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SETTLEMENT AND RECRUITMENT OF ECHINODERMS IN KELP BEDS AND BARRENS

by

Toby Balch

Submitted in partial fulfillment of the requirements
for the degree of Doctor of Philosophy

at

Dalhousie University
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The undersigned hereby certify that they have read and recommend to the Faculty of Graduate Studies for acceptance a thesis entitled "Settlement and Recruitment of Echinoderms in Kelp Beds and Barrens"

by Toby Balch

in partial fulfillment of the requirements for the degree of Doctor of Philosophy.

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ABSTRACT

This thesis examines temporal and spatial variability in settlement and recruitment of echinoderms in rocky subtidal habitats. A review of the literature revealed that the processes which regulate the transitions from early life stages through to adulthood, and thereby determine the distribution and abundance of echinoderm populations, remain poorly understood. However, a salient feature of most echinoderm populations is a high degree of temporal and spatial variability in settlement and recruitment. In this study, settlement of echinoderm species was measured on artificial collectors placed on and above the bottom in kelp beds and barrens at multiple sites and sampled over a variety of temporal (days to years) and spatial (metres to 100's of kilometres) scales. Settlement of echinoids (*Strongylocentrotus droebachiensis*) measured in 3 regions of the northwest Atlantic showed order of magnitude differences between regions, where settlement was highest in the Gulf of Maine, lowest in the Bay of Fundy and intermediate in Nova Scotia. Within each region, settlement differed between sites but was within the same order of magnitude. In Nova Scotia, settlement of ophiuroids (*Ophiopholis aculeata*, *Ophiura*) sampled over 3 day intervals was compared with concurrent hydrographic and meteorologic measures. A major settlement pulse occurred over one 3 day period and was associated with minor fluctuations in the physical environment. Sampling every 2 weeks over 3 years in kelp beds and barrens at 2 sites (exposed and sheltered) showed settlement pulses of ophiuroids (*O. aculeata*, *Ophiura*), asteroids (*Asterias*) and echinoids (*S. droebachiensis*, *Echinarachnius parma*) occurred between July and September of each year. Timing of settlement differed consistently among species, the magnitude of each pulse varied between years and species, and the year of maximum settlement differed between species. Settlement of all species was greater at the sheltered site but patterns were not consistent among species between habitats. Sampling settlement concurrently at different frequencies and on different collector types gave different estimates of settlement. This indicates the need for calibration across studies and assessment of sampling artifacts (e.g. changes in collector quality, post-settlement mortality or migration) which can occur over longer deployment intervals. For most species sampled, settlement predicted recruit density in natural populations the following year. However, the strength of the relationship varied between species, probably because of differing post-settlement processes.

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PREFACE

Some of the research described in this thesis has been published or is in press in the scientific literature. The references to the publications are as follows:

The literature reviewed in Chapter 1 is also presented in:

Balch T, Scheibling RE (in press) Larval supply, settlement and recruitment in echinoderms. In: Lawrence J, Jangoux M (eds) Echinoderm Studies 6. A.A. Balkema, Rotterdam

The research in Chapter 2 is also described in:

Balch T, Scheibling RE, Harris LG, Chester CM, Robinson SMC (1998) Variation in settlement of *Strongylocentrotus droebachiensis* in the northwest Atlantic: Effects of spatial scale and sampling method. In: Mooi R, Telford M (eds) Echinoderms: San Francisco. A.A. Balkema, Rotterdam, p 555-560

Written permission was obtained from A.A. Balkema (for Chapter 2) to include the material in this publication in my thesis.

The research in Chapter 3 is also described in:

Balch T, Hatcher BG, Scheibling RE (in press) A major settlement event associated with minor meteorologic and oceanographic fluctuations. Can J Zool

Chapter 1: General Introduction

The role of settlement and recruitment in determining population and community structure, or what has been coined "supply-side ecology" (Lewin 1986), has been the focus of intensive study for over a decade (reviewed by Underwood & Fairweather 1989, Ólafsson et al. 1994, Booth & Brosnan 1995, Caley et al. 1996, Hunt & Scheibling 1997). Settlement of benthic marine invertebrates is generally defined as the attachment of larvae to the substratum and attendant metamorphosis into the juvenile form (reviewed by Pawlik 1992). Recruitment is usually defined operationally as occurring some time after settlement when individuals can be reliably counted and some post-settlement mortality or migration may have occurred (*sensu* Keough & Downes 1982). Consequently, methodological differences often complicate comparisons of recruitment within and among taxa and habitats. Most studies on recruitment have involved sessile species, such as barnacles and mussels, in rocky intertidal habitats (e.g. Connell 1985, Gaines & Roughgarden 1985, Sutherland 1987, 1990, Raimondi 1990, Menge 1991, Minchinton & Scheibling 1991). Fewer studies have involved mobile species, such as echinoderms, for which patterns of distribution and abundance are influenced both by post-settlement mortality and migration (Hunt & Scheibling 1997).

Echinoderms are ubiquitous in all marine benthic habitats from the intertidal zone to the deep-sea. They are significant components of the trophic structure in many communities and serve important ecological roles as both predators and prey. In some cases, their impact as predators or grazers can be catastrophic. Population outbreaks of the asteroid *Acanthaster planci*, for example, have devastated coral reefs in the south Pacific (Moran 1986, Johnson 1992a) and intensive grazing by strongylocentrotid echinoids has destroyed kelp forests throughout the north Atlantic and Pacific (Harrold & Pearse 1987, Vadas & Elner 1992). Consequently, these species have been viewed as pests to be controlled or eradicated. In contrast, some holothuroids and echinoids, are valued food resources and form the basis of major fisheries around the world (Sloan 1984). Yet others, such as ophiuroids and crinoids, are suspension feeders comprising a large proportion of the macrofaunal biomass of sedimentary environments, particularly in the deep-sea (Haedrich et al. 1980).

In view of their considerable ecological and economic importance, the population ecology of many echinoderms, particularly asteroids and echinoids, has been extensively studied. However, the importance of early life-history events in determining population structure and dynamics remains poorly understood for most species. The larval phase is a critical component of the life-history of echinoderms and other marine invertebrates with meroplanktonic larvae. Factors determining larval supply to benthic habitats include abiotic (e.g. currents, temperature, salinity) and biotic factors (e.g. larval behaviour, food availability, predation) which regulate larval production, development and survival (reviewed by Young & Chia 1987, Rumrill 1990). Settlement can be induced by a variety of biological, physical and chemical factors (reviewed by Rodriguez et al. 1993) but their importance relative to pre- and post-settlement processes is not clear for echinoderms (reviewed by Chia et al. 1984, Pearce 1997). Ebert (1983) reviewed studies of recruitment in echinoderms and found that recruitment was spatially and temporally variable both within and among species. He concluded that many factors contribute to recruitment variability in ways that remain poorly understood. In many studies, researchers have made inferences about patterns of settlement and recruitment based on population size structure or distributional patterns of older individuals (Ebert 1983, Chia et al. 1984), although sampling constraints and the small scale of such observations have limited the strength or generality of the conclusions.

In this review, I summarise recent progress (much of it over the past 14 years since Ebert's 1983 review) in the search for links between larval supply, settlement, and recruitment in echinoderms, which ultimately determine the distribution and abundance of populations. The text is divided into 4 major sections based on different stages of the early life-history of echinoderms and the processes that influence them: 1) factors affecting larval supply, 2) induction of settlement, 3) spatial and temporal patterns of settlement and recruitment, and 4) post-settlement processes. The section on patterns of settlement and recruitment is central to the review and studies on this topic from the 4 most studied echinoderm classes are summarised in tabular form to facilitate comparisons within and between species, classes and geographic regions. My intent is to provide a comprehensive synthesis and critical evaluation of the literature on patterns and processes of larval supply, settlement and recruitment in echinoderms, and to identify gaps in our knowledge which may guide future research.

FACTORS AFFECTING LARVAL SUPPLY

Hydrodynamics

While in the water column, invertebrate larvae generally have little control over horizontal movement, although they may actively migrate vertically (reviewed by Young & Chia 1987). Echinoderm larvae usually are found near the sea surface (Rumrill 1988a, Pedrotti & Fenaux 1992) where ocean currents and wind may enhance larval dispersal (reviewed by Ebert 1983, Harrold & Pearse 1987, Pearse & Cameron 1991). Larval dispersal is also common in deep-sea echinoderms (Eckelbarger 1994, Pearse 1994, Tyler et al. 1994, Young 1994a, b) where larvae can be retained locally or advected away from spawning areas by currents (Mullineaux 1994). To fully understand the effect of hydrodynamics on larval supply to the benthos, various spatial scales must be considered. Because the arrival of planktonic larvae at suitable settlement sites is primarily dependant on advective transport, both local hydrodynamics and large-scale oceanographic features are important determinants of recruitment success (reviewed by Shanks 1995). Ebert and coworkers (Ebert 1983, Ebert et al. 1994) documented the existence of a latitudinal cline in settlement for *Strongylocentrotus purpuratus* and *S. franciscanus* and correlated settlement with general oceanographic processes along the California coast. They found settlement was more variable along the northern coast, which is subjected to greater offshore advection rates, than in the southern California Bight, which is thought to have a longer residence period and therefore retain larvae. Ebert & Russel (1988), however, did not observe this latitudinal cline in settlement of *S. purpuratus* in intertidal populations from central California to Oregon. They proposed that local topographic features such as capes and headlands reduced recruitment due to upwelling and cold water plumes that advect larvae away from the coast. At sites between headlands with no predictable upwelling, there was substantial annual recruitment. Further north in Washington, Paine (1986) found that recruitment of *S. purpuratus* occurred only 4 times in 22 years suggesting sporadic supply of larvae to the area. Although Paine (1986) found no consistent correlation with El Niño events at this latitude, recruitment was associated with above average sea temperatures which he assumes is an indication of transport of larvae in northward flowing currents.

Most echinoderm larvae have relatively long planktonic periods and are capable of delaying metamorphosis in the absence of suitable substrata (Strathmann 1978a, b, Bosch et al. 1989). Echinoid, asteroid and ophiuroid larvae have been found in offshore plankton tows in the central Pacific where currents may enable long distance dispersal between distant islands (Scheltema 1986). Once larvae are advected far offshore, however, the likelihood of settling in a suitable habitat is greatly diminished unless currents deliver them to coastal areas when they are competent to settle (Jackson & Strathmann 1981). In the absence of a settlement substrate, ophiuroids may metamorphose in the plankton or settle indiscriminately resulting in major losses (Hendler 1991). For example, Mileikovsky (1968) found post-larval ophiuroids in plankton tows down to 4000 m in the Oyashio Current (northwest Pacific) and attributed a decrease in numbers with depth to increasing mortality. Local hydrodynamic processes may act to retain larvae within the coastal region. Pedrotti & Fenaux (1992) found that ophiuroid and echinoid larvae remained in the surface layer in the Bay of Villfranche, Mediterranean and rarely occurred beyond a divergence zone 30 km offshore. At a smaller spatial scale, Sewell & Watson (1993) found high densities of asteroid larvae in plankton tows in an enclosed bay in Nootka Sound, British Columbia, where there was substantial recruitment of *Pisaster ochraceus*. They proposed that the larvae are spawned and retained within the bay where they settle and then disperse over time. Similarly, Lubchenco-Menge & Menge (1974) found atypically high densities of recruits of *P. ochraceus* at 1 site on San Juan Island, Washington, which they considered a nursery area.

By far the largest body of research on asteroid early life-history is based on 1 species, the Crown-of-thorns starfish *Acanthaster planci*. This research has been motivated by population outbreaks of *A. planci* which have had catastrophic effects on coral reefs throughout the western tropical Pacific (reviewed by Moran 1986, Birkeland & Lucas 1990). There is general recognition that larval supply, settlement and recruitment are critical aspects of this problem, although the relative importance of each of these processes in initiating population outbreaks remains speculative (Johnson 1992b). The genetic relatedness of populations of *A. planci* throughout the Pacific suggests that there is widespread dispersal of larvae and considerable gene flow within reef systems connected by ocean currents (Benzie 1992). Populations on the Great Barrier Reef are genetically homogeneous, suggesting that outbreak populations arise from a single source (Nash et al. 1988, Benzie 1992). Although the primary source of larvae is not known, the 2 series of outbreaks of *A. planci* recorded on the Great Barrier Reef during the past 4 decades have progressed from north to south (Johnson 1992b, Moran et al. 1992) presumably by advection of larvae (Nash et al. 1988). Hydrodynamic models of larval dispersal, correlated with data on reported outbreaks, showed that the severity of the outbreak decreases, and the proximity to the mainland increases, as larvae disperse southward (James & Scandol 1992, Scandol & James 1992). Black & Moran (1991) developed a numerical model of current patterns and larval supply to 6 reefs in the central Great Barrier Reef. They found a clear correspondence between observed and predicted distributions of populations of *A. planci* in all 6 simulations and concluded that hydrodynamics and larval supply are largely responsible for recruitment patterns. Recruitment of *A. planci* probably occurs in deeper water on the reef slope; subsequent migration up the reef slope results in outbreaks (Johnson et al. 1991).

Temperature and salinity

Thorson (1950) proposed that increased temperature may enhance settlement by accelerating larval development and reducing the period that larvae are exposed to planktonic predators. Evidence for a correlation between temperature and recruitment of echinoids was reviewed by Ebert (1983) who found a positive relationship for echinoids (species not stated) in Japan, an inverse relationship for *Strongylocentrotus purpuratus* in southern California, and no obvious relationship for *S. purpuratus* in Oregon. In a laboratory study, Hart & Scheibling (1988) showed that temperature has a strong positive influence on larval development of *S. droebachiensis.* By comparing sea temperature patterns off Nova Scotia in the early 1980's to recruitment events during the same period, they found that recruitment tended to occur in years of relatively warm spring sea temperature and not in colder years. Long term records for the same area show abnormally warm spring sea temperatures in 1960 and 1983, which preceded echinoid population outbreaks in the late 1960's and the early 1990's respectively (Hart & Scheibling 1988, Scheibling 1996). In accordance with Thorson's hypothesis, Hart & Scheibling (1988) proposed that increased larval survival during warm years results in recruitment pulses which lead to population outbreaks several years later. Other studies of this species, however, have suggested an inverse relationship between recruitment and sea temperature during larval development. Foreman (1977) attributed heavy recruitment of *S. droebachiensis* in British Columbia in 1969 to record low spring temperatures and Himmelman (1986) related weak recruitment at sheltered sites in Newfoundland to relatively high water temperatures. These equivocal findings suggest that temperature alone does not reliably explain recruitment patterns. Changes in sea temperature may simply reflect shifts in local hydrodynamics or other environmental factors, such as salinity, food availability or predator abundance, which may either enhance or limit larval survival.

The temperature dependence of developmental rate also has been proposed as a mechanism influencing settlement rates in asteroids. Laboratory experiments with *Acanthaster planci* have shown the length of the larval period ranges from 9 to 28 days and decreases with increasing temperature between 25 °C and 32 °C (reviewed by Moran 1986, Johnson 1992b). Larvae of *A. planci* are also found to respond to differences in salinity. Wide salinity ranges (21 to 33 ‰) can be tolerated but survival is greatest at 30 ‰ (reviewed by Moran 1986, Brodie 1992). However, Brodie (1992) concluded that fluctuations in temperature and salinity are relatively minor on the Great Barrier Reef and are probably not responsible for outbreaks of *A. planci* in that region.

Predation

Although predation in the plankton has long been recognised as a major component of larval mortality (Thorson 1950), few studies have examined predation of echinoderm larvae (reviewed by Ebert 1983, Harrold & Pearse 1987, Young & Chia 1987, Rumrill 1990, Scheibling 1996). Laboratory experiments on predation of embryos and larvae of *Dendraster exentricus*, *Strongylocentrotus franciscanus* and *S. purpuratus* showed that planktonic invertebrate predators, such as crustaceans, chaetognaths, medusae and ctenophores, selectively feed on embryos and early larval stages, whereas small planktivorous fish choose the larger plutei (Rumrill & Chia 1985, Pennington et al. 1986). Possible mechanisms which have been proposed to explain stage-specific predation include selection of prey size by predators, escape swimming behaviour of larvae, and larval structural defences (Rumrill & Chia 1985, Pennington et al. 1986).

As larvae approach the bottom they become exposed to a suite of suspension-feeding benthic invertebrates including mussels, ophiuroids, ascidians, anemones, and tunicates (Hooper 1980, Cowden et al. 1984). In the laboratory, Tegner & Dayton (1981) offered larvae of *Strongylocentrotus purpuratus* to 3 species of bryozoans and a serpulid polychaete which are common suspension feeders inhabiting kelp fronds. They found that only the polychaete could consume young plutei and that it had difficulty consuming larger, mature plutei. They concluded that it is unlikely that these filter feeders reduce larval abundance within a kelp forest, and suggested that planktivorous fish are more likely responsible (see also Gaines & Roughgarden 1987).

The coral *Pocillopora damicornis* and several species of fish have been observed to feed on eggs and/or larvae of *Acanthaster planci* (Yamaguchi 1973, and reviewed by Yamaguchi 1975, Moran 1986). However, laboratory studies have shown that some species of fish reject *A. planci* eggs and larvae, suggesting a chemical defence (reviewed by Yamaguchi 1975, Moran 1986). Lucas et al. (1979) found that pomacentrid fish rejected gelatin food particles with extracts of saponins from larval and adult *A. planci* and concluded that the concentrations of saponins in eggs and larvae are sufficient to limit predation. A chemical defence is also proposed for larvae of *Pisaster ochraceus* and for 3 species of echinoids which had higher survival rates than polychaete, gastropod or cirriped larvae when offered to mussels or ascidians in the laboratory (Cowden et al. 1984, but see also Young & Chia 1987).

Starvation

Starvation is a possible cause of larval mortality, although in reviewing the literature on nutrition of larval echinoids, Pearse & Cameron (1991) concluded that starvation is probably less important than predation in limiting larval survival. Strathmann (1996) reviewed several studies on feeding rates and natural densities of echinoderm larvae and concluded that death through starvation is unlikely under most conditions, although food limitation may occur in nutrient poor waters. Laboratory studies on larvae of the asteroid *Asterina miniata* showed that food limitation slows development, extends the time to metamorphosis, and reduces survival (Allison 1994, Basch & Pearse 1996). Basch & Pearse (1996) found that larvae of *A. miniata* reared in field enclosures developed faster than those in the laboratory where different hydrodynamic or light regimes may have reduced food capture or quality. In laboratory feeding experiments with larvae of *Acanthaster planci*, Lucas (1982) found that food limitation prevented development to the late brachiolaria stage. He suggested that starvation and/or increased predation associated with a longer larval period may reduce survival of larvae of *A. planci* on the Great Barrier Reef under food-limited conditions. However, Olson (1985) pointed out that food used in laboratory studies differs in composition from natural food resources and proposed that a mixed diet may not be limiting, even at the same particle concentrations. He used *in situ* culture chambers to examine larval survival of *A. planci* under natural food levels on the Great Barrier Reef. Surviving larvae did not appear to be food limited, although survivorship was relatively low (40 to 58 %). Olson (1985) attributed this to handling error but it is clear from discrepancies between laboratory and field studies that more experimentation is needed to resolve the issue of food limitation.

Birkeland (1982) correlated outbreaks of *Acanthaster planci* with heavy rainfall events and proposed that terrestrial runoff, which results in phytoplankton blooms, enhances larval survival, assuming the larvae normally are food limited. However, Moran (1986) pointed out some of the weaknesses with this correlational hypothesis and concluded that it is not well supported for some regions, such as the Great Barrier Reef (but see also Shanks 1995). Brodie (1992) reviewed several hypotheses relating enhanced larval survival of *A. planci* to various effects of runoff, including increased nutrient supply, increased mortality of predators, a reduction in salinity to an optimal level and increased temperature. Although he found the existing evidence for each of these hypotheses to be inconclusive, he suggested that biotic and abiotic effects of riverine input should not be discounted, and that further investigation may elucidate their roles in causing primary outbreaks.

Summary and Conclusions

Although much research has been done on larval behaviour in relation to the dynamics of dispersal, most studies on larval echinoderms have been conducted in the laboratory. Field studies have tended to focus on distribution in the water column and have not followed larvae through to settlement. Despite major advances during the past decade in methods of marking and tracking larvae (reviewed by Levin 1990), there remain substantial deficiencies in our present understanding of larval dispersal and dynamics. New methods such as the use of genetic markers for larval tracking may enable researchers to determine the discreteness of populations and identify potential sources of larvae (Palumbi 1995, Medeiros-Bergen et al. 1995). Hydrodynamic models of dispersal, which have been proven effective in predicting recruitment of *Acanthaster planci* (Black & Moran 1991), could be applied to other species to obtain a more general understanding of the relationship between physical factors and larval supply to benthic habitats. There is strong evidence for regulation of settlement by currents and hydrodynamic forcing. However, these factors can act at different spatial scales, all of which must be considered before fully understanding settlement patterns. The roles of larval predation and starvation in determining settlement and recruitment also remain unclear. Laboratory studies have identified some predators of echinoderm larvae and have shown that larvae possess chemical, structural, and behavioural defences to resist predation. Although starvation seems to be less important than predation in regulating larval abundance, this needs to be tested experimentally under realistic conditions of food availability and predator abundance, preferably in the field (e.g. Olson 1985).

INDUCTION OF SETTLEMENT

Numerous laboratory experiments (mostly with echinoids) have documented various cues for induction of settlement and metamorphosis of echinoderm larvae (reviewed by Strathmann 1978b, Chia et al. 1984, Chia 1989, Rodriguez et al. 1993, Pearce 1997). Larvae of regular echinoid species, including *Anthocidaris crassispina, Arbacia punctulata, Lytechinus pictus, Pseudocentrotus depressus, Strongylocentrotus droebachiensis* and *S. purpuratus*, have been found to settle in response to a variety of microbial and/or algal films that occur on natural substrata (Cameron & Hinegardner 1974, Cameron & Schroeter 1980, Rowley 1989, Pearce & Scheibling 1990a, 1991, Kitamura et al. 1993, reviewed by Morse 1992). Although specific inducers have been isolated, studies which have tested a variety of substrata suggest that larvae are responding less to a single cue than to a suite of signals which indicate the suitability of a habitat (Cameron & Schroeter 1980, Pearce & Scheibling 1991, but see also Rowley 1989). In contrast, irregular echinoids, such as *Dendraster exentricus* and *Echinarachnius parma* have been shown to settle selectively in the presence of a chemical cue associated with conspecifics, which largely restricts settlement to within adult populations (Highsmith 1982, Pearce & Scheibling 1990b).

Studies of settlement induction and substrate preferences in asteroids have involved only a few species. In Washington, Birkeland et al. (1971) found that larvae of the asteroid *Mediaster aequalis* were highly selective, settling only on the tubes of the polychaete *Phyllochaetopterus prolifica*. In New Zealand, Barker (1977) found that larvae of *Stichaster australis* settled only on the encrusting coralline alga *Mesophyllum insigne*, but that larvae of *Coscinasterias calamaria* were non-selective, provided there was a microbial film on the substrate. In a subsequent study in England, he also found that larvae of *Asterias rubens* and *Marthasterias glacialis* showed no marked substrate preference in laboratory experiments, but tended to settle on the undersides of various substrata, as was observed in the field (Barker & Nichols 1983). *Acanthaster planci* has been shown to settle on a wide variety of substrata, although many studies report only qualitative results (reviewed by Moran 1986) or are compromised by flawed methodology such as inadequate controls for spontaneous settlement (reviewed by Johnson 1992b). In laboratory experiments, Johnson et al. (1991) showed that some crustose coralline algae such as

Lithothamnium pseudosorum and/or associated bacteria are highly inductive to larvae of *A. planci*, whereas other coralline algal species are not. The authors proposed that *A. planci* on the Great Barrier Reef settle in deeper water at the base of reefs where these inductive substrata occur (see also Johnson 1992b). Alternatively, Zann et al. (1987) suggested that *A. planci* in Fiji settle on coral in shallow water. However, because of the limited number of settlers found in most studies (see Spatial and Temporal Patterns of Settlement and Recruitment) spatial patterns of settlement of *A. planci* remain unresolved.

Very little is known about possible cues to settlement in holothuroids (Smiley et al. 1991), crinoids (Holland 1991) and ophiuroids (Hendler 1991). Some species exhibit gregarious settlement, although the chemical or physical factors inducing metamorphosis and settlement have not been experimentally examined. Young & Chia (1982) showed that larvae of the holothurian *Psolus chitonoides* settle gregariously on or near adult conspecifics in laboratory and field studies in the San Juan Islands, Washington. In contrast, Hamel & Mercier (1996) found no evidence of gregarious settlement in another holouthurian *Cucumaria frondosa* in laboratory and field studies in the St. Lawrence Estuary. Rather, the larvae tended to settle on the undersides of rocks and avoided mud and sand bottoms. Mladenov & Chia (1983) showed aggregated settlement of *Florometra serratissima* on the bottom of culture dishes and concluded that gregarious settlement may account for the adult aggregations that they observed in the field. Larval ophiuroids often appear to settle indiscriminately or metamorphose in the water column in the absence of a substrate more so than other echinoderms (reviewed by Hendler 1991).

Summary and Conclusions

Although various cues for induction of settlement of echinoderms have been isolated, the evidence is often based on findings from laboratory studies or from anecdotal evidence from the field. Chia et al. (1984) and Pearce (1997) concluded that larval preferences for settlement substrata are generally less important than post-settlement processes, such as migration and mortality, in determining population distribution and abundance. This brings into question the relative importance of induction for most species of echinoderms and underscores the need to follow settlers in the field through to early juvenile stages to better understand the consequences of preferential settlement (e.g. Highsmith 1982, Young & Chia 1982).

SPATIAL AND TEMPORAL PATTERNS OF SETTLEMENT AND RECRUITMENT

Sampling methods

A variety of techniques have been used to record settlement and recruitment rates of echinoderms (Tables 1.1 to 1.4), but sampling accuracy remains a considerable methodological challenge. Conventional sampling methods, such as quadrat and grab sampling, are labour intensive and must be repeated frequently if recent recruits are to be enumerated. Harris et al. (1994) have used photographic sampling to measure recruitment of *Strongylocentrotus droebachiensis* in the Gulf of Maine, although the small size and cryptic nature of early juveniles limit the applicability of this approach. Typically, these methods either fail to detect or to accurately census recently settled individuals. Variation in sampling method and frequency among studies may significantly affect measures of recruitment rate, as has been shown for barnacles (Minchinton & Scheibling 1993, Miron et al. 1995), suggesting caution when interpreting data and comparing across studies using different methods.

Of the 52 studies of echinoids that I reviewed, 10 used artificial collectors to measure settlement or recruitment rates (Table 1.1). Bak (1985) monitored recruitment of *Diadema antillarum* on plastic collectors (light diffuser panels) suspended vertically 20 cm above coral reefs in Curaçao. He found that submergence times of more than 2 months resulted in reduced settlement due to fouling. Harrold et al. (1991) used plastic pipes containing either light diffuser panels or coralline algae (*Calliarthron* and *Bossiella*), and suspended 1 m above the seabed, to monitor settlement of *Strongylocentrotus purpuratus* and *S. franciscanus* in a kelp forest in California. They found that settlement over 30 to 41 day sampling intervals was greater in the plastic-filled than in the coralline-filled collectors, conflicting with their laboratory observations which showed greater settlement on corallines. However, there were more juvenile crabs and polychaetes in the coralline-filled collectors, which may have preyed upon the newly settled echinoids. Keesing et al. (1993) used plastic bio-filter spheres suspended 1 m off the bottom in mesh bags to compare settlement of several species of echinoderms on the Great Barrier Reef. They found a significant correlation between settler densities on collectors and those on the natural substrata for species from all 5 echinoderm classes. They also compared various sorting techniques and found that recovery rates of settlers varied from 52 to 100 %, and that the most time consuming method was required to collect all echinoderm settlers. Harris et al. (1994) used panels of plastic turf mounted on racks on the bottom to collect settlers of *S. droebachiensis* in the Gulf of Maine. They found much higher rates of recruitment (3 months after settlement) on the turf than on natural substrata such as bare rock and coralline algae. Ebert et al. (1994) and Schroeter et al. (1996) used scrub brushes suspended vertically 1 to 1.4 m off the bottom to monitor settlement of *Strongylocentrotus* spp. in California. Schroeter et al. (1996) concluded that patterns of recruitment on natural substrata observed during benthic surveys were similar to the patterns of settlement measured at weekly intervals in their collectors.

Many studies of ophiuroid recruitment have been done in the deep-sea where sampling is logistically difficult and confined to conventional methods (Table 1.3). Constraints on sampling frequency and the accuracy of site relocation limit conclusions about recruitment dynamics in such remote communities (Grassle 1994). Ophiuroids also are ubiquitous in shallow waters but there they typically are cryptic and hard to sample. In Denmark, Muus (1981) collected recent settlers (0.325 mm) of *Amphiura filiformis* in sediment samples sieved through a 0.265 mm mesh screen. She observed high rates of settlement and concluded that previous studies using larger mesh sizes did not sample settlers. Estimates of ophiuroid settlement often have involved back-calculation based on modal analysis of size distributions. These methods measure recruitment at best and the stacked age classes that usually occur seriously limit the accuracy of this technique (Gage 1985). Even methods of measuring the size of an ophiuroid have been debated and the reliability of some methods has been questioned (O'Connor & McGrath 1980, O'Connor et al. 1983, Duineveld & Van Noort 1986, Bosselmann 1989, Munday & Keegan 1992). In an effort to circumvent many of the problems with conventional sampling methods, artificial collectors have been used to measure ophiuroid settlement and have detected high rates of settlement in differing shallow water habitats (Keesing et al. 1993, Chapters 3 and 4).

Methods used to detect patterns of spatial and temporal variability in recruitment of holothuroids have varied among studies (Table 1.4). Compared to other echinoderms, holothuroids are particularly difficult to measure accurately due to their soft and flexible body wall. Cameron & Fankboner (1989) suggested that a single measurement of length or wet weight can be unreliable. Different methods of measurement could account for some of the variability observed both within and between studies, and may influence conclusions that are drawn from them.

Echinoidea

Many studies have documented large spatial and temporal variability (over tens of metres to thousands of kilometres and over months to years) in settlement and recruitment rates of echinoids (Table 1.1 and reviews by Ebert 1983, Harrold & Pearse 1987, Pearse & Cameron 1991). Pearse & Hines (1987) monitored populations of *Strongylocentrotus franciscanus* and *S. purpuratus* in central California from 1972 to 1981. Throughout this period there was only 1 significant pulse of recruitment of *S. purpuratus* (resulting in a 25-fold increase in population density) and little evidence of recruitment of *S. franciscanus*.

However, echinoids <10 mm were not accurately sampled in this study and the sampling frequency was inadequate to reliably distinguish and track cohorts over time. Estes & Duggins (1995) found episodic recruitment of *S. droebachiensis*, *S. purpuratus*, and *S. franciscanus* between 1972 and 1990 in southeast Alaska, although *S. polyacanthus* recruited heavily in each of these years in the Aleutian Islands. They suggest that large-scale oceanographic processes are responsible for differences in larval supply to each of the regions. Episodic recruitment also has been observed in *S. purpuratus* and *S. franciscanus* in California and Washington (Paine 1986, Watanabe & Harrold 1991) and *S. droebachiensis* in Nova Scotia (Scheibling 1986, Raymond & Scheibling 1987, Chapter 4). Rowley (1989) found recently settled *S. franciscanus* and *S. purpuratus* in echinoid barren grounds and kelp beds in southern California between April and July in each of 3 successive years (1984 to 1986), but only in May of the final year did he observe heavy settlement of both species (~1000 settlers m^{-2}). He noted a rapid reduction in settler densities within 10 days and suggested that other pulses during his 3 years of sampling may have gone undetected. Sloan et al. (1987) observed low overall recruitment and a high degree of variability among populations of *S. franciscanus* in southern British Columbia in 1984 and 1985. Although most studies of strongylocentrotids have shown recruitment to be quite patchy in space and time, there are some exceptions. For example, recruitment was temporally predictable and substantial over several years for *S. droebachiensis* in the Gulf of Maine (Harris et al. 1985, 1994, Harris & Chester 1996) and *S. purpuratus* in Baja California, Mexico (Pearse 1970 in Ebert 1983).

Watts et al. (1990) measured spatial and temporal variability in recruitment using the genetic characteristics of *Echinometra mathaei* in Western Australia. They found that populations within 4 km of each other had as much genetic variance as populations sampled over 1300 km of coast. The authors suggested that different populations of larvae are supplied to adjacent areas over different years, resulting in genetic heterogeneity. On Rottenest Island, Western Australia, Prince (1995a, b) measured spatial and temporal variability in recruitment of *Echinometra mathaei* at a variety of scales. She concluded that differences in both local hydrodynamics, such as eddy formation and wave action, as well as large-scale interannual variation in ocean currents determine patterns of recruitment.

Small-scale spatial variation in settlement and recruitment of echinoids has been related to differences in habitat (Pearse & Cameron 1991), particularly between kelp beds/forests and echinoid-dominated barren grounds (Pearse et al. 1970, Lawrence 1975). Lower rates of recruitment of *Strongylocentrotus franciscanus* and *S. purpuratus* have been recorded in kelp forests (*Macrocystis pyrifera*) than in adjacent barren areas in California (Tegner & Dayton 1981) and a similar pattern has been observed for *S. droebachiensis* in kelp beds (*Laminaria* spp.) in Nova Scotia (Scheibling 1986) and Norway (Leinaas & Christie 1996). Furthermore, Basch & Tegner (1995) found that recruitment of *Strongylocentrotus* spp. was lower within a kelp forest than at the seaward edge. A number of mechanisms have been proposed to account for these patterns. Various authors have suggested that kelp forests act as larval filters by harbouring species which consume larvae as they drift through the forest or settle on the bottom (Pearse et al. 1970, Bernstein & Jung 1979, Tegner & Dayton 1981, Dayton & Tegner 1984, Gaines & Roughgarden 1987, Harrold & Pearse 1987, Chapman & Johnson 1990). In addition, Jackson & Winant (1983) showed that kelp forests deflect currents which could act to reduce the number of incoming larvae (see also Dayton & Tegner 1984). Larval supply to a kelp forest also may be limited because larvae encountering a forest settle on the first suitable substrates along the forest edge (Bernstein & Jung 1979, Tegner & Dayton 1981, Harrold & Pearse 1987). Within the forest, post-settlement survival of recruits may be adversely affected by understory macroalgae which increase sedimentation or decrease water flow, light and microalgal cover, as has been shown for other benthic invertebrates (Eckman et al. 1989, Duggins et al. 1990).

Studies which have compared settlement rates of strongylocentrotids between kelp forests/beds and barren grounds have yielded equivocal results. Rowley (1989) reported no significant difference in the densities of newly settled *Strongylocentrotus franciscanus* and *S. purpuratus* between a kelp forest and an adjacent echinoid barren ground in southern California. However, the number of samples and size of the sampling units (200 cm^2 pieces of shale) may have been too small to provide a meaningful statistical comparison. Rowley also noted that the kelp canopy density was low during this study and might not have influenced larval supply to the kelp forest. Using artificial collectors (scrub brushes), Schroeter et al. (1996) found that kelp forests had no significant effect on settlement rates of *S. purpuratus*. However, settlement of *S. franciscanus* was low and variable (0 to 10 per collector) with some evidence of higher settlement 20 m offshore of the kelp forest. The authors concluded that kelp forests do not reduce larval supply or settlement but offer the caveat that their 2 year study period may have been too short (relative to natural cycles) to assess this. Using artificial collectors (plastic turf) in the Gulf of Maine, Harris & Chester (1996) found settlement of *S. droebachiensis* was greater within natural or artificial kelp beds than in adjacent barren grounds. In contrast, using similar collectors in Nova Scotia, we found the opposite pattern: settlement of this species was lower in kelp beds than in barrens (Chapter 4). These regional disparities may be attributable to differences between the Gulf of Maine and Nova Scotia in size and growth form of individual kelps, or in characteristics of the kelp bed (e.g. bed area and shape, kelp density, understorey species) or surrounding environment (e.g. depth, topography, hydrodynamic conditions), which may effect larval supply. Such differences are even more pronounced between the *Laminaria* beds of the northwest Atlantic and the *Macrocystis* forests of the northeast Pacific (see Harrold & Pearse 1987 for a description of different kelp habitats).

Differences in echinoid settlement rates also have been recorded between habitats on a tropical coral reef. Keesing et al. (1993) found that settlement of echinoid larvae (several species were grouped together including *Echinometra mathaei* and *Mespilia globulus*) on an artificial substrate (plastic biofilter spheres) was significantly greater on the windward edge than on the leeward edge of Davies Reef, Great Barrier Reef. The authors attributed this to different water residence times. Within a given reef there was no significant difference in settlement rate between collectors placed tens to hundreds of meters apart.

Although most studies of echinoid settlement and recruitment have focussed on horizontal variability, few studies have documented variability over a depth gradient. Harris et al. (1994) found settlement of *Strongylocentrotus droebachiensis* on artificial turf to be greatest at 6 to 8 m and orders of magnitude lower at 20 and 30 m. Himmelman (1986) also found decreased recruitment of *S. droebachiensis* with depth in Newfoundland. He attributed this pattern to reduced food and slower growth resulting in increased predation of juveniles. In contrast, DeRidder et al. (1991) found recruitment of *Echinocardium cordatum* was greatest at 15 to 25 m, much less at 5 to 10 m, and absent in the littoral zone.

Seasonal patterns in settlement have been documented for a few species of echinoids. In central California, Harrold et al. (1991) sampled artificial collectors in a kelp forest at monthly intervals for a year and found clear settlement peaks in April and November for *Strongylocentrotus purpuratus* and *S. franciscanus*. In northern and southern California, Ebert et al. (1994) monitored the same species on artificial collectors at weekly intervals between 1990 and 1993. They found that settlement of both species was strongly seasonal occurring between late winter and early summer and that settlement rate varied between species, among sites and among years. Settlement at southern sites tended to be higher and more consistently annual than at northern sites. In the Mediterranean, Pedrotti (1993) suggested that seasonal recruitment patterns of *Paracentrotus lividus* were related to biannual spawning (in spring and fall), as indicated by the presence of larvae in plankton samples.

Asteroidea

As with echinoids, asteroids show a high degree of spatial and temporal variability in settlement and recruitment throughout the distributional range of species (Table 1.2). The most extensive study of settlement for any echinoderm is that by Loosanoff (1964) of *Asterias forbesi* in Long Island Sound, Connecticut. From 1937 to 1961 he deployed oyster shell collectors twice weekly at 10 sites in 3 areas along 26 km of shore and at depths of 0 to 33 m. Loosanoff (1964) found that settlement increased with depth to 10 m and then decreased to 33 m (see also Ebert 1983). Settlement occurred between June and September but the settlement period varied between sites and years, ranging from 1 to 91 days (mean = 52 days). In years of heavy settlement, the settlement period was protracted; in years of light settlement, it occurred late in the year. Settlement intensity varied from a single peak in 1 week to relatively constant settlement over a period of 3 months. Total annual settlement varied by 5 orders of magnitude (0.3 to 1700 per collector) with no consistent pattern of high and low settlement years. Settlement varied between sites within areas but tended to increase from northeast to southwest. Both Loosanoff (1964) and Ebert (1983), who re-analysed Loosanoff's data, concluded that settlement was not correlated with preceding or subsequent adult density (but see also Burkenroad 1957). Ebert (1983) proposed that hydrodynamic conditions or planktonic predators regulating larval supply may be more important in determining settlement and subsequent recruitment of *A. forbesi* than settlement or post-settlement processes.

