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STRUCTURE AND DYNAMICS OF INTERTIDAL MUSSEL (*Mytilus trossulus, M. edulis*) ASSEMBLAGES

by

Heather L. Hunt

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

at

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ABSTRACT

This thesis examines the biological and physical processes influencing the structure and dynamics of mussel (*Mytilus trossulus, M. edulis*) assemblages in tidepools and on the surrounding emergent rock on a wave-exposed rocky shore near Halifax, Nova Scotia, Canada. Over 17 mo, more than 96% of mussels colonizing the natural substratum were too large to be settling larvae, indicating the importance of post-settlement dispersal of mussels. Patterns of colonization after 5-16 mo reflected patterns measured at sampling intervals of 2-7 d, suggesting that spatial variation in initial colonization is important in determining the abundance and distribution of mussels on this shore. I examined the relative roles of supply of colonists and substratum type in determining colonization patterns of mussels by comparing colonization rates on artificial collectors and natural substrata. Patterns of abundance and size distribution of mussel colonists differed markedly between artificial collectors and natural substrata. Colonization rate on natural substrata was related to a suite of biological (macroalgal and barnacle cover) and physical factors (water flux, tidal height, flushing time). I examined the effects of predation by the whelk *Nucella lapillus* on established mussel assemblages by manipulating the densities of whelk recruits and post-recruits. Reduction of the density of whelk post-recruits influenced the percentage cover and size distribution of mussels and had a greater effect on emergent rock than in tidepools, reflecting differences in density of whelk post-recruits between habitats. I could not detect an effect of whelk recruits on mussel cover or size distribution. I experimentally investigated the influence of rates of recruitment, immigration, predatory and non-predatory mortality, and growth of individuals by transplanting artificially constructed mussel patches to tidepools and emergent rock. In addition, I monitored the movement of tagged mussels and estimated the probabilities of wave dislodgment of mussels from measurements of water velocity and attachment strength of mussels. The structure and dynamics of mussel patches both in tidepools and on emergent rock were influenced by all of these processes. However, these experiments indicated that physical processes (wave dislodgment) were more important than biological processes (predation) in determining the structure and dynamics of mussel assemblages on this shore. The results of this thesis indicate that patterns of distribution and abundance of mussels on this shore develop slowly due to the slow growth rate of individuals. I conclude that dispersal and redistribution of juvenile and adult mussels by wave disturbance are very important in colonization by mussels and in the dynamics of established mussel assemblages.

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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 2 is also presented in:

Hunt, H.L., and R. E. Scheibling. 1997. Role of early post-settlement mortality in the recruitment of benthic marine invertebrates. Marine Ecology Progress Series 155: 269-301.

The research in Chapter 4 is also described in:

Hunt, H.L., and R. E. Scheibling. 1996. Physical and biological factors influencing mussel (*Mytilus trossulus, M. edulis*) settlement on a wave-exposed rocky shore. Marine Ecology Progress Series 142: 135-141.

Written permission was obtained from Inter-Research to include the material in these 2 publications in my thesis.

The research in Chapter 5 is also described in:

Hunt, H.L., and R. E. Scheibling. In press. Effects of whelk (*Nucella lapillus* (L.)) predation on mussel (*Mytilus trossulus* (Gould), *M. edulis* (L.)) assemblages in tidepools and on emergent rock on a wave-exposed rocky shore in Nova Scotia, Canada. Journal of Experimental Marine Biology and Ecology.

CHAPTER 1: General Introduction

Patchiness is a fundamental characteristic of most populations and communities. Many systems can be a viewed as a dynamic mosaic in which individuals are exchanged among patches (Pickett & White 1985). These patches may be small groups of individuals, disturbance-generated gaps in an assemblage, islands, or whole populations (Paine 1994). The dynamics of any system of patches will depend on a number of factors, including the area, shape, and spatial distribution of patches and the rates of patch formation, growth, and extinction (Paine 1994). Investigating patch dynamics has proven to be valuable in our understanding of population and community dynamics. For example, consideration of the effects of the number, size, and isolation of habitat patches on the dynamics of systems of local populations (metapopulations), and on the number of species found in individual patches or islands, has led to the theories of metapopulation dynamics and island biogeography (Hanski & Gilpin 1991). Assemblages of marine mussels present a good model system to investigate patch dynamics because they are relatively simple. Mussel assemblages are two-dimensional and effectively monocultures, although other species occur within the interstices of mussel beds (Seed & Suchanek 1992). Investigating the dynamics of mussel assemblages is also valuable in the context of understanding community organization on rocky shores. Mussels are often the dominant space occupiers on these shores (Menge & Farrell 1989), and their interactions with other species are known to affect overall community structure and dynamics (e.g., Paine 1966, 1974, Menge 1976, Lubchenco & Menge 1978, Robles 1987).

Because mussels can disperse in the water column both during the planktonic larval phase and after settlement (Seed & Suchanek 1992), the formation of a mussel aggregation begins with colonization by settling larvae and/or larger, postlarval individuals. The waterborne dispersal of young postlarval mussels (up to 2 mm shell length) is aided by long, mucous threads which increase hydrodynamic drag (Sigurdsson et al. 1976, De Blok & Tan-Maas 1977, Lane et al. 1985). Because mussels are often associated with macroalgae and other rough or filamentous substrata (Seed & Suchanek 1992), the patterns and rates of colonization by mussels are likely to depend on the type of substratum as well as on the supply of larval settlers and larger colonists. Once a mussel aggregation is established, its structure and dynamics will depend on the balance between processes which remove individuals and those which add individuals and increase their size (Petraitis 1995). On wave-exposed shores, for example, dislodgment by waves results in losses of mussels in intertidal and subtidal habitats (e.g. Paine & Levin 1981, Witman 1987). Another important cause of loss is predation by macroinvertebrates such as sea stars, crabs, lobsters, and whelks, which determines the spatial distribution and abundance of mussels on many shores (e.g. Paine 1966, 1974, Menge 1976, Robles 1987). Growth of individuals within an aggregation, which is highly variable and dependent on environmental conditions (Seed & Richardson 1990), can be important in offsetting losses of mussels from wave disturbance or predation (Reusch & Chapman 1997). Spatial and temporal variability in recruitment of new individuals also may offset predation and other losses, and influence the abundance and size structure of mussel assemblages (Robles 1997). Because mussels are not permanently attached to the substratum, redeposition of mussels by waves and active dispersal by crawling also may change aggregation size.

In this thesis, I examine mussel assemblages (*Mytilus trossulus* and *M. edulis*) in tidepools and on the surrounding emergent rock in the mid intertidal zone on a rocky shore on the Atlantic coast of Nova Scotia, Canada. The abundance and spatial distribution of mussels differ between these two habitats: mussels in tidepools generally occur in centimeter-scale patches (Hunt & Scheibling 1995), whereas those on emergent rock tend to form more extensive beds with centimeter-scale gaps (Minchinton et al. 1997). Differences in the pattern of distribution and abundance of mussels between tidepools and emergent rock may result from environmental differences between the two habitats. Because environmental fluctuations are less severe in tidepools than on emergent rock, tidepools are potentially important refuges from stressful conditions, particularly during low tide (Metaxas & Scheibling 1993). Between-habitat differences in environmental stress are predicted to influence the relative importance of biotic and abiotic factors in structuring communities and the intensity and outcome of biological interactions (Connell 1975, Menge and Sutherland 1976, 1987). However, there are few experimental studies of processes influencing species assemblages in tidepools for comparison to the wealth of studies on emergent rock (reviewed by Metaxas & Scheibling 1993). My thesis addresses the following specific questions:

1) What are the biological and physical processes influencing patterns of colonization by mussels in tidepools and on emergent rock?

2) What is the relative importance of initial patterns of colonization compared to post-colonization processes in determining patterns of distribution and abundance of musels?

3) What are the important causes of changes in cover of established mussel assemblages in tidepools and on emergent rock?

4) What is the relative importance of these processes in determining the structure and dynamics of mussel assemblages?

I begin by reviewing the literature on the role of early post-settlement mortality in the recruitment of benthic marine invertebrates (Chapter 2). In this review, I discuss the influence of patterns of settlement and early post-settlement mortality on patterns of abundance and distribution of recruits, a major focus of my thesis. In Chapter 3, I examine patterns and rates of colonization by mussel settlers and larger, postlarval mussels in tidepools and emergent rock and on ice-scoured and non-scoured areas of the shore. I examine the relative importance of initial colonization compared to post-colonization dispersal and mortality in determining the distribution and abundance of mussels by comparing patterns and rates of mussel colonization at sampling intervals of days to months over a 17 mo period. In Chapter 4, I examine the relative roles of supply of colonists and substratum type in determining patterns of colonization of mussels by comparing patterns of colonization on artificial and natural substrata. In Chapter 5, I examine the effects of predation by whelks on the cover and size distribution of established mussel aggregations in tidepools and on emergent rock. In Chapter 6, I examine the relative influence of growth, recruitment, immigration, predation, wave dislodgment, and movement on the structure and dynamics of mussel assemblages by transplanting artificially constructed mussel patches to both habitats. In the final chapter (Chapter 7), I discuss the contributions of these studies to our understanding of the dynamics of mussel assemblages in the rocky intertidal zone.

CHAPTER 2: Role of early post-settlement mortality in recruitment of benthic marine invertebrates

INTRODUCTION

Over the last 15 years, our understanding of recruitment variability of benthic marine invertebrates, and its role in population and community dynamics has increased considerably. Variation in recruitment rate has been shown to affect competitive interactions (Sutherland & Ortega 1986), predation (Fairweather 1988, Menge et al. 1994, Robles et al. 1995) and other community level processes on rocky shores (for review see Booth & Brosnan 1995), and there is increasing evidence that adult population size is limited by recruitment for species on hard substrata in both intertidal (e.g. Connell 1985, Sutherland 1987, 1990, Menge & Farrell 1989, Raimondi 1990, Menge 1991a) and subtidal habitats (e.g. Hughes 1990, Karlson & Levitan 1990). Consequently, recent models of population dynamics (Roughgarden et al. 1985, Roughgarden & Iwasa 1986, Alexander & Roughgarden 1996) and community organization on rocky bottoms (Menge & Sutherland 1987) incorporate recruitment variability as a limiting factor. Recruitment limitation has received less attention from researchers studying soft bottom communities (but see Peterson & Summerson 1992, Peterson et al. 1996, Butler & Herrnkind 1997). A recent review by Ólafsson et al. (1994) concluded that larval supply is generally not limiting, and therefore is probably not a major determinant of patterns of species distribution and abundance in sedimentary habitats. However, interactions between adults and settlers/recruits have been shown to affect recruitment rate (Peterson 1982, Peterson & Black 1993, Ólafsson et al. 1994, Thrush et al. 1996) and may limit the density of infauna (Thorson 1966, Woodin 1976, Peterson 1979).

Many factors can influence the intensity and variability of recruitment of benthic marine invertebrates. The abundance of larvae in the water column is influenced by adult reproductive cycles, larval mortality (Roughgarden et al. 1988), and settlement rate itself

(Gaines et al. 1985). Physical factors which affect dispersal of larvae include wind (Morgan et al. 1996, Bertness et al. 1996), linear oceanographic features (for review see Kingsford 1990), upwelling (Roughgarden et al. 1991, Farrell et al. 1991, Wing et al. 1995), cold water plumes (Ebert & Russell 1988), water residence time in estuaries (Gaines & Bertness 1992), and vertical distribution of larvae in the water column (Grosberg 1982, Le Fèvre & Bourget 1991, Miron et al. 1995). Settlement onto the substratum occurs once the larvae reach a suitable habitat. Settlement is a process that may include reversible or irreversible contact with the substratum, exploratory behaviour, orientation, and metamorphosis (which may occur before, during, or after contact with the substratum) (Pawlik 1992). At this time, the pattern of larval supply may be modified by larval response to various abiotic and biotic cues on the substratum including surface texture or chemistry, conspecifics, and the presence or absence of other macrobenthic species or microbial films (reviewed by Pawlik 1992). Hydrodynamic conditions may determine the scale at which active selection of a substratum occurs (Butman 1987).

In this review, I will focus on the period between settlement and recruitment. Monitoring newly settled individuals is difficult due to their small size and because sampling must be frequent enough to avoid confounding patterns of settlement with patterns modified by early post-settlement mortality. For convenience, most researchers measure recruitment days to months after settlement (e.g. Shanks & Wright 1987, Ebert & Russell 1988, Gaines & Bertness 1992, Ebert et al. 1994, Wing et al. 1995). Knowledge of early post-settlement events is critical in determining if and when recruitment patterns reflect settlement patterns. In situations where early post-settlement events substantially alter the abundance of recruits, they may regulate population size and adult distribution, and reduce the importance of interactions between adults. Gosselin and Qian (1997) recently reviewed 30 studies of rates of mortality of juvenile benthic invertebrates. They discussed causes of early post-settlement mortality, methods of quantifying mortality rates, and the influence of juvenile mortality on age at maturity. In my review, I strive for a more comprehensive examination of the major functional groups of benthic marine invertebrates, including sessile species on hard substrates, mobile epifauna, and infauna in sedimentary habitats. I begin by discussing problems with the definition of recruitment and the early post-settlement period. I then review the rates and patterns of early post-settlement mortality reported in the literature and discuss factors which affect the survival of newly settled and early juvenile individuals. Finally, I address the influence of mortality of recent settlers on patterns of abundance and distribution of recruits.

THE EARLY POST-SETTLEMENT PERIOD

Recruitment is an operational term rather than a biological event, and consequently, has been defined in many different ways. Definitions of recruitment of benthic marine invertebrates include (Booth & Brosnan 1995): 1) presence of juveniles after a specified time interval, 2) attainment of a specified size, 3) survival through a period of high early mortality, 4) survival to a size when the settlers become vulnerable to predators, and 5) retention on a particular sieve mesh size (in soft bottom studies, Butman 1987). Differences in the time interval to recruitment are inevitable due to differences in the life histories and lifespans of organisms. For example, it might not be reasonable to consider a barnacle which reaches maturity in 6 weeks and a slow growing coral which may live more than 20 years to be recruits after the same time interval. Also, the time interval before a settler can be censused by an observer (recruitment *sensu* Keough & Downes 1982) will differ among species because of variability in initial size and growth rate (Rumrill 1989) and also because of differences in our ability to sample different habitats.

Booth and Brosnan (1995) have suggested that survival through high (usually Type III, *sensu* Deevey 1947) mortality in the first few days to weeks after settlement may be a biologically meaningful definition of recruitment. This suggestion is reasonable, considering that early mortality often follows this pattern (see Table 2.1 and the following section). However, survival curves of early juveniles of some species exhibit other patterns, and this type of information is not available for many species. A combination of criteria may be necessary to define the early post-settlement stage for a particular species. For mobile epibenthic species, differences in behaviour and habitat between early juveniles and older juveniles and adults may help define the time at which recruitment occurs. Because recruitment is not a distinct biological event like settlement, definitions will continue to differ from species to species. However, efforts should be made to harmonize definitions of recruitment (or to redefine the term, see Conclusions and directions for future research) and to use biologically meaningful criteria when defining the early post-settlement period.

Comparisons of studies are complicated by differences in sampling interval. Variation in sampling interval has been shown to affect estimates of recruitment and (or) early post-settlement mortality of oysters (Michener & Kenny 1991) and barnacles (Minchinton & Scheibling 1993b, Gosselin & Qian 1996). Minchinton and Scheibling (1993b) found that estimates of recruitment and early post-settlement mortality of the barnacle *Semibalanus balanoides* decreased significantly when the sampling interval was changed from 1.3 days to 2.1 days, and continued to decrease exponentially with increasing sampling interval. Sampling interval also altered comparisons of early post-settlement mortality rate between intertidal zones. These results suggest that comparisons of studies with different sampling regimes should be made cautiously.

RATES AND PATTERNS OF EARLY MORTALITY

In the field, monitoring mortality immediately after settlement is difficult, if not impossible, for many species. However, without knowledge of events shortly after settlement, post-settlement mortality can be underestimated and settlement patterns can be confounded by patterns produced by or modified by mortality. Mortality rate in the field

Table 2.1. Summary of studies examining patterns of survival of recently settled benthic marine invertebrates. Location indicates if the settlers were monitored in their original location or if they were transplanted (trans) (nat=settled in field, lab=settled in laboratory); na: not applicable.

	Location	Sampling Interval	Sampling Period	Survival rate (%)	Survival Rate (% wk^{-1})	Survival Curve Type	Sources of Variability in Survival Rate	Reference
a) Sessile species								
Cirripedia								
Chthamalus fissus	Original	1 mo	18 mo	0-20	89-93 (1st 2 mo)	II, III	Cohort, site	Sutherland 1990
Chthamalus anisopoma	Original	3-7 d	60 d	65-80	91-92	II	Cohort	Raimondi 1990
	Trans (nat)	1 wk	90 d	0-90	92-99	III, II, I	Tidal height	Raimondi 1991
	Trans (nat)	5-15 d	40 d	10-90	84-98	III, II	Rock type, tidal height	Raimondi 1988b
Balanus eburneus	Trans (nat)	2-3 d	12 d	65-95	80-97	II, I	Site	Bingham 1992
Semibalanus balanoides	Original	1 d	2 mo	6-70	90-97	III	Cohort	Connell 1961
	Original	1 d	6 wk	5-90	85-98	mostly III	Cohort	Wethey 1986
Balanus amphitrite	Original	1 d	1-2wk	0-90	50-95	III, II, I	Cohort, panel, substrate	De Wolf 1973
Balanus crenatus	Original	1 d	2 wk	0-100	50-100	III, II, I	Cohort	De Wolf 1973
Balanus glandula	Original	1 d	42 d	22	87	III	Tidal height, exposure, cohort	Gosselin & Qian 1996
Ascidiacea								
Ascidia nigra	Original, trans (lab)	1d-1wk	45 d	2 to 18	85-87	III, II, I	Date, depth	Goodbody 1963
Diplosoma similis	Original	1 d	28 d	0	10 (1st wk)	III	Settlers in crevices (10%) not monitored	Stoner 1990
Podoclavella cylindrica	Original	1 d	30 d	11-78	79-95	III, II	Substratum	Davis 1987

Table 2.1 continued

	Location	Sampling Interval	Sampling Period	Survival rate (%)	Survival Rate (% wk^{-1})	Survival Curve Type	Sources of Variability in Survival Rate	Reference
Ascidiacea								
Didemnum candidum	Original	3 d		20-40	69-77	III	Depth, transplants between depths	Hurlbut 1991c
Diplosoma sp.	Original	3 d		10-25	65-70	III		
Phallusia nigra	Original	1 d	14 d	~15	57	I	na	Hurlbut 1991a
Didemnum candidum	Original	1 d	14 d	~60	80	I	na	Hurlbut 1991a
Diplosoma listerium	Original	1 d	14 d	~65	82	I	na	Hurlbut 1991a
Diplosoma sp.	Original	1 d	14 d	~40	70	I	na	Hurlbut 1991a
Botryllus schlosseri	Original, trans (nat)	3-10 d	22 d	0-100	68-100	III, II	Site, density	Osman et al. 1992
Botrylloides sp.	Original	2-30 d	45-57 d	5-10	85-90	III	Year, includes substrate loss	Worcester 1994
Bryozoa								
Alcyonidium hirsutum	Original	2-4 wk	1 yr	0-1	94-99 (1st 3 mo)	III	Year	Seed & Wood 1994
Octocorallia								
Alcyonium siderium	Original, trans (nat)	1 wk- 1 mo	1 yr	5-25	89-94 (1st 2 mo)	III	Year, distance from adult	Sebens 1983
Gastropoda								
Serpulorbis squamigerus	Original	6-10 wk	400 d	20-90	95-99 (1st 3 mo)	III, II	Site	Osman 1987
Bivalvia								
Crassostrea virginica	Trans (lab)	1 wk	30 d	<15	<80	III	Season	Roegner & Mann 1995

Table 2.1 continued

	Location	Sampling Interval	Sampling Period	Survival rate (%)	Survival Rate (% wk^{-1})	Survival Curve Type	Sources of Variability in Survival Rate	Reference
b) Mobile species								
Gastropoda								
Lacuna vincta	Original	1 mo	8 mo	4-5	97-98	III	Site, year	Fretter & Manly 1977
Haliotis rubra	Original	4-5 mo	4-5 mo	<5	<95	na	Site	McShane 1991
Aplysia juliana	Original	1 wk	30 d	0	77	III	na	Sarver 1979
Bivalvia								
Cerastoderma edule	Original	14 d-1 mo	1 yr	1-10	80-85 (1st mo)	III	Year	Guillou & Tartu 1994
Tapes japonica	Original	1-2 mo	9 mo	1	95-96 (1st 4 mo)	III	Adult clam density	Williams 1980a
Polychaeta								
Capitella sp. I	Trans (lab)	3-4 wk	60-90 d	25-50	91-96	III	Sibling group	Qian & Chia 1994
Decapoda								
Penaeus merguiensis	Original	2 wk	3 mo	<5	<93	III	Cohort-study lasted 3 yr	Haywood & Staples 1993
Echinoidea								
Strongylocentrotus purpuratus	Original	10-15 d	45 d	5-15	85-87	II/III	Habitat	Rowley 1990

during the first few hours or days after settlement is known for only 2 groups of benthic marine invertebrates: barnacles and ascidians. Survival rates of barnacle cyprids during the first 24-48 h range from 22-87% (*Balanus glandula*, Gosselin & Qian 1996; *Semibalanus balanoides*, Connell 1961, Bergeron & Bourget 1986, Kendall et al. 1985; *Chthamalus fragilis*, Young 1991) and mortality risk does not necessarily decline after metamorphosis (*S. balanoides*, Wethey 1986). In studies of colonial ascidians, 50 to >70 % of settlers survive the first 24 h (*Diplosoma similis*, Stoner 1990; *Podoclavella moluccensis*, Davis 1987). Mobile species probably also experience elevated mortality immediately after settlement, but survival rates have not been measured. Indirect evidence of high early mortality is provided by Eggleston and Armstrong's (1995) study of Dungeness crabs (*Cancer magister*): settlement patterns and density of first benthic instar crabs were decoupled in less than 48 h. The first day after settlement may be a critical period for many benthic invertebrates. Gosselin and Qian (1996) found that mortality of the barnacle *Balanus glandula* was 1.5 to 6 times higher during the first day after settlement than during the second day. Indeed, for 2 of the 3 cohorts monitored, mortality during the first day after settlement was almost as high as total mortality during the subsequent 44 days.

Mortality in the days to weeks after settlement is generally high (Table 2.1; Gosselin & Qian 1997). In 2 studies of tropical colonial ascidians (*Trididemnum solidum*, van Duyl et al. 1981; *Diplosoma similis*, Stoner 1990), all visible settlers disappeared during the 1-4 mo. monitoring period. However, neither study was able to follow the fate of individuals which settled in crevices or other protected microhabitats. Small individuals of some species have high survival rates. For example, 63% of settlers of the colonial ascidian *Podoclavella moluccensis* survived one month (Davis 1988a), and 65 to 80% of settlers of the barnacle *Chthamalus anisopoma* survived to reach maturity at six weeks of age (Raimondi 1990).

Survival curves of new settlers (Table 2.1) are often Type III: survival rate decreases rapidly and then levels off (Deevey 1947). Gosselin and Qian (1997) pooled data from 30 studies of juvenile benthic invertebrates to produce a general survivorship curve and found an interspecific trend of exponentially decreasing survivorship during the first days to weeks after settlement. Decreases in mortality rate of early juveniles with time also have been noted in studies which do not present survival curves (Keough 1986, Keough & Chernoff 1987, Günther 1992). A Type III pattern of mortality can even occur in the benign conditions of the laboratory (e.g. Roegner 1991). However, newly settled invertebrates also exhibit other patterns of survivorship. Hurlbut (1991a) found that mortality rate of a number of sessile species on subtidal panels was higher in the second week after settlement than in the first week, and suggested that the increase in mortality was due to density dependent predation. Early mortality may also follow a type II survivorship curve in which mortality is independent of age (Table 2.1). In some cases, however, the reported survival curve may represent only a portion of the overall curve. High mortality may have occurred in the first hours to days after settlement before survival was monitored, or mortality rate may level off over a longer time interval than the period of study. However, Gaines and Roughgarden (1985) found that weekly survivorship of the barnacle *Balanus glandula* was independent of age for the entire first year of life, and that survival rate of settlers monitored from the first low tide after settlement did not differ from that of older barnacles.

VARIABILITY IN EARLY POST-SETTLEMENT MORTALITY

Studies examining variability in early post-settlement mortality have found variation at several spatial and temporal scales. Spatial variability in mortality of barnacle settlers has been detected at scales of metres to kilometres (Meadows 1969, De Wolf 1973, Caffey 1982, 1985, Wethey 1986, Bingham 1992). However, in some of these studies, estimates of post-settlement mortality were based on counts of 1-2 month old juveniles (Meadows 1969, Caffey 1982, 1985), and consequently excluded mortality occurring shortly after settlement. Spatial variability in early post-settlement mortality at scales of kilometres also has been reported for the sea hare *Aplysia juliana* (Sarver 1979). In contrast, Keesing et al. (1996) found that early post-settlement mortality of the sea star *Acanthaster planci* did not vary significantly among habitats (front reef slope, reef flat, back reef lagoon) or sites within habitats.

A number of studies which have monitored barnacle cohorts have detected differences in mortality rate between cohorts settling within 1 or 2 days of one another (Connell 1961, De Wolf 1973, Wethey 1986, Kendall & Bedford 1987, Raimondi 1990, Sutherland 1990). Wethey (1986) suggested that temporal dispersion of settlement (i.e. an extended settlement season) is advantageous when there is no temporal trend in mortality, as was the case in his study of *Semibalanus balanoides*. In contrast, Raimondi (1990) and Connell (1961) found that earlier cohorts of barnacles (*Chthamalus anisopoma* and *Semibalanus balanoides* respectively) had higher survivorship. They suggested that early settlers fill up the most suitable settlement sites (pits or other concavities), leaving later settlers vulnerable to high temperatures and desiccation or gales. On a rocky shore in England, Bowman (1986) found that limpets (*Patella vulgata*) which settled earlier in the fall had a lower mortality rate than those which settled later. She hypothesized that limpets suffer high mortality if they are not large enough to emigrate from their settlement microhabitat before winter. Variation in mortality among cohorts (determined from size frequency analysis) also has been detected for 2 species of prawns in Australia, *Penaeus merguiensis* (Haywood & Staples 1993) and *P. esculentus* (O'Brien 1994a). For both species, cohorts which entered estuaries in summer (the wet season) suffered higher mortality than prawns settling in other seasons.

Intensity and variability of early post-settlement mortality can differ among species which are monitored simultaneously. Bingham (1992) transplanted recruits of mangrove epifaunal species to different channels in a mangrove island and found that mortality of barnacle *Balanus eburneus* recruits was greater and more variable than that of ascidians (*Symplegma viride*, *Diplosoma* [illegible], and *Botryllus planus*) or polychaetes (*Hydroides* sp.). Keesing et al. (1996) transplanted 1 month old sea stars from the laboratory to the field and found that the mortality rate of *Acanthaster planci* was 5 times higher than that of the larger *Nardoa novaecaledoniae*. Hurlbut (1991a) found that the intensity, age dependence, and density dependence of early post-settlement mortality differed among species in a sessile community on subtidal panels. Such variability in early mortality among species suggests that recruitment patterns measured for one species will not predict patterns for other members of the community, an assumption of some models which strive to predict the effect of recruitment strength on community organization (e.g. Menge & Sutherland 1987).

CAUSES OF EARLY POST-SETTLEMENT MORTALITY

Delay of Metamorphosis

For many invertebrate species, delay of metamorphosis eventually results in a decrease in larval condition, substratum selectivity, or ability to metamorphose (for review see Pechenik 1990). Extended larval life also has the potential to affect juvenile survival and condition in some species (Table 2.2). In the laboratory, delayed metamorphosis reduced survival of juveniles of the polychaete *Capitella* sp. I. (Pechenik & Cerulli 1991) and appeared to reduce stress tolerance of the sand dollars *Dendraster excentricus* and *Echinarachinus parma* (Highsmith & Emlet 1986). Prolonged larval life decreased survival of juveniles of the nudibranch *Phestilla sibogae* that were raised as lecithotrophic larvae but not of those raised as facultatively planktotrophic larvae (Miller 1993). Unlike planktotrophic larvae, lecithotrophic larvae experience depletion of stored nutrients during delay of metamorphosis, resulting in decreased size at metamorphosis (Miller 1993). An extended competency period had little effect on survival of juveniles of the barnacle *Balanus amphitrite* (Pechenik et al. 1993) and no effect on survivorship of

Table 2.2 Summary of studies examining sources of non-predatory early post-settlement mortality in benthic marine invertebrates. (Recr) indicates that recruitment rather than mortality was measured in determining effect on survival; obs: observations.

Factor	Species	Methods	Effect	Reference
Delayed metamorphosis				
	Echinoidea			
	Dendraster excentricus	Lab expt	Yes	Highsmith & Emlet 1986
	Echinarachinus parma	Lab expt	Yes	Highsmith & Emlet 1986
	Gastropoda			
	Crepidula fornicata	Lab expt	No	Pechenik & Eyster 1989
	Phestilla sibogae	Lab expt	Dependent on larval life history	Miller 1993
	Polychaeta			
	Capitella sp. I	Lab expt	Yes	Pechenik & Cerulli 1991
	Barnacle			
	Balanus amphitrite	Lab expt	Mixed	Pechenik et al. 1993
Biological Disturbance				
Grazers				
Gastropods				
	Cirripedia			
	Tesseropora rosea	Field expt	Yes	Denley & Underwood 1979
	Semibalanus balanoides	Lab expt	Yes	Miller & Carefoot 1989
		Field expt (recr)	Yes	Hawkins 1983
		Field expt (recr)	Yes	Connell 1961
		Field expt (recr)	Yes	Menge 1976
		Field obs	Yes	Hatton 1938
		Field expt(recr)	Yes	Petraitis 1983
	Balanus amphitrite	Field expt	Yes	Safriel et al. 1994
	Chthamalus fissus	Field obs	No	Sutherland & Ortega 1986
	Balanus glandula	Field obs	Yes	Stimson 1970
		Field expt (recr)	Yes	Dayton 1971
	not identified to sp.	Field expt (recr)	Yes	Turner & Todd 1991

Table 2.2 continued

Factor	Species	Methods	Effect	Reference
Biological Disturbance				
Grazers				
Gastropods				
	Gastropoda			
	Patella latistrigata	Field expt	Density dependent	Creese 1982
	Ascidiacea			
	Corella inflata	Lab expt	Yes	Young & Chia 1984
	Boltenia villosa	Lab expt		Young & Chia 1984
	Styela gibbsii	Lab expt		Young & Chia 1984
	not identified to sp.	Field expt(recr)		Turner & Todd 1991
	Bryozoa			
	ctenostome	Field expt(recr)	Yes	Turner & Todd 1991
	cheilostome	Field expt(recr)	Yes	Turner & Todd 1991
	Hydroida	Field expt(recr)	Yes	Turner & Todd 1991
	Polychaeta	Field expt(recr)	Yes	Turner & Todd 1991
Urchins	Anthozoa			
	Favia fragum	Field expt	Yes	Sammarco 1980
	Agaricia spp.	Field expt	Yes	Sammarco 1980
	Porites spp.	Field expt	Yes	Sammarco 1980
	Echinoidea			
	Echinometra mathaei	Field expt (recr)	No	Prince 1995
	Gastropoda			
	Turbo intercostalis	Field expt (recr)	No	Prince 1995
	Cypraeea caputserpentis	Field expt (recr)	No	Prince 1995
	Thais orbita	Field expt (recr)	No	Prince 1995
	Siphonaria zelandica	Field expt (recr)	Yes	Prince 1995
Crab				
	Ascidiacea			
	Podoclavella moluccensis	Field expt	Yes	Davis 1988b
Algae				
	Cirripedia			
	Semibalanus balanoides	Field expt	Yes	Grant 1977

Table 2.2 continued

Factor	Species	Methods	Effect	Reference
Biological Disturbance				
Adult infauna				
Macrofauna				
	Polychaeta			
	Streblospio benedicti	Field expt	No	McCann & Levin 1989
	Rhynchospio arenicola	Field and lab expts	Yes	Brenchley 1981
	Crustacea			
	Leptochelia dubia	Lab expt	Yes	Brenchley 1981
	Bivalvia			
	Sanguinolaria nuttallii	Field expt	Yes	Peterson 1977
	Mercenaria mercenaria	Lab expt	Dependent on sediment type	Ahn et al. 1993
	Macoma liliana	Lab expt	Yes	Cummings et al. 1996
Meiofauna				
	Bivalvia			
	mostly *Veneridae*	Field expt	Yes	Watzin 1986
	Mercenaria mercenaria	Lab expt	No	Zobrist & Coull 1994
	Polychaeta			
	Streblospio benedicti	Lab expt	No	Zobrist & Coull 1994
Physical Disturbance				
Storms				
	Cirripedia			
	Semibalanus balanoides	Field obs	Yes	Connell 1961
Hydrodynamics				
	Bivalvia			
	Argopecten irradians	Field expt	Yes	Eckman 1987
	Anomia simplex	Field expt	No	Eckman 1987

Table 2.2 continued

Factor	Species	Methods	Effect	Reference
Physiological Stress				
Aerial Exposure	Neogastropoda			
	Nucella emarginata	Field and lab expts	Yes	Gosselin & Chia 1995 a,b
	Archeogastropoda			
	Patella granularis	Lab expt	Yes	Branch 1975
	P. oculus	Lab expt	Yes	Branch 1975
	P. granatina	Lab expt	Yes	Branch 1975
	P. longicosta	Lab expt	Yes	Branch 1975
	P. cochlear	Lab expt	Yes	Branch 1975
	P. argenvillei	Lab expt	Yes	Branch 1975
	P. barbara	Lab expt	Yes	Branch 1975
	Cirripedia			
	Chthamalus anisopoma	Field expt	Yes	Dungan 1985
Tidal Height				
	Cirripedia			
	Tesseropora rosea	Field expt	Yes	Denley & Underwood 1979
	Tetraclitella purpurascens	Field expt	Yes	Denley & Underwood 1979
	Semibalanus balanoides	Field expt/obs	Yes	Foster 1971
		Field expt	Yes	Hatton 1938
		Field obs	Yes	Minchinton & Scheibling 1991
		Field expt	Yes-effect of algae	Minchinton & Scheibling 1993a
	Balanus cariosus	Field expt/obs	Yes	Strathmann & Branscombe 1979
	Chthamalus anisopoma	Field expt	Yes-effect of rock type	Raimondi 1988a,b, 1990, 1991
	Chthamalus montagui	Field obs	No	Kendall & Bedford 1987
	Pollicipes polymerus	Field obs	Yes	Hoffman 1989
	Bivalvia			
	Mytilus viridis	Field expt	Yes	Tan 1975
	Crassostrea virginica	Field expt	Yes	Roegner & Mann 1995

Table 2.2 continued

Factor	Species	Methods	Effect	Reference
Warm Weather				
	Cirripedia			
	Semibalanus balanoides	Field obs	Yes	Connell 1961
		Field obs	Yes	Foster 1971
	Bivalvia			
	Crassostrea virginica	Field expt	Yes	Roegner & Mann 1995
Light				
	Ascidiacea (colonial)			
	Diplosoma listeranium	Field expt	No	Hurlbut 1993
	Diplosoma sp.	Field expt	No	Hurlbut 1993
	D. candidum	Field expt	Yes	Hurlbut 1993
	Didemnum molle	Field expt	Yes	Olson 1983
Hypoxia/Anoxia				
	Bivalvia			
	Crassostrea virginica	Lab expt	Yes	Baker & Mann 1992
Siltation				
	Ascidiacea			
	Corella inflata	Field expt	Yes	Young & Chia 1984
	Ascidia callosa	Field expt	Yes	Young & Chia 1984
	A. paratropa	Field expt	Yes	Young & Chia 1984
	Pyura haustor	Field expt	Yes	Young & Chia 1984
	Boltenia villosa	Field expt	Yes	Young & Chia 1984
	Styela gibbsii	Field expt	Yes	Young & Chia 1984
	Diplosoma listeranium	Field expt	Yes	Hurlbut 1993
	Diplosoma sp.	Field expt	Yes	Hurlbut 1993

Table 2.2 continued

Factor	Species	Methods	Effect	Reference
Salinity and Temperature	Decapoda			
	Menippe adina	Lab expt	Yes	Brown & Bert 1993
	M. mercenaria	Lab expt	Yes	Brown & Bert 1993
		Lab expt	Yes	Brown et al. 1992
	Penaeus esculentus	Lab expt	Yes	O'Brien 1994a
		Field obs	No (temperature)	O'Brien 1994b
	Penaeus merguensis	Lab expt	Yes	Staples & Heales 1991
		Field obs	Yes (temperature)	Haywood & Staples 1993
	Amphipoda			
	Corophium volutator	Lab expt	Yes	Mills & Fish 1980
	C. arenarium	Lab expt	Yes	Mills & Fish 1980
	Asteroidea			
	Patiriella pseudoexigua	Lab expt	Yes	Chen & Chen 1993
	Demospongiae			
	Haliclona tubifera, Halichondria magniconulosa	Lab expt	Yes (only temperature tested)	Maldonaldo & Young 1996
Dinoflagellate Bloom	Bivalvia			
	Argopecten irradians	Field obs	Yes	Summerson & Peterson 1990
Competition/Overgrowth				
	Cirripedia			
	Tetraclitella purpurascens	Field expt	Yes	Denley & Underwood 1979
	Tesseropora rosea	Field expt	Yes	Denley & Underwood 1979
	Anthozoa			
	Pocillopora damicornis	Field and lab expts	Yes	Harriott 1983
	Capnella gaboensis	Lab expt	Yes	Farrant 1987

Table 2.2 continued

Factor	Species	Methods	Effect	Reference
Competition/Overgrowth				
	Octocorallia			
	Alcyonium siderium	Field obs	Yes	Sebens 1983
	Ascidiacea			
	Corella inflata	Field expt	Depth dependent	Young & Chia 1984
	Ascidia callosa	Field expt	Depth dependent	Young & Chia 1984
	A. paratropa	Field expt	Yes	Young & Chia 1984
	Pyura haustor	Field expt	Depth dependent	Young & Chia 1984
	Boltenia villosa	Field expt	Depth dependent	Young & Chia 1984
	Styela gibbsii	Field expt	Yes	Young & Chia 1984
	Podoclavella cylindrica	Field obs	Yes	Davis 1987
	Bryozoa			
	Bugula pacifica	Field obs	Yes	Young & Chia 1981
	Fouling community	Field expt	Yes	Osman & Whitlach 1995b
	Bivalvia			
	Crassostrea virginica	Field and lab expts	Yes	Osman et al. 1989
		Field and lab expts	Yes	Zajac et al. 1989
	Tapes japonica	Field expt	No	Williams 1980a
	Archeogastropoda			
	Patelloida latistrigata	Field expt	Yes	Creese 1982
	Cellana tramoserica	Field expt	Yes	Underwood et al. 1983

the gastropod *Crepidula fornicata* (Pechenik & Eyster 1989). To date, there is only indirect evidence of delay of metamorphosis in the field (for review see Pechenik 1990). The consequences of prolonged larval life for early post-settlement mortality will depend on how frequently delayed metamorphosis occurs and on how it affects juvenile survival in nature.

Biological disturbance

Accidental ingestion or "bulldozing" by grazers such as limpets, littorinids and sea urchins has been well documented as a cause of early post-settlement mortality and reduced recruitment of barnacles, limpets, ascidians, and corals (Table 2.2). Vulnerability to disturbance by grazers may decrease with size (age) (Miller & Carefoot 1989, Safriel et al. 1994) and substratum heterogeneity (Sammarco 1980, Miller & Carefoot 1989, but see Denley & Underwood 1979). Grazers can also influence the abundance of sessile invertebrates indirectly through their effects on algal abundance. For example, Petraitis (1990) attributed the negative effect of *Littorina littorea* on mussel recruitment to the gastropod's reduction of the algae on which mussels settle. Low densities of grazers may positively affect the abundance (Petraitis 1983), survival (Creese 1982), or condition (Sammarco 1980) of recruits, presumably due to reduction of the abundance of algae and other competitors which either prevent settlement or overgrow recently settled individuals.

On hard substrata, biological disturbance by organisms other than grazers has received less attention. Davis (1988b) found that crabs kill recruits of the colonial ascidian *Podoclavella moluccensis* by trampling them with their sharp dactyls. In the intertidal zone, fucoid algae have both positive and negative effects on barnacle recruitment (Dayton 1971, Hawkins 1983 and references therein). Fucoids have been hypothesized to decrease settlement of barnacles by a whiplash effect or by altering water flow, and to increase (by whiplash) or decrease (by reduced desiccation) early post-settlement mortality (for discussion see Grant 1977, Hawkins 1983). In the only study to directly measure canopy effects on barnacle mortality, Grant (1977) found that an artificial algal canopy (strips of inner tube rubber) decreased post-settlement survival of *Semibalanus balanoides*. Heavy cover of *Fucus* is also associated with decreased limpet (*Patella vulgata*) recruitment (Lewis and Bowman 1975).

Adult infauna in soft-bottom communities can cause mortality of newly settled macrofauna by bioturbation of the sediments (but see McCann & Levin 1989). Peterson (1977) found that removal of the ghost shrimp *Callianassa californiensis*, a deposit feeder, increased recruitment of the clam *Sanguinolaria nuttallii*. He suggested that burial and direct consumption of juvenile clams by *C. californiensis* were the most likely mechanisms for the negative effect of the shrimp on clam recruitment. Brenchley (1981) demonstrated that densities of spionid polychaetes (*Rhynchospio arenicola*) and tanaid crustaceans (*Leptochelia dubia*), particularly small individuals, were decreased by addition of macroinfaunal (the lug worm *Abarenicola pacifica* and the mud shrimps *Ugopebia pugettensis* and *Callianassa californiensis*) or macroepifaunal (the sand dollar *Dendraster excentricus*) burrowers. Addition of sediment also reduced densities, suggesting that physical events were important in the interaction between bioturbators and recruits (Brenchley 1981). In the laboratory, Ahn et al. (1993) found that the clam *Gemma gemma* reduced survival of recent settlers of another clam (*Mercenaria mercenaria*) in muddy sand but not in sand, and suggested that increased mortality in muddy sand was due to burial and exposure to pore water metabolites from sediment reworking by *G. gemma*. Interference with feeding can also cause early post-settlement mortality. Cummings et al. (1996) found that the tube building spionid polychaete *Boccardia syrtis* decreased survival of early juvenile clams (*Macoma liliana*) in the laboratory. The polychaetes did not ingest the clams but caused them to retract their siphons, and thus interrupted feeding. Meiofaunal burrowers also can cause mortality of newly settled macrofauna. In the field, Watzin (1986) showed that meiofauna other than turbellarians (primarily nematodes and copepods) decreased the survivorship of recently settled bivalves, most likely by sediment destabilization. However, Zobrist and Coull (1994) found that meiofaunal bioturbators (copepods, nematodes, foraminifera) did not affect the survival of newly settled bivalves (*Mercenaria mercenaria*) and polychaetes (*Streblospio benedicti*) in the laboratory. They suggested that meiofauna (with the possible exception of predaceous turbellarians) do not play a large role in early post-settlement mortality of macrofaunal species.

Physical Disturbance and Hydrodynamics

Physical disturbance has received relatively little attention as a cause of mortality for newly settled invertebrates. Connell (1961) found that mortality of both cyprids and newly metamorphosed barnacles (*Semibalanus balanoides*) increased during gales, when mortality was greater at convexities on the substratum than in more protected microhabitats such as crevices or depressions. Eckman (1987) determined that current speed affected post-settlement survival of one species of bivalve (*Argopecten irradians*) but not another (*Anomia simplex*) in eelgrass meadows. Survival of *Argopecten* was lower in regions with faster currents, possibly because recruits were dislodged (Eckman 1987). Survival of abalone (*Haliotis iris*) settlers transplanted to the field was greater in deep than shallow habitats, possibly due to reduced dislodgment by wave action (McShane & Naylor 1995).

Physiological Stress

Newly settled invertebrates are generally more susceptible than older juveniles and adults to physiological stress (Hatton 1938, Foster 1971, Branch 1975, Olson 1983, Dungan 1985, Baker & Mann 1992, Gosselin & Chia 1995a, but see Mills & Fish 1980). This has been attributed to a greater surface area to volume ratio (Vermeij 1972), an inferior ability to reduce energy consumption under conditions of stress (Baker & Mann 1992), and incompletely developed protective adaptations (e.g. pigment and calcareous spicules in the ascidian *Didemnun molle*, Olson 1983). For mobile species, the age dependence of tolerance to physiological stress may depend on the habitats of juveniles and adults. Branch (1975) showed, in the laboratory, that tolerance to desiccation remained fairly constant in non-migratory species of patellid limpets but increased rapidly with size in species which settled low on the shore and migrated upwards as juveniles. Survival of early juvenile invertebrates may also be reduced by stressful physiological conditions which interfere with larval development. Developmental abnormalities associated with extreme physical conditions have been documented (e.g. Watts et al. 1983), but their effects on juvenile survival have not yet been investigated.

In the intertidal zone, newly settled invertebrates are highly vulnerable to mortality from desiccation (Table 2.2). Hatchling whelks (*Nucella emarginata*) are unable to survive 4-6 hours emersion in the field or the laboratory unless they are in a protective microhabitat (Gosselin & Chia 1995 a,b). Survival of settlers often decreases with increasing height on the shore. Small barnacles which settle or are transplanted above the limit of the adult distribution generally die (*Semibalanus balanoides*, Hatton 1938, Foster 1971; *Balanus cariosus*, Strathmann & Branscomb 1979; *Tetraclitella purpurascens*, Denley & Underwood 1979; *Chthamalus anisopoma*, Raimondi 1988a, 1991). Hatton (1938) demonstrated that a small amount of dripping water could keep barnacle cyprids alive above the adult zone. Within the vertical range of distribution of adult barnacles, early post-settlement mortality may increase with tidal height (*Semibalanus balanoides*, Minchinton & Scheibling 1991, Bertness et al. 1992; *Pollicipes polymerus*, Hoffman 1989; *Chthamalus anisopoma*, Raimondi 1988b, 1990) or remain constant (*Chthamalus montagui*, Kendall & Bedford 1987). Early post-settlement mortality also has been shown to increase with tidal height for mussels (*Mytilus viridis*, Tan 1975) and oysters (*Crassostrea virginica*, Roegner & Mann 1995). Lewis and Bowman (1975) and Bowman & Lewis (1977) suggested that desiccation was responsible for the restriction of limpet (*Patella vulgata*) spat on the upper shore to crevices and pits. However, this distribution could also be due to preferential settlement or migration.

Weather and other conditions that influence desiccation rates can account for temporal variability in survival rates of young juveniles. Increased mortality of attached cyprids (Connell 1961) and early post-metamorphic juveniles (Foster 1971) of the barnacle *Semibalanus balanoides* has been observed during periods of warm weather and prolonged aerial exposure due to neap tides (Foster 1971) or diminished wave action (Connell 1961). Roegner and Mann (1995) showed that recently settled oysters (*Crassostrea virginica*) survived transplantation to 25 cm above mean low water in September, but not in June or July when aerial temperatures were > 30 °C. Substratum type also can affect the risk of mortality from desiccation. Schubart et al. (1995) demonstrated that settlement inside empty barnacle tests increased the survival of recently settled barnacles (*Balanus glandula*) in the high intertidal zone. Minchinton and Scheibling (1993a) found that early post-settlement mortality of the barnacle *Semibalanus balanoides* increased with tidal height in the absence but not in the presence of ephemeral algae. Raimondi (1988b) showed that survival of juvenile barnacles (*Chthamalus anisopoma*) was reduced at higher tide levels on basaltic rocks compared to granitic rocks, most likely because higher temperatures were attained by basalt. However, rock type did not affect the survival of early juveniles of the barnacle *Tesseropora rosea* in Australia (Caffey 1982).

Exposure to bright light is a cause of early post-settlement mortality for some species of ascidians (*Didemnum candidum*, Hurlbut 1993; *Didemnum molle*, Olson 1983), but not others (*Diplosoma listeranium* and *Diplosoma* sp., Hurlbut 1993). Siltation also causes mortality of recently settled ascidians, resulting in greater survival of new settlers on the undersides of panels (Young & Chia 1984, Hurlbut 1993).

In the laboratory, combinations of extreme temperature and salinity have been shown to cause mortality of recent settlers of several species of invertebrates (Table 2.2).

However, most species tested survived virtually all conditions they are likely to experience in the field (Mills & Fish 1980, O'Brien 1994b, Brown et al. 1992, Chen & Chen 1993). Field estimates of mortality of early juveniles were significantly related to temperature for one species of Australian prawn (*Penaeus merguiensis*, Haywood & Staples 1993), but not another (*Penaeus esculentus*, O'Brien 1994a). Laboratory experiments indicated that environmental temperatures were suboptimal for survival of *P. merguiensis* (Staples & Heales 1991), but less detrimental to survival of *P. esculentus* (O'Brien 1994b). Also, the field study (O'Brien 1994a) was carried out near the southern limit of the range of *P. esculentus* in Australia, where water temperatures were lower. For estuarine species, periods of anoxia or hypoxia may also be a source of early post-settlement mortality. Baker and Mann (1992) demonstrated that low levels of oxygen decreased survival of recently settled oysters (*Crassostrea virginica*) in the laboratory. The absence of adult barnacles from tidepools in New England has been attributed to early post-settlement mortality from decreased dissolved oxygen levels (Singletary & Shadlou 1983) or accumulation of toxins (e.g. substances secreted by the alga *Ulva lactuca*, Magre 1974) during tidal isolation. Blooms of toxic dinoflagellates also may result in mortality of early juveniles of benthic invertebrates. Summerson and Peterson (1990) found that recruitment of the bay scallop *Argopecten irradians concentricus* was extremely low (2% of previous years) during a red tide (*Ptychodiscus brevis*) outbreak in North Carolina, USA. The increased abundance of empty shells of juvenile scallops after the red tide suggests that the recruitment failure resulted at least partly from elevated early post-settlement mortality.

Despite the vulnerability of recently settled invertebrates to physiological stress, environmental conditions may not commonly cause mortality of early juveniles in the field. Most studies examining survivorship under conditions of physiological stress have transplanted settlers or modified the conditions to which they were exposed. Many individuals may avoid these sources of mortality by settling in (Connell 1961, Denley &

Underwood 1979, Olson 1983, Young & Chia 1984, Hurlbut 1993, Schubart et al. 1995) or migrating to (Gosselin & Chia 1995b) locations where environmental conditions are not lethal.

Predation

Mobile Epifauna

Predation on early juveniles has been documented most often for mobile epifaunal species (Table 2.3). Fish and crabs are the most commonly reported predators of early juveniles of many species including lobsters, crabs, shrimp, queen conch, scallops, and sea urchins (Table 2.3). These were the only types of predators, out of the 45 species of intertidal invertebrates tested in the laboratory by Gosselin and Chia (1995a), that preyed on recently hatched intertidal whelks (*Nucella emarginata*). Other predators of early juveniles include shrimp (preying on blue crabs), sea stars (on scallops and urchins), whelks (on scallops), octopus (on spiny lobster), lobster (on urchins), and urchins (on sea cucumbers) (Table 2.3). Some species of recently settled echinoderms are preyed upon primarily by small predators. In the laboratory, small individuals (< 1.5 mm) of the sand dollar *Dendraster excentricus* were heavily preyed upon by tanaid crustaceans but not eaten by gammarid amphipods or holothurians (Highsmith 1982). Survival of 1 month old sea stars (*Acanthaster planci* and *Nardoa novaecaladoniae*) in rubble on the Great Barrier Reef was decreased by epifauna consisting primarily of polychaetes, amphipods and gastropods (Keesing & Halford 1992, Keesing et al. 1996), but predators had little effect on survival of another species of *Nardoa* on the Okinawan Reef, Japan (Keesing et al. 1996). Rumrill (1989) was unable to find any significant predators of juveniles of *Asterina miniata* when he exposed them to crabs, other sea stars, and fish in the laboratory. Most of the studies of predation on early juveniles of mobile species have involved individuals several weeks to months after settlement (Table 2.3) and the vulnerability of recently settled individuals to predators may differ from that of slightly

Table 2.3. Summary of studies examining predation on recently settled or early juvenile benthic marine invertebrates. For experiments examining the effects of predator inclusion or exclusion on recruitment the age given is the duration of the experiment. For laboratory experiments and field tethering experiments, the size of the prey is indicated.

