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**The effects of sea otter (*Enhydra lutris*) foraging on shallow  
rocky communities off northwestern Vancouver Island, British  
Columbia**

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University of California, Santa Cruz, 1993

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SANTA CRUZ

THE EFFECTS OF SEA OTTER (*ENHYDRA LUTRIS*) FORAGING ON  
SHALLOW ROCKY COMMUNITIES OFF NORTHWESTERN  
VANCOUVER ISLAND, BRITISH COLUMBIA

A dissertation submitted in partial satisfaction of the  
requirements for the degree of

DOCTOR OF PHILOSOPHY

in

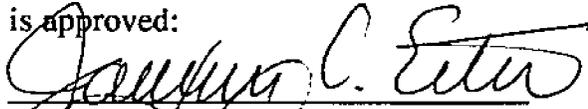
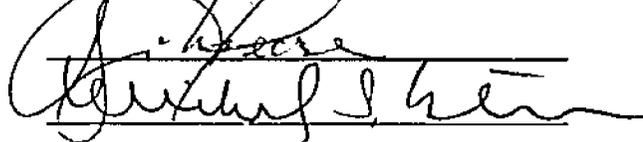
BIOLOGY

by

Jane Catherine Watson

March 1993

This dissertation of Jane Catherine Watson  
is approved:

  
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Dean of graduate studies and research

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**THE EFFECTS OF SEA OTTER (*ENHYDRA LUTRIS*) FORAGING ON  
SHALLOW ROCKY COMMUNITIES OFF NORTHWESTERN  
VANCOUVER ISLAND**

Jane Catherine Watson

**ABSTRACT**

The effects of sea otter foraging on rocky subtidal communities was examined off northwestern Vancouver Island, British Columbia. The Vancouver Island otter population originates from 89 animals re-introduced from 1969-1972. Since 1977 the population has increased 19.2% yr<sup>-1</sup> and expanded its range 15.3% yr<sup>-1</sup>.

The effects of otter foraging were inferred by comparing the species composition of 60 randomly selected sites, 40 in two areas without sea otters, and 20 in an area with otters. Areas without sea otters were dominated by urchins and brown algae were rare, whereas areas with otters were dominated by brown algae and urchins were rare. Patchy mosaics of urchins and algae observed at sites recently occupied by otters may represent a transitional stage between the otter-free and otter-dominated configurations.

The effects of otters were documented by monitoring species abundance at four sites before and after sea otters arrived. Two sites with sea otters and two without were monitored concurrently. Despite small changes in species abundance, community configuration did not change at sites with or without sea otters. With the arrival of sea otters, urchin abundance declined and algal abundance increased. The rate and pattern of change varied among sites, apparently affected by the frequency, intensity and seasonality of otter foraging.

The response of red urchins (*Strongylocentrotus franciscanus*) to damaged conspecifics was examined as a mechanism for the urchin/algal mosaics observed at sites recently invaded by otters. Red urchins avoided eviscerated conspecifics, creating

urchin-free patches which lasted at least 16 days. Urchin tests dropped by foraging otters may elicit an escape response in nearby urchins, creating urchin-free patches that allow algal recruitment and explain how mosaics of urchins and algae form.

Long-term succession was inferred by comparing algal assemblages at 12 sites where the modal age of *Pterygophora californica* was used to estimate when sea otters had arrived. Algal assemblages at sites occupied by otters for 3-4 yrs were unpredictable in composition or density, whereas assemblages at sites >7 yrs old were dominated by stipitate kelp and were highly predictable. Chance events appear to have little effect on the eventual composition of brown-algal assemblages in otter-dominated areas off western Vancouver Island.

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## CHAPTER 1

### Introductory Remarks

It was the remote and inhospitable character of northwestern Vancouver Island that led biologists to select it as a suitable location for re-introducing sea otters to Canada. Searching for potential sites, Karl Kenyon recommended that the "rock and islet-studded area south of the Brooks Peninsula appeared to offer ideal habitat" (Kenyon 1967). Consequently, from 1969-1972 eighty-nine sea otters, captured at Amchitka Island and Prince William Sound, Alaska, were released in Checleset Bay on northwestern Vancouver Island (Bigg and MacAskie 1978, Jameson et al. 1982).

