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Community structure and recruitment of decapods in shallow sub-littoral habitats

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A thesis submitted in fulfilment for the degree of Doctor of Philosophy to
Trinity College, University of Dublin

Department of Zoology
September 1999

Candidates Declaration

I hereby declare that this thesis is my own work, unless otherwise stated and has not been previously submitted to this or any other university. I also give my permission to the library to lend or copy this thesis on request.

M. Robinson

Martin Robinson

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SUMMARY

Although decapod crustaceans represent a major component of benthic fauna in many geographic localities around the world, little is known of their early benthic life history. This study examined the relative influences that larval supply, larval habitat choice and post-settlement processes have in shaping resultant community structure in sub-tidal rocky habitats. The habitat sampled contained high densities of numerous decapod species, some of which are commercially exploited, indicating that sub-tidal rocky substrates may represent important nursery grounds.

Temporal and spatial surveys of young of the year and adult decapod community structure were conducted. Divers using SCUBA apparatus took quantitative air-lift suction samples in a single cobble habitat in 1997 and five distinct habitats with varying physical complexity in 1998. Seasonal minima and maxima in decapod abundance and biomass were identified. Settlement and recruitment of numerous decapod species were detected. Multivariate and univariate statistical techniques revealed significant temporal variability in intra-annual community structure and population parameters. Some species that settled into habitats did not persist until the end of the year. Settlement and recruitment differed between habitats with varying physical complexity, with higher densities recorded in more complex substrates. Post-settlement processes significantly altered community structure within the first year. Changes in the community were more significant in less complex habitats.

The early benthic phase population dynamics of certain species were examined using length-frequency analyses. In some cases it was possible to produce detailed models of post-settlement mortality and growth. Aquaria experiments revealed that growth and survival of juvenile crab is not always negatively affected by the presence of larger conspecifics. Reduction in density of crab species was initially high after settlement, but in most cases declined with increasing size. Experimental enclosures indicated that dispersal did not significantly affect the density of most species or community structure as a whole, when compared with non-dispersal. A high proportion of hatchery-reared stage V juvenile lobster died within one month of release, with almost all survivors dispersing from the release site. Hatchery-reared juvenile lobster had no impact on most species present in the immediate release area, or on community structure as a whole.

Multi-species stock-recruitment models that describe the relationship between larval production and the subsequent density of young of the year decapods in the benthos were developed. Density dependant regulation of recruitment and overcompensation was evident in some habitats, while others showed no such constraint. The application of these models, and ways in which they could be further developed, are discussed.

INTRODUCTION

Decapod crustaceans often represent a major component of benthic fauna in many geographic localities throughout northern Europe (Smaldon, 1972; González-Sanjurjo, 1982; Anon, 1997; Kaiser *et al.*, 1998; Nickell & Sayer, 1998; Jennings *et al.*, 1999). Decapod species can be both numerically dominant and the major contributors to biomass in benthic communities. The sheer numbers or size of individuals can have direct effects on the surrounding environment and resident community due to physical disturbance (Warwick *et al.*, 1990), or by representing a resource to other species (Chesney & Iglesias, 1979; López-Jamar *et al.*, 1984; Friere & González-Gurriarán, 1995). Artisanal and major commercial fisheries are supported by exploitation of decapod crustaceans around the world. An understanding of the life history of crustacean stocks, and the causes and prediction of annual fluctuations in numbers, is essential for sustainable harvest. The life cycles of marine crustaceans can be difficult to study, and as a result the population dynamics of species are often poorly understood. Much of the information pertaining to decapod species is relevant to the more easily studied planktonic and adult stages. For many species, little is known of the early benthic and juvenile phases. The body size and cryptic nature of early benthic phase individuals have made detection and quantitative sampling difficult, especially in hard, physically complex substrata.

The importance of shallow water sites as nursery grounds for decapod species is only beginning to be realised. Gravel extraction, aquaculture, benthic trawling and pollution may cause serious degradation of these areas. Damage, alteration and reduced productivity has been recorded in many communities that have been subjected to anthropogenic disturbance (Pearson, 1975; Bamber, 1984; Agard *et al.*, 1993). Loss of such habitats, and the species within them, will result in a reduction in recruitment to nearby fisheries. It is vital that an understanding of the dynamics of shallow water nursery areas, and their importance to fisheries, is gained. Prediction and detection of intra-annual and inter-annual variation in the communities resident in sub-tidal nursery habitats will allow informed management of these areas and the fisheries that depend on them, permitting sustainable utilisation whilst conserving the resident decapod communities.

Larval life history

The majority of decapod species have a 2 stage life history and release dispersive larval propagules. The duration of incubation is species specific (Wear, 1974), and can be related to a number of physical and biotic factors (Richards & Wickens, 1979; Aiken & Waddy, 1986; Thompson & Ayers, 1989). Larvae develop through a number of stages in the plankton, the exact duration being determined by a number of factors, but predominantly by temperature (Valdes & Alvarez Osorio, 1983; Wickens & Beard, 1991). The larvae of some species spend prolonged periods in the plankton, while others released at later stages of development have a shorter planktonic life. Although initial larval production is related to the size of the adult spawning stock and fertilisation success, processes acting on larvae after release significantly affect subsequent larval abundance and settlement. Density independent and density dependent physical and biotic processes act on the larval population throughout development. Physiological stresses (Pechenik, 1987; Wang & Widdows, 1991), starvation (Boidron-Metairon, 1995; Baily *et al.*, 1997) and predation (Olson & McPherson, 1987) are believed to contribute to high levels of larval mortality (Rumrill, 1990; Kristiansen *et al.*, 1997). Oceanographic processes can lead to the retention of larvae in the locality of release (Alldredge & Hammer, 1980; Baily *et al.*, 1997; Swearer *et al.*, 1999), transport larvae away and then return them at a later stage of development (Shanks, 1983; McConaugha, 1988; Rothlisberg, 1988; Jones *et al.* 1999), or permanently remove larvae to new areas (Gaines *et al.*, 1985; Caley *et al.*, 1996; Baily *et al.*, 1997; Verdier-Bonnet *et al.*, 1997). Larvae delivered to new areas may encounter exploitable habitats unoccupied by conspecifics, areas already supporting genetically different populations of conspecifics, or grounds that are unsuitable for either settlement or subsequent development. Transportation of larvae to unsuitable habitats may represent a significant contribution to larval mortality (White *et al.*, 1988; Rumrill, 1990; Baily *et al.*, 1997). Recent studies have indicated that behavioural responses of postlarvae, including directional orientation, vertical migration and active swimming, are important for delivery to settlement habitats (Cobb *et al.*, 1989; Katz *et al.*, 1994; Condie *et al.*, 1999).

Defining settlement and recruitment

Interchanging of the terms associated with the transition between the pelagic and benthic phases of the life cycle has lead to confusion in the literature. In the following chapters terms are generally defined as the following unless otherwise stated. Settlement is the process whereby late stage pelagic larvae select a final substrate in which to settle and metamorphose into the benthic form. In some species, such as the European lobster *Homarus gammarus* (L.), postlarvae have moulted to the benthic form prior to settlement. The term settler or 1st crab stage is used to describe the newly settled individual at the first benthic moult instar. Young of the year is used to distinguish individuals that have settled to the benthos in the current season from all previously settled individuals. Recruitment refers to individuals reaching a certain stage of development, normally either the maturation of individuals or the attainment of a size that permits commercial exploitation when used in the context of fisheries. In this thesis young of the year crab remaining several months after settlement are referred to as recruits.

Substrate selection

Discriminatory ability increases as the time for settlement is approached (Welch *et al.*, 1998) and larvae respond to numerous cues within their surrounding environment. The postlarvae of many species have been shown to exhibit both positive and negative taxis towards various cues within the surrounding environment, including the presence of algae and seagrass (Forward *et al.*, 1996; Morgan *et al.*, 1996; Welch *et al.*, 1998), habitat complexity (Moksnes *et al.*, 1998; Stevens & Kittaka, 1998) and the presence or absence of conspecifics (Crisp & Meadows, 1962; Jensen, 1991) or predators (Boudreau *et al.*, 1993; Welch *et al.*, 1998; Diaz *et al.*, 1999). Exploration and rejection of unsuitable settlement habitats or conditions, and subsequent return into the water column has been documented (Cobb *et al.*, 1983). Delay of metamorphosis is a temporary measure to avoid marginal habitats, but eventually a final and sometimes fatal selection of habitat must be made (Connell, 1961; Strathman *et al.*, 1981). Substrate selectivity tends to decline as the delay in metamorphosis is extended (Crisp, 1974; Doyle, 1975; Rumrill, 1989). Settlement of some species can also be mediated by environmental cues, such as tidal periodicity (Morgan *et al.*, 1996; Eggleston *et al.*, 1998; Robinson & Tully, in press a), while others display no such association (Jones & Epifanio, 1995). Patchiness in larval distributions, caused by larval behaviour (Botero & Atema, 1982; Herrnkind & Butler, 1986) and hydrodynamic processes (Eckman, 1983; Clancy & Cobb, 1997;

Wahle & Incze, 1997), can result in inequalities in subsequent benthic distributions. Variation in settlement and subsequent benthic abundance can occur at numerous spatial scales ranging from metres to hundreds of metres (Hughes *et al.* 1999).

Spatial variation in settlement and community structure

Selection of suitable settlement habitat is likely to be one of the most important factors affecting species survival in shallow sub-littoral environments. Different species display varying degrees of substrate specificity at settlement, with some displaying no preference over a wide spectrum of substrates (Tupper & Boutilier, 1997), while others are extremely selective (Keough & Downs, 1982). The ability of individuals to select a suitable habitat can contribute to subsequent survival (Connell & Jones, 1991; Pile *et al.*, 1996; Tupper & Boutilier, 1997) and growth (Connell & Jones, 1991; Perkins-Visser *et al.*, 1996), and may define the resultant community structure. Physically complex habitats are generally accepted as supporting dense, rich faunal communities. Survival and growth are often higher in more complex habitats (Connell & Jones, 1991; Moksnes *et al.*, 1998; Stevens & Kittaka, 1998). Interstitial spaces in cobble and boulder substrata affords shelter (Wahle, 1992) from physical (Howard & Nunny, 1983) and biological hazards (Lavalli & Barshaw, 1986; Wahle & Steneck, 1992) to numerous species. Other factors, such as the occurrence of dense aggregations of prey species in complex habitats (Steele, 1999) may promote settlement. Risk (1997) suggested that the ability of larvae to choose favourable places to settle, and to persist there, may cause patterns of recruitment to differ from those of the larval supply. A combination of larval supply dynamics, larval substrate selection and post-settlement processes together determine resultant adult community structure (Gaines & Roughgarden, 1985;

Eggleston & Armstrong, 1995). The spatial variation in settlement and recruitment within several distinct sub-tidal habitats with varying degrees of physical complexity is examined in Chapter 1 of this thesis. A comparison of the spatial variability in young of the year and adult community structure is presented. The results suggest that habitat complexity may play an important role in determining the level of settlement and subsequent recruitment. Chapter 1 has been accepted for publication in Marine Ecology Progress Series (Robinson & Tully, in press b).

Seasonal variation in settlement and recruitment

Settlement and recruitment vary annually. The causes and magnitude of annual variation in settlement and recruitment success are poorly understood (Beukema, 1984; Aiken & Waddy, 1986; Ennis, 1986; Fogarty *et al.*, 1991; Lewis, 1991; Eggleston *et al.*, 1998). Annual variation can be detected in single species, complexes of species with similar habits or habitats, or in the community as a whole. Natural processes and anthropogenic activities can lead to increase, decrease or failure of settlement or recruitment. Intra-annual variation in settlement and recruitment is common in temperate latitudes, where the environmental conditions experienced by individuals can be markedly different over time. An understanding of intra-annual variation in decapod settlement, abundance and biomass is useful in the identification of the causes and magnitude of inter-annual variation. Identification of seasonal trends in these parameters may enhance the success of hatchery-release programs and the accuracy of annual stock prediction. The former may benefit from knowledge of community dynamics if seasonal minima in parameters representing the optimum time for release, that minimises competition, can be identified. Examination of seasonal settlement and recruitment can identify the most suitable time to conduct censuses of recruitment for annual predictions. Identifying the most influential species, or biological or physical factor, interacting with the target species, and accounting for variability in their recruitment success will enhance the accuracy of annual predictions. Seasonal variability in decapod community statistics and community structure in a sub-tidal cobble habitat is examined in Chapter 2 of this thesis. The duration and intensity of settlement of numerous decapod species, and distinct seasonal lows in species abundance and biomass, are identified. An abstract and poster of this chapter was presented at the 4th International Crustacean Congress (Robinson & Tully, 1998a). A full version of the chapter has been submitted to Marine Ecology Progress Series.

Post-settlement processes and population dynamics

A number of post-settlement processes are involved in shaping the benthic community (Roughgarden *et al.*, 1988). These fall into two general categories; those that affect survival and those that affect dispersal. Significant sources of mortality include predation (Lavalli & Barshaw, 1986; Wahle & Steneck, 1992; Fernandez *et al.*, 1993a; Moksnes *et al.*, 1998), cannibalism (Fernandez *et al.*, 1993a; Smith, 1995; Lovrich & Sainte-Marie, 1997; Moksnes *et al.*, 1997; Moksnes *et al.*, 1998), disease (Aiken & Waddy, 1986) physical disturbance (Howard & Nunny, 1983; Pile *et al.*, 1996) and environmental stress (Bertness, 1981). These pressures, whether density dependent (Pile *et al.*, 1996) or independent (Connell, 1985; Pile *et al.*, 1996), can result in the dispersal of individuals (Campbell, 1986; Fernandez *et al.*, 1993b; Lovrich *et al.*, 1995). Random movement of displaced individuals will often lead to the arrival of conspecifics as others leave (Iribarne *et al.*, 1994; Wahle & Incze, 1997). This will eventually result in an overall net loss or gain from the population.

Detecting density dependent regulation within such dynamic populations, that are often patchily distributed, can be extremely difficult (Hassell, 1987; Herrnkind & Bulter, 1994). Further confusion can occur when the population is prone to unpredictable stochastic disturbances (Pile *et al.*, 1996). However, it may still be possible to model recruitment, mortality and growth with sufficient life history data. As understanding of individual species dynamics increases, and the interactions within communities are examined, it may be possible to develop detailed ecological models of the population dynamics and interactions between the early life history stages of decapods. The population dynamics of a single species, the porcellanid crab *Pisidia longicornis* (L.), are examined in Chapter 3 of this thesis. This species represents an important component of shallow water nursery habitats as it provides a plentiful and readily available source of food for other decapods and fin fish species (Chesney & Iglesias, 1979; López-Jamar *et al.*, 1984; Friere & González-Gurriarán, 1995). Much of the analysis is based on length-based assessment of the population. The periodic shedding of the hard exoskeleton in crustaceans and lack of permanent hard body parts hampers age determination, precluding the use of conventional age-based assessment. Length-frequency distributions can often be used to identify annual cohorts within crustacean populations, and occasionally to distinguish successive instars. Subsequent length-based assessment of distinct components of the population can be used to model growth and survival (Sparre & Venema, 1992). Chapter 3 has been accepted for publication in the Journal of the Marine Biological Association of the United Kingdom (Robinson & Tully, in press a).

Post-settlement dispersal

Settlement into unsuitable habitats or saturation of desirable substrate will necessitate movement to other areas in order to survive. Ontogenetic shifts from nursery habitats have been documented in large and mobile species (Orth & van Montfrans, 1987; Pile *et al.*, 1996). The ability of mobile species to disperse is believed to play an important role in reducing inter-specific and intra-specific competition (Iribarne *et al.*, 1994). Avoidance of conspecifics and other species may become vitally important when considering the high density of individuals resident in shallow water rocky nursery habitats. Migration from habitats has been described for species that undergo a complete shift in habitat utilisation (Orth & van Montfrans, 1987; Pile *et al.*, 1996) and those that simply saturate suitable habitat (Wahle & Incze, 1997). In the latter, saturation density of the initial settlement substrate, when the required habitat type remains the same during development, is a decreasing function of increasing body size. The number of shelters available declines as larger interstitial spaces are required (Wahle, 1992). This leads to a habitat 'bottleneck' that requires movement to other areas to search for shelter, removal or vacation of another individual from a suitable shelter, or postponement of further growth until a suitable shelter becomes available (Caddy, 1986; Wahle & Steneck, 1991; Moksnes *et al.*, 1998). Movements by larger individuals, that are less dependent on shelter providing habitats (Wahle & Steneck, 1991), to less crowded areas with available shelter have been shown to smooth spatial variability in settlement densities (Wahle & Incze, 1997).

Over-fishing or natural depletion of crustacean stocks, together with increasing market prices and demand, has lead to the need for informed stock management and legislation. The lucrative export of quality shellfish to the continent represents a major source of revenue from fisheries in Ireland (Anon, 1999). As a result, methods of stock enhancement have been developed to augment natural stocks (Bennett, 1980; Bannister & Addison, 1998). A number of these methods have been commonly utilised in Ireland to replenish, sustain or increase stocks of the European lobster, *Homarus gammarus*, with varying degrees of success. Establishment of a minimum landing size to protect immature individuals, conferring protected status on 'V-notched' brood stock (Daniel *et al.*, 1989) and the release of hatchery-reared juveniles into the fisheries catchment area (Addison & Bannister, 1994) have been instigated by state bodies and fisheries co-operatives. The latter method involves the on growing of juveniles in hatcheries (Mercer & Brown, 1994), in an attempt to avoid the high mortality often experienced by newly settled invertebrates (Gosselin & Qian, 1997). The labour intensive and time consuming work involved with hatchery methodology can lead to high expenditure for each juvenile produced (Hicky, pers. coms.). Successful hatcheries often rely on the voluntary work or financial contribution from local fishermen. Past studies have refined release methodology to ensure juveniles are released safely to the benthos and quickly find shelter (Bannister, 1995; Cook, 1995). The subsequent fate of these juveniles, and the numbers surviving to recruit to the fishery are largely unknown (Walker, 1986; Bannister *et al.*, 1994; Bannister & Addison, 1998). Most release methods create temporary artificially high, localised densities of lobster juveniles which are believed to disperse into the surrounding area with time. Encounters between lobster can be assumed to be high initially, decreasing with time after release. Lobsters are solitary, territorial animals that readily fight (O'Neill & Cobb, 1979; Atema & Cobb, 1980), injure and cannibalise conspecifics in field and laboratory conditions. In less confined surroundings, physical encounters may lead to more rapid dispersal (Iribarne *et al.*, 1994) of released individuals. Displacement and movement in densely populated sub-tidal habitats, which are inhabited by numerous pelagic and benthic predators (Lavalli & Barshaw, 1986; Wahle & Steneck, 1992), increase the possibility of an unfavourable or fatal encounter. Anthropogenic alteration of the benthic community by release of juvenile lobster may have an adverse effect on the resident communities. No attempts have been made to characterise these effects in the past. The effect of confinement on both the young of the year and adult components of the population are examined in Chapter 4. Mortality and dispersal of hatchery-reared juvenile *Homarus*, which were released into the enclosures, are also presented. Experimental enclosures are used to examine the effects of confinement on both lobster and the natural decapod community resident in the release habitat. Although there is some question as to the 'reality' of caging and enclosure experiments, due to the presence of physical boundaries (Virnstein, 1978; Gee *et al.*, 1985), these are not relevant in the context of the present experiment. Comparisons between enclosures and controls are used to assess the importance of dispersal, rather than the effects of enclosure *per se*. An oral version of this chapter was presented at the 3rd International Conference on Shellfish Restoration and submitted to the conference proceedings printed in Hydrobiologia.

Population structure and growth

As stated previously, when saturation density is a negative function of body size a 'bottleneck' effect can occur. This can lead to a reduction in the growth rate of individuals. There is some experimental evidence to suggest that in densely populated areas the presence of conspecifics can reduce overall growth rate (Carlberg *et al.*, 1979). This is believed to be either a physically (Cobb & Tamm, 1974) or chemically (Nelson *et al.*, 1980) mediated response suppressing the metabolism and growth potential of smaller bodied individuals that are in close proximity to larger specimens (O'Donovan, 1998). Disproportion in body size or age between conspecifics sharing habitats is believed to reduce niche overlap and to effectively eliminate direct competition itself (Wilson, 1975; Polis, 1984). High densities of individuals can occur in shallow water nursery habitats throughout the growing season. As the settlement season progresses new settlers are increasingly likely to be in the locality of larger conspecifics, that settled in previous years or earlier in the same season. The possible reduction in growth rate that may occur when commercially exploited species are involved has implications for recruitment to fisheries, stock enhancement programs and the lag time from settlement to recruitment applied in stock-recruitment models. The edible crab, *Cancer pagurus* L., represents a significant proportion of the shellfisheries landings and export in Ireland (Cosgrove, 1998; Anon, 1999). Shallow water cobble habitats could represent vitally important nursery grounds for *C. pagurus* that recruit both to inshore and offshore fisheries (Robinson & Tully, 1998b). Juvenile *Cancer* are abundant in these habitats from low water mark on the shore, partially buried in coarse sand under cobble and boulder (pers. obs.). Chapter 5 examines the early life history of *Cancer pagurus*. The settlement and mortality of the species is described in a shallow water nursery habitat. The occurrence of smaller individuals in the close proximity of larger conspecifics in the field prompted examination of possible effects of this population structure on growth and mortality of younger conspecifics in particular in aquaria based experiments. The results of field surveys of seasonal *Cancer* abundance were presented to the ICES Study Group on crabs in 1998 (Robinson & Tully, 1998b).

Coupling of larval production and recruitment to the benthos

As understanding of the early life history stages of invertebrate's increases, debate still remains as to the relative contributions of larval supply, larval substrate selection and post-settlement processes in shaping the resultant benthic community (Eggleston & Armstrong, 1995). Interest in this area has increased with attempts to model the recruitment of commercially exploited species from larval production. Benthic sampling for juvenile decapods can be time consuming and labour intensive relative to plankton sampling. Although methods for quantitative sampling of complex rocky substrata have been developed with advances in SCUBA diving techniques (Wahle & Steneck, 1991; 1992), effort is often constrained by the time divers can remain at depth and the financial expenditure involved with even a small diving unit. Therefore, there are obvious advantages if recruitment can be predicted from larval production. If settlement and subsequent recruitment into the benthic habitat are under density dependent constraint and the area of habitat is limiting, then these life history processes could control the stock-recruitment relationship (if the population is closed), carrying capacity and production of the population within specific habitat types. In effect, estimates of recruitment can be made when a suitable time lag and mortality estimates are applied to known larval production. This may seem a gross simplification when the processes of dispersal and migration are considered and therefore the population is not closed. This has in turn led to the development of metapopulation analysis, which is suitable for mobile open populations or sedentary populations with pelagic larvae as it identifies the main locations for gains (sources) and losses (sinks) of larval production. Advances in predicting recruitment have been made in single species stock-recruitment models that examined settler-recruit relationships for the Australian rock lobster (Phillips &

Brown, 1989) and the American lobster (Incze & Wahle, 1991; Incze *et al.*, 1997). Multi-species models have been derived linking primary production to subsequent secondary production in the form of benthic invertebrates (Buchanan, 1993). No previous attempts have been made to link decapod larval production and recruitment in multi-species models. Failure to detect juveniles of some commercially exploited species, or to characterise their nursery habitat, has hampered formulation of stock management methods (Howard & Bennett, 1979). It may be possible to predict the recruitment of such species using multi-species stock-recruitment data and applying a model that represents the average stock-recruitment relationship for the species assemblage being studied. In Chapter 6, the relationship between larval production and subsequent benthic density of young of the year individuals for a number of decapod species are examined. The resultant models may be of benefit in predicting future recruitment of these and other species from the transfer efficiency of larval production. The results may suggest that the overall number of young of the year individuals across all species may be under density dependent regulation in some habitats and not others. This indicates that interaction between conspecifics and/or the community as a whole is significant at or soon after settlement in the majority of habitats. Chapter 6 has been submitted to the Canadian Journal of Fisheries and Aquatic Sciences.

Summary

In summary, this thesis consists of a number of field and laboratory based experiments that examine various aspects of the early benthic life history of decapod crustaceans in sub-littoral rocky habitats. Chapter 1, ‘Spatial variability in decapod community structure and settlement in sub-tidal habitats’, examines the community structure and abundance of both young of the year and previously settled individuals in several sub-littoral habitats. Chapter 2, 'Seasonal variation in decapod community structure, settlement and recruitment within a rocky sub-tidal benthic habitat', describes intra-annual variation in community structure and population parameters with a sub-littoral cobble habitat. A detailed account of the population dynamics of a single species, that is the numerically dominant decapod species in most rocky habitats in northern Europe, is presented in Chapter 3, 'Dynamics of a sub-tidal population of the porcellanid crab *Pisidia longicornis*'. The effect that dispersal has on decapod community structure and abundance is examined in Chapter 4, ' Mortality and dispersal in a benthic sub-tidal decapod community and of hatchery reared lobster, *Homarus gammarus*', along with that of released hatchery reared lobster for stock enhancement purposes. Chapter 5, 'Settlement, growth and mortality of early benthic phase edible crab, *Cancer pagurus*', examines the population dynamics of the edible crab and the effect that population size structure has on the growth and survival of conspecifics. The sixth and final chapter, 'Coupling of decapod larval production and subsequent recruitment to the benthos in a rocky sub-tidal habitat', examines the efficiency of transfer of larval production to the benthos, and discusses its application in the formulation of models for prediction of recruitment. The overall aim of this thesis is to provide new and informative data relating to the early life history of individual decapod species and of the decapod community as a whole. The rich and diverse decapod community studied, that is dominated numerically by *Pisidia longicornis*, ranges through most of the sub-littoral rocky habitats of northern Europe.

CHAPTER 1

SPATIAL VARIABILITY IN DECAPOD COMMUNITY STRUCTURE AND RECRUITMENT IN SUB-TIDAL HABITATS

ABSTRACT

Sub-tidal populations of decapod crustaceans from five distinct benthic habitats were sampled at the end of the main settlement season. Divers, using SCUBA equipment, estimated substrate characteristics and complexity, removed sediment samples, and collected quantitative samples of the resident communities using suction sampling at each of the sites. Adult and young of the year (YOY) components of the decapod assemblages were identified. Univariate and multivariate statistical techniques were used to detect between-site differences in the community structure and community statistics of each component. Although YOY individuals were detected at each of the sites, community structure and statistics for the YOY component varied significantly across sites. Between-site differences in the adult component of the community were also identified. Between-site differences in the YOY assemblages varied from that of the adult component, indicating that post-settlement processes, such as predation and migration, play an important role in shaping the community. Variation in physical complexity and other habitat characteristics appeared to contribute to the significant differences in the YOY and adult assemblages. Due to the close proximity of the sample sites, it seems unlikely that restrictions or spatial and temporal variations in larval supply resulted in the between-site differences observed. Substrate choice at settlement would appear to vary between species, with most species rejecting more marginal areas that offer little shelter to either postlarvae or individuals at later stages of development.

INTRODUCTION

Cohort strength in decapod crustaceans may be determined early in life history (Robinson & Tully, 1998b). Both density dependent (Iribarne *et al.*, 1994; Pile *et al.*, 1996) and density independent (Doherty, 1994) processes may operate at this stage.

If settlement and recruitment into the benthic habitat are under density dependent constraint and the area of habitat is limiting, then these life history processes could control the stock-recruitment relationship (if the population is closed), carrying capacity and production of the population within specific habitat types. Many marine invertebrates release dispersive planktonic propagules as part of their reproductive life cycle. The postlarvae of many species have been shown to exhibit both positive and negative taxis towards various cues within the surrounding environment, including presence of algae and seagrass (Forward *et al.*, 1996; Morgan *et al.*, 1996; Welch *et al.*, 1998), habitat complexity (Moksnes *et al.*, 1998; Stevens & Kittaka, 1998) and the presence or absence of conspecifics (Crisp & Meadows, 1962; Jensen, 1991) or predators (Boudreau *et al.*, 1993; Welch *et al.*, 1998; Diaz *et al.*, 1999). Late in the larval phase, at the time approaching metamorphosis when discriminatory ability increases (Welch *et al.*, 1998), the selection of a suitable habitat plays an important role in subsequent survival. In more mobile species, settlement often occurs into nursery habitats (Cobb & Wahle, 1994; Pile *et al.*, 1996; Moksnes *et al.*, 1998), with a subsequent habitat shift at a later stage of development. Settlement into less favourable environments, due to factors such as wind forced hydrodynamic processes (Young *et al.*, 1998) or ocean currents (White *et al.*, 1988; McConnaughey *et al.*, 1992), which can strongly influence larval supply, or simply the absence of preferred habitat at metamorphosis (Roughgarden *et al.*, 1988), can lead to a drastic increase in both the rate (Connell & Jones, 1991) and magnitude (Moksnes *et al.*, 1998) of initial mortality. Diving excursions by postlarvae to test the suitability of the benthic substrate, and subsequent rejection and return to the water column, have been documented (Cobb *et al.*, 1983). Although such excursions, and the ability to delay metamorphosis, must significantly increase the possibility of encountering a suitable habitat, postponement is not indefinite and a final, sometimes sub-optimal substrate remains the only choice.

Some species have been shown to be less selective when settling to the benthos. Tupper and Boutilier (1997) observed no significant habitat preference between rocky reef, cobble, seagrass and sand substrates in settling cunner, *Tautogolabrus adsperus* (Walbaum). The green shore crab *Carcinus maenas* (L.) settles in a variety of habitats ranging from complex cobble to filamentous algae (Moksnes, 1999). At the other extreme, some smaller sessile species make habitat choices on extremely small scales (Keough & Downs, 1982), which significantly affect subsequent mortality. There is evidence that the level of distinction in habitat selection may be closely related to the reproductive biology of the individual species (Cobb *et al.*, 1997; Palma *et al.*, 1998). Larvae of species that are highly fecund and receive little parental care, such as *Cancer* spp., tend to be less selective at settlement relative to less fecund species such as clawed lobsters. Whatever the scale of niche selection, post-settlement mortality is often reduced in more complex habitats (Connell & Jones, 1991; Pile *et al.*, 1996; Tupper & Boutilier, 1997) which afford organisms more shelter. However, recent work by Steele (1999) suggests factors other than mortality, such as increased abundance of prey species in complex habitat, may also influence post-settlement abundance. Mortality and displacement (Iribarne *et al.*, 1994) of early life history stages are often under density dependent control. Gosselin & Qian (1997) list numerous studies where population abundance, distribution and community structure are controlled/influenced by juvenile mortality of marine invertebrates. There is evidence that growth rate can also be promoted in certain species when habitat complexity is increased (Connell & Jones, 1991; Perkins-

Visser *et al.*, 1996). Complex habitats are generally accepted as supporting both higher densities and diversities of species.

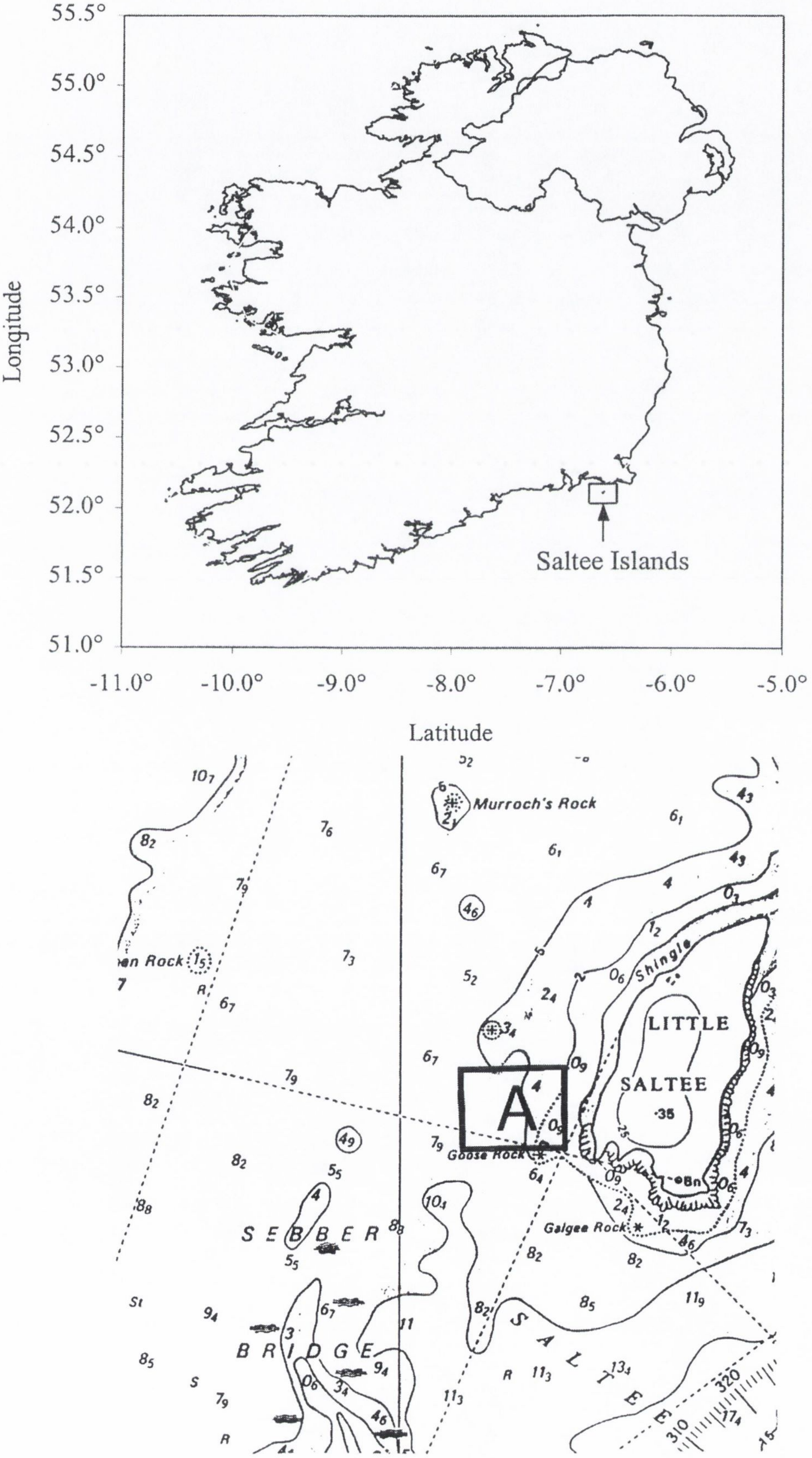
Recently there has been increasing interest in the effects that larval supply, larval choice, substrate selection, and density dependent mortality and displacement have on the postlarvae-settler-recruit relationships of decapods (Incze & Wahle, 1991; Incze *et al.*, 1997). Although these models may become valuable tools in the prediction of benthic recruitment, the relationship may be habitat specific, complicating interpretation of recruit relationship data. Recent work presented by Hughes *et al.* (1999) highlighted the need for consideration of spatial scales when examining variation in recruitment and adult distributions. Risk (1997) suggested that the ability of larvae to choose favourable places to settle, and to persist there, may cause patterns of recruitment to differ from those of the larval supply. Larval supply dynamics, larval choice in substrate selection, and post-settlement processes together determine the resultant adult community structure. In this chapter spatial variability in the community structure of settlers and adults in a number of discrete shallow sub-littoral habitats is compared. The results give an insight into the relative importance of larval supply, larval choice and post-settlement processes in determining the adult community structure.

MATERIALS AND METHODS

Study location

Samples were collected at five sites within a 0.5 nm^{-2} area in the Saltees Sound, County Wexford, Ireland (Figure 1.1). Sampling was conducted during daylight hours on the 22 September 1998. This date was identified from the previous

Figure 1.1. Location of study area in the Saltees Sound, Co. Wexford, Ireland, and approximate position of area (A) within which benthic samples were taken.



year as representing the approximate end of the settlement season for most species. The sediment structure and conditions at each site were known prior to sampling from information obtained during SCUBA and remote video surveys. Sites were selected to be representative of a number of habitats typical of the area encompassed within the bay. The area consists of bands of varying substrate orientated parallel to the shoreline, ranging from mud to solid bedrock. The area within the Saltees Sound contains patches of more solid substrate types.

Collection of samples and habitat characteristics

Divers using SCUBA equipment randomly positioned 0.5 x 0.5m quadrats. The area contained within each quadrat was sampled *in situ* using a diver operated suction sampler. The sampler consisted of a 2m length of 150mm diameter plastic pipe with an air feed fitting mounted 25mm from the base. Air supply to the sampler, estimated to be 200-300 l min^{-1}, was provided *via* a spare diving cylinder carried by the operator. *In situ* sampling permitted collection from sheltered lower surfaces and crevices of large rocks and boulders that support high densities of juvenile decapods. Sampling methodology employing grab samples or dredging fail to adequately sample such habitats. Four replicate samples were taken at each site. Although this represents a low number of samples, a large-scale temporal study in the previous year with greater replication (10-15 samples a day) had shown that community structure (but not abundance) was not significantly different between samples taken within a habitat on the same day (Chapter 2). All fauna was collected in rigid 1mm mesh bags. Substrate samples were taken by manually placing the contents of one quadrat from each site into lidded buckets. The same divers conducted surveys at each site, ensuring the same methodology was employed. The proportion of each area covered by solid bedrock was estimated, whether exposed on the surface or underlying loose rock cover. The proportion of the area covered by loose boulders larger than 150mm in diameter was estimated. Algal cover, mainly *Laminaria* spp. when present, was estimated at each of the sites. Finally, the percentage coverage of loose rock was estimated, defined as the area covered by stones larger than 50mm in diameter, which obscured the finer underlying material. The proportion of area covered by loose rock and cobble, and hence the interstitial space afforded as shelter (Wahle 1992), was considered a good indication of the physical complexity of the habitat sampled.

In the laboratory, samples were sieved, while submerged in seawater, through progressively smaller mesh sizes down to 1.0mm. Individual decapods were fixed in 5% formalin, containing 5% glycerol to maintain flexibility. Maximum carapace width of large crab (>3.0mm) were recorded to 0.1mm using digital callipers. Individuals smaller than 3.0mm were sized to the nearest 0.1mm, using a binocular microscope micrometer. Carapace length was recorded for Galatheidae, uropod length and eye width for Caridea and shield length for Paguridae. It was necessary to record different body dimensions so comparison could be made to samples taken in previous years that used this protocol. The total wet weight of individuals was recorded using a Sartorius three point balance. Sediment samples were sieved through progressively smaller meshes, to a size of <710μm. The substrate retained within each sieve was oven dried and weighed.