Group and Species	Size/Age	Predator	Methods	Patterns/ Conclusions	Reference
Echinodermata					
Acanthaster planci	1-16 mo old 1 mo old	Rubble epifauna	Transplant	High rate of mortality due to predation	Keesing & Halford 1992
Nardoa novaecaladoniae, A. planci		rubble epifauna	Transplant	Predation rate varied among sites within habitats and was higher for *A. planci* than for *N. novaecaladoniae.*	Keesing et al. 1996
Nardoa sp.	5 d old	Rubble epifauna and nektonic predators	Transplant	Mortality rate was very low	Keesing et al. 1996
Asterina miniata	8-27 mm	Crabs, sea stars, fish	Lab observation	Almost no predation occurred	Rumrill 1989
Dendraster excentricus	<2.5 mm	Crustaceans	Lab observation	Tanaids only ate sand dollars <1.5 mm	Highsmith 1982
Cucumaria frondosa	<25 mm	Urchins	Field/ lab observation	Direct observations of predation	Hamel & Mercier 1996
Actinopyga echinites	>3 g	Gastropods, fish	Predator exclusion cages	Exclusion of predators reduced mortality	Wiedemeyer 1994
Strongylocentrotus droebachiensis	3-6 mm	Fish, whelks, crabs, lobsters	Predator inclusion cages	No effect of whelks or green crabs. Cobbles (spatial reguge) decreased predation by rock crabs and lobsters	Scheibling & Hamm 1991
	0-30 mm	Fish	Lab experiment gut contents	Urchins were not preferred prey in lab (0-15 mm urchins eaten most often), but were primary prey in field	Ojeda & Dearborn 1991

Table 2.3 continued

Group and Species	Size/Age	Predator	Methods	Patterns/ Conclusions	Reference
Echinodermata					
Strongylocentrotus droebachiensis	<20 mm	Fish	Artificial reef	Construction of artificial reefs increased predator densities and decreased densities of juvenile urchins	Ojeda & Dearborn 1991
Strongylocentrotus franciscanus	<10 mm	Sea stars, fish, lobsters	Lab/ field observation	Direct observations of predation	Tegner & Dayton 1977
	<10 mm	Sea stars, fish, lobsters	Manual removal of adult urchins	Juveniles protected from predation under the spine canopy of adults. Removal of adults decreased juvenile abundance	Tegner & Dayton 1977
Gastropoda					
Nucella emarginata	2-8 d old	45 sp. tested	Lab observation	Only crabs and fish were significant predators.	Gosselin & Chia 1995a
		Crabs	Lab experiment	Predation was reduced for whelks in algae or in clumps of mussels and barnacles.	Gosselin & Chia 1995b
Strombus gigas	<54 mm	Decapods, fish	Field observation	Early juveniles occurred under sand	Sandt & Stoner 1993
	9-13 mm	Decapods, fish	Tethering	Predation was reduced in medium density eelgrass compared to sand	Ray & Stoner 1995
Trochus histrio	7-25 mm	Fish	Tethering	Predation rate was lower in branching coral than in open areas, and decreased with increasing snail size.	Scheibling & Hatcher 1997
Tectus pyramis	12-34 mm	Fish	Tethering	Predation rate negligible, even on small *T. pyramis* in open areas	

Table 2.3 continued

Group and Species	Size/Age	Predator	Methods	Patterns/ Conclusions	Reference
Bivalvia					
Argopecten irradiens	6-20 mm	Crabs, sea stars	Tethering	Predation decreased with increasing height of attachment on seagrass	Pohle et al. 1991
	12 mm	Crabs, whelks	Tethering	Predation decreased with increasing height of attachment on eelgrass	Ambrose & Irlandi 1992
Placopecten magellanicus	7-30 mm	Sea stars, crabs	Tethering	Predation rate was affected by predator species, scallop size and density, site and season	Barbeau et al. 1994
	7-30 mm	Sea stars, crabs	Tethering	Predation rate varied among seasons	Hatcher et al. 1996
	5-25 mm	Sea stars, crabs	Lab experiment	Crabs actively preferred large scallops, while the preference of sea stars for small scallops occurred passively.	Barbeau & Scheibling 1994a
	5-25 mm	Sea stars, crabs	Lab experiment	Predation rate increased with increasing temperature	Barbeau & Scheibling 1994b
Crassostrea virginica	1-30 mm	Blue and mud crabs	Lab experiment	Predation rate increased by decreased prey size or increased predator size, and affected by the species of predator	Bisker & Castagna 1987
	5-45 mm	Blue crabs	Lab experiment	Predation rate increased with decreasing prey size and increasing prey density.	Eggleston 1990
Mytilus californianus *M. trossulus*	1-5 mm	Whelks	Lab experiment	Early juvenile whelks strongly preferred mussels over other species of prey and consumed 1 and 2 mm SL mussels more often than larger individuals	Gosselin & Chia 1996

Table 2.3 continued

Group and Species	Size/Age	Predator	Methods	Patterns/ Conclusions	Reference
Bivalvia					
Mytilus trossulus *M. edulis*	0.5-8 mm	Whelks	Lab experiment	Size of mussels consumed increased with increasing size of juvenile whelks.	Chapter 5
	<2 mm	Whelks	Field observations	The majority of mussel shells drilled by juvenile whelks were <2 mm SL	Chapter5
	<2 mm	Whelks	Manual removal	No effect of removal of juvenile whelks on mussel cover or size distribution.	Chapter 5
M. edulis	Recruitment after 2.5 mo.	Whelks	Inclusion and exclusion cages	No effect of whelks on mussel recruitment. Barnacles were provided as alternative prey	Petraitis 1990
	Recruitment after 3-10 wk	Whelks	Exclusion cages	Predator exclusion cages had a small but significant effect on mussel recruitment	Petraitis 1991
Choromytilus chorus	7 mo (sampled montly)	Whelks	Settlement collectors	Mussel mortality greater on collectors attached to the substratum at several points than on those with a single attachment point	Moreno 1995
Chama echinata	Unspecified	Gastropods, crabs, fish	Manual removal and cages	Recruitment lower in presence of gastropods	Menge 1991a
Ostrea palmula	Unspecified	Gastropods, crabs, fish	Manual removal and cages	Recruitment lower in presence of predators	Menge 1991a
Cerastoderma edule	2-35 mm	Green crabs	Lab experiment	Predation decreased with increasing prey size and increased with increasing temperature	Sanchez-Salazar et al. 1987

Table 2.3 continued

Group and Species	Size/Age	Predator	Methods	Patterns/ Conclusions	Reference
Bivalvia					
Cerastoderma edule	2-6 mm	Green crabs	Field enclosure	Juvenile crabs prey on *C. edule*	Jensen & Jensen 1985
	2-6 mm	Green crabs	Lab experiment	Crabs preferred *C. edule* to *M. balthica* or annelids	Jensen & Jensen 1985
	< 5 mm	Polychaetes, nermertines	Inclusion and exclusion cages	Cage treatments were unreplicated. Juvenile cockles were found only in exclosures, and not in predator inclusion cages	Reise 1979
Mercenaria mercenaria	4.5-20 mm	Snapping shrimp	Lab experiment	Predation rate decreased with increasing prey size.	Beal 1983
Gemma gemma	1 mo survival	Polychaetes	Lab experiment	Polychaetes prey on juvenile *G. gemma*	Weinberg 1984
Macoma balthica	<0.3 mm	Amphipods	Lab experiment	Increased sediment depth decreased predation rate.	Elmgren et al. 1986
	0.25-0.3 mm	Nereid polychaetes	Lab experiment	Polychaete decreased survival of *M. balthica*	Ólafsson et al. 1989
	0.5-1.5 mm	Nereid polychaetes	Lab experiment	Predation rate decreased with increasing prey size.	Rönn et al. 1988
Mulinia lateralis	0.2-0.25 mm	Polychaetes	Lab experiment	Polychaetes decreased survival of *M. lateralis*	Luckenbach 1987
soft bottom bivalves	Recruitment after 49 days	Decapods, fish	Exclusion cages	Densities of bivalve spat were greater inside than outside predator exclusion cages	Möller 1986
Decapoda					
Panulirus argus	5-35 mm	Fish, crabs, octopus	Tethering	Predation rate on lobsters decreased with increasing prey size, and was greater for lobsters without shelter	Smith & Herrnkind 1992

Table 2.3 continued

Group and Species	Size/Age	Predator	Methods	Patterns/ Conclusions	Reference
Decapoda					
Panulirus argus	7-11 mm	Fish, crabs, octopus	Tethering	Predation rate on lobsters greater in open than in algae	Herrnkind & Butler 1986
Panulirus cygnus	<26 mm	Fish	Stomach contents	Small juveniles detected in stomach contents	Howard 1988
Homarus americanus	5-40 mm	Fish, crabs	Tethering	Predation rate decreased with increasing prey size, and was greater on bare or PVC substrate than on cobble	Wahle & Steneck 1992
	Post-larvae/ 1st benthic instar	Fish, crabs	Lab experiment	Fish predation occurred in eelgrass, sand and mud substrata but not in rock, while crab predation occurred on all substrata.	Lavalli & Barshaw 1986 Barshaw & Lavalli 1988
	1st benthic instar	Fish	Lab experiment	Predation rate was decreased by algae.	Johns & Mann 1987
Cancer magister	Recruitment after 48 h	Conspecifics, fish	Predator exclusion cages	Predation affected survival at 1 site but not at another	Eggleston & Armstrong 1995
	10-34 mm	Fish, conspecifics	Tethering	Total predation rate was less in shell than in mud substrate, but cannibalism was higher in shell	Fernandez et al. 1993a
	<8 mm	Conspecifics	Lab/ field experiment (recruit-ment)	Abundance of early juveniles was greater in unoccupied shell plots than in plots occupied by an earlier cohort	Fernandez et al. 1993b
Callinectes sapidus	11-100 mm	Fish, conspecifics	Tethering	Predation rate was lower in medium density than in low or high density sea grass. Prey size did not affect predation rate	Wilson et al. 1987

Table 2.3 continued

Group and Species	Size/Age	Predator	Methods	Patterns/ Conclusions	Reference
Decapoda					
Callinectes sapidus	11-70 mm	Fish, conspecifics	Tethering	Predation rate was lower in macroalgae than in celgrass or at an unvegetated site. Prey size affected predation rate only at the unvegetated site	Wilson et al. 1990
	1st, 3rd, 7th, 9th instar	Fish, conspecifics	Lab (tethering)	Predation rate was lower in vegetation and when prey were untethered and decreased with increasing prey size	Pile et al. 1996
	1st, 3rd, 7th, 9th instar	Fish, conspecifics	Field (tethering)	Predation rate was decreased by vegetation, increasing prey size, and storm and post-storm conditions, but not affected by prey density or location	Pile et al. 1996
	Megalopae	Shrimp	Lab experiment	Predation rate affected by predator species but not by substratum type or prey density	Olmi & Lipcius 1991
Panopeus herbstii	Megalopae	Fish, shrimp, crabs	Lab experiment	Predation rate was lower on shell substratum than on sand, marsh grass or *Ulva*. Predation rate by crabs was lower than that of the other predator species	Dittel et al. 1996
Penaeus esculentus	4-5 mm	Fish	Lab experiment	Predation rate was greater on bare substratum than in seagrass.	Kenyon et al. 1995
	8-12 mm	Fish	Lab experiment	Predation rate was decreased by artificial seagrass or thick sand (in day but not night).	Laprise & Blaber 1992

Table 2.3 continued

Group and Species	Size/Age	Predator	Methods	Patterns/ Conclusions	Reference
Decapoda					
Penaeus aztecus	8-32 mm	Fish	Lab experiment	Vegetation decreased the predation rate of most of the fish species.	Minello et al. 1989
	30-35 mm	Fish	Field-predator exclusion	The mortality rate of shrimp in predator exclusion cages was much lower than the mortality rate of cohorts outside of cages.	Minello et al. 1989
Cirripedia					
Tesseropora rosea	1 mo survival	Whelks	Exclusion fences	Exclusion of whelks had no effect on barnacle survival	Denley & Underwood 1979
Semibalanus balanoides *Balanus glandula* *Semibalanus cariosus*	Recruitment after 5-7 d	Gastropods sea stars	Exclusion fences	Exclusion of predators increased recruitment rate in a year with low settler densities but not during 2 years with high settler densities	Carroll 1996
Balanus inexpectatus	Recruitment after 1-4 mo	Gastropods, fish, crabs	Manual removal and cages	Predation by gastropods but not by fish or crabs decreased barnacle recruitment	Menge 1991a
Ascidiacea					
Botryllus schlosseri	1-3 d old	Gastropods	Transplantation	Very few newly recruited *B. schlosseri* survived when transplanted to a site where gastropods were present	Osman et al. 1992
Botryllus schlosseri *Botrylloides diegensis* *Diplosoma* sp.	Recruitment after 8-18 d		Inclusion cages	Predators affected recruitment of *B. schlosseri* and *Diplosoma* sp. throughout the settlement season, but had no effect on *B. diegensis*	Osman et al. 1992 Osman & Whitlach 1995a

Group and Species	Size/Age	Predator	Methods	Patterns/ Conclusions	Reference
Ascidiacea					
Trididemnum opacum	Recruitment after 1 mo.	Fish, urchins	Exclusion cages	Substratum heterogeneity decreased predation rate	Keough & Downes 1986
Podoclavella moluccensis	Recruitment after 3 wk	Fish, crabs	Exclusion cages	Fish predation had no effect on recruitment. The effect of crabs was due to physical disturbance rather than predation	Davis 1988b
didemnid ascidians	Recruitment (sampled every 2 mo)	Fish	Exclusion cages	3 species of spirorbids were unaffected by fish predation	Keough 1984
Bryozoa					
Tubilopora spp.	Recruitment after 3-4 wk	Fish	Exclusion cages	Spatial distribution and abundance affected	Keough & Downes 1982
Celleporia brunnea				Little effect on distribution or abundance	
Scrupocellaria bertholetti				Size distribution affected by predation.	
Crytosula pallasiana *Bugula turrita*	Recruitment after 8-18 d	Gastropods	Inclusion cages	Gastropods had only small effects on bryozoan recruitment	Osman et al. 1992 Osman & Whitlach 1995a
Polychaeta					
Spirorbis eximus	Recruitment after 3-4 wk	Fish	Exclusion cages	Predator exclusion cages had little effect on recruitment rate	Keough & Downes 1982
Phragmatopoma virgini	Recruitment after 1 mo	Snails, crabs, sea stars	Exclusion cages	Exclusion of consumers increased recruitment. Recruitment greater on rough substratum	Zamorano et al. 1995
Abarenicola pacifica	2 mo survival	Polychaetes, cumaceans	Lab experiment	Predators reduced survival of juveniles.	Wilson 1981

Table 2.3 continued

Group and Species	Size/Age	Predator	Methods	Patterns/ Conclusions	Reference
Polychaeta					
Capitella sp. I	2-3 wk survival	Polychaetes	Transplant	Predators reduced survival of juveniles	Qian & Chia 1994
Nerinides spp., *Nerinopsis* sp. *Armandia brevis*	7-10 d survival	Amphipods, tanaid crustaceans	Lab experiment	Some species of crustaceans had no effect on mortality rate of *Nerinides*. Anemones had no effect on survival of *Nerinides* or *Nerinopsis*. Increased sediment depth did not decrease the predation rate	Oliver et al. 1982 , Oliver & Slatterly 1985
Communities					
Sessile species on subtidal panels	Recruitment after 2 mo	Rock lobsters	Exclusion cages	Recruitment was increased by substratum complexity. The effects of predation differed between islands	Barkai & Branch 1988
Soft bottom	<2 mm	Meiofauna deposit feeders omnivores	Observations and gut contents	Literature review suggests high post-settlement mortality	Thorson 1966
Soft bottom estuary-polychaetes and crustacean	Recruitment after 2.5 mo	Not specified	Exclusion cages	Predators decreased the amplitude of the recruitment pulse but did not change the shape of the abundance curve.	Holland et al. 1987
Soft bottom macrofauna	Recruitment after 1-2 wk	Meiofauna	Cores with/ without predators	Predators reduced recruitment of macrofaunal species	Watzin 1983, 1986

older juveniles. However, several studies have found high predation rates on settling or recently settled decapods in the laboratory (Lavalli & Barshaw 1986, Johns & Mann 1987, Barshaw & Lavalli 1988, Olmi & Lipcius 1991, Dittel et al. 1996) and in the field (Eggleston & Armstrong 1995).

Tethering is the most common technique used to evaluate predation rates on early juveniles of mobile epifaunal species (Table 2.3). Recent papers have pointed out potential artifacts of tethering (Zimmer-Faust et al. 1994, Peterson & Black 1994, Barbeau & Scheibling 1994 c, Aronson & Heck 1995, Micheli 1996). For example, tethering may increase predation rates by limiting the escape response of prey, particularly for highly mobile species (Zimmer-Faust et al. 1994, Peterson & Black 1994, Aronson & Heck 1995), or by decreasing the ability of prey to burrow in certain substrates (Barshaw & Able 1990). Also, tethering may differentially affect predation by different predators, potentially complicating comparisons of predation rate among predator species (Barbeau & Scheibling 1994 c) and habitats (if predator species composition or behaviour differs among habitats) (Peterson & Black 1994, Micheli 1996). Despite these artifacts, tethering with thoughtful controls remains an effective way to assess predation on small, mobile invertebrates.

Predator inclusion or exclusion cages also have been widely used to measure predation rates of juveniles of mobile (and sessile) species (Table 2.3). There are various artifacts of caging (reviewed by Dayton and Oliver 1980, Hall et al. 1990) which are particularly relevant to studies of juvenile survival and recruitment. By altering the micro-environment (e.g. reducing water flow, shading, creating structure), cages may increase settlement rate and/or early post-settlement survival, which may confound an assessment of predator effects. Also, mesh size will determine the size of predators that are manipulated, including those which may not be part of the original experimental design. Thus, effects of excluding a particular predator may be confounded by other smaller and perhaps unknown predators (including juveniles of species that are being manipulated as adults) which can pass through the mesh and may even be attracted to cages. As with tethering, the use of adequate procedural controls to evaluate artifactual effects is crucial to the design of any caging experiment. However, only two (Denley & Underwood 1979; Reise 1979) of the 13 studies I reviewed that employed exclusion cages or fences also used inclusion or partial cages/fences to assess cage artifacts (although in Reise's study treatments were not replicated). Two other studies (Keough 1984, Eggleston and Armstrong 1995) measured settlement or short-term recruitment rates in caged and uncaged plots to determine if the presence of a cage altered settlement rates. Studies employing predator inclusion cages were less problematic, as most (6 out of 7) compared mortality or recruitment rates between cages with and without predators, which would share the same artifacts.

The risk of predation for early juveniles may vary with recruit size. In tethering experiments, the mortality rate of small juvenile lobsters (*Panulirus argus*, Smith & Herrnkind 1992; *Homarus americanus*, Wahle & Steneck 1992) was greater than that of larger individuals, but the effect of body size on predation rate on juvenile blue crabs varied among studies (Wilson et al. 1987, 1990, Pile et al. 1996). The effect of juvenile sea scallop size on predation rate depended on predator type, site, and season (Barbeau & Scheibling 1994a, Barbeau et al. 1994). For some species, predation risk may be greater for intermediate sized individuals than for early juveniles or adults. Gut contents of mobile benthic predators from the Gulf of Maine examined by Ojeda and Dearborn (1991) contained mostly juveniles or small species of invertebrates, but most predators did not seem to exploit the smallest size range of prey available. The bimodal size distribution commonly observed in sea urchin populations may be the result of increased predation on intermediate sized urchins in transition between the spatial refuge of the cryptic early juvenile stage and the size refuge of adults (for review see Scheibling 1996). Similarly, Wiedermeyer (1994) found that the importance of predation as a source of mortality for juvenile sea cucumbers (*Actinopyga echinites*) increased over time, and suggested that this increase in mortality resulted from a decrease in cryptic behaviour.

Predation risk for early juveniles varies among habitats and microhabitats for many invertebrate species including scallops, lobsters, crabs (but see Olmi & Lipcius 1991), shrimp, urchins, and gastropods (but see Scheibling & Hatcher 1997) (Table 2.3). Predation intensity is lower in vegetation and other structurally complex substrata (Table 2.3). Attachment above the bottom on vegetation (*Argopecten irradiens*, Pohle et al. 1991, Ambrose & Irlandi 1992) or occurrence near (*Dendraster excentricus*, Highsmith 1982) or under (*Strongylocentrotus franciscanus*, Tegner & Dayton 1977) adults can also offer protection from predation. Early juveniles of many species occur primarily in these protective habitats (e.g. Tegner & Dayton 1977, Highsmith 1982, Breen et al. 1985, Wahle & Steneck 1991, Garcìa-Esquivel & Bricelj 1993, Gosselin & Chia 1995b). Older juveniles may outgrow their spatial refuges or shift habitats as their vulnerability to predation decreases (Tegner & Dayton 1977, Scheibling & Hamm 1991, Smith & Herrnkind 1992, Garcìa-Esquivel & Bricelj 1993).

Predation risk for early juveniles also can be influenced by physical factors which affect predator-prey interactions. In laboratory and field experiments with juvenile sea scallops (*Placopecten magellanicus*), predation rate by crabs and sea stars increased with temperature due to increased predator activity and decreased effectiveness of the scallops' escape response (to sea stars) (Barbeau & Scheibling 1994b, Barbeau et al. 1994). In a tethering experiment with juvenile blue crabs (*Callinectes sapidus*), Pile et al. (1996) found that mortality was lower during and immediately after a storm than before the storm. They attributed the reduction in mortality to decreased predator activity resulting from altered physical conditions associated with the storm, such as a drop in water temperature, increased turbidity and turbulent flow, and increased salinity. Similarly, Scheibling and Hatcher (1997) observed that mortality of juvenile snails (*Trochus histrio*) tethered outside of a spatial refuge (live branching coral) was lowest during a gale which temporarily reduced the abundance of predatory fish.

Infauna

Early juveniles of macrofauna in soft bottom communities are vulnerable to predation by a variety of predators. Jensen and Jensen (1985) suggested that juvenile crabs (*Carcinus maenus*) were responsible for the rapid decline in the number of juvenile cockles (*Cerastoderma edule*) after the settlement peak in the Danish Wadden Sea. In the laboratory, *C. maenus* can consume large numbers of cockles and selectively preys on small individuals (Jensen & Jensen 1985, Sanchez-Salazar et al. 1987). Reise (1979) found that densities of early juveniles of *C. edule* in cages in the Wadden Sea were reduced in predator inclusion cages with a nereid polychaete or a nemertine, and increased in predator exclusion cages. However, his failure to replicate treatments may have confounded differences between treatments with differences between locations. In Sweden, Möller (1986) found that exclusion of epibenthic predators using cages also increased densities of spat of several species of bivalves, primarily *Mya arenaria* and *C. edule*. In Chesapeake Bay USA, Holland et al. (1987) showed that exclusion of fish and crabs increased the peak abundance of macrofaunal recruits in trays of azoic sediment. Beal (1983) found that two species of snapping shrimp (*Alpheus heterochaelis* and *A. normanni*) selectively prey on small juveniles of the clam *Mercenaria mercenaria* in the laboratory, suggesting they may be important predators of juvenile macrofauna. Meiofaunal predators (organisms <0.5 mm) also feed on recently settled macrofauna (Thorson 1966, Bell & Coull 1980). Watzin (1983, 1986) showed that increased densities of turbellarians reduced the survival of spionid and terebellid polychaetes, oligochaetes, and amphipods.

Deposit feeders, particularly surface-feeding species, ingest early juvenile macrofauna, as well as causing mortality by sediment reworking. Thorson (1966) calculated that deposit feeders could ingest large numbers of macrofaunal settlers, but suggested that some settlers may survive passage through the digestive tract. However, Mileikovsky (1974) reviewed reports of the presence of larvae and small juvenile invertebrates in the digestive tracts of deposit feeders and concluded that passage alive through the digestive system is probably rare and does not play an important role in recruitment. In the laboratory, adult polychaetes and crustaceans decrease the survival of recently settled individuals of several species of bivalves (*Gemma gemma*, *Mulinia lateralis*, *Macoma balthica*) and polychaetes (*Abarenicola pacifica*, *Nerinides* spp., *Nerinopsis* sp., *Armandia brevis*) (Table 2.3). Elmgren et al. (1986) tested the mechanism for the increased mortality of settlers of the bivalve *Macoma balthica* in the presence of adult amphipods (*Pontoporeia affinis*) and found crushed shells of *M. balthica* only in the aquaria in which *P. affinis* were present. Increased sediment depth, which would decrease the probability of physical contact between amphipods and early juvenile clams, increased the survival of *M. balthica* in the presence but not in the absence of *P. affinis*. Weinberg (1984) showed that the deposit-feeding polychaete *Polydora ligni* ingested recently settled clams (*Gemma gemma*) thereby reducing recruitment in the laboratory, but he did not find these clams in the gut contents of polychaetes collected in the field. However, Qian and Chia (1994) found that recently settled polychaetes (*Capitella* sp. I), which were marked with red dye and transplanted to the field, had high mortality in trays containing large numbers of deposit-feeding polychaetes and other predators.

Sessile Species

Exclusion of macrofaunal predators often results in increased recruitment of sessile subtidal invertebrates, which can ultimately affect community structure (Table 2.3). In California, Keough and Downes (1982, 1986) examined the effects of predators on patterns of recruitment of sessile invertebrates on subtidal rock walls off Santa Catalina

Island. Exclusion of predators (fish and urchins) with cages altered the abundance (the bryozoan *Tubilopora* spp.), spatial distribution (*Tubilopora* spp., the ascidian *Trididemnum opacum*), and size distribution (the bryozoan *Scrupocellaria bertholetti*) of recruits of several species, but had little effect on other species (the bryozoan *Celleporaria brunnea*, the polychaete *Spirorbis eximus*). In South Africa, Barkai and Branch (1988) demonstrated that high densities of rock lobsters prevented recruitment on uncaged plates in the subtidal zone of Malgas Island, while caged plates developed a community of barnacles and mussels. Caging also increased recruitment, although less dramatically, on plates at nearby Marcus Island where rock lobsters were nearly absent and whelks (*Burnupena* spp.) were the most abundant predators. Caging studies also have shown that predation on recent settlers has a major effect on the structure of fouling communities in New England. The small gastropods *Anachis lafresnayi* and *Mitrella lunata* prey on newly settled ascidians, resulting in a shift of community dominance from ascidians to bryozoans (Osman et al. 1992, Osman & Whitlach 1995a).

Predation by whelks is well known to be an important source of post-recruitment mortality for sessile invertebrates in the intertidal zone (e.g. Connell 1961, Dayton 1971, Menge 1976). However, studies of the effect of whelks on recently settled invertebrates have yielded conflicting results. Exclusion of the whelk *Morula marginalba* in Australia had no effect on survival of the barnacle *Tesseropora rosea* in the first few months after settlement (Denley & Underwood 1979). In contrast, Menge (1991a) found that recruitment of the barnacle *Balanus inexpectatus* in Panama was lower in the presence of predatory gastropods (including whelks), and that recruitment of the bivalves *Chama echinata* and *Ostrea palmula* was lower in the presence of various predators (gastropods, crabs, fish). However, gastropod removal treatments and controls were pseudoreplicated in his study, confounding differences between locations with differences between treatments. Carroll (1996) found that exclusion of whelks and sea stars increased recruitment of barnacles (*Semibalanus balanoides, S. cariosus, B. glandula*) in Alaska, USA, in a year with low settler densities, but had no effect in 2 years with higher settlement. In Maine, USA, the whelk *Nucella lapillus* had little (Petraitis 1991) or no (Petraitis 1990) effect on recruitment of the mussel *Mytilus edulis*. In southern Chile, Moreno (1995) found that recently settled mussels (*Choromytilus chorus*) only survived on filamentous algae or artificial collectors which were inaccessible to the whelk *Nucella crassilabrum*. However, much of the whelk predation probably occurred several weeks to months after the mussels settled. Also in southen Chile, exclusion of all consumers (including whelks and other carnivorous gastropods, crabs, and sea stars) increased recruitment of the reef-building polychaete *Phragmatopoma virgini* (Zamorano et al. 1995).

Researchers investigating predation on older individuals have commented that adult whelks were not observed feeding on newly settled barnacles (*Semibalanus balanoides*, Connell 1961; *Tesseropora rosea*, Fairweather 1988), although Connell (1970) noted that *Balanus glandula* was attacked by predators (primarily 3 species of *Nucella*) soon after settlement. Whelk recruits are probably more important predators of recently settled barnacles and mussels than adult whelks. In the laboratory, Gosselin and Chia (1996) found that 15 to 18 day old *Nucella emarginata* strongly preferred *Mytilus californianus* and *M. trossulus* over 4 other species presented (the barnacles *Balanus glandula, Chthamalus dalli* and *Pollicipes polymerus* and the bivalve *Lasaea* sp.). The whelks preferentially consumed the smallest (1 and 2 mm shell length) size classes of mussels offered. In Chapter 5 of this thesis, I found that recruits (<5 mm SL) of *Nucella lapillus* prey on a range of sizes of mussels (*Mytilus trossulus* and *M. edulis*) in the field and the laboratory, including individuals <1 mm shell length. Reduction of the density of recently recruited whelks had no effect on either cover or size distribution of *Mytilus*. However, manual removal of whelk recruits was not very effective because the high densities of recruits necessitated a small spatial scale of manipulation that was difficult to maintain.

A number of factors can modify the intensity of predation on recent settlers of sessile species. In the laboratory, predation on juvenile oysters (*Crassostrea virginica*) by blue crabs (*Callinectes sapidus*) decreases with increasing oyster size (Bisker & Castagna 1987, Eggleston 1990). For colonial species, the consequences of predation may also be greater for early juveniles than for adults. Davis (1988b) demonstrated that removal of all zooids (to simulate predation) of the ascidian *Podoclavella moluccensis* killed all juvenile (2-3 months old) colonies in < 24 days but did not cause mortality of adults which quickly regenerated. Certain substrata can offer protection from predation, as described above for mussels (Moreno 1995). Settlement beside adults decreased mortality of recently settled octocorals *Alcyonium siderium*, most likely because adults prevented urchin grazing (Sebens 1983). Protection from predation is probably also the reason for the increased survival of early juvenile vermetid gastropods which settle on bryozoans (Osman 1987).

Competition for Space and Food

For recently settled invertebrates, particularly sessile ones, overgrowth is an important cause of mortality. Overgrowth by algae is associated with decreased survival of recently settled corals (*Pocillopora damicornis*, Harriott 1983), ascidians (Young & Chia 1984), barnacles (*Tetraclitella purpurascens, Tesseropora rosea*, Denley & Underwood 1979), and limpets (*Patelloida latistrigata*, Creese 1982). Survival of early juveniles is increased by factors which decrease algal abundance, such as shade for ascidians (Young & Chia 1984) and the presence of adult limpets for the limpet *Patelloida latistrigata* (Creese 1982).

Overgrowth by other invertebrates is a common cause of mortality for encrusting species (e.g. Buss 1979, 1981, Grosberg 1981), and new settlers may be particularly vulnerable. Overgrowth by ascidians has been suggested as a cause of mortality for early juveniles of the octocoral *Alcyonium siderium* (Sebens 1983) and the bryozoan *Bugula* *pacifica* (Young & Chia 1981), and for several members of the fouling community in Long Island Sound, USA (Osman & Whitlach 1995b). Overgrowth also was the likely cause of decreased survival of settlers of the coral *Capnella gaboensis* on biofilmed substrata compared to bare substrata in the laboratory (Farrant 1987). In New South Wales, Australia, Denley and Underwood (1979) showed that survival of newly settled barnacles (*Tetraclitella purpurascens*) in the low intertidal zone was increased by removal of settling polychaetes (*Galeolaria caespitosa*). Also in Australia, mortality of the subtidal colonial ascidian *Podoclavella moluccensis* in the first month after settlement varied among sponge and bare wood substrata due to differences in the risks of overgrowth and dislodgment of substrata: ascidians preferentially settled on substrata on which their survival was increased (Davis 1987). Crowding and overgrowth in dense aggregations of settlers can result in density-dependent early post-settlement mortality (Weiss 1948), although crowding is more likely to cause post-recruitment mortality as the recruits grow and begin to contact one another. Flexibility of body form can lessen the effects of crowding. Young and Braithwaite (1980) reported that gregarious settlers of the ascidian *Chelyosoma productum* produce an epidermal ampulla to access the overlying water column for space to grow.

Limitation of food intake also can cause early post-settlement mortality. In laboratory and field experiments, mortality of newly settled oysters (*Crassostrea virginica*) increased with the density of fouling species, possibly due to food depletion (Zajac et al. 1989, Osman et al. 1989) although some overgrowth occurred (Osman et al. 1989). Increased food supply in the laboratory experiments had mixed effects on oyster spat survival, initially ameliorating density effects and later exacerbating them (Zajac et al. 1989). Underwood et al. (1983) showed that barnacles reduced survivorship of recruits of the limpet *Cellana tramoserica*, probably by decreasing the space available for grazing. In sedimentary habitats, competition for food may be less important as a source of early post-settlement mortality. Although recruitment rates of several species of bivalves in soft bottom habitats are inversely related to the density of adult conspecifics (e.g. Peterson 1979, Möller 1986, Thrush et al. 1996), this is attributed primarily to a reduction in settling larvae by filter feeding adults rather than early juvenile mortality (Ólafsson et al. 1994). For example, Williams (1980b) found that settlement of clams (*Tapes japonica*) on a beach in Washington was greater in areas with low or moderate densities of adult clams, but adult density had no effect on survival of early juvenile clams (Williams 1980a).

RECRUIT-SETTLER RELATIONSHIP

Relationship between recruit and settler density

A positive relationship between the abundances of recruits and settlers (measured at 1-4 day intervals) has been found in most studies of sessile species (mainly barnacles). Recruitment of the barnacle *Chthamalus fissus* in Costa Rica reflected settlement for the first 120 days (Sutherland 1990). Similarly, settlement explained >70% of the variance in the number of *Chthamalus anisopoma* reaching maturity (6 weeks of age) in the Gulf of California, Mexico (Raimondi 1990), and in the abundance of *Semibalanus balanoides* recruits at the end of the main settlement season in Nova Scotia, Canada (Minchinton & Scheibling 1991). Connell's (1985) analysis of unpublished data from several studies of barnacles revealed a positive relationship between recruit and settler density for *Tesseropora rosea* at 2 of 3 shore levels in Australia, and for *Semibalanus balanoides* in England but not in Scotland or Massachusetts, USA. In Rhode Island, USA, Bertness et al. (1996) found that interannual differences in abundance and distribution of recruits of *S. balanoides* reflected settlement patterns associated with wind-induced changes in larval concentrations. Davis (1988a) monitored settlement of the colonial ascidian *Podoclavella moluccensis* on wooden pilings in South Australia and found that settlement explained 86% of the variation in recruitment one month later. In California, zooid density of 2-4 week old bryozoans (*Membranipora membranacea*) was primarily related (68% of variance) to recruitment which was monitored bi-weekly (Yoshioka 1986).

Studies of the relationship between recruit and settler abundance for mobile species have produced variable results. In North Carolina, USA, density of settlers of the bay scallop *Argopecten irradians concentricus* on spat collectors explained 71% of the variance in the number of recruits 2 months later in 1988, but only 4% in 1989 when settlement was very high at 2 sites (Peterson & Summerson 1992). Herrnkind and Butler (1994) were unable to make consistent, accurate predictions of recruitment of the spiny lobster (*Panulirus argus*) over 3 years in Florida Bay, USA, based on samples of lobster larvae in the plankton, settlers on floating and benthic collectors, and information on geography and substratum type. More accurate models were generated based on data from a single year, but the most influential variables varied from year to year. Butler and Herrnkind (1997) experimentally tested the importance of settler abundance and availability of shelters for recruitment of *P. argus*. They found that the number of small juvenile lobsters increased at sites where artificial shelters were added, apparently as a result of reduced predation on small juveniles, but was not measurably increased by the addition of new settlers. In New Zealand, Morgan et al. (1982) found no clear relationship between density of juveniles of the rock lobster *Panulirus cygnus* and density of settlers on collectors 1-1.3 years earlier, although Chittleborough and Phillips (1975) had reported a significant relationship based on a smaller portion of the same data set. However, Phillips (1990) suggested that the estimates of densities of juvenile rock lobsters, based on mark-recapture methods, are inaccurate due to migration of lobsters among reefs. There appears to be a stronger relationship between abundances of the early life history stages of the American lobster (*Homarus americanus*) in the Gulf of Maine, USA. Incze and Wahle (1991) found that the number of 1-year-old lobsters (10-16 mm) was significantly correlated with the density of recent benthic recruits (7-8 mm carapace length) sampled the previous year. In Australia, the density of juvenile (> 3 mm carapace length) tiger prawns (*Penaeus semisulcatus*) was related to the density of recently settled benthic postlarvae (< 3 mm) 2 weeks earlier (Vance et al. 1996).

For soft bottom communities, studies examining temporal variability in early juvenile densities provide some information about the recruit-settler relationship. Muus (1973) monitored densities of 11 species of infaunal bivalves (<2 mm shell length) in Denmark. Abundances of most species decreased rapidly after settlement peaked and leveled off at a density unrelated to the peak settler abundance. In South Carolina, USA, Feller et al. (1992) examined the correspondence between peaks of abundance of meiofaunal (<0.5 mm) and macrofaunal-sized (>0.5 mm) polychaetes and bivalves in sediment samples and larvae in plankton tows. There was better correspondence between peaks of abundance of meiofaunal-sized individuals and planktonic larvae than between macrofauna and larvae, or between macrofauna and meiofauna, suggesting that mortality of new settlers was variable.

McGuinness and Davis (1989) have suggested that using correlation or regression to analyze the relationship between recruit and settler abundance (as was done in most studies described above) is not appropriate because recruit density is constrained to be equal to or less than settler density. However, the relationship between recruitment and settlement in these studies is generally clear even without the use of statistics. McGuinness and Davis (1989) suggested that statistical analyses should be confined to the relationship between mortality and initial settler density. Analysis of the relationship between mortality and settler density is useful, but may not reveal whether spatial or temporal patterns of recruitment reflect differences in settlement (see next section).

Under what conditions are recruit and settler densities positively related?

Connell (1985) suggested that recruitment will reflect settlement only when early post-settlement mortality is density independent. However, Holm (1990) pointed out that settlement and recruitment may still be positively related when mortality is weakly density dependent. When mortality is positively density dependent, predictions of recruitment will be most accurate when settler densities are low, whereas when mortality is inversely density dependent, predictions will be most accurate at high settler densities (Holm 1990).

Positive density dependence of early post-settlement mortality may result from density dependent predation (Hurlbut 1991a,c, Gaines & Roughgarden 1985), lack of suitable settlement sites (McShane 1991) or crowding (Weiss 1948). Crowding may be a less important cause of density dependent mortality for recent settlers than it is for recruits which have grown large enough to contact one another (e.g. barnacles: Grant 1977, Denley & Underwood 1979, Bertness 1989, Stephens & Bertness 1991). Inversely density dependent mortality of recent settlers may arise when conspecific settlers provide protection to one another from harsh physical conditions, as is the case for post-recruitment mortality of the barnacle *Semibalanus balanoides* in the high intertidal zone (Bertness 1989, Stephens & Bertness 1991).

Studies have reported a positive relationship between recruitment and settlement when mortality was density independent (most studies analyzed by Connell 1985, Davis 1988a, Raimondi 1990, Minchinton & Scheibling 1991) or inversely density dependent (Minchinton & Scheibling 1991). McGuinness and Davis (1989) reanalyzed the data of Davis (1988a) by weighted least-squares regression (to meet the assumption of homogeneity of variances), and those of Caffey (from Connell 1985) by pooling observations, and found significant inversely density-dependent mortality. These studies, all but one of which involved barnacles, are the only ones to have simultaneously examined the relationship between recruit and settler abundance and the density dependence of early post-settlement mortality. No consistent trend in the density dependence of early mortality has emerged from other studies of sessile invertebrates. Early post-settlement mortality was positively density dependent for the ascidian *Didemnum candidum* on floating docks (Hurlbut 1991c) and for barnacles (predominantly *Balanus improvisus*) on settlement panels (Weiss 1948). Hurlbut (1991a) found that mortality of 1 day old juveniles was density dependent for the 3 most abundant settlers on subtidal plates (the serpulid polychaete *Hydroides elegans*, the bivalve *Anomia nobilis*, and the bryozoan *Schizoporella unicornis*) but not for the less abundant ascidians (*Phallusia nigra*, *Didemnum candidum*, *Diplosoma listeranium*, and *Diplosoma* sp.). In laboratory studies, survivors of the coral *Porites porites* were clumped (Goreau et al. 1981), suggesting inversely density dependent mortality, while early post-settlement mortality of the oyster *Crassostrea virginica* was density independent (Roegner 1991). Mortality of bryozoans (*Bugula neritina*) transplanted to the field on artificial seagrass blades was either inversely density dependent or had no trend with density (Keough 1986, Keough & Chernoff 1987).

The density dependence of early post-settlement mortality of mobile species has been examined in fewer studies. McShane (1991) found that the decrease in recruit density (after 5 mo.) of the abalone *Haliotis rubra* in southeastern Australia depended on initial recruit density. In contrast, Haywood and Staples (1993) reported that mortality rate of cohorts of the prawn *Penaeus merguiensis* was not significantly related to prawn density, although densities decreased dramatically within 2 weeks of settlement regardless of initial density. Guillou and Tartu (1994) found that the decline in density of the bivalve *Cerastoderma edule* during the early post-settlement period was not clearly related to initial recruit density. Early post-settlement mortality of sea stars (*Acanthaster planci*) transplanted to the field was density independent (Keesing et al. 1996). Pile et al. (1996) found a hyperbolic relationship between densities of small instars of the blue crab *Callinectes sapidus*, indicating density-dependent processes. They suggested that this relationship was more likely due to emigration from the nursery habitat than to mortality.

Temporal or spatial variability in mortality may obscure any relationship between recruitment and settlement, even if early post-settlement mortality is density independent (Holm 1990). In the laboratory, Roegner (1991) found that temporal variability of mortality of the oyster *Crassosstrea virginica* precluded estimation of recruit density from settler density, despite density independent mortality.

EFFECTS OF SETTLEMENT AND EARLY POST-SETTLEMENT MORTALITY ON RECRUIT DISTRIBUTION

Sessile Species

Association with Substrata

Both selective settlement and early post-settlement mortality determine the distribution of recruits at small spatial scales, such as among microhabitats on the substratum. In California, USA, recruits of the ascidian *Trididemnum opacum* occurred primarily in pits and crevices because of both selective settlement and predation of more exposed settlers by fish and urchins (Keough & Downes 1986). Fish predation also determined the spatial distribution of recruits of the bryozoan *Tubulipora* spp., such that recruit abundance was related to the proportional surface area of microhabitat refuges, but it did not affect the distributions of 2 other bryozoans (*Scrupocellaria bertholetti* and *Celleporaria brunnea*) or a polychaete (*Spirorbis eximus*) (Keough & Downes 1982). In North Carolina, USA, early post-settlement mortality did not modify the distribution of recently settled barnacles (*Balanus amphitrite*) and bryozoans (*Bugula neritina*) on an artificial substrata (Lego) with uniformly spaced roughness elements (Walters 1992). Walters and Wethey (1996) found that both species selectively settled between the "bumps" which acted as refuges from predation during the first week after settlement. Larvae of 2 species (the bryozoan *Schizoporella errata* and the hydrozoan *Tubularia crocea*) with unlimited growth along the substrata (clonal encrusting and stolon-mat forms respectively) were less specific in their settlement locations and grew out of refuge locations within days (Walters & Wethey 1996).

Recruits of sessile species are also non-randomly distributed at small spatial scales on biotic substrata. In South Carolina, USA, Young (1991) found that preferential settlement resulted in greater recruitment of the barnacle *Chthamalus fragilis* in the axils of cordgrass (*Spartina alterniflora*), despite higher early post-settlement mortality in this location. In contrast, the distribution of the bryozoan *Bugula neritina* on seagrass (*Thalassia testudium*) blades in Florida resulted more from early mortality than from differential settlement (Keough 1986). Mortality of newly settled bryozoans on artificial seagrass blades transplanted to the field was lowest on the distal (oldest) parts of the blades where most adult colonies occurred; settlement accounted for < 20 % of the deviation from a uniform distribution (Keough 1986). Early post-settlement mortality also appeared to be important in determining the distribution of the colonial hydroid *Hydractinia echinata* on hermit crab shells (Yund et al. 1987). The entire surface of the shells was covered by settlement-inducing bacteria, but extensive differential mortality of juveniles resulted in the concentration of recruits on the undersurface of the shell, particularly at the aperture and siphon where polyps were bathed in the crab's feeding currents (Yund et al. 1987).

Early post-settlement mortality can also alter the association of settlers with particular substrata. Gotelli (1987) found that the association of the compound ascidian *Aplidium stellatum* with vertical surfaces in the field was stronger than the preference of larvae for vertical substrata in the laboratory, suggesting that juvenile mortality also contributed to the distributional pattern. Hurlbut (1991b) compared the distribution of settlers, juveniles, and adults of 2 species of bryozoans (*Flustrellidra hispida* and *Alcyonidium polyoum*) on various substrata in the rocky intertidal zone in New Hampshire, USA. For both species, survival of new settlers appeared to differ among substrata. The distribution of *F. hispida* seemed to result mainly from selective settlement on the most abundant alga *Ascophyllum nodosum*. However, *A. polyoum* occurred mainly on rock, although it selectively settled on the relatively rare algae *Fucus distichus* and *Chondrus crispus*. Osman (1987) found that the vermetid gastropod *Serpulorbis squamigerus* recruited primarily on encrusting bryozoans. Based on observations of newly settled individuals and measures of post-recruitment mortality, he suggested that although the general association of *Serpulorbis* with bryozoans resulted from both settlement and early post-settlement mortality, differences in recruitment among different bryozoan substrata were caused primarily by mortality.

Vertical distribution

The relative importance of settlement and early post-settlement mortality in determining the vertical distribution of barnacles differs among species. Numerous studies have noted that barnacles settle above the distributional limit of adults, usually in very small numbers, and that many of these settlers die shortly after settlement (for review see Connell 1985). The vertical distributions of some species of barnacles (*Tesseropora rosea* and *Tetraclitella purpurascens*, Denley & Underwood 1979; *Chthamalus anisopoma*, Raimondi 1988a, 1991) have been attributed to settlement patterns. The vertical range of settlement can be limited by the vertical distribution of larvae in the water column (*Balanus crenatus* and *Balanus glandula*, Grosberg 1982), induction of settlement by conspecifics (*Chthamalus anisopoma*, Raimondi 1988a, 1991), or larval avoidance of cues present on the upper shore (*Balanus cariosus*, Strathmann & Branscomb 1979). The frequency of settlement above the upper limit of adults can vary among geographic locations (Wethey 1984).

The abundance of recruits of subtidal sessile species often varies with depth. On floating docks in Hawaii, USA, non-random settlement resulted in greater abundance of the colonial ascidian *Didemnum candidum* at 0.25 m than 6 m depth, despite high density-dependent mortality of settlers (Hurlbut 1991c). Stoner (1990, 1992) demonstrated that vertical zonation of recruits of the ascidian *Diplosoma similis* in Hawaii was determined by directional larval swimming and active site selection. In contrast, post-settlement mortality appeared to determine the upper depth limit of subtidal ascidians in Florida (Dalby & Young 1992). The lack of recruits in the intertidal oyster zone did not result from larval zonation, as ascidians recruited to floating plates in this zone. Adults transplanted to the oyster zone died, primarily from physiological stress during emersion (e.g. desiccation, insolation, osmotic shock, or freezing), suggesting that new settlers, which are likely more vulnerable to these stresses, experience high mortality in this zone (Dalby & Young 1992).

Horizontal Distribution

At horizontal scales of hundreds of metres to kilometres, early post-settlement mortality appears to be less important than settlement in determining the distribution of recruits of sessile species. Gaines and Roughgarden (1985) attributed differences in the abundance of the barnacle *Balanus glandula* between 2 sites on a rocky shore in California to settlement rate since survivorship was similar or greater at the site with lower barnacle abundance. In the San Juan Archipelago, USA, Shanks and Wright (1987) found that barnacle cyprids were abundant in the convergence zone of internal waves, suggesting that cyprids (and other larvae) can be transported shoreward by these waves. Recruitment of barnacles (*B. glandula, Semibalanus cariosus*) was greater in areas of a bay where surface drifters were frequently transported by internal waves than in areas where drifters were seldom transported. In the intertidal zone of Galveston Bay, Texas, USA, differential settlement results in domination by oysters (*C. virginica*) within 10 m of shore and by barnacles (*Balanus eburneus*) further from shore (Bushek 1988). Greater settlement of barnacles on the farther pilings was attributed to both preferential settlement and a higher rate of larval supply due to greater water motion (Bushek 1988). Bingham (1992) showed that the distribution of epifaunal species among channels in a mangrove island in Florida was best explained by larval supply; early post-settlement mortality of settlers transplanted on panels was low, and varied among channels for only 1 of 5 species tested. A short larval lifespan appeared to explain the absence of the bryozoan *Bugula neritina* from some suitable sites in seagrass beds in Florida. Keough and

Chernoff (1987) found that early post-settlement mortality of transplanted bryozoans was lower at sites where adults were absent, suggesting that the patchy adult distribution results from limited dispersal of the short lived larvae rather than from post-settlement mortality. In a lagoon in the Great Barrier Reef, Olson (1985) showed that the distribution of recruits and adults of the colonial ascidian *Didemnum molle* matched the dispersal pattern of the short lived larval stage, indicating that early post-settlement mortality (which was not measured) did not modify the distribution of settlers. Also on the Great Barrier Reef, Sammarco and Andrews (1989) found that coral recruitment on plates decreased with distance from the reef, even though early post-settlement mortality due to overgrowth was higher on and directly adjacent to the reef. Coral spat were concentrated at stations with high water residence times.

Early post-settlement mortality appears to be responsible for the dominance of bryozoans in some New England, USA, fouling communities, although the contributions of larval supply and settlement to this pattern have not been examined. Osman et al. (1992) and Osman and Whitlach (1995a) found that micropredators (the gastropods *Anachis lafresnayi* and *Mitrella lunata*) dramatically reduced the recruitment of ascidians, resulting in dominance by bryozoans. The gastropods were fairly specific in their prey preference and were capable of affecting the recruitment of ascidians throughout the settlement season (Osman & Whitlach 1995a).

Mobile Species

The distributional pattern of settlers of mobile species can be modified by migration (e.g. the sea cucumber *Psolus chitonoides*, Young & Chia 1982; the gastropod *Lacuna vincta*, Martel & Chia 1991b) as well as early post-settlement mortality. Movement frequency of early juveniles of some species can be high. For example, Armonies (1994) estimated that juvenile bivalves (*Macoma balthica* and *Cerastoderma edule*) in a soft bottom community in the German Wadden Sea moved at least once a week during summer. For species with high rates of movement, patterns of settlement and early post-settlement mortality are likely to influence the distribution of recruits only at scales larger than that of the movement of early juveniles.

Several studies have found evidence that early post-settlement mortality influences the distribution of recruits of mobile epifauna. Eggleston and Armstrong (1995) found that differences between sites in settlement rate of Dungeness crab (*Cancer magister*) attributed to postlarval supply disappeared in less than 48 hours outside predator exclusion cages. The high densities of juveniles of the red and purple sea urchins (*Strongylocentrotus franciscanus* and *S. purpuratus*) beneath or near adults also have been attributed to early post-settlement mortality rather than preferential settlement or migration (Cameron & Schroeter 1980). However, Breen et al. (1985) found that juveniles of *S. franciscanus* in laboratory experiments actively associated with adults, particularly in the presence of predators, and suggested that the association in nature was due to migration rather than mortality. Early post-settlement mortality also has been implicated as a cause of between habitat differences in the distributions of *S. franciscanus* and *S. purpuratus*. After a large settlement pulse, Rowley (1989) observed high densities of recently settled urchins in both a kelp bed and an adjacent barrens area. The density of these juveniles declined more rapidly in the kelp forest than in the barrens, suggesting that the lower numbers of adult urchins in kelp forests than barren grounds results from greater mortality in the kelp habitat (Rowley 1990). However, the generality of Rowley's conclusions is limited by the lack of replicate sites and the observation of a single settlement event.

Despite the influence of both mortality and movement, settlement can in some cases determine the distribution of recruits of mobile epifauna. O'Connor (1993) found that the distributions of the fiddler crabs *Uca pugnax* and *U. pugilator* in a salt marsh in North Carolina were determined at settlement: the distributions of the 2 species differed within the marsh but the distribution of individuals of each species did not vary with age.

Early post-settlement mortality can influence the distribution of infauna in soft bottom communities. In an intertidal community in South Carolina, Luckenbach (1984) compared sites with different densities of the polychaete *Diopatra cuprea* and showed that, although *D. cuprea* tubes did not influence settlement of the bivalve *Mulinia lateralis*, they resulted in reduced numbers of bivalves in the smallest size class 1 month later. This reduction could have been due to emigration, but more likely resulted from interactions with other infauna (Luckenbach 1984). This conclusion was supported by a laboratory experiment (Luckenbach 1987) indicating reduced survival of recently metamorphosed *M. lateralis* in the presence of 2 polychaetes (*Nereis succinea* and *Streblospio benedicti*) which are common around *D. cuprea* tubes. Both settlement and post-settlement mortality appear to influence the distribution of male isopods (*Paragnatha formica*) in an English salt marsh (Upton 1987). Settlement is probably not indiscriminate as isopods were found only within a restricted vertical range and larval males were most abundant in core samples which contained adult males. However, juvenile males were disproportionately more abundant lower in the zone compared to adult males. Upton (1987) suggested that mortality of juveniles was greater lower in the zone where their molting chambers became waterlogged and anoxic. Settling larvae may be able to avoid some agents of early juvenile mortality. For example, larvae of the spionid polychaete *Pseudopolydophora kempi* appear to avoid the polychaete *Abarenicola pacifica*, whose defecation may have negative impacts on small infauna (Woodin 1985). After sediment cores were outplanted in the field for 1 week, densities of small spionids were greater in blank cores than in cores which contained an undamaged polychaete, a regenerating polychaete, or worm smell (worm removed before transplant to the field).

The vertical distribution in the deep sea of benthic invertebrates with planktonic larvae can be influenced by patterns of both settlement and early post-settlement mortality. In the Rockall Trough (2800-2900 m) off the Hebrides Islands ,U.K., Gage and Tyler (1981) found large numbers of juvenile ophuroids (*Ophiocten gracilis*), many of them corpses, in benthic samples collected in summer, but few in fall. The adult population of *O. gracilis* occurs from ca. 600 to 1200 m depth on the slope surrounding the Trough and is most likely the source of this non-viable settlement in deep water (Gage & Tyler 1981). In some cases, individuals which settle below the lower depth limit of the reproductive population survive. Mileikovsky (1961) argued, based on the hortizontal distribution of larval stages in a series of plankton samples, that the deep water population of the polychaete *Euphrosyne borealis* in the Norwegian Sea was a "pseudopopulation", existing only because of the influx of larvae from depths above 400 m.

CONCLUSIONS AND DIRECTIONS FOR FUTURE RESEARCH

Although our knowledge of the early post-settlement period is still limited, the number of studies addressing this topic is expanding rapidly. While the literature is currently biased towards a few groups of organisms (mainly barnacles and ascidians), the evidence to date suggests that early post-settlement mortality influences recruitment patterns of many different types of benthic marine invertebrates. The importance of events during this period arises from the very high rates of mortality of recent settlers (usually Type III survivorship, although mortality in the first few hours to days after settlement has only been observed for a few species) and the spatial and temporal variability of this mortality. Mortality patterns of early juveniles can not necessarily be predicted from those of adults because vulnerability to different sources of mortality often varies with size (age). In many studies, spatial patterns of settlement or early post-settlement mortality were found to influence the distribution and abundance of adults, underscoring the importance of studying events which occur in the early benthic stage. Reviews of recruitment in other groups of marine organisms [e.g. benthic algae (Vadas et al. 1992) and coral reef fish (Booth & Brosnan 1995)] also have suggested the importance of high rates of early post-settlement mortality, but have not as yet established a clear link between early juvenile mortality and the distribution and abundance of recruits.

Factors which are known to cause mortality of recent settlers of benthic marine invertebrates include biological and physical disturbance, delay of metamorphosis, physiological stress, predation, and competition for food and space (Gosselin & Qian 1997, this review). Predation has been the best documented cause of early post-settlement mortality, particularly for mobile invertebrates, but most studies have focused on individuals several weeks to months after settlement. Similarly, mortality of juvenile fish on coral reefs is most often attributed to predation (Hixon 1991, Booth & Brosnan 1995). Physical disturbance has received relatively little attention as a source of early post-settlement mortality of invertebrates, although wave action and water flow have been shown to cause mortality of macroalgal zygotes and germlings (for review see Vadas et al. 1992) and probably have the same effect on invertebrate settlers in the intertidal zone of rocky shores. Many causes of mortality of recently settled algae are similar to those reported for sessile invertebrates, including grazing, canopy effects, presence of algal turf, and desiccation (reviewed by Vadas et al. 1992). Disease and parasitism are potential causes of early post-settlement mortality which have not yet been addressed, although the importance of these agents of mortality among older life history stages of marine invertebrates is well known (Kinne 1980). Problems arising at or before metamorphosis, such as developmental abnormalities (Rumrill 1990), complications during metamorphosis (Roegner 1991), or insufficient energy reserves (Gosselin & Qian 1996), are other possible causes of early post-settlement mortality which should be investigated. Observations of recently settled individuals under benign conditions in laboratory aquaria may give some indication of the frequency of such problems and their influence on survivorship. Even at sublethal levels, disease, parasitism, developmental abnormalities, or poor physiological condition may increase mortality by increasing the susceptibility of recent settlers to predation or physical disturbance. Future studies of early post-settlement mortality should evaluate the influence of the various causes of mortality on patterns of abundance and distribution of recruits. Because of the lack of data on many of the causes of early post-settlement mortality, it is not presently possible to rank the various factors as selective pressures (Gosselin & Qian 1997).

Early post-settlement mortality did not obscure the relationship between recruit and settler abundance in most studies of sessile invertebrates (almost all of barnacles), but this relationship appears to be more variable among mobile species. When recruit and settler density were related, mortality was either density independent or inversely density dependent. However, there is still insufficient data to support general conclusions about the conditions under which recruitment rate can be predicted from settlement rate. Studies examining the relationship between recruit and settler density under conditions of both density dependent and density independent mortality, and over a range of settler densities, are needed before conclusions can be drawn. Both early post-settlement mortality and settlement patterns have been shown to affect the distribution of recruits of sessile species at small spatial scales, but there is less evidence of the influence of mortality at larger scales. In addition to migration, early post-settlement mortality modifies the distribution of recruits of some mobile species. Differences among spatial scales in the importance of early post-settlement mortality may result from variation in the relative importance of different causes of mortality. Variation in the processes operating at different spatial scales has been documented for settlement. For example, active habitat selection becomes important at scales of centimetres to metres, but larvae tend to be passively deposited at large spatial scales (reviewed by Butman 1987). However, the scale dependence of differing processes influencing early post-settlement mortality has not yet been addressed.

Early post-settlement mortality probably exerts strong selective pressure on settlement patterns of both sessile and mobile invertebrates. A number of invertebrate species selectively settle in locations where early post-settlement mortality is low (Highsmith 1982, Young & Chia 1984, Davis 1987, Hurlbut 1993). However, species with widely dispersing larvae may encounter different agents of mortality in different areas, resulting in "fatal errors of set" (Strathmann et al. 1981). There may be tradeoffs between early post-settlement survivorship and adult or juvenile mortality (Keough 1986, Schubart et al. 1995). These tradeoffs can only be assessed in studies which examine the spatial and temporal variability of mortality of both settlers and older individuals. Genotype-specific post-settlement selection has been documented for mussel populations (for review see Gosling 1992), but most studies have not isolated the stage at which selection occurs. Pedersen (1991) examined temporal variation in isozyme frequencies within *Mytilus trossulus* and found no evidence of early post-settlement selection. Further genetic studies contrasting settlers and recruits are necessary to determine whether post-settlement selection varies among different micro-habitats or under different environmental conditions.

Studies of barnacles and ascidians have contributed much of our knowledge of early post-settlement mortality of benthic invertebrates. More information is now needed for other groups of benthic marine invertebrates, particularly mobile ones. Obtaining information about the fate of settlers of mobile species, which may undertake frequent and extensive movements or remain cryptic or buried in sediment, is much more difficult than mapping sessile organisms on exposed substrata. A combination of methods will probably prove most useful. Field experiments involving tethering and predator enclosures or exclosures can be used to identify causes of mortality (e.g. Table 2.3). Settlement rate on collectors or in passive settlement traps can provide an index of larval supply for comparison with subsequent censuses of recruits (e.g. collectors: Morgan et al. 1982, Peterson & Summerson 1992, Herrnkind & Butler 1994, Forcucci et al. 1994, Eggleston & Armstrong 1995, Balch & Scheibling in press; tube traps: Wilson 1990), although patterns and rates of settlement on artificial substrates may differ from those on natural substrata (e.g. Chapter 4). Laboratory reared settlers can be transplanted to the field to examine mortality shortly after settlement when individuals from naturally settled cohorts are rare or difficult to detect (e.g. Keesing & Halford 1992, Ray & Stoner 1995, Keesing et al. 1996). Tagging and marking methods using dye (Qian & Chia 1994), microwire tags (Forcucci et al. 1994), nailpolish (Gosselin 1993), and plastic "bee" tags (Barbeau et al. 1996) have been developed which enable researchers to follow the fate of individuals or cohorts of very small invertebrates. Time-lapse video photography may reveal early mortality events such as predation or dislodgment, particularly at times (e.g. at night or during storms) when direct observations in the field are difficult or impossible.

The relative importance of the early post-settlement period compared to other life history stages can only be determined in studies which examine several stages. Studies examining larval supply, settlement, and early post-settlement mortality (or recruitment) are necessary to provide information about the contribution of the various components of recruitment (e.g. Davis 1988a, Bertness et al. 1992, Eggleston & Armstrong 1995). The importance of settlement and recruitment rates in regulating the dynamics of adult populations are best addressed in studies which follow individuals from settlement to adulthood (e.g. Davis 1988a, Raimondi 1990, Minchinton & Scheibling 1991) or compare patterns of abundance and distribution of various age classes over a time series (e.g. Peterson & Summerson 1992, Feller et al. 1992, Pile et al. 1996). Comparison of the distributions of different cohorts (settlers, recruits, and adults) at a single time also can provide valuable information (e.g. Grosberg 1982, Raimondi 1988a, Hurlbut 1991b,c, O'Connor 1993), but may confound temporal variation in abundance of cohorts with patterns of mortality. Matrix models can be used to explore the sensitivity of adult population size to changes in settlement rate and survivorship of various stages (e.g. Hughes 1990), although such models have seldom been applied to studies of marine invertebrates.

Finally, one of the major impediments to any synthesis of studies of recruitment in benthic marine invertebrates is the ambiguity in the operational definition of recruitment. While an operational definition of recruitment is appropriate to fisheries research (ie. the size at which new individuals join the harvestable stock), there is no clear analogue in ecological studies of the marine benthos. The body size at which new individuals are recorded in invertebrate populations will be determined by the growth rate of early juveniles and (or) their behavioural and morphological adaptations for crypsis (perhaps by the persistence and eyesight of the observer as well!). Thus, the utility of the term recruitment according to its current usage in ecological studies of benthic marine invertebrates is questionable. The input of new individuals to a population can be quantified by censusing juveniles (= recruits) at a particular size or time after settlement without invoking a term which may do more to obfuscate than clarify an ecological process. Recruitment may be more meaningful if it is used to quantify the addition of new individuals to the adult (breeding) population. This would require knowing the size (age) at sexual maturity for a given species, which can vary among populations and habitats but is easily measured in most cases. Recruitment as the number of individuals undergoing the transition to adulthood, a discrete biological event, would provide a more readily quantifiable and standardized measure of a demographic process than that given by current definitions of the term.

CHAPTER 3: Spatial and temporal variability of patterns of colonization by mussels (*Mytilus trossulus, M. edulis*) on a wave-exposed rocky shore

INTRODUCTION

Studies of the role of recruitment variability in the population and community dynamics of benthic marine invertebrates have focused largely on processes influencing patterns of settlement by planktonic larvae (reviewed by Butman 1987, Pawlik 1992, Rodriguez et al. 1993). However, many benthic marine invertebrates, particularly molluscs, can disperse in the water column as juveniles (e.g.Sigurdsson et al. 1976, Beukema & de Vlas 1989, Martel & Chia 1991a, Armonies 1992). When the rate of waterborne dispersal of juveniles is high, it may be an important determinant of the distribution and abundance of adults (Woodin 1991). Post-settlement transport of juvenile molluscs can be actively initiated (Martel & Diefenbach 1993), and is generally facilitated by the production of long byssal threads which increase hydrodynamic drag (Sigurdsson et al. 1976, De Blok & Tan-Maas 1977, Lane et al. 1985, Martel & Diefenbach 1993). Young post larval mussels can use threads to drift in the water column at least until they reach a size of ~2 mm shell length (Sigurdsson et al. 1976, De Blok & Tan-Maas 1977, Lane et al. 1985). Bayne (1964) demonstrated that *Mytilus edulis* entered a secondary pelagic phase at a size of 1-2 mm and moved from initial settlement sites on filamentous algae to a more permanent attachment on established beds of adult mussels. Although a temporary association between recently settled mussels and filamentous algae has been observed in several other studies (e.g. Seed 1969a, King et al. 1989), mussels also may settle directly onto adult mussel beds (McGrath et al. 1988, Cáceres-Martínez et al. 1993, 1994). Patterns of post-settlement dispersal may partially account for sporadic and unpredictable pulses of recruitment which characterize many populations of *Mytilus* (Seed & Suchanek 1992). Although byssal drifting in the water column generally involves small juveniles (<5 mm in length), larger mussels may be redistributed by wave action or may move by crawling (Chapter 6; Paine 1974).

In this chapter, I examine patterns and rates of colonization of mussels (*Mytilus trossulus, M. edulis*) in tidepools and on emergent rock, both in ice-scoured and non-scoured regions of an exposed shore in Nova Scotia, Canada. The abundance and spatial distribution of mussels differ between tidepools and emergent rock: mussels in tidepools generally occur in centimeter-scale patches, whereas those on emergent rock tend to form more extensive beds with centimeter-scale gaps (Hunt & Scheibling 1995, Minchinton et al. 1997). Tidepools and emergent rock differ in several aspects which may influence mussel colonization (see also Chapter 4). For example, they have different macroalgal assemblages (the substrata upon which mussels settle) and they are differentially affected by occasional ice-scour which generally disturbs tidepools less than emergent rock. To examine the relative importance of initial settlement/colonization compared to subsequent dispersal and mortality in determining the distribution and abundance of mussels, I compare patterns and rates of mussel colonization at sampling intervals of days to months over a 17 mo period.

MATERIALS AND METHODS

This study was conducted at an exposed rocky shore at Cranberry Cove (44° 28' N, 63° 56' W) near Halifax, Nova Scotia, Canada. The shore is composed of granite platforms and outcrops with occasional large boulders (glacial erratics). There are numerous tidepools in irregular depressions along the shore, ranging from a few decimeters to over 10 m in maximum dimension. The shore is exposed to southerly swells which may reach 10 m in significant wave height (average height of the largest 1/3 of all waves measured) in fall and winter (unpubl. data, Department of Fisheries and Oceans, Canada).

Because *M. trossulus* and *M. edulis*, the two species of mussels at my study site cannot be distinguished visually at small size, I used genetic assays to compare the relative abundance of the two species between habitats. A preliminary sample of 27 mussels (4 to 44 mm in shell length (SL)) was collected from tidepools and emergent rock in March 1996 and identified to species by polymerase chain reaction/restriction fragment length polymorphism assays using a marker for the female mitochondrial DNA lineage (Rawson & Hilbish 1995a,b) and a nuclear DNA marker for the adhesive foot protein (Rawson et al. 1997). In March 1997, I collected 32 mussels in 3 size classes, <5 mm (n=8), 5-9.9 mm (n=8), and 10-24.9 mm SL (n=16) from each of three tidepools and three adjacent areas of emergent rock. The mussels were identified to species using a polymerase-chain-reaction-based assay of a nuclear DNA segment (the ITS marker) described by Heath et al. (1995). DNA was extracted from the whole animal for mussels <10 mm, and from gill tissue for individuals ≥10 mm.

