Ecological Dynamics of the Green-lipped Mussel, *Perna canaliculus*, at Ninety Mile Beach, Northern New Zealand

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A thesis submitted in partial fulfillment of the requirements of the Degree of
Doctor of Philosophy in Marine Sciences,
The University of Auckland,
New Zealand

September 2001

ABSTRACT

The New Zealand green-lipped mussel, *Perna canaliculus*, is farmed by an aquaculture industry (> NZ$ 150 million/year) that is dependent on mussel juveniles (spat) collected from unpredictable and unreliable wild sources for more than 80 % of its mussel seed requirements. Most wild-caught spat is collected from the surf zone at Ninety Mile Beach, northern New Zealand, where unique environmental conditions cause the accumulation and transport of spat attached to drift algae, which arrive to the shore in great quantities (up to 100 tonnes at once). This study is the first to investigate the ecology of mussels at Ninety Mile Beach throughout their life history, including reproductive behavior, micro-scale settlement patterns on filamentous macroalgae, accumulation and transport of mussel spat to the shore, colonization of the rocky intertidal, and adult population dynamics. Histologic investigation of 4 intertidal and 2 subtidal populations revealed that females and males were well-synchronized throughout their reproductive cycles, with a prolonged spawning season from June to December, when temperatures were lowest and rising. Comparisons of gonad indices and maximum shell length indicated high productivity in certain populations, which likely contribute to the high larval availability of the area.

Experiments showed that mussel spat preferentially settled on fine-branching natural and artificial substrata, with correlation evident between mussel shell size and degree of branching. Furthermore, greater numbers of mussels settled on node versus internode areas within natural and artificial substrata. Chemical cues for mussel settlement also were studied using phytogel plates spiked with algal extracts, which were preferred over control plates by mussel larvae/post-larvae in the field, and by hatchery-reared larvae in the laboratory.

Three intertidal populations were investigated at different temporal and spatial scales. Mussel concentrations in seawater were higher after spawning for both small mussels (< 0.25 mm) in August, and for larger mussels (> 0.5 mm) in March. Settlement patterns within quadrats cleared of mussels in 2 habitats (adult mussel bed and adjacent areas covered with algae) were studied from July 1999-March 2001. Primary settlement (mussels < 0.5 mm) was found to dominate the algal habitats at the beginning of the spawning season in August, while secondary settlement (mussels > 2.0 mm) was higher in the adult mussel bed late in the spawning season (November-March). Monthly surveys of undisturbed quadrats indicated that a peak in new recruitment coincided with a peak in adult mortality in August. At Scott Point, massive mortality for 2 years in August was followed by a dramatic re-colonization of the empty spaces by juveniles.

Settlement patterns of mussels on suspended ropes in the water column were investigated at 3 water depths inside and outside Ahipara Bay during 2 spawning seasons (1999-2000). Mussel settlement was higher for small mussels (< 0.49 mm) in shallower water (2 m water depth) in August, and higher for larger mussels (> 1.0 mm) at greater depths (18 m water depth) in September-December. Mussels found on shallow-water ropes may have settled directly from the plankton, whereas mussels on ropes near the bottom (18 m) may have transferred from macroalgae tumbling on the seafloor.

Environmental conditions associated with mussel spat arrival to the beach (spatfall events) were studied by statistical analysis (1990-1998; daily, monthly, inter-annually) of wind speed/direction, tidal range, water temperature, swell height/direction, and records of spatfall events/amounts. Spatfall events/amounts were more abundant during days of strong offshore winds. Swell height in the onshore direction was significantly correlated with spatfall events/amounts. Storm events (wind speeds > 20 m/s) were most frequent between May-August; spatfall events/amounts were more numerous 4 months later (September-October). Years with more storm events (El Niño/La Niña episodes) were associated with significantly higher spatfall events/amounts.

ACKNOWLEDGMENTS

To my colleagues...

I am grateful for the constant support and guidance from my supervisors Andrew Jeffs and Bob Creese. I also would like to thank my collaborators Brian McArdle, Brent Copp, Shane Kelly, and Simon Hooker. Henry Kaspar, Kerry Rodgers, Murray Gregory, Bruce Hayward, Neville Hudson, and Marti Anderson often were sources of scientific and philosophical information.

To those who have assisted me...

This research could not have been possible without the amazing technical wizardry and/or field logistics from the Hensley and Morrogh families, Beryl Davy, Vivian Ward, Adrian Nelson, Ian MacDonald, David Todd, Bryony James, and Virginia Toy. My field work was enriched by the company and assistance of Dan Tasker, Mike Collins, Kirsty Hamlin, and Mary Sewell. I also am lucky to have friends who believed in me though this career experience, especially Kim Rush, Bryony James, Kerry Rodgers, and Dan Tasker. To all of you who have encouraged me to finish this degree, and who have helped make New Zealand my home, I thank you. Special thanks to members of the Geology Department who made me feel at home.

To my family...

My sister/friend, Ivana Alfaro, has always known how crazy I really am and still has supported me through my school years. My mother the scientist is the reason why I am submitting this doctoral thesis. Her inquisitive mind and love for nature slowly seeped into my life and created a desire to know and discover. With all my love, I dedicate this research to my mother, who thinks I can do anything. My life has been full of worldly adventures, positive learning experiences, and fascinating endeavors. The best part of this life, by far, is that I get to share it with my partner, Kathy Campbell – the scientist who inspires me, the Pisces who cares for me, the rock that grounds me, and the woman who means the world to me.

When I was a little girl, I saw my father disappear between the rocks in the low intertidal on a receding wave. After what seemed like hours, he re-appeared, running away from what seemed to me a tsunami wave. As he just escaped the wave, by what I thought was magic, I saw a bundle of sea urchins, which he had just collected. That was my first experience with the majestic powers of the sea and the beginning of my love and admiration for its wonders and delicacies.

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CHAPTER 1

General Introduction

The ecology of mussels is highly mediated by biotic and abiotic factors that interact in a variety of ways throughout the life history of a particular species. Numerous studies have focused on specific processes that affect mussels at some stage of their lives (Hunt and Scheibling, 1996; Buchanan and Babcock, 1997; Reusch and Chapman, 1997; Cáceres-Martínez and Figueras, 1998; Gardner, 2000; McQuaid et al., 2000). Some of these factors may involve physical processes such as wave action (Witman, 1987; McQuaid et al., 2000), temperature (Vélez and Epifanio, 1981; Hickman et al., 1991), salinity (Hickman et al., 1991; Dame, 1996), and desiccation (Dame, 1996), and biological factors such as reproductive maturity (Snodden and Roberts, 1997; Darrigran et al., 1999; Myrand and Himmelman, 2000), competition (Newell, 1990; Petraitis, 1995), and predation (Robles et al., 1995; Robles, 1997). Regardless of the particular process in question, most of these physical and biological influences act at various magnitudes within a range of temporal and spatial scales. Consequently, it is evident that the study of mussel ecology must, in the end, take a systems approach, where each major contributing force is given the adequate importance according to how it affects mussels at a given life stage. This multi-disciplinary approach to the study of a particular mussel species not only provides a better understanding of the species throughout its life history in the wild, but also provides important information that can be use for commercial purposes in the harvesting of mussels in the field the successful rearing of mussels in aquaculture farms.

The New Zealand green-lipped mussel, *Perna canaliculus*, supports one of the biggest mussel aquaculture industries in the world. The expanding New Zealand mussel industry produces more than 70,000 tonnes of mussels/ year, which are sold in the world markets (Jeffs et al., 2000). However, one of the weaknesses of the New Zealand mussel industry is the fact that it relies on mussel juveniles (spat) harvested from unpredictable and unreliable wild sources for more than 80 % of their mussel seed requirements (Jeffs et al., 2000). Most of the wild-caught mussel spat is collected, while still attached to drift algae from the surf zone at Ninety Mile Beach, northern New Zealand. The unique oceanographic conditions at Ninety Mile Beach allow for the accumulation of massive quantities of drift algae, covered with spat (up to 100 tonnes of algae with mussel spat) (C. Hensley, personal communication), which are found nowhere else in the country in such quantities. Unfortunately, very little is known about natural mussel populations and the environmental and physiological processes that promote and hinder their success in New Zealand (but see Buchanan and Babchock, 1997; Marsden and Weatherhead, 1999; Gardner, 2000). Thus, the present thesis contribution provides the first comprehensive study of wild mussel populations at Ninety Mile Beach, northern New Zealand. Specifically, this research focuses on 1) the reproductive behavior of the major adult intertidal and subtidal mussel populations, 2) the influences of morphological and chemical cues on settlement patterns, 3) the population dynamics of mussels from larval concentrations in the water column to primary and secondary settlement, recruitment, and mortality rates of the major intertidal populations, 4) the settlement processes of larvae and post-larvae on suspended subtidal ropes, and 5) the effects of wind patterns, tidal range, water temperature, and swell conditions on the arrival of mussel spat to the shore at Ninety Mile Beach.

An extensive histological study of *Perna canaliculus* from 6 intertidal and subtidal populations was conducted to identify patterns in reproductive behavior. Temporal and Spatial patterns were elucidated and evaluated according to their contribution to the massive mussel spat productivity of the area. Sex ratios throughout different size classes, hermaphroditism, parasitism, and shell size to sexual maturity were investigated within all populations. Spawning synchrony and seasonal spawning periods were identified through the reproductive cycle. Furthermore, calculated gonad indices and maximum mussel shell lengths within each mussel population were evaluated within 3 spatial scales; between exposed and sheltered populations, between intertidal and subtidal populations, and among intertidal populations along the 90 km coastal area.

Micro-scale settlement patterns of mussel juveniles were investigated within and among morphologically distinct natural and artificial substrata. Field experiments involved the identification of size-frequency distribution, abundance, and site selectivity of mussels settled on drift algae collected from the surf zone at Ninety Mile Beach. Size- and site-specific selectivity on filamentous substrata of different branching degrees also were investigated in the laboratory with artificial aquarium plants, which mimicked the natural algal and hydroid substrata found in the field.

Chemically-mediated settlement patterns were investigated in the field and the laboratory using algal extracts mixed with phytogel material to make smooth-surface settlement plates. Field experiments tested settlement patterns of wild spat on plates with extracts from 7 preferred algal species and control plates. These experimental gel plates were deployed subtidally (5 m water depth) at Ahipara Bay, Ninety Mile Beach for a period of 2 weeks. Two laboratory experiments tested the effect of chemical cues on settlement of mussel larvae reared at Cawthron Institute hatchery, Nelson, New Zealand, on treatment plates containing extracts from 1-2 algal species and control gel plates at the Leigh Marine Laboratory, The University of Auckland, New Zealand.

Larval availability, primary and secondary settlement, recruitment, and mortality rates were investigated at various spatial and temporal scales in the intertidal zone at Ninety Mile Beach. Larval concentrations in seawater adjacent to 3 intertidal mussel populations were evaluated during a 6-month period just after spawning. Primary and secondary settlement patterns were investigated during short-term (daily) and long-term (monthly) experiments involving manipulated quadrats in the intertidal zone. Short-term experiments involved quantification of settlement rates within cleared areas of all mussels within the adult mussel bed (bare rock) and adjacent algal-covered areas (algae with no mussels). Long-term experiments also tested settlement of mussels within different size classes on cleared quadrats, which contained mesh material as a settlement substratum, in the adult mussel bed and algal band habitats. Recruitment and mortality rates were monitored in each of the 3 intertidal mussel populations through monthly surveys of live and dead mussels within the adult mussel beds.

Direct settlement of mussels from the plankton to suspended ropes in the water column was investigated at Ahipara Bay, Ninety Mile Beach. Mussel spat-collecting ropes were placed at 3 different water depths within subtidal areas (18 m water depth) inside and outside of Ahipara Bay. Abundances of settled mussels within different size classes were compared among depths and between the 2 study sites during 2 spawning seasons in 1999 and 2000. Information on settlement patterns within spat-collecting ropes at Ahipara Bay may be useful to potential commercial harvesting ventures of mussel spat from the wild.

Historical records of wind speed and direction, tidal range, water temperature, and swell height and direction were examined to elucidate daily, monthly, and inter-annual patterns of mussel spat arrival to Ninety Mile Beach between 1990-1998. A statistical approach was use to model the effects of ocean and weather conditions on spatfall events and amounts. Based on the identified patterns within the historical data, possible ecological and oceanographic processes responsible for spat arrival to the shore were proposed.

While this multi-disciplinary study provides valuable information on various aspects of the ecology of *Perna canaliculus* populations at Ninety Mile Beach, it is clear that further research is needed on this mussel species. Future work may be focused on understanding the basic oceanographic processes involved in the transport and accumulation of larvae and juvenile mussels within this dynamic environment. More detailed investigation of subtidal mussel populations, which were shown to be highly productive, may be of great importance to potential conservation needs. Research on identifying and quantifying algal populations that provide the bulk of the drift material may be of critical importance to further understanding of temporal and spatial variability of spat arrives to the shore. Finally, the commercial feasibility of using spat-collecting ropes to harvest wild mussel spat may be evaluated, and may be utilized as a complementary source of mussel spat. Attention to these future research avenues should be promoted and supported by the mussel industry and other funding institutions if the

New Zealand mussel industry is to continue to be a leading revenue producer for this country and a food staple provider to the world.

CHAPTER 2

Reproductive Behavior of the Green-lipped Mussel, *Perna canaliculus*, in Northern New Zealand.

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In press: Bulletin of Marine Science

ABSTRACT

Wild populations of mussels, *Perna canaliculus,* in northern New Zealand supply the majority of seed mussels to the >70,000 tonnes per annum green-lipped mussel aquaculture industry. However, surprisingly little is known about the reproductive cycle in this mussel species or in these northern populations at Ninety Mile Beach. An extensive histological study of *Perna canaliculus* found that their reproductive biology was similar to that recorded for other mussels. The mussels were dioecious with a 1:1 sex ratio throughout all sizes; only one hermaphrodite individual was found. Mussels began to mature from 27 mm shell length, and by 40-50 mm, most individuals were sexually mature. Both female and male mussels appeared to have a consistent gonad cycle of gamete development, discharge, and redevelopment. Both sexes were well-synchronized reproductively, with a prolonged spawning season from June to December (Austral winter-spring) when water temperatures were at their lowest and rising. However, a small proportion of mussels was found spawning ripe gametes throughout the year, which could account for the continuing appearance of mussel seed outside the main spawning season. The spawning-spat catching season is more extensive at Ninety Mile Beach than has been recorded in more southerly parts of New Zealand, and these differences may be related to the generally warmer water conditions recorded in northern areas.

Key words: Mussels, Reproductive cycle, *Perna*, Bivalves, Histology, Gonad index

INTRODUCTION

Knowledge of reproductive patterns of natural mussel populations is important for mussel aquaculture, which in New Zealand depends entirely on wild-caught seed. For example, the frequency and duration of spawning events may be used to predict spat settlement and spatfall events within a particular population. However, there are great geographical and seasonal variations in reproductive cycles within mussel populations (Newell et al., 1982; Snodden and Roberts, 1997), and reproductive patterns cannot be generalized from one population to another. There is limited published data on the reproductive cycle of the New Zealand green-lipped mussel, *Perna canaliculus*, except for indirect observations on spat settlement (Greenway, 1975; Meredyth-Young and Jenkins 1978; Buchanan, 1994; Buchanan and Babcock, 1997), body condition index (Flaws, 1975; Hickmanand Illingworth, 1980; Buchanan, 1998), and initial histological work by Flaws (1975), Tortell (1976), and Buchanan (1998). The full gametogenic cycle of the genus *Perna* has been well studied in tropical regions (Virabhadra Rao et al., 1975; Walter, 1982). Several investigations report on the reproductive cycles of various temperate species of *Perna*, and most have used indirect methods such as larval appearance in the plankton (Booth, 1977), and settlement of spat (Greenway, 1968; 1969; 1975; Zaouali, 1973; Berry, 1978; Abda-Boudjema and Mouèza, 1981). These methods do not provide the precise assessment of mussel gonad development that can be attained with histological sections of gonad tissues (e.g., as for Moroccan *Perna* species in Shafee, 1989). In conjunction with environmental measurements such as water temperature and nutrient availability, histological gonad sections can provide information about the influence of exogenous and endogenous factors affecting the initiation and duration of various stages in the gametogenic cycle (Vélez and Epifanio, 1981; Newell et al., 1982; Nichols, 1996). For dioecious species with external fertilization such as mytilids, examination of histological sections may elucidate sex ratios, hermaphroditism, and level of gamete synchrony in the population (Brousseau, 1982; Jasim and Brand, 1989; Villalba, 1995).

Ninety Mile Beach, North Island, New Zealand, is the main source of wild mussel spat for commercial farms in Marlborough Sounds, South Island. About 100,000 tonnes/year of mussel spat, attached to seaweed, are collected from Ninety Mile Beach and transported about 1,000 kilometers to farms in Marlborough Sounds, where they provide about 80% of mussel farm spat requirements (Jeffs et al., 2000). However, the detailed reproductive cycle of wild populations of mussels at Ninety Mile Beach is largely unknown. Buchanan (1998) investigated the reproductive condition in *Perna canaliculus* at French Pass, Marlborough Sounds, with the aim to compare histological and visual techniques that could be used to measure mussel condition in farms. However, no other studies have focused on the reproductive patterns and potentials of the wild mussel populations that provide the bulk of seed mussels to the farms. The present study investigates the reproductive cycle of *Perna canaliculus*, the major commercial shellfish product of New Zealand, through histological sections of gonad tissues, which were prepared and analyzed from natural intertidal and subtidal green-lipped mussels from the main spat-source region of Ninety Mile Beach, northern New Zealand. Results are provided on the reproductive behavior of mussels from 6 sites along the 90 kilometer length of Ninety Mile Beach. More specific comparisons of reproductive variability among sites are presented elsewhere (Alfaro et al., in preparation).

METHODS AND MATERIALS

Mussel specimens were gathered for histological analysis from a total of six sites at Ninety Mile Beach, in northern New Zealand (Fig. 1). Collections from four rocky intertidal sites at Tonatona Beach, Ungaunga Bay, The Bluff, and Scott Point represented the sum total of all major intertidal mussel populations that occur along Ninety Mile Beach. Two subtidal sites at Wizard Rock and Blue House were chosen for additional sampling because these were the only subtidal populations known at the outset of the study (Fig. 1). Temperature records were obtained from a data logger placed 0.5 m below low water level at the south end of the study area at S 35°10.8' and 173°5.3' E.

Approximately 70 adult mussels (62-114 mm in length) were collected monthly from each of the six sites, for a total of about 420 mussels sectioned per month. Sampling took place from July 1998 to April 2000, with 21 months sampled. Exceptions to this regular sampling scheme took place only when weather conditions prevented access to the sites. In addition, 96 juvenile mussels (3-60 mm in length) were collected on 8 July 1998 and 24 April 2000 to determine the minimum size at sexual maturity. Intertidal mussels were collected haphazardly during low tide and subtidal mussels were dredged when weather conditions permitted. Immediately after collection, the mussels were sectioned dorsoventrally through the mid-body and fixed in Bouin's solution. Mussel tissues were embedded in paraffin, sectioned with a microtome at 5-7 μm, and stained with Haematoxylin-Eosin. The histological sections were viewed under a compound microscope to identify sex and stage of gametogenic development. Gonad developmental stages were identified for each sex according to a modified classification scheme based on Shafee (1989). Gonad tissues mostly were uniform in their stage of development, and mussels were assigned a developmental stage according to the state of the majority of the follicles in the gonad tissues. The presence of hermaphroditism and parasitism was recorded throughout the sampling period.

A 1:1 sex ratio in the mussels was tested with a Chi-square, goodness-of-fit test. Gonad indices were calculated according to King et al. (1989) and Galinou-Mitsoudi and Sinis (1994) with the following formula:

$$\text{G.I.} = \frac{\text{(number in each stage) (rank of stage)}}{\text{total sample size}} \times 100$$

where the rank system was:

Resting stage	0
Early development stage	1
Late development stage	2
Ripe stage	3
Spawning stage	2
Redevelopment stage	2

Spent stage	1

Frequency distribution graphs, including all developmental stages, were constructed to identify seasonal patterns of gametogenic and breeding activities.

RESULTS

Examination of gonad tissues of female and male mussels allowed delineation of six distinct development stages for each sex (Figs. 2 - 5). An indeterminate stage was recorded for mussels which showed no signs of follicle development in the tissues sectioned.

Female Gonad

Early developing stage (Fig. 2A & B): Small groups of germinal cells are scattered in the mantle. The follicles are irregular in size. Oogonia line the follicle wall. Mostly small, irregular-shaped oocytes bulge from the follicle wall. A few large oocytes are attached to the follicle wall by a cytoplasmic stalk. Oocyte nuclei are large and clear.

Late developing stage (Fig. 2C & D): The follicles are larger and more numerous than in previous stage. Oocytes have begun to accumulate yolk and have grown considerably. Early oocytes are still attached to the follicle wall by a slender stalk of cytoplasm. Some mature oocytes are free in the lumen. Oocyte nuclei are enlarged.

Ripe stage (Fig. 2E & F): The mantle is nearly filled with follicles. Most oocytes have reached maximum size, have become free from the follicle wall, and are now packed in the lumen. Oocytes have become compressed inside the follicle.

Spawning stage (Fig. 3A & B): A great number of ripe oocytes are still present in the expanded follicles. However, there is a reduction in the density of gametes which have left numerous empty spaces in the lumen. Some follicles have ruptured and a few oocytes may be left.

Redeveloping stage (Fig. 3C & D): Follicles do not occupy all the available mantle area. Remaining oocytes are arranged loosely in the follicle. New oocytes are visible along the follicle wall. More connective tissue is evident in this stage than before initial spawning.

Spent stage (Fig. 3E & F): Follicles collapse and degenerate. Amoebocytes attack unspawned gametes, often resulting in the lumen of the follicle becoming filled with a mass of cellular debris.

Male Gonad

Early developing stage (Fig. 4A & B): Small groups of germinal cells are scattered in the mantle. The follicles are often small and elongate. Spermatogonia line the follicle wall. The follicles start to fill with spermatocytes and spermatids. A few spermatozoa can be seen in the middle of the lumen.

Late developing stage (Fig. 4C & D): The follicles occupy a large portion of the mantle. Wide concentric layers of spermatogonia, spermatocytes, and spermatids are evident. Spermatozoa are apparent in the lumen, but they are not well organized.

Ripe stage (Fig. 4E &F): The mantle is nearly filled with follicles. A thin layer of spermatogonia line the follicle wall, although in some follicles this layer is not visible. Spermatocytes and spermatids are less apparent. Spermatozoa are clear and neatly arranged in layers, converging at the center of the lumen.

Spawning stage (Fig. 5A &B): A dense band of ripe spermatozoa is still present. The spermatozoa are less organized in a partially empty lumen. Very few or no spermatocytes and spermatids remain.

Redeveloping stage (Fig. 5C & D): Densely staining bands of spermatids give rise to new lamellae of spermatozoa, although gaps within the follicles are still present. Large follicles do not occupy all the available mantle area. More connective tissue is evident in this stage than before initial spawning.

Spent stage (Fig. 5E & F): Follicles collapse and degenerate. Amoebocytes attack unspawned gametes, often resulting in the lumen of the follicle becoming filled with a mass of cellular debris.

Reproductive Cycle

Maximum shell length measurements of adult mussels showed no differences in mean shell lengths between female and male individuals. The range of shell length for both female and male mussels was the same at 70-145 mm, and the mean (± SE) for each sex was 91±12 mm. Furthermore, similar numbers of females to males were found within the samples of adult mussels ($X^2 = 0.34$, $p > 0.05$).

Histological examination of small mussels (3-69 mm in length), from both intertidal and subtidal populations, indicated that about 50% of mussels from about 27 mm in length contained identifiable gonad tissues (Table 1). A Chi-square test for all female and male mussels between 3-69 mm in length indicated no statistical difference from a 1:1 sex ratio ($X^2 = 2.00$, $p > 0.05$). Both sexes were equally represented within the mussel size range, which suggests that female and male mussels mature at about the same size.

The gonad index analyses suggest that female and male mussel reproductive cycles were well synchronized across all sites (Fig. 6). A two-way ANOVA comparing gonad indices between all female and male mussels for the interval from July 1998 to April 2000 (sex and month as factors) showed no statistical difference in reproductive state between sexes (ANOVA; $F_{(1,134)} = 0.003$, $p > 0.05$) and the interaction (ANOVA; $F_{(19,134)} = 0.007$, $p > 0.05$), but highly significant monthly differences among sampling periods (ANOVA; $F_{(19,134)} = 6.119$, $p < 0.05$) (Fig 6).

The frequency distribution of all reproductive stages indicated a similar seasonal trend for female and male mussels (Figs. 7&8). Generally, gonad development started in December, with the early stage becoming increasingly dominant until around February. The late stage of development predominated in March. By April, mussels in the ripe stage became more numerous, and these were most abundant in May. The number of ripe mussels continued to be high through August-September. Spawning appears to have begun in June-July, with spawning continuing through December. Redevelopment of gonad tissue was present throughout the year, but was most significant from August to December (Austral winter-spring). No major inter-annual variations were observed between the 1998, 1999, and 2000 reproductive cycles. The number of mussel gonads in the resting stage of development was similar for female and male mussels. These resting gonads were more abundant (7±4%) from January to March, which is when high numbers of gonads were in the early stage of development. During the rest of the year, the percentage of resting gonads fluctuated between 0 to 4%.

Only one hermaphrodite mussel was found among 6720 mussels examined. The mean (± SE) number of parasitized mussels per site per month was 3.6±5.3 mussels, but with > 30% of parasitized mussels within a single monthly sample. Parasitized mussels were most common in samples taken in October 1999, July 1998, and April 2000. Two different parasites were found in the samples; *Bucephalus* sp. and *Nematopsis* sp., were equally abundant in the number of mussels they infested (66 and 57 respectively, of the 6720 mussels). No differences were observed in the level of parasitism between female and male mussels ($X^2 = 1.72$, $p > 0.05$), although in most cases the sex was not identifiable.

Water temperature records at Ninety Mile Beach ranged from 14 °C in winter to 22 °C in summer and had a mean (± SE) of 17±2 °C throughout the sampling period (Fig. 6).

DISCUSSION

Understanding the reproductive patterns of the wild mussel populations at Ninety Mile Beach is particularly important because their spat production is of considerable commercial importance to the extensive New Zealand mussel farming industry. Reproductive cycles of local mussel populations, together with oceanographic data (i.e. ocean currents, tidal range, and upwelling dynamics) and weather information (i.e. wind and temperature), may allow for temporal and spatial predictions of both spatfall events and the health of adult source populations.

The 1:1 sex ratio and synchronized reproductive development between sexes throughout the year in intertidal and subtidal populations at Ninety Mile Beach have been observed in other *Perna canaliculus* populations in New Zealand (Flaws, 1975; Tortell, 1976; Buchanan, 1998), and is found among other mussel species (Heffernan and Walker, 1989; Villalba, 1995; Nichols, 1996; Darrigran et al., 1999). Furthermore, no differences in maximum shell length, nor size at maturation, were found between females and males. These results suggest that female and male *Perna canaliculus* respond to similar spawning cues to ensure maximum chances of fertilization and larval production.

The shell length at onset of sexual maturity for wild mussel populations at Ninety Mile Beach appears to be around 27 mm, which indicates early development of gonad tissue. Hermaphroditism was rare, as in other wild mussel populations (Sunila, 1981;Villalba, 1995). By contrast, up to 5% hermaphroditism has been found in farmed mussels in Coromandel that were sourced from the same Ninety Mile Beach spat (Alfaro et al., unpublished). The overall level of parasitism of the mussel gonads was 3%, but differences were observed among the six sites (Alfaro et al., in preparation).

Gonad indices that are based on gonad developmental stages have been used extensively as a quantitative way to identify the larval/spat production of shellfish populations, and to compare results from different studies (Gabbott and Bayne, 1973; Kautsky, 1982; Brown, 1988; Borcherding, 1991). Results from Ninety Mile Beach gonad indices indicate that the potential production of larvae is low from about October to February, and productivity is highest in April-May.

The reproductive cycle of *Perna canaliculus* at Ninety Mile Beach reveals a spawning season starting in June and continuing through December. Together, the extended spawning season, and the large percentage of ripe and redeveloping mussels through most of the year, suggest that gonad production in mussel populations at Ninety Mile Beach is occurring in optimal environmental conditions. Prolonged reproductive periods have been observed in other mussel populations in tropical and subtropical waters (Lubet, 1981; Lee, 1986), but marked differences in the timing and frequency of spawning events have been reported in other mussel populations, even within the same species (Flaws, 1975; King et al., 1989; Villalba, 1995; Nichols, 1996). The prolonged spawning season of *Perna canaliculus* at Ninety Mile Beach greatly differs from the two spawning periods (early summer and autumn-spring) observed six degrees latitude to the south in Marlborough Sounds, New Zealand (Flaws, 1975; Tortell, 1976; Buchanan, 1998).

Water temperature has been suggested to be one of the most important factors responsible for spawning in marine bivalves (Kautsky, 1982; Newell et al., 1982; Brown, 1988; Dame, 1996). Rapid temperature changes (up or down) have been observed to trigger spawning events in many bivalves, including mussels (Newell et al., 1982; Hawkins et al., 1985; Grant, 1994; Hooker and Creese, 1995; Nichols, 1996). Furthermore, marked differences in spawning behavior have been attributed to regional climatic differences from one population to another (Shafee, 1989). In general, warm water mussels spawn throughout the year according to sudden climatic fluctuations such as favorable temperature changes (opportunistic behavior), whereas in temperate regions, gonad development and spawning are continuous through a season or conservative in behavior (Shafee, 1989). In the present study, spawning activity started in June-July, which corresponds to water temperatures of about 15 ºC, a value close to the lowest temperatures of the year (Figs. 6-8). Spawning continued through the warmer months in spring, until December, when water temperatures reached their highest values of 18-20 ºC. A factor that contributes to the extended spawning season of *Perna canaliculus* at Ninety Mile Beach is that water temperature rarely drops below 14 ºC, which is well above the temperature range (10-12 ºC) at which larval production ceases for other mussel species (Fraleigh et al., 1993; Nichols, 1996). Mean water temperatures in Marlborough Sounds of 10-11 ºC in winter and 20-21 ºC in summer (Tortell, 1976; Jenkins, 1985) may account for the observed differences in spawning patterns of mussels between these warmer northern and cooler southern regions of New Zealand. Thus, the shorter spawning intervals of Marlborough Sounds populations appear to be constrained by the relatively cooler climatic conditions they experience. Conversely, the less marked seasonality in reproductive cycle of the northern populations may be a result of the warmer subtropical climate of the area. Results from this study confirm that reproductive variability is great from one region to another in New Zealand, and that generalizations about the seasonal reproductive behavior may not be appropriate for this mussel species.

The presence of a clear redeveloping stage in Ninety Mile Beach mussels suggests that multiple spawning events take place throughout the year, and implies high reproductive output in these mussel populations. This potential high productivity, together with the prolonged spawning season from winter to spring, is consistent with the observation that Ninety Mile Beach has the highest wild spat abundances in the country (Jeffs et al., 2000). Finally, the extended spawning period of *Perna canaliculus* at Ninety Mile Beach has significant ecological implications for the maintenance of mussel populations in northern New Zealand. A better understanding of the factors that control spawning allows elucidation of geographic differences among regions, and may help overcome current difficulties in conditioning and spawning mussels in commercial hatcheries.

ACKNOWLEDGMENTS

We thank B. Davy for her invaluable assistance with processing of histological sections. The Morrogh and Hensley families, K. Hamlin, and D. Tasker helped in the field. B. Diggles identified parasites. K. Rodgers, K. Campbell, and B. James provided technical and editorial expertise. We also thank B. Creese, S. Genovese, and an anonymous reviewer for their helpful comments on this manuscript. Funding for this project was granted by the New Zealand Foundation for Research, Science and Technology.

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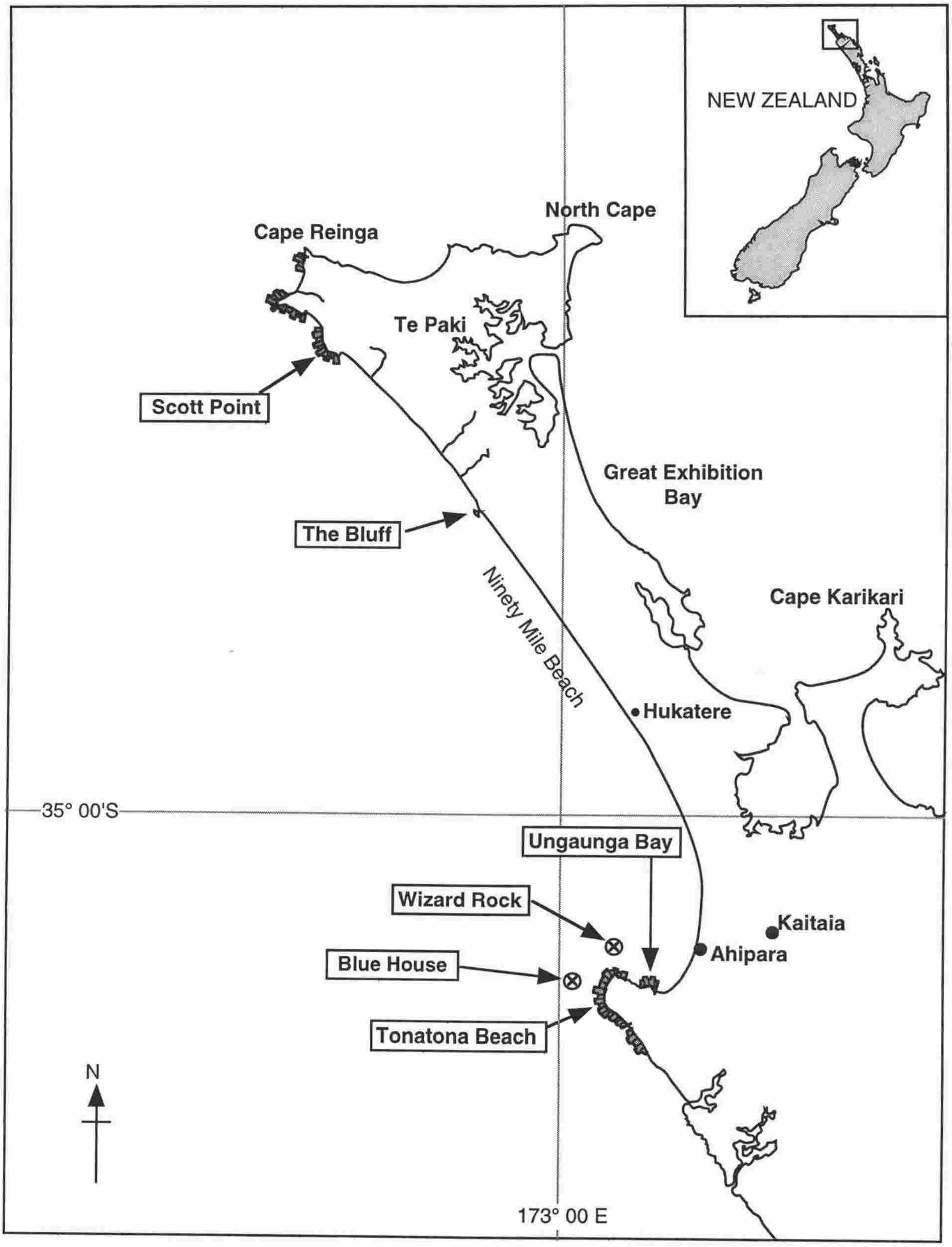

Figure1. Map of the study area at Ninety Mile Beach, northern New Zealand. Four intertidal collection sites are Tonatona Beach, Ungaunga Beach, The Bluff, and Scott Point. Two collection sites are Blue House and Wizard Rock.

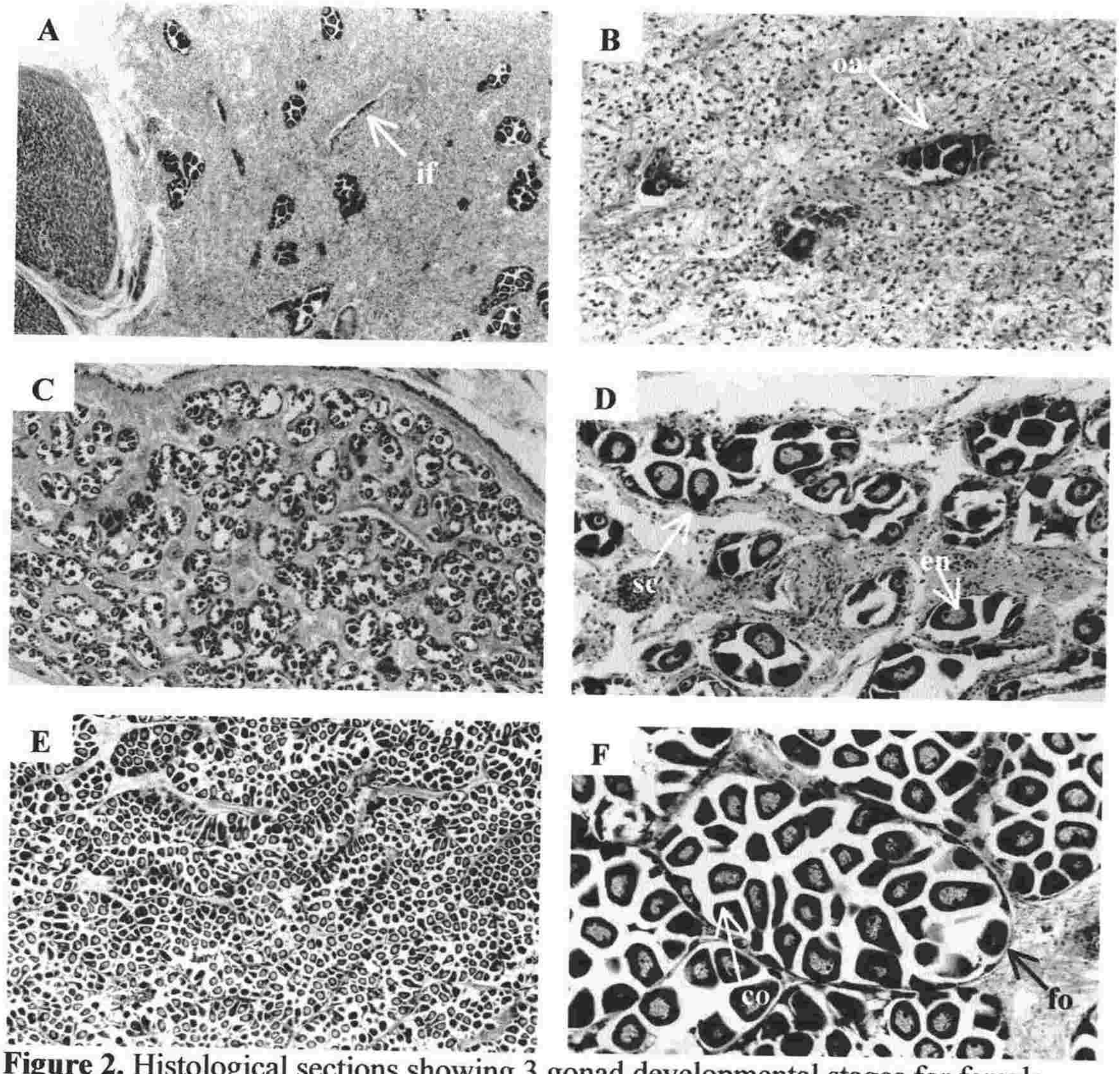

Figure 2. Histological sections showing 3 gonad developmental stages for female mussels. A) Early stage showing irregular follicles (if) with small oocytes; 4x, and B) oocytes attached to follicle wall (oa); 16x. C) Late stage of development showing larger follicles; 4x. D) stalk of cytoplasm (sc) between oocyte and follicle wall, and enlarged nuclei (en); 16x. E) Ripe stage with oocytes covering mantle area; 4x, and F) compressed free oocytes (co) inside follicles (fo); 16x.

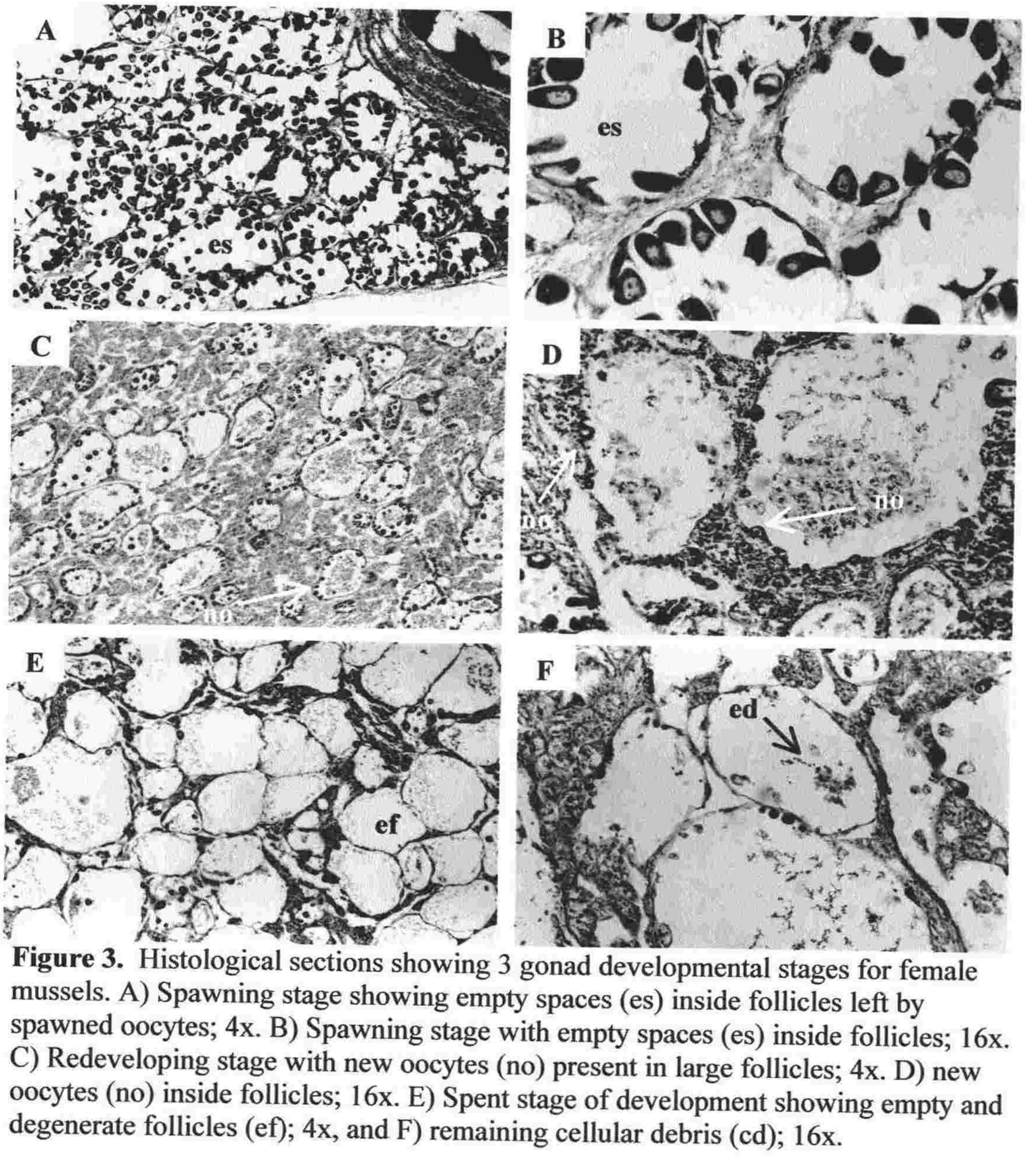

Figure 3. Histological sections showing 3 gonad developmental stages for female mussels. A) Spawning stage showing empty spaces (es) inside follicles left by spawned oocytes; 4x. B) Spawning stage with empty spaces (es) inside follicles; 16x. C) Redeveloping stage with new oocytes (no) present in large follicles; 4x. D) new oocytes (no) inside follicles; 16x. E) Spent stage of development showing empty and degenerate follicles (ef); 4x, and F) remaining cellular debris (cd); 16x.

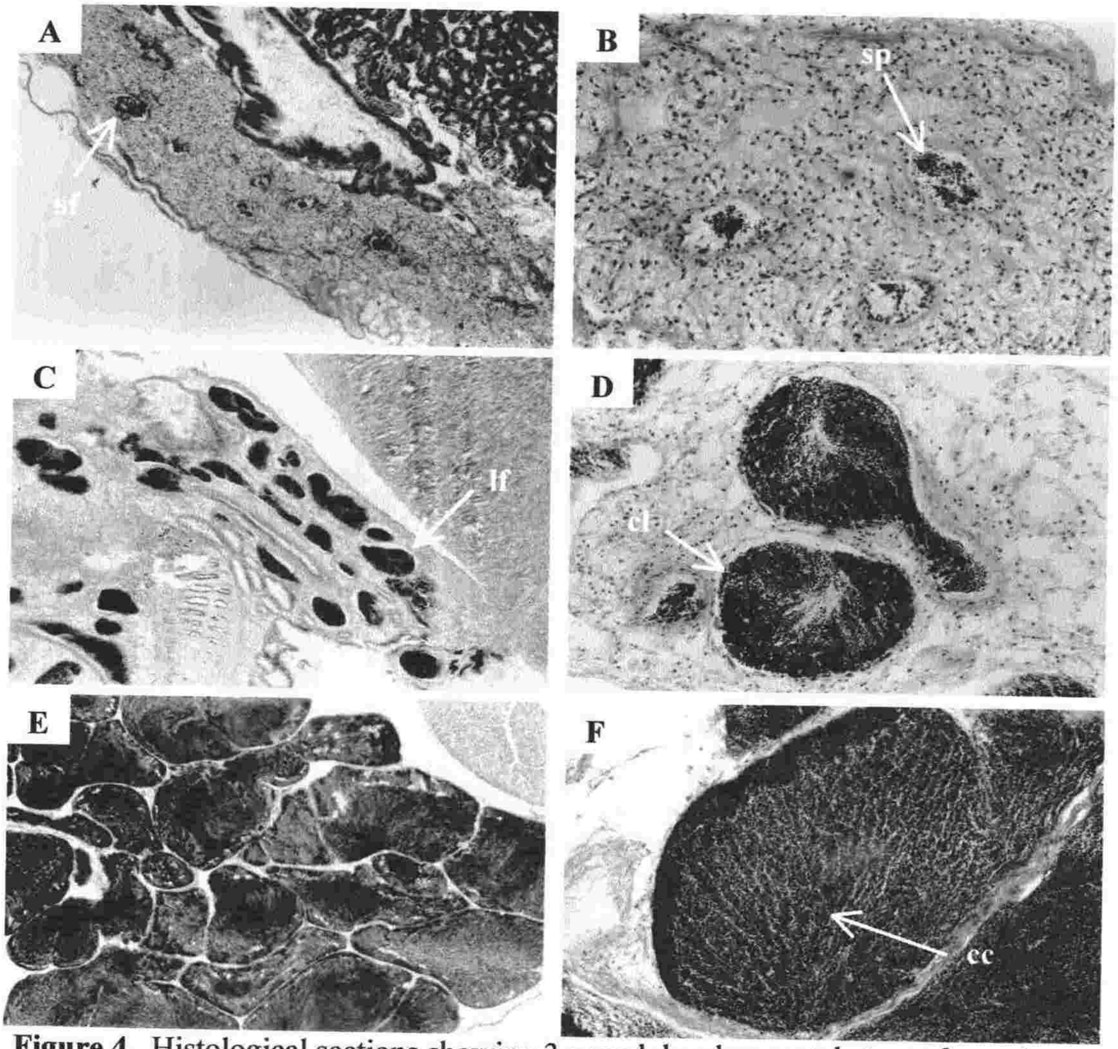

Figure 4. Histological sections showing 3 gonad developmental stages for male mussels. A) Early stage of development with small follicles (sf); 4x, and B) spermatogonia inside follicles (sp); 16x. C) Late stage showing larger follicles (lf); 4x, and D) concentric layer (cl) of spermatogonia; 16x. E) Ripe stage showing mantle filled with follicles; 4x, and F) spermatozoa converging at the center of the lumen; 16x.

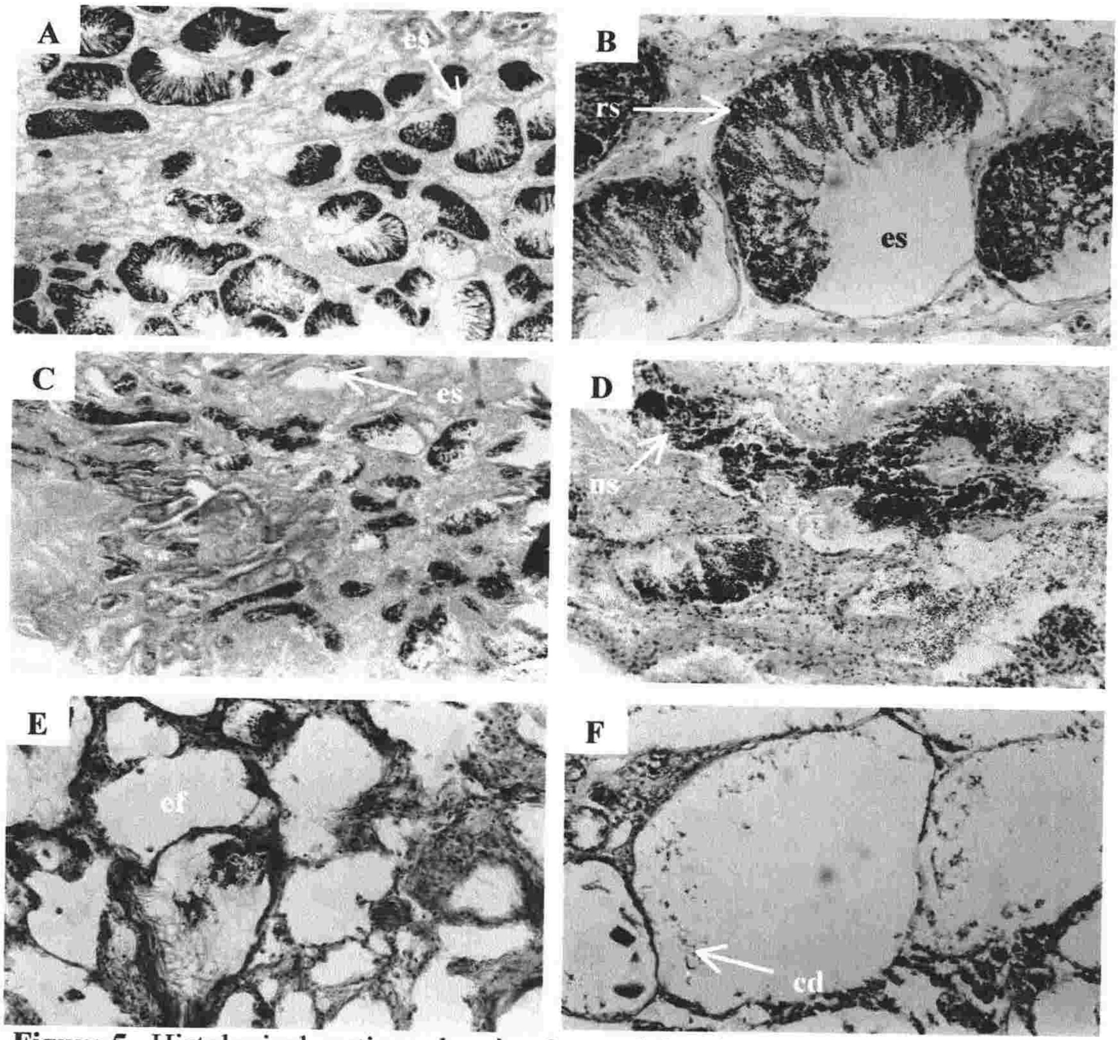

Figure 5. Histological sections showing 3 gonad developmental stages for male mussels. A) Spawning stage of development showing empty spaces (es) inside follicles after ejection of spermatocytes; 4x, and B) some ripe spermatozoa (rs) are still present; 16x. C) Redevelopment stage showing empty spaces (es) inside follicles; 4x, and D) new spermatids (ns) forming. E) Spent stage with empty follicles (ef); 4x, and F) cellular debris (cd) left inside follicles after spawning; 16x.