Data analysis

The number of young of the year (YOY) specimens within each sample was estimated by construction of length-frequency histograms. When the number of individuals sampled was sufficient gaps appeared in the distributions, distinguishing newly settled individuals from cohorts established in previous years. The number of individuals required to identify the YOY cohort varied with species but in general only one or two individuals were required. Growth data for YOY individuals of numerous species were collected during surveys throughout the previous settlement season of 1997 (Chapter 2). This time series of information was also used as a guide when identifying YOY individuals in the 1998 data. The component of the population referred to as adult in this study also includes immature individuals, and as such should be taken to refer to individuals settled in previous years.

The total number of species and individuals within each sample were used to calculate diversity (Shannon), evenness (Pielou), and dominance (Simpson) indices ($\log_e$) for the YOY and adult components of the community. Between-site differences in each of these parameters were examined using ANOVA. Although the number of samples taken from each site was small, variances were considered sufficiently homogenous (Cochran's test) to permit use of parametric statistics. Post hoc tests revealed sources of significant between-site differences. Analysis of abundance data was conducted on adult and YOY components separately after LN transformation. Due to the dominance of *Pisidia longicornis* (L.), between-site differences in abundance were also examined after removal of the species from the data matrix. Biomass was not treated in this way as the periodic occurrence of single large individuals, of species such as *Cancer pagurus* L., strongly affected the suitability of the analyses due to high within group variance.

Multidimensional Scaling Ordination (MDS) (Kruskal & Wish, 1978) was carried out on the adult and YOY components of the population separately using the computer package Primer © in order to examine between-site differences in community structure in more detail. Species that did not represent more than 4% of the total abundance in any one sample, were removed from the data matrix. Data was double-root transformed to reduce the influence of more dominant species. The significance of differences in between-site Euclidean dissimilarities were tested using the ANOSIM routine (Clarke & Warwick, 1994). Bray-Curtis similarities, which are more regularly associated with the analysis of biological data, were not used as joint absences of species were considered important in such variable sites where lack of larval supply was probably not a cause for absence. The program ANOSIM computes the average rank dissimilarity between within site samples and subtracts this from the average dissimilarity between samples from different sites (Warwick *et al.*, 1990). Significant variation between sites is identified when samples within sites are more similar than samples from other sites.

Within site differences between YOY and adult community composition were examined using ANOSIM after presence/absence transformation. This severe transformation removed the influence of the large differences between YOY and adult abundances, allowing a direct comparison of newly settled species and those already established in the area. The total proportion of individuals at each site representing the YOY component within the community was examined using ANOVA after arcsine transformation. Post hoc tests revealed sources of any significant between-site differences.

Environmental data in the form of diver estimates of overall sediment structure were compared to mean number of species and individuals by site, and to the derived diversity indices mentioned above, using Pearson's correlation.

RESULTS

Sediment composition & habitat characteristics

The proportion of the total weight of sediment samples represented by each size component were calculated and combined with diver estimates of site characteristics (Table 1.1). The substrate at site 1, that consisted of a stone and boulder surface layer overlaying a layer of finer sediment made up of sand and shell debris, was almost identical to site 4 in composition (Table 1.1). The only noticeable differences between the two sites were the proportion of algal cover, which was more extensive at site 4 (10% vs. 75%), and the additional depth at site 1 (12m vs. 8m). Site 2 consisted of a substrate similar to that of site 1 & 4, but with a higher coverage of overlaying stone and boulder (90-100%), a larger amount of underlying bedrock (60%), and a lower proportion of finer sediment (Table 1.1). There was an equally low proportion of fine sediment at site 5, which was entirely covered by solid bedrock. Only patches covered by loose stone and cobble, which covered approximately 25% of this solid ridge, were sampled. Areas consisting of only bedrock were not sampled as they offered little shelter, only the occasional large *Cancer pagurus* was encountered during inspection. The substrate at site 3 consisted almost entirely of fine sand (90%). A few small stones (5-49mm) were scattered around the site, but the availability of interstitial space of a size suitable to afford shelter to decapods was negligible.

Table 1.1. Sediment grain size composition expressed as proportion of sample dry weight (g) represented by each size component and diver estimates of substrate characteristics (marked *) from five distinct sub-tidal habitats. Substrate characteristics do not equal 100% as each is an independent estimation of coverage.

	Site 1	Site 2	Site 3	Site 4	Site 5
% Large Stone (50-149mm dia)	72.9	78.7	0.0	72.8	76.1
% Small Stone (5-49mm dia)	12.3	19.2	7.7	12.0	22.9
% Course sand (2-5mm dia)	1.5	0.4	2.1	1.2	0.4
% Fine sand (<2mm dia)	13.3	1.7	90.2	14.0	0.6
Total of above (%)	100	100	100	100	100
% Area covered by solid bedrock *	20	60	0	20	100
% Area covered by >150mm dia *	15	15	0	15	5
% Algal coverage *	10	75	0	75	35
% Area covered by loose rock *	75	95	0	75	25
Low water chart depth (m)	12	9	8	8	6

YOY individuals

A total of 4333 individuals from 17 decapod species were collected during the study. There was a large variation in the number of YOY individuals between sites (Table 1.2). The highest mean density of YOY individuals ($2220m^{-2}$) was at site 2, with lowest density ($36m^{-2}$) recorded at site 3 (Table 1.3). Low diversity in the YOY component of the population at sites 1,2 and 4 coincided with high dominance and low evenness. The mean density, number of species, and each of the diversity indices calculated for YOY individuals varied significantly ($p<0.05$) between sites (Table 1.3). The sources of between-site differences were identified using Scheffe Post Hoc Test (Table 1.4). The mean proportion of the population represented by YOY individuals was significantly ($p<0.05$) higher in sites 1 & 3 than in site 5 (Table 1.4). Although the mean proportion of settlers was also higher at sites 1 & 3 than 2 & 4, the difference was not statistically significant at the 5% level. Analyse of the abundance of YOY individuals showed significant between-site differences ($p<0.01$), before and after removal *Pisidia longicornis* (Table 1.3). Post hoc tests of YOY abundance (Table 1.4), including *Pisidia*, revealed differences between all sites except 1 & 4. When *Pisidia* was removed, site 3 differed from sites 4 & 2 at the 5% level, and from sites 1 & 5 at the 10% level. No other between-site differences in YOY abundance were observed.

Previously settled individuals

The greatest mean number of adult species (8) were encountered at sites 2 and 4, while the highest overall mean density of adult individuals ($292m^{-2}$) was at site 2. The lowest overall mean number of adult species (2) and individuals ($8m^{-2}$) occurred at site 3 (Table 1.3). Adult diversity, evenness and dominance were not calculated for

Table 1.2. Abundance of species sampled from five distinct sub-tidal habitats (1-5), four replicates taken from each site (A-D). Lower case y indicates young of the year component, individuals settled in previous years by a.

	1Ay	1Aa	1By	1Ba	1Cy	1Ca	1Dy	1Da	2Ay	2Aa	2By	2Ba	2Cy	2Ca	2Dy	2Da	3Ay	3Aa	3By	3Ba	3Cy	3Ca	3Dy	3Da	4Ay	4Aa	4By	4Ba	4Cy	4Ca	4Dy	4Da	5Ay	5Aa	5By	5Ba	5Cy	5Ca	5Dy	5Da
Anapagurus hyndmanni	3	0	3	0	0	0	2	0	0	2	3	1	1	1	13	1	0	1	0	0	0	0	0	0	4	2	4	0	0	0	3	0	2	0	0	0	0	1	0	0
Athanas nitescens	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	1	0	0	0	0	0	0	0	0	0	0
Cancer pagurus	0	0	1	0	1	0	2	0	3	0	5	1	3	2	1	0	0	0	0	0	0	0	0	0	1	1	5	0	0	3	1	1	0	2	1	0	4	3	0	0
Galathea intermedia	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Galathea squamifera	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	1	2	2	0	0	0	0	0	0	0	0	0
Hippolyte varians	0	0	0	0	1	2	0	0	2	2	3	2	0	0	0	1	0	0	0	0	0	0	0	0	1	5	2	4	1	4	3	4	0	1	1	6	0	0	0	2
Inachus phalangium	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	2	0	0	0	0	0
Necora puber	1	0	0	0	1	0	4	0	1	2	0	4	0	0	4	3	2	0	1	1	0	0	1	0	4	5	0	1	2	0	1	1	0	0	0	1	1	0	4	0
Pagurus bernhardus	0	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	0	1	0	0	0	1	0	1	0	0	0	0	0	0
Pilumnus hirtellus	0	0	0	0	0	0	0	0	1	2	1	1	2	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	2	0	0	0	0	0	1	1	0	0	3	1
Pirimela denticulata	2	1	1	0	0	0	1	0	1	0	0	0	0	0	2	3	0	0	1	1	1	0	0	0	1	1	0	1	0	0	0	0	1	2	0	0	2	1	0	0
Pisidia longicornis	112	0	127	6	103	8	163	6	533	75	490	48	479	67	644	37	9	0	11	0	3	0	3	0	138	13	226	26	95	13	238	39	24	2	42	9	37	4	47	9
Pontophilus fasciatus	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	2	0	0	0	1	0	1	0	1	0	1	0	1	0	0	0	2	0	0	0	0	0	0	0	0
Porcellana platycheales	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0
Processa canaliculata	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Thoralus cranchii	1	2	2	2	0	2	1	2	3	5	8	10	4	5	0	0	0	0	4	1	0	0	0	0	4	13	2	7	7	12	1	5	1	5	4	16	3	11	6	10
Xantho pilipes	0	1	3	0	1	0	0	0	0	2	1	3	3	3	5	2	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0

Table 1.3. Mean (± SD) values for community statistics for each site and results of ANOVA. Proportion YOY arcsine transformed prior to ANOVA. Abundances LN transformed. Values missing from adult indices involving site 3 due to occurrence of a single individual in two samples.

Source	Site 1	Site 2	Site 3	Site 4	Site 5	d.f.	Prob.%
% Proportion YOY	94 (3)	88 (4)	93 (9)	81 (4)	69 (5)	19	<0.001
Adult Species	3 (2)	8 (1)	2 (1)	8 (2)	5 (1)	19	<0.001
YOY Species	6 (1)	7 (2)	3 (1)	8 (1)	5 (1)	19	<0.001
Adult individuals $0.25m^{-2}$	9 (4)	73 (17)	2 (1)	44 (8)	22 (8)	19	<0.001
YOY individuals $0.25m^{-2}$	134 (29)	555 (79)	9 (6)	189 (67)	47 (13)	19	<0.001
Ad. Shannon div. (H')	0.93 (0.42)	0.93 (0.23)		1.44 (0.33)	1.30 (0.24)	19	0.09
YOY Shannon div. (H')	0.30 (0.07)	0.20 (0.05)	0.64 (0.22)	0.45 (0.18)	0.71 (0.10)	19	<0.001
Ad. Pielou even. (J)	0.84 (0.08)	0.45 (0.10)		0.69 (0.15)	0.81 (0.07)	19	<0.001
YOY Pielou even. (J)	0.17 (0.03)	0.10 (0.02)	0.75 (0.07)	0.22 (0.08)	0.46 (0.07)	19	<0.001
Ad. Simpson dom. (D)	0.48 (0.18)	0.61 (0.11)		0.36 (0.15)	0.33 (0.07)	19	0.04
YOY Simpson dom. (D)	0.89 (0.03)	0.94 (0.02)	0.61 (0.09)	0.83 (0.08)	0.67 (0.05)	19	<0.001

Table 1.4. Scheffe Post Hoc Test result for between-site differences in community statistics. Proportion YOY arcsine transformed. Total, YOY and adult individuals LN transformed. * indicates significant between-site differences at 5% level. Values missing from adult indices involving site 3 due to occurrence of a single individual in two samples.

	Pisidia removed												
	Prop. YOY	YOY. Sp.	Ad. Sp.	YOY. Ind.	Ad. Ind.	YOY. Ind.	Ad. Ind.	YOY. Div.	Ad. Div.	YOY. Even.	Ad. Even.	YOY. Dom.	Ad. Dom.
Sites	Prob.%	Prob.%	Prob.%	Prob.%	Prob.%	Prob.%	Prob.%	Prob.%	Prob.%	Prob.%	Prob.%	Prob.%	Prob.%
1 & 2	0.76	0.28	<0.01*	<0.01*	<0.01*	0.74	<0.01*	0.90	>0.99	0.56	<0.01*	0.89	0.59
1 & 3	0.99	0.02*	0.80	<0.01*	<0.01*	0.08	0.45	0.05		<0.01*		<0.01*	
1 & 4	0.19	0.10	<0.01*	0.90	<0.01*	0.88	<0.01*	0.68	0.21	0.90	0.27	0.76	0.65
1 & 5	0.01*	0.90	0.54	0.04*	0.07	>0.99	<0.01*	0.02*	0.46	<0.01*	0.97	<0.01*	0.51
2 & 3	0.51	<0.01*	<0.01*	<0.01*	<0.01*	<0.01*	<0.01*	<0.01*		<0.01*		<0.01*	
2 & 4	0.80	0.98	0.99	0.03*	0.57	>0.99	0.95	0.22	0.21	0.16	0.05	0.27	0.11
2 & 5	0.13	0.06	0.15	<0.01*	0.01*	0.79	>0.99	<0.01*	0.46	<0.01*	<0.01*	<0.01*	0.08
3 & 4	0.09	<0.01*	<0.01*	<0.01*	<0.01*	0.01*	<0.01*	0.47		<0.01*		<0.01*	
3 & 5	<0.01*	0.10	0.10	<0.01*	<0.01*	0.07	<0.01*	0.98		<0.01*		0.70	
4 & 5	0.61	0.02*	0.06	<0.01*	0.20	0.92	0.93	0.20	0.94	<0.01*	0.49	0.04*	>0.99

site 3 as two of the samples contained only one individual. This strongly influenced the values derived using these methods, resulting in a significant reduction in the homogeneity of variances. Although site 3 was excluded from subsequent ANOVA of adult indices, raw data (Table 1.2) would suggest that the adult community at this site differed from all other sites. The four remaining sites displayed between-site variation in evenness and dominance, but not in diversity (Table 1.3). Analyses of the abundance of adult individuals also showed significant between-site differences ($p<0.01$), before and after removal *Pisidia longicornis* (Table 1.3). Tests on adult (including *Pisidia*) abundance data revealed similarities between site 4 and sites 5 & 2, and between sites 5 & 1. Removal of *Pisidia* led to a similar result but with the addition of no differences between sites 1 & 3 and sites 2 & 5, and variation between sites 1 & 5 (Table 1.4).

Community Structure

Between-site differences in adult community structure were not immediately evident after MDS ordination (Figure 1.2). There was some degree of mixing of samples from different sites, with a trend of increasing abundance from left to right in the ordination. Subsequent ANOSIM analysis revealed underlying significant ($p<0.05$) between-site differences (Table 1.5). Differences in community structure were identified at the 6% level between all sites with the exception of sites 1 and 3, sites 1 & 5, and between sites 4 & 5. Identical analysis of YOY community structure revealed differences between all sites with the exception of sites 2 & 4 at the 6% level (Table 1.5). Clustering of site samples was slightly clearer than that of the adult ordination, especially within site 3 (Figure 1.3). Again, overall abundance of YOY individuals appeared to increase from left to right on the ordination plot. Analysis of

Figure 1.3. Multidimensional scaling ordination of young of the year decapod community abundance recorded in five distinct sub-tidal habitats. Grouping by dotted lines indicates replicate samples from each habitat.

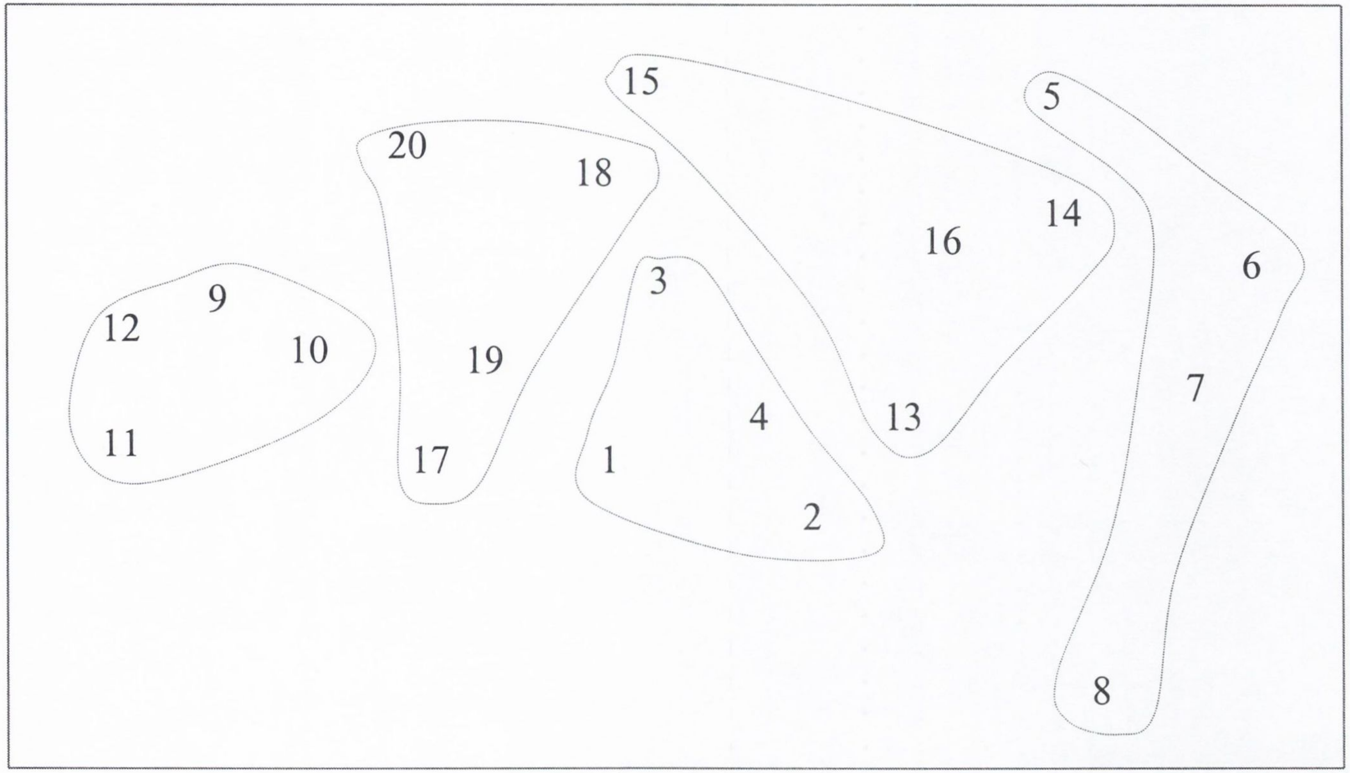


Figure 1.2. Multidimensional scaling ordination of adult decapod community abundance recorded in five distinct sub-tidal habitats. Grouping by dotted lines indicates replicate samples from each habitat.

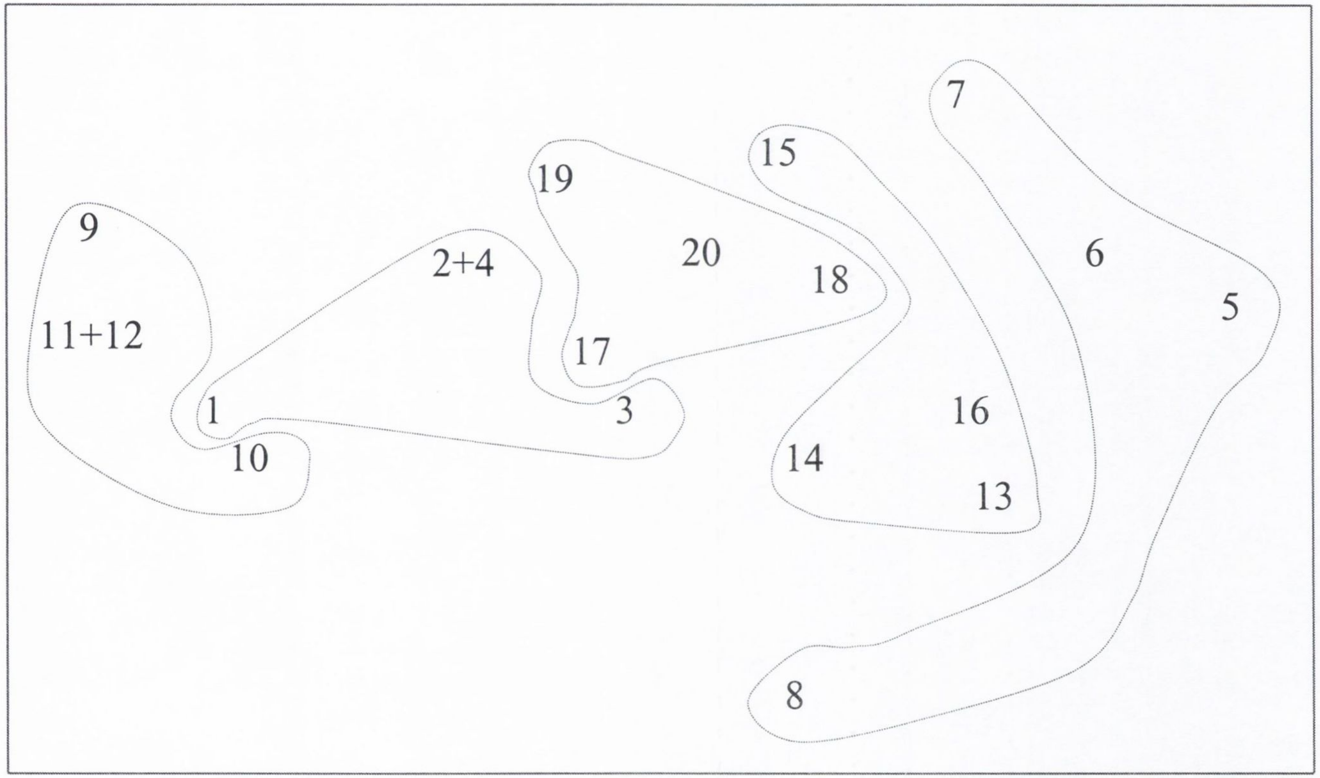


Table 1.5. Results of ANOSIM for between-site similarities in adult and young of the year (YOY) community components. * indicates significant between-site difference at 5% level.

	Adult Component		YOY Component	
Sites	Stat. (R)	Sign. %	Stat. (R)	Sign. %
1 & 2	0.72	2.9*	0.47	5.7
1 & 3	0.46	8.6	0.9	2.9*
1 & 4	0.56	5.7	0.52	5.7
1 & 5	0.06	28.6	0.35	5.7
2 & 3	1.00	2.9*	1.00	2.9*
2 & 4	0.42	5.7	0.25	11.4
2 & 5	0.56	2.9*	0.89	2.9*
3 & 4	0.99	2.9*	0.98	2.9*
3 & 5	0.98	2.9*	0.50	5.7
4 & 5	0.27	20.0	0.67	2.9*
Global R	0.62	<0.01	0.64	<0.01

presence/absence identified significant differences ($p<0.05$) between the species found within the YOY and adult components of the community at sites 1 & 3. The community composition of YOY and adult individuals was not significantly different at the other three sites.

Correlation analysis

A number of the estimated site characteristics correlated well to the community statistics (Table 1.6). The strongest correlation, $r = 0.991$, occurred between the extent of algal coverage and number of adult species. Density of adult individuals also correlated positively (0.926) to algal coverage. Although the density and number of species in the adult and YOY components displayed a positive relationship with rock coverage, the correlation was not quite significant at the 5% level. Diversity and evenness of YOY individuals showed significant negative correlation (-0.928 and –0.960 respectively) with rock coverage (Table 1.6). Dominance showed a significant correlation, 0.984, to rock coverage. Adult diversity, evenness and dominance were not correlated to site characteristics due to the difficulty in deriving indices for site 3.

The overall abundance of some individual species showed correlation with site characteristics. Both *Cancer pagurus* and *Necora puber* (L.) displayed significant (5% level) correlation (0.929 and 0.950 respectively) with algal cover. The hermit crab *Anapagurus hyndmanni* Thompson showed a strong correlation with rock coverage. *Inachus phalangium* (Fabricius) abundance was positively correlated with bedrock coverage.

Table 1.6. Pearson's Correlation (r_p) between community statistics and estimated substrate characteristics arcsine transformed. Critical value r_p for 3 d.f. =0.878. Diversity, evenness and dominance for YOY only.

	Ad. Spec.	YOY Spec.	Ad. Ind.	YOY Ind.	Shan. Div.	Piel. even.	Simp. Dom.
% Area covered by solid bedrock	0.228	-0.002	0.186	0.011	0.351	-0.035	-0.165
% Area covered by >150mm dia	0.189	0.083	0.056	-0.149	0.390	-0.083	-0.154
% Algal coverage	0.991	0.794	0.926	0.713	-0.377	-0.579	0.505
% Area covered by loose rock	0.706	0.859	0.785	0.869	-0.928	-0.960	0.984
Low water chart depth (m)	-0.230	0.214	-0.099	0.229	-0.736	-0.497	0.639

DISCUSSION

There were clear differences in the structural complexity of most of the sites sampled. The increase in number of species and individuals in habitats with higher rock coverage, although not quite significantly correlated at the 5% level, concurred with the findings of other studies (Connell & Jones, 1991; Pile *et al.*, 1996; Tupper & Boutilier, 1997; Steele, 1999). However, high densities of one particular species *Pisidia longicornis*, lead to the very low YOY evenness observed at more complex sites. Porcelain crab megalopae are gregarious and settle preferentially in areas inhabited by adults of the species (Jensen, 1991). The occurrence of this species in marginal areas containing no adults would suggest that megalopae are sometimes forced to choose sub-optimal habitats however. The increasing dominance of this species with higher physical complexity resulted in significant negative correlation between rock coverage and both YOY diversity and evenness. This illustrates how high densities of a single species can confuse interpretation if a single univariate measure of diversity is used to describe community diversity.

A clear distinction must be drawn between sites 3 & 5. Site 3 offered little shelter to any non-burrowing settler over its entire area, and as a result supported very few adult individuals. Of the three adult species encountered, two burrow readily into coarse sand, *Xantho pilipes* Milne Edwards and *Pirimela denticulata* (Montagu), while the third *Necora puber* is extremely mobile and ranges over most of the area within the Saltees Sound. No adults of the species *Pisidia longicornis* were collected. However, site 5 did afford a certain degree of shelter, in the scattered patches of loose rock overlaying the solid bedrock. Settlement into these patches may have been reduced due to slightly increased tidal currents sweeping over the ridge, but this is speculation as no current velocity data is available for the area. The loose rock patches did however support numerous adult species, so it seems likely that immigration occurred some time after settlement. Although the exposed bedrock surfaces were not sampled, and a light settlement into the close turf layer could be envisaged, substantial settlement or subsequent survival of decapod species is unlikely on these patches. Even small variations in physical complexity and site characteristics were observed to lead to significant differences in univariate community statistics. Although algal cover was the only apparent parameter separating sites 1 & 4, significant variation in the number of adult species and individuals were observed. The extent of the algal canopy strongly influenced the density of adult individuals between sites. Further increase in variation in habitat characteristics between sites 1 and 2 lead to even further variation in community statistics.

The higher abundance of certain species, especially *Pisidia longicornis*, with increasing habitat complexity contributed to the between-site differences in YOY and adult community structure observed. It is likely that the differences in community structure and the variation in numbers of adult individuals were caused by larval choice and post-settlement mortality and movement, rather than restrictions or spatial and temporal variations in larval supply. As all sample sites were contained within an area of several hundred square meters, it seems reasonable to assume that larval supply was fairly uniform over the entire season. Although small-scale current patterns may have effected settlement, it was assumed that these did not affect settlement strongly between sites. Therefore, the observed differences in YOY community structure between all sites, with the exception of 2 and 4, would indicate the importance of larval choice and early post-settlement processes in shaping the composition of the YOY community. Post-settlement processes that shape the community, such as predation and migration, appear to have different relative effects within each of the substrates sampled. The processes acting at sites 1 & 3 shaped the community composition such that YOY and adult assemblages were significantly different within-site. Recruitment failure of *Pisidia* and larval avoidance by other species at site 3 is probably directly related to the lack of shelter afforded to small decapod species that are vulnerable to predation. Small settlers that occupy any of the limited shelter available are likely to quickly outgrow their environment. Migration to a more suitable area that affords shelter becomes necessary when the nursery habitat is unsuitable for the adult organism. Such ontogenetic shifts are commonplace in mobile crustacean species (Cobb & Wahle, 1994; Pile *et al.*, 1996; Moksnes *et al.*, 1998) but are unlikely in a small, shelter dependent species such as *Pisidia*. Larger, more mobile species such as *Cancer pagurus* or *Necora puber* may be more capable of short migrations from less favourable sites. The influence of post-settlement processes in shaping the community were reflected in between-site differences in adult assemblages. Significant differences in adult community structure were detected across sites 2 and 4, which supported similar YOY assemblages. Conversely, similarities in adult structure were observed between sites where YOY structure varied significantly. Of the three pairs of sites displaying similarities, two involved sites 1 & 3, locations where YOY and adult assemblages varied within-site. It is likely that YOY species composition is altered to some degree at all sites before their second year, with more dramatic changes occurring at sub-optimal sites where processes have an increased influence on the community.

The high degree of between-site differences in YOY abundance of *Pisidia longicornis* initially suggested that the larvae of this species displays greater discrimination at settlement, preferring more physically complex habitats. This may be linked to the increased abundance of adult individuals, to which settling megalopae are attracted, in physically complex habitats (Jensen, 1991). However, the occurrence of the species in marginal areas, where they are unlikely to survive, would contradict this theory and suggest that *Pisidia* shows a low degree of substrate specificity at settlement. The presence of *Pisidia* settlers in site 3 together with the lack of adult individuals indicates a potential problem in predicting settler-recruit-adult relationships due to the failure of settlers to recruit to the mature population. These individuals are unlikely to survive to maturity, and as such habitats with substrate similar to site 3 will yield no future production of *Pisidia*. The most realistic theory for the presence of settlers in marginal areas would be that settlement by *Pisidia* is not totally mediated by the complexity of the benthic substrate or the presence of adults. However, subsequent mortality is directly related to the physical complexity of the substrate settled into. This would agree with the finding of Tupper & Boutilier (1997) for reef fish. Larvae may be transported to more marginal areas by unfavourable currents at a time when metamorphosis cannot be delayed further (Jensen, 1991). Heavy settlement pulses, timed to coincide with minimal tidal amplitudes, have been documented in other studies (Morgan *et al.* 1996) and have been observed in the current study area for *Pisidia* (Robinson & Tully in press a). It seems reasonable that many larvae would become competent to settle in the intervening period since the previous low spring tide, and must settle at the next opportunity within the few days when currents are reduced. Site 1 would also appear to represent a substrate where recruitment is reduced. Although this site was as physically complex as site 4, the proportion of adults in the population was unusually low (not statistically different from site 4 at 5% level). This may be due to the lack of algal cover or the additional depth of this site, as these were the only differences from site 4 observed, or other factors not considered in this study such as emigration.

The substrate specificity of settlers may vary from species to species, probably due to factors associated with reproductive strategy. Species that mature early and have high fecundity have been shown to display reduced settlement substrate specificity when compared to less fecund, later maturing species (Palma *et al.*, 1998). Of the species encountered in the current study area *Pisidia* is the most likely to be considered in the former group. Although adult individuals are small and not unusually highly fecund, their sheer numbers and maturation within their first year result in larval production fifteen times higher than any other species within the study site (Merin, 1998). Other species within the area may also display a similar lack of substrate specificity at settlement, but may not have been sampled or occur in sufficient numbers to persist long enough in marginal areas to be detected. It is however, more likely that many less productive or more habitat limited species show a greater degree of substrate specificity (Cobb *et al.*, 1997; Palma *et al.*, 1998), as with the avoidance of site 3 observed here. Further investigation into the reproductive strategy and substrate specificity of key species is warranted.

Although no larval abundance data is available for the study period, intra-annual spatial and temporal variation or restriction in larval supply would be unlikely to influence resultant community structure, especially when considering the small area from which all samples were taken. It would seem likely that the YOY decapod community structures within the habitats studied are strongly mediated by larval choice and early post-settlement processes, although it was not possible to separate their relative influences in this study. The substrate specificity displayed by settling species is variable, and may be linked to reproductive strategy of the species (Cobb *et al.*, 1997; Palma *et al.*, 1998). Larval choice and/or between-site variability in post-settlement processes, which may be determined by the nature of the substrate, lead to differences in community structure. The results presented here highlight the need for a detailed knowledge of larval supply processes and dynamics, and post-settlement processes acting on the post-larval population until recruitment and subsequent benthic production has occurred. Understanding of early life history processes is important in defining the shape and scaling of the production-settlement-recruitment model for use in stock prediction. Advances have been made in the development of such recruitment indices and forecasting methods for Australian rock lobster (Phillips & Brown, 1989), *Panulirus cygnus* George, and for the American lobster (Incze & Wahle, 1991; Wahle, pers. coms.), *Homarus americanus* Milne Edwards. There is excellent potential in the application of suction sampling methods with others, such as settlement tray deployment, to gather detailed and informative data pertaining to the spatial distribution and timing of settlement, and the processes affecting subsequent survival and growth of juvenile decapod species (Robinson & Tully, 1998b). However, the detection of significant between-site variation in YOY and adult community structure in this study suggests a need for caution with these pelagic-benthic models. The settler-recruit relationship is obviously affected by habitat complexity and other properties, so the area of each distinct habitat type available and spatial patchiness in larval supply regulate subsequent production and recruitment. Further studies should follow the recommendations of Hughes *et al.* (1999) in incorporating various spatial scales into the experimental design so that the data obtained accounts for spatial variability in recruitment, such as that revealed in the present study. Variation in physical complexity and other habitat characteristics lead to significant differences in YOY community structure across sites. Spatial variability in the magnitude of post-settlement processes acting on YOY communities, including mortality and dispersal, can alter community structure before the end of the second year. This may result in a smoothing of between-site inequalities in community structure, reducing spatial variability between more similar sites over time and allowing generalised categories of recruitment habitats to be defined.

CHAPTER 2

SEASONAL VARIATION IN DECAPOD COMMUNITY STRUCTURE, SETTLEMENT AND RECRUITMENT WITHIN A ROCKY SUB-TIDAL BENTHIC HABITAT

ABSTRACT

Sub-tidal rocky habitats provide shelter to a dense, species rich decapod community throughout the Northeast Atlantic. Monthly or more frequent quantitative suction samples of benthic decapod fauna were taken during 1997. Some species settled into the area, but failed to persist to the first winter, while others were present in high numbers throughout the year. The duration of settlement was species specific, ranging from several weeks to several months. Body size at settlement was related to the temperature during larval development. Growth potential and early mortality of a number of decapod species was recorded. Seasonal lows in abundance and biomass of young of the year and previously established decapod individuals were identified, and may represent the most suitable time to conduct juvenile release for stock enhancement purposes. In general, community structure differed between the settlement season and over-wintering periods. Young of the year community structure differed from that of previously established individuals. The data collected represents a baseline study of a widely distributed community that may support further work on species interactions, improving the accuracy of prediction of annual settlement and recruitment fluctuations.

INTRODUCTION

Sub-tidal rocky habitats often support dense, species rich marine communities. Decapod crustaceans can represent a major component of the overall species abundance and biomass within such communities. Some species settle into, and remain within, shallow water physically complex substrates, while others undergo a subsequent ontogenetic shift at a later stage of development (Cobb & Wahle, 1994;

Perkins-Visser, 1996; Pile *et al.*, 1996; Moksnes *et al.*, 1998). The importance of nursery habitats in the survival and development of decapod species has been well documented (Wahle & Steneck, 1992; Eggleston & Armstrong, 1995; Pile *et al.*, 1996). When the species is of commercial value the success of the fishery may well depend on recruitment from such areas.

Physical (Eckman, 1983; Hobbs *et al.*, 1992; Eggleston & Armstrong, 1995; Wahle & Incze, 1997) and biotic (Olmi & Lipcius, 1991; Eggleston & Armstrong, 1995) processes affect pre- and post-settlement processes, and influence subsequent recruitment (Phillips, 1990; Pile *et al.*, 1996). Cohort strength and subsequent population size in these species may therefore be determined early in the life history (Pile *et al.*, 1996; Robinson & Tully, 1998b). Studies directed at these critical life history phases can therefore greatly increase the understanding of population rate processes, such as settlement, post-settlement growth and mortality, and density dependent control on these processes. Mortality and displacement of early life history stages are often under density dependent control. Gosselin & Qian (1997) list numerous studies of marine invertebrates where population abundance, distribution and community structure are controlled/influenced by juvenile mortality. Density dependent mortality and displacement quickly shape the resultant community structure of the species within the habitat.

Initial mortality rates (Connell & Jones, 1991) of early benthic stages are generally accepted as being very high (Moksnes *et al.*, 1998). Both physical (Roughgarden *et al.*, 1988; White *et al.*, 1988; McConnaughey *et al.*, 1992; Young *et al.*, 1998) and biological (Phillips, 1990; Olmi & Lipcius, 1991; Eggleston &

Armstrong, 1995; Pile *et al.*, 1996) factors contribute to variation in inter-annual and within season recruitment variability. At temperate latitudes the conditions encountered by developing larvae can be markedly different over time. Inequalities in the magnitude of settlement and subsequent survival of settlers over prolonged periods during the settlement season can lead to short term variability in the abundance of the young of the year (YOY) cohort (Robinson & Tully, in press a). The causes and magnitude (Beukema, 1984; Aiken & Waddy, 1986; Ennis, 1986; Fogarty *et al.*, 1991; Lewis, 1991) of inter-annual variation in settlement and recruitment success has received increasing attention recently with the development of stock prediction models for fisheries management. Attempts have been made to relate levels of larval supply, settlement and subsequent recruitment to the standing stock of the fishable adult population after a suitable lag phase is applied. Advances have been made in the development of such recruitment indices and forecasting methods for Australian rock lobster, *Panulirus cygnus* George (Phillips & Brown, 1989), and for the American lobster, *Homarus americanus* Milne Edwards (Incze & Wahle, 1991; Wahle, pers. coms.). Examination of seasonal settlement and recruitment can identify the most suitable time to conduct censuses of recruitment for annual predictions. Identifying the most influential species, or biological or physical factor, interacting with the target species, and accounting for variability in their recruitment success will enhance the accuracy of annual predictions. For example, recruitment of the exploited species within a year may be average, while recruitment of a predator species may be exceptionally high. Censuses of the fished cohort in the following year may then reveal unexpectedly high mortality.