Sea otters once ranged throughout the northeast Pacific Ocean, from northern Japan to Baja California (Riedman and Estes 1990). Estimates suggest the population may have included 300,000 animals (Riedman and Estes 1990). Midden remains indicate that native peoples along the entire Pacific rim exploited sea otters long before the arrival of Europeans, perhaps even driving otter populations locally extinct (Simenstad et al. 1978).

The first well documented arrival of Europeans to the west coast of Vancouver Island occurred in 1774, when Spanish explorer Juan Perez Hernandez dropped anchor at the village of Yuquot at the entrance to Nootka Sound (Pethick 1980). Perez traded with the Mowachaht people for sea otter furs, but failed to recognize the fur's commercial value. Captain James Cook arrived at Yuquot in 1778. Unlike Perez, Cook stayed a month, overhauling his ships and surveying the area while trading for local goods, including over 300 sea otter skins (Arima 1983). Cook left Yuquot to explore what is now Alaska, searching for an ice free route between Europe and the Orient. Unsuccessful, Cook sailed to the Hawaiian Islands where he was killed in a local dispute. His crew

carried on to Canton, China where the sea otter pelts were sold for exorbitant prices (Arima 1983).

When Cook's journal was published 1784, the rush to acquire sea otter furs was well underway. By the end of the 18th century the west coast of North America was swarming with ships engaged in trading and hunting for sea otter pelts (Pethick 1980, Woolfenden 1985). The fur trade lasted only 60 years. By the late 1830's sea otters were scarce and although the occasional sea otter was taken, the sea otter fur trade ground to a halt (Robinson 1979). When sea otters were finally protected in 1911, under the International Fur Seal Treaty (Kenyon 1969), less than 2000 animals remained (Riedman and Estes 1990). The last known sea otter to inhabit British Columbian waters was shot in 1929 off of Kyuquot on the West coast of Vancouver Island (Cowan and Guiguet 1960).

The sea otter fur trade profoundly changed the cultural and political face of western North America. Aboriginal populations were ravaged by diseases introduced by Europeans. Resource-based regional economies were replaced by a dependence on European trade goods as the west coast was colonized (Robinson 1978, Arima 1983). In 1867, the Russians, who had moved steadily east and south in search of fur, sold what is now Alaska to the United States, believing its principal commodities, fur seals and sea otters, to be largely exhausted (Woolfenden 1985). While the historical consequences of the sea otter fur trade are well known, the ecological consequences of the sea otter's near extinction went largely unrecorded (Estes et al. 1989).

The importance of sea urchin grazing on the abundance and distribution of fleshy algae has been well described (Lawrence 1975, Harrold and Pearse 1987). In many temperate marine ecosystems sea urchin grazing denudes rocky substratum of fleshy algae, often restricting it to areas where water motion or unstable substrate provide a refuge from grazing (e.g. Keats 1991, Pace 1975, 1981, Druehl 1978, 1979). Red sea urchins

(*Strongylocentrotus franciscanus* Agassiz) are very abundant in British Columbia, occurring on rocky substrate in densities of up to 30 m<sup>-2</sup> (Breen 1980). In British Columbia mortality in adult red urchins is low and sea otters are seemingly the only predator capable of regulating urchin abundance (Breen 1980). The extinction of sea otters may thus have allowed urchin populations to increase to the point where urchin grazing reduced the abundance of fleshy algae, especially kelp, along much of British Columbia's coast (Pace 1975, Druehl 1978, 1979, Breen et al. 1982).

Kelp beds affect biological and physical processes in many nearshore ecosystems (reviews in Foster and Schiel 1985, Duggins 1988). Duggins et al. (1989) demonstrated that nearshore productivity in the Aleutian Islands was higher at islands with sea otters (and thus kelp) than at islands without sea otters (thus little kelp) and traced the source of increased productivity to kelp-derived carbon. Kelp beds enhance fish populations in California, Alaska and possibly British Columbia, increasing water-column complexity and providing habitat for adult and larval fishes (Leaman 1976, Simenstad et al. 1977, Bodkin 1986, 1988, Laur et al. 1988, Ebeling and Laur 1988, Carr 1989, 1991). Kelp beds reduce tidal currents and damp wave height (Jackson and Winant 1983, Jackson 1984, e.g. Schiel and Nelson 1990) which may affect recruitment and dispersal in many kelp bed organisms (Eckman 1983, Foster and Schiel 1985, Duggins et al. 1990).

