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Population dynamics and secondary production of the small copepods in the Menai Strait

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A Doctoral thesis in Marine Biology
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Abstract

Measuring zooplankton standing stock and production is a central problem in marine biology since zooplankton, particularly copepods, link primary productivity to fisheries productivity. The aim of the present study was to determine the seasonal and annual variation in the standing stock and secondary production of the main calanoid copepod species found in the Menai Strait, eastern Irish Sea. The zooplankton survey was carried out between January 1996 and December 1997. In addition, the reproduction and the respiration rate of the dominant copepod species, *T. longicornis*, was investigated between 1996 and 1998 during field and laboratory experiments to study its population dynamics. The temperature during January through to April differed between years, with the winter 1996 being colder than that of 1997 and 1998. The timing of the spring phytoplankton bloom also differed between years with the Chla maximum in 1996 occurring ~1 month later than in 1997 and 1998. *T. longicornis* produced eggs all year round with maximum carbon-specific egg production rates (EPR) of (~0.14 μg Egg-C μg fem.-$C^{-1}day^{-1}$) coinciding with the spring phytoplankton bloom and minimum rates (~0.01 μg Egg-C μg fem.-$C^{-1}day^{-1}$) in winter. The pattern of natural EPR variability indicates that individual fecundity was positively related to female weight and food quantity (possibly constrained by food size or quality) and negatively related to tidal range (i.e. total suspended sediment). In all three years, the hatching success (% HS) of the eggs laid decreased by ~80 % during peak phytoplankton production and was significantly negatively correlated ($r = -0.47$, $p<0.05$, d.f.= 96) with ambient Chl-a concentration. These non-hatching eggs could have been diapause eggs. The respiration rate of *T. longicornis* varied during the year increasing both with body weight and with temperature. The metabolic daily energy loss of an adult copepod account for between 4 % and 8 % of its body carbon (winter and summer respectively). The seasonal pattern of copepod abundance and species composition was typical of temperate coastal areas. The seasonal variation in the copepod community (by number and biomass) showed *T. longicornis* to be the most abundant in spring, *Centropages hamatus* and *Acartia clausi* in summer and *Pseudocalanus sp.* in autumn and winter. Maximum total copepod standing stock occurred during the spring phytoplankton bloom and minimum between autumn and winter with total annual standing stock in 1996 (618 mg-C m^{-3}) being ~ 4 times lower than in 1997 (2530 mg-C m^{-3}). Stage specific, copepod cephalothorax lengths varied with season and in most cases were negatively correlated with temperature. Individual weights and abundance of the copepods, together with measures of temperature, were used to predict weight specific growth and production rates using published empirical relationships. Calanoid copepod total annual production varied between 37-160 mg-C m^{-3} yr^{-1} for 1996 and 1997 respectively with *T. longicornis* accounting for ~50 % of the total followed by *C. hamatus* (~25 %), *A. clausi* (~20 %) and *Pseudocalanus sp.* (5 %). Annual carbon flow in the Menai Strait was estimated from copepod production with measures of primary production, production of bacteria (previous study) and ciliates at this site. It is suggested that since the spring increase in *T. longicornis* population could not be attributed to the EPR of over-wintering females alone, the excess of copepods may either originate from the hatching of resting eggs during winter or from transport of animals from southern regions. If resting eggs were implicated in copepod population dynamics the annual variation in copepod standing stock may be controlled by climate change through differential hatching rate of resting eggs in winter.

Foreword

Lasciate ogne speranza, voi ch'intrate
(Abandon all hope, ye who enter here)

Inferno - canto 1

Nel mezzo del cammin di nostra vita
mi ritrovai per una selva oscura
ché la diritta via era smarrita.

Ahi quanto a dir qual era è cosa dura
esta selva selvaggia e aspra e forte
che nel pensier rinova la paura!

Tant'è amara che poco è più morte;
ma per trattar del ben ch'i' vi trovai,
dirò de l'altre cose ch'i' v'ho scorte.

Io non so ben ridir com'i' v'intrai,
tant'era pien di sonno a quel punto
che la verace via abbandonai.

(Dante Alighieri, Inferno, Canto I, 1306-21)

MIDWAY upon the journey of our life
I found myself within a forest dark,
For the straightforward pathway had been lost.

Ah me! how hard a thing it is to say
What was this forest savage, rough, and stern,
Which in the very thought renews the fear.

So bitter is it, death is little more;
But of the good to treat, which there I found,
Speak will I of the other things I saw there.

I cannot well repeat how there I entered,
So full was I of slumber at the moment
In which I had abandoned the true way.

(Dante Alighieri, the Hell) Longfellow (1867) translation

Acknowledgements

First, I should thank Dott. Dante Alighieri, an eminent Florentine academic from the fourteen century, for providing his lyrics as an adequate foreword to the present work. I believe there are not better words to describe the cathartic journey through the darkness, misery and pain of a PhD existence. However hard, an educational journey to hell which is worthwhile.

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I am very grateful to several people for providing invaluable complementary data sources, which I have used in my thesis; Dr Richard Gowen provided me with the copepod abundance data collected in 1997 from the Western Irish Sea and the Liverpool Bay. Dr. Des Barton gave me the CTD data collected from the Ynys Faelog station in the Menai Strait between 1996 and 1998. Dr Kevin Hosborough allowed me to access the meteorological data collected by RAF station in Valley, Anglesey. Professor P. LeB. Williams provided me with the oxygen rate and bacterial numbers measured in the Menai Strait between 1992 and 1996.

A very special thank goes to Malcom Budd (M.Phil) for growing so "excellently" the *Rhinomonas reticulata* algae for feeding "my copepods"; to Dave Gill, Mike E. Jones and Elwyn Jones not only for building many "miraculous" experimental devices but also for their good humour; to John Rowlands, Ian Pritchard and to Berwyn Roberts for providing generously "everything at any time" and to Berwyn also for his skills in catching all those delicious Sea-bass.

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Chapter 1

General Introduction

1.1 Introduction

Research on the seasonal and long-term fluctuations in copepod community structure and standing crop has progressively gained importance (Colebrook, 1986; Kane, 1993; Escribano & McLaren, 1999; Beaugrand *et al.*, 2000). These studies have been particularly stimulated by observations, over the last 50 years, that changes in many fisheries were correlated with concomitant changes in the abundance of key copepod species (Reid *et al.*, 1998; Planque & Reid, 1998). Zooplankton are the major food for larval fish and are thus thought to be one of the key factors determining year class strength of commercial fish species (Cushing, 1978; Brander & Dickson, 1984). The inter-annual unpredictability of fishery recruitment is the major obstacle to devising acceptable, sustainable fisheries policies. Understanding the mechanisms which give rise to the variation in zooplankton abundance may therefore provide a scientific underpinning for the sustainable exploitation of marine fisheries.

Increasing interest in the fluctuations of planktonic communities has also been prompted by the knowledge that the plankton presents a sensitive indicator of environmental change (Sparks & Reid, 1999). Observed variations in standing stock and community structure of the North Atlantic copepod, through long-term time series analysis (Colebrook, 1985) have been shown to be correlated significantly with the North Atlantic Oscillation (NAO), an index of global climate changes (Hurrell, 1995; Fromentin & Planque, 1996). Thus, the changes in zooplankton dynamics reflect not only the sustainability of world fisheries (Costanza *et al.*, 1997), but also the effect of global changes (including human activity) on the health and biodiversity of marine life (Cook *et al.*, 1997).

Although they represent only a small area of the world's oceans, shelf and coastal seas are of great ecological and economic importance being highly productive, providing the nursery ground for many commercial fish stocks and being the recipients of increasing industrial, agricultural and human pollutants. In temperate latitudes the annual cycle of plankton is an obvious reflection of the annual cycle of physical

conditions in the sea (Valiela, 1995). The increase in light intensity, in spring coupled with nutrient availability and stabilisation of the water column (e.g. thermocline formation), promotes the spring phytoplankton bloom, which is in turn followed by increased zooplankton abundance (Mann & Lazier, 1991; Gowen *et al.*, 1998). Variation in the community structure and biomass of marine planktonic organisms is commonly observed at different spatial and temporal scales (Cushing, 1975; Raymont, 1980) occurring both on a latitudinal scale and seasonally on a local scale (reviewed by Heinrich, 1962). Thus, temperate and polar areas are usually characterised by a marked seasonal fluctuation in plankton productivity, while tropical and bathypelagic environments are essentially aseasonal with virtually constant standing crop (Cushing, 1959; Lalli & Parson, 1993).

Temperate shelf and coastal waters are classically characterised by a bi-annual zooplankton increase, the first and larger one taking place after the spring phytoplankton bloom and the second after the autumn phytoplankton increase (see review by Heinrich, 1962). Although, the causes of the spring bloom in phytoplankton, the summer peak in zooplankton, and the resurgence of phytoplankton in the autumn are broadly explicable (Smayda, 1980) it cannot be said that the cycle is understood in detail. Succession in different communities is observed to give rise to cyclical annual patterns in both the phytoplankton (Margalef, 1978) and the zooplankton (Mazzocchi & Ribera d'Alcala, 1995; Mauchline, 1998) but the factors that determine the presence of given species at a specific time or location are not clear (Levin, 1992; Verity & Smetachek, 1996). For instance, it is unclear why despite parallel seasonal reproduction patterns of *C. typicus* and *T. stylifera*, abundance peaks of these two species occurs at different times of the year (Halsband-Lenk *et al.*, 2001). In addition, *Calanus helgolandicus* is an important component (~ 50 %) of the mesozooplankton of the Celtic Sea but it is less abundant (~ 10 %) in the neighbouring Irish Sea where small copepod genera like *Temora*, *Pseudocalanus*, and *Acartia* are numerically dominant (Planque & Fromentin, 1996; Gowen *et al.*, 1999).

The copepod community in any coastal region is usually dominated by a few species with one species usually more common in term of number or biomass but usually both (McGowan, 1990). Seasonal succession of copepod species has been found in many areas (Ambler, 1985) with the different species dominating at different times during the year (Sullivan & McManus, 1986; Fransz *et al.*, 1991; Hirst *et al.*, 1999). For

instance, in the Gulf of Naples, a succession of different *Clausocalanus* species appears throughout the year (Mazzocchi & Ribera d'Alcala, 1995).

Conditions governing the seasonal changes in marine copepod communities in coastal seas tend to be more complex than in open oceans due to the added effect of local geography, river discharge and tidal rhythm (Mauchline, 1998; Hirst *et al.*, 1999). In coastal waters, the changes in a given plankton community in time and space are driven both by physico-chemical (e.g. temperature, salinity, turbulence, suspended sediment, advection) and biological (e.g. food sources, competition, predation, growth) parameters which can act independently or synergistically at different spatial and temporal scales (Mann & Lazier, 1991).

Temperature, for instance, is an important environmental variable for poikilothermic organisms, like copepods, since it directly influences their physiological rates (Vidal, 1980a), limits the extent of their geographical distribution and determines the seasonal occurrence of many species (Ikeda, 1970). The seasonal fluctuation of temperature in temperate regions has been shown to influence the size and the growth rate (i.e. egg production and development rate) of copepods both in the laboratory (Klein-Breteler *et al.*, 1995) and in the field (Evans, 1981) and the seasonal appearance of different copepod species (Walsh, 1981). *Pseudocalanus sp.*, for example, is a cold water form (Corkett & McLaren, 1978) which grows well at low temperatures (Vidal, 1980b) and intermittent food supply (Dagg, 1977) and dominates winter communities whereas *Centropages hamatus* does better in warmer temperatures and dominates summer communities (Walsh, 1981; Kane, 1993).

Separating the influence of variables both on standing crop and community structure is often difficult. For example, the spring increase in temperature, phytoplankton and microzooplankton in temperate coastal regions usually takes place simultaneously so that their relative influence on copepod physiology is often difficult to determine (Rodriguez *et al.*, 1995). Tidal regime has also been shown to affect the blooming and persistence of both phytoplankton (Roden, 1994; Lauria *et al.*, 1999) and copepod communities (Hirst *et al.*, 1999). Moreover, in open bays the variation in planktonic organisms is dictated by advective and dispersive forces, resulting in random copepod dominance order whereas in fjiords and other enclosed bays, these processes are minimised and the seasonal order of in copepod species dominance is stable from year to year (Williamson, 1987; Coyle *et al.*, 1990; Ban *et al.*, 1998).

Biological factors reputed as important for determining copepod species dominance and standing crop are competition for limiting food resources and/or predation by planktivorous fish (Fulton, 1984), jelly-fish, ctenophores and chaetognaths (Davis, 1984; Verity and Smetacek, 1996; Purcell, 1997).

The question of whether copepods in nature are food limited (Kiorboe, 1989; Kiorboe & Nielsen, 1994; Hopcroft & Roff, 1998) or not (Huntley & Lopez, 1992) is still unresolved. Clearly, the answer may be species specific (Kleppel *et al.*, 1996; Hirst & Lampitt, 1998) since copepods are a heterogeneous group of organisms. Different species have different resistance to starvation (Dagg, 1977), and have different preferences for the size and quality of their prey (Hansen *et al.*, 1994) as reflected by the variety in size and structure of the cephalic appendages of different copepod species (Anraku & Omori, 1963; Itoh, 1970). Copepods have been shown to feed selectively on different planktonic species (Uchima, 1988; Turner, 1991) being able to discriminate among, for instance, diatoms, microzooplankton and dinoflagellates and selecting these preferentially to flagellates, like *Phaeocystis sp.* (Hansen *et al.*, 1994; Verity and Smayda, 1989).

The Ctenophora and Cnidaria are major predators of copepods and their population densities have been found to often correlate inversely with copepod density both in the field (Deason & Smayda, 1982; Davis, 1987) and in mesocosm experiments (Harris *et al.*, 1982). The impact of these predators on copepod population can be quite severe. As an example, the accidental introduction from the Atlantic of the ctenophore species *Mnemiopsis laydii* in the Black Sea, has been held responsible for the collapse, in the late 80's, of the anchovy and other important commercial fisheries through the decimation of the copepod population (Shiganova, 1998). Yet, both the extent and the mechanisms through which different predator and prey species interact with copepods in their environment to give rise to the observed patterns in copepod species succession and standing crop await explanation (Verity & Smetachek, 1996).

Because of their variable environmental conditions, coastal water environments encourage the success of small copepod species (Williams *et al.*, 1994; Mauchline, 1998). Small copepods generally are well adapted to fluctuating coastal conditions. For instance, several species of coastal copepod deposit diapause eggs in the sediment which allow avoidance of mass mortality seasonally with the new population being regenerated at a later date from the diapause eggs (Marcus *et al.*, 1994). It is commonly

accepted that the resting egg stages make up part of the life history of many freshwater and marine copepods, and play an important role in the succession of copepod species (Kasahara *et al.*, 1974). Recently, the existence of viable egg banks representing a potentially important source for recruitment of nauplii into the plankton has been suggested (De Stasio, 1989; Marcus *et al.*, 1994).

Technical difficulties, however, exist in distinguishing, morphologically, between true diapause eggs and non-viable eggs for some copepod species. The appearance of diapause/non-viable eggs in the sediments often coincides with the simultaneous increase in the copepod population (Ban & Minoda, 1994; Guerrero & Rodriguez, 1998), the population of their predators (Hairston, 1987), the bloom of particular phytoplankton species (Miralto *et al.*, 1999), low food quality (Jónasdóttir, 1994), low temperature regimes (Sullivan & McManus, 1986), photoperiod (Marcus, 1982) giving rise to multiple correlation and hypothesis with respect to triggers for the production of diapause eggs or non-viable eggs.

Short generation times and continuous breeding typical of species belonging to the genera *Acartia*, *Centropages*, *Pseudocalanus* and *Temora*, are also considered adaptations to a changeable environment (Williams *et al.*, 1994; Mauchline, 1998). Estimating the parameters of population dynamics, like growth, fecundity, mortality and recruitment of continuously reproducing copepod species in general and small copepods in particular is technically difficult or impossible (Binet, 1977; Huntley & Lopez, 1992).

For instance, a variety of methods have evolved, over the course of the last century, for estimating the production of marine zooplankton which only requires the measurement of two parameters, namely, growth rate and biomass. Whereas, biomass can be relatively easily quantified through an appropriate sampling program, the estimation of *in situ* growth rate is more difficult and time consuming. Yet, the measurement of copepod growth is of crucial importance for the determination of secondary production of copepod populations. Although, there are different methods available for estimating primary production, routinely used for decades, zooplankton ecologists have not yet developed a commonly accepted and routine method for measuring copepod secondary production (Poulet *et al.*, 1995).

Two methods have been applied in the past, that is the cohort analysis (Manly, 1993) and the physiological method, (Omori & Ikeda, 1984; Huntley & Lopez, 1992: Poulet *et al.*, 1995) but none is entirely practical and/or satisfactory. The cohort method

allows both the measurement of growth and survival rate through the measurement of 1) time and weight increase between stages and 2) from the difference in the number of individuals counted in different stages, respectively, using time series field data. One of the major disadvantages is that it is extremely labour-intensive because time-specific and site specific weight at stage information is necessary (Berggreen *et al.*, 1988). The physiological method consists in estimating growth rates indirectly through the measurement of individual physiological components of the species energy budget. All the physiological functions which need to be estimated to build such a budget are influenced by intrinsic and extrinsic factors that may result in large errors in the estimation of growth rate. In concept, the physiological method is simple elegant and straight-forward but in practice it is almost impossible to carry out (Huntley & Lopez, 1992). The aim of many more recent methods in estimating copepod production based either on egg production and female copepod weight (Poulet *et al.*, 1995) or copepod weight and/or temperature (Huntley & Lopez, 1992; Hirst & Lampitt, 1998) is to obtain a simple and widely applicable mathematical relationship. These methods are, however, still rough approximations of the real copepod production since they propose equations for estimating production which either underestimate production by only taking into account the female stage (Poulet *et al.*, 1995) or which are bound to be affected by a large error since they cannot resolve the effect of physical and biological variables (Huntley & Lopez, 1992; Hirst & Lampitt, 1998) on copepod production which is, at least, site and time specific.

Observed patterns in plankton dynamics including copepod standing crop and species succession are the results of a close interaction between the physico-chemical environment, the biology of the organisms, the time scale at which events take place and the bias imposed by the perception of the observer. Because of the differences in time scale and spatial scale, many of which are technically hard to asses, the observed pattern of variation in planktonic communities is difficult to resolve and cause and effect not simple to determine (Steele, 1991). The need for a better understanding of the mechanisms stabilising marine ecosystems as opposed to the more popular and technically easier, energy flow measurements, advocated by Odum (1971) and Radach *et al.*, (1984) during the 70's and 80's, have been echoed throughout the 1990's. In his recently published MacArthur Award Lecture to the Ecological Society of America (ESA), Levin (1992) wrote: 'Understanding patterns in terms of the processes that

produce them is the essence of science'. The problem of scale and pattern represents the central issue in ecology in general (Platt & Sathyendranath, 1994; Levin, 1992). According to Levin (1992) there is not single scale at which ecological phenomena should be studied; systems generally show characteristic variability on a range of spatial, temporal and organisational scales. Interannual variation in the timing of the annual peak maxima in copepod biomass can be related to multiple causes spanning from strictly contingent ones including predation and limitation for food sources to long term ones like the effect of winter conditions as suggested by several authors (Colebrook, 1985; Hay *et al.*, 1991). Furthermore, facts like the production of diapausing eggs will create a temporal mismatch between cause and effect resulting in delays and feed-back loops to population densities which if ignored will lead to erroneous interpretation.

As Levin (1992) put it, the key to prediction and understanding lies in the elucidation of mechanisms underlying observed patterns. The nature of ecological studies is such that, large scale variability, like climate changes, superimposed on small scale variability, such as tidal effect and copepod's physiological conditions, often result in apparent random "noise" which is impossible to explain. Thus, the prediction of ecological causes and consequences requires the interfacing of phenomena that occur on very different spatial and temporal scales.

Progress in understanding the mechanisms stabilising marine communities has been often hampered by logistic and intrinsic difficulties in studying and manipulating such a dynamic and remote environment, that is the sea, as opposed to terrestrial ecosystems. As a result, terrestrial ecology has had the benefit of a seminal paper (Hairston *et al.*, 1960) that inquired into the mechanisms that determine the abundance of populations of species in different trophic levels. Conversely, in marine ecology even if we had an unambiguous depiction of food webs, we would still be a long way from understanding how these assemblages of organisms functions, what controls flow of matter and energy from one link to the next, and what determines abundance of different populations (Valiela, 1995).

In the past, there has been a tendency especially when modelling energy fluxes in marine food webs to aggregate organisms into functional groups constraining different species into single "boxes" (Fransz *et al.*, 1991a). Quite recently, an increasing number of theorethical (Levin, 1992; Verity & Smetacek, 1996), applied (Williams *et al.*, 1996; Adrian & Deneke, 1996) and modelling (Andersen & Nival, 1988) studies on plankton

ecology have stressed the importance of looking at the species rather than at the functional group if we have to gain a better understanding and to be able to predict future changes in the marine ecosystem. Selection operates, in fact, at the species level. The fauna of copepods, for instance, usually comprises an association of species that exhibit a wide variety of environmental preferences (Mauchline, 1998, Kane, 1993). Consequently different species will react in different ways to changes in environmental factors which give rise, for instance, to the intra- and inter-annual fluctuations documented in *A. clausi* and *P. elongatus* (Colebrook, 1978, 1982) or to the succession of *Acartia hudsonica* and *A. tonsa* in Narrangasett Bay (Sullivan & McManus, 1986).

In this respect, the Nantwich 1993 PRIME guest paper of Verity & Smetacek (1996) can be regarded as a milestone for the way in which it interprets, the new tendency of the scientific community to view plankton ecology. According to these authors:

"substantial advances in quantification and delineation of biogeochemical processes and provinces have not been accompanied by commensurate progresses in understanding of the mechanisms that structure pelagic ecosystems. Thus, the distribution patterns of dominant pelagic species are fairly well established, yet we do not know why they occur when and where they do. What is lacking is knowledge of the nature of properties that gear given species to specific environment and, which are responsible for their occurrence or persistence in given water masses".

This new awareness of the role of the species has partly sprung from putting together long time series, which have revealed long term changes in species composition in relation to environmental variables (Colebrook, 1982; Fromentin & Planque, 1996).

The marine environment is more sensitive than terrestrial ecosystems to climate changes since the ocean responds on a shorter time scales to atmospheric changes (Steele, 1991). With the current concern about climate change, there is increasing consensus among scientists that the past is the avenue to understanding the future. The starting point to view changes is through analysis of valuable time series (McGowan, 1990). Long temporal and spatial series can be used to examine similar patterns in the variation of climate and ecosystem components; only where scales of variation match there is at least the basis for investigation of mechanistic relationships (Levin, 1992). An

example is provided by the continuous plankton recorder surveys of the North Atlantic, providing data on spatial variations in the distribution of the phytoplankton and zooplankton over half a century (Reid *et al.*, 1998; Beaugrand *et al.*, 2000). The radical changes in climate are held responsible for a wide range of effects on the marine ecosystem including changes in the production of zooplankton and the distribution of fish, these changes being correlated with the North Atlantic Oscillation index (Fromentin & Planque, 1996; Reid *et al.*, 1998; Planque & Reid, 1998).

The North Atlantic Oscillation (NAO) is primarily a winter atmospheric oscillation which is associated with the position and strength of weather systems as they cross the North Atlantic, which in turn determine precipitation (Hurrell, 1995) and sea surface temperature (i.e. SST, Beker & Pauly, 1996; Planque & Taylor, 1998). An index of the NAO variability is defined as the difference between the normalised (by division of each seasonal pressure to the standard deviation between 1864-1994, Hurrel, 1995) winter, (December to March) sea level pressures (SLP) measured at Stikkisholmur in Iceland, to represent the Iceland low and at Lisbon Portugal, to approximate the high pressure cell. The strong positive phases of the NAO-index tend to be associated with above-normal temperatures and precipitation over northern Europe while the opposite pattern of temperature and precipitation anomalies are typically observed during strong negative phases of the NAO. Hurrel (1995) and Beker & Pauly (1996) have shown that the NAO-index is directly related with a considerable portion of the climatic fluctuations in sea surface temperatures. The NAO-index has strengthened during the last 30 years or so, rising from its low index state in the 1940's and 1950's to reach a historic maximum in the early 1990's which seems to have been reversing in the last couple of years (Karl *et al.*, 2000).

1.2 Aim of the thesis

The present study aims to study the seasonal and annual changes in standing stock and production of the small copepods living in the Menai Strait. In addition it aims to study the population dynamics of one of the dominant copepod species living in the Menai Strait, *Temora longicornis*.

Temora is used here as a model to investigate the nature of its success in comparison to other copepod species. In addition, the present study provides a

continuation of an existing data set on plankton compiled for the Menai Strait since the 1950's.

The Menai Strait is part of the Irish Sea. The Irish Sea is currently the subject of a major environmental review and the need for a better understanding of the changes in the marine ecosystem has been recognised in the integrated Science Programme for the Irish Sea commissioned by Departments of Environment in London, Belfast and Dublin (Boelans, 1995). The results from the present study may, therefore, provide relevant information on the factors affecting ecological changes within copepod communities not only on a global scale but also for local policy making.

The aim of the thesis was pursued considering the following:

1) Measurement of egg production rates (EPR) of *T. longicornis* in relation to physical and biological environmental conditions. The EPR was used to estimate copepod secondary production and copepod potential recruitment.
2) Measurement of respiration rate of *T. longicornis* in relation to natural field temperature conditions to test metabolic acclimation to temperature to estimate major inefficiency of production.
3) Seasonal and annual changes in the small copepod species community abundance and size structure in relation to food resources, predation and environmental factors.
4) Investigation of the population dynamics of *T. longicornis* over a two year time series has been undertaken to explore the factors affecting the inter-annual fluctuation in abundance of this species. Comparisons with other zooplankton time series compiled in the Menai Strait from the 50's have been undertaken.

1.3 The thesis plan

The thesis plan is organised as follows:

Chapter 1 is the general introduction. It explains the importance of plankton research in relation to the ecology of the marine environment and global climate changes. It briefly surveys the past research on zooplankton and justifies the aims of the thesis in the context of the new research tendencies.

Chapter 2 contains the general methodology. This chapter explains the methods used to acquire basic information relative to environmental variables including temperature, salinity chlorophyll and microzooplankton during the seasonal sampling in the Menai Strait. In addition it provides information about the general copepod maintenance carried out in the laboratory.

Chapter 3 presents a concise overview of the results obtained for relevant physico-chemical and biological characteristics of the sampling site. Temperature, salinity, sediments, chlorophyll-a and microplankton groups profiles are provided over the three years of the study spanning between 1996 and 1998.

Chapter 4 describes the seasonal pattern in egg production measured between 1996 and 1998 for *T. longicornis* in relation to biotic and abiotic variables.

Chapter 5 describes the seasonal pattern in egg hatching success measured between 1996 and 1998 for *T. longicornis* in relation to biotic and abiotic variables.

Chapter 6 presents the results obtained during a laboratory investigation on *T. longicornis* egg production and hatching success with different phytoplankton diets. The hatching rate of eggs produced over the ambient temperature range and at extreme environmental acclimation temperatures was also investigated.

Chapter 7 describes the seasonal changes in the respiration rate of *T. longicornis* measured at ambient temperature and acutely during laboratory experiments. In this chapter the hypothesis that *Temora* is able to acclimate to field temperature was tested. The survival rate of this copepod species acclimated at different ambient temperatures over a wide temperature range was also investigated.

Chapter 8 analyses the seasonal variation in the Menai Strait meso-zooplankton species composition and of the copepod community structure paying particular attention to, *T. longicornis*, the dominant species. Enumeration and identification to species level (when possible) of all the zooplankton groups found in the Menai Strait is reported. The stage and length frequency distribution and annual standing stock of the most abundant

calanoid copepods species is presented for 1996 and 1997. The mechanisms responsible for the seasonal and inter-annual fluctuations in species composition and biomass are considered. The chapter also investigates long-term changes in the Menai Strait copepod species composition and standing stock by comparing the data compiled from the late 50's with those collected during the present study.

Chapter 9 is the General Discussion. It brings together and justifies the various topics dealt with throughout this study and discusses the possible reasons for the observed pattern and success of *Temora longicornis* within the Menai Strait and the coastal regions of the eastern Irish Sea.

1.4 List of Contributions

- Description of seasonal and annual changes in the microzooplankton community and standing stock in the Menai Strait
- Measurement of seasonal and annual changes in egg production rate (EPR) and egg hatching success of *T. longicornis* in the Menai Strait
- Time course of acclimation to temperature of the respiration rate of *T. longicornis*
- Measurement of the respiration rates of *T. longicornis* at different *in situ* acclimation temperatures
- Measurement of seasonal and annual changes in community structure, abundance and biomass of the main calanoid copepod species living in the Menai Strait
- Estimation of calanoid copepod secondary production in the Menai Strait
- Estimation of carbon flow in the Menai Strait

Chapter 2

General Material and Methods

2.1 Description of the study site: The Menai Strait

The Menai Strait is a temperate, aquatic ecosystem. It is typified by complex biogeochemical cycles due to land and sea interactions, high primary productivity, pronounced seasonality and by mixing with adjacent off-shore water masses of distinct physico-chemical and biological characteristics. Local hydrographic conditions (e.g. currents, eddies, stratification, advection) and physico-chemical variables (e.g. temperature, salinity, wind speed/direction) must influence any zooplankton community (Aksnes *et al.*, 1997; Resgalla *et al.*, 2001), thus, the physical characterization of the study site becomes essential to the understanding of the dynamics of the zoo-planktonic community.

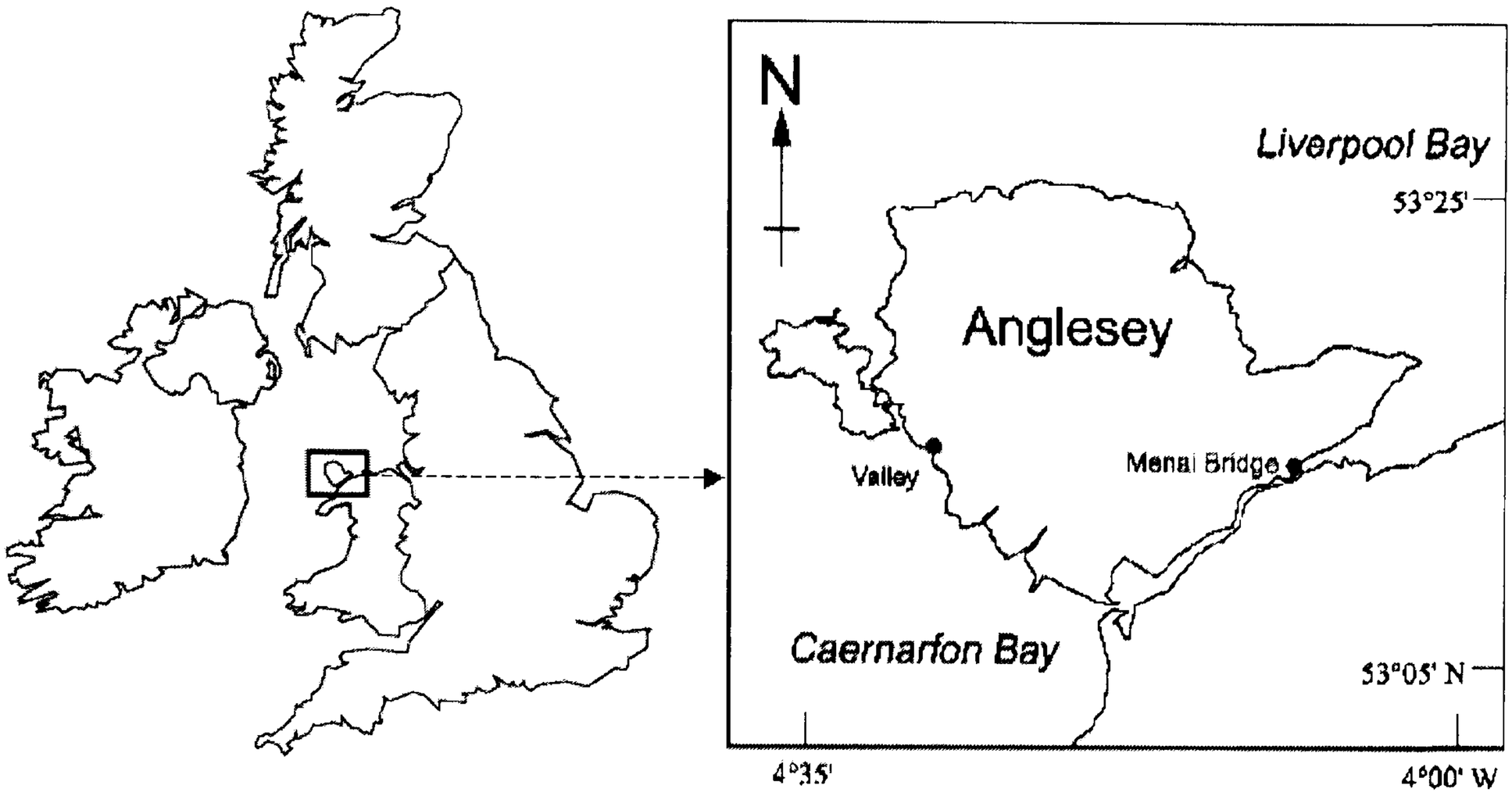
The physical chemical and biological characteristics of the Menai Strait have been extensively investigated. Sampling has been conducted from research vessels and also from the St George Pier, Menai Bridge. The pier is easily accessible from the School of Ocean Sciences and sampling at this site is considered representative (Jones & Spencer, 1970; Blight *et al.*, 1995) of what happens in the rest of the Menai Strait.

2.2 The hydrographic characteristics of the study site

The Menai Strait is the narrow channel separating the island of Anglesey in North Wales from the U.K. mainland (Figure 2.1). It runs for approximately 20 km from Fort Belan in the south-west, past the towns of Caernarfon, Port Dinorwic and Menai Bridge to Bangor in the north-west where it widens into Conwy Bay and the Irish Sea. The channel has a mean width of approximately 800 m narrowing to less than 300 m in an area known as the Swellies between Menai Bridge and Port Dinorwic. Tidal currents are generally fast and the bottom rocky and uneven. More sandy substrata can be found intertidally particularly where the channel widens, e.g. the Lafan Sands in Conwy Bay. Although depths between 1-5 m predominate along the Strait, water depths in the channel can be considerable reaching maximum of 22 meters around the Swellies at high spring tide (Admiralty Chart 1464,1986). Mean spring and neap tidal ranges and at Menai Bridge of 6.6 m and 3.4 m respectively are found with a predominantly semi-

diurnal rhythm. Due to these strong tidal currents and high tidal ranges the water of the Menai Strait never stratifies and is thoroughly mixed throughout the year.

Figure 2.1: Map of the sampling area.



The tidal pattern within the Menai Strait is complex and greatly influenced by the water masses from Liverpool Bay and Caernarfon Bay. The in-flowing tide enters at Abermenai Point at the south-west end and flows north but before it reaches the other end, the tidal flood has passed around Anglesey and has started to enter at the north end. As a result the two opposing in-flows meet between the Swellies and Bangor Pier becoming thoroughly mixed. Observations made by Harvey (1972) on diurnal and seasonal changes in water temperature have indicated that during average weather conditions the water sampled in the Menai Strait at the St George pier particularly at high tide originates mostly from the Liverpool Bay. In addition, studies of the flow regime in the Strait (Harvey, 1968; Simpson *et al.*, 1971) using drifters and electromagnetic current meters have demonstrated a net transport of water to the south-west during a semidiurnal tidal cycle. In the absence of significant wind forcing, the net transport is of the order of 30 million m^3 over a tidal cycle (approx. 700 m^3 s^{-1}) corresponding to a residual velocity of about 10-15 cm s^{-1}, so that the system has a flushing time of 2-3 days (Harvey, 1965 & 1968; Campbell *et al.*, 1998). The along strait wind component, however, may strongly influence the net transport, even to the extent that a strong south-westerly wind (12.5-20 m/s) may reverse the direction of the

residual flow especially during neap tides (Simpson *et al.*, 1971). A water mass is usually defined on the base of its physical (i.e. temperature and salinity) and biological (i.e. plankton community) characteristics (Bary, 1964). Based on their planktonic composition, Williamson (1956) has recognised in the Irish Sea up to four different water masses, namely 1) the north- going current, 2) the south-going current, 3) the central Irish Sea water and 4) the eastern coastal water. More recently Gowen *et al.*, (1995) have described, similarly to Williamson (1956) up to four different hydrographic regions looking at the degree of seasonal stratification of the water column and their primary production.

The circulation throughout the Irish Sea is weak and is driven by density gradients, tides and local weather (Ramster & Hill, 1969; Bowden, 1955; Norton, 1990) so that the entrance of water masses of Atlantic or off-shore origin in the Liverpool Bay and indeed in the Menai Strait is sporadic. The eastern Irish Sea particularly the Liverpool Bay water forms a backwater with a possible residence time longer than a year (Norton, 1990). In addition, the consistent presence of the Liverpool Bay front has been shown to act, for most of the year, as a natural barrier to planktonic organisms between coastal and offshore waters (Floodgate *et al.*, 1981; Savidge & Kain, 1991; Burkart *et al.*, 1995). Occasionally, storm events and strong south-westerly winds cause the water from the more central part of the Irish Sea (Ewins & Spencer, 1967) and to some extent the Atlantic (Harvey & Spencer, 1962) to enter the Menai Strait.

Fresh water input to the Strait *via* several small rivers (e.g. Conwy, Afon) is strongly dependent on local rainfall and the annual snow melt from the Snowdonia mountain range. On average, however, the total inflow of fresh water over a semi-diurnal period is less than 0.5 million m^3, whereas the total volume of water contained within the Strait is over 80 million m^3 (Simpson & Nunes, 1981) corresponding to as little as 0.6% of the total Strait water mass.

2.3 The study site

The Irish Sea is a semi-enclosed sea connecting with the Atlantic Ocean via channels in the north and south. The dynamics of the sea are dominated by the semi-diurnal tides. Fast currents in excess of 1 ms^{-1} are found near Wicklow and north of Anglesey. Weak currents occur to the south-west of the Isle of Man, where thermal stratification occurs in the summer. The regions of fast currents remain vertically mixed

all year. Intermittent stratification, at times of weak wind stirring, is found in the eastern Irish Sea, where there is a significant input of fresh water by rivers. There is some doubt as to whether the rivers and estuaries are sources or sinks of sediment in the Irish Sea (Nunny, 1978; Kirby & Parker, 1983). The major source of particles in suspension appears to be the stirring up of sediment from the sea-bed. Concentrations of suspended sediments respond to variations in the intensity of stirring, for example with the springs-neaps tidal cycle (Weeks & Simpson 1991). The important role of tidal stirring in the Irish Sea has been recognised for over 20 years (Simpson & Hunter 1974), mainly in connection with the vertical mixing of heat and the production of fronts (Hill *et al.*, 1997). Mitchelson (1984) and later Weeks (1989) observed a correlation between gradients of tidal stirring and those of turbidity (i.e. concentration of suspended sediments in the water column). Such a relationship might be expected because strong tidal currents will erode sediments from the sea-bed and keep them in suspension. Tidal stirring alone, however, cannot cause the reported seasonal variation of turbidity in the Menai Strait and in the Irish Sea, since the tides are essentially the same in winter and summer (Buchan *et al.*, 1967 & 1973). Weeks (1989) has discussed possible causes of the seasonal sediments cycle. The most likely cause is flocculation of particles in summer (Jones *et al.,* 1997) which will cause an increase in settling velocity and hence a decrease in turbidity (Bowers *et al.*, 1998). Other possible contributions to the seasonal variation could be greater wind stirring by storms in winter and trapping of sediment below the seasonal thermocline in summer (Buchan *et al.*, 1967 & 1973). Bagnold (1963) first suggested that there should be a correlation between suspended sediment concentration and tidal power dissipation. The observations so far in the Irish Sea have been by ship and hence have been of limited spatial coverage. Calibrated satellite images, however, have recently provide a much better spatial coverage and data set for testing the link between turbidity and tidal stirring (Bowers *et al.*, 1998).

2.4 Salinity and temperature measurement

Salinity and temperature data collection for this study was carried out in the Menai Strait between January 1996 and December 1998. The salinity of the Menai Strait varies between 32 p.p.t. in winter and 34 p.p.t. in summer, rarely falling below 31 p.p.t. or above 34 p.p.t. (Harvey & Spencer, 1962; Hidayat, 1995). Sea-water temperature reaches 17 ± °C in summer and 5 ± °C in winter (Haq, 1960; Harvey, 1972; Blight *et al.*,

1995) although extreme year to year variation can take place with maxima of 18 °C and minima of 0 °C being recorded (Haq, 1960).

In the current study, temperature and salinity were measured with a Braystoke CTD (Series 600), during boat sampling and continuously (virtually throughout the year apart from periods of maintenance or calibration) from a fixed CTD at, Lys Faelog, (courtesy of Dr D. Barton).

In addition, temperature was measured every time and at the same depth of plankton collection using a digital thermometer (Hanna instrument, model Checktemp-1) with a precision of ± 0.2 °C.

2.5 Micro-plankton sampling and biomass determination

The micro-plankton was quantitatively sampled at high tide with a fortnightly/weekly frequency. During the spring phytoplankton blooms of 1997 and 1998 the sampling frequency was increased to every two days to obtain more resolution. Duplicate samples of 100 ml or 50 ml were collected, from a depth of 1-2 m, in dark glass bottles filled with a bilge pump from the St. George's Pier and from 2 L Niskin Bottle on the boat.

Upon collection, samples were immediately fixed with Lugol's Iodine (final concentration 1-2%) (Nielsen & Kiorboe, 1994). Lugol's was chosen since the non loricate ciliates are better preserved than with buffered formaldehyde which can cause losses of 30 –70% of the organisms (Pace & Orcutt, 1981). Samples were then stored in the dark at 4 °C and analysed within one month.

Micro-plankton analysis was carried out by the Utermohl (1958) technique. Concentrated aliquots of 50 ml were allowed to settle for 24-48 hrs in sedimentation chambers at room temperatures not exceeding 19 °C before counting and sizing the ciliates by inverted microscopy (Utermohl, 1958). Preliminary observations showed that it was impossible to concentrate larger sample volumes, because of the large amount of sediment suspended in the Menai Strait water, particularly in autumn and in winter.

Micro-zooplankton counting and sizing was accomplished by using a phase contrast Nikon inverted microscope. Organisms were counted at x300 according to the type and density of the organism of interest by screening either 4 transects for each slide if the specimens were numerous or the whole slide if they were sparse (Unesco, 1978). To estimate ciliate volume, individual microzooplankton cell dimensions were

measured at an appropriate magnification (X600-X1200). The organism's shape was approximated to the nearest simple geometrical shapes and the estimated volumes converted to carbon content assuming a conversion factor of 0.19 pgC μm^{-3} cell volume (Putt & Stoecker, 1989).

The aloricate ciliates were identified with reference to Corliss (1979) and Lee *et al.*, (1985). Only a few of the naked ciliates species could be recognised, through gross morphological features and were identified to genus/species level. Although an excellent cell fixative, Lugol's iodine darkly stains the specimens, masking the finest taxonomic characters. Loricate ciliates (i.e Tintinnids) were much more easily identified on the basis of their lorica, which is unaffected by Lugol's fixation. Identification was made with reference to Marshall (1969) and Rampi & Zattera (1982). Other micro-plankton, including phytoplankton and dinoflagellates species, were enumerated from the same samples in the same way described for the ciliates and identified with reference to Drebes (1974).

2.6 Phytoplankton biomass determination

The phytoplankton biomass was approximated through fluorometric determination of Chlorophyll (Chl, henceforth) concentration (Holm-Hansen, *et al.*, 1965) as this is a widely used simple chemical method and is considered a good estimator of primary producer standing stock (Tett, 1987). Chl was determined from samples of 100 to 750 cm^3 of seawater filtered onto a 47mm ∅ Whatman GF/F filters and the phytopigment extracted in 8 ml of neutralised 90 % acetone solution for 24 hours at 4 °C in the dark. Chl concentration was measured by using a Turner 10 fluorometer in accordance with the recommendations of Tett (1987). This method is considered quite effective since it extracts at least 90 % of the phytopigments from the sample but it is not specific for chlorophyll-a. The fluorometric method measures not only chlorophyll-a but also its precursor chlorophyllide-a since when exposed to the 430 nm light of the fluorometer both these pigments have their emission peak at 670 nm (Tett, 1987). Thus, the Chl concentration [Chl] refers to chlorophyll-a plus chlorophyllide-a. The equations used to estimate the [Chl] were as follows:

$$f_o = (f_o^* - f_{o(b)}) / R$$

$$f_a = (f_a^* - f_{a(b)}) / R$$

$$[\text{Chl}] = \frac{k_f (f_o - f_a) * E}{V}$$

where, f_o and f_a represent the blank corrected fluorescence emitted at 670 nm, by the sample before and after acidification respectively. f_o^* and f_a^* represent the fluorescence of the sample, $f_{o(b)}$ and $f_{a(b)}$ are the fluorescence of the blanks before and after acidification respectively. R is the instrument range, E the extract volume in ml and V the filtered volume in litre. [Chl] is then the Chl concentration in ($\mu g\ L^{-1}$) given k_f, the fluorometric constant, of 0.098 $\mu g\ ml^{-1}$ over the time of the measurements.

2.7 Total suspended particulate matter

Due to the turbulent mixing of its waters the Menai Strait can be loaded with a large amount of particulate matter depending on the phase of the tidal cycle, weather conditions and the time of the year. With the exception of Buchan *et al.*, (1967 & 1973) and Floodgate (1965), information on the amount and characteristics of suspended material in the Menai Strait is very sparse. In general, minimum total suspended particle loads have been measured in summer (0.5 mg L^{-1}) while maximum (50 mg L^{-1}) in winter (Buchan *et al.*, 1967).

In the current study, information on total suspended particulate matter was indirectly estimated between January 1996 and December 1998 from the micro-plankton samples. Total suspended particulate matter (SPM) was visually determined from the micro-plankton slides by assigning the samples scores between 1 and 6, corresponding roughly to 0 to 50 mg L^{-1} (Buchan, *et al.*, 1967 and data from 1996 from Kratzer *et al.*, 2000) according to the percentage of the slide area covered by the detritus.

2.8 Copepod capture and maintenance for laboratory experiments

Temora specimens, for laboratory experiments, were captured from St. George Pier, Menai Bridge, at high tide at a depth of 1 to 2 m. A 270 μm mesh plankton net fitted with a non filtering cod-end was used held open by the water movement generated by the strength of the out-going tide. This sampling procedure was adopted since it minimised damage to the animals due to crowding and the high tow speed, which occurred during

the boat net tows. The copepods were then immediately transferred to an opalescent, polypropylene aspirator containing 20 L of natural seawater pre-screened to 250 μm and brought back to the laboratory. They were sorted within one hour of collection using a large bore plastic pipette to avoid damaging the specimens. Unless otherwise specified, the copepods were maintained at *in situ* temperature either in a cold room or in water-baths at densities of 15 copepods L^{-1} in 5 - 10 L glass jars. U.V. radiated, cartridge filtered (to 0.2 μm) seawater (U.V.F.S.W.) was used routinely and the animals fed *at libitum* with the flagellate alga *Rhinomonas reticulata* (Novarino, 1991) semi-continuously cultured in the laboratory.

Every other day, the water was changed by sieving the copepods in a submerged (to avoid damage to the animals) 200 μm sieve, the copepods poured gently with some remaining water in a cleaned vessel containing clean water and food at the appropriate temperature and concentration respectively. The experimental vessels were first cleaned overnight with a 1% solution of sodium hypochloride and then thoroughly rinsed with hot tap water to remove chemical residues.

Chapter 3

Seasonal trends in the Menai Strait

3.1 Introduction

The aim of this chapter is to offer the reader an overview of the seasonal trends in several physical (temperature, salinity, suspended sediments) and biological (Chl and microplankton) variables, measured in the present study, which are likely to influence copepod population dynamics in the Menai Strait.

3.2 Results

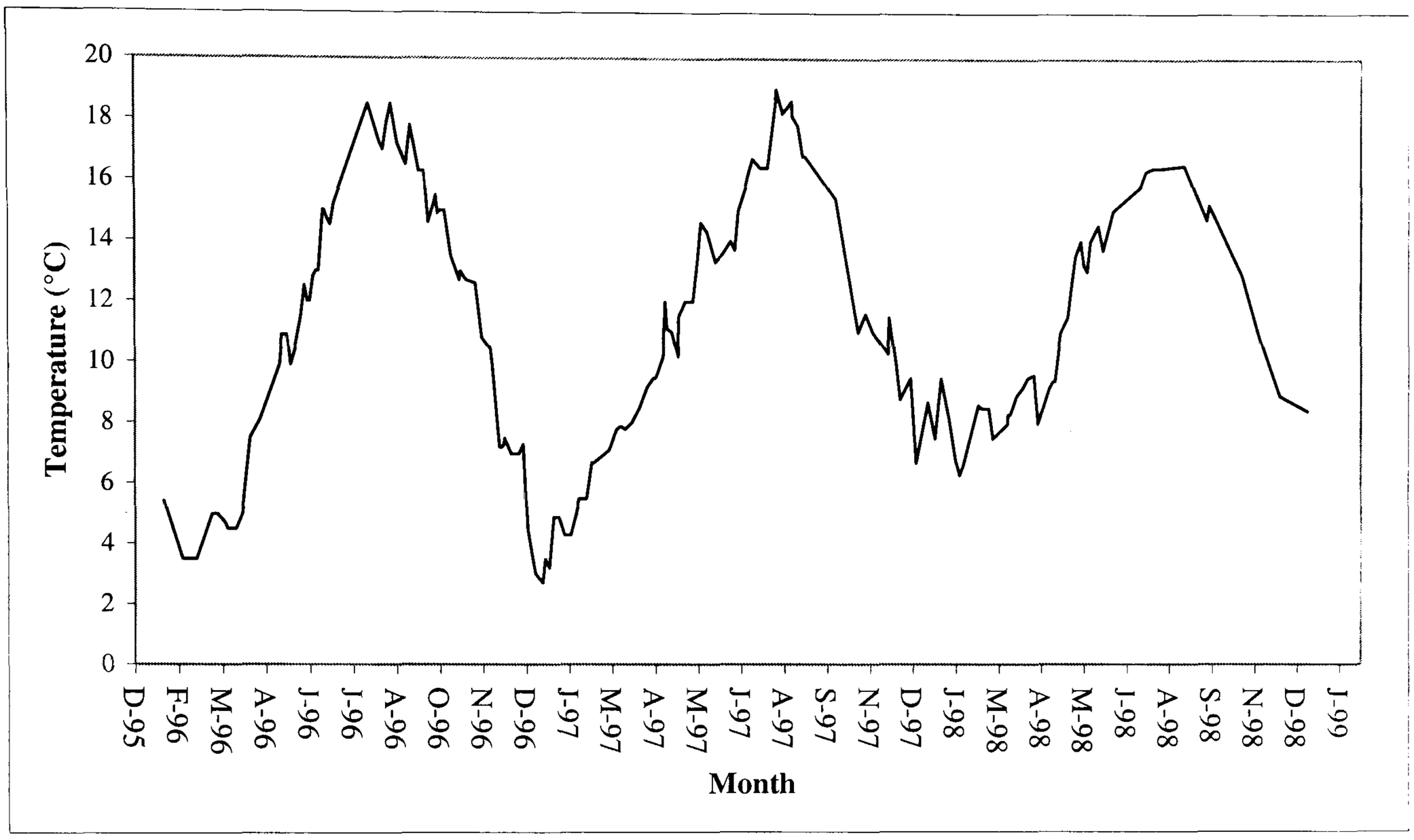
3.2.1 Temperature and salinity

The temperature cycle measured in the Menai Strait between 1996-1998 shown in Figure 3.1. Although, the overall seasonal temperature trend recorded in the Menai Strait followed a parabolic pattern typical of temperate latitudes with *minima* in winter and *maxima* in summer, the variation in magnitude and in the rate of temperature change differed considerably over the 3 years examined (Figure 3.1).

The greatest interannual variation occurred between January and mid-April while temperature fluctuated around similar values for the other seasons (Figure 3.1). Overall, the annual variation in temperature during 1996 and 1997 was higher than in 1998 which was characterised by a flatter temperature profile than the previous two years showing the highest minimum and the lowest maximum winter and summer values respectively. Essentially no winter minimum equivalent to that in 1995/96 and 1996/97 was evident in 1997/98. During winter 1996, seawater temperature stayed low between 3.5 °C and 5 °C increasing sharply at 0.1 °C day^{-1} (faster than for 1997 at 0.066 °C day^{-1} and for 1998 at 0.074 °C day^{-1}) only in spring. The lowest recorded annual temperature at the start of the winter 1997 at 2.7 °C, followed the sharp decrease measured at the end of December 1996 but there was a more gradual thermal increase (i.e. 0.066 °C day^{-1}) than that recorded in 1996 over the same period. In 1998 the winter temperatures were much higher than those recorded during the previous 2 years, following the mild temperatures recorded by the end of 1997, with values ranging

between 7.5 °C and 9.6 °C, excluding a sudden but brief drop in temperature to 6.3 °C at the end of January.

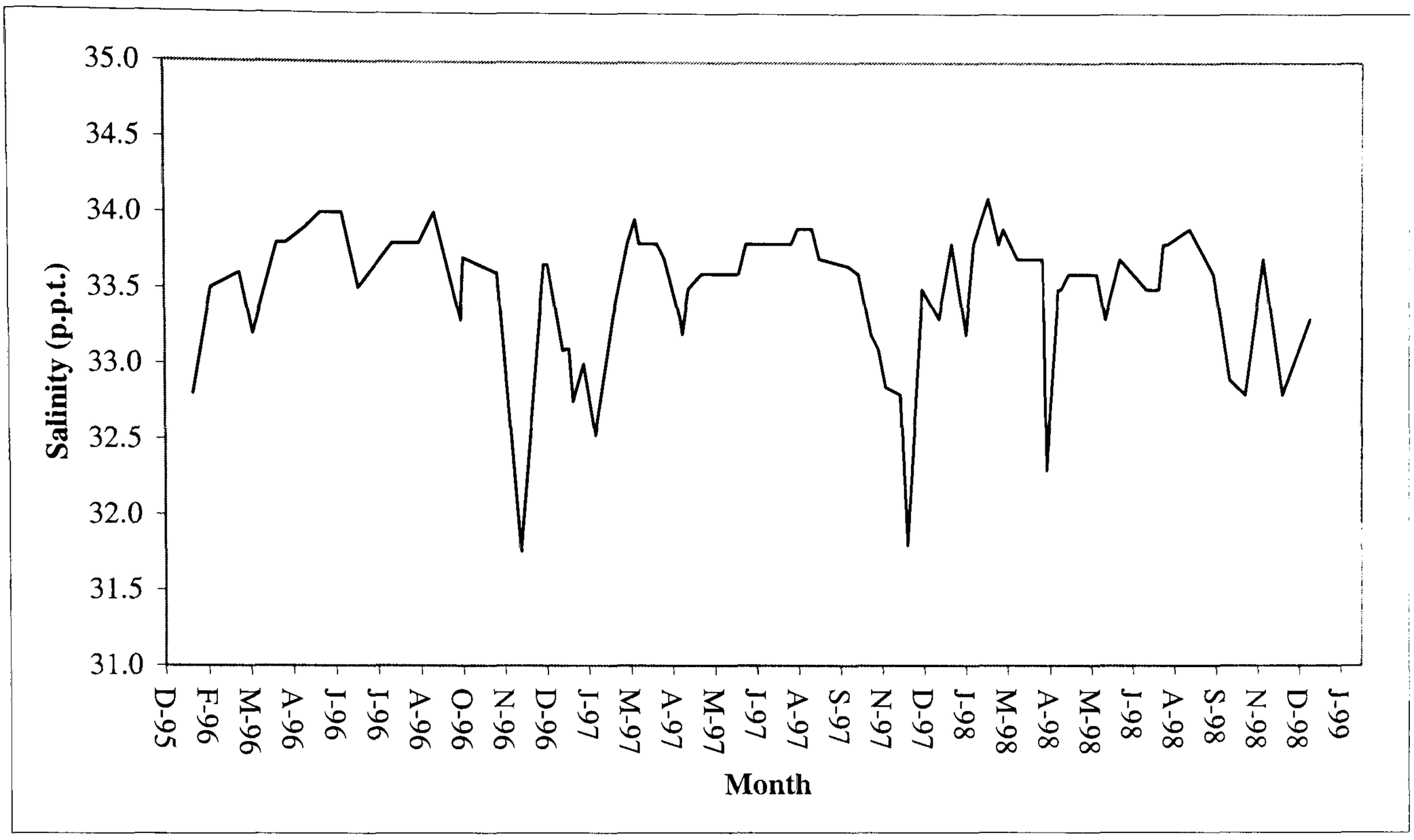
Figure 3.1: Seasonal variation in seawater temperature (°C) in the Menai Strait between January 1996 and December 1998.



As a result differences of about 3.5 °C and 4.5 °C were recorded at the beginning of April between 1996-97 and 1996-98 respectively. The annual maximum also varied among years with the highest values up to 18.5 °C being recorded at the end of July 1996 and in mid August 1997 and the lowest up to 16.5 °C at the end of July 1998.

The seasonal fluctuation in salinity in the Menai Strait showed maxima values in summer and minima in autumn winter months (Figure 3.2). The highest salinities, up to 34.1 p.p.t., were usually recorded in August while the lowest up to 31.7 p.p.t., were measured in November when local annual rainfall (i.e. 110 to 126 mm $month^{-1}$) is usually maximum (Royal Meteorological Society, Weather Log 1996-1998). Drops in salinity were, however, observed in spring around April particularly in 1998 following a temperature drop. During winter 1998 the unusually high temperature records were closely matched by consistently above average salinity for this time of the year. A significant positive correlation between temperature and salinity was found during 1997 (d.f.= 98; $r = 0.57$; $p < 0.001$) but not for either 1996 or 1998 or for the combined years.

Figure 3.2: Seasonal variation in seawater salinity (p.p.t.) in the Menai Strait between January 1996 and December 1998.



3.2.2 Chlorophyll-a and the microplankton

The Chlorophyll-a profile measured in the Menai Strait was characterised by a pronounced seasonal pattern, which was similar for the 3 years considered (Figure 3.3). Minimum Chl of 0.5-0.9 μg Chl L^{-1} characterised the winter period increasing to ~3-8 μg Chl L^{-1} only in early spring. The early increase in Chl was always almost exclusively diatomaceous and included a wide variety of species showing the alternate dominance of *Ditylum brightwelli*, *Skeletonema costatum*, *Chaetoceros sp.*, *Asterionella sp.* and *Thalassiosira sp.*. This early diatomaceous bloom declined to be replaced between April and June by a second and most pronounced bloom of mixed diatom and flagellates dominated by the Haptophyceae *Phaeocystis sp.* and by the diatom *Rhizosolenia delicatula*. The Chl characterising the 96-98 spring blooms ranged around ~16-26 μg Chl L^{-1}. The development of the spring bloom always took place during an extended spell of good weather characterised by very sunny days and calm weather conditions. The end of this bloom was usually followed and dominated by a flagellate community mainly composed of euglenoids and cryptomonas-like flagellates.

Figure 3.3: Seasonal variation in chlorophyll-a concentration (μg Chl L^{-1}) in the Menai Strait between January 1996 and December 1998.

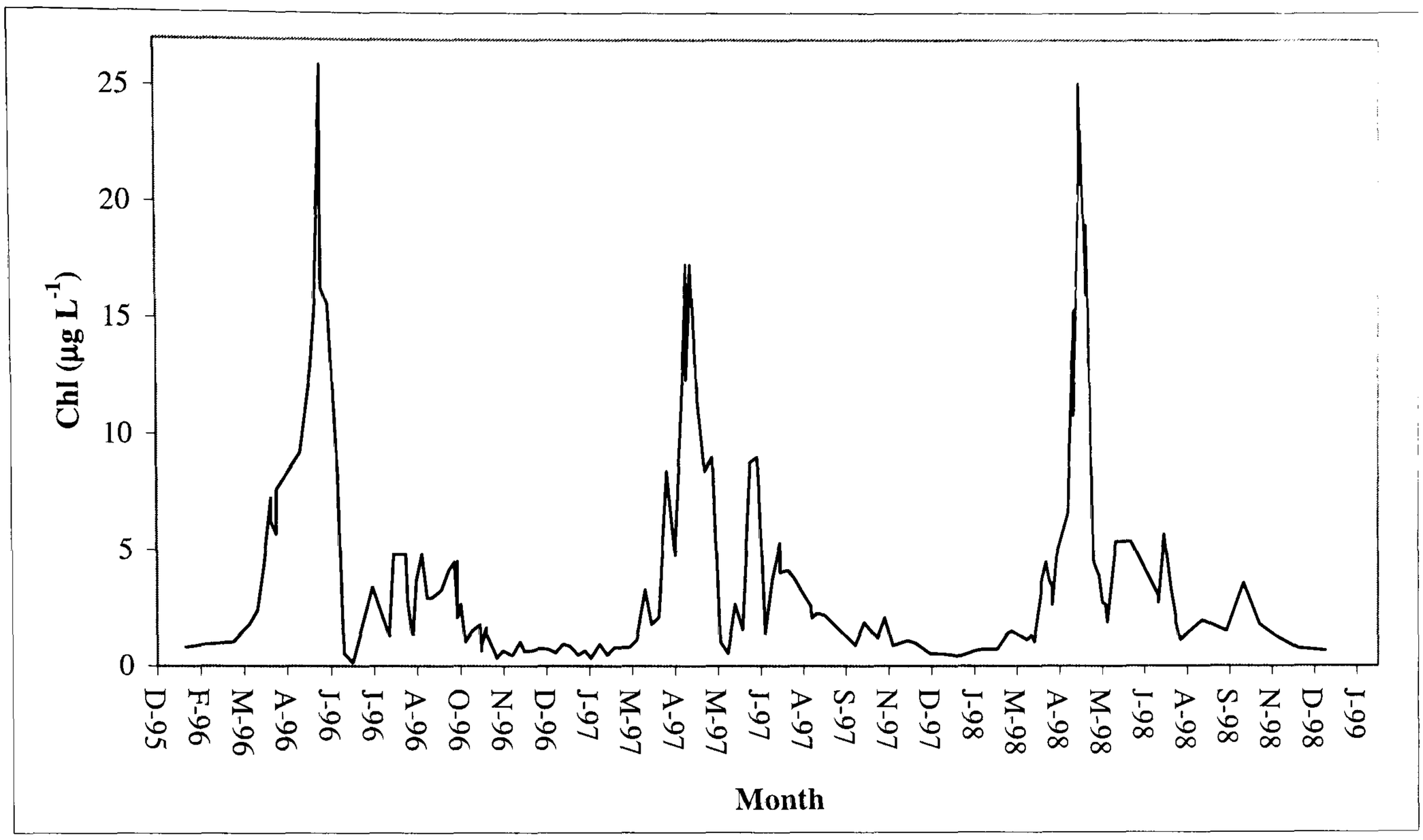
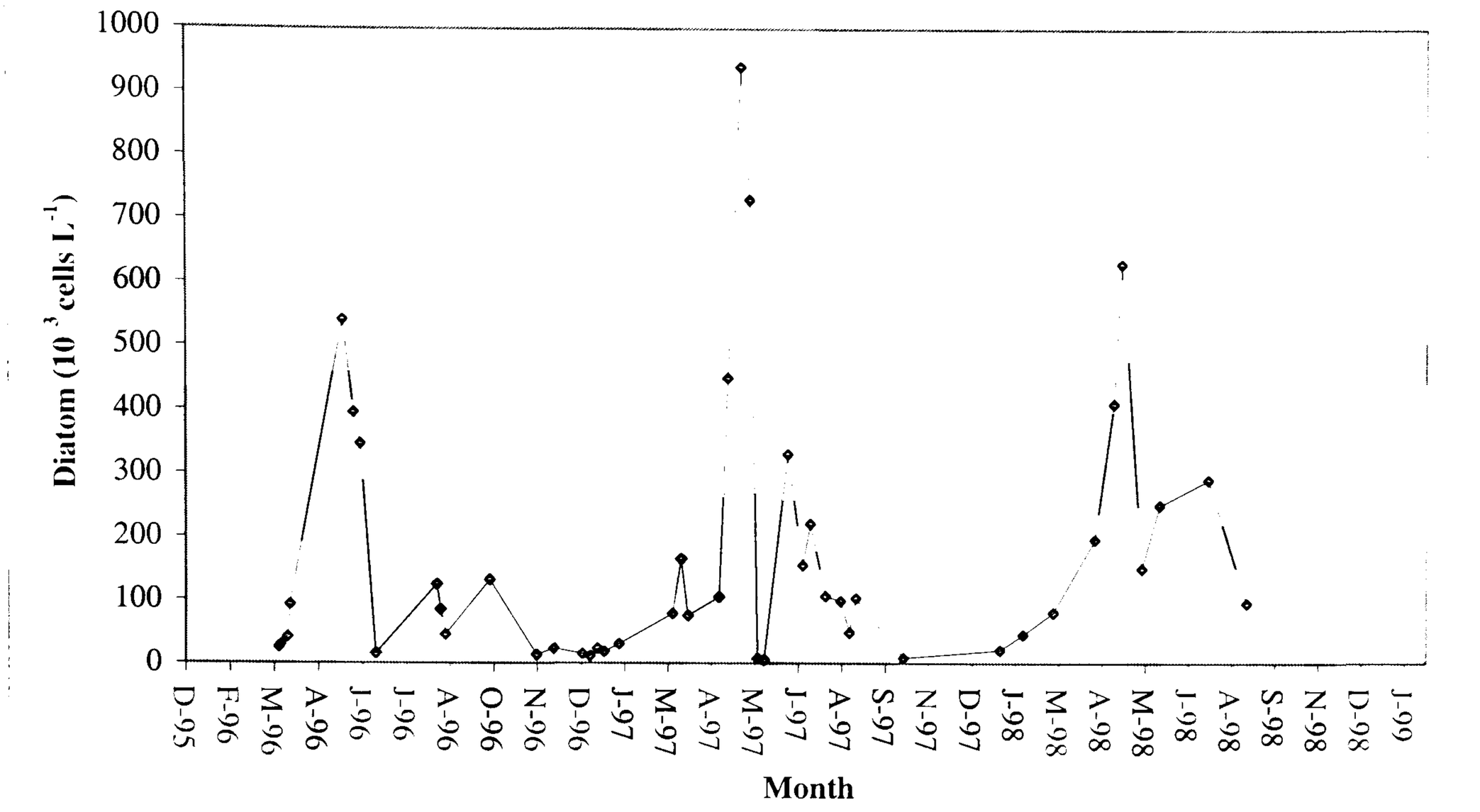


Figure 3.4 shows the seasonal variation in diatom abundance (x 10^3 cells L^{-1}) recorded in the Menai Strait between 1996 and 1998. The timing in the seasonal fluctuation of diatom abundance closely mirrored the variation in Chl concentration (Figure 3.4). The higher diatom abundance measured in spring 1997 as compared to spring 1996 and 1998 was the result of a larger bloom of *Rhizosolenia delicatula.*

In all the 3 years of study, a series of less conspicuous summer and autumn blooms developed with chlorophyll-a concentrations of ~3-8 μg Chl L^{-1}. The first summer bloom on July was usually dominated by *Leptocylindrus danicus*, followed by other monospecific diatom blooms of *Rhizosolenia styliformis* and *Guinardia flaccida.* The order of succession during the summer varied, however, between years. For instance, although *Leptocylindrus* was recorded blooming both in 1996 and 1997, in July just after the *Phaeocystis-Rhizosolenia* decrease, whereas in 1998 it was preceded by a mixed diatom bloom dominated by *Guinardia sp*. During autumn 1996-98 between September and November *Phaeocystis sp.* reappeared giving rise to a mixed flagellate-diatom bloom, smaller than the spring one, dominated by a variety of large diatoms like *Biddulphia sp.* and *Coscinodiscus sp.*

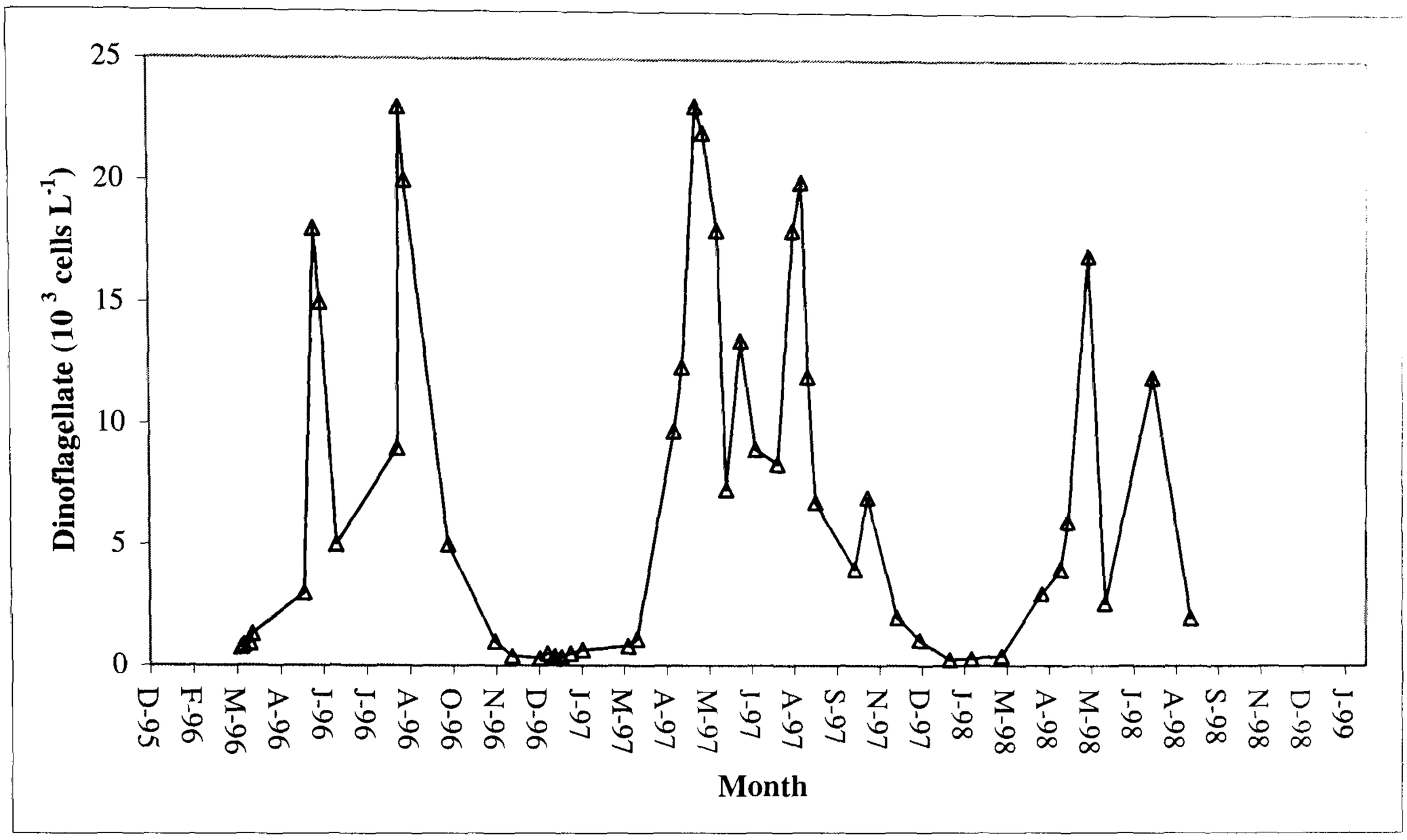
Figure 3.4: Seasonal variation in diatom abundance (x 10^3 cells L^{-1}) in the Menai Strait between January 1996 and December 1998.



The timing of occurrence of the 1996 spring bloom differed from that measured in 1997 and 1998. The initial Chl increase from the winter minima took place at the end of March for all the 3 years. While this initial increase continued during 1997 and 1998 developing into the spring bloom, in 1996 it slowed down so that the bloom occurred ~1 month later than in the following two years. The 1996 shift in the phytoplankton bloom did not affect the timing of the following summer and autumn blooms in respect to those measured in 1997 and 1998.

Figure 3.5 shows the seasonal variation in dinoflagellate abundance (x10^3 cells L^{-1}) recorded in the Menai Strait between 1996 and 1998. The dinoflagellates, started increasing in abundance just after the spring bloom with *Noctiluca scintillans* and *Gymnodinium sp.* blooming extensively between May and July. At this time dinoflagellate standing stock, excluding *N. scintillans*, varied between 17-23 x 10^3 cells L^{-1} or ~ 43-60 µg-C L^{-1}. Dinoflagellate belonging to the genus *Gymnodinium sp.*, *Peridinium sp. Protoperidinium sp.*, *Dinophysis sp.* and the species *Prorocentrum micans* gave rise to summer blooms of ~12 -23 x 10^3 cells L^{-1} corresponding to between ~ 16 - 59 µg-C L^{-1}. The dinoflagellates autumn population was dominated by several large species including *Ceratium furca*, *C. longipes* and *C. fusus*.

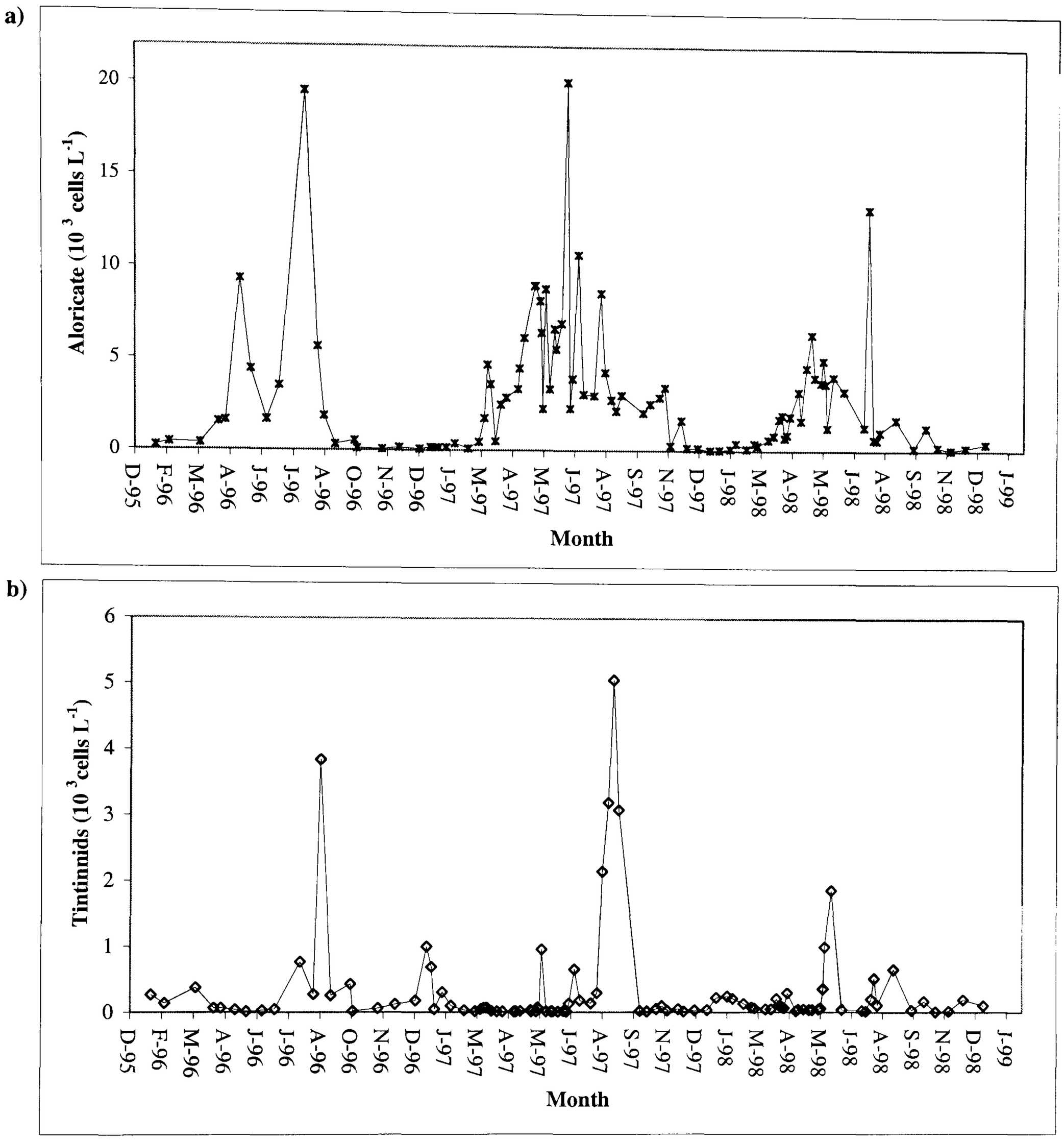
Figure 3.5: Seasonal variation in dinoflagellate abundance (x 10^3 cells L^{-1}) in the Menai Strait between January 1996 and December 1998.



The changes in abundance for aloricate and loricate ciliates measured in the present study are shown in Figure 3.6. As for the Chl and the other microplankton groups the ciliates living in the Menai Strait followed a consistent seasonal trend, although, the timing of occurrence, the presence of certain species and the ciliate standing stock varied between years.

The aloricate ciliates were more abundant between spring and mid summer giving rise to 2-3 distinct peaks of abundance, although, other minor increases took place during the rest of the year. The first peak (~ 4-8 x 10^3 cells L^{-1}) coincided with the spring phytoplankton bloom and was due to a mixed oligotrich community. The estimated spring ciliate increase recorded in 1996 (~10 µg-C L^{-1}) was smaller than in 1997 (~13 µg-C L^{-1}) and 1998 (~18 µg-C L^{-1}).

Figure 3.6: Seasonal variation in a) aloricate and b) tintinnid ciliates abundance (cells L^{-1}) in the Menai Strait between January 1996 and December 1998.



The annual aloricate maxima (~20 x 10^3 cells L^{-1}) took place in June during 1997-98 and in July in 1996. The ciliate standing stock measured during the ciliate annual maxima was greater in 1996 (~ 61 µg-C L^{-1}) than that recorded in 1997 (~ 41 µg-C L^{-1}) and almost double than that in 1998 (~34 µg-C L^{-1}). In 1996 and 1997 this bloom consisted of a mixed ciliate community dominated by the autotrophic species *Mesodinium rubrum* (Lindholm, 1985) and of the large mixotrophic ciliate *Loboea strobila* (Putt, 1990). During 1998, on the other hand, the maximum annual increase consisted of a mixed ciliated community dominated by large ciliate cells belonging to

the genus *Lohmaniella.* The 1998 *Mesodinium-Loboea* maximum increase occurred during a third biomass peak. Unlike the previous two years the *Mesodinium-Loboea* increase was outnumbered by a mixed community of small oligotrichs (~15-30 μm). In 1996 and 1997, during the *Mesodinium-Loboea* maximum the ciliate assemblage was always numerically dominated by *Mesodinium* (~ 2-15 x 10^3 cells L^{-1}) although *Loboea* (~ 2-4 x 10^3 cells L^{-1}) accounted for the majority of the standing stock representing up to ~ 65 % of the total ciliate carbon. Large predatory ciliates like *Didinium sp.* and *Askenasia sp* also appeared in summer during ciliate blooms. Other minor mixed and mono-specific ciliate peaks occurred during late summer and autumn but these never developed into the large blooms encountered in spring.

The Tintinnid seasonal cycle observed during the current study was usually characterised by 3 main peaks of abundance. The first and smaller one which occurred in winter, between January and March 1996-98, was initially dominated by *Tintinnopsis lobiancoi* (~1 x 10^3 cells L^{-1}) and followed by a mixed community of *Tintinnopsis sp..* The second increase, in July, mainly consisted of a monospecific bloom of *Helicostomella subulata* (~2 x 10^3 cells L^{-1}) which was very marked in 1997 and 1998 but not in 1996. During its peak of abundance *H. subulata* was observed to produce resting cysts which in 1998 accounted for up to 5.3 % of the active population of this species. Numerous empty loricas of *H. subulata* were also found at this time which accounted for ~ 25 % of the species active population. Other less abundant but large species recorded in the Menai Strait in summer were *Tintinnopsis campanula* and *Favella herenbergii.* A third and largest tintinnid increase (~5 x 10^3 cells L^{-1}) due to a mixed bloom dominated by very small (lorica size ~14 x 31 μm) unidentified species measured in late summer 1996 and 1997 but not in 1998.

3.2.3 Relationship between microplankton, chlorophyll-a and temperature

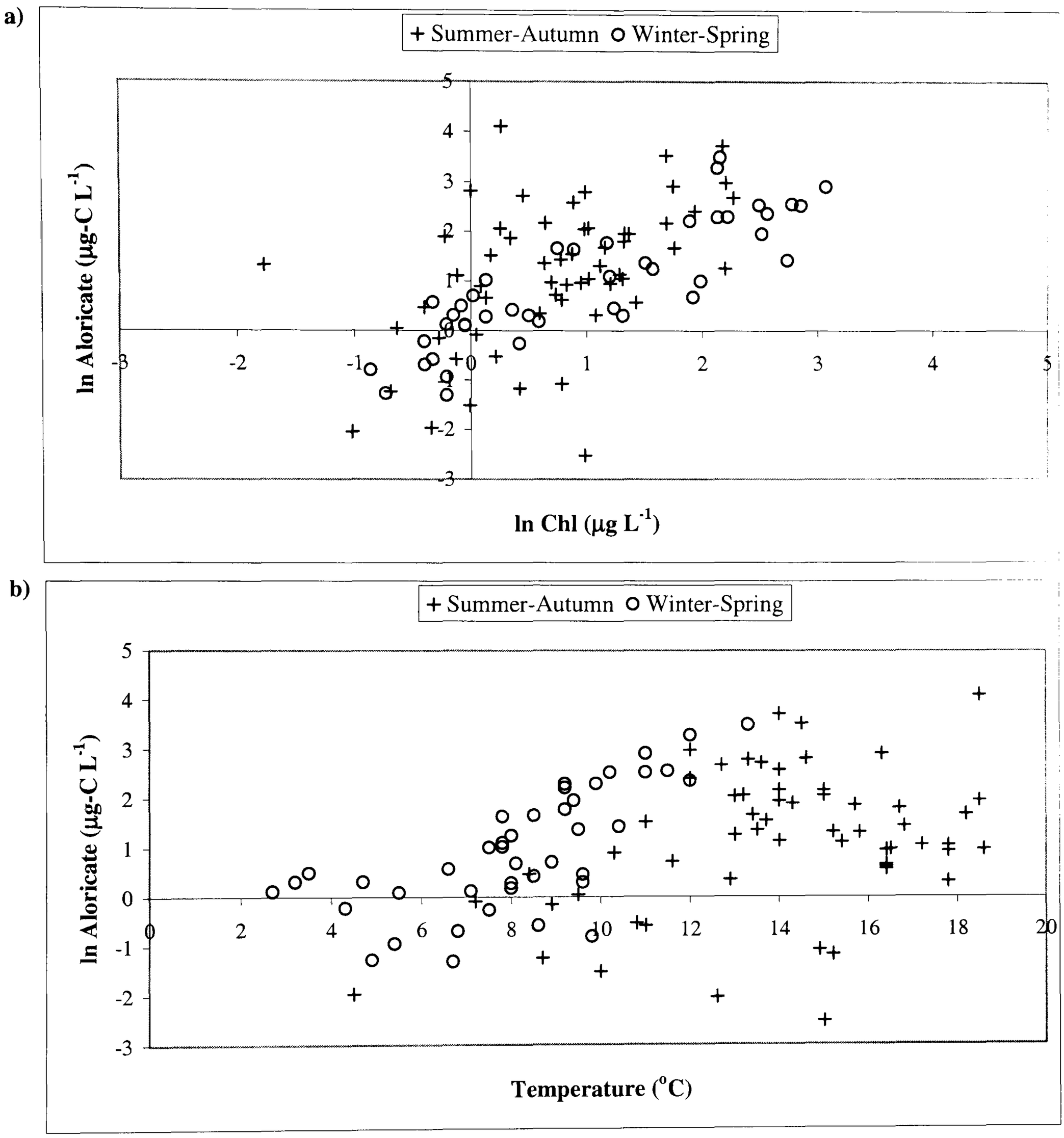
The seasonal distribution of the aloricate and loricate ciliate was quite different. While the heterotrophic aloricate ciliates were more abundant in spring early-summer increasing when Chl increased in the field, the tintinnids were usually more abundant in winter and late-summer when the Chl concentration was low (Chla < 1 μg L^{-1}). As a result, the aloricate ciliates were positively correlated to Chl for all the years and this correlation was stronger between winter and spring up to the maximum Chl concentration than for the rest of the year (Table 3.1).