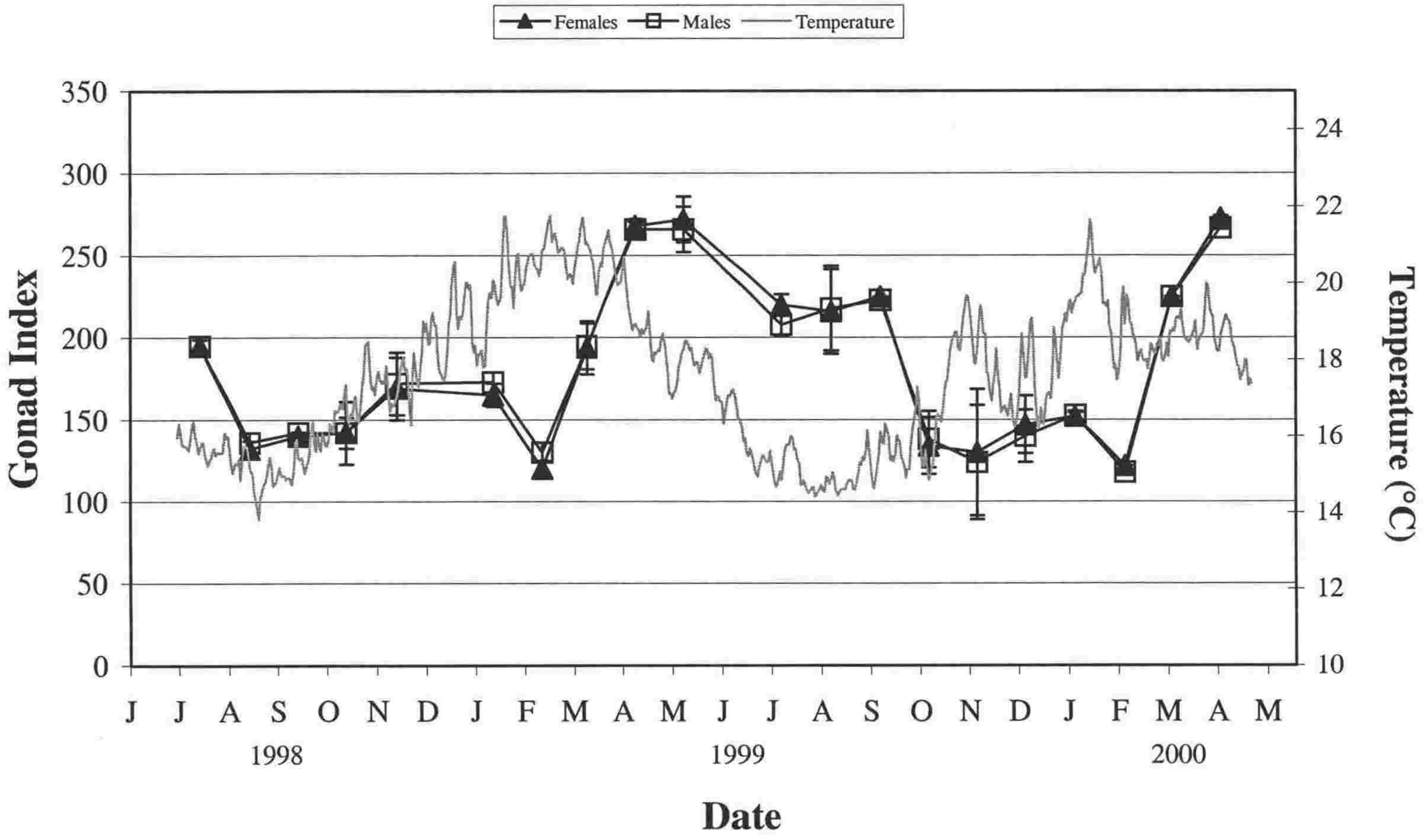

Figure 6. Mean (± SE) gonad indices for female and male mussels (combined data from 6 sites) and water temperature records for Ninety Mile Beach, northern New Zealand between July 1998 and April 2000.

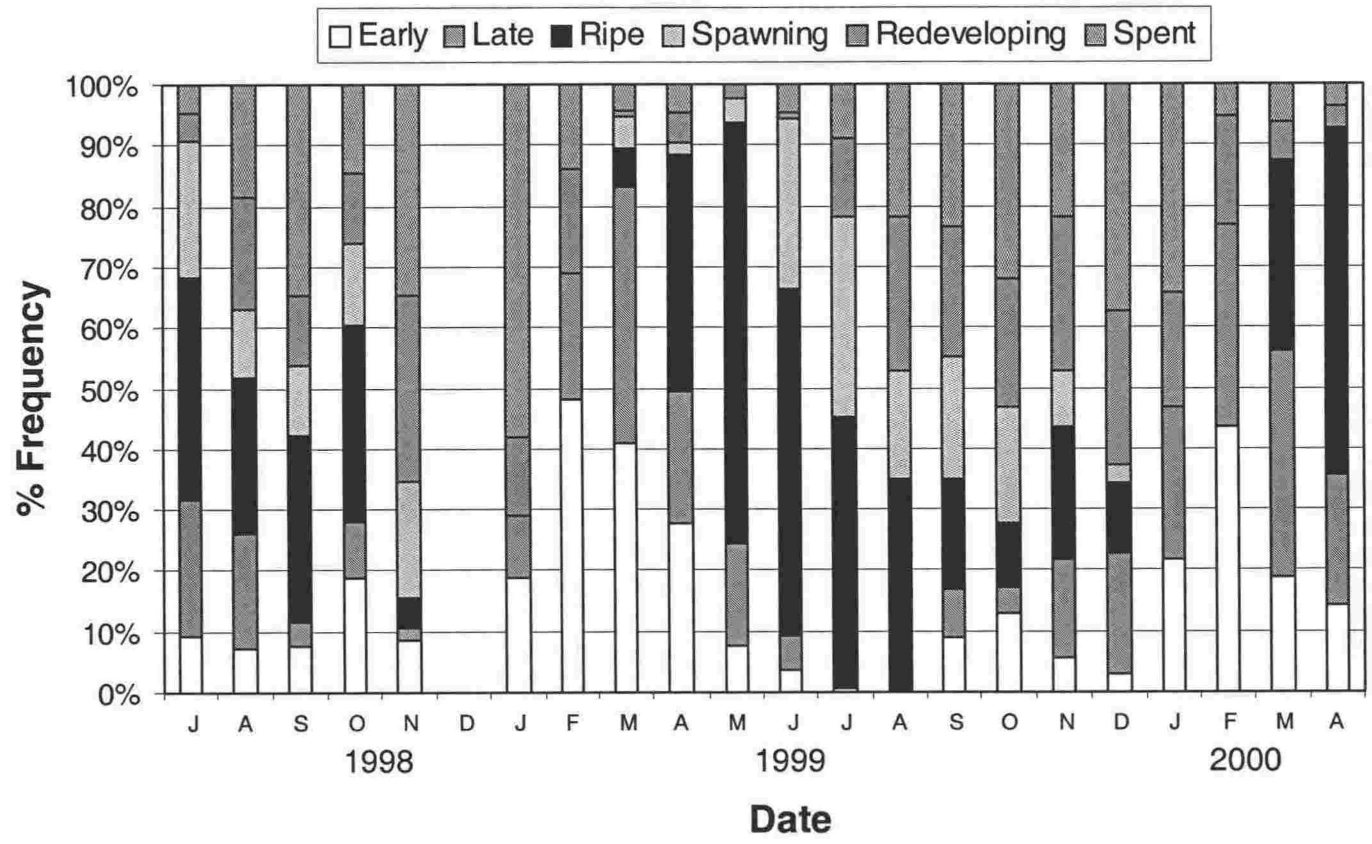

Figure 7. Percent frequency of the six female gonad developmental stages in the monthly samples from July 1998 to April 2000.

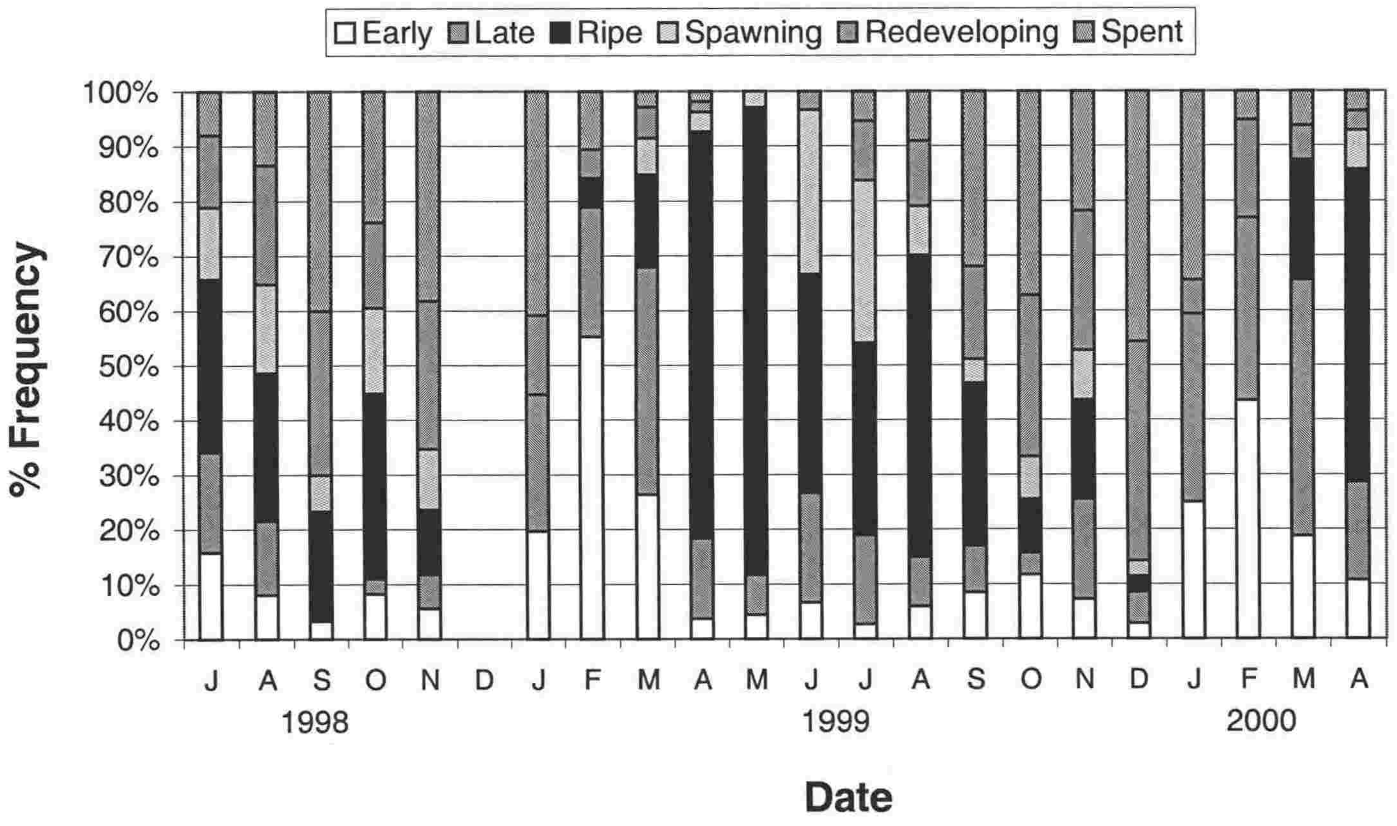

Figure 8. Percent frequency of the six male gonad developmental stages in the monthly samples from July 1998 to April 2000.

Table 1. Numbers and percentages of mussels (3-69 mm in length) within 7 size classes.

Size Range (mm)	Total Number	Number with Gonads (%)	% of Total
3-9	11	0	0
10-19	16	0	0
20-29	16	5 (31)	10
30-39	17	12 (71)	24
40-49	15	14 (93)	28
50-59	12	11 (92)	22
60-69	9	8 (89)	16
Total	96	50 (52)	100

CHAPTER 3

Spatial Variability in Reproductive Behavior of Green-lipped Mussel Populations of Northern New Zealand

Andrea C. Alfaro, Andrew G. Jeffs, and Simon H. Hooker

In review: Marine Biology

ABSTRACT

The reproductive behavior of 4 intertidal and 2 subtidal mussel populations were investigated within 3 spatial scales at Ninety Mile Beach, northern New Zealand, where large quantities of seed mussels are collected for aquaculture. Reproductive efforts were compared between exposed and sheltered populations, between intertidal and subtidal populations, and among intertidal populations along a 90 km coastal area. Histological sections of mussel gonads were used to identify the reproductive state of individual mussels collected monthly between July 1998 and April 2000. Gonad indices were calculated for entire population each month at each site. Frequency distributions of different gametogenic stages were plotted and differences in reproductive cycle among populations were identified. Mussel shell sizes were directly related to gonad indices and to percent ripe and spawning mussels within each population. While all intertidal and subtidal populations had extremely similar temporal variations in reproductive behavior, spatial patterns among various sites revealed clear differences in reproductive effort among populations. In particular, mussel shell size, gonad indices, and reproductive efforts were higher at exposed versus sheltered intertidal sites, and were higher for subtidal sites compared to their intertidal counterparts. Among intertidal mussel

populations, the northernmost population had the highest maximum shell length, gonad indices, and percent ripe and spawning individuals, followed by 2 populations at the southern end of Ninety Mile Beach. A small mid-beach mussel population had the smallest mussels with lowest gonad indices and few spawning mussels during the reproductive season. A prolonged spawning period was observed within the most productive populations (2 subtidal populations at the south end, and one intertidal population at the north end of the beach) between June-December. However, the reproductive cycle of 2 intertidal populations at the south end of the beach indicated 2-3 spawning events during the same period. Differences in mussel shell size and reproductive effort among sites are likely to be related to variations in environmental conditions throughout Ninety Mile Beach.

INTRODUCTION

The biology of the commercially important green-lipped mussel, Perna canaliculus, has received considerable interest in recent years, in part because the New Zealand aquaculture industry cannot produce sufficient hatchery spat to stock the mussel farms. Thus, the industry has continued to depend on the >140,000 tons/year of wild mussel spat (attached to macroalgae) collected from Ninety Mile Beach, in northern New Zealand (Jeffs et al., 2000). However, understanding the basic biology of natural mussel populations is critical if mussel spat are to be utilized reliably in terms of their availability and arrival to coastal areas along Ninety Mile Beach. The reproductive behavior of Perna canaliculus has been investigated for mussel farm populations in Marlborough Sounds (Flaws, 1975; Tortell, 1976; Hickman et al., 1991; Buchanan, 1998) and wild populations at Ninety Mile Beach (Alfaro et al., in press). However, differences in environmental conditions, such as water temperature, salinity, and food availability, make generalizations from one population to another difficult (Newell et al., 1982; Hickman et al., 1991; Snodden, 1997). The temporal variability in reproduction of mussels at Ninety Mile Beach, where the majority of the country's mussel spat is collected, has been investigated previously (Alfaro et al., in press). However, spatial variability in reproduction of mussel populations along the 90-kilometer coastal stretch, as described herein, provides important additional information as to the future sustainability of wild spat production from Ninety Mile Beach.

An in-depth study of the reproductive behavior of various mussel populations within a given geographical area can provide valuable information on variability of reproductive efforts at different spatial scales. This information then can be used to predict patterns of spatfall supplies to coastal areas, which can be utilized for commercial purposes. One way to quantify the reproductive efforts of a population is by using a gonad index as a standardized measure of the energy allocated to reproduction (Kautsky, 1982; Brown, 1988; King et al., 1989; Borcherding, 1991; Galinou-Mitsoudi and Sinis, 1994). Seasonal variations in reproductive cycle can be obtained and compared among populations, by quantifying the frequency of mussels within various reproductive stages in the populations at a given time (Kautsky, 1982; Shafee, 1898; Villalba, 1995; Nichols, 1996).

The aim of this study is to investigate differences in reproductive efforts of mussel populations within 3 spatial scales along Ninety Mile Beach. Reproductive patterns of 4 intertidal and 2 subtidal adult mussel populations are examined and evaluated as to their contribution to the massive spat production at Ninety Mile Beach, northern New Zealand.

MATERIALS AND METHODS

Six geographically distinct mussel populations likely to be affected by different environmental conditions were identified at Ninety Mile Beach, northern New Zealand. Four rocky intertidal mussel populations were located at Tonatona Beach, Ungaunga Bay, The Bluff, and Scott Point. Two subtidal populations were found at Wizard Rock and Blue House (Fig. 1). The Tonatona Beach population is exposed to strong swells from the northbound Westland current, while the mussel population at Ungaunga Bay is slightly more sheltered from strong wave action by its position inside Ahipara Bay (Fig. 1). These 2 southern intertidal populations also experience periodic sediment load disturbances from redistributed nearby sands. A mussel population at The Bluff also is exposed to high wave action and sand load disturbances. The northernmost population at

Scott Point experiences strong hydrodynamic regimes, but because of the extensive rock cover, the sediment load appears to be low in comparison with the other intertidal populations. The subtidal populations investigated in this study, Wizard Rock and Blue House, are located about 8 km apart near Ahipara Bay, and are in 13 and 15 m water depth, respectively (Fig. 1).

Histological analyses were made of mussel specimens from the 6 sites at Ninety Mile Beach. Approximately 70 adult mussels (50 to 145 mm in greatest length) were collected monthly from each of the 6 sites. Mussel collections were not possible during certain months due to poor weather conditions, or during months when collections were prohibited by cultural traditions of native Maori land owners. Sampling took place from July 1998 to April 2000, with 21 months sampled in at least one site per month. Intertidal mussels were collected haphazardly during low tide, whereas subtidal mussels were dredged when weather conditions permitted. Immediately after collection, the mussels were measured across their greatest shell length, sectioned dorsoventrally through the mid-body, and the tissues fixed in Bouin's solution. Mussel tissues were histologically processed and the resulting slides were analyzed under a microscope according to techniques developed for this species (Alfaro et al., in press). Gonad indices for each population were calculated following King et al. (1989), and Galinou-Mitsoudi and Sinis (1994), using the following formula:

$$\text{G.I.} = \frac{\text{(number in each stage) (rank of stage)}}{\text{total sample size}} \times 100$$

where the scoring system was:

Resting stage	0
Early development stage	1
Late development stage	2

Ripe stage	3
Spawning stage	2
Redevelopment stage	2
Spent stage	1

Frequency distribution graphs, including all developmental stages, were constructed to identify differences in gametogenic activity among the 6 sites investigated.

RESULTS

Mussel Shell Length

Maximum shell length measurements of adult mussels from intertidal and subtidal sites at Ninety Mile Beach indicatedin marked differences in mean maximum shell length among mussels from the 6 different sites. Generally, subtidal mussels were larger than intertidal mussels, mussels from Scott Point were consistently larger than mussels from all other intertidal sites, and The Bluff had the smallest mussels of any site at Ninety Mile Beach throughout the study period (Fig. 2). Mean (±SE) maximum shell lengths for Tonatona Beach, Ungaunga Bay, The Bluff, Scott Point, Wizard Rock, and Blue House were 86±0.3, 82±0.2, 68±0.2, 93±0.3, 101±0.4, and 99±0.4 mm in shell length, respectively; and ranges were 60-116, 59-111, 50-88, 64-125, 71-145, and 70-142 mm in shell length, respectively. Mussel shell length data were tested for statistical requirements and no transformations were necessary. Two-way ANOVA tests (site and date as fixed factors) were conducted to identify differences in mean maximum shell length between exposed (Tonatona Beach) and sheltered (Ungaunga Bay) sites, between the 2 subtidal sites (Wizard Rock and Blue House), among intertidal (combined Tonatona Beach and Ungaunga Bay) and subtidal (combined Wizard Rock and Blue House) sites, and among all intertidal sites (Tonatona Beach, Ungaunga Bay, The Bluff, and Scott Point). Equal sample sizes between and among sites were used within each of the 4 statistical tests. Thus, only sampling events that were shared by all sites in a given statistical test were used. All ANOVA tests resulted in statistical significance for all factors and interactions (Table 1).

Gonad Index and Reproductive Cycle

No major differences were observed in gonad indices and reproductive cycles between female and male mussels in any of the 6 sites studied, nor in months sampled between July 1998 and April 2000. This high level of reproductive synchrony allowed for female and male gonad indices to be pooled for further comparisons among sites and dates. All gonad index data satisfied statistical requirements. Temporal variability in reproductive behavior was remarkably similar among all sites. Generally, populations showed high reproductive maturity and spawning between March-December and very little spawning outside this reproductive season. Conversely, spatial variability in reproductive behavior among sites within 3 spatial scales was high.

Exposed versus Sheltered Intertidal Populations

Comparisons of reproductive behavior between mussels from Tonatona Beach (exposed site) and Ungaunga Bay (sheltered site) suggest that mussels exposed to the open ocean tended to have higher reproductive efforts than mussels from sheltered areas inside Ahipara Bay. The monthly mussel gonad indices of Tonatona Beach were consistently higher than those of mussels from Ungaunga Bay for the time period between July 1998 and April 2000 (Fig. 3). The mean (±SE) gonad index and range from Tonatona Beach mussels were 189±8 and 144-259, while Ungaunga Bay mussels had a gonad index mean (±SE) and range of 173±6 and 136-247. The frequency distribution of all reproductive stages for mussels within Tonatona Beach and Ungaunga Bay indicated similar reproductive cycles, although Ungaunga Bay mussels exhibited a greater number of mussels in the spent stage throughout the post-spawning periods (Fig. 4). Mussels from both sites showed 2 to 3 likely spawning events between June-November that were concurrent at both sites, followed by rapid redevelopment until the end of the spawning season in December (Figs. 3-4). A two-way ANOVA test without replication (mixed model; site as fixed factor and date as random factor), comparing mean gonad indices between Tonatona Beach and Ungaunga Bay between October 1999 and April 2000, resulted in statistical significance between sites (ANOVA; $F_{(1,33)} = 11.99$, $p = 0.001$), and among dates (ANOVA; $F_{(16,33)} = 7.55$, $p = 0.001$).

Intertidal versus Subtidal Populations

The reproductive behavior of two intertidal mussel populations (Tonatona Beach and Ungaunga Bay) was compared to the reproductive behavior of two subtidal populations (Wizard Rock and Blue House) at the southern end of Ninety Mile Beach. Intertidal mussels had lower gonad indices than subtidal mussels (Fig. 3). No major differences were observed between the 2 subtidal populations. Compared to the intertidal populations of Tonatona Beach and Ungaunga Bay (see previous section), the subtidal populations had gonad index means (±SE) and ranges of 220±10 and 158-268 for Wizard Rock, and 215±8 and 161-277 for Blue House, respectively. Furthermore, intertidal mussel populations had greater numbers of mussels in the spent stage of development than subtidal populations before the end of the spawning season in November/December (Figs. 4-5). Conversely, the percent of ripe and spawning mussels was higher for subtidal mussel populations than intertidal populations throughout the reproductive season (March to December) (Figs. 4-5).

Statistical comparisons of mean gonad indices between Wizard Rock and Blue House were conducted with a two-way ANOVA without replication (mixed model; site as fixed factor and date as random factor). No differences between the 2 subtidal sites were observed (ANOVA; $F_{(1,29)} = 3.46$, $p = 0.08$), but statistical significance was found among 15 dates between November 1998 and April 2000 (ANOVA; $F_{(14,29)} = 82.53$, $p = 0.001$). A two-way ANOVA with replication (mixed model; site as fixed factor and date as random factor) was performed to test differences in gonad indices between intertidal (combined Tonatona Beach and Ungaunga Bay) and subtidal (combined Wizard Rock and Blue House) sites among 15 months between November 1998 and April 2000. Statistical significance was found between the intertidal and subtidal sites (ANOVA; $F_{(1,30)} = 35.03$, $p = 0.001$), and among dates (ANOVA; $F_{(14,30)} = 16.01$, $p = 0.001$), but non-significant differences were found in the interaction (ANOVA; $F_{(14,30)} = 1.93$, $p = 0.06$)

Southern versus Northern Populations

Larger-scale comparisons in reproductive behavior were conducted among southern (Tonatona Beach and Ungaunga Bay) and northern (The Bluff and Scott Point) intertidal mussel populations. Comparisons of gonad indices among the four intertidal populations indicated that The Bluff had the lowest gonad indices (mean (±SE) of 146±4 and range of 136-177) during the sampled period, followed by the southern populations of Ungaunga Bay and Tonatona Beach (see previous section) (Fig. 6). Scott Point had the highest gonad indices of all intertidal populations with a mean (±SE) of 217±9 and a range of 180-262 (Fig. 6). Frequency distribution data suggest that the mussel population at Scott Point had the highest percentage of spawning mussels during the reproductive season (March to December) as compared to southern intertidal populations, with The Bluff population showing the lowest percent of spawning mussels (Fig. 7). Also, mussels in the spent developmental stage were more numerous in The Bluff population than the southern populations, while Scott Point had the lowest number of spent mussels during the reproductive season (Fig. 7). A two-way ANOVA without replication (mixed model; site as fixed factor and date as random factor) comparing gonad indices among the 4 intertidal sites (Scott Point, The Bluff, Tonatona Beach, and Ungaunga Bay) for 9 months between July 1999 and April 2000 resulted in statistical significance among sites (ANOVA; $F_{(3,24)} = 24.14$, $p = 0.001$) and among dates (ANOVA; $F_{(8,24)} = 4.27$, $p = 0.001$).

DISCUSSION

The timing and location of mussel spat arrival at Ninety Mile Beach have been previously unpredictable. The complexity of interacting physical and biological parameters that affect the green-lipped mussel life cycle have made the study of the ecology of this mussel challenging in the past. Research on the importance of various ecological processes of mussel populations at Ninety Mile Beach is underway and will provide clues to the factors responsible for the high spatial and temporal variability of mussel spat production in the area (Alfaro, unpublished data). The study of spatial variability in reproductive behavior among various intertidal and subtidal mussel populations provides evidence on the timing and magnitude of larval production at various locations along Ninety Mile Beach.

Marked differences in maximum shell length among all intertidal and subtidal populations are likely due to variations in environmental conditions that regulate feeding rates, such as food supplies, emersion time, hydrodynamic regime, sediment load, and temperature (Suchanek, 1985; Frechette and Grant, 1991; Alvarado and Castilla, 1996; Dahlhoff and Menge, 1996; McQuaid and Lindsay, 2000). Different environmental conditions also may result in different spawning times and duration, as well as more subtle variations in gametogenic cycles (Bayne et al., 1983; Nichols, 1996; Myrand et al., 2000). Experiments conducted by Myrand et al. (2000) in the Gulf of St. Lawrence revealed distinctive differences in timing and duration of spawning events, and in mortality between two populations of blue mussels, Mytilus edulis. The two mussel populations originated from the same initial stock but were subjected to different environmental conditions of temperature and water depth within the Magdalen Islands.

The high level of reproductive synchrony observed between female and male mussels in this study have been reported in other Perna canaliculus populations (Flaws, 1975; Tortell, 1976; Buchanan, 1998), and in other mussel species (Heffernan and Walker, 1989; Villalba, 1995; Nichols, 1996; Darrigran et al., 1999). Despite the significant differences in maximum shell length, varying environmental conditions, and large physical distances among populations (8-90 km) at Ninety Mile Beach, a remarkable temporal synchrony was observed in reproductive behaviors among populations (Fig. 3-7). These unique temporal patterns in mussel reproduction at Ninety Mile Beach indicate a prolonged spawning season between June-December, which differs from the 2 spawning periods reported for mussel populations in the South Island, New Zealand (Flaw, 1975; Buchanan, 1998; Alfaro et al., in press). Conversely, the present study shows clear differences in gonad indices and reproductive cycles among mussel populations within 3 spatial scales at Ninety Mile Beach.

Exposed versus Protected Intertidal Populations

The reproduction of mussels inhabiting sheltered intertidal areas inside Ahipara Bay (Ungaunga Bay population) exhibited overall lower gonad indices throughout the sampling period, compared to a similar population in an exposed intertidal area just outside Ahipara Bay (Tonatona Bay population). Differences in reproductive efforts among mussel populations mostly have been attributed to variations in temperature and food supplies (Vélez, 1981; Bayne et al., 1983; Thompson, 1984). While temperatures are likely to be the same for the 2 adjacent sites, food supplies inside Ahipara Bay are greater (Alfaro, unpublished data). Sheltered inner bay sites, such as Ungaunga Bay, tend to concentrate large quantities of food particles, but the lower hydrodynamic regime inside Ahipara Bay may reduce the rate at which food particles reach, and are ingested by, mussels in this bed. Low growth rates and metabolic rates of mussels elsewhere have been attributed to decreased particulate organic material in suspension, and low rates of food delivery to the mussel gills, due to low water flow conditions (Griffiths, 1981; van Erkom Schurink and Griffiths, 1993; McQuaid and Lindsay, 2000; McQuaid et al., 2000). These low feeding rates also have been attributed to reduced reproductive efforts in the mussel Mytilus edulis at various sites on the English and Welsh coasts (Bayne et al., 1983). Thus, mussels at Ungaunga Bay may have lower feeding rates that account for the lower gonad indices. The similar spawning behaviors of both intertidal populations may be related to similar water temperatures at the 2 sites. Rapid temperature changes in this area at the southern end of Ninety Mile Beach may be responsible for the distinctively rapid redeveloping and subsequent spawning periods through the season (March - December) for both populations (Alfaro et al., in press).

Intertidal versus Subtidal Populations

Comparisons of reproductive patterns among intertidal and subtidal mussel populations at Ninety Mile Beach indicate that subtidal populations have consistently higher gonad indices and a higher percent of ripe and spawning mussels compared to intertidal populations. Subtidal populations often have been associated with higher productivity than intertidal populations (Suchanek, 1978; Thompson, 1979; Griffiths, 1981; Reusch and Chapman, 1997). Furthermore, subtidal mussels tend to have higher growth rates and reproductive efforts due to the generally lower stresses from desiccation, temperature fluctuations, and predation (Suchanek, 1978; Griffiths, 1981, Bayne et al., 1983; Reusch and Chapman, 1997). Thus, mussel populations at subtidal Wizard Rock and Blue House may increase their reproductive efforts by re-allocating energy from maintenance to reproduction. Another indication of higher reproductive efforts is an increase in age and size, often associated with habitats that exhibit more constant environmental conditions (Griffiths, 1981; Bayne et al., 1983; Petraitis, 1995). Mussels from subtidal sites not only had the highest gonad indices but also maintained more ripe and spawning mussels through the season. Consistency of parameters in subtidal sites, such as temperature, compared to intertidal sites, also may account for the single but extended subtidal spawning period, with very few spent mussels in the populations until the end of the season. This reproductive pattern emphasizes the importance of subtidal populations as major contributors to the spat production at Ninety Mile Beach.

Southern versus Northern Populations

Spatial patterns of reproductive behavior at Ninety Mile Beach suggest great variability in overall gonad indices among northern and southern populations. The mussel population at The Bluff had the lowest gonad indices. Although data for this site are not available from July 1999 to April 2000, there is an indication that this population also had the shortest spawning period among all studied populations. Evidence of low reproductive effort at The Bluff is consistent with this population also exhibiting the lowest maximum shell length of any population at Ninety Mile Beach. It is difficult to explain why the population at the Bluff had such a low productivity when the nearest population (15 km to the north) at Scott Point had the highest reproductive effort at Ninety Mile Beach. Indeed, Scott Point had a consistently high and long spawning period with low numbers of spent mussels until November. It is possible that less favorable local conditions at The Bluff may contribute to the low productivity of this population. The Bluff is an isolated patch of rocks in the middle of a long stretch of sandy beach. Thus, the sediment load is high and may be a constant source of stress for mussels surviving on the rocks. Due to the generally straight coastal morphology of this area, food supplies tend to be irregular and dependent on the northbound nearshore current, with little residence time at The Bluff (Alfaro, unpublished data). Conversely, Scott Point is located at the northernmost end of the beach, where the mixing of the West Auckland and Westland currents, and the more complex coastal morphology of bays and shallow banks create a highly turbulent environment (Stanton, 1973). Thus, the dynamic ocean circulation and high delivery and residence time of food particles make the Scott Point area highly productive (Alfaro, unpublished data). Differences between the 2 northern mussel populations and the 2 southern populations at Ahipara suggest that the southern intertidal populations have intermediate reproductive behaviors. These large-scale spatial differences in reproductive behavior may be related to the 1-2 °C temperature difference between northern and southern areas (Alfaro, unpublished data).

Regional variations in reproductive behavior have been observed in many mussel populations throughout the world (Bayne et al., 1983; Thompson, 1984; Jasim and Brand, 1989; Nichols, 1996). This reproductive variability is believed to be a result of mussel adaptation to local conditions (Bayne et al., 1983; Nichols, 1996). Thus, variations in environmental conditions such as water temperature and food availability may be sufficient enough to cause dramatic differences in reproductive behavior among mussel populations (Hickman and Illingworth, 1980; Smit et al., 1992; Dorgelo and Kraak, 1993; Ram and Nichols, 1993; Nichols, 1996). For the green-lipped mussel, Perna canaliculus, in New Zealand, great variations in condition index, an indirect measure of reproductive effort, were found among populations throughout the country, including populations about 36 km apart between Ahipara Bay and Whangaroa Harbour (Hickman and Illingworth, 1980). Thus, the variations in reproductive effort among all intertidal and subtidal populations at Ninety Mile Beach may contribute, in various degrees, to the highly productive and sometimes spatially and temporally variable spatfall conditions observed in this unique coastal area of New Zealand.

In summary, spatial variability in reproductive behavior of mussel populations at Ninety Mile Beach can be observed at 3 spatial scales (between exposed and sheltered, between intertidal and subtidal, and among northern and southern populations) possibly related to varying environmental conditions, such as temperature and food supply. Exposed and sheltered intertidal habitats at Ahipara Bay may have significantly different mussel feeding rates, owing to their different water flow regimes, which may affect general reproductive behaviors. Differences in reproductive behavior between intertidal and subtidal populations may be due to the more constant environmental conditions of subtidal populations. As a consequence, subtidal mussels tend to be larger (high growth rates) and have one prolonged spawning period. This spawning behavior contrasts with the 2-3 spawning periods observed in the 2 intertidal populations and in Ahipara Bay. Regional differences in Ninety Mile Beach populations are exemplified by the disparate reproductive patterns among northern and southern mussel populations. Low reproductive efforts of mussels at The Bluff may be related to the high stress of sediment loads and irregular food supplies. Conversely, mussels at Scott Point benefit from higher water temperatures and high energy ocean conditions that ensure high and constant food supplies to these mussel beds. These favorable mussel habitats may result in the high reproductive effort of mussels at Scott Point, and may promote a prolonged spawning season. Mussel populations at Ahipara have intermediate reproductive behaviors compared to those at The Bluff and Scott Point.

Finally, the observed reproductive differences among mussel populations at Ninety Mile Beach suggest that the 2 subtidal populations at Wizard Rock and Blue House, and the northernmost intertidal population at Scott Point have the reproductive potential to make significant contributions to the spat production of the area. Careful monitoring and protection of these adult populations may ensure a more reliable and predictable commercial harvest of green-lipped mussel spat in New Zealand.

ACKNOWLEDGMENTS

We thank B. Davy for her invaluable assistance with processing of histological sections. The Morrogh and Hensley families, K. Hamlin, and D. Tasker helped in the field. K. Rodgers and K. Campbell provided technical and editorial expertise. The New Zealand Foundation for Research, Science, and Technology granted funding for this project.

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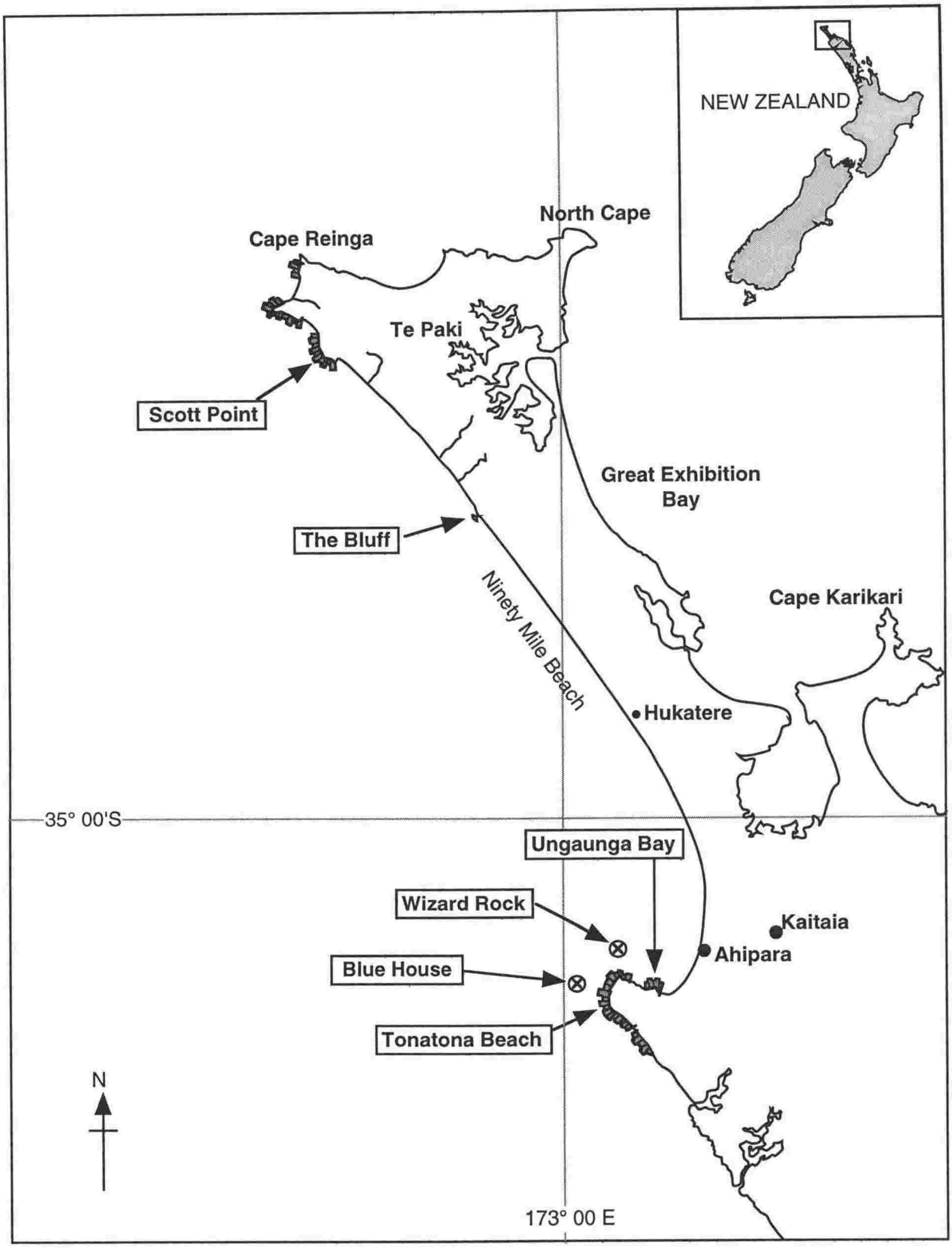

Figure 1. Map of the study site at Ninety Mile Beach, northern New Zealand. Four intertidal (Tonatona Beach, Ungaunga Beach, The Bluff, and Scott Point) and 2 subtidal (Blue House and Wizard Rock) mussel populations are shown.

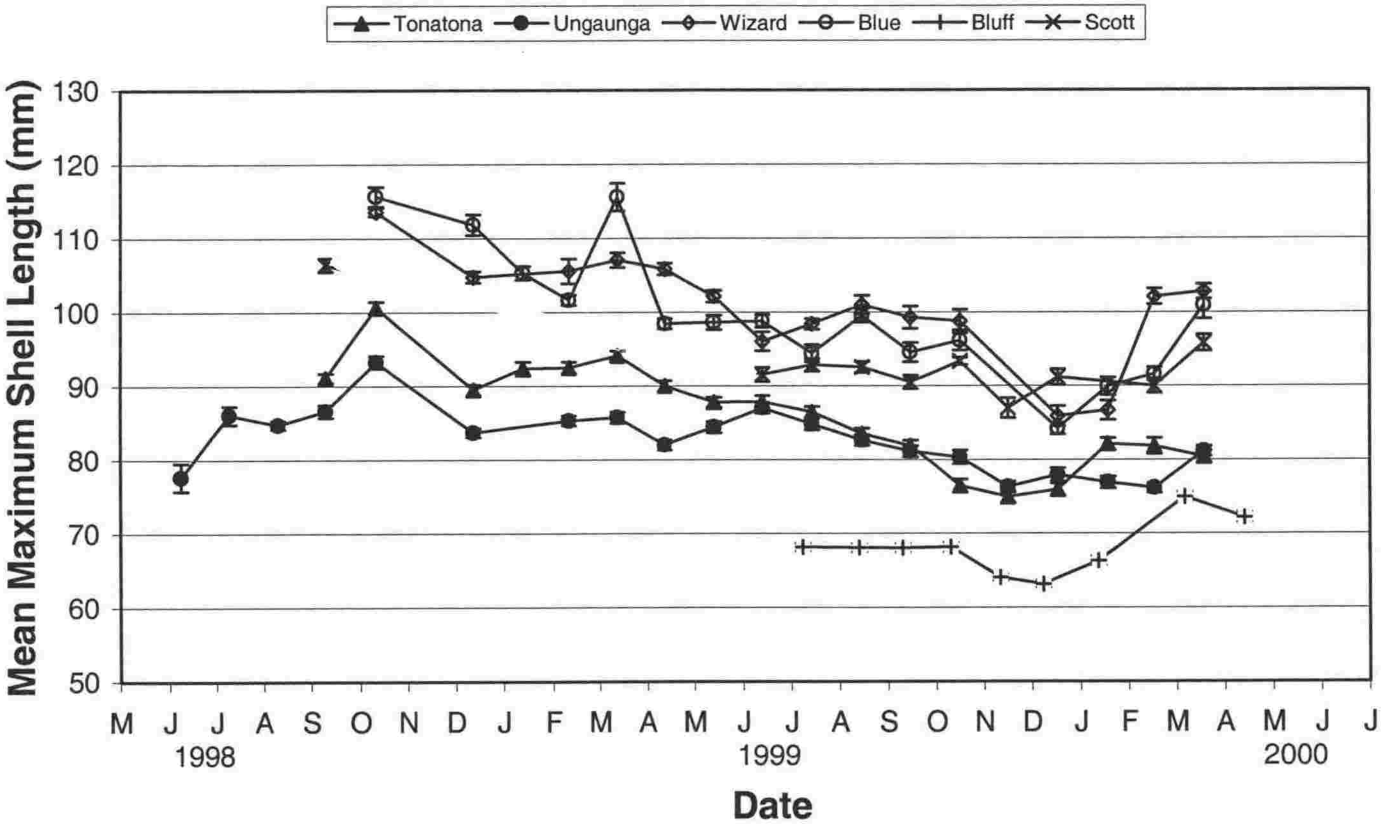

Figure 2. Mean (±SE) maximum shell length of mussels within 6 adult mussel populations sampled about monthly between July 1998 and April 2000. Means were calculated from 70 adult mussels on each date sampled within each site. Tonatona Beach, Ungaunga Bay, The Bluff, and Scott Point represent 4 intertidal populations, and Wizard Rock and Blue House constitute 2 subtidal mussel populations.

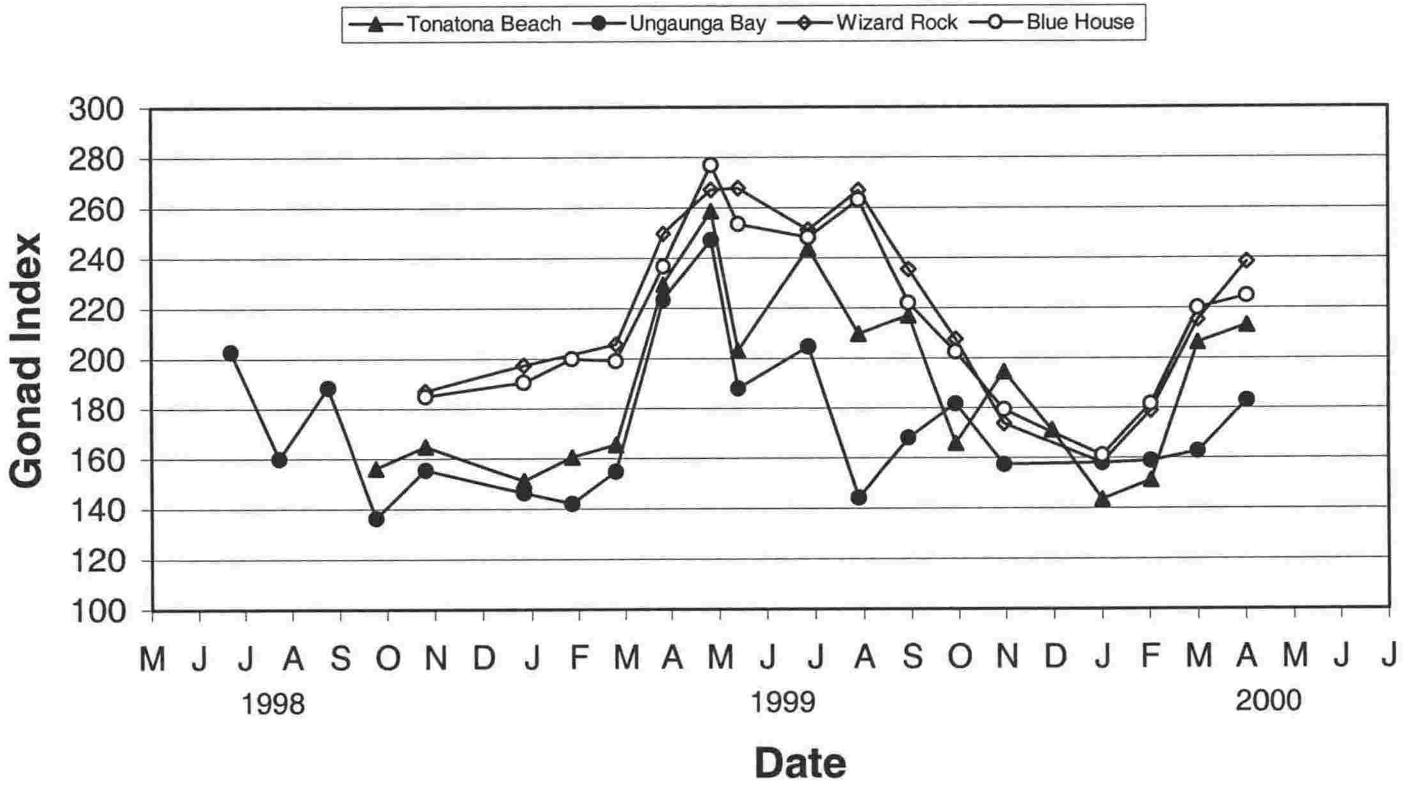

Figure 3. Gonad indices for 2 intertidal (Tonatona Beach, Ungaunga Bay) and 2 subtidal (Wizard Rock and Blue House) mussel populations at Ninety Mile Beach. A total of 70 mussels were sampled on each date and within each site to calculate a gonad index at a given date and site.

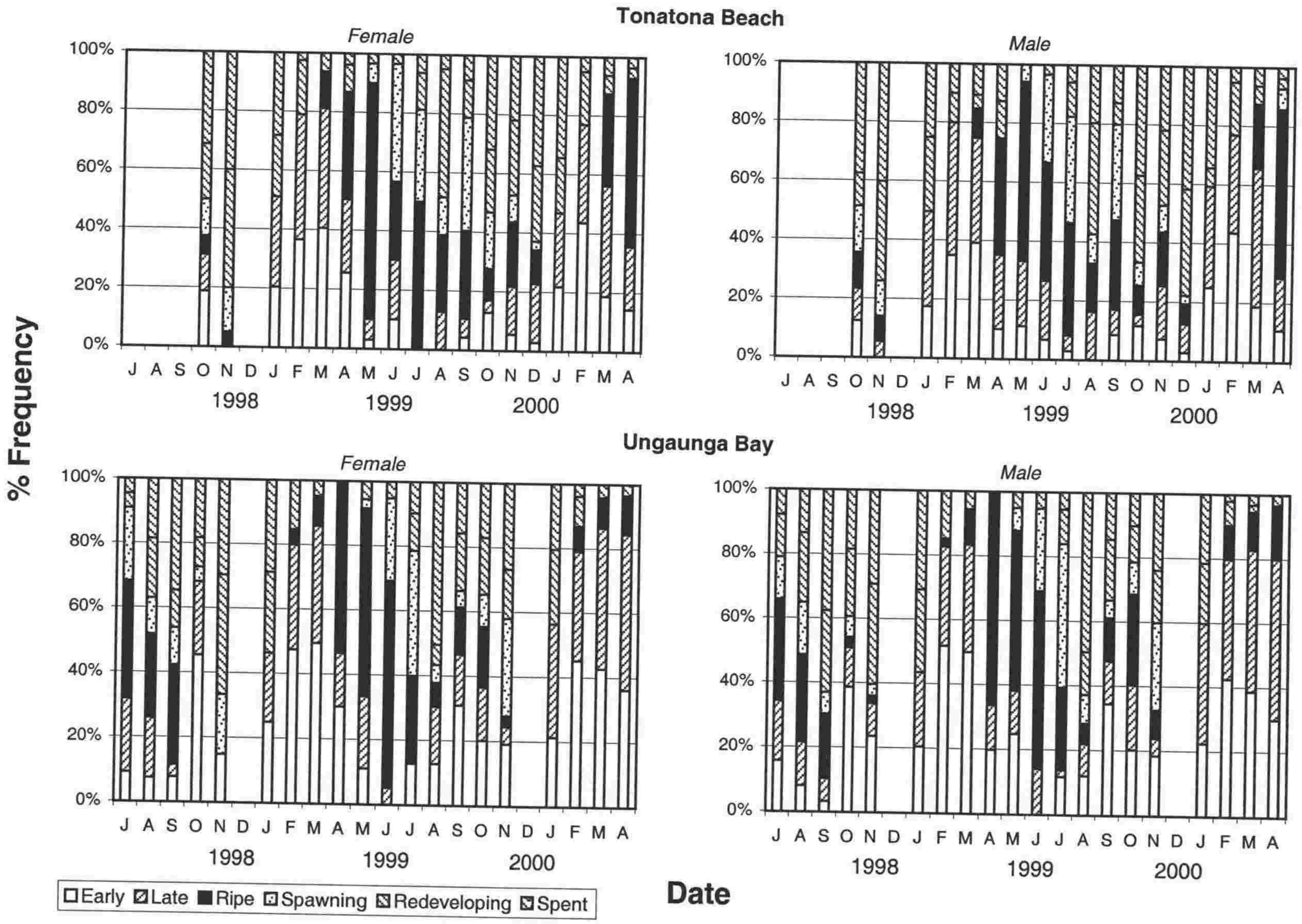

Figure 4. Frequency distribution of 6 developmental stages (early development, late development, ripe, spawning, redeveloping, and spent) of gonad reproductive state for female and male mussels at 2 intertidal sites (Tonatona Beach and Ungaunga Bay).