Between July 1993 and December 1994, I measured colonization by mussels in two habitats, tidepools and emergent rock, within each of two strata in the mid intertidal zone, areas scoured by sea ice and non-scoured areas. To set up a factorial design, I selected 12 plots (tidepools or areas of emergent rock) along a horizontal distance of ~ 1 km of shoreline to make up 3 replicates of each of the 4 combinations of habitat and stratum. Tidepools ranged from 2.7-7.2 m in length, 1.1-2.8 m in width, and 0.3-0.6 m in depth; plots of emergent rock were comparable in area. Non-scoured tidepools were somewhat higher on the shore (1.4-2.3 m above chart datum) than the other combinations of habitat and stratum (0.8-1.6 m) (Fig. 4.1a). An index of water flux was higher on emergent rock than in tidepools, and higher in ice-scoured than non-scoured areas (Fig. 4.1b). At the beginning of this study, emergent rock surfaces in areas scoured during winter 1992-93 were bare except for the scattered thalli of crustose macroalgae, whereas upright macroalgae remained in ice-scoured tidepools.

I recorded colonization by mussels within 10 x 10 cm quadrats on the natural substratum. I prepared 12 quadrats per plot in July 1993 by removing the existing mussels with forceps or a pipette to avoid disturbing the rest of the macrobenthic community. I also removed mussels (with a paint scraper) from a 10-cm border around each quadrat to limit migration into the quadrat. The quadrats were spaced at least 10 cm apart and marked by stainless steel screws in plastic anchors. I define initial colonization as the arrival of mussels in the quadrats by larval settlement and/or post-settlement dispersal (secondary settlement, sensu Bayne 1964). I examined the effects of post-colonization mortality and dispersal on patterns of initial colonization of mussels by sampling quadrats (i.e. collecting all mussel colonists) at different frequencies, since the extent of mortality and dispersal will be directly related to the interval between samples (Minchinton & Scheibling 1993b). I sampled three quadrats per plot at short sampling intervals, 2-7 d (spring to fall) to 30 d (winter), resulting in a total of 105 sampling dates over 17 mo. I examined patterns of longer term colonization over the same period by sampling mussels in three quadrats per plot at each of three successive 5 to 6 mo intervals, i.e. in November 1993 (5 mo), May 1994 (11 mo), and October 1994 (16 mo). To examine the effects of season on patterns of long term colonization, I collected colonists from the initial 5 mo quadrats at two other times, May and November 1994, after 5 to 6 mo periods. This enabled me to examine seasonal variation between a winter interval, November 1993-May 1994, and the preceding and subsequent summer/fall intervals (July-November 1993, May-October 1994). Mussels were collected from each quadrat using forceps or a pipette. A magnifying glass was used to detect settlers and small postlarval mussels. A small proportion of <0.5 mm mussels, particularly those in filamentous or jointed calcareous algae, may not have been detected. However, unless these individuals died or dispersed immediately, they would have been detected when they grew larger. After the short sampling intervals (2 to 7 d) and the first and second 5 to 6 mo intervals, mussels were collected without disturbing the rest of the macrobenthic assemblage. After the 11 mo interval, the 16 mo interval, and the third 5 to 6 mo interval, mussels were collected by removing all macroalgae from the quadrats. Removal of all of the macroalgae during sampling may have slightly increased the number of <0.5 mm mussels detected, but should not have introduced a large bias in the counts. Samples were frozen until they could be processed. Mussels were counted and shell length was measured in 0.5 or 1 mm size classes using an ocular micrometer on a dissecting microscope for the smallest individuals, or vernier calipers for larger ones (>5 mm SL).

I grouped the mussels collected at the shortest sampling intervals (2-7 d) into 4 size classes: <0.5, 0.5-1.9, 2-4.9, and >5 mm SL. I refer to mussels which are <0.5 mm SL as settlers because they are equal to or smaller than the maximum size of settling larvae (Bayne 1965). I grouped 0.5 to 1.9 mm mussels because individuals in this size class are capable of drifting using byssal threads and are known to disperse frequently in some populations (reviewed by Seed & Suchanek 1992). I summed, separately, the total number of mussels from each size class collected from each quadrat for each of the two main colonization periods in my study: July to November 1993 and May to November 1994. Short term colonization rate was negligible during winter/early spring (see Results). Analyses were carried out using ANOVA. Cumulative colonization based on short term samples was compared among plots, habitats (tidepool, emergent rock), and strata (scoured, non-scoured) for each size class in both the 1993 and 1994 colonization periods. In the analysis, Habitat and Stratum are fixed factors, each with two levels, and Plot is a random factor nested within Habitat x Stratum, with 3 levels. Effects of Habitat, Stratum, and the interaction between Habitat and Stratum were tested against the mean square error of Plot, and the effect of Plot was tested against the residual mean square error. The numbers of colonists at the end of the three 5 to 6 mo intervals were analysed using the same model. To compare colonization at the end of the 5, 11, and 16 mo intervals beginning in 1993, Time, a fixed factor with three levels (5, 11, 16 mo) was added to the model. Effects of time and the interactions between Time, Habitat, and Stratum, were tested against the mean square error of the interaction between Time and Plot. The interaction between Time and Plot was tested against the residual mean square error. Prior to ANOVA, the raw data were log or log (x+1) transformed to successfully remove heterogeneity of variance, as detected by Cochran's test ($\propto$=0.05). For post-hoc comparisons of means (α=0.05), I used t-tests for comparisons of two means and Student-Newman-Keuls (SNK) tests for comparisons of multiple means.

I measured the cover of macroalgae, barnacles (*Semibalanus balanoides*), and mussels on the substratum in each of the quadrats in September 1993, and April, July, and October 1994. A plexiglass panel with 20 random points was placed over a quadrat and the number of points overlying each species were counted and expressed as a percentage of the total. Macroalgae were assigned to functional form groups after Littler (1980) and Littler and Littler (1984): sheets, filamentous, coarsely branched, thick leathery, jointed calcareous and crustose forms.

RESULTS

Genetic Analysis

Analysis of the mussels collected in 1996 indicated that ~80% of mussels both in tidepools and on emergent rock were *M. trossulus* (tidepools: *M. trosslus*, 8, *M. edulis*, 2; emergent rock: 13, 3, respectively). I compared the frequency of *M. trossulus* and *M. edulis* (Table 3.1) collected in 1997 among size classes (<5, 5-9.9, ≥10 mm) and between tidepools and emergent rock using contingency tables. Hybrids were not included in the analysis because of their low abundance (≤3 individuals per size class per habitat). The frequency of occurrence of *M. trossulus* and *M. edulis* did not differ significantly among size classes in tidepools (G_2=1.93, p=0.38) or on emergent rock (G_2=5.64, p=0.06), where the difference was only marginally non-significant. The frequency of the two species (pooled across size classes) did not differ significantly between tidepools (76%) and emergent rock (66%) (G_1=1.20, p=0.27).

Colonization over short sampling intervals

Less than 4 % of mussels which colonized the quadrats sampled at short (2 to 7 d) intervals (Fig. 3.1) were settling larvae (<0.5 mm SL). Settlement occurred from August to November, while larger mussels colonized the quadrats over a more extended period from May to December. The daily colonization rate by all size classes of mussels was negligible in winter/early spring (January to April 1994). Settlement of <0.5 mm mussels peaked in September in 1993 and in August and October/November in 1994. Colonization by larger size classes was at a peak when sampling began in July 1993 and again in June/July 1994. Colonization by 0.5-1.9 mm mussels also peaked in September/October in both years.

ANOVA (Table 3.2) showed a significant interaction in the effects of habitat and stratum on the cumulative density of colonists for each size class of mussels in both years, except for 2-4.9 mm mussels in 1994 when the interaction was marginally non-significant and the cumulative density of colonists was significantly higher in tidepools than on emergent rock. Post hoc comparisons of means showed that settlers (<0.5 mm) were 1-2 orders of magnitude more abundant in tidepools than on emergent rock in ice-scoured areas, but did not differ significantly between habitats in non-scoured areas (Fig. 3.2, Table 3.2). Cumulative abundance of settlers was significantly higher in ice-scoured than in non-scoured areas in tidepools, but did not differ significantly between strata on emergent rock. In contrast, cumulative abundance of larger colonists was more similar among ice-scoured tidepools and non-scoured tidepools and emergent rock, but was consistently lowest on ice-scoured emergent rock (Fig. 3.2). Cumulative colonization by these larger mussels was significantly higher in tidepools than on emergent rock in ice-scoured areas, but did not differ significantly between habitats in non-scoured areas

(Table 3.2). Moreover, colonization by larger mussels was significantly higher in non-scoured than in ice-scoured areas on emergent rock, but did not differ between strata in tidepools. There was significant variation among plots for initial settlers in 1994 but not in 1993, and for 0.5-1.9 mm mussels in both years. Variation among plots in the cumulative colonization by 2-4.9 mm mussels was marginally non-significant in both years, but there was no significant effect of plot for >5 mm mussels. In both 1993 and 1994, the cumulative number of colonists summed across size classes was highest in ice-scoured tidepools and lowest on ice-scoured emergent rock (Fig. 3.2). I did not compare colonization between years because sampling in 1993 began in July when colonization by large mussels was at a peak.

I examined the size distributions of mussel colonists by pooling individuals over the main colonization periods in 1993 and 1994 (Fig. 3.3). Small mussels were proportionately more abundant in 1993, when sampling began in July, than in 1994, when sampling was carried out throughout the entire colonization period. In each year, ≤3% of colonists in any habitat/stratum combination were recent settlers (<0.5 mm). Mussels that were 0.5-1.9 mm represented the majority (50-81%) of colonists in 1993, while 2-4.9 mm mussels were the most abundant (53-71%) colonists in 1994. Mussels that were >5 mm represented 3-8% of colonists in 1993 and 11-16 % in 1994. For each year, I compared the size distributions of mussels between strata within each habitats and between habitats within each strata using Kolmogorov-Smirnov tests (Seigel & Castellan 1988) (Fig 3.3). Mussels were pooled across quadrats and plots within a habitat/stratum combination. In both years, mussels <1 mm were proportionately more abundant in ice-scoured tidepools than in the other combinations of habitat and stratum, such that the size distributions of colonists differed significantly between ice-scoured and non-scoured tidepools, and between ice-scoured tidepools and ice-scoured emergent rock. On emergent rock, size distributions of colonists did not differ significantly between non-scoured and ice-scoured areas in each year. In non-scoured areas, size distributions of colonists did not differ significantly between tidepools and emergent rock in 1993. However, this difference was statistically significant in 1994, which reflected larger sample sizes in 1994 since the degree of difference remained small (D_{max}=0.07).

Colonization over long sampling intervals

The pattern of long term colonization was similar to the pattern of cumulative short term colonization (summed over all size classes of mussels): abundance was highest in ice-scoured tidepools and lowest on ice-scoured emergent rock (Fig. 3.4). For the 5, 11, and 16 mo intervals beginning in July 1993, ANOVA showed a significant interaction in the effects of habitat and stratum on the density of mussel colonists (Table 3.3). Post hoc comparison of means showed that the patterns of differences between habitats within strata, and between strata within habitats were the same as those of cumulative short term colonization of mussels >0.5 mm, i.e., colonization was greater in tidepools than on emergent rock in ice-scoured areas, and greater on non-scoured than on ice-scoured emergent rock. Colonization increased significantly over time, but not in proportion to the time elapsed: abundance after 5 and 11 mo was 70% and 95%, respectively, of the abundance after 16 mo (159 mussels/100 cm^2, averaged across all habitat/stratum combinations). There were no significant interactions between time interval and either habitat or stratum, nor was there a significant three-way interaction. The density of colonists also varied significantly among plots within combinations of habitat and stratum. For each of the three 5 to 6 mo intervals, ANOVA showed a significant interaction in the effects of habitat and stratum on the density of mussel colonists (Table 3.4). Differences between habitats within strata, and between strata within habitats, were the same as for the 5, 11, and 16 mo intervals beginning in 1993, except for the third 5 to 6 mo interval when the difference between non-scoured and ice-scoured areas on emergent rock was marginally non-significant (Table 3.4). Colonization varied significantly among plots within combinations of habitat and stratum after the third, but not the first or second, 5 to 6 mo intervals.

After each of the longer term (5-16 mo) intervals, mussels <5 mm represented 72 to 100% of colonists and mussels >10 mm represented <10% (Fig. 3.5). I compared the size distributions of colonists between habitats within strata and between strata within habitats for each interval. Differences in the size distributions between combinations of habitat and stratum were not consistent over time and did not reflect the pattern observed in the size distributions of cumulative short term colonization (Fig. 3.5). However, after each of the 5 to 6 mo intervals, and the 11 and 16 mo intervals, mussels <1 mm SL were proportionately less abundant on ice-scoured emergent rock than in the other combinations of habitat and stratum. The absence of significant differences in size distributions in some of the comparisons with ice-scoured emergent rock resulted from the smaller sample sizes from this habitat/stratum combination and not from smaller differences between cumulative size frequency distributions. I did not statistically compare the size distributions among time intervals because the differences were clear and larger than the differences between habitats and strata within an interval, and the analyses would have necessitated a large number of comparisons. Mussels <1 mm were proportionately least abundant in May 1994, the end of the second 5 to 6 mo interval and the 11 mo interval, and proportionately most abundant in October 1994, at the end of the third 5 to 6 mo interval and the 16 mo interval. Mussels <0.5 mm were abundant only in October 1994.

Comparison of sampling frequencies

To explore the importance of post-colonization mortality and dispersal in determining the abundance of colonists at the end of the 5 to 16 mo intervals, I used regression analysis to examine the relationship between long term (5-16 mo) colonization and cumulative short term (2-7 d) colonization during each of these intervals (Fig. 3.6).

Long term colonization was significantly related to cumulative short term colonization during the 5, 11 and 16 mo intervals beginning in July 1993. The slope of the relationship approached the maximum value of one during the first 5 to 6 mo interval and the 11 mo interval, but was lower during the 16 mo interval. During the second 5 to 6 mo interval, long term colonization also was significantly related to cumulative short term colonization, and the slope of the relationship approached one. However, during the third 5 to 6 mo interval which corresponded to the end of the 16 mo interval, the relationship was marginally non-significant. Results of these analyses should be interpreted cautiously because long term colonization is constrained to be less than cumulative short term colonization (McGuiness & Davis 1989). However, the statistically significant relationships explained >69% of the variation which is unlikely due to chance.

Differences in the size distributions of colonists sampled at short and long sampling intervals can result from growth of individuals or size specific mortality or dispersal after initial colonization. I compared the size distributions of long term colonists to those of cumulative short term colonists for the first and third 5 to 6 mo intervals (Figs. 3.3 and 3.5) using Kolmogorov-Smirnov tests. In the first 5 to 6 mo interval, mussels <1 mm were proportionately more abundant when colonists were collected at short than at long sampling intervals in both non-scoured (D_{max}=0.17, $p<0.001$) and ice-scoured tidepools (D_{max}=0.33, $p<0.001$), but proportionately less abundant when colonists were sampled at short than at long intervals on non-scoured emergent rock (D_{max}=0.15, $p<0.001$). On ice-scoured emergent rock, where sample sizes were low, size distributions did not differ significantly between sampling frequencies (D_{max}=0.25, $p>0.10$). In each habitat/stratum combination during the third 5 to 6 mo interval, mussels <1 mm were not only proportionately (D_{max}: tidepools, ice-scoured=0.46, non-scoured=0.65; emergent rock, ice-scoured=0.37, non-scoured=0.50; $p<0.001$) but also absolutely less abundant when colonists were sampled at short than at long intervals. These results indicate that, in comparison to the quadrats sampled at short intervals, the abundance of small mussels (<1 mm) in the long term colonization quadrats was enhanced during the first 5 to 6 mo interval on non-scoured emergent rock and during the third 5 to 6 mo interval in all combinations of habitat and stratum.

Spatial and temporal variation in the macrobenthic assemblage

The macrobenthic assemblage in the short and long term colonization quadrats varied markedly between habitats and strata (Fig. 3.7). Jointed calcareous algae were found only in tidepools. Sheet algae were abundant in tidepools in April 1994, but rare on emergent rock (see also Metaxas et al. 1994). Conversely, thick leathery macroalgae and barnacles generally were rare in tidepools, but were more abundant on emergent rock. Ice-scoured emergent rock lacked filamentous algae (except in April 1994) and coarsely branched macroalgae, and had a lower cover of crustose macroalgae than non-scoured emergent rock and tidepools. In ice-scoured habitats, the macrobenthic assemblage differed between years: there was a greater cover of thick leathery algae and barnacles on ice-scoured emergent rock, and of coarsely branched algae in ice-scoured tidepools, and consequently less unoccupied space in October 1994 than in September 1993 .

For the quadrats sampled for long term colonization, I also estimated the cover of mussels. Percentage cover of mussels was less than 1% after each of the three 5 to 6 mo intervals, with the exception of ice-scoured tidepools after the third 5 to 6 mo interval (x=6% cover). On average, percentage cover was less than 3% after 11 mo in each combination of habitat and stratum. After 16 mo, percentage cover of mussels was <1% on non-scoured and ice-scoured emergent rock, ~8% in non-scoured tidepools, and ~17% in ice-scoured tidepools. Because many of the colonists were associated with macroalgae, my low estimates of mussel cover may partly reflect an artifact of my sampling method which recorded only the top species/group if there were several organisms at the same point on the substratum. However, the relatively small size and low abundance (less than 3 cm^{-2}) of mussel colonists at the end of each of the 5 to 6 mo interval, the 11 mo interval, and the 16 mo interval indicates that the cover of mussels was probably not greatly underestimated.

Table 3.1. Frequency of *M. trossulus*, *M. edulis*, and hybrids of the two species in three size classes (<5, 5-9.9, and 10-24.9 mm) of mussels collected from tidepools and emergent rock in March, 1997.

			Species	
Size Class	Habitat	*M. trossulus*	*M. edulis*	hybrids
<5 mm	Tidepool	13	6	1
	Emergent rock	20	3	0
5-9.9 mm	Tidepool	19	3	1
	Emergent rock	11	9	3
10-24.9 mm	Tidepool	36	10	1
	Emergent rock	30	13	3
Total	Tidepool	68 (76%)	19 (21%)	3 (3%)
	Emergent rock	61 (66%)	25 (27%)	7 (8%)

Table 3.2. Three-way ANOVA of the cumulative density (no. 100 cm^{-2}) of mussels of each of four size classes colonizing quadrats sampled at short intervals from July to November 1993 and from May to November, 1994. Factors are Habitat (H, tidepools and emergent rock), Stratum (S, ice-scoured and non-scoured), and Plot (nested within H x S). Degrees of freedom: $F_{P(HX\ S)}$=8, 24; F_H, F_S, and $F_{Hx\ S}$=1, 8. *p<0.05; ** p<0.01; *** p<0.001. The results of a posteriori tests are presented in the column labelled comparison.When there was a significant H x S interaction, means were compared between habitats within each stratum and between strata within each habitat using t-tests (TP=tidepool, ER=emergent rock, NS=non-scoured, S=ice-scoured). = indicates a non-significant result, while < or > indicates a significant result (α=0.05)

Size Class	Source	MS	F	p	Comparison
1993					
<0.5 mm	Plot (H x S)	0.07	1.48	0.22	TP: NS<S
	Habitat	2.01	27.72	<0.001***	ER: NS=S
	Stratum	0.81	11.14	0.01*	NS: TP=ER
	Habitat x Stratum	1.34	18.50	0.003**	S: TP>ER
	Residual	0.05			
0.5-1.9	Plot (H x S)	0.65	3.71	0.006**	TP: NS=S
	Habitat	11.46	17.64	0.003**	ER: NS>S
	Stratum	0.25	0.38	0.55	NS: TP=ER
	Habitat x Stratum	6.57	10.11	0.01*	S: TP>ER
	Residual	0.18			
2-4.9	Plot (H x S)	0.29	2.21	0.07	TP: NS=S
	Habitat	4.58	15.79	0.004**	ER: NS>S
	Stratum	2.39	8.23	0.02*	NS: TP=ER
	Habitat x Stratum	2.44	8.41	0.02*	S: TP>ER
	Residual	0.14			
>5	Plot (H x S)	0.07	0.89	0.54	TP: NS=S
	Habitat	2.45	34.39	<0.001***	ER: NS>S
	Stratum	0.88	12.30	0.008**	NS: TP=ER
	Habitat x Stratum	1.18	16.54	0.004**	S: TP>ER
	Residual	0.08			
1994					
<0.5 mm	Plot (H x S)	0.18	4.40	0.002**	TP: NS<S
	Habitat	3.82	21.56	0.002**	ER: NS=S
	Stratum	2.06	11.64	0.009**	NS: TP=ER
	Habitat x Stratum	1.79	10.07	0.01*	S: TP>ER
	Residual	0.04			

Table 3.2 continued

Size Class	Source	MS	F	p	Comparison
1994					
0.5-1.9 mm	Plot (H x S)	0.40	3.90	0.005**	TP: NS=S
	Habitat	6.26	15.75	0.004**	ER: NS>S
	Stratum	0.53	1.33	0.28	NS: TP=ER
	Habitat x Stratum	2.71	6.81	0.03*	S: TP>ER
	Residual	0.10			
2-4.9	Plot (H x S)	0.24	2.32	0.05	
	Habitat	3.70	15.50	0.004**	
	Stratum	0.06	0.26	0.62	
	Habitat x Stratum	1.18	4.96	0.06	
	Residual	0.10			
>5	Plot (H x S)	0.16	1.45	0.23	TP: NS=S
	Habitat	4.60	28.81	<0.001***	ER: NS>S
	Stratum	0.12	0.78	0.40	NS: TP=ER
	Habitat x Stratum	2.08	13.05	0.01*	S: TP>ER
	Residual	0.110			

Table 3.3. ANOVA of the number of mussel colonists in 100 cm^2 quadrats after the 5, 11, and 16 mo intervals beginning in July 1993. Factors are Habitat (H, tidepools and emergent rock), Stratum (S, ice-scoured and non-scoured), Plot (nested within H x S), and Time (T, 5, 11, and 16 mo). Degrees of freedom: $F_{P(HX\ S)}=8, 72$; $F_H=1, 8$; $F_S=1, 8$; $F_{HxS}=1, 8$; $F_T=2, 16$; $F_{P(HxS)xT}=16, 72$; $F_{HxT}=2, 16$; $F_{SxT}=2, 16$; $F_{HxSxT}=2, 16$. *$p<0.05$; ** $p<0.01$; *** $p<0.001$. The results of a posteriori tests are presented in the column labelled comparison. Since there was a significant H x S interaction, means were compared between habitats within each stratum and between strata within each habitat using t-tests (TP=tidepool, ER=emergent rock, NS=non-scoured, S=ice-scoured). Since there was a significant effect of Time, means were compared among time intervals (5=5 mo, 11=11 mo, 16=16 mo) using SNK. = indicates a non-significant result, while < or >indicates a significant result ($\alpha=0.05$)

Source	MS	F	P	Comparison
Plot (H x S)	1.09	4.64	<0.001***	
Habitat	25.6	23.54	0.001**	
Stratum	1.94	1.78	0.22	
Time	1.66	7.90	0.004**	5 < 11=16
Habitat x Stratum	25.8	23.73	0.001**	TP: NS=S
Time x Plot (H x S)	0.211	0.90	0.23	ER: NS>S
Habitat x Time	0.48	2.28	0.13	NS: TP=ER
Stratum x Time	0.43	2.04	0.16	S: TP>ER
Habitat x Stratum x Time	0.34	1.61	0.57	
Residual	0.24			

Table 3.4. ANOVA of the number of mussel colonists in 100 cm^2 quadrats after the three 5 to 6 mo intervals. Factors are Habitat (H, tidepools and emergent rock), Stratum (S, ice-scoured and non-scoured), Plot (nested within H x S). Degrees of freedom: $F_{P(HX\ S)}$= 8, 24; F_H=1, 8; F_S=1, 8; F_{HxS}=1, 8. *$p<0.05$; ** $p<0.01$; *** $p<0.001$. The results of a posteriori tests are presented in the column labelled comparison. When there was a significant H x S interaction, means were compared between habitats within each stratum and between strata within each habitat using t-tests (TP=tidepool, ER=emergent rock, NS=non-scoured, S=ice-scoured). = indicates a non-significantresult, while < or > indicates a significant result (α=0.05)

Interval	Source	MS	F	p	Comparison
1st 5 to 6 mo	Plot (H x S)	0.46	1.51	0.21	TP: NS=S
	Habitat	8.25	17.82	0.003**	ER: NS>S
	Stratum	0.26	0.55	0.48	NS: TP=ER
	Habitat x Stratum	12.93	27.93	<0.001***	S: TP>ER
	Residual	0.31			
2nd 5 to 6 mo	Plot (H x S)	0.36	2.09	0.08	TP: NS=S
	Habitat	3.81	10.51	0.01*	ER: NS>S
	Stratum	0.13	0.37	0.56	NS: TP=ER
	Habitat x Stratum	4.13	11.4	0.01*	S: TP>ER
	Residual	0.17			
3rd 5 to 6 mo	Plot (H x S)	1.16	8.95	<0.001***	TP: NS=S
	Habitat	1.46	1.27	0.29	ER: NS=S
	Stratum	0.01	0.01	0.95	NS: TP=ER
	Habitat x Stratum	11.02	9.53	0.02*	S: TP>ER
	Residual	0.13			

Fig. 3.1. Colonization rate (no. 100 cm^{-2} day^{-1}) of mussels of each of four size classes (<0.5, 0.5-1.9, 2-4.9, and >5 mm SL) in quadrats in ice-scoured and non-scoured tidepools and emergent rock monitored at short (2 to 7 d) sampling intervals from July 1993 to November 1994. Data were averaged across 3 quadrats per plot and across 3 plots within each combination of habitat and stratum.

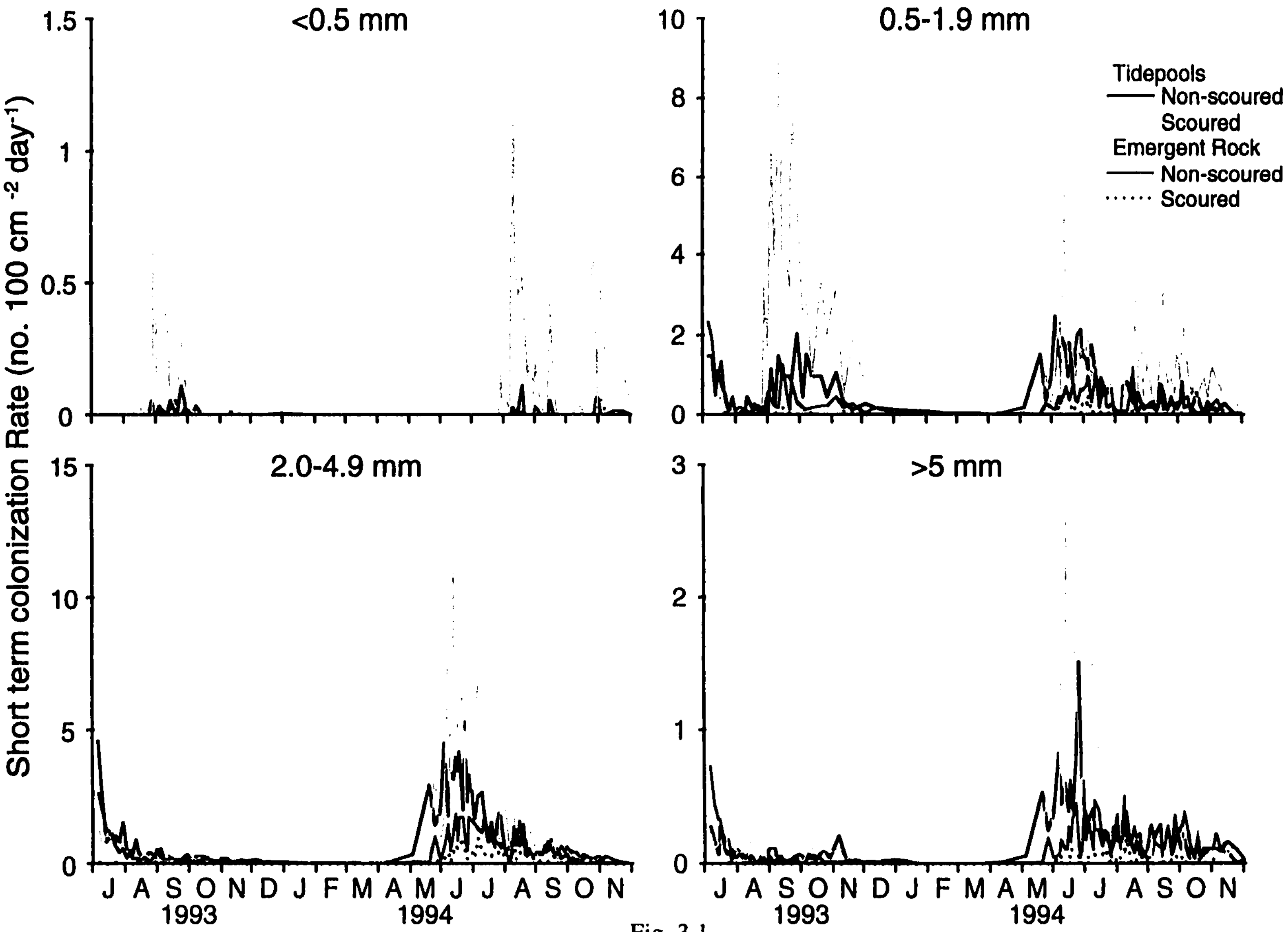

Short term colonization Rate (no. 100 cm -2 day-1)
<0.5 mm
1.5
1
0.5
0
0.5-1.9 mm
10
8
6
4
2
0
Tidepools
Non-scoured
Scoured
Emergent Rock
Non-scoured
Scoured
2.0-4.9 mm
15
10
5
0
>5 mm
3
2
1
0
J A S O N D J F M A M J J A S O N
1993
1994
J A S O N D J F M A M J J A S O N
1993
1994

Fig. 3.1

Fig. 3.2. Mean (+ S.E.) cumulative number of mussels (per 100 cm^2) collected from July to November 1993 and from May to November 1994 from the quadrats sampled at short intervals in ice-scoured and non-scoured tidepools (TP) and emergent rock (ER). Data were averaged across 3 quadrats per plot and across 3 plots within each combination of habitat and stratum.

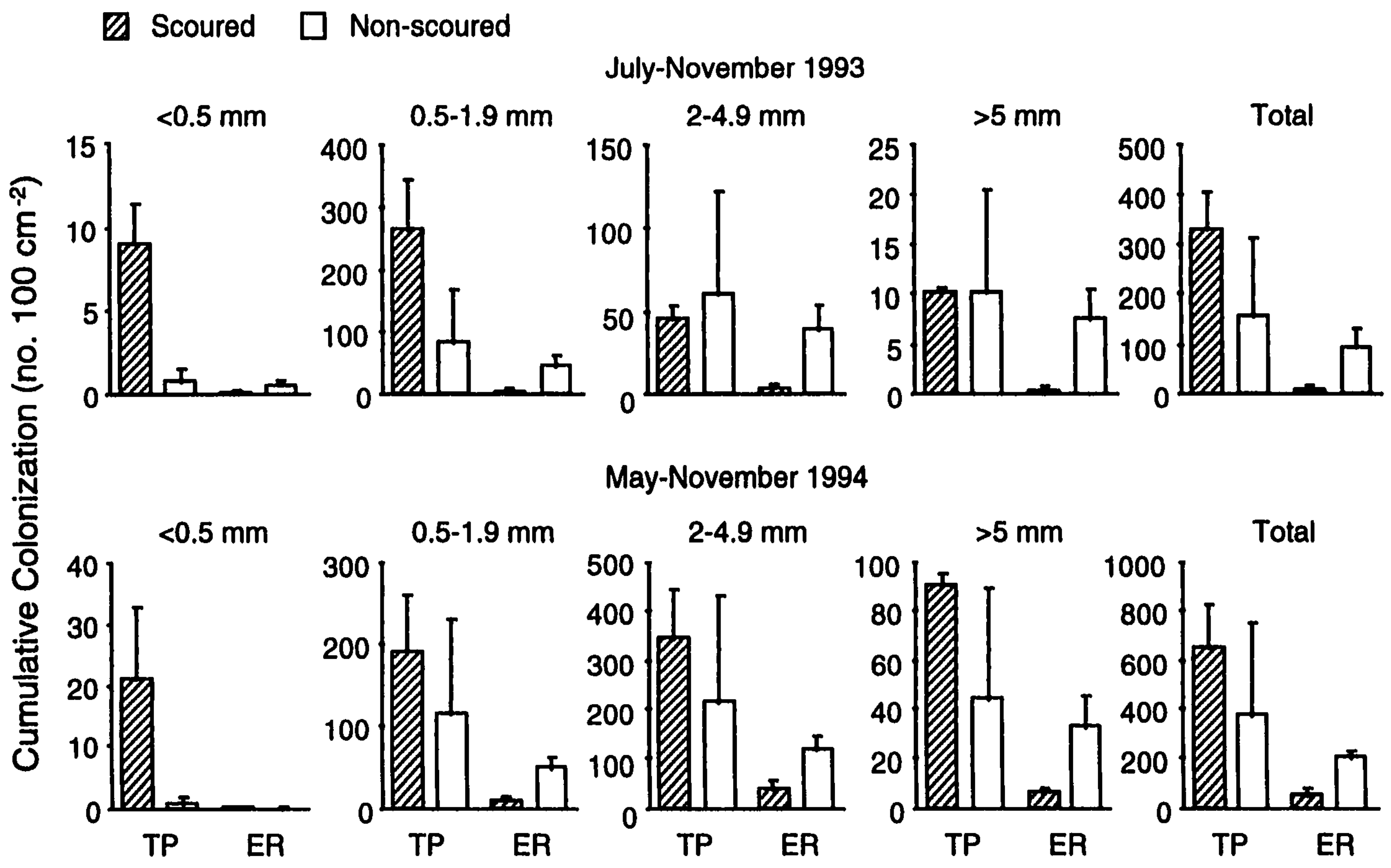
▨ Scoured
☐ Non-scoured
July-November 1993
<0.5 mm
0.5-1.9 mm
2-4.9 mm
>5 mm
Total
15
10
5
0
400
300
200
100
0
150
100
50
0
25
20
15
10
5
0
500
400
300
200
100
0
May-November 1994
<0.5 mm
0.5-1.9 mm
2-4.9 mm
>5 mm
Total
40
30
20
10
0
300
200
100
0
500
400
300
200
100
0
100
80
60
40
20
0
1000
800
600
400
200
0
TP
ER
TP
ER
TP
ER
TP
ER
TP
ER
Cumulative Colonization (no. 100 cm-2)

Fig. 3.2

Fig. 3.3 Size frequency distributions of mussels collected from July to November 1993 and from May to November 1994 from the quadrats of sampled at short intervals. Mussels were pooled across quadrats and plots within a combination of habitat and stratum. In the first bar, the black shading indicates settlers (<0.5 mm SL), while the gray shading indicates individuals which were 0.5-0.9 mm. Individuals in the last bar were >10 mm SL. Results of Kolmogorov-Smirnov tests are indicated above the panels (D_{max}, p). *** $p<0.001$, * $0.01<p<0.05$, ns $p>0.05$

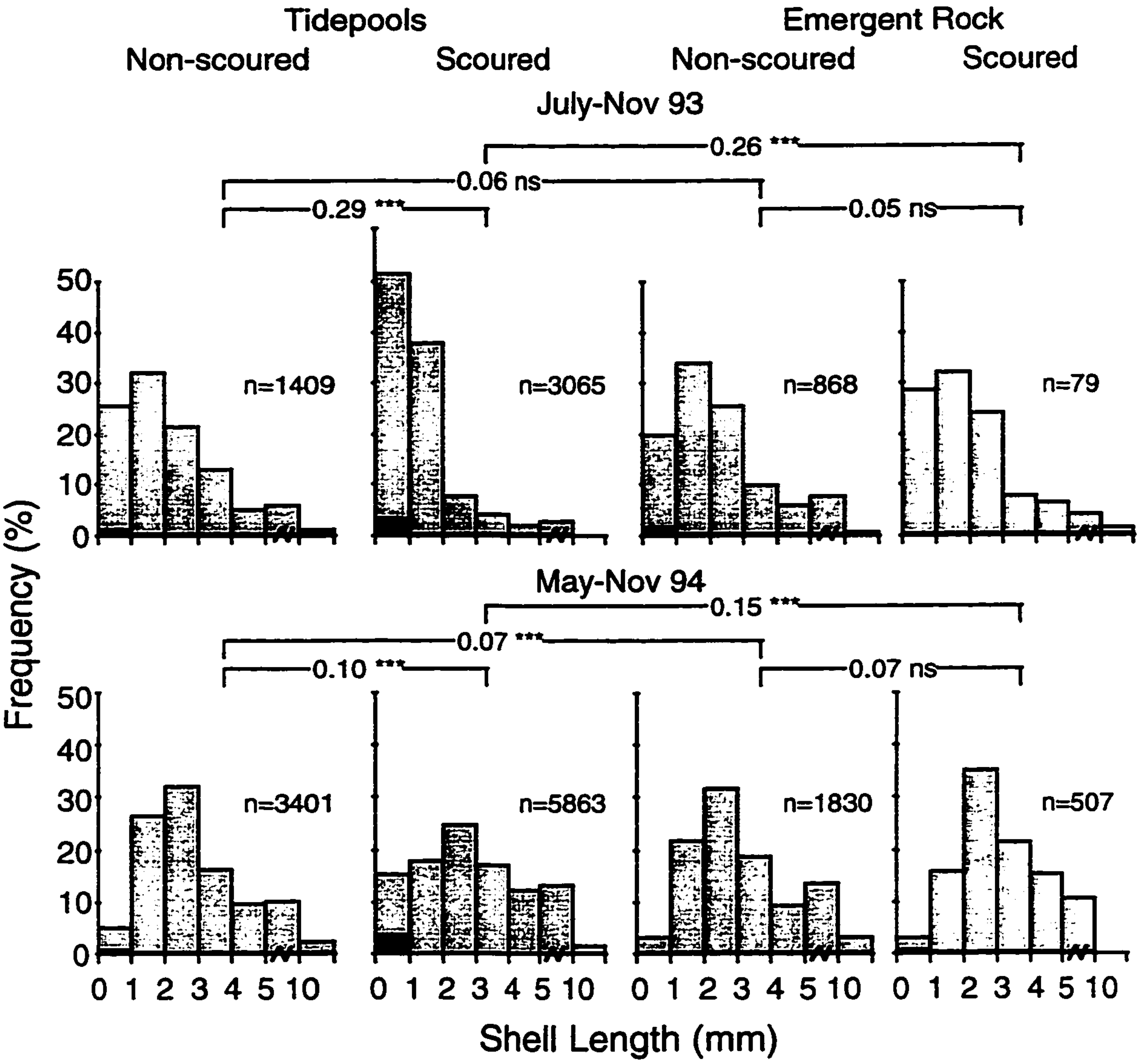

Tidepools
Emergent Rock
Non-scoured
Scoured
Non-scoured
Scoured
July-Nov 93
0.26 ***
0.06 ns
0.29 ***
0.05 ns
n=1409
n=3065
n=868
n=79
May-Nov 94
0.15 ***
0.07 ***
0.10 ***
0.07 ns
n=3401
n=5863
n=1830
n=507
Frequency (%)
0
10
20
30
40
50
0 1 2 3 4 5 10
Shell Length (mm)

Fig. 3.3

Fig. 3.4. Mean (+ S.E.) density of mussel colonists (no. 100 cm^{-2}) in ice-scoured and non-scoured tidepools and emergent rock after the 5, 11, and 16 mo intervals beginning in July 1993, and after the second and third 5 to 6 mo intervals. Data were averaged across 3 quadrats per plot and across 3 plots within each combination of habitat and stratum.

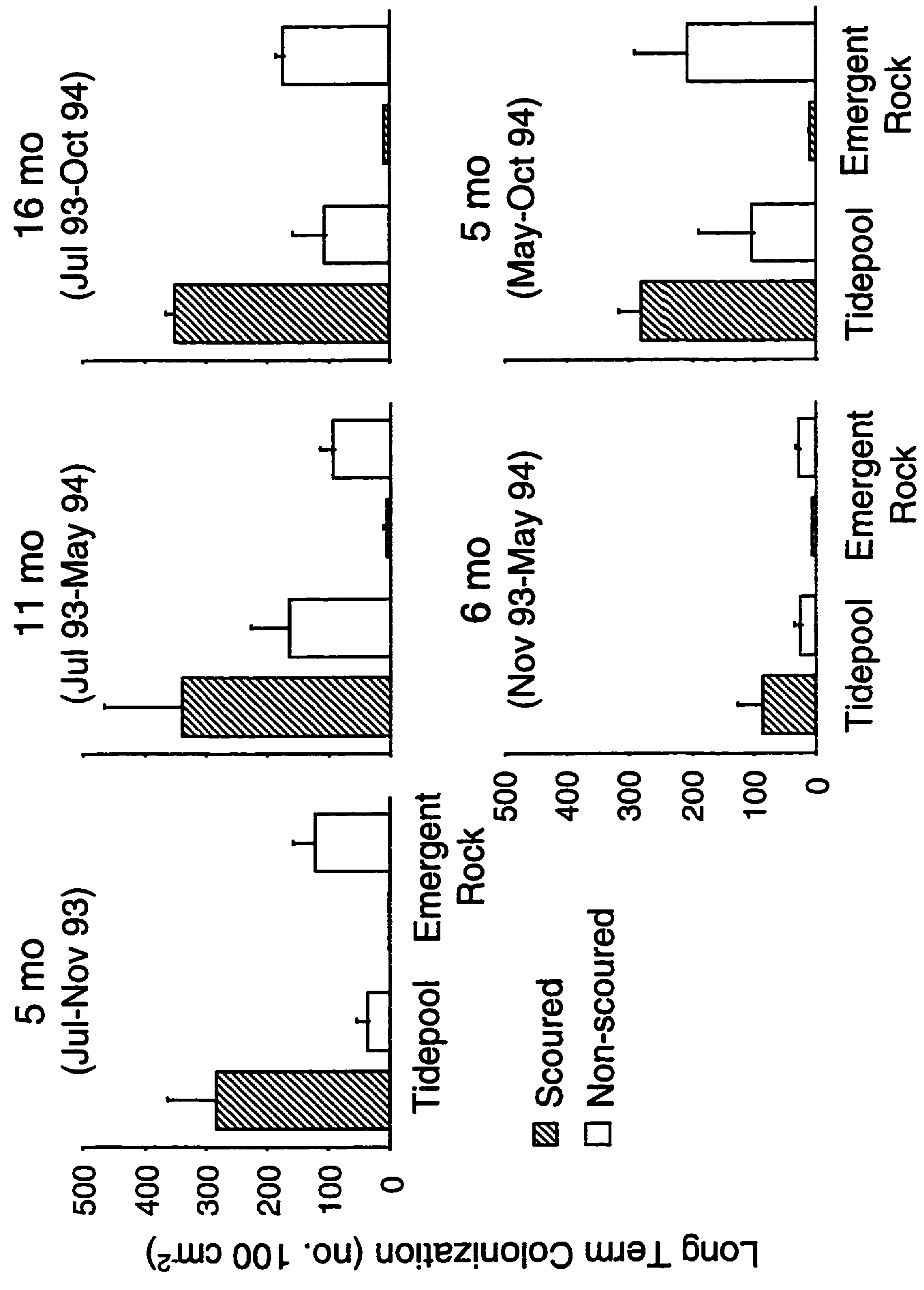

Long Term Colonization (no. 100 cm^{2})
500
400
300
200
100
0
5 mo
(Jul-Nov 93)
11 mo
(Jul 93-May 94)
16 mo
(Jul 93-Oct 94)
6 mo
(Nov 93-May 94)
5 mo
(May-Oct 94)
Tidepool
Emergent Rock
▨ Scoured
☐ Non-scoured

Fig. 3.4

Fig. 3.5. Size frequency distributions of mussels after the 5, 11, and 16 mo intervals beginning in July 1993, and the second and third 5 to 6 mo intervals. Mussels were pooled across quadrats and plots within a combination of habitat and stratum. In the first bar, the black shading indicates settlers (<0.5 mm SL), while the gray shading indicates individuals which were 0.5-0.9 mm. Individuals in the last bar were >10 mm SL. Results of Kolmogorov-Smirnov tests are indicated above the panels (D_{max}, p). *** $p<0.001$, * $0.01<p<0.05$, ns $p>0.05$

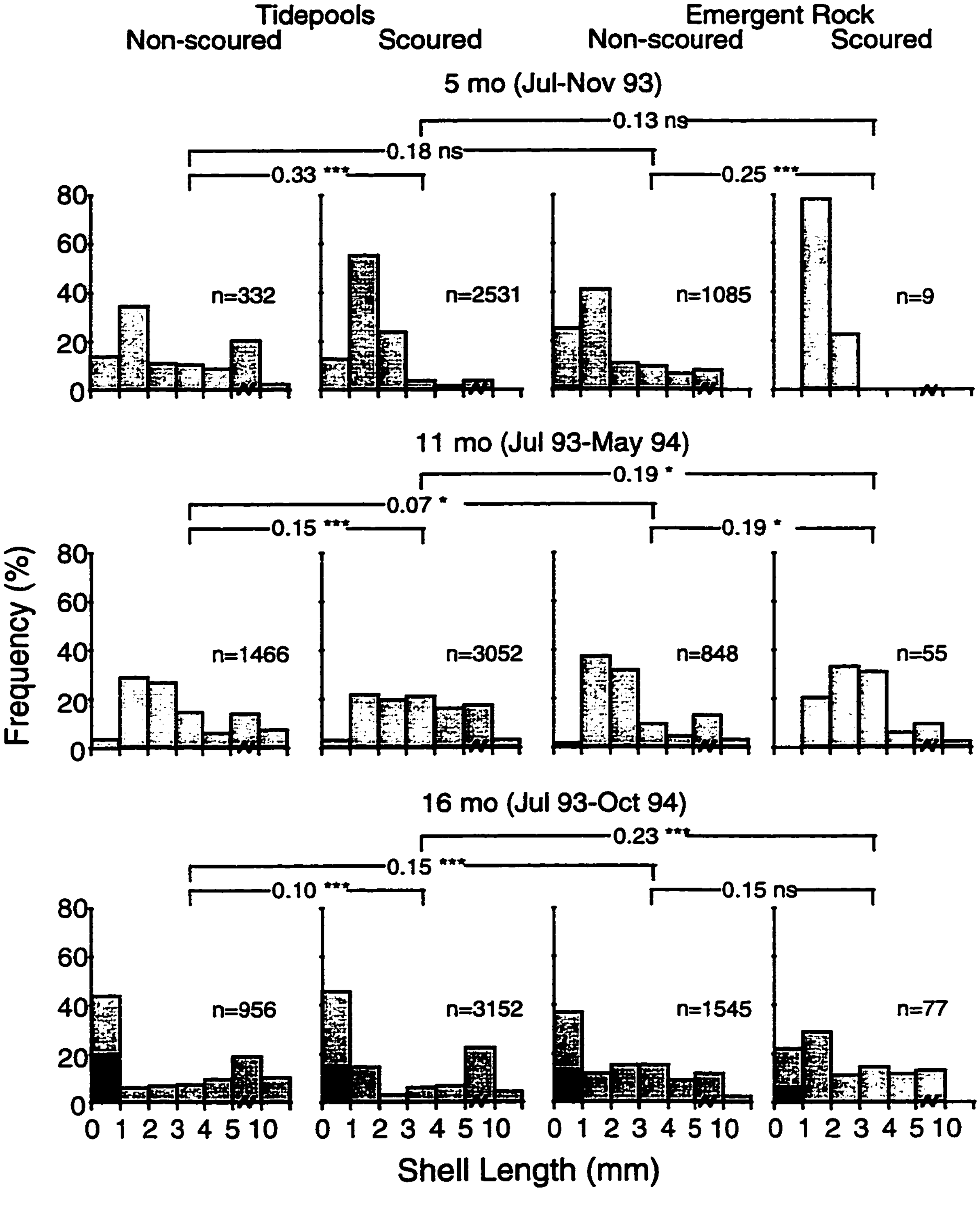

Tidepools
Non-scoured
Scoured
Emergent Rock
Non-scoured
Scoured
5 mo (Jul-Nov 93)
0.13 ns
0.18 ns
0.33 ***
0.25 ***
n=332
n=2531
n=1085
n=9
11 mo (Jul 93-May 94)
0.19 *
0.07 *
0.15 ***
0.19 *
n=1466
n=3052
n=848
n=55
16 mo (Jul 93-Oct 94)
0.23 ***
0.15 ***
0.10 ***
0.15 ns
n=956
n=3152
n=1545
n=77
Frequency (%)
0
20
40
60
80
0 1 2 3 4 5 10
Shell Length (mm)

Fig. 3.5

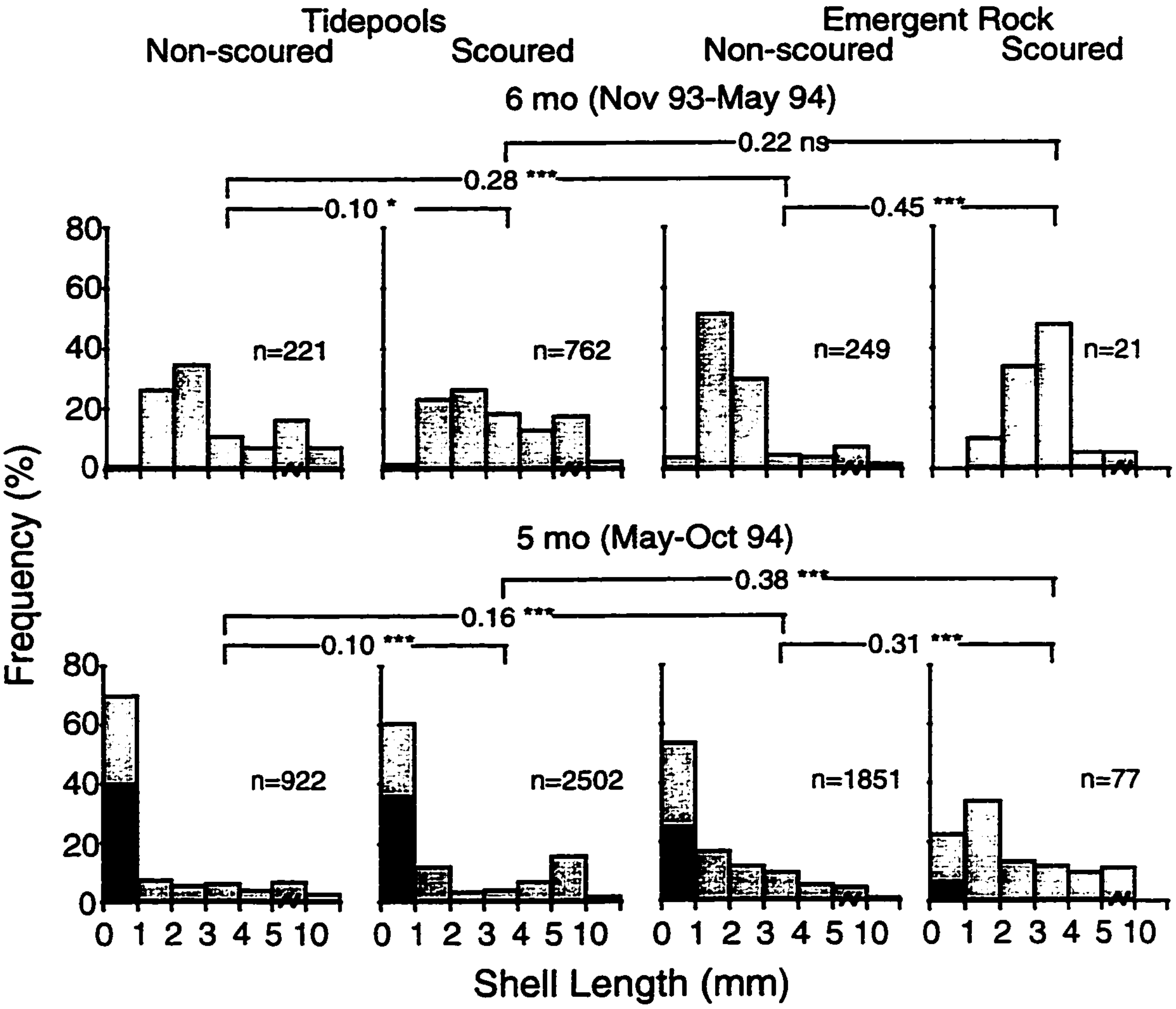


Fig. 3.5 continued

Fig. 3.6. Relationship between abundance of colonists (no. 100 cm^{-2}) after a 5-16 mo interval (L) and the cumulative short term colonization (no. 100 cm^{-2}) during that interval (S) for the 5, 11, and 16 mo intervals beginning in July 1993, and the second and third 5 to 6 mo intervals. Data are averages for 3 quadrats per plot. The dashed line is the one to one line, and the solid line is the regression line. The regression equation and statistical results are presented on each panel.

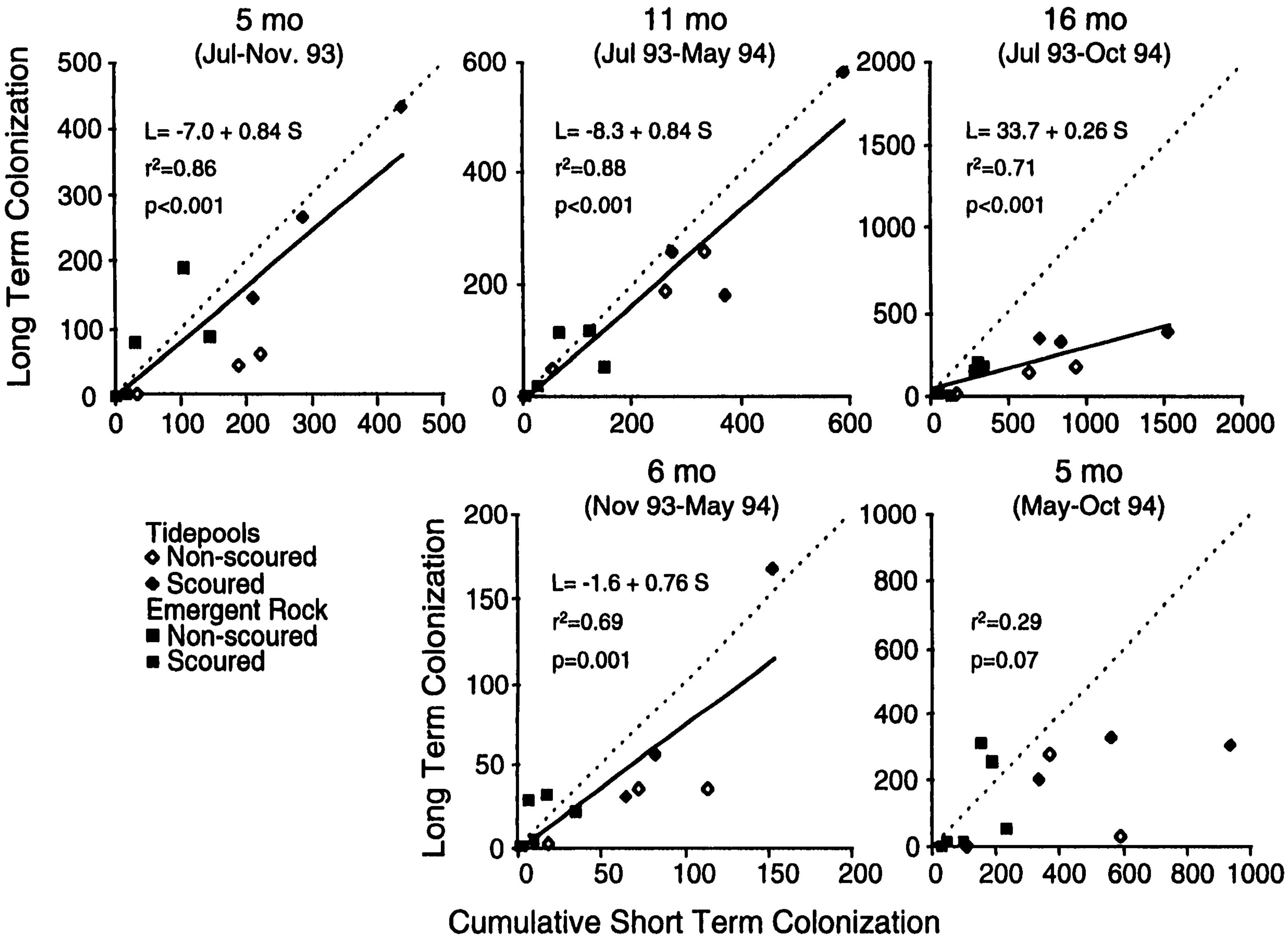

5 mo
(Jul-Nov. 93)
L= -7.0 + 0.84 S
r²=0.86
p<0.001
11 mo
(Jul 93-May 94)
L= -8.3 + 0.84 S
r²=0.88
p<0.001
16 mo
(Jul 93-Oct 94)
L= 33.7 + 0.26 S
r²=0.71
p<0.001
6 mo
(Nov 93-May 94)
L= -1.6 + 0.76 S
r²=0.69
p=0.001
5 mo
(May-Oct 94)
r²=0.29
p=0.07
Tidepools
◇ Non-scoured
◆ Scoured
Emergent Rock
■ Non-scoured
■ Scoured
Long Term Colonization
Cumulative Short Term Colonization
0
100
200
300
400
500
600
1000
1500
2000
50
150
800

Fig. 3.6

Fig. 3.7. Percentage cover of 6 functional form groups of macroalgae and of barnacles and unoccupied substratum in ice-scoured and non-scoured tidepools and emergent rock in September 1993 and April, August and October 1994. Data were averaged across short and long term colonization quadrats within a plot (12 per plot in September 1993, April 1994, 9 per plot in August and October 1994) and across 3 plots within each combination of habitat and stratum. Cover of mussels in the long term colonization quadrats was not included and percentage cover of macroalgae and barnacles in these quadrats was adjusted to total 100%.