Table 3.1: Correlation between logarithmically transformed aloricate and tintinnids ciliate biomass (ln µg-C L^{-1}) and Chlorophyll-a (ln µg Chl L^{-1}) or temperature (°C) for the whole year and during spring (i.e. up to the Chl maximum) during 1996 and 1998 in the Menai Strait.

Variables	n	r	p
ln Aloricate vs ln Chl	98	0.63	> 0.001
ln Aloricate vs ln Chl (spring)	38	0.87	> 0.001
ln Tintinnid vs ln Chl	98	- 0.24	0.016
ln Tintinnid vs ln Chl (spring)	38	- 0.54	> 0.001
ln Aloricate vs Temperature (spring)	38	0.64	> 0.001
ln Tintinnid vs Temperature (spring)	38	-0.48	0.006

Figure 3.7 shows the relationship between logarithmically transformed aloricate carbon (ln µg-C L^{-1}), Chl (ln µg Chl L^{-1}, Figure 3.7, a) and temperature (°C, Figure 3.7, b) between 1996 and 1998. Despite the logarithmic transformation the relationship between aloricate biomass and Chl was not linear increasing at a faster rate between ~ 0.5 µg Chl L^{-1} and ~ 2.7 µg Chl L^{-1} and at a lower rate thereafter. Figures 3.7 a) and b) show that aloricate ciliate abundance increased from low winter concentrations of ~ 0.5 - 2 µg-C L^{-1} at Chl concentrations above 1-2 µg Chl L^{-1} and temperature beyond ~ 7.5 °C. The pattern in ciliate variation observed during winter 1998 when spring like temperatures between 7 °C and 9 °C were recorded suggests that ciliate growth at this time of the year was limited (Figure 3.7, b). The tintinnids, however, were only poorly or negatively related to Chl concentration and negatively correlated with temperature in spring (Table 3.1).

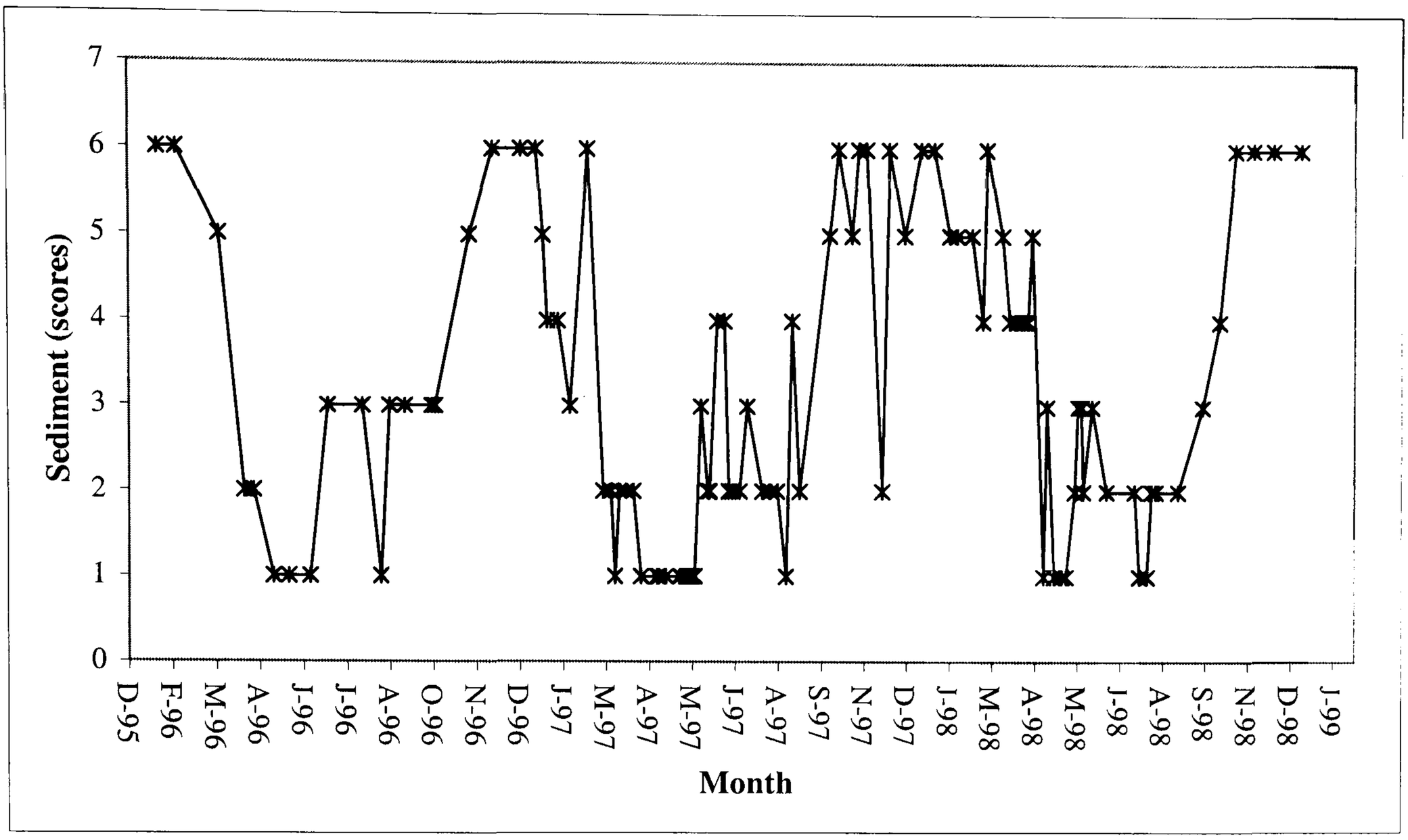
Figure 3.7: Scatter plot of natural log of aloricate ciliate carbon (ln µg-C L^{-1}) versus a) natural log of Chl (ln µg Chl L^{-1}) and b) temperature (°C) measured in the Menai Strait between 1996 and 1998.



3.2.4 Total suspended particulate matter

The SPM load in the water column followed a similar seasonal trend in all the three years studied (Figure 3.8).

Figure 3.8: Seasonal variation in suspended particulate matter (SPM, scores) in the Menai Strait water between January 1996 and December 1998.



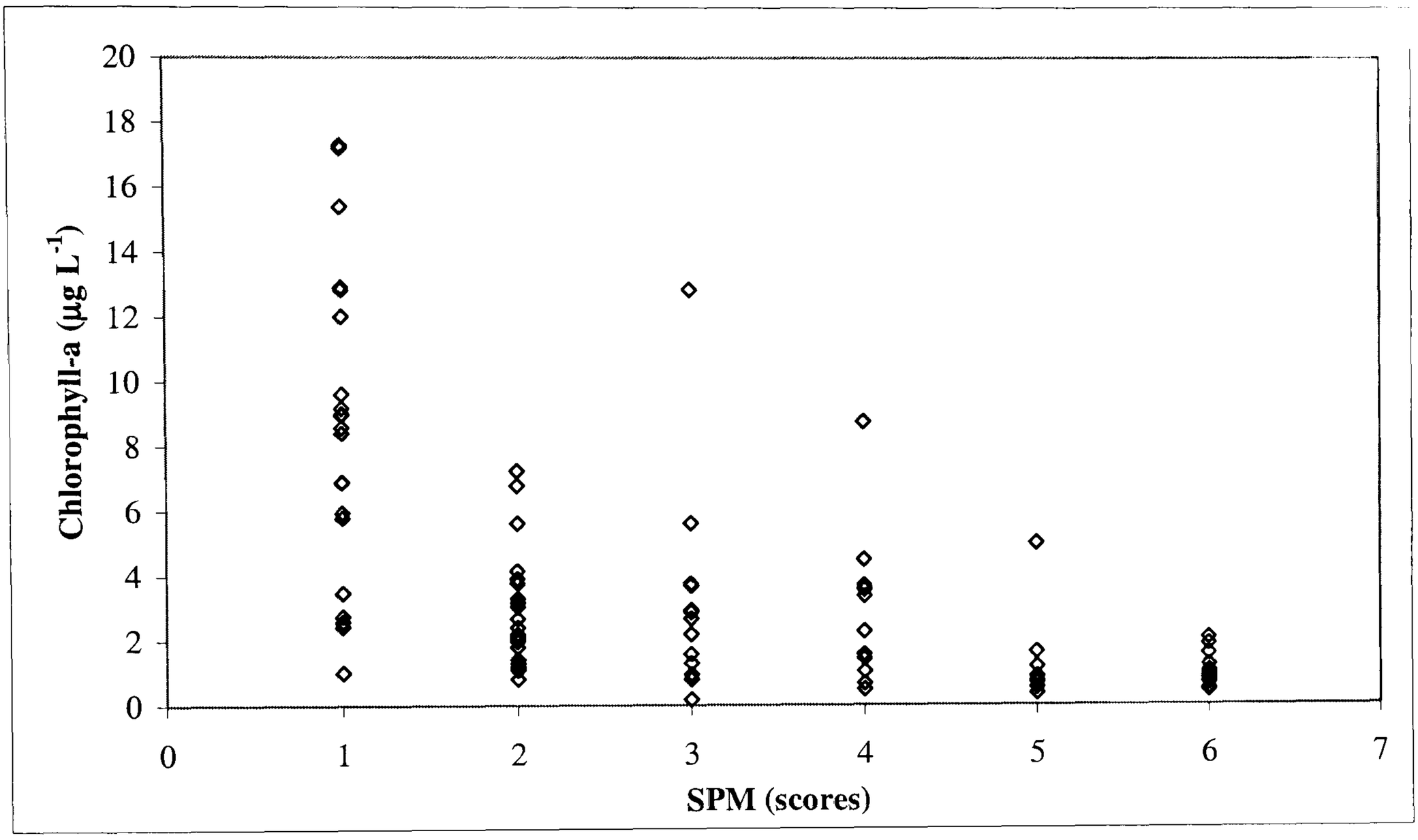
Seasonal high to maximum score values corresponding to between 5 and 50 mg L^{-1} were recorded during autumn-winter months, minima to low values ranging between 0.5 to 3 mg L^{-1} in late spring-early summer and intermediate values between 3-5 mg L^{-1} observed in late summer (Kratzer *et al.*, 2000). Increase in SPM in the water could be often noticed when weather conditions deteriorated as during strong wind and storms. So, although, sediment load was highest in autumn and winter relatively high amounts of sediment in the water could be also found in spring and summer depending on the prevailing weather conditions.

As shown in Figure 3.8, however, a difference in the timing of SPM concentration, particularly in spring, was evident between years. During 1996 SPM concentrations ~ 7-5 mg L^{-1} (Kratzer pers. comm) persisted until late spring up to the end of April. On the other hand, during 1997 and 1998 a decline in the SPM concentration occurred earlier in the year around the beginning of April (Figure 3.8).

Between 1996-98, the spring phytoplankton bloom was observed to occur always during protracted good weather conditions corresponding to minimal SPM concentration while low Chl in the field was associated with high SPM. Increase in Chl standing stock leading to the spring blooms only occurred when sediments load in the water was at its annual *minimum* (Figure 3.3 and Figure 3.8). A significant negative

correlation (Spearman, d.f. = 98; ρ = - 0.68; $p < 0.001$) was found between Chl concentration and SPM for the pooled 1996-98 data (Figure 3.9).

Figure 3.9: Scatter plot of Chl (µg Chl L^{-1}) and SPM (score) measured in the Menai Strait between 1996 and 1998 showing a negative relationship (Spearman rank correlation, d.f.= 98; ρ = - 0.68 ; $p < 0.001$).



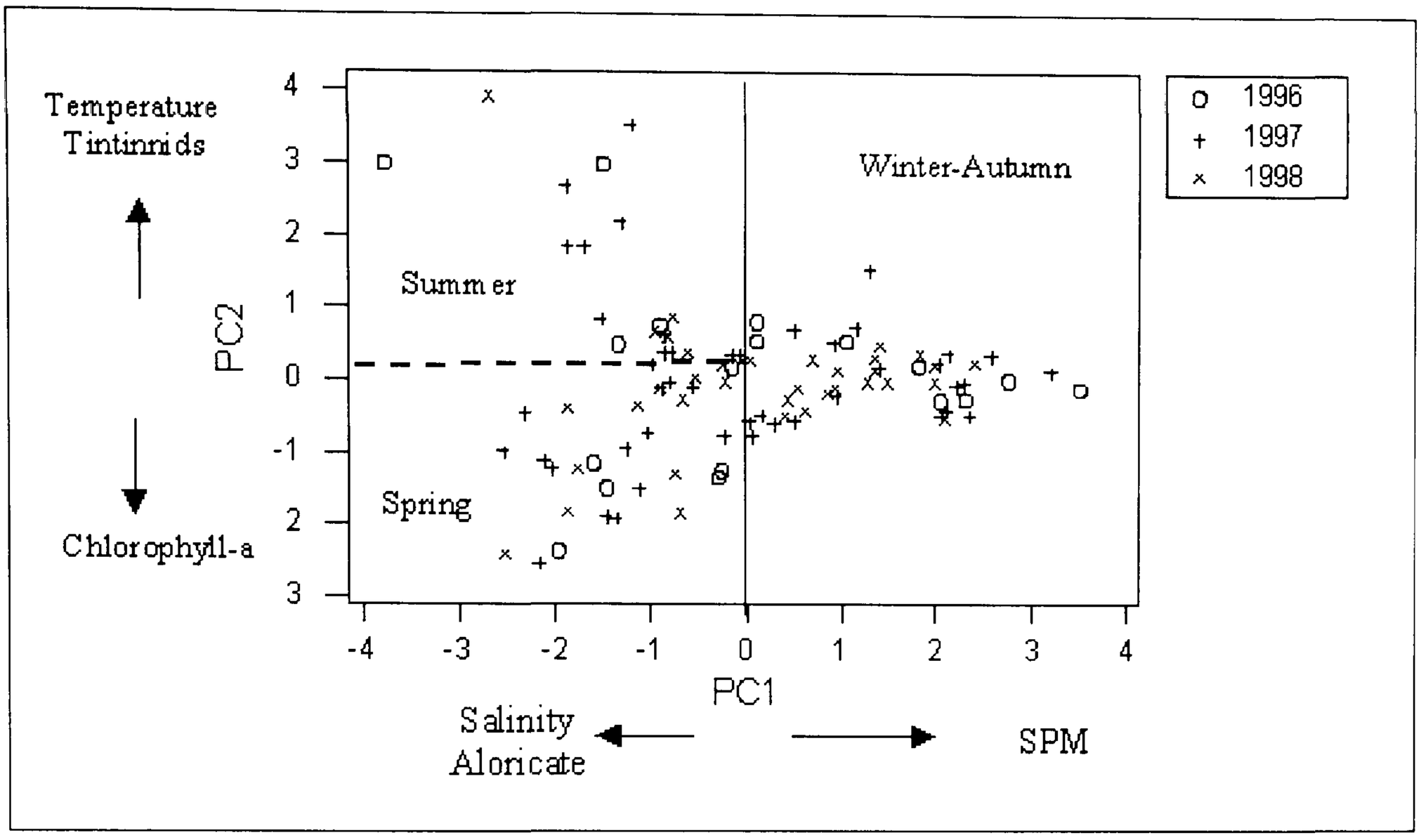
On the other hand, sea temperature was found to be negatively correlated to SPM (Spearman rank correlation, d.f.= 98; ρ = - 0.39 ; $p < 0.001$).

3.2.5 Overview and relationship among the measured variables

The information contained in the variables described in this chapter were analysed and condensed using a multiple comparison technique, the Principal Component Analysis (PCA). In the PCA the variables were compared by treating the days as replicates to avoid the effect of the temporal scale.

The first three principal components accounted for 77 % of the variability within the data set. An ordination of PC1 and PC2 is presented in Figure 3.10.

Figure 3.10: Ordination of the scores of variables derived from a Principal Component Analysis (PCA) of biotic and abiotic variables measured between 1996 (o), 1997 (+) and 1998 (x) in the Menai Strait. Each variable consists of a total number of 100 observations.



The main variables contributing to PC1 were SPM which contrasted with salinity and aloricate ciliates. On the other hand, the main variables contributing to PC2 were temperature and tintinnid ciliates contrasting with Chl.

Chlorophyll-a, aloricate and Tintinnid ciliates, which were high in spring and summer, were clearly separated from sediment loading which were high in autumn and winter. The tintinnid standing stock was separated from high concentration of Chl and aloricate ciliates but associated with high temperature. In the current study, the annual maximum standing stock of Tintinnids was, in fact, measured between July and August when temperature and Chl reached their maximum and minimum values respectively (Figure 3.1, Figure 3.3 and Figure 3.6 (b)).

As a result the PCA graph clearly shows that the data are divided in three distinct portions, one on the left and two on the upper and lower right (Figure 3.10). The data on the right-hand side of the graph correspond to the winter-autumn and are the least variable. On the other hand, the information in the left-hand side of the graph corresponding to the spring (lower group) and to summer-autumn (upper group) respectively is characterised by a wider spread (Figure 3.10).

There was a consistent similarity in the variables over the 1996-1998 period as suggested by the extensive overlapping of the symbols representing the different years.

3.3 Discussion

The pattern of the physical and biological parameters considered in the present study followed a seasonal cycle typical of mid latitude coastal waters (Tett, 1987).

Within their annual cycle, however, both the physical and the biological variables measured showed interannual variation in magnitude and/or timing of occurrence. For instance, the temperature profile recorded between January and April varied between the 3 years with 1996 being the coldest and 1998 the warmest. The long term positive values recorded for the NAO-index during the 1990's became negative in 1996 and since then the NAO-index has risen to reach a positive value in 1998 and 1999 (Karl *et al.*, 2000). The low water temperature measured in 1996, one of the coldest year ever recorded for northern Europe, corresponded to a NAO-index of –3.78, while the successive two years where milder with a progressive increase in the NAO-index to –0.20 and 0.72 for 1997 and 1998 respectively (Hurrell, 1995; Karl *et al.*, 2000). Thus, the mean winter water temperatures measured between 1996 and 1998, followed the shift in the NAO-index measured over the same period. It is worth noting that, the 3 years examined had a very different pattern in temperature changes during the first part of the year which is the time preceding the phytoplankton and the zooplankton spring increase. The trends for 1996-1998, however, are within the ranges reported for the Menai Strait by previous investigators (Reviewed by Rodriguez, 1998).

The pattern observed in the temperature was similar to the trend in salinity, although, more complex and less clear-cut. The lowest salinity was usually measured in winter and autumn while the highest occurred during spring and summer months. The pattern persisted through 1996 and 1997 despite the salinity drop in June 1997, corresponding to rainfall at Valley (i.e. TMP-V therein) of 102 mm which was recorded as the wettest of the century (Royal Meteorological Society, 1997). The persistent high salinity measured throughout the winter 98' and the drop in salinity in April 98' also seemed to follow the temperature recorded in that period. However, the consistent drop in salinity to minimum level in November, which is usually the wettest month of the year, observed in 1996 and 1997 but not in 1998 does not have an easy explanation since both October and November 1998 were even wetter months with a TMP-V of 121 mm and 126 mm respectively. The salinity measured over the period of study was similar to that reported for the Menai Strait in recent years (Hidayat, 1995; Kratzer *et al.*, 2000).

The delay of 1 month in the 1996 spring phytoplankton peak as compared to those measured in 1997 and 1998 is also noteworthy. The timing and the magnitude of the bloom occurrence in the Menai Strait has proven very variable in the historical data collection for the Menai Strait with Chl maximum records varying between early April and June (Haq, 1960; Jones & Spencer, 1970; Blight *et al.*, 1995). This Chl maximum has been attributed to the formidable increase of *Phaeocystis sp.* which during bloom time, may represent as much as 95% of the total phytoplankton biomass (Spencer, 1965; Jones & Spencer, 1970; Al-Hasan *et al.*, 1975; Lennox, 1979).

In the current study, increase in *Phaeocystis sp.* cells and the first appearance of the colonies were recorded between mid March-April during the initial spring diatom bloom for all 3 years. The fact that the initial *Phaeocystis* increase developed during 1997 and 1998 into the mixed *Rhizosolenia-Phaeocystis* maximum at the beginning of May but was delayed to the end of May in 1996 requires some consideration. The timing in the Chla increase corresponds to the rise in net community production conducted during the PRIME campaign (T. Bentley pers. comm.) by using the oxygen titration method (Gaarder & Gran, 1927; Williams & Jenkinson, 1982). In 1996 the net community production increased at the beginning of April to 18.5 $\mu M\text{-}O_2\ day^{-1}$ from a low winter value of 1.7 $\mu M\text{-}O_2\ day^{-1}$. After that, the net community production decreased to 6.4 $\mu M\text{-}O_2\ day^{-1}$ by mid April to increase again steadily between the end of April reaching the maximum value of 41.2 $\mu M\text{-}O_2\ day^{-1}$ for 1996 at the end of May, coincidentally with the Chl maximum recorded in the current study. Similarly in 1997 a high peak in net primary production of 25.5 $\mu M\text{-}O_2\ day^{-1}$ was recorded at the same time of the Chl maximum reported by the current study. Thus, two independent techniques provided evidence of accurate timing for the annual maximum of primary production measured during 1996 and 1997.

The appearance of the spring bloom in the Menai Strait usually takes place after a diatom increase, when nutrient concentrations (i.e. nitrate & silicate) have decreased to minimum annual values (Ewins & Spencer, 1967). Other physical factors, however, like wind intensity and direction together with general meteorological conditions (Spencer, 1987) and the magnitude of the temperature during winter and early spring (Jones & Haq, 1963) are thought to be influential. Unlike the spring 1997-98, during 1996 the second part of April and the first 2 weeks of May were characterised by very unstable cold weather conditions and by unusually strong wind (Royal Meteorological Society, 1996). A combination of strong persistent wind and the occurrence of a

maximum spring tide during the second part of April were probably the cause of the persistent high SPM recorded over this time.

An inverse relationship was found in this study between SPM and Chl. Several authors (Joint & Pomeroy, 1981; Gowen *et al.*, 1995) have reported that strong tidal mixing and turbidity in near-shore waters and estuaries may delay and/or prevent the start of the spring bloom, due to light limitation, so that nutrient enrichment has little effect in promoting algal growth. Blight (1996) reported that during spring 1994, most of the detritus had largely disappeared from the water column by day 123 and *Phaeocystis* bladders were observed for the first time on day 129 increasing thereafter to peak on day 145. In addition, Jones & Spencer, (1970) speculated that the turbidity of the water could be one of the factors responsible for the delay of the spring phytoplankton bloom they observed in the Menai Strait in 1962.

Consultation of the 1996-98 tide tables and the water pressure fluctuations recorded by the continuously recording CTD revealed that the peak of phytoplankton bloom consistently occurred at the time when the amplitude during the tidal cycle was at its minimum (i.e. neap tide) in all the 3 years studied. In 1996, *Rhizosolenia* reached its maximum abundance during the second week of May (Julian day 128) coincidentally with a minimum neap tide. The abundance maximum peak bloom dominated by *Phaeocystis*, on the other hand, only occurred at day 148 again during the neap tide, when the SPM in the water column reached its annual minimum. During the neap tide cycle obviously the energy of the water system is lower than during the spring tidal cycle conferring higher stability and lower SPM to the water column. Given the shallowness of the Menai Strait (i.e maximum depth 20 m), it is possible that the high increase in sediments in the water column in 1996 may have delayed the development of the *Phaeocystis sp.* by increasing water turbidity (so decreasing the light penetration in the water column). The importance of the interplay between weather conditions and the tidal rhythm in controlling the timing of species succession and the development of the spring bloom is apparent.

Jones and Haq, (1963) have observed the existence of a positive relationship between the onset of *Phaeocystis sp.* and the temperature of the water during the period prior the spring phytoplankton bloom outburst. Similarly to the present study, Buchan *et al.*, (1967) found a significant negative relationship between suspended sediments and temperature in the Menai Strait. It seems likely, therefore, that the protracted low temperature measured during 1996 was correlated to high sediment in the water and

consequently to the later appearance of the phytoplankton bloom in that year. Thus, it can be concluded that, the 1996 bloom peak was probably delayed by meteorological and physical parameters other than temperature but correlated with it.

As far as the variation of the magnitude of the Chl peak is concerned very high values ranging from 17 to 26 μg Chl L^{-1} were recorded during the spring blooms which occurred between 1996 and 1998. These values, are much higher than those measured previously in the Menai Strait (Jones and Spencer, 1970; Tyler, 1977; Blight *et al.*, 1995). Gowen *et al.*, (2000) have reported Chl concentrations up to 44 μg Chl L^{-1} during the 1997 spring bloom in the Liverpool Bay, which is the main supplier to the Menai Strait. Looking at the Chl values measured in the Menai Strait over the last 40 years it is apparent that there has been a general increasing trend in the Chl from the early 60's to the present. The early measurements ranged between ~7-11 μg Chl L^{-1} in the 1960' (Jones & Spencer, 1970) while values as high as ~15 μg Chl L^{-1} were reported in the early to mid 1990's (Blight, 1996; Rodriguez, 1998) and between ~17 to 25 μg Chl L^{-1} by the present study and by Kratzer (pers. comm). Reid *et al.*, (1998) have reported an increasing trend in the Chl since the 1940's for the North Sea and in the Atlantic between 52° and 58° N, which they related to the positive trend in the NAO-index. The similarity observed in the temperature and Chl trends between the Menai Strait and the North Atlantic (Reid *et al.*, 1998) is noteworthy and warrant further investigation. The increase in Chl during the spring phytoplankton bloom over the past 40 years appears to be related mainly to the progressive increase of *Phaeocystis sp.* which is not paralleled by a similar increase in nutrient concentration in the water (Menai Strait data base). On the other hand, the pattern of abundance and composition in other phytoplankton species described in the present study is overall similar to what reported by other authors (Haq, 1960; Jones & Spencer, 1970; Blight, 1996).

The present investigation has also identified a distinct year to year variation in the standing stock of ciliates living in the Menai Strait. The initial spring increase in aloricate ciliates, observed in this study, between 1996 and 1998, closely followed the field spring bloom Chl increase indicating a close coupling with the autotrophs. A significant correlation between ciliates and phytoplankton has already been reported by several authors for the Menai Strait (Blight *et al.*, 1995) and elsewhere (Smetacek, 1981).

The second ciliate increase corresponding to the ciliate annual maximum (both numerically and in term of biomass), however, was de-coupled from the Chl standing

stock and usually coincided with the increase of both the heterotrophic and the mixotrophic ciliates *Mesodinium* and *Loboea strobila*. Blight *et al.* (1995) reported the occurrence of three distinct peaks of ciliates following the 3 peaks of Chl increase recorded between March and June 1994 in the Menai Strait. In Blight's *et al.*, (1995) study, the third and largest peak (~10 x 10^4 cells L^{-1}), made of predominantly unidentified aloricate oligotrichs ciliates 20 μm in diameter, took place 1 week after the *Phaeocystis sp.* bloom peak indicating, according to these authors, a looser coupling between the autotrophs and the micro-heterothrophs. In this study about 50 % of the increase in ciliate biomass after the bloom in 1997 was due to the increase of the mixotrophic species *L. strobila* and the small autotrophic ciliate *Mesodinium rubrum*. It is possible, therefore, that the lack of correlation between the ciliate peak and the Chl reported by Blight *et al.* (1995) was due to the potential autotrophic nature of the ciliate species they measured.

The maximum annual ciliate abundance was recorded in this study always between June and July for all the 3 years studied. While in 1996 and 1997 maximum abundance (~20 x 10^3 cells L^{-1}) was associated with the *Mesodinium-Loboea* increase, in 1998 this was due to the increase of mixed aloricate ciliates *Strombidium sp. M. rubrum* forms extensive blooms in eutrophic coastal waters (Lindholm, 1985). It is a very ubiquitous organism with a remarkable tolerance to a wide range of temperature of 0-24 °C and salinity 3 to 36.9 p.p.t. (Taylor *et al.*, 1971; Lindholm, 1985). Thus, the fact that in 1998 there was no clear development of a *Mesodinium-Loboea* bloom cannot be easily explained by physico-chemical factors.

In general, the late summer aloricate ciliate population density recorded over all the three years, was lower than that measured during the phytoplankton spring bloom. Smetacek (1981) has argued that the decline in ciliate numbers observed in late spring and their low abundance during summer in the Kiel Bight could not be attributed to change in the amount of available food to the ciliates but must be the results of predation. Although, in the present study, the bacterioplankton and flagellates were not numerically quantified a large number of these cells were observed throughout the summer indicating that ciliates may not be food limited.

In the current study, despite being less common than the aloricate ciliates, the tintinnid populations showed appreciable oscillation in their number during the year, with increases in abundance in early winter and mid to late summer. The seasonal study on microzooplankton conducted by Blight *et al.*, (1995) was restricted to between

March and June 1994 and it did not distinguish between aloricate and loricate ciliates. Thus, it is not clear whether aloricate and loricate ciliates were merged in the same group by these authors or if they had missed the major tintinnid increases due to their low sampling frequency and limited survey.

The highest number of tintinnids found in summer 1996 and 1998 in the Menai Strait ranged between 4 to 5 x 10^3 cells L^{-1}. These values are higher than the <1 cell ml^{-1} reported by Montagnes *et al.*, (1999) and Edwards and Burkill, (1995) between April and June and the 1.5 x 10^3 L^{-1} measured in August 1988 by Graziano, (1989) for the eastern part of the Irish Sea.

With the exception of the July bloom of *Helicostomella subulata* the occurrence of the aloricate and loricate ciliates seemed mutually exclusive, with the former blooming in spring and at the start of the summer and the latter showing maximum abundance in late summer and winter when Chl was low. Similarly, Graziano (1989) reported maximum abundance of tintinnids in the Irish Sea during summer months when Chl was low and lowest during late spring and early summer when Chl reached its highest concentration. The importance of physical factors in regulating tintinnid dynamics is still poorly understood. A numbers of authors have observed maximum abundance to be associated with high temperature (Verity, 1987). Other authors (Sanders, 1987) have pointed out that temperature may not directly cause change in tintinnid abundance, since other parameters such as day length, food supply and predator abundance also increase in spring and summer. During late summer 1998 the tintinnid bloom was 6 to 10 times lower than those recorded for the same time of the year in 1996 and 1997. Since sampling frequency in 1998 was similar or higher than in the previous two years the reason for the lower tintinnid abundance measured in 1998 is not clear at the present and requires further consideration. Despite some inter-annual differences a very similar ciliate seasonal pattern occurred in the three successive years, suggesting that it was probably not due to random fluctuations but may represent an established temporal sequence between different populations.

Chapter 4

Egg production of *Temora longicornis* in the Menai Strait

4.1 Introduction

In nature, marine copepod egg production rate (EPR) is notoriously variable, changing widely both on a temporal and on a spatial scale (Ambler, 1985; Ianora *et al.*, 1992; Ianora & Poulet, 1993; Laabir *et al.*, 1995).

Copepod EPR is considered an important index of copepod productivity and has been routinely used in field-work studies (Hay *et al.*, 1991; Poulet *et al.*, 1995). Knowledge of factors determining the seasonal and inter-annual variability of copepod EPR is of growing interest since copepod eggs and nauplii are the main food source for many first-feeding fish larvae and consequently play a key role in determining fish recruitment (Runge, 1988; Cushing, 1995). Despite its importance, elucidating the causes of the variability and what limits population growth in marine copepods still represent key challenges to ecologists. A basic ecological principle is that populations have the potential for exponential growth and yet under most natural conditions maximum population growth rates in copepods are seldom achieved (Peterson & Kimmerer, 1994). Clearly any attempt to explain the population dynamics of copepods and thereby commercial fisheries' recruitment must start exploring what causes EPR variability (Poulet *et al.*, 1995; Ban *et al.*, 2000).

Although, laboratory experiments have shown that EPR depends on food concentration (Runge, 1985) and temperature (Uye, 1981), field studies have yielded contradictory results (Gomez-Gutierrez & Peterson, 1999; Ban *et al.*, 2000). In this respect, several investigations have suggested the importance of hydrographic (Gomez-Gutierrez & Peterson, 1999), physiological (Rey *et al.*, 1999) and methodological (Ohman *et al.*, 1996) factors in determining the observed variability in copepod fecundity.

The potential determinants of copepod EPR and egg survival cannot usually be easily and clearly identified from field studies as they are often significantly inter-correlated (Prestidge *et al.*, 1995; Saiz *et al.*, 1997). Laboratory and field studies have indicated that copepod fecundity is generally related to temperature and food supply (Kiorboe *et al.*, 1985; Runge, 1988; Peterson & Kimmerer, 1994), but the relative importance of these two parameters remains controversial. Huntley and Lopez, (1992)

have argued that copepod somatic growth and EPR in the field is not food limited and can be explained by temperature alone. On the other hand, there is mounting evidence from marine and freshwater environments which suggest that growth in copepods is primarily governed by the availability of the food sources (Bautista *et al.*, 1994; Richardson & Verheye, 1998; Koski & Kuosa, 1999). In some instances, however, the large variation in EPR found in field studies often do not correlate with either temperature or chlorophyll used as a measure of the available food (Gomez-Gutierrez *et al.*, 1999).

It has already been shown that crude Chl measurement is not always a reliable indicator of food availability since copepods may select prey according to their density (Kiorboe *et al.*, 1996, Verity & Paffenhofer, 1996), quality (Hansen *et al.*, 1993), size range (Berggreen *et al.*, 1988; Hansen, 1994) and are well known to supplement a vegetarian diet with heterotrophic organisms (Kleppel, 1993; Verity & Paffenhofer, 1996). Dam & Peterson (1991) and Bautista *et al.*, (1994) comparing *T. longicornis*'s ingestion rate for different Chl size fractions, have suggested that the degree to which herbivorous coastal copepods are food-limited will depend on the food-size spectrum and the quality (Jónasdóttir, 1994; Irigoien *et al.*, 2000) of the micro-plankton assemblage.

The chemical composition of the seston, e.g. carbon, nitrogen, C:N ratio and specific unsaturated fatty acids, has also been shown to be related to copepods EPR (Ambler, 1986; Jónasdóttir *et al.*, 1995). Although, a wealth of studies in aquaculture have largely demonstrated the importance of essential dietary components like vitamins and fatty acids in promoting high EPR for many crustacean species (Kanazawa, 1979; Harrison, 1990), similar studies in marine copepods are still few and lack direct evidence (Guisande & Harris, 1995; Pond *et al.*, 1996; Kleppel & Hazzard, 2000).

Studies looking at the detrimental effect of the microplankton on copepod fecundity have recently gained impetus but have yielded contradictory results. Whereas laboratory experiments have shown (Ban *et al.*, 1997) that some species of diatoms can dramatically reduce EPR in copepod, field observations, on the other hand could not find any evidence of diatom toxicity (Niehoff *et al.*, 1999; Irigoien *et al.*, 2000).

It is well known that females within the population are not all in the same reproductive condition (i.e. pre-, post- and reproductive) and this fact can cause a bias in secondary production estimates if copepod EPR measurements are derived from incubating together groups of females (Ohman *et al.*, 1996). Incubating individual females is very important because it not only gives information on the variability in EPR among individuals and in relation to their size but it also allows the investigation of the

reproductive physiological performance of individuals within the population (Rey *et al.*, 1999). Despite evidence, not many studies, however, have investigated the proportion of females producing eggs at any one time in the field and incubation for EPR measurements are still largely carried out incubating groups of females (Kleppel & Hazzard, 2000).

More recently a number of studies have indicated that factors like turbulence may play an important role in determining variation in copepods fecundity by changing the contact rate of the suspended particles and the copepods, both increasing the suspended matter and dispersing microplankton patches (Gomez-Gutierrez *et al.*, 1999). In coastal areas suspended particulate matter (SPM) can be quite conspicuous and its suspension in the water column varies in relation to tidal range, wind strength and currents (Lindsay *et al.*, 1996; Bowers *et al.*, 1998). Although, feeding rate may increase during turbulent periods the efficiency with which captured food is converted to body tissue or eggs production has been found to decrease during high turbulence conditions (Saiz *et al.*, 1992). Despite laboratory and field evidence indicating the detrimental effects of TSPM on both copepod feeding efficiency and fecundity (Butler, 1995) for different copepod species (White & Dagg, 1989), its impact on secondary production has not yet been fully evaluated.

Inter-annual variation in the weather pattern may also have a strong influence on the copepod fecundity and secondary production (Hay, 1995; Prestidge *et al.*, 1995). Hay (1995), for instance, has recently suggested that the effect of winter conditions on the over-wintering production and survival of copepod nauplii population may be of paramount importance in determining copepod secondary production in spring and the survival of the herring larvae in the North Sea.

Studies of copepod EPR (and hatching success) in the Irish Sea are sparse and have been mainly limited to few copepod species (Kleppel *et al.*, 1991; Prestidge *et al.*, 1995). Attempts to build predictive models of EPR in the Irish Sea have been carried out but the limited data set and the use of simple crude variables like Chlorophyll-a and temperature has yielded unsatisfactory results (Prestidge *et al.*, 1995).

The aim of the present chapter was to describe the seasonal and inter-annual variation in *Temora* EPR in the Menai Strait, eastern Irish Sea, in relation to relevant biological and physical field variables.

4.2 Material and Methods

Egg production rate and hatching success was measured for *T. longicornis* and more infrequently for *C. hamatus* since these are the two most abundant species encountered in the Menai Strait over the year. With the exception of April and July 1996 (when no data were collected) the EPR of *T. longicornis* females was measured every fortnight from March to August 1996 and weekly from September 1996 to December 1998. The EPR of *C. hamatus* was measured between April-May 1997 and it was specifically intended for comparisons of hatching success with *T. longicornis.*

The female copepods were incubated for EPR estimation within a maximum of 1 hour from their collection (see Chapter 2). A number of 25 to 30 intact active female *T. longicornis* were randomly selected from the catch and individually pipetted into 250 ml crystallising dishes filled with natural seawater pre-screened to 53 μm. The dishes were kept in a temperature controlled water-bath at the Menai Strait's ambient temperature ± 0.2 °C under artificial lighting with an ambient light/dark regime. An oxygen electrode, (Logit model) was also used to regularly monitor the oxygen concentration of the seawater close to the bottom of the dishes. After 24 hours the females were gently removed from the crystallising dishes with a large bore plastic pipette and the cephalothorax length was subsequently measured with an eye-piece graticule under a dissecting microscope. The dishes were then incubated in the water-bath for at least 1 week at ambient temperature to allow complete hatching of all the viable eggs produced. Hatching times for *T. longicornis* eggs ranged from 5 days at 5 °C to 2 days at 17 °C (see Chapter 6) hence the incubation time varied with field temperature.

After incubation the content of each dish was filtered through a 53 μm sieve. The eggs and nauplii retained were stained with Lugol's iodine and counted in a Bogorov tray under a dissecting microscope. The egg production rates of copepods found dead or moribund, at the end of the incubation time, were not taken into account.

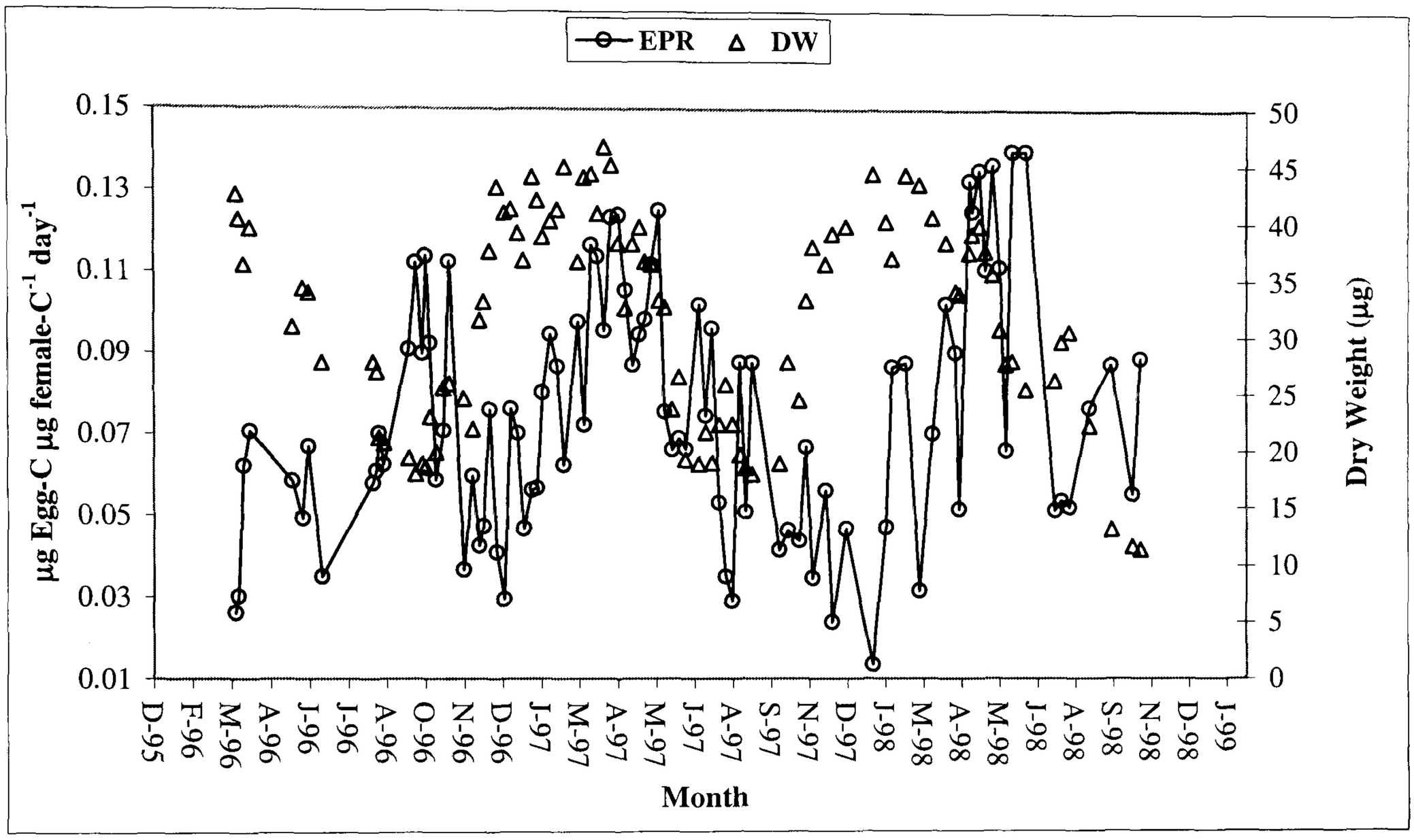
Over the year, 10-20 eggs, randomly chosen from a pool spawned by a large number of wild *T. longicornis* females, were measured with a high power phase-contrast Nikon microscope to establish the variation in egg size with season.

Egg production rates were converted to carbon production rates by assuming that an egg of *T. longicornis* contained 37.5 ng of carbon. This value was estimated assuming, an average *T. longicornis* egg diameter of 80 μm, hence egg volume 2.68×10^5 μm^3 and a carbon/volume ratio of 0.14×10^{-6} μg carbon μm^{-3} averaged from published values (Checkley, 1980; Ambler, 1985; Kiorboe *et al.*, 1985).

4.3 Results

Figure 4.1 shows the seasonal pattern in *T. longicornis* weight specific EPR, calculated only from egg producing females, recorded in the Menai Strait from March 1996 to October 1998.

Figure 4.1: Seasonal trend in mean EPR (circles, μg egg-C μg female-$C^{-1}day^{-1}$) and copepod dry weight (triangles, μg) in *Temora longicornis* in the Menai Strait between 1996 and 1998.



T. longicornis produced eggs all year round with maximum carbon-specific production (± SD) of ~ 0.14 ± 0.01 μg egg-C μg female-$C^{-1}day^{-1}$ or ~58 ± 6 egg $female^{-1}$ day^{-1} usually coinciding with the spring phytoplankton bloom and minimum rates ~ 0.01 ± 0.002 μg egg-C μg female-$C^{-1}day^{-1}$or 6 ± 1 egg $female^{-1}day^{-1}$ in winter.

Despite similarities, the pattern of *T. longicornis*'s EPR differed among years. During 1996 the spring maximum measured occurred 1 month later and was at least half that measured in the springs of 1997/98. In addition, in October 1996 an EPR autumn maximum of ~ 0.11 μg egg-C μg female-$C^{-1}day^{-1}$ or 32 ± 4 egg $female^{-1}day^{-1}$ was similar to that measured during the spring maximum in 1997/98. An autumnal increase in EPR was not obvious in either '97 or '98.

Unlike 1996, during 1997 and 1998 the EPR was similar both in magnitude and rate of increase. In 1997 and 1998 the rise in EPR from winter minima took place as early as February and reached a spring maximum of ~ 0.12 ± 0.01 μg egg-C μg female-

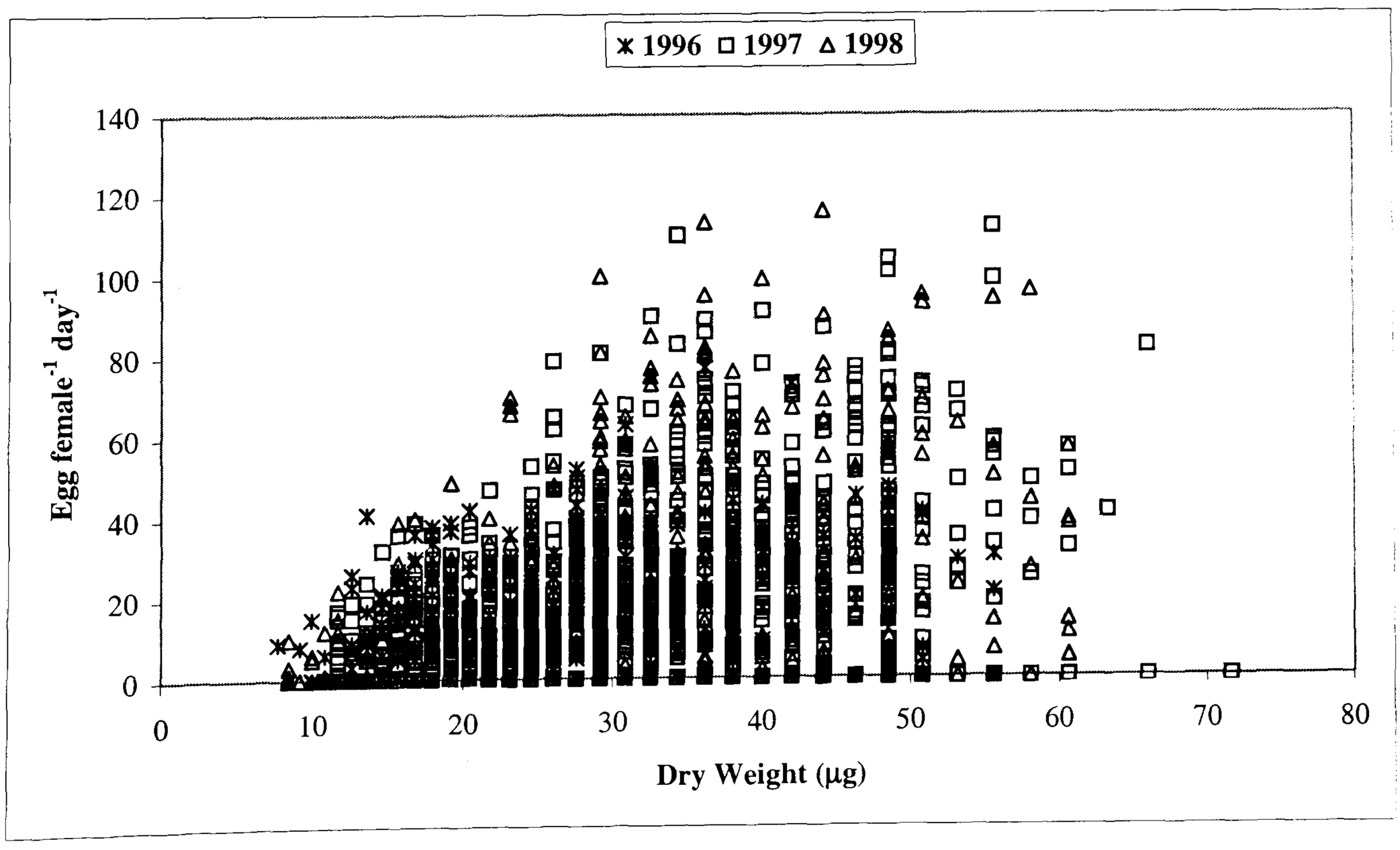
$C^{-1}day^{-1}$ (± SD) or 59 ± 5 egg $female^{-1}day^{-1}$ and 0.14 ± 0.01 µg egg-C µg female-$C^{-1}day^{-1}$ or 58 ± 6 egg $female^{-1}day^{-1}$ respectively.

4.3.1 Female dry weight vs EPR

The body weight of females *T. longicornis* varied seasonally with large copepods occurring in winter-spring and small ones appearing during summer and autumn (Figure 4.1). In 1996 the annual maximum weight specific egg production was recorded in autumn when copepods reached their smallest weights, whereas in 1997 and 1998 maximum annual EPR was measured in spring when copepod weight was largest (Figure 4.1).

Figure 4.2 shows the relationship between EPR and copepod dry weight for the 1996 to 1998. The range in egg producing copepods in the Menai Strait is between 9 to 67 µg dry weight. Copepod EPR is extremely variable for a given weight but the edge of the cloud of points clearly delineates a distinct relationship of increasing EPR with individual weight till 40 µg $female^{-1}$after which no further increase in EPR with weight was measured (Figure 4.2). The observation that similarly large copepods can produce the lowest and the highest weight specific EPR in winter and spring respectively suggests that adult copepod production in the field might have been limited (Figure 4.1 and Figure 4.2).

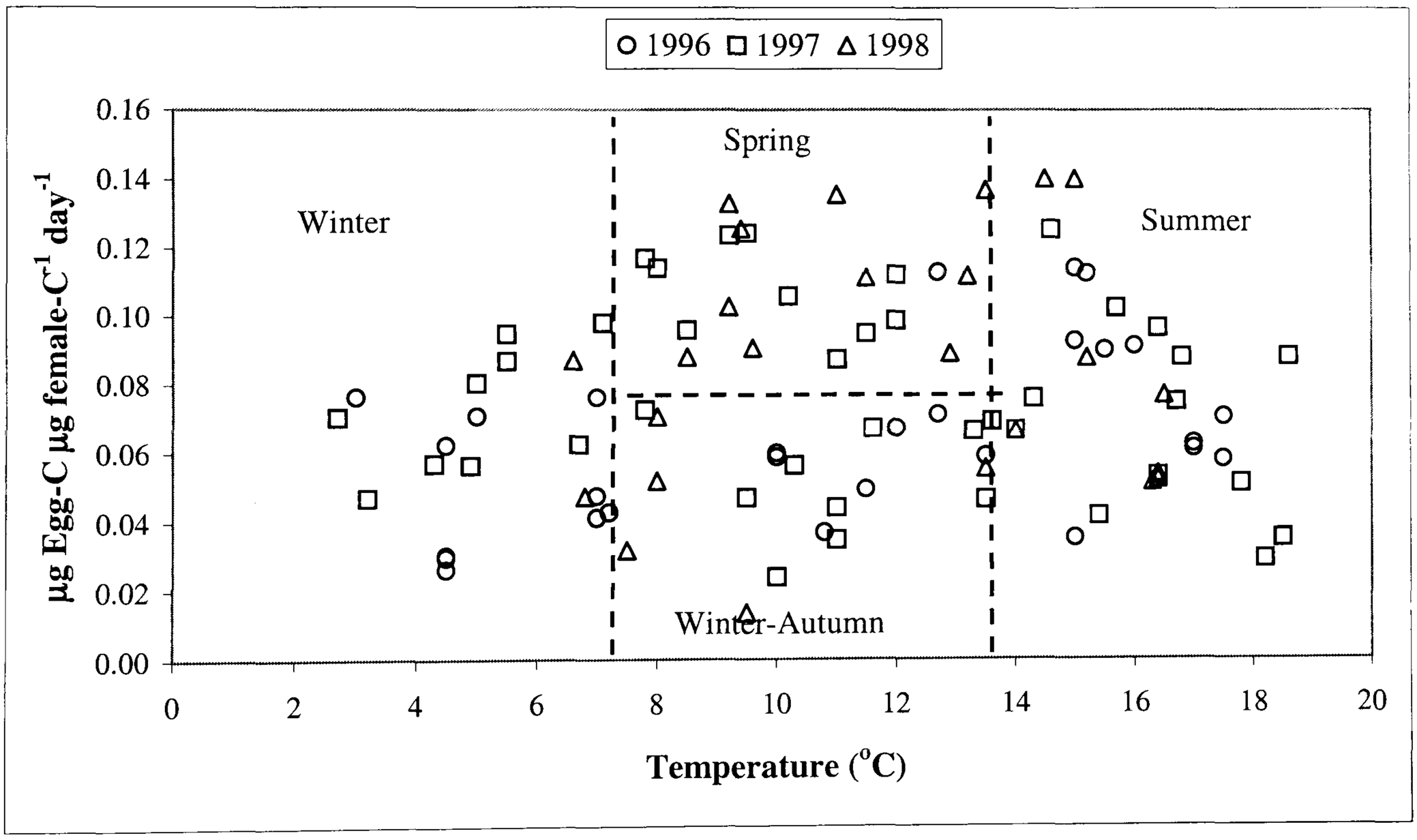
Figure 4.2: Scatter plot of individual *T. longicornis* EPR (egg $female^{-1}day^{-1}$) against body weight (µg) for pooled data between 1996 and 1998.



4.3.2 The effect of temperature on EPR

Figure 4.3 illustrates the scatter plot between field temperature and the pooled EPR data between 1996 and 1998. The outer boundary of the variable scatter of EPR versus temperature is characterised by a rise over low temperature to a plateau around 9 °C and 15 °C with declining production at higher temperatures (Figure 4.3). The central part of the plot is characterised by a large spread of the observations from the top boundary corresponding to high EPR in the spring and the lower EPRs occurring in the autumn time (See Figure 4.3). The highest and lowest EPR measured between 9 °C and 14 °C suggests, however, that copepod fecundity is controlled by factors other than temperature.

Figure 4.3: Mean carbon weight specific fecundity (μg egg-C μg female-$C^{-1}$$day^{-1}$) of *Temora longicornis* versus field temperature (°C) measured in the Menai Strait between 1996-98. The graph has been partitioned according to the season of the year to illustrate the relative changes of EPR over similar temperature ranges.



The pooled 1996 to 1998 EPR of *T. longicornis* was positively correlated with temperature (d.f. = 36; r = 0.145; p = 0.010) between winter and spring (i.e. up to 11.5 °C). However, the relationship between *T. longicornis* EPR and temperature differed for all the three years. Whereas in 1996 (d. f. = 5; r = 0.37; p = 0.42) and 1998 (d. f. = 11; r = 0.53; p = 0.061) EPR was not correlated with water temperature (d. f. = 5; r = 0.37; p = 0.42) in 1997 EPR (d.f. = 16; r = 0.66; p = 0.003) rose with temperature up to 11.5 °C.

4.3.3 The relationship between EPR and microplankton biomass

Figure 4.4 shows the scatter plot of *T. longicornis*'s EPR and the potential food species present in the field at the time of sampling including total Chl (μgL^{-1}, a), total ciliates (i.e. aloricates and tintinnids, as $\mu g\text{-}C\ L^{-1}$, b), total diatom ($\mu g\text{-}C\ L^{-1}$, c) and total dinoflagellate ($\mu g\text{-}C\ L^{-1}$, d). The scale of the x-axis was expanded using a semi-log plot to improve the resolution of the relationship between EPR and the different microplankton species.

Figure 4.4: The mean weight specific EPR (µg egg-C µg female-$C^{-1}day^{-1}$) of *T. longicornis* versus ln transformed a) chlorophyll-a (µg L^{-1}, for 1996 to 1998), b) diatoms (µg-C L^{-1}, for 1996 to 1998), c) dinoflagellates (µg-C L^{-1}, for 1996 to 1998) and d) ciliates (µg-C L^{-1}, for 1997 to 1998) biomass in the Menai Strait.

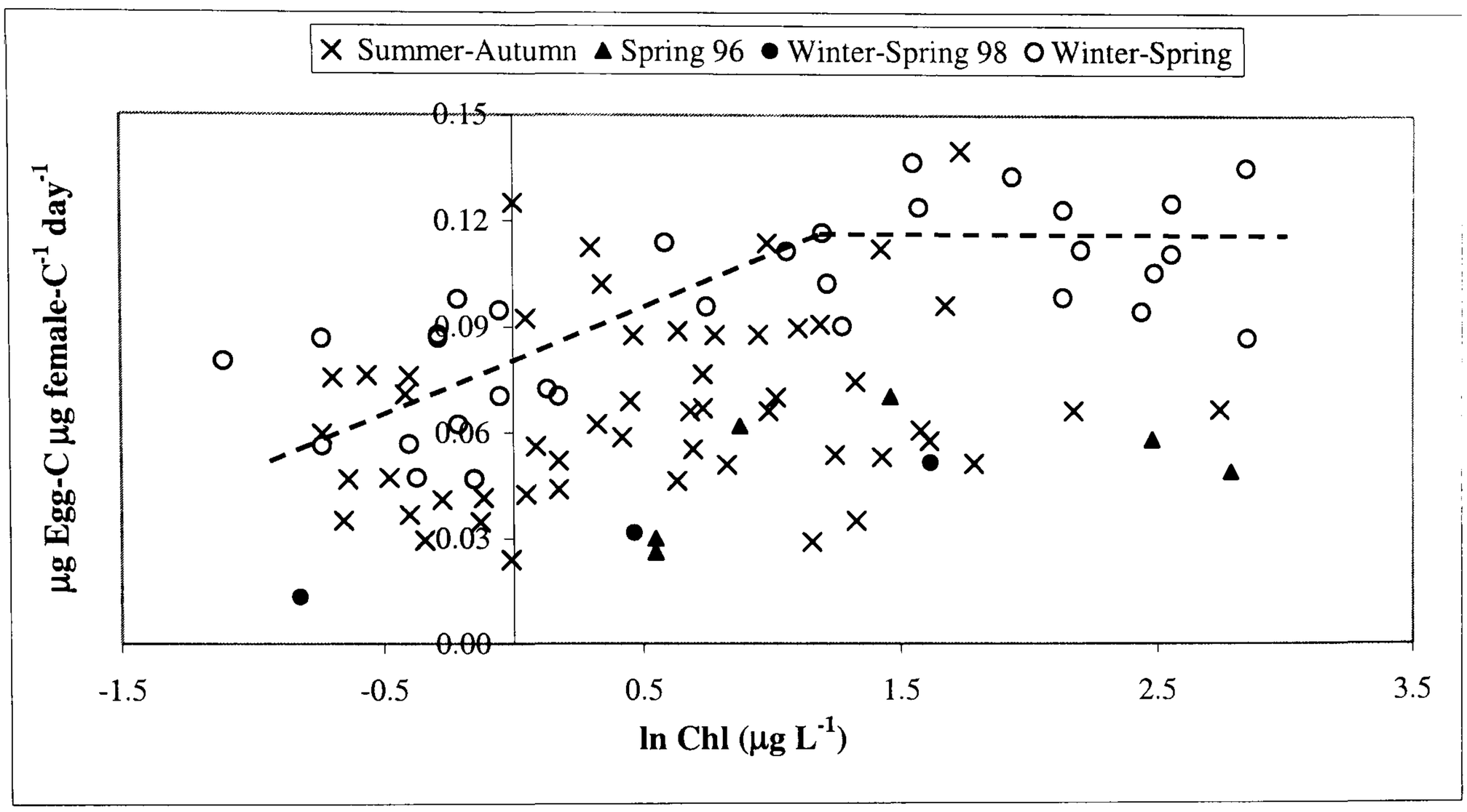
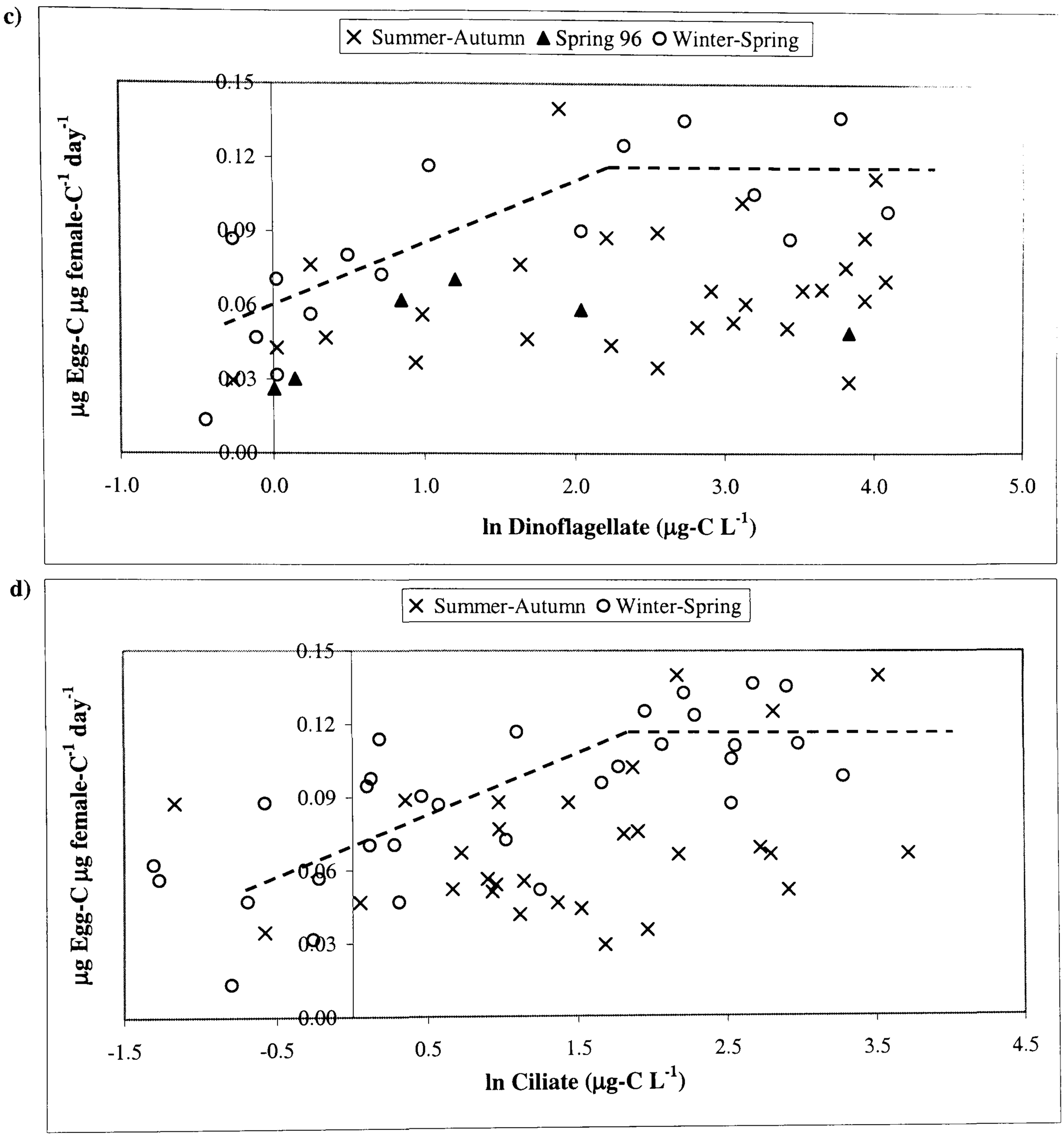


Figure 4.4: continued



T. longicornis's weight specific EPR increased asymptotically in relation to all the microplankton species considered (Figure 4.4). In 1997 and 1998 the relationship between copepod fecundity and Chl or the different microplankton groups was stronger during winter-spring than for the rest of the year when the change in EPR with the microplankton concentration appeared more variable (Figure 4.4; Table 4.1). The full black symbols in the plots represents EPR measurements recorded mostly during winter 1996 which deviate from the general winter-spring pattern.

Table 4.1 summarises the relationship found, over the linearly rising part of the curve (Figure 4.4), between the EPR of *T. longicornis* and the standing stock of the different microplankton groups measured in the Menai Strait between 1996 and 1998.

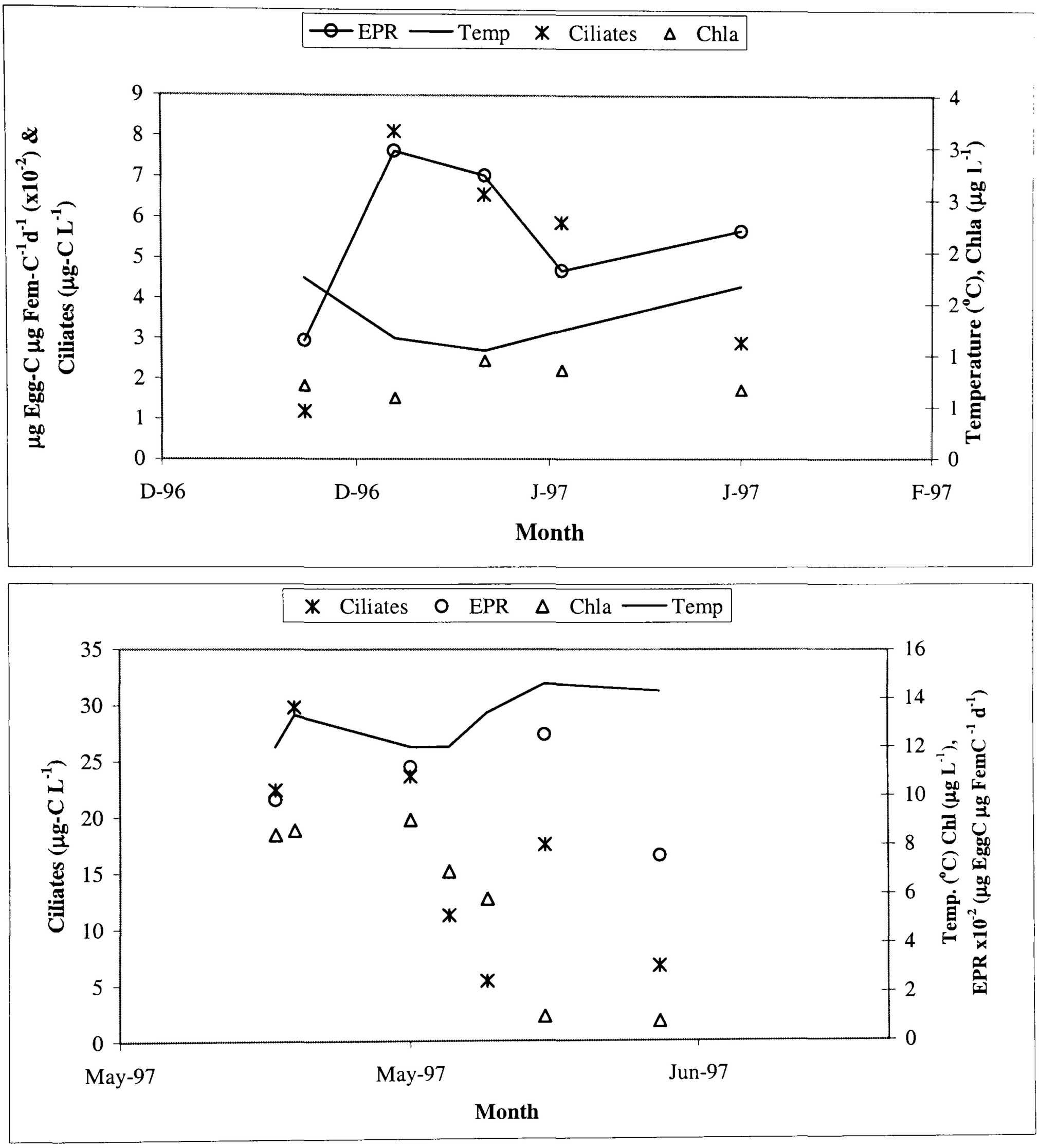
Table 4.1: Relationships between *T. longicornis* EPR (µg egg-C µg female-C^{-1}day^{-1}) and the natural logarithm of the biomass of different microplankton groups (µg-C L^{-1}) and Chlorophyll-a (µg L^{-1}). The number of observation (n), the intercept (a), the slope (b) of the regression are also shown. C.S. is the minimum microplankton (µg-C L^{-1}) and Chl (µg L^{-1}) concentration at which copepod EPR becomes maximum. The C.S as a proportion of the maximum microplankton and Chl concentration in the field is given in square brackets. The average maximum fecundity (EPR$_{max}$) beyond C.S. is also shown. The standard errors are given in round brackets.

Microplankton	n	a	b	C.S.	EPR$_{max}$	r	p
ln Chl	29	0.071 (± 0.006)	0.015 (± 0.007)	5 [25 %]	0.093 (± 0.009)	0.40	0.031
ln Chl (spring)	22	0.0816 (0.004)	0.0230 (± 0.005)	5 [25 %]	0.108 (± 0.007)	0.73	< 0.001
ln Diatom	46	0.048 (±0.009)	0.007 (± 0.002)	200 [10 %]	0.091 (± 0.012)	0.45	0.002
ln Diatom (spring)	18	0.028 (± 0.011)	0.0175 (± 0.003)	200 [10 %]	0.091 (± 0.011)	0.73	0.001
ln Dinoflagellate	27	0.048 (± 0.007)	0.0188 (± 0.006)	10 [20 %]	0.07 (± 0.006)	0.55	0.003
ln Dinoflagellate (spring)	16	0.050 (± 0.007)	0.023 (± 0.007)	10 [20 %]	0.095 (± 0.014)	0.63 8	0.008
ln Ciliate	51	0.063 (± 0.005)	0.012 (± 0.004)	12 [20 %]	0.10 (± 0.008)	0.43	0.001
ln Ciliate (spring)	29	0.071 (± 0.005)	0.018 (± 0.003)	12 [20 %]	0.112 (± 0.007)	0.74	< 0.001

As anticipated from Figure 4.4 the relationship between EPR and microplankton is stronger over the winter-spring period than for the whole of the year. Maximum copepod egg production occurred when the microplankton concentration in the field was relatively low representing approximately between ~10 % and 25 % of the maximum annual concentration measured in the Menai Strait between 1996 and 1998 (Figures 4.4 & Table 4.1).

Isolated *T. longicornis* EPR increases during winter (Figure 4.5, a) and summer (Figure 4.5, b) during low concentration of Chl (Chl ≤ 1 µg L^{-1}) and temperature relatively constant were associated with the rise of the ciliates indicating that this microplankton group could be important in supporting fecundity when phytoplankton is low.

Figure 4.5: *T. longicornis*'s EPR (µg egg-C µg female-$C^{-1}day^{-1}$), temperature (°C) ciliates (µg-C L^{-1}) and chlorophyll-a (µg L^{-1}) during winter 1996-97 (a) and summer 1997 (b).

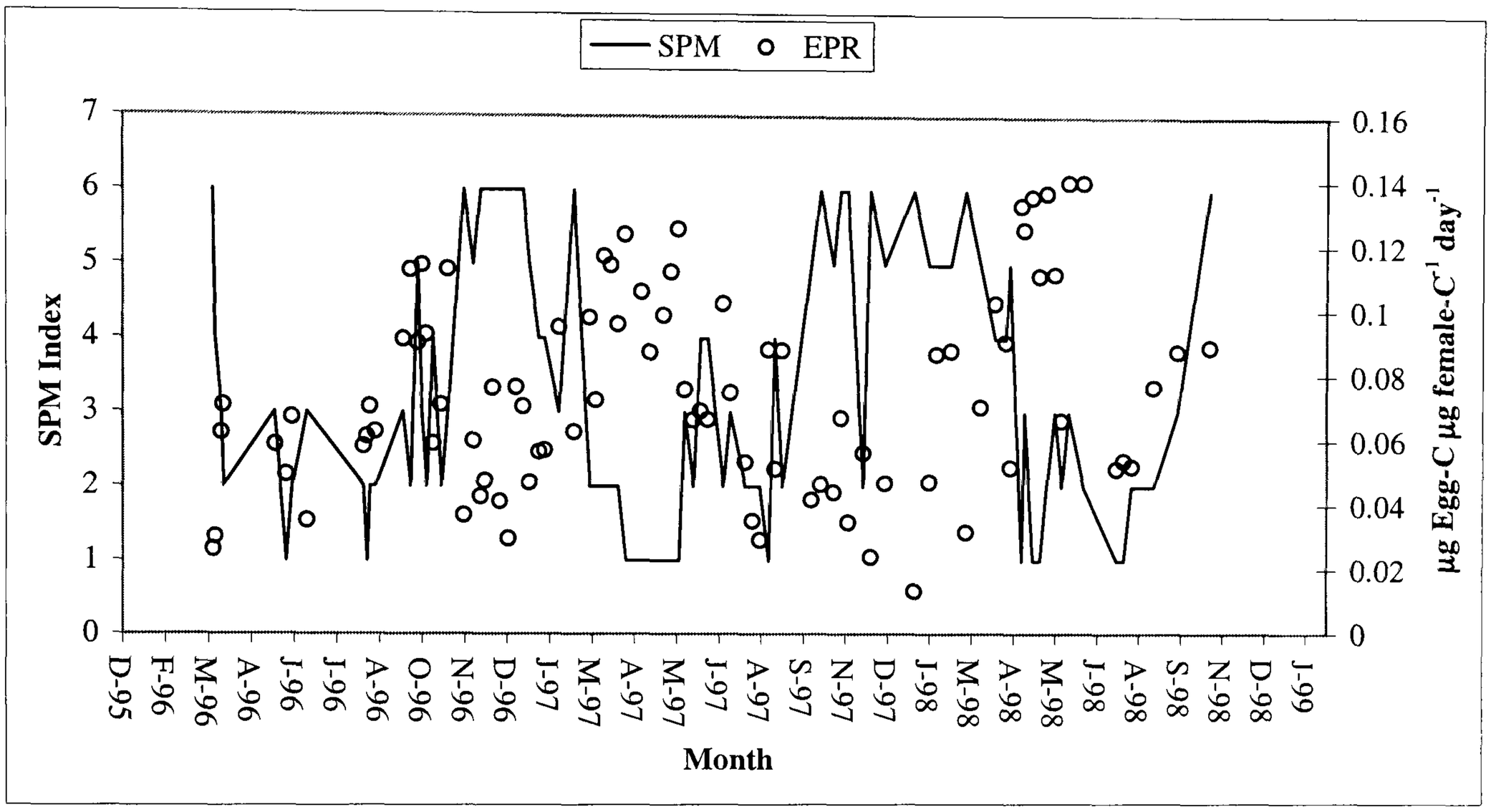


For instance, a sudden increase in EPR up to 0.075 µg egg-C µg female-$C^{-1}day^{-1}$ between December 1996 and January 1997 above the usual winter values of ~ 0.01-0.05 µg egg-C µg female-$C^{-1}day^{-1}$ coincided with the increase up to ~ 8 µg-C L^{-1} of the tintinnid *T. lobiancoi* (Figure 4.5, a). During summer 1997, despite the sharp decrease in total phytoplankton biomass from ~ 9 to 1 µg Chl L^{-1} copepods continued to sustain a high EPR which coincided with a bloom up to 16 µg-C L^{-1} of the tintinnid *H. subulata* (Figure 4.5, b).

4.3.4 EPR vs tidal range and suspended particulate matter

Figure 4.6 (a & b) shows the changes in EPR of *T. longicornis* and index of suspended particulate matter (SPM) between 1996 and 1998.

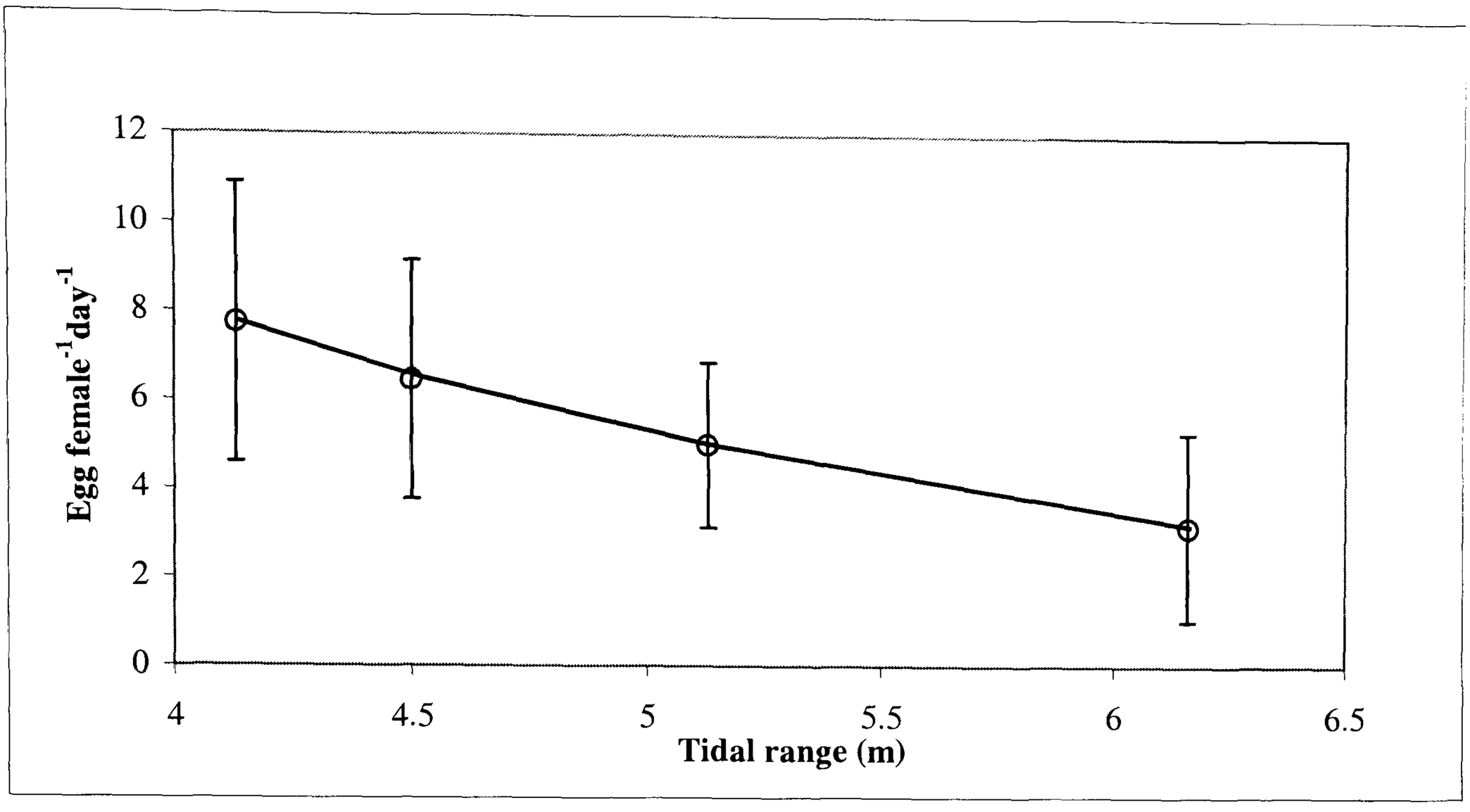
Figure 4.6: *T. longicornis* specific EPR (µg egg-C µg female-$C^{-1}d^{-1}$) and total suspended sediments (SPM, arbitrary units) in the Menai Strait between 1996 and 1998.



From Figure 4.6, high fecundity usually coincides with spring-summer when SPM index is at its lowest whereas minimum fecundity occurs in winter-autumn when the SPM index is highest. As a result a significant negative relationship (Spearman's rank correlation coefficient $\rho = -0.61$; $n = 96$, $p < 0.001$) was found between weight specific EPR and the SPM index.

Figure 4.7 shows an inverse relationship between EPR and tidal range over a single tidal cycle between November and December 1996 when values recorded in the field for Chl, temperature and micro-zooplankton were relatively constant with coefficient of variation being 8 %, 19 % and 33 % respectively.