There is a need for a detailed knowledge of larval supply processes and dynamics, and post-settlement processes acting on decapod post-larval population until recruitment and subsequent benthic production has occurred in order to understand the adult recruitment relationship in closed populations and density dependent constraints in early life history. Similar decapod assemblages, dominated by *Pisidia longicornis* (L.), are resident in sub-tidal cobble habitats to depths of 50+m throughout much of the north eastern Atlantic (Smaldon, 1972; González-Sanjurjo, 1982). This study is the first to report on the community dynamics, settlement and early post-settlement growth and mortality in this decapod assemblage. Seasonal variation in YOY community statistics and community structure are examined and related to the established decapod community.

MATERIALS AND METHODS

Study location

Samples were collected from an area with uniform habitat characteristics within the Saltees Sound, County Wexford, Ireland. Sampling was conducted on a monthly basis between December 1996 and November 1997, with more concentrated effort during the settlement season. The exact frequency and timing of each sampling effort, at this relatively exposed site, was often determined by conditions at sea. The substrate in the area consisted of gravel and shell material, overlain by boulders and rocks of various sizes. The finer sediment and interstitial spacing between cobble afforded shelter to high densities of numerous decapod species. Due to the perennial nature of the *Laminaria* species present, algal cover varied through the year, but was typically between 50-70% during the settlement season. Sampling was conducted at a depth of 8-10 meters. Temperature was monitored at 2hr intervals by a Seamon® temperature recorder deployed near the seabed.

Collection of samples

Divers using SCUBA apparatus randomly positioned 0.5 x 0.5m quadrats on the seabed. The area contained within each quadrat was sampled *in situ* using a diver operated suction sampler. Air supply to the sampler was provided *via* a spare diving cylinder carried by the operator. *In situ* sampling permitted collection from sheltered lower surfaces and crevices of large rocks and boulders that support high densities of juvenile decapods. All fauna was collected in rigid 1mm mesh bags.

In the laboratory, samples were sieved, while submerged in seawater, through progressively smaller mesh sizes down to 1.0mm. Individual decapods were fixed in 5% formalin, containing 5% glycerol to maintain flexibility. Maximum carapace width of large crab (>3.0mm) were recorded to 0.1mm using digital callipers. Individuals smaller than 3.0mm were sized to the nearest 0.1mm, using a binocular microscope micrometer. Carapace length was recorded for Galathidea, uropod length and eye width for Caridea and shield length for Paguridea. The total wet weight of individuals was recorded using a Sartorius three point balance.

Data analysis

The number of YOY specimens within each sample was estimated by construction of length-frequency histograms. The YOY cohort was easily distinguishable in these distributions if adequate numbers were sampled.

The total number of species and individuals within each sample were used to calculate diversity (Shannon), evenness (Pielou), and dominance (Simpson) indices ($\log_e$). Between-sampling date differences in each of these parameters and total decapod biomass were examined using ANOVA. Post hoc tests revealed locations of significant seasonal variation. Analysis of abundance data was conducted separately for adult and YOY components after LN transformation. High numbers of YOY individuals masked the abundance of adult individuals. Multidimensional Scaling Ordination (MDS) (Kruskal & Wish, 1978) was carried out using the computer package Primer ©, in order to examine seasonal variation in community structure in more detail. Only species that represented at least 4% of the overall species abundance in any sampling date were included in analyses. Data was double-root transformed to reduce the influence of more dominant species. The significance of differences in between-date Bray-Curtis similarities were tested using the ANOSIM routine (Clarke & Warwick, 1994). The program ANOSIM computes the average rank Bray-Curtis similarity between within-date samples and subtracts this from the average similarity between samples from different dates (Warwick *et al.*, 1990). Significant seasonal variation is identified when samples within a sampling date are more similar than samples from other periods.

Within sampling date differences between the YOY and adult community structures were examined using ANOSIM after presence/absence transformation. The severe nature of the transformation removed the influence of the large differences between YOY and adult abundances, allowing a direct comparison of the two components of the population. The component of the population referred to as adult also consisted of juvenile individuals, and as such should be taken to represent individuals settled in previous years.

Mean body size of settlers was related to the average daily temperature for 30 days prior to settlement. Thirty days was chosen as an arbitrary value for larval development of decapod species due to the poor availability of data for most species. Valdes & Alverez Osorio (1983) recorded a development time of 26 days at 15°C for *Pisidia longicornis* under laboratory conditions.

Seasonal growth estimates were derived for a number of species where the YOY component was clearly identified. Growth potential was estimated by comparing minimum size at settlement and the maximum size of individuals obtained at the end of the growing. Although the mean size at the start and end of the settlement season would be a more accurate assessment of growth potential it was not always possible to separate successive instars from composite length-frequency distributions (LFD). The growth range described was considered a reasonable approximation to the growth potential of individual species.

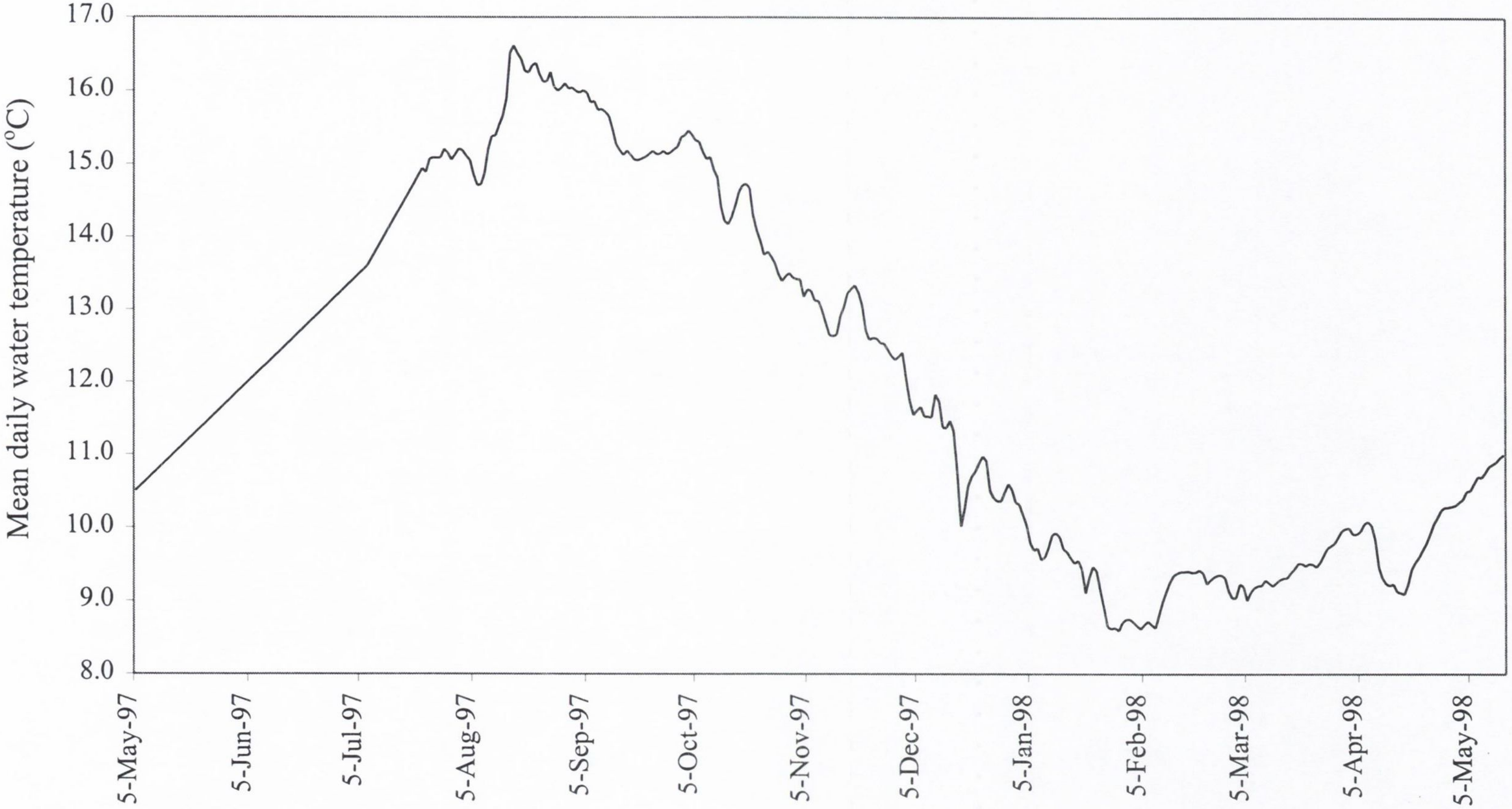
Reduction in the total number of individuals sampled over the entire year between crab stages II and IV were taken to represent early seasonal mortality. Total abundance of YOY crab were used as numbers sampled in individual sampling dates were often too small to permit modal progression analysis. Separation of normal distributions and calculation of instar density was conducted using MIX 2.3 (MacDonald & Green, 1988). Castro (1995) found MIX to be a robust and efficient method for separation of mixtures of normal distributions after a comparison of numerous length-frequency techniques. The program separates normal distributions from composite length frequency distributions by maximum likelihood estimation. Numbers of individuals within 1st crab stage were omitted as it was not possible to predict the exact timing of the end of the settlement season. Further additions to this group could have occurred after sampling, especially for species that displayed pulsed settlement. Numbers of this 1st crab stage in the LFD often appeared far lower than would be expected when accounting for reduction of individuals between instars. This may indicate that settlement was often incomplete at sampling or significant initial mortality had already occurred (Gosselin & Qian, 1997). Although a similar situation could be envisaged for later stages, as all individuals within settlement groups are unlikely to moult to the next stage in synchrony, estimates were thought to be less susceptible to bias than at the first crab stage. Instars after the first crab stage are dependent on the variability in the mortality of previously settled crab, rather than more large scale variations that can be associated with larval supply.

RESULTS

Temperature & tides

Average daily temperature at the site was calculated from the 12 daily recordings, for the period July 1997 to May 1998 (Figure 2.1). Although this does not coincide exactly with the duration of the study, it approximates to the usual annual temperature regime of the area. Two sets of remote recording were taken using a WTW temperature meter, on 23/01/97 (8.0°C) and 08/07/97 (13.6°C), prior to the deployment of the probe. The highest mean daily temperature of 16.6°C was recorded in mid August. July and September yielded comparable values of 15.0°C. Temperature dropped significantly at the onset of October, reaching a minimum

Figure 2.1. Mean daily seawater temperature calculated from 2 hourly recordings, from July 1997, Saltees Sound, Co. Wexford. Values from May-July 1997 estimated from single recordings taken in Jan and early July.



(8.5°C) in early February. Increasing temperatures were recorded from mid April onward. The remote WTW probe recording in early July was used when estimating missing temperature values between May and late July.

Tidal amplitude was estimated using the height of the morning high tide, from mid May to early December 1997 (Figure 2.2), as predicted by local Harbour Office tide tables (Kilmore Quay Harbour Office, 1997). The timing of consecutive sampling dates are indicated on the oscillating line by addition of asterisk (Figure 2.2).

Abundance

During the study 29 decapod species were recorded (Table 2.1). A number of species, that are indicated with an asterisk in Table 2.1, have not previously been described in this area (Healy & McGrath, 1988; Ingle, 1993; Smaldon, 1993; Ingle, 1996; Kelly *et al.*, 1996). The occurrence of species ranged from single observations of a lone individual, to high densities of individuals at all times. The small Anomuran crab *Pisidia longicornis* was always highly abundant, representing 78% of the total number of individuals sampled during the entire study. There were differences in the overall mean abundance of species over the entire year ($p<0.001$). However, high variation in numbers within sampling date lead to the detection of only three significant between-date differences at the 5% level. Abundance was significantly higher in late August than in May, and greater in September than both December and May. Numbers increased after the commencement of the main settlement season in June, and continued to rise until the approximate end of settlement in late September (Table 2.2). Numbers fell sharply between late September and November. Although

Figure 2.2. Height of morning high water at Kilmore Quay, Co. Wexford, June to December 1997. Consecutive sampling dates are indicated by asterix.

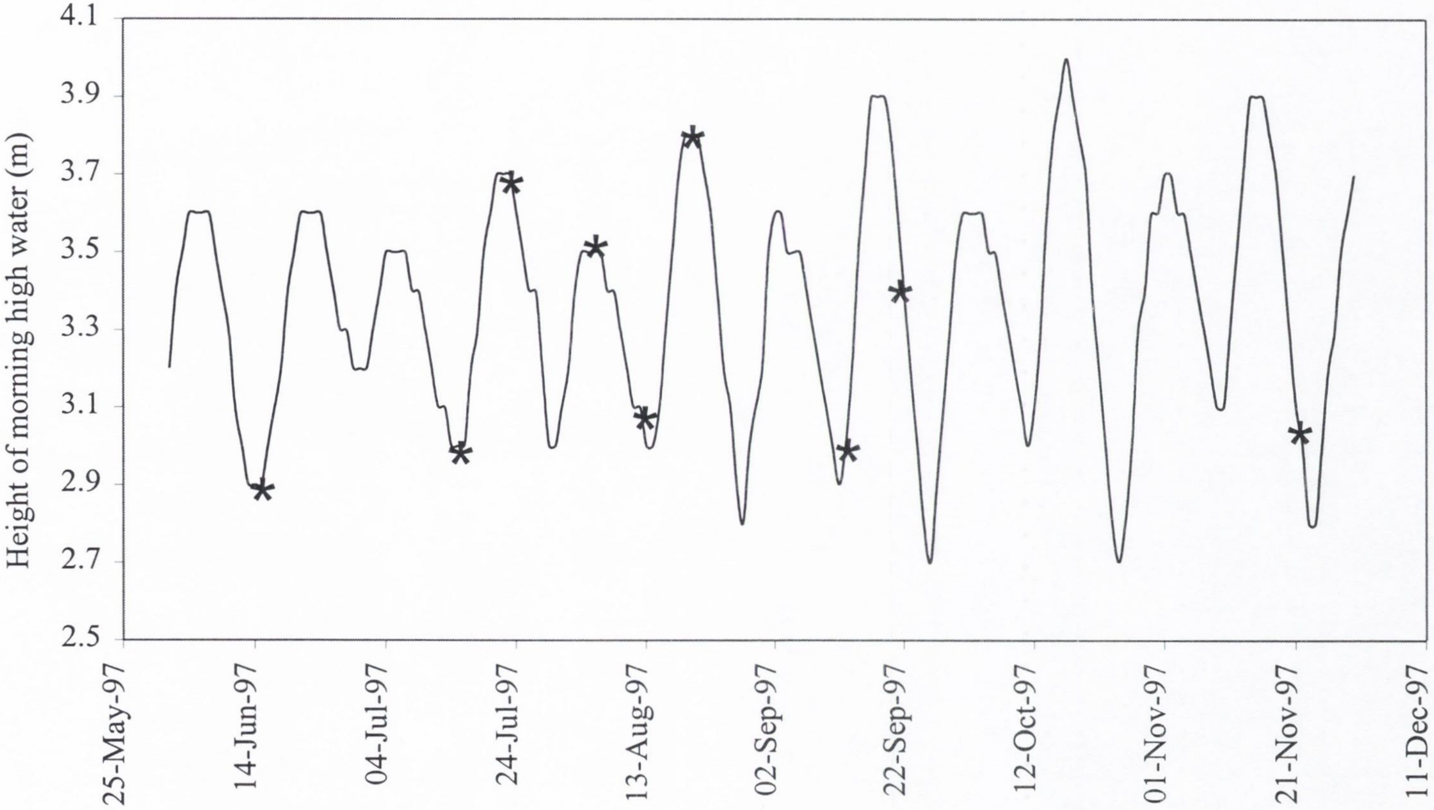


Table 2.1. Species contributing to decapod community structure Dec 96-Nov 97. P=Presence, G=Gravid females present, S=Settlement detected. *=First description of sp. for area.

	Dec	Jan	Mar	Apr	May	Jun	Jul-11	Jul-22	Aug-07	Aug-15	Aug-22	Sep	Nov	Total
Achaeus cranchii *				P	G			S	S	P	P	P		9
Anapagurus hyndmanni	P	P	P	G	G	GS	GS	G	G	G	G	G	P	343
Athanas nitescens			P	P	P	P		P	G	P		P		22
Cancer pagurus	P	P	P	P	P	P	S	S	S	S	S	S	P	260
Caridion gorgoni							P			P	P	P		4
Ebalia cranchii *				P										1
Eurynome aspera	P			P	P	P	P	P	S			P		17
Eurynome spinosa *		P		P						S				4
Galathea intermedia *			P	G	P			G		G	G			12
Galathea nexa *		P		P					P			S		24
Galathea squamifera	P	G	G	G	P	S	S	S	P	P	P	P	P	341
Hippolyte varians						P	GS	GS	GS	GS	GS	S		285
Inachus leptochirus			P	P		P					S	S		6
Inachus phalangium										S	P			4
Liocarcinus pusillus *					S	S	S		S		P			13
Macropodia rostrata *					P	P								3
Necora puber	P	P	G	G	P		S	S	S	S	S	P	P	197
Pagurus bernhardus	P	P		G	P		S	S	S	S	S	P	P	35
Pagurus cuanensis *										P				1
Pandalus montagui								P						1
Pilumnus hirtellus	P	G	P	P	P	P	P	S	P	G	S	GS	P	119
Pinnotheres pisum *			P											1
Pirimela denticulata	P	P	P	G	G	S	S	S	P	P	P	P		135
Pisidia longicornis	P	P	G	G	G	GS	GS	G	G	GS	G	S	P	10550
Pontophilus fasciatus			P	P	P	G		S	S	S	P	P	P	79
Porcellana platycheles	P	P										S		38
Processa canaliculata			P	P		P	S	G		P				8
Thoralus cranchii	P	P	P	G	G	GS	GS	GS	GS	GS	GS	S	P	795
Xantho pilipes	P	P	P	G	G	P	P	P	P	P	P	S	P	310
No. of Species	12	13	15	20	17	16	15	18	18	20	18	19	10	13617

Table 2.2. Mean abundance (individuals $0.25m^{-2}$) of decapod species recorded, Dec 96-Nov 97. Only species listed which were recorded at a mean density greater than 1 individual $0.25m^{-2}$ on at least one sampling date.

	Dec	Jan	Mar	Apr	May	Jun	Jul-11	Jul-22	Aug-07	Aug-15	Aug-22	Sep	Nov
Anapagurus hyndmanni	1	1	1	2	2	6	3	4	4	4	4	4	2
Athanas nitescens	0	0	0	0	0	1	0	0	0	0	0	0	0
Cancer pagurus	2	1	2	1	2	1	1	3	4	3	6	3	2
Eurynome aspera	0	0	0	0	0	1	0	0	0	0	0	0	0
Galathea nexa	0	0	0	0	0	0	0	0	0	0	0	1	0
Galathea squamifera	2	3	1	1	1	2	3	4	3	4	5	5	6
Hippolyte varians	0	0	0	0	0	4	2	2	3	4	6	8	0
Liocarcinus pusillus	0	0	0	0	0	1	0	0	1	0	0	0	0
Necora puber	1	1	3	1	0	0	1	2	2	4	3	1	3
Pagurus bernhardus	0	0	0	0	0	0	0	0	1	0	1	0	0
Pilumnus hirtellus	1	2	0	1	1	1	2	1	1	0	1	2	0
Pirimela denticulata	1	1	2	1	1	2	1	2	2	2	2	0	0
Pisidia longicornis	44	62	55	84	56	71	71	91	90	120	125	157	98
Pontophilus fasciatus	0	0	1	0	0	0	0	0	1	2	2	1	0
Porcellana platycheles	2	1	0	0	0	0	0	0	0	0	0	1	0
Thoralus cranchii	1	5	8	6	1	3	4	5	8	11	13	12	6
Xantho pilipes	2	1	6	5	4	5	1	1	1	2	2	3	1
Total Mean Abundance	56	79	78	103	69	97	89	115	119	156	169	201	120
Standard Deviation	41	34	38	67	77	28	19	25	47	40	39	78	45
Proportion of Total Abundance YOY (%)	0.00	0.00	0.00	0.00	0.18	11.43	58.48	69.94	77.56	79.86	74.50	78.07	73.12

the reduction in mean abundance of adults over the year was noticeable (Table 2.2), statistically significant differences existed only between April and early August, the seasonal maximum and minimum densities respectively. The YOY densities in May and June, the start of the settlement season (Table 2.1), were significantly lower than at all other dates ($p<0.01$). The mean abundance of individuals in early July was not significantly different (5%) from that of late July and early August, but varied from all subsequent dates. From late July onwards, there was no significant difference in YOY abundance, but there was a trend towards increasing numbers until late September. Densities were noticeably lower in November (Table 2.2). The proportion of the population constituted by the adult component of the population was minimal in mid August, when it represented only 20% of the community.

Biomass

There were no significant differences (5% level) in mean biomass between sampling dates. This was caused by the random occurrence of single large individuals in some samples, notably *Cancer pagurus* L., *Necora puber* (L.) and *Xantho pilipes* Milne Edwards. Within sampling date variation was reduced between June and early August, due to a reduction in the occurrence of such large individuals. There was a distinct period between early July and late August when mean biomass was at its lowest (Table 2.3). The biomass of YOY individuals increased from the onset of the settlement season to the end of the study in November. Mean adult biomass increased through August but declined after the end of August until November. The proportion of the population biomass represented by YOY individuals was highest (20%) in November.

Table 2.3. Mean biomass (g^{-1} 0.25m^{2}) of decapod species recorded, Dec 96-Nov 97. Only species listed which were recorded at a mean density greater than 1 individual 0.25m^{-2} on at least one sampling date (Table 2).

	Dec	Jan	Mar	Apr	May	Jun	Jul-11	Jul-22	Aug-07	Aug-15	Aug-22	Sep	Nov
Anapagurus hyndmanni	0.03	0.04	0.02	0.06	0.09	0.83	0.07	0.07	0.08	0.19	0.14	0.19	0.09
Athanas nitescens	0.00	0.00	0.01	0.01	0.01	0.03	0.00	0.02	0.03	0.01	0.00	0.03	0.00
Cancer pagurus	8.29	1.80	5.02	4.49	8.99	2.27	1.49	0.66	4.61	10.48	13.91	7.49	3.83
Eurynome aspera	0.03	0.00	0.00	0.01	0.01	0.03	0.02	0.01	0.00	0.00	0.00	0.00	0.00
Galathea nexa	0.00	0.23	0.00	0.01	0.00	0.00	0.00	0.00	0.06	0.00	0.00	0.55	0.00
Galathea squamifera	1.10	3.42	0.26	1.47	1.08	0.13	0.38	0.37	1.11	1.18	2.26	5.51	5.54
Hippolyte varians	0.00	0.00	0.00	0.00	0.00	0.07	0.06	0.09	0.06	0.09	0.11	0.08	0.00
Liocarcinus pusillus	0.00	0.00	0.00	0.00	0.00	0.03	0.00	0.00	0.01	0.00	0.01	0.00	0.00
Necora puber	1.03	2.77	5.04	3.73	0.08	0.00	1.68	4.27	0.05	5.76	7.09	0.39	2.70
Pagurus bernhardus	0.12	0.11	0.00	0.07	0.03	0.00	0.09	0.01	0.15	0.20	0.21	0.14	0.09
Pilumnus hirtellus	1.02	1.76	0.01	0.57	0.88	0.22	0.87	0.08	0.74	0.96	0.47	2.52	0.54
Pirimela denticulata	0.13	0.07	0.12	0.03	0.21	0.13	0.07	0.25	0.12	0.26	0.29	0.03	0.00
Pisidia longicornis	3.60	5.42	3.90	6.37	4.08	5.66	4.22	4.43	4.88	6.53	9.13	11.35	9.15
Pontophilus fasciatus	0.00	0.00	0.06	0.01	0.00	0.03	0.00	0.02	0.02	0.03	0.04	0.03	0.01
Porcellana platycheles	0.84	0.70	0.00	0.00	0.00	0.00	0.00	0.00	0.14	0.00	0.00	0.50	0.00
Thoralus cranchii	0.05	0.25	0.50	0.43	0.12	0.24	0.16	0.22	0.32	0.34	0.48	0.36	0.20
Xantho pilipes	1.22	0.28	5.79	7.57	4.38	5.77	1.05	0.84	0.28	1.01	1.81	6.30	4.36
Total Mean Biomass	17.47	16.85	20.71	24.84	19.97	15.45	10.15	11.34	12.65	27.04	35.94	35.47	26.51
Standard Deviation	27.9	13.3	15.9	28.4	17.9	10.9	5.1	11.4	11.5	25.9	28.6	20.7	8.8
Proportion of Total Biomass YOY (%)	0.00	0.00	0.00	0.00	0.01	0.84	3.49	5.09	10.29	7.68	7.05	12.92	20.13

Number of species & diversity indices

There was a general trend towards higher numbers of species during the settlement season. Significantly higher numbers of species (5% level) occurred in the four samples between early August and September than occurred in April and May. Some of the species, e.g. *Liocarcinus pusilus* (Leach) and *Hippolyte varians* Leach, present at settlement failed to persist into later samples.

There were no significant differences in diversity, evenness or dominance throughout the season. Evenness was always low due to the dominance of the species *Pisidia longicornis*. The high density of this species accounted for the relatively low values of Shannon diversity observed.

Community structure

Community structure varied during the year. Of the 77 possible comparisons between the 13 sampling periods, only 18 displayed similarities in community structure. A full list of similarities is given in Table 2.4. Most differences occurred between samples in the settlement season and those within the over-wintering period, although there were exceptions such as the similarity between April and early July, early and late August, and November. The presence/absence transformed species composition of the YOY component of the population was significantly different from that of the established adult component at all times.

Settlement

Settlement of 21 of the 29 species encountered during the study was detected. Settlement was detected on only one occasion for some species, while others

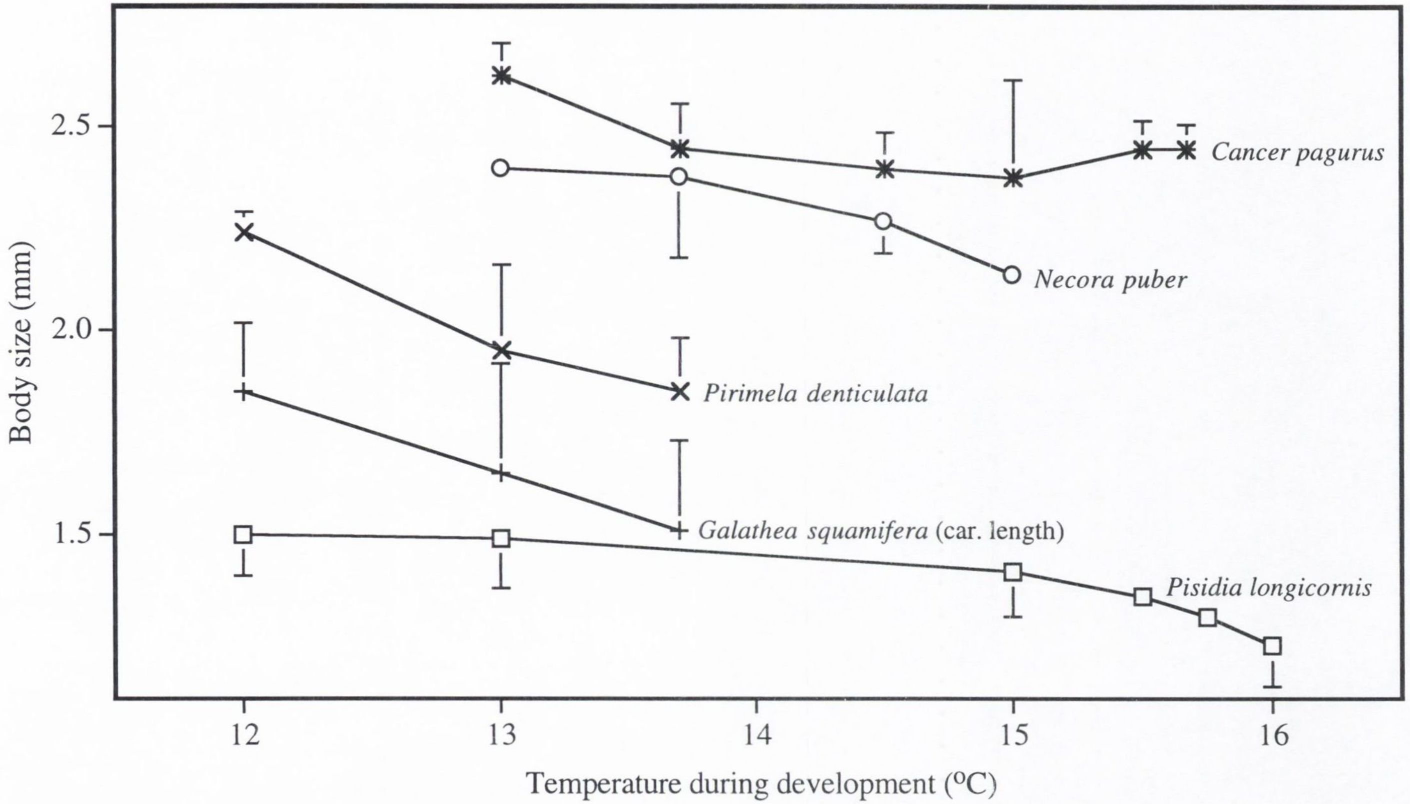
Table 2.4. Sampling dates displaying significant Bray-Curtis similarities in decapod community structure. Bracketed numbers represent date in month when sampling was conducted for months sampled more than once.

Dec-Jan	Jan-Apr	Mar-Apr	Apr-Jul(11)	May-Jun	Jul(11)-Jul(22)	Jul(22)-Aug(07)	Aug(15)-Aug(22)
Dec-Mar	Jan-Nov		Apr-Aug(15)	May-Nov		Jul(22)-Aug(15)	
Dec-Apr			Apr-Aug(22)			Jul(22)-Aug(22)	
Dec-May			Apr-Nov				

continued to settle over prolonged settlement periods (Table 2.1). Gravid female individuals were often present for extended periods for species subsequently displaying prolonged settlement (Table 2.1). There was clear evidence that settlement of the species *Pisidia longicornis* occurred only at periods when tidal velocity was minimal, as settlement was not detected at other times. Seven other species, *Anapagurus hyndmanni* Thompson, *Eurynome spinosa* Hailstone, *Galathea nexa* Embleton, *Inachus phalangium* (Fabricius), *Porcellana platycheles* (Pennant), *Processa canaliculata* Leach and *Xantho pilipes*, settled only during periods of low tidal velocity but none of these displayed a prolonged intermittent settlement, as displayed by *Pisidia*. Settlement of other species appeared to be unaffected by tidal amplitude. Several species displayed prolonged settlement over two months or more, such as *Cancer pagurus*, *Pagurus bernhardus* (L.), *Hippolyte varians*, *Necora puber* and *Thoralus cranchii* (Leach).

Body size at settlement decreased with increasing temperature during larval development (Figure 2.3). Although temperature during development was taken as an average daily figure from 30 days prior to settlement for all species, the more rapid moulting of smaller individuals, at higher temperatures, would reduce the moult increment and the duration of larval development. The high temperatures of mid-August also coincided with the recording of the smallest planktonic larvae in this area (Merin, pers. com.). Of the five species that occurred in sufficient numbers to calculate mean size at settlement for several temperatures, significant reductions in size were observed for *Cancer pagurus*, *Necora puber*, *Pirimela denticulata* (Montagu) and *Pisidia longicornis*.

Figure 2.3. Relationship between mean (±SD) size at settlement and mean temperature (°C) for 30 days prior to settlement in five decapod species. All sizes carapace width unless stated otherwise.



Growth

Minimum size at settlement and maximum body size obtained before the end of the growing season was determined for 13 of the species sampled (Table 2.5). Numbers of YOY individuals were too low to determine these sizes accurately for the other 8 species for which settlement was detected. It was not always possible to detect consecutive instars due to mixing of distributions, and so the number of moults from settlement to the cessation of growth before winter was determined for only 5 species. Of the crab species sampled, *Necora puber* displayed the highest growth rate, from 1.8mm carapace width to 19.6mm. The growth of some species was relatively low as they settled later in the season, reducing the time available for growth (*Xantho pilipes*).

Mortality

Early seasonal mortality estimates were derived for five decapod species where clear progression through instars could be detected (Figure 2.4). It was assumed that no YOY individuals migrated from the study area. In general, these represented the more abundant species at the site (Table 2.1). Mortality was higher between instars II & III for all species with the exception of *Pisidia longicornis*. The inter-moult duration between stage II & III for *P. longicornis* is short relative to the following period, resulting in the appearance of higher mortality during stage III & IV (Robinson & Tully, in press a). Of the five species, highest mortality rates were recorded for *Cancer pagurus* and *Necora puber*, with a 64% and 67% reduction in numbers between stage II & IV respectively. High rates of early mortality were evident in the LFD of these species (Figure 2.5). A number of factors prevented the separation of instar groups for other species, including low numbers of individuals

Table 2.5. Growth potential of decapod species, Saltees Sound, 1997. Caridea growth recorded by increase in weight (g), Paguridea (sl) by shield length (mm) and Galathidea (cl) by carapacelength (mm). Increase in carapce width (mm) recorded for other species.

Species	Minimum size	Maximum size	No. Moults
Achaeus cranchii	1.6	2.7	
Anapagurus hyndmanni (sl)	0.7	1.8	
Cancer pagurus	2.3	8.8	5 to 6
Galathea squamifera (cl)	1.2	9.5	
Hippolyte varians (g)	0.002	0.05	
Necora puber	1.8	19.6	8 to 10
Pagurus bernhardus (sl)	1.1	4.0	
Pilumnus hirtellus	1.3	8.4	
Pirimela denticulata	1.7	6.7	5 to 6
Pisidia longicornis	1.3	4.7	5
Pontophilus fasciatus (g)	0.002	0.05	
Thoralus cranchii (g)	0.001	0.08	
Xantho pilipes	1.8	3.6	1

Figure 2.4. Decline in numbers of five decapod species between the 2nd, 3rd & 4th crab stages, calculated from the total number of individauls sampled in each instar, Jun-Nov 1997.

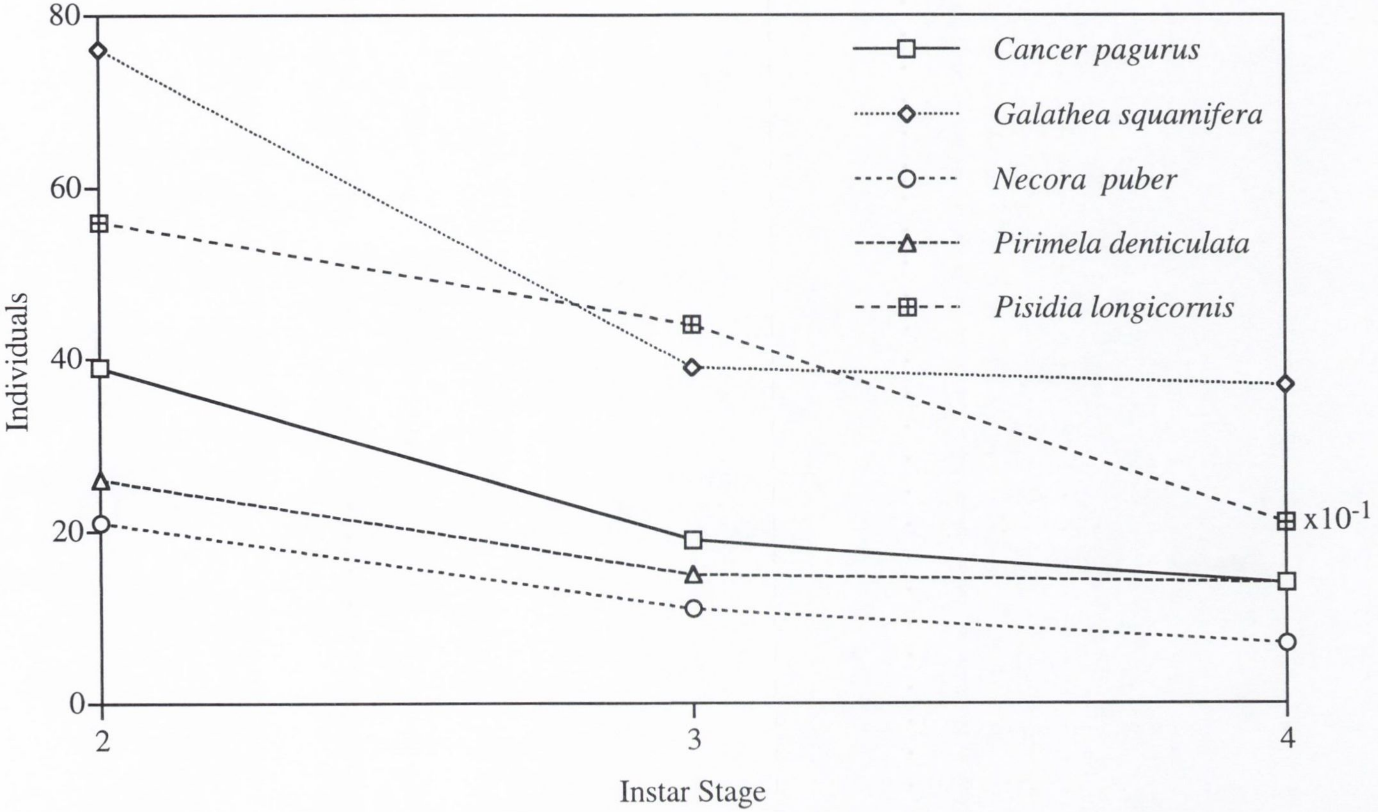
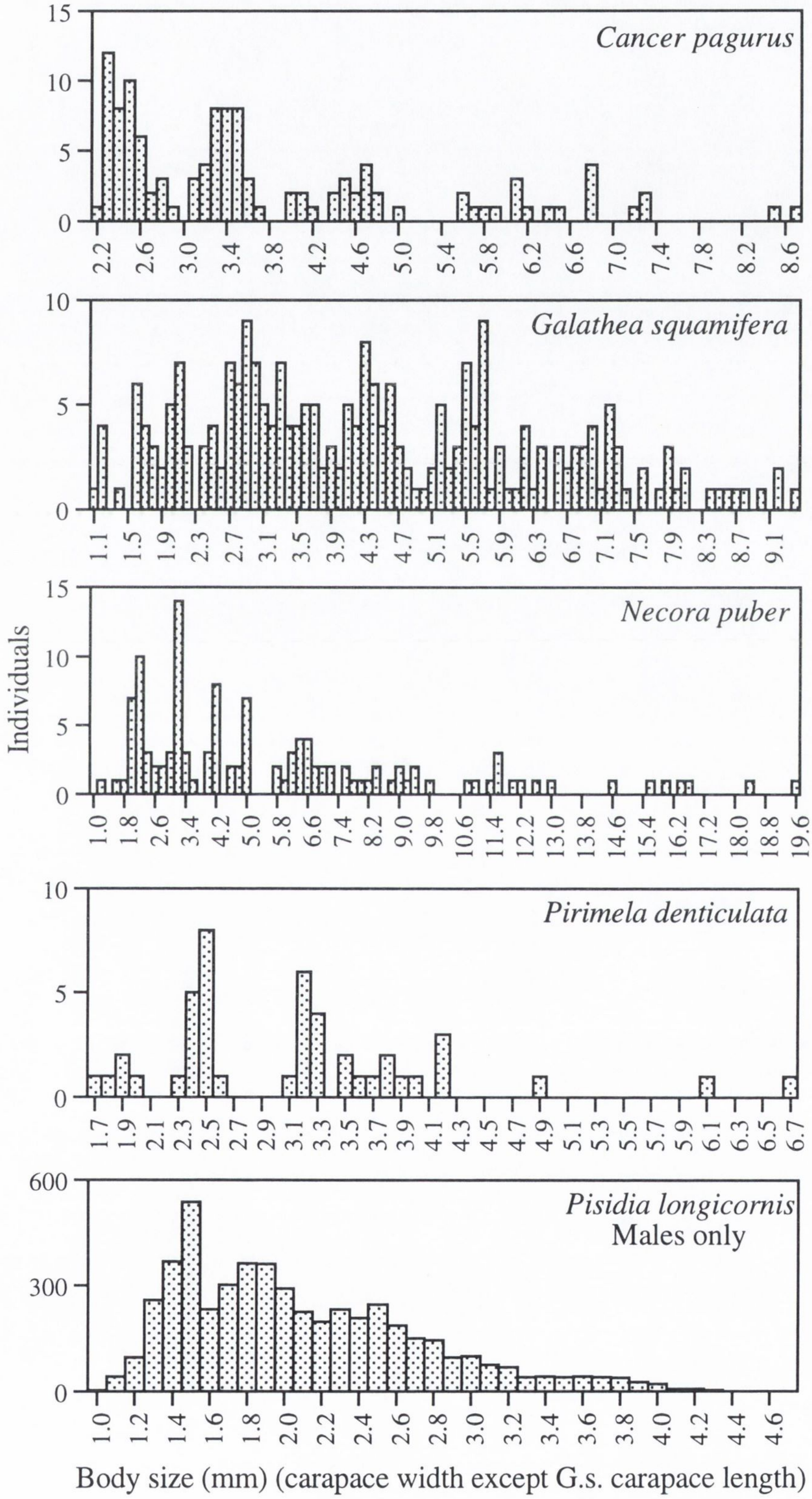


Figure 2.5. Length-frequency distributions of the young of the year cohort of five decapod species, Jun-Nov 1997.