Despite massive sampling efforts, most studies of *Acanthaster planci* found few settlers and these were patchily distributed in space and time (reviewed by Moran 1986, Johnson 1992b). During extensive searches at Iriomote-jima in the Ryukyu Islands, Yokochi & Ogura (1987) found only 9 juveniles of *A. planci* in 1984 and 13 in 1985. Fisk (1992) used various methods to measure recruitment of *A. planci* on Green Island in the northern Great Barrier Reef (considered a possible source for larvae that seed secondary outbreaks on reefs to the south) and found only 2 recruits between 1986 and 1990 (Fisk et al. 1988, Fisk 1992). In the central Great Barrier Reef south of Green Island, Doherty & Davidson (1988) destructively searched for *A. planci* on 16 reefs in 1986 and 1987 and found only 4 individuals < 30 mm in diameter (all in 1986), which Johnson (1992b) considered new recruits. From analysis of size-frequency distributions, they inferred low settlement rates in 1986 and 1987 and an order of magnitude higher settlement rate in 1985. However, Ebert (1983) and Moran (1986) pointed out that size- and diet-specific variation in growth rates complicates identification of cohorts from size distributions. *A. planci* individuals grow slowly at the early juvenile stage, when they feed on algae, and then undergo a dramatic increase in growth rate when they shift to a diet of coral. This dietary shift is not necessarily age-related and size at a given age can vary considerably (Moran 1986) indicating that more direct methods of measuring settlement and recruitment rates than size-frequency analysis are needed to accurately detect patterns. Keesing et al. (1993) found 11 asteroid settlers on artificial collectors on Davies Reef, Great Barrier Reef (3 *A. planci*, 5 *Choriaster granulatus* and 3 *Culcita novaeguineae*) in 1992 and concluded that it was a poor settlement year. Despite these meagre results, they suggested that collectors could be used to monitor settlement of *A. planci* in various habitats and to predict the location of outbreaks 3 years in advance.

Juveniles of *Acanthaster planci* have been found in Fiji where Zann et al. (1987, 1990) reported heavy recruitment in 1977, 1984 and 1987 in the intertidal zone of several coral reefs based on size-frequency analysis. Recruitment occurred over thousands of hectares in most years between 1979 and 1989, although intense recruitment in 1982 and 1983 occurred over only a few hectares. Zann et al. (1987, 1990) concluded that there is a high degree of spatial and temporal variability in recruitment of *A. planci* and that outbreaks originate from episodic events.

Differences in recruitment patterns of several co-existing species of temperate asteroids suggest that factors influencing settlement and recruitment may not operate uniformly across species. Sewell & Watson (1993) found that *Pisaster ochraceus* in British Columbia settled in all 5 years studied, whereas *Pycnopodia helianthoides* settled in 4 of 5 years and *Dermasterias imbricata* settled in only 1 year. Himmelman & Dutil (1991) found that differences in distribution of recruits of 3 asteroid species were associated with different habitat types across a depth gradient in the northern Gulf of St. Lawrence. Recruits of *Leptasterias polaris* were most abundant at 0 to 1 m and found only in boulders, cobble or bedrock; those of *Asterias vulgaris* were most abundant at 4 to 7 m and found only in boulders or cobble; and those of *Crossaster papposus* were only found on sedimentary bottoms deeper than 11 m.

Asteroids display a wide variety of reproductive strategies (Chia & Walker 1991) which may influence patterns of recruitment, but little is known about recruitment of species that reproduce by means other than planktonic larvae. For example, Ebert (1983) contended that increased parental investment in the form of brooding, should increase recruitment success and consequently decrease longevity. In support of this hypothesis, Menge (1975) found a broadcast spawner (*Pisaster ochraceus*) lived approximately 3 times longer than a brooding asteroid (*Leptasterias hexactis*) on San Juan Island, Washington. Menge (1975) proposed that brooding has co-evolved with small body size to ensure increased reproductive success and survival of *L. hexactis* in a competitive relationship with larger *P. ochraceus*. However, Himmelman et al. (1982) suggested that brooding is a fixed trait in the genus *Leptasterias* and doubts that it evolved from competitive interaction. Boivin et al. (1986) concluded that the large egg reservoir and long development time of *L. polaris* assure steady annual recruitment in the St. Lawrence Estuary.

There is indirect evidence for habitat selectivity in several asteroids based on the differential distribution of juveniles and adults. These differences may arise by selective settlement in a habitat different from that of adults (assuming that juveniles eventually migrate to the adult habitat) or because of between-habitat differences in post-settlement mortality. Migration to adult habitats may occur when juveniles reach a size refuge from predation or require an alternate food source. Birkeland et al. (1971) found various species of recently metamorphosed asteroids (*Mediaster aequalis*, *Luidia foliolata*, *Crossaster papposas*, *Henricia leviuscula*, *Solaster stimpsoni*, *S. dawsoni* and *Pteraster tesselatus*) on the tubes of the polychaete *Phyllochaetopterus prolifica* and not elsewhere. The authors suggested this habitat acts as a nursery ground for juveniles where there is an abundance of food.

Plant assemblages seem to be particularly attractive habitats for asteroid settlement. Scheibling (1980a) found juveniles of *Oreaster reticulatus* mainly within and adjacent to dense seagrass beds and suggested that settlement in seagrass beds provides refuge from predation by fish (Scheibling 1980a, b). Sewell & Watson (1993) found recruits of *Pisaster ochraceus*, *Pycnopodia helianthoides* and *Dermasterias imbricata* on various substrata including macroalgae such as *Laminaria saccharina* and *Sargassum muticum*. Rumrill (1988b) reported that *Pisaster ochraceus* in laboratory experiments preferentially settled on substrata collected from the *Laminaria* zone. Day & Osman (1981) found juvenile *Patiria miniata* under boulders in a California kelp forest whereas adults were on the exposed algal covered reef. They suggested that juveniles are either out-competed by adults on exposed reefs or removed by predation (see also Harrold & Pearse 1987).

Ophiuroidea

Unlike echinoids and asteroids, most studies of ophiuroids (including a number in the deep-sea) indicate consistent annual and seasonal patterns of settlement or recruitment (Table 1.3). Although the deep-sea has been considered an aseasonal environment, some species of ophiuroids (and other invertebrates) show seasonality in reproduction and/or recruitment (Schoener 1968, Tyler et al. 1982, Tyler 1988, Gage 1994). In the northeast Atlantic, Gage & Tyler (1981a, b, 1982b, c) found that *Ophiura ljungmani* and *Ophiocten gracilis* on the Hebridean continental slope (600 to 1200 m depth) and *Ophiura ljungmani* in the nearby Rockall Trough (2200 to 2900 m) reproduced seasonally, and that high densities of recruits dominated populations of *Ophiura ljungmani* in the Rockall Trough. From these studies, they inferred that settlement of both species occurs annually in summer. However, they also observed annual recruitment (indicating a settlement peak in May) of

Ophiomusium lymani which exhibited continual gametogenesis in the Rockall Trough (Gage & Tyler 1982a, b). They suggest that this pattern of recruitment in *Ophiomusium lymani* is related to the seasonal input of detritus from surface waters which may regulate larval survival. Other studies of *Ophiomusium lymani* from sites at 1100 to 2300 m depth in the northeast and northwest Atlantic and the northeast Pacific (reviewed by Gage 1982) showed several juvenile modes in population size distributions, suggesting seasonal and annual recruitment in the spring (Atlantic) or late summer (northeast Pacific).

Several studies of *Amphiura filiformis* from coastal waters of various regions have shown different patterns of recruitment, although these differences may partly reflect different sampling methods (Table 1.3). Very low and patchy recruitment of *A. filiformis* was observed over an 8 year period in Galway Bay, Ireland (O'Connor & McGrath 1980, O'Connor et al. 1983). Based on the reproductive cycle, settlement was assumed to occur from September to November. The authors concluded that they had missed sampling settlers because of high post-settlement mortality in the first year after settlement, although it is possible that settlement rarely occurs in this population. Off the coast of the Netherlands, Duineveld & Van Noort (1986) observed high recruitment of *A. filiformis* from July to September in each of the 2 years studied. They concluded that high mortality in the first year after settlement limits the number of intermediate size animals, but enough survive to sustain a low rate of renewal of the adult population. In the Øresund off Denmark, Muus (1981) also found high recruitment of *A. filiformis* in both years of a 2 year study, with a peak from September to November. Here too, post-settlement mortality was high and few recruits survived their first year, resulting in a relatively stable adult population. In contrast, *A. chiajei*, which began settling 3 months later than *A. filiformis*, was found in very low numbers in the same area (Muus 1981). In the Mediterranean, Pedrotti (1993) found larvae of *A. filiformis* comprised 70 % of the ophiuroids in plankton tows from November to February. The author concluded that mixed larval stages found at various times of the year were evidence for prolonged and variable recruitment.

Continual recruitment also has been reported for *Ophiura sarsi* at depths of 148 to 156 m in the Gulf of Maine (Packer et al. 1994). Small individuals were found throughout the year but the highest number of recruits occurred in January, suggesting a seasonal peak. Using artificial collectors at 6 to 10 m depth off Nova Scotia, we found that *Ophiura* sp. and *Ophiopholis aculeata* both settled in a pulse between late July and early August in 3 successive years (Chapter 4). However, highest settlement occurred in different years for each species suggesting that different processes control larval supply and settlement of the 2 species. The regional difference in settlement pattern of *Ophiura* between Nova Scotia and the Gulf of Maine may be due to differences in depth or geographic location. Alternatively, different species may have been sampled, since we could not distinguish between *Ophiura sarsi* and *O. robusta* (Chapter 4).

Ebert (1983) hypothesised that different reproductive strategies result in different recruitment patterns, and that brooders should have more predictable recruitment than spawners due to increased parental investment in brooding. He compared recruitment (based on size distributions) of *Ophioplocus esmarki* (a brooder) and *Ophionereis annulata* (a spawner) at False Point, California and found that the brooder showed higher or more frequent recruitment. Ebert (1983) also hypothesised that recruitment declines with depth, based on data from studies of the deep-sea ophiuroids *Ophiura ljungmani* and *Ophiomusium lymani*. Assuming a constant population where mortality equals recruitment, he estimated mortality rate and showed that mortality, and thus recruitment, decreases with depth. However, Ebert (1983) included data from Gage & Tyler (1982c) who found considerable variability in survivorship of these ophiuroids and suggested that depth is not a factor affecting their recruitment. Some support for Ebert's (1983) hypothesis comes from the observations of Fujita & Ohta (1990) that recruitment of *Ophiura sarsi* off the northeast coast of Japan was greater at 250 m than at deeper sites (350 to 550 m).

Many studies of ophiuroids are from deep water habitats with relatively uniform soft-bottoms; few studies have compared settlement or recruitment of the same species between different habitats. We found higher settlement of *Ophiura* sp. and *Ophiopholis aculeata* on artificial collectors in echinoid-dominated barren grounds than in kelp beds in Nova Scotia (Chapter 4). However, recruitment of both species did not differ between habitats 1 year later, suggesting differential post-settlement mortality. Keesing et al. (1993) compared settlement between 2 habitats on Davies Reef in the Great Barrier Reef. Using an artificial substrate, they found no differences in settlement of several combined species of unidentified ophiuroids between the windward and leeward edge of the reef. This pattern corresponded to observed recruitment to coral rubble in these habitats but Keesing et al. (1993) suggested that identification of separate species might yield different patterns.

Holothuroidea

Despite the predominance of spawners among the holothuroids (Smiley et al. 1991), most studies of recruitment are based on fissiparous or brooding species (Table 1.4). Ebert (1983) reviewed several studies of fissiparous populations of *Holothuria atra* in the South Pacific. He concluded that recruitment can be either continual or seasonal and that rates of fission alone can be enough to sustain the population. Rutherford (1973) sampled populations of the brooding holothuroid *Cucumaria pseudocurata* in the intertidal zone in northern California and found that they recruit annually in February. He also found a strong negative correlation between recruit survival and adult density leading him to conclude that recruitment is density dependent and that recruits are space limited. Sewell (1994) showed that *Leptosynapta clarki*, another brooder inhabiting intertidal mudflats of Bamfield Inlet, British Columbia, recruited annually in April/May. Cameron & Fankboner (1989) concluded that recruitment of *Parastichopus californicus* (a spawner) occurs over several months in fall and winter, based on an extended spawning period in southern British Columbia and Washington. They found that recruitment over a 6 year period varied markedly among sites, with regular recruitment in some areas and weak or no recruitment in others.

Differential settlement over a depth gradient has been observed for some holothuroid species which settle in the shallow range of their habitat. In the St. Lawrence Estuary, Hamel & Mercier (1996) found settlers of *Cucumaria frondosa* concentrated in shallow water (0 to 20 m) compared to adults which were more common in deeper water (40 and 60 m). Bulteel et al. (1992) found similar results for *Holothuria tubulosa* in 3 depth zones (6, 19 and 33 m) of a seagrass bed off Ischia Island, Gulf of Naples where small individuals dominated the shallowest zone.

Crinoidea

There is little information about settlement or recruitment of crinoids on natural substrata in the field. Mladenov & Chia (1983) were unable to find any settlers of *Florometra serratissima* in 2 years of study in Barkley Sound, British Columbia, suggesting that recruitment is low or sporadic. On Davies Reef (Great Barrier Reef), Keesing et al. (1993) found 15 crinoid settlers (unidentified species) on artificial collectors. 12 of the settlers were on the windward edge of the reef and only 3 on the leeward, but the sample size is too small to draw any conclusions about spatial trends in settlement.

Summary and Conclusions

Ebert (1983) identified spatial and temporal variability in recruitment as a salient feature of most echinoderm life histories. While this review supports this contention, it also demonstrates that various scales of spatial and temporal variability must be considered in establishing patterns of settlement and recruitment. Although most echinoderm species exhibit seasonal patterns of settlement, there is large inter-annual variation. Spatial variability in settlement occurs at a variety of scales including habitat, site and region, all of which introduce variables that are difficult to isolate. Although Ebert (1983) presents a number of "clines" that may explain large-scale patterns of recruitment, these are generally based on correlative data and the causative factor(s) are not known. Large spatial and temporal variability necessitates close monitoring of populations to detect ecologically relevant patterns of settlement and recruitment, and suggests caution in interpretation and generalisation of patterns from any particular study. Periodicity may operate on spatial and temporal scales greater than those sampled and thus go undetected. Alternatively, patterns may emerge that are of little consequence to the overall recruitment to a population. For example, low levels of recruitment observed during a particular study may become irrelevant when a single large recruitment event occurs before or after the sampling period. Of 88 studies which examined temporal variation in settlement and/or recruitment of echinoderms, 57 (65 %) were ≤3 years in duration (Fig. 1.1). Unfortunately, studies of this duration yield little information on long-term patterns. The length of most studies likely reflects funding periods for research grants, rather than a biologically meaningful time scale.

Traditional techniques of monitoring settlement and recruitment are time consuming, labour intensive, and often inaccurate in sampling and identifying small individuals. Identification of settlers to species level is often not done because of the lack of suitable descriptions of early post-metamorphic forms and the difficulty in discriminating taxonomic characteristics at microscopic scales. However, species identification recently has been facilitated by molecular genetic techniques (for ophiuroid species) which have broad applicability to future studies (Medeiros-Bergen et al. 1998). Of the 108 studies on settlement and/or recruitment patterns that I reviewed (Tables 1.1 to 1.4), only 57 detected individuals that might be considered recent recruits (<1 mm for ophiuroids and <2 mm for other classes).

Settlement and recruitment patterns often are inferred from infrequent measures of size distributions which are difficult to interpret (Botsford et al. 1994). Estimates of juvenile abundance can vary greatly between studies due to differences in sampling method, frequency and efficiency, which limit direct comparisons between studies. Of 82 studies which provide information on sampling frequency, 30 (37 %) sampled at intervals ≤1 month (Fig. 1.2), although sampling frequencies ≤2 weeks were achieved in only 12 (15 %) of these studies. Because mortality and migration of settlers can occur within days to weeks after settlement (Hunt & Scheibling 1997), studies with longer sampling intervals may be unable to reliably detect patterns of settlement. 21 of the 82 studies (26 %) sampled at yearly intervals providing information on interannual patterns of recruitment (Fig. 1.2), particularly when these studies extended over several years.

The use of artificial collectors promises an efficient and effective way of frequent monitoring which may enable reliable prediction of recruitment events. This is particularly important for species which can severely impact benthic community structure or for commercially important species. For example, artificial collectors have been used to sample settlers and predict catch rates of rock lobster 4 years in advance for the fishery in Western Australia (Phillips 1986, Pearce & Phillips 1994). Artificial collectors also may provide a means of rigorously examining spatial and temporal patterns of settlement and recruitment. However, collector results should be compared to measurements on natural substrata to identify artifactual effects. Also, different collector types should be standardised, or cross-calibrated (e.g. Chapter 2), to allow comparisons across studies.

POST-SETTLEMENT PROCESSES

Predation

Juvenile echinoids are prey to various invertebrate and fish predators but the relative importance of these predators as agents of mortality is not well understood (reviewed by Scheibling 1996). Highsmith (1982) found that the tanaid crustacean *Leptochelia dubia* consumed *Dendraster excentricus* which settled outside of adult sand dollar beds in the San Juan Islands, Washington. Larvae of *D. excentricus* that settled amongst adult conspecifics had higher survival rates because tanaids were excluded from sand dollar beds by bioturbation. Keats et al. (1985) concluded that size-selective predation of juvenile

Strongylocentrotus droebachiensis by cunner and winter flounder may play an important role in regulating recruitment to echinoid populations in Newfoundland. In a cobble bed in Nova Scotia, Scheibling & Hamm (1991) found that juvenile rock crabs, lobsters and sculpins had a significant effect on the survival of juvenile *S. droebachiensis* in predator inclusion cages. In a Californian kelp forest, Pearse & Hines (1987) observed a dramatic decline in the density of recently recruited *S. purpuratus*, which they suggested was due to disease and/or predation by asteroids. Also in California, Rowley (1990) attributed a higher rate of mortality of newly settled *S. purpuratus* in a kelp forest than in a nearby barren ground to a difference in predation between the 2 habitats, although he did not identify predators. In New Zealand, Andrew & Choat (1982) observed enhanced recruitment of *Evechinus chloroticus* in predator exclusion cages in barren grounds and suggested that fish are important predators of juveniles. They also found that survival of caged juveniles was much higher in sparse and dense kelp forests than in barren habitats and concluded that processes other than predation regulate echinoid abundance in algal covered habitats (Andrew & Choat 1985).

The importance of spatial refugia from predation has been demonstrated for several species of echinoids which find shelter in a variety of microhabitats. Mussel beds were shown to provide a spatial refuge for juvenile *Strongylocentrotus droebachiensis* from predation by fish, crabs and lobster in New England (Witman 1985). In cage experiments in Nova Scotia, Scheibling & Hamm (1991) recorded a lower rate of predation on juveniles of *S. droebachiensis* which sheltered among cobbles compared to those without a spatial refuge. Juveniles of *S. franciscanus* are often observed under the spine canopies of conspecific adults which provide protection from predators (Tegner & Dayton 1977, 1981, Tegner & Levin 1983, Breen et al. 1985, Sloan et al. 1987, Rogers-Bennett et al. 1995). In contrast, Andrew & Choat (1982, 1985) found no effect of conspecific adults on juvenile survival of *Evechinus chloroticus*.

Several studies have documented bimodal size distributions of echinoids with prominent juvenile and adult modes but low numbers of intermediate size animals (e.g. Tegner & Dayton 1981, Ojeda & Dearborn 1991, Rodriguez & Ojeda 1993, reviewed by Scheibling 1996). This pattern has been attributed to an ontogenetic shift in microhabitat as juveniles outgrow spatial refugia and are subjected to increased predation until they reach a refuge in size as adults (but see also Botsford et al. 1994). For example, Scheibling & Raymond (1990) found that juveniles of *S. droebachiensis* in a cobble bed declined in abundance once they outgrew refuges in the interstices and undersides of cobbles. This was attributed to predation since juveniles survived under boulders that were experimentally transplanted to the bed, providing a more suitable spatial refuge for larger individuals.

Predation of juveniles of the asteroid *Acanthaster planci* by a variety of animals (including fish, crabs, lobster, shrimp, gastropods, corals and worms) has been observed in field and laboratory studies (reviewed by Moran 1986, Keesing & Halford 1992a). Keesing & Halford (1992b) placed laboratory-reared juveniles of *A. planci* of different ages in open and closed cages to examine survival rates in the field. They found that juveniles move little in the presence of adequate food supplies, suggesting that preferential settlement in spatial refugia would enhance survival. They recorded high but declining rates of mortality (attributed to predation) for newly settled juveniles over the first 4 months, suggesting that early post-settlement mortality could substantially affect population dynamics. McCallum (1992) developed models to examine predation on juveniles as a mechanism of controlling populations of *A. planci* and concluded that our understanding of the stock-recruitment relationship and degree of openness of populations was insufficient to reliably address this problem.

Post-settlement predation has been less well documented for other species of asteroids. Dayton et al. (1974) concluded that populations of *Acodontaster conspicuus* and *Austrodoris mcmurdensis* are at least partially regulated by predation of juveniles by the detritivorous asteroid *Odontaster validus*. Day & Osman (1981) observed predation on juveniles of *Patiria miniata* by adult conspecifics and by cancrid crabs. In laboratory experiments, Rumrill (1989) recorded high survival rates for juveniles of *Asterina miniata* offered to a fish, 2 species of predatory crabs and 5 species of predatory asteroids. These results, combined with observations of juvenile abundance in the field, led him to conclude that post-settlement mortality due to predation is low.

Duineveld & Van Noort (1986) attributed the rapid decline in density of the ophiuroid *Amphiura filiformis* off the Netherlands to predation of juveniles by shrimp, crabs and polychaetes. They also proposed that high adult densities (1330 m^{-2}) might result in competition or cannibalism, but reported similar rates of post-settlement mortality at a nearby site with lower adult densities (300 m^{-2}). Packer et al. (1994) found that small *Ophiura sarsi* (3 to 13 mm) were the most common component of the stomach contents of American plaice (*Hippoglossoides platessoides*) in the Gulf of Maine. They concluded that, despite their low caloric value, juveniles were selectively preyed upon because of their abundance and/or accessibility.

Several predators of juvenile holothuroids have been identified but the impact of predation on recruitment to adult populations is not clear. Rutherford (1973) showed that recruits of the brooding holothuroid *Cucumaria pseudocurata* were reduced by 61 % after 1 month and by more than 96 % after 1 year, and suggested predation by the asteroid *Pycnopodia helianthoides* as a source of post-settlement mortality. In contrast, Sewell (1994) observed "no dramatic decrease in numbers of juvenile *Leptosynapta clarki* in the first month" and followed the cohort for 6 months until it merged with the adult population. This discrepancy could be a result of the different habitats sampled and different predator assemblages. In the St. Lawrence Estuary, Hamel & Mercier (1996) observed predation of juveniles of *Cucumaria frondosa* by the echinoid *Strongylocentrotus droebachiensis* and the asteroid *Solaster endeca*, but these occurrences were rare. In laboratory experiments, Cameron & Fankboner (1989) showed that *Solaster dawsoni* and a hermit crab *Pagarus hirsutiusculus* selectively preyed on juveniles of *Parastichopus californicus* and suggested that predation may limit recruitment to areas free of predators. In cage experiments off Okinawa Island, Wiedemeyer (1994) showed low rates of natural mortality (0.6 % mo^{-1}) of juvenile *Actinopyga echinites*. However, when the cage lids were removed and the juveniles exposed to potential predators (a gastropod and several species of fish), mortality rate increased 5 fold (to 3.3 % mo^{-1}) due to predation. This predation rate is still low compared to that observed for other holothuroid species, leading Wiedemeyer (1994) to suggest that the juveniles of *A. echinites* are defended by toxins.

Migration and dispersal

Migration of juvenile echinoids between distinct habitats such as kelp forests and barren grounds is generally discounted due to the large distances relative to the size and rates of movement of the juveniles (Rowley 1989) or because of the presence of some physical barrier such as sand (Watanabe & Harrold 1991). With increasing age and size, however, the likelihood of migration increases. DeRidder et al. (1991) found no recruitment of *Echinocardium cordatum* in the littoral zone and suggested that 2 to 4 year old echinoids migrated there from deeper water.

Small scale migrations have been observed for juvenile asteroids that settle in nursery areas and then move to adult habitats (reviewed by Chia et al. 1984). Birkeland et al. (1971) commonly found several asteroids (*Mediaster aequalis*, *Luidia foliolata*, *Crossaster papposas*, *Henricia leviuscula*, *Solaster stimpsoni*, *S. dawsoni*, *Pteraster tesselatus*) on the tubes of the polychaete *Phyllochaetopterus prolifica* and suggested they settle there and feed on epizoites before migrating to sandy areas to feed on larger prey. Scheibling (1980a, b) suggested that *Oreaster reticulatus* individuals settle in seagrass beds and then migrate to adult populations in open sandy areas. Similarly, Jost & Rein (1985) proposed that migration of juvenile *Astropecten bispinosus* from *Zostera marina* beds compensates for losses due to predation on a sand bottom. In contrast, Rumrill (1989) measured low rates of movement of settlers and juveniles of *Asterina miniata* in the laboratory and concluded that migration was limited in natural populations. Extensive migrations of juveniles or adults of *Acanthaster planci* to form aggregations of different year classes have been proposed as a causal mechanism for population outbreaks, although there is no obvious cue to trigger such behaviour (reviewed by Ebert 1983, Moran 1986, Johnson 1992b).

Post-settlement migration of holothuroids has been observed at small and large spatial scales. In laboratory and field studies in the San Juan Islands, Washington, Young & Chia (1982) showed that post-settlement migration of *Psolus chitonoides* toward shaded areas such as cracks and overhangs occurs within the first week of settlement. After 1 month, juveniles in the field could no longer be located and were presumed to have dispersed. Young & Chia (1982) suggest that post-settlement processes such as migration are more important than substratum choice at settlement in determining the spatial distribution of *P. chitonoides*. Hamel & Mercier (1996) showed a 3-stage migration of *Cucumaria frondosa* in the St. Lawrence Estuary: 4 to 5 months after settling on the undersides of rocks, juveniles migrate to crevices; after 19 months, when they reach a size refuge from predation (~ 35 mm), they move to exposed rock surfaces; finally, once sexual maturity is reached after ~ 3 years, the adults migrate to deeper water. Similarly, Bulteel et al. (1992) concluded that settlement of *Holothuria tubulosa* occurs in shallow seagrass beds and that some individuals migrate to deeper water to reproduce.

For small fissiparous or brooding echinoderms, rafting on drift algae may be an effective mode of dispersal for both adults and juveniles. Highsmith (1985) observed rafting on drift algae for several brooding species of invertebrates on San Juan Island, Washington, including the ophiuroid *Amphipholus squamata*. He concluded that the small size of brooders, especially the juveniles, makes them well suited to this mode of dispersal. Mladenov & Emson (1988) proposed that rafting on floating clumps of algae such as *Halimeda* and *Amphiroa* may serve as a dispersal mechanism for strictly asexual populations of the ophiuroids *Ophiactis savignyi* and *Ophiocomella ophiactoides* in

Jamaica. Sewell (1994) provides anecdotal evidence for dispersal of the brooding holothurian *Leptosynapta clarki* in Bamfield Inlet, British Columbia, by rafting, floating, swimming, and transport by waves or currents. In contrast, Hess et al. (1988) showed much greater gene flow between populations of *L. clarki* < 500 m apart than between those 11 to 24 km apart on San Juan Island, and concluded that dispersal between distant locations was limited due to barriers of unfavourable habitat.

Disease, starvation and other mortality

Disease can have catastrophic effects on echinoid populations, as evidenced by epizootics affecting *Strongylocentrotus droebachiensis* in Nova Scotia (Miller & Colodey 1983, Scheibling 1986) and *Diadema antillarum* in the Caribbean (Lessios et al. 1984, Hughes et al. 1985). Scheibling & Stephenson (1984) reported higher mortality of adults than juveniles of *S. droebachiensis* during a disease outbreak in Nova Scotia in 1983. They suggested that juveniles, which shelter beneath rocks and in crevices, are more likely to avoid exposure to a waterborne pathogen. Following mass mortality of *D. antillarum* in Barbados in 1983, recruitment in 2 successive years enabled populations to recover to within 57 % of their pre-mortality levels by 1985 (Hunte & Younglao 1988). In other areas, however, recruitment occurred at relatively low levels and recruits tended not to persist (Bak et al. 1984, Lessios 1988, 1994, Carpenter 1990, Karlson & Levitan 1990).

Mass mortalities have also been observed for juveniles of *Acanthaster planci* in Fiji (Zann et al. 1987, 1990). In some areas, the 1984 cohort suffered complete mortality by 1987 due to an undescribed sporozoan pathogen, while juveniles from the same cohort survived in other areas. Necrotic lesions are typically observed in juveniles that have been nutritionally stressed and Keesing & Halford (1992a) concluded that density-dependant mortality, in the absence of sufficient coral food, could limit survival of juvenile *A. planci*.

Abiotic sources of mortality such as storms and temperature and salinity fluctuations also may affect recruitment (Lawrence 1996). In British Columbia, mass mortality of recently settled *Strongylocentrotus droebachiensis* and *S. franciscanus* was attributed to rainwater runoff during the winter (Cameron & Fankboner 1989). In laboratory and field experiments Himmelman et al. (1983, 1984) showed that juveniles of *S. droebachiensis* suffered greater rates of mortality than adults when exposed to low salinity conditions.

Summary and Conclusions

Most species of benthic marine invertebrates suffer very high mortality within the first days to months of life after settlement (Gosselin & Qian 1997, Hunt & Scheibling 1997). Gosselin & Qian (1997) conclude that common processes may influence the early post-settlement survival of most species, which are at least as important as processes affecting larvae. However, the role of post-settlement processes in determining populations of echinoderms remains a poorly studied component of their early life history. High rates of settlement and recruitment are often recorded but the fate of recruits is usually unknown. Various factors such as migration, predation, disease, storms and reduced salinities have been implicated as sources of high post-settlement mortality or loss from a population. However, separating these factors and determining their relative importance has proven difficult, particularly in field studies. Although early survival can be tracked by using methods as simple as size or age distributions, the sampling resolution of most studies (Tables 1.1 to 1.4) is inadequate to make clear statements about meaningful time scales and possible causes of mortality. Many predators of juvenile echinoderms have been identified from laboratory studies and analysis of gut contents, but further field studies are required to quantify predation rates under natural conditions and to examine predator-prey interactions. Field enclosures and tethering are effective means of manipulating predators and prey, although they may introduce experimental artefacts which must be assessed using appropriate controls (Scheibling 1996, Hunt & Scheibling 1997).

Table 1.1. A summary of studies examining spatial and temporal patterns of settlement and/or recruitment of echinoids.

Species	**Location**	**Habitat, Depth**	**Sampling Method**	**Size***	**Sampling Period, Frequency**	**Patterns and Conclusions**	**Source**
North Temperate							
Strongylocentrotus droebachiensis	Vega Island, Norway	barrens and kelp, 2.5-10 m	0.25 m^2 quadrats	≥ 10 mm	Jul 1990, Apr and Jul 1991	Age/size-frequency analysis showed regular annual recruitment in barren areas; kelp beds inhibit recruitment.	Leinaas & Christie 1996
Strongylocentrotus droebachiensis	Isles of Shoals, New Hampshire, USA	barrens and kelp, 0-30 m	artificial collectors (plastic turf) and photo quadrats	0.49 mm	1990, 1992 and 1993, once in Jun-Jul	Substantial annual settlement decreasing with depth (after 9 m). Recruitment greater on artificial turf than rock.	Harris et al. 1994
Strongylocentrotus droebachiensis	Gulf of Maine, USA, Bay of Fundy and Atlantic coast of Nova Scotia, Canada	barrens, kelp, silt, 10 cm-8 m off bottom at 5-30 m	artificial collectors (plastic turf and scrub brush)	0.150 mm or cheese cloth mesh size	May to Sep 1994, 2-8 week intervals	Order of magnitude differences in maximum settlement between regions. Highest settlement in the Gulf of Maine (34008 m^{-2}), lowest in the Bay of Fundy (32 m^{-2}), and intermediate in Nova Scotia (1066 m^{-2}). Within regions, settlement differed between sites but was within the same order of magnitude. Settlement greater in the barrens than in adjacent kelp beds in the Gulf of Maine.	Chapter 2
Strongylocentrotus droebachiensis	St. Margaret's Bay, Nova Scotia, Canada	habitat not stated, intertidal-20 m	0.25 m^2 quadrats	2 mm	Jul 1968	A size-frequency distribution suggested annual recruitment in May and Jul, following Nov and Apr spawnings.	Miller & Mann 1973
Strongylocentrotus droebachiensis	St. Margaret's Bay, Nova Scotia, Canada	barrens	0.1 m^2 quadrat	> 5 mm	May-Sep 1975, monthly	Evidence for high recruitment in the year after destructive grazing of kelp.	Lang & Mann 1976

Table 1.1 continued

Species	**Location**	**Habitat, Depth**	**Sampling Method**	**Size***	**Sampling Period, Frequency**	**Patterns and Conclusions**	**Source**
Strongylocentrotus droebachiensis	Atlantic coast of Nova Scotia, Canada	barrens and kelp, 0.2 and 2.3 m off bottom at 5-10 m	artificial collectors (plastic turf) and 1.0 m^2 quadrat for recruits	0.150 mm and 1 mm mesh size	Jun-Nov 1992-1994, biweekly and recruits once per year 1993-1995	Settlement pulse in Jul of each year. Low settlement in 1992 and '93, high settlement in '94. Settlement greater in barrens than in kelp beds but not significant. Recruitment reflects settlement.	Chapter 4
Strongylocentrotus droebachiensis	Avalon Peninsula, Newfoundland, Canada	barrens, 0-24 m	0.2, 0.8 or 1.0 m^2 quadrat (depending on density)	2-3 mm	1968-1969, once or twice in summer	Decreased recruitment with depth as reduced food and slower growth results in increased predation. Suggested increased recruitment with exposure to wave action (fewer predators) and lower temperature (increased larval survival).	Himmelman 1986
Strongylocentrotus droebachiensis	Conception Bay, Newfoundland, Canada	barrens and macro-algae, 0-18 m	diver-operated air dredge in 0.1 m^2 quadrats	1 mm	summer 1979-summer 1983, once or twice per year	High recruitment in 1979 and '80 and low from '81-83. Juveniles most abundant in barren zone (6-9 m) particularily on rough coralline algae and rare in the macro-algal zones (0-3 m and12-18 m). Suggested that macro-algae inhibits recruitment but rough coralline algae in barren areas acts as a refuge from predation.	Keats et al. 1985

Table 1.1 continued

Species	Location	Habitat, Depth	Sampling Method	Size*	Sampling Period, Frequency	Patterns and Conclusions	Source
Strongylocentrotus droebachiensis	St. Lawrence Estuary, Québec, Canada	rock and cobble, intertidal-18 m	diver-operated "scraping devices and an air lift aparatus" in 0.25 m^2 quadrats	0-1 mm	once in 1978 or 1979 at 8 sites and from 1978-1980/81 at 2 sites, every 2-8 months	Single pulse of recruitment in 1977 and then none from '78-81. High recruitment at all depths in the lower estuary, but limited to below the fresh layer (0-2 m) further upstream. Suggested that low survival of juveniles in the upper estuary related to low salinity.	Himmelman et al. 1983
Strongylocentrotus droebachiensis	Strait of Georgia, British Columbia, Canada	urchin grazed and ungrazed bedrock in estuarine flow 30 km from river, 7.5-9 m	0.25 m^2 airlift	2.5 mm mesh size	1972-1975, once per year	First record of an urchin outbreak in the region. Recruitment in 1973 and '69 and none in '74 or '75. Recruitment success related to plankton bloom and cold winters which enhance larval survival.	Foreman 1977
Strongylocentrotus droebachiensis, *S. purpuratus*, *S. franciscanus* (Alaska), *S. polyacanthus* (Aleutians)	Aleutian Islands and SE Alaska, USA	rock/boulder bottom with or without kelp, 6-13 m	0.25 m^2 quadrats	≤ 2-3 mm	1972-1990, every 1-7 years (sites sampled for 3-15 years)	Heavy recruitment in Aleutians in most of the 19 years; low and episodic recruitment in SE Alaska. Regional differences related to larval transport and supply.	Estes & Duggins 1995
Strongylocentrotus purpuratus	Tatoosh Island area, Washington, USA	habitat and depth not stated	method not stated	1-2 mm "can be found"	1963-1985	Recruitment only observed in 1963, '69, '82 and '83. No consistent association with El Niño events affecting these waters but some association with warmer water temperatures suggested northward movement of water enhances recruitment in this area.	Paine 1986

Table 1.1 continued

Species	Location	Habitat, Depth	Sampling Method	Size*	Sampling Period, Frequency	Patterns and Conclusions	Source
Strongylocentrotus purpuratus	Sunset Bay, Oregon, USA	habitat and depth not stated	method not stated	2.5-5 mm	1964-1978, once per year	Good recruitment in 1963. Little or no recruitment during remainder of study.	Ebert 1983
Strongylocentrotus franciscanus, *S. purpuratus*	southern Oregon, USA	habitat not stated, 1 m off bottom and 4 m below surface at 18 and 22 m	plankton tows; artificial collectors (Astroturf)	0.202 mm mesh size (tow); 0.3 mm mesh size (collector)	Jan-Aug 1994 and Mar-Aug 1995, ~ every 2 days- 4 weeks	Larvae more abundant and occur earlier in the year in 1995 than '94 . Variable settlement between sites, species and years occurring from Mar-Aug with peak in mid-June of each year and greater in 1995 than '94. More settlement in bottom collectors. Aging indicated settlement events occurred over several days within a sampling period during relaxation of upwelling.	Miller & Emlet 1997
Strongylocentrotus franciscanus / S. purpuratus (not distinguished)	Bodega Head, California, USA	granitic rock and attached algae, 5 and 11 m	1 m^2 quadrats	5-20 mm (< 5 mm "not accurately sampled")	Oct 1988-Oct 1992, ~ quarterly	Juveniles more abundant, smaller and more cryptic at 5 m than 11 m. Greater proportion of adult *S. franciscanus* provided shelter under spine canopies at 5 m (28 %) than 11 m (2%). Suggested recruitment is greater in shallow water and in association with adults.	Rogers-Bennett et al. 1995

Table 1.1 continued

Species	Location	Habitat, Depth	Sampling Method	Size*	Sampling Period, Frequency	Patterns and Conclusions	Source
Strongylocentrotus franciscanus, *S. purpuratus*	northern California, USA	habitat not stated (1992); "rocky bottom" (1993), 0.5-1 m off bottom at 5-20 m (1992), 10-12 m (1993)	artificial collectors (scrub brush)	0.06 mm mesh size	Apr-Sep 1992 and 1993, weekly	No significant vertical (5-20 m) or horizontal (10-100's m) variation in settlement between collectors within a site. Low settlement of both species in 1992; mainly during an unusual upwelling relaxation event in Jul. Minimal settlement at 3 sites in 1993 but high at a 4th site where settlement of *S. purpuratus* during a relaxation event in Apr.	Wing et al. 1995a, b
Strongylocentrotus purpuratus	central California to central Oregon, USA	tide-pools	"thorough search"	0-2.5 mm	1985-1986, once in spring	Recruitment driven by physical events: low recruitment at upwelling sites (capes and headlands); high annual recruitment at sites between. No trend with latitude.	Ebert & Russell 1988
Strongylocentrotus franciscanus, *S. purpuratus*	northern and southern California, USA	habitat and depth not stated but variable, 1-1.4 m off bottom	artificial collectors (scrub brush)	0.436 mm mesh size	1990-1993, weekly with some gaps	Seasonal settlement (Feb-Jul) was higher and more regular in the south. Settlement correlated with general oceanographic processes.	Ebert et al. 1994
Strongylocentrotus purpuratus / *S. franciscanus* (not distinguished)	Pacific Grove, California, USA	kelp forest, 1 m off bottom at 10 m	artificial collectors (plastic light diffuser and coralline algae)	0.25 mm mesh size	Jul 1988-Jul 1989, ~ monthly	Two settlement peaks (Dec-Feb and Apr-Jul). Greater settlement in plastic collectors, probably due to fewer predators.	Harrold et al. 1991
Strongylocentrotus purpuratus, *S. franciscanus*	Pacific Grove, California, USA	kelp forest, 10 m	10 m^2 circular plots	> 10 mm (5-10 mm was variable)	Oct 1972-Aug 1981, every 2-12 months with a gap in 1973/74	*S. franciscanus* densities low throughout. Recruitment pulse of *S. purpuratus* in 1975-76. A massive reduction of urchins in 1976 due to predation or disease.	Pearse & Hines 1987