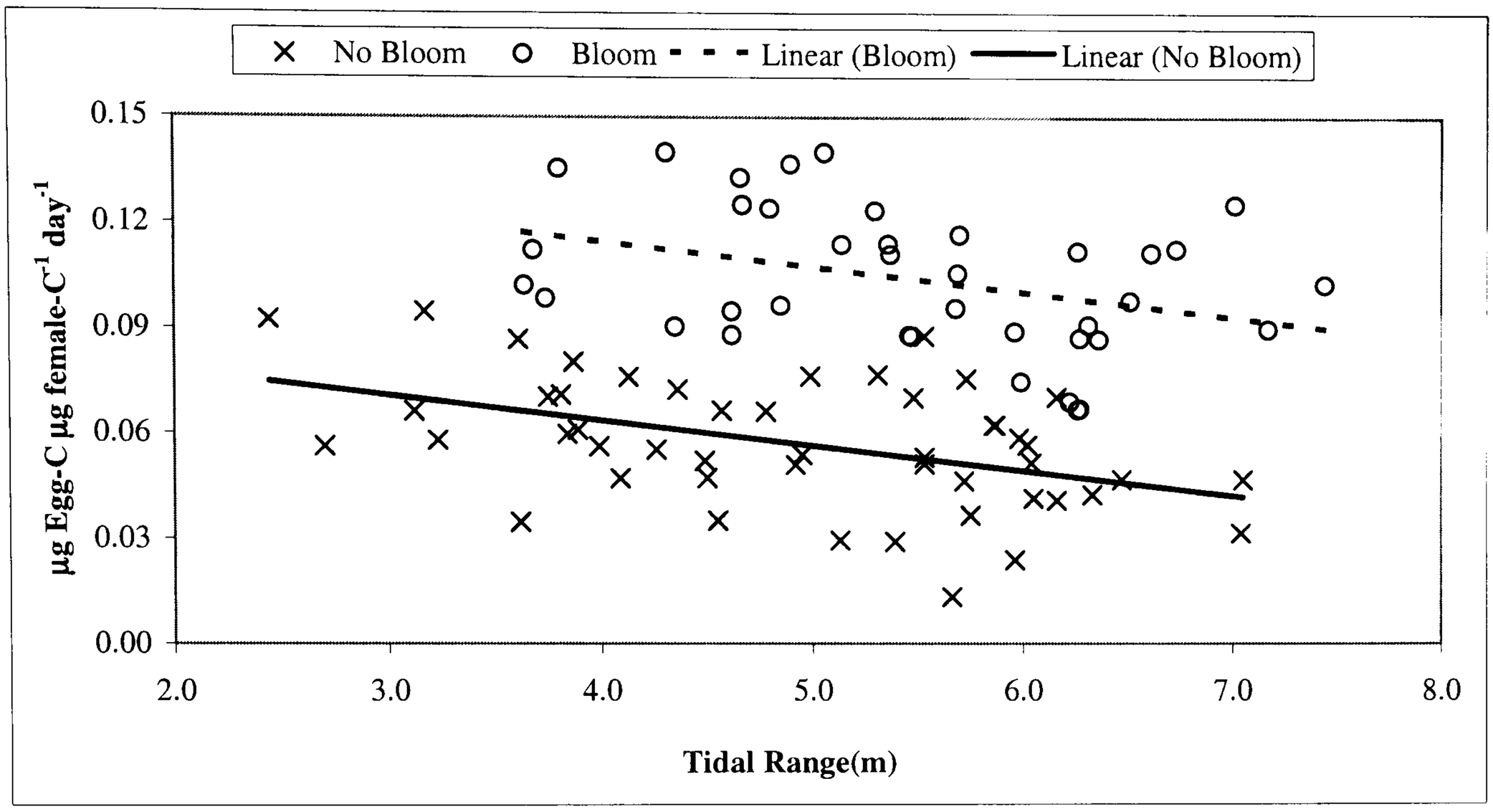
Figure 4.7: *T. longicornis* specific EPR (μg egg-C μg female-C^{-1}day^{-1}) with tidal range during November and December 1996.



Despite the limited data set, the present observation suggests that EPR is inversely related to tidal range (hence to SPM load in the water column). Given the observed inverse relationship between EPR and SPM the relationship between tidal range (considered a good proxy for SPM) and EPR was also investigated. In the eastern Irish Sea, tidal cycle has been found to be directly related to SPM (Bowers *et al.*, 1998).

Figure 4.8 shows the relationship between EPR and tidal range between 1996 and 1998. The data presented in Figure 4.8 show two different clusters of high EPR group or "Bloom" and a low EPR group or "no-Bloom". The "Bloom" group corresponded to eggs laid mostly during the spring and the autumn phytoplankton increase at Chl>1.5 μg L^{-1} when the microplankton assemblage was dominated by diatoms smaller than 50-100 μm (either as cell length or diameter). For instance, the highest EPR occurred when diatom species like *R. delicatula*, and *S. costatum* appeared in the water in high concentrations (i.e. Chl > 1.5 μg L^{-1}). The "non-Bloom" group corresponded to EPR measured mostly during winter and summer at Chl < 1.5 μg L^{-1}, when blooms of diatom species larger than 100 μm like *R. shrubsolei*, *R. setigera* and *G. flaccida* or when cryptomonas microflagellate species dominated the microplankton community.

Figure 4.8: The variation of *T. longicornis* specific EPR (µg egg-C µg female-C^{-1}day^{-1}) with tidal range at phytoplankton abundance equivalent to Chl concentrations above 1.5 µg L^{-1} (Bloom, circle) and below 1.5 µg Chla L^{-1} (No-Bloom, triangle) between 1996 and 1998. Lines fitted by least square regression.



A high EPR value recorded just after the spring bloom at low Chl ~1 µg L^{-1} during the increase of *H. subulata* to 4.4 µg-C L^{-1} and total microplankton concentration of ~100 µg-C L^{-1} was included in the "Bloom" group. However, high summer increases of other aloricate ciliates species up to 40 µg-C L^{-1}, dinoflagellate up to ~ 50 µg-C L^{-1} and total microplankton carbon concentrations comparable to or higher than the concentration in spring, did not coincide with comparably high EPR. Thus, the type of microzooplankton available to the copepods might also have been important in determining their fecundity.

Within both clusters EPR decreases significantly with tidal range ($r = -0.445$; d.f. = 47; $p = 0.001$ for "no-Bloom" and $r = -0.36$; d.f. = 36; $p = 0.026$ for "Bloom" conditions). The relationship between tidal range on EPR was also investigated with an analysis of Covariance. Some anomalous points (i.e. 7 out of 94) corresponding to low EPR values measured during the 1996 bloom did not fit the general pattern and were excluded from the calculation.

Table 4.2: Covariance analysis of *T. longicornis* weight specific EPR (µg egg-C µg fem-C $^{-1}$day^{-1}) with tidal range (T.R., in m) between "Bloom" and "non-Bloom" condition (See text for explanation). (Seq. =sequential, Adj = adjusted).

Source	DF	Seq SS	Adj SS	Adj MS	F-value	P-value
T.R.	1	0.000219	0.004788	0.004788	15.46	< 0.001
Bloom	1	0.052209	0.002142	0.002142	6.92	0.01
Bloom x T.R.	1	0.000014	0.000014	0.000014	0.04	0.841
Error	83	0.025701	0.025701	0.00031		
Total	86	0.078129				

Term	Coef	SE Coef	T	P
Constant	0.117809	0.009798	12.02	< 0.001
Tidal Ra	-0.00716	0.001821	-3.93	< 0.001
Tidal Ra*bloom	0.000052	0.001821	0.03	0.977

The results in table 4.2 show that *T. longicornis* EPR decreased significantly with tidal range (F = 15.46; p< 0.001) for both "Bloom" and "non-Bloom" conditions. There was no significant difference between the slopes of the "Bloom" (- 0.07 ± 0.003 µg egg-C µg fem-C $^{-1}$day^{-1}m^{-1}) and "non-Bloom" (- 0.07 ± 0.002 µg egg-C µg fem-C $^{-1}$day^{-1}m^{-1}) regressions (F = 0.04; p = 0.977) fitted to the scatter plot shown in Figure 4.9. Table 4.2 also shows that the intercepts of the two regression lines were significantly different (F = 6.92; p = 0.01), the "Bloom" EPR (0.14 ± 0.017 µg egg-C µg fem-C $^{-1}$day^{-1}) being higher than that measured during "non-Bloom" conditions (0.092 ± 0.011 µg egg-C µg fem-C $^{-1}$day^{-1}). Thus, EPR measured during "Bloom" and "non-Bloom" condition decreased with tidal range at the same rate but fecundity was significantly higher during spring and autumn when Chl concentration exceeded 1.5 µg L^{-1} and the phytoplankton community was dominated by the smaller microplankton species.

4.3.5 Reproductive active females (RAF)

The seasonal variation in the proportion of copepods producing eggs (thereafter, Reproductive Active Females or RAF) varied over the year with maximum up to 100 % in spring and summer and minimum of 21 % in autumn and winter (Figure 4.9).

Figure 4.9: Seasonal variation in % RAF of *T. longicornis* in the Menai Strait during 1996-98.

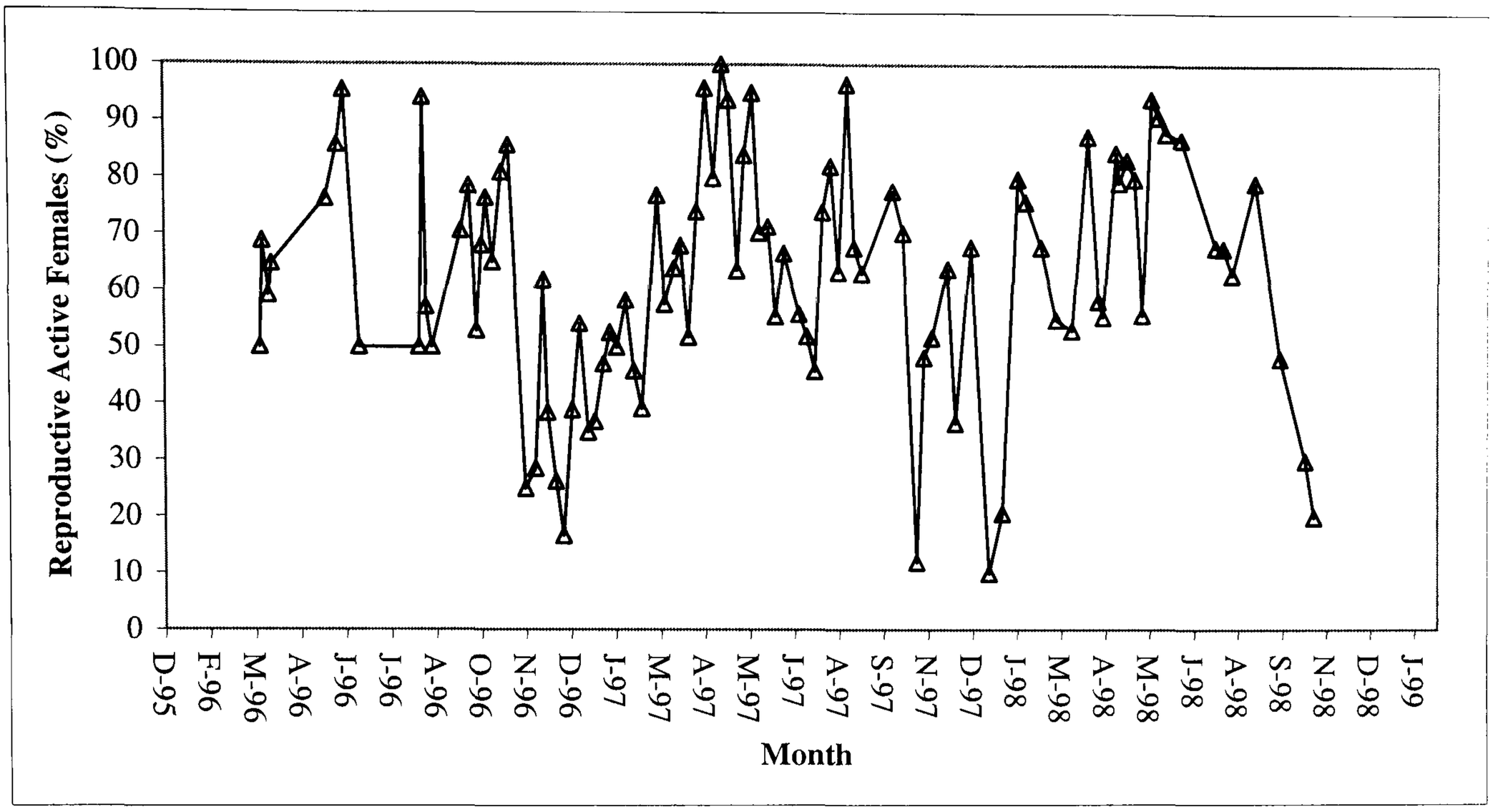


Figure 4.10: *T. longicornis* % RAF vs ln Chl (μg L^{-1}) in the Menai Strait during 1996-98.

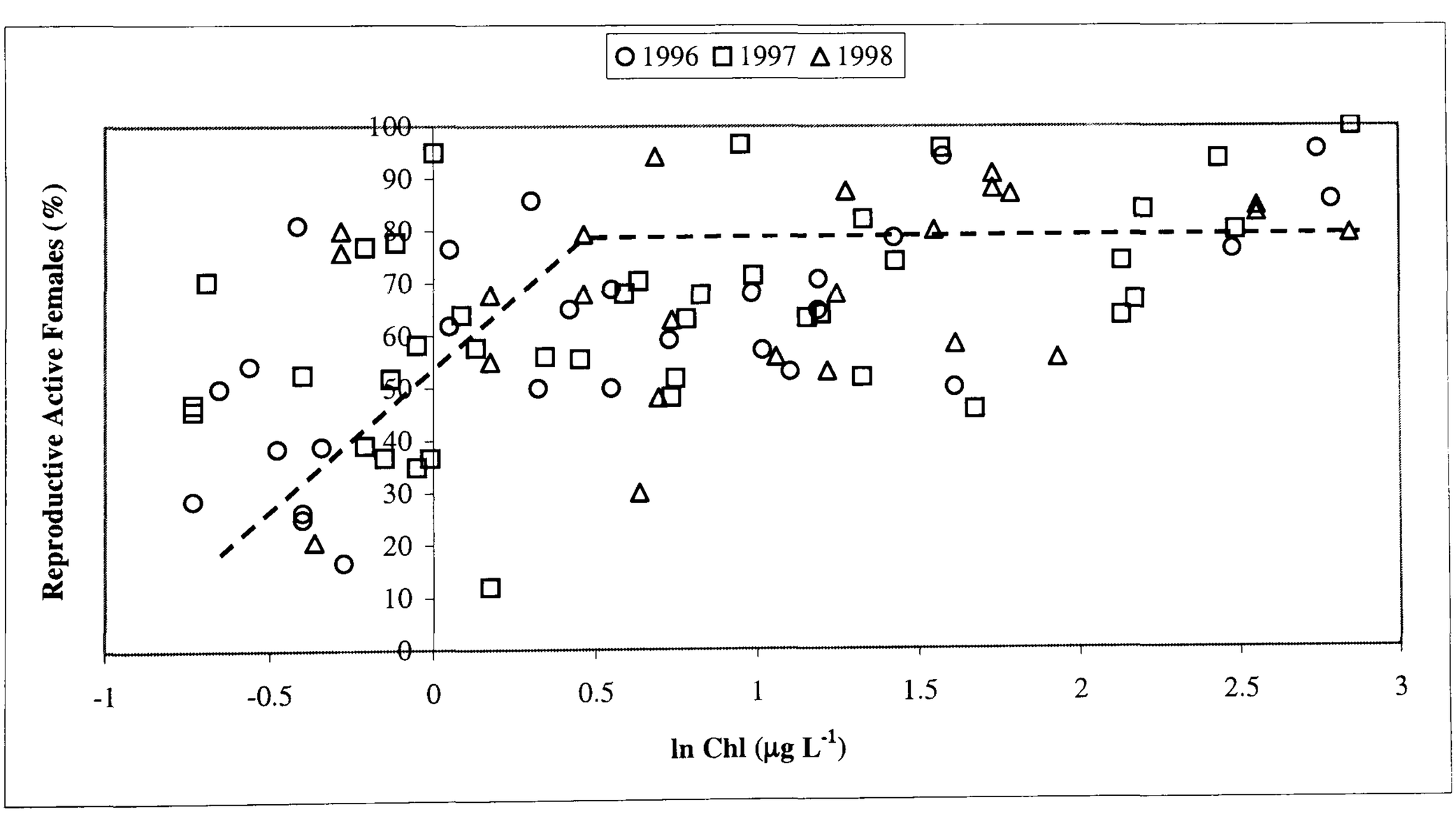


Figure 4.10 shows the relationship of *T. longicornis* % RAF and ln Chlorophyll-a between 1996-1998. The scale of the x-axis was expanded using a semi-log plot to improve the resolution of the relationship between % RAF and Chlorophyll-a. Although variable the % RAF increased asymptotically to 100 % at a Chl concentration as low as ~1.5 μg L^{-1} (Figure 4.10). The change in % RAF with temperature is shown in Figure

4.11. The proportion of RAF increases from ~ 30 % to ~ 100 % up to 9 °C after which an asymptote is reached. The lower circled group of data laying outside the general pattern corresponds consistently for all the three years to the data collected at the end of autumn (i.e. October-November). At that time the temperature in the Strait was comparable to that recorded in spring but the % RAF was 3-10 times lower (See Figure 4.11).

Figure 4.11: Scatter plot in *T. longicornis* % RAF vs temperature (°C) in the Menai Strait during 1996-98. Data in the oval represent observations made during autumn.

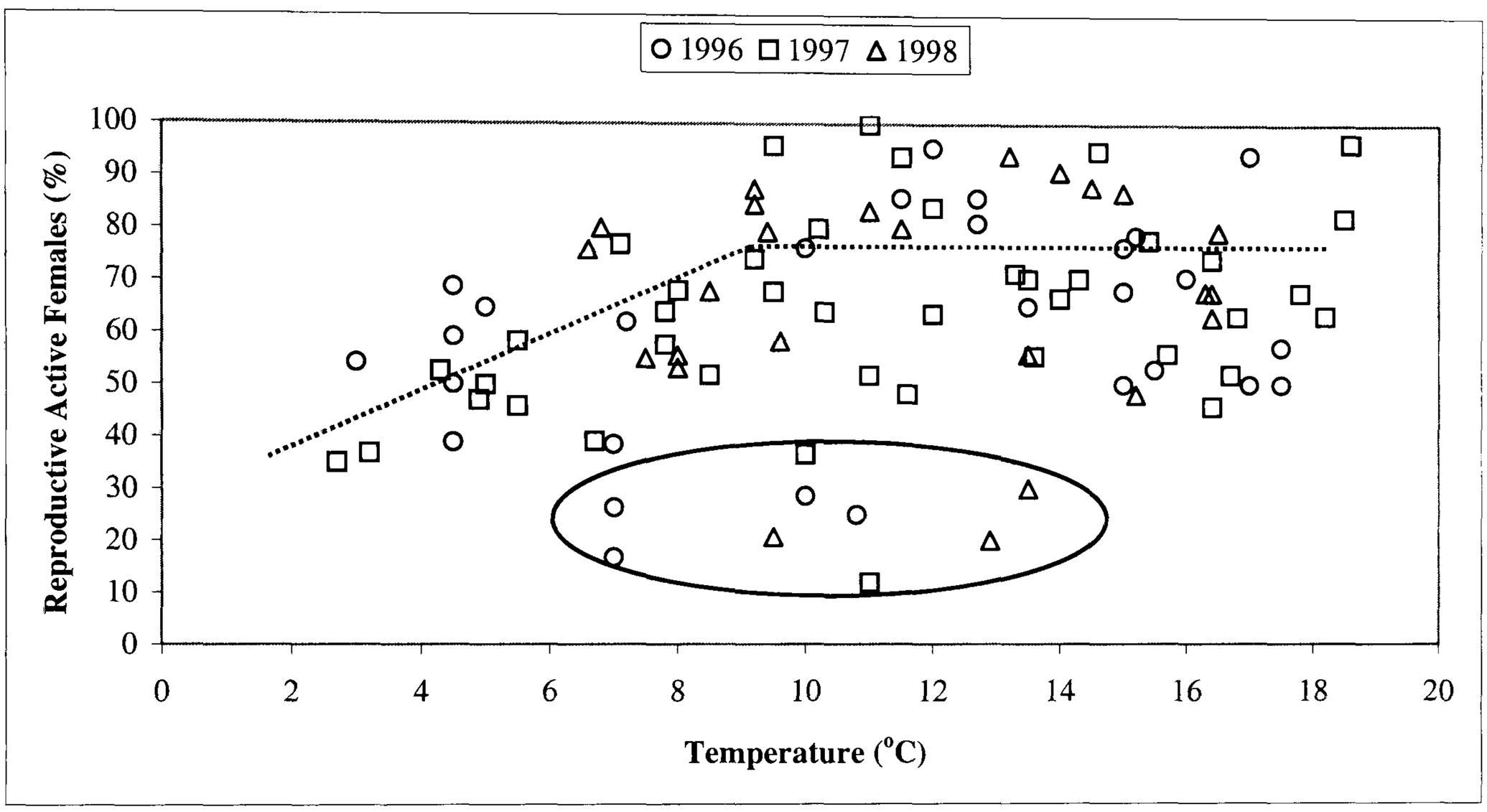
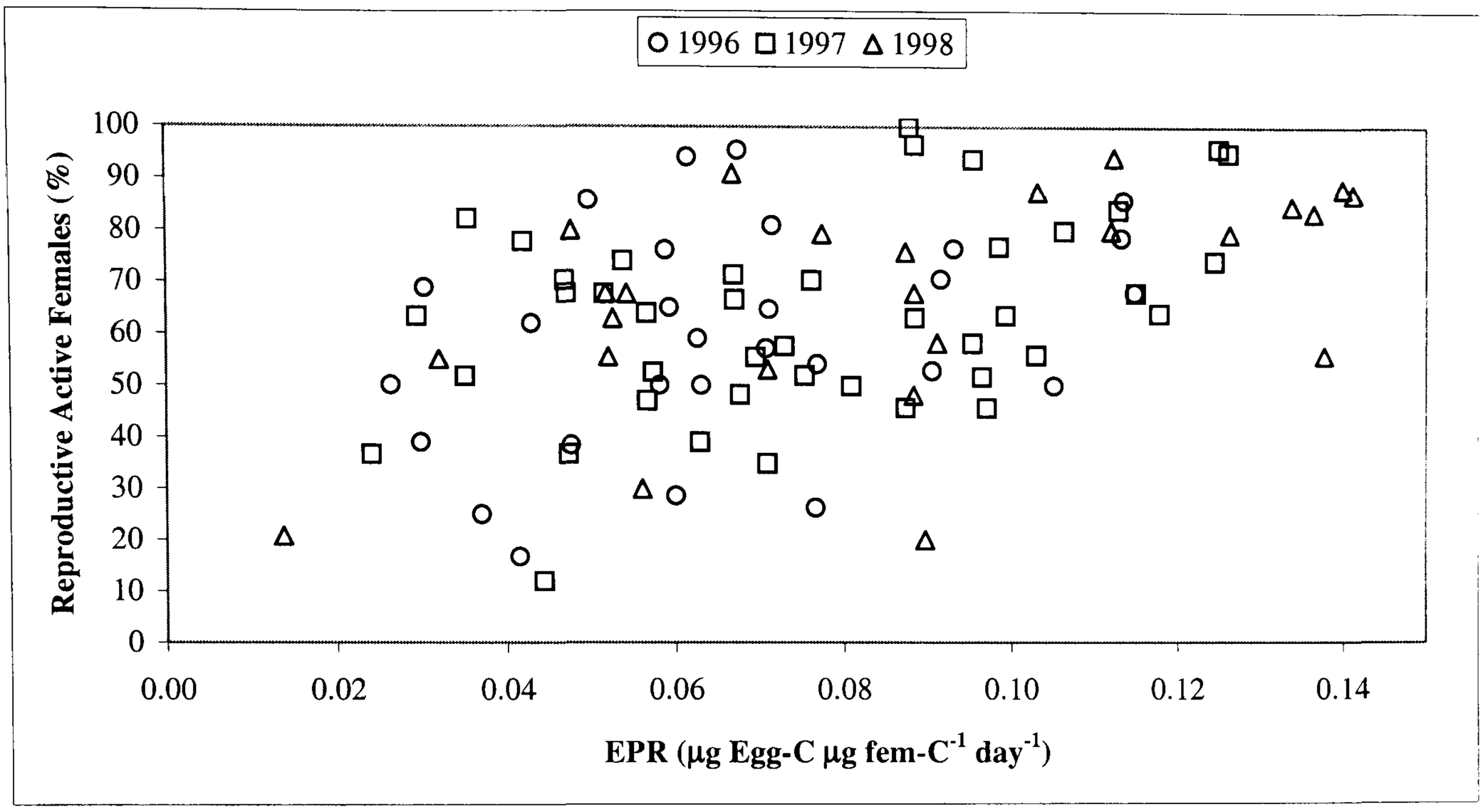


Figure 4.12 shows the relationship of *T. longicornis* % RAF and EPR between 1996-1998. A positive relationship was found between % RAF and mean EPR indicating that the total number of egg produced by the *T. longicornis* population in spring depends on the concomitant increase of both the proportion of RAF and the *per capita* copepod EPR (Figure 4.1, 4.9 & 4.12). Similarly to the EPR, the proportion of RAF was also found to decrease with increasing sediment load (Spearman's rank correlation coefficient, $n = 96$,

$\rho = -0.67$; $p < 0.01$).

Figure 4.12: *T. longicornis* % RAF vs EPR (µg egg-C µg fem-C $^{-1}$day^{-1}) in the Menai Strait during 1996-98.



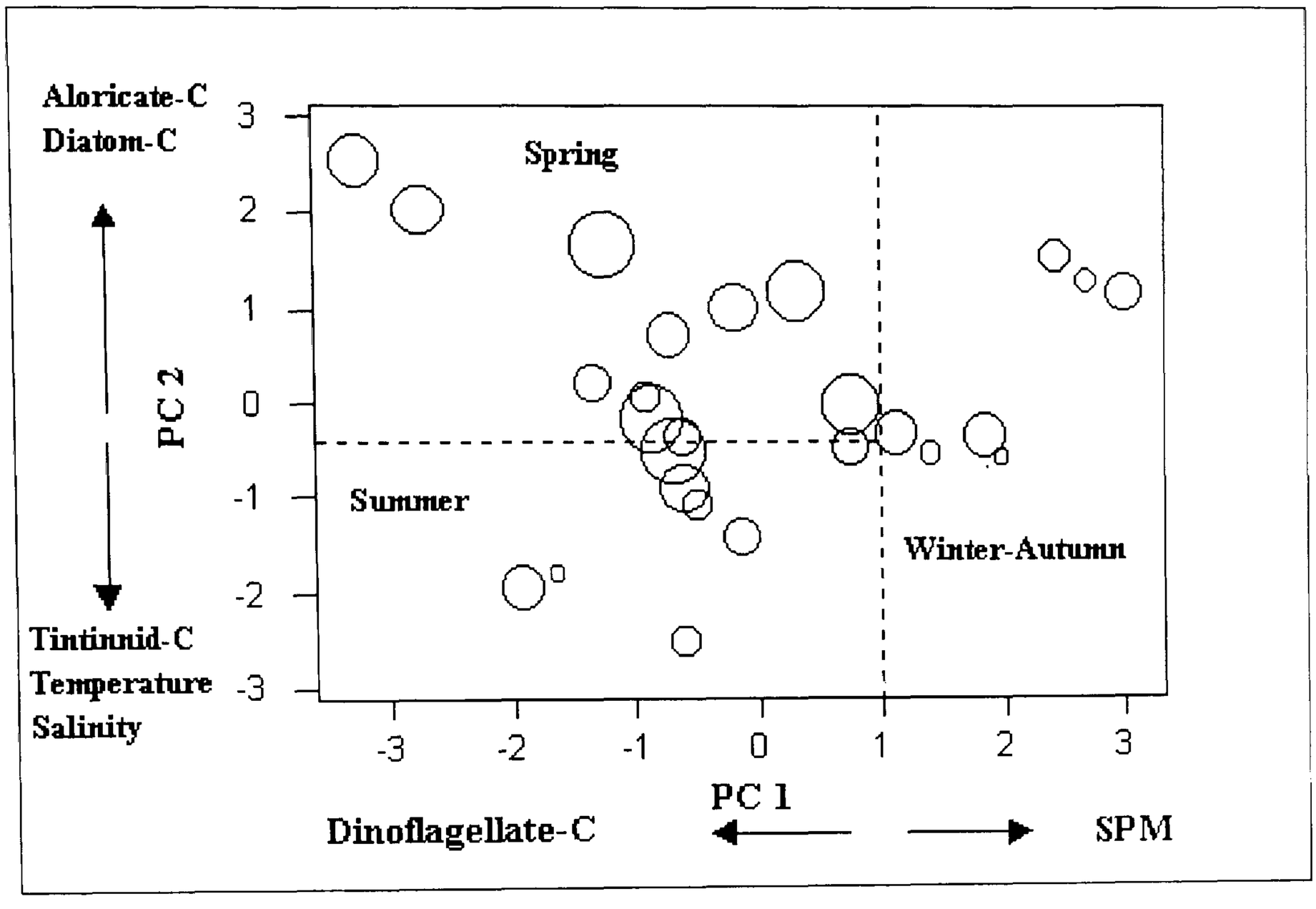
4.3.6 Principal component analysis

The principal component analysis (PCA) was conducted on a set of variables which are likely to influence the EPR and % RAF of *T. longicornis*. In the PCA the variables were compared by treating the days as replicates to avoid the effect of the temporal scale.

The first three principal components accounted for 78 % of the variability within the data set. Variables contributing to the PC1 were SPM, and dinoflagellate carbon whereas variables contributing to PC2 were temperature, diatom carbon, aloricate ciliates carbon, tintinnid ciliates carbon and salinity.

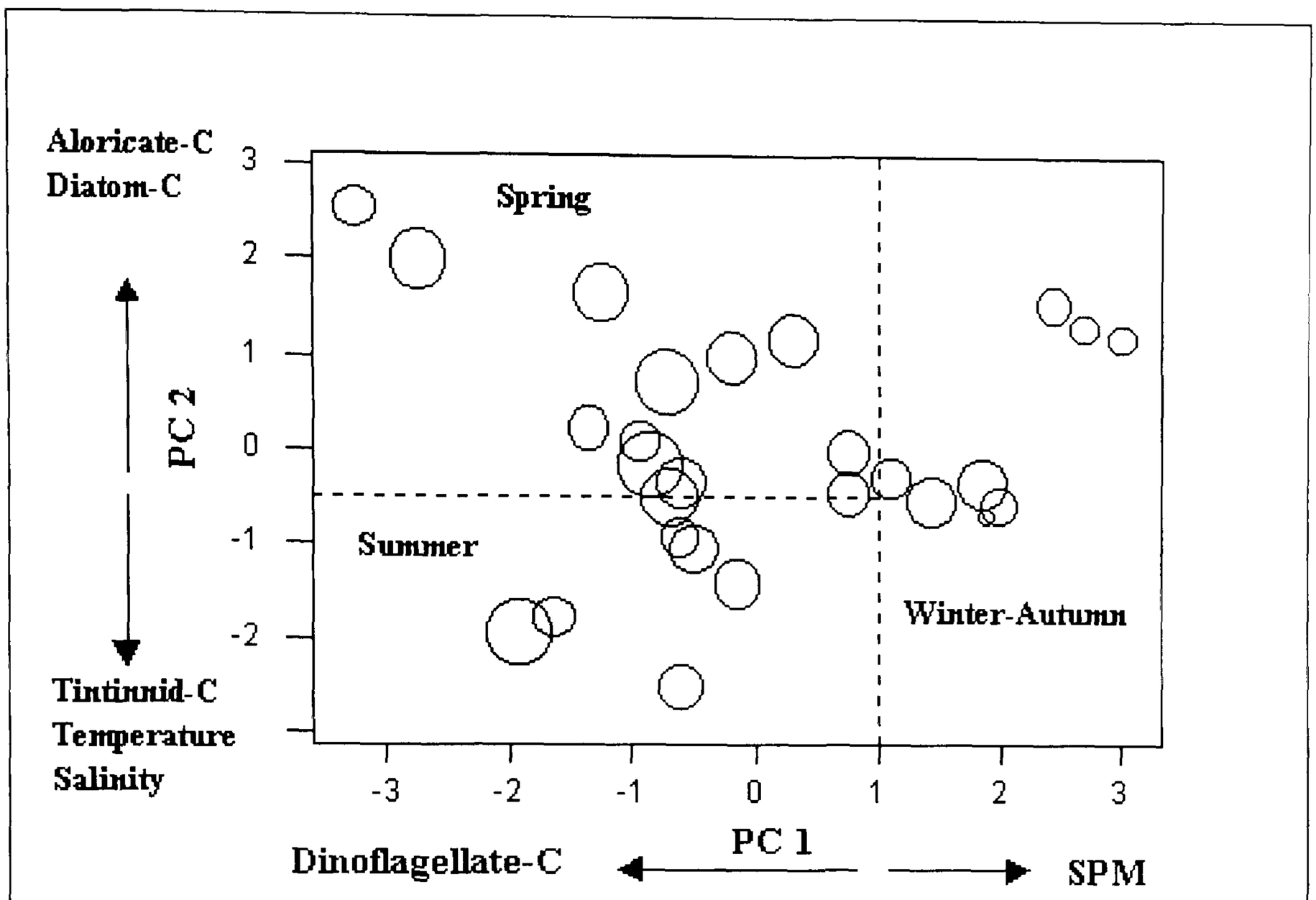
An ordination of PC1 and PC2 is presented in Figure 4.13 for EPR and in Figure 4.14 for the RAF. Spheres are scaled to EPR (0.013 to 0.14 (µg egg-C µg fem-C $^{-1}$day^{-1}) in Figure 4.13 and to RAF (21 to 100 %) in Figure 4.14. The size of the spheres and their position in relation to the PC1 and PC2 axis shows that periods of high and low EPR / % RAF are clearly separated (Figure 4.13 & 4.14). High copepod EPR was measured in spring and early summer and was associated with high diatoms, aloricate ciliates and dinoflagellates carbon whereas lower EPR were found in winter, late summer and autumn and were associated with high temperature, SPM, tintinnid carbon and salinity (Figure 4.13).

Figure 4.13: Ordination of the scores of variables derived from a PCA of biotic and abiotic variables measured between 1996 and 1998 in the Menai Strait. Spheres are linearly scaled to fecundity. Smallest spheres = 0.013 µg egg-C µg femC^{-1}day^{-1}; Largest Spheres = 0.14 µg egg-C µg femC^{-1}day^{-1}.



On the other hand, high % RAF were measured both in spring and summer and were associated with high diatoms, aloricate ciliates and dinoflagellates carbon, tintinnid carbon, temperature and salinity whereas the lowest RAF were associated with high SPM (Figure 4.14).

Figure 4.14: Ordination of the scores of variables derived from a PCA of biotic and abiotic variables measured between 1996 and 1998 in the Menai Strait. Spheres are linearly scaled to % actively reproducing female (RAF). Smallest spheres = 21 %; Largest spheres = 100 %.



4.4 Discussion

The present work has described the seasonal changes in the fecundity of *T. longicornis*, the numerically most abundant calanoid copepod living in the eastern Irish Sea. The EPR for 2240 females has been measured, individually, over a three years study in the Menai Strait.

Despite, recent investigations (Kleppel *et al.*, 1991) and attempts to model (Prestidge *et al.*, 1995) the EPR of several copepod species living in the Irish Sea, basic biological information on factors affecting the fecundity of even the best represented copepod species is still sparse. The present investigation thus represents, perhaps, the most comprehensive study carried out to date on the reproductive biology of *T. longicornis* in the Irish Sea.

By incubating individual females, the present study has measured both the individual variability in EPR and the proportion of females producing egg at any one time within the population. Several authors have already suggested that measurements of copepod egg production should consider fecund females only (Hay 1995; Ohman *et al.*,

1996). In nature copepods are not all in similar states of readiness for egg bearing (i.e. some may be too young, some too old and some damaged or dying) and including females which could not produce eggs in the calculation would underestimate copepod fecundity (Hay 1995; Ohman *et al.*, 1996). In addition, the high variability resulting from including non-reproducing females (as in estimates of EPR from incubation of more than one female at a time) information of individual variability is lost (Ohman *et al.*, 1996) and may obscure relationships between EPR and relevant variables.

T. longicornis's EPR in the Menai Strait varied widely both seasonally, with spring maxima being ~3-5 times the winter minima and annually with the fecundity maximum in 1996 being about a third of that measured during 1997 and 1998. The large seasonal fluctuation in *T. longicornis* EPR and its complex relationship with copepod body weight (See Figure 4.1 and 4.2) suggest that for most of the year fecundity in the Menai Strait is limited. The reason why copepods living in temperate latitudes cannot sustain maximum EPR over the whole year is still matter of some debate with temperature (Huntley & Lopez, 1992), food availability (Richardson & Verheye, 1998) or gonad maturation (Ianora and Scotto di Carlo, 1988; Rey *et al.*, 1999) usually proposed as the main explanation.

Laboratory experiments have shown that many biological rates including fecundity and gonad maturation generally increase with temperature, within the tolerance range of an organism (Runge, 1984). The dome shaped relationship found in the present study between EPR and temperature points to the existence of an optimal thermal range between 9 °C and 14 °C within which *T. longicornis* EPR can be maximal. The fact that this thermal optimum corresponded to both EPR spring maximum and autumn minimum, however, indicates the clear influence of factors other than temperature on copepod's ability to attain maximum EPRs. Although, *T. longicornis* EPR increased with temperature during the winter-spring of 1997, the high spring-like temperatures measured in the winter of 1998 did not promote high EPR.

In the present study, high EPR in *T. longicornis* up to ~58 egg fem^{-1} day^{-1} usually coincided with chlorophyll-a concentrations between ~1.5 - 21 μg Chl L^{-1}, particularly when the microplankton was dominated by the diatom *R. delicatula* and diatom species < 100 μm in cell length or diameter. Peterson & Kimmerer (1994) have suggested that EPR in *T. longicornis* in Long Island Sound was limited by low phytoplankton abundance reporting bursts of EPR in *T. longicornis* with Chl >5 to 21 μg L^{-1} in when phytoplankton cells > 10 μm accounted for 30-50 % of the total phytoplankton. Similarly, Kiorboe &

Nielsen, (1994) have reported *T. longicornis* maximum EPR of ~ 45 egg fem.$^{-1}$ day^{-1} coinciding with phytoplankton blooms up to ~ 11 µg Chl L^{-1} and low sea temperatures of ~ 5 °C in the southern Kattegat, Denmark. The results of Kiorboe & Nielsen (1994) indicate that *T. longicornis* can achieve maximum EPR production at temperatures as low as 5 °C (i.e. the average winter temperature in the Menai Strait).

The idea that food may be limiting for coastal copepod is surprising since many laboratory studies have shown that small copepods are able to achieve high EPR at relatively low Chl concentrations (Runge, 1984). For example, Uye (1981) found that maximum EPR in *A. clausi* and *A. steuri* could be achieved at 1 and 1.5 µg Chl L^{-1} respectively, while Runge (1984) reported that carbon concentration of 20 and 100 µg L^{-1} (corresponding to 0.4 and 2 µg Chl L^{-1} considering a C/Chl ratio of 50) could sustain maximum EPR in *A. clausi* and *Pseudocalanus parvus* respectively. In the current study, max EPR can be achieved at concentrations of Chl > 1.5 µg L^{-1} and microzooplankton carbon ranging from 12 µg-C L^{-1} to 200 µg-C L^{-1}, which are well below the measured annual maxima. Dam & Peterson, (1991) and Bautista *et al.*, (1994), comparing *T. longicornis* ingestion rate for different Chl size fractions, have suggested that the degree to which herbivorous coastal copepods are food-limited will depend on the size spectrum and the quality (Jónasdóttir, 1994) of the food encountered during the season. The particle type and size spectrum of potential food items encountered by *T. longicorni* during the year in the Menai Strait is very variable ranging from suspended detritus to a wide range of microplankton species (See Chapter 3). During 1997 and 1998 *T. longicornis* EPR annual maximum coincided with a mixed diatom-flagellate *Rhizosolenia-Phaeocystis* and ciliates spring increase ranging between 5 µm to 50 µm (i.e. as single cell) in length/diameter. It must, therefore, be assumed that the microplankton were of a suitable size and nutritional quality to sustain maximal EPR. Although, in the Menai Strait, *Phaeocystis sp.* can represent up to 90 % of the total biomass in spring, the diatoms, the ciliates and dinoflagellates also reach their annual maximum at around this time of the year (See Chapter 3).

A number of studies have indicated that the rates at which copepod ingest different prey items does not always reflect the relative abundance of the prey in the environment (Hansen *et al.*, 1993). For instance, during a mesocosm study *T. longicornis* was reported to graze on ciliates preferentially to *Phaeocystis sp.*, although the latter was more abundant (Hansen & Van Boekel, 1991; Hansen *et al.*, 1993).

Bautista *et al.*, (1994) have reported that the EPR of copepods including *C. helgolandicus* and *T. longicornis* appeared to be food limited during the *Phaeocystis sp.* bloom in the English Channel. Although, *T. longicornis* can feed on *Phaeocystis sp.* (Jones & Haq, 1963), this flagellate has poor nutritional value for zooplankton (Verity & Smayda, 1989) and copepods are likely to select more nutritious food when available (Hansen & Van Boekel, 1991; Hansen *et al.*, 1993). Furthermore, the high mucopolysaccaride, acrylic acid and dimethylsulphide (DMS) content of *Phaeocystis sp.* have already been shown to deter many marine organisms, including copepods, from feeding on it (Savage, 1931; Haq, 1960). It is likely, therefore, that the high EPR recorded for *T. longicornis* during the spring phytoplanton bloom in the Menai Strait was supported by copepod grazing on diatoms and ciliates rather than on *Phaeocystis sp.*.

Over the last decade, several studies have questioned the traditional role of diatoms in the diet of copepods. Ban *et al.*, (1997), for instance, have reported that out of 37 combinations of copepod and diatom species tested in the laboratory 25 exhibited reduced EPR and 29 exhibited reduced hatching success. During the present study, the maximum EPR took place when diatoms and in particular *R. delicatula* reached their maximum annual abundance in the Menai Strait. The presence of diatoms (or at least of *R. delicatula*), thus, had no apparent negative effect on *Temora*'s fecundity. Likewise, recent field studies have shown no negative effect of both diatom and flagellates like *Phaeocystis pouchetti* on the EPR of *C. helgolandicus* (Niehoff *et al.*, 1999; Irigoien *et al.*, 2000).

The low EPR recorded for *T. longicornis* during the summer at concentrations of Chl > 3-4 $\mu g\ L^{-1}$ in the Menai Strait is clearly not due to low phytoplankton concentration. Summer blooms in the Menai Strait are usually dominated by diatoms like the long chained *L. danicus*, the large celled *R. styliformis*, *R. shrubsolei* and *Guinardia flaccida* (see Chapter 3). Several authors (Gomez-Gutierrez & Peterson, 1999 and Saiz *et al.*, 1999) have argued that low EPR in small copepod species may depend on the poor handling efficiency of very large algal cells like *Chaetoceros sp.* and *Thalassiosira sp.* Thus, the low EPR measured during summer phytoplankton blooms might have been the result of low grazing efficiency on large phytoplankton cells, although, low nutritional quality of the food and reproductive incompetence by the copepod cannot be excluded. Likewise, the presence of large *Coscinodiscus sp.*, *D. Brigtwellii* and *Biddulphia sp.* which dominate the Menai Strait in late winter and

autumn blooms might also have been partly responsible for limiting the EPR of this small copepod species.

The significant correlation between Chl concentration and ciliate abundance, found in the present study (See Chapter 3), makes it difficult to clearly establish the dependency of *T. longicornis* fecundity on the type of food-source. Dam and Peterson (1991) have argued that up to 30 % to 40 % of the variance they found for *T. longicornis* ingestion rates could not be explained by algal concentration and size alone and must be related to omnivory. Moreover, the model of Prestidge *et al.*, (1995) has highlighted inconsistencies between predicted and empirical EPR estimates for *A. clausi* and *Calanus helgolandicus* in the Irish Sea suggesting that non-algal food sources may be responsible for maintaining the EPR of copepods when Chl concentrations are low. Kleppel *et al.* (1991) found that microzooplankton was an important dietary component for Irish Sea copepods and that microzooplankton biomass was positively correlated to EPR of the copepods tested.

Isolated winter and summer EPR increases coincident with low Chlorophyll-a (i.e. Chl <1 $\mu g\ L^{-1}$) but high ciliate abundance, suggesting that food sources other than phytoplankton e.g. microzooplankton or detritus, must be sustaining *T. longicornis* EPR when algal food is scarce. For instance, the sudden winter increase in EPR from ~ 0.03 μg egg-C μg female-$C^{-1}day^{-1}$ to ~ 0.075 μg egg-C μg female-$C^{-1}day^{-1}$ recorded in December 1996 coincided with increase in abundance of a large tintinnid, *T. lobiancoi* to ~10^3 cells L^{-1} or ~ 8 μg-C L^{-1} when temperature was 3 °C and Chlorophyll-a of 0.57 μgL^{-1} only. Furthermore, high *T. longicornis* EPR during June 1997 (~ 0.13 μg egg-C μg female-$C^{-1}day^{-1}$) measured during low Chlorophyll-a (~ 1 $\mu g\ L^{-1}$) was coincidental with an increase in the abundance of the tintinnid *H. subulata* to ~ 10^3 cells L^{-1} or ~ 16 $\mu g\ L^{-1}$. Both incidences indicate that the high EPR measured must have been supported by carnivourous and/or detrital feeding.

The C:N ratio of field microplankton and fatty acid content has often been used as crude indicators of particulate food quality for copepods (Ambler, 1986; Jónasdóttir & Kiorboe, 1996; Laabir *et al.*, 1998). The fecundity of several copepod species has been shown to be inversely related to the C:N ratio (Checkley, 1980; Ambler, 1986) and to be highest when the C:N ratio is below seven (Checkley, 1980; Laabir *et al.*, 1998). Although, the C:N ratio and fatty acid content of the seston were not measured in the current study, previous investigations carried out in the Menai Strait have consistently shown that the C:N ratio during the spring bloom ranges between ~15 and 20 as

compared to ~ 6 in the remainder of the year (Middleton, 1997; Rodriguez, 1998). Yet, despite the usually high spring C:N ratio the EPR of *T. longicornis* measured during the spring bloom of 1997 and 1998 reached its annual maximum indicating that the C:N cannot be generalised as a good indicator of dietary potential for copepods. The present observation is hardly surprising, since copepods tend to select their food sources or are limited by the size of food with C:N ratios which may be different from a crude filtered average. The high C:N reported during the spring bloom is probably due to the rich mucopolysaccharide matrix produced, in its colonial phase, by *Phaeocystis sp.* which dominated the Menai Strait waters during this time of the year (see Chapter 3) but it is not probably eaten in large amount by copepods (see above). Thus, it can be argued that relating fecundity to total or fractions of this index would be little different or worse than relating fecundity to total Chl since C:N ratio, particularly in coastal areas, may be overestimated for instance, by the presence of inorganic sediments (Rodriguez, 1998). It would be more helpful, therefore, if more studies would focus on the quality and quantity of the specific diet ingested by the copepods rather than trying to relate copepod EPR with the average composition of the potential food sources in the field.

Large amounts of flocculate material and detritus were observed in the Menai Strait throughout the autumn-winter possibly re-suspended from the sediments by the frequent storms and tidal activity. The ability of omnivorous coastal copepods to feed on suspended detritus has been reported in the past (Poulet, 1976; Roman, 1977& 1984; Finenko & Romanova, 1991; Buskey *et al.*, 1999). Although, detritus may have represented a source of food for *T. longicornis* in the autumn-winter months when food-stuff was limited, this source was evidently insufficient in quantity or quality to support high EPR.

The present study has shown that EPR in *T. longicornis* was significantly inversely related to both an index of total suspended particles and to tidal range even at times when potential food sources and temperature in the field were relatively stable. Very few studies have been conducted on the effect of suspended inorganic sediments on copepod feeding rates and EPR (White & Dagg, 1989; Butler, 1995) and none, to date, have been carried out on *T. longicornis*. Since suspended sediments are characteristic of coastal waters and shallow shelf seas it is surprising that their impact on copepod feeding and secondary production has not been rigorously addressed.

The important role of tidal stirring in the Irish Sea has been recognised for over 20 years (Simpson & Hunter 1974) and has long been correlated to water column

turbidity (Mitchelson, 1984; Weeks, 1989; Kratzer *et al.*, 2000). However, since tides are the same in winter and summer, tidal stirring alone cannot be representative of the seasonal variation of turbidity in the Irish Sea. Turbidity will, in fact, depend also on seasonal variation in wind strength (Weeks, 1989), riverine discharge (Lindsay *et al.*, 1996) and flocculation of particles (Jones *et al.* 1997). As a result, the influence of tidal range reflected sub-groups of EPR associated with "bloom" and "non-bloom" conditions. The distinctive high and low productivity clusters of EPR observations for essentially the same functional relationship between EPR and tidal range indicate that other factors such as food concentration/quality are clearly of greater impact than tidal range (hence presumably SPM). But in both cases (i.e. high and low productivity) the significant negative relationship with tidal range is indicative of lower production rates when sediment loading is high, even over a single neap/spring tidal cycle.

Butler (1995) has reported that all concentrations of suspended sediments significantly lowered the ability of the herbivorous fresh water copepod *Diaptomus ashlandii*, to locate and ingest micro-algae. Gasparini & Castel (1997) have suggested that the low fecundity of *Acartia bifilosa* in part of the Gironde estuary may be related to poor feeding conditions associated with high suspended particulate loading. Thus, it is not unreasonable that high sediment load in the water column might have also reduced *T. longicornis* EPR in the Menai Strait, through lowering ingestion rates. Bucham *et al.*, (1967) found that in the Menai Strait SPM was inversely correlated to temperature. Thus, the apparent increase in EPR with temperature observed during winter-spring 1997 when food sources increased little might have been due to the decline in suspended sediments rather than to a direct effect of temperature on copepod EPR.

The present study has shown that in the Menai Strait the spring-autumn EPR maxima increased between 1996 and 1998. The low *T. longicornis* EPR during spring 1996 when food sources for copepods were plenty has no easy explanation. Maximum *T. longicornis* EPR in the field usually coincided with the phytoplankton spring bloom and the ciliate increase. Since sampling rate during the spring phytoplankton increase for the 3 years is comparable it is unlikely that the sampling frequency biased the results. Moreover, since there was no apparent variation in the concentration and species composition of the food available to the copepods during the spring bloom, there are no apparent reasons to believe that the lower egg production in 1996 may be due to food quality. The annual variation in the proportion of copepods producing eggs, shows a

clear seasonal trend. The CV stage and adult females are very similar and, therefore, difficult to tell apart (WCM Klein-Breteler, pers.comm.). Thus, in routinely measuring of EPR it is likely that a proportion of non-fecund CVs may be included by accident in the measurements. The inclusion of these immature females will be more likely the higher is their proportion within the population. Although ~ 100 % of the copepods measured during spring 1996 produced eggs the per capita fecundity was as low as ~ 0.075 µg egg-C µg fem-$C^{-1}day^{-1}$. One of the most striking differences between 1996 and the other two years was the lower rate of increase in temperature and the later development of the spring bloom (See Chapter 3). Because both temperature and food availability affect the rate of development and growth in *T. longicornis* (Klein Breteler & Gonzalez, 1986), population growth must have been slower in 1996 than during 1997 and 1998. Slow population development may have resulted in an unusually high proportion of over-wintering old females (and possibly immature CVs) in the spring population. Zero or low EPR measured *in situ* or laboratory studies are attributed either to the immature stage of the female or to their senescence (Ianora *et al.*, 1989; Ohman & Runge, 1994; Rey *et al.*, 1999). Thus, a preponderantly aged/immature female population in 1996 may have resulted in low EPR (particularly weight specific) and slow population growth.

Chapter 5

Egg hatching success in *Temora longicornis*

5.1 Introduction

Compared with studies on egg production rates (EPR), there are only a few studies on *in situ* egg hatching success (HS) in copepods. Measuring fecundity is only the first step in analysing copepod population dynamics since not all eggs are inherently viable (Laabir *et al.*, 1999; Miralto *et al.*, 1999) and many copepod species produce resting eggs which will only hatch when suitable environmental and physiological conditions occur (Dahms, 1995; Castro-Longoria & Williams, 1999).

Estimates of egg HS in the field and in laboratory studies have demonstrated considerable variability with low HS usually attributed to factors like low oxygen concentration (Lutz *et al.*, 1992), lack of re-mating (Ianora *et al.*, 1992), post- and pre-reproductive female (Ianora & Poulet, 1993), inhibitory compounds produced by diatoms (Chaudron *et al.*, 1996), production of resting eggs (Sullivan & McManus, 1986), low egg organic content (Guisande & Harris, 1995), low or inappropriate egg fatty acid content (Pond *et al.*, 1996), the presence of predators (Hairston, 1987) and crowding of the adult copepods (Ban & Minoda, 1994).

Among these factors the low nutritional value of the potential food and the inhibiting effect of some microplankton groups have been recently considered as the main causes of egg mortality and abnormal nauplii measured in field and laboratory experiments (Guisande & Harris, 1995; Ianora *et al.*, 1999). Traditionally, diatoms have been regarded as providing the bulk of the primary food supporting pelagic food chains that lead, through suspension-feeding planktonic copepods, to top consumers and important fisheries (Riley, 1947). Very recently, however, the classic role of diatoms as a beneficial food for copepods has been questioned mainly on the basis of laboratory evidence showing the inhibitory effect of diatoms on the embryonic development of copepods (Ianora & Poulet, 1993; Laabir *et al.*, 1995; Uye, 1996). Poulet *et al.* (1994) demonstrated that extracts from the diatom, *Thalassiosira rotula*, inhibited embryogenesis in the marine copepod, *Calanus helgolandicus* and more recently Lee *et al.*, (1999) showed the detrimental effect of cultured diatoms on egg production and hatching success of *Pseudocalanus newmani* in the laboratory. Several studies (Ianora *et*

al., 1999; Miralto *et al.* 1999) have suggested that the cause of such inhibition should be attributed to the accumulation of aldehyde compounds, derived from the diatoms, in the ovary of female copepods that had been feeding on diatom blooms (Poulet *et al.*, 1995). Despite laboratory results, direct clear evidence of *in situ* deleterious effect of diatoms on HS is still lacking (Miralto *et al.* 1999; Ban *et al.*, 2000). Thus, Miralto *et al.*, (1999) reported low HS in *C. helgolandicus* and *A. clausi* during diatom blooms in the Adriatic Sea, whereas Ban *et al.*, (2000) on *P. newmani* and Irigoien *et al.*, (2000) on *C. helgolandicus* could find no similar effect during extensive diatom blooms. Given such contradictory evidence more field details is clearly required (Ban *et al.*, 2000).

Many marine and freshwater species, including copepods, undergo a period of suppressed development, dormancy, involving physiological and morphological changes (Danks, 1987; De Stasio, 1990). Copepod dormancy is expressed in various ontogenetic stages, such as resting eggs, juvenile and adult encystment or arrested development of non-encysted copepodids and adults (Dahms, 1995). The occurrence of the subitaneous (i.e. hatching) and resting egg phase in the life cycle of small marine calanoid copepods, including those belonging to the family *Temoridae*, is well documented (Marcus, 1996). The two types of egg may or may not be distinguishable morphologically from each other (Kasahara *et al.*, 1974). Whereas, the resting eggs of *Acartia sp.*, for example, differ from subitaneous eggs in having long spines, in *T. longicornis* resting and subitaneous eggs are morphologically indistinguishable (Dahms, 1995; Castro-Longoria & William, 1999).

Ecologically, dormancy is an energy saving trait allowing the individual to bridge periods of adverse environmental conditions (Marcus, 1996). The production of resting eggs is a recognised strategy that copepod species, particularly those living in coastal waters, have evolved as a means of maintaining their population against advective losses and to overcome unfavourable conditions occurring during strong seasonal fluctuations in the natural environment (Mauchline, 1998). The production of resting eggs in copepods is triggered by species specific environmental factors including changes in photoperiod, temperature, population density, food availability, biological clocks, competition and predation (Dahms, 1995).

Typically such copepod species disappear from the water column for portions of the year but remain in the region as benthic resting eggs. Resting eggs can become buried in the sediments but can remain viable for as long as 40 years (Marcus *et al.*, 1994) offering a potential mechanism to regenerate pelagic populations even after

several unfavourable years (Lindley, 1990). In the bottom sediments of several coastal areas in the Irish Sea, Lindley (1990) has reported the existence of banks of resting eggs of small calanoid species including *T. longicornis*, *C. typicus*, *C. hamatus* and *Acartia sp.*

The aim of the present study was to describe the seasonal and inter-annual variation in *T. longicornis* egg HS in the Menai Strait, Eastern Irish Sea, in relation to relevant biological and physical variables.

5.2 Material and Methods

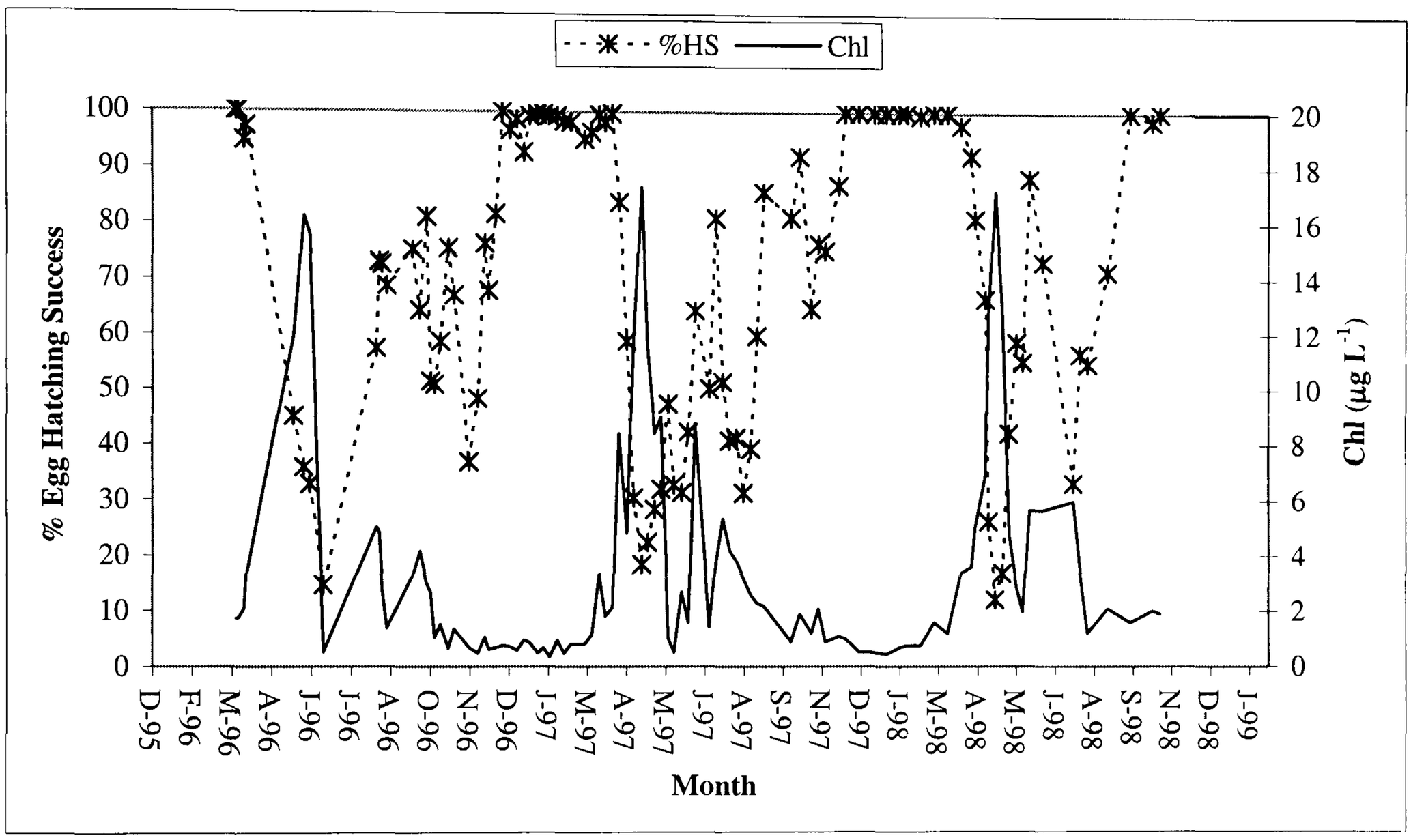
(See Chapter 4)

5.3 Results

5.3.1 Egg hatching success in the Menai Strait

The results of the seasonal egg HS survey carried out for *T. longicornis* in the Menai Strait between 1996 and 1998 is presented in Figure 5.1.

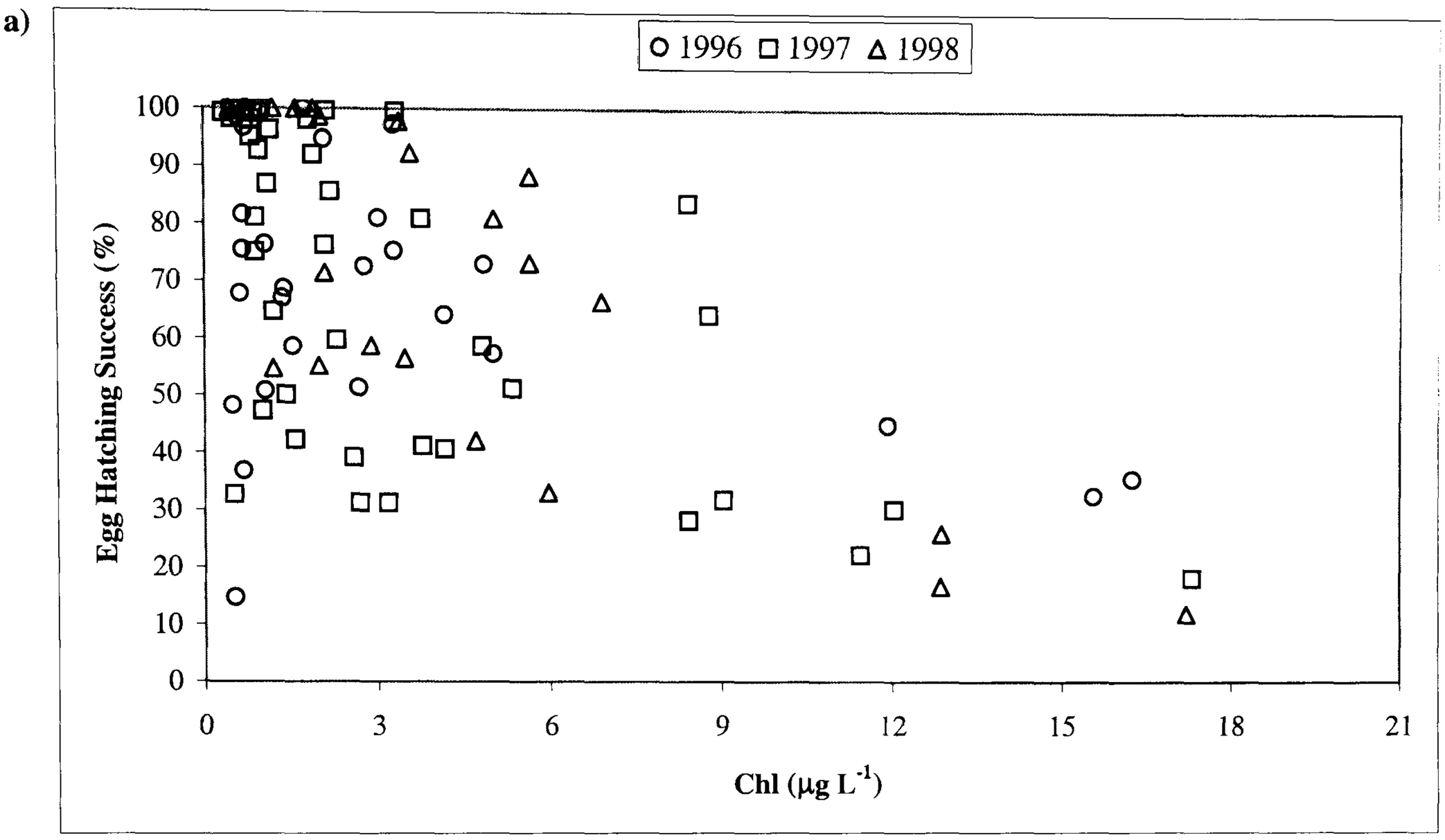
Figure 5.1: Seasonal trend of *T. longicornis* egg HS (%) measured in the Menai Strait between 1996 and 1998. The seasonal change in chlorophyll-a (Chl, μg L^{-1}) concentration is also shown.



The seasonal pattern in egg HS recorded in the field is very variable but very similar between years. Minimum HS ~ 12 % was measured in spring whereas maximum HS ~ 100 % was recorded in winter. The lowest HS recorded over the time of investigation always occurred when EPR reached their maximum field values (See Chapter 4, Figure 4.1). Figure 5.1 also shows that decrease in HS appeared to take place with increase in phytoplankton biomass (i.e. measured as Chl).

A plot of the HS versus Chl measured over the whole year indicated the presence of an inverse relationship (Pearson correlation coefficient $r = -0.61$; $p < 0.001$; d.f. = 95) with HS decreasing when ambient Chl rose to between 3 μg-Chl L^{-1} to 4 μg-Chl L^{-1} (Figure 5.2, a)).

Figure 5.2: Scatter plot of *T. longicornis* eggs HS (%) and Chl (μg L^{-1}) for (a) the whole year and (b) winter and spring only between 1996 and 1998.

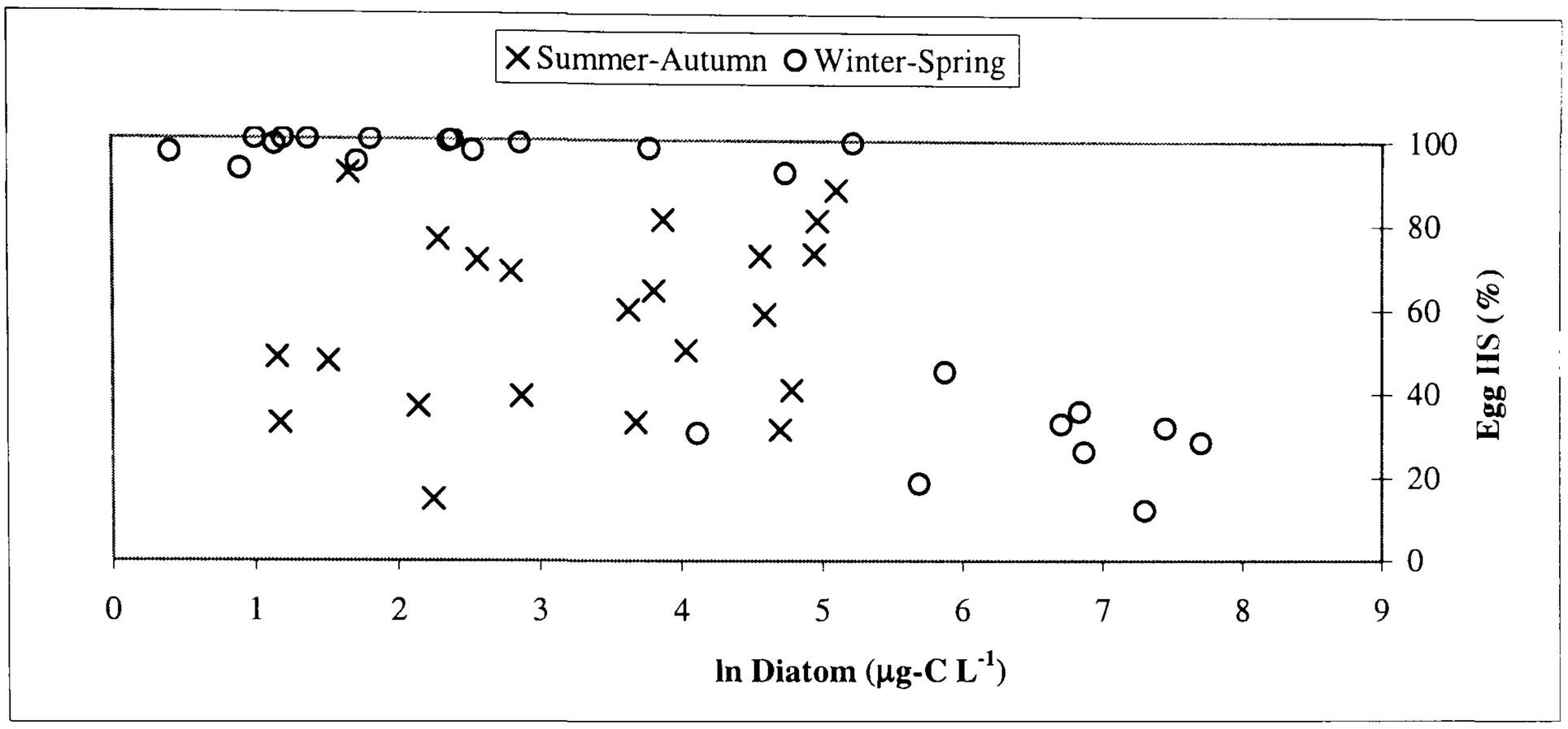


The lower correlation obtained between HS and Chl considering the whole year indicates a large spread in HS, which is only loosely related to Chl. The large spread of the observations with HS < 100% measured at relatively low Chl concentrations correspond mostly to observations collected after the phytoplankton bloom in summer and autumn. On the other hand, if the winter and spring data only are considered for all the 3 years (Figure 5.2, b) the relationship between HS and Chl becomes less variable (Pearson correlation coefficient $r = -0.94$; $p < 0.001$; d.f. = 39).

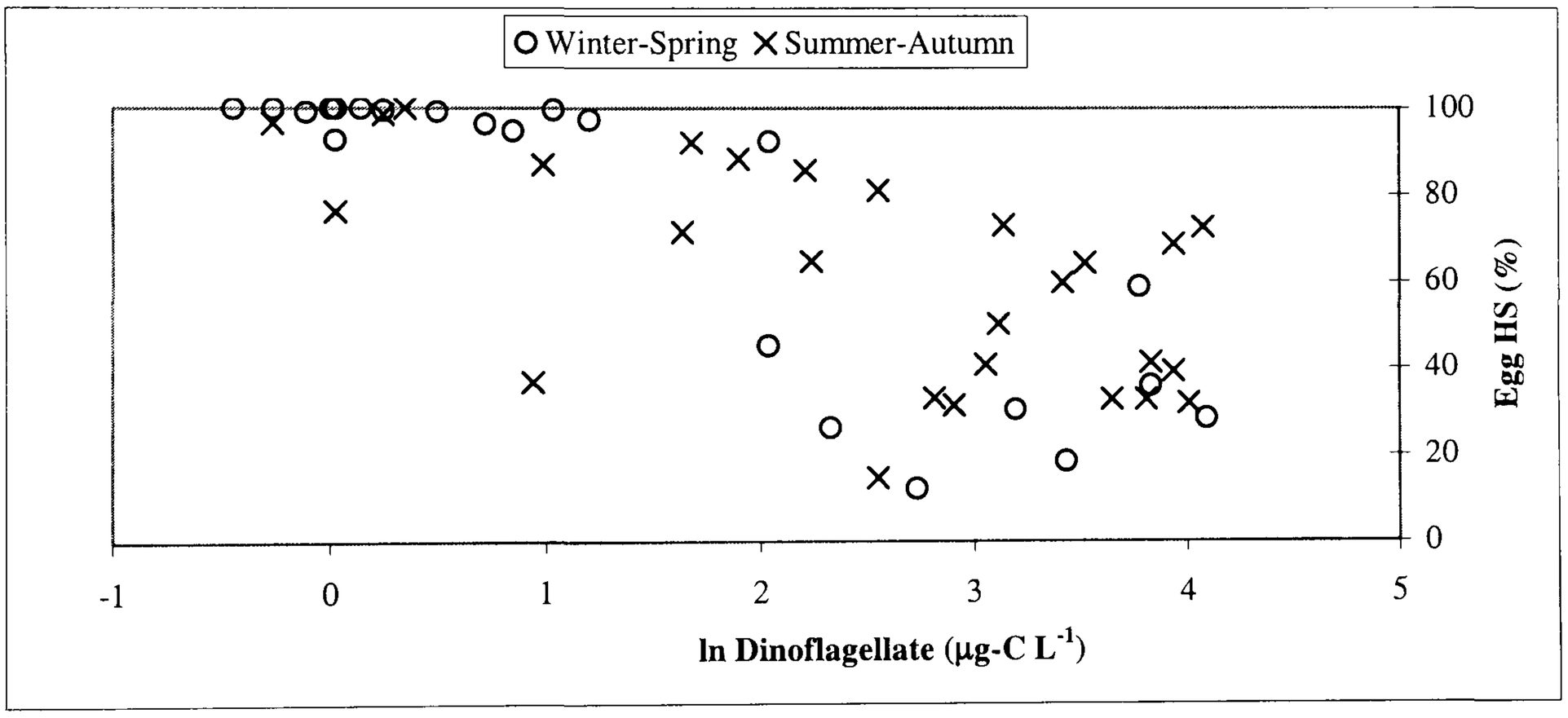
The scatter plots of egg HS and the natural log of diatom, dinoflagellate and ciliate abundance are shown in Figure 5.3, (i.e a-c).

Figure 5.3: Egg hatching success (HS, %) in *T. longicornis* in relation to the natural log of a) diatom (µg-C L^{-1}), b) dinoflagellate (µg-C L^{-1}) and c) ciliate (µg-C L^{-1}) between 1996 and 1998.

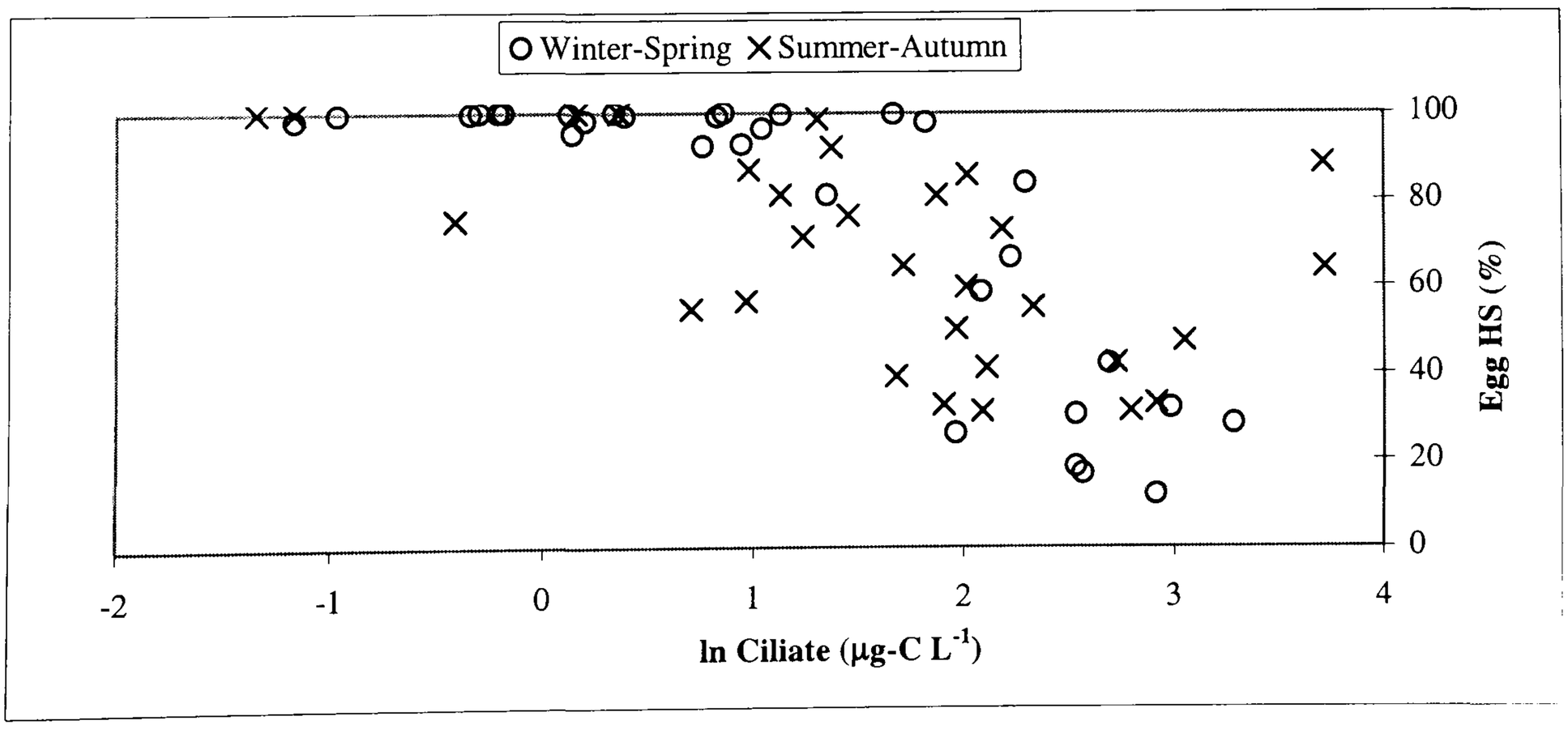
a)



b)



c)



Again, despite the large scatter Figure 5.3 show a decreasing trend in HS with ln diatom-C (Pearson Correlation, r = - 0.451; p =0.002; d.f. = 44), ln dinoflagellate-C (Pearson Correlation r = - 0.376, p = 0.008; d.f. = 47) and ln ciliate-C (Pearson Correlation r = - 0.465, p > 0.0001; d.f. = 59). Similarly to the HS vs Chl plot, the decrease in HS with diatom carbon showed a wider spread in summer/autumn than in winter/spring. Decline in egg HS occurred with diatom-C concentrations ~3 μg-C L^{-1} over the whole year, but at diatom-C concentration between ~54 and 150 μg-C L^{-1} in spring. In the case of the dinoflagellates and the ciliates the difference in egg HS between winter/spring and summer/autumn was less obvious. Decrease in HS with either dinoflagellate or ciliate carbon increase was recorded when the concentration of these two microplankton groups approached ~3 μg-C L^{-1}.

5.3.2 The EPR and HS of *T. longicornis* and *C. hamatus* during spring 1997

Table 5.1 shows the EPR and the HS of *T. longicornis* and *C. hamatus* during spring 1997.

Table 5.1: Results from two sample T-test between means (± 95% C.I.) of EPR and HS for 20 individual *T. longicornis* and *C. hamatus* females. The mean and range of the Cephalotorax lenght (C.L.) of the copepods is also shown.

Species	C. L. (μm)	EPR (± 95% C.I.)	HS (± 95% C.I.)
C. hamatus	1128 (940-1260)	60.35 (± 15.7)	38.9 (±11.8)
T. longicornis	1038 (860-1260)	41.45 (± 11.5)	31.2 (±10.8)

Although *C. hamatus* had, on average, higher EPR (i.e. as mean ± SE) ~ 60 ± 8 egg $female^{-1}$ day^{-1} (range 0-135) than *T. longicornis* ~ 41 ± 5.9 egg $female^{-1}$ day^{-1} (range 0-110) the two-sample T-test statistic showed that, during the spring phytoplankton bloom, there were no significant differences between the mean fecundity (t = 1.90; p = 0.065; d.f. = 38, Pooled StDev = 31.5) of these two copepod species.

Similarly, a Two-sample T-test on arcsine transformed percentage data showed no significant differences (t = 0.48; p = 0.63; d.f. = 35, Pooled StDev = 48.7) between the egg HS of the two copepod species (Table 5.1).

Similarly to *T. longicornis*, prior to the phytoplankton spring bloom, the HS of *C. hamatus* eggs always approached 100 %. The present findings indicate that during the

spring phytoplankton bloom in the Menai Strait high EPR coincided with low HS for both copepod species.

5.3.3 Observations on eggs size and morphology

The diameter of the eggs produced by *T. longicornis* in the Menai Strait from winter to summer 1997 are shown in Table 5.2.

Table 5.2: Mean (± SE) egg (n = 30) diameter (viz. ∅, in µm) of *T. longicornis* and temperature (T, °C) measured in the Menai Strait between January and August 1997.

Month	T (°C)	Egg ∅ (µm)
January	3.5	85.8 (± 0.76)
March	5	86.2 (± 0.63)
May	9	85.5 (± 0.65)
August	17	86.8 (± 0.65)

The mean (± SE) egg diameter ranging from 85.5 (± 0.76) µm to 86.8 (± 0.65) µm appeared to differ little through the months despite temperature change from 3.5 °C to 17 °C (Table 5.2.).

Table 5.3: Results of One-Way Anova comparing the means in *T. longicornis* egg diameter (in µm) with different temperature (i.e. T, in °C) measured in the Menai Strait during 1997 (See Table 4.5).

Source	DF	SS	MS	F-value	P-value
Egg diameter	3	25.6	8.5	0.62	0.6
Error	116	1582.7	13.6		
Total	119	1608.3			

The results of an Analysis of Variance shows that there were non significant differences between the mean diameter of eggs spawned by *T. longicornis* at different times of the year ($F_{[3, 116]} = 0.62$; $p = 0.6$, Table 5.3).

Microscopic observations were also carried out on eggs that hatched and those which did not. When observed under a high power microscope eggs that hatched

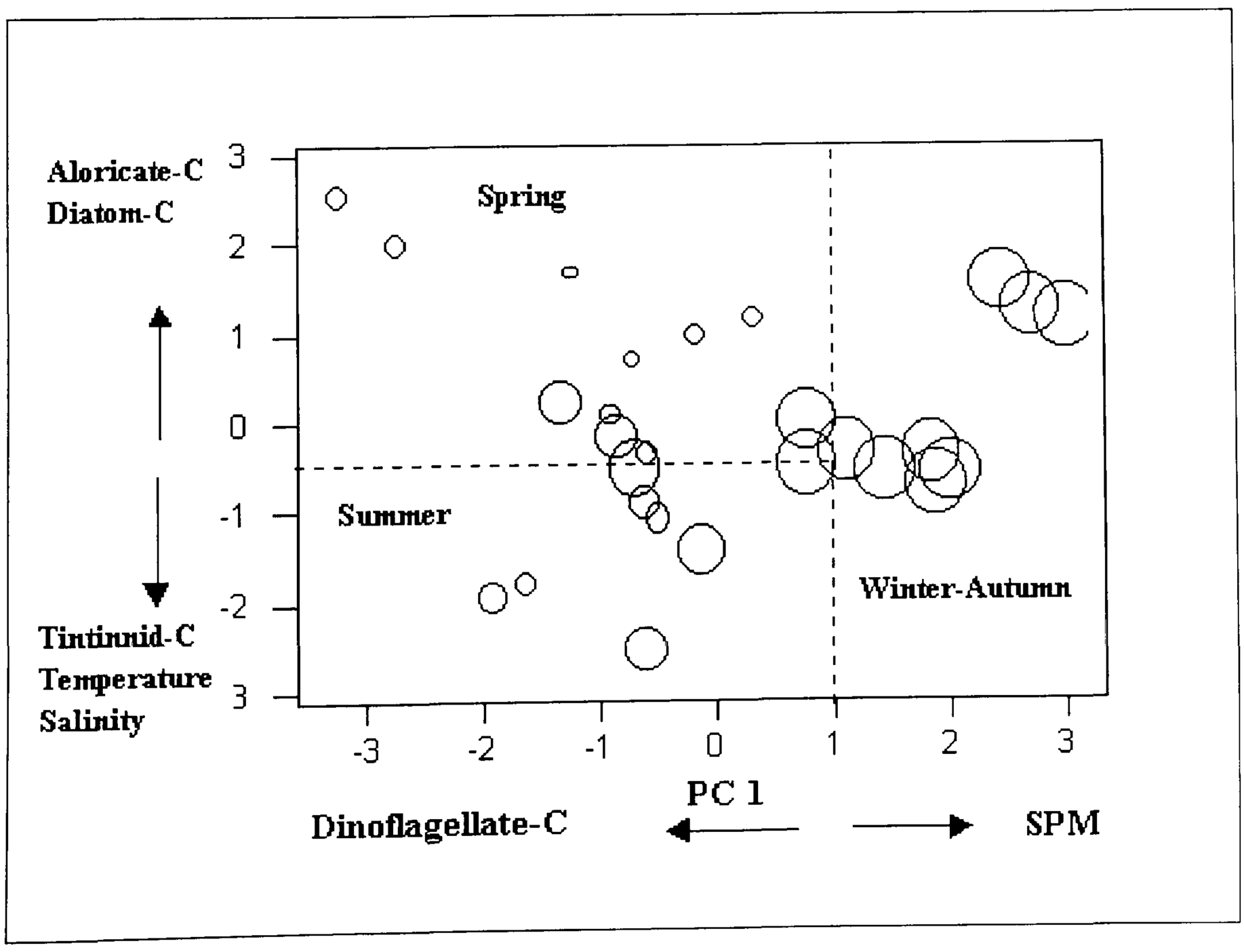
appeared translucent and smooth on the surface whereas the eggs that did not hatch always appeared opaque and with a granular surface.