(e.g. *Pagurus bernhardus*, *Galathea nexa*), early mixing of instar groups due to variable growth (*Thoralus cranchii*, *Hippolyte varians*) and late settlement (*Xantho pilipes*). However, reduction in numbers of individuals was observed with increasing body size for all species to some extent.

DISCUSSION

High densities of decapod species were recorded throughout the study period, some of which were not previously described at the study location. It is likely that the majority of species sampled, most of which were relatively small bodied, settle into and remain within the vicinity of the habitat sampled. More mobile or larger bodied individuals may make temporary movements or permanent migrations from the area. For species such as *Cancer pagurus*, which can undergo long migrations (Cosgrove, 1998), shallow water rocky nursery habitats probably represent a major source of recruitment to offshore fisheries. Competition for resources, low larval supply or sub-optimal habitat conditions are the likely explanation for species that settle into the area but fail to persist until the end of the season (*Liocarcinus pusillus*). Lewis (1991) stated that recruitment failures of barnacles stemmed from planktonic or initial settlement conditions. Several species that may have been expected in samples were noticeably absent. Although adults are fished in the area, no juvenile lobster, *Homarus gammarus* (L.), were detected. This may be an indication that the habitat requirements of juvenile lobster are not met in the area, and that settlement occurs elsewhere (Howard & Bennet, 1979). Other noticeable absences from the area include *Carcinus maenas* (L.) and *Galathea strigosa* (L.). Both of these species were recorded in planktonic samples (Merin, 1998).

Although trends in abundance and biomass could be seen, the significance of changes was often masked by high variance within sampling date. Grant (1991) stated the use of random samples in the presence of high heterogeneity can lead to large sampling variances which can make year to year differences difficult to detect (Bowman & Lewis, 1977). It is likely that small-scale patchiness within the habitat sampled causes similar difficulties within the seasonal data set presented here. Recent work by Hughes *et al.* (1999) incorporated numerous spatial scales in the experimental design. This allowed partitioning of variance within and between spatial scales for both newly settled and adult individuals. Differences in community structure, caused by between-site variation in settlement intensity (Gaines & Roughgarden, 1985) or post-settlement processes, may occur across spatial scales ranging from metres to kilometres. In the present study, similarity in community structure existed mainly between the dates before commencement of the settlement season, and between dates when settlement occurred. It seems reasonable to assume that community structure during the settlement season is transitional, and will quickly be shaped by post-settlement processes. The community structure at other times, although likely subject to stochastic alteration such as storm events, can then be considered a more accurate representation of the established decapod fauna in this area. Variations in seasonal and annual physical and biological parameters may alter the resultant species composition. In a parallel experiment to the present study, significant differences occurred in decapod abundance and community structure between habitats with varying degrees of complexity (Robinson & Tully, in press b). Identifying the factors that cause seasonal spatial variation in settlement, recruitment and community structure, both temporally and spatially, will allow a more detailed understanding of annual fluctuations and population dynamics.

The settlement of some species is mediated by tidal amplitude (Morgan *et al.*, 1996; Eggleston *et al.*, 1998), while others show no such association (Jones & Epifanio, 1995). The present study area is subjected to a strong tidal regime, and slack water period between turning tides lasts only a few minutes. Within that tidal regime some species appeared unable to settle to the benthos when tidal currents were significant. This may be due to physical inhibition of substrate selection of passive or weakly swimming larvae.

By the end of the settlement season YOY individuals were numerically dominant, due to both heavy settlement and decline in adult numbers. The reduction in adult numbers was due mainly to the mortality of short-lived individuals, such as *Pisidia longicornis*, soon after reproduction (Robinson & Tully, in press a). Grant (1991) stated that the small individual body size of YOY specimens suggested that their contribution to total biomass, and presumably their influence on other species and the environment, was less important. However, there is probably a high level of interaction between individuals within the YOY component itself, especially when individuals settling later in the season encounter earlier settlers. Density dependent cannibalism and predation are known to play an important role in shaping both abundance and community structure (Gosselin & Qian, 1997). However, these regulatory processes can be difficult to detect in patchily distributed populations (Hassell, 1987). The availability of information relating to the development rate of early benthic phase decapods is limited. It was possible to detect successive instars in a number of the species sampled in this study, and derive crude estimates of growth potential and mortality. These estimates could be substantially improved with knowledge of development rate. Although sampled in high numbers, there was difficulty in separating caridean instar groups due to early mixing of distributions. Fluctuating recruitment and mixing of broods in both sexes has also hampered the use of length-frequency data for estimation of the growth parameters of penaeid shrimp (Pauly *et al.*, 1984) and other crustacea. Instar duration, body size and activity are closely linked to environmental temperature and as such, different growth and mortality rates may be encountered by individuals settling at different times of the year. Survival may be directly related to size at settlement, with smaller size predisposing individuals to higher rates of mortality (Robinson & Tully, in press a). Although temperature during larval development would appear to influence body size at settlement, other factors not considered in the present study, such as food availability or the variation in body size of spawning stock may also illicit significant affects. The numbers of individuals of many of the species sampled during this study were too low at individual sampling times to warrant application of a time scale to growth and mortality estimates. More refined mortality estimates and seasonalised growth curves were derived for *Pisidia longicornis* (Robinson & Tully, in press a). It is possible that the reduced early mortality of *Pisidia* and *Galathea squamifera* Leach observed in this study may be linked to absence of cannibalism and reduced intra-specific competition, although both are preyed upon by other species in the laboratory and field (pers. obs.). Cannibalism is common and can account for a large proportion of early mortality in active predators (Lovrich *et al.*, 1995; Moksnes *et al.*, 1997) such as *Cancer pagurus* and *Necora puber*. Predation on moulting or newly moulted YOY individuals of these species, both by adults and other YOY individuals, has been regularly observed in mesocosm aquaria (pers. obs.).

If the magnitude of adult biomass and abundance are presumed to exert a greater influence on the community and environment, relative to the small bodied YOY component (Grant 1991), then seasonal minima in these parameters may be the most suitable time to release juvenile *Homarus gammarus* for enhancement purposes. In this enhancement method, hatchery reared juvenile lobster are grown on to later stages of development (Mercer & Brown, 1994) are released into the fishery catchment area (Addison & Bannister, 1994) in an attempt to avoid the high post-larval mortality rates experienced by recently settled larvae. Some doubt remains as to the subsequent fate of these lobsters, and the numbers that survive to recruit to the fishery (Walker, 1986; Bannister *et al.*, 1994; Bannister & Addison, 1998). Understanding the dynamics of existing wild populations may help in assessing the success of these stock enhancement methods. Seasonal lows in both biomass and abundance occurred during July and early August. Minimum density and biomass of YOY individuals also coincided with this period. After this time, the biomass represented by the adult component increased, due to summer growth of established individuals. Periods of reduced interspecific competition could therefore be identified.

Novel information pertaining to the early life history stages of numerous decapod species was gathered during the study using suction sampling methods. Although no implications are made regarding the interactions between species, conspecifics or the community as a whole, further laboratory and field experimentation could be conducted using seasonal data as a baseline. Examination of the interactions between YOY individuals, YOY and adults individuals and between the community and the environment will enhance understanding of decapod early life history and ecology in this geographically widespread community. Increasing knowledge of seasonal variations, and any patterns that may be associated with these fluctuations, will help to further development of methods for prediction of annual variations in settlement and recruitment.

CHAPTER 3

DYNAMICS OF A SUB-TIDAL POPULATION OF THE PORCELLANID CRAB *PISIDIA LONGICORNIS*

ABSTRACT

A sub-tidal population of the anomuran crab, *Pisidia longicornis* (L.) was sampled quantitatively throughout 1997. Divers, using SCUBA equipment, conducted suction sampling each month, with concentrated effort directed towards the settlement season. *Pisidia* occurred in very high densities, constituting the major component of decapod community abundance. Gravid females were detected between March and September. Newly settled megalopae were present in benthic samples from June until late September. Six distinct settlement events were detected during this period, with pulses coinciding with low spring tides. Body size at settlement decreased as temperature during larval development increased. The rapid growth of each distinct settlement group was followed over time through each subsequent crab stage up to maximum adult size. Growth was suspended between December and April. Survival within each distinct settlement group was density-independent during the first summers growth. Mortality increased between June and July settlement events, with the rate of decline remaining a linear function. There is excellent potential for the application of suction sampling methodology in conducting detailed examination of often poorly understood early benthic life history. The settlement and recruitment of commercially valuable species can be utilised in the prediction of future fishery performance.

INTRODUCTION

The commonly abundant anomuran decapod *Pisidia longicornis* (L.) can often represent the major component of both the biomass and abundance in the shallow water crustacean communities of northern Europe (Smaldon, 1972; Fernández *et al.*, 1990). Rocky substrates and other solid structures provide suitable habitats for this short-lived, suspension-feeding species. This less competitive feeding strategy may allow the species to be successful in the dense and diverse shallow water crustacean communities of Ireland. *Pisidia* forms an important and readily available source of food for many other species, some commercially valuable, within these communities (Chesney & Iglesias, 1979; López-Jamar *et al.*, 1984; Friere & González-Gurriarán, 1995).

Limited attention has been directed to the detailed examination of the early benthic life history of *Pisidia longicornis*, and indeed other species of decapod. Physical (Eckman, 1983; Hobbs *et al.*, 1992; Eggleston & Armstrong, 1995; Wahle & Incze, 1997) and biotic (Olmi & Lipcius, 1991; Eggleston & Armstrong, 1995) processes affect pre- and post-settlement processes, and influence subsequent benthic stages (Phillips, 1990; Pile *et al.*, 1996). Long-term sampling of juvenile blue crab *Callinectes sapidus* Rathbun distribution identified sequential early life history stages (Pile *et al.*, 1996) from which density dependent mortality rate was estimated. Robinson and Tully (1998b) examined the settlement density and growth of the edible crab *Cancer pagurus* L. through successive instars to their first winter. Cohort strength in decapod crustaceans may be determined early in the life history. Studies directed at these critical life history phases can therefore greatly increase the understanding of population rate processes, such as settlement, post-settlement growth and mortality, and density dependent control on these processes. These processes could therefore determine the relationship between recruitment and population egg production. The form of this relationship has rarely been demonstrated but is critical to the conservation of exploited species.

This chapter presents quantitative data on the settlement, growth, mortality and population structure of a sub-tidal population of *Pisidia longicornis* in order to examine both young of the year and adult life history in detail. Data on the development of *Pisidia*, from settling megalopae to full size adult is presented.

MATERIALS AND METHODS

Study location

Samples were collected from within a pre-determined area 0.5 x 0.5 nautical miles in area, in the Saltees Sound, County Wexford, Ireland. Sampling was conducted on a monthly basis between December 1996 and November 1997, with more concentrated effort during the summer settlement season. The exact frequency and timing of each sampling effort, at this relatively exposed site, was often determined by conditions at sea. The substrate in the area consisted of gravel and shell material, overlain by boulders and rocks of various sizes. Due to the perennial nature of the *Laminaria* species present, algal cover varied through the year, but was typically between 50-70% during the settlement season. Sampling was conducted at a depth of 8-10 meters. Temperature was monitored at 2 hour intervals by a Seamon® temperature recorder deployed near the seabed.

Collection of samples

Divers using SCUBA equipment randomly positioned 0.5 x 0.5m quadrats on the seabed. The area contained within each quadrat was sampled *in situ* using a diver operated suction sampler. The sampler consisted of a 2m length of 150mm diameter plastic pipe with an air feed fitting mounted 25mm from the base. Air supply to the sampler, estimated to be 200-300 $l\ min^{-1}$, was provided *via* a spare diving cylinder carried by the operator. *In situ* sampling permitted collection from sheltered lower surfaces and crevices of large rocks and boulders that support high densities of *Pisidia longicornis*. Sampling methodology employing grab samples or dredging may fail to adequately sample such habitats. All fauna was collected in rigid 1mm mesh bags.

In the laboratory, samples were sieved, while submerged in seawater, through progressively smaller mesh sizes down to 1.0mm. Once isolated, individuals were fixed in 5% formalin, containing 5% glycerol to maintain flexibility. Large specimens were sorted by sex by examination of abdominal width. Smaller individuals, down to a size of 2.0mm, were sexed by examination of the first pleopods using a binocular microscope (Smaldon, 1973). The sex ratio of the young of the year (YOY) with carapace width greater than 2.0mm was calculated. Individuals smaller than 2.0mm were allocated either to male or female distributions in proportions representative of the sex ratio observed at the time of sampling. Distribution of small individuals in this manner assumed that post-settlement mortality rates were identical for both sexes below a carapace width of 2.0mm. Maximum carapace width of larger specimens (>3.0mm) was recorded to 0.1mm using digital callipers. Individuals smaller than 3.0mm were sized to the nearest 0.1mm, using a binocular microscope micrometer.

Data analysis

Young of the year *Pisidia longicornis*, sub sampled from the catch before fixation, were maintained in a seawater re-circulation system to monitor growth. Moult increment averaged 19-25% of pre-moult carapace width. These increments were used as a guide in constructing length-frequency histograms of all individuals collected at each sampling date, such that successive moults could be detected. Bar widths were set at 0.1mm and the data smoothed by 3 point running average. Smoothed histogram bar counts were used as the input data to the computer package MIX 2.3 (MacDonald & Green, 1988), in order to isolate normal distributions, thought to represent instars, from the distribution mixtures. Castro (1995) found MIX to be a robust and efficient method for separation of mixtures of normal distributions after a comparison of numerous length-frequency techniques. The program separates normal distributions from composite length frequency distributions by maximum likelihood estimation. Individuals representing the newly settled cohort were treated separately during graphical analysis due to their large numbers that masked the much smaller scaled adult distributions.

In order to estimate growth, linkage of the means separated by MIX was carried out using the computer package FISAT (Gayanilo *et al.*, 1994). Not all means were selected for inclusion in this process. Neighbouring peaks were sometimes interpreted as containing individuals from one instar group that had not all moulted to the subsequent instar at the time of sampling. Lines of best fit applied to the series of means would pass through the centre of these temporarily split pairs to bisect the point recorded at the next sampling period. This was interpreted as the time when the majority of individuals from the group had moulted to the next instar. Linking means to either the higher or lower values in these cases produced unlikely curves deviating widely from the growth of other groups, with unrealistic increments or durations. For the purpose of growth curve estimation the adult linked means were appended to those of the YOY. The final means separated for the YOY in November 97 were not completely continuous with those of December 96, but similar enough for application of a von Bertalanffy growth curve (von Bertalanffy, 1938). The full set of growth increment data obtained from mean linkage was input into FISAT's Appeldoorn's method (Appeldoorn, 1987; Soriano & Pauly, 1989), to obtain refined parameter estimates for a seasonally oscillating von Bertalanffy growth curve (Pitcher & MacDonald, 1973; Cloern and Nichols, 1978). Estimated growth parameters include the asymptotic length ($L\infty$), calculated from the observed reduction in growth rate with increasing age, which is essentially the maximum size of infinitely old *Pisidia longicornis*. The rate at which $L\infty$ is approached is estimated from the overall curvature (K). The period of minimal growth is defined as the winter point (WP). The amplitude of seasonal oscillations in growth (C) becomes more pronounced as the value increases. The full equation takes the form:

$$L(t)=L\infty*[1-\exp\{-K*(t-t_0)-(CK/2\pi)*\sin(2\pi*(t-ts))\}]$$

, where the term ts is the summer point, the fraction of the year that has elapsed when growth rate is maximal.

The decline in numbers of individuals (m^{-2}) within three of the distinct YOY male settlement groups were taken as an indication of instantaneous mortality rates. Densities of megalopae, from the June, July and late August settlements, were not included as it was not possible to determine the exact point after which no new additions occurred. Regression analysis was applied to the density of individuals surviving to each subsequent instar beyond the 1st crab stage. The regression slopes derived were compared using the methodology described by Fowler & Cohen (1990).

RESULTS

Temperature and tides

Average daily temperature at the site was calculated from the 12 daily recordings, for the period July 1997 to May 1998 (Figure 3.1). Although this does not coincide exactly with the duration of the study, it is believed to approximate to the usual annual temperature regime of the area. Two sets of remote recording were taken using a WTW temperature probe, on 23/01/97 (8.0°C) and 08/07/97 (13.6°C), prior to the deployment of the probe. The highest mean daily temperature of 16.6°C was recorded in mid August. July and September yielded comparable values around 15.0°C. Temperature dropped significantly at the onset of October, reaching a minimum (8.5°C) in early February. Increasing temperatures were recorded from mid April onward. The remote WTW probe recording in early July was used when estimating missing temperature values between May and late July.

Tidal amplitude was estimated using the height of the morning high tide, from mid May to early December 1997 (Figure 3.2), as predicted by local Harbour Office tide tables (Kilmore Quay Harbour Office, 1997). The timing of consecutive sampling dates are indicated on the oscillating line by addition of asterisk.

Abundance

The highest recorded mean density, 640 individuals m^{-2}, occurred in early September (Figure 3.3). Means and standard errors were calculated, using bootstrapping techniques, for total population numbers. The population was comprised mainly of newly settled individuals at this time. Total numbers decreased rapidly until the end of the study in November, due to high mortality of newly settled

Figure 3.1. Mean daily seawater temperature calculated from 2 hourly recordings, from July 1997, Saltees Sound, Co. Wexford. Values from May-July 1997 estimated from single recordings taken in Jan and early July.

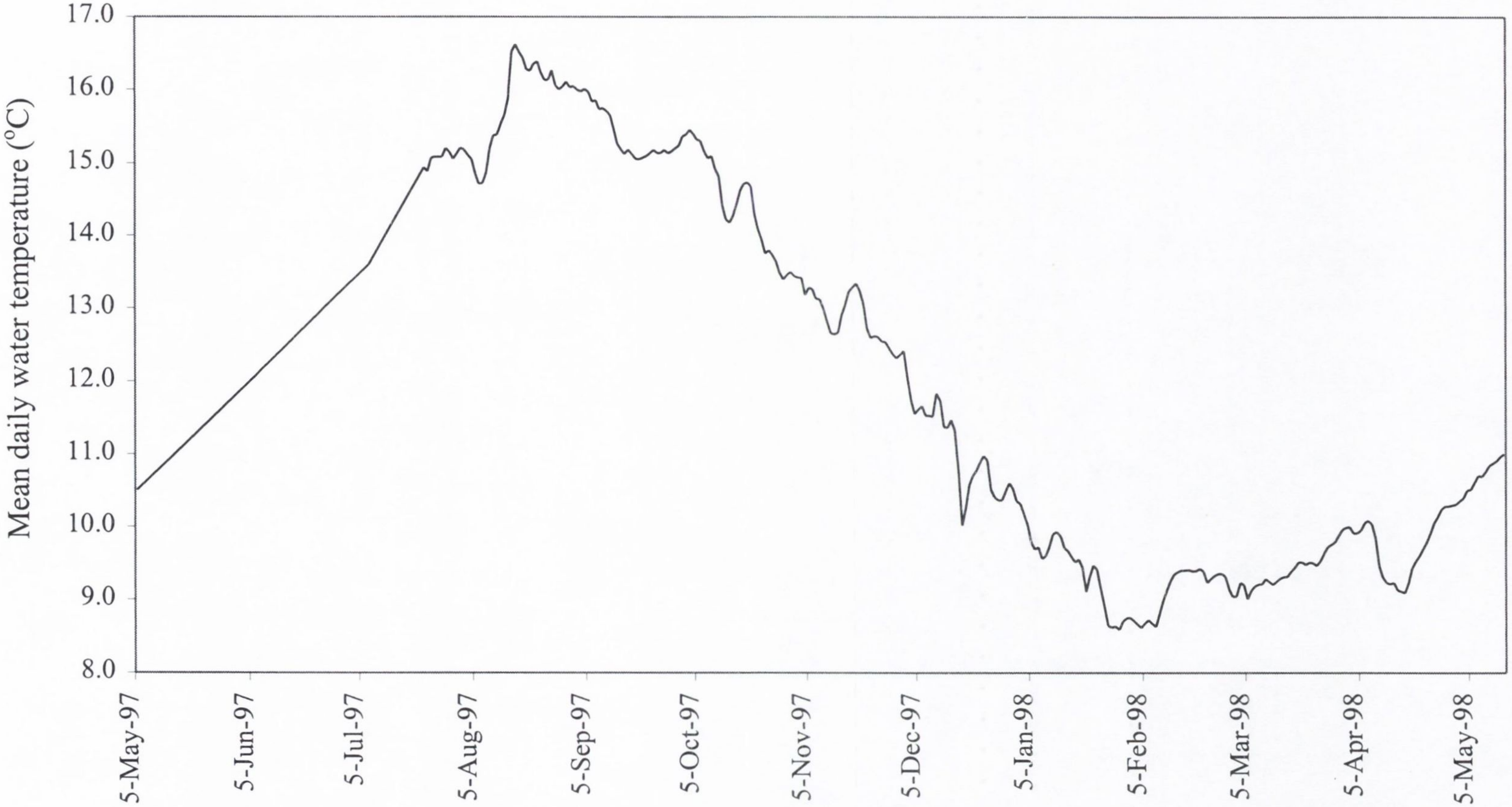


Figure 3.2. Height of morning high water at Kilmore Quay, Co. Wexford, June to December 1997. Consecutive sampling dates are indicated by asterix.

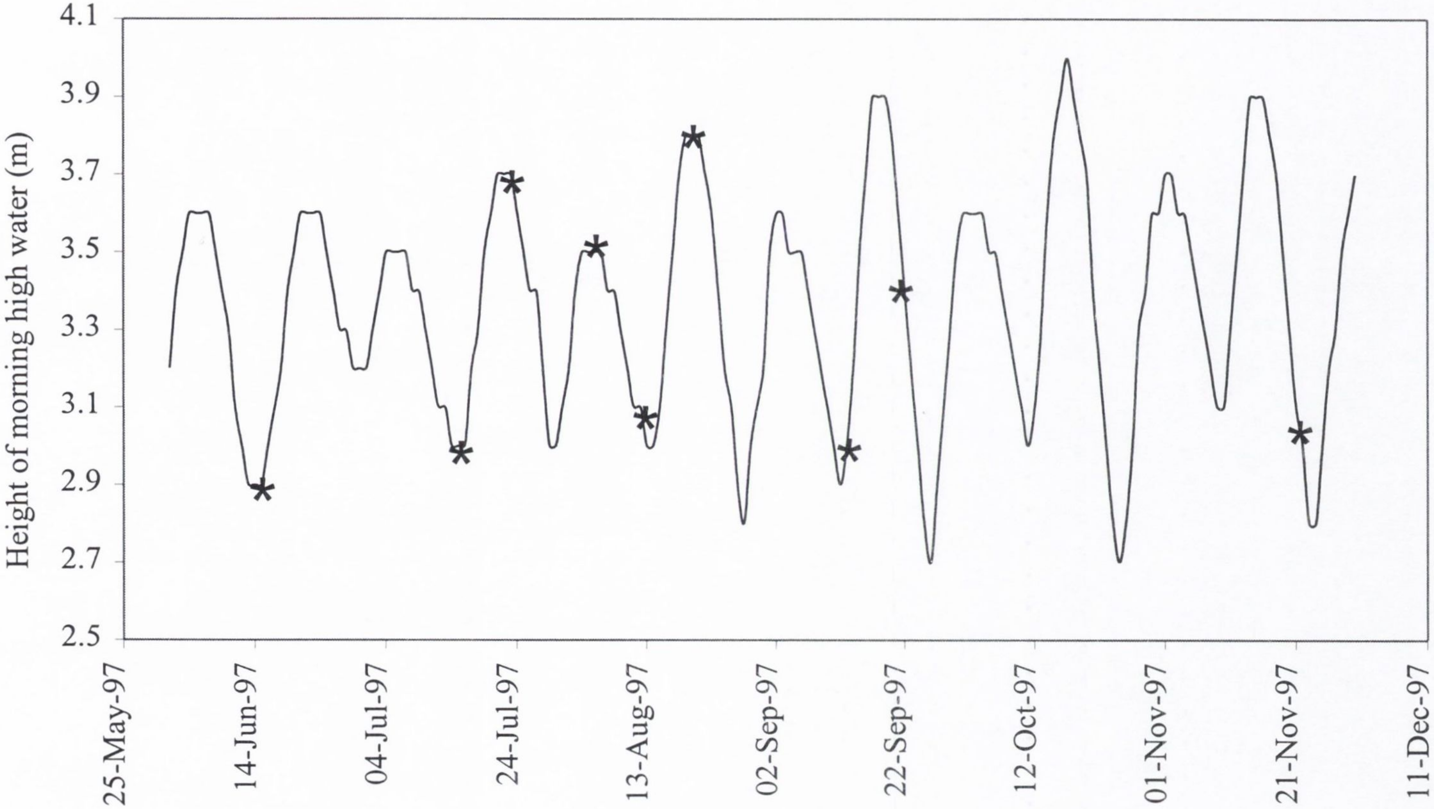
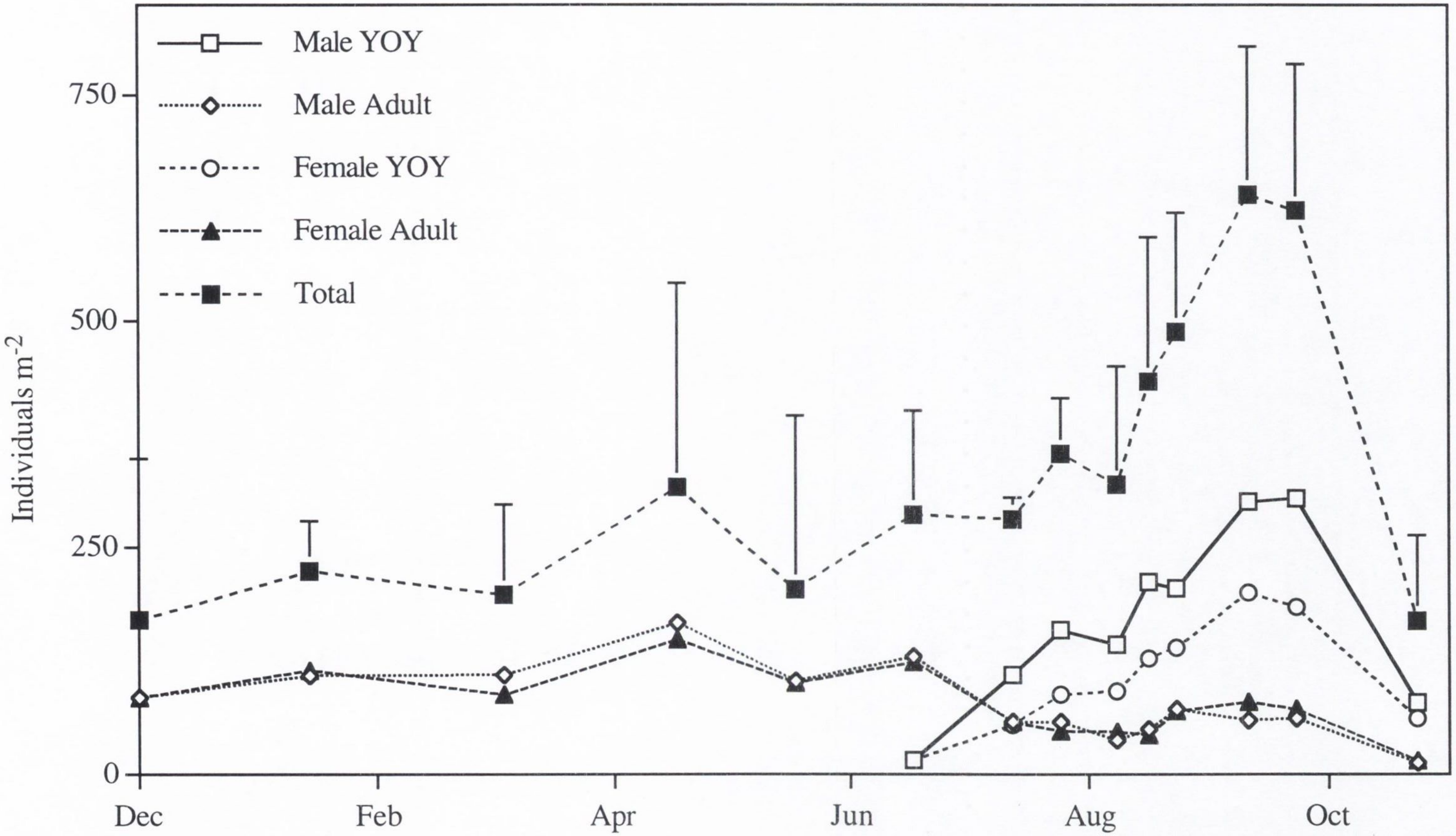


Figure 3.3. Mean abundance of sub-tidal *Pisidia logicornis* (m^{-2}), Dec 1996 to Nov 1997. YOY=Young of the year. Total abundance shown with bootstraped standard error.



individuals, and adults to a lesser extent. The similar densities recorded between December 96 and March 97 suggests that the population was more stable over winter. Numbers of male and female adults, that included immature juveniles that settled in 1996 and mature adults, decreased over the year.

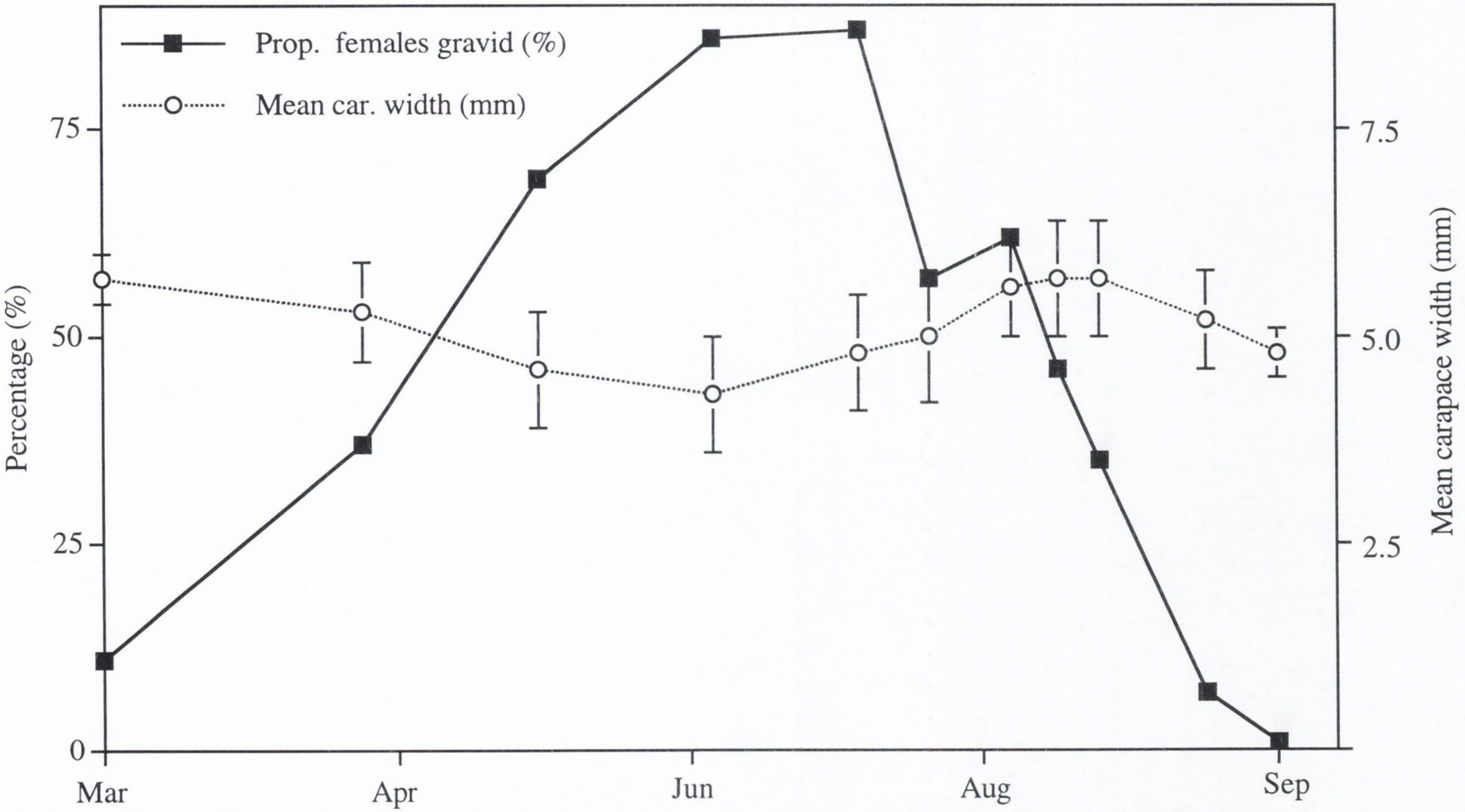
Female maturity

Gravid females were observed between March and September. The proportion of gravid individuals within the female population was highest during June and early July, with over 80% carrying eggs (Figure 3.4). Only large specimens were gravid during March and April, with mean (±SD) carapace width of 5.6 ±0.33mm and 5.3 ±0.55mm respectively. The mean size of gravid female decreased until June as younger individuals produced eggs after spring moulting (Figure 3.4). Mean carapace width increased again after June, reaching maximum, 5.7 ±0.72mm, in late August. Gravid individuals were detected until the end of September, but constituted less than 10% of females by the end of the month. The smallest gravid female observed was 3.0mm in carapace width. This would seem to be the minimum size at maturity for females, considering the large number of individuals sampled (n=4428).

Settlement pulses

Newly settled megalopae were detected in benthic samples from mid June until the end of September. Settlement pulses during this extended period were timed to coincide with periods when tidal amplitude was minimal (Figure 3.2). No new settlement was detected during sampling conducted between these tides. The actual timing of settlement pulses around the August 29 and September 29 were estimated after detection of the first crab stage in subsequent samples. Settlement in June and

Figure 3.4. Mean (±SD) carapace width (mm) and proportion (%) of female *Pisidia longicornis* (>3mm carapace width) gravid during 1997.



July occurred only on monthly low spring tides. Pulses occurred during all four spring and neap low tidal periods between August 13 until September 29. Planktonic stage II zoea larvae were detected over the study area between May and September (Merin, 1998).

YOY instars

Length-frequency histograms of the YOY male cohort were constructed for each of the nine sampling dates between June and November (Figure 3.5), with laboratory moult increment data used as a guide to bar width. The normal components contained within each distribution mixture represented the sequence of growth through each instar. Distinct groups of individuals, thought to represent those from discrete settlement pulses, were traced throughout the sampling period. Distinct groups within the male (Table 3.1) and female YOY distributions were successfully separated out using MIX. All Chi-square values for goodness of fit were significant to the 90% level. These values represent maximum likelihood solutions. Moult increments calculated from means separated by MIX compared closely to those observed in the laboratory. Six settlement events were detected between June and late September. Although the small June settlement failed to persist beyond late August, it is estimated that these individuals would have undergone six moults from megalopae before the end of the growing season. Late September settlers had time for only one moult before winter. This disproportion in length of growing season between groups lead to the wide range of carapace sizes observed within the cohort, with surviving July settlers reaching mean carapace width of 4.4mm by November, while late September settlers reached only 1.7mm before winter. The largest surviving YOY group settled with a mean carapace width of 1.5mm, increasing to 4.4mm by the

Figure 3.5. Length-frequency distribution of young of the year *Pisidia longicornis*, Jun-Nov 1997.