The direct ecological effects of sea otter foraging were first recognized by McLean (1962), who attributed the growth of "luxuriant" kelp beds off Carmel California to otter predation on urchins. Lowry and Pearse (1973) later noted that sea urchins and abalone in areas inhabited by sea otters were restricted to crevices which apparently provided refuge from foraging otters. A more general role for sea otters was proposed by Estes and coworkers. Comparing Aleutian Islands with and without sea otters they found that islands with sea otters were characterized by fleshy algae but had a low

biomass of urchins, whereas islands without sea otters were dominated by urchins and fleshy algae were rare (Estes and Palmisano 1974, Palmisano and Estes 1977, Estes et al. 1978). They concluded that sea otter predation played a major role in determining community structure in the Aleutian Islands. By preying on urchins sea otters released marine plants from intense grazing, which increased nearshore productivity and enhanced populations of organisms dependent on kelp-based food webs (Estes and Palmisano 1974). Subsequent studies in southeast Alaska (Duggins 1980, Estes and Duggins in prep), British Columbia (Morris et al. 1981, Breen et al. 1982) and Washington State (Kvitek et al. 1989) support these observations.

Recently the geographic generality of sea otter's role in structuring nearshore communities has been questioned (Foster and Schiel 1988, Foster 1990). While it is generally agreed that sea otters can affect community structure, Foster and Schiel (1988) suggest the importance of sea otters is less clear in California. They reviewed 224 subtidal surveys of California and concluded that sea urchins do not necessarily control marine plant biomass in California. Consequently they suggest that the importance of sea otter predation in regulating urchin populations and thus on community structure may be less important in California than elsewhere (Foster and Schiel 1988, Foster 1990). What emerges from this discussion is that geographic differences in the effects of sea otter foraging may exist (e.g. Duggins and Estes in prep.), and that such interactions must be studied over wide temporal and spatial scales.

In this dissertation, I examine the effects of sea otter foraging on rocky nearshore communities off northwest Vancouver Island. The dissertation is organized chronologically, with each chapter outlining a study that follows logically from the preceding chapter. Each chapter has been written so that it can be read independently making some repetition necessary.

**Chapter 2** outlines the history and present status of the sea otter population in British Columbia. This chapter is based on survey data and observations I collected between 1987 and 1991, but also summarizes the results of earlier, often unpublished studies. The British Columbia sea otters are probably the most poorly known of all of the re-introduced otter populations. The data summarized in this chapter suggest that the population is growing at 19.2% per year, a rate similar to other translocated populations. I describe range expansion and social organization in the otter population off Vancouver Island and draw comparisons to sea otter populations in Alaska and California.

**Chapter 3** examines community composition in areas with and without sea otters along the west coast of Vancouver Island. I compared the species composition of 60 randomly selected sites, 40 sites located in two areas without sea otters and 20 sites in one area with sea otters. The results I obtained support those of earlier qualitative studies (Morris et al. 1981, Breen et al. 1982), but benefit from a more rigorous approach. Areas with sea otters were dominated by brown algae and sea urchins were absent, in contrast areas without sea otters were dominated by urchins and brown algae were absent. Sites that had been recently invaded by sea otters appeared to be in a transitional state, a patchy mosaic of sea urchins and algae. My results suggest that although species abundance within otter-free and otter-dominated communities varies, sea otters appear to regulate the abundance of sea urchins and thus the abundance of fleshy algae in Checleset Bay.

**Chapter 4** examines the direct effects of sea otter foraging. The species composition of four permanently marked sites was compared before and after sea otters arrived. Four additional sites, two located in areas without sea otters and two located in areas with sea otters were monitored to document variability in community composition in areas with and without sea otters. Three of the sites re-inhabited by sea otters during the study changed from urchin-dominated to algal-dominated, while the fourth site, although re-occupied by sea otters, became a patchy mosaic of algae and urchins. The rate and pattern of change varied among sites, apparently affected by the seasonality, intensity and frequency of sea otter foraging. In contrast, community configuration did not change at sites continuously with or without sea otters, even though species abundance varied slightly.