Table 1.1 continued

Species	Location	Habitat, Depth	Sampling Method	Size*	Sampling Period, Frequency	Patterns and Conclusions	Source
Strongylocentrotus purpuratus, S. franciscanus	Carmel Bay, central California, USA	kelp forest and deforested rock reef, 16-29 m	1 m^2 quadrats	2-3 mm "some < 1 cm overlooked"	1986-1989, ~ twice per year	Evidence of recruitment in kelp in 1987-88. Suggested that heavy recruitment in 1984 was responsible for population increase and deforestation at both sites (but only one site recovered).	Watanabe & Harrold 1991
Strongylocentrotus purpuratus, S. franciscanus	Santa Barbara, California, USA	"patchy" kelp forest and coralline barren, 8-12 m	collected shale with resident organisms	0.243 mm mesh size	1984-1986, mostly during summer	Few settlers in Apr 1984/85 and many in May '86; similar patterns for both species but lower densities of *S. franciscanus*. No significant difference between habitats; concluded that post-settlement mortality is greater in the kelp.	Rowley 1989, 1990
Strongylocentrotus purpuratus, S. franciscanus	Point Loma, California, USA	inner, middle and outer kelp forest, 12, 15 and 18 m	1 m^2 quadrat "haphazardly placed over rock piles where urchins were abundant"	5-7.5 mm	1974-1977, ~ monthly	Substantial annual recruitment at all sites. *S. franciscanus* recruitment lower at inner (12 m) site and much higher outside the kelp canopy. Concluded that kelp and/or resident predators reduce recruitment.	Tegner & Dayton 1981
Strongylocentrotus purpuratus, S. franciscanus	Point Loma, California, USA	outer, middle and inner kelp forest, 18, 15 and 12 m	1 m^2 quadrats "haphazardly placed over aggregations of urchins in boulder piles"	"< 10 mm not quantitatively sampled"	1983-1987, ~ twice per year	Recruitment on outer edge of kelp forest was low from 1983-85 and increased in '86 and '87 to previous levels (1970's, see above); recruitment remained low within forest. Low recruitment related to El Niño conditions leading to reduced production/survival of larvae and altered currents.	Tegner & Dayton 1991

Table 1.1 continued

Species	**Location**	**Habitat, Depth**	**Sampling Method**	**Size***	**Sampling Period, Frequency**	**Patterns and Conclusions**	**Source**
Strongylocentrotus franciscanus, *S. purpuratus*	San Diego, California, USA	inshore, offshore and within 3 kelp forests, 1 m off bottom at 12-15 m	artificial collectors (scrub brush)	0.436 mm mesh size	Mar-May 1991 and Jan, Apr-Jul 1992, ~ weekly (range = 5-20 d)	Low settlement (0-10 per collector) in both years. Kelp forest had no effect on settlement of *S. purpuratus*. Variable settlement of *S. franciscanus* with some evidence for higher settlement offshore. Concluded that kelp forests do not affect larval supply or settlement.	Schroeter et al. 1996
Strongylocentrotus purpuratus	La Jolla, California, USA	habitat not stated	method not stated	0-2.5 mm	1970-1978, 6 months-3 years apart	Good recruitment in 1969, '71, '74 and substantial recruitment in '72 and '76.	Ebert 1983
Strongylocentrotus purpuratus	Papalote Bay, Baja California, Mexico	habitat not stated	method not stated	0-2 mm	1962-1969, once or twice per year	Substantial annual recruitment with more than one pulse in some years and variability in timing between years.	Pearse 1970 in Ebert 1983
Dendraster exentricus	Monterey Bay, California, USA	inshore sand dollar bed to offshore, 8-30 m	plankton tows; grab and core samples	0.202 mm mesh size (tow); 0.3 mm mesh size (grab)	1978-1981, monthly with gaps	Abundance of competent larvae peaked in summer. Variable inter-annual settlement within and outside adult sand dollar bed.	Cameron & Rumrill 1982
Echinarachnius parma	Middle Atlantic Bight and Georges Bank, northwest Atlantic	habitat not stated, 20-70 m	0.1 m^2 Smith-McIntyre grab	1 or 0.5 mm mesh size	Jul 1977-Jul 1985, every 2-13 months	Regular annual recruitment at 3 of 4 sites from Dec-Apr in Middle Atlantic Bight, from Nov-Jul on Georges Bank. No recruitment at the fourth site after 1978 attributed to anoxic conditions.	Steimle 1990

Table 1.1 continued

Species	Location	Habitat, Depth	Sampling Method	Size*	Sampling Period, Frequency	Patterns and Conclusions	Source
Echinus affinis	Rockall Trough, northeast Atlantic	habitat not stated, 1632-2300 m	3 m wide Agassiz trawl, epibenthic sledge, single-warp trawl or semi-balloon otter trawl	20, 16, 12, 10, 1 or 0.5 mm mesh size	Jun 1973-Apr 1985, 1 day-37 months apart	Mixed unimodal and bimodal size-frequency distributions, but variation in sampling methods and possible bias may have obscured patterns. Samples using small mesh sizes suggested recruitment is rare.	Gage & Tyler 1985
Echinocardium cordatum	German Bight, North Sea	fine sand, 25 and 35 m	vertical plankton tows with Nansen net; 10 cm^2 subsample from $0.017 m^2$ Reineck box core	0.15 mm mesh size (tow); 0.1 mm mesh size (core)	Apr 1985-Dec 1986, monthly	Larvae and settlers present from Jun-Aug in both years. Maximum settlement (26000 m^{-2}) in Aug; heavy post-settlement mortality eliminated recruits by Sep of both years. Suggested dense settlement enables population recovery in years following heavy adult mortality.	Bosselmann 1989
Echinocardium cordatum	Terschelling and Texel Islands, North Sea, Netherlands	sand, 7-18 m	0.2 m^2 Van Veen grab sampler	1 mm mesh size	1972-1982, ~ once per year from Apr-Jun	High recruitment (individuals < 1.5 cm) in 1973, '77 and '80; low or no recruitment in other years. Recruitment greatest at depths of 8-12 m and low above 8 m and below 12 m. Suggested that recruitment occurs infrequently but simultaneously over large areas (100's of km), and may be related to colder water temperatures.	Beukema 1985
Echinocardium cordatum	Bay of Seine, Normandy, France	sand, 0-25 m	0.1 m^2 grab samples	3-6 mm	1986-1987, once per year	Recruitment increased with depth; no recruits in littoral zone. Suggested that 2-4 year olds migrate to the littoral zone.	DeRidder et al. 1991

Table 1.1 continued

Species	Location	Habitat, Depth	Sampling Method	Size*	Sampling Period, Frequency	Patterns and Conclusions	Source
Sphaerechinus granularis	Penfret Island, Brittany, France	algae-encrusted shell debris, mud, *Zostera marina* and rock, < 5 m	"1 m wide dredge" or diver collected	20 mm mesh size or not stated	Dec 1988-Dec 1991, monthly with an 8 month gap in 1989/90	Consistent recruitment in Aug/Sep each year but of variable magnitude among years. Recruits found on algae whereas adults occur only on rocks. Suggested post-settlement migration from juvenile to adult habitats occurs both passively (with currents) and actively (with change in diet).	Guillou & Michel 1993a, b, see also Glémarec & Guillou 1996
Paracentrotus lividus, *Arbacia lixula* echinoplutei	Bay of Villefranche, Provence, France	6-52 km offshore, 10 m and 200-0 m	plankton tows	0.2 mm mesh size	1984-1988, every 2 weeks-3 months	Synchronous spawning twice per year (spring and fall). Larvae restricted to the surface layer, decreased with distance from the coast and rarely occurred beyond a divergence zone 30 km offshore. Timing of recruitment of *P. lividus* related to larval supply.	Pedrotti & Fenaux 1992, Pedrotti 1993
Clypeaster ravenelii	northern Gulf of Mexico	sand, 110 m	otter trawl	10 mm mesh size	Dec 1988-Jan 1991, bimonthly with gaps	Low numbers of juveniles (1-4 cm) noticed in Sept 1989, and May and Aug '90 but little evidence of substantial recruitment. Suggested that if recruitment occurs, it is episodic.	McClintock et al. 1994
South Temperate							
Evechinus chloroticus	Goat Island Marine Reserve, New Zealand	barrens, 5-8 m	0.25 m^2 quadrats "carefully searched"	> 5 mm "reliably found"	1975-1977, yearly; 1979-1981, monthly with gaps	Juveniles found at all sampling dates. Smaller proportions of juveniles in 1975-77 than in '79-81 suggested variable recruitment among years. Concluded that recruitment maintains populations in barrens.	Andrew & Choat 1982

Table 1.1 continued

Species	**Location**	**Habitat, Depth**	**Sampling Method**	**Size***	**Sampling Period, Frequency**	**Patterns and Conclusions**	**Source**
Centrostephanus rodgersii	central coast New South Wales, Australia	barrens	5 m^2 transects	> 3 mm	Jan 1985-Jan 1988, 1-3 times per year	Recruitment varied between 4 sites spanning 300 km from no recruitment over 4 years to high annual recruitment. Suggested differences in availability of spatial refugia (rock types) may result in variable rates of juvenile survival.	Andrew & Underwood 1989
Centrostephanus rodgersii	Botany Bay, New South Wales, Australia	barrens and foliose algae, < 6 m	"haphazard swim"	5-10 mm	Oct 1986-Jun 1988, ~ bimonthly	Recruitment observed at all 7 sites from Jan-Apr in both years. Suggested that growth of foliose algae (at 5 sites following mass mortalities of *C. rodgersii*) did not affect recruitment.	Andrew 1991

Table 1.1 continued

Species	Location	Habitat, Depth	Sampling Method	Size*	Sampling Period, Frequency	Patterns and Conclusions	Source
Tropical							
Araeosoma fenestratum, *Archaeopneustes hystrix*, *Aspidodiadema jacobyi* *Brissopsis* sp., *Cidaris blakei*, *Conolampas sigsbei*, *Linopneustes longispinus*, *Lytechinus euerces*, *Paleobrissus hilgardi*, *Paleopneustes cristatus*, *Paleopneustes tholoformis*, *Phormosoma placenta*, *Salenia goesiana*, *Stylocidaris lineata*	northern Bahamas	habitat not stated, 100-930 m	individually collected using suction device or scoop on submersible	≥ 5 mm	Oct 1985-Feb 1990, ~ twice per year (9 cruises)	Only *Phormosoma placenta* showed direct evidence of recruitment; small indivduals of other species not detected. Suggested recruitment of those species is sporadic and patchy, based on adult size distributions.	Young 1992
Diadema antillarum	Curaçao, Caribbean	coral reef terrace and slope, 3-30 m	transect survey	size not stated	May-Oct 1983, twice	After mass mortality due to disease, ≤ 1 mm recruits settled throughout the year. Larvae may have originated from an island 52 km up current not affected by disease.	Bak et al. 1984
Diadema antillarum	Curaçao, Caribbean	2 coral reefs 24 km apart, 20 cm off bottom at 8 m	artificial collectors (plastic light diffuser panels)	≤ 3 mm	1982-1984, biweekly with gaps	Continuous settlement with spring and fall peaks. Settlement similar between years but differed between sites.	Bak 1985

Table 1.1 continued

Species	**Location**	**Habitat, Depth**	**Sampling Method**	**Size***	**Sampling Period, Frequency**	**Patterns and Conclusions**	**Source**
Diadema antillarum	Barbados, Caribbean	fringing coral reef	10-250 m^2 search area	< 10 mm = settlers; 10-15 mm = recruits	Oct 1984-Dec 1985, monthly	Settlers found in Jun in cryptic habitats and aggregated with adults on offshore region of reefs. Populations recovered to 57 % of pre-mortality levels within 2 years after disease. Suggested recruitment is greater on reefs with higher adult densities.	Hunte & Younglao 1988
Diadema antillarum	St. Croix, US Virgin Islands, Caribbean	coral reef, 2-10 m	$1m^2$ quadrats	0-10 mm	Dec 1983-Mar 1986, 2-15 months apart	Low recruitment at 2 of 4 sites in Feb, Apr 1984 only. Paucity of larvae/settlers after mass mortalies from 1983-85 suggested population recovery is recruitment-limited.	Carpenter 1990
Diadema antillarum	St. John, US Virgin Islands, Caribbean	habitat previously stated	method previously stated	recruit = < 50 mm	1984-1988, ~ yearly	Annual recruitment rates were low (0.017-$0.534\ m^{-2}yr^{-1}$) after mass mortalities from 1983-84. Significant interannual variation but no significant variation between sites in the same bay. Highest recruitment in 1985, lowest in '88. Concluded that recruitment rate was density-independent but too low to enable populations to recover to pre-disturbance levels.	Karlson & Levitan 1990
Diadema antillarum	Molasses Reef, Florida Keys reef tract, USA	offshore reef, 1-2 m	140 m^2 quadrat	3-4 mm	Jul 1991-Aug 1992, every 1-4 months	Mass mortality in Jan/Feb 1991 reduced densities by 97 %. Low recruitment from Jul-Oct 1991, none in '92. Suggested populations will not recover because mortality rate exceeds recruitment.	Forcucci 1994

Table 1.1 continued

Species	**Location**	**Habitat, Depth**	**Sampling Method**	**Size***	**Sampling Period, Frequency**	**Patterns and Conclusions**	**Source**
Diadema antillarum	Panama, Caribbean	sand, coral and seagrass between 2 reefs, 0.5-2.5 m	3-2500 m^2 permanent quadrats	< 15 mm	1982-1987, biweekly-bimonthly	Recruitment immediately after mass mortality in 1983 but none during remainder of study. Experiments showed that predation, conspecific protection, settlement cues, and competition by other echinoids were not responsible for recruitment failure. Low fertilisation success and poor larval supply were likely the cause.	Lessios 1988
Diadema antillarum	Panama, Caribbean	coral reef	method not stated	size not stated	1983-1993, "continuously "	Since mass mortality in 1983, population density has been ≤ 10 % of pre-mortality level. Recruitment was very low over study period.	Lessios 1994 (abstract)
Anthocidaris crassispina	Hong Kong	habitat and depth not stated	diver-collected	5-10 mm	Jan 1983-Dec 1984, monthly	Recruitment from Feb-Jun in both years at 3 sites; no recruitment at fourth site probably due to adverse environmental conditions (low salinity).	Chiu 1986
several species including *Echinometra mathaei, Mespilia globulus* (could not be distinguished)	Davies Reef, Great Barrier Reef, Australia	windward and leeward coral reef, 1m off bottom at ~ 15 m	artificial collectors (100 plastic bio-filter spheres in a net bag), boxes of rubble	0.5 mm mesh size	Nov 1991-Jan 1992, rubble collected in Jan	Settlement was significantly greater on the windward edge than on the leeward edge of the reef which corresponds with observed recruitment to rubble. Within a given reef habitat there was no significant difference in settlement rate between collectors placed 1-100's of meters apart.	Keesing et al. 1993

Table 1.1 continued

Species	Location	Habitat, Depth	Sampling Method	Size*	Sampling Period, Frequency	Patterns and Conclusions	Source
Echinometra mathaei	Rottnest Island and other sites along Western Australia's coast	habitat and depth not stated	used 0.25 m^2 quadrats to collect size frequency data and genetic traits to distinguish groups	5-10 mm	1985 (Rottnest Island) and 1987 (all other sites)	Populations within 4 km of each other had as much genetic variance as populations sampled over 1300 km of coast. Suggested that, over time, variable recruitment supplies different sites with larvae from separate populations.	Watts et al. 1990
Polar							
Sterechinus neumayeri	McMurdo Sound, Antarctica	mud, sand and gravel, 6-18 m	diver-collected	30-31 mm	1989, 1990 and 1992, Dec of each year	Size-frequency analysis and ageing failed to detect recruitment between 1985 and '92. Suggested that recruitment in McMurdo Sound is rare and controlled by physical factors (current and ice activity) that vary interannually.	Brey et al. 1995

* Measurements are test diameters unless specified. Size is either the smallest individual recorded or deemed detectable, the smallest size-frequency range containing individuals, and/or the mesh size used to filter or collect samples.

Table 1.2. A summary of studies examining spatial and temporal patterns of settlement and/or recruitment of asteroids.

Species	Location	Habitat, Depth	Sampling Method	Size*	Sampling Period, Frequency	Patterns and Conclusions	Source
North Temperate							
Asterias forbesi	Long Island Sound, Connecticut, USA	habitat not stated, 0-33 m	collectors (100 clean oyster shells in wire mesh bags)	size not stated	1937-1961, twice per week	Settlement increased with depth to 10m and then decreased to 33 m. Timing and magnitude of settlement varied between sites and years, occurring between Jun and Sep and ranging in duration from 1-91 days (mean = 52 days). Settlement intensity varied from a single peak in 1 week to constant settlement throughout the period. Annual settlement increased from NE to SW and varied by 4 orders of magnitude (0-1700 collector^{-1}) with no pattern of good and bad years. Settlement not correlated with adult density.	Loosanoff 1964
Asterias vulgaris and/or *A. forbesi*	Atlantic coast of Nova Scotia, Canada	barrens and kelp, 0.2 and 2.3 m off bottom at 5-10 m	artificial collectors (plastic turf) and 1.0 m^2 quadrat for recruits	0.150 mm and 1 mm mesh size	Jun-Nov 1992-1994, biweekly and recruits once per year 1993-1995	Settlement pulse in Aug/Sep of each year. Highest settlement in 1993 and '94, intermediate settlement in '92. Settlement greater in kelp beds than in barrens. Recruitment reflects settlement.	Chapter 4
Asterias rubens (= *A. vulgaris*)	Torbay, southwest England	rocky intertidal shore	"carefully searched"	2-5 mm	1980-1981, monthly	Recruits first appeared in Jul 1980 and Sep '81 beneath boulders and in crevices. No recruits found in adjacent areas with similar topography.	Barker & Nichols 1983, Nichols & Barker 1984

Table 1.2 continued

Species	**Location**	**Habitat, Depth**	**Sampling Method**	**Size***	**Sampling Period, Frequency**	**Patterns and Conclusions**	**Source**
Asterias vulgaris, Leptasterias polaris, Crossaster papposus	Mingan Islands, Gulf of St. Lawrence, Canada	bedrock, boulders, cobble, sand/mud, intertidal-20 m	2 m^2 quadrat	≥ 5 mm	Aug-Sep 1984	*A. vulgaris* juveniles most abundant at 4-7 m and found only in boulders or cobble. *L. polaris* juveniles most abundant at 0-1 m and found only in boulders, cobble or bedrock. Small *C. papposus* juveniles found only on sediment bottoms > 11 m.	Himmelman & Dutil 1991
Pisaster ochraceus, Pycnopodia helianthoides, Dermasterias imbricata	Nootka Sound, British Columbia, Canada	bare and algae-covered rock, 1-9 m; 1-2 m (tows)	100 cm^2 quadrat for recruits; plankton tows	0-5 mm "ray length" of recruits; 0.125 mm mesh size (tows)	1987-1991, recruitment data once per year; plankton tows in May and Sep 1989	Recruitment varied between species, sites and years. Recruitment of *Pisaster ochraceus* was high in all years but mortality of recruits after 1 year was > 97 %. *Pycnopodia helianthoides* recruited in 1987-89 and '91. *D. imbricata* recruited in low densities in 1988. Highest densities of bipinnaria larvae found in plankton tows in a semi-enclosed bay. Proposed this area acts as a source of larvae.	Sewell & Watson 1993
Pisaster ochraceus	San Juan Island, Washington, USA	rocky intertidal	0.1-1 m^2 quadrats	1-10 mm	May 1969, Aug 1970 and Apr 1971	Annual recruitment at Point Caution over all 3 years. This site proposed as a nursery area because Gull Reef and other sites in region showed few recruits.	Lubchenco-Menge & Menge 1974
Pisaster ochraceus	Pacific northwest	habitat not stated (includes intertidal)	method not stated	size not stated	1984-1987	Size-structure varied markedly over 20 sites. Predictable and intense recruitment at sheltered sites. Density of recruits declined rapidly and survivors were restricted to crevices.	Rumrill 1988b (abstract)

Table 1.2 continued

Species	**Location**	**Habitat, Depth**	**Sampling Method**	**Size***	**Sampling Period, Frequency**	**Patterns and Conclusions**	**Source**
Asterina miniata	Barkley Sound, British Columbia, Canada	mud and cobble, 4-6 m	0.25 m^2 quadrats	2-4 mm "ray length"	Mar 1985-Aug 1987, bimonthly-yearly	Recruitment at 1 of 2 sites in 1983 and '84; none at either site from '85-87. Evidence that migration and juvenile mortality are not as important as pre- and early post-settlement events in determining recruitment.	Rumrill 1989
Mediaster aequalis, Luidia foliolata, Crossaster papposas, Henricia leviuscula, Solaster stimpsoni, S. dawsoni, Pteraster tesselatus	San Juan Islands, Washington, USA	sand and tube worm (*Phyllochaetopterus prolifica*) beds, 20 m	diver-collected	> 2 mm	"fall and winter, 1968-1969", 4 dives	Juvenile asteroids of all species were commonly found on polychaete tubes and rare elsewhere. Suggested tube worm beds are a nursery ground for juveniles, which subsequently migrate to sandy areas to feed on larger prey.	Birkeland et al. 1971
unidentified species	northern California, USA	habitat not stated, 0.5-1 m off bottom at 5-20 m	artificial collectors (scrub brush)	0.06 mm mesh size	Apr-Sep 1992, weekly	Low levels of settlement occurred throughout most of the sampling period at both sites, with a peak in settlement in Jul during an unusual upwelling relaxation event.	Wing et al. 1995a
Patiria miniata	Southern California Bight, USA	rock reefs and boulders	method not stated	5-10 mm	period not stated	Juveniles found under boulders and adults on reef surface. Suggested juveniles are either excluded by adults or subject to predation when exposed.	Day & Osman 1981

Table 1.2 continued

Species	**Location**	**Habitat, Depth**	**Sampling Method**	**Size***	**Sampling Period, Frequency**	**Patterns and Conclusions**	**Source**
Astropecten bispinosus, *A. aranciacus*	Sardinia, Italy	sand bottom (5-10 m) and seagrass (*Zostera marina*) beds (10-20 m)	25 m^2 grid	10-15 mm radius	Jul/Aug 1980	Recruitment never observed on sandy bottom where adults of both species coexist; suggested migration of juvenile *A. bispinosus* from seagrass beds compensates for loss via predation by *A. aranciacus*.	Jost & Rein 1985
Anseropoda placenta	Bay of Brest, Brittany, France	"muddy sand, sediments with shells and sandy gravel", 17-35 m	"0.8 m wide 'Charcot' dredge"	20 mm mesh size	Dec 1983-Nov 1986, monthly with a 6 month gap in 1984	Annual recruitment from Aug-May. Higher recruitment at deeper site (where shells provide a refuge); possible migration to shallower sites (where adults are more abundant).	Guillou & Diop 1988, see also Glémarec & Guillou 1996
South Temperate							
Stichaster australis, *Coscinasterias calamaria*	Maori Bay, and other sites around North Island, New Zealand	rock reefs and boulders, intertidal-5 m	"searched exhaustively on many occasions"	≥ 7 mm	1974-1976, "on many occasions"	*S. australis* settlers found only on encrusting coralline alga (*Mesophyllum insigne*) at all sites. *C. calamaria* settlers not found in Maori Bay (where juveniles and adults existed) but occurred on various algae at other sites.	Barker 1977
Stichaster australis	Maori Bay, New Zealand	a large (2 m^2) intertidal boulder	measured each juvenile found on the boulder	2-3 mm	1974-1979, monthly	Recruitment density varied by an order of magnitude between years. Timing of recruitment also varied between years.	Barker 1979

Table 1.2 continued

Species	Location	Habitat, Depth	Sampling Method	Size*	Sampling Period, Frequency	Patterns and Conclusions	Source
Tropical							
Oreaster reticulatus	Grenadines and St. Croix, Caribbean	seagrass beds and sand bottoms, 1-13 m	25-100 m^2 quadrats along a transect	> 20 mm radius	1974-1977, ~ every 1-4 months	Juveniles mainly observed adjacent to or within dense seagrass beds. Suggested that they settle in seagrass beds and migrate to adult populations in open sand areas once they reach a size refuge from predation.	Scheibling 1980a, b
Acanthaster planci	Iriomote-jima, Ryukyu Islands, Japan	fringing coral reef (flat and slope, floor of groove or base of coral), depth not stated (imply 5.5-18.5 m)	0.25 m^2 quadrats (20 or 10 cm layer of substrate collected by hand)	0.35 or 2 mm mesh size	Mar-Nov 1985, frequency and allocation of 191 samples not stated	Found 13 recruits in Sep and Nov 1985 (9 in '84). 12 of 13 found in 5.5-7 m and one at 18.5 m depth. 11 of 13 found on the reef floor and the other 2 on the reef slope.	Yokochi & Ogura 1987
Acanthaster planci	Suva Reef, Fiji Islands	coral reef crest, intertidal-? (imply 2 m)	1 m^2 quadrats	10-11 mm	1979-1987, monthly-yearly	Low recruitment for most of the 9 years except 1984 when massive recruitment (3 order of magnitude increase) over most of the reef flat resulted in a population outbreak and subsequent migration down the reef slope.	Zann et al. 1987

Table 1.2 continued

Species	**Location**	**Habitat, Depth**	**Sampling Method**	**Size***	**Sampling Period, Frequency**	**Patterns and Conclusions**	**Source**
Acanthaster planci	Suva, Nukubuco and other reefs, Fiji Islands	coral reef and rubble, intertidal-0.5 m	1 m wide belt transects, rubble searches, random 0.25 m^2 quadrats, spot dives and reef users' reports	10-30 mm	1979-1989, yearly	Massive recruitment in 1977 and '84, large recruitment in '87 and little or no recruitment in other years, over thousands of hectares. Intense recruitment over only a few hectares in 1982 and '83. No correlation between recruitment and terrestrial runoff associated with increased rainfall.	Zann et al. 1990
Acanthaster planci	Green Island, Great Barrier Reef, Australia	live coral and coralline algal-covered rubble, 2-12 m	rubble searches	≥ 2 mm	1986-1990, once or twice per year	Only 2 recruits (2 and 4 cm) found in 4 years, suggesting low or very patchy recruitment.	Fisk 1992, see also Fisk et al. 1988
Acanthaster planci	16 reefs in central Great Barrier Reef, Australia	coral reef base, crest and flat; 15 m below, 2-5 m below and on top of reef respectively	destructive sampling of 10 m^2 belt transects	> 10 mm	Jul-Nov 1986 and Nov 1987, monthly	Greater recruitment in the lower zones of the reef. Reduced recruitment with increasing distance downstream of the primary outbreak population. Recruitment in 1985 was an order of magnitude greater than in '86 and '87. Suggested that a single year of successful recruitment could result in outbreaks.	Doherty & Davidson 1988
Acanthaster planci, *Choriaster granulatus*, *Culcita novaeguineae*	Davies Reef, Great Barrier Reef, Australia	windward and leeward coral reef, 1 m off bottom at ~ 15 m	artificial collectors (100 plastic bio-filter spheres in a net bag), boxes of rubble	0.5 mm mesh size	Nov 1991-Jan 1992, rubble collected in Jan	Minimal settlement of asteroids (n = 11) on collectors with corresponding low recruitment to rubble. 7 of the 11 settlers, including all 3 *A. planci* found on the windward reef slope. Suggested collectors could be a useful tool in predicting outbreaks of *A. planci* 3 years in advance.	Keesing et al. 1993

Table 1.2 continued

Species	**Location**	**Habitat, Depth**	**Sampling Method**	**Size***	**Sampling Period, Frequency**	**Patterns and Conclusions**	**Source**
Acanthaster planci	Lord Howe Island, Australia	coral reef and unstated habitat, 1-40 m	500-5000 m^2 "searched systematically"	> 15 cm	1987 and 1989, once each year	Suggested that range of observed sizes (15-52 cm) indicates annual recruitment since 1985.	DeVantier & Deacon 1990
Polar							
Odontaster validus	McMurdo Sound, Antarctica	volcanic sediments, 10, 20 and 30 m	diver-collected	0-1 g wet weight	Oct 1984-Aug 1985, every 2-7 months	Size-frequency distributions showed no obvious recruitment over the year. Suggested that recruitment is low and temporally stable.	McClintock et al. 1988

* Measurements are diameters unless specified. Size is either the smallest individual recorded or detectable, the smallest size class containing individuals and/or the mesh size used to filter or collect samples.

Table 1.3. A summary of studies examining spatial and temporal patterns of settlement and/or recruitment of ophiuroids.

Species	Location	Habitat, Depth	Sampling Method	Size*	Sampling Period, Frequency	Patterns and Conclusions	Source
North Temperate							
Acrocnida brachiata	Douarnenez Bay, Brittany, France	sand, intertidal and 20 m	0.25 m^2 core (intertidal), 0.062 m^2 suction sample (subtidal)	0.16 mm mesh size (intertidal), 1 or 0.2 mm mesh size (subtidal)	Mar 1984-Jul 1986, ~ monthly with some gaps	Annual recruitment at both sites in Jun with high mortality in the subsequent 2 months. Higher recruitment in the subtidal zone is attributed to less harsh hydrodynamic conditions.	Bourgoin et al. 1990, see also Glémarec & Guillou 1996
Amphiura filiformis, *Ophiothrix fragilis*, *Ophiopluteus bimaculatus*, *O. compressus* ophioplutei	Bay of Villefranche, Provence, France	6-52 km offshore, 10 m and 200-0 m	zooplankton tows	0.2 mm mesh size	1984-1988, every 2 weeks-3 months	Larvae restricted to the surface layer, decreased with distance from the coast and rarely occurred beyond a divergence zone 30 km offshore. A mixture of larval stages at various times of the year suggested variable recruitment over most of the year.	Pedrotti & Fenaux 1992, Pedrotti 1993
Amphiura filiformis	Concarneau Bay, Brittany, France	muddy sand, 17 and 28 m	0.1 m^2 Smith McIntyre grab sampler	1 mm mesh size	May 1972-Oct 1973 and Jun 1977-Feb 1979, every 3-7 months	Recruitment in spring and fall each year. Suggested high post-spawning mortality of adults facilitates recruitment, particularly under unstable evironmental conditions.	Bourgoin & Guillou 1988, see also Glemarec & Guillou 1996

Table 1.3 continued

Species	Location	Habitat, Depth	Sampling Method	Size*	Sampling Period, Frequency	Patterns and Conclusions	Source
Amphiura filiformis	North Sea, off the Dutch coast	fine sand with silt, 30 m	0.06 m^2 Reineck box corer	1.0 and 0.2 mm nested sieves (measured disk size: "distance between alternating radial shields")	Sept 1982-May 1984, ~ quarterly	Stable size structure with large adult mode and seasonal recruitment from Jul-Sep each year. Density of recruits varied annually (mean: 3000-15000 $m^{-2)}$ but high mortality in their first year resulted in a low but steady rate of renewal of adult population.	Duineveld & Van Noort 1986
Amphiura filiformis	German Bight and the central North Sea	muddy fine sand, 38 and 54 m	0.1 m^2 van Veen grab; 0.017m^2 Reineck box sampler	0.5 mm mesh size; 0.125 mm mesh size (0.2-0.3 mm)	1983, 1984 and 1986-1988, every Mar/Apr (and Jun, Jul/Aug and Nov in 1983 and 1987); Mar and Dec 1987 and Apr 1988	Size-frequency analysis suggested annual recruitment with settlement beginning Jul/Aug. Data from several studies indicated a SW to NE progression in timing of settlement in the North Sea.	Künitzer 1989
Amphiura filiformis	Galway Bay, west coast of Ireland	silty sand, 20 m	0.12 m^2 van Veen grab or suction sampler	0.5 or 1 mm mesh size	Oct 1974-Sept 1976 and Nov 1978-Apr 1982, ~ every 1-7 months	High densities found at a permanent site (mean = 290-2226 m^{-2}) and throughout the bay, but only ~ 5 % were juveniles (< 4 mm). Very low and patchy recruitment observed over the 8 year period. Settlers were not sampled due to large sieve size, but peak settlement assumed to occur in the fall (Sep-Nov).	O'Connor et al. 1983, see also O'Connor & McGrath 1980

Table 1.3 continued

Species	Location	Habitat, Depth	Sampling Method	Size*	Sampling Period, Frequency	Patterns and Conclusions	Source
Amphiura filiformis, A. chiajei	the Øresund, off Denmark	muddy sand, 27 m	0.02 m^2 "mouse-trap" sampler	0.265 mm mesh size (settler = 0.325 mm)	Oct 1963-Oct 1965, biweekly	79 % of *A. filiformis* sampled were recruits (0.3-0.6 mm). Peak settlement (6-7000 m^{-2}) occurred annually during a 2-6 week interval in Sep-Nov. Few recruits survived their first year. Few juveniles (0.7- 4 mm) were present and adult cohorts overlapped with relatively stable densities (mean = 575 m^{-2}). *A. chiajei* were present in very low numbers and settlement started in Nov (~ 3 mo after *A. filiformis*).	Muus 1981
Amphiura chiajei	Killary Harbour, west coast of Ireland	soft mud, 14 m	0.02 m^2 "mousetrap" sampler and 0.12 m^2 van Veen grab	0.5 or 1.4 mm mesh size (measured oral width and disk diameter)	Nov 1985-Oct 1988, every 1-2 months with a 12 month gap in 1987/88	Limited and variable recruitment occurred over the sampling period. Suggested that low survival of recruits is due to competition with a dense adult population (~ 700 m^{-2}). Adult mortality during severe winters may allow for occasional heavy recruitment.	Munday & Keegan 1992
Amphipholis squamata	Firth of Forth, Scotland	"boulder-strewn rocky shore", low water	"200 ml of muddy gravel" from under boulders	0.5-1.0 mm	Dec 1975-Nov 1976, monthly	Juveniles recruited to the study population from Jun-Sep but declined in numbers over winter and spring.	Jones & Smaldon, 1989

Table 1.3 continued

Species	**Location**	**Habitat, Depth**	**Sampling Method**	**Size***	**Sampling Period, Frequency**	**Patterns and Conclusions**	**Source**
Amphipholis squamata	Firth of Forth, Scotland; South Devon, England	"loose muddy gravel between boulders", low water; tidepools, high water	200 ml of gravel; 150-200 ml of fringing turf	0-0.99 mm	Dec 1975-Nov 1976, monthly; Jul 1986-Jun 1987, monthly	Recruitment occurred from May-Aug in Scotland, but occurred in a pulse (in Aug) in England. Differences in recruitment patterns attributed to differences in adult survival: adults die in fall in England whereas they continue to brood through a second winter in Scotland.	Emson et al. 1989
Ophiomusium lymani	various sites in northeast and northwest Atlantic and northeast Pacific	habitat not stated, 1100-2300 m	epibenthic sled, Agassiz trawl, Megatrawl, Otter trawl, young fish trawl, Blake trawl	0-1 mm (various mesh sizes used)	1910-1981, variable	Re-analysed size distributions from various studies. Presence of several juvenile modes in all regions suggested seasonal and annual recruitment in spring in the Atlantic and late summer in the NE Pacific. Juvenile modes dominated most of the populations but survivorship low; variable presence of adult modes attributed to different rates of mortality with the NE Atlantic region showing lowest adult mortality.	Gage 1982, see also Gage & Tyler 1982a, Gage et al. 1980, Tyler 1988

Table 1.3 continued

Species	Location	Habitat, Depth	Sampling Method	Size*	Sampling Period, Frequency	Patterns and Conclusions	Source
Ophiomusium lymani	Rockall Trough, northeast Atlantic	silt, clay, and sand mixture, 2200 m	Agassiz trawl, epibenthic sled	0-2 mm (10 mm or 0.5 mm mesh size and/or "sorted on deck")	Apr 1978-Sep 1980, 1 day-7 months apart	Polymodal size distributions suggested annual recruitment with a settlement pulse in May (due to large mesh size, settlers were only effectively measured on 2 trawls in 1980). This conflicts with the observed lack of seasonal reproduction but may be explained by regulation of larval survival by seasonal inputs of detritus from surface waters. Concluded that high mortality of juveniles < 4 mm results in low rate of increase of adult population.	Gage & Tyler 1982a, b, see also Gage et al. 1980, Tyler 1988
Ophiocten gracilis	Rockall Trough and Outer Hebrides continental slope, northeast Atlantic	silt, clay, and sand mixture, 2200, 2900 and 600-1200 m	epibenthic sled or 0.25 m^2 box-core	0.75-1.0 mm (0.5 mm and unstated mesh size)	May 1975-Sep 1980, ~ every 2-7 months	Heavy settlement in early summer (May/Jun) at two sites in the Rockall Trough (2200 and 2900 m) where adults absent. Mortality at that time was high and no settlers survived the winter. Found a population on the Hebridean continental slope (600-1200 m) with a polymodal size distribution of juveniles suggesting annual and seasonal recruitment.	Gage & Tyler 1981a, see also Gage et al. 1980, Gage & Tyler 1981b, 1982b, c, Tyler & Gage 1980, Tyler 1988

Table 1.3 continued

Species	**Location**	**Habitat, Depth**	**Sampling Method**	**Size***	**Sampling Period, Frequency**	**Patterns and Conclusions**	**Source**
Ophiocten gracilis, *Ophiura ljungmani*	Rockall Trough and surrounding slopes, northeast Atlantic	silt, clay, and sand mixture, 704-2900 m	epibenthic sled and box core	0.25-0.5 mm (0.5 mm mesh size)	Jun 1973-Sep 1980, 1-43 months apart	Suggested uniform annual settlement over the observed depth range for both species. Adult breeding populations of *Ophiocten gracilis* (range = 704-2900 m) concentrated at ~ 1000 m with a high proportion of juveniles at all depths but decreased survivorship with depth. Adult *Ophiura ljungmani* (range = 1632-2900 m) concentrated at ~ 2900 m and juveniles dominated the shallower populations with no clear trend in survivorship. Concluded that both species showed considerable variability with depth and suggested that depth is not a direct controlling factor.	Gage and Tyler 1982c, see also Gage & Tyler 1981a, 1981b, Gage et al. 1980
Ophiura ljungmani	Rockall Trough, northeast Atlantic	silt, clay, and sand mixture, 2200 and 2900 m	epibenthic sled	0.25-0.5 mm (0.5 mm mesh size)	Nov 1975-Sep 1980, ~ 3 times per year	Time series of size distributions showed that high densities of recruits dominated the population. Suggested settlement occurs annually in summer but the timing and magnitude varies from year to year.	Gage & Tyler 1981b , see also Gage et al. 1980, Gage & Tyler 1982c, b, Tyler & Gage 1980, Tyler 1988

Table 1.3 continued

Species	Location	Habitat, Depth	Sampling Method	Size*	Sampling Period, Frequency	Patterns and Conclusions	Source
Ophiura robusta and/or *O. sarsi*, *Ophiopholis aculeata*	Atlantic coast of Nova Scotia, Canada	barrens and kelp, 0.2 and 2.3 m off bottom at 5-10 m	artificial collectors (plastic turf) and 1.0 m^2 quadrat for recruits	0.150 mm and 1 mm mesh size	Jun-Nov 1992-1994, biweekly and recruits once per year 1993-1995	Settlement pulse of both species in late Jul-early Aug of each year. Highest settlement in 1992 for *Ophiura* and in '93 for *Ophiopholis aculeata*. Settlement of both species greater in barrens than in kelp beds. Recruitment same between habitats.	Chapter 4
Ophiura sarsi	Gulf of Maine, USA	poorly sorted silt-clay, 148-156 m	Blake trawl	1 mm mesh size	Jul 1985-Aug 1986, every 1-4 months	Followed multiple cohorts over time. Small individuals (< 3 mm) in all sample dates with high numbers of recent recruits (< 1 mm) in Jan. Suggested continuous recruitment with an annual peak around Jan.	Packer et al. 1994
Ophiura sarsi	northeast Japan	mud, 200-600 m	trawl or dredge	1 or 5 mm mesh size	May 1987-Mar 1989, 2-7 times per site	Settlement not detected due to large mesh size. Size distribution showed strong recruitment at shallow depths and poor recruitment at deeper sites. Multiple modes at 250 m site suggested annual recruitment with a peak in Mar-May.	Fujita & Ohta 1990

Table 1.3 continued

Species	Location	Habitat, Depth	Sampling Method	Size*	Sampling Period, Frequency	Patterns and Conclusions	Source
Ophioplocus esmarki, *Ophionereis annulata*	La Jolla, California, USA	habitat and depth not stated	method not stated	2-3 mm	1971-1974, 1-6 months apart	Found few settlers of either species but conceded that they may have been missed. Size distributions showed that *Ophioplocus esmarki* (brooder) has higher or more frequent recruitment due to its positive skew than *Ophionereis annulata* (spawner) with its more normal distribution. Concluded that both species are at their geographic extreme and suggested they might show different recruitment patterns elsewhere.	Muscat 1975 in Ebert 1983
Hemipholis elongata, *Microphiopholis atra*	northern Gulf of Mexico	sand, silt and clay, 13 m	0.09 m^2 box-corer	0.5 mm mesh size	Sep 1981	Predominance of small individuals (< 1 mm) suggested heavy recruitment in both species. Based on a single sample of size distribution and no growth data, concluded that periods of recruitment overlap.	Turner & Miller 1988
Hemipholis elongata, *Microphiopholis atra*	Mississippi Sound, Gulf of Mexico	habitat and depth not stated	0.4 m^2 Shipek grab sampler	0.5 mm mesh size (measured oral diameter)	Apr 1986-Aug 1987, ~ biweekly	Recruitment of both species occurred year round with peak levels in Sep/Oct 1986 and Jul/Aug '87 for *M. atra*, and May-Sep '86 and Jun-Aug '87 for *H. elongata*. Only 5 and 3 % of recruits of *M. atra* and *H. elongata* respectively survived the first year. Concluded that interannual variability in recruitment has little effect on density and persistence of populations.	Valentine 1991

Table 1.3 continued

Species	**Location**	**Habitat, Depth**	**Sampling Method**	**Size***	**Sampling Period, Frequency**	**Patterns and Conclusions**	**Source**
Asteroporpa annulata	northern Gulf of Mexico	"substrate covered with rhodolith structures", 90 m	10 m semi-balloon trawl	15 mm mesh size	Oct 1988-Apr 1991, 19 times	Of 177 individuals sampled, only 4 were juveniles (3-4 mm) all of which were attached to adult aboral discs. Suggested gradual supply of juveniles that either actively or passively recruit to adult conspecifics.	McClintock et al. 1993
Tropical							
Ophiocomella ophiactoides	Discovery Bay, Jamaica	coralline algae on rock, < 2 m	hand collected samples of *Amphiroa* spp. (where *O. ophiactoides* resides)	1-1.5 mm	Jun-Aug and Dec 1981, Jul 1982, monthly	Only 6 juveniles found suggesting recruitment via larvae is rare. Concluded that continuous reproduction by fission and a high survival rate maintains large populations.	Mladenov et al. 1983
Ophiactis savignyi	Wanlitung, southern Taiwan	tidepools, 0.3-0.5 m deep	500-1000 g samples of the sponge *Haliclona* sp. (where *O. savignyi* resides)	0-0.9 mm (across widest part of disk)	Feb 1991-Jan 1992, monthly	Low numbers of recruits found from May-Dec with a pulse in Jun. Regeneration by fission occurred year round with a peak in Jul.	Chao & Tsai 1995

Table 1.3 continued

Species	Location	Habitat, Depth	Sampling Method	Size*	Sampling Period, Frequency	Patterns and Conclusions	Source
unidentified species	Davies Reef, Great Barrier Reef, Australia	windward and leeward coral reef, 1 m off bottom at ~ 15 m	artificial collectors (100 plastic bio-filter spheres in net bag), boxes of rubble	0.5 mm mesh size	Nov 1991-Jan 1992, rubble collected in Jan	Settlement did not differ significantly between habitats which corresponds with observed recruitment to rubble. Within a given reef habitat there were near-significant differences in settlement between collectors 100's of meters apart but no differences between those 1-2 m apart. Settlement increased from north to south between sites on the leeward reef.	Keesing et al. 1993

* Measurements are disk diameters (radial shield to opposite disk edge) unless specified. Size is either the smallest individual recorded or detectable, the smallest size-frequency range containing individuals, and/or the mesh size used to filter or collect samples.