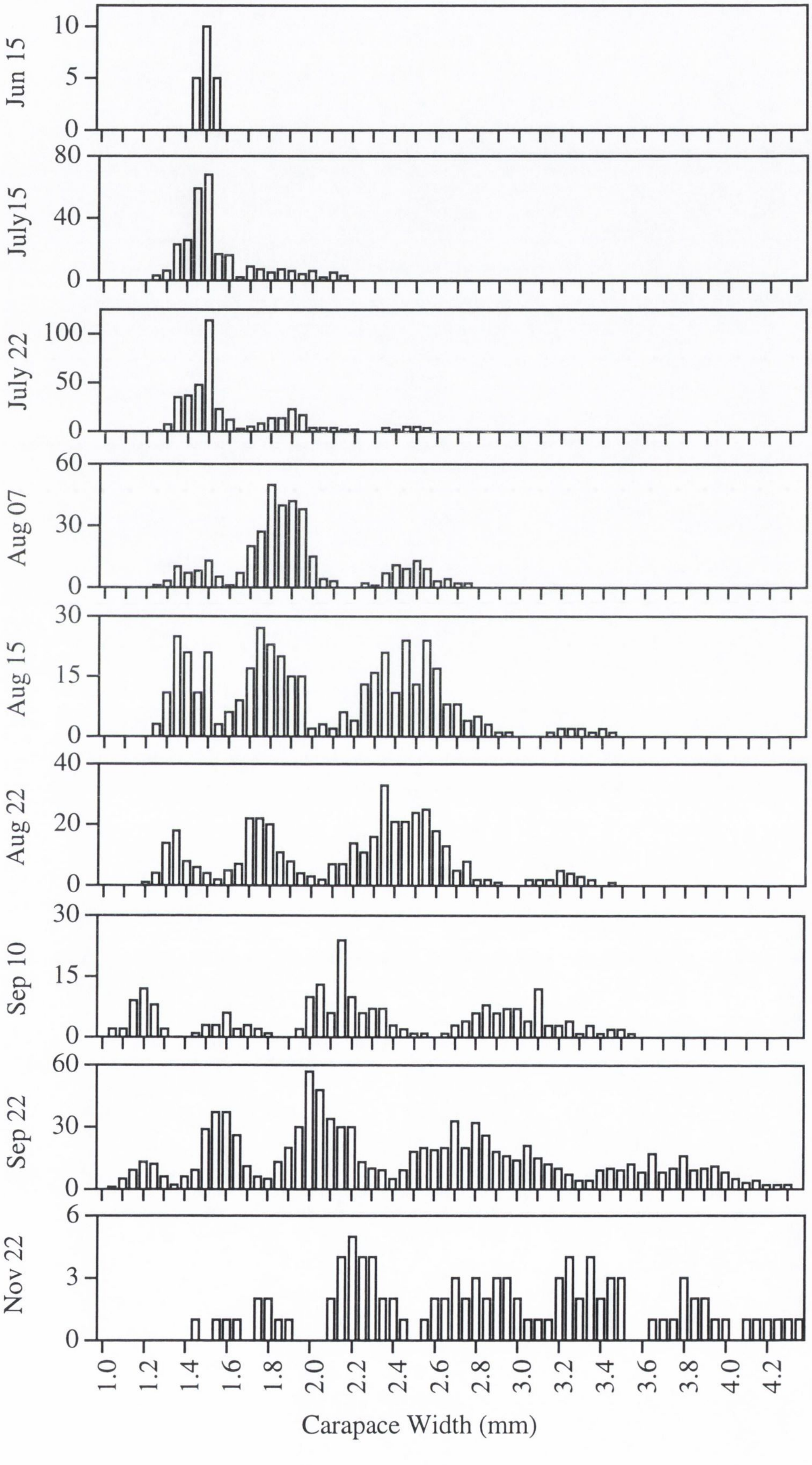


Table 3.1. Means (±SD) of normal components separated from male young of the year *Pisidia longicornis* length-frequency distributions using MIX. Numbered asterisk indicates successive linked means representing growth of distinct settlement groups.

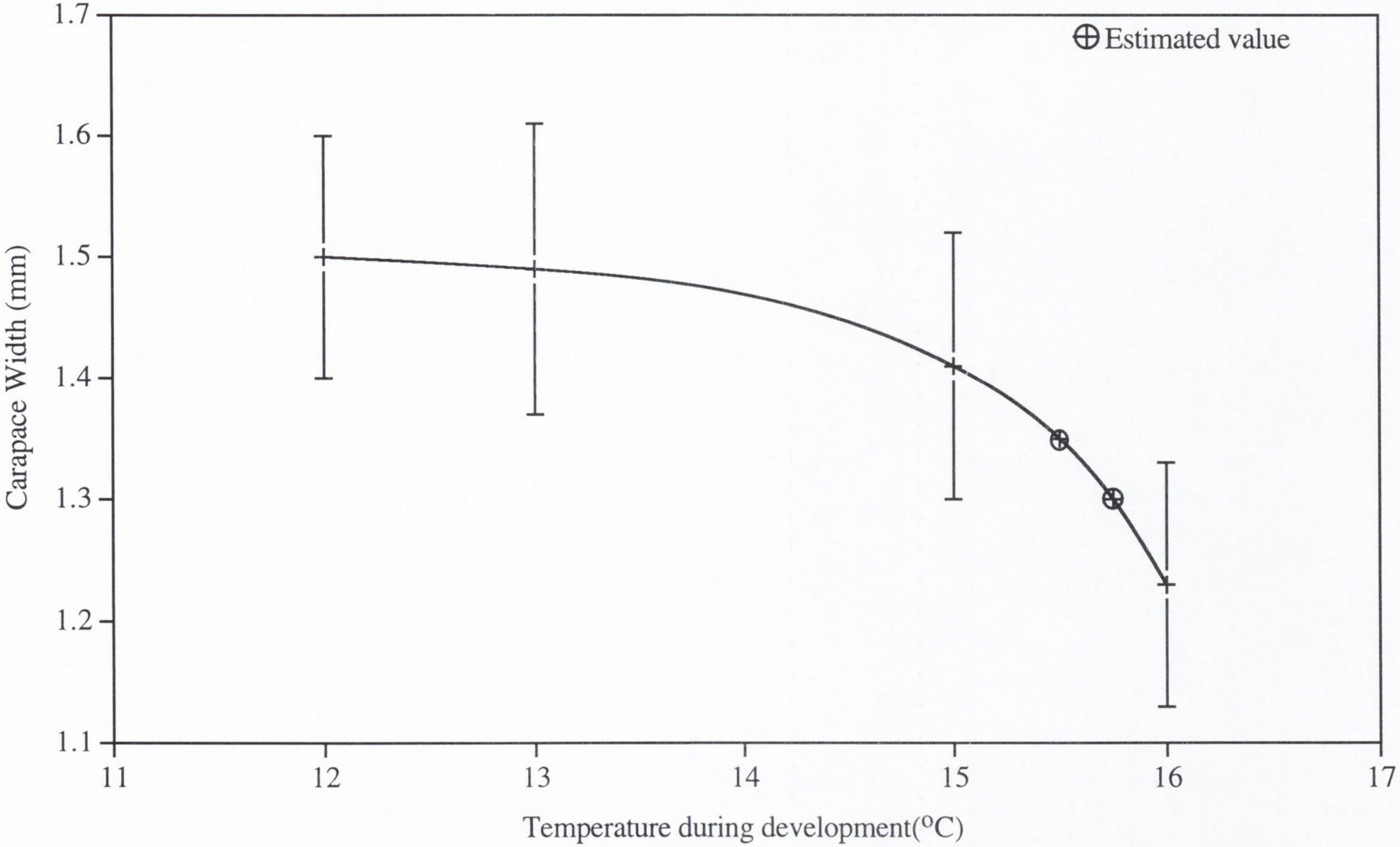
Date	Mean	SD	Group	Date	Mean	SD	Group
Jun-15	1.5	0.12	*1	Sep-10	1.23	0.11	*5
					1.64	0.10	*4
Jul-11	1.49	0.12	*2		2.18	0.15	*3
	1.89	0.24	*1		3.03	0.29	*2
Jul-22	1.5	0.12		Sep-22	1.60	0.24	*5
	1.93	0.12			2.10	0.12	*4
	2.45	0.16			2.80	0.29	*3
					3.76	0.27	*2
Aug-07	1.45	0.12					
	1.87	0.13	*2	Nov-22	1.71	0.17	*6
	2.51	0.14	*1		2.26	0.14	*5
					2.84	0.19	*4
Aug-15	1.41	0.11	*3		3.48	0.22	*3
	1.80	0.15			4.36	0.19	*2
	2.48	0.20					
	3.26	0.22		Estimated			
				Aug-29	1.74	N/A	*3
Aug-22	1.37	0.10		Aug-29	1.3	N/A	*4
	1.78	0.13		Sep-29	1.35	N/A	*6
	2.46	0.20	*2				
	3.25	0.12	*1				

end of November. The difference represented a 193% increase over a five month period, during which five moults took place. Individuals settling later in the season underwent fewer moults, with the late September settlers increasing only 21% in one moult before winter. Female distributions were almost identical to those of males with the exception of the July settlement group separated from the November distribution. YOY females were noticeably smaller than males in this group, with a mean carapace width of 3.9mm. The moult increment to this size from the previous instar was lower at 6%, representing the first moult from a pre-moult carapace width exceeding 3mm. Alternatively, the perceived increase in body size of this settlement group may represent sampling variability between dates when no growth occurred.

Temperature during larval development and size at settlement

There was evidence to suggest that temperature during larval development played an important role in determining body size at settlement (Figure 3.6). The mean (± SE) body size of newly settled groups decreased as the average daily temperature for the thirty days prior to settlement increased. Thirty days was chosen as an arbitrary value for larval development of *Pisidia*. Valdes & Alverez Osorio (1983) observed a development time of 26 days at 15.0°C in the laboratory. A mean carapace width of 1.5mm, corresponding to an average temp of 12.0°C, was recorded at the July settlement (Figure 3.6). This was significantly larger than 1.2mm recorded in early September, when temperature during development averaged 16.1°C. This difference in carapace width between groups at equivalent moult stages was reflected in subsequent juvenile instars and into the second year of growth, although it became less pronounced towards the end of the second growing season.

Figure 3.6. Relationship between mean size (±SD) of *Pisidia longicornis* at settlement and mean temperature (^oC) for 30 days prior to settlement, 1997.



Adult instars

Length-frequency histograms of adult male and female distributions contained mature adult individuals recruited in 1995 and immature, and possibly mature, individuals from 1996 (Figure 3.7). Means were successfully separated from male distributions only using MIX (Table 3.2). Values taken to represent instar growth are marked with a numbered asterisk in Table 3.2, the number corresponding to distinct groups identified earlier. All Chi-square values for goodness of fit were significant to the 90% level. These values represent maximum likelihood solutions. Seven groups were separated from male distributions between December 96 and April 97. Moulting first occurred between the samples taken in April and May. After this only five groups were detected, the four smallest of which persisted until the end of the study in November. In the 1997 juvenile group that appeared to be the equivalent of the July settlement group, mean carapace width increased from 4.2mm to 8.0mm between April and November. This represented a 92% increase in body size in six moults, over a seven month period. Due to a different pattern of growth, it was not possible to separate clear groups from female distributions. An area of doubt exists in the adult male distributions recorded in November as the total number of individuals taken was small. Sampling was conducted in heavy ground swell and only limited samples were taken in poor visibility. The resultant length-frequency distributions were fragmented but means were still separated. An increase in size was observed between late September and this time but the increments were small in relation to previous moults in the season. These small increments, 4-7% from largest to smallest group respectively, may represent an unusually small growth increment at the end of the growing season, which is unlikely in cooler temperatures (Figure 3.1), or merely

Figure 3.7. Length-frequency distribution of adult *Pisidia longicornis*, 1997. Female distributions are depicted on the top (positive) axis, with gravid individuals indicated in black. Male distributions are depicted on the bottom (negative) axis.

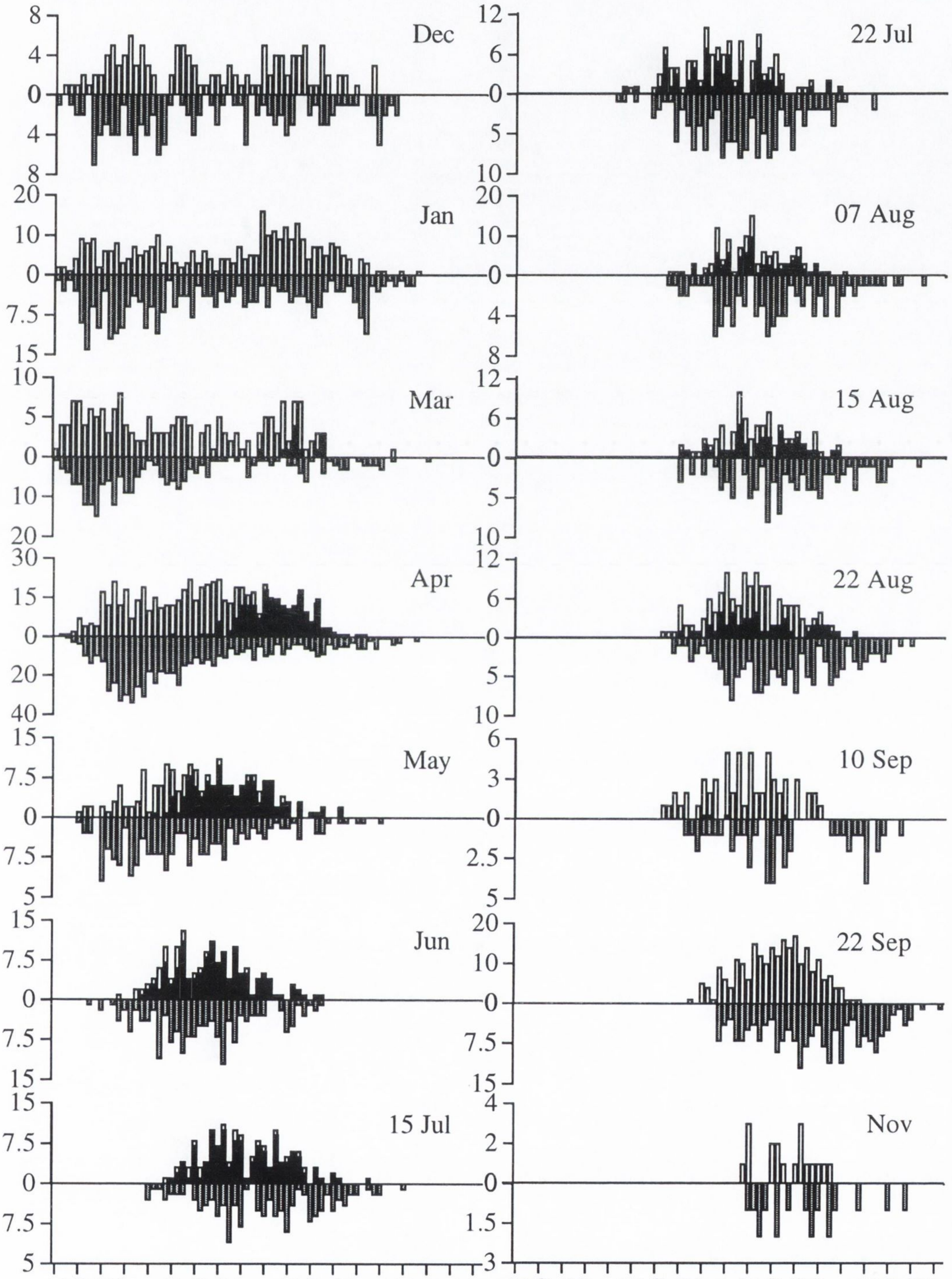


Table 3.2. Means (+SD) of normal components separated from adult male *Pisidia longicornis* length-frequency distributions using MIX. Numbered asterisk indicates successive linked means representing growth of distinct instar groups.

Date	Mean	SD	Group	Date	Mean	SD	Group
Dec-96	2.29	0.18	*1	Jul-11	3.47	0.26	*1
	2.82	0.17	*2		4.44	0.3	*2
	3.26	0.16			5.41	0.3	*3
	3.84	0.12	*3		6.23	0.29	*4
	4.24	0.12	*4		7.00	0.21	*5
	4.76	0.18	*5				
	6.00	0.25	*6	Jul-22	3.67	0.25	
	7.03	0.18	*7		4.53	0.24	
					5.31	0.30	
Jan-97	2.05	0.18	*1		6.14	0.26	
	2.56	0.18	*2		6.89	0.17	
	3.16	0.19					
	3.74	0.21	*3	Aug-07	4.38	0.16	*1
	4.32	0.27	*4		5.11	0.22	*2
	4.99	0.31	*5		5.89	0.21	
	5.84	0.25	*6		6.82	0.46	
	6.83	0.34	*7		7.83	0.13	
Mar-97	2.16	0.26	*1	Aug-15	4.48	0.16	
	2.78	0.16	*2		5.12	0.16	
	3.59	0.24	*3		5.83	0.31	
	4.14	0.11	*4		6.82	0.45	
	4.96	0.28	*5		7.81	0.12	
	5.78	0.15	*6				
	6.38	0.22		Aug-22	4.56	0.24	
	7.03	0.16	*7		5.20	0.18	
					6.00	0.40	*3
Apr-97	2.15	0.25	*1		6.91	0.23	*4
	2.79	0.42	*2		7.65	0.28	*5
	3.62	0.19	*3				
	4.17	0.29	*4	Sep-10	4.69	0.18	
	5.04	0.33	*5		5.44	0.27	*1
	6.09	0.38	*6		6.02	0.17	
	7.00	0.30	*7		7.44	0.29	
May-97	2.50	0.26	*1	Sep-22	5.48	0.32	
	3.20	0.21	*2		6.36	0.26	*2
	4.16	0.31	*3		7.02	0.23	*3
	4.91	0.27	*4		7.68	0.22	*4
	5.50	0.30	*5		8.25	0.21	*5
	6.14	0.36					
				Nov-22	5.84	0.23	*1
Jun-97	2.9	0.24	*1		6.79	0.24	*2
	3.33	0.12			7.42	0.08	*3
	3.72	0.19	*2		8.01	0.12	*4
	4.62	0.3	*3				
	5.62	0.15	*4				
Estimate	6.30	N/A	*5				

variation introduced by natural mortality or sampling effort, between dates when no growth occurred.

Growth

Growth of instar groups are represented by stepped links through separated means (± SE) in Figure 3.8. The vertical dashed line marks the break point where adult and YOY means, sampled during the same period, are joined. The vertical increase in progressing linked means represents the growth increment between successive instars. It was not possible to determine the exact point at which moulting occurred between sampling dates, and therefore the length of lines on the horizontal axis do not represent instar duration. Without the support of temperature development rate data for benthic stages it becomes difficult to accurately predict instar duration. Estimated von Bertalanffy parameters (± SE) were $L\infty=12.4mm \pm 2.5mm$, $K=0.503 \pm 0.158$, $C=1.0 \pm 0.1$ and $WP=0.06 \pm 0.02$. The winter point 0.06 indicated that growth was minimal during January. The value C=1 revealed strong seasonality in growth, with total suspension during part of the year. The bold central smoothed line, in Figure 3.8, represents the seasonalised von Bertalanffy growth curve derived from the parameters estimated using FISAT. The upper and lower lines represent growth curves one standard error from the central line.

Mortality

There was a linear decline in the densities of YOY male individuals from the June, July and late August settlements (Figure 3.9). The slope parameter derived for June settlement, taken to represent the instantaneous mortality rate, was significantly lower ($p=<0.05$) than those from the July and late August settlement. Variation

Figure 3.8. Instar growth pattern of *Pisidia longicornis*, 1997. Vertical dashed line separates groups within young of the year cohort (left) and adults (right) (N.B. Growth of the two groups actually occurred simultaneously). Stepped dotted lines, passing through linked means (±SE), represent growth of groups through progressive instars. Smoothed central line represents seasonalised von Bertalanffy growth curve. Upper and lower smoothed lines show standard error of estimated parameters. N.B. Stepped lines only indicate occurrence of growth and not instar duration.

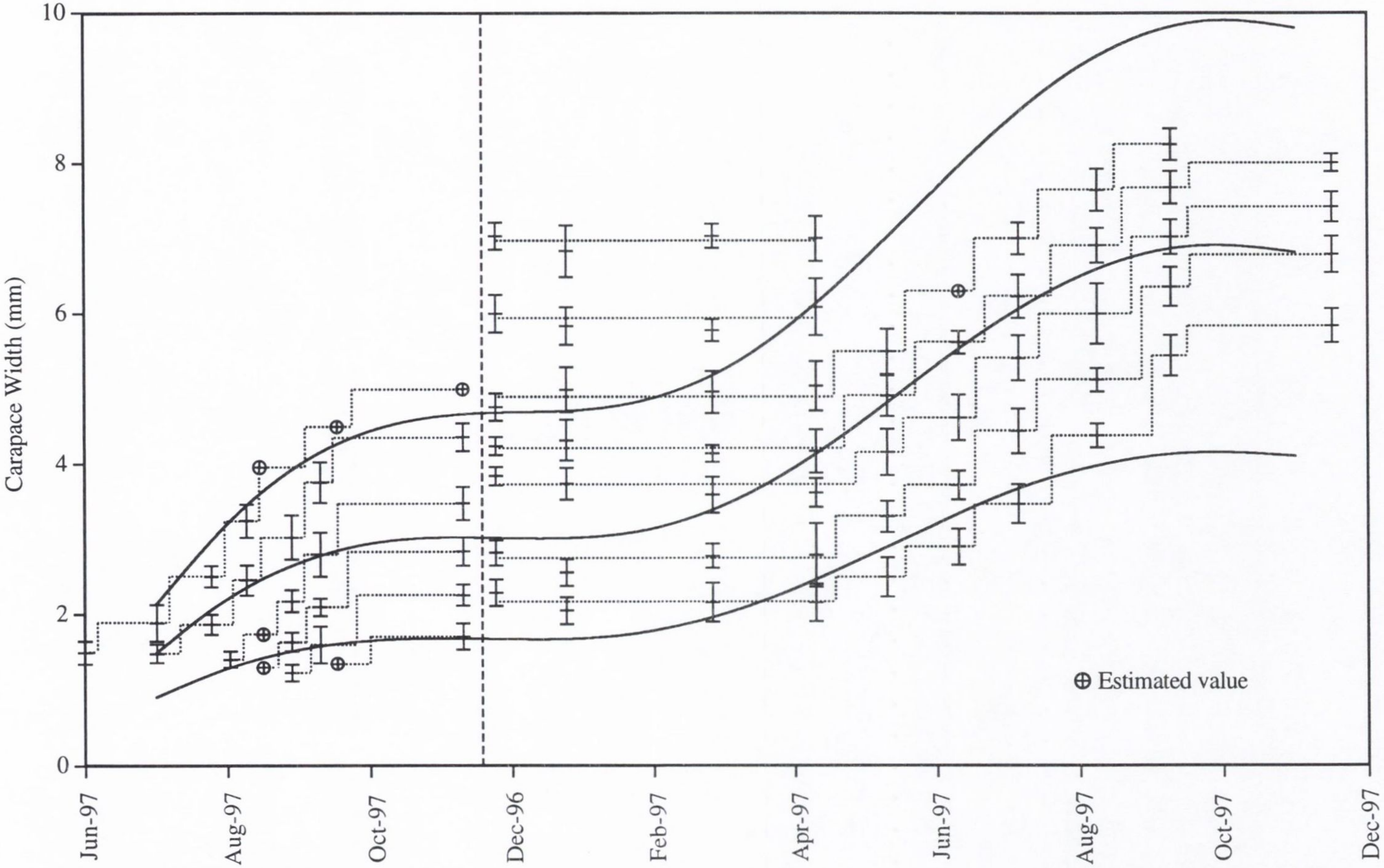
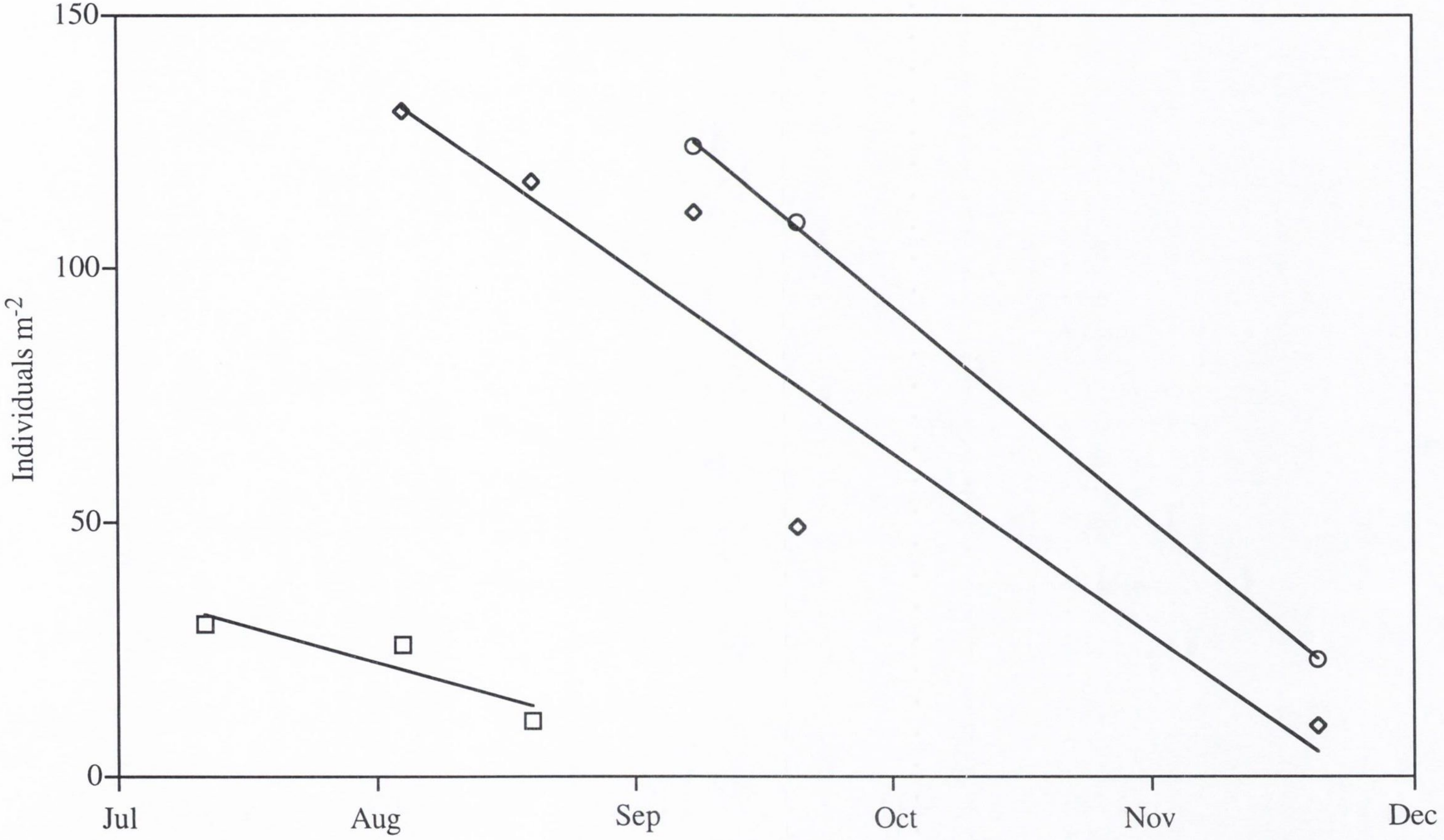


Figure 3.9. Decline in mean density of male individuals at each instar beyond the 1st crab stage in three distinct settlement groups of *Pisidia longicornis*, 1997.



between the mortality rates for July and August was not statistically significant, although this was mainly due to the high standard error associated with the July slope (Figure 3.9). Individuals settling in June, which developed in cooler waters, were larger than late August settlers (Figure 3.6). Numbers of adult individuals sampled within each instar were too small to accurately estimate mortality.

DISCUSSION

The densities of *Pisidia longicornis* observed during the course of the study were extremely high, exceeding those reported by Smaldon (1972) from sub-littoral depths. *Pisidia* was the most abundant decapod species within the benthic community throughout the study period. The density and biomass of all other decapod species sampled during the study were recorded (Chapter 2). Although small in size, the sheer number of individuals present often made the species the major component of crustacean biomass.

Planktonic stage II zoea larvae and megalopae were present in the area between May and September (Merin, 1998). Together with the continuous occurrence of gravid females between March and September, this would suggest that pulsed larval release is not the reason for the timing of the settlement events. The pulsed settlement observed, and the resultant size grouping within the cohort, is therefore most likely to be caused by settlement coinciding with periods of lowest tidal velocity. This may be an indication that higher near-bed current speeds inhibit settlement at other times (Eckman, 1983). This would imply that megalopae that develop in intervening periods postpone settlement until near bed current velocity declines. It is likely that mortality is significantly increased when the planktonic phase of development is prolonged.

Sampedro *et al.* (1997) recorded the occurrence of large numbers of gravid female *Pisidia longicornis* (>70% of females) for extended periods (Jan-Aug) in Northwest Spain. Smaldon (1972) observed a much shorter reproductive period between April and September in Wales, with >70% of females gravid between June and August. In the present study, females brooded between March and September, slightly earlier than the Welsh population. The highest proportions of ovigerous individuals (>69%) also occurred slightly earlier, between May and mid July. Wear (1974) observed an incubation period of approximately 30 days at 12-14°C for *Pisidia* in the laboratory. Multiple brooding was implied in the Spanish population of *Pisidia* inhabiting mussel rafts (Sampedro *et al.*, 1997). In the present study large females were gravid in March, before commencement of growth. It is likely that growth in these individuals is postponed until after they have released larvae. The subsequent reduction in numbers of large individuals would suggest that many females die at this point, while a few might moult, recover and possibly brood for a second time. If conditions allow, a limited number of larger females may persist into their third year, as seen in male distributions. These females probably represent the smaller individuals within the cohort, from later settlement groups. Smaldon (1972) stated that sub-littoral females from Oxwich Point were unlikely to survive into a third year due to high mortality during their second summer. Small females did not brood until growing to a carapace width exceeding 3mm. Although a large proportion of juvenile females had obtained this size by May, what appeared to be two or three of the smallest groups, had not. Assuming female size at maturity to be 3mm carapace width these individuals remained immature. Almost all individuals had moulted above 3mm carapace width by June, a period when incidence of brooding was high (86%). Smaldon (1972) only recorded gravid females with >3mm carapace width, and stated that spring growth probably represented the puberty moult for juveniles. The postponement of growth in larger individuals and the earlier growth and maturity of some juveniles lead to mixing of the cohorts in the present study. Blending of cohorts in this way confused interpretation of female length-frequency distributions and would inevitably have lead to large errors if attempts were made to separate components. Fluctuating recruitment and mixing of broods in both sexes has also hampered the use of length-frequency data for estimation of the growth parameters of penaeid shrimp (Pauly *et al.*, 1984).

Although developmental temperature was taken as an average daily figure from 30 days prior to settlement for all groups, the more rapid moulting of smaller individuals, at higher temperatures, would reduce the moult increment and the duration of larval development (Valdes & Alverez Osorio, 1983). The high temperatures of mid-August coincided with the recording of the smallest planktonic larvae in the area (Merin, pers. com.), contributing to the small size of early September settlers.

Length-frequency distributions of populations of *Pisidia* in South Wales were presented by Smaldon (1972), from littoral and sub-littoral environments. Seasonal anecdysis was observed in each population, with growth suspended between January and March. In the current study growth was not observed until April-May. The estimated winter point from the seasonalised von Bertalanffy growth function identified January as the month when no growth occurred. It was stated that the mean carapace width of immature crab (<3mm) in the Welsh population was observed to decrease in Aug-Sept, due to the settlement of megalopae. The clear gap maintained between YOY and adult distributions in this study made it possible to determine that all crabs settled prior to 1997 had obtained a carapace width greater than 3mm before July. Therefore, all crabs were presumed to be mature at this time, assuming males reached maturity before or at the same time as females. The apparent reduction or lack of growth in the female July settlement group may be due to maturation. These individuals had obtained a carapace width greater than 3mm, the size at female maturity. Somatic growth is reduced as a greater proportion of energy is invested in reproductive development (Hartnoll & Gould, 1988).

Assuming that appending adult distributions from 1997 to YOY of the same year offered an acceptable approximation to the normal growth progression through instars, then annual fluctuations in the number of settlement groups persisting in the population can be expected. For example, it appears that only two of the male groups that settled in 1995 persisted until December 96, while four settlement groups (1996 settlement) survived until November 97. Variability in environmental parameters are the most likely determinants of the survival of these older instar groups. Temperature is probably the most influential factor, affecting instar duration and moult increment, and therefore the time taken to reach maximum size. A persistent June settlement group may undergo eleven moults from time of settlement to death in the second year. This number is reduced in subsequent settlement groups that persist into a third year as they disappear in early summer before moulting to the larger sizes attained by earlier settlement groups. Therefore, in any one cohort some individuals might reach a maximum size and die within their second year, while others persist to contribute to production in the following year. The total number of settlement groups surviving or reaching maximum size in each year is probably dependent on the growth rate exhibited through the whole benthic life-cycle. In years with elevated temperature, or more prolonged periods with temperatures similar to those recorded in 1997, individuals may exhibit increased growth approximating more closely with the upper von Bertalanffy curve imposed on Figure 3.8. Similarly, growth in cooler years might be more accurately represented by the lower curve. Environmental factors are also likely to affect the number and survival of YOY settlement groups. It would appear that June 96 settlers may have survived into 97, while the 97 group did not persist beyond August. However, the late September settlement observed in 1997 did not survive or occur in 1996. The number and timing of settlement groups would depend on the tidal regime of that year.

Mortality of almost all decapod crustacean fauna was observed in depths to 7m immediately after violent storms in February. Burial of equipment left on the seabed, by approximately 75mm, would suggest that the substrate was very mobile during this period. The carcasses of many crustacean species were observed the following week. A gradual and full re-colonisation was observed over the following 2 months. Stochastic factors, such as storm events, can strongly influence the population structure, behaviour and survival of benthic communities (Reiswig, 1971; Pile *et al.*, 1996). Disturbance of the benthos and the resident communities by heavy ground swells can be common in exposed shallow waters. Disturbance events such as these may effect the longevity and number of groups within a cohort, especially if occurring during the settlement season.

The linear nature of the decline in YOY densities is an indication that density independent processes determine early mortality rates. Density independent processes, such as temperature, are more readily identified as influences on larval life history. Density dependent processes are believed to mediate the juvenile and adult components in a population (Phillips, 1990; Lipcus & Cobb, 1994; Pile *et al.*, 1996). It is impossible to determine exactly which process(es) most strongly influences mortality in the present study. It must be appreciated that the data presented is limited, and further examination of mortality is warranted before firm conclusions are made. The increase in mortality rate observed between June and August coincided with rising temperature and decrease in body size at settlement. Instar duration was shorter as temperature increased, possibly leading to higher mortality of smaller individuals. Survival may be directly related to size at settlement, with smaller size predisposing individuals to higher rates of mortality. Alternatively, predator activity may have increased with rising temperature. Predation of early benthic crab stages is probably curtailed both by *Pisidia*'s cryptic nature, and its preference for crevices and under-surfaces as habitat. Mortality is likely to be predominantly controlled by density dependent processes during the second year, when individuals are larger and less susceptible to variation in stochastic factors. Due to the small size and habitat requirements of *Pisidia*, immigration and emigration were considered negligible.

The maximum size of males observed during the study was significantly lower than that predicted by the seasonalised von Bertalanffy (VB) growth function. This was due to the VB function estimating growth continuing into a fourth year, based on the decay of growth increment observed. Somatic growth is generally expected to be reduced in older females, as a greater proportion of energy is invested in reproductive output (Hartnoll & Gould, 1988). This is often applicable to more long-lived species studied on a yearly basis. However, when the instar growth of short-lived species, such as *Pisidia*, is observed under the influence of oscillating temperature misinterpretations can occur. In this case the instar duration and growth increment remain high, although reduced, in the second year of growth leading to overestimation of maximum size. The use of the von Bertalanffy growth function may not be totally appropriate for short lived, cold water species. However this does not strongly influence the form of the growth curves presented. Smaldon (1972) did not observe individuals larger than those in the current study. The increase in size of both adult and YOY *Pisidia* over the entire growing season was substantial. It is possibly the large variation in the growth of YOY individuals that lead to Smaldon (1972) stating that after 1 year mean carapace widths of immature crabs had increased by up to 1.9mm. This appears to be an underestimation of the growth potential of *Pisidia,* that increased well above 3mm carapace width during the first year of growth in this study.

Numerous decapod species were collected during the course of sampling, including YOY, juvenile and adult stages of commercially exploited species, such as *Necora puber* (L.) and *Cancer pagurus*. New and informative data has become available pertaining to their often poorly understood early benthic life histories (Robinson & Tully, 1998b). Suction sampling *in situ* proved an efficient method of sampling all sizes of *Pisidia longicornis* from sub-tidal benthic habitats. There is excellent potential for combination of this method with settlement collectors (Beninger *et al.*, 1986) to investigate further the settlement, growth and mortality of numerous crustacean species. Settlement collectors and more frequent sampling would provide new information regarding moult duration, mortality and settlement rates. If small scale projects such as this study can be expanded it would be possible to gather vast amounts of novel information relating to the population dynamics and ecology of early life stages of many species. These methods can also be used to provide an index of recruitment success and its inter-annual and spatial variability. If correlated with fisheries performance, using an appropriate time lag, these indices can be a valuable stock forecasting tool in commercially exploited species. Recruitment indices and forecasting methods have been developed for the Australian western rock lobster, *Panulirus cygnus* George (Phillips & Brown, 1989), and the American lobster, *Homarus americanus* Milne Edwards (Incze & Wahle, 1991).

CHAPTER 4

MORTALITY AND DISPERSAL IN A BENTHIC SUB-TIDAL DECAPOD COMMUNITY AND OF HATCHERY REARED LOBSTER, *HOMARUS GAMMARUS*.