**Chapter 5** reports on an experiment designed to examine how the patchy mosaics of urchins and algae seen in areas newly invaded by sea otters form. Although the eventual outcome of sea otter foraging is to decimate sea urchin populations, the initial effect of otter foraging appears to be a change in the small-scale spatial distribution of urchins. In areas recently re-inhabited by sea otters urchin-free patches occurred around broken urchin tests, dropped by foraging sea otters. Urchin density in adjacent areas was often twice that normally observed. In many cases algae had recruited to the urchin-free patches. I proposed that urchin tests dropped by foraging sea otters evoke an avoidance response in nearby sea urchins. As urchins move away from the damaged tests they accumulate at increased densities in nearby areas. The presence of urchin-free patches allows algae to recruit, and a patchy assemblage of urchins and algae forms. I tested this idea by adding eviscerated urchins to the center of three 5 by 5 m quadrats. Red urchins moved away from damaged conspecifics and urchin density in two

of the three quadrats dropped to nearly zero and remained well below pretreatment levels for almost 16 days. By allowing temporally and spatially variable algal recruitment, this avoidance response may result in the development of patchy algal assemblages.

**Chapter 6** examines long-term successional processes in kelp forests in otter-dominated areas off northwest Vancouver Island. *Pterygophora californica* (Turner) is a long-lived kelp, that can be aged by annual rings in its stipe. *P. californica* recruits in the wake of sea otter foraging and can live up to 18 yrs (DeWreede 1984, Hymanson et al. 1990). Thus the age of *P. californica* populations within the otter range off Vancouver Island should provide an estimate of when sea otters arrived at a location, or the age of the algal assemblage. Furthermore, successional processes can be inferred by comparing the composition of algal assemblages of known ages. In this study I inferred long-term successional process by comparing the species composition, algal density and biomass of algal assemblages at 12 sites where assemblage age was estimated using the modal age of the *Pterygophora californica* population at that location. Algal assemblages at sites occupied by sea otters for 3-4 yrs were unpredictable in species composition and algal density while assemblages at sites occupied by sea otters for >7 yrs were highly predictable. Algal density at sites older than 12 years appeared to decline. My results suggest that chance events are most important in the early stages of algal succession but despite early differences, predictable algal assemblages develop after a maximum of 7 yrs. Thus differences in the seasonality, frequency and intensity of sea otter foraging, or the behavioral responses of red urchins, observed in the preceding studies may have little effect upon the long-term development of kelp forest communities.

In summary the results of this research add to the overall view of how sea otter foraging affects nearshore communities. Using a comparative, experimental and historical approach, I have examined variation in an otter-dominated community over differing spatial and temporal scales. I present testable, mechanistic explanations for some of the observed variation, but as with most ecological research, I raise more questions than I answer.

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## CHAPTER 2

### **The Growth, Expansion and Social Organization of the Sea otter Population in British Columbia**

#### **ABSTRACT**

The British Columbia sea otter population, originating from 89 animals reintroduced to Vancouver Island from 1969-1972, has increased at a finite rate of 19.2% yr<sup>-1</sup>, a rate similar to other reintroduced populations. In 1990, 612 sea otters were found between Yuquot Point, Nootka Island and Lawn Point, Quatsino Sound off Vancouver Island. In addition 104 sea otters were found near Goose Island, 125 km north of Vancouver Island. The origin of this latter group is uncertain. The geographic range of the Vancouver Island sea otter population has increased 15.3% yr<sup>-1</sup>. The ratio of pup-to-independent animals in Checleset Bay is 0.219 which is similar to populations elsewhere. Pupping appears to peak in April-May but can occur year round. On northwest Vancouver Island, as in other expanding populations, sea otters segregate spatially by sex. During the summer groups of peripheral subadult males were generally found at the ends of the sea otter's range. What appeared to be territorial males were located near female areas. Female groups were generally found in the center of the range.