Table 1.4. A summary of studies examining spatial and temporal patterns of settlement and/or recruitment of holothuroids.

Species	Location	Habitat, Depth	Sampling Method	Size*	Sampling Period, Frequency	Patterns and Conclusions	Source
North Temperate							
Cucumaria frondosa	western Gulf of Maine, USA	mussels, coralline algae and kelp holdfasts, 7.5-12.5 m	"haphazard samples of each substrate"	0.5-1.0 mm	Jun/Jul 1993, Oct 1994 and Apr-Jul 1995	Recruitment from May-Jul with peak in mid-Jun. Recruitment highest in mussel beds, lowest on individual mussels, and intermediate in kelp holdfasts and coralline algae.	Medeiros-Bergen & Miles 1997, see also Medeiros-Bergen et al. 1995
Cucumaria frondosa	St. Lawrence Estuary, Canada	bedrock, boulders and gravel, 0-60 m	200 m^2 "transect parallel to the coast"	0-15 mm, (measured "length")	spring 1992-winter 1993, "once at the beginning of each season"	Spawned mid-June 1992 and '93 and settled 3 weeks later. Settlers concentrated in shallow water (0-20 m). Concluded low annual recruitment and migration to deeper water at sexual maturity (~ 3 years).	Hamel & Mercier 1996
Cucumaria pseudocurata	Shell Beach, northern California, USA	rocky intertidal, + 0.3 m	"samples collected" for reproductive cycle; 16 cm^2 quadrats for size distributions	0-1 mg (dried weight)	Aug 1970-Jan 1972, ~ monthly for reproductive cycle; Feb and Mar, 1971 for size distributions	Seasonal reproductive cycle with spawning in Jan 1971 and '72. Recruits first observed in Feb 1971. All mature females in the population were found brooding, suggesting annual recruitment.	Rutherford 1973

Table 1.4 continued

Species	Location	Habitat, Depth	Sampling Method	Size*	Sampling Period, Frequency	Patterns and Conclusions	Source
Leptosynapta clarki	Bamfield, British Columbia, Canada	mid-intertidal mudflat	785.4 mm^2 perspex core	0.25 mm mesh size (length measured after relaxation in $MgCl_2$)	May 1990-Aug 1991, every 2 months	Recruitment pulse in Apr/May of both years. Noted "patchy distribution of juveniles".	Sewell 1994
Parastichopus californicus	Howe Sound, Clayoqout Sound, and Indian Arm, British Columbia, Canada and San Juan Islands, Washington, USA	algal mats, stipes or thalli, polychaete tubes, crevices in rock walls, 5-15 m (not stated for all habitats)	"qualitatively observed" or collected	0.004 "size index" = contracted length x width x scaling factor of 0.1	May 1979-Dec 1984, every 2-3 months (varied with site)	Extended spawning period suggested recruitment occured over several months at Canadian sites with no recruitment in the San Juan Islands. Followed growth of 2 cohorts that settled in 1981 and '83. Suggested recruitment is common and regular in some areas and weak or non-existent in others.	Cameron & Fankboner 1989
Holothuria tubulosa	Ischia Island, Gulf of Naples, Italy	seagrass (*Posidonia oceanica*) bed, 6, 19 and 33 m	diver collected	0-20 g "total wet weight"	May 1988-Dec 1989, every 2-4 months	Combining all sample dates showed a depth gradient in size distribution with smaller individuals (but of different ages and/or reproductive states) at shallow depths (6 m). Concluded that recruitment occurs in the shallow part of the seagrass bed and that some individuals migrate down-slope.	Bulteel et al. 1992

Table 1.4 continued

Species	Location	Habitat, Depth	Sampling Method	Size*	Sampling Period, Frequency	Patterns and Conclusions	Source
Tropical							
Holothuria atra, *H. leucospilota*, *Actinopyga echinites*, *Opheodesoma grisea*, *Synapta maculata*	Wanlitung and Nanwan, southern Taiwan	intertidal and subtidal "flats", intertidal-10 m	"search for small individuals"	recruits defined as either < 5 g or < 20 mm	Mar 1990-Feb 1992, monthly (intertidal); 1991, 3 times in summer (subtidal)	No recruits of *H. atra* at either site; recruits of other species were common on intertidal flats. Suggested that asexual reproduction by fission maintains populations of *H. atra*.	Chao et al. 1994

* Measurements are body length (anterior to posterior ends) unless specified. Size is either the smallest individual recorded or detectable, the smallest size-frequency range containing individuals, and/or the mesh size used to filter or collect samples.

Fig. 1.1. Frequency distribution of sampling duration for 88 studies which monitored temporal patterns of settlement and/or recruitment in 4 classes of echinoderms (Tables 1.1 to 1.4; studies using larval distribution or genetic analysis to predict patterns are excluded).

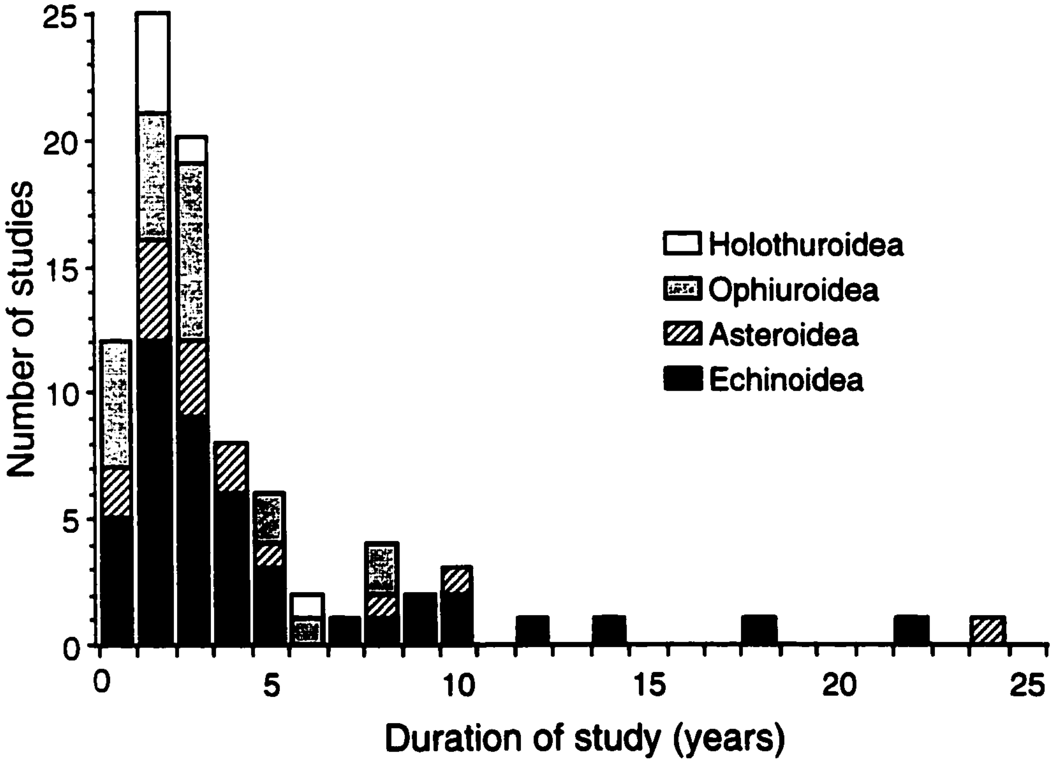

Number of studies
0
5
10
15
20
25
Duration of study (years)
0
5
10
15
20
25
Holothuroidea
Ophiuroidea
Asteroidea
Echinoidea

Figure 1.1

Fig. 1.2. Frequency distribution of modal sampling interval for 82 studies which monitored temporal patterns of settlement and/or recruitment in 4 classes of echinoderms (Tables 1.1 to 1.4; studies using larval distribution or genetic analysis to predict patterns, or with insufficient data to assess sampling interval, are excluded).

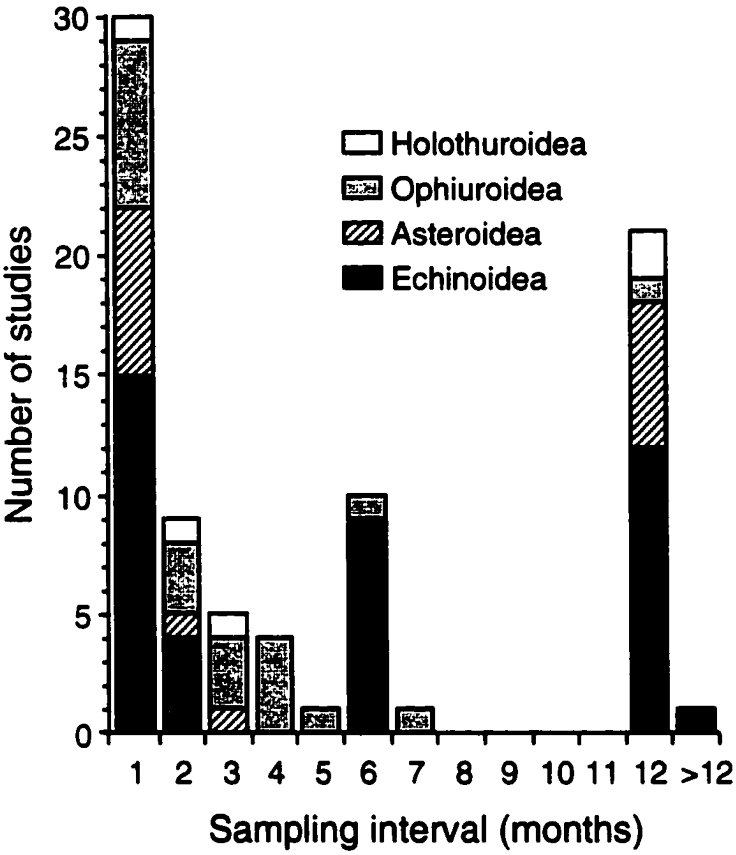

Number of studies
30
25
20
15
10
5
0
Holothuroidea
Ophiuroidea
Asteroidea
Echinoidea
1
2
3
4
5
6
7
8
9
10
11
12
>12
Sampling interval (months)

Figure 1.2

GENERAL CONCLUSIONS AND RECOMMENDATIONS FOR FUTURE RESEARCH

In the 14 years since Ebert's 1983 review, there has been a substantial increase in research on the early life-history stages of echinoderms, particularly in relation to settlement and recruitment patterns and processes. For example, of the 108 studies included in the tables, 80 were published after 1982. I have compartmentalised this research into three components: larval supply, settlement and recruitment. Most of the studies that I reviewed dealt with only one of these components, some in only a peripheral manner. In population studies, for example, it is often concluded that recruitment is highly variable and probably important in population regulation without strong empirical or experimental support for these conclusions. I contend that each of these components represents a critical stage of early life-history of echinoderms, and that studies which integrate all components for a given species will best enable us to understand the relative importance of each. Also, it is only through an integrated approach that we can reasonably parametrise population dynamics models (e.g. stage-based matrix or simultaneous differential equation models) to predict patterns of settlement and recruitment for echinoderm populations. To date, there has been little application of such models to benthic marine invertebrates in general (Eckman 1996). However, models will only be as good as the data used to construct them (Grant 1989) and, as indicated by this review, there remain many unanswered questions about the early life histories of echinoderms.

Many species of echinoderms produce vast quantities of planktonic larvae that are dispersed over great distances and suffer huge losses before settling. Larval supply is a crucial determinant of spatial and temporal patterns of recruitment in these species, and a potential bottleneck to population growth. However, the fate of larvae in the plankton remains the most poorly known aspect of echinoderm early life histories, a "black box" which we are only beginning to penetrate (McEdward 1995). The behaviour of echinoderm larvae has been studied almost exclusively in the laboratory (mostly under static conditions) and the relevance of observed behaviours to the situation in nature is difficult to predict. Experimental mesocosms may circumvent this problem by approximating natural conditions while enabling some degree of control over factors which regulate larval behaviour. Natural mesocosms such as tide pools also may prove useful in studies of larval behaviour (Metaxas & Scheibling 1993). Field studies may benefit from new methods of larval tracking (reviewed by Levin 1990) which, when combined with increasingly more sophisticated hydrodynamic models (e.g. Griffin & Thompson 1996), could yield more accurate predictions of advective transport of larvae from spawning sources, and elucidate physical factors which influence larval supply (e.g. Taggart et al. 1996).

Studies of settlement of echinoderm larvae also have been largely restricted to static conditions in the laboratory. These studies have shown that many species can be induced to settle on a variety of substrata, including microbial films, suggesting that settlement is not substratum specific (Pearce 1997). Settlement induction, therefore, may be less important than larval supply in determining rates and patterns of settlement. Once competent larvae are delivered to an area by large-scale hydrodynamic processes, specific settlement sites may be determined by variations in boundary-layer flow, either by passive deposition of larvae or active selection of particular substrates when flow conditions permit (Butman 1987). Field experiments which track competent larvae through to settlement, particularly in areas where they will encounter a variety of substrata or microhabitats, could advance our understanding of the role of larval behaviour in determining settlement patterns in nature. A logical extension of such studies would be to monitor the fate of settlers in different microhabitats to determine whether larvae tend to select sites to maximise post-metamorphic survival.

Although the number of studies examining spatial and temporal patterns of settlement and recruitment in echinoderms has increased markedly over the past 14 years, the distribution of these studies across taxa and geographic regions is highly skewed. Of the 108 studies on this topic that I reviewed (Tables 1.1 to 1.4), 77 were done in northern temperate waters and 36 of those were on echinoids, of which 27 were on strongylocentrotids. The work on *Strongylocentrotus* has revealed that recruitment patterns can be highly variable, both temporally and spatially, even within the geographic range of a species. However, this emphasis on a single northern temperate genus may bias our perception of recruitment variability among echinoderms in general. Only 24 of the studies on recruitment patterns have involved tropical echinoderms, and 14 of those have been on 2 species, *Diadema antillarum* and *Acanthaster planci*, which have undergone large population fluctuations, atypical of tropical species. Most studies of recruitment of *D. antillarum* have been aimed at investigating population recovery after a mass-mortality in the Caribbean, whereas studies *A. planci* have been prompted by attempts to understand population outbreaks on the Great Barrier Reef. Unfortunately, recruits rarely have been found in these cases, offering few insights for recruitment of even these most studied species. Furthermore, the paucity of studies from southern temperate (5) and polar (2, both Antarctic) regions provides little direct evidence to assess geographic variation in patterns and processes of recruitment of echinoderms. Because spatial and temporal variability in recruitment are common at all scales, among all echinoderm taxa, and throughout all geographic regions, data from one or a few species in a region will likely not be representative of other species in that area. Nevertheless, knowledge gained from intensively studied species can guide future research on the less studied species and geographic regions.

Although the importance of recruitment in determining the distribution and abundance of echinoderm populations is widely recognised, the inherent variability in the definition of recruitment often causes confusion when it fails to identify which stage of the early life-history is being considered (for a more general discussion of this problem, see Hunt & Scheibling 1997). Recruitment typically is defined operationally by the method used to sample juveniles which can vary greatly among studies, even of the same species

(Tables 1.1 to 1.4). Because post-settlement processes such as predation and migration can alter the pattern of juvenile abundance, the measure of recruitment may depend largely on the time elapsed since settlement. Without isolating the effects of these processes, the researcher is left without a clear understanding of the factors responsible for the pattern observed or whether it reflects the pattern of settlement. Although sampling early juveniles presents significant challenges, the development of new techniques for tagging and monitoring (e.g. time-lapse video) recruits in the field can greatly extend our ability to track cohorts from settlement or at least shortly thereafter. The use of artificial collectors, coupled with continuous temperature and current records, is facilitating the detection of settlement patterns over ecologically relevant spatial and temporal scales, and in relation to local hydrographic conditions (e.g. Miller & Emlet 1997, Chapters 2 to 4). Conventional procedures for tracking of cohorts and detecting recruitment events, such as modal analysis of size-frequency distributions, also have benefited from advancements in analytical methods and improved techniques of aging individuals. By increasing the efficiency and precision of sampling, these technological and methodological advances will enable future researchers to better understand the mechanistic links between the early life-history stages of echinoderms which cause the patterns that we observe.

RESEARCH OBJECTIVES

This thesis examines settlement of echinoderm species on artificial collectors at different spatial and temporal scales to identify patterns and processes determining population dynamics in the rocky subtidal zone. The major objectives are:

1) To compare settlement among distinct geographic regions (100's of kilometres apart), and relate differences to patterns of settlement at smaller scales among sites within regions (10's of kilometres) and among habitats within sites (10's of metres) (Chapter 2).

2) To assess the effect of collector type and sampling frequency on measures of settlement (Chapters 2 and 4).

3) To examine effects on larval supply and settlement of small-scale hydrodynamic forcing (Chapter 3).

4) To compare settlement of species with similar larval types at different temporal (days to years) and spatial (metres to 10's of kilometres) scales within a region (Atlantic coast of Nova Scotia) to resolve patterns and gain insight into the underlying processes (Chapter 4).

5) To compare recruitment of these species over the same scales to determine whether recruitment patterns reflect settlement or are shaped by post-settlement processes (Chapter 4).

Chapter 2: Variation in settlement of *Strongylocentrotus droebachiensis* in the northwest Atlantic: effects of spatial scale and sampling method

INTRODUCTION

The green sea urchin *Strongylocentrotus droebachiensis* is a common inhabitant of the rocky subtidal zone throughout the northwest Atlantic. In areas where this species is abundant, it is capable of drastically altering community structure by the destructive grazing of kelp (*Laminaria* spp.) to form sea urchin-dominated barren grounds (Chapman 1981, Wharton & Mann 1981, Miller 1985a, b, Scheibling 1986). Apart from its ecological importance, *S. droebachiensis* forms the basis of a rapidly growing sea urchin fishery, which has renewed interest in the processes that control sea urchin population dynamics (Scheibling & Hatcher 1994). Settlement and subsequent recruitment of sea urchins are seen as key factors in regulating urchin populations (Harrold & Pearse 1987). Many studies have shown recruitment of echinoderms to vary over a variety of spatial and temporal scales, from tens of metres to thousands of kilometres and from months to years (reviewed by Ebert 1983, Pearse & Cameron 1991). However, little is known about patterns of settlement due to the difficulties in sampling settlers before post-settlement processes such as mortality or migration occur. Recent studies using artificial collectors have shown that settlement of sea urchins can be effectively measured to better understand the processes that determine recruitment patterns (Harrold et al. 1991, Keesing et al. 1993, Ebert et al. 1994, Harris et al. 1994, Schroeter et al. 1996, Miller & Emlet 1997). Artificial collectors provide a uniform substrate for measurement of settlement and allow for consistent comparisons both within and between sites and habitats across large distances at relevant time scales. In this study, settlement of *S. droebachiensis* on three types of artificial collectors was compared in three regions of the northwest Atlantic: the Atlantic coast of Nova Scotia, the Bay of Fundy, and the Gulf of Maine. The objectives of the this study were to determine the scales of spatial variability of settlement and to compare different methods of settlement sampling.

MATERIALS AND METHODS

Settlement of *Strongylocentrotus droebachiensis* was measured at 20 sites in 3 geographic regions of the northwest Atlantic separated by 100's of km: 8 in the Gulf of Maine (Region A), 9 in the Bay of Fundy (Region B), and 3 along the Atlantic coast of Nova Scotia (Region C) (Table 2.1 and Fig. 2.1). Within each region most sites were separated by 0.5 to 100 km. Exceptions to this were: Star Island which was sampled at several depths along a rock ridge, White Island which included a sea urchin-dominated barren ground and a kelp bed habitat separated by a rock outcrop, and Mill Cove which included adjacent barren and kelp habitats (Table 2.1). Although the sites used in this study included a variety of habitat types (Table 2.1), they all contained populations of *S. droebachiensis*.

Settlement was measured using artificial collectors separated by 0.02 to 10 m and placed at 5 to 30 m depth (Table 2.1). Three different collector designs were used. Rack collectors were 0.01 to 0.04 m^2 rectangular sections of plastic turf mounted horizontally with cable ties on 35 x 65 cm plasticised wire racks (Fig. 2.2). Four or five replicates were mounted on each rack which was attached to bricks and therefore elevated 10 cm off the bottom. At one site (Tongue Shoal) several racks were suspended in 2 m increments up to 8 m off the bottom. Replicates were either on the same rack or on racks placed within 2 m of each other. The plastic turf used was either "mining turf" (PNS-3, Monsanto Canada Inc., La Salle, PQ, Canada) or sections of plastic doormats made of a similar material and with a similar configuration. Pipe collectors were made up of paired 20 cm x 14 cm diameter PVC pipes mounted on a plastic vane and attached to a rope by swivels to allow orientation into the current (Fig. 2.2). Each pipe was lined with 0.05 m^2 pieces of plastic turf (PNS-3, Monsanto Canada Inc.) and protected from predators by plastic light diffuser grating (1 cm aperture). Paired collectors were suspended in an array at 0.2 and 2.3 m off the bottom by a sub-surface float and anchored with two 20 kg cement blocks (Fig. 2.2). Each replicate array was placed 10 m apart within each site. Brush collectors consisted of two wooden scrub brushes with 0.014 m^2 of nylon bristles (#0115, National Brush Co., Aurora, IL, USA; from Ebert et al. 1994) which were deployed 1 m apart at one site in Maine (Nubble Lighthouse) and suspended vertically 15 cm off the bottom. Collectors were sampled at 2 to 10 week intervals from May to August 1994 (Table 2.1). Rack and brush collectors were sampled once over the settlement period and pipe collectors were sampled at 1 or 3 successive intervals over this period (Table 2.1). Data from pipe collectors at sites in Nova Scotia are presented for both an ~2 week interval (15 to 18 d) encompassing the peak of the settlement period to compare between sites within this region, and for 3 successive ~2 week intervals combined, for comparison with the rack collectors over the same 6 to 7 week period. Sampling intervals at all other sites (except Hardwood Island and Campobello Narrows which were terminated early) encompass most of the settlement period which ranged from June to early July in the Gulf of Maine, late June to July in Nova Scotia, and late July in the Bay of Fundy (Chapter 4, unpublished data).

The collectors were sampled by divers who removed the substrate and placed it into plastic bags which were returned to the laboratory for processing. Each substrate was soaked in 50 to 70 % Ethanol or 7 to 8 % Magnesium Chloride for 5 to 20 min and then gently agitated or rinsed with filtered sea water to remove settlers. The water was poured through a mesh screen (150 μm Nitex or cheese cloth) and settlers were retained for identification and enumeration under a dissecting microscope. Settler densities were compared between sites, collector types and collector heights using analysis of variance (ANOVA). Post hoc and paired comparisons were made using Student-Newman-Keuls

(SNK) tests or t-tests ($\alpha=0.05$). Statistical comparisons between regions (Fig. 2.3) were made using log transformed data [ln (n+1)] and all other comparisons (Figs. 2.4 to 2.6) used raw data.

Table 2.1. Description of study sites in regions A, B and C where artificial settlement collectors were deployed in 1994.

Region	Site	Code	Coordinates		Habitat	Depth (m)	Date		Duration (days)	Type	n
							In	Out			
A	White Island	WIb	42°58'N	70°38'W	Barren	8	May 17	Jul 14	58	rack	10
						8[b]	Jun 17	Jul 5	18	pipe	2
		WIk			Kelp	8	May 17	Jul 14	58	rack	10
						8[b]	Jun 17	Jul 5	18	pipe	3
	Star Island	SI8	42°59'N	70°37'W	Barren	8	May 17	Jul 5	49	rack	10
		SI20	42°58'N	70°37'W	Barren	20	May 17	Jul 5	49	rack	10
		SI30			Barren	30	May 17	Jul 5	49	rack	10
	Nubble Lighthouse	NL	43°10'N	70°36'W	Barren	8	Jun 1	Jul 6	35	rack	10
						8	Jun 1	Jul 6	35	brush	2
	Inner Green Island	IG	43°40'N	70°07'W	Kelp	8	Jun 3	Jul 19	46	rack	9
	Cliff Island	CI	43°41'N	70°07'W	Cobble	8	Jun 3	Jul 19	46	rack	10
B	Hardwood Island	HI	45°01'N	66°56'W	Barren/Silt	9	May 19	Jul 8	50	rack	5
						9[b]	May 19	Jul 8	50	pipe	2
	Fish Island	FI	45°01'N	66°56'W	Barren/Silt	7	Jun 19	Aug 25	67	rack	5
	Beaver Harbour	BH	45°04'N	66°43'W	Silt/Cobble	8	Jun 15	Aug 26	72	rack	5
	Biological Station	BS	45°05'N	67°05'W	Rock	7	Jun 20	Aug 9	50	rack	5
	Ministers Island	MI	45°06'N	67°02'W	Rock/Silt	7	Jun 19	Aug 25	67	rack	5
	Tongue Shoal	TS	45°04'N	67°01'W	Silt/Rock	13[c]	Jun 19	Aug 25	67	rack	4
	Campobello Narrows	CN	44°50'N	66°56'W	Cobble	8	Jun 19	Jul 20	31	rack	5
	Prescription Weir	PW	44°42'N	66°41'W	Cobble/Kelp[a]	7	Jun 9	Jul 30	51	rack	5
	Green Island	GI	44°37'N	66°46'W	Kelp/Cobble	5	Jun 9	Jul 30	51	rack	5

Table 2.1 continued

Region	Site	Code	Coordinates	Habitat	Depth (m)	Date		Duration (days)	Type	n
						In	Out			
C	Mill Cove	MCb	44°35'N 64°03'W	Barren	8	Jun 9	Jul 27	48	rack	10
					8[b]	Jun 9	Jul 27	48[d]	pipe	2
					8[b]	Jul 10	Jul 27	17	pipe	4
		MCk		Kelp	6	Jun 9	Jul 27	48	rack	10
					6[b]	Jun 9	Jul 27	48[d]	pipe	3
					6[b]	Jul 10	Jul 27	17	pipe	4
	Little Duck Island	LD	44°22'N 64°11'W	Barren	6.6[b]	Jun 13	Aug 1	49[d]	pipe	2
					6.6[b]	Jun 29	Jul 14	15	pipe	3

[a] comprised of drift kelp and kelp attached to cobble; [b] collectors suspended 0.2 m and 2.3 m above the bottom; [c] collectors suspended in 2 m increments to 8 m above the bottom; [d] 3 ~bi-weekly samples combined

Fig. 2.1. Map of 3 regions that include 20 study sites where artificial settlement collectors were deployed in 1994 in the northwest Atlantic (Region A: Gulf of Maine; Region B: Bay of Fundy; Region C: Atlantic coast of Nova Scotia).

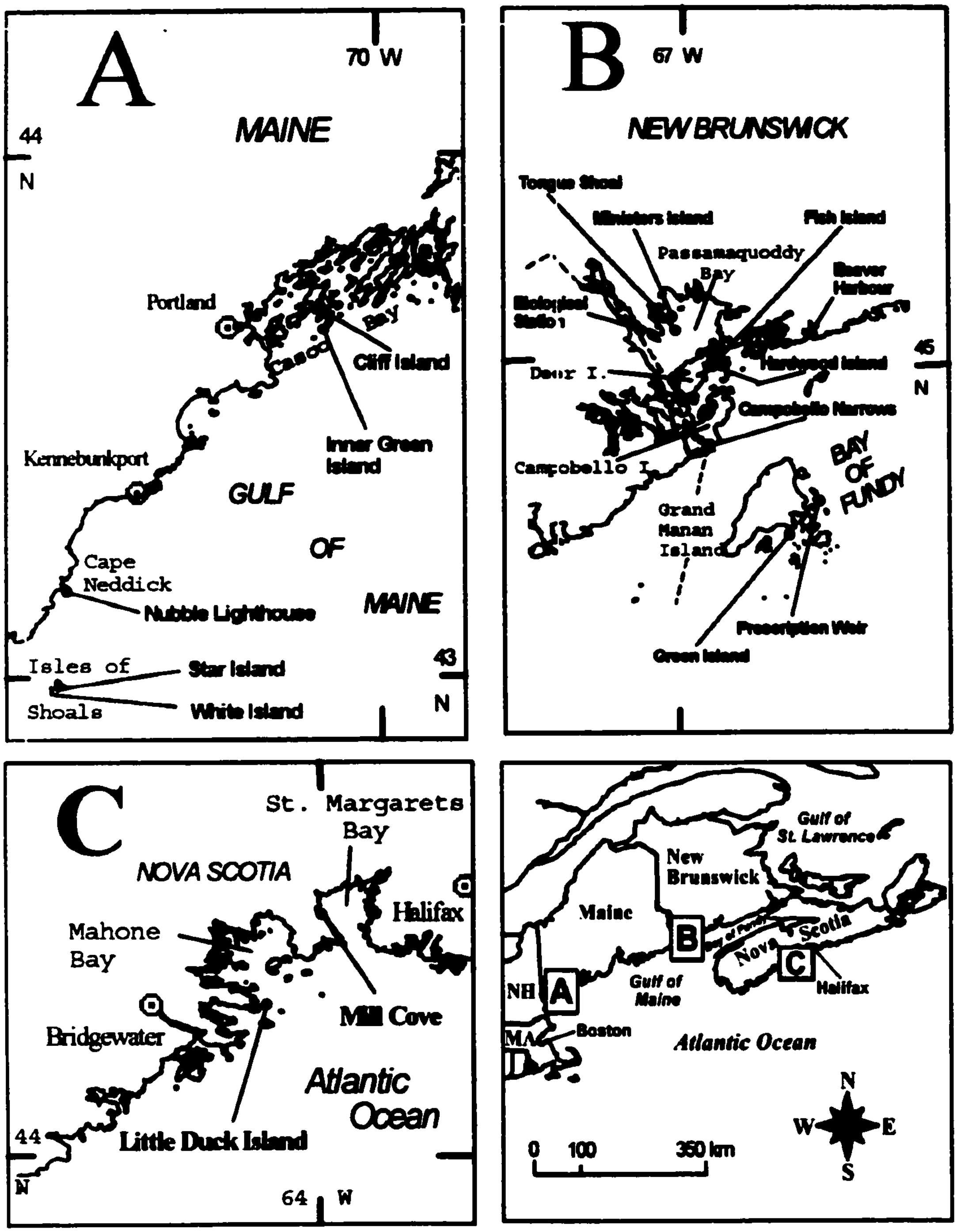

A
70 W
44
N
MAINE
Portland
Casco Bay
Cliff Island
Inner Green Island
Kennebunkport
GULF
OF
MAINE
Cape Neddick
Nubble Lighthouse
Isles of Shoals
Star Island
White Island
43
N
B
67 W
NEW BRUNSWICK
Tongue Shoal
Ministers Island
Fish Island
Passamaquoddy Bay
Beaver Harbour
Biological Station
Deer I.
Hardwood Island
45
N
Campobello Narrows
Campobello I.
BAY OF FUNDY
Grand Manan Island
Prescription Weir
Green Island
C
St. Margarets Bay
NOVA SCOTIA
Halifax
Mahone Bay
Bridgewater
Mill Cove
Atlantic Ocean
Little Duck Island
44
N
64 W
Gulf of St. Lawrence
New Brunswick
Maine
B
Nova Scotia
C
Halifax
NH
A
Gulf of Maine
MA
Boston
Atlantic Ocean
0 100 350 km
N
W
E
S

Figure 2.1

Fig. 2.2. Two different types of artificial settlement collectors which were deployed at 20 sites in the northwest Atlantic in 1994 to sample settlers of *Strongylocentrotus droebachiensis*. A rack collector (A) in a sea urchin-dominated barren ground and a pipe collector array (B) in a kelp bed (*Laminaria* spp.).

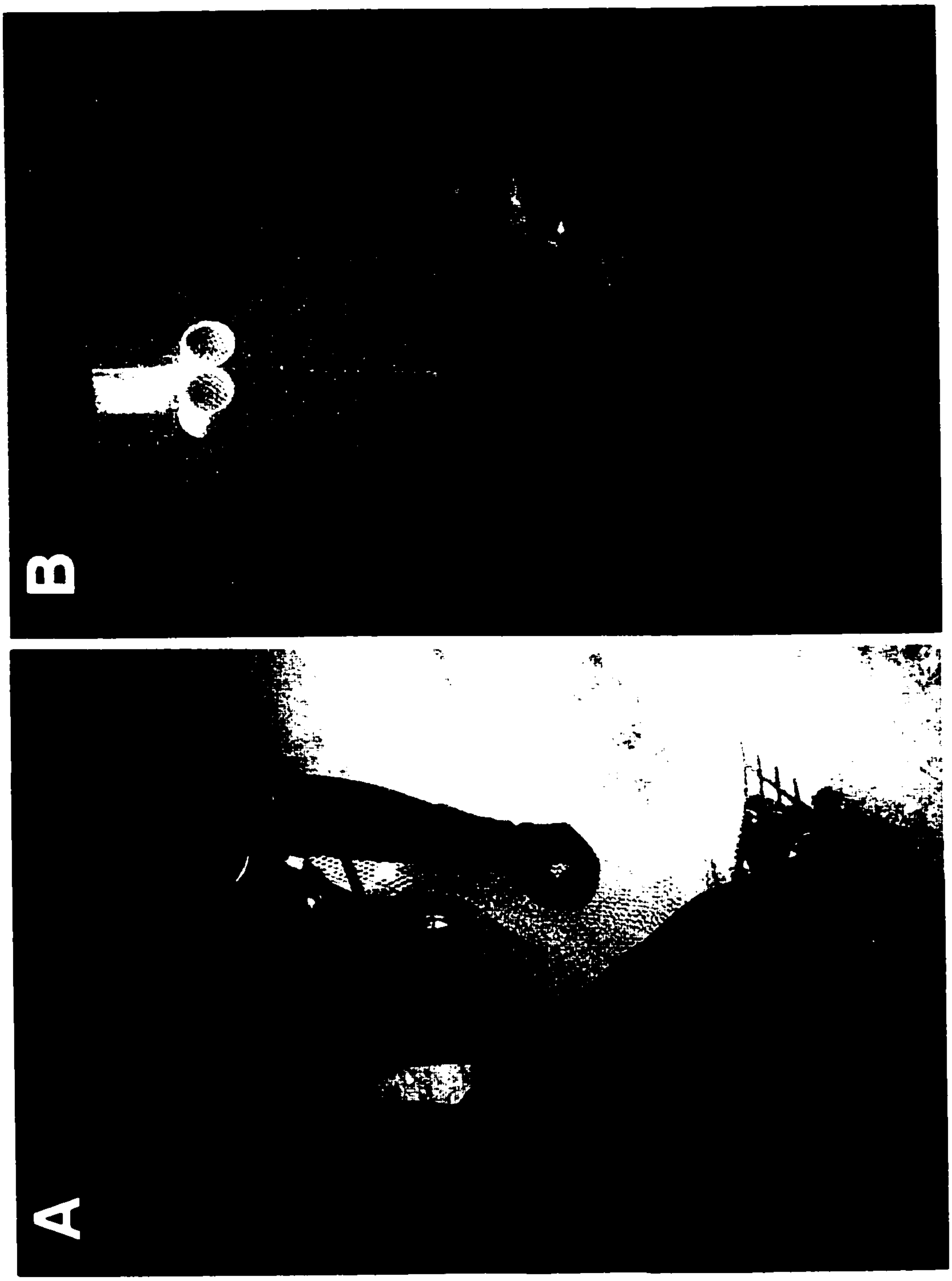


Figure 2.2

RESULTS

Both rack and pipe collectors showed significant differences between sites (rack: F=55.969, p=0.0001; pipe: F=18.912, p=0.0001) and order of magnitude differences in settlement between regions, with highest overall settlement (grand mean of the site means) in the Gulf of Maine (rack: 14481 individuals m^{-2}; pipe: 3724 individuals m^{-2}), lowest settlement in the Bay of Fundy (rack: 33 individuals m^{-2}; pipe: 20 individuals m^{-2}), and intermediate settlement in Nova Scotia (rack: 900 individuals m^{-2}; pipe: 302 individuals m^{-2}) (Fig. 2.3).