5.3.4 Principal component analysis

The principal component analysis (PCA) was conducted on a set of variables which are likely to influence the % egg HS of *T. longicornis*. In the PCA the variables were compared by treating the days as replicates to avoid the effect of the temporal scale. The first three principal components accounted for 78 % of the variability within the data set. Variables contributing to the PC1 axis were SPM, and dinoflagellate carbon whereas variables contributing to PC2 axis were temperature, diatom carbon, aloricate ciliates carbon, tintinnid ciliates carbon and salinity.

An ordination of PC1 and PC2 is presented in Figure 5.4 for HS. Spheres are scaled to HS in Figure 5.4. The size of the spheres and their position in relation to the PC1 and PC2 axis shows that periods of high and low % HS are clearly separated (Figure 5.4).

Figure 5.4: Ordination of the scores of variables derived from a Principal Component Analysis (PCA) of biotic and abiotic variables measured between 1996 to 1998 in the Menai Strait. Spheres are linearly scaled to % egg HS. Smallest spheres = 12 %; Largest Spheres = 100 %.



Low HS was measured in spring and early summer and was associated with high diatoms, aloricate ciliates and dinoflagellates carbon. High HS were found in winter, late summer and autumn and it was associated with both low and high temperature and high SPM, tintinnid carbon and salinity (Figure 5.4).

5.4 Discussion

The present investigation has shown that the egg HS of *T. longicornis* from the Menai Strait is very variable but characterised by a distinct seasonal pattern. The lowest HS ~12 % occurred during the spring phytoplankton bloom and maximum HS ~100 % in winter. Such cyclical variability in HS has not been reported previously in *T. longicornis*. Tang *et al.*, (1998), for instance, have recently shown that the annual HS in *T. longicornis* from Long Island Sound ranged only between 70 % and 90 % without notable seasonality. Variability in HS in *T. longicornis* may well be site specific and as such egg HS should always be measured in routine determinations of EPR for estimating copepod recruitment (Poulet *et al.*, 1995; Ban *et al.*, 2000).

Low HS in field and laboratory studies has been often attributed to the poor nutritional quality of the diet measured as either low C:N ratio, lipid or protein content (Jonasdottir & Kiorboe, 1996; Kleppel & Hazzard, 2000). The macro-nutrient content of the seston was not assessed in the present investigation. However, the lowest HS usually occurred when EPR was maximal and during high microplankton abundance and species diversity. High EPR suggests that the copepods did not suffer nutritional deficiency.

Low nutritional quality and reduced food availability may result in the production of smaller eggs by copepods. Guisande & Harris (1995) have attributed an increase in *C. helgolandicus* HS to an increase of up to 20 % in egg diameter. They argue that larger eggs contain more reserves, conferring higher chance of survival to the developing nauplii. The present study and Tang *et al.*, (1998) found no significant seasonal differences in the egg diameter of *T. longicornis* suggesting that the level of nutrient reserve was probably not a crucial factor affecting egg HS.

The decrease in HS in *T. longicornis* from the Menai Strait coincided with the spring phytoplankton increase in all the 3 years studied. Furthermore, there was a highly significant negative correlation between HS and phytoplankton biomass (measured as Chl). The spring Chl rise was mainly due to increased abundance of the diatom *R. delicatula* and the flagellate *Phaeocystis sp.* (See Chapter 2, Blight *et al.*, 1995).

Consequently, copepod's HS was also negatively correlated to total diatom abundance and to ciliates carbon both of which are positively correlated to Chl. Despite traditional opinion, a number of studies have questioned the role of certain groups of microplankton, particularly diatoms, as a staple food source for copepods (Ban *et al.*, 1997). In laboratory experiments, several diatom species have been found to prevent embryogenesis in copepods (Ianora *et al.*, 1996). Ianora *et al.*, (1999) and Miralto *et al.*, (1999) have identified aldehyde compounds, produced by diatoms, as the toxic agents inducing low HS. It has been argued that a negative correlation between HS (or EPR) and the abundance of different microplankton species may be indicative of a direct toxic effect of such organisms on copepods reproductive physiology or embryology. The negative correlation obtained in field studies between EPR and the density of the dinoflagellate *Gyrodinium aureolum* (Irigoien *et al.*, 2000) and between HS and the abundance of the diatom *Skeletonema costatum* and *Pseudo-nitzschia delicatissima* (Miralto *et al.*, 1999) have been considered strong evidence for an ecologically negative effect of the microplankton species on copepod production.

Reluctance to accept a possible toxic effect of diatoms on copepods stems from the fact that copepod EPRs generally increase during the spring diatom bloom (Present study, Niehoff *et al.*, 1999; Irigoien *et al.*, 2000). As already mentioned, however, the lowest HS in *T. longicornis* from the Menai Strait measured during the spring bloom usually coincided not only with high diatom concentrations (particularly *R. delicatula*) but also with the highest EPRs. Similarly, Ban *et al.*, (1997) (laboratory studies) and Miralto *et al.*, (1999) and Starr *et al.*, (1999) (field studies) found that EPR increased with diatom concentration whereas HS decreased. Ban *et al.*, (1997) found that in 29 out of 37 cases, a diatom diet significantly reduced copepod egg HS. With the exception of the present study, there have been no reports so far indicating whether *R. delicatula* can produce compounds that are toxic or significantly decrease HS in copepods.

The Prymnesiophyte *Phaeocystis sp.*, on the other hand, is known to produce, significant amounts of dimethylsulfopropionate (DMSP) which in turn gives rise to dimethylsulfide (DMS) and to acrylic acid, two known toxins (See Chapter 3). Although, DMSP and DMS may well be innocuous for *T. longicornis* (this species can sequester DMSP in its cell tissues and within its gut (Tang *et al.*, 2000) and DMS is very volatile) the effect of acrylic acid on copepod production is not yet known. Whether the decreased HS during the spring bloom in the Menai Strait was due to the diatom *R. delicatula* or to the Prymnesiophyte *Phaeocystis sp.* or else is difficult to

ascertain. It is clear, however, that even after the spring phytoplankton bloom, when other microplankton species were relatively more abundant than diatoms in the water column, many *T. longicornis* eggs were still not hatching. Only during the winter, with low temperatures and relatively low potential food abundance did egg HS approach a consistent 100 %.

The nature of the non-hatching eggs was not thoroughly investigated so that at the present it is not clear whether the low HS was due to high egg mortality or high numbers of resting eggs. Although, the resting eggs of *T. longicornis* have been found in the eastern Irish Sea (Lindley, 1990), the proportion of resting egg produced by copepods has seldom been assessed and the non–hatching eggs have usually been considered non viable (Ban *et al.*, 1997). Where there are no morphological differences to distinguish resting eggs from potentially viable ones (as in the case of *T. longicornis*) then long term incubations possibly over decades, are needed and even then it is essential to distinguish resting from dead eggs (Dahms, 1995). It is little wonder that routine determination of percentage resting egg in *T. longicornis* has hardly been attempted (Lindley, 1990).

On the other hand, the difference between egg surface, that is, translucent and smooth in hatching eggs vs opaque and granular in non-hatching eggs, suggests that the two types may be physiologically different eggs (Marcus, 1996). Although consistent the presence of a difference in the egg surface alone is not sufficient to determine whether the non-hatching eggs found were viable resting eggs or not. Further microscopic observations, looking at the surface pattern of the eggs using scanning electron microscope (SEM) and at the presence/absence of an outer thicker chorion using transmission electron microscope (TEM), would be required to investigate the nature of these eggs (Ianora & Santella, 1991).

The HS of the eggs produced by *C. hamatus* in spring was comparable to that of *T. longicornis* indicating that, whatever it was, the mechanism that reduced HS was common to both copepod species living in the Menai Strait at this time of the year.

Chapter 6

Factors affecting egg production, hatching rate and success in *Temora longicornis* in the laboratory

6.1 Introduction

In nature the production of marine animals depends on a number of physical and biological factors which are often inter-correlated. For this reason, the causal relationships existing between development /production and environmental variables have often been investigated in laboratory experiments to isolate major factors (Runge, 1985; Ianora *et al.*, 1995).

In recent years the composition and the characteristics of the diet have been increasingly identified as important factors for the productivity of copepods (Kleppel & Hazzard, 2000). For instance, differences in the reproductive responses of copepods have been attributed to subtle differences between microplankton types, such as the presence and absence of silica wall (e.g. diatoms vs flagellates), shape and size of cells, palatability or nutrient concentration per unit cell volume (Huntley *et al.*, 1986; Paffenhofer, 1988). Although, food composition plays a major role in the fecundity and HS of copepod eggs the food properties and characteristics responsible for these variations are not well established. Laboratory experiments have also shown that the development of the embryo and the hatching success of the brood of several marine invertebrates including copepods can be affected by the nutritional quality and/or the presence of toxic compounds in the diet of the adult female (Ban *et al.*, 1997). Recent laboratory studies have indicated that different diatom extracts or unialgal diatom diets may have a quite specific effects on the egg production rate and egg hatching success of different copepod species (Ban *et al.*, 1997).

Other studies have stressed the role of temperature (Huntley & Lopez, 1992) and remating (Parrish & Wilson, 1978; Ianora *et al.* 1989) in determining fluctuations in reproductive rates. In addition, the subitaneous eggs of some copepod species can be inhibited from hatching by darkness when covered, for instance, by sediments on the bottom of the sea (Lindley, 1997). In this respect, Landry (1975) has reported that darkness, could affect short term copepod productivity, by completely and immediately suppressing hatching of the eggs of *Acartia clausi*.

All estimates of the production of aquatic animals involve knowing the duration of the development period. The more exactly this is known, the more adequately and precisely may secondary production be estimated (Winberg, 1971; Guerrero *et al.*, 1994).

The duration of poikilotherm development depends upon temperature, whose range in nature may be very wide (Prosser & Brown, 1961; Schmidt-Nielsen, 1996). Thus, for production estimate purposes it is necessary to have some idea about the nature of the relationship between temperature and the duration of the development. The development time (D) in days from laying to hatching of copepod eggs has been classically represented as a curvilinear function of temperature T (in °C) by Belehradek's (1935) equation, $D = a*(T-T_0)^{-b}$ where a, T_0 and b are three constants to be estimated (McLaren, 1966). The Belehradek's (1935) equation has been the most commonly used mathematical model to describe the relationship of development to temperature in biological oceanography over the last 40 years (McLaren, 1963; Uye, 1988). However, there is no general agreement about the most appropriate model with which to relate development to temperature and other models have been preferred to that of Belehradek (Lindley, 1990; Miranda *et al.*, 1990; Guerrero *et al.*, 1994). Guerrero *et al.*, (1994) have claimed that other models like that of Arrhenius or Tauti, could better describe the temperature-development relationship as they relate development rate, d (i.e. d = 1/D), to temperature and require the estimation of only two rather than three constants (See Wimberg, 1971).

Embryonic development has been reported to vary not only with temperature exposure but also according to the time and direction of the thermal acclimation of the copepod (Landry, 1975; Hart & McLaren, 1978), the size and quality of the eggs (McLaren *et al.*, 1969).

The aim of the present section was to assess, through laboratory experiments, the effect of temperature and different algal diets on the embryonic development, EPR and hatching success of *T. longicornis*.

6.2 Material and Methods

6.2.1 Egg hatching time with temperature

An experiment was carried out to determine the hatching (hence incubation) time and hatching success of eggs produced by *T. longicornis* acclimated at different

(ambient) water temperatures. Collection of the copepods took place during January and August 1996 at the winter *minimum* (~5 °C) and summer *maximum* (~17 °C) environmental temperatures respectively.

Before the start of the experiment, copepods were maintained in the laboratory for at least 1 week in temperature controlled water baths at the temperature (i.e. either 5 °C or 17 °C) of the Menai Strait at the time of their capture as described in Chapter 3.

During the experiment, females and males *T. longicornis* were incubated together, for egg production, in groups of 10-15 in crystallizing dishes of 250 ml capacity containing U.V.F.S.W. and 10-50 cells μl^{-1} of *R. reticulata*. The crystallizing dishes were, then kept in temperature controlled water-baths at 5 °C and 17 °C ± 0.2 °C in January and August respectively. In these conditions animals produced eggs continuously over the 24 hours incubation time of the experiment. The dishes were monitored every 1-2 hours within a 10-20 minute screening session using a dissecting microscope and all the eggs produced were collected with a plastic pipette. In this way a large number of eggs (of similar age, i.e. 1-2 hours) produced by a wide number of females could be simultaneously collected in order to reduce any lag time in egg hatching rate due to the age of the egg. Batches of 20 to 30 eggs were incubated in 20 ml glass vials containing filtered seawater at the selected temperature and randomly allocated to a series of water-baths set at temperatures ranging from 0 °C to 25 °C.

During the experiment, the vials were monitored at increasingly shorter time intervals to determine the time at which egg hatching started. After the onset of hatching, observations were made every 15-30 minutes, depending on the incubation temperature, to determine the number of eggs hatched.

The data were recorded as the percentage of the total number of eggs in the experiment that hatched with time. Data on percentage hatch were regressed against time to determine the time at which 50% of the eggs hatched. Time to 50% hatch was the variable used throughout this study and equates to the "hatching time" herein (Landry, 1975).

6.2.2 Effect of phytoplankton diet on EPR and hatching success

During March 1996 a series of experiments on the effect of diatom versus flagellate diet on *T. longicornis* EPR and egg HS were carried out at 5 °C, the temperature of the Menai Strait at that time.

Preliminary experiments incubating individual females in March 1996 showed that any eggs produced after a week stopped hatching thus indicating the need for remating within a week of capture. Thus, each copepod female was always incubated together with a male copepod for the rest of the experiments. Forty copepod couples were incubated in 60 ml vials and fed *ad libitum* one of the flagellates *Pavlova lutherii*, *R. reticulata* and the *diatoms Chaetocerous calcitrans* and *S. costatum* for approximately 20 days. The copepod couples were transferred to a new vial containing fresh phytoplankton every day and the eggs produced counted and further incubated at the same temperature in clean filtered seawater. The eggs were transferred with a large bore plastic pipette to clean filtered seawater every day and the number of nauplii counted over the succeeding 7 days. Incubation was stopped after no nauplii had been produced for 10 days.

6.2.3 Effect of light on hatching success

An experiment was carried out to determine the effect of darkness on the hatching success of *T. longicornis* eggs. The eggs were obtained as described above. Groups up to 6, 60 ml replicate vials containing 30 eggs were incubated at 17 °C or 5 °C in constant darkness, in constant light and 12 hours-dark/12 hours-light regime. HS was evaluated again as above.

6.3 Results

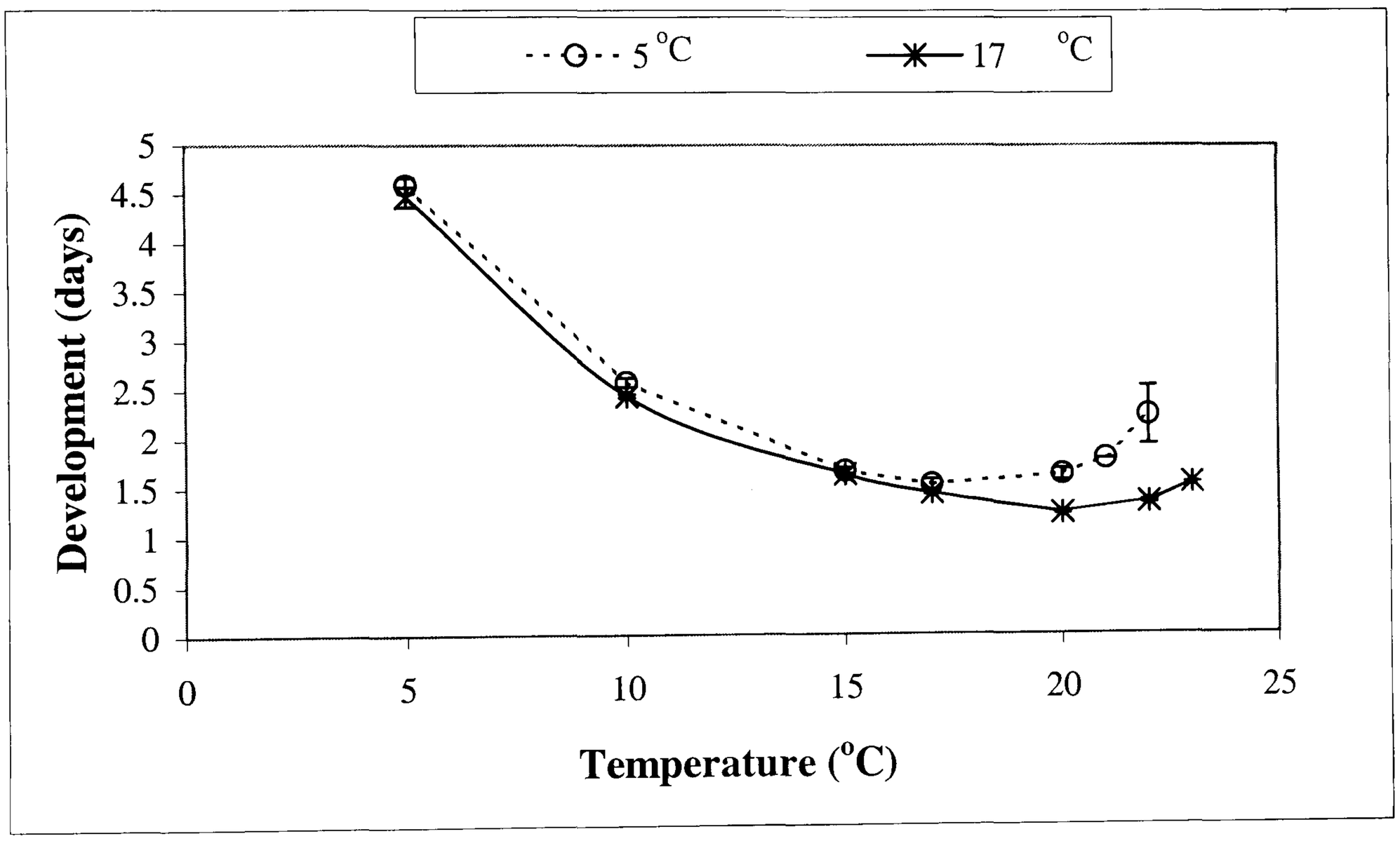
6.3.1 Eggs development and HS with temperature and thermal acclimation of the female

The plot of the development time of the eggs produced by females copepods acclimated to winter, i.e. 5 °C and summer, i.e. 17 °C temperatures is shown in Figure 6.1. *T. longicornis* egg development time (D) is characterised by a curvilinear decrease with short-term (i.e. acute) temperature rise followed by a subsequent increase beyond 17 °C and 20 °C (i.e. near and beyond the *in situ* temperature range), for cold and warm acclimated eggs respectively (Figure 6.1).

The D-temperature curve obtained for cold acclimated egg lays above that of warm acclimated eggs and this is particularly evident at high temperatures, indicating that warm

acclimated eggs can cope better than cold acclimated ones with high temperature extremes. Moreover, it is apparent that the variability in egg hatching time changes with both temperature and thermal acclimation with the development of cold acclimated eggs being less variable at low than at high temperatures and *viceversa* for the warm acclimated eggs (Figure 6.1). Although, summer acclimated females seem to produce eggs with higher thermal resistance (i.e. at least 3 °C) as compared to the winter the 95% C.I. (i.e. ± 2 x SE) of the two curves would overlap indicating no differences in D among acclimation temperatures over the temperature range examined.

Figure 6.1: Embryonic development time (D, in days) as mean (± SE) of *T. longicornis* eggs at different incubation temperatures (T, in °C) produced by females copepods acclimated at 5 °C (broken line) and 17 °C (continuous line).



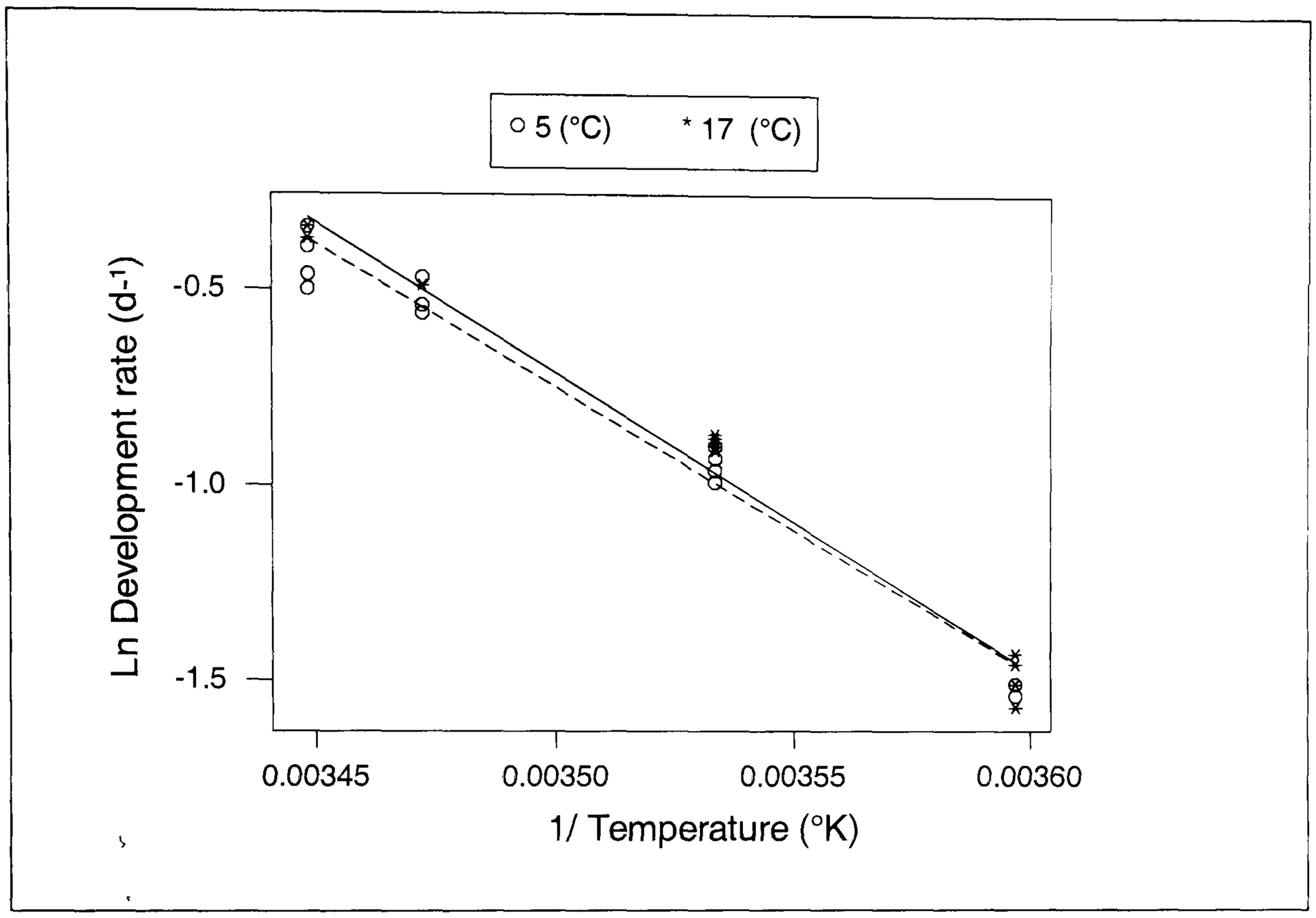
6.3.2 Comparison of egg development rates at the two acclimation temperatures

The plots presented in Figure 6.1 were linearised using the semi-log plot shown in Figure 6.2, of the Arrhenius equation (Eq 6.1),

$$\ln d = \ln a - \left(\frac{Ea}{RT} \right) \quad \text{(Eq 6.1)}$$

that is, plotting the natural log of the egg development rate (i.e. Ln d) against the reciprocal of the absolute temperature (T, in °K). In Eq 6.1, a is constant, R is the gas constant (i.e. 8.31 J $mole^{-1}$ $^{o}K^{-1}$) and Ea (i.e. in J mol^{-1}) is the activation energy constant.

Figure 6.2: Scatter plots of natural log transformed (Ln) mean (± SE) development rates (d, d^{-1}) with temperature (1/T, °K) for *T. longicornis* eggs for cold (i.e. 5 °C) and warm (i.e. 17 °C) acclimated females over the ambient temperature range. The fits of the regression equations calculated for the egg development rate of cold (continuous line) and warm acclimated (broken line) copepods are also shown.



The results of the regression analysis between *T. longicornis* embryonic development rate (d, in $days^{-1}$) and the reciprocal of the absolute temperature (T, in °K), i.e. the Arrhenius plot, are shown in Table 6.1.

Table 6.1: Regression analysis between *T. longicornis* embryonic development rate d ($days^{-1}$) with reciprocal of the absolute temperature T (in °K), i.e. Arrhenius plot, at two different acclimation temperatures (in °C). The regression equation intercept a, (± SE), the slope b (± SE), the degree of freedom (d.f.) and the Pearson correlation coefficient (r) are also shown.

Equation Type	Equation Model	Acclimation (°C)	a	b	d.f.	r	p-value
Arrhenius	$d = a \times e^{-b(1/T)}$	5	24.8 (± 1.29)	7297 (± 370)	13	0.98	>0.001
		17	26.0 (± 0.93)	7626 (± 265)	16	0.99	>0.001

Thus, the activation energy, Ea calculated from slope b (i.e. Ea/R) of the Arrhenius equation corresponded to 60.6 KJ mol^{-1} and 63.4 KJ mol^{-1} for eggs acclimated at 5 °C and 17 °C respectively.

The difference in d, between the cold and the warm acclimated eggs of *T. longicornis*, was investigated with the Two-way Anova (Table 6.2).

Table 6.2: Two-way Anova test between the means development rate of *T. longicornis* eggs with temperature (T in °C, between 5 °C and 17 °C) produced by warm (i.e. 17°C) and cold (i.e. 5°C) acclimated (i.e. A) females. AdJ=adjusted, Seq = sequential, SS = sum of square, MS= mean square.

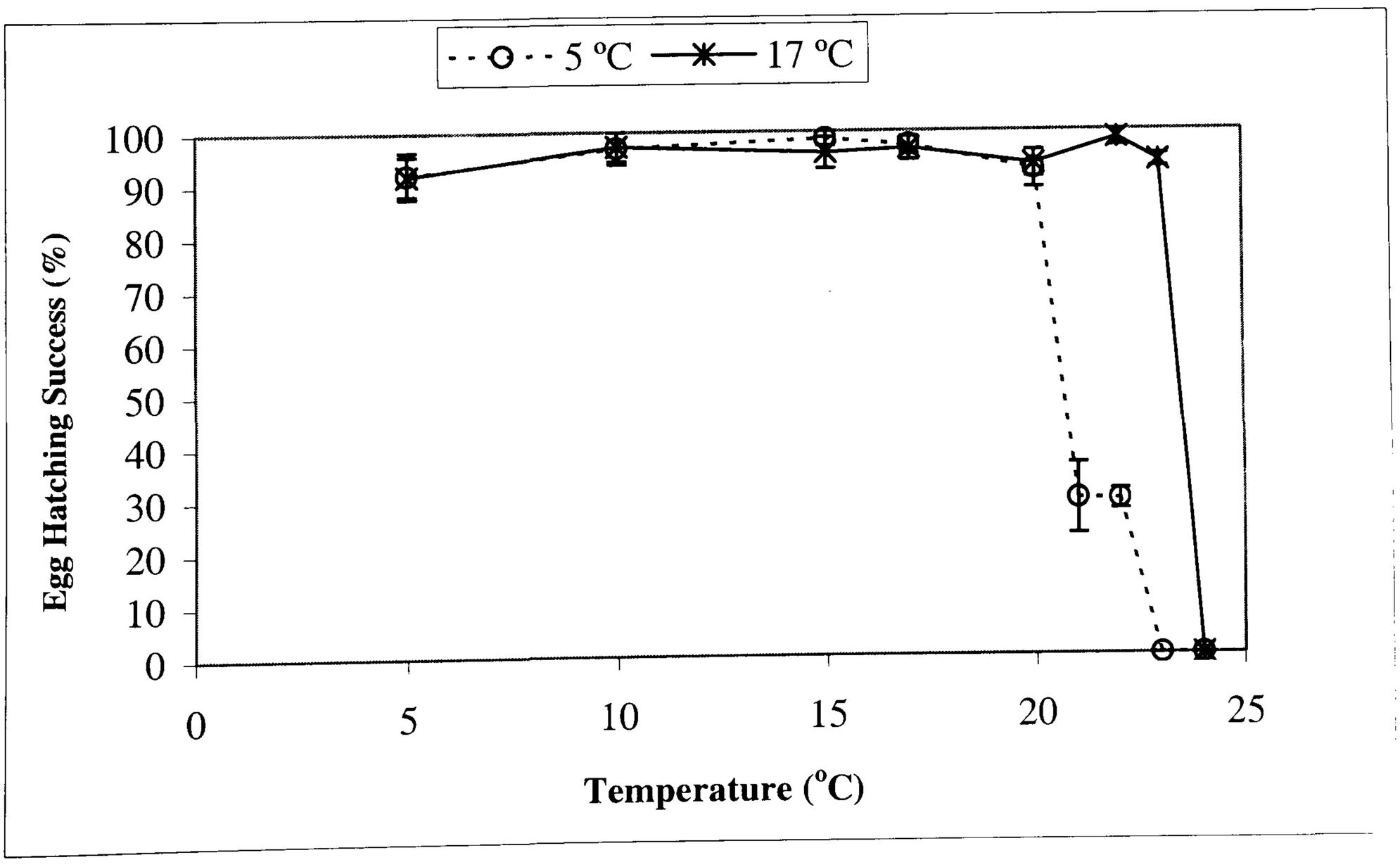
Source	DF	Seq SS	Adj SS	Adj MS	F-value	P-value
T	1	5.4521	5.0453	5.0453	1112	> 0.0001
A	1	0.0093	0.0026	0.0026	0.58	0.455
A x T	1	0.0025	0.0025	0.0025	0.54	0.468
Error	27	0.1225	0.1225	0.0045		
Total	30	5.5863				

The Two-way Analysis of Variance showed that there were no significant differences between the slopes ($F_{[1, 27]} = 0.54$; $p = 0.47$) of the two regression lines indicating that egg development rates was unaffected by acclimation temperature over the copepod ambient temperature range (i.e. 5-17 °C).

6.3.3 The hatching success of egg with acclimation temperature

The results of HS for eggs produced at 5 °C compared to those produced at 17 °C by acclimated *Temora* are shown in Figure 6.3. The egg HS has been recorded over a range of temperatures between 5°C and 25 °C.

Figure 6.3: The mean (± SE) HS (%) with temperature of *T. longicornis* eggs produced by cold (i.e. 5 °C, a) and warm (i.e. 17 °C, b) acclimated females.



HS was very close to 100 % for both winter and summer acclimated eggs exposed to between 5 °C to 19 °C, i.e. the temperature range experienced by *T. longicornis* in the field. A noticeable drop in HS was, however, evident for the summer acclimated eggs above 23 °C and for the winter acclimated eggs above 20 °C. The eggs produced by winter acclimated animals again had a slightly narrower tolerance range (c.f. development time).

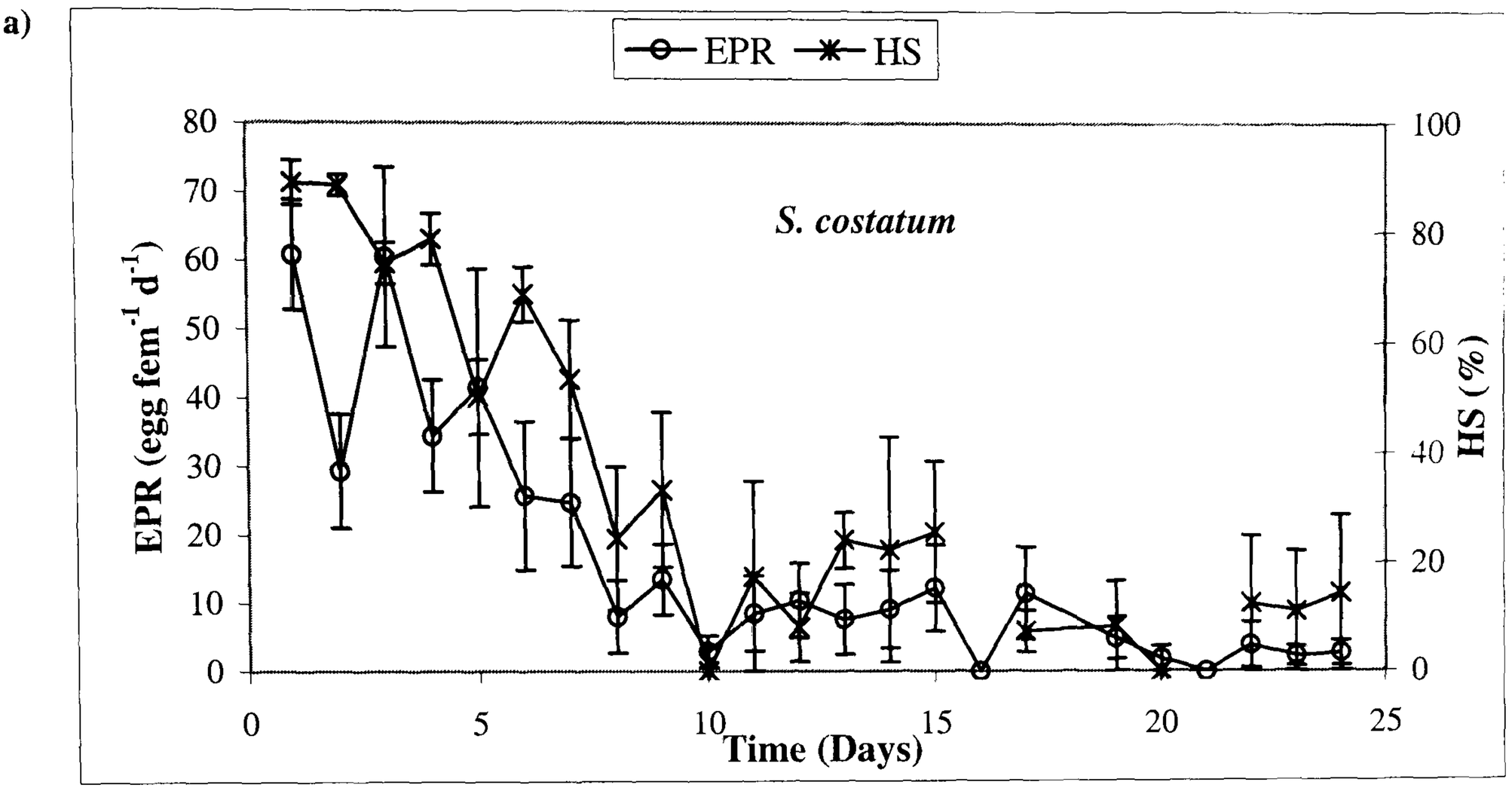
6.3.4 Effect of diet on copepod EPR and HS

The copepods fed on *P. lutherii* did not produce eggs and died 3 days after the start of the experiment. Microscopic examination of the debris found on the bottom of the experimental jar during egg counting showed the copepods fed on *P. lutherii* produced no faecal pellets. *P. lutherii* (diameter ~ 3 μm) is clearly too small or unpalatable to be utilised as food by *T. longicornis*.

The mean EPR and the egg HS of *T. longicornis* fed on laboratory cultured phytoplankton diets over 20-24 days are presented in Figure 6.4. Figure 6.4 shows that the initial trend in fecundity differed between diets. At the start of the experiment the EPR (mean ± SE) was relatively high for copepods fed on *S. costatum* (60.7 ± 22.6 egg female^{-1} day^{-1}) and *R. reticulata* (24.3 ± 35.2 egg female^{-1} day^{-1}) but very low for those fed on *C. calcitrans* (0.6 ± 1.9 egg female^{-1} day^{-1}, Table 6.4).

Over the first 2 weeks of the experiment the EPR of copepod fed on *S. costatum* declined steadily to ~ 6 ± 1.2 egg female^{-1} day^{-1} (Figure 6.4, a). The EPR of copepods fed on the diatom *C. calcitrans* increased only after day 4 up to 54 ± 13.2 egg female^{-1} day^{-1} but after that the pattern was very variable over the whole duration of the experiment (Figure 6.4, b). The EPR of the copepod fed on *R. reticulata* fluctuated throughout the 3 weeks from no eggs at all to averages up to 32 ± 15 egg female^{-1} day^{-1} (Figure 6.4, c). It is worth noting that the mean EPR pattern shown for each diet in Figure 6.4 is similar to the individual trend of copepod fecundity indicating that the differences measured derived from a consistent effect of the diets on copepod fecundity rather than random variation.

Figure 6.4: The mean (± SE) fecundity (egg female^{-1} day^{-1}) and HS (%) of three batches of ten *T. longicornis* copepods fed different alga diets (a) *S. costatum*, (b) *C. calcitrans* and (c) *R. reticulata*



The effect of the different diets on copepod fecundity was analysed comparing the total number of eggs produced over the first 20 days of the experiment using the Analysis of Variance test statistic after square root transformation of the data (Table 6.3).

Table 6.3: Anova test between the mean EPR (egg fem^{-1} day^{-1}) of *T. longicornis* fed on different cultured phytoplankton diets (i.e. *S. costatum*, *C. calcitrans* and *R. reticulata*) over 20 days from the start of the experiment. Data were square root transformed prior to analysis.

Analysis of Variance for square root transformed EPR					
Source	**DF**	**SS**	**MS**	**F-value**	**P-value**
Diet	2	134.7	67.3	2.97	0.077
Error	18	407.4	22.6		
Total	20	542.1			

Over the first 20 days of the experiment the mean EPR of the copepods fed different phytoplankton diets were not significantly different (Anova test, $F_{[2,18]} = 2.97$; $p = 0.077$). Although, the fecundity of copepods fed on different diets did not differ, the EPR measured with the diatom diets was on average higher than with the flagellate diet (Table 6.4).

Table 6.4: Summary of egg production rate (EPR, in egg fem^{-1} d^{-1}) and hatching success (HS, % range in brackets) of 10 individual females *T. longicornis* fed on natural microplankton and on three cultured phytoplankton diets over the first 20 days of the experiment. The EPR at the start of the experiment (EPR_T_0), the mean EPR (EPR_T_0-T_{20}), total EPR (EPR_T_{20}), the HS (HS_T_{20}), the females survived (%, SF_T_{20}) after 20 days from the start of the experiment and the copepod cephalotorax length (C.L. in µm ± SE) are also shown. Standard Error is given in round brackets whereas the range is in square brackets.

Species	C.L. (µm)	EPR_T_0 (egg fem^{-1} d^{-1})	EPR_T_0-T_{20} (egg fem^{-1} d^{-1})	EPR_T_{20} (egg fem^{-1} d^{-1})	HS_T_0 (%)	HS_T_{20} (%)	SF_T_{20} (%)
S. costatum	1114 (± 23.7)	60.7 (± 22.6)	19.3 [0-127]	367 (± 69.6)	100	4.7 [0-29]	100
C. calcitrans	1160 (± 30.6)	0.6 (± 1.9)	13.2 [0-109]	219 (± 28.5)	100	92.8 [70-100]	90
R. reticulata	1128 (± 30.3)	24.3 (± 35.2)	7.5 [0-104]	191 (± 72.9)	100	87.9 [77-95]	80
Natural diet	1148 (± 27.4)	5.9 (± 8.5)	-	-	100	-	-

Comparison of the initial (i.e. day 1) median copepod EPR showed that the copepod fed on either *S. costatum* (~ 61 ± 22.6 egg fem^{-1} d^{-1}, Mann-Whitney, W = 45; $p< 0.001$) or *R. reticulata* (~ 24 ± 35.2 egg fem^{-1} d^{-1}, Mann-Whitney, W = 50; $p< 0.001$) had significantly higher EPR than those feeding on natural microplankton in the field (~ 6 ± 8.5 egg fem^{-1} d^{-1}, Table 6.4). The sharp rise in fecundity, after day 4, of copepods fed on *C. calcitrans* well above the fecundity measured for copepods fed on natural microplankton suggests that a latent phase for energy storage might have been necessary prior of egg production on this diet (Table 6.4).

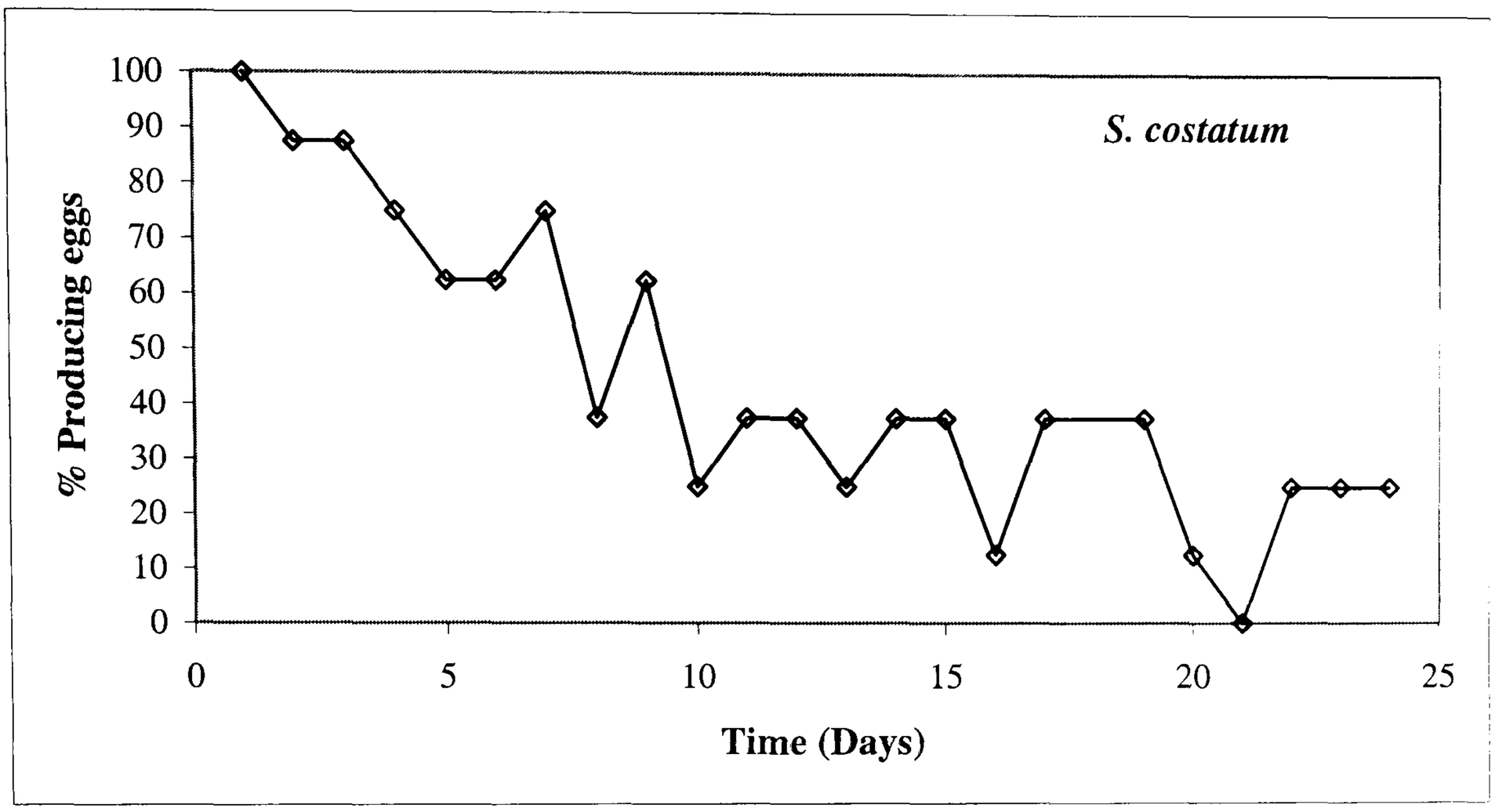
Egg HS also varied with algal diets (Figure 6.4 & Table 6.4). While the HS of females fed on *S. costatum* decreased dramatically from ~ 90 % to 25 % ($r = - 0.92$; $p< 0.001$) within the first week of the experiment, the HS of those fed on *C. calcitrans* ($r = 0.01$; $p = 0.99$) and *R. reticulata* ($r = -0.18$; $p = 0.67$) remained as high as for the copepods in the field ~ 70-100 %.

The changes in the percentage of females producing egg with the 3 different phytoplankton diets over a 25 days experimental trial is shown in Figure 6.5. The percentage females fed *S. costatum* producing eggs decreased steadily ($r = - 0.85$; $p< 0.001$) over the first 10 days from initially 100 % to ~ 30 % (Figure 6.5, a) in a manner paralleling the EPR reduction (Figure 6.5, a). In the reminder of the 3 weeks little change occurred with between 1 and 3 females (out of 10) always producing eggs. In the females fed *R. reticulata* ($r = - 0.17$; $p = 0.49$) or *C. calcitrans* ($r = 0.46$; $p = 0.13$) no major temporal trend was discernible and greater variability was measured. It took four days before more than 1 copepod produced eggs for the females fed with *C. calcitrans* but after that the numbers fluctuated between 1 and 6 producing eggs.

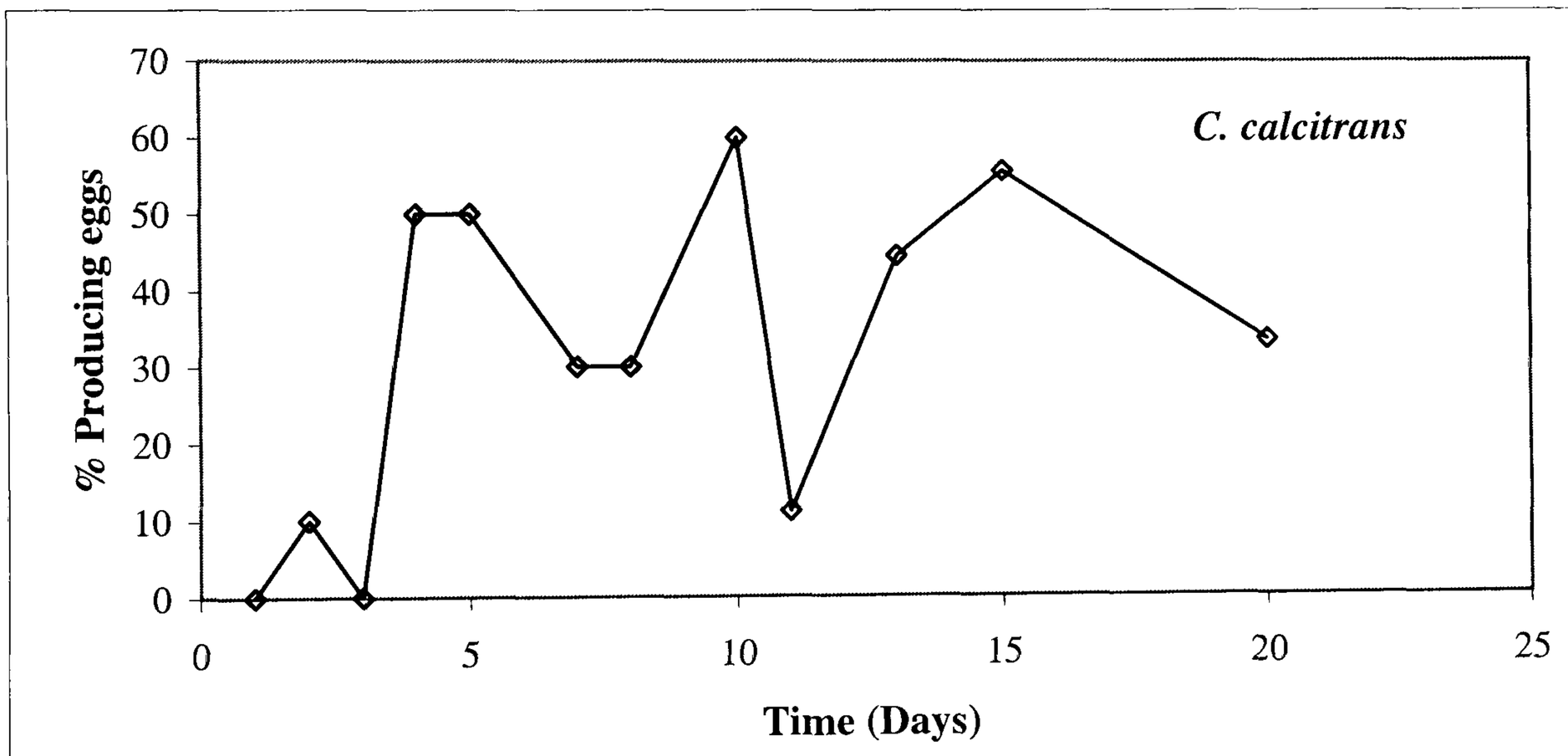
With the exception of those fed on *P. lutherii* the percentage of female copepods surviving on the different diets was high ranging from 80 % to 100 % (Table 6.4). All the dead females from the *R. reticulata* culture had multiple spermatophores (i.e. 4-10) attached to their genital pore.

Figure 6.5: Changes in the proportion (%) *T. longicornis* females producing egg with diatoms a) *S. costatum* and b) *C. calcitrans* and flagellate c) *R. reticulata* phytoplankton diets during 25 days of experiment.

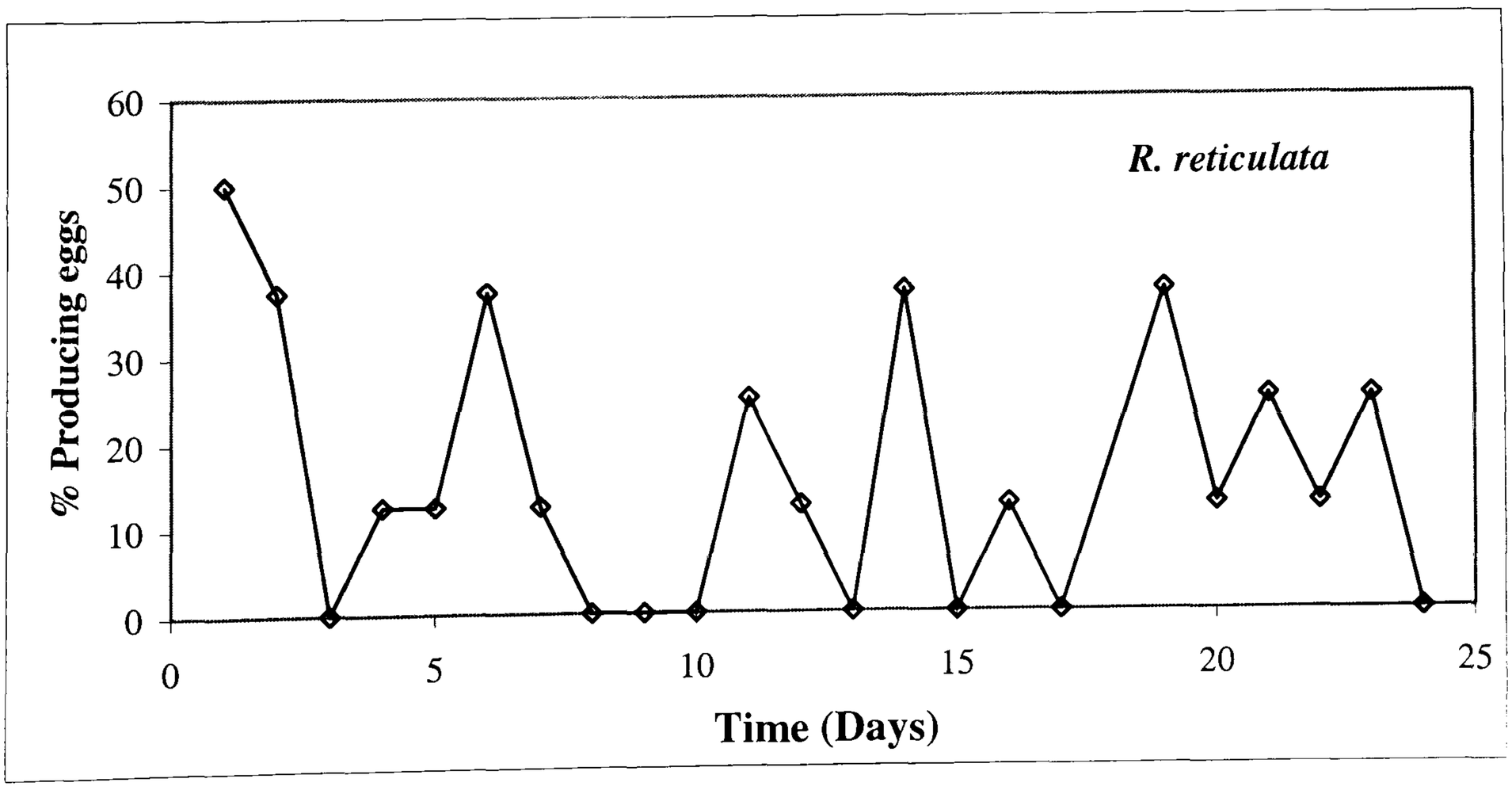
a)



b)



c)



6.3.5 Egg hatching success in light and dark

The results of the experiment carried out to assess the effect of light exposure on percentage HS in *Temora* are summarised in Table 6.5.

Table 6.5: Results hatching success (%, HS) of *T. longicornis* eggs exposed to different light conditions immediately after spawning. Continuous illumination (Light), continuous dark (Dark) and 12 hrs-Dark/12 hrs-Light (Light/Dark) at 17 °C. Data show the mean number of nauplii hatched from 3 batches of 30 eggs with the 95 % confidence interval (95 % C.I.) in brackets.

Treatment	Nauplii (± 95% C.I.)
Ligth	28 (± 2.45)
Dark	28 (± 3.92)
Light/Dark	29 (± 1.86)

The results from the One-Way Anova after arcsine transformation of the percentage HS showed that the type and duration of light exposure did not affect significantly ($F_{[2, 6]} = 0.27$; $p = 0.77$) the HS of *T. longicornis* eggs. Thus, 28-29 eggs or 92-97 % of the total eggs incubated hatched.

6.4 Discussion

The present investigation has shown that the duration of copepod embryonic development declines with temperature increase up to a point after which a prolongation of development occurs, similarly to what reported by other studies (Landry, 1975, in *A. clausi*, Uye, 1988 in *Calanus sinicus*). The observed increase of egg development time at high temperatures indicates the limits of temperature resistance of the eggs and can be attributed to the disruption of the enzymatic reactions involved in physiological temperature responses (Somero, 1995).

In the present study, the embryonic development rate of *T. longicornis* with temperature relationship was described by fitting the Arrhenius model to the part of the

curve corresponding to ambient (i.e. winter acclimated) or near-ambient (i.e. warm acclimated) temperatures only (Winberg, 1971). A number of studies examining the curvilinear functional relationships between temperature and egg development have used a wide range of equations ranging from complex exponential (Miranda *et al.*, 1990) to quadratic (Sarvala, 1979) to elliptic models (Bernard, 1971) to best describe their data sets. Although interesting from a physiological point of view, Winberg, (1971) has argued that the prolongation of development has only been observed under high temperatures in the laboratory, thus it is probably not ecologically meaningful. The Belehradek's model is a curvilinear mathematical function, which has often been used to describe the curvilinear relationship between copepod embryonic development and temperature (McLaren, 1969; Uye, 1988). The Belehradek's equation is defined by three parameters, a, T_0 and b which need to be estimated through non-linear fit by computer iteration. Although, McLaren, (1969) has advocated that the three parameters of the Belehradek's function have real biological significance their interpretation is still rather controversial (Heip, 1974; Blanco *et al.*, 1995). For instance, Guerrero *et al.*, (1994) have indicated that the high negative values of T_0, the so called "biological zero", often obtained using the Belerhadek's equation are meaningless because they are well below the freezing point of sea water at –1.9 °C.

The Arrhenius and Tauti's models are also curvilinear functions but relate development rate, d (i.e. d = 1/D), to temperature and have only two parameters, a and b, which can be easily estimated by linear regression after semi-log transformation of the data (Winberg, 1971; Guerrero *et al.*, 1994). Guerrero *et al.*, (1994) and Blanco *et al.*, (1995) have argued that the Arrhenius and the Tauti's equations should be preferred to the Belehradek function because the same information is given in two parameters which are easier to resolve, use development rates rather than development time (Winberg, 1971), do not use arbitrary values of b (i.e. b = 2.05) and have unequivocal solutions.

A Two way Analysis of Variance indicated that there were no significant differences in the development rates of eggs produced by warm and cold acclimated *T. longicornis* females. Although, Landry (1975) showed that in *A. clausi* females cold acclimated eggs hatch faster than warm acclimated ones, other authors failed to confirm his results and concluded that eggs produced throughout the year by *A. clausi* and other copepod species have similar physiological properties (Uye, 1980; Tester, 1985). Although, in the present study there were no significant differences among development times of the eggs produced by cold and warm acclimated females, the higher mean

development rate and the higher HS measured at high temperatures indicate that warm acclimated eggs have a tendency for higher physiological thermal resistance. This type of temperature response may constitute a competitive edge for the species under increasing trends in environmental temperature, which may arise, for instance, as a result of global warming.

In the present study the total number of eggs produced over a 20 day experiment by *T. longicornis* fed with the diatoms *S. costatum* and *C. calcitrans* was not different from that of copepod fed on *R. reticulata*. Results from this study contrast with previous reports where several copepod species fed or exposed to extracts of a single diatom diet had both lower fecundity (and egg HS) than those fed on flagellate or dinoflagellate diets (Ban *et al.*, 1997). For instance, Ianora *et al.*, (1995) have recently measured a decrease in EPR and HS for *Temora stilifera* fed on *S. costatum* and Ban *et al.*, (1997) have found that out of 37 combinations of copepods and diatoms species 25 reduced EPR and 29 egg HS

Consistently with other investigations, in this study, females fed on *S. costatum* produced an increasing number of non hatching eggs after 2-3 days from the start of the experiment to reach a minimum HS of about 26 % by day 11. The decrease in HS observed was obviously not due to mating because a male copepod was always present in each incubation jar and no decrease in HS was observed with the other diets tested over the same period. On the other hand, the present study has also shown that *T. longicornis* fed on the diatom *C. calcitrans* had egg HS as high as that of animals fed on the flagellate *R. reticulata* and on natural microplankton indicating that *C. calcitrans* had no detrimental effect on *T. longicornis* egg HS.

Ban *et al.*, (1997) have reported that the same cultured diatom species showed considerable differences in their impact on the fecundity and HS of different copepod species which they attributed to the copepod species specific feeding behaviours or variable intracellular composition of the algae. For example, *S. costatum* reduced fecundity and HS in *A. clausi*, fecundity but not HS in *C. helgolandicus* and neither of the two in *C. finmarchicus* (Ban *et al.*, 1997). Thus, it is likely that, in laboratory experiments, *S. costatum* may affect *T. longicornis* in a different way than for other copepods.

In the present study the pattern in copepod EPR and HS observed was very variable indicating that the field animals used in the experiments were possibly of different age and/or in different reproductive condition. The consistent trend in both

EPR and HS of individual copepods with each algal diet suggests that the reproductive pattern measured was probably the result of the type of phytoplankton rather than random variability. Food nutritional composition and characteristics like size, shape and palatability have been increasingly considered important factors in determining copepod productivity (Kleppel & Burkart, 1995; Kleppel & Hazzard, 2000). The differences in EPR and HS observed, in the present study, among cultured algal diets and copepods fed on natural microplankton must have been due not only to the concentration of the phytoplankton offered to the animals but also to the size and quality of the food. For instance, the high initial EPR/HS and steady decrease measured over time for copepods fed on *S. costatum* was striking and quite distinct from the random EPR pattern and high HS observed for animals fed on *R. reticulata*. Although all the tested cultured diets were offered *at libitum*, all the copepods fed on *P. lutherii* did not produce any eggs and died after 3 days of the start of the experimental trial. Since the copepods fed on *P. lutherii*, which is a small phytoplankton species (~ 3-5 μm in diameter), produced no faecal pellets it is possible that the animals did not feed efficiently on this diet. On the other hand, the consistently lower EPR measured over the first 3 days of the experiment with *C. calcitrans* also points to a specific effect of this diet. The delay observed suggests that a latent phase might have been necessary for the copepods to accumulate reserves for the development and/or conditioning of the ovary prior to egg production. Despite being similar in cell size to *P. lutherii* the chain-forming characteristic of *C. calcitrans* must have partly contributed to the feeding success and the high EPR of the copepods on this alga.

It is perhaps, worth noting that at the time of this investigation *S. costatum* concentration in the Menai Strait was high (~ 10^5 cells L^{-1}) and yet the EPR of copepods in the field was much lower (~ 6 egg $female^{-1}$ day^{-1}) and HS higher (~ 100 %) than that obtained in the laboratory over the same period. The fact that the EPR of copepod fed *ad libitum* in the laboratory, during the present study, was higher than the copepod EPR measured in the field suggest that the EPR of wild copepods was food limited. Similar conclusions were reported for *C. helgolandicus* from the English Channel by Laabir *et al.*, (1998). It is also likely that the decrease in egg HS, measured in the present study, was an artefact due to *S. costatum* fed to copepods at unrealistically high densities in laboratory trials as already suggested for other diatom species by Jonasdottir *et al.*, (1998).

Since, the copepods used during the present experiment were taken from the wild the variability in egg laying due to the age of the animals, although randomly allocated among diets, was beyond the control of the experimental design. The high variability in copepod's fecundity measured within each diet suggested, in fact, that the females might have been in different physiological conditions (post-, pre- and reproductive). For instance, some females never laid any egg from the beginning of the experiment while others stopped spawning completely at some stage during the experiment and others produced more eggs at the beginning than at the end. Despite this underlying high variability the different diets seemed to induce a specific response in the copepods in the pattern of EPR, HS and in the number of females producing eggs.

The present investigation has also shown that the HS of subitaneous eggs produced by *T. longicornis* is not affected by darkness. Landry (1975), on the other hand, found that *Acartia clausi* egg HS was immediately suppressed by darkness and concluded that the egg of this species could remain quiescent on the bottom of the sea when covered by sediments.

Chapter 7

Respiration rate of *Temora longicornis*

7.1 Introduction

After the fervent activity of research carried out during the first half of this century (Ostenfield, 1913; Putter, 1925; Raymont & Gauld, 1951; Gauld & Raymont, 1953; Zeuthen, 1953; Conover, 1959; Berner, 1962; Marshall & Orr, 1958, 1966), studies on the respiration rate of marine copepods have lagged behind advances in other taxonomic groups. In recent years, investigations on copepod respiration rates in general (Mayzaud, 1973, 1985; Kiorboe *et al.*, 1985; Pavlova, 1994) and on seasonal changes in respiration rate (Gaudy, 1973) in particular have been very sparse.

Furthermore, with the exception of the work of Nakamura & Turner (1997), research on copepod respiration rates since the late 80's, has mainly focused on large polar calanoids (Hirche, 1987; Bamstedt, 1988; Bamstedt & Tande, 1988), while the small coastal copepods from temperate areas have been largely neglected.

The measurement of respiration rate is ecologically important since it provides meaningful information on both the basic energetic requirements and the general physiological state of an organism. Copepods have considerable ecological importance both in terms of their abundance and for the trophic link they provide between the microplankton and higher trophic levels. Thus, research on copepod respiratory metabolism, has been traditionally undertaken to increase our understanding both of the animal-environment relationship (Gauld & Raymont, 1953) and to allow estimations of the energy flux within marine food webs (Petipa, 1978; Anderson, 1992). As a result, authors have monitored either seasonal variation in respiration rates or have measured the metabolic response to isolated experimental parameters.

In field studies, it has often been observed that the oxygen uptake is higher during the first hours after capture than subsequently (Marshall *et al.*, 1935; Berner, 1962; Fernandez, 1978) Most of the literature does not indicate whether these higher values at the beginning of the experiments are due to feeding, 'excitation' or represent normal rates in the environment, with the effects of starvation subsequently inducing lower rates (Le Borgne, 1986).

The seasonal fluctuation of copepod respiration rates in the field has been the object of many studies (Marshall & Orr, 1958; Alcrow, 1963; Berner, 1962; Haq, 1967; Conover and Corner, 1968; Gaudy, 1973, Bamstedt and Tande, 1988). Generally, a marked seasonal variation in oxygen consumption per individual is noted for many copepod species, the main change being a rise in early spring and a subsequent decline in early summer. The spring rise in copepod respiration has been attributed to various factors like the animal size (Marshall and Orr, 1958), the spring diatom bloom (Conover & Corner, 1968; Butler *et al.*, 1970), high reproductive activity (Conover, 1956), generational differences (Gauld & Raymont, 1953) rise in the field temperature (Anraku, 1964, Bamstedt & Tande, 1988), light and salinity (Marshall *et al.*, 1935). However, with the exception of the work of Conover & Mayzaud (1975) on mixed zooplankton species, none of the previous studies has attempted to describe the relationship between the seasonal fluctuation in copepod oxygen rate and physiological and environmental parameters.

Rates of metabolism are dependent on body size (Prosser & Brown, 1962). This dependency is probably one of the most studied biological phenomena and it is a classic topic of physiology (Rubner, 1902; Kleiber, 1961). As a general rule, metabolic rate is proportional to body weight and is usually described by a power function (introduced by Huxley, 1932). Bertalanffy (1957), studying a wide variety of animals, spanning unicellular organisms to man, has recognised three different types of metabolic dependencies on body size; Type 1, proportionality to body surface (or 2/3 of the body weight, Type 2, direct proportionality to body weight and Type 3 intermediate proportionality between weight and surface.

Several attempts have been made, in the past, to find a consistent relationship between oxygen uptake and some measurement of copepod body length, surface area or weight. Early attempts (Gauld & Raymont, 1953) have related metabolism with copepod body length (i.e. cephalothorax). Subsequent studies have measured the respiration in copepods of varying dry weights and calculated the appropriate relationship as a linear (Conover, 1959; Berner, 1962) or power function (Comita & Comita, 1964). The calculated exponents of power functions relating the respiration rate to body weight, differ considerably and range from 0.62 to 1.06 in different copepod species (Conover, 1968; Ikeda, 1970; Vidal & Whitledge, 1982). Several authors have found the metabolic rate/weight exponent to change during ontogeny (Epp & Lewis, 1980), with organism

phylogeny and body size (Zeuthen, 1953). Zeuthen (1953), for instance, working on marine crustaceans found direct proportionality of metabolism with body weight in animals containing > 0.1 mg N (i.e. Type 2 above), and between surface proportional and weight proportional (i.e. Type 3 above) for animal <0.1 mg N.

From an extensive survey of the respiration rate of marine zooplankton, including copepods, Ikeda (1970, 1974) found the weight exponent of the metabolism-weight relationship, for the combined species, to decrease significantly with ambient temperature. Others, however, have advocated that while the exponent for poikilotherms is independent of ambient temperature for both non-planktonic (Scholander *et al.*, 1953) and planktonic poikilotherms (Vidal & Whitledge, 1982), the intercept (the rate for an organism of unit weight) is not, with subtropical species having higher metabolic rates than boreal species.

Temperature has obvious effects on organisms since it limits species distributions and determines the rates of most processes (Prosser & Brown, 1962). The rates of all the physico-chemical reactions, biological or otherwise, are ultimately controlled by temperature. According to the collision and transition-state theory, which stems from an initial hypothesis formulated by the Swedish chemist Arrhenius in 1889, for a reaction to occur, reactant molecules must collide with a kinetic energy which is greater than some minimum value known as the activation energy (i.e. Ea, or μ). Thus, a temperature change may be expected to alter reaction rates through its effect on molecular activity and the kinetic energy of the enzyme system.

Unlike homeotherms, which can regulate their body temperature, to a greater or lesser extent, independently of external conditions, poikilotherm metabolism has been generally regarded as being at the mercy of the environment. As for other poikilotherms, temperature has a very marked effect on the respiration rate of copepods. Marshall & Orr, (1955) and Halcrow (1963) for *Calanus finmarchicus*, Gauld & Raymont, (1953) for *Temora longicornis*, *Centropages hamatus*, and *Acartia clausi*, Conover (1956) for *Acartia tonsa* and *A. clausi* and Hirche (1987) in polar copepods of the genus *Calanus* have all demonstrated the effect of temperature on copepod respiration.

One of the complicating factors affecting measurements of oxygen consumption is the level of activity of animals during the course of an experiment. It has been shown, for instance, that while the routine and active rate of metabolism in a wide variety of poikilotherms are temperature dependent and have a Q_{10}, between 2 and 3 over the normal

environmental temperature range, the standard rate is usually insensitive to temperature (Newell, 1973). Although increase in physiological rates with temperature has often been associated with the activity of the organism (e.g. Yule, 1984 in barnacle nauplii limb beat rate; Gill & Crisp, 1985 in *T. longicornis* limb beat rate), Hirche (1987) has found the respiration rate of *Calanus sp.* to be independent of activity.

The metabolic rate of many alleged poikilotherms animals has been shown, however, not to be totally governed by environmental temperature (Bullock, 1955). A large body of evidence has accumulated to show that many poikilotherms possess different degrees of thermal control to compensate for changes in habitat conditions and results have been generalised by the works of Pretch *et al.*, (1955), Pretch, (1958) and Prosser (1958).

Earlier experiments, carried out to test the capacity for seasonal temperature acclimation in marine copepods have shown that both *Calanus hyperboreus* (Conover, 1961) and *Calanus finmarchicus* (Halcrow, 1962) acclimate so that their oxygen uptake varies little with long term environmental temperature changes. Similar acclimation was apparent in *Oithona similis* (Nakamura & Turner, 1997) and for *O. divisae* measured between 5 °C and 30 °C (Hiromi *et al.*, 1988). Metabolic compensation to seasonal temperature fluctuation has also been reported in several species of small copepods not only in term of respiration rate (Conover, 1956; Anraku, 1964; Gaudy, 1973) but also for other physiological rates (Gill & Crisp, 1985).

Respiration rate experiments in copepods have been traditionally carried out in sealed chambers with the Winkler titration (Marshall & Orr, 1958) and the manometricaly (Gauld & Raymont, 1953). The techniques used require animals to be measured in groups over long incubation times in order to obtain a measurable drop in the oxygen concentration of the medium. Other techniques like the Cartesian-diver (Linderstrom-Lang, 1937) and the Clark and the polarographic oxygen electrode (Kanwisher, 1959), in which single animals are measured over short times, have also been used for small zooplanktonic organisms (Zeuthen, 1943). The use of oxygen electrodes in respiration rate experiments has been, however, mostly restricted to large calanoid copepods of the genus *Calanus* (Vidal, 1980; Teal & Halcrow, 1962; Halcrow, 1963; Nival *et al.*, 1971) and has never been used for studies on small copepods.

The present work investigates the seasonal respiratory physiology of *T. longicornis* and its metabolic response to short and long term exposure to temperature variation in the laboratory.

7.2 Material and Methods

7.2.1 Animal capture and maintenance

(See Chapter 2)

7.2.2 Respirometry

Respiration rate was measured using a polarographic oxygen electrode (pO_2-electrode) sensitive to changes in oxygen tension in a fluid media (Kanwisher, 1959). The apparatus is shown in Figure 7.1. The pO_2-electrode (Strathkelvin inst. 1302) was fitted to the base of a closed micro-respirometer chamber (Strathkelvin inst. RC 200) whose volume was adjusted between 100 to 150 µl depending on the temperature selected and on the size of the animals measured. Chambers were made in transparent material so that animal activity and behaviour could be monitored.

The temperature inside the respirometer was kept constant within ± 0.2 °C by a thermostat through a re-circulating water bath system, which allowed a continuous water flow in the chamber water jacket. The pO_2-electrode was connected to an O_2-meter (Strathkelvin inst. 781) to display the change in oxygen tension inside the chamber and the output recorded on a chart recorder.

Before each experimental session, the pO_2-electrode was calibrated with distilled water containing a little sodium dithionite to set the zero point on the O_2-meter, and then with air saturated U.V. radiated cartridge filtered (to 0.2 µm) sea water (i.e. U.V.F.S.W.) to set the 100 % air saturation level. The electrode response is linear from 0 % to 100 % of air saturation. The amount of oxygen present in the chamber was calculated from the algorithm of Green & Carrit (1967).

Correction for electrode and micro-organism consumption (i.e. blank) was performed at regular intervals (i.e. every other reading) at each experimental temperature by running an oxygen respiration measurement without the animal chamber. The average

blank between the experimental readings was then subtracted from the animal's oxygen rate measurement to obtain the actual oxygen consumption of the organism.

At the end of each recording session the cephalothorax length of each female was subsequently measured with an eye-piece graticule under a dissecting microscope. Copepod body dry weight was calculated from the relationship, ln D.W = 2.75 * ln C.L. - 15.9 ($r = 0.92$, $p<0.001$, d.f.= 29) where D.W. = Dry Weight (μg) and C.L.= chephalothorax length (μm), described for *T. longicornis* from the Menai Strait (see Chapter 8).

7.2.3 Routine metabolic activity in *T. longicornis*

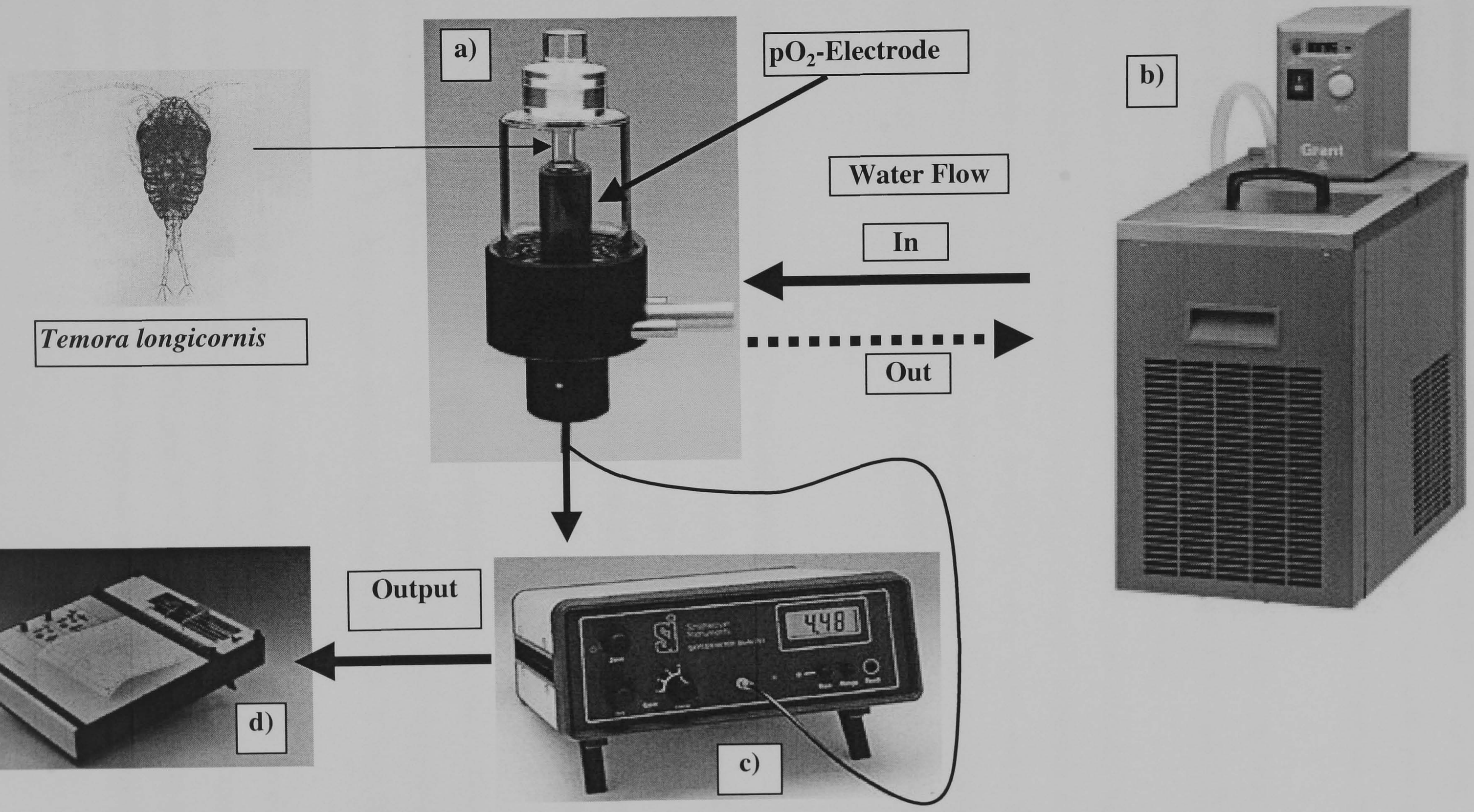
A preliminary study was carried out during April 1996 to assess the time required by freshly caught wild copepods to attain a stable respiration rate. That minimum time from capture was allowed to elapse, prior all further respiration measurements.

The respiration rate of individual copepods, captured within one hour and randomly chosen from a wide range of sizes, was continuously measured, at the average annual temperature of the Menai Strait (i.e. 9 °C), until the respiration rate stabilised.

7.2.4 Seasonal variation in copepod respiration rate in the field

The seasonal variation in "routine" oxygen consumption of *T. longicornis* was measured, at ambient sea water temperature (i.e. between 5 °C and 17.5 °C) for adult copepods over the full size range available at different times of the year. Before each experimental session copepods were left without food in batches of up to 30 animals in 3 L (approx. 100 ml animal^{-1}) glass jars filled with U.V.F.S.W. at ambient temperature between 12 and 24 hours to avoid any added effect of Specific Dynamic Action (S.D.A., Saunder, 1963).

Figure 7.1: The apparatus used for measuring the respiration rate of *T. longicornis*. The animal is placed in a) the respirometer chamber containing the pO_2-Electrode at its base. The chamber is kept at constant temperature by a b) re-circulating water-bath. The drop in oxygen measured by the pO_2-Electrode is displayed on a c) O_2-meter and the output is recorded continuously on d) a chart-recorder.



7.2.5 Time course of acclimation in metabolic rate with temperature

An experiment was carried out to determine whether copepods 1) are able to acclimate, 2) how long is required to acclimate and/or to achieve the stabilised rate which occurs after the initial temperature shock and 3) what is the magnitude and direction of the metabolic response to temperature changes.

The experiment was carried out on wild animals which had been captured in different seasons (i.e. different ambient temperatures) and maintained (see Chapter 2) in the laboratory at that same temperature over 1 week prior to measurements.

The time course of acclimation and the changes in metabolic rate associated with the temperature shift imposed, were measured by exposing a group of copepods to a higher or lower temperature and continuously by monitoring (*circa* every hour) the respiration rate of different individual copepods until rate stabilised. The experimental control consisted of a group of copepods kept and measured at the original acclimation temperature.

7.2.6 Acute effect of temperature on the respiration rate

The physiological response to temperature of *T. longicornis* was investigated by measuring the respiration rate of copepods acutely exposed to a wide range of temperatures. Copepods from the Menai Strait maintained in the laboratory for 1 to two weeks, prior experimentation, on a diet of *R. reticulata* in temperature controlled aquaria.

The experiment was carried out in two parts: in the first part copepods collected during different seasons of the years, i.e. winter (5 °C), spring (10 °C) and summer (17 °C) were acutely exposed to temperature ranging between 5 and 25 °C and their respiration rate measured.

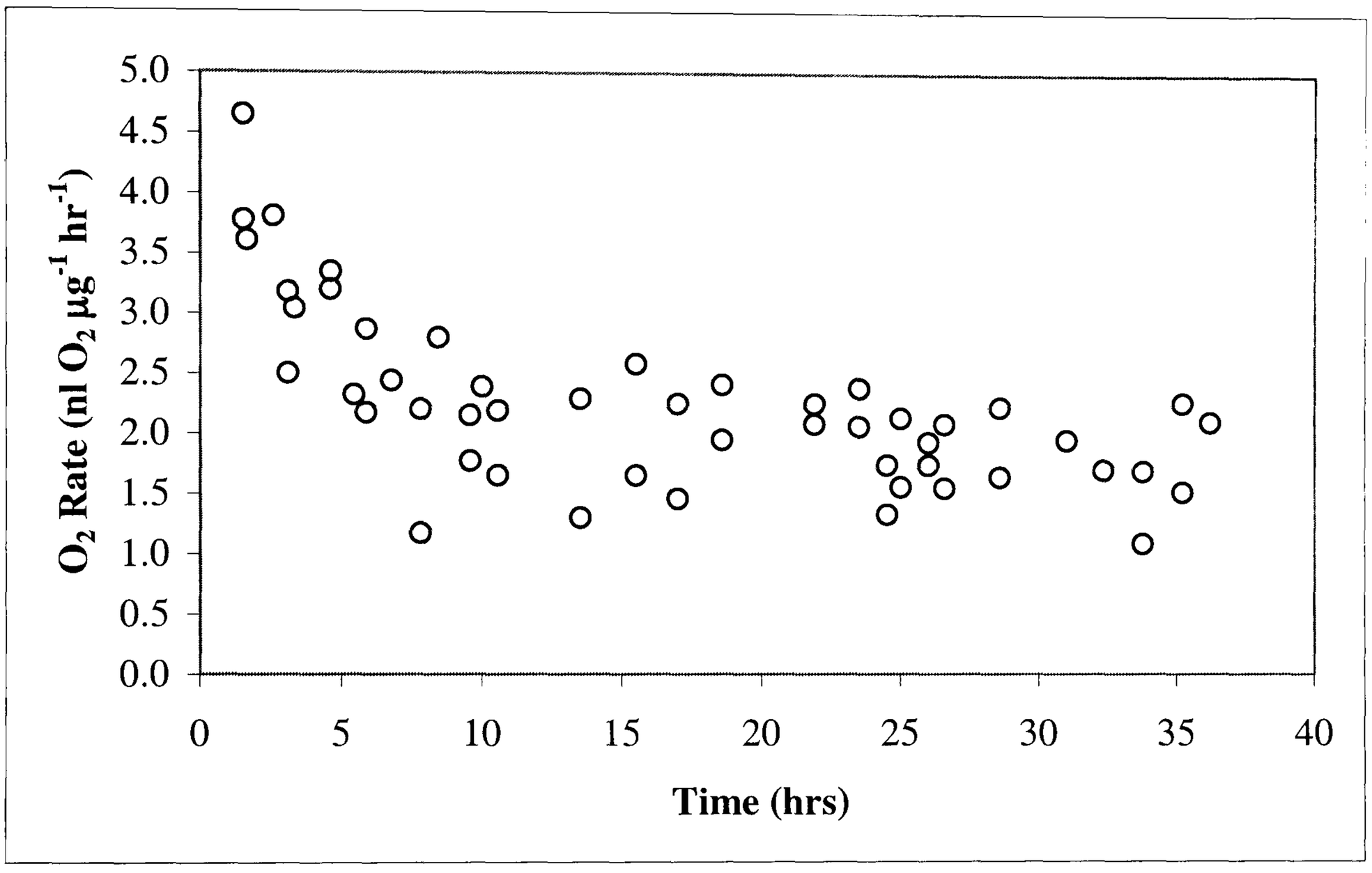
In the second part, a group of wild copepods, collected at the ambient temperature of 13 °C, were divided into 8 subgroups which were randomly allocated to 4 different temperatures (i.e 4 °C, 7.5 °C, 12.5 °C and 20 °C) for 10 days before the start of the experiment. The respiration rates of the copepods were then measured acutely between 5 °C and 20 °C.

