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Distribution of Nephrops norvegicus (Linnaeus, 1758) larvae in the western Irish Sea and its relation to physical structure

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University of Wales, Bangor
School of Ocean Sciences

Distribution of *Nephrops norvegicus* (*Linnaeus, 1758*) larvae in the western Irish Sea and its relation to physical structure

by

Maria Manuel Pimenta Angélico

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A dissertation submitted in candidature for the degree of Doctor of Philosophy at the University of Wales, Bangor, School of Ocean Sciences

May, 1999

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Abstract

Nephrops norvegicus, commonly known as Norway lobster or Dublin Bay prawn, is a commercially exploited benthic decapod crustacean widely distributed across the continental shelf of the northeastern Atlantic Ocean. During its life cycle, the species undergoes a planktonic larval phase, which includes three zoeal stages and lasts approximately 45 to 50 days, in total. The third zoeal stage is followed by metamorphosis into the postlarval form and settlement onto the sea bed, starting the adult, benthic, existence. The distribution of the adults is tightly controlled by the requirement for muddy substrata in which to construct burrows. That dependency on suitable areas for settlement, bring about the importance of the larval distribution in guaranteeing successful recruitment into the benthic habitat. In areas where muddy sediments occur in isolated patches, the viability of *N. norvegicus* populations is strongly reliant on retention of the larvae above the parental grounds. Understanding the mechanisms (physical and biological) assisting on larval retention may lead to better interpretation of recruitment patterns and can be a useful tool for stock assessement and management, resolutions.

In the Irish Sea, the most significant mud area is a geographically isolated patch in the deepest region of the western basin. In this region, where tidal stirring is weak, thermal stratification of the water column occurs every year, during the spring-summer period. Due to the local topography and water column stratification a seasonal, density-driven gyre develops in the region. When the surface waters heat up, a dome of cold, dense, water becomes trapped in the deepest trough and isolated from the surrounding mixed waters by horizontal bottom fronts which are then responsible for the development of the cyclonic gyre. The gyre is a stable, consistent circulation feature present each year during the surface heating season (spring-summer) which coincides with most of the Norway lobster larval season and may therefore constitute the mechanism promoting retention of the larvae above the mud patch.

In this study a comprehensive set of biological and hydrographic observations was gathered in order to investigate the possible role of the western Irish Sea gyre in the retention of *N. norvegicus* larvae and maintenance of the local population. Special attention was dedicated to simultaneous observation of oceanographic and larval distribution (spatial and vertical) patterns.

The observations from this study confirmed the stable and coherent nature of the western Irish Sea gyre and its retentive effect was clearly shown by the trajectories of Argos drifters. The distribution of *N. norvegicus* larvae closely matched the gyre circulation, particularly towards the end of May-June, when the gyre was fairly well developed, highlighting its influence on the retention of the planktonic lobsters above the mud patch and adult habitat. However, the larval hatching season was noted to start in March-April, when stratification of the water column and associated gyre was only starting to develop. At this stage of the season considerable numbers of larvae drifted away from the muddy area, especially on the southwestern side. The gyre circulation was strongest in July-August, when the larval season of *N. norvegicus* was already over. Despite the apparent mismatch between the peak of larval production, in May, and the period of maximum retention it appears that recruitment of lobsters into the adult habitat has remained stable. Spawning stock size estimated from larval abundances, for the 1995 season, did not differ significantly from equivalent calculations carried out for the 1982 and 1985 seasons. In addition, fishery statistics have shown steady, high, *N. norvegicus* landings figures for many years. Together, this information suggests that the western Irish Sea *Nephrops norvegicus* population is sustained by stable, successful recruitment and the gyre seems to be assisting in that process. The larvae which are lost from the population do not appear to be crucial for its survival.

The analyses of larval, spatial and vertical, distribution presented in this study constitute effective background information to include in biological/oceanographic models aiming at simulating the dispersal of *Nephrops norvegicus* larvae in the western Irish Sea. Such experiments can contribute to a better understanding of the recruitment patterns of the species and assist on stock assessement studies.

Acknowledgements

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A special thank you to Dr. Juan Brown, from the Centre for Environmental Fisheries and Aquaculture Science, for making plankton sampling part of his research surveys even when it meant using time on tedious LHPR casts instead of Scanfish surveying or drifters spotting. I am deeply grateful for the time, advice and encouragement given during this study. I also like to show my gratitude for the availability of hydrographic observations and assistance on gathering data on larval distribution from CEFAS and other institutions and finally for the warm welcome and access to the facilities at Lowestoft.

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Chapter I. Introduction

A great number of marine benthic invertebrate species, particularly from shelf ocean areas outside the polar regions, exhibit life cycles which include a planktonic larval phase. This type of development seems to confer some ecological advantages which are reflected in the wide distribution and sustenance of the organisms which have pelagic larval forms (Thorson, 1950; Mileikovsky, 1971). Although dispersal is an important rationale for planktonic larvae in benthic invertebrate, those with long pelagic larval stages can have major problems with over-dispersal far from settlement areas. This issue is even of greater relevance for substrate specific species inhabiting isolated areas like offshore banks, reefs or isolated mud patches. Unless recruitment is maintained by transport from other regions, retention of larvae over the parental habitat (or return to the area) is vital to the perpetuation of these populations. During the pelagic existence, dispersal depends on water circulation, larval behaviour and duration of the planktonic stages. Larval longevity and water movements establish the potential for dispersal (retention) whereas larval behaviour (vertical movements, swimming ability) often determines the actual degree of spread. Together, these aspects play an important role on larval distribution and ultimately on the recruitment to the benthic habitat and survival of the populations.

Recruitment of larvae into the adult populations is the most relevant natural process controlling population size in many species of marine fish and invertebrates but despite the numerous studies carried out on the subject its dynamics is still poorly understood (Boicourt, 1988; Roughgarden *et al.*, 1988). Variability in recruitment, one of the most important areas of study in fisheries science, has been hypothesised to result from timing of larval occurrence with plankton production cycles (the match-mismatch hypothesis, Cushing, 1975), predation pressure (Bailey & Houde, 1989) and advective losses of larvae (the retention, or member-vagrant, hypothesis, Sinclair, 1988). The physical, chemical and biological elements contributing to recruitment variability have long been identified however, only in recent years have serious attempts been made to understand the mechanics of its interactions. The increasing need for assessment and sustainable management of the world fisheries brought about a new perspective on fisheries oceanography which became a truly multidisciplinary science. The study of the relationship between the physics of the ocean and the living

organisms contained therein can enhance substantially our ability to attack the fundamental and perplexing problem of recruitment dynamics in marine populations.

Recently, a considerable number of studies have been dedicated to interpret the dispersal patterns of larvae from marine and estuarine species in relation to the hydrodynamics of the environment in which they live with the ultimate aim of understanding recruitment dynamics and temporal and spatial fluctuations in populations size. In some cases, larval behaviour has been identified as a crucial element on dispersal, particularly concerning considerably large and powerful larvae of fish and crustacean species, while in other examples, considering smaller less motile larval forms of for example polychaete, echinoderm and some bivalve species, the larvae seem to act as inert particles at the mercy of water circulation.

Frontal zones (*eg.* upwelling fronts, tidal fronts, river plume fronts) can influence the distribution of planktonic organisms and constitute a physical boundary to larval dispersal. Rougharden *et al.* (1988) observations showed that the distribution of barnacle larvae, *Balanus glandula*, along the North American Pacific coasts is strongly controlled by the intensity of the front associated with the Californian upwelling system. In the south of the Bay of Biscay, the existence of a shelf-break frontal zone appears to retain the larvae of bivalve and bryozoan species in the coastal waters (Fernandez *et al.*, 1993). Tidal fronts also promote aggregation and retention of planktonic larvae. Examples of such mechanisms have been observed for brachyuran crab larvae in Delaware Bay (Clancy & Epifanio, 1992), sea scallop larvae, *Placopecten magellanicus*, on Georges Bank (Tremblay & Sinclair, 1992), oyster larvae, *Crassostrea virginica*, in Cheasapeake Bay (Mann, 1988) and Atlantic herring larvae, *Clupea harengus*, in several areas of the north Atlantic Ocean, including the Irish Sea (Iles & Sinclair, 1982; Sinclair & Iles, 1985). River plume fronts also play an important part in larval retention of estuarine and coastal species, as it has been shown for polychaete, *Pectinaria koreni*, (Thiebaut, 1996) and fish (Sabates, 1990), larvae within the Seine and Rhone river plumes, respectively.

Species that are dependent on estuarine or river environments have been observed to have a distribution favouring retention in, or transport to, these regions. Some species exhibit ontogenetic and/or tidally rhythmic changes in depth that allow the larvae to take advantage of differing flow regimes in the water column resulting in retention in the estuary. The larvae of

the mud crab, *Rhithropanopeus harrissi*, found exclusively in estuaries, are retained via a timed vertical migration synchronised with the tide, their depth distribution is centred at the depth of no net flow reducing longitudinal transport during larval development (Cronin, 1982; Lambert & Epifanio, 1982).

Larvae from other crab species like *Uca spp.* (fiddler crab) and *Callinectes sapidus* (blue crab) are usually quickly flushed from the estuaries but while the first is retained in the inner shelf area (Epifanio *et al.*, 1988; Christy, 1989) the latter may be widely distributed across the continental shelf (Lambert & Epifanio, 1982; Little & Epifanio, 1991). McConaugha (1988) argues that usually, decapod larvae that are widely distributed across the shelf tend to be concentrated in the upper 3 metres of the water column, their transport being particularly correlated to wind currents, while larvae from species that move only short distances from the estuary are concentrated mainly at depth. Two mechanisms have been proposed to explain how *Uca* megalopae reach the adult habitat. The first, involves staying in the bottom waters where residual flood directed currents on the inner shelf will carry the postlarvae into the estuaries (Lambert & Epifanio, 1982; Epifanio, 1988) and the second considers remaining at the bottom during the day and upward movement with nocturnal flood tides (Epifanio *et al.*, 1988; Christy, 1989). Transport via the first process would be slow since bottom residual currents have low velocities; immigration by riding nocturnal flood tides would be faster because tidal flow is greater. The megalopae of *Callinectes sapidus* may also be carried back into the estuaries by the same mechanisms referred to above if the postlarval blue crab sinks to the bottom layers of the water column. Alternatively, surface dwelling megalopae (which appears to be the region of greater abundance) might be transported by shoreward wind-driven currents, which in the Chesapeake Bay region seems to be a prominent feature.

The postlarvae of the American lobster, *Homarus americanus*, also inhabits the superficial layers of the water column and its dispersal into the rocky coastal regions seems to be greatly dependent on wind events but active swimming also appears to contribute to transport to areas of settlement (Ennis, 1975; Harding *et al.*, 1983; 1987). Spiny lobsters generally have a very long larval pelagic life, sometimes of more than 20 months, during which they are exposed to adverse conditions and subjected to long distance transport from the spawning areas. However, an elaborate ontogenetic vertical migration pattern associated with water circulation and an unusual swimming ability allows the larvae to return towards the coasts. In the southeastern

Indian Ocean, the early larval stages of *Panulirus cygnus* are transported offshore with surface currents, sometimes to distances of several hundred kilometres. The late phyllosoma instars, on the other hand, avoid the surface layers of the water column becoming more subjected to subsurface flows which assist in their return towards the coasts. Metamorphosis into the puerulus stage, provided with an accurate sense of orientation and very developed swimming capacity, allows the young lobster to swim across the shelf and settle in the shallow inshore reef areas, where it starts its benthic existence (Phillips & McWilliam, 1986; Phillips *et al.*, 1978; Phillips & Olsen, 1975). Studies on the distribution of the larval forms of slipper lobsters (Scylaridae), in the same region of the Indian Ocean, showed that their larvae, in contrast to spiny lobster larvae, were able to remain closer to the coastal area due to their lower position in the water column. By avoiding the surface layers phyllossoma and nisto larval stages of Scylarid lobsters prevented transport offshore (Phillips *et al.*, 1981).

The persistence of many fish and invertebrate species in isolated reefs and islands have been related to the existence of mesoscale eddies, although the spatial and temporal scales of such events have not been clearly identified. This retention mechanism is evident in Hawaiian waters (Lobel & Robinson, 1986), in the Florida Coral Reefs (Lee *et al.*, 1992) and in the Australian Great Barrier Reef (Black & Moran, 1991). Flierl and Wroblewski (1985) proposed a model to account for the impact of warm core rings, in the Gulf stream, upon shelf water fish larvae distribution and abundance on the continental shelf. Stationary or moving warm core rings owing to their rotation may advect larvae off the shelf over a time interval exceeding the maximum period of competence to settle or entrain them and later return them to the shelf.

One of the better documented case studies on larval distribution, and recruitment patterns, in relation to the hydrodynamic structure is the Georges Bank system, in the northwest Atlantic Ocean. In this region, a permanent, barotropic, closed circulation structure occurs over the topographic elevation, due to rectification of the tidal currents. The presence of the gyre over the Bank, is of critical importance for the productivity of these waters and plays a major role in the retention of several species in the region, including molluscs, crustaceans and fish (Wiebe & Beardsley, 1996; references therein).

In recent years research in the western Irish Sea led to the discovery of another type of stably located structure - baroclinic mesoscale gyres, which form seasonally over topographic

depressions in shelf sea areas (Hill, 1993). During the spring-summer, every year, heating of the surface waters over isolated regions of weak tidal stirring, such as topographic depressions, can lead to the formation of domes of cold, dense bottom water beneath the thermocline. This pool of water, becomes isolated from the surrounding mixed waters by near bottom, horizontal fronts which drive a cyclonic, near surface circulation around the cold dome. The western Irish Sea gyre is a consistent, coherent circulation feature which is present every year during the spring-summer period and can constitute a retention mechanism for planktonic organisms (Hill, 1993; Hill *et al.*, 1994; Brown *et al.*, 1995; Hill *et al.*, 1996; 1997a; present study).

The western Irish Sea gyre occurs over an area of fine muddy sediments which supports a population of *Nephrops norvegicus*, a decapod crustacea which only inhabits regions with muddy sea bed substrata, where it constructs its burrows. Prior to the benthic existence *N. norvegicus* undergoes a planktonic larval phase, which includes three zoeal stages and lasts approximately 45-50 days, in total. Because the western Irish Sea mud patch is surrounded by sand and gravel sediments, none suitable for *N. norvegicus* burrowing, it is crucial that the hatched larvae remain above the parental ground in order to insure successful recruitment into the benthic habitat. The existence of the gyre, in spring-summer when the larval season occurs, may be a key factor controlling the retention of the larvae over the mud patch and consequently guaranteeing the survival of the population.

Maintenance of this *Nephrops norvegicus* population is particularly sensitive considering that it is the target of an intense, directed, fishing activity. The species, also known as Norway lobster or Dublin Bay prawn, is in fact the most valuable commercially exploited item in the Irish Sea, providing the bulk of the revenue for the local fishery industry. Since the mid fifties's market demand for Norway lobsters has increased considerably. In the last two decades an average 8000 tonnes of lobsters have been extracted each year from the western Irish Sea, amounting to a value of approximately £15 million per annum, at first sale.

The objective of this study was to gather information on the spatial and vertical distribution of *Nephrops norvegicus* larvae, in the western Irish Sea, and to try to establish its association with the local hydrography (gyre). The present study falls within the general approach within fisheries oceanography, to attempt to identify the relationship between larval dispersal, and recruitment patterns of marine species, and physical factors (*eg.* hydrodynamic aspects). The

understanding of larval dispersal and recruitment dynamics of the western Irish Sea *Nephrops norvegicus* population, may assist in the interpretation of the dynamics of other Norway lobster populations and also bring some contribution to the more general issue of understanding the mechanisms controlling population size and variability in time and space, of key planktonic organisms critical to fisheries.

Historical observations on the spatial and vertical distribution of the larvae, from several sources, were investigated together with a comprehensive set of simultaneous, planktonic and oceanographic data, collected during the period of this project. Observations included in this study constitute the first set of contemporaneous information on *N. norvegicus* larval distribution and oceanography of the western Irish Sea. The results from this research could constitute effective background information to be included in biological/oceanographic models designed to simulate the circulation in the western Irish Sea and dispersal of *N. norvegicus* larvae. This approach can produce useful material to understand the recruitment patterns of the species and assist in stock assessment studies.

This thesis has been organised in six chapters, following this general introduction. Chapter II presents a characterisation of the area of study and relevant aspects on the biology and ecology of *Nephrops norvegicus* and chapter III summarises the observational methods and instruments used during sampling. Chapter IV describes the oceanographic observations collected during campaigns in 1994, 1995 and 1996. The following chapters V and VI examine data on the seasonal and spatial distribution of the larvae and vertical distribution, respectively, analysed in conjunction with the oceanographic observations. Finally chapter VII includes an overall discussion of all the observations analysed.

Chapter II. Characterisation of the species and area of study

1. The study area

1.1. Geography, topography and sediment distribution

The Irish Sea is semi-enclosed, connected to the Atlantic Ocean by narrow entrances in the north (North Channel) and in the south (St. George's Channel) (figure 2.1).The North Channel is about 37 km wide from north-east Ireland to the Galloway peninsula and it then broadens out at the entrance to the Firth of Clyde. The waters of both the Irish Sea and the Firth of Clyde communicate with the Atlantic Ocean through the narrow section of the North Channel, only about 20 km wide between Tor Point and the Mull of Kintyre. At the southern end, St. George's Channel is about 73 km wide from Carnsore Point to St. David's Head. The Irish Sea is about 300 km long and of greatly varying width with a total area of about 47000 km^2. As a whole, the Irish Sea is relatively shallow with a deep north/south trough in the west, the eastern side is characterised by shallow embayments. The minimum depth along the axis of the trough is about 80 m whilst the maximum reachs over 200 m. The embayments are shallower than 50 m, the largest being Cardigan Bay and the eastern Irish Sea, east of the Isle of Man.

The Irish Sea receives the fresh water run-off from several rivers, the majority of them in the eastern Irish Sea, The Eden (Solway Firth), The Lune (Morecambe Bay) and The Mersey are among the ones with greater water discharge. Along the eastern Irish coast the river flow is comparatively small with the River Boyne, south of Dundalk Bay, and River Liffey, in Dublin Bay, being the more relevant. The fresh water input is highly variable on a daily basis, the peak flow down a major river during a flood can be up to 400 times the flow during a drought. The largest monthly discharge occurs between December and February and the smallest in July. From year to year the total river flow can vary by a factor of three (Anonymous, 1990). Bowden (1955) estimated a total river discharge of 6.2 km^3/year and 24.9 km^3/year along the western and eastern margins of the Irish Sea respectively, coupled with a direct addition (precipitation minus evaporation) of 10.6 km^3/year to give a net freshwater input of 41.7 km^3/year.

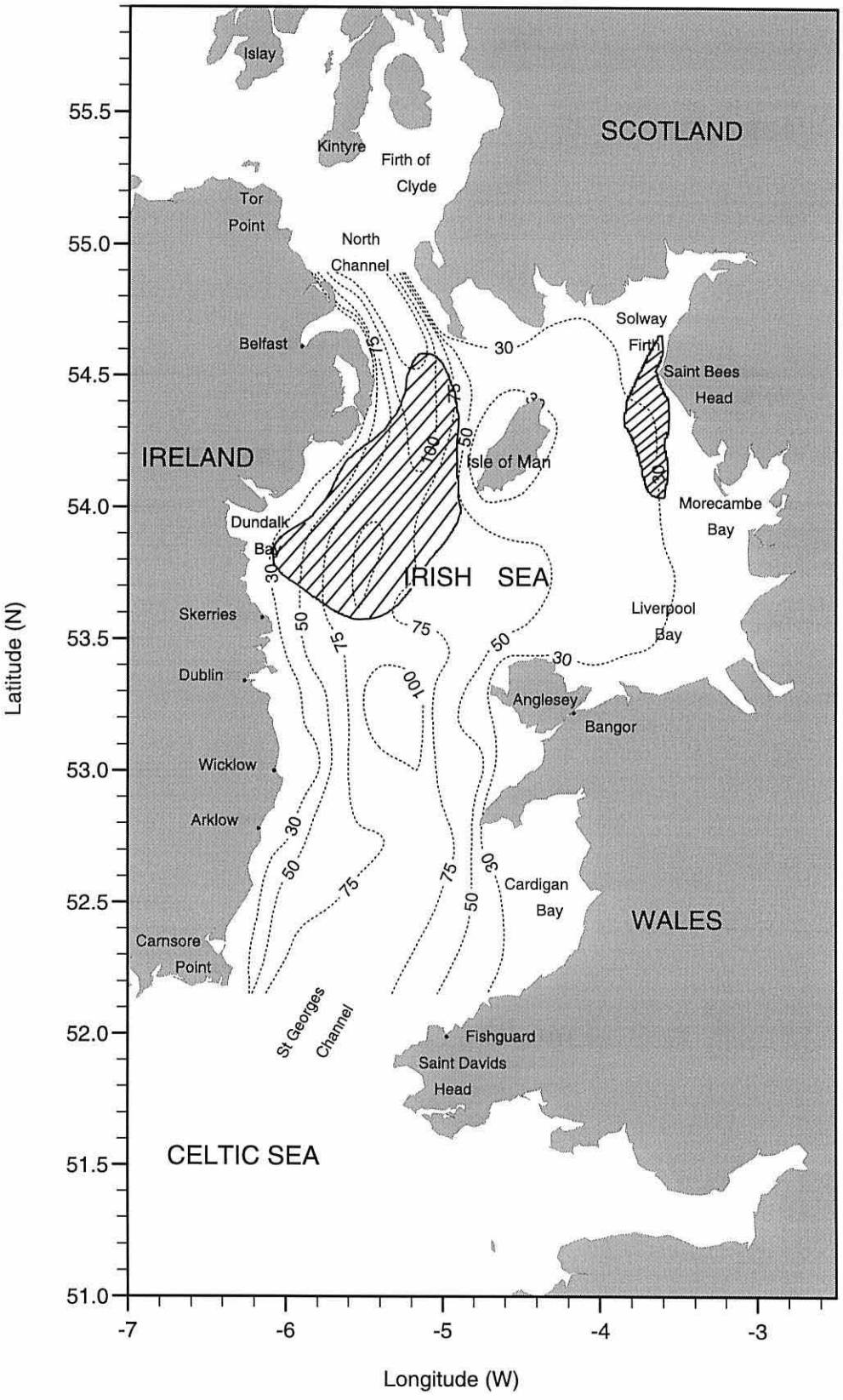
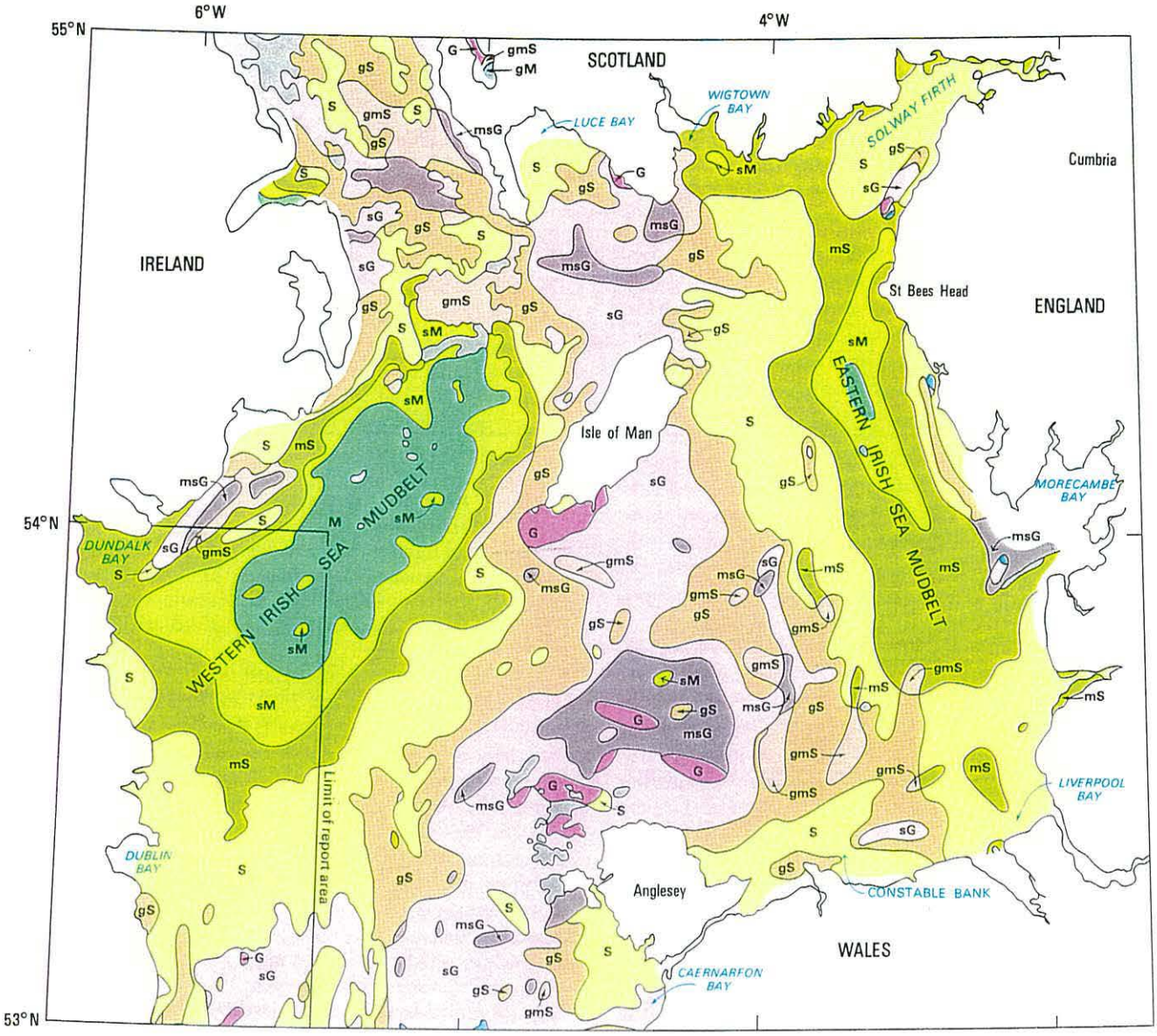
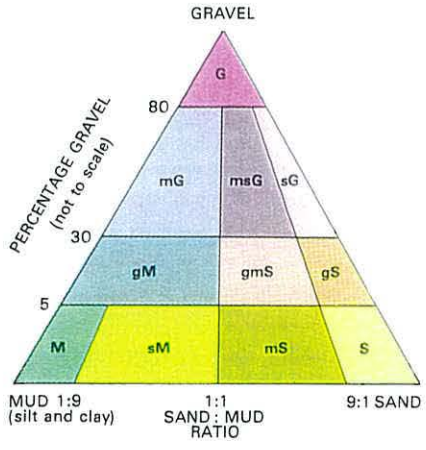


Figure 2.1. Irish Sea showing locations mentioned in the text, bathymetry (doted lines) and the muddy areas (black line) in the western and eastern basins, habitat of *Nephrops norvegicus*.

Although long term factors of earth crustal structure/rock development form the basic cause of the Irish Sea's existence, its shape and bathymetric complexity owe more to changes of recent geological time, the Quaternary. Most of the features are of glacio-fluvial/fluvial origin. Glacial deposition-erosion within the Irish Sea has radically altered the former hard rock surface topography. Subsequent marine inundation and related processes of hydrodynamic change, and sediment movement, have further modified the glacial landscape. The complex bathymetry and pattern of sediment distribution found at present, is a result of all the alterations over the years (Devoy, 1989), (figures 2.1 and 2.2).

The sediment distribution found today appears to be related to hydrodynamic factors though inheritance factors can not be overlooked. Coarser sediments are found where the tidal currents are stronger and finer ones where the tides are weaker. The major features of superficial sediment distribution in the northern Irish Sea are shown in figure 2.2. Gravelly sediment is widespread in St. George's Channel and in Cardigan Bay and extends northwards in a broad band along the central Irish Sea passing the Isle of Man through to the North Channel. Sandy sediments flank these gravels to the east and west covering an appreciable area of the Sea (Jackson, 1995). Several sand bank areas can be found off the Irish coast, south of Dublin, and in the Solway Firth. Within the sandy regions there are two main mud patches, one relatively small in the eastern Irish Sea, southwest of St. Bees Head, and the largest one southwest of the Isle of Man, roughly rectangular with dimensions of 50 km x 100 km (figures 2.1 and 2.2.). A very small area of muddy substrate is present off Holyhead on the Welsh coast (Anonymous, 1990; Jackson *et al.*, 1995). The existence of these mud regions will become central to the discussion presented later in this thesis.





M ..... Mud
sM ..... Sandy mud
gM ..... Gravelly mud
S ..... Sand
mS ..... Muddy sand
gmS ..... Gravelly muddy sand
gS ..... Gravelly sand
G ..... Gravel
mG ..... Muddy gravel
msG ..... Muddy sandy gravel
sG ..... Sandy gravel

The sediment classification used on the map is modified after Folk (1954)

Outcrop of till (Quaternary) with local and/or intermittent cover of sediment

Outcrop of rock (pre-Quaternary) with local and/or patchy cover of sediment

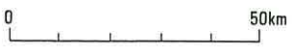


Figure 2.2. Sea bed sediment distribution in the Irish Sea (Jackson *et al.*, 1995).

1.2. Physical oceanography

The physical oceanography of the Irish Sea has been the subject of a considerable number of papers since the second half of last century. These works led to the current, quite good, understanding of the distribution of physical properties and the dynamics of the flow field in the area. Nevertheless, a comprehensive review of all the work done it is yet to be produced and perhaps more importantly, some conflicting hypotheses which have arisen from many years of research are still to be interpreted. Recent research is especially directed to the development of models for particular areas relevant from the economic and environmental point of view (*eg.* heavy metal and radionuclides distribution and dispersal in the eastern Irish Sea).

In the Irish Sea, like in other shelf sea areas, the presence of the bottom at a relatively shallow depth places a greater constraint on water movement. Currents near the bottom are generally quite large and bottom friction plays a significant part in their dynamics. The proximity of a coast line, almost all around the sea area, acts as a lateral constraint on water motion tending to divert currents so that they flow nearly parallel to it. The coastal barrier also causes surface slopes to develop which consequently will affect the flow. The influx of fresh water run-off from the land, which has the effect of reducing the salinity and hence the density of the coastal waters may, during some periods of the year, be relevant for the flow field description. Changes in water temperature due to surface heating by the sun also affect the structure of the water column with subsequent vertical and horizontal gradients usually developing. Coastal waters are generally areas of relatively large gradients of salinity, temperature and density, because of that, density-driven currents play an important role in the local circulation. Tides and tidal currents, due to the particular physiography of the Irish Sea are comparatively large and constitute the major forcing mechanism promoting vertical mixing with some areas remaining completely mixed all year round. Tidally driven water movements dominate the physical oceanography of the Irish Sea, with typical tidal streams of magnitude of 1 m/s and ranges of tidal elevation up to 9 m. Temperature and salinity distribution and the existence of a thermocline are very much controlled by the tidal regime. Wind stress and wind-driven currents also contribute to water mixing, strong winds may affect considerably the water movement in the Irish Sea.

1.2.1. Temperature and salinity distribution

Bowden (1955, 1980) presented a brief description of the distribution of mean values for temperature, salinity and density, in the Irish Sea, based on observations from a variety of sources along the years (figures 2.3, 2.4, 2.5). Pioneer research work showed that the majority of the Irish Sea, with the exceptions of a few areas, remains vertically mixed at all seasons and the vertical gradients of temperature and salinity are negligible. The exceptions are the deep area southwest of the Isle of Man, where the tidal currents are very weak, and some shallow regions off the northwest coast of England, where in summer the water stratifies.

The overall picture of distribution of temperature and salinity in the Irish Sea shows slightly warmer and more saline waters in the southern end, spreading along the western Irish Sea trough, while the waters far north and in the eastern Irish Sea remain cooler and less saline, fresh water run-off plays an important role in temperature and salinity distribution along the western coast of England. That pattern of temperature distribution, persists during winter but in summer the shallow waters of the eastern side show higher temperatures contrasting with the deeper waters from the western basin. The seasonal variation of temperature increases in range from the centre of the Sea towards the coasts.

The mean salinity distribution, characterised by a decrease from south to north and from the centre of the western basin towards the sides, with little variation during the year, has long been taken as an indication of a northerly flow of Atlantic water, the salinity of which is gradually reduced along its passage northward. The features of the temperature and salinity distribution in the Irish Sea depend on the properties of that inflowing water of Atlantic origin and on the extent to which these are modified by processes acting within the Sea itself. The temperature range in the shallow waters of the eastern Irish Sea is greater than in the western basin waters, minimum and maximum temperatures ocurring earlier in the year in the eastern side. The shallow waters also show the greatest diurnal variations due to the daily cycle of heating by solar radiation, during the day, and cooling by evaporation and back radiation, at night. Seasonal variations in salinity are most noticeable near the coasts and related to the annual cycle of river flow (Bowden, 1955; 1980).

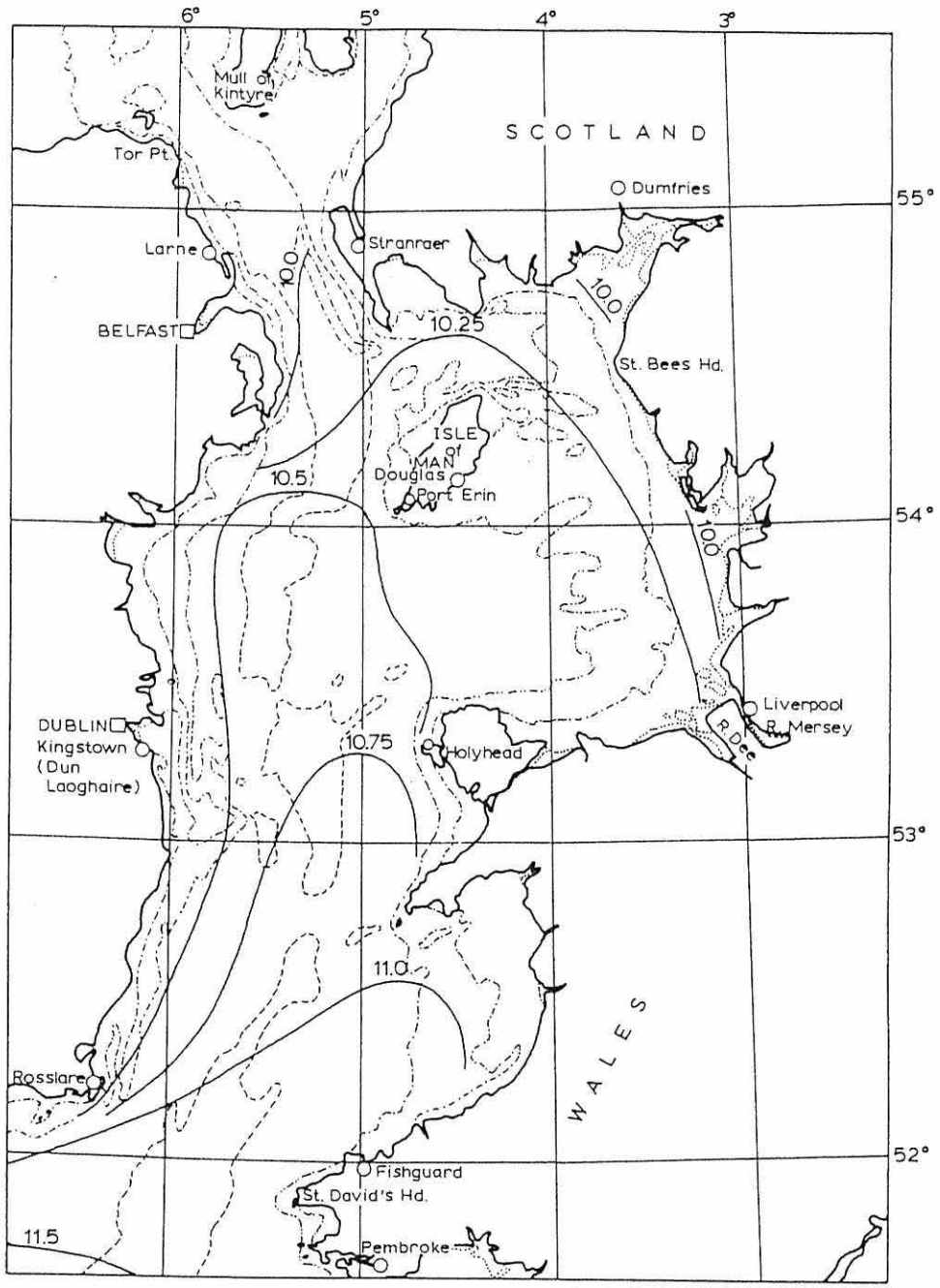


Figure 2.3. Annual mean surface temperature (°C) in the Irish Sea (Bowden, 1980).

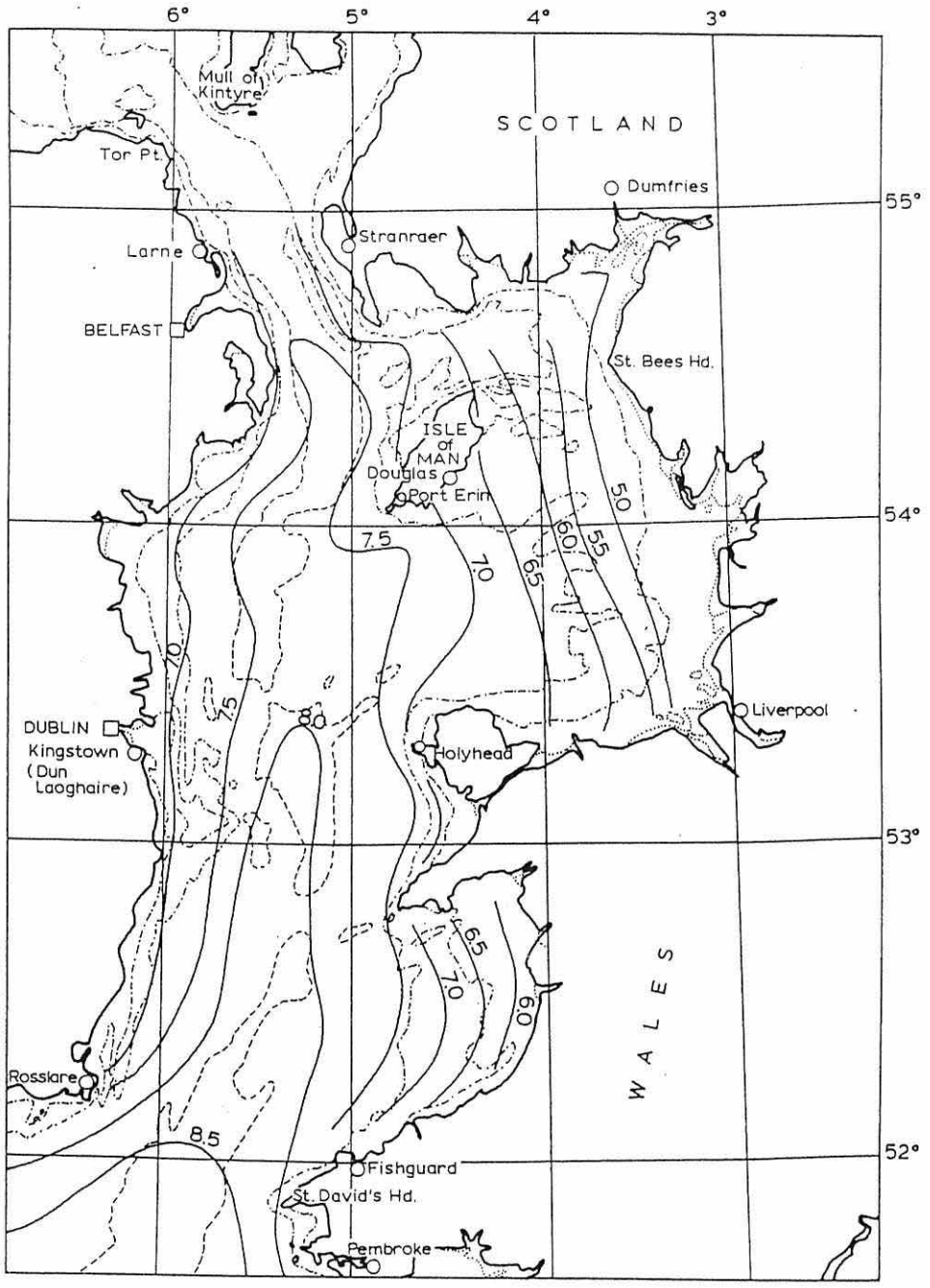


Figure 2.4. Mean surface temperature (°C) in the Irish Sea during February (Bowden, 1980).

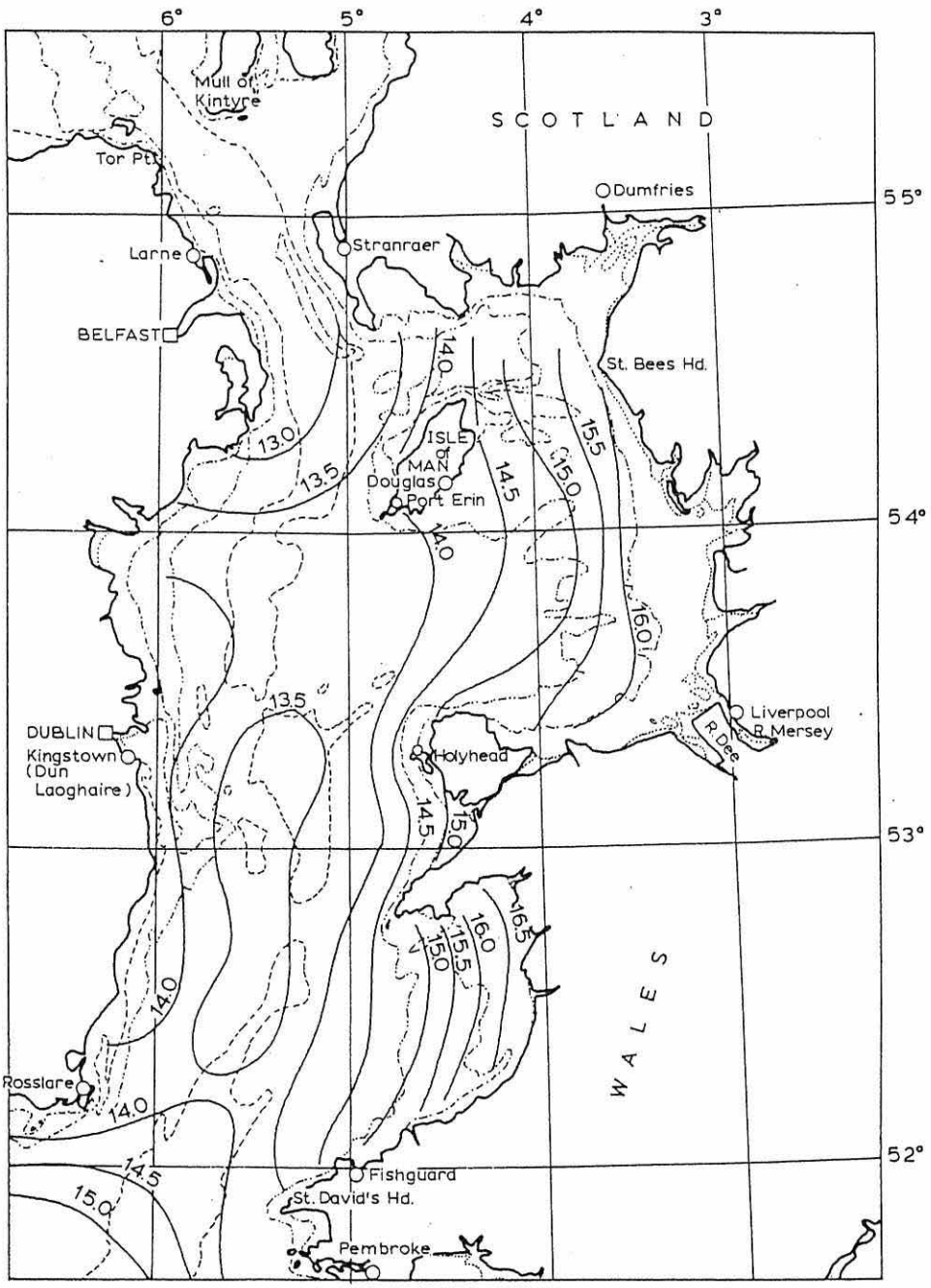


Figure 2.5. Mean surface temperature (°C) in the Irish Sea during August (Bowden, 1980).

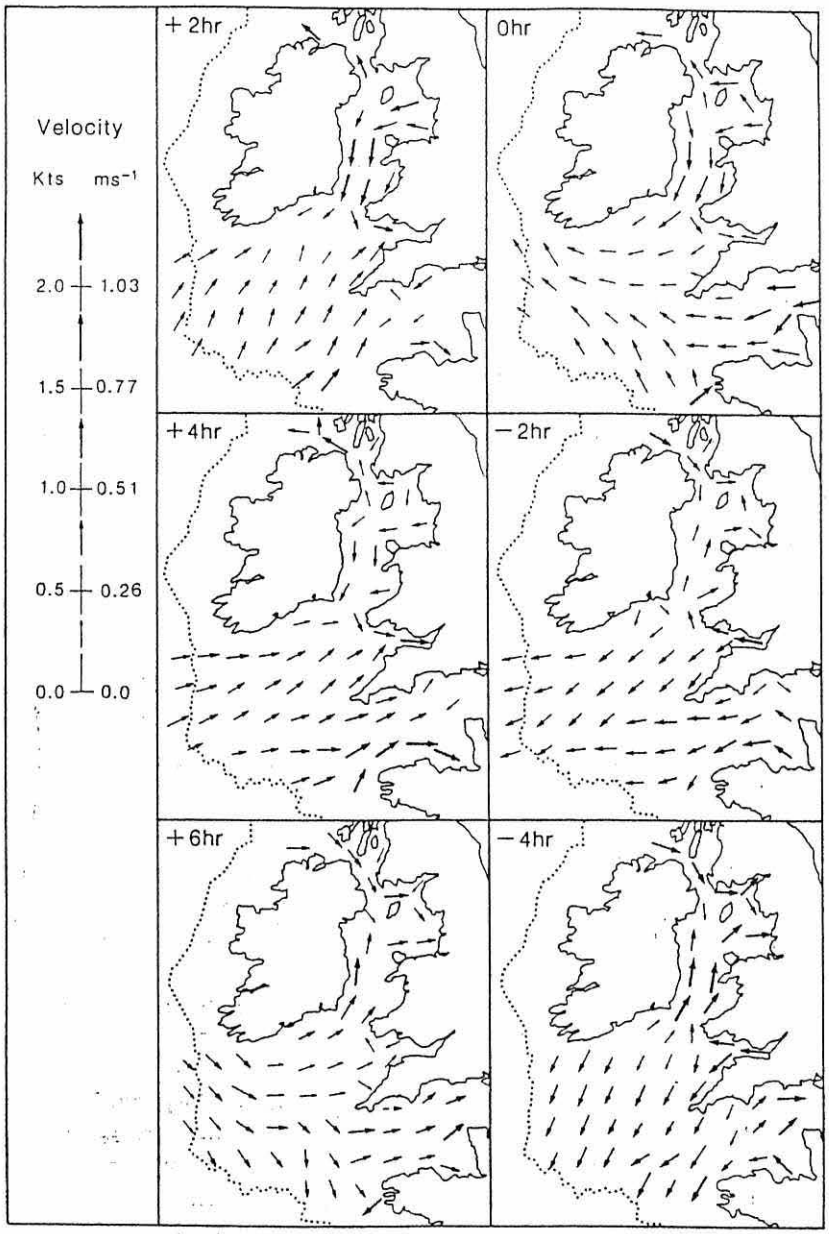


Figure 2.6. Tidal current velocity and direction for the M_2 tidal constituent (Huntley, 1980).

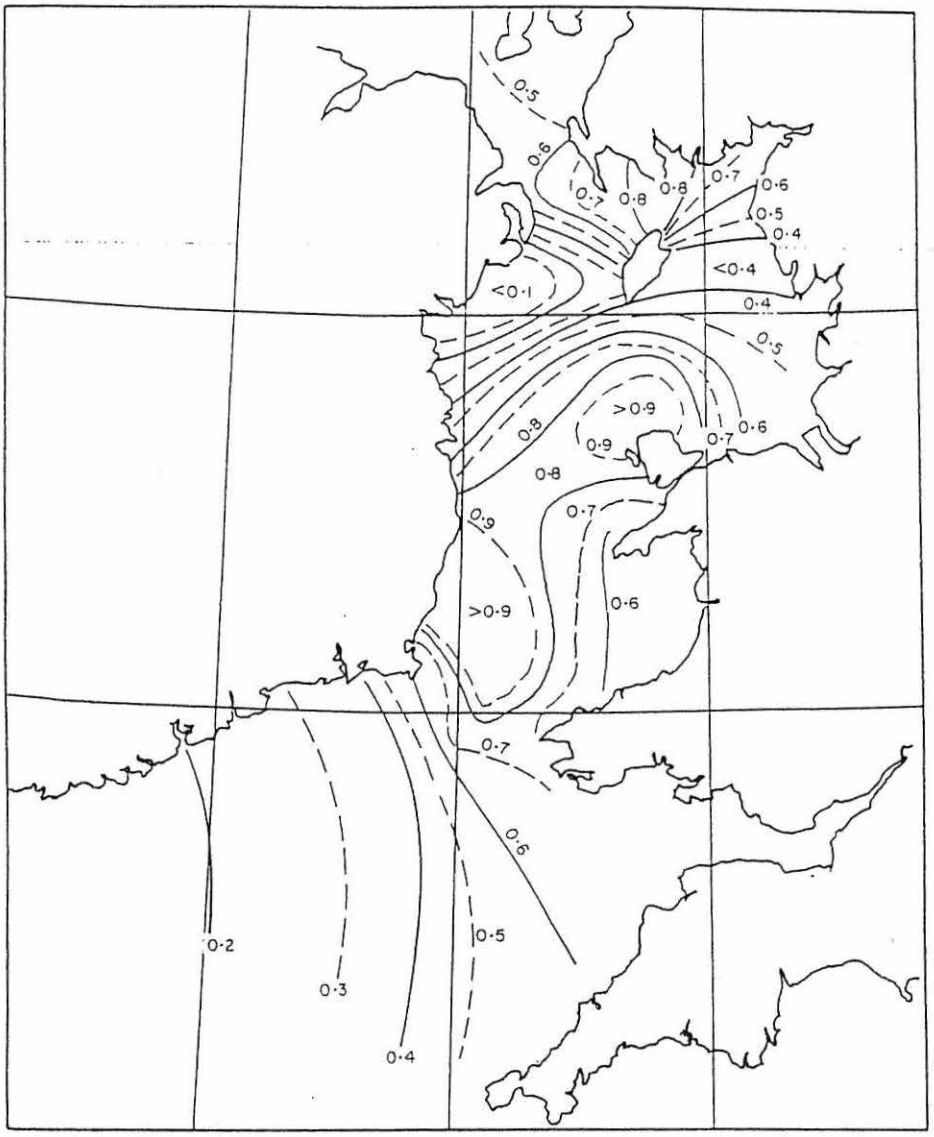


Figure 2.7. M_2 tidal streams, maximum velocity (m/s) (Robinson, 1979).

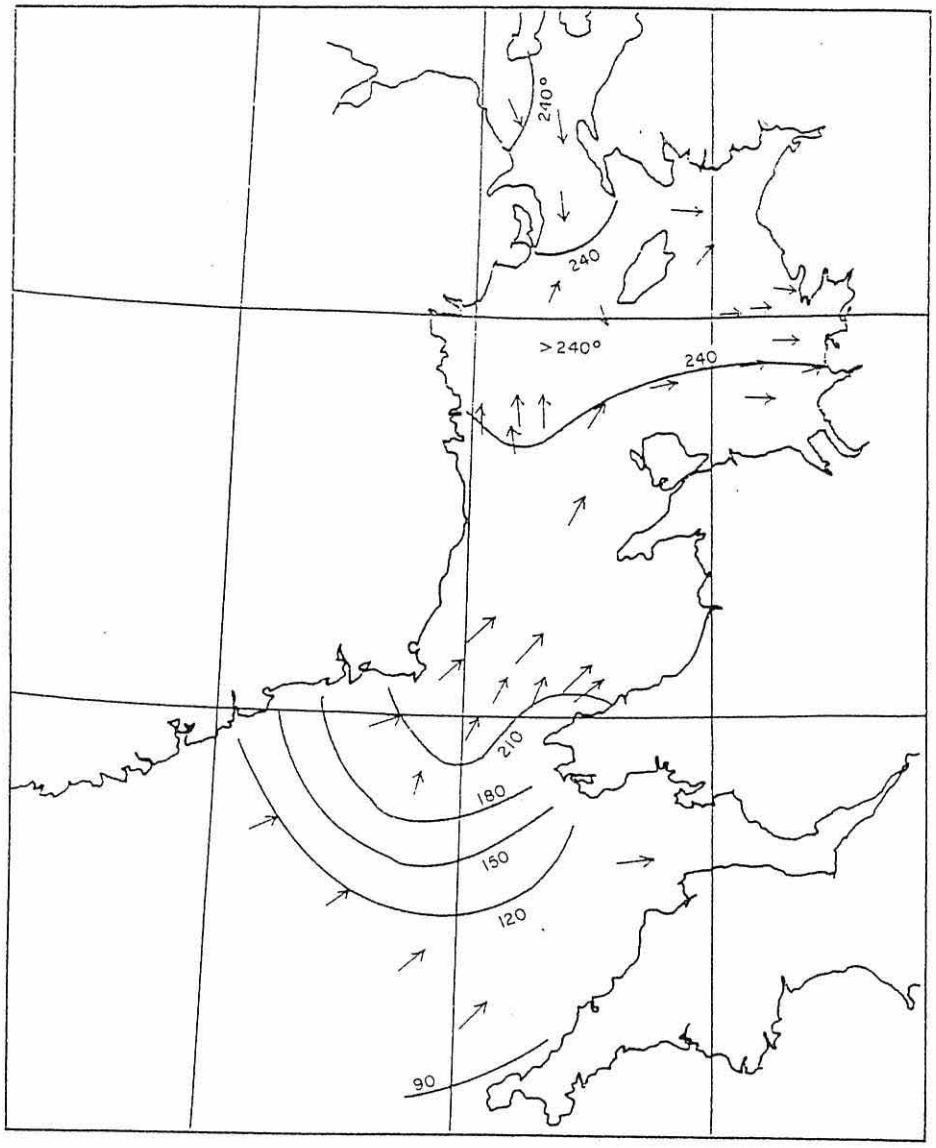


Figure 2.8. M_2 tidal streams, phase and direction of maximum velocity (Robinson, 1979).

Annual and seasonal mean values of temperature, salinity and density distribution give, obviously, just a broad picture of the Irish Sea water characteristics and can therefore only be interpreted in these terms. Particular areas and shorter time scale events must be considered in order to adequately understand the physical and dynamical oceanography of the region.

1.2.2. Tides

In the Irish Sea the most evident water movements are tidal streams associated with the tidal rise and fall of water level. Chief constituents of the tidal activity are recognised as being the M_2 (semi-diurnal cycle) and S_2 (spring-neap cycle). Most tidal variation in the Irish Sea is in response to a Kelvin type wave being generated by the Atlantic Ocean tidal system and then being reflected and resonated within the relatively narrow and shallow sea (Orford, 1989). Over 92% of the energy generated results from the Atlantic tidal input, especially that entering via St. Georges's Channel, the northerly input of tidal energy is comparatively low (Huntley, 1980).

A wave entering the Irish Sea through the St. George's Channel when it swings east, along the North Wales shores, towards the eastern basin is then reflected by the Lancashire coast back along its original path. These eastern shallow areas are important in controlling tidal amplification, surge resonation and wave shoaling, the depth of the water and friction of the bed reduces the velocity of the wave which in turn alters its wave length. The reflection of the adjusted tidal wave allows a near standing wave to be set up. Due to the Coriolis force and the east to west gradient of water elevation across St. George's Channel, caused by the Kelvin wave and the frictional effects in the shelf area, the nodal position moves westwards onshore in Ireland appearing to be found on a line between Fishguard and Arklow, west of the latter. This degenerate amphidromic point plays a major role in determining tidal range and tidal currents. The structure of co-tidal elevation is virtually the same for both M_2 and S_2 constituents, supporting the major influence of the amphidromic point on the Irish Sea tidal range. Water elevation due to M_2 is approximately twice the S_2 elevation. Higher tidal ranges are found on the eastern side of the Irish Sea. The longshore gradient of spring tidal elevation on the Welsh coast is approximately four times that of the Irish coast. Maximum tidal range on the east coast is associated with the shelf areas underlining the amplification potential of the shallow water. (Orford, 1989)

Robinson (1979) and Huntley (1980) presented a review of the major tidal currents in the Irish Sea (figures 2.6, 2.7, 2.8). The direction of rotation of the M_2 current vector is not uniform throughout the Irish Sea and appears to vary with depth. In the northern Irish Sea, east of the Isle of Man, the current vectors rotate counter-clockwise (Robinson, 1979) while a clockwise rotation of current direction, during the semi-diurnal cycle, is well defined for the Celtic Sea. The movement of water in and out of the Irish Sea shows a very strong bi-directional flow with some maximum current velocities greater than 1 m/s (Huntley, 1980).

Charts from Robinson (1979) (figures 2.7, 2.8) show contoured maximum tidal current velocities, timing and direction for the whole Irish Sea. The effects of the degenerate amphidromic point can be appreciated, an increase in maximum tidal current velocity occurs from south to north through St. George's Channel. For continuity reasons the volume of water passing across an amphidromic point must be accelerated in order to compensate for the lack of tidal elevation. Such an effect can be seen off Wexford, southeast Ireland, where the tidal stream is greater than 0.9 m/s. Off the Down coast, southwest of the Isle of Man, the lowest tidal currents (0.1 m/s) were registered. The high tidal range of the Lancashire coast is associated with only minor current speeds (0.4 m/s).

To the extent that they are purely oscillatory, tidal currents do not give rise to a residual current, measured at a fixed point. There may be a Lagrangian drift of the water, however, resulting from the mass transport associated with the tidal wave under certain circumstances. Hunter (1972) has estimated this drift to be of the order of 0.4 cm/s northwards in St. George's Channel. It could thus amount to about one fifth of the mean residual flow deduced from observations.

Figure 2.8 shows the phase of maximum tidal flow. Peak currents and tidal elevation peak for the M_2 tide, appear marginally out of phase in St. George's Channel and then progressively move further out of phase as the tidal peak moves into the north Irish Sea. In general, the residual direction of maximum velocity is northwards through the south Irish Sea and eastwards over Liverpool Bay. The secondary tidal flow through the North Channel meets with the northely flow southwest of the Isle of Man where some spatial partition of flow

occurs. The S_2 currents are very similar to the M_2 currents, the dynamics of the harmonics appear to be very similar, except for their relative magnitude (Robinson, 1979).

1.2.3. Vertical structure of the water column

The tides are a determinant factor for the vertical structure of the Irish Sea with tidal stirring providing most of the mechanical energy responsible for vertical mixing. Regions characterised by strong tidal turbulence usually remain well mixed throughout the year while in areas of weaker tidal streams a temperature gradient develops. The heating up of the sea surface layers by solar radiation, combined with the poor stirring power of the tides in these areas, induce the onset of a seasonal thermocline every spring-summer. Summer-time sea surface temperature pictures, of the region, demonstrate well the warmer waters in the stratified areas compared with the cooler waters present in the well mixed regions (figure 2.9). There is a very good agreement between those images and the maps of contoured tidal velocity, with stratification occurring where the tidal currents are weaker, of the order of 0.1 m/s, in the western Irish Sea, and around 0.4-0.6 m/s, in the shallow embayments of the eastern shores. Stratification results mainly from vertical gradients in temperature although vertical gradients in salinity, due to fresh water run off, may be of some importance especially during the early stages of the stratification season. Simpson (1971) reported surface to bottom temperature differences of more than 5° C for the western Irish Sea, during the summer months.

The boundaries of this strongly stratified area of the western basin are marked by strong horizontal gradients on the southern and eastern sides, with surface temperature changes of up to 1° C/km. Discontinuities as large as 3° C have been observed in the surface waters in June and July (Simpson, 1971; Simpson & Hunter, 1974). The dynamics of these regions, of high gradients, separating stratified and well mixed waters in shelf sea areas, tidal or shelf-sea fronts, was described by Simpson and Hunter (1974). These authors developed an energy argument which predicts the ocurrence of stratification and the location of these type of fronts. Their position is controlled by the competition between buoyancy input, by surface heating, and tidal and wind stirring. A front would be found where the intensity of turbulent mixing is just enough to continously overcome the barrier to mixing presented by

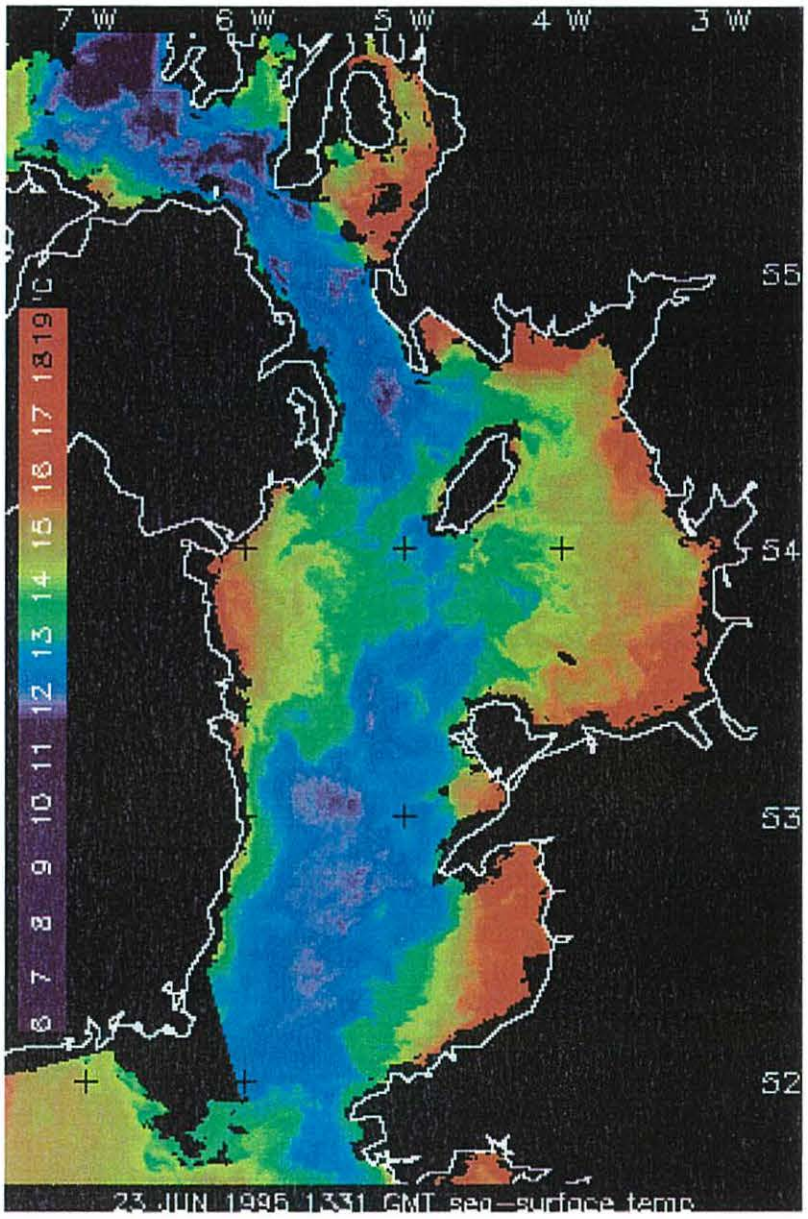


Figure 2.9. Sea surface temperature in the Irish Sea on 23 June 1995, (image processed by the NERC Remote Sensing Data Analysis Service, Plymouth, from channel 4 AVHRR).

stratification. It is commonly expressed by the ratio h/U^3, where h is the depth of the water in metres, and U is the absolute speed of the tidal flow in m/s, averaged over one tidal cycle.

The location of the Irish Sea frontal system, predicted by Simpson and Hunter's theory was successfully compared with observed data (Simpson & Hunter, 1974). Figure 2.10 presents contours of the stratification parameter ($\log_{10} h/U^3$) for the Irish Sea, Celtic Sea and English Channel, tidal fronts are predicted for areas with values between 2.0 and 2.5 (Simpson & Pingree, 1977). Simpson and Hunter's postulate, which has been refined to include the effects of wind mixing and variable levels of mixing efficiency (Simpson & Bowers, 1981; Bowers & Simpson, 1987), has proved to be very effective in predicting tidal fronts in various shelf sea areas.

1.2.4. Residual currents

In the Irish Sea the average residual current, after the tidal currents had been removed, is an order of magnitude, or even two, smaller than the tidal currents (Robinson, 1979, Bowden, 1980).

Residual flow may vary over periods of days, weeks or months, and may be related to wind effects, the density distribution or the inflow of Atlantic water. The first attempts to describe it for the Irish Sea were indirect, based on the distribution of temperature and salinity. Mean salinity distribution features led to the conclusion that the main flow through the Irish Sea was northwards, from the southern entrance to the North Channel. From the shape of the isohalines and isotherms it was deduced, at an early stage, that after passing northwards through St. George's Channel, the main flow turned eastwards and passed around the east coast of the Isle of Man instead of following the deeper channel west of it. More recent evidence has been less clear on this point. Slinn (1974) showed, considering the distribution of salinity from a number of cruises, a core of high salinity water over the deep trough on the west side of the Isle of Man, indicating that a considerable part of the flow passed to the west of the island.

Bowden (1950) estimated the mean flow across the Holyhead-Dublin line to be 0.3 km/day (0.35 cm/s) and 0.5 km/day (0.6 cm/s) through the North Channel, these figures were find

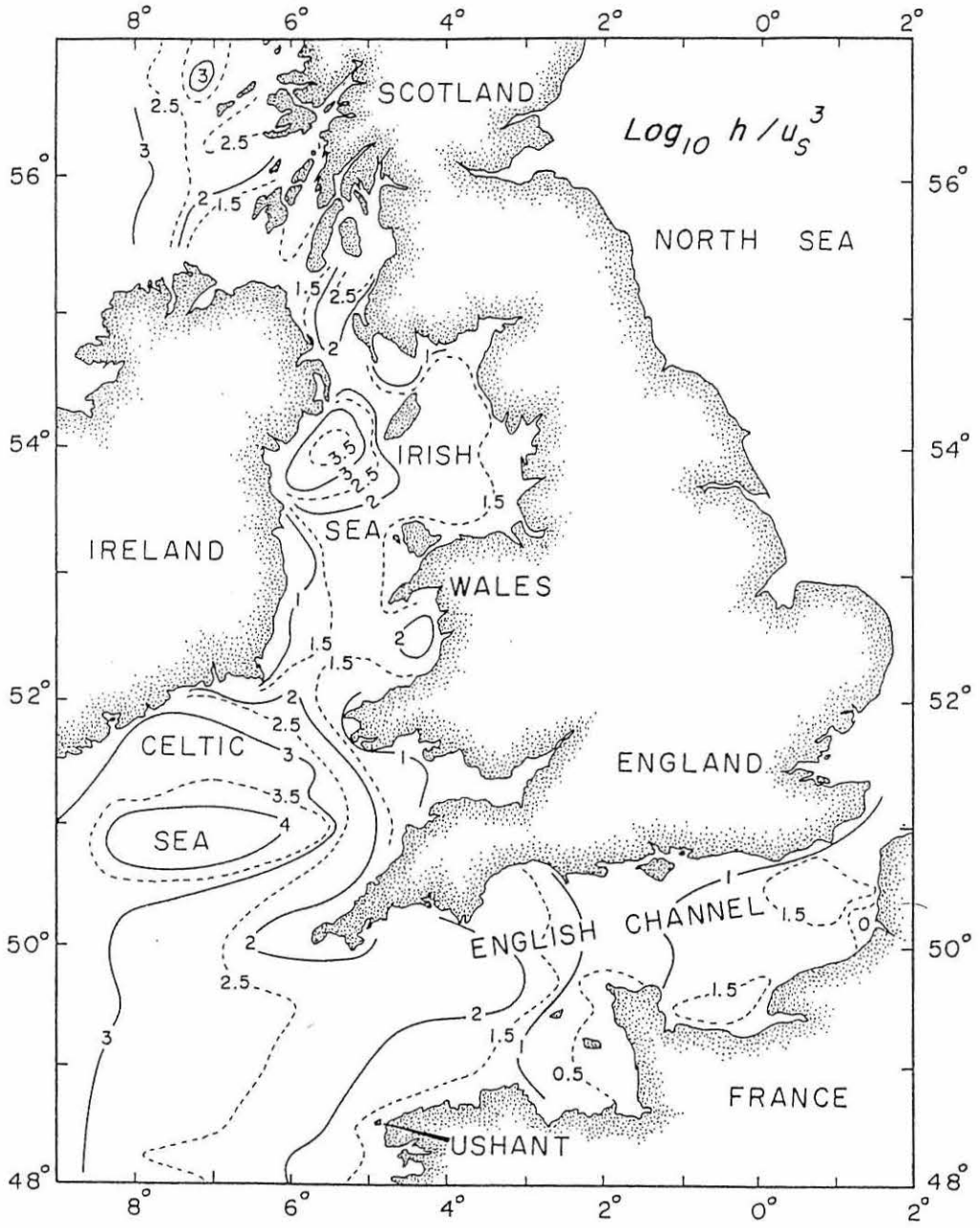


Figure 2.10. Stratification parameter $\log_{10} h/u^3$, h is the depth in metres and u the surface tidal stream amplitude in m/sec at mean spring tides (Simpson & Pingree, 1977).

considering quantitatively the continuity of salt and water. Wilson (1974), looking at the Caesium 137 distribution as a tracer of water movement in the St. George's Channel, came up with a current speed of 0.32-0.39 km/day (0.37-0.45 cm/s) across the Fishguard-Rosslare line and 0.28-0.34 km/day (0.33-0.39 cm/s) across the Holyhead-Dublin parallel.

Direct measurements of currents in the Irish Sea were first made using drift bottles, in the latter years of the last century. Those observations lead to a first outline of the flow field. Most of the recovered drift bottles, released in the Irish Sea never left it. Many were retrieved on the northeastern English, and southwestern Scottish, shores. A small number of the drift bottles passed through the North Channel and were found off the west coast of Scotland, the Orkneys and, in one case, Norway. None of the bottles passed southwards through the St. George's Channel (Bowden, 1980).

The first current meter measurements in the North Channel gave, surprisingly at the time, a residual flow towards the south, contrary to the evidence from the salinity distribution and the drift bottle experiments. Proudman (1938) found a southward (southeastwards) residual flow averaging 0.5 km/day (0.6 cm/s). It was then concluded, and it has been confirmed by later data, that this southerly flow is an indication of a coastal current close to the Irish shore, although the total transport through the North Channel is northwards. Several surveys were carried out later and data from Harvey & Buchan (1967 *in* Bowden, 1980), including temperature and salinity observations, current meter measurements and bottom drifter releases, confirmed the picture of a northerly flow, on the east side, with surface velocity about 4 cm/s, and a southerly flow on the west, with a velocity of about 3 cm/s. The wind stress was found to have a major contribution for the residual flow, strong winds can affect considerably the flow through the Irish Sea as a whole.

From the late sixties onwards, the amount of data on currents has been much increased by the use of current meters enabling continous records to be obtained for considerable periods. Using data from current meters and sea-bed drifters Ramster and Hill (1969) published charts of the surface and bottom currents in the Irish sea (figure 2.11). These maps are until the present the only attempt to describe the water circulation for the whole Irish Sea, based on observations, and were produced under the assumption that a reasonable consistent pattern of residual flow exists in the area. According to these authors, in the west side of the Irish Sea

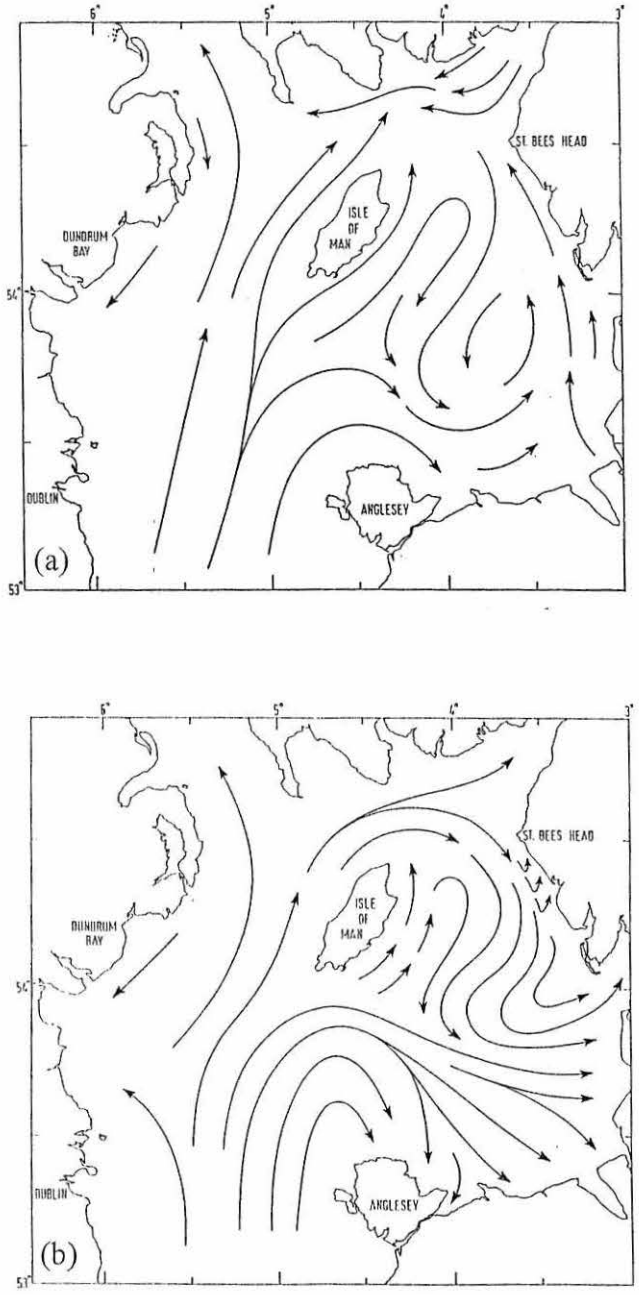


Figure 2.11. Residual circulation, (a) surface waters, (b) bottom waters (Ramster & Hill, 1969).

the surface and bottom currents show a similar pattern, both exhibiting a northward flow passing to the west of the Isle of Man and then reaching the North Channel. The remaining part passes eastwards between Anglesey and the Isle of Man. A southerly flow is present close to the Irish coast. On the east side of the Irish Sea the bottom and surface currents show a different behaviour. The surface currents take a turn north of Anglesey into Liverpool Bay, where they undergo an anticlockwise path eventually leaving the eastern Irish Sea along the English coast and southwest Scotland, in the direction of the North Channel. The bottom flow on the other hand, turns towards the English coast in several branches from the north of Anglesey up to the Solway Firth. Because of their simplicity these charts were, and are still, in use, specially by marine biologists and the fisheries research, communities.

Although very attractive and easy to interpret, these maps are perhaps a rather simplistic (incomplete) description of the flow field in the Irish Sea. Hill *et al.* (1997a) drew attention to the apparent inconsistency between Ramster and Hill (1969) hypothesis of a long term, stable, organized circulation in the Irish Sea, strong enough to be mapped, and the work of Bowden (Bowden, 1950, Bowden, 1980) and, Simpson and Hunter's (1974) theory. Bowden's studies led to the conclusion that the long term mean circulation is, northwards and, weak with average basin speeds of no more than 1-2 cm/s; consequently, the vertical temperature (density) structure, is controlled by local vertical (tidal) mixing processes (Simpson & Hunter's theory).

Since the total velocity signal consists of energetic, short-time scale motions, such as tides and wind driven events, a mean long-term circulation of the order of 1 cm/s is down at the noise level and therefore it may not be meaningful to infer a coherent, organized circulation pattern of mean currents from observations (Hill *et al.*, 1997a).

The discovery of a cyclonic, near-surface gyre in the western Irish Sea, brought a new dimension to the understanding of the circulation in the region (Hill, 1993; Hill *et al.*, 1994) and also provided the arguments to conciliate the two, apparently exclusive, views on the nature of the circulation in the region (Hill *et al.*, 1997a). These works led to the conclusion that elements of both theories are relevant because intense organised flow features (gyre) can co-exist within an overall frame work of weak mean flow in which local vertical exchange processes are dominant.

It would then be reasonable to construct a circulation picture, like Ramster-Hill's map which, would include the western Irish Sea gyre as a strong, consistent and coherent summer circulation feature.

1.3. The western Irish Sea gyre

In the previous section of this chapter some background information on the physical oceanography of the Irish Sea was presented, in this section attention will be turned to the major aspect of the local hydrodynamics which is relevant to the interpretation of the results presented in this study.

The crucial aspect of the physics in the western Irish Sea is the development of seasonal thermal stratification, the spatial distribution of which is controlled principally by topographic and tidal dynamics through the Simpson and Hunter (1974) h/U^3 (h, water depth; U, tidal current amplitude) criterion (Hill *et al.*, 1996).

The tidal currents in the western Irish Sea are exceptionally weak (<0.2 m/s) compared to the rest of the Irish Sea. The combination of deep water and weak tides in this region, leads to stratification of the water column during the spring and summer heating season, where there is insufficient tidally-generated turbulent kinetic energy to maintain vertical mixing against the input of surface buoyancy. Pronounced tidal mixing fronts are then evident separating thermally stratified and tidally mixed waters (Simpson & Hunter, 1974; Simpson, 1981).

The stratification season lasts for about 6 months, roughly from early April until September. Wind stress, acting on the surface layers and the tidal current energy, from the bottom are responsible for the breakdown of stratification at the end of the season, when the surface heating input is too weak to counterbalance vertical mixing. Although largely controlled by temperature the summer time density field in the western Irish Sea is also influenced by salinity during the begining of the season. Fresh water originating from the rivers along the Irish coast plays a part in the increase of buoyancy of the surface waters.

The seasonal thermocline is located at 20-40 m depth and outcrops at the surface as a front visible in sea surface temperature images. Associated with the onset of seasonal thermal stratification is the formation of a dome of cold (dense) bottom water in the deeper basin of the western Irish Sea. The dome is composed of water, left over from the previous winter, which becomes trapped beneath the thermocline as stratification develops during spring-summer, every year. This body of isolated, relict, water is separated from warmer, surrounding mixed waters by horizontal bottom fronts. Exchange with the neighbouring waters is limited and warming takes place very slowly by weak diffusion of heat across the seasonal thermocline. Low oxygen levels (Davies, 1972, Simpson & Hunter, 1974; Horsburgh *et al.*, submitted) and high concentrations of nutrients (Simpson & Hunter, 1974; Horsburgh *et al.*, submitted) confirm the limited exchange between the bottom mass of water and the surrounding waters.

The baroclinic density structure that develops in the western Irish Sea every spring-summer is responsible for the occurrence of a near surface cyclonic (anti-clockwise) circulation (gyre) above the cold water pool (and mud patch area). It is the bottom density gradients, occurring between the dense water dome and the neighbouring waters, that are dynamically significant and drive the baroclinic, cyclonic gyre, in accordance with thermal-wind balance, assuming zero flow parallel to the density contours at the bottom. The dome of cold dense water remains static while the water above it moves in a cyclonic way in order for geostrophic balance to be maintained. The geostrophic flow is concentrated in two narrow (~ 10 km wide), jet-like cores on either side of the dense water pool and centred just below the thermocline. These jets are located immediately above the strongest horizontal near bottom density gradients (Hill, 1993; Hill *et al.*, 1994; Hill, 1996).

The western Irish Sea gyre starts to develop at the begining of the stratification season and it is usually apparent by April-May. However, at this stage the system is not fully formed and 'leaks' in the cyclonic flow can be observed, particularly in the eastern arm of the gyre. As the season progresses, the isothermal mixed waters warm up much quicker than the bottom layers of the stratified side and consequently the horizontal bottom gradients sharpen up resulting in an increase in the gyre circulation velocity. By late June, the gyre is usually completely established and a closed circulation system is in place in the western Irish Sea. In July-August, when the gyre is at its maximum strength, water flow along the eastern (north-

flowing) and western (south-flowing) branches of the gyre reaches speeds of about 15-20 cm/s. The breakdown of the thermal stratification (and the gyre) occurs usually in late September-October.

The gyre was first observed in July 1990 (Hill, 1993; Hill *et al.*, 1994) using satellite-tracked free drifting buoys and it has been consistently identified whenever subsequent observations have been made during spring-summer time (Brown *et al.*, 1995; Hill *et al.*, 1996, 1997a; present study).

1.4. Plankton production and distribution

1.4.1. Phytoplankton production and distribution

The development of different water masses in the Irish Sea, a consequence of the diverse tidal stream regime, land influence, and Atlantic water effect, leads to distinct patterns in the spatial and temporal distribution of plankton and hence differences in production, biomass and species composition.

The annual cycle of plankton production in temperate seas is strongly influenced by the formation and breakdown of the seasonal thermocline (pycnocline). Stabilization of the water column by thermal stratification can stimulate primary production. During winter, when the solar radiation is not enough to increase the temperature of the sea surface layers and cause stratification, most of the water stays well mixed and therefore the phytoplankton are being circulated to the full depth of the mixed layer and hence spend a large proportion of their time below the euphotic zone. With the onset of surface warming and the formation of a much shallower mixed layer, phytoplankton cells are held for long periods in the well lit layer and can therefore take more advantage of it for growth and cell division. On the other hand, the thermocline (pycnocline) may constitute a barrier for nutrients, which would be recirculated from the sea bottom, because vertical mixing is strongly inhibited. Once all the nutrients available in the surface layers are used and new influx is not possible the production rate drops to minimum levels.

Simpson and Hunter (1974) found the distribution of nutrients and dissolved oxygen to be strongly correlated with the temperature structure in the western Irish Sea. In August, nitrate and phosphate concentrations, in the mixed water, were generally higher than in the surface layer of the stratified regime, but large concentrations of all the nutrients remained in the bottom water of the stratified regime, which was also characterised by depletion of the dissolved oxygen content. Concentrations of nitrate-nitrogen of the order of 2 μg/l were found in the tidally mixed waters while the content of the same nutrient in the surface water of the stratified region was less than 1 μg/l. At the same time, the deep water of the stratified side contained about 7 μg/l. Chlorophyll$_a$ measurements from the same survey showed concentrations of 1.5 μg/l for the isothermal waters and 0.5 μg/l for the surface water of the stratified side.

It was pointed out in later studies, that the concentration of chlorophyll$_a$ measured only for the surface layer does not give a good account of the phytoplankton biomass for the stratified waters (Richardson *et al.*, 1985). As the season progresses, the surface layer extends and so does the phytoplankton vertical distribution. Maximum concentrations of chlorophyll are then found in deeper water usually around the pycnocline where the light available is still enough and some nutrients are being transported from the bottom waters by vertical diffusion or internal wave activity (Simpson & Pingree, 1977). In addition, those cells produced on the surface layers that are not removed by grazing tend to sink. In the autumn, the phytoplankton are usually most abundant again in the surface of the stratified water due to new input of nutrients.

Richardson *et al.* (1985) showed good agreement between the stratification season and the annual cycle of phytoplankton production. Between 1980 and 1982, substantial spring phytoplankton outbursts were noted in the surface stratified water soon after water column stratification became established. The same authors, using data over the entire season of thermal stratification, also made the important observation that when averaged for the top 30 m, cholorophyll$_a$ concentration from isothermal waters, stratified waters and frontal zone did not show significant differences, in contrast with the results obtained from surface water measurements. Although not statistically significant, the results suggested that the mixed ([Chl$_a$] = 1.30 μg/l) region contained less chlorophyll than either the stratified ([Chl$_a$] = 1.75 μg/l) or the frontal ([Chl$_a$] = 2.17 μg/l) zone. These results do not agree with the work of

Simpson and Hunter (1974), who recorded higher concentration of chlorophyll$_a$ in the isothermal waters than in the stratified waters. It should however be pointed out that Simpson and Hunter's samples were taken late in the season, in August, and that the measurements only referred to the surface waters. Data from other sources showed a generally higher phytoplankton biomass for the surface water of the stratified region (Fogg *et al.*, 1985; Savidge & Kain, 1990 authors therein; Gowen *et al.*, 1995; Prestige & Taylor, 1995). However, part of the records of chlorophyll$_a$ concentration in mixed and stratified waters presented by Foster *et al.* (1976), Beardall *et al.* (1982) and Savidge *et al.* (1984) do not concur with the assumption that stratified waters always have a higher level of phytoplankton biomass.

Richardson *et al.* (1985) showed that over the entire season of thermal stratification the chlorophyll$_a$ concentration in surface waters was highest near the front as compared with mixed and stratified waters. This is a well reported occurrence, frontal zones are usually areas of increased biomass. The combined effects of vertical mixing and surface stabilization mantain favourable nutrient and light conditions for the growth of phytoplankton in frontal regions (Pingree *et al.*, 1975). To the stratified side of the front, mean concentration of chlorophyll in the thermocline and surface layer usually decreases with distance from the frontal boundary as the water column becomes more stable. It seems that, under adequate illumination, the standing crop of plant cells becomes directly dependent on the flux of nutrients (Holligan, 1981). In the surface mixed layer on the stratified side of the front, shortage of nutrients depresses growth, whereas in the tidally mixed bottom layer, shortage of light prevents growth. The pycnocline, however, is a region where phytoplankton are exposed to moderate illumination from above and to moderate rates of nutrient supply by diffusion from below. Flux through the thermocline is possible due to vertical gradient differences. Biological depletion of a nutrient in the mixed layer and thermocline causes an increase in the vertical gradient of that nutrient at the base of the thermocline, *i.e.* in the nutricline, this gradient would lead to an upward flux of the nutrient.

Several mechanisms have been mentioned to account for the increased biomass usually found in frontal zones. Savidge (1976) did not find any differences in primary production rates for either side of the western Irish Sea front, in August 1973, but recognised that the frontal zone constituted a distinct environment. The concentration of chlorophyll$_a$ was 1.3 μg/l at the front,

0.7 μg/l in the adjacent mixed waters and 0.95 μg/l in the stratified side. He suggested that mixing of the two different water types, mixed and stratified which may separately be deficient of some important nutrient, would originate a richer environment at the front which might lead to enhanced primary production.

Baroclinic eddies, formed along the frontal zone as a consequence of the strong mean flow parallel to the front often close in on themselves and break free, forming patches of cool water on the warm side, and *vice versa*. This cross-front process might be one of the explainations for the surface patches of high production in the vicinity of shelf-sea fronts. Savidge and Foster (1978) and Fogg (1985) found evidence of this phenomenon for the western Irish Sea frontal system. Although the residual currents are primarily along the tidal front a weak frontal circulation induced by internal friction is also expected and may play a significant role on the cross-frontal exchange of inorganic nutrients.

The mechanism most often cited to justify the enhanced biomass at shelf-sea fronts is the movement of the front during the spring-neap tidal cycle. During the spring tide period of maximum tidal currents the front is pushed back into the previously stratified area, so that nutrients are brought to the surface, when the tidal currents relax during the neap tides, the waters close to the front that have previously been tidally mixed become stratified and there is a burst of phytoplankton growth (Pingree *et al.*, 1975; Simpson & Pingree, 1977).

Moderate upwelling usually occurs on the mixed side of the front and convergence on the stratified region, both processes may also play a part in the increased phytoplankton standing crop in the frontal area.

Savidge (1976) pointed out that the absence of differences in the primary production rate from mixed and stratified waters does not necessarily mean that the phytoplankton growth strategies are the same. Furthermore, Fogg (1985) reported that the impression that the standing stocks in the frontal waters were only of slightly greater magnitude, than in the surface stratified waters, and largely determined by the amount of plant nutrients initially presented above the thermocline, might be misleading. In fact, the frontal waters differ markedly from the main part of the surface stratified waters, showing a much higher microbiological activity. This is reflected by the higher cellular ATP concentrations found,

which are not correlated with chlorophyll$_a$, bacterial biomass or zooplankton biomass but are more a measure of physiological activity.

The effects of the front were clearly seen in the phytoplankton species distribution. The composition of the phytoplankton populations on either side of the front was distinctive and the population found at the front was a mixture of both. On the stratified side the percentage contribution of diatoms to the total phytoplankton population is smaller than in the mixed waters region. A larger population of flagellates is present in the surface stratified waters (Beardall *et al.*, 1982; Fogg, 1985). Moreover, Coombs *et al.* (1994) argue that a more abundant and diverse particulate microzooplankton assemblage is found above the thermocline at stratified sites than anywhere else. Those observations can be interpreted from an ecological point of view. Diatoms which are fairly large cells without great means of controlling their vertical position tend to sink, and because of that flourish better under turbulent conditions which bring them back to the euphotic zone from time to time. Small flagellates, in stratified waters, form a subsurface patch close to the thermocline, where there is a small but steady vertical transport of nutrients. It is also possible that those organisms may make use of their locomotory power to control their vertical position and even undertake migrations in order to find the best place for nutrient uptake and light supply (Mann & Lazier, 1991). There is also some evidence of specific phytoplankton succession occurring along the season. When the waters are beginning to became stable small cells with high division rates are expected to predominate. As the season progresses and the water column stability increases, a complete succession from fast growing small celled diatoms to larger diatoms with lower growth rates and to large dinoflagellates with still lower growth rates should appear (Demers *et al.*, 1986; Coombs *et al.*, 1994).

Waters that become stratified in the summer months tend to exhibit peaks of production. The first peak usually occurs in early spring, after the onset of the thermocline when plenty of nutrients are still available in the surface waters. In the autumn, when the surface mixed layer extends new nutrients are brought into the euphotic layer and a second, smaller, peak of production normally appears. This seems to be the general pattern of phytoplankton production to be found in the Irish Sea (Slinn & Eastham, 1984; Savidge & Kain, 1990). Nevertheless, it is also possible that the secondary autumn maximum may or may not be present, Richardson *et al.* (1985) observations showed that in general, chlorophyll$_a$ increased

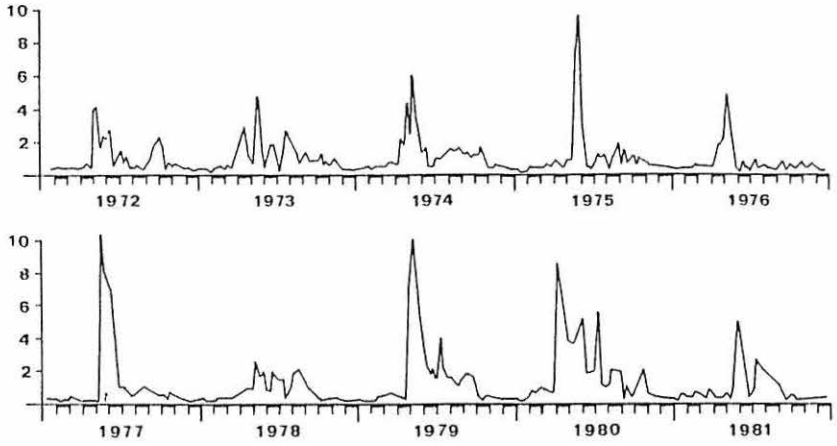


Figure 2.12. Variation of chlorophyll$_a$ (μg/l) in surface water at 54° 5.5' N 4° 50' W, during 1972-1981 (Slinn & Eastham, 1984).

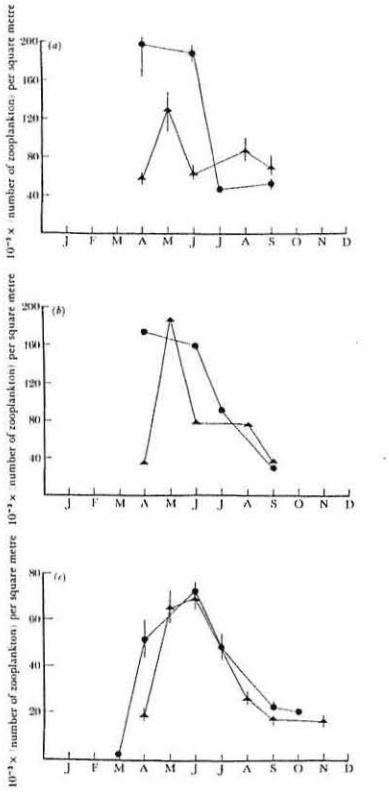


Figure 2.13. Total zooplankton mean monthly number per square metre for (a) stratified region, (b) frontal region and (c) mixed region, in the western Irish Sea during 1980 (circles) and 1981 (triangles) (Scrope-Howe & Jones, 1985).

in all regions soon after the onset of stratification and remained relatively high until stratification broke down in October. Only for the surface waters of the stratified region was there indication that the data fitted the classical primary production model of temperate waters. For many of the sampling stations the chlorophyll$_a$ peaks occurred intermittently throughout the period of stratification.

Considerable variability was observed in the recorded values of chlorophyll$_a$ for that survey and others undertaken in the Irish Sea. Differences in the magnitude and timing of the spring bloom are well evident in figure 2.12, which reports the variation of chlorophyll$_a$ in surface water for the period 1972-1981 from a fixed station, 5 km offshore on the western coast of the Isle of Man. For example, for 1980 the spring bloom developed rapidly over a period of a week or less achieving a maximum chlorophyll concentration of around 8.5 μg/l whereas in 1978 no defined spring bloom was found and maximum chlorophyll concentration reached only about 2 μg/l. In 1980, the spring bloom started in late March whereas in 1981 the bloom only got underway in mid May (Slinn & Eastham, 1984). Colebrook (1979) observations from 28 years of CPR (Continous Plankton Recorder) survey indicated that when compared to other areas around the British Islands, the major growth of phytoplankton, in the Irish Sea in spring, commences approximately one month later, around April-May. Primary production values for the Irish Sea have been considered to be 5 to 10 times lower then in the North Sea (Savidge & Kain, 1990 sources therin). But perhaps the most noticeable feature about the Irish Sea productivity is its considerable year to year variability in timing and magnitude, making predictions very difficult.

One of the reasons often given for the fluctuations and lower productivity values found in the Irish Sea, when compared to other shelf sea areas, is the generally cloudy conditions prevailing over the area. It is also possible that the patchiness in the plankton distribution could by itself explain most of the variability encountered but, conclusions should be taken with caution when comparing surveys which often were undertaken in very distinct locations, using different sampling strategies (*eg.* different depth of sampling, different time of the tidal cycle, sampling stations around the frontal zone) and very rarely interpreted together with hydrographic data.

Despite the considerable number of studies carried out in the Irish Sea along the years, details of the production season are still lacking. Gowen *et al.* (1995) give a more complete picture of the influence regional stratification differences have on the phytoplankton production season. Observations were made for the entire stratification season (from March to November) and cover the whole western Irish Sea (west of the Isle of Man and from a line between Dublin and Holyhead up to the North Channel).

Perhaps the most significant point brought about by this study is the suggestion that the regional hydrography of the area gives rise to several distinct systems with specific primary production characteristics. The particular physical and biological properties of tidally mixed waters and summer stratified waters have been well documented in many studies and in addition, Foster *et al.* (1976) drew attention to the fact that the coastal areas were yet a different system with high temperature and nutrient content, low salinity and a fairly consistent high phytoplankton production throughout the season. Gowen *et al.* (1995) go further to suggest that in fact the coastal area off the Irish shores are not only a particular environment for primary production but also must be seen as two separate regions. A northern coastal region (NCR), roughly north of Dundalk Bay, and a southern coastal region (SCR), from there, south. In the same way the isothermal mixed waters should be considered as a northern mixed region (NMR), in the North Channel and surroundings, and a southern mixed region (SMR), south and west of the summer stratified region (SSR). A transition zone between the stratified and mixed waters is also recognised.

For the 1992 season the onset of stratification started in late April-early May, only observed in the deeper central waters of the western basin (SSR), and lasted until August. The SSR did not have its primary production season under way until early May, it lasted about 4 months, until August, and the seasonal production rate registered was 101 gC/m^2. A rapid reduction in the concentration of nitrate and nitrite was noticed in that area during May but was not observed until approximately one month later in the mixed isothermal waters. The concentration of nitrate and nitrite were very low in the SSR and SCR compared to the mixed regions and NCR. Within the coastal area a progressive northwards delay in the timing of initial nutrient depletion and extent of it was noticed.

The phytoplankton production season started earlier in the coastal regions, around begining of April, and lasted approximately 6 months, until the end of summer. The highest season production rate was recorded for the SCR (155 gC/m^2) whereas the NCR had a lower production rate, around 127 gC/m^2. Accumulation of biomass was registered in the SCR but not in the NCR.

These observations in the costal regions are in good agreement with what is known about shelf sea areas that remain well mixed throughout the year. They do not, usually, have a limitation of nutrients and, the disadvantage that the lack of stratification may constitute are usually well compensated by the high nutrient abundance. If phytoplankton is being transported by turbulence throughout the water column, and is exposed to abundant nutrients, the onset of the spring bloom depends mainly on the seasonal increase in light, and not at all on the onset of stratification. Usually, the primary production cycle starts early in the season, as soon as the solar radiation available is enough to trigger the photosynthetic process, and it only decreases when the resuspension of sediments, in the autumn, is so strong that not enough light would penetrate into the water column. Within the tidally-mixed regions the offshore sites often have well marked peaks of production while, coastal sites have relatively high biomass throughout the spring and summer. Coastal waters generally show a higher summer production but a sharper decline in the autumn, depending on the extent of land runoff input (Mann & Lazier, 1991).

Gowen *et al.* (1995) data, also seemed to show that the offshore mixed waters of the western Irish Sea are the least productive and have a short primary production season. The NMR had the later start (late May/June) and only lasted for 2 months with a seasonal production rate of 96 gC/m^2. The SMR showed an increase in the phytoplankton biomass from early May although no enhacement in production was observed. The season lasted less than 2 months and the production rate was the lowest (66 gC/m^2).

Gowen *et al.* (1995) argued that the comparatively low productivity of the Irish Sea is probably due to the short late season to be found in most of the whole area. The delay in primary production consequentely causes a delay in secondary production and hence in food availability for larvae of fish and other planktotrophic animals, at the time of spring spawning. However, this apparent set back may be counterbalanced by the early and sustained

production in the SCR which, in fact happens to be one of the main spawning sites in the Irish Sea. Cod, haddock and whiting are among the species strongly dependent on that area for reproductive sucess.

1.4.2. Zooplankton production and distribution

The zooplankton production cycle, in the Irish Sea, is expected to show regional differences as a consequence of the distinct water properties and the different patterns of primary production. In stratified regions, because of the rapid warming up of the surface layers, grazing on phytoplankton starts relatively early in the season. In tidally mixed areas because warming of the surface waters is delayed, due to the lack of stratification, the zooplankton growth is slower and often does not peak until early summer (Mann & Lazier, 1991).

Scrope-Howe and Jones (1985) zooplankton survey evidenced only fine scale differences in the amplitude and timing of the seasonal zooplankton cycle for the distinct physical regions of the western Irish Sea. The stratified region contained the highest zooplankton production, which occurred, in the main, above the thermocline with an abundance maxima earlier in the year. The mixed isothermal region supported a lower density of total zooplankton and the maximum occurred at least one month later than in the stratified waters (figure 2.13). Mean monthly zooplankton densities, in 1980-1981, taken for the stratified, frontal and mixed regions did not reflect any substantial increase in zooplankton associated with the front. Fish eggs and larvae were found in appreciable numbers in the frontal zone.

The pattern of zooplankton species distribution is not as marked as the pattern of phytoplankton species distribution seems to be. The majority of the species were distributed right across the whole area with a few showing a more restricted distribution. The copepods *Pseudocalanus elongatus*, *Calanus finmarchicus*, *Acartia clausi*, *Oithona similis*, *Temora longicornis* and *Centropages hamatus* were the dominant zooplankton species throughout the western Irish Sea. *Sagitta elegans* was the only chaetognath found in the western basin (Scrope-Howe & Jones, 1985).

Temora longicornis and the nauplii of *Acartia clausi* were absent from the stratified surface waters whereas *Calanus finmarchicus* and *Membranipora membranacea* were absent from the

mixed waters. Williamson (1952) had already pointed out that *C. finmarchicus* was more abundant in the stratified region of the western Irish Sea and relatively rare in the mixed isothermal waters to the west and north of Anglesey. This author argued that the population of *C. finmarchicus* is not endemic to the region, their occurrence being associated with the southward flowing current originated from the north of Ireland, where this species is abundant. The copepod would enter the Irish Sea via the North Channel during spring-summer. *C. finmarchicus* population showed marked density fluctuations from year to year and had a great impact in the total zooplankton biomass for the area.

Edwards and Burkill (1995) looked at the smaller zooplankton (microzooplankton, <200 μm) in spring-summer, 1987-1989 and 1992, and also found a higher biomass in the surface stratified water above the thermocline. The frontal zone exhibited a lower biomass, about half the density present in the stratified waters, and the mixed isothermal waters had the lowest biomass of Protozoa and Metazoa.

The mixed waters in the eastern sector of the Irish Sea were dominated by small sized microzooplankton, whereas larger species dominated the stratified westerly waters. Up to 50% of the total biomass found at the westerly stations was in the >50 μm range while the samples from the eastern basin had a major biomass contribution from smaller organisms, in the fraction <50 μm. The spatial pattern encountered was related to the different hydrographic regimes but also reflected the distribution of particulate matter in the Irish Sea waters (Edwards & Burkill, 1995). Within the surface waters the detrital content of the particulate matter has been determined to be 52% in the western stratified region and 97% in the mixed water sites (Coombs *et al.*, 1994).

The low levels of particulates (high levels of detritus), in the total suspended particulate material, and low levels of chlorophyll concentration in the mixed waters sites are an indication of low heterotrophic activity which implies a relatively inefficient transfer of energy and it is reflected in the small copepod, dominant system, of these areas. On the other hand, stratified water sites show lower levels of detritus (higher levels of particulates) and higher chlrophyll concentration and consequently a more efficient transfer of energy from phytoplankton to larger copepods, which in turn will provide a higher nutritional value for fish larvae and other larger planktotrophic organisms (Coombs *et al.*, 1994).