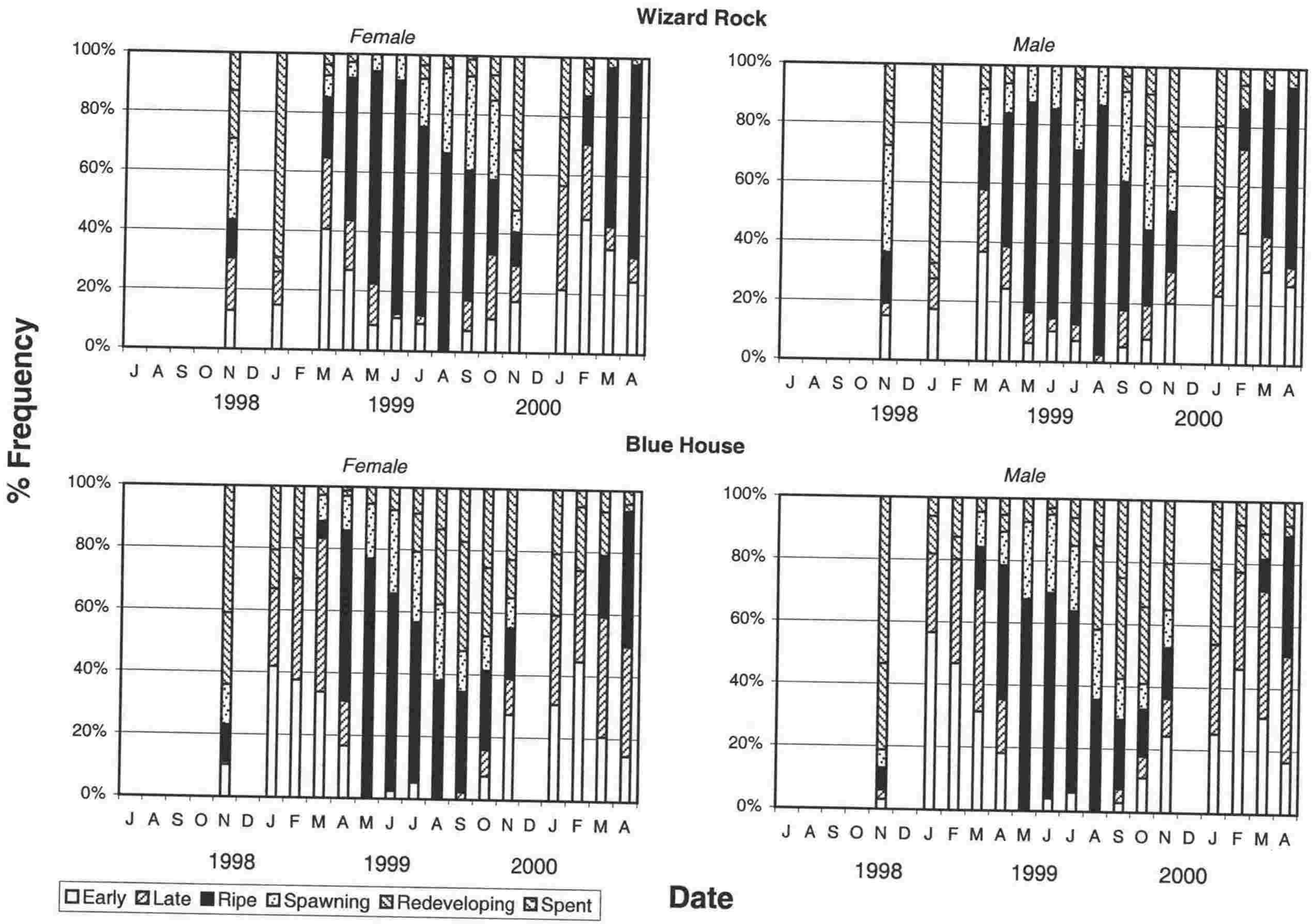

Figure 5. Frequency distribution of 6 developmental stages (early development, late development, ripe, spawning, redeveloping, and spent) of gonad reproductive state for female and male mussels at 2 subtidal sites (Wizard Rock and Blue House).

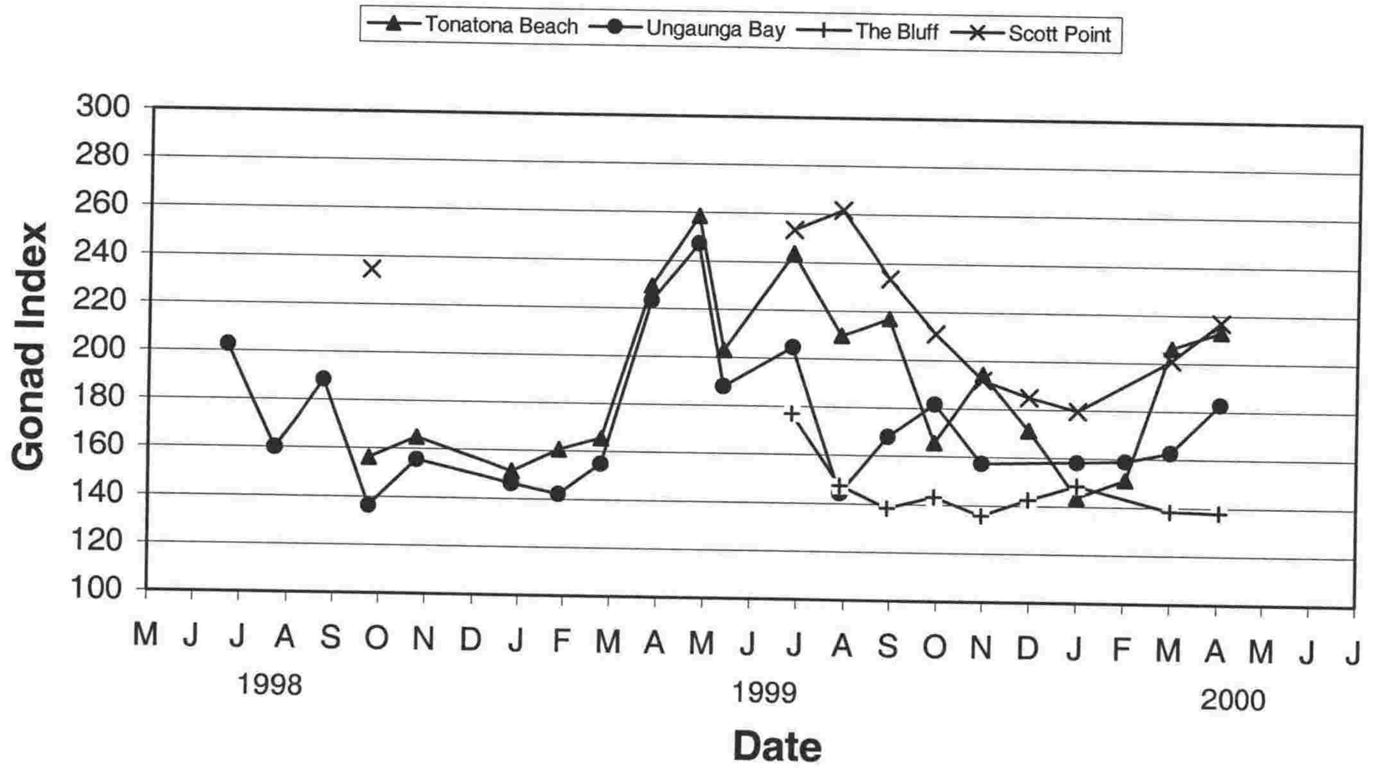

Figure 6. Gonad indices for 4 intertidal mussel population (Tonatona Beach, Ungaunga Bay, The Bluff, and Scott Point at Ninety Mile Beach. A total of 70 mussels were sampled on each date and within each site to calculate a gonad index at a given date and site.

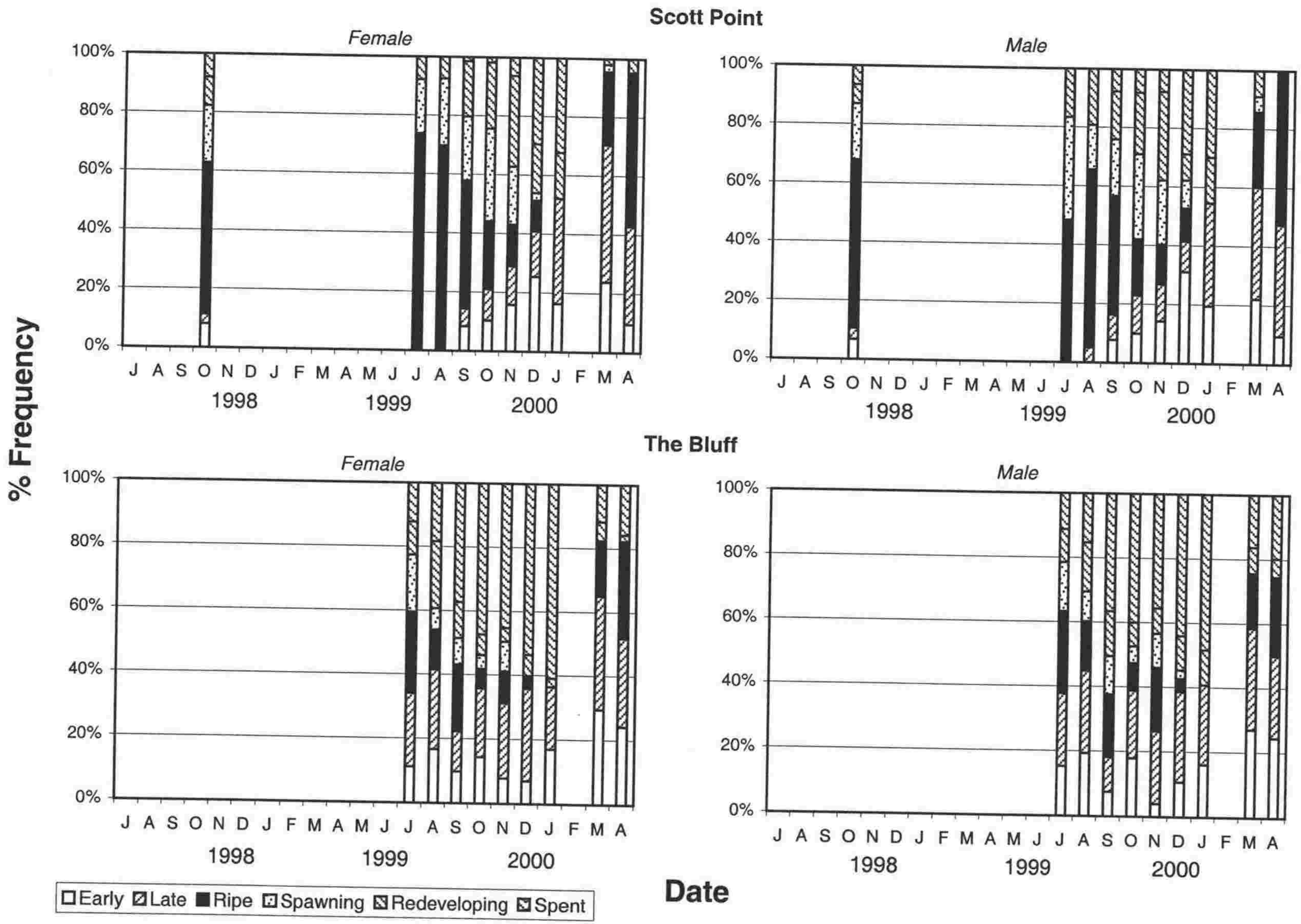

Figure 7. Frequency distribution of 6 developmental stages (early development, late development, ripe, spawning, redeveloping, and spent) of gonad reproductive state for female and male mussels at 2 intertidal sites (The Bluff, and Scott Point).

Table 1: Statistical analyses of maximum mussel shell length. Two-way ANOVA tests (Model I) are shown for each of 4 site comparisons (Site and Date as fixed factors). Statistical comparisons were made between exposed (Tonatona Beach) and sheltered (Ungaunga Bay) sites, between the 2 subtidal sites (Wizard Rock and Blue House), among intertidal (combined Tonatona Beach and Ungaunga Bay) and subtidal (combined Wizard Rock and Blue House) sites, and among all northern and southern intetidal sites (Tonatona Beach, Ungaunga Bay, The Bluff, and Scott Point).

Exposed versus Sheltered Sites

Source	df	F	p
Site	1	230.07	0.001
Date	16	93.96	0.001
Site x Date	16	10.14	0.001
Error	2346		

Subtidal Sites (Wizard Rock and Blue House)

Source	df	F	p
Site	1	23.14	0.001
Date	14	79.67	0.001
Site x Date	14	8.06	0.001
Error	2070		

Intertidal versus Subtidal Sites

Source	df	F	p
Site	1	3353.64	0.001
Date	14	140.12	0.001
Site x Date	14	17.94	0.001
Error	4169		

Northern versus Southern Intertidal Sites

Source	df	F	p
Site	3	1289.12	0.001
Date	8	35.16	0.001
Site x Date	24	11.18	0.001
Error	2484		

CHAPTER 4

Small-scale Mussel Settlement Patterns Within Morphologically Distinct Substrates at Ninety Mile Beach, northern New Zealand

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In press: Malacologia

ABSTRACT

Micro-scale settlement patterns of mussel juveniles Perna canaliculus were investigated within drift material at Ninety Mile Beach, northern New Zealand. Size- and site-specific selectivity on various morphologically distinct algal and hydroid species were identified within drift material and corroborated in laboratory experiments with similar artificial substrates. Mussel spat densities were greater within fine-branching natural (~ 28-57%) and artificial materials (~ 13-20%) compared to medium- and coarse-branching natural (~ 7-8%) and artificial (~ 2-3%) materials. Size-frequency distributions of mussel spat within natural and artificial materials suggested a relationship of increasing mussel size with decreased branching of substrates. Field and laboratory investigations indicated higher settlement of 1.5-2.0 mm mussel size classes in coarse-branching substrates, while fine-branching substrates had greater settlement of mussels within the < 0.5 mm size class. Mussel settlement comparisons within node and inter-node areas of all substrates in the field and in the laboratory indicated a strong preference of settlement in node areas over inter-node areas. The micro-scale settlement patterns observed in this study are argued to be indicative of a life strategy to maximize juvenile mussel survival within the dynamic environment of drift material in oceanic currents, before the potential arrival and re-settlement to rocky coastal areas. The present study is the first to elucidate settlement patterns of *Perna canaliculus* on drift material that washes up on Ninety Mile Beach, where > 70 tonnes/year of this material is collected and supplied to the New Zealand aquaculture industry to seed mussel farms.

Key words: Mussels; Small-scale settlement patterns; Micro-habitat selection; Size-frequency distribution; Drift algae.

INTRODUCTION

The complexity and diversity of planktonic larval settlement patterns has received a great deal of attention within various temporal and spatial scales (Butman & Grassle, 1992; Bourget & Harvey, 1998). Physical and biological factors have been investigated as potential contributors to passive and active settlement outcomes (Butman, 1987; Butman & Grassle, 1992; Grassle et al., 1992). For marine invertebrates, such as mussels, larval settlement on filamentous substrates represents an important intermediate step to the eventual recruitment to the adult population (Bayne, 1964; Davies, 1974; Highsmith, 1985; King et al., 1990; Harvey et al., 1993). However, the dynamics of these interactions are not well understood for most broadcast spawners (Dame, 1996).

Bayne (1964) first demonstrated that larvae of the mussel Mytilus edulis tended to settle on filamentous algae (primary settlement) and later moved to established adult mussel beds as secondary settlers (1-2 mm) through a bysso-pelagic phase. Bysso-pelagic drifting has since been shown to be a common means of dispersal among pelagic larvae and juveniles (Lane, 1985; Martel, 1993; Martel et al., 1994; Buchanan & Babcock, 1997). Buchanan & Babcock (1997) also found a size-specific settlement pattern for the New Zealand green-lipped mussel Perna canaliculus on various intertidal algae, hydroids, and adult mussel beds at Piha Beach, North Island, New Zealand. In their study, Buchanan & Babcock (1997) observed that mussels < 0.5 mm (primary settlers) were more abundant in attached filamentous algae and a hydroid species, while secondary settlers (> 0.5 mm) were numerous in coarser-branching algae and the adjacent intertidal mussel bed. Elsewhere in northern New Zealand, at Ninety Mile Beach (NMB), early juveniles or spat of Perna canaliculus also are found associated with floating algae and hydroids. Large quantities (> 70 tonnes per annum) of spat, attached to this drift material, are used to seed the extensive mussel farms in New Zealand, after collection from the surf zone (Jeffs et al., 2000). Nowhere else in New Zealand, but along the 90 kilometer stretch of NMB, are such vast amounts of wild spat concentrated in one place on detached material that can be conveniently and economically harvested to supply the mussel industry (Jeffs et al., 2000). Distinctive patches of filamentous substrates that arrive at the beach (wash-up events) may vary in substrate abundance and density, and spat size-frequency distribution (Hickman, 1982). A single wash-up at NMB may contain up to 70 tonnes of substrate and spat material (C. Hensley, personal communication). These filamentous substrates may derive from intertidal to deep subtidal regions in particular areas along NMB, and mussel settlement onto these substrates may take place before or after detachment of the alga or hydroid. Regardless of the timing of settlement, algal and hydroid materials appear to be essential to the transport of mussel spat, as they may not only provide a means for long-distance dispersal, but also an alternative habitat to maintain or increase physiological processes (Highsmith, 1985; Schneider & Mann, 1991a). If a size-specific mussel settlement pattern occurs on the filamentous substrates found within a wash-up event at NMB, it is likely that substrate selection is the predominant force behind mussel settlement patterns, rather than random physical encounters along this particularly high energy portion of the New Zealand coastline. The persistence of size-specific settlement patterns of mussels on drift material, while exposed to the energetic hydrodynamic regimes often encountered in the ocean, suggests a complex life history strategy. The aim of the present work is to elucidate micro-scale (cm) settlement patterns on the substrates found in wash-up events that occur along the 90 kilometer length of NMB. Thus, characterization of substrate types, and size- and site-specific settlement patterns upon various drift substrates, may provide a first step to understanding spat-substrate interactions at various spatial and temporal scales.

METHODS AND MATERIALS

Study Site

Samples of Perna canaliculus spat and associated substrates were collected from the surf zone at various locations along Ninety Mile Beach (NMB), Northland, New Zealand (Fig. 1). Each sample was collected from distinct wash-up events on 17 October 1998, 22 December 1998, and 16 May 1999. Wash-up samples were collected by net from the surf along the beach. Once collected, all samples were immediately frozen for later laboratory analyses at the University of Auckland, Auckland, New Zealand.

Natural Substrates

As a first step to investigate small-scale settlement patterns of mussel spat on various drifting natural substrates, two 100 g wet weight subsamples were taken from each of 3 wash-up samples. The original wash-up samples were between 1-5 tonnes (wet weight) of very homogeneous substrate and mussel wash-up material. All distinctive algal and hydroid substrates within each subsample were separated and grouped into 4 morphologically distinctive categories, with algal categories based on the level or degree of branching. The categories were: coarse-branching algae (Osmundaria colensoi, Carpophyllum angustifolium, and Rhodymenia dichotama); medium-branching algae (Melanthalia abscissa, Laurencia thyrsifera, Pterocladia lucida, P. capillacea, Gigartina marginifera, G. alveata, and Pachymenia lusoria); fine-branching algae (Champia laingii, Plocamium costatum, Haliptilon roseum, and Corallina officinalis); and hydroids (Amphisbetia bispinosa, Dictyocladium moniliferum, Crateritheca insignis, Aglaophenia acanthocarpa, and Lytocarpia incisa). The remaining material (shells, wood fragments, and other debris) did not contain attached mussels and was discarded. Mussels within each algal and hydroid substrate type were removed by vigorous agitation in water, and the removal of remaining mussels was achieved with forceps (Buchanan & Babcock, 1997). Mussels within 5 different size-classes (<0.49, 0.5-0.99, 1.0-1.49, 1.5-1.99, > 2.0 mm in length) were separated with a set of sieves of appropriate sizes. Previous research had verified this technique as an effective means of reliably sorting mussel material (A. Alfaro, unpublished data). The mussels were then dried to constant weight in an oven at 80°C. The number of mussels within each size class was initially determined by counting under the microscope. The number of dried mussels of each size class per unit volume was calculated, and volume subsequently was used to estimate numbers of mussels. Several test samples were processed initially to ensure the accuracy of the methodology. The surface area of flattened algal and hydroid samples was determined from video-computer images using NIH Image 1.61 software for the Macintosh (Harvey et al., 1993). All algae and hydroids were then dried in an oven at 80°C and weighed. Percent data sets of natural substrate abundance and mussel densities were arcsine transformed to normalize the data.

An additional 20 samples of ~ 25 g wet weight were taken from each wash-up sample to determine the number of mussels attached to nodes and inter-nodes of each of the 4 types of substrates (Fig. 2a). A node area was defined as a 1 cm^2 area including at least one axil, and an inter-node area as a 1 cm^2 area without an axil (Fig. 2b). Node and inter-node areas were randomly chosen from a large set of suitable areas. All mussels within node and inter-node areas on each substrate sample were removed with forceps and counted. The exact area occupied by each substrate within the 1 cm^2 region was determined from image analyses using NIH Image 1.61 software. The total number of mussels per unit area of node and inter-node was calculated for each sample of algal and hydroid substrates.

Artificial Substrates

In order to further examine the settlement dynamics of mussel spat onto morphologically distinct substrates, settling patterns onto artificial substrates of different shapes were monitored in the laboratory. Five to six 10 cm long plastic aquarium plants of 6 different types were placed in separate seawater tanks of 1.5 liters. The artificial substrates were standard aquatic plant replicas and, for consistency, also were classified as coarse-branching (Myriophyllum verticillatum, Ceratophyllum demersum, and Cabomba aquatica), medium-branching (Elodea densa, Elodea sp., and Rotala indica), and fine-branching (Vallisneria americana, V. spiralis, and Ceratopteris thalictroides) substrates to facilitate comparisons with the natural substrate experiments. Although the aquatic plants were not identical to the algae found in the wash-up samples, the surface area and degree of branching were very similar to the natural substrates, and the degrees of branching were distinctive among the 3 experimental groups. Mussel spat were collected from intertidal habitats at NMB, detached from their original algal substrates, and placed in a water tank with seawater on the same day. The density of mussels of different sizes was adjusted to be similar among size classes. From this mixture, subsamples of about 500 mussels, representing all sizes within 0.5 to 3.0 mm in length, were separated using a standard plankton splitter. The mussel subsamples were then placed in each of the 50 tanks containing artificial substrates. Each tank was aerated to ensure constant re-suspension of unattached mussels. The water temperature was maintained similar to the collection site at 15°C, and no food was added to the tanks during these short-term experiments. The light regime was set to mimic outdoor conditions. After 2 days, mussel abundance, size-frequency distribution, site of mussel re-settlement, and substrate area were determined with the procedures outlined for natural substrates. Percent mussel spat densities were arcsine transformed to normalize the data.

RESULTS

Natural Substrates

Substrate characterization in wash-up samples revealed overall differences in the total abundance of the four different settlement substrates, possibly due to seasonal changes in algal and hydroid productivity. The total amount of algal and hydroid material (± SE) from the original 100 g subsample for the 3 wash-up samples was 96±2.3% in October 1998, 31±5.2% in December 1998, and 64±3.5% in May 1999. However, the proportional algal and hydroid substrate comparisons among replicates and wash-up samples indicated that coarse-branching algae were more abundant than any other substrate for all 3 wash-up events (Fig. 3). The mean percent area (± SE) of coarse-branching algae was 69.1±2.7%, followed by medium-branching algae (14.1±1.4%), hydroids (12.1±1.4%), and fine-branching algae (4.6±1.2%). A two-way ANOVA of percent substrate among wash-up events (arcsine transformed data) showed no statistical significance among wash-up events (ANOVA; $F_{(2,12)} = 0.35$, $p > 0.05$), but a significant difference among substrate types (ANOVA; $F_{(3,12)} = 217.33$, $p < 0.05$). The interaction between wash-up and substrate type was not statistically significant (ANOVA; $F_{(6,12)} = 1.91$, $p > 0.05$). Tukey's pairwise comparisons of means failed to find significant differences between medium-branching algae and hydroids (Tukey test; $p = 0.799$).

The total number of mussels differed greatly among samples of different wash-up events. The first sample, collected on 17 October 1998 yielded mussel numbers ranging from 12 to 3866 mussels/cm^2 of substrate, and a mean (± SE) of 658.7±230.7 mussels/cm^2 of substrate. The second wash-up sample of 22 December 1998 contained very few mussels, ranging from 0 to 12 mussels/cm^2 of substrate and a mean (± SE) of 2.6±0.7 mussels/cm^2 of substrate. Finally, the third sample of 16 May 1999 had a range of 9 to 1632 mussels/cm^2 of substrate and a mean (± SE) of 255.2±123.5 mussels/cm^2 of substrate. While the absolute number of mussels among the three wash-up samples was very different, the percent of mussels within each substrate type was similar for all wash-up samples (Fig. 4). The mean percent of mussels between replicates and among wash-up events indicates that hydroid substrates consistently accumulated the greatest number of mussels compared to all other substrates (Fig. 4). The mean percent of mussels/cm^2 (± SE) among substrates was 57±4, 28±2, 8±2, and 7±2% mussels/cm^2 for hydroids, fine-branching, medium-branching, and coarse-branching algae, respectively. Results from a two-way ANOVA on the arcsine transformed data, with wash-up event and substrate type as factors, indicated that there was no statistically significant difference among wash-up events (ANOVA; $F_{(2,12)} = 0.57$, $p > 0.05$) and interaction (ANOVA; $F_{(6,12)} = 4.41$, $p > 0.05$), although there was a significant difference among substrate types (ANOVA; $F_{(3,12)} = 419.97$, $p < 0.05$). Tukey's test comparisons failed to find significant differences between coarse- and medium-branching substrates (Tukey test; $p = 0.714$).

Results from the size-frequency distribution of mussels within each substrate type revealed a relationship between increasing mussel size and decreased degree of branching of substrate. Coarse-branching algae had a greater percent of large mussels (1.5-1.99 mm in length), while fine-branching algae and hydroids had the greatest percent of small mussels (< 0.5 mm in length) (Figure 5 and Table 1). Two-way ANOVA's, with mussel size class and wash-up event as treatment, were performed for each substrate (Table 1).

Results from mussel density comparisons between node and inter-node areas within each of 4 natural substrates indicate that mussels were more abundant in node areas in all substrate types (Fig. 6). Furthermore, the relationship between increasing mussel abundance and decreased degree of substrate branching was generally apparent in these samples as well (Fig. 6). However, no difference between coarse- and medium branching algae was observed (Fig. 6). The mean number of mussels within node areas were 4.7±0.9, 52.4±9.5, 557.1±33.9, and 1055.0±41.5 individuals/cm^2, and within inter-node areas were (0.4±0.3, 23.7±6.0, 61.8±13.9, and 581.2±145.6 individuals/cm^2) for coarse-, medium-, and fine-branching, and hydroid substrates, respectively. Although size classes were not differentiated in this part of the study, the fact that the pattern is similar for all substrate types (which contained different predominate mussel size classes) suggests that mussels of all size classes were more abundant within node areas. In samples with low total mussel abundances, clumps of mussels within node areas were often clearly visible. As the total density of the sample increased, the clumps of mussels extended from inter-nodes along the branches, and in some cases, the entire algal or hydroid substrate was covered with mussels. A two-way ANOVA, with site of attachment (node versus inter-node) and substrate type, showed statistical significance for site of attachment (ANOVA; $F_{(1,472)} = 248.74$, $p < 0.05$) and substrate type (ANOVA; $F_{(3,472)} = 562.03$, $p < 0.05$). A statistically significant interaction (ANOVA; $F_{(3,472)} = 72.54$, $p < 0.05$) reflected the inability to differentiate settlement patterns between coarse- and medium-branching algae.

Artificial Substrates

While the absolute number of mussels that settled on the artificial substrates was much lower than the numbers recorded from the natural material found in wash-up samples, the general trend among morphologically distinct groups was consistent with the natural substrates (Fig. 7). Mussel settlement within coarse-branching artificial substrates ranged from 0 to 2 mussels/cm^2 of substrate and had a mean of 0.21±0.05 mussels/cm^2 of substrate. Medium-branching material had a settlement range from 0 to 6 mussels/cm^2 and a mean of 0.38±0.09 mussels/cm^2 of substrate. Finally, fine-branching material had a range of 0 to 25 mussels/cm^2 of substrate and had a mean settlement of 3.23±0.45 mussels/cm^2 of substrate. Three one-way ANOVA's, with artificial plant type as treatment, were run on the arcsine transformed data to test for settlement differences among plastic aquarium plants within each of the 3 experimental branching groups. The results of these tests showed no significant differences among any of the groups (ANOVA; $F_{(2,15)} = 0.02$, $p > 0.05$, ANOVA; $F_{(2,15)} = 0.07$, $p > 0.05$, and ANOVA; $F_{(2,15)} = 0.17$, $p > 0.05$ respectively for coarse-, medium-, and fine-branching substrates) (Fig. 7). However, a one-way ANOVA comparing mussel settlement on artificial substrates with different branching degrees found significant settlement differences among substrates (ANOVA; $F_{(2,51)} = 80.17$, $p < 0.05$) (Fig. 7). A one-way ANOVA comparing all coarse- and medium-branching substrates, regardless of plant species, resulted in non-significant substrate effects (ANOVA; $F_{(1,34)} = 1.06$, $p > 0.05$).

Frequency distribution results from the artificial substrate experiments also indicated greater settlement on fine-branching material than coarse- and medium-branching material (Fig. 8). Generally, fine-branching substrates had a higher percentage of < 0.99 mm mussel size classe, while coarse- and medium-branching substrates had a similarly high percentage of > 1.5 mm mussels, and very little to no settlement of < 1.5 sized mussels (Fig. 8). Results from statistical analyses, including two-way ANOVA's for each experimental group (degree of branching and mussel size as treatment), are shown in Table 2.

Settlement comparisons between nodes and inter-nodes areas within artificial substrates also resulted in greater mussel densities in node areas than in inter-node areas (Fig. 9). Again, no settlement differences between coarse- and medium-branching substrates were observed, but fine-branching substrates did contain greater settlement than the other 2 substrates (Fig. 9). Mussels often were observed extruding their foot to test surrounding substrates. In some cases, mussels were observed moving from the tip of an artificial plant to the nearest node. This migratory behavior sometimes resulted in clumping of mussels. A two-way ANOVA, with site of attachment (node versus inter-node) and substrate type, showed significant differences between node and inter-node attachment sites (ANOVA; $F_{(2,102)} = 13.40$, $p < 0.05$) among artificial substrate species

(ANOVA; $F_{(2,102)} = 41.60$, $p < 0.05$), and interaction (ANOVA; $F_{(2,102)} = 11.00$, $p < 0.05$).

DISCUSSION

One of the great interests in the field of invertebrate ecology is the question of how initial settlement patterns affect the distribution of adult broadcast spawners such as mussels. While oceanic-current dispersal of larvae and juveniles is a passive means of transport, some degree of habitat choice is exercised by individuals that encounter and attach to drift material. This initial settlement process on various morphologically distinct drift materials may be of significance to the survival and successful re-settlement of juveniles to the adult population. Thus, elucidation of micro-scale settlement patterns of mussel spat on natural drift substrates may enhance our understanding of the process of spat transport and arrival to coastal areas.

Substrate characterization within 3 wash-up events at NMB indicated that coarse-branching algal substrates consistently comprised the majority of settlement substrates found associated with wash-up events. Medium-branching algae, fine-branching algae, and hydroids were less abundant. Drift algal material may originate from rocky intertidal and subtidal areas. However, the majority of the material (mostly red algae) is subtidal in origin (Osmundaria colensoi, Carpophyllum angustifolium, and Rhodymenia dichotoma; Adams, 1994; Steneck & Dethier, 1994), indicating the importance of subtidal sources. The large amount of subtidal material in NMB wash-up samples also may be a result of the scarcity of rocky intertidal areas that could provide intertidal algal sources along the beach (Fig. 1). Furthermore, none of the intertidal areas at or near NMB contain the same species of algae found washed-up at NMB in enough abundance to indicate a likely source (A. Alfaro, personal observation). The often fresh and intact nature of the material which arrives at the beach suggests that the subtidal material comes from rocks situated just offshore (< 35 m water depth) of three rocky outcrops along the beach (Tauroa Point, The Bluff, and Scott Point). Indeed, algal beds have been observed off Tauroa Point (S. Hooker, unpublished), and extensive rocky substrates, likely to harbor algal material, have been noted by local fishers off Scott Point. Furthermore, spawning peaks of intertidal and subtidal mussels (< 35 m water depth), as well as algal seasonal cycles, may strongly influence the abundance, dispersal and colonization potential of spat within temporal and spatial scales (Alfaro et al., in review). However, more samples collected throughout the year are necessary to clarify these patterns.

Quantification of mussel spat among algal and hydroid substrates indicated that a greater number of spat settle on hydroids, followed by fine-branching algae; whereas fewer spat settle on medium- and coarse-branching algae. Laboratory settlement experiments with artificial substrates also resulted in greater settlement on fine-branching material over coarse- and medium-branching substrates. Buchanan & Babcock (1997) found a similar size-frequency distribution of mussel spat on intertidal algae at Piha, North Island, New Zealand. In their study, the authors found that primary settlement of mussels (< 0.4999 mm in length) was mostly on the hydroid Amphisbetia bispinosa, and fine- and medium-branching algae, while larger mussels in the dispersal (0.5-5.4999 mm in length) and stable (> 5.0 mm in length) stages of their life history tended to re-settle onto coarser-branching algae and the adult mussel bed. By contrast, the present study included consideration of a wider range of free-drifting algal-branching types (coarser red and brown algae), that are likely of mostly subtidal origin. Nonetheless, the size-frequency distribution of mussel spat on natural (in the field at NMB) and artificial (in the lab) substrates strongly corroborates observations at Piha by Buchanan & Babcock (1997). The field experiments at NMB indicated that the percent of mussel spat among the 4 algal and hydroid substrates was similar for all 3 wash-up samples and may indicate that settlement patterns are not affected by absolute variations in substrate abundance. Furthermore, mussel spat will settle predominantly on less abundant natural material even when existing spat densities may be quite high (~3800 individuals/cm^2 on hydroid material). This strong selectivity has been observed elsewhere (Butman, 1987; Schneider & Mann, 1991a,b; Butman & Grassle, 1992; Grassle et al., 1992; Harvey et al., 1993; Buchanan & Babcock, 1997). Schneider & Mann (1991a) found that there was a strong selectivity of epifaunal invertebrates to macroalgae with varying degrees of branching. The authors concluded that the relationship between invertebrate species and algal morphology benefited the associated invertebrates in terms of food source and living space provisions. It is unclear as to which different ecological properties may be provided by different substrates (such as coarse-branching algae versus hydroids) to the associated mussel spat, but it is likely that the relationship is based primarily on attaining a structurally secure place to inhabit. Indeed, results from the artificial substrate experiments suggested that mussels will preferentially settle onto filamentous substrates on the basis of their physical shape. While these experiments with artificial substrates do not rule out the possibility that chemical cues exuded by natural algae affect mussel settlement patterns, they do support the idea that substrate morphology alone strongly influences settlement of different-sized mussels. The observed movement of mussels from the tips of artificial aquarium plants to node areas suggest that attraction cues among mussels may exist, as well as substrate selectivity.

The size-frequency distribution of mussel spat on the various natural substrates within NMB wash-up samples (Fig. 5), and artificial substrates (Fig. 8), shows a general inverse relationship between spat size and degree of substrate branching. Thus, larger mussels (1.5-2.0 mm) appear to settle predominantly on coarse-branching substrates, while smaller mussels (<0.5 mm) preferentially settle on fine-branching material (Fig. 5 & 8). Buchanan & Babcock (1997) suggested that such size-specific settlement on morphologically distinct substrates in the intertidal zone may be largely a result of recolonization of natural substrates. Our results suggest that the selection process also may take place in subtidal habitats and in the water column, possibly within accumulated patches of drift algae and hydroids. Furthermore, this size-specific selection persists even after the mussels have been transported large distances by dynamic oceanographic conditions evident at NMB. The possibility exists that the observed relationship between spat size and substrate type is a result of differential growth rates that allow the less abundant spat on coarse- and medium-branching algae to attain a larger size due to lower crowding effect. However, the fact that all substrate types and mussel spat size classes were consistently represented in all 3 NMB wash-up samples suggests that differential growth rates of spat within patches of drift material is unlikely. Furthermore, artificial substrate experiments resulted in similar trends after a period of only 2 days, which was not long enough to note size differences due to growth.

A size-specific settlement pattern may represent a choice for scaled physical stability, where, for example, larger mussels may require larger morphologically stable substrates, such as the coarse- and medium-branching algae. However, smaller-scale selectivity also may contribute to stability requirements of mussel spat. Comparisons of settlement densities between node and inter-node areas within 4 different natural substrates (Fig. 6), and 3 artificial plant substrates (Fig. 9), indicate that node settlement is preferred by mussels settling in all types of substrates. Micro-scale selectivity has been demonstrated in laboratory flume experiments (Harvey et al, 1993; Harvey & Bourget, 1995; Bourget & Harvey, 1998). Bourget & Harvey (1998) found that recruits of 9 marine invertebrates, including 6 bivalve species, were more abundant in nodes as compared to inter-nodes, and that the rate of recruitment indicated that passive deposition alone was not sufficient to obtain such an outcome. The authors ruled out the influence of differential erosion and mortality on higher settlement patterns for nodes over linear areas. Evidence has been accumulating that points to behavioral responses to small scale (< 1 cm) substrate irregularities, such as pits, grooves, and depressions as determinants in micro-scale settlement preferences (Bourget et al., 1994; Nellis & Bourget, 1996; Bourget & Harvey, 1998). While chemical cues between spat and substrate, and among individual mussels, cannot be excluded as factors in the site-settlement preference experiments reported here, it is likely that morphology is the driving force to the strong habitat selectivity observed in this study.

The large volume of wash-up material (up to 70,000 tonnes/year; C. Hensley, personal communication) that can be collected only along NMB suggests that settlement on drift material may be an important part of the life history strategy for Perna canaliculus. Indeed, floating algal clumps have been found to provide alternative habitats and transport of invertebrates (Schneider & Mann, 1991a; Highsmith, 1985; Bologna & Heck, 1999). Micro-scale selectivity of mussel spat of different sizes onto morphologically distinctive substrate types may reflect a delicate level of organization within the transitional environment of drift material. Transport by drift material may be crucial to the invasion and retention of mussel spat onto new intertidal and subtidal sites (Highsmith, 1985). Pulses of new mussel settlements have been observed at Scott Point, NMB after large accumulations of drift material on the rocky shore (C. Hensley, personal communication). It is possible that entire rocky shore mussel communities may depend on the periodic arrival of spat from drift material. In the case of NMB, where rocky habitats constitute a very small portion of the coastal area, it appears that most wash-up events may arrive on the sandy beach where mussels have little chance of survival, unless collected by spat collectors and transported to mussel farms. Additional research on substrate availability and the dynamics of oceanographic transport of drift material at NMB is critical to further understanding of mussel dispersal, colonization, and maintenance of adult populations at various temporal and spatial scales.

AKNOWLEDGMENTS

We thank C. and R. Hensley, K. Campbell, and D. Tasker for their invaluable assistance with sample collections in the field. We are grateful for the technical support of A. Turner, I. MacDonald,V. Ward, and D. Todd. Algal identifications were done by W. Nelson, and S. O'Shea conducted the hydroid identifications. The Geology Department at the University of Auckland provided lab space and equipment for the size-frequency analyses. We thank K. Campbell and 2 anonymous reviewers for their comments on the manuscript.

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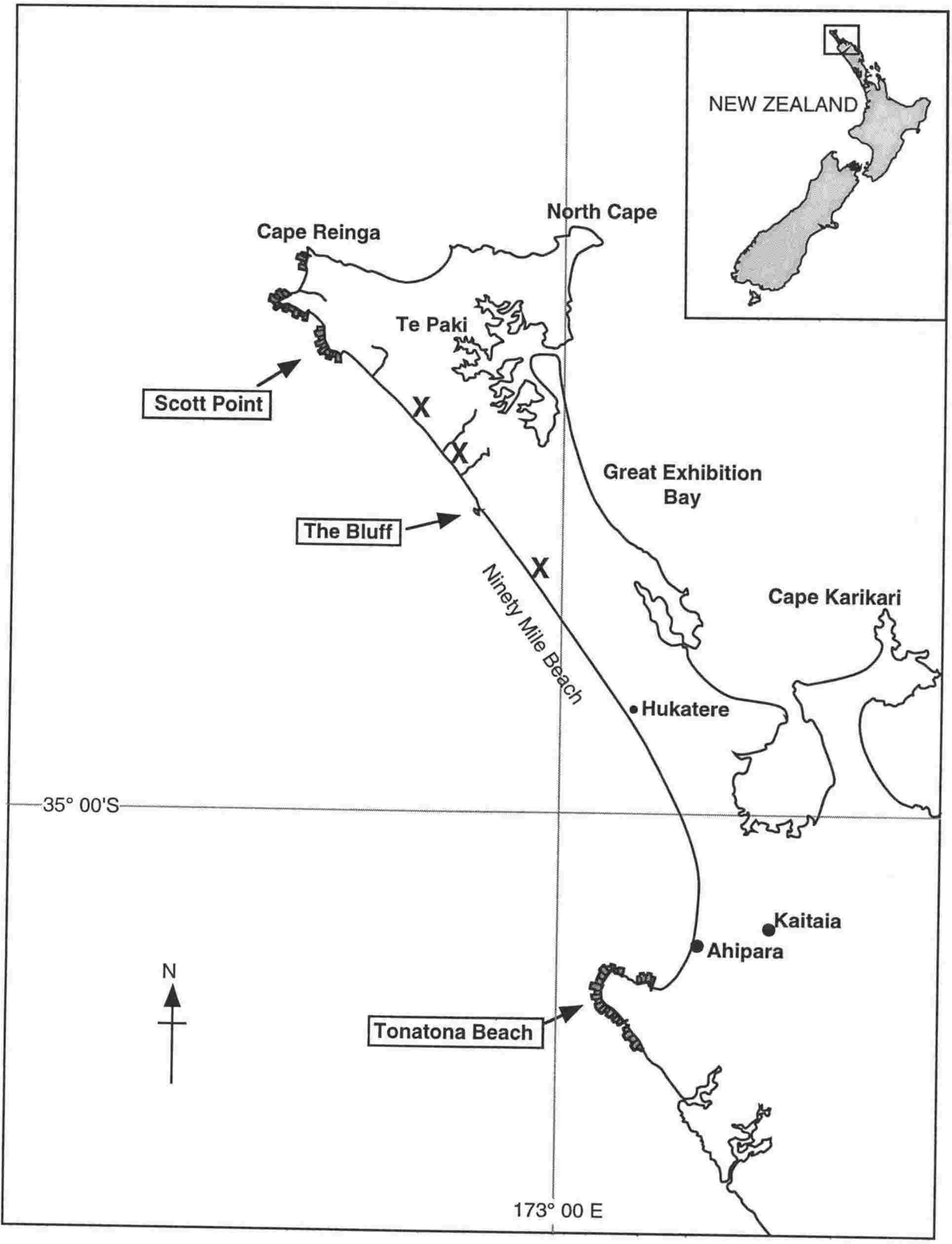

Figure 1. Location of study site at Ninety Mile Beach, northern New Zealand. Rocky intertidal areas are found at Tonatona Beach, The Bluff, and Scott Point. Spatfall collection sites on 17 October 1998, 22 December 1998, and 16 May 1999 are marked (X) along the beach.

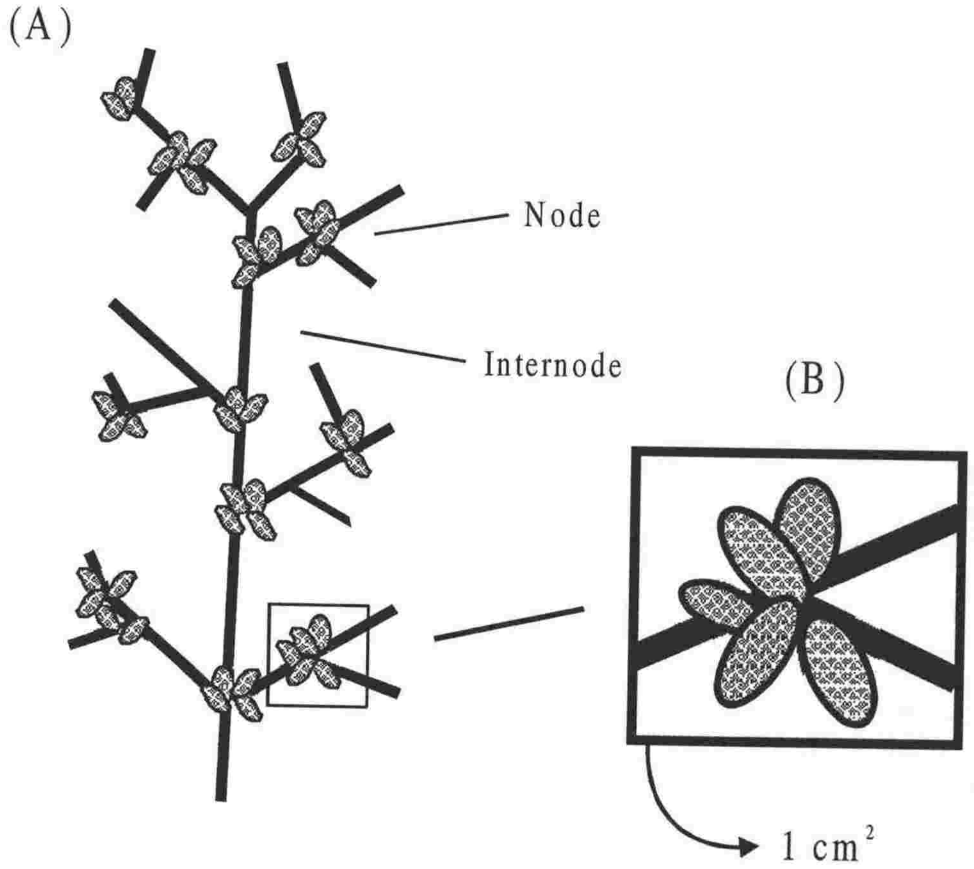

Figure 2. (A) Diagram depicting node and inter-node areas on a filamentous substrate. (B) Close-up of node and inter-node area (1 cm^2).

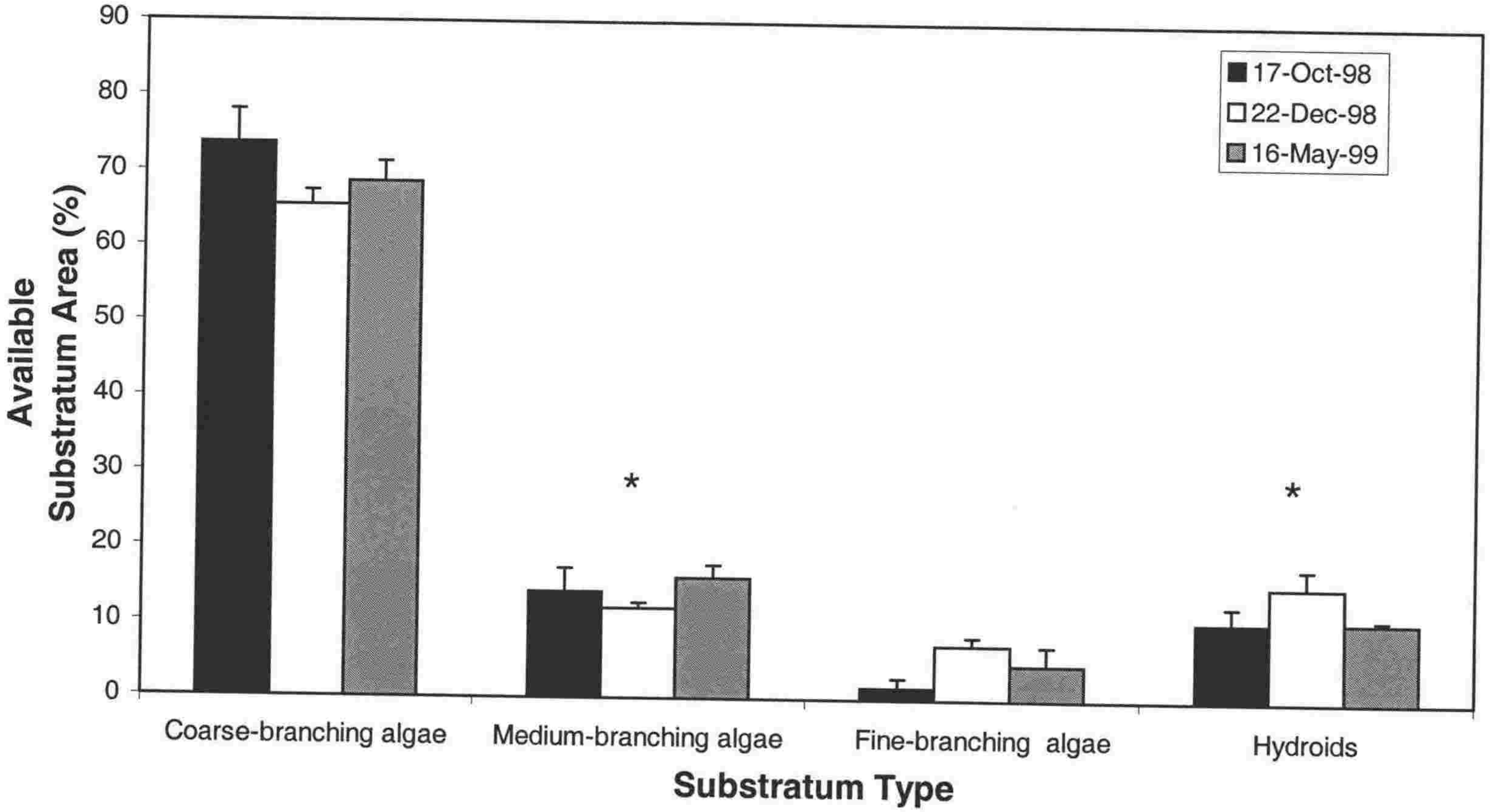

Figure 3. Percent area of 4 natural substrate types among 3 spatfall events. Non-significant Tukey tests for substrate differences are shown (*).