7.4 Results

7.4.1 Determination of routine respiration rate

The time required for the respiration rate of freshly collected *T. longicornis* copepods from the Menai Strait, to stabilise, is shown in Figure 7.2.

Figure 7.2: Time course of freshly caught individuals *T. longicornis* routine metabolism as weight specific respiration rate (nl O_2 μg^{-1} hr^{-1}) measured at the average annual ambient temperature of 9 °C over a 40 hours (hrs) experiment.



The weight specific respiration rate of copepods collected from the field at 9 °C, decreased from about 4.6 nl O_2 μg^{-1} hr^{-1} to an average of ~ 2 nl O_2 μg^{-1} hr^{-1} within ~ 10-12 hours. That rate remained relatively stable for the succeeding 28 hours. Thus, the stabilised rate was on average, less than half of the initial respiration rate measured just after the copepods capture (Figure 7.2). Therefore, routine respiration rate measurements were always carried out after keeping the copepod without food for approximately12 hours.

7.4.2 The seasonal variation in metabolic rate and the effect of body size on respiration

The results of the survey, carried out on the seasonal respiration rate of wild adult *T. longicornis* from the Menai Strait between 1996-97, are shown in Table 7.1.

The respiration rates varied from 17-130 nlO_2 $cop.^{-1}$ h^{-1} while the dry weight (D.W.) from 19 μg to 44 μg (Table 7.1). As expected copepod respiration rate increased with body weight. The variability of the respiration rate also increased with size, large copepods showing a wider spread. The relationships found between respiration rate and body weight of *T. longicornis* over the year were described by the power functions summarised in Table 7.1.

Table 7.1: Summary of the seasonal survey on the respiration rate of *T. longicornis* carried out during 1996-97 in the Menai Strait. The number of observations (N), the temperature (t in, °C), the cephalotorax length range (C.L., in μm), the dry weight range (D.W., in μg), the respiration rate range (VO_2, in nl O_2 cop^{-1} h^{-1}) are shown. The intercept a (nl O_2 $cop.^{-1}$ h^{-1}) and the slope b (nl O_2 μg $^{-1}$ h^{-1}), estimated with linear regression model fitted logarithmically (ln) transformed data for each month are presented with their 95 % confidence interval (95 % C.I.). The parameter r = Pearson's correlation coefficient.

Date	N	t	C.L.	D.W.	VO_2	a	b	r
Apr 96	24	6	900-1200	22-49	35.6-107	1.19 (0.23 - 5.9)	1.12 (0.66 –1.58)	0.72
May 96	31	10	800-1180	16-46	29-114	2.10 (0.55 - 7.9)	1.02 (0.63-1.41)	0.69
Jun 96	31	13	780-1160	15-44	30-132	2.91 (0.75 - 3.9)	0.97 (0.57-1.37)	0.67
Aug 96	28	17.5	840-1120	18-40	50-114	4.1 (1.16 - 3.5)	0.88 (0.5 - 1.27)	0.66
Sep 96	27	16	720-960	12-26	24-110	1.18 (0.27-5.3)	1.27 (0.78 - 1.76)	0.71
Oct 96	29	15	800-1000	16-29	34-101	2.5 (0.89- 7.0)	1.03 (0.7-1.36)	0.76
Nov 96	20	9	880-1040	20-33	40-79	2.6 (0.22 – 29)	0.91 (0.16-1.66)	0.47
Dec 96	20	5	880-1200	20-48	27-107	0.8 (0.19 – 2.9)	1.22 (0.84 – 1.6)	0.83
Feb 97	32	7	860-1240	19-53	17-113	0.6 (0.18 – 2.2)	1.26 (0.91- 1.61)	0.79
Apr 97	22	8	980-1280	28-53	38-105	0.98 (0.15 – 6.4)	1.15 (0.67 – 1.83)	0.72

The respiration rate to body weight relationships summarised in Table 7.1 were all significant regression equations. Although, the exponent of the equations (i.e. b) shown in Table 7.1, ranged from 0.88 to 1.26 none seemed to be significantly different from 1.The results of a two way Analysis of Variance testing the differences between the slopes of the power functions in Table 7.1 of ln-transformed data, are shown in Table 7.2.

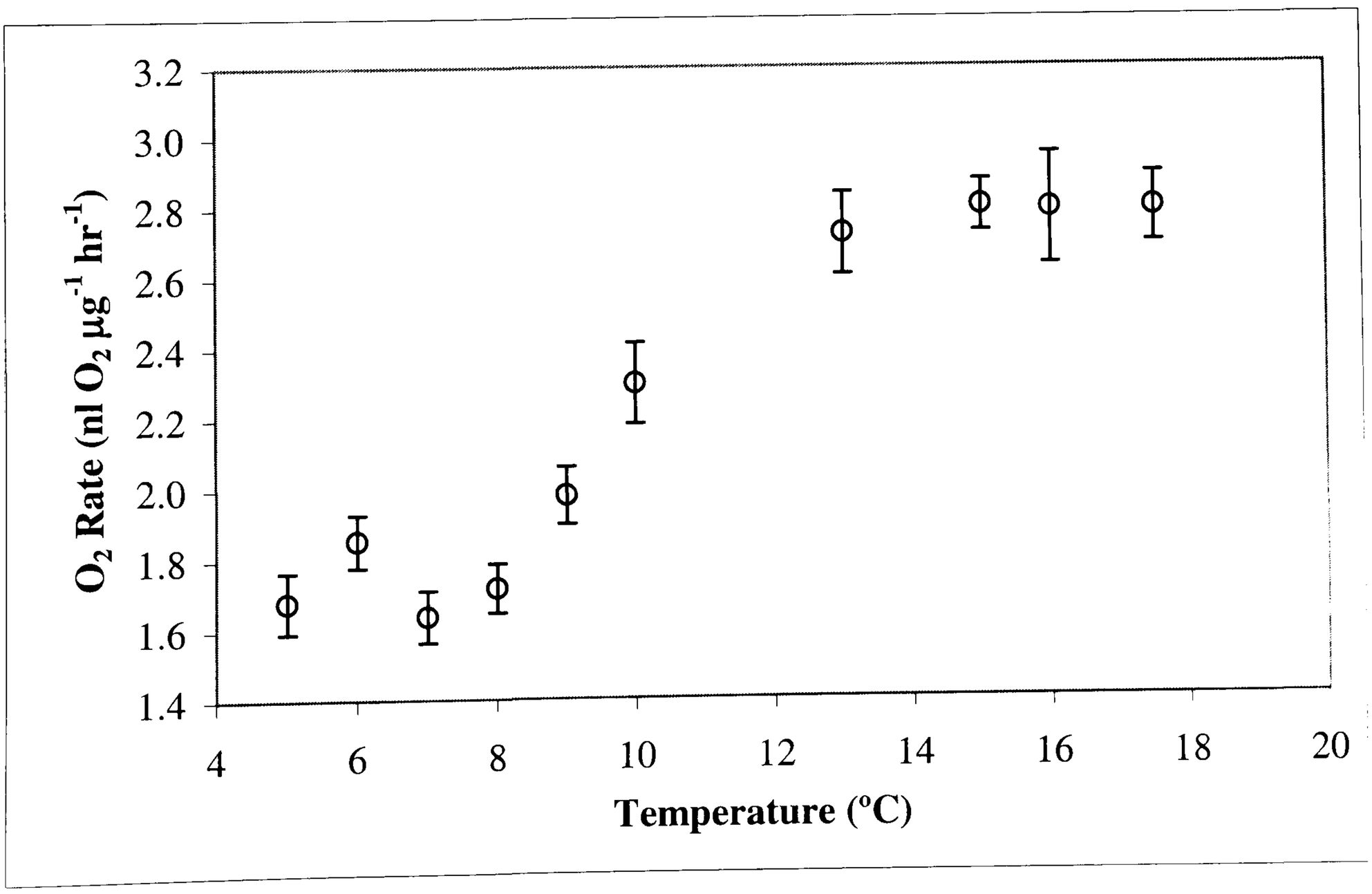
Table 7.2: Two way ANOVA of *T. longicornis* between ln-transformed respiration rate (ln nlO_2 cop.$^{-1}$ hr^{-1}), ambient temperature (t, in ^{o}C) and ln-transformed dry weight (ln D.W., in µg, covariate). Seq. = sequential, Adj. = adjusted for entry of order.

Source	DF	Seq SS	Adj SS	Adj MS	F-value	P-value
ln DW	1	9.4199	10.1007	10.1007	189.82	<0.001
t	9	10.3165	0.4278	0.0475	0.89	0.532
t x ln DW	9	0.2265	0.2265	0.0252	0.47	0.892
Error	244	12.9835	12.9835	0.0532		
Total	263	32.9463				

There were no significant differences (ANOVA, $F_{[1, 9]}$=0.47, p=0.89) between the slopes of the regressions (i.e. the exponents of the power functions) between months (Table 7.2). Furthermore, the intercepts of the regression lines (i.e. the respiration rates of a 1 µg copepod) were also not significantly different from each other (ANOVA, $F_{[1, 9]}$ = 0.89, p = 0.53). A general trend of increasing respiration rate with temperature for any given body weight is evident (Figure 7.3 & 7.4).

Figure 7.3 shows the mean monthly, weight specific, respiration rate against ambient field temperature for wild caught *T. longicornis*.

Figure 7.3: Mean weight specific respiration rate (nl O_2 µg^{-1} hr^{-1}) of wild adult *T. longicornis* versus ambient temperature. Vertical bars represent standard errors (± S.E.).



The metabolic rates appeared stable from 5 °C to 7 °C and from 13 °C to 17.5 °C, while between 7 °C and 13 °C, the respiration rate increased linearly with temperature increase. It is perhaps worth noting that the high mean respiration rate measured at 6 °C in April 1996 was similar to the means measured in November 1996 and April 1997 between 8 °C and 9 °C respectively.

Respiration rate was found to be correlated both to the natural logarithm of body dry weight (d.f. = 263, r = 0.54, p< 0.001) and to temperature (d.f. =263, r = 0.14, p< 0.001). Thus, the relationship between respiration rate, temperature and body size in *T. longicornis* was established with multiple linear regression analysis (Table 7.3).

Table 7.3: Results of multiple linear regression analysis of wild adults *T. longicornis* respiration rates (ln VO_2 in nlO_2 cop.$^{-1}$ hr^{-1}) for different ambient temperatures (t, in °C) and dry weights (ln D.W. in µg). The a) coefficients of the multiple regression and b) and the Analysis of Variance table are also shown.

a) Coefficients				
Predictor	**Coefficient**	**SE**	**T-value**	**P-value**
Constant	-0.3192	0.3306	-0.97	0.336
t	0.0895	0.0102	8.78	<0.001
ln DW	1.0479	0.0845	12.39	<0.001
S = 0.2468	r^2 = 57.8 %	r^2(adj) = 57.2 %		
b) Analysis of Variance				
Source	**DF**	**SS**	**MS**	**F-value**	**P-value**
Regression	2	11.1138	5.5569	91.22	<0.001
Residual Error	133	8.1016	0.0609		
Total	135	19.2154			

The multiple regression analysis was carried for the temperature interval 7 °C to 13 °C, where the respiration rate of *T. longicornis* was found to increase linearly with temperature (Figure 7.3). Thus, the relationship between the respiration rate, temperature and body weight of *T. longicornis* is described by the following equation:

$$\ln VO_2 = 0.32 + 1.05 \ln D.W. + 0.0895\, t \quad \text{(Eq 7.1)}$$

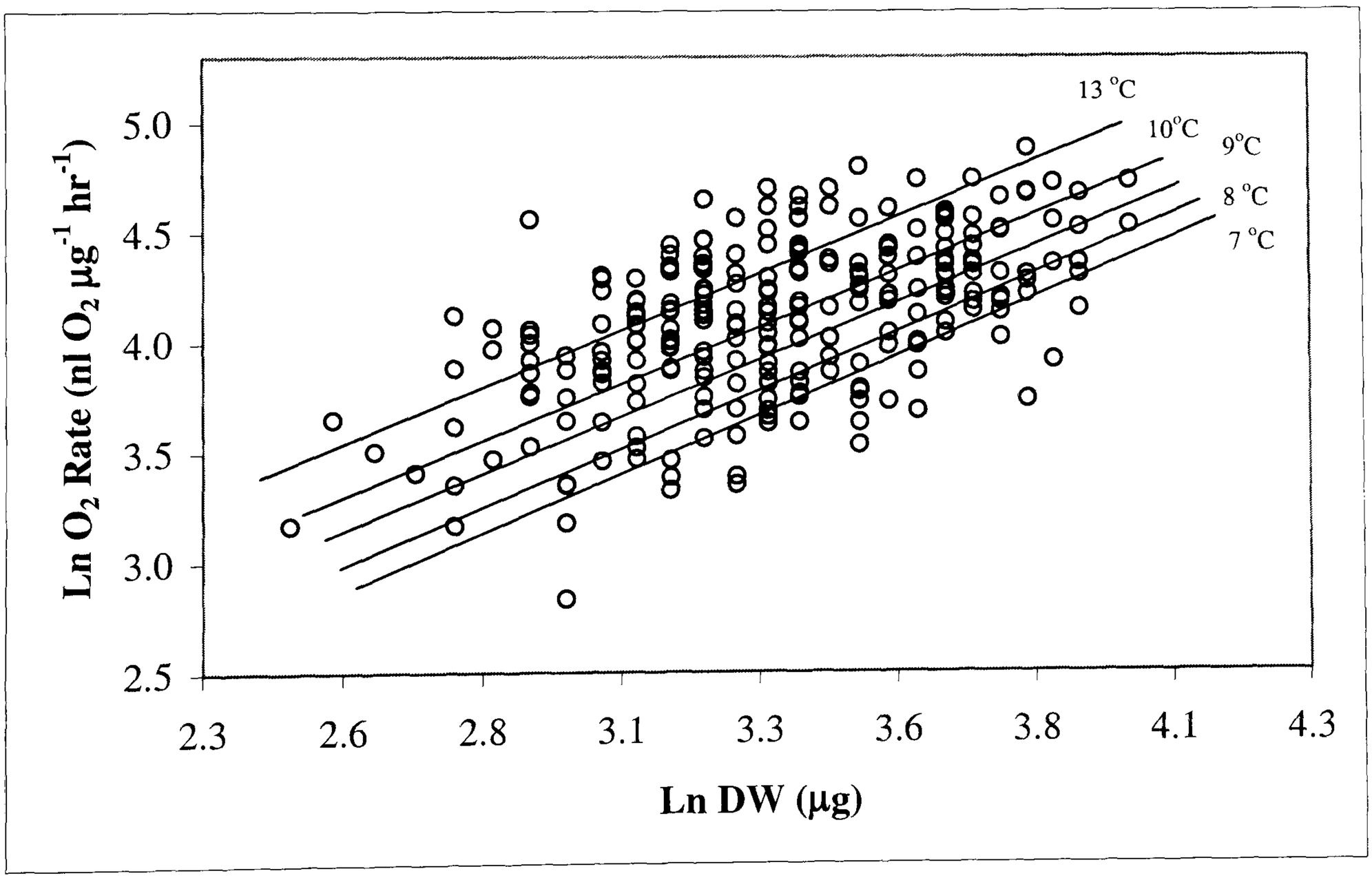
where, $\ln VO_2$ is the natural log of respiration rate in (nlO_2 cop^{-1} hr^{-1}), ln D.W. is the natural log of dry weight in (µg) and t is the acclimatisation temperature in (°C).

The Multiple regression analysis showed that the variation in copepod respiration rate (ln nlO_2 cop.$^{-1}$ hr^{-1}) during the year (Table 7.3 b), $F_{[2,\ 133]}$ = 91.2, p<0.001) depended both on weight (Table 7.3 a), ln µg, d.f.= 133, T=12.39, p< 0.001)

and ambient temperature (Table 7.3 a) °C, d.f. = 133, T = 8.78, p<0.001). The change in ln-respiration rate of *T. longicornis* for each °C at constant weight was 0.089 ± 0.01 nl O_2 cop^{-1} hr^{-1} (± SE). The change in copepod respiration rate of 1.05 nlO_2 hr^{-1} μg^{-1} ± 0.08 (± SE) for each µg of copepod's dry weight tissue at constant temperature was not significantly different from 1 (d.f. = 135, T = 0.63, p< 0.05). Thus, on average the respiration rate in *T. longicornis* was directly proportional to body dry weight.

Figure 7.4 shows the multiple regression model (Eq. 7.1) fitted to the data scatter plot of *T. longicornis* ln-respiration rate with ln-dry weight at different ambient temperatures between 1996 and 1997. Note that the multiple regression model has only been fitted to data between 7 °C and 13 °C where a linear increase in the *in situ* temperature acclimated respiration rate was recorded.

Figure 7.4: ln-respiration rate (VO_2, in nlO_2 $cop.^{-1}$ hr^{-1}) of wild adult *T. longicornis* versus ln-dry weight (D.W., in µg) measured at 10 different ambient temperatures (see text). Lines fitted with the Multiple linear regression model ln VO_2 (nlO_2 cop^{-1} hr^{-1}) = 0.32 + 1.05 ln D.W.(µg) + 0.0895 t (°C) between 7 °C and 13 °C (continuous lines).



As it can be seen in Figure 7.4, there is an evident positive trend of copepod respiration rate with both ambient temperature and dry weight.

A thermal coefficient for the respiration rate of *T. longicornis* can be calculated using the Van't Hoff equation (Eq. 7.2), where the coefficient of the change in rate per 10°C change in temperature is given by:

$$Q_{10} = \left(\frac{K_1}{K_2} \right)^{\frac{10}{(t_1 - t_2)}} \qquad \text{(Eq. 7.2)}$$

where K_1 and K_2 are the respiration rates at the temperatures t_1 and t_2. The model found (Eq. 7.1), therefore, predicts that the respiration rate of *T. longicornis* copepods acclimated to the natural range of temperatures measured between 7 °C and 13 °C in the Menai Strait will have a $Q_{10} = 2.44$. On the other hand, between 5 °C - 7 °C and 13 °C - 17.5 °C, for the lower and for the upper ambient temperature range respectively, the metabolic rate of copepods in the field, seemed to be relatively temperature insensitive, indicating a Q_{10} approximating unity.

7.4.3 The acute effect of temperature on copepods metabolic rate

The weight specific respiration rate of copepods acutely exposed to temperature changes was found to increase exponentially for all the 7 different acclimation temperatures considered. The metabolic rates of the copepod acclimated copepods increased with temperature up to a point after which a decline occurred (Figure 7.5, a-c). On the other hand, the respiration rate of the copepods reared in the laboratory, measured between 5 °C and 20 °C, always increased with temperature (Figure 7.5, d-f).

The weight specific respiration rate of copepods acclimated to 5 °C increased up to 20 °C beyond which, the animal behaviour became erratic and the rate declined. Copepods exposed to 23 °C were, in fact, often comatose at the end of the measurement resulting in the rates being lower than those measured at 20 °C (Figure 7.5, a). Observation carried out, in the present study, on *T. longicornis* thermal resistance showed that 23 °C was close to the upper lethal limit (i.e 24 °C) for copepods acclimated at 5 °C.

The respiration rate of copepods acclimated to 10 °C increased up to 24 °C beyond which again rate decreased and behaviour became intermittent with copepods spending the majority of the time hopping from the bottom of the chamber than swimming (Figure 7.5, b). In copepods acutely exposed at 24 °C the behaviour observed varied from animals frantically swimming to others jumping intermittently from the

base of the respirometer. This behaviour can probably account for the high variability, shown by the S.E. bars, obtained for the 24 °C acute exposure (Figure 7.5, b).

At 17 °C acclimation the respiration rate also declined beyond 24 °C (Figure 7.5, c). Although, respiration could be still measured at 25 °C, at this temperature, the majority of copepods were swimming erratically and died after just one hour. The variability (i.e. S.E. bars) of the respiratory response stayed quite homogeneous over the greatest part of the temperature range mostly increasing at the highest temperatures when the metabolic rates were declining.

Observations made, in the present study, on upper lethal temperature in *T. longicornis* showed that copepods acclimated at 17 °C could not survive for more than 24 hours at 25 °C and died instantly when exposed to 26 °C. Thus, 25 °C is a temperature close to the upper lethal temperature for *T. longicornis* acclimated at 17 °C. Thus, temperature seasonal acclimation, appeared to have shifted the upper lethal limits of the species' thermal tolerance of ~ 2 °C between the winter and spring-summer populations respectively.

When the reciprocal of the temperature, expressed in degrees Kelvin (°K) is plotted against the respiration rates, the dependence of respiration on temperature can be represented by the Arrhenius equation (Eq. 7.3)

$$k = A\, e^{-\frac{Ea}{RT}} \qquad \text{(Eq. 7.3)}$$

where k is the reaction velocity constant, A is the frequency factor constant, e is the natural base of the logarithms (i.e. 2.718..), T is the absolute temperature in °K, R is the gas constant (i.e. 8.31 J $mole^{-1}$ $^{o}K^{-1}$) and Ea (i.e. in J mol^{-1}) is the activation energy constant. The decrease in velocity for each degree change in temperature can be predicted from the proportionality constant Ea of an integrated form of the Arrhenius equation, that is

$$\ln\left(\frac{k_2}{k_1}\right) = \frac{Ea}{R\left(\frac{1}{T_1} - \frac{1}{T_2}\right)} \qquad \text{(Eq. 7.3)}$$

where k_1 and k_2 are the reaction velocities constant at temperatures T_1 and T_2 in °K.

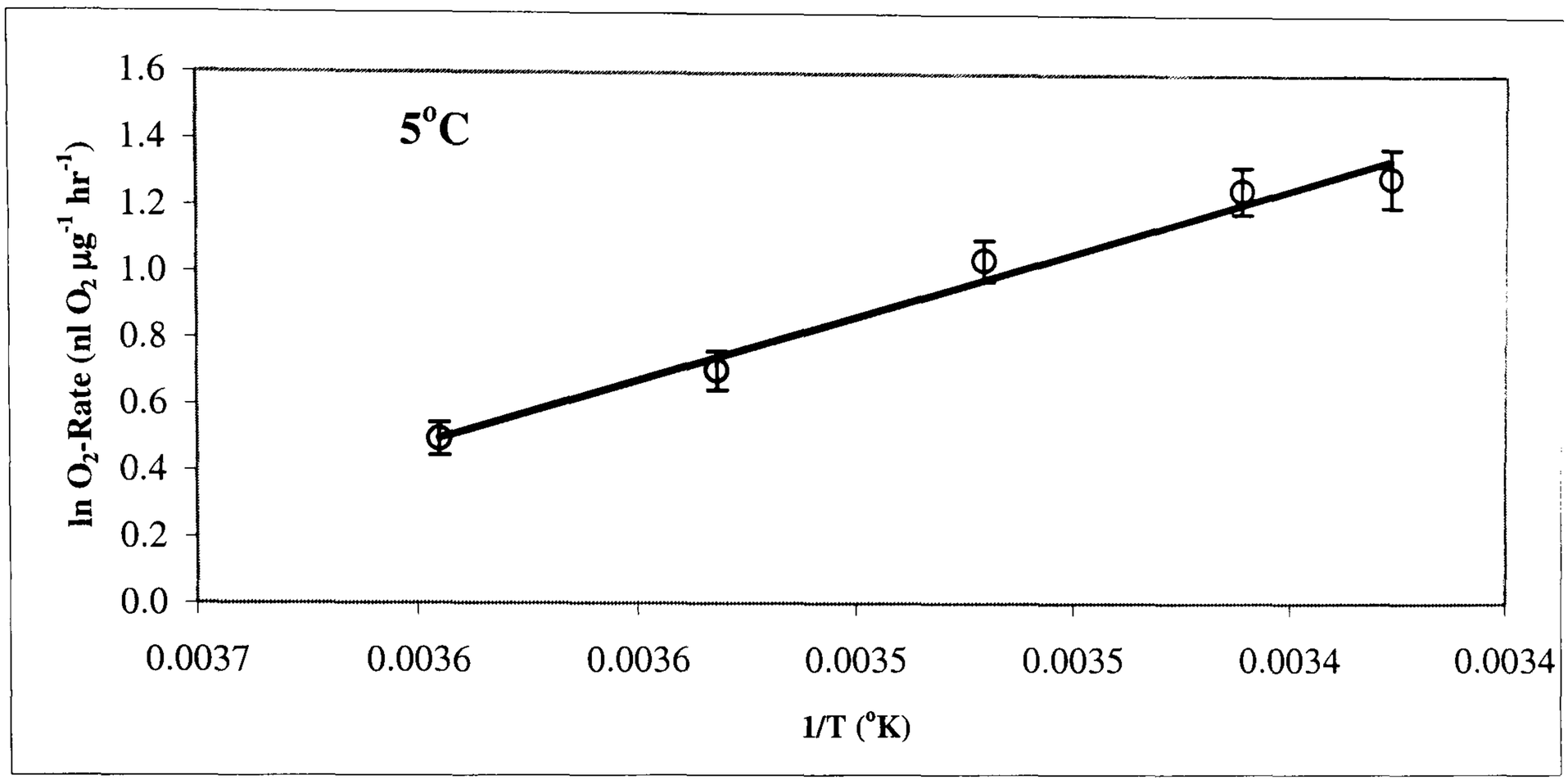
A graph of ln k against the reciprocal of the absolute temperature, that is the Arrhenius plot, gives a strait line of slope equal to Ea/R from which Ea can be calculated. The Arrhenius equations for *T. longicornis,* did not seem to deviate from linear relationships within the 4 °C to 20 °C temperature interval at any acclimation temperature. So the activation energies Ea, calculated from the slope Ea/R of the regression model shown in Eq. 7.3, were calculated from the expression:

$$Ea = \text{slope} * 8.31 \left(\text{J mol}^{-1} \right) \qquad \text{(Eq. 7.4)}$$

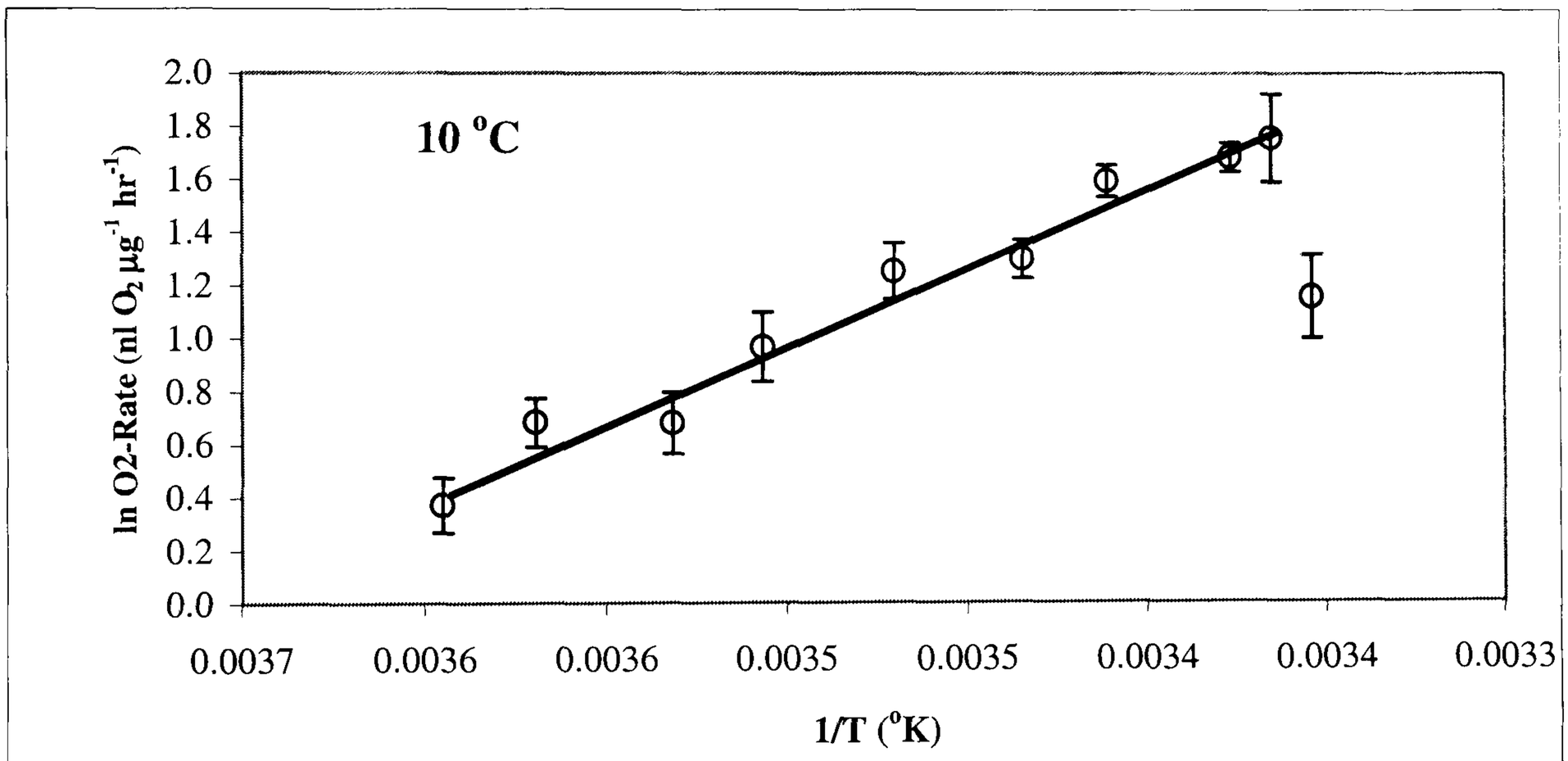
Figure 7.5 shows the Arrhenius plots of the mean ln-transformed specific respiration rate (ln nlO_2 μg^{-1} hr^{-1}) of *T. longicornis* and temperature (1/T, ^{o}K) at different acclimation temperatures.

Figure 7.5: Arrhenius plots of mean (± SE) weight specific O_2-rate (ln nlO_2 μg^{-1} hr^{-1}) versus temperature (1/T, °K) in *T. longicornis* acclimated in the field at a) 5 °C, b) 10 °C and c) 17 °C and in the laboratory at d) 4 °C, e) 7.5 °C , f) 12.5 °C and g) 20 °C. Trend line fitted with regression equations in Table 7.4.

a)



b)



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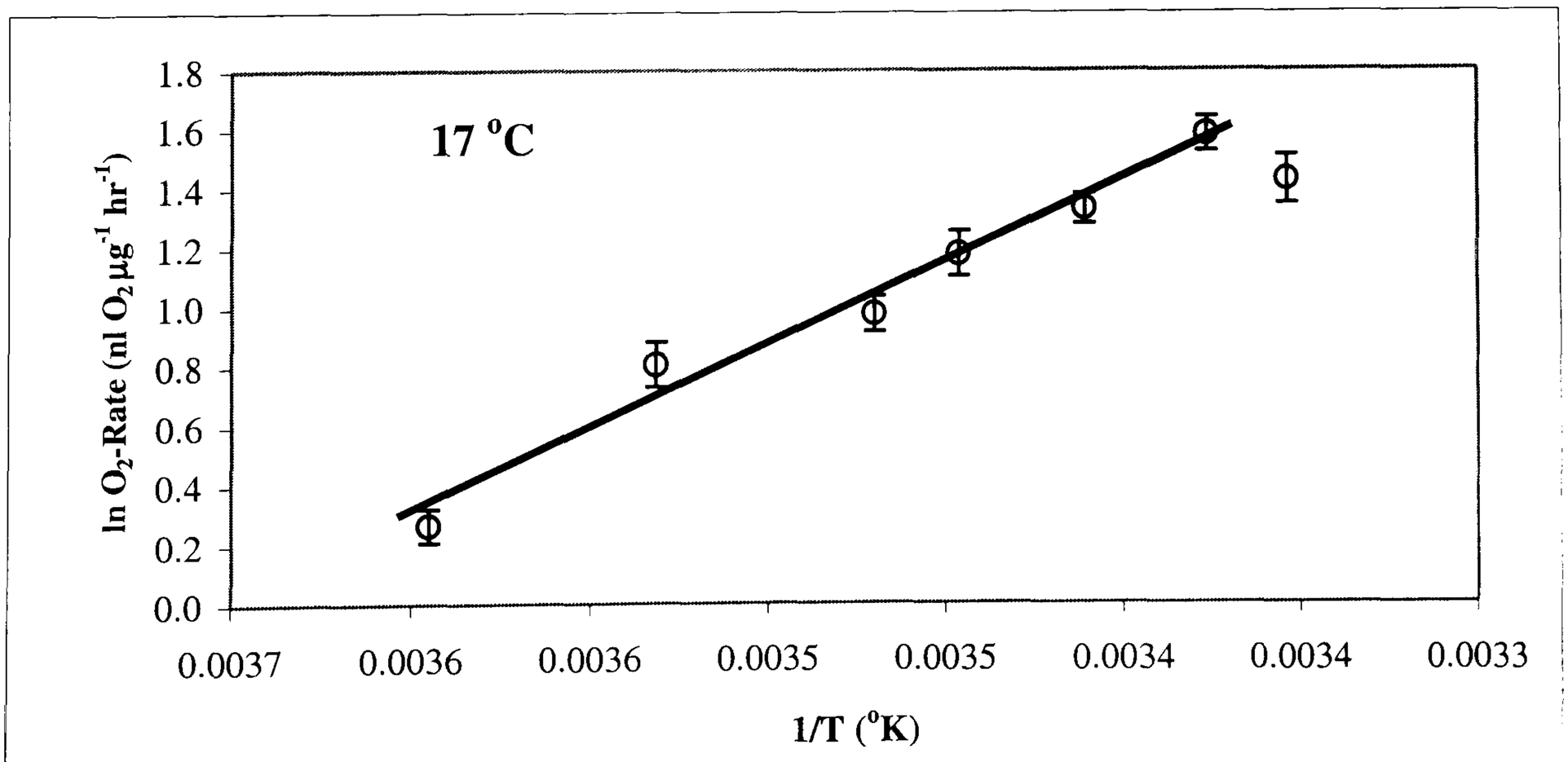


Figure 7.5: Continued

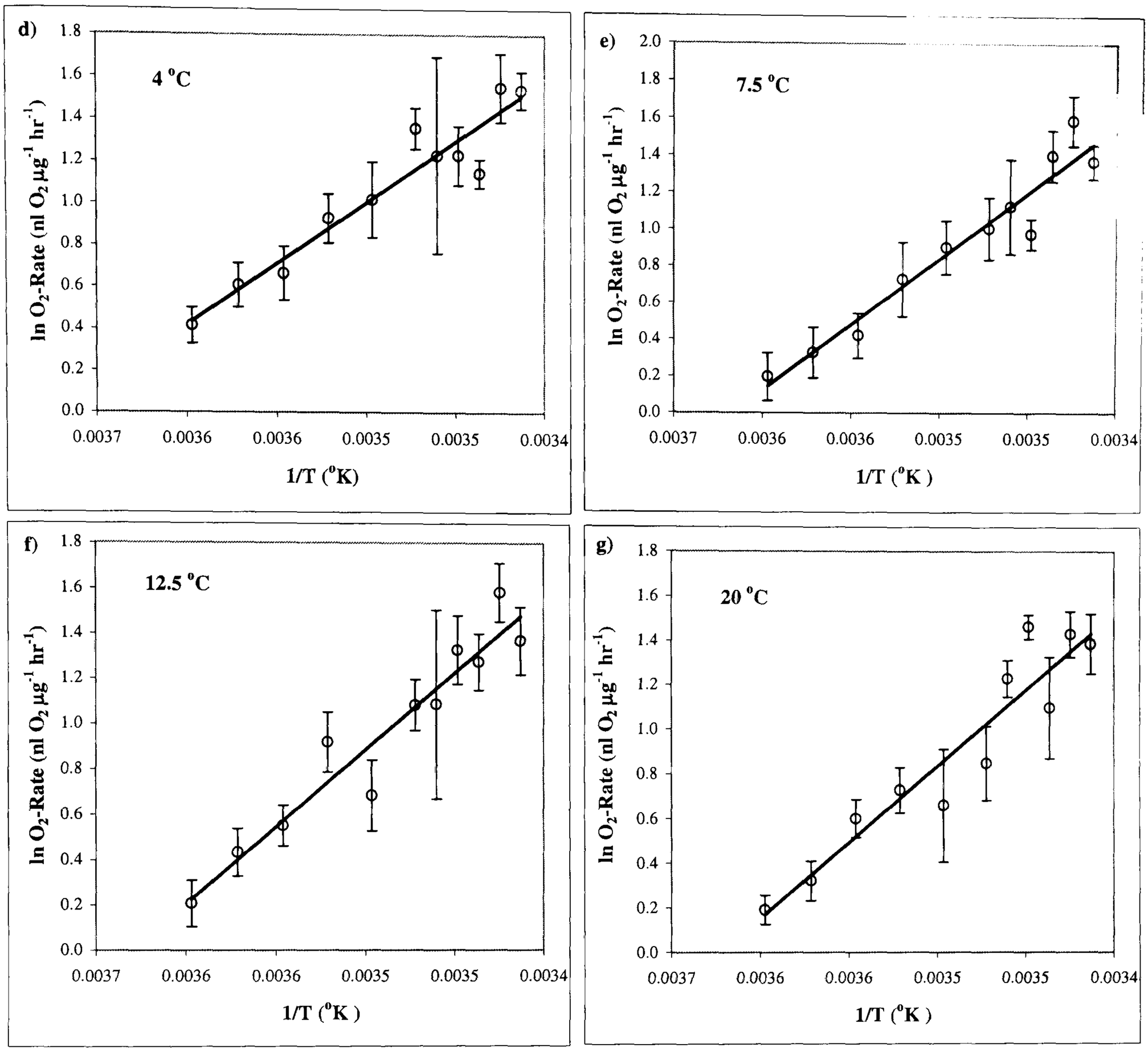


Table 7.4 summarises the regression analysis of the Arrhenius plots carried out between 5 °C and 20 °C where the copepod metabolic rate (ln nlO_2 μg^{-1} hr^{-1}) with temperature (1/T, °K) was linear for all the 7 different acclimation temperatures (See Figure 7.5).

Table 7.4 shows that the slopes of Arrhenius equations for copepods maintained at different temperatures were very similar. As a result the thermal coefficients μ and Q_{10} for *Temora* measured between 5 °C and 20 °C were also very similar with μ varying between 46 KJ mol^{-1} to 55 KJ mol^{-1} and Q_{10} between 1.94 and 2.35.

Table 7.4: Summary of Arrhenius equations for the weight specific respiration rate (ln nlO_2 μg^{-1} hr^{-1}) of *T. longicornis* acutely exposed to temperature between 5 °C and 20 °C for 7 different acclimation temperatures (i.e. Acclimation in °C). The Arrhenius equations are of the type $lnVO_2^*$ = ln a - b 1/T. VO_2^* is the weight specific respiration rate (nlO_2 μg^{-1} hr^{-1}), T is the temperature (°K), a (nlO_2 μg^{-1} hr^{-1}) is the intercept and b (nlO_2 μg^{-1} hr^{-1} $^oK^{-1}$) is the slope (i.e. μ / 8.31 J mol^{-1}) of the regression (± SE). The number of observations (N), the dry weight range (D.W., in µg), the activation coefficient (μ, in KJ mol^{-1}), the Q_{10} and the Pearson's correlation coefficient (r) are also shown.

Acclimation	N	D.W.	ln a	b	μ	Q_{10}	r
4	40	17-33	22.1 (± 2.24)	6031 (± 642)	50.11	2.03	0.83
5	37	21-44	21.4 (± 1.68)	5841 (± 482)	48.53	1.98	0.89
7.5	36	16-33	25.3 (± 2.54)	6986 (± 727)	58.05	2.35	0.85
10	50	17-48	22.2 (± 2.3)	6062 (± 657)	50.37	2.11	0.79
12.5	36	15-33	24.0 (± 2.48)	6599 (± 708)	54.83	2.24	0.84
17	56	11-20	20.3 (± 1.39)	5542 (± 400)	46.05	1.94	0.88
20	38	15-28	24.1 (± 2.05)	6642 (± 586)	55.19	2.26	0.88

The results of the comparisons between the regression equations fitted to the Arrhenius plots for copepods from the Menai Strait and reared in the laboratory are presented in Table 7.5.

Table 7.5: Results of two-way Analysis of Variance between specific respiration rate (ln nlO_2 μg^{-1} hr^{-1}) of *T. longicornis* vs temperature (1/T in °K; covariate) at 7 different acclimation temperatures (At in °C). Seq. = sequential, Adj. = adjusted for entry of order.

Source	DF	Seq SS	Adj SS	Adj MS	F-value	P-value
1/T	1	41.7609	41.5267	41.5267	690.96	<0.001
Acclimation	6	1.4573	0.2967	0.0495	0.82	0.553
Acclimation*1/T	6	0.3058	0.3058	0.051	0.85	0.534
Error	272	16.3473	16.3473	0.0601		
Total	285	59.8713				

Results from the analysis of variance in Table 7.8 indicated that there were no significant differences among the slopes ($F_{[1, 6]}$ = 0.85, p=0.534) and the intercepts ($F_{[1, 6]}$ = 0.82, p = 0.553) of the regression lines for copepods specific respiration rate vs

temperature for copepods maintained at different temperatures. Thus, the respiration rate of *T. longicornis* increases with temperature and copepods show no tendency to acclimate.

The model obtained by pooling the data of copepod acclimated to field and to laboratory temperatures was:

$$\ln VO_2^* = 22.4 - \frac{6134}{T}, \qquad r^2 = 69.8\% \quad \text{(Eq. 7.5)}$$

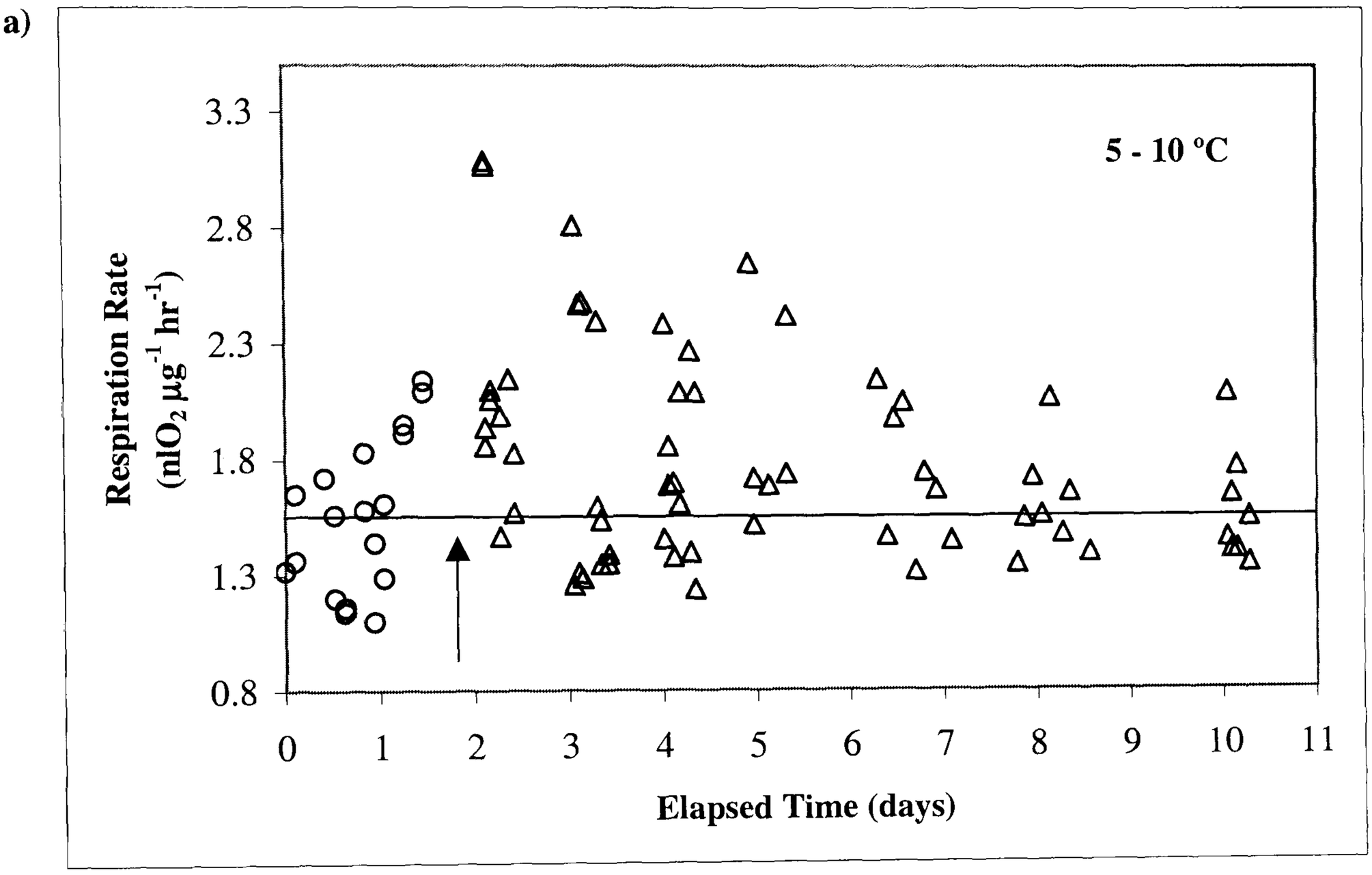
where, $\ln VO_2^*$ is the natural log of the copepods weight specific respiration rate (nl O_2 μg^{-1} hr^{-1}), T is the absolute temperature (^oK). Thus, the average thermal coefficients calculated over the temperature range 5 ^oC to 20 ^oC correspond to a μ = 50.9 KJ mol^{-1} and a Q_{10} = 2.10 (from Eq. 2).

7.4.4 Time course of acclimation of the metabolic rate of *T. longicornis* with temperature

The results of the acclimation of *T. longicornis* respiration rate to temperature changes in are shown in Figure 7.6. The initial average routine weight specific respiration rate of *T. longicornis* varied between 1.5 ± 0.08 nlO_2 μg^{-1} (± S.E.) to 2.8 ± 0.09 nlO_2 μg^{-1} (± S.E.) over the ambient temperature range of 5 °C to 15 °C respectively (Figure 7.6).

When copepods were exposed to a temperature change their respiration rate generally fell below the initial metabolic rate in cooling (Figure 7.6, f) and rose above it in warming (Figure 7.6, a-e). Coefficients of variation (c.v.) for the control measurements ranged from 22.1 % to 25.3 % showing no obvious trends with time and their averages were equivalent to those for experimental animals measured prior to the change in temperature (c.v. range 21.7 %- 24.5 %).

Figure 7.6: Time course of temperature acclimation in the respiration rate (nlO_2 μg^{-1} hr^{-1}) of *T. longicornis*. The scatter plots represent the metabolic response of the copepods shifted from the acclimation temperature (open circles) and a new temperature (open triangles) over the following temperatures intervals: a) 5-10 °C, b) 5-15 °C, c) 5-20 °C, d) 10-15 °C, e) 10-20 °C, f) 15-10 °C. The continuous line is the mean respiration rate for the control and the arrow indicates the time at which copepods were shifted to the new temperature.



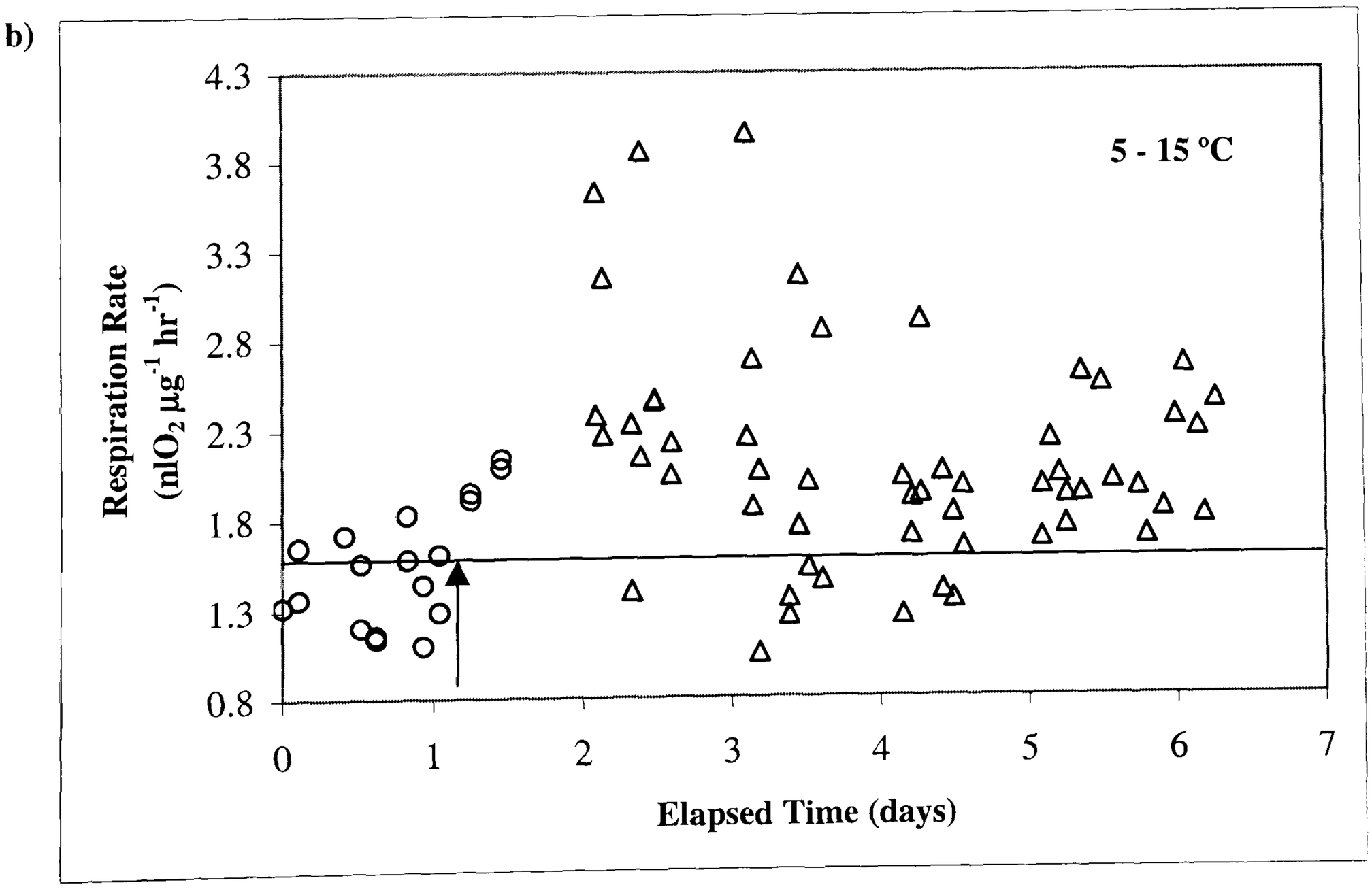
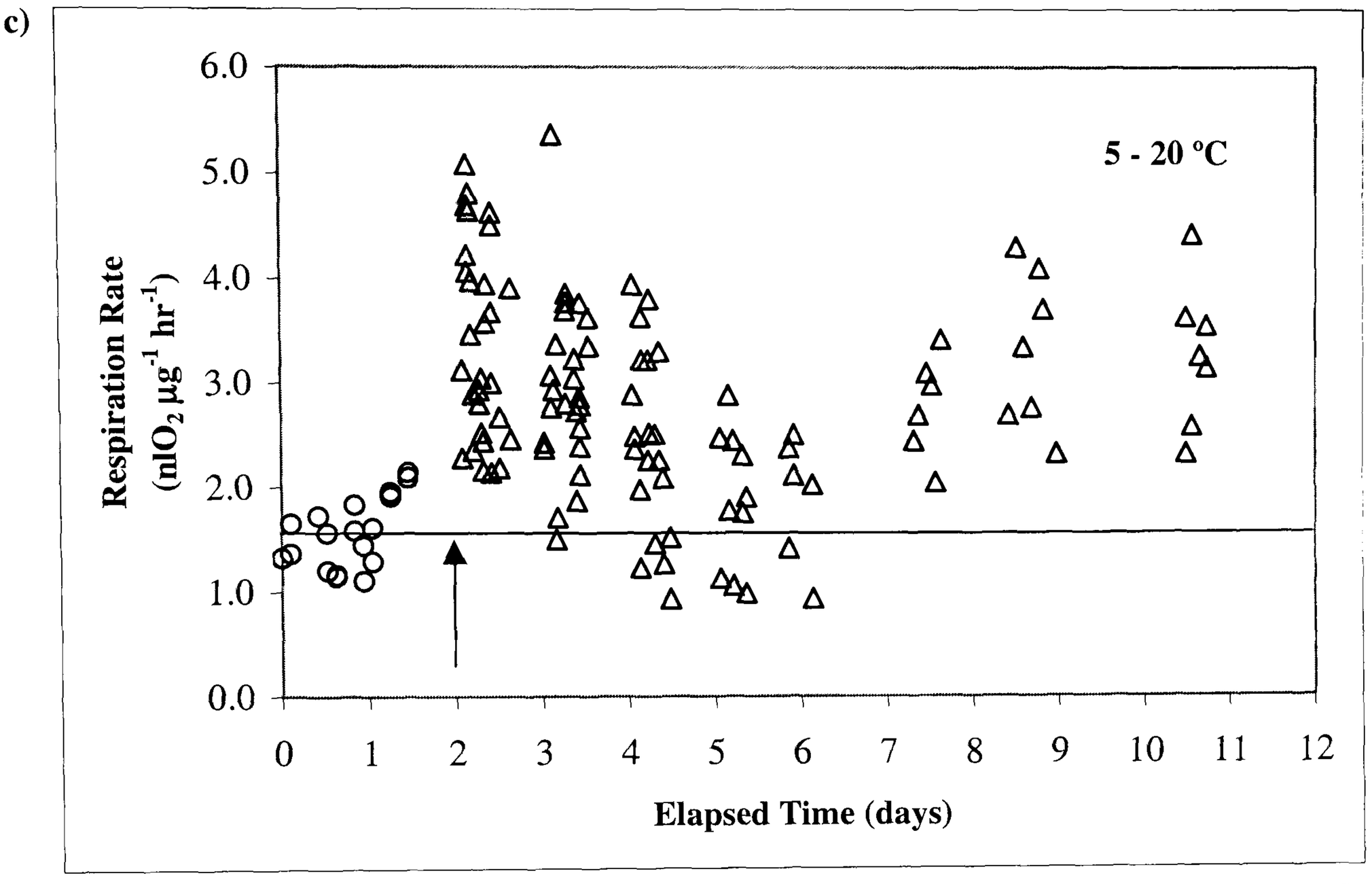


Figure 7.6: Continued



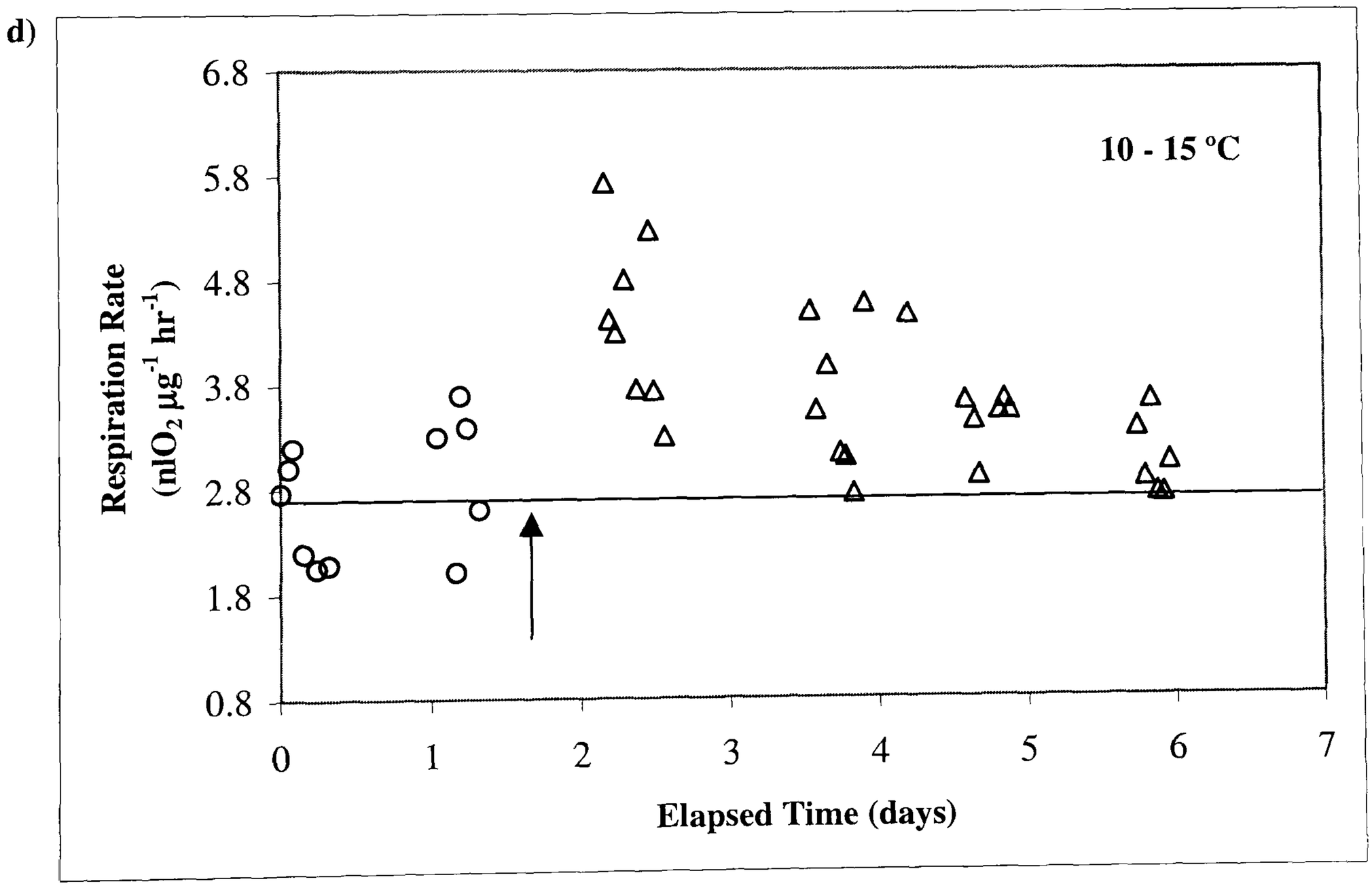


Figure 7.6: Continued

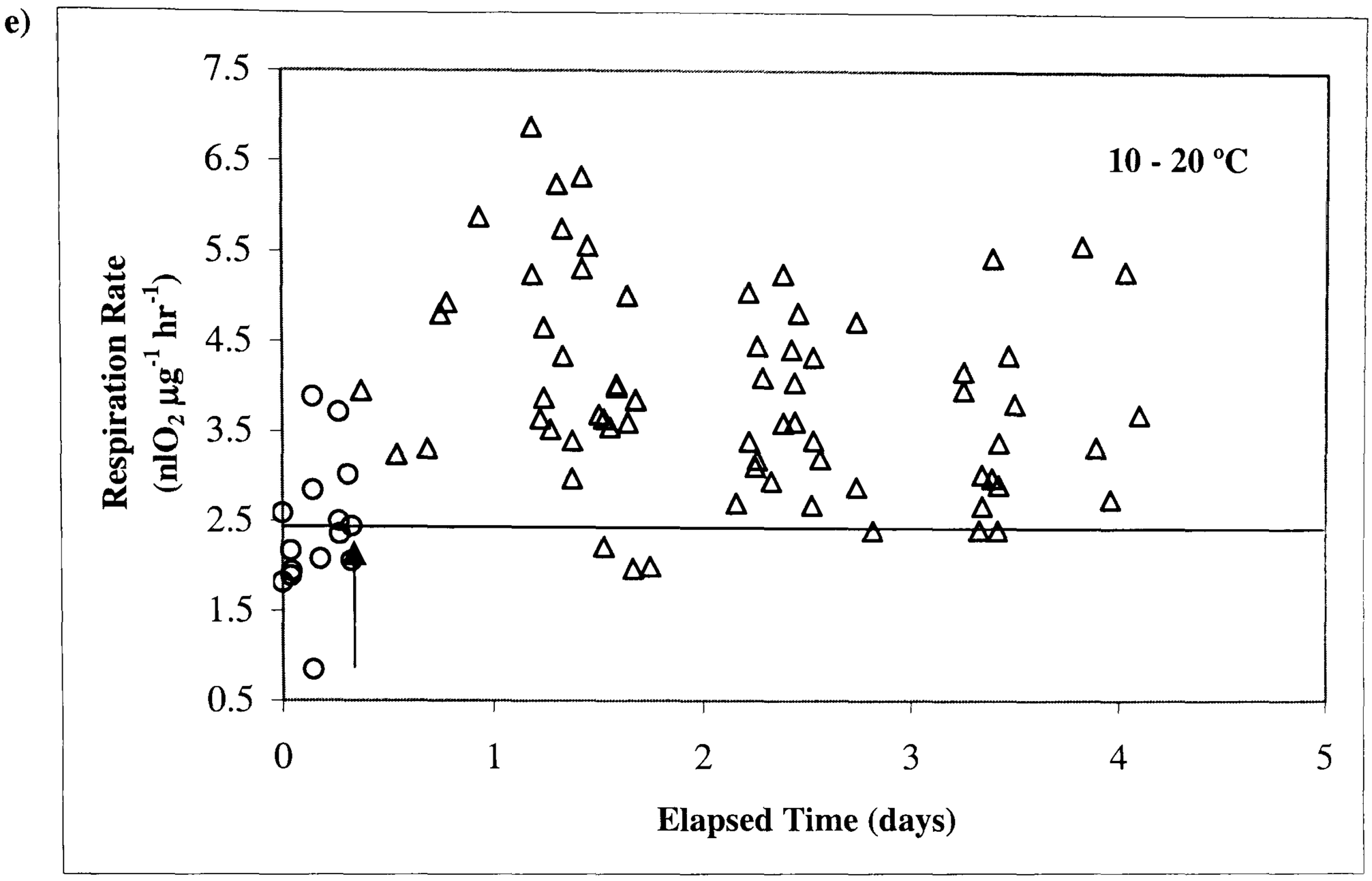


Table 7.9 summarises the trend in acclimation in the respiration rate of *T. longicornis* after the copepods have been exposed to a temperature shift as shown in Figure 7.8, a-f.

Table 7.9: Summary of the changes in respiration rate of *T. longicornis* copepods shifted from different acclimation temperatures (Acc.T.) over different temperature intervals (Δt). The percentage change immediately after the temperature shift (A.R.) and the percentage difference between the final stabilised rate (S.R.) and the mean control rates and the Q_{10} are shown. The approximate time needed to reach a stabilised rate after the temperature shift and the nature of any over/under compensation is also indicated.

Acc.T. (°C)	Δt (°C)	I.C. (%)	A.R Q_{10}	S.R. (%)	Time (days)	Compensation over/under
5	+ 5	+ 72	2.9	+ 9	3.5	No
5	+ 10	+ 120	2.2	+ 40	3.2	Slight-under
5	+ 15	+ 182	2.0	+ 113	6.2	Pronounced –under
10	+ 5	+ 93	3.7	+ 11	3.5	No
10	+ 10	+ 156	2.6	+ 72	3.2	Slight –under
15	- 5	- 81	3.2	0	3.1	No

There is a general consistency in the pattern of response in the copepod metabolic rate following the temperature change, which is largely independent of the acclimation temperature but related to the magnitude and direction of the temperature shift. Thus, the larger the temperature shift, the greater the increase in initial respiration rate and the larger the difference between the initial acclimated rate and the final stabilised rate (compare Figure 7.6, a to c). Similarly, the presence of a pronounced under-compensation on returning to a stable rate is related to a large (i.e. 15 °C) temperature shift (Figure 7.6, c). Only slight under-compensation is evident for a 10 °C shift and none at all for a 5 °C shift at any acclimation temperature and irrespective of the shift direction (Figure 7.6, f).

The initial rates recorded after the temperature shift showed the general characteristics of acutely measured R-T curves with shifts from 5 °C resulting in Q_{10}s ranging from 2.0 to 3.7 averaging 2.9. Using the final stabilised rates Q_{10}s ranged from 1 to 1.7 indicating the presence of acclimation (Table 7.9). The new stabilised rates attained after completion of the acclimation did not seem to vary a great deal when a 5 °C temperature change was applied. On the other hand, at higher temperature shifts of 10-15 °C the rate did not return at the original acclimation temperature but was

intermediate between the initial and the final rate conforming to the type-3 pattern described by Pretch (1958).

The time required to reach a stable rate after the temperature change varied between 3 to 6 days (average 3.3 days) showing no clear pattern except for the largest shift (from 5-20 °C) where it took nearly twice as long to establish a stable rate (Table 7.9).

7.5 Discussion

According to Le Borgne (1986) data for the time required to reach a stable routine metabolic rate is very variable and should be assessed for the species under investigation. The current study has shown that freshly collected *T. longicornis* from the Menai Strait, at 9 °C, reached a stable metabolic rate approximately 12 hours after capture. The present result contrasts with what found by Berner (1962) according to whom the minimum stable respiration rate in *T. longicornis* at 10 °C was reached only after 30 hours. High variability in the time required, by different copepod species, to reach stable routine metabolic rates does, however, pervade the literature. Halcrow (1963) found the metabolic rate in *C. finmarchicus* to decrease over 6-7 days, Fernandez (1978) over 40 and 50 hours for *T. stylifera* and *C. typicus*, Marshall & Orr, (1935) over 20 hours for *C. finmarchicus*, Ikeda (1977) over 9 hours in *A. tonsa*, Mayzaud (1976) over 6 hours in *A. clausi* and Conover & Corner (1968) found no change at all in *Calanus sp*.

High metabolic rates, measured after capture, have been largely attributed to the copepod's feeding history (Conover, 1956; Mayzaud, 1976; Ikeda, 1977) or animal "excitement" after capture (Conover & Corner, 1968; Marshall, 1973). The decrease in respiration rate of single *T. longicornis* from the present study was measured during the phytoplankton bloom when, in theory, animals were more likely to be influenced by food conditions and, therefore, the starvation time required should have been *maximum*. If animal 'excitement' played any part in altering copepod's respiration rate, methodologies involving high animal densities (Berner, 1962; Fernandez, 1978; Marshall *et al.*, 1935), might have needed longer stabilisation times of the metabolic rates due to animal to animal interaction (Conover, 1956).

The field acclimated respiration rate of *T. longicornis* was investigated monthly over a one year study between 1996 and 1997. Such investigations are very rare. Since

the early studies carried out by Marshall *et al.*, (1935), Conover (1968) and Berner (1962), there has been virtually no research conducted on the respiration rate of copepods in the field extending beyond two months.

The present work has shown that the respiration rate of *T. longicornis* taken freshly from the field increases with both ambient temperature and body size. Because of the high natural variability, which characterises copepod metabolic rates (Bamsted, 1988), there was a broad overlap between rates in different months especially at the lower and at the upper temperatures extremes. However, for any given size, the respiration rate of summer copepods was higher than that for winter copepods resulting in an approximate 40 % difference in the respiration rate or energetic requirement of copepods acclimated to seasonal temperature extremes (i.e. 5 ^{o}C and 17 ^{o}C). The multiple regression model found in the present study between 7 ^{o}C and 13 ^{o}C could explain about 58 % of the variability in the oxygen consumption measurements. A large part of the variability found in the present study probably arises from the different levels of activity shown by the animals as confirmed by observation made during the experiment.

The conclusions of the current investigation contrast with those of Conover (1959), Marshall & Orr (1966) and Butler *et al.*, (1970), who found copepod metabolic rates to peak in spring concomitantly with the occurrence of the phytoplankton bloom. If, for comparative purposes, the weight adjusted seasonal mean respiration rates of *T. longicornis*, from the current study, are plotted versus field temperature, the curve obtained (see Figure 7.4) shows more clearly a rise in respiration rate with temperature up to 15 ^{o}C beyond which rates remained approximately constant. Since these upper and lower temperatures extremes are close to the local ambient *maxima* and *minima* values, it is possible that at these values the temperature resistance mechanisms of the copepod become operative.

Berner (1962), investigating the seasonal variation in *T. longicornis* respiration rate in Milliport, could not detect any spring increase and attributed the lack of metabolic increase to the fact that his measurements were carried out after the diatom bloom. Although, Berner did not report field temperature values, the plot makes it evident that the mean copepod respiration rate, he measured, increased from May to July indicating a possible temperature effect similar to that found in the present study.

A comparison with previous work is often difficult due to the different experimental conditions adopted by different studies. Previous investigators have, in fact, traditionally reported mean copepod respiration rates derived from the incubation of groups of animals of various sizes rendering metabolic estimates approximate or at best imprecise. To complicate matters, in an attempt to standardise their results, in many of the previous studies, experiments were carried out at a single temperature irrespective of the acclimation temperature of the animals (Berner, 1962; Marshall & Orr (1966).

Table 7.10 has been drawn to illustrate comparisons of *T. longicornis* respiration rates from the literature. Respiration rate was measured in small coastal copepods, including *T. longicornis* by Marshall & Orr, (1966) and by Berner (1962), in *C. finmarchicus* by Marshall & Orr, (1958) at 10 °C, in small copepods by Conover (1959) at 20 °C, and in small and large copepods by Conover & Corner (1968) at 5-6 °C. The present study has shown that after a temperature shift of 5-15 °C the respiration rate of *T. longicornis* stabilises to the new temperature within 2 to 6 days. None of the studies cited above has taken into account the time required by the copepods to acclimate to a new temperature. If we assume, however, an average metabolic recovery time of 4 days, it is probable that most of time integrated measurements from previous investigations were something between an acute and an acclimated metabolic response to temperature. Thus, a combination of large animals in spring and low temperature exposure in summer may have resulted in many instances in the artefact reported of an increased respiration rate in spring.

If metabolic rates were measured at acclimated rather than at a single temperature it is probable that the seasonal respiration rates of many copepod species would prove not only weight dependent but also temperature dependent. As an example, Conover & Mayzaud (1975) found the seasonal average catabolism of fed mixed zooplankton species, measured at ambient temperature, to be directly proportional to temperature and dry weight while they could find no consistency in the effect of the food source.

The weight exponents of the monthly regression analysis, from the current study, between *T. longicornis* metabolism and body weight varied from 0.8 to 1.2 largely predicting a direct proportional increase corresponding to the Bertalanffy's (1957) type 2 relationship. Copepod metabolism has been reported to be related to the weight of the organism by an exponential weight coefficient varying between approximately 0.5 and 1

(Le Borgne, 1986). Conover (1959) reported a dry weight/metabolism exponent of 0.76 for *T. longicornis* from Southampton. However, the very high respiration rates in animals acclimated to 5 °C, strongly indicate that Conover (1959) data were biased by the elevated experimental temperature which he used (i.e.20 °C, see Table 7.10). The direct proportionality found, in the present study, between metabolism and weight was consistently measured for all the months investigated. As suggested by Conover (1959), however, exponents as high as 1 could depend on the relatively small size range analysed which does not include the copepodite stages and the very large adult *Temora* > 1300 μm C.L excluded from the present study because they were rare. According to Zeuthen's (1953) definition, on the other hand, since copepods in general and *Temora* in particular, fall in the group of organisms containing less than 0.1 mg of body Nitrogen content (Bamstedt, 1986), direct proportionality between respiration and body weight should be expected.

T. longicornis respiration rates from the present study, cannot be directly compared with the relationship found by Berner (1962) between some estimate of body surface (i.e. 1.2 x Length^2) and respiration rate, since his model was derived measuring copepods measured at 10 °C from different acclimation temperatures. However, the mean respiration rate of 32.1 $nlO_2\ cop^{-1}hr^{-1}$ measured at 10 °C for a *T. longicornis* of the average size of 800 μm C.L. from Berner (1962), is remarkably close with the rate of 31.7 $nlO_2\ cop^{-1}hr^{-1}$ estimated from the multiple regression model, from the present investigation (Table 7.10).

Table 7.10: Comparisons among *T. longicornis* respiration rates from the literature i.e. (1) with acclimated field rate estimated from the multiple regression equation (2) and from the metabolism-temperature curve relationship (3) found in this study. (C.L. = cephalotorax length in μm, D.W.= dry weigh in mg, E.t.= experimental temperature in °C, A.t.= acclimation temperature in °C, BPP = beyond the predictive power of the multiple regression, incubation time in squared brackets, 95% confidence interval in round brackets. All measurements reported were carried out between April and May.

C.L. (μm)	D.W.* (μg)	E.t (°C)	A.t (°C)	O_2-Rate (1) $nlO_2\ cop^{-1}hr^{-1}$	O_2-Rate (2) $nlO_2\ cop^{-1}hr^{-1}$	Acute (3) $nlO_2\ cop^{-1}hr^{-1}$	Method	Source
807	16	10	10 ?	32.1	31.78 (29.3-34.1)	34.55 (32.5-38.8)	Winkler [24]	Berner (1962) Milliport U.K.
941	25	10	10 ?	80	50.7 (48.4-51.9)	55.6 (51-60.7)	Winkler [24]	Marshall & Orr (1956) Milliport U.K.
859	19	15	7-8	142	49.4 (46.5-51.4)	56.5 (48, 58)	Manometer [3]	Raymont (1959) Harvard U.S.A.
861	19	20	5-10	130	B.P.P	81.8 (68.3-89.4)	Manometer [3]	Conover (1959) Southampton U.K.

*Dry weight estimated from the equation ln D.W.= -15.9 + 2.79 ln C.L, found for *T. longicornis* in the present study

Table 7.10 shows that the rates measured in *T. longicornis* by Berner (1962) and Marshall & Orr (1956) are closer to those measured during the present study, than to those from Raymont (1959) and Conover (1959) which are much higher than could even be predicted for acute temperature measurements. A possible explanation can be again partly found in the methodologies used. The rates reported by Berner (1962) and Marshall and Orr (1956), were possibly measured at temperatures close to the animal's field acclimation. In the case of Raymont (1959) and Conover (1959), on the other hand, animals were transferred from 5 °C to 15 °C and from 5-10 °C to 20 °C respectively after a mere acclimation of 15 minutes. Berner (1962) has suggested that the shaking procedure of the experimental flasks in the manometric technique had also contributed to the high respiration recorded by Raymont (1959) and Conover (1959). In all cases, however, sizes and metabolic rates reported in Table 7.10 represented averages that must hide even more variability.

The results of the present study show that the pattern and the time course of respiratory acclimation to temperature in *T. longicornis* was similar to the classical trends reported for a variety of other poikilotherms (Schlieper, 1950; Bullock, 1954; Pretch et al., 1955). Thus, in the present study, a sudden temperature rise induced an initial increase in the copepod's respiration rate, which persisted for about one day and was followed, by a steady decline and oscillation dependent on the magnitude of the thermal change. Respiration rates took 3 to 6 days, to stabilise at the new temperature. Conversely, a temperature decrease induced a mirror image of the acclimation pattern observed for an equivalent warming.

Despite the wealth of studies reporting on the existence of copepod metabolic acclimation in the field (Conover, 1956; Conover, 1961; Halcrow, 1963; Anraku, 1964; Gaudy, 1973; Hirche, 1987), Halcrow's (1963) experiment on the respiration rate of *C. finmarchicus*, is the only existing investigation carried out on the time course of metabolic acclimation to temperature in copepods. Halcrow (1963) reported an initial overshoot in the respiration rate, of *C. finmarchicus*, lasting for 4 hours after a temperature increase, followed by a stable rate (which he used for Q_{10} determinations). Grainger (1956), on the other hand, has reported that both increases and decreases in temperature, result in a metabolic undershoot, lasting minutes, in all the crustacean species he studied. The initial respiration rate measured after the temperature change in *T. longicornis*, in the present investigation, persisted for over one day and had the

characteristics of an acute temperature response with an average Q_{10} of 2.9. Thus, it probably represented the stabilised rate, which is usually taken for Q_{10} determinations, the time course of which has, till now, never been followed in small copepods.

Halcrow (1963) presented results collected from newly captured *C. finmarchicus* from the field, which were thus initially fed, and then subsequently deprived of food for the duration of the experiment. In the present investigation, copepods from the field were, first acclimated to laboratory conditions (including being fed) at their ambient temperature and then deprived of food 9-24 hours before measurements, to eliminate the effect of ASDA. Despite these methodological differences, the general trends found by Halcrow (1963) in *C. finmarchicus* are similar to those reported for *T. longicornis* in the present study. For instance, the correspondence of the magnitude of the initial acute respiration rate with the magnitude of the temperature shift, found in *T. longicornis* can also be observed from the plots presented by Halcrow (1963).

Stable respiration rates were established for *T. longicornis* within 3-3.5 days of temperature shifts between –5 °C and + 10 °C but took nearly twice as long (6 days) for the largest temperature shift employed (+ 15 °C). Halcrow (1963) reported minimal respiration rates in *C. finmarchicus* within 5-7 days for indeterminate temperature shifts of between –5 °C to +21 °C (note the time scale of his Figure 1, 20 °C, is out by 2 days given his warming period) and ultimate, possibly stable, rates after 11 to 13 days. If we assume the minimal rate observed in *C. finmarchicus* is equivalent to the undershoot we see for *T. longicornis* then it appears that the larger copepod takes nearly 3 times longer to acclimate to a change in temperature. Peterson and Anderson (1969), using *Salmo salar* and Widdows and Bayne (1971), using *Mitylus edulis* found no influence of initial acclimation temperature on the time course of acclimation to a constant temperature shift of 5 °C in their experimental organisms. It seems likely that, the increased acclimation time seen in *T. longicornis* shifted over + 15 °C is a consequence of the organism being forced to acquire resistance type adaptations towards the higher extreme of it's thermal environmental range (i.e. 4-17 °C, in the Menai Strait) in comparison to the capacity type adaptation required for the smaller thermal shifts.

The acclimated rates measured, in the present study, generally increased with temperature, although a ± 5 °C shift, caused insignificant changes in the acclimated rate over the control rate. The time course of temperature acclimation observed in *T. longicornis* respiration rate, in this study, resembled the Type-3 acclimation described

by Pretch et al., (1955) the final, stable, rate being intermediate between the acute phase rate and the original rate. Type-3 acclimation, "partial compensation", has been reported as the most frequent type of metabolic adjustment to temperature in both aquatic and terrestrial organisms (Prosser and Brown, 1961; Crisp and Ritz, 1967; Kalarani *et al.*, 1991).

In many studies of acute or acclimated responses of copepod metabolism to temperature, the dynamic respiratory pattern and its time course is generally not investigated. Since acclimation time varies from species to species and may also change, as suggested by the present study, according to the magnitude of the temperature change, preliminary experiments exploring the time course of acclimation are essential for adequate interpretation of the experimental results. The determination of both acute and acclimated metabolic rates in marine and freshwater crustaceans generally rely upon an arbitrary time scale, which may not correspond, to that of the rate measurement intended. For example, acute R-T curves, have been measured by Anraku (1964), Gaudy (1973) and Hirche (1987) in a variety of copepod species after 24 hours acclimation, by Mayzaud (1973) in *Acartia clausi* and by Halcrow (1963) in *C. finmarchicus* after 4 hours acclimation, by Comita (1965) in *Diaptomus sicilioides* after 18 hours acclimation, by Iguchi and Ikeda (1995) in the euphausid *Euphausia pacifica* after 3-12 hours acclimation. Obviously such variety in the timing of measurements needs to be explicitly justified. Understanding the time course of acclimation should be a prerequisite to studying the effect of any relevant environmental parameter, like temperature, on the metabolism of copepods, particularly if the results are intended for use in ecosystem modelling pertinent to seasonal fisheries production.

In the present study, acute exposure to temperature was found to affect the respiration rate of *T. longicornis* in a similar fashion reported for several copepod species by other authors (Gauld & Raymont, 1953; Raymont, 1959; Conover, 1959). The Arrhenius equations for *T. longicornis,* did not seem to deviate from linear relationships within the 4 °C to 20 °C temperature interval at any acclimation temperature. The acute effect of temperature on *T. longicornis* respiration rate, as estimated with the Q_{10} and the Arrhenius μ or Ea temperature coefficients, is summarised and compared with previous studies in Table 7.11.

The rate of increase measured for *T. longicornis*, in the present work, between 5 °C and 20 °C had temperature coefficients Q_{10} and Ea which were comparable to those

recalculated from Gauld & Raymont's (1953) data on *T. longicornis* (Table 7.11). The average Q_{10} found in this study was 2.10. According to Pretch *et al.*, (1955), Q_{10} values of less than 2 indicate that a homeostatic mechanism is operative.

The values for the temperature coefficients found in the present study are within the values of Q_{10} = 2-3 and Ea = 10.5 to 75 KJ mol^{-1} reported for most enzyme catalysed reactions (Hoar, 1966) and for the respiration rate of copepods and other crustacean species (Table 7.11). According to Hoar (1966), Ea, which theoretically represents the energetic barrier or master reaction (Crozier & Stier, 1924 & 1926) for the reaction to occur, is quite high for respiration achieving values around 70 KJ mol^{-1}. The similarities found between the Ea reported for most of the respiration rates of different crustaceans suggest that a similar enzyme system complex may be implicated in the control of the respiratory activity.