Within the Gulf of Maine, settlement differed significantly between sites (F=19.465, p=0.0001) but was within the same order of magnitude in most cases (Fig. 2.4). Exceptions are two sites in Casco Bay (Inner Green Island and Cliff Island) which showed lower settlement than most sites in the southern Gulf of Maine, and the adjacent sites at Star Island in the Gulf of Maine which showed order of magnitude reductions in settlement with depth from 8 to 30 m. Within Nova Scotia, settlement was not significantly different between sites (F=2.090, p=0.1861). Settlement was very low and variable in the Bay of Fundy and also did not differ significantly (F=0.697, p=0.6741). Sites in the Gulf of Maine and Nova Scotia, showed greater settlement in the barrens than in adjacent kelp beds, although the difference was not statistically significant in Nova Scotia (Fig. 2.4).

Pipe collector arrays suspended 0.2 and 2.3 m above the bottom showed no significant difference in settlement within sites located in all three regions (F=2.749, p=0.1582) (Fig. 2.5a). A collector array with racks suspended 0, 2, 4, 6 and 8 m above the bottom at one site (Tongue Shoal) also showed no significant difference in settlement at any height in the water column (F=1.324, p=0.3063) (Fig. 2.5b).

Comparison of different collector types within sites showed that rack collectors at both Mill Cove Barren and Mill Cove Kelp sampled twice as many settlers as pipe collectors over the same time interval, and 7 times more settlers at White Island (Fig. 2.6). However, these differences were not statistically significant at Mill Cove Kelp (t=1.192, p=0.2607), marginally non-significant at Mill Cove barren (t=2.225, p=0.0503), and confounded by a difference in sampling intervals between collector types (58 d for rack, 18 d for pipe) at White Island. There was also no significant difference between rack and pipe collectors at Hardwood Island (t=0.711, p=0.5092) where settlement was low and variable. Although settlement was high at Nubble Lighthouse, there was no significant difference between rack and brush collectors (t=0.327, p=0.7502).

Fig. 2.3. Mean (+ SE) density of settlers of *Strongylocentrotus droebachiensis* at sites across three regions of the northwest Atlantic using rack (A) and pipe (B) collectors. Horizontal bars indicate sets of non-significantly different sites (SNK, $p>0.05$).

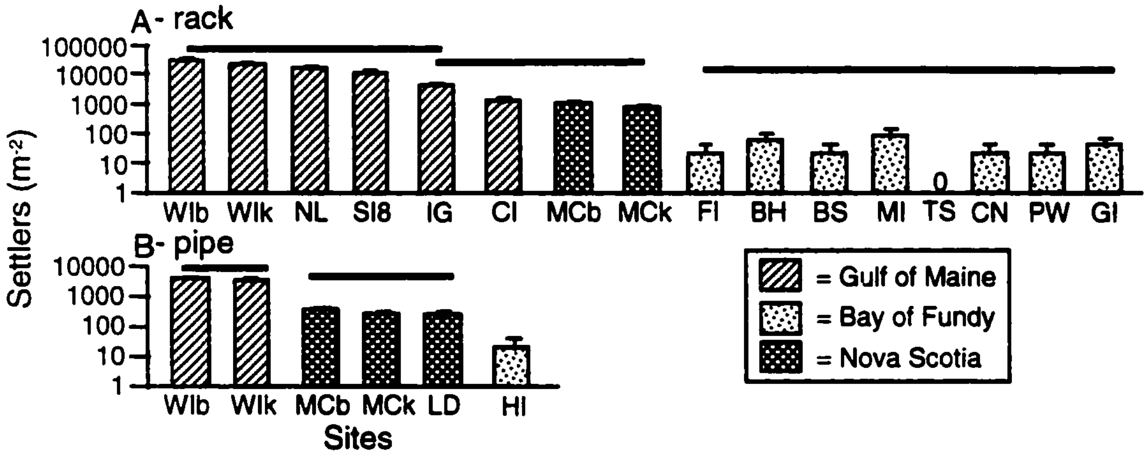

A- rack
100000
10000
1000
100
10
1
WIb
WIk
NL
SI8
IG
CI
MCb
MCk
FI
BH
BS
MI
TS
CN
PW
GI
0
Settlers (m-2)
B- pipe
10000
1000
100
10
1
WIb
WIk
MCb
MCk
LD
HI
Sites
= Gulf of Maine
= Bay of Fundy
= Nova Scotia

Figure 2.3

Fig. 2.4. Mean (+ SE) density of settlers of *Strongylocentrotus droebachiensis* at different sites within three regions of the northwest Atlantic. Horizontal bars indicate sets of non-significantly different sites (SNK, $p>0.05$). In the Bay of Fundy and Nova Scotia there were no significant differences between sites.

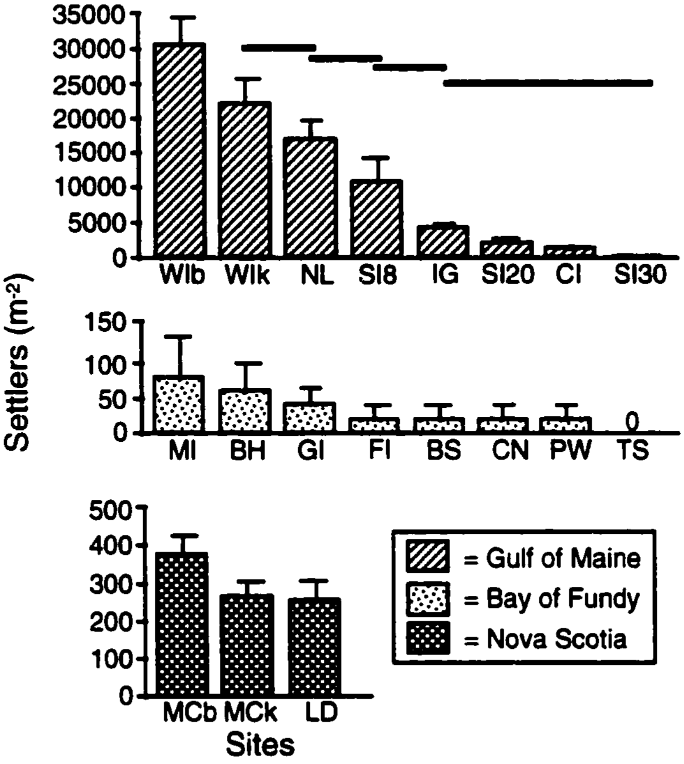

35000
30000
25000
20000
15000
10000
5000
0
WIb
WIk
NL
SI8
IG
SI20
CI
SI30
Settlers (m-2)
150
100
50
0
MI
BH
GI
FI
BS
CN
PW
TS
0
500
400
300
200
100
0
MCb
MCk
LD
Sites
= Gulf of Maine
= Bay of Fundy
= Nova Scotia

Figure 2.4

Fig. 2.5. Mean (+ SE) density of settlers of *Strongylocentrotus droebachiensis* suspended at different heights above the bottom using pipe collectors at 6 sites (A) and rack collectors at Tongue Shoal (B). Collector heights within sites were not significantly different (pipe: F=2.749, p=0.1582; rack: F=1.324, p=0.3063).

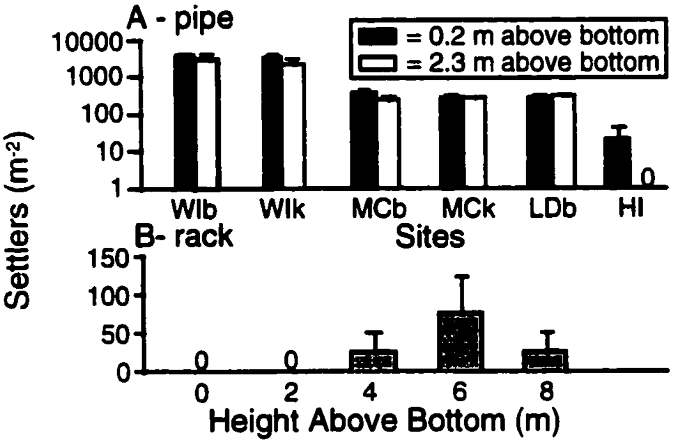

A - pipe
10000
1000
100
10
1
= 0.2 m above bottom
= 2.3 m above bottom
WIb
WIk
MCb
MCk
LDb
HI
0
Sites
Settlers (m-2)
B- rack
150
100
50
0
0
0
0
2
4
6
8
Height Above Bottom (m)

Figure 2.5

Fig. 2.6. Mean (+ SE) density of settlers of *Strongylocentrotus droebachiensis* from different collector types deployed within the same sites and habitats (NS=no significant difference between collector types; p>0.050: a=not tested due to unequal sampling intervals).

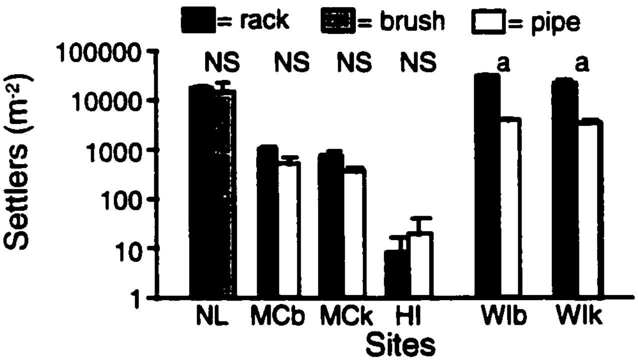

■= rack
▨= brush
☐= pipe
Settlers (m-2)
100000
10000
1000
100
10
1
NS
NS
NS
NS
a
a
NL
MCb
MCk
HI
WIb
WIk
Sites

Figure 2.6

DISCUSSION

Order of magnitude differences in settlement of *Strongylocentrotus droebachiensis* occur at large spatial scales between distinct geographic regions. This is likely due to differences in larval supply caused by large-scale oceanographic features. During the spring, when larvae are in the water column, there is net movement of water out of Passamaquoddy Bay and the Bay of Fundy which continues down the coast of Maine (Brooks 1985, Harris & Chester 1996). A counter-clockwise coastal gyre in the northeastern Gulf of Maine turns offshore at Penobscot Bay, in the central Gulf of Maine, where a separate coastal current moves onshore and in a southwesterly direction (Brooks 1985). These current patterns may act to enhance larval supply to the southwestern Gulf of Maine and to advect larvae away from the Bay of Fundy and northeastern Gulf of Maine (Harris & Chester 1996). Casco Bay is closer to the transition zone of offshore to onshore currents near Penobscot Bay and is a more contained area which may limit the supply of larvae when compared to points in the southwestern Gulf of Maine. Harris and Chester (1996) reported low recruitment of *S. droebachiensis* in the northeastern Gulf of Maine when compared to high rates of recruitment measured in the southwestern Gulf of Maine in 1995. The Atlantic coast of Nova Scotia typically is subject to unidirectional longshore coastal currents (NE to SW) with periodic upwelling (Han et al. 1997, Loder et al. 1997) suggesting that larvae may be advected away from the coast under certain conditions.

Factors related to larval survival such as food availability and temperature may also vary between regions with different hydrodynamic regimes. Regional differences in sea urchin abundance and reproductive output could also play a role in the differential supply of competent larvae. Although all sites in each region contained substantial populations of adults, the source of larvae is not clear.

Within each region, settlement of *Strongylocentrotus droebachiensis* differed between sites with no clear spatial trend, except in the Gulf of Maine where Casco Bay could be considered a sub-region due to its spatial separation from other sites and the reduced settlement there. This suggests that, within a relatively close geographic range (0.5 to 50 km), variability in urchin settlement is controlled by local hydrodynamic features that either enhance or limit settlement. Factors such as habitat, depth and stratification of larvae also may play a role. Higher settlement rates in barrens than in adjacent kelp beds were observed at sites in both Nova Scotia and the Gulf of Maine, suggesting that kelp beds have a negative effect on settlement. This could be due to differential mortality, hydrodynamic effects or selective settlement (Pearse et al. 1970, Lang & Mann 1976, Rowley 1989). At Star Island, settlement decreased with depth suggesting that larval supply and/or survival is greater in shallow water or that sea urchins prefer to settle in shallow water. Settlement in collectors placed on the bottom or at heights of up to 8 metres off the bottom showed no significant differences in settlement suggesting that competent larvae occur throughout the water column within the depth ranges sampled (4 to 13 m depth).

In order to be able to directly compare patterns of settlement, similar sampling methods should be used (Minchinton & Scheibling 1993, Miron et al. 1995). If different methods are employed, such as different collector types and/or substrata, these methods must be cross-calibrated. Our study determined that there were no differences in measurement of settlement between rack and brush collectors, although only two brush collectors were used. Studies by Ebert et al. (1994) and Schroeter et al. (1996) in California used the same brush collectors to sample settlement of *Strongylocentrotus franciscanus* and *S. purpuratus*, although the densities they reported were generally much lower than those we found in Maine. Settlement was consistently higher on rack compared to pipe collectors at Mill Cove and White Island indicating that these different collector types could be calibrated to make direct comparisons across regions. However, differences between these two collector types were not sufficiently large to obscure the pattern of large-scale variation in settlement of *S. droebachiensis* between regions in the northwest Atlantic.

Chapter 3: A major settlement event associated with minor meteorologic and oceanographic fluctuations

INTRODUCTION

For benthic marine invertebrates with planktonic larvae, spatial and temporal variability in larval supply and settlement are important determinants of population structure and dynamics (Gaines & Roughgarden 1985, Minchinton & Scheibling 1991, Gaines & Bertness 1993). Rates and patterns of settlement are influenced both by physical (e.g. currents, temperature and salinity) and biological (e.g. larval behaviour, food availability and predation) factors which regulate the development, survival and delivery of larvae (Young & Chia 1987, Rumrill 1990). Many invertebrate larvae have extended planktonic periods (weeks to months) which can result in high mortality (Morgan 1995) and long-distance dispersal (Shanks 1995).

The larvae of invertebrates are found throughout the water column over continental shelves but often aggregate near the sea surface where wind-driven currents may influence dispersal (Pearse & Cameron 1991, Shanks 1995, Young 1995). Most invertebrate larvae are weak swimmers and have little control over horizontal dispersal by currents, although they may migrate vertically and thus enhance dispersal in oscillating flow environments (Young & Chia 1987, Shanks 1995). Because the arrival of planktonic larvae at suitable settlement sites is primarily dependant on advective transport, both local hydrodynamics and large-scale oceanographic features can influence settlement success (Shanks 1995). Emphasis on coupling physical processes with patterns of larval supply and settlement have related successful settlement to the delivery of larvae via meso- to large-scale physical forcing, such as upwelling events (Johnson et al. 1984, Wing et al. 1995a, b) or tidally-induced internal waves (Pineda 1991, Leichter et al. 1998). The range of variability in the hydrodynamic environment that affects supply of larvae to the benthos demands that processes operating at various spatial and temporal scales be considered (Denman & Powell 1984).

This study is part of a larger project investigating spatial and temporal patterns of settlement and recruitment of several echinoderm species in Eastern Canada and the Gulf of Maine (Chapters 2 and 4). We found that settlement of most species occurred in a single, well defined pulse within an ~2 week period each year, but the magnitude of settlement during this pulse varied greatly between sites and years and the timing of the pulse varied among species. In this communication, we measure settlement of ophiuroid larvae at 3 day intervals over one of these 2 week pulses to isolate the timing of settlement, and relate it to local hydrographic conditions.

MATERIALS AND METHODS

From July 21 to August 5, 1993, the settlement of ophiuroid larvae was measured on collectors in two adjacent habitats, a sea urchin (*Strongylocentrotus droebachiensis*)-dominated barrens and a kelp bed (*Laminaria longicruris*), in the rocky subtidal zone (6 to 10 m below mean sea level) at Mill Cove (44° 34.9' N, 64° 3.2' W) in St. Margaret's Bay, a large semi-protected embayment along the Atlantic coast of Nova Scotia (Fig. 3.1). Collectors consisted of paired 20 x 14 cm diameter PVC pipes mounted on a plastic vane and attached to a rope by swivels to allow orientation into the current (Fig. 2.2). Each pipe was lined with an artificial substrate, 0.05 m^2 pieces of polyethylene plastic turf (PNS-3, Monsanto Canada Inc.), and protected from predators by plastic light diffuser grating (1 cm aperture). Paired collectors were suspended in an array at 0.2 m (Low) and 2.3 m (High) off the bottom by a sub-surface float and anchored with two 20 kg cement blocks. Four collector arrays were placed in line at 10 m intervals within each habitat (Barrens and Kelp), parallel to and ~15 m from the interface between habitats (i.e. ~30 m apart). The collectors were sampled at 3 d intervals when divers removed the plastic turf from one of each of the paired collectors (the other collector was used for another experiment) and replaced it with a new piece. Thus, settlers were sampled from 4 replicate collectors in each of 4 sampling strata (Kelp High, Kelp Low, Barrens High and Barrens Low) once every 3 d. Samples were immediately placed in sealed plastic bags and returned to the laboratory for processing within 6 h of collection. The turf was soaked in 50 % EtOH for 10 to 20 min and then gently agitated and rinsed with filtered sea water to remove settlers. The rinse water, together with the water from the plastic sampler bag, was filtered through a 150 µm Nitex® mesh screen (small enough to retain echinoderm settlers) and the retained contents of the sample were stored in 70 % EtOH for subsequent identification and enumeration of settlers under a dissecting microscope.

Current velocities and salinities were measured using two S4® current meters (InterOcean Systems, Inc., San Diego, CA, USA) mounted on stands secured to the bottom in the kelp bed at 6.6 m depth and in the barrens at 9.7 m depth. The meters were 33 m apart and located 10 m from one end of each collector line. Current velocity (1 $\mathrm{cm \cdot s^{-1}}$ and 2° accuracy) was measured electromagnetically in a torroid approximately 1 m dia. x 0.35 m high and centred at 70 cm above the bottom. Current direction is given relative to true north (T). Instantaneous current vectors were measured every 0.5 s and averaged over 1 min at 10 min intervals over the 15 d period. Current velocities were partitioned into alongshore and offshore component vectors, corresponding to the local bathymetry and shoreline. Positive alongshore currents (300° T) run parallel to shore in a WNW direction (into the bay), and positive offshore currents (30° T) run in a NNE direction (towards the middle of the bay), at Mill Cove (Fig. 3.1). Salinity was measured every 3 h from conductivity and temperature sensors on the two S4® meters.

Sea temperature was measured at 2.4 h intervals using HOBO®Temp data loggers (Onset®Computer Corp., Pocasset, MA, USA) deployed in sealed plastic (Nalgene®) bottles adjacent to one of the High and Low collectors in each habitat at Mill Cove. These data are compared to sea temperatures recorded hourly at two stations (3 and 10 m depth at

44° 32.8' N, 64° 1.2' W, and 17 and 37 m at 44° 33.0' N, 64° 1.1' W) at Northwest Cove (Fig. 3.1), near the mouth of St. Margaret's Bay ~4.5 km south of Mill Cove (unpublished data, Brian Petrie, Ocean Sciences Division, Department of Fisheries and Oceans, Bedford Institute of Oceanography, Halifax, NS, Canada).

Wave height and period were recorded (Marine Environmental Data Service, Department of Fisheries and Oceans Canada, Ottawa, ON, Canada) at Osborne Head Buoy (MEDS037) located 66 km ESE of Mill Cove and 5 km offshore (44° 29' N, 63° 25' W)(Fig. 3.1). Measures of significant wave height (average of the highest 1/3 of the waves in a wave field) and peak period (corresponding to the maximum energy wave component in the field) were calculated every 30 min. These measures serve as an index of general sea state which may have influenced large-scale hydrographic forcing in the area.

Instantaneous hourly measures of wind velocity and atmospheric pressure were recorded at the Shearwater Meteorological Station (44° 38' N, 63° 30' W)(Fig. 3.1) 63 km east of Mill Cove (Ocean Sciences Division, Department of Fisheries and Oceans, Bedford Institute of Oceanography, Halifax, NS, Canada). In contrast to the current data (but in accordance with meteorological convention) wind direction is expressed as the direction from which the winds were blowing relative to true north. The wind conditions we observed at Mill Cove were consistent with those recorded at the station.

Synoptic weather maps of eastern Canada (6 h intervals from July 23 to 29, 1993) were obtained from the Maritimes Weather Centre (Atmospheric Environment Service, Environment Canada). These maps provided an assessment of atmospheric features that influenced weather in St. Margaret's Bay during the study period.

Fig. 3.1. Map of the central Atlantic coast of Nova Scotia showing the locations of the study sites at Mill Cove and Northwest Cove in St. Margaret's Bay, the Shearwater Meteorological Station (SMS), the Osborne Head Buoy (OHB) and Little Duck Island in Mahone Bay (Chapters 2 and 4). The map is oriented relative to true north.

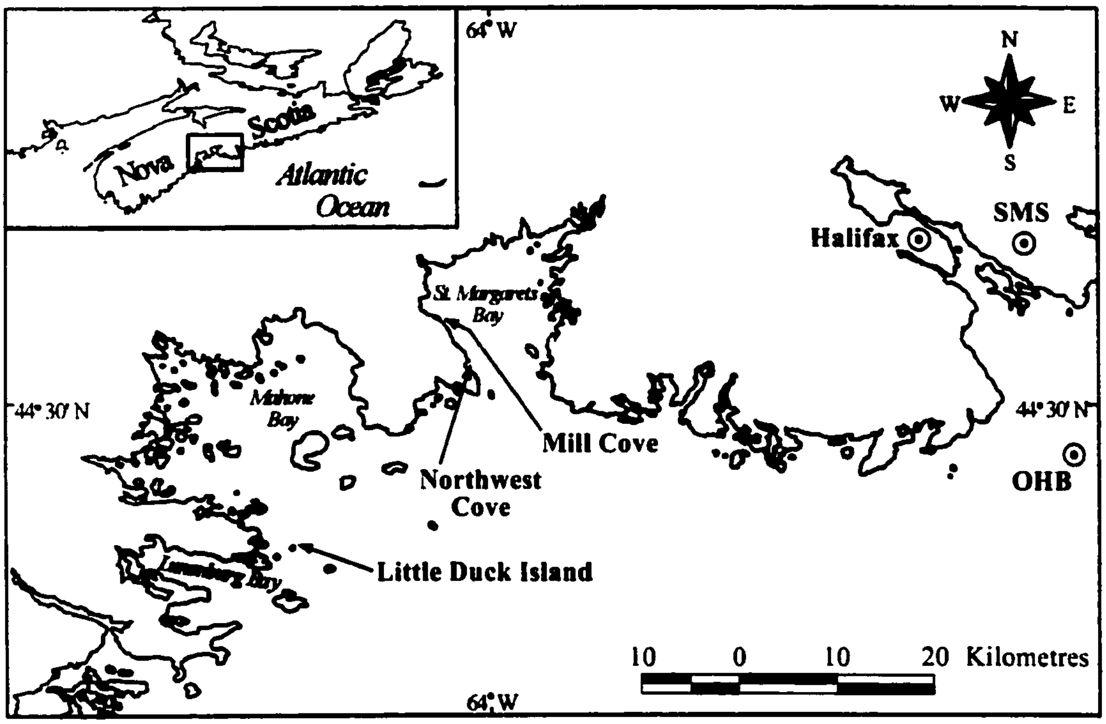

64° W
N
W
E
S
Nova
Scotia
Atlantic
Ocean
SMS
Halifax
St. Margarets Bay
Mahone Bay
44° 30' N
44° 30' N
Mill Cove
Northwest Cove
OHB
Little Duck Island
Lunenburg Bay
10
0
10
20
Kilometres
64° W

Figure 3.1

RESULTS

Larval ophiuroids (*Ophiopholis aculeata*, *Ophiura* spp.) settled in abundance during the 15 d study period (Fig. 3.2a). There was little or no settlement over the first 6 d and then a large pulse over the next 3 d (July 27 to 30) followed by declining settlement over the last 6 d. Settlement rates fluctuated synchronously among all four sampling strata (Kelp High, Kelp Low, Barrens High and Barrens Low), indicating uniform larval supply at the scale of our site (30 x 30 m). Settlement during the last 9 d of this study represented 63 % and 87 % of the total settlement for *Ophiura* and *O. aculeata* respectively in 1993, and 71 % of the total settlement of *O. aculeata* over a 3 year period (1992 to 1994) at Mill Cove (Chapter 4, unpublished data).

Sea temperature at Mill Cove rose from 11 to 15 °C over the study period (Fig. 3.2b). However, there were two ~24-h fluctuations in temperature that signalled a shift in water masses and established thermal stratification across the depth range of the sensors. On July 24, temperature fluctuated by ~2 °C and stabilised at 14 °C for a day before dropping to as low as 10 °C at the deepest sensor on July 26, during the second fluctuation. Temperature at all 4 sensor positions increased to 13 °C on July 27, when the settlement pulse began, then gradually rose over the remainder of the study period. During the second fluctuation, stratification was much stronger, and much lower temperatures were recorded at the deepest position (Barrens Low) than in the other 3 strata. A similar pattern in sea temperature was recorded at 3 and 10 m depth off Northwest Cove, although there was little fluctuation on July 24 (Fig. 3.3a). At 17 m, temperature declined gradually from 10 to 7 °C between July 24 and 26, then increased to 12 °C by July 30 before dropping gradually to 8 °C by the end of the study period. By July 31 the water column was well stratified between 10 and 17 m. The bottom temperature at 37 m remained stable at 4 to 6 °C throughout the study period.

Salinity in both the barrens and kelp bed fluctuated inversely with temperature at Mill Cove during the July 24 and 26 events, and declined gradually from 30.4 to 29.8 psu over the study period (Fig. 3.2c). Salinity was consistently higher in the barrens, with the greatest difference between habitats occurring during the second fluctuation, indicating an intrusion of colder, more saline water from deeper in the bay.

Mill Cove is generally sheltered from ocean swell except during severe storms. During the study period, wave heights were low (0.5 to 2 m) and wave periods were short (5 to 10 s), indicating a relatively calm sea state (Fig. 3.3b). The lowest wave energy occurred from July 24 to 27 when winds blowing off the coast likely damped the waves.

The S4® meter in the kelp bed malfunctioned, and reliable velocity data were not obtained from it during the study period. Current measures in the barrens showed a clear semi to diurnal tidal signal on the alongshore axis with generally weak flow over the study period: mean speed (± SD) = 2.73 $cm{\cdot}s^{-1}$ ±1.91 (Fig. 3.4). The offshore component remained relatively constant and weak at a mean speed of 1 $cm{\cdot}s^{-1}$ in a positive (NNE) direction while the alongshore component oscillated from positive (WNW) to negative (ESE). On July 26 the alongshore component strengthened and shifted to the negative direction only while oscillating about 5 $cm{\cdot}s^{-1}$ for 4 d before weakening on July 30.

From July 24 to 26, atmospheric pressure rose gradually from 1006 to 1022 hpa and then dropped to 1013 hpa by July 29 and stabilised for the remainder of the study (Fig. 3.3c). These minor fluctuations indicate the passage of weak pressure gradients. Surface Meteorological Analyses from July 23 to 29 confirm this, showing a weak low pressure area which passed over Nova Scotia at the start of the study and moved off to the NE by July 25 as a high moved down from northern Quebec and over Nova Scotia by July 26. This high pressure cell moved NE on July 27 and was replaced by unsettled weather through to July 29.

Winds were generally light and variable during the study, usually blowing from a southerly direction at speeds of ~5 $m{\cdot}s^{-1}$ (7.5 knots), with little evidence of a diabatic effect (Fig. 3.3d). Between July 24 and 26 however, the wind reversed direction and blew from the north at speeds up to 7 $m \cdot s^{-1}$, before switching back to winds from the south for the rest of the period.

Fig. 3.2. (a) Mean larval settlement density (+ SE; some error bars are obscured by data points) for 4 replicate collectors in each of 4 sampling strata (Kelp High, Kelp Low, Barrens High and Barrens Low) plotted at the midpoint of each 3 d sampling interval (staggered for graphical clarity), (b) sea temperature measured at 4 locations and (c) salinity measured at 2 locations in Mill Cove over a 15 d period in July/August 1993. All data are standardised to local time (AST). The shaded area indicates the period of maximum larval settlement.

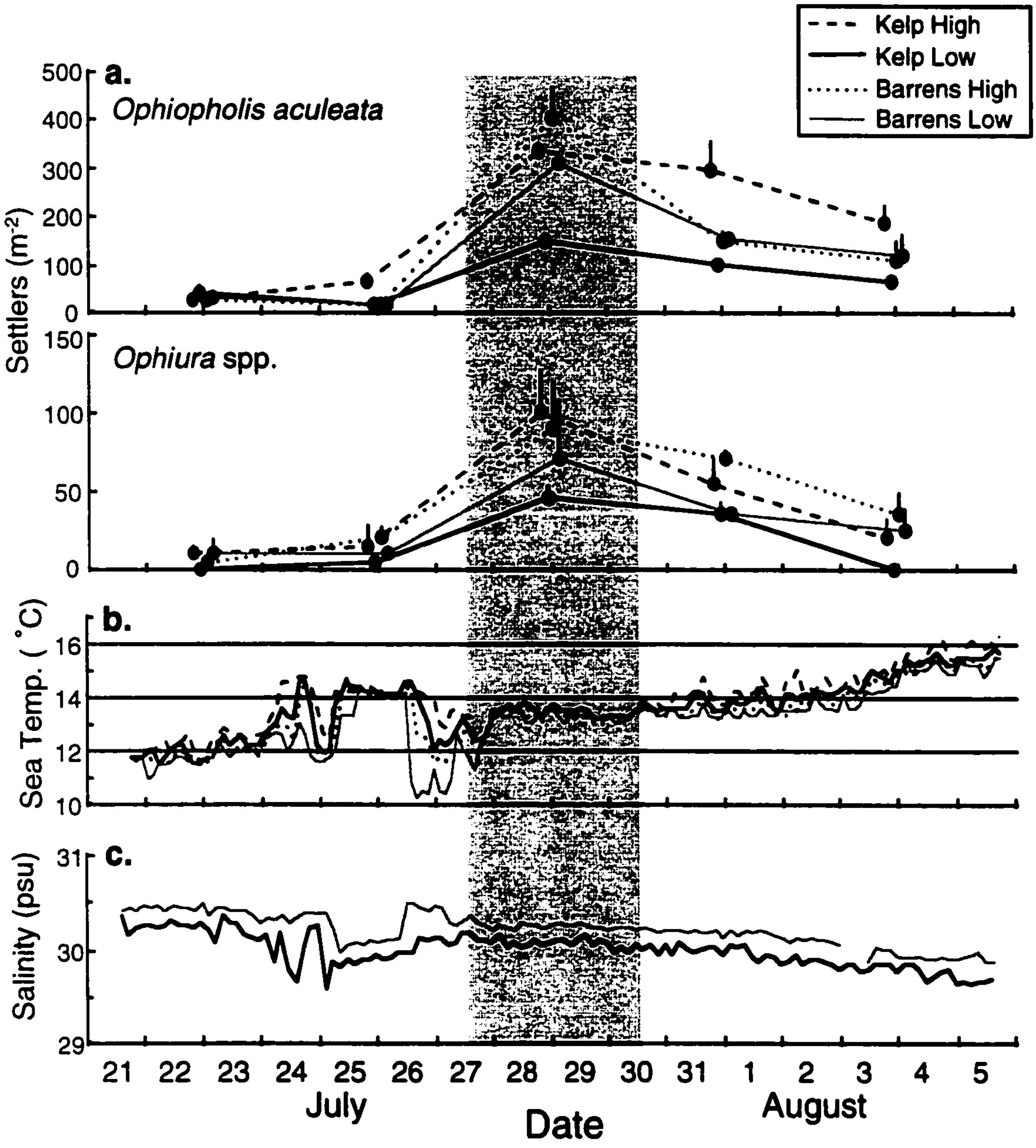

Kelp High
Kelp Low
Barrens High
Barrens Low
a.
Ophiopholis aculeata
Ophiura spp.
Settlers (m-2)
500
400
300
200
100
0
150
100
50
0
b.
Sea Temp. (°C)
16
14
12
10
c.
Salinity (psu)
31
30
29
21
22
23
24
25
26
27
28
29
30
31
1
2
3
4
5
July
Date
August

Figure 3.2

Fig. 3.3. (a) Sea temperature measured at Northwest Cove, (b) significant wave height and peak period measured at Osborne Head Buoy, (c) atmospheric pressure and (d) wind speed and direction measured at Shearwater Meteorological Station over a 15 d period in July/August 1993. All data are standardised to local time (AST). The shaded area indicates the period of maximum larval settlement.

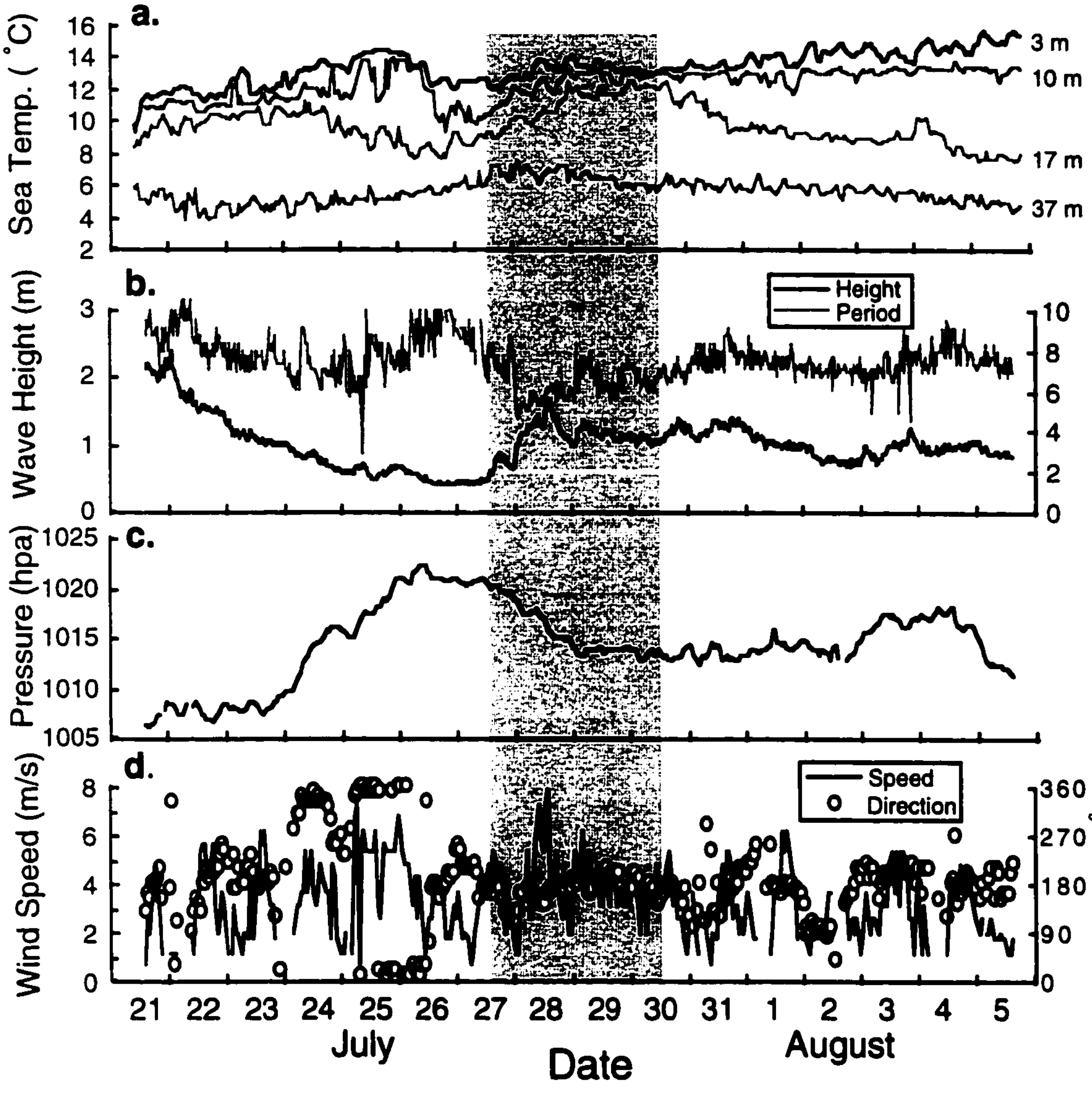

a.
Sea Temp. (°C)
16
14
12
10
8
6
4
2
3 m
10 m
17 m
37 m
b.
Wave Height (m)
3
2
1
0
Height
Period
Wave Period (s)
10
8
6
4
2
0
c.
Pressure (hpa)
1025
1020
1015
1010
1005
d.
Wind Speed (m/s)
8
6
4
2
0
Speed
Direction
Direction (°T)
360
270
180
90
0
21
22
23
24
25
26
27
28
29
30
31
1
2
3
4
5
July
Date
August

Figure 3.3

Fig. 3.4. Current velocity measured at 9 m depth in Mill Cove over a 15 d period in July/August 1993. Data are standardised to local time (AST) and given as alongshore and offshore component vectors relative to true north. The shaded area indicates the period of maximum larval settlement.

