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The ecology of Euspira pulchellus (Gastropoda: Naticidae)

Kingsley-Smith, Peter

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The Ecology of *Euspira pulchellus*

(Gastropoda: Naticidae)

Peter Kingsley-Smith

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School of Ocean Sciences,
University of Wales Bangor

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Summary

Euspira pulchellus is patchily distributed subtidally on muddy sand with significantly higher densities of individuals during summer (700 ha^{-1} May to August 2001) than winter (225 ha^{-1} November 200 to February 2001). Recruitment of *Euspira pulchellus* occurred over an extended period. Egg collar production in the laboratory occurred in females > 8-9.9 mm and was greatest during July and August. Largest individuals (14-15.9 mm) were most fecund despite ceasing egg collar production in late September. Smaller individuals (8-13.9 mm) laid egg collars until November. Small individuals (4-5.9 mm) grew rapidly during summer (April to September) whilst snails > 9 mm grew slowly. Egg collar wet weight was significantly correlated with the number of larvae released ($r = 0.932$, $p < 0.001$). Larvae metamorphosed 6-7 weeks after hatching (19-20° C) when exposed to muddy sand. Juveniles started drilling within 3 days of metamorphosis. Snails were size-selective in their choice of cockles and were cannibalistic. Inner and outer drill hole diameters were significantly ($p < 0.001$) correlated ($r = 0.899$ and 0.923 respectively) with shell length. Snails drilled cockles in the centre of the shell valve, with no preference for the left or right valve. Feeding rates were highest in July (14.57 cockles $snail^{-1}$ $month^{-1}$) and lowest in March (3.58 cockles $snail^{-1}$ $month^{-1}$) and like growth rates were related to seawater temperature. Statolith diameter and shell length were closely related ($R^2 = 0.972$). The larval statolith, settlement ring, first and second annual rings, and weaker rings were observed within the adult statolith. Variation in settlement ring and first ring diameters may reflect time of settlement and consequently time available for growth in the first year. First and second ring diameters were significantly correlated ($r = 0.844$, $p < 0.001$). Estimates of shell length from first and second ring diameters suggest that the prominent statolith rings are formed annually.

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Fig. 3a. Percentage frequency distribution of the shell lengths of *Euspira pulchellus*. estimated at the time of the deposition of the first prominent ring.

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Fig. 4. Relationship between the diameter of a) the first and second prominent rings and b) the settlement and first prominent rings.

Chapter 1

General Introduction

Drilling of prey species occurs in at least ten taxa, nine marine and one terrestrial, and therefore represents a taxonomically diverse and successful method of predation (see Kabat, 1990 for review). The mesogastropod families Capulidae, specialized ectoparasitic symbionts of molluscs and echinoderms, and Cassidae, specialist predators of tropical echinoids (Hughes and Hughes, 1981), penetrate the shells of their prey. The nudibranch *Okadala elegans* (Family Vayssiereidae) is also known to drill holes, in the calcareous tubes of spirorbid and serpulid worms (Carriker *et al.*, 1969, Kabat, 1990). *Octopus* spp. drill holes in the hard exoskeleton of their prey and drilling has also been reported for certain nematodes, an unusual polyclad turbellarian flatworm that feeds on oyster spat (Kabat, 1990), and the marine cottid fish, *Asemichthys taylori*, that predates gastropods (Norton, 1988). Shell drilling predation has also been reported amongst terrestrial molluscs, examples of which can be found within the pulmonate genus *Aegopinella,* species of which predate other gastropods (Mordan, 1977). In the marine environment, however, the dominant group of animals that predate organisms enclosed within calcified shells and tubes by drilling, is the prosobranch gastropods. The most studied are those within the families Muricidae and Naticidae (Morton and Chan, 1997).

Examples of drilling gastropods within the Muricidae include the dogwhelk, *Nucella lapillus*, the rough tingle *Ocenebra erinacea* and the oyster drill, *Urosalpinx cinerea* (Fretter and Graham, 1994). There are, however, indications that the drilling of prey by prosobranch gastropods may be more widespread than previously thought. Three publications briefly mention the occurrence of shell-drilling amongst the Nassariidae (Fischer, 1962, Reyment, 1966, Ilina, 1987), a family that contains herbivorous, carnivorous and scavenging members of the Neogastropoda. Whilst these three studies lack confirmative evidence, Morton and Chan (1997) claim to provide the first evidence, obtained somewhat serendipitously, of shell-drilling by a member of this family, in the species *Nassarius festivus* from Hong Kong. Newly settled individuals were left unfed over a holiday period of five days, after which eight individuals were found to have died. Upon examination, single drill holes were discovered on the ventral surfaces of the main body whorls. As adult nassariids have never been shown to drill their prey, the authors were unsure as to whether this observation represented a potential predation strategy for the adult whelk, or a post-larval behaviour that frees juveniles from competition with larger adults for carrion.

Both naticids and muricids species leave a permanent record of their predation in the valves of their prey in the form of characteristic drill holes (Carriker, 1981). Estimating the predatory impacts of other gastropod families tends to be more difficult. The two buccinid species *Cominella eburnea* and *C. tasmanica* from Western Australia are capable of drilling the venerid bivalve *Katelysia scalarina* (Peterson and Black, 1995). The drill holes of these two species, however, are indistinguishable from those of the muricid *Bedeva paivae* also found in the area. These *Cominella* species are believed to contribute considerably to the high mortality of *Katelysia* spp. that is attributable to drilling gastropods in the lagoonal systems of southwest Australia. It should be noted, however, that drilling of *Katelysia* spp. by *Cominella* spp. appears to be restricted to smaller, thinner-shelled individuals (Peterson and Black, 1995). The family Marginellidae, specifically members of the genus *Austroginella,* also includes species that drill animals enclosed within shells (Ponder and Taylor, 1992). The discovery of gastropod families previously not known to include species that drill holes in their prey generates the possibility of ascribing the predation of both fossil and Recent drilled prey to gastropod families thus far less extensively studied than the Muricidae and Naticidae.

Populations of drilling gastropods have been found in every coastal region of the world that has been examined (Carriker, 1981). Species are, however, predominantly found in subtropical and tropical areas, as diversity increases towards the equator (Taylor *et al.*, 1980). The distribution of drilled shells indicates that drilling gastropods occur from the intertidal down to a depth of 2700m (Carriker, 1961) but are less abundant at greater depths (Taylor *et al.*, 1980). The greatest abundance of muricid and naticid drilling gastropods occurs in the shallow waters around continents at tropical latitudes (Carriker, 1961, Taylor *et al.*, 1980). Since drilling gastropods have yet to be found in freshwater, and are less abundant in deeper water, it has been proposed that the drilling habit evolved in the shallow, tropical waters in which these animals are most abundant (Carriker, 1961, Taylor *et al.*, 1980). Naticids formed an abundant, though not diverse, part of the Jurassic and Lower Cretaceous fauna yet drilled shells of their bivalve prey are not commonly encountered in fossil strata from this time. The abundance of drilled shells increases greatly in late Cretaceous rocks and even more so in those from the early Tertiary period, coincident with the major diversification of the primary groups of extant drilling gastropods.

Since the late Cretaceous, drill holes have been found in the fossil shells of a diverse range of taxa including the Foraminifera, Brachiopoda, Gastropoda, Pelecypoda, spirorbid polychaetes, echinoids and ostracods (Sohl, 1969). A drilling habit in the Naticidae is likely to have evolved during the late Cretaceous, prior to which, during the Jurassic and Lower Cretaceous, naticids fed by some other means. The marine Mesozoic revolution, which included the Cretaceous radiation of the Naticidae, witnessed an increase in shelled prey and the evolution of a diverse range of predators capable of predating upon them (Vermeij, 1977, Benton, 1986). These predators included teleost fish, decapod crustaceans and drilling gastropods which gave rise to the diverse range of modern marine predators that are seen today. Drill holes characteristic of those left by naticid gastropods have been recorded in bivalve shells from the Triassic some 220 million years ago (Fürsich and Jablonski, 1984). The strength of the affinity between the gastropods responsible for these drill holes and Recent naticids, however, is uncertain (Sohl, 1969). The current view remains that the drilling habit of Recent gastropods arose in the Polinicinae during the Upper Cretaceous around 100 million years ago (Carriker and Yochelson, 1968, Sohl, 1969). Verification of a more ancient evolution of the drilling habit in naticid gastropods relies upon the discovery of fossilized naticid gastropods, sufficiently similar to those found today, both in appearance and the nature of their drilling, within geological strata from equivalent localities and time periods.

Drilling represents a rare case of predation which can be recognized after death, and is therefore preserved in the fossil record. Changes in the co-evolutionary relationships between naticid predators and their prey over millions of years can therefore be investigated (DeAngelis *et al.*, 1985). The overall strategy of naticid predation appears to have changed relatively little since the Upper Cretaceous period (Kitchell, 1987), with the same preferences for particular shell valves and drilling positions from the Cretaceous and Tertiary periods persisting in Recent shell assemblages (Sohl, 1969). Some alternative methods of prey entry to drilling may represent advancements in naticid predation techniques. Included in these is 'edge-boring', as opposed to more conventional 'side-boring', in which prey are drilled through the commissure of the valve margins (Taylor, 1980, Vermeij, 1980, Ansell and Morton, 1985). 'Edge-boring' is thought to be restricted to the predation of thick-shelled or heavily sculptured prey species by tropical species of *Polinices*. Ansell and Morton

(1987) reported the consumption of prey by *Polinices tumidus* without drilling; prey were suffocated following their envelopment in mucus by the predator. *P. tumidus* is capable, therefore, of three separate methods of predation; conventional 'side-boring' through prey valves, 'edge-boring' through the commissure, and non-boring predation by suffocation (Ansell and Morton, 1987). Drilling constitutes a high proportion of total handling time (Kitchell *et al.*, 1981, Hughes, 1985) such that methods of entry that do not involve time-consuming drilling may be highly advantageous. Colder water species seem to be more conventional in their predatory behaviour and normally drill the shells of their prey in a manner characteristic of naticids (Kitchell *et al.*, 1986).

Naticid gastropods are regular members of infaunal invertebrate communities at all latitudes (Taylor and Taylor, 1977) and are specialist predators of shelled prey, most commonly bivalve species. The diets of naticids comprise over 80 families of gastropods and bivalves, mainly restricted to those taxa inhabiting soft substrata, in particular *Donax*, *Tellina*, *Macoma* and *Mactra*, but also *Mya*, *Abra*, *Spisula*, *Chamelea* and *Nucula* (Piéron, 1933, Ziegelmeier, 1954, Fretter and Graham, 1994). Naticids are reported to prefer bivalve species with thinner shells, but also those with a permanent gape (Fretter and Graham, 1994). Ansell (1960) reported that *Lunatia alderi* and *L. catena* feed primarily upon bivalves, particularly those within the family Tellinidae, whilst Giglioli (1949) recorded the drilling of other gastropods by naticids, as well as cannibalistic activity. There are even reports of naticid species penetrating the cases of skate eggs (Jensen, 1951). Naticids are, however, generally less catholic in their diet than muricids, feeding primarily upon live infaunal bivalve and gastropod prey, whilst muricids also predate barnacles, small crabs, encrusting bryozoans and fish carrion (Kabat, 1990). The dogwhelk, *Nucella lapillus*, feeds mainly on mussels (Hughes and Dunkin, 1984) and limpets by drilling, and on barnacles, which some of the time it drills, but on other occasions predates by prising apart the plates (Dunkin and Hughes, 1984, Hughes, 1986).

Naticid gastropods are characterized by an extremely large and broad foot relative to the size of their shell. The foot is employed both in locomotion and in the capture, subjugation and manipulation of prey. The foot is thought to be distended by the uptake of seawater through pores, into internal spaces (Fretter and Graham, 1994), which is subsequently expelled from the foot tissue upon its retraction. The large foot of naticids permits rapid locomotion over soft substratum and is also used as a plough for burrowing. The latter is an extremely costly process requiring an estimated ten-fold increase in energy expenditure compared to crawling over the sediment surface (Trueman and Brown, 1976). The cost of entering the substratum is in the main due to the relatively large shell present in naticids (Trueman and Brown, 1989). A large aperture and foot has allowed the development of powerful muscles that assist in pulling the animal through the sediment when it is submerged. Muscular locomotor waves are generally not seen in groups of gastropods living on soft, mobile substrata as these habitats do not permit sufficient purchase for locomotion by this means. Members of the Naticidae, Tonnidae, Cassidae and a variety of neogastropods, in particular those in the families Nassariidae, Olividae and Conidae, exhibit locomotion that depends in most cases either largely or solely upon ciliary activity (Miller, 1974).

Naticids possess a well-developed gill which is housed within a large and effectively isolated mantle cavity. During locomotion, the front part of the foot, referred to as the propodium, is extended and reflected anteriorly over the shell, thereby regulating the pallial stream and preventing all but the smallest particles entering the mantle cavity. An extension of the opercular lobe of the metapodium is raised over the posterior part of the shell, concealing the operculum. Due to these extensions of the foot, the shell is virtually hidden during locomotion. During the process of prey capture naticids 'pick up' the prey using the propodium and secrete large quantities of mucus that reduces the likelihood of the prey escaping. Once the prey has been captured it is transferred to a posterior region of the foot and towed beneath the sediment until the predator comes to rest. The prey is then brought forward such that the apex of the prey lies at the anterior end of the propodium ready for drilling (Fretter and Graham, 1994).

Early controversy surrounded the precise nature of the drilling process, specifically in resolving whether it was entirely mechanical or involved a chemical component. Carriker and Williams (1978) hypothesised that naticids employ a combination of enzymes, including carbonic anhydrase, an inorganic acid, possibly hydrochloric acid, and possibly chelating agents, for the chemical dissolution of the prey shell. Carriker (1981) finally clarified that both muricids and naticids drill by a combination of chemical and mechanical means. The drilling mechanism of predatory gastropods is a time-consuming process that involves the alternate application of the radula and the accessory boring organ (ABO) to the shell surface (Carriker and Williams, 1978, Carriker, 1981, Palmer, 1982, Kabat, 1990). Connell (1970) stated that the drilling process can take up to 70% of the feeding period, which itself may comprise up to 99% of the total foraging time in thaidid gastropods (Menge, 1974). All 33 naticid and muricid species and subspecies studied by Carriker (1961) possess an ABO. In the Naticidae, the ABO is situated on the anterior ventral tip of the proboscis, whilst in the Muricidae it lies in a pit in the sole of the foot (Carriker, 1981). ABOs are essential to the process of drilling; this is clearly shown by the excision of the ABO from the muricid *Urosalpinx cinerea* which leaves the animal unable to drill until the ABO has been regenerated (Carriker and van Zandt, 1972). The ABO is thought to have evolved independently in the Muricidae and Naticidae (Morton and Chan, 1997) representing a case of convergent evolution, that has no known homologues in other taxa (Kabat, 1990). The evolution of the proboscis and the ABO must have opened up a broad range of prey species that would previously have been inaccessible to drilling gastropods. Taylor *et al.* (1980) proposed a hypothetical scenario for the evolution of the shell-drilling habit, starting from proboscis probing, supplemented by manipulation by the foot, leading eventually to a variety of methods of shell penetration, including drilling, chipping and pedal suffocation. Earlier stages were effectively pre-adaptations to drilling. The evolution of the proboscis and ABO, in addition to the regeneration of these organs following their damage or removal (Carriker and van Zandt, 1972) have been largely responsible for the ubiquity and survival of the muricid and naticid gastropods over geological time.

The radulae of naticids and muricids are long slender structures with only a few interlocking teeth in each transverse row. The wear resulting from drilling activity is countered by the continuous formation of new teeth within the radular sac that ensures a supply of sharp teeth for successive periods of drilling (Isarankura and Runham, 1968). During drilling, the prey is held by the propodium, the mid-anterior region of which retracts deeply to form a fleshy tube with a groove into which the proboscis is everted from the cephalic haemocoel. The proboscis becomes engorged causing the eversion of the radula and ABO (Kabat, 1990). The tips of the propodium curve dorsally, ensuring a firm grip on the prey (Fretter and Graham, 1994). The proboscis is rotated in 90° sectors to the right or left and applied to the shell surface. As radular strokes progress from the outside to the inside of the hole, the proboscis untwists. The centre of the drill hole receives the least efficient rasping by the radula resulting in a characteristic boss in the centre of an incomplete naticid drill hole (Ziegelmeier, 1954, Carriker, 1981). Periods of radular rasping are interspersed with periods during which the ABO is in contact with the drill hole. Chemical secretions from the ABO partially dissolve the inter-crystalline matrix of the shell and the radula scrapes away the exposed crystals. Once the drill hole is complete, and penetration through the shell is possible, the proboscis is inserted into the hole and the radula drags out the soft tissues that are severed by a set of jaws (Fretter and Graham, 1994). Ziegelmeier (1954) gave a detailed account of the shell-penetration process by *Lunatia nitida*. Direct observation of naticid feeding behaviour is, however, made difficult by the envelopment of the prey within the foot of the predator, and its occurrence when both the predator and the prey are buried within the sediment (Fretter and Graham, 1994).

Naticid drill holes are countersunk, truncated, spherical paraboloids, which is to say that the enlarged outer margin is bevelled or tapered (Benton, 1986). In contrast, muricid drill holes tend to be cylindrical with straight rather than bevelled edges, and may also be more variable in vertical section (Carriker and Yochelson, 1968). Both types of drill hole are generally circular and perpendicular to the shell surface. It is valuable to be able to distinguish between mortality caused by the drilling of muricids and naticids, the two major drilling groups of prosobranch molluscs (Kabat, 1990).

Five species of naticid gastropod are found around the coast of Britain. *Euspira pallida* is a circumpolar species and reports of this species around the British Isles are scarce, and in the main restricted to northern latitudes. *Euspira pallida* lives on clay sediments from 10m down to 2000m. *Polinices fuscus* is a southern species that ranges from the Mediterranean to the British Isles, where it has been found from the western parts of the Channel along Irish and Scottish coasts. *Polinices fuscus* lives sublittorally on muddy sand, is reportedly only common off the west coast of Ireland, and is absent from the North Sea. Most reports of *Polinices montagui* around the British Isles are from northern areas but is also known to occur off the coast of Northern Ireland, in the Celtic Sea and south to the Mediterranean (Graham, 1988). *Polinices montagui* is reported to preferring finer sediments than *Euspira catena* and *E. pulchellus*, and is only obtained by dredging soft bottoms at 15 to 200m (Graham, 1988). Compared to the other three species, *Euspira catena* and *Euspira pulchellus* are reportedly common around the coast of Britain on sandy substrates in shallow inshore waters, occurring both intertidally and subtidally (Hayward *et al.,* 1995). Ansell (1982) collected *P. alderi* (= *E. pulchellus)* near the low water mark at low tide from a population at Gullane beach on the south shore of the Firth of Forth.

Euspira pulchellus and *Euspira catena* were the only two naticid gastropods collected around the Anglesey coast during this study, and on no occasion were found to occur intertidally. Hayward *et al.* (1995) use the names *Polinices polianus* and *Polinices catenus* respectively for these two species, whilst Howson and Picton (1997) referred to these species as *Polinices pulchellus* and *Euspira catena* respectively, placing both of these species in the subfamily Polinicinae. The synonyms of *Polinices pulchellus* listed by Howson and Picton (1997) included *Polinices polianus, Euspira poliana, Lunatia alderi, Lunatia poliana, Lunatia pulchella* and *Natica alderi. Euspira catena* is listed as synonymous with *Lunatia catena, Natica catena* and *Polinices catena.* Unravelling the taxonomy of the Naticidae is complex due in no small part to the number of different genera that have been applied to a relatively small number of species. For a full review of the taxonomy of the Naticidae see Kabat (1991). Kabat (pers. comm.) states that *Polinices* is almost exclusively a tropical genus that rarely enters warm temperate waters whereas *Euspira* comprises an assemblage of cold-temperate and arctic species that were formerly placed within the genus *Polinices.* Some of the species currently placed within the genus *Euspira* may therefore be moved following further study. A problem arises with the generic placement of certain naticid species due to the fact that the type species of both *Lunatia* and *Euspira* are fossil species. Often a species is placed within a genus solely on the basis of the similarity of its shell to the type species. Kabat (pers. comm.) states that concluding that species from two locations are conspecific based upon shell descriptions alone is unsatisfactory without additional comparisons made from live or at least well-preserved specimens. Kabat (pers. comm.) therefore raised the question of whether the naticid species from the Mediterranean referred to both as *poliana* and *pulchella* is indeed conspecific with the species from Scandinavia, Britain and Northern France that has variously been called *poliana, pulchella* and *alderi.* A lack of taxonomic clarity here is highlighted by Ansell (1982), in which the author refers to his study as the "feeding, growth and reproduction in *Polinices alderi* from Scottish waters......while work on the Mediterranean species at Marseille is being described elsewhere (Macé, 1981a, b, c)" implying that this species may be different, despite the fact that Macé named the species as *Polinices alderi* in the title. Regrettably, no light can be shed on this conundrum by the present study as no collections from the Mediterranean were made. Based on the recommendation of Alan Kabat, in reference to work carried out as part of this thesis, the names *Euspira pulchellus* and *Euspira catena* will be used. When referring to work carried out elsewhere, however, the scientific names used in the original papers will be retained. For this reason the synonyms for these species have been listed above.

In this thesis, the findings from a wide ranging investigation into the ecology and biology of *Euspira pulchellus* are presented. Chapter 1 has introduced the subject through an extensive review of the literature. In Chapter 2, the subtidal distribution and population structure of this species within Red Wharf Bay are presented. The results of long-term monitoring of egg collar production in the laboratory and the effects of parental size and temperature on this process are documented in Chapter 3, whilst the growth, development and metamorphosis of the veliger larvae released from egg collars are described and presented photographically in Chapter 4. The feeding behaviour, including prey size selection, seasonal rates of consumption and growth, and determination of prey signature parameters are investigated in Chapter 5. In Chapter 6, an innovative method of investigating shell growth rates is presented, wherein the statoliths of *E. pulchellus* are used to interpret the age and growth of this species from the larval stage through to the adult. Finally, the results from all the chapters are drawn together and discussed in Chapter 7.

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Chapter 2

Distribution and population structure

INTRODUCTION

The importance of predation in structuring rocky intertidal communities has been well documented (Paine, 1966, Connell, 1970, Menge, 1976). Thaidid snails, for example, have been shown to be important in controlling intertidal prey populations under certain tidal regimes and exposure conditions (see Menge *et al.*, 1994 for review). In comparison, the role of predation in structuring soft sediment habitats has received less attention. Ambrose (1991) stated that "...the effect of predation by infauna on infaunal populations has barely been investigated." This bias towards hard substratum communities, however, has begun to change, in response to an increased interest in the role of predation as a structuring influence in soft sediment communities (Ambrose, 1991). Most of the work investigating the effects of predators on the structure of these communities has concentrated on large, conspicuous epibenthic predators (see Peterson, 1979 for review). Infaunal predators, in contrast, are generally smaller and less conspicuous. Their ecological role, therefore, has perhaps been assumed to be less important and has consequently received less attention. Naticid gastropods have frequently been overlooked as important predators in comparison with more obvious groups such as fish, crabs and starfish (Commito and Ambrose, 1985). Naticids are the only British mesogastropods that are restricted in their distribution to large sandy bays (Fretter and Graham, 1994), in which they are predators of a wide range of subtidal bivalve species. Naticids also have an ecological influence through the provision of vacant shells following their death which can be inhabited by small hermit crabs.

At the start of the present study, no data were available on the distribution of either *Euspira pulchellus* or *Euspira catena* in Red Wharf Bay, Anglesey. Hayward *et al.* (1995) reported that *E. pulchellus* occurs on sand and gravel bottoms and that *E. catena* can be found on sand. A lack of information on the fine-scale distribution of seabed sediment types in Red Wharf Bay, however, made the initial location of a sampling area for either of these species, based upon their association with particular sediment types, difficult. The aims of this chapter, therefore, were i) to identify a population of naticid gastropods around the coast of Anglesey that could be regularly sampled ii) to study the spatial distribution of individuals within that population iii) to investigate the size-frequency distribution of individuals within the population iv) to determine how (ii) and (iii) change seasonally, and finally v) based upon the appearance of small individuals in the population, to study the pattern of recruitment of *E. pulchellus* into the population.

MATERIALS AND METHODS

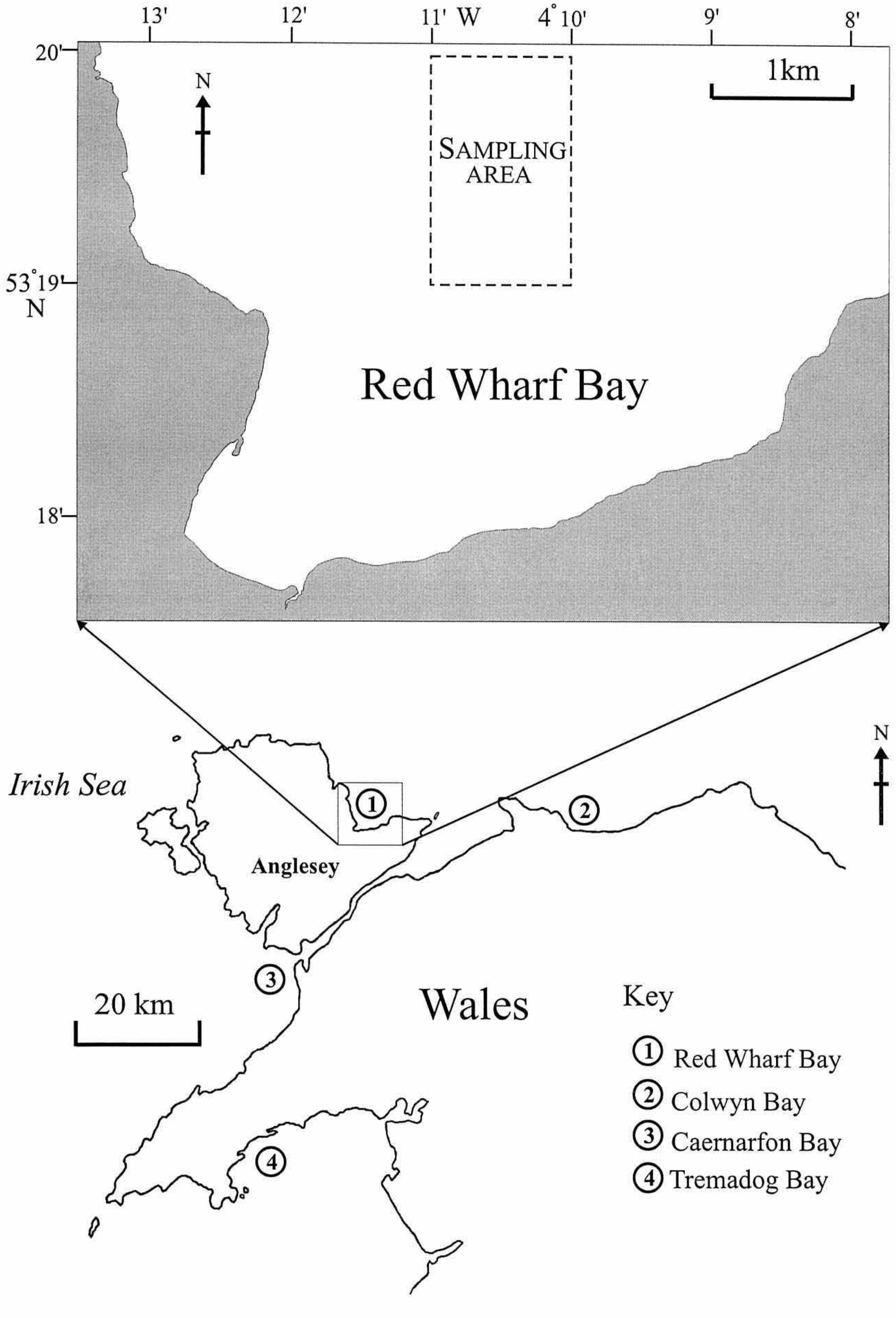
The initial sampling trips investigated the occurrence of *Euspira catena* and *E. pulchellus* within a sampling area previously used to study *Astropecten irregularis* (Freeman, 1999). The work of Freeman (1999) revealed the presence of naticid gastropod species within the stomach of *A. irregularis*, supporting the earlier findings of Christensen (1970). Naticids were collected from Red Wharf Bay, progressing in a westerly direction from the *Astropecten irregularis* study site established by Freeman (1999) using beam trawling. Additional sampling trips were also made initially, on single occasions, to Colwyn Bay, Tremadog Bay and Caernarfon Bay (Figure 1). From March 2000 onwards Red Wharf Bay was the only location that was visited for sampling. Each month samples were obtained using a standard 2 m beam trawl, fitted with three sizes of polypropylene mesh. The first section of the net comprised 10 mm diameter mesh, that led to a 3 mm diameter mesh cod end. An outer sheet of 45 mm diameter mesh protected the net as it was towed over the seabed. A chain of 60 mm steel links was attached across the beam itself, increasing the depth of sediment that was sampled. The beam trawl was towed at between 1 and 1.5 knots behind a Cheverton workboat. Global Positioning System (GPS) co-ordinates were recorded at the start and end of each trawl from readings given by a Raytheon Raystar 90 GPS Navigator. Bathymetric data were collected using an onboard Incastec Echopilot Classic Plus echo-sounder at the start of each trawl. The period of trawling varied (5-10 min) depending upon how effectively the beam trawl dug into the seabed, how quickly the cod end filled with material, the nature of the sediment, and the state of the flood or ebb tide. A hydraulic winch was used to lift the beam trawl to the side of the boat, from where it was manually lifted into the boat, limiting the size of catch that could be handled. When naticids were collected the co-ordinates of the trawls were used as references points for subsequent sampling trips. Trawl contents were transferred directly from the net into a large, grey plastic fish tub and hand-sorted at the side of the boat using 2 mm nylon mesh sieves. All naticids were removed and stored in seawater for further study. On returning to the laboratory, the shell length (tip of the spire to the base of the aperture at the lip of the shell), of each *E. pulchellus* and *E. catena* was measured (to nearest 0.1 mm) using vernier callipers. The number of individuals of each naticid species caught in each trawl was also recorded. The data presented for April and August 2001 represents the combination of two separate sampling trips taken in both of these months.

From the longitude and latitude data recorded using GPS, the distance covered by each trawl (assuming that trawls were made in straight lines) was calculated and used to calculate the area of the seabed sampled. Using these data, together with the numbers of individuals caught, the densities of snails per hectare of seabed trawled were calculated. For the *E. pulchellus* data only, size-frequency histograms were plotted for each monthly sample and the method of Bhattacharya (1967) was used to identify the different cohorts present within the population each month (as explained in the results section, insufficient numbers of *E. catena* were caught to carry out this analysis for both species). The method of Bhattacharya (1967) identifies the modal size classes within a frequency distribution and calculates the mean and standard deviation of each normal distribution identified as a separate cohort. The means were then plotted over time in order to represent the growth of the cohorts and to provide information on the time of year at which recruitment to the population occurred.

RESULTS

Beam trawl samples collected from the study area where the burrowing starfish *Astropecten irregularis* had been previously collected (Freeman, 1999) contained few naticids and therefore the area was considered an unsuitable sampling location for the present study. Sampling trips to locate populations of naticid gastropods within Colwyn Bay, Tremadog Bay and Caernarfon Bay yielded no *E. pulchellus* and only a single specimen of *E. catena* and these sites were not investigated further. By March 2000, an area of Red Wharf Bay, equivalent to 2 km^2, within the boundaries 53°19.000'N and 53°20.000'N latitude and 04°10.000'W and 04°11.000'W (Figure 1), had been identified from which *E. pulchellus* could regularly be collected.

Figure 1. Beam trawling sites around the coast of North Wales and (inset) the sampling area within Red Wharf Bay from which *Euspira pulchellus* were regularly collected during the period March 2000 to October 2001.


13'
12'
11' W
4° 10'
9'
8'
20'
53°19'
N
18'
N
SAMPLING
AREA
1km
Red Wharf Bay
Irish Sea
Anglesey
①
②
③
④
N
20 km
Wales
Key
① Red Wharf Bay
② Colwyn Bay
③ Caernarfon Bay
④ Tremadog Bay

Euspira pulchellus and *E. catena* were the only naticid species ever collected around the coast of Anglesey. The two species of *Euspira* were clearly distinguishable from each other at all sizes collected, based upon the descriptions of Hayward *et al.* (1995). The size ranges of individuals caught were markedly different for *E. pulchellus* and *E. catena*, (Figure 2). *Euspira pulchellus* ranged from 3.2 mm to 16.2 mm in shell length, whilst *E. catena* were generally caught at a larger size than *E. pulchellus*, ranging from 10.3 mm to 31.1 mm in shell length. *Euspira pulchellus* were most frequently caught at a size of 12-13.9 mm (47.2%), whilst *E. catena* were collected in approximately equal proportions at sizes ranging from 14 mm to 22 mm (Figure 2). Hayward *et al.* (1995) stated that the maximum sizes reached by *E. pulchellus* and *E. catena* are 16 x 14 mm and 30 x 30 mm respectively (shell length x shell width), which closely match the findings of the present study. The seawater depth at the start of trawls yielding *E. pulchellus* ranged between 4 m and 17 m (Figure 3a), with a mean of 8.46 m ± 0.40 (95% C.I intervals of the mean, n = 135). The number of samples collected in a particular month varied between 6 and 22 trawls (Figure 3b) due to weather conditions affecting the length of time that the boat was at sea. The number of trawls for which densities could be calculated varied due to the occasional loss of a reliable GPS signal. Figure 3b shows the number of trawls that were 'successful', in that they yielded *E. pulchellus,* or 'unsuccessful', in that they did not. Trawling was particularly 'successful' during the summer months of May to July 2001 during which all trawls contained *E. pulchellus*. Nevertheless, even late in the study (August and September 2001) some trawls yielded no *E. pulchellus*.

During sampling trips to Red Wharf Bay, it was observed that the sediment varied considerably over short distances in its relative proportions of silt, mud and sand. After extensive trawling it became clear that *E. catena* occurred more frequently in areas of clean sand, as determined by the associated fauna and presence of sediment either in the net itself or on the skids of the beam trawl. In contrast, *E. pulchellus* were generally absent or only present in low numbers on such ground, but occurred in much greater numbers in areas of muddy sand, where *E. catena* were usually absent. The maximum number of *E. catena* caught in a trawl was 10. On most occasions (41.98%) when *E. catena* was present, however, it was caught singly. In contrast, the maximum number of *E. pulchellus* collected in a single trawl was 213. *Euspira pulchellus* was the only naticid species that could be collected in sufficient numbers to

Figure 2. Size-frequency distributions of the naticid gastropods *Euspira pulchellus* and *Euspira catena* collected from Red Wharf Bay.

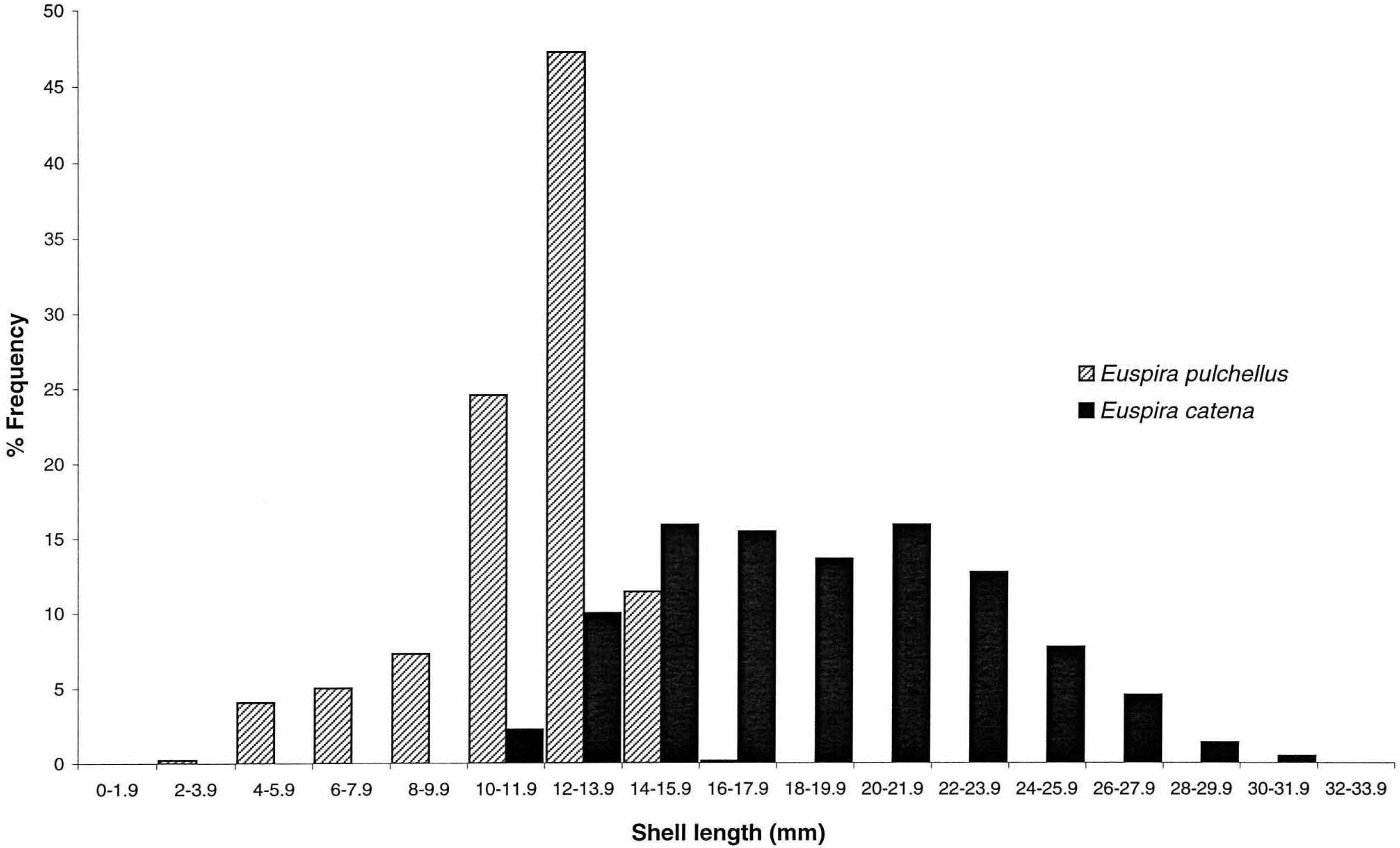
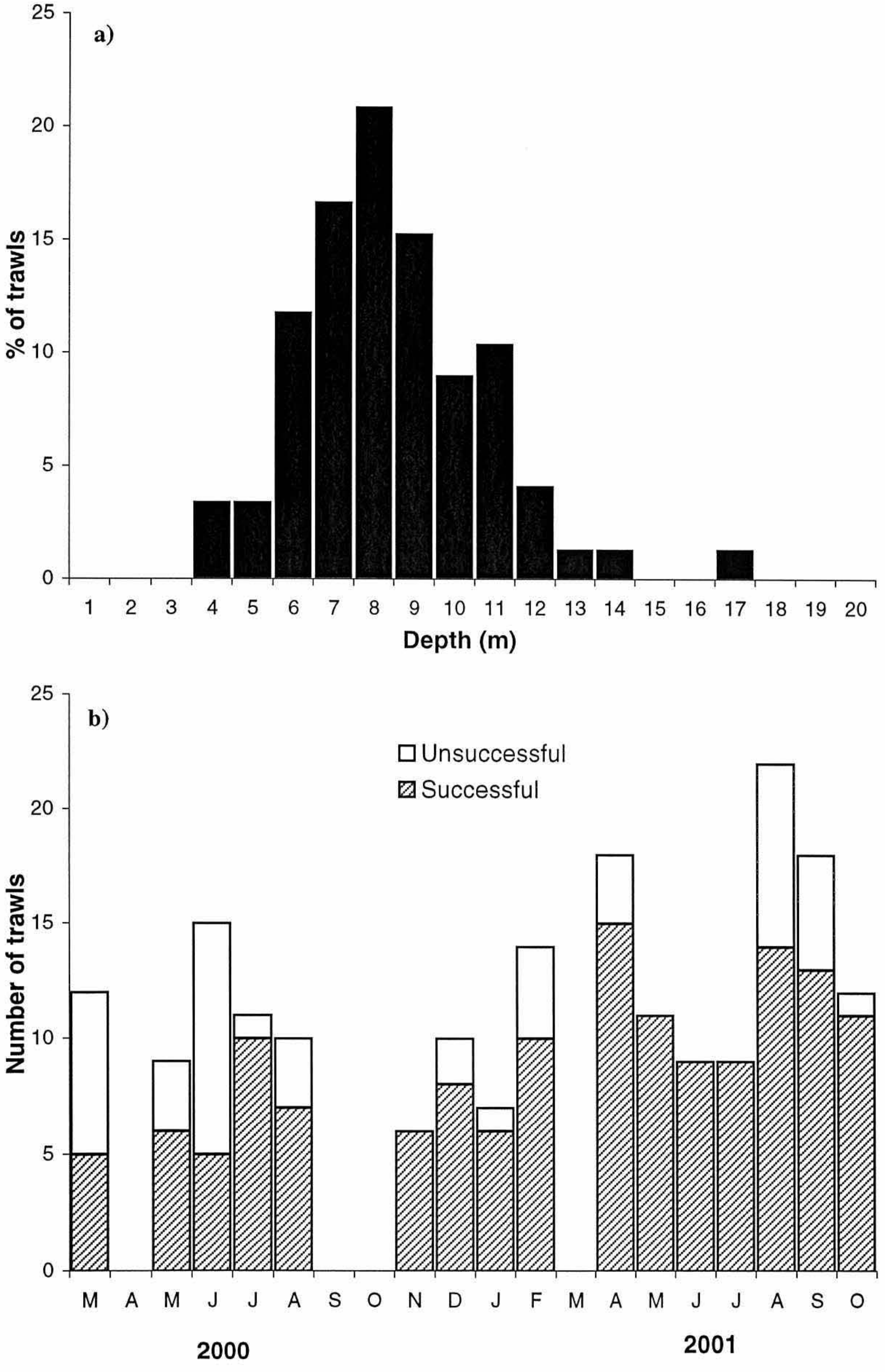

50
45
40
35
30
25
20
15
10
5
0
% Frequency
▨ *Euspira pulchellus*
■ *Euspira catena*
0-1.9
2-3.9
4-5.9
6-7.9
8-9.9
10-11.9
12-13.9
14-15.9
16-17.9
18-19.9
20-21.9
22-23.9
24-25.9
26-27.9
28-29.9
30-31.9
32-33.9
Shell length (mm)

Figure 3. a) Depths of seawater at which beam trawl samples were collected during monthly trips to Red Wharf Bay between March 2000 and October 2001. b) The number of 'successful' (caught *Euspira pulchellus*) and 'unsuccessful' (caught no *Euspira pulchellus*) trawls collected in each sampling month for the same period.


a)
% of trawls
0
5
10
15
20
25
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
Depth (m)
b)
☐ Unsuccessful
▨ Successful
Number of trawls
0
5
10
15
20
25
M
A
M
J
J
A
S
O
N
D
J
F
M
A
M
J
J
A
S
O
2000
2001

allow the size-frequency distribution of a naticid population to be studied over time. A decision was therefore made, as a result of these early fieldwork observations, to concentrate this Ph.D. study on *E. pulchellus* such that beam trawling sampling was directed towards areas of muddy sand in Red Wharf Bay.