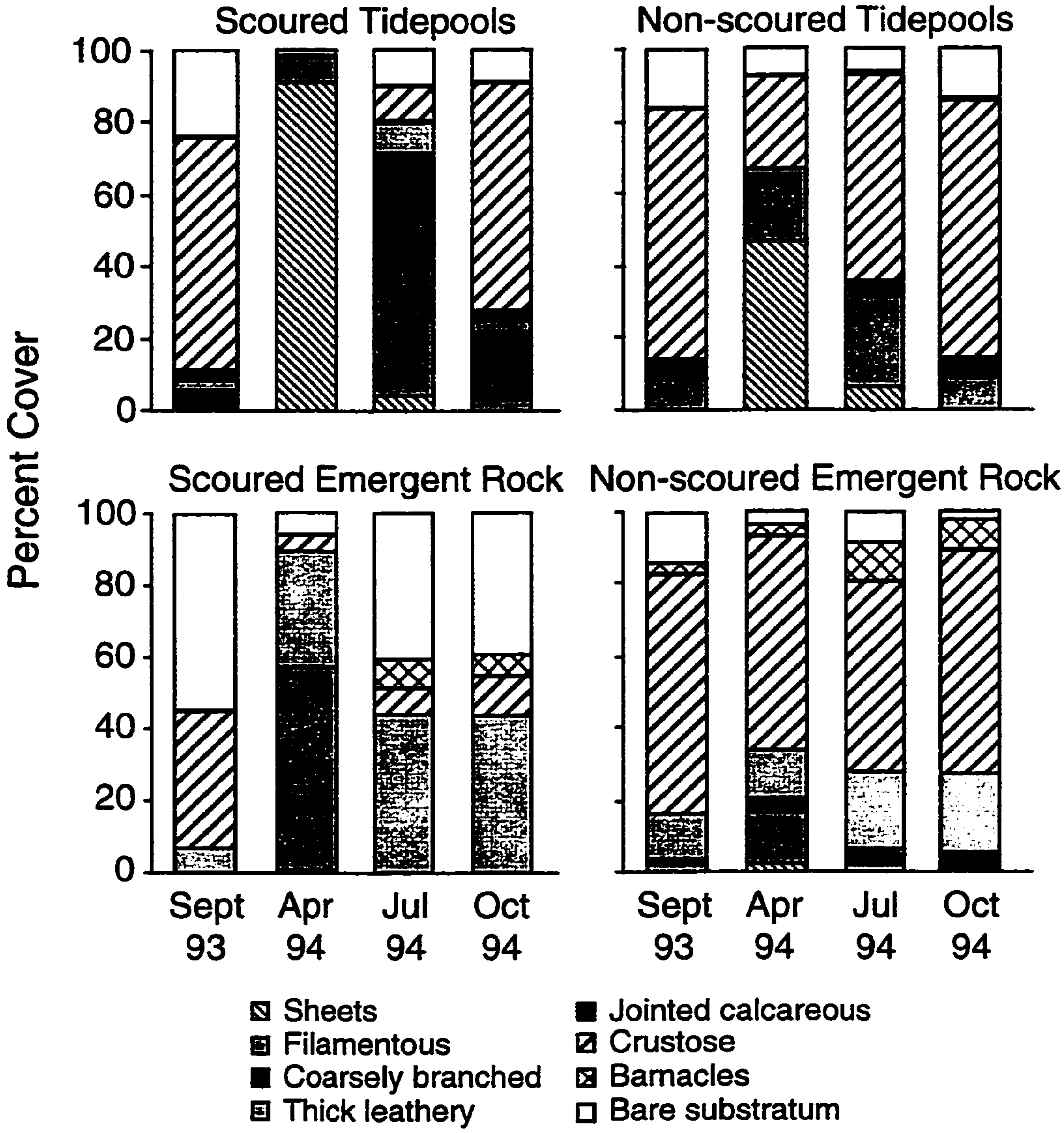

Scoured Tidepools
Non-scoured Tidepools
Scoured Emergent Rock
Non-scoured Emergent Rock
Percent Cover
100
80
60
40
20
0
Sept 93
Apr 94
Jul 94
Oct 94
Sheets
Filamentous
Coarsely branched
Thick leathery
Jointed calcareous
Crustose
Barnacles
Bare substratum

Fig. 3.7

DISCUSSION

Size of colonists and temporal pattern of colonization

Sampling at short intervals (2 to 7 d) indicated that more than 96% of mussels colonizing the natural substratum were too large (>0.5 mm) to be settling larvae. Most of these mussels (67-82% in 1994) were >2 mm and some were as large as 20-25 mm. Because mussels of this size are probably too heavy to drift in the water column using threads (Sigurdsson et al. 1976, De Blok & Tan-Maas 1977, Lane et al. 1985), their redistribution occurs either by dislodgment and deposition by waves, or by crawling (Chapter 6; Paine 1974). In a tagging study, I found that mussels larger than 5 mm SL usually moved <5 cm over 4 weeks (Chapter 6). Because I cleared a 10 cm border around my sampling quadrats, it is unlikely that postlarval colonists entered the quadrats by crawling. The size range of colonizing mussels encompassed most of the size range of the mussel population at Cranberry Cove: ~90 % of mussels are smaller than 5 mm and <5% are larger than 20 mm (Chapter 5; Hunt & Scheibling 1995). Since growth rates are low (≤ 0.4 mm mo^{-1} for mussels >5 mm, Chapter 6), the large size of many of the colonists indicates that they are several years old.

Sampling at short intervals indicated that the colonization rate of mussels >2 mm SL peaked in June to July in both 1993 and 1994. In contrast, settlement occurred in August to October, similar to the pattern observed by Pedersen (1991) at another wave-exposed shore ~30 km from my site. The peak of colonization of large mussels in late spring and summer may be associated with the low wave action at this time of year. In June and July of both years, <9% of measurements of significant wave heights recorded at the mouth of Halifax Harbour (44.483 °N, 63.417 °W, ~ 40 km from my study site) were >2 m (unpubl. data, Department of Fisheries and Oceans, Canada). In contrast, from September 1993 to May 1994, 11 to 45% of records in each month were >2 m. Decreased wave action is associated with decreased attachment strength of mussels to the substratum (Chapter 6; Price 1980, 1982, Witman & Suchanek 1984). Consequently, during periods of low wave heights, the probability of a mussel's dislodgment by occasional large waves may have been increased.

The influence of colonization by mussels >2 mm is not usually considered in studies of the dynamics of mussel assemblages on hard substrata, although dispersal by smaller postlarval mussels is well known (reviewed by Seed & Suchanek 1992). Detection of the movement of large mussels may depend on the substratum used to monitor colonization. Most studies of patterns of settlement or recruitment of mussels have monitored artificial substrata (usually filamentous) and have found no evidence of colonization by mussels >5 mm (e.g. De Blok & Geelen 1958, King et al. 1990, Cáceres-Martínez et al. 1994). In contrast, Paine (1974) observed that large *M. californianus* (>3 cm) colonized plots of the natural substratum which had been cleared of mussels. I found that mussels that colonized natural substrata were larger than those which colonized an artificial filamentous substrate, suggesting that filamentous substrata are more suitable for smaller than for larger mussels (Chapter 4). The high rates of colonization by large mussels in my study compared to others also may result from differences between mussel species. Genetic analysis indicated that ~70-80% of mussels at my study site were *M. trossulus*, while most of the studies employing artificial substrata examined *M. edulis* or *M. galloprovincialis*.

Patterns of colonization among habitats and strata

Colonization by *Mytilus*, measured both at short (2-7 d) and long (5-16 mo) sampling intervals, differed consistently among combinations of habitat and stratum. Mussel colonization was greatest in ice-scoured tidepools and lowest on ice-scoured emergent rock. Although spatial distribution is known to vary among some of the closely related species in the *M. edulis* species complex (e.g. *M. edulis* and *M. galloprovincialis*, Skibinski et al. 1983, Gosling and McGrath 1990), variation in the distribution of *M.*

trossulus and *M. edulis* probably did not contribute to the pattern I observed, since genetic analysis indicated that the frequency of occurrence of the two species did not differ between tidepools and emergent rock.

I investigated the factors influencing the pattern of mussel colonization among habitat/stratum combinations by comparing colonization rates on natural and artificial substrata (Chapter 4). In contrast to the natural substratum, colonization of artificial substrata was greatest on ice-scoured emergent rock in direct relation to water flux (Chapter 4). The difference in colonization pattern between artificial and natural substrata suggests that colonization on natural substrata is influenced by variation in the macrobenthic assemblage between habitats and strata. In fall 1994, colonization rate on natural substrata was related to a suite of biological (macroalgal and barnacle cover) and physical factors (water flux, tidal height, flushing time) (Chapter 4). I observed mussel colonists on a variety of substrata, including filamentous algae (*Cladophora* sp., *Spongomorpha* sp.), jointed calcareous alga (*Corallina officinalis*), holdfasts of thick leathery macroalgae (*Fucus vesiculosus*, *Chondrus crispus*) barnacle tests, and pits and crevices in rock covered by crustose algae (*Phymatolithon* sp., *Hildenbrandia rubra*). In contrast, I rarely observed mussel colonists on smooth, otherwise unoccupied substrata. During the 17 mo period of this study, the macrobenthic assemblage differed among the habitat and stratum combinations, and the percentage cover of different macroalgal groups and barnacles varied over time. Ice-scoured emergent rock, the habitat/stratum combination with the lowest abundance of colonists, generally lacked filamentous and coarsely branched algae, substrata with which recently settled mussels are often associated (pers. obs., see also Chapter 4; Seed & Suchanek 1992). Filamentous algae were abundant on ice-scoured emergent rock only in April 1994 when the short term colonization rate of mussels was negligible. Ice scoured emergent rock also had less crustose macroalgae than the other habitat and stratum combinations.

The patterns of colonization on natural substrata correspond to patterns of distribution and abundance of mussels on ice-scoured but not on non-scoured regions of the shore. Colonization rate of ice-scoured emergent rock was low during all sampling intervals and mussels are rare in these areas. In non-scoured areas, the spatial distribution and abundance of mussels differs between tidepools and emergent rock, but I did not detect a difference in colonization rate between non-scoured tidepools and non-scoured emergent rock. However, the small size and low percentage cover of mussels after 16 mo ($\leq$17 %) suggests that differences in the mussel assemblage between the two habitats develop slowly.

Sampling Frequency

Patterns of mussel colonization among habitats and strata were similar regardless of the length of the sampling interval. This indicates that, over time scales up to 16 mo, patterns of initial colonization were more important than post-colonization processes in determining the pattern of spatial distribution of mussels. In addition, the long term abundance of colonists was linearly related to the cumulative short term abundance during each interval except the third 5 to 6 mo interval. With the exception of the 16 mo interval, there was approximately a one to one relationship between long term and cumulative short term colonization, implying that little post-colonization mortality or dispersal occurred during these intervals. The low percentage cover of mussels after each of the intervals indicates that there was probably little or no competition for space. However, some post-colonization mortality or dispersal may have been offset by enhanced settlement in the presence of conspecifics in the long term colonization quadrats. As evidence of this, the abundance of <1 mm mussels after the third 5 to 6 mo interval, immediately after a settlement peak in 1994, was greater than the cumulative abundance based on short term sampling over the same interval. This disparity was not observed after the first 5 to 6 mo interval in 1993 when quadrats were sampled a month after the settlement peak. An increase in the estimate of settlement in quadrats from which individuals have not been cleared is contrary to the observations for barnacles (Connell 1985, Bertness et al. 1992, Minchinton & Scheibling 1993a,b). However, barnacles require free space on the substratum for settlement, wheareas mussels generally settle on filamentous or rough substrata, which can include the byssal threads of conspecifics.

The lack of a significant relationship between long term and cumulative short term colonization for the third 5 to 6 mo interval suggests that density-dependent post-colonization processes were more important during this interval, when cumulative short term colonization was highest, than during the other 5-16 mo intervals. Post-colonization processes also influenced the size distributions of colonists. On ice-scoured emergent rock (except in fall 1994) the size range of long term colonists was more limited than that of colonists sampled at short intervals. This suggests that ice-scoured emergent rock is not a suitable substratum for some sizes of mussels, particularly those <1 mm, and that many mussels died or emigrated after initial colonization. Small mussels were relatively more abundant in ice-scoured tidepools than in the other combinations of habitat and stratum at short sampling intervals, but this pattern was not as apparent at long sampling intervals. This change could result from differences among habitat and stratum combinations in the rates of mortality, dispersal, or growth of small mussels. I found that growth rates of large mussels (>5 mm) were slightly higher in tidepools than on emergent rock over 5 mo intervals (Chapter 6). The size distributions of long term colonists also may be influenced by an increased attractiveness of the substratum to settling larvae due to the presence of conspecifics, as discussed above.

This study demonstrates the potential importance of post-settlement dispersal in determining the distribution and population dynamics of benthic marine invertebrates which remain mobile for a period of time after settlement. I found that dispersing postlarval mussels were considerably more abundant than settlers and that mussels >2 mm represented a large proportion of colonists. Colonization by mussels >2 mm may be overlooked in many studies of mussel colonization because most researchers use a filamentous artificial substratum, which may be more suitable for smaller than for larger postlarval mussels. My results indicate that, over time scales up to 16 mo, patterns of initial colonization by settlers and larger post-larval mussels were more important than post-colonization mortality and dispersal in determining patterns of distribution and abundance of mussels on this shore.

CHAPTER 4: Physical and biological factors influencing mussel colonization on a wave-exposed rocky shore

INTRODUCTION

Spatial variation in settlement of larvae of benthic marine invertebrates arises through a combination of passive (hydrodynamic) and active (behavioural) processes operating at various scales (reviewed by Butman 1987). Larvae tend to be passively deposited at large spatial scales (tens of metres to tens of kilometres) since horizontal advection usually exceeds larval swimming speeds, although some larvae can vertically migrate between water masses. Active habitat selection becomes important at smaller scales (centimetres to metres) as larvae respond to various abiotic (e.g. surface texture and chemistry) and biotic (e.g. microbial films, conspecifics, other macrobenthic species) cues associated with the substratum (reviewed by Pawlik 1992). However, hydrodynamic processes, such as turbulent eddies around biotic roughness elements, may also influence the small-scale distribution of settlers (e.g. Eckman 1983, Eckman 1987, Havenhand & Svane 1991, Harvey et al. 1995).

Since mussels continue to disperse after larval settlement (Chapter 3; Sigurdsson et al. 1976, De Blok & Tan-Maas 1977, Lane et al. 1985), patterns of mussel colonization may arise by the influence of passive and active processes on both settlement and post-settlement dispersal. In their natural habitat, recently settled and small postlarval mussels (*Mytilus* spp.) are usually associated with filamentous substrata (primarily macroalgae) and small crevices or depressions in the bottom (reviewed by Seed 1976, Seed & Suchanek 1992). Laboratory studies have shown that larvae of *M. edulis* and postlarvae of *M. galloprovincialis* almost exclusively colonize natural or artificial filamentous substrata (Bayne 1965, Petersen 1984, Eyster & Pechenik 1987, Cáceres-Martínez et al. 1994). A variety of artificial substrata (including rubberized hair pads, panels, ropes, jute pads, shag rug, plastic pot scrubbers) have been used to collect mussel colonists (Menge

1978b, King et al. 1990 and references therein, Petraitis 1991, Cáceres-Martínez et al. 1994, Menge et al. 1994, Molares & Fuentes 1995), since they provide a standardized surface which is easy to sample. The abundance of mussel colonists on artificial substrata probably reflects supply of colonists in the water column, as observed for settlement of freshwater zebra mussels (Martel et al. 1994) and estuarine Dungeness crabs (Eggleston & Armstrong 1995). King et al. (1990) observed that the temporal pattern of mussel colonization on an artificial substratum (nylon pot scrubbers) was similar to that recorded on filamentous algae and adult mussels at the same site.

In the previous chapter, I described the patterns and rates of mussel (*M. trossulus* and *M. edulis*) colonization on natural substrata in ice-scoured and non-scoured tidepools and emergent rock on a wave-exposed shore on the Atlantic coast of Nova Scotia. Patterns of mussel colonization among habitats (tidepools, emergent rock) and strata (ice-scoured, non-scoured areas) were similar over short (2 to 7 d) and long (5 to 16 mo) sampling intervals, indicating that patterns of initial colonization were important in determining the pattern of spatial distribution of mussels. Colonists were most abundant in ice-scoured tidepools and least abundant on ice-scoured emergent rock. Variation in mussel colonization among habitats and strata may result from differences in the macrobenthic assemblage (the substratum for colonization) (Chapter 3) or in the supply of colonists. In addition, colonization may continue during the period of tidal isolation in tidepools but not on emergent rock. In this chapter, I compare colonization rates of *Mytilus* on artificial collectors and natural substrata to examine the relative roles of supply of colonists (as reflected by colonization on collectors) and substratum type in shaping colonization patterns of mussels. I relate the observed patterns of colonization to physical and biological characteristics of the local environment.

MATERIALS AND METHODS

Physical Environment

I examined colonization of mussels in two habitats (tidepools and emergent rock) within each of two strata (areas scoured by ice during winter 1992-93 and non-scoured areas) at Cranberry Cove, Nova Scotia. Sampling was carried out in 12 plots (tidepools and areas of emergent rock) along a horizontal distance of ~ 1 km of shoreline which made up 3 replicates of each of the 4 combinations of habitat and stratum (see Chapter 3 for further description of the study site and sampling plots). By fall 1994, when this study was carried out, foliose macroalgae had become re-established in ice-scoured areas, and mussels were abundant in all areas except ice-scoured emergent rock. I measured the height of each plot above chart datum using a transit level in May 1995. I measured flushing time for each of the 6 tidepools in August 1993 and June 1994 as the time taken for a fluorescent red dye (Rhodamine B, Sigma Chemicals), added at low tide at an initial concentration of 1.4 to 6.4 mg. l^{-1}, to become undetectable in a spectrophotometer (Perkin-Elner, Lambda 3B). I measured isolation time of tidepools (the period during which there is no sea water input) on the same dates as flushing time.

I measured relative water flux at each plot as the dissolution rate of dental stone (calcium sulfate) (Yund et al. 1991). The dental stone (Denstone® Golden, Miles Dental Products, South Bend, Indiana, USA) was cast in cylindrical molds 2 cm high and 11 cm in diameter. After drying at room temperature for at least 24 h and at 40 °C for 24 h, the sides and bottom of the cylinders were coated with polyurethane so that only the top surface was exposed to flow. The cylinders were then dried for a further 24 h at room temperature. The cylinders were fastened to 11 x 15 cm rectangles of galvanized mesh (0.6 cm mesh size) with epoxy putty (Z*Spar A-788 Splash Zone Compound®, Kop-Coat Inc., Los Angeles, California, USA), dried at 40 °C for 24 h, and then weighed. I measured relative water flux for 2, 5-6 d periods (May 15-20 and June 30-July 6, 1995). During each period, 2 cylinders were bolted to the substratum in each plot; another 2 cylinders were deployed above the tidal range as controls for losses not due to water flow, such as transport and rain. After each period, the cylinders were returned to the laboratory, rinsed in fresh water, dried at room temperature for 48 h and at 40 °C for an additional 24 h, and then weighed. In July, dissolution rate was not measured for one plot because both cylinders were abraded by macroalgae. However, the missing value was estimated from a regression equation relating dissolution rates in July (J) to those in May (M) in all other plots ($J=0.933M-12.719$; $r^2=0.802$, $F_{1,9}=36.344$, $p<0.001$). The ranks of dissolution rates in May and July were strongly correlated (Spearman Rank Correlation: $r_s=0.944$, $p<0.001$), and averaged to give an index of water flux for multiple regression and principal components analysis (see Statistical analysis).

Larval/postlarval abundance

I measured the availability of *Mytilus* larvae and postlarvae in sea water at high tide on September 24 and October 8, 1994, the same dates that artificial collectors were deployed (see Colonization). Three 30-l samples of sea water were collected at each of 3 (September) or 4 (October) positions separated by 100-400 m along ~1 km of shoreline. I hand-pumped the water with a bilge pump through a hose fastened to the substratum at the same height on the shore as my artificial collectors (see Colonization). The water sample was filtered through a 60 µm filter, which was rinsed with filtered sea water and preserved in 70% ethanol. Larvae and postlarvae were enumerated and measured in the laboratory under a dissecting microscope.

Colonization

I deployed artificial collectors to sample *Mytilus* colonists on September 24 and October 8, 1994. The collectors [similar to those used by Pearce & Bourget (1996) for scallop spat] were made of 9 x 11 cm pouches of plastic Vexar mesh (3 mm mesh size), filled with ~ 1.5 g of polyester wool for aquarium filters ("Poly" Filter Wool®, Rolf C.

Hagen Inc., Montreal, Quebec, Canada). The collectors were placed in running sea water in the laboratory for ~ 1 wk before use to allow colonization by microflora. In each plot, 4 collectors were bolted to the substratum (through a grommet in the center of the pouch) before tidal immersion, and removed after 6.5-10 h when the tide receded. A second set of collectors was placed in the tidepools at this time, and removed after 2.5-5.5 h, before immersion by the incoming tide. The collectors were returned to the laboratory and frozen until they were processed. Mussels from each collector were counted and shell length (SL) was measured using an ocular micrometer (accuracy: ± 30 µm). Mussels on both filter wool and Vexar mesh were counted, but those on the mesh were rare.

In each plot, I also sampled colonization of *Mytilus* in 3, 10 x 10 cm quadrats on the natural substratum (see Chapter 3 for further description). I collected mussel colonists from each quadrat using forceps or a pipette after 2, 5-d intervals (September 22-26 and October 7-11, 1994). The mussel samples were returned to the laboratory and frozen until they were processed as described above. In October 1994, I estimated the cover of macroalgae and barnacles (*Semibalanus balanoides*, the only sessile macrofaunal species besides *Mytilus*) in each of the quadrats of natural substratum (see Chapter 3 for further description). Macroalgae were assigned to functional form groups after Littler (1980) and Littler and Littler (1984): filamentous, coarsely branched, thick leathery, jointed calcareous and crustose forms.

Statistical analysis

I used 3-way analysis of variance (ANOVA) to analyze the colonization rate of *Mytilus* on artificial collectors and natural substrata. Habitat (tidepool, emergent rock) and Stratum (scoured, non-scoured) were fixed factors, each with two levels, and Plot was a random factor nested within Habitat x Stratum, with 3 levels. Effects of Habitat, Stratum, and the interaction between Habitat and Stratum were tested against the mean square error of Plot, and the effect of Plot was tested against the residual mean square error. If Plot was non-significant at $\alpha=0.250$, I removed this term from the analysis and calculated a pooled estimate of the residual error (Winer 1971). If Plot was significant at $\alpha=0.05$, I examined the Plot effect within each combination of Habitat x Stratum. I used Student-Newman-Keuls (SNK) tests ($\alpha=0.05$) for post-hoc comparisons of means. If necessary, counts of mussels (x) were ln (x+1) transformed to homogenize variances (Cochran's C test, $\alpha=0.05$).

I used Kolmogorov-Smirnov tests (Seigel & Castellan 1988) to compare size distributions of mussels among habitats and strata for samples from both artificial collectors and natural substrata.

I used forwards stepwise multiple regression to examine the relationship between colonization rate of *Mytilus* on artificial collectors and the physical characteristics of the plots (water flux index, tidal height, and flushing time). I did regressions for tidepools and emergent rock separately, as well as for the two habitats combined. For analysis of colonization on natural substrata, I used principal components analysis (PCA), based on both the physical and the biological (cover of macroalgal groups/barnacles) characteristics of the plots, to reduce the number of variables needed to explain the total variance in the data (Kleinbaum et al. 1988). Only principal components factors with eigenvalues >1 were used in stepwise regression. Also, I analyzed 2 size classes of mussels (<2 mm and >2 mm SL) separately because the larger mussels (postlarvae >2 mm) may have different substratum preferences than smaller ones (Seed 1969a). Counts of mussel colonists on natural substrata were ln (x+1) or square transformed if necessary to homogenize variances (as detected in plots of residuals).

RESULTS

Environmental variability

The height of the sampling plots ranged from 0.80 to 2.33 m above chart datum (Fig. 4.1a), and did not differ significantly between tidepool and emergent rock habitats ($F_{1,8}$=1.01, p=0.344) or between ice-scoured and non-scoured strata ($F_{1,8}$=3.04, p=0.119), and there was no significant interaction between Habitat and Stratum ($F_{1,8}$ =1.22, p=0.301). Ice-scoured tidepools were flushed within 2.8-3 h after low tide, significantly faster (t_4 =5.329, p=0.006) than non-scoured tidepools which were flushed in 4.0-5.0 h (Fig. 4.1c). Average isolation times during low tide were 3.8-4.8 h for scoured tidepools and emergent rock, and 6.5-8 h for non-scoured tidepools.

The water flux index, measured as the dissolution rate of dental stone, differed significantly with Habitat ($F_{1,16}$=37.55, p=0.0001), Stratum ($F_{1,16}$= 48.14, p=0.0001), and Sampling Date ($F_{1,16}$=91.79, p=0.0001), but there were no significant interactions between these factors (p>0.40). Water flux was higher on emergent rock than in tidepools and greater in ice-scoured than non-scoured areas (Fig. 4.1b). Although water flux and mussel colonization were measured at different times of year, significant wave heights (x±SD) recorded at the mouth of Halifax Harbour (44.483 °N, 63.417 °W, ~ 40 km from my study site were similar during both measurement periods: 1.62±0.54 m and 0.73±0.18 m during water flux measurements in May and June 1995 respectively, and 0.97±0.23 m and 0.86±0.17 m during sampling of mussel settlement in September and October 1994 respectively (unpubl. data, Department of Fisheries and Oceans, Canada).

The macrobenthic assemblage varied markedly between habitats and strata (Fig. 4.2). Filamentous and jointed calcareous macroalgae were found only in tidepools. Conversely, thick leathery macroalgae were rare (< 3% cover) in tidepools, but common on emergent rock (24% and 50% for scoured and non-scoured strata respectively). Ice-scoured emergent rock lacked coarsely branched macroalgae and had a much lower cover

(5%) of crustose macroalgae than other Habitat x Stratum combinations (59-72 %). Barnacle cover was somewhat higher on emergent rock (6% and 7% for scoured and non-scoured strata respectively) than in tidepools (<1%).

Larval/postlarval availability

The abundance of *Mytilus* larvae and postlarvae >250 μm (the size at competency, Bayne 1965) in the sea at high tide (Fig. 4.3) did not vary significantly along ~1 km of shoreline within my study site, in either September ($F_{2,6}$=1.750, p=0.252) or October ($F_{3,8}$=2.465, p=0.137). However, the mean proportion of mussels >250 μm in these samples increased from 16% (n=37) to 92% (n=91) between the 2 sampling periods (Fig. 4.3).

Colonization on artificial collectors

In September 1994, colonization rate of *Mytilus* on the artificial collectors did not vary significantly with Plot (within Habitat x Stratum), Stratum or Habitat (Table 4.1; Fig. 4.4a). In October 1994, colonization rate also did not vary significantly with Plot, but it was significantly higher in the ice-scoured than non-scoured stratum and significantly higher on emergent rock than in tidepools; there was no significant interaction between Stratum and Habitat (Table 4.1; Fig. 4.4a). In September, 33% and 38% of colonists in scoured and non-scoured tidepools respectively were collected during the period of tidal isolation (combining counts for all collectors: n=12 and n=13 respectively). In October, however, no colonists in non-scoured tidepools and only 8% (n=69) of those in scoured tidepools were collected during tidal isolation.

Mytilus sampled on the artificial collectors were <7 mm in shell length (SL) and the size distribution was highly skewed to the right (Fig. 4.5). In September, 0.5-1 mm mussels were the most abundant size class (Fig. 4.5), and size distributions did not differ significantly between scoured and non-scoured tidepools ($D_{13,12}$=0.378, p=0.281); strata were not compared for the emergent rock habitat because of the small sample size (n=5 mussels) for non-scoured areas. There was no significant difference between tidepools and emergent rock when strata were combined ($D_{25,21}$=0.316, p=0.178; Fig. 4.5). In October, >76% of mussels in all Habitat x Stratum combinations (n=17-110) were <0.5 mm SL (Fig. 4.5). The size distribution of mussels did not differ significantly between scoured and non-scoured tidepools ($D_{52,17}$=0.182, p=0.758) or emergent rock ($D_{110,40}$=0.241, p=0.069). There was a statistically significant difference in size distribution ($D_{69,150}$=0.233, p=0.012) between tidepools and emergent rock when these strata were combined, although the distributions were very similar (Fig. 4.5).

Regression analysis showed no significant relationship between mussel colonization rate on artificial collectors and the physical characteristics of plots (water flux, tidal height, flushing time) when tidepools and emergent rock were analyzed separately. However, when plots in both habitats were included in the same regression analysis, there was a significant positive relationship between colonization rate and water flux in October ($F_{2,9}$=9.653, p=0.006; water flux p=0.002, tidal height p=0.074).

Colonization on natural substrata

The colonization pattern of *Mytilus* on natural substrata differed markedly from that on the artificial collectors. In September 1994, colonization rate varied significantly with Plot, mainly because of differences among ice-scoured tidepools ($F_{2,24}$=3.792, p=0.037); differences among plots for other Habitat x Stratum combinations were non-significant (Table 4.1, Fig. 4.4b). There were no significant differences in colonization rate with Habitat or Stratum, and no significant interaction between Stratum and Habitat (Table 4.1, Fig. 4.4b). In October 1994, however, there was no significant variation in colonization rate among plots but there was a significant interaction between Habitat and Stratum (Table 4.1): colonization rate was significantly higher in ice-scoured tidepools than on the scoured emergent rock (SNK, p<0.05), but did not differ significantly among the other Habitat x Stratum combinations (Fig. 4.4b).

In contrast to artificial collectors, the size distributions of *Mytilus* on the natural substratum were relatively uniform and the mussels were larger (Fig. 4.6). In October, only 4% (n=52) of mussels in tidepools and no mussels on emergent rock were <0.5mm SL, the dominant size class on artificial collectors. I only found 1 mussel >5mm on artificial collectors; however, mussels sampled on the natural substratum were up to 12 mm, and 31% (n=109) in September and 20% (n=69) in October were >5 mm. The size distributions of mussels did not differ significantly between ice-scoured and non-scoured pools for either sample period (September: $D_{53,24}$=0.152, p=0.803; October: $D_{32,20}$= 0.262, p=0.321); strata were not compared for the emergent rock because of the small sample sizes in scoured areas (n = 2, 3 in September, October). The size distributions of mussels in tidepools and on emergent rock were similar in September ($D_{77,32}$=0.241, p=0.131), but differed significantly in October ($D_{52,17}$=0.519, p=0.002) when mussels <1 mm were absent on emergent rock, but comprised the most abundant size class in tidepools (Fig. 4.6).

To examine the relationship between mussel colonization rate on the natural substratum and the physical and biological characteristics of plots, I used 3 PCA factors for tidepools (94.9% of variance) and emergent rock (92.8% of variance) and 4 PCA factors for the combined habitats (87.7% of variance) (Table 4.2). There was no consistent relationship between colonization rate and PCA factor scores between sample periods and mussel size classes (Tables 4.2, 4.3). In September, mussels <2mm SL on emergent rock varied significantly with a factor (Factor 1) with high positive component loadings for water flux and crustose macroalgae. In October, mussels <2mm SL in tidepools varied significantly with a factor (Factor 1) with high negative component loadings for flushing time, bare space, tidal height, and water flux index. When both habitats were combined in the same analysis, mussels >2mm SL in September varied significantly with one factor (Factor 3) with a positive loading for coarsely branched algae and a negative loading for bare space, and another (Factor 4) with a positive loading for thick leathery macroalgae and a negative loading for coarsely branched macroalgae. In contrast, mussels <2mm SL in October varied significantly with one factor (Factor 1) with positive loadings for crustose macroalgae, water flux, and jointed calcareous and filamentous algae, and another (Factor 2) with a positive loading for tidal height.

Table 4.1. Three-way ANOVA of abundance of *Mytilus* colonists on artificial collectors (no. collector^{-1}. tidal cycle^{-1}) and natural substrata (no. 100cm^{-2}. 5d^{-1}) in September and October 1994. Factors are Habitat, Stratum, and Plot (nested within Habitat x Stratum). For artificial collectors, degrees of freedom are: Plot (H x S)= 8,36; Habitat, Stratum and H x S=1,8 if $p_{Plot(HXS)}<0.25$ and df=1,44 if $p_{Plot(HXS)}>0.25$. For natural substrata, degrees of freedom are: Plot (H x S)= 8,24; Habitat, Stratum and H x S=1,8 if $p_{PlotHXS)}<0.25$ and df=1,32 if $p_{Plot(HXS)}>0.25$. Pooled error is the estimate of experimental error when Plot is removed from the model (when $p_{PlotHXS)}>0.25$). *** $p < 0.001$; ** $p < 0.01$; * $p < 0.05$.

	Source	MS	F	p
Colonization of Artificial Collectors				
September	Plot (HxS)	1.50	1.07	0.41
	Habitat	0.33	0.23	>0.25
	Stratum	3.00	2.11	0.10< p <0.25
	Habitat x Stratum	2.08	1.47	0.10< p <0.25
	Residual	1.40		
	Pooled Error	1.42		
October	Plot (HxS)	11.52	1.93	0.086
	Habitat	133.33	11.57	0.009 **
	Stratum	225.33	19.56	0.002 **
	Habitat x Stratum	24.08	2.09	0.186
	Residual	5.97		
Colonization of Natural Substrata				
September	Plot (HxS)	23.97	3.19	0.013 *
	Habitat	56.25	2.35	0.164
	Stratum	0.03	0.001	0.974
	Habitat x Stratum	90.25	3.77	0.088
	Residual	7.53		
October	Plot (HxS)	1.50	0.42	0.898
	Habitat	34.03	11.12	<0.005 **
	Stratum	0.03	0.01	>0.25
	Habitat x Stratum	14.69	4.80	<0.05 *
	Residual	3.58		
	Pooled Error	3.06		

Table 4.2. Results of PCA of physical and biological characteristics of plots at Cranberry Cove, Nova Scotia. Only factors with eigenvalues >1 and components with loadings >0.5 or <-0.5 are shown. Components are listed in order of descending loadings. n=6 plots for tidepools or emergent rock and n=12 when the habitats are pooled. Functional form groups of macroalgae: FIL=filamentous, CB=coarsely branched, JC=jointed calcareous, TL=thick leathery, CR=crustose. BA=barnacles, BE=bare substratum. Physical characteristics: TID=tidal height, WFI=water flux index, FLU= flushing time.

Habitat	Eigenvalue	% Variance Explained	Components
Tidepool			
Factor 1	3.801	47.51	-FLU, -BE, -TID, -WFI, FIL, JC, CB
2	2.724	34.05	-CB, FIL, JC, CR, WFI
3	1.068	13.35	-CR
Emergent Rock			
Factor 1	2.945	42.07	WFI, CR, -BE, TID
2	2.202	31.46	-TL, BA, BE
3	1.347	19.24	CR, -TID
Combined Habitats			
Factor 1	3.571	39.68	CR, WFI, JC, FIL, -TL, -BA, -BE,
2	1.839	20.43	TID, -FIL
3	1.444	16.05	CB, -BE
4	1.039	11.54	TL, -CB

Table 4.3. Significant forwards stepwise multiple regressions relating abundance of <2mm and >2mm SL *Mytilus* colonists on natural substrata in September and October 1994 to factor scores obtained by PCA on physical and biological characteristics of plots at Cranberry Cove, Nova Scotia. F1-F4= PCA factors from Table 4.2. Independent variables with significant partial F-values are shown in bold.

Habitat	Month	Size	Model	R^2	F	p
Tidepool	Oct.	< 2 mm	3.093 + 2.194(**F1**)	0.925	49.25	0.002
Emergent Rock	Sept.	< 2mm	0.333 + 0.248(**F1**)	0.692	8.98	0.040
Combined Habitats	Sept.	> 2mm	1.972 + 1.141(**F3**) -1.013(**F4**)	0.672	9.21	0.007
	Oct.	< 2mm	0.861 + 0.634(**F1**) -0.485(**F2**) -0.287(F4)	0.800	10.68	0.004

Fig. 4.1. Physical characteristics of the sampling plots. Mean (±S.E.) a) height of plots above chart datum (m) b) water flux index: dissolution of dental stone ($g{\cdot}d^{-1}$) c) Flushing time: number of hours required after low tide for the tidepool to be flushed with new sea water.

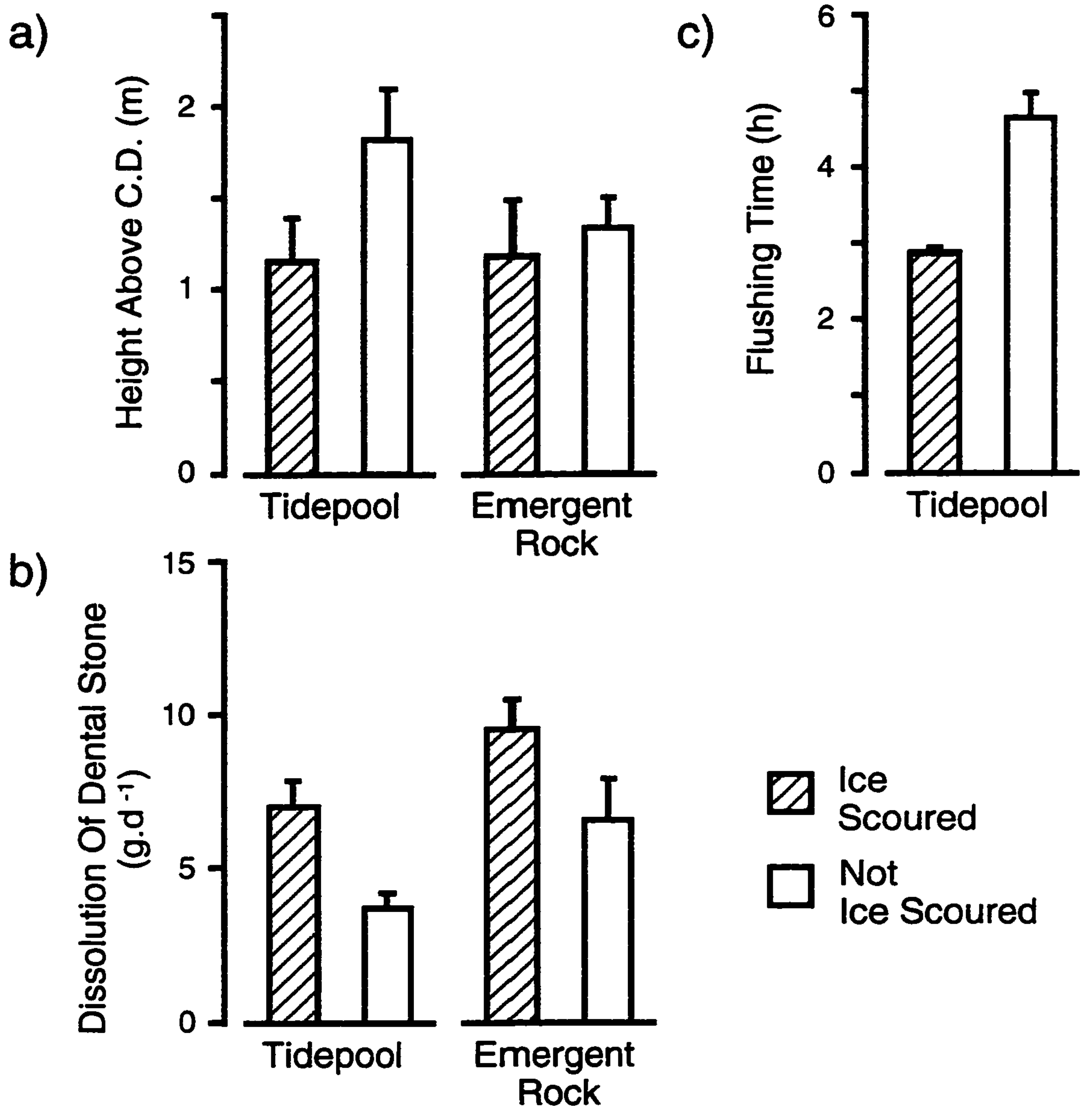

a)
Height Above C.D. (m)
0
1
2
Tidepool
Emergent Rock
b)
Dissolution Of Dental Stone (g.d^{-1})
0
5
10
15
Tidepool
Emergent Rock
c)
Flushing Time (h)
0
2
4
6
Tidepool
▨ Ice Scoured
☐ Not Ice Scoured

Fig. 4.1

Fig. 4.2. Mean percentage cover of 5 functional form groups of macroalgae and of bare substratum and barnacles in ice-scoured (S) and non-scoured (N-S) tidepools and emergent rock in October 1994.

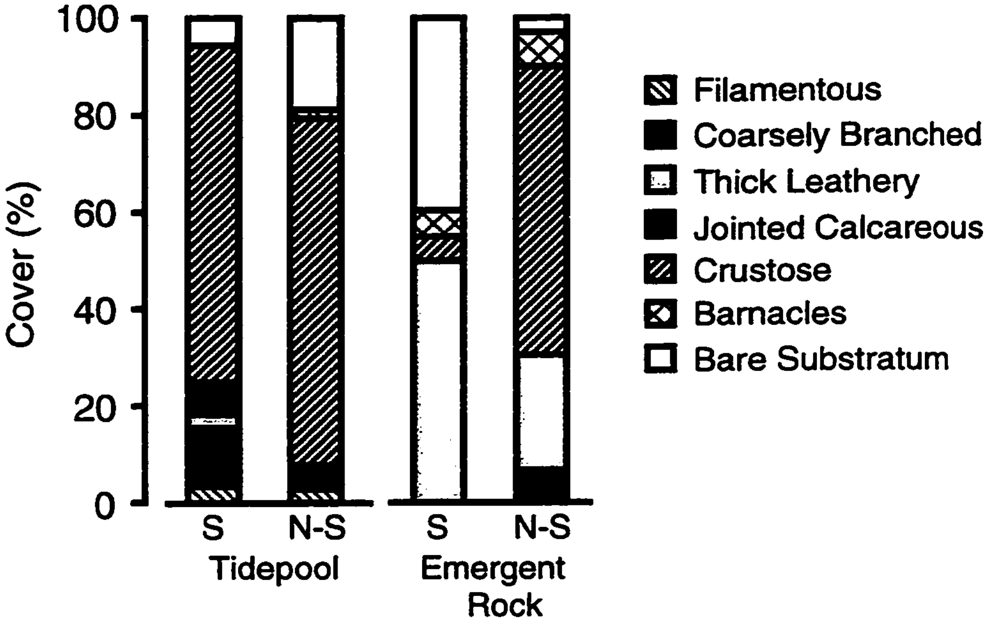

100
80
60
40
20
0
Cover (%)
S
N-S
Tidepool
S
N-S
Emergent Rock
Filamentous
Coarsely Branched
Thick Leathery
Jointed Calcareous
Crustose
Barnacles
Bare Substratum

Fig. 4.2

Fig. 4.3. Mean (±S.E.) concentration of *Mytilus* larvae and postlarvae (no. $30l^{-1}$) in sea water at high tide at four locations at Cranberry Cove, Nova Scotia (total horizontal distance ~ 1 km) on September 24 and October 8, 1994. n=3 samples at each location. ND=no data.

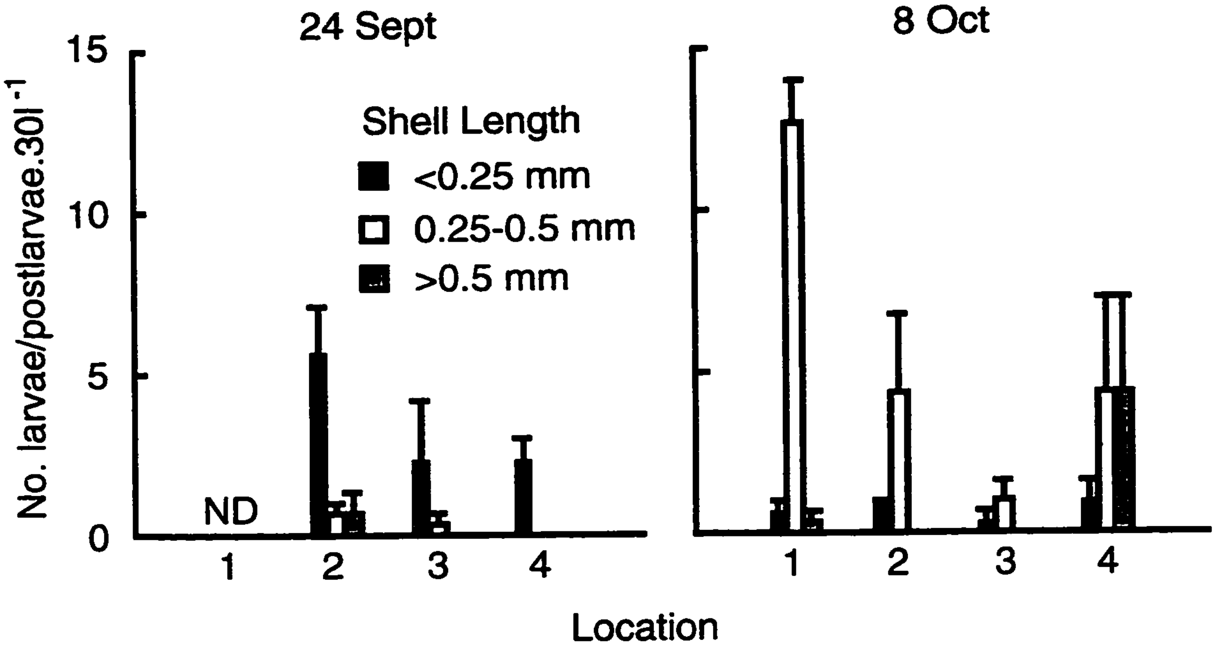
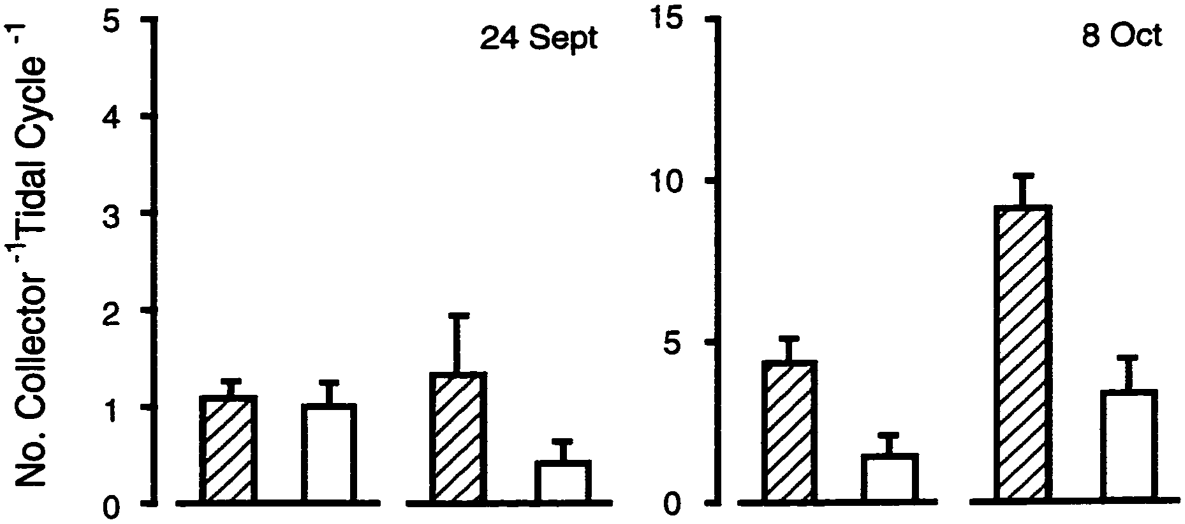

24 Sept
8 Oct
Shell Length
<0.25 mm
0.25-0.5 mm
>0.5 mm
No. larvae/postlarvae.30l -1
15
10
5
0
ND
1
2
3
4
1
2
3
4
Location

Fig. 4.3

Fig. 4.4. Mean (±S.E.) abundance of *Mytilus* on a) artificial collectors (no.collector^{-1}.tidal cycle^{-1}) on September 24 and October 8, 1994 (n=4 collectors per plot) and on b) natural substrata (no. 100 cm^{-2}.5 d^{-1}) September 22-26 and October 7-11, 1994 (n=3 quadrats per plot) in ice-scoured and non-scoured tidepools and emergent rock (n=3 plots per habitat/stratum combination) at Cranberry Cove, Nova Scotia.

a) Artificial Substratum



b) Natural Substratum

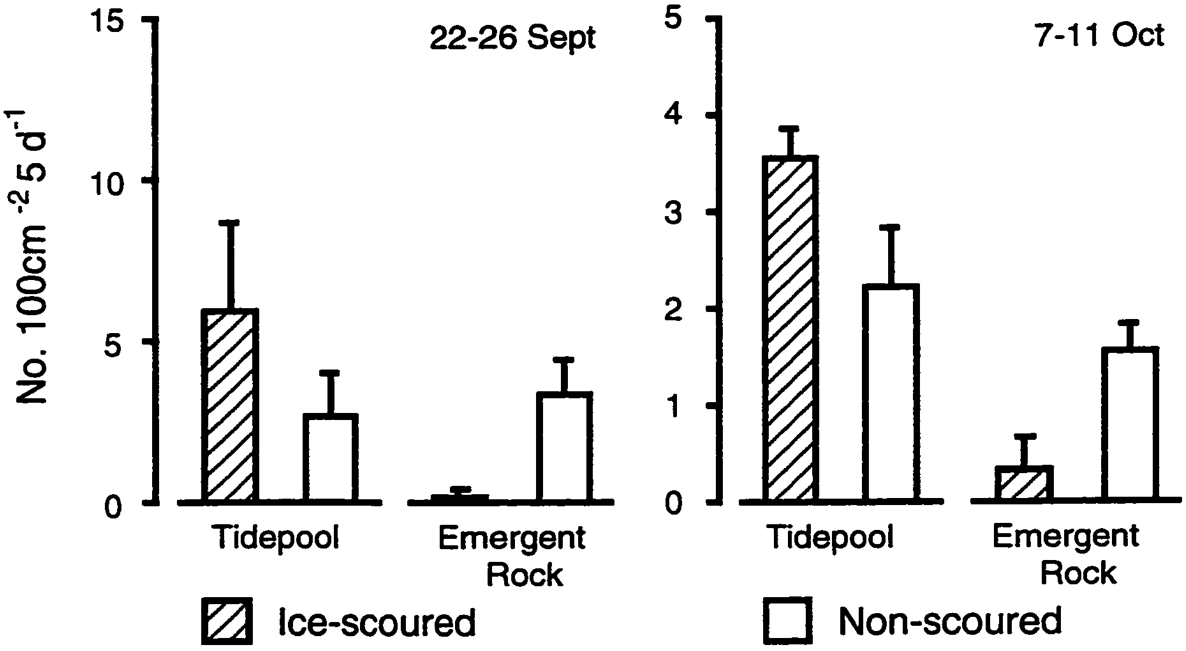


Fig. 4.4

Fig. 4.5. Size-frequency distributions of *Mytilus* on artificial collectors in a) tidepools and on b) emergent rock on September 24 and October 8, 1994 at Cranberry Cove, Nova Scotia. Mussels from all collectors (n=4 per plot, n=6 plots) from a habitat, including those from both ice-scoured and non-scoured strata, are pooled. In tidepools in October, animals in the last column are 5.05-7 mm SL.

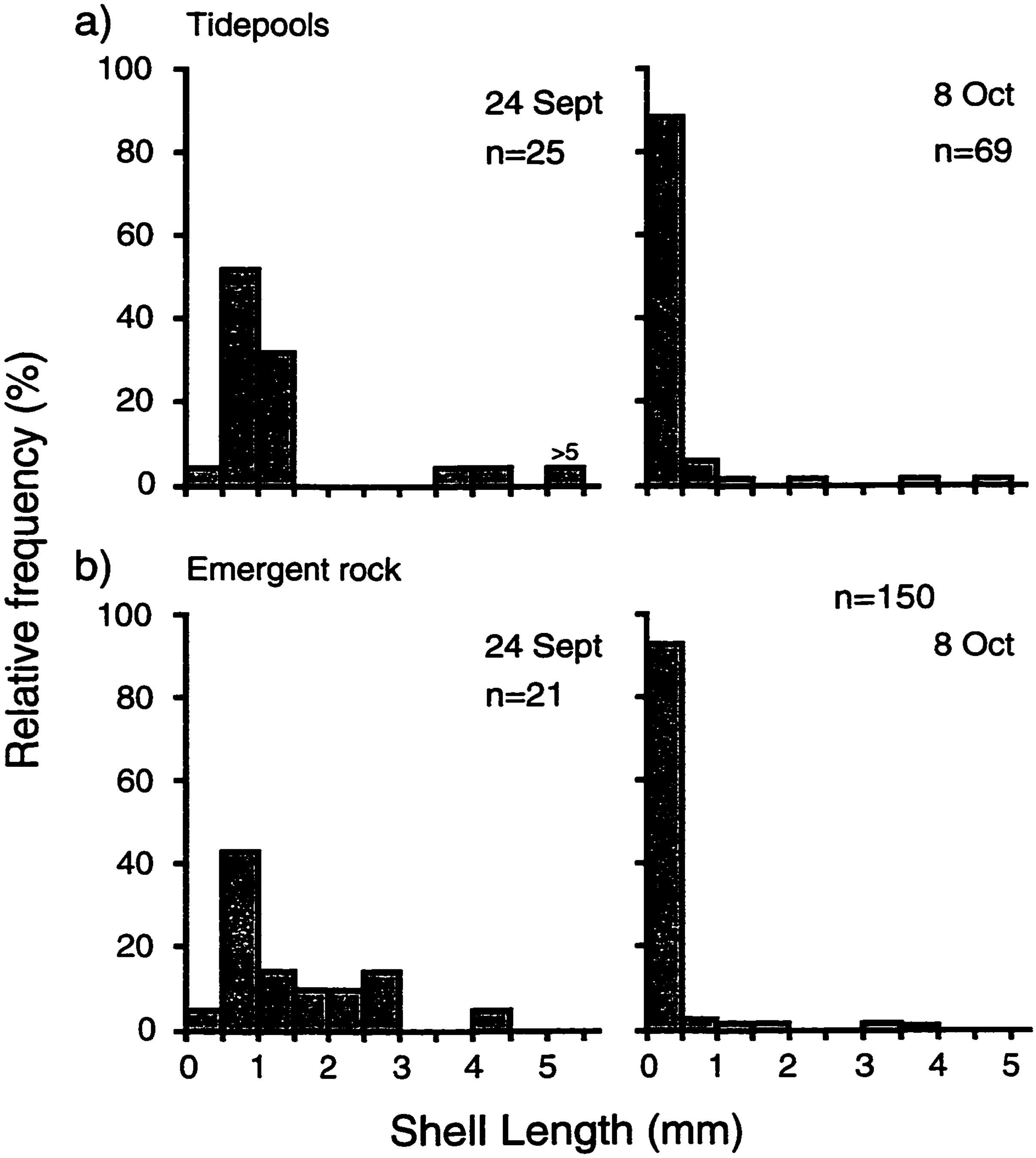

a)
Tidepools
100
80
60
40
20
0
24 Sept
n=25
>5
8 Oct
n=69
Relative frequency (%)
b)
Emergent rock
100
80
60
40
20
0
24 Sept
n=21
n=150
8 Oct
0
1
2
3
4
5
0
1
2
3
4
5
Shell Length (mm)

Fig. 4.5

Fig. 4.6. Size frequency distributions of *Mytilus* on natural substrata in a) tidepools and on b) emergent rock September 22-26 and October 7-11, 1994 at Cranberry Cove, Nova Scotia. Mussels from all quadrats (n=3 per plot, n=6 plots) from a habitat, including those from both ice-scoured and non-scoured strata, are pooled. Animals in the last column are 6.05-12 mm SL.

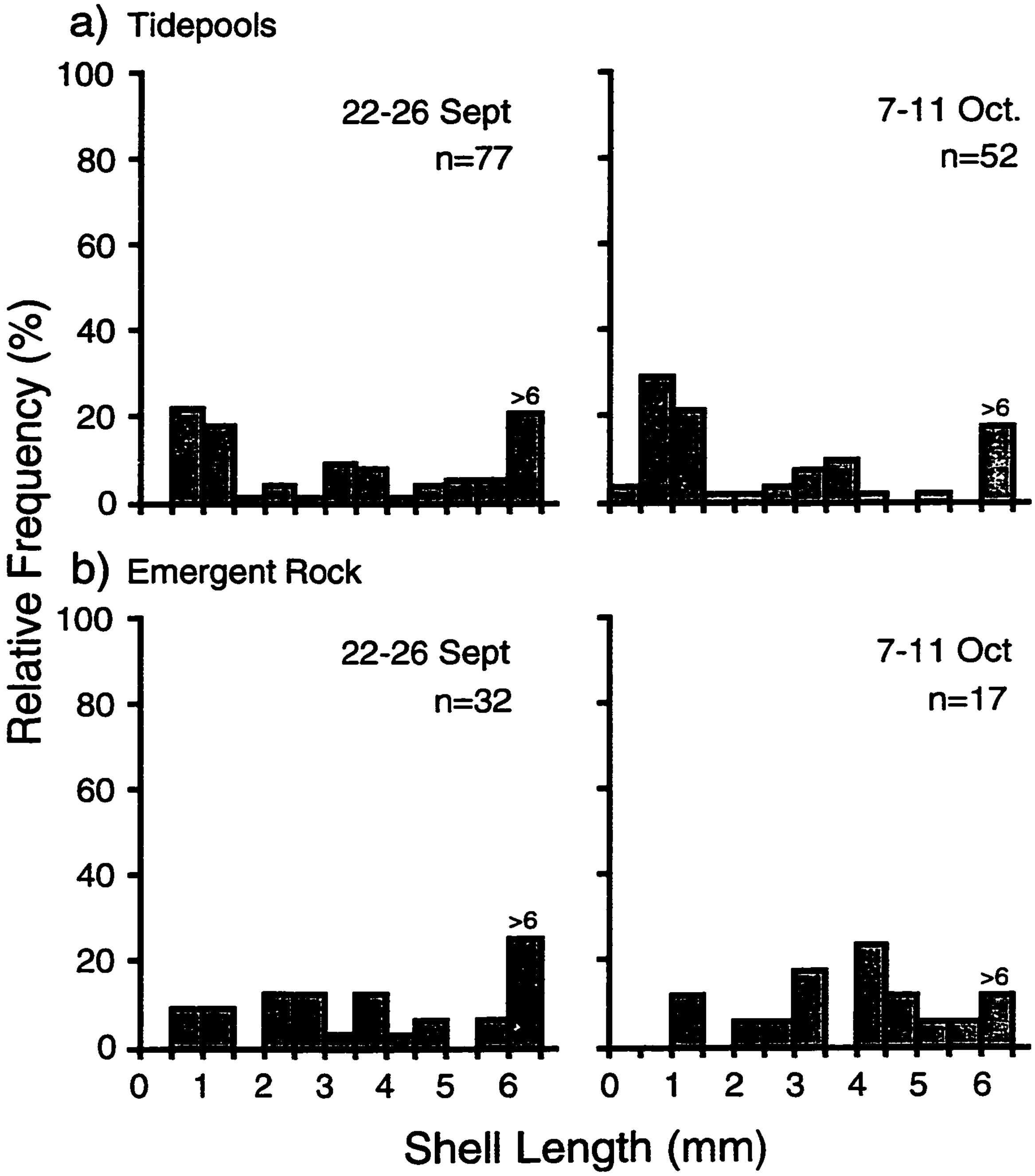

a) Tidepools
22-26 Sept
n=77
7-11 Oct.
n=52
>6
>6
b) Emergent Rock
22-26 Sept
n=32
7-11 Oct
n=17
>6
>6
Relative Frequency (%)
0
20
40
60
80
100
0
1
2
3
4
5
6
Shell Length (mm)

Fig 4.6

DISCUSSION

Colonization rate of *Mytilus* on artificial collectors was directly related to water flux, and was highest on ice-scoured emergent rock and lowest in non-scoured tidepools. This pattern probably reflects an increase in supply of colonists with increased water flux. Bushek (1988) found a similar positive relationship between barnacle settlement rate and water motion which he attributed to both larval supply and selective settlement. In my study, colonization on collectors placed on ice-scoured emergent rock may also have been enhanced by the apparent unsuitability of the surrounding substratum (where colonization rate was low). A similar effect has been reported by Pineda (1994) who found that barnacles settled at higher densities at sites surrounded by unsuitable sandy substratum. Horizontal variability in the availability of colonists did not contribute to the pattern, since the abundance of competent larvae and of postlarvae in the surrounding sea water did not vary significantly over the 1 km of shore spanning my sampling plots.

Artificial collectors have been widely used in studies examining colonization by mytilids (and references therein King et al. 1990, Cáceres-Martínez et al. 1994, Molares & Fuentes 1995), but such studies can not fully explain colonization patterns between habitats or sites because they do not account for the spatial variability of the natural substratum. In my study, the colonization patterns of *Mytilus* differed markedly between artificial collectors and natural substrata. In contrast to the collectors, colonization on natural substrata was greatest in ice-scoured tidepools and minimal on scoured emergent rock (see also Chapter 3). The difference in colonization patterns between artificial and natural substrata is probably related to variation in the macrobenthic assemblage between habitats and strata (see also Chapter 3). Ice-scoured emergent rock was devoid of filamentous or coarsely branched macroalgae, which settlers and small postlarval *Mytilus* are known to be associated with (Chapter 3; reviewed by Seed 1976, Seed & Suchanek 1992), and had less crustose macroalgae than the other habitat and stratum combinations.

Multiple regression did not reveal a consistent relationship between colonization rate on natural substrata and any particular macroalgal group, but there were some associations between either small or large colonists and a suite of biological and physical factors.

In October, mussels <1 mm on natural substrata were common in tidepools but absent on emergent rock. Filamentous and jointed calcareous algae, which were found only in tidepools, may be more suitable sites for mussel larvae and early postlarvae than thick leathery macroalgae, the predominant erect form on emergent rock. Also, mussels <1 mm colonize tidepools during the period of tidal isolation, although only a small proportion of colonists on artificial collectors were collected during tidal isolation in October.