Table 7.11: Temperature coefficients Ea (i.e.activation energy) and Q_{10} for physiological rates in crustacean species calculated from published data., t = temperature in (°C), CV= copepodite stage 5, *= assuming a dry weight of 200 µg copepod^{-1}.

Species	Stage	Parameter	t (°C)	Ea (KJ mole^{-1})	Q_{10}	Source
Temora longicornis	Adult	Respiration rate	5 – 20	45 – 58	1.94 – 2.35	Present study
Temora longicornis	Adult	Respiration rate	10 – 20	61.1	2.43	Gauld & Raymont (1953)
Temora longicornis	Adult	Limbs beat frequency	2.5 – 22.5	28 - 40.5	1.8	Gill & Crisp (1985)
Centropages hamatus	Adult	Respiration rate	6 – 20	59.9	2.42	Gauld & Raymont (1953)
Acartia clausi	Adult	Respiration rate	10 – 20	44.7	1.91	Gauld & Raymont (1953)
Calanus finmarchicus	Adult female	Respiration rate	0-10	77.5	3.31-3.44	Hirche, (1987)
Calanus finmarchicus	Adult female	Respiration rate	0-10	36.9*	-	Marshall *et al.*, (1935)
Calanus hyperboreus	Adult female	Respiration rate	0-10	56.22	2.38-2.44	Hirche, (1987)
Calanus hyperboreus	CV	Respiration rate	0-10	49.7	2.15-2.22	Hirche, (1987)
Calanus hyperboreus	CV	Respiration rate	0-10	38.4	-	Conover (1962)
Calanus glacialis	CV	Respiration rate	0-10	95.9	4.39-4.6	Hirche, (1987)
Metridia longa	Adult female	Respiration rate	0-10	46.1	2.04-2.09	Hirche, (1987)
Metridia longa	-	Respiration rate	0-10	63.3	-	Haq, (1967)
Penaeus monodon	Postlarva-Adult	Respiration rate	20 – 30	58.6	1.8-1.9	Kurmaly *et al.*, (1989)

Bullock (1955) has emphasised that acutely measured metabolic rates are among the most variable parameters measured in animals. Indeed the Arrhenius plots were characterised by a broad variability of the metabolic rates of the copepods. The interpretation of M-T curves can often be complicated by the variability if the respiration rates are measured only at few temperatures (Conover, 1961; Halcrow, 1962; Anraku, 1964; Gaudy, 1973). In the present study, measurements were carried out mostly at 1 or 2 ^{o}C interval over the full environmental temperature range so that the plots obtained should be truly representative. The Arrhenius equations of *T. longicornis* respiration rate obtained at different acclimation temperatures were not significantly different. Thus, according to Pretch's (1953) definition, *T. longicornis* from the Menai Strait does not show metabolic acclimation to temperature.

The physiological response of copepods to seasonal and latitudinal temperature variation, based on the interpretation of M-T curves, from the literature, has proven very variable and to some extent contradictory. Climatic adaptation with seasonal changes in the Q_{10} have been reported for several coastal Mediterranean copepods species (Gaudy, 1973) and for a variety of Atlantic species (Anraku, 1964). Conover (1956), on the other hand, found significant differences in the respiration of winter and summer acclimated *A. clausi* but not in *A. tonsa*. Seasonal temperature acclimation has also been reported by Marshall *et al.*, (1935) and Halcrow, (1962) in *C. finmarchicus* and by Conover (1961) in *C. hyperboreus*. Hirche (1987), however, found no indication of cold adaptation for Arctic *Calanus sp.* including *C. finmarchicus*. Bamstedt & Tande (1985) found that *C. glacialis* living at low temperatures had lower respiration rate of *Calanus* species from warmer latitudes. Vidal & Witledge (1982), recalculating Ikeda's (1970, 1974) data on zooplankton species by taking into account body lipid content, found that boreal species had a lower respiration rate than subtropical ones contrary to the conclusion of the author.

Gill and Crisp (1985) have reported *T. longicornis* limb beat frequency to acclimate to temperature (type IV, of Pretch, 1953). Different physiological rates have, however, been found to respond differently to temperature variation even in the same organism (Hoar, 1966) so that results, from this study, may not be comparable with those of Gill and Crisp (1985). The fact that no differences, however, were found among the M-T curves of copepods measured during different seasons, rules out any possibility

that generational differences could affect the Q_{10} of *T. longicornis* respiration rate as found for limb beats by Gill and Crisp (1985).

T. longicornis does not appear to exert any appreciable degree of control over its body metabolism independent of temperature on a short term exposure. Some evidence of metabolic adjustment was, however, present when either the M-T curves of animals from different seasonal acclimation were compared at temperature extremes or when long term acclimation studies were conducted. In the case of the M-T curves, for instance, the rates of warmer acclimated species declined at higher temperatures than those for colder acclimated copepods indicating that temperature acclimation occurs to some extent and it can influence and 'stretch' the limits of temperature tolerance of this species. Likewise, the long-term acclimation experiments, carried out in the present study, have shown that, after the initial acute phase following the temperature shift, an intermediate stabilised rate was reached for the new acclimation temperature, which was comparable to the acclimated rate measured in *T. longicornis* from the field.

Emphasis, has been put on the need for a satisfactory and consistent interpretation of the M-T curves because of their use in the calculation of secondary production (Gaudy, 1973). The present study has shown that Q_{10} calculated from the multiple regression model varied from 2.44 between 7 °C and 13 °C and ~1.0 below 5 °C and beyond 13 °C (average Q_{10} = 1.68). On the other hand, the Q_{10} obtained from the pooled M-T curves averaged ~ 2.1.

Thus, a correct use of the Q_{10} in ecological modelling studies would require knowledge of the variation of Q_{10} for acclimated metabolic rate (rather than acute) over the natural temperature range experienced by the copepods. For instance, applying the Q_{10} from the M-T relationship would lead to the overestimation of the energy demand of the copepods at the extreme of the temperature ranges.

Metabolic studies based on the O:N ratio have indicated that the main substrate catabolized in small calanoid copepods is protein (Ikeda, 1974; Mayzaud, 1976; Bamstedt, 1985) while lipids and carbohydrates are usually not stored in large quantities (Klein-Bretler *et al.*, 1990; Bamstedt, 1985). Thus, considering a respiratory quotient R.Q.= 0.8 for protein catabolism (Schmidt-Nielsen, 1996) and the expression µg carbon catabolized = µl O_2 day^{-1} respired x 12 g C mol^{-1}/ 22.4 L mol^{-1}, the daily carbon required, for body maintenance only, by a 1000 µm C.L *T. longicornis*, would be 470 ng C at 5 °C in winter and 870 ngC at 17 °C in summer, as estimated from the multiple regression model.

corresponding to 4 % and 7.5 % of the animal body carbon respectively. Therefore, a daily carbon requirement of 5.2 % of body weight at 10 °C for a *T. longicornis*, from the present study, is identical to the 5.2 % calculated from Berner (1962) while is lower than the 8.2 % estimated from Marshall & Orr, (1956) at similar temperatures.

Although, considerable research has been carried out on the physiological and biochemical adaptations which organisms make at different temperatures (Pretch *et al.*, 1955; Bullock, 1955) clearly little is known regarding the significance of these adjustments.

Chapter 8

Seasonal changes in zooplankton species composition, biomass and production in the Menai Strait

8.1 Introduction

Zooplankton biomass and production in temperate marine ecosystems undergo dramatic annual and seasonal changes (Roff *et al.*, 1988; Bautista & Harris, 1992; Kane, 1993; Kiorboe & Nielsen, 1994; Gowen *et al.*, 1998). According to the classic theory of plankton production cycle, in temperate waters, increase in zooplankton abundance from low winter levels takes place after the spring peak of the phytoplankton (Cushing, 1959; Heinrich, 1962). Typically, phytoplankton biomass shows several seasonal peaks with blooms in early spring, autumn and occasionally summer whereas meso-zooplankton is characterised by a unimodal seasonal distribution with peak abundance and biomass during late spring and summer before returning to low winter densities (Wimpenny, 1944; Colebrook, 1979; Kiorboe & Nielsen, 1994; Gowen *et al.*, 1998). Thus, the seasonal zooplankton cycle lags behind the spring burst of primary production and phytoplankton abundance. In summer, zooplankton abundance may be largely unrelated to either primary production or phytoplankton standing stock (Fransz, 1976; Kiorboe & Nielsen, 1994).

It has often been observed, however, that in many coastal areas the peak abundance of zooplankton occurs during, rather than after, the spring phytoplankton bloom, largely as a result of a sudden increase in copepod densities between April and May (Fransz, 1975 & 1992; Gowen *et al.*, 1998). If the peaks of abundance of phytoplankton and zooplankton are in phase, the potential for transfer of energy from primary production to secondary producers is obviously greater than when the peak abundances are widely separated (Platt & Sathyendranath, 1992). Thus, differences in the timing of the phytoplankton-zooplankton increase will have obvious implications for the production and the energy transfer of plankton to the higher trophic levels of marine food-webs.

Planktonic copepods generally dominate the meso-zooplankton and their importance in the early life history of many commercial fish species (Cushing, 1989; Thompson & Harrop, 1991) has focused attention on the causes of the seasonal and annual variation observed in copepod biomass and production in different areas

(Colebrook, 1984; Fransz *et al.*, 1991). The size and species composition of copepod populations are controlled by a variety of factors including, food availability, fecundity, rates of juvenile growth, temperature, advection, emigration or immigration, parasites and predation (see review by Mauchline, 1998). The direct effects of all these factors are very difficult to quantify in natural populations and frequently involve a time lag between cause and effect (Levins, 1992). Consequently the causes of the observed seasonal and annual variation in zooplankton biomass and production are still incompletely understood (Kiorboe & Nielsen, 1994).

A variety of methods have evolved, over the course of the last century, for estimating the production of marine zooplankton which only requires the measurement growth rate and biomass. Whereas, biomass can be relatively easily quantified through an appropriate sampling program, the estimation of *in situ* growth rate is more difficult and time consuming. Despite the numerous approaches proposed to measure copepod growth rate none of these is completely satisfactory and as a result there is still not a definitive routine method for measuring secondary production in the marine environment (Poulet *et al.*, 1995).

Early approaches, particularly for the measurement of copepod growth rate (Kimmerer, 1987), were based on the study of cohort development (Winberg, 1971). However, since continuous recruitment is characteristic of many copepod species, natural cohorts are difficult or impossible to identify even with intensive sampling (Binet, 1977; Huntley & Lopez, 1992). In addition, the experimental manipulation necessary to distinguish cohorts involves time consuming sorting of the animals (Klein Breteler, 1986) with the risk of introducing artefacts due to handling (Miller *et al.*, 1984).

Another approach, based on egg production has also been proposed which allows fast and accurate estimation of the production of adult copepod females (Poulet *et al.*, 1995) and it is highly sensitive to changes in environmental variables (Saiz *et al.*, 1997). Unfortunately, the equivalence between the growth rate of the females and the juvenile stages has not been generally established for different copepod species and for different *in situ* trophic conditions (Fryd *et al.*, 1991; McLaren & Leonard, 1995; Uye and Sano, 1998; Calbet *et al.*, 2000).

Some authors have proposed the use of empirical global predictive models, based on existing laboratory and/or *in situ* measurements, to estimate copepod growth using only body size and/or temperature (Huntley & Lopez, 1992; Hirst & Lampitt,

1998). Although of potential practical use, the validity of copepod growth estimates derived from the application of these models, however, has not been widely accepted (Kleppel *et al.*, 1996) and it is still being evaluated (Hirst & Sheader, 1997).

Detailed information on zooplankton diversity at a regional scale is essential for understanding the year-to-year fluctuations of planktonic communities (Beaugrand *et al.*, 2000). This is particularly true for coastal areas where the anthropogenic influence is usually greater and where the nursery grounds of many commercial fish species are found. The seasonal cycle in copepod abundance can vary with species and geographical location. For instance, whereas, *P. elongatus*, *A. clausi* and *C. hamatus* are more restricted to summer months, *T. longicornis* is the dominant species in spring and early summer for the southern North Sea (Fransz *et al.*, 1976; Fransz & van Arkel, 1983). In the central North Sea *C. hamatus* is present in May but is replaced by *C. typicus* in summer (Fransz *et al.*, 1984). Despite the importance of marine copepods in food webs detailed information on their regional biodiversity and the causes determining this variability remains largely unexplored (Beugrand *et al.*, 2000).

The Irish Sea zooplankton community has been relatively well studied over the last century. The earliest recorded zooplankton surveys undertaken by Scott (1906) and Riddel (1914), off the north coast of Wales, were only qualitative and the first quantitative studies on the meso-zooplankton were those by Williamson (1956) and later by Colebrook (1979) and Williams *et al.*, (1994).

Compared to zooplankton studies in the western Irish Sea (Herdman 1921, Scrope-Howe & Jones, 1985; Gowen *et al.*, 1998 & 1999) information for the eastern Irish Sea is more sparse. Generally, most of these zooplankton studies have been limited only to part of the year for both off-shore (Williamson 1952) and coastal regions (Floodgate *et al.*, 1981; Kendaris, 1974) with few regular, seasonal surveys undertaken (Haq, 1960; Kenchington, 1968; Hidayat, 1995).

Previous studies, have mainly focused on species composition and abundance providing limited information if any on the seasonal variation in zooplankton biomass or productivity. Further more, whereas attempts have been made to relate the seasonal abundance of copepods to phytoplankton biomass and production in the western Irish Sea (Fogg *et al.*, 1985; Graziano, 1988; Gowen *et al.*, 1998) no such investigation has been attempted for the eastern Irish Sea. The aim of the present study was to investigate the seasonal changes in copepod species composition, standing stock and production in

the Menai Strait and indicate the potential for such data as representative of coastal waters in the eastern Irish Sea.

8.2 Material and Methods

8.2.1 Mesozooplankton sampling

Seasonal sampling for meso-zooplankton took place with a fortnightly to monthly frequency between January 1996 and December 1997. Triplicate samples were collected at 1-2 meter depth with two different nets; a 270 μm was used to sample the copepods and zooplankton larval stages and a 500 μm mesh-sized plankton net to sample the ctenophores and medusae. The nets where fitted with a non filtering cod-end to avoid damage to the animals caught and towed, one at the time, behind a small research vessel, the "RV Sand Pebbler". A back-stop digital flow-meter Kiel-Hydrobios (model 438 110) fitted in the net mouth allowed the total volume of the water filtered to be estimated.

A previous zooplankton study (Hidayat, 1995) showed no significant differences in total number of individuals in catches collected at selected fixed stations along the Menai Strait. Thus, sampling was undertaken at no fixed station and at high tide, to sample the water incoming from the Liverpool Bay. Net clogging was, however, largely avoided by restricting the towing time to 3 to 5 minutes (Unesco, 1968). Severe clogging of the net almost certainly would result in losses of the catch from the net (Unesco, 1968). The volume of water filtered varied due to the direction and speed of the tide in relation to that of the boat and to the density of the plankton in the water. However, only in few instances mainly coinciding with the spring phytoplankton bloom and the summer *N. scintillans* bloom, the sampling was affected by severe net clogging and the volumes filtered dropped to below 1-2 m^3.

The net was always retrieved before the boat was completely stopped to avoid overflowing of the catch from the net due to the backlash effect. Once retrieved, the content of the net was washed into a plastic bucket to which formaldehyde was immediately added to make a 4% final concentration. Temperature and salinity were measured at 1 meter interval throughout the water column deploying a CTD (model) from the boat, while Chlorophyll-a and microplankton samples were obtained by sampling at 1 m depth with a Niskin bottle (see general methodology in Chapter 3).

8.2.2 Zooplankton counting and species identification

The plankton was kept for a minimum of 1 week in the formalin solution to allow complete fixation of the animal body tissues (Unesco, 1976). After that, samples were thoroughly rinsed with tap water, in a fume cupboard, and preserved in a solution of alcohol (70 %) and glycerol (30 %) (Omori and Ikeda, 1984).

Prior to analysis larger objects including non-planktonic material like benthic filamentous algae and the large zooplankton (e.g.Ctenophores, chaetognaths and fish larvae) were extracted from the samples to facilitate the sub-sampling and counting procedures. Each sample was then appropriately diluted/concentrated, to obtain counts of at least 250 organisms in 5 ml sub-sample (Omori and Ikeda, 1984). The plankton was gently, mixed to obtain a homogeneous suspension of all the zooplankters present. The suspension was sub-sampled with a 5 ml dipper and all the organisms in the sub-sample counted in a Bogorov tray and identified. This procedure was repeated at least 4 times per sample (Unesco, 1968). The abundance of each species was estimated by counting and identifying all the individual zooplankton present in the sub-sample. To avoid inhalation of the toxic fumes released by the preserved samples, measurements were carried out under a stereomicroscope whose stage was encased in an airtight and plastic laminated ply-wood box mounted with an aspirator fan, connected through a flexible plastic exhaust pipe to a nearby window.

The copepod species and their larval stages were identified according to Klein Breteler (1982) and Wilson (1931), while other zoo-planktonic species consulting Fiches d'identification du zooplankton (various authors and years), Newell & Newell, (1977) and Todd & Laverack (1991). *Pseudocalanus elongatus* and *Paracalanus parvus* were considered as a single grouping (i.e. *Pseudocalanus sp.*) they occur at the same time and they are difficult to separate in samples.

8.2.3 Zooplankton sizing and biomass estimation

Data collection for the seasonal size frequency distribution of the copepod species was obtained by measuring the cephalothorax length, (width and depth) of at least 100 individual copepod species per each replicate samples. Speciation, sizing, staging and sex determination of adult and copepodite copepods, were carried out with an eyepiece graticule under a dissecting microscope Walburg-Wild-32 model to the nearest 20 μm. A length/weight calibration was obtained for fresh (non-fixed) *T. longicornis* from thirty groups of 20-30 copepods, covering the full size range, which were dried in an oven at 50

°C and weighed to the nearest 1 μg with a Cahn Microbalance. The copepods used ranged in cephalothorax length from 820-1465 μm (corresponding to 16-63 μg dry weight).

Body dry weight (D.W., μg) could then be estimated by measuring the cephalothorax length (C.L., μm) from the relationship:

$$\ln D.W = 2.75^{*} \ln C.L. - 15.9 \ (r = 0.92, p<0.001, d.f. = 29).$$

Weight was then converted to carbon assuming that ~ 40 % of the dry weight is carbon (Omori & Ikeda, 1984). The linear measurements obtained for *C. hamatus*, *Pseudocalanus sp.* and *A. clausi* were converted into biomass using length/ ash free dry weight (AFDW) relationships from the literature (Klein Breteler *et al.,* 1982; Berggreen *et al.*, 1988) and the assumption that 45 % of AFDW is carbon (Kiorboe *et al.*, 1985). No correction was made to these measurements, as shrinkage due to preservation is minimal (Durbin & Durbin, 1978).

Total body length of the ctenophores *P. pileus* (excluding tentacles) were measured under a stereo microscope Walburg-Wild-32 model to the nearest 1 mm. *P. pileus* were sized measuring length and width of fresh non-fixed samples. The *P. pileus* body carbon was estimated from length-carbon relationships from the literature (Miller & Daan, 1989).

8.2.4 Zooplankton standing stock and copepod production

Mean annual counts (ind. m^{-3}) and biomass (μg-C m^{-3}) were derived for each zooplankton group separately using trapezoidal integration between points.

Production was determined by multiplying weight specific growth (g) for each individual copepod by its calculated *in situ* biomass (μg-C m^{-3}). Copepod production was estimated from growth rates calculated from two different equations extrapolated by Hirst and Lampitt (1998) and Huntley and Lopez (1992) from published data in the literature. Thus, the first estimate of copepod growth rate was estimated with the "globally predictive" equations derived by Hirst and Lampitt (1998):

$$\mathbf{Log_{10}\, g = 0.0208\ (T) - 0.3221\ (log_{10}\, BW) - 1.1408} \quad (r = 0.66)$$

where g (d^{-1}) is the weight specific growth, T (°C) is the *in situ* temperature and BW (μg-C ind^{-1}) is individual body weight, adult males were assumed not to grow. The second

estimate of copepod growth rate was obtained using the equation of Huntley and Lopez (1992):

$$\mathbf{g = 0.0445 * e^{0.111 * T}} \quad (r = 0.95)$$

where g (d^{-1}) is the weight specific growth, T (°C) is the *in situ* temperature.

Annual production (mg-C m^{-3} yr^{-1}) was derived for each copepod species separately using trapezoidal integration between points. Total annual production was derived simply as the sum of production for each copepod species.

8.2.5 Cohort analysis

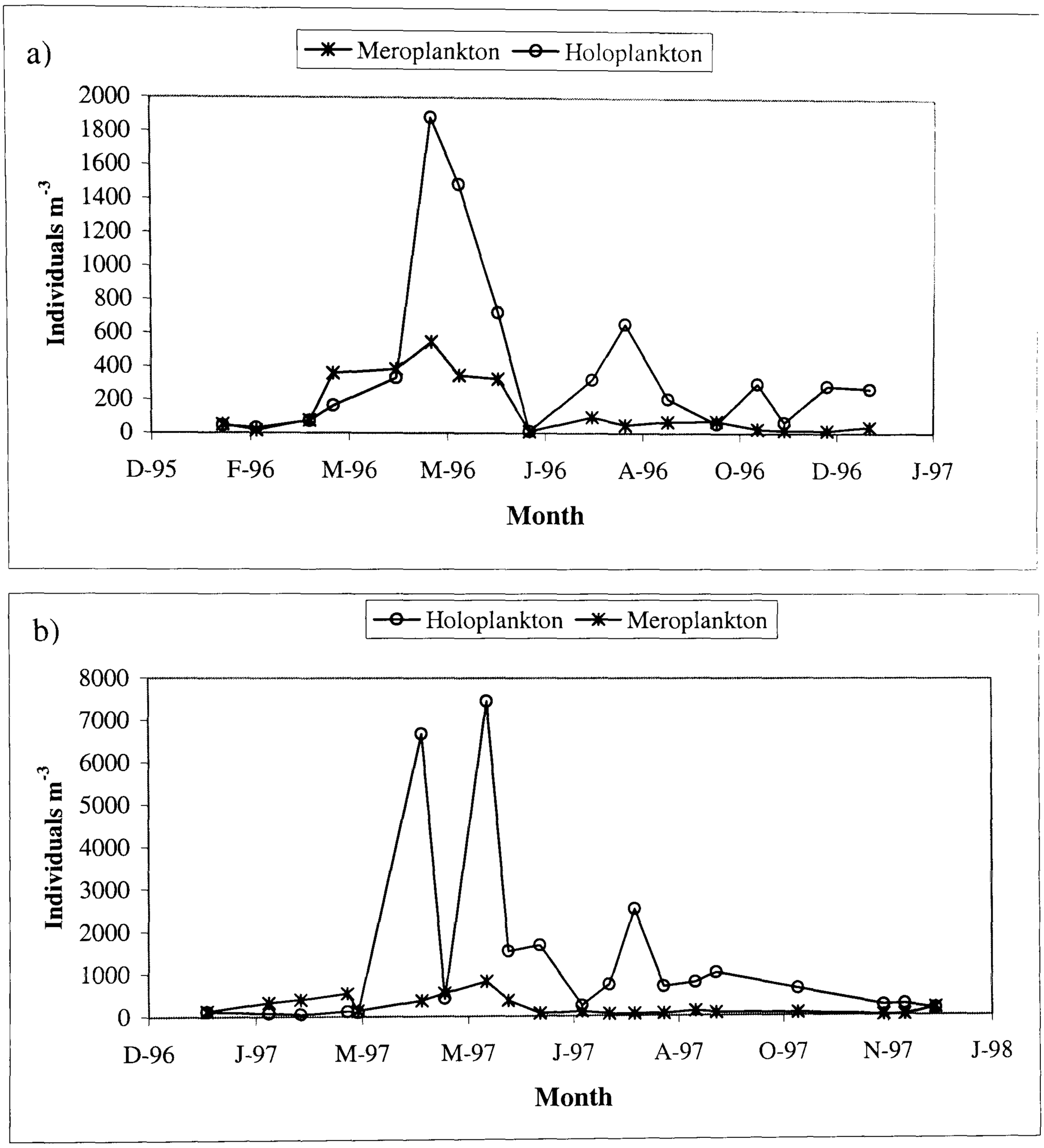
Inferences about copepod population dynamics in the natural environment can be made from measurements of the following: 1) absolute numbers of individuals of each developmental stage, 2) relative abundance of the stage 3) seasonal changes of adult size and 4) seasonal change of adult sex ratio (Ueda, 1978). In the present investigation the second and third method were used following McLaren (1978) and Uye (1982). If the population is reasonably synchronous, the relative abundance of the chosen stage should show well-defined pulses through time. In this study the stages CIV was chosen and its relative abundance as a percentage of the total copepodites was used to trace the cohorts, the appearance of which were simply defined as time of the peak of relative abundance. According to McLaren (1978), adult females that have grown up from naupliar stage under that temperature regime would have a period of stability in size followed by rapid change, followed by a period of stability at a new size after the old generation is numerically overwhelmed by the new. Thus, a pulse in copepodites should be followed by a changes in female cephalothorax length which should also indicate the numbers of cohorts during a year.

8.3 Results

8.3.1 Seasonal variation in merozooplankton and holoplankton

The seasonal variation of the zooplankton living in the Menai Strait during 1996 and 1997 was determined by the relative changes in the community and abundance of the meroplankton and the holoplankton (Figure 8.1).

Figure 8.1: Seasonal variation in abundance (ind. m^{-3}) in merozooplankton and holoplankton in the Menai Strait between a) 1996 and b) 1997.



The temporal variation in total zooplankton abundance, in the Menai Strait, is characterised by a low density during the winter months followed by a gradual increase in abundance of the meroplankton in early March-April and of the holo-plankton during April and May (Figure 8.1). During both 1996 and 1997 the highest mero- and holo-plankton abundance took place in spring whereas the summer and autumn were characterised by the appearance of several minor peaks of abundance before returning to the low winter densities.

Table 8.1 shows the mean annual abundance and the percentage seasonal changes for the main meso-zooplankton groups found in the plankton catches between 1996 and 1997.

Table 8.1: Annual mean abundance (ind. m^{-3}) calculated using trapezoidal integration, annual range (ind. m^{-3}) and relative proportion (%) of the main zooplankton groups found in the Menai Strait during 1996 and 1997.

Group	1996			1997		
Holoplankton	**Mean**	**Range**	**%**	**Mean**	**Range**	**%**
Calanoid Copepods	322	30 – 1810	67.39	1144.4	50-7270	83.28
Appendicularians	9.0	0 – 80	1.89	17.3	0 – 96	1.26
Chaetognaths sp.	8.8	0 – 62	1.84	4.9	0 – 18	0.36
Ctenophores sp.	0.3	0 – 1.5	0.06	0.3	0 – 1.7	0.02
Medusa sp.	1.4	0 – 16	0.29	4.4	0 – 27	0.32
% of Total Zooplankton	71.47			85.24		
Meroplankton						
Cirripede larvae	49.0	0 – 322	10.27	65.2	0 – 315	4.75
Decapod larvae	9.3	0 – 44	1.95	17.8	0 – 159	1.30
Bivalve larvae	3.3	0 – 26	0.69	3.8	0 – 12	0.28
Gastropod larvae	3.0	0 – 25	0.63	6.6	0 – 36	0.48
Gastropod eggs	49.0	0 – 273	10.27	52.3	0 – 295	3.81
Polychaete larvae	12.7	0 – 85	2.66	18.3	0 – 291	1.33
Bryozoan larvae	9.9	0 – 36	2.08	38.8	0 – 321	2.82
% of Total Zooplankton	28.53			14.76		

As shown in Table 8.1 the Menai Strait zoooplankton is dominated for most of the year by the holoplankton particularly calanoid copepods representing ~ 67 % and ~ 83 % of the total number of individuals in 1996 and 1997 respectively.

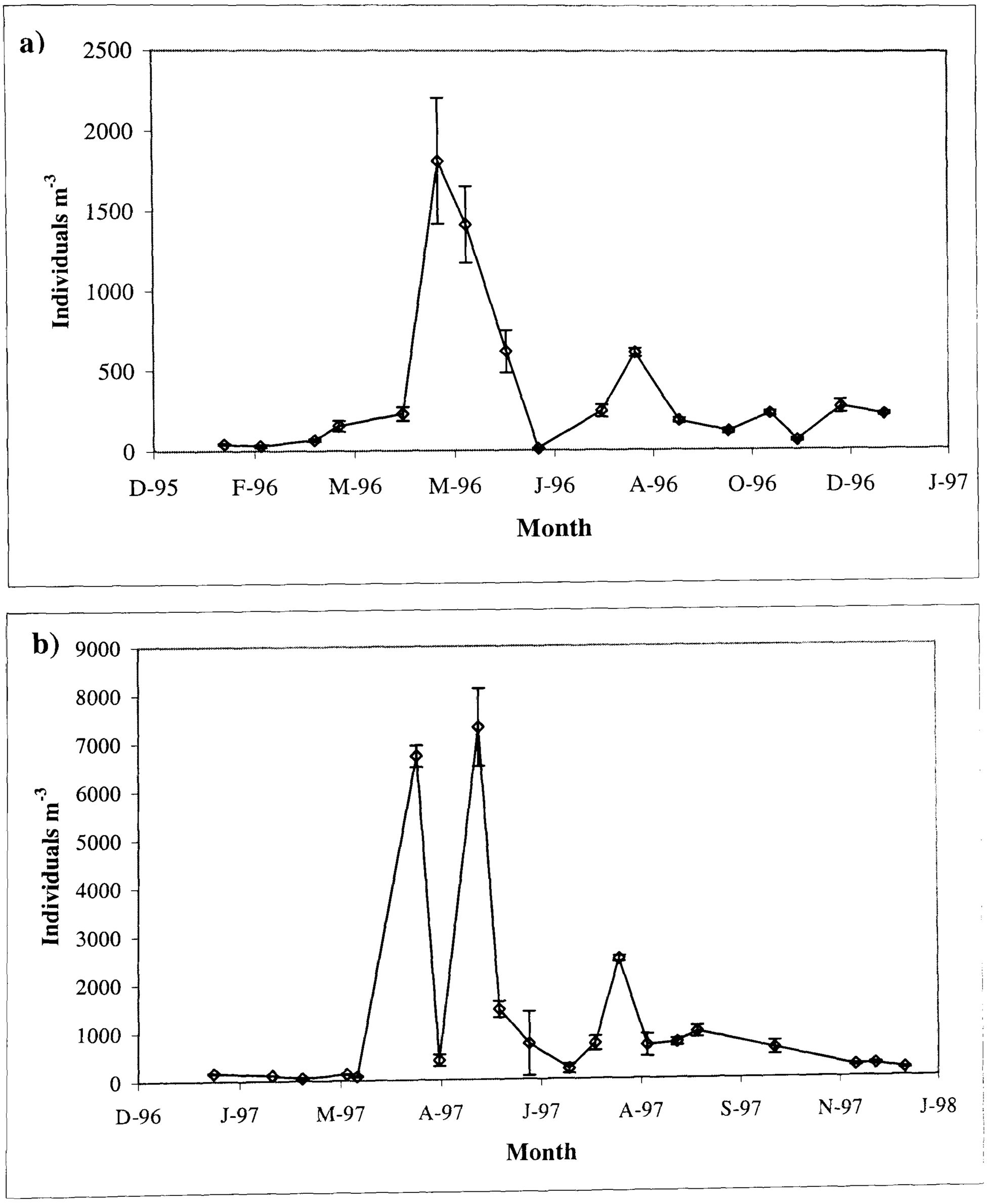
The higher total zooplankton abundance measured during 1997 as opposed to 1996 was mainly due to the higher spring and summer increase of the copepods although a similar higher trend could be observed also for decapods, polychaetes and bryozoan larvae (Table 8.1, Figure 8.14).

8.3.2 Seasonal variation in copepod abundance and species composition

The seasonal variation of copepod abundance (ind. m^{-3}) in the Menai Strait during 1996 and 1997 is shown in Figure 8.2. The copepod abundance began to increase from low winter levels towards the end of March to peak in May and in April for 1996 and 1997 respectively (Figure 8.2 & Chapter 3). The total copepod abundance at the end of the winter 1996 and 1997 was comparable (i.e. ~ 150 ind. m^{-3}). During spring, however, the total copepod number increased 12 and 45 fold above the winter levels for 1996 and 1997 respectively. Hence, the maximum copepod abundance recorded in spring 1996 (i.e. ~ 2000 ind. m^{-3}) was about 3.5 times lower than that recorded in 1997

(i.e. ~ 7000 ind. m^{-3}, Figure 8.3, a & c). Figure 8.3 also shows that a secondary peak of increase was also measured for both years during summer. As with the spring peak in 1996 the summer copepod population peak occurred about two weeks later and was about four times lower (i.e. August, ~ 600 ind. m^{-3}) than in 1997 (i.e. July, ~ 2500 ind. m^{-3}).

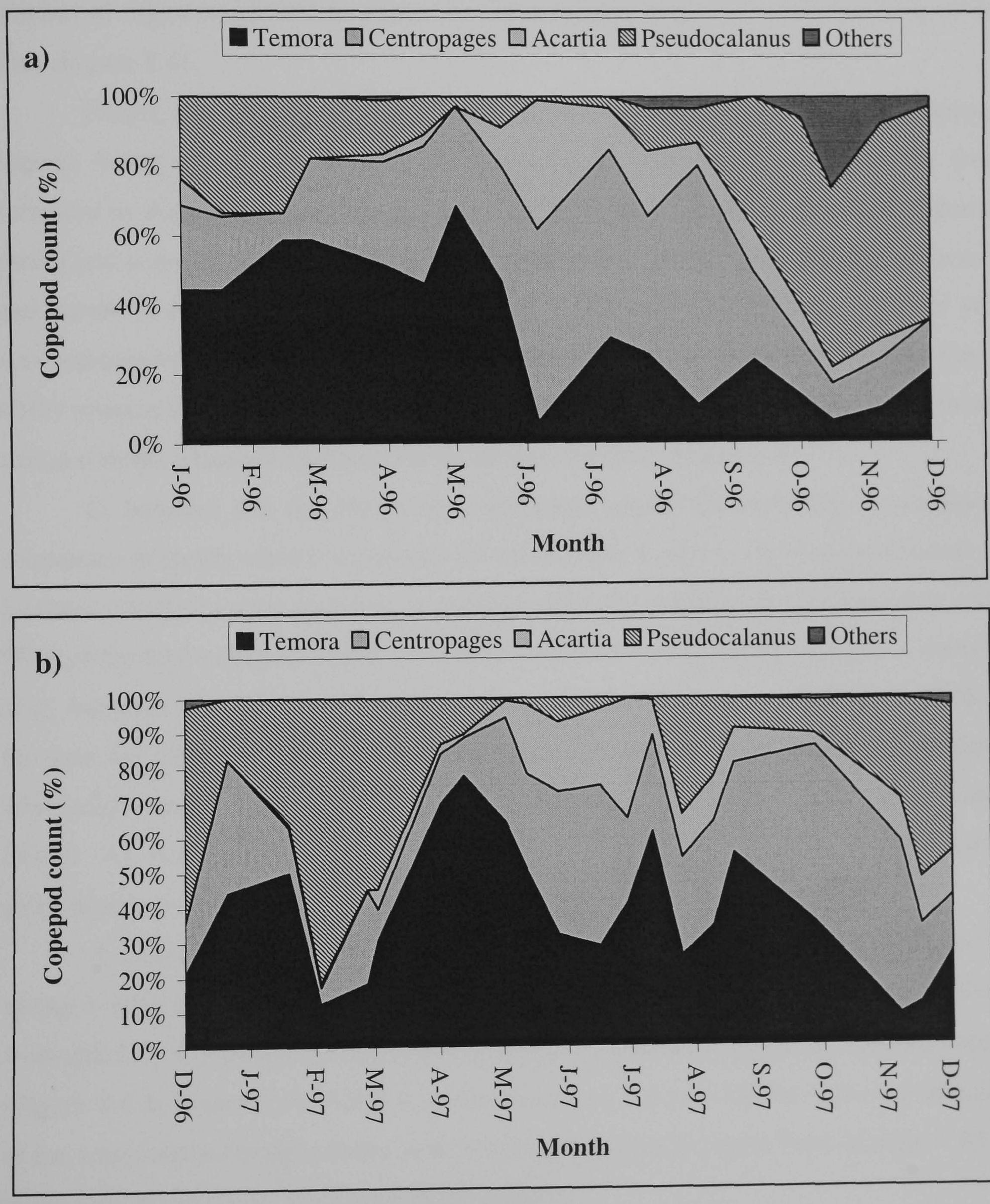
Figure 8.2: Seasonal changes in total mean (i.e. ind. m^{-3} ± S.D.) copepod abundance in the Menai Strait during a) 1996 and b) 1997.



8.3.3 Copepod species relative abundance and stages composition

Figure 8.3 shows the seasonal changes in the relative abundance of the copepod species composition whereas Figure 8.4 shows the seasonal changes in the copepod stages for each species.

Figure 8.3: Seasonal changes in relative (i.e. %) copepod abundance of different copepod species living in the Menai Strait during a) 1996 and b) 1997.



The Menai Strait waters are largely dominated by four species of calanoid copepods, namely *T. longicornis*, *C. hamatus hamatus*, *Pseudocalanus sp.* and *A. clausi clausi* (Figure 8.3).

The relative abundance of the different copepod species and their stage composition was broadly consistent between the years investigated (Figure 8.3 and 8.4 a & b). Whereas all the stages (CI-CIV) are shown for *T. longicornis* and *C. hamatus* only adults and total copepodites were counted for *Pseudocalanus sp.* and *A. clausi* as the number of organisms found for these two latter species was very sparse for most of the year (Figure 8.4).

During the 1996-97 survey *T. longicornis* was the dominant calanoid copepod species living in the Menai Strait (Figure 8.3). *T. longicornis* was abundant from February to August representing up to ~ 75 % of the total copepods counted during spring and summer. Its proportion declined to between ~ 8 and 30 % during the autumn and winter months. The highest proportion of *T. longicornis* abundance over the year was represented by the juvenile stages, particularly during spring and summer (i.e. > 60%) whereas the adults were relatively more abundant ~50 %-70 % during autumn and winter months when the total population density was low (Figure 8.4).

C. hamatus was the second most abundant species also reaching its maximum abundance in spring when it accounted for up to 30-40 % of the total copepod counts. *C. hamatus* usually became dominant in summer and early autumn representing up to ~ 55-70 % of the total copepod counts. As with *T. longicornis*, the spring population increase of *C. hamatus* was dominated by the juvenile stages representing ~ 80 % and ~70 % of the total for 1996 and 1997 respectively. Unlike *T. longicornis*, however, *C. hamatus* adult stages tended to be relatively more abundant than juveniles not only during winter (60-80 %) but also throughout the summer and autumn months showing peak proportions up to ~ 80 % particularly during 1996 (Figure 8.3 & Figure 8.4).

A. clausi was the least abundant calanoid species found in the Menai Strait. In spring it only represented ~3 % of the total copepod counts yet, in summer, between June and July it's population represented up to ~ 30-35 % of the total copepod counts (Figure 8.4 & Figure 8.5). Adult *A. clausi* tended to account for the highest proportion of the total counts throughout the year whereas the juvenile stages were at most ~ 63 % of the total during peak abundance in the summer.

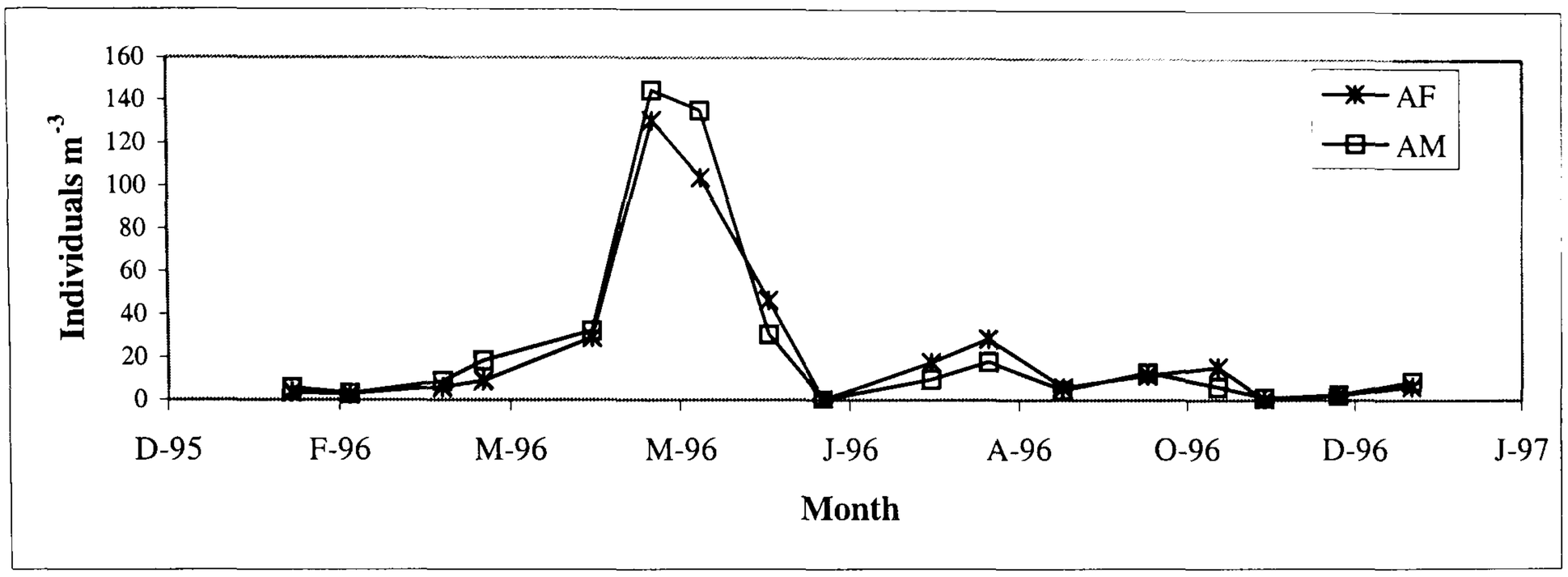
It is apparent from Figure 8.5 that stages younger than CIV (300-490 μm) were always less numerous than the older stages for all the species probably from under-

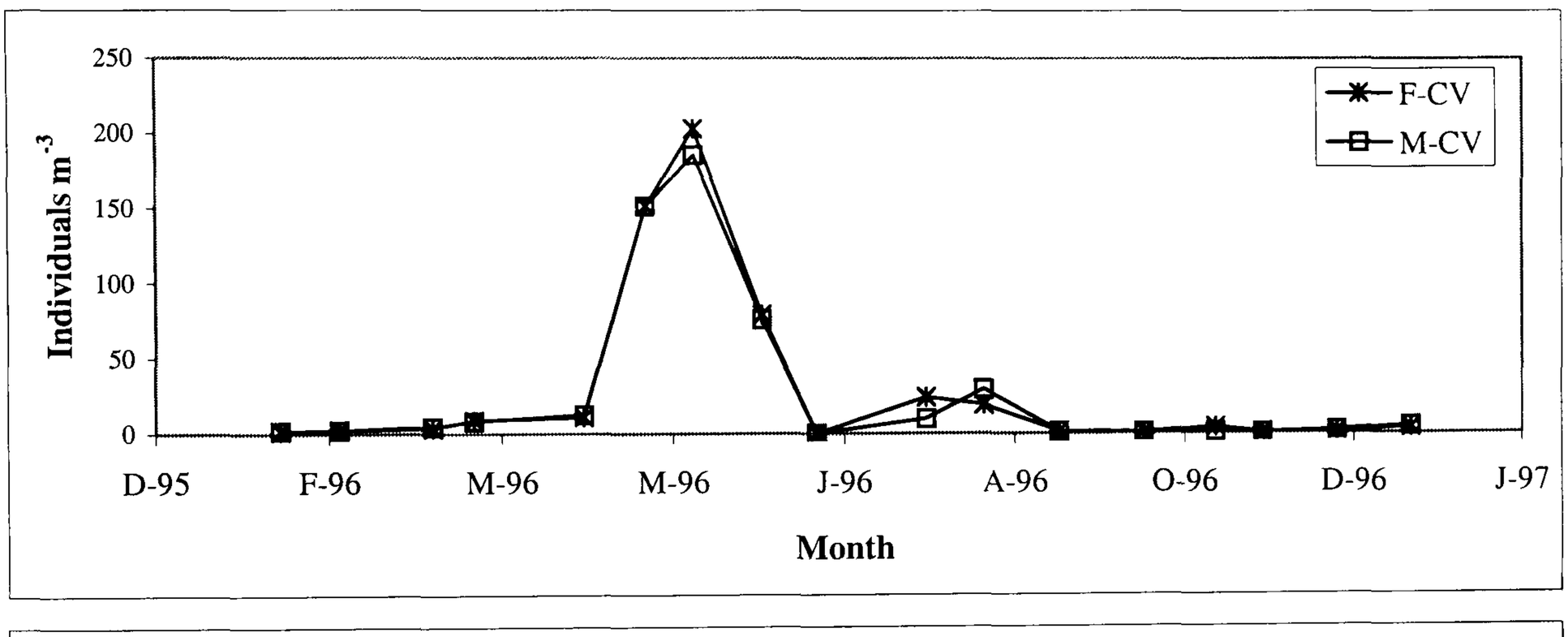
sampling by the 270 μm mesh size net. Overall, the seasonal change in the stage abundance for the four main species of calanoid copepod living in the Menai Strait followed a similar pattern. All the stages showed an annual maximum peak of abundance in spring and a secondary peak during summer.

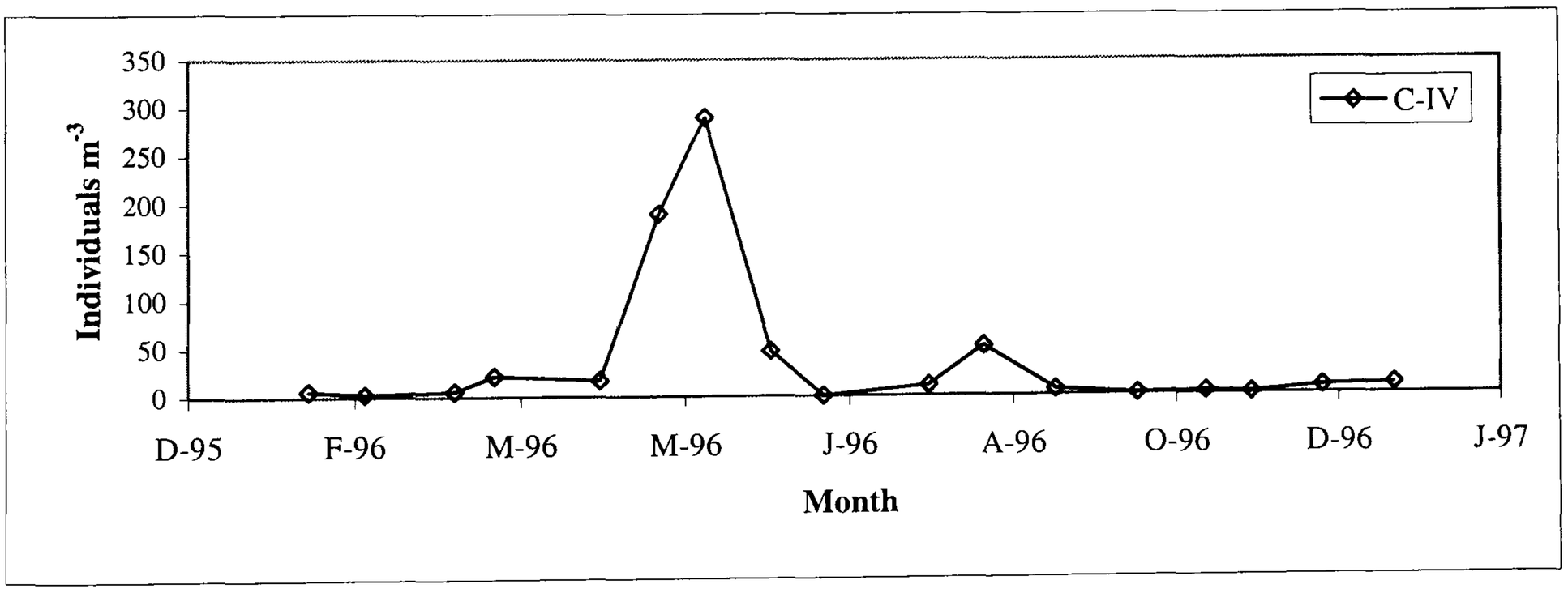
Other copepod species including *Calanus sp* and *Oithona sp.* and epibenthic harpacticoids, were present but in very low numbers. *Calanus sp* adults and nauplii were present particularly in autumn and winter but they were never numerically dominant. The cyclopoid copepod *Oithona sp.* (300 μm) was also found in the Menai Strait particularly towards the end of summer and in autumn, but also in very low numbers (i.e. < 1% of the total). Once again, the mesh size used was too coarse to sample this small species quantitatively. The harpacticoid *Euterpina acutifrons* was the best represented planktonic copepod and mainly appeared in the plankton catches during autumn and winter storm events when resuspension of bottom sediment was greatest.

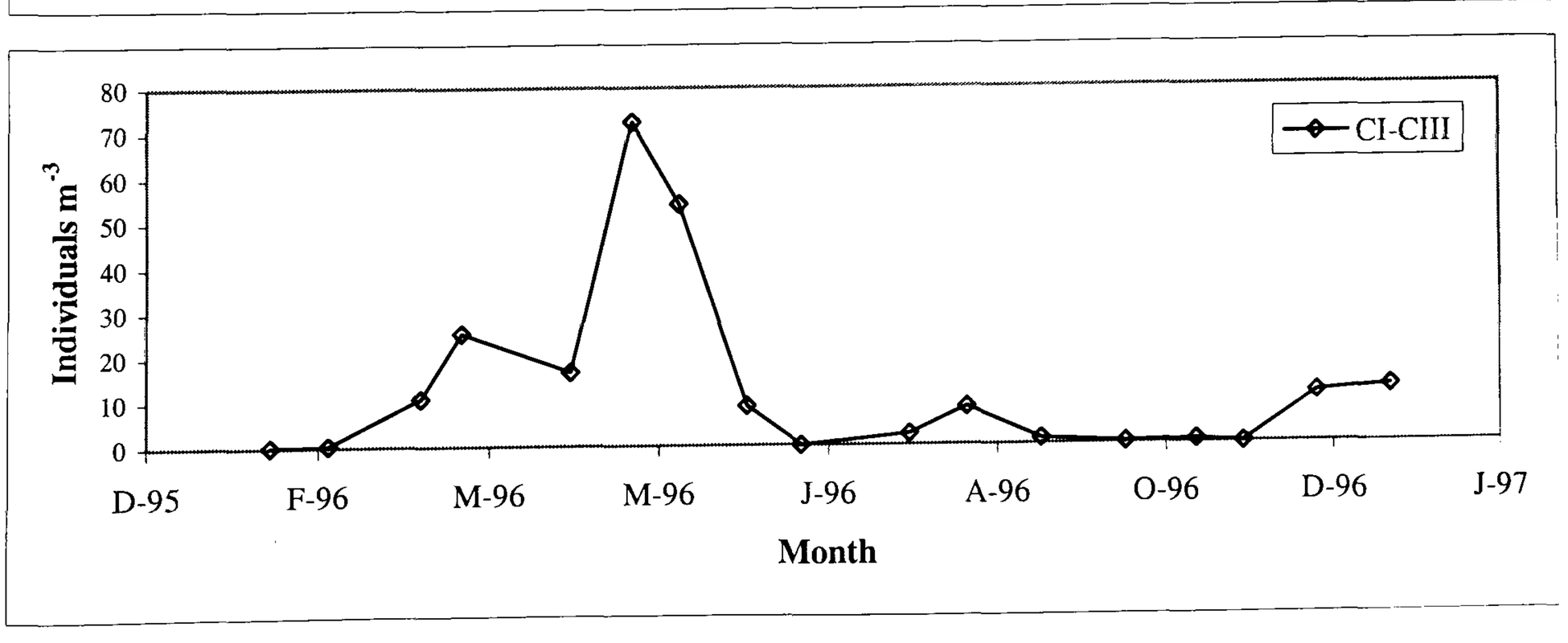
Figure 8.4: Seasonal change in stages abundance of *T. longicornis* in the Menai Strait during a) 1996 and b) 1997.

a)

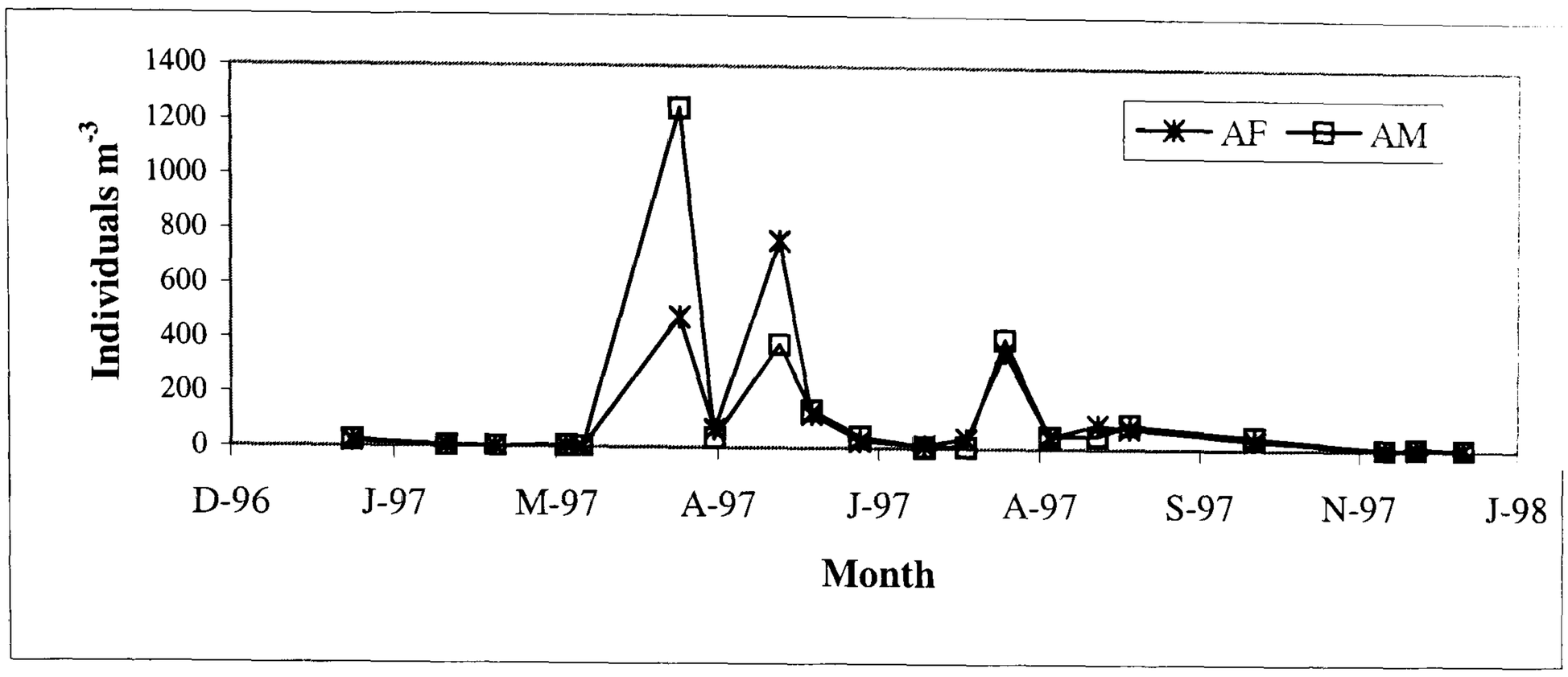








b)


Individuals m-3
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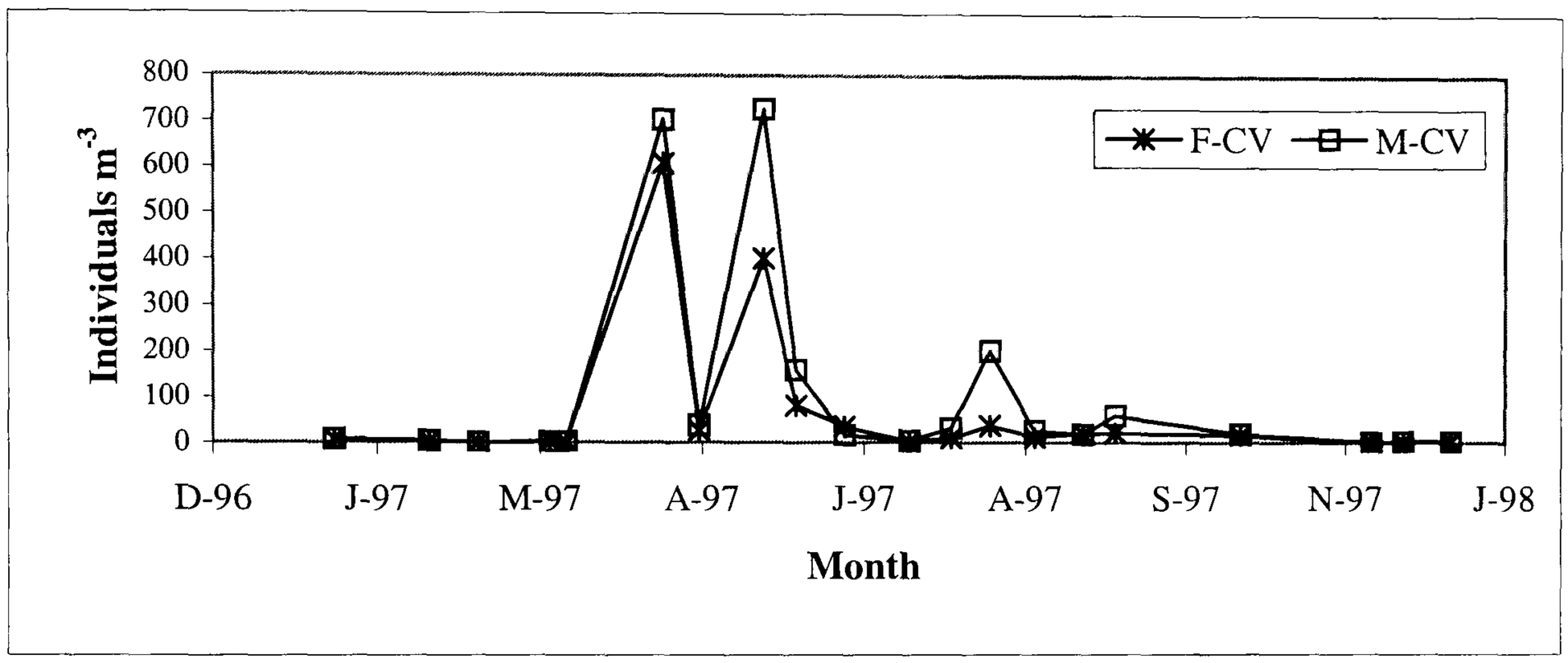
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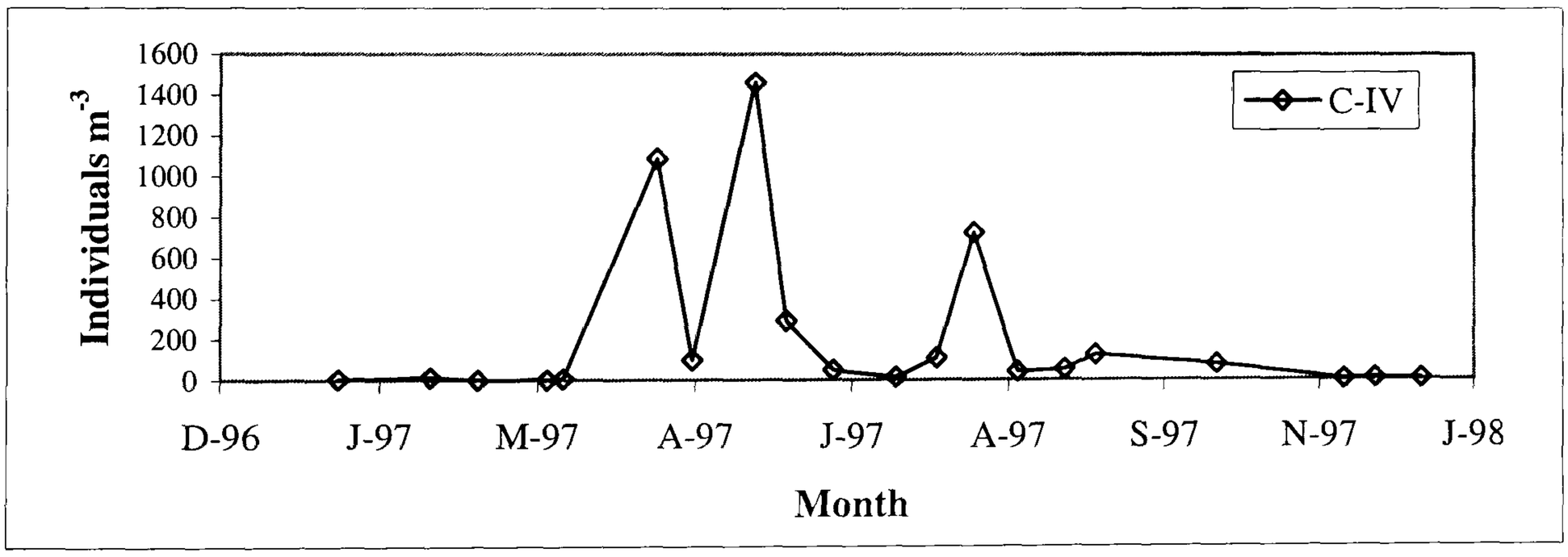
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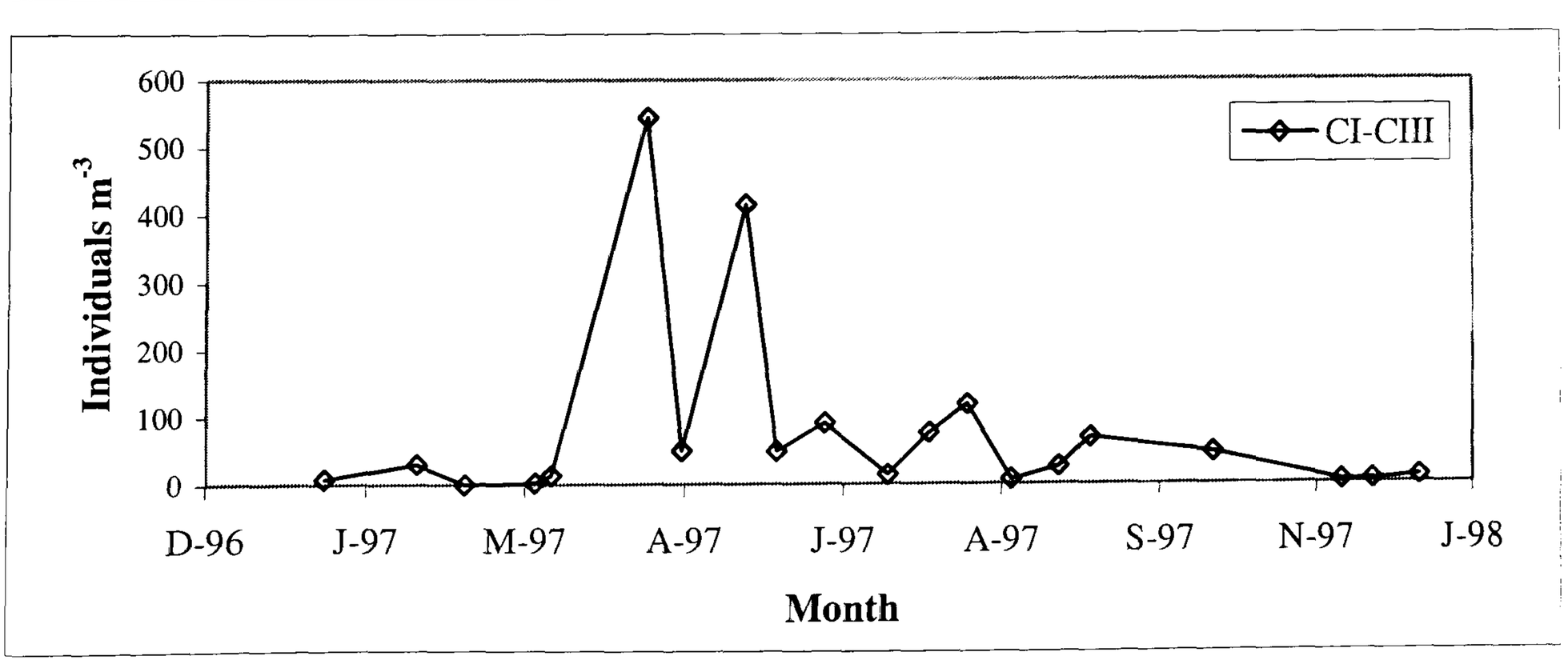
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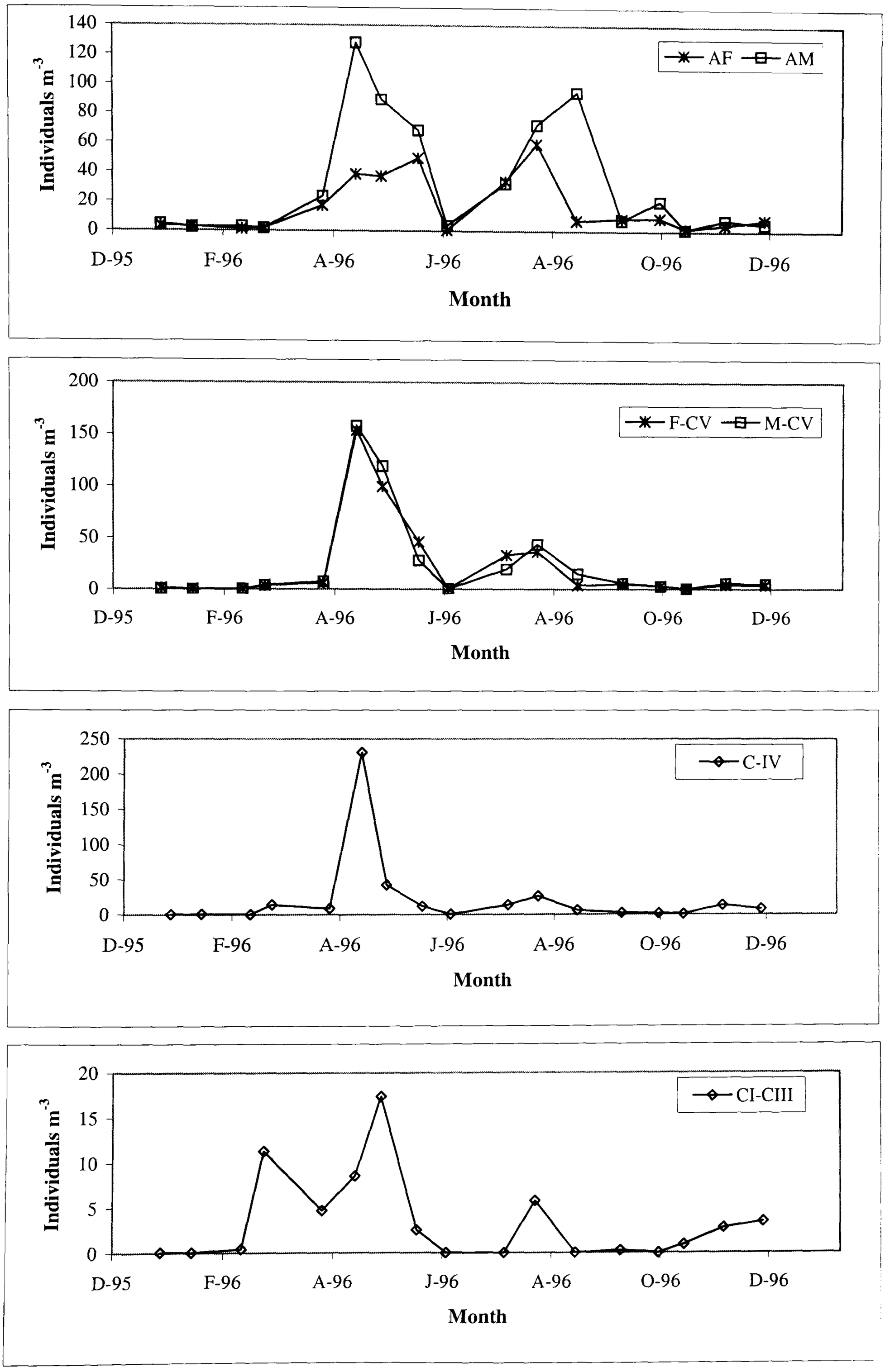
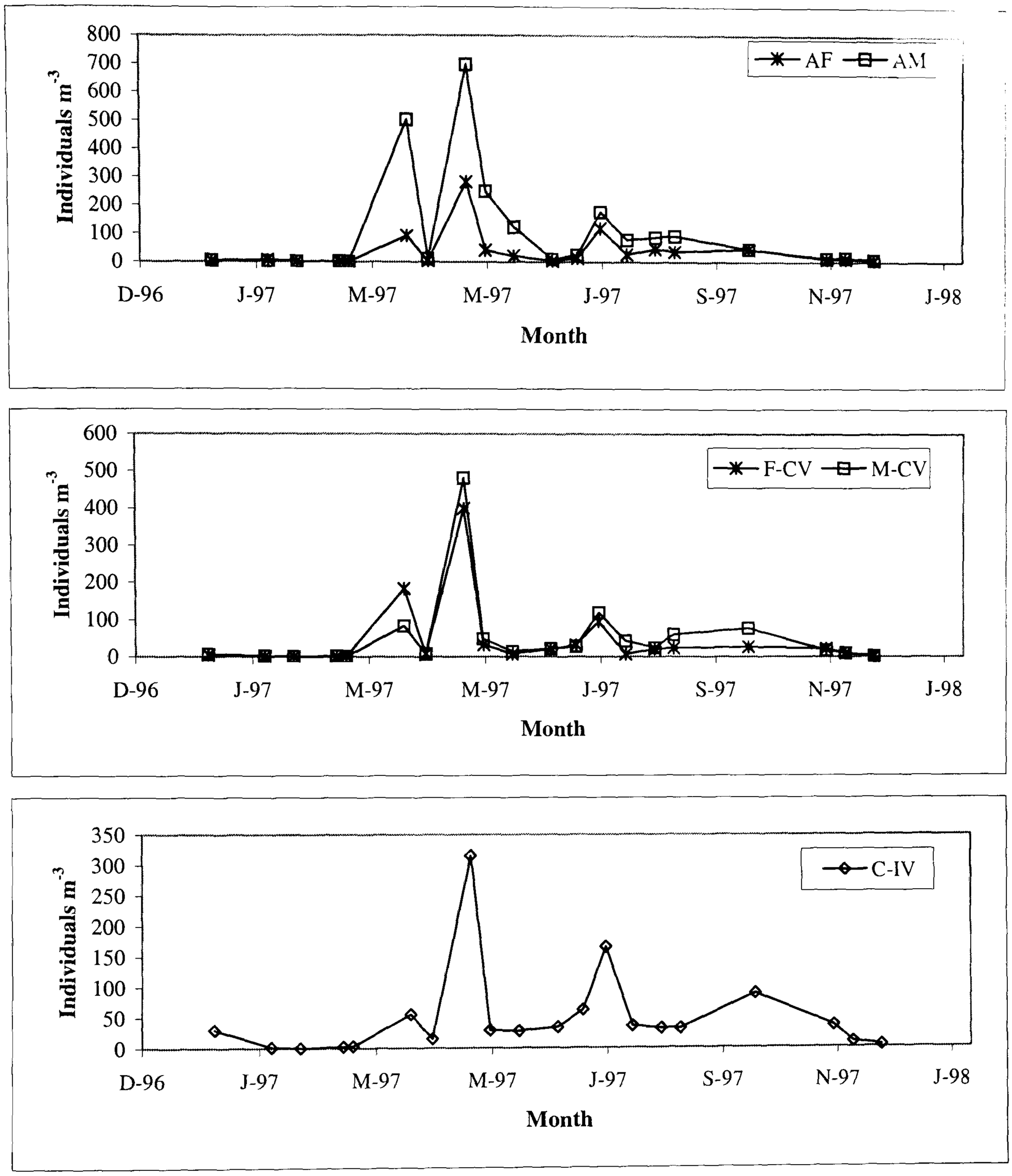
Month

Figure 8.5: Seasonal changes in stages abundance of *C. hamatus* in the Menai Strait during a) 1996 and b) 1997.

a)



b)


Individuals m-3
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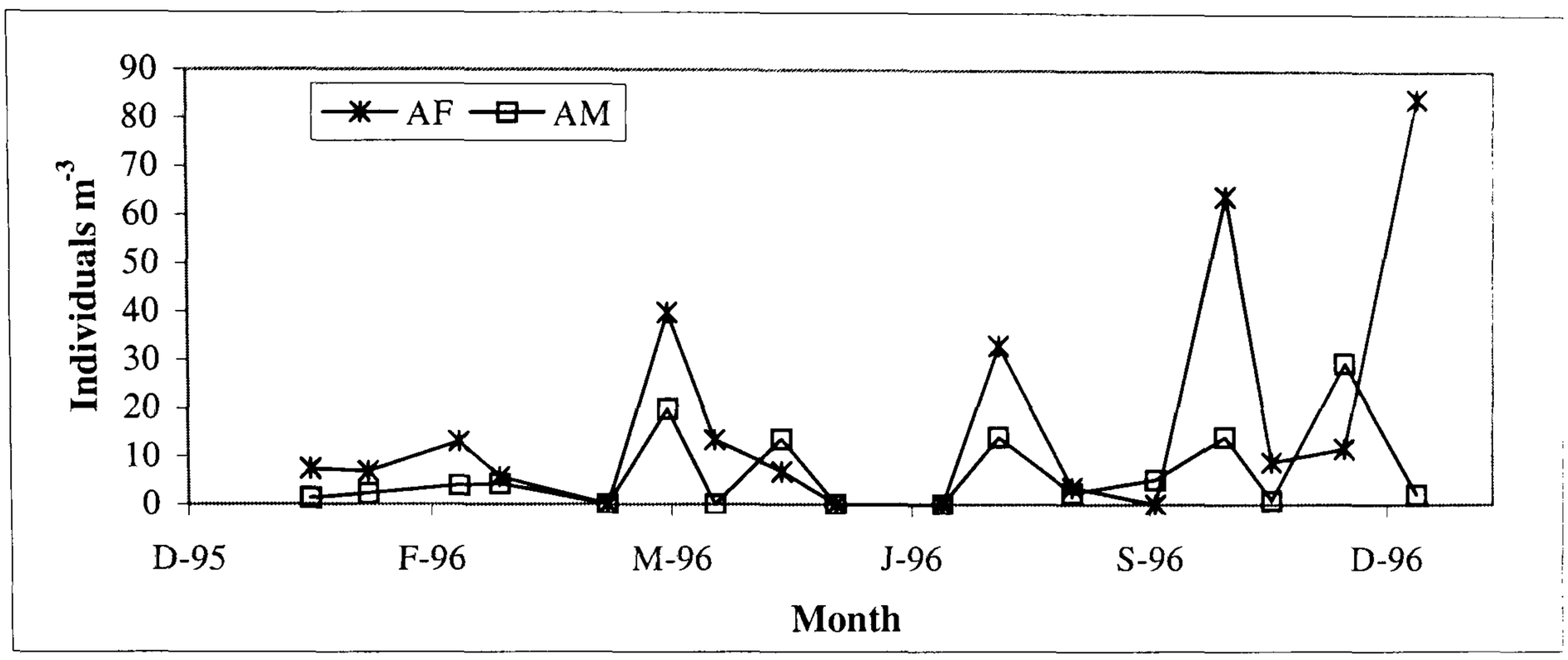
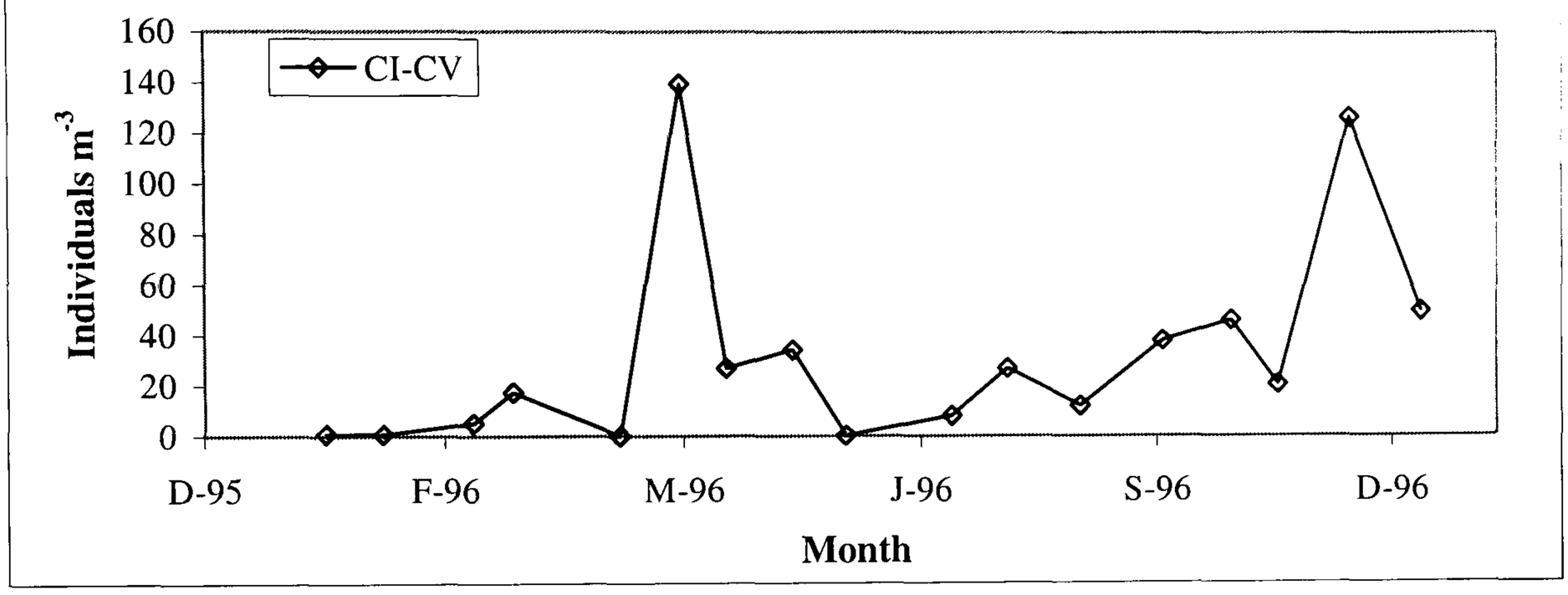
J-97
S-97
N-97
J-98
Month
Individuals m-3
600
500
400
300
200
100
0
F-CV
M-CV
D-96
J-97
M-97
M-97
J-97
S-97
N-97
J-98
Month
Individuals m-3
350
300
250
200
150
100
50
0
C-IV
D-96
J-97
M-97
M-97
J-97
S-97
N-97
J-98
Month
Individuals m-3
120
100
80
60
40
20
0
CI-CIII
D-96
J-97
M-97
M-97
J-97
S-97
N-97
J-98
Month

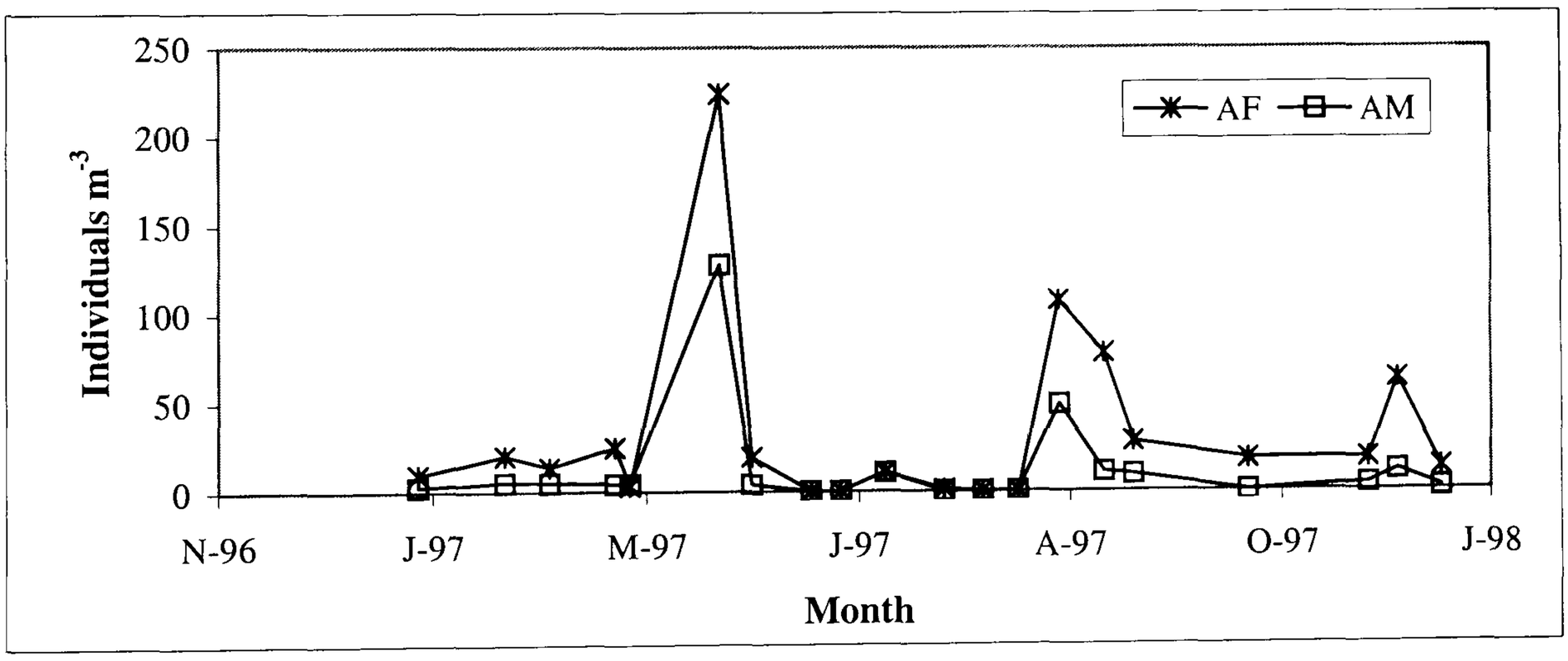
Figure 8.6: Seasonal change in stages abundance of *Pseudocalanus sp.* in the Menai Strait during a) 1996 and b) 1997

a)





b)



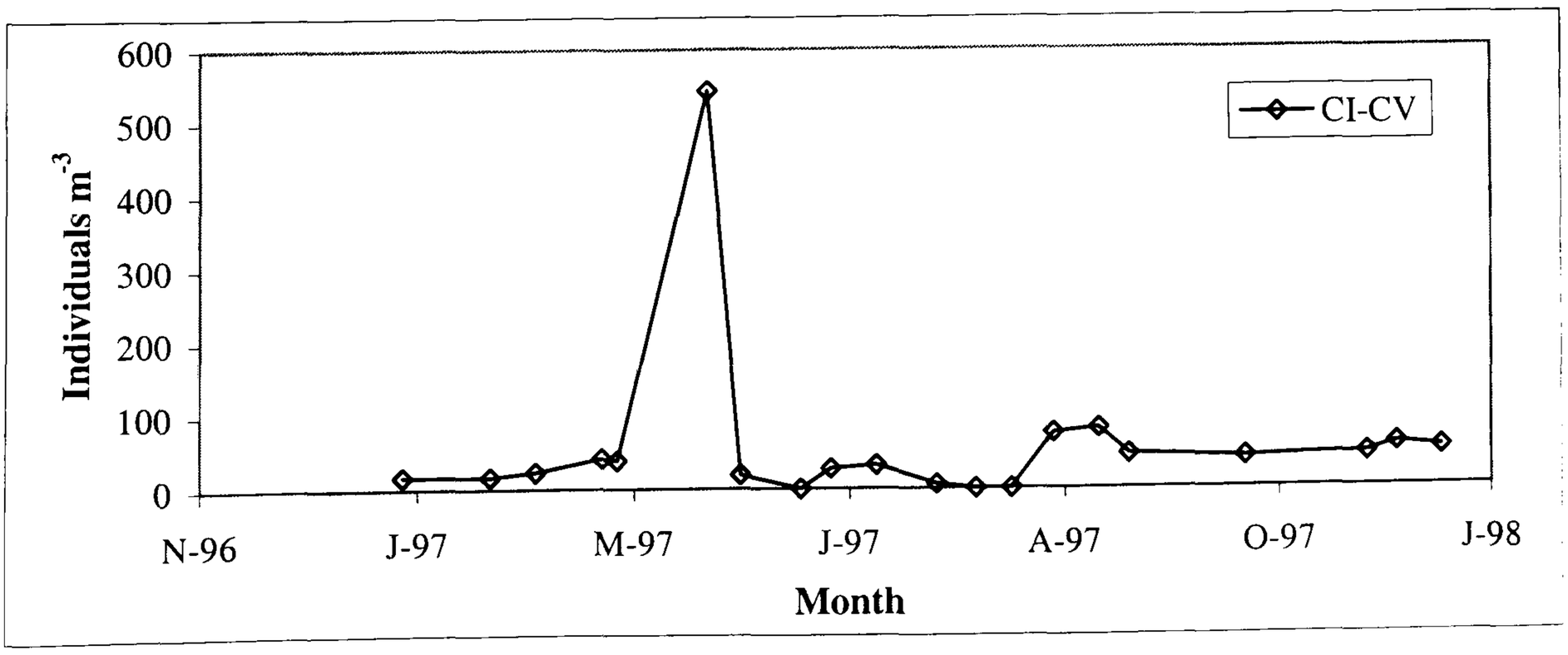
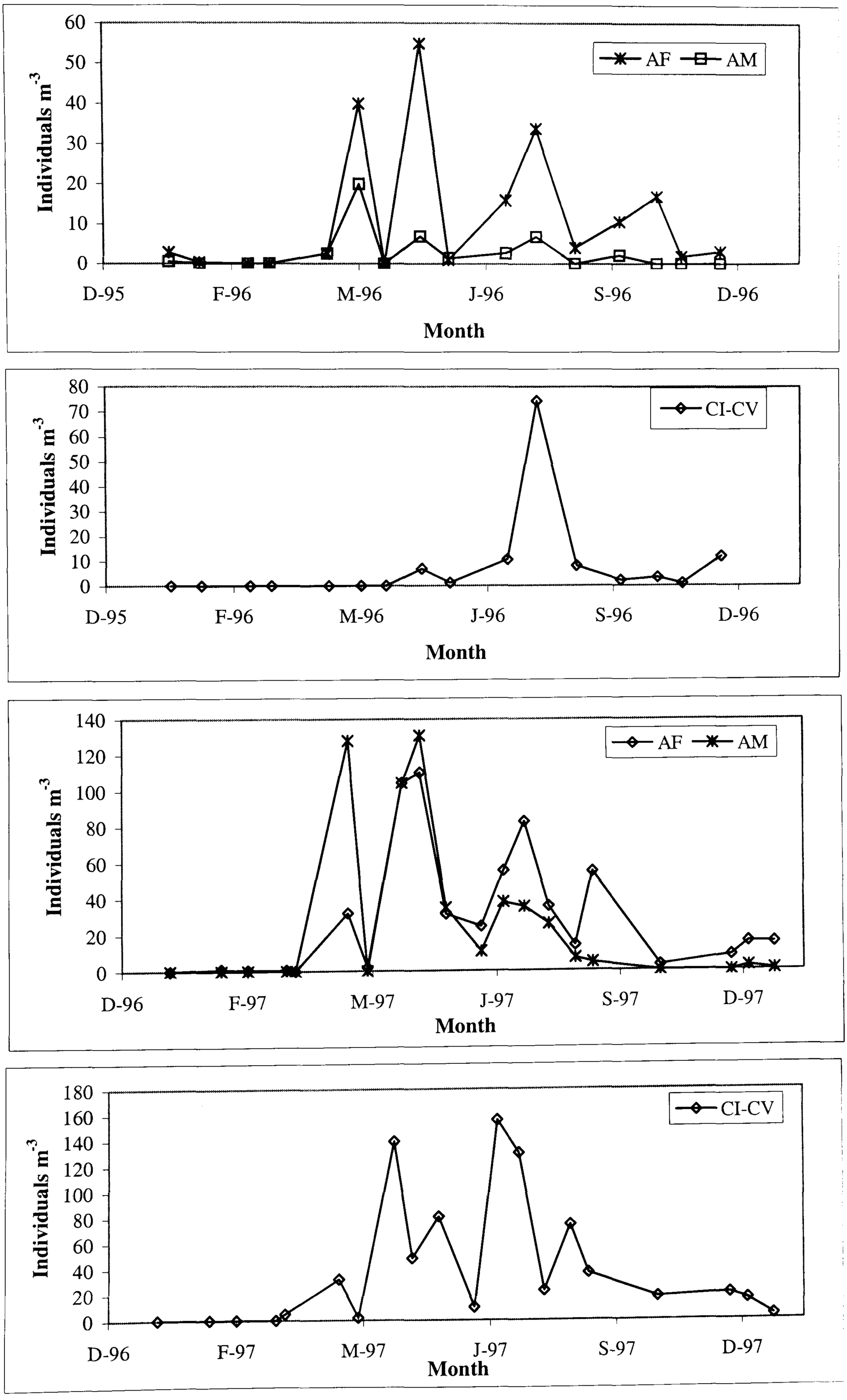


Figure 8.7: Seasonal change in stages abundance of *A. clausi clausi* in the Menai Strait during a) 1996 and b) 1997

a)



8.3.4 Sex ratio

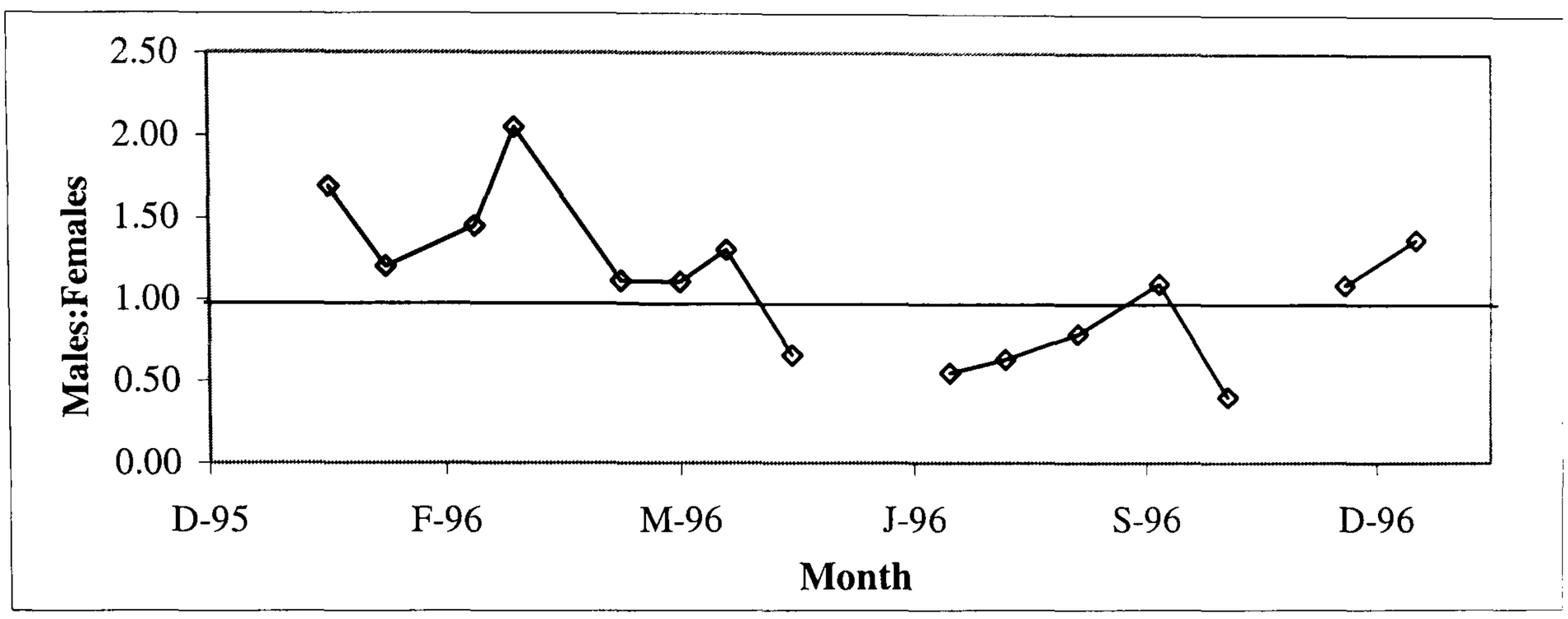
The copepod sex ratio, defined as the abundance of males to that of females, changed seasonally (Figure 8.8).