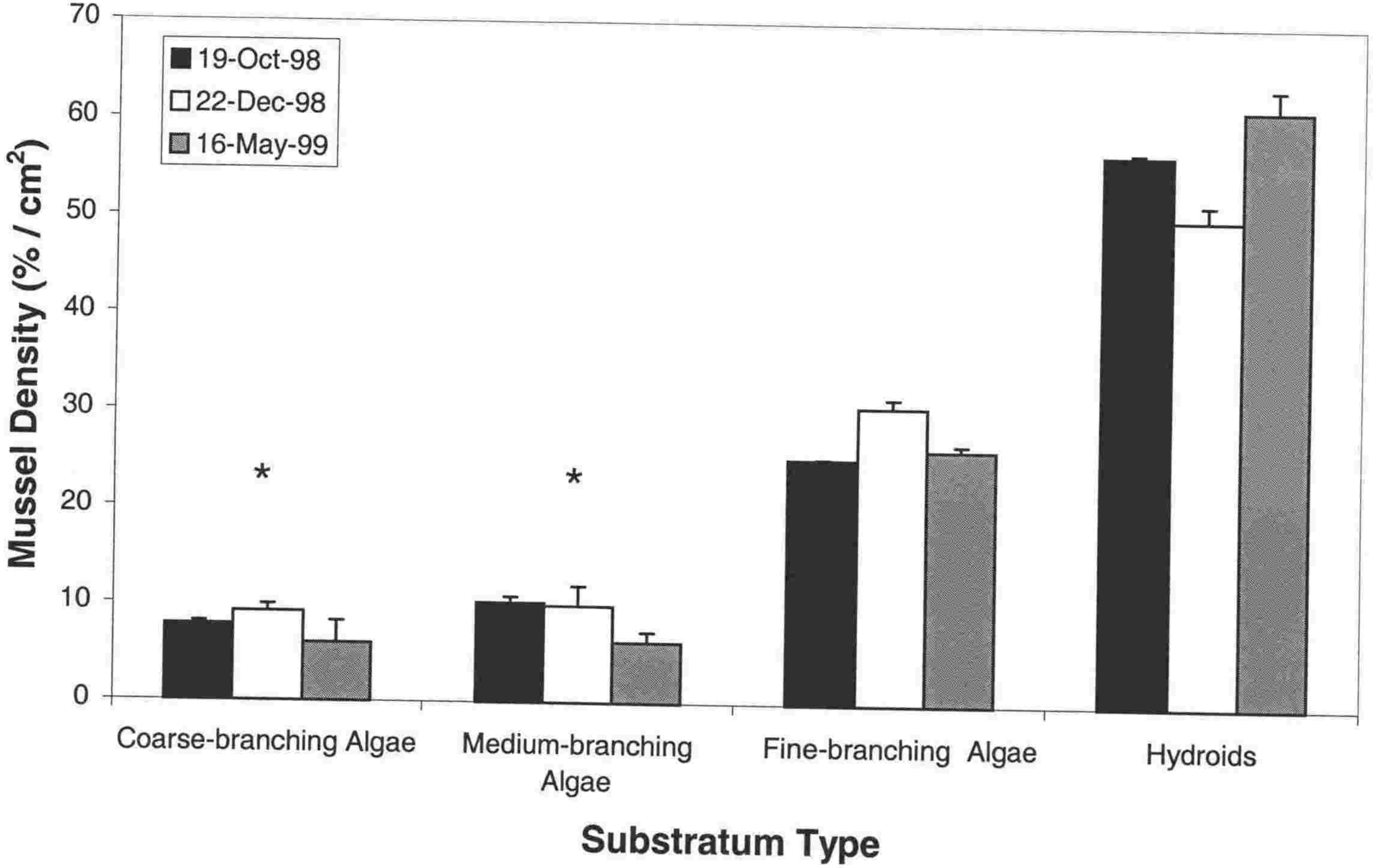

Figure 4. Mussel densities within 4 natural substrate types and 3 events samples. Non-significant Tukey tests between substrates are shown (*).

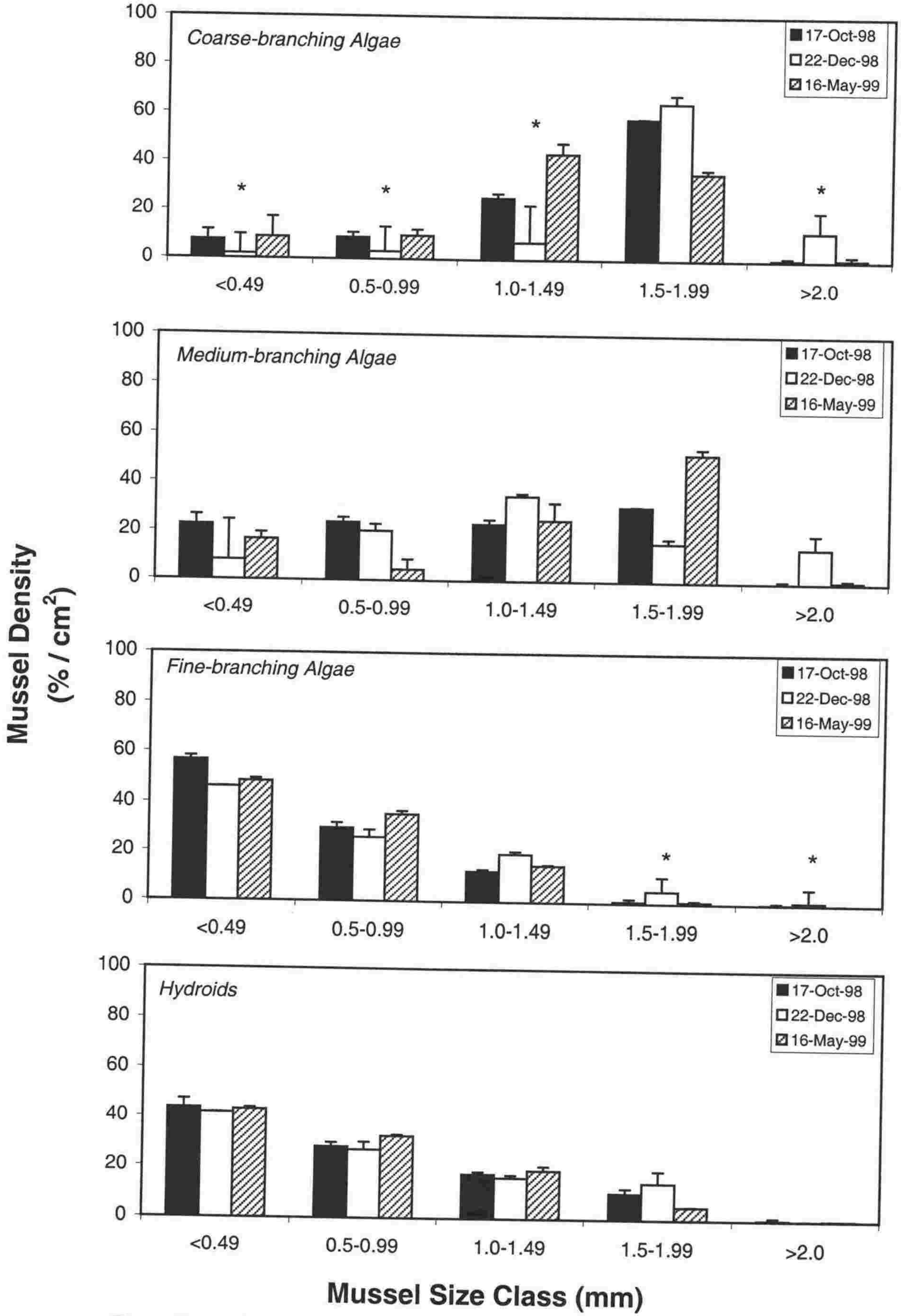

Figure 5. Size-frequency distribution of mussels within 5 size classes and 3 spatfall events for 4 natural substrate types. Pairwise comparisons (Tukey test) were performed for substrates that showed non-significant interactions (coarse-branching algae, medium-branching algae, and hydroids) in an overall ANOVA test and are shown (*).

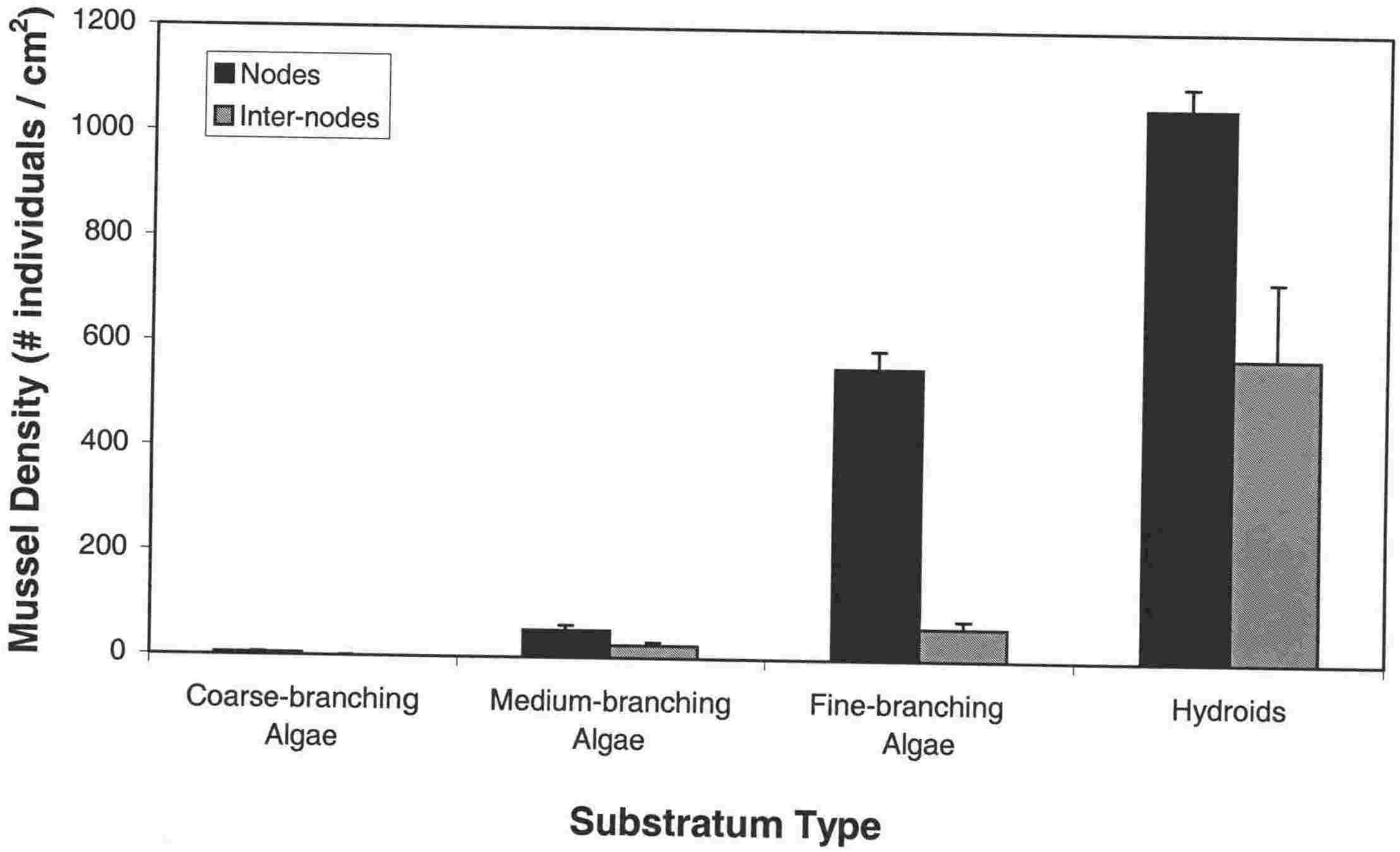

Figure 6. Mussel densities within node and inter-node areas within 4 natural substrate types. (n = 20).

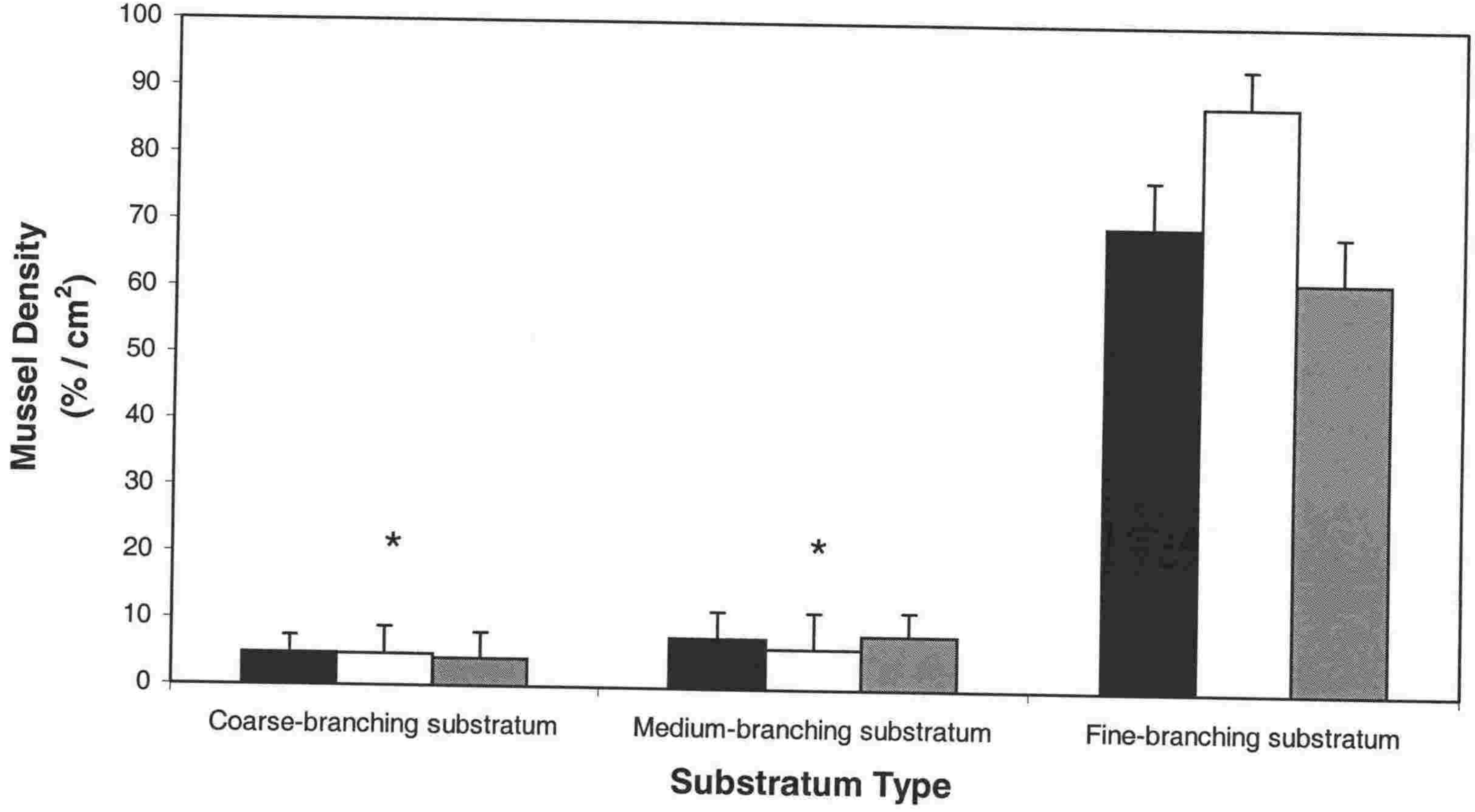

Figure 7. Mussel densities within 3 experimental groups containing artificial substrates. A significant ANOVA test (*) between coarse- and medium-branching algal substrates only are shown (*). (n = 6). See text for further explanations. Three one-way ANOVA's, with artificial plant types as treatment, resulted in no significant differences among substrate types.

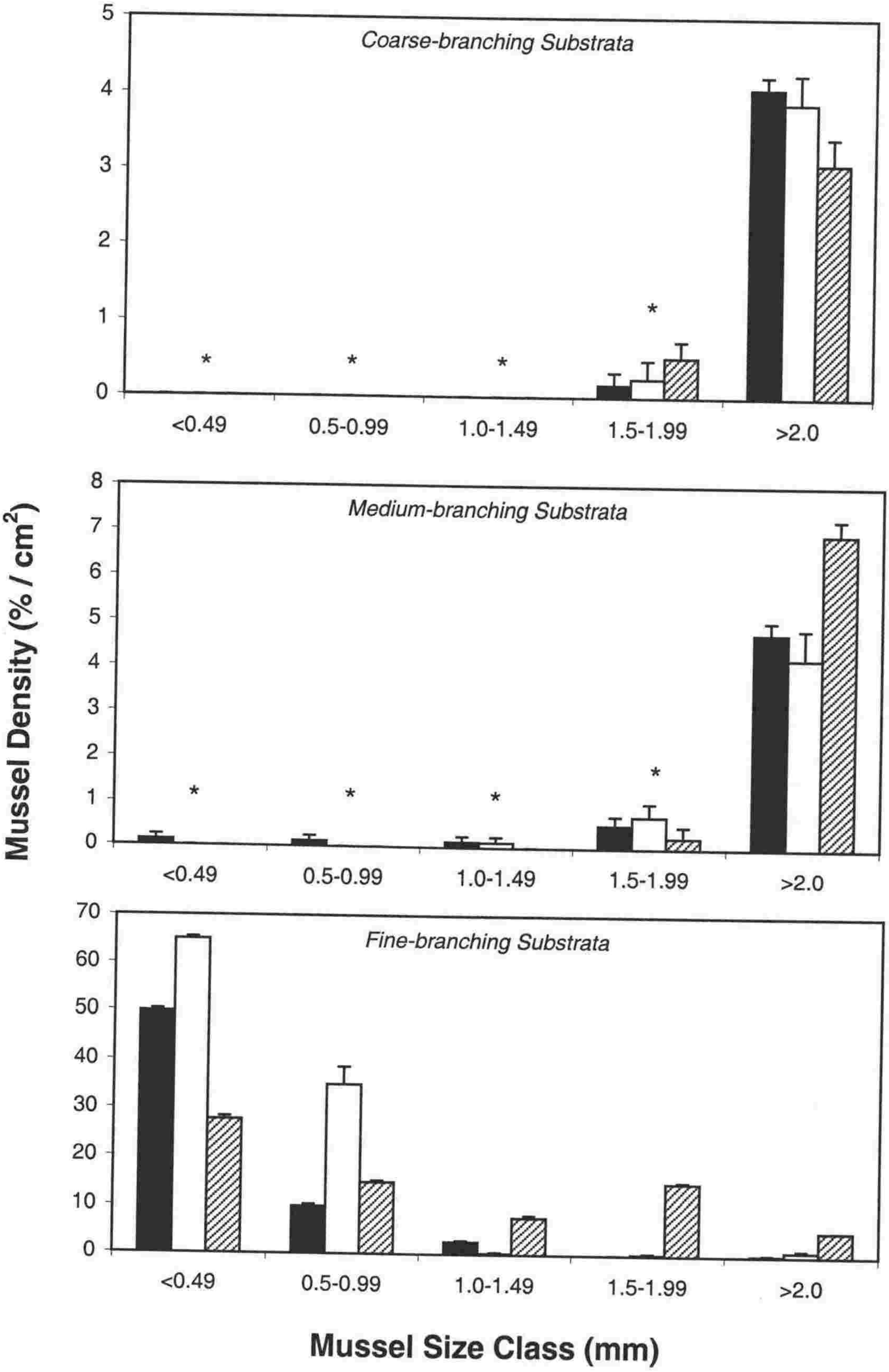

Figure 8. Size-frequency distribution of mussels within 5 size classes and 3 experimental groups of artificial substrates. Pairwise comparisons (Tukey test) were performed for substrates that showed non-significant interactions (coarse- and medium-branching substrates) in an overall ANOVA test and are shown (*).

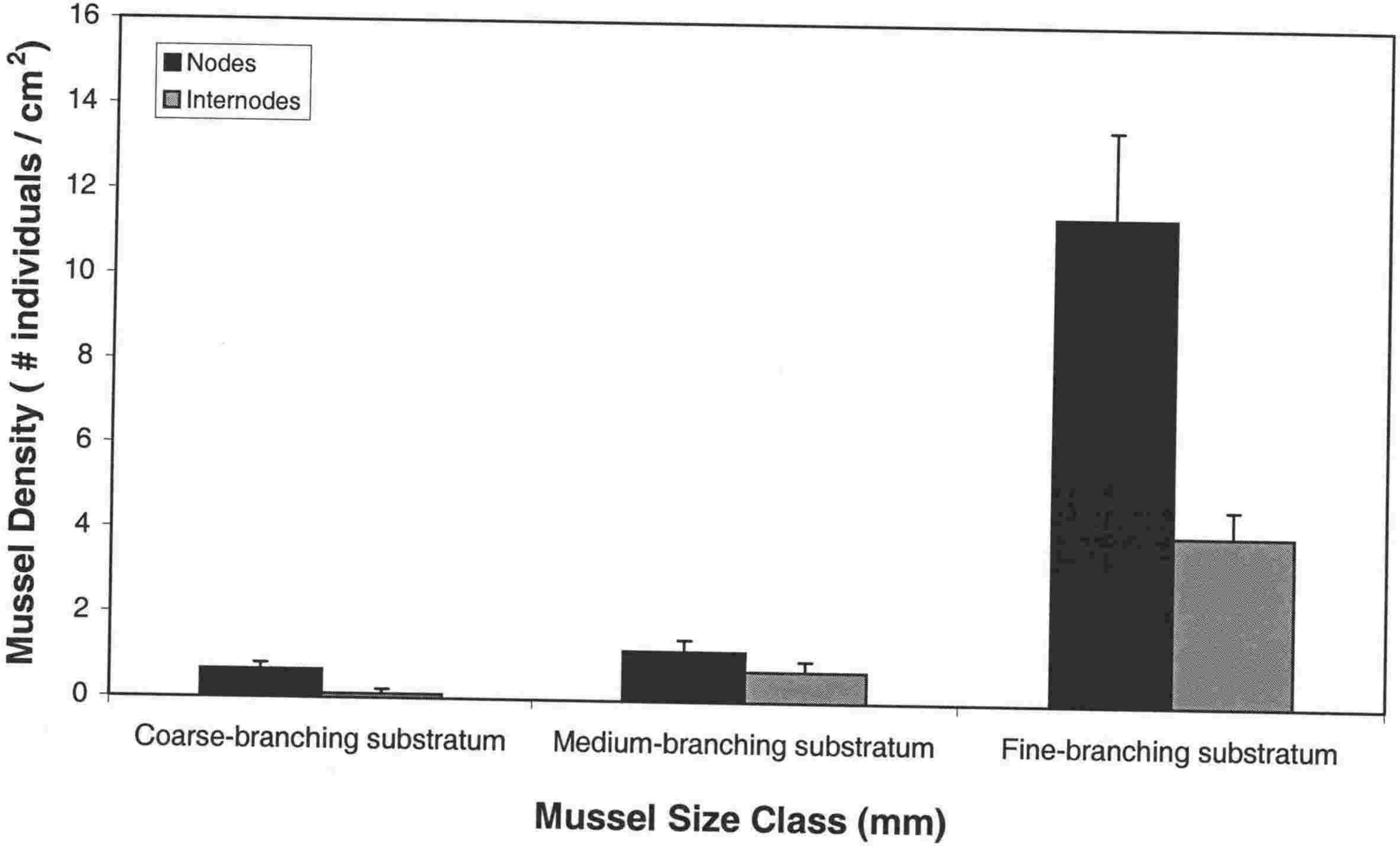

Figure 9. Mussel densities within node and inter-node areas within 3 artificial substrate types. (n = 6).

Table 1. Mean (±SE) percent mussel density within each of 5 size classes for 4 natural substrate types. Two-way ANOVA's are shown for each substrate type. Data were arcsine transformed for statistical analyses and back transformed to obtain the means.

Substrate Type	Mussel Size Class	Mean±SE	ANOVA				
	(mm)	%/cm^2	Source	df	F	p α = 0.05	
Coarse-branching Algae	< 0.49	5.62±3.50	Sample	2	0.20	0.819	ns
	0.5-0.99	6.74±3.10	Size	4	17.63	0.000	
	1.0-1.49	23.31±6.30	Sample x Size	8	2.33	0.075	ns
	1.5-1.99	52.63±3.34					
	>2.0	2.75±3.97	Error	15			
Medium-branching Algae	< 0.49	15.15±4.94	Sample	2	0.10	0.906	ns
	0.5-0.99	14.77±3.64	Size	4	10.44	0.000	
	1.0-1.49	27.35±2.37	Sample x Size	8	3.52	0.017	
	1.5-1.99	31.85±4.23					
	>2.0	2.57±4.35	Error	15			
Fine-branching Algae	< 0.49	50.48±1.26	Sample	2	1.08	0.365	ns
	0.5-0.99	30.57±1.46	Size	4	167.10	0.000	
	1.0-1.49	15.57±1.10	Sample x Size	8	2.23	0.086	ns
	1.5-1.99	1.76±2.28					
	>2.0	0.17±1.76	Error	15			
Hydroids	< 0.49	42.81±0.96	Sample	2	0.11	0.894	ns
	0.5-0.99	29.27±1.15	Size	4	173.34	0.000	
	1.0-1.49	17.60±0.71	Sample x Size	8	1.82	0.150	ns
	1.5-1.99	9.50±2.22					
	>2.0	0.05±0.48	Error	15			

Table 2. Mean (±SE) percent mussel density within each of 5 size classes for 3 artificial substrate types. Two-way ANOVA's are shown for each substrate type. Data were arcsine transformed for statistical analyses and back transformed to obtain the means.

Substrate Type	Mussel Size Class	Mean±SE	ANOVA				
	(mm)	%/cm^2	Source	df	F	p α = 0.05	
Coarse-branching Substrates	< 0.49	0.00±0.00	Substrate	2	0.00	0.998	ns
	0.5-0.99	0.00±0.00	Size	4	20.61	0.000	
	1.0-1.49	0.00±0.00	Sample x Size	8	0.12	0.998	ns
	1.5-1.99	0.29±0.06					
	>2.0	3.66±0.09	Error	75			
Medium-branching Substrates	< 0.49	0.01±0.01	Substrate	2	0.24	0.786	ns
	0.5-0.99	0.01±0.01	Size	4	15.79	0.000	
	1.0-1.49	0.05±0.03	Sample x Size	8	0.33	0.953	ns
	1.5-1.99	0.46±0.07					
	>2.0	5.23±0.13	Error	75			
Fine-branching Substrates	< 0.49	47.26±0.30	Substrate	2	3.14	0.049	
	0.5-0.99	18.79±0.54	Size	4	41.75	0.000	
	1.0-1.49	2.65±0.15	Sample x Size	8	5.34	0.000	
	1.5-1.99	2.15±0.23					
	>2.0	1.44±0.09	Error	75			

CHAPTER 5

Chemical Settlement Cues from Algae in the green-lipped mussel, Perna canaliculus.

Andrea C. Alfaro, Brent Copp, Shane Kelly, and Andrew G. Jeffs

ABSTRACT

Field and laboratory experiments were undertaken to test the effects of chemical cues from algal extracts on settlement of mussel larvae, Perna canaliculus. Extracts from 7 algae were mixed with phytogel to make settlement plates. These treatment plates and control plates (phytogel with no algal extract) were placed subtidally (5 m water depth) at Ahipara Bay, Ninety Mile Beach, northern New Zealand for a period of 2 weeks. Mussel settlement occurred in 5 out of 7 algal extract plates, but not in any of the control plates. Algal extract plates from 1-2 of the algal species used in the field experiments also were used in two laboratory experiment to test settlement of Perna canaliculus larvae which were reared at the Cawthron Institute hatchery, Nelson, New Zealand. These laboratory experiments conclusively indicated that algal extract plates attract a greater number of settling larvae than control plates. Although it is not known whether the chemical(s) that induced larval settlement are exuded from the algae themselves or the bacterial films which are likely to have covered the initial algal surfaces, these field and laboratory experiments are the first to indicate that chemical cues, in addition to known morphological cues from suitable substrata, are involved in the settlement process of the

New Zealand mussel, Perna canaliculus. These results may have relevant commercial implications for development of chemically-treated ropes to induce mussel settlement, which may be used reliably to harvest mussel spat from the wild to seed the aquaculture farms and could be used in a commercial hatchery.

INTRODUCTION

Larvae of many benthic marine invertebrates can to prolong their planktonic life stage until they encounter suitable physical and/or biological conditions that act to trigger settlement and metamorphosis of the larvae. Some physical factors involved in larval settlement are water flow, light, gravity, and shape and texture of the substratum (Sebens, 1983; Morse, 1991; Pawlik et al., 1991; Tamburri et al., 1996; Walters and Wethey, 1996; Abelson, 1997). However, biological factors, such as aggregative behavior, microbial films, and natural chemicals generally have been recognized as the most influential cues of larval settlement (Pawlik and Hadfield, 1990; Pearce and Scheibling, 1990; Pawlik, 1992a; Keough and Raimondi, 1995; Toonen and Pawlik, 1996). Considerable interest has revolved around the study of chemically-mediated settlement processes for a range of marine invertebrates (reviews in Rodríguez et al., 1990; Pawlik, 1992a). Chemical cues have been attributed to stimulate settlement in many marine invertebrates, such as abalone (Morse and Morse, 1984; Barlow, 1990), echinoderms (Pearce and Scheibling, 1990; Johnson et al., 1991), barnacles (Maki et al., 1990; Wright and Boxshall, 1999), polychaetes (Toonen and Pawlik, 1996; Walters et al., 1996), and bivalves (Fitt et al., 1990; Tritar et al., 1992; Turner et al., 1994). The nature of these chemical cues, in relation to the settlement of larvae, tends to fall in the categories of chemicals exuded by conspecifics, algae, and bacterial films. For example, settlement of larvae from the tube worm, Hydroides dianthus was attributed to be a direct response to water-borne compound(s) exuded by nearby live adult conspecifics (Toonen and Pawlik, 1996). Furthermore, the effects of bioorganic films on settlement of larvae for a number of species, including polychaetes, bryozoans, barnacles, protozoans, sponges, and ascidians showed a definite response by several larvae to microbial films prepared in the laboratory (Keough and Raimondi, 1995). Experiments with algal substrata, which often are covered by bacterial films, also have identified positive relationships between chemical cues versus larval metamorphosis and settlement rates (Morse and Morse, 1984; Pearce and Scheibling, 1990; Johnson et al., 1991; Walters et al., 1996). For instance, abalone larvae, Haliotis rufescens, were shown to initiate settlement as a response to chemical exudates from 3 foliose red algae (Laurencia sp., Gigartina sp., and Porphyra sp.) (Morse and Morse, 1984). Moreover, the green sea urchin, Strongylocentrotus droebachiensis was found to metamorphose on direct contact with aqueous extracts of the coralline red algae, Lithothamnion glaciale (Pearce and Scheibling, 1990). Considerable work has been undertaken to isolate and identify the specific chemicals involved in the settlement and metamorphosis of various larval species (Bonar et al., 1990; Pawlik, 1990; Pawlik and Hadfield, 1990; Zimmer-Faust and Tamburri, 1994). Chemicals such as gamma-aminobutyric acid (GABA), and L-3-4-dihydroxyphenylalanine (L-DOPA), which have been found in many organisms, have been identified as major inducers of larval settlement and metamorphosis (Barlow, 1990; Bonar et al., 1990; Fitt et al., 1990). However, because chemical inducers may be difficult to identify, many studies often start with testing settlement responses to algal or bacterial extracts, and later progress to more specific compounds (Fitt et al., 1990; Pearce and Scheibling, 1990; Johnson et al., 1991; Turner et al., 1994). For example, Fitt et al. (1990) found that veliger larvae of the oyster, Crassostrea gigas had a settlement response to an unknown compound, similar to L-DOPA, which came from a bacterial supernatant.

The evolutionary importance or advantages of chemically-mediated interactions continue to be debated (Schmitt et al., 1995). However, the clear advantages of settlement induced by conspecifics, and herbivorous species induced to settle by algae upon which the herbivore will feed, have been supported by numerous studies (Barlow, 1990; Pearce and Sceibling, 1990; Walters et al., 1996; Boettcher and Targett, 1998). For bivalve species, such as oysters and mussels, the advantages of settling on adult shells and macroalgae may provide 1) increased chances of survival in suitable habitats, 2) a transport vehicle via algal drift, 3) a transition stage from the plankton to the rocky shore, and 4) fertilization success. An important step in the life history of mussel species is a direct association with macroalgae either attached to the bottom or free-floating in the water column. A dramatic example of this relationship between mussel juveniles (spat) and macroalgae is seen at at Ninety Mile Beach, northern New Zealand, where massive quantities of algal drift material, covered with settled mussel spat, are collected from the shore and transported to mussel farms to seed aquaculture farms. The morphology of the filamentous algae or hydroids upon which these mussels settle have been identified to be an important determinant in the settlement rates of different sizes of mussel spat (Alfaro and Jeffs, in press). However, chemical cues exuded by different macroalgae also are believed to be involved in the mussel settlement process.

One of the major problems of undertaking experiments on chemically mediated settlement is the difficulty in obtaining viable larvae (Pawlik, 1992b). Larval collections from the field are confounded by the high temporal and spatial variability in larval abundance. Furthermore, spawning and maintaining larval cultures in the laboratory are often challenging (Pawlik, 1992b). Nevertheless, experiments on larval settlement responses to chemical signals are extremely valuable to the New Zealand aquaculture industry in terms of potentially increasing their seed stock from field collections of chemically treated ropes and better retention of mussel seeds on growth ropes. A unique opportunity to access hatchery-spawned mussel larvae, Perna canaliculus, from one of the few successful hatcheries in New Zealand, Cawthron Institute, Nelson, allowed for the first experiments to be undertaken to test for chemically-mediated settlement of this mussel species on various preferred macroalgae. Settlement of Perna canaliculus larvae on agar plates containing algal extracts and on control plates was investigated in the field, at Ninety Mile Beach, northern New Zealand, and in laboratory experiments at Leigh Marine Laboratory, The University of Auckland, New Zealand.

METHODS AND MATERIALS

Field Experiments

Extracts from 7 algal species, which are preferred by Perna canaliculus as settlement substrata, were prepared in the laboratory and added to phytogel mixtures and poured into separate plates (plastic petri dishes of 50 mm in diameter). The algae were Scytothamnus australis, Melanthalia abscissa, Corallina officinalis, Carpophyllum maschalocarpum, Plocamium costatum, Osmundaria colensoi, and Gigartina alveata. A flat plastic rack (about 1 m^2) was constructed and used to secure the gel plates. Two replicate gel plates for each of the 7 algal extracts, 2 control plates (phytogel without algal extract), and 2 blank plates (no phytogel nor algal extract) were placed randomly in the rack and suspended in the water column at Ahipara Bay, Ninety Mile Beach, northern

New Zealand. The rack was secured perpendicular to the surface at about 5 m below the water surface with four ropes anchored from each corner of the rack to the seafloor (about 18 m water depth). The rack was kept afloat by surface buoys. After 2 weeks, the rack was retrieved and the number of mussels settled in each of the gel plates enumerated. Retrieval of the rack was not possible before 2 weeks due to poor weather conditions that prevented access to the study site. A one-way ANOVA test was conducted on the log-transformed (log (X+1)) data, and a Tukey test was used to identify settlement differences among gel plates. Specific methodology for chemical procedures is not described herein due to pending patten submission.

Laboratory Experiments

Two algal species, which had the greatest number of mussels that settled in the field experiment were used in the laboratory experiments. Algal extracts of Scytothamnus australis and Melanthalia abscissa were processed as described above, to produce 6 replicate gel plates for each alga. Three algal extract plates from each algal species were placed in each of 2 tanks (50 x 60 x 60 cm) of filtered seawater. In addition, 3 control plates (phytogel with no algal extract) also were added to each of the water tanks. The 9 plates were randomly placed on the bottom of each water tank. The tanks had free-flowing water with a 60-μm mesh in the intake and outflow pipes to prevent larvae from entering and exiting the experimental tanks. Both water tanks were aerated throughout the experiment to provide adequate oxygenation to the larvae and to ensure a constant mixing of water in the tanks. The tanks also were kept in the dark to prevent the color of gel plates and light stimuli to interfere with the chemical cue experiments.

Late stage or pediveliger mussel larvae, Perna canaliculus, were transported for 5 hours at 5 °C from Cawthron Institute to Leigh Marine Laboratory, The University of Auckland. Once at the laboratory, about 3,000 larvae were immediately placed in each of the 2 experimental seawater tanks. The larvae were fed only before leaving the commercial hatchery and not during the experiment. After 24 hours, the gel plates were removed carefully from the water tanks and all settled mussels on the plates were examined and enumerated under the microscope. Analyses of variance and Tukey post hoc tests were used to statistically analyze the log-transformed (log (X+1)) data from this laboratory experiment.

A second laboratory experiment was conducted in the same manner as the previous experiment with algal extract plates of Scytothamnus australis only. Four replicate algal extract plates and 4 control plates were placed in each of 2 water tanks as above. The number of mussels settled on the 16 treatment and control plates were counted at the end of the experiment.

RESULTS

Field Experiments

Although the overall number of mussels settled on gel plates in the field were low, 5 out of 7 algal extract plates had settled mussel, whereas none of the control nor blank plates contained any mussels. The mean (±SE) abundance of mussels on algal extract plates was 1.5±0.5 mussels/ plate, and the range was 0-6 mussels/plate. While clear differences were observed between control and blank plates versus treatment plates, a one-way ANOVA test among the 5 algal extract plates which had settled mussels indicated no significant difference among mean mussel abundances among plates (ANOVA; $F_{(4,5)} = 0.908$, $p = 0.524$). A Tukey test also resulted in no significant differences among any combination of treatment, control, and blank plates (Tukey test; $p > 0.05$). (Fig. 1).

Laboratory Experiments

Results from the first laboratory experiments with Scytothamnus australis and Melanthalia abscissa algal extract plates clearly showed higher larval settlement on treatment plates compared to control plates. Mean (±SE) abundance of mussels on S. australis and M. abscissa algal extracts, and control plates were 88±16, 73±26, and 2±1 mussels/plate, respectively. Mussel abundance ranges were 33-142, 9-174, 0-5 mussels/ plate for S. australis and M. abscissa algal extract, and control plates, respectively. A two-way ANOVA test, with tank and treatment (2 algal extract plates and 1 control plate) as fixed factors, resulted in a non-significant difference between tanks (ANOVA; $F_{(1,12)} = 0.54$, $p = 0.478$), and significant differences among treatments (ANOVA; $F_{(2,12)} = 55.18$, $p = 0.001$) and interaction (ANOVA; $F_{(2,12)} = 5.13$, $p = 0.025$). A Tukey test found no significant difference between S. australis and M. abscissa algal extract plates (Tukey test; $p = 0.415$), but highly statistical differences between S. australis and control plates (Tukey test; $p = 0.001$) and between M. abscissa and control plates (Tukey test; $p = 0.001$). (Fig. 2).

The second laboratory experiment, which tested the effect of chemical cues from Scytothamnus australis, resulted in a clear difference among treatment and control plates. However, the total number of mussels settled in this experiment was much lower that the first laboratory experiment. The mean (±SE) abundance and range of mussels in plates with S. australis extract were 13±2 and 2-21 mussels/ plate. Conversely, no mussels settled on the control plates at all. (Fig. 3).

DISCUSSION

The distribution and abundance of adult populations of broadcast spawners, such as mussels, are highly dependant on the physical and biological factors that affect larvae during their pelagic life. Oceanographic processes, such as ocean currents, wind conditions, and water temperature, may determine the transport and survival of larvae in the water column. Smaller scale interactions between larvae and potential settlement substrata are determinants in the successful transition between larval life stage and the settled juvenile.

Adult populations of Perna canaliculus at Ninety Mile Beach, northern New Zealand, are maintained by a dynamic transition between spawned gametes and by larval and post-larval mussel arrivals back to the rocky shore. In the water column, mussel larvae may encounter and settle on abundant filamentous red algae (Alfaro and Jeffs, in press). These settlement materials may drift, and periodically accumulate, in exceedingly high quantities at Ninety Mile Beach (up to 100 tonnes of algae with mussel spat) (C. Hensley, personal communication). The arrival of these massive quantities of drift algae, covered with mussel spat (up to 100% cover) are an indication that the settlement process of mussel larvae onto algal material may be mediated by specific morphological and chemical cues.

Previous work on small-scale settlement patterns of Perna canaliculus within morphologically distinct natural and artificial algae revealed strong size- and site-specific selectivity by settling mussels (Alfaro and Jeffs, in press). Field and laboratory experiments indicated that large mussels (1.5-2.0 mm in shell length) preferentially settled on coarse-branching natural and plastic algae, and that small mussels (< 0.5 mm in shell length) settled in greater numbers on fine-branching substrata (Alfaro and Jeffs, in press). Furthermore, mussel settlement was significantly higher on highly branched algae, and higher on node areas versus internode areas within both natural and artificial algae (Alfaro and Jeffs, in press). Within the present research, the morphological component of the algae was removed by introducing natural algal extracts on phytogel plates used as settlement surfaces. Thus, this study provides the first indication that chemical cues also may be involved in the settlement process of Perna canaliculus on various algal species.

Initial field settlement experiments with algal extract, control, and blank gel plates resulted in mussel settlement on 5 out of 7 algal extract plates and no settlement on control nor blank plates. These results suggest that chemicals within the algal extracts stimulated mussel settlement even within the low mussel abundances observed within the field experiment. Mussel settlement on the gel plates may have been underestimated by the fact that mussels could have attached and detached from the gel plates during the 2 week field experiment. Conversely, leaching of water-soluble compounds from the algal extracts would have probably taken place within a few days after deployment of the plates. Thus, if the settlement inducers were water-soluble, the algal extract plates would have been effective attractants only at the beginning of the experiment period. During the 2-week period, bacterial films are likely to have formed on the gel plates and these films potentially may have produced chemical cues. Keough and Raimondi (1995) found that total recruitment of various larvae from polychaetes, bryozoans, barnacles, protozoans, sponges, and ascidians species increased within experimental plates exposed to microbial films for up to 6 days in the laboratory and then placed in the field to test larval recruitment for up to 6 days. However, the results from the present study suggest that the potential chemical influence of bacterial films formed during the experiments did not interfere with the testing of settlement differences among control and treatment plates. On the other hand, because bacterial films are likely to have formed over the original natural algal material (before chemicals were extracted from the algae), these experiments could not distinguish whether settlement was enhanced by chemicals within the algae themselves or the bacteria covering the algae. Johnson et al. (1991) conducted settlement experiments with starfish larvae, Acanthaster planci, which showed preferential settlement on the crustose coralline algae, Lithothamnium pseudosorum. However, further experiments indicated that settlement, in fact, was chemically induced by bacterial films, which readily formed on the surface of the coralline algae (Johnson et al., 1991).

Two controlled laboratory experiments on mussel larval settlement on algal extract gel plates resulted in significantly higher settlement on plates with algal extracts of Scytothamnus australis and Melanthalia abscissa species compared to control plates. These results also suggest that chemical cues from the algae, or bacterial films on the surface of the algae, may induce settlement of Perna canaliculus. It is possible that compounds such as GABA and L-DOPA exuded by the algae or bacterial films may be responsible for the clearly high settlement rate of mussels on treatment plates compared to control plates. However, elucidation of specific chemicals involved in the triggering of mussel larval settlement needs further investigation. While both laboratory experiments conclusively indicated a preference in mussel settlement to treatment gel plates, the second laboratory experiment resulted in lower overall settlement than in the first laboratory experiments. These different results were attributed to the fact that larvae used in the second experiment were younger, and most were not ready to settle.

Active exploratory behavior has been observed in several invertebrate larvae near the time of settlement (Barlow, 1990; Fitt et al., 1990; Zimmer-Faust and Tamburri, 1994). Observation of the behavior of settling and newly settled mussels in the present laboratory experiments suggest that Perna canaliculus utilized foot exploration and crawling techniques to test the substratum before producing byssi threads. Barlow (1990) used video techniques to observe an increased foot exploratory behavior in the abalone Haliotis rufescens when the larvae were exposed for a few minutes to GABA. Crawling behavior also was observed prior to settlement in the oyster larvae, Crassostrea gigas, when the larvae were exposed to an unknown dissolved chemical from cultured Alteromonas colwelliana and Vibrio cholerque bacteria (Fitt et al., 1990). Furthermore, the fact that all treatments were in the same tank implies that settlement cues for this species may be on contact rather than a water-borne chemical trigger.

The results from the first laboratory experiment with Perna canaliculus larvae involving Scytothamnus australis and Melanthalia abscissa extract plates indicated no significant differences in mussel settlement between these 2 algal extracts. Although both S. australis and M. abscissa extract plates may have contained similar chemicals that induced similar mussel settlement rates, these experiments may have been biased slightly due to uneven surface of one plate containing M. abscissa extract in tank A. This treatment plate had a rugose surface instead of the smooth surfaces of the other plates. Mussel larvae were observed in higher numbers (174 mussels) attached to small depressions and distinct indentations on this particular plate. Although this experimental bias did not affect the results and conclusions of these experiments, the attachment behavior to a rugose surface is in agreement with previous work reporting on increased mussel settlement on nodes within branching algae (Alfaro and Jeffs, in press).

The chemically-mediated settlement preferences reported herein, and the substratum morphologic selectivity previously reported (Alfaro and Jeffs, in press), suggest that the mussel Perna canaliculus is well adapted to settle on filamentous algae. Specific filamentous algae, such as S. australis and M. abscissa, may provide a mechanism for transport and dispersal of larvae and post-larvae to suitable rocky habitats. Furthermore, drift algae and attached algae on the rocky shore also may provide a microhabitat where mussels can attain a large enough size before transitioning from the water column to the adult mussel bed, where the competition for space and food are high.

ACKNOWLEDGEMENTS

We thank the Morrogh familiy for their helped in the field. This project could not have been possible without the generous assistance of H. Kaspar, S. Fox, and the Cawthron Institute, Nelson, New Zealand who provided the mussel larvae. We also thank A. Morgan, Darshani, and the Leigh Marine Laboratory at The University of Auckland, New Zealand for assistance with the laboratory experiments. K. Campbell provided technical and editorial expertise. This research partly was funded by a grant from the New Zealand Foundation for Research, Science and Technology, and a Graduate Research Grant to A. C. Alfaro from The University of Auckland, New Zealand.

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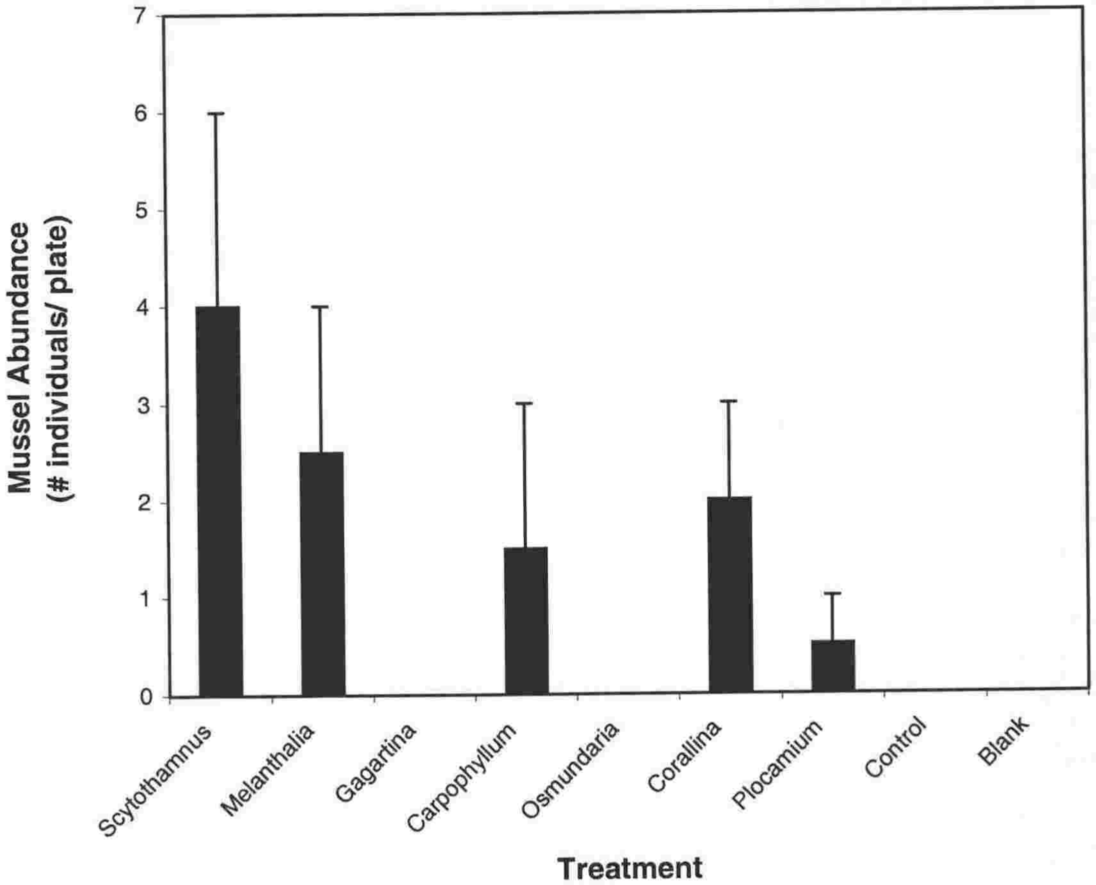

Figure 1. Mean (± SE) abundance of mussels settled on gel plates containing extracts from 7 different algal species (Scytothamnus australis, Melanthalia abscissa, Corallina officinalis, Carpophyllum maschalocarpum, Plocamium costatum, Osmundaria colensoi, and Gigartina alveata), and control and blank plates at Ahipara Bay, Ninety Mile Beach, northern New Zealand.