Scrope-Howe and Jones (1986) reported evidence of diel vertical movements in the zooplankton from both, the mixed isothermal waters and the stratified waters. It was also evident that the thermocline significantly influenced the vertical distribution of the zooplankton, the majority of the animals were found in the surface waters, with only a small part of the total zooplankton present in the bottom, below the thermocline or actually in the discontinuity layer. *Oithona similis* was concentrated around the pycnocline, while *Microcalanus pusillus*, a deep water species, was found only in the bottom stratified water. When chlorophyll$_a$ levels above the thermocline were relatively low and diffuse, the zooplankton seemed to carry out normal diel vertical movements with respect to the light cycle but without crossing the thermocline into the cooler bottom waters. When chlorophyll$_a$ levels were high and became concentrated into discrete subsurface layers, the zooplankton ceased migration and aggregated within these patches.

1.5. Benthic organisms and fish

Mackie (1990) presented a generalised distribution of the macrobenthic communities in the Irish Sea based especially on differences caused by different sediment types. Seven main soft-sediment macrofaunal communities were considered. Areas of hard substrate with particular epifauna which may include elements from some soft-bottom communities were also recognised. In the Irish Sea, the Norway lobster, *Nephrops norvegicus* occurs in areas characterised by Mackie (1990) as the '*Brissopsis* community' and the '*Amphiura* community'.

The '*Brissopsis* community' (referred to as the 'Boreal Offshore Mud Association' by Jones (1950)) arise in the deeper, muddy area of the western basin below about 70 m and on the eastern basin, on the shallower mud patch off the Cumbrian coast. This community is characteristic of offshore muds at shallow to moderate depth (15-100 m), typical species include the urchin *Brissopsis lyrifera* and the brittle-star *Amphiura chiajei*.

The '*Amphiura* community' (referred by Jones (1950) as the 'Boreal Offshore Muddy Sand Association') is typical of offshore sandy-muds at shallow to moderate depths (15-100 m). Occurs in the Irish Sea bordering the mud areas described above, in the western and eastern

basins. Typical species include the brittle-star *Amphiura filiformis*, the urchin *Echinocardium cordatum* and the tower shell *Turritella communis*. Smaller patches are present in inshore areas such as the Liverpool and Cardigan bays.

The benthic macrofauna of the western Irish sea mud patch is mainly composed of polychaete worms. About 80% of the infauna taxa observed by Hensley (1996) were members of the families Capitellidae, Cirratulidae, Paraonidae, Spionidae (sedentary species) or Glyceridae, Lumbrineridae (errant species).

Although much of the fauna was ubiquitous in the area sampled a change in trophic structure was observed, with tubiculous polychaetes less common in the deeper, soft sediments where, non-selective or mobile burrowers, deposit-feeding species predominated. Hensley (1996) considered five distinct regions which correlate with depth and differences in the superficial sediments: central area, first peripheral and second peripheral, northern and frontal.

The stations from the frontal area were very different from the rest, showing the highest abundance and species richeness. In addition, some taxa were only present there, one of them being the decapoda *Goneplax rhomboides*. The amphipoda *Harpinia pectinata*, very abundant on the frontal region, was also absent from everywhere else. Total taxa observed and abundance was considered to be low within the central region fine sediments, where the lowest values were registered. A trend of declining species richness was generally observed towards the centre of the patch. The northern and peripheral regions were distinguished on the basis of, high counts of the Cirratulidae *Monticellina dorsobranchialis*, in the first case, and on high counts of Cirratulidae polychaete in general and low numbers of the mollusca *Nuculla* spp., for the first peripheral area. The second peripheral region showed low numbers of Cirratulidae which were then absent from the central area.

The grounds of *Nephrops norvegicus* in the Irish Sea also support a diverse fish fauna. The burrowing gobiidae, Fries's goby (*Lesueurigobius friesii*) is the most indicative species of the muddy habitat. Other typical species of soft sediment, four-bearded rockling (*Enchelyopus cimbrius*), long-rough dab (*Hippoglossoides platessoides*) and witch (*Glyptocephalus cynoglossus*), are also frequent. The red band fish (*Cepola rubescens*) and the snake blenny

(*Lumpenus lampretaeformis*), two other burrowing species, occur seasonally in the catches (Nash, 1990).

The seasonally stratified waters of the western basin and the area off the Cumbrian coast are also the main spawning and/or nursery areas for many species including, cod (*Gadus morhua*), whiting (*Merlangius merlangus*), haddock (*Melanogrammus aeglefinus*), pouting (*Trisopterus luscus*) and ling (*Molva molva*) (Hillis & Grainger, 1990; Nichols *et al.*, 1993). The pelagic species sprat (*Sprattus sprattus*), herring (*Clupea harengus*) and mackerel (*Scomber scrombus*) are also abundant. Other common species include the lesser spotted dogfish (*Scyliorhinus caniculus*) and the spurdog (*Squalus acanthias*). Dab (*Limanda limanda*) and plaice (*Pleuronectes platessa*) also occur in the catches (Nash, 1990).

2. *Nephrops norvegicus*, some aspects of its biology and ecology

2.1. Identity

Nomenclature

Nephrops norvegicus (Linnaeus, 1758)

Taxonomy

Kingdom Animalia
Subkingdom Metazoa
Phylum Arthropoda
Class Crustacea
Subclass Malacostraca
Series Eumalacostraca
Superorder Eucarida
Order Decapoda
Suborder Reptantia
Section Macrura
Superfamily Nephropoidea
Family Nephropidae

Vernacular names

Fao names

English: Norway lobster
French: Langoustine
Spanish: Cigala

Local names

Iceland: humar, leturhumar
Ireland: Dublin Bay prawn
United Kingdom: Norway lobster, prawn, Dublin Bay prawn, scampi
Spain: langostino, cigala
Portugal: lagostim
Italy: scampo, scampolo, astracio
Morocco: langoustine

External morphology

Adult phase (fig. 2.14)

Exoskeleton pale orange with some zones with a stronger coloration, particulary evident on the carapace and claws. Rostrum fairly long and slender, ending in a sharp point which is slightly curved upwards, and with each of the side edges bearing 2-4 sharp teeth fringed with hair. Carapace with a distinct antennal spine, and at the base of the rostrum a few spines arranged in more or less distinct longitudinal rows; cervical groove distinctly marked and its rear edge bearing four small spines. Eyes with a very broad and kidney shaped cornea. First abdominal segment with an interrupted transverse groove dorsally; subsequent segments with a front groove wich is usually uninterrupted and a rear groove which is broken; rear most segments with clear connections in the middle of the segment between those two grooves. Epimeres of the abdominal segments ending in a sharp point directed to the rear. Telson short, rather longer than broad, tapering slightly towards the rear, its rear edge rounded off and both extremities provided with a spine. Uropods short, broad and triangular in shape. Exopodites clearly divided. (Fisher, 1973; Farmer, 1975)

The sexes are easly distinguished by the form of the first pair of pleopods. In females, they appear as a single flagellum bearing a large number of chitinous hairs and in males, consists of a firm and rigid structure with a longitudinal groove running along the inner wall of its terminal half. Other minor differences appear on the other pleopods and in the proportions between carapace and abdomen width, the abdomen being always wider in females. Males

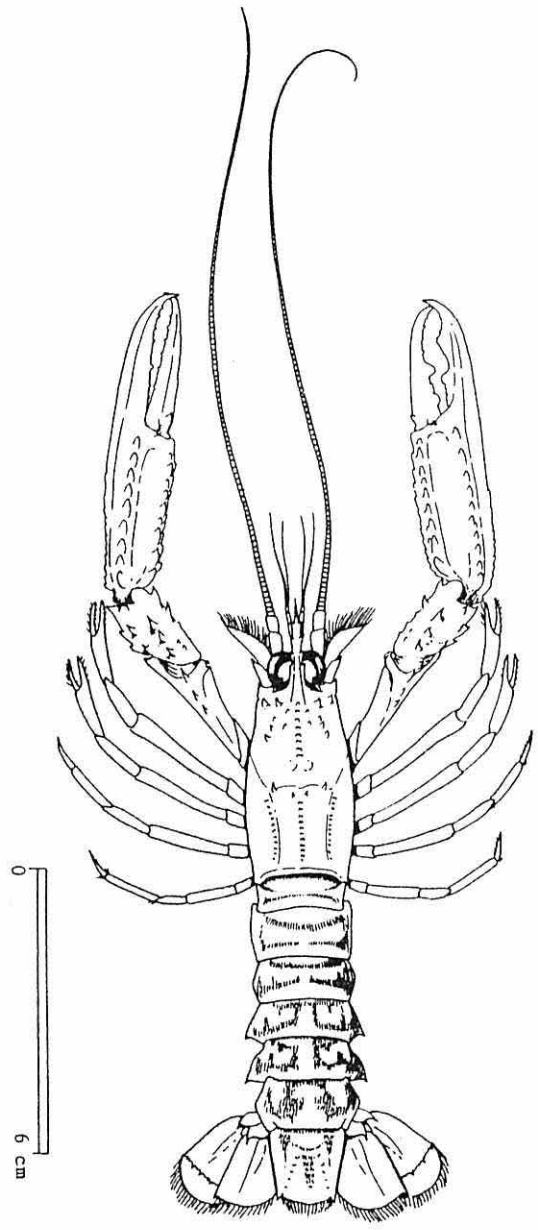


Figure 2.14. *Nephrops norvegicus*, adult form (Fisher, 1973).

attain an overall length up to 290 mm (93 mm carapace length) while females do not exceed 230 mm (73 mm carapace length) (Farmer, 1975).

Larval phase (fig. 2.15)

Farmer (1974a) revision on *N. norvegicus* development defines four larval stages. The first is a pre-zoea stage, of very short duration and yet to be found in plankton samples, followed by three planktonic zoea stages (stages I to III). After zoea stage III the larvae metamorphose into a postlarval form, the settling stage. The first instars of these juvenile phase are sometimes found in plankton samples.

Pre-zoea - Generally similar to first zoea, except smaller, and without setae on the natatory appendages. More or less curled up in the position of the embryo (Farmer, 1974a; Farmer, 1975).

First zoea (stage I) - The length of this stage, measured from the tip of the rostrum to the angle of the caudal fork is between 5.5 mm and 7.0 mm. The first abdominal segment is entirely hidden beneath the carapace and both it and the following one are devoid of dorsal spines. The third, fourth and fifth abdominal segments each bear one median dorsal spine. The sixth abdominal segment has two divergent dorsal spines. The telson is divided into two lateral projections and the uropods are still absent. The rostrum in the first larval stage is entirely devoid of armature and the supra-ocular spines, present in the next stages, are not yet developed. The great claws and the two following pairs of appendages are already chelate. All five pairs of pereiopods bear exopodits. Towards the end of this stage the appendages of the second to fifth abdominal segments can be seen as small buds beneath the cuticle (Jorgensen, 1925; Farmer, 1975).

Second zoea (stage II) - The average overall length of this stage is 7.5 mm to 10.0 mm. The pleopods are now present as small biramous structures but devoid of setae. The segments of the antennae are more fully differentiated than they were in the previous stage, and the large supra-ocular spines have appeared. The eyes are stalked. Dorsal spines and telson are more or less as in the previous stage. Uropods are still absent (Jorgensen, 1925; Farmer, 1975).

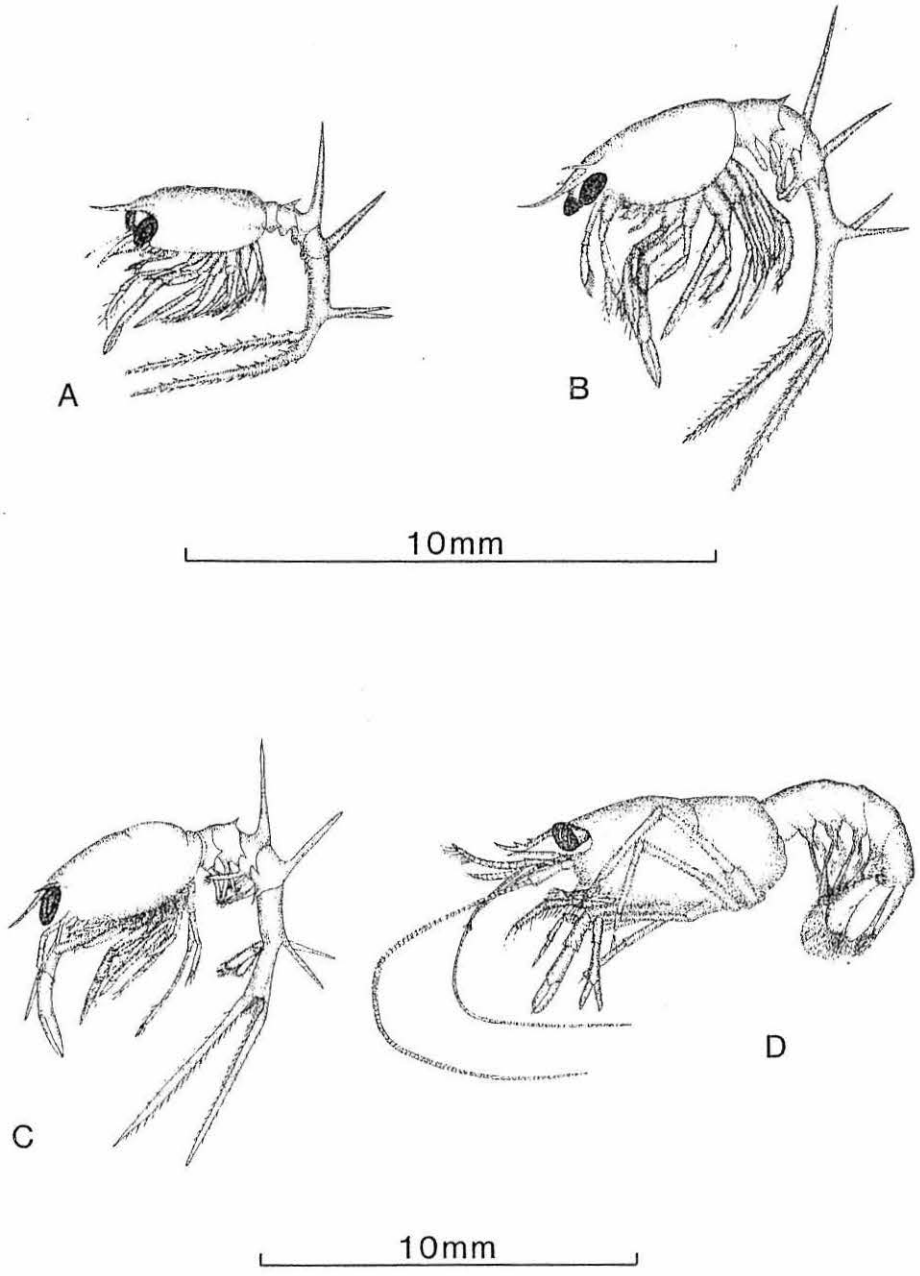


Figure 2.15. *Nephrops norvegicus*, larval stages. (A) stage I, (B) stage II, (C) stage III, (D) first postlarval stage (stage IV) (Nichols *et al.*, 1987).

Third zoea (stage III) - Larvae at this stage measure 10.5 mm to 12.0 mm, overall length. When the third and last larval stage is reached the pleopods of the second to the fifth abdominal segments are fully developed, and with short setae, as are also the uropods, but the first abdominal segment is still devoid of appendages. The rostrum now bears three pairs of teeth dorsolaterally and the caudal fork is segmented off from the last abdominal segment. Dorsal spines and telson more or less like in the previous stages (Jorgensen, 1925; Farmer, 1975).

All larval stages have yellow spots present at the base and points of the pereiopods, in addition to the orange/red chromatophores present over most of the body surface (Jorgensen, 1925; Farmer, 1974a; 1975).

Postlarval phase - On reaching the postlarval stage the small lobster no longer retains the long spines, the caudal fork, the exopodites of the pereiopods and assumes, in general, the characteres of the adult. The endopodit of the second antenna has now elongated to become the flagellum, and the whole appendage has the characteristic form of the adult structure, about three quarters of the total body length. The rostrum has now four pairs of dorso-lateral teeth and a single ventral tooth near the tip. Groups of setae are present on various parts of the carapace, and small protuberances, the precursors of teeth present in the cardiac region in later stages, are now visible. The telson also approximates to the adult form and the sculpturing on the terga of the abdominal segments is beginning to make its appearance (Jorgensen, 1925).

First stage postlarvae are less transparent then the zoea and second stage postlarvae are less transparent than first stage postlarvae. Following the moult into the third postlarval stage the animal resembles a miniature adult. Postlarvae within the third and fouth stages show the same red and white markings as the adults and appear to possess fully calcified exoskeletons. Although the major metamorphosis in *N. norvegicus* occurs between the third zoeal and first postlarval stages there is also evidence of a slight secondary metamorphosis between the first and second postlarval stages. The first postlarval stage still have some vestiges of the thoracic exopods while second stage postlarvae have lost these structures. The abdominal pleura in first stage postlarvae extends into sharp posteriorly pointing spines whereas the corresponding feature in second stage postlarvae is less pronounced. Second stage postlarvae possess spines

at the posterior corners of the telson but these structures are not yet present in postlarval stage one (Smith, 1987).

2.2. Geographical distribution

The Norway lobster, *Nephrops norvegicus*, is widely distributed on the continental shelf of the northeast Atlantic and in the Mediterranean Sea. It is found off Greenland and Iceland in the north, and as far south as Morocco. It has been reported in depths from 20 to 800 metres (Fisher, 1973; Farmer, 1975). The discontinous distribution is related to the nature of the sea bed substrata. The occurrence of adults is tightly controlled by their requirement for muddy substrates in which to construct burrows.

In the Irish Sea, *Nephrops norvegicus* occurs in two isolated areas, the only places with suitable sea bottom substrate. In the western basin, southwest of the Isle of Man, the species colonises a mud patch of about 100 km by 50 km, and in the eastern side, it appears in a much smaller muddy region of about 900 km^2, off the Cumbrian coast (figure 2.1, 2.2 and 2.16). Figure 2.16 shows the location of *N. norvegicus* in the Irish Sea and other grounds around Great Britain and Ireland.

2.3. Habitat and factors affecting distribution

2.3.1. Larval phase

After hatching the larvae of *Nephrops norvegicus* are generally concentrated above the adults grounds but because they are planktonic free swimming organisms, their distribution can be affected by the local hydrodynamic regime either concentrating or dispersing the individuals. Larval behaviour (vertical migration) may also influence the distribution of the planktonic lobsters. These are the aspects that will be investigated in this study.

Laboratory studies showed that the larvae can successfully complete their development at water temperatures ranging from 12° C to 18° C (Figueiredo & Vilela, 1972; Smith, 1987; Thompson & Ayers, 1989). Larvae hatched and kept at lower temperatures (5-12° C) did not survive. Temperature above 18° C also seems to be lethal. Overall, these experiments showed

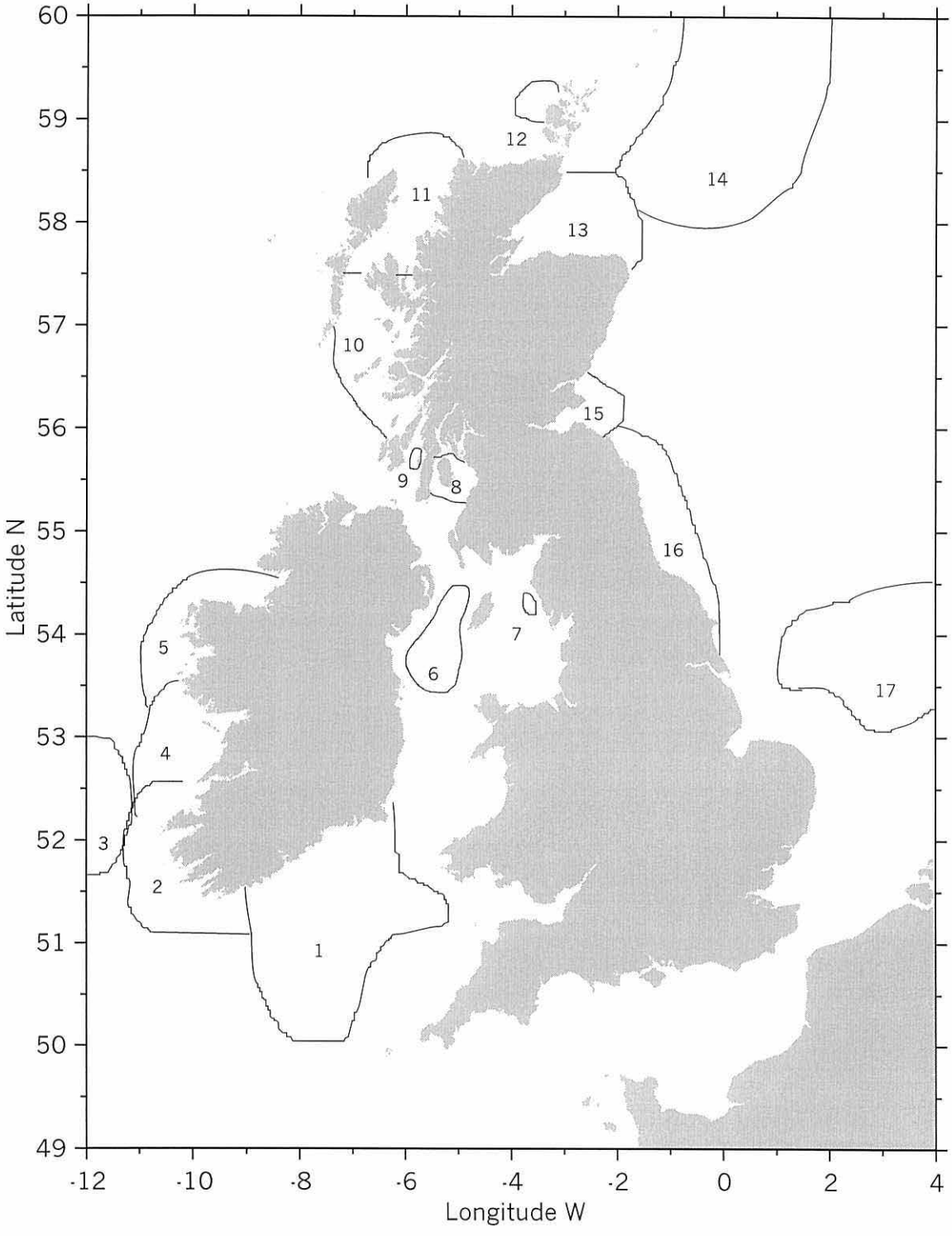


Figure 2.16. Schematic representation of *Nephrops norvegicus* grounds around Great Britain and Ireland 1. Celtic Sea, 2. Southwest Ireland, 3.Porcupine Bank, 4. Aran grounds, 5. Northwest Ireland, 6. Western Irish Sea, 7. Eastern Irish Sea, 8. Clyde Sea, 9. Sound of Jura, 10. South Minch, 11. North Minch, 12. Noup, 13. Moray Firth, 14. Fladen ground, 15. Firth of Forth, 16. Farn Deeps, 17. Botney Gut and Silver Pit (Adapted from ICES, 1997).

that optimum temperature for development ranges from 12° C to 16° C. A reduction in development time is observed with increasing temperature. The laboratory experiments mentioned above, also suggested that stage I larvae are less sensitive to temperature than larvae of stages II and III. Larval survival and development in artificial conditions, do not necessarily reflect what happens in the natural environment, where other factors, such as the quality and availability of food items, may play an important part in larval development.

Salinity does not seem to present a constraint for larval development. Figueiredo and Vilela (1972) successfully reared *N. norvegicus* larvae at salinities ranging from 33 to 40.

Food supply is thought to be an important factor controlling larval ocurrence and development but very little is known about *N. norvegicus* larvae natural diet. The larvae are planktotrophic and likely to feed on a variety of species found in the wild such as copepods, small mysids, other decapod larvae, small *Saggitta* spp. etc. Laboratory studies showed that the larvae actively pursue their preys which they capture with vigorous swimming movements (Farmer, 1975). Cannibalism has been reported to occur in laboratory conditions (Figueiredo & Vilela, 1972; Smith, 1987). The natural predators of *N. norvegicus* larvae are likely to include plankton feeding fish, ctenophores, medusea, fish larvae and other decapod larvae.

2.3.2. Adult phase

Juvenile and adult *Nephrops norvegicus* are benthic and construct burrows in the soft substrate on which they live. The species is substrate specific only occurring on cohesive muds, stable enough to support unlined burrows (Farmer, 1975; Chapman, 1980).

Various types of mud, differing in the relative proportions of their constituent clay, silt and sand particles, appear to be suitable. Field studies in Scottish waters showed that adult Norway lobsters can inhabit a range of sediments in which the silt and clay component varies from 30% to almost 100%, sand comprising the remaining fraction (Bailey *et al.*, 1986; Chapman & Bailey, 1987, Chapman & Howard, 1988; Tuck *et al.*, 1997). In the western Irish Sea the species was observed in some regions where the silt-clay content was as low as 4% (Tully & Hillis, 1995). Minerals associated with clay particles confer some of the cohesive properties required for burrow construction and stability, but the lower limit for the

proportion of these fine particles in the sediment is not known precisely (Bailey *et al.*, 1986; Chapman & Bailey, 1987).

Laboratory experiments on substrate selection by postlarval stages of *N. norvegicus* showed their clear preference for fine mud sediment. The majority of the young lobsters chose sediments with 100% or 80% mud content to settle. The first postlarval stage showed very little interest in burrowing. Individuals within this stage generally spend much of their time in exploratory behaviour but do not actually begin to construct their burrows, this phase is considered to be a transition between the planktonic and benthic environments. Second and older stage postlarvae actively showed their aptitude to burrow (Smith, 1987). The observations from that study supported the generally held view that juvenile *N. norvegicus* actively select substrata of a similar type to that which sustains the adult populations.

N. norvegicus spends the majority of its life within its burrow, sheltered and protected from predators, emerging periodically to forage. The duration of the foraging excursions seems to be dependent on the degree of vulnerability of the individuals. Newly moulted individuals are especially fragile and tend to stay in their burrows until their exoskeleton is fully formed. Juveniles and females also remain confined to their burrows for long periods. The young lobsters spend the first year of their benthic existence within their refuge and the berried females do not abandon the burrows during the period of incubation (approximately 8-9 months, in the Irish Sea). Large males are less dependent on the burrows and spend more time on the surface of the mud (Farmer, 1974b; Chapman *et al.*, 1975; Chapman, 1980). Activity outside their shelters, is restricted to several short excursions during favourable periods of the day (usually related to the light reaching the sea bed). During any period of activity only part of the population is active at any one time, it has been estimated that only 10% to 30% of the population may emerge at the same time (Chapman , 1980). As a consequence of the rhythms of emergence, commercial catches show large diel (daily emergence behaviour) and seasonal fluctuations (females are more available during the spring-summer period).

The structure of the burrows found in the wild varies greatly from single burrows with one or two openings to a system of linked burrows with several entrances. Most burrow systems have only one occupant but it is not unusual to find animals of different sizes sharing the

same system. When that happens, each individual occupies its own tunnel within the complex (Chapman, 1980).

Associations between adults and juveniles are common (Chapman, 1980; Tuck *et al.*, 1994) and even associations with other burrowing species have been reported (Rice & Chapman, 1971; Atkinson, 1974; Tuck *et al.*, 1994). There is some evidence that on settlement, juvenile *N. norvegicus* preferentially construct burrows within existing adult burrows. The narrow tunnels of a juvenile's burrow gives it protection from predation by the adult whose presence at the same time, keeps other predators away. The young lobsters, confined to their refuges, may also benefit from any food reserves the adults may carry to the burrow. As the juvenile grows, it extends its own tunnel, away from the adult burrow, developing an independent section which eventually loses all the links with the adult sector. In this way, aggregations of individual burrows develop from the original adult-juvenile complexes. Fishing and natural mortality will periodically remove the larger individuals and growth of the juveniles will modify the spatial distribution of the burrow system (Tuck *et al.*, 1994).

Apart from the nature of the substrate, few other factors have been reliably linked to changes in the distribution of *N. norvegicus*. References to temperature, salinity and oxygen exist in the literature but conclusive results on the way these factors affect the species distribution and behaviour have been scarce.

The maximum and minimum temperatures limiting the distribution of *N. norvegicus* are not known, although recorded bottom temperatures from inhabited areas range from about 5° C to 15 °C (Farmer, 1975, Chapman, 1980). At very low bottom temperatures, it is believed that the animals remain in their burrows (Chapman, 1980).

On the other hand, when the levels of dissolved oxygen in the water close to the bottom are low, the lobsters seem to be forced out, onto the mud surface. Baden *et al.* (1990) reported, in the Kattegat-Skagerrak area, low (<1 ml/l, 15% O_2 saturation) oxygen concentrations at the end of summer which forced the individuals to leave their burrows. During severe hypoxia conditions, even berried females were forced onto the surface. A significant decrease in the lobster biomass during these critical periods was also noted.

Differences in salinity do not seem to have a great relevance on the distribution of the Norway lobster but it is suggested that the absence of the species from the Baltic Sea is due to its inability to tolerate very low salinities. Salinity values ranging from 29 to 38 were observed in regions colonised by the species (Farmer, 1975).

Fish species are considered to be the main predators of *N. norvegicus*. Amongst all species, cod is the most important predator (Thomas, 1965a; Armstrong, 1982; Brander & Bennett, 1989). Lesser spotted dogfish (Thomas, 1965a; Tuck, 1993), thornback ray (*Raja clavata*) (Thomas, 1965a), pouting and poor cod (*Trisopterus minutus*) (Armstrong, 1982, Tuck, 1993) also include Norway lobsters in their diet. The octopus (*Eledone cirrhosa*), when in areas of considerable abundance, can also be an important predator (Tuck, 1993).

The macrobenthic species most common in the *N. norvegicus* grounds (section 1.5) are usually present in its diet. The species is in fact reported to be a varied feeder, taking available organisms indiscriminately. Polychaetes, brittle stars, other decapod, and bivalves are among the potential prey items (Farmer, 1975; Lagardere, 1977; Baden *et al.*, 1990).

2.4. Population structure

The information available on the size composition and sex ratio of *Nephrops norvegicus* populations is often derived from sampling of the commercial catches and therefore likely to underrepresent the smaller length classes which are not available for the fishery. Moreover, the length composition and size of catches vary diurnally and seasonally, larger males are more exposed to fishing because they spend more time outside the burrows and ovigerous females are usually absent from trawl catches between November and April. In consequence, the sex ratio and length composition of catches, and the overall catch per unit of fishing effort, fluctuates according to the phase of the breeding cycle in different areas and the activity rhythms of the individuals. Furthermore, changes in the fisheries legislation and market practices have occurred over the years adding extra bias to the information from fisheries statistics. For these reasons, analyses on population structure and dynamics based on data from the fishery should be considered with caution. Apart from information from the commercial catches other methods of sampling have been used in order to assess population characteristics and stock sizes, in different regions. Research as been carried out using

trawling with smaller mesh size nets, diving and underwater photography and filming and plankton surveying (Chapman, 1980; Chapman & Bailey, 1987; Briggs, 1997).

Despite the difficulty of observing females during part of the year, the fact that its proportion is close to 50% at certain times of the year (between egg hatching and egg laying), suggests that the true sex ratio is probably near 1:1. In the western Irish Sea females are well represented in catches only during the second and third quarters of the year, particularly between June and August (O'Riordan, 1964; Farmer, 1974a; ICES, 1997). Briggs (1995) observations, showed that the proportion of females in the Northern Ireland landings from July to September, over the period 1982-1993, has been around 55%, suggesting that the real sex ratio is close to 1:1. The sex ratio of the annual landings, from the eastern Irish Sea has been very near 1:1 since 1993, in earlier years the fishery was dominated by males (ICES, 1997).

After reaching sexual maturity the male *N. norvegicus* moults more frequently than the female consequently growing faster; mature females are only able to moult once per year, whereas males and immature females moult more frequently. As a result the males account for an increasing proportion of the larger size categories in the population and in catches while the females outnumber the males in the smaller size classes (Chapman, 1980).

It has long been recognised that western Irish Sea *Nephrops norvegicus* have a lower mean size than lobsters from other areas (O'Riordan, 1964; 1965a; 1965b; Cole, 1965; Farmer, 1974c; 1975). The fraction of animals below 25 mm carapace length is much higher in the Irish Sea than in the Scottish areas of the Minch and Clyde and also greater than in the Celtic Sea (Briggs, 1987). Observations carried out aboard a commercial vessel in the area off Dundalk Bay showed a size range from 21.7 to 30.5 mm, for males and 20.7 to 26.9 mm, for females. Size frequency distribution from an area in the southern end of the western Irish Sea ground presented median lengths between 22.4 and 27.8 mm, for males and between 22.5 and 25.7 mm, for females (Tully & Hillis, 1995). Mean sizes in catches carried out by Northern Ireland trawlers in the western Irish Sea, from 1994 to 1996, varied from 26.2 to 28.5 mm carapace length, for males and between 24.3 to 25.9 mm, for females. In the Republic of Ireland catches the mean sizes, for the same period, oscillated between 25.4 to 25.8 mm, for males and between 22.8 to 23.8 mm, for females. The mean sizes from catches

in the eastern Irish Sea grounds, during the same period, varied from 32.1 to 33.5 mm, for males and between 31.6 and 32.3 mm, for females (ICES, 1997).

The relationship between size and age in *N. norvegicus* populations is not clearly known due to the difficulty of determining age in a species with no permanent calcified structures and problems of separating cohorts in length frequency data. Laboratory studies indicated that the species reaches a size of about 14 mm (carapace length) after one year and approximately 20.8 mm, after two years (Farmer, 1973). Maturity, in western Irish Sea lobsters, appears to occur around age 2 for females and age 3 for males (Farmer, 1973; 1974a; Hillis, 1979; Briggs, 1988; Hillis & Tully, 1993). O'Riordan (1964) noted that in the Irish grounds, males generally did not exceed 180 mm, total length (~ 56.3 mm carapace length), and the maximum size for females was around 130 mm (~ 40.6 mm).

Differences in size composition between areas probably reflect differences in growth rate. The slow growth rate of the western Irish Sea *Nephrops norvegicus* population (Farmer, 1973; 1974c; Hillis, 1979) has been found to be similar to the growth rate of the species in the Sound of Jura, which also showed a similar size composition (Bailey *et al.*, 1986, Brander & Bennett, 1989).

Studies carried out in Scottish waters revealed variations in the density of *N. norvegicus* populations and an apparent relationship between population density and mean size of the lobsters. High densities were usually found in places where the size of the lobsters was predominantely small in size and *vice versa* (Chapman, 1979; Bailey *et al.*, 1986; Chapman & Howard, 1988; Tuck *et al.*, 1997). Differences in fishing activity between the areas were initially suggested to explain the size variability between sites but fishing pressure alone did not account for the variations observed. For example, the population structure of the Sound of Jura lobsters seemed to have remained virtually unchanged since the fishery started (Thomas, 1965b).

Although fishing mortality definitely plays a role in the size composition and density of the populations other factors, environmental factors, such as sediment type and food availability were pointed out as having an affect on population structure and abundances. In the Scottish grounds, high densities of small individuals were observed in areas with coarse sandy-muds

with a low silt-clay content while lower densities of predominantely larger individuals, were present in finer sediments with a higher silt-clay component (Chapman, 1980; Bailey, 1986; Bailey *et al.*, 1986; Chapman & Bailey, 1987; Chapman & Howard, 1988). Slower growth rates in locations with high densities can be explained by competion for food and space or changes in social behaviour but it is more difficult to understand why the lowest densities and biomass of *N. norvegicus* should occur in silt-clay sediments which seem to provide the most favourable conditions for adult life (more suitable to construct burrows and with higher food availability).

Observations on size composition and density of *N. norvegicus* in relation to substrate composition in the western Irish Sea, appeared to contradict the results described above. Studies in the southern end of the western Irish sea ground, showed lower densities of larger lobsters in coarser sediments and higher concentrations of smaller individuals in finer sediments (Hillis, 1987; Hillis, 1988a; Tully & Hillis, 1990; Hillis & Tully, 1993). Density was shown to correlate negatively with mean size and growth rates, in the northern and southern western Irish Sea ground (Briggs, 1989; Tully & Hillis, 1990; Hillis & Tully, 1993) but the observations in the northern region (Briggs, 1989) did not demonstrate a relation between sediment structure and lobster size.

More recent analyses, appear to indicate that the relationship between sediment composition and lobster size is not linear, a plot combining the information from several areas showed that peak abundances, and smaller lobster sizes, occurred at intermediate particle sizes (ICES, 1996). Moreover, it has also been pointed out that the studies carried out in Scottish waters and in the western Irish Sea, covered areas of very different sediment composition. The clay-silt content in the area studied in the Irish Sea was much lower (4-49%) than in the Scottish grounds (30-96%) and hence the apparent discrepency between the analyses (Tully & Hillis, 1995; Tuck *et al.*, 1997). Tully & Hillis (1995) highlighted that the negative relationship between *N. norvegicus* mean size and the silt-clay content of the sediment holds only for the restricted range in silt-clay component found in the area studied.

Other factors that have been suggested could be involved in the variability in structure and biology of *N. norvegicus* populations, include: bottom temperature (Hillis & Tully, 1993; Tully & Hillis, 1995), oxygen levels (Baden *et al.*, 1990; Maynou & Sarda, 1997), sediment

carbon content and benthic production (Bailey *et al.*, 1986; Chapman & Bailey, 1987) and hydrographic conditions which may favour plankton survival, concentration of larvae and settlement (Chapman & Bailey, 1987; Chapman & Howard, 1988; Tully & Hillis, 1995).

In the western Irish Sea, higher densities of individuals in finer sediments may reflect higher retention of larvae over the area, due to the local hydrodynamics (gyre), rather than sediment composition directly (finer sediments exist in regions of lower water mixing energy). A conclusive understanding of the variability encountered in structure and dynamics of *Nephrops norvegicus* populations is yet to be achieved. A combination of the aspects discussed is likely to be responsible for the differences observed and probably different factors have different contributions in distinct areas. In the western Irish Sea a degree of patchiness appears to exist in the population structure and biology, within the mud patch area. Variations in lobster sizes, densities, female maturity and sex ratio were observed between short distance sites (Briggs, 1995). This author concluded that *N. norvegicus* occurs in 'stocklets', which show different population characteristics.

2.5. Reproductive cycle

In the western Irish Sea, female *Nephrops norvegicus* reaches maturity at a size of between 20 to 25 mm carapace length (~ 2 years) and the male at slightly larger size (~ 3 years) (Farmer, 1973; 1974a; Hillis, 1979; Briggs, 1988; Hillis & Tully, 1993). The mature lobsters of both sexes moult during the period from May to July, with a peak in May, and mating takes place shortly after moulting when the female exo-skeleton is still soft. A spermatophore is injected into the thelycum of the females and fertilization probably occurs internally. Eggs are layed between August and September. The eggs are incubated (8-9 months) on the pleopods until the following April-June, when hatching occurs. A proportion of about 90% of the adult females is believed to carry eggs every year (Farmer, 1974a). Associated with their wide distribution, Norway lobsters show great variations in their breeding cycle, which are believed to be related to sea water temperature variability. The incubation period in the warmer waters of the Mediterranean Sea and off the coasts of Portugal is shorter (~ 6 months), hatching occurring earlier in the season while for example in the Faroe Islands spawning is probably biennial with the incubation period lasting for up to 12 months. Details of the reproductive cycle for other areas are given in table 2.1.

Table 2.1. Details of the breeding cycle of *N. norvegicus* in different areas.

Area	Egg laying (spawning)	Egg hatching	Incubation period	Periodicity of spawning	Reference
Faroe Islands	Jun-Aug	May-Aug	9-12	biennial (?)	Anderson 1962, *in* Chapman (1980)
Scottish grounds	Aug-Nov	May-Jun	9-10	annual	Thomas & Figueiredo (1965)
Clyde Sea	Aug-Nov	Apr-Jul	9	annual	Smith (1987)
NE England	Aug-Sept	May-Aug	10	biennial	Symonds (1972)
Central North Sea	Sept-Nov	May-Jun	9-10	biennial	Sterk & Redant (1989)
Western Irish Sea	Aug-Sept	Apr-May	8-9	annual	O'Riordan (1964)
Western Irish Sea	Aug-Sept	Apr-Jun	8-9	annual	Farmer (1974a)
Western Irish Sea		Apr-Jun			Hillis (1974a)
Western Irish Sea		Apr-Jun			Nichols *et al.* (1987)
W Ireland (Galway)		Feb-May			Bhaldraithe (1976)
Ligurian Sea	Apr-Nov	Dec-Mar	5-6	annual	Relini & Relini (1989)
Adriatic Sea	Jul-Dec	Jan-Jun	6	annual	Froglia & Gramitto (1981)
Portugal	Aug-Sept	Feb-Mar	6	annual	Figueiredo & Barraca (1963)

Fecundity also varies considerably between geographical areas, and according to the size of the females (Chapman, 1980; Sarda, 1995, references therein). In the western Irish Sea an approximate number of eggs per female between 340-1360 is derived from Farmer (1974a) study. During the incubation period a significant number of eggs are lost. Figueiredo *et al.* (1983) estimated that by the time hatching occurred, in Portuguese waters, only about 32% of the initial number of eggs produced were still attached to the pleopods. A lower figure of egg loss (45%) was presented by Morizur *et al.* (1980) for the Bay of Biscay. Nichols *et al.* (1987) estimated the mean effective fecundity for western Irish Sea *N. norvegicus* females to be in the range from 578 to 889 eggs.

On hatching, a short pre-zoeal stage (yet to be collected in plankton samples), which is unable to swim, appears. This stage quickly moults to the first of three zoeal stages which are planktonic. After the third stage zoea the larvae metamorphose into the postlarval stage (also commonly referred as stage IV) (Farmer, 1974a). Settlement is believed to occur after the first moult of the postlarvae (Smith, 1987). The larval stages have been described in section 2.1. The rate of development of the larvae are dependent on water temperature and food supply. Development times in relation to water temperature given by Nichols *et al.* (1987) study, in artificial conditions, estimates an overall duration of the planktonic phase of 44.4 days at 10^{o} C. The developmental time equations, for each zoeal stage, derived from this study are presented, and used, in chapter V. Another laboratory experiment (Smith, 1987) produced a slightly longer duration for the larval stages.

2.6. Fishery

The Irish Sea *Nephrops norvegicus* populations have been subjected to fishing activity for many decades. Landing statistics from the 1940's, indicated that an average of 23.5 tonnes of lobsters were being extracted from the area, every year. From 1950 onwards the commercial demand increased substantantially and as a consequence the economic value of the species rose and landings became greater each year (O'Riordan, 1964). Since its start, the fishery has been dominated by Northern Ireland and Republic of Ireland vessels. Other countries (England, Wales, Belgium, France), shared a much smaller proportion of the landings.

In the Irish Sea, Norway lobsters are mainly caught in a directed fishery, using an otter trawl. The fishery operates all year round but the bulk of the catches occur during the spring-summer period (when the females are also available for the fishery). A small by-catch of *N. norvegicus* occurs during trawling for white fish, especially cod (Briggs, 1997).

Most landings from the western Irish Sea are by Northern Ireland (6000 tonnes per annum, in recent years) and the Republic of Ireland (2000 tonnes), with a combined annual sale value of about £10 million, making it the most valuable fishery in these waters. Smaller quantities (~ 600 tonnes/year) are landed from the eastern Irish Sea predominantly by English vessels (Briggs, 1997).

Table 2.2 shows fishing effort ('000 hours), LPUE (landing per unit effort), catch and landing figures from the western Irish Sea by Northern Ireland trawlers for the period from 1987 to 1996. Total landings (including all countries involved in the fishery) are also presented. For the period considered, an average 8400 tonnes have been consistently removed from this population, every year. The total landings from 1996 are believed to be underestimated due to incomplete information from the Republic of Ireland fishery. Although some variability has been observed, effort and LPUE, during that 10 years period, have been fairly stable.

Size frequency distributions expressed as carapace length have been routinely measured for samples from the Irish Sea since the mid 1960's. Early analyses of these data suggested a declining trend in mean carapace length of catches however, more recent studies have drawn attention to the high variability between samples, even over short distances (greater variability in space than it has been observed in long term temporal trends), suggesting that any general conclusions should be carefully constructed (Briggs, 1987; Briggs, 1995). Changes in legislation (minimum sizes of net mesh and minimum size of individuals) and market practices (whole individuals or tails) should also, always be taken into account when looking at size information derived from fisheries data. Recent data from ICES (International Council for the Exploration of the Sea) statistics (ICES, 1997) showed that the mean size of *N. norvegicus* in the Northern Ireland fishery remained stable for a number of years but there has been an increasing trend since 1994 (table 2.3).

Table 2.2. Irish Sea west, effort (' 000 hours Northern Ireland trawlers), LPUE (kg/hour Northern Ireland trawlers), total landings (tonnes, UK, Isle of Man, Ireland, France) for the period 1987-1996 (ICES, 1997).

Year	Effort (NI)	LPUE (NI)	Catches NI (tonnes)	Landings NI (tonnes)	Total Landings (tonnes)
1987	164.5	30.3	5775	4990	9331
1988	156.4	33.4	5712	5220	8630
1989	191.4	28.8	5945	5517	8084
1990	189.9	29.0	5679	5505	8278
1991	200.6	29.5	6132	5925	9468
1992	194.1	26.1	5692	5058	7502
1993	184.1	28.8	6085	5295	8111
1994	185.9	31.1	6599	5480	7628
1995	167.8	32.2	6240	5401	8817
1996	165.4	33.9	6312	5600	7946

Table 2.3. Irish Sea west: Mean sizes (CL mm) of male and female *N. norvegicus* from Northern Ireland vessels, 1987-1996 (ICES, 1997).

Year	Catch		Landings		Discards	
	Males	Females	Males	Females	Males	Females
1987	26.3	24.7	27.2	25.9	22.1	21.6
1988	28.2	25.3	29.1	26.2	21.5	21.0
1989	26.6	24.9	27.4	25.9	20.8	20.5
1990	26.9	24.5	27.4	25.0	20.5	19.6
1991	26.7	23.6	27.3	24.2	20.8	19.8
1992	27.4	25.7	28.4	27.1	22.5	22.4
1993	25.9	24.2	27.1	25.6	21.3	21.0
1994	26.2	24.3	27.2	25.6	21.1	20.9
1995	27.7	24.9	29.0	26.0	22.0	21.6
1996	28.5	25.9	29.9	27.0	22.3	22.0

Table 2.4. Irish Sea east, effort (' 000 hours UK trawlers), LPUE (kg/hour UK trawlers), total landings (tonnes, UK, Isle of Man, Ireland, Belgium) for the period 1987-1996 (ICES, 1997).

Year	Effort	LPUE	Total Landings (tonnes)
1987	23.3	15	534
1988	19.7	18	516
1989	18.5	17	438
1990	17.8	24	644
1991	20.0	26	859
1992	18.6	20	495
1993	23.8	18	618
1994	17.8	22	514
1995	21.1	19	504
1996	17.1	22	450

Table 2.5. Irish Sea east: Mean sizes (CL mm) of male and female *N. norvegicus* from UK vessels landing in England and Wales , 1987-1996 (ICES, 1997).

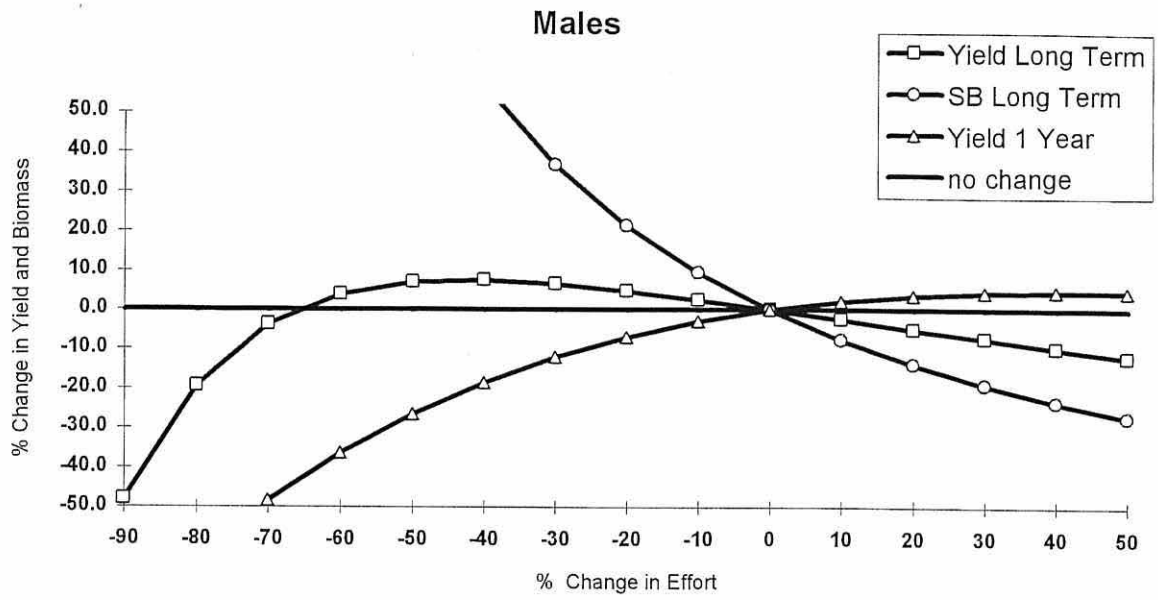
Year	Catch		Landings		Discards	
	Males	Females	Males	Females	Males	Females
1987	not avail.	not avail.	35.9	32.5	not avail.	not avail.
1988	not avail.	not avail.	37.9	36.4	not avail.	not avail.
1989	not avail.	not avail.	not avail.	not avail.	not avail.	not avail.
1990	not avail.	not avail.	not avail.	not avail.	not avail.	not avail.
1991	30.0	29.5	32.1	33.5	26.9	26.6
1992	30.1	30.5	32.2	32.8	26.9	26.0
1993	31.6	30.6	35.0	34.6	26.7	26.5
1994	33.2	32.3	33.9	32.9	28.2	28.1
1995	32.1	31.6	32.6	32.1	27.5	27.3
1996	33.5	32.0	34.2	32.6	28.2	28.1

Table 2.6. Landings (tonnes), effort (hours), LPUE (landings per unit effort) for statistical rectangles in the western Irish Sea (ICES, 1997).

Year		35E4 (53-53.5° N, 5-6° W)	35E5 (53-53.5° N, 4-5° W)	36E4 (53.5-54° N, 5-6° W)	36 E5 (53.5-54° N, 4-5° W)	37E4 (54-54.5° N, 5-6° W)	37E5 (54-54.5° N, 4-5° W)	38E4 (54.5-55° N, 5-6° W)
1987	Landings	2.4	0	2608.8	35.5	1820.3	610.7	17.3
	Effort	190	0	70738	1212	64705	24265	949
	LPUE	12.6	0	36.9	29.3	28.1	25.2	18.2
1988	Landings	4.3	0	2358.0	26.8	2303.0	642.4	11.3
	Effort	80	0	66632	794	77888	25289	1003
	LPUE	53.6	0	35.4	33.7	29.6	25.4	11.19
1989	Landings	5.4	0	2235.2	28.3	2475.0	839.4	6.5
	Effort	109	0	66978	777	88758	35266	667
	LPUE	49.5	0	33.3	36.4	27.9	23.8	9.7
1990	Landings	1.9	0.003	2167.5	29.9	2676.6	656.4	4.3
	Effort	183	18	68748	841	95745	25821	548
	LPUE	10.4	0.2	31.5	35.6	28.0	25.4	7.8
1991	Landings	2.9	0.5	2454.2	62.8	2571.6	885.0	15.5
	Effort	263	72	71315	1598	93409	34857	1521
	LPUE	10.9	6.2	34.4	39.3	27.5	25.4	10.2
1992	Landings	0.087	0	2272.2	21.1	2146.6	631.6	15.9
	Effort	7	0	73411	672	91000	26180	2581
	LPUE	12.4	0	31.0	31.5	23.6	24.1	6.1
1993	Landings	16.1	0	2383.5	55.8	2311.2	578.6	19.4
	Effort	316	0	76209	1773	81347	24451	1846
	LPUE	50.8	0	31.3	31.5	28.4	23.7	10.5
1994	Landings	5.5	0	2364.1	27.1	2890.0	519.8	23.9
	Effort	191	0	70579	1189	93756	20326	3308
	LPUE	28.8	0	33.5	22.8	30.8	25.5	7.2
1995	Landings	1.9	0.07	2254.5	33.1	2527.7	634.5	47.6
	Effort	146	15	63453	1324	83497	21134	3730
	LPUE	13.2	4.7	35.5	25.0	30.2	30.0	12.8
1996	Landings	7.5	0.04	2650.7	21.0	2343.9	588.3	41.1
	Effort	679	6	67524	1134	75107	19947	4116
	LPUE	11.0	6.5	39.3	18.5	31.2	29.5	10.0

Table 2.7. Landings (tonnes), effort (hours), LPUE (landings per unit effort) for statistical rectangles in the eastern Irish Sea (ICES, 1997).

Year		35E6 (53-53.5° N, 3-4° W)	36E6 (53.5-54° N, 3-4° W)	37E6 (54-54.5° N, 3-4° W)	38E6 (54.5-55° N, 3-4° W)
1987	Landings	0.053	12.5	509.1	7.4
	Effort	231	1559	41245	1302
	LPUE	0.2	8.0	12.3	5.7
1988	Landings	0.013	4.5	485.8	20.5
	Effort	8	1179	32474	3589
	LPUE	1.6	3.8	15.0	5.7
1989	Landings	0	6.8	428.0	2.2
	Effort	0	613	29896	803
	LPUE	0	11.1	14.3	2.7
1990	Landings	0	6.1	623.2	2.9
	Effort	0	740	30556	397
	LPUE	0	8.3	20.3	7.2
1991	Landings	0.03	4.1	828.0	1.5
	Effort	3	792	34057	127
	LPUE	10	5.2	24.3	11.6
1992	Landings	0.695	20.7	460.7	1.9
	Effort	77	1686	28745	420
	LPUE	9.0	12.3	16.0	4.6
1993	Landings	0	44.4	502.7	4.7
	Effort	0	3290	31541	909
	LPUE	0	13.5	15.9	5.2
1994	Landings	0	46.5	450.6	5.7
	Effort	0	2431	22914	733
	LPUE	0	19.1	19.7	7.8
1995	Landings	0	32.2	458.3	5.0
	Effort	0	4401	27947	1097
	LPUE	0	7.3	16.4	4.6
1996	Landings	0	23.6	409.6	12.9
	Effort	0	2787	22157	1883
	LPUE	0	8.5	18.5	6.9



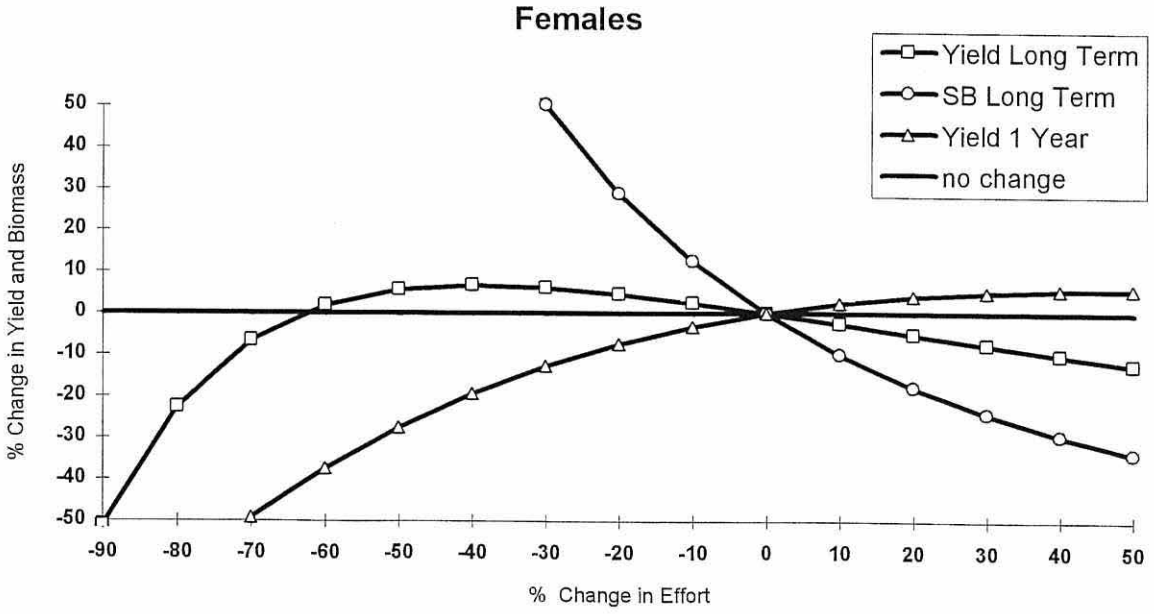
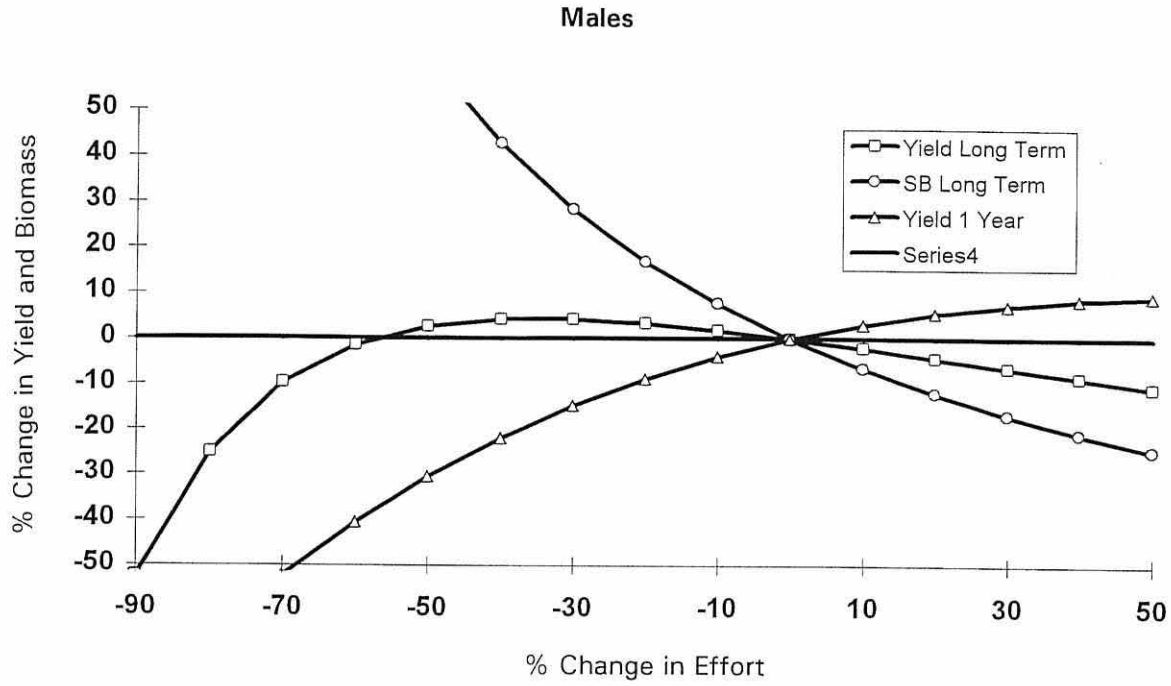


Figure 2.17. Irish Sea west (FU15), percentage changes in long term landings and stock biomass, and short term landings following various changes in fishing effort, males and females shown separately (ICES, 1997).



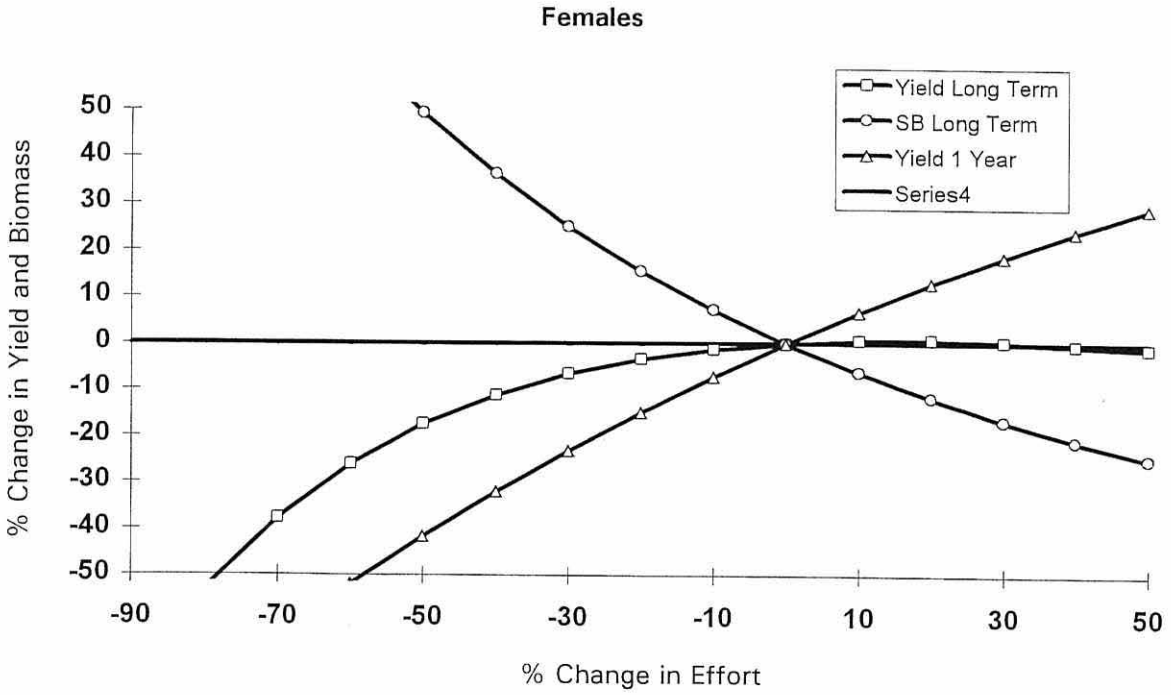


Figure 2.18. Irish Sea east (FU14), percentage changes in long term landings and stock biomass, and short term landings following various changes in fishing effort, males and females shown separately (ICES, 1997).

Information on effort, LPUE and total landings from the eastern Irish Sea population, for the same period (1987-1996), are presented in table 2.4 Effort and LPUE has not suffered significant changes. For the period considered total landings averaged approximately 560 tonnes per year. The mean size data (table 2.5) suggests that *N. norvegicus* mean size in the eastern Irish Sea ground is slightly larger than in the western Irish Sea waters. Small inter-annual variations have been observed. (ICES, 1997).

Landings and effort data per ICES statistical rectangle are presented in table 2.6, for the western Irish Sea, and table 2.7 for the eastern Irish Sea. Those rectangles are fairly large (half a degree in latitude per degree in longitude), however it can be appreciated that in the western Irish Sea the bulk of the fishery comes from rectangles 36E4 and 37E4, on the western side of the basin. This information also shows that although in small numbers, lobsters have been collected south of line 53.5° N (35E4, 35E5), which has been reported to be the limit of the mud patch area. In the eastern Irish Sea, the majority of the catches were carried out, in rectangle 37E6, in the centre of the muddy substrate area.

Fisheries regulations are advised by ICES and recommended by the European Commission to the European Council of Ministers. At present, the minimum landing size from Irish Sea waters (ICES division VIIa, Functional units 14 (east) and 15 (west)) is 20 mm carapace length and the minimum mesh size allowed for the fishery is 70 mm (Briggs, 1997). A total allowable catch (TAC) is recommended by the ICES Advisory Committee on Fishery Management (Working Group on *Nephrops* stocks) every 2 years, and subsequentely discussed and legislated by the European Council of Ministers. Catch allowances are given for ICES divisions, which usually include several *N. norvegicus* grounds.The Irish Sea waters are included in ICES division VII which also incorporates the grounds on the south and west coasts of Ireland.

Stock assessment is carried out by the ICES Working Group and until the present it has been mainly based on catch, landing, mean sizes and effort data. The methods employed are length cohort analysis (LCA), and after slicing length compositions into ages, virtual population analysis (VPA), which are performed separately for males and females (ICES, 1997). Accurate assessement of the status of the stocks depends upon reliable information on several biological parameters (*eg.* length, weight, maturity, mortality, age). Because age

determination in crustacean species is still imprecise, population assessement techniques are not yet as developed as the methods applyed for fish species. Recent research has provided considerable improvement on growth rate estimates but alternative methods of stock assessment have also been tested (*eg.* underwater television surveying and assessment from larval production) (Briggs, 1997).

The results from the last Working Group meeting (ICES, 1997) suggested that both, the western and eastern Irish Sea stocks are withstandings the current levels of fishing mortality. For the western Irish Sea population (FU 15) fishing mortalities generated by the 1997 LCA and VPA assessements were similar to those predicted by the 1995 analysis. LCA results gave a relatively flat topped Y/R (Yield per recruit) curve and suggested that the current fishing mortality (F) is about 20-30% beyond F_{max} (at which yield is maximised), for both males and females (figure 2.17). A flat topped curve indicates that reduction in effort would only produce a small long-term increase in yield however, increase in effort would result in a steady decline in long-term yield. The LCA results for the eastern Irish Sea population (FU 14) suggested that current F is above F_{max}, for males, though the Y/R curve is also flat topped. The female long-term Y/R curve produced is very flat topped, with current F a little below F_{max} (figure 2.18).

Sustained catches and stable recruitment led the ICES meeting to consider that the Irish Sea populations are enduring the current fishing pressure but fishing effort should not be allowed to increase (ICES, 1997). It is also a concern of the ICES scientists that the policy to establish TAC for considerably large areas (ICES divisions), including distinct *Nephrops norvegicus* populations, should be reviewed. Variability between populations (biology and structure) should be taken into account during management decisions.

Chapter III. Observational methods and instruments

The data analysed in this study includes observations on the spatial and vertical distribution of *Nephrops norvegicus* larvae, collected from 1982 to 1996, including surveys carried out during this project in 1994, 1995 and 1996. Oceanographic data was acquired during the same campaigns in 1994, 1995 and 1996.

1. Zooplankton sampling

1.1. Spatial distribution

1.1.1. Sampling

During this study four research cruises including physical and biological surveys were undertaken. In addition, to complement these observations, several sources of historical and contemporary data were investigated.

Several institutions were contacted in order to assess the possibility of access to their data on the distribution of *Nephrops norvegicus* larvae in the western Irish Sea. Sampling of the larval stages of the species has been used for stock assessement purposes and therefore a reasonable amount of information has been gathered over the years. Most of the data used in this study was made available by, or via, the Centre for Environment, Fisheries and Aquaculture Science (CEFAS).

Another source of plankton observations was the Sir Alister Hardy Foundation for Ocean Science (SAHFOS) data base. The laboratory is responsible for the collection and analysis of plankton samples provenient from a variety of commercial ship routes in the North Sea and in the North Atlantic, since the early thirties. A number of 'ships of opportunity' deploy the high speed sampler - Continous Plankton Recorder (CPR) once or twice a month during their regular trips, the plankton samples are then analysed at SAHFOS.

The CPR survey has some of their regular sampling routes through the Irish Sea area, habitat of the population under study. An enormous number of plankton samples (each sample being

the result of a 10 mile tow) have been collected over the years (once or twice a month since 1970) in the area. By looking at those samples the possibility of gaining some insight on long term trends on the larvae abundance was investigated.

In order to pursue this line of investigation I analysed 490 CPR samples at SAHFOS. All samples from routes IN (Liverpool-Dublin) from 1970 to 1994 and IB (Liverpool-Bay of Biscay) from 1986 to 1994, taken in the area between 52° N and 55° N and 4° W and 6° W, which had the presence of decapod larvae registered in the data base. SAHFOS scientists do not identify all the organisms present in the samples, the presence of decapod larvae is recorded but no further identification is undertaken.

The data on the spatial distribution of the larvae analysed during this study was collected using a modified version of the Gulf III type plankton sampler, the Lowestoft High Speed Sampler (HSTN), with the exception of the samples from Corystes 7/94 (see table 3.1). During this survey no HSTN sampler was available and a standard net (1 metre mouth diameter and 200 μm mesh size) was used instead, to perform vertical hauls. This method proved to be clearly inappropriate to sample the area, strong tidal currents, clogging of the net and the absence of reliable information on depth and volume of the water filtered made the work very difficult and of little reliability.

The HSTN data used to study the spatial distribution of the larvae are listed in table 3.1 which, also shows the research institutes that made the information available and the type of gear used for sampling. The survey code reference shown will be used throughout the text. The area sampled and number of stations visited are also shown. A detailed picture of the grid of stations sampled during each survey is presented in chapter V, where the spatial distribution of the larvae is analysed. Surveys in which I participated are indicated.

An extensive set of data was gathered, during the period from 1982 to 1996 over 2400 sampling stations were visited and these observations will, for the first time, be analysed together. However, because the surveys were not all part of a same programme, sampling is scattered in time, and sites and time of sampling were not maintained from year to year.

Table 3.1. Zooplankton sampling, spatial distribution.

Survey code	Date	Vessel	Source	N. sts	Area	Gear
Corella 5/82	9-13 April 82	Corella	CEFAS	60	WIS, NEIS	A
Clione 6/82	28 April-21 May 82	Clione	CEFAS	117	WIS, NEIS	A
Clione 7/82	21 May-5 June 82	Clione	CEFAS	160	WIS, NEIS	A
Cirolana 5.1/84	25 May-1 June 84	Cirolana	CEFAS/SOS	67	SWIM	A
Cirolana 5.2/84	12-13 June 84	Cirolana	CEFAS/SOS	14	SWIM	A
Clione 5/85	15-19 April 85	Clione	CEFAS	77	WIS, NEIS	A
Clione 6/85	11-26 May 85	Clione	CEFAS	166	WIS, NEIS	B
P. Madog 1/85	27 May-6 June 85	Prince Madog	SOS/CEFAS	91	WIS, NEIS	A
Cirolana 5/87	14-24 May 87	Cirolana	CEFAS	79	WIS	A
Cirolana 4/88	20 Apr-2 May 88	Cirolana	CEFAS	165	WIS, NEIS	A
Cirolana 4/89	16-28 April 89	Cirolana	CEFAS	89	SWIM, EIS	C
Cirolana 5/92	29 Apr-3 May 92	Cirolana	CEFAS	10	SWIM	A
Cirolana 5/93	8-30 May 93	Cirolana	CEFAS	107	SWIM	A
Cirolana 5/94	29 April-3 May 94	Cirolana	CEFAS	14	SWIM	D
Corystes 7/94*+	17-30 June 94	Corystes	CEFAS	51	WIS	E
Cruise 2/95	11-19 February 95	Cirolana	CEFAS	100	WIS, EIS, CB	A
Cruise 3/95	21-27 February 95	Cirolana	CEFAS	91	WIS, EIS, CB	A
Cruise 5/95	8-14 March 95	L. Beltra/Roagan	DOM/PEML	65	WIS, EIS	A
Cruise 6/95	15-22 March 95	Lough Foyle	DANI/QUB	103	WIS, EIS, CB	A
Cruise 8/95	30 March-6 April 95	Corystes	CEFAS	106	WIS, EIS, CB	A
Cruise 9+10/95	10-21 April 95	L. Beltra/Roagan	DOM/PEML	106	WIS, EIS, CB	A
Cruise 11/95	18-25 April 95	Lough Foyle	DANI/QUB	106	WIS, EIS, CB	A
Cruise 12/95	30 April-7 May 95	Lough Foyle	DANI/QUB	105	WIS, EIS	A
Cruise 13/95	14-20 May 95	Philomena	PEML	87	WIS, EIS	A
Corystes 5b/95*+	15-20 May 95	Corystes	CEFAS/SOS	54	WIS	A
Cruise 14/95	23-28 May 95	Cirolana	CEFAS	94	WIS, EIS	A
Cruise 15/95	5-14 June 95	Roagan	PEML	60	SWIM, EIS	A
L. Foyle 11/95	18-20 June 95	Lough Foyle	DANI/QUB	37	SWIM	A
Cirolana 4b/96*+	13-23 April 96	Cirolana	CEFAS/SOS	59	WIS	D
Corystes 9/96*+	12-14 July 96	Corystes	CEFAS/SOS	35	WIS	D

Legend:

WIS:	Western Irish Sea	Gear A:	76 cm HSTN, 270 μm net, 40 cm nose cone
EIS:	Eastern Irish Sea	Gear B:	76 cm HSTN, 400 μm net, 40 cm nose cone
NEIS:	North-Eastern Irish Sea	Gear C:	53 cm HSTN, 270 μm net 33 cm, nose cone
SWIM:	South-West of Isle of Man	Gear D:	53 cm HSTN, 270 μm net 20 cm, nose cone
CB:	Cardigan Bay	Gear E:	1 m diameter net, 200 μm mesh size

CEFAS - Centre for Environment Fisheries and Aquaculture Science
SOS - School of Ocean Sciences, University of Wales, Bangor
DOM - Department of Marine, Fisheries Research Centre, Republic of Ireland
PEML - Port Erin Marine Laboratory
DANI - Department of Agriculture Northern Ireland
QUB - Queens University Belfast

* Indicates surveys in which I participated
+ Indicates surveys during which zooplankton and environmental observations were made

In 1995, between February and June, a series of plankton surveys (12) was carried out as part of a project to calculate the spawning stock biomass of cod, sole and plaice.The laboratory work involved the identification of eggs and larvae of the target species but *N. norvegicus* larvae numbers and stages were also recorded. These observations are of particular interest because an extensive grid of sampling stations (see table 3.1) was visited two or three times a month throughout the whole hatching season. Moreover, these surveys coincided, in great part, with comprehensive hydrographic sampling of the western Irish Sea carried out, during a joint programme, by CEFAS and the School of Ocean Sciences (SOS), University of Wales, Bangor (see table 3.3).

In addition, during Corystes 5b/95, Cirolana 4b/96 and Corystes 9/96 surveys, zooplankton sampling and extensive oceanographic observations were carried out together.

1.1.2. Instruments and operation

Continous Plankton Recorder (CPR)

The CPR is a high speed plankton sampler designed to be towed from commercially operated ships over long distances. The original CPR was designed by Sir Alister Hardy and was operational in mid-late twenties. Since then several changes have been introduced but the basic design and principles remain unaltered. Data collected by the CPR survey have been used to describe the seasonal and long term changes in phytoplankton and zooplankton populations.

CPR samplers are towed in the surface mixed layer at an approximate depth of 10 m. Water enters the CPR through a 1.27 cm square entrance aperture and travels down a tunnel wich expands to cross-sectional dimensions of 5x10 cm where it passes through a silk filtering mesh (270 μm) before exiting via a rectangular exit aperture (dimensions 10x3 cm) at the back of the instrument. The movement of the sampler through the water turns an external propeller which, via a drive-shaft and gear-box, moves the silk across the tunnel at a rate of approximately 10 cm per 10 nautical miles of tow. As it leaves the tunnel, the filtering gauze is covered by a second band of gauze so that the plankton is sandwiched between the two net layers. The net and plankton enclosed are then reeled into a storage chamber containing

formaldehyde which fixes and preserves the sample. On return to the laboratory, the silk is cut into sections equivalent to 10 nautical miles for microscope analysis. About 400 phytoplankton and zooplankton species are routinely identified, counted and entered into the data base. Decapod larvae are counted but no further identification has been done (SAHFOS, 1994; Warner & Hays, 1994).

High Speed TinTow Net (HSTN)

The HSTN (Lowestoft, High Speed Sampler) is a modified version of the Gulf III sampler developed in the early 1950's. The samplers used by CEFAS have also undergone some alterations over the years. The standard sampler consists basically of a 76 cm diameter glass reinforced plastic tube enclosing a conical nylon filtering net, 185 cm long. Since the early seventies the length of the sampler has been increased from 213 cm to 275 cm, to house a greater net area and an improved flowmeter design has been adopted (Milligan & Riches, 1983; Brander *et al.*, 1993, Nash *et al.*,1998).

The mesh of the net usually used, for mesozooplankton and macrozooplankton sampling, has an aperture of 270 μm and a porosity of 46%, but in areas of high phytoplankton standing stock a 400 μm mesh size net is often preferred to avoid clogging. The water enters the net via a 40 cm nose cone and the sample is then retained at the end of the filtering net in the end bag.

A smaller version of the sampler (53 cm diameter with a nose cone of 33 cm or 20 cm) is also in use. The smaller sampler is made of 0.33 cm thickness marine grade aluminium and has the advantage of having hinged doors fitted to the top half of the body which allows easier access to the net for washing down at the end of each haul (Milligan & Riches, 1983; Brander *et al.*, 1993).

The HSTN incorporates both internal and external electromechanical flowmeters. The internal flowmeter is fixed centrally inside the nose cone whilst the external flowmeter is mounted in a tube 30 cm clear of the sampler body. The internal flowmeter is used to measure the volume of water filtered in conjuction with the external flowmeter, in this way the efficiency of the sampler is assessed. A real time indication of clogging of the net can be

monitored by the ratio of internal/external velocity displayed in the deck unit (Brander *et al.*, 1993; Nash *et al.*, 1998). The sampler is operated fom the stern of the vessel at towing speeds of 4 to 5 knots. By paying out and hauling the cable at constant speed, the sampler performs a v-shaped cast providing an equivalent sample of each part of the water column. The sampler is operated to as close to the sea bed as possible.

A Guildline, conductivity, temperature and depth (CTD), probe (Nash *et al.*, 1998) is attached to the sampler frame. Continously (every 2 seconds) readings are sent to the deck unit and stored in a computer for further analysis.

The samples were taken from the bag end and stored in a solution of, Borax (sodium tetraborate) buffered, formalin (37%-40% formaldehyde) at 4 %, in sea water (Omori & Ikeda, 1984). Back at the laboratory the samples were sorted out and all *N. norvegicus* larvae counted and identified by stage. I carried out the laboratory work on the samples from the surveys in which I participated.

1.2.Vertical distribution

1.2.1. Sampling

How *Nephrops norvegicus* larvae are vertically distributed in the water column is fundamental to understanding their dispersal patterns and of particular interest to interpret the processes leading to settlement onto the specific area of muddy substrate.

Nevertheless, with the exception of Hillis (1974a) and Lindley *et al.* (1994), there is a notable absence of studies on the vertical distribution of the Norway lobster larval stages. This fact, is mainly due to the difficulties in adequately sampling the water column for *N. norvegicus* larvae, a relatively scarce plankter with a patchy distribution. Net trawling at specific depth *strata* does not give a good enough picture of the whole vertical distribution and water pumping systems, while restricted in the area and volume sampled, are easly avoided by the relatively large and quite motile larvae.

The Longhurst-Hardy Plankton Recorder (LHPR) represents a great improvement over the conventional nets because it permits short discrete tows throughout the whole water column. It is however, not easy to operate and requires some time for preparation before launching and afterwards to separate and wash out the multiple samples. The Multiple Opening/Closing Net and Environmental Sensing System (MOCNESS) is another efficient sampler commonly used to study the vertical structure of planktonic organisms. It has however, a limitation on the number of nets that can carry which may be a problem in deep water sampling but because it operates separate nets for each *stratum* being sampled, problems of contamination of the discrete samples taken is prevented. This aspect is probably the only disadvantage the LHPR presents because the filtering net used is the same throughout the cast. Nevertheless, several trials, done over the years, have shown that any contamination of the samples that may occur is negligible (Brander & Thompson, 1989).

No field study has been devoted solely to study the vertical distribution of *N. norvegicus* larvae in the Irish Sea but some information has been gathered over the years, although not much of it has been analysed. The data available is, for all that, dispersed spatially and in time and consequently complex to analyse.

A compilation of data collected from 1984 to 1996, and made available by the Centre for Environment Fisheries and Aquatic Science (CEFAS) and the Plymouth Marine Laboratory (PML), was analysed with the aim of finding a more clear description of the vertical distribution of *N. norvegicus* larvae and their dispersal patterns.

Sampling sites are shown in figure 6.1 (chapter VI) and the dates and times of the hauls are listed in table 3.2. The institutions that made the data available and location and site depths are also presented. Only the stations that were analysed during this study are listed (36), 50 sampling stations were actually examined but whenever the number of larvae caught was less than 10, those stations were not considered. The original sampling station references, shown in the table, will be maintained throughout this text. This study includes three sampling stations which were visited, three times each, at night and day time, during the period of this project (Cirolana 4b/96). This survey also includes comprehensive hydrographic sampling.

Table 3.2. Zooplankton sampling, vertical distribution.

Station	Source	Location	Date	Time (GMT)	Depth (m)	Gear
18	CEFAS/PML	53.80 N, 5.80 W	11.4.88	23:29	55	LHPR 200 μm net
19	CEFAS/PML	53.80 N, 5.80 W	12.4.88	11:56	55	LHPR 200 μm net
22	CEFAS/PML	53.90 N, 5.50 W	24.4.88	23:23	105	LHPR 200 μm net
20	CEFAS/PML	53.80 N, 5.50 W	25.4.88	12:09	105	LHPR 200 μm net
35	CEFAS/PML	53.80 N, 6.08 W	21.4.89	23:01	30	LHPR 200 μm net
34	CEFAS/PML	53.83 N, 6.10 W	21.4.89	12:29	30	LHPR 200 μm net
36	CEFAS/PML	53.80 N, 5.48 W	22.4.89	23:09	105	LHPR 200 μm net
37	CEFAS/PML	53.80 N, 5.48 W	23.4.89	12:42	105	LHPR 200 μm net
61*	CEFAS/SOS	53.86 N, 5.92 W	19.4.96	18:35	45	LHPR 270 μm net
56*	CEFAS/SOS	53.86 N, 5.91 W	19.4.96	09:59	45	LHPR 270 μm net
62*	CEFAS/SOS	53.86 N, 5.75 W	19.4.96	20:35	65	LHPR 270 μm net
57*	CEFAS/SOS	53.84 N, 5.75 W	19.4.96	12:43	65	LHPR 270 μm net
63*	CEFAS/SOS	53.86 N, 5.58 W	19.4.96	22:48	105	LHPR 270 μm net
71*	CEFAS/SOS	53.86 N, 5.58 W	20.4.96	10:21	105	LHPR 270 μm net
63	CEFAS	54.18 N, 5.17 W	30.4.94	15:21	80	LHPR 270 μm net
123	CEFAS	54.56 N, 5.10 W	6.5.94	14:20	120	LHPR 270 μm net
135	CEFAS	53.67 N, 5.91 W	8.5.94	08:06	55	LHPR 270 μm net
140	CEFAS	53.66 N, 5.91 W	8.5.94	14.22	55	LHPR 270 μm net
119	CEFAS	54.00 N, 5.51 W	5.5.94	22:20	100	LHPR 270 μm net
130	CEFAS	54.00 N, 5.55 W	7.5.94	10:06	100	LHPR 270 μm net
135	CEFAS	53.80 N, 6.10 W	15.5.93	21:05	30	LHPR 270 μm net
206	CEFAS	53.87 N, 6.11 W	21.5.93	20:05	30	LHPR 270 μm net
136	CEFAS	53.83 N, 5.89 W	15.5.93	22:54	45	LHPR 270 μm net
314	CEFAS	53.84 N, 5.88 W	30.5.93	14:16	45	LHPR 270 μm net
222	CEFAS	53.40 N, 5.79 W	22.5.93	18:56	65	LHPR 270 μm net
288	CEFAS	53.42 N, 5.76 W	29.5.93	19:00	70	LHPR 270 μm net
12	CEFAS/PML	53.82 N, 5.53 W	27.5.87	23:11	85	LHPR 200 μm net
14	CEFAS/PML	53.48 N, 5.82 W	30.5.87	15:11	75	LHPR 200 μm net
25	CEFAS/PML	53.80 N, 5.60 W	25.5.88	00:13	100	LHPR 200 μm net
26	CEFAS/PML	53.80 N, 5.50 W	25.5.88	12:47	100	LHPR 200 μm net
28	CEFAS/PML	53.80 N, 5.80 W	25.5.88	23:41	40	LHPR 200 μm net
139	CEFAS/PML	53.85 N, 5.70 W	6.6.84	20.57	70	LHPR 200 μm net
140	CEFAS/PML	53.85 N, 5.70 W	7.6.84	00:25	70	LHPR 200 μm net
141	CEFAS/PML	53.88 N, 5.73 W	7.6.84	03:10	70	LHPR 200 μm net
142	CEFAS/PML	53.85 N, 5.70 W	7.6.84	10:53	70	LHPR 200 μm net
145	CEFAS/PML	53.54 N, 5.53 W	7.6.84	18:59	105	LHPR 200 μm net

Legend:

CEFAS - Centre for Environment Fisheries and Aquaculture Science
PML - Plymouth Marine Laboratory
SOS - School of Ocean Sciences, University of Wales, Bangor

* Sampling carried out during Cirolana 4b/96, survey in wich I participated

1.2.2. Instruments and operation

Longhurst-Hardy Plankton Recorder (LHPR)

Sampling was carried out using a LHPR, fitted with net and filtering gauze of 200 or 270 μm mesh size, as indicated in table 3.2.

The LHPR sampler body (76 cm diameter) is identical to the HSTN, already described, it consists of a conventional net enclosed in a tubular structure, mounted in a stainless steel frame; the water enters the net via a conical nose cone (40 cm diameter aperture). The volume of water filtered and efficiency of the sampler, is assessed by an internal and external flowmeter. Conductivity, temperature and depth information is collected during the cast by a CTD probe installed in the sampler's frame. The LHPR sampler is operated in the same way as the HSTN, performing a double oblique haul.

In order to collect discrete samples through the water column, the net is attached to a special unit in place of the normal bag end. This unit operates by the Hardy principle, filtering the plankton continuosly from the water passing down a tunnel into a long strip of bolting gauze. The organisms caught are stored between the filtering gauze and another identical strip when the gauze is advanced. A motor remotely activated by the deck unit, controls the movement of the filtering gauze according to the depth interval to be sampled, the used net ends up wound up like a film in a photographic camera. When back on deck the net is unwound and cut in pieces corresponding to the discrete samples which are then washed out into separate containers and preserved in a solution of buffered formalin at 4% (Longhurst *et al.*, 1966; Williams *et al.*, 1983). The samples were analysed back in the laboratory, where all *N. norvegicus* were counted and identified by stage (I analysed the samples from the surveys in which I participated).

2. Environmental sampling

2.1. Sampling

A good description of water column properties and structure and local hydrodynamics is crucial to understanding plankton distribution and dispersal patterns. Water properties (temperature, nutrients, phytoplankton and zooplankton biomass, etc.) have a major influence on the larvae location and local circulation ultimately controls their dissemination. Although relatively able swimmers (especially on the vertical plane) the small *N. norvegicus* larvae are extremely subject to the currents prevailing in the waters where they develop.

Associated hydrographic and biological observations are needed in order to adequately interpret *N. norvegicus* larvae distribution in the western Irish Sea and to assess the role the seasonal gyre plays on their retention over the mud patch. The problem more often encountered from zooplankton and hydrographic joint surveys is the scale of sampling. Plankton patchiness and diel rythyms can only be addressed with a fine spatial and temporal sampling scale. On the other hand, hydrographic sampling does not usually require such a detailed survey. Water properties and structure are more permanent, a broader (in space and time) survey is normally sufficient to characterise the hydrodynamics of a region. For these reasons, research cruises planned for either planktonic or hydrographic sampling usually lack an adequate and complete procedure for a multidisciplinary study. A compromise between both objectives is the more common, and less expensive, alternative. During this project an effort was made to simultaneously sample larvae distribution and environmental parameters in as much detail as possible.

The data collected by the Guildline CTD, mounted on the HSTN and LHPR samplers, is read simultaneously with the zooplankton sampling and therefore of great importance for the interpretation of the larvae distribution patterns in relation to the physical environment. Nevertheless, this information is limited and not always very reliable, the Guildline probe is an antiquated instrument with a very low sampling frequency (at 2 seconds intervals). A better coverage of the surrounding environment and the utilisation of more accurate hydrographic instruments are desirable in order to adequately characterise the water column

structure and circulation patterns. However, studies where both components, biological and environmental, were simultaneously and comprehensively sampled have been infrequent.

During this project a considerable effort was put into contemporaneous sampling of biological and physical parameters. Between 1994 and 1996 a joint programme, to study the hydrodynamics of the western Irish Sea, was carried out by CEFAS and SOS, University of Wales, Bangor. These surveys included comprehensive oceanographic sampling of the area in study (see table 3.3). Associated observations of larvae distribution and physical parameters were undertaken during research cruises Corystes 5b/95, Cirolana 4b/96 and Corystes 9/96. During the spring-summer of 1995 several hydrographic surveys were carried out simultaneously with the zooplankton programme referred to in section 1 of this chapter. Table 3.3 lists the oceanographic surveys (cruise reference and dates) and observations carried out as well as the equipment used during each cruise. All the research surveys undertaken during the CEFAS/SOS project are listed to show the extension of the sampling programe although only selected observations were used for this particular study. Surveys in which I participated are indicated.

The oceanographic observations presented in this study include temperature, salinity and density fields sampled using conventional CTD stations and an undulating probe installed in a Scanfish, this instrument also carried a fluorescence sensor. Velocity field measurements were made using a ship-mounted Acoustic Doppler Current Profiler (ADCP) and the Lagrangian water movement was assessed using free-drifting satellite tracked buoys. Water bottle samples were taken at discrete depths for calibration purposes and for nutrients and suspended load determinations.

2.1.2. Instruments and operation

Profiling CTD's

Discrete sampling stations were sampled using , a CTD, Rosette sampler during the Prince Madog surveys. The CTD unit used on most surveys was a Niel Brown Mark III. The instrument used on cruise Prince Madog 6/95 was a Seabird SBE19 CTD and the two 1996 surveys employed a Seabird 911+ CTD. The sampler was deployed at a constant speed of 1

Table 3.3. Hydrographic sampling.

Survey Code	Date	Observations, Gear
Corystes 7/94 *+	17-30 June 94	CTD, Scanfish, Argos drifters, ADCP
Corystes 13/94	24 October-17 November	CTD, Scanfish, ADCP
Corystes 5b/95 *+	4-20 May 95	CTD, Scanfish, Argos drifters, ADCP
Prince Madog 1/95 *	30 May-2 June 95	CTD, Argos drifters, ADCP
Prince Madog 2/95	12-16 June 95	CTD, Searover, Argos drifters, ADCP
Prince Madog 3/95	19-21 June 95	CTD, Argos drifters, ADCP
Cirolana 5/95	22-24 June 95	Scanfish, Argos drifters, ADCP
Prince Madog 4/95	17-21 July 95	CTD, Argos drifters, ADCP
Prince Madog 5/95	24-28 July 95	CTD, Argos drifters, ADCP
Prince Madog 6/95	14-18 August 95	CTD, Argos drifters, ADCP
Prince Madog 7/95	28 August-1 September 95	Searover, ADCP
Prince Madog 8/95	21 September 95	CTD
Corystes 10/95	29 September-13 October 95	Scanfish, Argos drifters, ADCP
Prince Madog 9/95	31 October-2 November 95	CTD
Cirolana 4b/96 *+	12-25 April 96	CTD, Scanfish, Argos drifters
Corystes 9/96 *+	4-18 July 96	CTD, Scanfish, Argos drifters, ADCP
Prince Madog 1/96 *	22-26 July 96	CTD, ADCP
Prince Madog 2/96	29July-2 August 96	CTD, ADCP

Legend:

* Indicates surveys in which I participated.
+ Indicates surveys during wich zooplankton and environmental observations were made.

m/s. The downward cast is usually analysed because the probe sensor travels through the water column prior to any disturbance created by the cable or Rosette frame. The performance of the sampler is monitored by the computer in the control deck room and the observations are stored for subsequent analysis. Temperature was calibrated against reversing, platinum resistance, digital thermometers and salinity was calibrated with water samples which were subsequently analysed in the laboratory. The grid of CTD stations occupied during Prince Madog cruises consisted of 53 sites along eight lines of latitude, at 16 miles intervals, from 53.3 ° N to 54.5 ° N. Along each section, the stations were located at 10 miles from each other (due to weather conditions the whole grid was not always sampled). The location of the transects presented in this study is shown in figure 4.17 (chapter IV).

The CTD probe used during CEFAS surveys, mainly for calibration purposes and when water samples were collected, was a Falmouth Scientific Inc. (FSI) and on other occasions a precision Guildline.

Undulating CTD (CEFAS surveys)

Water column structure was studied in more detail using a Scanfish MK II (Geological & Marine Instrumentation, GMI). The Scanfish is a towed computer-controlled vehicle, of 80x160x14 cm dimensions, which can be fitted with several sensors, CTD, turbidity and fluorometer sensors were used for this study. The device is towed, at speeds between 2.5 and 5.0 m/s, in an undulating fashion performing v-shaped profiles between the surface and sea bottom. The rate of dive and climb was set at 1 m/s. The pressure sensor on the CTD provides information on depth and an altimeter, mounted on the underside of the vehicle indicates the height above the sea bed. A computer in the deck control room monitors the Scanfish trajectory and stores the data being collected for subsequent analysis (Brown *et al.*, 1996).

Each Scanfish section in the western Irish Sea took between 4 and 5 hours and comprised approximately 250 individual profiles. This system allows a great, vertical and spatial, coverage of the area under study in considerable less time than conventional CTD stations sampling. The CTD unit aboard the Scanfish was a FSI. Scanfish transects covered the entire western Irish Sea starting at latitude 53.1° N. For location of the sections analysed in this study see figure 4.16 (chapter IV).

The fluorometer (Haart) consists of a light source that illuminates a small volume of water along the pass of the scanfish and an optical system to image this illuminated volume onto a photodetector. The illuminating radiation is optically filtered to produce blue light which if falls on any chlorophyll containing plankton, will result in fluorescent light being emitted from the chlorophyll, and then registed by the photodetector. Fluorescence readings are then converted into chlorophyll concentrations.

Acoustic Doppler Current Profiler (ADCP)

During surveys carried out using the research vessel Corystes (CEFAS), velocity field measurements were made using a ship mounted Acoustic Doppler Current Profiler (ADCP) (RD instruments, 153.6 KHz with a vertical resolution of 2 m (bin size) and an horizontal resolution of approximately 250 m. A numerical model was used to remove tides from the ADCP data and verified against data from current meters moorings layed in the western Irish Sea (Fernand, in preparation).

Drifters

The drifters consisted of a free drifting surface buoy equipped with an Argos platform transmitter terminal (PTT) connected to a sub-surface holey sock drogue (Sybrandy & Niiler, 1991). Two different drifter designs were used. One type consisted of a cylindrical surface unit connected to a 0.7 m diameter, 2.5 m long holey sock drogue via a surface float which decoupled the drogue from the drifter. The other form, comprised a pear shaped fibre glass buoy (Booth & Ritchie, 1983) connected by an elasticated tether to a 1.5 m diameter, 7m long holey sock drogue. An experiment conducted to assess differences in the behaviour of the two types of drifter showed that no appreciable separation could be observed and therefore no distinction is drawn between the two designs (Horsburgh *et al.*, submitted).

All drogues were centred at 24 m depth (depth of the base of the thermocline, known from previous observations) except for two drifters deployed in 1996 which had their drogues centred at 8.5 m depth. These buoys were released in order to examine differences between surface flows and those at the thermocline.

In the spring-summer of 1995, 41 deployments were made with a mean duration of 21 days and a maximum of 55 days. 24 drifters were subsequentely recovered while the remaining were either lost, mainly due to the intense fishing activity in the region, or grounded. To examine the circulation during the break down of stratification, a further 5 buoys were deployed in October 1995. In 1996, 9 drifters were released.

The positions obtained via satellite were acquired from the Argos service in Toulouse. On average 12 Argos fixes were available per day for each of the buoys.

Water samples

Samples taken at discrete depths using Van Dorn (1 or 5 litre) water bottles, mounted on the Rosette frame, were collected to calibrate the CTDs and fluorometer and to measure nutrient (nitrogen, phosphate, silica), oxygen and suspended load concentrations. During CEFAS surveys a continuous surface water pumping system was also used for collection of water samples for calibration purposes.

Chapter IV. Hydrodynamics of the western Irish Sea during the spring-summer period

1. Introduction

Over the northwest European shelf, like in other tidally energetic continental shelves, the long term mean circulation has been estimated to be very weak, with mean speeds (averaged over a month or more) of the order of 1-2 km/day (0.01-0.02 m/s) (Simpson, 1981). However, in some places in these shelf sea regions strong, persistent, organised flow patterns have been identified. Among the organised flow structures which have been observed to exist in continental waters are the permanent, barotropic, residual flows resulting from tidal rectification over topographic elevations (banks) or around headlands and islands. These stably located hydrographic features often emerge as closed circulation systems (gyres) which have long been recognised of particular importance in the dispersal of organisms (plankton) and other tracers (*eg.* pollutants) which drift with these waters. An example of such a structure which has been very well documented occurs over George's Bank in the western Atlantic waters. The gyre which is present over the Bank, has been recognized of crucial importance in the productivity of this waters and plays a major role in the retention of several species, including molluscs, crustaceans and fish, in the region (Wiebe & Beardsley, 1996, references therein).

Hill (1993) pointed out the existence of another type of stably located structure-baroclinic mesoscale gyres, which form seasonally over topographic depressions in shelf sea areas. During spring-summer, every year, heating of the surface waters over isolated regions of weak tidal stirring, such as topographic depressions, can lead to the formation of domes of cold, dense bottom water beneath the thermocline. The dense bottom water is isolated from the surrounding mixed waters by near bottom horizontal fronts which drive a cyclonic near surface circulation around the cold pool. One such structure was found to occur in the western Irish Sea (Hill, 1993; Hill *et al.*, 1994). Its development and influence on the sustenance of the local *Nephrops norvegicus* population is the subject of this thesis.

The first evidence of the existence of a seasonal cyclonic gyre in the region arose when two radio-tracked drifters (drogued at 27 m depth) were deployed in 1971. One of these buoys described a loop centred at approximately 53° 55' N, 5° 30' W (Hunter, 1972). The trajectory of this drifter together with geostrophic calculations, from dynamical topography (Davies, 1972), was suggestive of cyclonic circulation in the upper layers of the stratified western Irish Sea. In 1990, nine satellite-tracked Decca-Argos buoys, drogued at 15 m depth, and observations of the density field from CTD profiles and ADCP observations, provided the confirmation of the existence of a strong cyclonic near surface flow around the dense dome (Hill *et al.*, 1994). Further drifter deployments in 1993 and 1994 verified the occurrence of the western Irish Sea gyre (Brown *et al.*, 1995; Hill *et al.*, 1996; 1997a).

Although the existence of the gyre was by then confirmed, its spatial extent, seasonal evolution and associated velocities were still to be investigated. In the spring-summer of 1994, 1995 and 1996 a comprehensive hydrographic survey programme (CEFAS/SOS) was set up to observe the seasonal evolution of the 3D density field, to measure the residual currents and assess the full spatial extent of the western Irish Sea gyre and its retentive properties. Part of this project was devoted to studying the influence the gyre plays in the retention of *Nephrops norvegicus* larvae above the mud patch (adults grounds) in the western Irish Sea. Together with the hydrographic observations, extensive zooplankton sampling was carried out to observe the distribution of the larvae and its relation to the local hydrography.

In this chapter, a description of part of the hydrographic observations carried out in the western Irish Sea during the spring-summer period of 1994, 1995 and 1996 is presented. Special attention is devoted to data collected during the surveys which also included zooplankton sampling.

2. Methodology

2.1. Sampling

The hydrographic observations presented in this study were obtained during an extensive programme carried out in the western Irish Sea in 1994, 1995 and 1996. Table 3.3 (chapter III) lists all the surveys undertaken and measurements carried out. The data presented here are only a part of the results obtained and were chosen in accordance to the objectives of this study: to comprehensively characterise the western Irish Sea local hydrography with special relevance to the development and evolution of the water column stratification and associated spring-summer gyre which is relevant for the distribution of *Nephrops norvegicus* larvae in the area. Priority was also given to the observations carried out during the surveys in which I participated (and plankton sampling was undertaken).

The data analysed includes transects of temperature, salinity, density, chlorophyll$_a$ and flow field velocities. Spatial distribution of surface and bottom temperature, in the whole area are presented and the stratification of the water column is also assessed by potential energy anomaly calculations. The Lagrangian water circulation was observed using free-drifting, satellite tracked, buoys.

2.2. Data processing

Salinity and density were calculated according to international standard procedures for sea water (UNESCO, 1981). Salinities were determined on the practical salinity scale (UNESCO, 1978).

The density distribution was used to calculate the density-driven current field using the thermal wind equation:

$$\frac{\partial v}{\partial z} = -\frac{g}{\rho f}\frac{\partial \rho}{\partial x},$$

where z is the depth and $\partial v / \partial z$ the vertical velocity shear, g is gravitational acceleration, ρ is density and $\partial \rho / \partial x$ the density gradient in the x direction (Pond & Pickard, 1989).

Flow field data derived from ADCP observations was detided using a numerical model and verified against data from current meter moorings layed in the area (Fernand, in preparation).

The stratification of the water column was estimated using values of the potential energy anomaly (ϕ), which represents the amount of energy required to completely vertically mix a water colum of unit area as defined by Simpson (1981). The value of ϕ increases with increasing stratification and ϕ=0 represents complete vertical homogeneity.

$$\phi = \frac{1}{h}\int_{-h}^{0}(\bar{\rho} - \rho)gzdz \quad \text{where } \bar{\rho} = \frac{1}{h}\int_{-h}^{0}\rho dz$$

and z is the depth beneath the sea surface (negative), h is the total water depth and $\bar{\rho}$ is the depth average density.

Hydrographic data collected during CEFAS surveys were processed by L. Fernand (CEFAS) and the observations undertaken during SOS cruises were analysed by K. Horsburgh (SOS).

3. Results

The seasonal development of the 3D temperature and salinity distribution and associated density field in the western Irish Sea, can be examined by looking at the sections presented in figures 4.1 to 4.14. Figures 4.1 to 4.3 show the earliest observations in the heating season. The data were collected, in mid April (15-17) (Cirolana 4b/96), along three west-east transects (for location of the scanfish legs see figure 4.16). Temperature contours showed a predominantly mixed water column but there was a slight horizontal gradient (~ 0.2-0.3° C) with cooler waters close to the Irish coast, consistent with cold fresh water. Water temperature ranged from 7.5 to 7.7° C. Top to bottom temperature differences were very small indicating that thermal stratification was only starting. Despite that, a clear pycnocline was already developing at 20 to 30 m depth. This fact was particulary noticeable in section 17 (figure 4.2) across the deeper region of the western Irish Sea basin. The similarity between the pattern of distribution of isohalines and isopycnals point up the controlling role of salinity on the density field, at this stage of the heating season. When the surface waters were only starting to warm up, the distribution of salinity contributed significantly to the vertical structure of the water column as a result of fresh water input along the Irish coast. As it can be observed salinity increased gradually from west to east varing from 34.2 to 34.8. The horizontal salinity gradient was stronger at the begining of the season, in April-May, becoming less evident towards the summer.