The data presented in this chapter represent the measurements of *E. pulchellus* present in samples collected each month between March 2000 and October 2001, with the exceptions of April, September and October 2000 and March 2001. Both the numbers of *E. pulchellus* caught (Figure 4) and the calculated densities of *E. pulchellus* per hectare of seabed (Figure 5) were highly variable between trawls on a particular day. For example, when trawling in May 2001, the number of *E. pulchellus* varied from 3 to 213 between individual trawls, and the densities calculated from these values were 57.1 and 4072.7 *E. pulchellus* ha^{-1} respectively. The calculations of the monthly mean densities of *E. pulchellus* ha^{-1} and the 95% confidence intervals of these means (Figure 6) revealed that there were significant differences between December 2000 compared with June, July and August 2001, also between June 2000 and these three months, and finally between May 2000 compared with July and August 2001. The densities in June 2000 appear anomalous in comparison with the high mean densities of *E. pulchellus* during the summer of 2001. This is not explained by a lesser number of trawls taken on that particular day as shown in Figure 3b. If the individual densities of *E. pulchellus* for November 2000 to February 2001 are combined and taken to represent 'Winter 2000' and the data for May 2001 to August 2001 are combined to represent 'Summer 2001', mean densities of 224.92 and 699.97 *E. pulchellus* ha^{-1} are obtained, which are highly significantly different (2-sample T-test, $T = -5.98$, $p < 0.001$). *Euspira pulchellus*, therefore, was more densely distributed within the sampling area in Red Wharf Bay during the summer months than during winter months (Figure 7). As an example, the mean densities of *E. pulchellus* in December 2000 and January 2001 were 135.66 ha^{-1} and 131.01 ha^{-1} respectively, compared with 847.33 ha^{-1} in May 2001 (Figure 6).

The dispersion of a population determines the relationships between the variance (σ^2) and arithmetic mean (μ), in accordance with the following scheme (Elliott, 1971):

Figure 4. Number of *Euspira pulchellus* caught in individual beam trawl samples collected from Red Wharf Bay between March 2000 and October 2001. Sampling occasions varied in the number of trawls taken, with only successful trawls shown in this figure.

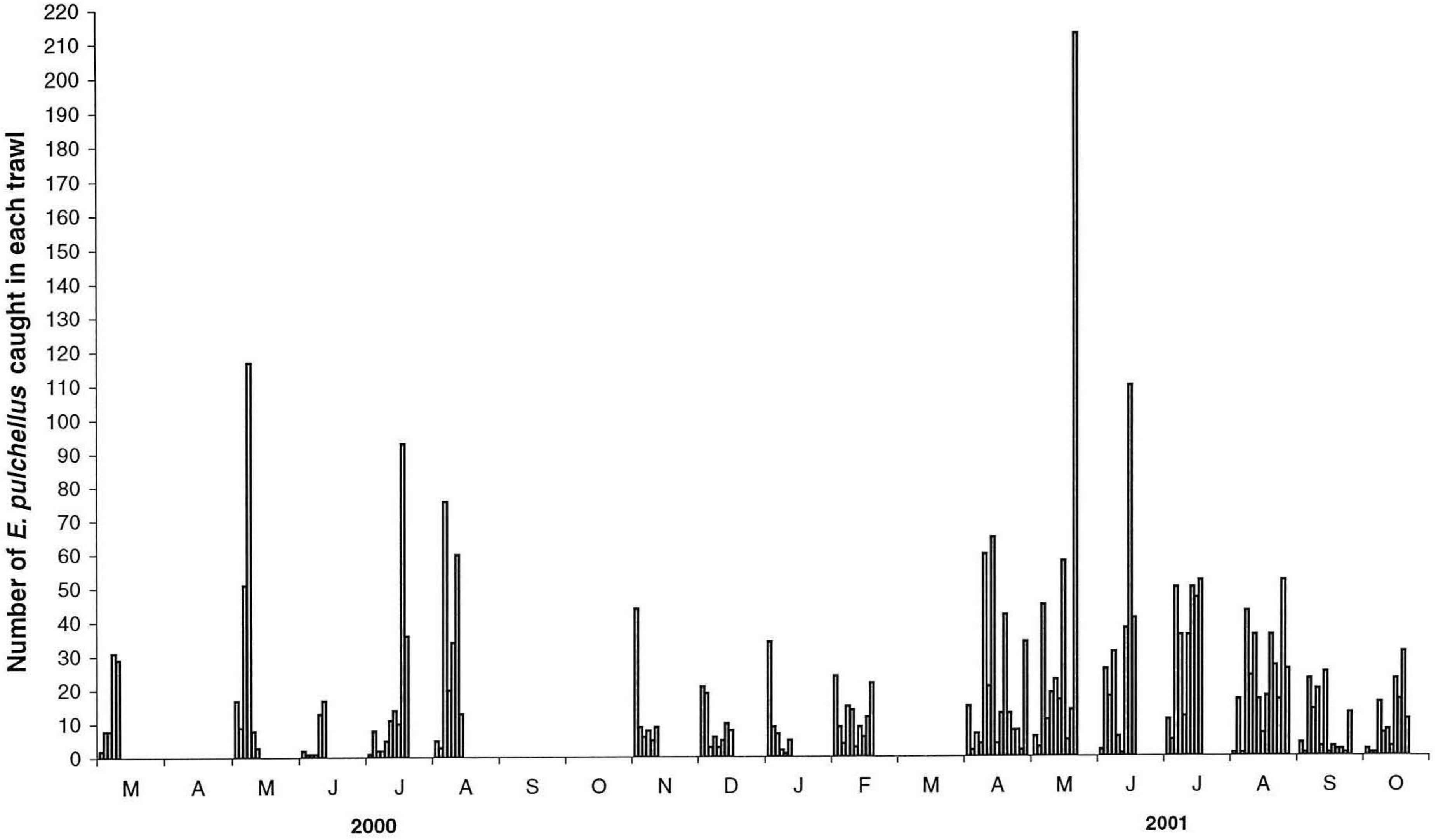

Number of *E. pulchellus* caught in each trawl
220
210
200
190
180
170
160
150
140
130
120
110
100
90
80
70
60
50
40
30
20
10
0
M
A
M
J
J
A
S
O
N
D
J
F
M
A
M
J
J
A
S
O
2000
2001

Figure 5. Number of *Euspira pulchellus* per hectare calculated from the numbers caught in individual beam trawl samples collected from Red Wharf Bay between March 2000 and October 2001.

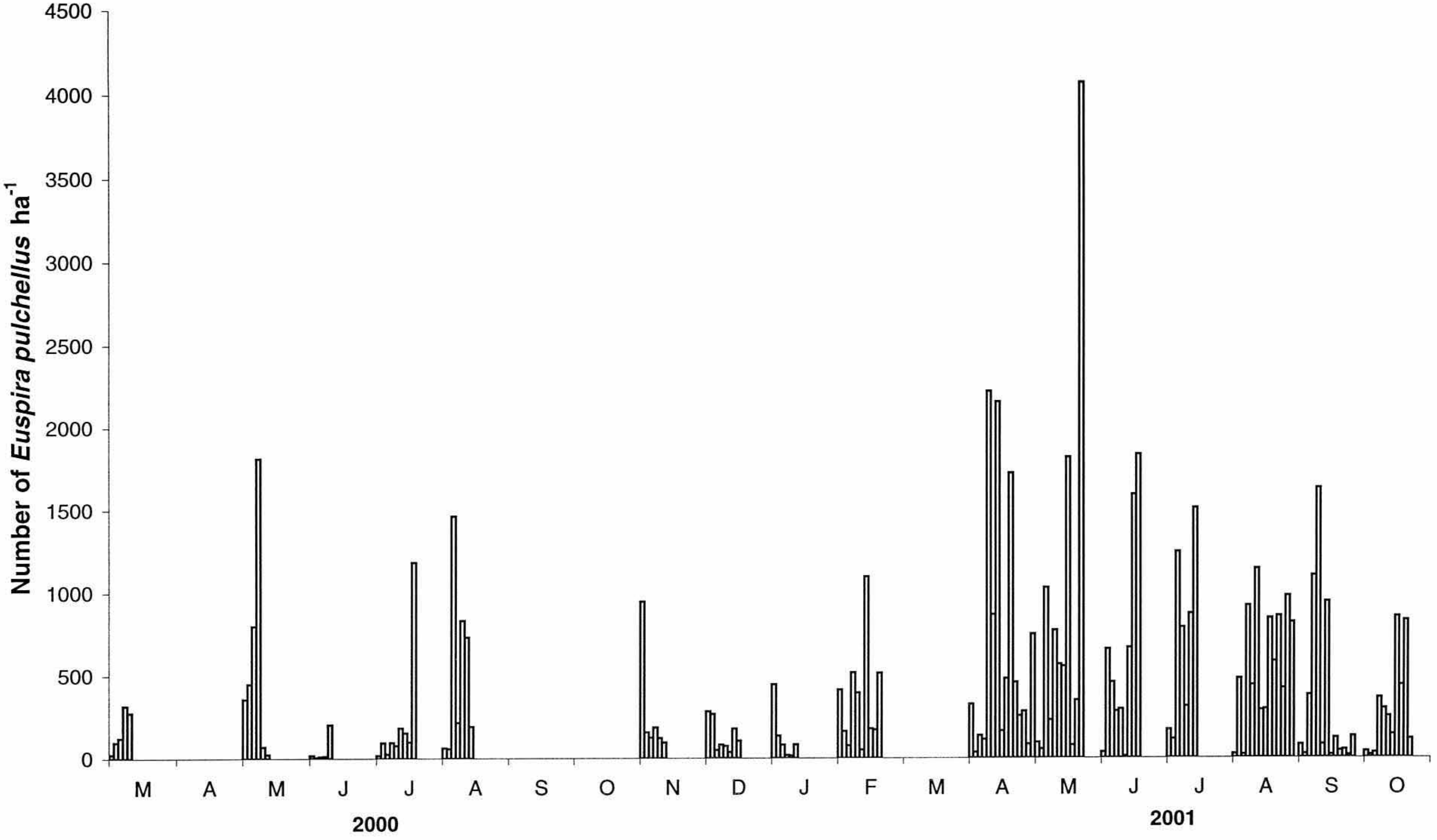
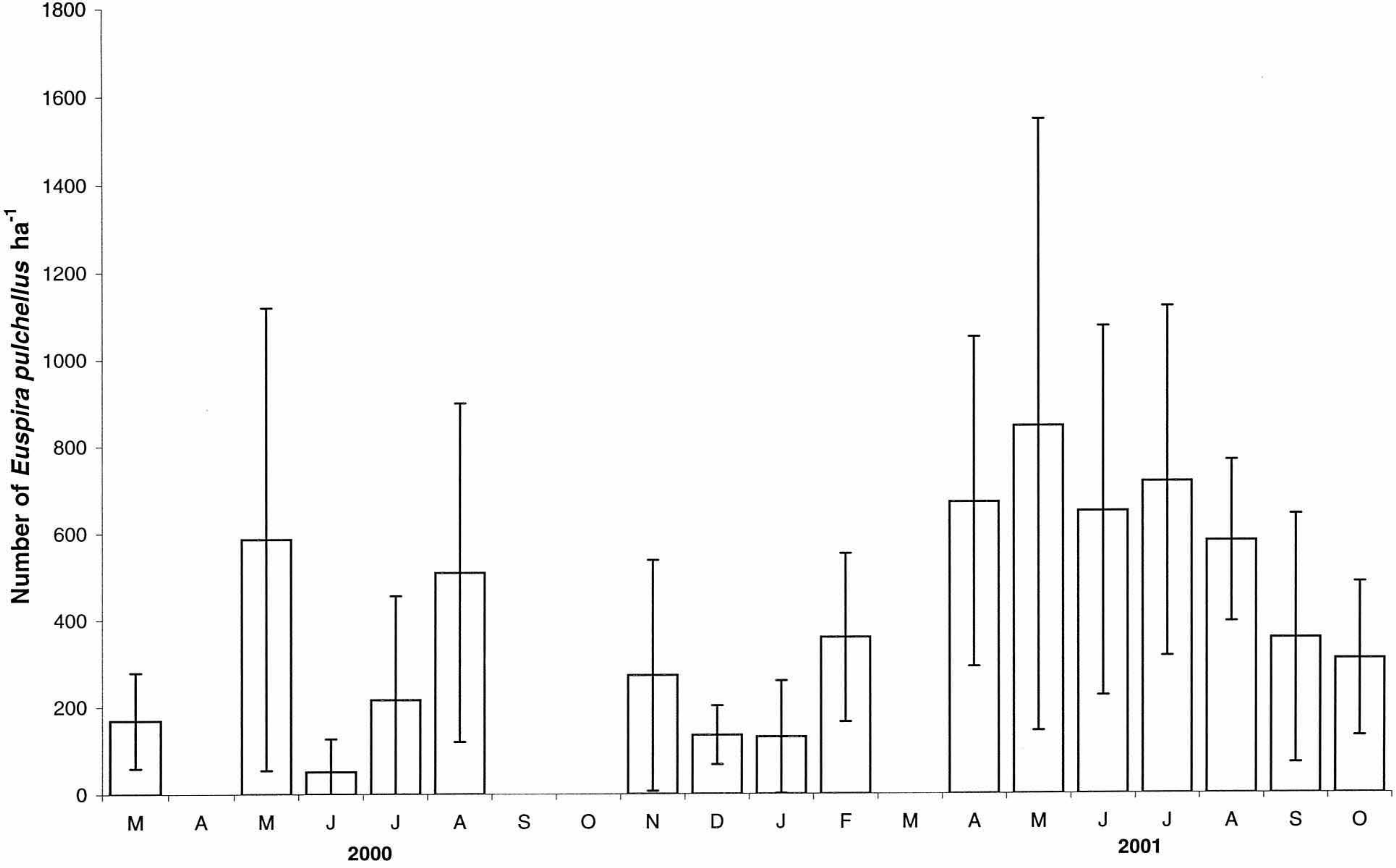

Number of Euspira pulchellus ha-1
4500
4000
3500
3000
2500
2000
1500
1000
500
0
M
A
M
J
J
A
S
O
N
D
J
F
M
A
M
J
J
A
S
O
2000
2001

Figure 6. Seasonal changes in the mean density of *Euspira pulchellus* per hectare within the sample areas of Red Wharf Bay between March 2000 and October 2001 (bars represent the averages for the successful trawls in each month ± 95% confidence intervals).


Number of *Euspira pulchellus* ha-1
0
200
400
600
800
1000
1200
1400
1600
1800
M
A
M
J
J
A
S
O
N
D
J
F
M
A
M
J
J
A
S
O
2000
2001

1) random distribution: variance equal to mean ($\sigma^2 = \mu$)

2) regular distribution: variance less than mean ($\sigma^2 < \mu$)

3) contagious distribution: variance greater than mean ($\sigma^2 > \mu$)

Regular distributions (2) are also referred to as being under-dispersed, uniformly or evenly distributed, whilst contagious distributions (3) are also referred to as being over-dispersed, clumped or aggregated (Elliott, 1971). A Poisson series ($\sigma^2 = \mu$) has been shown to be a suitable model for a random distribution (Elliott, 1971). A χ^2 test of the variance to mean ratio for agreement with a Poisson series was used to test whether or not individuals within the population were randomly distributed. In all months, the variance (σ^2) was considerably higher than the mean (μ) density of *Euspira pulchellus* ha^{-1}, by more than two orders of magnitude in many cases. χ^2 values for all months fell outside the 5% significance levels of the Poisson distributions for a given number of degrees of freedom (see Elliott, 1971), such that the distribution of *E. pulchellus* departed significantly ($p < 0.05$) from a random distribution. *Euspira pulchellus* had an aggregated or patchy distribution at all times between March 2000 and October 2001.

The shell-length frequency histograms for each sampling month between March 2000 and October 2001 are shown in Figure 8. From March 2000 until July 2001 the population consistently contained a cohort whose mean shell length was in the range 12-12.9 mm. In August 2001 this mean increased to fall within the 13-14.9 mm size class interval. The population was consistently dominated by snails of this size (Figure 8), and rarely were animals larger than this size (e.g. 15-15.9 mm) collected. Vacated shells of *E. pulchellus* that contained the hermit crab *Pagurus bernhardus* were frequently collected. These shells were not damaged or abraded and the markings on the shells were still clearly visible, suggesting that the original inhabitants had died recently. Small *E. pulchellus* (4-6 mm shell length) were consistently present in low numbers in the population compared to larger size classes (e.g. 12-12.9 mm), except during September and October 2001, at which time no *E. pulchellus* of this size (4-6 mm) were caught. From the size-frequency distributions shown in Figure 8 there appears to be a gradual increase over time in the size of these small individuals that become incorporated into the larger size classes. Using the

Figure 7. Seasonal difference in *Euspira pulchellus* density, measured as the number of individuals per hectare, between 'Winter 2000' (November 2000 to February 2001 inclusive) and 'Summer 2001' (May 2001 to August 2001 inclusive).

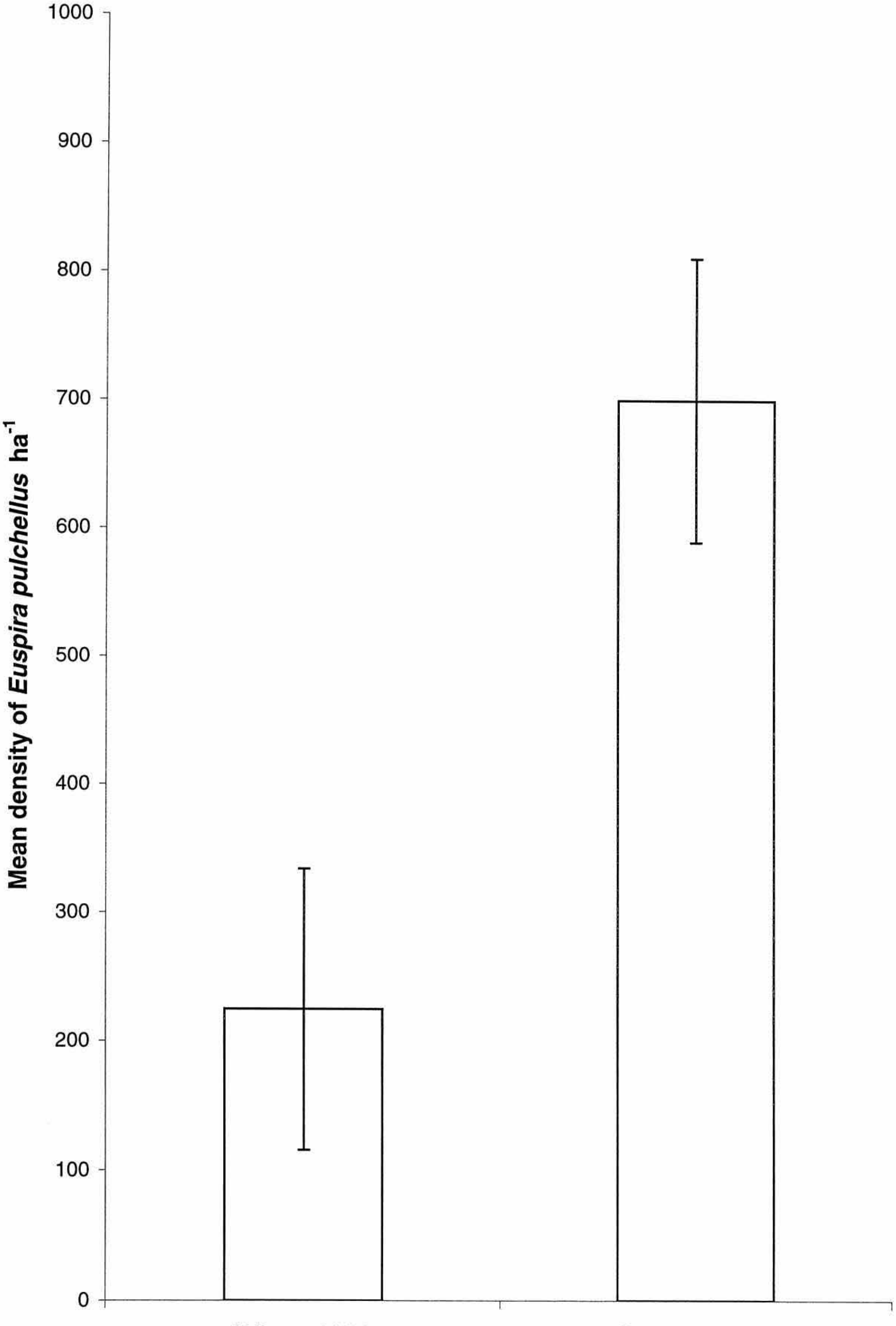

Mean density of *Euspira pulchellus* ha^{-1}
1000
900
800
700
600
500
400
300
200
100
0
Winter 2000
Summer 2001

Figure 8. Seasonal changes in the shell length percentage frequency distribution of *Euspira pulchellus* within the sample area of Red Wharf Bay between March 2000 and October 2001. Hatched bars indicate those shell length intervals that include means of normal distributions identified using the method of Bhattacharya (1967), representing the different cohorts within the population.

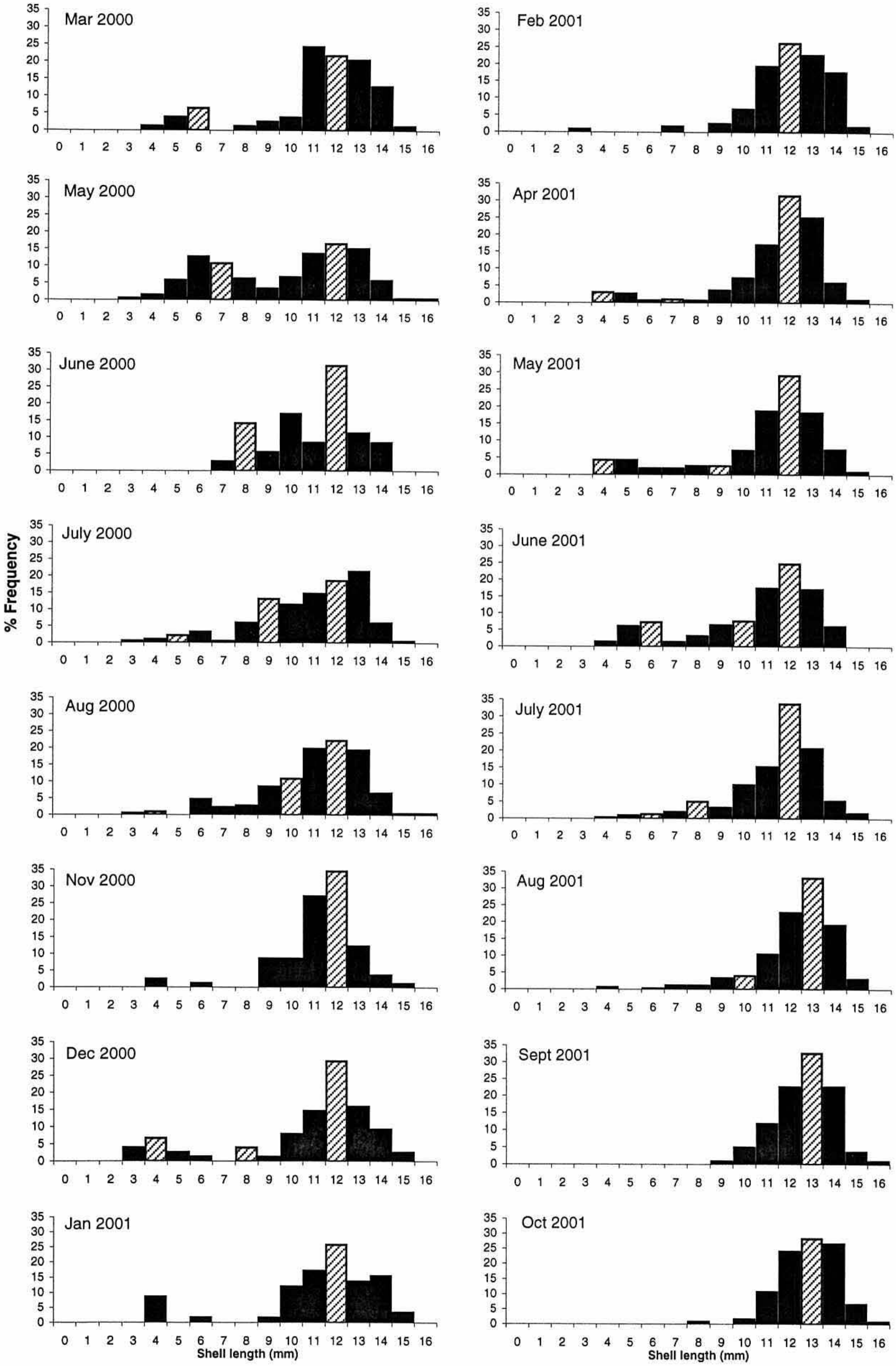
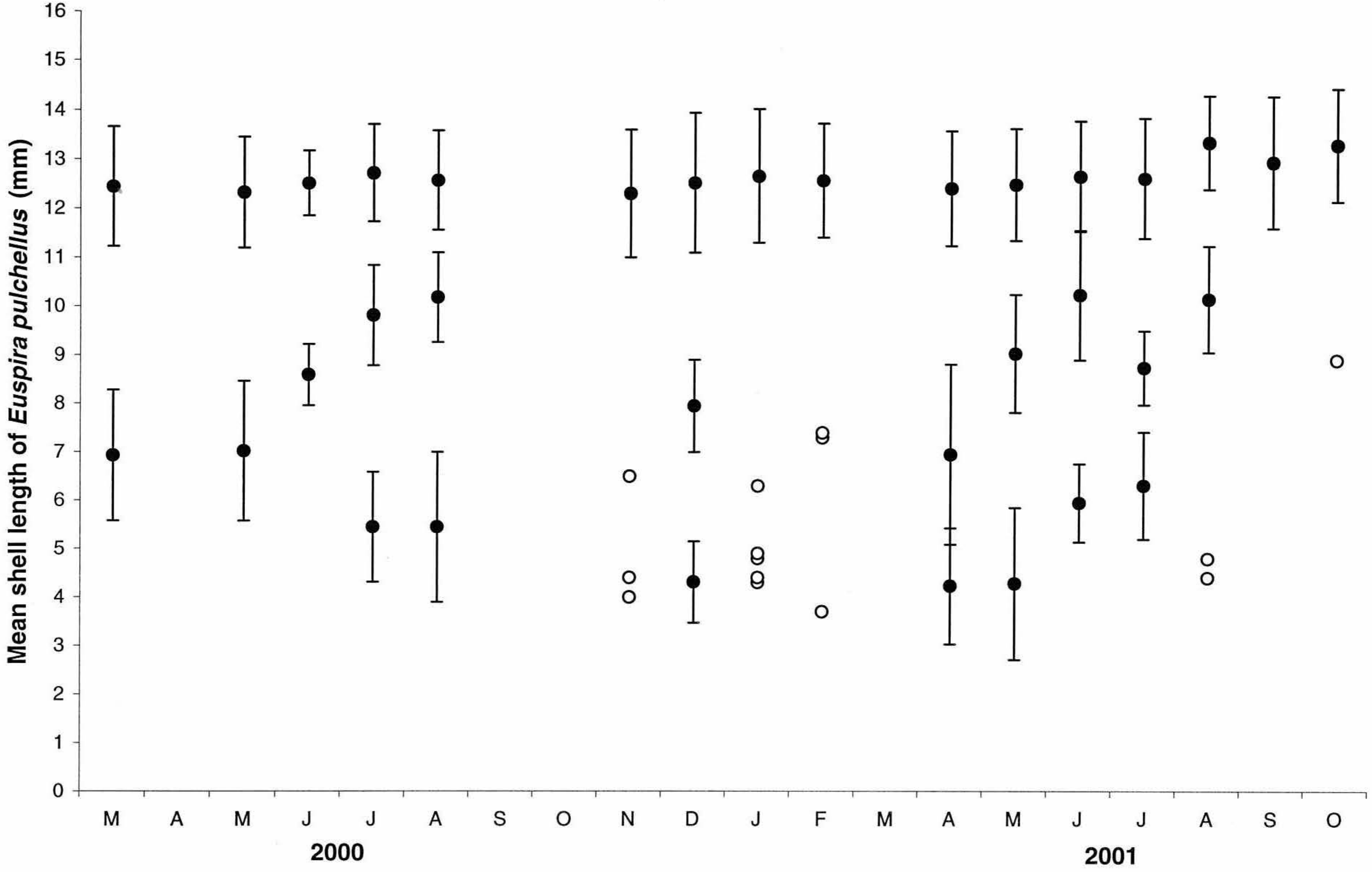

Mar 2000
May 2000
June 2000
July 2000
Aug 2000
Nov 2000
Dec 2000
Jan 2001
Feb 2001
Apr 2001
May 2001
June 2001
July 2001
Aug 2001
Sept 2001
Oct 2001
% Frequency
0 5 10 15 20 25 30 35
0 1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16
Shell length (mm)
Shell length (mm)

Figure 9. Seasonal growth and recruitment of *Euspira pulchellus* to Red Wharf Bay between March 2000 and October 2001 based upon the method of Bhattacharya (1967). Solid circles represent mean shell lengths ± S. D. and hollow circles represent the shell lengths of individual snails that were not part of the modal size classes.


Mean shell length of Euspira pulchellus (mm)
16
15
14
13
12
11
10
9
8
7
6
5
4
3
2
1
0
M
A
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method of Bhattacharya (1967), the growth of the different cohorts, identified by this method, can be determined (Figure 9). This method similarly demonstrated that the population was consistently numerically dominated by 12-12.9 mm individuals that grew slowly, if at all, over long periods of time. This method reveals that small individuals in the population grew rapidly within short periods of time, particularly between April and August in both 2000 and 2001. The cohort with a mean shell length of 6.93 mm in March 2000 had a mean of 10.18 mm by August 2000 and by November 2000 appear to have been incorporated in the dominant 12-12.9 mm cohort. In July 2000, a third cohort was present, however the growth progression of this cohort is more difficult to follow due to a lack of data for September and October 2000. Three separate cohorts were also present in December 2000 and individuals within the smaller two cohorts grew rapidly from April 2001 onwards. Following the growth of groups of individuals by eye in Figure 9 indicates that small individuals (~ 4 mm) present at certain times represent recent additions to the population.

DISCUSSION

The high variability of *Euspira pulchellus* between trawls on a particular day within the 2 km^2 sampling area of Red Wharf Bay indicates that *E. pulchellus* is patchily distributed, a finding supported by the comparison of the mean densities with a Poisson distribution (see method described above and in Elliott, 1971). The data presented in this chapter represent the first quantification of the density of *Euspira pulchellus* in its natural habitat. While other studies, referred to later in this discussion, have quantified the density of other naticid species, all were carried out on intertidal populations, such that samples collected were considerably smaller than those collected subtidally during this study. The variable success in catching *E. pulchellus,* even after extensive periods of study, can be explained by observations that *E. pulchellus* was associated with muddy sand, which was patchily distributed within the Red Wharf Bay. Relatively small shifts in trawling across the seabed resulted in a change from trawls which yielded high numbers of *E. pulchellus* to those which contained only a few *E. pulchellus* or none. Despite the high variability between samples, there was a highly significant difference ($p < 0.001$) between the mean density of *E. pulchellus* per hectare during the months of May to August 2001

('Summer 2001') compared with the period from November 2000 to February 2001 ('Winter 2000'). A possible explanation for this may be that *Euspira pulchellus* aggregates during the summer in order to mate. Alternatively, the patchy settlement of bivalve species during the summer months may cause *E. pulchellus* to aggregate in areas that present favourable conditions for feeding and growth. It is clear that naticids are strongly attracted to aggregations of suitable prey, such that the success of bivalve recruitment in a particular year will in turn affect that of the predator population. Broom (1982) recorded densities of between 0.02 and 0.82 *Natica maculosa* 0.4 m^{-2} on the intertidal mudflats of West Malaysia, whilst Wiltse (1980a) recorded a mean density of *Polinices duplicatus* in Barnstaple Harbour in 1975-6 of 1.8 m^{-2} consisting mainly of juveniles 3 to 5 mm in shell diameter, but an average density of 0.53 m^{-2} for individuals > 6 mm. In caging experiments in Barnstaple Harbour, Massachusetts, Edwards and Huebner (1977) calculated an overall density of 0.45 *Polinices duplicatus* m^{-2}, whilst in nearby locations, Hanks (1953) and Russell-Hunter and Grant (1966) recorded densities of 0.59 and 0.62 *P. duplicatus* m^{-2} respectively. Within an experimental *Mya arenaria* sub-area, however, Edwards and Huebner (1977) recorded densities of 1.4 and 2.2 *P. duplicatus* m^{-2} in 1969 and 1.5 *P. duplicatus* m^{-2} in 1970, demonstrating that *P. duplicatus* densities could be elevated by the experimental introduction of suitable prey. Similarly, Turner (1949, 1950) recorded densities of 1.9 and 3.4 *P. duplicatus* m^{-2} respectively 2 months after seeding *Mya arenaria.*

The unpredictable nature of bivalve spatfall has the potential to lead to occasional crises in the populations of predatory gastropod (Fretter and Graham, 1994). Broom (1982) demonstrated that fluctuations in *Natica maculosa* could be related to changes in the abundance of young *Anadara* prey. Berry (1982) proposed that large changes in the abundance, particularly of preferred size classes, of the trochid *Umbonium vestiarium*, the sole prey species of *N. maculosa* on a Penang shore in Malaysia, were also capable of determining the survival of *N. maculosa.* The settlement and distribution of bivalve prey species have also been shown to influence the larval stages of certain species of naticid gastropod. Wiltse (1980b) demonstrated that larvae of *Neverita duplicata* settle in the autumn, close to populations of the bivalve *Gemma gemma,* enabling them to begin feeding on this species shortly after they have metamorphosed into juveniles. Furthermore, Griffiths (1981) noted that the new spat settlement of the mussel *Choromytilus meridionalis* occurred every 4 to 6 years at Bailey's Cottage, False Bay, South Africa, providing the opportunity for the settlement, growth and consequent increase in density of juvenile *Natica tecta.* Due to rapid growth rates, however, within one year the mussels had attained a size refuge from predation by *N. tecta*, and the mussel bed had been so depleted of small mussels that only large *N. tecta* could subsequently survive. It was therefore concluded that the predator and prey population densities and size-frequency distributions were inter-dependent. A similar effect was observed by Ansell (1960) for the predator *Natica alderi* (= *E. pulchellus*) in response to population fluctuations in its prey, *Venus striatula* (= *Chamelea gallina*).

The size-frequency distributions and densities per hectare data obtained for *Euspira pulchellus* in this study provide the first information on the population structure and spatial distribution of *E. pulchellus* in a subtidal habitat. The population was characterised by large numbers of animals with a mean shell length of 12-12.9 mm, smaller than the maximum size at which *E. pulchellus* was collected (~ 16 mm). Few small individuals (4-6 mm) were present over an extended period, appeared to grow rapidly into the most abundant size classes present in the population (e.g. 4 mm individuals in December 2000 reached a size of 10 mm by the following June), and were apparently replaced by new arrivals to the population. These data indicate that there is no single annual recruitment event in *E. pulchellus* that adds large numbers of small individuals to the population, but rather that there is a steady trickle of recruitment to the population over an extended period of time. The time of year at which particular individuals settle will affect the size at which they over-winter. This can be seen (Figure 8) by the three cohorts present in December 2000. The smallest of these cohorts (4 mm) will have settled later in 2000 than the middle cohort (8 mm), which would have experienced more of the warmer period over which to grow. These cohorts, therefore, pass the winter at different sizes, and both show growth from April 2001 onwards towards the modal size of 12-13.9 mm. The growth of younger cohorts comprising smaller individuals was greatest during the period of April to August, during both 2000 and 2001, at the start of which the seawater temperature starts to rise.

A population as a whole may be comprised of several cohorts and therefore the size frequency of the population at any one time may be made up of distinct frequency distributions for the morphometric character in question. Individual populations are frequently polymodal, due to the presence of several individual age-groups. Bhattacharya (1967) devised a mathematical method for the resolution of a distribution into Gaussian components, each comprising a normal distribution, enabling the separation of a population into its constituent parts, each representing an age-group. When the method of Bhattacharya (1967) was used to separate the size frequency distributions of the burrowing starfish *Astropecten irregularis* (Freeman *et al.*, 2001) it was demonstrated that between October 1995 and September 1996 a single cohort was present which showed growth in arm length over this period. In October 1996 a second cohort was identified in the population. The increase in arm length of the starfish in this cohort could be identified in November 1996 and in June, July and August 1997. No other recruitment events were identified indicating that recruitment of *Astropecten irregularis* into the population occurred as a single discrete event. This is a consequence of the external fertilisation and synchronized spawning of *A. irregularis* and contrasts with the pattern of recruitment proposed for *E. pulchellus*.

An important consideration that must be made when interpreting size-frequency distributions is that they may only be used to speculate as to the pattern of recruitment within a population. Knowledge of the growth rates, periods of reproductive activity, and also the probable age composition of certain size classes or cohorts within the populations aid in the interpretation of the nature of recruitment. Similarities can be drawn between the size-frequency distributions of *Euspira pulchellus* presented in this chapter and the population of *Modiolus modiolus* in Strangford Lough, Northern Ireland studied by Seed and Brown (1975). The *M. modiolus* population was characterized by a high frequency of large mussels, which Seed and Brown (1975) explained by the slow but almost continuous recruitment by *M. modiolus*. Investigation of the condition of the gonad found it to be more or less ripe throughout the year. *M. modiolus* showed no pronounced seasonal cycle and therefore differed from *Cerastoderma edule,* which spawned over a restricted period of June to September, giving rise to a well defined polymodal distribution, following the relatively uniform growth rates of individuals within each year class. *Modiolus*

modiolus reached a refuge in size from predation and was estimated to be over 20 years old in some cases, whilst *C. edule* was subject to high levels of predation from oystercatchers, *Haematopus ostralegus*, shore crabs, *Carcinus maenas*, and flatfish, and rarely survived beyond its second or third winter (Seed and Brown, 1975). The determination of patterns of reproduction, growth and age allow the pattern of recruitment to be interpreted from the size-frequency distributions of a particular species, which may also be influenced by size-selective predation. These aspects of the biology of *E. pulchellus* are therefore examined in subsequent chapters and used to further explain the findings of this field study.

SUMMARY

In Red Wharf Bay, *Euspira pulchellus* occurs subtidally on areas of muddy sand, in contrast with *Euspira catena*, which occurs on clean sand. *E. pulchellus* was patchily distributed, such that there was high variability between trawls, both in the number of *E. pulchellus* caught and the density of *E. pulchellus* per hectare. Mean density of *E. pulchellus* ha^{-1} was higher during the period May 2001 to August 2001 than during the period November 2000 to February 2001, suggesting that *E. pulchellus* may aggregate during the summer months in order to mate. The population contained high numbers of 12-13.9 mm shell length individuals and low numbers of small individuals (4-6 mm shell length) throughout much of the year. It is proposed that *E. pulchellus* has low levels of recruitment spread over much of the year, that small individuals (~4 mm shell length) grow rapidly during the warmer, summer months (April to August), and that larger individuals (> 9 mm shell length) grow slowly.

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Chapter 3

Egg collar production

INTRODUCTION

Gastropod egg masses take a variety of shapes and forms. Soliman (1987) categorised the spawn of prosobranchs and opisthobranchs into one of the four following types; gelatinous egg masses (not ribbons or strings), egg capsules, egg ribbons and egg strings. Indeed, the manner of egg release and deposition among prosobranch gastropods is more varied than in any other group of mollusc. Spawn masses produced by mesogastropods and neogastropods are released from the pallial duct and in most cases are attached to a firm substratum selected by the parent. In soft sediment habitats snails may take advantage of firm substrata on which to lay their eggs, which may be weed in the case of *Nassarius reticulatus* (Barnett *et al.*, 1980). Other neogastropods requiring a firmer surface will use stones, the shells of congeners or even construct a holdfast from a few empty egg capsules, as seen in *Conus* spp. (Kohn, 1961). Epitonnids embed sand particles into the walls of egg capsules that are formed in chains, but the most complex spawn of this type is that produced by gastropods in the family Naticidae.

The sexes are separate in naticids and following internal fertilisation of eggs through copulation, reproductively mature females lay spawn, containing many egg capsules, that takes the form of characteristic egg collars made of mucus, strengthened with sand, and moulded by the foot. At times when eggs are escaping from the genital apertures of these animals, mucus, mainly produced by the front part of the foot, is passed into the mantle cavity and the two become mixed. Sand particles are incorporated into this mass as it is forced out of the mantle cavity between the body and the mantle skirt. This creates a smooth mass of secretion comprising egg capsules with sand grains in the intervening mucous matrix and produces the characteristic collar shape that causes naticids to also be referred to as necklace or sand-collar snails (Fretter and Graham, 1994). Not all naticids, however, produce the typical form of egg collar described above. Four Australian naticid species belonging to the genus *Conuber* produce large sand-free egg collars (Murray, 1963, 1966). Giglioli (1955) presents a classification scheme for the egg collars of the Naticidae based on descriptions from nine species from British, European and Canadian Atlantic waters in an attempt to improve the ability to identify parentage. Her study also includes detailed descriptions of the structure and formation of egg collars within this family. Ansell (1982a) states that naticid egg collars are produced in the sand and subsequently placed on the sand surface when completed.