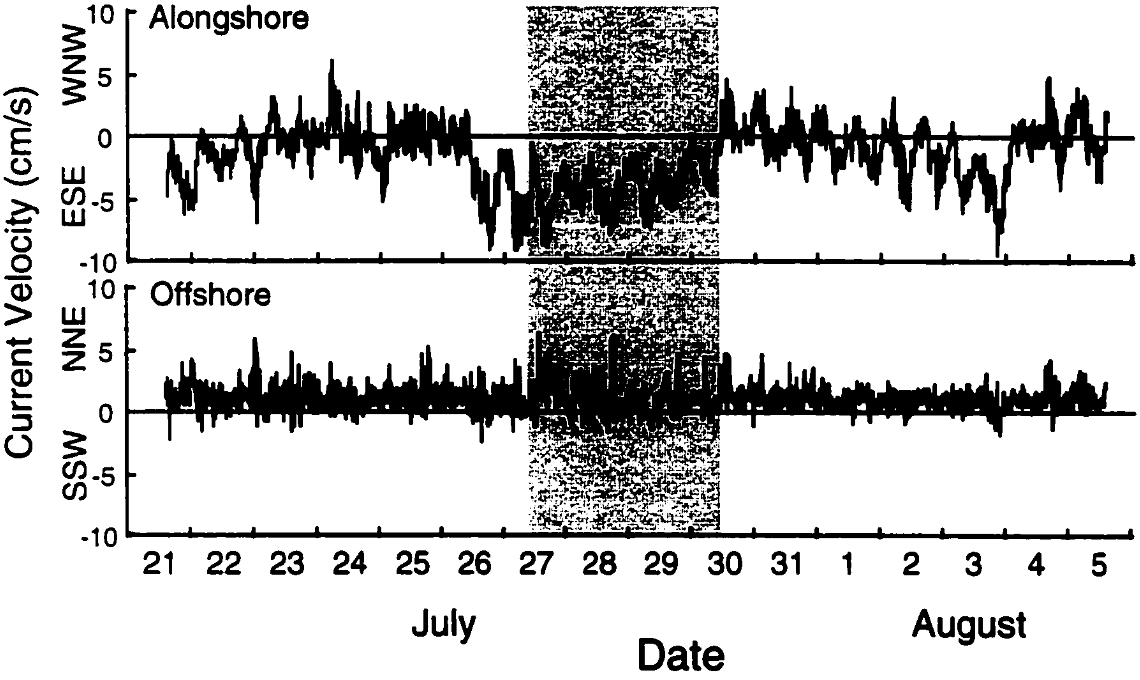

Current Velocity (cm/s)
WNW
ESE
10
5
0
-5
-10
Alongshore
NNE
SSW
10
5
0
-5
-10
Offshore
21
22
23
24
25
26
27
28
29
30
31
1
2
3
4
5
July
August
Date

Figure 3.4

DISCUSSION

The timing of ophiuroid settlement in relation to local hydrographic fluctuations suggests that water mass intrusions resulting in settlement pulses can occur during relatively weak weather conditions. Unlike some other oceanographic systems (e.g. Wing et al. 1995b), it is unlikely that a dominant physical event determines ophiuroid settlement off Nova Scotia. Rather, local bathymetry probably modifies bay- or shelf-scale forcing to produce upwelling which may deliver or induce competent larvae.

After infusions of cold water from July 24 to 27 and subsequent mixing of the water column above 17 m, a shift in currents apparently supplied competent larvae to the site at Mill Cove which settled there in high numbers between July 27 and August 5. The typical flow of water in St. Margaret's Bay is in a counter-clockwise motion (Heath 1973a) which argues for the delivery of larvae to the site from water masses within the bay and is coincident with the current direction measured during the settlement pulse at Mill Cove. Although we collected ophiuroid larvae during a 1 to 2 month settlement window in each of 3 years, the majority of settlement occurred within two weeks (Chapter 4). The settlement pulse described here (the only one for which we have corresponding physical data) may reflect the advective delivery of a discrete batch of larvae at the scale of our sampling grid (30 m square) or greater. Alternatively, competent larvae may be ubiquitous in surface waters during a longer period and the upwelled water might provide a trigger for mass settlement.

Our measures of temperature and salinity are typical for St. Margaret's Bay in summer, when water can either be stratified or mixed depending on local conditions (Sharaf El Din et al. 1970, Heath 1973a, b, Platt & Irwin 1979). The rapid fluctuations in salinity and temperature at Mill Cove and correlated changes in temperature stratification observed at Northwest Cove indicate that changes are occurring on at least a bay-scale. Although the shift in wind on July 26 is coincident with the change in currents, it is unlikely that this represents an Ekman upwelling response, given the relatively small size of

St. Margaret's Bay (i.e. somewhat less than the internal Rossby radius). Possible mechanisms for the observed hydrographic fluctuations include the setup-setdown of water within the bay due to changes in atmospheric pressure or windstress (Heath 1973b) or local expression of shelf-scale upwelling (Petrie et al. 1987). Given the limited oceanographic and atmospheric data, and complex coastal bathymetry, it is not possible to unequivocally identify the causative mechanism of upwelling on the west side of St. Margaret's Bay during this study.

The most striking finding of this study is that settlement of species with long-lived planktonic larvae (e.g. up to 7 mo for *Ophiopholis aculeata*; Strathmann 1978a), can occur over a few days in association with low amplitude fluctuations in the physical environment, which may be typical but not easily predicted. These pulses can account for most of the settlement of a species at a given site over several years. Our observations underscore the importance of measuring settlement and oceanographic processes at short time scales to understand settlement variability over much longer periods.

Chapter 4: Temporal and spatial variability in settlement and recruitment of echinoderms in kelp beds and barrens in Nova Scotia

INTRODUCTION

The importance of larval supply, settlement and recruitment as determinants of population structure and dynamics of marine invertebrates with planktonic larvae has been the subject of considerable research over the past 2 decades (reviewed by Underwood & Fairweather 1989, Ólafsson et al. 1994, Booth & Brosnan 1995, Caley et al. 1996). In particular, many studies have shown that temporal and spatial variability in settlement are important in regulating recruitment, and can occur at temporal scales that range from days to years, or even decades, and spatial scales of metres to kilometres (reviewed by Ebert 1983, Butman 1987, Chapter 1).

Most studies have inferred patterns of settlement from those of recruitment, which may confound settlement with post-settlement mortality or migration (reviewed by Connell 1985, Gosselin & Qian 1997, Hunt & Scheibling 1997). For example, variation in sampling method and frequency have been shown to significantly affect measures of barnacle recruitment in relation to differences in post-settlement mortality (Minchinton & Scheibling 1993, Miron et al. 1995). The increasing use of artificial settlement collectors enables direct quantification of settlement by sampling at frequent intervals, and thereby minimizing the effects of predation and migration (e.g. Harrold et al. 1991, Keesing et al. 1993, Ebert et al. 1994, Harris et al. 1994). Sampling collector arrays facilitates replication in space and time and separation of settlement from post-settlement processes (Harrold et al. 1991). However, different collector types should be calibrated for comparisons across studies (Chapter 2) and related to recruitment in natural habitats to determine links between larval supply and population structure and dynamics.

Differences in population densities of echinoids have been attributed to lower rates of recruitment in kelp beds/forests than in echinoid-dominated barrens in the northwest Pacific (Tegner & Dayton 1981), and northwest (Scheibling 1986) and northeast (Leinaas & Christie 1996) Atlantic. However, studies comparing settlement rates of echinoids between these two habitats have yielded inconsistent results and the relative roles of settlement verses post-settlement processes in determining recruitment patterns remains poorly understood (reviewed in Chapter 1). Along the Atlantic coast of Nova Scotia, large tracts of the rocky subtidal zone fluctuate between kelp beds and barrens on a decadal time scale (Chapman 1981, Wharton & Mann 1981, Miller 1985a, b, Scheibling 1986, Scheibling et al. in press). During the early 1990's, this region was in transition from kelp beds to barrens because of destructive grazing of kelp by the echinoid *Strongylocentrotus droebachiensis* (Scheibling et al. in press). This provided a rare opportunity to compare settlement and recruitment between these adjacent habitat types without the potential confounding effects of between-site variability.

To determine whether the factors that regulate settlement and recruitment are habitat or species-specific, we sampled several species of echinoderms with dispersing planktotrophic larvae that are typical of many marine benthic invertebrates (Strathmann 1987). Most of the species occur in high densities at our sites (Dempsey 1996, unpublished data) and are dominant components of the rocky subtidal ecosystem along the Atlantic coast of Nova Scotia. To determine the importance of scale in regulating settlement and recruitment of these species, we measured settlement in artificial collectors, and recruitment to natural substrata, at temporal scales of days to years, and spatial scales of 10's of metres between and within habitats (kelp beds and barrens), and kilometres between sites. We relate settlement to recruitment and show that both general patterns and species-specific variability are important in establishing and maintaining these populations in the rocky subtidal ecosystem.

MATERIALS AND METHODS

Site descriptions

Patterns of echinoderm settlement and recruitment were measured at 2 sites selected for their differing hydrodynamic regimes: Mill Cove (44° 34.9' N, 64° 3.2' W) in St. Margaret's Bay, a large semi-protected embayment, and Little Duck Island (44° 22.0' N, 64° 11.0' W), an exposed island at the mouth of Mahone Bay (Fig. 3.1). The substratum at Mill Cove consists of granitic boulders and bedrock pavement at 6 to 10 m depth (below mean sea level). At Little Duck Island, broad ridges of grooved basalt form the seabed at 5 to 7 m depth. Both sites encompassed an echinoid (*Strongylocentrotus droebachiensis*) - dominated barrens and a kelp bed (*Laminaria longicruris*), with high densities of *S. droebachiensis* (up to 400 m^{-2}) aggregated at the interface between habitats and destructively grazing the kelp. This echinoid front advanced shoreward 10 to 15 m during the study period (Scheibling et al. in press) creating new barrens, dominated by encrusting coralline algae, in its wake. Kelp morphology differed between sites in accordance with the differing flow regimes (Gerard & Mann 1979): *Laminaria longicruris* had longer stipes and longer and broader fronds at Mill Cove than at Little Duck Island. This resulted in a higher canopy at Mill Cove, although the kelps at this more protected site usually lay along the substratum whereas those at Little Duck Island often were suspended by wave surge. The understory in the kelp bed was composed of turfs of articulated coralline algae (*Corallina officinalis*) and various other red algae (e.g. *Ceramium rubrum, Chondrus crispus, Palmaria palmata*). For a further description of the sites and destructive grazing by the echinoid front see Scheibling et al. (in press).

Seasonal fluctuation in sea temperature was measured at 2.4 h intervals in 1993 and 1994 using HOBO®Temp data loggers (Onset®Computer Corp., Pocasset, MA, USA) deployed at 0.2 m and 2.3 m off the bottom (the height of settlement collectors, see below) in each habitat at both sites.

Settlement sampling

Settlement collectors were constructed from 20 x 14 cm diameter PVC pipes mounted on a plastic vane and attached to a rope by swivels to allow orientation into the current (Fig. 2.2). Each pipe was lined with 0.05 m^2 pieces of polyethylene plastic turf (PNS-3, Monsanto Canada Inc.) which served as a settlement substrate. The turf liners were protected from macro-predators by plastic light diffuser grating (1 cm aperture). The collector design was modified after Harrold et al. (1991) to accommodate the plastic turf, which Harris et al. (1994) showed to be an effective settlement surface for *Strongylocentrotus droebachiensis.*

Paired collectors were suspended in an array at 0.2 m (Low) and 2.3 m (High) off the bottom by a sub-surface float and anchored with two 20 kg cement blocks. Low collectors were located within the kelp canopy at both sites. High collectors were intended to measure larval supply in the water column above each habitat. Because paired Low and High collectors are sampling different regions of the water column with different flow rates and temperatures (Chapter 3), we considered them to be independent in statistical analyses. Four collector arrays were placed in line at 10 m intervals within each habitat (barrens and kelp bed) giving 4 sampling strata (Kelp High, Kelp Low, Barrens High, Barrens Low). Within each habitat we positioned collector arrays at a fixed distance from the interface between habitats and at the same depth to limit potential confounding effects of location, and we spaced these arrays equally to increase the likelihood of obtaining a representative sample with few replicates. The two lines were parallel and ~15 m from the interface (i.e. ~30 m apart). At the beginning of each year, the position of the lines was adjusted to maintain a similar distance from the interface which shifted because of the advancing echinoid front.

Collectors were sampled by divers who removed the plastic turf, immediately placed it in a sealed plastic bag and replaced it with a new piece of turf and cleaned plastic grating. Replacement turf was pre-soaked in tanks of flowing 50 µm filtered seawater for

~1 week prior to deployment to allow for growth of a microbial film (Pearce & Scheibling 1991, Pearce 1997). Samples were returned to the laboratory for processing within 6 h of collection. The turf was soaked in 50 % EtOH or 7 to 8 % $MgCl_2$ for 10 to 20 min and then gently agitated and rinsed with filtered sea water to remove settlers. The rinse water, together with the water from the sample bag, was filtered through a 150 µm Nitex® mesh screen (small enough to retain echinoderm settlers). The retained contents of the sample were stored in 70 % EtOH for subsequent identification and enumeration of settlers using a Bogorov tray under a dissecting microscope.

Settlers of echinoids (*Strongylocentrotus droebachiensis* and *Echinarachnius parma*) ophiuroids (*Ophiopholis aculeata* and *Ophiura*) and asteroids (*Asterias*) were identified from descriptions in the literature (Agassiz et al. 1883, Gordon 1929, Russell-Hunter 1979, Pearse et al. 1987, Todd & Laverack 1991, Medeiros-Bergen et al. 1998). Adults of *Ophiura robusta* occur in low numbers at both sites, although some settlers may have been *O. sarsi* which is common in deeper waters (Packer et al. 1994). *Asterias vulgaris* and *A. forbesi* occur at both sites with *A. vulgaris* being the more common species. Because we were unable to speciate the settlers of *Ophiura* and *Asterias*, we refer to them by genus.

Settlement was monitored in one of the paired collectors at each stratum in an array at bi-weekly intervals from 11 June to 20 November 1992, 26 May to 11 November 1993, and 9 June to 16 October 1994. Sampling was staggered between sites by ~1 week for logistical reasons. Settlers from two replicate arrays (20 m apart) were initially counted to record temporal patterns in settlement. The remaining 2 arrays also were counted for the 2-week period of highest settlement for each species, site and year. From 11 to 24 July 1992, we concurrently sampled all of the paired collectors to examine spatial variability within habitats at Mill Cove.

We define settlement operationally as the number of larvae of a species (genus) that attach to the turf during each 2-week period. We assume that the short sampling period and the design of our collectors minimise post-settlement mortality and emigration. To determine the effect of sampling frequency on our estimate of settlement, the second of the paired collectors was sampled at different intervals at Mill Cove. Thus, settlement at successive 3 d intervals from 21 July to 5 August 1993 was summed and compared to measures from concurrent bi-weekly samples for each combination of collector height and habitat. Similarly, settlement summed over 3 successive 16 d intervals from 9 June to 27 July 1994 was compared to concurrent 48 d samples at Mill Cove. The amount of algal/detrital fouling on collectors and the abundance of herbivorous gammarid amphipods (which could reduce fouling) also were measured in the 48 d samples to examine their potential effects on settlement at different collector heights. As an index of fouling we measured the thickness (in mm) of layers of sediment and flocculent material in standardised sample bottles.

Recruitment sampling

We define recruitment operationally as juveniles that survive to be counted ~1 year after settlement. The size of 1-year-old echinoderm recruits was determined from published growth rates and inspection of size-frequency distributions based on field samples (see below). We designated echinoids ≤8 mm (horizontal test diameter) as recruits of *Strongylocentrotus droebachiensis* based on growth rates for this species of 6 to 8 mm in the first year measured under laboratory and field conditions in Nova Scotia (Raymond & Scheibling 1987). We designated asteroids ≤10 mm (radius) as recruits of *Asterias*, which is consistent with early growth rates of *Asterias vulgaris* measured in the field in temperate waters (Smith 1940, Barker & Nichols 1983, Nichols & Barker 1984, Himmelman & Dutil 1991). We combined juvenile *Asterias vulgaris* and *A. forbesi* with small individuals that could only be identified to genus. Identifying ophiuroid recruits was complicated by a lack of juvenile growth data for *Ophiopholis aculeata* and *Ophiura robusta*, and the absence of distinct cohorts in our samples. Packer et al. (1994) reported growth rates of *Ophiura sarsi* of 2 to 4 mm in the first year at 150 m depth in the Gulf of Maine. Because modal size of *O. sarsi* from this population is ~7 times larger than *Ophiura robusta*, and ~3 times larger than *Ophiopholis aculeata*, at our sites, we designated individuals ≤2 mm (disc diameter) as recruits of *Ophiura robusta* and individuals ≤4 mm as recruits of *Ophiopholis aculeata*.

To compare the density of echinoderm recruits between years, sites and habitats, we collected and measured all individuals of each species from 6 to 10 quadrats of 1 m^2 randomly positioned along a belt transect of 4 m x 50 m (*Strongylocentrotus droebachiensis* in both habitats at Mill Cove in 1995 and in the barrens at Little Duck Island in 1993 were measured in only 4 quadrats). Each transect extended alongshore in each habitat at each site, parallel to and ~5 m from the line of collector arrays (in the direction of the echinoid front). Quadrats were sampled by divers between 30 August and 21 October 1993, 14 July and 2 September 1994, and 13 July and 31 August 1995. The location of the transect was staggered by <3 m each year to avoid overlap with previous transects and to maintain a similar position relative to the collector arrays and the advancing echinoid front.

Within each 1 m^2 quadrat, a 0.1 m^2 inset quadrat was sampled using a suction device to sample individuals as small as 1 mm. The remainder of the quadrat (0.9 m^2) was carefully searched by divers who removed and manually sorted through algal turfs and broke up coralline crusts to locate small and cryptic individuals. For each quadrat, echinoderms (and other invertebrates) were placed in sealed plastic bags. Samples were sorted in the laboratory where echinoderms were identified and measured with vernier calipers (0.1 mm accuracy). Measures from the 0.9 m^2 and 0.1 m^2 quadrats were combined to obtain the density of recruits per 1 m^2. The comparability of the two methods in sampling recruits was assessed by calculating the ratio of the number of recruits collected in the 0.9 m^2 portion to those collected in the 0.1 m^2 portion, pooled over all quadrats within each transect. In most cases, the ratio approximated 9, indicating that differences in sampling methodology or sampling scale had little effect on our estimates of recruitment. Exceptions to this were samples in the kelp bed at Little Duck Island of *Strongylocentrotus droebachiensis* in 1995, and *Asterias* in 1993 and 1994, where ratios ranged from 1.4 to 3.2, indicating that recruitment may have been a slightly underestimated in the 0.9 m^2 quadrats. Individuals of each species (genus) were pooled over all quadrats in a habitat to record size distributions.

Statistical analyses

Effects on settlement and recruitment of site, habitat, collector height (for settlement) and year were examined using factorial ANOVA. Analysis of settlement is based on 4 replicate collectors sampled over the 2-week period of highest settlement. Effects on settlement of sampling frequency, habitat and height also are examined by factorial ANOVA based on 4 replicate collectors. All analyses are based on counts of settlers per collector (i.e. 0.05 m^2 of turf) but converted to settlers per m^2 for comparability with recruitment measurements. Periods of low settlement (mean density ≤2 settlers per collector) within a site were excluded from statistical analysis. Analysis of recruitment data is based on 6 to 10 (occasionally 4) replicate quadrats sampled in each site, habitat and year. All factors are considered fixed, including site because the sites were selected to represent two different hydrodynamic environments. Cochran's test was conducted prior to ANOVA to test the assumption of homogeneity of variance (α=0.05). Where necessary, raw data were log transformed [ln (x+1)] to satisfy this assumption. Post-hoc comparisons are made using Tukey's HSD test (α=0.05).

RESULTS

Temporal and spatial patterns of settlement

Settlement of echinoderms in the kelp bed and barrens mainly occurred over an ~2 week period between July and September of each year (Figs. 4.1 to 4.4). The magnitude and timing of each settlement peak varied between species and years, and the year of maximum settlement differed between species. Most settlement occurred during the summer months when sea temperature was at or near the yearly maximum (Fig. 4.5). During the settlement period, temperature was slightly higher on average but more variable at Mill Cove than Little Duck Island. Temperatures at both sites were lower on average and more variable in 1994 than 1993.

Settlement of the echinoid *Strongylocentrotus droebachiensis* was consistently low at both sites in 1992 and 1993 but increased by an order of magnitude in 1994 (Fig. 4.6). Analysis of the 1994 settlement peak indicated no significant difference between habitats ($F_{1,12}$=0.962, p=0.346) or collector heights ($F_{1,12}$=3.200, p=0.099) at Mill Cove. There also was no significant interaction of habitat and height ($F_{1,12}$=2.427, p=0.145). Missing data from the kelp bed at Little Duck Island in 1994 limited between-site comparisons to the barrens, where there was no significant effect of site ($F_{1,10}$=0.267, p=0.617), or height ($F_{1,10}$=0.966, p=0.349), or interaction of height and site ($F_{1,10}$=3.671, p=0.084).

The irregular echinoid *Echinarachnius parma* settled in collectors only once over the 3 year sampling period, at Mill Cove from 8 to 22 September 1994. Settlement of *E. parma* did not differ significantly between habitats ($F_{1,12}$=0.531, p=0.480)(mean ± SE, averaged over collector heights, n=8: kelp, 65.0 ± 42.6 m^{-2}; barrens, 120 ± 76.0 m^{-2}) but was an order of magnitude greater in High (172.5 ± 76.9 m^{-2}) than in Low (12.5 ± 7.5 m^{-2}) collectors (averaged over habitats), although this difference was marginally non-significant ($F_{1,12}$=4.320, p=0.060). There was no significant interaction of habitat and collector height ($F_{1,12}$=0.014, p=0.909).

Settlement of the asteroid *Asterias* was highly variable at both sites in all years resulting in a significant 4-way interaction of year, habitat, height and site (Fig. 4.7, Table 4.1). Post-hoc comparisons indicate greater settlement in 1993 and 1994 than in 1992, but between-site differences were significant in only 2 cases (Barren Low in 1994, Kelp Low in 1992). Settlement tended to be greater in High than in Low collectors, particularly at Mill Cove. With the exception of Little Duck Island in 1992, settlement of *Asterias* in High collectors was consistently greater above the kelp bed than above the barrens. However, this difference was statistically significant in only one case (Little Duck Island in 1994). At Mill Cove, a second pulse of settlement occurred at the end of the sampling period in September/October 1994. Again, settlement was greater in the High than in the Low collectors ($F_{1,12}$=14.453, p=0.003), but there was no significant difference between habitats ($F_{1,12}$<0.001, p=0.993) and no interaction of these factors ($F_{1,12}$=0.084, p=0.776).

The ophiuroid *Ophiopholis aculeata* settled in significantly greater numbers in High than in Low collectors and there were no interactions between collector height and any of the other factors (Fig. 4.8, Table 4.2). However, there were significant 2-way interactions between year and site and between habitat and site. Post-hoc comparisons show that settlement (averaged over habitats and heights) differed between years (1993>94>92) at Mill Cove but not at Little Duck Island and was greater at Mill Cove than Little Duck Island in 1993 but not 1992 or 1994. Also, settlement (averaged over years and heights) was greater in the barrens than the kelp bed at Little Duck Island and greater in both habitats at Mill Cove than Little Duck Island.

Settlement of the ophiuroid *Ophiura* decreased over the 3 years to very low numbers in 1994. ANOVA of settlement in 1992 and 1993 indicated a significant 3-way interaction between year, habitat and height and a 2-way interaction between year and site (Fig. 4.9, Table 4.3). Post-hoc comparisons show that settlement (averaged over habitats, heights and sites) was greater in 1992 than in 1993 and greater at Mill Cove than Little Duck Island in both years. Settlement in Low collectors (averaged over sites) was greater in the barrens than in the kelp beds in 1992, but not in 1993, and greater in High than in Low collectors in the kelp bed in 1992. *Ophiura*, the only species that settled in abundance at Mill Cove in 1992, also was used to test the effect of array position within habitats in a nested ANOVA. The analysis showed that the effect of position, the nested factor, was not significant (kelp bed: $F_{3,16}$=0.456, p=0.717; barrens: $F_{3,16}$=2.021, p=0.152) nor was the interaction of height and position (kelp bed: $F_{3,16}$=0.706, p=0.562; barrens: $F_{3,16}$=1.150, p=0.359), indicating little variation among collector arrays within each habitat.

Effect of sampling frequency

At Mill Cove, sampling at 3 d intervals showed that most settlement of *Ophiopholis aculeata* and *Ophiura* during the ~2-week settlement period in 1993 occurred within 6 d (see also Chapter 3). A comparison of settlement of these ophiuroids summed over 5 successive 3 d intervals with that recorded over the same 15 d interval (Fig. 4.10a, b) indicated no significant effect of sampling frequency (*Ophiopholis aculeata*: $F_{1,24}$=3.543, p=0.072; *Ophiura*: $F_{1,24}$=0.488, p=0.492) or interaction of sampling frequency with habitat ($F_{1,24}$=0.081, p=0.778; $F_{1,24}$=0.025, p=0.877) or height ($F_{1,24}$=0.090, p=0.767; $F_{1,24}$=0.059, p=0.811). A comparison of settlement of *Strongylocentrotus droebachiensis* and *Ophiopholis aculeata* summed over 3 successive 16 d intervals to that recorded over the same 48 d interval in 1994 (Fig. 4.11a, b) indicated a significant interaction of sampling frequency and height (*S. droebachiensis*: $F_{1,24}$=16.097, p=0.001; *Ophiopholis aculeata*: $F_{1,24}$=12.326, p=0.002). Post-hoc comparisons show that settlement for both species (averaged over habitats) was greater in High than in Low collectors in the 48 d sample but not in the summed 16 d samples, and greater in the 48 d sample than in the summed 16 d samples in High collectors but not in Low collectors. *Ophiura* settled in low numbers during 1994 and most settlement of *Asterias* occurred later in the year (Fig. 4.11c). For both species there was no significant effect of sampling frequency (*Ophiura*: $F_{1,24}=0.800$, $p=0.380$; *Asterias*: $F_{1,24}=3.960$, $p=0.058$) nor significant interaction with habitat ($F_{1,24}\approx0$, $p\approx1$; $F_{1,24}=3.960$, $p=0.058$ respectively) or height ($F_{1,24}=0.200$, $p=0.659$; $F_{1,24}=0.615$, $p=0.441$ respectively).

ANOVA of the fouling index after 48 d shows that High collectors were more fouled than Low collectors ($F_{1,12}=151.742$, $p<0.001$), collectors in the kelp bed were more fouled than those in the barrens ($F_{1,12}=9.484$, $p=0.010$), and that there was no significant interaction of habitat and collector height ($F_{1,12}\approx0$, $p\approx1$)(Fig. 4.12). This difference in fouling, in part, could be due to differences in the abundance of herbivorous amphipods. ANOVA of amphipod abundance in the 48 d sample showed greater numbers in Low than in High collectors ($F_{1,12}=14.878$, $p=0.002$), no difference in abundance between habitats ($F_{1,12}=1.653$, $p=0.223$), and no interaction of habitat and collector height ($F_{1,12}=1.653$ $p=0.223$)(Fig. 4.12). To further examine the relationship between fouling and settlement, and between amphipod abundance and fouling, we used regression analysis (Fig. 4.13). Settlement of both *Strongylocentrotus droebachiensis* ($r^2=0.280$, $p=0.035$) and *Ophiopholis aculeata* ($r^2=0.775$, $p<0.001$) was positively related to fouling in the 48 d sample, but there was no significant relationship in each of the 16 d samples ($p>0.2$)(Fig. 4.13). Fouling was negatively related to amphipod abundance in the 48 d sample ($r^2=0.367$, $p=0.013$).

Temporal and spatial patterns of recruitment

Size distributions of *Strongylocentrotus droebachiensis* from 1993 to 1995 were skewed towards juvenile size classes (≤16 mm), reflecting recent recruitment (Fig. 4.14). In 1995 in particular, echinoid populations in both habitats at each site were dominated by recruits from the previous year (≤8 mm). Analysis of recruit density indicated significant differences between years ($F_{2,85}=123.092$, $p<0.001$), habitats ($F_{1,85}=76.000$, $p<0.001$) and sites ($F_{1,85}=34.315$, $p<0.001$)(Fig. 4.18) but no significant 2-way (year x habitat: $F_{2,85}=1.934$, $p=0.151$; year x site: $F_{2,85}=1.235$, $p=0.296$; habitat x site: $F_{1,85}=0.033$, $p=0.856$), or 3-way ($F_{2,85}=2.409$, $p=0.096$) interactions. Recruitment of *S. droebachiensis* was greater in barrens than in kelp beds, greater at Mill Cove than Little Duck Island, and greater in 1995 than 1994 (by an order of magnitude) and in 1994 than 1993 (Fig. 4.18).

Recruitment of the irregular echinoid *Echinarachnius parma* was not recorded at either site; only 10 small individuals, from barrens at Mill Cove (8 in 1993 and 2 in 1994) were collected during this study.

Size distributions of *Asterias* were heavily skewed towards juveniles (≤10 mm) in both habitats at each site in 1994 and 1995, and in the kelp bed at Little Duck Island in 1993 (Fig. 4.15). Analysis of recruit density indicated a 3-way interaction of year, habitat and site (Fig. 4.18, Table 4.4), largely because of differences in magnitude, rather than direction, of recruitment. Post-hoc comparisons indicated that recruitment generally was greater in 1995 and 1994 than in 1993, greater in kelp beds than barrens, and greater at Mill Cove than Little Duck Island.

Size distributions of *Ophiopholis aculeata* were approximately normal at both sites in all years, but slightly skewed towards the smallest size classes (≤4 mm) at Mill Cove in 1995 (Fig. 4.16). Modal size tended to be smaller at Mill Cove (4 to 6 mm) than Little Duck Island (7 to 9 mm) between 1993 and 1995. Analysis of recruit density indicated significant differences between years ($F_{2,92}=11.726$, $p<0.001$) and sites ($F_{1,92}=19.807$, $p<0.001$), but not between habitats ($F_{1,92}=0.405$, $p=0.526$)(Fig. 4.18). There were no significant 2-way (year x habitat: $F_{2,92}=0.287$, $p=0.751$; year x site: $F_{2,92}=0.713$, $p=0.493$; habitat x site: $F_{1,92}=0.217$, $p=0.643$) or 3-way ($F_{2,92}=0.624$, $p=0.538$) interactions.

Recruitment was greater at Mill Cove than Little Duck Island and greater in 1995 than 1994, and in 1994 than 1993.

Ophiura robusta occurred in low numbers at both sites and with approximately normal size distributions (Fig. 4.17). Recruits were rare or absent between 1993 and 1995 precluding any statistical analysis (Fig. 4.18).

Relationship between settlement and recruitment

We used regression analyses to examine the relationship between mean settlement in the Low collectors during the ~2 week peak each year (1992 to 1994) to mean recruitment ~1 year later (1993 to 1995) from each combination of site, habitat and year (Fig. 4.19). Logarithmic transformation of the means [log (x+1)] strengthened the relationship in 3 out of 4 cases (for *Ophiura* it remained non-significant). For *Strongylocentrotus droebachiensis*, recruitment strongly reflected settlement in the previous year: 84 % of the variation in recruitment is explained by the variation in settlement. Low settlement of echinoids in 1992 and 1993 resulted in low recruitment in the subsequent years, but a large settlement event in 1994 resulted in high recruit density in 1995 at both sites and in both habitats. Although settlement and recruitment rates of *Asterias* were more variable, 42 % of the variation in recruitment is explained by variation in settlement. Recruitment of *Ophiopholis aculeata* was consistently low, although settlement varied by almost 3 orders of magnitude. Nevertheless, 38 % of the variation in recruitment of this ophiuroid is explained by variation in settlement. *Ophiura* exhibited a similar variation in settlement as *O. aculeata* but recruits were so rare each year that there was no significant relationship between recruitment and settlement.

Table 4.1. Results of a 4-factor ANOVA and Tukey's HSD test for settlement of *Asterias* at Mill Cove and Little Duck Island sampled over 3 years in 2 habitats (barrens, kelp bed) at 2 heights (High, Low). Statistically significant post-hoc comparisons of each treatment level are given with levels increasing in magnitude; those with common underlines do not differ significantly (α=0.05). Data are log transformed [ln(x+1)]. MC: Mill Cove, LD: Little Duck Island, K: kelp bed, B: barrens, H: High, L: Low

Source	df	Sum of Squares	Mean Square	F-Value	P-Value
Year	2	105.869	52.935	248.804	.0001
Habitat	1	2.664	2.664	12.522	.0007
Height	1	23.233	23.233	109.198	.0001
Site	1	4.778	4.778	22.457	.0001
Year * Habitat	2	.814	.407	1.913	.1550
Year * Height	2	.351	.175	.824	.4428
Year * Site	2	10.689	5.345	25.121	.0001
Habitat * Height	1	1.136	1.136	5.341	.0237
Habitat * Site	1	.701	.701	3.296	.0736
Height * Site	1	2.311	2.311	10.862	.0015
Year * Habitat * Height	2	.441	.221	1.037	.3596
Year * Habitat * Site	2	.846	.423	1.989	.1443
Year * Height * Site	2	.526	.263	1.237	.2963
Habitat * Height * Site	1	.107	.107	.502	.4809
Year * Habitat * Height * Site	2	3.148	1.574	7.399	.0012
Residual	72	15.318	.213		

Source:	Year	Habitat	Height	Site
	MCKH: 92 94 93	LDH94: B K	MCB94: L H	BL94: MC LD
	MCKL: 92 94 93		MCK92: L H	KL92: MC LD
	MCBH: 92 94 93		MCK93: L H	
	MCBL: 92 94 93		MCK94: L H	
	LDKH: 92 93 94		LDK94: L H	
	LDKL: 92 94 93			
	LDBH: 92 94 93			
	LDBL: 92 93 94			

Table 4.2. Results of a 4-factor ANOVA and Tukey's HSD test for settlement of *Ophiopholis aculeata* at Mill Cove and Little Duck Island sampled over 3 years in 2 habitats (barrens, kelp bed) at 2 heights (High, Low). Statistically significant post-hoc comparisons of each treatment level are given with levels increasing in magnitude; those with common underlines do not differ significantly (α=0.05). Data are log transformed [ln(x+1)]. MC: Mill Cove, LD: Little Duck Island, K: kelp bed, B: barrens, H: High, L: Low

Source	df	Sum of Squares	Mean Square	F-Value	P-Value
Year	2	26.866	13.433	44.783	.0001
Habitat	1	6.080	6.080	20.268	.0001
Height	1	11.835	11.835	39.456	.0001
Site	1	17.897	17.897	59.663	.0001
Year * Habitat	2	.034	.017	.057	.9450
Year * Height	2	.094	.047	.157	.8546
Year * Site	2	19.010	9.505	31.688	.0001
Habitat * Height	1	.368	.368	1.226	.2719
Habitat * Site	1	2.365	2.365	7.885	.0065
Height * Site	1	.129	.129	.430	.5142
Year * Habitat * Height	2	1.326	.663	2.211	.1172
Year * Habitat * Site	2	.438	.219	.729	.4859
Year * Height * Site	2	.534	.267	.891	.4149
Habitat * Height * Site	1	.027	.027	.091	.7640
Year * Habitat * Height * Site	2	.190	.095	.318	.7290
Residual	70	20.997	.300		

Source: Year	Habitat	Height	Site
MC: 92 94 93	LD: K B	all pooled: L H	93: LD MC
			K: LD MC
			B: LD MC

Table 4.3. Results of a 4-factor ANOVA and Tukey's HSD test for settlement of *Ophiura* at Mill Cove and Little Duck Island sampled over 3 years in 2 habitats (barrens, kelp bed) at 2 heights (High, Low). Statistically significant post-hoc comparisons of each treatment level are given with levels increasing in magnitude; those with common underlines do not differ significantly ($\alpha=0.05$). Data are log transformed [ln(x+1)]. MC: Mill Cove, LD: Little Duck Island, K: kelp bed, B: barrens, H: High, L: Low

Source	df	Sum of Squares	Mean Square	F-Value	P-Value
Year	1	33.824	33.824	155.674	.0001
Habitat	1	12.118	12.118	55.772	.0001
Height	1	8.749	8.749	40.267	.0001
Site	1	26.294	26.294	121.015	.0001
Year * Habitat	1	.633	.633	2.915	.0942
Year * Height	1	.106	.106	.487	.4885
Year * Site	1	1.440	1.440	6.628	.0132
Habitat * Height	1	1.439	1.439	6.621	.0132
Habitat * Site	1	.683	.683	3.145	.0825
Height * Site	1	.056	.056	.259	.6133
Year * Habitat * Height	1	1.366	1.366	6.286	.0156
Year * Habitat * Site	1	.021	.021	.097	.7570
Year * Height * Site	1	.234	.234	1.077	.3046
Habitat * Height * Site	1	.017	.017	.080	.7786
Year * Habitat * Height * Site	1	.610	.610	2.806	.1004
Residual	48	10.429	.217		

Source: Year	Habitat	Height	Site
BH: 93 92	L92: K B	K92: L H	92: LD MC
BL: 93 92			93: LD MC
KH: 93 92			
KL: 93 92			
MC: 93 92			
LD: 93 92			

Table 4.4. Results of a 3-factor ANOVA and Tukey's HSD test for recruitment of *Asterias* at Mill Cove and Little Duck Island sampled over 3 years in 2 habitats (barrens, kelp bed). Statistically significant post-hoc comparisons of each treatment level are given with levels increasing in magnitude; those with common underlines do not differ significantly (α=0.05). Data are log transformed [ln(x+1)]. MC: Mill Cove, LD: Little Duck Island, K: kelp bed, B: barrens

Source	df	Sum of Squares	Mean Square	F-Value	P-Value
Year	2	43.304	21.652	56.190	.0001
Habitat	1	80.524	80.524	208.970	.0001
Site	1	22.188	22.188	57.581	.0001
Year * Habitat	2	6.357	3.179	8.249	.0005
Year * Site	2	7.943	3.972	10.307	.0001
Habitat * Site	1	5.142	5.142	13.344	.0004
Year * Habitat * Site	2	3.203	1.601	4.156	.0182
Residual	108	41.617	.385		

Source:	Year	Habitat	Site
	MCK: 93 94 95	MC94: B K	K93: LD MC
	LDB: $\underline{93\ 94}$ 95	MC95: B K	B95: LD MC
	LDK: 93 $\underline{94\ 95}$	LD93: B K	K95: LD MC
		LD94: B K	
		LD95: B K	

Fig. 4.1. Mean density of settlers of *Strongylocentrotus droebachiensis* in collectors at 2.3 and 0.2 m off the bottom (High and Low) in 2 habitats (kelp bed and barrens) from June to November 1992 to 1994 at Mill Cove and Little Duck Island. Data are plotted at the midpoint of each bi-weekly sampling interval (n=2 to 4).