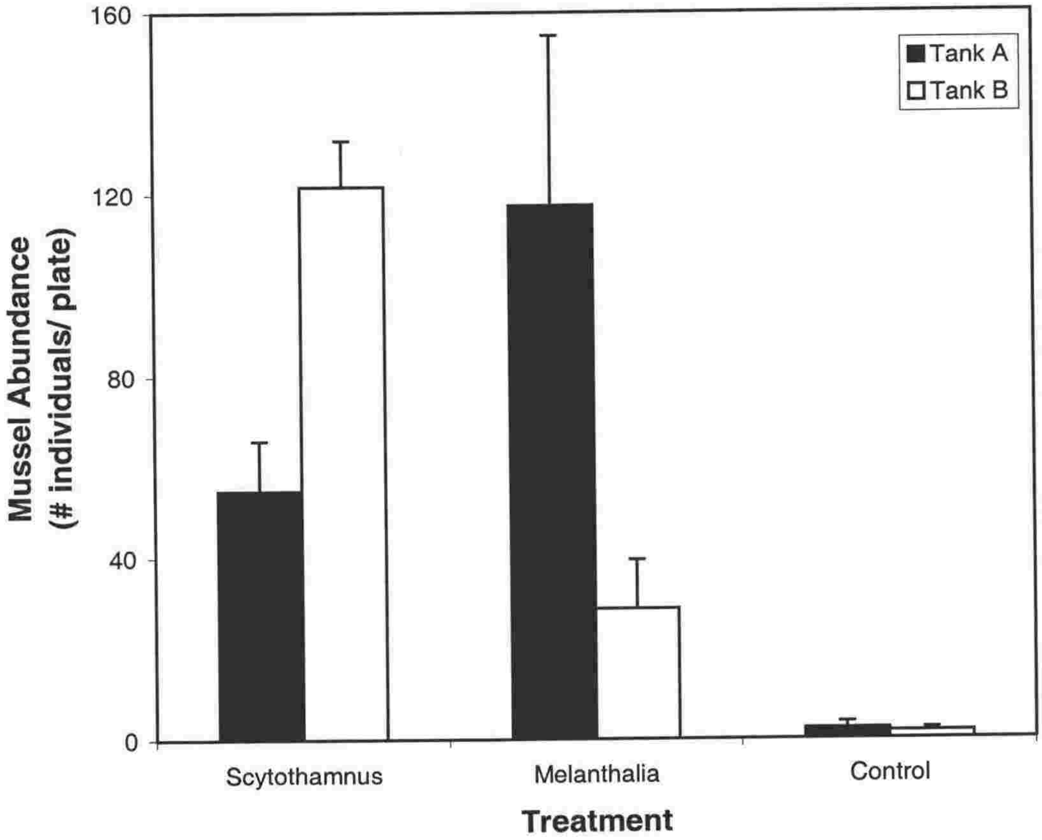

Figure 2. Mean (± SE) abundance of mussel larvae settled on gel plates containing extracts from 2 different algal species (Scytothamnus australis and Melanthalia abscissa), and control plates in laboratory experiments.

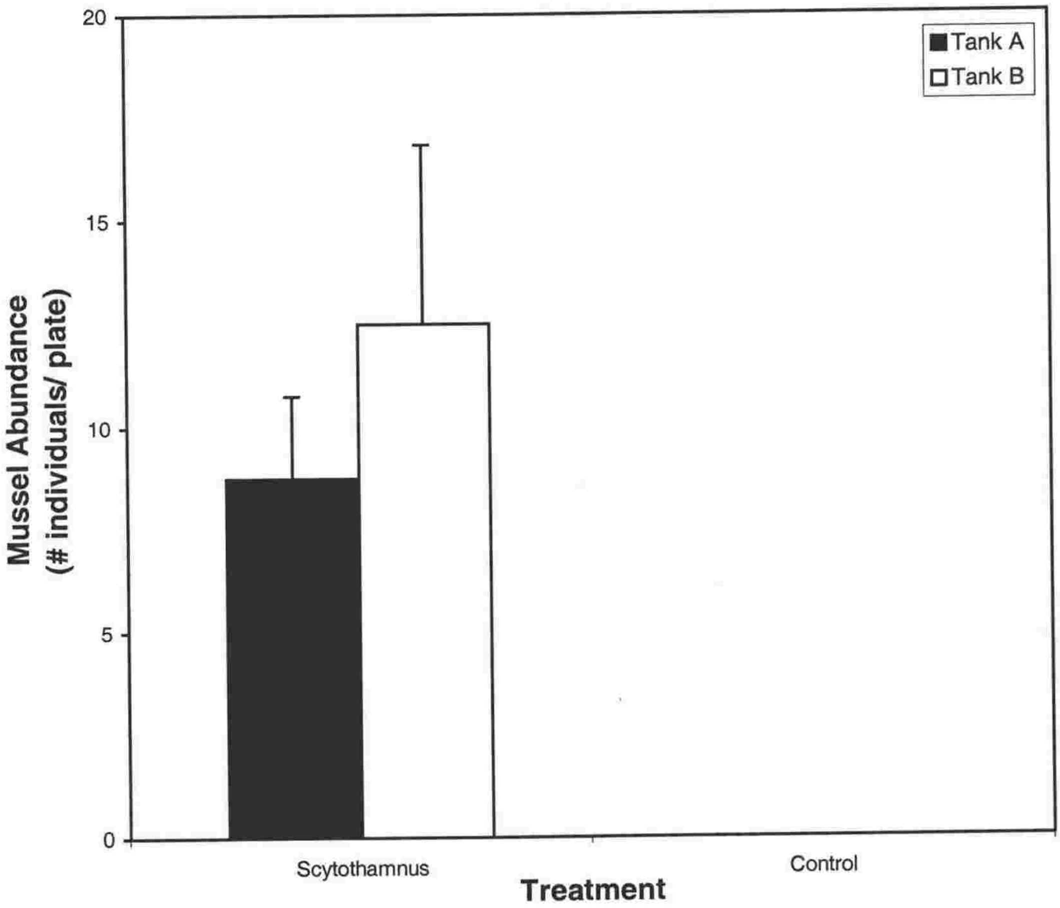

Figure 3. Mean (± SE) abundance of mussel larvae settled on gel plates containing extracts from the alga Scytothamnus australis, and control plates in laboratory experiments.

CHAPTER 6

Population Dynamics of the Green-lipped Mussel *Perna canaliculus* at Various Spatial and Temporal Scales in Northern New Zealand

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In submission: Ecological Monographs

ABSTRACT

Ecological processes that differentiate and maintain intertidal populations of mussels, *Perna canaliculus,* were studied within 3 sites at Ninety Mile Beach, northern New Zealand. At these 3 sites (Scott Point, The Bluff, and Tonatona Beach), the dynamics of larval availability, primary and secondary settlement, recruitment, and mortality rates were investigated at various spatial and temporal scales. 1) Mussel concentrations in seawater were variable with respect to study site and time of year, with highest abundances at the northernmost population (Scott Point) and lowest concentrations at the middle population (The Bluff). In seawater at all 3 sites, small mussels (<0.25 mm in shell length) were more abundant in August 2000, while larger mussels (>0.5 mm in shell length) were more abundant in March 2001. 2) Primary and secondary settlement patterns were investigated during short-term (daily) and long-term (monthly) settlement experiments, within quadrats that were cleared of all mussels in both the mussel bed and in adjacent algal band habitats. At all sites, primary settlement (<0.5 mm in shell length) was high within the algal band habitat in August 1999, 2000, and 2001. Conversely, secondary settlement (>2.0 mm in shell length) was high within cleared areas in the mussel beds in November-March 1999-2000, 2000-2001. 3) Abundance of mussels settling on artificial substrates placed in the intertidal did not differ greatly from comparable areas of natural substrates (bare rock or algae within cleared quadrats). 4) Recruitment and mortality rates were recorded during monthly surveys of the adult populations. Within 3 mussel size classes (<24, 25-74, >75 mm in shell length), peak recruitment coincided with high mortality in August of the 2 years studied. However, the most dramatic turnover of the population was observed at Scott Point in both years, following a spawning event. In adjacent waters at Scott Point, large accumulations of drift algae covered with juvenile mussels (up to 100% cover) may deplete food supplies usually delivered to intertidal adult mussels, causing their demise. Mats of adult mussels were observed "peeling-off" from the rocky shore at this time of the year, making space available to the new recruits. Where nearshore algal accumulations were moderate to low, only moderate to low mussel turnovers were observed (e.g. Tonatona Beach and The Bluff).

Key words: Mussels; Spatial Scales; Temporal Scales; Population Dynamics; Settlement Patterns; Recruitment; Mortality; Drift Algae; *Perna*.

INTRODUCTION

Most intertidal invertebrates depend on the successful settlement and recruitment of dispersing larvae to maintain viable populations. Successful recruitment to an adult population may be highly variable in space and time, reflecting the demographic diversity of a population (Hughes 1990; Doherty & Fowler 1994; Hunt & Scheibling, 1997; Reusch & Chapman, 1997). Numerous studies have focused on the physical and biological processes that influence settlement patterns of planktonic larvae on morphologically and chemically distinct substrates (Butman, 1987; Schneider & Mann, 1991a, b; Butman & Grassle, 1992; Grassle et al., 1992; Pawlik, 1992; Bourget & Harvey, 1998; Alfaro & Jeffs, in press). However, many marine invertebrates, such as mussels, may re-settle several times on different substrates during their post-larval and juvenile stages (Armonies 1992; Buchanan & Babcock 1997; Hunt & Scheibling, 1998; Alfaro & Jeffs, in press). Re-settlement may take place through passive waterborne dispersal, mucous-drifting, and crawling behavior (Bayne 1964; Kennedy, 1984; Lane et al., 1985; Martel, 1993; Buchanan & Babcock 1997). Bayne (1964) first recognized the importance of filamentous algae as the primary settlement substrate of larvae (< 0.5 mm) of the mussel *Mytilus edulis*, which later move to the adult mussel beds as secondary settlers (1-2 mm) through a bysso-pelagic phase. Juvenile mussels in the primary and secondary settlement phases actively explore and choose settlement substrates by a crawling behavior that involves foot movements and anchoring with mucous threads and filaments (Sigurdsson, 1976; Board, 1983; Kennedy, 1984). Further studies on settlement patterns of mussel larvae and juveniles on filamentous substrates have revealed size-specific selectivity to morphologically distinct algae and hydroid species from subtidal to intertidal areas (King et al., 1990; Hunt & Scheibling, 1996; Buchanan & Babcock 1997; Alfaro & Jeffs, in press). Thus, algal substrates, especially those found near adult mussel beds, may provide an important transition stage for primary mussel settlers to attain a large enough size before transferring to the adult mussel bed. By entering the adult mussel bed as larger juveniles, these mussels may reduce the risks of ingestion by adult conspecifics and increase their ability to compete for space.

While the mussel settlement process is dynamic and may involve various settlement substrates and transitions to new substrates, recruitment involves the successful establishment of individuals in the adult mussel bed. Variations in recruitment rates among populations reflect differences in larval and post-larval availability and/or early mortality of post-settlers (Connell, 1985; Hunt & Scheibling, 1997; Jenkins et al., 1997). The balance between initial settlement on the mussel bed and early mortality is regulated by biological processes, such as larval production, competition, and predation, and physical processes, such as water motion, temperature, salinity, and desiccation, of a particular geographical area.

Due to the unique oceanographic conditions at Ninety Mile Beach, northern New Zealand, large quantities (> 140 tons per year) of drift algae with associated mussel juveniles, or spat, accumulate nearshore. The drift algae serve as primary settlement sites for 0.25 mm to 5 mm sized spat, and can transport spat along shore for several kilometers before being washed ashore onto the beach. These wash-up or spatfall events are unique in New Zealand and are harvested to supply about 80% of the seed requirements for the national mussel industry (Jeffs et al., 2000). Such pulses of floating algae and attached mussel spat are likely to have a major effect in the structuring of adult mussel populations of the area. The populations themselves also may be regulated by biological and physical factors that affect adult mussels, such as competition, predation, hydrodynamic forces, temperature, and salinity. The sum total of these biological and physical factors is likely to be reflected in the growth rates and mortality rates of mussels within various populations. Therefore, comparisons among mussel populations must take into account a combination of interacting factors that affect mussels at various life-history stages. This study addresses the spatial and temporal variability in abundance and size-specific settlement patterns, recruitment, and mortality rates that affect the population dynamics of the major intertidal mussel populations at Ninety Mile Beach, northern New Zealand.

METHODS AND MATERIALS

Study Site

Settlement experiments were conducted at 3 intertidal sites along Ninety Mile Beach, northern New Zealand (Fig. 1). Rocky intertidal areas at Scott Point, The Bluff, and Tonatona Beach support the only intertidal mussel populations along the 90-kilometer stretch of sandy coast (Fig. 1). The coast at Ninety Mile Beach is exposed to a strong hydrodynamic regime. The oceanographic conditions are mediated by the predominantly southwesterly winds and swells, and the confluence of the northbound Westland and the southbound West Auckland currents (Stanton, 1973; Sharples, in press). The rocky outcrop at Scott Point is mostly covered with mussels, year around. At the subtidal fringe, a dense band or zone of filamentous red and brown algae defines the lower edge of the intertidal mussel bed. Mussels at this site are healthy and fast growing, as indicated by the bright green concentric growth lines and the brown radial color lines, which also are found in farm-grown mussels. The Bluff is a small rocky intertidal area mid-way along Ninety Mile Beach (Fig. 1). Mussel beds at this site are not extensive, but mussel abundances are consistent throughout the year. The sub-optimal growing conditions for these mussels may be inferred from records of low growth rates and relatively high levels of parasite infestation (Alfaro et al., in press; A. C. Alfaro, unpublished data). An algal band also is prominent just below the adult mussel bed at The Bluff, but these algae are of low abundance, especially in the winter. Mussels at the southernmost site, Tonatona Beach, are of intermediate abundance and growth rates relative to the other 2 sites (A. C. Alfaro, unpublished data). A mixture of old and young mussels often is apparent through the year, although abundances fluctuate. Algal cover is high at the low tide mark and more abundant in the summer.

Mussel Concentrations in Seawater

To quantify the larval and post-larval mussel concentrations at the shoreline, water samples were collected from seawater adjacent to the 3 adult mussel beds. Three replicate 20-liter water samples were collected during the spawning season in August, October, and December 2000, and March 2001 from each of the 3 sites. Water samples were collected with a hand pump, and filtered though a 100-µm mesh according to Hunt & Scheibling (1996). The samples were fixed in 10 % formaldehyde, and mussels were counted and measured under the microscope in the laboratory. Mussel concentrations within 3 size classes (< 0.25, 0.25-0.5, and >0.5 mm in length) were determined for each site during the sampling period.

Mussel Settlement and Recruitment

Because mussel spat (including *Perna canaliculus*) may utilize various substrates before reaching their final destination, the distinction between settlement and recruitment often is difficult to ascertain. In this study, settlement refers to post-larval mussels of generally < 5 mm, which often attach to filamentous materials before transferring to a more physically stable hard substrate. Recruitment is used, herein, to refer to juvenile mussels of generally > 5 mm, which are likely to attach to rocky substrates and remain in the adult population. These definitions are consistent with previous work on size-specific settlement patterns of *Perna canaliculus* on algal and mussel substrates in rocky intertidal areas of New Zealand (Buchanan, 1994; Buchanan & Babcock 1997; Alfaro & Jeffs, in press).

Short-term Settlement Experiments

Mussel settlement patterns within quadrats of natural and artificial substrates were examined during five 2-5 day intervals at 3 rocky intertidal sites between August 1999 and March 2000. Within each of the 3 sites, 2 habitats (mussel bed and algal band) and 2 substrates (mesh and natural algae or bare rock) were examined in a factorial design (Fig. 2). In the mussel bed habitat, four 225 cm^2 areas or quadrats were cleared of mussels and left as bare rock substrate, while another 4 quadrats were cleared of mussels and mesh material was attached to the rock with concrete nails. The mesh material used was strips of window screening material (2 mm mesh size) of a total area of 200 cm^2 per quadrat. Another 8 quadrats of the same size were cleared of mussels in the algal band habitat. Four of these quadrats were left with natural algal substrates, but all mussels were removed carefully from the algae by hand or with forceps. The other four quadrats in the algal band habitat were cleared of mussels and algae, and mesh material was attached in place, as described above. A 5 cm border also was cleared of all mussels and algae around all experimental quadrats to prevent mussels from crawling into the quadrats from adjacent areas (Hunt & Scheibling, 1998). All quadrats were established randomly within each habitat and were at least 50 cm away from one another. Each quadrat was marked with concrete nails driven into the rock and its position mapped for later identification. To ensure consistent algal abundance among quadrats, that also was similar to the mesh cover (200 cm^2), algal substrates within the quadrats in the algal band habitat were thinned out from areas of 100% algal cover. Algal surface areas were determined using methods described in Alfaro & Jeffs (in press). After the 2-5 day settlement experiments, all natural and artificial substrate material and all mussels within each quadrat were removed and frozen until mussels were counted and measured at a later date. Daily settlement rates for each habitat and substrate combinations were determined using new quadrats with new algal and mesh substrates in each of the 5 sampling events. Mussel settlement rates within 3 different size-classes (<0.49, 0.5-1.99, > 2.0 mm in length) were obtained from each of the 2 habitats and 2 substrate types using laboratory methods described in Alfaro & Jeffs (in press).

Long-term Settlement Experiments

Long-term settlement experiments were conducted in both mussel bed and algal band habitats in each of the 3 study sites, but only mesh substrates within cleared quadrats were used. From the short-term settlement experiments, it was established mussel settlement rates did not greatly differed between algal and mesh material. Thus, mesh material was used in the long-term experiments as a standard substrate within which mussel settlement could be monitored for longer periods of time. These quadrats were established in the same manner as in the short-term experiments. The sampling period for these experiments varied from 24 to 43 days. The experiment was repeated 13 times at each study site between July 1999 and March 2001, with more intensive sampling just after the spawning season (July to December). Mussel settlement rates within each of the 2 habitats (mussel bed and algal band) were standardized to 30-day sampling periods for each of the above mussel size classes to facilitate comparisons among different months. Seasonal differences were tested by conducting separate analyses for each of the 2 years (July 1999-June 2000 and July 2000-March 2001).

Population Dynamics of Mussel Beds

The abundance and size-frequency distribution of mussels within mussel beds at the 3 intertidal populations at Ninety Mile Beach were monitored between July 1999 and March 2001. Four 625 cm^2quadrats were randomly placed within each of 3 mussel beds at Scott Point, The Bluff, and Tonatona Beach 13 times during the 21-month sampling period. Each time, all mussels inside each quadrat were removed using a metal scraper, frozen, and later counted and measured. All mussels were classified into 3 size-classes (< 24, 25-74, and > 75 mm in shell length).

Recruitment Rates

Recruitment rates were determined by recording the abundance of mussels between 5-24 mm in shell length within quadrats sampled in the population dynamics experiments between July 1999 and March 2001. Comparisons of recruitment abundances among sites and dates were performed separately for each of the 2 years sampled.

Mortality Rates

Mortality rates of mussels within each of the 3 intertidal populations were estimated by quantifying the number of empty shells found within quadrats sampled in the adult mussel bed between July 1999 and March 2001. In order to prevent recounting of individuals, only right valves of dead mussels were counted. The right valves were then measured and classified under 2 size classes (< 25, and > 25 mm in shell length). Empty shells were examined for any marks (i.e. holes, scrapes, broken edges) that may have indicated death due to predation (i.e. predatory snails, sea stars, and crabs). Dead mussels that had no sign of predation were assumed to have died of other causes (i.e. lack of food, or poor health). The number of mussels eaten by predators was compared to the number of unmarked empty shells among sampling times and among sites. The percent mortality of new recruits (5-24 mm in shell length) and adult mussels (25-121 mm in shell length) were compared among site, date, and cause of death (definite predation or unknown causes).

Algal Abundances

To determine the predominant algal species within the algal band habitats, 4 randomly chosen 625 cm^2 quadrats were sampled at each of the 3 study sites. A new set of 4 quadrats was sampled on 5 occasions between August 2000 and March 2001 at each study site. All algal material within each of the quadrats was removed with a metal scraper and frozen for later analyses. The algal species were identified and their abundances quantified by surface area in the laboratory. Algal abundances were compared among sites and among sampling times for each year.

Statistical Analyses

Analyses of variance were used to identify statistical differences among processes affecting various aspects of the population dynamics of 3 intertidal mussel populations at Ninety Mile Beach. Data were tested for normality, independence, homoscedasticity, and transformations were performed where necessary.

RESULTS

Mussel Concentration in Seawater

Larval and post-larval concentrations in seawater were highly variable in space and time. The overall trend among samples indicated that the sea water near Scott Point had greater concentrations of mussels than Tonatona Beach, and that Tonatona Beach had greater concentrations than The Bluff throughout the sampling period (Fig. 3). The total mean (±SE) mussel concentrations for Scott Point, Tonatona Beach, and The Bluff were 37±4, 5±2, and 13±2 individuals/ 20 L, respectively, and the ranges were 18-58, 0-16, and 1-25 individuals/ 20 L, respectively. Monthly variability in mussel concentration between August 2000 and March 2001 indicates that mussel larvae and post-larvae (< 0.25 mm) were more abundant at the beginning of the spawning season in August, and least abundant after the spawning season in December 2000 and March 2001 (Fig. 3). However, larger mussels (> 0.5 mm) increased in abundance through the sampling period, especially at Scott Point. Mussel abundances were log-transformed to meet statistical requirements. A 2-way ANOVA comparing mean concentrations of mussels among sites and dates for 3 mussel size classes are shown in Table 1. Result from Tukey tests comparing levels within factors show no statistical differences between various sites and months for medium-sized mussels (0.25-0.5 mm), which indicates a transition trend between the inverse abundance relationship between small and large size classes (Table 1).

Short-term Settlement Experiments

Daily settlement patterns between August 1999 and March 2000 revealed marked differences in mussel settlement between mussel bed and algal band habitats at each of the 3 study sites (Fig. 4). However, differences in mussel settlement between mesh and natural substrates were apparent only at Scott Point (Fig. 4 & Table 3). Mussel abundances generally were higher at the beginning of the spawning season (August) for mussels < 1.99 mm in shell length. However, at the end of the spawning season (December and March), mussel abundances were higher for larger individuals (> 2.0 mm in shell length) (Fig. 4). Total mean mussel densities (±SE) within 2 habitats, 2 substrates, and 3 sites for the short-term experiments are shown in Table 2. Four-way ANOVA tests (site, habitat, substrate, and date as fixed factors) of mean mussel abundances for each mussel size class are shown in Table 3. Tukey test pair-wise comparisons also are shown in Table 3.

Long-term Settlement Experiments

Results from the long-term experiments follow a similar pattern to those from the short-term settlement experiment. Monthly settlement patterns for quadrats in the algal band habitat suggest that small mussels (< 1.99 mm) are more abundant during the spawning season (August- December), but densities of larger mussels (> 2.0 mm) generally were less variable over time (Fig. 5). Mussel settlement inside the mussel bed habitat indicates that small mussels also were more abundant during the spawning season; however, even more accentuated is the trend that larger mussels (> 2.0 mm) are more numerous between spawning seasons (December-July) (Fig. 5). Total mean mussel abundances (±SE) and ranges for both habitats at the 3 sites are shown in Table 2. A three-way ANOVA test comparing mean mussel abundances among 3 sites, between 2 habitats, and among dates, resulted in statistical significance in all factors and interactions for all 3 mussel size classes for years 1 and 2 (Table 4&5). Non-significant pair-wise comparisons with Tukey tests also are shown in Table 4&5.

Population Dynamics of Mussel Beds

Results from studies of the population dynamics of mussel beds within 3 intertidal areas at Ninety Mile Beach indicate that there were clear differences in total abundance and size-frequency distribution of mussels over the 2-year sampling period. Total mussel abundances were higher at Scott Point, followed by Tonatona Beach, and finally The Bluff (Fig. 6). For year 1, the means (±SE) for Scott Point, ' The Bluff ι, and Tonatona Beach were 1133±140, 116±4, and 308±34 individuals/ 625 cm^2, respectively, and the ranges were 88-2395, 85-145, 70-705 individuals/ 625 cm^2, respectively. For year 2, the means (±SE) for Scott Point, ' The Bluff ι, andTonatona Beachwere 1056±115, 119±5, and 215±20 individuals/ 625 cm^2, respectively, and the ranges were 56-1946, 56-152, and 66-504 individuals/ 625 cm^2, respectively. Populations at Scott Point and Tonatona Beach had similar monthly fluctuations in mussel abundance during the 2-year study (Fig. 6). High mussel abundances occurred during the spawning season (August-December), followed by a gradual decline in number through to June and marked increase in July-August (Fig. 6). The seasonal patterns within these 2 populations revealed an inverse relationship between mussel abundance and mean mussel shell size, possibly due to the lower number of large mussels that can fit in a unit of area compared to smaller mussels. Conversely, mussel abundance patterns for the population at The Bluff did not differ greatly throughout the 2 years sampled (Fig. 6). Results from a one-way ANOVA test comparing total mussel abundance among sites during year 1 and 2 revealed statistical significance among sites (ANOVA; $F_{(2,69)} = 50.2$; $p < 0.05$, and $F_{(2,81)} = 67.0$; $p < 0.05$, respectively).

Great variability also was found in the size-frequency distribution of mussels among study sites. The population at Scott Point had a clear increase in mean mussel shell size from August to its peak in July, followed by a rapid decline in July-August of both years (Fig. 7). Similar, but less dramatic patterns were observed at Tonatona Beach and The Bluff over the 2-years of the study (Fig. 7). To facilitate comparisons of mussel abundances among size-classes, the data were analyzed as percent frequency and were arcsine-transformed to meet statistical requirements. Results from a 2-way ANOVA comparing mussel abundances among sites and dates for each mussel size class during year 1 and 2, and non-significant Tukey test comparisons are shown in Table 6.

Recruitment Rates

Results of recruitment measurements indicate that Scott Point had the highest recruitment rates, followed by Tonatona Beach, and that The Bluff had the lowest recruitment rates over the 2-year sampling period (Fig. 8). Seasonal changes in recruitment rates were similar for all 3 populations. Peaks in recruitment were observed in August, followed by a gradual decline through to December of each year (Fig. 8). Mean (±SE) mussel abundances of new recruits for year 1 at Scott Point, The Bluff , and The Bluff were 859±152, 20±4, and 126±37 individuals/ 625 cm^2, respectively, and the ranges were 1-2351, 0-69, and 0-605 individuals/ 625 cm^2, respectively. Mean (±SE) mussel abundances of new recruits for year 2 at Scott Point, The Bluff , and Tonatona Beach were 811±137, 25±4, and 93±19 individuals/ 625 cm^2, respectively, and the ranges were 0-1863, 0-74, and 0-404 individuals/ 625 cm^2, respectively. Results from a two-way ANOVA on the log-transformed data for year 1 (July 1999 to February 2000) and for year 2 (July 2000 to March 2001) indicated significant differences in mean abundance of new recruits (< 24 mm in shell length) among sites, among dates, and interactions (Table 6).

Mortality Rates

Analyses of empty shells within sampled quadrats in the adult mussel beds suggest that more mussels died of unknown causes (unmarked shells) than through predation (predator marks) at all 3 sites (Fig. 9). The overall abundance of unmarked shells was greatest at Scott Point and lowest at The Bluff (Fig. 9). The mean (±SE) for unmarked shells at Scott Point, Tonatona Beach, and The Bluff for year 1 were 25±4, 9±1, and 4±0 individuals/ 625 cm^2, respectively; and for year 2 were 19±4, 8±2, and 3±0 individuals/ 625 cm^2, respectively. The ranges for unmarked shells for year 1 were 1-70,1-10, and 1-20 individuals/ 625 cm^2; and for year 2 were 0-66,0-9, and 0-29 individuals/ 625 cm^2 for Scott Point, Tonatona Beach, and The Bluff, respectively. The seasonal variability among large (> 25 mm) unmarked empty shells indicated that a greater number of empty shells were present in August, and subsequently their numbers declined through to December, but little seasonal variability was observed among empty shells of young mussels (< 25 mm) at all 3 sites (Fig. 9). Conversely, mussel shells with predator marks were not only less common, but little seasonality was observed in the abundance of adult (> 25 mm) and young (<25 mm) mussel shells at the 3 study sites (Fig. 9). Mean (±SE) number of mussel shells marked by predators at Scott Point, Tonatona Beach, and The Bluff for year 1 were 1±0, 1±0, and 1±0 individuals/ 625 cm^2, respectively; and for year 2 were 2±0, 1±0, and 1±0 individuals/ 625 cm^2, respectively. The ranges for predator-marked shells for year 1 were 0-8, 0-4, and 0-4 individuals/ 625 cm^2, and for year 2 were 0-8, 0-4, and 0-4 individuals/ 625 cm^2 for Scott Point, Tonatona Beach, and The Bluff, respectively. Results from statistical analyses of mortality rates due to unknown causes and predation at Scott Point, The Bluff, and Tonatona Beach during year 1 and 2 are shown in Table 7&8.

Algal Abundances

The results of the algal abundance experiments within the algal habitats at the 3 intertidal sites indicate that overall algal abundances were greater at Scott Point with 128±8 % algal cover, followed by Tonatona Beach with 66±4 % algal cover. The Bluff had the lowest overall percent algal cover with a mean (±SE) of 35±4 % (Fig. 10). Ranges in percent algal cover were 60-220, 10-70, and 40-125 % for Scott Point, The Bluff, and Tonatona Beach, respectively. The algal species found at all 3 sites were Algal turf, *Corallina officinalis*, *Champia laingii*, *Plocamium costatum*, *Scytothamnus australis*, *Melanthalia abscissa*, *Gigartina alveata*, and *Osmundaria colensoi*), except for *Scytothamnus australis*, which was not found at The Bluff. Data for algal abundances were arcsine-transformed to meet statistical requirements. A three-way ANOVA test of mean percent algal cover among algal types (Algal turf, *Corallina officianalis*, *Champia laingii*, *Plocamium costatum*, *Scytothamnus australis*, *Melanthalia abscissa*, *Gigartina alveata*, and *Osmundaria colensoi*), among sites (Scott Point, The Bluff, and Tonatona Beach), and among dates (August, September, October, and December 1999, and March 2000) are shown in Table 9.

DISCUSSION

A number of studies have focused on the ecology of intertidal mussels, including larval supply, settlement patterns, recruitment rates, growth, mortality, and reproduction (e.g., Petraitis, 1991; Stirling & Okumuş, 1995; Bourget & Harvey, 1998; Cáceres-Martínez & Figueras, 1998; Hunt & Scheibling, 1998; Alfaro et al., 2001). A good understanding of the dynamics of a population can be attained best by abundances and size-frequency distributions at all life history stages within various temporal and spatial scales. In the case of the New Zealand green-lipped mussel, the unique ecological conditions that support mussel populations at Ninety Mile Beach are of critical importance to the mussel industry, which depends on the wild mussel seed collected in this area. Ecological knowledge of *Perna canaliculus* at Ninety Mile Beach is limited to a few studies on growth, reproductive behavior, and settlement patterns (Hickman, 1979; Alfaro & Jeffs, 2001; Alfaro, et al., 2001). The present study furthers our understanding of larval availability, settlement patterns, recruitment and mortality rates, and the overall population dynamics of adult mussel populations at Ninety Mile Beach.

Mussel Concentrations in Seawater

The high variability of mussel concentrations in seawater among the 3 study sites may be a result of different oceanographic conditions and/or local larval production. Thus, Scott Point may have higher accumulation and retention of larvae and post-larvae than Tonatona Beach, and Tonatona Beach higher than The Bluff. The inverse relationship between abundance of small (< 0.25 mm) and large (> 0.5 mm) juvenile mussels over time is consistent with known spawning periods, which at Ninety Mile Beach start around July-August and persist through December (Alfaro et al., in press). Older mussels (> 0.5 mm) present in the seawater samples may represent secondary drifters from nearby intertidal areas. This temporal and spatial variability in plankton samples has been observed for many mussel species (Lewandowski, 1982; Legendre & Demers, 1984; Martel et. al., 1993; Hunt & Scheibling, 1996; Cáceres-Martínez & Figueras, 1998). Cáceres-Martínez & Figueras (1998) found that the abundance of mussel larvae and post-larvae for *Mytilus galloprovincialis* varied greatly between two adult mussel populations, and that the larval abundances were closely related to the spawning periods of adult mussels. Furthermore, Martel et al. (1994) also found a strong realtionship between settlement rates and veliger concentrations of the mussel *Dreissena polymorpha* in the water column near Wheatley, Ontario, which the authors attributed to local wind-driven hydrodynamics. Thus, the higher larval abundances in the vicinity of Scott Point suggest that more larvae are available for settlement on the shore of this northern site. Conversely, the lower larval abundances in seawater adjacent to Tonatona Beach and The Bluff equate with the observed lower settlement patterns there.

Settlement Patterns - Spatial Variability

Investigations on settlement patterns in the intertidal zone at Ninety Mile Beach were conducted at 3 different spatial scales - among sites (100 km), between habitats (10 m), and between substrates (1 m). Results from the short- and long-term settlement experiments were in agreement with the abundance and size-frequency patterns exhibited by mussels on the shore.

Settlement patterns among sites indicate that mussel abundances were generally higher at Scott Point than Tonatona Beach, and that the lowest settlement rates were observed at The Bluff. Differences in settlement patterns among coastal populations elsewhere have been attributed to variability in larval supply, dispersal and transport by local oceanographic conditions, and early mortality (Keough & Downes, 1982; King et al., 1989; Martel et al., 1994; Hunt & Scheibling, 1996; 1997). For all 3 intertidal populations in the present study, reproductive monitoring during the same sampling period suggests that the population at Scott Point has a greater gamete production than Tonatona Beach, and that Tonatona Beach has a higher gamete production than The Bluff (Alfaro et al., 2001b). Thus, it is likely that varying reproductive efforts and larval concentrations in the nearby water column, may directly affect the observed variations in settlement rates among sites. Different oceanographic conditions among the 3 sites also may have a significant effect on the settlement differences. For example, the presence of eddies may act to retain larvae, whereas straight coastlines tend to accelerate the flow of larval transport. Further research on the local hydrodynamics likely would provide valuable information as to the physical mechanisms that may cause these site-specific settlement patterns at Ninety Mile Beach.

The most dramatic settlement differences among intertidal sites were observed in the algal band habitat for the smaller mussel size-classes or primary settlers. Scott Point had the greatest number of primary settlers, especially during the peak spawning season. These primary settlers often covered up to 100% of the available substrate within quadrats. Conversely, algal substrates were never completely covered with primary settlers at Tonatona Beach during the sampling period. These settlement differences between the northernmost and southernmost intertidal sites at Ninety Mile Beach suggest that larval abundance adjacent to the mussel bed may not be limited at Scott Point. In contrast, at Tonatona Beach, mussel concentrations in seawater may not have been enough to saturate the available algal substrate. A combination of low mussel concentrations in seawater and low algal availability may have been responsible for the consistently low settlement rates at The Bluff throughout the year. Elsewhere, vegetated nearshore habitats have been recognized to support higher densities of colonists, when settler availability is not limited in nearby waters, as compared to nearby unvegetated areas (Edgar, 1990; Edgar et al., 1994; Boström & Bonsdorff, 1997; Reusch; 1998).

No significant differences were observed in settlement rates of mussels > 1.5 mm among the 3 study sites. These results, in conjunction with the fact that quadrats in the mussel beds were never recorded to have 100% mussel cover, indicate that secondary settlement into the adult mussel beds were not limited by space at any of the sites. Moreover, it is evident that secondary settlement rates normally range between 0-15 mussels/ 225-cm^2/ day in these natural intertidal populations. These settlement patterns are in strong agreement with findings by Bayne (1964), who first postulated that primary mussel settlers (< 0.5 mm) almost exclusively settle on filamentous substrates, and then transfer to the adult mussel bed as older/larger mussels or as secondary settlers (> 0.5 mm). The present study also is consistent with previous reports that primary settlement is not limited to adjacent filamentous substrates, but also takes place in the adult mussel beds, although usually at low frequencies (Bayne, 1964; McGrath et al., 1988; Buchanan, 1994).

Similarities in the total number of mussels settled on mesh material and on natural substrates suggest that the mesh material used in these experiments may serve as an appropriate proxy to natural substrates. Numerous artificial substrates have been used with various degrees of success in mussel settlement experiments (King et al., 1990; Bourget et al., 1994; Harvey & Bourget, 1995; Bologna & Heck, 1999). For example, King et al. (1990) found that settlement of *Mytilus edulis* on nylon pad scourers served as a good indicator of settlement events in filamentous algae and the adult mussel bed. The authors also suggested that these artificial materials could be used to monitor mussel recruitment cycles in the rocky shore (King et al., 1990). The present results imply that there is a strong selectivity for juvenile mussels to settle on filamentous substrates regardless of the composition of the material (i.e. algae versus plastic). However, further studies are needed on the potential influences of physically- and chemically-mediated settlement patterns in order to clearly elucidate differences between natural and artificial filamentous substrates. Several studies have shown size-specific settlement differences among substrates with various patterns of branching (Buchanan & Babcock 1997; Bologna & Heck, 1999; Alfaro & Jeffs, 2001). These morphologically based preferences may represent an ecological strategy for mussels to settle according to shell size on the appropriate physical/ morphological structures, and thus reduce the chance of detachment by waves or currents (Bologna & Heck, 1999; Alfaro & Jeffs, 2001). In this study, the relative abundances of different-branching algae in quadrats were similar throughout the sampling period for all sites. Thus, the relative size-specific settlement patterns based on substrate morphology would have been similar for all quadrats with algae and in agreement with quadrats with artificial substrates.

Settlement Patterns - Temporal Variability

Inter-annual variations in mussel abundance for all mussel size classes were quite low between 1999-2001 at the 3 intertidal sites. However, monthly settlement patterns showed high mussel abundances in August, which corresponded with the peak spawning period, as well as a consistent decrease in mussel abundance through December. Similar results were obtained by Buchanan (1994), who observed that mussel populations at Piha (~ 240-320 km south of the intertidal sites at Ninety Mile Beach) had a peak settlement in September, followed by a decrease through December-January. Buchanan (1994) also observed low levels of settlement throughout the year. At Ninety Mile Beach, there was no evidence of trickle settlement, which concurs with the lack of any substantial spawning peak between January and April (Alfaro et al., 2001). Thus, settlement differences between Ninety Mile Beach and Piha populations may be a result of regional differences in reproductive behavior. Furthermore, at Ninety Mile Beach, settlement of small mussels (< 0.5 mm) was consistently high during spawning periods (August-December) in both years, while larger mussels (> 0.5 mm) were more abundant between spawning periods (December-July). These meso-scale temporal patterns also support Bayne's (1964) hypothesis that mussels first settle on filamentous algae as a transition stage between the water column and the adult situation attached to the rocks.

Results from the daily settlement experiments indicate that there were no significant temporal differences in the total mean mussel abundance among sites, between habitats and between substrate types throughout the study period. Daily settlement patterns also indicate that settlement of small mussels (< 0.5 mm) was highest in August and lowest in March. An inverse pattern was observed for larger mussels (> 0.5 mm), which were more abundant in March and less abundant in August. These settlement results reveal strong settlement trends that are consistent among the 3 temporal scales for mussel populations at Scott Point, The Bluff, and Tonatona Beach. Furthermore, these trends are in agreement with reproductive behavior studies of the same mussel populations in the area (Alfaro et al., 2001), and mussel abundance and size-frequency distribution records within spatfall samples collected along the extent of the beach during the study period. (A. C. Alfaro, unpublished data).

Population Dynamics of Mussel Beds

The population dynamics of mussel populations at Ninety Mile Beach varied considerably in space and time during the 2-year sampling period. The mussel population at Scott Point was the most dynamic intertidal population at Ninety Mile Beach. Mussels at Scott Point appeared to follow a yearly cycle that started with a high recruitment period in August-December. Mussels continued to grow in shell size from December to July. In July, a high mortality event almost entirely killed off the adult population and created new empty space on the rocky shore for a new cohort of mussels. Young mussels, which had increased in shell size to over 0.5 mm, while attached to nearby filamentous algae, started to transfer to empty spaces in the adult mussel bed. While the effects of early mortality on these newly settled mussels in the adult mussel bed may be high, high recruitment greatly influenced the dynamics of the population at Scott Point during July. A similar pattern occurred at Tonatona Beach. However, the seasonal changes from one yearly cohort to the next were less clear, possibly due to the less dramatic mortality of adult mussels in July, and the lower abundance of available juvenile mussels in the seawater and adjacent algal beds. The effect of early mortality may be a significant factor in the low retention of juvenile mussels in this population. However, more short-interval sampling of mussel settlement would have to be conducted to clearly elucidate this effect at Tonatona Beach. The population dynamics at The Bluff were markedly different, with only very small seasonal changes between recruitment and mortality rates. A combination of low mussel abundance in seawater, low settlement/ recruitment rates and low retention of young mussels may be responsible for the low temporal variability at this site. The persistence of this mussel population at The Bluff may be a result of the larval production of the few local mussels that do survive to adulthood. It also is possible that sporadic larval pulses from other mussel populations at Ninety Mile Beach may supply mussels to The Bluff. Whatever the reason, environmental and biological conditions at The Bluff do not seem to provide the best growing conditions needed for maintaining a substantial resident population.

The dramatic differences in population dynamics among sites at Ninety Mile Beach are likely to stem from local oceanographic conditions that often concentrate algal drift material covered with young settled mussels at Scott Point. Large rafts of drift algae with mussel spat (up to 1 km long) have been observed to travel northbound along the coast (moving about 5 km/ day), and accumulate for up to a week at Scott Point (A. Alfaro personal observations, and C. Hensley personal communication). It is possible that the large number of spat in the algal rafts (up to 10^6 mussels/ kg of wet algae) is able to decrease the food concentration in the seawater adjacent to the shore (c.f., Stirling and Okumuş, 1995). The rapid deletion of food particles in the water column may starve, and/ or significantly decrease the survival chances of mussels already in the rocky intertidal area. Adult mussels may be especially vulnerable to reduced food availability, since most are at the peak or just past the peak of reproductive output during this time

(Alfaro et al., 2001b). Field observations revealed large numbers of moribund mussels during this time. Many mussels had open valves that did not close quickly when disturbed. When examined closely, these mussels appeared to have highly diminished soft tissues. Furthermore, mats of mussel were observed being ripped off from the rocks by strong wave action during winter. Presumably, the mussels were not able to continue to generate byssal threads to maintain a strong hold on the rock during this time. Massive mortality in this adult population during 2 consecutive years of observations is consistent with the hypothesis that these large mussels cannot compete with young incoming settlers for a limited food supply and space. Disturbance effects causing drift algal strandings have been inferred to dramatically change the population structure of several nearshore populations (Soares et al., 1996; Bell & Hall, 1997; Holmquist, 1997; Ingólfsson, 1998; Knowles & Bell, 1998). For example, Soares et al. (1996) observed a significant decrease in biomass and density of adult clams, *Donax serra,* on beaches that had high cover of stranded kelp, but juvenile abundance was affected only when the quantity of kelp was exceedingly high. The authors concluded that the zonation patterns of *Donax serra* were a direct result of the disturbance effect caused by stranded kelp, especially in pocket areas along the coast where drift algae can accumulate (Soares et al., 1996).

Populations at both Tonatona Beach and The Bluff do not seem to be impacted as severely by drift algae. The environmental and biological conditions at Tonatona Beach appear more moderate in their seasonal changes, so that only part of the adult population is replaced each year by new cohorts. Instead of rafts of algal material with mussel spat accumulating at this site, and creating a rapid turnover in the adult population, small but frequent pulses of mussel settlement cause a slow change in the population dynamics during the spawning season. Drifting algae may bypass The Bluff on their way north via a nearshore water current, but no significant accumulation nor retention of algae were observed that might cause a measurable change in the population dynamics at this intertidal site.

Predation pressure, as inferred from surveys of empty shells on the adult mussel beds of the 3 intertidal sites, revealed similar patterns among sites. Mortality from predation was similar throughout the year for young and adult mussels at all 3 sites. Natural mortality, as indicated by the unmarked empty shells found in quadrats sampled within the adult mussel beds, appeared to be highest when the populations had attained the greatest number of adult mussels (August). Although the number of empty shells found within quadrats is not necessarily an accurate indicator of mortality rates in the population, occurrences of large empty spaces during August, which previously had been filled with adult mussels, appear to substantiate this high mortality event. Mortality of young mussels may have been underestimated, since these mussels often have a weak byssal attachment and readily dislodge with passing waves.

In summary, ecological differences among populations at Ninety Mile Beach may be attributed to a combination of biological and physical processes that interact at various spatial and temporal scales. Scott Point is the most dynamic intertidal population, owing to the high concentration of mussels in nearby seawater, the high settlement of primary settlers on the algal band habitat in August, and the high secondary settlement/ recruitment on the mussel bed in March. These settlement and recruitment patterns coincide with a peak in mortality in the adult mussel bed, which provides empty spaces on the rocky substrate for new recruits. The high mortality in August may be a consequence of depleted of food supplies in the water column and low energy reserves of adult mussels just past their reproductive peak. Depletion of food supplies in the water column is attributed to a periodic, but seasonal, accumulation of young feeding mussels in drift algae in nearby waters. Similar ecological patterns, with less marked transitions among biological components, were observed at the Tonatona Beach, and were even less pronounced at The Bluff. It is argued that drift algae do not accumulate readily at these 2 southernmost sites at Ninety Mile Beach because of the northbound transport of algal and spat material via local oceanographic currents. These interacting processes create dynamic ecological system, which ensures the success of mussel populations at Ninety Mile Beach, and provides a consistent supply of mussel spat for New Zealand's mussel industry.

ACKNOWLEDGMENTS

I thank the Hensley family, K. Campbell, D. Tasker, K. Hamlin, M. Collins, and M. Sewell for their assistance in the field. K. Campbell, A. Jeffs, and Bob Creese provided editorial expertise. I also thank the Geology Department at The University of Auckland, New Zealand for the use of lab space and computer support. This research was funded by a Graduate Research Grant from The University of Auckland, New Zealand

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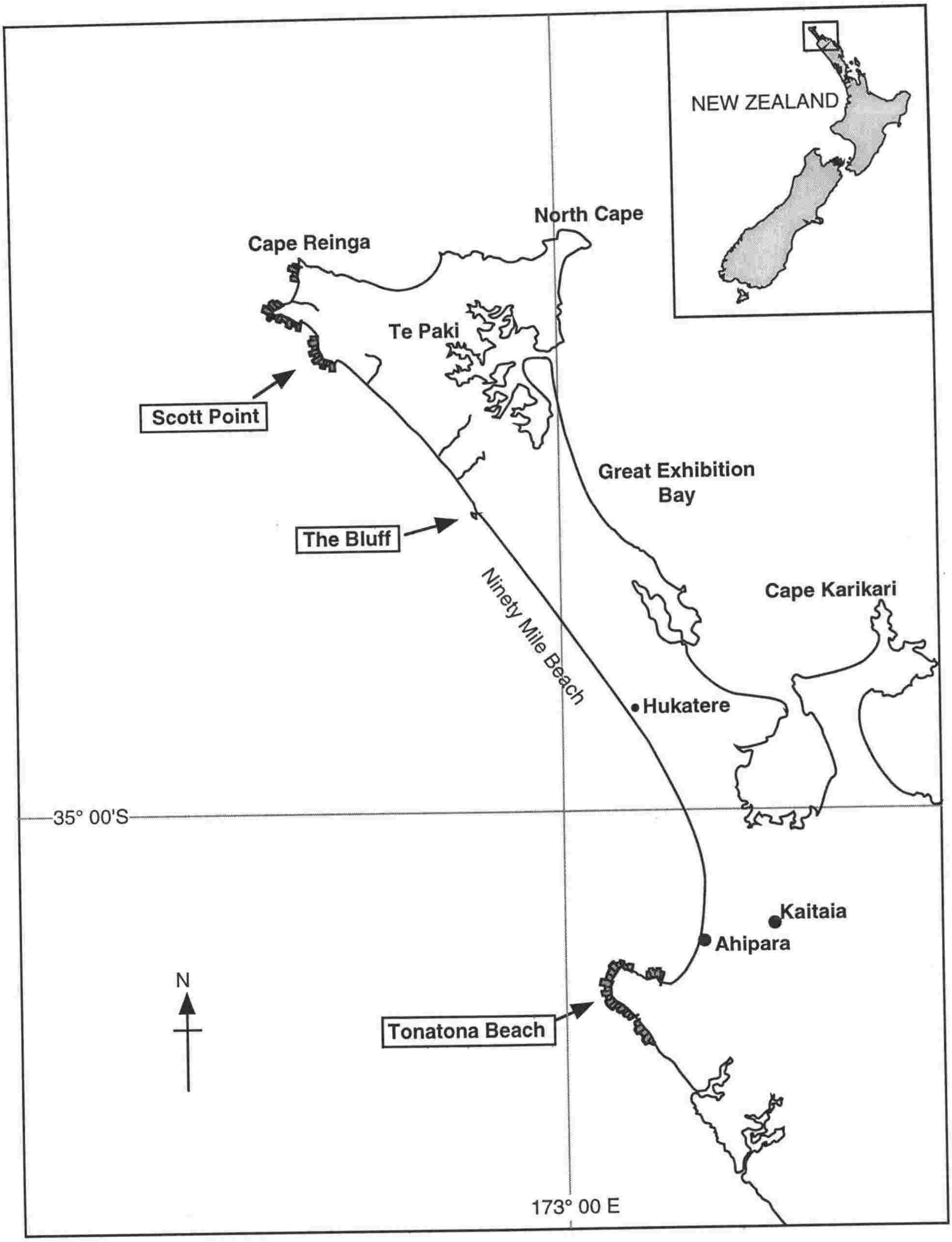

Figure 1. Location of 3 intertidal study sites (Tonatona Beach, The Bluff, and Scott Point) at Ninety Mile Beach, northern New Zealand.