In *T. longicornis* the sex ratio oscillated around 1 (Mean ± SD; 1.1 ± 0.45 in 1996 and 1.2 ± 0.12 in 1997) through most of 1996 and 1997. Higher proportions of *T. longicornis* adult males (2-3 males: 1 female) were usually recorded in early spring and autumn-winter for both years (Figure 8.5, a-b). The changes in the sex ratio for adult *C. hamatus* were larger in amplitude than in *T. longicornis*, males being generally more abundant (2.6 ± 0.79 in 1996 and 2.5 ± 1.7 in 1997) than females for most of the year (Figure 8.5,c-d). The highest proportions of adult males were recorded in late spring (6 males:1 female) to end of summer (13 males:1 female) in both years (Figure 8.5, c-d). Since these extreme ratios were obtained from large samples (i.e.> 100 adults), these figures must be considered representative. The sex ratios measured for *T. longicornis* ($r = 0.55$; $p = 0.033$; d.f. =16) and *C. hamatus* ($r = 0.71$; $p = 0.001$; d.f. = 16) in 1996 were positively correlated with the relative abundance of these two species suggesting a higher number of males during population increase of either species. However, the concomitance in population and males increase observed in 1996 for *T. longicornis* and *C. hamatus* could not be confirmed for 1997. By contrast, *Pseudocalanus sp.* (0.36 ± 0.28 in 1996 and 0.38 ± 0.36 in 1997) and *A. clausi* (0.48 ± 0.51 in 1996 and 0.86 ± 1.06 in 1997) females were almost always more numerous than males. Only once in 28 samples were *Pseudocalanus sp.* males more numerous than females (spring 1996) and 3 times in 20 samples were *A. clausi* males more numerous than females (late spring and early summer 1996 and 1997).

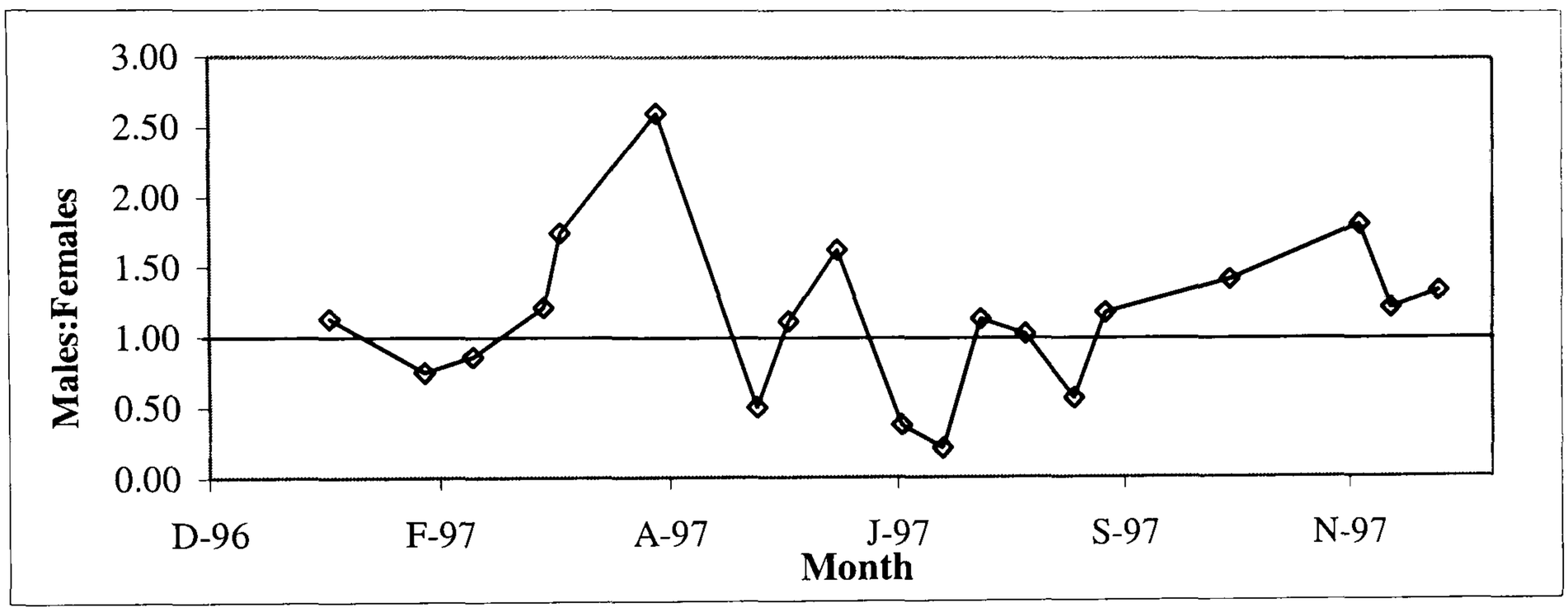
The calculated ratios for *T. longicornis* and *C. hamatus* were obtained from samples of between 20 and 200 adults. Those for *A. clausi* and *Pseudocalanus sp.* were calculated from between 10 and 30 copepods (i.e. excluding samples containing less than 10 adults).

Figure 8.8: Seasonal variation in the sex ratio of a-b) *T. longicornis*, c-d) *C. hamatus*, e-f) *Pseudocalanus sp.* and g-h) *A. clausi* in the Menai Strait during 1996 and 1997.

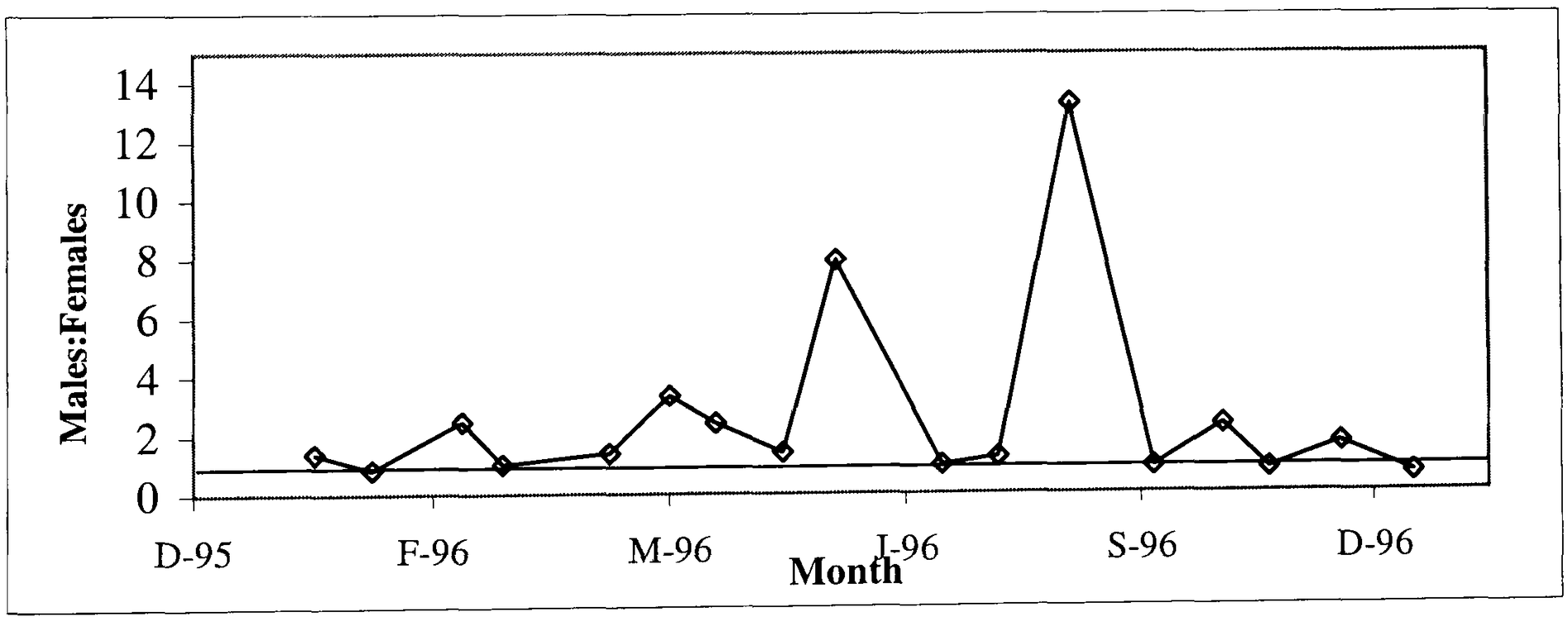
a)



b)



c)



d)

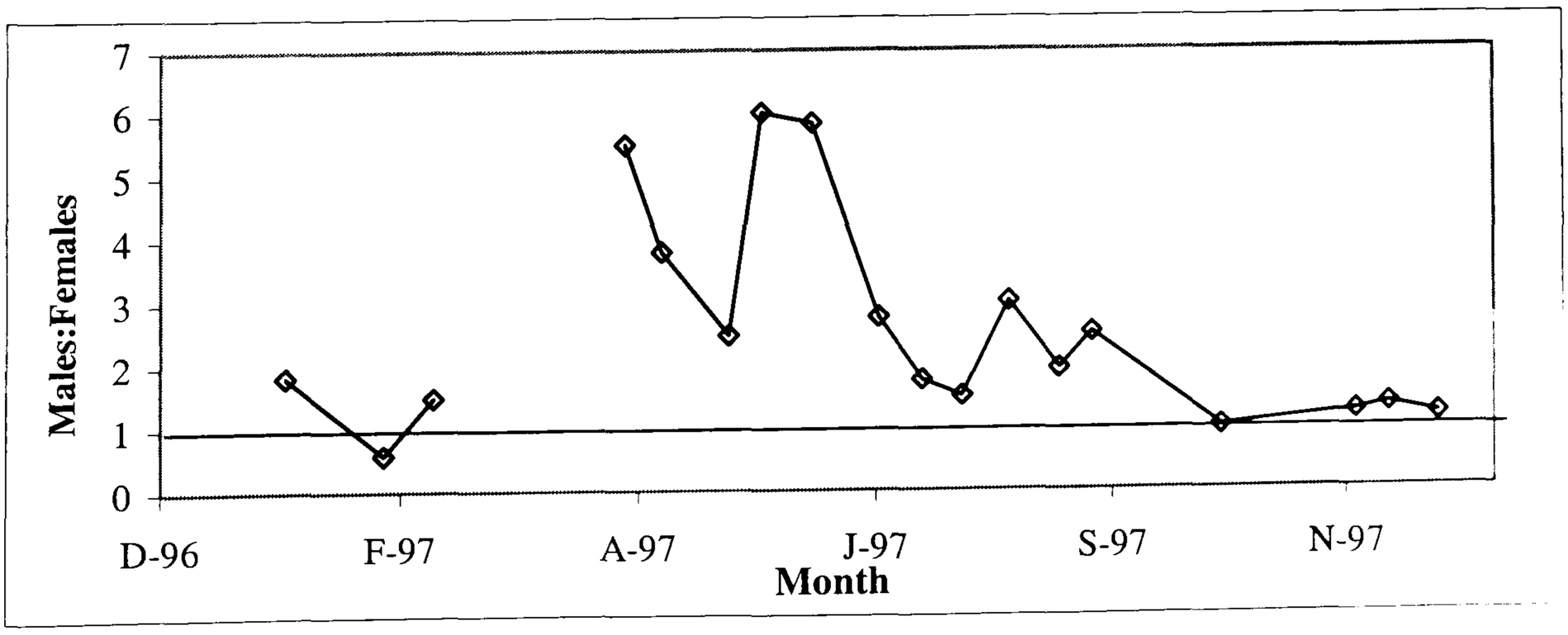
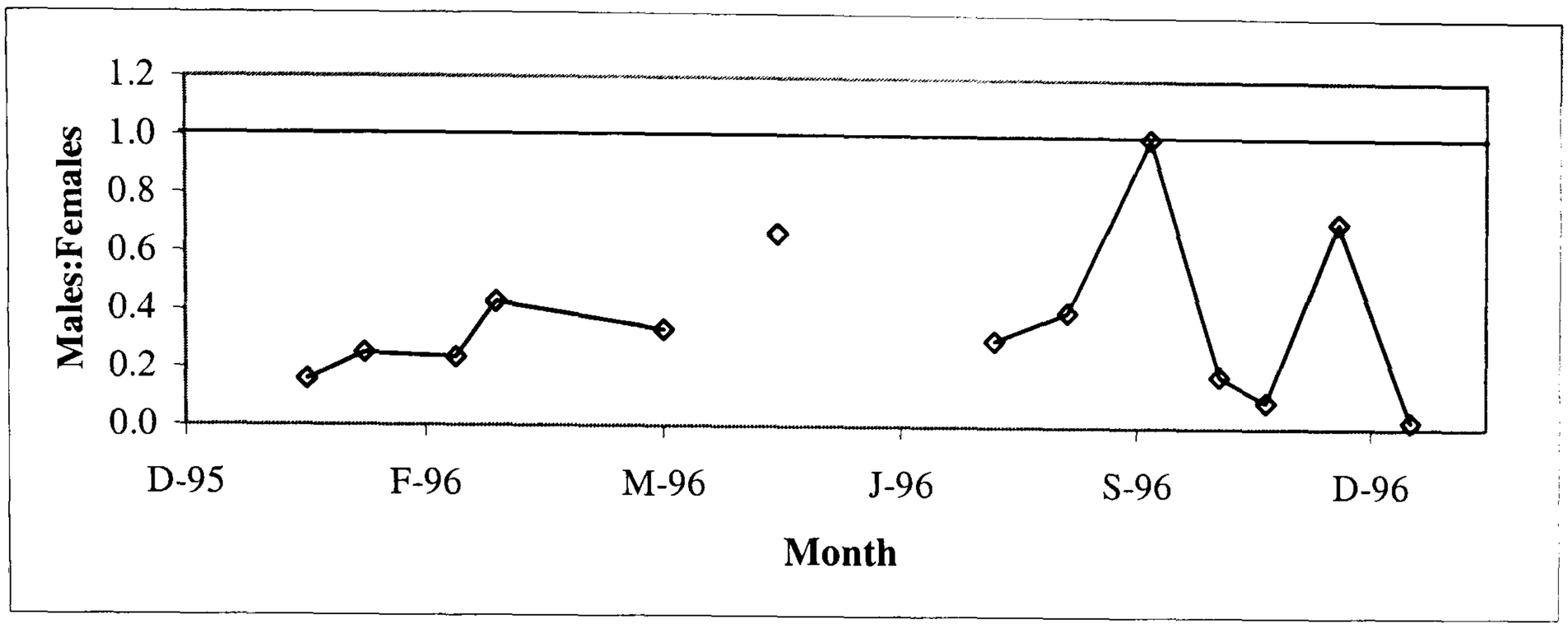
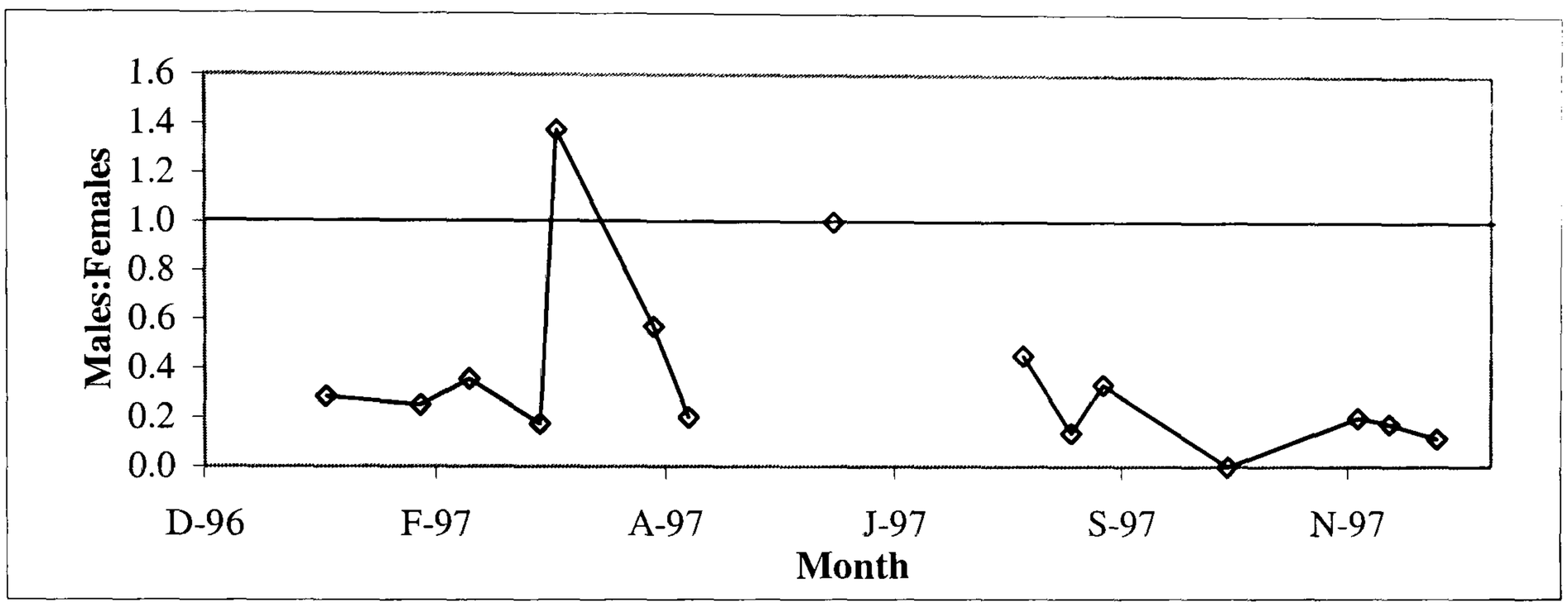


Figure 8.8: Continued

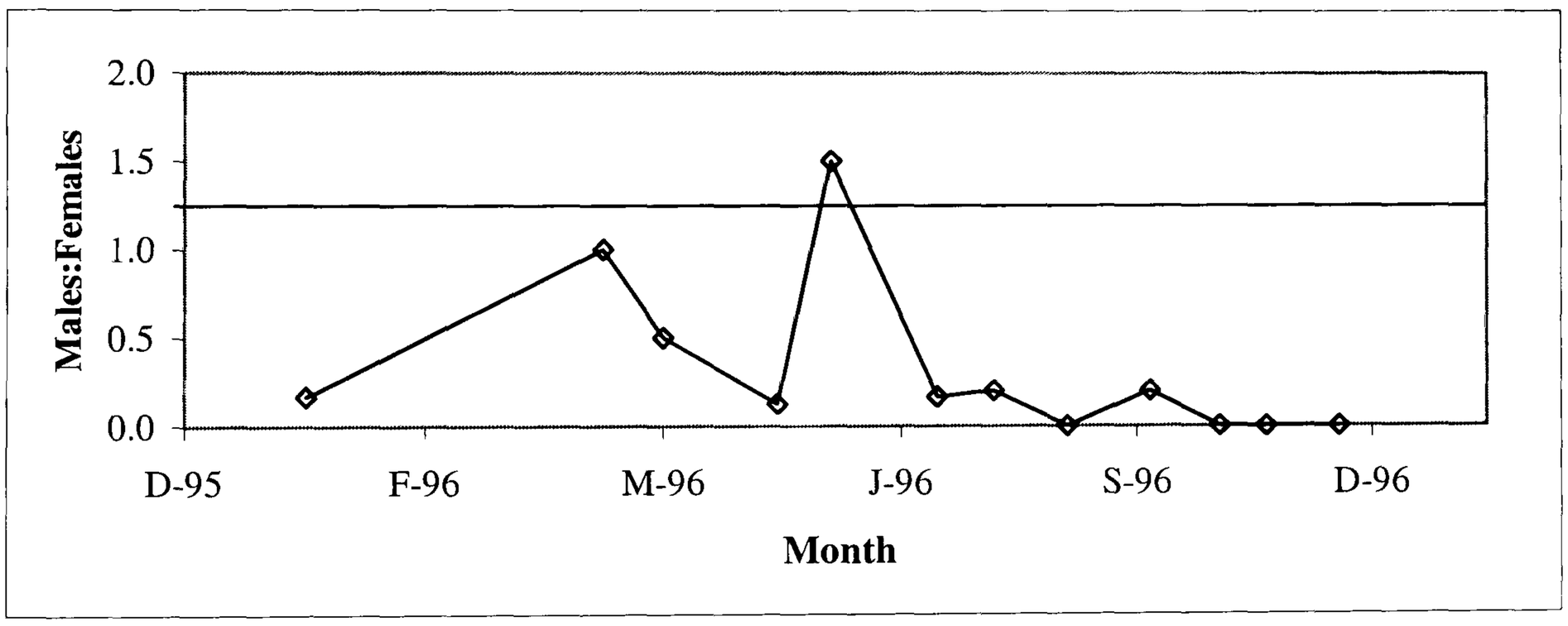
e)



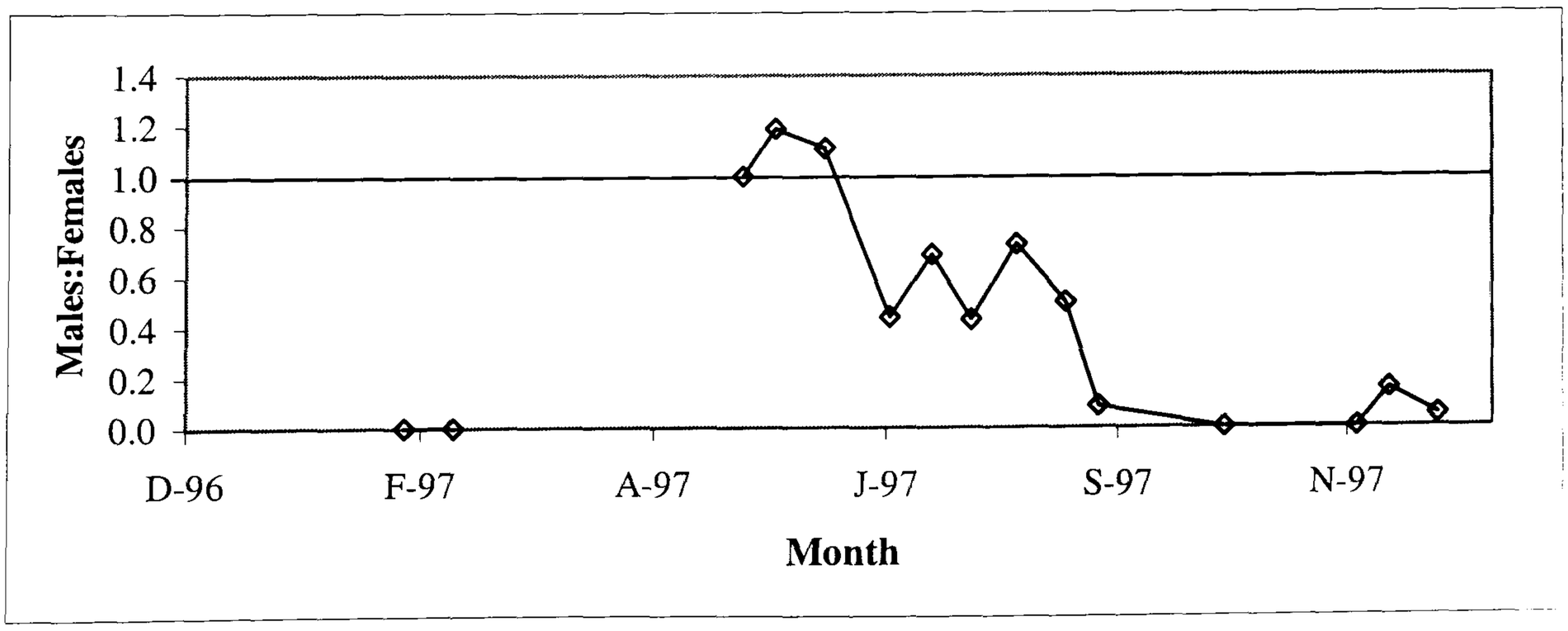
f)



g)



h)



8.3.5 Seasonal and interannual variation in copepod length

Figure 8.6 shows the seasonal changes in the cephalothorax length of the different stages (i.e. CI-CIV) of *T. longicornis*, *C. hamatus*, *Pseudocalanus sp.* and *A. clausi* present in the Menai Strait between 1996 and 1997. Copepod length varied over the year with the larger individual being measured in winter-spring and the smaller in summer autumn for all the copepod species investigated. Figure 8.6 shows that, in general, the adult and the older stages of all the species had greater seasonal length variability than the younger stages probably as a result of a cumulative effect throughout the copepod's life cycle (Figure 8.6). As already mentioned for the stage analysis, copepodite stages younger than CIV were poorly represented throughout the samples.

The seasonal changes in mean cephalothorax length for copepodite stages (CI-CV) and adults (AF & AM) of *T. longicornis* were similar between years (Figure 8.6, a-I & a-II). In *T. longicornis* cephalothorax length was maximal from January to April decreasing thereafter to reach an annual minimum between July and August. After that the length of the copepods started to increase again towards maximum levels (Figure 8.6, a). During the winter-spring 1996 *T. longicornis* adults mean (± Standard Deviation, SD) cephalothorax length varied between 945 ± 73 μm and 983 ± 90 μm and for males and between 1017 ± 87 μm and 1112 ± 94 μm for females. After this the cephalothorax length decreased to a summer-autumn minimum of 653 ± 58 μm and 703 ± 73 μm in males and females respectively at the end of July 1996. During 1997 a maximum of 1033 ± 81 μm 1135 ± 83 μm was measured in March and minimum of 700 ± 51 μm and 781 ± 79 μm in July for males and females respectively.

In *C. hamatus* adult cephalothorax lengths increased throughout the winter reaching an annual maximum of 1040 ± 68 μm and 1184 ± 112 μm in males and females respectively in spring 1996 (Figure 8.6, b). After this the cephalothorax length decreased to a summer-autumn minimum of 726 ± 43 μm and 808 ± 86 μm in males and females respectively. The 1997 trend in mean cephalothorax length measured in *C. hamatus* was similar to that measured in 1996 (Figure 8.6, b).

The seasonal pattern of changes in mean cephalothorax length recorded for *Pseudocalanus sp.* and *A. clausi* were similar to that of *C. hamatus* with maximum mean cephalothorax values only recorded in spring and minimum in summer (Figure 8.6, c & d). In 1997, when more data are available *Pseudocalanus sp.* reached the maximum annual cephalothorax length at the end of February with 833 ± 40 μm and

920 ± 122 μm for males and females respectively (Figure 8.6, c). After that, *Pseudocalanus sp* cephalothorax length decreased to reach a annual minimum in summer of 658 ± 21 μm and 644 ± 30 μm for males and females respectively (Figure 8.6, c).

The seasonal changes in *A. clausi* cephalothorax length are also described for 1997 when more data were available. *A. clausi* reached the annual mean cephalothorax length maximum in spring with 883 ± 25 μm and 945 ± 78 μm in males and females respectively (Figure 8.6, d). Annual minima of 762 ± 23 μm and 696 ± 75 μm were measured in summer for males and females respectively (Figure 8.6, d).

Figure 8.9: Seasonal changes in mean (± SE) cephalothorax length (µm) of *T. longicornis longicornis* during 1996 and 1997. Lines joining symbols are only given when individuals were found in consecutive samples.

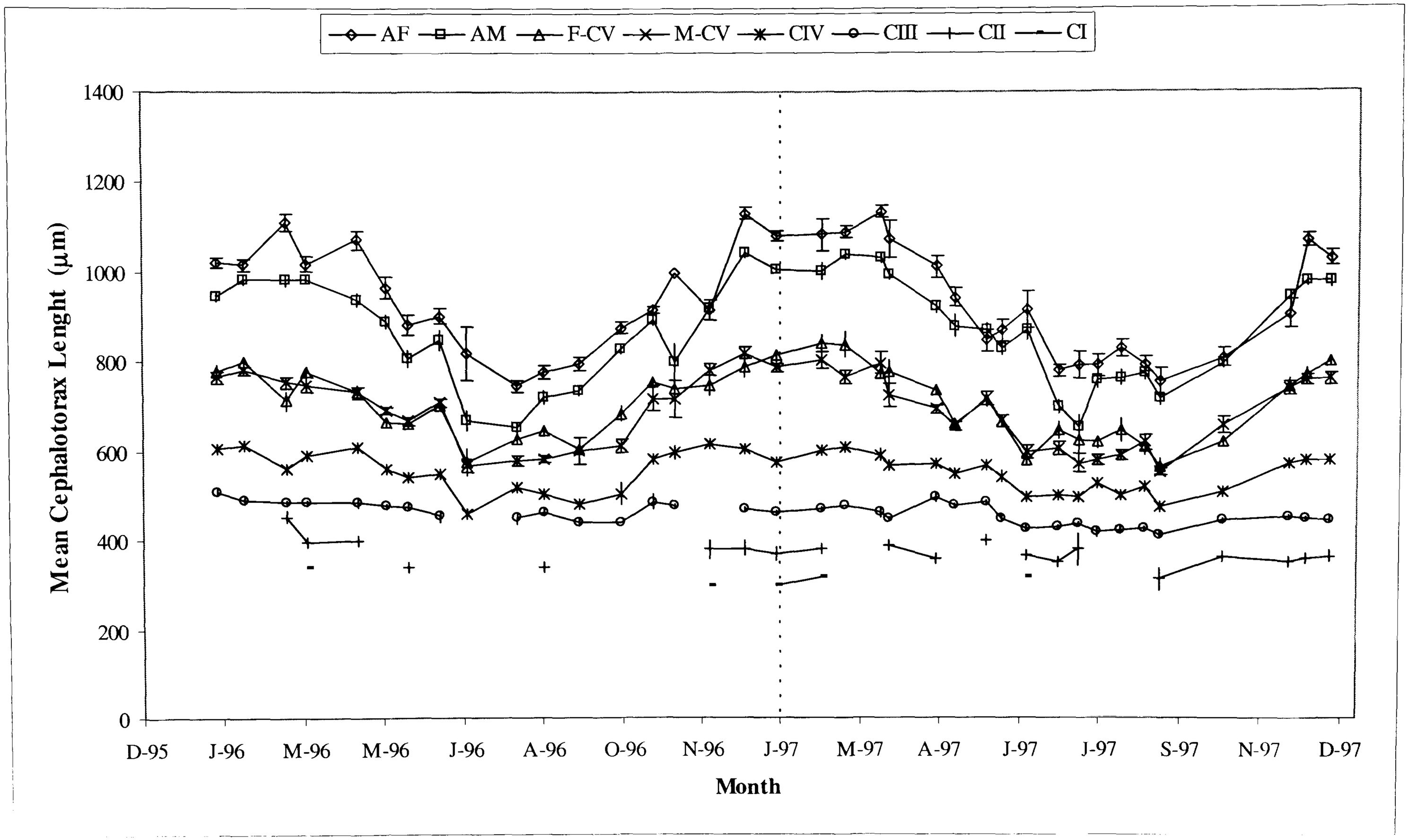


Figure 8.10: Seasonal changes in mean (± SE) cephalothorax length (µm) of *C. hamatus hamatus* during 1996 and 1997. Lines joining symbols are only given when individuals were found in consecutive samples.

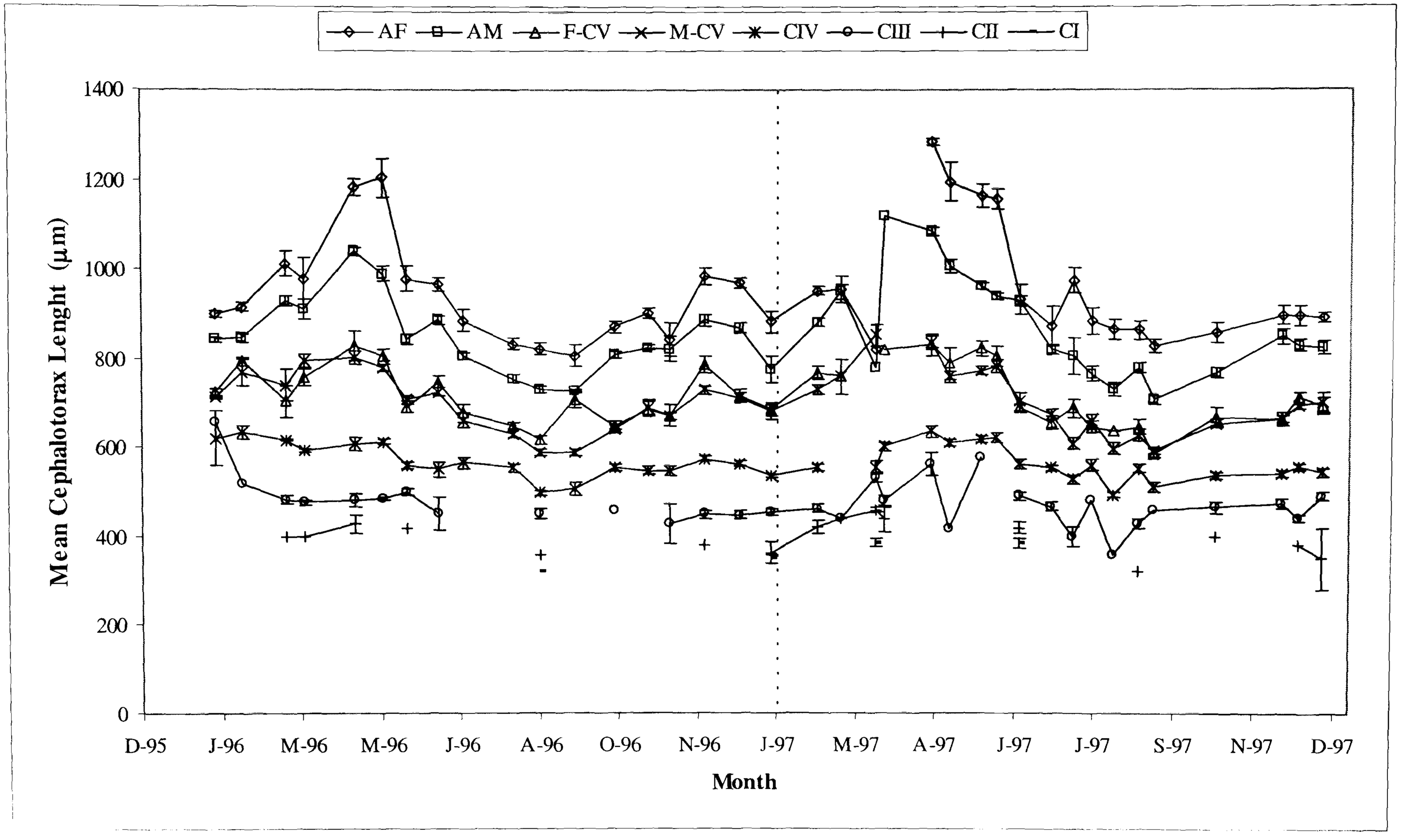


Figure 8.11: Seasonal changes in mean (± SE) cephalothorax length (µm) of *Pseudocalanus sp.* during 1996 and 1997. Lines joining symbols are only given when individuals were found in consecutive samples.

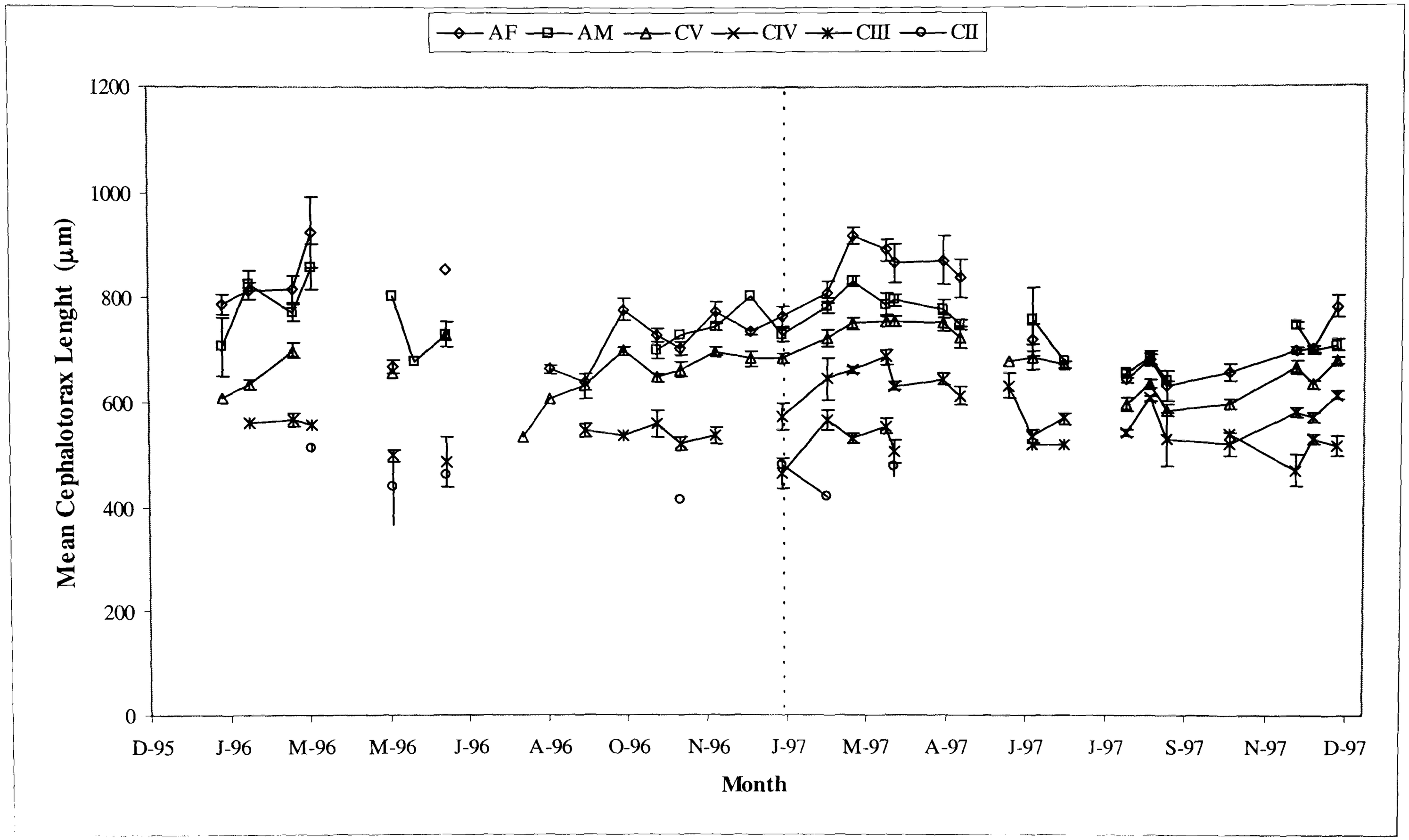
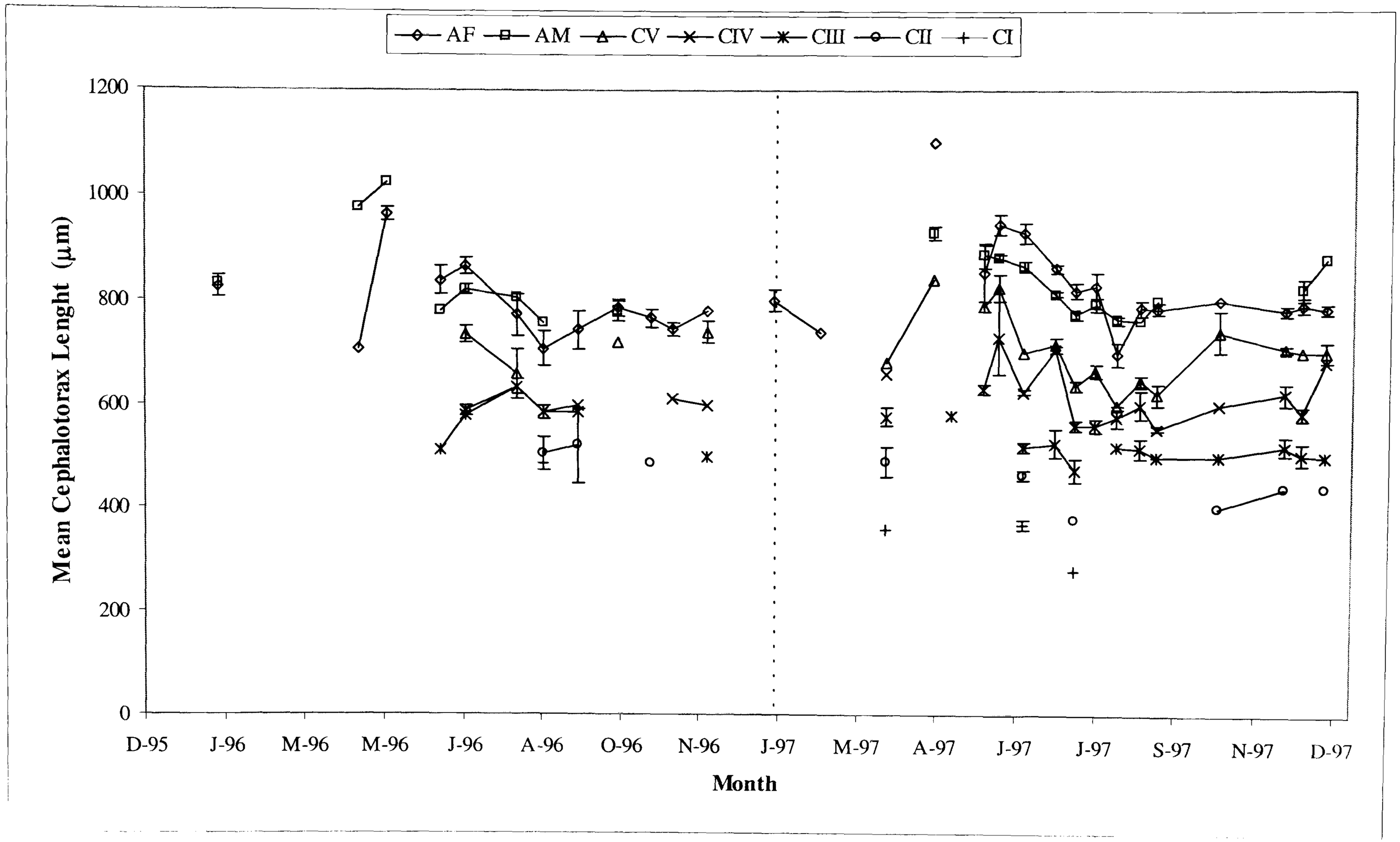


Figure 8.12: Seasonal changes in mean (± SE) cephalothorax length (µm) of *A. clausi clausi* during 1996 and 1997. Lines joining symbols are only given when individuals were found in consecutive samples.



8.3.6 Copepod length variation with Temperature and Chlorophyll-a

The results of the relationship between copepod length (CIII-adults) with the temperature and chlorophyll-a (used as a proxy for available food source) at the time of sampling and that for the previous month (i.e. data lagging) in both 1996 and 1997 are summarised in Table 8.2. Data for stages younger than CIII were very sparse so it was not possible to use them in the analysis.

Comparisons between 1996 and 1997 showed that there were no differences in changes in the cephalothorax length (C.L.) with temperature for the different copepod stages. Thus, the 1996 and 1997 data were merged together. For most stages the copepod C.L. were significantly negatively correlated with in situ temperature contemporaneously and for the previous month (Table 8.2). *T. longicornis* C.L. was more strongly correlated with the in situ temperature at the time of sampling than with those of the previous month (Figure 8.7 & Table 8.2). Conversely, in *C. hamatus, Pseudocalanus* and *A. clausi* the largest animals were measured at around the time of the phytoplankton bloom when temperature reached the annual average of 9-10 °C (See Figure 8.6 and Chapter 3). As a result the relationship of body size of these three copepod species and temperature was not linear. The mean body lengths of each stage were therefore plotted against the temperature measured during the previous sampling date (i.e. 15 to 30 days lag time).

In the case of *C. hamatus* the fit of relationships found between body size and temperature were better with the previous month temperature. Stage CIII *C. hamatus*, however, was only significantly correlated with the temperature at the time of sampling. Better fits of the regression between C.L. and temperature were also obtained for the stages of *Pseudocalanus sp.* and *A. clausi*, with the exception of the adult female of *Pseudocalanus sp.* and for the CIII stages of *Pseudocalanus sp.* and *A. clausi*, by using the previous month temperatures (Table 8.2). The lower correlation found for the *Pseudocalanus sp.* and *A. clausi* data is possibly due to the fact that the body length means used in the analysis were based on a lower number (therefore less representative of the population mean) of observations.

Table 8.2: Regression analysis between mean cephalothorax length (μm) for different copepod species and stages and temperature (T in °C) and Chlorophyll-a (Chl-a in μg L^{-1}) and for the combined 1996 and 1997 data set. Equations are presented only if the regression is significant i.e. p< 0.05. N is the number of sampling occasions, r is the Pearson correlation coefficient and p is the probability.

Concurrent Temperature and Chlorophyll-a								Previous Temperature and Chlorophyll-a						
T. longicornis longicornis			Temperature (°C)		Chl-a (μg L^{-1})			Temperature (°C)				Chl-a (μg L^{-1})		
Stage	**N**	**R**	**P**	**Equation**	**r**	**p**	**Equation**	**N**	**r**	**p**	**Equation**	**r**	**p**	**Equation**
CIII	35	- 0.66	< 0.001	C.L.= 502 - 3.63 T	0.03	0.844	-	35	- 0.68	< 0.001	C.L.= 504 – 3.81 T	- 0.14	0.437	-
CIV	37	- 0.87	< 0.001	C.L.= 642 - 7.87 T	- 0.15	0.389	-	37	- 0.73	< 0.001	C.L.= 633 – 7.08 T	- 0.36	0.027	C.L.= 568 – 4.34 Chla
CV-F	37	- 0.84	< 0.001	C.L.= 866 - 14.3 T	- 0.28	0.089	-	37	- 0.73	< 0.001	C.L.= 847 – 12.6 T	- 0.40	0.014	C.L.= 734 – 8.34 Chla
CV-M	37	- 0.89	< 0.001	C.L.= 865 - 15.6 T	- 0.22	0.198	-	37	- 0.77	< 0.001	C.L.= 842 – 13.5 T	- 0.32	0.055	-
AF	37	- 0.88	< 0.001	C.L.= 1193 - 22.9 T	- 0.22	0.178	-	37	- 0.86	< 0.001	C.L.= 1191 – 22.7 T	- 0.37	0.026	C.L.= 976 – 11.9 Chla
AM	37	- 0.88	< 0.001	C.L.= 1122 - 22.4 T	- 0.19	0.239	-	37	- 0.78	< 0.001	C.L.= 1094 – 19.9 T	- 0.35	0.036	C.L.= 907 – 10.9 Chla
C. hamatus hamatus														
Stage	**N**	**R**	**P**		**r**	**p**		**N**	**r**	**p**		**r**	**p**	
CIII	31	- 0.42	0.017	C.L.= 527 – 4.99 T	0.04	0.812	-	31	- 0.34	0.058	-	-0.033	0.857	-
CIV	36	- 0.56	< 0.001	C.L.= 620 – 4.62 T	0.25	0.136	-	36	- 0.62	< 0.001	C.L.= 626 –5.18 T	0.037	0.829	-
CV-F	36	- 0.57	< 0.001	C.L.= 809 – 8.09 T	0.29	0.087	-	36	- 0.68	< 0.001	C.L.= 828 – 9.76 T	0.146	0.396	-
CV-M	36	- 0.69	< 0.001	C.L.= 821 – 10.4 T	0.24	0.155	-	36	- 0.78	< 0.001	C.L.= 839 – 11.9 T	0.023	0.893	-
AF	36	- 0.28	0.095	-	0.55	< 0.001	C.L = 889 + 18.0 Chl	36	- 0.46	< 0.005	C.L.= 1093 – 12.4 T	0.322	0.056	-
AM	37	- 0.47	0.003	C.L.= 976 – 10.2 T	0.32	0.051	-	37	- 0.61	< 0.001	C.L.= 1012 – 13.4 T	0.140	0.408	-
Pseudocalanus sp														
Stage	**N**	**R**	**P**		**r**	**p**		**N**	**r**	**p**		**r**	**p**	
CIII	21	- 0.12	0.599	-	- 0.34	0.13	-	21	- 0.14	0.548	-	-0.382	0.087	-
CIV*	17	- 0.54	0.024	C.L.= 664 – 6.0 T	0.003	0.99	-	17*	- 0.74	0.001	C.L.= 800 – 10.6 T	-0.225	0.384	-
CV	30	- 0.51	0.004	C.L.=736 – 5.94 T	0.202	0.283	-	30	- 0.57	0.001	C.L.= 750 – 6.98 T	0.155	0.413	-
AF	28	- 0.66	< 0.001	C.L.= 891 – 12.2 T	0.05	0.788	-	28	- 0.75	< 0.001	C.L.= 910 – 13.4 T	-0.049	0.806	-
AM	26	- 0.66	< 0.001	C.L.= 830 – 8.56 T	- 0.20	0.317	-	26	- 0.78	< 0.001	C.L.= 849 – 10.3 T	-0.216	0.290	-
A. clausi clausi														
Stage	**N**	**R**	**P**		**r**	**p**		**N**	**r**	**p**		**r**	**p**	
CIII	18	- 0.32	0.191	-	0.03	0.902	-	18	0.087	0.733	-	-0.131	0.604	-
CIV	20	- 0.40	0.079	-	0.43	0.058	-	20	0.49	0.029	C.L.= 719 – 7.34 T	0.077	0.747	-
CV	19	- 0.51	0.025	C.L.= 821 – 8.66 T	0.38	0.107	-	19	0.47	0.04	C.L.= 825 – 8.60 T	0.236	0.330	-
AF	28	- 0.17	0.374	-	0.41	0.030	C.L.= 775 + 12.2 Chl	28	0.34	0.075	-	0.342	0.075	-
AM	20	- 0.66	0.002	C.L.= 996 – 11.9 T	0.45	0.049	C.L.= 795 + 10.6 Chl	20	0.78	< 0.001	C.L.= 1021 – 14.3 T	0.033	0.890	-

*** 1997 data only**

Investigation of the relationship between body length and chlorophyll-a showed no or low correlation for most of the species (Table 8.2). C.L. was significantly positively correlated with chlorophyll-a only for adult *C. hamatus* females and for adults *A. clausi* with the temperature at the time of sampling. The C.L. of for *T. longicornis* was negatively correlated to field chlorophyll-a, only for the adults, females CV and CIV when with the previous month temperature suggesting an indirect correlation (Table 8.2).

The observed differences in the length of different copepod species between winter and spring suggest that the over-wintering *C. hamatus* and *Pseudocalanus sp.* may derive from copepods born at the end of the previous year when *in situ* temperatures were higher, whereas the over-wintering for *T. longicornis* copepods developed at colder temperatures.

8.3.7 Number of copepod cohorts

Measurement of the number of cohorts during the year was attempted for *T. longicornis* and *C. hamatus* since *Pseudocalanus sp.* and *A. clausi* were only found occasionally in small number. The analysis of copepod stages and female modal C.L. changes showed that *T. longicornis* and *C. hamatus*, each had ~5 generations a year. The estimates of copepod generation times of 40-100 days were, however, much longer than those predicted on the basis of temperature alone using the Belehradek's equation (McLaren, 1978). The discrepancy measured between predicted and observed generation length was larger at higher temperatures when predicted generation times were as long as or shorter than sampling frequencies. Thus, given the sampling frequency of every two weeks to 1 month, interpretation of female length and good approximation of the timing of CIV pulses was possibly unreliable.

8.3.8 Copepod standing stock and production

The seasonal variation in biomass and production estimated for dominant copepod species in the Menai Strait is shown in Figure 8.13 a and b.

Figure 8.13, a): Seasonal variation in total calanoid copepod biomass (mg-C m^{-3}) for the Menai Strait during 1996 and 1997.

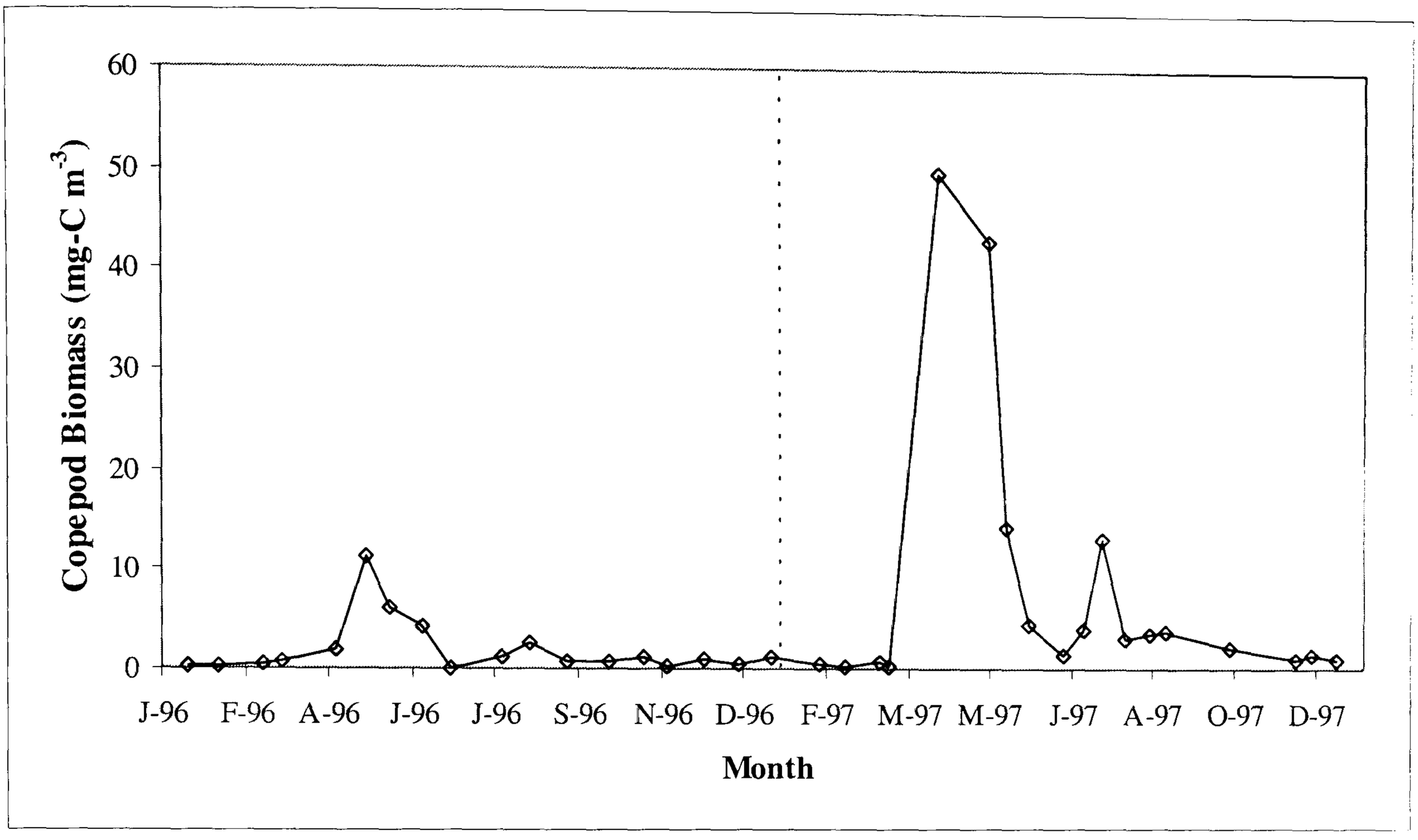
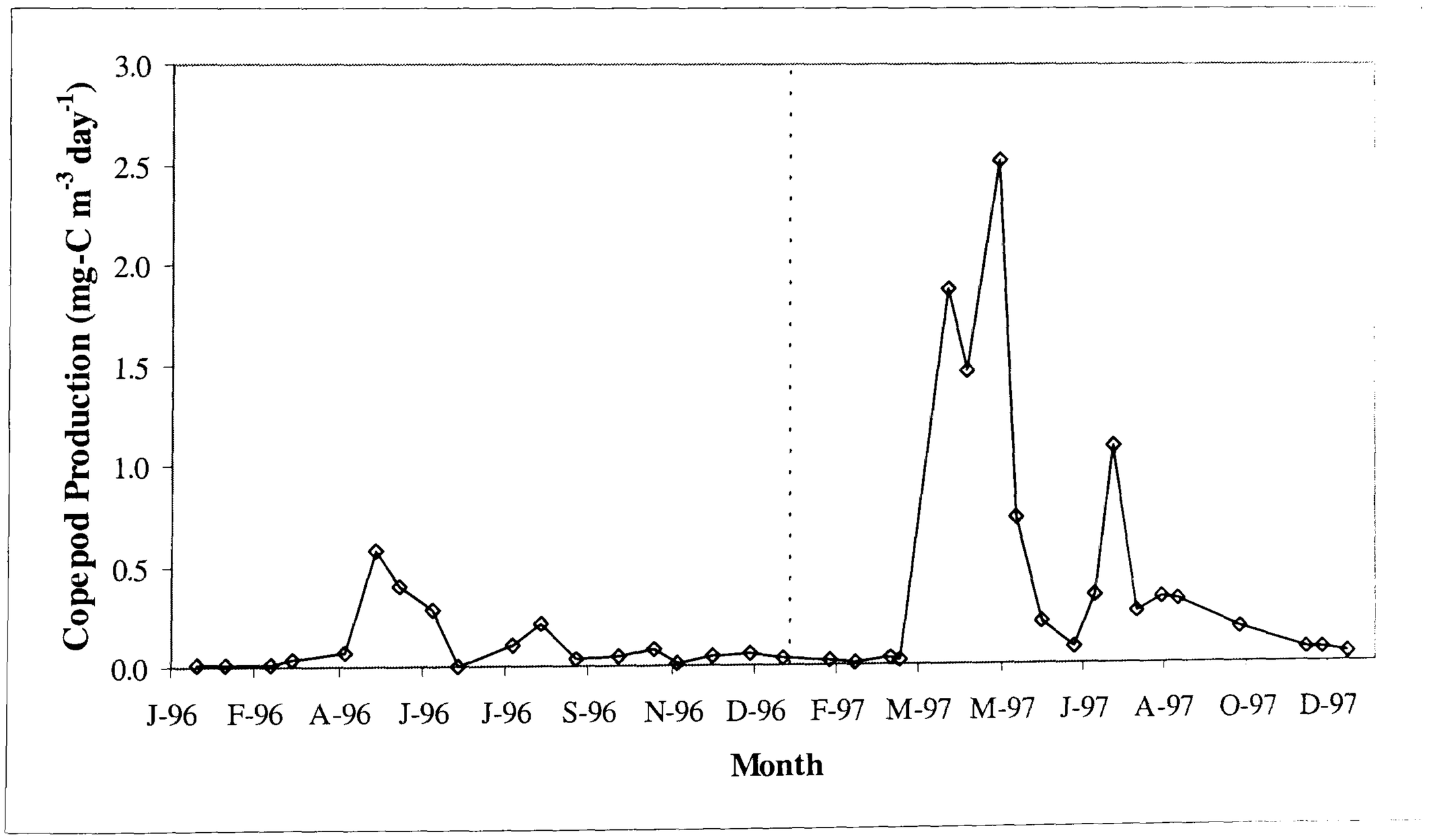


Figure 8.13, b): Seasonal variation in total calanoid copepod production (mg-C m^{-3} day^{-1}) for the Menai Strait during 1996 and 1997.



Total copepod biomass pattern of changes in the Menai Strait broadly reflected the changes in the numerical density of each copepod species. Copepod biomass ranged between ~ 0.3 - 11 mg-C m^{-3} in 1996 and from ~ 0.5 - 50 mg-C m^{-3} in 1997. The highest annual standing stock was always measured in spring when *T. longicornis* contributed between 50 % and 70% of the total copepod biomass, followed by *C. hamatus* (15-30 %), *A. clausi* (12-16%) and *Pseudocalanus* (5-7 %).

The annual standing stock (mg-C m^{-3}) and production (mg-C m^{-3} yr^{-1}) calculated using the equations of Hirst *et al.*, (1999) and Huntley & Lopez (1992) for the four different copepod species measured in the Menai Strait during 1996 and 1997 is shown in Table 8.3.

Table 8.3: Annual total standing stock (i.e. B, mg-C m^{-3}) and production (i.e. P, mg-C m^{-3} yr^{-1}) calculated according to Hirst & Lampitt, (1998) i.e. H and Huntley & Lopez 1992 i.e. H.L for the main copepod species found in the Menai Strait during 1996 and 1997. The annual biomass range (mg-C m^{-3}, in parenthesis) and the proportional (i.e. %) contribution of each species are also shown. Total annual estimates were obtained using trapezoidal integration.

Year	1996				1997			
Species	B		P		B		P	
		%	H	H.L		%	H	H.L
T. longicornis	283.8 (0.02-5)	45.89	16.83	32.46	1288.3 (0.09-32)	50.91	97.27	179.14
C. hamatus	172.3 (0.2-4)	27.86	10.72	25.35	545.1 (0.5-13)	21.54	28.04	55.33
A. clausii	113.1 (0.09-2)	18.29	4.76	19.62	560.5 (0.16-8)	22.15	23.42	71.06
Pseudocalanus sp.	49.2 (0.01-0.5)	7.96	4.68	4.61	136.7 (0.1-3.7)	5.40	11.07	12.69
Total	618.4 (0.3-11)		36.99	82.04	2530.5 (0.5-50)		159.80	318.22

The highest contribution to total copepod biomass was made by for *T. longicornis* followed by *C. hamatus*, *A. clausi* and finally *Pseudocalanus sp.* for both years. The two different estimates of production obtained using either Hirst & Lampitt, (1998) or Huntley & Lopez (1992) equation were quite different, the former estimating approximately half of the production calculated using the latter (i.e. 45.1 % and 50.2 % for 1996 and 1997 respectively). Given that the mesh used will not catch all the copepod stages (i.e. the nauplii and most of the copepodites (i.e. CI-CIII), the presented values underestimate the existing copepod standing stock and production.

8.3.9 Seasonal variation in other zooplankton species

Figure 8.14 shows the seasonal trend of abundance of the other main zooplankton species found in the Menai Strait during 1996 and 1997. Overall there was a consistently higher concentration during 1997 than during 1996 for most of the species considered.

8.3.9.1 Gastropod eggs

Gastropod eggs represented the most numerous planktonic organism reaching densities up to 70-100 ind. m^{-3} during winter months and up to ~ 300 ± 7.74ind. m^{-3} March and May during both 1996 and 1997 (Figure 8.14, a). Gastropod and bivalve veligers increased in number briefly during May but reached peak densities up to ~ 25 to 35 ind. m^{-3} in late summer and early autumn.

8.3.9.2 Cirripede nauplii

he barnacle nauplii were mostly found between early spring to autumn. Their largest increase was recorded in early March when they reached a mean (± S.D.) density of ~ 322 ± 47.5 and ~ 315 ± 21.4 ind.m^{-3} for 1996 and 1997 respectively (Figure 8.14, b). Smaller increases up to 50 ± 3.9 ind. m^{-3} were recorded in summer during July for both years.

8.3.9.3 Polychaete larvae

The number of larvae started to increase in spring around the end of March and April-May up to a mean (± S.D.) density of ~ 85 ± 7.9 to ~ 291 ± 78.3 ind. m^{-3} for 1996 and 1997 respectively (Figure 8.14, c). The most common groups included the Sillids, spionids magellonids and terebellids. The highest increase usually recorded during May was due to the sudden increase of the terebellid species *Lanice conchilegia* that at this time reached densities of 70 and 236 ind. m^{-3} in 1996 and 1997 respectively. The increase recorded in summer 1996 up to 14 ind. m^{-3} was mainly due to the species *Pectinaria sp.* The pelagic species *Tomopteris helgolandica* was present in the plankton samples during August and September 1997 but not in 1996.

8.3.9.4 Cladocera

The only cladoceran found in the Menai Strait belonged to the families *Podon sp.* and *Evadne sp.* These two groups only made a brief appearance in the Menai Strait during mid summer summer reaching concentrations of ~ 45 ind. m^{-3} and.~ 850 ind. m^{-3} during July 1996 and June 1997 respectively (Figure 8.14, d).

8.3.9.5 Appendicularia

Appendicularia belonging to the family *Oikopleura sp.* were found in the Menai Strait from spring to autumn reaching mean (± S.D.) peaks of increase up to ~ 82 ± 51.6 to ~96 ± 0.66 ind.m^{-3} in summer between May and June (Figure 8.14, e).

8.3.9.6 Bryozoa

The bryozoan larvae started increasing in densities also in spring after March and reached their mean (± S.D.) annual maximum of ~36 ± 16.4 and 321 ± 71.8 during May 1996 and June 1997 respectively and secondary peaks during autumn (Figure 8.14, f). In 1997 the annual summer maximum was ~ 9 times higher than during 1996 whereas the autumn increase were comparable between years.

8.3.9.7 Crab zoea

The crab zoea increased during late spring persisting throughout the summer (Figure 8.14, g). In 1997 the crab zoea mean (± S.D.) densities of ~159 ± 14.8 ind.m^{-3} recorded during the spring annual maximum were ~ 4 times those recorded in 1996 up to ~ 44 ± 14.4 ind.m^{-3}, whereas the summer increases were comparable.

8.3.9.8 Chaetognatha

The arrow-worms found in the Menai Strait belonged to the species *Sagitta elegans* and *S. setosa*. *S. elegans* was found exclusively during the winter months between January and March whereas *S. setosa* appeared in spring and autumn for both 1996 and 1997 (Figure 8.14, h).

During 1996 *Sagitta sp.* increased in summer with the highest concentration recorded during autumn with mean (± S.D.) up to ~ 62 ± 14.7 ind. m^{-3} whereas in 1997 maximum mean (± S.D.) increase was recorded in spring up to ~ 25 ± 16.8 ind. m^{-3} with smaller increases in summer between ~ 6 and ~11 ± 2.47 ind. m^{-3}. The summer and autumn increase in 1997 occurred about one month earlier than in 1996. The variability

among replicate samples was very high indicating patchiness in the distributions of this species.

8.3.9.9 Ctenophora and Cnidaria

The seasonal trend in the densities of the ctenophore *Pleurobrachia pileus* was similar between 1996 and 1997 (Figure 8.14, i). The first increase was measured in winter between January and February with densities between ~ 0.5-1 ind. m^{-3}. The winter increase was followed by a spring annual maximum up to 1.5 ± 0.6 and ~ 1.7 ± 1.16 ind. m^{-3} for 1996 and 1997 respectively. After that densities declined until December during which the numbers of ctenophores started to increase back to the winter concentrations. During the year fresh *P. pileus* individuals ranged in size from ~3 to 15 mm length corresponding to an estimated ~ 6.5-33.5 µg dry weight or ~ 3.6 % of their wet weight. *Beroe sp.* was very numerous during June and September 1997 reaching up to ~ 2.5 - 4.5 ind. m^{-3} and up to 0.5-1 ind. m^{-3} respectively but none was found in the 1996 samples. The hydromedusae *Phialidium sp.* was found in comparable numbers during both during 1996 and 1997. The first population increase was measured during May with maximum densities between ~ 17-21 ind. m^{-3} and secondary increases during late summer between ~ 6 - 28 ind. m^{-3}.

8.3.9.10 Euphausida

The euphausids *Meganictiphanes sp.* were found very infrequently and in low numbers both in 1996 and 1997 between January and February concomitantly with the appearance of *S. elegans* in the plankton catches.