Ziegelmeier (1961) provides a description of a mechanical device for the escape of *Euspira pulchellus* veliger larvae from an egg collar based on the deterioration of the structure of the egg collar when the veligers are ready to hatch. Ziegelmeier (1961) postulated that larvae are incapable of rupturing the walls of the egg capsules, and that the deterioration of the mucus causes the sand grains to fall under gravity, rupturing the walls of the egg capsules mixed within it and liberating the larvae. The timing of this disintegration of the egg collar is coincident with the veligers reaching a developmental stage at which they are ready to be released. Mechanisms of hatching from egg capsules are reviewed by Davis (1968). Depending upon the naticid species in question, the eggs hatch from the collar to give rise to swimming, planktotrophic larvae, shorter-lived lecithotrophic swimming larvae or crawl-away juveniles (Thorson, 1935, 1950, Giglioli, 1955, Amio, 1955, Bernard, 1967). This is discussed in greater detail in the following chapter.

Individuals of many species that are usually solitary come together in pairs for copulatory purposes and in some cases there are mass movements of individuals associated with reproduction. This spawning migration by adults may take the form of movement up the shore, as is seen in *Urosalpinx cinerea* which move from deeper water into the intertidal zone (Carriker, 1955, Hancock, 1959). Numerous females of *Nucella lapillus* (Feare, 1970) gather in damp, shady areas to deposit egg capsules at certain times of year and do not feed, a phenomenon that also occurs in *Thais canaliculata* (Houston, 1971). Males of these species, on the other hand, remain dispersed. Generally speaking, temperate-water prosobranchs have extended periods of spawning, however, the pattern is basically seasonal. For these seasonal species, most spawn during the summer, but some also spawn in the winter months (Webber, 1977).

The aims of this chapter were i) to observe the process of egg-laying in *Euspira pulchellus* and to investigate (ii) the seasonality of egg-laying in *Euspira pulchellus* (iii) the size at which *E. pulchellus* reaches sexual maturation iv) the relationship between adult size and egg collar production (v) the effect of temperature on the time taken for egg collars to hatch and (vi) the relationship between egg collar wet weight and the number of veliger larvae.

MATERIALS AND METHODS

1) Video observation of egg-laying

A 3.5 litre aquarium, supplied with running seawater from the Menai Strait, Anglesey, was filled to a depth of 2 cm with rinsed and sieved coarse sand collected from the high shore at Red Wharf Bay, Anglesey. Seawater supplied to aquaria throughout this study had first passed through settling tanks prior to being supplied to experimental areas. Ten *E. pulchellus* (12-13.9 mm shell length) were placed in the aquarium and offered ten cockles, *Cerastoderma edule*, of 10-12 mm shell height. The aquarium was placed in a dark room at ambient temperature and continuously illuminated with infra-red lamps. The surface of the sand was monitored continuously using a CCD video camera connected to a Panasonic AG6720 Time Lapse Video Cassette Recorder, which captured 1 frame second^{-1}. The aquarium was checked daily for a period of two weeks and any dead prey visible on the surface of the sand were removed and replaced.

2) Egg collar production

Six 3.5 litre aquaria, maintained at ambient air temperature and supplied continuously with running seawater from the Menai Strait, Anglesey, were filled to a depth of 1-2 cm with rinsed and sieved coarse sand collected from the high shore at Red Wharf Bay, Anglesey. Due to the difficulty of sexing *E. pulchellus* and in order to ensure that each aquarium yielded egg collars, snails were held in groups of five to encourage mating. The continued presence of males in each aquarium ensured that females were not limited in their access to mates, as would be the case if females were kept in isolation for extended periods. Whilst females remain capable of producing egg collars in the absence of males, this may occur at a lower rate than would occur in the continued presence of males.

At the start of the experiment, each of the six aquaria contained a different size range of snails as follows: 4-5.9, 6-7.9, 8-9.9, 10-11.9, 12-13.9 and 14-15.9 mm and are referred to as Tanks A-F for the sake of convenience. Fifteen cockles, *Cerastoderma edule,* 5 to 9.9 mm from umbo to shell margin were offered as prey every 7 days in each of the six tanks. Every four weeks the contents of each aquarium were washed through a 1mm sieve and the shell lengths of each *E. pulchellus* measured with vernier callipers to the nearest 0.1 mm, from the tip of the shell spire to the base of the outer lip of the shell aperture. Drilled cockles were collected, dead cockles without drill holes were discarded, and any live cockles were returned to the aquaria. Throughout the course of the experiment the temperature of the seawater was monitored using a Tiny Talk Temperature Logger placed in a separate aquarium supplied with running laboratory seawater taken from the Menai Strait. The logger recorded the temperature at half-hourly intervals and was downloaded and re-deployed at the end of each month. From the data recorded by the logger average daily temperatures were calculated, and an average temperature, with 95% confidence intervals, was calculated for each 4-week period. Between April and November the aquaria were checked daily for egg collars. Only egg collars visible on the sediment surface were removed and weighed. The sediment was not sieved to search for collars within the sand, to avoid interfering with snails that were in the process of drilling prey or laying egg collars. Egg collars were blotted dry on paper roll to remove excess water and were weighed on a balance to the nearest 0.01 g.

Following the termination of the experiment, the numbers and wet weight of egg collars produced in each tank were grouped into the following 4-week periods: April 26th-23rd May, 24th May-20th June, 21st June-18th July, 19th July-15th August, 16th August-12th September, 13th September-10th October, 11th October-7th November. In combination with the data collected on the shell lengths of the snails in each tank at the start of each 4-week interval, the number and wet weights of egg collars collected from the tanks were assigned to one of the following shell length size class of females; 4-5.9, 6-7.9, 8-9.9, 10-11.9, 12-13.9 and 14-15.9 mm. At the end of the experimental period all snails were removed from the tanks, dissected and examined for the presence of a penis in order to determine the number of females present in each tank. From the results of the dissections and using the measurements of shell length of snails in each tank at the start of the 4-week period, the number and wet weight of egg collars produced per female during each 4-week period for each size class of female as classified above were calculated. By manipulating the data in this way, the size classes of female *E. pulchellus* capable of laying egg collars could be investigated, along with any seasonal and size-related differences in the numbers and wet weight of egg-collars produced on a per female basis. (An assumption here is that all females present in a tank from which egg collars were collected produced egg collars. This assumption is unavoidable unless females are kept in isolation, as egg collars could not be assigned to a particular female, only to the two or three females present in that tank).

3) Relationship between egg collar wet weight and number of larvae released and the effect of temperature on hatching time

The aims of the following experiments were two-fold: i) to investigate the relationship between wet egg collar weight and the number of veliger larvae released and ii) to investigate the effect of temperature on the time taken for veligers to develop. Freshly collected egg collars of a range of sizes collected over the course of the summer of 2001 were placed individually in 2 litre Pyrex beakers containing 0.2 μm filtered, ultra-violet irradiated seawater (FSW hereafter). Beakers were maintained in a 13-14° C water bath and egg collars left to develop and the larvae to hatch. This temperature was chosen based on average summer surface water temperature for Red Wharf Bay (Mitchelson-Jacob, unpubl.). Attempts were also made to hatch egg collars and raise larvae at an elevated temperature of 19-20° C in order to determine whether the process of hatching could be accelerated. During development and hatching, the seawater in the 2 litre beakers containing the egg collars was not aerated but was replaced on alternate days. Once hatching had commenced, the water around the egg collar was vigorously pipetted manually, in order to accelerate the disintegration of the egg collar. This was carried out for up to 5 minutes, by which time if intact portions of the egg collar remained, the egg collar was left until the following day before repeated pipetting. This process aimed to overcome the artificial nature of larvae hatching in still water and was intended to ensure that all the larvae were released. Once the egg collar had completely disintegrated, which took a matter of hours to approximately one day from the start of hatching, the water containing the swimming veligers was decanted into a sterilised 2 litre beaker. Larvae were distributed evenly through the water column by the vertical movement and rotation of a plunger, that consisted of a plastic rod with a Perspex disk attached to the ends with holes drilled through it. Ten 1ml samples were removed using a glass pipette and each sample was placed in a watch-glass. The number of larvae in each 1 ml sample was counted with the aid of a dissecting microscope.

RESULTS

1) Preliminary observations of egg collar production

Observations of video footage of *E. pulchellus* during the summer of 1999 captured images of adults pushing egg collars to the surface of the sediment, indicating that although egg collars may well be produced beneath the surface, they are ultimately deposited on the sediment surface. Preliminary observations of the seasonality of egg collar production both by experimental animals and by those fed *ad libitum* in holding tanks found that *E. pulchellus* produced egg collars all year round, provided that access to mates and food availability were sufficient. *Euspira pulchellus* held individually in tanks from the start of April 1999, and fed a size range of cockles (5-15 mm shell height) *ad libitum*, produced egg collars up until the last week of July. During June and July these individuals, ranging from 10 to 15 mm shell length, produced 1-3 egg collars per week. A prolonged period of egg laying in the absence of contact with males indicates that female *E. pulchellus* are capable of storing sperm for a matter of months and are capable of producing viable egg collars without having repeated access to a mate. In August, however, egg collar production in these particular animals ceased, whilst newly collected animals at this time produced egg collars immediately. Similarly, when the former animals were put in contact with freshly collected snails in late September they began producing egg collars once more and continued to do so from October to February, at which time observations ceased. Having established that egg collars were produced throughout the year, it was decided to concentrate on egg–laying behaviour between late April and early November 2001.

2) Seasonal egg collar production

If the female snails are considered collectively and not separated into the distinct size classes, a seasonality of egg collar production, both in terms of the number (Figure 1a) and wet weight (Figure 1b) of egg collars produced can be observed. In addition there is a peak in egg collar production that is related to temperature. Both the total number and total wet weight of egg collars collected from all six tanks was greatest during the 4-week period from 19th July to 15th August. The seawater temperature was maximal between 19th July and September 16th, peaking on August 2nd at 18.1 °C. If, however, the data for the separate size classes of female snails in tanks A to F are considered (Figures 2a-2f), then at the start of the experiment no egg collars were produced in tanks A and B, which contained the smallest snails (4-7.9 mm shell length). An egg collar was first collected from tank A on the September 22nd and from tank B on July 7th. Snails 8-15.9 mm in shell length in tanks C to F, however, produced egg collars in the 4 week period commencing on April 26th. By grouping all the snails together (Figure 1) or by dividing egg collar production into the separate tanks (Figure 2) no account is taken of the growth of the snails during the experiment. Nor, therefore, is the possible increase in number of sexually mature females present as a result of this growth.

3) Differences in growth during egg-laying

Considerable differences in the growth of different sized snails were apparent during the course of the egg collar monitoring period (Table 1, Figure 3). More rapid growth occurred in the smaller size classes of snails, in particular those in Tanks A and B, than in the larger size classes of snails. The growth of one female snail in tank A was considerable, reaching a shell length of 13.5 mm by November 8th. Generally the larger size classes showed less growth during this experiment. Snails in Tank F grew little if at all during the course of this experiment, as might be expected as this is close to the maximum size reached by *E. pulchellus* (~16 mm). Table 2 shows the number and sizes of females present at the end of the experiment determined from the measurements of the shell lengths of all the snails taken every 4 weeks during the experiment and the dissection of the snails in all the tanks on November 8th. From the number of females present in each tank (Table 2) and the data for the growth of the

Figure 1. Egg collar production by *Euspira pulchellus* (n = 30, 5.3 mm to 15.7 mm shell length) during each 4-week period: a) the total numbers of egg collars and b) the total wet weight of egg collars laid. The line represents the seawater temperature change during the experiment, with points representing the average for the period and the error bars the 95% confidence intervals.

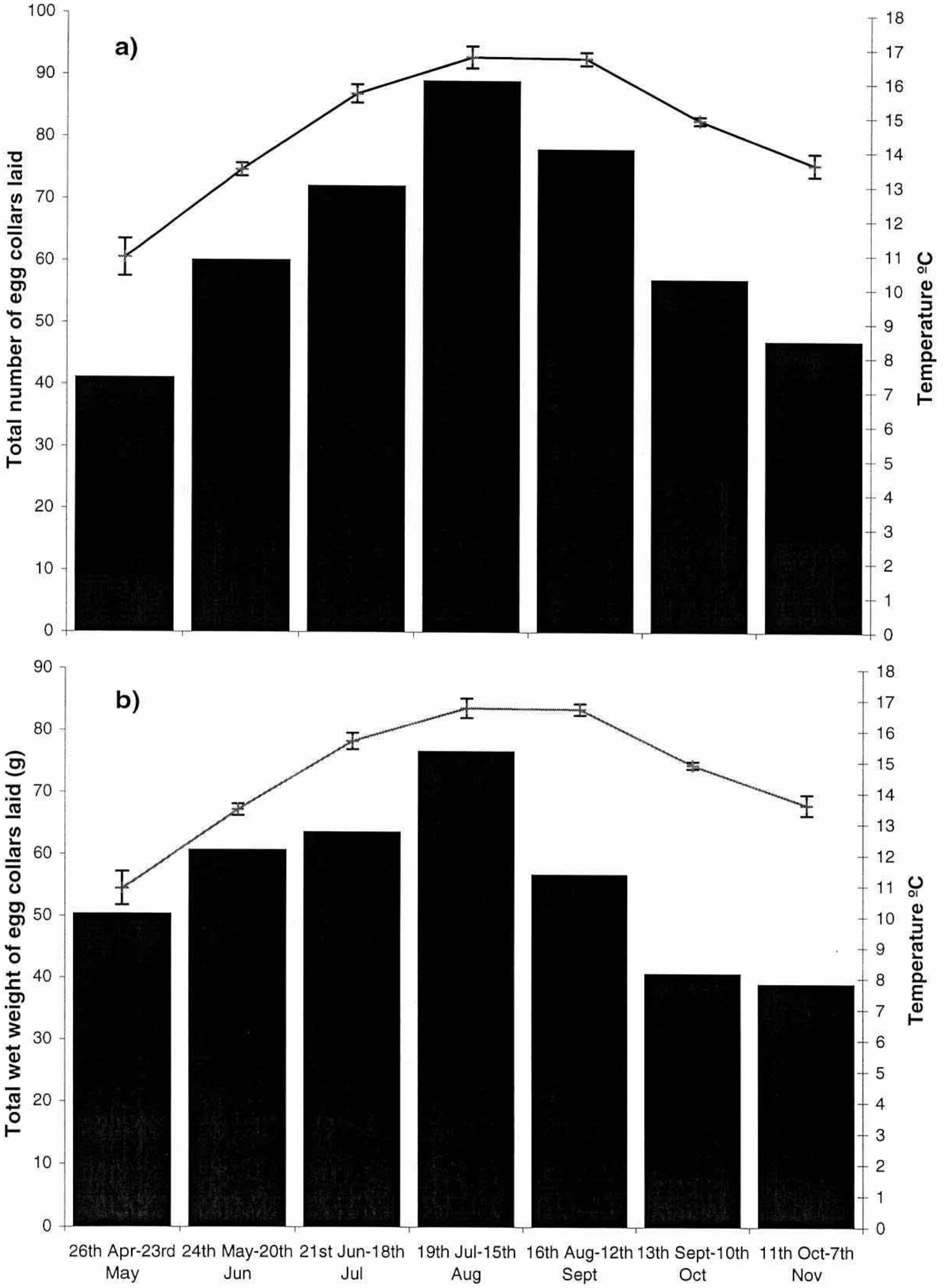

a)
Total number of egg collars laid
100
90
80
70
60
50
40
30
20
10
0
Temperature ºC
18
17
16
15
14
13
12
11
10
9
8
7
6
5
4
3
2
1
0
b)
Total wet weight of egg collars laid (g)
90
80
70
60
50
40
30
20
10
0
Temperature ºC
18
17
16
15
14
13
12
11
10
9
8
7
6
5
4
3
2
1
0
26th Apr-23rd May
24th May-20th Jun
21st Jun-18th Jul
19th Jul-15th Aug
16th Aug-12th Sept
13th Sept-10th Oct
11th Oct-7th Nov

Figure 2. Number of egg collars collected from the six individual tanks during each 4-week period. The initial size ranges of the snails in each tank were as follows a) 4-5.9 mm b) 6-7.9 mm c) 8-9.9 mm d) 10-11.9 mm e) 12-13.9 f) 14-15.9 mm.

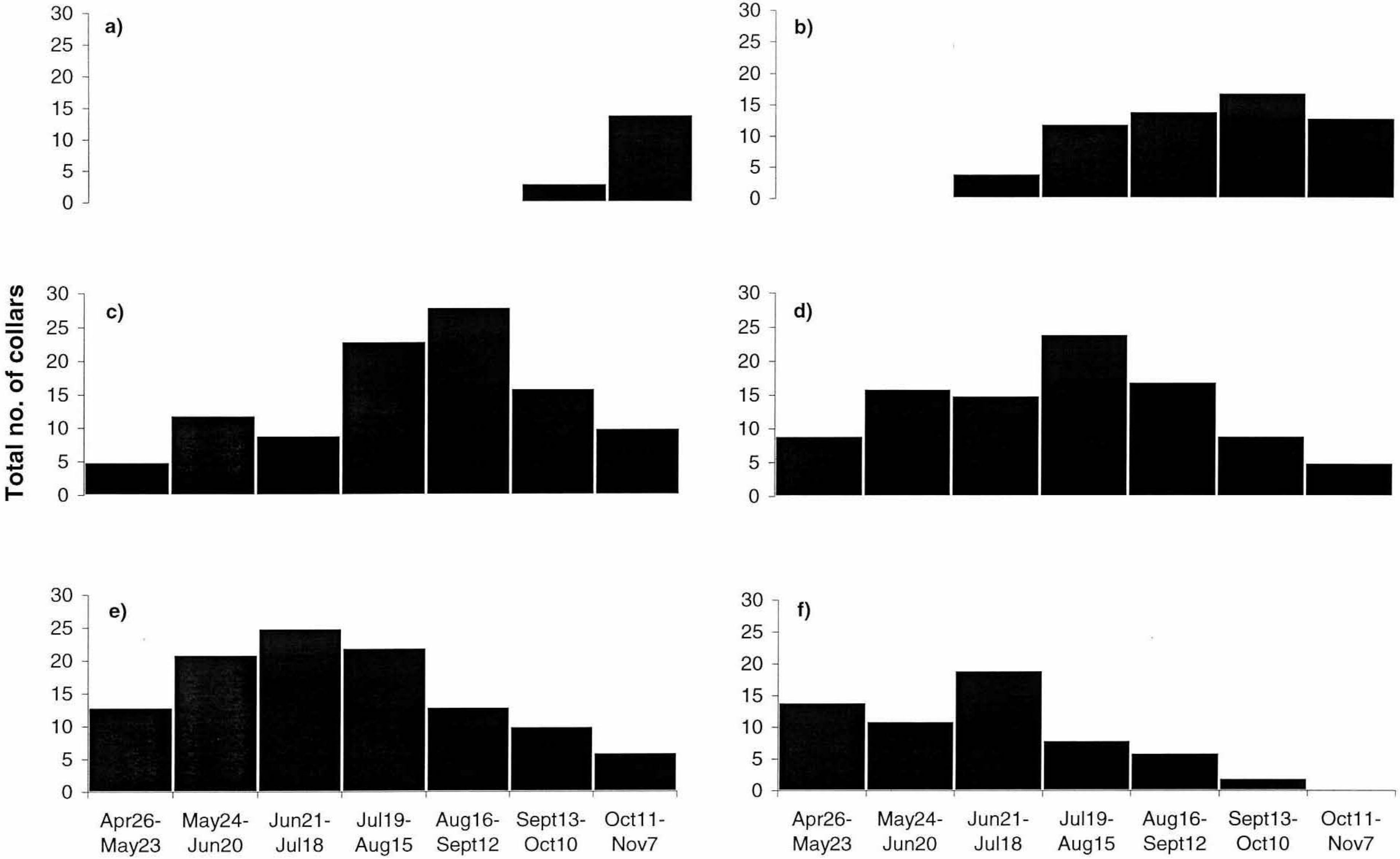

Total no. of collars
a)
b)
c)
d)
e)
f)
0
5
10
15
20
25
30
Apr26-May23
May24-Jun20
Jun21-Jul18
Jul19-Aug15
Aug16-Sept12
Sept13-Oct10
Oct11-Nov7

Table 1. Growth of *E. pulchellus* during the egg-laying experiment, expressed as the mean shell length in millimetres (± SD, n = 5) of the snails in each tank (A-F) at the start and end of the experiment.

Tank	April 26th 2001	November 8th 2001
A	5.58 ± 0.16	11.32 ± 1.50
B	6.82 ± 0.62	11.28 ± 0.87
C	9.06 ± 0.42	11.38 ± 0.69
D	10.94 ± 0.34	12.56 ± 0.56
E	13.06 ± 0.50	13.46 ± 0.43
F	14.82 ± 0.20	15.14 ± 0.38

Table 2. The number and shell lengths (mm) of female *E. pulchellus* present in each tank (A-F) at the end of the experiment on November 8th 2001.

Tank	Number of females	Shell length of females (mm)
A	3	11.8, 11.9, 13.5
B	2	11.4, 12.8
C	2	11.1, 12.1
D	2	13.0, 13.2
E	3	13.0, 13.6, 13.8
F	2	14.6, 15.1

Figure 3. Growth of *E. pulchellus* during the egg-laying experiment for each of the initial size ranges of snails (n = 5) a) 4-5.9 mm b) 6-7.9 mm c) 8-9.9 mm d) 10-11.9 mm e) 12-13.9 mm f) 14-15.9 mm.

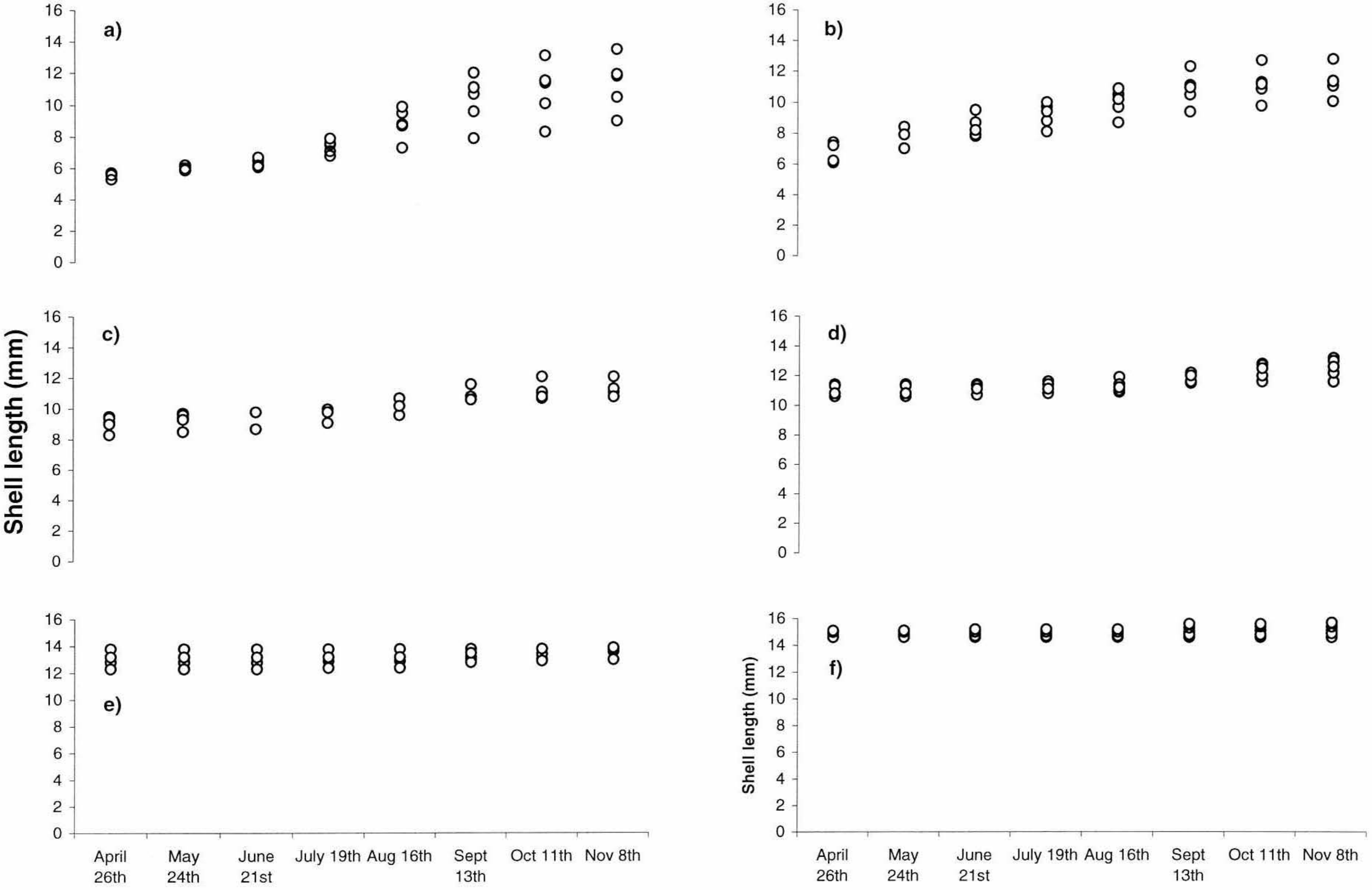
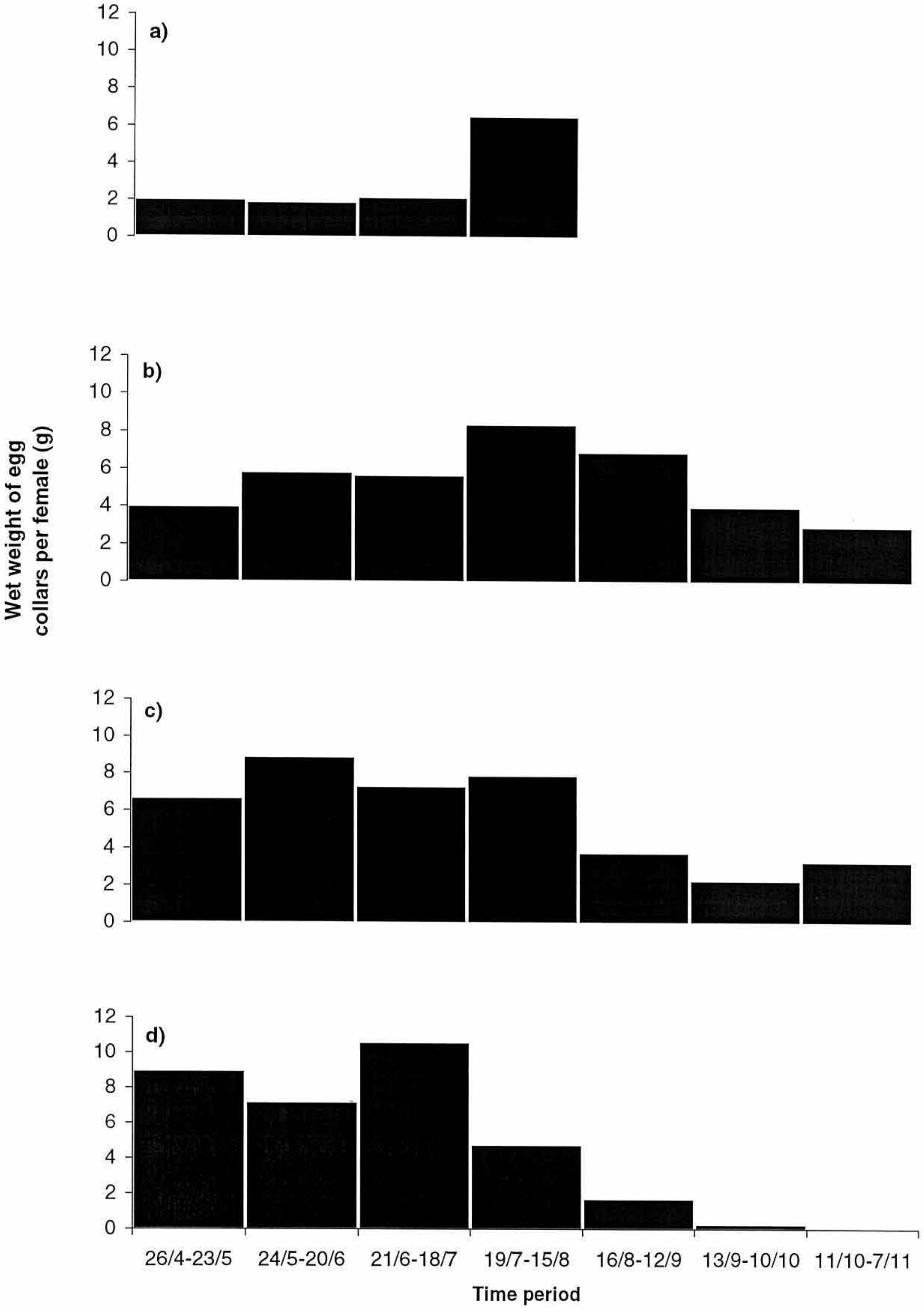
Shell length (mm)
a)
b)
c)
d)
e)
f)
0
2
4
6
8
10
12
14
16
April 26th
May 24th
June 21st
July 19th
Aug 16th
Sept 13th
Oct 11th
Nov 8th
Shell length (mm)

Figure 4. The wet weights of egg collars produced per female during each 4-week period for the following size classes of female *E. pulchellus* a) 8-9.9 mm b) 10-11.9 mm c) 12-13.9 mm d) 14-15.9 mm.


a)
b)
c)
d)
Wet weight of egg collars per female (g)
0
2
4
6
8
10
12
26/4-23/5
24/5-20/6
21/6-18/7
19/7-15/8
16/8-12/9
13/9-10/10
11/10-7/11
Time period

snails, (Figure 4), the size of each female during each 4-week period was estimated, and the number of females in each size class present during that period determined. These data are used to investigate egg collar production on a per female basis. Table 2 shows that of the five individual snails placed in each aquarium at the start of the experiment either 2 or 3 were female and the rest were male. Females, therefore, had access to males throughout the experiment and were not limited in their production of egg collars by non-access to mates. Examination of Tables 1 and 2 demonstrates that the individuals in Tanks A and B had a mean shell length of 5.58 mm and 6.82 mm respectively on April 26th 2001, and showed rapid growth over the summer, the females amongst them measuring 11.8, 11.9 and 13.5 mm, and 11.4 and 12.8 mm respectively on November 8th 2001. The snails in Tanks C and D that had mean shell lengths of 9.06 mm and 10.94 mm respectively on April 26th had grown to 11.1 mm and 12.1 mm, and 13.0 mm and 13.2 mm respectively by the same date. In contrast, the females in Tanks E and F had very slow growth rates during the equivalent period.

4) Numbers and wet weight of egg collars produced per females of different size classes

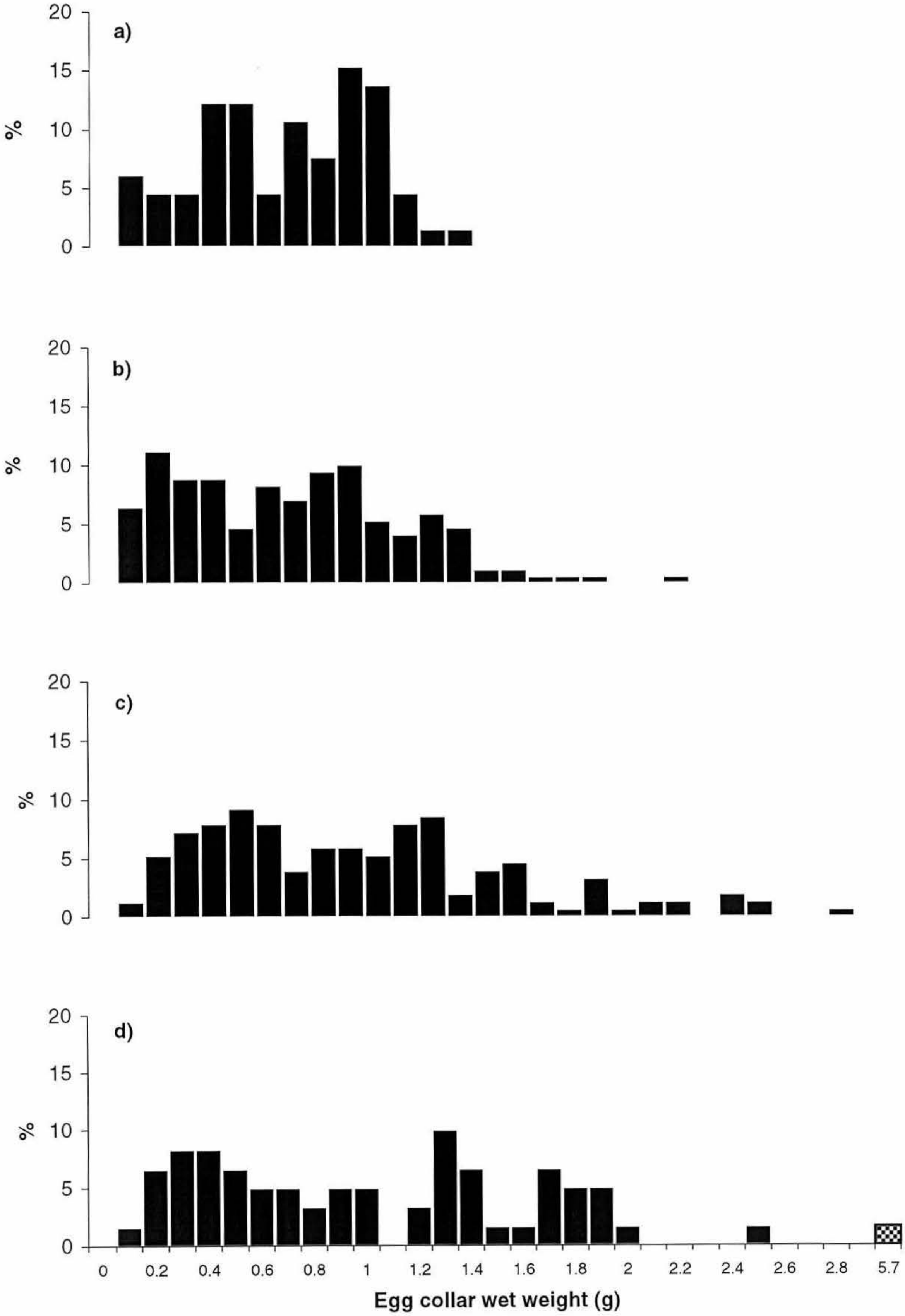
When the egg collar data are re-calculated on a per female basis, then the increase in the number of mature females capable of producing egg collars during the course of the experiment can be determined. Plotting both the numbers and wet weights of egg collars produced per female reveals similar seasonal patterns for the different size classes of female. Due to the slow growth of larger animals (12-15.9 mm), plotting egg collar production by tank or by size class for these individuals shows little difference. The seasonal patterns of egg collar production and those for different size classes of individuals are therefore adequately shown by Figure 4. Attributing egg collars to specific size class of females (4-5.9 mm, 6-7.9 mm, 8-9.9 mm, 10-11.9 mm, 12-13.9 mm and 14-15.9 mm), it was found that no egg collars were produced in tanks in which the females were < 7.9 mm. Egg collars were only produced once females reached a size > 8-9.9 mm. No data are available for 8-9.9 mm females for the time periods after August 15th (Figure 4a) because firstly, females in Tank A did not start laying egg collars until September 22nd, by which time they had reached a shell length > 10 mm, and secondly, by August 16th the females in Tank B had similarly reached a shell length > 10 mm. For the 8-9 mm females, therefore, it is not possible to state whether the wet weight of egg collars produced between 19th July and 15th August represents a peak in egg collar production, as data for later periods are unavailable (Figure 4). For the 10-11.9 mm females, egg collars were produced in greatest number and wet weight per female between 19th July and 15th August, after which the rate of egg collar production declined (Figure 4b). The larger individuals, 12-13.9 mm (Figure 4c) and 14-15.9 mm (Figure 4d), reached their peak wet weight of egg collars production slightly earlier during the period June 21st to July 18th, before showing a decline in egg collar production. The last egg collar produced by the 14-15.9 mm females, present only in Tank F throughout the experiment, was collected on October 7th.

5) Individual egg collar wet weight frequency distributions

The egg collars collected from Tanks A to F ranged from partial revolutions or whorls of mucus, sand and eggs through to more than a complete revolution. No attempt is made to distinguish between these on the basis of wet weight and egg collars can be thought of as existing as a continuum from part revolutions through to approximately two complete revolutions in the largest egg collars collected. In order to investigate further differences that might occur in the wet weights of individual egg collars produced by females of different sizes, the raw data of individual wet weights of egg collars were attributed to the same female size class categories used previously, irrespective of the time of year at which they were produced. The wet weights of egg collars collected from the tanks were classified into the categories 0-0.09 g, 0.10-0.19 g, 0.20-0.29 g and so on up to 2.90-2.99 g. All but one egg collar could be included in this range. One outlying data point arose from an unusually large egg collar produced on June 19th by a 14-15.9mm female that had a wet weight of 5.75g.

There is a considerable spread of data for the egg collar wet weights produced by the four size classes of female from which egg collars were collected (Figure 5). Nevertheless, it is possible to identify peaks in the distributions of the wet weights of the egg collars. There are two peaks in the egg collar wet weights for the 8-9.9 mm females which may correspond to partial egg collars and complete egg collars, the first spanning 0.40-0.49 g and 0.50-0.59 g, and the second occurring at 0.90-0.99 g (Figure 5a). A clear difference between the distribution of egg collars wet weights for

Figure 5. Percentage frequency distributions of the wet weights of individual egg collars produced by the four size classes of mature female *E. pulchellus* a) 8-9.9 mm b) 10-11.9 mm c) 12-13.9 mm d) 14-15.9 mm.


a)
b)
c)
d)
%
0
5
10
15
20
0
0.2
0.4
0.6
0.8
1
1.2
1.4
1.6
1.8
2
2.2
2.4
2.6
2.8
5.7
Egg collar wet weight (g)

the 8-9.9 mm females and those produced by the three larger size classes is the absence of a far-reaching right-hand tail to the distribution, particularly apparent in the distributions for the 12-13.9 mm (Figure 5c) and 14-15.9mm females (Figure 5d). No egg collars were collected from the 8-9.9 mm females that had a wet weight of greater than 1.34 g, whilst the maximum wet weight of an egg collar for the 10-11.9 mm, 12-13.9 mm and 14-15.9 mm size classes were 2.11 g, 2.73 g and 5.75 g (followed by 2.58 g) respectively. As snails increase in size, so too does the range of wet weights of egg collars and the largest size of egg collar produced.

6) Effect of temperature on time taken to hatch

From the cultures of egg collars in filtered seawater, temperature strongly affected the time that veligers took to develop within the egg capsules of the egg collars and to subsequently hatch. Egg collars maintained at 13-14° C released their larvae after 14-15 days, whilst eggs within collars incubated at 19-20° C showed an accelerated rate of development at the elevated temperate and hatched after 9-10 days.

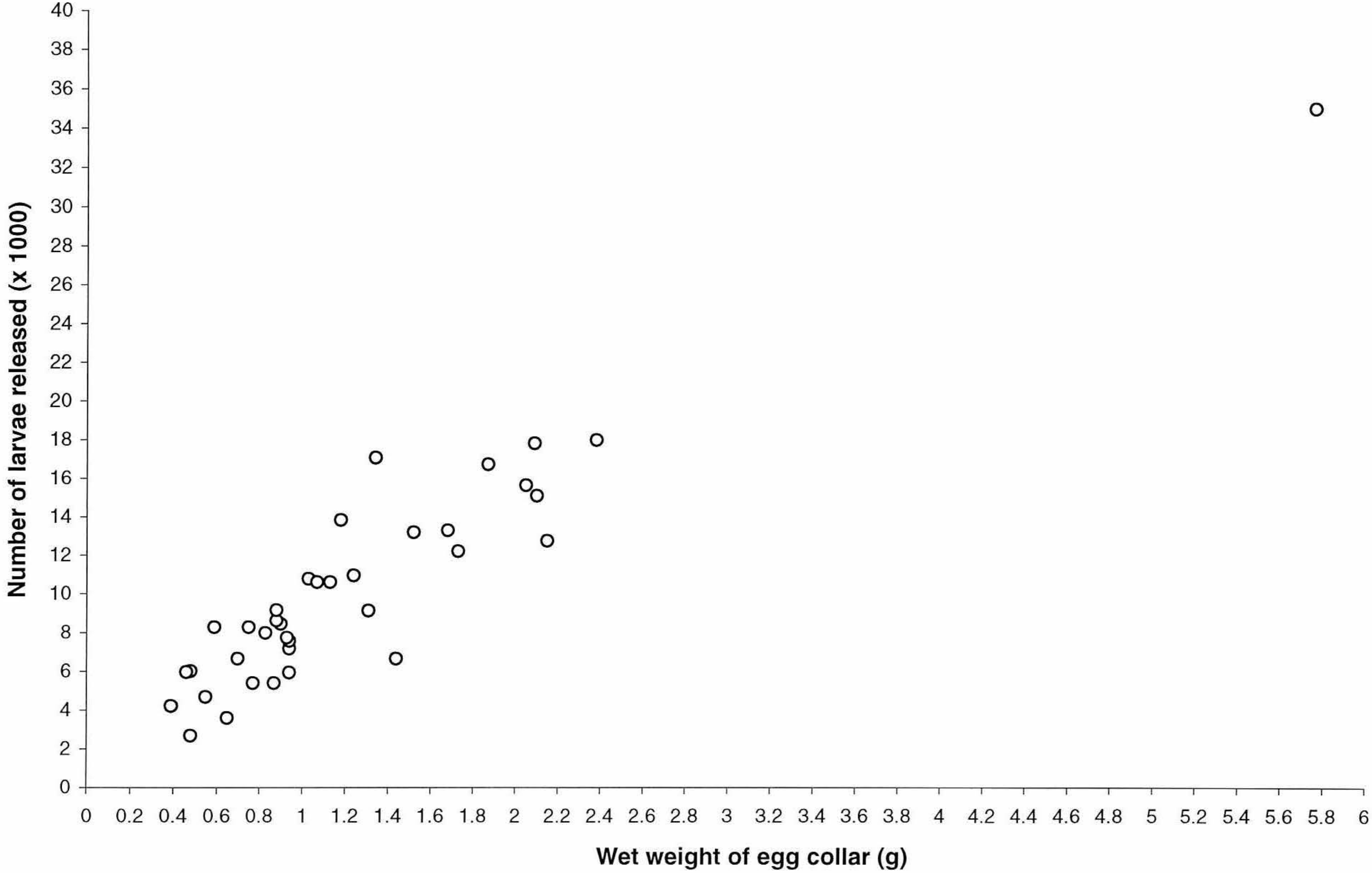
7) Egg collar wet weight and the number of veligers released

A significant relationship exists between the wet weight of an egg collar and the number of larvae released ($r = 0.932$, $p < 0.001$). This is expected if, as the egg collar increases in wet weight, the number of eggs mixed with the sand that are incorporated into it by the female as it is constructed increases (Figure 6). The outlier mentioned above arising from the 5.75 g egg collar was excluded from the regression, thereby restricting the data set used for the regression to the range of wet weights of egg collars usually collected. The relationship between wet weight of egg collar and the number of larvae released, in the absence of the outlier was found to be linear and produced the regression equation:

Number of larvae released = 8137 x wet weight of egg collar (g)

Until this point no mention has been made of the differences in fecundity of different sizes of female *Euspira pulchellus*. Having established a linear relationship between egg collar wet weight and the number of larvae released, however, this can now be

Figure 6. The relationship between egg collar wet weight and the number of veliger larvae released.