ABSTRACT

Depletion of decapod stocks has lead to a number of stock restoration programs in northern Europe. One such method utilised for the enhancement of European lobster *Homarus gammarus* (L.) involves the release of hatchery-reared juveniles onto the seabed. Due to the scarcity of data pertaining to the habitat requirements of wild juvenile *H. gammarus*, stage V hatchery reared lobsters are commonly released into habitats similar in characteristics to those occupied by adults. The fate of hatchery-reared lobster, and their effect on the decapod communities resident in the release areas is unclear. Certain release methodologies result in localised, short-term high densities of juvenile lobster. Juvenile lobsters were released at high density into enclosed and unconfined experimental plots containing existing wild fauna within a commonly utilised release ground. Twelve percent of the initial seeded lobsters were recovered from enclosures after one month, compared to a one percent recovery from unconfined plots. Overall density at the end of the experiment, 4.8 individuals m^{-2}, may represent a rough approximation to the saturation density of juvenile *H. gammarus*, although wild densities are unlikely to reach this level. Assuming that enclosure had no affect on any species the presence of juvenile lobsters reduced the abundance of young of the year porcellanid crab *Pisidia longicornis* (L.), but did not affect any other species, or community structure as a whole.

INTRODUCTION

Regulation of benthic marine populations is generally believed to be under density dependent control. The processes regulating the population, including cannibalism, predation and migration, can significantly affect initial settlement patterns, and alter subsequent abundance and community structure (Roughgarden *et al*, 1988; Eggleston & Armstrong, 1995; Lovrich & Sainte-Marie, 1997). These processes can often be difficult to detect and quantify in patchily distributed (Hassell, 1987) or mobile species (Moksnes *et al.*, 1997). Patchiness in larval supply to the benthos (which is often determined by physical processes) or saturation of suitable nursery habitat can result in strong spatial heterogeneity in benthic recruitment and crowding (Iribarne *et al.*, 1994; Wahle & Incze, 1997; Moksnes *et al*, 1998). Individuals may become increasingly subject to crowding and antagonistic interactions as they grow, and be forced to move from the initial settlement site (Wahle & Incze, 1997). Physical interactions between conspecifics have been shown to strongly affect crab density (Iribarne *et al.*, 1994). The ability of mobile decapod species to disperse can significantly reduce losses due to cannibalism and predation (Iribarne *et al.*, 1994; Lawton & Lavalli, 1995). These sources of mortality may therefore be greater in less mobile species that do not have other adaptations to reduce their effect (Jensen, 1991).

Over fishing and the resultant population depletion in some species of decapod has lead to the development of technical measures to restore spawning stocks (Bennett, 1980; Bannister & Addison, 1998). Several methods have been utilised in Ireland to enhance, restore or conserve stocks of the European lobster, *Homarus gammarus* (L.), including release of hatchery-reared lobster, minimum body-size catch restrictions, and conferring protection on brood-stock by V-notching. In the first method, hatchery reared lobster are grown to development stage five or beyond (Mercer & Brown, 1994) and released onto the seabed (Addison & Bannister, 1994), in an attempt to avoid the high larval mortality in the water column and high postlarval mortality rates experienced by recently settled decapod larvae (Moksnes *et al.*, 1998). Previous studies have perfected release methodology, ensuring that juveniles are delivered safely to the benthos and quickly find suitable shelter (Bannister, 1995; Cook, 1995). Release into the Co. Wexford fishery in Ireland has utilised commercial crab or lobster pots used in the inshore fishery. High densities of individuals, each confined within a small plastic cell covered by fine paper, are placed in pots before they are deployed. The crab pot mesh is of a size that does not restrict juvenile movement, while affording some localised shelter from benthic and demersal predators. The fine paper dissolves 10-20 minutes after reaching the seabed and juveniles emerge and seek shelter, creating a localised artificially high density of individuals. In late June 1997, the authors released 200 hatchery-reared lobster into a $5m^2$ sub-tidal cobble area. Suction sampling of the release plots and some of the surrounding area 3 weeks later recovered only one juvenile lobster (unpublished data). No quantitative data exists as to the fate of released lobsters, and the numbers that survive even the initial weeks after release or subsequently recruit to the fishery is unknown (Walker, 1986; Bannister *et al.*, 1994; Bannister & Addison, 1998).

Considering its commercial importance, little is known of the early benthic phase life history of *Homarus gammarus*. The preferred habitat of wild juvenile individuals is unknown, so release onto grounds that support adults of the species is the accepted compromise. Previous studies have failed to discover and catalogue the occurrence of juvenile *H.gammarus* in the adult habitat. This has lead to the conclusion that either juvenile lobsters occur in such low densities that their detection becomes extremely difficult, or that juvenile habitat requirements differ from those of the adult (Howard & Bennett, 1979). The former hypothesis may be supported by continued failure to detect juveniles in the adult habitat even after a number of independent surveys have been conducted towards locating juveniles in recent years (Howard & Bennett, 1979; Anon, 1997; Chapter 2; Wahle, pers. coms.). If the second proposal is true then juvenile release has been directed towards habitats with sub-optimal characteristics. This may have an adverse effect on the survival and growth of both the lobsters and the decapod fauna present in these areas. The aim of the present study was to examine the role of dispersal as opposed to mortality on a rocky sub-tidal decapod community and on the known decline in abundance of hatchery-reared lobsters that occurs after release. The results provide further insight into the early recruitment dynamics of the decapod crustacea of sub-tidal cobble habitats, while evaluating the potential value of juvenile lobster release to augment natural stocks.

MATERIALS AND METHODS

Study location

The experiment was conducted in the Saltees Sound, Co. Wexford, Ireland, during 1997. The substrate in the locality of the experimental enclosures consisted of coarse sand and shell material, covered by a dense layer of cobble and boulder. Algal species of the genus *Laminaria* formed a canopy over approximately 70-80% of the area. Tidal velocity in the Sound is relatively high, preventing sedimentation of enclosures. An extreme low water chart depth of 4m is specified for the study site.

Experimental enclosures

Experimental enclosures consisted of a weighted 0.5 x 0.5m plastic pipe frame, covered with 2mm mesh to prevent escape of species under the side skirting

(Figure 4.1). A 200mm high mesh (2mm) skirt was attached around the edge of the base, and the top joined to another air-filled plastic frame of identical dimensions to the base. The slightly buoyant top frame, which was affixed with a mesh lid to seal the enclosure, prevented the skirt edge from collapsing. Enclosures were deployed at the site approximately two weeks prior to commencement of the experiment, allowing natural biofilms to establish.

In mid July, enclosures were positioned randomly within a localised area of approximately 8m^2. Divers used an air-lift suction sampler to collect sediment and fauna from a randomly selected 0.25m^2 area in the vicinity of each enclosure. Collection bags were constructed from 1mm mesh. All fauna and sediment was then carefully tipped into the enclosure. Each enclosure was then seeded with ten stage V hatchery-reared lobster, *Homarus gammarus*, and sealed using cable ties and draw-strings. A 0.25m^2 area was pegged out 0.5m from the edge of each enclosure, by hammering coloured pins into the substrate (Figure 4.1). These areas were not altered or enclosed in any other way. Ten stage V juvenile lobsters were then released onto each of these control patches. In order to quantify mortality of decapods due to the sampling procedure a number of further suction samples were taken in the area, away from experimental plots, and lifted to the surface. The contents were emptied into sorting trays and the mortality of species recorded. Less that 5% of individuals were moribund at this time. Specimens of numerous species that were transplanted into seawater aquaria survived for longer than the duration of the experiment.

After one month the contents of the enclosures and control patches were recovered by suction sampling. In the laboratory, samples were sieved whilst submerged in seawater and all fauna removed. Decapod crustacea were fixed in 5% formalin and preserved in alcohol. Maximum carapace width of larger specimens (>3.0mm) was recorded to 0.1mm using digital callipers. Individuals smaller than 3.0mm were sized to the nearest 0.1mm, using a binocular microscope micrometer.

Data analysis

Length-frequency histograms were constructed for each of the species sampled. When numbers of individuals were sufficient clear gaps appeared in the distributions, distinguishing young of the year (YOY) from other individuals. Length-frequency data from a parallel survey conducted throughout 1997 were used as a guide when constructing histograms (Chapter 2). Although the term 'adult' is used in this study when referring to individuals settled prior to 1997, some of these individuals were still immature juveniles.

The densities of 1st crab stage individuals of a number of species were used to assess whether the mesh prevented or reduced settlement into experimental enclosures. These individuals were determined to have settled after deployment of the enclosures by referring to the length-frequency histograms constructed from the parallel survey mentioned above. The size ranges of the 1st crab stage of four of the more abundant species in the area were identified using MIX 2.3 (MacDonald & Green, 1988). This procedure isolated normal distributions, representing successive instars, from the composite length-frequency histograms. The number of 1st stage individuals in each enclosure and control, for *Cancer pagurus* L., *Galathea squamifera* Leach, *Necora puber* (L.) and *Pisidia longicornis* (L.), was determined. The significance of any differences between enclosures and controls were tested using a paired t-test. Neighbouring enclosures and controls were paired due to the small-scale patchy nature of settlement in the area (Robinson & Tully, 1998b; Robinson & Tully, in press b).

The abundance and number of species of YOY and adult individuals present in controls and enclosures were compared using paired t-test. Due to the numerical dominance of the species *Pisidia longicornis* in the YOY component, the test was repeated after removal of the species. The community structure of the YOY and adult components within enclosures and controls was compared using the computer package Primer© (Clarke & Warwick, 1994). The routine CLUSTER was used to construct a matrix of Euclidean dissimilarities, and the significance tested using ANOSIM. This routine computes the average dissimilarity between enclosures and compares it to the dissimilarity between controls. Only species that represented 4% of the YOY or adult component of the population in any one sample were included in the data matrix. Data was double route transformed to reduce the influence of dominant species.

RESULTS

All lobsters were observed to find shelter within several minutes of release. Encounters between individuals on the surface of the substrate often resulted in a 'tail-flick' avoidance response by one or both lobsters. This led to some individuals crossing the perimeter of control patches almost immediately, while enclosed lobsters were restrained by the mesh skirting. 'Tail-flick' responses were short in duration and were always succeeded by a rapid return to shelter seeking.

Although some fouling of the mesh, mainly by ascidians, had occurred by the end of the experiment, there were no obvious signs of major obstruction or sedimentation around the enclosures. Examination of the overall structural integrity of enclosures showed no evidence of wear that could have compromised the retention of individuals. A total of 25 species were encountered in the samples as a whole, ranging from single individuals to high densities in all enclosures and controls (Table 4.1). The total number of species per enclosure varied between 9-15 species $0.25m^{-2}$. Overall abundance ranged between 58-210 individuals $0.25m^{-2}$, with YOY densities between 50-169 individuals $0.25m^{-2}$ and adults 6-80 individuals $0.25m^{-2}$. *Homarus gammarus* were recovered from 8 of the 10 enclosures. A total of twelve lobsters were recovered, with 4 enclosures containing 2 individuals and the remaining 4 a single specimen (Table 4.1). This represented a 12% recovery of the original numbers. A single lobster was recovered from all control (unenclosed) plots combined, representing a 1% recovery.

There were no statistically significant differences (5% level) between the level of recent settlement (1st crab stage) into paired enclosures and controls for the four species examined. No significant differences existed between the abundance or number of species represented by the adult component between enclosures and controls, or the number of species in the YOY component. There was a significant difference ($p=0.03$) in the abundance of YOY individuals between enclosures and controls when the numerically dominant species *Pisidia longicornis* was included in the analysis. No significant differences ($p=0.84$) were detected with *Pisidia* removed. A comparison of the numbers of *Pisidia* in each of the four YOY instars present revealed increasing differences in densities between enclosures and controls with

Table 4.1. Occurrence of young of the year (YOY) and adult (Ad.) decapod individuals recovered from paired enclosures (E) and controls (C) after one month in a rocky sub-tidal habitat.

	E1	E1	C1	C1	E2	E2	C2	C2	E3	E3	C3	C3	E4	E4	C4	C4	E5	E5	C5	C5	E6	E6	C6	C6	E7	E7	C7	C7	E8	E8	C8	C8	E9	E9	C9	C9	E10	E10	C10	C10
Species	yoy	Ad.	yoy	Ad.	yoy	Ad.	yoy	Ad.	yoy	Ad.	yoy	Ad.	yoy	Ad.	yoy	Ad.	yoy	Ad.	yoy	Ad.	yoy	Ad.	yoy	Ad.	yoy	Ad.	yoy	Ad.	yoy	Ad.	yoy	Ad.	yoy	Ad.	yoy	Ad.	yoy	Ad.	yoy	Ad.
Achaeus cranchii	0	0	1	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Anapagurus hyndmanni	1	0	2	0	5	0	1	0	1	0	0	1	2	1	6	2	3	0	5	0	1	1	3	2	5	2	1	0	7	0	1	0	5	0	2	0	3	0	2	1
Athanas nitescens	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Cancer pagurus	1	2	2	1	7	4	2	3	2	1	0	0	2	2	3	1	1	3	2	1	0	0	3	0	1	1	4	3	5	3	3	1	5	0	6	2	4	2	3	3
Caridion gorgoni	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Eurynome aspera	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Eurynome spinosa	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Galathea intermedia	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	1	0	0
Galathea squamifera	4	0	3	0	1	0	4	1	1	0	3	2	5	1	7	0	1	0	3	1	4	0	5	0	4	1	9	0	3	0	2	0	2	0	5	2	3	1	4	2
Hippolyte varians	3	0	1	0	2	0	0	0	0	0	1	0	10	0	2	0	1	0	6	0	5	0	4	0	17	0	10	0	4	0	1	0	4	0	5	0	4	0	3	0
Homarus gammarus	2	0	0	0	1	0	1	0	2	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0	2	0	0	0	0	0	0	0	1	0	0	0	2	0	0	0
Inachus leptochirus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
Inachus phalangium	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
Liocarcinus pusillus	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0
Necora puber	2	0	2	0	5	0	1	0	1	1	1	0	1	0	4	1	1	0	4	0	2	0	6	0	0	0	2	0	3	0	8	0	2	0	3	0	5	1	1	0
Pagurus bernhardus	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	2	1	0	0	0	0	0	0	0	4	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0
Pagurus cuanensis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pilumnus hirtellus	0	2	0	1	0	1	0	1	0	0	0	2	0	1	0	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	3	1	1	0	0
Pirimela denticulata	0	0	1	0	2	0	0	3	1	0	0	0	2	0	0	0	0	0	0	0	3	4	3	1	1	0	2	4	2	0	2	1	1	0	0	0	1	0	1	1
Pisidia longicornis	75	29	112	10	91	29	118	42	42	4	37	24	57	39	123	24	58	28	130	18	43	14	105	17	67	28	93	50	119	30	135	27	44	35	80	66	104	32	78	15
Pontophilus fasciatus	1	0	1	0	5	0	1	0	0	0	1	0	0	0	1	0	0	0	1	0	6	0	2	0	0	0	4	0	0	0	0	0	0	0	5	0	4	0	4	0
Porcellana platycheles	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Processa canaliculata	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Thoralus cranchii	14	1	18	5	16	1	8	0	2	0	7	1	31	2	16	0	4	0	9	2	2	0	4	1	11	1	15	0	13	0	16	3	3	0	24	3	7	0	6	2
Xantho pilipes	0	0	0	3	0	2	0	1	0	0	0	0	0	3	0	2	0	1	0	0	0	0	0	1	0	2	0	1	0	1	0	3	0	1	0	3	0	2	0	1

successive instar. There were 19% more 1st crab stage individuals from all controls combined compared to enclosures. This disparity increased progressively between the 2nd, 3rd and 4th instars to 39%, 64% and 123% respectively. There were no significant differences in community structure between the control and enclosure treatments for either the YOY or adult components of the population.

DISCUSSION

The only noticeable effect of the addition of lobster on the rest of the community, assuming the enclosures had no effect, appeared to be the reduction in the overall abundance of *Pisidia longicornis*, although this was not significant between paired treatments for the 1st crab stage. A single or combination of several factors may have accounted for the reduction in numbers of this species. Firstly, initial sampling and transplantation into enclosures may have resulted in mortality of this relatively small crab. This seems unlikely when considering the low mortality observed in test samples, and the reduction in overall numbers between the 1st and 2nd instar groups. These two groups settled into the established enclosures at some point after the disturbance at the start of the experiment, but overall numbers were still lower. From the increasing inequality between overall densities of *Pisidia* in enclosures and controls across all instars, it seems likely that an increased mortality rate was responsible, rather than a reduction in numbers caused by experimental manipulation. The mortality rate of early benthic phase *Pisidia* has been shown to be a density independent linear function for the first summers growth (Robinson & Tully, in press a). It is possible that the rate of mortality is controlled in part by the species ability to disperse, although as a filter feeder cannibalism plays no active role. The influence of confinement could increase with subsequent growth if the saturation density of the species is assumed to be a declining function of body size. Some species of porcelain crab are known to settle gregariously in response to adults, seeking shelter underneath larger specimens immediately after settlement. The adults appear to tolerate this for some time after settlement until the younger crab becomes too large and moves into its own space (Jensen, 1991). Wahle & Incze (1997) suggested that the American lobster, *Homarus americanus* Milne Edwards, could become subject to increased crowding as they grow, leading to a need to move from the initial settlement site. The physical presence of the enclosures may have reduced the availability of particulate food for *Pisidia*, leading to increased mortality, although this may be contradicted by the even settlement of 1st stage crab into paired treatments. Alternatively, the presence of boundaries may have reduced the foraging area of other species, including *Homarus*, concentrating disturbance or predation of *Pisidia*, which represents a food source for several decapod species (Friere & González-Gurriarán, 1995; pers obs.). Due to the duration of the experiment, whatever process was active in the progressive inequality in YOY abundance of *Pisidia* with increasing moult stage would have had more time to impact on older YOY individuals.

The absence of other detectable effect on the established population indicates that movement has little effect on these species in the short term. Post-settlement movements however, are known to regulate population density (Moksnes, 1999). It is possible that enclosure may have lead to deterioration of the population over longer periods of time. The experiment was conducted at a time when productivity was high, reducing competition for available food. The study area represents an important nursery area, supporting high densities of numerous species (Chapter 2). The benefits of dispersal, from physically complex sites affording many spatial refuges, may become of limited benefit when conspecifics and other species occupy all surrounding areas. The apparent low level of dispersal for most species may indicate that their saturation density has not been reached. The influence of dispersal may become less important for species below saturation density resident in physically complex habitats with a plentiful food supply.

The initial seeding density of *Homarus gammarus* was by far in excess of that which could be expected for wild lobster, although this cannot be confirmed due to lack of knowledge pertaining to the early life history of the species. Wahle & Incze (1997) observed unconfined seeded *Homarus americanus* density to fall from a mean of 24 individuals m^{-2} to 5.3 individuals m^{-2} only 24h after release. The mean density of lobsters recovered after 1 month in this study was equivalent to 4.8 individuals m^{-2}. It is possible that the high seeding densities used in this study, which approximate to those occurring immediately after release when crab pots are used, combined with enclosure may have forced resultant densities below the level of the natural carrying capacity for this species. This would have implications for technical measures that increased larval supply to a level beyond the carrying capacity of the settlement habitat available. A number of sources would have contributed to the overall high mortality observed in the enclosures, including predation and cannibalism. Antagonistic interactions and cannibalism between *Homarus* conspecifics are commonly observed in artificially confined conditions (O'Neill & Cobb, 1979). It seems reasonable to assume that the frequency of interactions between conspecifics declined more rapidly in control plots as juveniles dispersed freely. However, overall survival of these free individuals may not have been higher as they were presumably vulnerable to more predators, including benthic and pelagic fish species, which could not gain access to enclosures. Assuming that the enclosure had no effect on the survival of juvenile lobster the results of this experiment suggested that 88% of the observed decline in abundance of lobsters after release was due to mortality and 11% to dispersal from the release site. Further experimentation should be directed towards quantifying the trade-off between dispersal and mortality for this species.

The density of *Homarus gammarus* remaining in enclosures after one month were similar to the saturation levels of new recruits suggested by Wahle & Incze (1997) (5.7 individuals m^{-2}) for unconfined *Homarus americanus* in dense cobble habitats. It is unclear whether the saturation density of *H. gammarus* would be lower in unconfined areas as the nursery habitat of this species has not been discovered to date. Densities of YOY European lobsters are probably lower than that of American populations when considering the more diverse array and frequent occurrence of predatory species acting on the former (pers. obs.). Mortality of released lobster can be expected to be high initially, reducing rapidly with time as individuals increase in size. The numbers of *H. gammarus* juveniles surviving to recruit to the adult fishery remains unclear. Although the habitat examined here, comparable to the dense cobble described by Wahle & Incze (1997) (pers. obs.), appears to represent a suitable nursery habitat for short-term survival of juvenile European lobster, its suitability relative to the habitat requirements of wild individuals is unknown.

CHAPTER 5

SETTLEMENT, GROWTH AND MORTALITY OF EARLY BENTHIC PHASE EDIBLE CRAB, *CANCER PAGURUS*.

ABSTRACT

In northern Europe, the edible crab *Cancer pagurus* L. contributes significantly to shellfish landings. Little is known of the early benthic life history of this species. Divers conducted field surveys on the Southeast coast of Ireland throughout 1997 to examine settlement, abundance and early post-settlement processes affecting *Cancer* in a rocky sub-tidal habitat. *Cancer* settled between June and late September, with highest mean density, 25 individuals m^{-2}, recorded in late August. Maximum density of first stage benthic juveniles occurred between late July and early August. The number of first stage crab decreased after this period, and there was an increase in abundance of crabs in subsequent size classes and high mortality. Young of the year *Cancer* attained a carapace width between 5-8mm before their first winter. Surveys of other shallow water habitats during 1998 revealed variable density of both the young of the year cohort and individuals settled in previous years. Abundance of *Cancer* was higher in more physically complex habitats with algal coverage. Growth in aquaria was not significantly different to that in the field. Growth of individuals held in isolation was similar to individuals held with conspecifics at the average maximum density recorded in the field (24 individuals m^{-2}). The presence of larger conspecifics did not affect the survival or growth of smaller sized crabs.

INTRODUCTION

The abundance of juvenile benthic crabs is influenced both by larval supply and post-settlement processes. Cohort strength in decapod crustaceans may be determined early in the life history. Density dependent mortality may operate at this stage either through intra-specific or inter-specific competition. Little is known about the substrate specificity of postlarvae, timing and magnitude of settlement or the processes controlling recruitment into benthic habitats for the commercially exploited species *Cancer pagurus* L. *Cancer* contributes significantly to both shellfish landings and export in Ireland, Britain and France (Anon, 1998; Anon, 1999). Utilisation of the species has increased in recent years with the development of offshore fisheries (Anon, 1998).

Recent studies have highlighted the importance of intra-specific interactions in regulating the survival (Moksnes *et al.*, 1998), dispersal (Iribarne *et al.*, 1994) and growth (Carlberg *et al.*, 1979; Wahle, unpublished data) of early benthic phase decapods. The abundance of previously settled conspecifics in densely populated or space/resource limited nursery habitats, and hence the level of interaction with newly settled individuals, is believed to represent a source of population self-regulation (Moksnes *et al.*, 1998; Moksnes, 1999). Dispersal is believed to play an important role in reducing inter-specific and intra-specific competition (Iribarne *et al.*, 1994). Avoidance of conspecifics and other species may become vitally important when considering the high density of individuals resident in shallow water rocky nursery habitats. There is some experimental evidence to suggest that in densely populated areas the presence of conspecifics can reduce overall growth rate (Carlberg *et al.*, 1979). This is believed to be caused by either a physically (Cobb & Tamm, 1974) or chemically (Nelson *et al.*, 1980) mediated suppression of the metabolism and growth potential of smaller bodied individuals that are in close proximity to larger conspecifics (O'Donovan, 1998).

This chapter presents data on monthly changes in density of early crab stages of *Cancer pagurus* in shallow sub-littoral cobble habitats. Settlement of individuals into distinct habitat types is examined and related to densities in subsequent years. Growth is examined in the laboratory in isolation and in the presence of conspecifics. The results present novel information pertaining to the early benthic life history of this commercially valuable species.

MATERIALS AND METHODS

Temporal data set

Early benthic phase *Cancer pagurus* juveniles were collected, using a SCUBA diver operated suction sampler, on a number of occasions during 1997. The contents of randomly positioned 0.5 x 0.5m quadrats collected in 1mm mesh bags at the end of the suction sampler. Sampling was more concentrated during June and November, representing the settlement period for decapods within the area. Sampling was conducted at a depth of 8-10m, in the Saltees Sound, Co. Wexford, Ireland. The substrate sampled consisted of a mixture of sand, shell fragments and stones, overlaid by approximately 50-70% cobble and boulder. Algal cover was variable, normally consisting of 40-80% *Laminaria* spp. Account was taken of the abundance and biomass of other decapod species sampled (Chapter 2). The decapod community was dominated numerically by the porcellain crab *Pisidia longicornis* (L.).

Spatial variability in settlement and abundance

Samples were collected (using the methodology described above) at five sites within a 1km^2 area in the Saltees Sound, in mid-September 1998, the period identified from the previous year as representing the end of the settlement season for most species. The sediment structure and conditions at each site were known prior to sampling from information obtained during SCUBA and remote video surveys. Sites were selected to be representative of a number of habitats typical of the area encompassed within the bay. The area consists of bands of varying substrate lying parallel to the shoreline, ranging from mud to solid bedrock. The area within the Saltees Sound contains patches of more solid substrate. A sediment sample was taken from each site, and general habitat characteristics recorded, including extent of rock, bedrock and algal coverage and water depth. Four replicate benthic samples were taken at each of the five sites, that included a dense cobble substrate with algal cover, a less dense cobble habitat with algal cover, a cobble habitat with no algal cover, a cobble habitat on solid bedrock with limited algal cover and a coarse sand and stone substrate with no algal cover.

Aquaria based growth in isolation and with conspecifics

Juvenile *Cancer pagurus* were sub-sampled from suction samples and transferred to laboratory based aquaria. Individuals were maintained in isolated compartments containing shell and stone substrate, and their growth rates monitored. All individuals were fed a combination diet of frozen Krill (*Euphasia*), frozen brine shrimp (*Artemia*) and fish. Temperature was maintained at $15 \pm 1^{\circ}$C using a looped cooling unit. Salinity ($32^{o}/_{oo}$) and pH (8) were monitored and maintained at twice weekly intervals.

Sixteen 0.5 x 0.5m experimental cells were seeded with six *Cancer pagurus* of various sizes. This density approximated to the average maximum density recorded in monthly samples (25 individuals m^{-2}). Each cell contained 75-100mm of shell and small stone, overlain 70% by cobble removed from the Wexford sampling site. The aquaria were maintained at $17 \pm 1^{\circ}$C. Each cell was seeded with 1 individual from each of the size ranges 10-20mm, 20-30mm, 30-40mm, 40+mm carapace width. A randomly allocated group of four cells from sixteen were then seeded with a further two individuals from the smallest size class, another four with two individuals from the next size class, and so on (Table 5.1) in order to examine growth and survival in treatments with identical density, and variable size class distribution and biomass. Food was added in quantities that reflected differences in the biomass contained within cells. Newly shed carapaces and moribund crabs were removed from the cells where evident, which were otherwise left undisturbed. All surviving individuals and intact shed carapaces were removed after seven weeks.

RESULTS

Temporal data set

Settlement of *Cancer pagurus* was detected between early July and late September. Specimens were generally collected from under cobble, fully or partially buried in the underlying coarse sand. The size of first crab ranged between 2.2-2.7mm carapace width (Table 5.2). Modal progression of the cohort and growth increment data indicated that settling juveniles attain a carapace width of approximately 5-8mm in the first summer of growth, depending on the timing of settlement. Moult increment approximated to a 27-29% increase from pre-moult carapace width. The magnitude of size increment was smaller (26%) after the first moult.

The highest average density of *Cancer*, 25 individuals m^{-2}, was observed in late August, at the end of the heavy settlement period and before extensive loss of the new cohort occurred (Table 5.3). The maximum density recorded during the study,

Table 5.1. Allocation of *Cancer pagurus* to experimental treatments with identical density and variable size class distribution and biomass.

	Individuals in size class (carapace width)			
	10-20mm	20-30mm	30-40mm	40+mm
4 x Treatment 1	3	1	1	1
4 x Treatment 2	1	3	1	1
4 x Treatment 3	1	1	3	1
4 x Treatment 4	1	1	1	3

Table 5.2. Mean density (individuals m^{-2}) of newly recruited *Cancer pagurus* in a sub-tidal rocky benthic habitat, Dec 1996-Nov 1997, Saltees Sound, Co. Wexford.

	Carapace Width (mm)					
Date	2-3 mm	3-4 mm	4-5 mm	5-6 mm	6-7 mm	7-8 mm
Dec	0	0	1	0	0	0
Jan	0	0	0	0	0	0
Mar	0	0	1	0	0	0
Apr	0	0	0	0	0	0
May	0	0	1	0	0	0
June	0	0	0	0	0	0
11-Jul	1	0	0	0	0	0
23-Jul	6	0	0	0	0	0
07-Aug	6	2	0	0	0	0
15-Aug	2	4	1	0	0	0
22-Aug	3	9	4	0	0	0
22-Sep	1	1	2	1	2	0
22-Nov	0	0	1	2	1	0

Table 5.3. Mean density (individuals m^{-2}) of *Cancer pagurus* in a sub-tidal rocky benthic habitat, Dec 1996-Nov 1997, Saltees Sound, Co. Wexford.

	Carapace Width (mm)									
Date	0-5 mm	5-10 mm	10-15 mm	15-20mm	20-25 mm	25-30mm	30-35mm	35-40 mm	40+ mm	Total
Dec	1	3	1	1	0	0	0	0	1	7
Jan	0	2	0	0	1	1	0	0	0	4
Mar	1	5	0	0	1	0	1	1	2	11
Apr	1	2	1	0	0	0	0	0	1	5
May	1	2	3	0	2	0	0	1	1	10
June	0	5	0	0	0	0	0	0	1	6
11-Jul	1	1	1	0	0	0	0	0	0	3
23-Jul	6	2	2	0	0	0	0	0	0	10
07-Aug	8	2	4	0	0	0	0	0	0	14
15-Aug	7	2	1	0	0	1	0	0	2	13
22-Aug	16	0	3	2	0	2	0	1	1	25
22-Sep	4	4	1	0	0	0	1	0	1	11
22-Nov	1	4	0	2	1	1	0	1	0	10

on the 7th August, was 44 individuals m^{-2}. Of this number, 28 individuals could be identified as young of the year.

Highest density of first stage benthic juveniles occurred between late July and early August. The number of first stage crab decreased significantly after this period and corresponded with an increase in abundance of crabs in subsequent size classes due to growth of settlers (Table 5.2). It was evident however, from the decline in density of crab entering subsequent instars that mortality was high. The rapid and large decrease in numbers of individuals with increasing size was evident from the overall length-frequency histogram from the entire sampling period which showed an exponential decline in numbers with increasing size, assuming constant inter-annual recruitment (Figure 5.1). The total number of individuals in each group believed to represent the previous 4 cohorts (1-7mm, 8-15mm, 16-30mm & 31-45mm) declined with increasing size (167, 79, 34 & 17 respectively). The decrease in number of individuals represented 53% mortality between the 0+ and 1+ cohorts, 56% between the 1+ and 2+ cohorts, and 50% between 2+ and 3+.

The largest individual caught during the 1997 sampling measured 80mm carapace width. Crabs with a carapace width >40mm never constituted more than 19% of the total monthly catch (Table 5.3). Crabs of this size were also absent from >50% of the sampling efforts.

Spatial variability in settlement and abundance

There were clear differences in the structural complexity of most of the sites sampled (Table 5.4). No young of the year (YOY) or individuals established in

Figure 5.1. Length-frequency distribution of *Cancer pagurus* collected from the Saltees Sound, Co. Wexford, Dec 1996 to Nov 1997. The fitted line represents the exponential decline in numbers with increasing size.

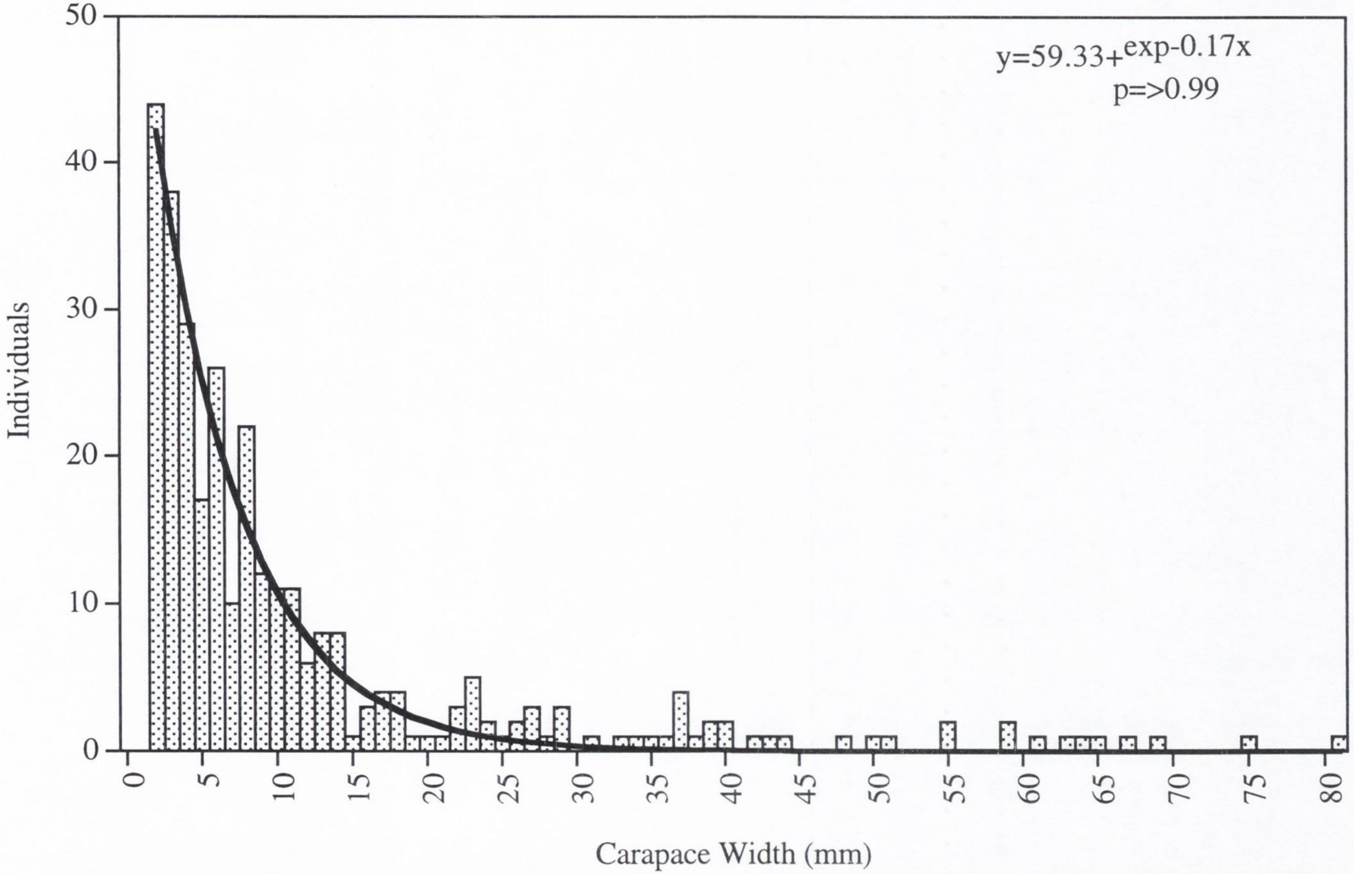


Table 5.4. Sediment grain size composition expressed as proportion of sample dry weight (g) represented by each size component, diver estimates of substrate characteristics (marked *) and range of densities (individuals m^{-2}) recorded for *Cancer pagurus* in five distinct sub-tidal habitats (YOY=Young of the year PC=Previously settled cohorts).

	Site 1	Site 2	Site 3	Site 4	Site 5
% Large Stone (50-149mm dia)	72.9	78.7	0.0	72.8	76.1
% Small Stone (5-49mm dia)	12.3	19.2	7.7	12.0	22.9
% Course sand (2-5mm dia)	1.5	0.4	2.1	1.2	0.4
% Fine sand (<2mm dia)	13.3	1.7	90.2	14.0	0.6
% Area covered by solid bedrock *	20	60	0	20	100
% Algal coverage *	10	75	0	75	35
% Area covered by loose rock *	75	95	0	75	25
Overall range of *Cancer* density (m^{-2})	0 - 8	4 - 24	0	8 - 20	0 - 28
Range of YOY *Cancer* density (m^{-2})	0 - 8	4 - 20	0	2 - 20	0 - 16
Range of PC *Cancer* density (m^{-2})	0	0 - 12	0	0 - 12	0 - 12

previous cohorts were encountered within the habitat at site 3 that consisted of coarse sand and small stone. This substrate afforded little shelter to decapods in the form of interstitial spaces. Only low densities (0-8 individuals m^{-2}) of YOY were detected in physically complex cobble (Site 1), overlying coarse sand, with a very limited algal canopy (Table 5.4). No individuals from previously settled cohorts were recorded at this site. Higher densities of *Cancer* (8-20 individuals m^{-2}), both YOY and previously settled, were recorded at the cobble site of similar physical complexity but with an extensive algal cover (Site 4). An almost identical range of densities were recorded for YOY and previously settled individuals in the denser cobble substrate (Site 2) with similar algal coverage, although overall density (4-24 individuals m^{-2}) was more variable. Overall (0-28 individuals m^{-2}) and YOY (0-16 individuals m^{-2}) densities differed in isolated cobble patches overlying solid bedrock that offered no substrate to burrow in, while density of previously settled individuals was identical to sites 2 and 4 (Table 5.4). Overall abundance of *Cancer* was significantly correlated to the extent of algal coverage (r=0.93).

Aquaria based growth in isolation

Absolute increase in carapace width (as a proportion of pre-moult size) of individuals held in isolated cells tended to decline as the pre-moult carapace width increased. A mean increase of 32% in carapace width from pre-moult size was recorded for individuals moulting from a pre-moult carapace width between 6-10mm (n=10). This fell to 29% for individuals between 10-20mm carapace width (n=13), 28% for individuals between 20-30mm (n=13) and 27% between 30-40mm (n=10). Moult death syndrome (MDS), failure to fully extract the body from the old exoskeleton, occurred in approximately 5% of individuals.