Figures 4.1 to 4.3, also show that at the beginning of stratification of the water column at this stage in the season, was more clear in the deeper, central area illustrated in transect 17 (figure 4.2). Along this section the halocline (pycnocline) was more evident than south (section 21, figure 4.1) or north (section 15, figure 4.3) of this line. It can also be observed that a pool of denser water was becoming apparent in the deep, central channel.

Observations carried out later in the season, in May (10-13) (Corystes 5b/95) are presented in figures 4.4 to 4.7 (see figure 4.16 for location of the scanfish legs). Four transects were chosen to characterise the structure of the water column, leg 68 (Corystes 5b/95) was sampled along the same line as leg 17 from the April survey (Cirolana 4b/96) while section 70 (Corystes 5b/95) corresponds to the same location as leg 15 (Cirolana 4b/96). It must be remarked at this stage, that the set of data presented in this study includes surveys carried out

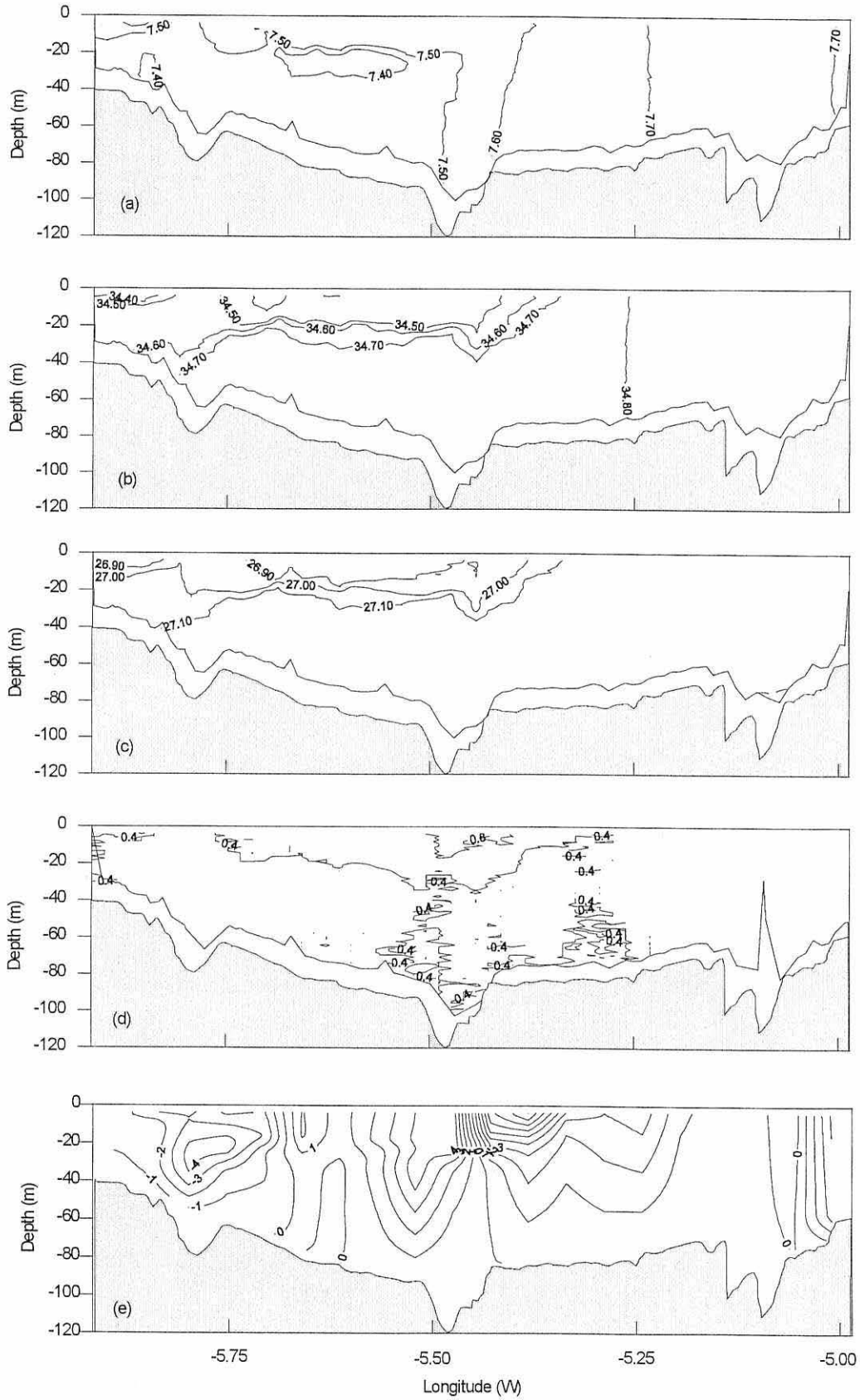


Figure 4.1. West-east Scanfish section of the western Irish Sea at latitude 53.5° N (leg 21, Cirolana 4b/96, see figure 4.16 for location) on 17 April 1996. Showing (a) temperature (°C), (b) salinity (psu), (c) density (σ_t), (d) chlorophyll$_a$ (µg/l), (e) geostrophic velocity computed relative to an assumed level of no motion at the sea bed; positive isotachs indicate flow into the page and negative values correspond to flow away from the page.

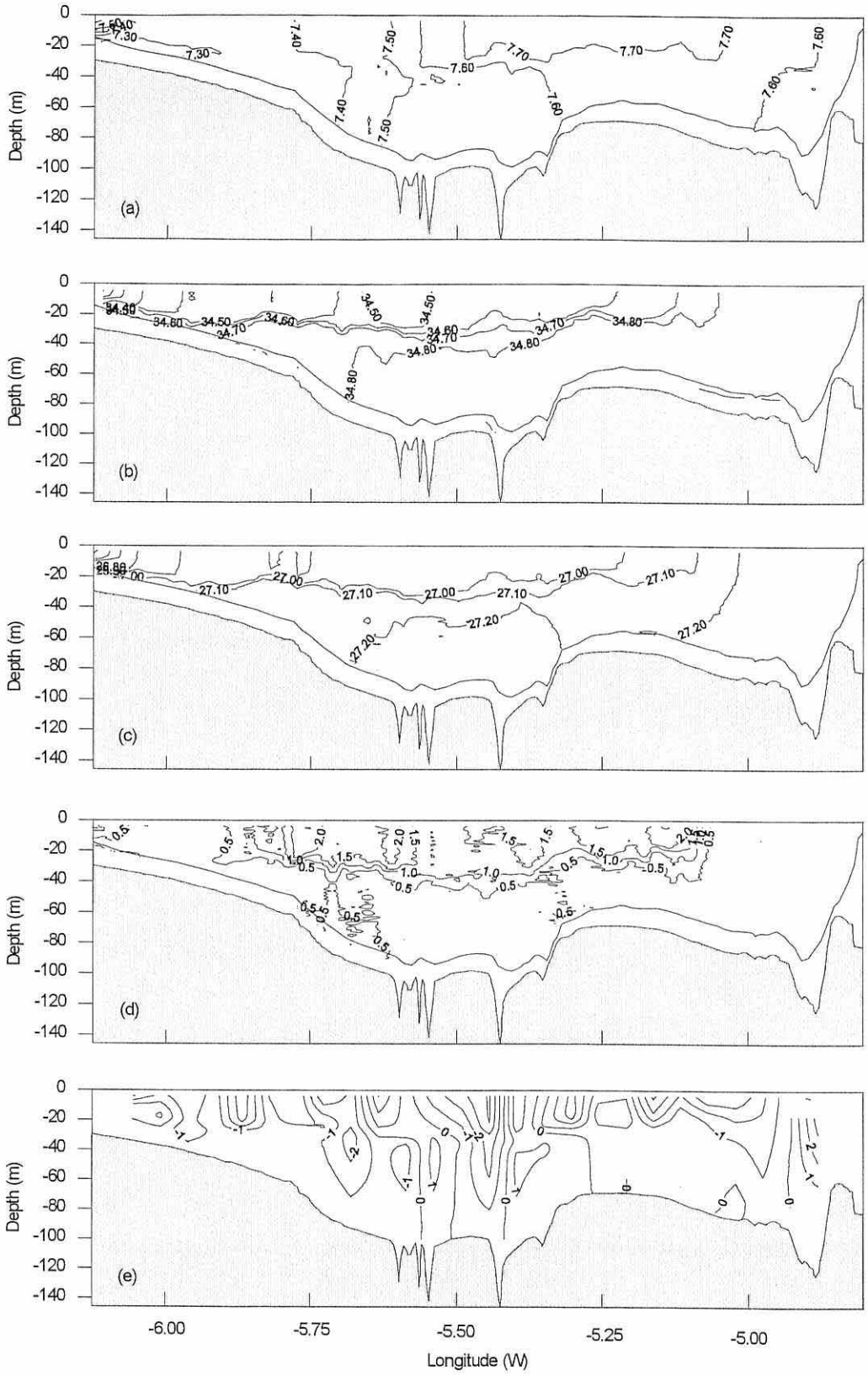


Figure 4.2. West-east Scanfish section of the western Irish Sea at latitude 53.8° N (leg 17, Cirolana 4b/96, see figure 4.16 for location) on 16 April 1996. Showing (a) temperature (°C), (b) salinity (psu), (c) density (σ_t), (d) chlorophyll$_a$ (µg/l), (e) geostrophic velocity computed relative to an assumed level of no motion at the sea bed; positive isotachs indicate flow into the page and negative values correspond to flow away from the page.

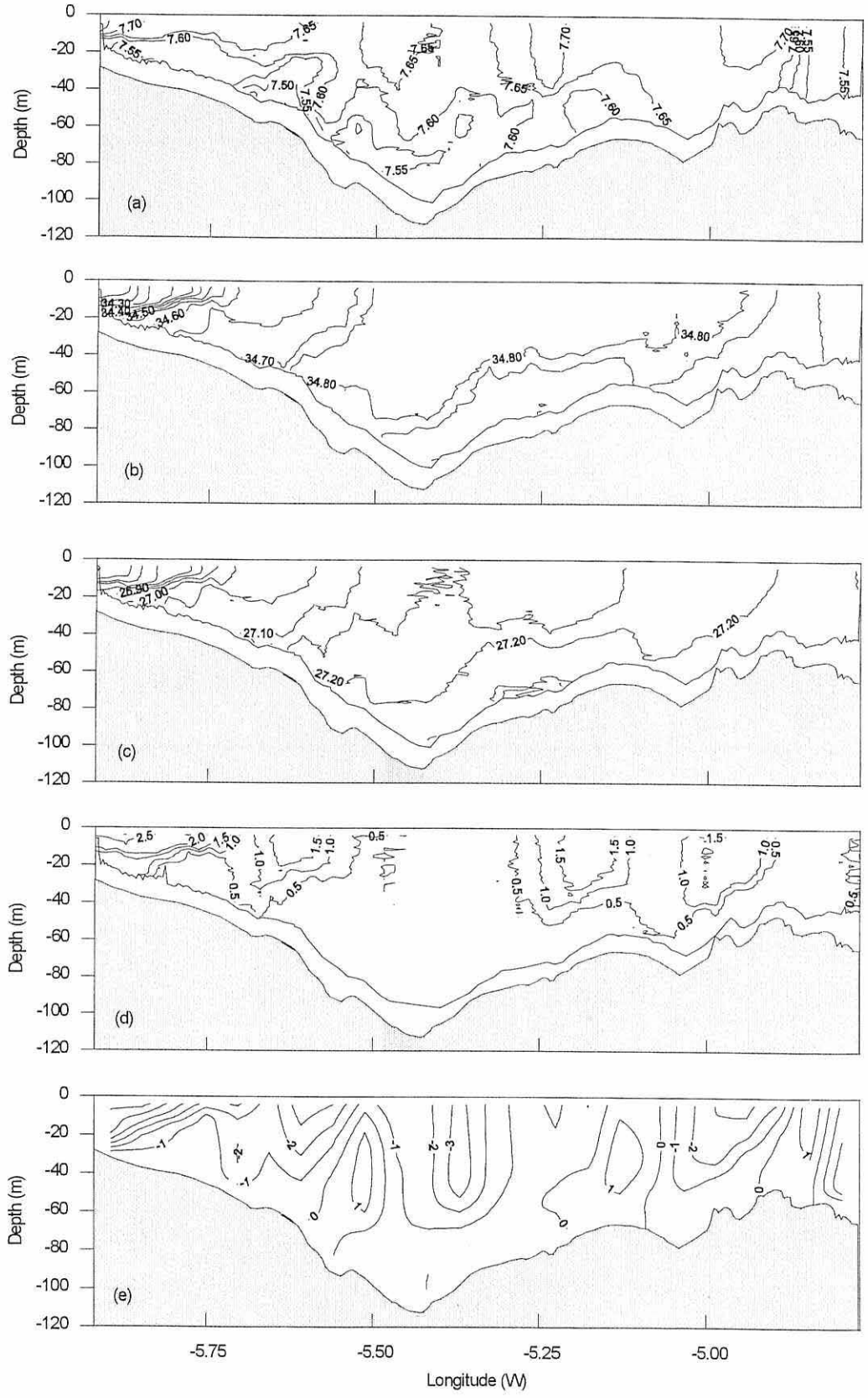


Figure 4.3. West-east Scanfish section of the western Irish Sea at latitude 54° N (leg 15, Cirolana 4b/96, see figure 4.16 for location) on 15 April 1996. Showing (a) temperature (°C), (b) salinity (psu), (c) density (σ_t), (d) chlorophyll$_a$ (µg/l), (e) geostrophic velocity computed relative to an assumed level of no motion at the sea bed; positive isotachs indicate flow into the page and negative values correspond to flow away from the page.

in different years and therefore some caution must be applied when analysing the seasonal evolution of the water column based on these observations (the date of each survey can easily be identified by the reference in brackets and the list in table 3.3, chapter III)

During the mid May observations (Corystes 5b/95) the qualitative similarity between isopycnals and isohalines was still apparent but the effect of temperature on the water column structure was more clear. Sections 68 and 70 (figures 4.5 and 4.6) show the increasing importance of temperature on water stratification. Still, the effect of fresh water runoff from the Irish rivers appeared to be crucial to the structure of the water column during this early phase of the heating season. Later in the season by June-July, salinity contributed negligibly to the vertical structure.

The isolation of a dome of colder, denser water was again particularly clear in the deeper, central region of the western Irish Sea as illustrated in sections 68 and 70. These observations are consistent with the centre of the summer stratified region and the gyre. A clear thermocline (pycnocline) was present in this area at depths between 20-30 m. Top to bottom temperature difference was 1.5° C, in the central area of section 68 and 1.25° C, in section 70. The temperature of the bottom water in the central area of these transects was 8.5° C. Section 74 (figure 4.7), sampled across a deep region, in a more northern area, also started to show the establishement of a thermocline (pycnocline) at 20-30 m depth, this region coincides with the second centre of stratification which will be referred to later. Transect 64 (figure 4.4), sampled along the southern limit of the summer stratified area, demonstrated the slower development of stratification in this area.

Figure 4.8 shows the temperature, salinity and density fields sampled between 30 May and 2 June/95 (Prince Madog 1/95) and 17 and 21 July/95 (Prince Madog 4/95), along latitude 53.83° N, same line as leg 17 (Cirolana 4b/96) and leg 70 (Corystes 5b/95) (see figure 4.17 for location). These observations serve to illustrate that from June onwards, when the surface waters warm up appreciably temperature becomes the main controlling parameter on the vertical structure of the water column. A strong thermocline (pycnocline) was evident at 20-30 m depth and the dome of colder, denser water in the deeper region, was completely isolated from the surrounding waters by sharp bottom fronts. Top to bottom temperature differences of 1.5° C were in place by the begining of June/95 (Prince Madog 1/95); and

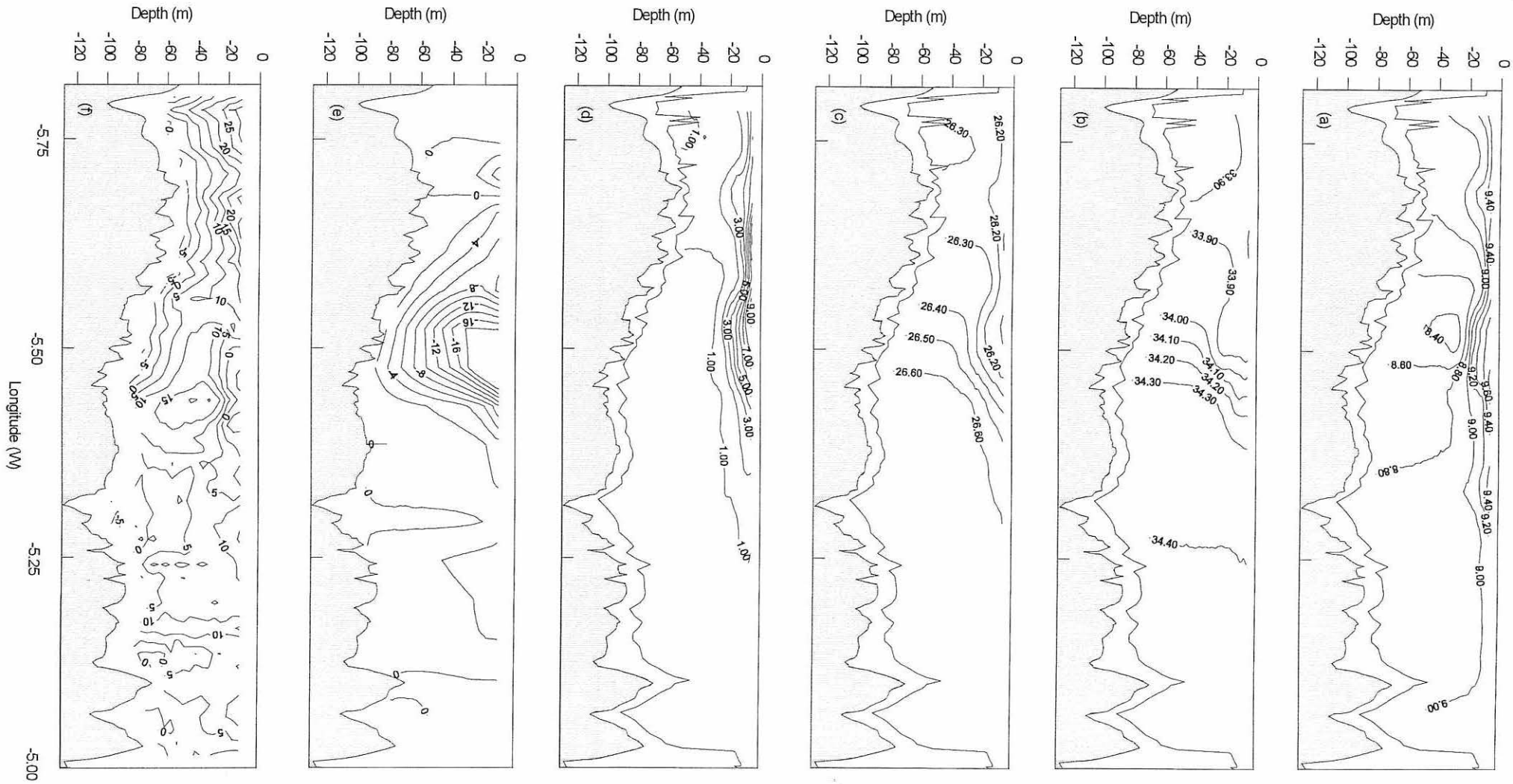


Figure 4.4. West-east Scanfish section of the western Irish Sea at latitude 53.4° N (leg 64, Corystes 5b/95, see figure 4.16 for location) on 10 May 1995. Showing (a) temperature (°C), (b) salinity (psu), (c) density (σ_t), (d) chlorophyll$_a$ (µg/l), (e) geostrophic velocity computed relative to an assumed level of no motion at the sea bed (f) detided ADCP velocities (north/south components). Positive isotachs indicate flow into the page and negative values correspond to flow away from the page.

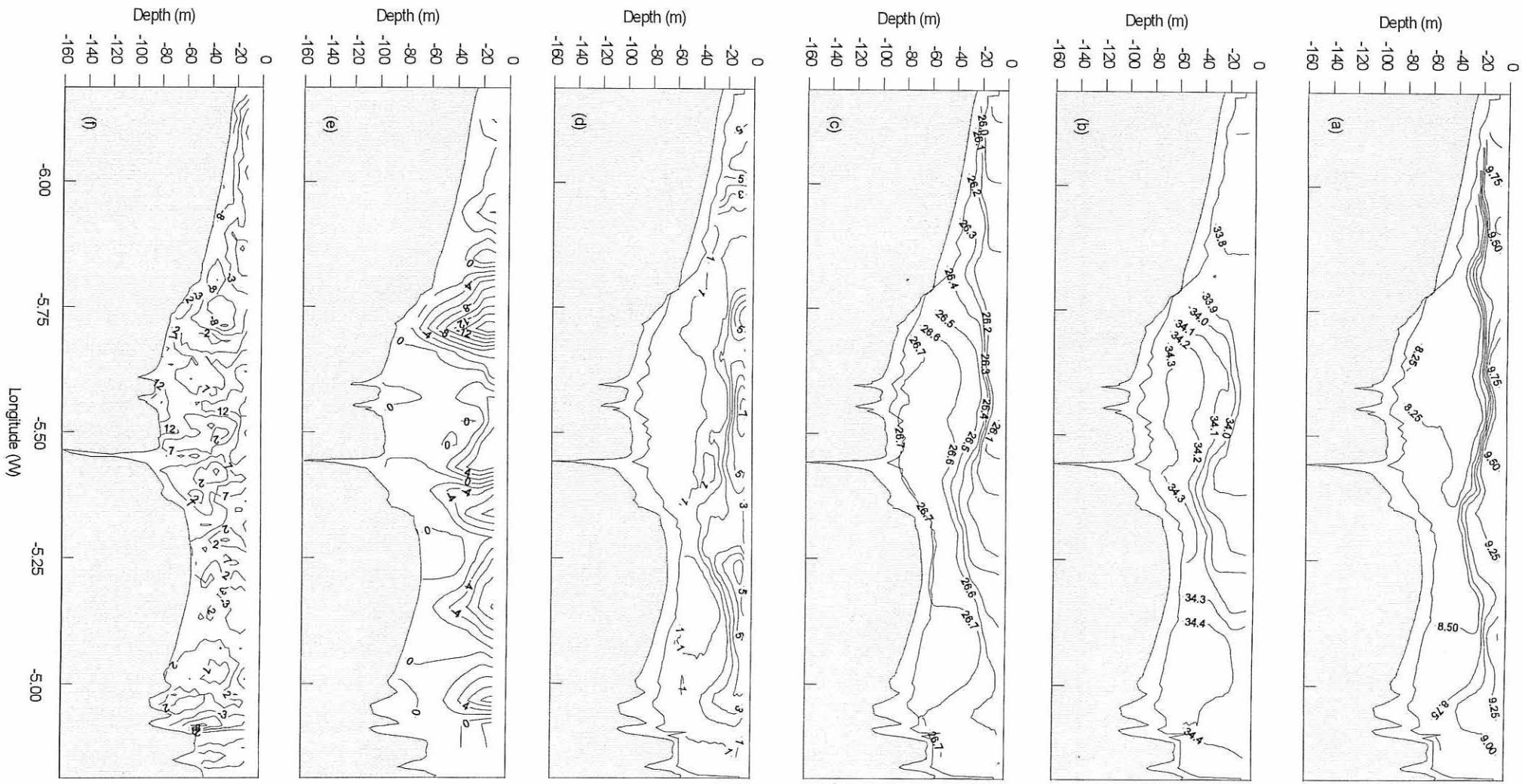


Figure 4.5. West-east Scanfish section of the western Irish Sea at latitude 53.8° N (leg 68, Corystes 5b/95, see figure 4.16 for location) on 11 May 1995. Showing (a) temperature (°C), (b) salinity (psu), (c) density (σ_t), (d) chlorophyll$_a$ (µg/l), (e) geostrophic velocity computed relative to an assumed level of no motion at the sea bed (f) detided ADCP velocities (north/south components). Positive isotachs indicate flow into the page and negative values correspond to flow away from the page.

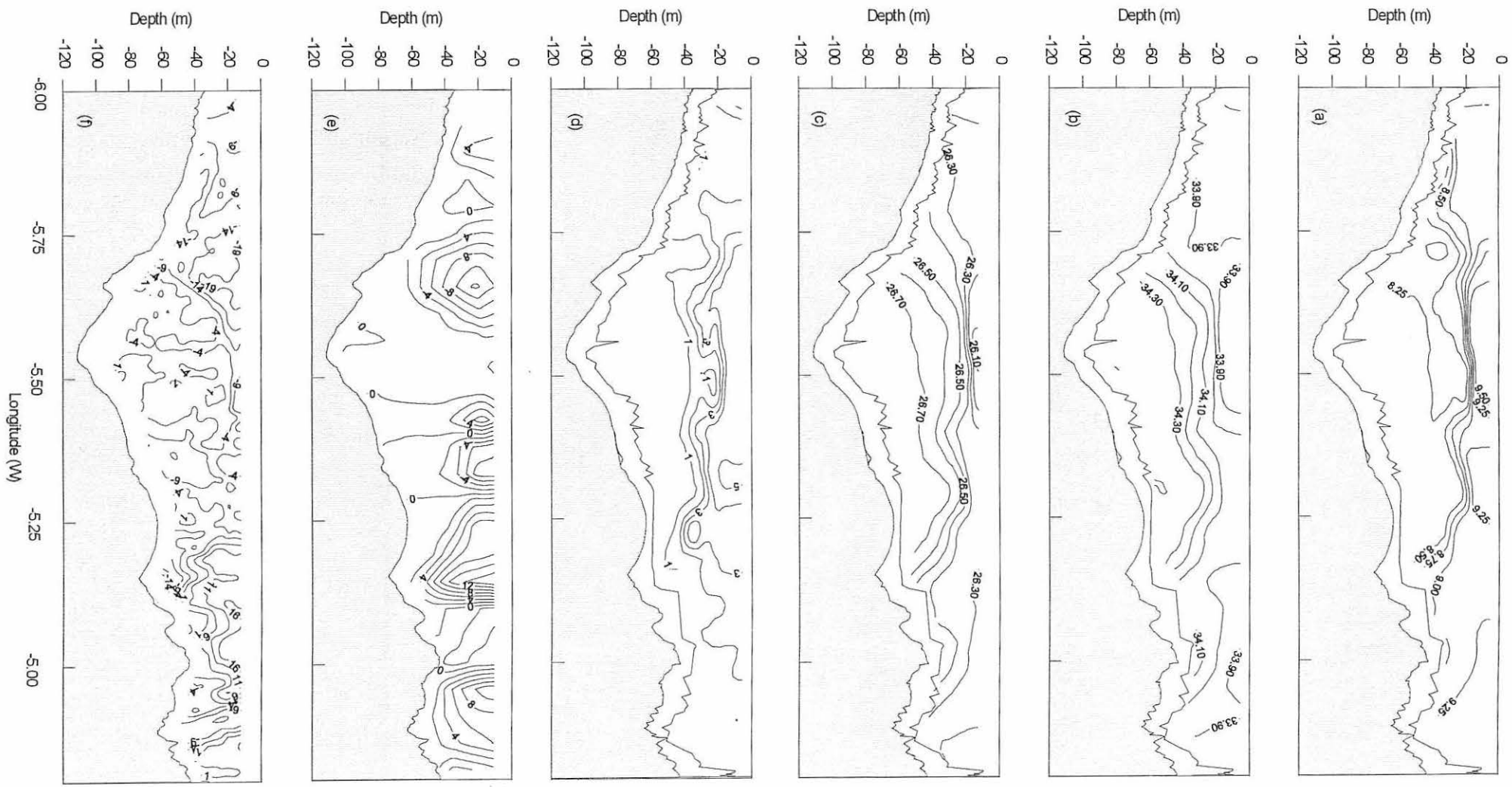


Figure 4.6. West-east Scanfish section of the western Irish Sea at latitude 54° N (leg 70, Corystes 5b/95, see figure 4.16 for location) on 12 May 1995. Showing (a) temperature (°C), (b) salinity (psu), (c) density (σ_t), (d) chlorophyll$_a$ (µg/l), (e) geostrophic velocity computed relative to an assumed level of no motion at the sea bed (f) detided ADCP velocities (north/south components). Positive isotachs indicate flow into the page and negative values correspond to flow away from the page.

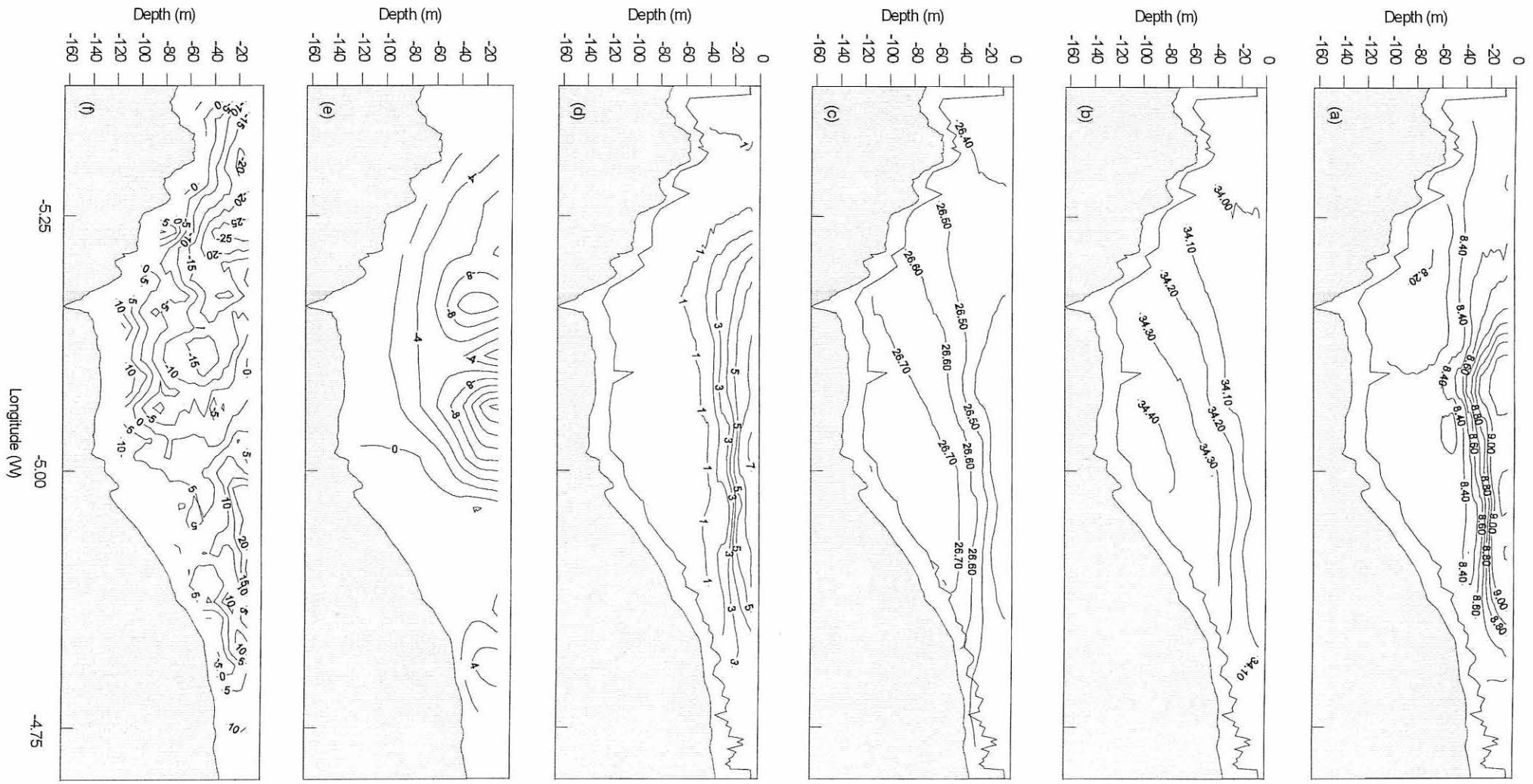


Figure 4.7. West-east Scanfish section of the western Irish Sea at latitude 54.3° N (leg 74, Corystes 5b/95, see figure 4.16 for location) on 13 May 1995. Showing (a) temperature (°C), (b) salinity (psu), (c) density (σ_t), (d) chlorophyll$_a$ (µg/l), (e) geostrophic velocity computed relative to an assumed level of no motion at the sea bed (f) detided ADCP velocities (north/south components). Positive isotachs indicate flow into the page and negative values correspond to flow away from the page.

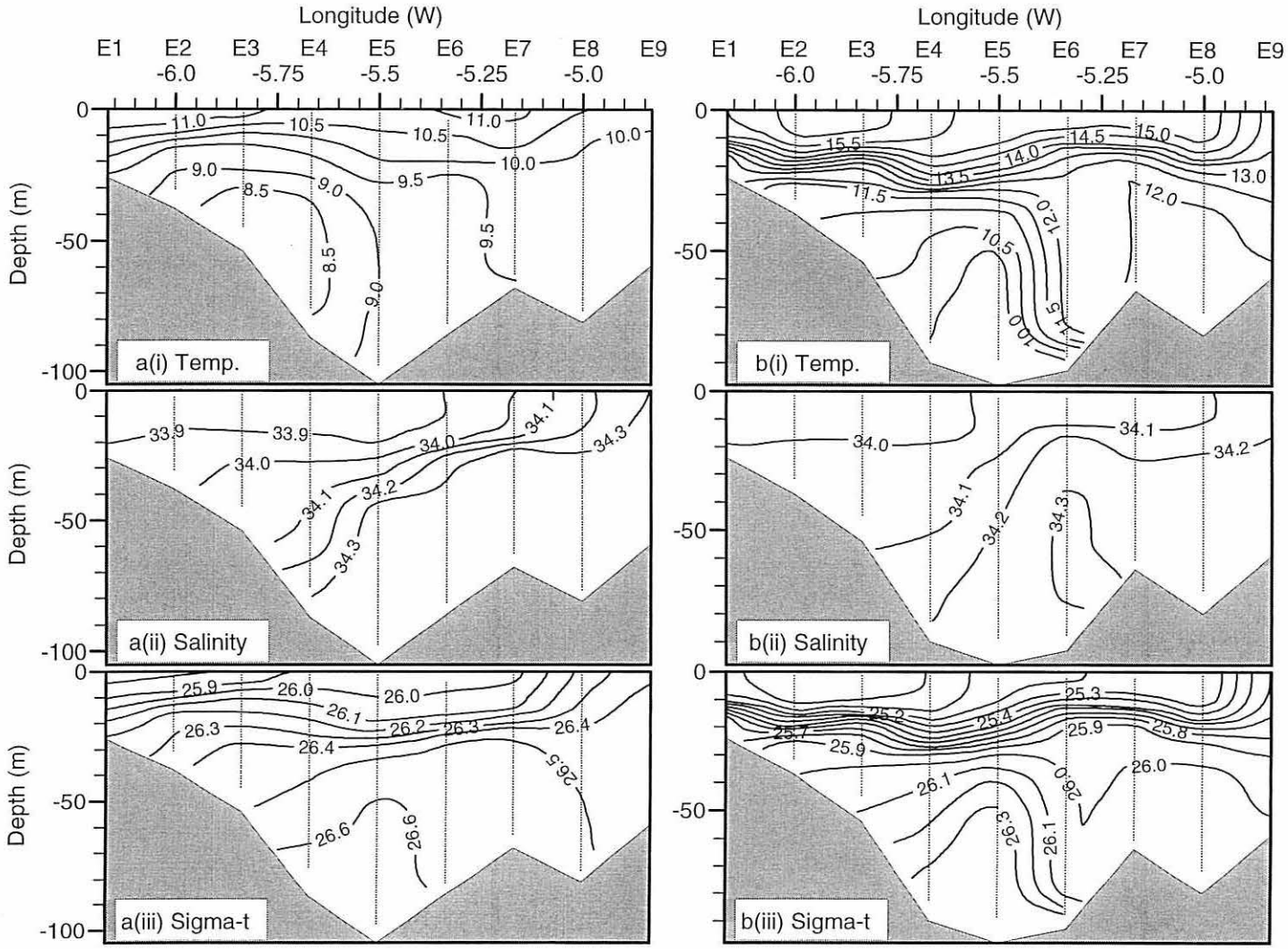


Figure 4.8. West-east CTD section of the western Irish Sea at latitude 53.8° N (section E, see figure 4.17 for location) on (a) 30 May-2 June 1995, P. Madog 1/95 and (b) 17-21 July 1995, P. Madog 4/95. Showing (i) temperature (°C), (ii) salinity (psu), (iii) density (σ_t).

amounted to 5.5° C in mid July/95. The bottom water remained fairly cold (8.5-9.0° C in June and 10.0° C in July) denoting the slow warm up of the isolated bottom water.

Data collected during Corystes 7/94 survey (19-22 June/94) are shown in figures 4.9 to 4.11. Three transects from this survey are included in this study (see figure 4.16 for location of the transects). Leg 72 from Corystes 7/94 corresponds to the same location as leg 68 from Corystes 5b/95, leg 17 from Cirolana 4b/96 and leg 70 from Corystes 9/96. Leg 101 from Corystes 7/94 was sampled along the same latitude as leg 74 from Corystes 5b/95 and leg 73 from Corystes 9/96. Leg 49 from Corystes 7/94 represents the same section as leg 21 from Cirolana 4b/96.

During the June survey in 1994 (Corystes 7/94) top to bottom temperature differences in the central region of the western Irish (section 72, figure 4.10) reached 3° C and the thermocline (pycnocline) was clearly established, at 20-30 m depth. It was also clear that thermal stratification controlled the vertical density structure. Sections 49 and 101 (figures 4.9 and 4.11) respectively on the southern and northern borders of the stratified region, show a less clear stratification of the water column. Observations from these areas also appeared to be considerably 'noisy'. Despite that, it is apparent that thermal stratification of the water column was already established. Top to bottom temperature differences of 2.5° C and 1° C were found in the southern and northern transects, respectively.

Figures 4.12 to 4.14 show the distribution of hydrographic parameters along three sections (see figure 4.16 for locations), in July (7-8) 1996 (Corystes 9/96). Transect 70 (figure 4.13) corresponds to the central line across the western Irish Sea shown in figure 4.2 (leg 17, Cirolana 4b/96), figure 4.5 (leg 68, Corystes 5b/95) and figure 4.10 (leg 72, Corystes 7/94). The distribution of temperature and density show evidence of the well established thermocline (pycnocline) at 20-30 m depth. The presence of a halocline was not as clear. It is also apparent that the temperature of the surface waters in mid July 1996 was lower (12.5° C) than for the same period in 1995 (Prince Madog 4/95), when surface water temperature reached 16.0° C. Despite that, the vertical structure of the water column appeared very stable. The pool of bottom colder, denser, water was very clearly isolated below the thermocline (pycnocline). The same pattern of water properties distribution was present along the northern most transect (leg 73, figure 4.14). Figure 4.12, on the southern end of western Irish Sea area

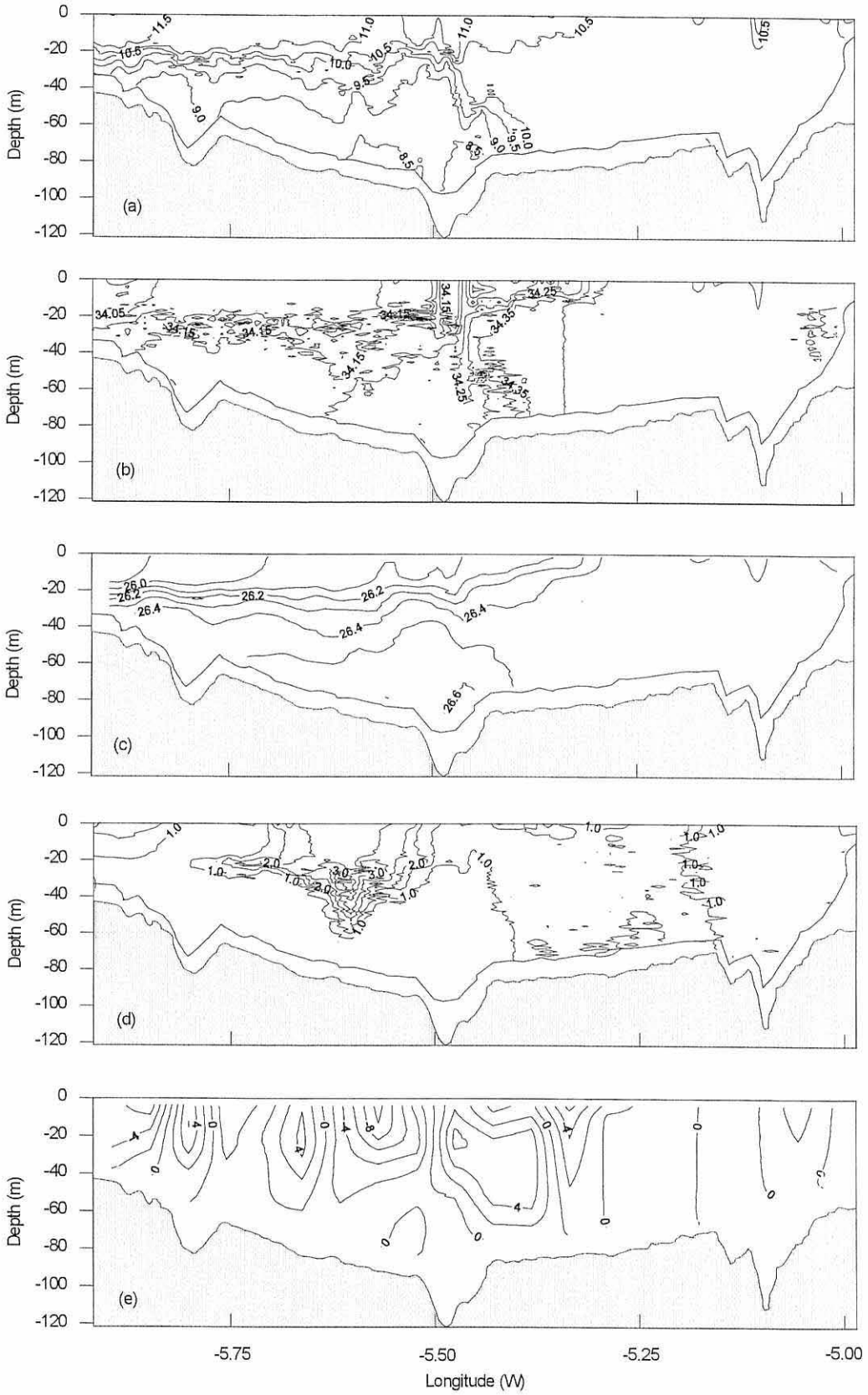


Figure 4.9. West-east Scanfish section of the western Irish Sea at latitude 53.5° N (leg 49, Corystes 7/94, see figure 4.16 for location) on 19 June 1994. Showing (a) temperature (°C), (b) salinity (psu), (c) density (σ_t), (d) chlorophyll$_a$ (µg/l), (e) geostrophic velocity computed relative to an assumed level of no motion at the sea bed; positive isotachs indicate flow into the page and negative values correspond to flow away from the page.

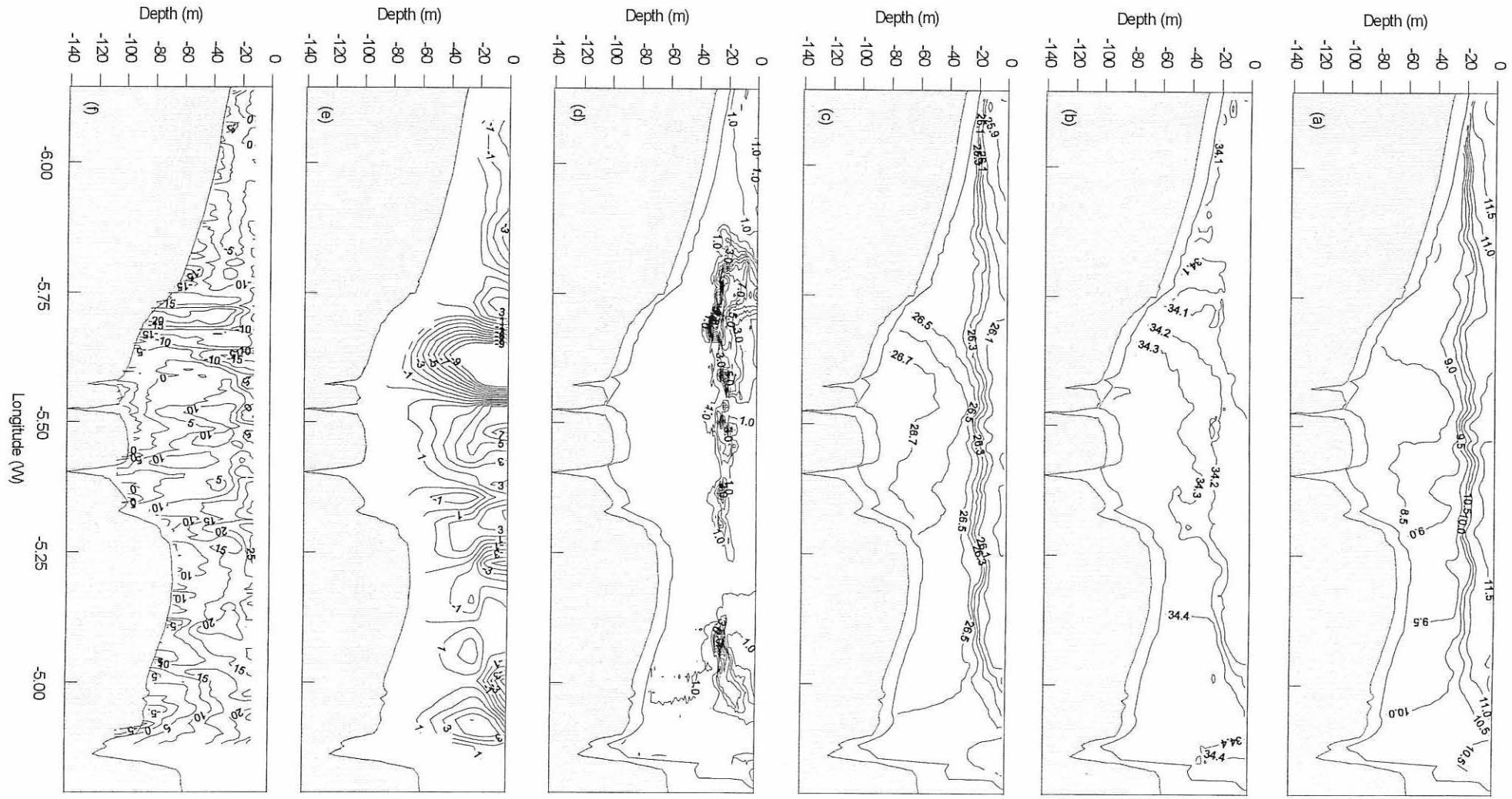


Figure 4.10. West-east Scanfish section of the western Irish Sea at latitude 53.8° N (leg 72, Corystes 7/94, see figure 4.16 for location) on 20 June 1994. Showing (a) temperature (°C), (b) salinity (psu), (c) density (σ_t), (d) chlorophyll$_a$ (µg/l), (e) geostrophic velocity computed relative to an assumed level of no motion at the sea bed. (f) detided ADCP velocities (north/south components). Positive isotachs indicate flow into the page and negative values correspond to flow away from the page.

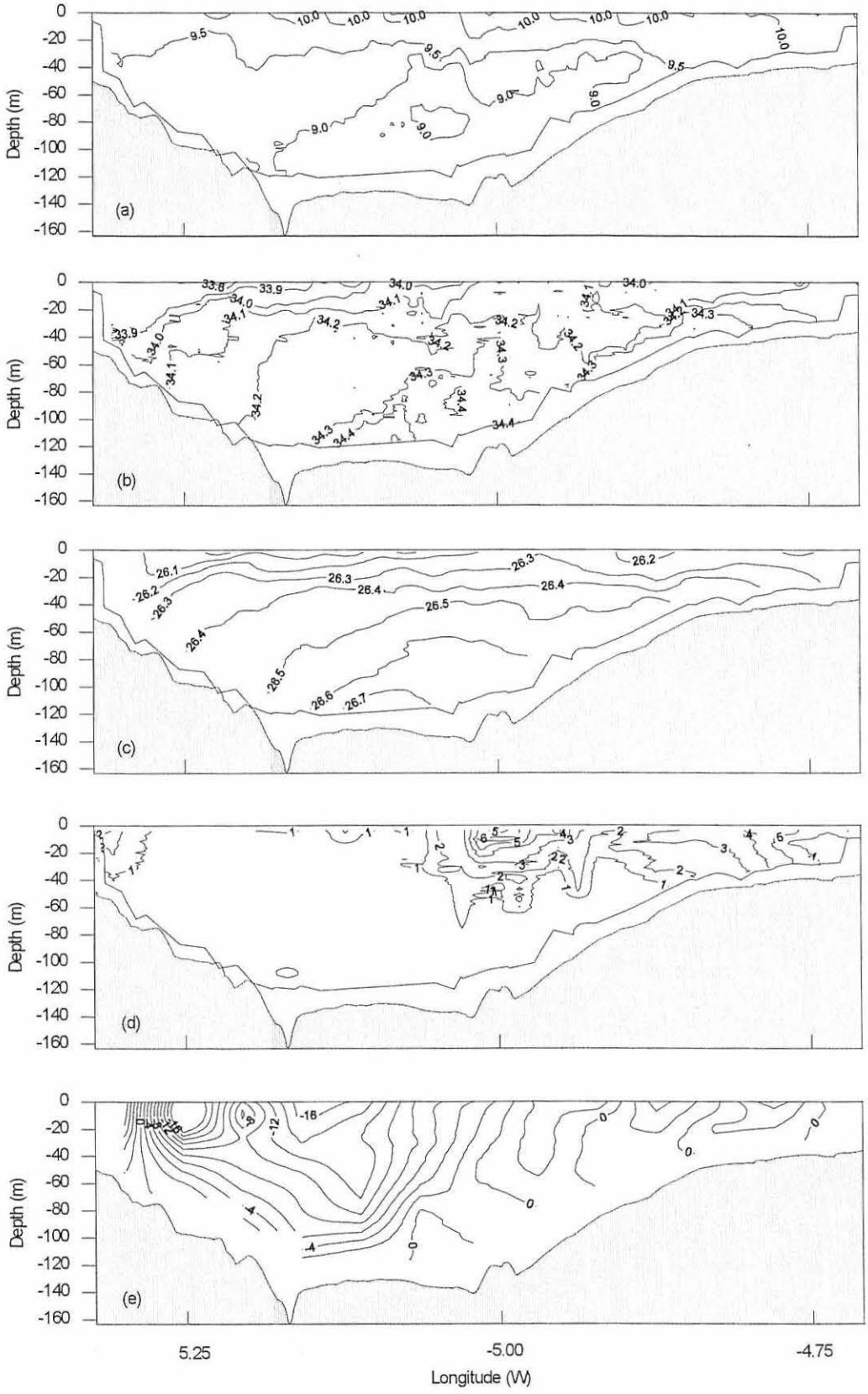


Figure 4.11. West-east Scanfish section of the western Irish Sea at latitude 54.3° N (leg 101, Corystes 7/94, see figure 4.16 for location) on 21-22 June 1994. Showing (a) temperature (°C), (b) salinity (psu), (c) density (σ_t), (d) chlorophyll$_a$ (µg/l), (e) geostrophic velocity computed relative to an assumed level of no motion at the sea bed; positive isotachs indicate flow into the page and negative values correspond to flow away from the page.

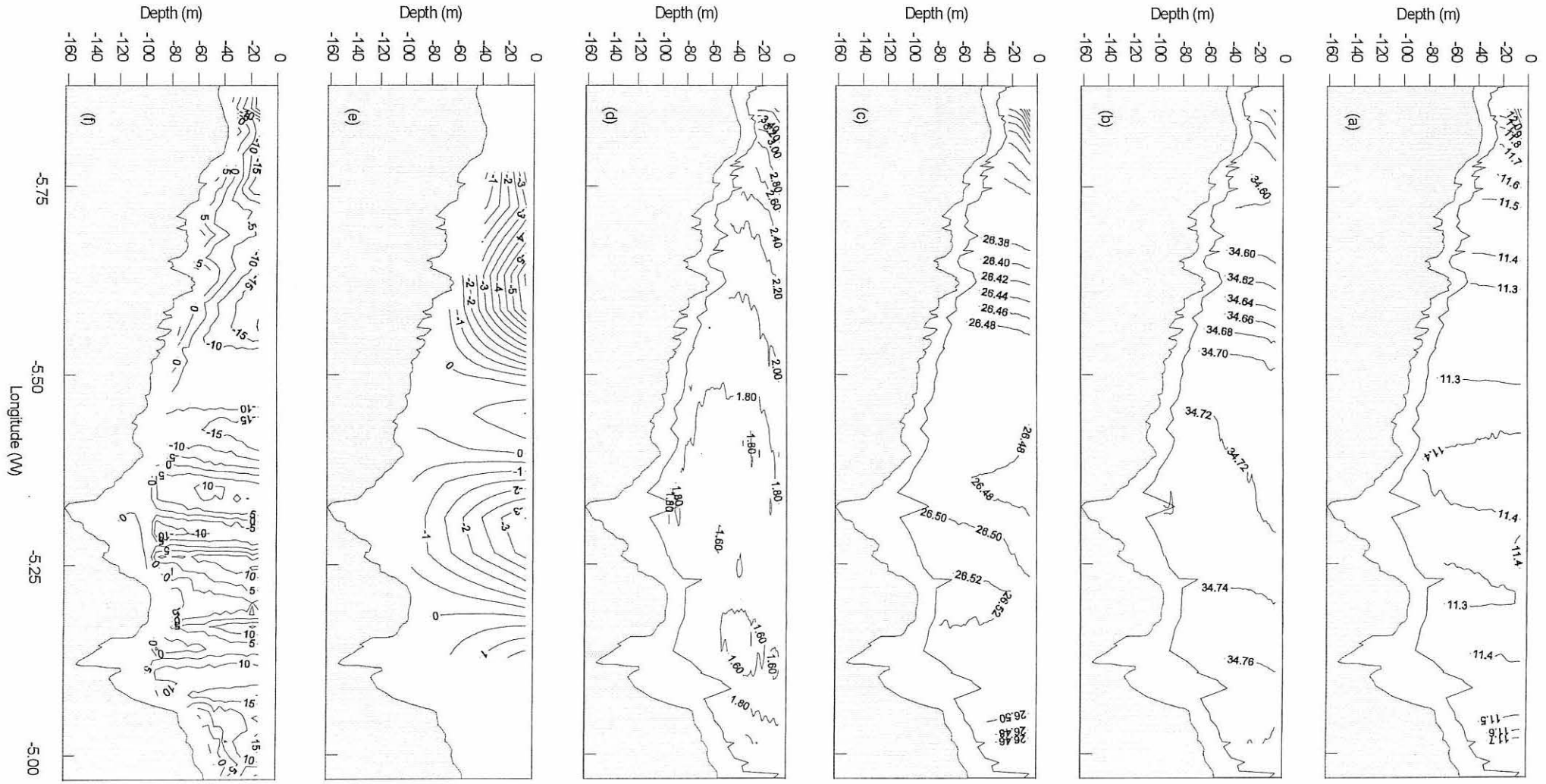


Figure 4.12. West-east Scanfish section of the western Irish Sea at latitude 53.35° N (leg 67, Corystes 9/96, see figure 4.16 for location) on 7 July 1996. Showing (a) temperature (°C), (b) salinity (psu), (c) density (σ_t), (d) chlorophyll$_a$ (µg/l), (e) geostrophic velocity computed relative to an assumed level of no motion at the sea bed. (f) detided ADCP velocities (north/south components). Positive isotachs indicate flow into the page and negative values correspond to flow away from the page.

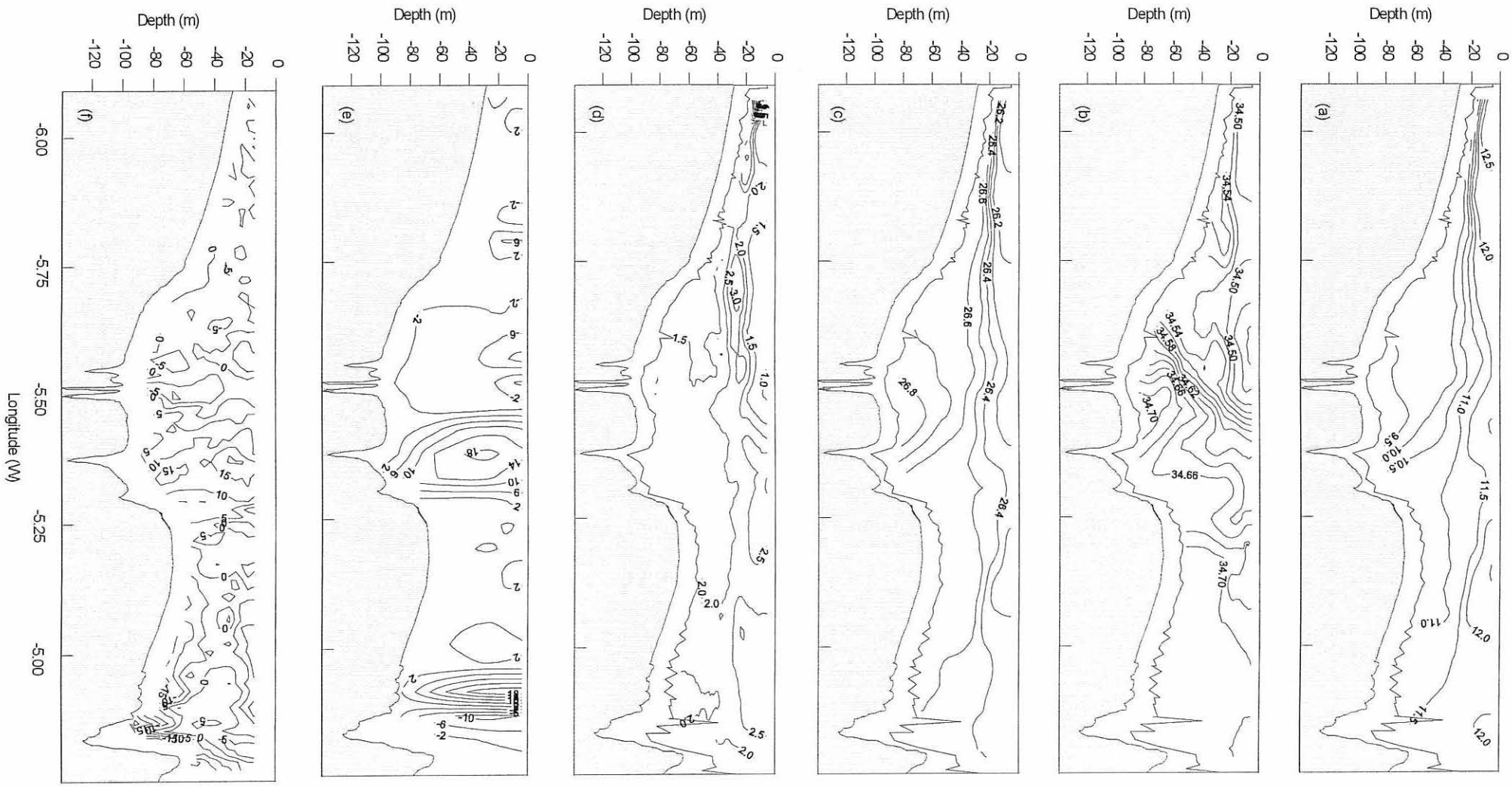


Figure 4.13. West-east Scanfish section of the western Irish Sea at latitude 53.8° N (leg 70, Corystes 9/96, see figure 4.16 for location) 7-8 July 1996. Showing (a) temperature (°C), (b) salinity (psu), (c) density (σ_t), (d) chlorophyll$_a$ (µg/l), (e) geostrophic velocity computed relative to an assumed level of no motion at the sea bed. (f) detided ADCP velocities (north/south components). Positive isotachs indicate flow into the page and negative values correspond to flow away from the page.

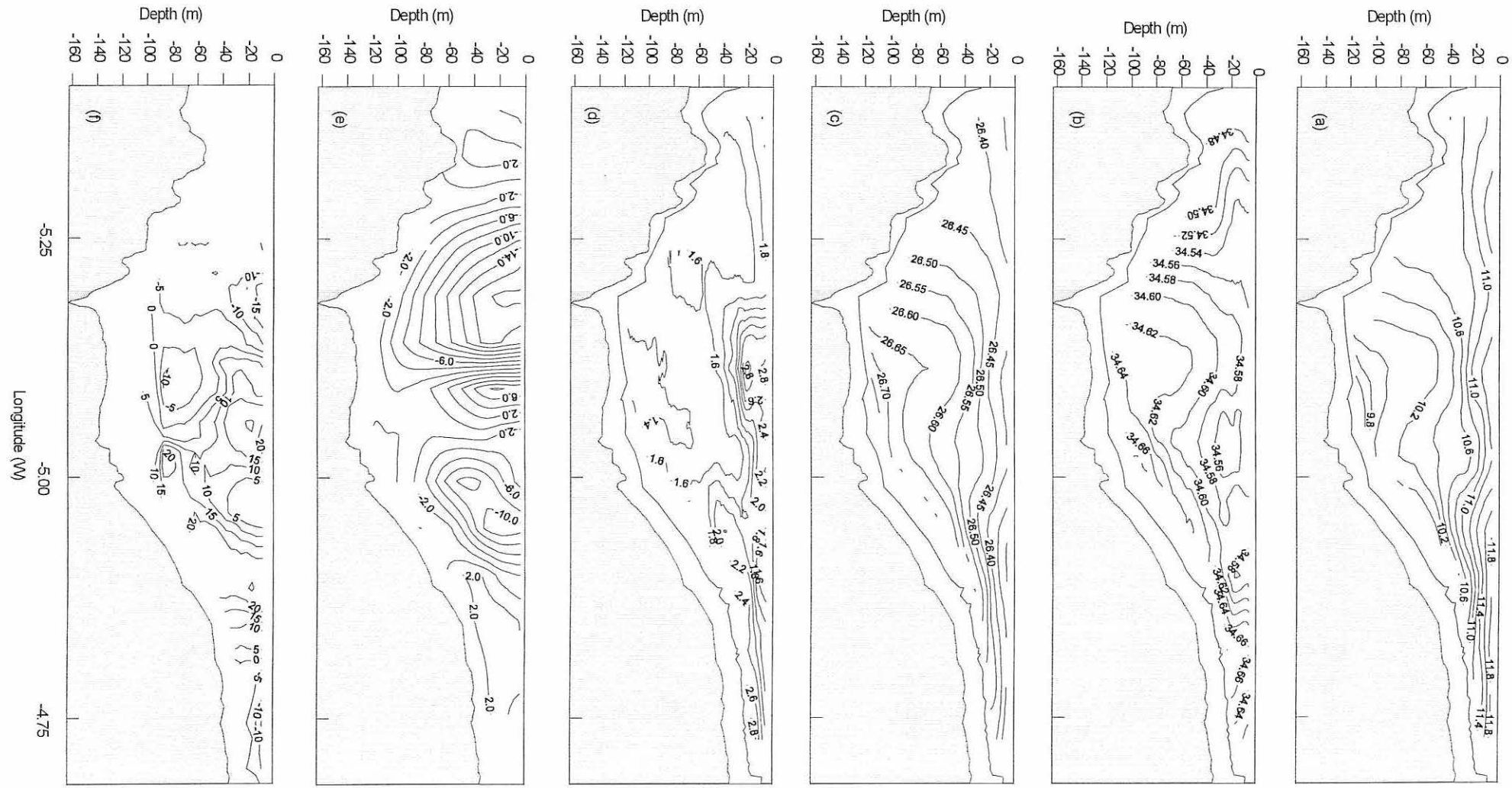


Figure 4.14. West-east Scanfish section of the western Irish Sea at latitude 54.3° N (leg 73, Corystes 9/96, see figure 4.16 for location) on 8 July 1996. Showing (a) temperature (°C), (b) salinity (psu), (c) density (σ_t), (d) chlorophyll$_a$ (µg/l), (e) geostrophic velocity computed relative to an assumed level of no motion at the sea bed. (f) detided ADCP velocities (north/south components). Positive isotachs indicate flow into the page and negative values correspond to flow away from the page.

(leg 67), shows a predominantly mixed water column consistent with the limit of the stratification region.

Figures 4.1 to 4.14 also present the vertical distribution of chlorophyll$_a$. During the first survey (Cirolana 4b/96, figures 4.1d, 4.2d, 4.3d) in mid April, maximum concentrations of chlorophyll$_a$, along the transects presented, reached 2.5 μg/l, indicating that the spring phytoplanktonic bloom had started. In places where samples of water were collected, concentrations of up to 12 μg/l were recorded in conjunction with surface depletion of nutrients. Identification of the phytoplankton composition, revealed that large diatoms dominated the spring bloom at this stage of the production season. The presence of some species of flagellates was also registered (CEFAS, unpublished data). Across section 17 (figure 4.2d) maximum concentrations of chlorophyll appeared in the surface waters above the pycnocline. In the bottom waters in the deeper central area, where the dome of colder denser water was starting to show, levels of chlorophyll were very low. Along transects 21 (figure 4.1d) and 15 (figure 4.3d) the phytoplankton seemed to be more homogeneously distributed in the water column. Along line 15 higher values of chlorophyll appeared towards the Irish coast, just north of Dundalk Bay.

By May, in 1995, (Corystes 5b/95, figures 4.4d to 4.7d) the levels of chlorophyll, recorded with the scanfish fluorometer, reached 9 μg/l. Higher concentrations of phytoplankton were found along transect 64 (figure 4.4d), the line on the southern limit of the stratification area. The high occurrence of phytoplankton in this area does not necessarily mean that production is higher there. Accumulation of cells in the surface waters in this area may occur due to the southward flowing current present along the Irish coast (the presence of this current is confirmed by the hydrographic results presented here). Phytoplankton occurrence was very clearly concentrated in the surface waters, above the thermocline (pycnocline), zone that probably also define the limit of the euphotic layer. Patches of cells appeared over the whole region but in transect 68 (figure 4.5d), 70 (figure 4.6d) and 74 (figure 4.7d) higher concentrations occurred over the central stratified area. High levels of chlorophyll were also evident at the frontal regions on both, eastern and western sides of the gyre; this pattern was particularly clear in section 68.

Chlorophyll$_a$ concentrations observed during Corystes 7/94 survey (figures 4.9d to 4.11d), in June, reached 6 μg/l. The pattern of distribution was similar to what was described for the survey in May.

In July 1996 (Corystes 9/96, figures 4.12d to 4.14d) maximum values of chlorophyll were just above 3 μg/l in the coastal region of section 67 (figure 4.12d), the southern most line. In this area, the vertical distribution of phytoplankton seemed to be fairly homogenous. Further north, at transects 70 (figure 4.13d) and 73 (figure 4.14d) the highest concentration of cells remained in the top 20-30 m of the water column but some patches of chlorophyll were observed in deeper waters.

The spatial distribution of temperature (surface, bottom and surface-bottom, Δt) observed during mid May (Corystes 5b/95), early June (Prince Madog 1/95) and mid July (Prince Madog 4/95) is presented in figure 4.15. The seasonal evolution of the thermal stratification of the water column can be appreciated in this sequence of maps. In May (Corystes 5b/95) stratification was in its early stages being particularly noticeable in the central area, the limits of the region were not yet clearly defined. By June (Prince Madog 1/95) temperature stratification was evident (maximum Δt 2.0° C) and the cold bottom water of less than 9.0° C remained in the central deep channel. The cold water was then clearly isolated in a patch at the central western Irish Sea by July (Prince Madog 4/95). Vertical temperature differences of more than 5° C were observed in the central region. It is also important to note that the bottom gradients of temperature were generally stronger at the bed than at the surface and closed contours of bottom temperature were observed. From mid May to mid July (1995) the bottom temperature increased from 8.5° C to 10° C. This slow warm up of the bottom waters did not lead to any appreciable change in the horizontal gradients, confirming the stability and seasonal persistence of the central mass of cold bottom water and the density gradients associated with it. The coldest temperatures were registered in the region between 53.7-53.8° N and 5.5-5.7° W, which define the centre of the cold pool and the deeper area of the western Irish Sea.

In summary, the density structure of the water column in the western Irish Sea seemed to be influenced by fresh water input, from the Irish coast, early in the season with temperature begining to exert dominant control over density by June. A considerable strengthening of the

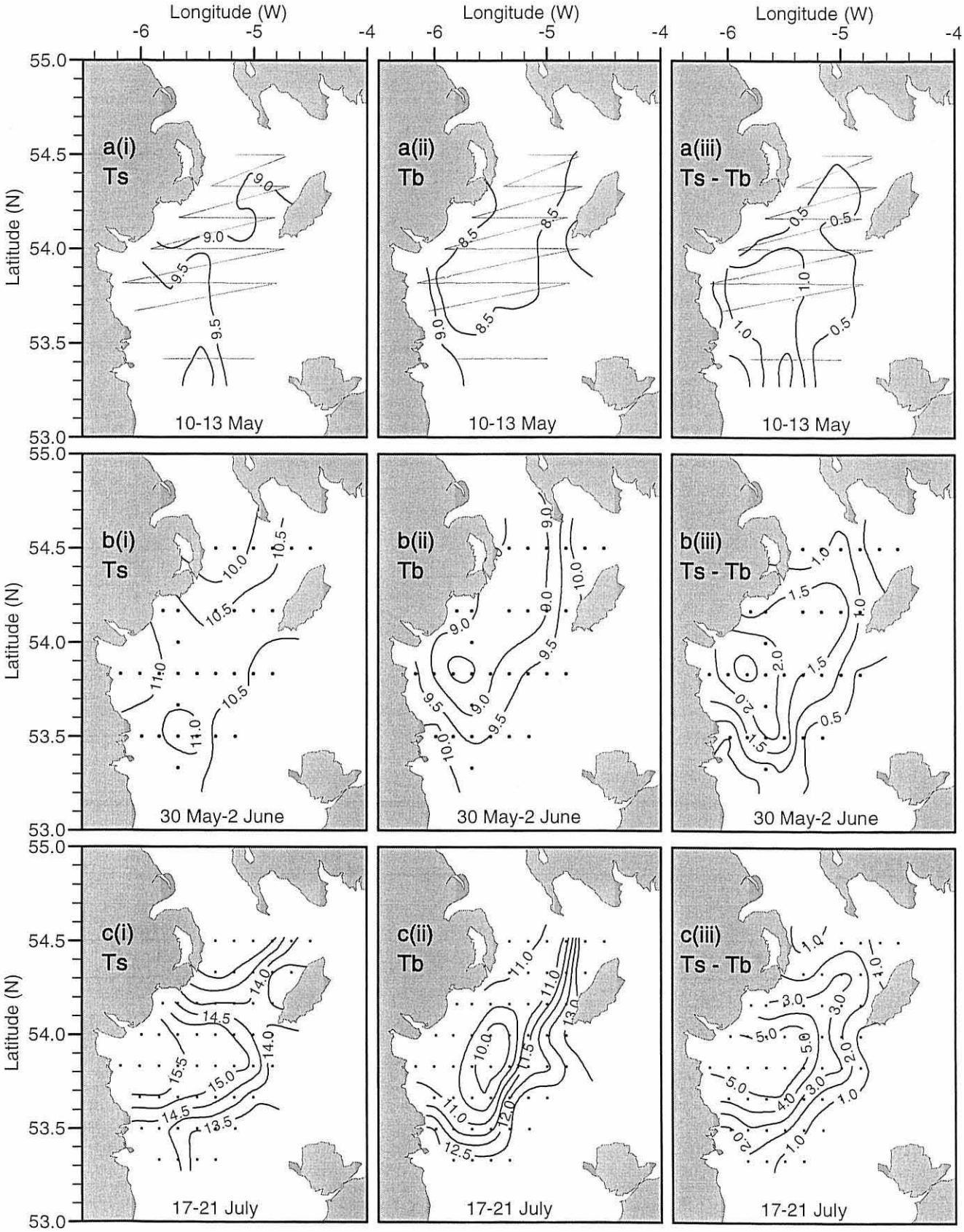


Figure 4.15. Seasonal development of the temperature field (°C) in 1995. (a) Corystes 5b/95, (b) P. Madog 1/95, (c) P. Madog 4/95. Showing (i) surface temperature, (ii) bottom temperature, (iii) difference between surface and bottom temperature.

pycnocline was then apparent. The dome of cold dense bottom water was observed throughout the spring-summer season with maximum horizontal density gradients being reached in July. Density gradients were generally stronger on the eastern side of the dense pool (except when fresh water runoff dominated the density structure, during the early stages of the heating season). The location of the bottom fronts changed little over the season occurring between 5.25° W and 5.42° W, on the eastern flank and at approximately 5.67 °W, on the western side. The depth of the pycnocline remained fairly constant, at 20-30 m, throughout the season. The bottom fronts are responsible for the occurrence of a near surface cyclonic circulation (gyre) about the western Irish Sea. Evidence of the gyre is confirmed by the flow field data and the Argos drifters trajectories described ahead. By July-August, when thermal stratification of the water column reachs its peak the gyre attains its maximum strength.

The break down of stratification (gyre) occurs by the end of the summer, in late September-October (by then, the planktonic phase of *Nephrops norvegicus* has already finished). Observations carried out at the end of the stratification season are not included in this study but can be confirmed in Horsburgh *et al.* (submitted).

Figures 4.16 and 4.17 show contours of potential energy anomaly (ϕ) calculated for the six surveys being described in this chapter. These observations confirmed the results already outlined. At the begining of the season in April (Cirolana 4b/96, figure 4.16a) values of ϕ were small (maximum 30 J/m^3), indicating a tenuous stratification of the water column. As the season progressed, the stratification of the water column intensified as it can be seen by the increase in ϕ (maximum values of around 50 J/m^3 in May (Corystes 5b/95, figure 4.16b and Prince Madog 1/95, figure 4.17a) and June (Corystes 7/94, figure 4.16c). The highest values of potential energy anomaly were observed during July (Corystes 9/96, figure 4.16d and Prince Madog 4/95, figure 4.17b). Maximum values of ϕ (120-130 J/m^3) were noted during survey Prince Madog 4/95. It is also important to note the closed contours of ϕ (particularlly noticeable in July, Prince Madog 4/95 survey) defining the extent of the stratified area and the gyre in the western Irish Sea. The southern limit of the stratified region (and gyre) was located approximately along the 53.4° N parallel and the northern boundary appeared around latitude 54.6° N. These limits coincide with the mud patch region in western Irish Sea. The distribution of ϕ also show the existence of two centres of stratification in the

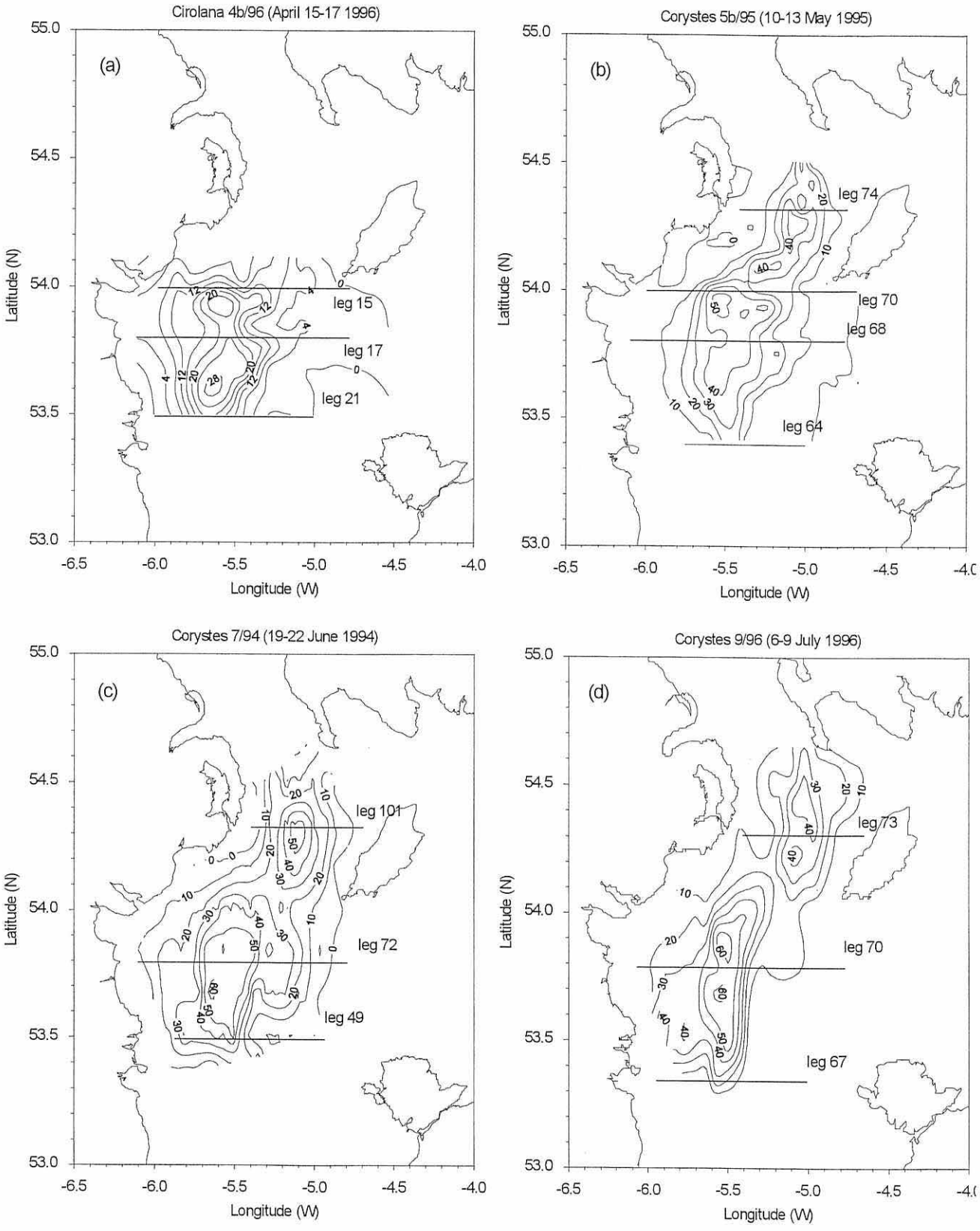


Figure 4.16. Contours of potential energy anomaly (J/m^3) for (a) Cirolana 4b/96, (b) Corystes 5b/95, (c) Corystes 7/94, (d) Corystes 9/96. Also shown the location of the Scanfish sections.

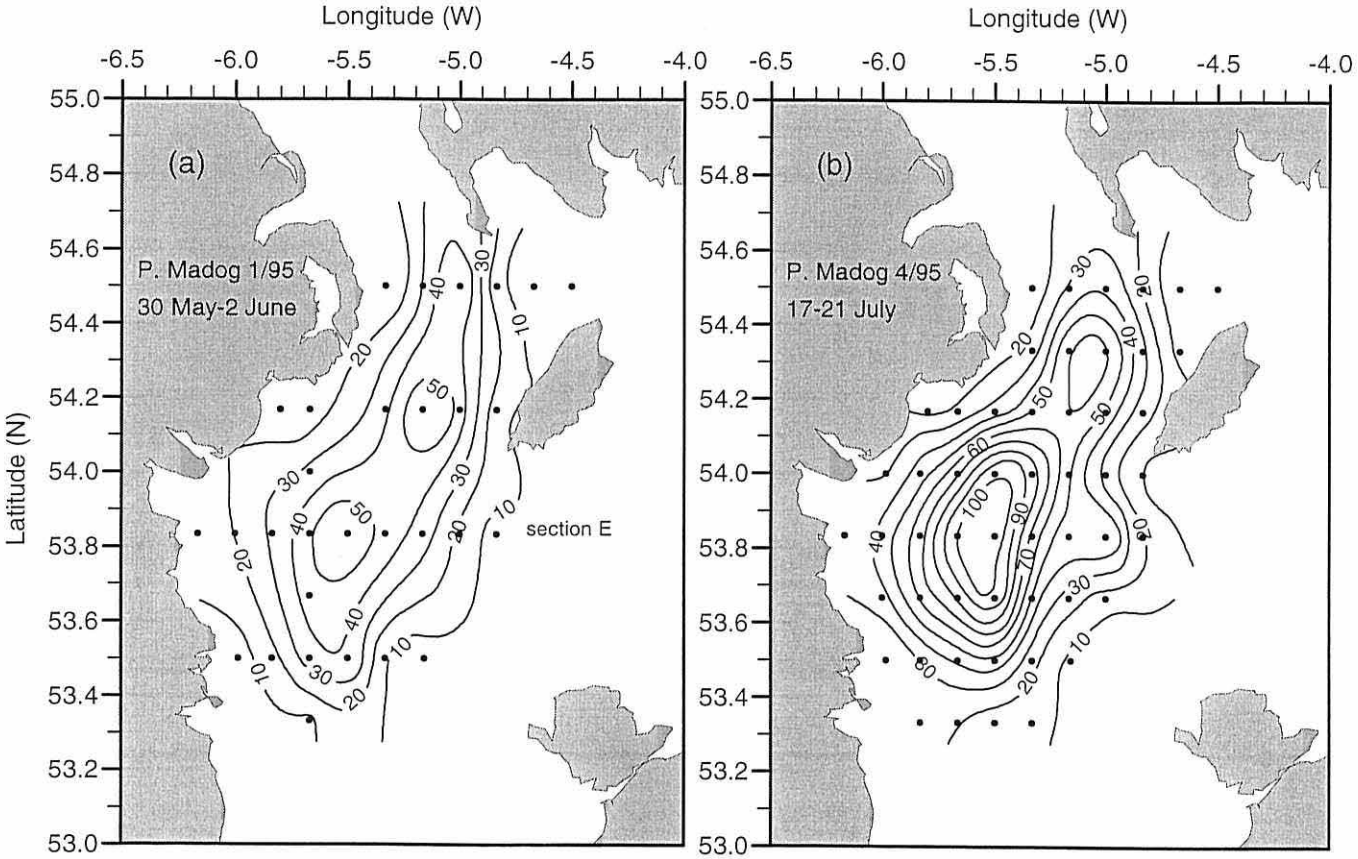


Figure 4.17. Contours of potential energy anomaly (J/m^3) for (a) P. Madog 1/95 (b) P. Madog 4/95. Also shown the location of CTD section E.

western Irish Sea, as it was suspected by observing the latitudinal transects presented before. The lines of potential energy anomaly also represent well the residual circulation in the area, as will also be shown by the drifters tracks (figures 4.18 and 4.19).

A total of 50 Argos drifters were deployed in the western Irish Sea in spring-summer of 1995 (41) and 1996 (9). From those, 20 were either lost or grounded while the remaining 30 were recovered. From the 40 that were active for 4 or more days only 2 showed anticyclonic tendencies. In figure 4.18 a selection of 25 drifter tracks are presented to illustrate the Lagrangian movement of water around the region. The drifters had their drogues at 24 m depth, consistent with the depth of the pycnocline, with the exception of drifters f24056 and f24062, which had the drogues placed at 8.5 m.

Several consistent features are obvious from the individual tracks. The first relevant point to make is that few drifters escaped the western Irish Sea area. Those that did so, left in a eastward direction, south of the Isle of Man (*eg.* a17830 and d24058). This pattern was noticed preferentially during the early stages of the stratification season. One buoy (a3911) exited the western Irish Sea through the North Channel but this tracer had lost its drogue and its track maybe indicative of a more superficial flow or wind driven current.

A southward flow along the Irish coast (*eg.* a24056, a3945, a24020, a17823, b6372) seemed to be a consistent pattern of movement, particularly noticeable in the earlier deployments. Drifter a24020 also showed evidence of an inflow through the North Channel. Coherent northeastward flow along the eastern front of the gyre was illustrated by buoys b24055, b17804, b17802 and c17823. Speeds of up to 20 cm/s were apparent in this area while southward flow along the western flank was of the order of 9 cm/s.

Cyclonic turn around the southern end of the gyre was clear from the tracks of buoys a17830, a6372, b24055 and f21575. Anti-clockwise flow in the northern boundary was shown by instruments b24055 and b17802, which recirculated around the northern centre of the gyre. One drifter (b17804) made a complete circuit in 55 days; after negligible movement for 13 days it then took 42 days to encircle the gyre at an average speed of 10 cm/s.

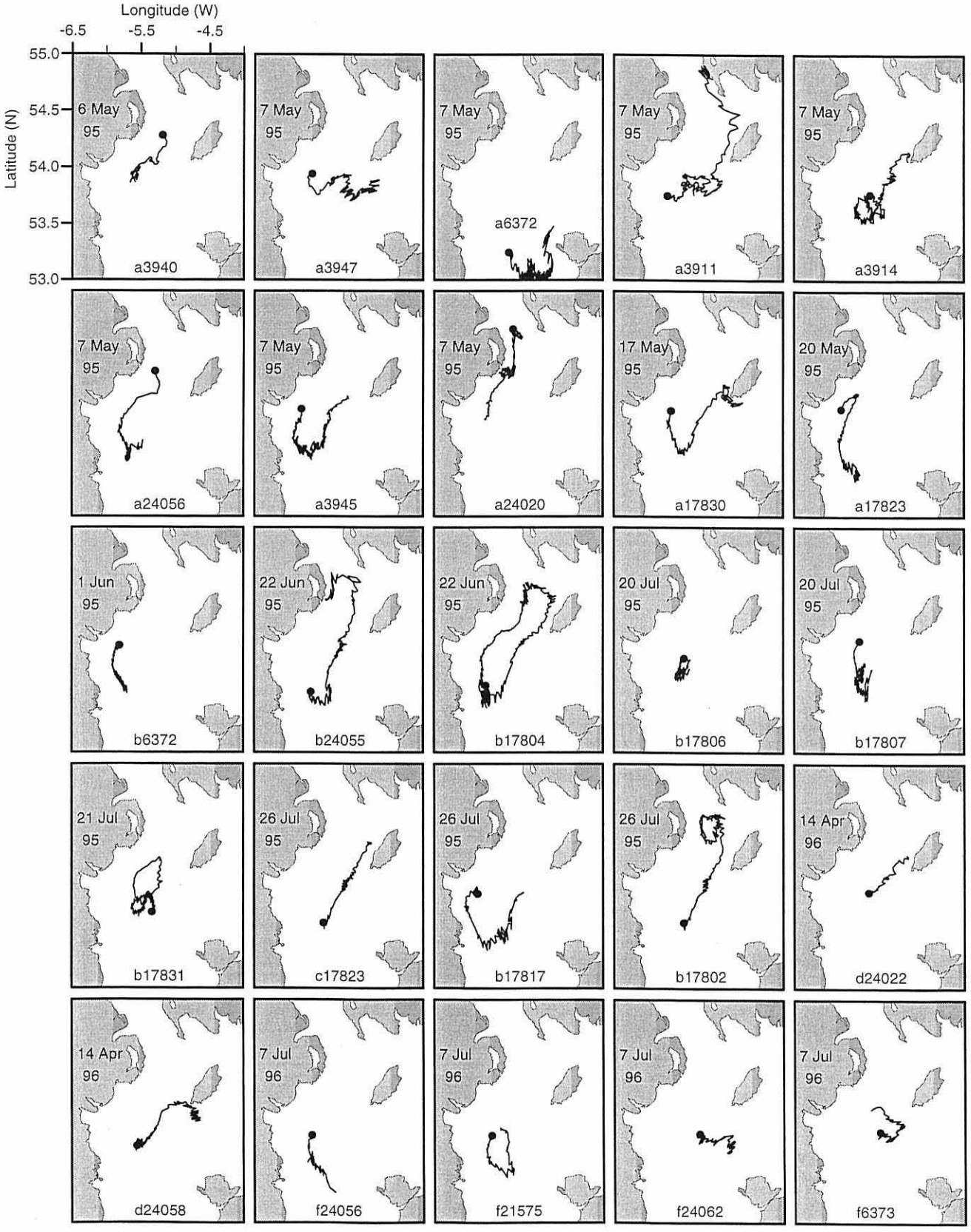


Figure 4.18. Argos drifters trajectories (unfiltered) in 1995 and 1996. Panels are presented in chronological order of release date which is shown in the top left corner. Drifter identification appears at the bottom of each panel. Solid circles denote the position of deployment.

Instruments drogued close to the surface (drogues placed at 8.5 m, f24056 and f24062) and the one that lost the drogue (a3911) seemed to be influenced by wind driven currents which affected their retention in the western Irish Sea. The turn northeastwards, about the southern end of the gyre also seemed to be 'helped' by the wind in two occasions (buoys a17830, a3945) when strong southwesterly winds were blowing.

A final consistent pattern of movement clearly shown by some drifters is exemplified by instruments b17806 and b17807, layed in the centre of the stratified area (and gyre). These buoys remained fairly static, showing very little drift confirming that the central area of high stratification appears to be a stagnation region for residual flow.

A striking feature of the drifters tracks is the similarity between the pattern of their trajectory and the spatial distribution of potential energy anomaly. This good agreement between the buoys trajectories and the contours of ϕ (figure 4.19) implies that the flow field in the western Irish Sea is density driven.

Geostrophic velocities presented in figures 4.1e to 4.7e and 4.9e to 4.14e also point out that the observed circulation is due to the baroclinicity of the density field. Geostrophic calculations showed that the magnitude of the observed residual flow is consistent with baroclinic forcing. As it can be seen in the transects shown, the predicted geostrophic flow is concentrated in two narrrow (approximately 10 km wide) bands on each side of the dense dome and centred just below the thermocline. These jets (southward flowing, in the western flank and northward flowing, in the eastern side) are located immediately above the strongest gradients of density, near the sea bed. At the begining of the heating season (Cirolana 4b/96, figures 4.1 to 4.3), when stratification of the water column is in its early stages and the gyre is only starting to develop, the currents are relatively weak (2-3 cm/s). It is also worth noting at this stage of the heating season, the presence of a southward flowing current along the Irish coast. This current was predicted by the evidence of fresh water input and the drifters tracks. As the season progressed, and the gyre strengthened, geostrophic velocities increased. Calculated geostrophic flows in May (Corystes 5b/95, figures 4.4e to 4.7e) reached 16-18 cm/s.

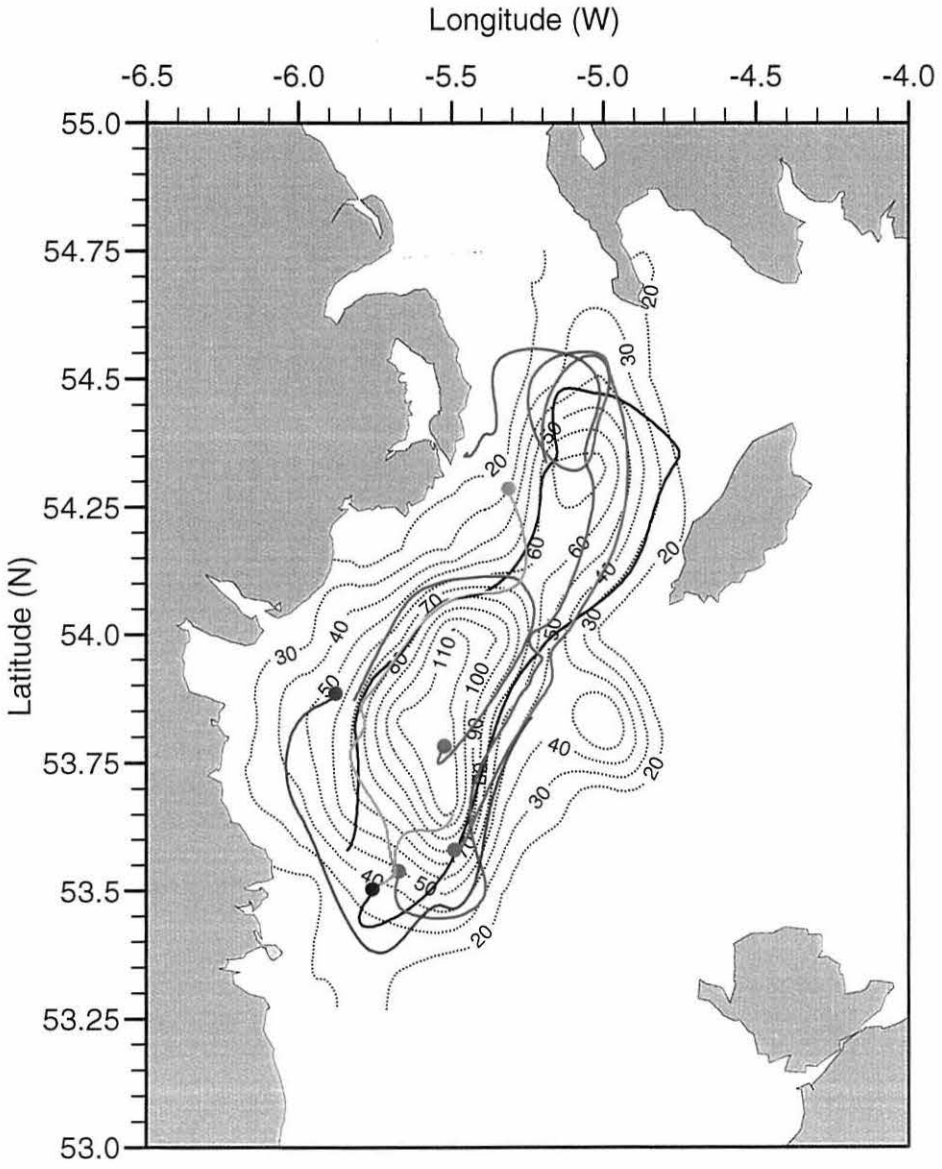


Figure 4.19. Filtered tracks of six chosen Argos drifters overlayed on the spatial distribution of potential energy anomaly (J/m^3) from survey P. Madog 4/95, 17-21 July 1995.

The detided currents, derived from ADCP observations (presented in figures 4.4f to 4.7f, 4.10f, and 4.12f to 4.14f, the only available ADCP observations) are similar to the geostrophic flows. Minor disagreements between the ADCP data and the geostrophic calculations are probably due to problems created by the model used to filtrate the tidal component of the flow.

4. Discussion

The results presented in this chapter, although including only part of the observations carried out in the western Irish Sea during the period from 1994 to 1996, give a comprehensive picture of the local hydrodynamics for the spring-summer term, when the larvae of *Nephrops norvegicus* are present in the water column. The extent of the stratification and development of the gyre, over the area of the mud patch, are clearly shown.

The observations from the drifters define the area of the western Irish Sea gyre and its retentive properties. Only 8 buoys, from a total of 50 escaped the area. Drifter tracks superimposed with the distribution of ϕ and calculations of the geostrophic flow field highlighted the baroclinicity of the density field as the driving force behind the development of the gyre, supporting the explanation by Hill (1993; 1996) and subsequent studies carried out in the region (Hill *et al.*, 1996; 1997a).

Data collected during Cirolana 4b/96 survey, in April , constitute the first comprehensive set of hydrographic results obtained early in the heating season, when the gyre starts to develop and the hatching season of *N. norvegicus* is already in progress. Observations from this survey, showed that fresh water input along the Irish coast plays a part in the establishment of stratification of the water column at the begining of the heating season. As the season progresses, and the surface waters warm up, thermal stratification becames the dominant factor defining the density structure of the water column. Associated with the fresh water input, a southward flowing current occurs along the Irish coast. This flow, is confirmed by the trajectories of drifters deployed in the area and it is also in agreement with the geostrophic calculations.

The pool of colder, denser bottom water, in the deep channel of the western Irish Sea was apparent early in the season in April-May becoming from then on, completely isolated from the surrounding waters. The sharp bottom density gradients, separating this mass of water from the adjacent mixed waters, and responsible for the cyclonic circulation of the surface waters above them, were particularly strong from June onwards. The bottom waters warmed up slowly and never reached temperatures above 10° C. Further evidence for the isolation of this mass of water is provided by the results from nutrients and oxygen analyses. Total

oxidised nitrogen (NO_3+NO_2) and phosphate (PO_4) concentrations, were relatively high in the dense pool compared to the waters from the euphotic zone, above the thermocline. Low levels of dissolved oxygen were registered in the bottom waters, consistent with little exchange between these waters and the surface layers (Horsburgh *et al.*, submitted). In July (Prince Madog 4/95) when the surface waters attained its maximum temperature (up to 16° C), top to bottom temperature differences of up to 5° C were recorded.

Contours of potential energy anomaly, a good indicator of the stratification of the water column, showed maximum values (> 100 J/m^3) in mid July (Prince Madog 4/95) when the gyre attained its maximum strength. Observations presented in the study by Horsburgh *et al.* (submitted) study, show that stratification of the water column in the western Irish Sea reaches its peak in July-August and the gyre is then at its strongest point, providing a retention system about the region. An Argos drifter released on the 22 of June 1995 described a complete circuit of the gyre in 42 days. Some buoys layed earlier in the season, drifted away from the area of the gyre, especially on the eastern flank, leaving to the southeast of the Isle of Man. These observations confirm the idea that before June the retention system may be not so effective. It is also important to note that tracers that had the drogues centred in more superficial waters, above the depth of the pycnocline, seemed to be not so well retained in the area probably responding to surface currents generated by the wind. The residual flow field predicted by geostrophic calculations and ADCP observations, showed that maximum currents occur above the bottom density fronts at about 20 to 30 m depth, appearing, in the sections presented in figures 4.1 to 4.7 and 4.9 to 4.14, as two narrow jets on each side of the stratified area.

The distribution of ϕ, and the tracks of drifters a3914, b1780 and f21575, verify the existence of two centres of high stratification, which seems to be associated with the two deeper regions in the western Irish Sea basin.

The distribution of $chlorophyll_a$ concentrations in the area of study, showed that by the time the first survey took place, in mid April (Cirolana 4b/96) the spring phytoplankton bloom was already in progress. At this stage of the season, the shallower waters close to the Irish coast, off Dundalk Bay, exhibited the highest levels of chlorophyll. These observations are in agreement with the studies by Gowen *et al.* (1995) and Gowen and Bloomfield (1996) which

describe that the primary production season in this area, starts earlier than in the rest of the western Irish Sea, even before the thermal stratification of the water column fully develops. This area also seems to have the highest primary production during the spring-summer season, which lasts longer (6 to 7 months) than in the rest of the western Irish Sea. In the central stratified region, the production season is underway slightly later, by the begining of May (as it is also apparent by the present study), and lasts about 4 months. The more northerly areas, coastal and offshore, exhibit a short (2-3 months), late (late May-June), intense production season.

The early, and sustained primary production found in the coastal region occurs despite the weak thermal stratification of these waters. During the survey described in Gowen *et al.* (1995), from March to November, surface to bottom temperature difference in that region never exceeded 0.6^{o} C. In these shallow waters, the onset of the spring bloom probably depends mainly on the seasonal increase in light and not at all on the onset of stratification. If phytoplankton is being transported by turbulence throughout the water column, and is exposed to abundant nutrients, the onset of the spring bloom depends mainly on the seasonal increase in light, and not at all on the onset of stratification. In such areas, the primary production cycle usually starts early in the season, as soon as the solar radiation available is enough to trigger the photosynthetic process, and it only decreases when the ressuspension of sediments, in the autumn, is so strong that not enough light would penetrate into the water column.

In deeper waters, primary production is more dependent on the stabilization of the water column and onset of a surface mixed layer. Prior to stratification of the water column the phytoplankton cells are being circulated to the full depth of the mixed layer and hence spend a large proportion of their time below the euphotic zone, reducing the chances of growth and multiplication.When stratification develops, primary production in the surface waters is usually high but the presence of a thermocline (pycnocline) acts as a barrier to the influx of nutrients from the bottom waters and once all the nutrients available in the surface layers are used, production ceases. In consequence, the production season in the thermally stratified waters is usually shorter than in isothermal regions.

The study by Gowen and Bloomfield (1996) revealed that by the end of May the highest phytoplankton standing crop was found in the central area of the western Irish Sea (chlorophyll$_a$ concentrations of up to 16 μg/l), and in June-July a pronounced subsurface chlorophyll maximum was found at depths of around 20 to 35 m, in these stratified waters. This pattern of phytoplankton distribution had already been observed by Richardson *et al.* (1985). As the season progresses and the surface layer extends, the distribution of phytoplankton deepens, maximum concentrations of chlorophyll are then found around the pycnocline, where the light available is still enough and some nutrients are transported from the bottom waters by vertical diffusion or internal wave activity. The hydrographic data presented in this study does not show any considerable change in the depth of the pycnocline during the period from mid April to July but sub-surface patches of chlorophyll concentration were apparent in the observations from June (section 72, Corystes 7/94) and July (section 70, Corystes 9/96). In addition, in places over the deep central areas during May and June surveys, echosounder and ADCP observations revealed strong patches of particles at depths around the pycnocline, which were likely to be an indication of concentration of zooplankton (and phytoplankton) at those depths.

Results from Gowen and Bloomfield (1996) suggest that the area on the southern limit of the stratified region, is a zone of high concentration of phytoplankton (observation supported by the present study, section 64, Corystes 5b/95) but not of high productivity suggesting, that plankton produced in other areas (north) drifts into this region.

The beginning of the autumnal decline in the phytoplankton standing stock in the western Irish Sea occurs usually during the month of August (Gowen & Bloomfield, 1996). A smaller autumn peak in primary production has been observed for the stratified region of the western Irish Sea (Slinn & Eastham, 1984; Richardson *et al.*, 1985; Savidge & Kain, 1990; Gowen *et al.*, 1998), but it seems not to be present every year (Slinn & Eastham, 1984).

Observations from Slinn & Eastham (1984), at a fixed station in the stratified region, during a period of 10 years, demonstrated the great variability on timing and magnitude of the primary production in the western Irish Sea. Observations of the spring bloom starting as early as March and as late as May were registered in consecutive years, whilst for one season no bloom was apparent at all. Moreover, Richardson *et al.* (1985) survey showed that for many

sites chlorophyll$_a$ peaks may appear intermittently throughout the period of stratification. Fluctuations in the plankton production of the Irish Sea, and the general low productivity, compared to other shelf sea areas, are usually explained by the variable, but generally high, cloud cover over the region.