Figure 8.14: Seasonal changes in the concentration (ind. m^{-3}) of zooplankton species

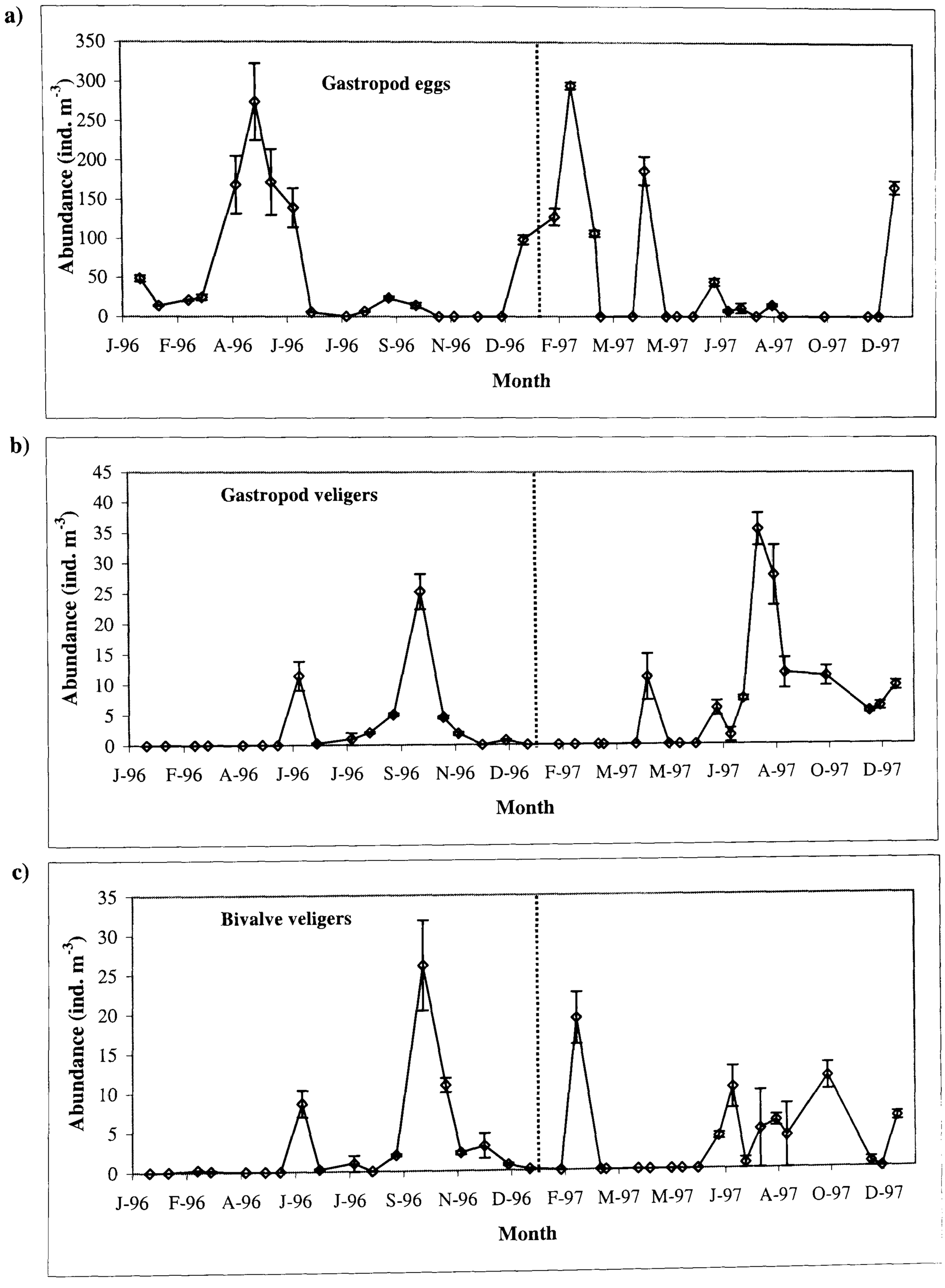
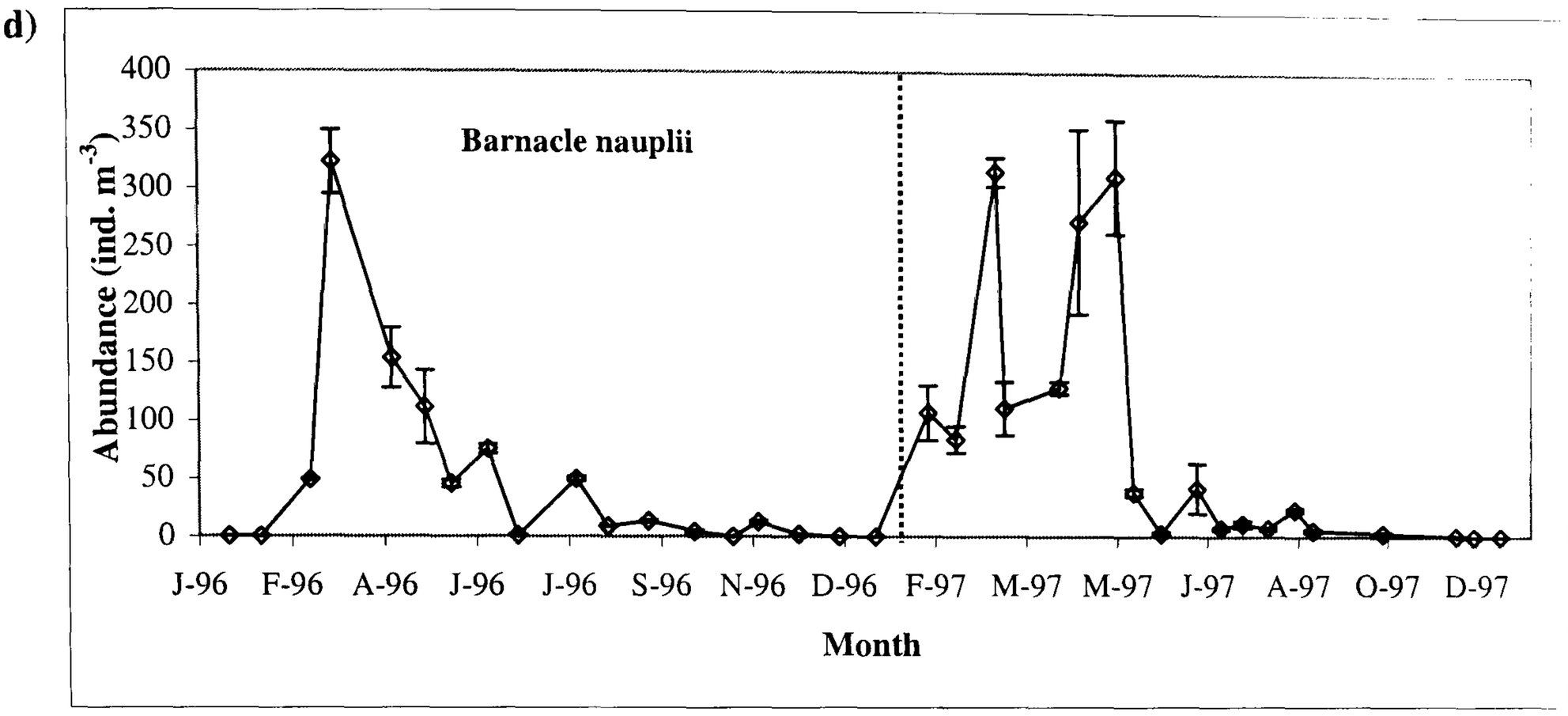
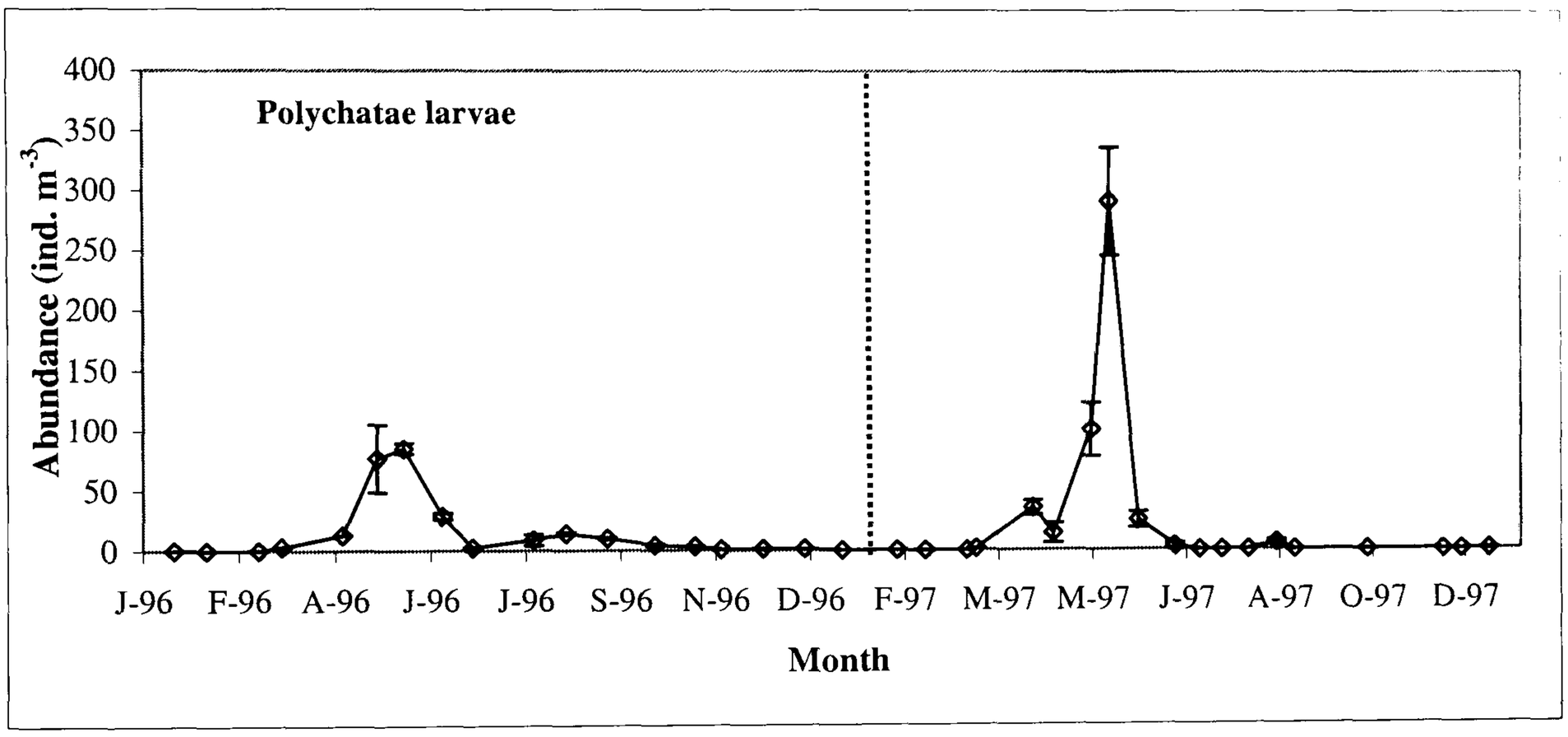


Figure 8.14 Continued





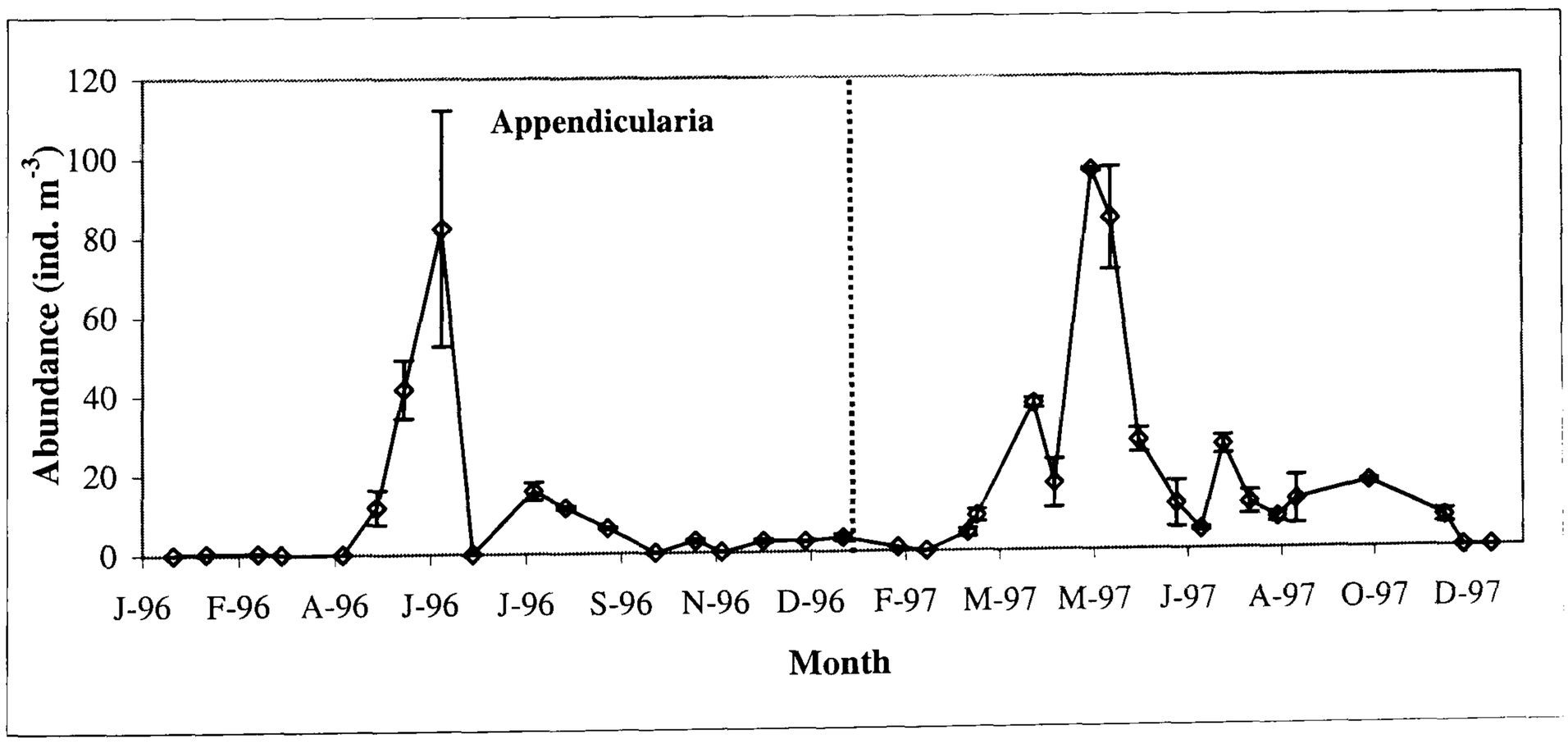


Figure 8.14 Continued

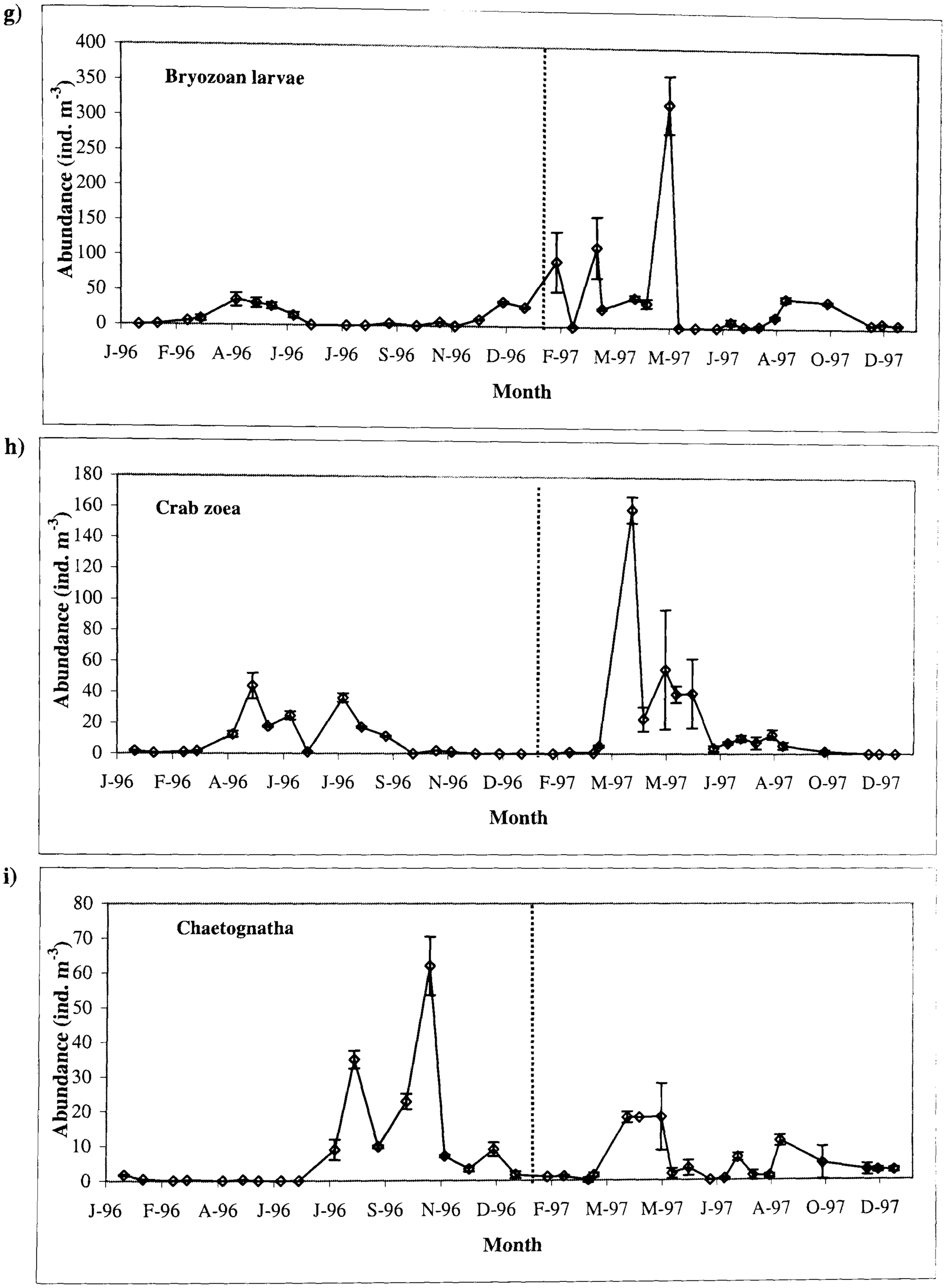
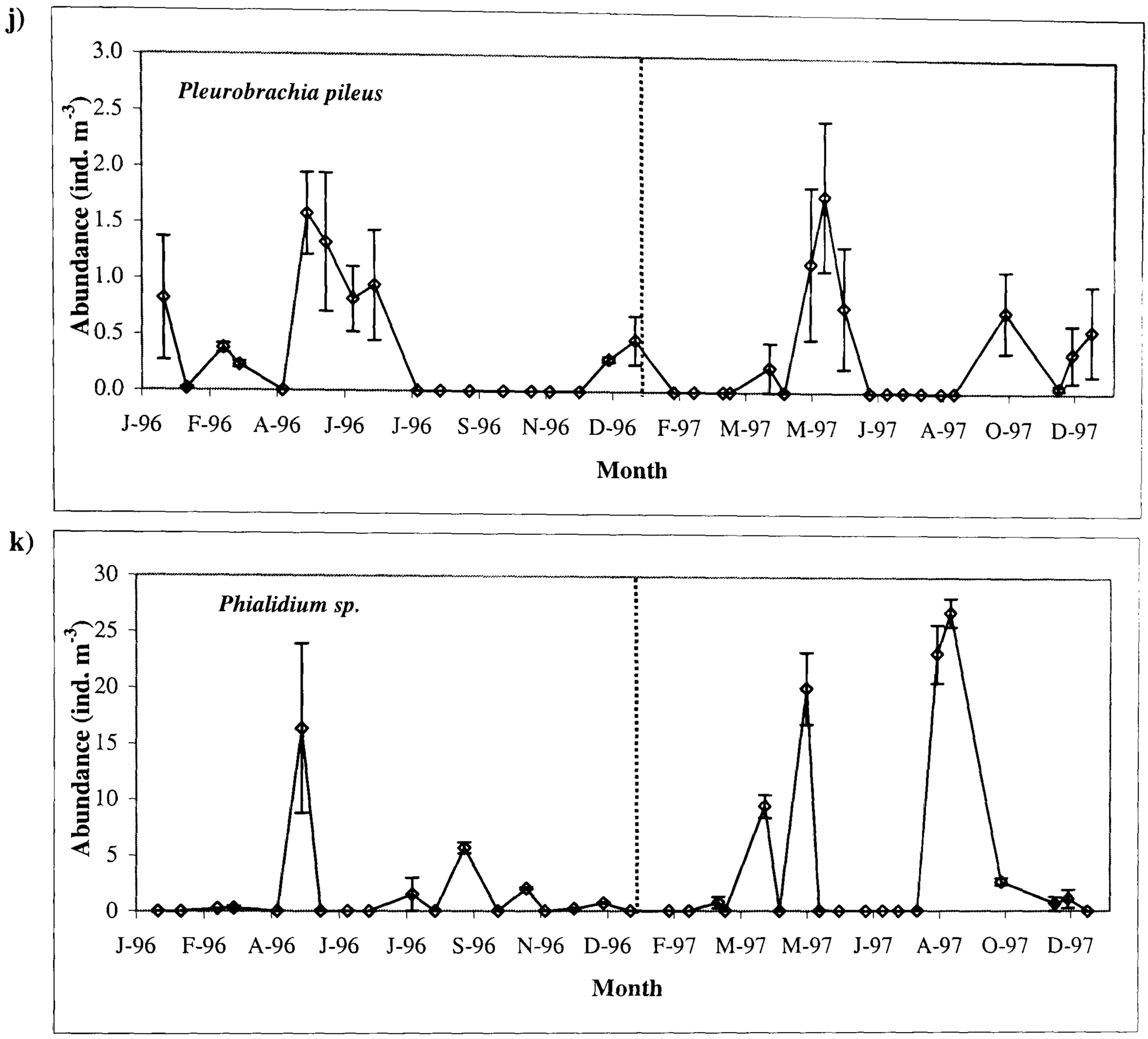


Figure 8.14 Continued



8.4 Discussion

8.4.1 Seasonal trend in succession of the copepods from the Menai Strait

The large number of surveys undertaken on the seasonal cycle of the Menai Strait's phytoplankton (Haq, 1960; Ewins & Spencer, 1967; Jones, 1968; Al-Hasan, 1976; Tyler, 1977; Lennox, 1979; Bajpai, 1980; Blight *et al.*, 1995) is in stark contrast with the limited work carried out on the zooplankton (Haq, 1960; Kenchington, 1968; Hidayat, 1995). Consequently, there is still a basic lack of knowledge on the seasonal ecology, population dynamics and productivity of the meso-zooplankton living in the Menai Strait as well as for the rest of the eastern Irish Sea (Savidge & Kain, 1990).

During the 1996-97 survey the copepod assemblage of the Menai Strait was characterised by relatively few copepod species including *T. longicornis*, *C. hamatus*, *Pseudocalanus sp.*, *A. clausi*, *Oithona sp. Calanus sp.* and *Euterpina acutifrons*.

The present study has shown that, as with many other temperate coastal areas, the meso-zooplankton number and biomass in the Menai Strait was mainly dominated by the copepods (Raymont, 1980). Total meroplankton abundance was higher than that of the copepods for a short time during winter (Littorina eggs), early-spring (barnacle nauplii). The surveys of Haq, (1960), Kenchington (1968) and Hidayat (1995) noted a very similar pattern.

During 1996-97, the annual copepod maxima of ~1800-7000 ind. m^{-3} always occurred in spring whilst minor peaks peaks up to ~ 600 (in 1996) ind. m^{-3} and 2500 (in 1997) ind. m^{-3} were measured during the late summer months. Haq (1960) has reported copepod peaks in spring between 6000-12000 ind. m^{-3} and copepod annual maximum in autumn 24000 ind. m^{-3}. Similarly, Hidayat (1995) recorded a lower total copepod abundance (~ 800 ind. m^{-3}) in spring than in summer when densities rose to ~ 1600 ind. m^{-3}. More consistent with the present study, however, Kenchington (1968) described copepod annual maxima in spring/summer of up to 1500 ind. m^{-3} and lower summer/autumn peaks of up to ~1000 ind.m^{-3}.

The copepod spring maximum in the Menai Strait was dominated by *T. longicornis*. Despite peaks of abundance in the spring, *C. hamatus*, *Pseudocalanus sp.* and *A. clausi* only became numerically dominant at other times. During the 1996-97 copepod spring increase *T. longicornis* reached annual peaks between ~ 800 ind. m^{-3} and ~ 4600 ind. m^{-3} between April and May accounting for up to ~ 50 % to 75 % of the total copepod numbers. Previously *T. longicornis* densities reached up to 71 % in May 1957 (Haq, 1960) and in June 1967 (Kenchington, 1968) and 62 % in May 1995 (Hidayat, 1995) of the total copepods number.

In the present study *C. hamatus* was the second most abundant species reaching annual maximum also in spring at up to ~ 30 % of the total copepod numbers. In his zooplankton survey in 1957 Haq (1960) reported *C. hamatus* as the second most important copepod species increasing in spring up to ~ 6000 ind. m^{-3} representing ~ 45 % of the total copepod numbers. Kenchington, (1968) found *C. hamatus* to be the least abundant copepod species in 1967 with numbers fluctuating between ~100 to ~145 from April to December and with no noticeable annual maximum. On the other hand, Hidayat (1995) reported a moderate spring increase in *C. hamatus* abundance followed by a

summer annual maxima of ~ 520 ind. m^{-3} representing >30 % of the total copepod density

During the present 1996-97 plankton survey, *Pseudocalanus sp.* was absent in summer months being best represented between October and April with 200 and 800 ind. m^{-3} and accounting for between 13 % and 55 % of the total copepod assemblage. Kenchington (1968) and Hidayat (1995) also measured spring and autumn peak abundances in *Pseudocalanus sp.* up to ~ 200 and ~ 100 ind. m^{-3} respectively, whereas Haq (1960) reported the highest concentrations only in spring of ~ 750 ind. m^{-3} with no records of its occurrence from summer onwards.

In the present study *A. clausi* was the least numerically represented species in the Menai Strait being only found in spring and summer between June-July when it reached a population annual maximum of ~ 115-250 ind. m^{-3} or ~ 37 % of the total copepod numbers. Previous studies reported *A. clausi* population density peaks only in the summer, between July-September, up to about 400 ind. m^{-3} (Haq, 1960), ~ 540 ind. m^{-3} (Kenchington, 1968) and ~ 260 ind. m^{-3} (Hidayat, 1995).

The seasonal trend in copepod abundance and species composition described in the present study shows that little has changed in the Menai Strait zooplankton over the last 40 years (Haq, 1960; Kenchington, 1968; Hidayat, 1995). Differences in the annual abundance and species dominance between studies are evident but general patterns are virtually identical. One of the main differences in copepod dominance emerging among the zooplankton studies in the Menai Strait is the autumn annual maxima recorded by Haq (1960) for the cyclopoid *Oithona nana* and *E. acutifrons*. In Haq's (1960) survey *O. nana* and *E. acutifrons*, both peaking in autumn with between 5,000-15,000 copepods m^{-3} and about 2,500-9,000 copepods m^{-3} respectively, were the numerically dominant copepod species. On the other hand, in the present, in Kenchington's and Hidayat's studies, *Oithona sp.*, reached a maximum of ~1 % of total copepod counts between the end of summer and autumn.

The year to year discrepancies in copepod abundance and species composition, observed among the Menai Strait studies, are difficult to ascertain given the lack of a standard sampling methodology both throughout and among the different surveys. In the present study bi-monthly to monthly sampling was carried out with a 270 μm mesh size filtering between 10-60 m^3 of water over 3-5 minutes to avoid net clogging. The survey of Haq (1960) was based on pumped water samples of only 0.7 to 0.9 m^3 filtered through a 200 mesh per inch (m.p.i. or 60 μm). Kenchington's (1968) used a 12"

fibreglass version of the Gulf-III High Speed Sampler (Geringer, 1952) to filter weekly. an estimated 200 m^3 of water with a 56 m.p.i. (i.e. 308 μm) and no flow-meter, for the first 7 months, and a 72.5 m.p.i. (i.e. 190 μm) with flow-meter, over the rest of the study. In his study, Hidayat (1995) made relatively long monthly samplings of ~ 10 mins duration (200 m^3 water filtered in non net-clogging conditions) with a 250 μm mesh sized net.

Kenchington (1968) has already pointed out that the differences recorded in species dominance and abundance between Haq's and his study probably arose as a result of the different net mesh sizes used. Paffenhofer (1998) has observed that most adult *Oithona sp.* would go through a 200 μm mesh and should be regarded as microzooplankton. Thus, whereas Haq's study places more emphasis on the smaller sized copepod species and stages, Kenchington's (1968), Hidayat's (1995) and the present investigation offer a better resolution of the seasonal changes of the larger calanoid copepod species underestimating the small *Oithona sp.*, *Euterpina acutifrons* and the younger stages.

8.4.2 Temperature effect on species interannual variations

In the present study, the spring peak of total copepods always coincided with the phytoplankton bloom peak both in 1996 and in 1997. Although, Haq (1960) is the only author to have reported a similar relationship for the Menai Strait, the coincidence between phytoplankton and copepod population maxima is also evident compiling data from previous studies (Jones, 1968; Kenchington, 1968; Hidayat, 1995; Pers. observ. in 1995). Fransz (1981) reported that inter-annual variation in zooplankton biomass and composition in the western Wadden Sea was irregular and probably based on shifts in the coincidence of the zooplankton development and the phytoplankton spring bloom and species composition. Such a concomitant occurrence between phytoplankton and zooplankton increase indicates a close coupling between the algae and the copepods. *T. longicornis*, which is a typical coastal spring copepod species, has been observed to increase in relation to phytoplankton increase and may be more dependent than other copepod species on the spring phytoplankton bloom (Fransz, 1975 & 1992).

The inter-annual variability in copepod abundance recorded in the Menai Strait, within the same study, over two consecutive years by Haq (1960) and by the present investigation is quite remarkable. Cushing (1980) reporting Herdman's (1921) results on the variability in copepod abundance in the Irish Sea, between 1907 and 1916.

calculated coefficient of variations as high as 40 % in *T. longicornis* and 80 % in *Calanus sp*. It is, perhaps, worth noting at this stage that although *T. longicornis* pre-bloom population in 1996 (~ 90 ind. m^{-3}) was ~ 3 times higher than for 1997 (~ 30 ind. m^{-3}) *T. longicornis* population maximum in 1997 (~ 4600 ind. m^{-3}) became ~ 6 times higher (~ 800 ind. m^{-3}) than in 1996 (see Figure 8.4). Thus, despite starting from a higher number of individuals, over the same period of time, the 1996 population increased at a lower rate than the 1997 population (Figure 8.4). Similarly, the relative inter-annual variation of *C. hamatus sp.* abundances recorded by different studies is also note worthy. Haq (1960) comparing seasonal cycle of copepod abundance during 1957 and 1958, argued that the colder winter of 1958 resulted in the decrease in the magnitude of the spring copepod peak of abundance in *T. longicornis* and *C. hamatus* which in that year showed no definite increase suggesting that *C. hamatus* was much more influenced by low temperature than *T. longicornis*. Similarly, a lack of a definite peak in *C. hamatus* abundance during the cold year of 1967 was recorded by Kenchington (1968). These observations contrast with records made in relatively warmer winters (5 -10 °C between January and March 1995) in the 1990's during which *C. hamatus sp.* showed peak abundance and/or dominated summer copepod numbers (Hidayat, 1995; Present study). *C. hamatus* has been often reported to thrive at higher summer temperatures (Kane, 1992; Fransz, 1991) and to be a potential sensitive indicator of environmental temperature changes (P. Reid pers. comm.). Thus, differences in the Menai Strait's winter temperature regime (i.e. 1996 'cold' and 1997 'warm', see Chapter 3), may have had an effect on the growth of the population of different copepod species later on in the year as already suggested by Colebrook (1985) for the North Sea. Further studies should validate the present observation by identifying the mechanisms leading to the inter-annual variation in copepod species abundance and whether these differences should be related to the characteristic thermal physiology of different copepod species.

8.4.3 Copepod decline and predation

Following the phytoplankton spring bloom a sharp decline in total copepod species was consistently observed for both 1996 and 1997 after which a population recovery gave rise to a secondary peak of abundance during the late summer months. A similar decline in copepod population has been observed by other studies and it has been variously related to mortality due to decreased food levels, poor food quality,

increased predation (Daan *et al.*, 1988; Roff *et al.*, 1988) and decline in birth rate (Fransz, 1989; Peterson and Kimmerer, 1994).

In the present study, the decline in the copepod populations coincided with the increase in the numbers of the ctenophore species *Pleurobrachia pileus* which are notorious predators of copepods (Larson, 1987). Reduction in the numbers of mesozooplankton, particularly copepods, and negative predator-prey abundance relationships have often been observed during periods when gelatinous predators are abundant (Burrel and Van Engel, 1976; Deason and Smayda, 1982; Lucas and Williams, 1995). However, evidence of the structuring influence of gelatinous zooplankton simply through examination of abundance changes (i.e. correlation analysis), may lead to erroneous conclusions regarding the true predator impact as often predator density cannot account for the observed decrease in their prey (Miller and Daan, 1989).

Maximum recorded biomass of *P. pileus* in coastal waters ranges from 0.6 up to 21 mg-C m^{-3} recorded for the North Sea and British Columbia respectively (Fraser, 1970; Larson, 1987; Harris *et al.*, 1982; Miller and Daan, 1989). Thus, the annual maximum *P. pileus* standing stock of 1.3 mg-C m^{-3} measured in the Menai Strait was at the lower range of the abundance reported for other coastal waters. Whereas, Haq (1960) and Hidayat (1995) show scarce or no record of ctenophores, Kenchington (1968) measured peaks of abundance of *P. pileus* of ~5 ind. m^{-3} in autumn, <1 ind. m^{-3} in summer and none in spring.

Miller and Daan, (1989) have reported *P. pileus* weight specific clearance rate between 8 and 12 °C, of ~ 0.1-0.6 mg-C copepod mg-C ctenophore^{-1} day^{-1} measured under quasi-natural conditions in Dutch coastal waters at mean *P. pileus* biomass 0.9-5.43 mg-C m^{-3} and copepod biomass of ~ 31-274 mg-C m^{-3}. Using Miller and Daan, (1989) ctenophore clearance rates, a peak spring ctenophore biomass of 1.3 mg-C m^{-3} at copepod standing stocks up to ~ 11-50 mg-C m^{-3} in the Menai Strait would clear at most 1 % of the copepod biomass per day. Therefore, during their annual maximum occurrence between spring and early summer ctenophore would remove at most between 6 % (in 1997) and 37 % (in 1996) of the copepod standing stock, that is, much less than the 92 % decline in copepod biomass measured in both years.

Although, in the present study, towing times were kept low (i.e. 3-5 minutes) to avoid net clogging (Unesco, 1968) by *Phaeocystis sp.* this organism was probably responsible for the sharp copepod population decline observed during the peak

phytoplankton spring bloom. Fast clogging of the plankton net was also observed, to some extent during the massive increase of *Noctiluca sp.* at the end of the phytoplankton bloom in June and July when this dinoflagellate species reached its annual maximum density in the Strait. However, since decline in copepod numbers occurred long before the *Noctiluca sp.* increase the drop in copepod density observed must have been real and not simply due to reduced filtration efficiency of the net. Thus, other factors like natural mortality and/or decrease in the reproductive rate were probably largely at the base of the early summer decrease in copepod numbers observed in the present study as advocated by other authors (Fransz, 1992; Peterson & Dam, 1994).

8.4.4 Seasonal changes in copepod body size

None of the previous studies conducted in the Menai Strait has investigated in any detail the seasonal changes in the copepods stage composition and body length. The present investigation has shown that copepod size varied with the time of the year. The ranges of copepod lengths found in the Menai Strait throughout 1996 and 1997 were similar to those reported for temperate regions by other investigators (Digby, 1954; Marshall, 1949; Hirst, 1996).

Maximum body length was usually found in winter and spring and minima in summer and autumn. Seasonal changes in copepod body size have been positively related to food concentration (Digby, 1950; Klein Breteler & Gonzalez, 1982; Bergreen *et al.*, 1988; Christou & Verriopoulos, 1993) and negatively related to temperature, both in nature (Marshall & Orr, 1955; Deevey, 1960; Evans, 1977; Christou &Verriopoulos, 1993; Hirst, 1996) and in the laboratory (Kimoto *et al.*, 1986; Uye, 1991). In the present study correlation analysis with temperature and Chla (as a proxy for food concentration) and copepod body length for each separate stage and sex, indicates strong negative correlation with temperature and no correlation with Chla. Similarly to the present study, Deevey (1960) has reported that Chla was not significantly related to prosome length of *P. minutus*, *T. longicornis*, *A. clausi* and *A. tonsa* in Long Island Sound. The lack of a clear relationship between copepod C.L. and Chla found by the present and past studies (Deevey, 1960; Hirst, 1996) is not surprising. Direct measurement of the food ingested and its quality would be necessary to establish the relative contribution of food to copepod growth and production (Kleppel & Hazzard, 2000). The relationships between temperature and body length was, however, not significant in all the cases for

all stages and sexes. The poor relationship found for the younger stages (i.e. CI-CIII) and some of the species like *A. clausi* and *Pseudocalanus sp.* may be also due to the relative paucity of data available for these two latter species. Nevertheless, higher direct relationship (no lagging) between body length and temperature measured in *T. longicornis* rather than for the other copepod species has already been reported by other studies (Deevey, 1960; Hirst, 1996). Thus, *T. longicornis* growth may be more directly influenced than other species by temperature changes, hence suggesting physiological differences among copepod species.

8.4.5 Sex ratio

A consistently higher abundance of male *T. longicornis* and *C. hamatus* and female *A. clausi* and *Pseudocalanus sp.* was observed during both 1996 and 1997 Although, male dominance is not very common in copepods (Bogorov, 1939), it has been observed in the past by several authors (Marshall, 1949; Digby, 1950; Fransz, 1975; Schnack, 1978). For instance, Fransz (1975) for the Dutch coastal waters and Schnack, (1978) for the Kiel Bay reported a consistently higher concentration of male over female *T. longicornis*. Similarly, Marshall (1949) in Loch Striven and Digby (1950) off Plymouth found higher proportions of both *C. hamatus* and *T. longicornis* males in their zooplankton catches. Marshall & Orr, (1955) have suggested that in spring *Calanus* males may develop faster than females. In the present study, all the copepod species considered showed sexual dimorphisms with adult males being shorter than females throughout the year. The smaller size of calanoid males (also measured by the present study) is generally attributed to their shorter development span (Corkett & McLaren, 1981) which allows the male to fertilise the female of its own generation as they moult (Landry, 1978). Nevertheless, the seasonal changes in the sex ratios for the Menai Strait's copepod species are difficult to explain. The data obtained in the present study provide no evidence of *C. hamatus* and *T. longicornis* male numbers increasing prior to female numbers as the sampling frequency was low. Since sex determination in copepods is mainly phenotypic (Takeda, 1950) it is also possible that the observed male dominance might have been induced by existing environmental factors or alternatively that the survival rate of the two sexes differed. Despite the low number of observations available, female dominance in *A. clausi* and *Pseudocalanus sp.* was consistently measured between years. These consistent differences in copepod sex ratios observed in

the present study and generally in the literature for different copepod species point to differential reproductive strategies that warrant further investigation.

8.4.6 Copepods stages composition and number of generations

The present study has shown that the copepodites (CIII-CIV) occurred throughout the year indicating that in the Menai Strait continuous recruitment take places for *T. longicornis* and *C. hamatus*. Observations made in the North Sea in early spring indicate that small-sized neritic copepods hibernate at all developmental stages during the winter (Fransz *et al.*, 1991). In the present study, the numbers of *T. longicornis* and *C. hamatus* copepodites increased simultaneously during the phytoplankton bloom with no apparent juvenile peak preceding the adult spring increase. Some authors (Fransz, 1976; Koeller *et al.*, 1979) have argued that because the nauplii of small copepod species, like *T. longicornis*, are not known as resting stages, presumably there is a continuous reproduction at low level during winter. It has already been reported that all stages of small copepod species increase in abundance, in response to the phytoplankton spring bloom, either simultaneously (Fransz, 1976) or in succession (Bossicart, 1980). According to Fransz *et al.*, (1991) copepods cohorts can remain distinct when periods of increased egg production or release of nauplii from bottom sediments (Lindley, 1986) are short and the number of emerging nauplii has a gaussian distribution in time. On the other hand, continuous reproduction and isochronal growth of stages in combination with a rather similar stage distribution in summer and winter tend to stabilise the ratio of age classes, which leads to simultaneous fluctuations (Fransz *et al.*, 1991). In the present study, the lack of distinct copepodite cohorts prior to the adult copepod spring increase was probably the result of a sampling artefact as the net used had a 270 μ mesh (as opposed to a 200 μ or less usually used in this kind of surveys). Thus, most of the younger stages (CI-CIII) did probably go through the net during sampling.

Generations in nature have been detected from analysis of cohorts and changes in the body length of adult copepods measured at weekly or shorter intervals (Evans, 1977; McLaren, 1978). The analysis of copepod stages and female modal length changes carried out for *T. longicornis* and *C. hamatus*, in the present study, resulted in estimates of copepod generation times higher than those predicted by the Belehradek's equation or those reported in the literature (McLaren, 1978; Review by Mauchline, 1998). It is likely that, the fortnightly to monthly sampling, carried out in the present

study, although allowing the recognition of most cohorts and changes in female body length was too coarse to permit a meaningful estimation of generation time let alone copepod growth rate from field data. Thus, in the present study the cohort method could not be utilised to measure copepod growth to estimate secondary production.

8.4.7 Biomass

The trend of copepod biomass, measured in the Menai Strait during 1996 and 1997, followed a similar pattern of total copepod abundance. The lowest biomass values of ~ 0.3 mg-C m^{-3} were recorded in winter whereas maximum values up to 50 mg-C m^{-3} were measured in spring. Reports of copepod biomass for the whole of the Irish Sea are very sparse. However, using 31 years (1960-1990) of CPR data Williams *et al.*, (1994) reported total copepod dry weight ranging between 178 and 3133 mg m^{-2} for the mixed welsh coastal waters during April and May. Considering the reported sampling depths of 20-45 m and a dry weight to carbon conversion factor of 40 % (Omori & Ikeda, 1984), the values reported by Williams *et al.*, (1994) correspond to 1.6-3.6 and 27.8-62.6 mg-C m^{-3} which are figures not dissimilar from those measured by the present investigation.

In the Menai Strait, *T. longicornis* was the single most dominant copepod species also in terms of biomass with spring annual maxima up to 32 mg-C m^{-3} representing 64 % of total calanoid copepod biomass. The annual maxima biomass values estimated in the present study are similar to the annual biomass maximum of 24 mg-C m^{-3} reported by Fransz (1981) for *T. longicornis* living in the western Dutch Wadden Sea.

8.4.8 Copepod production

With the exception of the limited spring survey of Prestidge *et al.*, (1995) on the EPR of *C. helgolandicus* and *A. clausi*, there are virtually no reported estimates of meso-zooplankton production neither for the Menai Strait nor for the whole of the Irish Sea. The 1996-97 total annual copepod production calculated for the Menai Strait estimated using Hirst & Lampitt (1998) equation, i.e. ~37-160 mg-C m^{-3} yr^{-1} was approximately half of that estimated using the Huntley & Lopez, (1992) relationship, i.e. ~82-318 mg-C m^{-3} yr^{-1} (see Table 8.2). The large differences in production found using the two different methods were clearly to be attributed to the higher specific

growth rates predicted by the Huntley & Lopez, (1992) as opposed to the Hirst & Lampitt (1998) equation (see Table 8.2 & 8.4).

Table 8.4 shows the biomass and production calculated in 1996 and 1997 for *T. longicornis* females only using the weight specific growth rate (i.e. EPR), measured in the present study, and the two above mentioned equations.

Table 8.4: *T. longicornis* annual females biomass (B_f, mg-C m^{-3}) and production (P_f, mg-C m^{-3} yr^{-1}) derived from carbon specific daily growth rates (d^{-1}, annual range) calculated using egg production rate (i.e. EPR, this study), the equation of Hirst & Lampitt, (1998) i.e. H and 0f Huntley & Lopez (1992) i.e. H.L. The total 1996 and 1997 annual estimates of copepod biomass and production were obtained using trapezoidal integration.

Year	1996			1997		
Method	EPR	H	H.L	EPR	H	H.L
B_f (mg-C m^{-3})	92.88			473.45		
Growth rate (d^{-1})	0.02- 0.09	0.04 -0.12	0.08 - 0.35	0.02- 0.12	0.04 -0.12	0.08 - 0.35
P_f (mg-C m^{-3} yr^{-1})	3.81	6.16	14.01	42.46	34.27	62.68

Annual *T. longicornis* female biomass in the Menai Strait was 92.9 mg-C m^{-3} and 473.5 mg-C m^{-3} representing ~ 32.7 % and ~ 36.75 % or about a third of the total annual biomass of this species for 1996 and 1997 respectively (Table 8.3 and Table 8.5). Female *T. longicornis* production estimated with the EPR method, in the present study, was closer to that calculated using Hirst & Lampitt, (1998) than that estimated using Huntley & Lopez's (1992) equation again due to the differences in specific growth rates estimated by the two methods (Table 8.4). Overall, the female production (EPR method), measured in the present study, represented between ~23 % and ~ 44 % of *T. longicornis*'s total annual production estimated with the Hirst & Lampitt, (1998) equation for 1996 and 1997 respectively (Table 8.3 & Table 8.4).

Kiorboe & Nielsen, (1994) also concluded that adult female copepod production in the Kattegat was less than the maximal value estimated on the base of temperature developmental rates of copepods alone (Huntley & Lopez, 1992). Whereas, the Huntley & Lopez, (1992) model estimates copepod growth rate using temperature as the only parameter (i.e. assuming equal growth rate of all copepod stages and no food limitation), the Hirst and Lampitt (1998) equation takes into account copepod weight. Thus, the present study supports the view that by including copepod size the Hirst &

Lampitt (1998) model probably gives more realistic estimates of copepod production than those obtained with the model proposed by Huntley & Lopez, (1992).

Table 8.5 compare copepod production in the Menai Strait in relation to that reported for other temperate coastal areas. Overall, many investigations of neritic and coastal water have demonstrated copepod production rates in excess of 100 to 1000 mg-C m^{-3} yr^{-1} when integrated over the total column depth (Landry, 1978; Uye, 1982; Roff *et al.*, 1988; McLaren *et al.*, 1989; Kiorboe & Nielsen, 1994).

Table 8.5: Copepod biomass range (mg-C m^{-3}) and total annual production in coastal areas (mg-C m^{-3} yr^{-1}). Maximum depth (m) of the sampling location and annual temperature range (°C) are also shown.

T (°C)	Depth (m)	Biomass	Production	Location	Author
3-18	20	0.3-50	37-160	Menai Strait, Eastern Irish Sea, UK	This study
6-18	15	>0.001-1.77	32.2	Calshot, Solent, Southampton, UK	Hirst *et al.*, (1999)
4-18	28	3.5-35	429	Southern Kattegat, NL	Kiorboe & Nielsen (1994)
-	50	-	178-763	Northumberland, North Sea, UK	Roff *et al.*, (1988)
7-16	20	-	176	Gulf of Maine, USA	Montagnes *et al.*, (1988)
27-29	27	0.4 - 6	406	Lime Cay, Jamaica	Chisholm & Roff, (1990)

Total zooplankton production converted from KJ assuming 1 g DW = 6 Kcal (Tremblay & Roff, 1983), 40 % of DW is Carbon (Omori & Ikeda, 1984) and 1 Kcal = 4.1855 KJ.

Fransz (1975) has reported annual maximum daily copepod production of 4.5 mg-C m^{-3} day^{-1} for Dutch coastal waters, which is higher than the of 0.58 to 1.9 mg-C m^{-3} day^{-1} estimated in the present study using Hirst & Lampitt (1998) equation. Although, the copepod production estimates for the Menai Strait are at the lower range of productivity reported for other coastal waters (Table 8.5) these figures certainly represent an underestimate of total copepod production as they exclude the cyclopoid *Oithona* and the early copepodite stages.

Chapter 9

General Discussion

The aim of the present study was to determine the standing stock, secondary production and population dynamics of the small copepod species captured in the Menai Strait. It was also envisaged that the data might be generally applicable to the mixed coastal waters of the eastern Irish Sea. To date, numerous surveys have been carried out on the Irish Sea phytoplankton and zooplankton, but only fragmentary published work appears to be available on copepod standing stock (i.e. as biomass, Scrope-Howe & Jones, 1985; Williams *et al.*, 1994) and their productivity (i.e. as EPR, Prestigdge *et al.*, 1995). Measuring zooplankton standing stock and production is a central problem in marine biology since zooplankton links primary productivity to fisheries productivity (Cushing, 1989). By comparing fish production between different shelf areas around the British Isles, Brander & Dickson (1984) observed that the Irish Sea yield per unit area was consistently lower than elsewhere. High fish production has been associated with high water column stability which enhances primary and zooplankton production and provides better feeding conditions for fish larvae (Frank & McRuer, 1989; Coombs *et al.*, 1992). Within the Irish Sea, larval fish are reported to be more abundant in the seasonally stratified waters in the west than in the permanently mixed waters in the east (Brander & Dickson, 1984; Coombs *et al.*, 1992, 1994). In much of the Irish Sea a combination of strong tidal flow and shallow water ensure that the water column remains vertically mixed throughout the year. The mixed water is characteristic of the shallow (~ 50 m), eastern Irish Sea, whereas the western Irish Sea is deeper (~110 m) and becomes thermally stratified offshore in spring-summer. The western Irish Sea becomes separated from the vertically mixed regions by tidal fronts (Simpson & Hunter, 1974). With 31 years of data, Williams *et al.*, (1994) have shown that the spring peak in zooplankton standing stock per unit area is generally higher in the stratified regions of the western Irish Sea as compared to that in the mixed regions in the eastern Irish Sea.

Differences in productivity have been classically attributed to the fact that tidally mixed coastal waters support a less ecologically efficient community than stratified and offshore waters (Cushing 1989). Shallow coastal waters have a plankton community dominated by the smaller copepods genera such as *Pseudocalanus sp.*, *Acartia sp.*, *Temora sp.*, *Centropages sp.* and well developed microzooplankton and microbial communities. Conversely, the seasonally thermally stratified waters of the European

shelves are dominated by larger herbivorous species e.g. *Calanus sp.* and Euphausids e.g. *Meganictiphanes sp.* which are considered to transfer energy from phytoplankton to fish more efficiently (Cushing 1989; Runge 1988). In addition, Coombs et al., (1994) have argued that in the Irish Sea mixed waters have higher detrital load than thermally stratified waters, which can affect the feeding success of copepods and fish larvae. Williams *et al.*, (1994), estimated that the highest zooplankton standing stock, in the central thermally stratified site of the Irish Sea, was due to the presence of the large *Calanus sp.* although, the smaller copepods were numerically dominant at all sites. However, in the mixed coastal waters of North Wales, the spring copepod standing stock (largely dominated by *T. longicornis*) can reach levels comparable to that of the thermally stratified western Irish Sea (Williams *et al.*, 1994). Similarity between the copepod biomass of the stratified and the eastern coastal regions suggests that the energy transfer from phytoplankton to copepods in Welsh coastal waters is not less efficient than that in the central stratified area. Although high larval fish production is often attributed to the presence of the large *Calanus sp.* the survival of first feeding larvae of many commercial fish species will depend on small calanoid copepods. According to Thompson and Harrop, (1991) in the western Irish Sea cod larvae are mostly abundant in the coastal area and those within 4 to 12.5 mm length will mainly feed on nauplii of 260 μm length and copepodite of 750 μm cephalothorax length (C.L.) of *Temora sp.*, *Pseudocalanus sp.* and *Oithona sp.*. Thus, potentially, the Welsh coastal area could support similar larval fish biomass per unit area as the central stratified region in the western Irish Sea. The mechanisms controlling the observed variation in the copepod biomass of different regions in the Irish Sea have not been fully clarified (Savidge & Kain, 1990; Williams *et al.*, 1994; Boelans, 1995).

Given its success in the Welsh coastal waters, *T. longicornis* population dynamics, production and ecological importance within the Irish Sea warranted further investigation. Thus, in the present study, particular emphasis was put on *T. longicornis* studying its seasonal changes in standing stock, EPR, egg hatching success and respiration rate with temperature to assess the variation in the energy losses by the copepods at different times of the year.

9.1 Hydrographic considerations

Atlantic water flows through the St. George's channel into the Irish Sea in a northerly direction but its influence on the composition of planktonic organisms is

thought to be weak (Williamson, 1956; Norton, 1990). Williamson (1956), for instance. was surprised by the number of Atlantic plankton species which fail to occur in the Irish Sea. According to some authors (Ewin & Spencer, 1967; Harvey & Spencer, 1962), water masses of offshore Atlantic origins can also penetrate coastal waters particularly in winter due to the severity of the weather conditions. On the other hand, in the eastern Irish Sea (e.g. Liverpool Bay), water masses have possible residence time longer than a year due to a localised hydrographic circulation (Norton, 1990; See Chapter 2). In addition, the consistent presence of the Liverpool Bay front has been shown to act, for most of the year, as a natural barrier to the transport of planktonic organisms between coastal and offshore waters (Floodgate *et al.*, 1981; Savidge & Kain, 1990; Burkart *et al.*, 1995). Several studies have shown that the body of water sampled in the Menai Strait has a residence time of 2 days (Campbell *et al.*, 1998) and comes from Liverpool Bay (Harvey, 1968; Simpson *et al.*, 1971). As a result, the Menai Strait water has been considered representative of Liverpool Bay waters by generations of biologists (Jones & Spencer, 1970; Blight *et al.*, 1995). Yet, there have been no observations providing direct evidence that planktonic organisms sampled in the Menai Strait originate from Liverpool Bay.

9.2 Comparisons between the Menai Strait and the Liverpool Bay plankton in 1997

Comparisons of the copepod communities in the Menai Strait with that in the Liverpool Bay (R. Gowen, unpublished data) for 1997 show a very similar pattern in both the timing of copepod abundance and their relative species composition (Figure 9.1 and Table 9.1).

The increase in copepod abundance measured in Liverpool Bay at the beginning of April corresponded to that measured in the Menai Strait. Similarly, the sharp drop in copepod numbers recorded in 1997 in Liverpool Bay between April and May coincided with that recorded for the Menai Strait during the same time. Such a sudden drop was possibly the result of the net clogging by *Phaeocystis sp.* during the Chla maximum (see Chapter 8 and Figure 9.1). The lower copepod density recorded the Liverpool Bay as compared to that measured in the Menai Strait is probably due to the lower sampling frequency (R. Gowen, pers. comm.). Further similarities between these two data sets can be also observed in the summer.

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Table 9.2 shows the average percentage rate of daily increase for the main calanoid copepod species over approximately one month during May 1996 and April 1997 when the copepod population was booming. The abundance of all the copepod species increased during the spring months, hence the change in community composition does not relate to a decline in numbers of one species relative to another (Table 9.2).

Table 9.2: Geometric mean rate of daily increase (%) in the main copepod species number during the spring copepod population increase in 1996 and 1997 in the Menai Strait.

Species	1996 (%)	1997 (%)
T. longicornis	12	16
C. hamatus	14	11
A. clausi	15	13
Pseudocalanus sp.	9	8

Despite *A. clausi* and *C. hamatus* having a faster population rate of increase during 1996 than *T. longicornis* the latter species became numerically dominant in spring also possibly due to its higher (~ 5 times) over-wintering population stock. It is worth noting, on the other hand, that the over-wintering population of *Pseudocalanus sp.* was approximately twice that of *T. longicornis* and 5-8 times that of *C. hamatus* and *A. clausi* respectively. Thus, the higher population growth rate of *T. longicornis*, *C. hamatus* and *A. clausi* during spring may put *Pseudocalanus sp.* at a disadvantage during spring.

9.3.2 *T. longicornis* EPR of over-wintering females

The consistent spring dominance of *T. longicornis* observed in the present and previous studies is quite remarkable. In 1997, for example, *T. longicornis* abundance increased 180 times within one month between March and April. With generation times. at spring temperatures with excess food available of the order of 40 days how is such a dramatic population increase possible?

During both spring 1996 and 1997, *T. longicornis*'s population maxima must have originated from eggs produced prior to the EPR maximum which was coincident with the copepod abundance maximum. Is it possible for the spring population peak to have resulted solely from a cohort of eggs spawned by the over-wintering female population?

The birth date of the spring *T. longicornis* cohort can be estimated using McLaren's (1978) development rate with temperature equation ($D = 16988 \times (t + 10.4)^{-2.05}$, D is egg-adult development time in days, t is the temperature in °C) estimated for *T. longicornis* reared in the laboratory (Harris & Paffenhofer, 1976). Since the temperatures experienced by the copepods were between 8-10 °C the birth date of the spring cohort would have been ~ 40 days earlier, i.e. 9/03/97. Since the stages measured during the spring peak were adults, CV and CIV, the eggs giving rise to the peak must have been produced over 9 days (i.e. 3 days stage^{-1} x 3 stages). The egg production rate and number of females present over the 9 days spawning period considered, results in a total of 1080 eggs m^{-3} (i.e. 6 fem. m^{-3} x 9 days x 20 eggs fem^{-1}day^{-1}) giving rise to the initial cohort in spring 1997.

Since, the total *T. longicornis* number during the 1997 spring peak was ~ 4600 copepods m^{-3}, even assuming an impossible 100 % survival egg-adult, about 77 % of the copepods must have derived from a different source. Even considering the much slower development rate of ~ 80-110 days (6-8 days/stage) measured by Klein Breteler & Gonzalez (1982) for *T. longicornis* cultured in limited food conditions between 5-10 °C, the number of eggs produced between January and March 1997 would still only be ~ 1170-1560 eggs m^{-3}. Thus, the initial copepod spring peak could not have been generated by the existing winter population of females as their number and reproductive output was too low (See Chapter 8 & Chapter 4). The same logic applies to 1996 where peak numbers were ~ 850 (ind. m^{-3}) and estimated total egg production was ~ 450 eggs m^{-3}.

9.3.3 Resting eggs

Discarding water movement and *in situ* egg production as the cause of the observed copepod spring increase the next logical step to be considered as the likely source of such a fast and extraordinary increase in *T. longicornis*'s population is the hatching of resting eggs from the sediments. Species of the families *Acartidae*, *Temoridae* and *Centropagidae* all produce resting eggs which can survive deposition in

the sediments for more than 40 years (Marcus, 1994; Marcus, 1996). It has been often speculated that, the population densities of small copepod species increase dramatically as the result of the mass hatching of the resting eggs. Conversely, the mass production of resting eggs coupled with the natural mortality will result in similar rapid decline in population densities (De Stasio, 1990; Marcus, 1984; Marcus, 1996). Thus, several authors have proposed that the development of the first generation of neritic copepod populations following winter depends on the hatching of resting eggs from bottom sediments (Marcus 1984; Uye, 1985; Lindley, 1986; Fransz *et al.*, 1992). For instance, the population of *T. longicornis* in Loch Striven in January and February consisted almost entirely of nauplii and Marshall (1949) concluded that they originated from resting eggs (confirmed by Petersova, 1974). The causes of the sharp decrease in copepod populations at the end of spring could not be entirely attributed to the feeding impact of gelatinous predators (Chapter 8). Population density dependent mechanisms in copepods leading to population decrease through the production of resting eggs has been demonstrated by Ban & Minoda, (1994) and suggested by Castro-Logoria & Williams (1999). Hairston, (1987) has even shown that predation pressure can cause a switch from producing resting eggs rather than subitaneous eggs in the freshwater copepod *Diaptomus sanguineus*. Low spring copepod egg hatching success in the Menai Strait was observed during maximum predator densities and maximum copepod population densities. It could be suggested that, the best time to produce resting eggs would be when the population is peaking and food is most abundant as EPR, encounter rate with potential mate and genetic variability are at their highest. In addition since predators are usually increasing with the increase of their prey producing resting eggs may represent the best way to avoid extinction.

Peterson & Kimmerer (1994) and Fransz *et al.*, (1992) have suggested that the low recruitment of individuals to the *T. longicornis* population in Long Island Sound after spring was caused primarily by high rates of egg mortality (or resting egg production) and food limitation. Although, summer phytoplankton standing stock in the Menai Strait was often high, the cell sizes of *R. styliformis*, *R. shrubsolei*, *Guinardia flaccida* and the long chain forming diatoms *Eucampia zodiacus* and *Leptocylindrus danicus* might have been too large for efficient ingestion by copepods resulting in lower fecundity (Chapter 4 & 5). High summer temperatures also gave rise to smaller sized copepods in the population with higher weight specific respiration rate (Chapter 7). Thus, a combination of reduced copepod hatching success, higher weight specific

energy requirement, food limitation and predation pressure might have combined to reduce population densities sharply at the beginning of summer (see Chapter 8).

The present study has shown a significant positive correlation between the number of non hatching eggs and the concentration of Chla in the Menai Strait suggesting that the phytoplankton or a co-related factor had a detrimental effect on egg hatching success in *T. longicornis*. Although, a deleterious effect of phytoplankton on egg hatching success (Miralto *et al.*, 1999) at the time of maximum EPR and population increase cannot be ruled out, it has been argued that phytoplankton toxicity towards eggs should be accompanied by reduced egg production (Irigoien *et al.*, 2000). This was obviously not the case of the present investigation where *T. longicornis* maximum EPR coincided with the lowest hatching success.

Monitoring of non-hatching eggs for an additional or >10 days beyond the time required by subitaneous eggs for complete hatching, showed no further hatching (Chapter 6). Marcus, (1984) has observed that it is unlikely that subitaneous eggs would remain viable for more than few days due to the lack of a hard protective coating characteristics of resting eggs (Ianora & Santella, 1991). Moreover, dead copepod eggs will deteriorate quickly as pointed out by Marcus (1996) and as observed in other crustaceans (D.A. Jones pers. comm.). The opaque egg cover observed in the present study in non-hatching eggs further suggests that the eggs produced during the spring phytoplankton bloom were resting eggs (Chapter 6).

In a study of the distribution of resting eggs in the sediments around the British Isles, Lindley (1990) and Lindley *et al.*, (1999) identified a broad sandy area within the eastern Irish Sea coast as a likely resting egg repository. The area, which extends from the Isle of Man along the Cumbrian coast down into Liverpool Bay, is far wider than any other potential resting 'egg bank' site within the Irish Sea. It is possible that the higher *T. longicornis* population abundance measured off the Welsh coast in comparison to that of the Irish coast is due to the existence of a larger 'egg bank' on the eastern side of the Irish Sea.

9.4 Carbon flux

One of the main limitations to our understanding of the Irish Sea productivity has been the fragmentary nature of the data available from a number of independent local research centres with no central co-ordination (Savidge & Kain, 1990). Moreover, with few exceptions (Fogg *et al.*, 1985a, b) the majority of studies conducted on the

Irish Sea have looked at biological and the hydrographic components separately. Given the high interannual variability in the Irish Sea it would be difficult to draw reliable conclusions from existing sources (Cushing, 1980; Savidge & Kain, 1990; Williams *et al.*, 1994). Hence, the following analysis draws largely on the current study for a crude estimate of the carbon flux dynamics in the Menai Strait.

9.4.1 Phytoplankton

Phytoplankton daily production was derived from the equation of Gowen & Bloomfield (1996) which relates chlorophyll-a standing stocks to estimates of daily primary production measured in the Irish Sea with the ^{14}C technique. Using the Gowen & Bloomfield (1996) equation, the annual productivity of phytoplankton in the Menai Strait would correspond to 8300 mg-C m^{-3} yr^{-1} and 7300 mg-C m^{-3} yr^{-1} for 1996 and 1997 respectively. During their 1997 survey in the Liverpool Bay, Gowen *et al.* (2000) have calculated (also using the equation of Gowen & Bloomfield, 1996) an annual productivity of phytoplankton of 9100 mg-C m^{-3} yr^{-1}. On the other hand, the average annual gross primary production, estimated between 1992 and 1997 for the Menai Strait from measurements of oxygen consumption, would be 31400 mg-C m^{-3} yr^{-1} (Net primary production = 16035 mg-C m^{-3} yr^{-1}). The primary production estimates calculated in the present section do not include the dissolved (DOC) and particulate organic carbon (POC) which are likely to represent an energy source for bacteria and at least micro-planktonic organisms.

9.4.2 Bacteria

Bacterial numbers in the Menai Strait varies during the year from ~ 0.4 x 10^6 cells ml^{-1} in winter up to a maximum of 7 x 10^6 cells ml^{-1} in spring just after the decline of the spring phytoplankton bloom (Blight *et al.*, 1995; Rodriguez, 1997). The bacterial production estimated from the bacterial numbers and growth rates reported by Blight *et al.*, (1995) and Rodriguez (1997) for the Menai Strait, assuming 20 ftg-C $cell^{-1}$ (Ducklow & Carlson, 1992) varied from 2 mg-C m^{-3} day^{-1} in winter to 30 mg-C$m^{-3}day^{-1}$ in the spring. The bacterial production estimated for the Menai Strait shows a wider range than the 3-13 mg-C m^{-3} day^{-1} range reported for the central western Irish Sea by Turley & Lochte (1985) but are within the range of 0.7 -192 mg-C m^{-3} day^{-1} reported by Ducklow & Carlson, (1992) for temperate coastal waters. The total annual bacterial production estimated for the Menai Strait from data of Blight *et al.*, (1995) is ~ 4800

mg-C m^{-3} yr^{-1}. Bacterial carbon demand estimated from production rate and assuming a 25 % bacterial gross growth efficiency (Azam *et al.*, 1983; Del Giorgio & Cole. 2000) would correspond to ~19400 mg-C m^{-3} yr^{-1}. On the other hand, bacterial carbon demand estimated for the Menai Strait from their respiration rate, assuming a respiratory quotient of 1.3, would correspond to an annual value of ~24600 mg-C m^{-3} yr^{-1} (P. LeB. Williams, Pers. comm.). The fact that the bacterial carbon demand is comparable or may exceed the primary production calculated above, suggests that the DOC pool would need to be taken into account as a energy source to explain bacterial production in the Menai Strait.

9.4.3 Ciliates

The annual production of ciliates in the Menai Strait was estimated using an equation that predicts ciliate growth from individual size and temperature (Montagnes *et al.*, 1988). Biomass estimates were ~ 2.4 g-C m^{-3} yr^{-1} for both years whereas production estimates were 197 mg-C m^{-3} yr^{-1} in 1996 and 247 mg-C m^{-3} yr^{-1} in 1997 (Chapter 3).

Ingestion demand by ciliates estimated from their production assuming a gross growth efficiency of 30 % (Straile, 1997) was 657 mg-C m^{-3} yr^{-1} and 823 mg-C m^{-3} yr^{-1} for 1996 and 1997 respectively.

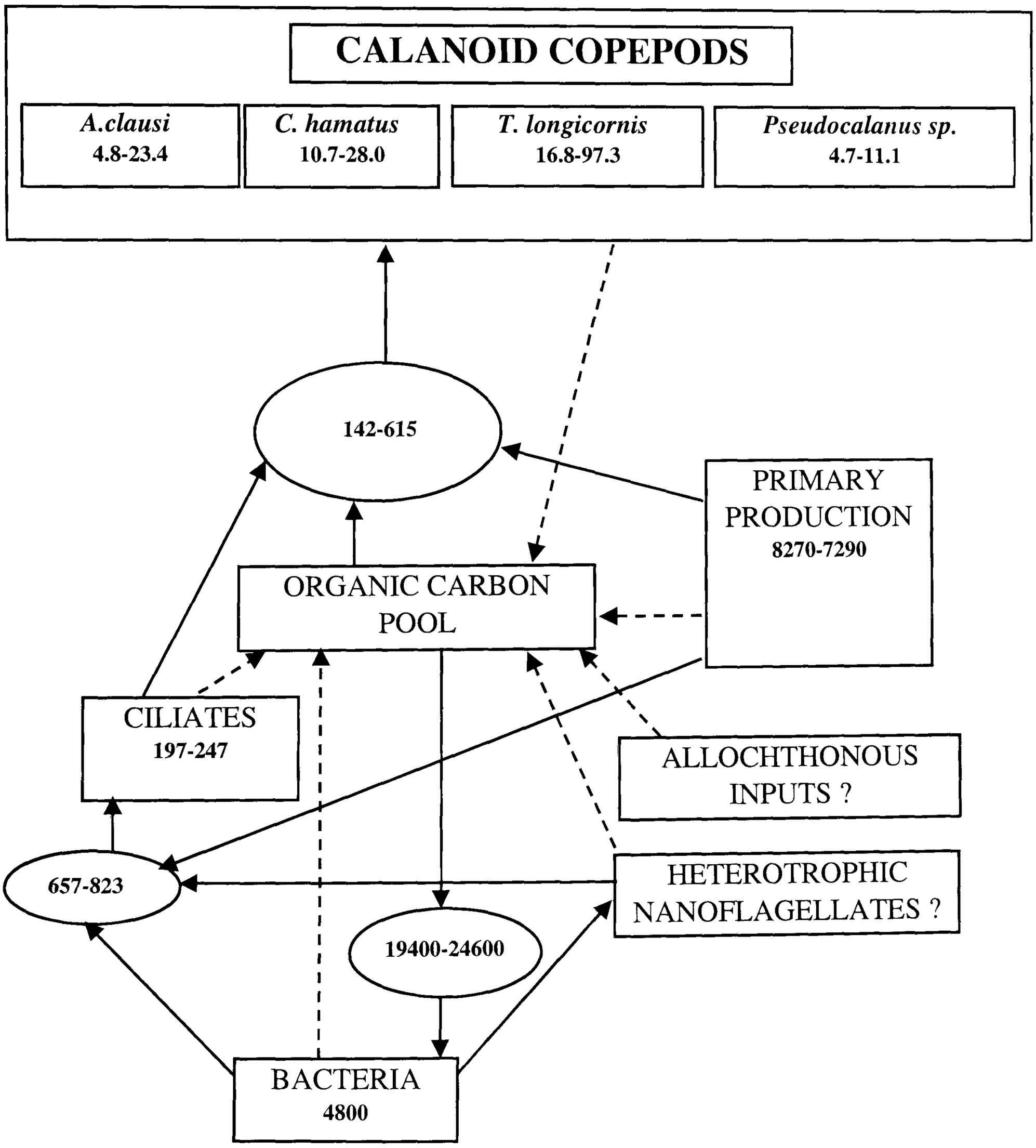
9.4.4 Copepods

The total annual copepod production estimated by the present investigation using the equation of Hirst & Lampitt, (1998) from measured standing stock (biomass, See Chapter 8) was ~ 37 mg-C m^{-3} yr^{-1} and ~ 160 mg-C m^{-3} yr^{-1} for 1996 and 1997 respectively. Annual ingestion demand estimated from copepod production assuming 26 % Gross Growth Efficiency (Straile, 1997) was ~ 142 mg-C m^{-3} yr^{-1} and ~ 615 mg-C m^{-3} yr^{-1} corresponding to ~ 1.7 % and ~ 8.4 % of the primary production for 1996 and 1997 respectively.

Figure 9.2 shows a carbon flow diagram based on the productivity estimates for the various ecosystem components measured in the present study. The ingested food sources for small calanoid copepods are likely to be algae > 10-20 μm (Dam & Peterson, 1991) which during the 1996-97 spring bloom represented between 20 % to 99 % of total phytoplankton carbon biomass (Chapter 3). Gowen *et al.*, (1999) estimated that during the 1997 spring phytoplankton bloom in the coastal western Irish Sea up to 56 % of daily production and 26 % of the total bloom production was grazed by

copepods. The phytoplankton timing, abundance and species composition during the 1997 spring bloom in the Menai Strait and Irish coast were very similar (See Chapter 3: Gowen *et al.*, 1999). Thus, using ingestion rates from Gowen *et al.*, (1999) for adults copepods (i.e. 12-112 ng-C ind.$^{-1}$ day^{-1}) and from Bautista & Harris, (1992) for juveniles (i.e. 14 ng-C ind.$^{-1}$ day^{-1}), the grazing impact on the primary production would correspond to a maximum of ~ 70 % per day and to ~ 13 % of the total phytoplankton production over the whole of the spring bloom.

Figure 9.2: Carbon flux through the biological community in the Menai Strait during 1996 and 1997. Values in the boxes are production estimates (mgC m^{-3}yr^{-1}), those in the ellipses are ingestion demands (mgC m^{-3} yr^{-1}). Solid arrows represent ingestion of carbon whereas dashed arrows represent movement to a non-living organic carbon 'pool'.



The grazing impact estimated in the present study is higher than the 1-5 % figures reported by Nicolajsen *et al.*, (1983), Joiris *et al.*, (1982) and Dagg *et al.*, (1982) indicating a tighter coupling between the phytoplankton and the copepods in these Welsh coastal waters.

Blight *et al.*, (1995) concluded, solely from the literature, that the mesozooplankton in the Menai Strait, would show no numerical increase during a phytoplankton bloom and, therefore, must have a small impact on primary production and on the flux of organic matter in this coastal area. Yet, in the Menai Strait as in the rest of the Irish Sea copepods reach their population maximum during the spring phytoplankton peak (see Fig. 9.1, Chapter 3 and Chapter 8).

In 1997 the highest value for the whole community respiration rate (DCR = 68.4 μmol O_2 $L^{-1}day^{-1}$, Bentley pers. comm.) was measured, in the Menai Strait, after no more than 6 days from the second peak of copepod abundance. Annual bacterial respiration in the Menai Strait averages ~ 49 % of the DCR reaching up to 70 % during the early phases of the *R. delicatula* and *Phaeocystis sp.* blooms (Blight *et al.*, 1995). The rapid 1997 spring increase in DCR together with estimated high grazing impact suggest that bacterial activity was fuelled by copepod grazing alongside any natural algal decay and exudation.

Lochte (1985) has observed that in the Irish Sea bacterial productivity was correlated to zooplankton abundances and concluded that the production of bacterial growth substrates via zooplankton grazing activity (through 'sloppy feeding') may be more important than substrate production from phytoplankton photosynthetic activity. Thus, the present investigation indicates that the mesozooplankton may have a larger contribution than previously thought (Blight *et al.*, 1995) to the "carbon flux" in the Menai Strait.

Ciliates were very abundant during the 1996 and 1997 spring bloom and chemical analysis of copepod gut content indicated ciliates and dinoflagellates to be a preferred food for the copepods in the Irish Sea (Kleppel *et al.*, 1991). It is possible that ciliates and dinoflagellates represented an important component in the copepod diet. The annual energy demand calculated for copepods living in the Menai Strait is, however, higher than the annual production estimated for the ciliates for both 1996 and 1997. During the 1997 spring bloom when the copepod population growth and biomass (14-50 μg-C L^{-1}) were highest, the standing stock of dinoflagellates was 8-46 μg-C L^{-1},

of diatoms 60-2200 μgC L^{-1}, of microflagellates 14-235 μg-C L^{-1} (figure for Liverpool Bay from Gowen *et al.*, 2000) and of ciliates 9-32 μg-C L^{-1}.

During the spring phytoplankton bloom, copepod standing stock carbon demand of 3-10 μg-C $L^{-1}day^{-1}$ for growth (from production assuming a 26 % gross growth efficiency) or even for basic maintenance of ~2 μg-C $L^{-1}day^{-1}$ (calculated from Eq. 7.1, Chapter 7) was higher than ciliate production of 0.6-2.5 μg-C $L^{-1}day^{-1}$. Since the ciliate standing stock increased over the period considered, it is clear that the copepod grazing impact on them was minimal.

Phaeocystis sp. is of a suitable size and abundance during the spring bloom for small copepods to eat. Nevertheless, Claustre *et al.*, (1990) have shown that it is not grazed to a great extent (<1.5 % d^{-1} of total *Phaeocystis sp.* biomass) by copepods in Liverpool Bay. Despite, lacking production estimates for many of the microplankton groups, biomass density alone suggests that the diatoms have the required biomass, hence, probably productivity to satisfy the energy demands of the copepods at least during their spring increase. Finally, since the estimated Ctenophore predation on copepods was low (1 % day^{-1} of the copepod standing stock, see Chapter 8) it is likely that most of the copepod production during spring would be potentially available for larval fish production.

The carbon flow consideration for the Menai Strait discussed in the present work must be regarded as crude estimations. The energy demand figures used in the present study were, in fact, not directly measured and the gross growth efficiency figures used for their estimation are known to vary widely (Straile, 1997).

Table 9.3 summarises and compares the annual production rates (mg-C $m^{-3}yr^{-1}$) of microbial and metazoan zooplankton calculated for the Menai Strait with those of other coastal areas. Although, phytoplankton production measured in the present study is comparable to or higher than many other locations, ciliate and copepod production were among the lowest reported (Table 9.3). In the Menai Strait, copepod production was proportional to copepod standing stock with maximum production occurring in spring. If the initial copepod population increase was set by the number of resting eggs hatching these must have also determined the differences between the 1996 and 1997 copepod standing stock and production measured during spring in the Menai Strait since primary production between years was comparable.

Table 9.3: Annual production rates (mg-C m^{-3} yr^{-1}) of microbial and metazoan zooplankton in different coastal areas.

Primary Production	Secondary Production			Site	Author
	Bacteria	Ciliates	Zooplankton		
8270-7290	4800	197- 247	37 -160	Menai Strait, eastern Irish Sea, UK	Present Study
4850	-	-	-	Irish Coast, western Irish Sea, U.K.	Gowen *et al.*, (2000)
6667	8300	2500	32	Calshot, Solent, U.K.	Hirst *et al.*, (1999)
8742	-	896	1589	Inland Sea of Japan	Uye & Shimazu, (1997)
10357	-	2036	429	Southern Kattegat, DK	Kiorboe & Nielsen, (1994) Nielsen & Kiorboe, (1994)
7998	1199	586	878	Lime Cay, Jamaica	Roff *et al.*, (1990)
12097	2419	132	176	Gulf of Maine, USA	Montagnes *et al.*, (1988)
38500	-	3300	4745	Narrangasett Bay, USA	Verity, (1987)

Note: Table adapted from Hirst *et al.*, (1999)

Low annual estimates of total copepod production of 37.7 mg-C m^{-3} yr^{-1} for Southampton water were partly attributed by Hirst *et al.*, (1999) to the high suspended sediment in the estuary. Although, coastal copepods may be better adapted to feed in turbid conditions, the inverse correlation shown in the present study between EPR in *T. longicornis* and tidal range suggests that copepod production might have been similarly limited by suspended sediment.

9.5 Plankton interannual variability and global climate

Inter-annual variation in weather patterns may have a strong influence on the productivity of fisheries via phytoplankton abundance and copepod egg production particularly for species such as cod, herring and sprat whose larval stages are heavily dependent on copepod nauplii and juveniles (Runge, 1988; Coombs *et al.*, 1992; Thompson & Harrop, 1991).

In 1997 the main mixed *Phaeocystis-Rhizosolenia* spring bloom in the Menai Strait occurred ~1 month earlier than in 1996. Similarly the copepod abundance maximum was coincident with the phytoplankton/ microplankton bloom (i.e. it too occurred 1 month later in 1996). Coincidentally the temperature recorded during winter 1996 was lower than in 1997. Similar observations for the Menai Strait were made by Blight *et al.*, (1995), Jones & Haq (1963) and (Haq, 1960) who suggested that the water temperature in early spring influenced the timing of the phytoplankton bloom and the magnitude of the *T. longicornis* and *C. hamatus* populations increase.

The measurements of water temperature made in the present study offer support for this contention, although, other factors such as detrital loading (Jones & Spencer, 1970; the present study) might have also played an important role in delaying the phytoplankton and the zooplankton increase. Since water temperature and suspended sediments in the Menai Strait are inversely related (Bucham *et al.*, 1967) a deterioration of the weather pattern in 1996 might have led, through the persistent increase of high sediment load in the water column, to the delay in the 1996 phytoplankton bloom. The delay in the 1996 spring bloom might have caused a delay in the zooplankton increase and possibly affected the production of the over-wintering female copepods since they were all producing eggs at a lower rate than in 1997 and 1998 (Chapter 4).

Hairston (1996) has advocated that increasing temperature resulting from climate change can affect resting egg banks. Temperature is, in fact, one of the most important cues stimulating the hatching of copepod resting eggs. For example, chilling

followed by warming resulted in synchronous hatching of resting eggs in *Eurytemora affinis* (Ban & Minoda, 1994) and in *Labidocera aestiva* (Marcus, 1980). Chen & Folt (1996) suggested that an increase in autumn water temperature may cue the eggs of the copepod *Epischura lacustris* to hatch at a maladaptive time of the year leading to the loss of the species from the lake. Thus, the lower winter temperature measured in 1996 might have delayed the hatching and possibly induced a lower number of resting eggs to hatch during spring resulting in the low population density measured.

It has already been mentioned in Chapter 3 that the temperature trend measured during the winter periods of 1996 to 1998 corresponded to an ongoing increasing trend in the NAO-index, which is considered an indicator of the weather pattern in the North Atlantic (Hurrel, 1995; Karl, 2000). Relationships between NAO-index and standing stock of *C. finmarchicus* has already been reported in long term studies even though the nature of this relationship is not fully understood (Backhaus *et al.*, 1994; Fromentin & Planque, 1996). The annual trend between EPR in *T. longicornis* and the NAO-index reported, in the present study, although based only on 3 data points is nevertheless consistent and indicative of a possible response of copepod production to changes in weather pattern.

9.6 Copepod species distribution in the Irish Sea

Williams *et al.*, (1994) have suggested that the diversity in copepod species composition is at the base of variation in the copepod productivity in different regions of the Irish Sea and other European shelf seas. In the pelagic realm, current spatial patterns in diversity are the result of evolutionary, biogeographic and more local abiotic, biotic and ecological factors (Angel, 1998). Over the last 40 years, a great deal of information on the spatial and temporal diversity of zooplankton has been acquired through the long-term use of the CPR particularly for the Northern Atlantic and the North Sea (Colebrook, 1984; Beaugrand *et al.*, 2000). The maps thus obtained have played a significant role in identifying potential factors responsible for observed pattern on a global scale although the mechanisms maintaining the diversity particularly at regional level remain unexplained (Beaugrand *et al.*, 2000).

The copepod species composition and timing of the spring population increase described for the Menai Strait is similar to that measured in the Irish coastal region and quite distinct from the central stratified region of the Irish Sea (Scrope-Howe & Jones, 1985; Williams *et al.*, 1994; Gowen *et al.*, 1998 and 1999, Table, 9.1).

Whereas the spring zooplankton increase in the western and eastern inshore waters is dominated mainly by *T. longicornis* the off-shore waters in the western Irish Sea are dominated by *Pseudocalanus sp* and *Calanus sp.* (Table 9.1, Williams *et al.*. 1994; Gowen *et al.*, 1998 and 1999). During winter and autumn *Pseudocalanus sp* is abundant in the Menai Strait but it virtually disappears during summer. *Pseudocalanus sp.* can reach higher numbers than *T. longicornis* in other coastal locations (e.g. English channel and Kattegat) in both spring and summer (Kiorboe & Nielsen, 1994; Bautista & Harris, 1992). Thus, it is possible that in the Menai Strait *Pseudocalanus sp.* during spring is out-competed by *T. longicornis* and *C. hamatus*. *Calanus sp.*, on the other hand, is never abundant in the Menai Strait or in the Liverpool Bay (Haq, 1960; Kenchington, 1968; Kendaris, 1974; Hydaiat, 1995; Gowen *et al.*, 2000).

The distribution and abundance of over-wintering stocks of planktonic organisms has been shown to be a critical factor influencing their overall distributions (Colebrook, 1982a) and seasonal population dynamics (Colebrook, 1982b) not to mention long-term variations in abundance (Colebrook, 1985). The rapid increase in abundance of *T. longicornis* and *C. hamatus* possibly as a result of winter hatching of resting eggs may be responsible for maintaining these copepod species in coastal waters while limiting the increase of *Pseudocalanus sp.*

Dominance of *Pseudocalanus sp.* and *Calanus sp.* occurs off-shore where these species may be able to cope better than other with low/patchy food (Dagg, 1977), can avoid high temperature undergoing vertical migration to cooler deeper waters and where coastal copepods resting eggs may not survive or may be cut-off from relevant environmental clues necessary for their hatching. Thus, both reproductive strategies and physiological characteristics of different copepod species and abiotic factors operating at regional scale (e.g. depths, currents, wind, temperature) are probably at the base of the observed difference in species distribution in the Irish Sea and elsewhere.

In the western Irish Sea first the majority of fish larvae are spawned in shallow (< 40 m) vertically mixed coastal regions during spring (Coombs *et al.*, 1992; Burkart *et al.*, 1995; Dickey-Collas *et al.*, 1996). Within this coastal region there is an early spring bloom of phytoplankton (Gowen *et al.*, 1995) and high zooplankton standing stock early in the year (Thompson & Harrop, 1991). In the western Irish Sea the importance of zooplankton living in coastal regions in supporting the early life stages of commercial species of fish is already well established (Brander & Symonds, 1984; Thompson & Harrop, 1991; Nichols *et al.*, 1993; Dickey-Collas *et al.*, 1996). According to Dickey-

Collas *et al.*, (1996) the early development of small copepods in coastal waters will support the first feeding larvae before they move off-shore as juveniles to start feeding on *Pseudocalanus sp.* and *Calanus sp.* which peak during summer in stratified waters. Thus, the timing and abundance of copepods in the coastal populations would represent the first crucial step for the recruitment of many commercially important fish species. To the knowledge of the present investigation, there is no published literature assessing the link between copepod and larval fish production in the eastern Irish Sea. Given the high standing stock of copepods early in the year, the importance in this coastal region for larval fish recruitment should deserve more attention in future studies.

9.7 Conclusions and limitation of the study

The present study has mainly focused on the eco-physiology of *T. longicornis*, the numerically dominant calanoid copepod species found in the North Wales coast. For the first time, seasonal changes of the biomass and production of *T. longicornis* and other main copepod species have been measured in the Menai Strait and used to give indications of the carbon flux through the planktonic food web. Despite being a simplified approximation, it is the first attempt to quantify annual secondary production and carbon flux in the Menai Strait and Irish Sea waters in general.

From the present study, it emerges that the standing stock and productivity in spring have high annual variability, possibly dependent on the effect of winter temperature (weather pattern) on the hatching of *T. longicornis* resting eggs.

The relatively high biomass, productivity and timing of the spring population increase indicate that the population dynamics of the copepods, particularly *T. longicornis* may be crucial for the survival of the larval fish spawned in the eastern Irish Sea in spring.

The following qualify some of the conclusions made above:

- Lack of hydrographic measurements including estimation of advection and currents during the study means that the populations measured in the Menai Strait may originate from elsewhere (e.g. transport of copepods from southern warmer areas).
- Measurement of copepod ingestion rates on natural microplankton assemblage and determination of prey size and type ingested in relation to EPR and egg hatching success limits estimates of carbon demand and preferred food type to literature sources.

- Lack of measurement of EPR of the other species of copepods living in the Menai Strait limits estimates of total copepod production and explanation of community structure
- Measurement of growth rate of juvenile copepods would be necessary to determine direct site specific production.
- Limited investigation on the viability of the non-hatching eggs. It is not known at the present if the non-hatching eggs were resting eggs.
- The use of a 270 μm mesh size net when larval sizes are smaller means that no direct estimates of recruitment are available.
- The use of a 270 μm mesh size also means that small copepod species like *Oithona sp.* where not included in the standing stock. Thus, both copepod standing stock and production must be considered underestimates.

9.8 Future research and recommendations

The study has highlighted the need for investigations in the following areas to be undertaken:

- Measurement of growth of juveniles copepods for site specific estimation of production
- Clarify the contribution of the various components of the microplankton (type, size, quality and concentration of suspended preys/particles) to the diet of the different copepod species.
- Investigate the reproductive physiology of copepods, particularly in winter conditions, in relation to body fat content, feeding rates and food sources and gonad development.
- Discover the fate of eggs which do not hatch in phytoplankton bloom conditions
- Investigate the importance in annual variation of small coastal copepod biomass to production of larval fish
- Assess larval fish abundance and feeding preferences

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