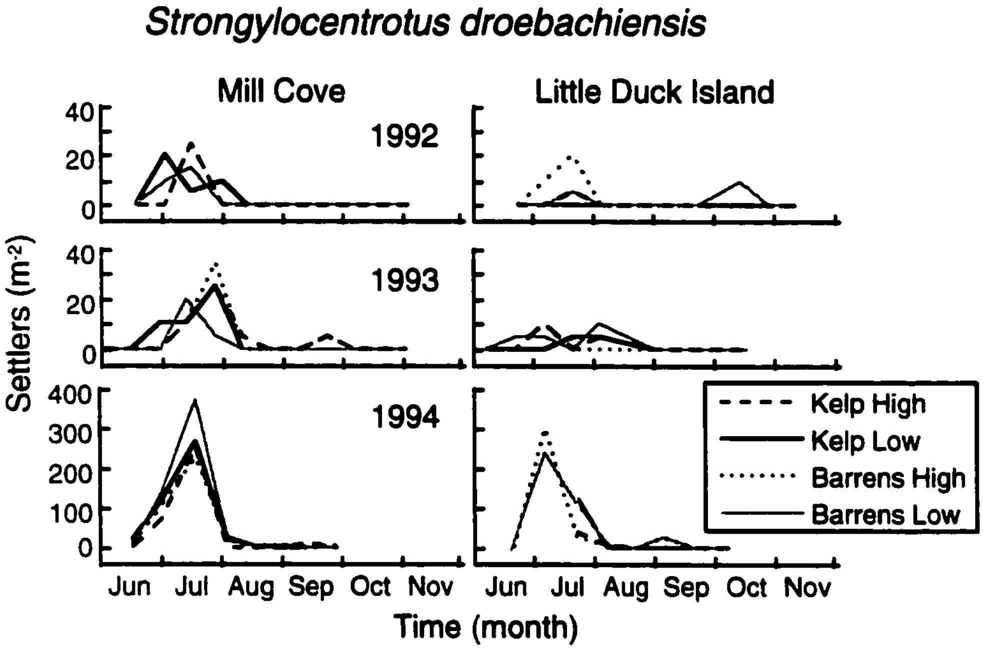

Strongylocentrotus droebachiensis
Mill Cove
Little Duck Island
1992
1993
1994
40
20
0
40
20
0
400
300
200
100
0
Settlers (m^{-2})
Jun
Jul
Aug
Sep
Oct
Nov
Jun
Jul
Aug
Sep
Oct
Nov
Time (month)
Kelp High
Kelp Low
Barrens High
Barrens Low

Figure 4.1

Fig. 4.2. Mean density of settlers of *Asterias* in collectors at 2.3 and 0.2 m off the bottom (High and Low) in 2 habitats (kelp bed and barrens) from June to November 1992 to 1994 at Mill Cove and Little Duck Island. Data are plotted at the midpoint of each bi-weekly sampling interval (n=2 to 4).

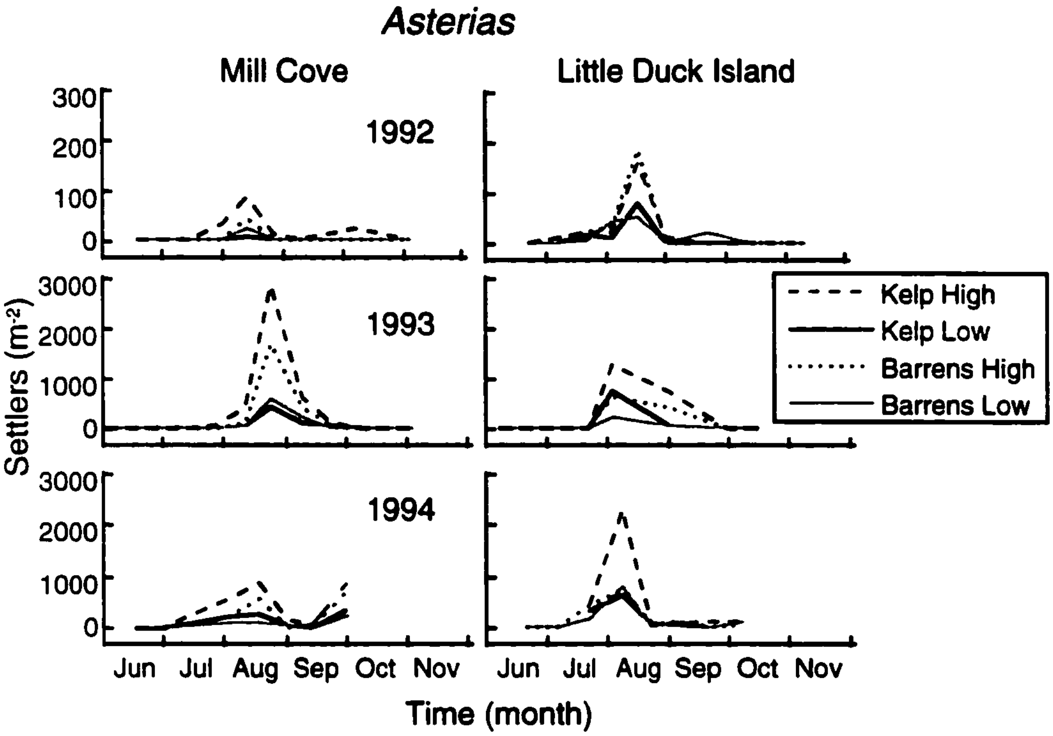

Asterias
Mill Cove
Little Duck Island
1992
1993
1994
300
200
100
0
3000
2000
1000
0
3000
2000
1000
0
Settlers (m-2)
Kelp High
Kelp Low
Barrens High
Barrens Low
Jun
Jul
Aug
Sep
Oct
Nov
Jun
Jul
Aug
Sep
Oct
Nov
Time (month)

Figure 4.2

Fig. 4.3. Mean density of settlers of *Ophiopholis aculeata* in collectors at 2.3 and 0.2 m off the bottom (High and Low) in 2 habitats (kelp bed and barrens) from June to November 1992 to 1994 at Mill Cove and Little Duck Island. Data are plotted at the midpoint of each bi-weekly sampling interval (n=2 to 4).

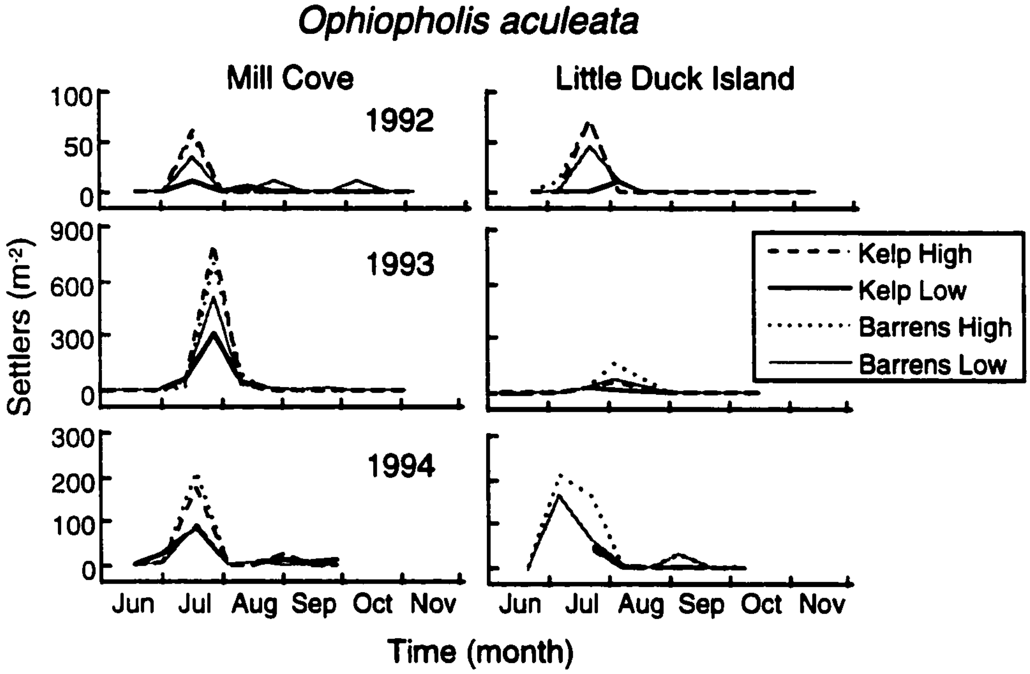

Ophiopholis aculeata
Mill Cove
Little Duck Island
1992
1993
1994
100
50
0
900
600
300
0
300
200
100
0
Settlers (m-2)
Kelp High
Kelp Low
Barrens High
Barrens Low
Jun Jul Aug Sep Oct Nov
Jun Jul Aug Sep Oct Nov
Time (month)

Figure 4.3

Fig. 4.4. Mean density of settlers of *Ophiura* in collectors at 2.3 and 0.2 m off the bottom (High and Low) in 2 habitats (kelp bed and barrens) from June to November 1992 to 1994 at Mill Cove and Little Duck Island. Data are plotted at the midpoint of each bi-weekly sampling interval (n=2 to 4).

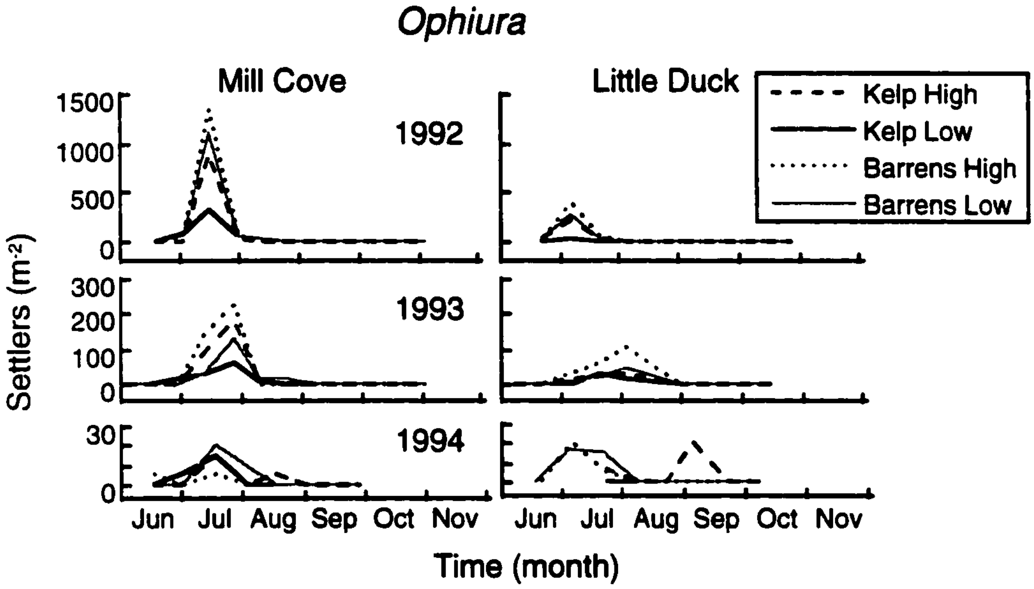

Ophiura
Mill Cove
Little Duck
1992
1993
1994
Kelp High
Kelp Low
Barrens High
Barrens Low
Settlers (m-2)
1500
1000
500
0
300
200
100
0
30
0
Jun
Jul
Aug
Sep
Oct
Nov
Jun
Jul
Aug
Sep
Oct
Nov
Time (month)

Figure 4.4

Fig. 4.5. Sea temperature measured at 2.3 and 0.2 m off the bottom (High and Low) in 2 habitats (kelp bed and barrens) in 1993 and 1994 at Mill Cove and Little Duck Island.

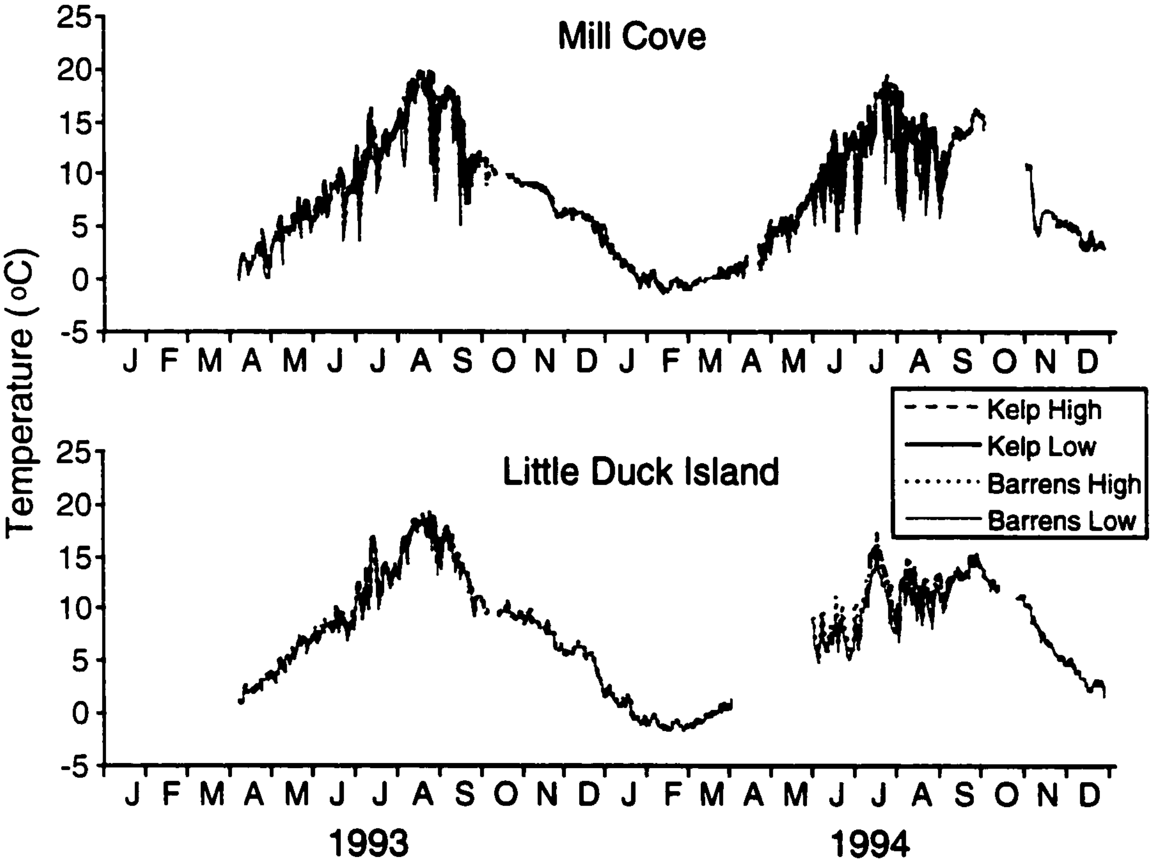

Mill Cove
Little Duck Island
Temperature (oC)
25
20
15
10
5
0
-5
J F M A M J J A S O N D J F M A M J J A S O N D
1993
1994
Kelp High
Kelp Low
Barrens High
Barrens Low

Figure 4.5

Fig. 4.6. Mean (± SE) density of settlers of *Strongylocentrotus droebachiensis* sampled in 4 replicate collectors at 2.3 and 0.2 m off the bottom (High and Low) in 2 habitats (kelp bed and barrens) during the bi-weekly period of peak settlement in each year (1992 to 1994) at Mill Cove and Little Duck Island.

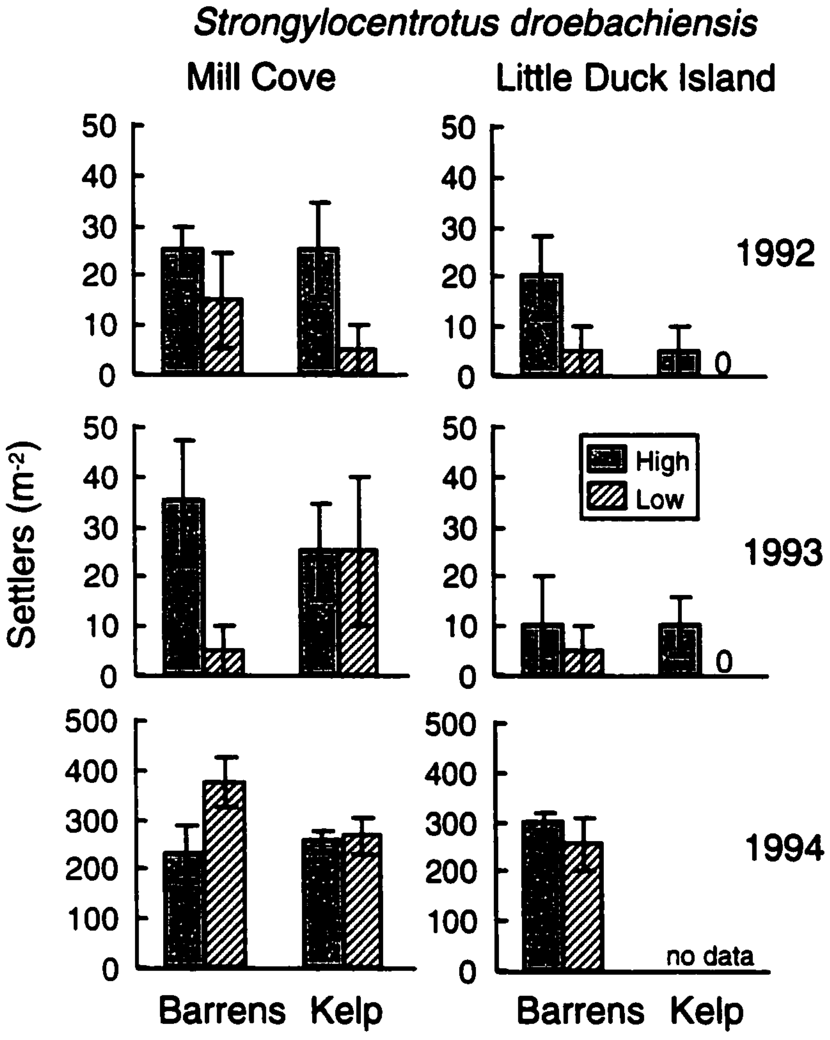

Strongylocentrotus droebachiensis
Mill Cove
Little Duck Island
Settlers (m⁻²)
0
10
20
30
40
50
100
200
300
400
500
1992
1993
1994
High
Low
no data
Barrens
Kelp

Figure 4.6

Fig. 4.7. Mean (± SE) density of settlers of *Asterias* sampled in 4 replicate collectors at 2.3 and 0.2 m off the bottom (High and Low) in 2 habitats (kelp bed and barrens) during the bi-weekly period of peak settlement in each year (1992 to 1994) at Mill Cove and Little Duck Island.

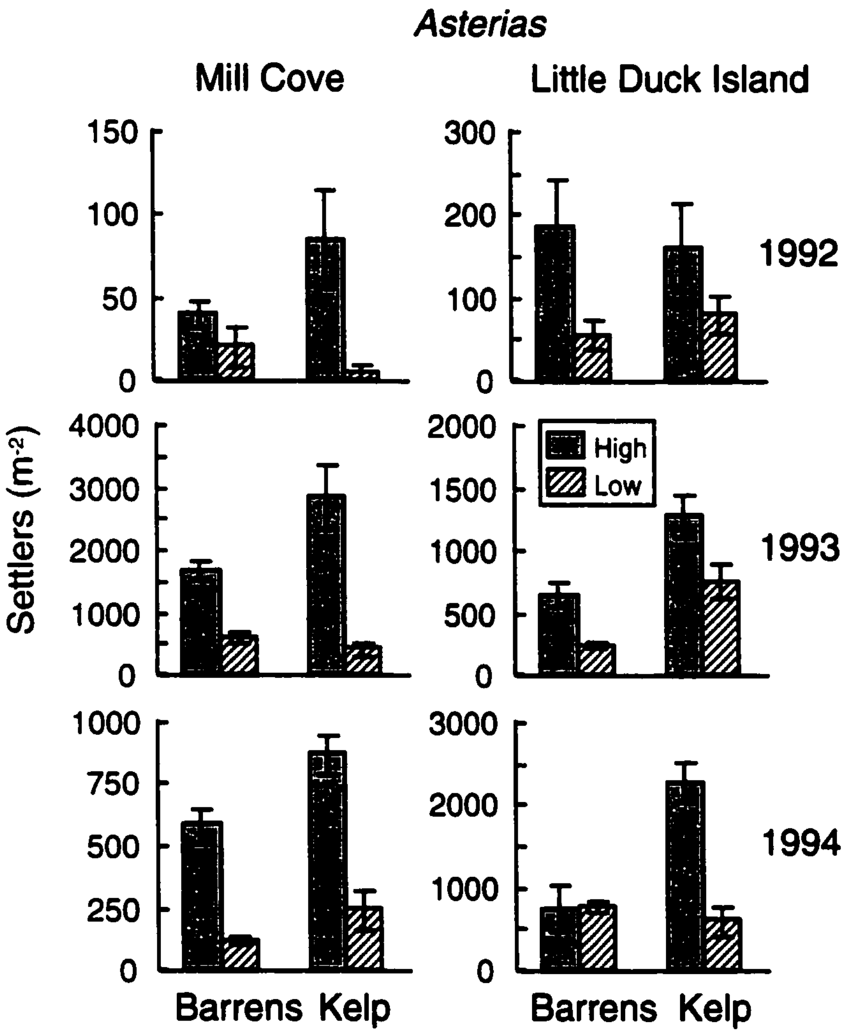

Asterias
Mill Cove
Little Duck Island
Settlers (m-2)
150
100
50
0
300
200
100
0
1992
4000
3000
2000
1000
0
2000
1500
1000
500
0
High
Low
1993
1000
750
500
250
0
3000
2000
1000
0
1994
Barrens
Kelp
Barrens
Kelp

Figure 4.7

Fig. 4.8. Mean (± SE) density of settlers of *Ophiopholis aculeata* sampled in 4 replicate collectors at 2.3 and 0.2 m off the bottom (High and Low) in 2 habitats (kelp bed and barrens) during the bi-weekly period of peak settlement in each year (1992 to 1994) at Mill Cove and Little Duck Island.

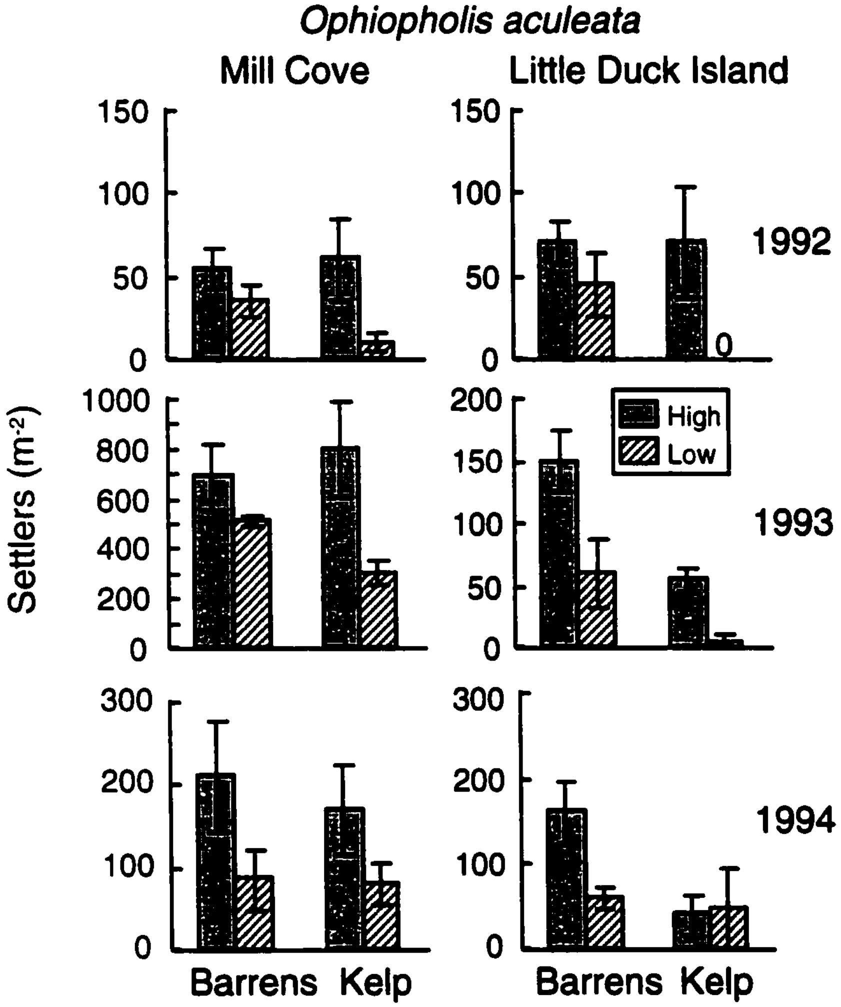
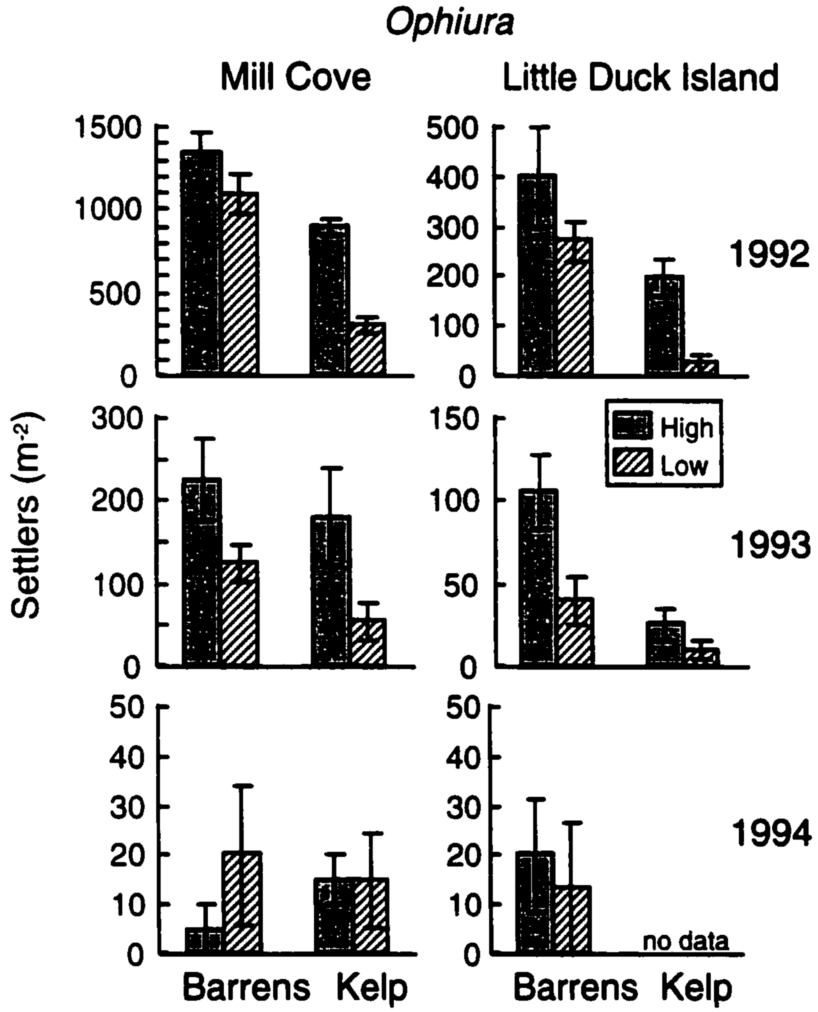

Ophiopholis aculeata
Mill Cove
Little Duck Island
Settlers (m-2)
150
100
50
0
1000
800
600
400
200
200
150
300
1992
1993
1994
High
Low
Barrens
Kelp

Figure 4.8

Fig. 4.9. Mean (± SE) density of settlers of *Ophiura* sampled in 4 replicate collectors at 2.3 and 0.2 m off the bottom (High and Low) in 2 habitats (kelp bed and barrens) during the bi-weekly period of peak settlement in each year (1992 to 1994) at Mill Cove and Little Duck Island.



Ophiura
Mill Cove
Little Duck Island
Settlers (m-2)
1500
1000
500
0
500
400
300
200
100
0
1992
300
200
100
0
150
100
50
0
High
Low
1993
50
40
30
20
10
0
1994
no data
Barrens
Kelp
Barrens
Kelp

Figure 4.9

Fig. 4.10. Mean (+ SE) density of settlers of (a) *Ophiopholis aculeata* and (b) *Ophiura* in 4 replicate collectors in each of 4 sampling strata (Kelp High, Kelp Low, Barrens High, Barrens Low) over a 15 d period in Jul/Aug 1993 at Mill Cove. Settlement summed over 5 successive 3 d (5x3 d) intervals is compared to a single 15 d measure over the same period.

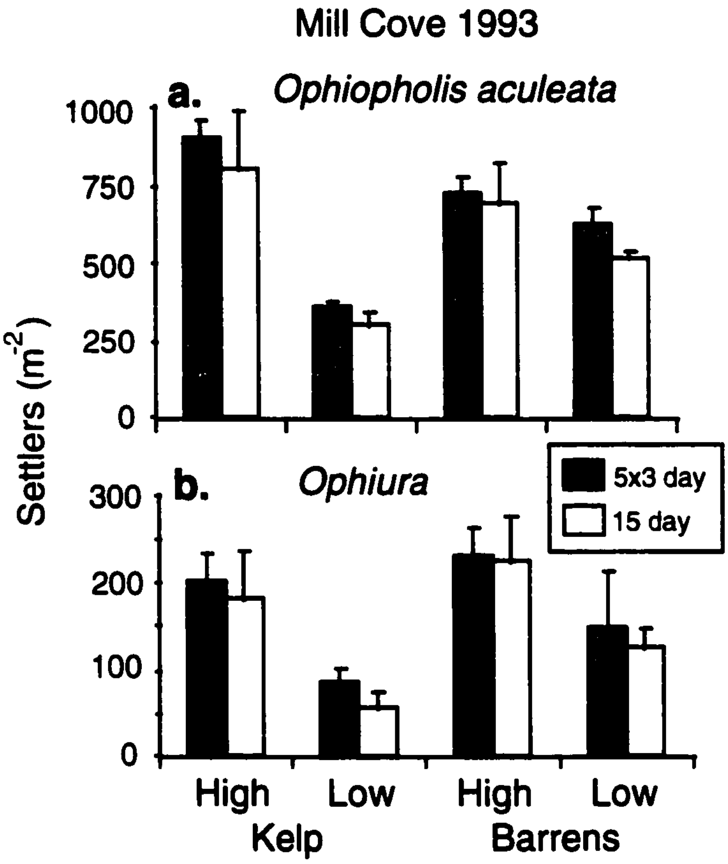

Mill Cove 1993
a.
Ophiopholis aculeata
1000
750
500
250
0
Settlers (m^{-2})
b.
Ophiura
300
200
100
0
5x3 day
15 day
High
Low
High
Low
Kelp
Barrens

Figure 4.10

Fig. 4.11. Mean (+ SE) density of settlers of (a) *Strongylocentrotus droebachiensis*, (b) *Ophiopholis aculeata* and (c) *Asterias* in 4 replicate collectors in each of 4 sampling strata (Kelp High, Kelp Low, Barrens High, Barrens Low) over a 48 d period in Jun/Jul 1994 at Mill Cove. Settlement summed over 3 successive 16 d (3x16 d) intervals is compared to a single 48 d measure over the same period.

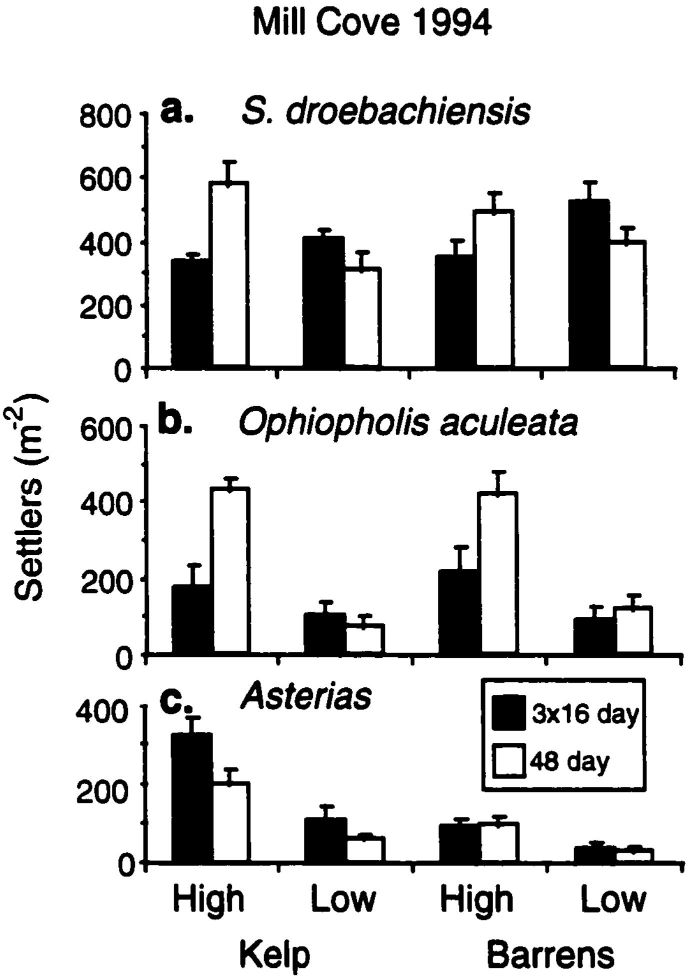

Mill Cove 1994
a. S. droebachiensis
800
600
400
200
0
b. Ophiopholis aculeata
600
400
200
0
c. Asterias
400
200
0
Settlers (m-2)
3x16 day
48 day
High
Low
High
Low
Kelp
Barrens

Figure 4.11

Fig. 4.12. Mean (+ SE) of fouling index and density of amphipods in 4 replicate collectors in each of 4 sampling strata (Kelp High, Kelp Low, Barrens High, Barrens Low) over a 48 d period in Jun/Jul 1994 at Mill Cove.

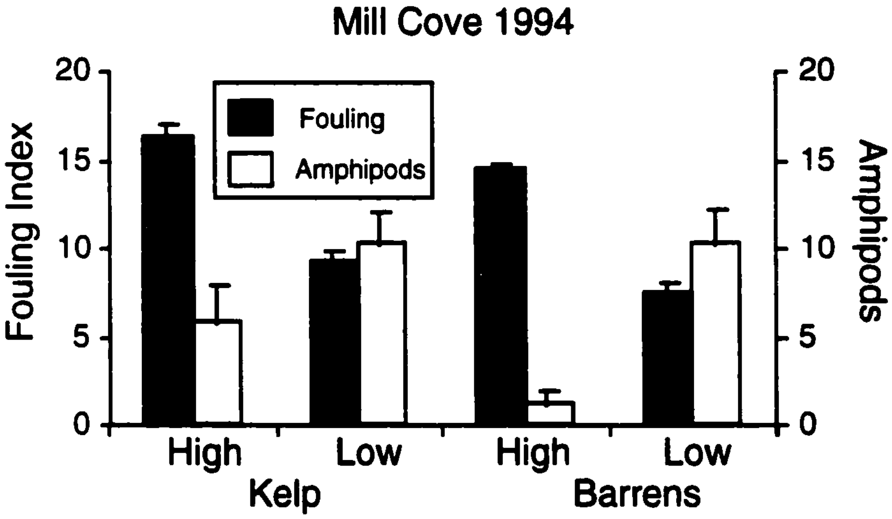

Mill Cove 1994
Fouling Index
Amphipods
20
15
10
5
0
Fouling
Amphipods
High
Low
High
Low
Kelp
Barrens

Figure 4.12

Fig. 4.13. a) Relationship between settlement of *Strongylocentrotus droebachiensis* (○) and *Ophiopholis aculeata* (●) and fouling index, and b) relationship between fouling index and amphipod abundance in 4 collectors in each of 4 sampling strata (Kelp High, Kelp Low, Barrens High, Barrens Low) over a 48 d period in Jun/Jul 1994 at Mill Cove. Also shown are regression lines for each set of grouped data (n=16).

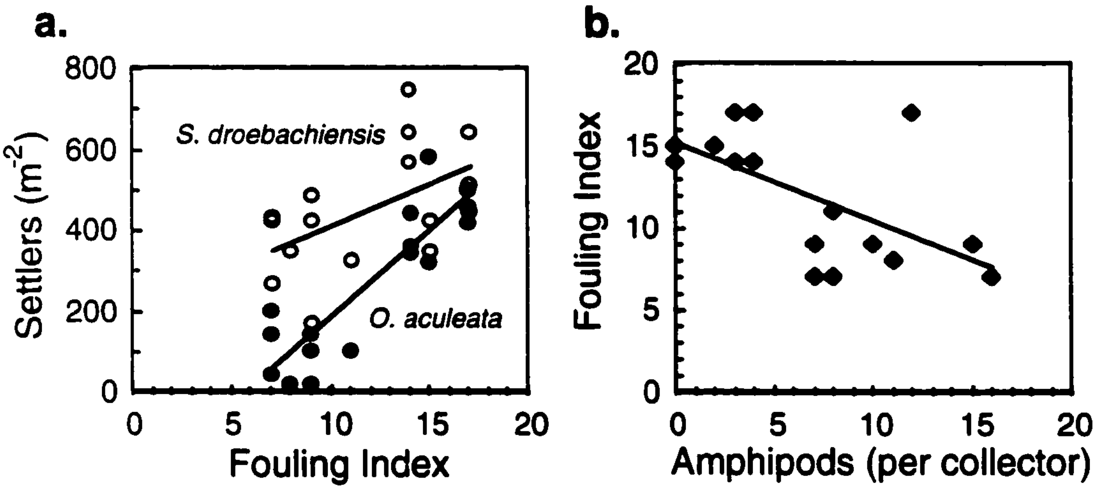

a.
800
600
400
200
0
Settlers (m-2)
S. droebachiensis
O. aculeata
0
5
10
15
20
Fouling Index
b.
20
15
10
5
0
Fouling Index
0
5
10
15
20
Amphipods (per collector)

Figure 4.13

Fig. 4.14. Size-frequency distributions (horizontal test diameter, mm) of *Strongylocentrotus droebachiensis* collected in 1.0 m^2 quadrats (n=4 to 10) in 2 habitats (kelp bed and barrens) between July and October 1993 to 1995 at Mill Cove and Little Duck Island. Recruits (shaded black) are individuals ≤8 mm.

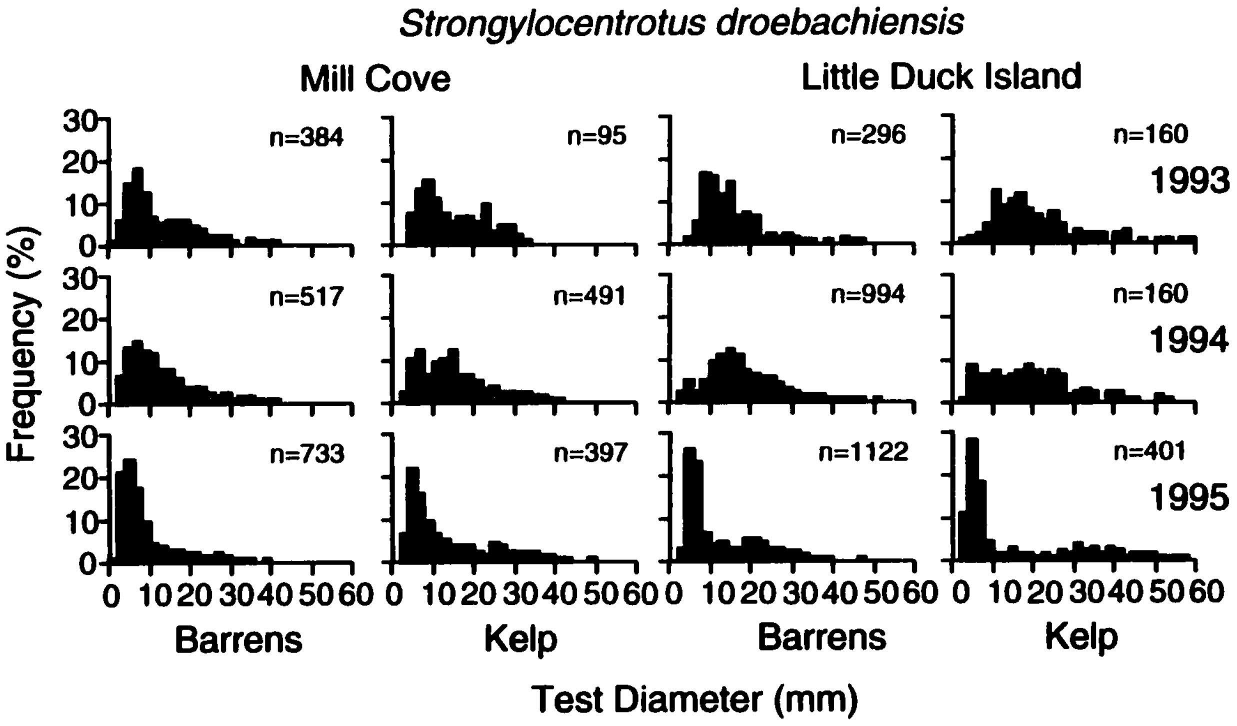

Strongylocentrotus droebachiensis
Mill Cove
Little Duck Island
Frequency (%)
30
20
10
0
n=384
n=95
n=296
n=160
1993
n=517
n=491
n=994
n=160
1994
n=733
n=397
n=1122
n=401
1995
0 10 20 30 40 50 60
Barrens
Kelp
Barrens
Kelp
Test Diameter (mm)

Figure 4.14

Fig. 4.15. Size-frequency distributions (radius, mm) of *Asterias* (*A. vulgaris* and *A. forbesi* combined) collected in 1.0 m^2 quadrats (n=10) in 2 habitats (kelp bed and barrens) between July and October 1993 to 1995 at Mill Cove and Little Duck Island. Recruits (shaded black) are individuals ≤10 mm.