Number of larvae released (x 1000)
40
38
36
34
32
30
28
26
24
22
20
18
16
14
12
10
8
6
4
2
0
0
0.2
0.4
0.6
0.8
1
1.2
1.4
1.6
1.8
2
2.2
2.4
2.6
2.8
3
3.2
3.4
3.6
3.8
4
4.2
4.4
4.6
4.8
5
5.2
5.4
5.6
5.8
6
Wet weight of egg collar (g)

done. The largest snails (14-15.9 mm shell length) showed the greatest fecundity for any size class of snail during a particular period (Figure 4), namely between June 21st and July 18th. The wet weight of egg collars produced per female, and therefore the number of larvae potentially released, was greatest by these animals during this period than by any other animals during any other 4-week period. The period of spawning in these individuals, however, was concentrated into a shorter period from April to August. Those snails between 10 and 13.9 mm (Figures 4b and 4c) showed lower levels of fecundity than the largest snails but spawned for longer, between April and November. The smallest mature females (8-9.9 mm) had the lowest fecundity during the early part of the year (April to July) presumably having become sexually mature recently.

DISCUSSION

The reproduction of *Euspira pulchellus* was strongly influenced by temperature in that both the highest numbers and wet weights of egg collars produced were associated with the warmest seawater temperatures recorded in the aquaria. The absence of egg collars from the two smallest size classes of snails, in tanks A and B, early in the experiment was due to a lack of sexual maturity in these individuals at that time. By September and July respectively, however, females had reached sufficient size to begin laying egg collars. The size at which female *E. pulchellus* become capable of producing egg collars was not known prior to the experiments carried out in this study. Individuals produced egg collars at different rates at different times of the year and this was determined by their size. The time at which a particular female begins to lay egg collars, at 8 to 9.9 mm shell length, will be influenced by the time of year at which metamorphosis and recruitment to the benthos occurs. This in turn determines the conditions, specifically temperature, for growth, and therefore the time taken for females to reach a size at which they are sexually mature and commence egg collar production. The growth data in this chapter show that small individuals (4-5.9 mm) at the start of May are capable of considerable growth over the course of a summer and reach sexually maturity and begin egg collar production by mid to late September.

Observations of long term cultures of *E. pulchellus* in this study, and in the work of Ansell (1982a), have shown that *E. pulchellus* is capable of producing egg collars year round. In Red Wharf Bay, from these findings, different size classes of females can be expected to produce different numbers of egg collars at different times of the year. Larger, older individuals will produce egg collars at high rates in the summer months, show reduced rates as the seawater temperature decreases, or as seen in this study may stop producing egg collars altogether in late September. In contrast, younger individuals that become sexually mature during the summer will lay egg collars at maximum rates in the summer months and continue to produce egg collars throughout the winter, resulting in year-round production by the population as a whole, as seen in the laboratory. The cessation of egg collar production by the larger snails in early October may have been due to these animals becoming senescent.

Ansell (1982a) found that *Polinices alderi* (= *Euspira pulchellus*) fed *Tellina tenuis* in the laboratory produced egg collars at a maximum rate in May and June and minimum rates in October and November and that the consumption of *Tellina* was reflected in the energy demands associated with reproductive output (Ansell, 1982a). Following transfer to the laboratory *P. alderi* frequently showed an initial growth phase prior to the commencement of egg collar production, which led to a reduction in growth rates (Ansell, 1982a). These patterns of activity are certainly supported by the findings of these experiments. Once mature, naticid gastropods enter cycles of growth and reproduction that succeed each other annually (Ansell, 1982a). Essentially the life of naticids is characterised by a growth phase prior to sexual maturity followed by cycles of growth and reproduction, during which growth is limited (Ansell, 1982a).

Few data are currently available on the reproductive biology of the other common naticid species found around the British coasts, namely *Euspira catena*. However, egg collar production by *Polinices* (= *Euspira*) *catena* in laboratory cultures was shown to begin in May, 22 months after hatching from egg collars as juveniles (Ansell, 1982b), and this author stated that *P. catena* grows to a 'relatively large size' before reaching sexual maturity and is a direct-developer, whilst *P. alderi* becomes sexually mature at 'a smaller size', producing egg collars from which hatch pelagic, planktotrophic veliger larvae. The development of these larvae will be examined in the following chapter. Preliminary observations by Ansell (1982a) indicated that *P. catena* had lower rates of egg collar production than *P. alderi,* and observations during the course of this study indicated that *Euspira catena* in the laboratory produces egg collars rarely in comparison with *E. pulchellus* kept under similar conditions. More work is required to investigate the comparative reproductive potentials of *E. catena* and *E. pulchellus*.

Webber (1977) found considerable variability between gastropod species in the size at which the onset of gametogenesis occurs. General speaking, sexual maturity is prior to prosobranch gastropods reaching their maximum size and age. This is certainly true for *E. pulchellus* from the findings in this chapter. Reaching sexual maturity before reaching a maximum size, 8-9.9 mm and 16 mm respectively for this species, results in demands for both somatic and reproductive processes throughout the reproductive cycle. Moore (1937) and Feare (1970) found that *Littorina littorea* and *Nucella lapillus* respectively stopped shell growth during sexual maturation. This is not always the case, however, as Williams (1964) demonstrated that shell growth in *Littorina littorea* became reduced during times of active reproduction rather than stopping completely.

Although the average wet weights of egg collars per female did not differ considerably between different size classes of females, differences were seen in the individual wet weights of egg collars produced by different sizes of female. What may be required to further clarify this situation are more data on the numbers and wet weights of egg collars laid by individual females, of a range of sizes, monitored over extended periods in isolation. In order to keep producing egg collars, female *Euspira pulchellus* require renewed mating (Ansell, 1982a); however, as stated in the initial observations, female *E. pulchellus* are capable of producing egg collars for a considerable period of time after isolation, as a result of their ability to store sperm. Ansell (1982a) found that females isolated in July, despite ceasing egg collar production in September-October subsequently produced egg collars in the following June, almost a year after isolation. Ansell (1982a) concluded that sperm from one season were stored and used to fertilise eggs produced in the following year.

The unusually large egg collar weighing 5.75 g collected on 19th June from the 14-15.9 mm size class of *E. pulchellus* presents an interesting biological curiosity and the reason for it can only be speculated upon. The female responsible for laying this egg collar may for some reason have stored up a large number of eggs and was unable to, or chose not to, release the eggs in smaller quantities, but rather released them all in one egg collar. The regression equation arrived at in this study closely matches that calculated by Ansell (1982a) of 8154 ± 602 larvae g^{-1} fresh weight of egg collar that he determined from a limited number of measurements (cf. 8137 x wet weight of egg collar (g) from the regression analysis carried out in this study).

Most marine prosobranchs are perennial and iteroparous. Commonly, the amount of reproductive effort shown by iteroparous animals increases with age, as has been demonstrated in species of *Conus* (Perron, 1982). Semelparity has evolved secondarily in terrestrial prosobranchs supposedly in response to reduced resource availability and the need to produce eggs without adequate food to produce more developed juveniles at hatching (Calow, 1978). Adult size must also play a part as numerous small marine gastropods with access to abundant resources are also semelparous. The effect of parental size on reproductive mode has been investigated in several cases of closely related invertebrate species. For example, *Asterina gibbosa* has direct development, producing around 1000 benthic eggs, whereas *A. phylactica*, a fifth the size of its congener, produces only 60 eggs which are brooded (Emson and Crump, 1979). *Alcyonium digitatum* is planktotrophic compared with *A. hibernicum* which broods (Hartnoll, 1977) and *Crepidula fornicata* is planktotrophic while *C. convexa* brood its eggs, (Hoagland, 1978). Similarly, *Pisaster ochraceus* has planktotrophic larvae whilst *Leptasterias hexactis*, a starfish a twentieth its size, due to the interactions with its superior competitor *P. ochraceus*, broods its eggs (Menge, 1975). In all these cases the smaller of the two species adopts what could be regarded as the less risky method of reproduction. Menge (1975) states that *L. hexactis* is "too small" for planktotrophy to be successful, however, as Grahame (1982) points out *Lacuna vincta* is a fraction of the size of *L. hexactis* and yet survives with planktotrophic development. A more plausible explanation for the situation described by Menge (1975) is that brooding in the genus *Leptasterias* is a fixed trait (Himmelman *et al.*, 1982) rather than a "coadaptive consequence of competition-induced small size". Furthermore, Hines (1982) challenges the notion that life-history traits are able to evolve freely in response to demographic influences.

Underwood (1979) proposed that there may be two size thresholds at work amongst the prosobranchs that could explain the modes of reproduction adopted by particular species. The author proposed that firstly, the largest animals have both lecithotrophy and planktotrophy as possible options, or may brood their offspring. Intermediate-sized animals, however, are unable to produce enough lecithotrophic eggs and are therefore constrained to either planktotrophy or brooding, and finally, the smallest species revert to lecithotrophy combined with cryptic habits as a mode of reproduction. More work is required to investigate thoroughly the energetics and demographics of the small species which have not been as extensively studied. Underwood (1979) suggested that small molluscs are in something of a dilemma, being unable to produce sufficient and large enough eggs to successfully adopt direct development and yet being incapable of producing enough larvae to overcome the high mortality associated with planktotrophic development. As well as being costly, using resources that could otherwise be devoted to other activities, reproduction is also risky. Menge (1974) reports that *Leptaterias hexactis* broods fewer eggs on exposed than sheltered shores, and that brooding individuals seem to be at greater risk of being washed away due to having less tube feet attached to the substratum.

It has been suggested here and elsewhere (Ansell, 1982a) that temperature has a strong influence on the rates of egg collar production in *E. pulchellus*. Ansell (1982a) found that rates of egg collar production were maximal between 15° C and 20° C, but that temperature had little effect on the timing or extent of the reproductive period in mixed-sex cultures. Despite temperature frequently being cited as an important factor in gonadal development (Giese and Pearse, 1974), few data exist for prosobranch gastropods (Webber, 1977). Many organisms reproduce at specific times of the year, and in areas where temperature changes seasonally, this is likely to act as a cue for reproduction. Egg-laying may not occur below a critical temperature and this temperature may vary with location, as in the case of *Urosalpinx cinerea*, which does not spawn below 20° C in Virginia (Federighi, 1931, Nelson, 1931) and Connecticut (Manzi, 1970) compared with 15° C in Delaware (Stauber, 1950) and 12-13° C in Britain (Cole, 1942). Whilst temperature appears to be the major environmental influence on spawning, other factors also play a role, not least the attainment of a size at which individuals are sexually mature. In many gastropod species, however, there are specific triggers that bring about spawning. Spawning cues in prosobranchs include temperature, salinity, lunar periodicity, tidal rhythms and possibly surf. High surf stimulating spawning has been reported for *Patella vulgata* (Orton *et al.*, 1956) and *Littorina* (= *Melarhaphe*) *neritoides* (Polant and Fishelson, 1968). Certain species may co-ordinate their breeding with phases of the spring-neap cycle such as in the case of *Littorina littorea*, which whilst releasing eggs on both spring and neap tides, shows increased spawning activity on spring tides, presumably to enhance the dispersal of egg capsules at times when tidal flow is greatest (Grahame, 1975; Fish 1979). *Littorina littorea* also has a tendency to spawn daily on high tides (Tattersall, 1920).

Food availability for planktotrophic larvae may also influence the timing of spawning. Himmelman (1975, 1979) demonstrated that a number of invertebrates spawn at the time of the spring phytoplankton bloom in order to ensure adequate food availability for their offspring. Such animals only began to spawn in the laboratory immediately after phytoplankton was introduced despite temperature and light conditions being manipulated. More recently Starr *et al.* (1990) similarly found a peak in the abundance of planktotrophic larvae linked to phytoplankton blooms. The Arctic species *Semibalanus balanoides* avoids the risk of insufficient phytoplankton availability for its progeny by the mediation of the release of its nauplii by a pheromone-like substance (Crisp, 1956, Crisp and Spencer, 1958). Underwood (1979) demonstrated that certain benthic gastropods time their breeding so that larvae settle at times when predators, specifically brittlestars, were breeding, and consequently not feeding. Thorson (1953, 1966) proposed the concept of the simultaneous larval settlement of predator and prey species such that prey settlement occurs during periods of reduced predation associated with the reproductive activity of the predators themselves. Nevertheless, this process does not seem to "universally" save juvenile prey spat from heavy losses or indeed their complete destruction by a new cohort of predators (Mileikovsky, 1974). Thorson (1966) himself reported the simultaneous settlement in the German Wadden Sea of the bivalve *Spisula subtruncata* and the two predators *Natica alderi* and the brittlestar *Ophiura texturata* that resulted in the complete destruction of the spat by the newly settled predators. The coincidence of reproductive activity of predators and prey to avoid excess predation upon juvenile prey is disputed by the observation that the pelagic larvae and early juveniles of many marine bottom invertebrates commonly pass alive through the feeding apparatus of suspension and deposit feeding benthic invertebrates (Mileikovsky, 1974). Christensen (1970) reports that the predatory starfish *Astropecten irregularis* ingests the gastropod *Natica* spp. but is unable to digest it and this predatory gastropod is egested alive and unharmed having spent between two and three weeks in the stomach of *A. irregularis*. Mileikovsky (1974), however, rejects the notion that this phenomenon has any adaptive significance or plays any important role in the maintenance and recruitment processes of the species involved or the marine benthos as a whole. Certain times of year therefore may present better or worse times for the survival of juveniles. Predation of larvae and spat in the plankton by not only carnivores but also suspension-feeders is also a consideration. A variety of factors therefore exist that are capable of influencing the time of year at which reproductive fitness can be optimised.

SUMMARY

In preliminary experiments, collectively *Euspira pulchellus* produced egg collars all year round. Following on from this initial work, egg collar production in the laboratory was shown to be greatest during July and August and only occurred in females > 8-9.9 mm shell length. The largest individuals (14-15.9 mm shell length) had the highest fecundity and ceased egg-laying in late September, whereas smaller individuals (8-13.9 mm shell length) laid egg collars until November. Small females (4-5.9 mm) grew rapidly during the warmer, summer months (April to August), became sexually mature and began laying egg collars in mid-September. The range of wet weights of egg collars and the highest wet weight of an individual egg collar produced both increased with increasing size class of female. A significant linear relationship exists between the wet weight of egg collars and the number of larvae released. Temperature strongly affected the time taken for larvae to hatch from an egg collar, which occurred after 9-10 days at 19-20° C and 14-15 days at 13-14° C.

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Chapter 4

Growth, development and metamorphosis of the veliger larvae

INTRODUCTION

Prosobranch gastropods have been shown to display three developmental strategies; oviparity, semiovoviviparity and ovoviviparity (Fretter and Graham, 1994). Oviparous animals deposit spawn on a substratum, which gives rise to crawl-away juveniles in species with direct development, or to larvae which may or may not feed in the plankton. Semiovoviviparous animals release their young as veligers from egg capsules that are retained within the mother. This reproductive mode is rare amongst mesogastropods and neogastropods. Ovoviviparous animals provide fertilized eggs with albumen and hold them within a brood pouch until they hatch as young snails, thereby investing the greatest amount in the protection of their offspring (Carriker, 1955, Mileikovsky, 1971). Encapsulated eggs protect the developing larvae from physical damage. The larvae of *Ilyanassa obsoleta*, *Nucella lamellosa* and *N. lima* are additionally protected from osmotic shock, following the dilution of their immediate environment, by the buffering of the environment surrounding the developing embryo by the egg capsule (Pechenik, 1982). Simpson (1977) distinguished between ovoviviparity and viviparity, and discounted the classification of encapsulated eggs held within the adult gastropods as viviparity, due to the lack of derivation of nutrition by the developing embryo through close contact with maternal tissues, without the interposition of egg membranes.

Prosobranch gastropods are subdivided into three major groups, the Archaeogastropoda, the Mesogastropoda and the Neogastropoda. The archaeogastropods are considered to be most like the ancestral gastropods and their reproductive biology is relatively simple. The Mesogastropoda is the largest of the three groups and its members display the most diverse reproductive biology. Primarily marine neogastropods are considered the most advanced group of gastropods, however, their reproductive biology generally follows the patterns shown by the Mesogastropoda (Webber, 1977). The Archaeogastropoda, of which limpets are common examples, are mostly broadcast spawners, releasing mature gametes and exhibiting external fertilization. The lack of care associated with broadcast spawning is reflected in higher fecundities, thereby increasing the chances of successful fertilizations. In most prosobranchs, however, there is internal fertilization achieved through copulation and in males a penis is present that is situated behind the right tentacle (Webber, 1977). Archaeogastropods possess a larval stage, firstly in the form of a trochophore. In the limpet *Patella vulgata,* the trochophore develops 24 hours after the start of cleavage and lasts between 24 and 36 hours. It is followed by a veliger stage, or more specifically in these animals a 'protoveliger' stage, due to the absence of certain characteristics of the veligers produced by higher prosobranchs (Fretter and Graham, 1994). The larval life of archaeogastropods is dominated by the development of the trochophore into the 'veliger', mainly through the process of torsion. The free veliger stage of the archaeogastropods is of short duration and feeding by this stage is minimal.

In contrast, all mesogastropods and neogastropods, collectively referred to as the monotocardians, pass the trochophore stage within the spawn mass or egg capsule and larvae hatch as post-torsional veligers. Typical monotocardian larvae are planktotrophic veligers that spend extended periods feeding on nanoplankton and microplankton, principally flagellates and to a lesser extent diatoms. Their lives are dominated by actions of the velum, a structure that is responsible for both swimming and feeding (Fretter, 1972). Food is collected at the velar edge by numerous long, compound cilia, which are under nervous control. These form a pre-oral band bordering a food groove, which contains shorter cilia which create a current directing food particles into the mouth. As in the adult, a current of water passes from the left to the right of the animal through the mantle cavity. This current is maintained whilst the veliger swims, and also when the animal is partly contracted, but ceases should adverse conditions cause a rapid withdrawal of the animal into its shell. As a result of torsion, in newly hatched monotocardian planktonic veligers, the mantle cavity, lying dorsally over the head is sufficient in volume to accommodate both the velum and the foot when the animal is withdrawn into the shell by the larval retractor muscle (Fretter, 1969). Torsion arose from a mutation that occurred in the larval stage of pre-gastropods and that was subsequently beneficial to the adult (Fretter, 1969). Once withdrawn, the animal is protected not only by its shell but also by an operculum attached to the foot.

Thorson (1946) studied the larvae of marine invertebrates found in the Øresund prior to drawing more general conclusions on the classification of larval types (Thorson, 1950). Mileikovsky (1971) reviewed this classification and found that it remained valid, and it is still widely used today. Thorson (1950) remains one of the most significant contributions to our present understanding of the different modes of development and larval biology of marine invertebrates. Thorson (1950) distinguished between planktotrophic and non-planktotrophic modes of development in gastropods by examining larval shell morphology in his "Apex Theory" that was later expanded upon by Shuto (1974). The relationship between larval shell morphology and reproductive mode and its application to achieving a better understanding of ecological processes, both in Recent and fossil records, has proved rewarding (Thorson, 1950, Scheltema, 1978, Jablonski and Lutz, 1983, Lima and Lutz, 1990). Thorson (1946) stated that larvae belong to one of three types:

i) *long-lived planktotrophic larvae*

Larvae of this type spend between 1 week and 2 or 3 months in the plankton feeding on other planktonic organisms, usually phytoplankton. The main advantage of this larval type is seen as the capacity for dispersal, with a trade-off of high mortality in the plankton. Larval mortality has been estimated to be as high as over 99% (Thorson, 1950, 1966, Mileikovsky, 1971). Due to this "waste", larvae of this type are produced in high numbers and are considered "cheap" in that they are small and have small provisions of yolk in the egg. Despite the losses, the extraordinary numbers of larvae produced are sufficient to ensure the continued survival of species adopting this reproductive mode. It is worth noting that while predation in the plankton may account for significant losses of larvae, predation upon benthic egg capsules and egg masses from a wide range of predators may also be intense (Spight, 1977, Pechenik, 1979).

ii) *short-lived planktotrophic larvae*

Larvae of this type change very little in size and organization during their time in the plankton. Feeding is not obligatory since in some species larval settlement occurs without feeding. They are referred to as 'planktotrophic' as they possess a fully developed, apparently functional gut upon hatching.

iii) *lecithotrophic pelagic larvae*

Lecithotrophic larvae are usually larger than planktotrophic larvae, at least when they hatch, due to the provision of considerable amounts of yolk which provide all the energy needed by the larvae until they metamorphose into juveniles.

There are, however, marine invertebrate species, not least amongst the prosobranch gastropods, the life history strategies of which lack a larval period. In gastropod species with 'direct development', juveniles hatch from encapsulated eggs that are laid on a substratum chosen by the female. Direct development in monotocardians is associated with the necessary provision of food for the embryo in the form of yolk or albumen, present in various amounts in almost all species (Webber, 1977). A variety of cells exist that provide nutrition for the developing ova and embryos. The phenomenon of embryos completing their development through the consumption of neighbouring food eggs or early embryos is referred to as adelphophagy, (Mileikovsky, 1971). Its occurrence is erratic even within a genus (Fretter and Graham, 1994), for example *Euspira catena* is the only naticid found to provide food eggs (Ankel, 1930, Thorson, 1946). Each egg capsule within the egg collars of *E. catena* contains 50 to 180 eggs, however, only between 2 and 19 of these hatch, with the remainder comprising food eggs that are disintegrated by the velar cilia and ingested by the developing embryos.

Different schemes of describing different reproductive modes will often reflect an author's particular interest. Those interested in dispersal will distinguish between planktonic and non-planktonic strategies, whilst those more interested in resource use, or feeding strategies, will emphasise planktotrophy and lecithotrophy (Jablonski and Lutz, 1980, Grahame and Branch, 1985). Reproductive strategies in marine invertebrates were recently reviewed by Giangrande *et al.* (1994). In addition, the different patterns of life history exhibited by marine invertebrates were described and summarized by Grahame and Branch (1985), including much information regarding prosobranch gastropods. Life history tactics were reviewed by Stearns (1976) and refer to "bet-hedging", in which the crucial factor is the predictability of the mortality of a particular stage in the animal's life. Stearns (1976) proposed that reduced reproductive effort, smaller clutches and longer adult life, particularly repeated breeding or iteroparity, are favoured by unpredictable juvenile mortality, whilst unpredictable or heavy adult mortality favours large and early investment in reproduction, large clutches and semelparity. For example, *Nassarius pauperatus* increases its fecundity when presented with unfavourable conditions for future adult survival, such as a shortage of food (McKillup and Butler, 1979).

A criticism of early work that attempted to categorise developmental patterns is that it does not take account of the plasticity that exists within species. Distinct populations of the same species inhabiting closely situated locations, or different individuals within the same population, may exhibit different types of larval development, a phenomenon referred to as poecilogony (see Hoagland and Robertson 1988, and Bouchet, 1989 for reviews). The reproductive strategy of the naticid *Polinices triseriata* in the coastal waters of Canada has been reported to be dominated by direct development in years with cool, wet summers and by "semiplanktonic" development in years with dry, hot summers (Giglioli, 1955). In the latter case, once hatched, larvae were reported to spend a few hours drifting passively in the plankton, unable to determine their position in the water column. This study went on to state that it seems likely that both strategies are employed each year but that one or other dominates depending on the weather conditions. Bouchet (1989) disputes that this represents a true case of poecilogony, as in neither case are the larvae planktotrophic, and the difference merely represents one of a few hours in the timing of hatching and metamorphosis. Poecilogony has also been reported as occurring in the naticid species *Euspira catena*. Thorson (1935) reported direct development for this species whilst Lebour (1936) described free-swimming larvae for this species. Lebour (1936, 1937) described the eggs and larvae of those prosobranchs species found in the waters around Plymouth, and included in Lebour (1936) was the tentative attribution of a naticid pelagic larva to *E. catena*. Thorson (1950) believed this discrepancy to be based on the erroneous identification by Lebour of a larva of *Polinices montagui*. Thorson (1946) described the larva hatching from collars of *E. catena* collected from Danish waters as being non-pelagic, which seems likely to be based on the presence of nutritional nurse eggs, unique to this species within the family Naticidae (Ankel, 1930, Thorson, 1946). The findings of Lebour (1936) have not since been repeated despite the common nature of this species. Another discrepancy over reproductive strategies within the Naticidae has arisen in *Polinices lewisii*. Bernard (1967) reported short-term, lecithotrophic larvae for *P. lewisii*, whereas Giglioli (1955) predicted planktotrophic larvae for this species on the basis of the dimensions of embryos and egg capsules of preserved egg masses. Planktotrophy is confirmed for *P. lewisii* by Pedersen and Page (2000) based upon the collection of egg masses during four successive years around Vancouver Island, British Columbia, Canada and the subsequent rearing of larvae that were released. Pedersen and Page (2000), however, are reluctant to dismiss the findings of Bernard (1967) lightly, as he described the presence of a large foot in the newly hatched larva. Pedersen and Page (2000) consider the possibility of cryptic sister species, distinguishable by different types of development. Cases previously thought to represent poecilogony are now considered instead to involve cryptic species that were previously considered single species. Bouchet (1989) dismisses the existence of poecilogony in the family Naticidae and furthermore was unable to present a single indisputable case of poecilogony in the prosobranchs or shelled opisthobranchs. However, Bouchet (1989) states that poecilogony certainly exists in the Ascoglossa and also possibly amongst the nudibranchs.

Marine prosobranchs with indirect development, of which *Euspira pulchellus* is an example, have two critical stages in their life cycle, namely hatching and metamorphosis. The termination of larval life firstly involves settlement, presumed to be under nervous control (Scheltema, 1974), which involves the change from a planktonic to a benthic existence and is reversible. Metamorphosis, presumed to be under endocrine control (Scheltema, 1974), is irreversible as it involves morphological and physiological alteration to the adult form. In gastropod veligers metamorphosis is characterised by the loss of the velum (Crisp, 1974). Metamorphosis represents an abrupt end to larval life and a marked ontogenetic shift in feeding habit, in the case of naticids from the velar capture of microalgae to the drilling of molluscan prey.

The main aims of the work covered in this chapter were to investigate the development and growth of the veliger larvae of *Euspira pulchellus,* from hatching through to settlement and metamorphosis and to document the changes in morphology and behaviour that occur during the early life history of *E. pulchellus*. This includes an investigation into the early feeding behaviour of post-metamorphic newly settled juveniles.

MATERIALS AND METHODS

1) Larval culture and the measurement of larval growth

Veliger larvae remaining in the 2 litre beaker after counting (see Chapter 3) were collected on a 63μm plankton mesh sieve and washed back by pipette into another 2 litre beaker of filtered seawater (FSW, for details see "Materials and Methods" Chapter 3). Larvae were raised on a diet of *Rhinomonas reticulata* and *Pavlova lutheri* at cell concentrations of 10 cells per μl and 40 cells per μl respectively. Larvae were transferred to fresh FSW on alternate days and the algal mixture replenished. Attempts were made to raise veligers at 13-14° C by placing culture beakers in a water bath under thermostatic control. Culture beakers were also stored in a thermostatically controlled cabinet set at 19-20° C. The cabinet was maintained on a 8L:16D light-dark cycle. All beakers were covered with a sheet of perspex, preventing material falling into the culture and minimising evaporation. At weekly intervals after hatching, a sub-sample of 15 larvae was transferred to a cavity slide using a sterile glass pipette and these larvae were killed by the addition of 10ml of 70% industrial methylated spirit (IMS). The shell lengths of these larvae were then measured (to the nearest 5 μm) using an inverted microscope with a calibrated eyepiece graticule. Figure 2a shows the orientation of the larva used to measure shell length. The shell length of each veliger was measured by positioning the lines of the graticule parallel to visualised tangents to the two curved surfaces of the larval shell, at the left and right sides of the animal in Figure 2a. Only larvae that had bright red stomachs when observed under the inverted microscope were measured, indicating that they had recently been feeding upon *Rhinomonas reticulata cells*. The presence of newly deposited shell material at the shell margin was also a sign that larvae were growing and such larvae were also measured.

2) Photography of developmental stages

In order to document the development of veliger larvae, photographs were taken of a sub-sample of larvae from cultures on the day of hatching and at weekly intervals thereafter. This required the transfer of larvae from the culture beaker to a smaller container using a sterile glass pipette. For the first 6 weeks after hatching this container comprised a perspex slide 75 mm x 35 mm x 6 mm thick with a 15 mm diameter circular portion cut out of it in the centre. A glass cover-slip was permanently attached to one side of the slide using DPX in order that the cavity could hold a small volume of seawater in which the veligers could swim or crawl. Once the larvae had been placed in a small volume of seawater in this cavity and the slide placed on the microscope stage, a second cover-slip was placed on the slide. Care was taken in lowering the cover-slip onto the slide to minimise the amount of air trapped between the two cover-slips and therefore avoid the curvature of the image when close to the edge of the cavity.

From 6 weeks post-hatching onwards animals to be photographed were instead transferred to a small glass Petri dish, 50 mm in diameter and 10 mm in depth, which held a small volume of seawater. A Leitz Laborlux S compound microscope was used to view the larvae up until 6 weeks post-hatching. Beyond this age larvae had grown too large to be viewed under the compound microscope. Pediveligers (6-7 weeks post-hatching), newly settled individuals (~7 weeks post-hatching) and juveniles up to 1 month post-metamorphosis were viewed using a Wild M3Z stereomicroscope. Images of the developmental stages of *E. pulchellus* were captured by attaching a Panasonic F15 High Sensitivity video camera to one or other microscope, depending on the age of the animals to be photographed. The video camera was connected to a Panasonic AG6720 Time Lapse Video Cassette Recorder. Still images of veligers, pediveligers, settlers and juveniles were then captured from the VHS footage using Adobe Première software, that allowed desired sections of footage to be recorded from the video cassettes onto the PC to create a digital version of the footage which could be advanced frame by frame to obtain the clearest images.

3) Induction of metamorphosis of competent pediveligers.

Sub-samples of larvae from the culture beakers were examined individually on a daily basis under a Wild M3Z stereomicroscope in order to determine if they had reached metamorphic competence. Larvae were deemed to be competent to metamorphose if they were able to crawl across the bottom of the glass Petri dish, whilst still in possession of a velum. Competent individuals are subsequently referred to as 'pediveligers'. The presence of a 'swimming-crawling' stage was termed the 'pediveliger' by Carriker (1956) and although originally used in the context of the development of bivalve larvae, is equally appropriate to be used for another class of the Mollusca, namely the gastropods.

Up to 50 pediveligers were transferred to a separate 2 litre beaker of FSW and algal mixture. A sample of sediment from the area of Red Wharf Bay in which *E. pulchellus* had been collected in high numbers during the sampling trips (Chapter 2) was collected using a small hand-operated grab. On returning to the laboratory, the sediment sample was stored at 5° C overnight. The following day the sediment was washed through a 500 µm stainless steel mesh sieve to remove any macrofauna. A 1-2 mm depth layer of this sediment was placed on the bottom of the sterilised 2 litre perspex beaker and 1800 ml of FSW and algal mixture was added. The beaker was left to stand to allow the sediment to settle, in an attempt to recreate the situation in which the pediveligers might encounter the sediment when they descend from the water column to the seabed. Pediveligers were then added to the beaker containing the sediment and left overnight. The following day the overlying water was decanted to leave sufficient volume to wash the retained sediment over the bottom of a white plastic tray to a depth of ~1 mm. Animals were retrieved from the sediment by the observation of trail marks that appeared when the animals began to crawl. Trail marks stood out clearly against the white of the tray provided that the sediment was spread sufficiently thinly. Once located by this method, animals were removed using a glass pipette and examined individually in a small glass pipette under a dissecting stereomicroscope in order to determine whether or not they had lost their velum and therefore undergone metamorphosis and adopted a benthic habit.

4) Delay of metamorphosis

In order to investigate the possibility of delayed metamorphosis in *Euspira pulchellus*, one culture of veligers that hatched on September 6th 2001 was kept alive until no healthy larvae remained, with continued changes of water and algae on alternate days. The culture was examined each morning for the presence of extended vela in the animals.

5) Investigation of early feeding behaviour

Following the successful induction of metamorphosis by the method described above, newly settled juveniles were held individually in small glass Petri dishes 50 mm in diameter and 10 mm in depth with glass lids placed on top. Dishes were filled with seawater and each juvenile offered two prey items (2-4 mm), which were checked daily. Any prey items that had been drilled or had died were replaced. Dishes were held in a thermostatically controlled cabinet maintained at 19-20° C. The bivalves *Lasaea adansoni* and *Cerastoderma edule* were chosen as a suitably small prey species that could be collected in sufficient numbers to be offered as prey to newly settled juveniles. *Lasaea adansoni* was collected from patches of *Lichina pygmaea* growing in rock crevices, high on exposed shores both at Treaddur Bay and Aberffraw, Anglesey, North Wales. *Lasaea adansoni* occurs at high tidal levels on exposed, wave-swept rocky shores inhabiting empty barnacles, mussel shells, crevices, tufts of *Lichina*, *Corallina* holdfasts and intertidal seaweeds. *Lasaea adansoni* tends to be found patchily but in high numbers and its gregariousness is due to its ovoviviparous reproductive behaviour, whereby embryos are brooded in a suprabranchial chamber. After approximately two weeks of feeding upon *L. adansoni*, juvenile *E. pulchellus* were offered the common cockle, *Cerastoderma edule* (3-4 mm from umbo to shell margin) that were collected from the high shore at Traeth Melynog, near Newborough, Anglesey.

RESULTS

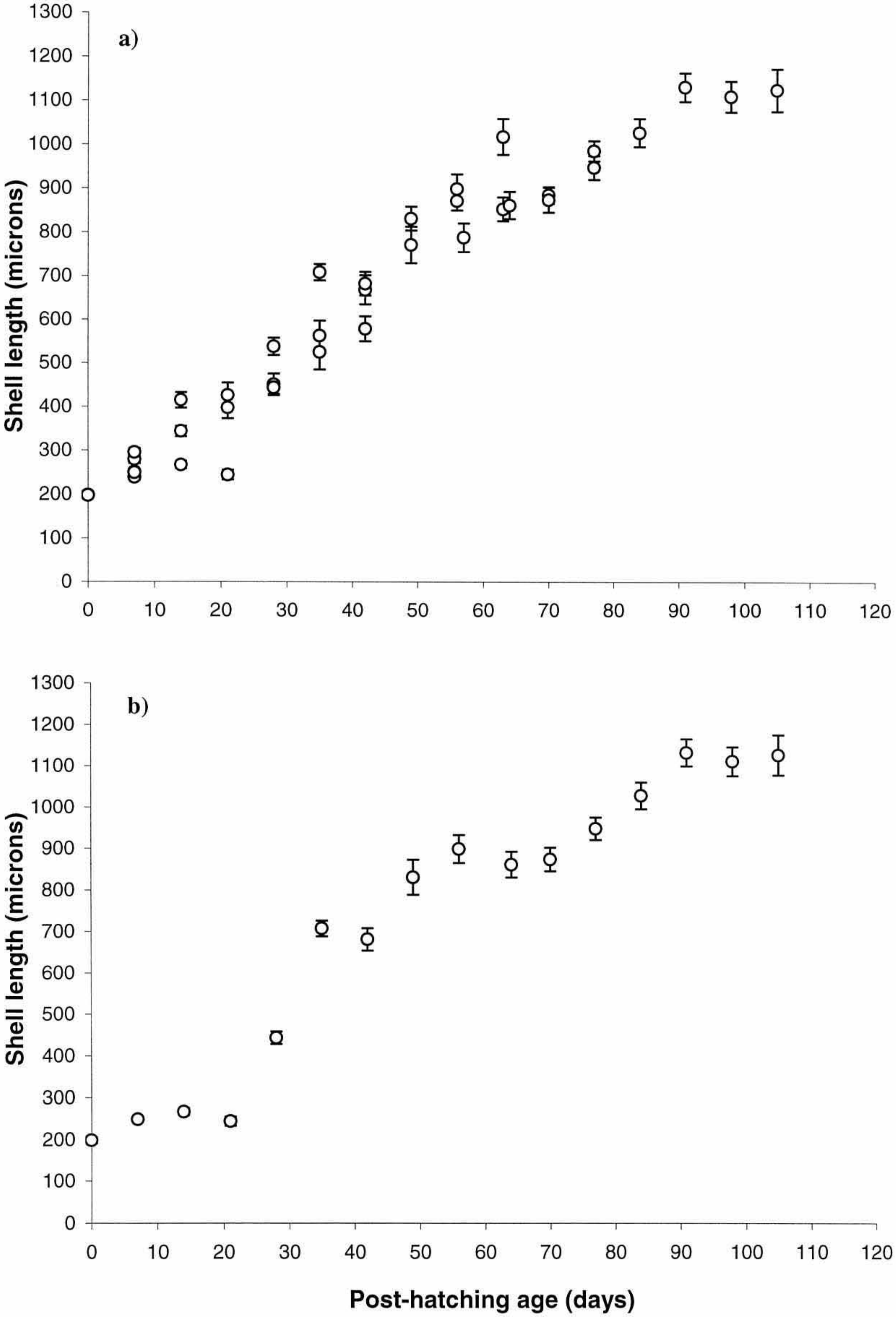
1) Behaviour of veligers

As the shell is the heaviest part of *E. pulchellus*, it is generally orientated downwards whilst the veliger is swimming, with the aperture and expanded velum orientated upwards. Furthermore, the direction of swimming tends to be in the vertical dimension. Veliger larvae are well-equipped to alter their depth by either swimming upwards or by retracting their velum and sinking. They are, however, less well-equipped to swim horizontally, for example in the manner displayed by copepods. Veligers are able to swim without feeding, however, any feeding activity in planktonic gastropod larvae requires swimming. Attempts to attract newly hatched veligers towards a fibre optic light source did not produce any noticeable change in the distribution of larvae within the water column. Newly hatched veligers spent most of their time close to the surface presumably as a result of continuous feeding activity. Upon contacting the water surface the velar cilia stopped beating, the velum folded and the larva sank a short distance before swimming resumed. Larvae feeding near the surface therefore frequently displayed discontinuous movements as a result of the interruption of feeding and consequent sinking on reaching the surface of the water in the beaker. As larvae became older they tended to spend less time at the surface, as they spent less time feeding and a greater proportion of time assessing the nature of substrata. On certain occasions older larvae ventured up into the water column again when observed during the dark hours of the light-dark cycle in the laboratory. As larvae approached metamorphic competence, however, they were rarely seen anywhere other than close to the bottom of the beaker irrespective of the direction or intensity of light falling on the beaker.

2) Larval growth

Repeated attempts to raise *E. pulchellus* veligers at 13-14° C were unsuccessful such that a comparison of growth at different temperatures was not possible. Figure 1a shows the shell lengths of larvae at different ages for all cultures of larvae raised at 19-20° C over the summer of 2000. Each data point represents the mean shell length

Figure 1. Growth of *Euspira pulchellus* veligers grown at 19-20° C a) collective data b) 15th March 2000 culture only. Points represent the mean shell lengths of the sub-samples of larvae and the error bars are the 95% confidence intervals of those means.


a)
b)
Shell length (microns)
Shell length (microns)
0
100
200
300
400
500
600
700
800
900
1000
1100
1200
1300
0
10
20
30
40
50
60
70
80
90
100
110
120
Post-hatching age (days)

of a sample of 15 larvae on a particular day after hatching and the error bars represent the 95% confidence intervals for that mean. Figure 1b shows only the data for one particular culture that hatched on the 15th March 2000 in which the larvae were kept alive for 105 days (15 weeks) before being discarded. Both these figures show the growth of veliger larvae at 19-20° C. The growth of the shell of the veliger larvae was linear up until day 90 but reached an asymptote between day 90 and 110 (beyond the point at which competence is reached).

3) Developmental changes in veligers

Figure 2 shows the changes that occurred to the veligers from the day that they hatched (Figures 2a and 2b), with increasing age (Figures 2c-2e), up until metamorphic competence was attained (Figures 2f and 2g), and eventually individuals settled as juveniles (Figure 2h). The most notable external changes that occurred in the morphology of veliger larvae as they grew larger and older, occurred in the velum and the foot. Figure 2b shows a newly hatched veliger with its bi-lobed velum fully extended as the larva swims. In terms of sensory organs, veligers are equipped with a pair of eyes spots (Figure 2b), tentacles (Figure 2f) and statoliths that control balance, one of which is visible through the shell of a newly hatched veliger in Figure 2a. During the first week after hatching, the velum broadened and began to develop pigmentation at the four corners of the velum. By the end of the second week after hatching this pigmentation was fully developed (Figure 2d). By the end of the fourth week after hatching all healthy larvae had a velum that had become bifurcated into four velar arms, as opposed to the two lobes present on hatching. The pigmentation at the ends of the velar arms was well developed by this time, however, larvae were still unable to crawl. During weeks 5 and 6 post-hatching there was a considerable increase both in the size and degree of black pigmentation of the foot, and by 6 weeks post-hatching most larvae were able to crawl (Figure 2g). The foot is differentiated into the propodium at the front and the metapodium at the back, to which the operculum is attached. These 6-week larvae still possessed a velum, which was visible either through the shell when the animal was withdrawn into its shell, fully extended when the animal was swimming, or protruding at the front of the shell as the animal crawled along (Figure 2g). Another structure visible in late *E. pulchellus* veligers is the gill, a longitudinal fold of the mantle skirt. In higher mesogastropods, including *E.*

Figure 2. a) Lateral view of a newly hatched *Euspira pulchellus* veliger (day 0) retracted into its shell (SH) with the shell aperture closed by the operculum (OP). One of the pair of statoliths (ST) is visible through the transparent shell. b) View from above of a day 0 veliger swimming with its bilobed velum (VL) fully expanded. Pair of eyes (E) present that are directed upwards. c) Lateral view of a 1-week old veliger swimming. Little enlargement of the foot (FT) at this stage. d) 2-week old veliger showing broadened and pigmented velar lobes (PVL). e) 4-week old veliger in which the velar lobes have undergone bifurcation (BF) resulting in four velar arms, the distal regions of which are now strongly pigmented as a result of microalgae consumption. f) 6 week-old pediveliger with well-developed tentacles (T) and an enlarged foot. g) 6-week old pediveliger capable of crawling and metamorphically competent. Gill (GL) visible lying close to the inner surface of the shell. Propodium (PP) well developed. h) Post-metamorphic *Euspira pulchellus* without velum. Foot differentiated into posterior metapodium (MP) and anterior propodium (PP).