#### **INTRODUCTION**

Historically, sea otters (*Enhydra lutris* Linn.) ranged across the north Pacific, from the northern Japan to the central Pacific coast of Baja California (Kenyon 1969, Riedman and Estes 1990). European exploitation of sea otters, which were valued for their pelts, began in British Columbia in 1778, when Captain James Cook arrived on the

west coast of Vancouver Island (Pethick 1980). By 1830, British, American, Spanish, Russian and aboriginal hunters had extirpated the sea otter from much of its historic range (Monroe 1985, MacAskie 1987, Kenyon 1969, Riedman and Estes 1990).

When sea otters were protected in 1911 under provisions of the International Fur Seal Treaty, fewer than 2000 animals remained in 13 relict populations (Kenyon 1969). One of these populations was located off the Queen Charlotte Islands in British Columbia (Jameson et al. 1982). It disappeared and the last sea otter known to inhabit British Columbia waters was shot in 1929, at Kyuquot, on Vancouver Island (Blood 1967, Cowan and Guiguet 1960, Kenyon 1969).

From 1969-1972, 89 Alaskan sea otters were reintroduced to the Bunsby Islands on northwestern Vancouver Island; 29 in 1969, 14 in 1970 and 46 in 1972 (MacAskie 1971, 1975, Bigg and MacAskie 1978). Survival was probably poor in the first translocation because the animals had badly soiled pelage when they were released. In subsequent translocations, the sea otters were held in floating pens before release and survival was probably higher (MacAskie 1971, Bigg and MacAskie 1978).

By 1972, sea otters had been sighted as far north as the Queen Charlotte Islands and as far south as Barkley Sound, suggesting that some of the translocated animals had dispersed (Bigg and MacAskie 1978). In 1977 four aerial surveys of Vancouver Island located 70 sea otters; 55 near the Bunsby Islands, and 15 off Bajo Reef, Nootka Island, 75 km east. Mothers and pups were seen in both areas (Bigg and MacAskie 1978). In 1984, 345 sea otters were counted from Bajo Reef to Checleset Bay indicating that the British Columbia sea-otter population had increased in size and geographic range (MacAskie 1984, 1985, 1987).

Despite their status as an endangered species in Canada (COSEWIC<sup>1</sup>, MacAskie 1985, 1987), and their impact on commercial shellfish stocks (VanBlaricom 1984, Estes and VanBlaricom 1985, Johnson 1984, Breen et al. 1982), surprisingly little is known about sea otters in British Columbia. Research has included periodic surveys (MacAskie 1984, 1987, Bigg and MacAskie 1978, Morris et al. 1979, 1981) and studies of their effects on community structure (Morris et al. 1979, 1981, Stewart et al. 1981, Breen et al. 1982).

In 1989, oil from a ruptured barge threatened the Vancouver Island sea otter population (Waldichuck 1989). Attempts to monitor the effects of the oil emphasized how little was known about the distribution and habits of these animals. This chapter, based primarily on survey data and observations from 1987-1992, examines the recent distribution, growth and social organization of the British Columbia sea otter population.

## METHODS

### Description of the study area

Most sea otters in British Columbia occur along a remote and rugged portion of northwestern Vancouver Island (Fig. 2.1). The convoluted shoreline of sheltered bays, islands, barrier reefs, and fjords offers ideal sea otter habitat and supports a diversity of hard and soft bottom communities in water depths of less than 50 m (Breen et al. 1982).

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<sup>1</sup> Committee on the Status of Endangered Species of Wildlife in Canada.

### **Sea otter surveys**

Several methods have been used to census the sea otter population off Vancouver Island. Aerial surveys were conducted from an altitude of 150 m during summer months. Fixed-wing aircraft were used from 1977-1987 and helicopters from 1989-1991. Opportunistic boat surveys were conducted from 1978-1987 and standardized weekly boat surveys were conducted during summers 1988-1991 in Checleset Bay and Kyuquot Sound. Boat surveys conducted after 1987 distinguished pups from independent animals until September, when large dependent pups became difficult to recognize. The area west of Brooks Peninsula was surveyed by boat in 1990 and 1991, Nootka Island was surveyed annually by boat or helicopter from 1987-1991 and Goose Island, 125 km north-west of Vancouver Island, was surveyed by boat in May 1991 (Figs. 2.1 & 2.2).