The zooplankton cycle in the western Irish Sea follows the classical pattern found in shelf sea areas of temperate zones. The study by Gowen *et al.* (1998) carried out for the central region, showed spring and autumn peaks in primary production, associated with stratification, and a lag, of two to four weeks, between the timing of the spring bloom and the increase in copepod abundance. Zooplankton surveys by Scrope-Howe and Jones (1985) evidenced some differences in amplitude and timing of the seasonal zooplankton cycle for the stratified and isothermal areas of the western Irish Sea. The stratified region contained the highest zooplankton production, which occurred mainly above the thermocline, with an abundance maxima earlier in the year in April-May. The mixed isothermal waters, east of the stratified region, supported a lower density of total zooplankton and the maximum occurred at least one month later than in the stratified region. Tidally mixed areas because warming of the surface waters is delayed, due to lack of stratification, usually show a slower zooplankton growth which often does not peak until early summer. Although the thermal stratification in the Irish coastal waters has been observed to be weak throughout the season, because this region is very shallow and the tides relatively weak, warming up of the water column occurs earlier than in the mixed waters to the east of the stratified region, a deeper area with stronger tidal currents. Therefore, zooplankton peak abundances are likely to occur earlier in the western coastal region, than in the isothermal waters of the eastern area. Copepod abundances observed in early May by Burkart *et al.* (1995) along a transect from Dundalk Bay to North Wales, revealed higher concentrations in the western coastal region followed by the central stratified area and then the mixed waters to the east. Mean abundances in the coastal region, were roughly two times larger than in the central area and six times greater than in the eastern region.

A final important point to emphasise about the hydrodynamics of the western Irish Sea which may be crucial for the plankton production and distribution in the area, is the stability and coherence of the seasonal gyre. Repeated observations in the region during spring-summer showed the coherence and stability of the system. The depth of the pycnocline, remained

fairly stable throughout the season and the gradients of density at the bottom, once established, changed little. For this reason, the gyre arises as a very stable and persistent system, until the breakdown of the stratification of the water column in late summer. The erosion of the cold pool of water, in 1995, was noted to occur during October. By the 31 of October the water column was vertically mixed at all the stations sampled (Horsburgh *et al.*, submitted).

The existence of the western Irish Sea gyre may be of particular importance in providing a mechanism for retention of *Nephrops norvegicus* larvae in the area above the mud patch, where the postlarvae must settle in order to survive. Although the gyre starts to develop in early spring, in April, it is not until July-August that it attains its maximum strength. By then, as it will be shown in the next chapter, the larval season of the Norway lobster, which usually reaches its peak during the month of May, is virtually over. It seems then, that at the time the planktonic larvae are present in the water column the gyre is not completely developed and therefore retention over the area may not be so effective (larval distribution and its relationship with the local hydrography is the subject of the next chapter).

Chapter V. Spatial and seasonal distribution of *Nephrops norvegicus* larvae

1. Introduction

Nephrops norvegicus, commonly known as Norway lobster, is a benthic species widely distributed over much of the continental shelf of the northeastern Atlantic Ocean. Its life cycle comprises a planktonic larval phase, which lasts approximately 45 to 50 days, followed by settlement onto muddy substrata where the adults construct burrows. Because of the burrowing requirement the species is confined to regions where suitable sea bed sediments are available.

In the Irish Sea there are two areas with muddy substrata, a small region off the Cumbrian coast of northeast England and a much larger area in the western Irish Sea (figure 2.1, chapter II). These patches, both support *N. norvegicus* populations which are targeted by intense fishing activity.

Since the the muddy areas are surrounded by none suitable settling sediments the species is presented with a serious constraint: the planktonic larvae must remain (or return) over the parental ground in order to guarantee successful recruitment into the benthic habitat and assure the survival of the population.

In the western Irish Sea, the mud patch region is also an area of weak tidal energy where thermal stratification of the water column occurs every year, during the spring-summer period. Due to the local topography and water column stratification a seasonal, density-driven, gyre develops in the region. The presence of this circulation feature coincides with most of the larval season of *N. norvegicus*, and may therefore confer a mechanism for retention of the larvae in the area.

In this chapter, the hypothesis that the seasonal gyre may provide a retention mechanism for *N. norvegicus* larvae over the mud patch region is investigated. Although the idea has been advanced in previous studies (Hill *et al.*, 1994; Hill *et al.*, 1996) the data available were

limited. More importantly, previous to this study no set of observations included contemporaneous information on the larval distribution and hydrography of the region.

The data presented here include a large set of observations on the larval distribution collected during the period from 1982 to 1996 (including 4 surveys carried out as part of this study). The 1995 season was particularly important because 13 surveys were carried out from February until June in this year. Oceanographic observations were gathered during several cruises undertaken during this project, in 1994, 1995 and 1996 (chapter IV).

2. Larval distribution during the 1995 season

2. 1. Methodology

2.1.1. Sampling

Plankton samples were collected by operating standard double oblique hauls with a HSTN sampler as described in chapter II. The data presented in this section was collected during the spring-summer period of 1995 in the western and eastern Irish Sea. A total of 13 plankton surveys were carried out covering both areas comprehensively over the entire hatching season. The cruise dates, gear used and extent of the sampling programme are listed in table 3.1 (chapter III). The cruise code references presented in this table are maintained throughout this text. Twelve of the thirteen surveys were undertaken as part of a project to assess the spawning stock biomass of several fish species in the area. Identification of *Nephrops norvegicus* larvae was also carried out and that information was subsequentely made available via CEFAS. Survey Corystes 5b/95 was included in the SOS/CEFAS research programme, of which the present work is part, to study the western Irish Sea seasonal gyre and its influence on the distribution of *N. norvegicus* larvae. During this cruise, extensive hydrographic observations were made together with the zooplankton sampling (see chapter IV). Oceanographic data from the fish egg and larvae surveys was limited to the information collected by the Guildline CTD probe aboard the plankton sampler. This source of data was not always available due to the unreliability of the instrument. Other hydrographic data (presented in chapter IV) was collected in 1995 during the SOS/CEFAS project.

2.1.2. Data processing and analysis

Estimates of concentration of plankters from surface-bottom-surface oblique hauls, are average values for the whole water column assuming that the zooplankton are evenly distributed with depth. However, as it will be shown in chapter VI, *N. norvegicus* larvae are concentrated in the top 40 m of the water column and therefore concentrations relative to the volume of water filtered would be underestimated in sampling sites where the water column is much deeper. Thus, in order to describe the spatial distribution of each zoeal stage (I,II,III),

and total larvae, for each survey the abundances are plotted as absolute numbers. The sampling site positions are presented at the mid point of each v shaped haul.

In order to calculate abundances for the whole area and estimate daily productions, for each cruise date, and the seasonal production, the numbers of each stage per haul were converted to numbers per square metre of sea surface using the flowmeter readings and the depth data for each tow.

The survey areas (western and eastern Irish Sea) were divided into a grid of rectangles (1/4° latitude x 1/2° longitude; approximately 15x18 nautical miles) and the arithmetic mean of observed number of larvae per metre square within each box, was multiplied by the unit's area to calculate total abundance of each stage within each grid rectangle. The western basin area was bounded between 53° N and 54.5° N and 6.5° W and 5° W, covering the entire western Irish Sea. The eastern Irish Sea region was limited between 53.75° N and 54.75° N and 4.5° W and 3.0° W, including the whole area where plankton sampling was carried out (see figure 5.1). The dimensions of the elements of the grid were selected in order to have a comparable number of sampling stations per unit, in most cases 2 to 3 sampling stations fell in each box. This method of assessing the abundances for the study regions was compared to a similar approach using the areas from contour plots and the results obtained were identical. The first technique was preferred due to the simplicity of its calculations and because the data in this format was also used for other analyses.

For each unit of the grid, daily larval production at the time of each survey was calculated by dividing the abundances by the larval stage duration at that time, estimated from regressions of development time against temperature derived by Nichols *et al.* (1987):

Stage I: $\ln(\text{days}) = 4.02 - 0.14(t^{\circ}C)$

Stage II: $\ln(\text{days}) = 4.22 - 0.16(t^{\circ}C)$

Stage III: $\ln(\text{days}) = 3.53 - 0.07(t^{\circ}C)$

The sea temperature values were determined from the vertical integrated temperature readings from the Guildline CTD probe, for each haul and averaged for each grid rectangle. The daily production figures for each unit and larval stage were summed and plotted against time, at the

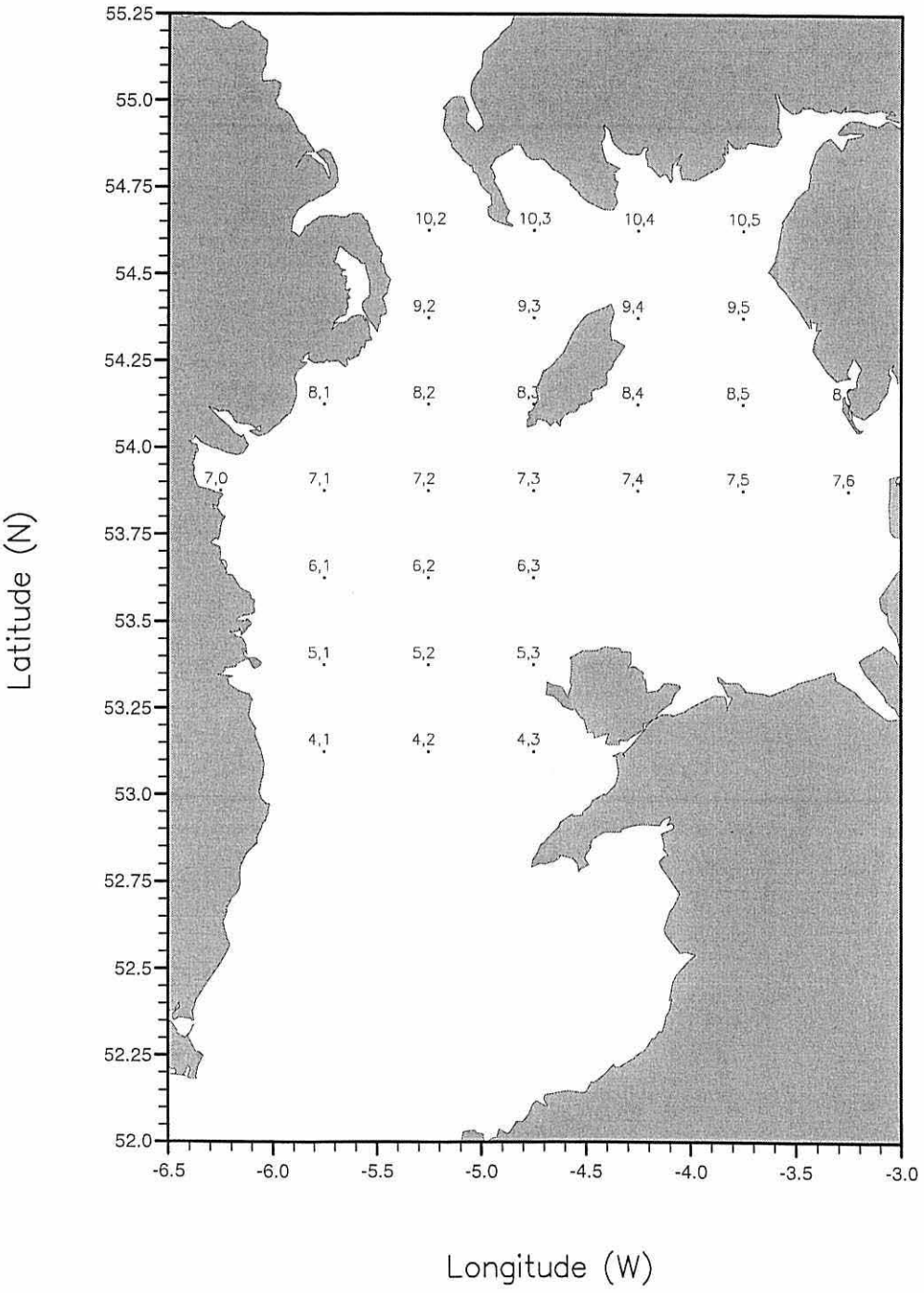


Figure 5.1. Grid units, each box is a 1/4 degree in latitude per 1/2 degree in longitude; the centre point for each unit is denoted by a row and column reference.

mid point of each survey, to produce a seasonal production curve. The area beneath each of these seasonal curves was measured, by calculating the area of the trapezia beneath each segment of the curve, to give estimates of total numbers produced in each stage during the hatching season. The numbers produced for each stage were used to compute the total losses occurring between each stage and also to compute the intercept value of the mortality regression at zero time. Using the total stage production, the instantaneous coefficient of larval mortality per day (Z) was calculated for each stage from the equation:

$$N_t / N_0 = e^{-Zt},$$

where N_0 is the initial numbers of larvae and N_t the numbers surviving to the next stage in the period t days, the mean stage duration for the season, calculated applying Nichols *et al.* (1987) equations with a mean sea temperature value calculated for the season.

The numbers of stage I zoea calculated by the survival curve (intercept at time zero) and from the seasonal production curve, were utilised to predict the spawning stock size using fecundity estimations presented by Nichols *et al.* (1987). The mean effective fecundity for the species in the western Irish Sea is thought to be in the range from 578 to 889 viable eggs per female.

In order to examine the extent to which environmental data is related to ("explains") the observed distribution of *N. norvegicus* larvae in the western Irish Sea, information from selected cruises was analysed. The surveys (Cruise 8, Cruise 11, Corystes 5b, Cruise 14 and Prince Madog 1) were chosen because of the availability of environmental data and in order to cover different periods of the larval season. The approach adopted was firstly to analyse the biotic data (larvae abundance) and then assess how well the information on environmental variables (sediment type, site depth, surface water temperature, bottom water temperature and potential energy anomaly), as a whole, matched the distribution patterns.

This sequential procedure, has been strongly supported in recent studies (*eg.* Clarke & Ainsworth, 1993; Clarke & Warwick, 1994; Somerfield *et al.*, 1995) and has the advantage over more complex techniques, such as Canonical Correlation, and variants of Correspondence Analysis (which by embedding the biotic and abiotic data at an early stage

influence their individual representations), of allowing an easier interpretation of the results. The link between the final picture and the original data is relatively transparent and easier to explain (Clarke & Ainsworth, 1993).

The data used to perform the analyses was in the gridded format referred to earlier in this section. Each sample, at this stage, representing a rectangle unit of the grid for which the arithmetic mean of the different variables had been calculated, using the original sampling sites observations (figure 5.1). This approach allowed the analysis of biotic and abiotic data in a similar frame otherwise unworkable due to the nature of planktonic and physical variables observations and the way they have to be sampled. Moreover, by reducing the number of samples under analysis, the interpretation of the results becomes less complex. On the other hand, variance between samples within each grid unit may preclude an accurate analysis and some of the detail provided by a larger set of data is lost in this way.

Differences in larval abundance ($\sqrt{x+0.5}$ transformed), of the three zoeal stages, between sites (1.over the stratified, mud patch (gyre) region; 2. outside 1) and the possible distinct distribution of the stages in these sites was investigated by analysis of variance (2 factors ANOVA: Site, Stage and Site x Stage). The observations were tested for homogeneity of variances and normality (Sokal & Rolf, 1995; Fry, 1996). The analyses were performed using the General Linear Model (GLM) routine of the statistics package Minitab.

The environmental information was analysed by Principal Component Analysis (PCA) which is an effective ordination technique for abiotic data. Abiotic variables, are usually relatively few in number, are generally continuously scaled, zeros do not predominate and their distribution can be transformed to approximate normality. Hence, standard correlation coefficients and Euclidean distances are appropriate ways of describing their inter relationships and PCA an effective way of ordinating the data (Clarke & Warwick, 1994). In PCA ordination plots, the samples are mapped in (two or more dimensions) in such a way that the distances between pairs of samples reflect their relative dissimilarity of composition of variables.

The PCA was performed on normalised Euclidean distance (dissimilarity) matrices because the variables have different units of measurement and need normalising to a common scale

(correlation rather than covariance matrices should be used on such data). In order to approximate normality, transformation should be applied to the variables according to necessity. In the present case, variables were log transformed with the exception of depth and sediment type. PCA analyses and ANOSIM tests were carried out using the Statistics package Primer.

To establish differences between sites selected *a priori* (1. central, summer stratified region over the mud patch; 2. region outside 1) ANOSIM (Clarke & Warwick, 1994) tests were carried out on the environmental data. These non-parametric tests were performed on the (ranked) normalised Euclidean distance (dissimilarity) matrices. This test uses the statistic:

$$R = (\bar{r}_b - \bar{r}_w) / (M/2),$$

where $\bar{r}_w$ is defined as the average of all rank similarities (dissimilarities) among replicates within sites, $\bar{r}_b$ is the average of rank similarities (dissimilarities) arising from all pairs of replicates between different sites and $M = n(n-1)/2$; n is the total number of samples considered.

In order to assess the relationship, if any, between the larvae distribution and the environmental variables observed, abundances were superimposed on the environmental ordination plots. Moreover, in an attempt to correlate the biotic and abiotic variables a linear regression, of log transformed larval abundances against the PC axis scores of the environmental PCA, was carried out (Clarke & Warwick, 1994).

2.2. Results

2.2.1. Larval distribution

Figures 5.2 to 5.11 show the spatial distribution of *Nephrops norvegicus* larvae during the surveys undertaken in 1995, from the begining of March throughout to mid June, when the entire western and eastern Irish Sea regions were sampled comprehensively. In the western basin, the muddy substratum extends from 53.3° N to 54.5° N and between longitude 4.8° W and 6.0° W. In the eastern Irish Sea a small patch is present off the Cumbrian coast, between the Solway Firth and Morecambe Bay, approximately between 3.5° W and 4.0° W (see figure 2.1 in chapter II). These isolated areas provide a suitable habitat for the Norway lobster when it becomes benthic and it can therefore be expected that the larval production will occur over these regions.

During the first and second surveys, cruises 2 (11-19 February) and 3 (21-27 February) no larvae were collected (see table 5.1). Stage I zoea started to appear in early March, during Cruise 5 (8-14 March, figure 5.2a). At this early stage in the season larvae were found in only 3 of the sampling sites visited and in very small numbers. The few stage I larvae collected occurred in the central western Irish Sea. No larvae were caught in the eastern Irish Sea. During the following survey (Cruise 6, 15-22 March, figure 5.2b) the numbers of stage I zoea increased slightly and they were present over a wider region in the western Irish Sea. Although in small numbers the concentration of the planktonic lobsters, at this period, seemed to be confined to the regions on the border of the mud patch, in the shallow waters off Dundalk Bay and on the southwestern limit of the muddy area, just north of Dublin Bay and to the west of line 5.6° W. Some individuals also appeared in the stations southwest of the Isle of Man on the eastern edge of the adults ground. In the eastern Irish Sea, stage I larvae were collected in the area over the Saints Bees Head mud patch. It is also worth noting the presence of some individuals in an area southeast of the Isle of Man, between the western and eastern mud patches, at approximately 53.8° N to 53.9° N and 4.1° W to 4.4° W.

By the end of March beginning of April (Cruise 8, 30 March-6 April, figure 5.3), the numbers of stage I larvae collected, increased substantially and were found all over the western Irish Sea basin. Higher concentrations were now apparent in the inshore waters (west

of 5.7° W), from Dundalk Bay to south of Dublin, on the limit of the sampling area (53.1° N). Although the mud patch extends nearly to the entrance of the North Channel very few larvae were collected north of the parallel 54.1° N. In the western Irish Sea, stage II zoea were observed approximately 22 days after the first stage I larvae were collected. These stage II larvae occurred in two sites in the most inshore region between Dundalk Bay and Skerries, north of Dublin Bay. In the eastern basin, the numbers of zoea I increased slightly and spread across the region between the Isle of Man and the Cumbrian shores. Some stage I lobsters were also caught south of the Isle of Man between 53.8° N and 53.9° N. At this stage in the season, the larval populations from the western and eastern basins appeared to be almost linked, with some individuals, although in very small numbers, found in the area between the two regions.

Figure 5.4 shows the larval abundances during Cruise 9+10 (10-21 April). The pattern of distribution of stage I zoea remained similar to that observed during the previous survey, with the majority of the larvae occurring in the southwestern area of the western Irish Sea. Although the higher numbers were still found in the waters close to the Irish coast, during the period of this survey more larvae were collected in the centre of the basin than before. This fact is particularly evident in the distribution of stage II zoea. Nevertheless the higher concentration of stage II larvae was present in the coastal waters off Dundrum Bay. During this cruise, no larvae were collected in the region south of the Isle of Man between the western and eastern basins of the Irish Sea. In the eastern side, stage I lobsters were caught in very small numbers, suggesting that hatching in this area had declined. Stage II larvae appeared over the Cumbrian mud area, approximately 25 days after the first stage I zoea were observed in the region.

In mid-late April (Cruise 11, 18-25 April, figure 5.5) the concentration of lobster larvae continued to increase, more stage I zoea were found in the central western Irish Sea but the higher abundances were still observed in the inshore waters southwest of the adults grounds, particularly in the region between Skerries and Dublin Bay. The larval distribution also extended to the area north of the parallel 54.1° N, up to the entrance of the North Channel. Stage II zoea appeared dispersed over the western basin but the higher numbers seemed to have drifted southwards to the same region were most stage I larvae were collected. The first stage III larvae were noted, in the same area, between latitude 53.1° N and 53.6° N and west

of 5.5° W , approximately 40 days after the hatching season had started and 20 days after the first stage II zoea were collected in the western Irish Sea. No larvae were observed south of the Isle of Man in the area between the western and eastern basins. In the eastern Irish Sea, the numbers of stage I larvae increased after the decline observed during the previous survey. The majority of the planktonic lobsters were then found slightly further offshore than before, in an area west (3.8° W to 4.1° W) of the Cumbrian coast mud patch.

During survey Cruise 12 (30 April-7 May, figure 5.6) the lobster larvae were fairly well distributed over the whole mud patch area in the western basin. Concentration of larvae over the central deeper area was at this point clearly evident. Numbers in the northern most region had also increased and at the same time the distribution still included the southern most area sampled. Stage III zoea were still scarce but were now dispersed over the central western Irish Sea. In the eastern basin, stage I larvae were found all over the region between the Isle of Man and the English coast and also north of the Isle of Man up to the entrance of the Solway Firth. Zoea stage III were first observed in the eastern Irish Sea during this survey, approximately 45 days after the first stage I were collected and 20 days after the appearance of stage II larvae was recorded.

Peak abundances of *N. norvegicus* larvae, in total, were recorded during Cruise 13 (14-20 May, figure 5.7). During this survey, 1516 larvae (221 larvae/m^2) of which 976 zoea II (142.4 larvae/m^2) were collected in only one sample (53.38° N, 5.88° W). At the same sampling site (just off the northern edge of Dublin Bay), the highest concentration of stage III larvae was found 360 (52.5 larvae/m^2). The largest number of stage I zoea (360, 40.5 larvae/m^2) was recorded off Dundalk Bay (53.88° N, 6.12° W). The abundance of lobster larvae during the period of this cruise was generally high over the entire Irish Sea but numbers of stage II larvae exceeded the numbers of stage I zoea indicating that the peak of hatching had probably occurred sometime between the previous survey and this one (7 and 14 May). In addition to the significant increase in the numbers of stage II larvae, stage III zoea appeared also in much large numbers then before. The spatial distribution pattern was generally similar to what had been observed before, with high abundances all over the western Irish Sea but with a tendency for the sites on the edges of the mud patch, specially in the southwestern flank, to present the largest amount of larvae. A considerable number of larvae was also observed south of the Isle of Man (53.6° N-53.9° N) on the eastern side of the mud patch. It is also

interesting to note the occurrence of larvae in nearly all sampling stations along the southern most sampling line, from Dublin Bay to Anglesey. In the eastern Irish Sea, *N. norvegicus* larvae were observed all over the region between the Isle of Man and the English coast and north of the Isle of Man towards the Scottish shores and as far south as Morecambe Bay.

During Corystes 5b (15-20 May, figure 5.8) survey, undertaken during the same period as Cruise 13 the number of lobsters collected was much lower highlighting the great variability involved in plankton sampling. The higher number of larvae was collected off Dublin Bay (53.38° N, 5.62° W) a total of 88 larvae/m^2 (586 individuals). Despite less larvae were collected during this survey than during Cruise 13, the pattern of distribution was identical, with larvae all over the western Irish Sea but higher concentrations on the southwestern region of the mud patch. The abundance of stage II larvae was greater than the abundance of zoea stage I as it was observed during Cruise 13. An important aspect of this survey was that the southern limit of the sampling grid was extended to latitude 52.6° N and it was therefore possible to assess the southern limit of the larval distribution. Stage I zoea were collected along the transect at latitude 53.1° N but not any further south. Stages II and III were observed all through to the parallel 52.9° N. Along this line and the one immediately north, larvae were observed across all the region from Ireland to the Welsh shores, suggesting that advection of the planktonic stages to the south, is not confined to the region along the Irish coast. Moreover, a small spot of muddy substrate has been mapped in a region southwest of Anglesey over which some lobster larvae were caught. On the sampling line furthest south, roughly along 52.6° N, no lobster larvae were collected.

By the last quarter of May (Cruise 14, 23-28 May, figure 5.9) the abundances of stages I and II zoea had decreased significantly and the peak of stage III larvae was then clear. Stages II and III larvae spread as far south as 53.1° N but the majority of zoea I were then found in the central western Irish Sea. In general, more larvae were observed over the deeper central region than in the inshore waters off Ireland. A considerable number of individuals were collected at a site (53.13° N, 5.12° W) half way from Ireland and the southern opening of the Menai Strait on the Welsh coast. The occurrence of significant numbers of larvae at that particular station had also been observed during Corystes 5b survey. In the eastern Irish Sea, the numbers of stage I larvae were still higher than stages II or III and fairly concentrated

over the small muddy area off Saint Bees Head. Stages II and III appeared more spread to the south and west of the mud patch.

Cruise 15 (5-14 June, figure 5.10) was the last survey in the season to include the eastern Irish Sea but no sampling was done west of longitude 5.5° W therefore only covering part of the western basin. Stage I larvae were no longer observed during this sampling period suggesting that the hatching season was probably over. In general the abundance of larvae was very low. Lobster larvae stage II and III were caught in very small numbers and none above the eastern Irish Sea mud patch although a few individuals were still observed to the northeast of the Isle of Man. In the western basin some individuals were observed in isolated sites.

The last survey for the 1995 season (Lough Foyle 11, figure 5.11) was carried out during the period 18 to 20 of June but only covering the western Irish Sea between latitudes 53.4° N and 54.2° N. In this area an appreciable number of stage III zoea were still observed over the central region. Stage I larvae were still present indicating that although declining the hatching season was not completely over.

In summary, during the 1995 hatching season, larvae were first observed in the western Irish Sea in mid March with abundances increasing up until mid May when the peak production (total larvae) took place. From then on the numbers started to decline but by the end of the sampling period, in mid-late June, there were still some stage I larvae present indicating that the production season was not yet completed and at least later stage larvae would probably be present up until July. In the western basin a common pattern of distribution, was the high numbers found along the Irish coast and includes areas beyond the southern limit of the local mud patch. This feature was particularlly apparent during the surveys earlier in the season, first for stage I zoea and later specially for larvae stages II and III. Observations during May and June showed greater numbers of larvae over the central western Irish Sea. The occurrence of larvae in the area north of latitude 54.1° N, was noted slightly later then from there south, suggesting that hatching took place later or the first zoeae from the area on the northern limit of the mud patch, drifted south. Planktonic lobsters were observed all over the western basin from the entrance of the North Channel to as far south as 52.9° N, well outside the limit of the adults ground. It also seemed evident that some individuals drifted between the western and

eastern basins of the Irish Sea particularly along the south of the Isle of Man but also north of this island. In the eastern Irish Sea the production season seemed to have started slightly later and ended a little earlier. The abundance of larvae over the eastern muddy region was more irregular spatially and in time with a decline in production observed during early May after it had peaked in late April, earlier than on the western basin. This finding should nevertheless be read with caution because it may just be an artificial feature derived from a patchy distribution of the larvae. On the eastern basin, larvae were collected from the Scottish coast down to latitude 53.8° N, south of Morecambe Bay.

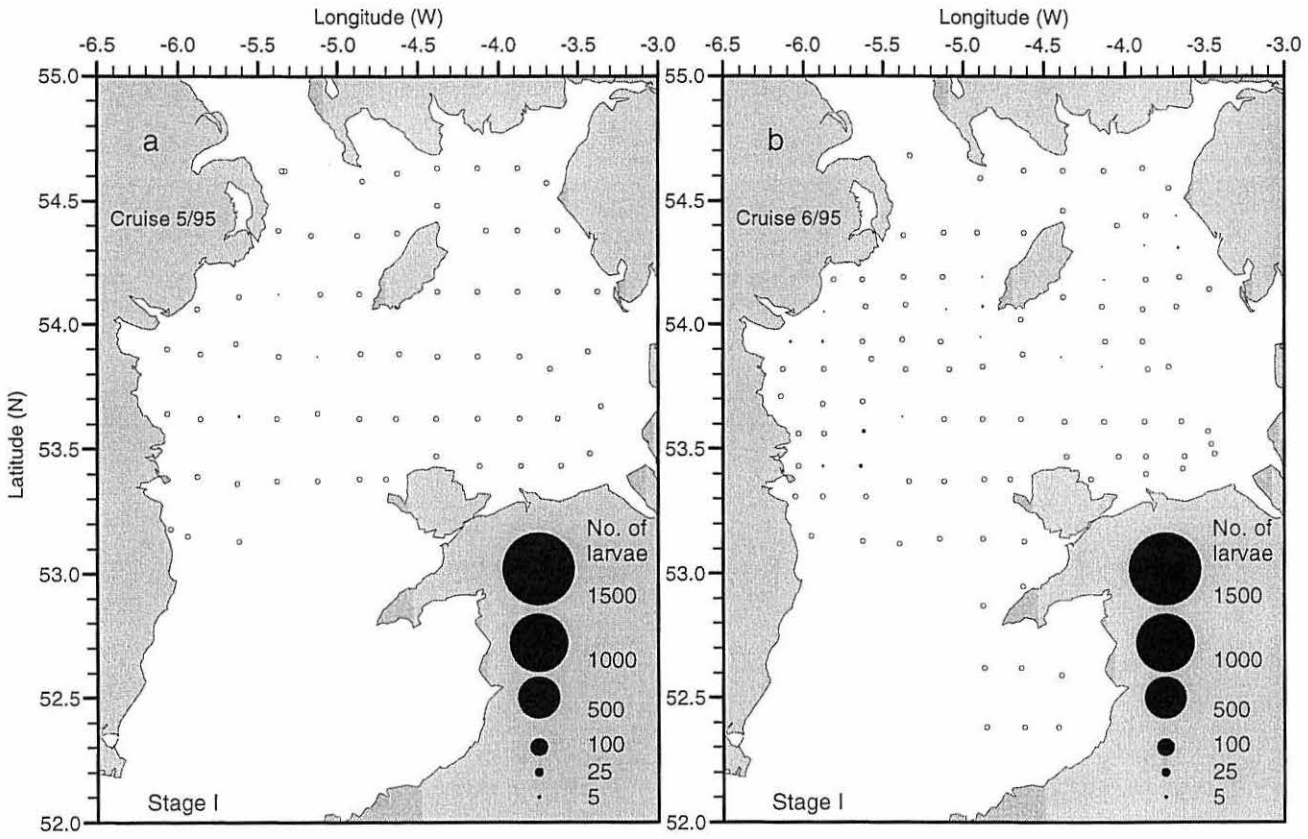


Figure 5.2. Number of *N. norvegicus* larvae from surveys (a) Cruise 5/95, 8-14 March 1995, (b) Cruise 6/95, 15-22 March 1995. Open circles denote sampling sites where no larvae were observed.

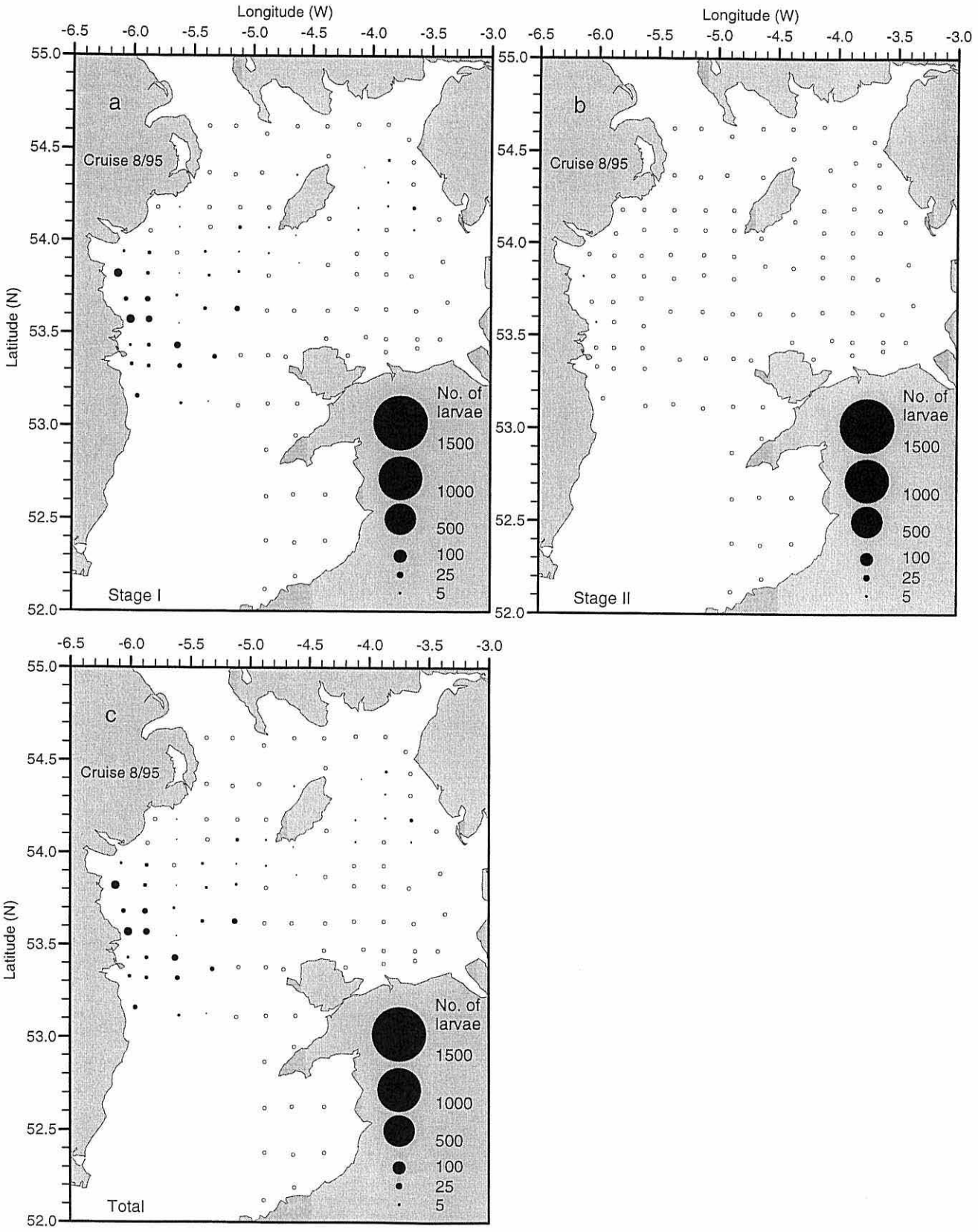


Figure 5.3. Number of *N. norvegicus* larvae per developmental stage from survey Cruise 8/95, 30 March-6 April 1995. (a) stage I, (b) stage II, (c) total. Open circles denote sampling sites where no larvae were observed.

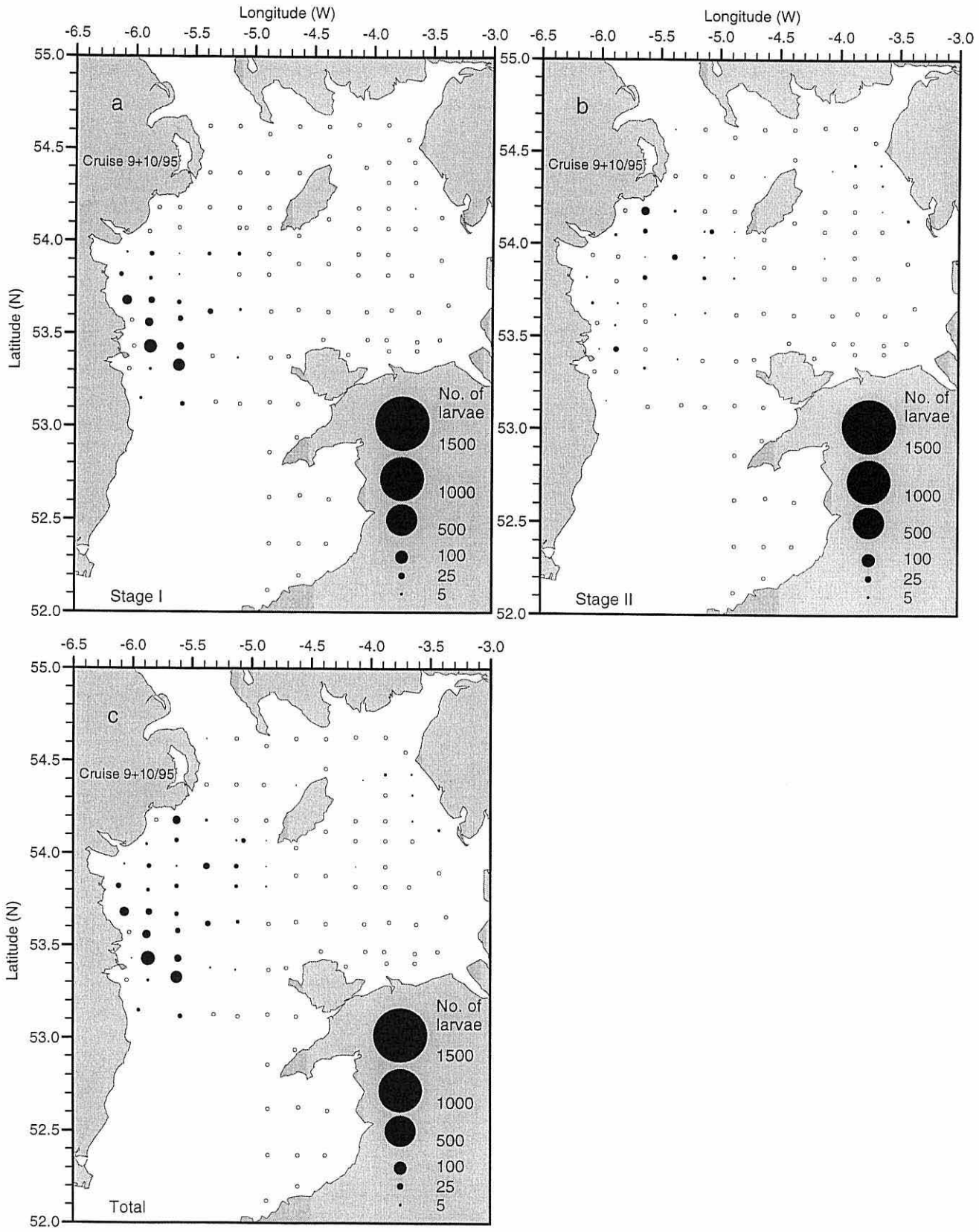


Figure 5.4. Number of *N. norvegicus* larvae per developmental stage from survey Cruise 9+10/95, 10-21 April 1995. (a) stage I, (b) stage II, (c) total. Open circles denote sampling sites where no larvae were observed.

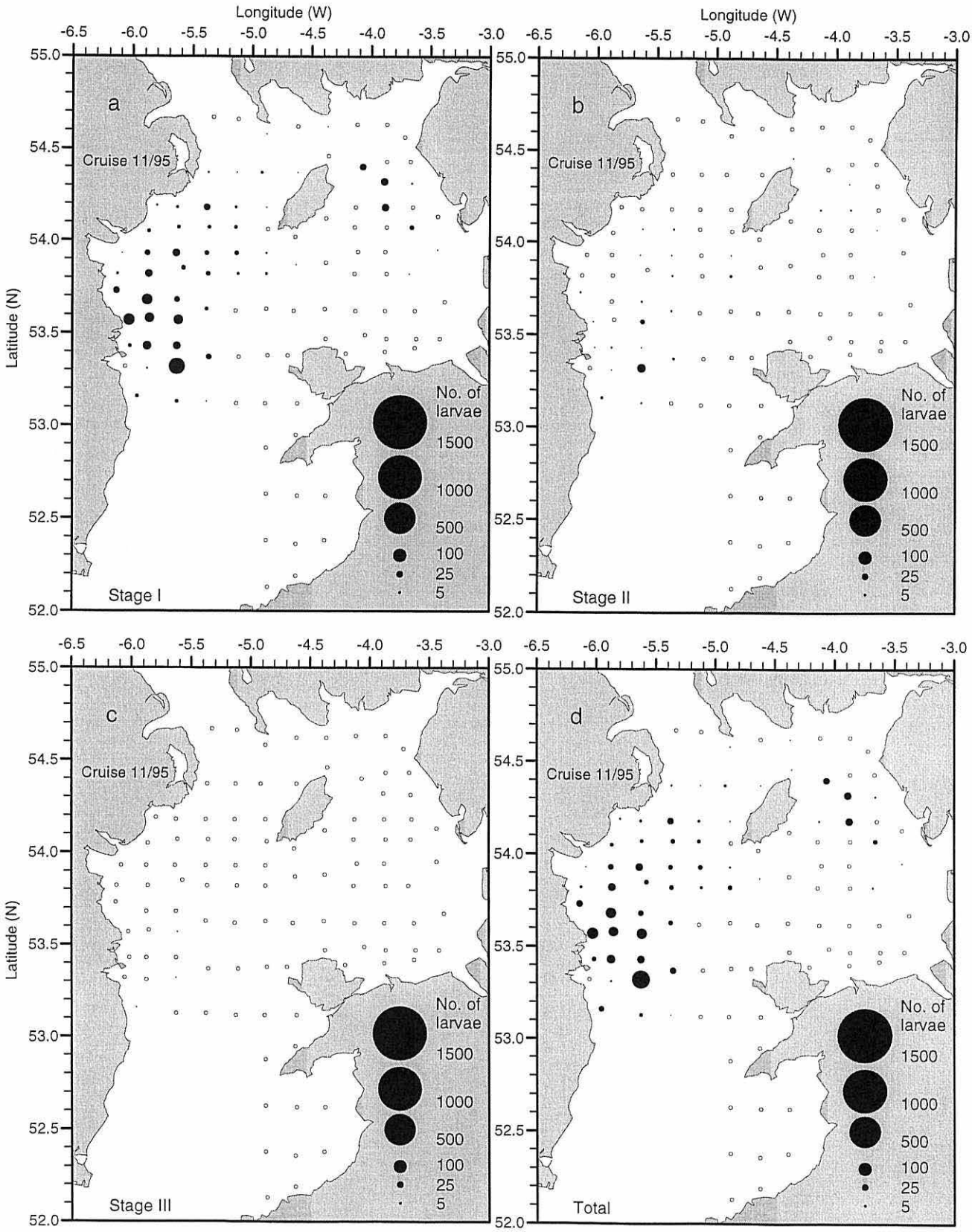


Figure 5.5. Number of *N. norvegicus* larvae per developmental stage from survey Cruise 11/95, 18-25 April 1995. (a) stage I, (b) stage II, (c) stage III, (d) total. Open circles denote sampling sites where no larvae were observed.

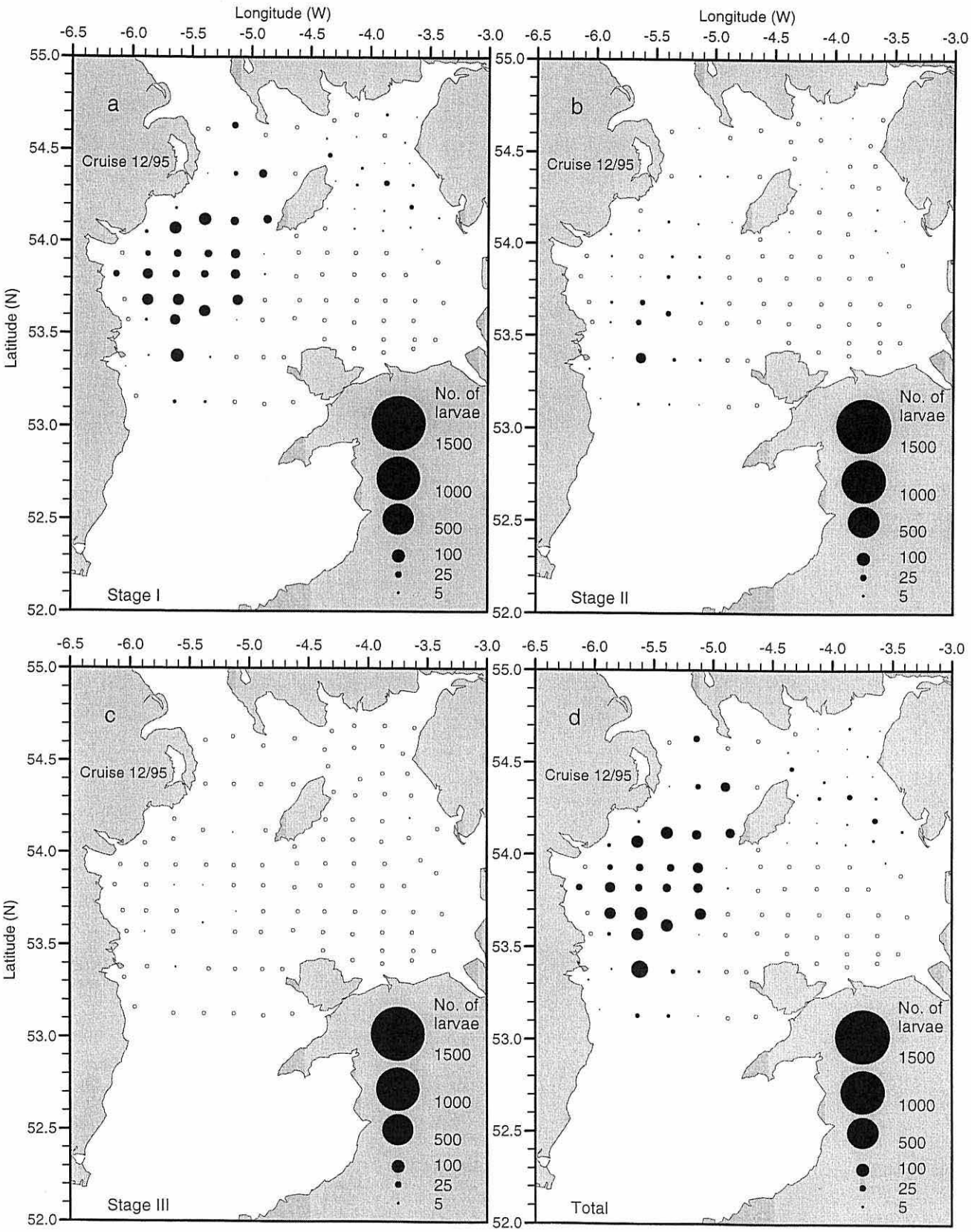


Figure 5.6. Number of *N. norvegicus* larvae per developmental stage from survey Cruise 12/95, 30 April-7 May 1995. (a) stage I, (b) stage II, (c) stage III, (d) total. Open circles denote sampling sites where no larvae were observed.

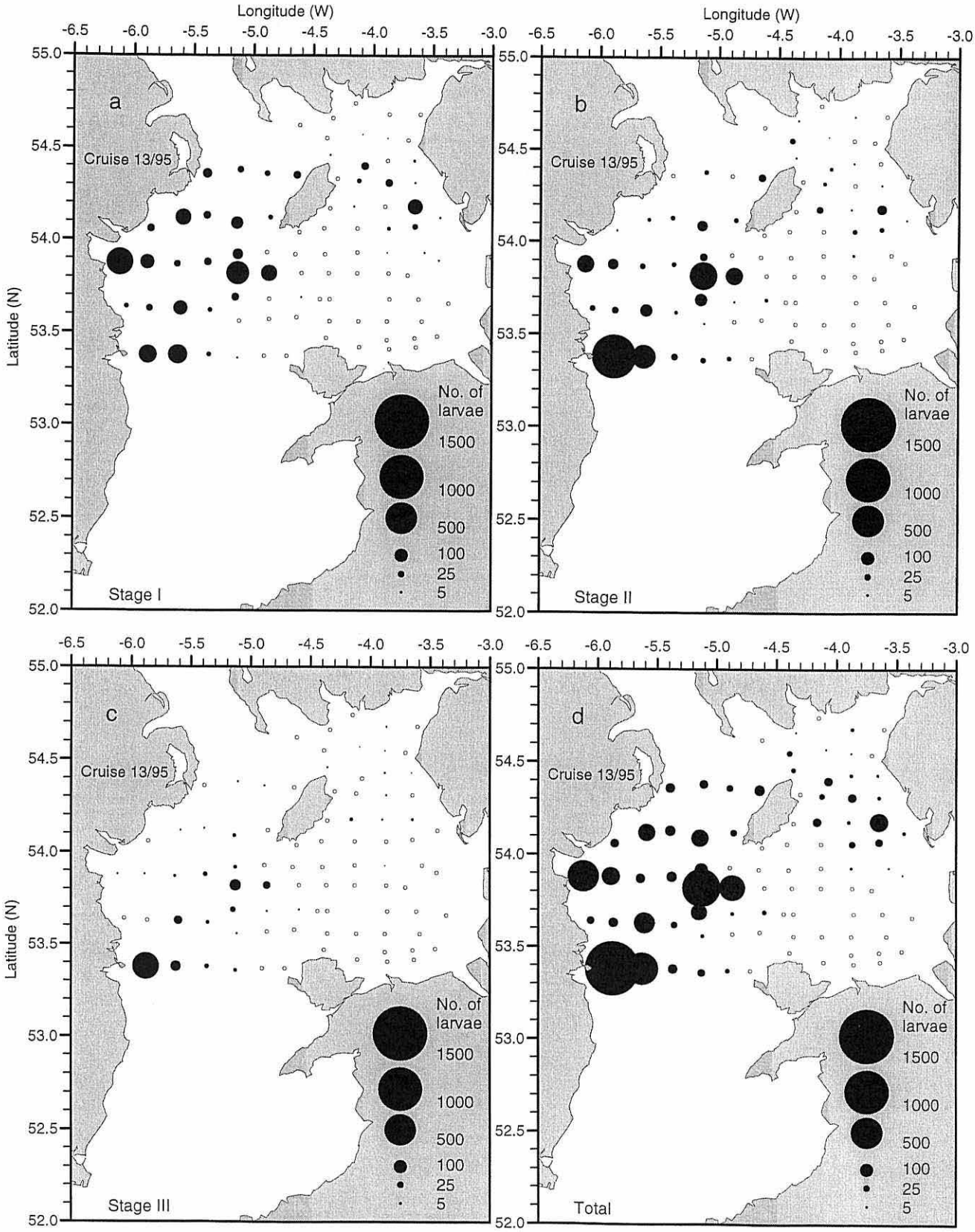


Figure 5.7. Number of *N. norvegicus* larvae per developmental stage from survey Cruise 13/95, 14-20 May 1995. (a) stage I, (b) stage II, (c) stage III, (d) total. Open circles denote sampling sites where no larvae were observed.

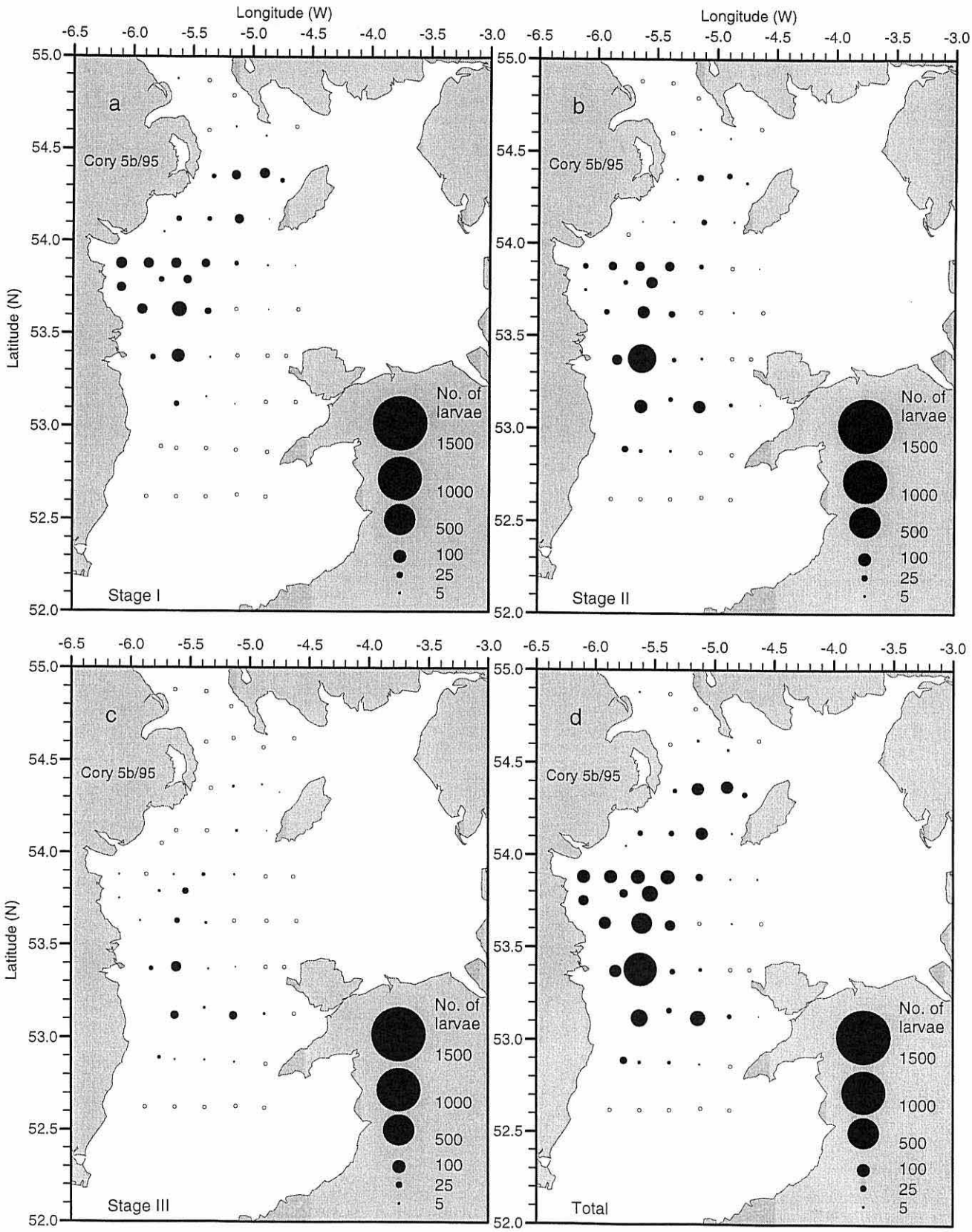


Figure 5.8. Number of *N. norvegicus* larvae per developmental stage from survey Corystes 5b/95, 15-20 May 1995. (a) stage I, (b) stage II, (c) stage III, (d) total. Open circles denote sampling sites where no larvae were observed.

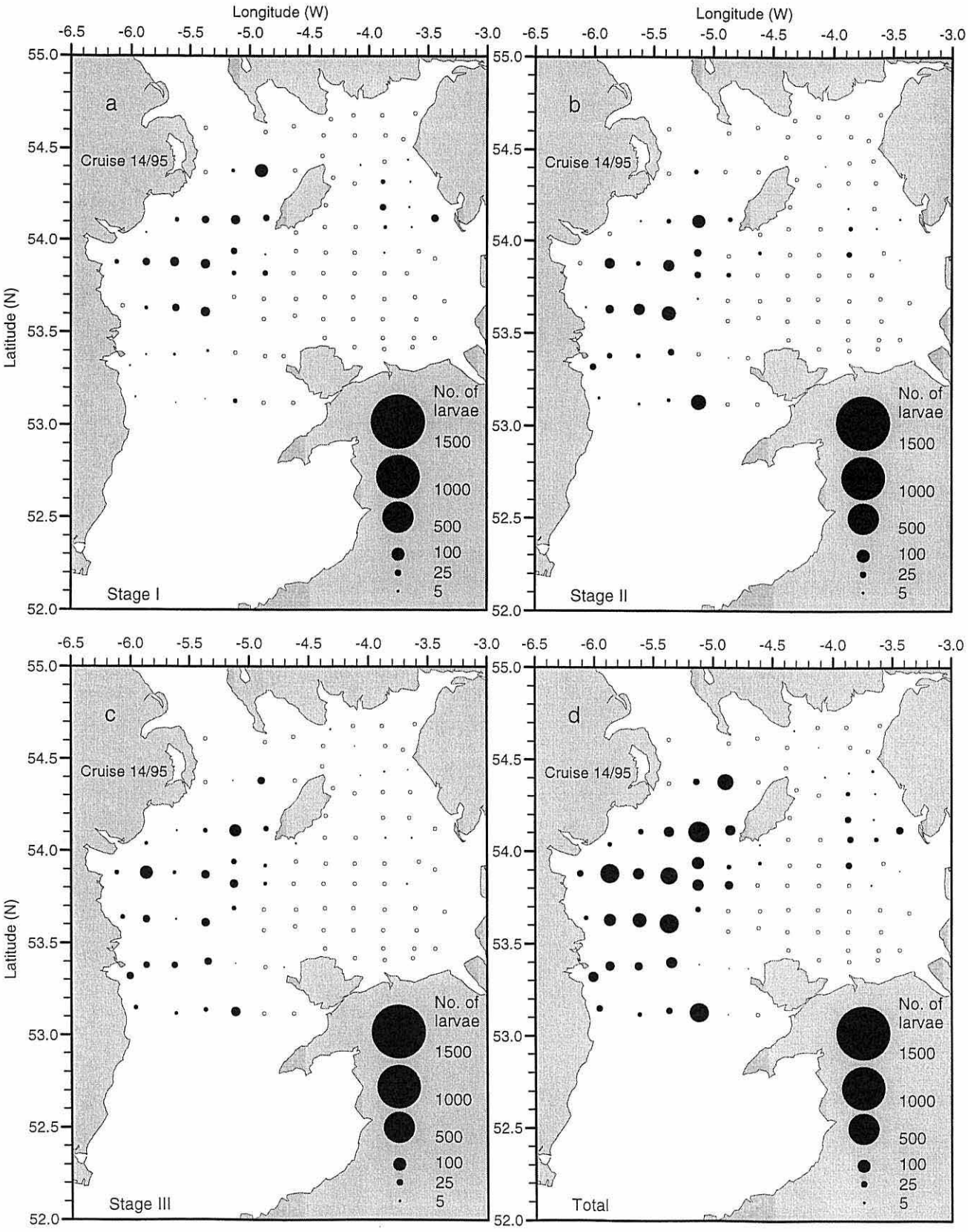


Figure 5.9. Number of *N. norvegicus* larvae per developmental stage from survey Cruise 14/95, 23-28 May 1995. (a) stage I, (b) stage II, (c) stage III, (d) total. Open circles denote sampling sites where no larvae were observed.

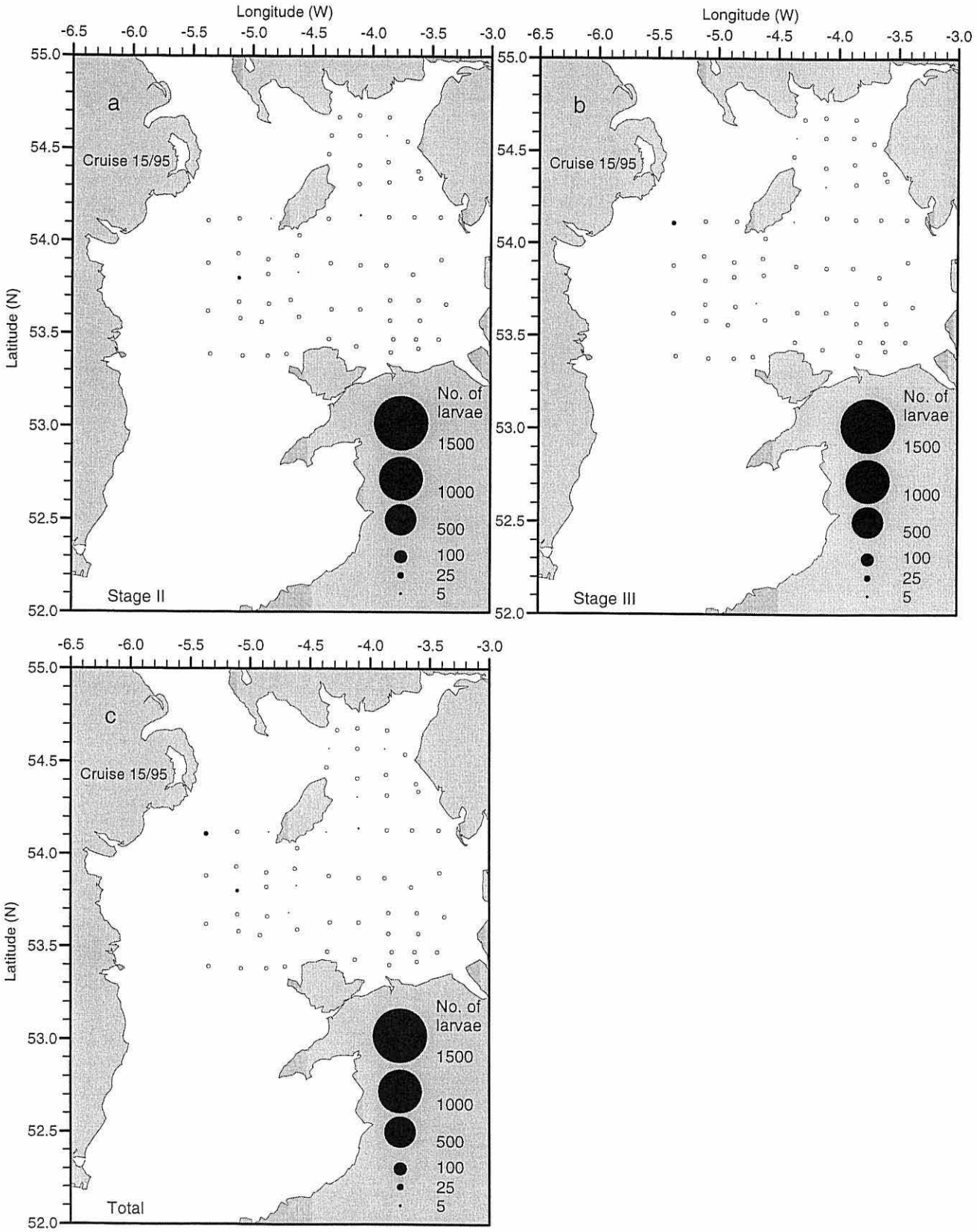


Figure 5.10. Number of *N. norvegicus* larvae per developmental stage from survey Cruise 15/95, 5-14 June 1995. (a) stage I, (b) stage II, (c) total. Open circles denote sampling sites where no larvae were observed.

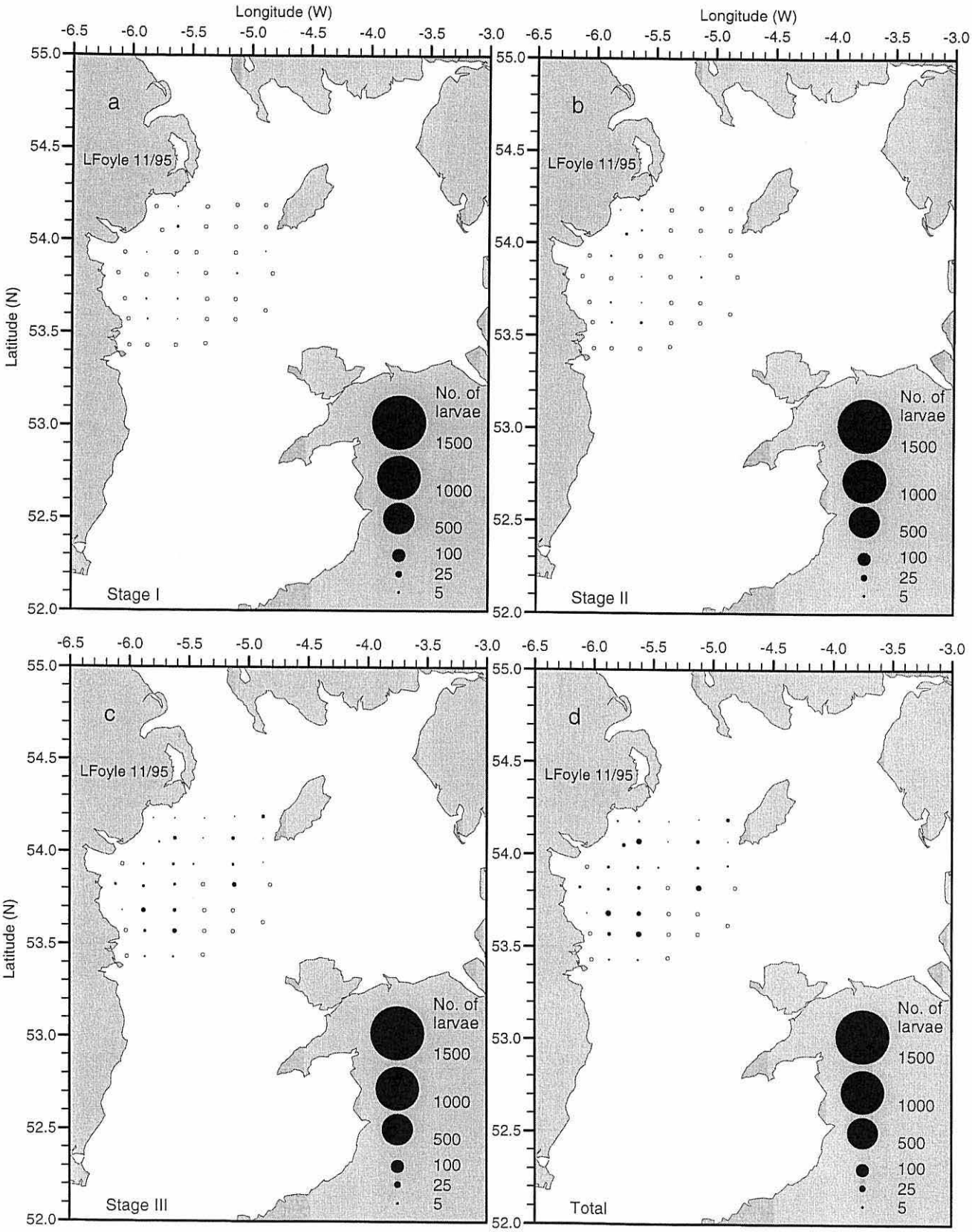


Figure 5.11. Number of *N. norvegicus* larvae per developmental stage from survey L. Foyle 11/95, 18-20 June 1995. (a) stage I, (b) stage II, (c) stage III, (d) total. Open circles denote sampling sites where no larvae were observed.

Table 5.1. Number of larvae collected during all the surveys from 1982 to 1996.

Survey reference	Date	Area	N. sts	Stage I	Stage II	Stage III	Stage IV	Total
Corella 5/82	9-13 April 82	WIS, NEIS	60	638	6	———	———	644
Clione 6/82	28 April-21 May 82	WIS, NEIS	117	4221	1380	123	———	5724
Clione 7/82	21 May-5 June 82	WIS, NEIS	160	2785	3167	2176	87	8215
Cirolana 5.1/84	25 May-1 June 84	SWIM	67	1520	2476	1271	22	5289
Cirolana 5.2/84	12-13 June 84	SWIM	14	75	202	499	20	796
Clione 5/85	15-19 April 85	WIS, NEIS	77	2765	354	3	———	3122
Clione 6/85	11-26 May 85	WIS, NEIS	166	6485	4507	1065	6	12063
P. Madog 1/85	27 May-6 June 85	WIS, NEIS	91	1678	1994	1059	2	4733
Cirolana 5/87	14-24 May 87	WIS	79	2136	345	49	———	2530
Cirolana 4/88	20 Apr-2 May 88	WIS, NEIS	165	7448	2498	442	1	10389
Cirolana 4/89	16-28 April 89	SWIM, EIS	89	1511	101	———	———	1612
Cirolana 5/92	29 Apr-3 May 92	SWIM	10	473	215	7	———	695
Cirolana 5/93	8-30 May 93	SWIM	107	1403	2136	1345	———	4884
Cirolana 5/94	29 April-3 May 94	SWIM	14	28	135	———	———	163
Corystes 7/94*+	17-30 June 94	WIS	51	13	30	55	2	99
Cruise 2/95	11-19 February 95	WIS, EIS, CB	100	———	———	———	———	———
Cruise 3/95	21-27 February 95	WIS, EIS, CB	91	———	———	———	———	———
Cruise 5/95	8-14 March 95	WIS, EIS	65	4	———	———	———	4
Cruise 6/95	15-22 March 95	WIS, EIS, CB	103	34	———	———	———	34
Cruise 8/95	30 March-6 April 95	WIS, EIS, CB	106	367	7	———	———	374
Cruise 9+10/95	10-21 April 95	WIS, EIS, CB	106	474	215	———	———	689
Cruise 11/95	18-25 April 95	WIS, EIS, CB	106	919	106	3	———	1028
Cruise 12/95	30 April-7 May 95	WIS, EIS	105	1239	224	14	———	1477
Cruise 13/95	14-20 May 95	WIS, EIS	87	2299	2750	713	———	5762
Corystes 5b/95*+	15-20 May 95	WIS	54	941	1241	291	1	2474
Cruise 14/95	23-28 May 95	WIS, EIS	94	670	874	745	1	2290
Cruise 15/95	5-14 June 95	SWIM, EIS	60	———	16	17	———	33
L. Foyle 11/95	18-20 June 95	SWIM	37	18	32	135	———	185
Cirolana 4b/96*+	13-23 April 96	WIS	59	644	158	1	———	803
Corystes 9/96*+	12-14 July 96	WIS	35	8	1	1	———	10

Legend:

WIS: Western Irish Sea
EIS: Eastern Irish Sea
NEIS: North-Eastern Irish Sea
SWIM: South-West of Isle of Man
CB: Cardigan Bay

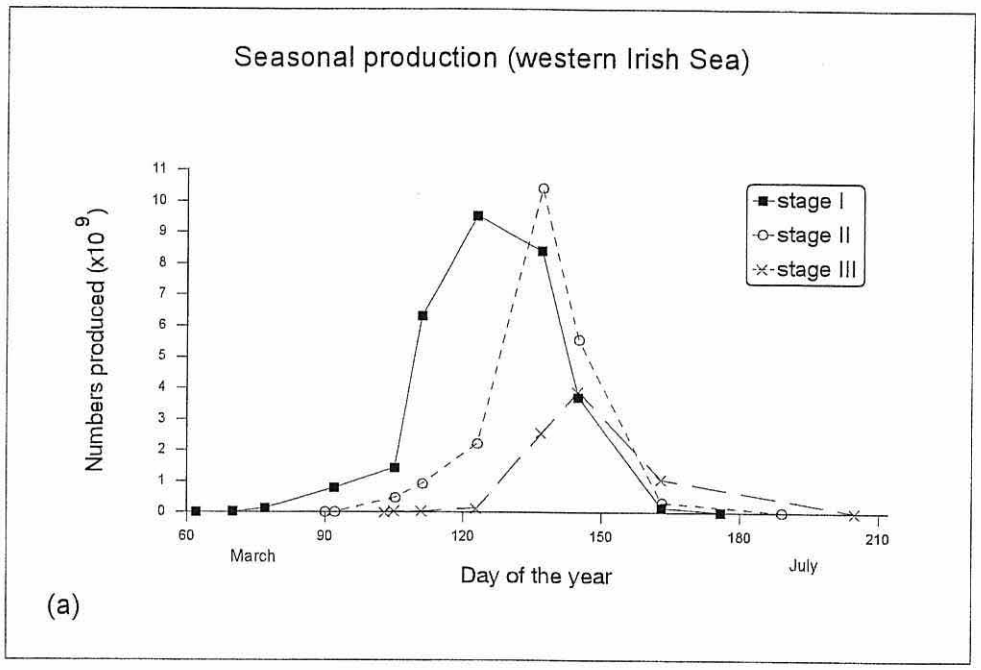
* Indicates surveys in which I participated
+ Indicates surveys during which zooplankton and environmental observations were made

2.2.2. Seasonal production and spawning stock estimate

Western Irish Sea

The temporal distribution of *N. norvegicus* larvae is best represented in figure 5.12a which shows the seasonal production curve for the three zoeal stages in the western Irish Sea. In the western basin, stage I larvae started to appear, in very small numbers, in mid March and a slow increase in production occurred until the middle of April. From then until the begining of May a sharp increase in numbers was observed. The peak of abundance of stage I zoea was observed during Cruise 12 (30 April-7 May) ($159x10^9$ zoea I, an average of 9.5 larvae/m^2) and the daily production in the area, at this time, was estimated to be $9.51x10^9$ larvae (see table 5.2). However, from the shape of the production curves for stages I and II it seems that the peak of production probably occurred between 7 and 14 of May. Between mid May and mid June the numbers of stage I zoea progressively declined and by the end of the sampling period, (20 June) the hatching season was close to its end. Stage II zoea were observed from the begining of April with a slow increase until early May. The highest density of zoea II was observed during mid May (14-20), Cruise 13+Corystes 5b ($162x10^9$ zoea II, an average of 9.7 larvae/m^2) when the daily production was estimated to be $10.4x10^9$ (table 5.2). From this date onwards the numbers declined and the end point of the production curve was estimated to occur in early-mid July. Stage III larvae were first observed in mid April and the peak of abundance occurred in late May (23-28). Abundance of stage III larvae during Cruise 14 was $68.7x10^9$ and the daily production estimated at $3.89x10^9$ larvae (~0.23 zoea III/m^2). It was predicted, according to local water temperature and related development rates and densities of the earlier stages, that some later zoeal stage of *N. norvegicus*, would be present in the western Irish Sea waters until the last quarter of July.

Calculation of the area of each production curve gave an estimate of seasonal production of stages I, II and III respectively $349.26x10^9$, $235.22x10^9$ and $113.06x10^9$ larvae (table 5.3). The percentage loss between stage I and II was therefore 32.65 and between stage II and III 51.93. Losses between stages I and III amounted to 67.63%. The daily mortality rate between zoea I and II larvae was estimated to be 2.37 %, 4.59% between stages II and III and 3.43% between stages I and III. According to the water temperatures recorded during each survey and the abundances of each stage along the season, the mean duration for stage I, stage II and stage



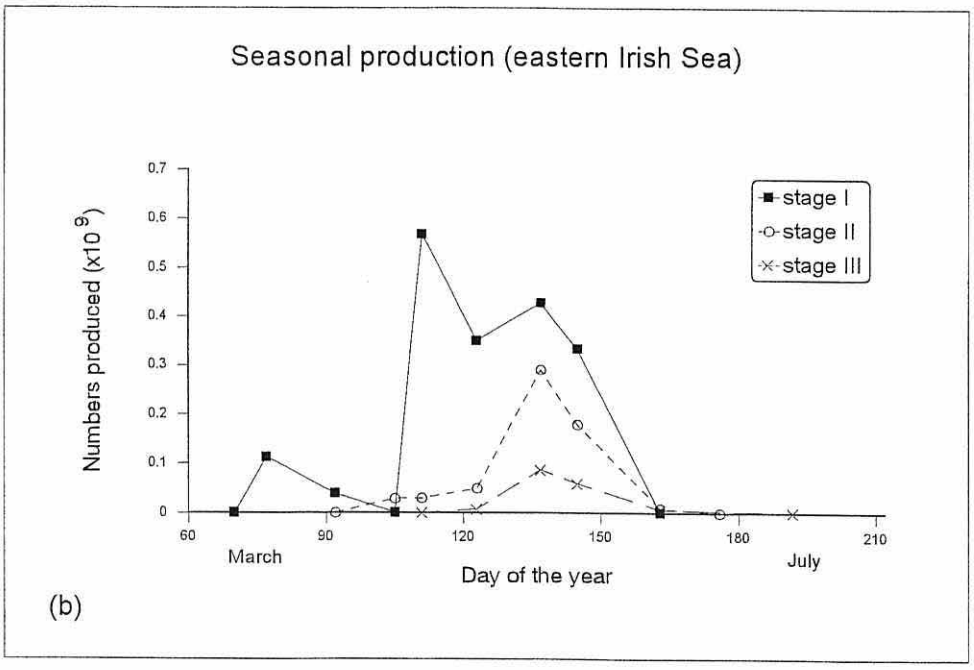


Figure 5.12. Seasonal production curves for stages, I, II and III *N. norvegicus* zoea from the 1995 season. (a) western Irish Sea, (b) eastern Irish Sea.

Table 5.2. Larval abundance ($x10^9$) and daily production ($x10^6$) for zoeal stages I,II,III on 11 survey dates in the western Irish Sea in 1995.

Survey	Mean sea temperature (°C)	Larval Abundance ($x10^9$)			Daily Production ($x10^6$)		
		Stage I	Stage II	Stage III	Stage I	Stage II	Stage III
Cruise 2 (11-19 February)	8.31	———	———	———	———	———	———
Cruise 3 (21-27 February)	7.95	———	———	———	———	———	———
Cruise 5 (8-14 March)	7.56	0.289	———	———	16	———	———
Cruise 6 (15-22 March)	7.45	2.47	———	———	128	———	———
Cruise 8 (30 March-6 April)	7.76	14.7	0.191	———	782	9.7	———
Cruise 9+10 (10-21 April)	8.23	25.0	8.58	0.736	1420	459	37.4
Cruise 11 (18-25 April)	8.23	113	16.6	0.568	6320	915	29.8
Cruise 12 (30 April-7 May)	8.82	159	37.9	2.44	9510	2220	131
Cruise 13+Cory 5b (14-20 May)	9.15	130	162	45.9	8390	10400	2570
Cruise 14 (23-28 May)	9.6	56.2	84.2	68.7	3710	5570	3890
Cruise 15+L. Foyle 11 (5-20 June)	10.46	1.90	4.12	17.6	146	313	1070

Table 5.3. Seasonal production and mortality of *N. norvegicus* larvae in the western Irish Sea in 1995.

Stage	Mean duration (days)	Mean sea temperature (°C)	Total production ($x10^9$)	% Loss	Z	% Daily mortality
I	16.18	8.58	349.26		0.024	2.37
II	15.61	8.89	235.22	32.65	0.047	4.59
III	17.50	9.08	113.06	51.93		
I-III				67.63	0.035	3.43

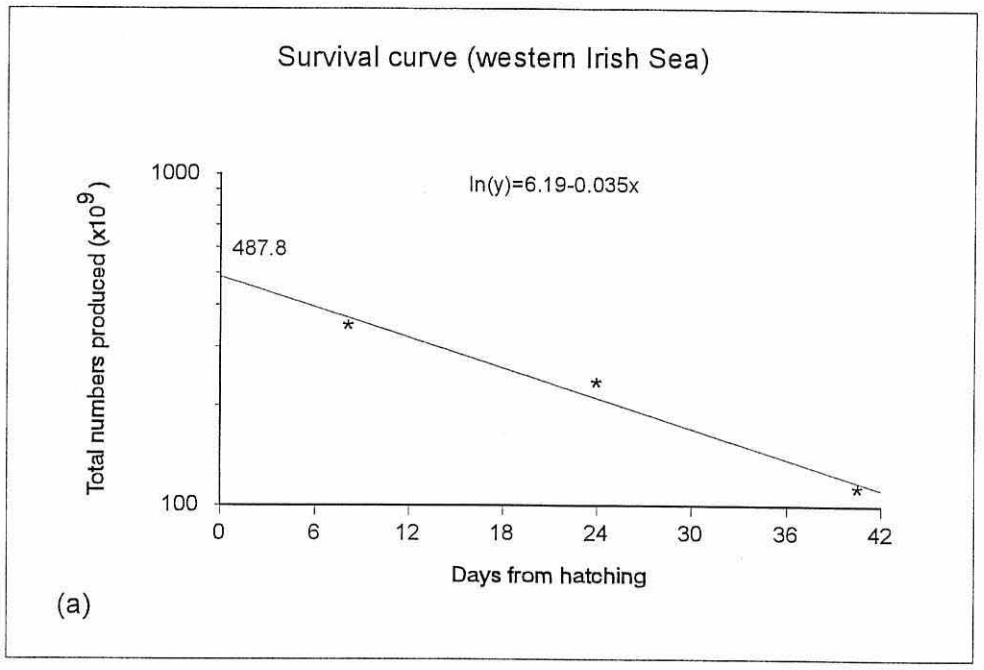
III larvae during the 1995 season, was predicted to be 16.18, 15.61 and 17.5 days, respectively.

Using the mortality regression (figure 5.13a) a value of 487.8×10^9 larvae was estimated for instant production (production of stage I larvae at time zero). Considering the fecundity estimates (578-889 viable eggs/female) presented by Nichols *et al.* (1987) for the western Irish Sea and the above value for instant production of larvae, it was predicted that during the 1995 hatching season the female spawning stock was in the range between 5.49×10^8 and 8.44×10^8 individuals. The same calculations using the total production of stage I larvae predicted a number of adult females ranging from 3.93×10^8 to 6.04×10^8.

Assuming a mean length of the spawning females of 27.5 mm carapace length, which corresponds to an individual of a mean weight of approximately 12.5 g (Nichols *et al.*, 1987) and applying it to the predicted number of breeding females in 1995 the spawning stock biomass can be estimated. Using the number of adult females predicted by the seasonal production curve of stage I larvae a spawning stock biomass of 4913 to 7550 tonnes is obtained. When the number of females involved in spawning is derived from the instantaneous production of stage I zoea (mortality regression), the adult mature female stock biomass predicted is between 6863 and 10550 tonnes.

Eastern Irish Sea

Abundances of the three zoeal stages and daily productions in the eastern Irish Sea area during the 1995 campaign are presented in table 5.4 and the seasonal production curves are shown in figure 5.12b. The numbers of stage I lobsters in the area, during the 1995 survey period, showed several fluctuations with three peaks detectable in the production curve. Stage I zoea were first detected in mid March (15-22) but the abundances then dropped and by mid April very few zoea I were collected. A sharp increase was then observed and peak abundance (10.6×10^9 larvae, approximately 11.4 larvae/m^2) reached during the next survey (Cruise 11) in the second half of April (18-25). The daily production at this point in time was estimated to be 0.569×10^9 larvae. From this peak the abundance then declined only to increase again in mid May (14-20) (6.22×10^9 larvae). After this survey the abundances dropped sharply and no stage I larvae were observed during the last survey in June (5-20),



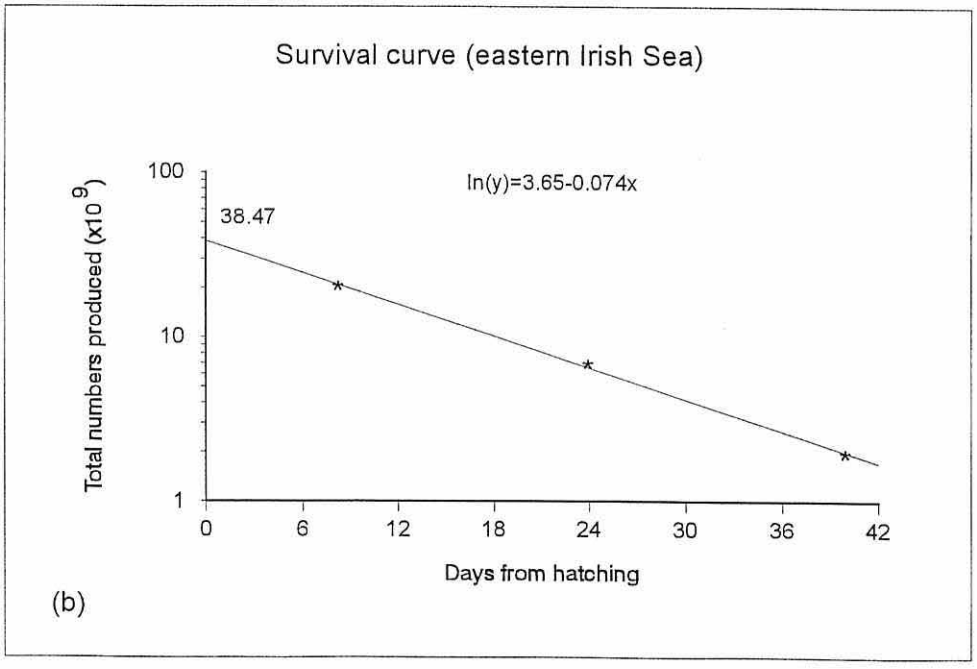


Figure 5.13. Survival curve for *N. norvegicus* zoea in 1995. Numbers of larvae produced at each stage plotted against their mean age in days from hatching. Also shown the fitted regression equation and the intercept value at time zero. (a) western Irish Sea, (b) eastern Irish Sea.

Table 5.4. Larval abundance ($x10^9$) and daily production ($x10^6$) for zoeal stages I,II,III on 11 survey dates in the eastern Irish Sea in 1995.

	Mean sea temperature (°C)	Larval Abundance ($x10^9$)			Daily Production ($x10^6$)		
		Stage I	Stage II	Stage III	Stage I	Stage II	Stage III
Cruise 2 (11-19 February)	6.80	———	———	———	———	———	———
Cruise 3 (21-27 February)	6.61	———	———	———	———	———	———
Cruise 5 (8-14 March)	6.38	———	———	———	———	———	———
Cruise 6 (15-22 March)	6.37	2.42	———	———	113	———	———
Cruise 8 (30 March-6 April)	6.66	0.873	———	———	39.4	———	———
Cruise 9+10 (10-21 April)	7.48	0.0186	0.605	———	0.92	28.8	———
Cruise 11 (18-25 April)	7.86	10.6	0.577	———	569	30.1	———
Cruise 12 (30 April-7 May)	8.65	5.89	0.854	0.140	350	49.9	7.52
Cruise 13+Cory 5b (14-20 May)	9.58	6.22	4.31	1.52	428	290	87.1
Cruise 14 (23-28 May)	10.11	4.47	2.43	1.0	334	179	59.3
Cruise 15+L. Foyle 11 (5-20 June)	11.21	———	0.112	0.0978	———	9.4	6.14

Table 5.5. Seasonal production and mortality of *N. norvegicus* larvae in the eastern Irish Sea in 1995.

Stage	Mean duration (days)	Mean sea temperature (°C)	Total production ($x10^9$)	% Loss	Z	% Daily mortality
I	16.48	8.70	20.52		0.066	6.39
II	14.88	9.50	6.92	66.28	0.084	8.1
III	17.18	9.80	1.97	71.53		
I-III				90.40	0.075	7.22

suggesting that the hatching season was complete. The production curves for stages II and III do not show the fluctuations that were observed for stage I seasonal production. This fact may indicate that the oscillations shown in the production curve of stage I larvae are probably not real. Only one peak of abundance was detected during the production season for stage II and III larvae. Stage II zoea were first collected in mid April (10-21) and a slow increase in numbers was observed until the beginning of May. A rapid increase in numbers was then registered and peak values ($4.31x10^9$ larvae, 4.63 larvae/m^2) recorded in mid May (14-20). Abundances then declined but by the end of the sampling period there were still some stage II larvae present in the water column. Stage III larvae were noted in early May (30 April-7 May) and the peak of abundance ($1.52x10^9$ larvae, 1.63 zoea III/m^2) observed during the following survey (14-20 May). The daily production for this period was estimated to be $0.087x10^9$ larvae. From this peak the numbers declined, at first slowly, and by the time of the last survey very few stage III zoea were collected. It was predicted that planktonic lobsters would probably be observed in the eastern Irish Sea area nearly to the middle of July.

The percentage losses between stages, in the eastern Irish Sea were very high, 66.28% between stages I and II and 71.53% between stage II and III. On average less than 10% of the larvae produced reached the last zoeal stage. The instantaneous coefficient of mortality (Z), calculated from the total abundance of each larval stage, and the percentage daily mortality through the larval season was found to be 6.39% between stages I and II, and 8.1% between stages II and III. The daily mortality between stages I and III was 7.22%. The mean duration for each larval stage during the 1995 hatching season in the eastern Irish Sea, was predicted to be 16.48 days for stage I larvae, 14.88 days for stage II zoea and 17.18 days for the last zoeal stage (table 5.5).

The total production of larval stages I, II and III was calculated to be $20.52x10^9$, $6.92x10^9$ and $1.97x10^9$, respectively (table 5.4). When these values were plotted against the mean larval age for each stage (figure 5.13b) the intercept value for production at time zero encountered was $38.47x10^9$ larvae. Using this production value and the effective fecundity figures presented by Nichols *et al.* (1987), the female spawning stock size was estimated to be between $4.33x10^7$ and $6.66x10^7$ adult females. When the total production of stage I considered is estimated by the production curve ($20.52x10^9$ stage I larvae) the number of adult females in the population is predicted to be between $2.31x10^7$ and $3.55x10^7$.

Assuming an average weight of the mature female of 12.5 g (Nichols *et al.*, 1987), the predicted spawning stock biomass, derived from the number of females estimated by seasonal production curve of stage I larvae, is between 289 and 444 tonnes. When the number of breeding females is estimated by the instantaneous production of stage I larvae (mortality regreession) the spawning stock biomass predicted is 541 to 833 tonnes.

2.2.3. Temperature, salinity and potential energy anomaly distributions

Figures 5.14 and 5.15 show the spatial distribution of sea surface temperature collected during the 1995 period of survey. In figure 5.16, surface salinity maps are presented for the surveys from which these observations were available. Although the validity of the absolute measurements from the Guildline CTD is of doubtful oceanographic value, due to the unreliability of the instrument and absence of calibration measurements, it was thought worth presenting in order to appreciate the general patterns of distribution of some physical properties, observed simultaneously with the plankton sampling.

Sea surface temperature contours show significantly lower values in the eastern Irish Sea than in the western basin, up until April. These observations are consistent with high levels of fresh water input from the rivers along the English and Scottish coasts, during the winter period. The maps of surface salinity give further evidence for this occurrence, with highly pronounced haline gradients visible in the eastern Irish Sea. In the western basin, surface salinity values are more homogenously distributed but it is clear the influence of, more saline, Atlantic waters entering the Sea via its south opening. The temperature distribution also shows the path of the warmer Atlantic waters spreading across the central western Irish Sea. The influence of river runoff is also apparent in the properties of the waters along the Irish coast, which up until April were clearly colder and less saline than the waters in the regions further offshore. The warming up of the surface waters is evident from April onwards. By the end of the survey period, surface temperatures had increased approximately 4^{o} C. The warmer temperatures were observed in the shallow coastal regions of the eastern Irish Sea but also in the centre of the western basin, where summer stratification occurs.

Evidence of water column stratification is clearer in the plots of potential energy anomaly shown in figure 5.17. Data were only available to construct ϕ distribution maps for four of the survey dates. These figures show evidence of water column stratification on the eastern Irish Sea during February which is consistent with haline stratification due to the fresh water input outlined on the salinity maps. In the western Irish Sea, stratification of the water column in the central deeper area was apparently in place very early in the season. While thermal stratification justifies the contours of potential energy anomaly observed during April and May it is not so clear what may have caused the apparent stratification during February. Some

less saline water entering via the North Channel may have had some influence but it seems more likely that the measurements taken by the CTD probe may have misrepresented the water column structure.

Figures 5.18 and 5.19 present contours of larval density distribution, in the western Irish Sea, for stage I zoea and total numbers of larvae, respectively. The patterns of distribution already described are confirmed by this representation of larval densities. Higher numbers of *N. norvegicus* larvae were observed along the Irish coast early in the season when a displacement towards south was also apparent. Towards the end of the season larval concentrations were higher in the central western Irish Sea. These plots serve also to highlight the similarity between the larval distribution contours and the maps of ϕ. This aspect is made particularly clear by comparing larvae densities and ϕ distributions observed during the month of May (figures 5.18 and 5.19f and g and figure 5.17d and figure 4.16b and 4.17a, chapter IV).

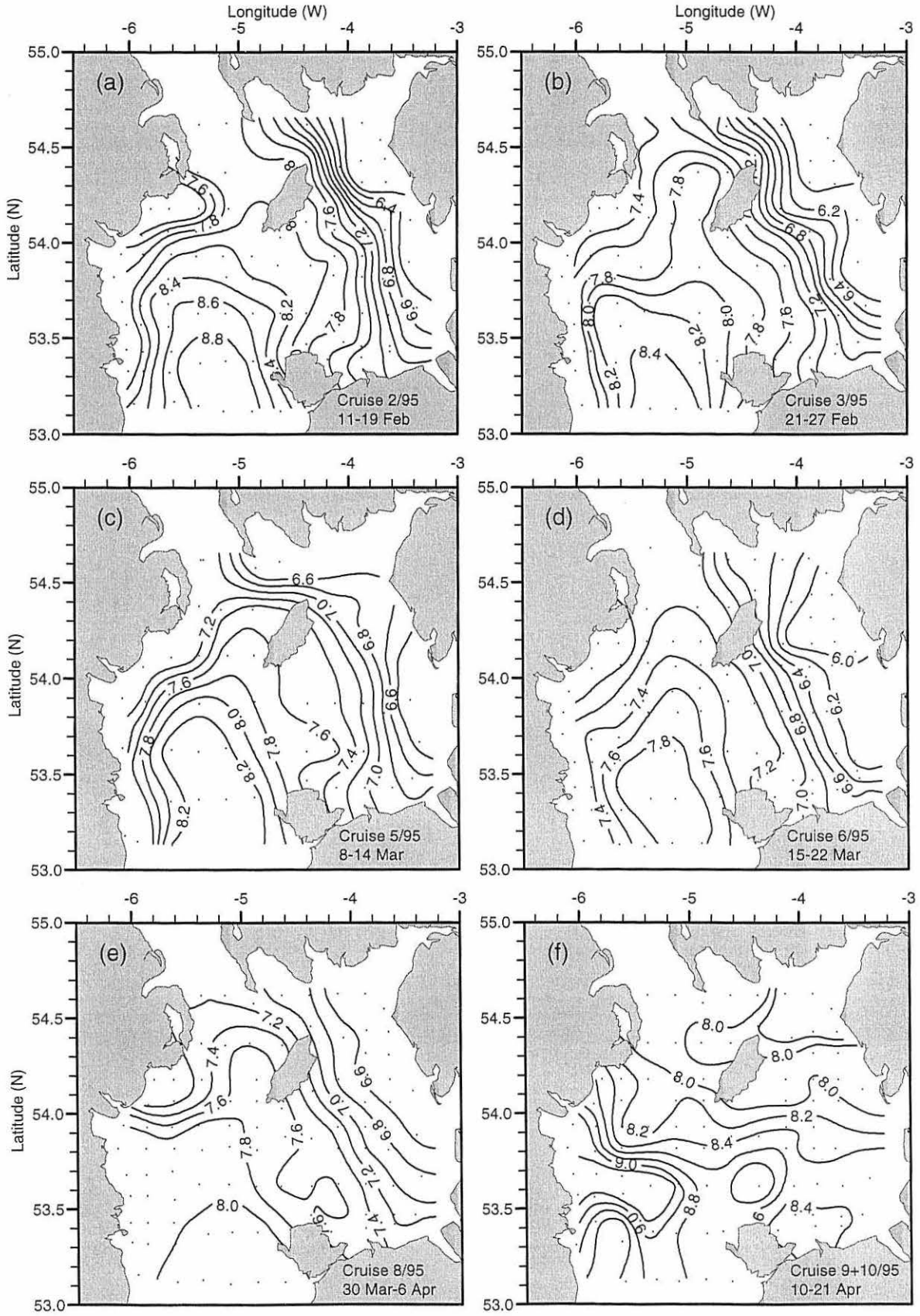


Figure 5.14. Seasonal development of the surface temperature field (°C) in 1995 (observations from the Guildline CTD probe). (a) Cruise 2/95, (b) Cruise 3/95, (c) Cruise 5/95, (d) Cruise 6/95, (e) Cruise 8/95, (f) Cruise 9+10/95.

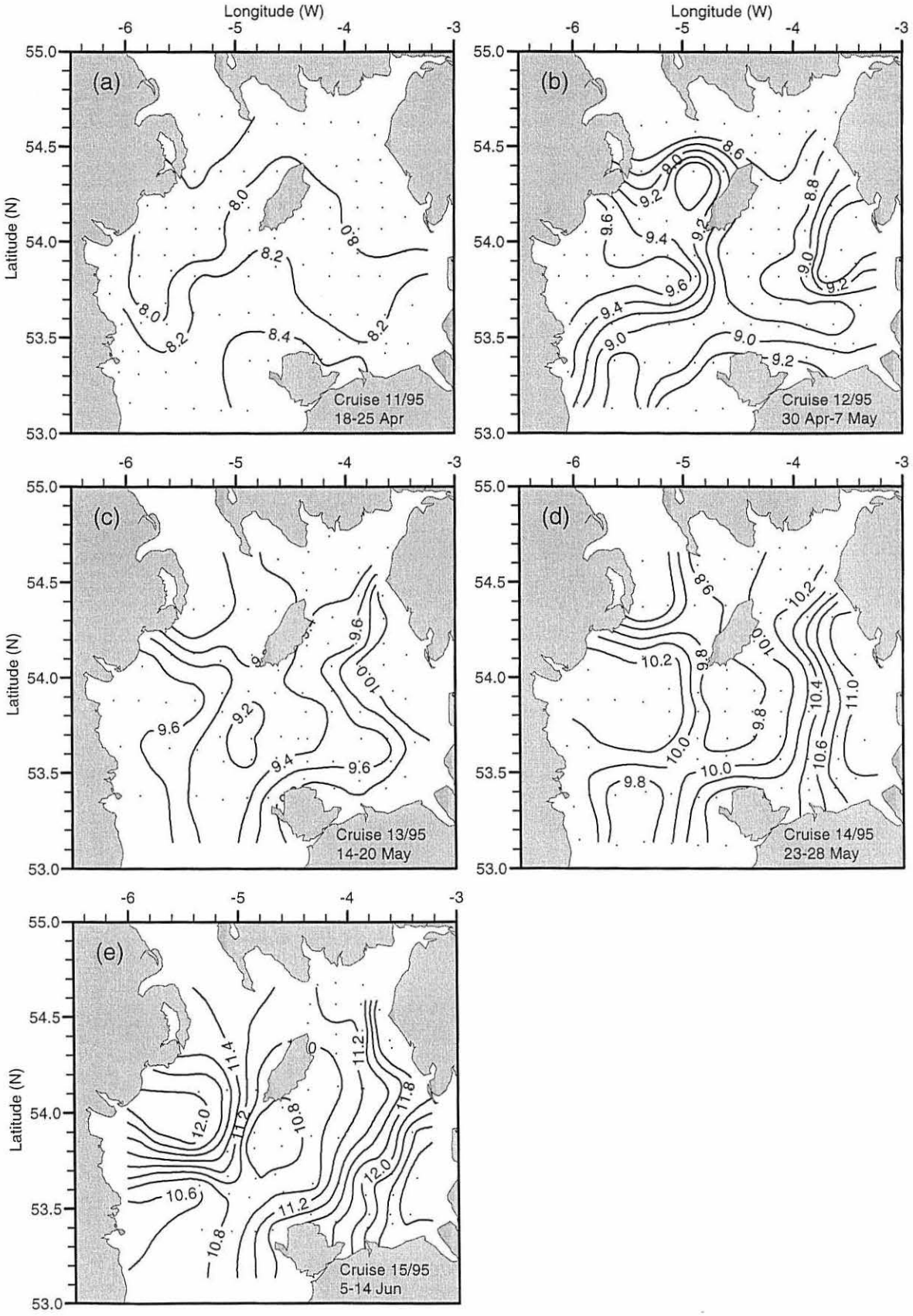


Figure 5.15. Seasonal development of the surface temperature field (°C) in 1995 (observations from the Guildline CTD probe). (a) Cruise 11/95, (b) Cruise 12/95, (c) Cruise 13/95, (d) Cruise 14/95, (e) Cruise 15/95.

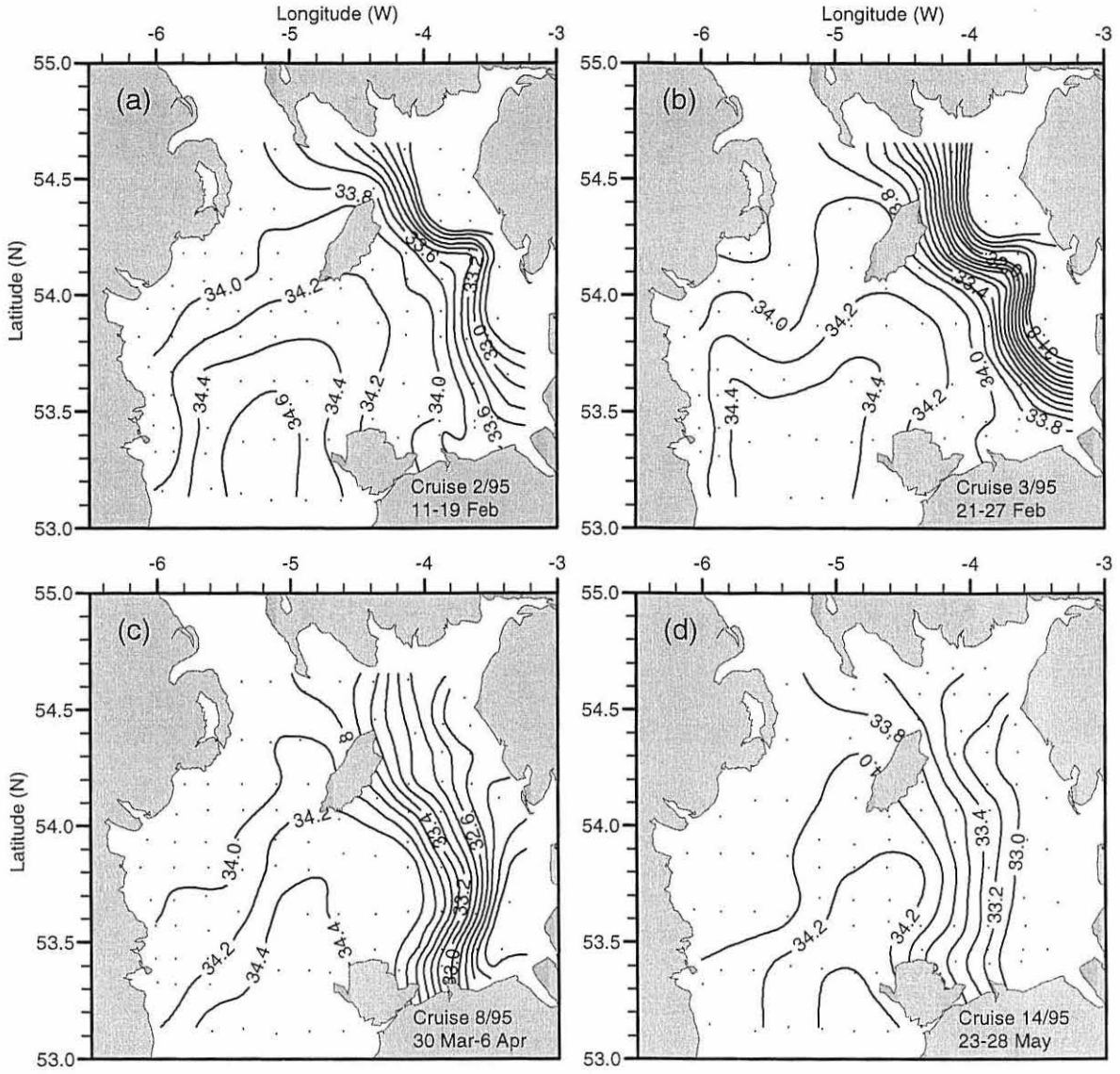


Figure 5.16. Contours of surface salinity (psu) in 1995 (observations from the Guildline CTD probe). (a) Cruise 2/95, (b) Cruise 3/95, (c) Cruise 8/95, (d) Cruise 14/95.