The relationship between the colonization rate of *Mytilus* and macroalgal substrata may depend upon both active substratum choice and passive hydrodynamic processes, and the processes and cues involved probably vary with spatial scale. Active substratum choice by *Mytilus* was suggested by Bourget et al. (1994) who examined the establishment of an epibenthic community on panels with various combinations of scales of substratum heterogeneity (1, 10, 100 mm wide grooves). Bivalve settlers, including *M. edulis*, were aggregated at particular scales of heterogeneity, suggesting they are active settlers (in contrast, bryozoans were uniformly distributed suggesting they are passive settlers). However, Harvey et al. (1995) found that passive settlement processes were sufficient to explain settlement patterns at decimetre scales (on plastic filamentous substrata) of several species of bivalves, including *M. edulis*. Cáceres-Martínez et al. (1994) have suggested that the association of postlarvae of *M. galloprovincialis* with filamentous substrata results from passive ensnarement of these substrata by byssus threads secreted by the postlarvae, rather than active selection.

Most *Mytilus* colonists in this study (with the exception of those on artificial collectors in October) were >0.5 mm SL and were too large to be settling larvae. This is consistent with the pattern I observed on the natural substratum over 17 mo (Chapter 3).

In this study, the size distribution of mussel colonists was much smaller on artificial collectors than on natural substrata. I found only one mussel >5 mm SL on a collector, which is consistent with the small sizes reported in previous studies using artificial collectors (e.g. Bayne 1964, Bohle 1971, King et al. 1990). In contrast, 20 to 30% of colonists on natural substrata were >5mm SL, suggesting that postlarval mussels in this population move repeatedly (see also Chapter 3). Paine (1974) also observed that relatively large large *M. californianus* (>3 cm) colonized cleared plots in the intertidal zone in Washington, USA. The filamentous substrata generally used in artificial collectors may be more suitable for smaller, early postlarvae than for larger, later mussels (Seed 1969a). Also, mussels >5 mm SL may disperse by crawling but are probably too heavy to drift on mucous threads, reducing the likelihood of sampling them in studies which use collectors suspended in the water column.

The results of this study indicate that rates and patterns of colonization by mussels on this shore were influenced by both biological (macroalgal/barnacle cover) and physical factors (water flux, tidal height, flushing time). The low colonization rates on natural substratum on ice-scoured emergent rock was not due to a limited supply of colonists to these areas, since the highest colonization rates were recorded on artificial collectors on ice-scoured emergent rock. This study underscores the importance of measuring colonization on both a standardized artificial substrate and on the natural substratum to unravel the relative roles of supply and substratum type in determining patterns of colonization in a spatially variable environment.

CHAPTER 5: Effects of whelk predation on mussel assemblages in tidepools and on emergent rock on a wave-exposed rocky shore

INTRODUCTION

Environmental factors, such as temperature and wave action, which influence predator-prey interactions may be important determinants of community structure in the marine benthos. Changing environmental conditions may alter the behaviour and/or relative abundance of predators, resulting in variation in feeding rate (Menge 1978a,b, 1983, Barbeau et al. 1994, Carroll & Highsmith 1996, Pile et al. 1996, Scheibling & Hatcher 1997), susceptibility of prey to capture (Barbeau & Scheibling 1994b), or size selectivity of predators (Richardson & Brown 1990, Hughes & Burrows 1991). Menge and Sutherland (1987) have proposed a model of community organization for rocky shores that predicts that increased environmental stress reduces the importance of predation, assuming predators are more affected by these stresses than their prey. The model is based on experimental studies of the impact and intensity of predation by whelks (Menge 1976, 1978a, 1978b, 1983, Lubchenco & Menge 1978) and grazing by littorinid snails (Lubchenco 1986) along a gradient of wave action.

Predation on mussels, which are often the dominant sessile organisms (Menge & Farrell 1989), can have dramatic effects on intertidal community structure on temperate rocky shores (Paine 1966, 1974, Menge 1976, Lubchenco & Menge 1978, Robles 1987, Robles & Robb 1993, Carroll & Highsmith 1996). The whelk *Nucella lapillus* is a common predator of mussels on wave-exposed rocky shores in the North Atlantic (Stephenson & Stephenson 1972). Its predation rate is affected by various abiotic and biotic factors which moderate the intensity of physical disturbance and desiccation stress, including wave forces, height on the shore, weather, substratum heterogeneity, and the presence or absence of canopy algae (Menge 1978a,b, 1983, Burrows & Hughes 1989, Gosselin & Bourget 1989, Hughes & Burrows 1990, 1991). Previous studies of the effects of whelks on mussel assemblages have focused on adult whelks and mussels. Newly recruited whelks are much less visible than adults, but can be seasonally abundant. Predation by recently recruited whelks has been examined in a few laboratory studies (Largen 1967a, Palmer 1990, Gosselin & Chia 1994), but the effects of recruits on natural prey assemblages in the field are unknown.

Along the Atlantic coast of Nova Scotia, the mussels *Mytilus trossulus* and *M. edulis* co-occur in the low and mid intertidal zones (Pedersen 1991, Mallet & Carver 1995). The cover and spatial distribution of *Mytilus* differs among intertidal habitats. Mussels in tidepools generally occur in centimetre-scale patches (Hunt & Scheibling 1995), whereas those on emergent rock tend to form more extensive beds (personal observations; Minchinton et al. 1997). Colonization rates of mussels do not differ between these habitats (Chapters 3 and 4), suggesting that this pattern reflects lower post-settlement mortality of mussels on emergent rock. Predation by *N. lapillus*, which is likely an important source of mortality for mussels in both habitats, may be influenced by environmental differences between tidepools and emergent rock. Predators such as whelks may have more time to search for prey in tidepools, where organisms are continually submerged, than on emergent rock. Also, tidepools provide a refuge from extreme fluctuations in environmental conditions which may influence the feeding rate of predators (Metaxas & Scheibling 1993).

In this chapter, I compare predation on *Mytilus* by *N. lapillus* between tidepools and emergent rock. During the study, I observed a large recruitment event of whelks, indicating that recently recruited whelks can be numerically dominant. In a field experiment, I manipulated the density of recently recruited whelks and of older juveniles and adults (hereafter post-recruits) to test their relative effects on percentage cover and size distribution of mussels. I compare the feeding rate and size selection of recently recruited and older whelks preying on mussels in both the field and the laboratory, and use these data to estimate the direct and indirect effects of whelk predation on the mussel assemblage.

MATERIALS AND METHODS

Laboratory experiments

Nucella lapillus drills through mussel shells by scraping with its radula and secreting an erosive chemical (Hughes & Burrows 1993), resulting in a distinctive, approximately circular drill hole (Palmer, 1990). Laboratory experiments were conducted to determine the relationship between the size of *Nucella lapillus* and their drill holes, and to investigate size selective predation of *Mytilus* by the whelks. Thirty four whelk post-recruits 5-26 mm in shell length (SL) were used in an experiment in May 1995; 32 recruits <5 mm were used in a second experiment in October 1995. In each experiment, individual whelks were presented with two mussels from each of four size classes: <5, 5-9.9, 10-14.9, and 15-24.9 mm SL for post-recruits; <2, 2-3.9, 4-5.9, and 6-7.9 mm for recruits. Whelks and mussels were collected from my field site (see Field Experiment).

Each experiment was conducted in a seawater table supplied with running sea water at a flow rate of ~ 3 $l^{-1}min^{-1}$. Water temperatures ranged from 5.5 to 8 °C in May and 9.5 to 16.5 °C in October. Natural lighting was provided by windows in the laboratory. Post-recruits were held in cages (diameter 15 cm, height 7 cm) constructed of PVC pipe and 3 mm Vexar mesh. Recruits were held in glass dishes (diameter 6.5 cm, height 5 cm) covered with cheesecloth. The duration of the experiment was 26 d for post-recruits and 34 d for recruits. Whelks which did not feed during the experiments (5 recruits and 3 post-recruits) were excluded from the analysis.

The experiments were monitored daily and dead (predated) mussels were replaced. Dead mussels were examined for a drill hole using a dissecting microscope. Drill hole diameter and whelk and mussel shell length were measured using an ocular micrometer (accuracy ± 0.03 mm) or vernier calipers (whelks and mussels >5 mm, accuracy ± 0.05 mm). Mean drill hole diameter was related to whelk shell length by non-linear regression after pooling the data from the two experiments (n=58).

Field Experiment-Manipulation of whelk densities

Methods

I compared the effect of predation by recruits and post-recruits of *Nucella lapillus* on the percentage cover and size distribution of *Mytilus* between tidepools and emergent rock at Cranberry Cove, Nova Scotia. For a detailed description of the study site, see Chapter 3. The experiment was set up in four blocks separated by at least 50 m to intersperse treatments along ~1 km of shoreline. Four plots in each block were selected: two tidepools and two areas of emergent rock (Fig. 5.1). The boundaries of plots of emergent rock were defined by crevices and other topographic features. Tidepools ranged from 1.5 to 4 m^2 in area and 0.2 to 0.4 m in depth. Plots of emergent rock were comparable in area. Distances between plots within a block ranged from 1 to 5 m. Height of each plot above chart datum (C.D.) was measured in August 1996 using a transit level: plots of emergent rock were 0.7 to 1.6 m above C.D. and tidepools were 0.6 to 2.2 m above C.D.

In June 1995, whelk post-recruits (≥5 mm SL) were manually removed from one of the two plots within each habitat (tidepool and emergent rock) in each block; the remaining plots served as controls (Fig. 5.1). In late September, about two weeks after a large recruitment event, recently recruited whelks (<5 mm SL) were manually removed from two 0.04 m^2 quadrats and from a 2-cm-wide border around each of these quadrats in each plot (Fig. 5.1). Two other 0.04 m^2 quadrats in each plot served as controls in which recruits were not manipulated. Quadrats were marked in two corners with stainless steel screws. Treatments with reduced densities of post-recruits or recruits were monitored every 3 to 10 d until mid November 1995 and invading whelks were counted and removed.

Densities of whelk recruits and post-recruits were measured in 5 randomly placed 0.04 m^2 quadrats in the experimental plots where densities of post-recruits were not manipulated. Whelk densities were recorded at 1-2 mo intervals from June to December 1995, and in June and October 1996. Because of extremely high densities of recruits in September and December 1995, they were counted in a 0.01 m^2 quadrat nested within each 0.04 m^2 quadrat. In December 1995, densities of recruits were estimated both in plots where densities of post-recruits were not manipulated and in plots where they were reduced. In September and December, the sizes of whelks in the sample quadrats were measured with vernier calipers (accuracy ± 0.1 mm). Densities of whelk recruits and post-recruits were recorded in a similar manner in one tidepool plot and one plot of emergent rock in each of four other blocks on the shore (which did not correspond to the experimental blocks) at 1-2 mo. intervals from July 1994 to October 1995 and in June and October 1996.

Percentage cover of *Mytilus* was estimated in each of the four permanently marked 0.04 m^2 quadrats in each plot in June (before manipulation of the density of post-recruits) and in August, October, and November 1995. A plexiglass panel with 60 random points was placed over a quadrat and the number of points overlying mussels were counted and expressed as a percentage of the total. The size distribution of *Mytilus* was determined from samples collected in random 12 cm^2 quadrats in late September (3 from each plot where post-recruits were not manipulated) and in late November or early December (from all permanently marked 0.04 m^2 quadrats). Empty shells with drill holes also were measured. Predator size was determined from the drill hole diameter using the relationship determined in the laboratory (see Results). Drill holes less than 0.34 mm were considered to have been made by recently recruited (<5 mm) whelks. Whelks experienced with feeding on mussels will sometimes attack small individuals between the posterior margins of the shell (Hughes & Burrows 1993). I was able to detect these attacks and estimate the size of the predator from the semi-circular mark left on the shell margin.

Statistical Analysis

ANOVA was used to examine spatial and temporal patterns in whelk abundance and to test the effects of experimental factors on mussel cover and size structure. All analyses were conducted as randomized block designs. Because of the lack of replication within blocks, the full model including interactions with block could not be tested. However, Tukey's test for non-additivity (α=0.05) indicated that additive models (i.e., interactions with block pooled as the residual error) were appropriate (Kirk 1995) for all analyses. Prior to ANOVA, Cochran's test was used to ensure that the data satisfied the assumption of homogeneity of variances (α=0.05). Where necessary, raw data were transformed to satisfy this assumption.

Peak densities of whelk recruits and post-recruits were compared between habitats (tidepool, emergent rock), years (a fixed factor with 2 or 3 levels), and blocks using three-way ANOVA. Post-recruit and recruit density was ln (x) or ln (x+1) transformed to remove heterogeneity of variance (Cochran's C test, α=0.05).

Due to preexisting differences in *Mytilus* cover between habitats, change in percentage cover of mussels was used as the dependent variable in ANOVA to examine the effects of habitat and reduction of whelk density on mussel cover. Mussel cover was averaged for the four 0.04 m^2 quadrats in each plot. Change in cover between June and August and between August and October 1995 was analysed by 3 way ANOVA. Habitat (tidepool, emergent rock) and Post-Recruit Density (reduced, natural density) were fixed factors, each with two levels, and Block was a random factor with 4 levels.

Change in mussel cover from October to November 1995, when density of recruits was manipulated, was analysed by four-way ANOVA using a split plot design (Damon & Harvey 1987). Each plot existed in one habitat (tidepool or emergent rock) and one block and received one of the levels of the treatment of post-recruits, but received both of the levels of the recruit density treatment (the split plot factor). To minimize the effects of spatial variability within plots, replicates of recruit density treatments were randomly located within plots rather than assigned to opposite sides of each plot (Fig. 5.1). Before analysis, mussel cover was averaged for the 0.04 m^2 quadrats with and without recruits respectively for each plot. Effects of Block, Habitat, Post-Recruit Density, and Habitat x Post-Recruit Density were tested among plots. The interactions of Habitat and Post-Recruit Density with Block were pooled as the error term. Recruit Density (a fixed factor with two levels: reduced, natural density), Recruit Density x Post-Recruit Density, Recruit Density x Habitat, and Recruit Density x Habitat x Post-Recruit Density were tested within plots. Interactions containing both Block and Recruit Density were pooled as the within-plot error term.

Three way ANOVA was used to compare the percentage of mussels <2 mm SL (recruits) between September and December, with Month and Habitat as fixed factors (each with two levels), and Block as a random factor with 4 levels. For samples collected in December, four-way split plot ANOVA (as described above) was used to compare the percentage of mussel recruits between blocks, habitats, and recruit and post-recruit density treatments.

Kolmogorov-Smirnov tests (Seigel & Castellan 1988) were used to compare the size distributions of whelks, live mussels, and empty mussel shells drilled by recruits or post-recruits between dates (September and December 1995) and habitats for plots where post-recruits were not manipulated. Due to low numbers of drilled shells in December, shells drilled by recruits were pooled across recruit density treatments. Kolmogorov-

Smirnov tests also were used to compare size distributions of live and drilled mussels in September and December 1995 and to compare size distributions of live mussels between habitats and whelk density treatments (recruits and post-recruits) in December 1995.

Comparison of feeding rates of whelk post-recruits in tidepools and on emergent rock

The feeding rate of *N. lapillus* on artificially constructed mussel patches with a specific composition (number and size distribution) was examined in tidepools and on emergent rock using cage enclosures in September and October 1995 and June 1997. Mussel patches were constructed in the laboratory. Each patch consisted of 150 mussels (109 <5 mm, 23 5-9.9 mm, 14 10-14.9 mm, and 4 15-24.9 mm) which were placed on a 12.5 x 12.5 cm piece of fiberglass window screen (mesh size=2 mm). This size distribution is the average of the size distributions of mussels in tidepools (Hunt & Scheibling 1995) and on emergent rock (unpubl. data) at Cranberry Cove. Patches were held in running sea water in the laboratory for two weeks before transplantation to the field. During this time, patches were placed on rings of PVC pipe to prevent mussels from attaching through the mesh to the bottom of the tank. While in the laboratory, patches were placed in front of the tank inflow for several days to stimulate stronger byssal attachment to the mesh and were removed from the water once a day for several hours to acclimate to emersion.

Mytilus patches for the first caging experiment were transplanted to the field on June 25, 1995. The mesh base of each patch was fastened to the substratum with marine epoxy putty (Z*Spar A-788 Splash Zone Compound). Patches were covered with another piece of fiberglass window screen for several days to reduce wave stress while the mussels attached to the substratum. Three mussel patches on emergent rock and two in tidepools were selected to examine feeding rates of whelks from August 26 to November 2 1995. Any dead mussels were removed from the patches before each was enclosed in a round cage constructed of PVC pipe (height 7 cm, diameter 15 cm, three 4 x 13 cm holes cut in the sides) and covered with 3 mm Vexar mesh. The cages were fastened to the substratum with epoxy putty and one whelk (15.5 to 16.5 mm SL) was enclosed in each cage. Two of the patches on emergent rock were exposed to whelk predation for 36 and 52 days (because damage to cages by storms and the death of the enclosed whelks interrupted the experiment); the other patches were exposed to whelk predation for 68 days. A second caging experiment was set up on June 13, 1997. Three mussel patches in each habitat were enclosed for 10 days in cages containing two adult whelks (15 to 17.5 mm). The number of mussels eaten by each whelk was determined from the number with drill holes. Any empty mussel shells with drill holes too small (based on the regression equation from the laboratory experiment) to have been created by the enclosed whelk were considered to have been consumed by invading whelk recruits and were excluded from the analysis.

RESULTS

Laboratory experiments

Drill hole diameter (D) was positively related to whelk length (L) (Fig. 5.2) as given by the regression equation:

$$D(\text{mm}) = 0.135 \times L(\text{mm})^{0.576} \; (r^2=0.986).$$

This equation predicts that whelk recruits (<5 mm) create drill holes <0.34 mm in diameter. To determine if mussel size affected drill hole size, drill hole diameters in two size classes of mussels (5-9.9 and 15-24.9 mm SL for post-recruits, n=7; 2-3.9 and 4-5.9 mm for recruits, n=13) were compared using paired t-tests for whelks which consumed individuals of both size classes. There was no significant effect of mussel size on drill hole diameter of recruits ($T_{12}=-0.106$, $p=0.918$) or post-recruits ($T_6=0.640$, $p=0.419$). A significant relationship between drill hole size and gastropod size also has been reported for adult (>5 mm SL) *Ocenebra lurida* feeding on limpets (Palmer 1988) and for juvenile (<7 mm SL) *N. emarginata* feeding on barnacles (Palmer 1990).

The feeding rate (FR) of *N. lapillus* recruits in October was significantly related to mean body size (L, average of initial and final length):

FR (mussels week^{-1})= 2.32 + 0.992 x L (mm), r^2=0.403, $F_{1,25}$=16.8, p=0.0004) (Fig. 5.3). Whelk recruits (mean SL±S.E.=3.5±0.2 mm) consumed an average of 1.2±0.2 mussels week^{-1} (X±S.E.). In contrast, the feeding rate of post-recruits in May was not linearly related to whelk size (r^2=0.08, $F_{1,29}$=2.65, p=0.11) (Fig. 5.3). On average, post-recruits (mean size =15.4±1.1 mm) consumed 0.7±0.1 mussels week^{-1}.

There was a significant positive relationship between mean size of mussels (M) consumed and mean size (L, average of initial and final length) of both whelk recruits and post-recruits (Fig. 5.4):

Recruits M(mm)=2.594 + 0.546 x L(mm), r^2=0.371, $F_{1,25}$=14.77, p=0.001

Post-recruits M(mm)= 8.485 + 0.312 x L(mm), r^2=0.254, $F_{1,29}$=9.88, p=0.004.

Although large recruits (>3 mm SL) rarely consumed mussels <2 mm SL and post-recruits rarely consumed mussels <5 mm SL, both recruits and post-recruits were capable of consuming the full size range of mussels presented to them.

Whelk Manipulation Experiments

Whelk density and size distribution

Peak densities of post-recruits of *N. lapillus* in both experimental plots (1995-96) and in plots in adjacent areas (1994-1996) varied significantly between habitats and among blocks along the shore but not between years, and there was no significant interaction between habitat and year (Table 5.1, Fig. 5.5). During my field experiment in 1995, post-recruits were three times more abundant on emergent rock than in tidepools. Peak densities of whelk recruits varied significantly between each of the years (Student-Newman-Keuls Test, p<0.05): densities in 1995 were forty times higher than in 1994 and ten times higher than in 1996 (Fig. 5.5, Table 5.1). Densities of recruits also differed significantly among blocks, but there was no significant effect of habitat and no significant interaction between habitat and year. Manual removal was an effective technique for reducing densities of post-recruits of *N. lapillus* at this site, resulting in densities 10-12% of initial values from July to November (Fig. 5.6). Removal of recruits reduced densities to 15-27% of initial densities during October and November (Fig. 5.6). However, because whelk densities were declining naturally in the fall, densities of recruits in particular did not differ greatly between treatment and control quadrats.

After the peak of whelk recruitment in September, recruits were numerically the dominant component of the population (Fig. 5.7). The size distributions of whelks in unmanipulated control plots did not differ between emergent rock and tidepools in September ($D_{819,620}=0.04$, $p>0.10$) or December ($D_{47,70}=0.18$, $p>0.10$). However, the size distributions differed significantly between months (habitats pooled, $D_{1439,117}=0.41$, $p<0.01$) as whelks <3 mm SL were less abundant in December than in September (Fig. 5.7). When post-recruits (≥5 mm SL) were analysed separately, the size distributions differed between tidepools and emergent rock in September ($D_{119,92}=0.25$, $p<0.01$), when post-recruits were larger in tidepools than on emergent rock, but not in December ($D_{20,23}=0.11$, $p>0.10$).

Effects on mussel cover

In the field experiment, mussel cover generally remained stable where densities of whelk post-recruits were reduced and decreased, particularly on emergent rock, where whelk density was not manipulated. However, the magnitude of the effect of whelk density varied over the course of the experiment. Before whelk density was manipulated in June 1995, percentage cover of *Mytilus* (averaged over plots in both habitats) was significantly greater on emergent rock than in tidepools, but did not differ significantly among blocks along the shore or between plots assigned to the different post-recruit density treatments, and there was no significant interaction between habitat and post-recruit density treatment (Fig. 5.8, Table 5.2). Between June and August 1995, mussel cover decreased by 5% in unmanipulated control plots and increased by 6% where densities of post-recruits were reduced (Fig. 5.8). Change in percentage cover of mussels varied significantly among blocks and differed significantly between whelk density treatments, but did not vary between habitats, and there was no significant interaction between habitat and post-recruit density (Table 5.2). Between August and October, percentage cover of mussels declined by 43% on emergent rock and by 9% in tidepools in unmanipulated control plots (Fig. 5.8). In plots where densities of post-recruits were reduced, percentage cover of mussels remained relatively constant (Fig. 5.8). Change in percentage cover was significantly greater on emergent rock than in tidepools and greater in control plots than in plots where post-recruit densities were reduced; there was no significant effect of block and no significant interaction between habitat and post-recruit density (Table 5.2).

Following a large recruitment event of whelks in September 1995, manipulation of the density of recently recruited whelks was added as a factor in the experiment. Between October and November, mussel cover changed by less than 7% in any combination of whelk density treatment and habitat (Fig. 5.8) and did not vary significantly among blocks, between habitats, or between treatments with reduced or unmanipulated densities of whelk recruits or post-recruits; there were no significant interactions between any of the factors (Table 5.2).

Effects on size distribution of mussels

Size distributions of live mussels differed significantly between tidepools and emergent rock in September for the control treament where post-recruit density was not manipulated ($D_{2080, 2895}=0.215$, $p<0.001$), and in December for each post-recruit density treatment (reduced: $D_{2629,2709}=0.13$, $p<0.001$, not manipulated: $D_{3101,2961}=0.19$, $p<0.001$;

data pooled across recruit density treatments, which were not significantly different) (Fig. 5.9). In December, size distributions of live mussels also differed significantly between post-recruit density treatments in each habitat (tidepools: $D_{2961,2709}=0.05$, $p<0.01$, emergent rock: $D_{3101,2629}=0.09$, $p<0.001$) (Fig. 5.9). ANOVA indicated that the percentage of mussel recruits (< 2 mm SL) in December was significantly greater in tidepools than on emergent rock, but did not differ significantly among blocks or between whelk density treatments, and there were no significant interactions (Table 5.3; Fig. 5.9). Size distributions of mussels in the control treatment where density of post-recruits was not manipulated differed significantly between September and December both in tidepools ($D_{2080,2961}=0.05$, $p<0.01$) and on emergent rock ($D_{2895,3101}=0.13$, $p<0.01$) (Fig. 5.9). ANOVA indicated that the percentage of mussel recruits in the control treatment was significantly higher in tidepools than on emergent rock, but did not differ significantly between blocks or between months, and there was no significant interaction between habitat and month (Table 5.3, Fig. 5.9).

Drill hole analysis

The size distribution of drilled mussels indicated that the percentage drilled by whelk recruits was greater than that drilled by post-recruits in control plots in both September and December (Fig. 5.10). Although only 2-10% >10 mm SL were drilled by whelk recruits, mussels as large as 22 mm SL were drilled (estimated whelk size: 3.8 mm SL). In September, the size distribution of shells drilled by whelk recruits differed significantly from the size distribution of live mussels in tidepools ($D_{64,2080}=0.23$, $p<0.01$), where the proportion of shells <1 mm SL was lower for drilled than for live mussels, but not on emergent rock ($D_{146,2985}=0.10$, $p>0.10$) (Fig. 5.9, 5.10). In December, the size distributions of drilled and live mussels did not differ significantly in either habitat (tidepools: $D_{30,2961}=0.25$, $0.05<p<0.10$; emergent rock: $D_{42,3101}=0.17$, $p>0.10$). In control plots where post-recruits were not manipulated, the size distribution of shells drilled by recruits did not differ significantly between tidepools and emergent rock in September ($D_{64,146}$=0.20, p>0.10) or December ($D_{30,42}$=0.10, 0.05<p>0.10), and did not differ significantly between months when habitats were pooled ($D_{210,72}$=0.12, p>0.10) (Fig. 5.10).

The size distribution of shells drilled by whelk post-recruits indicated that they consumed mainly the largest mussels, although small post-recruits (estimated whelk size: 6 mm SL) drilled mussels as small as 1-2 mm SL (Fig. 5.10). In September, the size distribution of shells drilled by post-recruits in control plots differed from the size distribution of live mussels both in tidepools ($D_{20,2080}$=0.94, p<0.001) and on emergent rock ($D_{31,2895}$=0.64, p<0.001) (Fig 5.9, 5.10). The size distribution of shells drilled by post-recruits differed between tidepools and emergent rock ($D_{20,31}$=0.52, p<0.01): mussels <10 mm SL comprised 74% of shells drilled by post-recruits on emergent rock but only 35% of those in tidepools (Fig. 5.10). In December, low sample sizes of shells drilled by post-recruits precluded further analysis.

Estimated mortality due to whelk predation

The mean feeding rates of post-recruit *N. lapillus* enclosed in cages did not differ significantly between tidepools and emergent rock in fall 1995 (0.82 and 0.77 *Mytilus* week^{-1} respectively; T_2=2.15, p=0.165) or June 1997 (0.58 and 1.4 *Mytilus* week^{-1} respectively; T_2=2.21, p=0.157). The size of mussels consumed did not differ significantly between habitats in fall 1995 (mean SL, emergent rock: 13.1 mm, tidepool: 13.5 mm; T_2=0.554, p=0.618) or June 1997 (mean SL, emergent rock: 11.0 mm, tidepool: 12.5 mm; T_2=0.633, p=0.599).

To estimate the reduction in mussel density due to predation by post-recruits between June and October 1995 (115 d), I multiplied the maximum density of *N. lapillus* (115 and 320 whelks m^{-2} in tidepools and on emergent rock respectively) by the estimated mean feeding rate of individual whelks (0.70 and 1.09 mussels week^{-1} based on the average of the cage experiments) during this period. According to this calculation, whelk predation accounted for the loss of 1,326 mussels m^{-2} in tidepools and 5,701 mussels m^{-2} on emergent rock. For comparison, I estimated the reduction in mussel density represented by the decrease in percentage cover of mussels over the same period (40% and 10% on emergent rock and in tidepools respectively). I assumed that the mean densities of mussels in December in plots where post-recruit density was reduced (all sizes for tidepools and emergent rock respectively: 121,836 and 126,663 mussels m^{-2}; >10 mm SL: 5,714 and 7,776 mussels m^{-2} >10 mm SL on emergent rock and in tidepools respectively) were representative of the densities at the start of the experiment. According to this calculation, the decrease in mussel cover represented a loss of 12,798 mussels m^{-2} in tidepools and 49,242 mussels m^{-2} on emergent rock. Assuming that the size distribution of mussels >10 mm SL in December in the plots where densities of post-recruits were reduced was representative of the size distribution during the summer in plots where densities of post-recruits were not manipulated, the estimated loss of these large mussels was 786 mussels m^{-2} in tidepools and 3,361 mussels m^{-2} on emergent rock. Thus, although my estimates of whelk predation only accounted for ~1% of the estimated reduction in the total density of mussels, it could account for all of the estimated reduction in the density of large mussels if whelks selectively preyed on mussels >10 mm SL.

Predation by post-recruits probably has greater effects on mussel cover than on mussel density because post-recruits selectively prey on large mussels. I estimated the reduction in percentage cover of mussels due to whelk predation between June and October. I assumed, based on the laboratory study (Fig. 5.5), that post-recruits consumed only mussels >10 mm SL, but that they selected mussels within this size range in proportion to their abundance. I assumed that the size distribution of mussels >10 mm SL in December in the plots where densities of post-recruits were reduced was representative of the size distribution during the summer in plots where densities of post-recruits were not manipulated. I used a non-linear regression equation based on a sample of 33 mussels in December to relate mussel shell length (SL) to cross sectional area (A, for an ellipsoid):

$$A\ (cm^2)=0.003 \times SL(mm)^{1.833}\ (r^2=0.987).$$

For mussels in each 1 mm size interval >10 mm SL, I calculated the estimated loss in mussel cover which could be attributed to whelk predation by multiplying the estimated loss of mussel density (the number of mussels consumed by whelks multiplied by the proportion of mussels in that size class) by the estimated cross-sectional area. I then summed these decreases in mussel cover across size classes. The estimated losses of mussel cover due to whelk predation were 635 $cm^2\ m^{-2}$ in tidepools and 2028 $cm^2\ m^{-2}$ on emergent rock. These estimated losses due to whelk predation accounted for 63% of the reduction in mussel cover in tidepools (1010 $cm^2\ m^{-2}$) and 51% of the reduction on emergent rock (4042 $cm^2\ m^{-2}$) between June and October 1995.

Nucella lapillus were the only abundant predators of mussels at my field site. Sea stars (*Asterias vulgaris*) were never observed in the experimental plots (although a few new recruits were observed in adjacent tidepools). Green crabs (*Carcinus maenus*) were observed only on two occasions, once in a tidepool plot and once on a plot of emergent rock.

Table 5.1: Three-way ANOVA of peak density (no. m^{-2}) of recruits and post-recruits of *N. lapillus* in experimental plots where densities of post-recruits were unmanipulated and in other plots on the shore at Cranberry Cove, Nova Scotia. Peak density of whelk post-recruits was recorded in June or July and that of whelk recruits in September or October. Factors are Block, Habitat (tidepool, emergent rock), and Year (1995, 1996 or 1994, 1995, 1996). Tukey's test for non-additivity was non-significant: experimental plots $F_{1,2}<0.02$, $p>0.25$, other plots $F_{1,5}<1.4$, $p>0.25$. *** $p < 0.001$; ** $p < 0.01$; * $p < 0.05$.

	Source	df	MS	F	p
Experimental Plots					
Whelk Post-recruits	Block	3	3.1	6.4	0.013*
	Habitat	1	12.3	25.1	0.0007***
	Year	1	0.7	1.4	0.272
	Habitat x Year	1	1.0	2.0	0.194
	Residual	9	0.5		
Whelk Recruits	Block	3	2.7	5.7	0.018*
	Habitat	1	0.3	0.7	0.416
	Year	1	23.5	50.8	0.0001***
	Habitat x Year	1	0.03	0.07	0.791
	Residual	9	0.5		
Other Plots					
Whelk Post-recruits	Block	3	2.2	3.9	0.031*
	Habitat	1	6.6	11.5	0.004**
	Year	2	0.7	1.3	0.306
	Habitat x Year	2	0.8	1.4	0.284
	Residual	15	0.6		
Whelk Recruits	Block	3	2.3	3.8	0.033*
	Habitat	1	0.001	0.002	0.967
	Year	2	24.4	39.6	0.0001***
	Habitat x Year	2	0.2	0.3	0.768
	Residual	15	0.6		

Table 5.2: Three-way ANOVA of percentage cover of *Mytilus* in June 1995, before density of whelk post-recruits was manipulated, and of change in percentage cover of *Mytilus* between June and August and August and October 1995, and four-way split plot ANOVA of change in *Mytilus* cover from October to November 1995, at Cranberry Cove, Nova Scotia. Factors are Block, Habitat (tidepool, emergent rock), Post-recruit Density and Recruit Density (October-November only). Tukey's test for non-additivity was non-significant: June $F_{1,2}$=0.98, p>0.25, June-August $F_{1,2}$=0.02, p>0.25, August-October $F_{1,2}$=16.2, 0.05<p>0.10, October-November within plots $F_{1,2}$=0.32, p>0.25, among plots $F_{1,2}$=0.01, p>0.25. *** p < 0.001; ** p < 0.01; * p < 0.05.

	Source	df	MS	F	p
June					
(Pre-manipulation)	Block	3	431	2.92	0.09
	Habitat	1	762	5.15	0.049*
	Post-recruit density	1	12	0.08	0.78
	Habitat x Post-recruit density	1	261	1.76	0.22
	Residual	9	148		
June to August					
	Block	3	270	4.36	0.04*
	Habitat	1	123	1.98	0.19
	Post-recruit density	1	486	7.86	0.02*
	Habitat x Post-recruit density	1	45	0.73	0.42
	Residual	9	62		
August to October					
	Block	3	47	0.56	0.65
	Habitat	1	927	10.96	0.009**
	Post-recruit density	1	1342	15.87	0.003**
	Habitat x Post-recruit density	1	226	2.67	0.137
	Residual	9	85		

Table 5.2 continued

	Source	df	MS	F	p
October to November	**Among Plot**				
	Block	3	43.8	1.52	p>0.25
	Habitat	1	1.1	0.04	p>0.25
	Post-recruit density	1	70.5	2.44	0.10<p>0.25
	Habitat x Post-recruit density	1	97.4	3.37	0.10<p>0.25
	Whole Plot Error	9	28.9		
	Within Plot				
	Recruit density	1	29.7	1.21	p>0.25
	Habitat x Recruit density	1	0.5	0.02	p>0.25
	Post-recruit density x Recruit density	1	2.6	0.11	p>0.25
	Habitat x Post-recruit density x Recruit density	1	1.1	0.04	p>0.25
	Split Plot Error	12	24.5		

Table 5.3: Three-way ANOVA of percentage of live *Mytilus* < 2 mm SL in September and December 1995 in plots where whelk post-recruits were unmanipulated and four-way split plot ANOVA of percentage of *Mytilus* <2 mm SL in December 1995 in all plots. Factors are Block, Habitat (tidepool, emergent rock), Month, Post-recruit Density (December only) and Recruit Density (December only). Tukey's test for non-additivity was non-significant: September vs December $F_{1,2}=0.015$, $p>0.25$, December within plots $F_{1,2}=1.14$, $p>0.25$, among plots $F_{1,2}=0.09$, $p>0.25$. *** $p < 0.001$; ** $p < 0.01$; * $p < 0.05$.

	Source	df	MS	F	p
September vs. December	Block	3	42	0.4	0.78
	Habitat	1	1848	15.7	0.003**
	Month	1	21	0.2	0.68
	Habitat x Month	1	12	0.1	0.76
	Residual	9	117		
December	**Among Plot**				
	Block	3	248	1.4	p>0.25
	Habitat	1	2539	14.2	p<0.005**
	Post-recruit density	1	26	0.1	p>0.25
	Habitat x Post-recruit density	1	234	1.3	p>0.25
	Whole Plot Error	9	179		
	Within Plot				
	Recruit density	1	0.2	0.002	p>0.25
	Habitat x Recruit density	1	18	0.3	p>0.25
	Post-recruit density x Recruit density	1	5	0.07	p>0.25
	Habitat x Post-recruit density x Recruit density	1	2	0.03	p>0.25
	Split Plot Error	12	68		

Fig. 5.1. Schematic diagram of one of four blocks in the field experiment in which densities of whelk recruits and post-recruits were manipulated at Cranberry Cove, Nova Scotia. Tidepool plots are indicated in grey and plots of emergent rock (white) are indicated by a dashed line. The boundaries of plots of emergent rock were defined by crevices, ridges, and other topographic features. Within a block, plots were separated by 1 to 5 m. Density of post-recruits (large snail symbol) was manually reduced (no snail symbol) in one plot in each habitat (tidepool, emergent rock) and not manipulated (snail symbol present) in the second plot in each habitat. Within each plot, density of recruits (small snail symbol) was manually reduced in two 0.04 m^2 quadrats (no snail symbol in quadrat) and not manipulated (snail symbol in quadrat) in two other 0.04 m^2 quadrats.

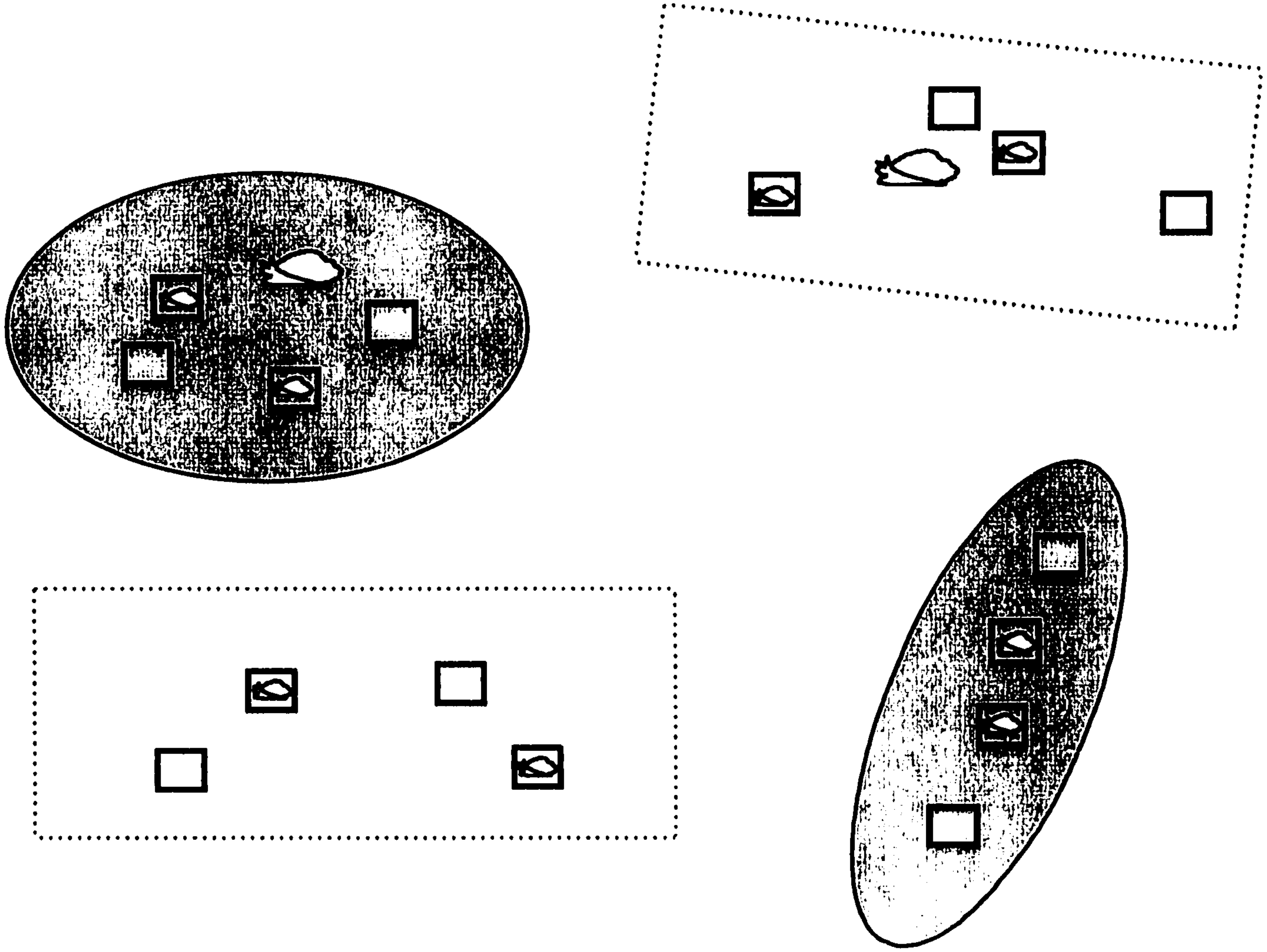


Fig. 5.1

Fig. 5.2. Relationship between the mean diameter of drill holes made in *Mytilus* and shell length of *Nucella lapillus*. Sample size=58.

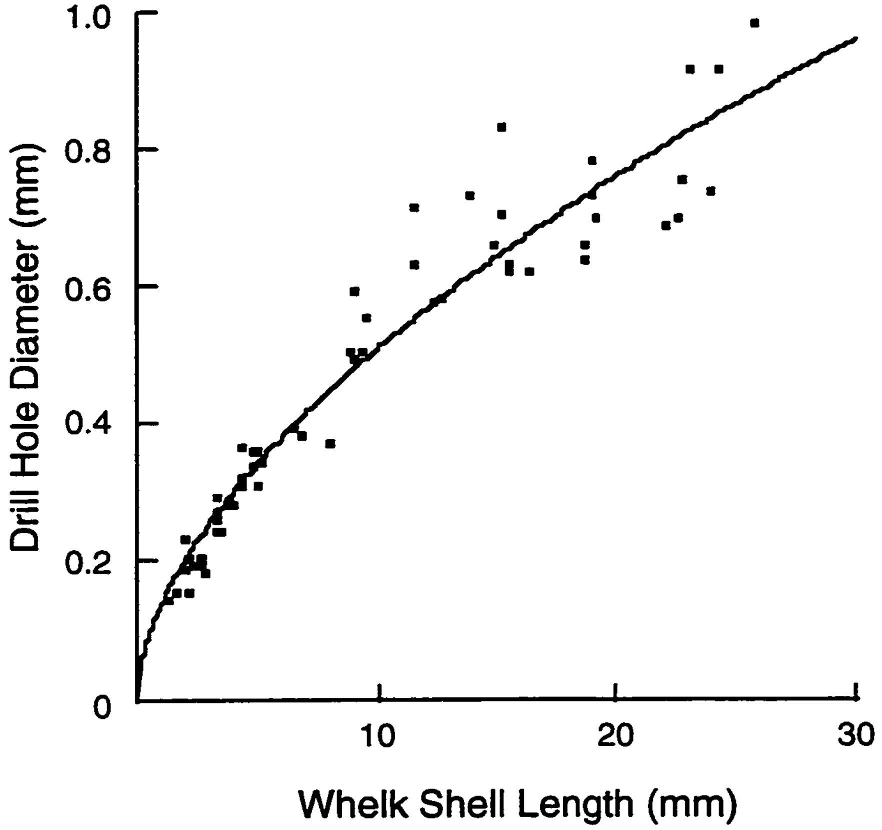

1.0
0.8
0.6
0.4
0.2
0
Drill Hole Diameter (mm)
10
20
30
Whelk Shell Length (mm)

Fig. 5.2

Fig.5.3. Mean number of *Mytilus* week^{-1} consumed by *Nucella lapillus* as a function of mean whelk shell length (mm, average of initial and final length): recruits (<5 mm SL) offered mussels 0.2-8 mm SL in October (n=27) and post-recruits offered mussels 1-25 mm SL in May (n=31).

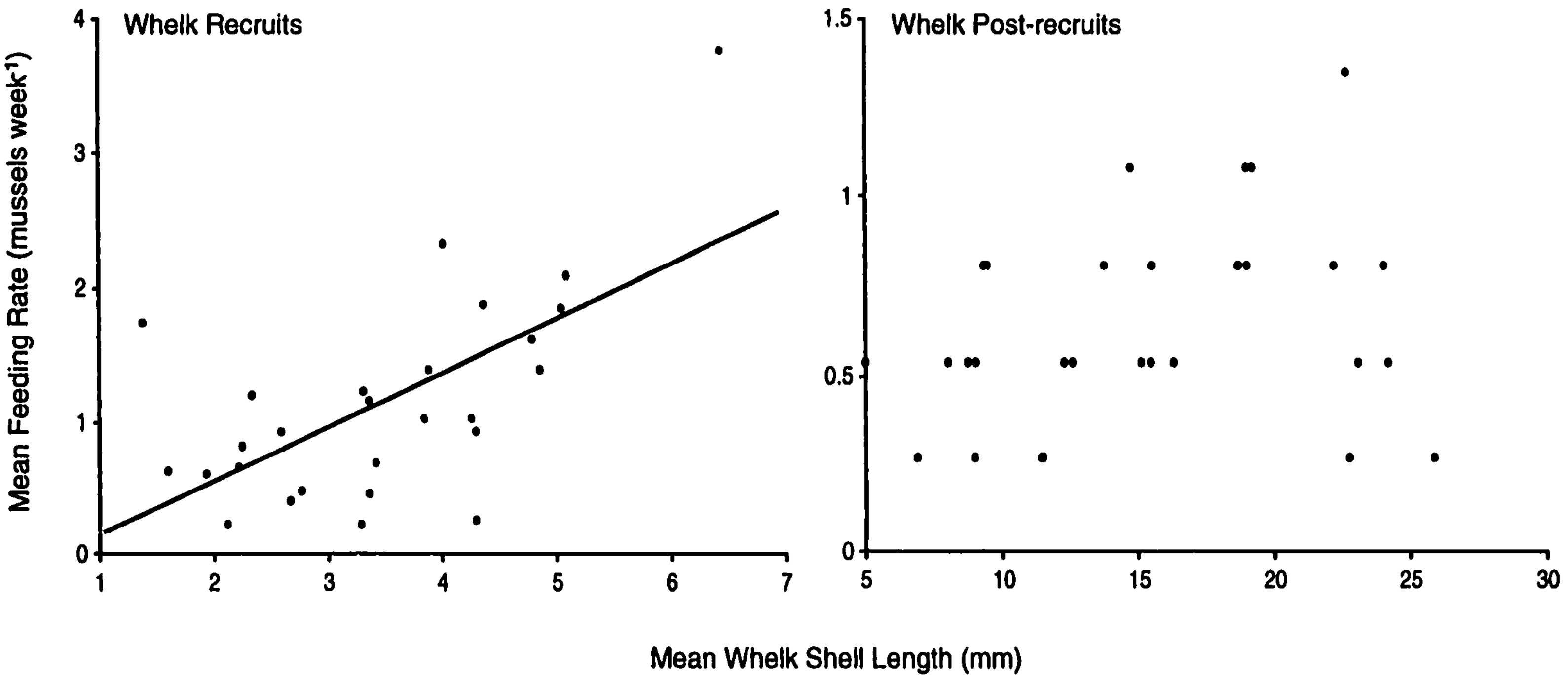

Whelk Recruits
Whelk Post-recruits
Mean Feeding Rate (mussels week^{-1})
Mean Whelk Shell Length (mm)
0
1
2
3
4
1
2
3
4
5
6
7
0
0.5
1
1.5
5
10
15
20
25
30

Fig. 5.3

Fig. 5.4. Mean size (mm) of *Mytilus* consumed by *Nucella lapillus* as a function of mean whelk shell length (mm, average of initial and final length): recruits (< 5 mm SL) offered mussels 0.2-8 mm SL (n=27) and post-recruits offered mussels 1-25 mm SL (n=31).

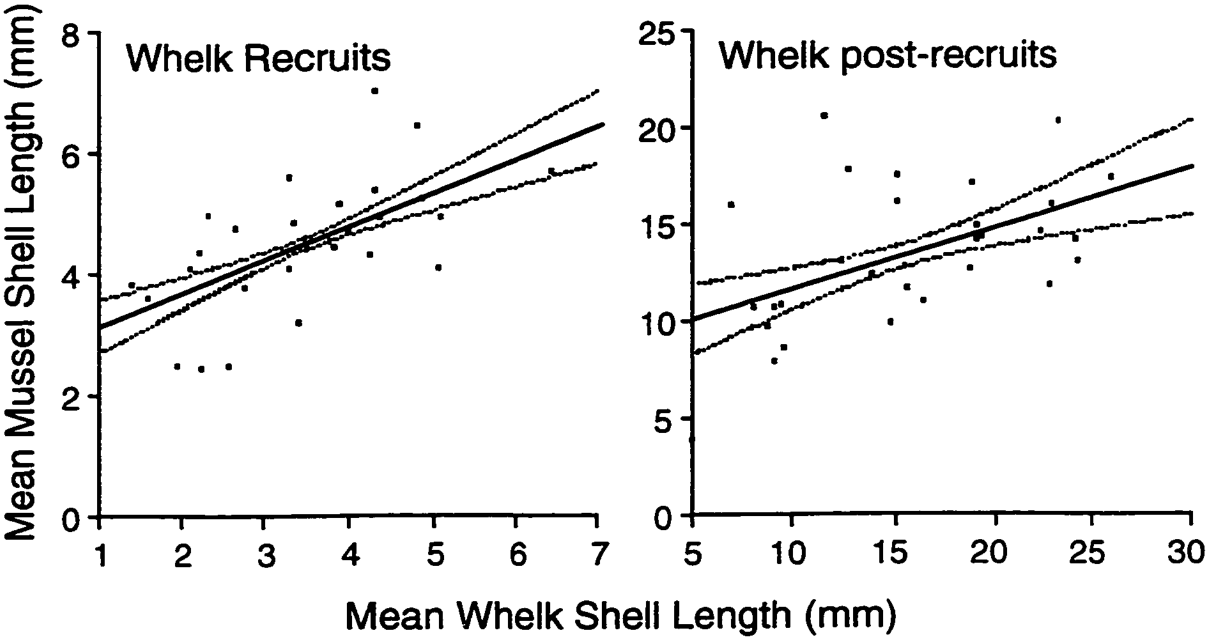

Whelk Recruits
Whelk post-recruits
Mean Mussel Shell Length (mm)
Mean Whelk Shell Length (mm)
0
2
4
6
8
1
2
3
4
5
6
7
0
5
10
15
20
25
5
10
15
20
25
30

Fig. 5.4

Fig. 5.5. Mean (±S.E.) densities (no. m^{-2}) of post-recruits (≥5 mm SL) and recruits (<5 mm SL) of *N. lapillus* in tidepools and on emergent rock (averaged for 4 blocks per habitat) between July 1994 and October 1996 at Cranberry Cove, Nova Scotia.

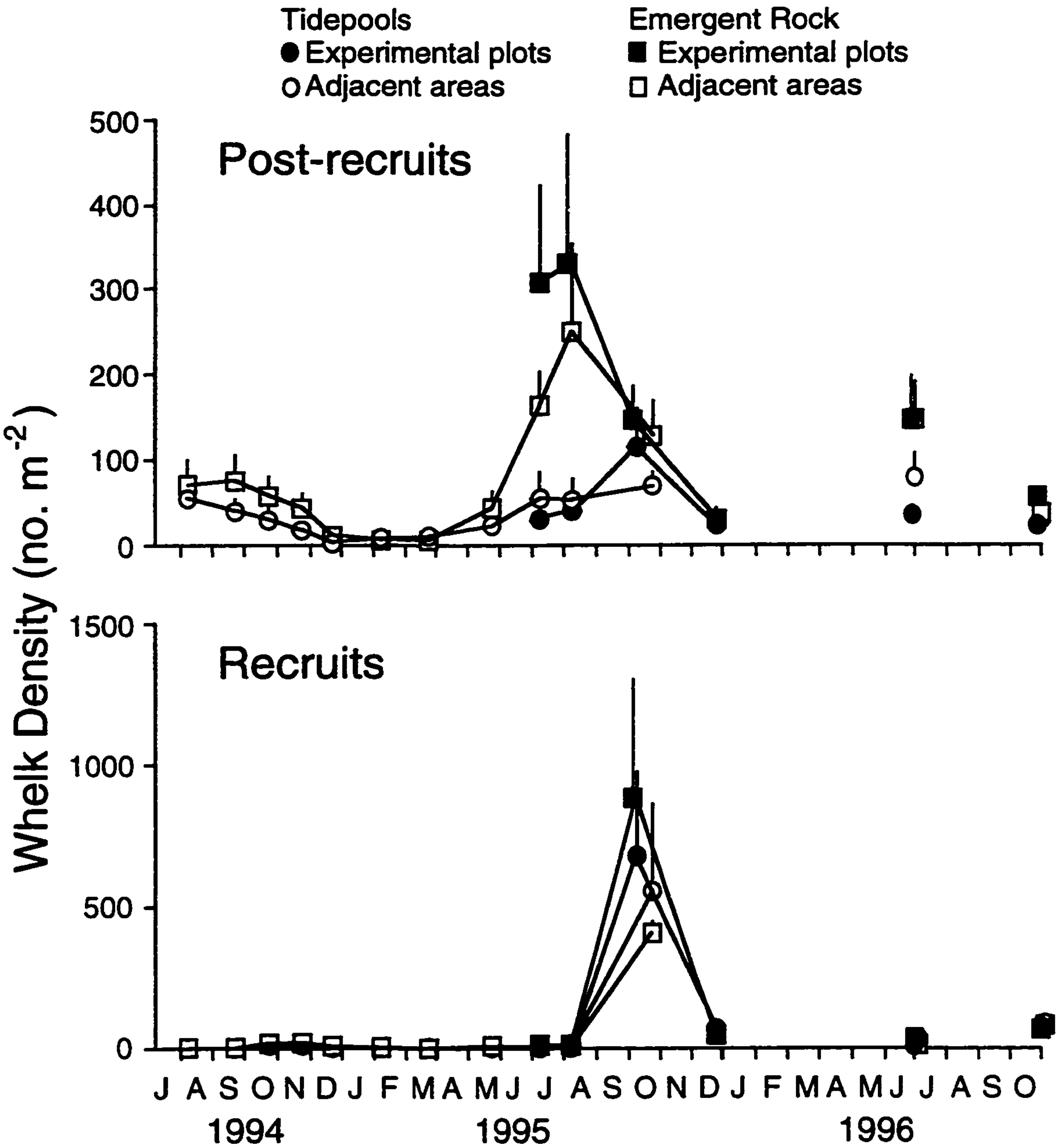

Tidepools
● Experimental plots
○ Adjacent areas
Emergent Rock
■ Experimental plots
□ Adjacent areas
Post-recruits
Recruits
Whelk Density (no. m^{-2})
500
400
300
200
100
0
1500
1000
500
0
J A S O N D J F M A M J J A S O N D J F M A M J J A S O
1994
1995
1996

Fig. 5.5

Fig. 5.6. Mean (±S.E.) densities (no. m^{-2}) of post-recruits (≥5 mm SL) and recruits (<5 mm SL) of *N. lapillus* in whelk density treatments in tidepools and on emergent rock (averaged for 4 blocks per habitat) between June and December 1995 at Cranberry Cove, Nova Scotia. Where densities of post-recruits were reduced, pre-manipulation densities of recruits were recorded only for quadrats from which juveniles were removed. The dashed lines indicate the start of manipulation of densities of recently recruited or post-recruit whelks.

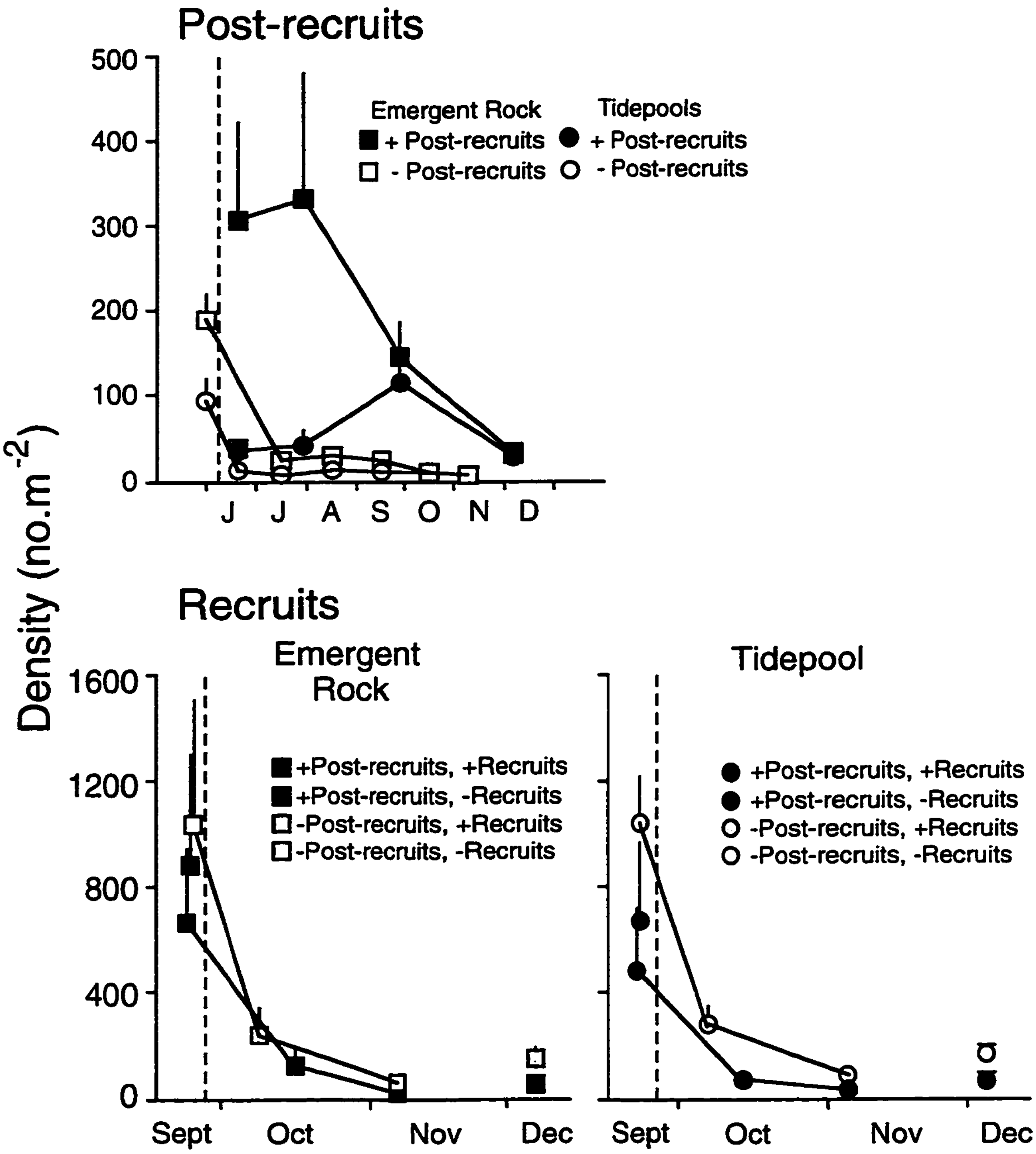

Post-recruits
500
400
300
200
100
0
J J A S O N D
Emergent Rock
■ + Post-recruits
□ - Post-recruits
Tidepools
● + Post-recruits
○ - Post-recruits
Density (no.m-2)
Recruits
Emergent Rock
1600
1200
800
400
0
Sept Oct Nov Dec
■ +Post-recruits, +Recruits
■ +Post-recruits, -Recruits
□ -Post-recruits, +Recruits
□ -Post-recruits, -Recruits
Tidepool
Sept Oct Nov Dec
● +Post-recruits, +Recruits
● +Post-recruits, -Recruits
○ -Post-recruits, +Recruits
○ -Post-recruits, -Recruits

Fig. 5.6

Fig. 5.7. Size frequency distributions of *N. lapillus* in September and December 1995 in tidepools and on emergent rock in plots where density of post-recruit *N. lapillus* was not manipulated. Whelks were pooled over quadrats and blocks (n=20) within a habitat (September for tidepools and emergent rock respectively: n=620, 819; December: n=70, 47).