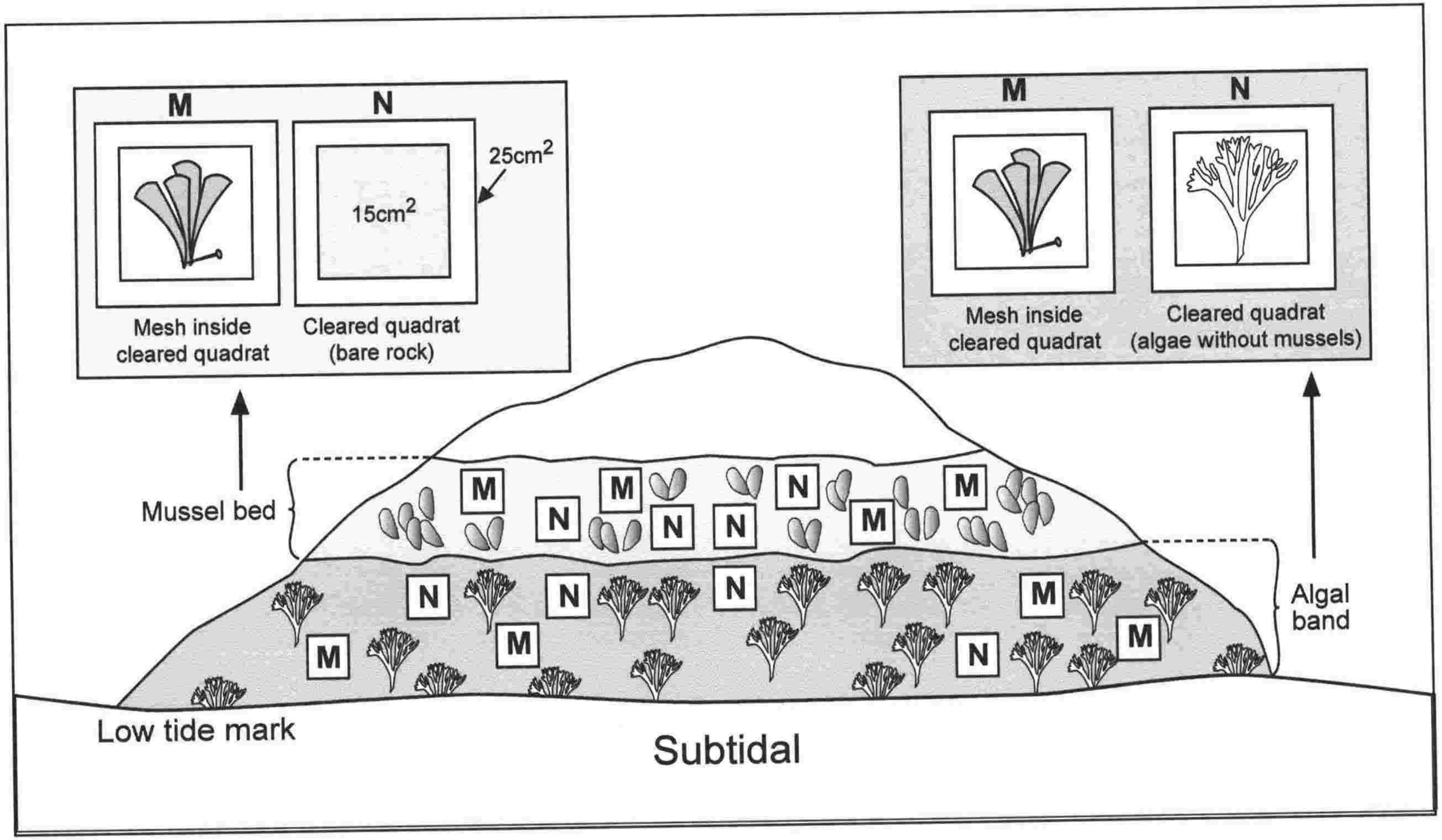

Figure 2. Diagrammatic representation of settlement experiments undertaken at 3 intertidal sites (Tonatona Beach, The Bluff, and Scott Point). Experimental quadrats were established within 2 habitats (mussel bed and algal band). Within each habitat, 4 quadrats were cleared of all mussels and algae and replaced with mesh material as settlement substrate. Another 4 quadrats in each habitat were cleared of all mussels, but algae were left in the algal band habitat. All quadrats were 225 cm^2, with a 5 cm skirt. See text for details.

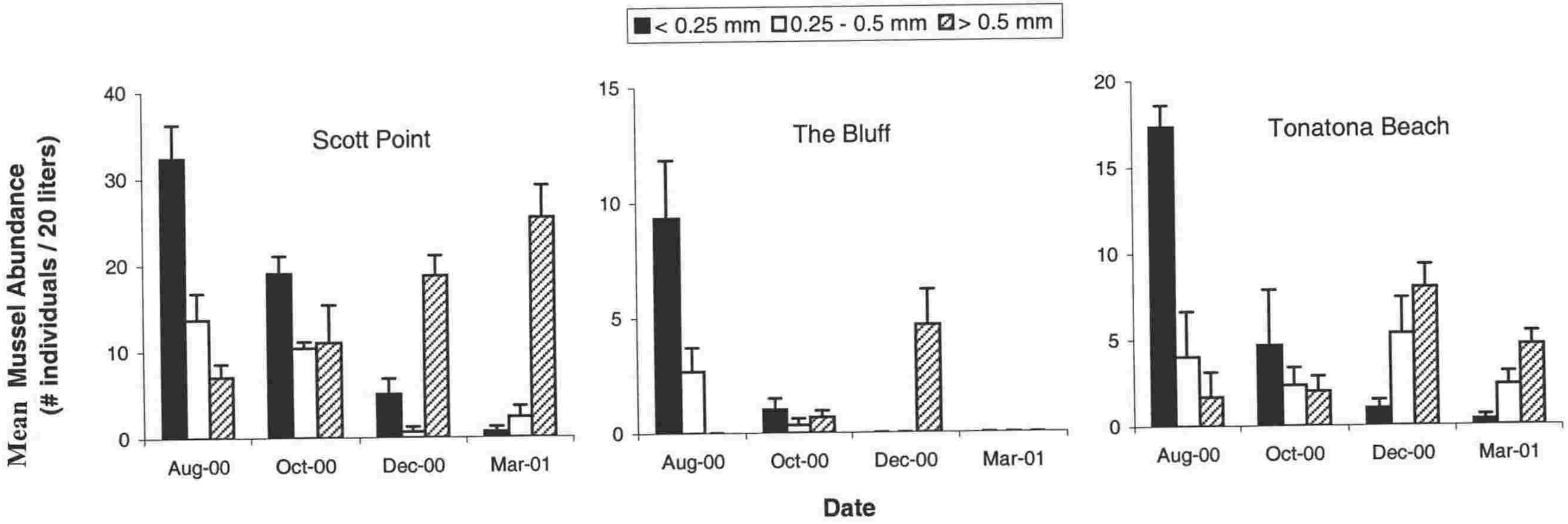

Figure 3. Mussel larval abundances (± SE) in seawater adjacent to 3 intertidal sites (Tonatona Beach, The Bluff, and Scott Point). Three replicate samples were taken each month (August, October, and December 2000, and March 2001). Larval abundances are shown for 3 mussel size classes (<0.25, 0.25-0.5, and >0.5 mm in shell length).

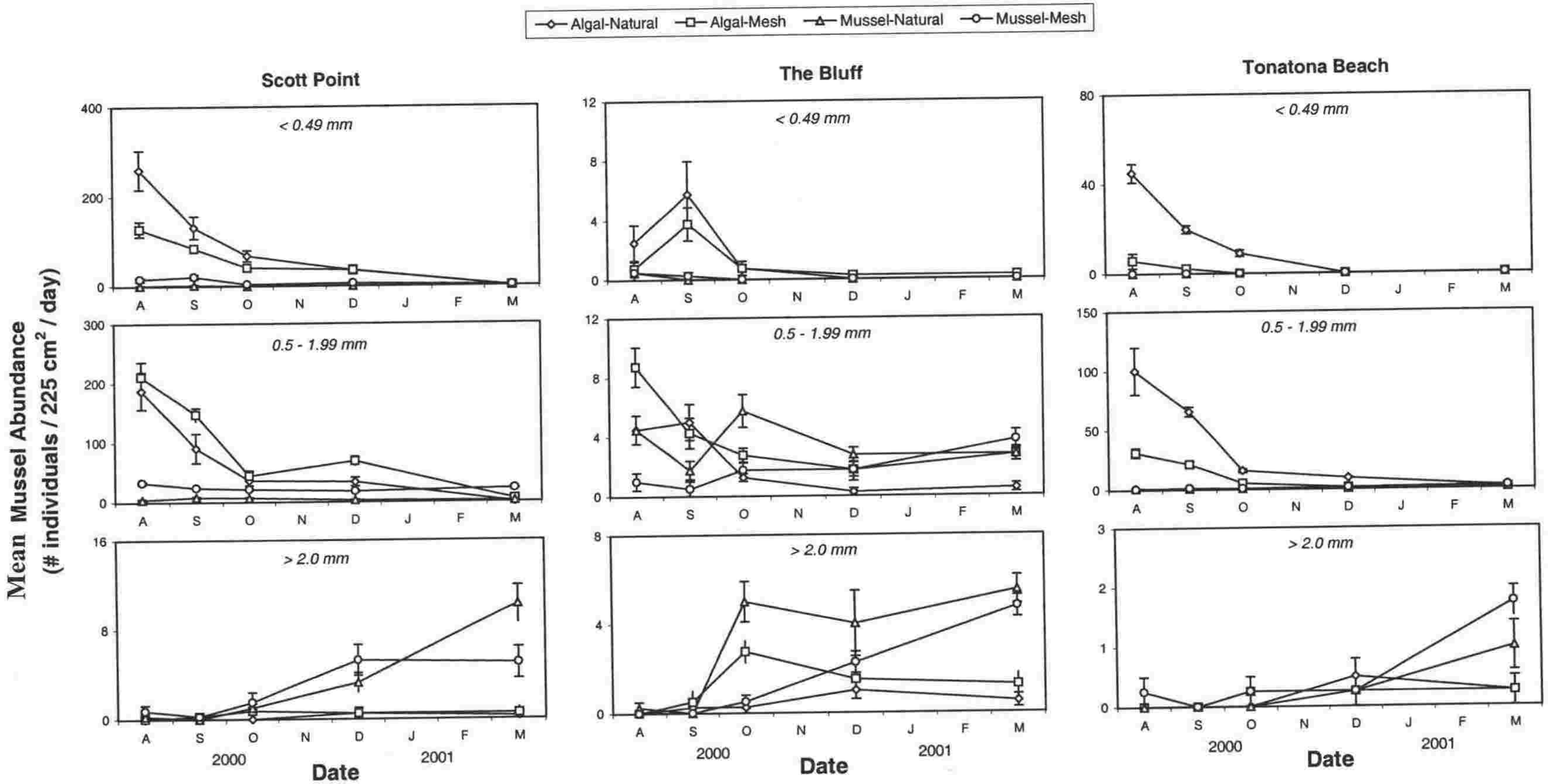

Figure 4. Daily mussel abundance (± SE) within quadrats in 2 habitats (algal band and mussel bed) and within 2 substrate types (natural and mesh) at 3 intertidal sites (Tonatona Beach, The Bluff, and Scott Point) between August 1999 and March 2000. Mussel abundances are shown for 3 mussel size classes (<0.49, 0.5-1.99, and >2.0 mm in shell length).

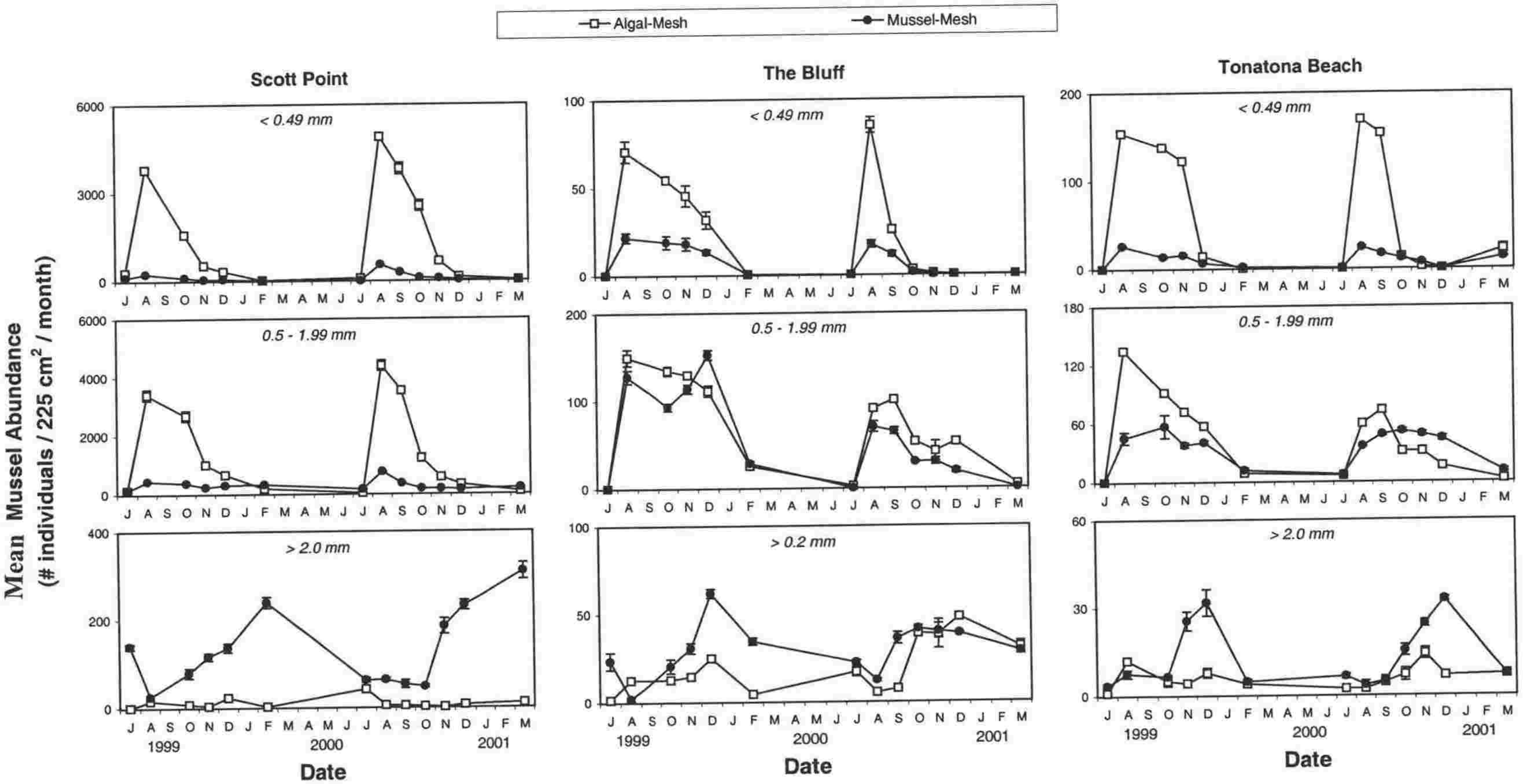

Figure 5. Monthly mussel abundance (± SE) on mesh material within quadrats in 2 habitats (algal band and mussel bed) at 3 intertidal sites (Tonatona Beach, The Bluff, and Scott Point) between July 1999 and March 2001. Mussel abundances are shown for 3 mussel size classes (<0.49, 0.5-1.99, and >2.0 mm in shell length).

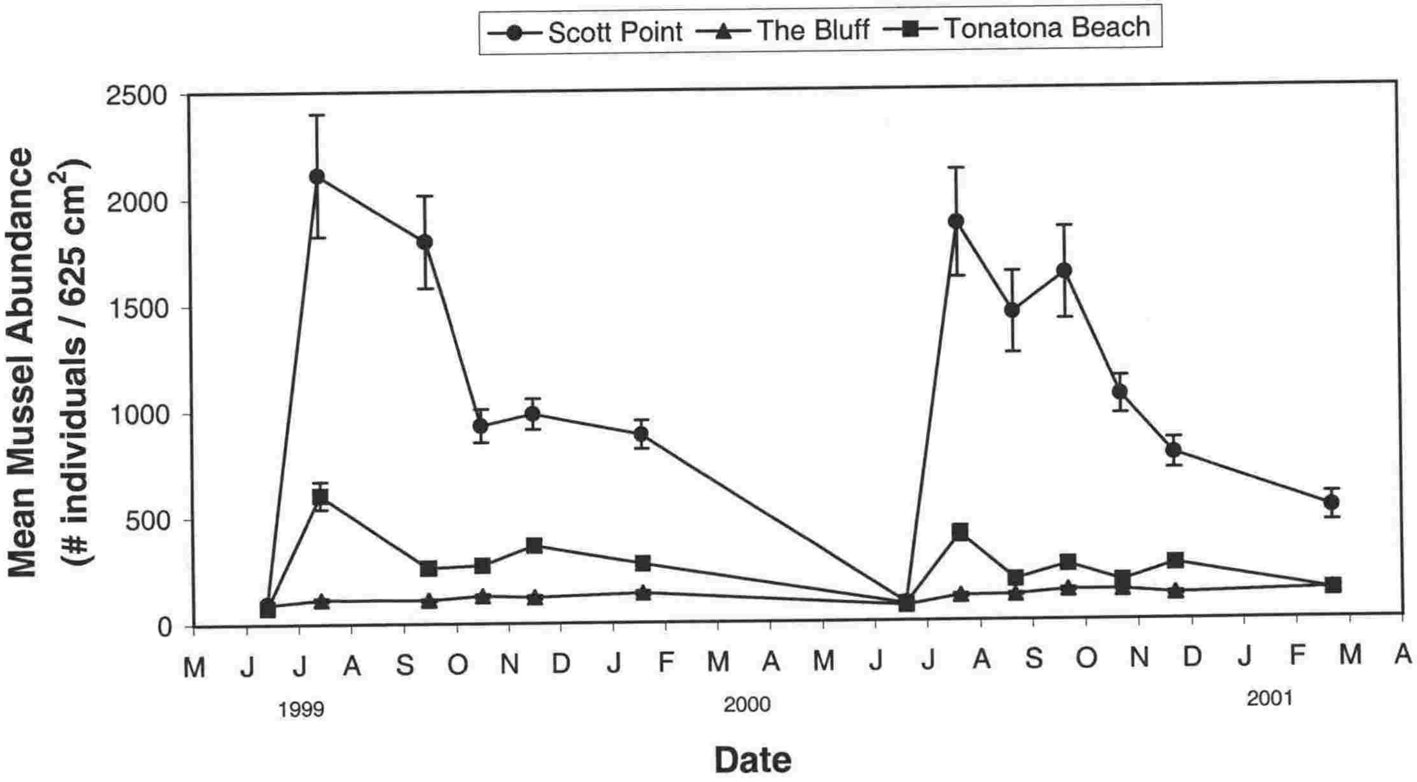

Figure 6. Mean mussel abundance (± SE) within quadrats in the adult mussel bed at 3 intertidal sites (Tonatona Beach, The Bluff, and Scott Point) between July 1999 and March 2001.

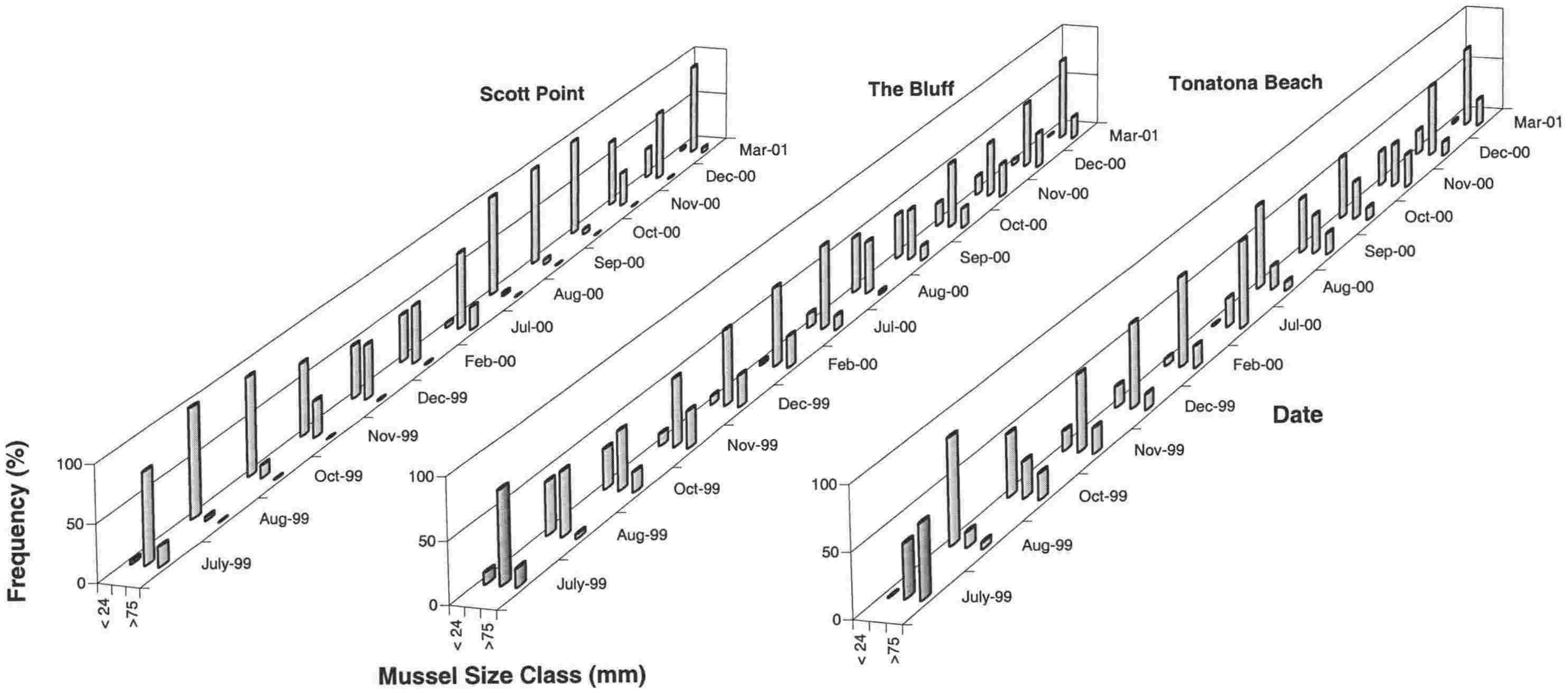

Figure 7. Frequency distribution of mussels within 3 size classes (<24, 50-74, and >75 mm in shell length) at 3 intertidal sites (Tonatona Beach, The Bluff, and Scott Point) between July 1999 and March 2001.

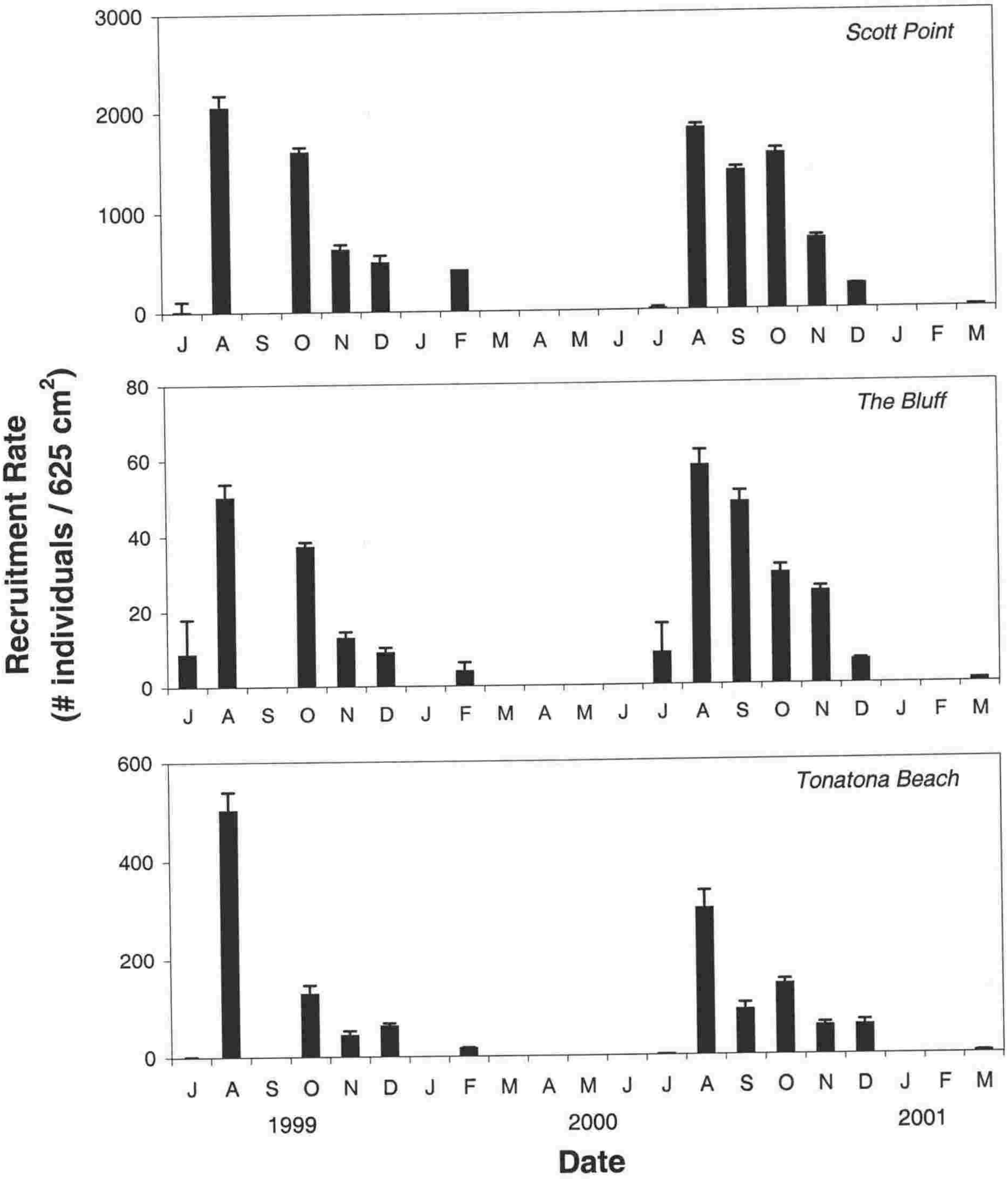

Figure 8. Recruitment rate of mussels (<24 mm in shell length) within quadrats in the adult mussel bed at 3 intertidal sites (Tonatona Beach, The Bluff, and Scott Point) between July 1999 and March 2001.

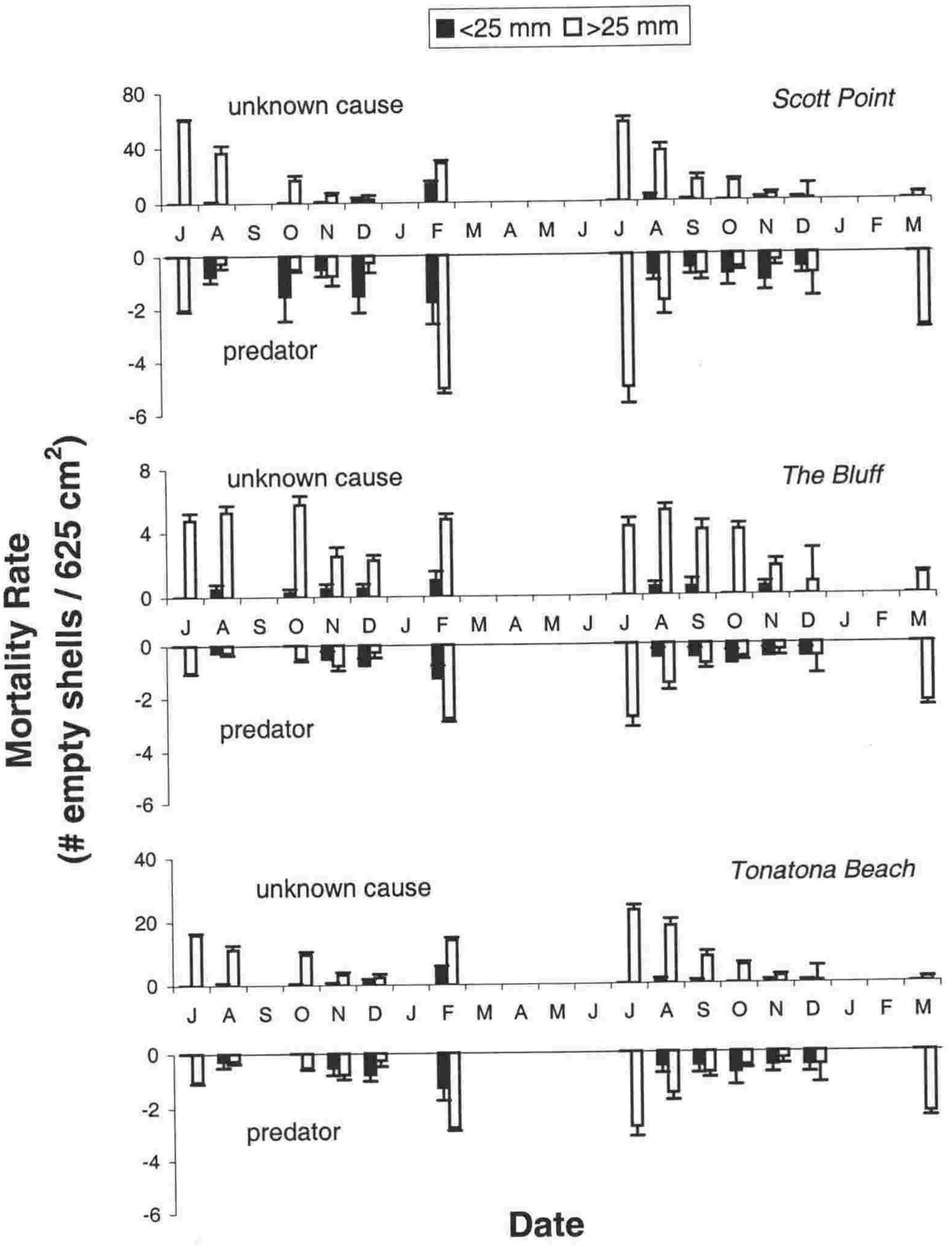

Figure 9. Mortality rate of mussels within quadrats in the adult mussel bed at 3 intertidal sites (Tonatona Beach, The Bluff, and Scott Point) between July 1999 and March 2001. Mussels are shown within 2 size classes (<25 and >25 mm in shell length). Mortality rates are shown for mussel that were killed by predators and by unknown causes.

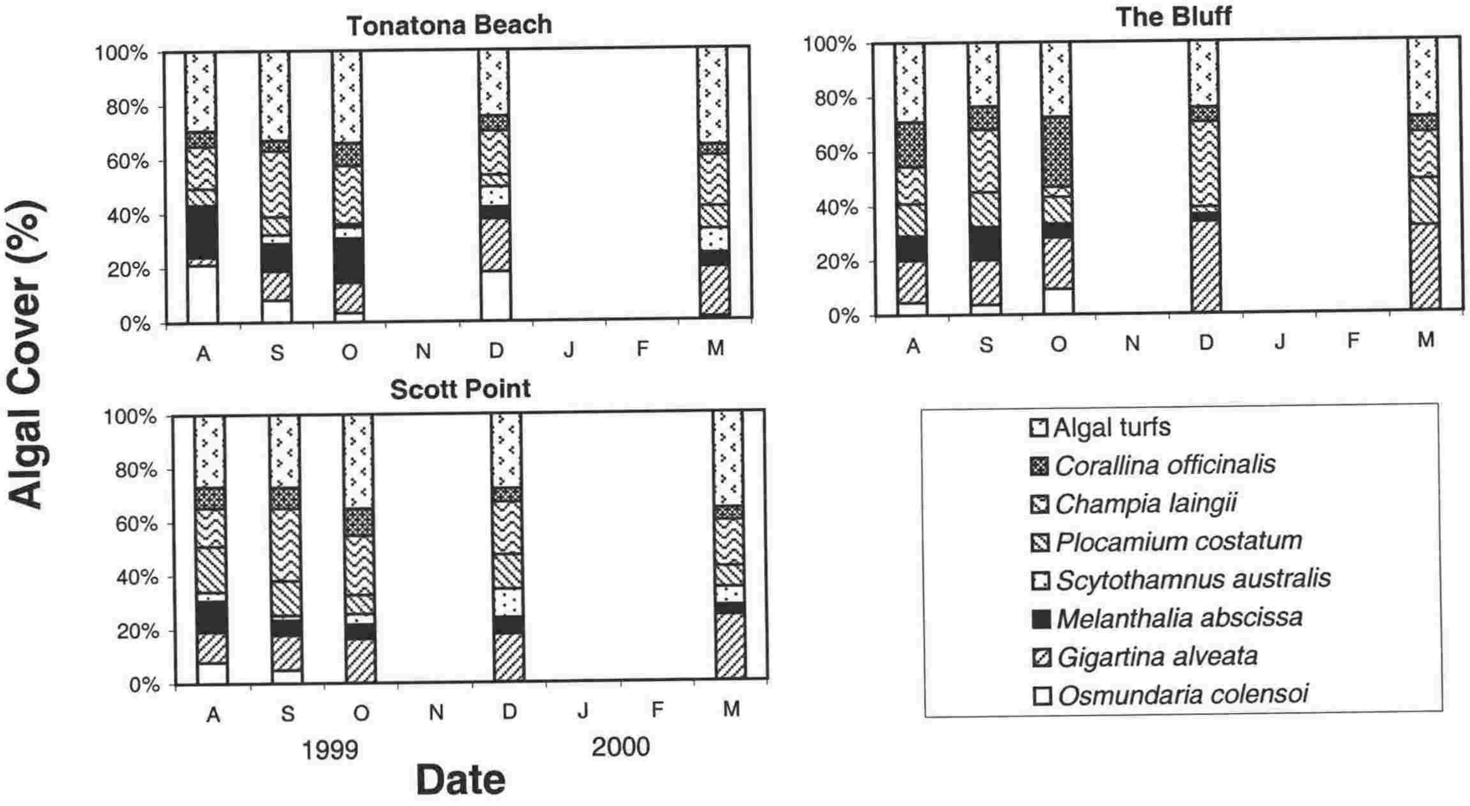

Figure 10. Percent algal cove for 8 algal types (Algal turf, *Corallina officianalis, Champia laingii, Plocamium costatum, Scytothamnus australis, Melanthalia abscissa, Gigartina alveata, and Osmundaria colensoi*) at 3 intertidal sites (Tonatona Beach, The Bluff, and Scott Point) between August 1999 and March 2000. The total percent algal cover within quadrats for Scott Point, Tonatona Beach, and The Bluff were 128±8%, 66±4%, and 35±4%, respectively.

Table 1: Statistical analyses of mussel concentrations in seawater. Two-way ANOVA tests (Model I) are shown for each of 3 mussel size classes (<0. 25, 0.25-0.5, and >0.5 mm in shell length). Fixed factors are site (Scott Point, The Bluff, and Tonatona Beach) and date (August, October, and December 1999, and March 2000). Tukey tests are shown for non-significant pair comparisons. S = Scott Point, B = The Bluff, T = Tonatona Beach, A = August 1999, O = October 1999, D = December 1999, and M = March 2000. Data were log- transformed. Non-significant tests at α = 0.05 are noted (ns).

		<0.25 mm		0.25-0.5 mm		>0.5 mm	
Source	df	F	p	F	p	F	p
Site	2	18.5	0.001	12.3	0.001	59.6	0.001
Date	3	37.6	0.001	4.9	0.008	13.7	0.001
Site x Date	6	1.9	0.128 ns	3.7	0.010	2.4	0.058 ns
Error	24						
Tukey tests							
		B x T	0.080 ns	S x T	0.394 ns	A x O	0.341 ns
		D x M	0.218 ns	A x O	0.462 ns	O x M	0.330 ns
				O x D	0.310 ns	D x M	0.058 ns
				O x M	0.325 ns		
				D x M	1.000 ns		

Table 2: Mean mussel abundances (±SE) and ranges for mussels in the short-term and long-term settlement experiments. Three sites (Scott Point, The Bluff, and Tonatona Beach), 2 habitats (mussel bed and algal band), and 2 substrates (bare rock and algae) are indicated for each experiment.

Short-term Settlement Experiments				
Study Site	Habitat	Substrate	Mean±SE	Range
Scott Point	Mussel Bed	Bare Rock	8±1	3-17
		Mesh	36±2	24-59
	Algal Band	Algae	168±35	0-606
		Mesh	153±25	4-388
The Bluff	Mussel Bed	Bare Rock	7±1	0-12
		Mesh	3±1	0-10
	Algal Band	Algae	5±1	0-17
		Mesh	6±1	2-13
Tonatona Beach	Mussel Bed	Bare Rock	1±0	0-4
		Mesh	1±0	0-4
	Algal Band	Algae	53±12	0-202
		Mesh	14±3	0-53

Long-term Settlement Experiments			Year 1		Year 2	
Study Site	Habitat	Substrate	Mean±SE	Range	Mean±SE	Range
Scott Point	Mussel Bed	Mesh	527±23	344-714	574±68	231-1419
	Algal Band	Mesh	2447±528	194-7525	3204±673	94-9884
The Bluff	Mussel Bed	Mesh	127±14	17-244	66±6	19-128
	Algal Band	Mesh	137±19	0-258	9±10	12-197
Tonatona Beach	Mussel Bed	Mesh	56±7	2-112	60±5	12-86
	Algal Band	Mesh	138±24	0-312	90±18	5-242

Table 3: Statistical analyses of short-term settlement experiments. Four-way ANOVA tests (Model I) are shown for each of 3 mussel size classes (<0.49, 0.5-1.99, and >2.0 mm in shell length). Fixed factors are site (Scott Point, The Bluff, and Tonatona Beach), habitat type (mussel bed and algal band), substrate type (natural and mesh), and date (August, September, October, and December 1999, and March 2000. Tukey tests are shown for non-significant pair comparisons. S = Scott Point, B = The Bluff, T = Tonatona Beach, A = August 1999, O = October 1999, D = December 1999, and M = March 2000. Non-significant tests at $\alpha = 0.05$ are noted (ns).

		<0.49 mm		0.05-1.99 mm		>2.0 mm	
Source	df	F	p	F	p	F	p
Site	2	186.7	0.001	205.8	0.001	40.2	0.001
Habitat	1	207.3	0.001	299.9	0.001	109.3	0.001
Substrate	1	15.9	0.001	1.7	0.191 ns	0.5	0.487 ns
Date	4	49.4	0.001	78.2	0.001	51.9	0.001
Site x Habitat	2	142.9	0.001	120.3	0.001	24.4	0.001
Site x Substrate	2	5.7	0.004	26.8	0.001	1.0	0.377 ns
Site x Date	8	32.5	0.001	30.6	0.001	9.3	0.001
Habitat x Substrate	1	30.6	0.001	1.3	0.262 ns	11.3	0.001
Habitat x Date	4	41.8	0.001	72.3	0.001	35.3	0.001
Substrate x Date	4	6.7	0.001	0.8	0.502 ns	1.4	0.229 ns
Site x Habitat x Substrate	2	14.8	0.001	8.8	0.001	7.7	0.001
Site x Habitat x Date	8	27.1	0.001	26.7	0.001	7.0	0.001
Site x Substrate x Date	8	2.9	0.005	2.6	0.011	3.5	0.001
Habitat x Substrate x Date	4	8.9	0.001	1.2	0.298 ns	4.6	0.002
Site x Habitat x Substrate x Date	8	4.2	0.001	2.6	0.010	5.4	0.001
Error	18 0						
Tukey tests							
		B x T	0.340 ns	Substrates	0.189	S x B	1.000 ns
		O x D	0.703 ns	O x D	1.000 ns	Substrates	0.486 ns
		D x M	0.226 ns	D x M	0.054 ns	A x O	1.000 ns
				D x M	0.052 ns		

Table 4: Statistical analyses of long-term settlement experiments for year 1. Three-way ANOVA tests (Model I) are shown for each of 3 mussel sizes classes (<0.49, 0.5-1.99, and >2.0 mm in shell length) between 1999-2000. Fixed factors are site (Scott Point, The Bluff, and Tonatona Beach), habitat type (mussel bed and algal band), and date (6 months between July 1999 and February 2000. Tukey tests are shown for non-significant pair comparisons. B = The Bluff, T = Tonatona Beach, J = July 1999, O = October 1999, N = November 1999, D = December 1999, and F = February 2000. Non-significant tests at α = 0.05 are noted (ns).

Size-frequency		Year 1					
		<0.49 mm		0.05-1.99 mm		>2.0 mm	
Source	df	F	p	F	p	F	p
Size	2	2095.3	0.001	1186.2	0.001	582.1	0.001
Habitat	1	1913.9	0.001	593.4	0.001	1039.1	0.001
Date	5	707.9	0.001	221.5	0.001	65.7	0.001
Size x Habitat	2	1500.4	0.001	537.6	0.001	560.4	0.001
Size x Date	10	587.8	0.001	165.1	0.001	41.7	0.001
Habitat x Date	5	562.3	0.001	153.5	0.001	77.6	0.001
Size x Habitat x Date	10	487.7	0.001	136.9	0.001	44.4	0.001
Error	108						
Tukey tests		Year 1					
		B x T	0.169 ns	B x T	0.054 ns	J x O	0.098 ns
		J x D	0.994 ns	J x F	0.303 ns	J x N	0.543 ns
				N x D	0.478 ns	D x F	1.000 ns

Table 5: Statistical analyses of long-term settlement experiments for year 2. Three-way ANOVA tests (Model I) are shown for each of 3 mussel size classes (<0.49, 0.5-1.99, and >2.0 mm in shell length) between 2000-2001. Fixed factors are site (Scott Point, The Bluff, and Tonatona Beach), habitat type (mussel bed and algal band), and date (7 months between July 2000 and March 2001). Tukey tests are shown for non-significant pair comparisons. B = The Bluff, T = Tonatona Beach, J = July 2000, A = August 2000, S = September 2000, O = October 2000, N = November 2000, D = December 2000, and M = March 2001. Non-significant tests at $\alpha = 0.05$ are noted (ns).

Size-frequency		Year 2					
		Scott Point		The Bluff		Tonatona Beach	
Source	df	F	p	F	p	F	p
Size	2	1814.7	0.001	1220.4	0.001	458.7	0.001
Habitat	1	1554.0	0.001	641.8	0.001	723.6	0.001
Date	6	412.7	0.001	126.8	0.001	83.4	0.001
Size x Habitat	2	1302.5	0.001	612.8	0.001	524.3	0.001
Size x Date	12	353.2	0.001	123.9	0.001	51.6	0.001
Habitat x Date	6	281.1	0.001	76.6	0.001	56.6	0.001
Size x Habitat x Date	12	245.3	0.001	71.9	0.001	67.4	0.001
Error	126						
Tukey tests		Year 2					
		B x T	0.463 ns	B x T	0.986 ns	J x S	0.090 ns
		J x D	1.000 ns	J x N	0.908 ns	J x O	0.998 ns
		J x M	1.000 ns	J x M	0.953 ns	A x S	0.965 ns
		D x M	0.996 ns	A x S	0.472 ns	S x O	0.290 ns
				O x D	0.802 ns	D x M	0.769 ns
				N x D	0.227 ns		
				N x M	1.000 ns		
				D x M	0.161 ns		

Table 6: Statistical analyses of population dynamics of the mussel bed experiments for years 1 and 2. Two-way ANOVA tests (Model I) are shown for each of 3 mussel size classes (<24, 25-74, and >75-99 mm in shell length) for 2 years (1999-2000 and 2000-2001). Fixed factors are site (Scott Point, The Bluff, and Tonatona Beach) and date (6 months for 1999-2000 and 7 months for 2000-2001). Tukey tests are shown for non-significant pair comparisons. B = The Bluff, T = Tonatona Beach, J = July, A = August, S = September, O = October, N = November, D = December, F = February, and M = March. Data were arcsin- transformed. Non-significant tests at $\alpha = 0.05$ are noted (ns).

				Year 1			
		<24 mm		25-74 mm		>75 mm	
Source	df	F	p	F	p	F	p
Site	2	265.3	0.001	48.7	0.001	139.5	0.001
Date	5	232.5	0.001	68.6	0.001	32.2	0.001
Site x Date	10	18.1	0.001	14.7	0.001	7.5	0.001
Error	54						
Tukey tests				Year 1			
		N x D	0.241 ns	J x D	0.988 ns	B x T	0.987 ns
				J x F	0.977 ns	O x N	0.530 ns
				D x F	0.742 ns	O x D	0.986 ns
						O x F	0.617 ns
						N x D	0.896 ns
						N x F	1.000 ns
						D x F	0.939 ns

				Year 2			
		<24 mm		25-74 mm		>75 mm	
Source	df	F	p	F	p	F	p
Site	2	204.8	0.001	131.4	0.001	772.9	0.001
Date	6	275.3	0.001	211.7	0.001	183.4	0.001
Site x Date	12	23.9	0.001	54.7	0.001	71.0	0.001
Error	63						
Tukey tests				Year 2			
		J x M	0.070 ns	A x S	0.148 ns	S x O	0.991 ns
		S x O	0.756 ns	S x O	0.335 ns	N x M	1.000 ns

Table 7: Statistical analyses of mortality rates in the mussel bed experiments for year 1. Three-way ANOVA tests (Model I) are shown for each of 2 mussel size classes (<25, and >25 mm in shell length) for the year 1999-2000. Fixed factors are site (Scott Point, The Bluff, and Tonatona Beach), cause of death (unknown and predation), and date (6 months between 1999-2000). Tukey tests are shown for non-significant pair comparisons. B = The Bluff, T = Tonatona Beach, J = July 1999, A = August 1999, O = October 1999, N = November 1999, D = December 1999, and F = February 2000. Data were log-transformed. Non-significant tests at α = 0.05 are noted (ns).

		Year 1			
		<25 mm		>25 mm	
Source	df	F	p	F	p
Site	2	9.5	0.001	48.5	0.001
Death	1	6.2	0.015	766.7	0.001
Date	5	24.3	0.001	50.9	0.001
Site x Death	2	1.5	0.219 ns	31.3	0.001
Site x Date	10	2.0	0.045	4.5	0.001
Death x Date	5	4.2	0.002	21.3	0.001
Site x Death x Date	10	2.3	0.017	2.8	0.004
Error	108				
Tukey tests		Year 1			
		B x T	0.284 ns	J x F	0.586 ns
		J x O	0.565 ns	A x O	0.990 ns
		A x O	0.751 ns		
		A x N	1.000 ns		
		A x D	0.184 ns		
		O x N	0.826 ns		
		N x D	0.137 ns		

Table 8: Statistical analyses of mortality rates in the mussel bed experiments for year 2. Three-way ANOVA tests (Model I) are shown for each of 2 mussel size classes (<25, and >25 mm in shell length) for the year 2000-2001. Fixed factors are site (Scott Point, The Bluff, and Tonatona Beach), cause of death (unknown and predation), and date (7 months between 2000-2001). Tukey tests are shown for non-significant pair comparisons. S = Scott Point, B = The Bluff, T = Tonatona Beach, J = July 2000, A = August 2000, S = September 2000, O = October 2000, N = November 2000, D = December 2000, and M = March 2001. Data were log- transformed. Non-significant tests at $\alpha = 0.05$ are noted (ns).

		Year 2			
		<25 mm		>25 mm	
Source	df	F	p	F	p
Site	2	3.6	0.031	21.8	0.001
Death	1	0.1	0.983 ns	217.0	0.001
Date	6	9.8	0.001	41.0	0.001
Site x Death	2	1.5	0.230 ns	14.6	0.001
Site x Date	12	0.9	0.510 ns	2.1	0.019
Death x Date	6	3.1	0.008	19.2	0.001
Site x Death x Date	12	0.5	0.920 ns	1.7	0.073 ns
Error	126				
Tukey tests		Year 2			
		S x T	0.228 ns	J x A	0.062 ns
		B x T	0.576 ns	S x O	0.794 ns
		Deaths	0.983 ns	S x M	0.452 ns
		J x O	0.338 ns	O x M	0.998ns
		J x M	1.000 ns	N x D	0.853 ns
		A x N	0.893 ns		
		A x D	0.090 ns		
		S x O	0.983 ns		
		S x N	0.577 ns		
		S x D	1.000 ns		
		O x N	0.132 ns		
		O x D	0.942 ns		
		O x M	0.338 ns		
		N x D	0.726 ns		

Table 9: Statistical analyses of algal cover experiments. A three-way ANOVA test (Model I) was conducted to test mean differences in algal abundance among algal types (Algal turf, *Corallina officianalis, Champia laingii, Plocamium costatum, Scytothamnus australis, Melanthalia abscissa, Gigartina alveata, and Osmundaria colensoi*), among sites (Scott Point, The Bluff, and Tonatona Beach), and among dates (August, September, October, and December 1999, and March 2000). All data were arcsin-transformed. Non-significant tests at $\alpha = 0.05$ are noted (ns).

Abundance

Source	df	F	p
Alga	7	38.1	0.00
Site	2	4.1	0.06 ns
Date	3	0.4	0.77 ns
Alga x Site	14	4.1	0.00
Alga x Date	21	1.8	0.02
Site x Date	6	0.2	0.98 ns
Alga x Site x Date	42	0.5	0.99 ns
Error	180		

CHAPTER 7

Variability in Mussel Settlement on Suspended Ropes Placed at Ahipara Bay, Northland, New Zealand

Andrea C. Alfaro and Andrew G. Jeffs

In review: Aquaculture

ABSTRACT

Unique physical and biological conditions at Ninety Mile Beach, northern New Zealand, are responsible for an accumulation of unusually high amounts of mussel spat, Perna canaliculus, found nowhere else in the country. These massive quantities of mussel spat are collected from the beach (>140,000 tonnes/ year) and transported to the aquaculture farms, where they supply 80% of the industry's mussel seed requirements. Direct settlement of mussels, Perna canaliculus, from the plankton to suspended ropes in the water column was investigated at Ninety Mile Beach, northern New Zealand. Mussel spat-collecting ropes were placed at two sites (inside and outside Ahipara Bay) and at 3 different depths. The abundances of mussels within 3 size classes were recorded monthly during 2 spawning seasons in 1999 and 2000. Small mussels (<0.49 mm) were found to be more abundant at shallower depths (2 m water depth) in August 2000, just after the spawning of nearby mussel populations. Conversely, larger mussels (>1.0 mm) were more abundant at greater depths (18 m water depth) in September-December. Larger mussels are thought to have transferred from tumbling algae covered with mussels, which are readily transported by hydrodynamic processes near the seafloor. Although higher mussel abundances generally were found at the site inside the bay, these differences were not strongly supported by statistical analyses. The present research provides the first evidence that artificial ropes deployed at Ahipara Bay may be of commercial value to spat collectors on the beach and the mussel farm industry. These ropes could be used as indicators of arrival of spatfalls, which are collected at the beach and used to seed the mussel farms. Furthermore, ropes could be used as a new way of harvesting the massive quantities of mussel spat available at Ninety Mile Beach, northern New Zealand.

Key words: Mussels; Settlement Patterns; Size Classes; Suspended Ropes; Perna.

INTRODUCTION

Mussel settlement patterns on natural and artificial substrates are highly variable in space and time (King et al., 1990; Hickman et al., 1991; Fuentes and Morales, 1994; Martel et al., 1994; Ramírez and Cáceres-Martínez, 1999). This variability has been attributed to the timing and magnitude of larval supplies, and the physical conditions of the environment, such as ocean currents, wind patterns, and temperature (King et al., 1990; Kingsford, 1990; McConnaughey et al., 1992; 1994; Miller and Emlet, 1997). Local oceanographic conditions and weather patterns further contribute to the dispersion and concentration of larvae and juveniles at various spatial and temporal scales (Kingsford, 1990; 1992; McConnaughey et al., 1994; Martel et al., 1994).