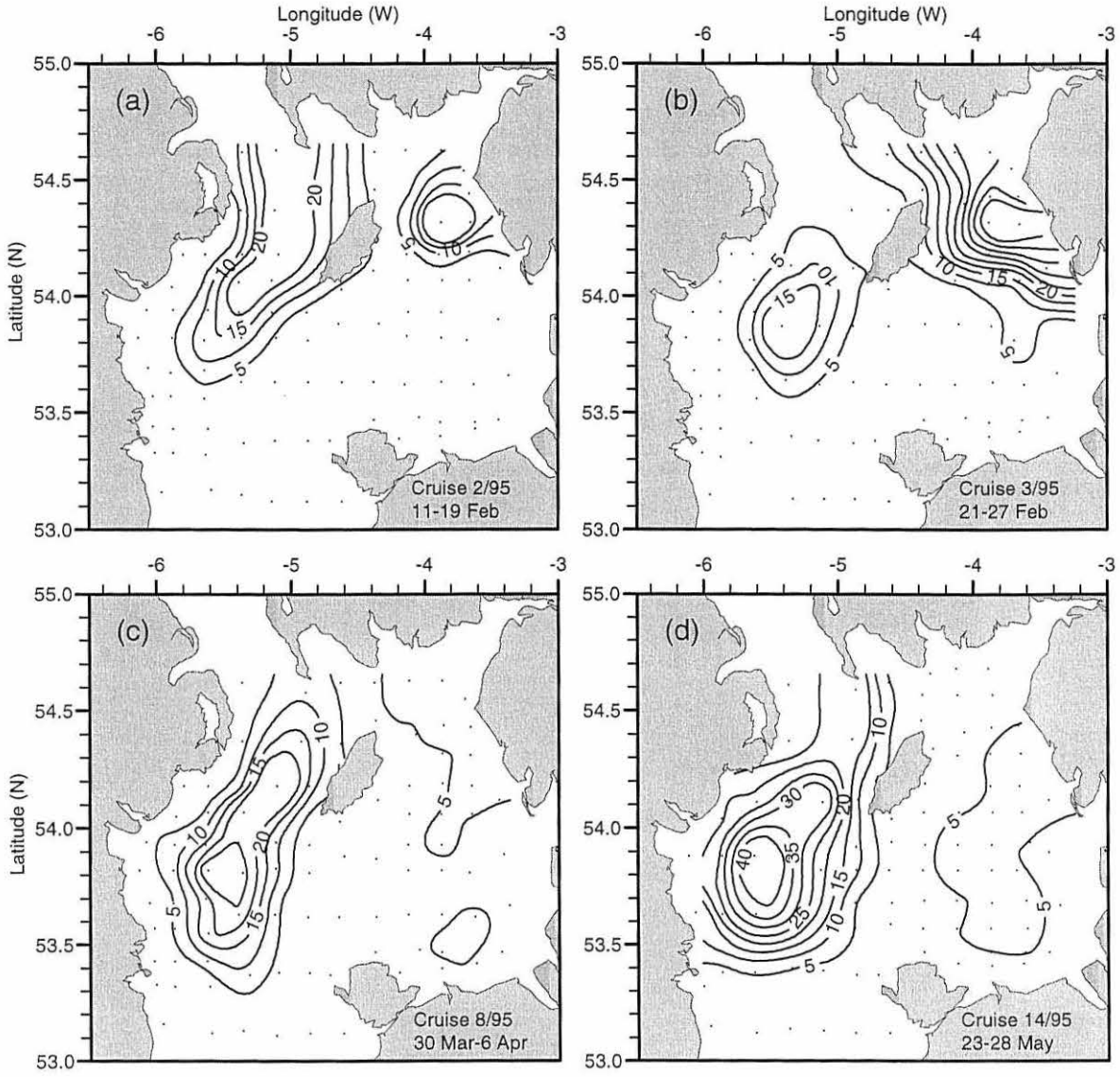


Figure 5.17. Contours of potential energy anomaly (J/m^3) (observations from the Guildline CTD probe) for (a) Cruise 2/95, (b) Cruise 3/95, (c) Cruise 8/95, (d) Cruise 14/95.

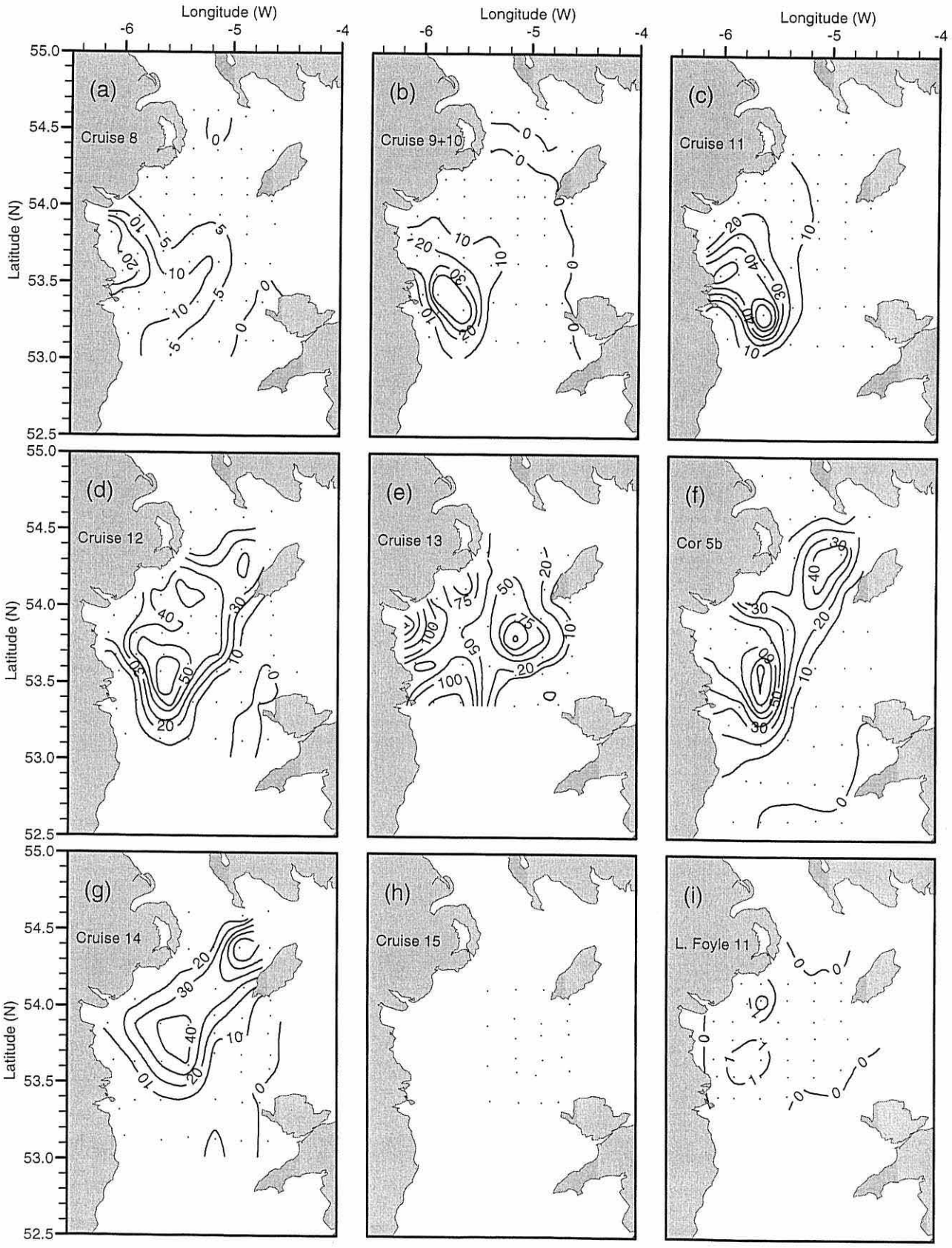


Figure 5.18. Distribution of *N. norvegicus* stage I larvae as numbers/m^2 in 1995 (a) Cruise 8/95, (b) Cruise 9+10/95, (c) Cruise 11/95, (d) Cruise 12/95, (e) Cruise 13/95, (f) Corystes 5b/95, (g) Cruise 14/95, (h), Cruise 15/95, (i) L. Foyle 11/95.

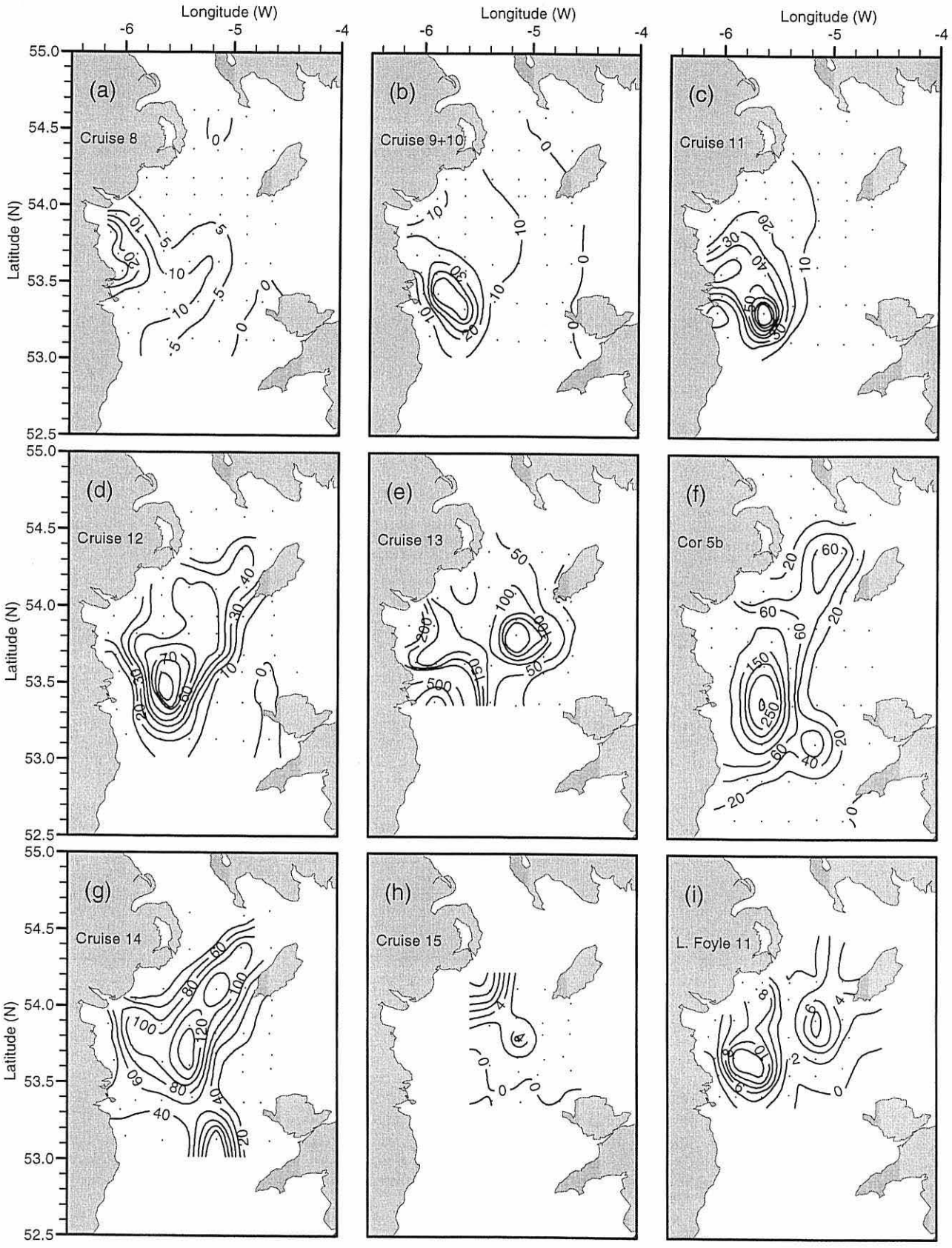


Figure 5.19. Distribution of total *N. norvegicus* larvae as numbers/m^2 in 1995 (a) Cruise 8/95, (b) Cruise 9+10/95, (c) Cruise 11/95, (d) Cruise 12/95, (e) Cruise 13/95, (f) Corystes 5b/95, (g) Cruise 14/95, (h), Cruise 15/95, (i) L. Foyle 11/95.

2.2.4. Larval distribution in the western Irish Sea and its relationship with environmental data

In order to assess differences in the larvae distribution (spatially and at different periods of the larval season) and between sites defined by a set of environmental variables and the relationship between the latter and the larvae abundances, information from surveys Cruise 8, Cruise 11, Corystes 5b, Cruise 14 and Prince Madog 1 was analysed. Samples considered were grid units: 6,1; 6,2; 7,1; 7,2; 8,1; 8,2; 8,3; 9,2; 9,3 constituting region 1. over the muddy substrate, summer stratified (gyre) region and grid units: 5,1; 5,2; 5,3; 6,3; 7,0; 7,3; 10,2; 10,3 outside area 1 (see figure 5.1).

Larval abundances, by stage, in two distinct areas (1. over the mud patch, stratified water (gyre) region; 2. outside region 1) and the hypothesis of dependency between sites and larvae of different stages distributions, was investigated by a 2 factors ANOVA (Site, 2 levels; Stage, 3 levels; and Site x Stage) for the surveys referred above. The results from the ANOVA are summarised in tables 5.6 to 5.9.

The analyses show that no significant differences, in *N. norvegicus* larvae abundances, were encountered between the two sites (over the mud region and outside this area) during surveys Cruise 8 (30 March-6 April; F=1.23, P=0.28), Cruise 11 (18-25 April; F=0.49, P=0.49) and Corystes 5b (15-20 May; F=2.06, P=0.16). Cruise 8 was carried out at the beginning of the hatching season when small numbers of larvae started to appear and stratification of the water column (gyre) is only starting to develop. Cruise 11 (18-25 April) and Corystes 5b (15-20 May), were carried out later in the season when higher larval productivity occurs but the gyre is still only setting up. The absence of (statistically significant) differences in the larval abundance between the two regions implies that larvae were 'equally' distributed across the study area analysed.

During Cruise 14 (23-28 May) statistically significant differences were encountered between the two areas (F=27.62, P=0.0). This survey was carried out towards the end of the larval season when larvae had been in the water column for a longer period but the local gyre is considerably developed. A higher concentration of larvae was observed in the central western

Table 5.6. ANOVA results, Cruise 8.

Source of variation	Df	Sum of Squares	Mean Square	F	P
Site	1	9.852	9.852	1.23	0.277
Stage	1	46.824	43.975	5.47	0.026
Site x Stage	1	11.516	11.516	1.43	0.241
Error	30	241.271	8.042		
Total	33	309.463			

Table 5.7. ANOVA results, Cruise 11.

Source of variation	Df	Sum of Squares	Mean Square	F	P
Site	1	0.790	0.79	0.49	0.488
Stage	2	35.665	17.174	10.61	0.000
Site x Stage	2	3.527	1.763	1.09	0.345
Error	45	72.866	1.619		
Total	50	112.849			

Table 5.8. ANOVA results, Corystes 5b.

Source of variation	Df	Sum of Squares	Mean Square	F	P
Site	1	16.012	16.012	2.06	0.158
Stage	2	55.406	26.636	3.43	0.041
Site x Stage	2	10.901	5.450	0.70	0.501
Error	45	349.471	7.766		
Total	50	431.790			

Table 5.9. ANOVA results, Cruise 14.

Source of variation	Df	Sum of Squares	Mean Square	F	P
Site	1	102.608	102.608	27.62	0.000
Stage	2	0.269	0.180	0.05	0.953
Site x Stage	2	1.998	0.999	0.27	0.765
Error	45	167.174	3.715		
Total	50	272.049			

Irish Sea than in the surrounding areas outside the mud patch (gyre) region. These results are in agreement with the description of the larval distribution presented in section 2.2.1.

No significant interaction between factors Stage and Site, was found for any of the surveys analysed. This fact suggests that the larval distribution of the three zoeal stages is not dependent on any of the 2 sites considered. In other words, their distribution is, 'statistically similar', regardless of the region. This result is not in contradiction with the interpretation of the larval distribution plots presented in section 2.2.1. because it actually does not cover totally the most southern region, where more late stages were found during the mid season surveys. In order for the samples between surveys to be comparable, and also to include the same area from which physical variables were available, the southern most sampling lines had to be excluded from the analyses. The differences between the abundance of the three zoeal stages (Cruise 8, Cruise 11, Corystes 5b) reflect the natural sucession of their appearance along the season.

PCA analyses of the environmental variables were performed for surveys Cruise 8, Corystes 5b, Cruise 14 and Prince Madog 1 (30 May-2 June). During Corystes 5b and Prince Madog 1 oceanographic observations were carried out and the variables considered were: site depth, sea bed sediment type, surface water temperature, bottom water temperature and potential energy anomaly. Salinity distributions were not used because it was considered not to add any extra relevant information to the characterisation of the environment and its relationship to the larvae distribution and also because they are already reflected on the ϕ data. Site depth and sea bed sediment type were derived from charted information. The set of environmental variables included in the analyses, were selected considering that they produce a good characterisation of the local environment and identify the spring-summer gyre in the study area. Availability of information was also a consideration. For surveys Cruise 8 and Cruise 14 the physical data available were collected by the probe attached to the plankton sampler and less reliable than the information from the oceanographic surveys. For these cruises, the variables considered were as defined above but bottom water temperature was not available. Data from the survey Prince Madog 1 were analysed in association with the plankton samples from Cruise 14. Figures 5.20 to 5.23 show combinations of all the variables included in the analyses, these plots (Draftman's plot) are not only useful to visualise the data under analysis

but also produce a way of detecting colinearity between pairs of variables (no added information is achieved by retaining 2, or more, variables if they are highly correlated).

PCA ordination plots are presented in figures 5.24a to 5.27a and the analyses results shown in tables 5.10 to 5.13. The distances between samples on the ordination plot reflect the corresponding dissimilarities in the environment structure. The amount of information (% of the original total variance) explained by the new variables (principal components) PC1 and PC2 was 69.6% for Cruise 8, 71% for Corystes 5b, 79.1% for Cruise 14 and 78% for Prince Madog 1 (tables 5.10 to 5.13). Guidelines for an acceptable level of percentage variance contained in the first two components are difficult to set. Generally, a picture that accounts for as much as 70-75% of the original variation is likely to describe the overall structure quite well (Clarke & Warwick, 1994). Looking at the ordination plots and PC1 and PC2 equations (these components are linear combinations of the old variables):

Cruise 8	PC1=0.61sed+0.42dep.+0.09surftemp+0.67ϕ
	PC2=0.21sed+0.1dep-0.97surftemp-0.1ϕ
Corystes 5b	PC1=0.27sed+0.5dep-0.42surftemp-0.5bottemp+0.51ϕ
	PC2=0.74sed-0.1dep+0.31surftemp+0.44bottemp+0.39ϕ
Cruise 14	PC1=-0.6sed-0.07dep-0.5surftemp-0.62ϕ
	PC2=0.18sed+0.84dep-0.5surftemp+0.14ϕ
Prince Madog 1	PC1=0.48sed+0.4dep-0.25surftemp-0.55bottemp+0.5ϕ
	PC2=-0.43sed+0.5dep-0.7surftemp-0.02bottemp-0.35ϕ

it is possible to identify which (original) variables make the greatest contribution for the construction of the axes and detect meaningful gradients of these new variables.

In Cruise 8 ordination plot (figure 5.24a), along PC1 a gradient from less to more stratified and lower to higher mud content, can be detected. Samples 6,2; 7,1; 7,2; 8,2; 9,2 (central western Irish Sea) all with a higher percentage of muddy substrate, and also slightly more stratified appear on the right of the picture. Samples 5,1; 5,3; 6,3; 7,3; with a lower mud content (area outside the mud patch) are placed on the left of the plot. Other samples (5,2; 6,1; 7,0; 8,3; 9,3) with intermediate values for these two properties (sediment, ϕ) are located in between the two groups referred to. Samples 8,1; 10,2; 10,3, on the northern area and 8,1

close to the coast of Ireland, are displaced along PC2 due to their slightly lower surface temperatures, surface temperature is the variable with higher contribution on the definition of the second component.

The ordination plot for Corystes 5b (figure 5.25a) show a gradient of lower to highest ϕ, an increase in depth and a decrease in bottom temperature, along PC1. PC2 separates the samples along a gradient essentially defined by sediment. Samples 6,1; 6,2; 7,1; 7,2; 8,1; 8,2; 8,3 9,2 (central western Irish Sea) are grouped towards the right of PC1 and on top half of PC2. The remaining samples, with the exception of 7,0, are placed in the bottom half of PC2. Sample 7,0 (Dundalk Bay) appears separated from the rest of the samples.

Figure 5.26a shows the ordination plot for the data from Cruise 14. For this survey the PC1 is mainly defined by ϕ and sediment which decrease along the axis. PC2 orders the samples essentially in respect of their depth. Sites from the central stratified region over the mud patch (6,1; 6,2; 7,1; 7,2; 8,1; 8,2), appear on the left of the picture. Samples from the regions on the borders of the stratified area (5,1; 5,3; 6,3; 7,0; 7,3; 8,3; 9,3; 10,3) are placed on the right side of the plot. Sites 9,2 and 10,2, from the deeper northern area, are located on the top right of the plot.

The PCA analysis of Prince Madog 1 produced perhaps a less clear ordination of the samples (figure 5.27a). Bottom temperature and ϕ have a major contribution to the construction of the first axis and surface temperature for the second. Samples on the southwestern region of the study area (5,1; 5,2; 5,3; 6,3; 7,3), with higher bottom temperature and lower ϕ, appear on the left of the plot. Sites from the centre of the basin are placed to the right of this group. Samples 8,2 and 9,2 (in the deeper, highly stratified region) are plotted on the far right extreme of the graphic and 10,2 (northern region) appears separated along PC2. Samples 7,0 and 7,1, off Dundalk Bay are isolated on the bottom of the picture, the first on the left and the second towards the right.

In summary, although the variables contributing the most for the ordination along the two first components varied a little between data sets (surveys) a general pattern could be identified. The ordinations separated quite clearly samples (sites) in the central western Irish Sea (more stratified, higher content of mud, gyre region) from sites outside this region. These

results were confirmed by tests (ANOSIM), performed *a priori*, in which the two regions were compared. For all the surveys, significant differences between the two areas were encountered (Cruise 8, R=0.46, P=0.1%; Corystes 5b, R=0.33 P=0.1%; Cruise 14, R=0.33, P=0.3%; Prince Madog 1, R=0.37, P=0.1%).

In order to investigate the relationship between the environmental variables and the abundance and distribution of *N. norvegicus* larvae, larval abundances (from corresponding samples) were superimposed on the ordination pictures from the environmental data. These effects can be appreciated in figures 5.24 to 5.27 (b, stage I; c, stage II; d, stage III). For survey Cruise 8 (figure 5.24), more larvae (stage I) were observed in all the stations at the bottom of the picture (sites in the central western Irish Sea and surrounding areas). No clear association was detected between larvae occurrence and the group of samples from the central sites which contain a higher percentage of muddy substrate which are placed on the right of the ordination plot. The sites that were separated essentially due to their lower surface temperatures show very low larval abundances.

In figure 5.25b (Corystes 5b) a cluster of high abundances of stage I zoea is apparently superimposed with the set of environmental samples, corresponding to the central, stratified area with high mud content, which were placed towards the right of PC1 and on the top half of PC2. Samples 7,0 (Dundalk Bay) which was isolated by the PCA ordination, also show a high number of stage I lobsters. Stages II and III larvae also appear associated with the samples from the central western Irish Sea 'grouped' by the ordination on environmental data. The highest abundance was however registered for sample 5,1 (off Dublin Bay), outside the stratified (gyre) region.

The larval abundance data superimposed on the environmental ordination plots for surveys Cruise 14 and Prince Madog 1 was collected during Cruise 14 (these two surveys were carried out at approximately the same period). *N. norvegicus* larvae appeared during these surveys more associated with the group of samples from the central more stratified region. For Prince Madog 1 (figure 5.27) these sites are located on the right of the the PCA ordination. This pattern is more evident for stage I zoea. The association between larval abundances and the sites in the central western Irish Sea (gyre region) is perhaps clearer for Cruise 14 (figure 5.26), particularlly for stages II and III zoea. The ordination plot for this

survey shows the samples from the stratified central area over the mud patch, placed on the left of the picture where the higher concentrations of larvae stages II and III were detected.

In an attempt to provide statistical support for the relationship between the environmental variables and the larvae abundances (and distribution) a linear regression was performed between the scores of the PC's and larvae abundances. Not much expectation was put in such an approach due to the undefined association between the ordination of the environmental variables and the larval abundances shown in figures 5.24 to 5.27 and also because PC1 and PC2 variables did not account for a considerable percentage of the variance existent in the original data. Figure 5.28 to 5.30 show the scatter plots of larvae abundances (log transformed) versus the scores of PC1 and PC2 for Corystes 5b. The regression analyses produced poor results indicating that a cause and effect relationship between PC1 and PC2 and larvae abundances, respectively, is not apparent.

	R^2	F	P
PC1 vs stage I	0.55	5.97	0.028
PC1 vs stage II	0.32	1.64	0.221
PC1 vs stage III	0.20	0.58	0.460
PC1, PC2 vs stage I	0.66	5.07	0.024
PC1, PC2 vs stage II	0.48	1.90	0.188
PC1, PC2 vs stage III	0.50	2.6	0.155

Although the regressions between stage I and the scores of PC1 (log stage I abundance =0.92+0.32PC1) and PC1, PC2 (log stage I abundance=0.98+0.21PC1+0.26PC2) were statistically significant it would be rather ambitious to assume that the relationship between the environmental variables considered (and represented by PC1 and PC2) and *N. norvegicus* larvae are well represented by these relations. No further regression analysis were carried out for the other surveys.

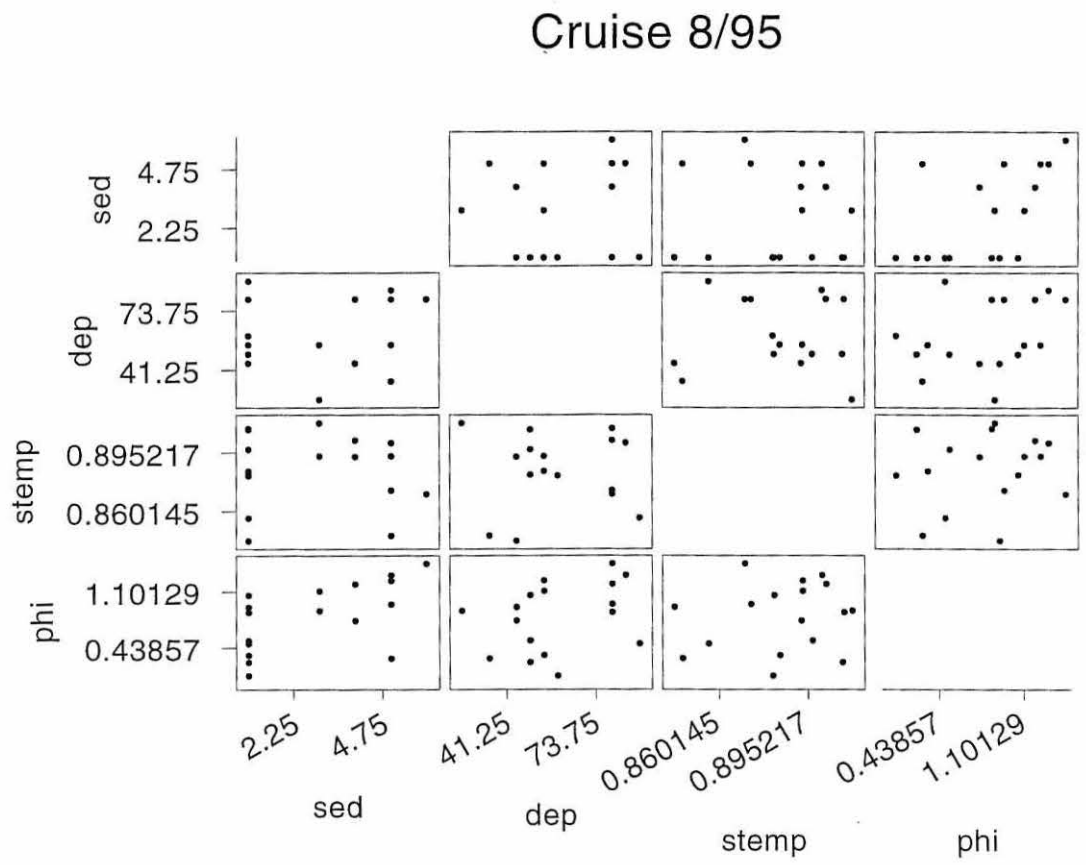


Figure 5.20. Western Irish Sea. 'Draftsman' plot, showing the relation between environmental variables for each sampling unit: sediment type, site depth, surface temperature and potential energy anomaly from Cruise 8/95 (30 March-6 April).

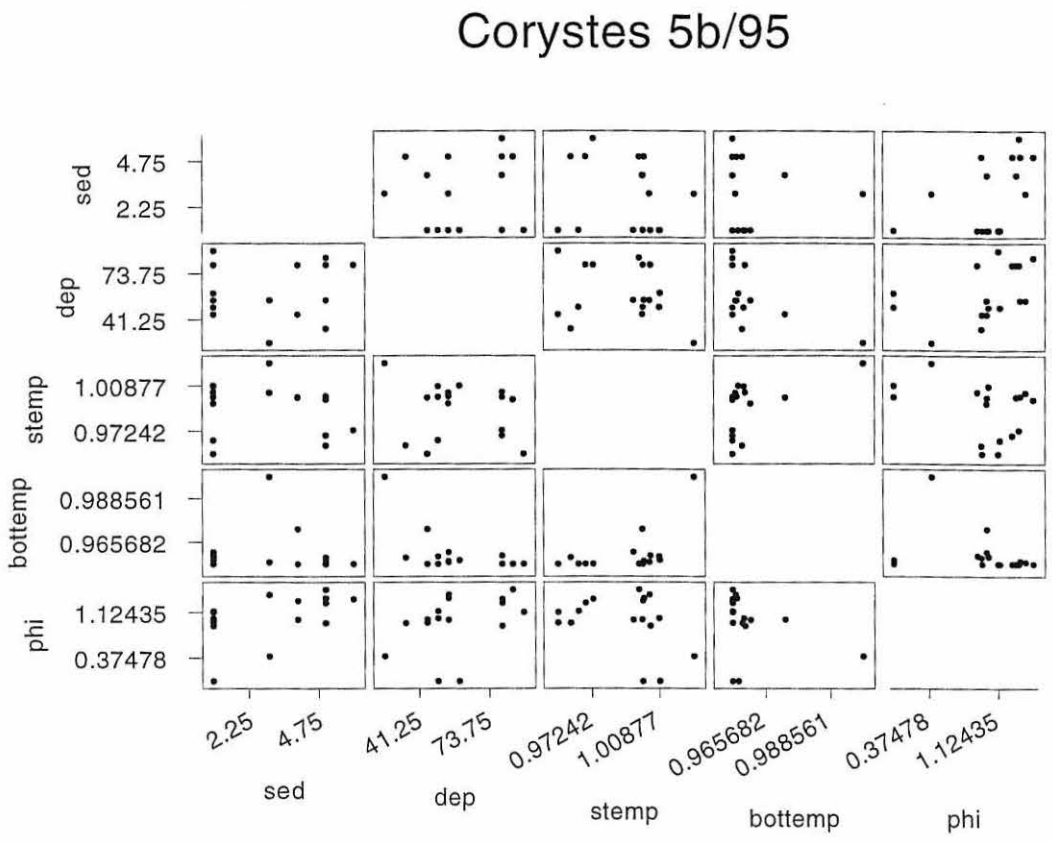


Figure 5.21. Western Irish Sea. 'Draftsman' plot, showing the relation between environmental variables for each sampling unit: sediment type, site depth, surface temperature, bottom temperature and potential energy anomaly from Corystes 5b/95 (15-30 May).

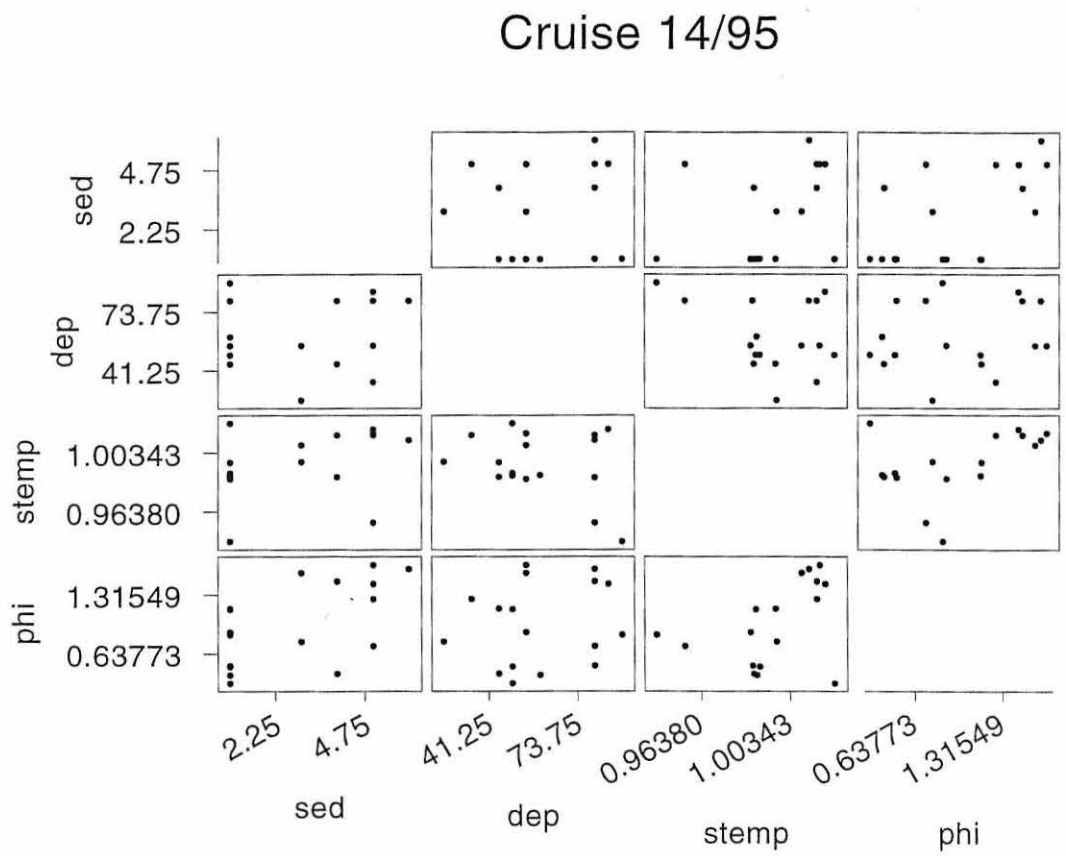


Figure 5.22. Western Irish Sea. 'Draftsman' plot, showing the relation between environmental variables for each sampling unit: sediment type, site depth, surface temperature and potential energy anomaly from Cruise 14/95 (23-28 May).

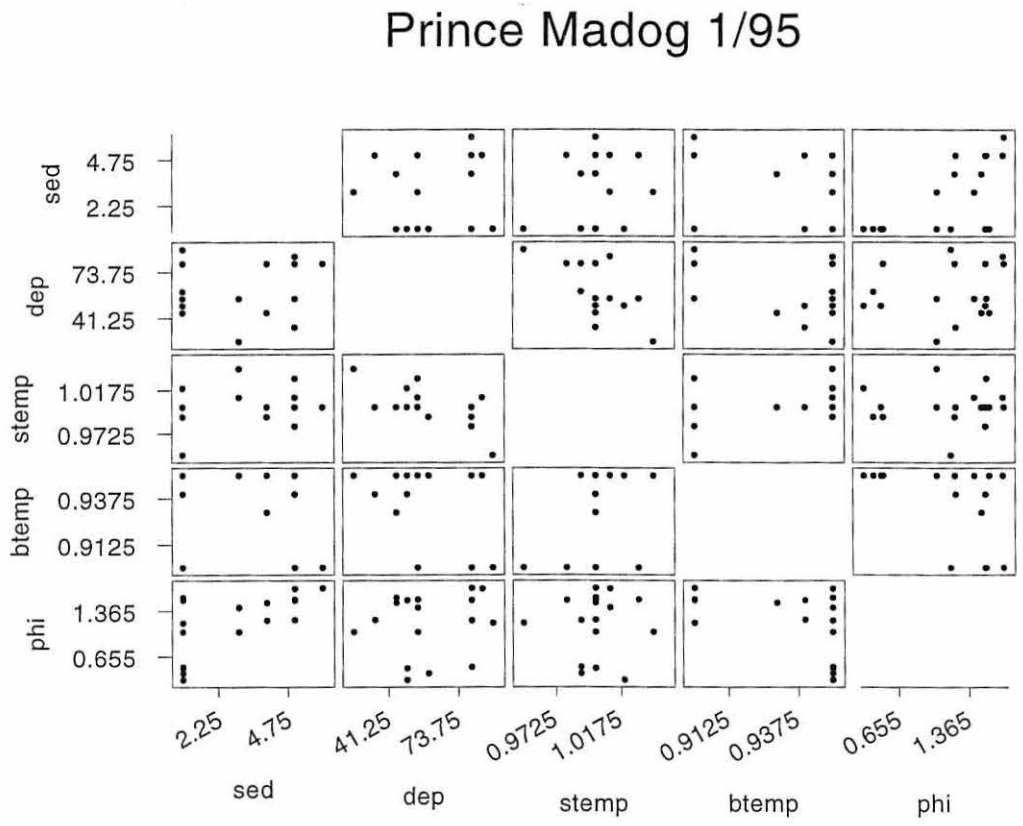
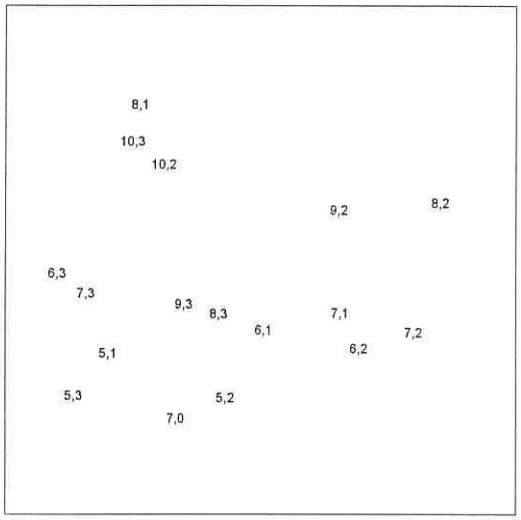
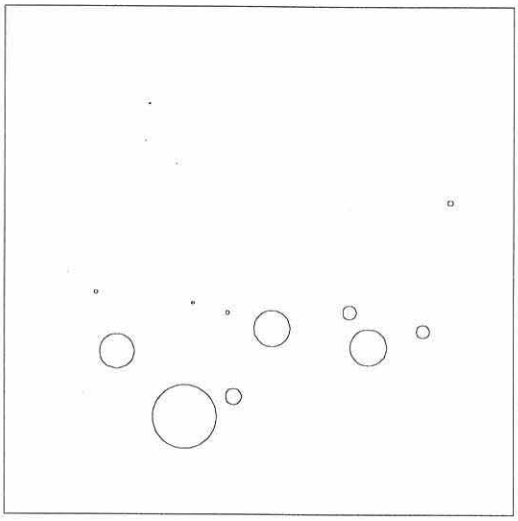


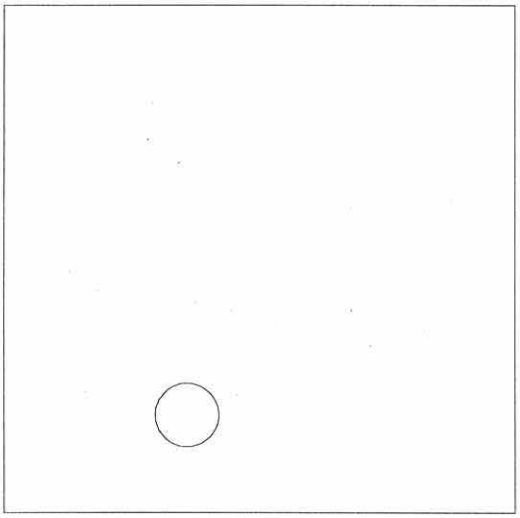
Figure 5.23. Western Irish Sea. 'Draftsman' plot, showing the relation between environmental variables for each sampling unit: sediment type, site depth, surface temperature and potential energy anomaly from P. Madog 1/95 (30 May-2 June).



(a)



(b)



(c)

Figure 5.24. PCA analysis for data from Cruise 8/95 (30 March-6 April). (a) PCA ordination plot for environmental variables, for sites indicated by grid unit reference in accordance with figure 5.1, (b) and (c) abundance of *N. norvegicus* stage I and II larvae, respectively, superimposed on the ordination plot of environmental variables.

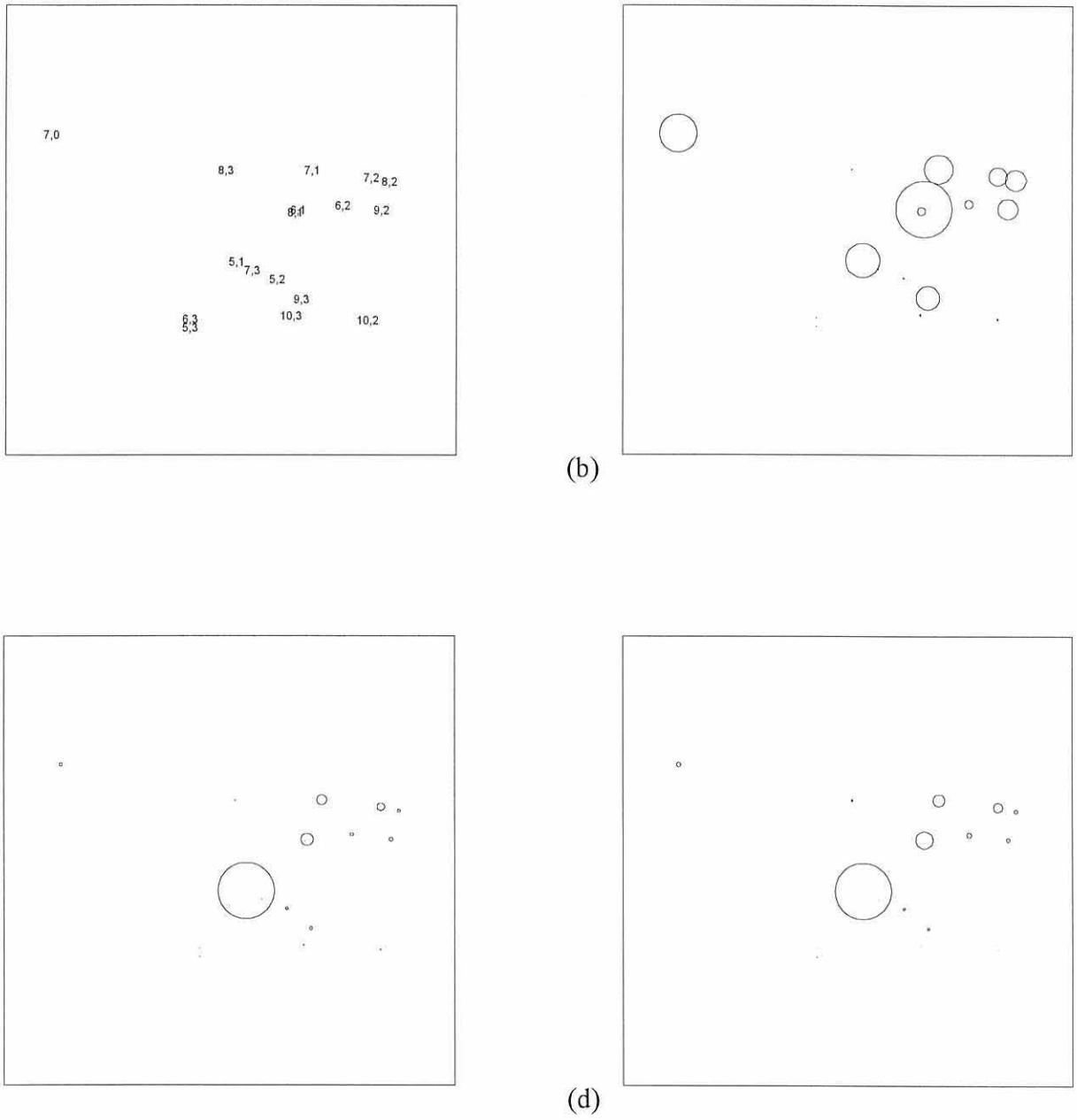
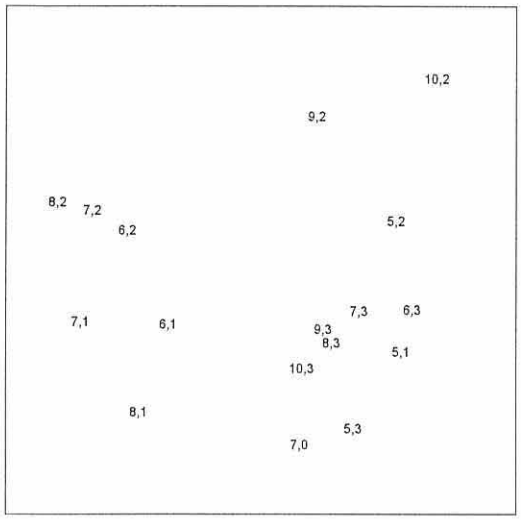
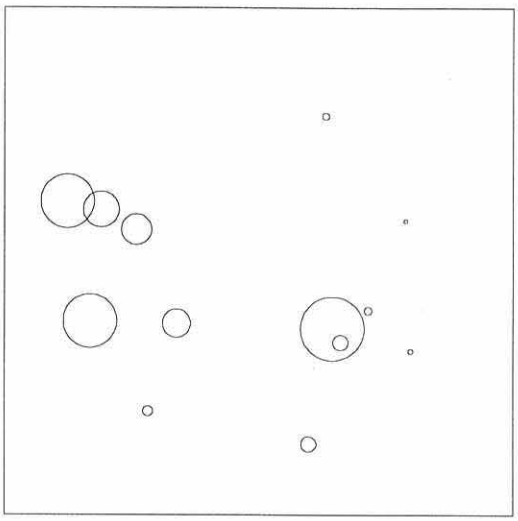


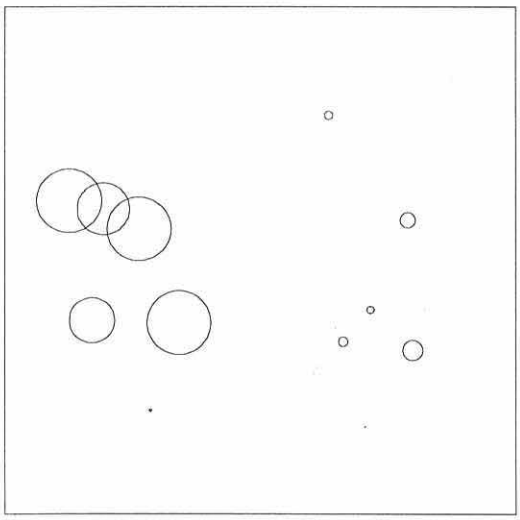
Figure 5.25. PCA analysis for data from Corystes 5b/95 (15-20 May). (a) PCA ordination plot for environmental variables, for sites indicated by grid unit reference in accordance with figure 5.1, (b) to (c) abundance of *N. norvegicus* stage I, II and III larvae, respectively, superimposed on the ordination plot of environmental variables.



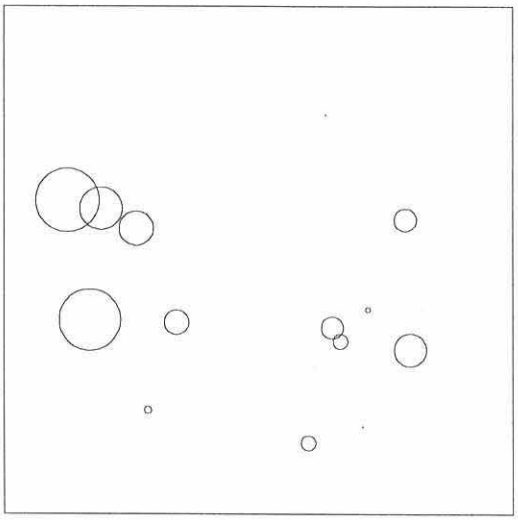
(a)



(b)



(c)



(d)

Figure 5.26. PCA analysis for data from Cruise 14/95 (23-28 May). (a) PCA ordination plot for environmental variables, for sites indicated by grid unit reference in accordance with figure 5.1, (b) to (c) abundance of *N. norvegicus* stage I, II and III larvae, respectively, superimposed on the ordination plot of environmental variables.

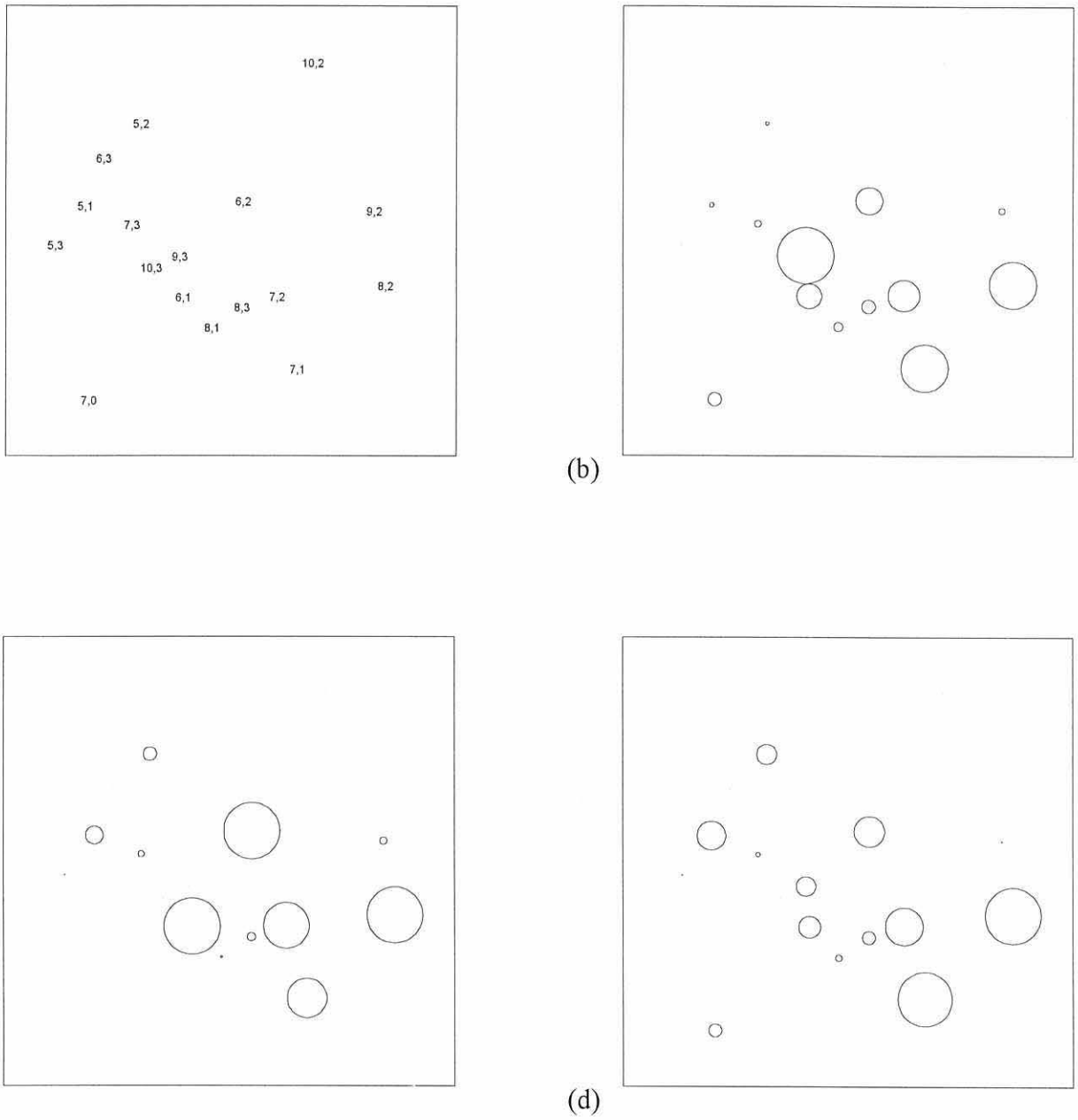


Figure 5.27. PCA analysis for data from P. Madog 1/95 (30 May-2 June). (a) PCA ordination plot for environmental variables, for sites indicated by grid unit reference in accordance with figure 5.1, (b) to (c) abundance of *N. norvegicus* stage I, II and III larvae, respectively, from survey Cruise 14, superimposed on the ordination plot of environmental variables.

Table 5.10. PCA, Cruise 8.

	Eigenvalues	% Variation	Cum. % Variation
PC1	1.75	43.8	43.8
PC2	1.03	25.8	69.6
PC3	0.86	21.6	91.1
PC4	0.35	8.9	100.0

Variable	PC1	PC2	PC3	PC4
Sediment	0.603	0.205	0.464	-0.616
Depth	0.422	0.099	-0.876	-0.213
Surface temperature	0.094	-0.967	-0.007	-0.235
Potential energy anomaly	0.670	-0.111	0.136	0.721

Table 5.11. PCA, Corystes 5b.

	Eigenvalues	% Variation	Cum. % Variation
PC1	2.30	46.0	46.0
PC2	1.25	24.9	71.0
PC3	0.76	15.3	86.2
PC4	0.37	7.5	93.7
PC5	0.32	6.3	100.0

Variable	PC1	PC2	PC3	PC4	PC5
Sediment	0.270	0.742	0.121	0.60	0.040
Depth	0.494	-0.099	-0.654	0.070	-0.561
Surface temperature	-0.421	0.310	-0.736	-0.073	0.424
Bottom temperature	-0.50	0.437	0.108	-0.293	-0.679
Potential energy anomaly	0.507	0.390	0.067	-0.738	0.207

Table 5.12. PCA, Cruise 14.

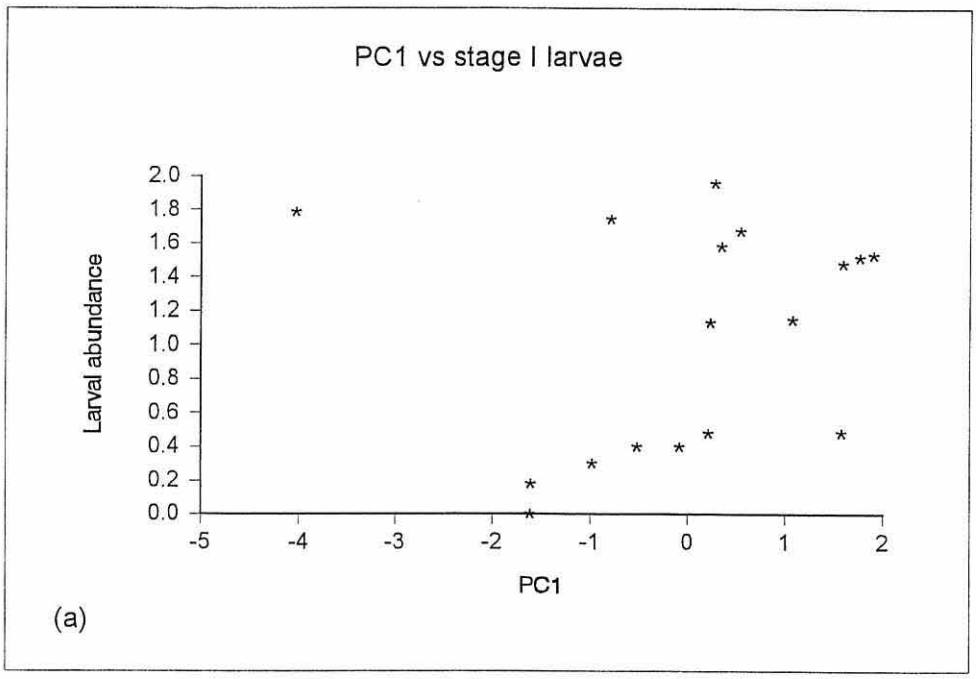
	Eigenvalues	% Variation	Cum. % Variation
PC1	1.93	48.2	48.2
PC2	1.24	30.9	79.1
PC3	0.47	11.6	90.7
PC4	0.37	9.3	100.0

Variable	PC1	PC2	PC3	PC4
Sediment	-0.596	0.175	0.726	0.296
Depth	-0.070	0.837	-0.406	0.361
Surface temperature	-0.500	-0.500	-0.496	0.504
Potential energy anomaly	-0.624	0.141	-0.250	-0.727

Table 5.13. PCA, Prince Madog 1.

	Eigenvalues	% Variation	Cum. % Variation
PC1	2.27	45.3	45.3
PC2	1.63	32.6	78.0
PC3	0.49	9.7	87.7
PC4	0.41	8.2	95.9
PC5	0.20	4.1	100.0

Variable	PC1	PC2	PC3	PC4	PC5
Sediment	0.481	-0.428	0.273	-0.418	-0.580
Depth	0.402	0.497	0.578	-0.266	0.431
Surface temperature	-0.246	-0.671	0.150	-0.330	0.599
Bottom temperature	-0.552	-0.019	0.737	0.265	-0.287
Potential energy anomaly	0.492	-0.345	0.161	0.759	0.192



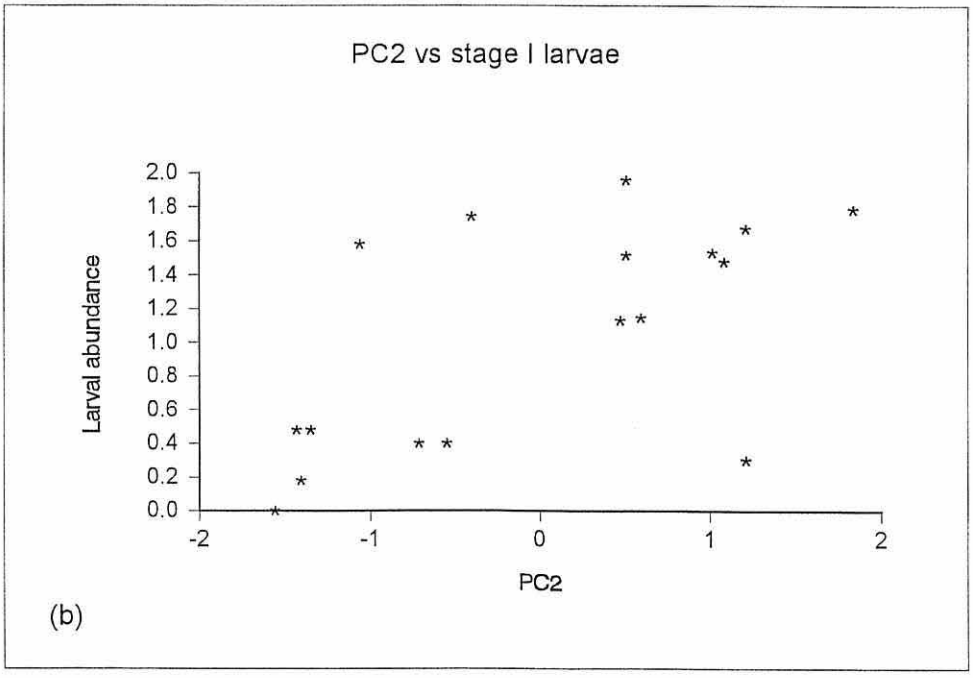
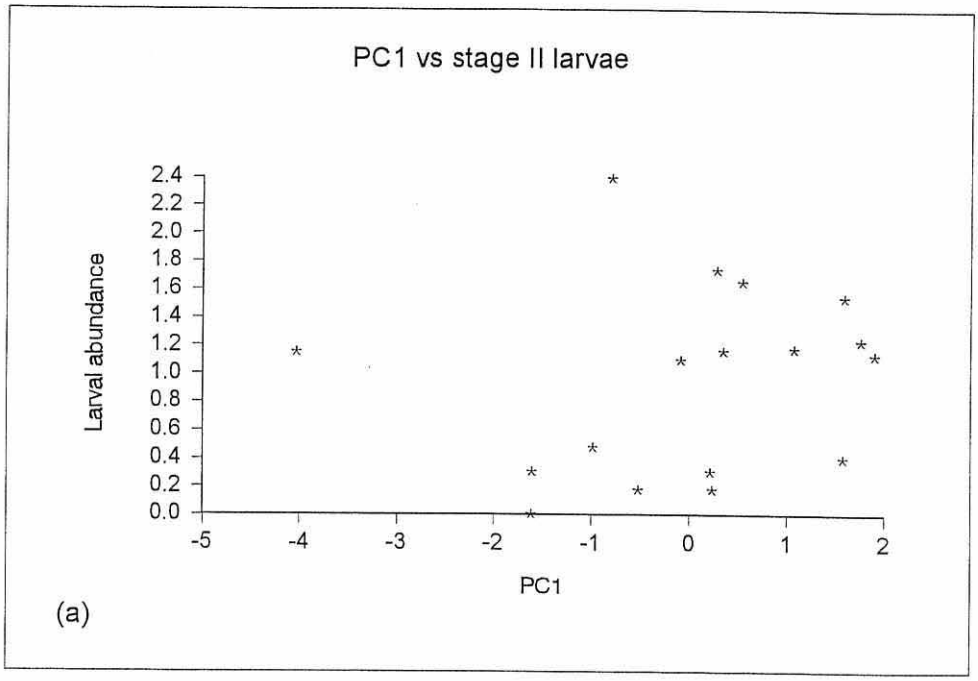


Figure 5.28. Scatter plot of (a) Scores of PC1 against abundance of *N. norvegicus* stage I larvae (log transformed), (b) Scores of PC2 against abundance of *N. norvegicus* stage I larvae (log transformed), for survey Corystes 5b/95.



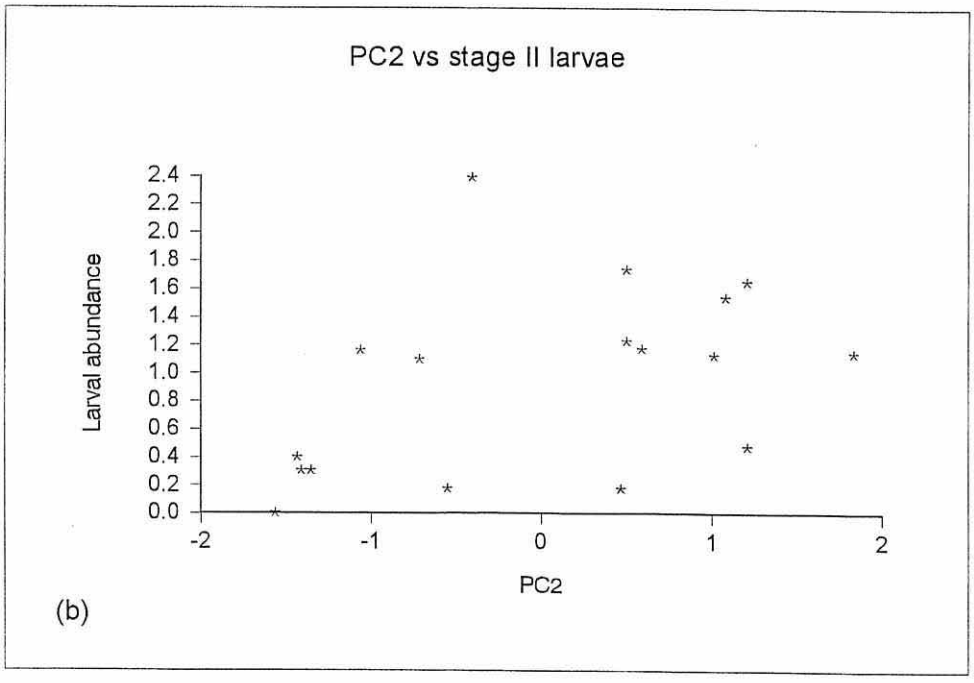
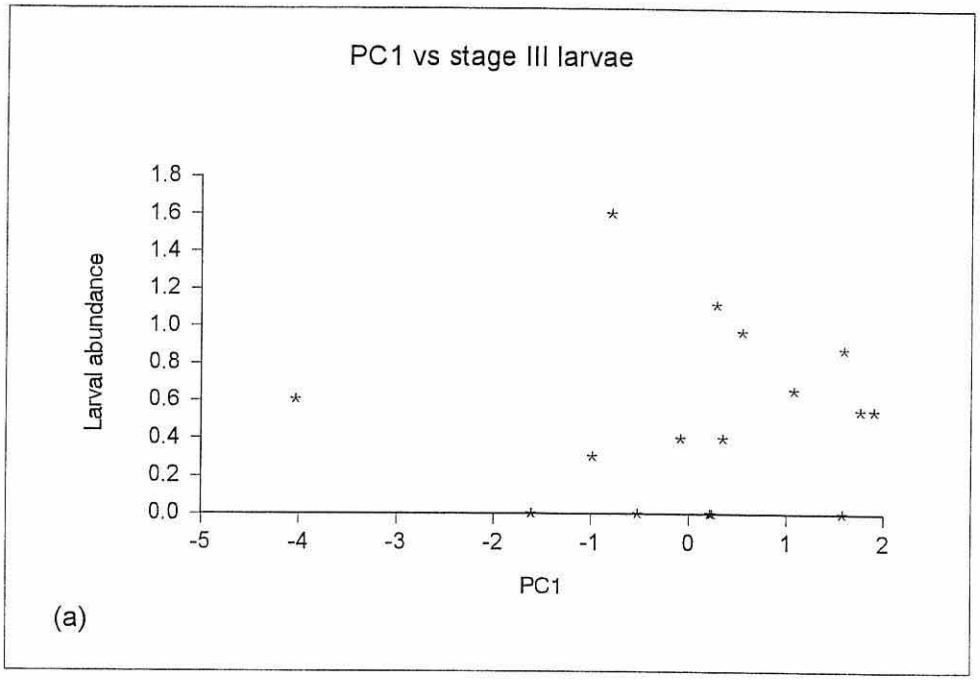


Figure 5.29. Scatter plot of (a) Scores of PC1 against abundance of *N. norvegicus* stage II larvae (log transformed) (b) Scores of PC2 against abundance of *N. norvegicus* stage II larvae (log transformed), for survey Corystes 5b/95.



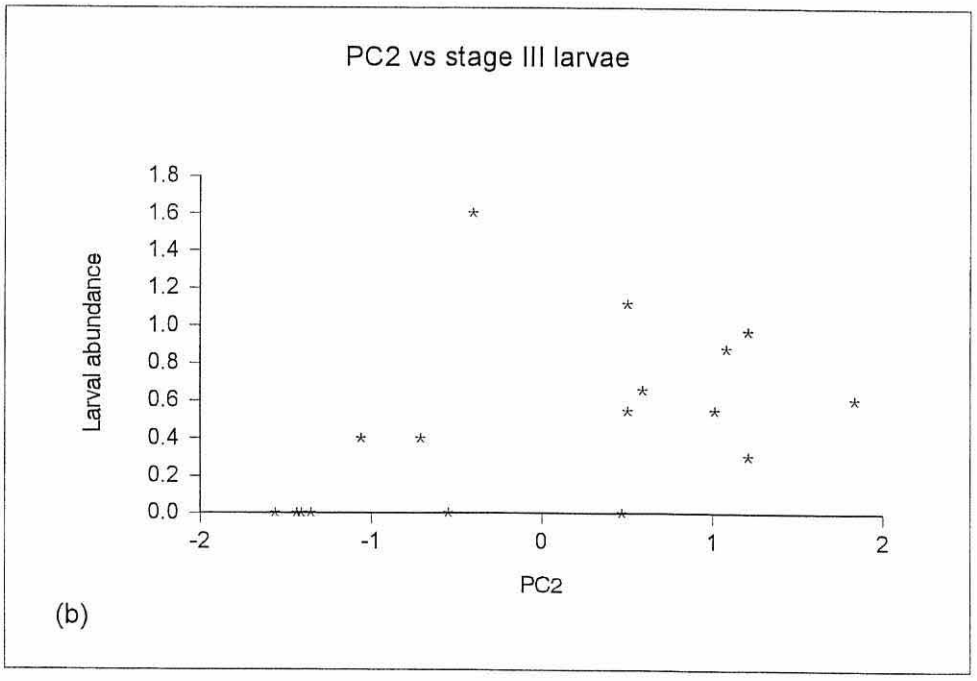


Figure 5.30. Scatter plot of (a) Scores of PC1 against abundance of *N. norvegicus* stage III larvae (log transformed), (b) Scores of PC2 against abundance of *N. norvegicus* stage III larvae (log transformed), for survey Corystes 5b/95.

3. Larval distribution during the period from 1982 to 1994 and 1996

3.1. Methodology

3.1.1. Sampling

Plankton samples were collected using a HSTN sampler. The data presented in this section derives from 17 plankton surveys carried out over a period of 15 years, from 1982 to 1996. This information is therefore dispersed in time and the area sampled also variable. Cruise dates, extent of the sampling programmes, gear used and source of the data can be read in table 3.1 (chapter III). As before, the survey references presented in that table are maintained in this presentation.

Corystes 7/94, Cirolana 4b/96 and Corystes 9/96 surveys were included in the SOS/CEFAS research programme, of which the present work is part. During these cruises, extensive hydrographic observations (discussed in chapter IV) were made together with the zooplankton sampling. Oceanographic data from the remaining surveys was limited to some observations collected by the Guildline CTD and only available for part of the surveys.

3.1.2. Data processing and analysis

Larval abundances and daily productions were estimated for the western Irish Sea, in the same way as described in section 2.1.2. This procedure was only applied for selected surveys, which presented a good coverage of the area. Larvae distribution is presented in bubble plots of absolute numbers of lobsters per stage.

3.2. Results

3.2.1. Larval distribution

Figures 5.31 to 5.47 show the spatial distribution and abundances of *N. norvegicus* larvae during the surveys carried out over the period from 1982 to 1994 and 1996. This set of data essentially includes information on the western Irish Sea, which was sampled regularly over the period considered (15 surveys from 1982 to 1994 plus 2 cruises in 1996). Nevertheless, the extent of the sampling programmes varied quite considerably, in some instances more than a 100 samples were collected while in other occasions only 12 to 14 stations were visited (see table 5.1). In addition, for the majority of the years only one survey was available and the same sampling dates were not maintained from season to season. During 1982 and 1985 seasons three cruises (April, May and June) were carried out and in 1984 the area was visited twice (May and June). During 1996 two research surveys (April and July) were undertaken as part of the present study. The distribution plots for all surveys available are presented here in chronological order.

Figures 5.31 to 5.33 show the distribution of *N. norvegicus* larvae on three occasions during the 1982 season. The first survey (Corella 5/82, figure 5.31) was carried out between 9 and 13 April, the second (Clione 6/82, figure 5.32) between 28 April and 21 May and the third (Clione 7/82, figure 5.33) from 25 May to 5 June. When Corella 5/82 sampling took place, the hatching season was already well underway, a considerable number of stage I zoea were observed and stage II larvae were collected in small numbers. Sampling off the Cumbrian coast, in the eastern Irish Sea, was limited to a few stations and no lobsters were detected in the region. Stage I lobsters were observed all over the western Irish Sea from latitude 54.5° N to 53.15° N. The larval concentration over the area of muddy substrate was appreciable but by far the location where most individuals were noted was off Dublin Bay, south of the adults ground. Stage II zoea were recorded in small numbers and all in a band between 53.3° N and 53.5° N, in the same area south of the mud patch. No stage III larvae were collected during this survey. Compared to a corresponding period in 1995 (Cruise 9+10/95), the distribution of larvae in 1982 seemed more dispersed over the entire basin, apart from the one location mentioned above. Abundance of stage I was greater during the 1982 survey but more stage II were collected in 1995 when zoea III were also already noted (see also tables 5.2 and 5.14).

During the following survey (Clione 6/82, figure 5.32), the number of stage I lobsters increased approximately 3 times and were well represented in the whole western basin from the entrance of the North Channel, in the northern limit, to as far south as 53.0° N. Large numbers of larvae were collected off Dublin Bay, as before, but the distribution spread further south than it was observed during the previous survey. Abundances of larvae during Clione 6/82 survey were comparable to the figures estimated for approximately the same period in 1995 (Cruises 12/95, Cruise13+Corystes 5b/95). In the eastern basin, stage I larvae were observed over the local mud patch. Stage II larvae abundances increased greatlly between Corella 5/85 and Clione 6/82 surveys and appeared then distributed all over the western Irish Sea. The highest concentrations were nevertheless observed between 52.8° N and 53.5° N, on the southern limit of the sampling area. Stage II and III larvae appeared to be more dispersed towards the south than stage I zoea. This particular pattern was also noted during surveys Corystes 5b/95 and Cruise 14/95 at a correspondent period in 1995. It seems that zoea II and III reached areas further south than stage I lobsters which suggest the advection of the first zoea, originated in the central area, towards the south. During the period the larvae are drifting south metamorphosis to the subsequent stages takes place.

When Clione 7/82 (figure 5.33) survey was carried out, in late May beginning of June 1982, the numbers of stage I lobsters had decreased substantially and were by then more concentrated over the central western Irish Sea. Stage II zoea appeared dispersed over the whole area from the entrance of the North Channel to the south end of the sampling area (52.8° N). Stage III larvae were also observed over the whole area but in higher numbers south of latitude 53.7° N. Stage II and III larvae continued to be found in more southern locations than stage I lobsters. The highest concentrations of stages II and III, for the 1982 surveys, were observed during this period of sampling. Zoea II abundances were nearly double the figure from the previous survey while larvae stage III numbers increased by a factor of 15 (see table 5.14). Abundances of the later stages during this survey were similar to the ones estimated for Cruise 14/95 (end of May) but stage I concentrations were higher in 1995. These comparisons should, however, be made with caution because survey dates in 1982 and 1995 do not exactly match. In the eastern Irish Sea the numbers of stage I larvae increased substantially and stage II were also identified. No stage III larvae were noted in the

area. During the Clione 7/82 survey a significant number of postlarvae of *N. norvegicus* were collected (table 5.1), these observations will be reported later in this chapter.

Figures 5.34 and 5.35 present the larval distribution observed during two surveys in 1984. During Cirolana 5.1/84, carried out in late May (25 May-1 June, figure 5.34), all three zoeal stages were present in considerable numbers over the central area of the western Irish Sea. As for other surveys undertaken at a corresponding period of the season, zoea II larvae seemed to be the more abundant stage. Stages II and III larvae also appeared in higher numbers than stage I in the area just south of the mud patch between 53.5° N and 53.0° N. The following survey in 1984, Cirolana 5.2/84 (12-13 June, figure 5.35) included only a very small number of stations and it provides therefore a limited picture of the distribution of the larvae. Even with such limited number of samples available some of the general patterns of distribution described before can be recognised. Higher numbers of larvae were observed on the southwestern region of the muddy area and stages II and III were more represented in the southern stations. Stage III zoea at this stage were present in higher numbers than stage I and II larvae. It was also observed that *N. norvegicus* larvae appeared in all sites sampled on the line across the eastern boundary of the mud patch. During both surveys in 1984, a considerable number of postlarvae of the species were collected (table 5.1), these observations will be presented later in this chapter.

During the 1985 season three surveys were carried out Clione 5/85 (15-19 April, figure 5.36), Clione 6/85 (11-26 May, figure 5.37) and Prince Madog 1/85 (27 May-6 June, figure 5.38). This succession of cruises was undertaken at approximately the same time as the three surveys in 1982. In mid April, Clione 5/85 (figure 5.36), all three zoeal stages were noted. The number of stage I larvae was nearly twice as large as for the same period in 1982 (Corella 5/82) but of comparable magnitude to the value estimated for Cruise 11/95 in 1995 (see tables 5.2 and 5.14). Stage I larvae were observed in high concentrations in the central western Irish Sea over the adults habitat and towards the Irish coast. Although abundances were still high off Dublin Bay not many individuals were collected south of line 53.3° N. The distribution of stage II zoea was similar but abundances much lower. Stage III larvae were noted in three sites on the south and west of the muddy area. In the eastern Irish Sea, only four sites were sampled but stage I larvae were observed in two of those, no stages II or III were collected in the region.

By mid May, Clione 6/85 survey (figure 5.37), the production of all three stages had increased substantially but particularly stages II and III abundances. The highest number of stage I larvae, for the 1985 surveys, was recorded during this survey. This peak value was nevertheless considerably smaller than the maximum production registered for the 1982 and 1995 seasons (tables 5.2 and 5.14). The pattern of distribution of the larvae is identical to the previous survey but with more larvae, of all stages, appearing to the south of latitude 53.5° N, in May. In the eastern basin, the number of stage I lobsters increased appreciably over the whole region between the Isle of Man and the Cumbrian coast. Stage II larvae were also noted, in the region, in small numbers but zoea III were not detected.

The last survey of the 1985 season (Prince Madog 1/85, figure 5.38) was carried out in late May begining of June. During this period the abundance of stage I larvae had dropped considerably but stages II and III reached the peak of production for the 1985 survey series. Abundances of these stages were comparable to estimations presented for the last survey in 1982 and Cruise 14/95 (tables 5.2 and 5.14). As pointed out before during the 1995 season no cruise was carried out at the begining of June in the western Irish Sea and comparisions may be merely especulative. The last surveys in 1995 (Cruise 15 and Lough Foyle 11/95) were limited in the area between 53.4° N and 54.2° N and therefore the full extent of the larvae distribution was not assessed. 1982 and 1985 June surveys show *N. norvegicus* larvae occurring over the entire western Irish Sea from approximately 52.8° N to 54.7° N. In the eastern basin stages I and II larvae were observed in significant numbers and stage III zoea were also collected.

Figures 5.39 to 5.47 show the distribution of *N. norvegicus* larvae from surveys, one in each season, in 1987 (Cirolana 5/87, 14-24 May, figure, 5.39), 1988 (Cirolana 4/88, 20 April-2 May, figure 5.40), 1989 (Cirolana 4/89, 16-28 April, figure 5.41), 1992 (Cirolana 5/92, 29 April-3 May, figure 5.42), 1993 (Cirolana 5/93, 8-30 May, figure 5.43) and 1994 (Cirolana 5/94, 29 April-3 May, figure 5.44). The larval distribution observed during these surveys followed the general patterns already described. The April surveys in 1988 and 1989 (Cirolana 4/88, figure 5.40 and Cirolana 4/89, figure 5.41) show a high proportion of the planktonic lobsters in the inshore waters close to the Irish coast and few south of latitude 53.5° N. The hatching season in 1989 seemed to be at an earlier stage than it was at

approximately the same time in 1988 and indeed some other years *eg.* 1985, 1995 and 1996 (tables 5.2 and 5.14). The abundances of stage I and, particularlly, stage II larvae in 1989, were lower than at a corresponding time during the other years. In addition, no stage III zoea were identified during Cirolana 4/89 while for the other mid-late April surveys their presence was already noted. May surveys (Cirolana 5/87, figure 5.39 and Cirolana 5/93, figure 5.43) showed the lobster larvae more dispersed towards the south with many observations registered in the area between Skerries and Dublin Bay and further south, particularly during survey Cirolana 5/93. This survey covered most of the month of May and therefore comparisons of production values with other surveys are impossible to judge. The abundances of larvae estimated for Cirolana 5/87 were lower than the calculations made for a similar period in 1995 (Cruise 13+Corystes 5b/95). Cruises Cirolana 5/92 (figure 5.42) and Cirolana 5/94 (figure 5.44) comprised a very limited number of sampling sites but were carried out at exactly the same dates in 1992 and 1994, respectively. In the small area between 53.6° N and 54.0° N and 5.5° W and 6.1° W, covered in both surveys, a higher number of lobster larvae was observed during the 1992 survey than during the 1994 cruise. Observations from the 1992 sampling study showed the presence of all three zoeal stages while during the 1994 survey only stages I and II were detected.

The observations from cruise Corystes 7/94 (17-30 June 1994, figure 5.45) can not be compared with the data from the other surveys because sampling was carried out by operating vertical hauls with a standard, 1 m diameter, net. This method proved quite inadequate to sample *N. norvegicus* larvae. The operation of the net was difficult due to the tidal currents and no means of assessing the volume of water filtered was available. Vertical hauls also sample a relatively small volume of water compared to the amount that goes through the net during a double oblique tow performed by a HSTN sampler. For this reason, and also because Corystes 7/94 was carried out towards the end of the season, very few lobster larvae were collected during this survey. It is nevertheless interesting to look at the plot of the observations from this cruise because it included several sampling sites across the North Channel, an area not covered by any of the other studies. In this region, lobster larvae were observed along the four transects sampled. It is impossible to determine the origin of these individuals. The Irish Sea, the Clyde Sea and the Sound of Jura, all areas where *N. norvegicus* populations are established, are possible sources.

Figures 5.46 and 5.47 show the distribution and abundance of larvae during two surveys in 1996. The first survey (Cirolana 4b/96) was carried out at the begining of the hatching period, between 13 and 23 April, and the second, at the end of the season between 12 and 14 of July. During Cirolana 4b/96 survey (figure 5.46), the distribution of larvae showed the general features highlighted during other studies carried out at the same time of the year. Larvae were present mainly in the deeper, central western Irish Sea, over the adults ground. The distribution did not extented south of 53.5° N but was evident in the northern section up to the North Channel, a pattern that was not observed during the 1995 season (Cruise 9+10) but was noticed during surveys Corella 5/82 and Clione 5/85, carried out roughly during the same period of the year. As for Clione 5/85, but not Corella 5/82 or Cruise 9+10/95, stage III larvae were already present although in very small numbers. The abundance of stage I zoea during Cirolana 4b/96 was comparable to the figure estimated for Clione 5/85 but larger than the values for Corella 5/82 and Cruise 9+10/95 (tables 5.2 and 5.14). Stage II production was higher during Cirolana 4b/96 than in the other surveys mentioned above.

By July, during the same year, (Corystes 9/96, figure 5.47) very few lobster larvae were detected. It is however interesting to note that individuals of all three zoeal stages were collected and that in fact more stage I larvae were observed than stages II or III (see also table 5.1). Although a few larvae were collected during this survey it is probably right to assume that the hatching season was virtually over. Maybe the very few larvae still present were produced by late, out of season, hatching by some females that had spawned late in the previous summer. There is no evidence to suggest a second peak of production of *N. norvegicus* larvae in the western Irish Sea. Still, these results may indicate that some recruitment may occur as late as July. During this survey no postlarvae were observed.

In summary, the larval distribution observations in the western Irish Sea during the period from 1982 to 1994 and 1996 showed the general patterns highlighted during the 1995 season. Earlier in the season (April), *N. norvegicus* zoea were observed dispersed over the centre of the basin but also with a clear concentration of individuals over the southern limit of the adults habitat and further south to a region south of Dublin Bay. The first larvae to be observed in this southern areas were stage I zoea. Stages II and III zoea appeared in the same region in subsequent surveys when they dominated the larval population in the region. In general, the distribution of stages II and III larvae were more spread towards the south than

the distribution of stage I lobsters. However, during this set of observations it seemed that the displacement of larvae to the south did not reach the magnitude observed during the 1995 season. The high number of lobster larvae in the coastal waters of Ireland, noted in 1995, was not as evident, either. The suggestion that hatching may start later in the northern region of the western Irish Sea than in the southern sector, outlined during the 1995 season, was not confirmed by the results presented in this section. This fact implies that either the timing of hatching in the northern region in 1995 was somehow uncharacteristic, or that the larvae produced in this region earlier in that season drifted south. The distribution of the planktonic lobsters during the second half of the larval season was more dispersed over the entire western Irish Sea basin and lower concentrations of larvae were then observed south of 53.5° N, the limit of the mud patch region. The ensemble of data presented in this section also shows indication of some variability in the timing and magnitude of the larval production from sesaon to season. However, it seems apparent that the hatching peak occurs during the second quarter of May and that the production drops considerably towards the end of May begining of June. Larvae of all stages, in small numbers, can however be observed until July.

Distribution of postlarvae

Postlarvae of *N. norvegicus* (also commonly known as stage IV) are very rarely collected by plankton samplers, and indeed by any other sampling apparatus, and their distribution is not clearly known. During the 30 surveys included in this study only 142 postlarvae were observed (0.19% of the total larvae). Their absence from these surveys may partly be explained by the lack of sampling during the end of the season, in June, when they are more likely to occur in higher numbers. Considering that the peak of hatching occurs during the first half of May and that on average it takes about 50 days for a larvae to go through the three zoeal stages (results from this study) the majority of the postlarvae are likely to appear towards the end of June and even begining of July. High mortality during the previous stages (during the 1995 season in the western Irish Sea the losses between stages I and III amounted to 67.6%) also imply that abundance of individuals at this stage of development is much lower than the concentration of the zoeal stages. In consequence the probability of collecting postlarvae in significant numbers is much lower. In addition, it is thought that the postlarvae live in the bottom layers of the water column, close to the sea bed, and therefore probably below the reach of plankton samplers.

During the surveys considered in this study postlarvae were observed in considerable numbers in three occasions, Clione 7/82 (21 May-5 June), Cirolana 5.1/84 (25 May-1 June) and Cirolana 5.2/84 (12-13 June) (see table 5.1). The distribution of postlarvae from these cruises is presented in figures 5.48, 5.49 and 5.50, respectively. During Clione 7/82 survey, 160 sampling stations were visited and 87 postlarvae were collected representing 1% of the total larvae observed. The postlarvae were detected on the edges of the mud patch region particularly on the south between latitude 52.8° N and 53.5° N. The highest concentrations were observed on the central area of the line between Dublin Bay and Holyhead. 21 postlarvae were observed at a site located at 53.34° N, 5.52° W, representing 4.3% of the total larvae collected at that station (4.2 postlarvae/m^2). At a neighbouring sampling station (53.33° N, 5.28° W), 14 individuals (6.2 postlarvae/m^2) at this stage of development were collected, representing 14.4% of the total *N. norvegicus* catch. A little further south (53.17° N, 5.23° W), 11 postlarvae (3.0 postlarvae/m^2) were observed representing 18.0% of the total larvae collected at that station. Some individuals were also noted south of the Isle of Man, to the east of the muddy region. On average during this Clione 7/82 survey the abundance of postlarvae in the study area was 0.18 individuals/m^2.

During Cirolana 5.1/84 (figure 5.49) and 5.2/84 (figure 5.50) studies, postlarvae were collected all over the central western Irish Sea over the region of the adults habitat, this fact is clearer during the first survey which included a greater number of sampling sites. For the first, survey 67 stations were sampled and 22 postlarvae collected, representing 0.4% of the total larvae observed. During the second survey (the latest in June not considering Corystes 7/94) only 14 sites were visited and 20 postlarvae were collected, representing 2.5% of the total catch of larvae. During Corystes 7/94 (17-30 June), 2 postlarvae were identified representing 2% of the total number of individuals collected during that survey. Table 5.1 shows that postlarvae of *N. norvegicus* were noted as earlier as begining of May (Cirolana 4/88) but particularly in late May and June.

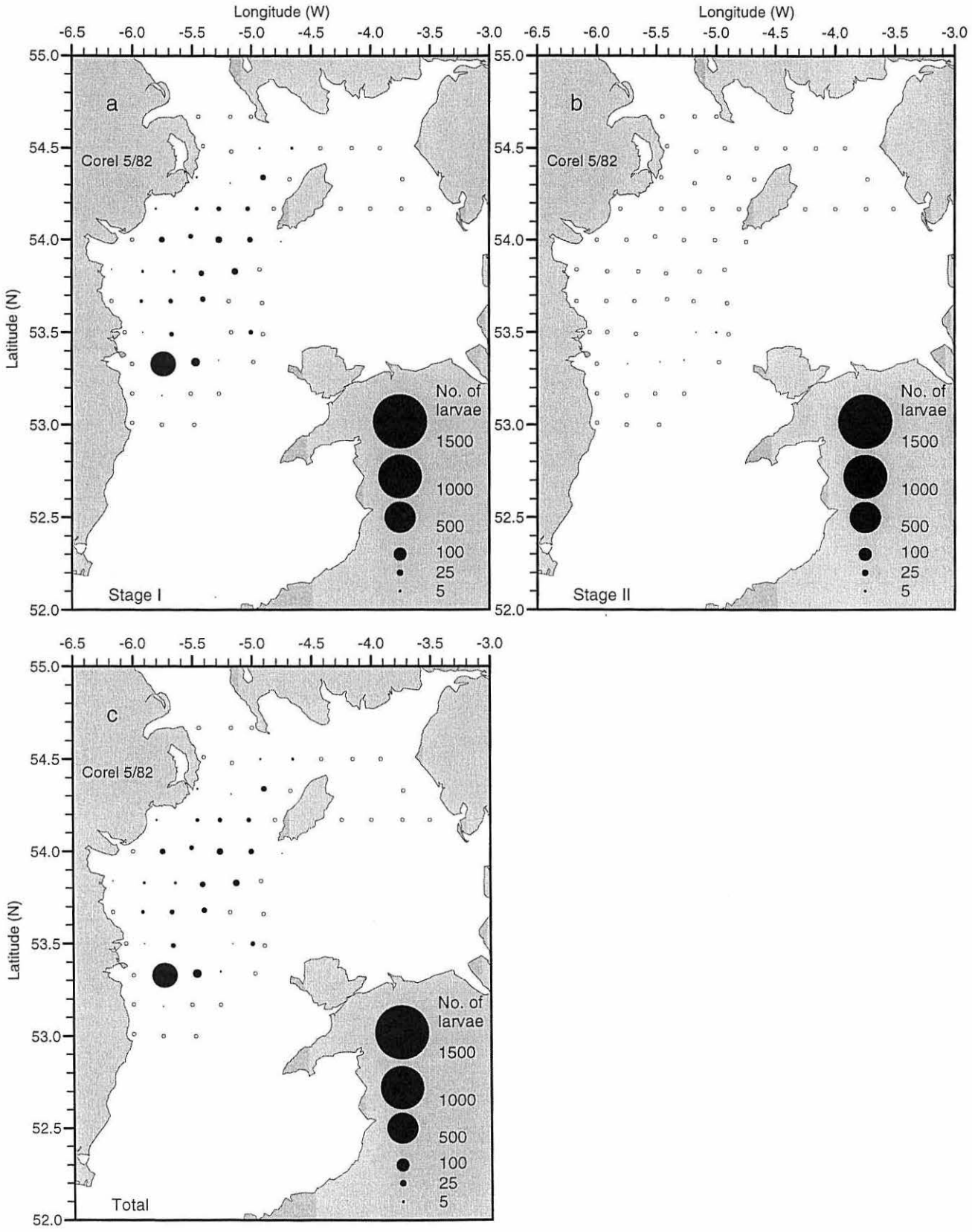


Figure 5.31. Number of *N. norvegicus* larvae per developmental stage from survey Corella 5/82, 9-13 April 1982. (a) stage I, (b) stage II, (c) total. Open circles denote sampling sites where no larvae were observed.

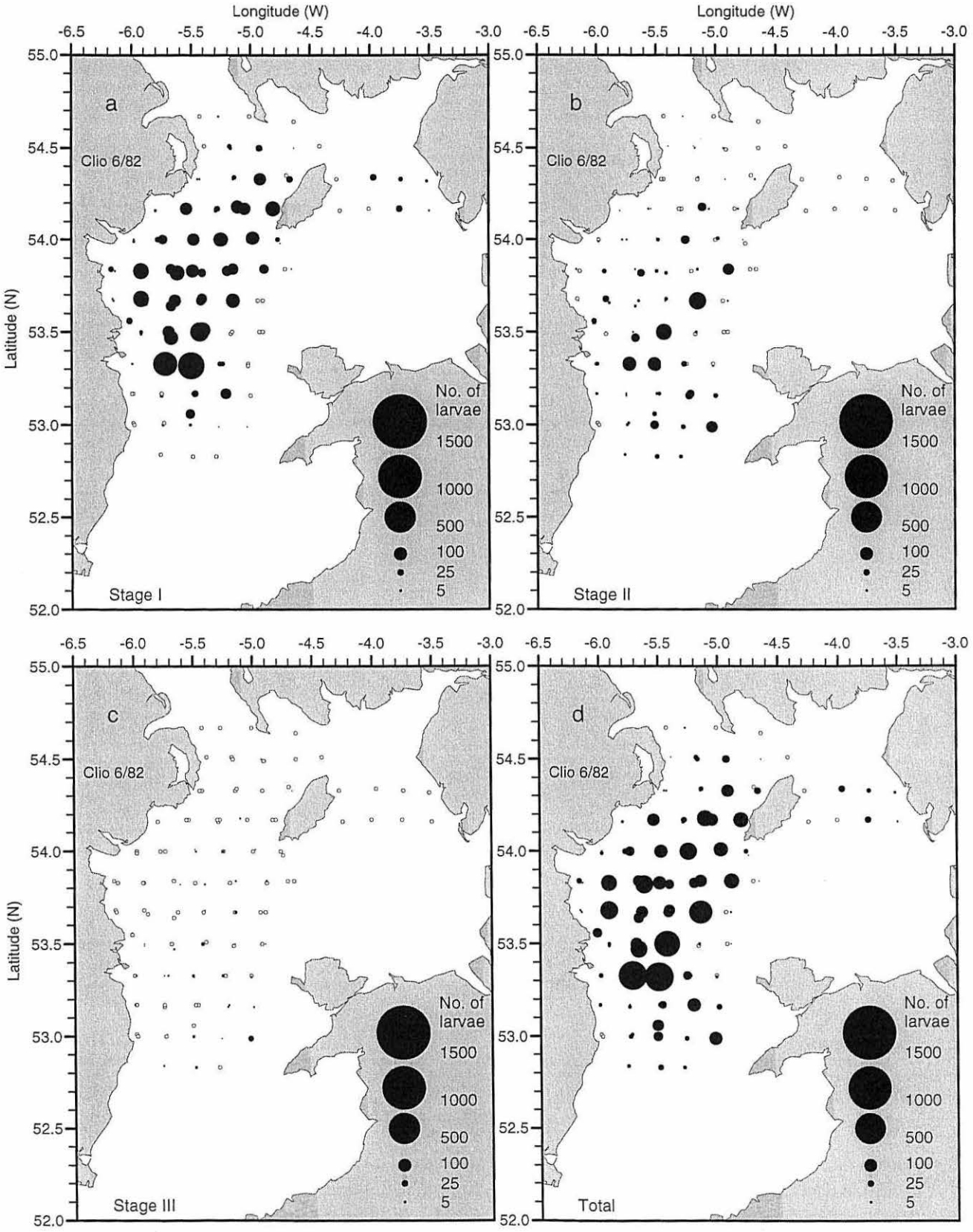


Figure 5.32. Number of *N. norvegicus* larvae per developmental stage from survey Clione 6/82, 28 April-31 May 1982. (a) stage I, (b) stage II, (c) stage III, (d) total. Open circles denote sampling sites where no larvae were observed.

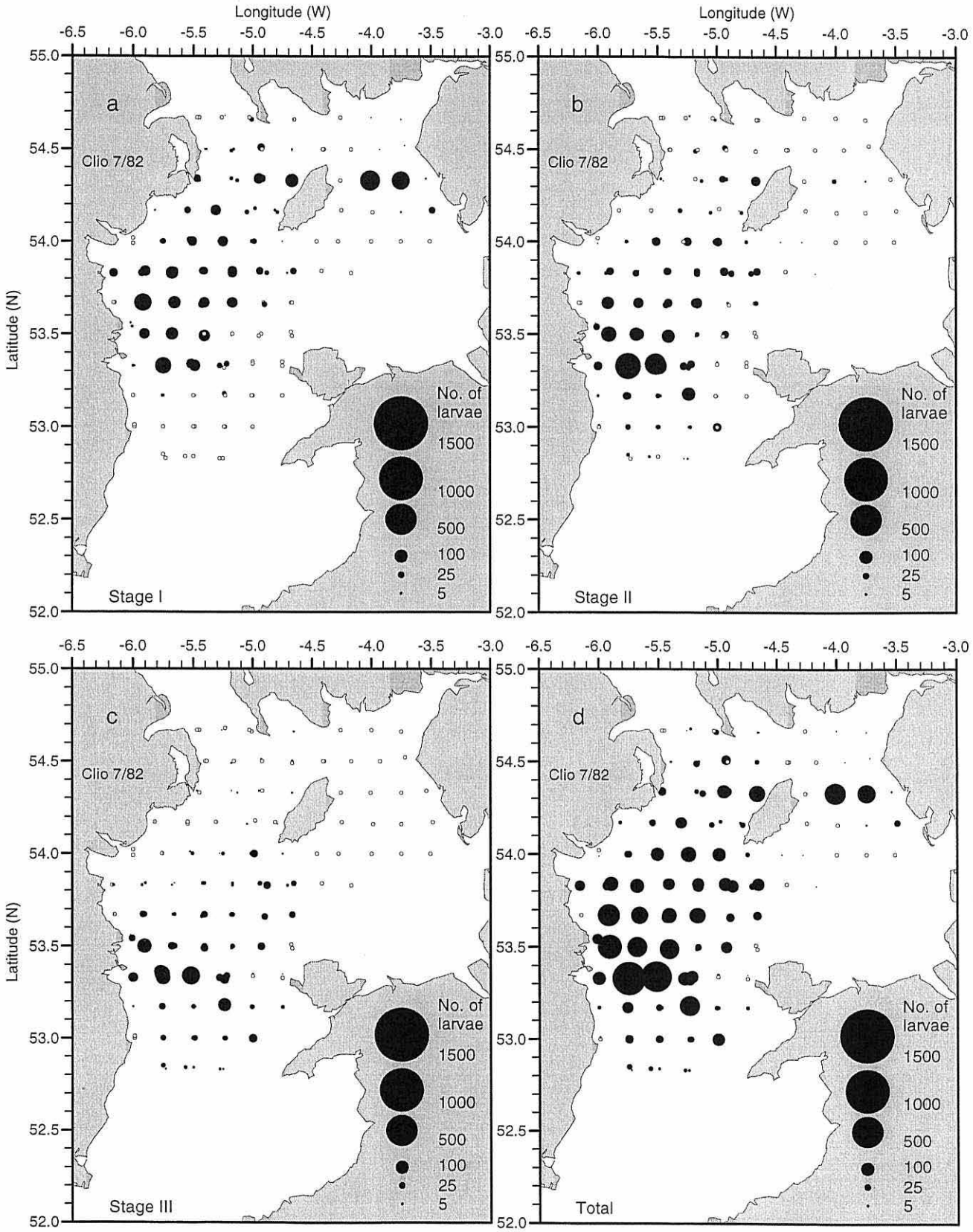


Figure 5.33. Number of *N. norvegicus* larvae per developmental stage from survey Clione 7/82, 21 May-5 June 1982. (a) stage I, (b) stage II, (c) stage III, (d) total. Open circles denote sampling sites where no larvae were observed.

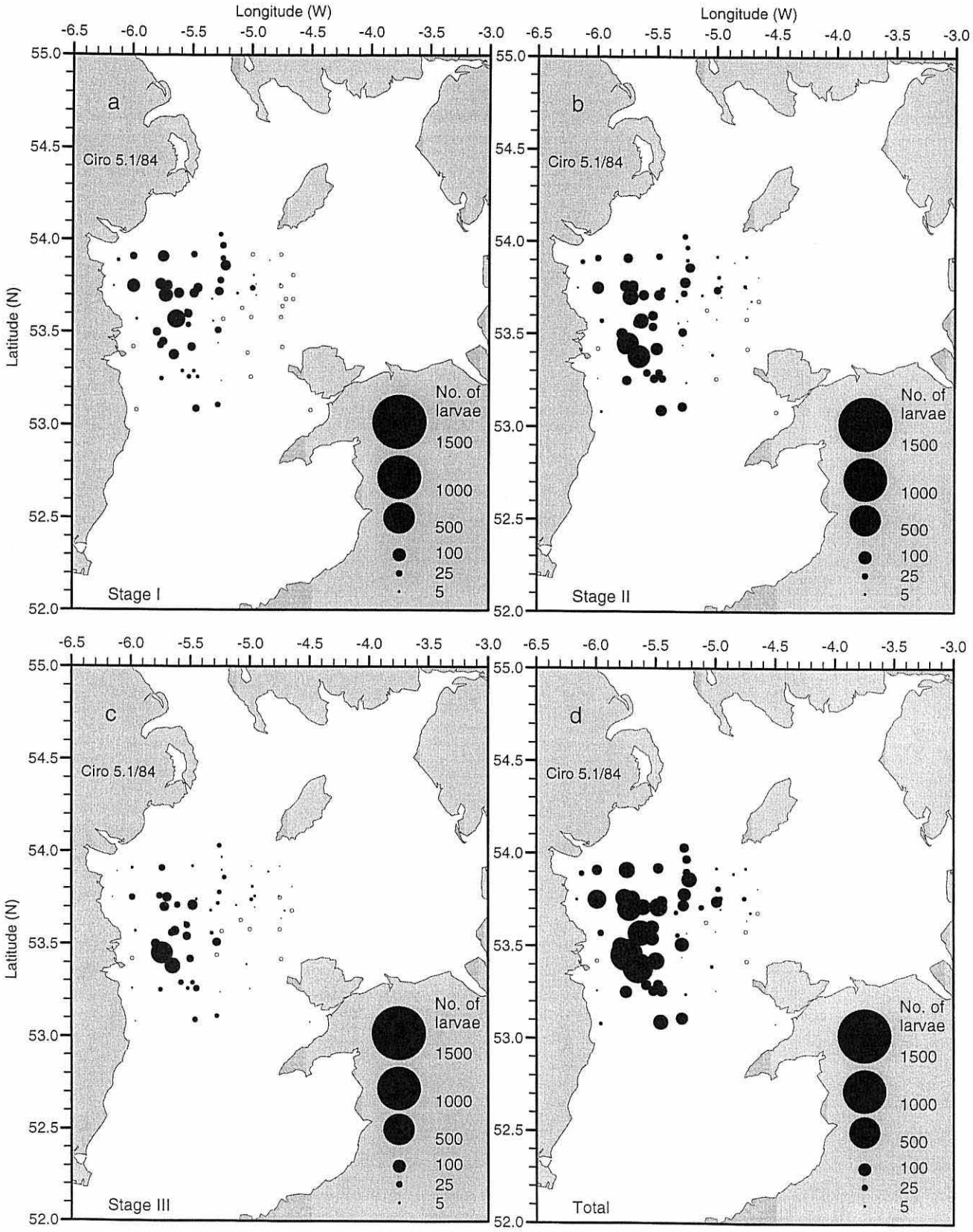


Figure 5.34. Number of *N. norvegicus* larvae per developmental stage from survey Cirolana 5.1/84, 25 May-1 June 1984. (a) stage I, (b) stage II, (c) stage III, (d) total. Open circles denote sampling sites where no larvae were observed.