Aquaria based growth with conspecifics

Of the 24 crabs placed into each treatment group at the start of the experiment, most were recovered from the second treatment (Table 5.5). Similar numbers of individuals were recovered from each of the remaining treatment groups (Table 5.5). In both of the cells containing a single crab, it was the largest or second largest individual placed into the cell at the start of the experiment that remained. Both of these remaining crabs were female. In the cell where two crabs remained, the smaller was physically damaged with five missing limbs including both chelae, while the larger was an undamaged female. All of the visible crab remains that were removed during the course of the experiment, approximately one third of total losses, were partially predated during or immediately after ecdysis. It was not possible to determine what proportion of these predated crabs were attacked during or after a successful moult, and how many failed to complete moulting due to MDS and were subsequently consumed.

There was no significant difference ($p=0.05$) in the average growth within each crab size class between treatments (Table 5.6). Although average growth of crabs with an initial carapace width between 10-20mm was greatest in cells with the smallest size distribution at 32% increase from pre-moult width, this was not significantly greater than crabs of the same size in other treatments (Table 5.6). There was a significant difference in growth between the smallest and two largest groups in treatment 1, and between the smallest and largest size group in treatment 2 (Table 5.6). The overall average growth increment of each crab class in each treatment did not differ from that of individuals grown in isolation. In general, average growth tended to decrease in larger sized crabs.

Table 5.5. Number of *Cancer pagurus* surviving in aquaria-based experimental cells after seven weeks, from six individuals at the start of the experiment. Size class distribution and biomass varied with treatment. Numbers in brackets represent numbers of survivors in each size class from smallest to largest.

Size class (Carapace Width)	4 x Treatment 1 4 crabs 10-60mm (+2 10-20mm)	4 x Treatment 2 4 crabs 10-60mm (+2 20-30mm)	4 x Treatment 3 4 crabs 10-60mm (+2 30-40mm)	4 x Treatment 4 4 crabs 10-60mm (+2 40+mm)
Cell 1	6 (3,1,1,1)	6 (1,3,1,1)	5 (1,1,2,1)	5 (1,1,1,2)
Cell 2	5 (2,1,1,1)	6 (1,3,1,1)	2 (0,1,1,0)	5 (1,1,1,2)
Cell 3	1 (0,0,1,0)	6 (1,3,1,1)	5 (1,1,2,1)	5 (1,1,1,2)
Cell 4	5 (2,1,1,1)	5 (1,2,1,1)	5 (1,0,3,1)	1 (0,0,0,1)

Table 5.6. Mean growth increment as proportion of pre-moult carapace width (mm) in *Cancer pagurus* held in aquaria, with identical density and variable size class distribution and biomass.

Size class (Carapace Width)	4 x Treatment 1 4 crabs 10-60mm (+2 10-20mm)	4 x Treatment 2 4 crabs 10-60mm (+2 20-30mm)	4 x Treatment 3 4 crabs 10-60mm (+2 30-40mm)	4 x Treatment 4 4 crabs 10-60mm (+2 40+mm)	Average	d.f.	F	Prob.
10-20mm class	32%	27%	30%	29%	30%	16	1.2	0.34
20-30mm class	27%	28%	25%	30%	28%	19	0.4	0.75
30-40mm class	20%	20%	23%	22%	21%	16	0.3	0.98
40+mm class	18%	18%	19%	18%	18%	14	0.2	0.92
Average	24%	23%	24%	25%				
d.f.	15	20	15	15				
F	8.2	3.4	2.2	2.2				
Probability	<0.01	0.04	0.14	0.14				

DISCUSSION

Early crab stages of *Cancer pagurus* were found in cobble habitats in shallow water during this study. The limited number of larger crabs recorded suggests that the high mortality experienced by early benthic phase crabs results in few individuals surviving to maturity, or that crabs move to other habitats at some stage during development. Ontogenetic shifts have been observed in other species of decapod (Orth & van Montfrans, 1987; Pile *et al.*, 1996). Tag recovery experiments showed that mature crabs that are targeted by offshore fisheries undertake seasonal migrations between Ireland and Scotland (Cosgrove, 1998). Recruitment from shallow water nursery grounds may replenish both inshore and offshore fisheries, and as such further investigation into the fate of shallow water individuals is warranted.

Cancer pagurus settled into physically complex habitats which provided some degree of shelter in the form of interstitial spaces. *Cancer* is a highly fecund species that invests limited energy into individual offspring. Recent work (Cobb *et al.*, 1997; Palma *et al.*, 1998) suggested that substrate specificity and early benthic survival of such ‘r-strategists’ is reduced when compared to ‘k strategy’ species that produce fewer eggs with proportionally greater investment in each offspring. Larval production is known to be high at the site examined in the present study (Merin, 1998). The subsequent high mortality, even in physically complex habitats, relative to other species recorded during sampling (Chapter 2) would concur with the findings of Palma *et al.* (1998). The mechanisms controlling the apparently high mortality of settlers and early crab stages remain unknown. Failure to detect *Cancer* in the less complex sand and stone habitat may be attributed either to larval avoidance at settlement, rapid early mortality before sampling could be conducted or immediate post-settlement movement to more complex habitats. Significant movements by small shelter dependent early benthic phase *Cancer*, exposed to predation (Lavalli & Barshaw, 1986; Wahle & Steneck, 1992; Fernandez *et al.*, 1993a; Moksnes *et al.*, 1998) and physical stresses (Howard & Nunny, 1983; Pile *et al.*, 1996), seems highly unlikely.

Juvenile *Cancer pagurus* grew quickly after settlement. The frequency and magnitude of moults in decapods is often reduced over time, as a proportion of energy is redirected from somatic to reproductive development (Hartnoll & Gould, 1988). Unlike *Homarus gammarus* (L.) and *Homarus americanus* Milne Edwards (Carlberg *et al.*, 1979), the presence of larger bodied conspecifics did not affect the growth of *Cancer*. Although cannibalism by *Cancer* was observed in the laboratory in this study, the species is slightly less antagonistic towards conspecifics than either *Homarus* species (pers. obs.). *Homarus* species are solitary, territorial decapods that readily fight, injure and cannibalise each other in artificial conditions (O'Neill & Cobb, 1979). In the present study, when held in high densities in the laboratory with no shelter, *Cancer* generally moved apart when physical contact was made, even when one individual was significantly larger than the other (pers. obs.). Physical contact between conspecifics is believed to be a strong regulatory mechanism of juvenile dispersal (Iribarne *et al.*, 1994). Significant difference in body size or age between individuals can lead to niche diversification and reduced competition, possibly due to differences in resource utilisation (Wilson, 1975; Polis, 1984).

Although the density of juvenile conspecifics settled in previous years or earlier in the current settlement season has been shown to regulate YOY densities through cannibalism (Fernandez *et al.*, 1993a; Smith, 1995; Lovrich & Sainte-Marie, 1997; Moksnes *et al.*, 1997; Moksnes *et al.*, 1998) and dispersal (Campbell, 1986; Fernandez *et al.*, 1993b; Iribarne *et al.*, 1994; Lovrich *et al.*, 1995), survival of *Cancer* at the density set for the current aquarium experiment was high (76% overall). It is possible that in cells where more than one mortality was recorded, the largest or remaining crab had displayed some form of territoriality. From the condition of the smaller individual in the cell with two survivors, and the removal of partially eaten conspecifics from these cells during the course of the experiment, it seems likely that territoriality was manifested as direct attack and cannibalism of conspecifics. It is possible that this behaviour was induced by confinement in an artificial environment, and does not occur outside captivity. A significant proportion of death was attributable to MDS when individuals were kept in isolation, and it is likely to have accounted for a number of the mortalities in the experiment with conspecifics. It is believed that MDS in captive decapods is caused by nutritional deficiency due to poor diet or other physiological stresses. It is unclear whether similar losses occur in wild populations. If so, then MDS would account for a significant source of mortality in early life history. The mortality estimates calculated from the number of *Cancer* in the previous four cohorts recorded in the field are likely to be influenced by inter-annual recruitment variability. The larvae of highly fecund species such as *C. pagurus* are believed to experience far greater mortality relative to species that invest more energy into the development of fewer larvae (Cobb *et al.*, 1997). This combined with the lower substrate specificity of the postlarvae of highly fecund species (Palma *et al.*, 1998), contributes to inter-annual variability in recruitment that is determined by physical and biological fluctuations in the population or the environment.

If the sub-tidal environments studied here are found to represent the major nursery grounds of commercially exploited stocks of *Cancer pagurus*, including offshore grounds, then they must be protected and monitored to safeguard continued recruitment. There is excellent potential for the application of suction sampling methods and settlement tray deployment to gather detailed and informative data pertaining to the spatial distribution and timing of settlement, recruitment, and the processes effecting subsequent growth and survival of juvenile *C. pagurus*.

CHAPTER 6

COUPLING OF DECAPOD LARVAL PRODUCTION AND SUBSEQUENT RECRUITMENT TO THE BENTHOS IN A ROCKY SUB-TIDAL HABITAT.

ABSRACT

Planktonic and benthic sampling for decapod crustaceans was conducted in a localised area during the summer of 1997 on the Southeast coast of Ireland. The rocky sub-tidal habitat sampled supported high densities of 21 decapod species. Larval production estimates were compared to subsequent young of the year (YOY) densities of twelve species in the benthos. Additional habitats with varying degrees of physical complexity were sampled during 1998. Plots of larval production against subsequent densities of YOY in the benthos conformed to significant density dependent or linear functions depending on the habitat type. Density dependent regulation and overcompensation was observed when no interaction between species was assumed. Larval supply or early post-settlement processes would appear to constrain recruitment in habitats were linear functions were fitted. Density dependence was observed at high levels of larval production when all species were considered interactive. The density of individuals within the community approached but did not reach the saturation density predicted by the fitted model. Further additions to settlement into these habitats may not result in higher recruitment when the saturation or compensation point is reached. When certain assumptions are made, it is possible that multi-species stock-recruitment curves may assist in the evaluation of habitat enhancement, highlight the sources of any constraints on recruitment and provide indications of the form of the stock-recruitment relationship in these species.

INTRODUCTION

Recently there has been increasing interest in the effects that larval supply, larval substrate selection, and density dependent mortality and displacement have on the postlarvae-settler-recruit relationship in decapods (Incze & Wahle, 1991; Incze *et al.*, 1997). These models attempt to predict recruitment, to the benthos or the adult population, from larval production after a suitable lag phase is applied. Of the few models developed, some have concentrated on variation in the annual spawning stock-recruitment relationship of single species (Phillips & Brown, 1989; Incze & Wahle, 1991), while others have linked primary production to subsequent densities of benthic invertebrate fauna (Buchanan, 1993).

Processes acting on the early life history of decapod species can determine subsequent cohort strength (Robinson & Tully, 1998b). Both density dependent (Iribarne *et al.*, 1994; Pile *et al.*, 1996) and density independent (Doherty, 1994) processes may operate at this stage. Mortality and displacement (Iribarne *et al.*, 1994) of early life history stages are often under density dependent control. Gosselin & Qian (1997) list numerous studies where population abundance, distribution and community structure are controlled/influenced by juvenile mortality of marine invertebrates. If settlement and recruitment into the benthic habitat are under density dependent constraint and the area of habitat is limiting, then early post-settlement processes could control the stock-recruitment relationship, carrying capacity and production of the population within specific habitat types.

Many marine invertebrates release planktonic larvae as part of their life cycle. Larvae can be transported over large distances or be retained in the localised area of release by wind forced hydrodynamic processes (Young *et al.*, 1998) or ocean currents (White *et al.*, 1988; McConnaughey *et al.*, 1992) and fronts (Alldredge & Hammer, 1980). Larvae that are transported away from the site of production may be returned at a later date (Shanks, 1983; McConaugha, 1988; Rothlisberg, 1988), or remain in areas far removed from the point of origin. These may represent new areas that can be colonised by the species, grounds already occupied by a genetically distinct population of conspecifics, or unsuitable habitats that cannot support either juvenile or adult individuals. Transportation to unsuitable grounds may represent a significant source of loss from the larval population (Rumrill, 1990). Settlement into less favourable environments, due to oceanographic processes which can strongly influence larval supply, or simply the absence of preferred habitat at metamorphosis (Roughgarden *et al.*, 1988), can lead to a drastic increase in both the rate (Connell & Jones, 1991) and magnitude (Moksnes *et al.*, 1998) of initial mortality.

As the point of metamorphosis is approached and the discriminatory ability of larvae increases (Welch *et al.*, 1998), postlarvae respond to numerous cues from the surrounding environment. Positive and negative taxis towards various cues have been reported, including habitat complexity (Moksnes *et al.*, 1998; Stevens & Kittaka, 1998), presence of algae and seagrass (Forward *et al.*, 1996; Morgan *et al.*, 1996; Welch *et al.*, 1998), and the presence or absence of conspecifics (Crisp & Meadows, 1962; Jensen, 1991) or predators (Boudreau *et al.*, 1993; Welch *et al.*, 1998; Diaz *et al.*, 1999). In more mobile species, settlement often occurs into nursery habitats (Cobb & Wahle, 1994; Pile *et al.*, 1996; Moksnes *et al.*, 1998), with a subsequent habitat shift at a later stage of development. Smaller, less-mobile species may remain permanently in the initial settlement habitat. The importance of nursery habitats in the survival (Wahle & Steneck, 1992; Eggleston & Armstrong, 1995; Pile *et al.*, 1996; Moksnes *et al.*, 1997; Moksnes *et al.*, 1998) and development (Connell & Jones 1991; Perkins-Visser *et al.*, 1996) of decapod species has been well documented. When the species is of commercial value the success of the fishery may well depend on recruitment from such areas (Wahle & Steneck, 1991; Pile *et al.*, 1996; Moksnes *et al.*, 1997).

The aim of the present study was to examine the form of the relationship between larval production and subsequent benthic recruitment in a rocky, sub-tidal decapod community. Non-linearity in this relationship may indicate whether larval supply or post-settlement processes limit or control recruitment, and whether transfer efficiency varies between species. The models presented may be useful for estimating the future recruitment of species from larval production estimates. The apparent scarcity of, or failure to detect, juveniles of some commercial exploited species have hampered formulation of such recruitment models. In these cases it may be possible to predict levels of recruitment from larval production estimates using models formulated for the recruitment of other species within the decapod community if the larval production-recruitment transfer efficiency is known and generally similar across species.

MATERIALS AND METHODS

Study location

Sampling was conducted in the vicinity of the Saltees Sound, Co. Wexford, Ireland, during 1997. The area, approximately one and a half nautical miles from the mainland, lies between the two Saltee islands. Strong tides predominate in the area with >4m heights at HWS. Diver surveys and video footage from remote camera tows revealed that the habitat type within the study area is patchy, ranging from solid bedrock to coarse sand. The majority of the area consists of a mixture of coarse sand and bedrock overlain by dense cobble and boulder, with 50-70% algal (*Laminaria* spp.) cover. Larval sampling was conducted at five stations positioned evenly along each of two 2.4km long parallel transects (Figure 6.1) 1.2km apart which passed directly over the benthic sampling site and extended to the north and south. Benthic sampling was conducted within a localised area (Figure 6.1) approximately 1km^2. An average depth of 8m is charted for the whole study area. Bottom temperature at the site was recorded every two hours by a Seamon® recorder.

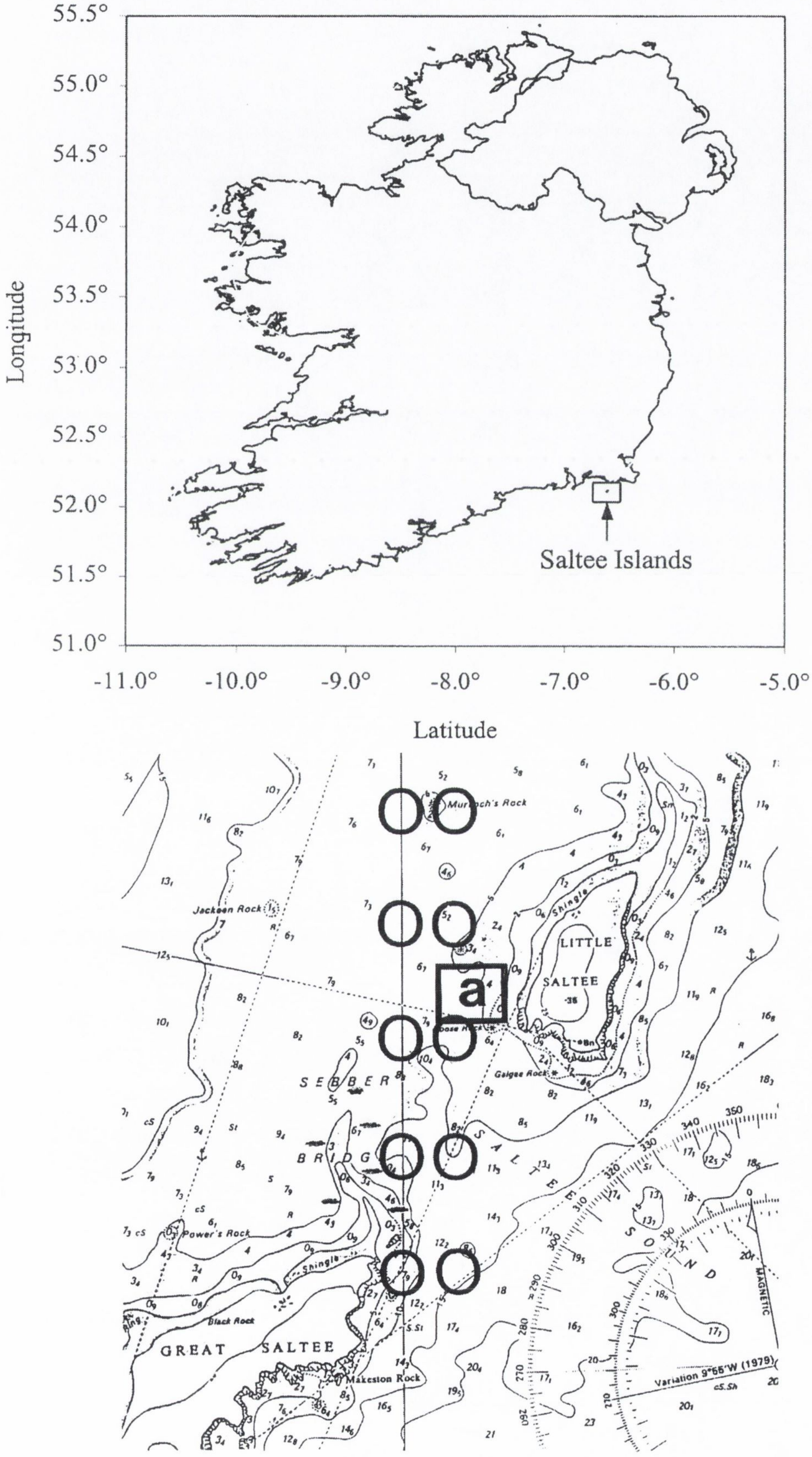
Larval sampling

Larval sampling was conducted on 6 dates between June and November 1997. Poor conditions at sea prevented earlier sampling, so a supplementary sample was taken in May 1998 and added to the data set. Larval tows were conducted at 2 knots from an 8m long chartered fishing vessel, using a standard 333μm mesh plankton net (Merin, 1998). The net was towed for 10min at a depth of 2m at each station. The volume of water passing through the mouth of the net was recorded using a flow meter. Samples were fixed immediately in 5% formal-saline.

Benthic sampling

Benthic sampling, which was conducted throughout 1997, detected settlement of decapod fauna between May and September. Sampling was carried out on eight occasions during these months. The predominant habitat type in the area, described above, was sampled on each occasion. A diver operated suction sampler was used to take quantitative benthic samples from a number of random selected 0.25m^2 areas. Sampling *in situ* allowed collection of individuals from the under-surfaces and interstitial spaces between cobble, and specimens berried in coarse sand. Methods

Figure 6.1. Location of study area in the Saltees Sound, Co. Wexford, Ireland, and position of ten areas within which plankton tows were conducted (O), and the approximate area (a) within which benthic samples were taken.



using grab sampling or trawls fail to quantitatively sample such complex habitat. Fauna sampled by suction sampling was retained in 1mm mesh bags.

Processing larval samples, density and seasonal production

Each plankton sample was diluted with seawater to a volume of 1l. Five random 50ml sub-samples were removed by pipette after mixing the sample. This procedure resulted in 50 sub-samples for each sampling date. A dissection microscope was used to identify decapod larvae and determine its stage of development using the keys of Ingle (1992), Paula (1996) and Williamson (1982). The abundance of larvae in each sample was converted to density estimates (m^{-3}) using flow meter readings (Merin, 1998).

Trapezoidal integration was carried out on densities of zoea I larvae to obtain larval production estimates for the entire season for each individual species or higher taxonomic group. This involved the extrapolation of larval densities recorded at each sampling date to half way between the previous and the next sampling date. In the absence of daily larval abundance data, this method made some allowance for seasonal variation in production. The normal procedure for estimating larval production involves back calculation of the decline of the natural logarithm of successive zoeal stages. Densities of zoea I larvae were used in this study, as decline in density with successive zoeal stages was not always observed. The densities of zoea I larvae were divided by the stage duration at the temperature recorded during sampling to derive daily production estimates (m^{-3}). As temperature related stage duration data was available for only three species at 15°C, *Cancer pagurus* L. 8 days (Nichols *et al.*, 1982), *Necora puber* (L.) 8 days (Valdes & Alvarez Osorio, 1983) and

Pisidia longicornis (L.) 9 days (Valdes & Alvarez Osorio, 1983), an average of 8 days was applied to all species. Confidence intervals were calculated for larval production estimates by addition of the squared variances associated within sub-sample, station and date. The variation associated with larval production estimates was partitioned to sampling components after ANOVA, using the methodology described by Sokal & Rohlf (1995).

Larvae of the European lobster, *Homarus gammarus* (L.), were not detected in plankton samples during 1997. The sampling methodology employed was not suitable for quantitative sampling of this species, which occurs in the neuston at dawn and dusk. Therefore, larval production estimates were calculated from the density of larvae collected in neuston tows in the Saltees Sound (Figure 6.1) on the 15 September 1996. Average density was calculated from hourly tows conducted between 4am-9am and 7pm-10pm, as the majority of the larval population are in deeper water and unavailable to the neuston sampler at other times (Tully & O'Céidigh, 1987).

There were some other limitations in the calculation of larval production estimates. Sampling did not commence early enough in the season in the first year, and although some effort was made to rectify this problem the following year, estimates from separate years are unlikely to be interchangeable without some loss of accuracy. The intervals between sampling efforts were also too long leading to broad extrapolation of abundance that may not have accounted for short-term variation in seasonal production. Temperature, which significantly effects development rate, food availability, larval size and survival, was variable over relatively short periods. The scarcity of temperature-development rate data lead to further generalisations. The geographic limits of the production area were not defined, and transport to and from the area may have affected subsequent transfer efficiency to the benthos. Finally, although a number of possible species may have contributed to the abundance of Portunid larvae of the sub-family Polybiinae, it was not possible to distinguish individual species. The larval abundance of Polybiinae was divided by the number (6) of species previously described in the local Wexford area (Healy & McGrath, 1988; Ingle, 1996; Kelly *et al.*, 1996), and multiplied by the number of species that were found on the habitat type sampled (2). Other sub-families or groups that were not identified to species level (*Galathea* spp. & *Inachus* spp.) consisted of species that were recorded in the benthic habitat sampled.

Processing benthic samples & identifying settlers

Decapods were isolated from benthic samples by sieving the sample through progressively smaller mesh sizes down to 1mm while submerged in seawater. Individuals were fixed in 5% formal-saline and subsequently preserved in 70% alcohol. The sizes of specimens >3mm carapace width were recorded to the nearest 0.1mm using digital callipers. Smaller individuals were measured to the nearest 0.1mm using a dissection microscope micrometer. The duration of the settlement season varied with species, with some displaying extended settlement over several months, and others for less than one month. Young of the year (YOY) settlers could be distinguished from individuals settled prior to 1997 in length-frequency distributions as there were clear gaps separating YOY and other cohorts. The total number of YOY individuals remaining on the 22 September, which represented the approximate end of the settlement season for most species, was calculated and expressed as individuals m^{-2}. Thirteen samples were taken on this date.

Benthic sampling in various habitat types

On the 22 September 1998, five distinct settlement habitats were suction sampled, including a cobble habitat over shale with no algal cover (a), a very dense cobble habitat over shale with algal cover (b), a sand and gravel substrate with no algal cover (c), a cobble habitat over shale with algal cover (d) and a cobble substrate on solid bedrock with limited algal cover (e). Four replicate benthic suction samples were taken from each habitat. As no plankton sampling was conducted in 1998, identical larval production estimates were assumed to be identical to 1997.

Modelling the relationship between larval production and recruitment

Stock-recruitment or linear models were fitted to data sets where appropriate. The Ricker stock-recruitment model (Ricker, 1954) takes the form:

$$[R=R1*S*^{\exp}(-R2*E)]$$

where S=production, R1and R2 are constant parameters and R=recruitment. The resultant density dependent model rises to an asymptote and declines when further addition to density results in overcompensation. A number of assumptions are made when fitting this function to data sets presented in this paper:

-The position on the R axis is only related to the level of S and not to species specific stock-recruitment relationships.

-Intra-specific constraints determine the position on R.

-Inter-specific competition is presumed absent (species are independent).

-Each species can occupy any position in a given window within the model that is determined by constraints, especially on S (reproductive constraints).

The second density dependent model of Beverton & Holt (1957) expressed as:

$$[R=(S/(S+g*Rmax))*Rmax]$$

where g and R(max) are parameters, differs from the first in that does not decline after the asymptote is reached, regardless of the magnitude of further additions. The assumptions of this model as applied in this paper to the species cumulative larval production and recruitment are:

-The position of on the R axis is only related to the level of S.

-Inter-specific and intra-specific competition are equal (complete interaction), with the addition of 1 individual of species x having the same saturating effect as the addition of 1 individual of species y.

-The model is constrained to move only positively (cumulative).

Due to its high densities *Pisidia longicornis* masked the general production-recruitment relationship in this species assemblage, and was excluded from all fitted models with the exception of habitat c) sampled in 1998, where abundance was low and could be viewed with the other species sampled.

RESULTS

Average daily temperature at the site was calculated from the 12 daily recordings of the Seamon probe, for the period July 1997 to May 1998 (Figure 6.2). Although this does not coincide exactly with the duration of the study, it is believed to approximate to the usual annual temperature regime of the area. Two sets of remote recording were taken using a WTW temperature metre, on 23/01/97 (8.0°C) and 08/07/97 (13.6°C), prior to the deployment of the probe. The highest mean daily temperature of 16.6°C was recorded in mid August. July and September yielded comparable values around 15.0°C. Temperature dropped significantly at the onset of October, reaching a minimum (8.5°C) in early February. Increasing temperatures were recorded from mid April onward. The WTW probe recording in early July was used when estimating missing temperature values between May and late July.

A total of 30 species were recorded in plankton samples, compared to the detection of settlement of 21 species in benthic samples. Twelve species were recorded in both plankton and benthic samples (Table 6.1). No juvenile *Homarus gammarus* were detected in benthic samples. Other species that occurred in plankton samples and not in benthic samples consisted mainly of those which inhabit other substrate types (*Atelecyclus* spp. and *Corystes cassivelaunus* (Pennant). The majority of species that were not detected in plankton samples but were present in benthic samples occurred in densities far lower than the least abundant species of the twelve common to plankton and benthic samples *Achaeus cranchii* Leach. Most of these species were recorded only once during benthic sampling (*Eurynome* spp., *Pagurus cuanensis* Thompson and *Macropodia* spp.) and were likely to be rare and difficult to detect in plankton samples. The variance component in the plankton data associated

Figure 6.2. Mean daily seawater temperature calculated from 2 hourly recordings, from July 1997, Saltees Sound, Co. Wexford. Values from May-July 1997 estimated from single recordings taken in Jan and early July.

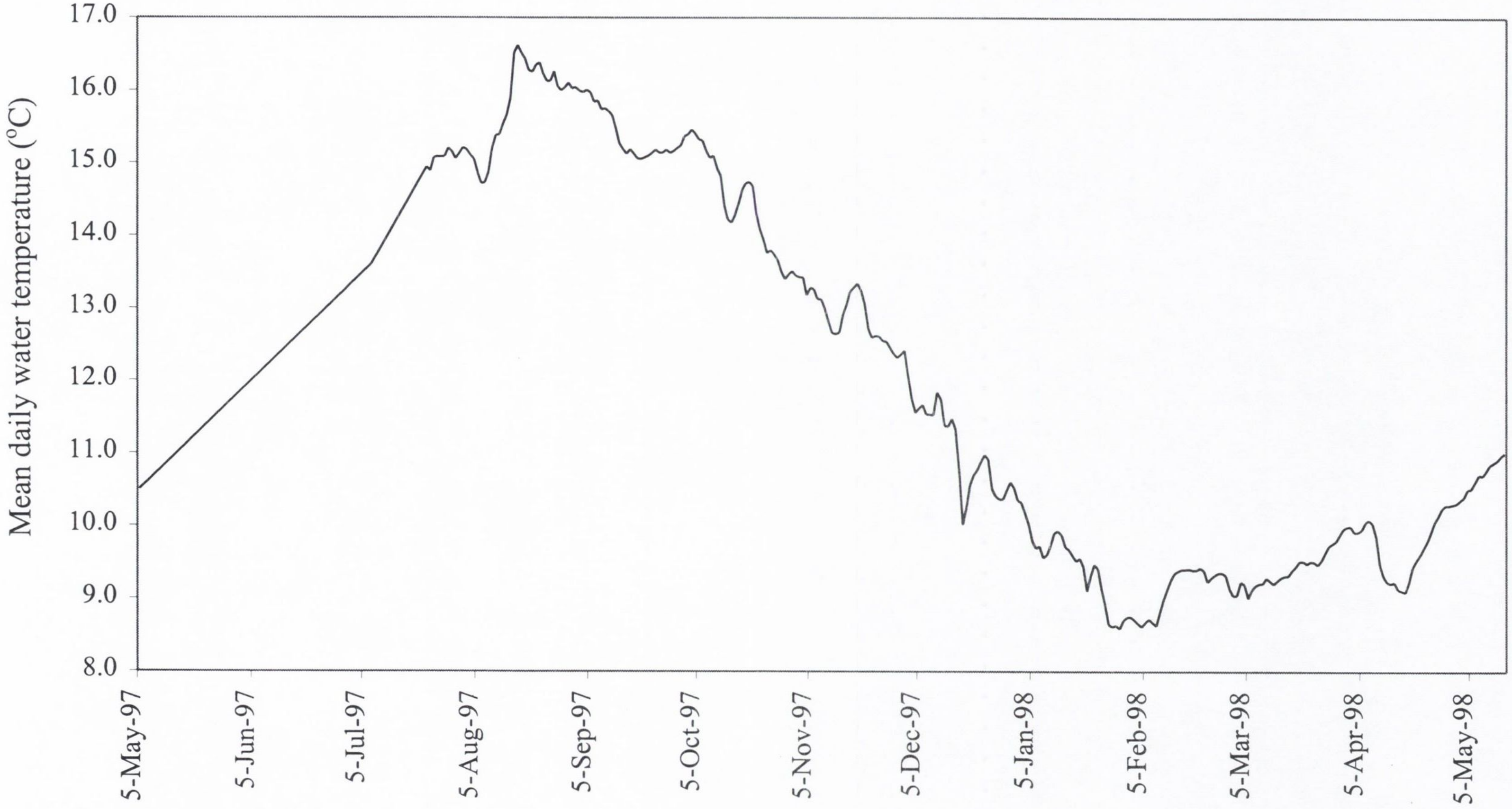


Table 6.1. Larval production estimates and subsequent densities of young of the year decapods in the benthos for twelve sub-tidal species or groups, 1997.

Species	Larval production Individuals m^{-3}	95% Confidence Interval	Benthic density Individuals m^{-2}	95% Confidence Interval
Pisidia longicornis (Pl)	373	0 - 5869	488	320 - 655
Polybiinae spp. (Psp)	25	0 - 115	6	3.6 - 8.4
Xantho pilipes (Xp)	22	14 - 30	5	2.6 - 7.4
Pilumnus hirtellus (Ph)	22	15 - 29	7	6.0 - 8.0
Cancer pagurus (Cp)	13	0 - 100	8	4.4 - 11.6
Galathea spp. (Gsp)	11	0 - 46	18	13.5 - 22.5
Pagurus bernhardus (Pb)	6.2	5.0 - 7.3	2	1.4 - 2.6
Pirimela denticulata (Pd)	5.2	0 - 49	5	4.2 - 5.8
Porcellana platycheles (Pp)	1.0	0.8 - 1.2	1	0.05 - 2.0
Inachus spp. (Isp)	0.3	0.2 - 0.3	1	0.2 - 1.8
Achaeus cranchii (Ac)	0.02	0.01 - 0.02	1	0.4 - 1.6
Homarus gammarus (Hg)	0.003	0.003 - 0.004	0	N/A

with differences between stations made the smallest contribution to error for each species (Table 6.2). Decreasing sub-sample variance corresponded to an increase in sampling date variance which was associated with increasing larval abundance (Table 6.2).

Seasonal larval production was compared to subsequent densities of YOY individuals (Figure 6.3 inset). The high seasonal production and settlement of *Pisidia longicornis* masked the larval production-settlement relationship of other species, so the data was re-plotted with this species removed (Figure 6.3). There was large variation in the proportion of transfer from larval production to subsequent benthic densities between species. A Ricker model fitted with all species except *Pisidia* included was insignificant (R^2=0.49, p=0.41). *Galathea* spp. displayed particularly strong settlement in relation to larval production estimates. The benthic abundance of polybinid crab, less than half that of *Galathea* spp., was low relative to larval production estimates. When *Galathea* spp. were removed from the fitted linear model the relationship between larval production and the density of YOY decapods in the benthos (Figure 6.3) was statistically significant (R^2=0.95, p=0.06). The fitted model reached an asymptote and declined after larval density reached 12 individuals m^{-3} and density of YOY decapods in the benthos was 9 individuals m^{-2}. Best fit functions applied to the five habitats sampled in 1998 (Figure 6.4a-e) were either linear (a & c) or density dependent (b, d & e). Of these relationships, only c) was significant at the 5% level.

Cumulative larval production by ranked species abundance was calculated and compared to the corresponding cumulative density of YOY individuals in the benthos

Table 6.2. Proportion of variance (%) in larval density estimates due to sub-sampling, station and date in data for 11 decapod species or groups, 1997.

Species	Sub sample (error) (%)	Station (%)	Sampling date (%)	Interaction (dat*sta) (%)	Total (%)
Achaeus cranchii	86.3	1.4	9.9	2.5	100
Cancer pagurus	33.7	4.8	36.6	24.9	100
Galathea spp.	70.3	5.8	10.7	13.2	100
Inachus spp.	96.8	0.9	0.9	1.5	100
Pagurus bernhardus	37.5	11.1	14.0	37.3	100
Pirimela denticulata	62.6	1.1	11.2	25.1	100
Pilumnus hirtellus	17.0	2.7	59.9	20.4	100
Pisidia longicornis	6.0	4.3	60.5	29.2	100
Polybiinae spp.	16.6	2.0	58.2	23.2	100
Porcellana platycheles	38.4	3.1	21.2	37.4	100
Xantho pilipes	3.8	4.7	61.4	30.1	100

Figure 6.3. Relationship between larval production and subsequent density of YOY decapods in the benthos for twelve species or groups, 1997. Models stated do not include *Pisidia* . Full species names listed inTable 1.

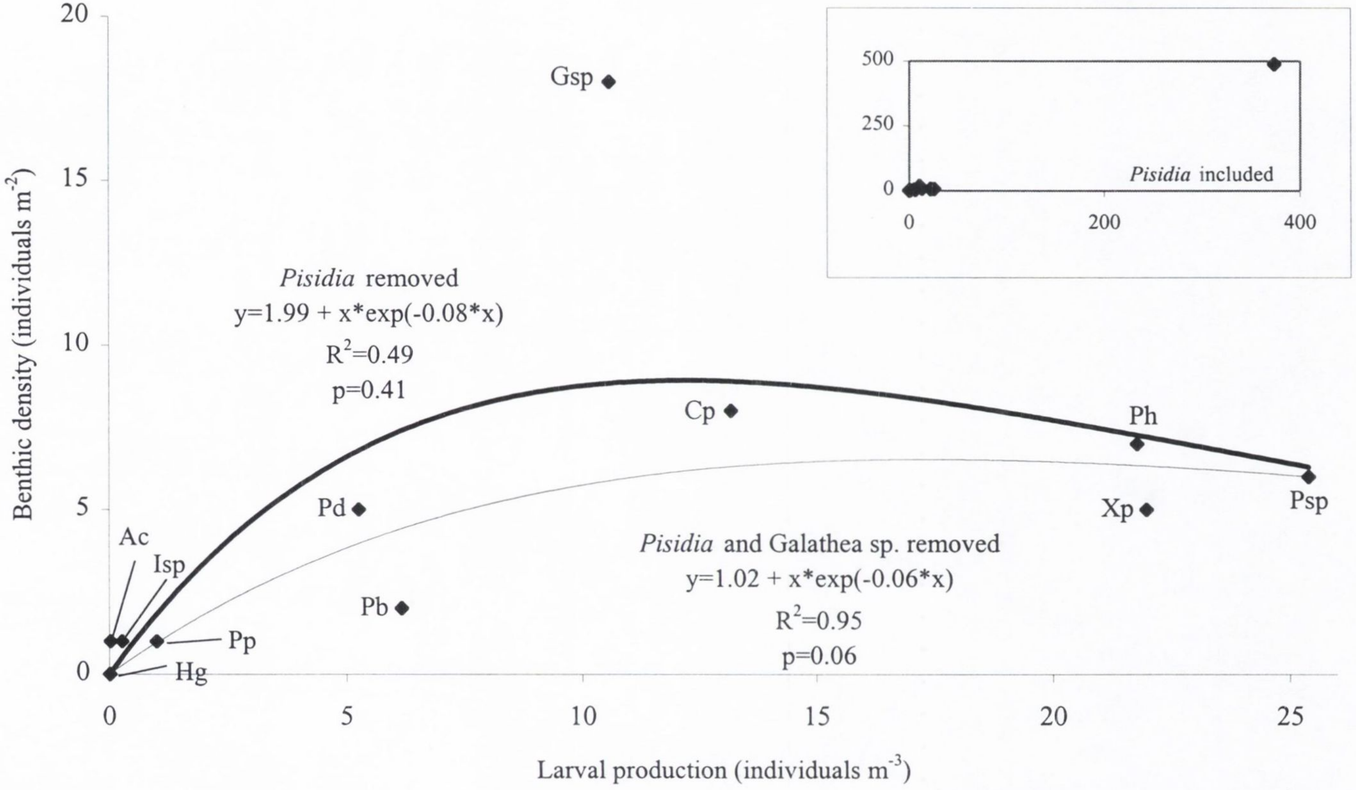


Figure 6.4a-e. Relationship between larval production and subsequent density of YOY decapods in the benthos from five distinct benthic habitats, 1998. Only model c) includes *Pisidia*. Benthic density (ind.m^{-2}) of *Pisidia* stated on other graphs corresponds to a larval production of 373 individuals m^{-3}.