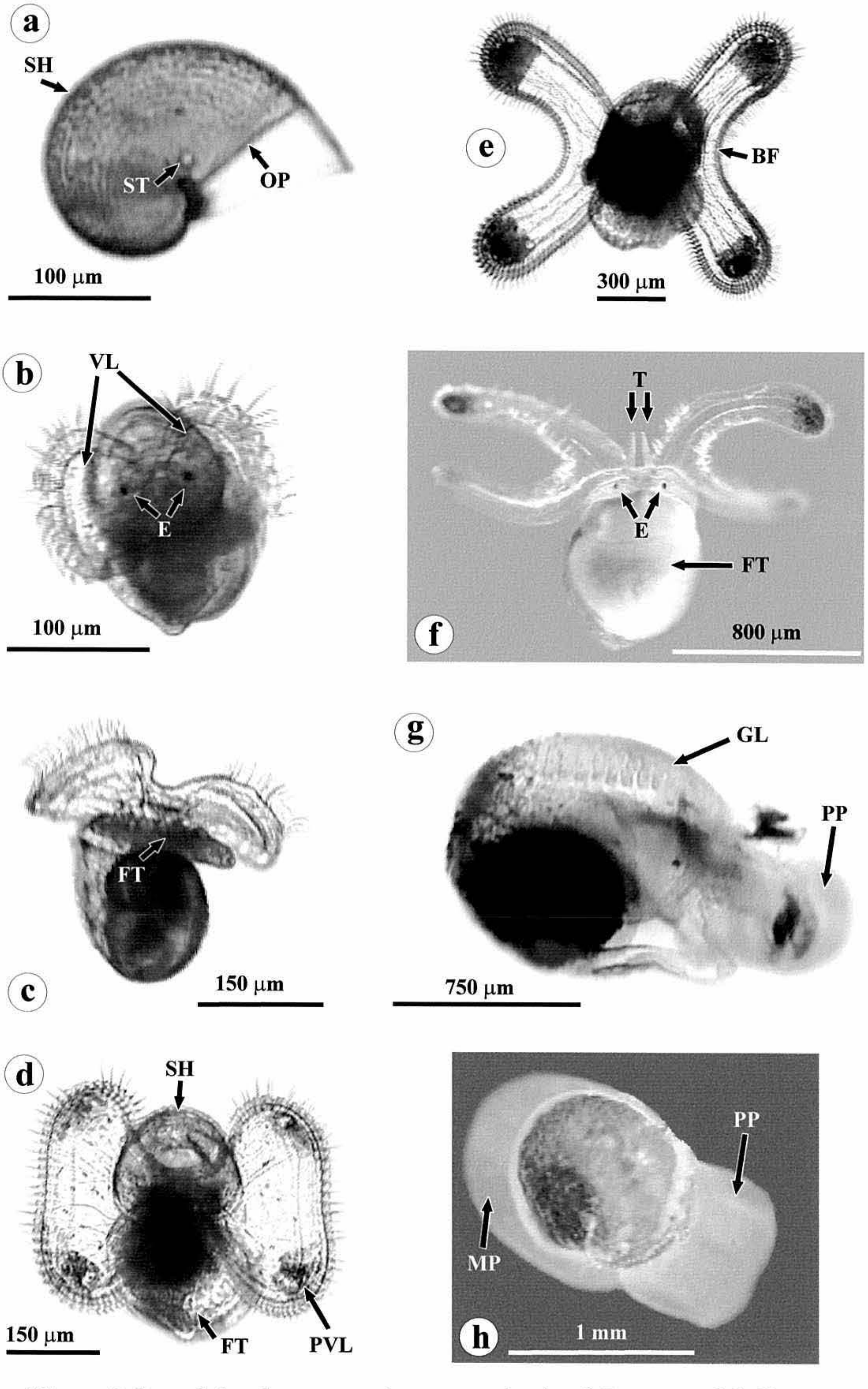


Figure 2. Larval development and metamorphosis of *Euspira pulchellus*.

pulchellus, and in the neogastropods, this fold is differentiated into gill leaflets by the late veliger stage (Figure 2g), whilst in other prosobranchs differentiation of the gill does not occur until metamorphosis (Fretter and Graham, 1994).

4) Metamorphosis

Pediveligers which were exposed to sediment collected from the adult habitat overnight, had lost their velum and therefore had successfully been induced to metamorphose by the following morning. The ability to observe the pigmented regions of the velar arms through the shells of pediveligers was useful in the identification of individuals that were still in possession of the velum and had therefore not metamorphosed, in animals that were not swimming at the time they were observed. Metamorphosed animals were also distinguishable by the projection of the cephalic tentacles beyond the rim of the shell aperture when the animal was crawling. If the velum was still present it was not possible to observe these tentacles when the animal was crawling. Tentacles could also be seen in swimming pediveligers in which the velum was extended, as shown in Figure 2f.

5) Delayed metamorphosis

Pediveligers left in filtered seawater containing the mixed algal suspension, and not exposed to sediment, retained the velum and did not metamorphose. No cases of spontaneous metamorphosis were ever recorded in the course of the investigations. Having developed the ability to crawl by 6-7 weeks, larvae remained at the bottom of the beaker with their velum extended. In the absence of sediment, veligers changed little in appearance and neither died nor metamorphosed, for at least 4 months after reaching metamorphic competence supporting the notion of delayed metamorphosis. The length of time for which larvae remain capable of being induced to settle has yet to be determined. Larvae were regularly found dead, desiccated and stuck to the sides of the beaker above the level of the water. Such individuals may have been searching for a suitable substratum on which to settle. By 6 months post-hatching all but a few of the larvae had perished in this way, and those that had remained alive still possessed a velum but showed little activity. The appearance of the velum in these

Figure 3. a) Left valve of *Lasaea adansoni* drilled by a recently settled *Euspira pulchellus*. b) *E. pulchellus* cannibalised by conspecifics in its first month after settlement, with drill hole (DH) visible. c) The common cockle, *Cerastoderma edule*, drilled by 1-month old (post-settlement) *E. pulchellus*. d) Close-up of the predation signature left in the cockle in figure (c) showing the characteristic countersunk bevelled drill hole (DH) left by naticid gastropods. e) *E. pulchellus* attached to a live *C. edule* with its siphons (SI) out and filtering, with its foot (FT) extended as it attempts to escape. f) *E. pulchellus* firmly attached to *C. edule* close to the umbo in the process of drilling the shell valve. g) Anterio-lateral view of 1-month of *E. pulchellus* showing early development of the shell patterning. h) Foot inflated into shovel-like shape with the propodium reflected anteriorly over the front region of the shell, effectively closing off the mantle cavity during locomotion. i) Shell-length view of *E. pulchellus* demonstrating its globose shape and the major contribution of the last whorl to the overall shell dimension.

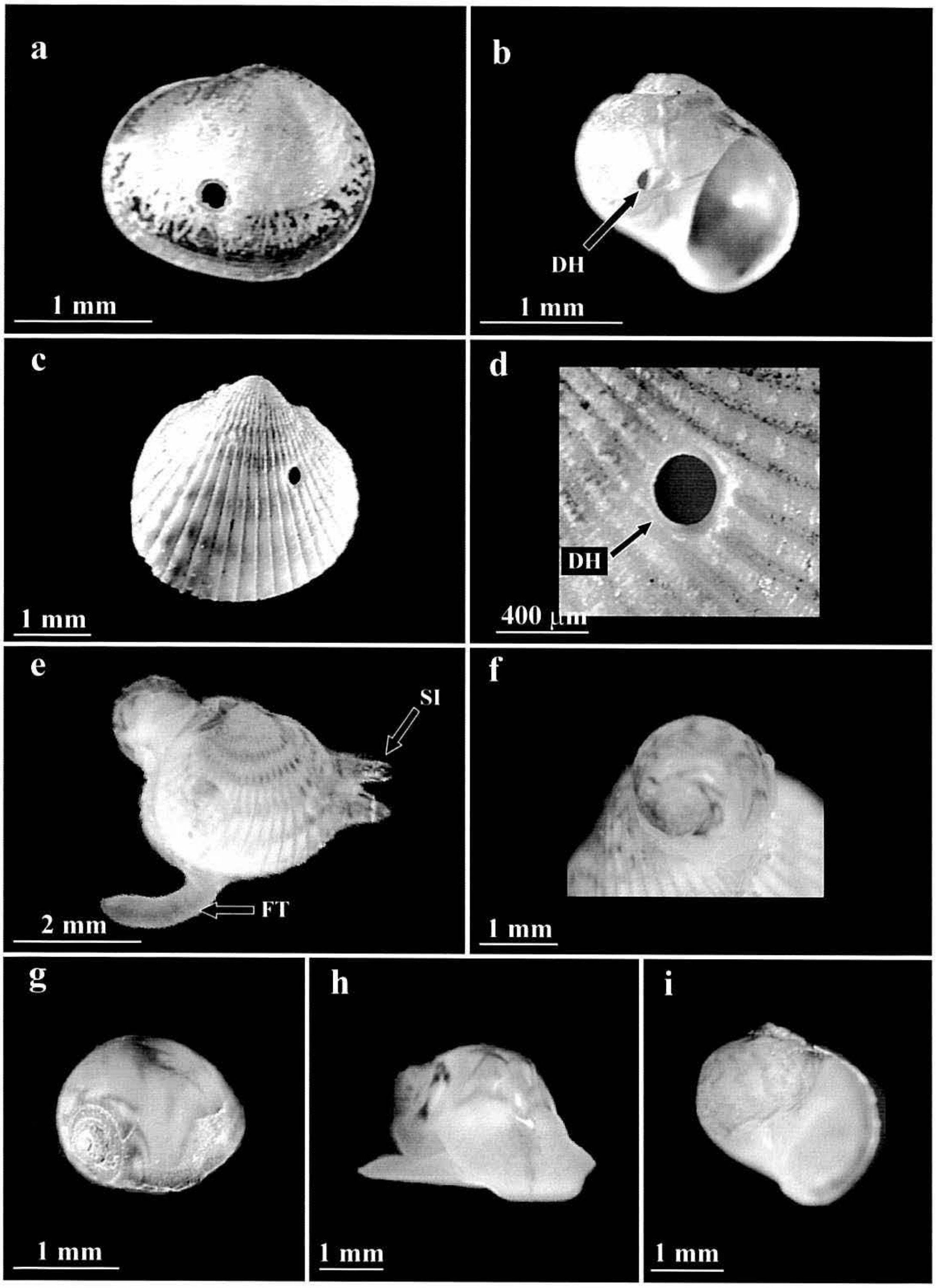


Figure 3. Early post-settlement feeding behaviour in *Euspira pulchellus*

individuals had changed, with the disappearance of all pigmentation, particularly at the distal regions of the velar arms.

6) Early feeding behaviour

Within 3 days of metamorphosis, juvenile *E. pulchellus* drilled ~2 mm *Lasaea adansoni* (Figure 3a) and by 2 weeks post-metamorphosis drilled 3-4 mm *Cerastoderma edule* (Figures 3c and 3d). Juvenile *E. pulchellus*, therefore, were capable of drilling prey that were considerably larger than themselves (Figure 3e) and were capable of remaining attached to *C. edule* despite its vigorous attempts to escape. In Figure 3e the bivalve foot is fully extended as the cockle crawls across the bottom of the glass Petri dish. Figure 3f shows the drilling position adopted by juvenile *E. pulchellus*. Shell laid down after settlement by *E. pulchellus* could be distinguished from the larval shell by the fact that the former showed patterning similar to that seen in the adult, whilst the larval shell lacked any pattern, being plain and fawn in colour. In juvenile *E. pulchellus* a pigmented band was also noticed running longitudinally down the centre of the propodium (Figure 3h). In the absence of bivalve prey, juvenile *E. pulchellus* readily cannibalised conspecifics (Figure 3b).

DISCUSSION

The first response on hatching of the typical monotocardian veliger is to rise through the water column with the velum fully expanded and the foot uppermost, aggregating in areas of high light intensity. This response, however, gradually changes as larvae get older as they spend more time at greater depths exploring the benthos in search of a suitable substratum on which to settle. Barile *et al.* (1994) demonstrated that *Strombus gigas* veligers had a strong attraction to light early in their development and swarmed at the surface in both light and dark conditions, indicating a role of geonegativity. This attraction decreased as veligers became older, with competent veligers showing the lowest response to light fields (see also Thorson, 1964 for review). *Phestilla sibogae* gastropod veligers have been shown to be photopositive when young but increasingly indifferent to light with increasing age (Miller and Hadfield, 1986). Thorson (1964) proposed that the maintenance of young gastropod larvae near the surface of the water column, by a combination of photopositive and geonegative behaviour, increases the dispersal of these larvae by surface currents. *Euspira pulchellus* veligers showed a change in behaviour with time although no photopositive response was observed. It is necessary to distinguish between the presence of larvae in the surface layers of the water column as a result of their attraction to light and their presence there due to upward movement associated with swimming behaviour that is concurrent with feeding. The diurnal vertical migration of gastropod larvae may be due to the alternation between feeding and non-feeding with certain species migrating upwards nocturnally and others migrating upwards in broad daylight or at twilight (Doyle, 1975).

It has been noted that veligers as a rule do not gather food immediately after hatching but rather have a preliminary non-feeding period of planktonic life. This occurs despite the presence of the velum, indicating that veligers are structurally equipped to feed immediately upon hatching (Fretter, 1969). *Lacuna vincta, Rissoa parva, Crepidula fornicata, Nassarius incrassatus* and *N. reticulatus* do not start to feed until 24-72 hrs after hatching from their benthic egg capsules, presumably when yolk reserves have been exhausted (Fretter and Montgomery, 1968). In contrast, Pedersen and Page (2000) observed algal cells within the stomachs of recently hatched *Polinices lewisii* larvae an hour after being placed in seawater containing *Isochrysis galbana*. Similarly, in this study *Rhinomonas reticulata* cells could be seen in the stomachs of *Euspira pulchellus* within an hour of transfer to the culture beaker. The pigments of plant cells ingested by veligers colour the ingesting cells of the gut (Fretter and Montgomery, 1968) and the intensity of this colour, visible through the shell of young veligers examined using light microscopy, gives an indication of both the start of feeding behaviour and the amount of food ingested. The bright red pigmentation of *R. reticulata* was particularly advantageous in this regard.

The larval shell is comprised of organic matrix laid down as sheets of extensible fibres upon which calcification of the shell is initiated, and this allows the viscera to expand (Fretter and Pilkington, 1971). This material is secreted by groups of cells situated close to the mantle edge. New material is only laid down when the edge of the mantle is in contact with the edge of the shell (Fretter and Pilkington, 1971) at times when the veliger is actively swimming and feeding and the velum and mantle edge are distended with blood. Growth lines in the larval shell are formed in response to the cessation of activity in the glands responsible for secreting new shell, such as at times when the larva is inactive. Rates of growth are mainly a function of the quantity and quality of food that larvae ingest and assimilate. Food may include dissolved organic matter (Hines, 1986), in particular amino acids, present in low concentrations in seawater, which may be significant in at least maintaining the condition of the larvae at times when other food is scarce (Fretter and Graham, 1994).

There is compelling evidence that larval growth rates are affected by temperature. Scheltema (1962a) found that *Nassarius obsoletus* completed its veliger stage in 6 to 7 days at 20° C but took 2 months at 12° C. Attempts to rear *P. lewisii* larvae at 12° C failed to produce larvae that were competent to settle after 3½ months, whilst larvae raised at 20 to 22° C were competent to settle 4-5 weeks after hatching (Pedersen and Page, 2000). The failure of larvae to reach competence at this lower temperature surprised these authors, as it fell within the temperature range of the waters around southern Vancouver Island where this species is found. *Polinices lewisii* occurs from the low intertidal down to the shallow subtidal in fine sediment embayments occurring along the West Coast of North America. Pedersen and Page (2000) speculated that *P. lewisii* larvae may require these higher temperatures to complete their development, and therefore remain within the warmer waters of shallow protected embayments. Scheltema (1962a) found that temperatures required for larval growth may differ from those required for metamorphosis. In the case of Nassarius obsoletus, growth was only found to occur at temperatures above 11.5° C, whilst metamorphosis only occurred at or above 16-17° C (Scheltema, 1962a). Similarities can be seen between the development of *Euspira pulchellus* in this study and the Pacific naticid species *Polinices lewisii* (Page and Pedersen, 1998, Pedersen and Page, 2000) in that the most apparent morphological changes occur in the velum and the foot. Metamorphosed larvae of both species are distinguishable by the loss of the velum and the projection of the cephalic tentacles beyond the rim of the shell aperture. Pedersen and Page (2000) noted that 6 days post-hatching each of the enlarging velar lobes in *P. lewisii* had acquired two red spots and by 9 days each lobe had begun to bifurcate, a pattern similar to that observed in *E. pulchellus* in this study.

The duration of the veliger stage is generally short and lasts for a matter of days in archaeogastropods, but tends to be longer in mesogastropods and neogastropods with planktotrophic larvae, lasting between two weeks (Scheltema, 1962a) and two months (Fretter, 1967). *Lacuna vincta* eggs hatch as free-swimming veligers after 2-3 weeks and the planktonic period is long (Thorson, 1946) and ends by the settlement and rapid metamorphosis of this species on algae (Fretter, 1972). Development of the egg in the neogastropod *Nassarius reticulatus* is slower lasting 1-2 months and veligers remain planktonic for 2-3 months prior to metamorphosis (Fretter, 1972). At 18-20° C, *Polinices duplicatus* veligers are released from egg collars after 10 to 12 days and after 25 days as planktonic individuals, whereupon having fed on phytoplankton, they possess a well-developed foot and metamorphose after approximately 30 days (Hanks, 1963). Thorson (1961) brought together data for the duration of the planktonic larval period in 195 species. Most data were taken from laboratory cultures, however, some were derived from field observations. Thorson (1961) related these durations to transport by oceanic currents, choosing the highest figure for the time to reach metamorphosis, the rationale being that at least some will be transported for this length of time. Thorson (1961) emphasised that development times in laboratory conditions in most cases will be longer than in nature, but may be offset by artificially elevated laboratory temperatures. Thorson (1961) concluded that the planktonic life of prosobranch gastropod veligers is short, with no species studied at that time having duration in the plankton greater than 9 weeks, and that in general larvae of temperate-water species are planktonic for 2 to 6 weeks.

Although cases of long-distance transport of prosobranch larvae were known at the time, these larvae were omitted as they had not successfully been reared through to metamorphosis. Many of these 'teleplanic' (Scheltema, 1971) larvae have spines on their shell thought to reduce losses to predation during their long stay of up to 6 months in the plankton. True long-distance larvae occur amongst specialized prosobranch groups and decapod crustaceans, and are mostly associated with tropical and subtropical seas. Most prosobranch larvae, therefore, are thought to be restricted to short distance dispersal. In the absence of a suitable cue to metamorphose, however, the larvae of *E. pulchellus* have been shown to be capable of surviving for a considerable period of time beyond the point at which they reach metamorphic competence.

During metamorphosis, gastropod larvae demonstrate sporadic contractions of the velar retractor muscles. These contractions cause the attachments between the head and the velum to be severed, and the velar lobes are generally resorbed (Franc, 1940, Fretter, 1967, 1972). Alternatively, the large and presumably nutritious velar lobes may be consumed by the newly metamorphosed larvae, as has been reported in *Lacuna vincta* and *Crucibulum spinosum* (Fretter,1972), or may simply be discarded in the case of *Nassarius* (Scheltema, 1962b, Fretter, 1969, 1972). The vulnerability of larvae during metamorphosis, either due to predation or through nutritional stress imposed by an inability to feed, make rapid metamorphosis advantageous or even a necessity for survival. The speed with which these changes take place is highlighted by the short time after metamorphosis that naticids are able to drill prey. Newly settled *Euspira pulchellus* drilled small cockles, *Cerastoderma edule*, and the bivalve *Lasaea rubra* within 3 days of metamorphosis. In contrast, Bernard (1967) reported that *Polinices lewisii* consumed both *Ulva* and diatoms, until it reached 5-6 mm in shell length at which time it switched to feeding on bivalves. Pedersen and Page (2000), however, found no evidence of juvenile *P. lewisii* feeding upon *Ulva*, and rather that *P. lewisii* started drilling bivalves and ostracods within 3 to 5 days of the metamorphic loss of the velum. Kabat (1990) speculated that ostracods might be an important source of food for juvenile naticids. Berg (1976) found that *Natica gualtieriana* were able to drill and ingest small gastropods shortly after metamorphosis, whilst newly settled *Polinices duplicatus* juveniles were carnivorous and fed mainly upon very small gastropod and bivalve prey (Hanks, 1963).

Berg (1976) demonstrated that stereotyped feeding behaviour is present from the moment naticid snails metamorphose. The presence of drill holes of less than 0.4 mm diameter in *Gemma gemma* (Wiltse, 1980) suggests that *Neverita duplicata* begins drilling shortly after metamorphosis at a size of less than 1 mm (Hanks, 1960). The abundance of small drilled *G. gemma* shells indicates that this species represents an important prey for small *Neverita duplicata* (Wiltse, 1980). Juvenile *Neverita duplicata* that have recently emerged from egg collars have been observed to be attracted to young prey, drill holes in them and feed on the soft tissues (Wiltse, 1980).

Early drilling behaviour may also encompass predation upon conspecifics. Cannibalism has been reported in both the Naticidae and the Muricidae (Giglioli, 1949, Edwards and Huebner, 1977, Carriker, 1981, Fretter and Graham, 1994). *Euspira pulchellus* readily cannibalised conspecifics; newly settled juveniles preyed on each other whilst adults were observed to cannibalise smaller individuals. Ansell (1982) reported the occurrence of cannibalistic behaviour in the absence of alternative prey within broods of *Polinices* (= *Euspira*) *catena,* whilst Kitchell *et al.* (1981) observed that cannibalism by the genus *Neverita* was the result of selective predation to maximize energy gain, rather than a consequence of the absence of other suitable prey, a finding supported by Kelley (1991). Dietl and Alexander (1995) demonstrated that the naticids *Euspira heros* and *Neverita duplicata* were selective of their confamilial prey using information gleaned from correlations of predator and prey size determined from predation signatures and prey width respectively. The earliest report of confamilial predation in the fossil record comes from the Ripley Formation, Tennessee of Campanian age during the Cretaceous, in which a multiply-drilled specimen of *Euspira rectilabrum* was discovered (Kitchell *et al.*, 1986). A study of the Nigerian Eocene fauna revealed that approximately 15% of naticid shells contained naticid drill holes (Adegoke and Tevesz, 1974), whilst Kabat and Kohn (1986) determined that during the Fijian Pleistocene naticid predation upon *Natica* spp. accounted for 27% of the mortality of this genus, whilst that upon *Polinices* and *Sinum* spp. accounted for only 3% of deaths. This difference was explained by the greater mobility of the latter genera and therefore a greater ability to evade predation.

The likelihood of encountering a suitable site for transition into the adult habitat, as well as rates of growth and development, influence the time larvae spend in the plankton. Planktonic dispersal carries with it the possibility that larvae may be transported away from their preferred adult habitat. This can partly be overcome by the specific response of larvae to habitat cues and by the ability to delay metamorphosis until a suitable habitat is encountered (Thorson, 1950, 1966, Strathmann, 1978, Crisp, 1984, Pechenik, 1990). The ability to delay metamorphosis acts to promote the placement of individuals in habitats that will support future survival and reproduction (Thorson, 1950, Scheltema, 1961, Crisp, 1974) rather than the larvae being forced to settle in inhospitable surroundings simply because metamorphic competence has been attained. The length of time for which species are capable of delaying metamorphosis is highly variable. Scheltema (1961) found that veligers of the mudsnail *Nassarius obsoleta* in the absence of an optimal substratum, are capable of delaying metamorphosis for up to 20 days. *Nassarius* spp. have been shown to be able to precipitate or delay metamorphosis according to the nature of the substratum and metamorphosis is triggered by exposure to some soluble substance emanating from a favourable substratum into the adjacent water (Scheltema, 1962a, b). Hinegardner (1969) found that larvae of the echinoderm *Lytechinus picta* are capable of delaying metamorphosis for up to 60 days, compared with only 7 days in larvae of the bivalve *Lyrodus pedicellatus* (Turner and Johnson, 1971), 2-5 days in larvae of *Mytilus edulis* (Bayne, 1965), 2 weeks to a month in *Crepidula fornicata* (Pechenik, 1980) and only 12 hours in *Spirorbis borealis* (Williams, 1964). In some cases the end of the delay is brought about by spontaneous metamorphosis, as larvae become "less choosy" as they get older (Knight-Jones, 1953, Crisp, 1974). Alternatively it may arise from the mortality of the larva, either due to a finite larval energy supply at hatching (Knight-Jones, 1953; Eggleston, 1972, Pechenik *et al.* 1979) or to the resorption of feeding structures (Bayne, 1965).

An extended period of metamorphic competence by delaying metamorphosis has been shown to have adverse effects on both larval and post-larval life history traits, in particular by reducing post-larval growth rates (Pechenik, 1990, 1999, Miller, 1993, Pechenik *et al.*, 1998). A reduction in post-larval growth may act to increase the length of time for which individuals are vulnerable to predation due to their small size. Several cases of reduced growth or survival of juveniles arising from an extended planktonic period have been reported (see Pechenik, 1999 for review). These may be partly offset in lecithotrophic larvae by facultative planktotrophy (Miller, 1993). Kempf and Hadfield (1985) found that the lecithotrophic larvae of the nudibranch *Phestilla sibogae* started to feed on plankton if deprived for sufficient time of suitable conditions for settlement, thereby extending the period available to find such conditions. The majority of evidence for delaying metamorphosis comes from laboratory studies and the frequency with which, and conditions under which, it takes place in the field have yet to be clearly defined (Pechenik, 1990). Work has concentrated on the induction of settlement in relation to adult distributions (see Meadows and Campbell, 1972, Crisp, 1974, Burke, 1983 for reviews) rather than on defining capacities for delaying metamorphosis. In the field, delayed metamorphosis may occur rarely as larvae are likely to encounter an environment that contains suitable cues or conditions for metamorphosis. The identification of delayed metamorphosis in larvae collected from the field requires the unequivocal determination of metamorphic competence, based either upon morphological criteria or the ability to trigger metamorphosis in the laboratory. Delayed metamorphosis in the field implies that avoiding predation in the plankton may not be as critical as finding a suitable substratum for juvenile survival and growth (Pechenik, 1999).

A number of studies have shown that the settlement of benthic invertebrate larvae is far from a random process (see Crisp, 1974 for review). The cues that elicit metamorphic responses from larvae include the physical properties of sediments (Knight-Jones, 1953, Gray, 1974, Wethey, 1986, Skilleter and Underwood, 1993) and the microflora and macromolecules associated with particular habitats (Morse and Morse, 1984, Pawlik, 1992). Certain prosobranch species occur on certain species of algae following the specific settlement of their veligers onto these surfaces. *Rissoa splendida* and *Bittium reticulatum* veligers settle in response to chemical stimuli from *Cytoseira* (Kiseleva, 1967). Alternatively, larvae may settle in response to exudates, such as mucous trails, from conspecific adults (Wells and Buckley, 1972) or to encountering a particular prey species. The opisthobranch *Adalaria proxima*, for example, metamorphoses in the presence of the bryozoan *Electra pilosa* on which it browses (Thompson, 1958). Crisp (1974) referred to this type of settlement as "associative settlement" as opposed to the settlement of larvae in response to some chemical recognition of their own or closely-related species or groups of species which Knight-Jones referred to as "gregarious settlement." *Polinices lewisii* larvae metamorphose in response to sediment from the intertidal zone in which the adults are found, but do not respond to this material once it had been autoclaved (Pedersen and Page, 2000). Whilst the present study has demonstrated that sediment from the adult habitat is capable of inducing metamorphosis in *Euspira pulchellus*, the precise nature of the cue has yet to be determined.

Metamorphosis substratum specificity may be problematic in that, by the nature of their metamorphic response, juveniles may be restricted to suboptimal habitats, due to an inability to settle in habitats other than those in which they are usually found that present better conditions for survival and growth (Stoner *et al.*, 1996). The large herbivorous gastropod *Strombus gigas*, a species that is abundant throughout the

Caribbean, has a low metamorphic response to certain habitats, in particular the sea grass *Thalassia testudinum*, despite its ability to support very high post-larval growth rates (Stoner *et al.*, 1996). Choices made by *S. gigas* larvae appear to be influenced by the protective advantages offered by habitats with greater structural complexity. The study of the settlement of marine invertebrates therefore needs to take into consideration the cost-benefit trade-offs facing larvae that are competent to settle. Larvae are faced with a variety of sources of potential mortality and clearly do not settle purely in response to those habitats that offer the optimal conditions for post-larval growth.

Larvae can be thought of in one regard as suspended particles and are therefore affected by hydrodynamic processes. Larvae are also capable, however, of behaviour that can modify the patterns of settlement that would arise through physical processes alone. Nevertheless, hydrodynamics control the fate of larvae through large scale transport and, on a smaller scale, their flux past a particular area of benthos (Ólafsson, *et al.*, 1994). The flow regime may also determine whether larvae are able to settle and exhibit habitat selection. Reduced flow can affect the abundance of benthic invertebrate species with planktonic larvae either though influencing settlement choices or by increasing the settlement of larvae through hydrodynamics alone. Greater recruitment arising from increased settlement leading to higher adult abundances may be explained through hydrodynamic factors rather than active habitat selection. The physical disturbance of soft sediment habitats can also affect levels of post-settlement mortality disputing the notion of Thorson (1950) that spatial and temporal variability in adult populations of soft-sediment invertebrates are generated by the variability of successful recruitment of planktonic larvae due to the risky nature of this stage. Thorson (1950) argued that longer larval periods generate greater variability in zygote survival, settlement rates and adult populations, such that adult populations of species with long larval phases show greater variability than those arising from lecithotrophic larvae or direct developers.

Two originally conflicting hypotheses were proposed to explain patterns of larval settlement, namely active habitat selection and passive deposition (see Butman, 1987 for review). The passive deposition hypothesis states that competent planktonic larvae reach the seafloor at sites where passively sinking particles with fall velocities similar to larvae initially settle (Hannan, 1984). Following this, other biological or physical processes may alter this distribution. Active habitat selection models concentrate on the cues for inducing larval settlement and metamorphosis. Such experiments fall into two broad categories; those of habitat selection in which larvae are given a choice of substrata, and those which study the environmental or biological factors that induce metamorphosis. Butman (1987) stated that those in the first category can provide direct evidence of active habitat selection, while those of the second type only imply selection. Direct choice experiments have shown that larvae preferentially settle in sediments that characterize their natural habitat. Investigations of settlement and metamorphosis cues have primarily been carried out through laboratory experiments in still water. Nevertheless, these types of study are useful for resolving the nature of the inductive factor. Recently, it has been suggested that the hypotheses of active habitat selection by and passive deposition of larvae need not necessary be in conflict but rather may be complementary, and merely operate over different temporal and spatial scales. Butman (1987) suggested that larvae may "be passively deposited and accumulate at large spatial scales (tens of metres to tens of kilometres), which apply to sediment transport and deposition, and that active habitat selection occurs over much smaller scales, of centimetres to metres, within these broad depositional areas". Woodin (1991) reiterated this paradigm of larval recruitment, stating that whilst much of the emphasis has been upon metamorphic responses to positive cues, negative cues and the rejection of unsuitable habitats may be equally important in terms of habitat selection and the resulting infaunal distributions.

Despite the evolutionary trend towards their loss (Pechenik, 1999), planktonic larval stages remain common components of the life histories of benthic invertebrates (Strathmann, 1985, Levin and Bridges, 1995). Their widespread nature is not explained by energetic considerations (Grahame, 1977, 1982, Strathmann, 1985) and the major advantage usually given for their presence, namely dispersal (Mileikovsky, 1971, Underwood, 1974, Jablonski and Lutz, 1983, Graham and Branch, 1985) may be a consequence of rather than a selective force in the maintenance of larvae in life cycles (Pechenik, 1999). Certain invertebrate groups, however, including the prosobranch gastropods, demonstrate a biased transition from planktonic to aplanktonic development, suggesting that larvae may be something to get rid of if possible (Pechenik, 1999). The selection pressures against them, however, are probably not large and adults usually produce enough larvae to overcome the losses incurred through planktonic development (Thorson, 1950). Larvae are also not easily lost from the life history of species whose populations are largely or entirely renewed by the influx of individuals from other populations (Pechenik, 1999). At the very least, dispersive larvae are capable of enabling species to exploit temporally and spatially sporadic niches (Underwood, 1979, Gallardo and Perron, 1982), to overcome local overcrowding, problems of inbreeding (Scheltema, 1971, 1986) and over-specialization (Crisp, 1974), and may reduce competition for resources between parents and offspring (Havenhand, 1995) and be favourable in terms of reduced mortality from epibenthic predators (Pechenik, 1979, Strathmann, 1985).

SUMMARY

Euspira pulchellus produced planktotrophic veliger larvae that hatched from egg collars after 9-10 days at 19-20° C and 14-15 days at 13-14° C. Larvae began feeding within an hour of hatching and the bright red cells of *Rhinomonas reticulata* were visible in the guts of the animals. Newly hatched veligers spent most of their time close to the surface as a result of concurrent swimming and feeding activity, using the velum. Attempts to raise larvae at 13-14° C were unsuccessful. Morphological changes, most notably in the velum and the foot, were observed in larvae raised at 19-20° C as they increased in size and age. During the first four weeks of larval development the velum broadened and bifurcated into four velar arms, the distal regions of which acquired a deep red coloration. In weeks 5 to 6 after hatching, the foot increased considerably in size and also in its degree of black pigmentation. By 6-7 weeks after hatching, larvae, termed 'pediveligers', were able to crawl and competent to metamorphose. Exposure to sediment collected from the adult habitat induced metamorphosis, larvae lost their vela and became benthic. Larvae survived for 4-6 months after reaching metamorphic competence, indicating that they were capable of delaying metamorphosis. Within 3 days of metamorphosis, juveniles began drilling small bivalves (~2 mm) and were also cannibalistic.

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Chapter 5

Prey selection

INTRODUCTION

Much has been written on the subject of optimal foraging and one of the primary aims of research in this field has been to demonstrate that predators select those prey that maximize their net energy gain and therefore their rate of growth (Schoener, 1971, Pyke *et al.*, 1977, Krebs, 1978, Hughes, 1980). Prey should therefore be selected according to their 'profitability' (*sensu* Charnov, 1976), as selection is affected by a variety of prey parameters. Prey selection by naticid gastropods has been shown to conform to a strategy of energy intake maximization, governed by prey size, predator size and the ratio of prey biomass to prey shell thickness (Kitchell *et al.*, 1981, Boggs *et al.*, 1984). It is generally believed that gastropod drilling is the consequence of highly stereotyped behaviour that follows an inflexible sequence of events, particularly with regard to the manipulation of the prey (Kitchell *et al.*, 1981, 1986). The stereotypy of drilling behaviour frequently results in the clustered distribution of drill holes for particular predator-prey interactions. Non-random siting of drill holes by the Naticidae is widely reported (Taylor, 1970, Berg and Porter, 1974, Berg and Nishenko, 1975, Rosewater, 1980 and Kitchell *et al.*, 1981). The relationships between the sizes of gastropods and the prey that they select have been investigated for a wide variety of species, many examples of which are included in the discussion of this chapter. The opportunity to monitor the feeding of *Euspira pulchellus* over a protracted period was used to study in detail not only the seasonal changes in predation rates, but also the parameters of the drilling process itself in order to elucidate the decisions made and behaviour involved in prey selection. The aims of this chapter, therefore, were to investigate:

i) seasonal changes in the feeding rate of *E. pulchellus* in relation to seawater temperature
ii) size-selective predation upon the common cockle, *Cerastoderma edule*
iii) the relationship between the size of *E. pulchellus* and drill hole diameter
iv) the possible occurrence of a left or right valve preference
v) the relationships between predator size, prey size and the location of the drill hole in terms of the region of the valve drilled and the distance of the drill hole from the umbo

MATERIALS AND METHODS

At the beginning of February 2001, 24 *Euspira pulchellus* ranging in size from 4.0 to 15.3 mm in shell length (spire to base of aperture) collected by trawling in Red Wharf Bay (Chapter 2) were individually placed in 1.5 litre aquaria. The aquaria were supplied continuously with running seawater taken from the Menai Strait, Anglesey; prior to its delivery to experimental areas this seawater had been coarsely filtered by being passed through settling tanks. Seawater temperature was recorded every 30 minutes using a Tiny Talk Temperature Logger placed in a separate aquarium located adjacent to the experimental aquaria and supplied with running seawater. Temperature data were downloaded on the last day of each month and the logger re-deployed immediately. No sediment was placed in any of the aquaria in this experiment. Common cockles, *Cerastoderma edule,* were collected by hand from Traeth Melynog, an intertidal mudflat near Newborough, Anglesey. Each *Euspira* was offered one cockle, from each of the following shell height size classes: 0.1-4.9, 5-9.9, 10-14.9, 15-19.9 mm. Each tank was checked every morning and any dead or drilled cockles replaced with those from the equivalent size class. All drilled prey recovered from the aquaria were measured and placed in separate labelled bags recording the date, tank number and shell heights (umbo to shell margin) of drilled prey in millimetres. The shell length of each snail was measured at the start of the experiment, at 4-weekly intervals and finally at the end of the experiment. All measurements of predator shell lengths and prey shell heights were made using vernier callipers (to 0.1 mm). In the event of the death of a predator in a particular tank, it was replaced with an animal of similar size from a stock of animals collected during previous sampling trips. Measurements of shell lengths of replacement snails were made on the day of their addition to the experiment and thereafter at 4-weekly intervals following that date.

The daily records of cockle consumption by each snail were initially collated into fortnightly periods for the purpose of investigating seasonal effects of feeding rates. Data for partial fortnights arising from the addition of replacement snails following mortality events and consumption data during the fortnight prior to that in which the mortality occurred were not included as a precaution against reduced feeding rates of moribund animals. The shell heights of cockles drilled were classified into 1 mm size classes e.g. 0-0.9, 1-1.9, 2-2.9 and so on up to 20-20.9 mm. Using the 4-weekly measurements of the predators, drilled cockles were assigned to one of the following shell length classes of *E. pulchellus*; 4-5.9, 6-7.9, 8-9.9, 10-11.9, 12-13.9 and 14-15.9 mm. Fortnightly data sets of cockle consumption for each size class of predator were converted to rates per snail and combined to produce monthly figures. A subset of 70 drilled cockles encompassing the size range drilled by the predators during the experiment was selected for further study. The drilled valves were examined using a Wild M3Z stereomicroscope and a live image was relayed to a PC using a Panasonic F15 High Sensitivity video camera. Images were then captured using a Matrox Rainbow Runner video capture card and measurements of these images taken using the image analysis software SigmaScan Version 3.0 from Jandel Scientific. For each of the 70 specimens the following parameters were recorded:

- predator size (shell length of *E. pulchellus* in mm)
- prey size (shell height of *C. edule* in mm)
- the position of the drill hole on the shell valve (Figure 1a).
- the inner and outer drill hole diameter (μm) (Figure 1b).
- valve drilled (left or right)
- the distance from the centre of the drill hole to the umbo (mm)

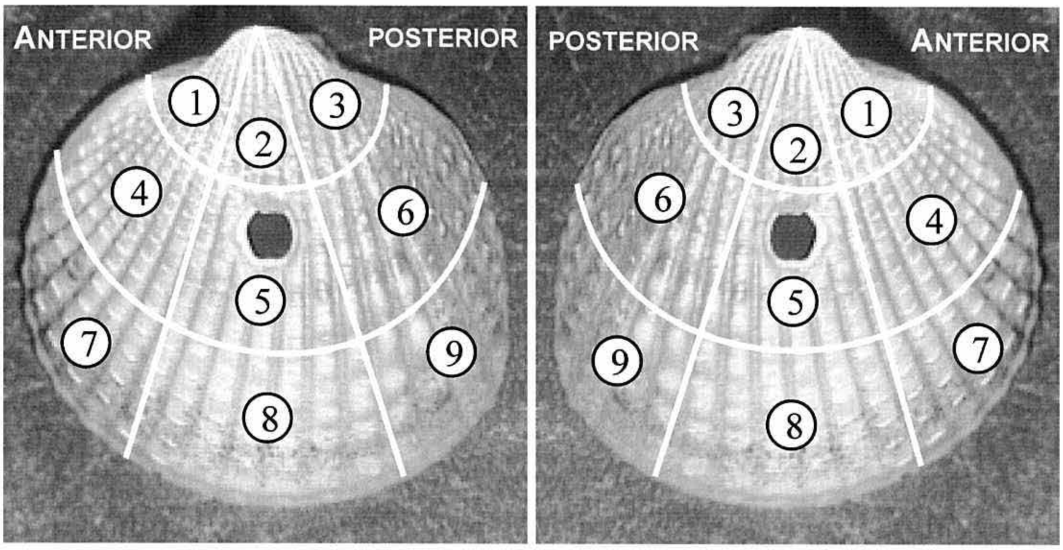
The location of the drill hole in the valve was categorized by ascribing it a number based upon the system shown in Figure 1a. Figure 1b demonstrates a vertical cross-section through a typical drill hole produced by *Euspira pulchellus* in the shell valve of *Cerastoderma edule* examined by sectioning a shell valve through the centre of a drill hole using a diamond saw.