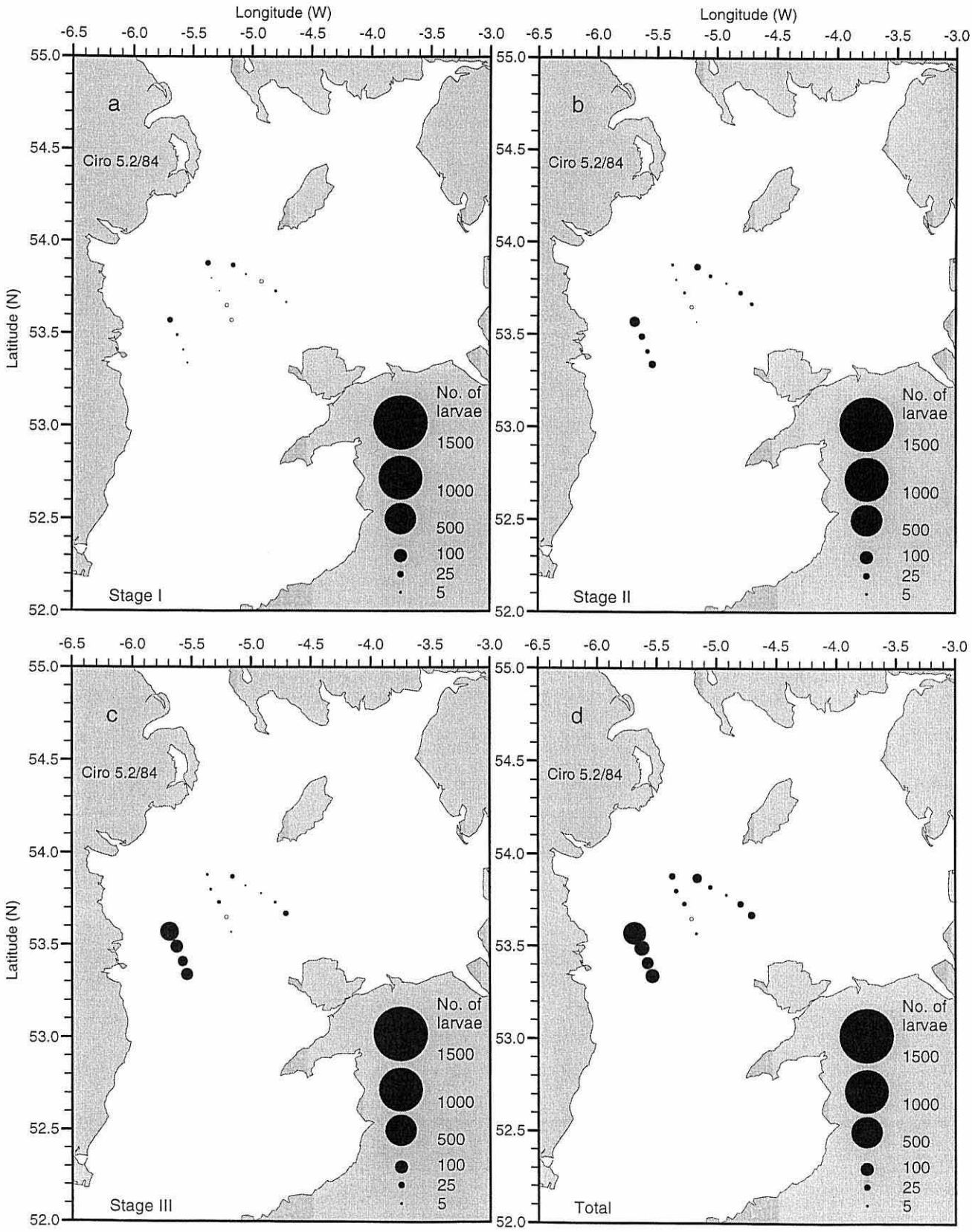


Figure 5.35. Number of *N. norvegicus* larvae per developmental stage from survey Cirolana 5.2/84, 12-13 June 1984. (a) stage I, (b) stage II, (c) stage III, (d) total. Open circles denote sampling sites where no larvae were observed.

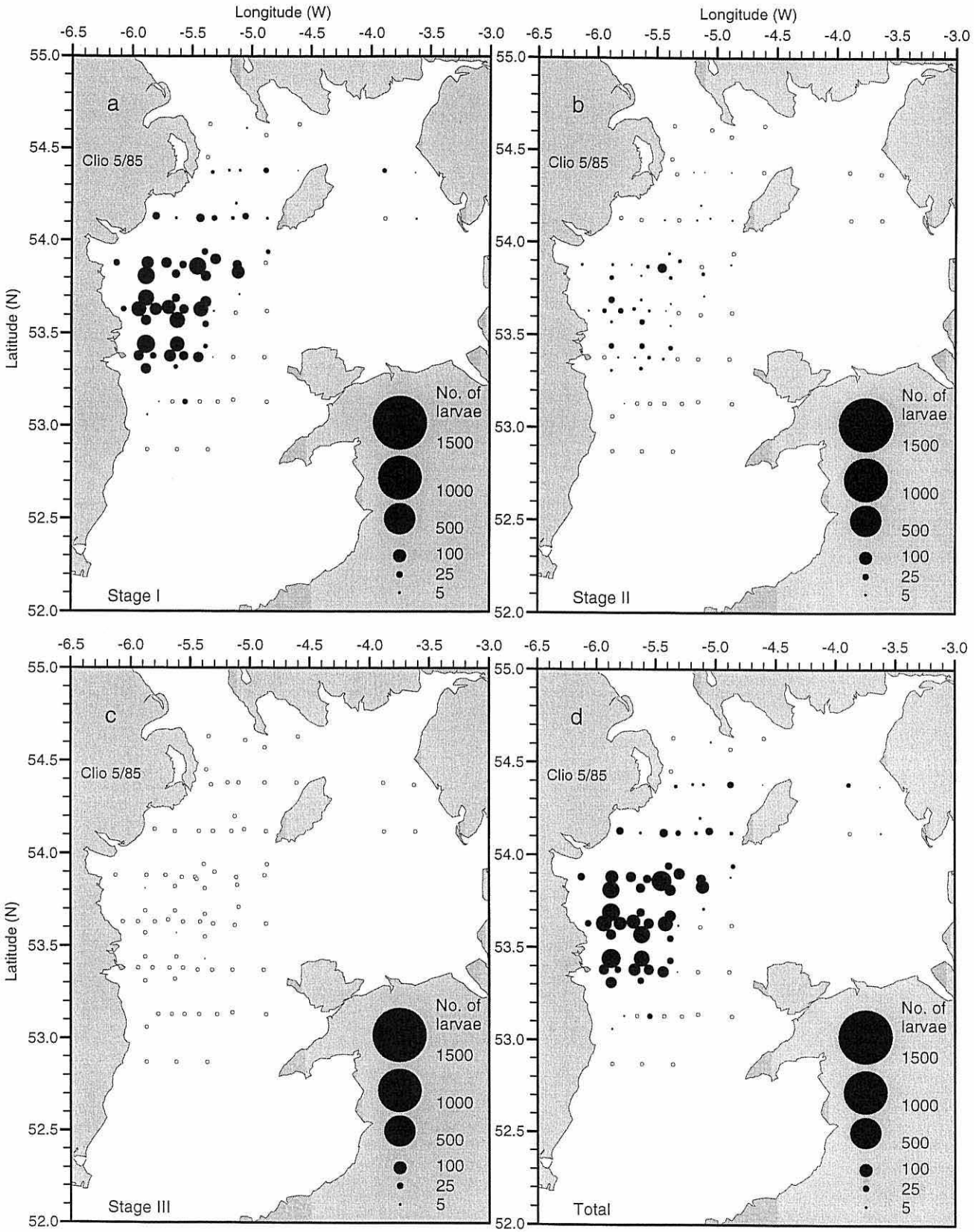


Figure 5.36. Number of *N. norvegicus* larvae per developmental stage from survey Clione 5/85, 15-19 April 1985. (a) stage I, (b) stage II, (c) stage III, (d) total. Open circles denote sampling sites where no larvae were observed.

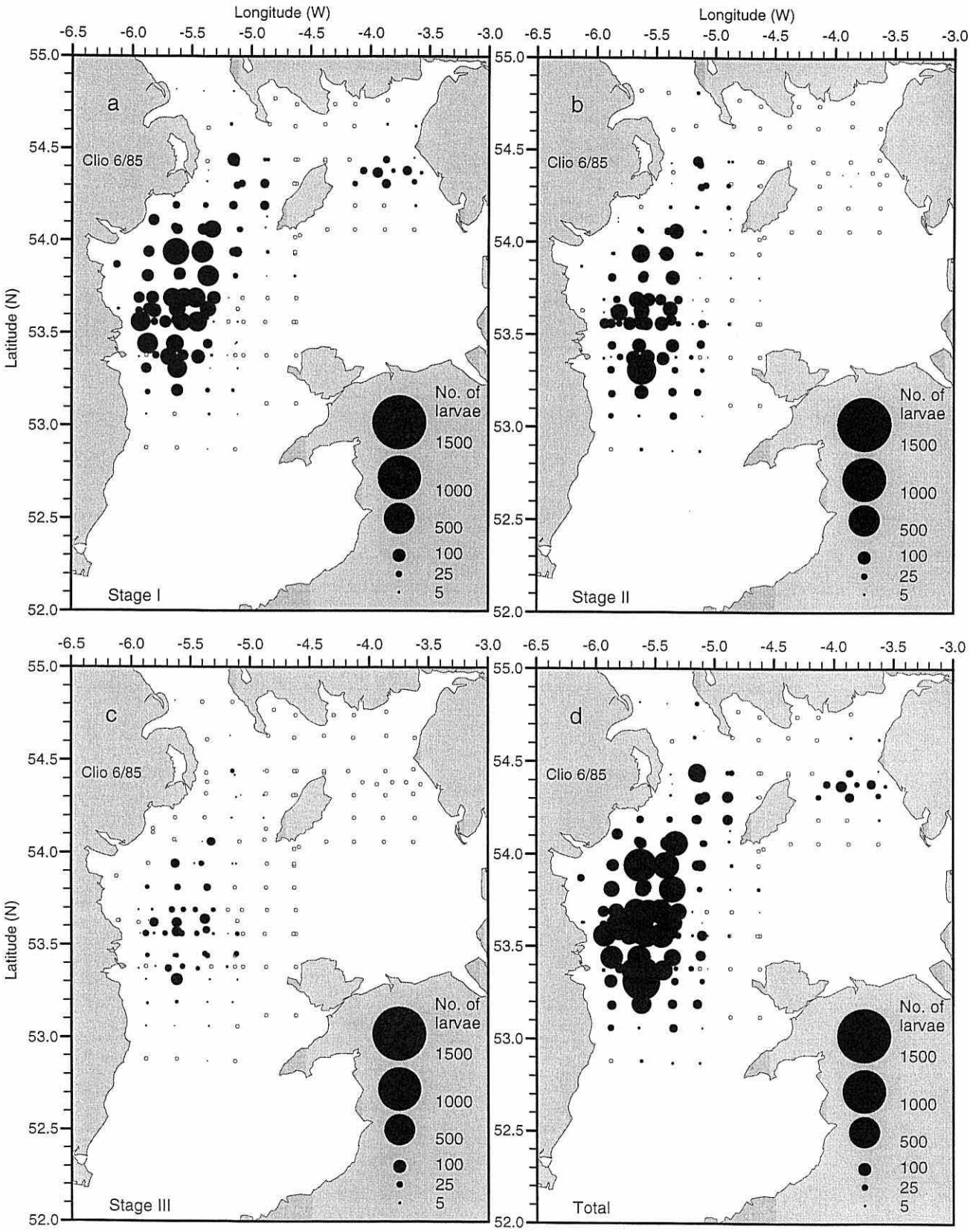


Figure 5.37. Number of *N. norvegicus* larvae per developmental stage from survey Clione 6/85, 11-26 May 1985. (a) stage I, (b) stage II, (c) stage III, (d) total. Open circles denote sampling sites where no larvae were observed.

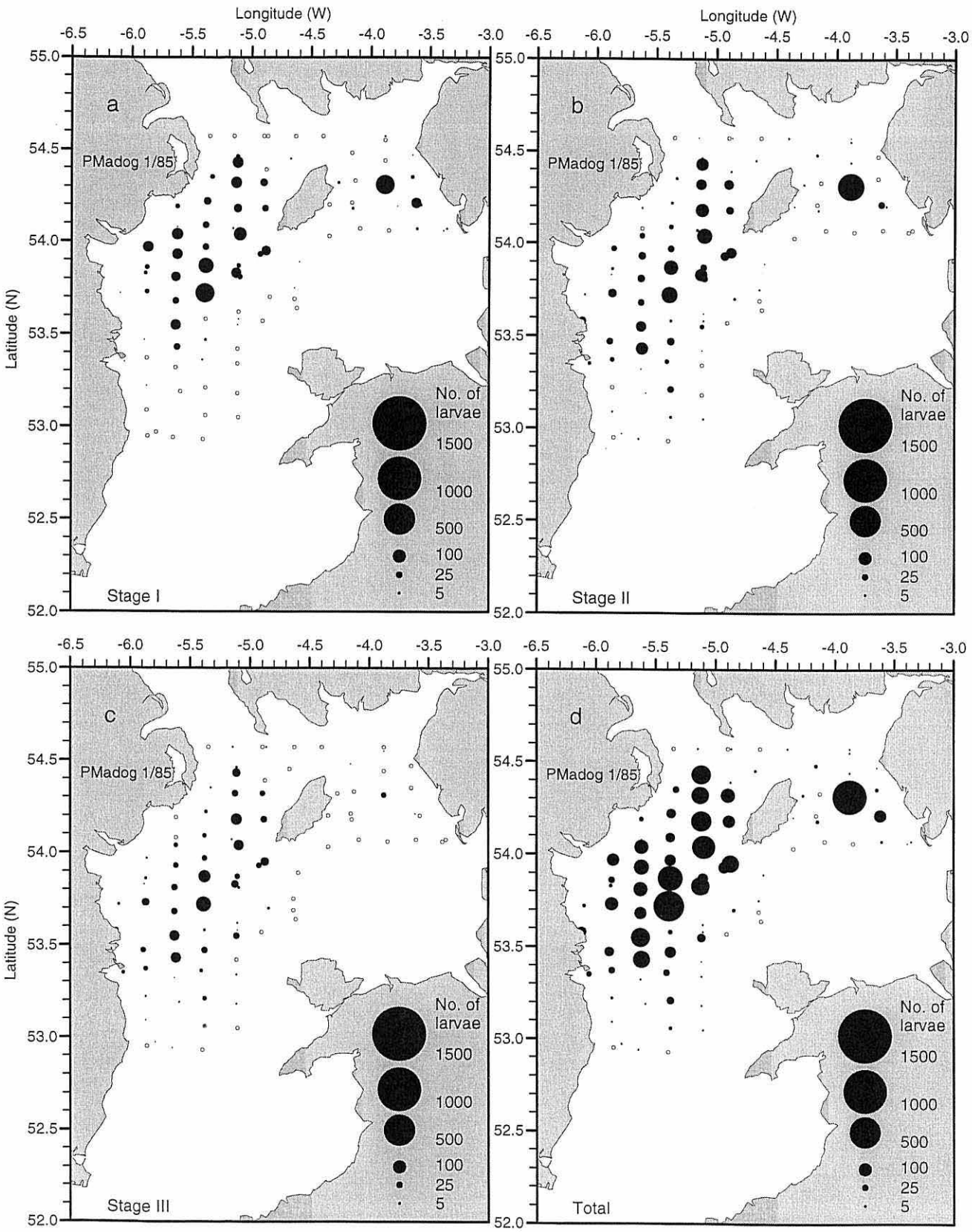


Figure 5.38. Number of *N. norvegicus* larvae per developmental stage from survey P. Madog 1/85, 27 May-6 June 1985. (a) stage I, (b) stage II, (c) stage III, (d) total. Open circles denote sampling sites where no larvae were observed.

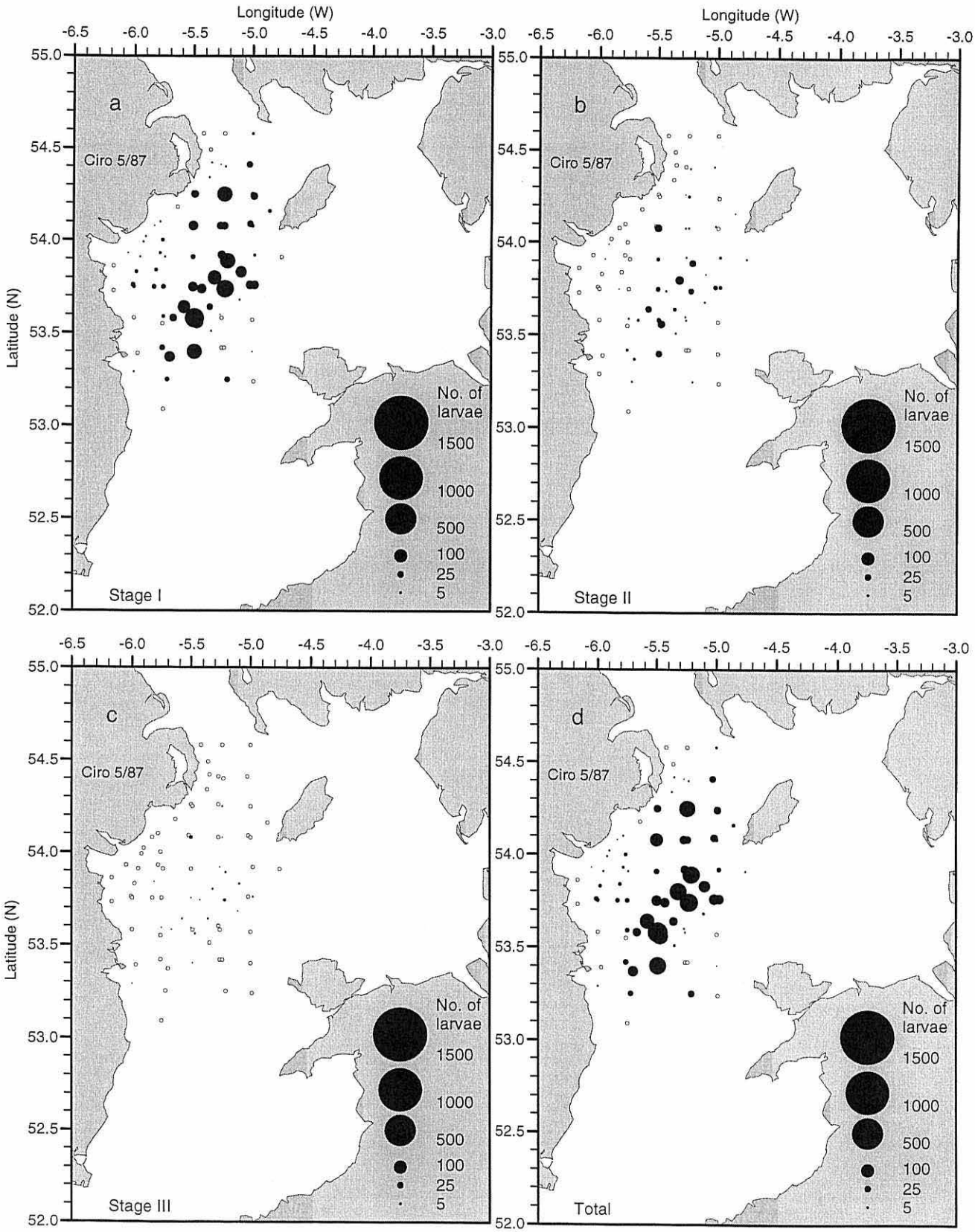


Figure 5.39. Number of *N. norvegicus* larvae per developmental stage from survey Cirolana 5/87, 14-24 May 1987. (a) stage I; (b) stage II, (c) stage III, (d) total. Open circles denote sampling sites where no larvae were observed.

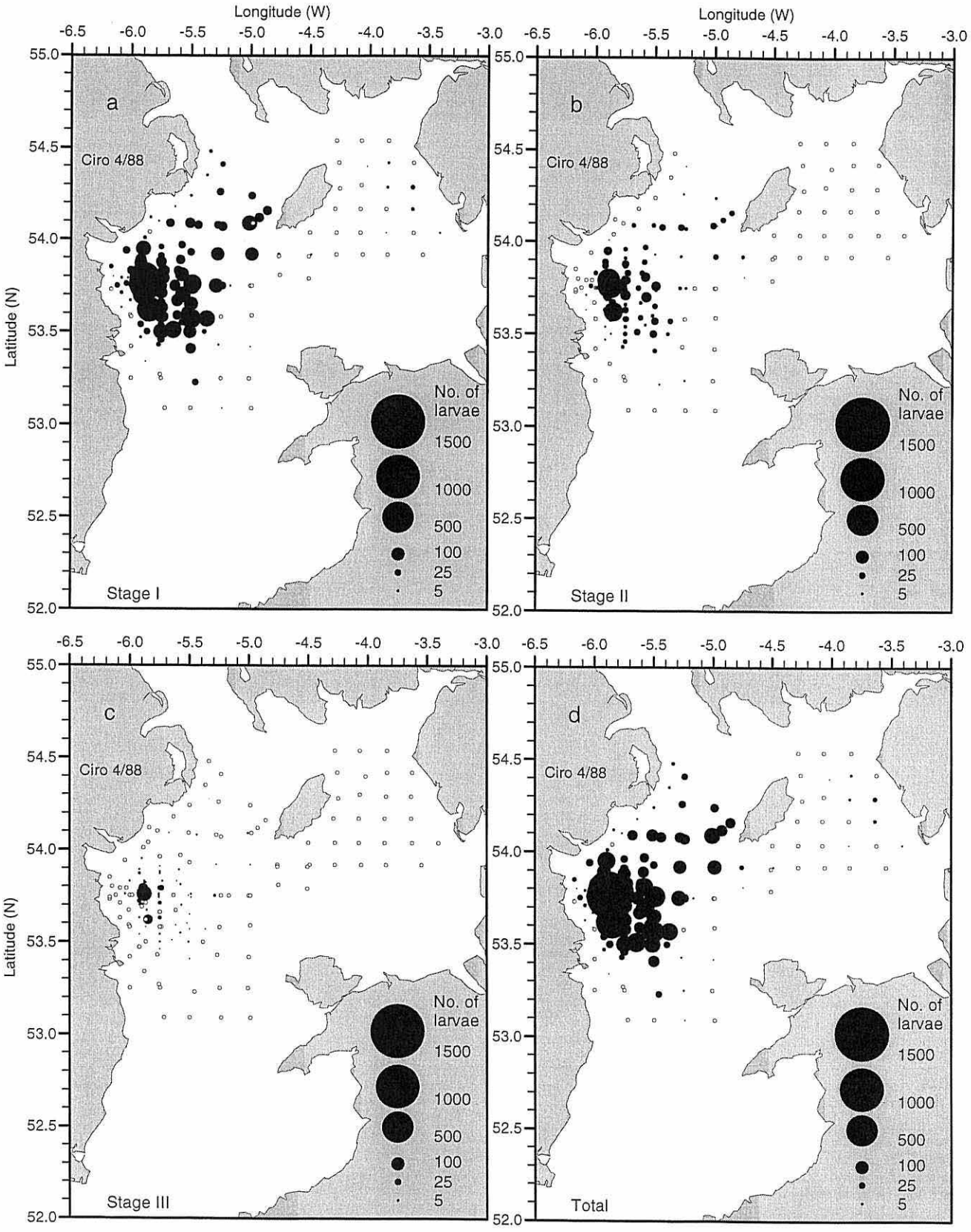


Figure 5.40. Number of *N. norvegicus* larvae per developmental stage from survey Cirolana 4/88 , 20 April-2 May 1988. (a) stage I, (b) stage II, (c) stage III, (d) total. Open circles denote sampling sites where no larvae were observed.

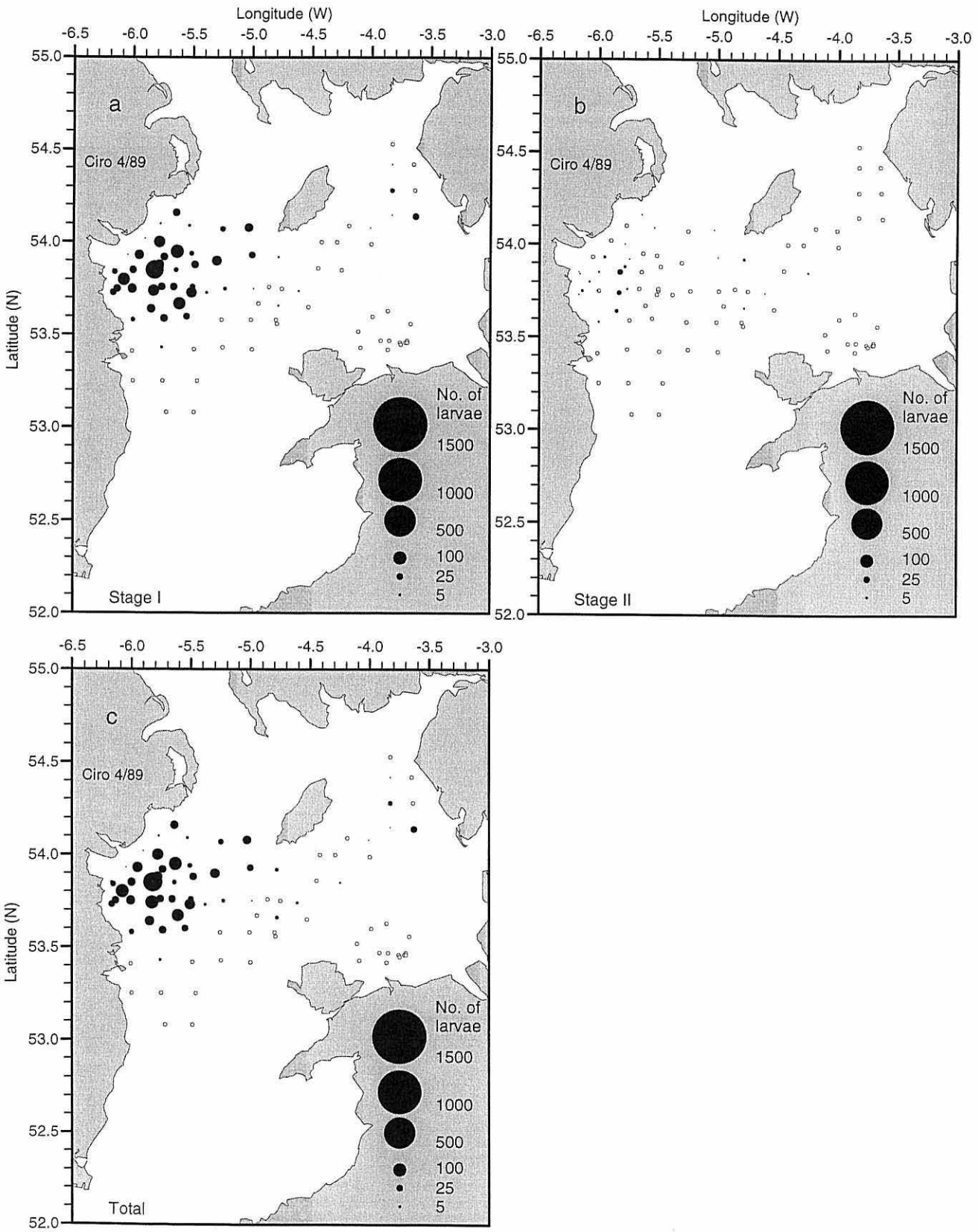


Figure 5.41. Number of *N. norvegicus* larvae per developmental stage from survey Cirolana 4/89, 16-28 April 1989. (a) stage I, (b) stage II, (c) total. Open circles denote sampling sites where no larvae were observed.

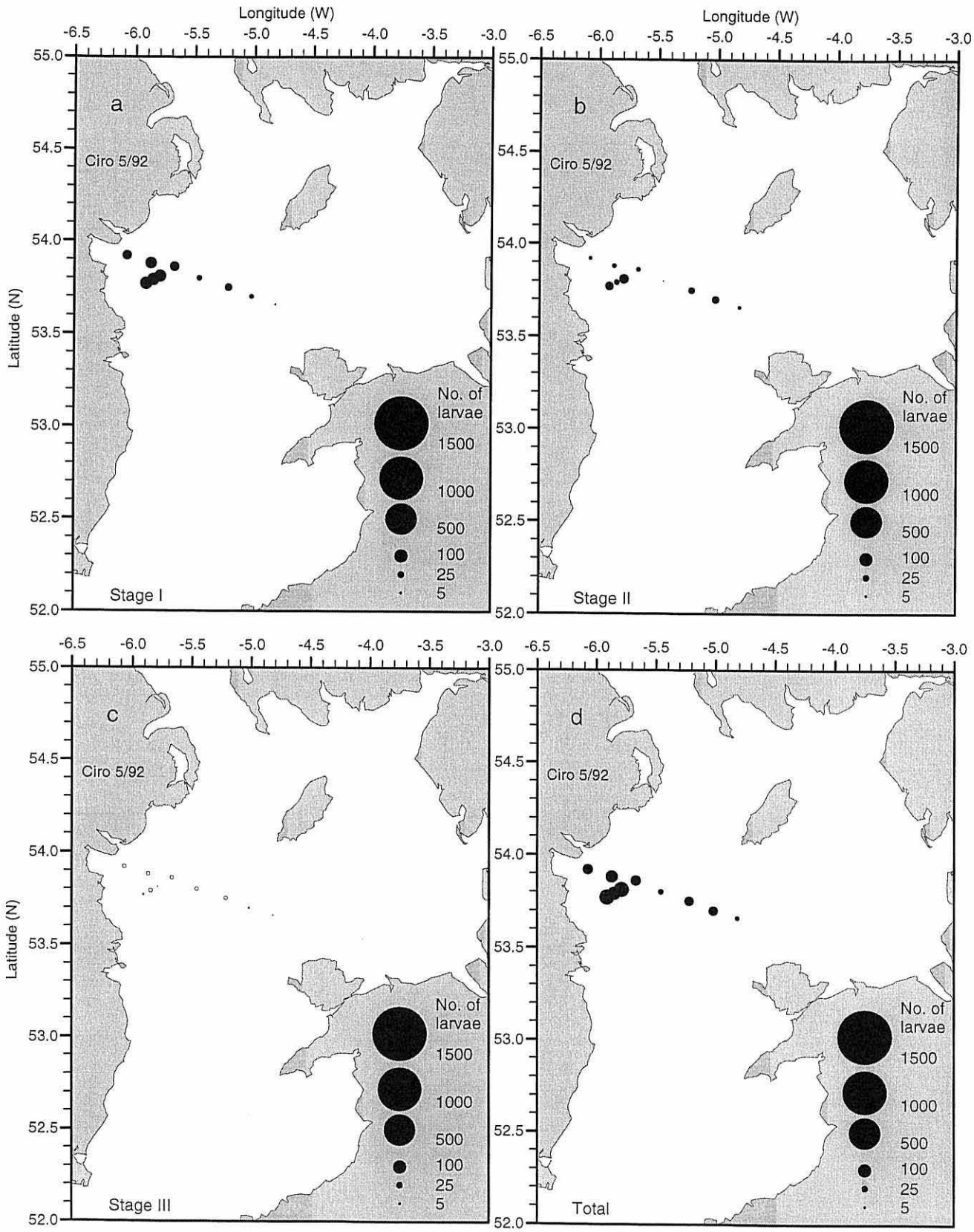


Figure 5.42. Number of *N. norvegicus* larvae per developmental stage from survey Cirolana 5/92, 29 April-3 May 1992. (a) stage I, (b) stage II, (c) stage III, (d) total. Open circles denote sampling sites where no larvae were observed.

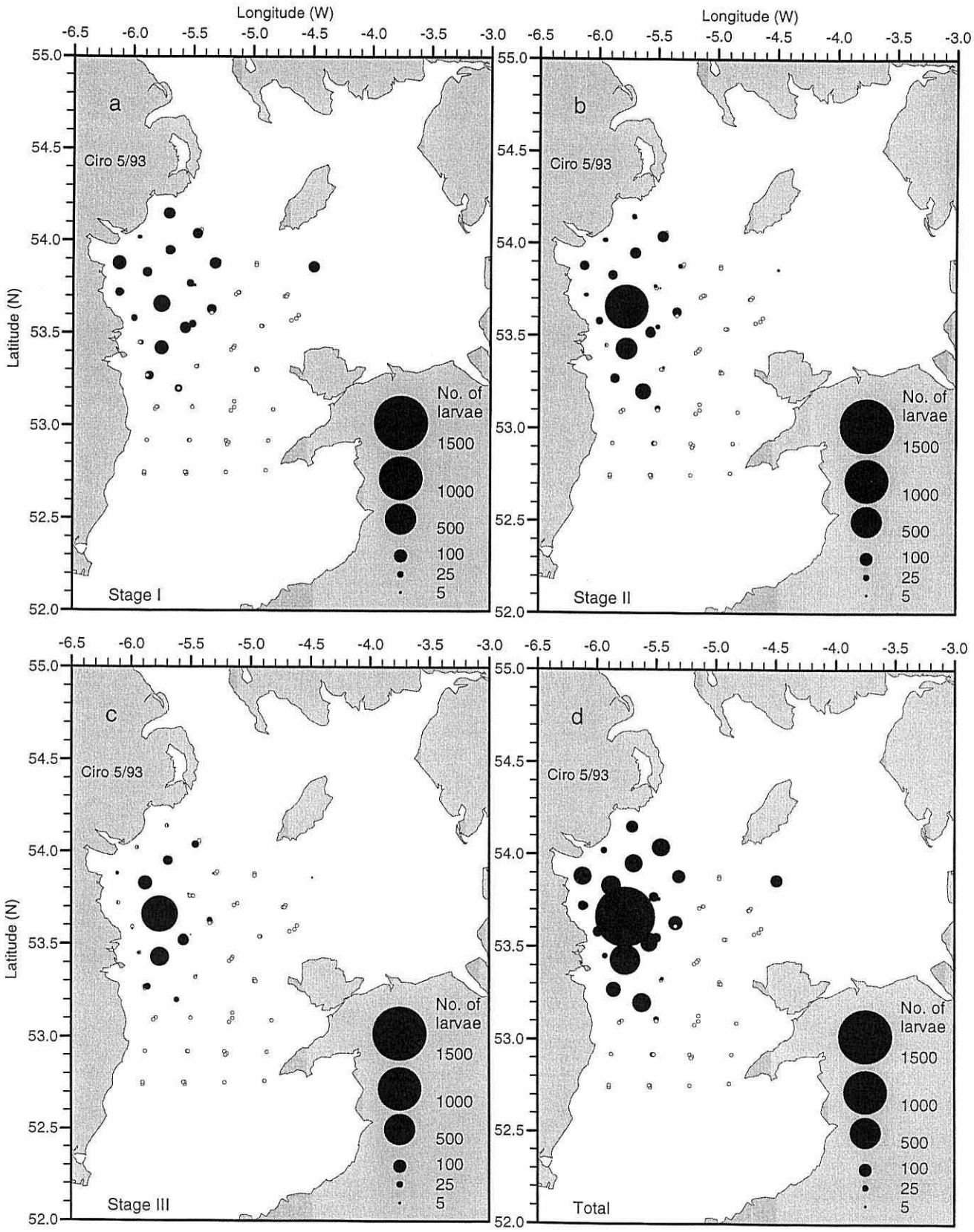


Figure 5.43. Number of *N. norvegicus* larvae per developmental stage from survey Cirolana 5/93, 8-30 May 1993. (a) stage I, (b) stage II, (c) stage III, (d) total. Open circles denote sampling sites where no larvae were observed.

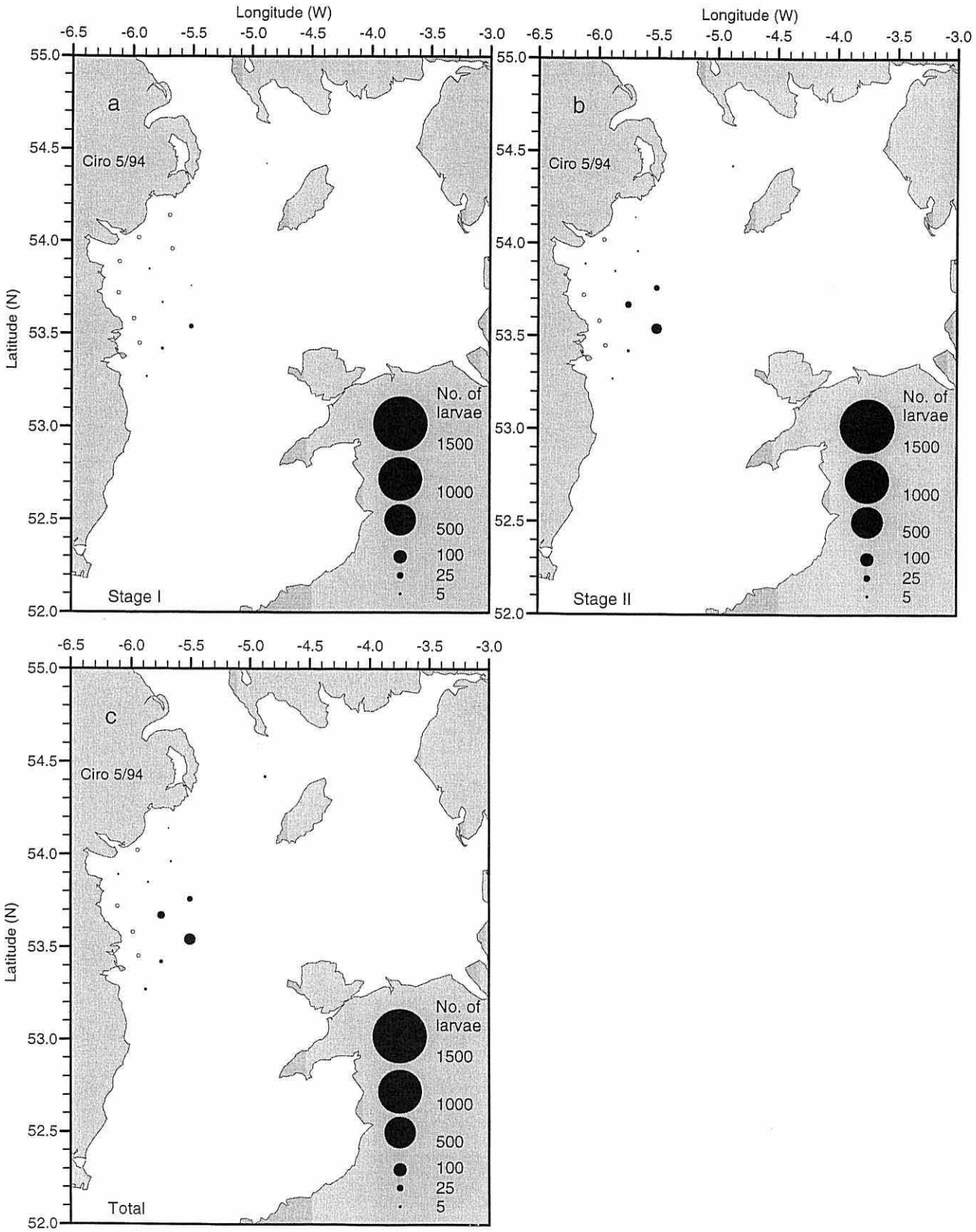


Figure 5.44. Number of *N. norvegicus* larvae per developmental stage from survey Cirolana 5/94, 29 April-3 May 1994. (a) stage I, (b) stage II, (c) total. Open circles denote sampling sites where no larvae were observed.

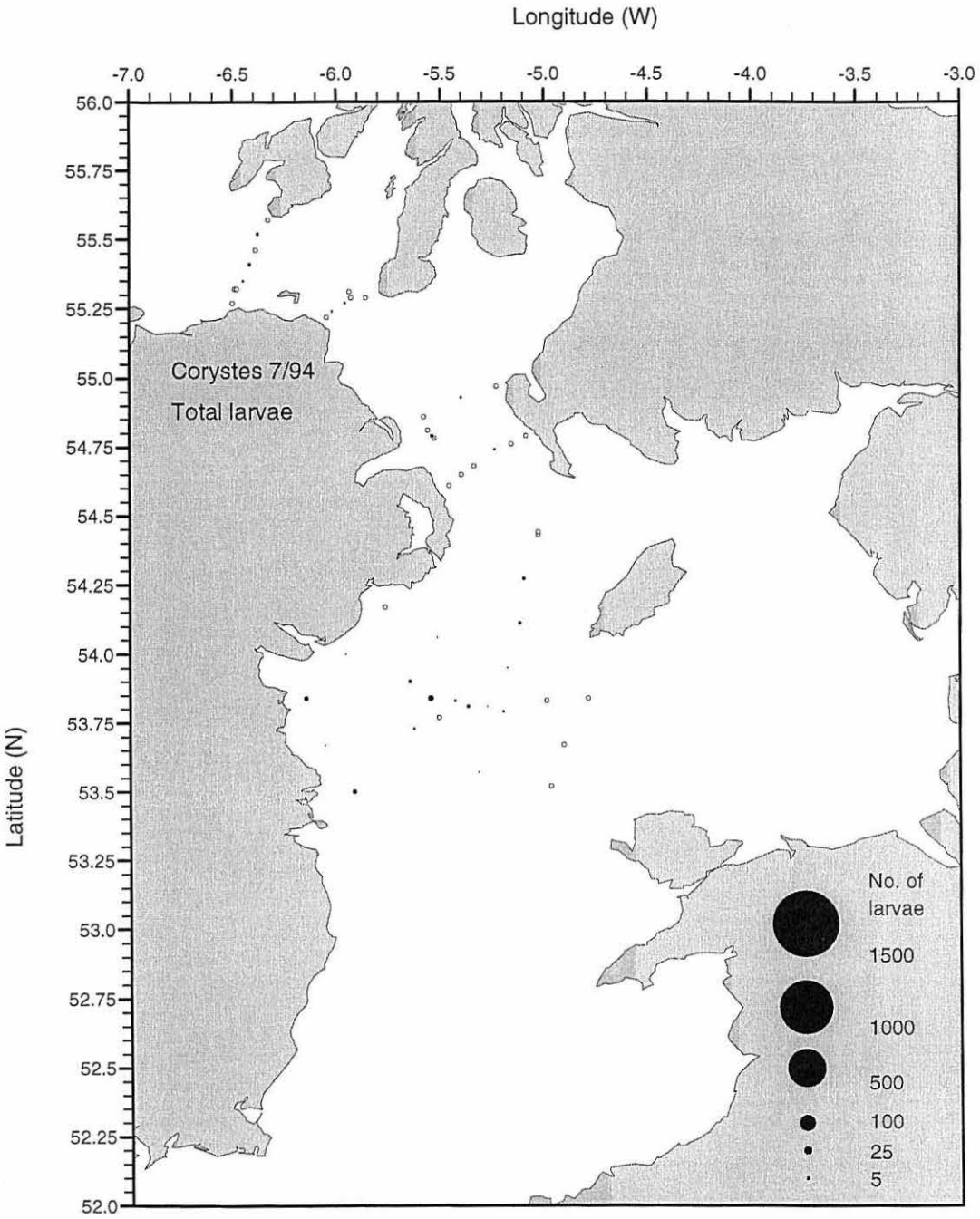


Figure 5.45. Number of *N. norvegicus* total larvae from survey Corystes 7/94, (17-30 June 1994). Sampling was carried out by vertical hauls using a 1m diameter, 200 μm mesh size, net. Open circles denote sampling sites where no larvae were observed.

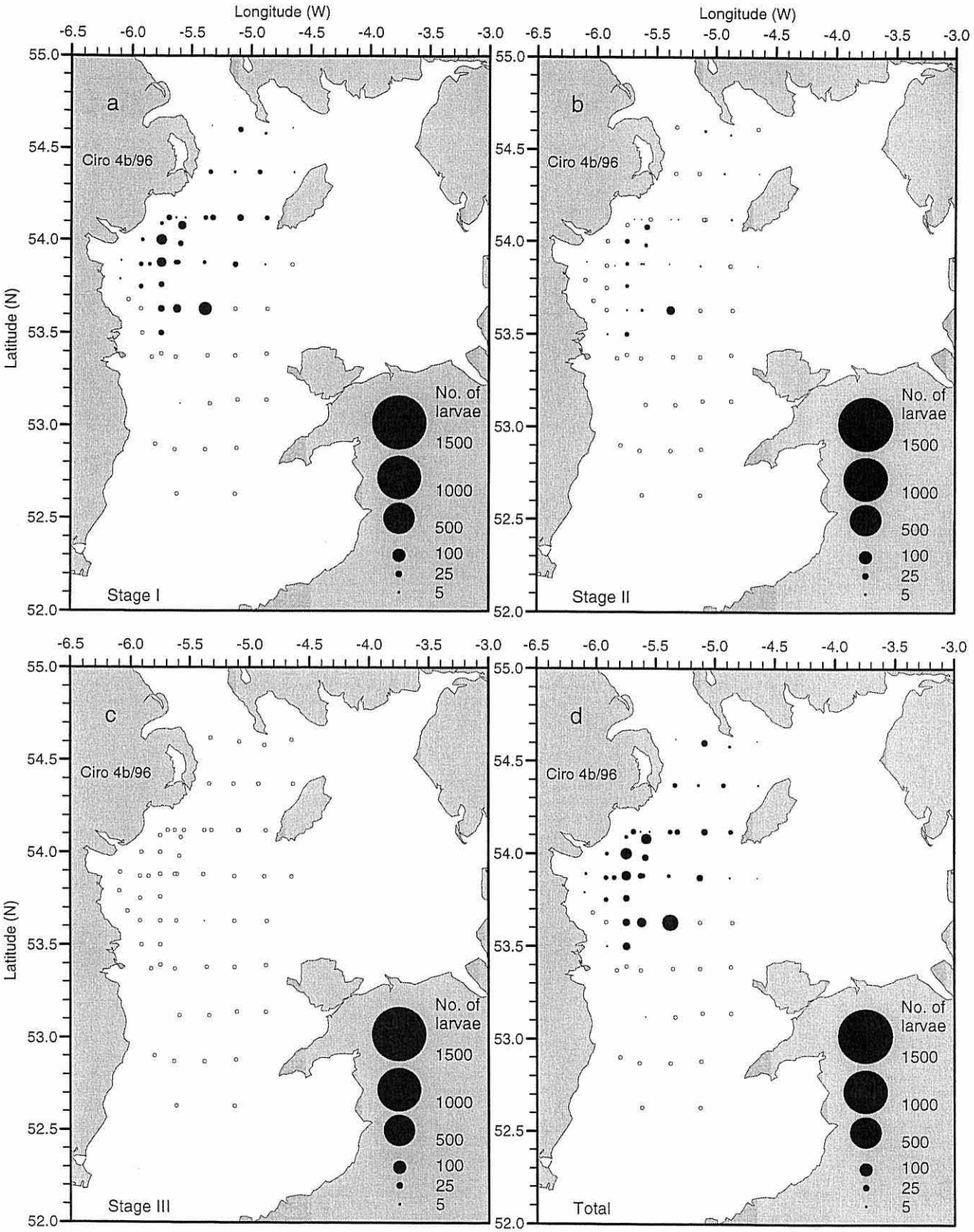


Figure 5.46. Number of *N. norvegicus* larvae per developmental stage from survey Cirolana 4b/96, 13-23 April 1996. (a) stage I, (b) stage II, (c) stage III, (d) total. Open circles denote sampling sites where no larvae were observed.

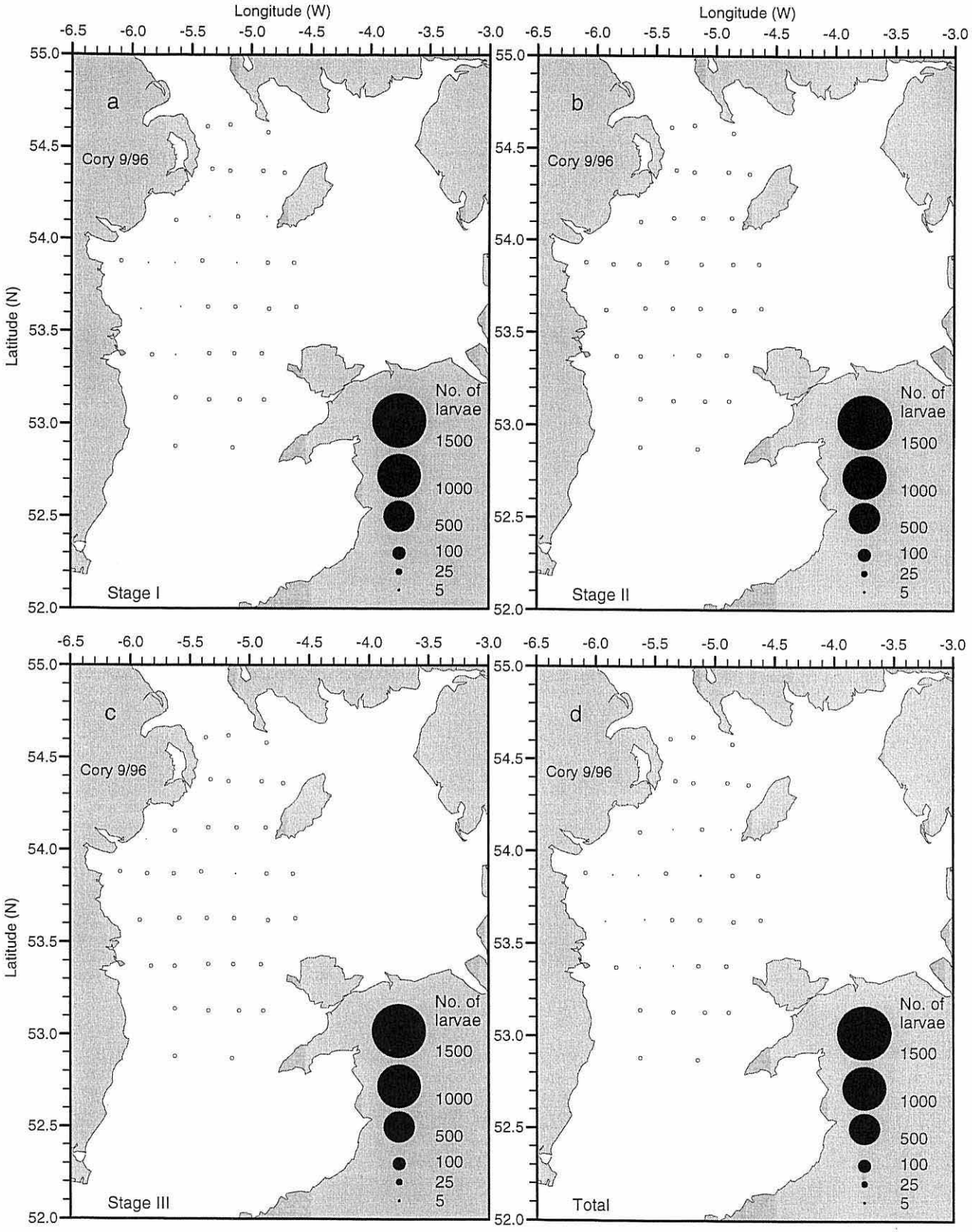


Figure 5.47. Number of *N. norvegicus* larvae per developmental stage from survey Corystes 9/96, 12-14 July 1996. (a) stage I, (b) stage II, (c) stage III, (d) total. Open circles denote sampling sites where no larvae were observed.

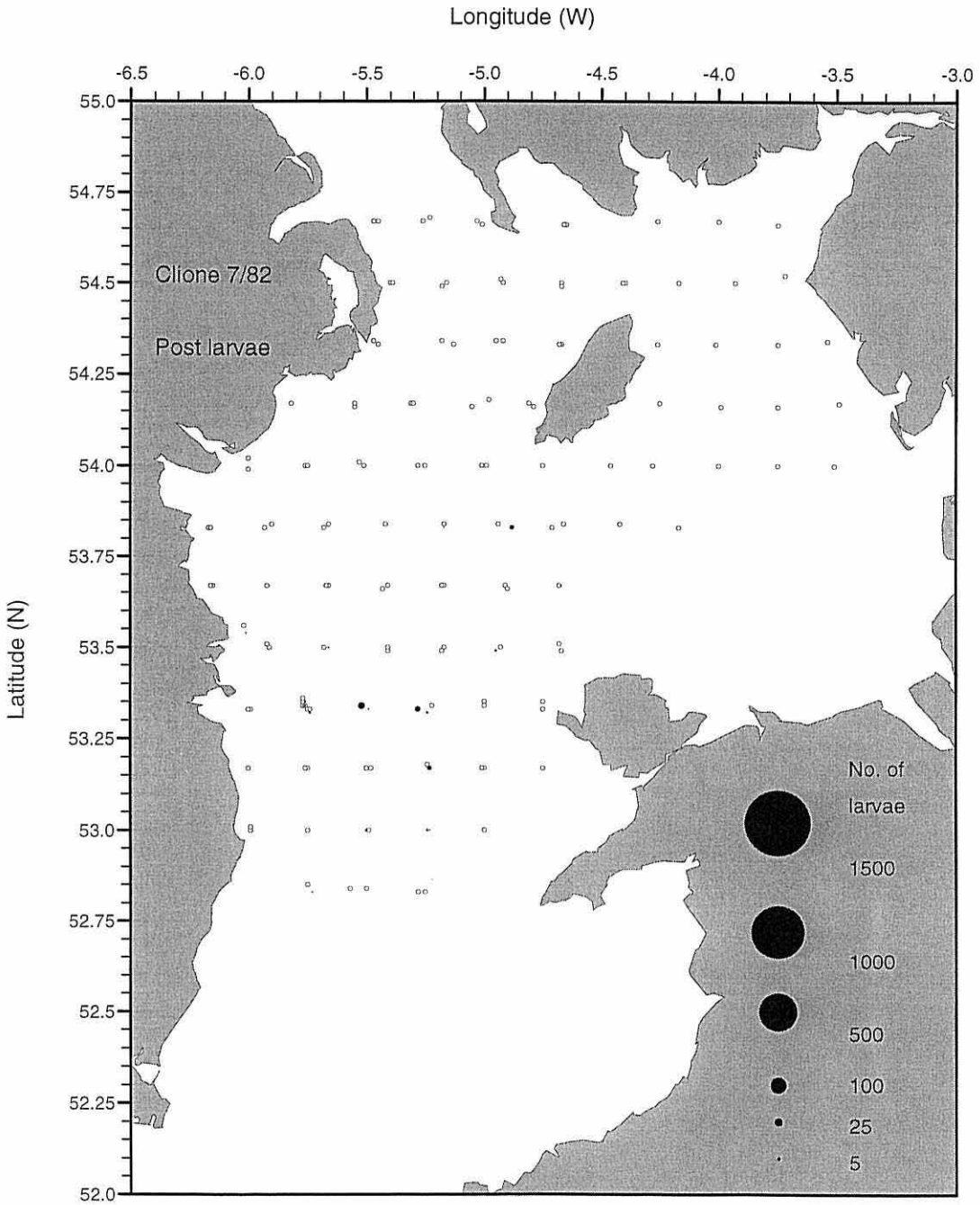


Figure 5.48. Number of *N. norvegicus* postlarvae from survey Clione 7/82 (21 May-5 June 1982). Open circles denote sampling sites where no larvae were observed.

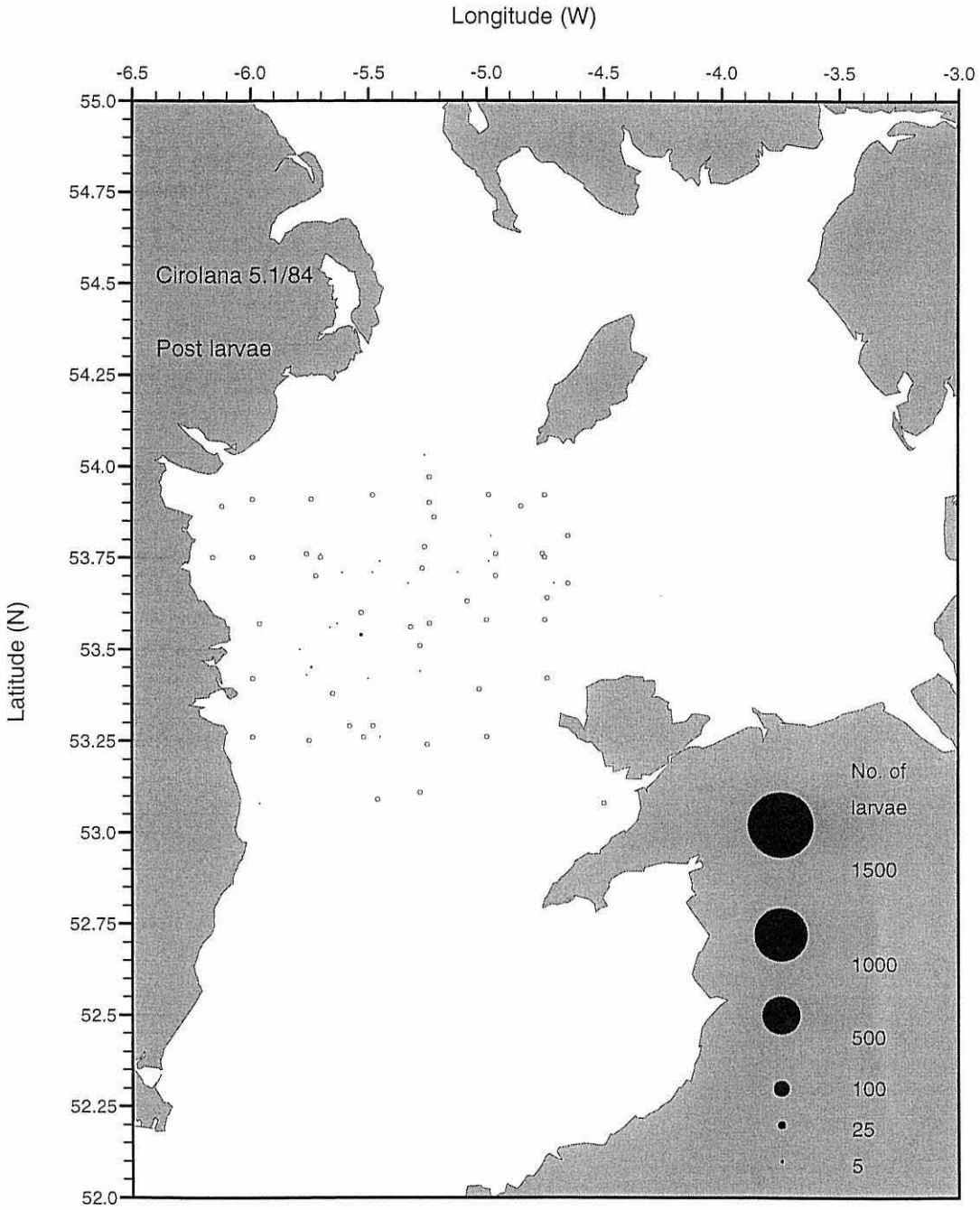


Figure 5.49. Number of *N. norvegicus* postlarvae from survey Cirolana 5.1/84 (25 May-1 June 1984). Open circles denote sampling sites where no larvae were observed.

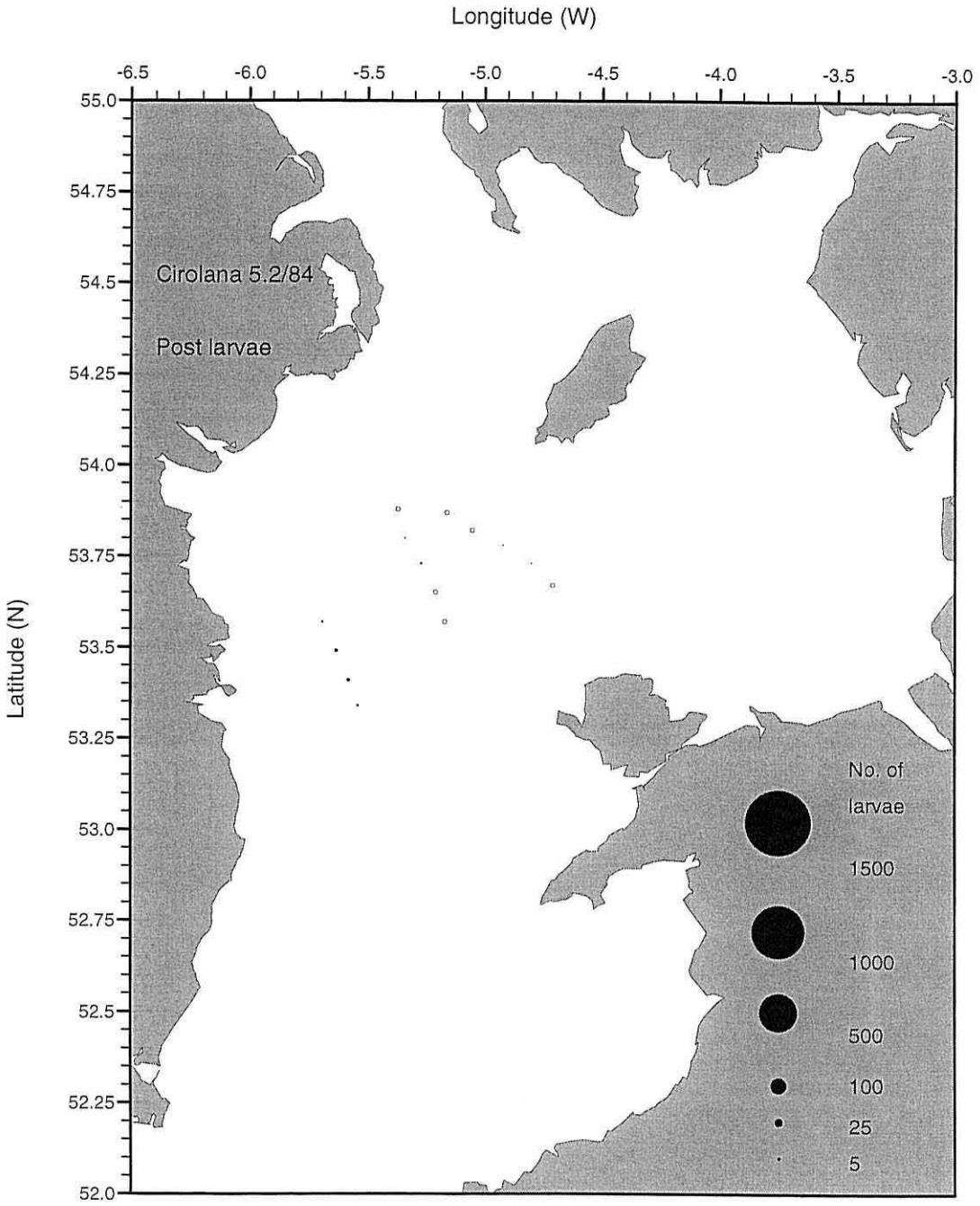


Figure 5.50. Number of *N. norvegicus* postlarvae from survey Cirolana 5.2/84 (12-13 June 1984). Open circles denote sampling sites where no larvae were observed.

3.2.2. Abundances and daily production estimates

Table 5.14 and figure 5.51 show larval abundance and daily production estimates, per stage, for the western Irish Sea, for 12 of the surveys carried during the period from 1982 to 1996. These calculations were only made for the surveys which included a good sampling coverage of the area. From the set of data available, it was impossible to assess total productions for the entire seasons in question because the number of surveys carried out for each particular year was in most cases reduced to a single sampling period. During 1982 and 1985 seasons, observations were collected during 3 surveying dates (April, May, June) (figure 5.52). Still, because sampling was limited to only part of the hatching season, estimates of the seasonal larval production for these periods are incomplete.

Figure 5.51, shows larval abundances and daily productions at the time of each survey. It can be appreciated that the data under analysis is scattered in time. Observations were carried out irregularly over the period from April to the begining of June and one survey was undertaken during mid July.

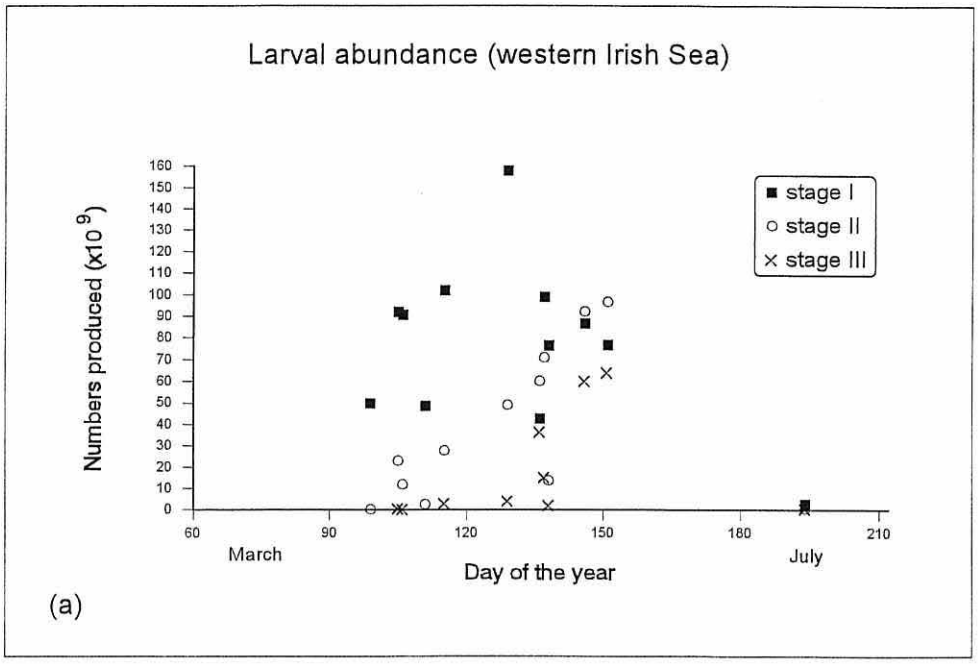
Higher abundances (and daily production) of stage I larvae were observed from late April to the second half of May. The highest value was recorded ($158x10^9$ zoea I, approximately 9.4 larvae/m^2) during Clione 6/82 survey (28 April-21 May in 1982) and it seemed from the data available that it may have been the peak of production of the 1982 season (figure 5.52a). The daily production estimated for this period ($9.3x10^9$ stage I) was similar to the value encountered for Cruise 12/95 ($9.5x10^9$ stage I), during the 1995 season, when the peak abundance of stage I larvae was observed ($159x10^9$ zoea I, on average 9.5 larvae/m^2) (tables 5.2 and 5.14). It must nevertheless be pointed out that the period of sampling for these two surveys is distinct. The majority of the abundance estimates for stage I larvae fell in the range between $40x10^9$ ($2.4x10^9$ larvae/m^2) and $110x10^9$ (6.5 larvae/m^2) individuals. The pattern of distribution of the values for stage I production presented in figure 5.51, and the estimates for the 1995 season (figure 5.12a) suggest that the peak of the hatching season for *N. norvegicus* in the western Irish Sea usually occurs around the second week of May. Inter annual variability in numbers and timing of the production peak are also suggested by the disparity of the estimates for equivalent periods in different years.

Figure 5.51 also shows that production of stage II and III larvae increased all through the period of surveying available and that the peak of production for these stages probably occurs towards the end of May. During the 1995 season, the peak of production for stages II ($162x10^9$ zoea II ~ $9.6x10^9$ larvae II/m^2, Cruise 13+Corytes 5b/95, 14-20 May) and III ($68.7x10^9$ zoea III ~ $4.1x10^9$ larvae III/m^2, Cruise 14/95, 23-28 May) was observed during the second half of May. For the set of data presented in figure 5.51 (see also figure 5.52) and table 5.14, the highest abundances of stage II larvae were observed during the 1982 (Clione 7/82, 21 May-1 June, $92.1x10^9$ zoea II, ~ $5.5x10^9$ larvae/m^2) and 1985 (P.Madog 1/85, 27 May-6 June, $96.6x10^9$ zoea II ~ $5.8x10^9$ larvae/m^2) seasons. The highest abundances of stage III lobsters were also estimated for Clione 7/82 ($60x10^9$ zoea III ~ 3.6 larvae/m^2) and Prince Madog 1/85 ($64x10^9$ zoea III ~ 3.8 larvae/m^2).

Since no surveys were carried out after the first week of June it is difficult to predict the shape of the production curves towards the end of the larval season. Even considering the comprehensive surveying programme carried out during 1995, the latter period of the larval season is not satisfactory illustrated. From the information available it seems however reasonable to suggest that the abundance of *N. norvegicus* zoeal stages, in the western Irish Sea, drops considerably during the second half of June, when the season is close to its end. A small number of larvae are still likely to exist until July. Observations during Corystes 9/96 survey, carried out in July 1996 (12-14), showed the presence of stage I ($2.6x10^9$ zoea I ~ 0.15 larvae/m^2), stage II ($0.26x10^9$ zoea II ~ 0.015 larvae/m^2) and stage III ($0.38x10^9$ zoea III ~ 0.023 larvae/m^2) larvae.

Table 5.14. Larval abundance ($x10^9$) and daily production ($x10^6$) for zoeal stages I,II,III in the western Irish Sea during 12 surveys dates over the period 1982 to 1996.

Survey	Mean sea temperature (°C)	Larval Abundance ($x10^9$)			Daily Production ($x10^6$)		
		Stage I	Stage II	Stage III	Stage I	Stage II	Stage III
Corella 5/82 9-13 April 1982	7.11	49.8	0.28	———	2420	12.7	———
Clione 6/82 28 April-21 May 1982	8.46	158	49.1	4.01	9290	2830	214
Clione 7/82 21 May-1 June 1982	10.23	86.6	92.1	60	6750	6980	3560
Clione 5/85 15-19 April 1985	7.43	90.6	11.9	0.102	4580	571	5.05
Clione 6/85 11-26 May 1985	8.71	99.1	70.9	15.2	5900	4110	810
Prince Madog 1/85 27 May-6 June 1985	9.21	76.7	96.6	64	4870	6080	3540
Cirolana 5/87 14-24 May 1987	8.50	76.4	13.7	1.98	4470	779	105
Cirolana 4/88 20 April-2 May 1988	8.23	102	27.9	2.89	5700	1510	149
Cirolana 4/89 16-28 April	8.35	48.7	2.68	———	2760	148	———
Cirolana 5/93 8-30 May	9.60	42.7	60.3	36.2	2980	4070	2060
Cirolana 4b/96 13-23 April 1996	7.79	92.1	23	0.27	4877	1173	13.7
Corystes 9/96 12-14 July 1996	11.76	2.6	0.26	0.38	238	25.2	25.5



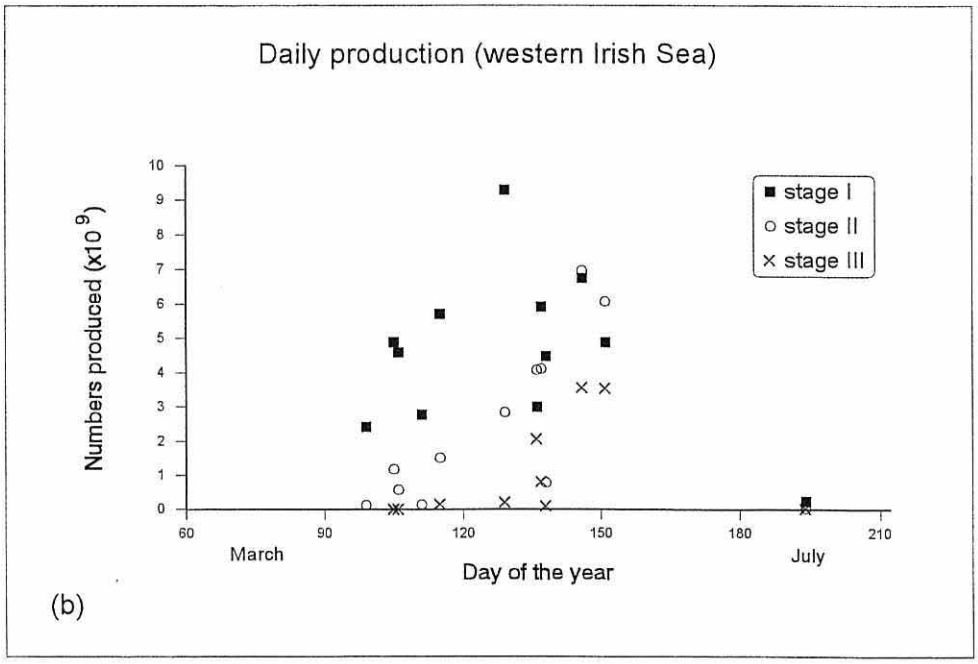
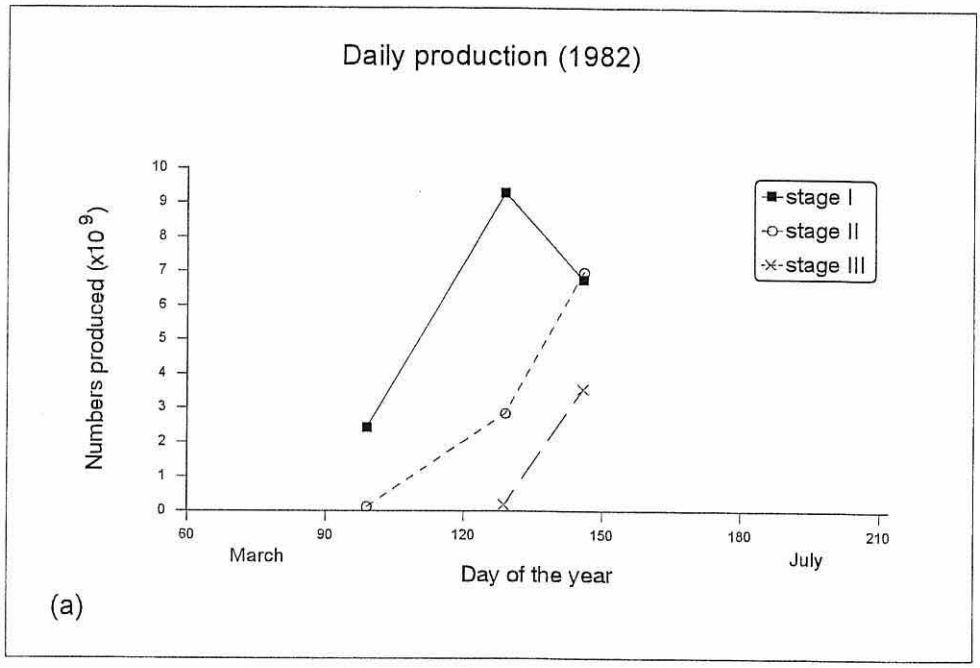


Figure 5.51. *N. norvegicus* (a) abundances and (b) daily productions for stages I, II and III zoea, in the western Irish Sea from surveys, from 1982 to 1996, shown in table 5.14.



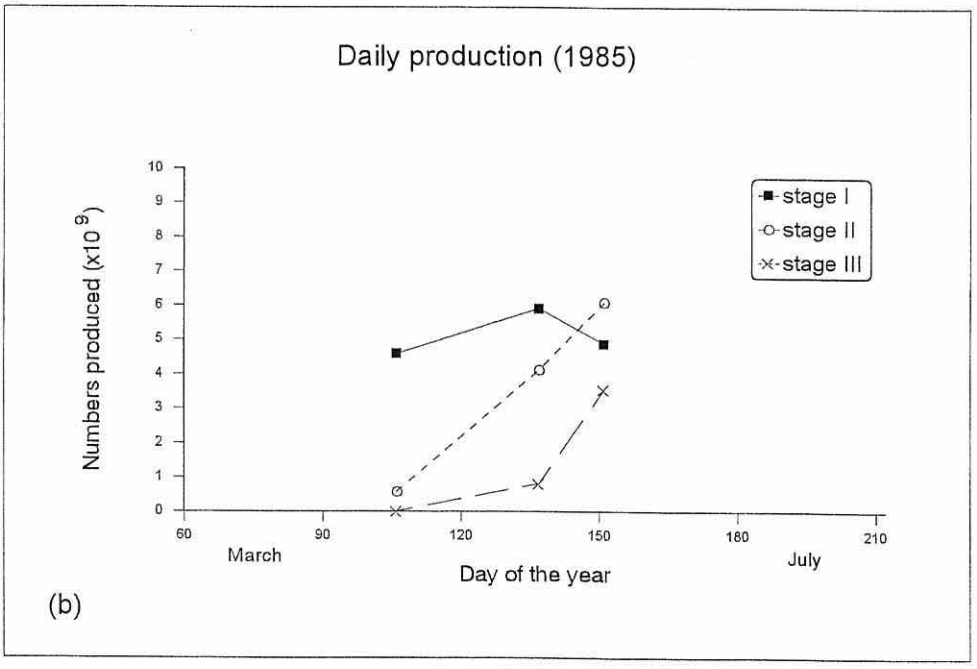


Figure 5.52. *N. norvegicus* daily production for stages I, II, III zoea, in the western Irish Sea for 3 survey dates in (a) 1982, (b) 1985.

3.2.3. Temperature and potential energy anomaly distributions

The distribution of sea surface temperature in the western Irish Sea (when information was available), for the surveys carried out during the period from 1982 to 1996, is shown in figure 5.53 and 5.54. Temperatures were lower during the April surveys (Corella 5/82, figure 5.53a; Clione 5/85, figure 5.53d; Cirolana 4/89, figure 5.54c; Cirolana 4b/96, figure 5.54e), on average below 8.0° C. Also apparent is the influence of slightly warmer waters, of Atlantic origin, in the southern area of the study area. During the end of April begining of May (Clione 6/82, figure 5.53b; Cirolana 4/88, figure 5.54b) and particularly in May (Clione 6/85, figure 5.53e; Cirolana 5/87, figure 5.54a; Cirolana 5/93, figure 5.54d) the temperature of the surface waters increased appreciably. The warming up of the surface waters over the deeper, central region, where thermal stratification becomes established was also apparent. This fact was clearer during the May-June surveys (Clione 7/82, figure 5.53c; Prince Madog 1/85, figure 5.53f). The higher temperatures were observed during the July survey (Corystes 9/96, figure 5.54f). The shallow waters close to the coast of Ireland also seemed to warm up significantly from May onwards.

The degree of stratification of the water column, during some of the above surveys can better be perceived in the contours of potential energy anomaly presented in figures 5.55 and 5.56. In April 1989 (Cirolana 4/89, figure 5.55c) the water column structure seemed to be quite homogenous. During surveys later in the year high values of ϕ were observed, May surveys Cirolana 5/87 (figure 5.55b) and Cirolana 5/93 (figure 5.55d) but particularly during the late May-June survey in 1982, Clione 7/82 (figure 5.55a). The succession of surveys in 1985 (figure 5.56a,b,c) showed clear evidence of water column stratification in the deeper, central western Irish Sea, during the whole sampling period. Curiously the highest values of ϕ were observed during the April survey (Clione 5/85).

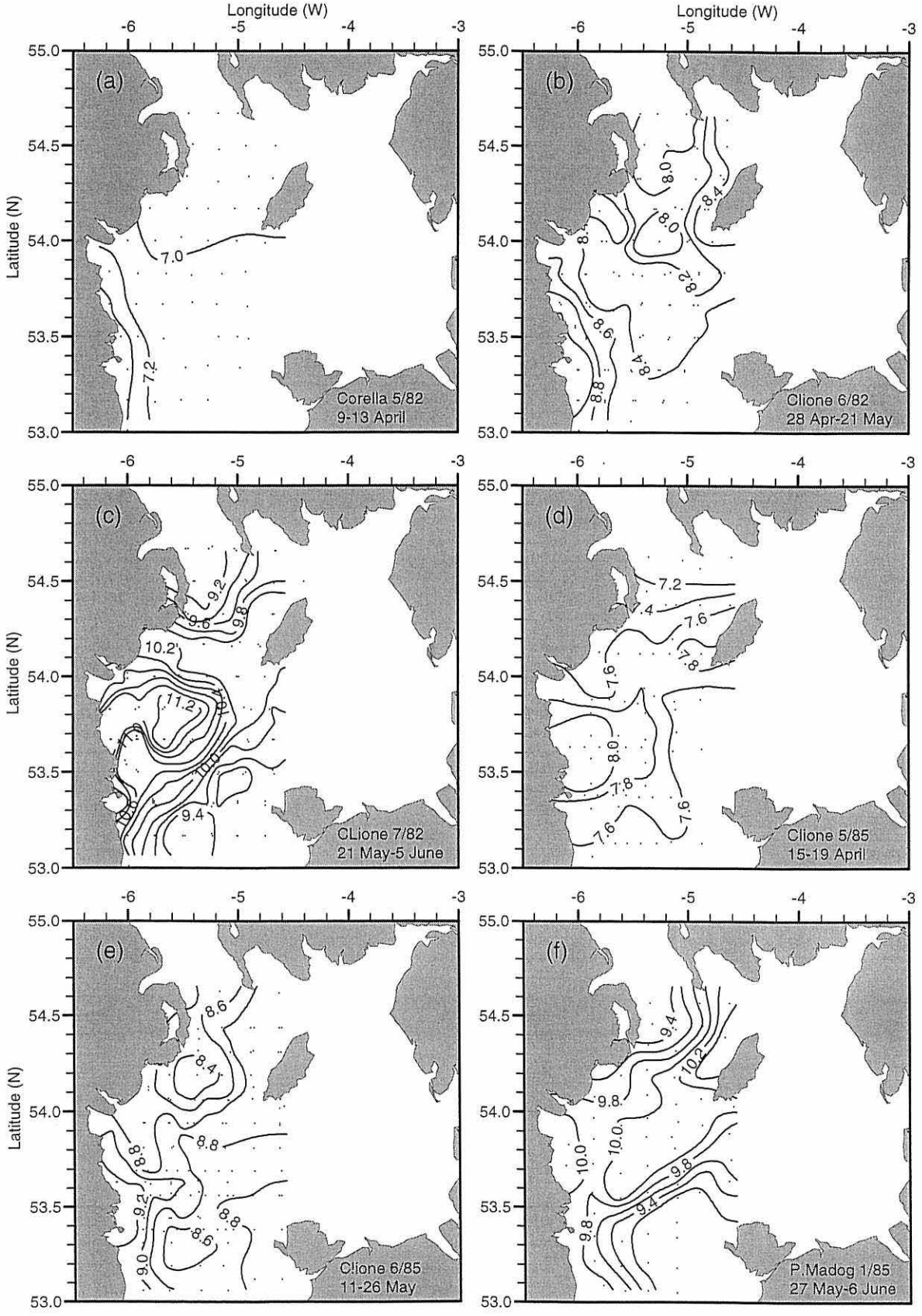


Figure 5.53. Contours of sea surface temperature (°C) from surveys in 1982, (a) to (c) and 1985, (d) to (f) (observations from the Guildline CTD probe).

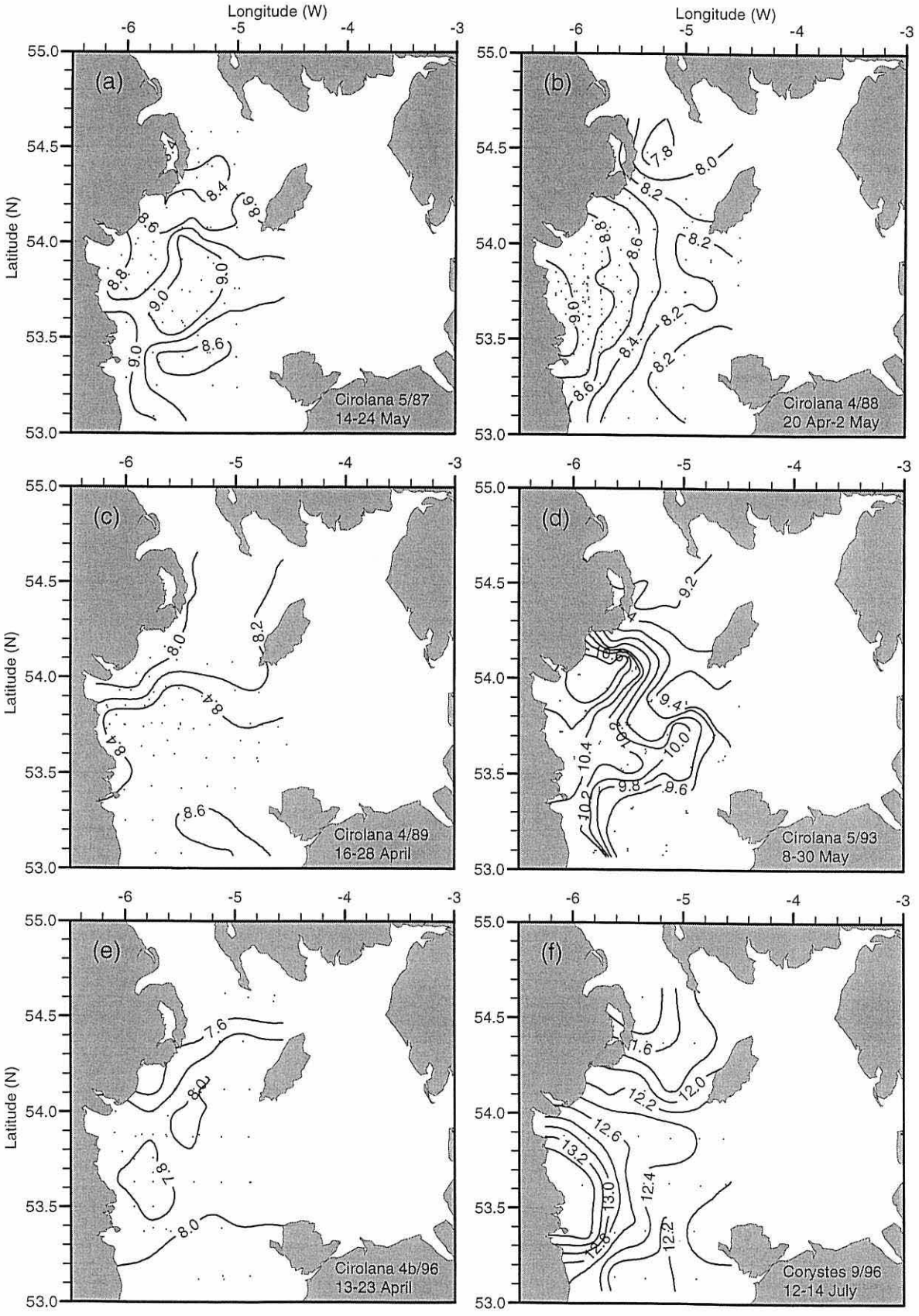


Figure 5.54. Contours of sea surface temperature (°C) from surveys in 1987 (a), 1988 (b), 1989 (c), 1993 (d) and 1996 (e) and (f) (observations from the Guildline CTD probe).

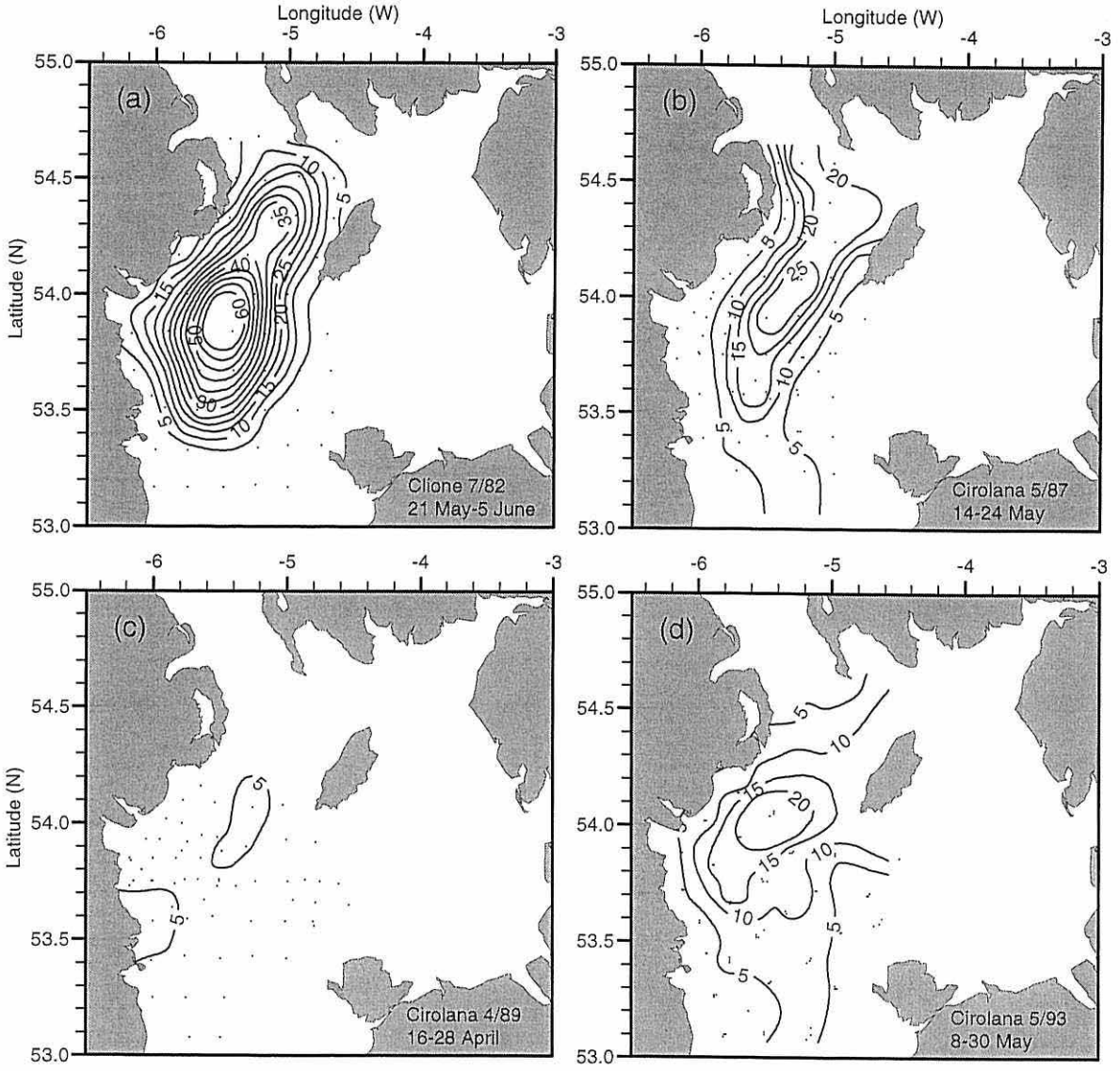


Figure 5.55. Contours of potential energy anomaly (J/m^3) for (a) Clione 7/82, (b) Cirolana 5/87, (c) Cirolana 4/89, (d) Cirolana 5/93 (observations from the Guildline CTD probe).

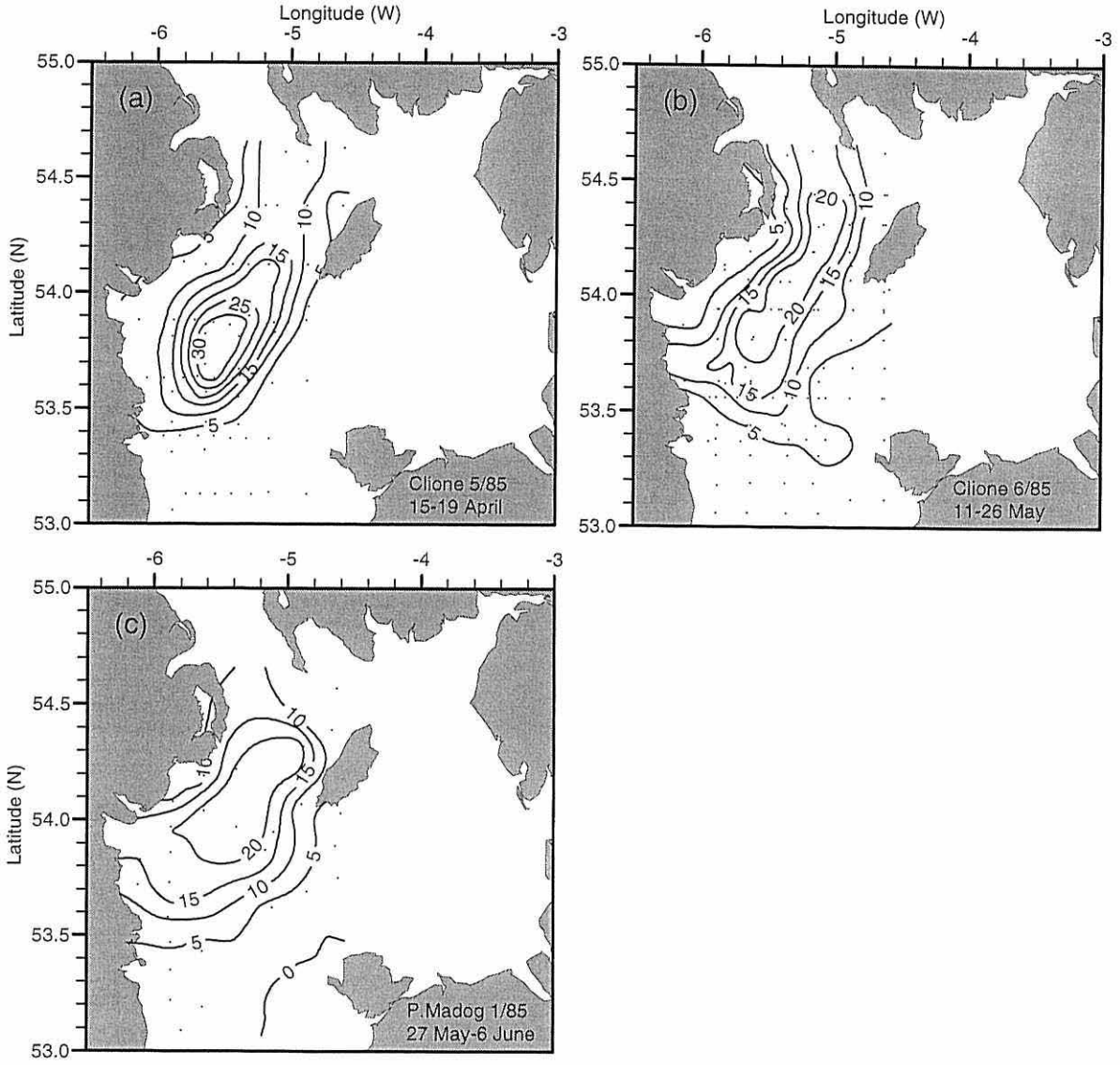


Figure 5.56. Contours of potential energy anomaly (J/m^3) for (a) Clione 5/85, (b) Clione6/85, (c) P. Madog 1/85 (observations from the Guildline CTD probe).

4. Larval abundances in Continuous Plankton Recorder samples (1970-1994)

4.1. Sampling

All CPR samples taken in the area between 52° N and 55° N and 4° W and 6° W, route IN during the period from 1970 to 1994 and route IB during the period from 1986 to 1994, with recorded presence of decapod larvae, were analysed to identify the presence of *N. norvegicus* larvae. A total of 490 samples were analysed.

4.2. Results

The information on abundance and distribution of *N. norvegicus* larvae derived from CPR sampling is presented in table 5.15 and figure 5.57. The results from this source were very poor, very few larvae were collected by the CPR sampler. From a total of 490 samples analysed, only 21 had lobster zoea and the total number of larvae observed was 45. More larvae were collected during sampling along the IN route (Dublin-Liverpool) which passes just south of the western Irish Sea mud patch. In this area, larvae were observed from March (sample 76IN8, 1977) until July (sample 92IN8, 1978) but their presence was not noted regularly over the spring-summer period for every year. The majority of the observations were made in the area between 53.35° N and 53.45° N and 5.25° W and 5.45° W. Along the IB route (Liverpool-Bay of Biscay) the presence of *N. norvegicus* larvae was only observed in two samples from 1991, in April and May. These individuals (stage I zoea) were collected far from the mud patch region, in the area between 52.75° N and 53.0° N and 5.05° W and 5.35° W. Its interesting to note that one postlarvae was collected by the CPR (sample 135IN5) in an area northwest of Anglesey.

The results presented here are of little significance for the study of *N. norvegicus* larval distribution and highlight the fact that the CPR is inadequate for sampling the species, which are large and scarce plankters with a patchy distribution. The standard CPR sampler operates at a constant depth (approximately 10 m) and the volume of water filtered per sample is only approximately 3 m^3. In addition, the only routes included in the CPR survey do not cover the area over the central western Irish Sea, were lobster larvae are more likely to be observed.

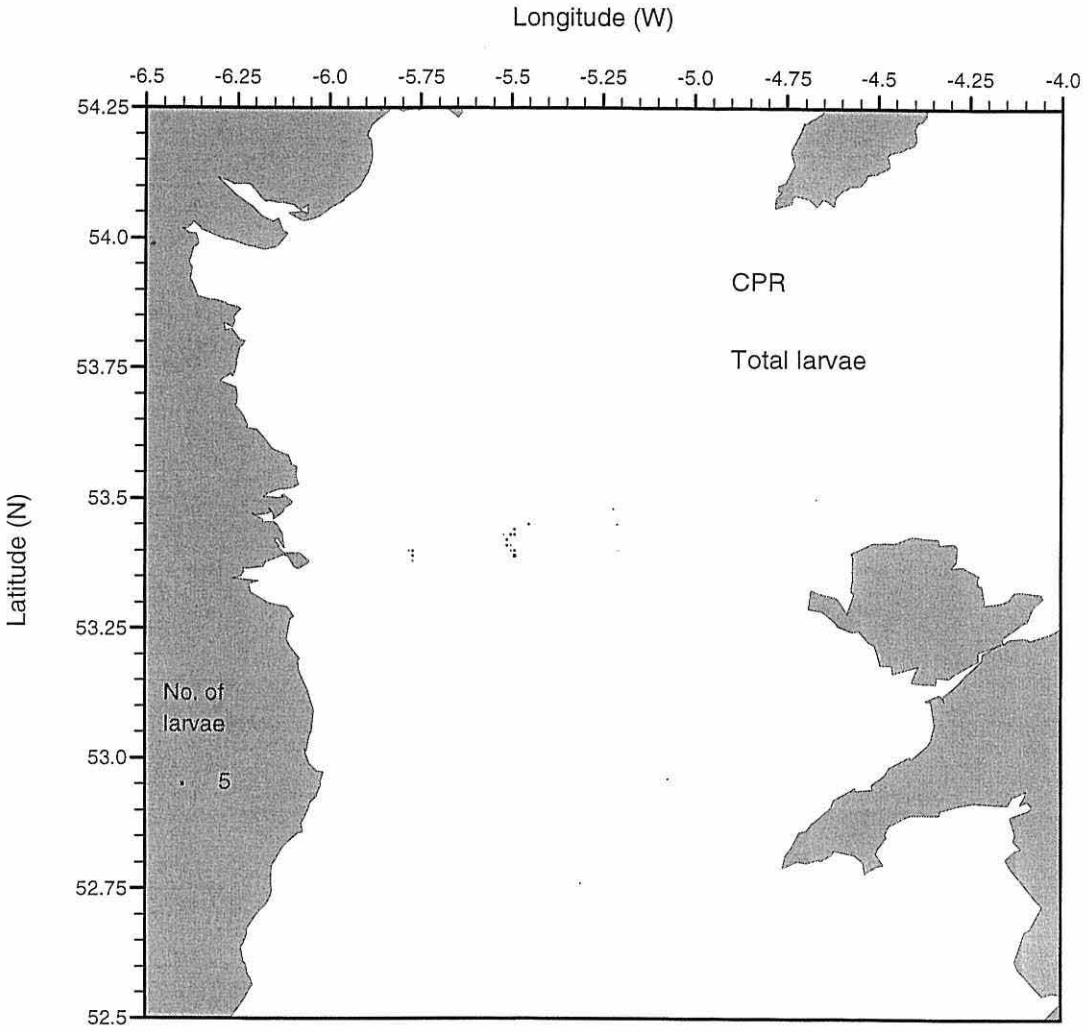


Figure 5.57. Total number of *N. norvegicus* larvae in CPR samples from routes IN and IB from the period 1970-1994.

Table 5.15. Occurrence of *N. norvegicus* larvae in CPR samples from routes IN and IB for the period 1970-1994.