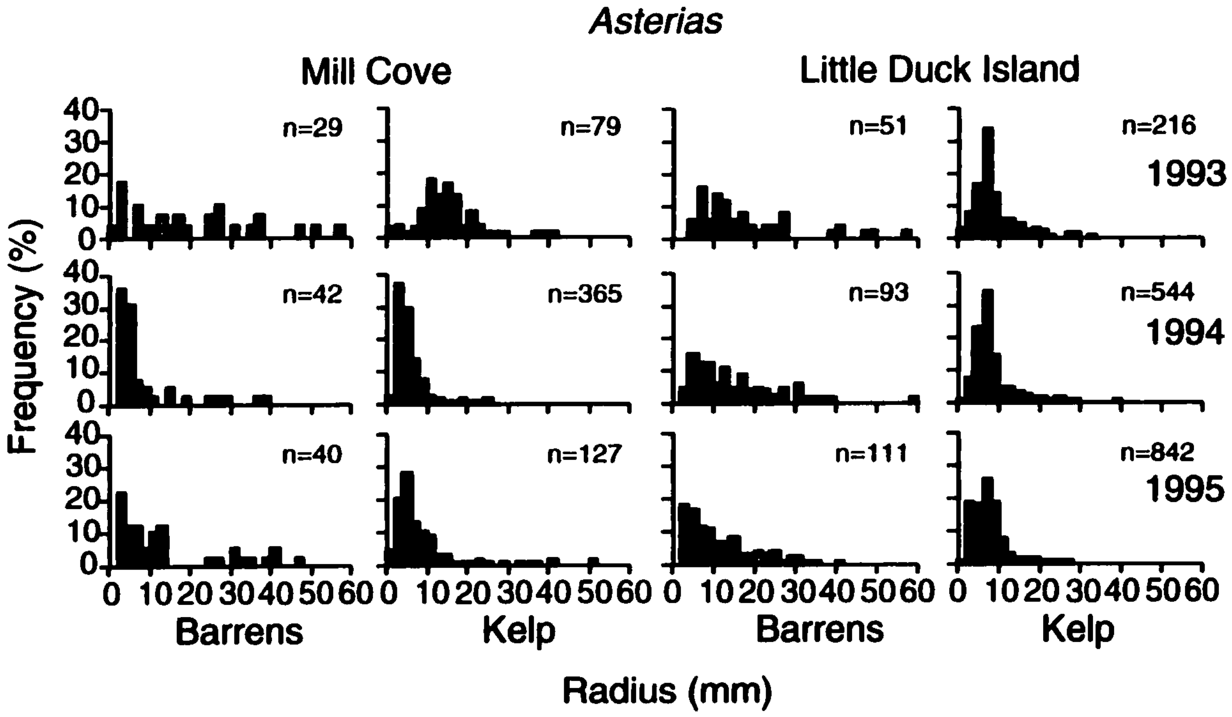

Asterias
Mill Cove
Little Duck Island
Frequency (%)
40
30
20
10
0
n=29
n=79
n=51
n=216
1993
n=42
n=365
n=93
n=544
1994
n=40
n=127
n=111
n=842
1995
0 10 20 30 40 50 60
Barrens
Kelp
Barrens
Kelp
Radius (mm)

Figure 4.15

Fig. 4.16. Size-frequency distributions (disc diameter, mm) of *Ophiopholis aculeata* collected in 1.0 m^2 quadrats (n=6 to 10) in 2 habitats (kelp bed and barrens) between July and October 1993 to 1995 at Mill Cove and Little Duck Island. Recruits (shaded black) are individuals ≤4 mm.

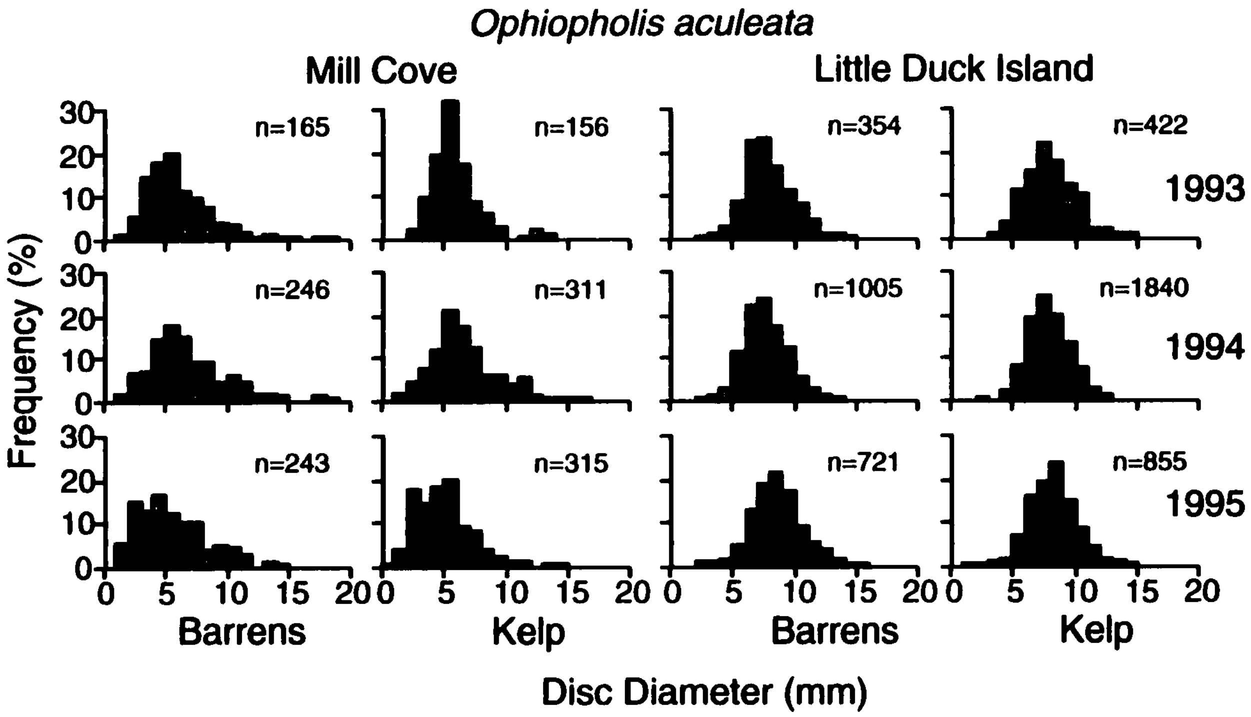

Ophiopholis aculeata
Mill Cove
Little Duck Island
n=165
n=156
n=354
n=422
1993
n=246
n=311
n=1005
n=1840
1994
n=243
n=315
n=721
n=855
1995
Frequency (%)
0
10
20
30
0
5
10
15
20
Barrens
Kelp
Barrens
Kelp
Disc Diameter (mm)

Figure 4.16

Fig. 4.17. Size-frequency distributions (disc diameter, mm) of *Ophiura robusta* collected in 1.0 m^2 quadrats (n=10) in 2 habitats (kelp bed and barrens) between July and October 1993 to 1995 at Mill Cove and Little Duck Island. Recruits (shaded black) are individuals ≤ 2 mm.

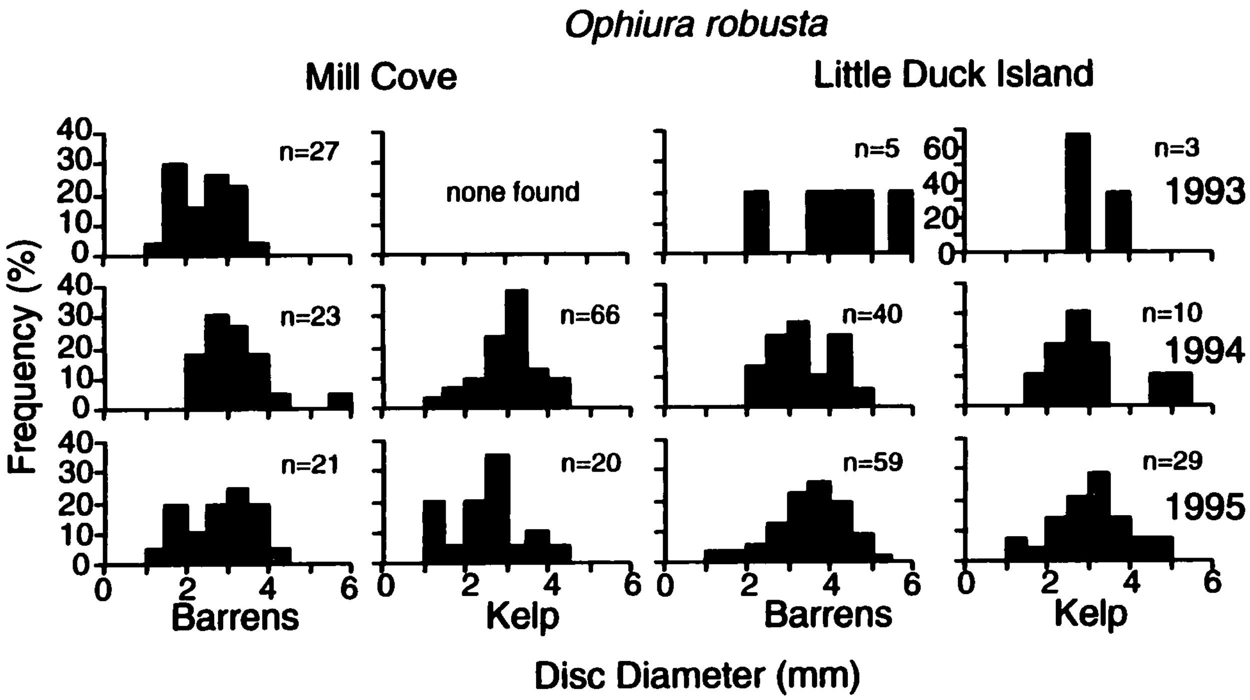

Ophiura robusta
Mill Cove
Little Duck Island
Frequency (%)
40
30
20
10
0
60
40
20
0
n=27
none found
n=5
n=3
1993
n=23
n=66
n=40
n=10
1994
n=21
n=20
n=59
n=29
1995
0
2
4
6
Barrens
Kelp
Barrens
Kelp
Disc Diameter (mm)

Figure 4.17

Fig. 4.18. Mean (± SE) density of recruits of *Strongylocentrotus droebachiensis*, *Asterias*, *Ophiopholis aculeata* and *Ophiura robusta* collected in 1.0 m^2 quadrats (n=4 to 10) in 2 habitats (kelp bed and barrens) between July and October 1993 to 1995 at Mill Cove and Little Duck Island.

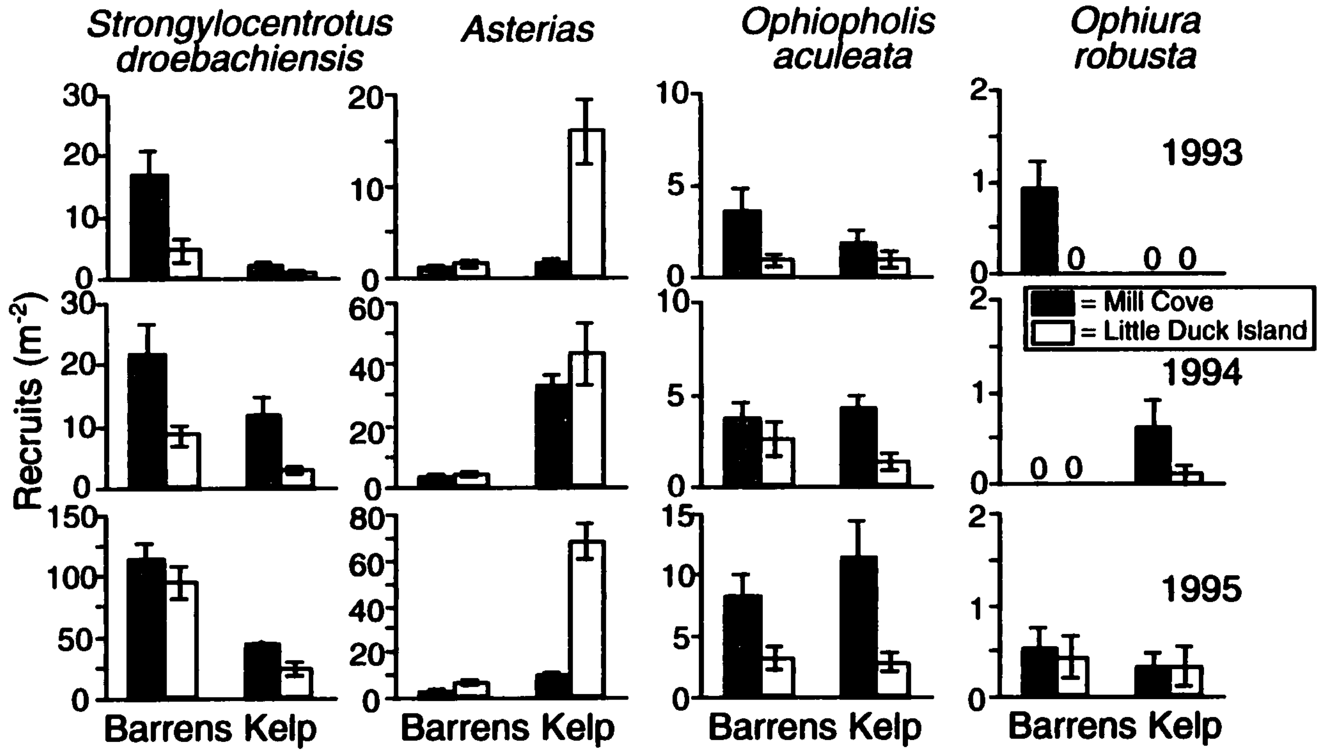

Strongylocentrotus droebachiensis
Asterias
Ophiopholis aculeata
Ophiura robusta
Recruits (m^{-2})
30
20
10
0
150
100
50
60
40
80
15
5
2
1
1993
1994
1995
0 0 0
0 0
= Mill Cove
= Little Duck Island
Barrens Kelp
Barrens Kelp
Barrens Kelp
Barrens Kelp

Figure 4.18

Fig. 4.19. Relationship between mean settlement (1992 to 1994) and mean recruitment in the subsequent year (1993 to 1995) of ***Strongylocentrotus droebachiensis*, *Asterias*,** *Ophiopholis aculeata* and *Ophiura* measured in 2 habitats (kelp bed and barrens) at Mill Cove and Little Duck Island. Means are calculated from settlers sampled in 4 Low collectors during the bi-weekly interval of peak settlement in each year (1992 to 1994) and from recruits collected from 4 to 10 quadrats of 1.0 m^2 between July and October 1993 to 1995. Also shown are regression lines and exponential equations relating recruit density (y) to settler density (x) and the associated r^2 and p value of this relationship.

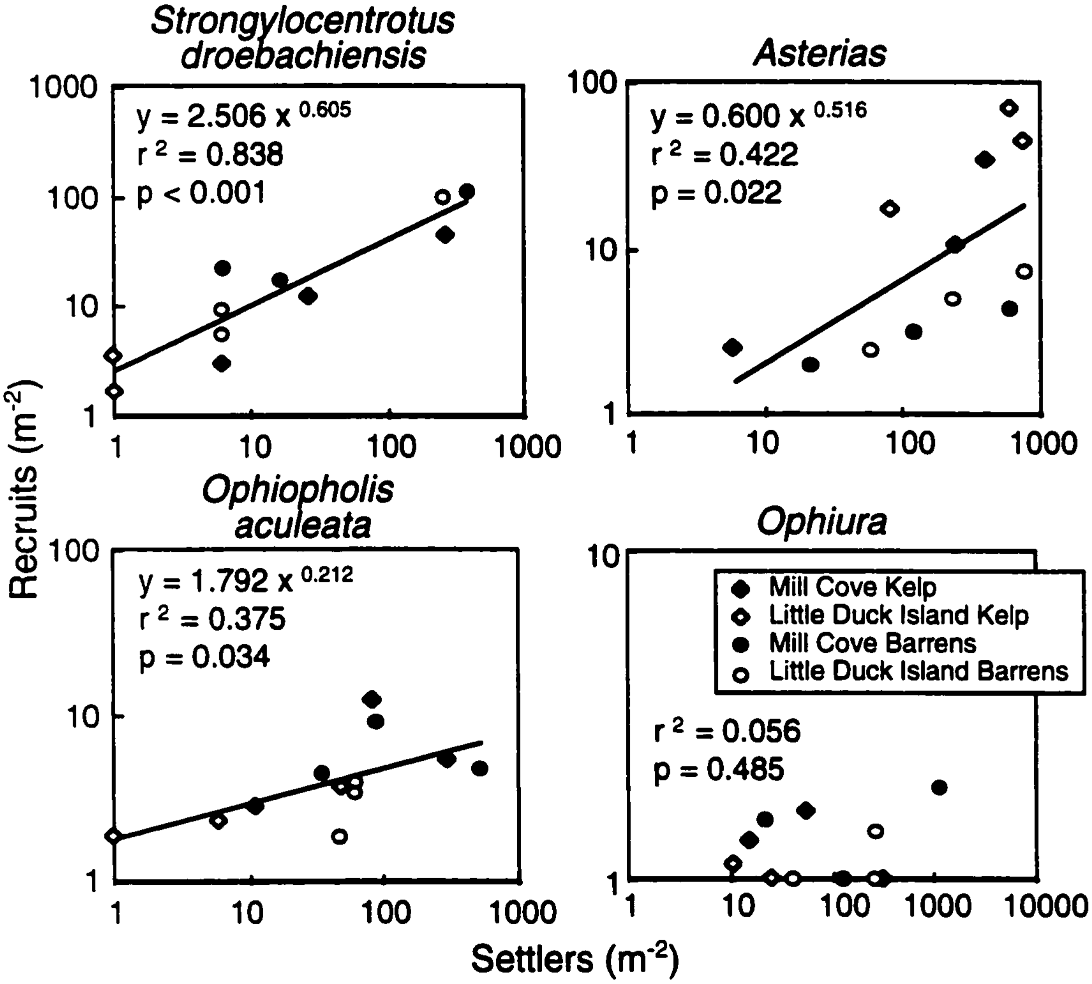

Strongylocentrotus droebachiensis
y = 2.506 x 0.605
r 2 = 0.838
p < 0.001
1000
100
10
1
1
10
100
1000
Asterias
y = 0.600 x 0.516
r 2 = 0.422
p = 0.022
100
10
1
1
10
100
1000
Ophiopholis aculeata
y = 1.792 x 0.212
r 2 = 0.375
p = 0.034
100
10
1
1
10
100
1000
Ophiura
r 2 = 0.056
p = 0.485
10
1
1
10
100
1000
10000
◆ Mill Cove Kelp
◇ Little Duck Island Kelp
● Mill Cove Barrens
○ Little Duck Island Barrens
Recruits (m-2)
Settlers (m-2)

Figure 4.19

DISCUSSION

Temporal patterns of settlement

Timing of settlement of echinoderms in our study differed consistently among species, in relation to differences in timing of spawning and larval development. Almost all settlement of *Strongylocentrotus droebachiensis* occurred in July but low numbers of settlers were found as late as October. *Strongylocentrotus droebachiensis* spawns in March/April at both sites (Meidel & Scheibling 1998) and laboratory-reared larvae settle 4 to 22 weeks post-fertilization at temperatures within the range they experience along the coast of Nova Scotia (Strathmann 1987, Pearce & Scheibling 1990a, Meidel et al. 1999). We recorded settlement of *Echinarachnius parma* in September 1994, but we may have missed the settlement peak for this species because our sampling ended in October/November. Spawning of *E. parma* in the Gulf of Maine begins in August and peaks in November (Cocanour & Allen 1967) and laboratory-reared larvae settle within 5 to 10 weeks (Highsmith & Emlet 1986). Settlement of *Asterias* at our sites was variable among years occurring from late July to early October, which may in part be explained by the occurrence of two species. In New England and Prince Edward Island, *A. vulgaris* spawns from April to July, whereas *A. forbesi* spawns in July/August (Smith 1940, Boolootian 1966, Menge 1986). Thus, the second peak in settlement at Mill Cove in September/October 1994 could be that of *A. forbesi*. Settlement of *A. forbesi* over a 24 to year period in Long Island Sound occurred between June and September each year (Loosanoff et al. 1955, Loosanoff 1964). The ophiuroids, *Ophiopholis aculeata* and *Ophiura*, settled from July to early August each year. Spawning of *Ophiopholis aculeata* occurs in April/May in Norway (Olsen 1943) and laboratory-reared larvae settle within 12 to 31 weeks (Strathmann 1978a). *Ophiura sarsi* spawns from March to June in Washington (Strathmann 1987) but Packer et al. (1994) suggest deep water populations of *O. sarsi* in the Gulf of Maine spawn year round with a peak from January to April. Thus, the summer/fall settlement peak that we observed for each echinoderm species along the

Atlantic coast of Nova Scotia was consistent with their respective annual reproductive cycles and measured larval periods.

The infrequent occurrence of major settlement events observed in our study underscores their potential importance in determining population structure and abundance in this region. For most of the species that we measured, settlement was minimal during 1 or 2 out of the 3 years of our study and, within each year, the majority of settlement occurred over a period of 2 weeks or less. For example, *Strongylocentrotus droebachiensis* settled in abundance only in the first 2 weeks of July in 1994. In contrast, *S. droebachiensis* in the southern Gulf of Maine settle in large numbers each year in June and early July (Harris et al. 1994, 1985, Harris & Chester 1996), and *S. franciscanus* and *S. purpuratus* in California and Oregon settle over a protracted period each year from December to July (Harrold et al. 1991, Ebert et al. 1994, Wing et al. 1995a, Miller & Emlet 1997). Unlike *S. droebachiensis*, *Asterias* settled in high but variable numbers each year of our study, which concurs with the long term observations by Loosanoff (1955, 1964) on *A. forbesi* in Long Island Sound.

Variation in the magnitude of settlement between species and years at our sites suggests that large-scale environmental factors, such as fluctuations in sea temperature or shelf-scale upwelling events do not regulate settlement. Temperature is known to increase the rate of larval development (reviewed by Strathmann 1987) and higher than normal spring temperatures have been suggested to enhance settlement of *Strongylocentrotus droebachiensis* in Nova Scotia (Hart & Scheibling 1988, Scheibling 1996). In our study however, interannual variation in temperature alone can not explain settlement patterns, because species with similar larval development and timing of settlement, settled in greatest abundance in different years. For the same reason, shelf-scale upwelling and relaxation events, which periodically occur along the Atlantic coast of Nova Scotia in the summer (Petrie et al. 1987), are also not likely to regulate settlement as has been suggested for echinoderm larvae in other systems (Johnson et al. 1984, Wing et al. 1995a, b, Miller &

Emlet 1997). Rather, differences between species in interannual settlement patterns may be related to differences in reproductive output and larval survival, which determine larval availability in a given year. Because the same interannual pattern was observed at both sites for each species, larval delivery probably is determined by hydrodynamic forcing at scales of at least 10's of kilometres.

Spatial patterns of settlement

Although we detected few statistically significant differences between sites, settlement of echinoderms, and particularly of ophiuroids, tended to be greater at Mill Cove than Little Duck Island. This may be related to local differences in hydrodynamic conditions resulting in greater larval supply to Mill Cove. The predominant southwesterly flow along the Atlantic coast of Nova Scotia (Han et al. 1997, Loder et al. 1997) suggests that larvae arriving at both sites probably originate from spawning populations to the northeast. Mill Cove is in a large semi-enclosed embayment characterized by a unidirectional counter-clockwise flow that may retain larvae (Heath 1973a, b). In contrast, Little Duck Island is a more exposed site subjected to variable, wave-induced flows that are more likely to disperse than retain larvae supplied to the area. Similarly, Ebert & Russel (1988) suggest that settlement of *Strongylocentrotus purpuratus* in California and Oregon is lower off capes and headlands which experience more upwelling than the more sheltered bays and coves in between.

Although settlement differed between kelp beds and barrens for some species, kelp beds did not exhibit a consistent or strong inhibitory effect on settlement. The ophiuroids, *Ophiopholis aculeata* and *Ophiura*, showed a trend toward greater settlement in the barrens, whereas *Asterias* settled in greater numbers above kelp beds (i.e. on High collectors). Unlike the other species, however, *Asterias* recruits were observed on kelp fronds suggesting that the kelp itself may filter out settlers, reducing the number available to settle within the bed (i.e. on Low collectors). Our limited data on settlement of

Strongylocentrotus droebachiensis indicate higher settlement on average in barrens at Mill Cove in 1994 (the only year of heavy settlement) although the difference was not statistically significant. This may have been due to insufficient power in our test of a habitat effect resulting from low replication. We calculated that 12 replicates would have been required to conclude that the habitat effect we observed in Low collectors (with n=4) was statistically significant (α=0.05) assuming adequate power (1-β=0.80). Previous studies comparing settlement of echinoids between kelp beds/forests and barrens also have yielded equivocal results (reviewed in Chapter 1). Regional differences in kelp morphology and kelp bed/forest structural complexity may account for some of these disparities. For example, kelp beds in Nova Scotia typically extend only 1 to 2 m above the bottom and probably do not deflect currents (and therefore incoming larvae) in the same way as the kelp forests of the northwest Pacific, where the canopy extends to the surface (Jackson & Winant 1983, Dayton & Tegner 1984, Harrold & Pearse 1987).

Although echinoderm larvae generally are found near the surface (0 to 30 m depth) in nearshore waters (Rumrill 1988a, Pedrotti & Fenaux 1992, Miller & Emlet 1997), there is little resolution of larval distribution within the surface layer. In our study, echinoderm larvae generally settled in greater numbers in High than Low collectors. High collectors were intended to measure larval supply independently of habitat effects, including decreased flow in the benthic boundary layer (Eckman et al. 1989). However, the kelp bed at each site is 2 to 3 m shallower than the barrens which may have resulted in High collectors sampling different strata of the water column containing different numbers of larvae. Furthermore, collectors closer to the surface and exposed to more light become more fouled, which may enhance settlement in shallower collectors (see Sampling frequency). Therefore, between-habitat differences in settlement in High collectors (e.g. *Asterias*) may simply reflect depth-related differences in larval abundance or degree of collector fouling. Settlement in Low collectors is less likely to be affected by small differences in bottom depth since these were further from the surface, and in a region where settlement is more likely influenced by bottom features (reviewed by Butman 1987).

Sampling frequency

Comparisons of settlement measured at shorter or longer intervals show that our bi-weekly samples measured settlement with minimal confounding by post-settlement processes or temporal changes in collector efficacy. Because our collectors were isolated from the substratum and excluded many potential predators, early post-settlement mortality or migration probably was minimized. Thus, although most settlement of *Ophiopholis aculeata* and *Ophiura* in 1993 occurred over 6 days within a 2-week period (Chapter 3), there was no difference in settlement measured every 3 days for 15 days compared to a single measure over the whole interval. In contrast, settlement of *Strongylocentrotus droebachiensis* and *O. aculeata* pooled over 3 successive 16 day intervals was significantly less than that measured over the same 48 day interval. This may be because of fouling during long deployment times which enhances the quality of the settlement surface or its ability to passively trap settlers. Greater fouling in High than in Low collectors, and in kelp beds than in barrens may be related to the difference in depth between habitats (see Spatial patterns of settlement) and/or to the greater number of herbivorous amphipods in Low collectors which reduced algal fouling. Artifactual effects of sampling design, such as the presence of migrating or settling grazers or predators in collectors (Harrold et al. 1991) or differential light availability as a function of depth or shading (Eckman & Duggins 1991) may bias results and limit comparability between studies, or locations in the same studies.

Temporal and spatial patterns of recruitment

Interannual patterns of recruitment of echinoderms in our study are similar to patterns of settlement in the previous year, with major recruitment events occurring in only 1 or 2 out of 3 years. Sporadic recruitment has been documented for many species of echinoderms in various geographic regions, and is often attributed to variable settlement (reviewed by Ebert 1983, Chapter 1). Although we recorded recruitment of all species in all years, it is these strong recruitment events which probably have a disproportionate contribution to overall population abundance and demographic structure.

Species-specific differences in recruitment between kelp beds and barrens probably are a result of differences in both settlement and post-settlement mortality between habitats. Recruitment of *Strongylocentrotus droebachiensis* was ~2 times greater in barrens than in kelp beds, although there was no statistically significant difference between habitats in settlement (but see Spatial patterns in settlement). This suggests that juveniles suffered higher mortality in kelp beds. We observed the opposite effect of habitat on *Asterias* for which recruitment was up to an order of magnitude greater in kelp beds than barrens. Settlement of asteroids also tended to be greater in and above kelp beds but differences between habitats were not as great (the ratio of recruits in kelp beds relative to barrens, pooled over sites and years, is 9.4; the ratio for settlers pooled over sites, years and collector heights, is 1.7), suggesting higher post-settlement mortality in the barrens. This also appears to be the case for *O. aculeata* since there was no difference in recruitment of this ophiuroid between habitats but settlement was greater in the barrens. Kelp creates structure that may offer spatial refuges from predation to juveniles of some species, such as *Asterias* which settles on kelp fronds and *O. aculeata* which shelters within the holdfasts. Kelp beds also harbour predators that consume juveniles of these and other species (such as *S. droebachiensis*) which are not found on the fronds or may be less cryptic in the early juvenile stages. Between-habitat differences in post-settlement mortality also may be related to differences in the assemblage of predators, which have different prey preferences or predation rates. Juvenile echinoderms are prey to various invertebrate and fish predators but the role that predation plays in differential post-settlement survival remains unclear (reviewed by Scheibling 1996, Chapter 1).

Greater recruitment of most echinoderm species at Mill Cove than Little Duck Island was consistent with greater settlement at Mill Cove, but this also may be related to differences in availability of suitable refugia, or the types or abundance of predators at the two sites. For example, the boulders at Mill Cove provide undersides and crevices that may shelter juveniles from predation more effectively than the more open substratum at Little Duck Island. In caging experiments in a cobble bed in Nova Scotia, Scheibling & Hamm (1991) recorded a lower rate of predation on juveniles of *S. droebachiensis* which sheltered among cobbles and small boulders compared to those without a spatial refuge.

Does settlement predict recruitment?

Settlement of the dominant species of echinoderms at our sites does predict recruitment, however the strength of the relationship varies, probably because of differing post-settlement processes. *Strongylocentrotus droebachiensis* showed a strong relationship whereby recruitment in all years, sites and habitats was proportionate to settlement measured in the same location one year earlier. This suggests that rates of settlement of this species could be used to predict recruitment of one year-olds, which may be beneficial for management of the local echinoid fishery (Hatcher & Hatcher 1997). Fluctuating patterns of settlement of *Asterias* among sites, habitats and years resulted in a weaker relationship, although recruitment was generally greater in kelp beds. The strength of the relationship between settlement and recruitment for *Ophiopholis aculeata* was similar to that for *Asterias*, but the slope of the regression line was much lower indicating greater post-settlement mortality of these ophiuroids. There was no relationship between settlement and recruitment of *Ophiura*: recruitment was minimal throughout the study, despite at least one year of high settlement, indicating high post-settlement mortality (possibly because of a lack of suitable sedimentary habitat at our rocky sites). The absence of recruits of *Echinarachnius parma* at our sites clearly reflects the unsuitable substratum: a large population of this species occupied a sandy bottom ~100 m from our site at Mill Cove.

Echinarachnius parma has been shown to selectively settle in response to cues from conspecifics (Pearce & Scheibling 1990b), although a few settlers were found in our collectors.

Our study demonstrates the importance of settlement and post-settlement processes in determining the population structure, distribution and abundance of mobile benthic marine invertebrates with dispersing larvae. For most of the echinoderm species we studied, recruitment did reflect settlement patterns, although the importance of post-settlement processes in determining recruitment varied among species, habitats and sites. Heavy settlement events occurred sporadically at our sites and in different years for different species. These events clearly were important determinants of subsequent recruitment, although the causes of such events and mechanisms regulating supply of larvae and survival of juveniles are not well understood. The temporal and spatial variability that we observed within and between species/genera underscores the need to monitor settlement and recruitment at varying scales of space and time to better understand their role in population dynamics.

Chapter 5: General Conclusions

This thesis examined temporal and spatial variability in settlement and recruitment of echinoderms in rocky subtidal habitats. A review of the literature (Chapter 1) revealed that numerous studies have addressed settlement and recruitment patterns of echinoderms, particularly species (mainly echinoids and asteroids) of ecological or economic importance. However, the processes which regulate the transitions from early life stages through to adulthood, and thereby determine the distribution and abundance of echinoderm populations, remain poorly understood. The supply of planktonic larvae of echinoderms to benthic populations is regulated by a complex interaction of biotic and abiotic factors such as hydrodynamics, sea temperature, predation and starvation. Echinoderm larvae have been induced to settle on various substrata in laboratory studies and specific chemical inducers have been isolated in some cases. However the importance of settlement induction and substratum preferences in determining settlement patterns in natural habitats is not clear. A salient feature of most echinoderm populations is a high degree of temporal and spatial variability in settlement and recruitment. Settlement variation exists at spatial scales ranging from metres between adjacent habitats to hundreds of kilometres between regions. Seasonal settlement is common among echinoderm species but interannual variation in settlement and/or recruitment is often high, and several years may elapse between successful recruitment events. Some of this variability is likely attributable to measurement inaccuracies associated with sampling individuals which are small, cryptic and transient, and procedural inconsistencies among different studies. A variety of post-settlement processes including predation, migration, disease and starvation may alter observed patterns of settlement and play an important role in regulating recruitment rates and patterns.

To assess variability in settlement over large and small spatial scales and to compare sampling techniques, settlement of *Strongylocentrotus droebachiensis* was measured on 3 different collector types in 3 regions of the northwest Atlantic (Chapter 2). Different collectors types in the same locations measured different settlement rates suggesting limited comparison of results across studies without first calibrating collectors. However, these differences did not obscure the order of magnitude differences in settlement between regions (100's of kilometres), with highest settlement in the Gulf of Maine, lowest settlement in the Bay of Fundy and intermediate settlement in Nova Scotia. These large-scale patterns are likely due to differences in larval supply caused by large-scale oceanographic features. Within each region (10's of kilometres), settlement differed between sites but was within the same order of magnitude. Within sites, (10's of metres) settlement decreased with depth and was lower in kelp beds than barrens but these differences were not always significant. At the scale of regions, patterns of settlement are clearly related to larval supply but within a region, and between habitats within a site, settlement patterns are less clear and likely controlled by factors such as larval behaviour, predation and small-scale hydrodynamics.

Settlement of ophiuroids (*Ophiopholis aculeata*, *Ophiura*), measured over 3 day intervals during their annual 2 week settlement period at Mill Cove was associated with minor fluctuations in the physical environment (Chapter 3). Hydrographic (temperature, salinity, current velocity, wave height and period) and meteorologic conditions (atmospheric pressure, wind velocity) were recorded concurrently at the site or nearby locations. A major settlement pulse occurred over one 3 day period with declining settlement over the following 6 days. This pulse was associated with a shift in current direction and preceded by rapid temperature and salinity fluctuations. Similar changes in temperature occurred at a second site (4.5 km away) indicating at least bay-scale forcing. This period was characterised by the passage of weak atmospheric pressure gradients and a low-energy sea-state. These meteorologic and oceanographic fluctuations were within the normal range for this time of year, indicating that major settlement events can occur over very short time periods and are not likely regulated by major oceanographic events such as shelf-scale upwelling.

Settlement of various echinoderm species, measured in different habitats (kelp beds, barrens) at different sites (Mill Cove, Little Duck Island) and over periods of days to years, demonstrated the importance of variability at different scales in understanding settlement patterns and inferring processes which shape them (Chapter 4). Settlement pulses of ophiuroids (*Ophiopholis aculeata* and *Ophiura*), asteroids (*Asterias*) and echinoids (*Strongylocentrotus droebachiensis* and *Echinarachnius parma*) occurred between July and September of each year at both sites. Timing of settlement differed consistently among species, in relation to differences in timing of spawning and larval development. The magnitude of each pulse varied between years and species, and the year of maximum settlement differed between species. Variation between species suggests that large-scale environmental factors, such as fluctuations in sea temperature or shelf-scale upwelling events do not regulate settlement. Similar interannual patterns at both sites suggest that larval delivery probably is determined by hydrodynamic forcing at scales of at least 10's of kilometres (see also Chapter 3). However, consistently greater settlement at Mill Cove (a sheltered site within a large bay) may be related to bay-scale circulation which retains larvae, compared to a more variable hydrodynamic regime at Little Duck Island (an exposed site) which is more likely to disperse larvae. Although settlement differed between habitats for some species, kelp beds did not exhibit a consistent or strong inhibitory effect on settlement as suggested by previous studies. Ophiuroids showed a trend toward greater settlement in the barrens, whereas asteroids settled on kelp fronds and in greater numbers in and above kelp beds. The echinoid, *S. droebachiensis*, tended to settle more in barrens, although the difference was not statistically significant.

Settlement sampled at intervals of 3 days to 7 weeks showed that biases in estimates of settlement can occur between habitats and collector heights within a site (Chapter 4). For example, greater settlement in High (2 m off bottom) than Low (0.2 m off bottom) collectors over 7 weeks may result from greater fouling of High collectors because of increased exposure to light and/or decreased exposure to small grazers. However, settlement measured over 5 successive 3 day intervals demonstrated that patterns based on bi-weekly sampling were not obscured by post-settlement mortality or changes in collector quality.

Interannual patterns of recruitment of echinoderms were similar to patterns of settlement in the previous year, with major recruitment events occurring in only 1 or 2 out of 3 years (Chapter 4). These settlement/recruitment events probably have a disproportionate contribution to overall population abundance and demographic structure. Greater recruitment of all echinoderm species at Mill Cove than Little Duck Island was consistent with greater settlement at Mill Cove, but this also may be related to differences in availability of suitable refugia, or the types or abundance of predators at the two sites. Species-specific differences in recruitment between kelp beds and barrens probably are a result of differences in both settlement and post-settlement mortality between habitats. Regression analyses showed that, in most cases, settlement of echinoderms does predict recruitment, however the strength of the relationship varies between species, probably because of differing post-settlement processes.

This thesis has shown that variability in settlement and recruitment of echinoderm species occurs over a range of temporal (days to years) and spatial (metres to 100's of kilometres) scales. To understand how this variability influences population structure and dynamics, future studies must address the biotic and abiotic processes which determine the observed patterns. This will require both detailed monitoring and careful experimentation in differing habitats and over extended periods. In particular, future research should attempt to resolve sources and sinks of larvae, the relative importance of biological and physical processes determining larval supply and settlement, and the factors which regulate early post-settlement mortality.

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