### **Sea otter population growth**

The finite growth rate of the Vancouver Island sea otter population was estimated for 1977-1990, using the exponential growth equation  $N_t = N_0 e^{rt}$ , where  $N_t$  = population count in year  $t$ ,  $N_0$  = the population count in some preceding year 0 and  $r$  = the instantaneous rate of increase. A linear regression on  $\ln(\text{counts})$  versus time was done to obtain the best fit to exponential population growth. For years with multiple population estimates, the highest count was used.

An annual pup-to-independent ratio for Checleset Bay and Nootka Island was calculated from the total number of animals counted in all surveys conducted in July and August of each year. A mean pup-to-independent ratio was calculated from the annual ratios.

### **Geographic expansion of the sea otter population**

Range expansion was calculated by using a planimeter to measure the length of the sea otter range, including offshore islands and reefs, from 1977-1991. The rate of expansion was calculated from a linear regression of  $\ln(\text{range length (km)})$  versus time. Sea otters were designated as having occupied an area when three or more individuals were observed.

### **Social organization of sea otters in Checleset Bay and Kyuquot Sound**

Female/pup areas and male areas in Checleset Bay and Kyuquot Sound were identified during boat surveys conducted from 1987-1991. Female areas were indicated by the presence of females with dependent pups and male areas by rafts of sea otters without pups (Kenyon 1969, Garshelis et al. 1984). Animals unaccompanied by pups were further examined through binoculars and their sex determined by the presence or absence of a penile ridge. Animal age (subadult or adult), when determined, was based on size and pelage color as suggested for sea otters in Prince William Sound (Garshelis 1984), however these may vary geographically (Riedman and Estes 1990).

## **RESULTS**

### **Geographic Range**

In 1990, the sea otter population off northwest Vancouver Island was composed of two groups: a) a western group of at least 469 animals, that extended from McQuarrie Rocks, Kyuquot Sound, north to Lawn Point, Quatsino Sound and b) an eastern group, of at least 143 animals, that extended from Nuchatlitz Islands east to Yuquot Point, Nootka Island (Fig. 2.2, Table 2.1). Although separated by a distance of about 20 km, sea otters appeared to move between these two areas because one individual with a dis-

tinative scar on its left forelimb, travelled regularly between Yuquot Point and Kyuquot Village (S. Kayra pers. comm.). A third group of at least 104 sea otters occurred in the Goose Island Group (Fig. 2.1, Table 2.1). Single sea otters have been periodically observed in the Goose Islands since 1976 (Bigg and MacAskie 1978, G. Ellis pers comm.), but mother/pup rafts were first reported in 1989 (D. Powers unpub.).

### **Population growth**

The results of the linear regression indicate that the sea otter population off northwestern Vancouver Island has increased at a finite rate of 19.2%  $\text{yr}^{-1}$  ( $r^2 = 0.937$ ), from a population of at least 70 individuals in 1977, to 612 in 1990 (Fig. 2.3, Table 2.1). Population growth was calculated from 1977 onwards because some of the introduced sea otters dispersed from the area after release in 1969-1972 (Bigg and MacAskie 1978). When otters in the Goose Islands are included in the analysis (1989-1990), population growth for British Columbia is 19.6%  $\text{yr}^{-1}$  ( $r^2 = 0.939$ ). Probability, studentized and Cook's distance plots of the residuals (Wilkinson 1990) indicated that they were normally distributed, had a constant variance and were independent in both regressions.

Portions of the Vancouver Island sea otter population may be approaching equilibrium density or at least undergoing density dependent reduction in growth rate. The number of sea otters within Checleset Bay, which has been surveyed since 1977, appeared to peak in 1989 and declined from 1990-1992 (Fig. 2.4, Table 2.1). However variability in population estimates from 1987 onwards (Table 2.2) make statistical analysis of this pattern difficult.

In the western sea otter group (Checleset Bay/Kyuquot Sound) the population birth rate or mean pup-to-independent ratio was 0.219 (range=0.12-0.33) from 1978-1991. The pup-to-independent ratio for the eastern group (Nootka Island) was 0.12. This

is undoubtedly an underestimate of pup production because surveys were conducted in September when pups born during peak pupping were difficult to identify and because pups are born year round.