Sample	Location		Date	Time	Stage I	Stage II	Stage III	Stage IV	Total
	Latitude	Longitude							
8IN8	53.42	5.51	21 May 71	2:12	2	2	———	———	4
19IN8	53.43	5.52	14 April 72	4:19	1	———	———	———	1
20IN8	53.44	5.49	13 May 72	2:31	———	———	2	———	2
31IN8	53.39	5.49	15 May 73	1:38	3	2	———	———	5
42IN8	53.43	5.50	9 April 74	3:03	2	1	———	———	3
55IN8	53.43	5.49	5 June 75	1:43	———	2	———	———	2
55IN9	53.40	5.77	6 June 75	2:30	———	2	———	———	2
66IN9	53.39	5.77	8 May 76	2:38	1	3	———	———	4
76IN8	53.40	5.50	20 March 77	18:44	1	———	———	———	1
91IN8	53.45	5.45	15 June 78	4:40	———	2	1	———	3
92IN8	53.41	5.51	16 July 78	21:08	———	2	1	———	3
122IN8	53.41	5.50	15 April 81	22:53	———	1	———	———	1
124IN9	53.38	5.77	16 June 81	21:59	———	———	1	———	1
134IN7	53.48	5.22	15 May 82	3:13	———	1	———	———	1
134IN8	53.43	5.49	15 May 82	3:48	2	2	———	———	4
135IN5	53.50	4.67	10 June 82	0:51	———	———	———	1	1
135IN8	53.40	5.49	9 June 82	23:16	———	1	2	———	3
157IN7	53.45	5.21	17 April 84	3:14	1	———	———	———	1
222IN9	53.40	5.78	4 April 92	18:39	1	———	———	———	1
59IB1	52.96	5.07	22 April 91	22:59	1	———	———	———	1
60IB9	52.76	5.31	25 May 91	1:30	1	———	———	———	1

5. Discussion

5.1. Seasonal production and stock estimate

In this chapter an extensive number of surveys on the larval distribution of *N. norvegicus* in the Irish Sea was collated, including four sampling cruises which were carried out during the period of this study. The data presented spans from 1982 to 1996 but for the majority of the cases only one survey per season was available and the period of sampling was not consistent from year to year. The information from the 1995 season was of particular interest because the study area was covered extensively during 13 surveys, from February until June. During the same year several hydrographic surveys were also carried out, in the western Irish Sea, throughout the season.

Western Irish Sea

In 1995, the first larvae of *N. norvegicus* were detected in the western Irish Sea in early-mid March (Cruise 5). By the end of the sampling period, in late June, the hatching season appeared to be nearly complete but a few planktonic lobsters were still observed. The peak production of larvae was observed during the second quarter of May. These results are in agreement with other studies, carried out in the region, which have shown the main hatching period to occur in April-May (O'Riordan, 1964; Hillis, 1974a; Farmer, 1974a; Nichols *et al.*, 1987).

The planktonic phase of the Norway lobster in the Irish Sea waters, appears to start slightly earlier than in the Clyde Sea (Thomas & Figueiredo, 1965; Smith, 1987) and than in several areas in the North Sea (Symonds, 1972; Sterk & Redant, 1989), but a little later than off the west coast of Ireland (Bhaldraithe, 1976) (see table 2.1, chapter II).

When the hatching season started in the western Irish Sea in 1995 (March-April) the temperature of the water column was still below 8° C and the seasonal thermocline was not yet evident. In fact, the water temperature remained below 8° C up until mid April. At that temperature the full development through all three zoeal stages would take approximately 57 days based on equations from Nichols *et al.* (1987) for development time in relation to water

temperature). Metamorphosis to the second zoeal stage would be expected to occur approximately 18 days after hatching and the third zoea would occur about 19 days after the first metamorphosis. During the 1995 season the first stage II larvae were detected (late March begining of April) approximately 22 days after the first stage I individuals were collected. Stage III zoea were first observed (mid-late April) approximately 40 days after the begining of the hatching season and 20 days after stage II larvae were recorded.

During April-May the water temperature gradually increased as a thermocline (pycnocline) and associated local gyre began to develop (see chapter IV). A high level of primary production was also noticed in the surface waters. During the same period a sharp increase in the abundance of larvae was observed and peak production was detected during the second week of May (Cruise 13, Corystes 5b). By mid May (Corystes 5b/95) a pycnocline was evident at about 20-25 m depth and the surface waters reached temperatures of the order of 9.5° C to 10.0° C. Bottom temperatures remained below 9° C. *N. norvegicus* larvae occur mainly in the top 30 m of the water column occupying the warmer water layers (chapter VI). Larvae hatched in May would have taken about 44 days to reach the postlarval stage assuming an average surface water temperature of about 10.0° C.

A rapid decline in larval production was observed during late May-June, this period corresponded to the presence of a well defined thermocline (and strengthening of the gyre) with lower temperatures in the bottom waters. Surface temperatures at this stage of the season, in the central western Irish Sea, ranged from 11° C to 12° C and bottom temperature was still about 9° C (chapter IV and Horsburgh *et al.*, submitted).

The production curve of *N. norvegicus* larvae in the western Irish Sea showed a clear peak in early-mid May and a decrease in production from then on. The end of the larval season seems to occur in late June-early July. This fact is based in the presence of larvae, of all three zoeal stages, during the last survey in June 1995 and also in the occurrence of some larvae during the July survey, in 1996. The presence of stage I zoea in the water column as late as July, may also indicate the lack of synchronicity in hatching for a few females which had probably spawned a little later than the majority of the population, during the previous summer.

It is evident from the results presented in this study that short term fluctuations in larval abundance occurred in the area and that from year to year, fluctuations in timing and magnitude of production also existed. It is, however, clear that the peak of larval production in the western Irish Sea occurs between the second and third weeks of May.

Survival and growth of the planktonic larvae is dependent upon temperature but food availability is also an important aspect. Although laboratory studies have shown very little success in maintaining larvae below 12° C (Figueiredo & Vilela, 1972; Smith, 1987; Thompson & Ayres, 1989) it is clear from field studies that the lobsters zoea survive and complete their planktonic life when the water temperature is much lower than 12° C (thermal water structure and abundance of larvae is further discussed in chapter VI). The seasonal changes in the composition of the food organisms available to *N. norvegicus* may in fact be a more important factor in determining the timing and extent of the larval season than water temperature, directly.

Lower bottom temperatures and perhaps more importantly a strong thermocline ($\Delta t \sim 5^{\circ}$ C) in late summer, may also play a role in defining the better timing for settlement and therefore the begining of the hatching season. Although no studies exist relating the success of settlement of the species to thermal (density) gradients it is known that sharp thermoclines may reduce severely the settlement of the American lobster, *Homarus americanus*. Boudreau *et al.* (1992) work showed that temperature gradients of 3.5° C to 4.0° C affect significantly the settlement of this species of lobster (this aspect is further discussed in chapter VI).

The estimated values for seasonal production of larvae stages I, II and III during the 1995 season in the western Irish Sea (tables 5.2 and 5.3), were of approximately the same magnitude as the predictions given by Nichols *et al.* (1987) for the same area for the 1982 season and by Thompson *et al.* (1986) for 1985. Nichols *et al.* (1987), estimated a seasonal production of zoea I, II and III of 391.3×10^9, 246.4×10^9 and 131.8×10^9 individuals, respectively, in 1982. The total production of stage I, II and III larvae, for the 1985 season was 341.2×10^9, 182.9×10^9 and 63.4×10^9 individuals, respectively (Thompson *et al*, 1986). The production calculations from the present study predicted a production of 349.3×10^9 stage I larvae, 235.2×10^9 stage II zoea and 113.1×10^9 stage III lobster.

Using the total production of zoea I and a fecundity value of 578 to 889 viable eggs per female, the total number of adult females in the western Irish Sea population was estimated to be between $440x10^6$ and $680x10^6$ (5502-8463 tonnes) in 1982, and between $384x10^6$ and $590 x10^6$ (4800-7375 tonnes) in 1985 (Nichols *et al.*, 1987; Thompson *et al.*, 1986). The spawning stock size derived from the present study's calculations was between $393x10^6$ and $604x10^6$ individuals (4913-7550 tonnes). Using estimates of stage I larvae production derived from the mortality regression, the predicted number of adult females in the population, in 1995, increased to $549\text{-}844x10^6$ (6863-10550 tonnes). The same calculations for the 1982 and 1985 seasons, estimated $585\text{-}900x10^6$ (7313-11250 tonnes) and $620\text{-}954x10^6$ (7750-11925 tonnes) females respectively (Thompson *et al.*, 1986; Nichols *et al.*, 1987).

The rates of daily larval mortality for each larval stage, in the western Irish Sea, found in this study (Z stage I-II, 0.024; Z stage II-III, 0.047; Z stage I-III, 0.035) were comparable with those of Nichols *et al.* (1987) for the 1982 season, (Z stage I-II, 0.031; Z stage II-III, 0.041; Z stage I-III, 0.035) but sligtly lower than the figures produced by Thompson *et al.* (1986) for the 1985 season (Z stage I-II, 0.035; Z stage II-III, 0.058; Z stage I-III, 0.047). Higher rates of instantaneous daily mortality between stages I and II (Z=0.116) have been estimated for populations from the northeast coast of England (Milligan & Nichols, 1988). Results from the Clyde Sea (Smith, 1987; Tuck, 1993) showed considerably higher mortality rates for all zoeal stages. However, this fact can be partly due to the mean stage duration times used in the Clyde Sea studies, different equations for development time against temperature were used. Nichols *et al.* (1987) equations, used in this study, produce shorter development times and therefore lower estimates of overall mortality.

The mean stage duration for the 1995 season (stage I, 16.18 days; stage II, 15.61 days, stage III, 17.5 days) were slightly higher than the rates found by Nichols *et al.* (1987) for 1982 (stage I, 15.04 days; stage II, 15.15 days, stage III, 16.98 days) but lower than the durations estimated by Thompson *et al.* (1986) for 1985 (stage I, 17.7 days; stage II, 18.27 days, stage III, 18.53 days). The variability encountered is due to the temperature of the water during the different seasons but it may also be attributed to differences resulting from the use of temperature values representing different layers of the water column. During this study a depth integrated value of temperature was used for the calculations.

Despite the removal, by the fishery, of an annual average of around 8000 tonnes of *Nephrops norvegicus* during the period from 1985 to 1994 (Hillis, 1988b; Briggs, 1989; ICES, 1997), there has apparently been no significant change in the spawning stock size. The close agreement between the spawning stock estimates for this study and the figures given for the 1982 and 1985 seasons, supports the view that the western Irish Sea *N. norvegicus* stock is fairly stable despite the intense fishing activity in the area. This fact has been highlighted by recent analysis of landings statistics (Briggs, 1987; 1995, see also section 2.6, chapter II). Although a trend of decline in the size of *N. norvegicus* in catches, had been observed during the 1960's and 1970's (Hillis, 1984, 1988b; Briggs, 1987 references therein) a more detailed analysis of recent data (Briggs, 1987; 1995), showed a great inter-sample variability on the size of the species. These observations are consistent with considerable variations in population structure occurring within relatively small geographic areas (Briggs, 1987; 1995). This fact, together with the recognition that several changes in the fishery (gear, mesh size, minimum legal landing size) and market demands have occurred along the years suggest that the conclusions drawn from the earlier studies and analysis of long term temporal trends should be treated with caution. Moreover, recent statistics have shown an increasing trend in the mean size of *N. norvegicus* in catches, by both the Northern Ireland and the Republic of Ireland vessels, since 1994 (ICES, 1997, and see section 2.6, chapter II).

The last report of the ICES Working Group on *Nephrops* Stocks, indicated that fishing mortality (F) in the western Irish Sea (Functional Unit 15) is about 20-30 % beyond F_{max} (at which yield is maximized). However, the LCA results show a relatively flat topped Y/R curve, indicating that a reduction in the current fishing effort would only produce a small long-term increase in yield. The 1997 ICES meeting indicated that although the present level of fishing mortality, in the western Irish Sea population, is high ('fully or slightly over-exploited'), the catches and recruitment have been relatively stable. These facts, together with evidence of effort reduction, led to the conclusion that this population is withstanding the current fishing pressure and no alterations on the TAC's have been recommended (for the whole area VII which includes the Irish Sea). It has however been a general practice for the agreed TAC, achieved in Council of Ministers of the member countries, to be slightly higher than the TAC recommended by the ICES Advisory Committee on Fishery Management. The aggreed quotas have been relatively unchanged during this decade (ICES, 1997).

Assuming a sex ratio of 1:1 (O'Riordan, 1964; Farmer, 1974a; Chapman, 1980), and using the predicted number of mature females mentioned above the total number of adult *Nephrops norvegicus* in the western Irish Sea can be estimated. When the seasonal production curve is used to calculate the spawning stock, a total of $786x10^6$ to $1208x10^6$ adult lobsters is predicted. Using the number of females estimated from the instantaneous production of stage I zoea, the total adult population is predicted to be between $1098x10^6$ and $1688x10^6$ individuals.

Considering that the area of suitable substrate for *N. norvegicus* in the western Irish Sea is approximately 5000 km^2 and the above figures for abundance of adults, an average estimate of density of adults in the area can be produced. Using a mean value of abundance (arithmetic mean for the ranges given above), the density of adult lobsters is estimated to be 1 individual per 5 m^2, when the estimations are derived from the seasonal production curve, and 1 individual per 4 m^2, if the estimation is based on the instantaneous production of larvae. These figures are in agreement with density observations obtained by Hillis (1974b) during diving surveys off the Irish coast. However, the density estimates presented here, average density for the whole area, should be read with caution because it is known that the spatial structure of the western Irish Sea population varies considerably within the area (Briggs, 1995, Tully & Hillis, 1995). Moreover, stock estimates using larval abundances are only reliable if the larvae collected represent well the real population and the fecundity rates and larval development times used are accurate. Stock assessement of *Nephrops norvegicus* using larval production data is a method which is still being tested. Laboratory work to verify the mean realised fecundity and larval development rates for the Irish Sea population is being carried out.

Eastern Irish Sea

In the eastern Irish Sea, the first larvae of *Nephrops norvegicus* during the 1995 season, were observed in mid March (Cruise 6), slightly later than in the western basin. By the end of the sampling period in mid June (Cruise 15), no stage I zoea were collected and the number of stages II and III were very low, indicating that the hatching season was probably complete. The seasonal production curve for stage I larvae showed great fluctuations but those variations were not evident on the curves for stages II and III. There is evidence for a second

peak of larval production in other areas (north Clyde Sea, Smith, 1987; northeast coast of England, Milligan & Nichols, 1988) but the same conclusion can not be drawn to the eastern Irish Sea, from the observations in this study. It is more likely that the fluctuations observed in this area are related to high mortality of stage I larvae and/or advection of larvae from the region. The peak of production of stage I larvae was observed in late April, slightly earlier than in the western basin. The larval season in 1995, seemed to be shorter in the eastern Irish Sea than in the western side.

The timing and extent of the larval season in the eastern Irish Sea may be influenced by the local hydrography and evolution of the water column structure during spring-summer time. In this shallow region off the Cumbrian coast, stratification of the water column was observed in February, due to river runoff, but later in the season there was no evidence of stratification (figures 5.14-5.17). This fact may suggest that the spring primary production, and consequently secondary production, ceases earlier in the season, when high suspension of particles in the water column (due to mixing) may prevent enough light to be available for production. There is also evidence that water temperature, in this shallow area, increases slightly earlier in the warming season, than in the deeper western basin, perhaps allowing for the zooplankton to develop earlier in the season. However, this arguments can not be verified by the present study because no hydrographic surveys were carried out in the region. Plus, information on the primary and secondary productions in this area are not available.

The estimated values for seasonal larval production of stages I, II and III in the eastern Irish Sea, in 1995 was 20.52×10^9, 6.92×10^9 and 1.97×10^9, respectively. The spawning stock size, derived from the production curve of stage I, was predicted to be between 2.31×10^7 and 3.55×10^7 mature female. The total biomass of adult females was therefore estimated to range from 289 to 444 tonnes. When the number of breeding females was obtained from the mortality regression the spawning stock size was estimated to be between 4.33×10^7 and 6.66×10^7 individuals and the correspondent biomass was predicted to range from 541 to 833 tonnes.

Considering that the sex ratio is approximately 1:1 (ICES, 1997) an average number of adult *Nephrops norvegicus* between 4.62×10^7 and 7.1×10^7 can be obtained from the lower estimate (production curve), and 8.66×10^7 to 13.32×10^7 from the higher estimation (instantaneous

production of stage I zoea). Taking the arithmetic mean between the two values for each estimation and considering that the area of suitable substrate, in the eastern Irish Sea, is approximately 900 km^2, the average density of adult lobsters in the region is 1 individual per 15 m^2 for the lower estimate, and 1 individual per 8 m^2 for the higher abundance estimate. Under-water video surveys carried out in this region, showed that *Nephrops norvegicus* burrows were more abundant in the softer muds in the centre of the muddy patch (approximately between 54.25° N and 54.40° N). In this substrate where the silt-clay makes up approximately 80% of the sediment, the density of lobster burrows at one sampling site was estimated to be 1.3 burrows/m^2. Sampling stations on the edges of the patch where the content of sand is higher (muddy sand) showed no evidence of *N. norvegicus* burrows (Hughes & Atkinson, 1997). Burrow density may not correspond directly to population size because some burrows may be unoccupied (Chapman & Rice , 1971) or have several occupants (Tuck *et al.*, 1994).

The spawning stock size estimated for the 1995 season ($2.31x10^7$ to $3.55x10^7$ mature female) was similar to the predictions obtained by Thompson *et al.* (1986) for the 1985 season ($2.05x10^7$ to $3.15x10^7$ mature females). During the 1985 season, fluctuations in the production of stage I larvae were also observed. However, the peak of production was detected considerably later in 1985 than in 1995. Higher abundances of all three zoeal stages were detected during the last survey of the season in early June (3-5). This fact may indicate that the production values for that season were underestimated. The authors of that study suggested that hatching of *N. norvegicus* larvae in the eastern Irish Sea, would continue through June and possibly July. These results are not verified by the present study, which predicted the larval season of the species, in the region, to be completed during mid-late June. The observations carried out in 1995, in the eastern Irish Sea, showed the peak production of stage I zoea to occur in late April. By the time of the last survey in early-mid June (5-14) no stage I larvae were collected. The difference in the timing of peak hatching between the two seasons compared, suggest high inter-annual variability in the larval production of the species in the eastern Irish Sea. This fact may be due to differences in water temperature and onset of primary production. The lack of continued observations in the area precludes further discussion of these aspects. The examination of some of the historical data presented in section 3 of this chapter, suggest that perhaps the 1995 larval season in the eastern Irish Sea, was completed earlier than in other years. However, because not many surveys have been

carried out towards the end of the season, it is difficult to assess the full duration of the larval season in the area.

The estimated values for daily mortality for the 1995 season in the eastern Irish sea (Z stage I-II, 0.066; Z stage II-III, 0.084; Z stage I-III, 0.075), were considerably higher than the predictions made for the western area. Daily mortality rates for stage I larvae, in this region, were however lower than the values predicted for the Clyde Sea (Smith, 1987; Tuck, 1993) and the eastern coast of England (Milligan & Nichols, 1988). The mortality rate of stage II zoea, estimated in the present study, is considerably higher than the rates predicted for any of the other regions mentioned.

The predicted mean stage duration for stages I, II and III, for the 1995 season in the eastern Irish Sea, was 16.5, 14.9 and 17.2 days, respectively. These figures are slightly lower than the estimates obtained for the western Irish Sea and conform with the generally higher temperature of the water column observed in the eastern basin, during the 1995 season.

The ICES statistics show that *N. norvegicus* landings from the eastern Irish Sea ground (Functional Unit 14) declined in the last two or three years (ICES, 1997, see section 2.6, chapter II). However, LCA results indicated that the stock has remained fairly stable. The current fishing mortality for males is slightly beyond F_{max}, but for the females the present levels of fishing are still below F_{max}. As the long term Y/R curves are flat topped small changes in effort would not affect substantially the yield. However, the stock assessment for the eastern Irish Sea population is not yet of the same quality as for other regions, namely the western Irish Sea, due to the lack of information on some biological parameters for the analysis, for this specific population. The report from the last ICES Working Group on *Nephrops* Stocks meeting indicated that since the current levels of fishing mortality, for both sexes, are close to F_{max}, they should not be increased (ICES, 1997).

5.2. Larval distribution in the western Irish Sea and its relationship with environmental variables

The spatial distribution of *Nephrops norvegicus* larvae in the western Irish Sea, was found to be mainly concentrated above the mud patch region. This result is as expected since this region provides a suitable substrate on which the adults live and therefore production of larvae can be anticipated to occur in the area. However, the abundance of larvae did not appear to be uniformly distributed over the muddy region and a fairly high number of planktonic lobsters were also observed outside the area. Furthermore, the pattern of distribution seemed to change throughout the season.

The results from the 1995 and 1996 campaigns and the historical data, showed that at the begining of the larval season (March-April), the higher densities of larvae consistently occur over, and beyond, the southwestern edge of the muddy ground and often in the inshore region off Ireland. This feature has been reported previously by Hillis (1974a), Nichols *et al.* (1987) and White *et al.* (1988) studies. Several factors, or a combination of those, can account for this pattern of distribution: this area, may have a higher density of adults, it may provide better environmental conditions (*eg.* water temperature and food availability) for production and development of larvae and it may constitute an area of concentration of larvae advected from other regions.

Evidence from the fishery statistics (catch (landing) and catch (landing) per unit effort) suggest that higher densities of adults occur in the ICES rectangles 36E4 and 37E4 which include the southwest region of the *Nephrops norvegicus* grounds (see table 2.6, chapter II). However, these rectangles are very large (1 degree in longitude by 1/2 degree in latitude) and it is not clear where exactly, within the area, the higher catches are obtained. Differential fishing results may also relate to distinct performance of the fishing gear under different conditions, such as sediment type and topography. Still, O'Riordan (1964) identified 2 pockets of higher concentration of adults in the southwestern region of the western Irish Sea ground. The first of these spots was located off Cloger Head (just south of Dundalk Bay) on the western edge of the mud patch and the second one, further south, off the Skerries. The same author also observed the highest concentration of *N. norvegicus* larvae to occurred over the regions of greater adult densities.

Hillis (1988a) and Tully and Hillis (1995) working, in the southern area of the western Irish ground (area between 53.5° N and 53.83° N) showed that the highest density of, smaller, adult *N. norvegicus* was associated with the finer sediments, in the centre of the study area whereas in the borders of this region, where the sediments are coarser, the concentration of lobsters was lower but the individuals attained a larger size. These observations and studies elsewhere (Bailey *et al.*, 1986; Chapman & Bailey, 1987; Chapman & Howard, 1988; Maynou & Sarda, 1997; Tuck *et al.*, 1997) have led to a prolific discussion on the factors beyond the variability in structure and biology of *N. norvegicus* populations (some of these aspects are presented in chapter II, section 2.5). Although, it is clear that sediment composition affects the distribution of this burrowing lobster, the mechanism by which this factor controls biological parameters and population dynamics it is still not fully understood. Other environmental factors such as variable benthic production and differences in larval survival and settlement have also been pointed out as possible causes for the variability encountered between different Norway lobster populations. In the western Irish Sea, there also appears to exist a degree of patchiness in the size composition and biology of the population within the muddy ground. Variations in lobster density, size, female maturity and sex ratio were observed between short distance sites (Briggs, 1995). In view of these facts the author suggested that in the western Irish Sea *Nephrops norvegicus* occurs in 'stocklets', each of which exhibiting its own population characteristics.

In respect to planktonic standing stock there is evidence to suggest that the area southwest of the western Irish Sea ground is a zone of high concentration of phytoplankton (and probably zooplankton) but not of high productivity (Gowen & Bloomfield, 1996, see also figure 4.4d and discussion in chapter IV). This fact implies that plankton produced in other areas (north) drifts into this region.

Conversely the inshore waters off Ireland appear to constitute the region of highest primary production in the western Irish Sea. In this area planktonic production starts earlier than in the rest of the western Irish Sea, even before warming up is noted in water temperatures, and lasts longer (6 to 7 months) (Gowen & Bloomfield, 1996). This region is also recognised to have a high level of secondary production. High concentrations of copepods, twice as large as in the central area, were observed by Burkart *et al.* (1995). The inshore areas off the coast of Ireland

are also identified as the spawning sites for several fish species during spring (Nichols *et al.*, 1993; Dickey-Collas *et al.*, 1996a; 1997; Fox *et al.*, 1997). It can therefore be especulated that these inshore waters may provide higher food availability for *N. norvegicus* larvae, especially at the beginning of the season. At the same time, this region probably also supports a larger number of potential predators.

It is not clear how the larvae of *N. norvegicus* occur in these inshore waters, to the west of the adults ground. Studies by O'Riordan (1964) and Farmer (1972) suggest that some migration of adults towards the Irish coast may occur during the winter. This hypothesis has never been confirmed and it is believed that the berried females do not leave their burrows during the period of incubation which in the Irish Sea starts at the end of the summer (Farmer, 1974a; Chapman, 1980). The southward, density driven current found along the Irish coast, at the begining of spring, may have some influence on the dispersal of the early larvae into the shallow areas to the west of the mud patch. This pattern of distribution is a recurrent event observed at the begining of the season, every year.

The southward flowing current (about 3-5 cm/s) is clearly visible in the geostrophic velocity profiles and it was confirmed by current meters moored in the area and the tracks of some drifters released in the spring of 1995 and 1996 (chapter IV). This current is also likely to be responsible for the advection of *N. norvegicus* larvae into the area south of the adults ground. The distribution of the different larval stages, in consecutive surveys, at the begining of the season, suggested that the larvae were being carried in a southward direction. In 1995, the first larvae to appear in the area south of the mud patch (south of 53.5° N) were stage I zoea which were observed there in early and mid April (Cruises 8, Cruise 9+10). During the following surveys, until mid May (Cruise 11, Cruise 12, Corystes 5b, Cruise 13) concentrations of stage II and III larvae dominated the larval assemblage in that region. By this time, stage I larvae occurred, in higher numbers and, more uniformly distributed above the adults habitat. It was also evident that stage II and III zoea appeared more wide spread towards the south than stage I larvae. The same pattern of distribution of the larvae was also noted during the consecutive surveys carried out in 1982 and 1985.

These observations seemed consistent with a continuous drift of the larvae, produced in the central western Irish Sea, in a southward direction. During the period the newly hatched

lobsters were being carried with the currents, metamorphosis into successive zoeal stages would have taken place. This development would explain the higher concentrations of the later stages in the area further south. The observed density driven flow was likely to have been responsible for this pattern of dispersal. A rate of advection of the order of 3 cm/s (2.6 km/day) would explain the observed displacement of the larvae. It seems that the planktonic lobsters could had been carried distances of up to 50 km south of their expected point of origin. The observations from Corystes 5b/95 survey, showed the southern limit of the larval distribution of stages II and III larvae to be around latitude 52.9° N. No larvae were collected along the furthest south sampling line (~ 52.6° N).

The larval distribution plots, also showed that although the core of the southward displacement was concentrated on the western side, along the Irish coast, some larvae appeared to be following paths in more central areas.

Apart from the coastal current mentioned, it must also be considered that during late April-May, when the western Irish Sea gyre is developing, the currents generated on the western front may also promote a southward displacement of the *N. norvegicus* larvae. At this stage of the season, stratification of the water column and the associated gyre are clearly apparent but its structure is not fully developed and therefore a closed circulation feature is not yet present. 'Leaks' in the gyre circulation, were evident on the trajectories of some drifters deployed during May 1995. One instrument (a17823) which was being transported southward in the western jet of the gyre travelled to the south of the stratified region. However, the majority of the buoys transported along the western flank of the gyre eventually made a turn northeastwards following the gyre circulation. No drifters were observed to be carried as far south as the region where *N. norvegicus* larvae were collected. This fact suggests that the larvae were probably subjected to more superficial currents, above the gyre flow. The buoys, because their centres of mass were located at the depth of the core of the gyre flow, followed its path more closely. Two drifters which had the drogues centred at 8.5 m (f24056, f24062), demonstrated the difference between the surface flows and those at the pycnocline.

Another area where some drifters 'escaped' the gyre circulation was the southwest of the Isle of Man. Two instruments (d24058, a3947) deployed in April and early May were carried in a eastward direction just south of this island. *Nephrops norvegicus* larvae were observed along

the same path on a few occasions. This pattern was more evident at the begining of the larval season, end of March begining of April (Cruise 6, Cruise 8). During the early April survey, in 1995 (Cruise 8), although in small numbers some larvae were observed right across the Irish Sea, along a corridor south of the Isle of Man, between the western and eastern *N. norvegicus* grounds. Observations from other years also showed the presence of some larvae in this region to the east of the western Irish Sea *N. norvegicus* patch.

Slightly later in the season, by the end of April and particularly during the month of May (Cruise 11, Cruise 12, Cruise 13), some planktonic lobsters were also collected in the area between the western and eastern basins on the north of the Isle of Man. Although no drifters were deployed in the area, studies on the concentration of radioactive isotopes discharged from the Sellafield plant (Cumbrian coast) have shown the transport of such chemicals in a northwest direction, towards the North Channel (Leonard *et al.*, 1997). *N. norvegicus* larvae produced in the eastern Irish Sea ground may be carried along the same path.

Up to this point, the larval distribution during the first half of the season has been described and it has been pointed out that considerable numbers of individuals were advected from the area above the western Irish Sea mud patch, particularly during the early spring. During the second half of May and begining of June in 1995 (Cruise 14, Cruise 15, L. Foyle) higher abundances of *N. norvegicus* larvae were observed in the central region of the western Irish Sea, above the adults ground. By this time, the larvae were more uniformly distributed over the whole area and advection of individuals from the region, seemed less evident. This pattern of distribution, was also noted for surveys carried out during May-June in other years (1982, 1984, 1985, 1987).

This period of the season coincides with considerable intensification of the water column stratification and consequently strengthening of the cyclonic gyre. These aspects were clearly visible in the temperature, density and velocity, profiles and contours of potential energy anomaly. During mid May (Corystes 5b/95), surface to bottom temperature differences of 1.5° C were registered, in the deeper region of the western Irish Sea, and ϕ values of up to 50 J/m^3 were calculated for that region. By the end of May (P. Madog 1/95), top to bottom temperature differences of the order of 2.5° C were observed in the central area. Contours of potential energy anomaly showed values of around 50 J/m^3 in the centre of the basin. In mid

June (1994), surface to bottom temperature differences reached 3.5° C, in the central region, and ϕ values over 60 J/m^3 were estimated (Corystes 7/94). It is also important to note that for the surveys from mid May onwards (until the end of summer), the plots of Δt and ϕ showed closed contours of these properties, indicating the isolation of the stratified waters over the western Irish Sea basin and the establishement of the gyre as a closed circulation feature (chapter IV, Horsburgh *et al.*, submitted). This aspect was further verified by the trajectories of several drifters layed in the region. Buoys released during this stage of the season, in the region of the gyre flow, were clearly describing the cyclonic circulation. One instrument deployed on the 22 June 1995 (b17804) described an organized flow about the region, circumnavigating the western Irish Sea in 42 days, at an average speed of 10 cm/s. During May (Corystes 5b/95) the currents along the western (southward) and eastern (northward) edges of the gyre were of the order of 10 to 15 cm/s. By June (Corystes 7/94), velocities of up to 20 cm/s were observed at the cores of the jet flow (25-30 m depth), on both sides of the gyre.

The strengthening of the gyre seemed to have had some influence on the retention of the lobster larvae over the adults habitat. This fact was highlighted by the results of the ANOVA and PCA analysis performed for the 1995 data. Two regions were considered for the analysis on the larvae distribution: over the mud patch and surrounding area. The ANOVA results showed no significant differences between the abundance of *N. norvegicus* larvae between the two regions for the surveys in early-mid season (Cruise 8, Cruise 11, Corystes 5b). This fact is indicative that the larvae were 'equally' distributed in both areas during the period of those surveys. Towards the end of May (Cruise 14), the abundance of larvae in the two regions considered, was found to be significantly different. This period coincides with higher abundance of larvae over the mud patch and less individuals being carried away from the area.

Despite these results, when the larval abundance for the three zoeal stages was superimposed on the PCA ordination of sites, based on environmental variables, the association of larval occurrence and physical data was not very clear. PCA analysis ordinated fairly well the different sites according to sea bed substrate type and degree of stratification of the water column (ϕ), other variables like surface temperature and site depth seemed to explain less of the original variance between the samples. A few environmental variables were available to

perform the PCA, the introduction of other ambiental descriptors (*eg.* nutrient concentrations, phytoplankton concentration, zooplankton biomass, density of adults) would probably have improved the analysis. Nevertheless, the results presented here still showed a higher association of the larvae with the group of sites from the central stratified region, over the mud patch, for the survey in late May (Cruise 14) than for the earlier surveys. These results were consistent with the highest abundance (retention) of lobster larvae observed in the area over the adults ground, at this stage of the larval season.

This discussion has so far highlighted that during the earlier stages of the season considerable numbers of *N. norvegicus* larvae were observed outside the area of suitable settling substrate and that this pattern was reversed during mid May-June, when higher larval abundances were detected over the adults ground. It must now be added that the retention of larvae in the suitable area for settlement, which seemed to be assisted by the existence of the local gyre, would probably be largely reduced if this hydrographic feature did not exist. Although the larval season does not coincide exactly with the period when the gyre is at it strongest point (end of July-August) (Hill *et al.*, 1997a; Horsburgh *et al.*, submitted), retention of larvae, particularly during May-June, seemed to be clearly favoured by the existence of this circulation feature. In the western Irish Sea the long term mean residual flow is weak, of the order of 1-2 cm/s (0.9-1.7 km/day) in a northward direction (Bowden, 1950) however, currents of this magnitude would probably be enough to carry most of the lobster larvae away from the area of settlement, before the competent stage had been attained. This fact stresses the importance of the gyre as a retention mechanism by which the larvae may be presented with a much higher chance of successful recruitment.

It can be argued that, if retention of *N. norvegicus* larvae over the mud patch is crucial to the survival of the population, a better matching between the larval production season and the appearance of the local gyre would be expected to exist. However, other aspects such as larval dietary requirements and environmental conditions at the time of settlement (*eg.* water column structure) may also be critical. The timing of larval hatching probably results from a compromise between improved chances of retention and other environmental constraints, like the ones mentioned above. One other factor that may have some influence on the timing of larval occurrence is the physiological condition of the females. It is believed that the females remain inside their burrows during the incubation period (8-9 months in the western Irish

Sea) and are therefore subjected to restricted food intake for several months. In order to produce viable eggs and those to be fertilized (to hatch during the next season) the adult females would need to be able to restore their body nutrient reserves. Food items are likely to be available in higher concentrations during the spring-early summer period and therefore it would be advantageous for the females not to be restricted to their burrows during this period.

While it is likely that a proportion of the larvae that are retained above the western Irish Sea mud patch eventually metamorphose into the postlarval stage and find a place to settle, the fate of the individuals which are advected away from the region is unclear. Some larvae may reach other areas where suitable substrata may be available for settlement and some, not carried too far away, may somehow manage to return into the area, but the majority would probably die.

The plots of larval distribution presented in this chapter suggested that some larvae may be transported between the western and eastern (and *vice versa*) Irish Sea *N. norvegicus* grounds. The larvae observed south of latitude 53.5° N, in early season, could conceivably be carried to grounds to the south of Ireland. For that to occur the larvae would need to be transported for distances of about 150 km, which would probably require the whole period of their larval existence (~ 50 days) and a consistent southwest flow of the order of 3 cm/s. This scenario is, at present, only especulative because no information exists to confirm the existence of such a coherent southwest current from the northwestern Irish Sea to the south coast of Ireland. Moreover, the probability of the larvae surviving such a journey and finding a suitable settling spot are not known. When zooplankton sampling was carried out along latitude 52.6° N in May 1995 (Corystes 5b) no lobster larvae were detected.

The hypothesis that *N. norvegicus* larvae may delay metamorphosis into the postlarval stage while 'searching' for a place for settlement (Smith, 1987), may increase the chances of the individuals which are advected from the parental grounds to survive and eventually encounter a settling area.

Some of the lobster larvae which were detected just south of the western Irish Sea mud patch may actually be settling in that area on the edge of the muddy region. Although the limit of the muddy substrate has been described to be at latitude 53.5° N, some suitable sea bed spots

may still exist south of that line, adult *N. norvegicus* have been found in substrates with a silt-clay content of as less as 4% (Tully & Hillis, 1995). Fisheries statistics data, show that catchs of the species have been recorded for ICES rectangles 35E4 (53-53.5° N, 5-6° W) and 35E5 (53-53.5° N, 4-5° W) (table 2.6, chapter II).

Another possibility is that larvae washed away from the region over the mud patch, may be able to return to the area, before metamorphosis into the postlarval stage occurs. It is unlikely that the juveniles may travel along the sea bed back into the adults grounds, on what would be a very hazardous journey. The young juveniles are believed to be considerably dependent on the existence of adults burrows for shelter and to start their benthic existence (Tuck, *et al.*, 1994).

How the planktonic stages may return to the adult area is very uncertain. Surface currents, mainly induced by wind events, could play a role in the dispersal of the larvae back into the area of settlement. In the western Irish Sea, the winds blow predominantly from a southwest direction and therefore wind driven currents may promote the return of some individuals into the area of the mud patch. The depth distribution of the larvae, especially during the night (chapter VI), places the individuals in the layers that might be affected by surface currents. If the larvae became, by that means, entrained into the gyre circulation then the probability of retention over the mud patch would be considerable. When the gyre is established, currents of the order of 15-20 cm/s are in place in the area around the mud patch. It is very improbable that *N. norvegicus* larvae would be able to isolate themselves from the influence of such strong currents. There is no information about the swimming ability of *N. norvegicus* larvae in flowing waters but laboratory trials, using static water conditions, showed that *N. norvegicus* zoeae are capable of upward and downward displacement at speeds of 2-3 cm/s (Smith, 1987). Despite the possibility of vertical displacement at such speeds it is unlikely that the larvae would be able to counteract the gyre jet flow. Once entrapped in the gyre circulation, transition to the waters in the centre of the gyre would occur and then conditions for settlement would be favoured because this region is mainly an area of stagnant flow.

The larvae which were observed in the inshore waters to the west of the mud patch may also become entrained in the gyre circulation and subsequently be retained in the favourable area for settlement. Dickey-Collas *et al.* (1997) suggested that pelagic juvenile fish of several

species which occur in the western Irish Sea at the same time as *N. norvegicus* larvae, are passively retained in the stratified area, although the mechanism by which the transition from the spawning grounds, inshore, to the deeper central area, is achieved was not clearly described. The prevailing offshore winds may have some influence on the transport of the larvae into the central area. Horsburgh *et al.* (submitted) suggested another mechanism which may assist the entraining of the planktonic organisms into the gyre. Downslope Ekman flows in the bottom boundary layer beneath a coastal current can cause density to be advected offshore until it reaches a depth where vertical shear produces a frictionally induced upslope flow which balances the offshore buoyancy flux. In this way, isopycnals can be moved downslope and an initially weak density anomaly can be intensified into bottom frontal gradients near the coast in the absence of an associated surface front.

Although it is not clear how some species reach the area of influence of the gyre, a considerable amount of evidence has become available to support the view that the existence of the gyre promotes retention of planktonic organisms in the western Irish Sea (Nichols *et al.*, 1993; Bukart *et al.*, 1995; Dickey-Collas *et al.*, 1996b; 1997; Fox *et al.*, 1997; Gowen *et al.*, 1998).

Bearing in mind that the existence of a planktonic larval phase is a trait favouring dispersal, even though *N. norvegicus* is a substrate specific species during the adult phase, it is not surprising that a proportion of the larvae produced may drift away from the parental ground. What is however crucial for the survival of the population is that enough individuals may be capable of remaining in (attaining) the suitable area for settlement in order to guarantee recruitment into the benthic environment. In the western Irish Sea, it appears that the existence of the gyre may provide the mechanism for retention of *Nephrops norvegicus* larvae in the area. Some other populations of the species seem to inhabit regions where similar hydrographic conditions occur (*eg.* Fladen Ground in the North Sea (Bailey *et al.* 1997)).

The western Irish Sea *Nephrops norvegicus* population has been subjected to intense fishing activity since the 1950's (~ 8500 tonnes/year, ~ 600×10^6 individuals/year), however it seems that it has been withstanding those rates of mortality. This fact supports the view that successful regular recruitment to the population is occurring.

Using the number of larvae produced during the 1995 season and the overall % loss figures and assuming a moulting survival of approximately 30% for the postlarval stages (Smith, 1987: a figure of 50% moulting survival for the first postlarval phase is likely to be an overestimate), the overall numbers available for settlement in the western Irish Sea were $6.8/m^2$ ($33918x10^6$ individuals). It must, however, be pointed out that this is an average density value and the considerable spatial variability in larval density observed during this study would suggest local variability in settlement. This value is also, only a very rough estimate of potential settlers, which does not take into account mortality of juveniles and is also likely to overestimate the number of individuals retained in the area. The lack of observations on the density and distribution of the postlarva, and juveniles does not permit accurate predictions of recruitment of the species.

Chapter VI. Vertical distribution of *Nephrops norvegicus* larvae in the western Irish Sea

1. Introduction

Most larvae are small animals, heavier than seawater, that move at low Reynolds numbers where inertial forces are very low and completly overwhelmed by the effects of viscosity. In general, therefore larvae move only when swimming appendages and/or cilia are actually in motion and they stop completely, sinking, when swimming ceases (Young, 1995).

Crustacean larvae are among the invertebrate larvae with a more developed locomotory system and can propel themselves using the muscles in their appendages and tails. Swimming speeds high enough to counteract water currents have been registered for several species (see Chia *et al.*, 1984; Shanks, 1985). As an illustration, megalopae larvae of the crab *Pachigrapsus crassipes* swim well enough (average speeds of 9.5 cm/s in laboratory experiments) to resist the downwelling currents at surface convergence zones marked by slicks (Shanks, 1985) and stage IV larvae of the lobster *Homarus americanus* are capable of upward swimming speeds of 6.2 cm/s (Ennis, 1975). Crustacean zoeae and more advanced stages also have a bilaterally symetrical arrangement of appendages that allow them to swim in a more or less straight path. Large larvae, like late stages of crab and lobster larvae, are even capable of using horizontal swimming to migrate considerable distances. The best example is probably the powerful puerulus stage of spiny lobsters. *Palinurus cygnus* larvae are able to swim, at speeds up to 33 cm/s (Phillips & Olsen, 1975), across shelf areas for distances of 40 to 60 Km (Philips *et al.*, 1978). Despite cases like the latter, the major function of larval locomotion is to control their position in the water column either maintaining a relatively constant depth or exhibiting a migratory behaviour.

Vertical displacements may occur on a daily basis (diel vertical migration-DVM) or over longer periods; seasonal in which an organism occurs at different depths at different times of the year and ontogenetic in which different developmental stages of a species occur at different depths (Longhurst, 1976). Seasonal and ontogenetic migrations are often in fact one and the same thing especially when referring to holoplanktonic species which have several

generations each year. Ontogenetic migrations are also common among meroplankters, larval stages of many marine benthic invertebrates occupy distinct depths at different stages in their planktonic life.

Three basic patterns of DVM have been recognised by Hutchison (1967): (1) nocturnal migration, characterized by a single daily ascent with minimum depth reached between sunset and sunrise and maximum depth attained during the day. (2) twilight migration, characterised by a rise to a minimum depth at dusk and dawn, downward movement during the day and scatter throughout the water column at night. (3) reverse migration, consists of an ascent to a minimum depth during the day and descent to a maximum depth at night. More recently, migrations in estuarine and shallow water species have shown to correlate with tidal rhythms, thus adding a fourth pattern of migration, tidal migration (Cronin & Forward, 1979).

Although conflicting views still persist regarding the adaptive significance of vertical distribution patterns and the factors that trigger such behaviours, its relevance in the species life history is widely acknowledged. Both the proximal (causal) and ultimate (adaptive) reasons for vertical distribution patterns have been investigated. Proximate causes include responses to stimuli such as light, temperature, hydrostatic pressure and chemical cues and endogenous factors such as state of feeding and biological rhythms. Feedding advantages, metabolic energy saving, predator avoidance and horizontal transport have been postulated as possible driving forces (or evolutionary adaptations) behind migratory or non-migratory behaviours. (see Longhurst, 1976; Ohman, 1990; Haney, 1993 and Lampter, 1993 for reviews on causal and adaptive factors of vertical distribution patterns)

In this chapter, the objective is to discuss the effect the vertical distribution of the larvae may have on their spatial distribution and dispersal. It is clear from a large body of evidence that many larvae control their horizontal distribution and dispersal by navigating vertically in the water column. Examples in which horizontal dispersal is controlled by migrating with respect to current shear include small, weak swimmers like polychaete larvae (Mathivat-Lallier & Cazaux, 1990; Thiebaut *et al.*, 1992) or bivalve larvae (Wood & Hargis, 1971; Manuel *et al.*, 1997) larvae, as well as more motile larvae of crab (Cronin, 1982; Epifanio, 1988; Zeng & Naylor, 1996a; 1996b), lobster (Rimmer & Phillips, 1979; Phillips *et al.*, 1981; Phillips &

McWilliam, 1986) or fish (Fortier & Leggett, 1983; Sinclair & Iles, 1985; Werner *et al.*, 1993; Bartsch & Knust, 1994) larvae.

Although some reservations may remain concerning the extent to which some small larvae may actively influence their position in the water column, the evidence for an active behaviour in that control is less disputable in cases involving decapod and fish larvae.

Perhaps the least controversial cases supporting the hypothesis that larval migration is directed towards transport producing effects arise from examples in the estuarine and inshore waters environments. Vertical migration synchronized with the tides, where the larvae avoid being flushed out of estuaries by migrations centered on the depth of no net flow (Cronin, 1982; Thiebaut *et al.*, 1992) or by resting close to the bottom during ebb tides and migrating up in the water colum on flood tides (Wood & Hargis, 1971; Epifanio *et al.*, 1988) or reinvading those areas by travelling with flood currents (Epifanio *et al.*, 1988; Christy, 1989; Lawler *et al.*, 1988) conform to the theory of active behaviour in the control of larvae dispersal.

Other cases, show that coexisting species adopting different vertical positions in the water column have distinct dispersal patterns. The phyllosoma of the spiny lobster (*Panulirus cygnus*) and slipper lobster (*Scyllarus bicuspidatus*) inhabiting the same area in the western coasts of Australia exhibit a distinct migration behaviour. The larvae of both species undergo diel vertical migrations, with the peak abundances of early stages centered closer to the surface and mid and later stages deeper in the water column. Early stages are carried offshore by the surface wind drift but mid and later stages, by avoiding the surface layers during most of their larval phase, become more subject to the subsurface circulation which returns them to near the coast. The adoption of a deeper position in the water column by *S. bicuspidatus* planktonic stages makes them less exposed to offshore transport than *P. cygnus* larvae (Phillips *et al.*, 1981; Phillips & McWilliam, 1986).

Evidence also suggests that different larval displacement strategies may lead to similar transport effects (retention within an area) for a same species occupying distinct habitats. *Placopecten magellanicus* larvae from Georges Bank and Passamaquoddy Bay are retained over their respective parental grounds due to distinct migration behaviour. While

Passamaquoddy Bay veligers minimise dispersal by swimming up at slack waters and down when currents are stronger, Georges Bank larvae utilize the vertical differences in tidal phase to avoid being flushed out of the Bank (Manuel *et al.*, 1996; Manuel *et al.*, 1997).

From all the examples mentioned, and others in the literature, it seems fair to say that whatever the contribution larvae behaviour may have, an almost inevitable consequence is that their vertical distribution will influence their horizontal distribution. A complete study on the spatial distribution and dispersal patterns of a planktonic organism should consequently include the investigation of its vertical distribution. The objective of this chapter is therefore to cover this aspect of the larvae distribution for the species under study. How *Nephrops norvegicus* larvae are vertically distributed in the water column is fundamental to understand their dispersal patterns in the western Irish Sea and ultimately of interest in the interpretation of the processes leading to settlement onto the mud patch.

Although the hypothesis of retention of *N. norvegicus* larvae over the western Irish Sea mud patch has been advanced in previous research (Hill *et al.*, 1994) and further discussed by (Brown *et* al, 1995 and Hill *et al.*, 1996), the influence that the vertical distribution of the larval stages may have on their spatial distribution has never been discussed.

There is in fact a notable absence of research on the vertical distribution of the Norway lobster larvae. Hillis (1974a) and Lindley *et al.* (1994) are the only published studies on this subject. However, both studies are inconclusive due to limitations derived by the sampling strategies adopted. Problems arise due to the difficulties of adequately sampling the water column for *N. norvegicus* larvae, a relatively scarce and quite motile plankter with a patchy distribution.

In this chapter, a compilation of historical data and some information collected during this project are analysed aiming to find a more clear description of the vertical distribution of *N. norvegicus* larvae and its effects on their dispersal patterns. Environmental data (temperature, density, chlorophyll and flow field profiles) are used in conjuction with the larvae distribution profiles in order to assess the relationship between the biotic and abiotic components of the system.

2. Methodology

2.1. Sampling

Sampling was undertaken using a multiple-serial plankton recorder (LHPR). Sampling sites, 36 in total, are shown in figure 6.1 and the dates and times of the hauls and site depths are presented in table 6.1. The institutions that made the historical data available, and the location are shown in table 3.2 (chapter III). The original sampling station references, shown in tables 3.2 and 6.1, will be maintained throughout this text; station numbers denote haul numbers rather than sites. This study includes three sampling stations which were visited, three times each, at night and day time, during the period of this project (Cirolana 4b/96).

Hydrographic data (temperature, salinity, density, chlorophyll, potential energy anomaly, geostrophic velocities, ADCP derived velocities and drifters trajectories) from Cirolana 4b/96 (April), Corystes 5b/95 (May) and Corystes 7/94 (June) surveys are used for the analysis presented in this chapter. References to observations made during other surveys in the spring-summer of 1995 and 1996 are also included. (These hydrographic observations were already discussed in chapter IV). Profiles of temperature obtained by the CTD probe attached to the LHPR sampler are also presented.

2.2. Data processing and analysis

A total of 50 sampling stations were available but from those only 36 are analysed in this study. The remaining samples, all containing less than 10 larvae, were not considered.

The LHPR is always deployed by performing a double oblique haul, collecting samples during the dive of the net and on the way up. However, some of the historical data made available only included data from the downward cast. For this reason, to assure uniformity between the samples, only the downward casts were analysed. Because of the way the sampler is deployed, downward and upward casts tend to collect unequal sample sizes.

The original numbers of larvae for each depth interval sampled, were integrated into standardized 5 m depth intervals. The data in this format was subsequentely used for plotting and statistical analyses.

An estimate of the mean depth of occurrence of the larvae was calculated as the weighted mean depth (Sokal & Rolf, 1995):

$$\text{Mean depth} = \frac{\sum f_i d_i}{\sum f_i},$$

where f_i is the frequency of larvae in the *i*th depth interval, and d_i is the mid depth of the *i*th interval. The weighted mean depth is also defined as the centre of mass of the distribution by Fortier & Leggett (1983), this quantity is meaningful only when the aggregation of larvae is substantial (Tremblay & Sinclair, 1990). As a measure of dispersion of the larvae through the water column, two statistics were considered: the standard deviation, of the frequency distribution, and the coefficient of variation (CV: standard deviation/mean) of larval concentration in the different intervals (Elliot, 1977; Sokal & Rolf, 1995). A high CV indicates strong aggregation of larvae while a low CV indicates that the larvae are more evenly distributed through the water column (Tremblay & Sinclair, 1990).

Analysis of variance (ANOVA) (Sokal & Rolf, 1995) was used to assess the differences between the mean depth of occurrence of the larvae for each profile. Four, crossed, factors were considered: time of sampling (day and night), site depth ($\leq$ 50 m, 50-75 m, $\geq$ 75 m), season (April, May, June) and developmental stage (I, II, III). Depth distributions were only considered when 10 or more individuals belonging to a particular stage were present. The analysis was performed using the GLM (General Linear Model) routine from the statistics package Minitab. Tests for homogeneity of variances and normality of errors were performed to guarantee that the results from the ANOVA could be relied upon (Sokal & Rolf, 1995; Fry, 1996).

When the information was available, temperature profiles were plotted using the data from the Guildline CTD, mounted on the LHPR. The depth of the surface mixed layer was estimated as the maximum depth at which the temperature was still constant. The difference

between surface and bottom temperature (Δt) is used as an indication of the stratification of the water column.

Association between the mean depth distribution of the larval stages and the depth of the surface mixed layer and between the CV of the distribution across the depth intervals and surface to bottom temperature difference, was analysed using the Pearson's product-moment correlation coefficient (Sokal & Rolf, 1995).

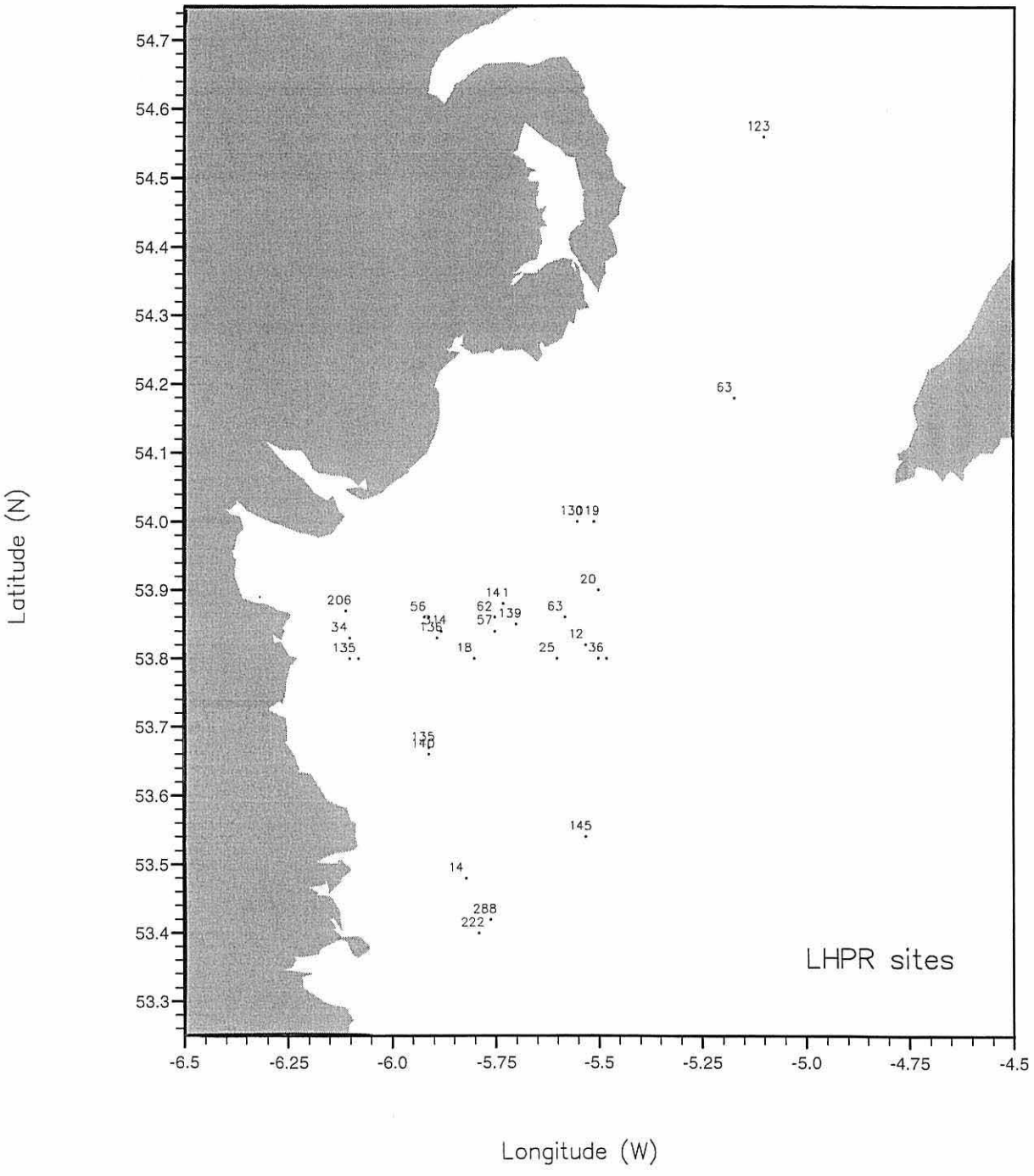


Figure 6.1. Location of LHPR sampling sites. Details on dates and times are shown in table 6.1.

Table 6.1. LHPR observations, date, time, depth and Δt. Number of larvae collected by stage and mean depths of occurrence and respective standard deviation and coefficient of variation.

Station	Date	Time	Depth (m)	Δt (°C)	Total /m²	Total	Stage I	Stage II	Stage III	Stage IV	Mean dep. Stage I	Stdev. Stage I	Coef. Var. Stage I	Mean dep. Stage II	Stdev. Stage II	Coef. Var. Stage II	Mean dep. Stage III	Stdev. Stage III	Coef. Var. Stage III
18	11.4.88	23:29	55	0.50	13.4	25	23	2	——	——	11.92	8.67	1.19	24.23	2.76	2.0	———	———	———
19	12.4.88	11:56	55	0.50	33.1	63	52	11	——	——	18.73	4.40	0.31	18.06	4.1	0.32	———	———	———
22	24.4.88	23:23	105	0.50	11.4	26	26	——	——	——	19.21	24.02	1.78	———	———	———	———	———	———
20	25.4.88	12:09	105	0.60	9.3	25	25	——	——	——	21.20	6.75	2.08	———	———	———	———	———	———
35	21.4.89	23:01	30	0.30	6.9	29	25	4	——	——	10.31	5.42	1.02	20.83	2.36	1.57	———	———	———
34	21.4.89	12:29	30	0.42	12.4	37	35	2	——	——	17.60	2.41	1.88	19.40	2.48	1.67	———	———	———
36	22.4.89	23:09	105	0.42	19.1	42	41	1	——	——	10.13	7.75	2.35	14.17	2.36	2.47	———	———	———
37	23.4.89	12:42	105	0.40	9.0	23	22	1	——	——	19.82	12.89	2.0	17.5	———	———	———	———	———
61	19.4.96	18:35	45	0.71	16.9	39	39	——	——	——	10.79	3.75	1.58	———	———	———	———	———	———
56	19.4.96	09:59	45	0.43	3.9	10	10	——	——	——	20.26	4.29	1.47	———	———	———	———	———	———
62	19.4.96	20:35	65	0.33	64.2	138	101	34	3	——	18.16	7.07	1.32	17.32	5.98	1.39	24.50	2.45	2.40
57	19.4.96	12:43	65	0.32	20.2	60	43	16	1	——	25.4	6.44	1.96	23.89	3.40	2.92	22.50	———	———
63	19.4.96	22:48	105	0.41	4.6	5	3	2	——	——	30.85	2.35	3.43	10.50	2.45	3.10	———	———	———
71	19.4.96	10:21	105	0.33	10.5	11	8	3	——	——	29.62	3.76	2.71	31.41	3.89	2.64	———	———	———
63	30.4.94	15:21	80	0.31	5.3	13	9	4	——	——	18.49	12.98	2.54	15.0	2.50	2.72	———	———	———
123	6.5.94	14:20	120	0.59	12.2	30	21	9	——	——	23.50	7.02	2.30	20.0	7.88	2.21	———	———	———
135	8.5.94	08:06	55	1.53	9.1	53	35	18	——	——	10.99	4.89	3.23	10.23	2.49	3.44	———	———	———
140	8.5.94	14:22	55	1.76	3.8	24	16	8	——	——	18.49	4.08	1.70	17.77	3.85	1.74	———	———	———
119	5.5.94	22:20	100	0.78	3.7	22	17	5	——	——	13.50	7.82	1.37	12.50	5.0	2.47	———	———	———
130	7.5.94	10:06	100	1.29	2.8	11	9	2	——	——	20.69	6.14	2.24	29.82	2.49	3.10	———	———	———
135	15.5.93	21:05	30	0.04	65.0	280	167	88	25	——	7.50	6.59	1.18	10.85	7.97	0.70	8.91	7.75	1.23
206	21.5.93	20:05	30	0.76	15.2	54	31	15	8	——	9.14	3.51	1.28	6.30	3.09	1.40	7.81	3.71	1.17
136	15.5.93	22:54	45	0.26	20.1	55	28	26	1	——	22.64	12.03	0.40	22.80	12.85	0.56	19.51	2.45	2.09
314	30.5.93	14:16	45	0.73	74.7	226	41	110	75	——	26.10	6.87	1.07	26.20	5.35	1.31	28.08	4.30	1.50
222	22.5.93	18:56	65	0.54	24.2	52	14	30	8	——	15.37	4.47	2.89	10.59	9.82	1.77	4.46	3.97	3.05
288	29.5.93	19:00	70	0.69	106.1	304	26	148	129	1	21.70	10.51	1.68	23.95	13.89	1.03	18.42	11.44	1.40
12	27.5.87	23.11	85	2.26	17.3	31	11	15	5	——	20.05	21.29	2.02	17.06	19.88	1.50	6.11	2.19	3.17
14	30.5.87	15:11	75	1.98	11.4	25	25	——	——	——	26.35	11.07	1.55	———	———	———	———	———	———
25	25.5.88	00:13	100	2.70	18.3	61	23	13	25	——	18.81	7.25	1.86	12.75	5.44	2.0	15.33	6.23	1.80
26	25.5.88	12:47	100	2.60	8.9	14	3	4	7	——	24.53	2.47	4.60	24.08	2.27	3.40	25.90	3.35	2.40
28	25.5.88	23:41	40	2.12	5.7	17	13	3	1	——	15.67	9.40	0.75	11.59	7.63	1.08	9.50	2.45	1.85
139	6.6.84	20:57	70	——	42.7	147	18	51	75	3	10:33	3.84	2.31	13.0	6.1	1.64	17.0	8.92	1.15
140	7.6.84	00:25	70	——	51.8	180	26	81	71	2	7.81	5.57	1.81	10.30	6.9	1.44	12.86	8.78	1.23
141	7.6.84	03:10	70	——	24.1	38	3	10	25	——	27.05	2.53	3.0	22.19	2.04	1.71	25.19	11.26	1.22
142	7.6.84	10:53	70	——	77.2	309	44	153	112	——	24.11	3.54	2.13	22.96	5.92	1.61	21.74	7.54	1.32
145	7.6.84	18:59	105	——	40.3	111	7	49	51	4	26.41	6.68	2.27	21.23	7.30	0.48	22.08	9.49	1.89

3. Results

3.1. Vertical distribution of *Nephrops norvegicus* larvae

Figures 6.2 to 6.7 show percentage depth distribution of *Nephrops norvegicus* larvae, for each stage, for all the sampling stations assembled. The plots are presented in sequence according to the period of the year in which the samples were collected (April, May, June), dates and times for each profile are shown in table 6.1. Paired histograms represent night/day hauls undertaken at a same site.

Sampling carried out in April (figures 6.2 and 6.3) included mainly individuals at developmental stage I although some stage II larvae were also collected. Throughout May (figures 6.4, 6.5 and 6.6) the proportion of stage II larvae increased but numbers of individuals at stage III became only appreciable during the second half of the month (figures 6.5 and 6.6). By the end of the sampling period, in early June (figure 6.7), the density of stage I lobster larvae had decreased considerably but stages II and III seemed to be equally abundant. Postlarvae (stage IV) are rarely found in plankton samples and that fact is supported by this set of data, from the 2590 individuals collected by the LHPR only 10 were at stage IV. *N. norvegicus* postlarvae were detected in, late May-early June, samples 288/93, 139/84, 140/84 and 145/84. This information is not shown in the graphics due to its small representation in the samples (see table 6.1).

The present results seem to indicate no differences in the number of larvae caught during night and day time hours. Avoidance of the LHPR, during day light, has been reported for fish larvae (Brander & Thompson, 1989), but it appeared not to be the case for *N. norvegicus* larvae. For the sites where repeated night and day hauls were carried out (paired histograms), 6 cases showed larger numbers per m^2 by night than by day and 4 vice-versa (see table 6.1). The average density was 18.3 larvae/m^2, in the night samples and 18.7 larvae/m^2, in the day samples. In total, the night time catches (18 stations) averaged 23.6 larvae/m^2 and the day time samples (18 stations) 25.0 larvae/m^2 ($T=0.63$, $p=0.53$, $df=32$). The overall proportions of the four stages were: stage I - 40.2 %, stage II - 35.4 %, stage III - 24.0 % and stage IV - 0.4 %.

The distribution of the larvae throughout the water column is fairly aggregated with the bulk of the larvae occurring in the top 40 m. The mode of the distribution appeared, in most cases, in the top 25 to 30 m. The degree of aggregation, reflected by relatively small standard deviations and high CV's (see table 6.1), did not seem to differ much between places, stages or period of the year. There were however a few larvae appearing deeper in the water column. Stations 22/88 (figure 6.2b), 12/87 (figure 6.6a) and 141/84 (6.7c), all night time samples, show a more dispersed distribution, which could indicate a weaker aggregation of the larvae during the night. Stations 63/94 (figure 6.4a), 14/87 (figure 6.6b) and 145/88 (figure 6.7d), sampled during the day also show occurrences below 40 m. Sample 288/93 (figure 6.5f), also revealed larvae at the bottom of the water column, this station was sampled close to dusk.

The results presented here, indicate a clear diel migration of the zoeal stages of *N. norvegicus*, with significant movement at night towards the surface. Evidence for ontogenetic migration behaviour was not found. No differences were apparent between the depths occupied by the different developmental stages either at night or day. The mode of the day distributions was located around 25-30 m, in the majority of the cases, and night time profiles had modes generally between 10 and 20 m. Due to the great disparity in the time of sampling between the samples analysed, a more detailed description of the daily movements of the larvae is not appropriate.

Figure 6.8 show that stage I larvae migrate from an average day time depth of 21.1 m to 13.8 m (7.3 m displacement), individuals at stage II, move from a mean day time depth of 20.9 m to 14.3 m at night (amplitude of migration 6.6 m), and stage III lobsters show an average day time depth of 22.6 m, moving to an average 13.2 m during the night (9.4 m migration). Considering the 95 % confidence intervals calculated for those mean depths, stage I larvae show a possible amplitude of migration of 12.4 m, stage II zoea can migrate vertically 15.1 m and individuals at developmental stage III may have a displacement of 26.2 m. The latter value should be treated with caution because the number of samples available to calculate the depth of occurrence of stage III zoea was small.

The vertical distribution of the postlarval stage (stage IV), in the present samples, seemed to be very variable. Lobsters at this phase of development, were found from the very superficial waters, top 10 m, to much deeper in the water column, below 80 m. From the 10 postlarvae

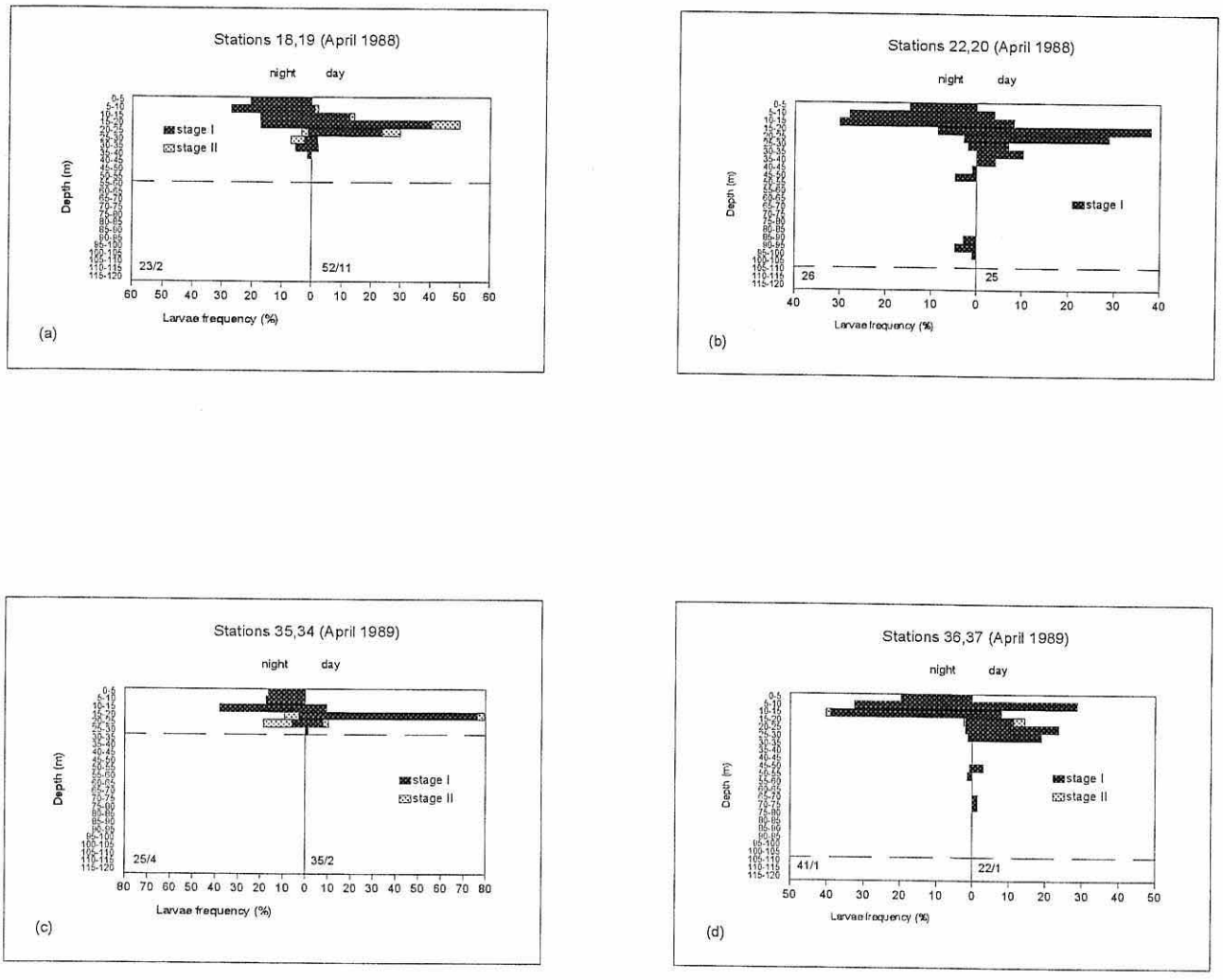
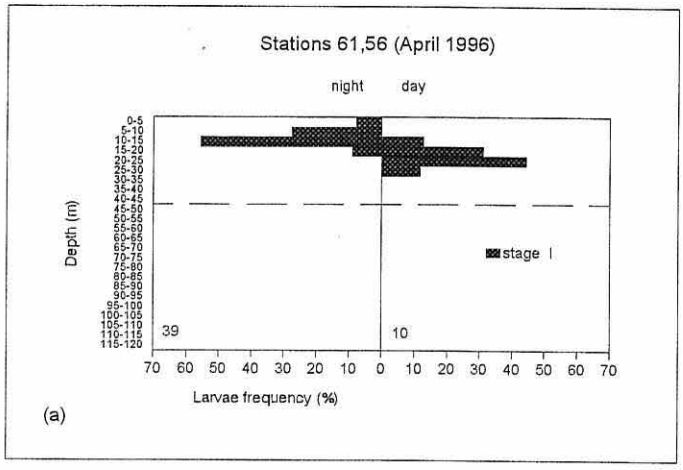
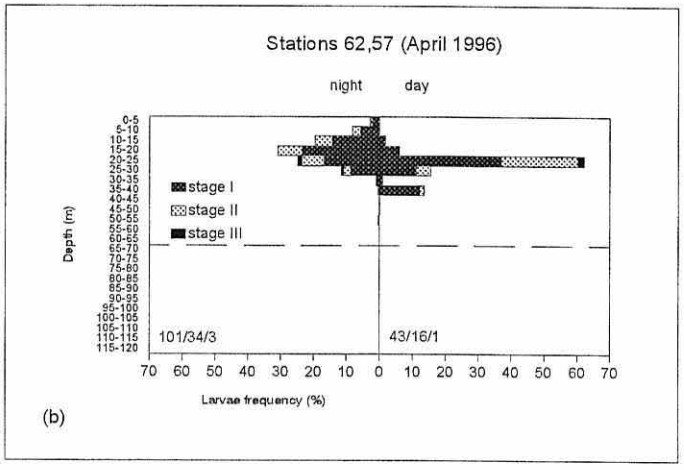


Figure 6.2. *N. norvegicus* vertical distribution for sites sampled during the month of April. Each plot shows distribution, per larval stage, during night and day hauls carried out at the same location (the dashed line indicates the total depth at each site). The number of individuals collected for each larval stage is presented in the bottom left corner.





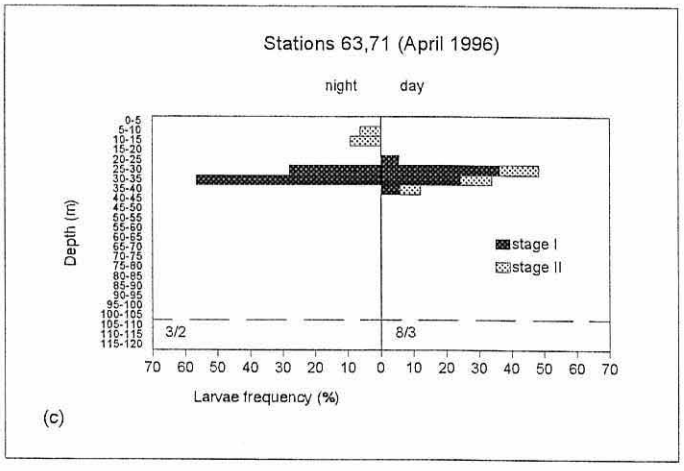
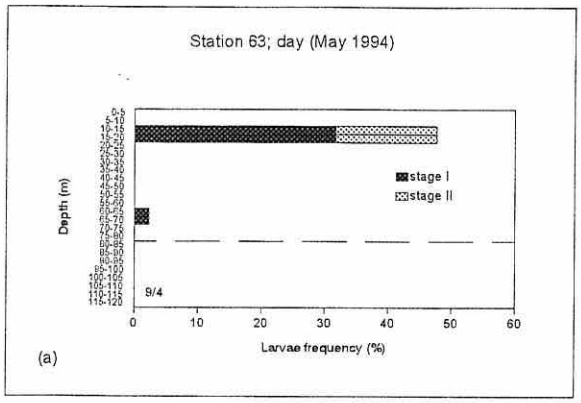
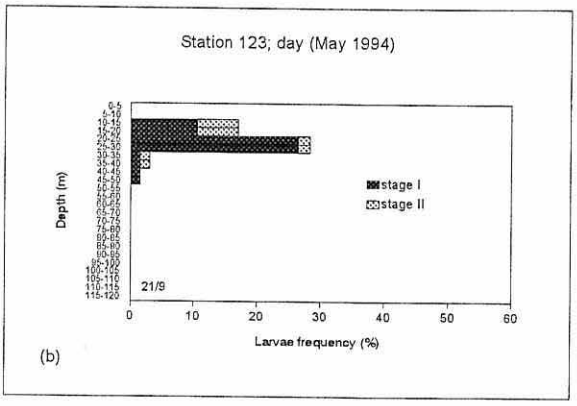
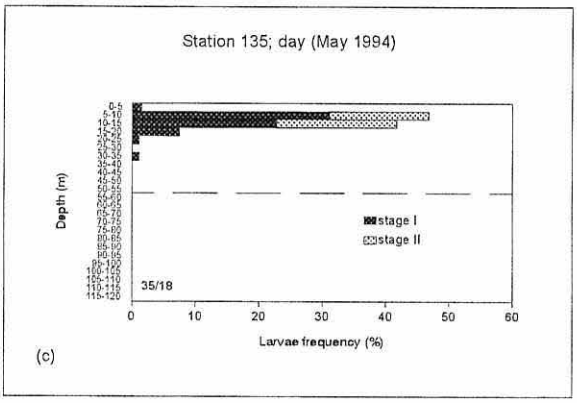
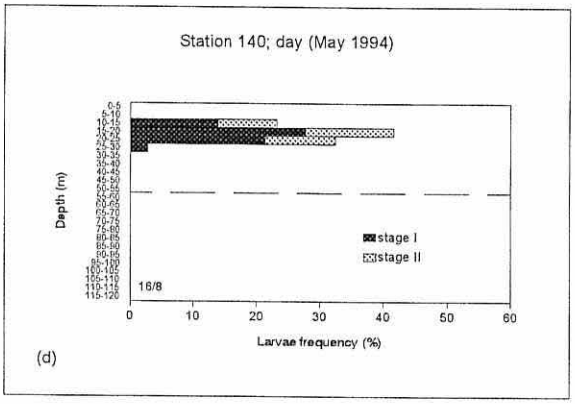


Figure 6.3. *N. norvegicus* vertical distribution for sites sampled during the month of April in 1996 (Cirolana 4b/96). Each plot shows distribution, per larval stage, during night and day hauls carried out at the same location (the dashed line indicates the total depth at each site). The number of individuals collected for each larval stage is presented in the bottom left corner.









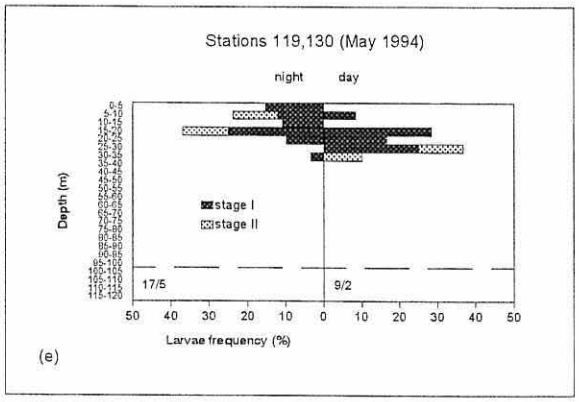
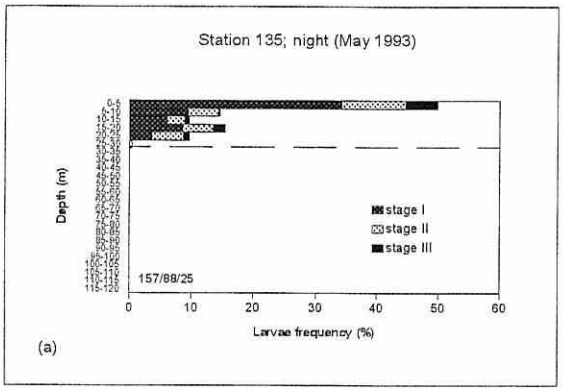
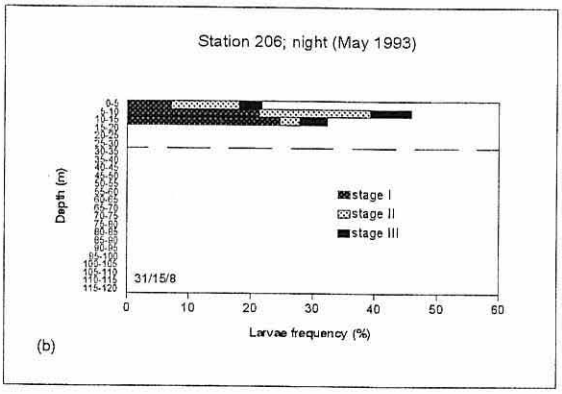
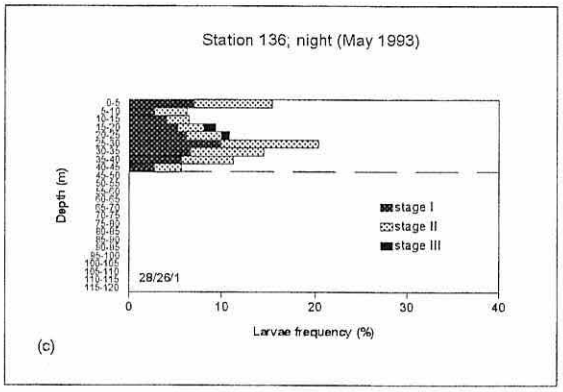
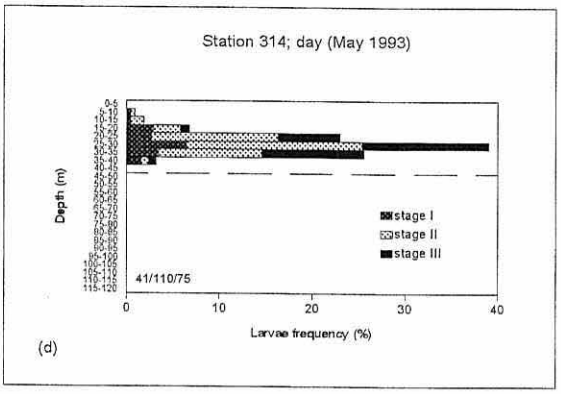


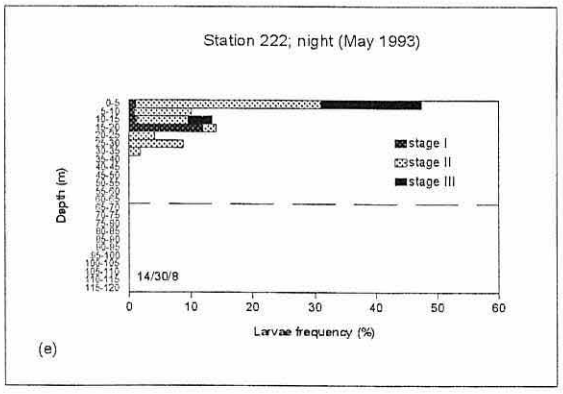
Figure 6.4. *N. norvegicus* vertical distribution for sites sampled during the month of May in 1994. The number of individuals collected for each larval stage is presented in the bottom left corner. (a) to (d) are day time hauls, (e) paired hauls carried out at the same location during night and day time. (c) and (d) are samples from approximately the same location, (the dashed line indicates the total depth at each site).











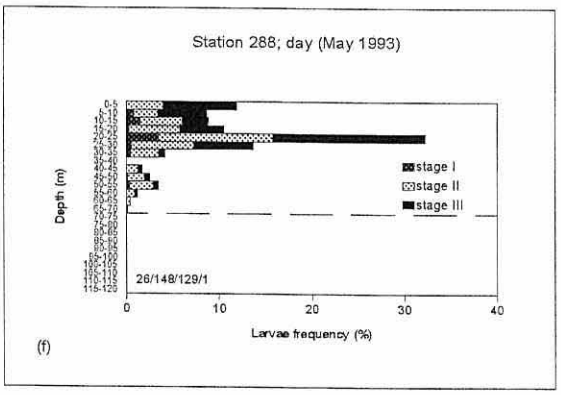
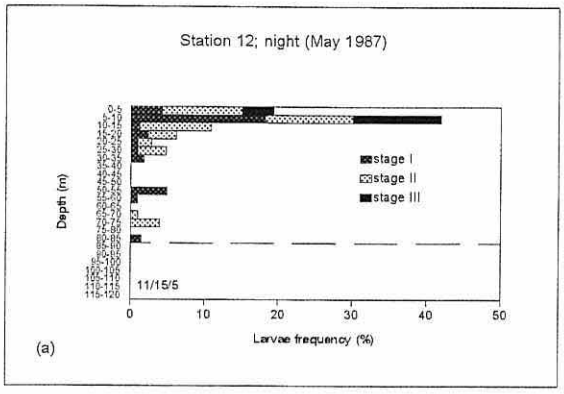
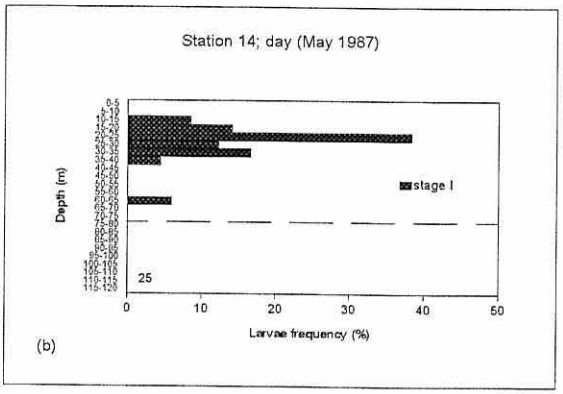
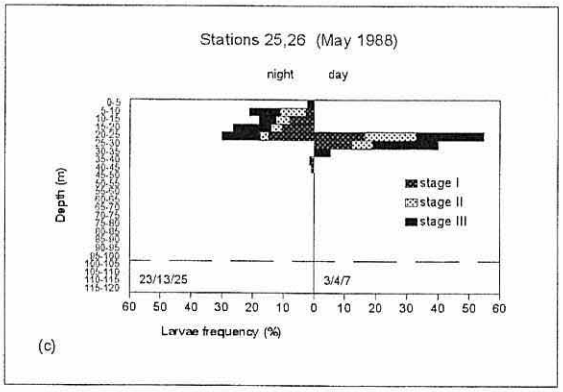


Figure 6.5. *N. norvegicus* vertical distribution for sites sampled during the month of May in 1993. The number of individuals collected for each larval stage is presented in the bottom left corner. (a), (b), (c) and (e) are night time hauls, (d) and (f) are day time hauls, (the dashed line indicates the total depth at each site).







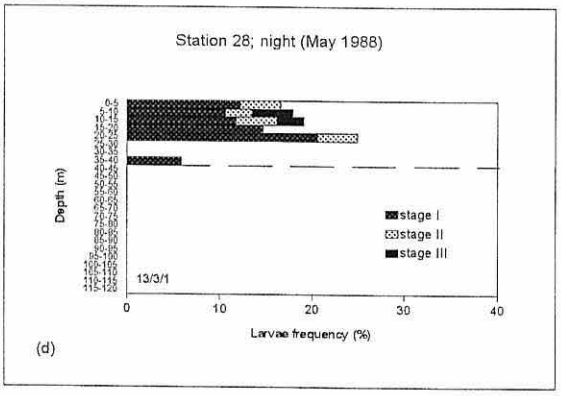


Figure 6.6. *N. norvegicus* vertical distribution for sites sampled during the month of May. The number of individuals collected for each larval stage is presented in the bottom left corner. (a) and (d) are night time hauls, (b) is a day time haul and (c) paired hauls carried out at the same location during night and day time, (the dashed line indicates the total depth at each site).

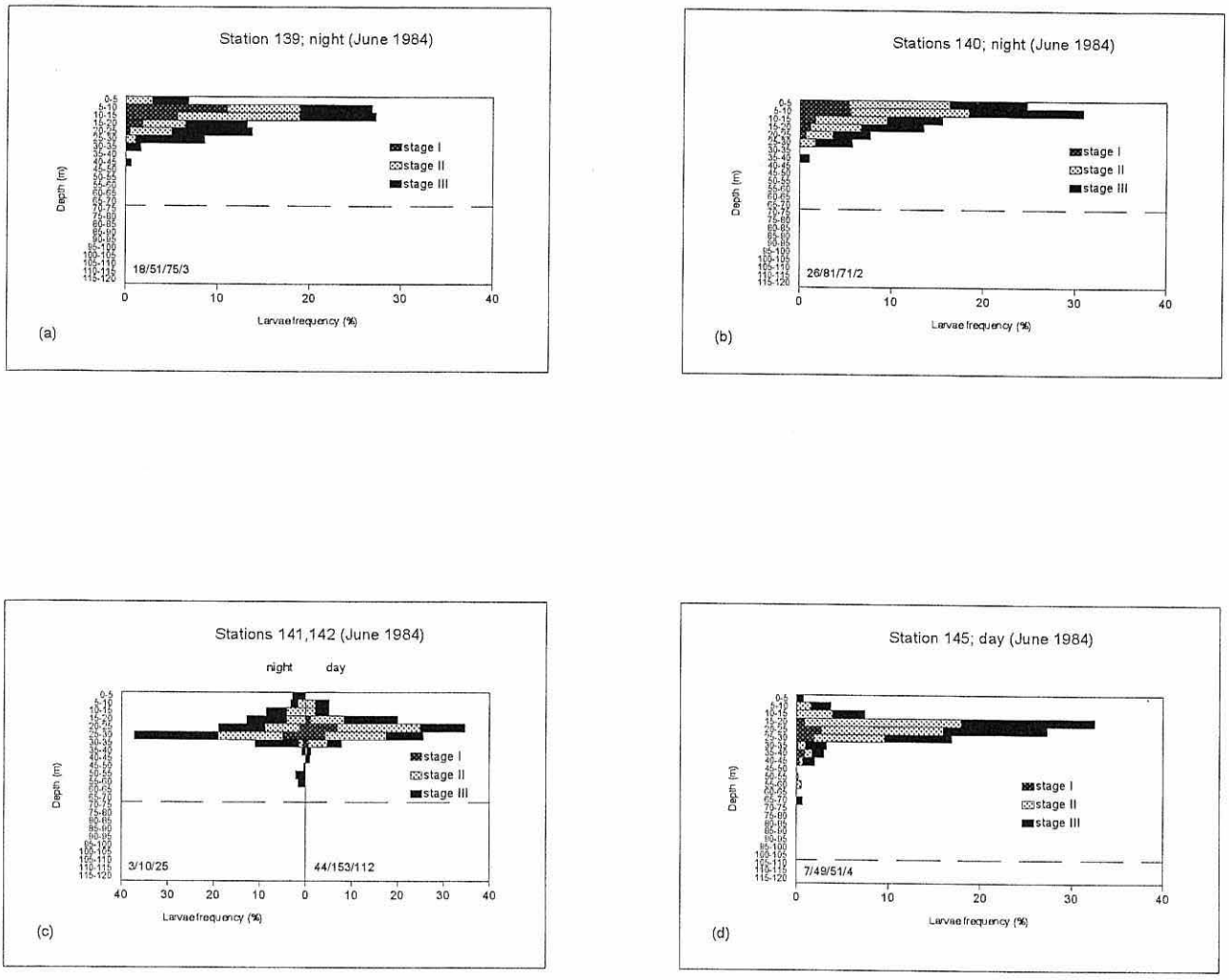


Figure 6.7. *N. norvegicus* vertical distribution for sites sampled during the month of June. The number of individuals collected for each larval stage is presented in the bottom left corner. (a) and (b) are night time hauls carried out at the same location, (c) paired hauls carried out at the same location during night and day time, (d) day time haul, (the dashed line indicates the total depth at each site).

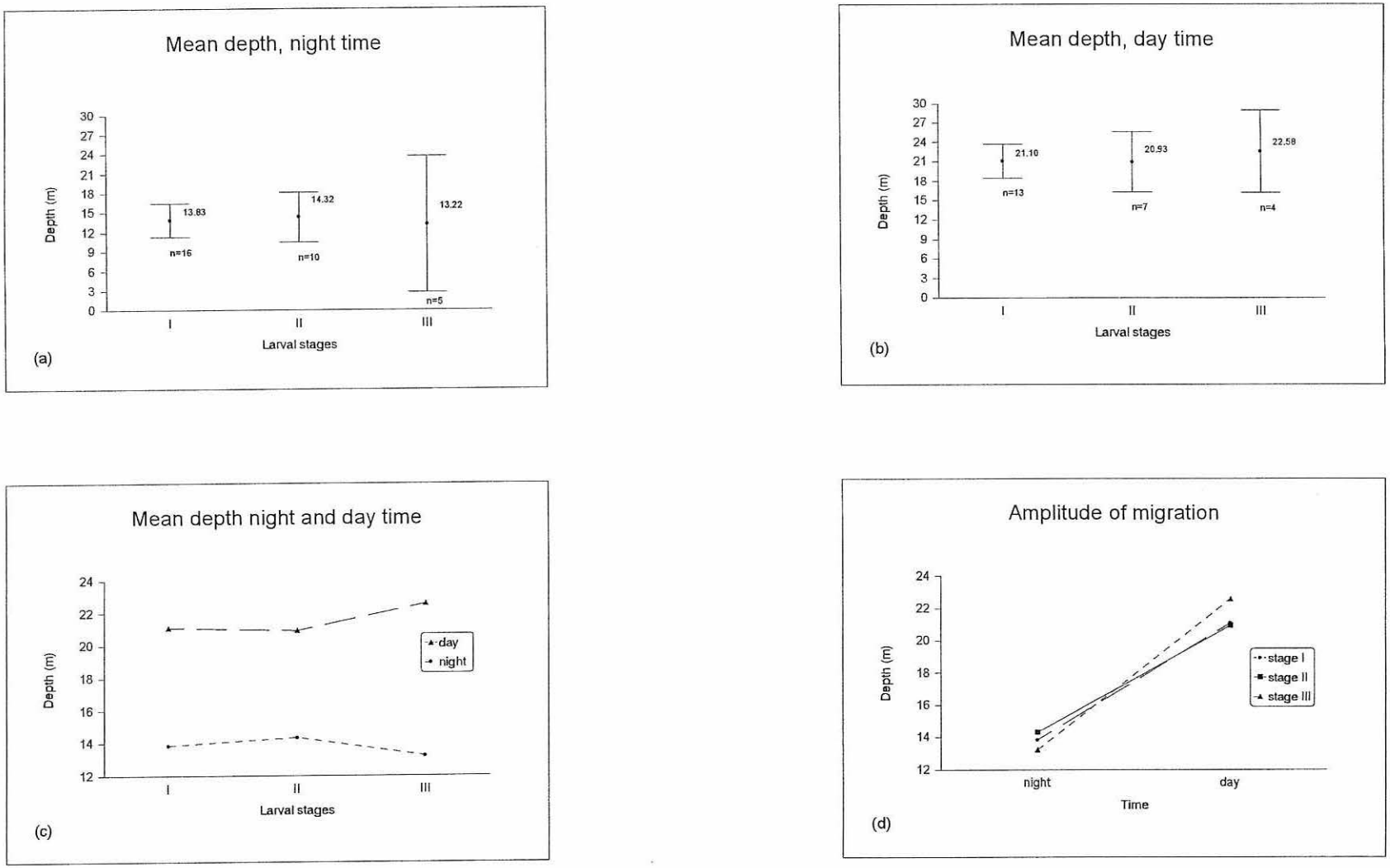


Figure 6.8. Mean depth of occurrence of *N. norvegicus* stage I, II and III zoea. (a) night time distribution, (b) day time distribution. Bars denote 95% confidence intervals for the mean values calculated. Also presented the number of samples (n) considered and the mean depth of occurrence calculated for each stage. (c) the same information shown in (a) and (b) plotted together to show the difference between night and day depths of occurrence. (d) amplitude of migration for stages I, II and III.

Table 6.2. ANOVA table.

Source of variation	Df	Sum of Squares	Mean Square	F	P
Time	1	610.0	610.0	23.45	0.0 **
Season	2	11.53	5.77	0.22	0.802
Stage	2	0.99	0.49	0.02	0.981
Site depth	2	19.45	9.72	0.37	0.691
Time x Season	2	98.65	49.32	1.90	0.166
Time x Stage	2	1.17	0.59	0.02	0.978
Time x Site depth	2	243.15	121.58	4.67	0.016 *
Stage x Site depth	4	78.77	19.69	0.76	0.516
Time x Stage x Site depth	4	123.61	30.90	1.19	0.334
Error	33	858.26	26.01		
Total	54				

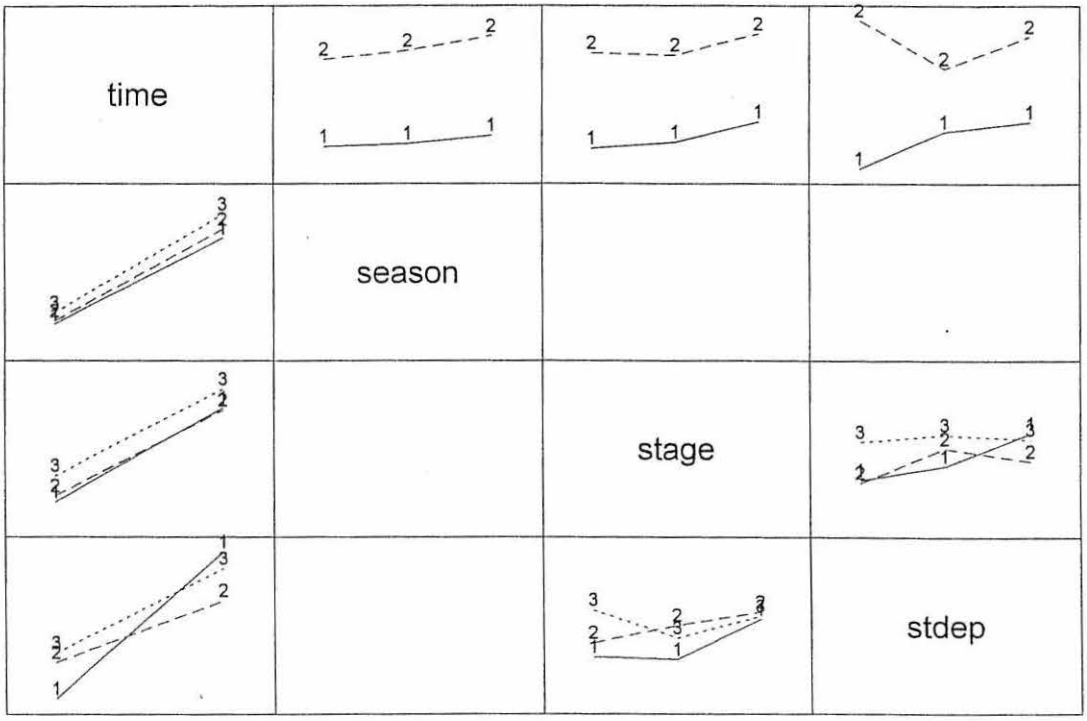


Figure 6.9. ANOVA plot showing interactions between factors: time, season, stage and site depth (stdep). Time (1, night; 2, day), Season (1, April; 2, May; 3, June); Stage (1, stage I; 2, stage II; 3, stage III), Site depth (1, ≤ 50 m; 2, 50-75 m; 3, ≥ 75 m).

collected, 50% were observed in the top 25 m of the water column. The postlarvae were detected mainly in samples taken over the western and southern edges of the mud patch zone. Four stage IV lobsters were observed in station 145/84 (53.54° N, 5.53° W), where they showed a very dispersed distribution. One individual appeared in very superficial waters, in the depth interval between 4 and 8 m, two occurred in the layer between 75 and 85 m and another one was observed very close to the sea bed, just below 100 m.

The results from the analysis of variance (table 6.2 and figure 6.9) confirmed the occurrence of diel vertical migration. Mean day time depths were significantly different from mean night time depths ($F=23.45$, $p<0.0001$). It also showed that the depth of occurrence of the larvae did not change for the three periods considered (April, May and June) or between the different site depths considered (≤50 m, 50-75 m and ≥75 m), and no ontogenetic migration was apparent. The only statistically significant interaction of factors ($F= 4.67$, $p=0.015$) was observed between site depth and time. The individuals occurring at shallower stations seemed to be involved in nocturnal migration with a larger amplitude. When compared to the behaviour exhibited in the central deeper sites, the larvae from the inshore, shallower areas, seemed to migrate from deeper day time depths, to more superficial waters, by night (this fact is clear in the interactions plot presented in figure 6.9).

3.2 Larval distribution and water column structure

The temperature profiles, obtained by the Guildline CTD, attached to the plankton sampler, are presented in figures 6.10 to 6.15, data for the samples carried out in June was not available. The quality of this information is questionable because these probes have a very low sampling frequency which does not permit a very detailed profile of the water column structure. In addition, calibration of the instruments was not carried out during the surveys. Despite that, the degree of stratification of the water column can, to a certain extent, still be inferred and the occurrence of a thermocline can also be detected.

The difference between surface and bottom temperature for the stations sampled in April ranged from 0.30° C to 0.71° C (figures 6.10, 6.11, 6.12 and table 6.1). Stratification of the water column was slightly more pronounced during the 1988 sampling period but in general, no differences were apparent between the temperature structure in the sites in the deeper

central area and the shallower coastal stations. A weak thermocline, located around 25 to 35 m, seemed to become noticeable in the sites in the deeper central channel (samples 22/20-88, figure 6.10c,d; 36/37-89, figure 6.11c,d and 63/71-96, figure 6.12e,f).

Sampling in May, was carried out early in the month in 1994 (stations 63, 123, 135, 140 and 119/130; figure 6.13a to f), in mid month in 1993 (stations 135, 206, 136, 314 222, 288; figure 6.14a to f) and by the end of the month in 1987 (stations 12 and 14; figure 6.15d, e) and in 1988 (stations 25/26; figure 6.15b, c; station 28 figure 6.15a). Top to bottom temperature differences were greater towards the end of the month (between 1.98° C and 2.7° C) and were slightly higher in the stations in the central area (stations 25/26 and 12) (see table 6.1). A thermocline appeared at depths around 25 to 30 m. Samples from 1993 showed indication of very weak stratification (Δt ranging from 0.04° C to 0.76° C), especially in the shallow sites in Dundalk Bay area. Local wind events may explain the lack of stratification but it can also indicate that the atmospheric temperature, at this point in time in 1993, was not as high as for a corresponding period in other years. Temperature profiles observed during early May in 1994 seemed to indicate that for that year the warming (stratification) season was more advanced than at a correspondent time in 1993, differences in surface to bottom temperatures over 1.5° C were already in place. However, the sampling sites are not exactly in the same locations and that fact alone may explain the differences encountered between temperature profiles. During the 1994 survey the sampling sites were located in deeper regions of the western Irish Sea and some in more northerly areas. Station 63 is above the 54° N parallel and sample 123 was collected at the entrance of the North Channel, both these samples showed a weaker stratification of the water column (Δt 0.31 ° C and 0.59° C, respectively) than the sites further south (Δt ranging from 0.78 ° C to 1.76 ° C).

When the depth distribution of the larvae (figures 6.2 to 6.7) is examined in association with the temperature structure of the water column (figures 6.10 to 6.15 and 6.16) it can be observed that in general, day time samples showed a distribution of *N. norvegicus* larvae below the bottom of the surface mixed layer. Most zoeae, from all developmental stages, were located in the temperature discontinuity layer occupying a range of depths between around 20 to 30 m. The nocturnal migration brought the individuals into more superficial waters, in some sites the larvae appeared just above the thermocline while in others they remained still in the temperature gradient zone. A clear nocturnal migration of the larvae,

from depths within the thermocline layer to just above it was observed in samples 22/20-88 (figures 6.2b and 6.10c, d) and 36/37-89 (figures 6.2d and 6.11c, d). There was no apparent change in the migratory behaviour of the larvae with the progression of the season.

Despite the association of the vertical distribution of the larvae with the thermal structure of the water column, observed in the histograms and temperature profiles, no significant correlation was found between the mean depth of occurrence of the lobsters and the depth of the surface mixed layer, either during the day or night samples (Night samples - mean depth of stage I vs. depth of surface mixed layer: r=-0.206, df=12; Day samples - mean depth of stage I vs. depth of surface mixed layer: r=-0.527, df=10). Figure 6.16 shows scatter plots for mean depth of occurrence of the three zoeal stages and the depth of the surface mixed layer for correspondent samples, during night and day time. The day time sampling (figure 6.16b) showed that during that period the majority of the larvae were located below the bottom of the surface mixed layer. The pattern of distribution observed during night time sampling (figure 6.16a) was less clear, although the larval distribution was clearly concentrated in more superficial waters in some cases the lobsters appeared at depths above the thermocline in other samples they remained below the bottom of the surface mixed layer.

In order to investigate the possible effect of water column structure stability on the degree of aggregation of the larvae, the correlation between surface to bottom temperature differences (Δt) and the coefficient of variation (CV) of the larvae distribution was assessed. It is common to observe a more aggregated distribution of plankters in stable (stratified) waters than in mixed (isothermal) conditions. However, the results from the correlation analysis in the present case (CV stage I *versus* Δt), showed no evidence for such behaviour (Night samples: CV stage I vs. $\sqrt{\Delta t}$: r=0.171, df=12; Day samples: CV stage I vs. $\sqrt{\Delta t}$: r=0.217, df=10). The plots presented in figure 6.17 highlight the lack of association between CV and Δt.