Monitoring mussel settlement rates on various natural and artificial substrates is an important tool for assessing the population dynamics of nuisance species (Fraleigh et al., 1993; Martel et al., 1994) and commercial species (Meredyth-Young and Jenkins, 1978; Fuentes and Morales, 1994; Ramírez and Cáceres-Martínez, 1999). For example, Fuentes and Morales (1994) found that settlement of the mussel Mytilus galloprovincialis was high at shallower depths in a seaward site of the Ría de Arousa Bay in northeastern Spain. In New Zealand, settlement studies have been limited to farm areas, such as Marlborough Sounds in the South Island, and Coromandel in the North Island. Meredyth-Young (1978) found variations in settlement of the mussel Perna canaliculus at different sites in Marlborough Sounds, but no depth differences in mussel settlement. However, Hayden and Kendrick (1992) found that the same mussel species settled in higher numbers in deeper areas (15 m water depth) compared to shallower areas (5 m water depth) in both Marlborough Sounds and Coromandel.

While harvesting of mussels settled on suspended ropes near mussel farm areas in New Zealand is an important supplement to the industry's total requirement for seed mussels, the majority of the mussel spat (about 80 %) is collected from wash-ups of large quantities of spat-covered drifting macroalgae at Ninety Mile Beach, northern New Zealand (Hickman et al., 1991; Jeffs et al., 2000). The dependency of the mussel industry on these natural supplies of mussel spat from Ninety Mile Beach stems from the fact that nowhere else in New Zealand do algal drift material covered with mussel spat (up to 100 % cover) wash to the shore in such massive quantities (>140,000 tonnes/year of mussel spat attached to macroalgae). However, the spatial and temporal dynamics of mussel spat arrival to the beach are highly variable and poorly understood (Jeffs et al., 2000).

The purpose of this research was to investigate the temporal and spatial patterns of mussel settlement, Perna canaliculus, on suspended ropes inside and outside of Ahipara Bay at Ninety Mile Beach, northern New Zealand. Settlement differences among mussel size classes were investigated at different water depths during several months within 2 spawning seasons (July 1999-December 2000). The importance of these findings are discussed both in terms of the potential use of suspended ropes at Ninety Mile Beach to predict spatfalls and wash-ups, and the possibility to collect newly settled mussel spat attached to the ropes, which could be transported directly to the mussel farms.

METHODS AND MATERIALS

Mussel settlement patterns were monitored from spat-collecting ropes, which were placed at two sites at Ninety Mile Beach, northern New Zealand (Fig. 1). Two to 4 anchor lines with spat-collecting ropes were placed at each of the 2 sites (inside and outside Ahipara Bay), and the spat-collecting ropes were sampled monthly between October-December 1999, and between July-December 2000. However, owing to rough weather conditions, entanglement with passing trawlers, and vandalism, only one anchor line per month for 6 months inside the bay and 4 months outside the bay were retrieved for sampling. All anchor lines were placed at about 20 m water depth and suspended with a buoy at the surface. From these vertical ropes, two smaller spat-catching ropes (50 cm in length) were attached 1 m apart from each other at 2, 10, and 18 m water depth, for a total of 6 spat-collecting ropes per anchor line. The spat-collecting ropes were made of furry plastic (Kinnears Rope Ltd. "christmas tree" rope), which are used extensively for mussel spat collection at other sites in New Zealand. Each month, a new set of spat-collecting ropes were replaced for the old ropes, which were returned to the laboratory for analysis. All mussels were removed from the ropes by vigorous agitation, and with forceps. The mussels were then sorted into 3 size classes (<0.49, 0.5–0.99, and >1.00 mm in shell length) by passing the mussels through different-sized sieves (Alfaro and Jeffs, in press). Mussel abundances within the 3 mussel size classes were obtained from ropes retrieved each month, among the 3 depths and between the 2 sites.

Mussel abundances were first log-transformed to satisfy assumptions of statistical analyses. Analysis of variance tests were conducted separately for each of the 2 years and for each mussel size class, since size classes were not independent of each other. Thus, for October 1999, a two-way ANOVA per mussel size class incorporated site (inside and outside the bay), and depth (2, 10, and 18 m water depth) as fixed factors. In 2000, a three-way ANOVA included month (July, August, and September for 2000), site (inside and outside of the bay), and depth (2, 10, and 18 m water depth) as fixed factors. November 1999 and December 2000 were not included in the statistical analyses because only ropes inside the bay were retrieved. Although the initial intention was to compare mussel settlement inside and outside the bay, the loss of replicate anchor lines made the site factor pseudoreplicated. Thus, site comparisons are made with caution since their differences cannot be separated from the natural spatial variability of the environment. Similarly, differences among months may include the inherent temporal variability of the natural environment. Post hoc comparisons within factors were conducted with Tukey-tests and used to make interpretations among factor levels and interactions.

RESULTS

The temporal patterns of mussel settlement within suspended ropes at Ahipara Bay, northern New Zealand, indicated higher settlement in August, and decreasing settlement to December. Monthly abundances (mean ± SE) for small mussels (<0.49 mm in shell length) were highest in August 2000 (2028±577 mussels/ 0.5 m rope) and lowest in November 2000 (61±11 mussels/ 0.5 m rope) (Fig. 2-3 & Table 1). Conversely, large mussels (>1.0 mm in shell length) were most abundant inNovember 2000 (1141±605 mussels/ 0.5 m rope) and least abundant in July 2000 (866±181 mussels/ 0.5 m rope) (Fig. 2-3 & Table 1).

Mussel settlement differences between the 2 sites (inside and outside the bay) resulted in generally higher settlement inside the bay compared to outside the bay for all mussel size classes (Fig. 2-3 & Table 1). The mean (±SE) mussel abundances inside the bay for the entire sampling period were 1381±274, 714±136, and 468±139 for small, medium, and large mussels, respectively. Outside the bay, mean (±SE) mussel abundances were 1081±276,1281±268 and 422±103 for small, medium, and large mussels, respectively.

A direct relationship between mussel size class and water depth was found in ropes sampled among months and between sites. Small mussels (<0.49 mm in shell length) were more abundant at the surface (2 m water depth), and had a total mean (±SE) of 2086±403 individuals/ 0.5 m rope, while larger mussels were most abundant at water depths of 18 m (1704±318 individuals/ 0.5 m rope) (Fig. 2-3 & Table 1).

For October 1999, a two-way ANOVA for each of the 3 mussel size classes resulted in significant differences among mean mussel abundances for all factors (site and depth) and interactions, except for site within 0.5-0.99 mm mussels and the interaction within >1.0 mm mussels (Table 2). For 2000, three-way ANOVA's for each mussel size class, which also included month as a factor (July, August, and September), resulted in significant differences among mean abundances for all sites and interactions, except for site within 0.5-0.99 and >1.0 mm mussels, and for 2 first order interactions within 0.5-0.99 mussels (Table 3).

DISCUSSION

A central concern in the field of larval ecology is the need to identify factors responsible for the variability of larval abundance and size-frequency distribution in the ocean. Studies on spawning cycles, larval transport by means of hydrodynamic processes, and mortality rates in the water column have improved understanding of biological variability in the ocean (e.g. Kingsford, 1990; Nichols, 1996; Hunt and Scheibling, 1997; Miller and Emlet, 1997; Snodden and Roberts, 1997). In particular, use of artificial collectors, when well correlated with larval distribution in the water column, can be a straightforward and effective way to identify temporal and spatial fluctuations in spatfalls (Davies, 1974; Fuentes and Morales, 1994; Martel et al., 1994; Ramírez and Cáceres-Martínez, 1999). At Ninety Mile Beach, northern New Zealand, the time and place of spatfall arrivals at the beach is of critical importance to the spat collectors and mussel farms, which utilize the seed mussels. However, the large number of interacting physical and biological factors that affect the abundance and distribution of larvae and juvenile mussels in the water column have hindered previous attempts to make predictions for future spatfall events (A. Alfaro, unpublished data). The present study is the first to investigate mussel settlement patterns on suspended spat-collecting ropes at Ninety Mile Beach, northern New Zealand. Vertical and horizontal settlement variability was identified inside and outside of Ahipara Bay, and among 3 water depths within various months in 1999 and 2000.

Higher mussel settlement of small mussels (<0.49 mm in shell length) was recorded in August and settlement decreased through December. These temporal patterns agree well with the observed spawning period of the nearby adult population in July-August, and decreasing through December (Alfaro et al., in press). A direct relationship between spawing periods and subsequent settlement of post-larval juveniles has been shown for several mussel species (Kautsky, 1982; King et al., 1989; 1990; Fuentes and Morales, 1994; Snodden and Roberts, 1997; Ramírez and Cáceres-Martínez, 1999). Snodden and Roberts (1997) concluded that spawning events of Mytilus edulis in Dundrum Bay, northern Ireland, coincided with the arrival of primary settlers on nearby collection pads 6 weeks later. On rocky intertidal areas of west Ireland, King et al. (1990) also attributed the appearance of new settlers (<0.3 mm) of the mussel Mytilus edulis on collecting pads to direct settlement of larvae from the plankton just after spawning times. At Ninety Mile Beach, the arrival of larger mussels (>1.0 mm) from September to December likely represents secondary settlers that transferred from floating algae tumbling on the bottom to the spat-collecting ropes at 18 m water depth. King et al. (1990) also observed larger settlers (>0.75 mm) on their collecting pads, which the authors attributed to migration from benthic habitats. Although these temporal patterns cannot be attributed fully to seasonal patterns due to the lack of replication among months, the trends are likely to be due to variations in mussel abundances caused by the spawning season cycle. Analyses of mussel spat samples that arrived at the beach on washed-up algae during the same sampling period also indicate that higher abundances of small mussel (<0.49 mm) were present in August and larger mussels (>1.0 mm) were more abundant in September-December (A. Alfaro, unpublished data).

Site differences indicate greater mussel settlement inside compared to outside Ahipara Bay only for s all mussel size classes). However, these differences are confounded by lack of replication and the interacting factors of month and depth. Therefore, it is likely that the observed differences in mussel abundances between sites also incorporate some degree of natural spatial variability. Mussel settlement differences among sites have been observed in many studies, especially those comparing habitats inside and outside bays and estuaries (Kautsky, 1982; Petraitis, 1991; Fuentes and Morales, 1994; Snodden and Roberts, 1997). These differences may be due to the greater level of accumulation and retention of biological material in geographically confined areas, compared to open, higher energy environments. Ahipara Bay is likely to be affected by eddy currents that would tend to accumulate larvae and juvenile mussels, especially when concentrations of small pre-settlers are high just after spawning periods. However, testing this hypothesis will require further investigation.

Mussel abundances were generally higher for smaller mussels (<0.49 mm) at shallower water depths, and higher for larger mussels (>1.0 mm) at greater depths. This relationship between mussel size and water depth may be related to the greater buoyancy and migratory capability of smaller mussels compared to the generally heavier, larger mussels that are ready to settle (King et al., 1990; Martel et al., 1994; Buchanan and Babcock, 1997). Small mussels of, Perna canaliculus, (<0.6 mm) were shown to slow their rate of descent in the water column by 30% by using mucus threads, while larger mussels were less likely to produce mucus threads (Buchanan and Babcock, 1997). In addition, these small mussel size classes are highly mobile (Lane et al., 1985; Armonies, 1992; Martel, 1993; Buchanan and Babcock, 1997), which implies that some small mussels may have settled and left the settlement ropes during the sampling period, thus underestimating the total abundance of mussels settled at shallower depths. Red filamentous algae and hydroids covered with mussels (0.2-3 mm) form drifting patches of up to 1 km in length at Ninety Mile Beach (A. Alfaro, personal observation). This algal material covered with growing mussel spat is negatively buoyant and is readily transported by hydrodynamic processes acting near the seafloor (A. Alfaro, unpublished data). Thus, it is quite likely that larger mussels transferred from loose algae rolling on the bottom, to the spat-collecting ropes placed at 18 m (2 m above the bottom).

The statistical analyses conducted for all 3 mussel size classes during 1999 and 2000 resulted in significant interactions for most first and second order interactions. These results indicate that differences in mussel abundance between sites, and among depths (and among months for 2000), vary according to the particular combinations among levels within factors. With a significant second order interaction, it is difficult to ascertain the magnitude and direction of the contribution of each main factor. However, post hoc comparisons suggest that small mussels were more abundant in August and that abundances were not significantly different between July and September. These differences may be more pronounced inside compared to outside the bay, and may be more evident at shallower depths. Although there also was a significant second order interaction for medium-sized mussels, this significance was mostly due to the interacting effects of month and site. Depth appeared to be of little contribution to the interaction and suggests higher settlement at greater depths in October-December 1999 (including mostly large mussels) and shallower depths in July-November 2000 (including mostly small mussels). Statistical comparisons for larger mussels in 1999 resulted in a significant relationship between mussel abundance and depth, and higher settlement inside versus outside the bay. In 2000, all 3 factors (month, site, and depth) contributed to a significant second order interaction, and it can only be suggested that higher settlement of larger mussels took place in September at greater depths.

Although more replicate samples would have benefited this research, the results of this first subtidal rope settlement experiment at Ninety Mile Beach indicate that ropes may be a useful way of monitoring spatfall events, and they may be a feasible method for collecting spat in the area. Besides showing a good correlation between settlement and spawning periods, and between settlement and spat arrival at the beach, it also is apparent that different mussel size classes may be collected separately by placing ropes at different water depths. More research is necessary to identify sites of optimal mussel settlement at Ninety Mile Beach. However, the identification of generally higher settlement inside Ahipara Bay suggests that commercial settlement ropes may be better placed inside the protection of Ahipara Bay.

ACKNOWLEDGMENTS

We thank the Morrogh and Hensley families, M. Collins, and M. Sewell for their helped in the field. K. Campbell and M. Anderson provided technical and editorial expertise. We also thank the Geology Department at The University of Auckland, New Zealand for the use of lab space and computer support, and Kinners Ropes Ltd. for their contribution of rope material. This research partly was funded by a grant from the New Zealand Foundation for Research, Science and Technology, and a Graduate Research Grant to A. C. Alfaro from The University of Auckland, New Zealand.

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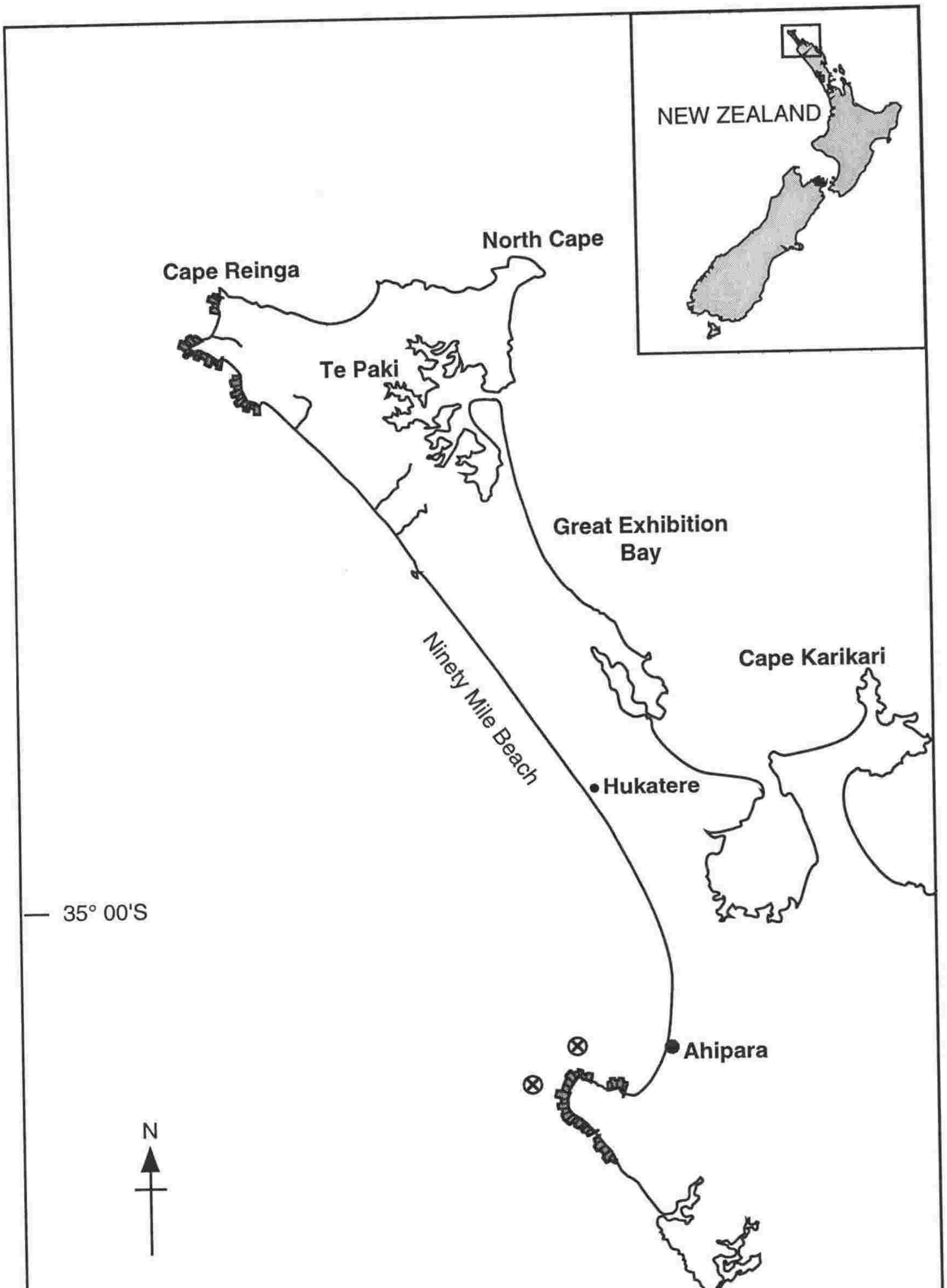

Figure 1. Map of the study area at Ninety Mile Beach, northern New Zealand. Two sites, where mussel settlement ropes were deployed, are shown (circled x) inside and outside of Ahipara Bay.

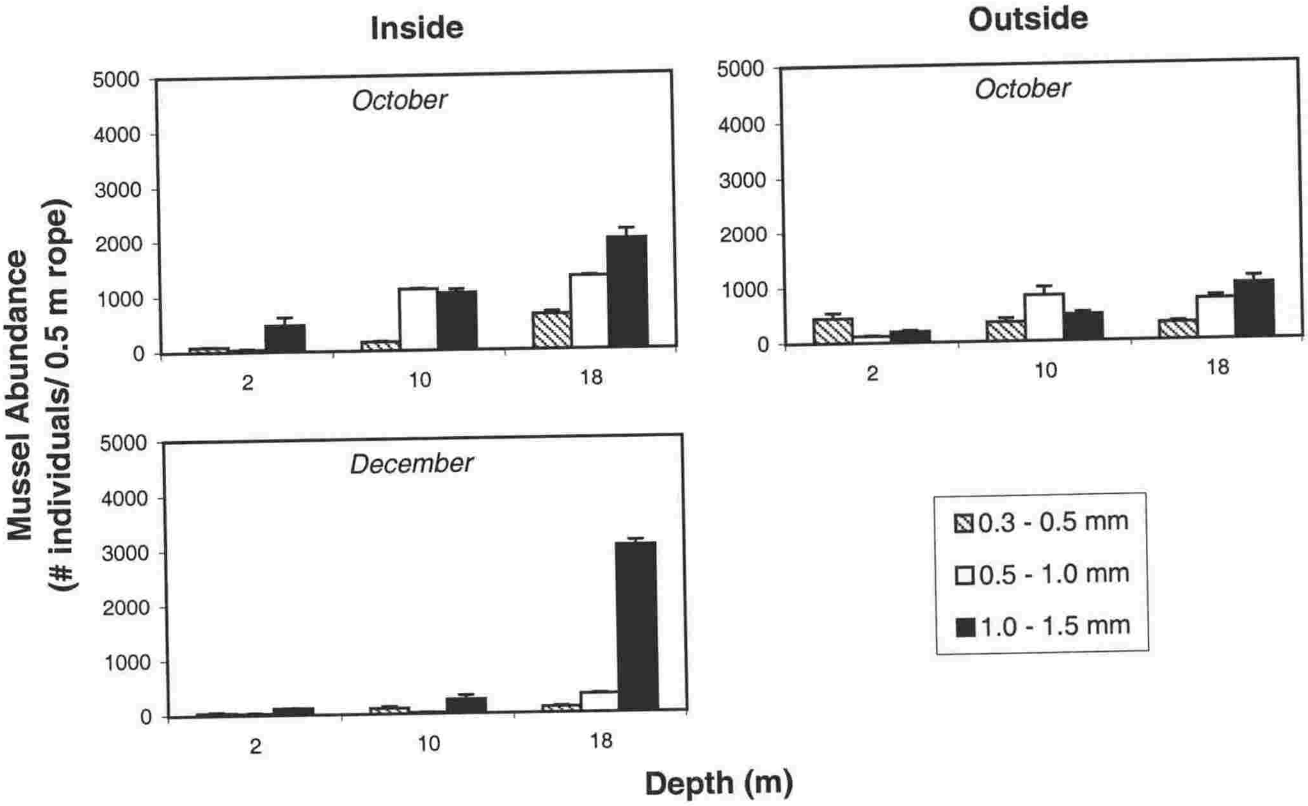

Figure 2. Mean (±SE) abundance of mussels within 3 size classes (<0.49, 0.5-0.99, >1.0 mm in shell length) settled on suspended ropes at 3 water depths (2, 10, and 18 m), 2 sites (inside and outside of Ahipara Bay), and 2 months in 1999.

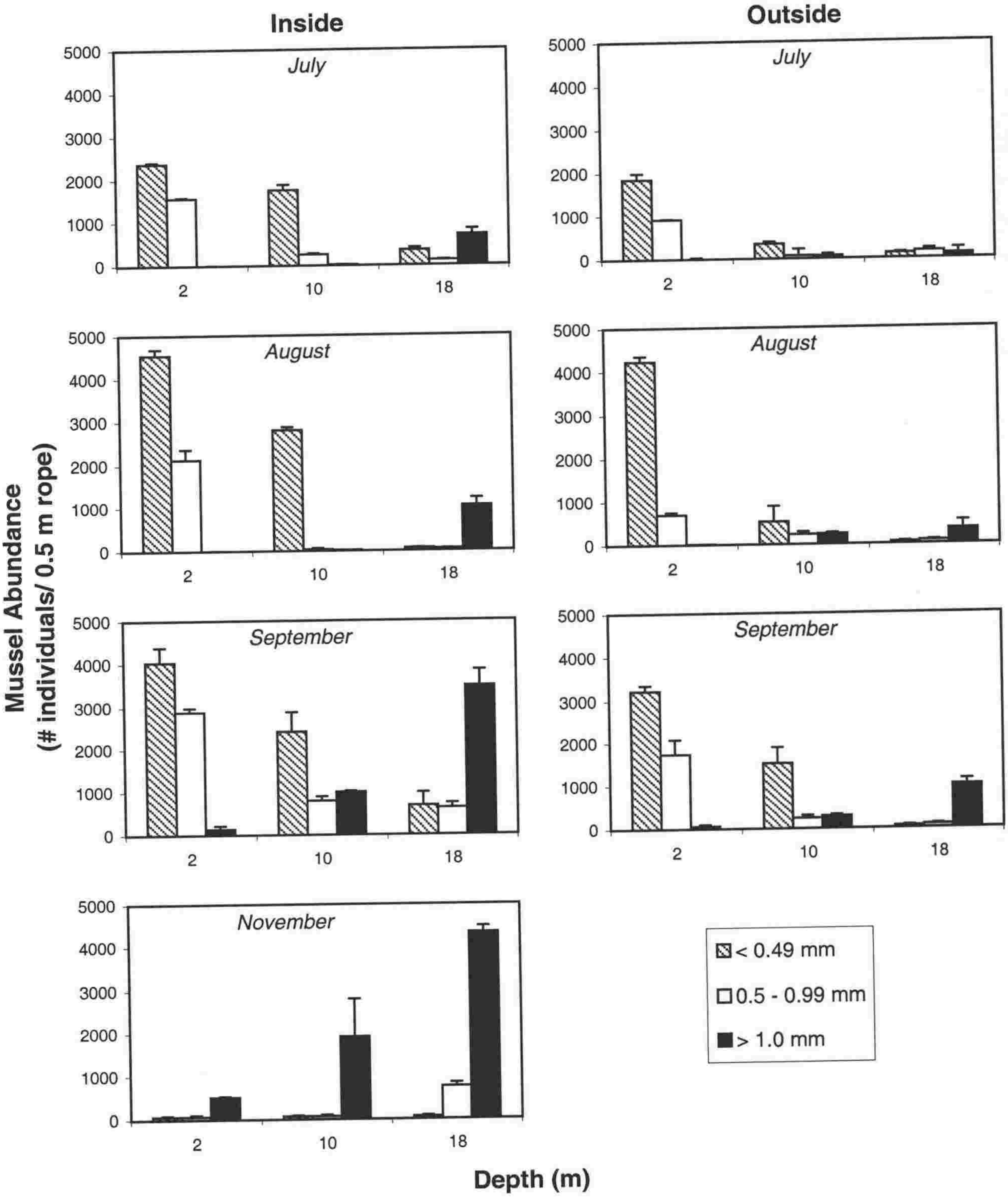

Figure 3: Mean (±SE) abundance of mussels within 3 size classes (<0.49, 0.5-0.99, >1.0 mm in shell length) settled on suspended ropes at 3 water depths (2, 10, and 18 m), 2 sites (inside and outside of Ahipara Bay), and 4 months in 2000.

Table 1: Mean (±SE) mussel abundances and ranges within 3 mussel size classes (<0.49, 0.5-0.99, and >1.0 mm in shell length) settled on suspended ropes at 3 water depths (2, 10, and 18 m), and 2 sites (inside and outside Ahipara Bay), between October-December 1999 and July-November 2000.

1999							
		Mussel size class					
Site	Depth	<0.49 mm		0.5-0.99 mm		>1.0 mm	
		Mean (SE)	Range	Mean (SE)	Range	Mean (SE)	Range
Inside	2 m	58 (14)	24-89	30 (6)	16-46	299 (120)	113-625
	10 m	126 (22)	61-164	564 (316)	12-1123	647 (230)	179-1108
	18 m	375 (157)	89-690	829 (284)	324-1342	2525 (314)	1821-3135
Outside	2 m	454 (93)	574-361	119 (10)	109-128	198 (21)	177-219
	10 m	356 (68)	288-424	829 (151)	678-980	477 (49)	428-526
	18 m	315 (30)	285-345	732 (59)	673-791	1004 (127)	877-1130
2000							
Inside	2 m	2749 (663)	42-4678	706 (218)	98-1583	177 (116)	0-826
	10 m	1756 (407)	38-2884	594 (338)	2-2359	42 (16)	0-112
	18 m	282 (113)	32-982	255 (99)	32-738	404 (154)	2-1218
Outside	2 m	3096 (439)	1709-4347	1425 (465)	489-2985	1536 (642)	58-3842
	10 m	787 (269)	134-1887	675 (347)	56-2073	442 (185)	24-1131
	18 m	65 (17)	23-132	292 (147)	30-837	2251 (744)	476-4477

Table 2: Statistical analyses of mussel abundances on suspended ropes in 1999. Two-way ANOVA tests (Model I) are shown for each of 3 mussel size classes (< 0.49, 0.5 - 0.99, and > 1.0 mm in shell length). Fixed factors are site (inside and outside Ahipara Bay), and depth (2, 10, and 18 m water depth). Sample size n = 2. Non-significant tests at α = 0.05 are noted (ns).

		< 0.49 mm		0.5 - 0.99 mm		> 1.0 mm	
Source	df	F	p	F	p	F	p
Site	1	29.78	0.002	0.81	0.402 ns	37.43	0.001
Depth	2	22.20	0.002	214.37	0.001	48.70	0.001
Site x Depth	2	40.56	0.001	21.01	0.002	0.12	0.893 ns
Error	6						

Table 3: Statistical analyses of mussel abundances on suspended ropes in 2000. Three-way ANOVA tests (Model I) are shown for each of 3 mussel size classes (< 0.49, 0.5 - 0.99, and > 1.0 mm in shell length). Fixed factors are month (July, August, and September 2000), site (inside and outside Ahipara Bay), and depth (2, 10, and 18 m water depth. Sample size n = 2. Non-significant tests at $\alpha = 0.05$ are noted (ns).

		< 0.49 mm		0.5 - 0.99 mm		> 1.0 mm	
Source	df	F	p	F	p	F	p
Month	2	20.60	0.001	16.31	0.001	129.51	0.001
Site	1	12.99	0.002	3.90	0.64 ns	0.17	0.683 ns
Depth	2	155.00	0.001	74.53	0.001	285.26	0.001
Month x Site	2	11.17	0.001	9.86	0.001	16.18	0.001
Month x Depth	4	12.89	0.001	1.85	0.163 ns	7.23	0.001
Site x Depth	2	8.19	0.003	1.28	0.303 ns	21.06	0.001
Month x Site x Depth	4	5.31	0.005	7.32	0.001	5.67	0.004
Error	18						

CHAPTER 8

Multi-scale effects of wind conditions, temperature, and tidal range on the dynamics of mussel spat transport and arrival on coastal areas of northern New Zealand

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In preparation: Journal of Marine Research

ABSTRACT

Historical records of wind speed and direction, tidal range, water temperature, and modeled swell height and direction were examined to elucidate daily, monthly, and inter-annual patterns of mussel spat (*Perna canaliculus*) arrival to Ninety Mile Beach, northern New Zealand between 1990 and 1999. For the long-term data set, a statistical approach was taken to identify the conditions that favored spatfall events and amounts. Spatfall events and amounts correlated well with strong offshore winds. On days with high tidal range, there was a suggestive increase in spatfall amount, but this trend was non-significant. Daily and seasonal water temperature records did not show significant effect on the timing nor the scale of spatfall events nor spatfall amounts. However, low swell height in the onshore direction was highly significant to spatfall events and amounts. Within the 9-year data set, storm events (wind speeds > 20 m s^{-1}) were most frequent between May-August. An average lag time of 4 months was found between peak storm events and the subsequent peak in spatfall events and amounts in September-

October. Years with a greater number of storm events also were associated with significantly higher spatfall events and amounts. Storminess and water temperature may be associated with El Niño/ La Niña episodes, which greatly influence the wind climate of New Zealand. Possible ecological and oceanographic processes are put forward to explain the observed relationships between spatfall events and natural forces, such as winds, tides, and swell.

INTRODUCTION

Numerous hydrological studies have attempted to relate oceanographic information to the distribution and transport of marine invertebrate larvae and juveniles (Farrell, et al., 1991; Wing, et al., 1995; 1998). The widespread dispersal of planktonic larvae of many sessile invertebrates is highly dependent on both the population dynamics of adult populations and oceanographic processes. Settlement and recruitment of invertebrate larvae to coastal areas may occur over spatial scales of 1 to 100's of kilometers, and temporal scales of 1 day to several years (Farrell, et al., 1991; Elbert et al., 1994; McConnaughey et al., 1994; Miller and Emlet, 1997). During the dispersal or transport phase, larvae and juvenile invertebrates may be associated with drift algae, which provide micro habitats, as well as a vehicle for dispersal (Kingsford, 1992; Kingsford and Milicichi, 1987; Ingólfsson, 1998; Norkko, 1994). These larval and juvenile pulses to the coast are likely to be directly related to ocean currents, tidal ranges, and the wind patterns that influence local hydrodynamic processes, such as surface currents, eddies, and upwelling events (Epifanio et al., 1989; Kingsford, 1990; Clancy and Cobb, 1997; Miller and Emlet 1997; Chiswell and Roemmich, 1998; Eggleston et al., 1998; Stoner and Smith, 1998).

Hydrodynamic transport of marine larvae and juveniles and their recruitment to coastal areas have been extensively studied, especially for commercial species such as crabs (Eggleston et al., 1998a; McConnaughey et al., 1992; McConnaughey et al., 1994; Epifanio, 1995) and lobsters (Katz, et al., 1994; [Comeau and Drinkwater, 1997]; Eggleston et al., 1998b). Many of these studies have addressed the effect of wind-generated currents as a major contributor to the transport and subsequent arrival of invertebrate larvae to coastal areas. A commonly proposed transport mechanism is that of an onshore surface movement of larvae due to significant onshore winds (Hudon and Fradette, 1993; Katz et al., 1994; McConnaughey et al., 1994). Other mechanisms influencing larval recruitment to the shore involve oceanographic processes such as upwelling, selective tidal transport, river mouth advection, and Ekman transport (Hernández-León, 1991; McConnaughey et al., 1994; Thorrold et al., 1994; Wing et al. 1995; Grimes and Kingsford, 1996; Eggleston et al., 1998a). However, these transport mechanisms apply to surface-transported pelagic organisms. Many marine invertebrates may disperse while in association with "loose-lying" or bottom drifting algae (Holmquist, 1994; 1997; Norkko, 1998). Conceptual oceanographic models for bottom drifting or benthipelagic organisms have been lacking (but see Epifanio et al., 1989).

In the case of the New Zealand green-lipped mussel, *Perna canaliculus*, the dispersal and recruitment potentials of larvae and juveniles in the water column are not only influenced by hydrodynamic processes but also are strongly dependent on the availability of algal material that provide the majority of the substrates for primary and even secondary settlement of juveniles (Hickman, 1982; Buchanan and Babcock, 1997; Alfaro and Jeffs, in press). Mussel juveniles or spat will preferentially settle on filamentous algal material, either attached to the bottom or drifting in the water column, although mussel settlement also takes place on other fibrous materials such as hydroids and artificial debris (Buchanan and Babcock, 1997; Alfaro and Jeffs, in press). Unattached subtidal algae (mostly red algae), unlike some detached brown algae and kelps (i.e. *Sargassum, Macrocystis*), are "loose-lying" on the bottom and are transported by bottom currents (Norton and Mathieson, 1983). Mussel larvae and juveniles may settle on these drifting materials until a more suitable substrate, such as bare rock, is encountered. However, the ultimate survival of mussels to adult size within suitable rocky substrates is limited to a small percentage (< 1%) of the initially settled mussels within algal and other fibrous materials (A. C. Alfaro, unpublished data).

At Ninety Mile Beach, in northern New Zealand, periodic pulses (spatfall events) of drift algal material with attached mussel spat (up to 100% coverage) arrive along the 90 km long beach. Spatfall events generally consist of distinct clumps (10-100 m^2 horizontal extent) of mussel spat (0.3-2 mm, and in occasion 0.3-10mm in length) with drift algae (mostly red algae), hydroids, and debris (Alfaro & Jeffs, in press). Because only about 5% of the intertidal area is covered by rocky habitat suitable for mussel beds, most of the mussel spat that strands on the sandy beach has little chance of survival. Nevertheless, their arrival (up to 140 tonnes of wet algae with spat per year) is of great economical value to the spat collectors who supply the seed spat, still attached to the drift material (up to 10^6 mussels/kg of wet algae), to mussel farms for subsequent aquaculture production (A. C. Alfaro, in preparation). These spatfall events or wash-ups are unique in New Zealand and provide about 80% of the mussel industry seed requirements, which converts to > $150 M/ year revenues to the country (Jeffs et al., 2000). Consequently, research on the local oceanographic and climatic conditions are essential to the understanding of why mussel spat accumulate in such massive quantities at Ninety Mile Beach, and why are spat sometime absent for up to 9 months of the year. A useful approach to investigate temporal and spatial patterns in larval and juvenile transport and landings in nearshore environments is the use of physical and biological historical data.

Based on records such as wind speed and direction, water temperature, and fishery landings, models have been derived to reduce unpredictability in nearshore fisheries, which have been regarded previously as highly variable in time and space (McConnaughey et al., 1994; Clancy and Cobb, 1997).

In the present study, the relationships between spatfall events at Ninety Mile Beach, northern New Zealand, and local physical forcings (wind patterns, water temperature, tidal range, and swell conditions) were investigated in historical records between 1990 and 1998. Patterns within temporal scales of days, months, and years were examined to attempt to elucidate the dynamics of spat arrival to the beach.

METHODS AND MATERIALS

Study Site

The study site encompasses 90 km of coastal area at Ninety Mile Beach, northern New Zealand (Fig. 1). The virtually straight sandy beach stretches from Ahipara Bay to Scott Point, with only three intertidal rocky areas suitable for mussel bed formation (Reef Point, The Bluff, and Scott Point) (Fig. 1). Reef Point and Scott Point contain large rocky intertidal habitats with extensive adult mussel populations that may extend subtidally (M. Morrison, unpublished data). These intertidal and subtidal populations are likely to be the predominate sources of larvae in the area. The offshore subtidal environment is quite even, shallow sloping, containing a soft sediment seabed to an offshore distance of 60 km and up to depths of 200 m. The local oceanographic regime is dominated by the interaction of the southbound West Auckland current and the northbound Westland current (Stanton, 1973; Sharples, in press). The predominant winds affecting the shelf waters at Ninety Mile Beach are from the south-west (Reid, 1982; Sharples, in press) (Fig. 1). These southeasterly winds have been observed to create strong upwelling in the area (Stanton, 1973). However, easterly and northeasterly winds also are strong in the summer, and are associated with the passage of tropical cyclones to the north of New Zealand (Moir et al., 1986; Sharples, in press). The tidal environment around New Zealand is dominated by a coastally-trapped Kelvin wave traveling anti-clockwise around the shelf with an elevation amplitude of less than 1-2 m and a tidal current amplitude of about 10-20 cm s^{-1} (Sharples, in press). El Niño effects in New Zealand are associated with lower sea surface temperatures (Gordon, 1986). Lower sea surface temperatures have been attributed to increasing southerly winds from the Antarctic and a large-scale diffusive upwelling phenomenon caused by the reduction in the source of tropical water to the Australasian region (Sprintall et al., 1995; Sharples, in press). Accompanying the southeasterly winds, swells from the south-west also create a high level of exposure to the coast line (Moir et al., 1986).

Physical Data

Wind records were obtained from nearby Cape Reinga meteorological station (S 34° 26’ and 173° 5.3’ E). The station’s anemometer is located 226 m above sea level and it is well exposed to the winds. Wind records from this station are known to be representative of the entire Ninety Mile Beach area (Kaitaia wind report; G. Daw, personal communication). The wind data included hourly measurements of wind speed and direction from May 1990 to May 1999. Wind speeds > 20 m s^{-1} were considered strong winds or storm events suitable to cause significant water movement, and potentially to dislodge and transport drift algae and mussel spat.

Tidal range data were provided by The National Institute of Water and Atmospheric Research. The data were generated for a mid-point along Ninety Mile Beach using a CashCanz model. Daily tidal information also covered the sampling time between May 1990 to May 1999.

Water temperature records were obtained from a data logger placed 0.5 m below low water level at the south end of the study area S 35° 10.8' and 173° 5.3' E for the period of January 1991 to May 2000. Three gaps in the water temperature data set were between 19 August to 12 October 1992, 16 October 1993 to 26 April 1994, and 1 January to 1 July 1998.

Swell height and directions were obtained from a model generated for Ninety Mile Beach. Swell data were available only between May 1990 and December 1993.

Records of Southern Oscillation Index were extracted from the New Zealand National Climate Database, maintained by The National Institute of Water and Atmospheric Research. These records covered the period between 1990 to 2000.

Spat Collection Data

Detailed records of the dates and amounts of spatfall from May 1990 to May 2000 were obtained from 6 spat collectors at Ninety Mile Beach. Spat collectors patrol the extent of the beach daily in search of algal drift patches close enough to the shore to be collected with hand nets. Some algal patches may drift offshore from Ninety Mile Beach, but unique oceanographic conditions tend to accumulate and transport distinctive patches of algal material to the surf zone, where almost all the spat is collected. The algal patches may drift northward along the coast during the course of a few days until the majority of the material is collected or the ocean conditions change and push the algal patch offshore. For the purpose of this research, a particular collection of algae with attached spat on a given day is referred to as a spatfall event. The amount (wet weight) of algae with spat collected from each spatfall event also was obtained, but because the amount of algae with spat collected was influenced by spat demands from the mussel farms, results from these data were used only in general ecological interpretations. Variations in mussel spat within algal material are not included in this research because they were assumed to have no effect on the dynamics of spatfall arrival to the beach.

Statistic Analyses

Statistical models were used to elucidate daily relationships between spatfall events and amounts, and the physical factors of wind speed, wind direction (onshore versus offshore), tidal range, water temperature, and swell height in the onshore direction during the 9-year data set. Because data for some physical parameters were not available for the entire 9 years, 3 different statistical models had to be fitted with the available data and each tested for each response variable (spatfall events and spatfall amounts). One model was constructed with the mean daily wind speed, wind direction, and tidal range for the period May 1990 to May 1999. Thus, strong winds in a given direction were expected to enhance the probability of a spatfall event and high spatfall amounts. Tidal range was incorporated in this model with the *a priori* expectation that spring tides would bring greater spatfall amounts than neap tides. For the second model, water temperature was added to the physical parameters of wind speed, wind direction, and tidal range. This model included data from May 1990 to May 1999 excluding the periods between 19 August to 12 October 1992, 16 October 1993 to 26 April 1994, and 1 January to 1 July 1998. Finally, a third model included swell in the onshore directions with wind speed, wind direction, and tidal range for the period January 1990 to December 1993. The expectation for this model was that low swells would enhance spatfall events and amounts at Ninety Mile Beach.

Because the spatfall data were binary and episodic (spatfalls often occurred over a number of days) classical analytic methods based of normal independent data could not be used. Re-sampling methods were used for the significance tests. Thus, 2 response variables were modeled with each of the 3 different physical data sets. First, logistic regression was used to model the probability that a spatfall event would take place (any amount of algae and spat collected on a given day). Second, least squares regression was used to fit models that included the spatfall amount (wet weight of algae with spat) that arrived to the beach on a spatfall event. It was considered unlikely that there would be any spatfall in the absence of any wind. Therefore, the models were fitted with no intercepts, which simplified the analysis considerably. Thus, all 6 analyses focused of the slopes of the relationships between the physical parameters and spatfall events or the physical parameters and spatfall amounts. A separate slope of wind speed was generated for both wind directions (onshore and offshore) within each analysis. Seasonal changes within the physical and biological data also were identified from the models.

After the models had been fitted, the test statistics for the parameter groups were compared to null distributions prepared by a permutation procedure. Since the null hypotheses were that the time sequence of the spatfall events (and amounts) were unrelated to the time sequences of the environmental factors, the permutation method randomized the starting point of the spatfall sequence relative to the physical factors. To preserve the data sequence, the data were wrapped around to produce a random association between the spatfall events (and amounts) and the factors that preserved both the correlations among the factors and their autocorrelation structure.

The same models (logistic and linear) were fitted using the daily mean length of the hourly wind vectors (a proxy for wind directional stability) instead of wind speed. Thus, a steady wind in a given direction was expected to enhance the probability of a spatfall event. However the results were so similar to those from mean wind speed that they are not presented here.

RESULTS

Daily Patterns

Results from the statistical models incorporating wind speed, wind direction, tidal range, and spatfall events indicated that the only significant effects on the probability of a spatfall event occurring on a given day *(prob(S))* was the mean wind speed/direction interaction (Table 1; Fig. 2). An offshore wind had a significantly higher probability of generating a spatfall event than an onshore wind (Tables 1; Fig. 2). For an offshore direction in the wind, the odds of a spatfall event occurring on a given day *prob(S)/(1-prob(S))* increased by an estimated 13% for each 10 kmh^{-1} increase in wind speed. If the wind was in the onshore direction, the probability of a spatfall event decreased by an estimated 40%. Thus, results from this model suggest that spatfall events tended to be associated with strong offshore winds. With regard to the effect of wind speed, wind direction, and tidal range on the spatfall amount (total weight of algae with spat) that arrived at the beach, an offshore wind increased the amount of spatfall by an estimated 181% for every 10 kmh^{-1} increase in mean wind speed. If the wind was in the onshore direction, the amount of spatfall decreased by an estimated 12% for every 10 kmh^{-1} increase in mean wind speed.

The effects of tidal range on the spatfall events and amounts were non-significant for all 6 analyses. However, a slight indication that a large tidal range may have increased the chances of a large spatfall amount was found within the first model (including wind speed, wind direction, and tidal range) (Table 2; Fig. 3).

Analyses that included water temperature as an added physical forcing failed to detect any effect of water temperature on both, the probability of spatfall events and the averaged daily spatfall amounts (Table 1&2; Fig. 4). However, the models including swell height in the onshore direction detected a strong negative effect for both spatfall events and amounts. Thus, for every meter increase in the swell height, the odds of a spatfall event were reduced by 81% and the spatfall amounts were reduced by 39% (Table 1&2; Fig. 5).

Monthly Patterns

Monthly records of storm events and spatfall events between January 1991 and December 1998 showed distinctive seasonal patterns. The number of storm events, defined as maximum wind speeds >20 m s^{-1}, per month indicated that the months of May through October had the greatest number of storms of the year (Fig. 6). Monthly spatfall events were highest between September and October (Fig. 6). Thus, a lag time of about 4 months is apparent between peak number of storms and peak number of spatfall events (Fig. 6). Similar trends were observed for spatfall amounts, which also peaked between September and October. The monthly mean number (2.36±2.36) of storms through the calendar month, regardless of year, varied from 0.66 events in February to 5.11 events in June. The average number of spatfalls ranged from 8.5 in May to 46.1 in October. The spatfall amounts ranged from 23550-178659 kg/month in May and September, respectively.

Results from the relationship between mean monthly swell height and number of spatfall events and spatfall amounts between 1991 and 1993 revealed a generally inverse relationship between swell height and both, spatfall events and amounts. Mean swell height was highest in August and lowest in December-January for months between 1991 and 1993 (Fig. 7). The number of spatfall events peaked in February and October, when swell conditions were generally low. Spatfall amounts were low between February and July, when the mean swell height was rising. However, peak spatfall amounts took place in August-October, when swell conditions were highest (Fig. 7). The monthly mean swell height varied from 1.4±0.1 events in December to 2.3±0.1 events in August. The number of spatfall events ranged from 1 in May to 16 in October, and the total spatfall amounts ranged from 480 kg/month in July and 103340 kg/month in August.

Yearly Patterns

Inter-annual patterns of high wind speeds and spatfall events show a direct relationship between the number of high wind speed events (wind speeds >20 m s^{-1}) and spatfall events between 1991 and 1998. Two peaks of strong wind speeds were observed in 1992 and 1996 (Fig. 8). Within the 8-year period, 1993 had the lowest number of strong wind speeds (14 events), whereas 1996 had the greatest number of strong wind speed events (41). Similar peaks in 1992 and 1996 were observed in the spatfall data (Fig. 8). The range of spatfall events within the 8-year data period was from 20 events in 1991 to 74 events in 1996 (Fig. 8). Spatfall amounts followed a similar direct relationship with the number of storm events except during1993-1994 (Fig. 8).

Records on the Southern Oscillation Index directly related to the number of storm events (wind speeds > 20 m s^{-1}) and the number of spatfall events that took place at Ninety Mile Beach between 1991 and 1998 (Fig. 9). An El Niño event affected New Zealand between 1991 and 1995 (Fig. 9). This 4-year El Niño was particularly strong between 1993-1994, which coincided with the lowest point in the number of storm and spatfall events within the sampled period (Fig. 8&9). A strong La Niña event in 1996 clearly matched a peak in number of storms and spatfalls the same year (Fig. 8&9). A recorded El Niño in 1997 and La Niña in mid-1998 again were closely followed by the number of storms and spatfall events at Ninety Mile Beach (Fig. 8&9).

DISCUSSION

For bottom dispersers or negatively buoyant larvae and juveniles, a subtidal transport mechanism is required for dispersal (Epifanio, 1995). In the case of mussel larvae, settlement often takes place on filamentous algal material, which is neutrally or negatively buoyant. As the density and size of mussels increase, the spat/algal material becomes heavier, and forms dense clumps where often the initial algal substrate is no longer visible. Under strong water currents, such as storms and cyclones, algal material may becomes dislodged and form algal patches that tumble near the bottom. Studies of the effects of wind-driven subtidal currents on the transport of negatively buoyant materials are lacking. However, Reusch and Chapman (1995) observed the movement of adult mussel clumps with wind speeds of less than 10 m s^{-1} in a shallow subtidal habitat in the Western Baltic. Storm events have been associated with dislodgment and onshore transport of adult mussels (Witman and Suchanek, 1984; Witman, 1987; Reusch and Chapman, 1995), but no detailed studies have been undertaken to record the movement of bottom-drifting algal/spat clumps (but see Bonsdorff, 1992; Holmquist, 1994).

Daily Patterns

In the present study, offshore winds correlated well with a spatfall event on the beach. Rapid cross-shelf transport responses to wind conditions have been observed in other invertebrate larvae (Stoner and Smith, 1998). Stoner and Smith (1998) found that larvae from the gastropods *Strombus gigas* and *S. costatus*, which inhabit the upper few meters of the water column, have a lag response to arrival at the shore of 6-8 hours after a strong onshore wind condition. Lag times of less than 12 hours have been suggested to be associated with larval transport of the crab, *Callinectes sapidus*, although it is still unclear as to whether the transport is through surface and/or bottom waters (Epifanio, 1995). Surface drift algae, with their associated invertebrate communities, also have been observed to move with slight breezes (Ingólfsson, 1998). *Macrocystis pyrifera* clumps (1-2 kg) have been reported to move under wind speeds of 3.6-5.1 m/s (Kingsford, 1995). However, it is unknown to what extent strong wind speeds can move bottom-drifting material.

Upwelling conditions may upwardly transport heavier material, such as algal/spat clumps, to near-shore surface waters. Upwelling events have been recorded along the west coast of New Zealand's North Island, including Cape Reinga (Fig. 1) (Stanton, 1973, Sharpless, in press). However, these upwelling events are normally caused by southerly winds that move water northward along the coast. Then, Ekman transport carries surface water away from the land such that upwelling of deeper water takes place. Southerly winds are the predominant winds at NMB and these wind conditions may be responsible for upwelling and the onshore transport of algal clumps in spatial scales of 100 km. It is possible that, in conjunction with an upwelling mechanism to bring algal/spat material near shore, a smaller scale and closer to shore process is responsible for the accumulation of spat/algae in the surf zone. Our data showed that northerly and northeasterly winds were more likely to be associated with spatfall events and high spatfall amounts on the same day. It is possible that strong offshore winds may act to decrease the onshore swells allowing for smaller scale (10-100 m) entrapment of algal material in the surf zone. Low swell conditions in the onshore direction where found to increase the probability of a spatfall event and the probability of a large spatfall amount. However, more detailed oceanographic studies would need to be conducted in the area to elucidate the effects of local ocean dynamics on spat/algal transport.

Tidal rage did not significantly affect the arrival of algae and spat to the beach. However, there was a slight indication that spring tides resulted in higher spatfall amounts. Spring tides have been associated with greater onshore transport than neap tides (Kingsford, 1990).

Monthly Patterns

Monthly mean storm events within the 1991-1998 data show a distinct peak in June, whereas the number of spatfall events peaked in October. These data support the notion that a high number of storm events in May-August result in a high number of spatfall events in September-October. This 4-month average lag time between peak storm events and peak spatfall events may reflect the time scale within which algae are dislodged by storms from subtidal habitats, and are transported to the surf zone. Algal clumps tumbling on the bottom have been recorded to move more than 0.5 km in 24 hours (Holmquist, 1994), although algal patches near the surf zone at Ninety Mile Beach have been observed to move with the along-shore currents up to 5 km per day (C. Hensley, personal communication). However, bottom transport in deeper areas may be slower and accumulation of drift algae may require several days to months.