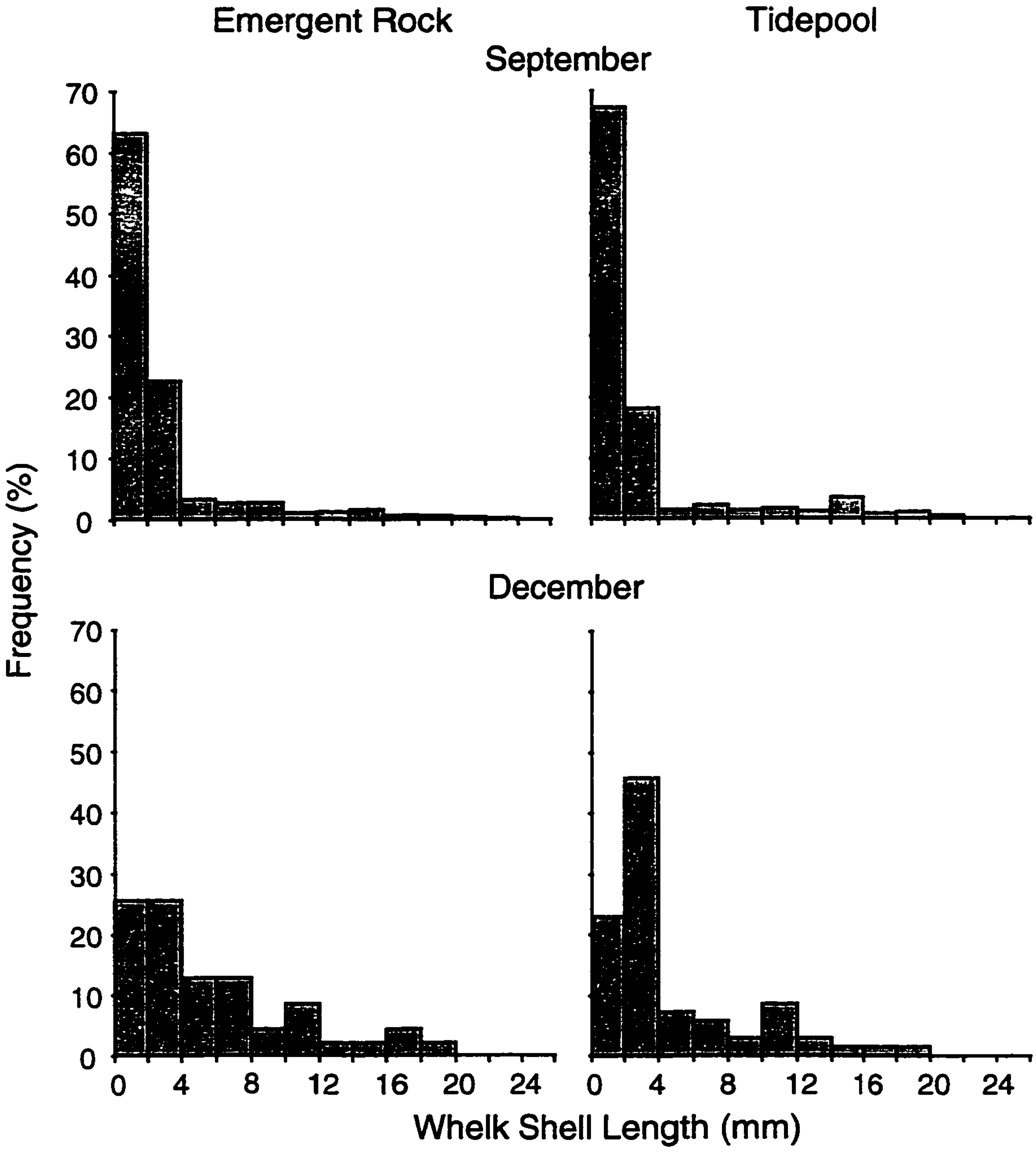

Emergent Rock
Tidepool
September
December
Frequency (%)
0
10
20
30
40
50
60
70
0
4
8
12
16
20
24
Whelk Shell Length (mm)

Fig. 5.7

Fig. 5.8. Mean (±S.E.) percentage cover of *Mytilus* in whelk density treatments in tidepools and on emergent rock (averaged for 4 blocks per habitat) from June to November 1995 at Cranberry Cove, Nova Scotia. The dashed line indicates the start of manipulation of densities of post-recruits.

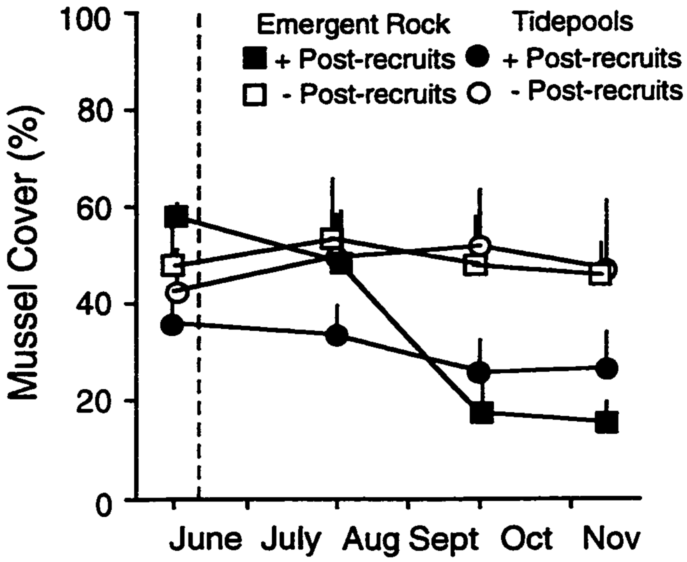

100
80
60
40
20
0
Mussel Cover (%)
Emergent Rock
■ + Post-recruits
□ - Post-recruits
Tidepools
● + Post-recruits
○ - Post-recruits
June
July
Aug
Sept
Oct
Nov

Fig. 5.8

Fig. 5.9. Size frequency distributions of *Mytilus* in September and December 1995 in tidepools and on emergent rock in plots where density of post-recruit *N. lapillus* was not manipulated (September and December) and where it was reduced (December only). Mussels were pooled over quadrats and blocks (September: n=12, December: n=16) within a habitat, including treatments with reduced and unmanipulated recruit density (n=2629-3101). Mussels in the last bar are 10.05-33.7 mm SL.

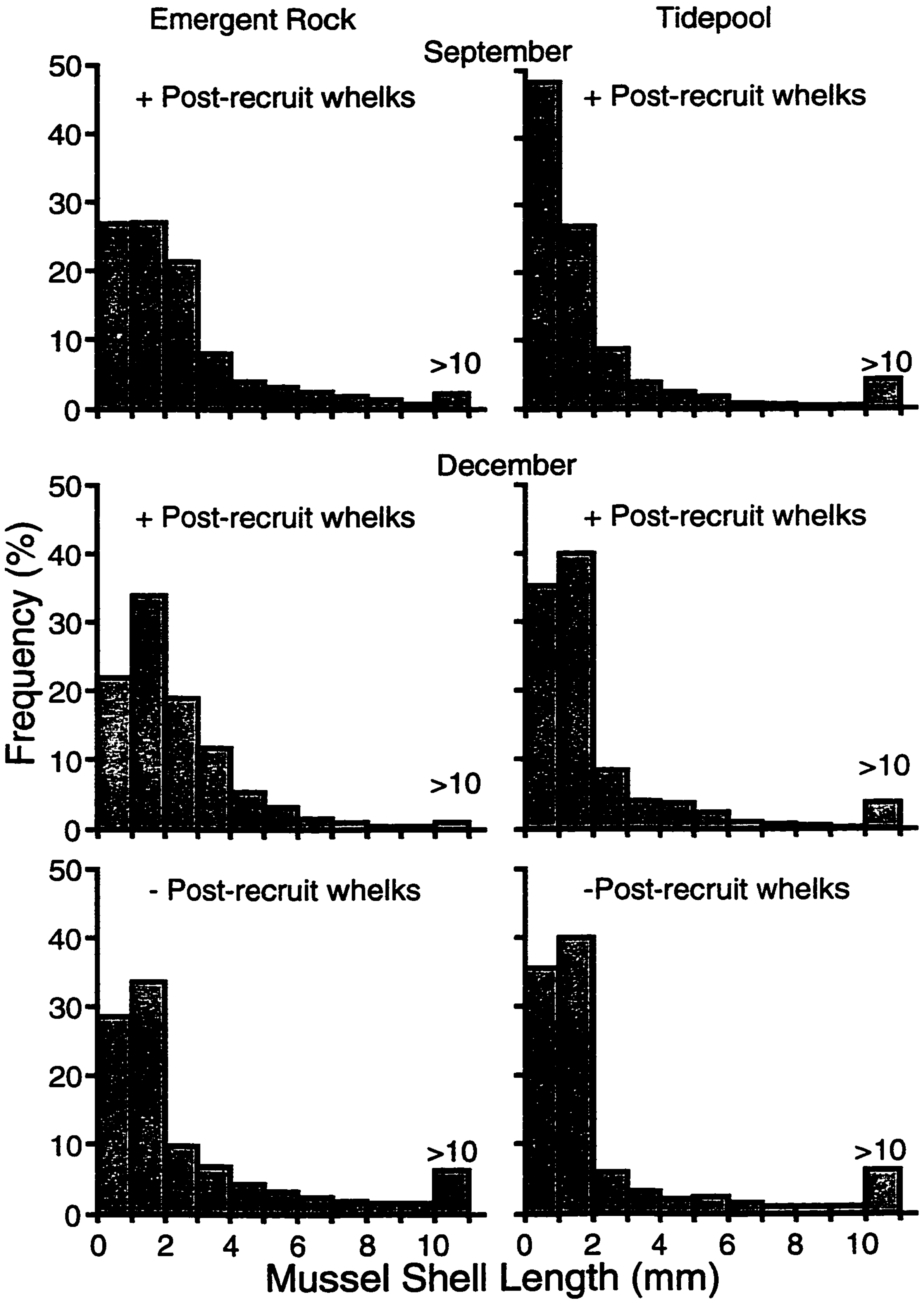

Emergent Rock
Tidepool
September
+ Post-recruit whelks
+ Post-recruit whelks
>10
>10
December
+ Post-recruit whelks
+ Post-recruit whelks
>10
>10
- Post-recruit whelks
-Post-recruit whelks
>10
>10
Frequency (%)
0
10
20
30
40
50
0
2
4
6
8
10
Mussel Shell Length (mm)

Fig. 5.9

Fig. 5.10. Size frequency distribution of empty *Mytilus* shells drilled by whelks in September and December 1995 in tidepools and on emergent rock in plots where density of post-recruit *N. lapillus* was not manipulated. Mussels were pooled over quadrats and blocks (September: n=12, December: n=16) within a habitat, including treatments with reduced and unmanipulated recruit density (September for tidepools and emergent rock respectively: 64, 146 drilled by recruits, 20, 31 drilled by post-recruits; December: 30, 42 drilled by recruits, 5, 13 drilled by post-recruits).

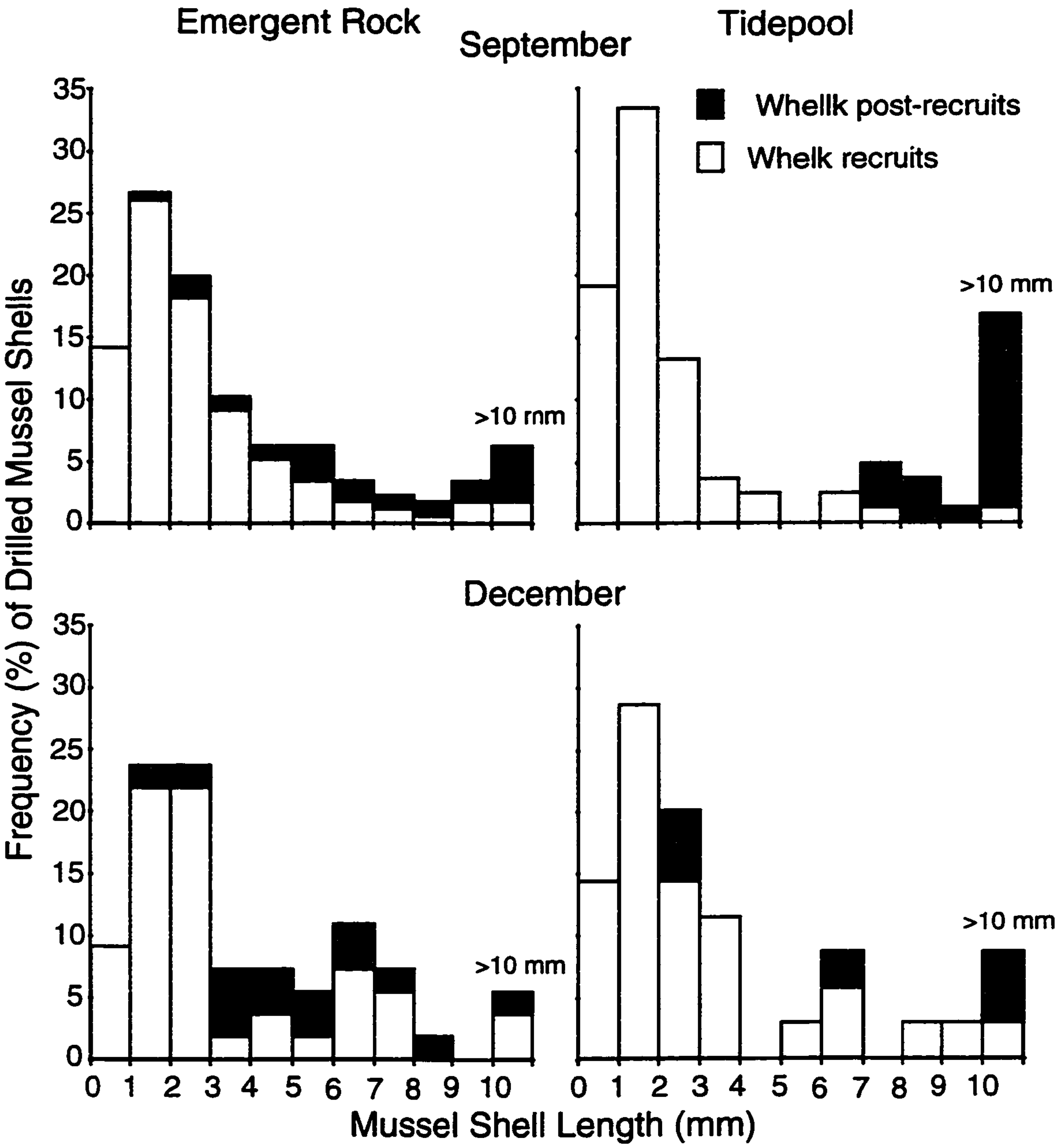

Emergent Rock
September
Tidepool
Whellk post-recruits
Whelk recruits
Frequency (%) of Drilled Mussel Shells
35
30
25
20
15
10
5
0
>10 mm
>10 mm
December
>10 mm
>10 mm
0 1 2 3 4 5 6 7 8 9 10
0 1 2 3 4 5 6 7 8 9 10
Mussel Shell Length (mm)

Fig. 5.10

Fig. 5.11. Frequency distribution of significant wave heights recorded from June to November in 1995 and from 1970-1995 at the mouth of Halifax Harbour, Nova Scotia (44° 50' N, 63° 25' W).

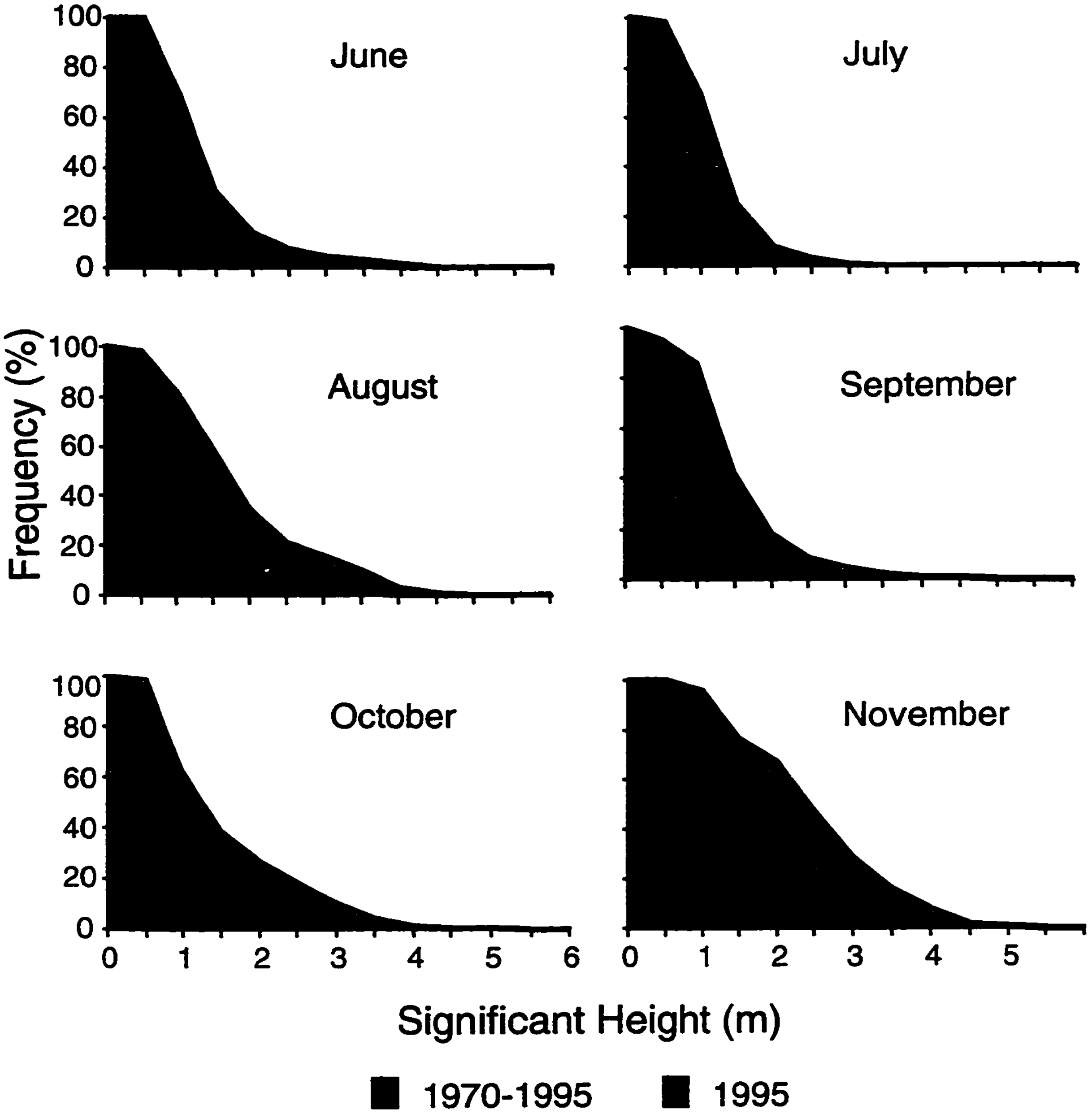

June
July
August
September
October
November
Frequency (%)
100
80
60
40
20
0
0
1
2
3
4
5
6
Significant Height (m)
■ 1970-1995
■ 1995

Fig. 5.11

DISCUSSION

Predation by post-recruits of *N. lapillus*

Removal of post-recruits of *N. lapillus* had a significant effect on percentage cover of *Mytilus* during my experiment. Cover of mussels between June and October remained relatively stable where the density of post-recruits was reduced but declined where whelks were not manipulated. The size distribution of mussels also differed at the end of the experiment between whelk removal treatments and controls. From October to November, mussel cover remained relatively stable and no effects of habitat or density of post-recruits were detected. During this period, however, densities of whelks in the intertidal zone declined markedly as they migrated to the subtidal zone for winter. Furthermore, decreasing temperatures probably depressed the feeding rates of whelks (Largen 1967b, Bayne & Scullard 1978, Stickle et al. 1985) which would lessen their impact on mussel abundance.

Manipulation of densities of whelk post-recruits also has been shown to affect *Mytilus* cover on temperate rocky shores in other regions. In New England, USA, Menge (1976) and Lubchenco and Menge (1978) found that exclusion of *N. lapillus* from cleared plots resulted in the eventual replacement of *Semibalanus balanoides* by *M. edulis* in the mid and low (where other predators also were excluded) intertidal zones at moderately wave protected sites but not at wave exposed sites. In contrast, at a sheltered shore in Maine, Petraitis (1990), found no effects of *N. lapillus* on recruitment of *M. edulis* when barnacles were provided as alternative prey. Petraitis (1990) suggested that the abundance of *M. edulis* is controlled by the presence of barnacles which provide a settlement site for mussels and are the preferred prey of *N. lapillus*. However, Menge (1991b) reanalyzed Menge and Lubchenco's data, controlling for initial barnacle cover, and found that predation still had a strong effect on mussels at wave-sheltered sites. In Oregon, USA, Navarette (1996) found that exclusion of *N. emarginata* and *N.*

canaliculata in the mid intertidal zone resulted in increased cover of *M. trossulus* and *M. californianus*, but that varying the intensity and frequency of whelk predation had unpredictable effects on mussel cover. In the mid-low zone where the sea star *Pisaster ochraceus* is abundant, whelks significantly affected the survival of transplanted *M. trossulus* in the absence but not in the presence of *Pisaster* (Navarette & Menge 1996). In Alaska, Carroll and Highsmith (1996) observed that, after a severe freeze greatly reduced the abundance of *M. trossulus*, mussels did not recover spatial dominance at sites with high densities of the whelk *N. lima*. In field experiments, they recorded significant decreases in mussel cover within two weeks in cages with average densities of *N. lima* compared to exclusion cages without whelks (Carroll & Highsmith 1996). In contrast, Wootton (1994) found that manually reducing densities of whelks had no significant effects on cover of any sessile species, including *M. californianus*, in the mid intertidal zone in Washington State.

In my study, the reduction in *Mytilus* cover attributed to whelk predation was greater on emergent rock than in tidepools. This probably reflects differences between habitats in whelk densities, since feeding rates and sizes of mussels consumed by post-recruits enclosed in cages in the two habitats were similar. However, I did not assess cage artifacts and must assume that any effects of caging on whelk behaviour did not differ between emergent rock and tidepools. The greater reduction in mussel cover on emergent rock than in tidepools is contrary to predictions of the model of Menge and Sutherland (1987) that the importance of whelk predation should diminish along a gradient of increasing environmental stress. However, this model may be more applicable to habitats where stress gradients are large and conditions are relatively severe (Menge & Olson 1990), and may be less appropriate for contrasts between tidepools and emergent substrata on the same shore.

My calculations indicate that predation by whelk post-recruits accounts for ~63% of the reduction in mussel cover in tidepools, and ~51% of the reduction on emergent rock. I attribute this between habitat difference to an interaction between whelk predation and wave action. Dislodgment of the shells of predated mussels by waves would remove small mussels associated with the empty shells and weaken the surrounding mussel matrix. Because whelk predation is more intense on emergent rock than in tidepools, losses due to this interaction between whelk predation and wave action were probably greater on emergent rock, particularly in August 1995 due to the passage of Hurricane Felix. During each month of the experiment, significant wave heights recorded at a station ~ 40 km from the study site (unpubl. data, Department of Fisheries and Oceans, Canada) were larger in 1995 than in a pooled data set from 1970-1995 (Fig. 5.11). In August 1995, 16% of observations of significant wave heights were ≥3 m compared to 1% of observations in the long term record (Fig. 5.11). This study suggests that predation by whelks on exposed rocky shores may have a greater impact than would be predicted from whelk density and feeding rate because of the indirect effects of wave action.

Size selection of mussels by post-recruits of *N. lapillus* in the laboratory has been well documented (for review see Hughes & Burrows 1993). However, analysis of mussels collected in the field suggests that post-recruits may have a greater impact on juvenile mussels than predicted from laboratory studies. In my laboratory feeding experiment, post-recruits appeared to avoid preying on mussels <5 mm SL. Similar results were reported for adult *N. emarginata* preying on *M. trossulus* and/or *M. californianus* (Gosselin & Chia 1994). The mean size of mussels consumed in the laboratory increased with increasing whelk size (for both recruits and post-recruits), although individual whelks consumed a broad size range of mussels. In the field, whelk post-recruits were size selective, but small post-recruits would consume *Mytilus* as small as 2 mm SL and >35% of mussels drilled by post-recruits were <10 mm SL. Shells drilled by post-recruits were larger in tidepools than on emergent rock, perhaps because of the between-habitat difference in size of post-recruits in September. Although wave action may remove large shells more rapidly than small shells, potentially biasing these estimates, these results demonstrate that predation by whelk post-recruits on mussels <5 mm SL is not unusual in the field. In contrast, Hughes and Burrows (1990, 1991), who recorded the diets of individual whelks in Yorkshire, UK, found that whelks consumed few to no mussels <5 mm SL, primarily preying on individuals 10-20 mm SL. Size selection by whelks at my field site may be influenced by the relatively small size of post-recruits (cf Hughes 1972; Hughes et al. 1992) and by the highly skewed size distribution of mussels (Fig. 5.9; see also Hunt & Scheibling 1995).

A number of studies have shown that the feeding rate of *N. lapillus* is strongly temperature dependent (Largen 1967b, Bayne & Scullard 1978, Stickle et al. 1985). However, the feeding rate of post-recruits in my field enclosures in September and October (0.8 mussels week^{-1}) was similar to the feeding rate in my laboratory study in May (0.7 mussels week^{-1}), despite large differences in temperatures (5.5-8 °C in the laboratory in May and ~ 15 °C in the field in October). Bayne and Scullard (1978) measured drilling and ingestion time as well as time between meals for *N. lapillus* preying on mussels at various temperatures in the laboratory. Using their data, I have calculated a feeding rate (2.4 mussels week^{-1}) for whelks of 16 mm SL (the size used in my cage enclosures) at 16 °C in October which is three times higher than that measured in my field enclosures. The relatively low feeding rate of post-recruits in the cage enclosures is presumably due to constraints on foraging in the field by factors such as desiccation and wave action (Burrows & Hughes 1989, Hughes & Burrows 1990, 1991). The feeding rate of post-recruits in the laboratory in May at 5.5-8 °C is higher than the feeding rate (0.16 mussels week^{-1}) reported by Largen (1967b) at 7 °C (month and size of whelks not reported) but is similar to the feeding rate of whelks of 16 mm SL at 9 °C in March (0.8 mussels week^{-1}) calculated from Bayne and Scullard's data.

Predation by recruits of *N. lapillus*

My laboratory studies showed that feeding rate of *N. lapillus* is directly related to body size for recently recruited whelks but not for post-recruits. Bayne and Scullard (1978) found that time spent drilling and ingesting *M. edulis* did not vary with body size for whelks 8.5-34 mm SL (probably because smaller whelks drilled smaller mussels) but that time between meals decreased with increasing body size. The feeding rate of whelk recruits in my study at 9.5-16.5°C in October (1.2 mussels week^{-1}) is 50% of that which I calculated from Bayne and Scullard's (1978) data for whelks of 16 mm SL at 16°C in October (see previous paragraph). Extrapolating Bayne and Scullard's (1978) data to a whelk of 3.5 mm SL (the mean size of recruits in my laboratory experiment) gives a predicted feeding rate (1.4 mussels week^{-1}) similar to that measured for recruits in my laboratory study.

Although size of *Mytilus* consumed generally increases with whelk size, whelk recruits are not constrained to preying on recently recruited mussels. In the laboratory, recruits were able to consume the largest mussels offered to them (8 mm SL). Examination of empty shells collected from the field indicated that recruits of *N. lapillus* are capable of consuming even larger mussels than those offered in the laboratory study, up to 22 mm SL. The ability of recruits to consume prey much larger than themselves has been reported in other laboratory studies (*N. lapillus*, Largen 1967a; *N. emarginata*, Palmer 1990). The size distribution of shells drilled by recruits was similar to the size distribution of live mussels except in tidepools in September where mussels <1 mm SL were proportionally less abundant as drilled shells than as live mussels.

In contrast to the marked effect of post-recruits of *N. lapillus* on mussel assemblages in my field experiment, reduction of the density of recently recruited whelks had no effect on either cover or size distribution of *Mytilus*. Manual removal of whelk recruits was less effective than removal of post-recruits because the high densities of recruits necessitated a smaller spatial scale of manipulation which was harder to maintain. Furthermore, although densities of recruits were reduced to 15-20% of initial values, whelk abundance was declining naturally during this period due to mortality and migration to the subtidal zone. Therefore, the difference in density between recruit treatments was small (Fig. 5.6). However, examination of drilled shells suggests that whelk recruits consumed large numbers of mussels during this period. In both September and December, the percentage of mussels which had been drilled by recruits was greater than that drilled by post-recruits, although differential removal of large empty shells by wave action may bias this comparison. The empty mussel shells in these samples likely reflect predation which occurred after August 1995 when waves from Hurricane Felix probably removed the large numbers of empty shells which had accumulated during the summer due to intense predation by post-recruits. Although I was unable to detect a significant effect of whelk recruits on mussel assemblages in my experiment, the high abundance of recruits following a large recruitment event in September 1995, their high feeding rate relative to their body size, and their ability to consume mussels larger than themselves all suggest they can have an important impact on mussel assemblages. This is the first study to attempt to examine the effects of predation by recently recruited whelks in the field, and more research is necessary.

Patterns of abundance and distribution of mussels and the role of whelk predation

Predation by *N. lapillus*, particularly post-recruits, affects mussel assemblages both in tidepools and on emergent rock, but does not fully explain the differences between habitats in the patterns of distribution and abundance of mussels. In my field experiment, the reduction in mussel cover was greater on emergent rock, where mussel patches are larger and more continuous, than in tidepools. This disparity between the effects of whelk predation and the pattern of abundance of mussels may have resulted, in large part, from the interaction between whelk predation and unusual wave action in August 1995 which may not be typical of this shore. At the end of the experiment in December 1995, mussel cover in control plots (where density of post-recruits was not manipulated) was lower on emergent rock than in tidepools, in contrast to the more typical pattern observed at the start of the experiment in June. However, densities of post-recruits were greater on emergent rock than in tidepools each summer between 1994 and 1996, although the difference between habitats was greatest in 1995. Because feeding rates of whelk post-recruits are similar in tidepools and on emergent rock, whelk predation at this site is probably usually at least as intense on emergent rock as in tidepools. The long term effects of whelk predation on mussel assemblages will depend on the balance between rates of predation by whelks and rates of growth and recruitment of mussels (Petraitis 1995). Recently recruited whelks may have long term effects on mussel cover by limiting recruitment and preying on fast-growing juvenile mussels.

CHAPTER 6: Patch dynamics of mussels in contrasting intertidal environments

INTRODUCTION

Many populations and communities can be viewed as dynamic mosaics of patches or islands among which individuals are exchanged (Pickett & White 1985, Paine 1994). Assemblages of marine mussels are a good model system to examine patch dynamics because of their simplicity: they are effectively monocultures in a two-dimensional matrix. Mussels are common on rocky shores in many parts of the world in aggregations that range in size from patches a few centimeters in diameter (e.g. Hunt & Scheibling 1995) to large beds containing meter scale gaps (e.g. Paine & Levin 1981). The structure and dynamics of mussel assemblages will depend on the balance between processes decreasing the size of aggregations and those increasing their size (Petraitis 1995). For example, predation is important in determining the distribution and abundance of mussels on many shores (e.g. Paine 1966, 1974, Menge 1976, Robles 1987). Under certain conditions, high individual growth rates of mussels enable the persistence of mussel patches subjected to intense predation (Reusch & Chapman 1997). On wave-exposed shores, dislodgment by waves is a major cause of loss of mussels in the intertidal zone (Paine & Levin 1981) and the shallow subtidal zone (for mussels overgrown by algae Witman 1987). Because mussels are not permanently attached to the substratum, aggregation size also may change due to passive dispersal of mussels by wave dislodgment or active dispersal by crawling. Redeposition by waves and movement of large mussels have been shown to be important in structuring mussel assemblages on soft substrata (e.g. Bertness & Grosholz 1985, Reusch & Chapman 1997), but these processes have received little attention in studies on rocky shores.

In this chapter, I continue my examination of mussel assemblages (*Mytilus trossulus* and *M. edulis*) in tidepools and on the surrounding emergent rock in the mid intertidal zone on a rocky shore on the Atlantic coast of Nova Scotia, Canada. The abundance and spatial distribution of mussels differ between these two habitats: mussels in tidepools generally occur in centimeter-scale patches (Hunt & Scheibling 1995), whereas those on emergent rock tend to form more extensive beds with centimeter-scale gaps (personal observations; Minchinton et al. 1997). In both habitats, the scale of the aggregations and the size of the individuals in them are smaller than those described in most previous studies of mussel patch dynamics. Previous studies of mussels have focused on a single habitat, either emergent rock in the intertidal zone or the subtidal zone (e.g. Paine & Levin 1981, Svane & Ompi 1993, Petraitis 1995, Reusch & Chapman 1997). There are few experimental studies of processes influencing the structure and dynamics of species assemblages in tidepools compared to emergent rock (reviewed by Metaxas & Scheibling 1993).

Differences in the pattern of distribution and abundance of mussels between tidepools and emergent rock may result from environmental differences between the two habitats. Strong gradients or differences in environmental stress are predicted to influence the relative importance of biotic and abiotic factors in structuring communities and the intensity and outcome of biological interactions (Connell 1975, Menge & Sutherland 1976, 1987). For example, these models of community structure, which are based on research in the rocky intertidal zone, predict that predation will decrease with increasing environmental stress, which inhibits consumers more than their prey. Tidepools fluctuate in temperature, salinity, oxygen saturation, and pH over the tidal cycle, but the degree of environmental fluctuations is less than on emergent rock (reviewed by Metaxas & Scheibling 1993). Most importantly, organisms in tidepools are continually submerged and do not experience desiccation during low tide. Thus, tidepools are potentially important refuges from stressful environmental conditions on emergent rock which may explain differences in the structure and dynamics of species assemblages in tidepools compared to emergent rock (Metaxas & Scheibling 1993).

To monitor the dynamics of mussel patches and investigate processes influencing patch size and structure both in tidepools and on emergent rock, I transplanted artificially constructed patches with a specific composition (size and number of mussels) to each habitat at a wave-exposed rocky shore for different periods and in different seasons of the year. I measured rates of recruitment, immigration, predatory and non-predatory mortality, and growth of individuals in these experimental patches and monitored changes in patch area and biomass, and in the size distribution of individuals. In addition, I monitored the movement of tagged mussels and estimated the probabilities of wave dislodgment of mussels from measurements of water velocities and attachment strengths of mussels. Collectively, these mensurative experiments provide insight into the relative importance of interacting physical and biological processes in determining the structure and dynamics of mussel assemblages and their role in shaping the patterns of distribution and abundance observed in these two different habitats.

MATERIALS AND METHODS

Transplantation Experiment

Design

This study was carried out at an exposed rocky shore at Cranberry Cove, Nova Scotia (for further description, see Chapter 3). I constructed experimental mussel patches in the laboratory on 12.5 x 12.5 cm (156 cm^2) panels of fiberglass window screen (mesh size=2 mm). Each patch consisted of 150 mussels in four size classes: 1) <5.0 mm SL (n=109), 2) 5.0-9.9 mm (n=23), 3) 10.0-14.9 mm (n=14), and 4) 15.0-24.9 mm (n=4). This size distribution was based on the average of the size distributions of mussels in tidepools (Hunt & Scheibling 1995) and on emergent rock (unpubl. data) at Cranberry Cove prior to this study. The experimental patches were submerged in a flowing (~ 3 L/min) seawater tank at ambient temperature. The patches were elevated on rings of PVC pipe to prevent mussels from attaching to the bottom of the tank and placed by the tank inflow for several days to stimulate byssal attachment to the mesh. The mussels were tightly aggregated in the patches which were roughly circular (Fig. 6.1). Patch area was ~14 cm^2, based on the average of 4 patches. Patch biomass was ~4.8 g dry mass after drying in an oven for 48 hours at 80 °C, based on the average of 5 patches (range 4.1 to 5.1 g). After 1-4 weeks in the laboratory, I transplanted the experimental mussel patches to tidepools and emergent rock at Cranberry Cove. The mesh base of each patch was fastened to the substratum with marine epoxy putty (A-788 Splash Zone Compound; Z*Spar, Los Angeles) (Fig. 6.1). Patches were covered with another panel of fiberglass window screen for several days to reduce wave stress while the mussels attached to the rock substratum.

My transplantation experiments were set up in four blocks along ~1 km of shoreline with at least 100 m between blocks. I selected two plots in each block: one tidepool and one area of emergent rock. Tidepools ranged from 4.6 to 9.5 m^2 in area and from 0.3 to 0.6 m in depth. Plots of emergent rock were comparable in area and delineated by crevices and other topographic features. The height of plots above chart datum (C.D.), measured in May 1995 and August 1996 using a transit level, ranged from 0.7 to 1.8 m. Maximum tidal range is approximately 2 m. To examine changes in patch structure over a 15 mo period, I transplanted 9 mussel patches to each plot in July 1994 and collected three patches per plot at successive 5 mo intervals, i.e. in December 1994 (5 mo), April 1995 (10 mo), and October 1995 (15 mo). To examine the effects of transplantation date on patch structure and dynamics, I transplanted an additional three patches to each plot at two other times, December 1994 and May 1995, for 5 mo periods. This enabled me to examine seasonal variation between a winter interval, the second 5 mo set (December 1994-April 1995), and the preceding and subsequent summer/fall intervals (July-December 1994, May-October 1995). The first set of 5 mo patches was used in both the time-series and seasonal comparisons.

In July 1994, many of the mussels in the 10 and 15 mo patches on emergent rock died shortly after they were transplanted to the shore on a hot, sunny day. The first set of 5 mo patches was transplanted 3 days later on a cool, cloudy day and subsequent mortality was negligible. I transplanted a new series of 10 and 15 mo patches to emergent rock two weeks later. To avoid further mortality, I acclimated the replacement patches, and the additional patches transplanted in December 1994 and May 1995, by removing them from the water once a day for 2 to 6 hours at room temperature (for patches transplanted in spring/summer) or in a 10 °C cold room (for patches transplanted in December). At the end of each experimental interval, patches were collected by chiseling the epoxy and mesh base off the rock. The mussels remained attached to the mesh and to one another by their byssal threads. In some cases, a few mussels had attached to the outside of the epoxy ring or recruited to the rock substratum under the mesh. I did not collect these mussels for analysis. Patches were frozen in the laboratory until they could be processed.

Patch Structure and Dynamics

In each plot, I measured the area of the experimental patches and of 3 natural patches (initially similar in size to the experimental patches) in each plot within 2 to 6 weeks of transplantation and then at 5 mo intervals (before sets of patches were collected). Patches were photographed or their outlines were traced on acetate sheets if algal growth or light conditions prevented photography. Computer images were created from photographic slides using a dissecting microscope connected to a black and white video camera and a computer. Tracings of patch outlines were scanned. Images from photographs and tracings were analyzed using a computerized image analysis system (NIH Image, Version 1.59; National Institutes of Health, Bethesda, Maryland, USA). Because the camera angle was not directly perpendicular to the substratum and because of the low resolution of computer images obtained from photographic slides, photographs underestimated patch area by ~12% compared to tracing, as assessed by comparison of photographs and tracings of 22 patches. Patch areas calculated from photographs were therefore adjusted to compensate for this underestimation.

After each set of experimental patches was collected, I counted and measured the mussels in each patch. Mussels were measured in 1 mm size classes using an ocular micrometer on a dissecting microscope for the smallest individuals or vernier calipers for larger ones. I measured final patch biomass as total mass of mussels (excluding empty shells) in each patch after drying for 48 hours at 80 °C.

Growth and Immigration

To measure individual growth rates, the mussels were marked with calcein (ICN Biochemicals, Inc., Cleveland, Ohio), a dye which binds to calcium and fluoresces under UV light. The mussels were immersed in a 125 mg/L solution (Wilson et al. 1987) for 40 hours before being assembled into patches. After the patches were collected from the field, mussels ≥5 mm SL in the three sets of 5 mo patches, and the set of 10 mo patches, were examined for the presence of the calcein mark. Shells were placed in 10% sodium hypochlorite bleach for 15 to 18 h to remove the periostracum and any other organic material, and then examined under long wave (peak 365 nm) ultraviolet light (Blak Ray UVL-22 lamp, Ultraviolet Products Inc., San Gabriel, California USA) with a dissecting microscope. Initial (exposure to calcein) and final shell length of all individuals with a visible calcein mark was measured with calipers or an ocular micrometer. Mussels <5 mm were not examined for calcein marks because the preparation of the shells made them brittle and difficult to examine. Mussels in the 15 mo patches were not examined for calcein because most of the patches contained no individuals >5 mm SL.

I also used the calcein marks to estimate the number of immigrant mussels in each set of experimental patches at the time they were collected from the field. To determine the proportion of mussels exposed to calcein which had a visible mark, I held 60 to 90 marked mussels in the laboratory for comparison with each set of experimental patches, except the third 5 mo set. While in the laboratory, mussels were held in sand-filtered running seawater at ambient temperature; no additional food was provided.

Mortality

I recorded the number of whelks (*Nucella lapillus*) present on the experimental patches at approximately weekly (in summer) or monthly (in winter) intervals. From June to October 1995, I recorded the number of whelks on the natural patches at approximately weekly intervals. I compared the number of whelks on experimental and natural mussel patches to determine if the mesh base and epoxy attachment of the transplanted patches altered whelk behavior.

To assess sources and rates of mussel mortality, I collected empty mussel shells in the experimental patches on the same dates as I recorded the number of whelks. Empty shells were measured and examined for a drill hole indicative of whelk predation (Chapter 5). Whelks experienced with feeding on mussels will sometimes attack small individuals between the posterior margins of the shell (Hughes & Burrows 1993). I was able to detect these attacks from the semi-circular mark left on the shell margin. I summed, separately, the number of empty shells with whelk drill holes and the number of non-drilled empty shells collected from each patch. The cumulative number of drilled shells collected from a patch provides an index of predation intensity. The cumulative number of non-drilled shells provides an index of mortality resulting from causes other than predation, assuming they did not result from sea star predation because sea stars were rare at my site. Some empty shells were undoubtedly dislodged by waves before they could be collected, and mortality of mussels <5 mm SL was probably less detectable than that of larger individuals. I did not include mussels that died after the last date a patch was checked for empty shells but before the patch was removed because these shells were included in the final patch area and I wanted to examine the relationship between cumulative mortality and final patch area.

Statistical Analysis of Transplantation Experiment

I excluded from analysis data from one of the 4 blocks for the second and third 5 mo sets, December 1994-April 1995 and May-October 1995. Most experimental patches from these sets in this block were detached and washed away by waves within days of transplantation and before the mesh covers were removed. As a result, comparisons of the three sets of 5 mo patches include only 3 blocks while comparisons of the 5, 10, and 15 mo patches which were transplanted in July 1994 include 4 blocks.

Most analyses were carried as randomized block designs using ANOVA. Data were averaged across patches for each plot. Because of the lack of replication of plots within blocks, the full model including interactions with block could not be tested. My choice of blocks was arbitrary and, although I consider block a random factor, I do not wish to draw inferences about the population of blocks from which they were selected. With the exception of one analysis, Tukey's test for non-additivity ($\propto$=0.05) indicated that there were no significant interactions resulting from multiplicative effects of differences due to blocks and those due to the other factors (Kirk 1995). Therefore, I used an additive model, assuming no interactions with block (see Newman et al. 1997 for discussion of models for analysing block designs). Block was a random factor with 3 or 4 levels, habitat (tidepool and emergent rock) was a fixed factor with 2 levels, and patch age (5, 10, or 15 mo, transplanted in July 1994) or transplantation date (the three sets of 5 mo patches) was a fixed factor with 3 levels. The effect of each of these factors was examined against the residual error. In the single case where Tukey's test was significant, I used a non-additive model. In this case, the effect of habitat was examined against the habitat x block interaction term, the effect of patch age was examined against the patch age x block interaction term and the effect of the habitat x patch age interaction term was examined against the habitat x patch age x block interaction term; no tests of the effect of block or of any the interactions between block and the other factors could be carried out. Prior to ANOVA, Cochran's test was used to ensure that the data satisfied the assumption of homogeneity of variances (α=0.05). Where necessary, raw data were log or log (x+1) transformed to satisfy this assumption.

Wave forces and probabilities of mussel dislodgment

I measured maximum water velocities in tidepools and on emergent rock from October 1994 to April 1995 using meters based on the design of Bell and Denny (1994). Each meter consists of a practice golf ball attached to a spring in a plastic housing which is anchored to the substratum. I used a spring with a tension similar to the tension of the stiff spring described by Bell and Denny (1994), but modified the attachment system slightly: each meter was fastened to the substratum by hooking it to a stainless steel fishing swivel attached to the substratum by a stainless steel screw. Two or three velocity meters were deployed in each habitat and checked and reset at 10 to 43 d intervals. The extension of the spring (x, in m) was converted to water velocity (u, m/s) using the relationship $u = \left(\frac{kx + c}{a}\right)^{\frac{1}{b}}$ where k and c are constants (2924 and 5, respectively) which are properties of the spring determined from the relationship between force (F) and spring extension, F=k x + c, ($F_{1,5}$=101.6, p<0.001, r^2=0.95). The constants a and b (0.575 and 1.93, respectively, Bell and Denny 1994) are hydrodynamic properties of the practice golf ball. To compare these velocity measurements to wave heights, I obtained records of significant wave heights from a buoy at the mouth of Halifax Harbour (44.483 °N, 63.417 °W, depth 56.7 m) ~ 40 km from the study site (unpubl. data, Department of Fisheries and Oceans, Canada).

I measured attachment strength of mussels in natural assemblages as the force required to dislodge them from the substratum. In July and August 1997, I measured dislodgment forces for 10 mussels from both the tidepool and the emergent rock plot in each of 3 experimental blocks. The problematic fourth block was excluded because there were very few large mussels (>10 mm), precluding sampling of the entire experimental size range. In July 1997, I also measured dislodgment forces for an additional 10 mussels from both a tidepool and an emergent rock plot in each of 3 areas adjacent to the experimental blocks. Dislodgment force was measured perpendicular to the substratum because mussels are most strongly affected by hydrodynamic forces acting in this direction (Denny 1987). A thin multifilament fishing line was tied around each mussel and attached to a 250 g or 2000g spring scale (Ohaus). The dislodgment force was measured on the scale by pulling it at a right angle to the substratum until the mussel was detached. Shell length (SL, mm) of each detached mussel was measured and converted to cross-sectional area (A, cm^2) using the relationship: $A=0.003 \times SL^{1.833}$ (Chapter 5). I was not able to measure dislodgment force for mussels in the center of patches, or for individuals <5 mm SL, because of difficulties in tying the line around these individuals. Because dislodgment force of mussels in the center of patches is generally lower than that of individuals at the edge (Witman & Suchanek 1984), my measurements may overestimate average dislodgment force.

I pooled dislodgment forces of mussels across blocks within a habitat for the analysis. I used Denny's (1995) method to calculate probabilities of wave dislodgment using the measured dislodgment forces and estimates of the hydrodynamic forces imposed on mussels. The data relating dislodgment force (f) to mussel size (A, cross-sectional area) were fit to an allometric model: $f_p=j + m A^q$ where f_p is the predicted dislodgment force and j , m, and q are constants fit to the power curve for each date using a nonlinear, simplex iterative procedure (Systat, Wilkinson 1992). Each measured dislodgment force was normalized by dividing the measured force by the dislodgment force predicted by the allometric model. The normalized dislodgment forces ($f_n=f/f_p$) were ranked in ascending order and the probability (P) that an individual had a normalized dislodgment force less than a force of rank i was estimated as: $P(f_n \leq f_{n,i}) = i / (N + 1)$

where N is the total number of individuals sampled. The cumulative probability distribution of normalized dislodgment force ($P(f_n)$) was estimated by fitting a modified Weibull model: $P(f_n)= \exp\{-[(a- bf_{fn})/(a-bc)]^{1/b}\}$, where a, b, and c are constants.

I then predicted the hydrodynamic force which would be imposed on mussels. Water movement exerts three types of forces on benthic organisms: lift, drag, and the acceleration reaction (Denny et al. 1985, Denny 1987, 1995). In a tightly packed mussel patch, mussels shield their neighbors from hydrodynamic forces acting along the direction of flow (drag and acceleration) and provide physical support in resisting these forces (Denny 1987). However, lift forces, which are caused by a difference in pressure between the top and bottom of a mussel and act perpendicular to the direction of water motion, can potentially dislodge mussels (Denny 1987). The relationship between lift (L) and maximal water velocity (U) is: $L=(1/2\rho U^2)C_l A$ where ρ is the density of seawater (1025 kg/m^3), C_l is the coefficient of lift and A is the cross-sectional area of a mussel (Denny 1987). Denny (1987) estimated that C_l for M. *californianus* is 0.88. Because the relationship between shell height, length, and width of *M. trossulus* is similar to that of *M. californianus*, 0.88 is also a reasonable estimate of the lift coefficient for *M. trossulus* (Bell & Gosline in press). Using this equation, I calculated lift forces imposed on mussels of 4 sizes, the midpoints of the experimental size classes (2.5, 7.5, 12.5, 20 mm SL), from maximal water velocities measured by my wave meters in tidepools and on emergent rock. I normalized the calculated lift force for each mussel size by dividing it by the predicted dislodgment force (f_p) for a mussel of that size (see above), and used this as the normalized force (f_n) in the Weibull model (see above) to obtain the probability of dislodgment.

Movement of Mussels

I investigated the mobility of mussels in tidepools and on emergent rock by tagging individuals from ~5 to 25 mm SL with numbered plastic bee tags (Steele &

Brodie Ltd., Hampshire, England). These tags are small (2.6 mm diameter, 0.02 mm thickness) and lightweight (0.0014 g) and presumably have no measurable effect on movement of mussels. The same tags have been used to study swimming movements of juvenile scallops within a similar size range (Carsen et al. 1995). I tagged the mussels in situ after draining the water from the tidepools. I dried one shell valve on each selected mussel, cleaned it with acetone, and affixed a tag using cyanoacrylate glue. Mussels <5 mm were not tagged because their small size made it difficult to attach a tag without gluing the valves shut. In August 1994, I tagged 15 individuals in each of two tidepools (outside of the experimental blocks) and two plots of emergent rock (in two of the experimental blocks) and monitored them for 2-3 weeks. In July and August 1995, I tagged 20 mussels in both a tidepool and an adjacent plot of emergent rock (in one of the experimental blocks) and monitored them for ~4 weeks. I determined the location of each tagged mussel at 2-10 d intervals by measuring the distances between the mussel and 2 reference bolts drilled into the rock. Tagged mussels were grouped into two categories of initial position: in patches (at center or edge) and isolated (alone or in a small group, or on top of the monolayer of mussels in a patch). Mussels on top of a patch were considered to be isolated rather than in a patch because their frequencies of movement and disappearance were more similar to those of mussels which were alone than to those in patches. Contingency tables (G-test) were used to compare the frequency of movement and disappearance of mussels between habitats, positions, and dates. I converted the distances of the mussels from the reference bolts to x and y coordinates and calculated the total distance moved by each mussel trigonometrically.

RESULTS

The Physical Environment

Tidepool salinity was relatively constant and similar to sea surface salinity (Fig. 6.2). Mean water temperature in tidepools was usually a few degrees higher than mean sea surface temperature in spring and summer. Tidepool temperatures closely tracked air temperatures (Fig. 6.2). Although I sampled once a month, air temperatures on my sampling dates were representative of average maximum air temperatures. Monthly means of maximum air temperature ranged from -0.2 °C in February 1995 to 23.9 °C in July 1994 and 22.6 °C in July 1995 (unpubl. data, Environment Canada). Variability in temperature and salinity among tidepools was low, probably because these mid-zone pools were isolated from seawater input during low tide for only 3-8 h (pers. obs).

Patch dynamics

The mean area of experimental patches remained relatively constant over successive measurements of patches of different ages (5, 10 and 15 mo), and of 5 mo patches transplanted at different times (Fig. 6.3). The final area of patches transplanted in July 1994 did not differ significantly between habitats ($F_{1,15}$=0.52, p=0.48), blocks ($F_{3,15}$=1.70, p=0.21), or patch ages (5, 10, and 15 mo, $F_{2,15}$=0.46, p=0.54), and there was no significant interaction between habitat and patch age ($F_{2,15}$=0.66, p=0.53). Similarly, the change in area of natural patches over the same 15 mo period did not differ significantly between habitats ($F_{1,3}$=0.05, p=0.84) or blocks ($F_{3,3}$=4.0, p=0.14). Also, there was no significant variation in final patch area of the three different sets of 5 mo patches between habitats ($F_{1,10}$=0.13, p=0.73), blocks ($F_{2,10}$=0.22, p=0.81) or transplantation dates ($F_{2,10}$=0.37, p=0.70); there was no significant interaction between habitat and transplantation date ($F_{2,10}$=0.001, p=0.99). Despite the constancy of mean patch area, the area of individual mussel patches (experimental and natural) varied markedly. Many patches disappeared or decreased considerably in size. For example, ~44% of experimental patches in tidepools and 25% of those on emergent rock were <5 cm^2 in final area (i.e. <45 % of the mean area at the first sampling date after transplantation, 11 cm^2). Large increases in patch area were less common than decreases:

~10% of experimental patches had a final area of >25 cm^2 (i.e. ~225 % of the mean area area after transplantation).

Final patch biomass for each set of experimental patches was, on average, lower than the estimated initial biomass of 4.8 g (Fig. 6.4a) For the experimental patches transplanted in July 1994, final patch biomass varied significantly with patch age ($F_{2,15}$=6.7, p=0.01): final biomass of the 15 mo patches was significantly lower than that of the 5 and 10 mo patches, which did not differ significantly (SNK, p<0.05). Final biomass did not differ signficantly between habitats ($F_{1,15}$=1.3, p=0.27) or blocks ($F_{3,15}$=2.5, p=0.10), and there was no significant interaction between habitat and patch age ($F_{2,15}$=1.5, p=0.25). For the three sets of 5 mo patches, final patch biomass did not differ significantly between habitats ($F_{1,10}$=0.78, p=0.40), blocks ($F_{2,10}$=0.38, p=0.69) or transplantation dates ($F_{2,10}$=0.96, p=0.42); there was no significant interaction between habitat and transplantation date ($F_{2,10}$=0.03, p=0.97).

Final number of mussels in a patch was greater than the initial number of 150 individuals, except for the second (winter) set of 5 mo patches (Fig. 6.4b). Final number of mussels in the experimental patches transplanted in July 1994 did not differ significantly between habitats ($F_{1,15}$=0.42, p=0.53), blocks ($F_{3,15}$=2.05, p=0.15), or patch ages ($F_{2,15}$=0.94, p=0.41), and there was no significant interaction between habitat and patch age ($F_{2,15}$=0.55, p=0.59). For the three sets of 5 mo patches, variation in final number of mussels in a patch with transplantation date was marginally non-significant ($F_{2,10}$=3.48, p=0.07), indicating a trend towards a lower number of mussels in the patches from the second (winter) set of 5 mo patches compared to the other sets of experimental patches. There were no significant differences between habitats ($F_{1,10}$=0.01, p=0.91) or blocks ($F_{2,10}$=1.61, p=0.25) and no significant interaction between habitat and transplantation date ($F_{2,10}$=0.02, p=0.98).

The size distribution of mussels in experimental patches changed after transplantation as the proportion of small mussels (<5 mm SL) increased in both habitats.

The size distribution of mussels in the experimental size classes (<5, 5-9.9, 10-14.9, 15-24.9 mm), compared using contingency tables (G-test) differed significantly from the initial size distribution in the 5, 10 and 15 mo patches transplanted in July 1994 (mussels pooled across patches and blocks; emergent rock, G_3=63.3, 156.5, 420.3, respectively; tidepools, G_3=128.4, 187.3, 218.1, respectively; $p<0.001$), in the second set of 5 mo patches on emergent rock (G_3=14.8., p=0.002) but not in tidepools (G_3=3.3., p=0.35), and in the third set of 5 mo patches in both habitats (emergent rock, G_3=186.6; tidepools, G_3=81.9; $p<0.001$). Mussels <1 mm SL were proportionately more abundant in tidepools than on emergent rock (Fig. 6.5) such that, in Kolmogorov-Smirnov tests, size distributions (in 1 mm size classes) differed significantly between habitats in the 5, 10 and 15 mo patches transplanted in July 1994 (D_{max}=0.15, 0.09, 0.12 respectively, $p<0.001$) and the third set of 5 mo patches (D_{max}=0.08, $p<0.001$), but not the second set of 5 mo patches (D_{max}=0.06, $p>0.10$). Small mussels (<2 mm SL) are also proportionately more abundant in tidepools than on emergent rock in natural mussel assemblages (Chapter 5). In each habitat, cumulative size distributions also differed ($D_{max}>0.11$) among patches of different ages (5 vs 10, 10 vs 15, 5 vs 15 mo: tidepools, D_{max}=0.11, 0.24, 0.35, respectively; emergent rock, D_{max}=0.10, 0.23, 0.28, respectively; $p<0.001$) and transplantation dates (1st vs 2nd, 2nd vs 3rd, 1st vs 3rd set of 5 mo patches: tidepools, D_{max}=0.40, 0.15, 0.28, respectively; emergent rock, D_{max}=0.29, 0.16, 0.24, respectively; $p<0.001$). Overall, the proportion of mussels <1 mm decreased with patch age and was greater in the first set of 5 mo patches than in the second or third set (Fig. 6.5). In tidepools, mussels >5 mm were proportionately less abundant after 15 mo than after 5 or 10 mo in patches transplanted in July 1994 (Fig. 6.5).

Growth

Marking with calcein indicated that transplanted mussels grew slowly: mean change in shell length of mussels >5 mm ranged from 1.2 to 2.2 mm among the 3 sets of

5 mo patches (Fig. 6.6). These growth rates were consistent with my previous estimates for mussels in tidepools at Cranberry Cove, based on external rings on the shell (Hunt & Scheibling 1995). Prior to ANOVA, change in shell length was averaged across mussels (n=4-32) within a patch and then across patches within a block for each habitat. Mean change in shell length of the three sets of 5 mo patches varied significantly among blocks ($F_{2,10}$=10.69, p=0.003) and was significantly greater in tidepools than on emergent rock ($F_{1,10}$=17.91, p=0.002) and significantly lower for the second set of 5 mo patches (December 1994-April 1995) than for the first and third sets ($F_{2,10}$=16.55, p=0.001, SNK $p<0.05$) (Fig. 6.6); there was no significant interaction between habitat and transplantation date ($F_{2,10}$=1.19, p=0.344). In contrast, change in shell length of the 10 mo patches did not differ between habitats ($F_{1,3}$=0.45, p=0.55) or blocks ($F_{3,3}$=0.89, p=0.54) (Fig. 6.6). These results indicate that growth rates of mussels in 5 mo, but not 10 mo patches, were slightly higher in tidepools than on emergent rock and that growth rate was lower in winter than in summer and fall. Mean change in shell length (±1S.D.) of mussels held in the laboratory was 1.9±1.2 mm and 0.6±0.3 mm for mussels in the first and second 5 mo sets respectively, and 1.1±1.0 mm for mussels in the 10 mo patches, indicating that growth rates in the laboratory were similar to those in the field.

As growth rates of mussels often vary with size (Seed & Richardson 1990), I examined the relationship between change in shell length and initial shell length of marked individuals. I used ANCOVA to compare this relationship between tidepools and emergent rock (block was not included as a factor). If there was no significant interaction between habitat and initial shell length, patches from both habitats were pooled in a regression. If the interaction was significant, regressions were carried out separately for tidepools and emergent rock. There was a significant relationship between change in shell length and initial shell length for mussels in the first ($F_{1,153}$=8.68, p=0.0037, r^2=0.054) and third sets of 5 mo patches ($F_{1,130}$=6.33, p=0.013, r^2=0.22). Change in shell length of mussels in the second set was significantly related to initial shell length on emergent rock ($F_{1,130}$=15.8, p<0.001, r^2=0.11) but not in tidepools ($F_{1,117}$=0.15, p=0.70). However, the low values of r^2 in these analyses indicate that initial shell length explains little of the variance in growth rate of mussels in the three sets of 5 mo patches. There was no significant relationship between change in shell length and initial shell length for mussels in the 10 mo patches ($F_{1,169}$=0.023, p=0.88).

Since individual growth rates of mussels may be influenced, either negatively or positively by neighbouring mussels in a patch, I examined the relationship between individual growth rate and patch size using the same procedure I employed with initial shell length. Mean change in shell length (pooled over habitats) was significantly positively related to patch area and the number of mussels in a patch for 10 mo patches (area: $F_{1,15}$=4.83, p=0.04, r^2=0.243; number: $F_{1,15}$=7.26, p=0.02, r^2=0.346) (Fig. 6.7). Individual growth rate in the second set of 5 mo patches also was significantly related to patch area on emergent rock ($F_{1,7}$=7.72, p=0.03, r^2=0.56) (Fig. 6.7), but not in tidepools ($F_{1,6}$=1.0, p=0.36). In contrast, mean change in SL of mussels in the second set was not significantly related to number of mussels in a patch (pooled over habitats, $F_{1,13}$=0.12, p=0.74). There was no significant relationship between mean change in shell length and patch area or number of mussels in a patch in the first (area, $F_{1,16}$<0.001, p=0.99; number, $F_{1,16}$=4.18, p=0.06) and third sets of 5 mo patches (area, $F_{1,16}$=4.5, p=0.07; number, $F_{1,5}$=2.07, p=0.21 for emergent rock only as there were insufficient numbers of patches with marked mussels from tidepools). These results indicate that over a 10 mo interval (and in some cases over 5 mo), a positive relationship develops between the growth rate of individual mussels and the size of a mussel patch, at least among mussels >5 mm SL.