Hydrographic surveying contemporaneous with LHPR sampling was only carried out during the present study, in April 1996 (Cirolana 4b/96, leg 17 and LHPR samples 61/56, 62/57 and 63/71). However, because the structure of the water column and its evolution during spring-summer, in the western Irish Sea, is remarkably consistent from year to year (Hill *et al.*, 1997a; Horsburgh *et al.*, submitted) non-simultaneous oceanographic observations can still

provide adequate information for examining the larval distribution in relation to the physical environment. Three Scanfish transects carried out along the line 53.8° N (area where the majority of the LHPR samples were collected) in April (1996), May (1995) and June (1994) are considered in the present analysis. These observations have already been discussed in chapter IV, here a reminder of the more relevant aspects is summarised to assist in the interpretation of the vertical distribution of the lobster larvae.

Section 17, sampled on the 16 of April (Cirolana 4b/96), passed through the plankton sampling sites visited three days later (samples 61/56, 62/57 and 63/71). Figure 4.2 (chapter IV) shows the temperature, salinity, density, chlorophyll$_a$ and geostrophic velocity profiles observed across transect 17 in April 1996. Temperature contours, showed a predominantly mixed water column but a slight horizontal difference in temperature (around 0.3° C) with cooler waters close to the Irish coast was noted at the time. Despite the absence of thermal stratification a clear pycnocline (halocline) was already developing at 20 to 30 m depth. The density pattern exhibited was mainly due to the contribution of salinity. Less saline waters originated from fresh water runoff along the Irish coast, made a major contribution to the stratification of the water column at this early stage of the warming up season. Contours of chloroplyll revealed aggregation of phytoplankton above the pycnocline in the top 20 to 30 m of the water column (maximum concentrations around 2 µg/l). Geostrophic velocity profiles showed weak residual flows in the western Irish Sea, yet a southward current along the Irish coast, consistent with the fresh water input, was noted.

Observations carried out along the same transect on the 11 May 1995 (section 68, Corystes 5b/95, figure 4.5, chapter IV) showed that stratification of the water column was clearer in May (1995) than it was in April (1996). It was also evident that temperature played a more definitive role on the density structure of the water column at this stage of the season. A clear thermocline was present at 20 to 25 m depth and maximum surface to bottom temperature differences (Δt = 1.5 ° C) were observed in the deeper central channel. The shallow coastal zone on the west, was mixed vertically extending approximately to 5.8° W. The profiles showed a dome of denser, colder water in the deeper region. The dynamical effect of this density structure (gyre) was patent on the flow field observations. A maximum southward velocity of around 15 cm/s was apparent along the western edge of the deep basin at depths to about 20 m. On the eastern side of the stratified area, northward flowing, currents of around 8

cm/s were observed. Chloroplyll$_a$ concentrations of up to 7 µg/l were observed in the top 25 m of the water column.

The same line (section 72, Corystes 7/94, figure 4.10, chapter IV) was sampled on the 20 June 1994. At this stage in the season, a strong, temperature controlled, pycnocline was observed at approximately 20 m depth. In the deep central channel the dome of dense water was clearly isolated by well defined bottom fronts. Surface to bottom temperature differences of around 3.5° C were registered in the central area. Velocities of up to 20 cm/s, centered at about 30 m depth, were observed on the western (southward flow) and eastern (northward flow) arms of the gyre. Phytoplankton abundance, assessed by chloroplyll$_a$ concentrations, was clearly higher in the surface waters of the central stratified area.

The vertical distribution of *N. norvegicus* larvae examined in conjuction with the hydrographic observations, seems to indicate that the zoeae were present at depths mainly within the density discontinuity layer, during the day. Nocturnal migration brought the planktonic lobsters into more superficial waters, mostly into the surface mixed layer. Some individuals remained in the pycnocline region. The larvae were concentrated in the area of higher phytoplankton abundance which is also a zone of abundance of potential zooplanktonic prey. The depth distribution of the larvae also suggested that they may be subject to the local density driven flow (gyre). More superficial currents generated by fresh water run off along the Irish coast, during the begining of spring, and wind driven effects may also play a role on the distribution of the pelagic stages of *N. norvegicus* in the western Irish Sea. The larvae are more likely to be subjected to such surface flows during the night, when their position in the water column is closer to the surface.

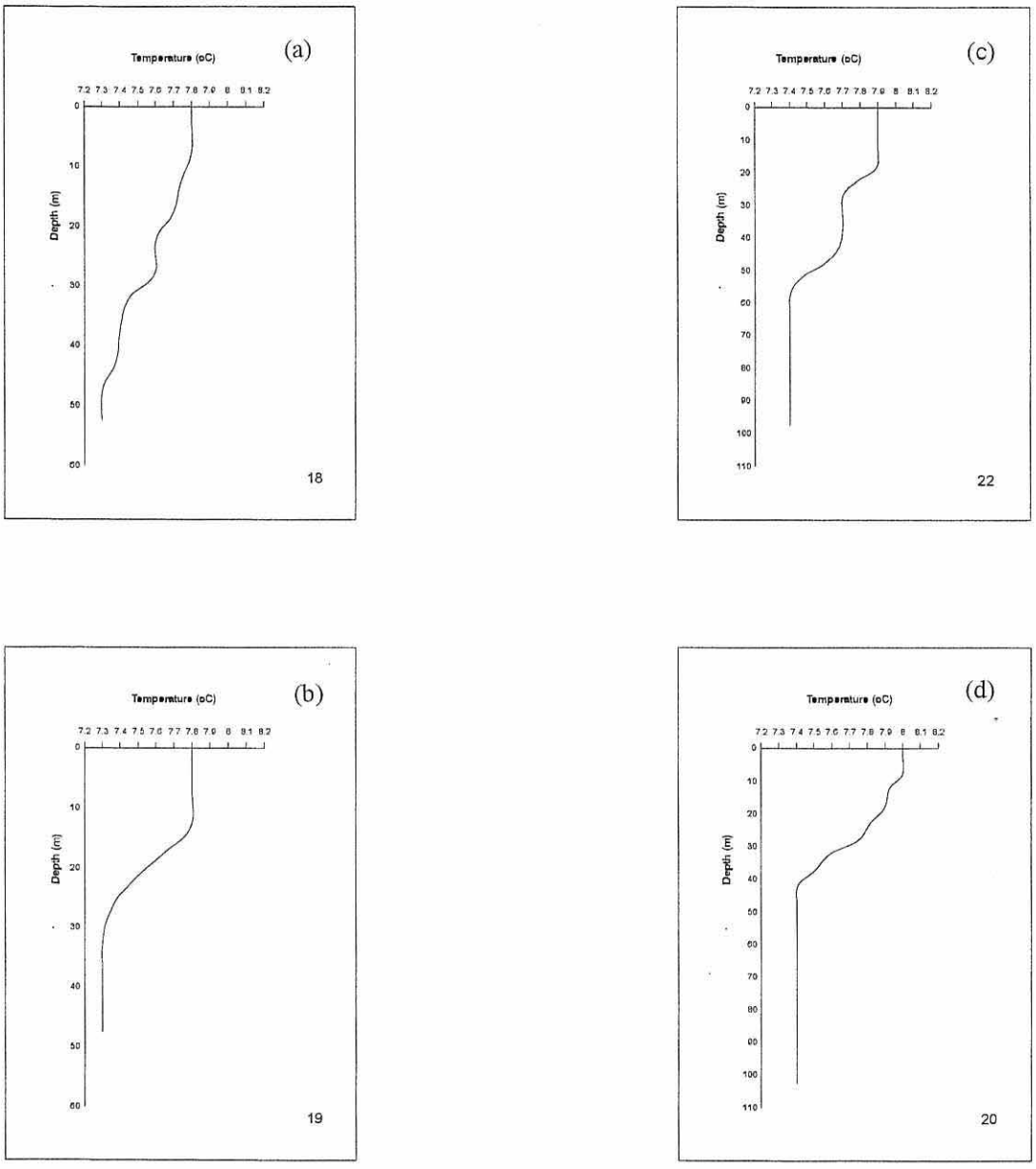


Figure 6.10. Temperature (°C) profiles for sampling stations from April 1988 surveys (larval distribution shown in figure 6.2). Sampling station references are presented in the bottom right corner. (a) and (b), (c) and (d) are night and day casts, respectively, at a same location.

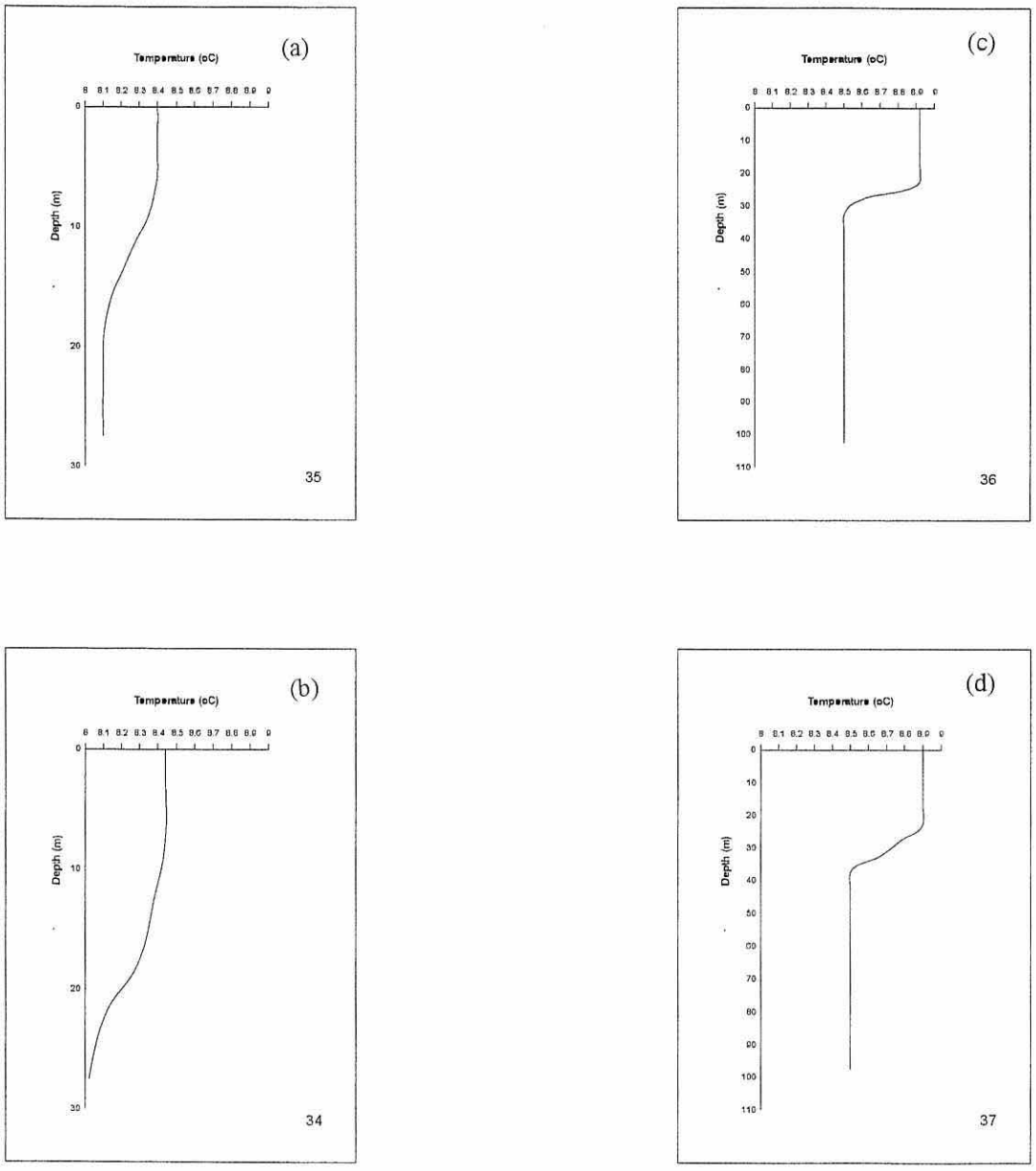


Figure 6.11. Temperature (°C) profiles for sampling stations from April 1989 surveys (larval distribution shown in figure 6.2). Sampling station references are presented in the bottom right corner. (a) and (b), (c) and (d) are night and day casts, respectively, at a same location.

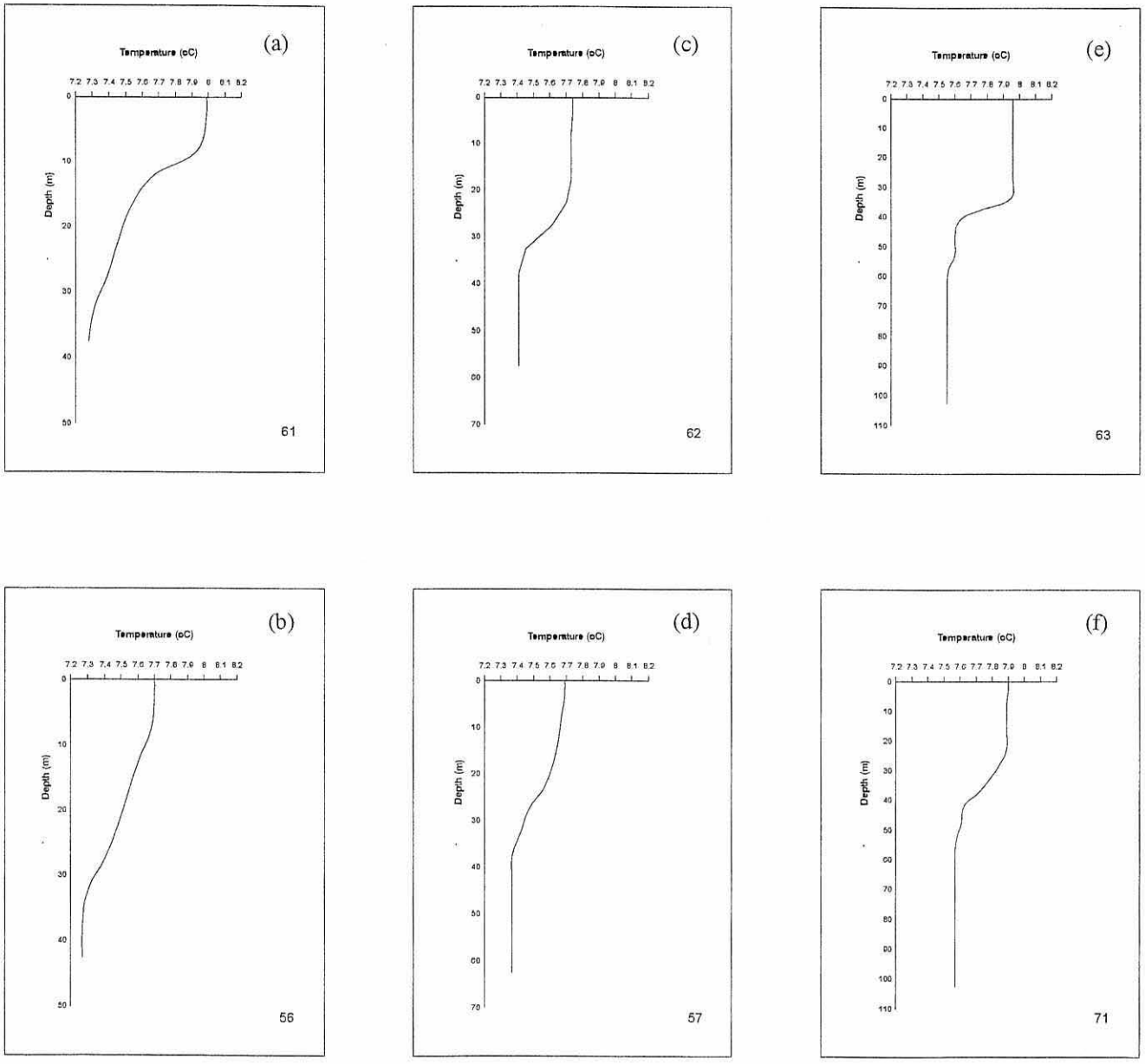


Figure 6.12. Temperature (°C) profiles for sampling stations from April 1996 surveys (Cirolana 4b/96) (larval distribution shown in figure 6.3). Sampling station references are presented in the bottom right corner. (a) and (b), (c) and (d), (e) and (f) are night and day casts, respectively, at a same location.

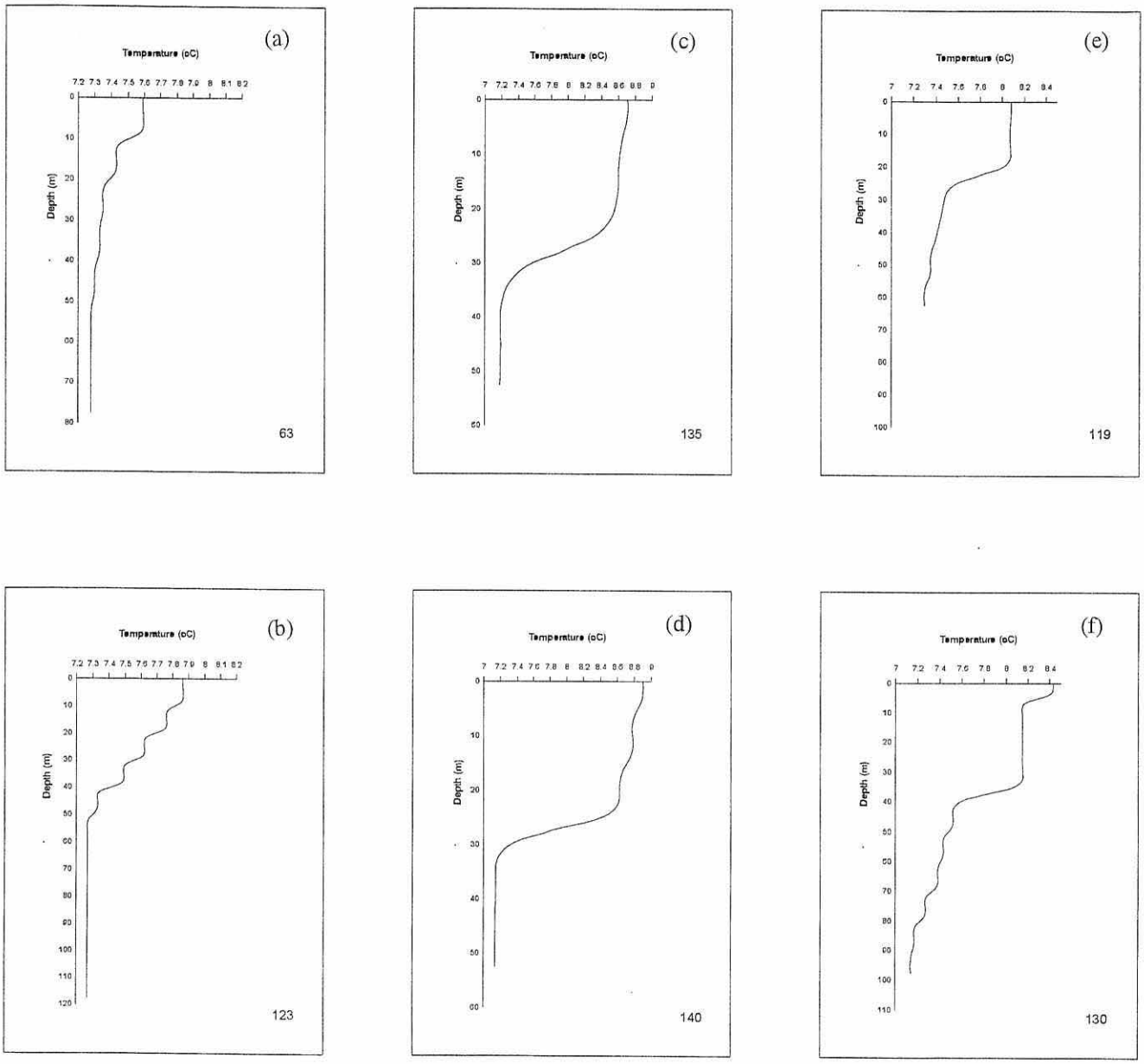


Figure 6.13. Temperature (°C) profiles for sampling stations from May 1994 surveys (larval distribution shown in figure 6.4). Sampling station references are presented in the bottom right corner. (c) and (d) are day casts at a same location (e) and (f) are night and day casts, respectively, at a same location.

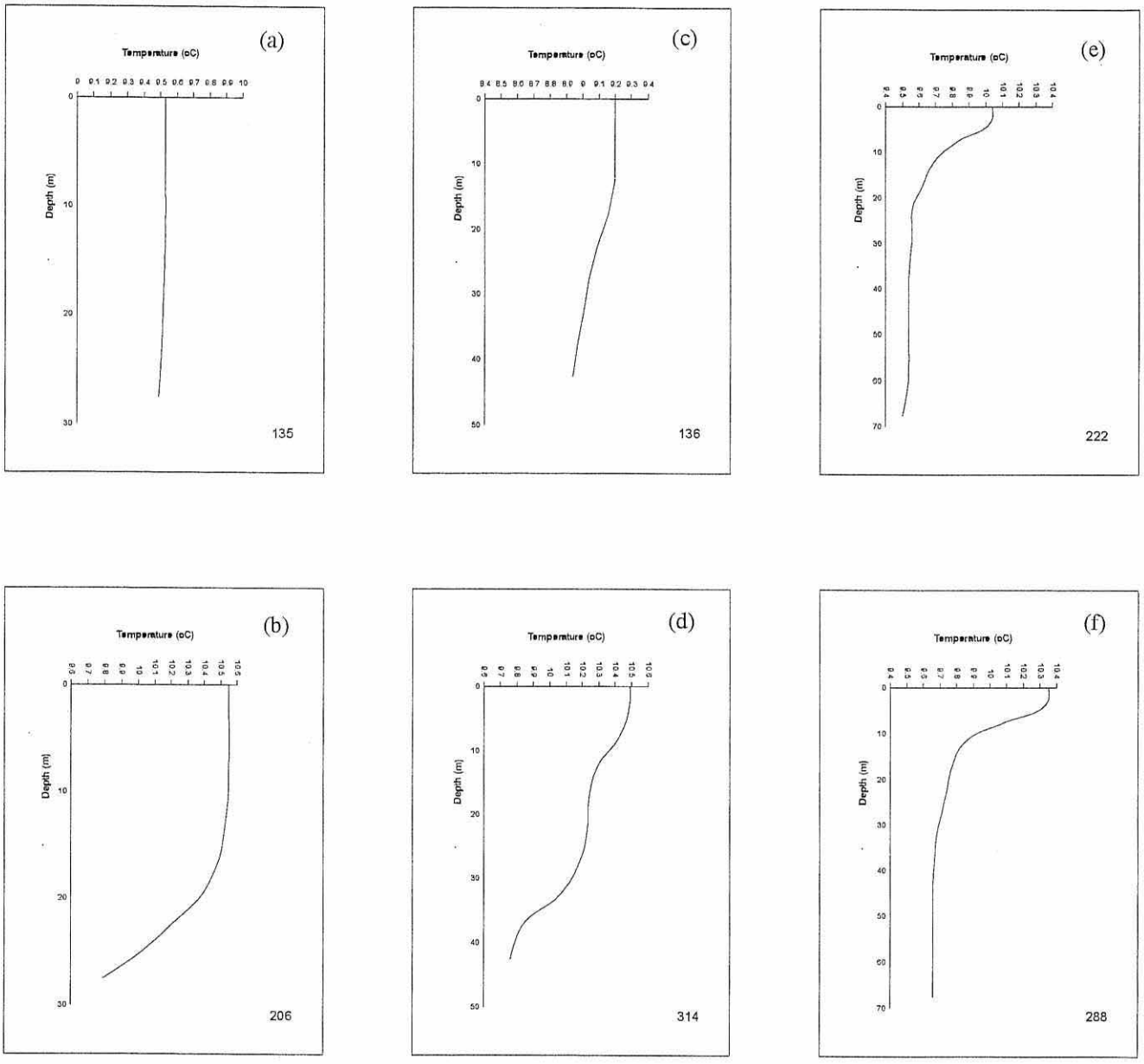


Figure 6.14. Temperature (°C) profiles for sampling stations from May 1993 surveys(larval distribution shown in figure 6.5). Sampling station references are presented in the bottom right corner. (c) and (d) are night and day casts, respectively, at a same location.

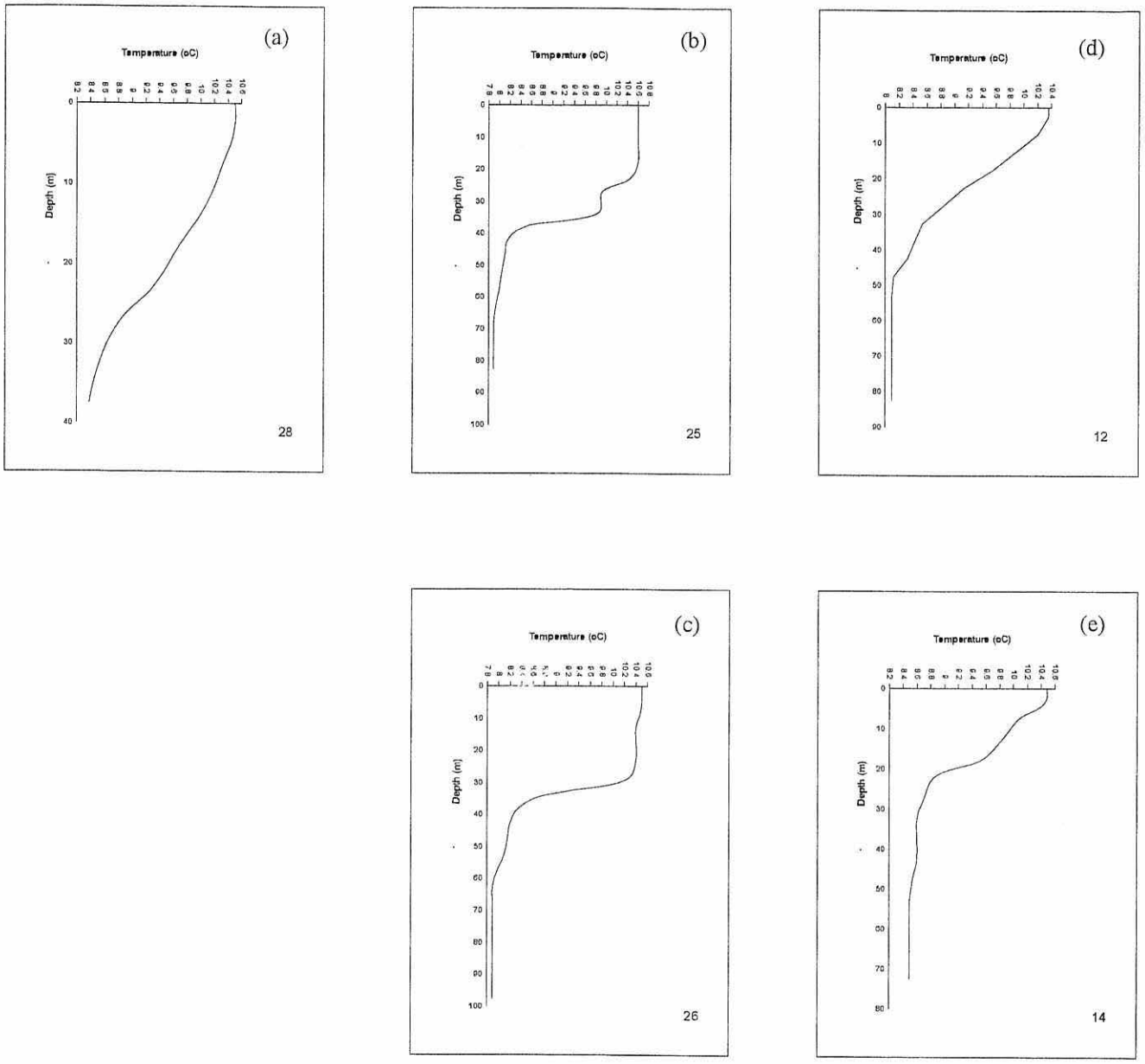
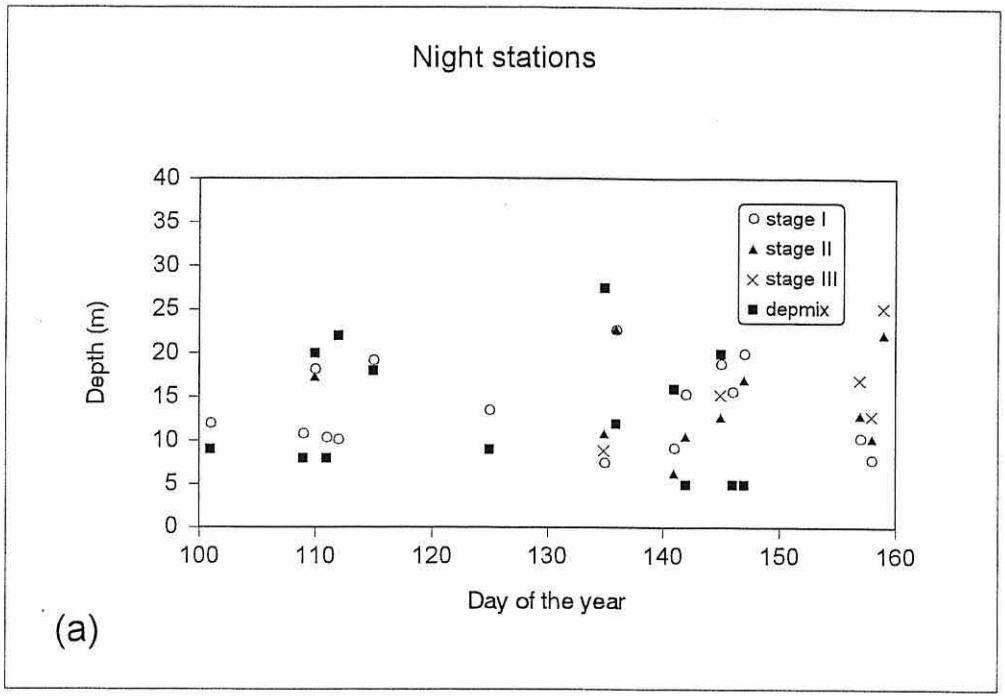


Figure 6.15. Temperature (°C) profiles for sampling stations from May surveys (larval distribution shown in figure 6.6). Sampling station references are presented in the bottom right corner. (b) and (c) are night and day casts, respectively, at a same location.



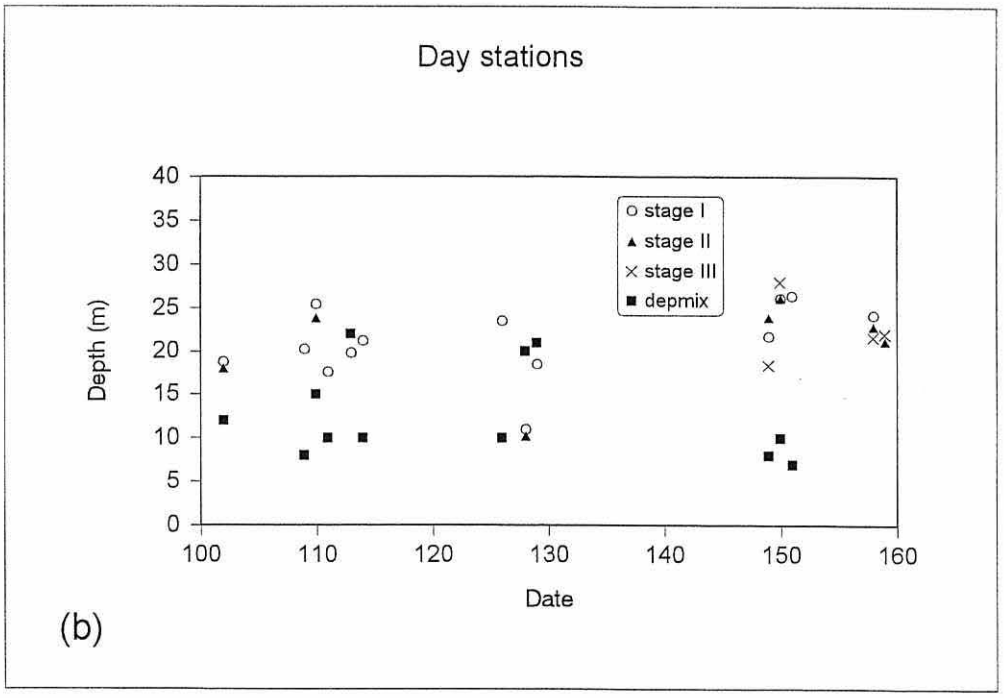
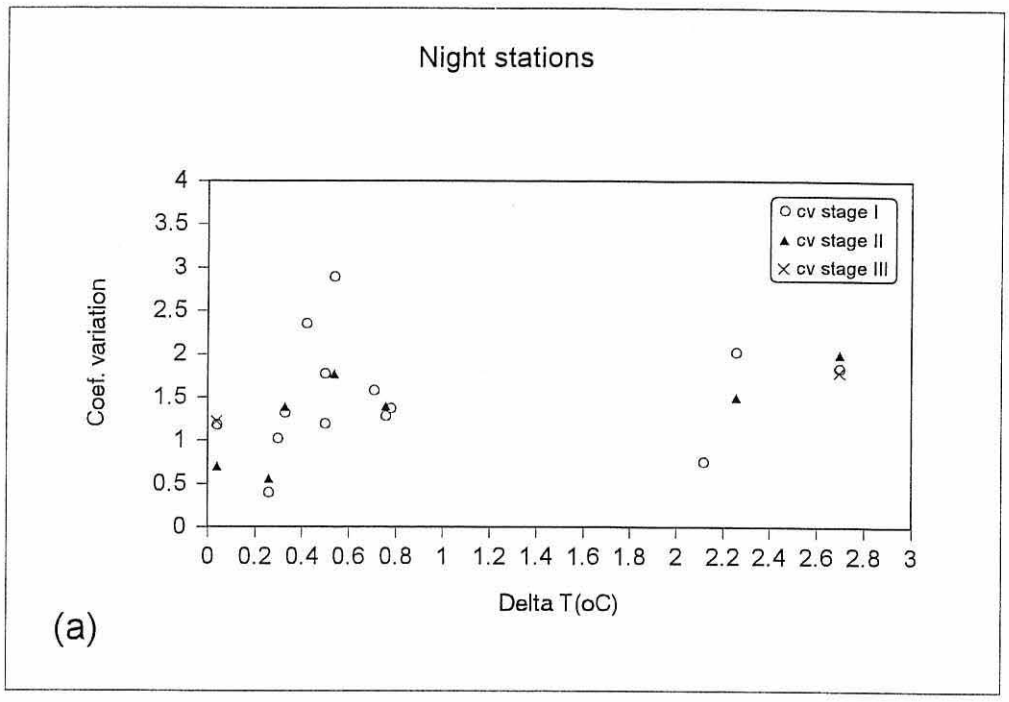


Figure 6.16. Mean depth of occurrence of *N. norvegicus* larval stages I, II and III from all samples considered for analysis. Also shown the depth of the surface mixed layer. (a) night stations, (b) day stations.



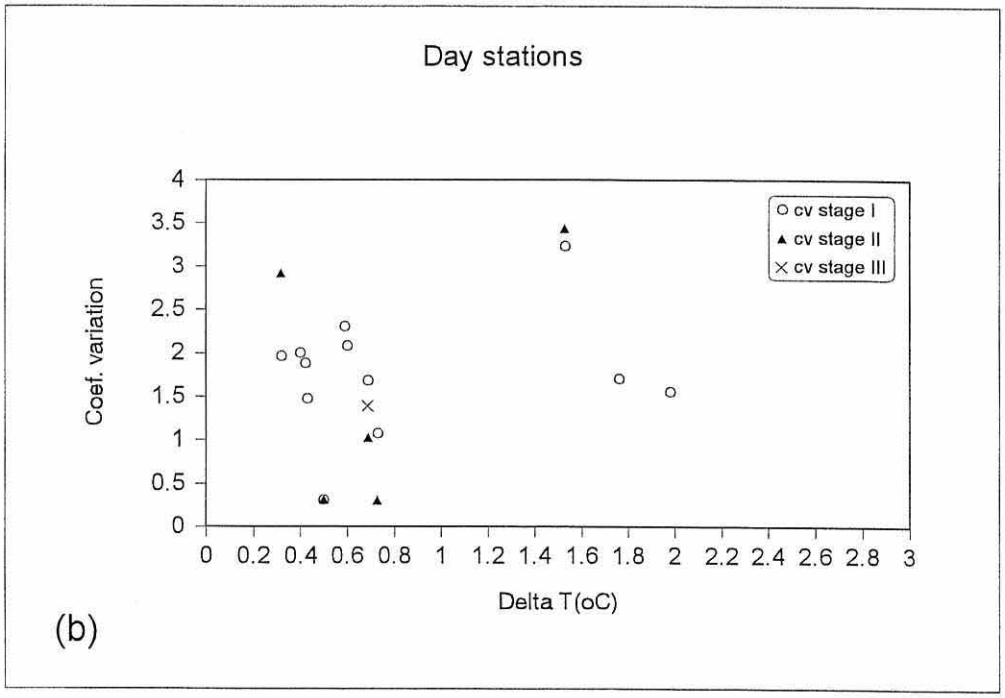


Figure 6.17. Scatter plot of surface to bottom temperature differences (Δt, in °C) against coefficient of variation of the depth distribution of *N. norvegicus* larval stages I, II, III, for (a) night and (b) day, samples.

4. Discussion

The data on the vertical distribution of *Nephrops norvegicus* larvae presented in this chapter resulted from a compilation of information collected over a period of 12 years. Sampling sites and time at which the hauls were carried out varied from survey to survey. The analysis of these LHPR observations is therefore quite complex and variability due to the sampling procedure must be taken into account. In addition, hydrographic surveying contemporaneous with the plankton sampling was not available for most cases which created another constraint to the analysis. However, owing to the fact that the pattern of water stratification in the western Irish Sea and its evolution is remarkably consistent from year to year (Hill *et al.*, 1997a; Horsburgh *et al.*, submitted; present study), the interpretation of the vertical distribution of *N. norvegicus* larvae in association with the hydrographic data available, is still conceivable.

The results presented in this study show that the depth distribution of the zoeal stages of the Norway lobster in the western Irish Sea was fairly aggregated, with most individuals occurring in the top 40 m of the water column. The mode of the distribution appeared, in the majority of the cases, in the top 25 to 30 m of the water column. These observations are in agreement with the study by Hillis (1974a), carried out in the same area. This author pointed out that very few larvae appeared below 27 m depth but he also suggested that the depth at which the planktonic lobsters live may increase with the progression of the season. From the present observations there is no evidence to support this hypothesis, no noticeable change in the vertical distribution of the larvae was found between the periods analysed. However, the data included in the present study, contained only a restricted number of samples obtained within a single year and that fact could have prevented the detection of deepening of the larvae distribution throughout the season. On the other hand, the relatively small number of samples and individuals caught by Hillis (1974a) survey could have also misrepresented the distribution of the zoeae. Stations 18/19-88 (figure 6.2a) and 25/26-88 (figure 6.6c), and 22/20-88 (figure 6.2b) and 28-88 (figure 6.6d) were sampled in approximately the same area in April and in May of the same year. Despite the fact that more stage III zoea were collected during May, no difference seemed to exist between the depth distribution of the larvae between these two periods. It is however impossible to exclude the possibility of that occurring later in the season.

The vertical distribution of *N. norvegicus* zoeae observed by Smith (1987) in the Clyde Sea suggested, that the larvae can be found throughout the whole water column, although the bulk of the catches during that study, came from nets fishing at 16 and 27 m depth. A considerable number of larvae was also collected at the bottom of the water column during night time sampling. Owing to the fact that hatching activity in *N. norvegicus* occurs during the night (Moller & Branford, 1979) and that Smith (1987) collected mainly stage I zoea, this author pointed out that the individuals found at greater depths were possibly newly hatched lobsters. Although a very small number of larvae were collected at the bottom of the water column during the surveys included in the present study, night time hatching activity may explain some of the observed distributions. Stations 12/87 (figure 6.6a) and 22/88 (figure 6.2b), sampled during night time hours, showed some larvae occurring at the bottom of the water column. However, at site 12/87 stage II zoea were also present in deeper waters. At site 141/84 (figure 6.7c), another night time haul, larvae at stages II and III were caught in depths close to the sea bed, as well. Other samples, collected during the day (63/94, figure 6.4a; 14/87, figure 6.6b; 145/88, figure 6.7d) also uncover the presence of some lobster zoea deep in the water column. Asynchrony in movement may account for the pattern exhibited, not all individuals may be engaged in migratory behaviour at the same time. Still, the typical bimodal distributions characteristic of asynchrony in migration (Pearre, 1979) are not evident. Another possibility is that larvae from different generations may move as separate groups.

Despite the occasional occurrence of some individuals in deeper waters, it seems reasonable to say that *N. norvegicus* larvae in the western Irish Sea exihibited a fairly aggregated vertical distribution, occupying mainly the top 40 m of the water column. No correlation was found between water column stability, assessed by top to bottom temperature differences, and the dispersion of the zoea through the water column. The vertical distribution of the lobster larvae seemed equally aggregated in waters where stratification was evident and in isothermal sites.

The present study indicate that *N. norvegicus* larvae in the western Irish Sea, were involved in diel vertical migration with significant movement towards the surface at night. The mode of the day distributions was located around 25 to 30 m and night time profiles showed modes at depths from 10 to 20 m. No difference seemed to occur between the depth distribution of the

three zoeal stages, either at day or night. Stage I zoea migrated from a day time depth of 21.1 m (±2.57) to 13.8 m (±2.56), during night time hours, stage II lobsters moved from 20.9 m (±4.65) during the day, to 14.3 m (±3.85) by night, and stage III larvae appeared at 22.6 m (±6.4) by day, moving upward to 13.2 m (±10.47), by night. The amplitude of migration observed was therefore 7.3 m for stage I zoea, 6.6 m for stage II larvae and 9.4 m for stage III lobsters. These figures are in the same range as the vertical displacements referred in Hillis (1974a) study. This author observed that the greatest number of larvae were at depths around 18 m during the day ascending to around 9 m by night.

Hillis (1974a) also suggested that the minimum depth is reached around dusk. The data included in the present study does not permit the verification of this hypothesis. However, when a sequence of four samples was collected at approximately the same site for a period of 16 hours starting at sunset (stations 139, 140, 141, 142 in June 1984, figure 6.7a, b, c), that pattern was not evident. Although the majority of the individuals were located at the depth interval between 5 and 15 m by sunset (station 139), the highest concentration of larvae in the top 10 m of the water column occurred during hours of darkness (00:25, station 140). By sunrise (station 141) the larvae had begun to concentrate around day time depths and around 11 o'clock (station 142) the bulk of the larvae were in the depth interval between 20 and 30 m. Observations in the Clyde Sea (fixed location, every 2 hours for a period of 24 hours) did not support Hillis (1974a) suggestion of a twilight migration pattern for *N. norvegicus* larvae. A nocturnal ascent with larval concentration around 5 m depth, was reported during Smith (1987) study.

However, in order to detect small changes in larval depth distribution over short periods of time, high frequency sampling should be carried out and the whole water column must be sampled. Neither of the studies on *N. norvegicus* vertical distribution, available to present, has followed a sampling procedure that could give very fine detail of the larval depth distribution throughout a 24 hours period. Although Hillis (1974a) reported an ascent of the larvae by dusk, the survey from which he obtained evidence for that behaviour, was not performed over a period of 24 hours. In addition, studies by both Hillis (1974a) and Smith (1987), were carried out using plankton nets sampling at discrete depths. The absence of observations through the whole water column may preclude an accurate representation of the vertical distribution of the larvae and its movements.

The results from the present study showed a clear displacement of the larvae between a mean day time depth of around 22 m, to an average night time depth of 14 m, approximately. These results are nevertheless not without fluctuation, the confidence intervals calculated for the mean depths showed a possible variation of around 5 m for the mean depths of stage I zoea, about 8 m for stage II larvae and more than 10 m in the case of stage III lobsters. Part of that variability is likely to derive from natural fluctuations in the vertical distribution of the larvae but variability due to the sampling programme, number of samples used to calculate the mean depths and assumptions made during the analysis should also be considered. The overall mean depths of occurrence were calculated by dividing the samples available in two groups, night and day samples. Due to the disparity between the sampling times, this approach almost certainly added an extra component to the variance of the depths calculated. Yet, the results from the analysis of variance clearly supported the existence of a different mean depth of occurrence by day and by night.

The statistical analysis also indicated no difference between the depth of occurrence of the three zoeal stages of *N. norvegicus* and no interaction between stage and time. These results contrast with Hillis (1974a) suggestion that the older stages show a tendency to occupy a lower position in the water column than the younger stages, although no attempt was made by this author to test the significance of such differences. Ontogenetic variation in the vertical distribution of stage I and stage II larvae was also mentioned for one of the samples collected during Lindley (1994) study (station 25/88, also presented here). But in that instance the depth of occurrence of stage II larvae was shallower than the depth occupied by stage I zoea. Lindley (1994) included a limited number of samples which were analysed separately, for differences in the depth of occurrence of the larvae. When a larger number of samples is considered, as in the present study, and the analysis is performed for the whole data set, single variations like the case reported by Lindley (1994), have little weight for the overall variance. The results from the analysis of variance presented here indicated that no significant variation in the vertical distribution of the three zoeal stages existed. Perhaps a larger number of samples with stage III zoea would have been useful in order to confidently assess their distribution. The statistical results also indicated no differences between the depth of occurrence of the larvae for the three site depths ($\leq$ 50 m, 50-75 m, $\geq$ 75 m), or the three periods (April, May, June), analysed.

When the interaction of factors was analysed there was evidence for some association between time and site depth. It seemed that the larvae occurring in the shallower sites, inhabit deeper waters by day and more superficial waters during the night, when compared to the individuals from the deeper, more central areas. It is uncertain whether this apparent larger amplitude of migration, exhibited by the larvae from the shallower areas, was real or merely an artifact of the analysis due to the way the samples were categorised. One possible explanation for this apparent behaviour, of the larvae from the coastal region, may lay on predator avoidance. These inshore areas are recognized as the spawning sites for several fish species during spring (Nichols *et al.*, 1993; Dickey-Collas *et al.*, 1996a; 1997; Fox *et al.*, 1997), the high abundance of potential predators may have some influence on the migratory behaviour of the lobster larvae. Predator avoidance is acknowledged as a major factor behind vertical migration and the strength of DVM by some species has been significantly related to the predation impact caused by their natural predators (Ohman, 1990; Frost & Bollens, 1992). During the study by Hillis (1974a) a reduction on the depth of maximum concentration of *N. norvegicus* larvae in the shallower sites was also noticed but the author did not give any further details on the amplitude of migration of the larvae from such areas. It was suggested that the high turbidity of these waters was responsible for the shallower depth of occurrence of the larvae. Turbidity measurements carried out during survey Cirolana 4b/96, showed that the inshore waters off the Irish coast presented higher turbidity levels than the surface waters on the stratified region. This fact is consistent with the lack, or lower degree, of water stratification in the coastal region.

Temperature profiles observed at the begining of the season, in April, showed a fairly mixed or only slightly stratified water column, with maximum top to bottom temperature differences of around 0.7^{o} C. The scanfish survey, in mid April (1996) revealed that although a thermocline was not yet in place a pycnocline was already developing at depths around 25 to 30 m depth. Values for the stratification parameter (ϕ) were lower than 25 J/m^3 (chapter IV). Despite the weak stratification of the water column found during the April survey, there was evidence that the spring phytoplankton bloom had already begun in the central and western parts of the study area. High levels of $chlorophyll_a$, up to 12 μg/l, were recorded in places, in conjuction with surface depletion of nutrients (CEFAS, unpublished data). Chlorophyll concentrations ranging from 0.5 to 2.0 μg/l were derived from the scanfish fluorescence

profiles. Information from other sources (Coombs *et al.*, 1994 and Lindley, 1994) showed that in April 1988 (data contemporaneous with LHPR sampling presented in this study) chlorophyll$_a$ concentrations of up to 12 μg/l were already present.

Observations by Gowen *et al.* (1995) and Gowen and Bloomfield (1996) showed that the phytoplankton production season in the inshore waters off the Irish coast, usually starts at the begining of April, earlier than anywhere else in the western Irish Sea. This area, also seems to have the highest primary production during the spring-summer season which lasts longer (6-7 months) than in the surrounding waters (see chapter IV).

Profiles of temperature and density observed in May (1995) showed a fairly stratified water column ($\Delta t \sim 1.5\ ^{o}C$, $\phi \sim 40\text{-}50\ J/m^3$, in the central area) with a pycnocline located at around 20 m depth. Chlorophyll concentrations, derived from the fluorescence readings from the scanfish survey, showed a high abundance of phytoplankton (up to 6 μg/l) in the top 20 m of the water column, in the whole western Irish Sea.

By June (1994), the stratification of the water column was stronger, top to bottom temperature differences of around 3.5^{o} C were found in the central area ($\phi \sim 50\text{-}60\ J/m^3$). The pycnocline was centred at around 20 m depth and chloprophyll concentrations up to 8 μg/l were recorded in the surface waters of the stratified region. The occurrence of subsurface patches of phytoplankton was also noted at this stage of the production season.

The results from the present study indicate that *Nephrops norvegicus* larvae were engaged in diel vertical migration irrespective of the degree of stratification of the water column. A similar behaviour was observed for several zooplanktonic species (Scrope-Howe & Jones, 1986) and decapod larvae (Lindley, 1994) collected in isothermal and stratified waters in the western Irish Sea. However, Scrope-Howe and Jones (1986) study revealed a relationship between the DVM exhibited by the plankters and the stage of the primary production season, which was not evident in the case of the lobster larvae. Scrope-Howe and Jones (1986) showed that, DVM persisted when chlorophyll levels above the thermocline were low and diffuse but ceased when the phytoplankton was concentrated in discrete subsurface layers, where the animals then aggregated. The migratory behaviour exhibited by *N. norvegicus* larvae did not seem to be altered with the occurrence of these patches of phytoplankton

although they may also be aggregations of potential prey organisms. When the LHPR samples presented in this study, were collected the phytoplankton spring production was already underway and secondary production was also evident. Despite that, the lobster larvae exhibited DVM throughout the season regardless of the potential accumulation of organisms in patches. In contrast, Lindley (1994) observations showed that in some areas, before the onset of the spring bloom some decapod larvae were not engaged in vertical movements and in the permanently well mixed waters off the Welsh coast, where the tides are fairly strong, some species were never engaged in vertical migration. Icthyoplankton distribution observed by Conway *et al.* (1997), revealed little evidence of vertical movement throughout the season. The fish larvae were mainly concentrated in the top 40 m of the water column with subsurface peaks at 10-15 m, for some species.

The depth distribution of *N. norvegicus* zoeae observed during this study, also revealed that the planktonic lobsters were mainly present at depths within the pycnocline during the day, and at depths just above it during the night. These results are in agreement with the observations made during Smith (1987) survey in the Clyde Sea. This author reported that the majority of the larvae were distributed at depths within the discontinuity layer.

The distribution of the lobster larvae in the water column also coincided with the richest layers of phytoplankton and zooplankton, concentrations. During the Norway lobster larval season, several potential prey like copepods, mysids, and other invertebrate larvae, are largely available in the western Irish Sea. High densities of zooplankton have been observed in the inshore waters off the Irish coast from early May (Burkart *et al.*, 1995) and in the surface mixed layer of the central region from April-May until later in the summer (Lee & Williamson, 1975; Scrope-Howe & Jones, 1985; 1986; Burkart *et al.*, 1995; Edwards & Burkill, 1995; Gowen *et al*, 1998). Below the pycnocline, the zooplankton biomass is relatively small with only a few deep water species occurring at these depths. Distinct patterns of vertical migration (nocturnal, twilight, reverse, no migration) have been identified for zooplanktonic organisms in the western Irish Sea (Scrope-Howe & Jones,1986).

Despite the clear association of *N. norvegicus* larvae with the layers of higher abundance of planktonic organisms, very little is known about their prey items. Likewise, their natural predators, which are likely to include plankton feeding fish, fish larvae, other crustacean

larvae and ctenophores, are not clearly identified. Hence, the difficulty in trying to examine their vertical movements in relation to feeding behaviour and/or predation avoidance. Whether there is any adaptive significance to the diel vertical migration undertaken by *N. norvegicus* larvae for either improved feeding or predator avoidance it is unclear from the present investigation. In order to assess the influence of such factors on the migratory behaviour of the lobster larvae studies on their potential prey and predators must be carried out.

It is uncertain what direct effect *in situ* temperatures have on *Nephrops norvegicus* larvae development and survival. Owing to the fact that the species inhabit regions from the cool Artic waters off the Icelandic coasts to the warm subtropical waters of the Meditteranean, it is expected that the temperature range found in the western Irish Sea would not constitute a limitation to development.

Laboratory studies have shown that at temperatures above 16° C high rates of mortality occur and 12° C was the lowest temperature at which complete development to the first postlarval stage took place (Smith, 1987). Figueiredo and Vilela (1972) found that the best survival rates were obtained with temperatures between 11-14° C and Thompson and Ayers (1989) observed the best survival rates at 15° C. Very high mortality was observed in the laboratory experiments at temperatures between 7° C and 9° C (Smith, 1987, Thompson and Ayers, 1989). From Nichols *et al.* (1987) equations for intermoult periods, larvae reared at 12° C would be expected to have a planktonic life of 35 days, while from Smith (1987) experiment, at the same temperature, 46 days is the predicted time for the lobsters to reach the postlarval stage.

Although hatching and development under laboratory conditions has not been very successful at temperatures below 12° C, it is clear that in the western Irish Sea the larvae hatch and undergo, at least, part of their development when the temperature of the water is much lower (below 9° C). In the sea, natural diet and other environmental conditions probably guarantee a more successful development under low temperatures and the pelagic phase is also likely to take considerably less time than the laboratory experiments seem to indicate. Hillis (1974a) suggested that the full larval phase at normal sea temperatures in the western Irish Sea may be not much longer than 40 days.

As shown in the previous chapters, when the hatching season for *N. norvegicus* started in the western Irish Sea, in late March-early April typical water temperatures did not exceed 8° C and the water column was generally well mixed. Data from mid April (Cirolana 4b/96), showed a fairly isothermal water structure with temperatures ranging from 7.3° C, in the west, to 7.8° C in the surface waters of the central region. Regardless of the low temperature, considerable numbers of stage I and stage II larvae were collected and some stage III zoea were also observed.

By May, when the density of *N. norvegicus* larvae reached its peak, surface temperature were usually 2-3° C higher but bottom temperature in the deep central channel were still relatively low, generally below 9°C. Surveys in mid (Corystes 5b/95) and late (Prince Madog 1/95) May, revealed surface temperatures of around 10° C and 11° C, respectively while bottom temperatures in the central trough remained at around 8.5° C for the earlier survey, reaching 9° C in the latter.

In mid-late June, when the larval season was close to its end, surface temperatures of up to 13° C were observed but the central deeper waters usually remained below 9.5° C. In June 1994 (Corystes 7/94), the dome of denser water in the central area showed temperatures of around 8.5° C but the surface waters had reached temperatures between 11-12° C. In June 1995 (Prince Madog 2/95), surface temperatures of 12° C were registered whilst the bottom temperatures in the central region were still below 9° C.

In July, when the planktonic phase of *N. norvegicus* was finished, the stratification of the waters column was at its strongest point ($\phi \sim$ 100-120). Top to bottom temperature differences of up to 5° C were observed in mid-late July in 1995 (Prince Madog 4/95) and 1996 (Prince Madog 1/96). The temperature at the bottom, in the central area was 10°C while the surface temperatures ranged from 13° C to 15° C (Prince Madog 4/95, Corystes 9/96, Prince Madog 1/96). The depth of the pycnocline (thermocline) throughout the stratification season, until the end of August, remained fairly stable, centred at an average depth of approximately 25 m.

Results from the present investigation suggest that the larval phase of *Nephrops norvegicus* is mainly completed in the upper warmer layers of the water column. Still, the larvae hatched at the beginning of the season, will experience temperatures of 8-10° C for most of their pelagic lifes and probably will reach the competent stage before the water had warmed up to 11-12° C. On the other hand, zoea hatching during May will encounter warmer temperatures, between 10-14° C in the surface waters, but by the time settlement will take place a strong thermocline (pycnocline) may be present ($\Delta t > 4^{\circ}$ C). It is not known what effect the pycnocline has on lobster larval behaviour. Results from this study indicated that diel vertical displacements through depths including the top of the discontinuity layer, occur throughout the season, at the start when the thermocline is not fully formed ($\Delta t \sim 0.8^{\circ}$ C) and later when differences in temperature of 2 to 3° C may be encountered. The gradients of temperature found in the western Irish Sea are much smaller than the 12.5° C needed to inhibit the migration of the larvae of the crab *Callinectes sapidus* (McConnaughey & Sulkin, 1984) but smaller differences may still alter larval behaviour (Young, 1995). Studies by Boudreau *et al.* (1992) showed that gradients of 3.5-4.0° C were sufficient to reduce significantly the proportion of postlarval settlement of the American lobster *Homarus americanus*. Likewise, steep gradients of temperature (density) in mid-late summer in the central western Irish Sea may affect the settlement of *Nephrops norvegicus* larvae.

Settlement occurs after the third zoeal stage metamorphosis into the postlarval phase. This phase is recognised as the transitional stage between the planktonic and benthic environments. Metamorphosis into the postlarval stage is thought to happen in the bottom waters. It appears that the first postlarvae constitute an exploratory phase in order to find suitable places for eventual settlement which then occur after the subsequent moult, which is slightly metamorphic (Smith, 1987). Laboratory observations made by this author suggested that the postlarvae progressively loose their swimming capabilities and tend to remain at the bottom of the water column.

Little is known about the distribution of the postlarval stage of *N. norvegicus* in nature. This is due to the fact that very few lobsters at this phase of development have ever been collected. The results from the present investigation also showed the fact that the postlarvae are very rare in plankton samples, from a total of 2535 samples, obtained during a period of more than 12 years, 78570 larvae were collected but only 152 (0.19%) were at the postlarval phase

(stage IV). Moreover, the collection of 5 postlarvae during bottom water trawling was reported by Hillis (1974a). It is, therefore, generally thought, that *N. norvegicus* postlarvae reside in the bottom layers of the water column, close to the sea bed, below the reach of the plankton samplers being used.

However, the results from the present study showed that at least some individuals at this stage of development live in the water column, well above the sea bed. Ten postlarvae (not identified in more detail) were collected during the LHPR surveys, 50 % of which in the top 25 m of the water column. Only one individual was found close to the sea bed, below 100 m. Owing to the fact that most lobsters at this stage were collected in sampling sites on the borders of the adults ground, it could be speculated that they may be individuals that failed to settle. Alternatively metamorphosis may take place in surface waters and the postlarvae may retain a pelagic existence until a suitable settling area is found. Several marine benthic invertebrates, including lobster and crab species, have postlarval stages which occur in surface waters. The postlarvae of *Homarus americanus* (Ennis, 1986; Katz *et al.*, 1994) and *H. gammarus* (Nichols & Lovewell, 1987) inhabit very superficial waters, taking advantage of superficial currents to reach suitable areas for settlement. Likewise, the puerulus stage of the spiny lobster *Panulirus cygnus* actively swims in the top centimetres of the water column, in inshore waters prior to settlement (Phillips & Olsen, 1975; Phillips *et al.*, 1978).The megalopa of the Dungeness crab, *Cancer magister*, also seems to be able to attain the settling habitat due to their position in near surface waters which it occupies during its DVM (Hobbs *et al.*, 1992; McConnaughey *et al.*, 1992).

Any hypotheses on the behaviour of the postlarval stage of *N. norvegicus* put forward at present is highly speculative. More research should be carried out in order to identify the distribution of *N. norvegicus* postlarvae. Knowledge of their distribution and behaviour may be crucial to understand the species recruitment patterns.

During spring-summer, the water circulation in the western Irish Sea is dominated by the density driven flow (gyre), which develops as a consequence of the stratification of the water column over the central deep basin. The cores of the gyre flow are concentrated in two narrow bands (approximately 10 Km), on each side of the dense pool, centred just below the thermocline, at approximately 25 m. The gyre is a persistent cyclonic circulation feature over

the duration of the stratification season each year. Prior to the onset of stratification and associated gyre, the velocity field is dominated by weak residual currents. Net long-term circulation through the western Irish Sea is northward with basin averaged speeds of no more than 1-2 cm/s (Bowden, 1950; Hill *et al.*, 1996; 1997a).

At the begining of the *N. norvegicus* hatching season, in early April, the gyre is only starting to develop and the geostrophic currents associated with it are weak. During this early part of the season a southward flow of less saline water derived from fresh water runoff, appears along the Irish coast. In May, when the peak density of lobster larvae occurs the gyre is fairly developed and flows along the western (southward) and eastern (northward) flanks of the gyre are about 10-15 cm/s. The centre of the stratified region is essentially a stagnant area of flow. By June, the gyre is established and currents of up to 20 cm/s have been observed along the western and eastern edges. Later in the season at the peak of the summer, when the lobster larval season is finished, the gyre reachs its maximum strength. A strong cyclonic, closed, circulation is then in place over the western Irish Sea deep basin.

The LHPR samples analysed in the present study were collected mainly along the western side of the western Irish Sea. Some observations were made on the western side of the western front, some in the area of the southward flowing arm of the gyre and some in the deep central area. No apparent difference in behaviour seemed to exist between the larvae collected in these three regions. Irrespective of the stratification of the water column and currents, the lobster zoeae were engaged in diel vertical migration. The vertical distribution of the larvae in the shallow inshore waters, in the frontal region and in the deeper stratified area seemed to be identical.

The inshore waters to the west of the western flank of the gyre (west of 5.8° W, approximately) remain fairly mixed throughout the season and the currents there are predominantely weak (~1-3 cm/s) with variable direction. The long term circulation is of the order of 1 cm/s in a northward direction but data from current meters moored in the region showed a south-easterly flow of around 2 cm/s (CEFAS, unpublished data). A geostrophic flow of 3-5 cm/s in a southward direction, was observed in the coastal, surface waters in April-May.

The LHPR observations and the results presented in the previous chapter, showed that a considerable number of *Nephrops norvegicus* larvae occur in these inshore waters close to the Irish coast. The fate of these larvae appearing outside the area of the mud patch is uncertain. It does not seem probable that the larvae could swim horizontally, back into the adults ground (see also discussion in chapter V). Still, the depth of occurrence of the larvae during the night, which takes them into superficial waters may play a role in the dispersion in a eastward direction (into the mud patch region). Local winds, which in the area are predominantly from a southwesterly direction, may provide a mechanism for the return into the stratified region and by becoming entrained into the cyclonic circulation the larvae may be retained over the mud patch region. The depth of occurrence of the larvae, specially during the night (mainly in the top 15 m of the water column) is within the layer that might be affected by wind driven currents. However, wind generated currents are occasional events which usually do not last more than 3 days and therefore dispersal by that means would be very uncertain.

The wind field observed during the period of the 1995 surveys (Horsburgh *et al.*, submitted) showed the irregular nature of wind events and also revealed changes in the direction of the wind. Predominant winds blowing in a northeast direction at an average speed of around 10 m/s were observed at periods during the spring-summer season. Larvae residing near to the surface can be transported nearly downwind at around 3% of the wind speed, larvae lower in the water column will experience a slower transport and in a direction slightly to the right of the wind direction (Shanks, 1995). Wind speeds of around 10 m/s lasting for 2-3 days, can conceivably sustain a 20-30 km transport of the larvae which could take them back to the central area above the mud patch. Surface currents generated by southwesterly winds have been observed in many occasions in the Irish Sea, transport of debris (Brown, 1991) has shown clearly this effect. During this study observations of near surface drifters (with drogues centred at 8.5 m depth) and a couple of instruments which have lost their drogues gave further evidence of such surface currents.

Although uncertain, wind driven currents have been related to transport of *H. americanus* larvae into settling areas in the east coast of USA and Canada (Harding *et al.*, 1982; 1983; Ennis, 1986). But directional swimming by the postlarval stage of this lobster is believed to play a considerable role in the recruitment of the species to the coastal areas (Katz *et al.*, 1994). No information exists as either *N. norvegicus* larvae or postlarvae, are capable of

directional swimming although horizontal movement has been observed in other crustacean larvae (Phillips & Olsen, 1975; Chia *et al.*, 1984). The possibility of displacement of the larvae associated with tidal currents is unlikely to occur in the western Irish Sea, where the tides are very weak (maximum currents of 0.1-0.3 m/s for the M_2 constituent) and orientated along a north-south axis (Robinson, 1979, Huntley, 1980). Besides, the amplitude of the DVM undertaken by *N. norvegicus* larvae is very small to have any significant effect for tidal transport (Hill, 1995).

The larvae occurring in the frontal zone, where the currents are stronger (10-15 cm/s in May, up to 20 cm/s in June) are likely to become entrained in the gyre circulation and therefore be retained above the adults ground. The vertical distribution of the larvae concentrated at depths around the thermocline (20-30 m), especially during the day (mean day time depth around 22 m), places the individuals within the region of strongest flow. At the begining of the season when the gyre is still weak and leaky, this position in the water column may lead to advection of the larvae to areas outside the influence of the cyclonic circulation. On the other hand, when the gyre is established, the vertical distribution of the larvae may guarantee retention over the adults ground and the chance of successful recruitment. Flow field observations using free drifting buoys (with drogues located at 24 m) showed that some instruments released at the begining of the season, were carried away from the central western Irish Sea but once the gyre was established its coherent nature and retention effects were clearly demonstrated by the drifters tracks.

The vertical distribution of the lobster larvae collected in the region of stratified water, was identical to the one found in the frontal and shallow water sites. This region in the centre of the gyre, is essentially a stagnant area of flow, and therefore it would be expected that the larvae would remain in the area. Buoys deployed in this area showed very little displacement.

The analysis of the vertical distribution of *N. norvegicus* larvae together with the hydrographic observations, seems to indicate that their depth of occurrence and vertical displacement is not directed towards transport (retention) promoting effects. The fact that the larval distribution appears to be similar, regardless of the structure of the water column and associated currents, in the different sites surveyed gives further support for that hypothesis.

It is more likely that the distribution of *N. norvegicus* larvae observed in the western Irish Sea and the nocturnal migration exhibited are related to feeding and predator avoidance behaviours. However, the lack of information on their food items and natural predators precludes further discussion of that hypothesis. Notwithstanding, while probably not directed at dispersal, the distribution of the larvae still provides them with the chance of retention within the area of suitable substrate for settlement, once the gyre is established.

The results from this study suggest that the depth distribution and vertical displacement of *Nephrops norvegicus* larvae should be taken into account in biological-hydrographic models developed to predict the distribution and settling sites of the species in the Irish Sea. Furthermore, surface currents, not very well explained by geostrophic and ADCP derived, calculations, should be examined with more attention in order to completely understand larval dispersal. The present observations also indicate that the distribution and behaviour of the three zoeal stages is identical but more studies should be carried out in order to investigate the distribution of the postlarvae.

Chapter VII. Overall discussion

The oceanographic observations presented in this study (chapter IV), produced a comprehensive description of the hydrodynamics in the western Irish Sea for the spring-summer period, when the planktonic larval phase of *Nephrops norvegicus* occurs. The onset and evolution of thermal stratification of the water column and associated gyre, over the mud patch region and adults ground, was clearly shown by the set of data analysed. Furthermore, the retentive effects of the seasonal western Irish Sea gyre, were well demonstrated by the trajectories of satellite tracked drifters. These observations, in conjuction with previous studies (Hill *et al.*, 1996; 1997a), verified the coherent and persistent nature of the closed circulation system, which develops in the region (deep basin with weak tidal currents) during spring-summer, every year. Drifter tracks superimposed on potential energy anomaly contours and geostrophic flow field calculations, highlighted the baroclinicity of the density field as the driving force behind the development of the gyre, confirming the interpretation by Hill (1993; 1996).

In April, when the first hydrographic survey was carried out, and the larval season of the Norway lobster was already underway, stratification of the water column was only starting to be apparent and the gyre not fully developed, although the isolation of a cold pool of bottom water was already noticeable. At this stage of the season, some buoys drifted away from the stratified area (mud patch). A southward flow along the Irish coast, consistent with fresh water input, was noted. On the eastern side of the western Irish Sea basin, some buoys were observed being carried in an eastward direction, just south of the Isle of Man.

By May, when the peak of larval production was observed, water column stratification and the gyre had strengthened. Potential energy anomaly values of up to 50 J/m^3, were observed in the central, deeper region of the western Irish Sea, where top to bottom temperature differences were observed to be around 1.5° C (mid May) to 2.5° C (late May). Although retention in the region had become more evident, some drifters did still leave the area of influence of the gyre. The southward current along the Irish shores was still apparent.

During June-July, when the larval season was close to its end, thermal stratification was stronger and the gyre apparent as a closed circulation feature. Maximum bottom density

gradients, responsible for the cyclonic circulation of the surface waters, were observed in July-August. At this point in the season, surface to bottom temperature differences, in the central western Irish Sea, reached 5.5° C and ϕ values above 100 J/m^3 were observed (Horsburgh *et al.*, submitted). The retentive properties of the gyre were clearly ilustrated by the trajectories of the drifters (drogued at the depth of the thermocline). One buoy released on the 22 June 1995, circumnavigated the whole western Irish Sea (and mud patch region) in 42 days, after 13 days of negligeble movement, at an average speed of 10 cm/s. The cores of the gyre flow were centred at a depth between 20 and 30 m, at the base of the thermocline. The depth of the thermocline (pycnocline) and gyre jet, were very consistent throughout the season with negligible change.

The begining of the larval season of *Nephrops norvegicus*, in the western Irish Sea in 1995, was noted in mid-late March and lasted probably until late June-July. The end of the season was not clearly identified due to the absence of observations after the 20 June. In mid July 1996, a small number of larvae, of all three zoeal stages, were collected. The peak production of stage I larvae, in 1995, was observed during the second week of May. These results are in agreement with observations from other studies carried out in the region, which showed that the larval season occurs mainly in the period between April and June, with a peak during the month of May (Farmer, 1974a; Hillis, 1974a; Nichols *et al.*, 1987). Fluctuations on the timing and magnitude of the larval production were apparent from the set of historical observations (1982-1994).

Data on the spatial distribution of *Nephrops norvegicus* larvae from 30 surveys (chapter V), highlighted the major dispersal patterns in the western Irish Sea. At the begining of the season, a considerable number of planktonic lobsters were observed in the inshore waters close to the Irish coast and also in the southwest end of the adults ground. High numbers of larvae in the southern limit of the mud patch had been observed in previous studies (Hillis, 1974a; Nichols *et al.*, 1987; White *et al.*, 1988). This region, just south of Dublin Bay, has also been recognised to have a large phytoplankton standing stock, during spring-summer, but evidence of high productivity was not noted in the area. Plankton produced in other areas (north) seems to be transported into this region. Conversely, the shallow region off the Irish coast appears to be an area of high phytoplankton production which also lasts longer than anywhere else in the western Irish Sea (Gowen *et al.*, 1995; Gowen & Bloomfiled, 1996). High concentrations of

chlorophyll$_a$ were also observed in these two regions during surveys carried out during this study. During the early stages of the stratification season, a few *N. norvegicus* larvae were also observed outside the mud patch, on the eastern side of the basin. This pattern is in agreement with the path followed by some of the drifters which were carried eastwards along the south of the Isle of Man. The full extent of the lobster larvae distribution was shown to be between latitude 54.7° N and 52.9° N.

As the season progressed, more *N. norvegicus* were observed over the central western Irish Sea, and mud patch region, and the apparent drift of plankton away from the region was less evident. This aspect was particularly noticed towards the end of May-June, consistent with strengthening of the gyre and retention in the area. Good agreement between the larvae distribution and plots of potential energy anomaly isolines, gave further evidence for the retentive effect of the western Irish Sea gyre. By late May-June, concentration of lobster larvae over the adults grounds was clearly observed. At this stage of the season, planktonic lobsters were observed in high numbers above the muddy region in the entire basin, in accordance with the observed extent of the gyre.

It is not clear what happens to the larvae which were observed outside the suitable settling area (muddy region). It is probable that the majority of the individuals that drift away from the adults ground will die but some may reach other suitable areas for settlement, for example in the south of Ireland or eastern Irish Sea grounds. No drifters were observed to be transported all the way to these regions. The majority of the buoys once on the southwestern limit of the stratified region made a turn northeastwards continuing travelling along the gyre path. But it must also be pointed out that the routes of drifters which left the area of influence of the gyre were not fully investigated. Two drifters drogued in more superficial waters (8.5 m) showed a more erratic circulation probably responding to surface currents generated by the wind. It is possible that some individuals, not carried too far away from the muddy region, may be able to return into the area probably influenced by wind driven currents (the predominant winds in the region blow from the southwest). The vertical distribution of the larvae, particularly during night time, places the individuals in superficial waters more affected by wind driven currents. During the day the lobster zoea concentrated mainly at the depth of the thermocline and gyre flow. Once the larvae reach the area of influence of the gyre they may become entrapped in its circulation and therefore increase its chances of recruitment into the suitable settling region.

There is evidence that a high concentration of adult lobsters inhabit the region on the southern limit of the mud patch (Tully & Hillis, 1995). Some individuals may even be settling just south of parallel 53.5° N (southern limit of the mud patch), where the composition of the sediment may still be favourable for burrowing. Fisheries statistics indicate that catches of *N. norvegicus* have been occurring in this region. The lack of observations on the distribution of the postlarvae, and juveniles, precludes a complete understanding of the recruitment patterns of the species.

The spatial pattern of distribution of *N. norvegicus* larvae in the western Irish Sea shows similarities to the distribution of planktonic species (Burkart *et al.*, 1995; Dickey-Collas *et al.*, 1996b; Gowen *et al.*, 1998) and fish larvae (Nichols *et al.*, 1993; Dickey-Collas *et al.*, 1996a; 1997; Fox *et al.*, 1997) in the region, which have been related to the local structure of the water column. *N. norvegicus* populations from other regions, seem to inhabit areas where similar closed circulation systems are apparent (Fladen ground, Bailey *et al.*, 1997; Celtic Sea, J. Brown, pers. com.) or other retention mechanisms occur (Minch, Hill *et al.*, 1997b), stressing the importance of larval retention on the survival of such populations.

The observations from this study showed a clear association between *Nephrops norvegicus* larval distribution and the western Irish Sea gyre, particularly towards the end of the larval season in late May-June. The number of larvae retained over the suitable area for settlement seems to be assuring the survival and stability of the population. The individuals that may be advected away from the region are probably not crucial for the maintenance of the stock. Support for this idea was given by the little change observed between the spawning stock estimated from this study, for the 1995 season, and equivalent calculations carried out for the 1982 (Nichols *et al.*, 1987) and 1985 (Thompson *et al.*, 1986) seasons. These observations together with indications that the population is withstanding the current, high, levels of fishing mortality (Briggs, 1995; ICES, 1997), stable annual fishery landings around 8000 tonnes, support the view that recruitment has been stable. The western Irish Sea gyre appears to be the mechanism assisting in that process. The absence of a hydrographic system conducive to retention, almost certainly would lead to a great number of the larvae being carried away from the suitable area for settlement before reaching the competent stage (larval duration approximately 44 days, estimated for the 1995 season), considering that the long term residual

currents in the area are about 1-2 cm/s (0.8-1.7 km /day), in a northward direction (Bowden, 1950).

The apparent mismatch between the peak of the larval season and the period of maximum retention (gyre is at its maximum strength in late July-August) is possibly related to larval food requirements, which are more likely to be attained at the time of peak zooplankton production, in May. The actual timing of the larval season is therefore probably, the result of a compromise between favourable feeding conditions and retention in the suitable settling region.

The presence of sharp temperature (density) gradients ($\Delta t \sim 5^{\circ}$ C) on the stratified waters (mud patch) during the summer, may also have some influence on the timing of *N. norvegicus* larval production. The possibility that a strong thermocline may be present at the time of settlement may create a constraint for the transition from the pelagic environment to the benthic habitat. In the event that these circunstances may in fact be relevant, settling would be favoured earlier in the season, when temperature differences between the surface layers and the bottom waters are not so sharp. At present, this hypothesis is merely especulative because no observations exist to verify it. Information on the depth distribution of *N. norvegicus* larvae, from this study, showed that the planktonic lobsters migrated through gradients of up to 2-2.5° C. However, settlement in other lobster species (*Homarus americanus*) have been observed to be affected by temperature gradients of the order of 3.5-4.0° C (Boudreau *et al.*, 1992).

Data on the vertical distribution of *Nephrops norvegicus* larvae from several sites, collected at distinct periods of the larval season (chapter VI), showed a clear diel vertical migration pattern. Indistinctly of period of the season and site location (shallow, mixed; frontal; deep, stratified), the lobster larvae were observed to be engaged in DVM with a mean day time depth of approximately 22 m and a mean night time depth of around 14 m. The larvae, occurring in stratified waters, were observed to migrate from depths within the thermocline layer, during the day, to above it, during the night.

No differences were observed between the depth distribution and behaviour of the three zoeal stages. Stage I larvae migrated from a day time depth of 21.1 m to 13.8 m, during night hours,

stage II zoea moved from 20.9 m, day depth, to 14.3 m, during the night and stage III lobsters appeared at 22.6 m, during day time moving upwards to 13.2 m, by night.

The results presented in this study do not permit the identification of a possible adaptive significance for the DVM pattern observed. The indistinct pattern of displacement observed between sites with different water column structure and currents (mixed, frontal, stratified) suggest that DVM behaviour is not directed towards transport (retention) promoting effects. Feeding and predator avoidance are probably more likely factors behind the diel movements observed. However, the lack of information on the actual prey organisms and predators (and their distribution) of *N. norvegicus* larvae prevents the discussion of this hypothesis.

Notwithstanding, while probably not directed at dispersal, the vertical distribution of the larvae in the western Irish Sea, will affect their spatial distribution. The depth distribution of the larvae places the individuals, occurring in the region of influence of the gyre, within the layers of stronger currents, especially, during the day. At night time, the location of the larvae in the water column is more superficial and therefore potentially subjected to surface currents (*eg.* wind-driven currents). The results from this study indicate that information on the vertical distribution should be considered when analysing the dispersal patterns of *N. norvegicus* larvae, in the western Irish Sea.

The extensive observations presented in this study, highlighted the vertical and spatial distribution patterns of *Nephrops norvegicus* larvae in the western Irish Sea, and its association with the local hydrography. These results constitute effective background information to include in coupled biological and oceanographic models to predicted *Nephrops norvegicus* larval dispersal in the western Irish Sea. Such experiments can contribute to a better understanding of the recruitment patterns of the species and assist on stock assessement studies. Oceanographic models capable of simulating the circulation in the region have been developed in the School of Ocean Sciences, University of Wales, Bangor, (Hill, 1993; Hill *et al.*, 1996; 1997a; Horsburgh, in preparation) and can now be used to predict larval transport.

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Annexes

Annex 1. Cruise 5/95 (8-14 March 1995), number of *N. norvegicus* larvae per square metre (grid box as shown in figure 5.1).

Row	Column	Longitude (W)	Latitude (N)	Stage I/m^2	Stage II/m^2	Stage III/m^2
6	1	5.75	53.63	0.16	———	———
7	2	5.25	53.88	0.08	———	———
8	2	5.25	54.13	0.07	———	———

Annex 2. Cruise 6/95 (15-22 March 1995), number of *N. norvegicus* larvae per square metre (grid box as shown in figure 5.1).

Row	Column	Longitude (W)	Latitude (N)	Stage I/m^2	Stage II/m^2	Stage III/m^2
5	1	5.75	53.38	1.05	———	———
6	1	5.75	53.63	0.44	———	———
6	2	5.25	53.63	0.23	———	———
7	0	4.75	53.63	0.35	———	———
7	1	6.25	53.88	0.17	———	———
7	3	4.75	53.88	0.11	———	———
8	1	5.75	54.13	0.05		
8	2	5.25	54.13	0.14		
8	3	4.75	54.13	0.38		
7	4	4.25	53.88	1.43	———	———
8	4	4.25	54.13	0.85	———	———
9	5	3.75	54.38	0.32	———	———

Annex 3. Cruise 8/95 (30 March-6 April 1995), number of *N. norvegicus* larvae per square metre (grid box as shown in figure 5.1).

Row	Column	Longitude (W)	Latitude (N)	Stage I/m^2	Stage II/m^2	Stage III/m^2
4	1	5.75	53.13	1.29	———	———
4	2	5.25	53.13	0.06	———	———
5	0	6.25	53.38	0.69	———	———
5	1	5.75	53.38	2.27	———	———
5	2	5.25	53.38	1.21	———	———
6	0	6.25	53.38	3.11	0.22	
6	1	5.75	53.63	2.44	———	———
6	2	5.25	53.63	2.09	———	———
7	0	4.75	53.63	2.88	0.19	———
7	1	6.25	53.88	1.21	———	———
7	2	5.25	53.88	0.83	———	———
7	3	4.75	53.88	0.38	———	———
8	1	5.75	54.13	0.07	———	———
8	2	5.25	54.13	0.42	———	———
8	3	4.75	54.13	0.32	———	———
9	3	4.75	54.38	0.07	———	———
8	4	4.25	53.88	0.19	———	———
8	5	4.25	54.13	0.46	———	———
9	4	4.25	54.38	0.05	———	———
9	5	3.75	54.38	0.25	———	———

Annex 4. Cruise 9+10/95 (10-21 April 1995), number of *N. norvegicus* larvae per square metre (grid box as shown in figure 5.1).

Row	Column	Longitude (W)	Latitude (N)	Stage I/m^2	Stage II/m^2	Stage III/m^2
4	1	5.75	53.13	2.34	0.12	———
5	0	6.25	53.38	———	0.08	———
5	1	5.75	53.38	11.56	1.36	———
5	2	5.25	53.38	0.2	0.25	———
6	0	6.25	53.38	3.84	0.47	———
6	1	5.75	53.63	6.21	0.26	———
6	2	5.25	53.63	2.82	0.69	———
7	0	4.75	53.63	1.03	0.19	———
7	1	6.25	53.88	1.48	0.72	0.05
7	2	5.25	53.88	1.06	2.52	0.05
7	3	4.75	53.88	———	0.24	0.08
8	1	5.75	54.13	———	1.63	0.17
8	2	5.25	54.13	———	1.07	0.44
8	3	4.75	54.13	———	0.08	———
9	3	4.75	54.38	———	0.05	———
7	4	4.25	53.88	———	0.06	———
8	5	4.25	54.13	0.02	0.02	———
8	6	3.25	54.13	———	0.35	———
9	4	4.25	54.38	———	0.05	———
9	5	3.75	54.38	———	0.27	———

Annex 5. Cruise 11 (18-25 April 1995), number of *N. norvegicus* larvae per square metre (grid box as shown in figure 5.1).

Row	Column	Longitude (W)	Latitude (N)	Stage I/m^2	Stage II/m^2	Stage III/m^2
4	1	5.75	53.13	5.9	2.73	0.31
4	2	5.25	53.13	0.38	———	———
5	0	6.25	53.38	1.6	0.14	———
5	1	5.75	53.38	38.03	7.62	0.18
5	2	5.25	53.38	5.36	1.79	———
6	0	6.25	53.38	11.14	0.37	———
6	1	5.75	53.63	22.7	2.33	0.12
6	2	5.25	53.63	2.65	0.8	———
7	0	4.75	53.63	1.49	———	———
7	1	6.25	53.88	18.45	0.15	———
7	2	5.25	53.88	7.21	0.54	———
7	3	4.75	53.88	1.4	1.05	———
8	1	5.75	54.13	2.23	0.13	———
8	2	5.25	54.13	6.09	0.44	———
8	3	4.75	54.13	0.24	———	———
9	2	5.25	54.38	0.9	———	———
9	3	4.75	54.38	2.61	———	———
7	5	3.75	53.88	0.12	0.12	———
7	6	3.25	53.88	0.21	———	———
8	5	4.25	54.13	———	0.11	———
9	4	4.25	54.38	6.2	0.2	———
9	5	3.75	54.38	2.81	0.08	———
10	4	4.25	54.63	0.42	———	———

Annex 6. Cruise 12 (30 April-7 May 1995), number of *N. norvegicus* larvae per square metre (grid box as shown in figure 5.1).

Row	Column	Longitude (W)	Latitude (N)	Stage I/m^2	Stage II/m^2	Stage III/m^2
4	1	5.75	53.13	1.42	1.09	———
4	2	5.25	53.13	2.3	1.62	———
5	0	6.25	53.38	0.17	0.34	———
5	1	5.75	53.38	19.46	12.56	0.84
5	2	5.25	53.38	0.76	4.84	———
6	1	5.75	53.63	24.37	5.62	0.16
6	2	5.25	53.63	29.32	6.53	1.07
7	0	4.75	53.63	2.47	———	———
7	1	6.25	53.88	12.88	0.42	0.14
7	2	5.25	53.88	19.63	3.15	0.15
7	3	4.75	53.88	0.62	0.12	———
8	1	5.75	54.13	10.82	0.39	———
8	2	5.25	54.13	21.98	1.52	0.26
8	3	4.75	54.13	6.64	0.15	———
9	2	5.25	54.38	6.38	1.3	———
9	3	4.75	54.38	14.85	1.32	———
7	5	3.75	53.88	0.05	0.05	———
8	4	4.25	53.88	0.28	———	———
8	5	4.25	54.13	1.67	0.36	0.15
8	6	3.25	54.13	0.65	0.16	———
9	4	4.25	54.38	1.62	0.13	———
9	5	3.75	54.38	1.78	———	———
10	4	4.25	54.63	0.37	0.12	———
10	5	3.75	54.63	0.47	0.17	———

Annex 7. Cruise 13 (14-20 May 1995), number of *N. norvegicus* larvae per square metre (grid box as shown in figure 5.1).

Row	Column	Longitude (W)	Latitude (N)	Stage I/m^2	Stage II/m^2	Stage III/m^2
4	1	5.75	53.13	4.02	21.53	10.41
4	2	5.25	53.13	0.3	9.14	4.53
5	1	5.75	53.38	18.05	70.25	19.05
5	2	5.25	53.38	0.89	3.66	1.22
6	0	6.25	53.63	9.17	1.92	0.35
6	1	5.75	53.63	19.47	12.44	3.28
6	2	5.25	53.63	4.13	6.39	1.79
6	3	4.75	53.63	0.12	0.33	0.18
7	0	4.75	53.63	27.43	6.22	0.87
7	1	6.25	53.88	13.49	10.05	1.68
7	2	5.25	53.88	13.42	16.39	3.21
7	3	4.75	53.88	3.38	3.78	0.71
8	1	5.75	54.13	7.69	0.5	0.05
8	2	5.25	54.13	8.55	4.15	0.79
8	3	4.75	54.13	0.69	0.84	0.14
9	2	5.25	54.38	7.66	3.02	0.57
9	3	4.75	54.38	5.71	3.87	0.39
7	5	3.75	53.88	0.07	0.16	0.03
7	6	3.25	53.88	0.27	———	———
8	4	4.25	53.88	0.08	0.57	0.16
8	5	4.25	54.13	3.34	1.89	0.79
8	6	3.25	54.13	0.42	0.42	———
9	4	4.25	54.38	1.23	0.52	0.14
9	5	3.75	54.38	1.62	0.24	0.33
10	4	4.25	54.63	0.04	0.9	0.04
10	5	3.75	54.63	0.02	0.16	0.18

Annex 8. Cruise 14 (23-28 May 1995), number of *N. norvegicus* larvae per square metre (grid box as shown in figure 5.1).

Row	Column	Longitude (W)	Latitude (N)	Stage I/m^2	Stage II/m^2	Stage III/m^2
4	1	5.75	53.13	0.47	1.57	2.64
4	2	5.25	53.13	2	15.38	7.44
5	0	6.25	53.38	0.17	2.14	2.66
5	1	5.75	53.38	0.8	3.51	5.43
5	2	5.25	53.38	0.56	2.45	3.51
5	3	4.75	53.38	———	0.12	0.14
6	0	6.25	53.63	———	0.63	1.9
6	1	5.75	53.63	4.51	11.2	4.29
6	2	5.25	53.63	6.38	14.29	7.22
7	0	4.75	53.63	1.48	———	1.48
7	1	6.25	53.88	8.97	8.6	11.55
7	2	5.25	53.88	6.18	9.76	7.86
7	3	4.75	53.88	1.46	1.4	0.96
8	1	5.75	54.13	1.52	0.44	0.87
8	2	5.25	54.13	11.11	13.96	13.45
8	3	4.75	54.13	1.7	1.13	1.9
9	2	5.25	54.38	1.57	2	0.14
9	3	4.75	54.38	12.71	4.07	4.57
7	5	3.75	53.88	0.23	1.15	0.24
7	6	3.25	53.88	———	0.08	———
8	5	4.25	54.13	1.26	1.06	0.33
8	6	3.25	54.13	2.92	0.37	———
9	4	4.25	54.38	0.09	0.05	0.05
9	5	3.75	54.38	1.05	———	0.3
10	4	4.25	54.63	———	———	0.17

Annex 9. Cruise 15+L.Foyle (5-20 June 1995), number of *N. norvegicus* larvae per square metre (grid box as shown in figure 5.1).

Row	Column	Longitude (W)	Latitude (N)	Stage I/m^2	Stage II/m^2	Stage III/m^2
5	1	5.75	53.38	———	———	1.55
6	0	6.25	53.63	———	———	0.17
6	1	5.75	53.63	0.99	1.68	6.25
6	3	4.75	53.63	———	———	0.03
7	0	4.75	53.63	———	———	1.07
7	1	6.25	53.88	0.3	0.42	3.76
7	2	5.25	53.88	0.15	0.81	1.98
7	3	4.75	53.88	0.11	0.02	0.11
8	1	5.75	54.13	0.49	1.47	1.5
8	2	5.25	54.13	———	———	1.94
8	3	4.75	54.13	———	0.03	1.52
8	4	4.25	54.13	———	0.09	0.05
9	4	4.25	54.38	———	———	0.02
10	4	4.25	54.63	———	———	0.04
10	5	3.75	54.63	———	0.03	———

Annex 10. Corella 5/82 (9-13 April 1982), number of *N. norvegicus* larvae per square metre (grid box as shown in figure 5.1).

Row	Column	Longitude (W)	Latitude (N)	Stage I/m^2	Stage II/m^2	Stage III/m^2
4	1	5.75	53.13	0.05	———	———
5	1	5.75	53.38	25.99	0.08	———
5	2	5.25	53.38	5.09	———	———
6	1	5.75	53.63	2.74	———	———
6	2	5.25	53.63	1.7	0.09	———
6	3	4.75	53.63	1.53	———	———
7	0	4.75	53.63	0.21	———	———
7	1	6.25	53.88	1.38	———	———
7	2	5.25	53.88	6.14	———	———
7	3	4.75	53.88	0.15	———	———
8	1	5.75	54.13	2.31	———	———
8	2	5.25	54.13	3.91	0.13	———
9	2	5.25	54.38	0.2	———	———
9	3	4.75	54.38	2.03	———	———

Annex 11. Clione 6/82 (28 April-21 May 1982), number of *N. norvegicus* larvae per square metre (grid box as shown in figure 5.1).

Row	Column	Longitude (W)	Latitude (N)	Stage I/m^2	Stage II/m^2	Stage III/m^2
4	1	5.75	53.13	1.4	1.56	0.18
4	2	5.25	53.13	4.9	4.05	0.38
4	3	4.75	53.13	———	3	0.9
5	1	5.75	53.38	29.37	12.57	0.76
5	2	5.25	53.38	15.15	3.08	0.4
6	0	6.25	53.63	1.1	0.6	0.03
6	1	5.75	53.63	17.1	2.15	0.03
6	2	5.25	53.63	19.34	11.21	0.6
6	3	4.75	53.63	———	0.2	0.05
7	0	4.75	53.63	0.95	0.15	———
7	1	6.25	53.88	22.88	3.56	0.04
7	2	5.25	53.88	16.15	1.75	0.38
7	3	4.75	53.88	3.04	4.08	0.1
8	1	5.75	54.13	6.45	0.37	———
8	2	5.25	54.13	14	3.57	0.34
8	3	4.75	54.13	11.32	0.5	0.04
9	2	5.25	54.38	1.17	0.1	———
9	3	4.75	54.38	5.12	0.2	0.08

Annex 12. Clione 7/82 (21 May-5 June 1982), number of *N. norvegicus* larvae per square metre (grid box as shown in figure 5.1).

Row	Column	Longitude (W)	Latitude (N)	Stage I/m^2	Stage II/m^2	Stage III/m^2
4	1	5.75	53.13	0.25	1.84	1.06
4	2	5.25	53.13	0.42	4.7	5.81
4	3	4.75	53.13	———	2.92	4.6
5	1	5.75	53.38	4.32	18.79	17.34
5	2	5.25	53.38	8.38	14.77	9.18
5	3	4.75	53.38	———	0.1	0.38
6	0	6.25	53.63	0.3	1.17	1.2
6	1	5.75	53.63	13.71	14.64	6.94
6	2	5.25	53.63	8.45	7.55	3.9
6	3	4.75	53.63	1.18	1.9	3.68
7	0	4.75	53.63	4.6	1.35	0.55
7	1	6.25	53.88	10.96	3.86	0.92
7	2	5.25	53.88	9.65	6.42	1.67
7	3	4.75	53.88	4.45	6.57	3.73
8	1	5.75	54.13	4.2	1.76	0.34
8	2	5.25	54.13	10.77	3.9	1
8	3	4.75	54.13	1.65	2.53	1.57
9	2	5.25	54.38	2.64	1.14	0.32
9	3	4.75	54.38	7.02	2.98	0.26

Annex 13. Clione 5/85 (15-19 April 1985), number of *N. norvegicus* larvae per square metre (grid box as shown in figure 5.1).

Row	Column	Longitude (W)	Latitude (N)	Stage I/m^2	Stage II/m^2	Stage III/m^2
4	1	5.75	53.13	1.06	0.01	———
5	1	5.75	53.38	14.34	1.83	———
5	2	5.25	53.38	4.48	1.18	0.05
6	0	6.25	53.63	1.47	0.22	———
6	1	5.75	53.63	18.58	2.65	0.03
6	2	5.25	53.63	8.28	0.32	———
7	0	4.75	53.63	3.33	0.69	———
7	1	6.25	53.88	16.07	1.5	0.03
7	2	5.25	53.88	16.22	2.87	———
7	3	4.75	53.88	1.82	0.22	———
8	1	5.75	54.13	2.32	———	———
8	2	5.25	54.13	4.04	0.36	———
8	3	4.75	54.13	1.54	0.66	———
9	2	5.25	54.38	1.01	0.11	———
9	3	4.75	54.38	2.68	0.12	———

Annex 14. Clione 6/85 (11-26 May 1985), number of *N. norvegicus* larvae per square metre (grid box as shown in figure 5.1).

Row	Column	Longitude (W)	Latitude (N)	Stage I/m^2	Stage II/m^2	Stage III/m^2
4	1	5.75	53.13	4.82	7.35	0.78
4	2	5.25	53.13	1.34	4.91	0.46
5	1	5.75	53.38	15.2	15.97	3.06
5	2	5.25	53.38	3.06	5.31	1.37
6	0	6.25	53.63	0.41	0.08	———
6	1	5.75	53.63	17.37	13.08	3.41
6	2	5.25	53.63	10.23	7.1	2.25
6	3	4.75	53.63	———	0.1	———
7	0	4.75	53.63	4.17	0.42	———
7	1	6.25	53.88	16.98	8.85	2.39
7	2	5.25	53.88	11.98	4.67	1.3
7	3	4.75	53.88	0.49	0.24	———
8	1	5.75	54.13	7.44	0.69	0.02
8	2	5.25	54.13	6.06	3.18	0.8
8	3	4.75	54.13	1.26	0.45	0.07
9	2	5.25	54.38	4.1	3.16	0.33
9	3	4.75	54.38	1.52	0.56	0.07

Annex 15. P. Madog 1/85 (27 May- 6 June 1985), number of *N. norvegicus* larvae per square metre (grid box as shown in figure 5.1).

Row	Column	Longitude (W)	Latitude (N)	Stage I/m^2	Stage II/m^2	Stage III/m^2
4	1	5.75	53.13	0.05	0.13	0.38
4	2	5.25	53.13	———	3.63	2.19
5	0	6.25	53.38	0.2	2.16	1.96
5	1	5.75	53.38	1.14	5.49	4.19
5	2	5.25	53.38	0.8	4.82	3.91
6	0	6.25	53.63	0.5	3.92	1.77
6	1	5.75	53.63	8.63	9.61	9.19
6	2	5.25	53.63	10.34	9.39	9.64
6	3	4.75	53.63	———	0.34	0.28
7	1	6.25	53.88	8.67	4.42	2.25
7	2	5.25	53.88	9.43	10.69	5.85
7	3	4.75	53.88	4.99	6.85	3.91
8	1	5.75	54.13	4.34	1.32	0.84
8	2	5.25	54.13	10.01	13.88	9.08
8	3	4.75	54.13	5.33	7.77	5.1
9	2	5.25	54.38	15.25	15.31	6.98
9	3	4.75	54.38	2.7	4.02	1.24

Annex 16. Cirolana 5/87 (14-24 May 1987), number of *N. norvegicus* larvae per square metre (grid box as shown in figure 5.1).

Row	Column	Longitude (W)	Latitude (N)	Stage I/m^2	Stage II/m^2	Stage III/m^2
5	1	5.75	53.38	4	0.67	0.03
5	2	5.25	53.38	7.36	1.41	0.05
5	3	4.75	53.38	0.24	———	———
6	1	5.75	53.63	8.38	1.95	0.3
6	2	5.25	53.63	17.26	2.4	0.39
7	0	6.25	53.88	0.77	———	———
7	1	6.25	53.88	2.25	0.11	0.04
7	2	5.25	53.88	17.1	3.95	0.34
7	3	4.75	53.88	3.2	1.2	0.13
8	1	5.75	54.13	0.86	———	———
8	2	5.25	54.13	8.04	2.36	0.73
8	3	4.75	54.13	3.87	0.08	0.07
9	2	5.25	54.38	4.77	0.3	0.05
9	3	4.75	54.38	3.93	0.3	———

Annex 17. Cirolana 4/88 (20 April-2 May 1988), number of *N. norvegicus* larvae per square metre (grid box as shown in figure 5.1).

Row	Column	Longitude (W)	Latitude (N)	Stage I/m^2	Stage II/m^2	Stage III/m^2
4	2	5.25	53.13	1.22	0.1	———
5	1	5.75	53.38	1.38	0.62	0.03
5	2	5.25	53.38	3.66	1.07	0.06
5	3	4.75	53.38	0.21	———	———
6	0	6.25	53.63	0.74	0.14	———
6	1	5.75	53.63	14.55	4.72	0.84
6	2	5.25	53.63	20.14	3.03	0.14
7	0	6.25	53.88	3.41	0.59	0.08
7	1	6.25	53.88	14.05	5.68	1.08
7	2	5.25	53.88	16.88	2.65	0.38
7	3	4.75	53.88	3.26	0.71	0.03
8	1	5.75	54.13	3.56	0.98	0.04
8	2	5.25	54.13	16.14	7.3	0.42
8	3	4.75	54.13	6.75	2.23	———
9	2	5.25	54.38	3.23	0.15	———

Annex 18. Cirolana 4/89 (16-28 April 1989), number of *N. norvegicus* larvae per square metre (grid box as shown in figure 5.1).

Row	Column	Longitude (W)	Latitude (N)	Stage I/m^2	Stage II/m^2	Stage III/m^2
5	1	5.75	53.38	0.38	———	———
6	0	6.25	53.63	6.43	0.27	———
6	1	5.75	53.63	9.65	0.88	———
6	2	5.25	53.63	0.26	———	———
6	3	4.75	53.63	0.22	0.14	———
7	0	6.25	53.88	5.21	0.35	———
7	1	6.25	53.88	11.22	0.72	———
7	2	5.25	53.88	4.99	———	———
7	3	4.75	53.88	1.49	0.27	———
8	1	5.75	54.13	6.13	0.14	———
8	2	5.25	54.13	6.35	0.11	———

Annex 19. Cirolana 5/93 (8-30 May 1993), number of *N. norvegicus* larvae per square metre (grid box as shown in figure 5.1).

Row	Column	Longitude (W)	Latitude (N)	Stage I/m^2	Stage II/m^2	Stage III/m^2
4	1	5.75	53.13	0.84	3.87	1.16
4	2	5.25	53.13	0.06	0.51	0.03
5	1	5.75	53.38	4.26	6.28	4.38
5	2	5.25	53.38	0.02	0.12	0.07
6	0	6.25	53.63	4.64	1.18	0.23
6	1	5.75	53.63	9.36	35.23	24.24
6	2	5.25	53.63	1.91	1.39	0.45
7	0	6.25	53.88	6.35	2.79	0.59
7	1	6.25	53.88	7.18	4.67	4.43
7	2	5.25	53.88	3.2	0.65	0.08
8	1	5.75	54.13	2.57	1.12	0.17
8	2	5.25	54.13	5.5	6.99	3.07

Annex 20. Cirolana 4b/96 (13-23 April 1996), number of *N. norvegicus* larvae per square metre (grid box as shown in figure 5.1).

Row	Column	Longitude (W)	Latitude (N)	Stage I/m^2	Stage II/m^2	Stage III/m^2
6	1	5.75	53.63	10.07	2.97	———
6	2	5.25	53.63	28.47	13.07	0.29
7	0	6.25	53.88	1.25	0.16	———
7	1	6.25	53.88	10.5	2.31	———
7	2	5.25	53.88	9.67	0.97	———
7	3	5.25	53.88	0.96	0.26	———
8	1	5.75	54.13	9.38	2.33	———
8	2	5.25	54.13	8.09	0.28	———
8	3	4.75	54.13	8.57	1.43	———
9	2	5.25	54.38	6.5	———	———
9	3	4.75	54.38	4.95	0.9	———

Annex 21. Corystes 9/96 (12-14 July 1996), number of *N. norvegicus* larvae per square metre (grid box as shown in figure 5.1).

Row	Column	Longitude (W)	Latitude (N)	Stage I/m^2	Stage II/m^2	Stage III/m^2
5	1	5.75	53.38	0.56	———	———
5	2	5.25	53.38	———	0.28	———
7	1	6.25	53.88	0.69	———	———
7	2	5.25	53.88	0.41	———	0.41
8	3	4.75	54.13	0.56	———	———