### **Geographic expansion of the sea otter population.**

Since 1977, the range length of the Vancouver Island sea-otter population has increased  $15.3\% \text{ yr}^{-1}$  ( $r^2=0.986$ , Fig. 2.5); from 29.6 km in 1977 to 239 km in 1991 (Fig. 2.2 & 2.5). The range of the western group increased  $13.1\% \text{ yr}^{-1}$  ( $r^2=0.992$ , Fig. 2.5), although this rate underestimates range expansion because westward expansion was poorly documented after 1989 and range expansion was measured only at the eastern edge of the range. The eastern group of sea otters expanded east and west along Nootka Island at a rate of  $17.8\% \text{ yr}^{-1}$  ( $r^2=0.977$ , Fig. 2.5).

### **Social organization of sea otters in Checleset Bay and Kyuquot Sound**

A large raft of male sea otters was observed predictably at the eastern extent of the western sea otter group from 1987-1991. During the summer months this group was composed primarily of subadult males. The raft formed every evening or in poor weather and dispersed each morning or when weather permitted. However, this pattern may have been influenced by boat traffic which often sent the animals porpoising away at speeds of  $9\text{-}10 \text{ km hr}^{-1}$ . These large subadult groups appeared to form the leading edge of the expanding population and relocated to the east at approximately two year intervals. Large single males were sighted repeatedly at predictable locations during summer months often in close proximity to female areas.

Females with pups were consistently sighted at offshore islets located at the center of the western group's range. Mother-pup rafts of up to 138 animals were observed in the late morning and early afternoon. Smaller groups of mother-pup pairs were

observed in Kyuquot Sound, near the eastern boundary of the western group and throughout Checleset Bay. Single animals and mother pup pairs were seen foraging throughout the sea otter's range.

## DISCUSSION

### Population growth

The sea otter population off northwest Vancouver Island may be increasing at near maximum rate. The finite growth rate of 19.2% yr<sup>-1</sup> ( $r=0.176$ ) I obtained is identical to the estimate of 17.7% yr<sup>-1</sup> (instantaneous rate) Estes (1990a) calculated using survey data from 1977, 1984, and 1987. These rates are comparable to those of sea-otter populations off southeast Alaska, Washington State and Attu Island. These near maximum rate ( $r_{max}$ , Caughley 1977) increases may occur because populations are below equilibrium density and are thus not resource limited (Estes 1977, 1990a, 1990b). The Goose Group sea otters were not included in the analysis, because their history is unknown and there is speculation that this group, located in an inhospitable and poorly charted portion of coast, may represent a relict population (G. Ellis pers comm.).

The high coefficient of determination ( $r^2=0.937$ ) from the regression of  $\ln(\text{count})$  vs. time, demonstrates that the data were highly concordant with an exponential growth model. However the variety of procedures used to estimate sea otter population size make it difficult to accurately assess population growth rate.

The accuracy of sea otter surveys in British Columbia is impossible to assess. A wide range of population estimates were obtained each year, largely because fog, wind and choppy seas meant that censuses were conducted in variable and often difficult

conditions. Furthermore, the patchy distribution of sea otters meant that rafts of animals were easily overlooked. Sea otter surveys are known to be affected by a variety of factors including time of day (Geibel and Miller 1984), lighting, sea conditions, sea otter group size (Drummer et al. 1990) and sea-otter activity (Estes and Jameson 1988, Garshelis et al. 1990, Estes 1990b, Ralls and Siniff 1990). In addition, the behavior and distribution of sea otters is thought to be influenced by weather and sea state (Estes 1980, Ribic 1982a, 1982b, Riedman and Estes 1990). The highest population estimates off Vancouver Island were achieved in summer surveys conducted before storms when sea conditions were still suitable but the sea otters had moved inshore. During extended periods of calm sea otters tended to disperse to offshore areas and were difficult to count. Winter surveys conducted in 1989 consistently obtained low population estimates, principally because the distribution of sea otters during the winter months differed from that seen in the summer (Watson 1990).