Figure 4a. Cobble with no algal cover

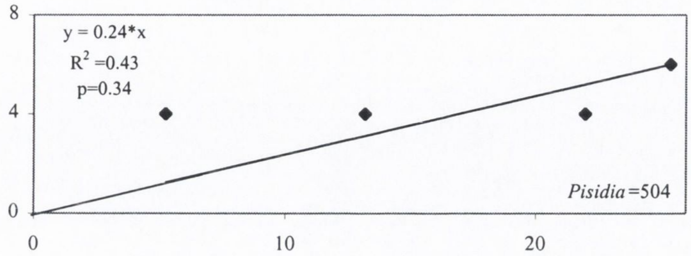


Figure 4b. Dense cobble with algae

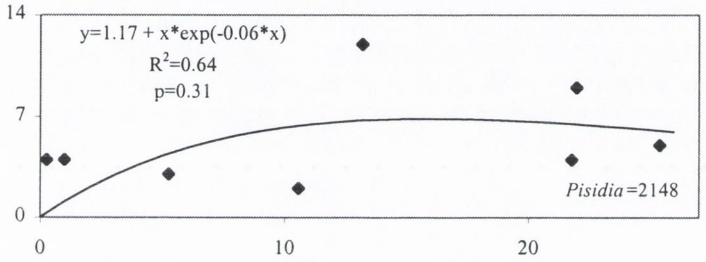


Figure 4c. Course sand and stone

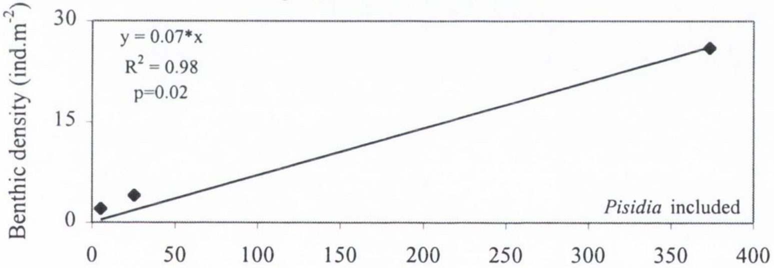


Figure 4d. Cobble with algal cover

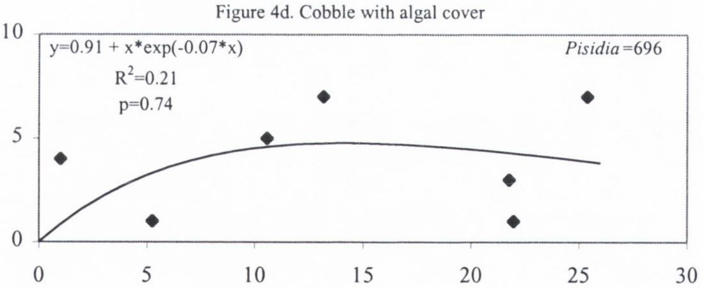
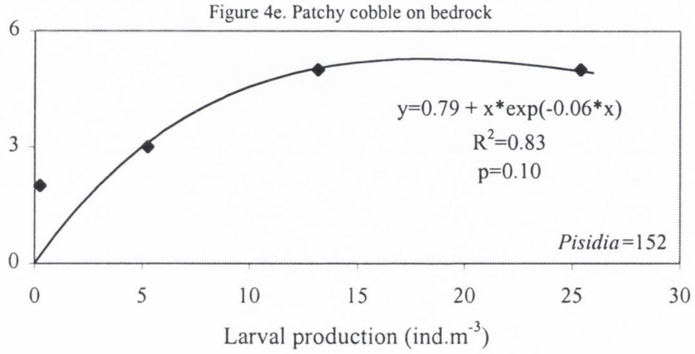


Figure 4e. Patchy cobble on bedrock



(Figure 6.5 inset). Again, the high density of *Pisidia longicornis* distorted the overall relationship. Removal of this species revealed a significant (R^2=>0.99, p=<0.01) density-dependent relationship (Figure 6.5) described by the Beverton-Holt stock-recruitment function. The R(max) asymptote value of 81 YOY benthic individuals m^{-2}, that represented the saturation density, was higher than the 54 individuals m^{-2} recorded in the population (excluding *Pisidia longicornis*).

Significant linear (Figure 6.6a & c) or density-dependent (Figure 6.6b, d & e) relationships were observed in models of the cumulative ranked larval production and subsequent density of YOY benthic individuals in the five habitats sampled in 1998 (Figure 6.6a-e). The R(max) or saturation value was greatest (63 individuals m^{-2}) in the dense cobble habitat (b). The actual cumulative density of YOY benthic individuals recorded in each of the sites b, d & e was lower than the R(max) saturation value predicted by the Beverton-Holt fitted models. The density of *Pisidia longicornis* varied widely, with extremely high densities recorded in dense cobble habitat (Figure 6.7 inset). The densities of some species, such as *Necora puber* and *Pirimela denticulata* (Montagu), were similar within each of the five habitat types sampled during 1998 (Figure 6.7). Other species such as *Cancer pagurus* and *Xantho pilipes* Milne Edwards were similarly abundant in more complex habitats, but were absent from areas that afforded less shelter. The density of benthic YOY *Galathea* spp. recorded in 1997 was more than twice that of those recorded at any site in 1998. The average density of YOY benthic individuals recorded in 1998, 5.2 individuals m^{-2}, would position *Galathea* spp. close to the average stock-recruitment curve proposed in Figure 6.3. Benthic densities for most species tended to be within a relatively close

Figure 6.5. Relationship between cumulative larval production ranked by species abundance and subsequent density of YOY decapods in the benthos for twelve species or groups, 1997. Species ranked in accordance with Table 1.

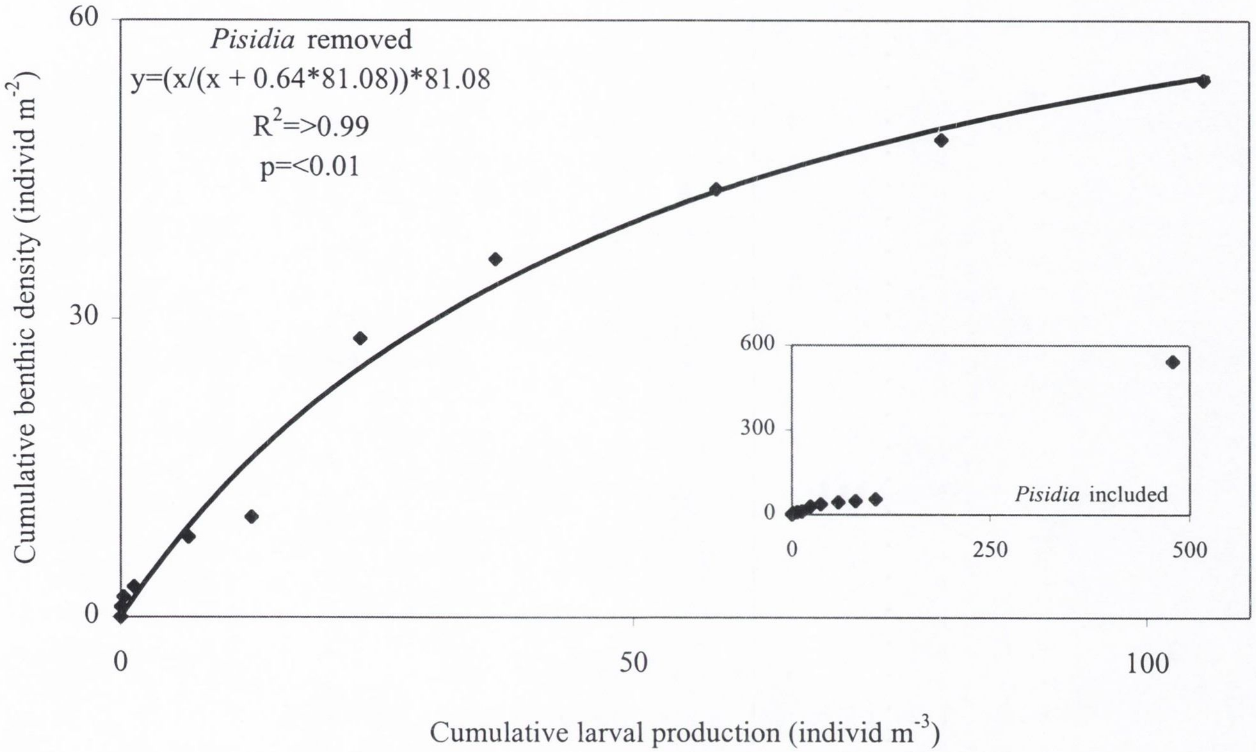


Figure 6.6a-e. Relationship between cumulative larval production ranked by species abundance and subsequent cumulative density of YOY decapods in the benthos for 12 species or groups from five distinct benthic habitats, 1998. Only c) includes *Pisidia*. Benthic density (ind.m^{-2}) of *Pisidia* stated on other graphs corresponds to an increase of 373 ind.m^{-3} in larval production

Figure 6a. Cobble with no algal cover.

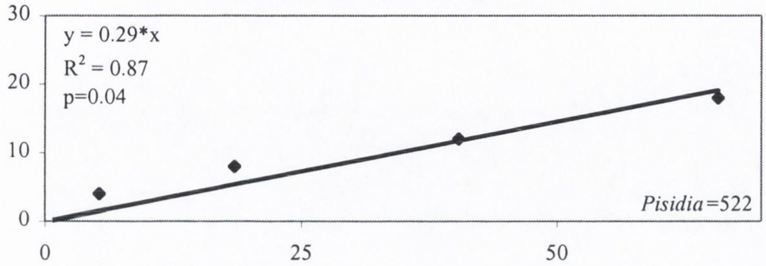


Figure 6b. Dense cobble with algae.

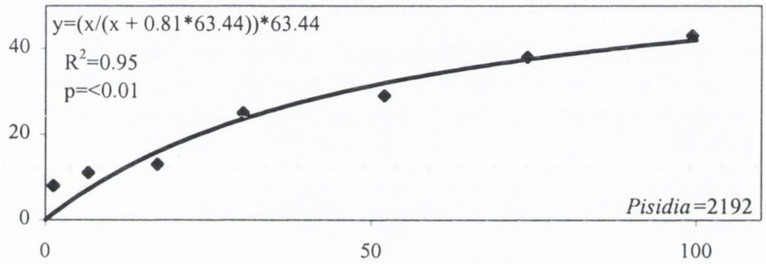


Figure 6c. Course sand and stone.

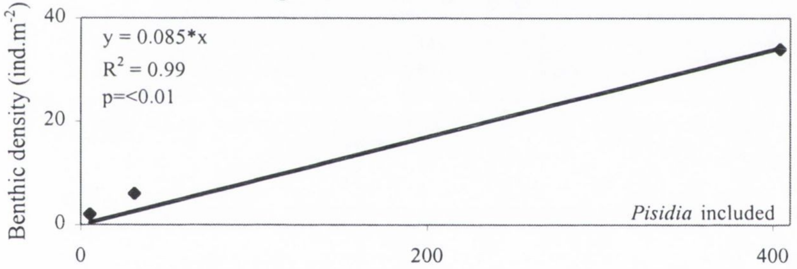


Figure 6d. Cobble with algal cover.

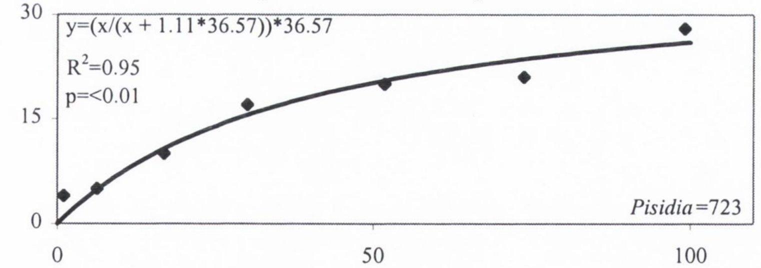


Figure 6e. Patchy cobble on bedrock.

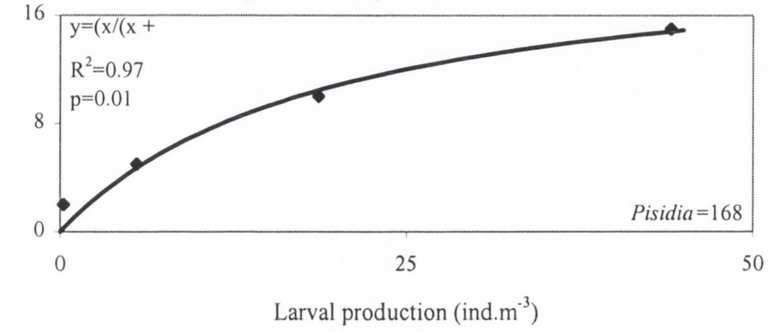
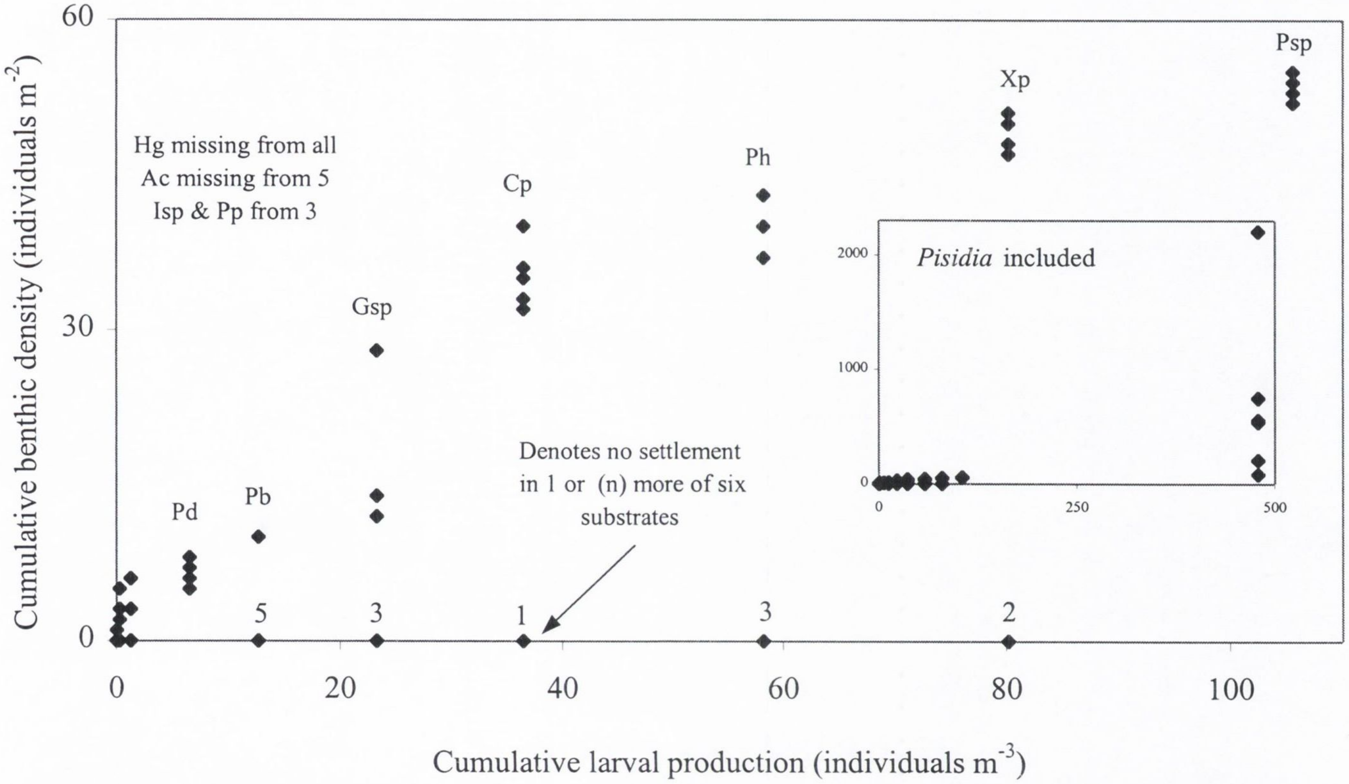


Figure 6.7. Relationship between cumulative larval production ranked by species abundance and subsequent cumulative density of YOY decapods in the benthos for twelve species or groups from a single habitat in 1997 and five distinct habitats in 1998. Full species names stated in Table 1.



range in suitable habitats, and undetectable in one or more less favourable sites (Figure 6.7).

DISCUSSION

Data were presented which allowed estimation of the relationship between larval production and the subsequent post-settlement densities of 12 decapod species. The models presented suggested that density dependence occurred with increasing levels of larval production. It would appear that the saturation density of the habitat was surpassed in the first model presented, which lead to overcompensation and less transfer (recruitment) to the benthos at high larval production. The saturation density predicted by the Beverton-Holt model was higher than the observed cumulative density.

The upper limits of the position species occupy on the larval production axis (x) in the multi-species stock-recruitment model is governed by the reproductive constraints on the adult population and factors affecting larval survival and transport. Adult body size, which is governed by growth rate and the maximum body size attainable, determines the number of eggs that can be successfully brooded (Reid & Corey, 1991; Somers, 1991). Egg loss through development due to crowding, caused by increase in egg size during development, has been documented (Sampedro *et al.*, 1997). The density and population size of mature adult brood stock determines total reproductive potential. The reproductive strategy of each species will also effect the number of eggs brooded. Species that are ‘k selective’ (McArthur & Wilson, 1967) invest relatively more energy and/or brooding time into each larvae produced when compared to ‘r strategists’. Although the lower energy investment into each individual produced by ‘r selected’ species may lead to higher rates of larval mortality, far greater numbers of offspring are produced. The reproductive strategy of a species can also affect the settlement behaviour of postlarvae (Palma *et al.*, 1998), with ‘k selected’ species exhibiting greater substrate specificity. It seems likely that the position of each species in the multi-species stock-recruitment space will vary annually within the constraints mentioned above, in response to fluctuations in physical and biological factors, and is capable of taking any position within a localised area in the model. ‘r strategists’, such as *Cancer pagurus*, often display greater annual recruitment variability relative to ‘k strategists’ such as *Homarus gammarus* (Cobb *et al.*, 1997), and are likely to occupy a position within a larger ‘window’ in the model.

Larval production estimates are affected by larval mortality in the plankton (Rumrill, 1990) due to physiological stresses (Pechenik, 1987; Wang & Widdows, 1991), starvation (Boidron-Metairon, 1995) and predation (Olson & McPherson, 1987). Transport of larvae away from the site of release by physical processes will also affect production estimates when larvae are not subsequently returned (Gaines *et al.*, 1985; Verdier-Bonnet *et al.*, 1997). The multi-species stock-recruitment model presented assumes that the position of a species on the recruitment (y) axis is defined by its level of larval production and not by species specific variation in the stock-recruitment relationships. Furthermore it assumes intra-specific rather the inter-specific competition is the mechanism determining the observed density dependence i.e. each point is independent.

Although the model assumes that recruitment is determined solely by the level of larval production, other factors can control the level of recruitment. Wind forced hydrodynamic processes (Young *et al.* 1998), ocean currents (White *et al.* 1988, McConnaughey *et al.* 1992) and tidal periodicity (Morgan *et al.*, 1996; Eggleston *et al.*, 1998) or magnitude (Robinson & Tully, in press a) can affect larval supply to suitable nursery habitats and the ability of postlarvae to settle. Favourable tidal periodicity may be required for delivery to suitable settlement habitats, while tidal magnitude may determine near-bed current speeds. The availability of suitable settlement substrate (Roughgarden *et al.* 1988), or the availability of shelter or refuges (Wahle & Steneck, 1991), will also determine population size. Mortality of early benthic phase juveniles can be rapid (Connell & Jones 1991) and of high magnitude (Moksnes *et al.* 1998). Significant sources of mortality include predation (Lavalli & Barshaw, 1986; Wahle & Steneck, 1992; Fernandez *et al.*, 1993a; Moksnes *et al.*, 1998), cannibalism (Fernandez *et al.*, 1993a; Smith, 1995; Lovrich & Sainte-Marie, 1997; Moksnes *et al.*, 1997; Moksnes *et al.*, 1998), disease (Aiken & Waddy, 1986) physical disturbance (Howard & Nunny, 1983; Pile *et al.*, 1996) and environmental stress (Bertness, 1981). In open populations, changes in juvenile abundance can occur due to dispersal (Iribarne *et al.*, 1994; Wahle & Incze, 1997), although decapods are often shelter dependent during early life (Wahle & Steneck, 1991) and are unlikely to undertake significant migrations during their first year.

The models presented without *Pisidia longicornis* conformed to a density dependent function with some saturation or compensation point reached, beyond which no further, or reductions, in abundance occurred. Significant intra-specific competition (Fernandez *et al.*, 1993a; Smith, 1995; Lovrich & Sainte-Marie, 1997;

Moksnes *et al.*, 1997; Moksnes *et al.*, 1998), saturation of suitable settlement habitats (Iribarne *et al.*, 1994; Wahle & Incze, 1997; Moksnes *et al*, 1998) or redirection of predator activity at higher density (Moksnes, 1999) may prevent further increases in benthic abundance. The linear functions presented for two habitats sampled in 1998 showed no signs of constraint within the confines of the data sets. The density of YOY decapods in the benthos within habitats with linear models fitted would appear to be constrained by larval supply, or the unsuitable nature of the substrate as a settlement habitat for decapods (Lipcius *et al.*, 1997). Low species number and overall decapod abundance at these two sites, relative to the others habitats sampled, may account for the lack of obvious density dependence.

The suggestion of density dependence was supported by the relationship between species in the cumulative model. This model assumes that the addition of each species has the same effect with open interaction between conspecifics and other species. The position occupied by each species in the model is likely to be influenced by the relative position of other species within the community. Although accumulation of benthic settlers appears to conform to a density dependent function, with the exception of *Pisidia longicornis*, this may be falsely suggested if the species at the higher end of the larval production scale have poor settlement ability bending the fitted line downwards. The model may be considered a simplification of the actual relationship between larval production and settlement, as settlement of species occurred simultaneously and not consecutively in rank order of larval production. Further additions to the larval production of certain species, or the introduction of a new species may result in the asymptote or saturation density, predicted as 81 individuals m^{-2} by the cumulative model, being reached. The saturation density was not reached in any of the habitats sampled. In a stable population, it is again possible that the exact position of each species in the model will fluctuate vertically within a pre-determined area which is defined by species ecology and habitat type. More severe variations within the community or environment may result in an interchanging of species along the line, alteration of the saturation density and the rate at which it is reached, or the elimination of one or more species. Intra-specific interactions may play an important role in determining the relative position of each species in the model. Juveniles of the two Polybiinae species recorded in benthic samples, *Necora puber* and *Liocarcinus pusilus* (Leach), and the edible crab *Cancer pagurus* readily predate smaller or soft-shelled conspecifics (pers. obs.). Early benthic mortality of these species is exceptionally high (Robinson & Tully, 1998b; Chapter 2), possibly contributing to their low benthic densities relative to larval production. Interaction between conspecifics may be less important for more gregarious non-predatory species such as *Pisidia longicornis* and *Galathea* spp.

The provision of artificial shelters and extension of natural preferred settlement habitats have been the subject of a number of studies in which attempts were made to increase production of decapod species (Scarratt, 1968; Sheehy, 1982). Artificial reefs have been shown to attract and support lobster in densities higher than surrounding areas (Scarratt, 1973) and in previously uninhabited substrates (Collins *et al.*, 1990). Some doubt remains as to whether these structure increase production or merely concentrate stocks (Addison & Bannister, 1994). Models like those presented in this paper may be of use when evaluating the effect of habitat enhancement. The position of species within the models (community structure), species composition, or the form of the models themselves may change in response to habitat manipulation.

An increase in the asymptote of the fitted model may not correspond to an increase in the recruitment of the desired species if its position in the model is lowered due to an increase in the upper constraints of recruitment for other species due to habitat enrichment. Similarly, no change or a decline in the asymptote of the stock-recruitment curve may not indicate failed enhancement if the upper constraints on recruitment increase for the target species.

Fogarty & Idoine (1986) recorded a significant density dependent relationship between the density of stage IV *Homarus americanus* Milne Edwards larvae and subsequent adult stock size 5-7yrs later. The Beverton-Holt model fitted to this single species relationship had a steep increase in recruitment at low larval production. The slope of the model fitted in this study was shallow at low levels of larval production indicating less transfer and evidence of overcompensation. The lower transfer efficiency may be a result of greater competition that is likely to occur in the more dense and diverse decapod community of northern Europe, relative to the species poor community of north eastern America and Canada.

The porcellanid crab *Pisidia longicornis* displays a larval production recruitment relationship that is distinct from all other species. Conspecifics of this small filter-feeding species co-exist in very high densities far in excess of any other decapod species in the area (Robinson & Tully, in press a). The YOY benthic density of this species was extremely high relative to the larval production of other species in models 1 & 2. Newly settled individuals grow rapidly and are capable of reproduction in the following spring. Very few individuals survive their second summer to contribute to production in the third year (Robinson & Tully, in press a).

Although individual fecundity is not considered particularly great (Sampedro *et al.*, 1997), the high density of individuals and extended settlement season leads to larval production and YOY benthic density far in excess of any other decapod species in the area. However, the high levels of recruitment observed in cobble were not reflected in less physically complex substrates, such as the sand and gravel habitat. Much lower densities of YOY *Pisidia* were detected in several habitats from which the adult was absent. Accordingly, the position of *Pisidia* in models describing the level of pelagic-benthic transfer in different habitats varied significantly.

The main substrate type studied in 1997 was similar to habitat (d) in 1998 in physical complexity and habitat characteristics. The 1998 study examined spatial variability in the magnitude and species composition of the YOY component, and the subsequent community structure persisting after one year. Significant differences in settlement densities and community structure were related to physical complexity of the nursery habitat (Robinson & Tully, in press b). In more marginal areas, with relatively low complexity, post-settlement processes lead to a YOY community structure significantly different to the resident species assemblage. This was not the case at site (d) where YOY and established community structure were similar. If the community within this habitat type is relatively stable, and a sufficient time series of data can be gathered, then larval production figures may be a useful stock predictor for species where level of transfer to the benthos is known (Phillips & Brown, 1989; Incze & Wahle, 1991). The transfer of larvae to benthic YOY production, and the resultant models, are strongly dependent on the physical complexity of the settlement substrate however.

If the stock-recruitment relationship in decapods can be described reliably by an average curve and the mechanisms controlling recruitment are therefore viewed as common across species then it may be possible to estimate recruitment from larval production in species which cannot be located on the sea bed. Widespread efforts to locate and characterise the nursery habitat and abundance of early benthic phase juvenile lobster, *Homarus gammarus*, have been unsuccessful to date (Howard & Bennett, 1979; Wickens, 1994; Anon, 1997). This is an obstacle in the management and prediction of stocks. It may be possible to utilise multi-species models to make estimations of recruitment for such poorly understood species if the fitted model represents the average stock-recruitment curve for decapod species. Larvae of *H. gammarus* can be sampled with neuston nets. Larval densities can then be used to estimate recruitment to the benthic habitat. The position of *Homarus* in the mutli-species stock-recruitment models here seemed to suggest that recruitment is constrained by limited larval supply, and that technical or operational measures to increase egg production in their exploited populations may be beneficial. Little extra production may result however, when the community as a whole is accounted for in the cumulative model where the saturation density seems to be approached. Using the models presented in the current study, if the transfer efficiency of *Achaeus cranchii*, the least abundant species, was assumed to be similar to that for the larval production estimate for *Homarus* then 18.4m^2 of seabed could be expected to contain a single YOY lobster. The author of this paper sampled 34m^2 of sub-tidal cobble habitat during the last two years. Failure to detect a single early benthic phase lobster during sampling of this scale, and in other recent studies of sub-tidal cobble substrates throughout Europe (Anon, 1997), may suggest sampling effort is being targeted towards habitats that do not represent the nursery grounds of this species.

The models presented here may also have value in the prediction and monitoring of the affect of the introduction of a new species. Introduced species can have a dramatic effect on existing fauna, significantly altering community structure (Grosholz & Ruiz, 1995; Lafferty & Kuris, 1996). Further work to determine the mechanisms controlling recruitment and where bottlenecks occur could use benthic pelagic migration traps (Moksnes, 1999) and settlement collectors (Benninger *et al.*, 1986) to examine the relationship between production-settlement-recruitment. This may provide additional information on constraints on recruitment due to larval supply and the effect that post-settlement processes have on early benthic decapod communities. Development of models for various habitat types within a defined recruitment area would assist in the evaluation of habitat enhancement, highlight the sources of any constraints on recruitment and improve the accuracy of stock-recruitment estimates.

GENERAL DISCUSSION

The aim of this study was to examine the early benthic life history of decapods within sub-tidal rocky cobble habitat. The decapod community studied, which is dominated numerically by the porcelain crab *Pisidia longicornis* (L.), is representative of most sub-tidal cobble habitats throughout northern Europe (Smaldon, 1972; González-Sanjurjo, 1982; Anon, 1997). A number of the species found in this community were of commercial importance, suggesting that the habitat studied may represent an important nursery ground from which juveniles recruit to the adult population. Prior to this study little was known of the structure or population dynamics of this decapod community in northern Europe. The data presented here represents the first description of settlement into these habitats, and the post-settlement processes that define subsequent recruitment, population parameters and community structure.

Larval supply, larval substrate selection and post-settlement processes together determine resultant adult community structure in benthic habitats (Gaines & Roughgarden, 1985; Eggleston & Armstrong, 1995). The spatial variation in community structure and population parameters between habitats with varying degrees of physical complexity described in this study appeared to be caused by the selectivity of settling megalopae and between-site differences in post-settlement processes, assuming larval supply was constant between such closely situated sites. It is likely however, that larval supply also determines resultant benthic communities on a broader spatial scale. Oceanagraphic processes can lead to the retention of larvae in the locality of release (Alldredge & Hammer, 1980), transport larvae away and then return them at a later stage of development (Shanks, 1983; McConaugha, 1988;

Rothlisberg, 1988), or permanently remove larvae from the area (Gaines *et al.*, 1985; Verdier-Bonnet *et al.*, 1997). The behavioural responses of postlarvae, including directional orientation, vertical migration and active swimming, are also important for delivery to settlement habitats (Cobb *et al.*, 1989; Katz *et al.*, 1994; Condie *et al.*, 1999). A major assumption of the stock-recruitment models presented in the current study was that the larvae production sampled within the area was subsequently delivered directly to the benthos below. No account was taken of the origin of the larval production recorded in the area, or the losses and gains of production due to physical oceanographic processes or larval behaviour, leaving the boundaries of the production area and the population itself undefined. The community studied was effectively considered a self-contained population unit, closed to immigration, emigration and recruitment of larvae from other areas (Orensanz & Jamieson, 1998). Multi-species models of the kind presented in the current study could be developed to include data that accounts for losses (sinks) and gains (sources) of larval production. Modelling of physical oceanographic processes such as currents, drifts, jets, tides and wind driven hydrodynamics contribute to models of larval transport (Fogarty, 1998; Wing *et al.*, 1998; Condie *et al.*, 1999). Larval behaviour such as vertical migration and settlement, and their effect on larval transport, can also form inputs to recruitment modelling (Condie *et al.*, 1999). The methodology for the linking of sub-populations by accounting for sources and sinks of larval production in this way (i.e. metapopulation analysis) is only now being developed for single species models (Fogarty, 1998; Wing *et al.*, 1998; Condie *et al.*, 1999). Knowledge of in spatial and temporal variability in larval supply, and in subsequent settlement and recruitment (as described in the current study) is necessary for accurate metapopulation analysis (Wing *et al.*, 1998)

Although the spatial variability between habitats with varying degrees of physical complexity described in this study appeared to be caused by the substrate specificity of settling larvae and differences in post-settlement processes, it was not possible to separate their relative influences. The magnitude and timing of settlement *per se* was not measured. The number of first crab stage individuals that were quantified in benthic samples may have already been affected by rapid (Connell & Jones 1991) and high (Moksnes *et al.* 1998) initial mortality, and should not be used as a reliable indication of larval supply to the benthos or subsequent settlement. Benthic pelagic migration traps (Moksnes, 1999) and settlement collectors (Benninger *et al.*, 1986) could be used in future studies to quantify settlement accurately. Although settlement was not quantified, it appears that many of the species in the community studied display some degree of substrate specificity at settlement, avoiding more marginal areas that offer little shelter to either the settler or individuals at a later stage of development. The ability of larvae to settle into and persist in suitable habitats is believed to cause patterns of recruitment to differ from those of larval supply (Risk, 1997). Settlement of larvae into habitats that do not support the adult of the species, indicating that these larvae are unlikely to recruit to the adult population and contribute to future production, represents a loss of production. Areas that attract settlement of species into habitats they are not suited to can be regarded as sinks for the larval population (Lipcius *et al.*, 1997). The results presented in this thesis highlight the need for a detailed knowledge of the benthic habitat characteristics of settlement areas, especially when extrapolating production or recruitment estimates over large areas with patchy or discontinuous habitat.

Post-settlement processes acting on the population generally fall into two categories; those that effect mortality and those that effect displacement. Differences between the community structure of the young of the year cohort (YOY) and previously settled individuals in less physically complex habitats in the current study indicated the importance of post-settlement processes in shaping the resultant community. It is likely that YOY species composition was altered to some degree in all the habitats sampled before their second year, with more dramatic changes occurring at sub-optimal sites where post-settlement processes have an increased influence on the community. Adult abundance and community structure is likely to be decoupled from larval supply, settlement rate and juvenile abundance through the effects of varying habitat quality upon post-larval and juvenile survival (Lipcius *et al.*, 1997). It is often difficult to separate the relative influences of mortality and displacement regulating benthic communities. Mortality of YOY crab stages was high for most species examined in this study, but declined with increasing body size. Although habitat shifts and movements of decapod crustaceans have been documented (Campbell, 1986; Orth & van Montfrans, 1987; Fernandez *et al.*, 1993b; Iribarne *et al.*, 1994; Lovrich *et al.*, 1995; Pile *et al.*, 1996; Wahle & Incze, 1997), it seems unlikely that shelter dependent benthic juveniles undertake significant movements during their first year. The lack of detectable effects between enclosed and unenclosed experimental populations for most species in this study would support this theory. Movement is likely to become increasingly important for species that are required to relocate due to resource shortage 'bottlenecks' (Caddy, 1986; Wahle & Steneck, 1991; Wahle & Incze, 1997; Moksnes *et al.*, 1998) or where habitat requirements change during development (Orth & van Montfrans, 1987; Pile *et al.*, 1996). The ability to disperse is believed to play an important role in reducing intra-specific competition in mobile species (Iribarne *et al.*, 1994). High localised densities of conspecifics can result in reduced growth due to physically (Cobb & Tamm, 1974) or chemically (Nelson *et al.*, 1980) mediated suppression of the metabolism of smaller individuals (Carlberg *et al.*, 1979; O'Donovan, 1998). The reduction of growth and survival with increasing density or presence of larger conspecifics could influence the time to recruit to commercial size. The results presented in this study suggest that the growth potential of *Cancer pagurus* L. was unaffected by the presence of larger conspecifics however. Relaxation of growth suppression is important when the high density of juvenile crabs from numerous cohorts and species recorded in this study is considered, especially if sub-tidal habitats represent the main nursery ground for these species.

Previous studies have encountered difficulty in defining the annual stock-recruitment relationship in single species models (Phillips & Brown, 1989; Incze & Wahle, 1991; Incze *et al.* 1997). This has hampered attempts to define the constraints placed on recruitment and the sources of 'bottlenecks' in population growth (Caddy, 1986; Wahle & Steneck, 1991; Moksnes *et al.*, 1998). The stock-recruitment curves presented in this study represent the first attempt to define the relationship between larval production and subsequent density of YOY in the benthos in a multi-species framework. When certain assumptions are made, models of this type may provide information on constraints on recruitment due to larval supply or saturation/availability of suitable benthic habitat. Development of models for various habitat types within a defined recruitment area would assist in the evaluation of habitat enhancement, highlight the sources of any constraints on recruitment and improve the accuracy of stock-recruitment estimates. The predictive power of these models could be improved when temporal data sets such as the one presented in this study are used as a guide for selecting periods to conduct benthic sampling to 'ground truth' recruitment predictions. Intra and inter-annual variation identified by time series benthic sampling may help refine the models in describing sources and causes of annual recruitment fluctuation. Variation in the form of the stock-recruitment relationship between habitats, and the spatial variability in community structure and population parameters with physical complexity highlights the need for caution when extrapolating recruitment estimates over large areas with patchy substrate characteristics. Even when the sources of error associated with larval production estimates in the models are considered, together with the simplicity and assumptions of the models, the significance and clarity of the relationships presented are encouraging.

Exploitation of decapod species by commercial fisheries is likely to increase (where stock size permits) as the size, range and efficiency of vessels increases (Anon, 1999). Further development of informed stock prediction and stock management will be required to maintain sustainable yield, and to protect both the target species and other non-commercial species in the community. The importance of shallow water sites as nursery grounds for decapod species is only beginning to be realised. A comprehensive understanding of decapod early life history and the relative effects that larval supply, larval substrate selectivity, habitat availability and post-settlement processes have in shaping decapod communities is required. Prediction and detection of intra-annual and inter-annual variation in settlement and recruitment of species resident in the communities of sub-tidal nursery habitats will allow informed management of these areas and the fisheries that depend on them, whilst conserving the resident decapod communities. This study has utilised novel methods to provide quantitative information on these communities and the processes that control their development.

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