Recruitment

Based on the low growth rates, mussels <2 mm SL were considered to be recent recruits to the patches. Mussels recruited to each set of experimental patches (Fig. 6.8).

When recruit abundances per patch were compared among patches of different ages, there were no significant differences among blocks ($F_{3,15}$=2.5, p=0.10), habitats ($F_{1,15}$=0.003, p=0.96), or patch ages ($F_{2,15}$=0.43, p=0.66), and no significant interaction between habitat and patch age ($F_{2,15}$=0.47, p=0.63) (Fig. 6.8). When recruit abundances were compared among sets of 5 mo patches with different transplantation dates, recruit abundance was significantly lower in the second (winter) set than in the first or third (summer/fall) sets ($F_{2,10}$=5.30, p=0.027, SNK $p<0.05$) (Fig. 6.8), but did not vary significantly among blocks ($F_{2,10}$=2.88, p=0.103) or between habitats ($F_{1,10}$=0.32, p=0.585); there was no significant interaction between habitat and transplantation date ($F_{2,10}$=0.038, p=0.963). These results indicate that recruit abundance in a patch did not differ between tidepools and emergent rock or among patches of different ages, but was lower in 5 mo patches transplanted in winter than in those transplanted in summer.

Since recruitment rate may be influenced by the presence of conspecifics, I examined the relationship between recruit abundance in a patch and patch area using the same procedure I employed for change in shell length. Recruit abundance was significantly positively related to patch area for 5, 10, and 15 mo patches transplanted in July 1994 (5 mo, $F_{1,19}$=9.14, p=0.007, r^2=0.33; 10 mo , $F_{1,19}$=7.37, p=0.01, r^2=0.28; 15 mo, $F_{1,12}$=56.6, p=0.0001, r^2=0.83) and for the third set of 5 mo patches ($F_{1,14}$=24.9, p=0.0002, r^2=0.64) but not for the second set, although this relationship was only marginally non-significant ($F_{1,15}$=3.77, p=0.07) (Fig. 6.9). Because the area available for mussel settlement (the mesh bases of the experimental patches) was the same size for all experimental units, this positive relationship is directly or indirectly attributable to the abundance of conspecifics.

Immigration

The increase in area of some experimental patches was too large to be accounted for by gains due to growth and recruitment. Large increases in patch size often occurred within a few days between observations and were associated with storms, suggesting that waves deposited large mussels on the patches. For example, a patch which increased in area to 50 cm^2 contained 25 mussels larger than 15 mm in December 1994, 5 mo after it had been transplanted to the shore with only 4 mussels in this size range. Given the low growth rates of mussels at Cranberry Cove, these large individuals must be immigrants. I estimated the number of immigrant mussels > 5mm SL (the size limit for detecting the calcein mark) in a patch by subtracting the estimated number of mussels exposed to calcein from the total number of mussels >5 mm. The number of mussels >5 mm exposed to calcein was estimated by dividing those with a visible calcein mark by the proportion of mussels exposed to calcein and held in the laboratory which had a visible mark (32-39%, Table 6.1). This assumes no difference between mussels held in the laboratory and those transplanted to the field in the proportion with a detectable calcein mark. Calcein marks which were not visible were probably very close to the edge of the shell or obscured by disturbance rings formed when the mussels were brought into the laboratory. For the 5 and 10 mo patches transplanted in July 1994, the percentage of mussels with a visible calcein mark in the field (29-36%) was not significantly different from that in the laboratoy (36-39%) (Table 1) (habitats pooled: 5 mo, G_1=2.64, p=0.10; 10 mo, G_1=0.76, p=0.39). At the end of these intervals, the number of mussels >5 mm estimated to have been present at the time of transplantation (i.e. non-immigrants) was always lower than or similar to the known initial number of mussels >5 mm. The percentage of mussels with a visible calcein mark in the second set of 5 mo patches was significantly higher in the field than in the laboratory (habitats pooled, G_1=18.0, p<0.001) (Table 1). I have no explanation for this discrepancy and consequently I did not estimate immigration for this interval.

According to my calculations, the percentage of mussels >5 mm SL which were immigrants ranged from 15 to 26 % in the 5 and 10 mo patches and did not differ significantly between habitats (5 mo, t_6=0.51, p=0.63; 10 mo, t_6=0.32, p=0.76). The percentage of immigrants in the third set of 5 mo patches was estimated using the mean percentage of mussels with a visible calcein mark in the laboratory during the other time intervals. According to this calculation, the percentage of immigrants was significantly higher in tidepools (55 %) than on emergent rock (16 %) (t_4=7.50, p=0.002).

Whelk Predation and Other Mortality

Whelks were often present on the experimental patches in summer and fall. The mean number of whelk post-recruits (>5 mm SL) per patch was 0.11 and 0.04 in tidepools and on emergent rock, respectively, from July to October 1994, and 0.10 and 0.20, respectively, from May to October 1995 (Fig. 6.10). No whelks were observed on the experimental patches from November 1994 to March 1995. Mean number of post-recruits per patch from July to October 1994, and from May to September 1995, did not differ significantly between tidepools and emergent rock ($F_{1,9}$=0.04, p=0.85) or among blocks ($F_{3,9}$=0.72, p=0.56) or between the two time intervals ($F_{1,9}$=2.1, p=0.19); there was no significant interaction between habitat and time interval ($F_{1,9}$=3.16, p=0.11).

To determine if the mesh base and epoxy attachment of the transplanted patches altered whelk behavior, I compared whelk densities on experimental and natural mussel patches. I compared whelk densities rather than number of whelks per patch because natural patches were slightly larger than experimental patches (Fig. 6.3). Mean whelk density (number/cm^2 of mussel patch) on patches from June to October 1995 did not differ between experimental (third set of 5 mo patches) (0.01/cm^2) and natural patches (0.03/cm^2) ($F_{1,6}$=4.29, p=0.084), between habitats ($F_{1,6}$=0.30, p=0.607), or between blocks ($F_{2,6}$=0.57, p=0.592), and there was no significant interaction between habitat and patch type ($F_{1,6}$=1.30, p=0.30). Therefore, I conclude that, both in tidepools and on emergent rock, whelks encountered experimental and natural mussel patches at a similar rate and exhibited natural foraging behavior on experimental patches. The pattern of whelk abundance on the experimental and natural patches also was similar to that observed at the larger scale of the plots: mean densities of whelk post-recruits in the plots peaked in 1994 at $58/m^2$ and $76/m^2$ in tidepools and on emergent rock, respectively, and in 1995 at $68/m^2$ and $250/m^2$ respectively (Chapter 5). Whelk densities were $<10/m^2$ in both habitats in winter.

The cumulative number of empty shells with whelk drill holes collected from the experimental patches provides an index of predation rate. I compared the cumulative number of drilled shells between habitats for the first (July-December 1994) and third (May-October 1995) sets of 5 mo patches using a non-additive model since Tukey's test indicated significant non-additivity ($p<0.05$). I did not include the second set of 5 mo patches (December 1994-April 1995) in my comparisons since no drilled shells or whelks (Fig. 6.10) were observed in the patches during this winter period. I did not compare between habitats for the 10 and 15 mo patches because mussels in tidepools were exposed to whelks for 2 weeks longer than patches on emergent rock at the start of the experiment. For the first and third sets of 5 mo patches, the cumulative number of drilled shells per patch did not differ significantly between habitats (non-additive model, $F_{1,2}=1.2$, $p=0.39$), or transplantation dates ($F_{1,2}=0.02$, $p=0.91$), but there was a significant interaction between habitat and transplantation date ($F_{1,2}=173.6$, $p=0.006$). The cumulative number of drilled shells per patch was significantly higher in tidepools (8.4/patch) than on emergent rock (1.7/patch) for the first set of 5 mo patches, but significantly lower in tidepools (3.9/patch) than on emergent rock (7.7/patch) for the third set of 5 mo patches (t-tests, $p<0.05$) (Fig. 6.11). The cumulative number of drilled shells per patch was significantly higher for the first than the third set of 5 mo patches in tidepools, while the reverse was true on emergent rock (t-tests, $p<0.05$). Regression analysis indicated that the number of drilled shells collected from a patch was significantly related to the number of whelks observed on a patch (pooled over habitats and sets of patches, $F_{1,38}=8.94$, $p=0.005$, $r^2=0.19$). These results indicate that whelk predation was greater in patches in tidepools than on emergent rock in 1994, but lower in patches in tidepools than on emergent rock in 1995.

The cumulative number of non-drilled empty shells collected in mussel patches provides an index of non-predatory mortality. No non-drilled empty shells were observed in the patches during the winter. The cumulative number of non-drilled empty shells was significantly higher for the first set of 5 mo patches (5.7/patch) than the third set of 5 mo patches (0.8/patch) ($F_{1,6}$=46.9, $p<0.001$), but did not differ significantly between habitats ($F_{1,6}$=0.18, p=0.69) or blocks ($F_{2,6}$=1.5, p=0.29); there was no significant interaction between habitat and transplantation date ($F_{1,6}$=0.07, p=0.80). Mussels in the 10 and 15 mo patches in tidepools probably experienced some physiological stress shortly after transplantation when patches on emergent rock died (see Methods, Transplantation Experiment). For 10 and 15 mo patches, there was a trend towards a higher cumulative number of non-drilled empty shells per patch from July to December 1994 for patches in tidepools (x±S.E.=6.4±1.7 and 6.3±2.2, respectively) than for the replacement patches on emergent rock (0.8±0.6,1.1±0.4, respectively). However, the number of non-drilled shells did not differ significantly between habitats (sets pooled, $F_{1,3}$=4.4, p=0.13) or blocks ($F_{3,3}$=0.6, p=0.66). These results indicate that non-predatory mortality was similar in tidepools and on emergent rock and that, for patches transplanted in spring or summer, it was lower for those which were acclimated to emersion before transplantation (10 and 15 mo patches on emergent rock, 3rd set of 5 mo patches) than for those that were not acclimated (1st set of 5 mo patches, 10 and 15 mo patches in tidepools).

To determine whether mussel mortality influenced patch size, I examined the relationship between final patch area and the cumulative number of drilled and non-drilled empty shells collected from a patch. Because most drilled mussels are >5 mm SL, whelk predation probably has a greater effect on patch area than on the number of mussels in a patch. However, regression analysis showed no significant relationship between final patch area and the number of drilled mussels collected from July to December 1994 (all patches, $F_{1,64}$=2.3, p=0.14, r^2=0.04) or from May to October 1995 (3rd set of 5 mo patches, $F_{1,15}$=1.69, p=0.21, r^2=0.10). Similarly, there was no significant relationship between final patch area and number of non-drilled mussels collected from July to December 1994 (all patches, $F_{1,64}$=2.4, p=0.12, r^2=0.04) or from May to October 1995 (3rd set of 5 mo patches, $F_{1,15}$=1.54, p=0.23, r^2=0.09). The low values of r^2 indicate that cumulative mussel mortality explains little of the variation in size among patches.

Wave Disturbance

Mean maximum water velocities between November 1994 and April 1995 ranged from 5.2 to 11.2 m/s in tidepools and from 7.6 to 12.2 m/s on emergent rock (Fig. 6.12). These water velocities correspond to maximum forces of 14 to 72 N, which are comparable to the maximum wave forces measured (with the same type of wave meter) by Blanchette (1997) at a wave-exposed site in Oregon, USA. The greatest water velocities were measured in February 1995 when significant wave heights of up to 9.4 m (Fig. 6.12), and a maximum wave height of 14.5 m, were recorded. Mean maximum water velocities were significantly greater on emergent rock than in tidepools ($F_{1,12}$=5.9, p=0.032) and differed significantly among dates ($F_{4,12}$=15.4, p=<0.001); there was no significant interaction between habitat and date ($F_{4,12}$=0.6, p=0.69) .

In July and August 1997, the force required to dislodge mussels ranged from 0.5 to 18 N, increasing with increasing mussel size (Fig. 6.13a). In both months, dislodgment force was significantly related to mussel cross-sectional area (July, $F_{1,116}$=36.1, p=0.0001; August, $F_{1,56}$=50.5, p=0.0001), but did not differ significantly between habitats (July, $F_{1,116}$=0.8, p=0.13; August, $F_{1,56}$=3.61, p=0.06). Although the difference between habitats was only marginally non-significant in August, this was mainly due to the influence of the high dislodgment forces measured for two of the largest mussels in tidepools. There was no significant interaction between mussel area and habitat (July, $F_{1,116}<0.001$, $p=0.98$; August, $F_{1,56}=3.38$, $p=0.07$). Consequently, I pooled measurements from the two habitats before fitting the data to the allometric model (see Methods, Wave Dislodgment). The relationship between dislodgment force and shell area was exponential in July but nearly linear in August (Fig. 6.13a). As a result, dislodgment forces were higher in August than in July for mussels within the range of the experimental size classes (up to 1.1 cm^2 cross-sectional area, 25 mm SL), but similar in both months for larger (>1.1 cm^2) mussels (Fig. 6.13a). This change in dislodgment force (attachment strength) may be a response to increased wave action between the measurement dates. The maximum significant wave heights in the 3 weeks preceding the July measurement were <2 m (unpubl. data, Department of Fisheries and Oceans, Canada). Between the July and August measurements, recorded wave heights were also <2 m (unpubl. data, Department of Fisheries and Oceans, Canada) with the exception of one day when they were >4 m (T. Balch, surfer, pers. comm.). As previously described, I converted each measurement of dislodgment force (f) to a normalized force (f_n) by dividing it by the predicted force (f_p) from the allometric model and then calculated the probability (P) that an individual had a normalized dislodgment force less than a force of rank i (see Methods, Wave Dislodgment). The Weibull model provided a good estimate of the cumulative probability distribution of the normalized dislodgment forces in both July and August ($r^2>0.99$, Fig. 6.13b).

For comparison with dislodgment forces, I predicted the hydrodynamic lift force exerted on mussels of each of 4 sizes, the midpoints of the experimental size classes (2.5, 7.5, 12.5, 20 mm SL, which correspond to cross-sectional areas of 0.02, 0.12, 0.31, and 0.73 cm^2 respectively), over a range of water velocities. Water velocity in tidepools averaged 87% of that on emergent rock, based on the five intervals when wave meters were deployed in both habitats (Fig. 6.12). Consequently, at a given time, predicted lift forces exerted on mussels were up to 1.3 times higher on emergent rock than in tidepools (Fig. 6.14). Predicted lift forces increased with increasing water velocity and mussel size. For example, lift forces on 7.5 and 20 mm mussels were 0.1 and 0.82 N, respectively, at 5 m/s and 1.2 and 7.4 N, at 15 m/s (Fig. 6.14).

I estimated the probability of dislodgment of each of the 4 sizes of mussels by water velocities of up to 15 m/s using the predicted lift forces (Fig. 6.14) and the cumulative probability distribution of dislodgment forces (Fig. 6.13b). The probability of dislodgment of mussels in the smallest size class (2.5 mm SL) was ~ 0 in both tidepools and emergent rock but it increased markedly with increasing mussel size (Fig. 6.15) because lift forces increased faster with size than dislodgment forces. Because of the difference in water velocities between tidepools and emergent rock, the probability of dislodgment, at a given time, of mussels from 7.5 to 20 mm SL was higher on emergent rock than in tidepools (Fig. 6.15). For 12.5 and 20 mm SL mussels, probabilities of dislodgment were 2-5 times greater in July than August 1997 because of differences in dislodgment forces. Probabilities of dislodgment increased with increasing water velocity (Fig. 6.15). For example, maximal water velocities of 6 m/s, such as those observed during the last period (April 18-27, 1995) during which wave meters were deployed, maximum significant wave height=3.4 m, (Fig. 6.12), were predicted to dislodge <3 % of mussels in either July or August. By comparison, maximal water velocities of 9 m/s on emergent rock (7.8 m/s in tidepools), such as those observed March 12-April 18, 1995 (maximum significant wave height=4.5 m) (Fig. 6.12) were predicted to dislodge ~27 % of large mussels (12.5 and 20 mm SL) on emergent rock and ~15 % in tidepools in July. In contrast, these velocities would only dislodge 3-7% of large mussels on emergent rock, and 1-2% in tidepools in August. Probability of dislodgment would, of course, be higher in the largest storms, but mussels are probably more strongly attached in fall and winter when large storms are most frequent. Overall, this model indicates that mussels >10 mm SL are vulnerable to dislodgment by waves and that mussels on emergent rock will be dislodged more frequently than those in tidepools.

Movement

The tagging study indicated that mussels of 5-20 mm SL are mobile, although they move infrequently and for short distances. In August 1994 and July 1995, 21 to 56% of mussels in patches and 67 to 86% of isolated mussels moved within 13-27 days (Fig. 6.16). In October 1995, only 7-10% of mussels in patches and 43-66% of isolated mussels moved within 30 days (Fig. 6.16). The percentage of mussels that moved did not differ significantly between tidepools and emergent rock during each study period (August 1994: in patches, G_1=2.87, p=0.09; isolated, G_1=0.27, p=0.60; July 1995: in patches, G_1=1.44, p=0.23; isolated, G_1=0.07, p=0.79; October 1995: in patches, G_1=0.11, p=0.74; isolated, G_1=0.56, p=0.46). Isolated mussels in both habitats were significantly more likely to move than those in patches (habitats pooled; August 1994, G_1=6.66, p=0.01; July 1995, G_1=10.48, p=0.001; October 1995, G_1=11.49, p=0.001). In 1995, a higher percentage of mussels in patches moved in July, when maximum significant wave heights were 2.8 m (Fig. 6.12), than in October (habitats pooled, G_1=4.93, p=0.03), when wave heights reached 4.9 m (Fig. 6.12). The percentage of isolated mussels that moved did not differ significantly between these dates (habitats pooled, G_1=1.16, p=0.28).

Distances moved by tagged mussels were usually <5 cm with a modal class of 1-2 cm, although 6 out of 68 individuals moved 10-49 cm (Fig. 6.17). I pooled all mussels since distance moved during each of the study periods did not differ significantly between tidepools and emergent rock (August 1994, pooled across plots: $F_{1,22}$=1.20, p=0.29; July 1995, $F_{1,26}$=0.84, p=0.37; October 1995, isolated mussels: t_7=0.49, p=0.64, there were insufficient data to include mussels in patches in the analysis), or between mussels in patches and isolated mussels (August 1994: $F_{1,22}$=0.009, p=0.93; July 1995, $F_{1,26}$=0.008, p=0.93), and there was no significant interaction between habitat and position (August 1994: $F_{1,22}$=0.93, p=0.35; July 1995: $F_{1,26}$=0.37, p=0.55).

During each of the study periods, some tagged mussels were not relocated. These mussels probably were dislodged by waves and moved beyond my limited survey range of ~50 cm radius around their initial location. These disappearances were unlikely to have been tag losses because some tags from 1994 were still visible in 1995. In August 1994 and July 1995, 10 to 22% of mussels in patches and 13-27% of isolated mussels disappeared (Fig. 6.16). In October 1995, when wave heights were greater (up to 4.9 m), 42% of mussels in patches in tidepools and 17% of those on emergent rock and 44-50% of isolated mussels in both habitats disappeared (Fig. 6.16). The frequency of disappearance of mussels in July 1994 and August 1995 was too low to permit statistical comparisons of disppearance rate between habitats and positions. In October 1995, the frequency of disappearance did not differ significantly between tidepools and emergent rock, both for mussels in patches, (G_1=3.40, p=0.065), where the difference was only marginally non-significant, and for isolated mussels (G_1=0.13, p=0.72). The frequency of disappearance also did not differ significantly between mussels in patches and isolated mussels (habitats pooled, G_1=2.38, p=0.12). In 1995, the frequency of disappearance in tidepools was significantly greater in October than in July, both for mussels in patches (G_1=10.8, p=0.002) and isolated mussels (G_1=6.5, p=0.011). In contrast, the frequency of mussel disappearance on emergent rock did not differ significantly between dates for mussels in patches (G_1=0.14, p=0.710) and for isolated mussels, although this difference was marginally non-significant (G_1=3.2, p=0.07). These results indicate that the frequency of mussel disappearance was generally similar between positions (in patches, isolated) and habitats with the exception of the higher frequency of disappearance in October than in July 1995 for mussels in tidepools but not those on emergent rock.

Patch Dynamics: effects of growth, recruitment, immigration, mortality, and other losses

I graphically examined the relationship between mean shell area and number of mussels in a patch to relate changes in this relationship to changes in patch size, and to examine the contributions of mortality, growth, and recruitment to these changes (Petraitis 1995, Reusch & Chapman 1997) (Fig. 6.18). For calculation of final mean shell area of each set of experimental patches, I used the mid point of each 1 mm size class as the shell length of mussels in that size class and converted shell length to cross-sectional area (see Methods, Wave Dislodgment). Mean shell area before transplantation could only be roughly estimated from the number of mussels in each of the 4 experimental size classes. For this calculation, mussels in the smallest size class (0.1-4.9 mm) were assumed to be 1 mm SL based on the size distribution of mussels at this site (Chapter 5; Hunt & Scheibling 1995), and the midpoint of each of the other three size classes (7.5, 12.5, and 20 mm respectively) was used as the shell length of mussels in that size class.

In the graph (Fig. 6.18), changes within the transplanted mussel patches are expressed as vectors from the initial mean conditions to the final mean for each set of patches. These changes in the relationship between shell area (y-axis) and number of mussels in a patch (x-axis) reflect the effects of mortality, growth, and recruitment (defined here as the arrival of new individuals and their growth during the time interval) (Petraitis 1995). Vectors which are parallel to the axes can be attributed to growth (if parallel to the y-axis and increasing) or non size-specific mortality (if parallel to the x-axis and decreasing) (Fig. 6.18). Recruitment leads to decreases in the mean size of mussels and increases in the number of individuals in a patch. The isoclines (dotted lines on the graph) represent lines of zero change in patch area which were calculated by assuming that patch area was constant when mean shell area multiplied by number of mussels in a patch was constant. Packing of mussels was assumed to be constant.

The graph of changes in cross-sectional shell area and number of mussels in a patch (Fig. 6.18) indicates that each set of patches decreased from the initial size after transplantation. This initial decrease likely resulted from dislodgment by waves of loosely attached mussels. Trajectories of change in shell area and mussel number in the two habitats diverged over 15 mo (Fig. 6.18a). On emergent rock, patches exhibited a trend of decreasing shell area and increasing mussel number, consistent with effects of recruitment, which resulted in a relatively constant patch area after 10 mo. In tidepools, mean shell area decreased considerably over 15 mo as mussel number increased slightly, resulting in a decrease in patch area. For the three sets of 5 mo patches, vectors of patches in tidepools and on emergent rock were similar (Fig. 6.18b). Mean shell area decreased from July to December 1994 and May to October 1995, presumably as a result of both recruitment and mortality. From December 1994 to April 1995, number of mussels in a patch decreased but shell area remained relatively constant, consistent with non-selective mortality.

I estimated the influence of processes resulting in increases (growth, recruitment, immigration) and decreases (predatory and non-predatory mortality) in patch area in tidepools and on emergent rock for each set of experimental patches (Fig. 6.19). Because losses of mussels from patches due to wave dislodgment or emigration by crawling were not directly measured, I estimated the percentage of decreases in patch area which could not be accounted for by mortality. To estimate the increase in patch area due to recruitment, I multiplied mean recruit abundance by recruit shell area. I assumed an average size of 1 mm SL for recruits and converted this to area (Methods, Wave dislodgment). According to these calculations, recruitment alone would increase patch area by <1 cm^2 for each set of experimental patches, assuming no mortality or other losses, accounting for <9% of potential increases in patch area (Fig. 6.19). This calculation does not take into account growth after recruitment. To estimate the increase in patch area due to growth, I multiplied the change in shell area for mussels in each of the four size classes by mean number (average of initial and final number) of mussels in that size class and then totalled the increases across size classes. For this calculation, I assumed that the average initial size of mussels was 1 mm for the smallest size class (<5 mm SL) and 7.5, 12.5, and 20 mm (the midpoints of size classes) for progressively larger size classes. I used mean growth rates in my calculations, since initial shell length explained little of the variance in growth rate. According to these calculations, growth alone would increase patch area by as much as 6 cm^2 in 5 mo and 13 cm^2 in 15 mo, approximately doubling patch area, if I assume no mortality or other losses (Fig. 6.19). Growth was estimated to account for >54% of increases in patch area.

I estimated the increase in patch area resulting from immigration by multiplying the number of immigrants in a size class by the estimated average shell area of that size class (7.5, 12.5, 20 mm, as described above). To simplify the calculation, I assumed that the percentage of immigrants was the same in all size classes. For a conservative estimate, I used the lowest percentage from the other sets of patches as the percentage of immigrants in the second set of 5 mo patches and the 15 mo patches. According to my calculations, immigration of individuals larger than 5 mm accounted for 23-37% of potential increases in patch area for the first and second sets of 5 mo patches (Fig. 6.17). For the third set of 5 mo patches, in which the estimated proportion of immigrants was higher in tidepools than on emergent rock, immigration of individuals > 5 mm was estimated to account for 37% of potential increases in patch area in tidepools and 16% on emergent rock. Immigration accounted for an estimated 12-14% and 4-5% of potential increases in area of the 10 and 15 mo patches, respectively. Because the estimated percentage of immigrants in the 10 and 15 mo patches was relatively similar, the lower percentage increase in patch area attributable to immigration for 15 mo patches is a consequence of a decrease in number of mussels larger than 5 mm in a patch.

I estimated the decrease in patch area due to the death of mussels that I collected as drilled and non-drilled shells. I multiplied the number of empty shells in a size class by the area of a mussel in that size class (assuming average sizes of 1, 7.5, 12.5, and 20 mm for successive size classes, as described above). Because mean patch area remained relatively constant or decreased (Fig. 6.3, 6.18), decreases in area due to mortality must have been equal to or greater than increases due to growth, recruitment, and immigration. I calculated the losses which could not be accounted for by empty shells by subtracting the area accounted for by the empty shells from the sum of the increases in patch area due to growth, recruitment, and immigration. Mortality of mussels was negligible in the second set of 5 mo patches (December 1994 to May 1995) since no empty shells were collected from this set of patches. For patches transplanted in July 1994, predatory mortality accounted for a greater percentage of decreases in area of patches in tidepools than of patches on emergent rock: drilled empty shells accounted for 29% of decreases in area of 5 mo patches, 18% of decreases in 10 mo patches, and 35% of decreases in 15 mo patches in tidepools and 7%, 1%, and 5%, respectively, on emergent rock. In contrast, for the third set of 5 mo patches (May to October 1995), drilled empty shells accounted for 7% of decreases in patch area in tidepools and 31% of decreases on emergent rock. Predation undoubtedly accounted for a greater percentage of decreases in patch area than my estimates since some empty shells would have been washed away by waves before they were collected. These results indicate that whelk predation accounted for a greater percentage of decrease in patch area in tidepools than on emergent rock for patches transplanted in 1994, while the reverse occurred in 1995.

According to my calculations, non-predatory mortality accounted for 22% of decreases in patch area in tidepools and 54% on emergent rock for the first set of 5 mo patches, and 1% and 5%, respectively, for the third set of 5 mo patches. For the 10 and 15 mo patches, non-predatory mortality accounted for 21 and 28%, respectively, of decreases in patch area in tidepools and 3 and 2%, respectively, of decreases in patch area on emergent rock. The percentage of decreases in area accounted for by non-predatory mortality in the experimental patches is probably higher than in natural patches because of the stress of transplantation. For the experimental patches, much of the variability in the percentage of decreases in area in patch area accounted for by non-predatory mortality may be attributable to differences in acclimation to emersion in the laboratory. The sets of patches and habitats for non-predatory mortality accounted for the greatest decreases in patch area are those in which mussels were transplanted to the shore in July 1994 without acclimation to emersion. However, differences in the stress imposed by transplantation likely did not influence variation in size among patches within a habitat or transplantation date since the number of non-drilled empty shells collected from a patch was not significantly related to final patch area.

The percentage of decreases in patch area not accounted for by mortality (as measured by the empty shells collected from the patches) is attributable to active and passive dispersal of mussels. Passive dispersal by wave dislodgment is probably the most important loss not due to mortality, although tagging indicates that mussels may also actively disperse by crawling. For the second set of 5 mo patches (December 1994 to April 1995), 100% of decreases in patch area were unaccounted for by mortality (Fig. 6.19). The percentage of decreases in patch area not accounted for by mortality was similar in tidepools and on emergent rock for first set of 5 mo patches (48% and 39%, respectively), lower in tidepools than on emergent rock for 10 (61 and 96%, respectively) and 15 mo patches (37 and 89%, respectively), and greater in tidepools than on emergent rock for the third set of 5 mo patches (92 and 64%, respectively). These calculations suggest that the percentage of decreases in patch area due to losses other than mortality varies over time and between habitats, although not consistently, and that these losses are important in maintaining the balance between increases and decreases in patch size.

Table 6.1. Mean (±1S.E.) percentage of mussels >5 mm SL with a visible calcein mark for mussels held in the laboratory and those from patches transplanted to tidepools and emergent rock. The mean percentage of immigrants in transplanted patches is estimated from the number of mussels in these patches with visible marks and the percentage of mussels exposed to calcein which have visible marks in the laboratory. Sample size, n=60 to 90 individuals in the laboratory. Data from the field were averaged across patches (n=10-56 individuals/patch) within a block and then averaged for 3 blocks per habitat for the second and third sets of 5 mo patches and for 4 blocks for the first set of 5 mo patches and the 10 mo patches. ND indicates no data, NA indicates that the calculation was not applicable.

Interval	Percentage of Individuals with Visible Mark			Percentage Immigrants	
	Laboratory	Field			
		Tidepool	Emergent Rock	Tidepool	Emergent Rock
5 mo: Jul-Dec 94	36.0	29.0±5.3	31.0±2.1	26.3±11.4	20.4±2.4
5 mo: Dec 94- Apr 95	31.9	58.3±2.1	56.1±4.2	NA	NA
5 mo: May-Oct 95	ND	15.9±0.8	32.3±4.0	55.5±2.3	16.3±4.7
10 mo: Jul 94-Apr 95	39.4	35.8±3.9	36.1±1.7	17.7±6.2	15.2±4.7

Fig. 6.1. a) Tidepool (tp) and emergent rock in the mid intertidal zone at Cranberry Cove, Nova Scotia. Fucoid algae (*Fucus vesiculosus*, *Ascophyllum nodosum*) and extensive beds of mussels (mb) are visible on emergent rock b) Patches of mussels (p) and macroalgae in a tidepool (scale bar=10 cm) c) and d) Experimental mussel patches on emergent rock (scale bar=1 cm).


A

Fig. 6.2. Mean (±1S.D.) a) tidepool and sea surface salinities (ppt, measured by refractometer) and b) tidepool, sea surface, and air temperatures (° C, measured by mercury thermometer) between July 1994 and October 1995 at Cranberry Cove, Nova Scotia. Tidepool measurements are averaged across four tidepools and sea surface measurements are averaged for two locations (2 measures per tidepool and location). A single reading of air temperature was taken on each date.

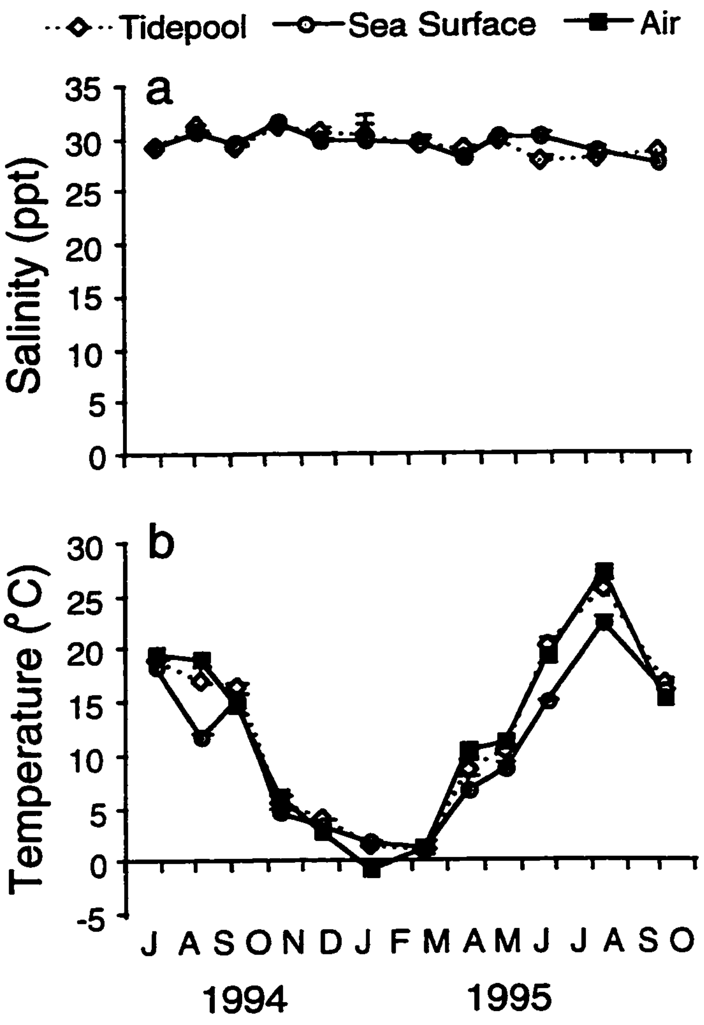

Tidepool
Sea Surface
Air
a
Salinity (ppt)
35
30
25
20
15
10
5
0
b
Temperature (°C)
30
25
20
15
10
5
0
-5
J A S O N D J F M A M J J A S O
1994
1995

Fig. 6.2

Fig. 6.3. Mean (±1S.E.) area (cm^2) of natural mussel patches and of 5, 10 and 15 mo experimental patches and the 2nd and 3rd sets of 5 mo patches, in tidepools and on emergent rock between July 1994 and October 1995. Patch area was first measured 2-6 weeks after transplantation (the date of transplantation is indicated by an arrow; the second arrow for the 10 and 15 mo patches indicates the date of transplantation of the replacement patches on emergent rock). Data for the 5, 10, and 15 mo patches transplanted in July 1994 are averaged for 4 blocks per habitat; those for the second and third set of 5 mo patches are averaged for 3 blocks per habitat.

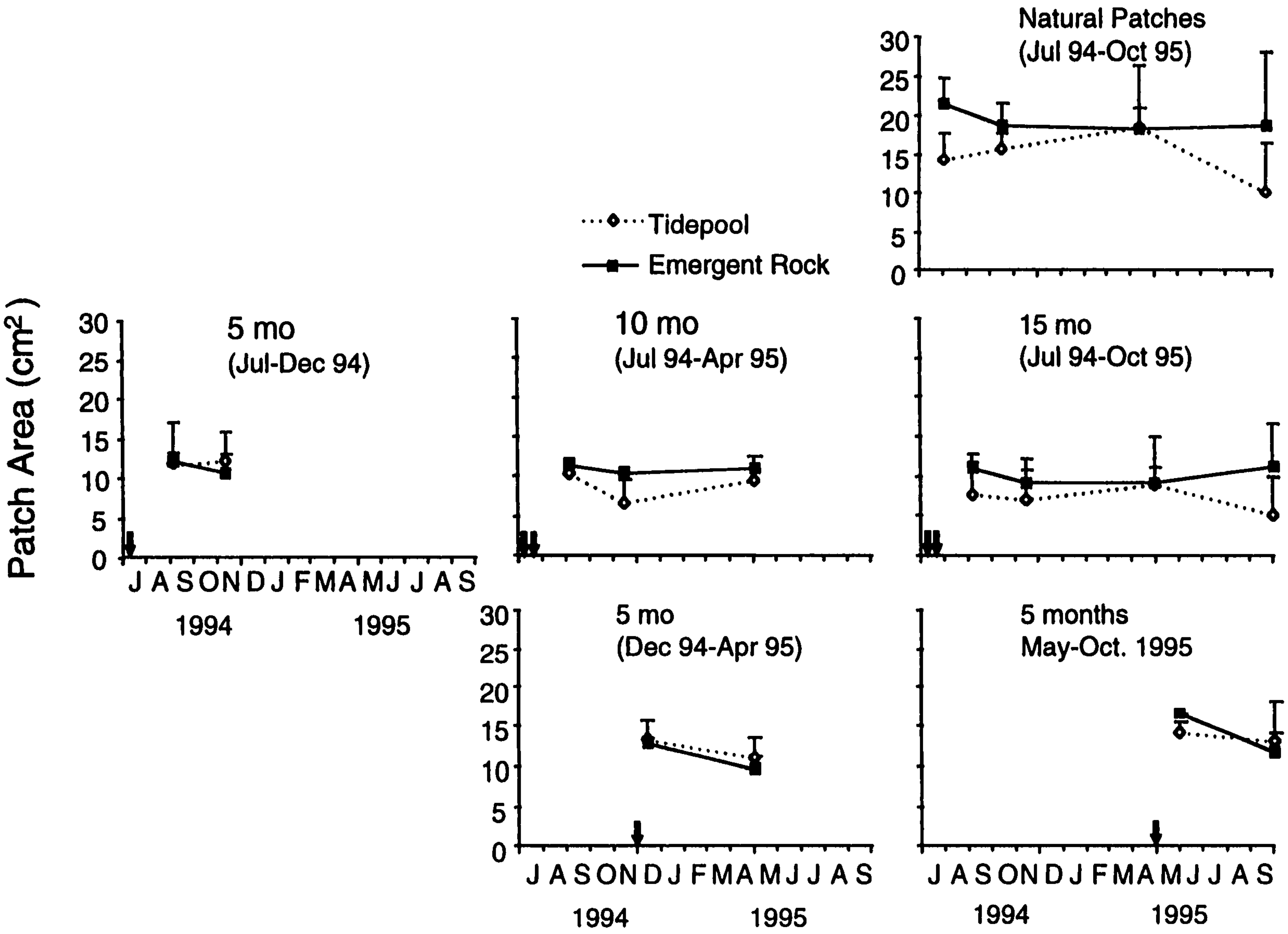

Natural Patches
(Jul 94-Oct 95)
Tidepool
Emergent Rock
5 mo
(Jul-Dec 94)
10 mo
(Jul 94-Apr 95)
15 mo
(Jul 94-Oct 95)
5 mo
(Dec 94-Apr 95)
5 months
May-Oct. 1995
Patch Area (cm²)
0
5
10
15
20
25
30
J A S O N D J F M A M J J A S
1994
1995

Fig. 6.3

Fig. 6.4. Mean (±1S.E.) a) dry mass (g) of experimental mussel patches and b) number of mussels in a patch in tidepools and on emergent rock for 5, 10, and 15 mo patches transplanted in July 1994 and for the second and third sets of 5 mo patches. Data for the 5, 10, and 15 mo patches transplanted in July 1994 are averaged for 4 blocks per habitat; those for the second and third set of 5 mo patches are averaged for 3 blocks per habitat.

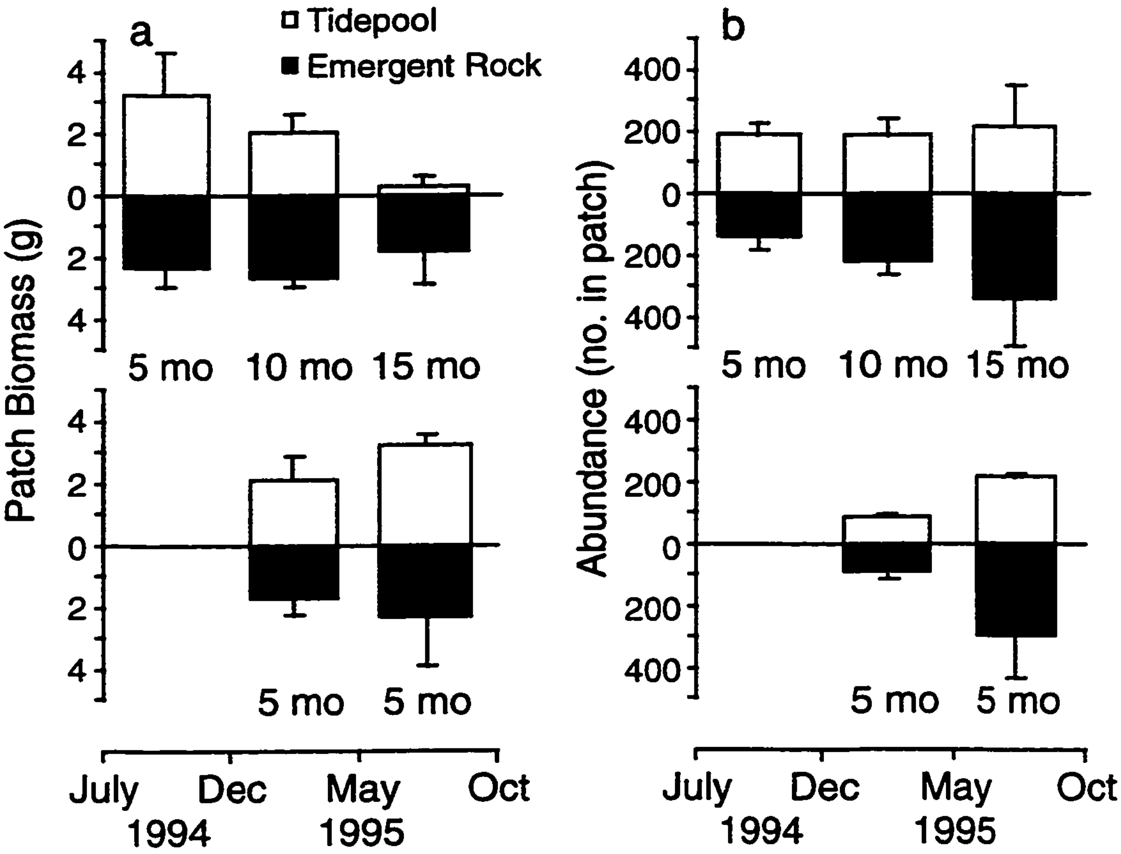

a
b
□ Tidepool
■ Emergent Rock
Patch Biomass (g)
Abundance (no. in patch)
4
2
0
2
4
400
200
0
200
400
5 mo
10 mo
15 mo
5 mo
5 mo
July
Dec
May
Oct
1994
1995

Fig. 6.4

Fig. 6.5. Size frequency distributions (SL, mm) of mussels in tidepools and on emergent rock in 5, 10, and 15 patches transplanted in July 1994 and in the second and third sets of 5 mo patches. Mussels were pooled over patches and blocks within a habitat. Data for the 5, 10, and 15 mo patches transplanted in July 1994 are from 4 blocks; those for the second and third set of 5 mo patches are from 3 blocks.

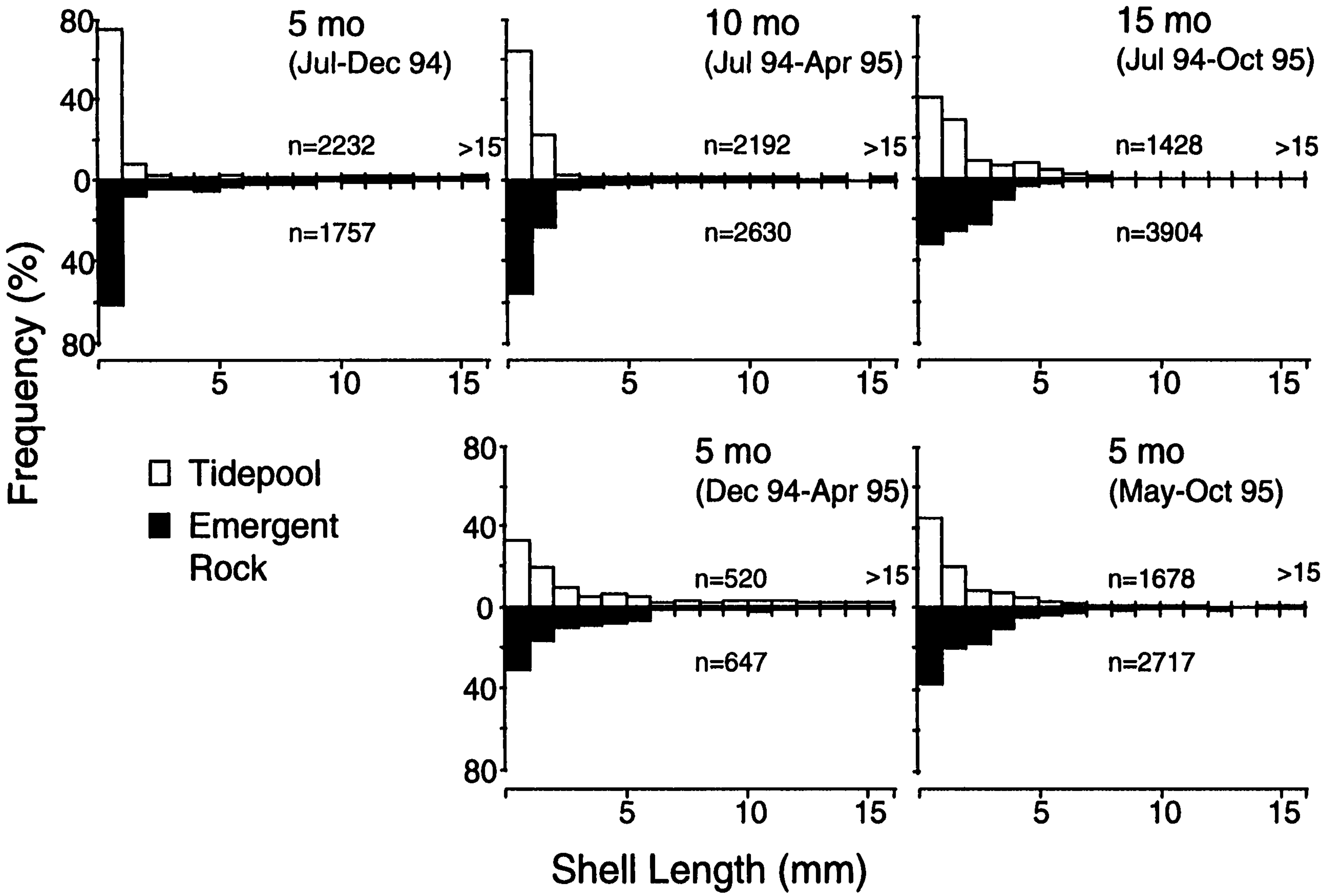
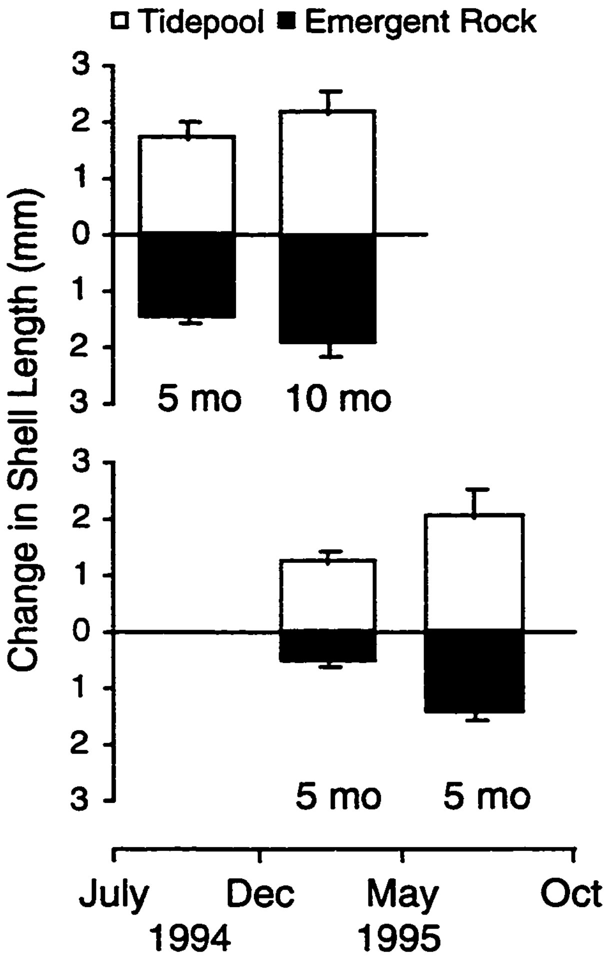
5 mo
(Jul-Dec 94)
n=2232
n=1757
10 mo
(Jul 94-Apr 95)
n=2192
n=2630
15 mo
(Jul 94-Oct 95)
n=1428
n=3904
5 mo
(Dec 94-Apr 95)
n=520
n=647
5 mo
(May-Oct 95)
n=1678
n=2717
>15
80
40
0
40
80
5
10
15
Frequency (%)
Shell Length (mm)
□ Tidepool
■ Emergent Rock

Fig. 6.5

Fig. 6.6. Mean (±1S.E.) growth rate (change in shell length, mm) of mussels in experimental mussel patches in tidepools and on emergent rock in 5, 10, and 15 mo patches transplanted in July 1994 and in the second and third sets of 5 mo patches. Data were averaged across individuals (n=4-32) within a patch and across patches within a block for each habitat. Data for the 5, 10, and 15 mo patches transplanted in July 1994 are averaged for 4 blocks per habitat; those for the second and third set of 5 mo patches are averaged for 3 blocks per habitat.



□ Tidepool ■ Emergent Rock
Change in Shell Length (mm)
3
2
1
0
1
2
3
5 mo
10 mo
3
2
1
0
1
2
3
5 mo
5 mo
July
Dec
May
Oct
1994
1995

Fig. 6.6

Fig. 6.7. Relationship between mean growth rate (change in shell length, mm) and final patch area (cm^2) and number of mussels in a patch for mussels in tidepools and on emergent rock for the second set of 5 mo patches (n=15) and the 10 mo patches (n=17).

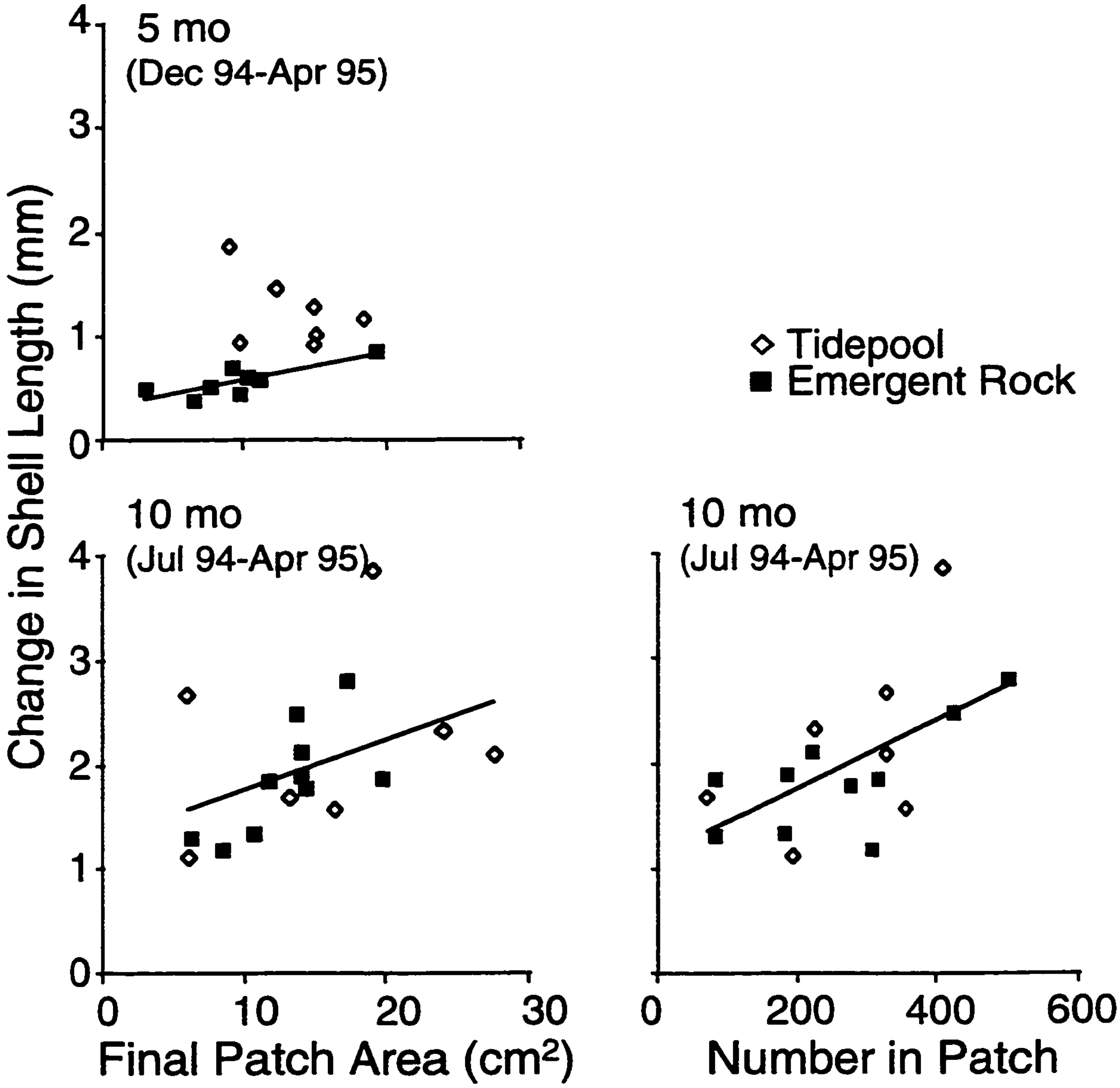

5 mo
(Dec 94-Apr 95)
10 mo
(Jul 94-Apr 95)
10 mo
(Jul 94-Apr 95)
Change in Shell Length (mm)
0
1
2
3
4
0
10
20
30
Final Patch Area (cm²)
0
200
400
600
Number in Patch
◇ Tidepool
■ Emergent Rock

Fig. 6.7

Fig. 6.8. Mean (±1S.E.) abundance of recruits (<2 mm SL) in experimental mussel patches in tidepools and on emergent rock in 5, 10, and 15 mo patches transplanted in July 1994 and in the second and third sets of 5 mo patches. Data for the 5, 10, and 15 mo patches are averaged for 4 blocks per habitat; those for the second and third set of 5 mo patches are averaged for 3 blocks per habitat.

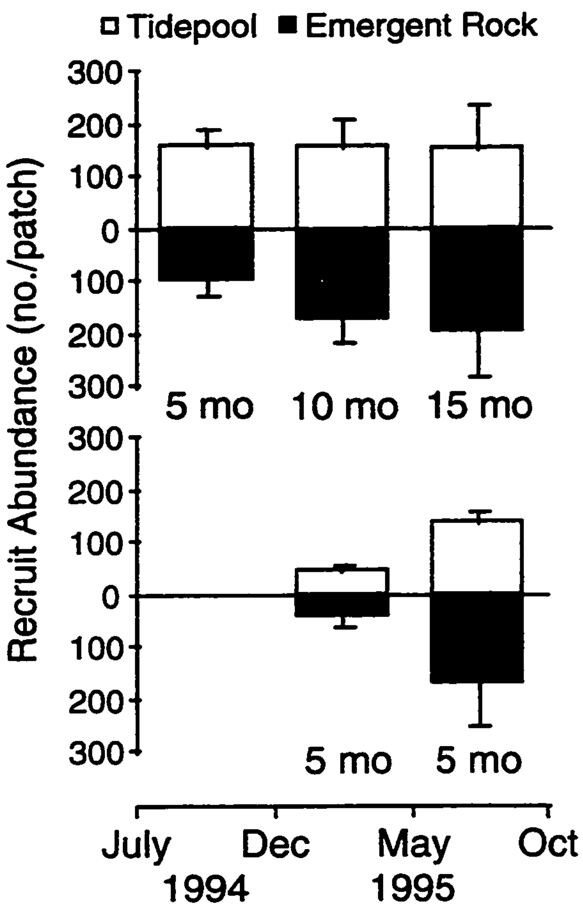

□ Tidepool ■ Emergent Rock
Recruit Abundance (no./patch)
300
200
100
0
100
200
300
5 mo
10 mo
15 mo
300
200
100
0
100
200
300
5 mo
5 mo
July
Dec
May
Oct
1994
1995

Fig. 6.8

Fig. 6.9. Relationship between mean number of *Mytilus* recruits (<2 mm SL) in a patch and patch area (cm^2) in tidepools and on emergent rock in 5, 10, and 15 mo patches transplanted in July 1994 and in the second and third sets of 5 mo patches. One patch which increased in size to 50 cm^2 within a few days between observations was excluded from analysis. Sample size, n=14 to 21. Note that data for the third set of 5 mo patches were log transformed prior to analysis and therefore are plotted on a log scale.

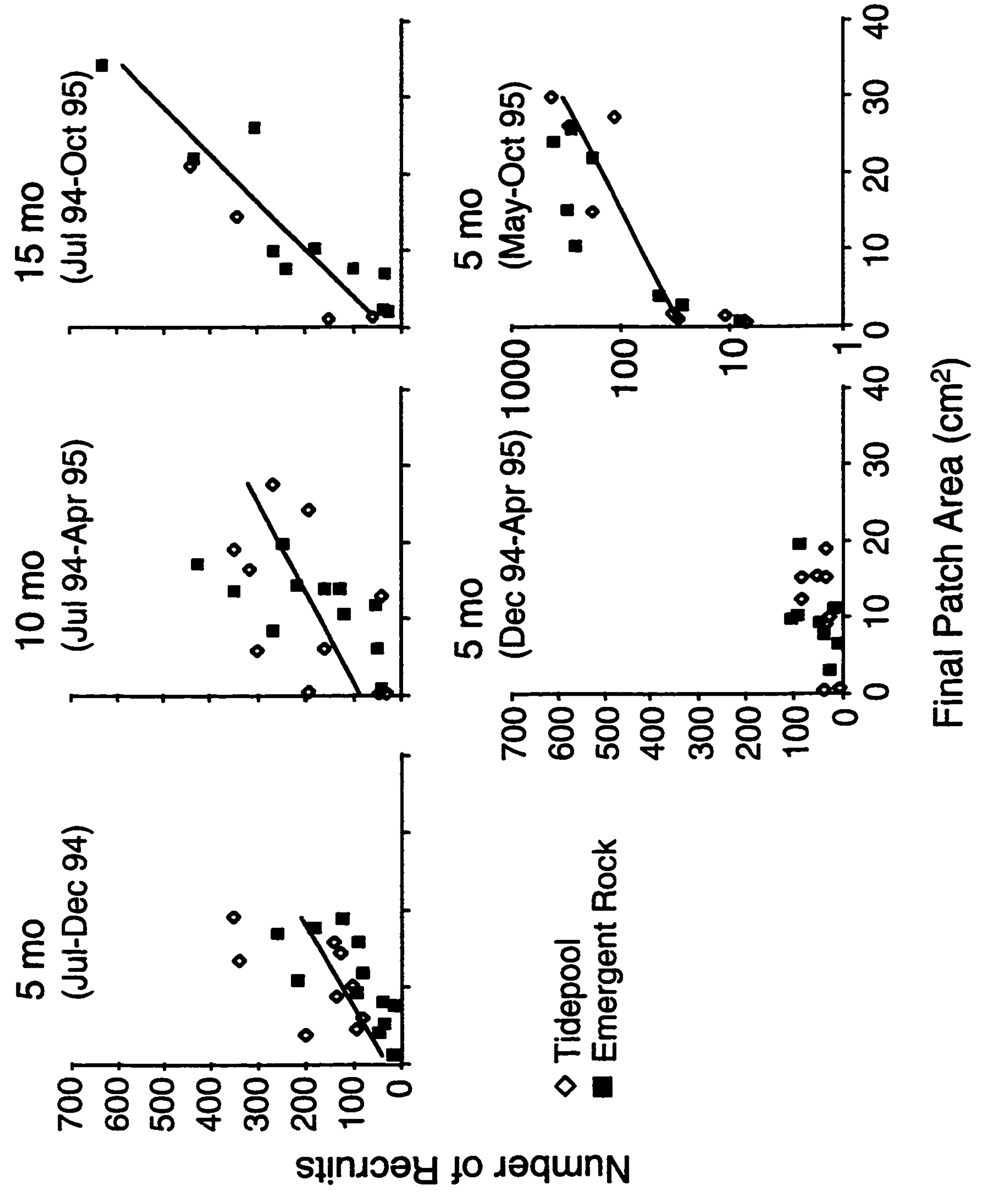

5 mo
(Jul-Dec 94)
10 mo
(Jul 94-Apr 95)
15 mo
(Jul 94-Oct 95)
5 mo
(Dec 94-Apr 95)
5 mo
(May-Oct 95)
Number of Recruits
700
600
500
400
300
200
100
0
1000
100
10
1
0
10
20
30
40
Final Patch Area (cm²)
◇ Tidepool
■ Emergent Rock

Fig. 6.9

Fig. 6.10. Mean (±1S.E.) number of whelks (*N. lapillus*) >5 mm SL on a experimental mussel patch in tidepools and on emergent rock between July 1994 and October 1995. Data are averaged across 4 blocks per habitat. From July 1994 to April 1995, nine mussel patches (first or second 5 mo, 10 mo, 15 mo) were monitored per block per habitat except the problematic block in which only 6 patches (10 mo, 15 mo) were monitored from December 1994 to April 1995. From May to October 1995, six patches (3rd 5mo, 15 mo) were monitored per block per habitat except the problematic block in which only 3 patches (15 mo) were monitored.