RESULTS

1) Prey size selection

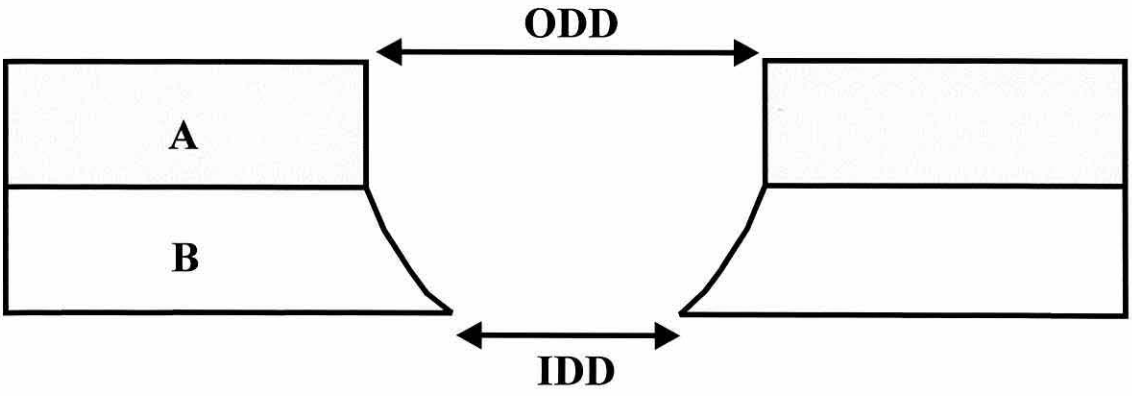
Certain size classes of cockle prey were not available throughout the year due to the seasonal changes in the size-frequency of the prey population at Traeth Melynog. *Cerastoderma edule* spat settle during a discrete period of the year between late June and September (Seed and Brown, 1975) and grow quickly during the summer, such

Figure 1a. Schematic illustration used to categorise the positions (1-9) of drill holes produced by *Euspira pulchellus* when feeding upon the common cockle, *Cerastoderma edule*.



a) Left valve of *Cerastoderma edule* b) Right valve of *Cerastoderma edule*

Figure 1b. Schematic illustration of a typical *Euspira pulchellus* drill hole through the shell valve of *Cerastoderma edule* to demonstrate the difference between the inner drill hole diameter (IDD) and outer drill hole diameter (ODD). The crossed lamellar layer (A) and complex crossed lamellar layer (B) are also represented.



that the smallest cockles (0.1-4.9 mm) were only available during the late summer months. Nevertheless, whilst the modal sizes of *C. edule* in the Traeth Melynog population change over time as individual size classes grow, cockles from each of the three larger prey size categories (5 to 19.9 mm) were collected successfully throughout the period February to November 2001. The smallest snails (4-5.9 mm) only fed upon cockles between 3.0 and 8.9 mm shell height during the experiment and fed most frequently on cockles in the size range 4-4.9 mm (Figure 2a). Snails in the second size class (6-7.9 mm) similarly consumed a high proportion of 4-4.9 mm cockles but also consumed a greater proportion of 6-6.9 mm cockles (Figure 2b) than the smallest snails (4-5.9 mm). Larger predators (> 8 mm) consumed a greater overall size range of cockles and a greater proportion of larger cockle size classes (10-19.9 mm) (Figures 2c-f). On rare occasions 6-7.9 mm *E. pulchellus* drilled cockles in the 12-12.9 mm size class. Large *E. pulchellus* (8-9.9 mm) (Figure 2c) and (10-11.9 mm) (Figure 2d) drilled a higher proportion of 7-7.9 and 8-8.9 mm cockles than the smaller predators (Figures 2a and 2b). There is a general trend of increasing prey size with increasing predator size, with the exception of the 14-15.9 mm snails (Figure 2f). The frequency of cockles drilled in the size range 15-19.9 mm was consistently low. All size classes of predators drilled more cockles in the size ranges 0-4.9 and 5-9.9 mm than those > 10 mm. No cockles > 10 mm were drilled by the smallest (4-5.9 mm) snails. These larger cockles were only drilled to any great extent by the 12-13.9 mm and 14-15.9 mm *E. pulchellus* (Figures 2e and 2f).

2) Seasonal variation in feeding rates

Consumption of cockles by the smallest snails (4-5.9 mm) showed a steady increase between February and July (Figure 3a). By early August, these *E. pulchellus* had reached > 6 mm and are included in the next size category of snail (6-7.9 mm). Consumption rates by all size classes of *E. pulchellus* were low between February and April, ranging from 1.5 to 5.25 *C. edule* animal $^{-1}$ month $^{-1}$. Consumption of cockles by the 6-7.9 mm sized snails peaked in June and by October showed signs of decreasing (Figure 3b). The number of *C. edule* consumed by the 8-9.9 mm sized snails showed a sharp increase from June to July, remaining at a high level between July and September and then declining in October to a minimum rate in November (Figure 3c). A very similar pattern was seen in the 12-13.9 mm animals (Figure 3e).

Figure 2. Size-selective predation by *E. pulchellus* offered a range of sizes of the common cockle, *Cerastoderma edule*. Figure titles a)-f) refer to the sizes of *E. pulchellus*.

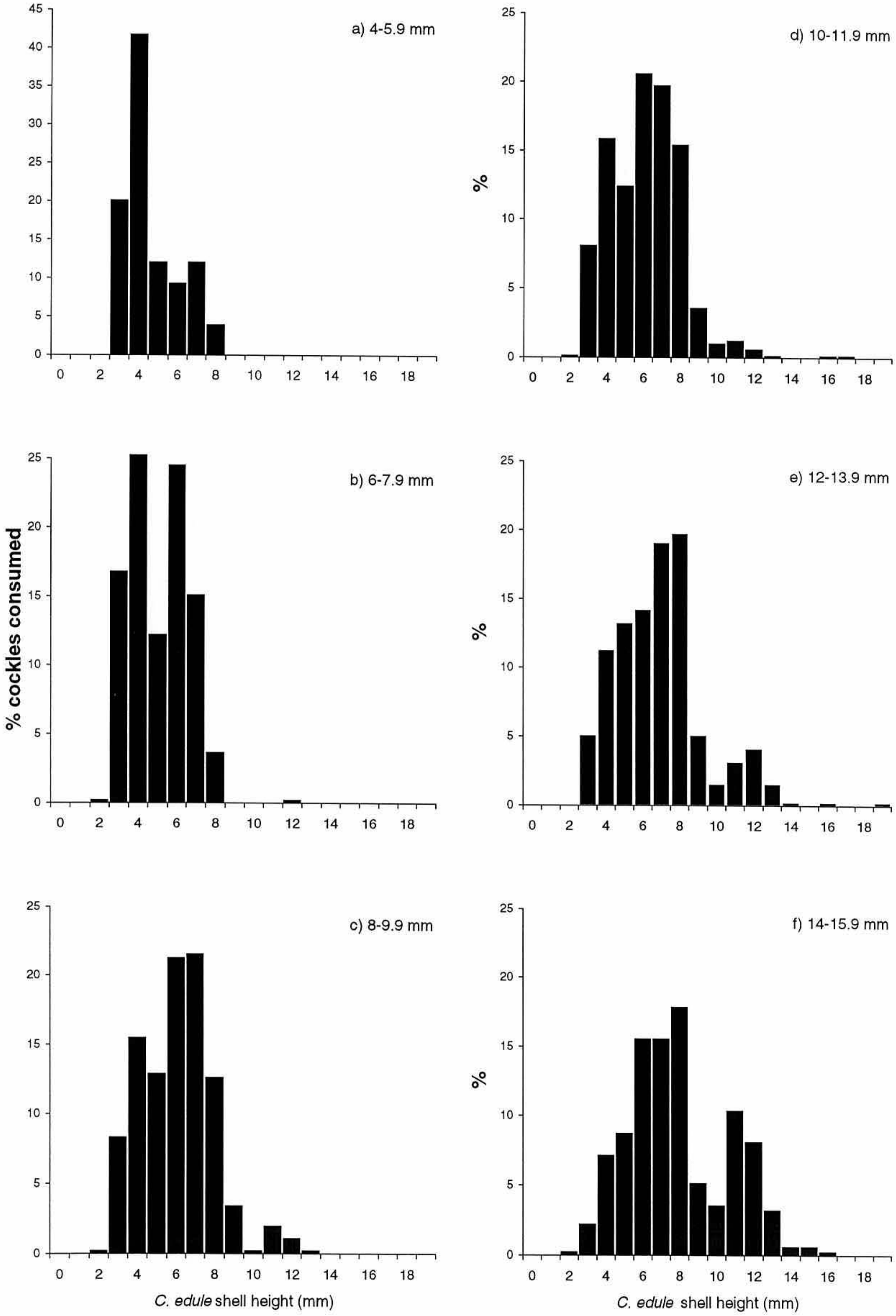
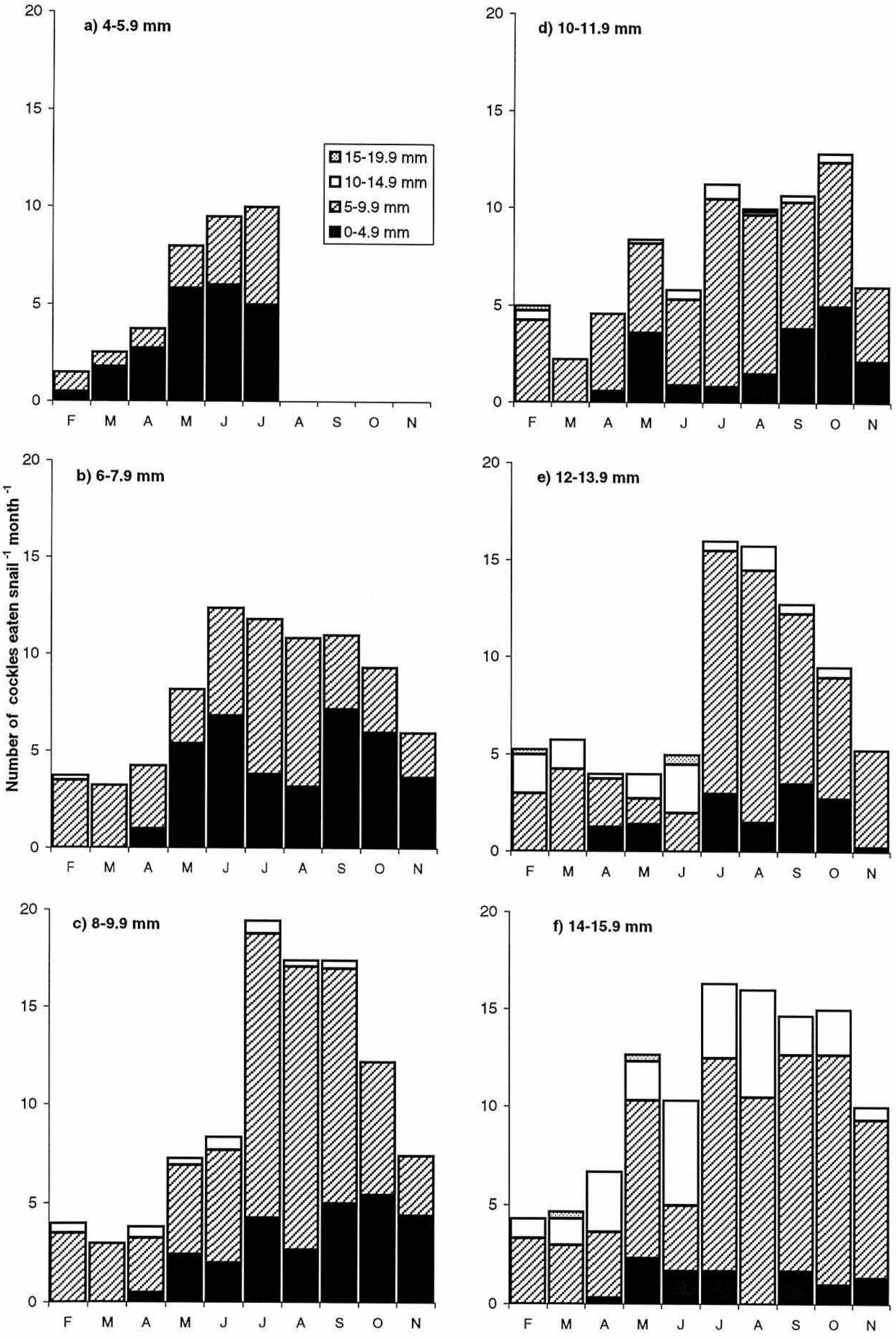

a) 4-5.9 mm
b) 6-7.9 mm
c) 8-9.9 mm
d) 10-11.9 mm
e) 12-13.9 mm
f) 14-15.9 mm
% cockles consumed
%
%
%
0
5
10
15
20
25
30
35
40
45
0
2
4
6
8
10
12
14
16
18
C. edule shell height (mm)
C. edule shell height (mm)

Figure 3. Seasonal predation rates of *E. pulchellus* held in the laboratory between February and November 2001 showing the proportions of different prey size classes consumed each month.


a) 4-5.9 mm
b) 6-7.9 mm
c) 8-9.9 mm
d) 10-11.9 mm
e) 12-13.9 mm
f) 14-15.9 mm
▩ 15-19.9 mm
☐ 10-14.9 mm
▨ 5-9.9 mm
■ 0-4.9 mm
Number of cockles eaten snail $^{-1}$ month $^{-1}$
0
5
10
15
20
F
M
A
M
J
J
A
S
O
N

Consumption by the 10-11.9 mm sized snails was high (10 to 12.86 *C. edule* animal $^{-1}$ month $^{-1}$) during the period July to October and again declined in November (Figure 3d). The consumption rate of the 14-15.9 mm sized snails was high in May, declined slightly in June, increasing once more in July, remained at a high level through to the end of October, before starting to decline in November (Figure 3f). Between February and November, the proportion of the smallest cockles (0-4.9 mm) consumed decreased and the occurrence of larger prey sizes in the diet increased, as predator size increased (see Figure 2 and 3). Generally, there was also a pattern of increased consumption by the larger individuals although the largest monthly consumption rate was seen in July for the 8-9.9 mm sized animals (19.47 cockles snail^{-1} month^{-1}). For all sizes of *E. pulchellus,* consumption rates were higher in the summer and autumn (between July and November) than in the winter and spring months (February to June) (Figure 3).

3) Growth of E. pulchellus experimental animals

Measurements of the snails involved in the feeding experiments at 4-weekly intervals allowed differences in the rates of shell growth of different sized animals to be investigated. Figure 4a shows the growth of individuals which survived the entire period between February and November, whilst Figures 4b-4e show the growth of animals that were added to tanks to replace those which died during the experiment; these snails were therefore monitored for shorter periods of time. The patterns of growth here can be described concisely. Most snails > 9-10 mm grew little if at all during the period February to November (Figures 4a, c, d and e). In contrast, most animals that were small (4-8 mm) at the start of the experiment showed considerable shell growth during the course of the experiment (Figure 4a), and grew most rapidly between April and September. From Figure 4a it can be seen that individuals measuring 4.0 mm and 7.6 mm on February 2nd attained sizes of 9.0 mm and 11.4mm respectively by November 9th (9 months), whilst animals > 12 mm were not seen to increase by any more than 0.2-0.4 mm over the same period of time.

Patterns of growth and rates of consumption are related to seawater temperature (Figure 5a-c) as this will affect the metabolic rate of the animals that live in it. Figure 5a shows the change in daily average seawater temperature in the aquaria between

Figure 4. Growth of *Euspira pulchellus* at ambient laboratory seawater temperatures. a) individuals that survived the experimental period between February and November 2001. b)-e) individuals that were added to the experiment at a later date to replace individual snails that had died.

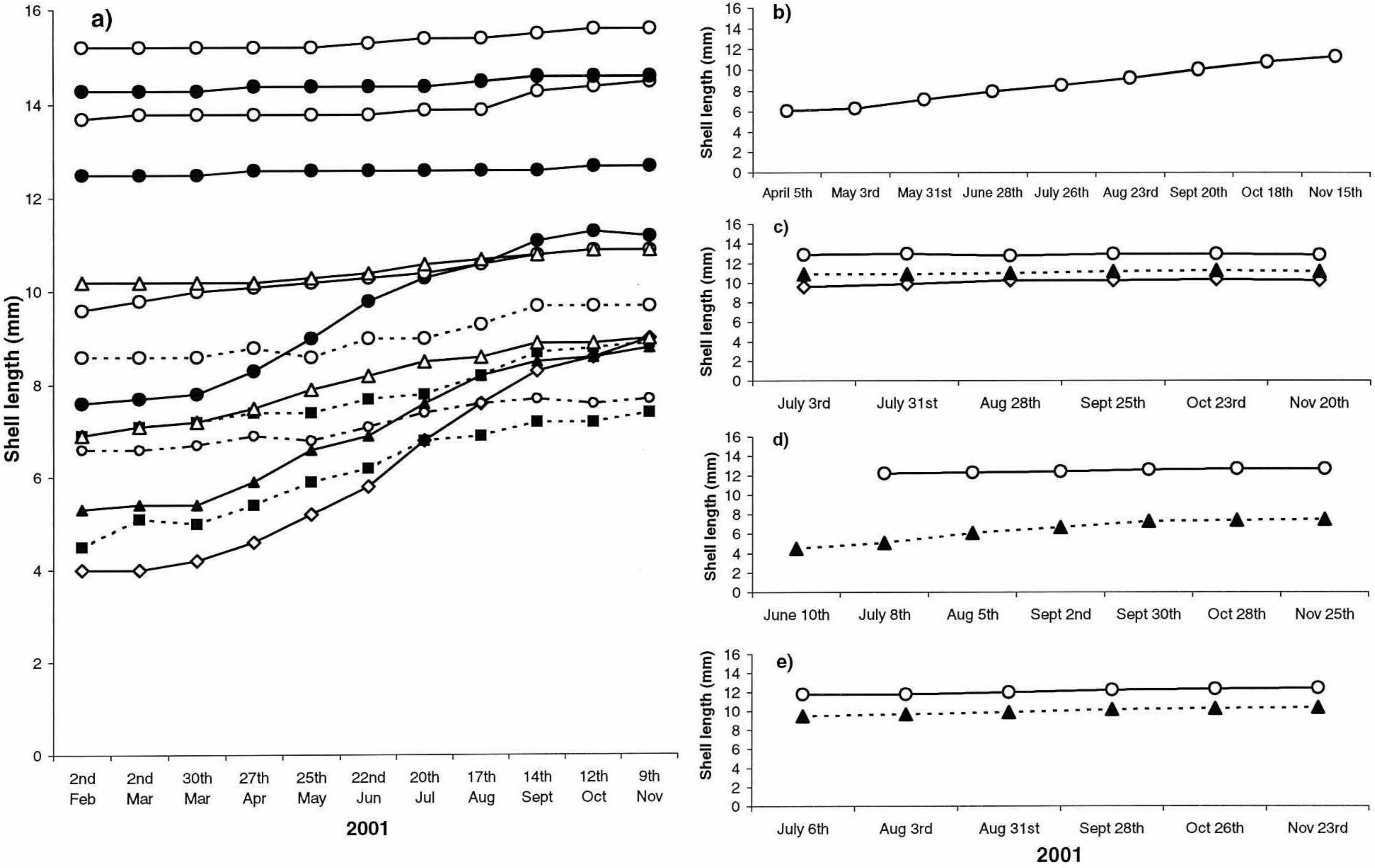
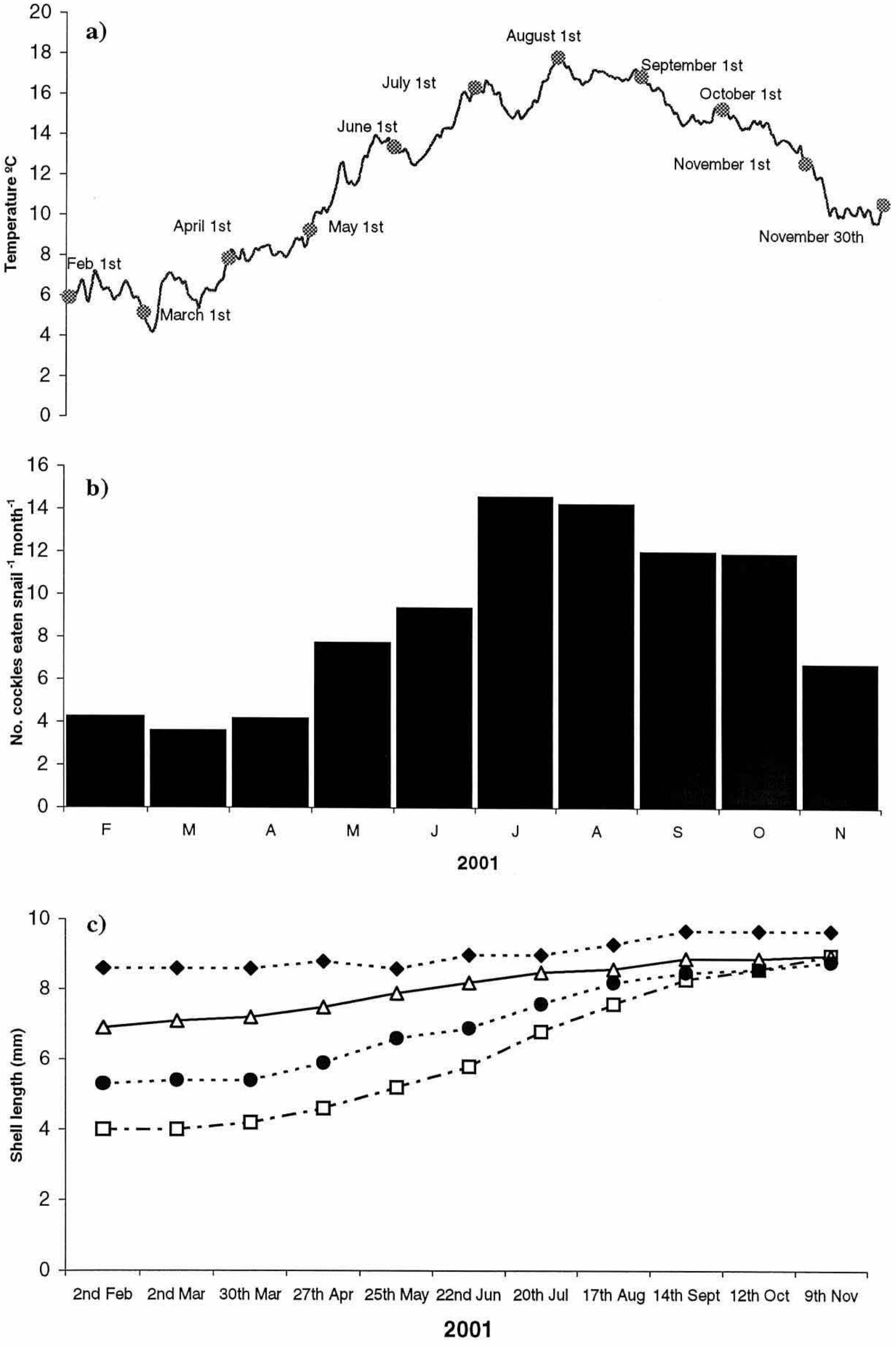

a)
Shell length (mm)
0
2
4
6
8
10
12
14
16
2nd Feb
2nd Mar
30th Mar
27th Apr
25th May
22nd Jun
20th Jul
17th Aug
14th Sept
12th Oct
9th Nov
2001
b)
Shell length (mm)
April 5th
May 3rd
May 31st
June 28th
July 26th
Aug 23rd
Sept 20th
Oct 18th
Nov 15th
c)
Shell length (mm)
July 3rd
July 31st
Aug 28th
Sept 25th
Oct 23rd
Nov 20th
d)
Shell length (mm)
June 10th
July 8th
Aug 5th
Sept 2nd
Sept 30th
Oct 28th
Nov 25th
e)
Shell length (mm)
July 6th
Aug 3rd
Aug 31st
Sept 28th
Oct 26th
Nov 23rd
2001

Figure 5. The effect of seawater temperature on the rates of feeding and growth in *Euspira pulchellus*. a) Average daily seawater temperature in an aquarium adjacent to those containing the experimental animals b) Consumption rates of *E. pulchellus* (6-15.9mm) expressed as the number of cockles eaten per snail each month c) The increase in shell length of four *E. pulchellus* between February and November 2001.


a)
Temperature ºC
20
18
16
14
12
10
8
6
4
2
0
Feb 1st
March 1st
April 1st
May 1st
June 1st
July 1st
August 1st
September 1st
October 1st
November 1st
November 30th
b)
No. cockles eaten snail ⁻¹ month⁻¹
16
14
12
10
8
6
4
2
0
F
M
A
M
J
J
A
S
O
N
2001
c)
Shell length (mm)
10
8
6
4
2
0
2nd Feb
2nd Mar
30th Mar
27th Apr
25th May
22nd Jun
20th Jul
17th Aug
14th Sept
12th Oct
9th Nov
2001

February 1st and November 30th determined from the half-hourly readings collected by the Tiny Talk data logger. From this it can be seen that the temperature was still low in February and early March (4-6 °C) before starting to increase from mid-March onwards. The daily average seawater temperature peaked on August 2nd at 18.1 °C and displayed a precipitous drop from 15 °C at the start of October to 10 °C by mid-November. Figure 5b shows the number of cockles consumed per *E. pulchellus* during the experiment, not including those measuring 4-5.9 mm as data for these were not available after July. The number of cockles consumed was at its lowest level in March during which consumption rate was 3.58 cockles snail^{-1} month^{-1}. From March onwards, consumption rate showed a steady increase from March until July and August, when it reached 14.57 cockles snail^{-1} month^{-1}and 14.23 cockles snail^{-1} month^{-1} respectively, before decreasing slightly in September (12.00 cockles snail^{-1} month^{-1}) and October (11.91 cockles snail^{-1} month^{-1}) and considerably more so in November (6.73 cockles snail^{-1} month^{-1}). Consumption rate closely followed the seawater changes shown in Figure 5a. Figure 5c shows the increase in shell length of four individual *E. pulchellus* and demonstrates the general pattern that was seen of a reduction in growth rate with increasing size. The increase in the rate of shell growth in small individuals (4-8 mm) from April onwards was coincident with the onset of the warming of the seawater.

3) Predator size vs. drill hole diameters

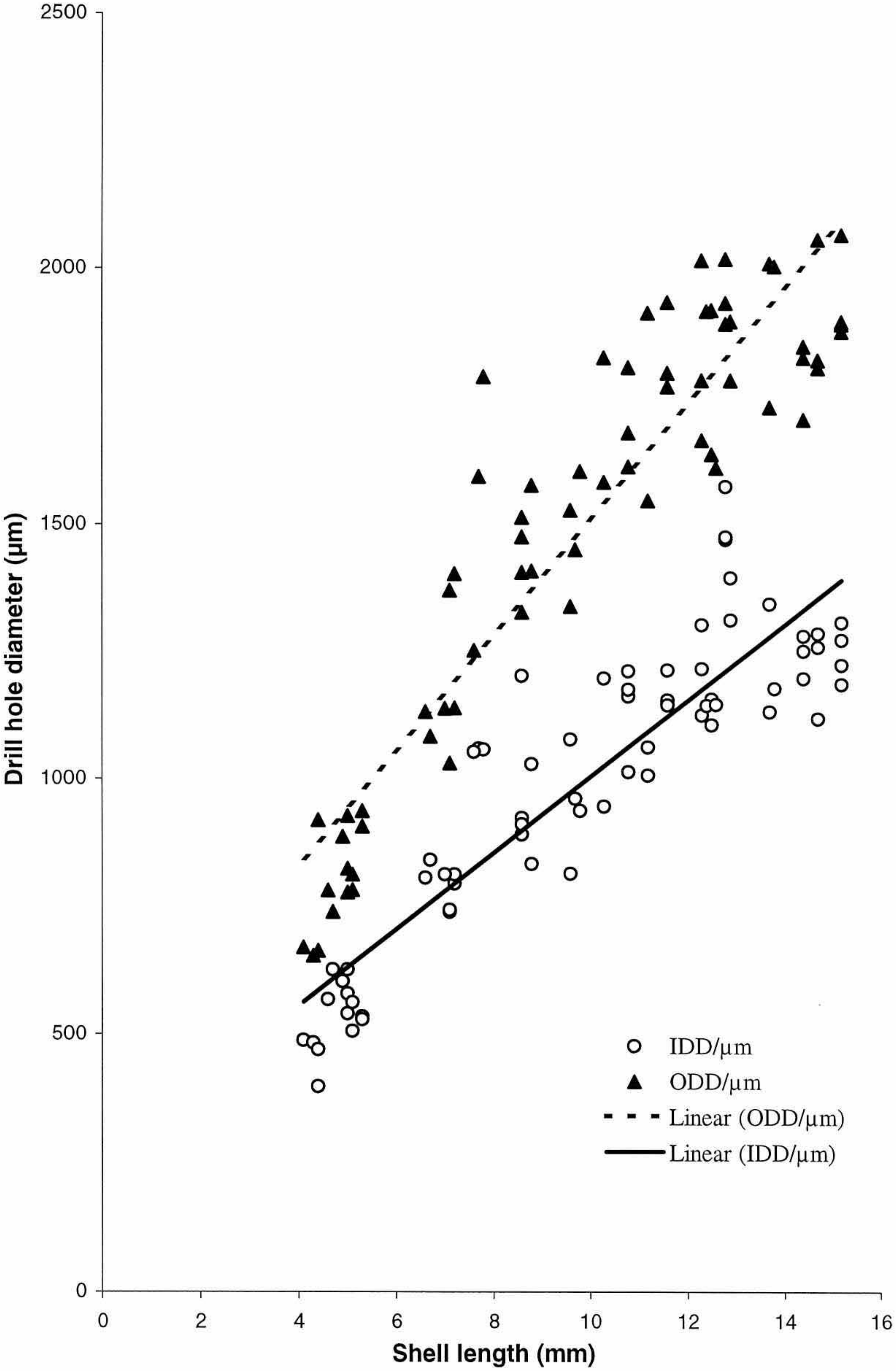
Inner drill hole and outer drill hole diameters were significantly correlated with *E. pulchellus* shell length (Figure 6), with a more robust Pearson's correlation co-efficient for the outer diameter ($r = 0.923$, $p < 0.001$ compared with 0.899, $p < 0.001$). The relationships between inner and outer drill hole diameter and *E. pulchellus* size are described by the following equations:

Inner drill hole diameter (μm) = 74.8 *E. pulchellus* shell length + 256 μm

Outer drill hole diameter (μm) = 112.8 *E. pulchellus* shell length + 382 μm

The R^2 values of these two regressions equations were 0.808 and 0.852 respectively and ANOVA of both regression lines demonstrated that both slopes and both

Figure 6. Linear relationships between predator size (shell length) and the inner and outer diameters of drill holes produced in *Cerastoderma edule* by *Euspira pulchellus*. IDD refers to the inner drill hole diameter and ODD refers to the outer drill hole diameter (see Figure 1b).



2500
2000
1500
1000
500
0
Drill hole diameter (µm)
0
2
4
6
8
10
12
14
16
Shell length (mm)
IDD/µm
ODD/µm
Linear (ODD/µm)
Linear (IDD/µm)

intercepts were significantly different from zero ($p < 0.001$). From the shape of the drill holes produced by naticid gastropods (see Figure 1b), the inner drill hole diameter is expected to be smaller than the outer drill hole diameter, which explains the differences in the values of the intercepts in these two equations. Tukey's method was used to calculate whether or not there was any significant difference between the slopes of these regression lines. As the confidence interval of the difference between the standard errors of the two lines included zero, it was concluded that the slopes of the two lines were not significantly different from one another. Therefore, as drill holes increase in diameter with increasing predator size, the relative inner and outer diameters remain geometrically similar, such that the vertical profile of the drill hole does not change with predator size. From a small number of *C. edule* valves that were sectioned, the profile of the drill hole was vertical in the exterior crossed lamellar layer but became sloped in the interior complex lamellar layer (see Figure 1b).

4) Investigation of valve preference

Of the representative subset of 70 *Cerastoderma edule* shell valves, 33 were drilled through the right valve and 37 through the left valve. No significant difference was found between the proportion of left and right valves of *C. edule* drilled by *E. pulchellus* ($\chi^2 = 0.229$, $p > 0.05$, $df = 1$).

5) Drill hole location

Categorisation of the location of the drill holes in the 70 valves using the scheme shown in Figure 1a produced the distribution shown in Figure 7. Snails drilled most frequently (64-73%) in the centre of the valve, in sector 5, and to a lesser extent (14-27%) in sector 8, close to the shell margin. Rarely (2.7-5.4%) were either left or right *C. edule* valves drilled in sectors 1, 3, 4, 6, 7 and 9.

6) Relationships between predator size, prey size and umbo to drill hole distance

The distance from the umbo to the centre of the drill hole (UDH) as a proportion of the shell height of the prey was not significantly correlated with predator shell length (Figure 8) ($r = -0.012$, $p = 0.923$). Distance from the umbo to the drill hole divided by

Figure 7. The distribution of drill holes across the surface of the shell valves of *Cerastoderma edule*.

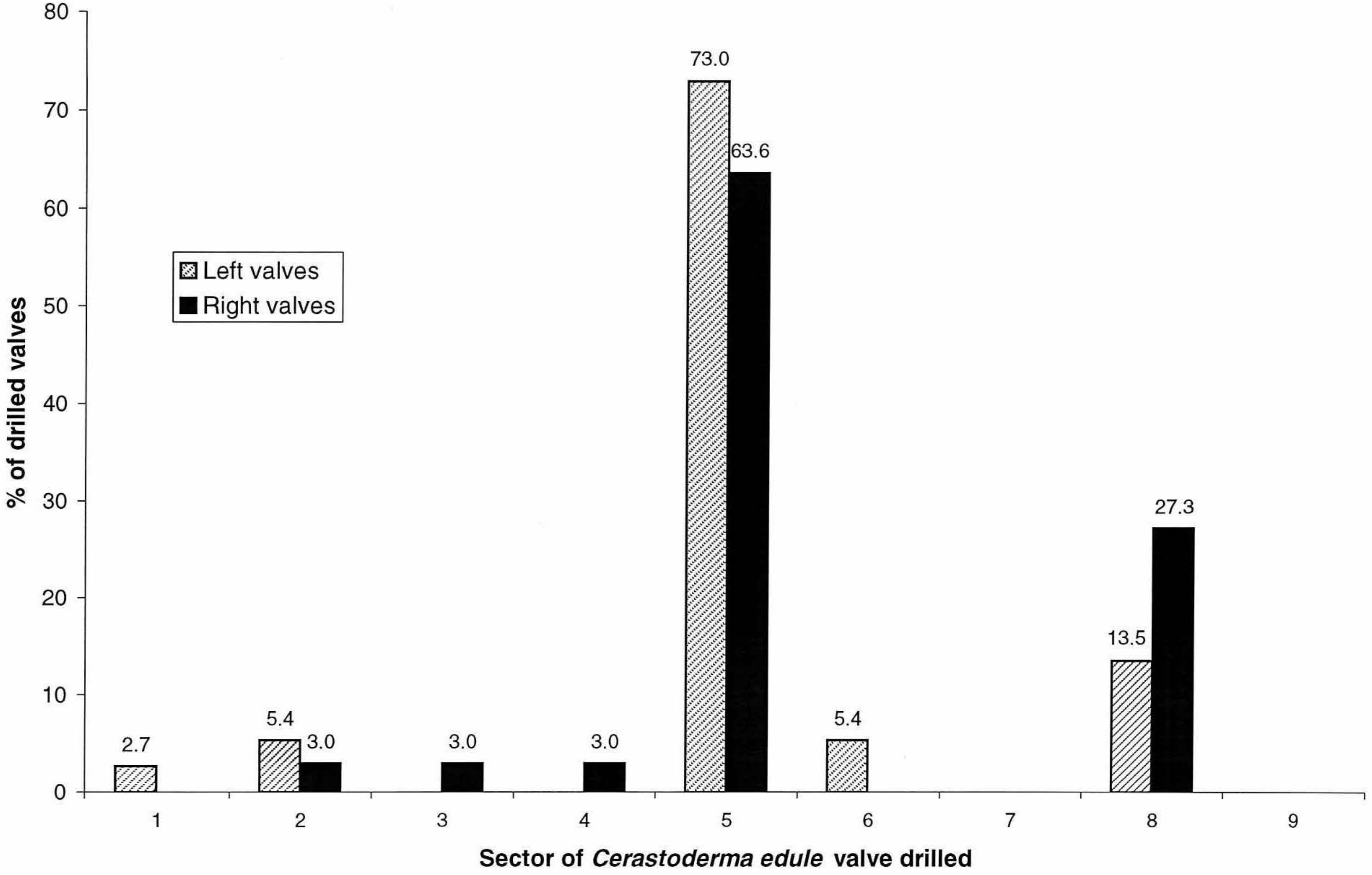
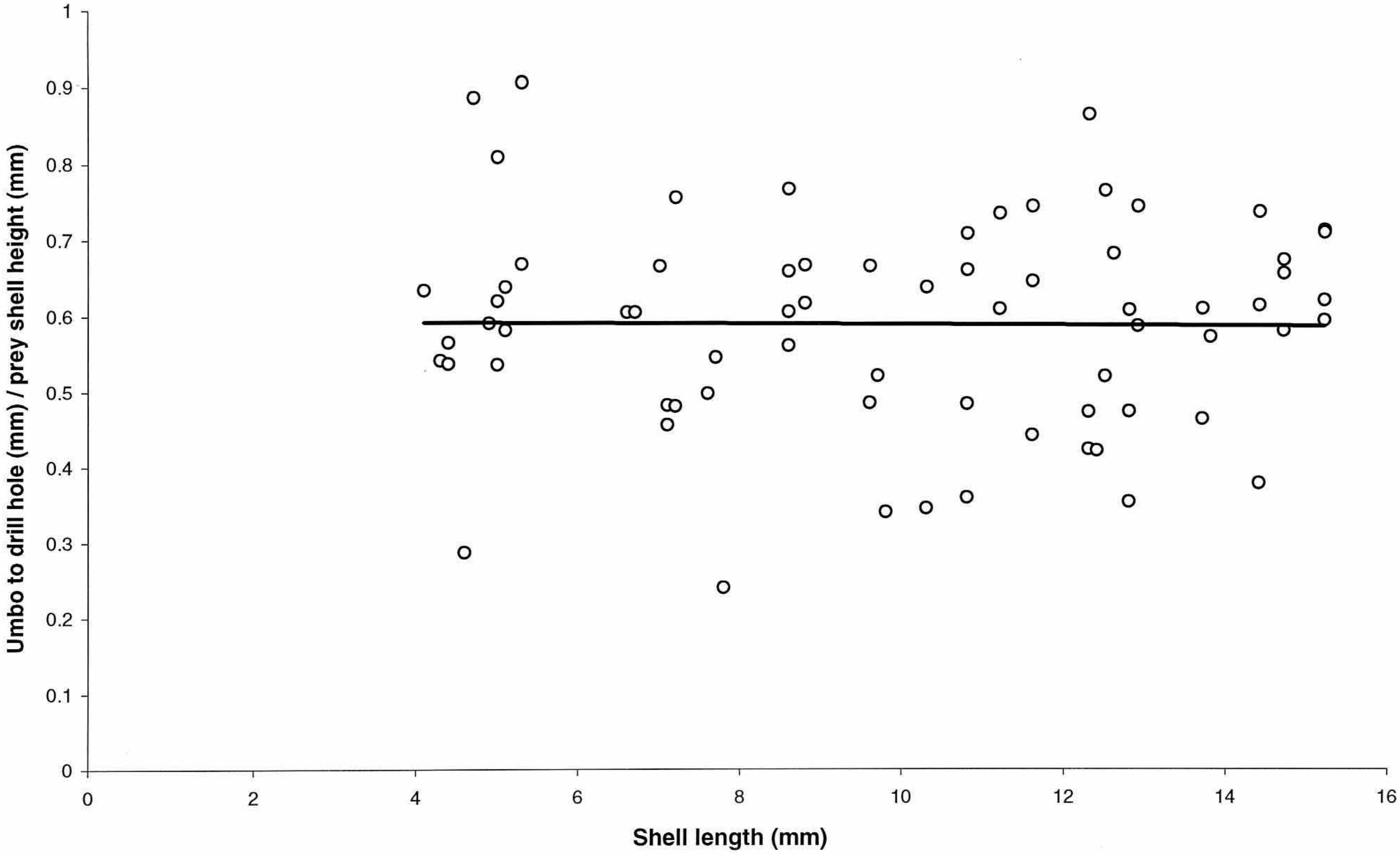

80
70
60
50
40
30
20
10
0
% of drilled valves
▨ Left valves
■ Right valves
2.7
5.4
3.0
3.0
3.0
73.0
63.6
5.4
13.5
27.3
1
2
3
4
5
6
7
8
9
Sector of *Cerastoderma edule* valve drilled

Figure 8. Relationship between predator size and the relative distance of the drill hole from the umbo of the drilled valve.