The mussel spawning season at Ninety Mile Beach is during winter-spring (Alfaro et al., in press). Thus, the peak in spatfall events also may reflect a time when mussel larvae are available in quantities large enough to saturate most of the floating algal substrate available in the water column. Once algal substrates have attracted large numbers of settlers, the material becomes quite negatively buoyant and may only be moved by subtidal hydrodynamic processes. Thus, the time of the year over which the peaks of storm/spatfall events take place may be related to a combination of factors including frequency of storm events, availability of algal material, mussel spawning events, and subtidal water flow dynamics. Climatic conditions for the area predict increased wind speeds in winter months, as shown by our historical data and Moir et al. (1986). Attached algal biomass has been recorded to be highest in summer months when the temperature is highest (Kingsford, 1992), and algal abundances are high until winter storms dislodge them (Rees et al., 1977; Lenanton et al., 1982; Dobbs and Vozarik, 1983; Kingsford, 1992). Although there is little information about oceanographic conditions of the area, the biological and physical factors mentioned, may be responsible for the distinctively large number of spatfall events recorded in September-October.

Yearly Patterns

Within a larger temporal scale, the present data suggest strong inter-annual agreement between the number of storm events, the number of spatfall events, and El Niño/ La Niña years between 1991 and 1998. A peak number of storm and spatfall events in 1996 coincided with the strongest La Niña period recorded by the Southern Oscillation Index. A strong El Niño event in 1993-1994 related well with a drop in the number of storm and spatfall events in that period. The Southern Oscillation Index directly relates to sea surface temperatures, such that, an El Niño period is reflected in an increase in sea surface temperature and a deepening of the thermocline (Goring & Bell, 1999). There are 3 possible processes by which El Niño/ La Niña events may affect the observed spatfall event patterns. 1) while sea surface temperatures and depth of the thermocline may have little effect on the availability and arrival of algae to the beach, it is possible that higher temperatures and lower nutrients (caused by lowering of the thermocline) may reduce the number of mussel spat available for settlement in the water column. Because this study only reflects spatfall events that contained a substantial number of spat attached to the algae to make their collection commercially viable, it is likely that low numbers of mussel spat, not algae, may have resulted in the low number of spatfall events during El Niño years. 2) during El Niño years, changes in wind-driven Ekman transport also have been noted a have been associated with reduced coastal upwelling (Mysak, 1986). The suggestion that arrival of algal material with spat to the surf zone necessitates a net transport of bottom water to the surface is substantiated by the findings that less spatfall number were recorded in El Niño years and greater numbers were recorded in La Niña years. 3) it also is possible that El Niño/ La Niña climatic conditions do not directly affect the number of mussel spat, but the number of storm events. The number of storm events, in turn, affects the amount of algae that is ripped off from the bottom and becomes available for transport to the beach.

Finally, spatfall events and amounts arriving at the beach appear to be affected by a combination of physical factors that vary considerable within small and large temporal scales. Wind speed and direction and swell height in the onshore direction have significant effects on the dynamics of spatfall arrivals to the beach. However, more detail information is needed to elucidate the specific mechanisms involved in the accumulation and transport of bottom drifting material. The oceanographic and weather conditions at Ninety Mile Beach are highly complex and poorly understood. Thus, further studies are needed to investigate other oceanographic processes, such as water circulation, vertical and horizontal advection, and internal waves, that greatly affect the dynamic west coast of New Zealand.

ACKNOWLEDGMENTS

We would like to thank 6 spat collectors who provided historic spatfall information. We are grateful for the generous assistance of the Henley family. D. Goring from The National Institute of Water and Atmospheric Research provided tidal range data. J. Lumley from Metservice, New Zealand provided wind records. B. Mullan from The National Institute of Water and Atmospheric Research facilitated Southern Ocean Index data. The modeled swell data was generated with CashCanz by D. Goring from The National Institute of Water and Atmospheric Research. Technical advise for this project was provided by J. Wilkin, A. Graham, B. Stanton, and D. Goring.

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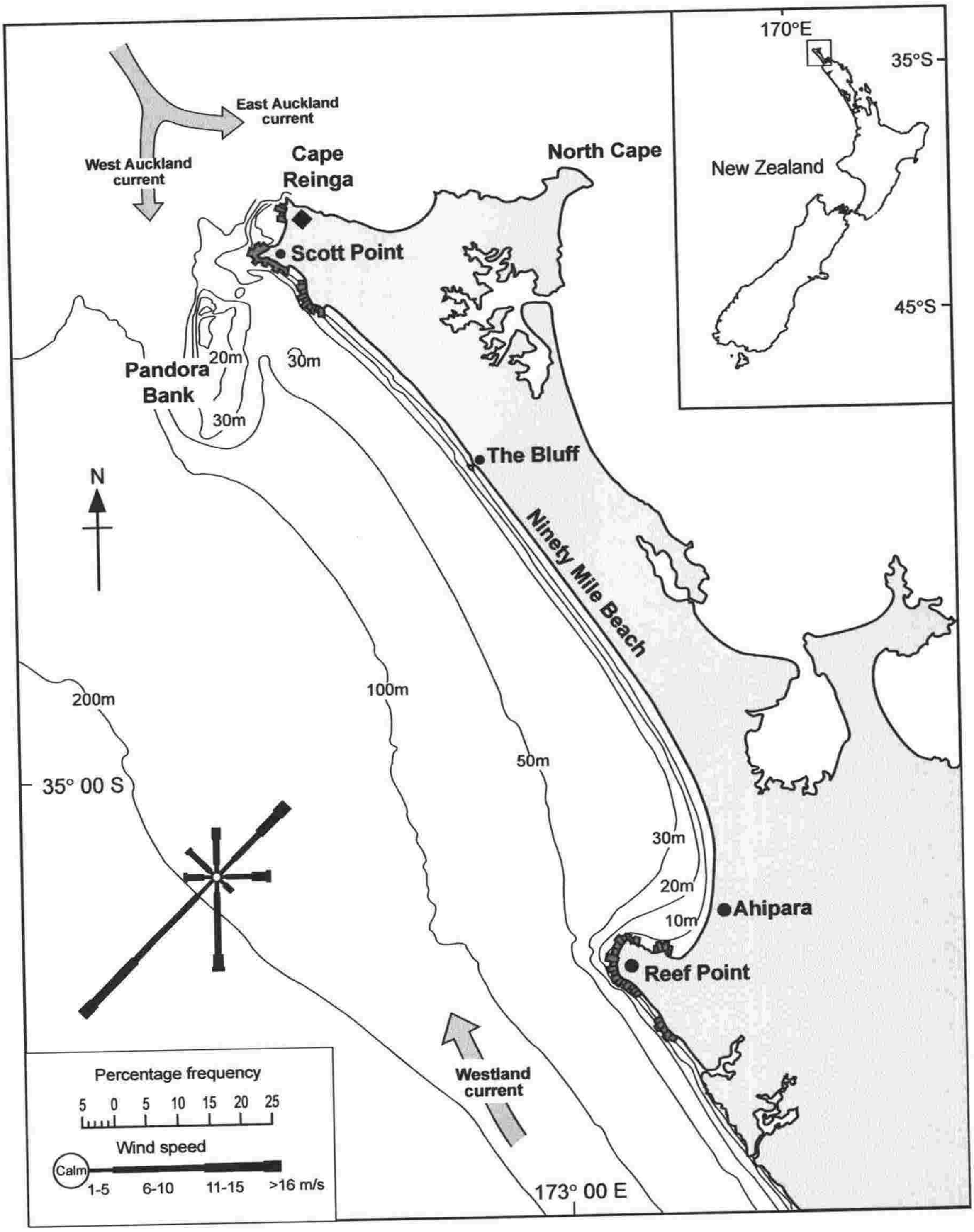


Figure 1. Map of the study site at Ninety Mile Beach, northern New Zealand. Three major intertidal mussel populations are found at Reef Point, The Bluff, and Scott Point. Two major currents that affect the area are The West Auckland current and the Westland current. Predominant winds are from the southwest direction. The location of Cape Reinga meteorological station is noted with a black diamond.

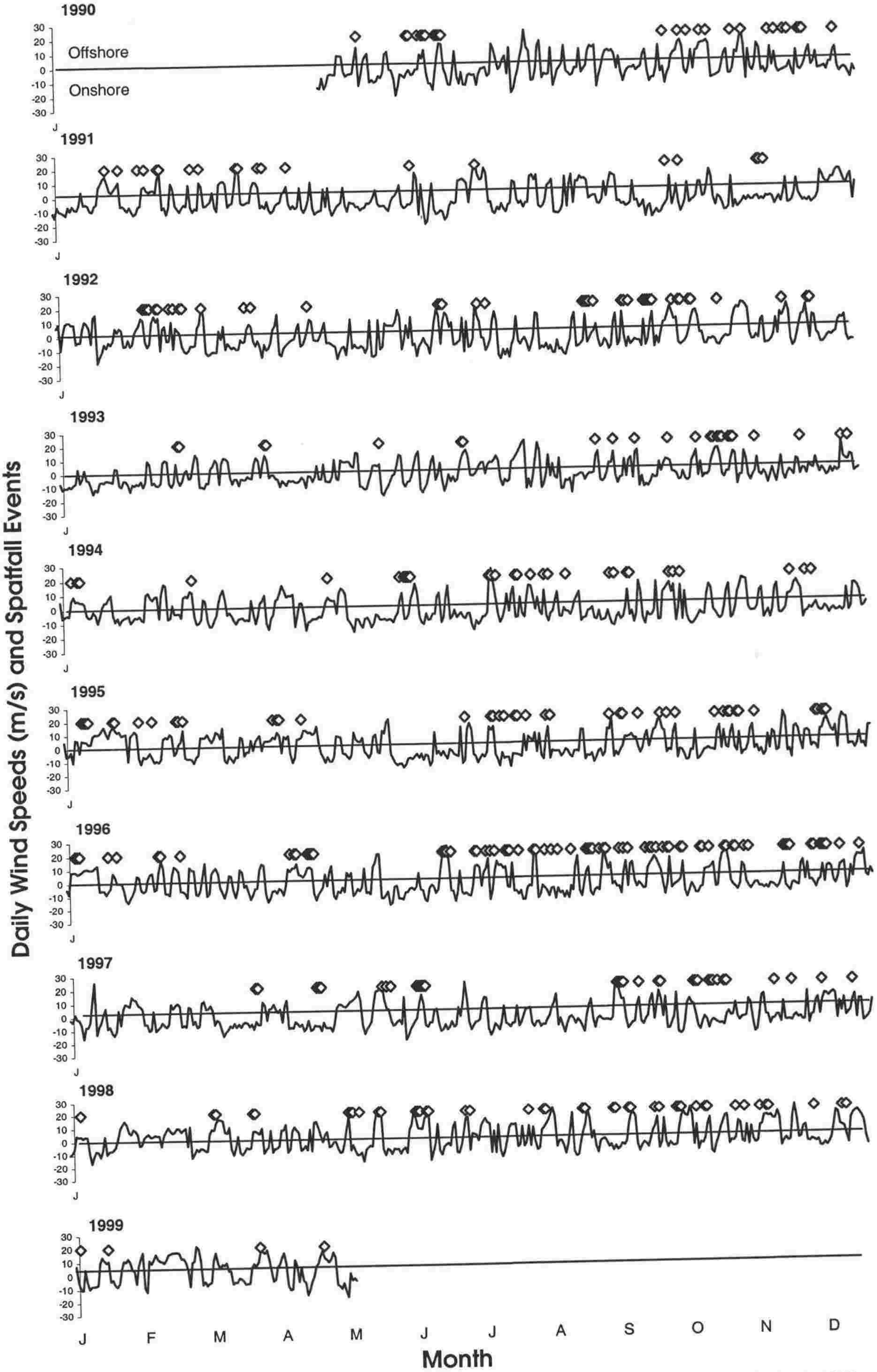


Figure 2. Daily wind speeds (m/s) and spatfall events (diamonds) between March 1990 and March 1999. Positive wind speeds are in the offshore direction and negative wind speeds are in the onshore direction.

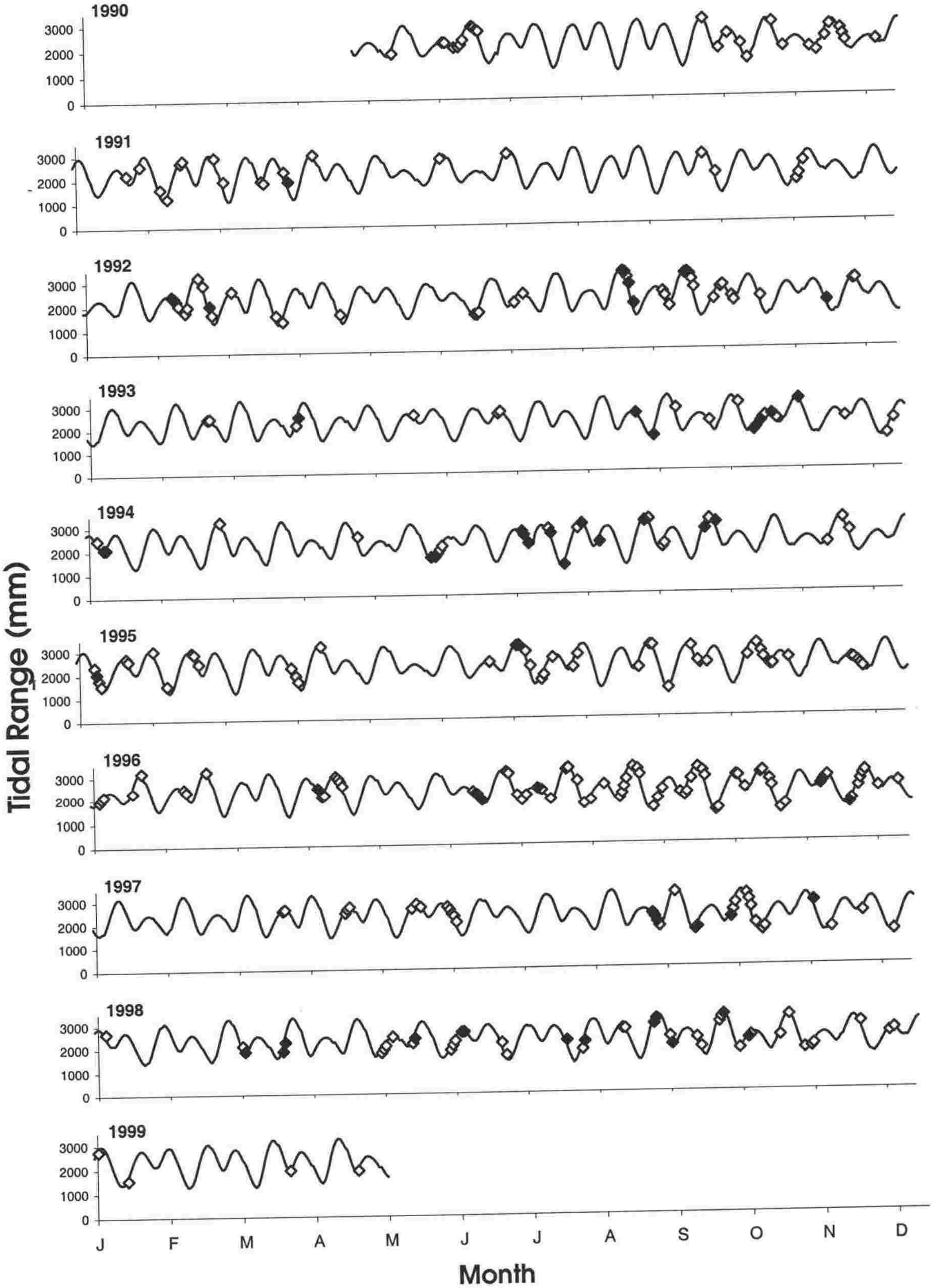


Figure 3. Tidal range (mm) and spatfall events (white diamonds) between March 1990 and March 1999. Spatfall events which had > 5000 kg of wet algae and spat are plotted on the tidal range curve (black diamonds).

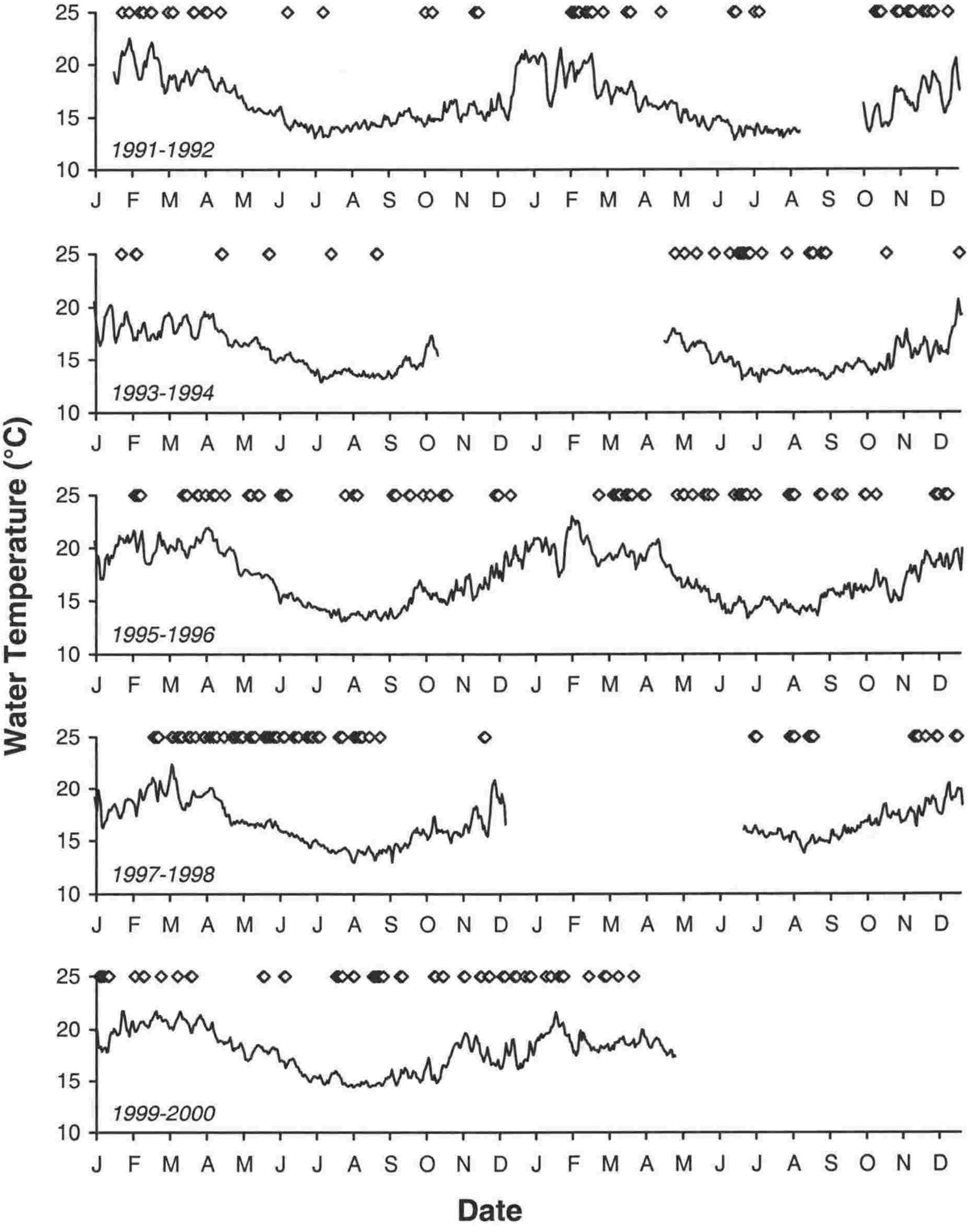


Figure 4. Daily water temperature records (ºC) and spatfall events (diamonds) between January 1991 and May 2000 with missing gaps.

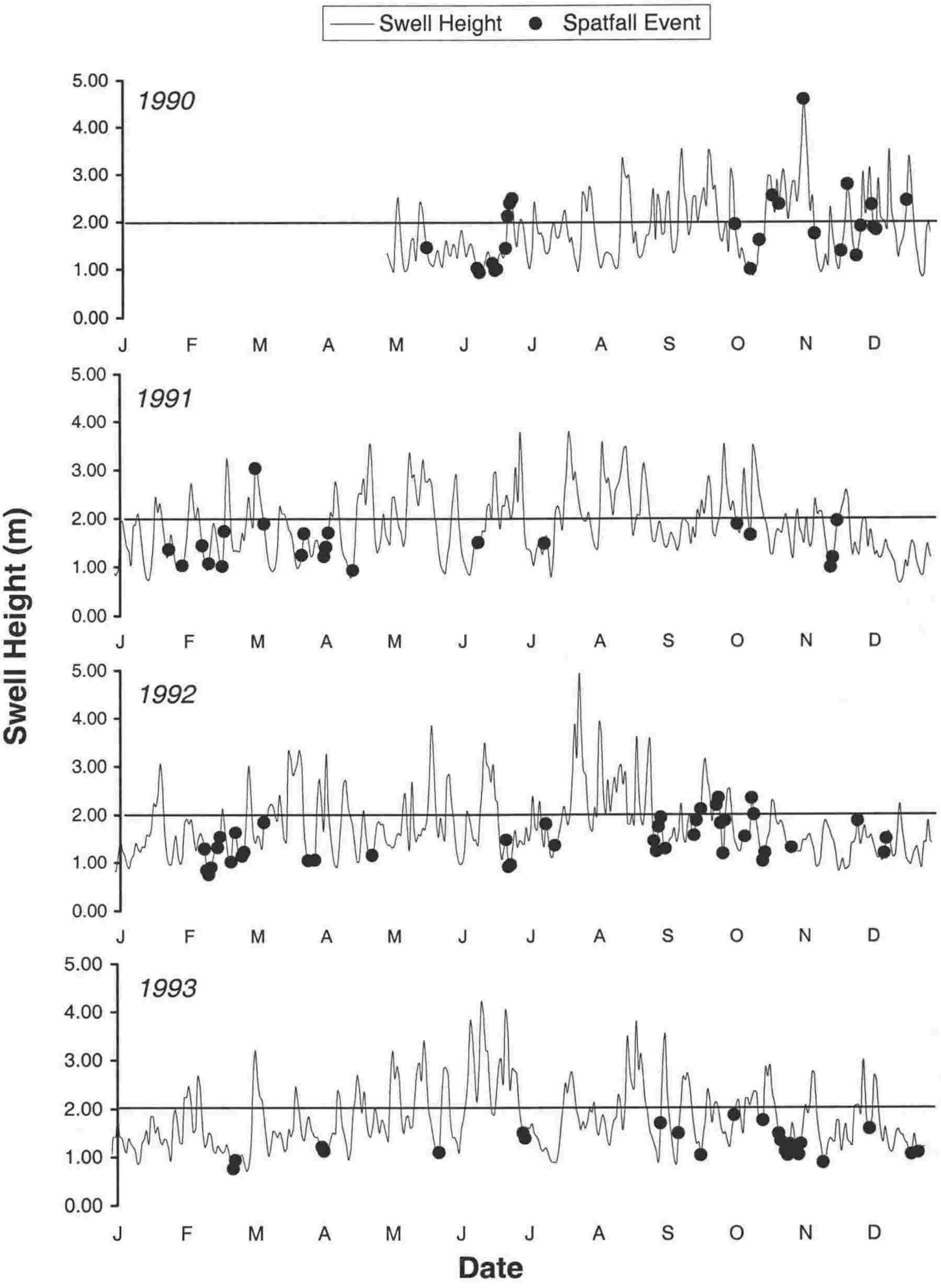


Figure 5. Daily swell height (m) and spatfall events (black circles plotted on the swell curve) between May 1990 and December 1993. An axis line at 2 m represents the average swell height.

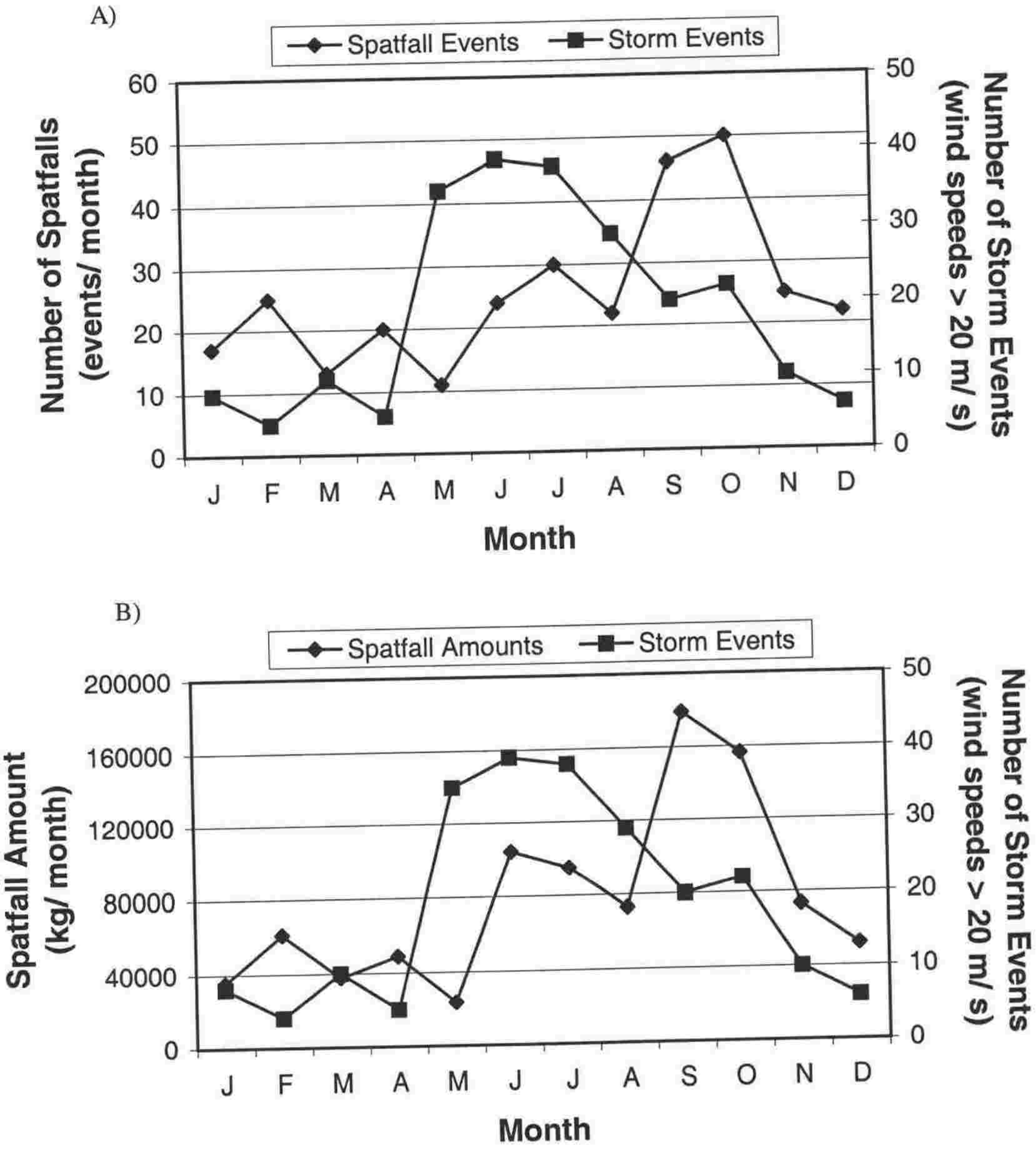
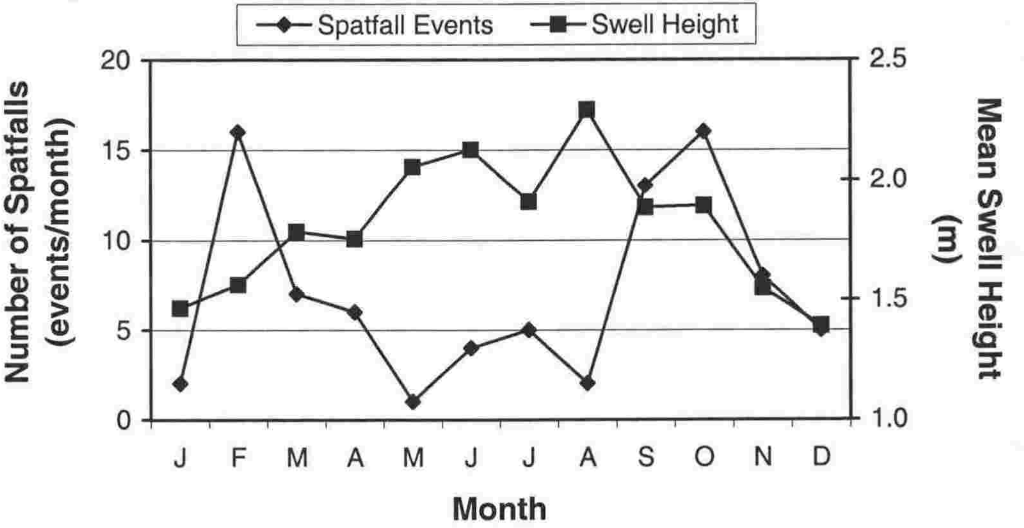


Figure 6. Monthly storm events (wind speeds > 20 m/s) between January 1991 and December 1998. A) number of spatfall events and B) spatfall amounts within the same time period.

A)



B)

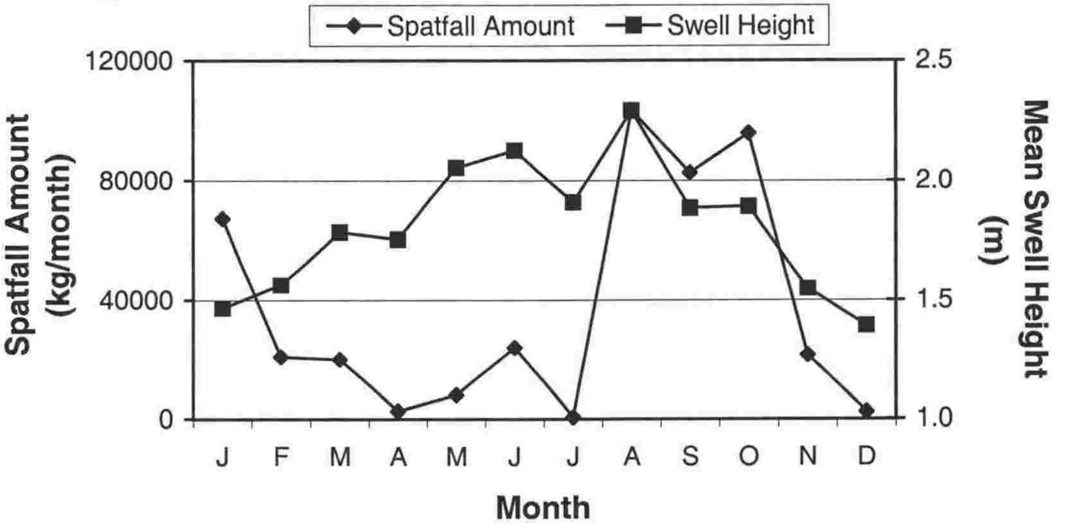


Figure 7. Monthly swell height (m) between January 1991 and December 1993. A) number of spatfall events and B) spatfall amounts within the same time period.

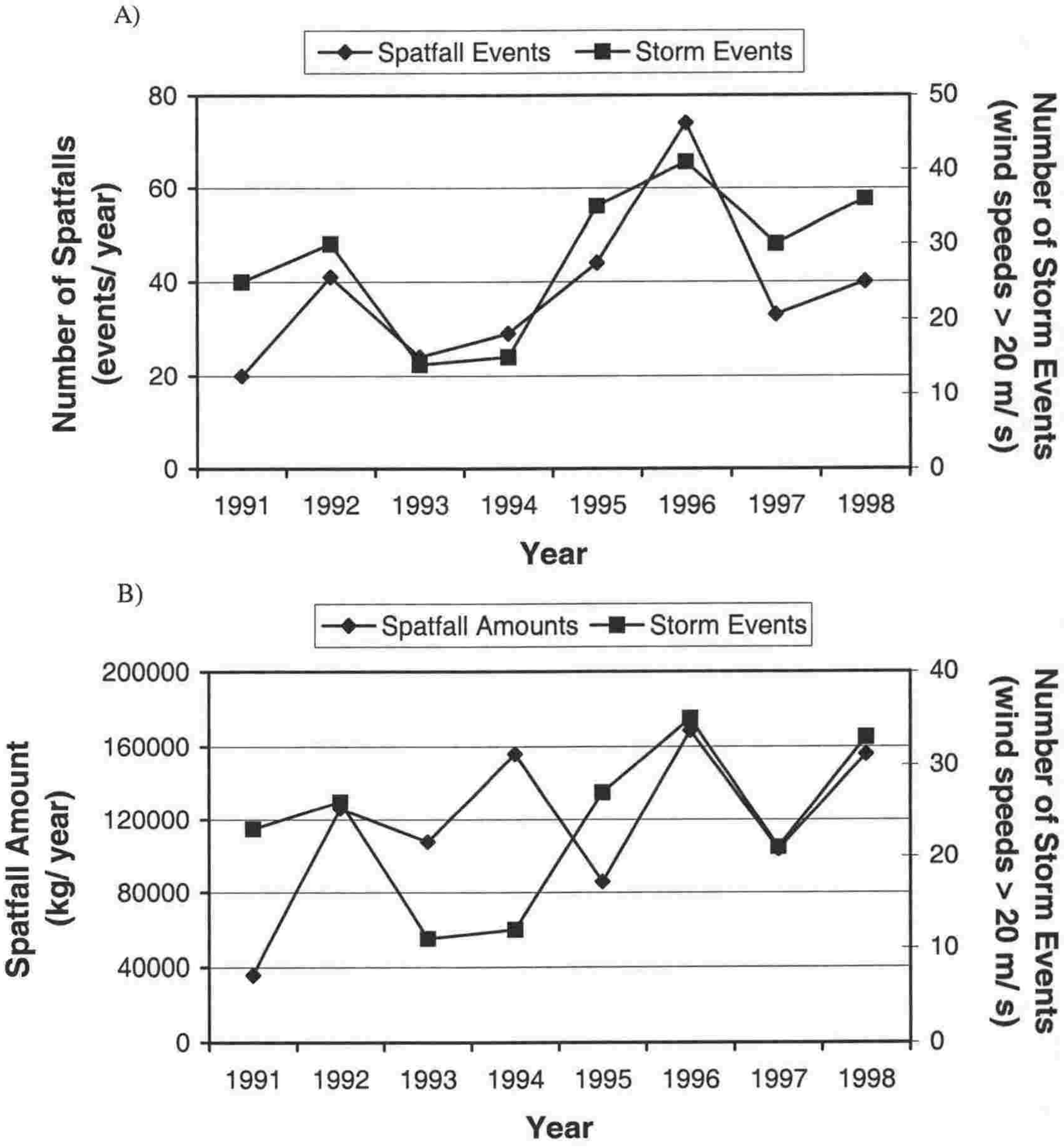


Figure 8. Yearly storm events (wind speeds > 20 m/s) between 1991 and 1998. A) number of spatfall events and B) spatfall amount within the same time period.

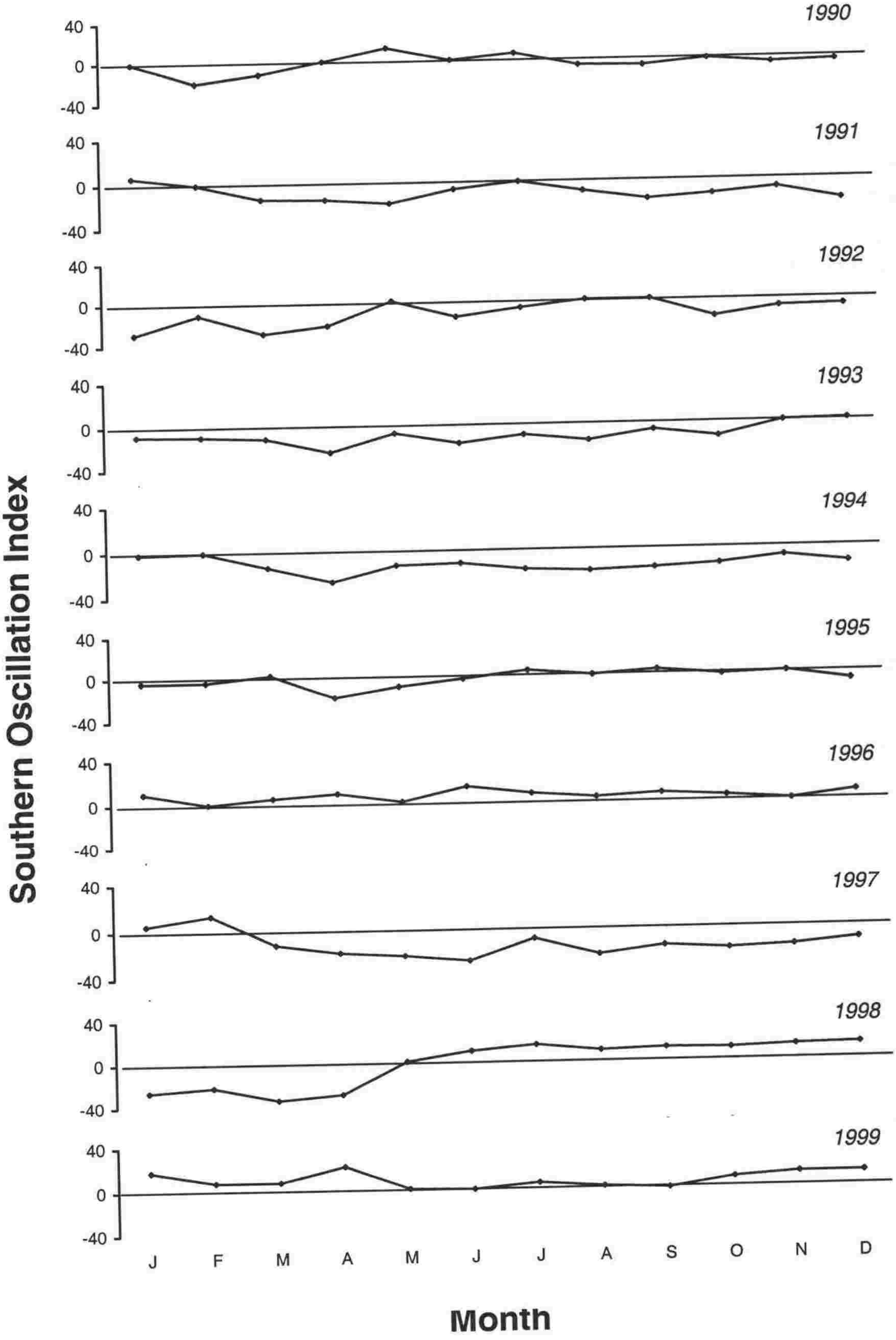


Figure 9. Southern Oscillation Index records for 1990 to 1999. More positive values indicate La Niña conditions and more negative values indicate El Niño conditions.

Table 1. Logistic regression model fitted on the probability of spatfall events (any amount of algae and spat collected on a given day). F-statistics are presented for 3 models containing different parameters. Parameters include A) mean wind speed (m/s), wind direction (onshore and offshore), tidal range (mm), and date (January 1990 to December 1998), B) water temperature (ºC) was added to the model, and C) swell height (m) was added to the model, and C) swell height in the onshore direction was added to the model. Each logistic model contains 5000 permutations.

A

Parameter	p - value
p(wind speed)	0.050
p(wind direction)	0.301
p(date)	0.191
p(wind speed x wind direction)	0.001
p(wind speed x date)	0.288
p(wind speed x wind direction x date)	0.205
p(tidal range)	0.138

B

Parameter	p - value
p(wind speed)	0.759
p(wind direction)	0.514
p(date)	0.359
p(wind speed x wind direction)	0.004
p(wind speed x date)	0.819
p(wind speed x wind direction x date)	0.436
p(tidal range)	0.965
p(temperature)	0.202

C

Parameter	p - value
p(wind speed)	0.001
p(wind direction)	0.024
p(date)	0.229
p(wind speed x wind direction)	0.001
p(wind speed x date)	0.382
p(wind speed x wind direction x date)	0.104
p(tidal range)	0.258
p(swell)	0.001

Table 2. Least squares regression model fitted on the probability of spatfall amounts (amount of algae and spat collected on a given day, in kilograms). F-statistics are presented for 3 models containing different parameters. Parameters include A) mean wind speed (m/s), wind direction (onshore and offshore), tidal range (mm), and date (January 1990 to December 1998), B) water temperature (°C) was added to the model, and C) swell height (m) in the onshore direction was added to the model.

A

Parameter	p - value
p(wind speed)	0.548
p(wind direction)	0.689
p(date)	0.141
p(wind speed x wind direction)	0.001
p(wind speed x date)	0.647
p(wind speed x wind direction x date)	0.448
p(tidal range)	0.093

B

Parameter	p - value
p(wind speed)	0.759
p(wind direction)	0.514
p(date)	0.359
p(wind speed x wind direction)	0.004
p(wind speed x date)	0.819
p(wind speed x wind direction x date)	0.436
p(tidal range)	0.965
p(temperature)	0.302

C

Parameter	p - value
p(wind speed)	0.752
p(wind direction)	0.108
p(date)	0.409
p(wind speed x wind direction)	0.013
p(wind speed x date)	0.850
p(wind speed x wind direction x date)	0.291
p(tidal range)	0.999
p(swell)	0.001

CHAPTER 9

General Discussion

Within the past 20 years, our understanding of mussel ecology has increased considerably. The role of reproductive behavior (Darrigran et al., 1999; Myrand and Himmelman, 2000), larval abundance and distribution (Martel et al., 1994; Cáceres-Martínez and Figueras, 1998), settlement and recruitment patterns (Hunt and Scheibling, 1997; 1998), and population dynamics (Hunt and Scheibling, 1996; McQuaid et al., 2000) have been extensively investigated for a number of mussel species. Furthermore, these detailed studies have contributed substantially to the identification of major population dynamics and community structure trends in the rocky shore (Pawlik, 1992; Petraitis, 1995; Hunt and Scheibling, 1997; Reusch and Chapman, 1997; Robles, 1997). Conversely, the level of spatial and temporal variability observed within different life stages in many mussel species, has made it difficult to apply general models to specific populations. Therefore, research intending to elucidate ecological patterns within and among mussel populations first necessitates a good understanding of the basic biology of the species and the major environmental factors acting on such populations. Further evaluation of the main biotic and abiotic processes affecting the population at different spatial and temporal scales can provide a solid understanding of the system as a whole.

For mussel species such as, *Perna canaliculus*, a good understanding of the ecological forces acting to maintain wild populations is essential to successful aquaculture practices. This need for field-based knowledge is accentuated for wild mussel populations extending intertidally and subtidally along Ninetly Mile Beach, northern New Zealand. Prior to this research project, the physical and biological processes that contribute to the availability, accumulation, and transport of massive quantities of mussel spat, attached to macroalgae, to the beach were almost entirely unknown. The organism-environment interactions that exist at the reproductive, larval, settlement/recruitment, and adult population dynamic stages of this species create a complex ecological system at Ninety Mile Beach. Using techniques from a variety of scientific disciplines, directed laboratory and field experiments were conducted to elucidate ecological patterns that contribute to the maintenance and success of this highly productive mussel system.

Studies on the reproductive behavior of the major intertidal and subtidal populations of *Perna canaliculus* at Ninety Mile Beach indicated that these mussels generally had a well-synchronized and prolonged spawning period between June-December, when the water temperature was low and rising. This spawning period is more extensive than southern areas such as Marlborough Sounds, New Zealand, and these differences may be attributed to the overall warmer water temperatures at Ninety Mile Beach. Identification of clear redeveloping gonad stages within mussels studied at Ninety Mile Beach also implies that multiple spawnings take place throughout the year. Furthermore, a prolonged spawning season and the occurrence of multiple spawnings point to a potentially high production of larvae that may account for the massive spatfall events at Ninety Mile Beach. Differences in gonad indices among intertidal and subtidal populations also indicated that subtidal populations at the southernmost end and one intertidal population at the northernmost end of Ninety Mile Beach have the greatest gonad indices of all populations studied, and may be the greatest contributors to the high spatfall productivity of the area.

Once the gametes are in the water column and fertilization has taken place, larvae will begin their search for suitable substrata to settle on. Macroalgae, mostly filamentous red algae, are the main substrata that larvae and juvenile mussels will settle on. Morphological and chemical cues were shown to directly mediate the settlement selectivity of larval and post-larval mussels. Field and laboratory experiments indicated that young mussels of different size classes preferentially settled and re-settled on various substrata according to the branching degree of the substratum, the specific site of attachment within the substratum, and the chemical composition of the substratum. Thus, small mussels (< 0.5 mm in shell length) tended to settle on fine-branching natural and artificial substrata, while larger mussels (1.5-2.0 mm in shell length) tended to settle (or re-settle) on coarser-branching substrata. Furthermore, young mussels preferred to settle on node versus internode areas within natural and artificial substrata. When the morphological component was removed from the settlement experiments by placing algal chemical extracts on phytogel plates, mussels settled in greater numbers on plates containing algal extracts compared to control plates, which only had phytogel. This clear morphological and chemical settlement specificity may be an adapted strategy for mussel larvae and post-larvae to increase their survival chances by settling on filamentous algae. Filamentous algae may provide a protective microhabitat of concentrated food supplies where young mussels may survive for long periods of time. Because macroalgae are readily dislodged from their original substrata, and are able to survive for a considerable time in the water column before disintegrating in the water column, these substrata also may provide an effective mechanism for transport and dispersal for mussels attached to this drift material.

Within the drift algae, juvenile mussels may continue to grow until they reach a suitable rocky shore. Once near the rocky shore, mussels may detach from the drift algae and mucous drift and re-settle onto other algal substrata attached to the rocks, or in a few instances, directly onto the adult mussel bed. Field experiments conducted to elucidate patterns of larval availability, primary and secondary settlement, recruitment, and mortality rates within intertidal populations at Ninety Mile Beach indicated that a clear and specific pathway may exist for mussels to transfer from their early life in the water column (and drift algae) to the adult mussel bed in the rocky shore. Larval availability in seawater adjacent to the studied intertidal areas was higher for small mussels (< 0.25 mm in shell length) in August, just after the start of the spawning season, and higher for larger mussels (> 0.5 mm in shell length) later in the season in March. Results from short- and long-term settlement experiment on adult intertidal mussel beds and adjacent algal areas suggest that primary settlement takes place predominantly on the algal substrata. Then, mussels may transfer from these algae to the adult mussel bed as larger mussel recruits more able to compete for space and food with their adult conspecifics. Peaks in recruitment rates also coincided with peaks in mortality rates in August, indicating the importance of early mortality effects on intertidal populations of the area. A particular population at the northernmost end of Ninety Mile Beach had a dramatic turn-over of individuals in August of the 2 years studied. During this time, the intertidal zone suffered an almost 100 % mortality of adult mussels, which were soon replaced by young mussels, which were abundant on the attached and free-floating algae nearby. The mortality of mussels within this population was attributed to a combination of low energy levels of mussels, which had just spawned, and a periodic accumulation of large quantities of drift algae covered with mussel juveniles (up to 100 % cover), which may have smothered adult mussels by depleting the food supplies of the area. As a consequence, mussels of large shell size, but diminished body tissue size, were observed "peeling-off" from the rocks, making space available for new recruits. The high turn-over rates of some intertidal populations at Ninety Mile Beach, together with the massive strandings of mussel spat along the stretch of the beach, suggest that a powerful oceanographic mechanism may continuously act to accumulate and deliver the negatively buoyant algal material covered with spat to the shore in un-limiting quantities.

While the high abundance of mussel spat at Ninety Mile Beach is unique in this country, the arrival of spatfall material to the surf zone is more sporadic and irregular. Unreliable sources of mussel spat collected from the surf zone may be complemented with mussels harvested from settlement ropes placed subtidally inside Ahipara Bay, Ninety Mile Beach. Field experiments that tested settlement patterns on suspended ropes at 3 different water depths inside and outside Ahipara Bay indicated that mussel settlement was high for small mussels (< 0.49 mm in shell length) at the shallowest depths (2 m water depth) just after the start of the spawning season in August. Conversely, larger mussels (> 1.0 mm in shell length) were more abundant at greater depths (18 m water depth), and were thought to have transferred as secondary settlers from tumbling algae on the seafloor. Although settlement differences between inside and outside the bay were not statistically significant, results from these experiments suggest that settlement ropes placed inside Ahipara Bay may be used reliably as indicators of the arrival of spattfalls to the beach, and as an alternative source of mussel spat, which can be harvest directly from the water column.

An attempt to elucidate temporal variability in spatfall events on the beach was undertaken by comparing historical records of wind speed and direction, tidal range, water temperature, and modeled swell height and direction with records of spatfall events for the period 1990-1998. Specifically, a statistical model was used to identify oceanographic and weather conditions that favored spatfall events and amounts within daily, monthly, and inter-annual temporal scales. Analyses of the large data sets resulted in a significant increase in spatfall events and amounts during days of strong offshore winds and low swell, and a suggestive increase in spatfall amount with high tidal range. After removing seasonal variability, water temperature was found to have no significant effect on spatfall events nor amounts. Monthly storm events (wind speeds > 20 m/s) were most frequent between May-August, while spatfall events and amounts were greater 4 months later in September-October. Years with a greater number of storm events also were associated with significantly higher spatfall events and amounts. These weather and oceanographic patterns may be associated with El Niño/La Niña events, which greatly influence the climate in New Zealand.

It is clear that the dynamic life history processes of *Perna canaliculus* at Ninety Mile Beach make this mussel species well adapted to the complex and energetic ocean conditions of the northwest coast of New Zealand. These favorable environmental conditions allow for a prolonged spawning season, especially from productive subtidal populations, which generate unlimited amounts of mussel larvae in the water column. These larvae readily saturate the abundant drift macroalgae, which tumble on the seafloor. A combination of favorable ocean currents which meet offshore of Ninety Mile Beach appear to accumulate this drift material and periodically push it to the nearshore, where mussel spat are able to re-colonize and maintain adult populations, as well as provide the major source of mussel spat to support the mussel farms in New Zealand.

Finally, this thesis is submitted to The University of Auckland, New Zealand in the hope that it may provide a foundation for continued research in the field of mussel ecology at Ninety Mile Beach. It is suggested that the appropriate private and government organizations extend funding opportunities for future work on the ecology of this important commercial species. Further studies may target research on the basic oceanographic patterns of the area, identification and quantification of the main sources of macroalgae, and continued monitoring of mussels within drift material and within intertidal and subtidal populations at Ninety Mile Beach, northern New Zealand. The study of this mussel species, endemic to New Zealand, also provides a unique opportunity for this country to export valuable ecological knowledge to the scientific community of the world.

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