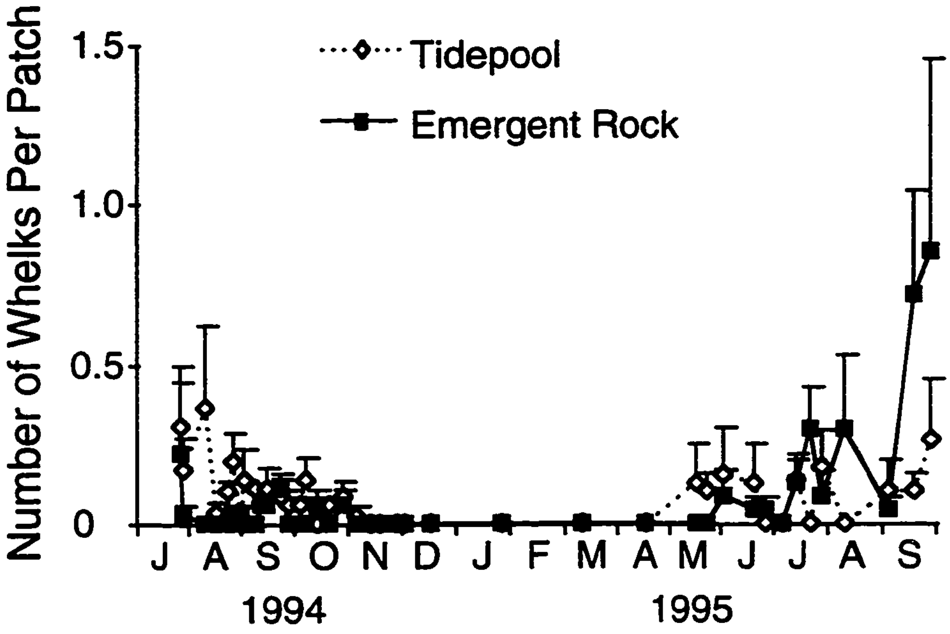

Number of Whelks Per Patch
1.5
1.0
0.5
0
Tidepool
Emergent Rock
J
A
S
O
N
D
J
F
M
A
M
J
J
A
S
1994
1995

Fig. 6.10

Fig. 6.11. Mean (±1S.E.) cumulative number of empty mussel shells with and without a drill hole (indicative of whelk predation) collected per patch from the first (July to December 1994) and third (May to October 1995) sets of 5 mo patches. Data were averaged for 4 blocks per habitat for the first set of 5 mo patches and 3 blocks per habitat for the second set.

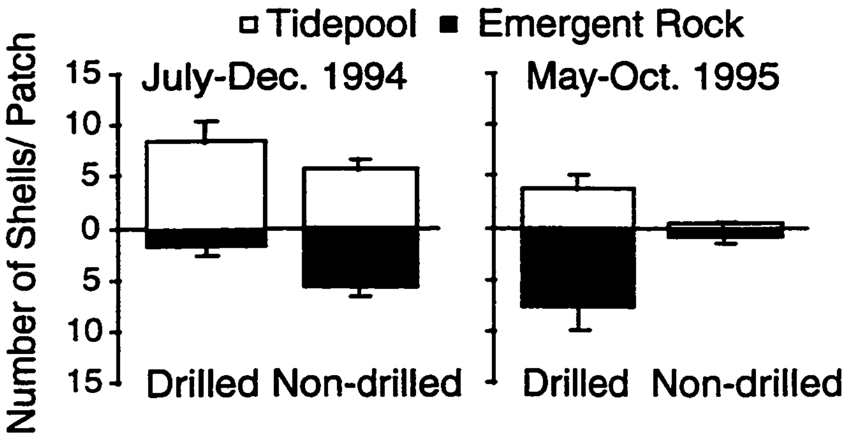

□ Tidepool ■ Emergent Rock
July-Dec. 1994
May-Oct. 1995
Number of Shells/ Patch
15
10
5
0
5
10
15
Drilled
Non-drilled
Drilled
Non-drilled

Fig. 6.11

Fig. 6.12. Daily maximum significant wave heights (m, solid line) at a nearshore oceanographic buoy between July 1994 and December 1995 and mean (±1S.D.) maximum water velocities (m/s, symbols) in tidepools and on emergent rock (averaged across 1-3 velocity meters per habitat) at Cranberry Cove between December 1994 and April 1995. There are gaps in the record of maximum significant wave heights when the buoy was not functioning.

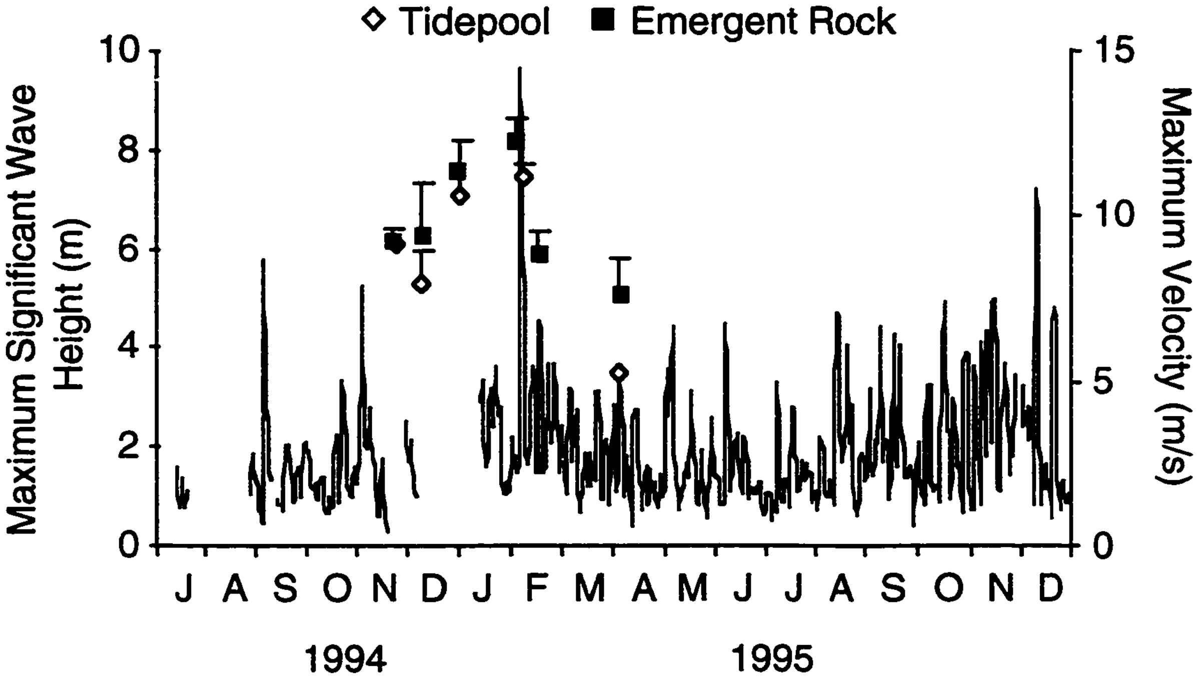

◇ Tidepool
■ Emergent Rock
Maximum Significant Wave Height (m)
10
8
6
4
2
0
Maximum Velocity (m/s)
15
10
5
0
J
A
S
O
N
D
J
F
M
A
M
J
J
A
S
O
N
D
1994
1995

Fig. 6.12

Fig. 6.13. a) Relationship between the force (f, N) required to dislodge a mussel and mussel cross-sectional area (A, cm^2) in tidepools and on emergent rock in July and August 1997. The curve is fitted using the allometric model of variation in predicted dislogment force (f_p) with mussel area: $f_p=j + m A^q$ where j, m, q are constants (1.43, 5.64, 2.12, respectively, in July, $r^2=0.80$; 0.67, 7.23, 0.89, respectively, in August, $r^2=0.80$). b) Cumulative probability distribution of normalized forces ($f_n = f/f_p$) in July and August 1997 (habitats pooled) fitted using the modified Weibull model: $P(f_n)= \exp\{-[(a- bf_{fn})/(a-bc)]^{1/b}\}$ wherea, b, c are constants (0.24, -0.22, 0.70, respectively, in July, $r^2=1.0$; 0.30, -0.09, 0.77, respectively, in August, $r^2=0.998$). Sample size, n=60 per habitat in July and 30 per habitat in August.

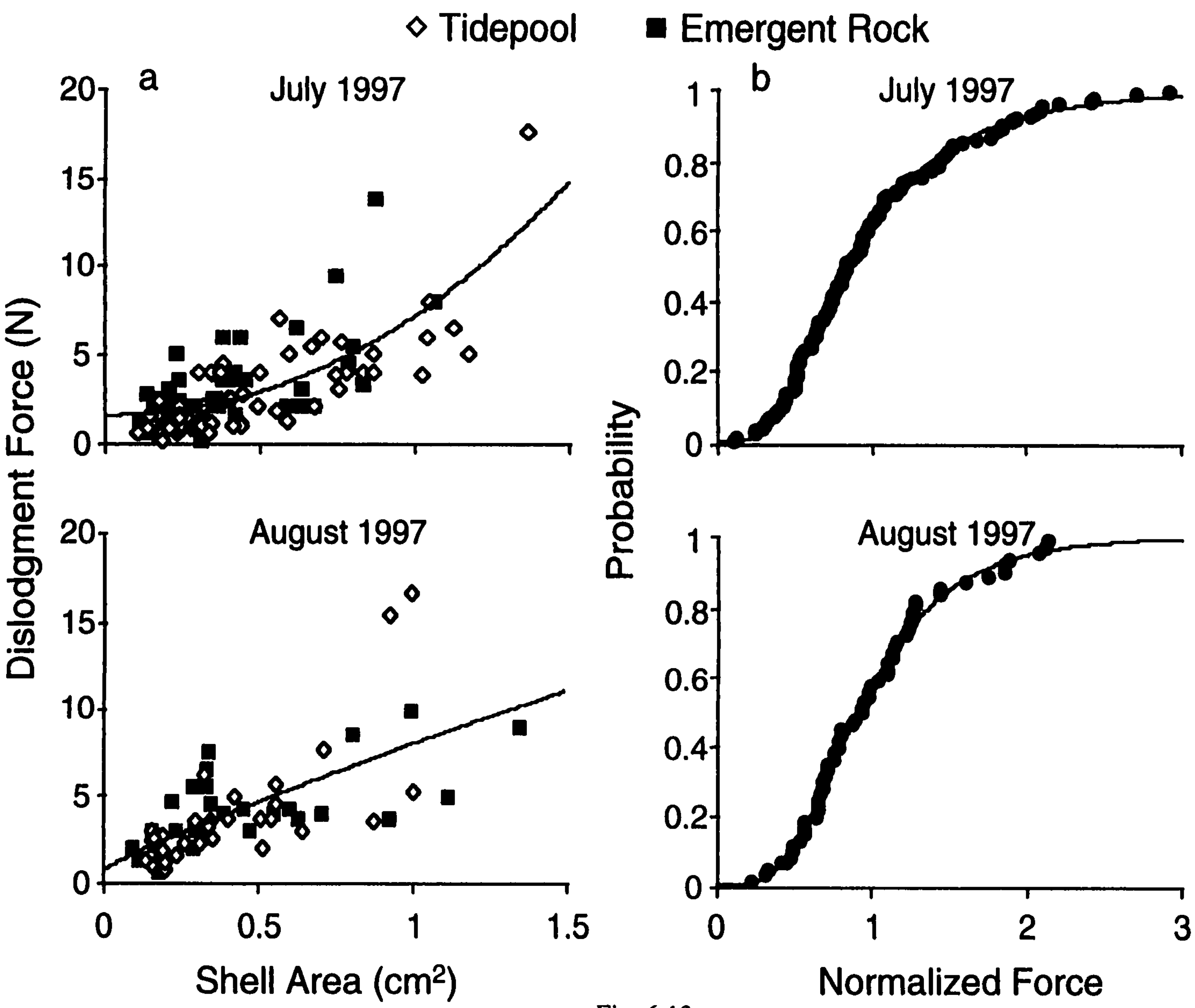
◇ Tidepool
■ Emergent Rock
a
b
July 1997
August 1997
Dislodgment Force (N)
0
5
10
15
20
Shell Area (cm²)
0
0.5
1
1.5
Probability
0
0.2
0.4
0.6
0.8
1
Normalized Force
0
1
2
3

Fig. 6.13

Fig. 6.14. Relationship between predicted hydrodynamic lift force (N) and water velocity (m/s) for mussels of 2.5, 7.5, 12.5, and 20 mm SL in tidepools and on emergent rock. The different scales used for water velocity indicate that, at a given time, water velocities in tidepools are 87% of those on emergent rock.

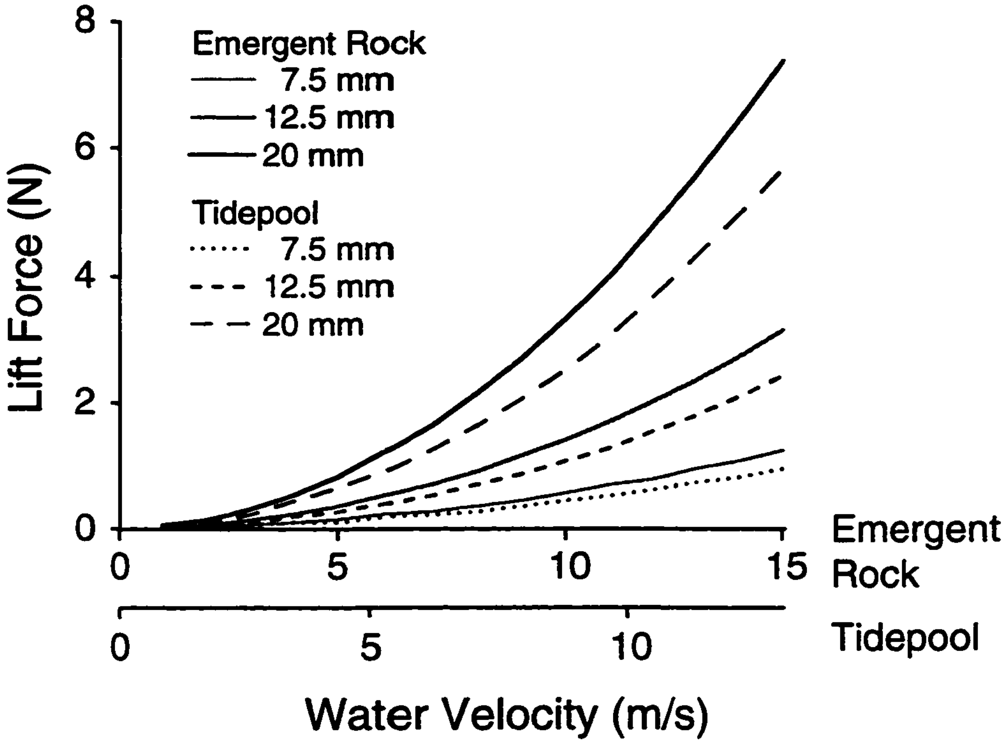
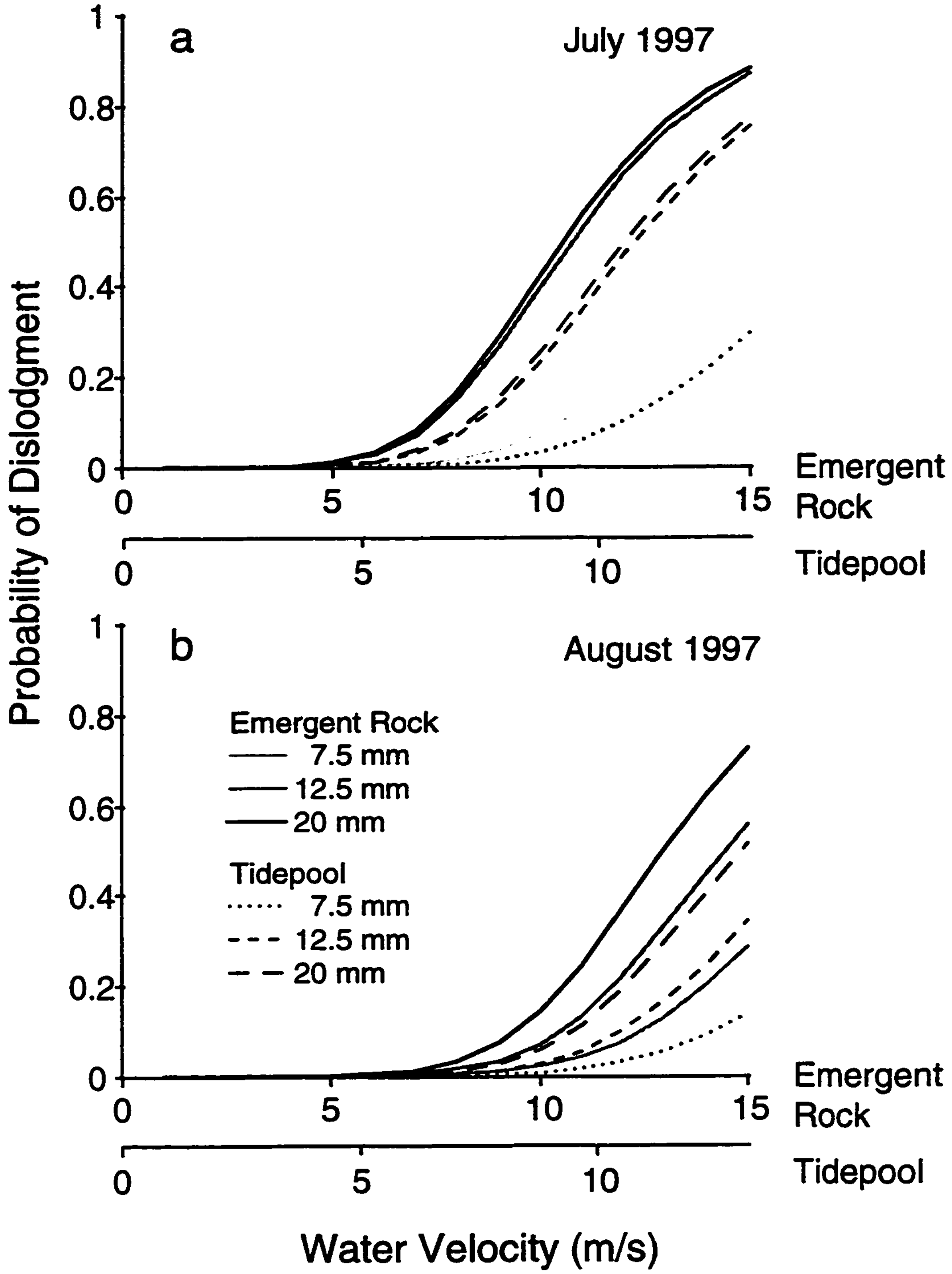

Lift Force (N)
8
6
4
2
0
Emergent Rock
7.5 mm
12.5 mm
20 mm
Tidepool
7.5 mm
12.5 mm
20 mm
0
5
10
15
Emergent Rock
0
5
10
Tidepool
Water Velocity (m/s)

Fig. 6.14

Fig. 6.15. Relationship between probability of dislodgment and water velocity in a) July and b) August 1997 for mussels of 2.5, 7.5, 12.5, and 20 mm SL in tidepools and on emergent rock. The different scales used for water velocity indicate that, at a given time, water velocities in tidepools are 87% of those on emergent rock.



Probability of Dislodgment
a
July 1997
1
0.8
0.6
0.4
0.2
0
0
5
10
15
Emergent Rock
0
5
10
Tidepool
b
August 1997
Emergent Rock
7.5 mm
12.5 mm
20 mm
Tidepool
7.5 mm
12.5 mm
20 mm
1
0.8
0.6
0.4
0.2
0
0
5
10
15
Emergent Rock
0
5
10
Tidepool
Water Velocity (m/s)

Fig. 6.15

Fig. 6.16. Frequency (%) of movement and disappearance of tagged mussels in patches and isolated (alone or in small group, or on top of the monolayer of mussels in a patch) in tidepools and on emergent rock in August 1994 (pooled across plots within a habitat) and July and October 1995. Frequency of movement was calculated as a percentage of the mussels which were tracked throughout a monitoring period. Frequency of disappearance was calculated as a percentage of the total number of tagged mussels. Sample size, n, is indicated in parantheses.

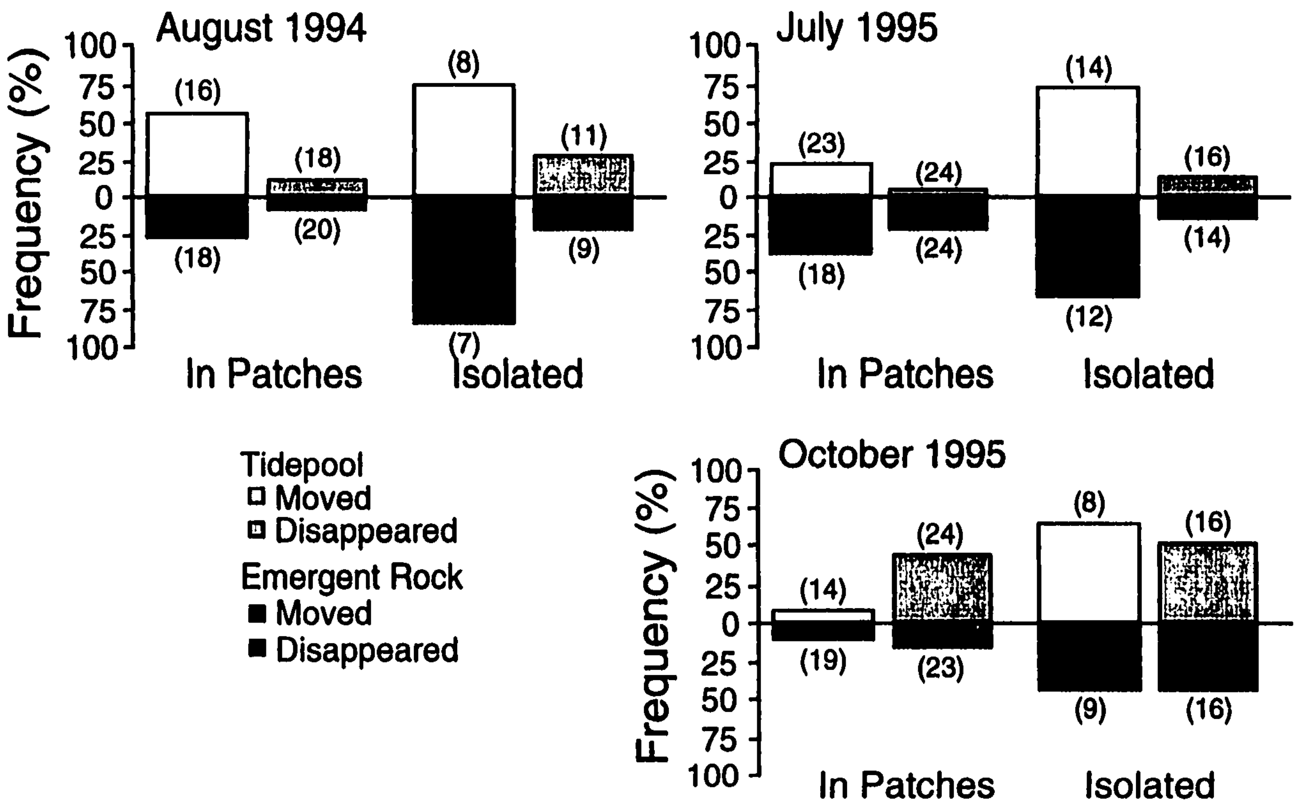

August 1994
July 1995
October 1995
Frequency (%)
100
75
50
25
0
25
50
75
100
(16)
(18)
(18)
(20)
(8)
(7)
(11)
(9)
(23)
(18)
(24)
(24)
(14)
(12)
(16)
(14)
(14)
(19)
(24)
(23)
(8)
(9)
(16)
(16)
In Patches
Isolated
Tidepool
□ Moved
▨ Disappeared
Emergent Rock
■ Moved
■ Disappeared

Fig. 6.16

Fig. 6.17. Frequency distribution of distances moved by tagged mussels. Mussels were pooled over habitats (tidepools, emergent rock), positions (in patch, isolated) and dates (August 1994, July and October 1995). Sample size, n=68.

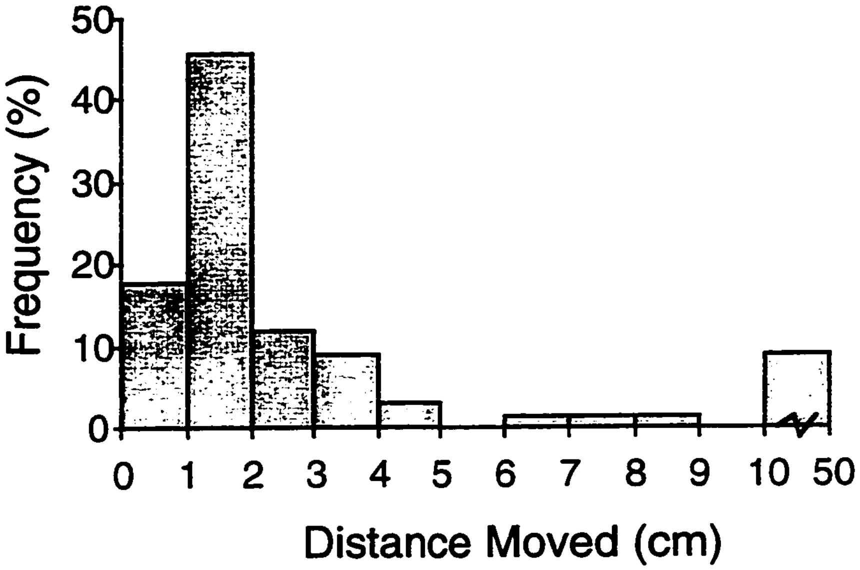


Fig. 6.17

Fig. 6.18. Partioning of changes in mussel patch area into changes in mean shell area of individuals (mm^2) and mean number of mussels in a patch. Vectors connect the initial conditions with mean conditions in tidepools and on emergent rock a) 5, 10, and 15 mo after transplantation to the shore in July 1994 and b) 5 mo after transplantation on different dates: July 1994, December 1994, May 1995, respectively. Dashed lines indicate ratios of individual shell area and number of individuals giving the same patch area; a trajectory which is not parallel to these lines indicates a change in patch area. Effects of growth, recruitment, and non size-selective mortality are shown in the inset.

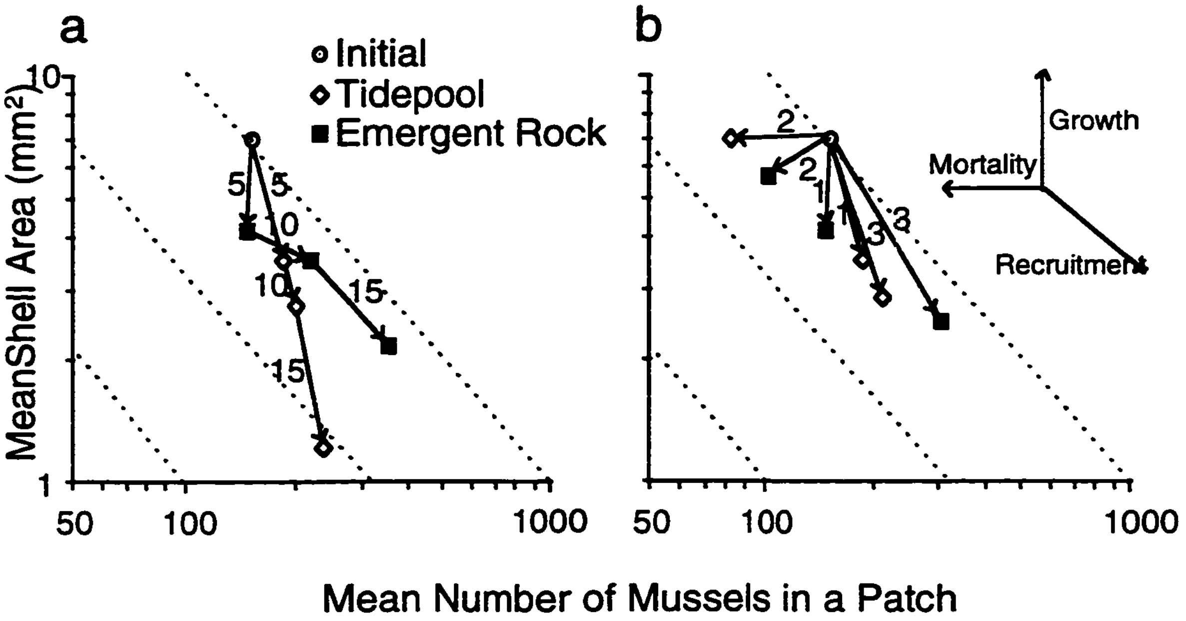

a
b
○ Initial
◇ Tidepool
■ Emergent Rock
MeanShell Area (mm^2)
10
1
50
100
1000
5
5
10
10
15
15
2
2
1
1
3
3
Growth
Mortality
Recruitment
Mean Number of Mussels in a Patch

Fig. 6.18

Fig. 6.19. Balance between increases in patch area due to immigration, recruitment, and growth and decreases in area due to predation, other mortality, and other losses for 5, 10, and 15 mo experimental mussel patches transplanted in July 1994 and for the second and third sets of 5 mo patches in tidepools (TP) and on emergent rock (ER). Patch area at the first sampling date after transplantation was ~ 11 cm^2.

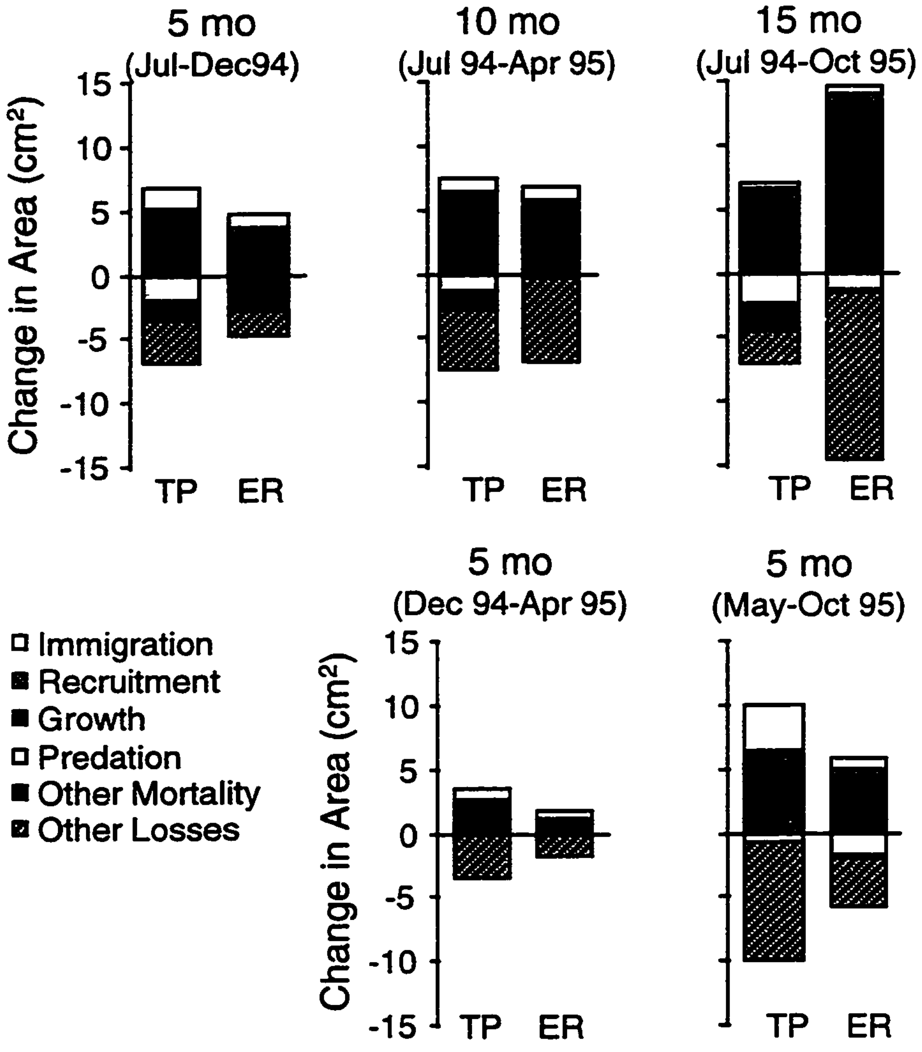

5 mo
(Jul-Dec94)
10 mo
(Jul 94-Apr 95)
15 mo
(Jul 94-Oct 95)
5 mo
(Dec 94-Apr 95)
5 mo
(May-Oct 95)
Change in Area (cm²)
15
10
5
0
-5
-10
-15
TP
ER
□ Immigration
■ Recruitment
■ Growth
□ Predation
■ Other Mortality
▨ Other Losses

Fig. 6.19

DISCUSSION

Determinants of patch structure and dynamics

Mean area of both the experimental and natural mussel patches remained relatively constant over each of the experimental time intervals, suggesting that, on average, processes increasing patch size (growth, recruitment, immigration) were balanced by processes decreasing patch size (mortality, wave dislodgment, and emigration). Despite this constancy in average patch size, individual patches varied in size and mean size of individuals decreased while numbers of individuals in a patch increased.

Growth

Growth of mussels can potentially be important in offsetting mortality and maintaining the spatial dominance of mussel assemblages (Petraitis 1995). The growth rates of *Mytilus* in this study and a previous one (Hunt & Scheibling 1995) (≤ 0.4 mm mo^{-1}) were low compared to those reported in most previous studies of this species on rocky shores (e.g. Bayne & Worrall 1980, Gardner & Thomas 1987), but were comparable to the growth rate measured for *M. edulis* in Yorkshire, UK (Seed 1969b, Seed 1973). At these low growth rates, my calculations suggest that growth can balance losses of patch area of no more than 6 cm^2/5 mo. In contrast, Reusch and Chapman (1997) concluded that a high growth rate (~30 mm/yr) enabled subtidal patches of the mussel *M. edulis* in the Baltic Sea to persist in spite of intense predation by sea stars.

Previous studies have found a negative relationship between mussel growth rate and patch size (Okamura 1986, Newell 1990, Svane & Ompi 1993), presumably due to competition among mussels for food and space. Interestingly, I found a positive relationship between growth rate and patch size for the 10 mo patches in both habitats and for the second set of 5 mo patches on emergent rock, but not in tidepools. There was no significant relationship between growth rate and patch area for the other sets of experimental patches. Because the mussel patches in my study were small and exposed to high flow rates on a wave-exposed shore, food was not likely to become depleted above a patch. A positive relationship between growth and patch size may result from effects of mussels on water flow: larger mussel patches may increase water turbulence and enhance the delivery of food to the substratum compared to smaller patches. Butman et al. (1994) found that a mussel bed significantly enhanced turbulent stress compared to a smooth bottom in flume experiments. On emergent rock, patch size also may affect the microenvironmental conditions to which a mussel is exposed. During low tide, individuals in large patches may gain some protection from their neighbors from desiccation and freezing.

Recruitment, Movement, and Immigration

The relationship between changes in mean shell area and number of mussels in a patch suggests that recruitment contributed to the changes in the size structure of each set of experimental patches, except the second set of 5 mo patches which was transplanted in winter when settlement rate of *Mytilus* is negligible (Chapter 3; Pedersen 1991). Recruitment rates of mussel on the experimental patches (mean 2-4 recruits/cm^2 of patch area per month) were comparable to those measured on other rocky shores in the northeast Atlantic (Petraitis 1991). I found a positive relationship between recruitment rate of mussels and patch area which may have resulted from a hydrodynamic effect, as suggested for growth rate, or because mussels selectively settled on conspecifics. *Mytilus* are known to settle on a wide variety of filamentous substrata, including byssal threads of adult conspecifics (reviewed by Seed & Suchanek 1992).

The ability of mussels to crawl along the substratum using their foot has been shown to influence the population dynamics of the mussel *Geukensia demissa* in salt marshes (Bertness & Grosholz 1985), but is not usually considered in studies of the dynamics of mussel assemblages on hard substrata. I found that 22-56% of mussels in patches in summer moved within 4 wk. Anthony and Svane (1995) recorded a higher movement frequency for *M. edulis* in a subtidal mussel bed (94% moved within 4 wk) possibly because lower water velocities in the subtidal permit mussels to be less strongly attached to the substratum. The distances moved by tagged mussels in this study were generally small (<10 cm), resulting in changes in the position of a mussel within a patch or, less frequently, in immigration to a new patch (natural patches were usually separated by 5-15 cm). Movement within a patch may result in changes in growth rate or risk of predation, as these factors may vary with position in a patch (Okamura 1986). Movement of mussels among patches by crawling is probably more important in natural assemblages than in the experimental patches because I cleared the substratum (up to 10 cm) around the patches as part of the attachment process.

Immigration of mussels probably also occurs by dislodgment and deposition of individuals by waves, as suggested by the sudden large increases in area of some of the experimental and natural patches. Comparison of the percentage of mussels with visible calcein marks in the field with those held in the laboratory suggested that immigrants constituted >10% of mussels larger than 5 mm in each set of experimental patches. At Cranberry Cove, mussels larger than 5 mm SL arrive in plots cleared of mussels at a rate of up to 3 mussels day^{-1} 100cm^{-2} (Chapter 3). Dislodgment and reattachment of large mussels is known to be an important mode of dispersal in soft bottom habitats (Reusch & Chapman 1997), but has received less attention in studies on rocky shores (but see Paine 1974, Wooton 1993).

Predation and Wave Dislodgment

Predation by whelks can have dramatic effects on mussel assemblages (e.g. Menge 1976, Lubchenco & Menge 1978, Carroll & Highsmith 1996). I found that drilled shells indicative of whelk predation accounted for up to 36% of the decrease in patch area. As wave action would have removed some empty shells before they were collected, the percentage of mortality resulting from whelk predation was certainly higher.

I examined the effect of whelk predation on mussel assemblages at Cranberry Cove (Chapter 5) by reducing densities of whelk post-recruits in 1.5 to 4 m^2 tidepools and plots of emergent rock. Mussel cover decreased in unmanipulated control plots in both habitats, more so on emergent rock than in tidepools, but remained constant in plots where whelk densities were reduced. In this study, however, final area of mussel patches was not significantly related to the cumulative number of drilled shells collected from a patch. This suggests that, although whelk predation can be an important cause of mussel mortality, it was not an important source of variation in patch area.

Mussels living on wave-exposed shores are subjected to large wave forces, particularly during fall and winter storms. Most studies of wave disturbance of mussels on hard substrata have involved *M. californianus*, the dominant mussel on exposed shores in the north east Pacific. Disturbance by waves is known to cause gaps in beds of *M. californianus* in Washington, USA (Levin & Paine 1974, Paine & Levin 1981) and Denny (1995) calculated that *M. californianus* experience forces near their modal breaking force. Dislodgment by waves may be even more important as a cause of mortality of other mytilids, such as *M. edulis, M. trossulus,* and *M. galloprovincialis*, since their byssal attachment (per unit of cross sectional area) is much weaker than that of *M. californianus* (Harger 1970, Witman & Suchanek 1984, Bell & Gosline in press).

My calculations of the probability of wave dislodgment of mussels at Cranberry Cove suggest that mussels >10 mm SL are vulnerable to dislodgment by water velocities ≥7 m/s. My predicted dislodgment rates are in the same range as those calculated by Bell and Gosline (in press) for *M. trossulus* on a moderately exposed shore in British Colombia, Canada. The importance of wave dislodgment as a cause of mussel mortality at my site is supported by the high proportion (37-100%) of decreases in area of the experimental patches which were not accounted for by in situ mortality (empty shells), and by the greater percentage of tagged mussels which disappeared in tidepools in October (when wave heights were greater) than in July and August. Dislodgment by waves of one or a few mussels in a patch would render the remaining mussels more vulnerable to hydrodynamic forces acting parallel to the substratum, drag and the acceleration reaction, and could lead to the dislodgment of many other mussels in a patch (Denny 1987). Wave action may also interact with other causes of mortality. For example, when I experimentally reduced whelk densities (Chapter 5), predation could not entirely account for the decrease in mussel cover and abundance which occurred in unmanipulated plots. I attributed this discrepancy to wave action, as dislodgment of the shells of predated mussels would remove recruits associated with the drilled shells and weaken the surrounding mussel matrix.

Attachment strength of mussels depends on the number of byssal threads anchoring them to the substratum (Bell & Gosline in press). Unlike the permanent attachment of a barnacle, these threads decay and must be replaced to maintain a constant attachment strength, which can be metabolically costly (Hawkins & Bayne 1985). Mussels respond to their flow environment by varying their attachment strength (Price 1980, 1982, Witman & Suchanek 1984). I found that attachment strength was higher, and, consequently, probability of dislodgment by a given water velocity was lower, after mussels had been exposed to 4 m high waves than during a period of low wave heights (<2 m). At Cranberry Cove, probability of dislodgment by a given water velocity is probably lower in fall and winter (when large waves are more common) than in summer. Seasonal variation in attachment strength may counteract seasonal changes in wave action to dampen any seasonality in the probability of wave dislodgment. Similar probabilites of dislodgment during infrequent hurricane-generated storms in summer, compared to winter storms with greater wave heights, may partly account for the lack of seasonality in mean patch size.

In summary, these results suggest that variation in individual patch area was probably due primarily to wave dislodgment and immigration of larger mussels, since the largest increases and decreases in patch size usually occurred suddenly and were often associated with storms. Recruitment and size-selective mortality due to whelk predation and/or wave dislodgment seemed to be the most important determinants of patch structure. Low growth rates undoubtedly also contributed to the small mean size of mussels but growth was important in balancing mortality and other losses. The importance of wave dislodgment in the structure and dynamics of mussel patches at Cranberry Cove is typical of many wave-exposed rocky shores (e.g. Harger & Landenberger 1971, Levin & Paine 1974, Paine & Levin 1981). However, predation seems to be less important in structuring these mussel assemblages than those at many other sites, particularly those where seastars or crustaceans are the dominant predators (e.g. Kitching et al. 1959, Paine 1966, 1974, Robles 1987, Reusch & Chapman 1997). The intense predation in those mussel assemblages is generally balanced by much higher growth rates than at Cranberry Cove.

Effects of habitat on mortality, growth, and recruitment

My observations at Cranberry Cove over 6 years indicated that the cover and spatial distribution of mussels differed between tidepools and emergent rock. When I transplanted mussel patches to both habitats in this study, the divergence in patch structure and size developed slowly. Mean area of experimental patches remained relatively constant during the 15 mo experiment and did not differ significantly between tidepools and emergent rock. However, there was a clear trend of decreasing patch biomass and area in tidepools. When each set of experimental patches was collected, except the second set of 5 mo patches (December 1994 to April 1995), small mussels were relatively more abundant in experimental patches in tidepools than on emergent rock. Differences in size distributions likely resulted from greater mortality of large mussels in tidepools than on emergent rock since recruit abundance did not differ significantly between habitats. I observed a similar between-habitat difference in the size distribution of natural mussel assemblages at Cranberry Cove in fall 1995 (Chapter 5).

I compared rates of mussel growth, recruitment, and mortality between tidepools and emergent rock to determine if they were influenced by environmental differences between the habitats. I found that growth rates of mussels were significantly higher in tidepools than on emergent rock for each of the sets of 5 mo patches, particularly for the second set in winter. However, these between-habitat differences in growth rates were small and there were no significant differences in growth rate between tidepools and emergent rock for mussels in the 10 mo patches. My results are inconsistent with the prediction of Clarke and Griffiths (1990) who concluded that scope for growth of the mussel *Choromytilus meriodionalis* in South Africa was lower in tidepools than on emergent rock. They reasoned that mussels in tidepools would continue filtering water during low tide even though the pools would be rapidly depleted of food, while aerially exposed individuals on emergent rock would reduce their metabolism and conserve energy. At Cranberry Cove, however, Metaxas and Scheibling (1994) found that total abundance of phytoplankton in mid-zone tidepools did not decrease during the period of tidal isolation, suggesting that mussels either do not deplete their food resources during tidal isolation or cease feeding during this time.

Recruitment rate of mussels did not differ significantly between tidepools and emergent rock in any of the sets of experimental patches. Although mussels could potentially settle in tidepools throughout the tidal cycle, only a small proportion of mussels colonize tidepools during low tide (Chapter 4). In the present study, the substrate available for mussel settlement (the experimental patch and mesh base) was the same in both habitats, unlike the natural substratum (macroalgal assemblage) which differed considerably between tidepools and emergent rock (Chapter 3). However, I found that colonization of *Mytilus* on the natural substratum did not differ between the habitats in areas of the shore that were not recently scoured by ice (Chapter 3).

Based on models of the effects of environmental stress on predation (Connell 1975, Menge & Sutherland 1987), whelk predation on mussels would be expected to be greater in tidepools than on emergent rock because of increased time available for foraging. In 1994, I found significantly more drilled shells in patches in tidepools than in those on emergent rock, which is consistent with this prediction. In 1995, however, the number of drilled shells was greater in patches on emergent rock than in tidepools and manipulation of whelk densities had greater effects on emergent rock than in tidepools (Chapter 5). The between-year difference probably reflects changes in whelk densities since the cumulative number of drilled shells collected from a patch was related to the mean number of whelks observed on a patch. Feeding rates of whelks held in cages are similar between tidepools and emergent rock (≈ 1 mussel/whelk/week, Chapter 5), suggesting that foraging time is not a major factor controlling whelk predation rates on this shore. Predation rates of whelks probably differ more consistently between tidepools and emergent rock in places where canopy-forming algae, which provide shelter from desiccation (and possibly wave dislodgment) for foraging whelks (Menge 1978a), are less abundant on emergent rock than they are at Cranberry Cove.

My calculations suggest that the probability of dislodgment of mussels larger than 5 mm SL is approximately twice as high on emergent rock as in tidepools. The greater probability of dislodgment on emergent rock than in tidepools results from 15% higher maximal water velocities, since attachment strength of mussels did not differ between habitats. Between-habitat differences in probabilities of dislodgment are larger than differences in water velocities because hydrodynamic forces exerted on mussels are related to the square of water velocity. Predicted probabilities of dislodgment of small mussels (2.5 mm) are negligible in both habitats. However, small mussels are often attached to the byssal threads or shells of a larger individual, and would likely be lost if the larger mussel was.

In summary, my results indicate that differences in environmental conditions between tidepools and emergent rock did not strongly affect predation rates on mussels. My estimates of the probability of dislodgment of mussels by waves were considerably higher for emergent rock than for tidepools, but rates of growth and recruitment were similar in both habitats. Over the time scale of this experiment (15 mo), differences between habitats in rates of mortality, wave dislodgment, and growth cannot account for the observed differences between the two habitats in the patterns of mussel abundance and distribution. This suggests that differences in mussel distribution and cover between tidepools and emergent rock develop gradually and can be altered by stochastic events, such as ice scour (Chapter 3) and hurricanes which generate large wave forces (Chapter 5).

Comparison with other shores

The scale of mussel aggregations and the size of the component individuals are smaller at Cranberry Cove than those described in most other studies. At my site (and elsewhere in Nova Scotia), mussels occur in centimetre-scale patches in tidepools and in larger beds (with centimetre-scale gaps) on emergent rock. In a previous study (Hunt & Scheibling 1995), I recorded ~150 mussel patches/m^2 in tidepools at this site (unpubl. data). In contrast, Levin and Paine (1974) and Paine and Levin (1981) modelled the dynamics of gaps of up to 6 m^2 in mean size in extensive beds of *M. californianus* (a much larger mussel than *M. edulis* and *M. trossulus*) in Washington, USA. Reusch and Chapman (1997) described patches of *M. edulis* up to 5 m^2 on subtidal soft substrata in the Baltic Sea. The size distribution of mussels at Cranberry Cove is highly skewed towards small individuals: ~90 % are <5 mm (Chapter 5; Hunt & Scheibling 1995). Mean size of mussels in the experimental patches at the end of each of the experimental intervals was only 2-4 mm SL. This is much smaller than the size of individuals described in most studies of intertidal mussel assemblages (e.g. Mossop 1921, Gardner & Thomas 1987, Petraitis 1995, Reusch & Chapman 1997). For example, Petraitis (1995) reported that the mean length of *M. edulis* on a sheltered rocky shore in Maine was 31 mm. The size structure of mussel assemblages at Cranberry Cove is similar to those of *M. edulis* on exposed rocky shores in Yorkshire, UK (Seed 1969a,b), where growth rates are comparable, and *M. galloprovincialis* on Santa Catalina Island, California (Robles 1987), where growth rates and predation intensity on larger mussels are much higher. The smaller size of aggregations and component individuals in my study compared to most previous studies of *M. edulis* and *M. trossulus* probably result from the low individual growth rates at Cranberry Cove. The size distribution of mussels also is probably influenced by size selective loss due to wave dislodgment and predation. Differences between *M. trossulus/edulis* and *M. californianus* likely result from life history differences between species: *M. californianus* attains a greater maximum size, is longer lived, and is better protected from predators by a thicker shell than *M. trossulus* (Suchanek 1981). *M. californianus* also appears to be better adapted to strong wave action due to stronger byssal attachment (Harger 1970, Witman & Suchanek 1984, Bell & Gosline in press).

At Cranberry Cove, I found that mean size of experimental patches was relatively constant over time despite high variability among individual patches. Natural patches also exhibited a lack of seasonality in patch size, both in this study and in my previous work at this site (Hunt & Scheibling 1995), which is inconsistent with other studies of *Mytilus*. Gaps in beds of *M. edulis* in New England (Menge 1976) and of *M. californianus* in Washington (Paine & Levin 1981) form more frequently in winter than in summer. In Oregon, Navarette and Menge (1996) described extensive beds of *M. trossulus* which covered >70% of the substratum the low intertidal zone in spring, but were eliminated by predators by mid summer. As previously discussed, seasonality in the probability of wave dislogment may be dampened by seasonal variation in attachment strength. In addition, the magnitude of seasonal variation in growth rate was relatively small because growth rates were low.

In summary, there are a number of differences in spatial scale and in ecological and physiological rates between the mussel assemblages at Cranberry Cove and those examined in other studies. These include differences in scale of aggregations, size of component individuals, individual growth rates, seasonality in patch size, and the relative importance of wave dislodgment compared to predation. My results, in particular, emphasize the importance of wave disturbance as a cause of both redistribution and loss of mussels. By demonstrating the variation which exists among regions in the structure and dynamics of mussel assemblages, and in the relative importance of processes which influence them, this study cautions against generalizing pattern and process across different spatial and temporal scales.

CHAPTER 7: General Discussion

This thesis examines the biological and physical processes influencing the structure and dynamics of mussel assemblages in tidepools and on emergent rock on a temperate rocky shore. Sampling mussel colonization at short intervals (2 to 7 d) indicated that most colonists (>96%) on the natural substratum were postlarval mussels (usually >2 mm) rather than settling larvae (Chapter 3). Mussels that colonized natural substrata were larger than those which colonized an artificial filamentous substrate, indicating that detection of the dispersal of large mussels may depend on the substratum used to monitor colonization (Chapter 4). Comparison of colonization on artificial collectors and natural substrata revealed that differences in rates of colonization among non-scoured and ice-scoured tidepools and emergent rock were influenced by differences in the substratum (Chapter 4). Colonization rate on natural substrata was related to a suite of biological (macroalgal/barnacle cover) and physical factors (water flux, tidal height, flushing time). Comparison of colonization patterns on the natural substratum at sampling intervals of days to months indicated that, over time scales up to 16 mo, patterns of initial colonization were more important than post-colonization processes in determining the pattern of abundance and distribution of mussels (Chapter 3).

Size of established mussel patches varied over time, but mean patch area remained relatively constant (Chapter 6). This constancy suggested that, on average, processes increasing patch size were balanced by processes decreasing patch size. Growth of individuals was important in balancing losses of mussels, although individual growth rates were low in comparison to other shores (Chapter 6). Increases in patch area also occurred by increases in the number of individuals, including immigration of mussels >5 mm. Predation by the whelk *Nucella lapillus* was an important cause of mussel mortality in the experimental patches (Chapter 6), as it was in plots in which the density of whelk post-recruits was manipulated (Chapter 5). However, whelk predation was not an important source of variation in area among the experimental mussel patches (Chapter 6). I predicted probabilities of wave dislodgment of mussels using measures of water velocity and attachment strength of mussels (Chapter 6). These calculations suggested that wave disturbance was an important cause of loss of large (> 10 mm) mussels and that probabilities of dislodgment at a given water velocity varied over time because of changes in attachment strength. My results suggest that wave disturbance is more important than predation in determining the structure and dynamics of mussel patches on this shore (Chapter 6), although effects of wave disturbance and predation may interact. When I experimentally reduced whelk densities (Chapter 5), predation could not entirely account for the decrease in mussel cover and abundance which occurred in unmanipulated plots. This discrepancy is most likely due to dislodgment by waves of the shells of predated mussels, as well as the live mussels surrounding the empty shells.

Over the time scale of these studies (up to 17 mo), rates and patterns of colonization, growth, mortality, and wave dislogment could not account for the observed differences in the distribution and abundance of mussels between tidepools and emergent rock. On non-scoured areas of the shore, rates of colonization of mussels over both short (2 to 7 d) and long (5-16 mo) sampling intervals did not differ between habitats (Chapter 3). Rates of recruitment in the experimental mussel patches were similar in tidepools and on emergent rock (Chapter 6). Individual growth rates were slightly higher in tidepools than on emergent rock, particularly in winter, but these differences were relatively small (Chapter 6). Between-habitat differences in effects of whelk predation varied between years and were dependent on whelk density, since feeding rate of whelks held in the two habitats were similar (Chapters 5, 6). The higher probabilities of wave dislodgment of mussels on emergent rock than in tidepools (Chapter 6) cannot account for the larger beds of mussels on emergent rock. Patterns of distribution and abundance of mussels appear to develop slowly on this shore, primarily due to low individual growth rates. This is illustrated by the low cover and small size of individuals after 16 mo of colonization

(Chapter 3). In addition, in the experimental mussel patches, mean size of individuals and patch biomass began to diverge between tidepools and emergent rock only after 10 mo. Further understanding of differences in the distribution and abundance of mussels between tidepools and emergent rock will probably require studies of longer duration. It may also be valuable to examine interactions of mussels with other species, such as the snail *Littorina littorea* which is abundant in tidepools (Metaxas et al. 1994) but rare on emergent rock (pers. obs.). Littorinids may influence mussel abundance by causing early post-settlement mortality through biological disturbance (Chapter 2) or by indirect effects through their influence on the macroalgal assemblage.

The results of this thesis extend our understanding of the structure and dynamics of mussel assemblages by demonstrating the importance of wave disturbance as a cause of redistribution as well as loss of mussels. Dislodgment and reattachment of large mussels has been reported in other studies on rocky shores (e.g. Paine 1974) and is known to be an important mode of dispersal in soft bottom habitats (Reusch & Chapman 1997), but has not been recognized as a major determinant of the structure and dynamics of mussel assemblages on hard substrata. Because the substratum used to monitor mussel colonization may influence the size of colonists (Chapter 4), the relative importance of colonization by large mussels is unlikely to be recognized in the many studies using artificial filamentous substrata. The results of this study also emphasize the importance of wave disturbance as a cause of loss of mussels. Attachment strength of mussels, and consequently, probability of dislodgment by a given water velocity, is variable (Chapter 6). The interacting effects of seasonal variation in wave action and attachment strength on probability of wave dislodgment require further investigation. Future directions for research also include examination of the response time of attachment strength to changes in wave action, and the potential tradeoffs between allocation of resources to byssal attachment and other activities such as reproduction.

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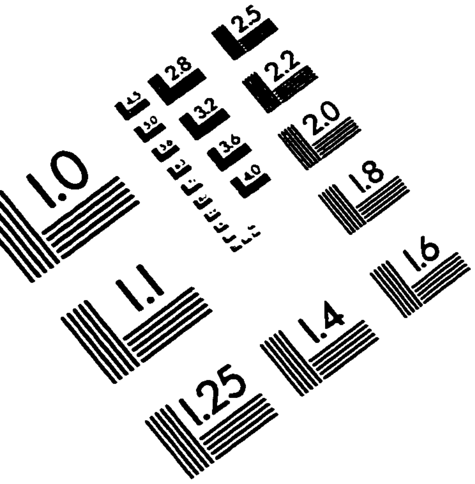
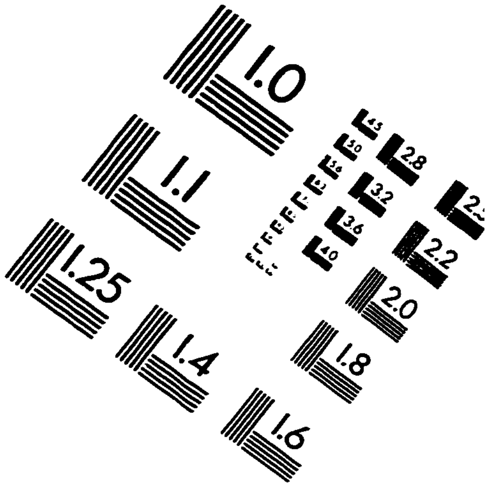
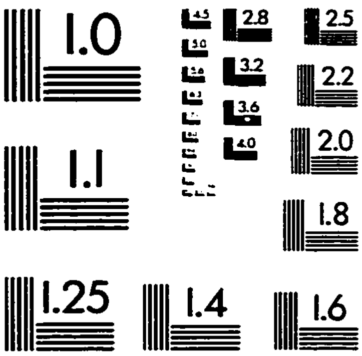
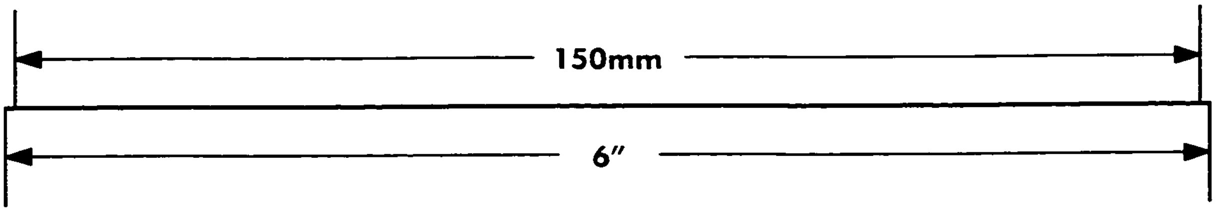
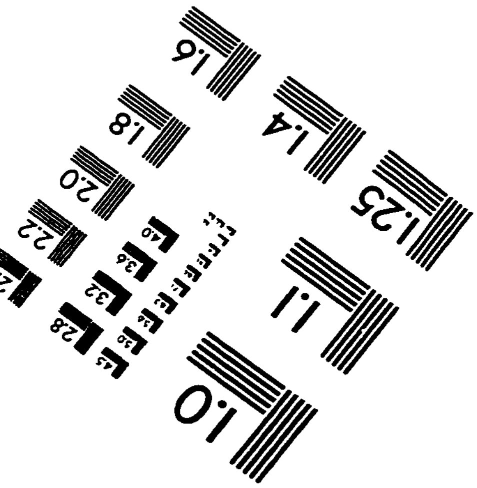
IMAGE EVALUATION TEST TARGET (QA-3)











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