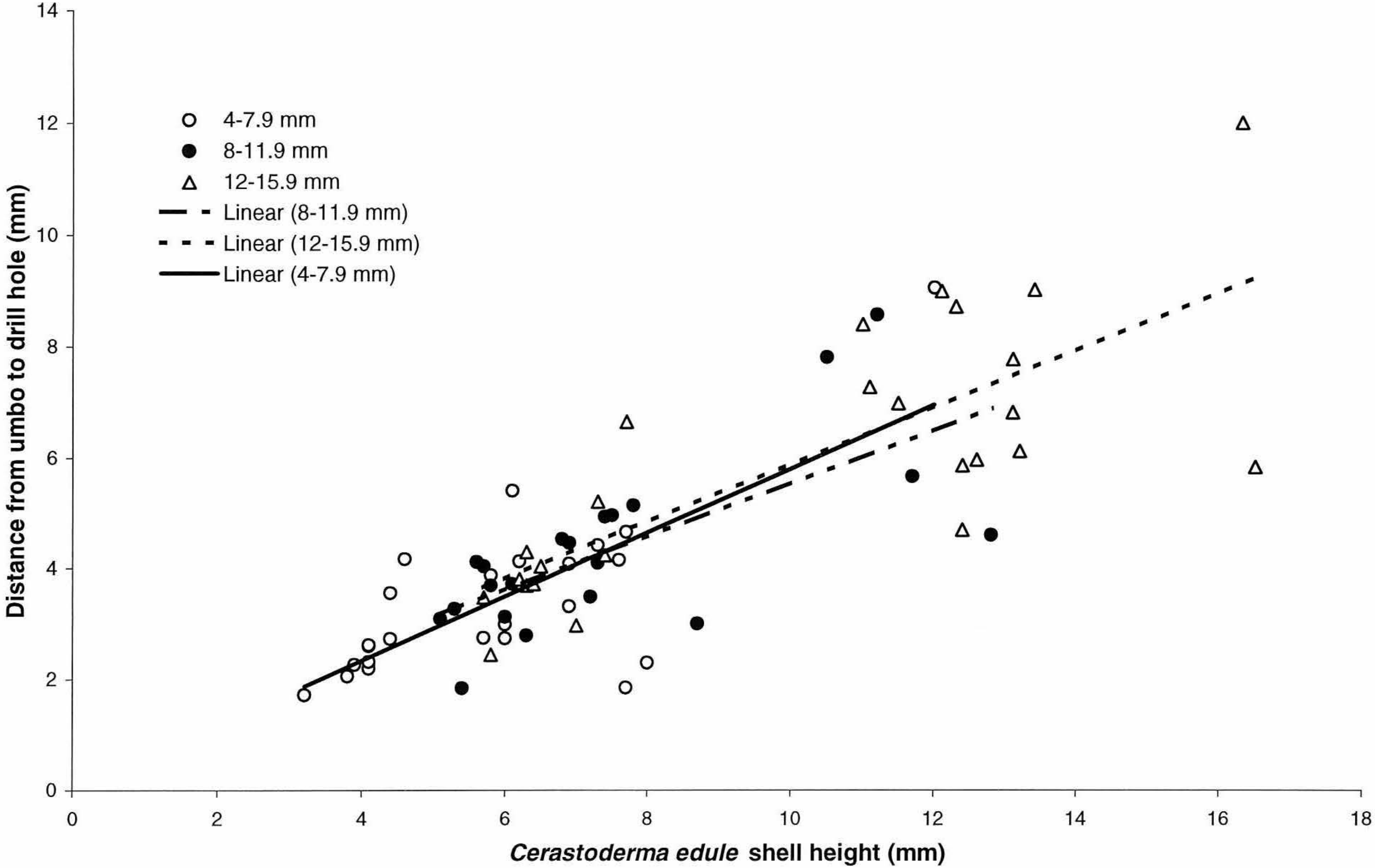

Umbo to drill hole (mm) / prey shell height (mm)
1
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
0
2
4
6
8
10
12
14
16
Shell length (mm)

prey size was therefore not related to predator size. The intercept of the regression line 0.594 (from the equation $y = -0.0005x + 0.594$) suggests that on average cockles were drilled 59.4% of the distance from the umbo to the shell margin irrespective of predator size (Figure 8). Prey size and UDH for all sizes of *E. pulchellus* were further investigated and found to be significantly correlated ($r = 0.815$, $p < 0.001$) and described by the linear regression equation $y = 0.547x + 0.295$ ($R^2 = 0.665$), in which the slope is significant ($p < 0.001$) and the intercept is not ($p = 0.464$). As prey increase in size, the absolute distance of the drill hole from the umbo increases, resulting in the concentration of drilling locations in the centre of the valve. There is a close similarity between the value of the intercept in the first analysis (0.594) (see Figure 8) and the slope of the line describing the relationship in this analysis (0.547). To investigate the effect of predator size on the relationship between UDH and prey size, the data were separated into three size categories of *E. pulchellus*: 4-7.9, 8-11.9 and 12-15.9 mm. These three subsets of data are each representative of the complete data set in that they consist of a similar range of prey sizes and number of observations. Analysis of the three subsets of data produced significant correlations for prey size against the umbo-to-drill hole distance ($r = 0.732$, $p < 0.001$, $r = 0.691$, $p = 0.001$ and $r = 0.769$, $p < 0.001$ respectively). Linear regression on the three data sets produced the following equations:

a) 4-7.9 mm snails: $y = 0.578x + 0.031$ ($R^2 = 0.536$)
b) 8-11.9 mm snails: $y = 0.485x + 0.710$ ($R^2 = 0.478$)
c) 12-15.9 mm snails: $y = 0.519x + 0.703$ ($R^2 = 0.591$)

Figure 9 demonstrates that these three lines lie very close to one another. ANOVAs of the regression lines a)-c) found that all slopes were significant ($p < 0.001$, $p = 0.001$ and $p < 0.001$ respectively) and that none of the intercepts were significant ($p = 0.966$, $p = 0.443$ and $p = 0.473$ respectively). The slopes of these three regression lines were not significantly different from one another using Tukey's method. Therefore, predators of different size do not drill *C. edule* in different locations, rather an equivalent relationship exists between UDH and prey size for the entire size range of *E. pulchellus* investigated. Drilling by all sizes of *E. pulchellus* concentrates drilling in the centre of the valves of *Cerastoderma edule* across a wide range of sizes.

Figure 9. Relationships between prey size and the absolute distance of the drill hole from the umbo, for three size classes of *Euspira pulchellus*.


Distance from umbo to drill hole (mm)
0
2
4
6
8
10
12
14
○ 4-7.9 mm
● 8-11.9 mm
△ 12-15.9 mm
Linear (8-11.9 mm)
Linear (12-15.9 mm)
Linear (4-7.9 mm)
0
2
4
6
8
10
12
14
16
18
Cerastoderma edule shell height (mm)

DISCUSSION

It has been widely reported that *Euspira pulchellus* feeds on a wide variety of bivalve species, by drilling through their shells whilst buried beneath the sediment surface (Ansell, 1960, Thorson, 1971, Fretter and Graham, 1994). Whilst the predation of only one prey species was investigated during this study, Bayliss (1986) demonstrated that *Polinices alderi* (= *E. pulchellus*) has hierarchical species prey preferences when offered a choice of seven bivalve species. The most preferred species were also those that had thinner shells, namely *Mya arenaria* and *Spisula subtruncata*. However, prey species preferences were not entirely explicable by shell thickness as *Cerastoderma edule* and *Parvicardium scabrum,* which have robust and thickly calcified shells, were preferred to the thin-shelled species *Spisula elliptica*, whilst *Arctica islandica* and *Corbula gibba,* which do not have particularly thick shells compared with the other species, were not predated. Kitchell *et al.* (1986) demonstrated that surfclams, *Spisula solidissima* vary in shell thickness in a predictable manner both dorso-ventrally and anterior-posteriorly, whilst Harper and Morton (1997) showed that in six species of Hong Kong bivalves a linear relationship exists between valve height and valve thickness. Considering that bivalves accrete marginally, whilst continuing to lay down calcareous material across the inner shell surface, this relationship might be expected. Shell thickness strongly affected the bivalve species preferences of the muricids *Morula musiva* and *Thais clavigera* in their study (Harper and Morton, 1997). Furthermore, Tull and Boehning-Gaese (1993) found that both naticid and muricid drilling gastropods preferred the thinner-shelled *Turritella leucostoma* to the thicker-shelled, co-existing species *Turritella gonostoma.*

Thicker shelled prey will take longer to drill and assuming the same energy content per gram of prey tissue, a prey with a thinner shell, but of equivalent size, will be more profitable. It has, however, been shown that artificially thinned bivalve shells do not alter prey size preferences of the drilling gastropod *Neverita duplicata* (Boggs *et al.*, 1984) and *Neverita didyma* (Rodrigues *et al.*, 1987), such that it is questionable whether shell thickness is a critical determinant of prey size-selection (Wiltse, 1980, Boggs *et al.*, 1984, Bayliss, 1986, Rodrigues *et al.*, 1987). *Polinices alderi* has been shown to spend a constant proportion of its time drilling such that when faced with thicker shelled prey they consume fewer individuals (Bayliss, 1986). Nevertheless, any prey characteristic that increases the handling time of the predator must substantially increase the likelihood that the predator will be deterred from selecting that prey, and that the prey survives. Kelley (1982, 1987, 1988) proposed that over evolutionary time there has been a general increase in bivalve shell thickness without a discernable increase in prey volume, thereby reducing the value of bivalves to drilling predators. Other prey characteristics that have been shown to influence the species preferences of drilling gastropods include; the microstructural composition of bivalve shells (Gabriel, 1981), a low spire, narrow or toothed opening in gastropod shells (Seed and Hughes, 1995), or the absence of a persistent gape in burrowing bivalves (Vermeij, 1983). Spines and ornamentation have been proposed as acting as efficient deterrents to predation (Palmer, 1979, Bertness *et al.*, 1981, Bertness and Cunningham, 1981, Vermeij, 1987). However, Ray and Stoner (1995) concluded that growing to a large overall size and forming aggregations are more important anti-predator traits for the queen conch, *Strombus gigas*, than having a heavy shell or longer spines.

The most obvious prey characteristic that affects prey selection decisions, however, is size. It is well established that as naticid gastropods increase in size they select larger prey (Edwards and Huebner, 1977, Griffiths, 1981, Berry, 1982, Rodrigues *et al.*, 1987), presumably to meet increasing demands for food to support greater amounts of somatic tissue, and also reproductive tissues once sexually mature. Vignali and Galleni (1986) concluded that in general bivalve predation mortality initially increases with prey size up to a maximum representing the preferred size, and thereafter progressively decreases towards the maximum size at which a particular prey species is found. Bayliss (1986) demonstrated that 9 mm *Polinices alderi* (= *Euspira pulchellus*) predated most heavily on *Spisula subtruncata* and *S. elliptica* in the 9 mm size class, with a sharp reduction in the selection of larger size classes. Vignali and Galleni (1986) found a lack of drill holes in *S. subtruncata* greater than 10 mm in length, and proposed that larger size classes are less favourable because they are more difficult to manipulate. The current study found that as *Euspira pulchellus* increased in size, snails consumed larger prey sizes and also a wider range of prey sizes. Similarly, Brown (1997) demonstrated that small southern oyster drill, *Stramonita haematoma,* were only able to feed on small oysters, *Crassostrea virginica,* whilst larger snails were able to consume a greater range of prey sizes, a trend supported by other authors (Griffiths, 1981, Hughes and Dunkin, 1984). Intermediate and large snails, however, were unable to consume the largest oysters offered, indicating that the largest oysters reach a size refuge. Size-selective predation also operates in the cannibalistic predation of *Neverita duplicata* in that successful attacks have been shown to occur most frequently upon individuals in the < 25 and 25 to 39 mm size ranges (Dietl and Alexander, 1995). The examination of empty, drilled shells has revealed that naticid predation is generally most intense on medium-sized bivalves (Edwards and Huebner, 1977, Franz, 1977). Vignali and Galleni (1986) in their study of a beach shell assemblage demonstrated that naticid predation on *Donax trunculus* was concentrated almost exclusively on individuals greater than 20mm in length, whilst *Donax semistriatus* was scarcely drilled, possibly due to its smaller size. Size-selective predation, therefore, has the potential to influence the population structure of a prey species through the depletion of vulnerable size classes of small individuals (Ebling *et al.*, 1964, Paine, 1974, 1976, Seed and Brown, 1975, Commito, 1982, Summerson and Peterson, 1984). Wilson (1988) demonstrated that naticids predated selectively on 6 and 7 yr old *Nucula turgida* such that the chances of this species surviving beyond 7 years and achieving a size greater than 10 mm was thought to be slight. Naticids are therefore potentially important limiting factors of bivalve populations.

The relative sizes of predators and their prey frequently determine whether or not a predation event is successful (Paine, 1976, Kitchell *et al.*, 1981, Palmer, 1990). Consequently, prey size can provide a refuge from predation, either by the prey attaining a size at which it can no longer be efficiently manipulated by the predator, as Ansell (1960) proposed for *Natica alderi* (= *Euspira pulchellus*) feeding *upon Venus striatula* (= *Chamelea gallina*) (see also Franz, 1977, Hughes, 1985, Dietl and Alexander 1997), or by the prey reaching a size at which it is less profitable to the predator than other available prey. A spatial refuge from predation can be reached by an increased burial depth at a larger size by the possession of longer siphons, as Edwards and Huebner (1977) demonstrated for the interaction between *Mya arenaria* and *Neverita duplicata*. Commito (1982) rarely found *M. arenaria* valves greater than 30 mm that had been drilled by *Euspira heros,* whilst *Macoma balthica* of all sizes and ages (up to 25 mm) were predated. The survival of *M. balthica* was, however, higher than for *Mya arenaria* of an equivalent size due to the longer siphons present in *M. balthica* than in *M. arenaria*. Peitso *et al.* (1994), in contrast, demonstrated that the surf clam *Protothaca staminea* did not achieve a refuge in size from predation by *Polinices lewisii,* as even the largest clams offered, that were close to the maximum size encountered at the study site, were drilled successfully. Dietl and Alexander (1997) found that *Spisula solidissima,* greater than 120 mm shell width were not drilled in any of their study sites, whilst Franz (1977) recorded *S. solidissima* valves 160 mm in width that had been drilled. The size at which a species reaches a refuge, therefore, appears to vary between populations, depending upon the sizes of predators that are present (Dietl and Alexander, 1997).

In the current study, there was considerable overlap in the sizes of *Cerastoderma edule* that were drilled by *E. pulchellus*. In terms of the cost of drilling and the amount of tissue obtained, the small size classes of *C. edule* may have been most profitable to *E. pulchellus* of a range of sizes. Determining the costs of naticid predation is problematic due to the considerable practical difficulties of accurately recording the times taken for naticids to drill and consume particular prey items. These difficulties arise from the envelopment of the prey within the foot and also the burial of both predator and prey within the sediment during drilling. As yet no apparatus has been devised to permit the close viewing of the drilling process in naticids. Much of the data presented for the times taken to drill are based upon the deliberate interruption of predators, the examination of the progress made in drilling and consuming the prey and the extrapolation thereafter to complete the task. Berry (1982) found that *N. maculosa* took between 10 and 18 hours to drill and consume large *Umbonium vestiarium*. Bayliss (1986) reported that *Polinices alderi* took 10.5 hours to drill through 0.11 mm thick shells of *Mya arenaria* (0.0105 mm hr^{-1}), 15.9 hours for 0.146 mm thick *Spisula subtruncata* (0.0092 mm hr^{-1}) and 35.5 hours for 0.334 mm thick shells of *S. elliptica* (0.0094 mm hr^{-1}). On average *Acanthina punctulata* was found to take approximately 14 hours to drill and 14 hours to consume a littorinid in the field (Menge, 1974). Ziegelmeier (1954) reported a drilling rate of 0.6 mm per day or 0.025 mm hr^{-1} by *Euspira nitida,* whilst *Neverita duplicata* has been shown to have an almost constant rate of drilling of 0.0223 mm hr^{-1} across a range of prey species, predator sizes and times elapsed (Kitchell *et al.*, 1981). Drilling times were obtained by Carriker and van Zandt (1972) for predation by the oyster drill *Urosalpinx cinerea*

(Family Muricidae) by attaching a hydrophone directly to the prey valve and recording the vibrations resulting from drilling. This would be difficult, if not impossible, for naticids for the reasons outlined.

Cost-benefit curves, such as those derived for *Polinices duplicatus* (Wiltse, 1978), reveal that larger prey are more profitable up to a certain point, beyond which profitability decreases (Palmer, 1980). Kitchell *et al.* (1981) reported that yields per handling times for several bivalve species by naticid predators increase monotonically with prey length, a relationship that has also been demonstrated for the dogwhelk *Nucella lapillus* feeding on mussels (Dunkin and Hughes, 1984). Although larger prey, with thicker shells, take longer to drill, this should be compensated for by an increased yield of flesh due to the greater internal volume of larger shells (Bayliss, 1986). Kitchell *et al.* (1981) stipulated that naticids select their prey in a manner that optimises their energy gain by the development of a behaviour pattern that determines the likelihood of a successful attack, based on the size-ratio of predator and prey, prey availability and potential prey value. Their theory was corroborated by a study of fossil shell assemblages (Kitchell *et al.*, 1986).

Variation in the predation rate of *Polinices alderi* (= *Euspira pulchellus*) is affected by temperature, predator size and annual cycles of growth and reproduction (Ansell, 1982a). In the absence of food limitation, predation rate is governed largely by temperature but also by the internal state of the animal (Ansell, 1982c). Under conditions of food limitation, the amount of food that can be obtained determines the metabolic activity of the animal, rather than the metabolic activity of the animal governing the rates of food intake and predation (Ansell, 1982c). Experiments with sub-optimal prey (Edwards, 1975) have shown that such a diet is able to depress the rate of somatic growth of the predator. Feeding *P. alderi* a diet of *Spisula*, *Donax* and particularly *Chamelea*, which have a low yield of tissue in comparison to *Tellina tenuis,* results in reduced growth performance (Ansell and Macé, 1978). Once mature, food limitation has an effect on both growth and reproduction, usually resulting in the reduction of reproductive output to maintain a balance between somatic growth and reproductive output (Ansell, 1982c). The peak rate of consumption by *Euspira pulchellus* in this study was seen in July in the size class of the predator of 8-9.9 mm shell length. This may be due to high rates of growth in these animals at a time when they are also becoming sexually active for the first time, as demonstrated in Chapter 3. Energy maximization models have been devised for both naticids (Kitchell *et al.*, 1981) and the temperate muricid *Nucella lapillus* (Hughes and Dunkin, 1984, Hughes and Burrows, 1990) whilst attempts have also been made to determine energy budgets for *Neverita duplicata* (Edwards and Huebner, 1977), *Natica maculosa* Broom (1982) and *Polinices alderi* (Ansell, 1982a, b). Naticids appear to show high growth efficiencies when young, as demonstrated by the rapid growth of small individuals in the present study. Growth efficiencies, however, decline with age, as seen by the comparatively negligible growth of larger and older individuals in Chapter 2. Ansell (1982b) recorded gross growth efficiencies in *P. alderi* of 48% for the 2 year age class and 16% for the 4 year age class. Huebner and Edwards (1981) reported gross growth efficiencies of 35% for *Polinices duplicatus* that varied inversely with snail size. The construction of energy budgets requires the knowledge of the amount of tissue consumed. Edwards and Huebner (1977) reported that only 80% of the tissue of *Mya arenaria* was consumed by *Neverita duplicata*, which the authors attributed to the unpalatable nature of the mantle and siphonal tissue.

The present study demonstrated a strong relationship between predator size and both the inner and outer diameters of drill holes left in the shell valves of bivalve prey. A significant relationship between outer drill hole diameter and predator size has also been demonstrated in *Polinices lewisii* (Peitso *et al.*, 1994) *Neverita duplicata* (Wiltse 1980, Kitchell *et al.*, 1981), *Natica tecta* (Griffiths, 1981) and *Ocenebra lurida* (Palmer, 1988). If the diameter of the drill hole is indicative of the size of the predator (Piéron, 1933, Ansell, 1960) then it is possible to determine the size of predator responsible for prey mortality by measuring either the inner or outer diameter of the drill hole without the need for direct observations of the predation event, for example by collecting drilled shell valves from the field. Vignali and Galleni (1986) used this approach to conclude that small naticids feed on small *Glycymeris glycymeris*, whilst adult predators prefer to attack larger specimens. Furthermore, Dietl and Alexander (1995, 1997) showed that naticid size, as determined from outer drill hole diameter, increased with prey size for predation attacks upon molluscan prey and for cannibalistic attacks amongst *Euspira heros* and *Neverita duplicata*. Harper and Morton (1997), however, did not find a significant relationship between the size of muricids collected from Cape d'Aguilar Marine Reserve, Hong Kong and the diameter of the holes that they drilled. Some flexibility in the size of holes drilled by individual predators appeared to exist, as 'edge-bores' were generally smaller in diameter than 'side-bores'. In fact, the sizes of the drill holes themselves generally seemed to be highly variable. Individual predators in laboratory experiments were also not particularly consistent in the positioning of their drill holes (Harper and Morton, 1997). No significant correlation was found between predator size and size of prey selected (Harper and Morton, 1997) as has previously been reported from correlations of drill hole diameters and the sizes of prey in which they are found (Carriker and van Zandt, 1972, Palmer, 1990). An important difference may exist between muricids and naticids. A naticid holds its prey in its foot, manipulating and consuming the prey in a stereotyped fashion, and therefore it might be expected that stronger relationships between prey size and predator size exist for naticids than for muricids, which frequently crawl over their prey. Muricids, therefore, have greater flexibility in both the sizes of prey and drilling positions that they are able to choose, as prey are not required to be manipulated in the manner observed in naticids.

Euspira pulchellus showed no preference for the left or right of the equivalve species of prey offered in this study, namely *Cerastoderma edule*. In prey species with asymmetric valves, however, a greater degree of drilling in one valve than the other might be expected, due to a greater ease of manipulation or to differences in the costs associated with drilling the two valves (Fretter and Graham, 1994). *Neverita didyma* has been shown to preferentially drill the left valve of *Ruditapes philippinarum* (Rodrigues *et al.*, 1987), whilst the well-developed periostracum on the left valve of corbulid bivalves is an effective deterrent to drilling gastropod predators, such that they tend to be drilled through the right valve only (Lewy and Samtlebergen, 1979). A higher degree of drilling in one or other shell valve may occur due to the orientation of the bivalve in the sediment that results in a greater susceptible of one valve to attack. The validity of this, however, is equivocal considering that naticids manipulate their prey prior to drilling, and also that infaunal burrowing bivalves lie with their posterior-anterior axis perpendicular to the sediment surface such that each shell valve would be equally susceptible to drilling. The majority of studies, including that by Dietl and Alexander (1997) on the predation of *Spisula solidissima* by *Euspira heros* and *Neverita duplicata*, have found no preference for left or right valves. This is perhaps not surprising bearing in mind the equivalve nature of most infaunal bivalve species (Kabat, 1990). The present study found that in most cases *Euspira pulchellus* drilled *Cerastoderma edule* in the centre of the shell valve and rarely at the margins or close to the umbo. Shell thickness tends to be greater near the umbo than at the edges of the shell valve such that it would be disadvantageous for naticids to drill in this position (Vignali and Galleni, 1986). *Polinices alderi* (= *E. pulchellus*) has been shown to preferentially drill in the mid-region of the valves of *Spisula subtruncata* and *Spisula elliptica,* and if forced to drill prey larger than the preferred size, drilling occurred in less favourable regions of the valves (Bayliss, 1986). Ansell (1960) found that *Natica alderi (= Euspira pulchellus)* drilled *Venus striatula* (= *Chamelea gallina)* in sites that were mostly at the shell margin, which according to Ansell (1960) directs drilling over the thinnest part of the shell. Yet elsewhere it has been reported that *C. gallina* is drilled mainly near the umbones (Vignali and Galleni, 1986, Martinell and De Porta, 1980). This is resolvable if different naticid species manipulate particular prey species in different ways. Drilling through the mid-region of shell valves has also been demonstrated by Griffiths (1981), Aitken and Risk (1988) and Vermeij *et al.*, 1989). Numerous studies, however, have also demonstrated that naticids drill close to the umbones (Piéron, 1933, George, 1965, Bernard, 1967, Sohl, 1969, Kitchell *et al.*, 1981, Ansell and Morton, 1985, Vignali and Galleni, 1986, Reid and Gustafson, 1989, Peitso *et al.*, 1994).

The distance from the umbo to the shell margin may be an important factor in size preference by *E. pulchellus* as it may be this that determines the limit of manipulation of the prey. Kabat (1990) proposed that the important factors influencing the positions of drill holes were the relative sizes of the predator and the prey, shell thickness and sculpturing of the prey, and any other factors relating to the manipulation of the prey. Other authors have stated that the position of the drill hole will vary with the particular predator-prey combination (Ansell, 1960, Massé, 1963), prey shell size (Sohl, 1969) and predator size (Verlaine, 1936, Negus, 1975). Early studies suggested that the stereotyped nature of drilling sites was aimed at directed entry over the prey gonads or digestive tissues (Pelseneer, 1924, Verlaine, 1936, Black, 1978). Verlaine (1936) suggested that *Natica alderi* (= *Euspira pulchellus*) drilled *Macoma balthica* in a position directly over the underlying gonad. Drilling over the digestive gland may be particularly beneficial in the presence of interlopers for two reasons. Firstly, it allows faster access to the most energetically rewarding tissues, and secondly, it leaves the adductor muscles intact, delaying gaping, both of which would reduce the likelihood of the predator being disturbed following the attraction of other predators (Pratt, 1974, 1976, Hughes and Dunkin, 1984). The muricid gastropod, *Haustrum baileyanum* selectively drills in a concentrated area of the shell of the abalone, *Haliotis rubra*, where the abalone muscle is attached (Thomas and Day, 1995). Unusually, *Acanthina punctulata* always drills its littorinid prey at the columellar despite the fact that this is the thickest part of the shell (Menge, 1974). It is, however, the point at which the prey is attached to its shell by the columellar muscle, such that severing this connection, or possibly introducing a toxin at this point, may facilitate the removal of the prey from its shell (Menge, 1974). It has also been suggested that drilling by some naticids occurs near the shell margin of their bivalve prey where the shell is thinner and there is no sculpturing (Ansell, 1960, Ansell and Morton, 1985, 1987).

The distribution of drill holes on prey shells may be a function of prey manipulation and result from the best grip the predator can obtain on the prey using its foot (Ansell, 1960, Carriker and Yochelson, 1968, Negus, 1975, Griffiths, 1981, Bayliss, 1986). Predators might be expected to hold the prey in the most secure manner, so that the prey is neither dropped or escapes before it is penetrated by drilling. The pattern of drill holes produced by *Euspira catena* feeding upon *Donax vittatus* is thought to be explicable by the manner in which the prey is manipulated by the foot (Negus, 1975). Similarly, the sitings of drill holes produced by *Natica tecta* feeding on *Choromytilus meridionalis* (Griffiths, 1981), or *Polinices tumidus* feeding on bivalves (Vermeij, 1980) are thought to arise from the manner in which prey are held. Berry (1982) observed that the trochacean gastropod *Umbonium vestiarium* is held by the foot of *Natica maculosa* with its ventral surface uppermost and the aperture to the rear and therefore drill holes were found almost entirely in the ventral surface of the shell.

Drill hole site stereotypy has been shown for *Euspira heros* and *Neverita duplicata* feeding on the surfclam *Spisula solidissima*, with more than 90% of drillholes being found in the mid-dorsal or umbonal area of the shell (Dietl and Alexander, 1995, 1997). Berg and Porter (1974) have also documented such stereotypy for these naticid species when predating molluscan prey, but found different patterns for the two species, whilst Dietl and Alexander (1995) demonstrated drill hole site stereotypy for these species when involved in cannibalistic activity. Berg (1975) suggested that behavioural differences in the way that prey are captured and manipulated influence the distribution patterns of drill holes for particular predator-prey combinations. Harper and Morton (1997) found that each of the six most abundant bivalve species found bysally attached in the shell gravels of Lobster Bay in the Cape d'Aguilar Marine Reserve, Hong Kong had a stereotyped drill hole site resulting from muricid predation. Harper and Morton (1997) concluded that at their particular study site in Hong Kong, the muricids of the low tidal zone were acting as generalist, opportunistic predators. The phenomenon of specialist predators acting as ecological generalists is referred to as Liem's paradox (Robinson and Wilson, 1998), and can partly be explained by the notion that some resources are intrinsically easy to use, such that predators are capable of developing specializations to exploit non-preferred resources without compromising their ability to consume preferred resources. This has been used to argue against the importance of competition as a diversifying force (Liem, 1984, 1990).

The nature of drilling in naticid gastropods appears to be highly stereotyped, so much so that in some cases it becomes inefficient. If interrupted during drilling, naticids do not resume where they had previously been drilling, but rather leave an incomplete drill hole and commence a new drill hole elsewhere, despite their previous investment in drilling (Kitchell *et al.*, 1981). The drilling behaviour of naticids appears to be insufficiently flexible to allow the predator to resume drilling at its previous location or to recognise an incomplete drill hole (Vermeij, 1982, Kitchell *et al.*, 1986). In the long-term, however, stereotypic drilling behaviour may be beneficial to the predator (Boggs *et al.*, 1984).

SUMMARY

Euspira pulchellus were size-selective in their choice of *Cerastoderma edule*. Large predators (12-15.9 mm shell length) selected both larger and a wider range of cockles than smaller individuals (4-11.9 mm shell length). However, there was considerable overlap in the sizes of cockles frequently drilled by different size classes of snail, indicating that certain sizes of cockles may be most profitable to a wide range of predator sizes. Feeding and growth rates were both strongly affected by seawater temperature. Small individuals (4-6 mm shell length) grew rapidly between April and September, whilst larger individuals (> 9-10 mm shell length) grew slowly, if at all. Inner and outer drill hole diameters were both correlated with predator size and the morphology of the drill hole was geometrically similar across a range of predator sizes. *Euspira pulchellus* showed no preference for either the left or right valve and drilled most cockles in the centre of the shell valve. The relationship between the distance of the drill hole from the umbo and prey size was unaffected by predator size, such that predators of different sizes were not found to drill cockles in different positions. When disturbed during drilling, incomplete drill holes were abandoned and when drilling resumed it occurred in new locations on the surface of the shell valve. The findings of this chapter highlight the stereotyped nature of drilling behaviour seen in the family Naticidae.

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Chapter 6

Age and growth determined using statoliths

INTRODUCTION

The hard skeletal structures of bivalves, gastropods and cephalopods contain not only a record of the past growth history of the animal, but also of the conditions surrounding the animal as it grew (see Richardson, 2001 for review). Rosenberg and Runcorn (1975) and Rhoads and Lutz (1980) are cited as landmark papers in this particular field and were the inspiration for much of the work that followed. Much use has been made of the growth rings, or annuli, both on the surface and within the internal shell structure of bivalve molluscs, to investigate seasonal and tidal cycles of shell growth, and also to determine age. The bivalve shell is frequently sectioned whole, or embedded in resin and then sectioned from umbo to shell margin, in order to study the micro-growth bands and growth lines present in the internal structure of the shell (Richardson, 2001). The 'limpet shape' of the majority of archaeogastropods also enables the shells of these animals to be sectioned, allowing growth bands, particularly those produced tidally, to be studied and estimates of age to be made. Species upon which such work has been carried out include the abalone, *Haliotis rubra* (Prince *et al.*, 1988), *H. midae* (Erasmus *et al.*, 1994), *H. corrugata* (Shepherd and Avalos-Borja, 1997) and *H. fulgens* (Shepherd *et al.*, 1995), the slipper limpet, *Crepidula fornicata* (Ekaratne and Crisp, 1982) and the limpets *Patella vulgata* (Ekaratne and Crisp, 1982, 1984), *Siphonaria gigas* (Crisp *et al.*, 1990) and *Cellana toreuma* (Richardson and Liu, 1994). In contrast, the helical configurations of the shells of mesogastropods and neogastropods make the production of continuous growth series sections by such methods difficult. Consequently, comparatively little work has been carried out on the shells of these higher gastropods. Nevertheless, Ekaratne and Crisp (1982, 1984) were able to demonstrate the production of tidally produced growth bands in the newly formed margin of the shells of *Littorina littorea* and *Nucella lapillus.*

Prosobranch gastropods, as well as other molluscs, possess sense organs known as statocysts which control the orientation of the animal. This function was first proposed by Delage (1887) and later proven by Tschachotin (1908). Statocysts were formerly referred to as otocysts or auditory capsules (Lacaze-Duthiers, 1872), at a time when they were thought to have a role in sound perception rather than in maintaining equilibrium. The statocyst comprises a fluid-filled cavity, the inner surface of which is ciliated, with an outer wall formed from connective tissue. Within the statocyst floats either a single calcareous statolith or several smaller statoconia. Statoconia are considered primitive and are found in all archaeogastropods, whilst statoliths are considered to be more advanced (Fretter and Graham, 1994).

There has been considerable work on the statoliths of cephalopods (e.g. Clarke, 1978, Lipinski, 1980 and see reviews by Jackson, 1994 and Richardson, 2001), whilst the published work on statoliths in gastropods is thus far limited to those of prosobranch and opisthobranch larvae (Bell, 1982, 1983, 1984, Grana-Raffucci and Appeldoorn, 1997). Larval statoliths can be viewed directly through the almost transparent shell of the intact animal and the formation of increments has been claimed to arise from a daily response to light-dark cycles, rather than to discrete feeding episodes (Bell, 1982, 1983, 1984). Work has, however, been carried out at the School of Ocean Sciences, Menai Bridge on the statoliths of *Buccinum undatum* (Karageorgopoulos, 1997) and *Nucella lapillus* (Saurel, unpubl.), from a range of intertidal gastropods collected from the Menai Strait (Taylor, unpubl.), and on the invasive gastropod *Rapana venosa* in collaboration with the Virginia Institute of Marine Science (Richardson, Kingsley-Smith, Mann and Harding, unpubl.).

The data presented in this chapter represent the first in-depth use of statoliths from adult gastropods to interpret the life-history of an adult gastropod in the field, in terms of its growth, age and timing of recruitment. The aims of the work presented here were to investigate:

i) the relationship between statolith size (diameter) and shell size ii) the patterns of rings within the statoliths of *Euspira pulchellus* of different sizes and to ascertain whether these structures can reliably be used to determine the age and growth rates of individuals of this species iii) the structure of statoliths from animals collected at different times of the year in order to determine the time of year at which prominent rings are formed iv) the diameter of the first ring in statoliths of animals collected at different times of year to determine the effect of recruitment time on growth during the first year.

MATERIALS AND METHODS

Information regarding the anatomy of the nervous system, and the relative positions of other parts of the animal, enable gastropods to be dissected in such a way as either to locate the statoliths directly or to produce a section of tissue in which the statoliths are likely to be contained. For all gastropods, the operculum and viscera can be discarded, leaving only the tissue of the head and foot. In large gastropods, such as adult *Buccinum undatum* and *Rapana venosa*, further dissection of the foot is necessary in order to produce a section of tissue containing the statoliths. This involves cutting dorsoventrally through the animal perpendicular to the long axis of the foot, in front of and behind the tentacles. If necessary, further parallel sections can be produced posterior to this initial section. Sections can then either be examined under the microscope for the presence of statoliths or digested in NaOH solution. In smaller gastropods, such as *Urosalpinx cinerea*, *Nucella lapillus* and *E. pulchellus,* the amount of foot tissue remaining following the removal of the operculum and viscera is sufficiently small it can be placed in NaOH solution in its entirety. (Note: In *Nucella lapillus* it is extremely difficult to observe the ganglia within the tissue of the animal (Saurel, pers. comm.) in comparison with ganglia in *Buccinum undatum* which were readily observed (pers. obs) presumably due to their greater size).

From those *Euspira pulchellus* collected from Red Wharf Bay in January, May and September 2001 (Chapter 2), a sub-sample of 20-30 animals was selected in order to give as wide a range of shell lengths as was available. Collectively these animals fell within the shell length size range 4 to 16 mm. These animals were stored in a freezer until required for dissection. Kristensen (1980) states that the use of weak acids, such as formalin, in the preservation of animals should be avoided if work on statoliths is to be carried out, as such substances are capable of dissolving these structures. Rodhouse and Hatfield (1990) reported that freezing is a much better method of preservation as the statoliths of squid frozen for 18 months were just as clear as those from freshly caught specimens. Once thawed, snails were removed from their shells, using fine forceps, by severing the attachment between the columellar muscle and the shell. The operculum was removed and together with the shell placed in a small labelled plastic bag. The viscera were then dissected away and discarded. Each animal was placed in a small glass Petri dish with its foot stretched out flat, as if in the crawling position. 10-15 mls of 1.0 M NaOH solution were added to each Petri dish in sufficient volume to cover the foot, in order to dissolve the tissue. A lid was placed over each dish and the dishes were left overnight in a fume cupboard. The following morning the dishes were observed under a Wild M3Z stereomicroscope. Statoliths are generally located close to the pedal ganglia in neogastropods and mesogastropods. The pedal ganglia tend to be concentrated anteriorly and the nerve innervating the statocysts runs from the cerebral ganglion through the cerebropedal connective. For this reason, it appears to originate from the pedal ganglion itself. The cerebral, pleural and pedal ganglia in higher gastropods form a ring that surrounds the gut (Fretter and Graham, 1994). Provided that the dishes were not disturbed too much in transit from the fume cupboard to the microscope stage, the statoliths were frequently easy to locate, as the nerves within the foot of the animal could be used as reference points. Once the statoliths had been located, the surrounding tissue was teased away using fine forceps and the statoliths transferred from the Petri dish into individual 500 μl Eppendorf tubes containing 70% industrial methylated spirits (IMS) solution.

A permanent slide preparation was made for each statolith or pair of statoliths from each animal. In most cases, both statoliths from a particular animal were extracted and prepared together on a single slide. Each statolith was picked out of the Eppendorf tubes using fine forceps, rinsed in 70% IMS, placed in 100% ethanol for 2 minutes, transferred to Histoclear for 2 minutes and finally transferred to a drop of DPX on a glass microscope. Each statolith was then manipulated, before the DPX began to set, so that it rested flat on its longest axis. (This orientation is optimal for viewing rings within the statolith). A cover-slip was then placed over each drop and the slides were left on a flat bench to dry naturally for 7 days.

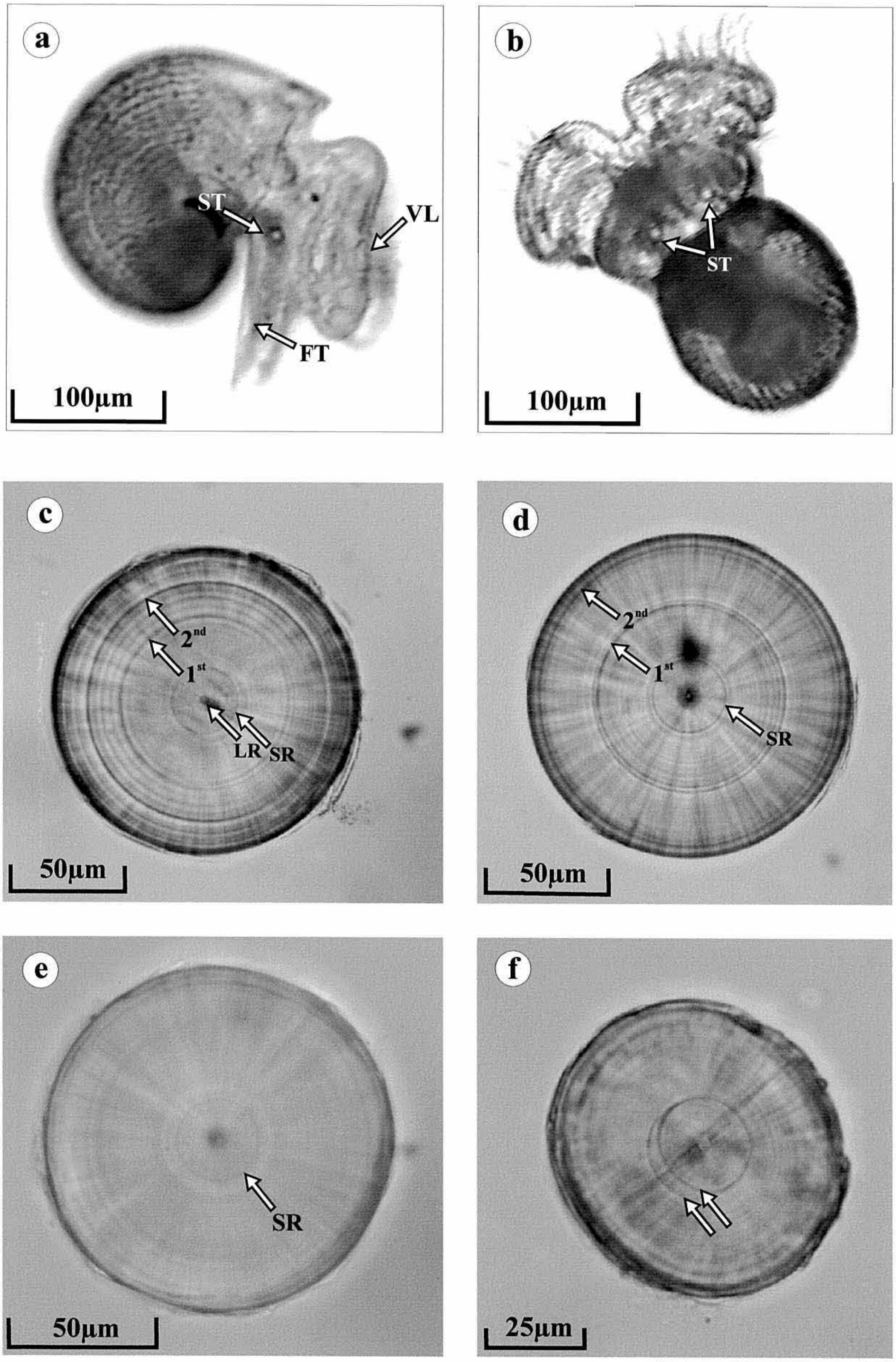
Statoliths were photographed and measured using a computer based image analysis system. Digital images were measured using Image Pro Plus v. 2.0 (1995) software made by Media Cybernetics, Silver Spring, Maryland, U.S.A. A photo-library was compiled of a representative selection of pairs of statoliths of a range of sizes of *E. pulchellus* from the January, May and September samples to allow the examination and comparison of the patterns of rings within the statoliths. The photo-library was compiled from captured images of the statoliths of 16-18 animals that ranged in shell length from 4.3 to 14.9 mm, 4.7 to 15.8 mm and 9.4 mm to 16.0 mm for the January, May and September samples respectively.

RESULTS

The positions of the statoliths in newly hatched *Euspira pulchellus* veliger larvae, reared as part of the work described in Chapter 4, are shown in Figures 1a and 1b. As in the adult, the statoliths are situated within the tissues of the foot and are visible through the shells of newly hatched larvae, and for approximately the first two weeks after hatching. Proliferation and differentiation of the foot tissues as the animal approaches metamorphic competence requires the dissection of the animal to observe and extract the statoliths in older individuals. The larval statolith, the proposed settlement ring and a first and second prominent ring can be seen in Figures 1c and 1d in statoliths extracted from adult *E. pulchellus* (see Figure 1 legend for details). In most of the statoliths examined, the settlement ring and the first and second prominent rings could be observed against a background pattern of less strongly defined regularly deposited rings. In a few specimens, however, statoliths were difficult to interpret as prominent first and second rings could not be seen (Figure 1e). Considerable variation occurred in the settlement ring and first ring diameter, the distance between these two rings and in the ability to observe a prominent second ring.

Figure 1f demonstrates the elliptical nature of the statoliths of adult *E. pulchellus* and highlights the importance of orientating the statolith appropriately in order to view the rings optimally. Failure to do so results in the appearance of 'double' rings resulting from the 3-dimensional and semi-transparent nature of these microstructures, such as in the case of the settlement ring shown in Figure 1f. Measurement of the statoliths from captured images of 10 newly hatched veliger larvae from the work described in Chapter 4 revealed that these structures had a mean diameter of 7.95 μm (95 % C.I = 0.43, n = 12). The mean diameter of the larval statolith within the adult statoliths, measured from images captured in this chapter, was 3.05 μm (95% C.I. = 0.31, n = 8), a value significantly smaller than that determined from the statoliths of newly hatched veligers.

Figure 1. a) Lateral view a newly hatched *Euspira pulchellus* veliger larva, partly emerged from its shell, showing the position of one of the statoliths (ST) in relation to the foot (FT) and the velum (VL). b) Newly hatched veliger swimming with velum fully extended, showing both statoliths (ST). c) Statolith from *E. pulchellus* (13.2 mm shell length collected in January 2001) with larval ring (LR), settlement (SR), first and second prominent rings visible, in addition to regular weaker rings. d) Statolith from *E. pulchellus* (13.4 mm shell length collected in January 2001) demonstrating the variation in ring patterns in which the second ring is nearer the margin than in (c). e) Statolith from *E. pulchellus* (10.1 mm shell length collected in (May 2001) in which only the settlement ring (SR) is clearly distinguishable. f) Statolith from *E. pulchellus* (5.2 mm shell length collected in May 2001) orientated to demonstrate the elliptical shape of these microstructures and the importance of ensuring the statoliths are positioned as in (c)-(e) to avoid the illusion of double rings (indicated by arrows).


a
ST
VL
FT
100μm
b
ST
100μm
c
2nd
1st
LR
SR
50μm
d
2nd
1st
SR
50μm
e
SR
50μm
f
25μm

Statoliths from snails (4.3 to 16.0 mm shell length) collected in January, May and September measured between 64.76 μm and 150.05 μm in diameter respectively. In all statoliths observed, a dark ring was present that ranged in diameter from 19.65 μm to 45.21μm with a mean of 29.84 μm (95% C.I = 0.804). It is proposed that this ring is deposited at metamorphosis following larval settlement (SR in Figures 1c to 1e). The measurement of statoliths extracted from newly settled individuals raised in Chapter 4 would have supported this argument, however, the small number of larvae successfully brought through to metamorphosis and the necessity of keeping them alive for use in other work prevented this.

The total diameters of the statoliths from the animals collected in January, May and September were significantly correlated with shell length ($r = 0.842$, $p < 0.001$) and linear regression analysis produced the equation:

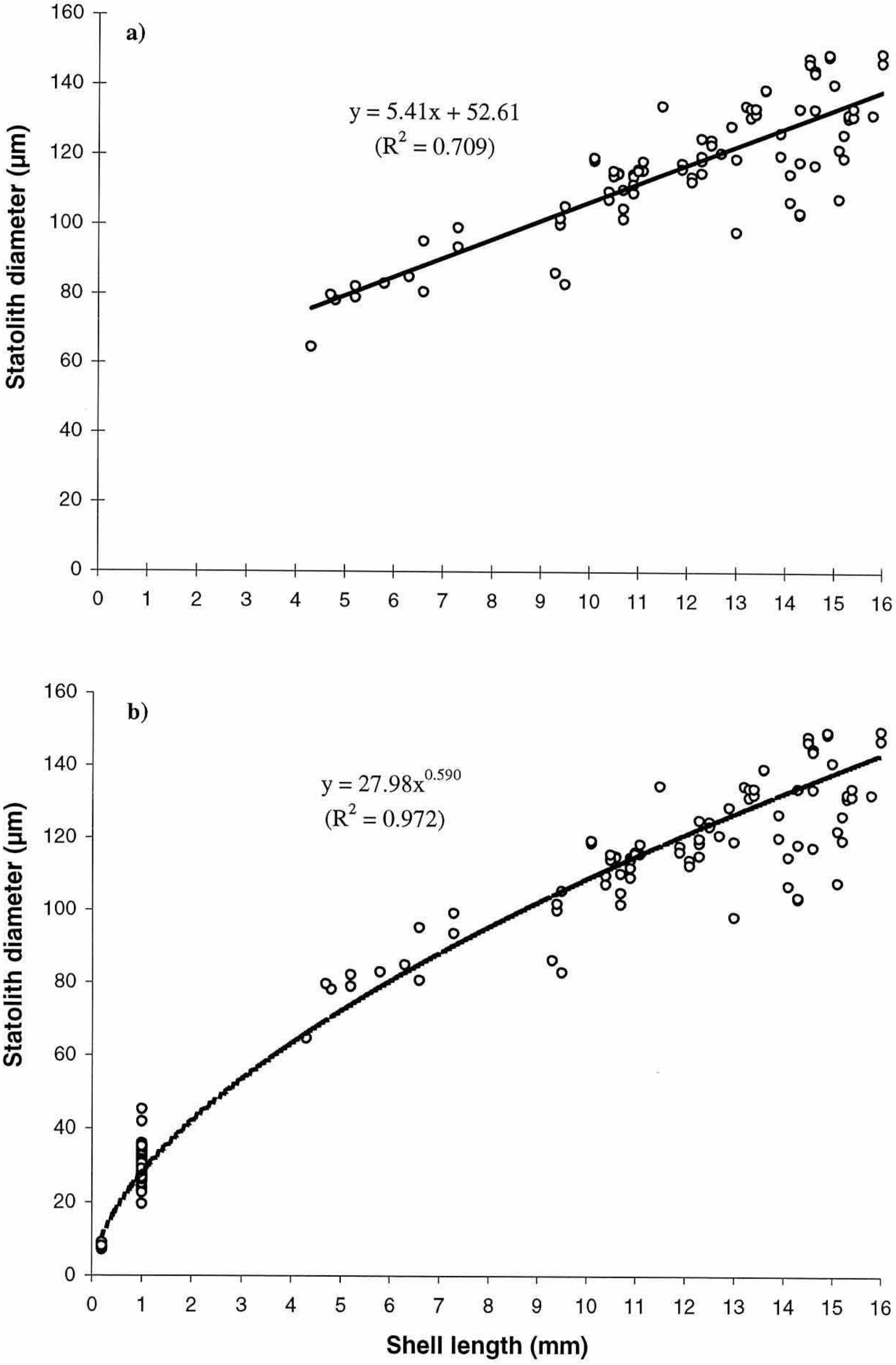
Statolith diameter (μm) = 5.41 x shell length (mm) + 52.61 μm (Equation 1)
($n = 88$, $R^2 = 0.709$)

ANOVA of this regression equation demonstrated that both the slope and the intercept were significant (Figure 2a). If the data for larval statolith and settlement ring diameters are included, however, in conjunction with shell lengths of animals at hatching and at settlement (200 μm and 1 mm respectively – see Chapter 4), the relationship between shell length and statolith diameter is improved and appears more curvilinear. Fitting a curve to the extended data set gives rise to the following equation:

Statolith diameter (μm) = 27.98 x (shell length in mm) $^{0.590}$ (Equation 2)
($n = 186$, $R^2 = 0.972$)

Having established the relationship between statolith diameter (Figure 2b) and shell length from the larva up to the maximum shell length reached by *Euspira pulchellus* (16 mm), it is possible, using equation 2, to back-calculate the shell length of the snail at the time when a particular statolith ring was formed. From the calculation of these shell length data, the variation in shell length at the deposition of the prominent first ring (not including the settlement ring) was investigated. From the shell lengths at

Figure 2. Relationship between *Euspira pulchellus* shell length (mm) and statolith diameter (µm) for a) 4 mm to 16 mm animals collected in January, May and September 2001 from Red Wharf Bay and b) including data on the statolith diameters from newly hatched veligers (200 µm), newly settled individuals (1mm) and adults (4-16 mm) (plotted in (a)).


a)
y = 5.41x + 52.61
(R^2 = 0.709)
Statolith diameter (µm)
0
20
40
60
80
100
120
140
160
0
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
b)
y = 27.98x$^{0.590}$
(R^2 = 0.972)
Statolith diameter (µm)
0
20
40
60
80
100
120
140
160
0
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
Shell length (mm)

both the first and second prominent rings the pattern of growth in this species can also be investigated and compared with that determined in Chapter 2, using the method of Bhattacharya (1967), and Chapter 5, from direct measurements of animals held in the laboratory. Variation in shell length at the time the first prominent ring was deposited may reflect variations in the timing of settlement. A size-frequency analysis of back-calculated shell lengths reveals that there is considerable variation in the shell length of snails at the time the first ring is deposited, ranging from 2 mm to 9 mm, but in most cases occurs between 4 and 4.9 mm (Figure 3a). Back-calculation of the shell lengths of animals for both the first and second prominent rings determined using equation 2 produced mean shell lengths of 5.02 mm (95% C. I. = 0.416) and 8.96 mm (95% C. I. = 0.550) respectively. In Figure 3b the line plotted through these points is fitted by eye. Attempts to fit the growth of this species to the Von Bertalanffy growth equation, $L(t) = L\infty\ (1-\exp^{-k(t-t0)})$, based upon the data derived from the first and second rings indicated that the pattern of growth in this species does not fit the model. The model fitted a line that was almost linear to the three data points and produced an $L\infty$ value of 62.08 mm and a value of K of 0.07. As the model requires data which has an asymptote, the linear nature of the growth data based upon statolith ring diameters means it is not suitable for use in the von Bertalanffy model.

A significant correlation was found between the diameter of the first and second rings ($r = 0.844$, $p < 0.001$) (Figure 4a). Linear regression on this data set produced the equation:

Second ring diameter (μm) = 0.66 x First ring diameter (μm) + 56.50 μm

(Equation 3)

Both the intercept and slope were significantly different from zero ($p < 0.001$ in both cases) and ANOVA of the regression was also significant ($p < 0.001$). A significant correlation was also found between the settlement ring diameter and first ring diameter ($r = 0.443$, $p < 0.001$). There was considerable scatter of the data, however, and a clear relationship between these two variables could not be seen (Figure 4b). No clear differences were found between the samples collected in January, May and September in the distance from the second ring to the edge of the statolith and

Figure 3. a) Percentage frequency distribution of the shell lengths of *Euspira pulchellus* estimated at the time of the deposition of the first prominent ring; shell lengths were calculated from equation 2 for the relationship shown in Figure 2a. b) Mean shell lengths (± 95% confidence intervals) of *E. pulchellus* estimated at the time of the deposition of the first and second prominent rings using the same equation.

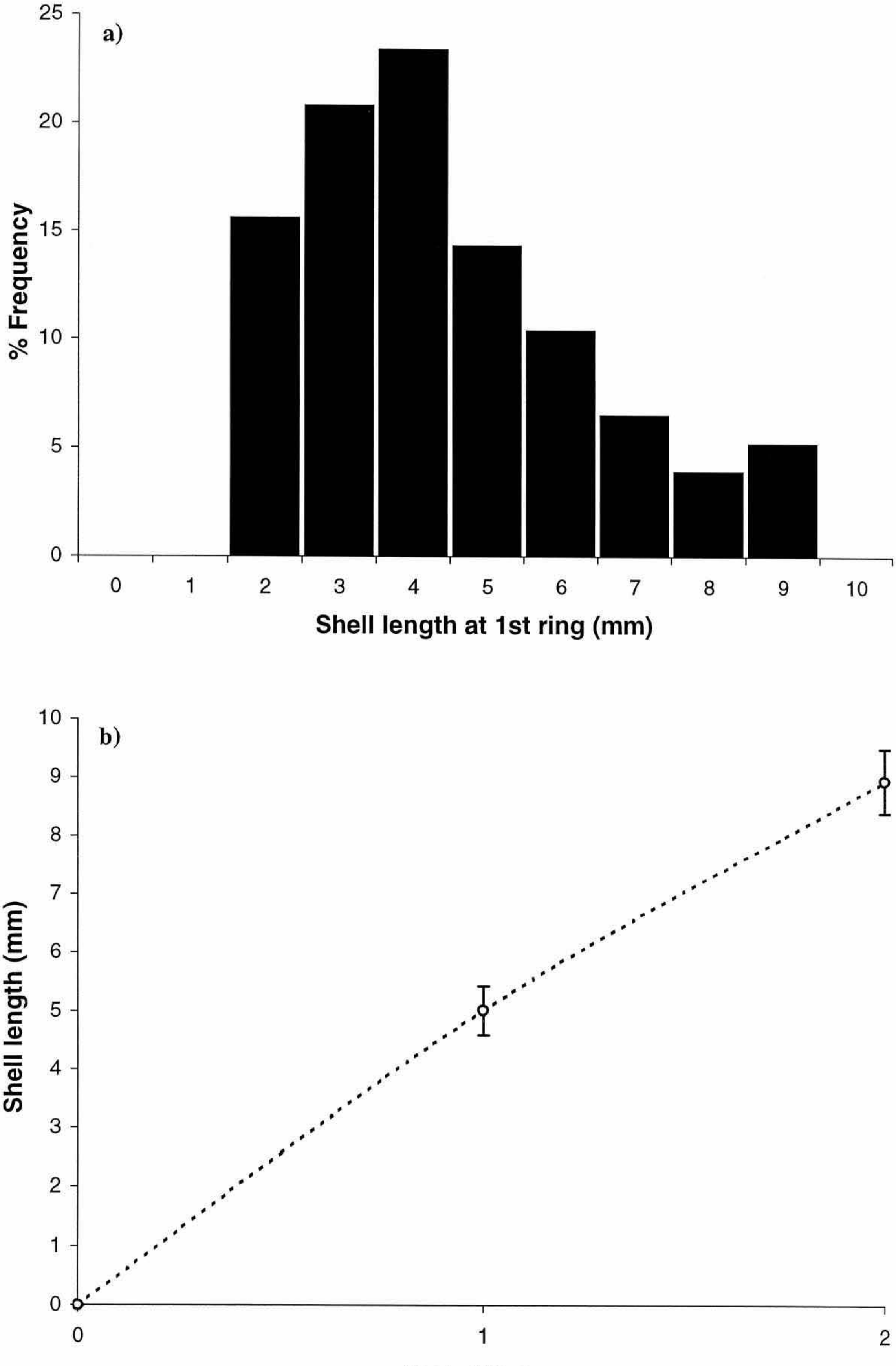
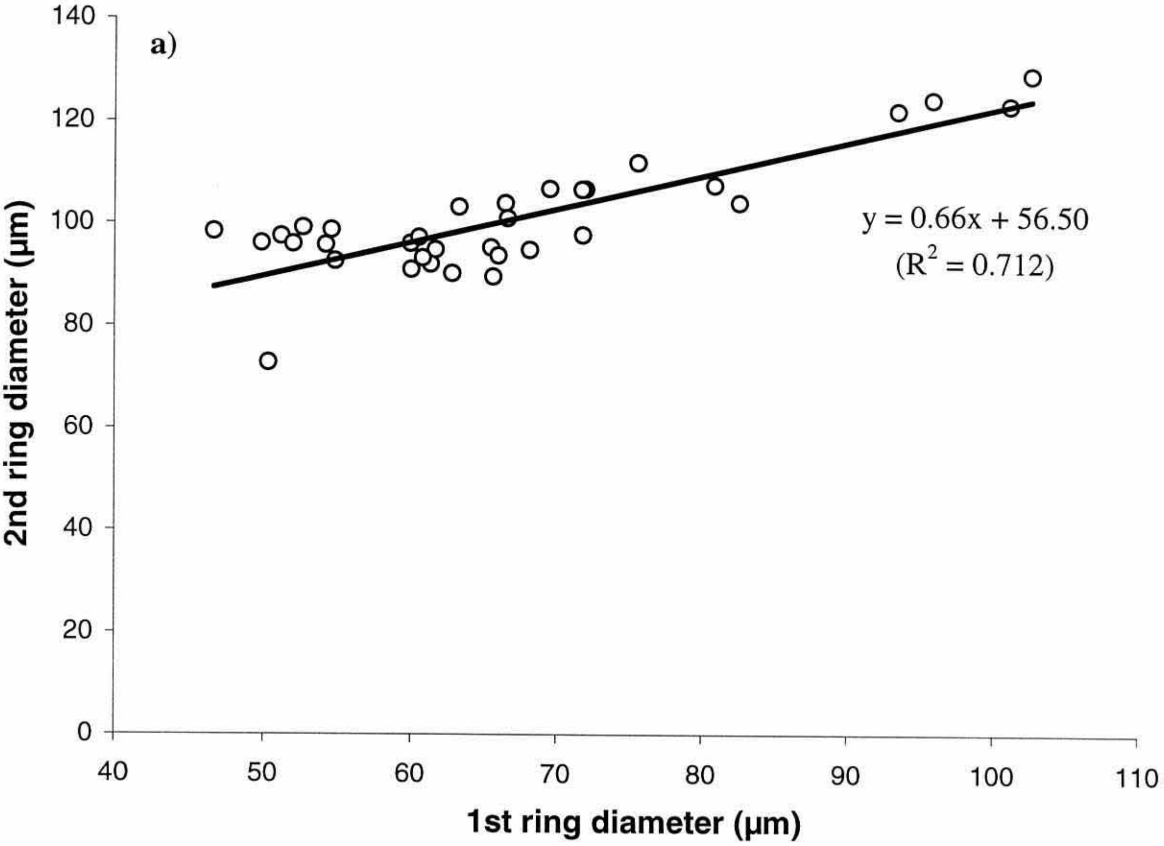
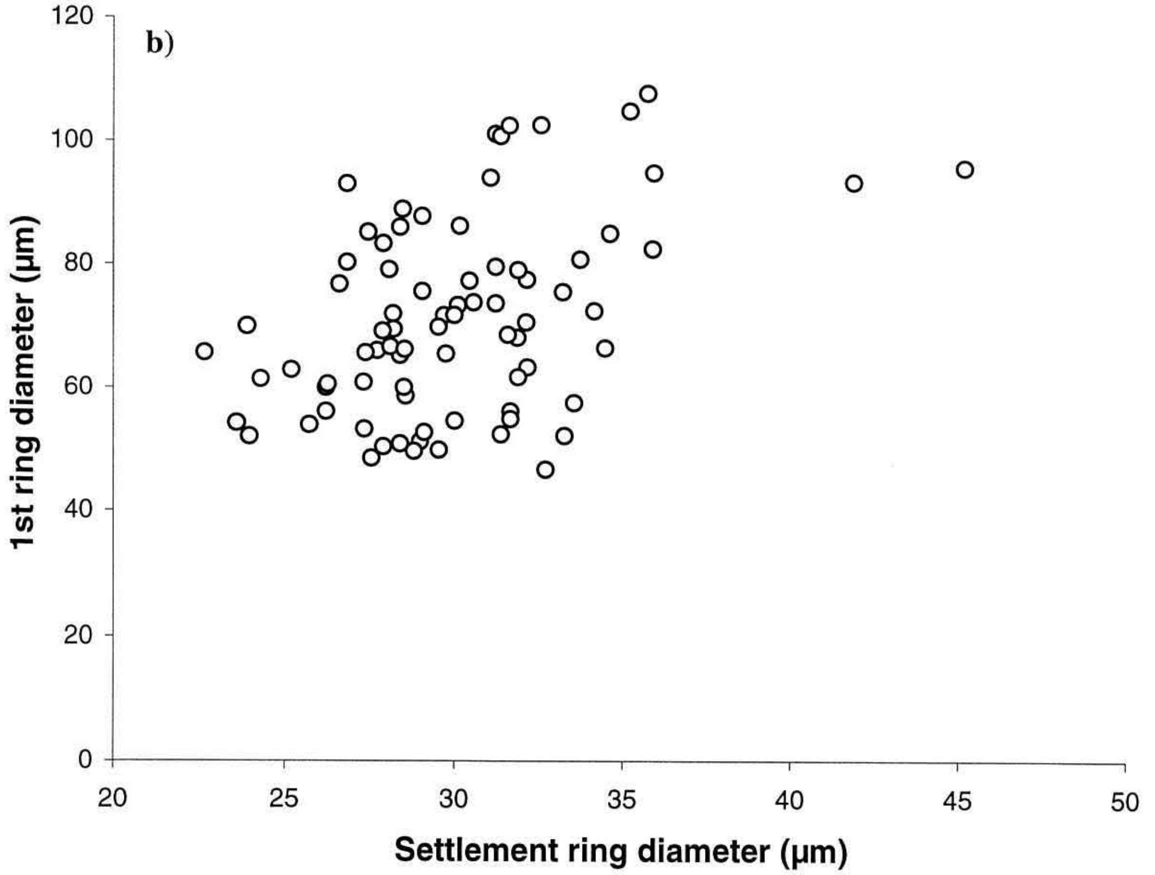

a)
% Frequency
25
20
15
10
5
0
0
1
2
3
4
5
6
7
8
9
10
Shell length at 1st ring (mm)
b)
Shell length (mm)
10
9
8
7
6
5
4
3
2
1
0
0
1
2
Statolith ring

Figure 4. Relationship between the diameter of a) the first and second prominent rings and b) the settlement and first prominent rings observed in the statoliths of *Euspira pulchellus* collected from Red Wharf Bay.


a)
140
120
100
80
60
40
20
0
2nd ring diameter (µm)
40
50
60
70
80
90
100
110
1st ring diameter (µm)
y = 0.66x + 56.50
(R^2 = 0.712)


b)
120
100
80
60
40
20
0
1st ring diameter (µm)
20
25
30
35
40
45
50
Settlement ring diameter (µm)

therefore it was not possible to determine the time of year at which the first and second rings are formed.

DISCUSSION

By establishing the relationship between the shell lengths of *Euspira pulchellus* and their statolith diameters, it is proposed that statoliths can be used to reconstruct the growth history of the animal. This includes growth during the larval stage through settlement and metamorphosis up until the animal reaches its maximum size. The change in feeding niche between the planktotrophic veliger and the carnivorous juvenile (as discussed in Chapter 4) is reflected in the structure of the statolith, as indicated by the proposed presence of a settlement ring. Furthermore, it is proposed that variation in the diameter of this ring may reflect differences in the period of time spent in the plankton. Had attempts to raise larvae at different temperatures been successful in Chapter 4, the effect of temperature on larval development rates and therefore statolith settlement ring diameters could have been used to support this hypothesis.

The discrepancy between the larval statolith diameters obtained from newly hatched larvae and from the larval statolith within the statoliths extracted from the adults, may have arisen from one of two possible sources of error. Firstly, it was difficult to get a clear image of the larval ring in the adult statolith due partly to their small size and partly due to the necessity to focus through a 3-dimensional structure. This could be overcome by sectioning the statoliths but this in itself is difficult due to the size and fragile nature of these microstructures (see Karageorgopoulos, 1997). The other possibility is that what was actually measured from the captured still images of the newly hatched larvae was the statocyst, rather than the statolith within it. Nevertheless, it is still proposed that the structure discernible at the centre of the adult statolith represents the statolith present in newly hatched larvae.

Variation in the shell length of this species at the deposition of the first ring may correspond to differences in the timing of settlement, with individuals that settle earlier in the year depositing a greater amount of statolith material than later settlers prior to the formation of this ring. Although there was no clear relationship between settlement ring diameter and first ring diameter when plotted, the significant correlation suggests that a relationship may exist. If variation in settlement ring diameter does indeed represent differences in the length of time that individuals spend as planktonic organisms, which is itself affected by temperature, settlement rings could be used to determine the time of year at which particular larvae were released. Larvae released early in the year when water temperatures are lower will take longer to develop, producing a larger settlement ring. As a result of earlier recruitment, these individuals will spend a longer period growing in the benthos in their first year before the deposition of the first prominent ring in winter. Larger settlement rings should, therefore, correspond with larger first ring diameters, as suggested by the positive correlation. The strong correlation and clear linear relationship between the first and second ring diameters indicates that individuals that settle early and grow to a larger size during their first year also grow more rapidly during their second year. Attaining a larger size in the first year, therefore, confers an advantage on *Euspira pulchellus* in terms of growth in its second year, despite the onset of sexual maturity. In contrast, the common cockle *Cerastoderma edule*, grows rapidly and becomes sexually mature in its first year, but grows more slowly in its second year, as somatic growth is compromised by reproduction (Seed and Brown, 1978).

There was considerable variation in the statolith diameters and ring patterns such that clear differences in the patterns between the January, May and September statoliths were difficult to unravel. Resolving the time of year at which the prominent rings are deposited, may require the examination of statoliths from snails collected on more occasions within the year, and a closer examination of the statoliths extracted from small animals, say 4-6 mm in shell length, in which rates of statolith diameter increase are greater than in larger individuals.

The causes of the pattern of weak regular rings and the deposition of prominent rings seen in the statoliths of *E. pulchellus* have yet to be determined. The presence of daily increments have been demonstrated in the statoliths of gastropod larvae (Bell, 1982, 1983, 1984, Grana-Raffucci and Appeldoorn, 1997) and are well documented in the statoliths of a range of cephalopod species (e.g. Hurley *et al.*, 1985 and see review by Richardson, 2001). The weak regular rings seen in the statoliths of *E. pulchellus* are, however, unlikely to be deposited on a daily basis. The congruency of the mean shell lengths calculated from the first and second rings with the growth data, not only from the experiments carried out in Chapter 5, but also the results of the method of Bhattacharya (1967) in Chapter 2, supports the conclusion that prominent rings are deposited annually. Mean shell lengths of 5.02 mm and 8.96 mm, calculated from the statolith diameters of the first and second rings, are appropriate sizes at which *E. pulchellus* could over-winter. It is well established that cephalopod statoliths are deposited incrementally and the close relationship between statolith diameter and shell length of *E. pulchellus* suggests that the growth of the animal is reflected in the growth of the statolith. Reduced feeding rates and slower growth due to lower seawater temperatures may cause the increments in the statolith to be more closely packed, resulting in a dark band that has been referred to as the first or second prominent ring in this chapter. Villanueva (2000) demonstrated that the statoliths of the squid *Loligo vulgaris* grow more slowly in the winter months when water temperatures are lower supporting the hypothesis that the prominent rings observed in the statoliths of *E. pulchellus* represent winter cessation in growth. It is not possible, however, to categorically state that the rings in the statoliths of this species are annual without corroboration from statoliths extracted from animals of known age and history.

Following the successful development of a method for rearing *Euspira pulchellus* (Chapter 4), it would now be possible to raise snails over extended periods from larvae through to juveniles and adults. Experiments in which external factors such as light, temperature and feeding regime are controlled, and growth and reproductive behaviour of animals of known age monitored, would greatly strengthen the conclusions that have been made about the nature of the rings in the statoliths of this and other gastropod species. In the absence of such experimentation, the possibility remains that checks in the growth of the animal, and also therefore in the statolith, leading to the formation of a prominent ring, may arise from other sources. Shell growth in bivalves has been shown to be interrupted by a variety of factors including extreme seasonal temperature shocks (Pannella and MacClintock, 1968, Cunliffe and Kennish, 1974, Kennish, 1980), spawning (Pannella and MacClintock, 1968, Kennish, 1980, Sato, 1995), storms (Cunliffe and Kennish, 1974, Kennish, 1980), disturbance by fishing gear (Gaspar *et al.*, 1994, Robinson and Richardson, 1998, Ramsay *et al.*,

2000) or manipulation by predators (Ramsay and Richardson, unpubl. obs., Richardson *et al.*, 1980). Such disturbances of shell growth might be expected to be reflected in the structure of the statolith as well as the shell of the animal. Without controlling external factors the interpretation of the structure of the statolith and conclusions that rings are annual remains equivocal.

SUMMARY

In most statoliths examined from adult *Euspira pulchellus*, the larval statolith, settlement ring and first and second prominent rings were visible against a background of weaker, regularly formed rings. Statolith diameter and shell length were closely related for data gathered from larvae through to fully grown adults (16 mm). This relationship was used to calculate the shell lengths of snails at the time that particular statolith rings were formed, and to interpret the growth of a range of sizes of snails. Both settlement ring and first ring diameters varied considerably, which it is proposed reflect differences in the time spent in the plankton and the time available for growth prior to the onset of winter respectively. First ring and settlement ring diameter were significantly correlated such that the duration of these two phases appear to be related. First ring and second ring diameters were also significantly correlated, indicating that rapid growth during the first year is maintained during the second year. Attaining a larger size during the first year, therefore, confers an advantage in terms of growth on the animal during its second year. Estimates of mean shell length from the first and second ring diameters, when compared with measurements made of animals collected from the field and grown in the laboratory, support the conclusion that prominent rings are formed annually. Further experiments are required to determine both the causes and timings of the formation of weak and prominent rings in adult gastropod statoliths.

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Chapter 7

General Discussion

Naticid gastropods are specialist predators of infaunal invertebrate communities, feeding preferentially on thin-shelled bivalve species (Fretter and Graham, 1994). *Euspira catena* and *Euspira pulchellus* are both reportedly common around the coast of Britain on sandy substrates in shallow inshore waters (Hayward *et al.* 1995) and have particular preferences for bivalves within the family Tellinidae (Ansell, 1960). Beam trawling revealed that the abundance of *E. pulchellus* and *E. catena* in Red Wharf Bay varies according to sediment type. *E. catena* was generally associated with areas of clean sand, whilst *E. pulchellus* was associated with areas of muddy sand, where *E. catena* was usually absent.

The investigation of the size-frequency distributions of individuals within the Red Wharf Bay population revealed that small individuals (4-6 mm shell length) were present in low numbers over an extended period of time, implying that recruitment to the benthos may have been occurring at low levels throughout the year, rather than as a discrete event at a particular time each year. This hypothesis was supported by the production of egg collars by females held at ambient temperature in the laboratory throughout the year, with maximum rates occurring during the summer months. Egg collars were, however, only produced by females in the laboratory once they had reached a size between 8 and 9.9 mm in shell length. Different sizes of female *E. pulchellus* displayed different patterns of egg collar production in the laboratory. Larger individuals had greater fecundity and produced egg collars over a shorter period of time than smaller individuals. Statements regarding the fecundity of *E. pulchellus* based upon numbers and wet weights of egg collars could be made having established a linear relationship between the wet weight of egg collars and the number of veligers released. Individuals that were 4 to 6 mm shell length in April became sexually mature during the course of the summer with females commencing egg collar production in September and continued to produce egg collars after larger, older individuals (14-15.9 mm shell length) had ceased laying. This suggests that these larger individuals had become senescent. *Euspira pulchellus* females are capable of laying egg collars over an extended period of time in the absence of contact with males, as a result of their ability to store sperm. These aspects of the reproductive biology of *E. pulchellus* adequately explain the pattern of recruitment of *E. pulchellus* in Red Wharf Bay.

Although the number of *E. pulchellus* caught was highly variable between trawls, the mean density of *E. pulchellus* was higher during the warmer, summer months than during winter. Higher densities of *E. pulchellus* during the summer months may be explained by the aggregation of individuals in order to mate. The *E. pulchellus* population in Red Wharf Bay was consistently dominated by individuals 12-12.9 mm shell length. Monitoring the increase in shell length of cohorts in the field and by measuring animals kept in the laboratory revealed that the shell growth of small individuals (4-6 mm) was rapid until a shell length of 9-10 mm was attained, and thereafter growth rate declined. The rapid growth of small individuals to a size at which they were indistinguishable from the most abundant size classes present in the field population throughout the year indicated that this cohort may be made up of more than one year class. Rates of feeding and growth in *Euspira pulchellus* were both related to seawater temperature which started to increase in April.

The size at which females become sexually mature and the size at which growth rates decline are both approximately 9 mm shell length, considerably below the maximum size reached by *E. pulchellus* (16 mm), such that somatic growth at some stage might be expected to be compromised by gametogenesis. The life histories of naticids are characterised by a growth phase prior to sexual maturity followed by cycles of growth and reproduction during which, according to Ansell (1982a), growth is limited. Ansell (1982a) demonstrated that variation in predation rate in this species is affected by temperature, predator size and annual cycles of growth and reproduction. In the absence of food limitation, predation rate has been shown to be governed largely by temperature, but also the internal state of the animal (Ansell, 1982b); however, when food is limited, the amount of food obtained determines the metabolic activity of the animal, rather than *vice versa* (Ansell, 1982b).

The veliger larvae of *E. pulchellus* were successfully reared and induced to metamorphose during this study and the behavioural and morphological changes occurring during development were documented for the first time. When raised at 19-20° C in filtered seawater and a mixed algal suspension, veligers were competent after 6-7 weeks and were induced to settle and metamorphose when exposed to sediment collected from the adult habitat. The association of *E. pulchellus* with areas of muddy sand in Red Wharf Bay, as opposed to other sediment types, therefore, may be explained by an active habitat choice made by the larvae. The precise nature of the cue, however, has yet to be identified. In light of the possibility of transport away from the adult habitat, a specific metamorphic response and the ability to delay metamorphosis in the absence of an appropriate cue, as shown in this study, should act to promote the placement of individuals in habitats that support future survival, growth and reproduction (Thorson, 1950, Scheltema, 1961, Crisp, 1974). The frequency with which delayed metamorphosis occurs in the field has not been investigated and may occur rarely given that larvae can be expected to encounter a suitable cue for metamorphosis. The identification of delayed metamorphosis in larvae collected from the field requires the identification of metamorphic competence, based either upon morphological or behavioural characteristics, or by the induction of metamorphosis in the laboratory. Considering that veligers of *E. pulchellus* remain planktonic for several weeks, the potential for transport of larvae is considerable. The influences of the currents within Red Wharf Bay on the dispersal of larvae and the consequent distribution of adult populations have yet to be investigated. A short-fall of many field-based experiments has been the difficulty in distinguishing between differential larval settlement and differential post-settlement survival such that the importance of differential larval settlement in determining adult distributions is open to debate. The lack of evidence that there is clear imprinting onto adult populations from variation in settlement, due to post-settlement processes, brings into question a long and rich literature on the consequences of larval ecology for the population dynamics of marine invertebrates. Factors determining adult populations that are independent of those influencing planktonic larvae include post-settlement mortality from mobile epibenthic predators (Frid and James, 1988) and food limitation (Òlafsson *et al.*, 1994). Predation upon *E. pulchellus* has not been investigated and the effect of this process upon the ecology of this species warrants further study.

The extended period of recruitment exhibited by *E. pulchellus* indicates that its recruitment does not coincide with that of its prey. The early commencement of drilling and pattern of recruitment in *E. pulchellus,* therefore, have implications for the recruitment and post-settlement survival of a range of subtidal bivalve species over an extended period. Early in its life-history, *E. pulchellus* has been shown to be size-specific in its selection of bivalve prey, whilst other work has demonstrated species preferences by this species (Bayliss, 1986). During the course of the present study, a high proportion of small size classes of cockles (4-8 mm) were drilled by a wide range of sizes of *E. pulchellus*, indicating that these small prey may be the most profitable. *Cerastoderma edule* were most frequently drilled in the centre of the valve, irrespective of the size of the predator or the prey. It is proposed that such drilling results from the manner in which prey are held, rather than prey shell thickness or the siting of drilling to gain access to particular underlying tissues. The comparison of the distributions of drill holes in bivalve shells that differ markedly in shape may explain the siting of drill holes by *E. pulchellus*.

The inner and outer diameters of drill holes produced by *E. pulchellus* in the valves of the common cockle were significantly correlated with the shell length of the predator. Drilled bivalve shells collected from the field, therefore, can be used to obtain information on the sizes and rates of predation of *E. pulchellus* in the field. The structuring role of *E. pulchellus* in benthic soft-bottom communities, specifically those of Red Wharf Bay, and of British naticids generally, requires further scrutiny. Size-selective predation, by the depletion of certain size classes, has the potential to influence the prey population structure as prey may be more vulnerable when they are small (Ebling *et al.*, 1964, Paine, 1974, 1976, Seed and Brown, 1975, Commito, 1982, Summerson and Peterson, 1984). Ecologists intending to study the population dynamics of soft sediment marine habitats, specifically from the point of view of invertebrate predator-prey relationships, should also consider the possible roles of gastropod predators outside the Naticidae and Muricidae, particularly the buccinids (Peterson and Black, 1995, Morton and Chan, 1997).

The helical configuration of the shells of higher gastropods makes the production of a continuous growth series to study growth and determine age difficult, such that little research of this kind has been carried out. This study has shown that statoliths, due to the incremental nature of their formation can be interpreted chronologically. Whilst considerable work has been carried out on the statoliths of cephalopods (Clarke, 1978, Lipinski, 1980 and see reviews by Jackson, 1994 and Richardson, 2001), the published work on gastropod statoliths is limited to the study of larval stages (Bell, 1982, 1983, 1984, Grana-Raffucci and Appeldoorn, 1997), in which statoliths can be viewed directly through the shell. Examination of the statoliths of adult *E. pulchellus* in this study revealed the presence of a central larval statolith, settlement ring, and first and second prominent rings, against a background of weaker rings. The change in feeding niche between the planktotrophic veliger and the carnivorous juvenile and a distinct change in growth is presumed to be responsible for the appearance of a dark ring at the time of settlement.

It is proposed that the prominent rings represent annual checks in statolith growth. From the close relationship established in this study between the shell length of *Euspira pulchellus* and statolith diameter ($R^2 = 0.972$), the shell lengths at the time that particular rings in the statoliths were formed were calculated. It is proposed that variation in the diameters of settlement rings results from differences in the length of time spent by larvae in the plankton prior to settlement. Larvae released earlier in the year when seawater temperatures are lower will take longer to develop and are presumed to have a larger settlement ring. Individuals that recruit to the benthos earlier in the year will have a longer period available for growth in their first year prior to the deposition of the first ring in winter. Larger settlement ring diameters, therefore, correspond with larger first ring diameters, and these two parameters were significantly correlated ($r = 0.443$, $p < 0.001$). The extended period of recruitment in *E. pulchellus* and consequent variation in the period of time between settlement and the subsequent winter is expected to produce variation in the diameter of the first ring. Calculation of the shell lengths of *E. pulchellus* at the time first prominent rings were deposited ranged from 2 mm to 9 mm, but most frequently fell within the interval 4 to 4.9 mm. First and second ring diameters were significantly correlated ($r = 0.844$, $p < 0.001$) indicating that individuals that attain a larger size in their first year maintain a more rapid growth rate in their second year, such that reaching a greater size in the first year, following earlier recruitment, confers an advantage in terms of growth in the second year. The mean shell lengths of *E. pulchellus* at the formation of the first and second prominent rings were appropriate sizes at which *E. pulchellus* might pass their first and second winters. It is therefore proposed that these prominent rings are produced in the winter and represent annual checks in statolith growth. The precise causes of the production and timings of the weak, regular rings and darker, prominent statoliths rings, however, have yet to be determined. The reduced rates of growth and feeding at lower water temperatures during winter may cause statolith increments to be more closely packed resulting in a dark band, as demonstrated by Villanueva (2000) for the statoliths of the squid *Loligo vulgaris*.

The successful development of a technique for the culture of *E. pulchellus* larvae enables the production of animals of known age that could subsequently be used in experiments in which light, temperature and feeding regime were controlled, and growth and reproductive output measured. Such work could elucidate the causes of both the regular and more prominent rings seen in the statoliths of *E. pulchellus*. As a third annual ring was not seen in the statoliths of any *E. pulchellus* examined, this species does not appear to be long-lived. *E. pulchellus* demonstrates a strategy of rapid growth to a size at which it is sexually mature (~ 9 mm). Female *E. pulchellus* have an extended period of egg-laying, which occurs continuously from the first summer through the winter before declining and stopping in the oldest animals after their second summer in September. From the information gathered on the growth, reproductive biology and population structure of *E. pulchellus,* this species may only live for 2 to 3 years. The senescence of larger individuals, indicated by the cessation of egg-laying activity, may be followed by the death of individuals in their second or third year. Mortality of *E. pulchellus* appeared to be a common occurrence in the population of Red Wharf Bay based upon the abundance of *E. pulchellus* shells inhabited by the hermit crab, *Pagurus bernhardus*.

Predatory snails, particularly naticids, have been regarded as unusually voracious, possibly consuming 25% of their own body weight per day (Thorson, 1971) and have therefore been regarded as competitors with Man for benthic resources. Edwards and Huebner (1977), however, reported that in Barnstaple Harbour, Massachusetts, *Neverita duplicata* consumed only 1% of its body weight per day annually of its preferred prey species, *Mya arenaria.* Naticids may have come to be regarded as voracious predators, along with crabs and starfish, due to the permanent record that their predation activity leaves behind. Whilst other invertebrate predators (e.g. crustaceans) and fish frequently destroy the shells of their prey during consumption, naticid and muricid drill holes provide an indication of how the prey species died. As a result, naticids have become the scapegoats in some areas for declining shellfish stocks, such as in the case of *Neverita duplicata* and declining clam yields in the coastal waters around Massachusetts (Edwards and Huebner, 1977). Despite the apparently low rate of consumption by *N. duplicata* (Edwards and Huebner, 1977) the structuring role of naticid gastropods requires further scrutiny. Wiltse (1980) investigated the effect of predation by *Neverita duplicata* on the infaunal sandy shore community at Barnstaple Harbour, Massachusetts. The exclusion of this predator from caged areas of the seabed led to a more diverse, richer community with denser associations of both molluscan and non-molluscan species within the cages, with both higher species richness and evenness components. In uncaged, fenced snail enclosures, intense predation pressure was shown to remove individuals and species from the infauna, in particular thin-shelled tellins, a favoured prey of naticids, which were generally rare (Wiltse, 1980). The selective feeding behaviour of naticids, particularly upon non-dominant forms has the potential to affect the faunal diversity of an area by altering the balance between supply and demand.

The disturbance of the sediment made by snail trails has also been shown to decrease the number of spionid polychaetes within a community, as well as the total non-molluscan fauna (Woodin, 1978). The author also reported fewer species and lower densities of surface-feeding polychaetes in areas disturbed by other epibenthic predators, namely the horseshoe crab *Limulus polyphemus* and the blue crab *Callinectes sapidus*. Conversely, Kelley (1982) proposed that extensive naticid predation has the potential to increase species diversity by reducing competitive interactions. Trophic interactions involving naticids can be rather complicated since both asteroids and naticids feed upon bivalves, and some asteroids also feed upon naticids (Christensen, 1970, Freeman, 1999). Whilst much is known on the biology of a number of naticid species around the world, their ecological role and their potential to structure subtidal benthic communities, particularly around British coasts, requires greater study.

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