Estimates of population birth rate were variable. Sea otter pup production off Vancouver Island (0.22 pups/adult) was similar to that observed in California and Alaska. Estes (1980, 1990a) reported 0.20 pups per adult in California and 0.30 pups per adult in Alaska. However, because sea otters segregate spatially by sex, the number of pups is easily over or under-estimated if areas of high and low pup production are not equally surveyed (Simon-Jackson 1986, Jameson et al. 1986, Estes 1990a). Furthermore, if pupping is asynchronous, pup production will be underestimated (Pitcher 1989, Estes 1990a). Although synchrony in pupping has not been examined in British Columbia, the number of large, dependent pups during July suggests peak pupping occurs in April-May as has been observed in the Aleutian Islands and Prince William Sound (Payne and Jameson 1984, Garshelis et al. 1984, Riedman and Estes 1990). However, as with sea

otter populations elsewhere (Schneider 1972, *in* Riedman and Estes 1990), newborn pups have been observed year-round in Checleset Bay (G. Ellis and J. Watson unpub. data).

### **Expansion of the sea otter range**

Estes (1990a) suggested that increases in sea otter populations are achieved mainly through range expansion rather than increased density. This appears to be true on northwest Vancouver Island where exponential population growth has been accompanied by a similar exponential increase in range length. This pattern contrasts with California, where sea otter range has increased in a linear but inconsistent manner (Lubina and Levin 1988). In California sea otters at the southern end of the range have expanded their range more rapidly than those at the northern end. Major habitat discontinuities, such as substrate type or water depth, and differential mortality at the northern end of the range appear to affect expansion rates (Lubina and Levin 1988, Estes 1990b). Incidental mortality in a set net fishery (Wendell et al. 1986 *in* Riedman and Estes 1990), attack by great white sharks (*Carcharodon carcharias*, Ames and Morejohn 1980) and reduced habitat quality are suggested as responsible for the low rate of population increase and range expansion in California (Estes 1990a). Although sources of sea otter mortality have not been studied in British Columbia, such factors do not appear to affect the British Columbia population.

Starvation is probably the major cause of death at Amchitka Island, where sea otters are at equilibrium density (Riedman and Estes 1990). Other than humans, predators include bald eagles, (*Haliaeetus leucocephalus*, Kenyon 1969, Sherrod et al. 1975, Riedman and Estes 1990), killer whales, (*Orcinus orca*, Nikolaev 1965, *in* Riedman and Estes 1990) and sharks (Ames and Morejohn 1980). Bald eagles are common in British Columbia and killer whales, although probably an insignificant source of mortality, were

seen pursuing and consuming sea otters in Kyuquot Sound in 1990 (L. Kayra pers. comm.).

### **Social organization and behavior in Checleset Bay and Kyuquot Sound**

The social organization of sea otters has been described in Alaska and California (reviewed in Riedman and Estes 1990). Sexual segregation has been reported repeatedly, with males and females often occupying spatially distinct areas (reviewed in Riedman and Estes 1990). These patterns vary somewhat with season. In general males and females rest in different locations, with the exception of adult males which occupy territories that overlap female areas during breeding season (Riedman and Estes 1990). In California and Alaska large groups of males are found at the edges of the sea-otter range. These groups are composed primarily of subadult males, with breeding males joining them outside of breeding season. Males generally expand into new areas first (Lensink 1962, Loughlin 1980, Garshelis et al. 1984, Wendell et al. 1986, Pitcher 1989), while females use areas which have been occupied by sea otters for longer periods, and expand into areas vacated by male groups (Garshelis et al. 1984).

Patterns of sea otter organization observed in British Columbia appear similar to those observed in Alaska and California. During the summer months the large group of males at the eastern end of the western group appeared to be composed of largely subadult males, but may have been joined by breeding males during the winter (Ellis and Watson unpub.). Over a period of three years, several solitary males were sighted sleeping in predictable locations in the center of the sea otter range. These sea otters may have been territory holders. Individual males are known to rest in the same location within their territories in California (Jameson 1989) and Prince William Sound (Garshelis et al. 1984). Rafts of resting females with pups were found at predictable lo-

cations in the center of the sea otter range. Female rafts have been sighted at these locations for ten years. Females have also expanded into areas recently vacated by male sea otters (Watson unpub.).

Continued increase and expansion of the British Columbia sea otter population will have ecological consequences. By feeding on sea urchins, sea otters indirectly promote the growth of fleshy algae and effect nearshore community structure (Estes and Palmisano 1974, Breen et al. 1982). The ecological impact of sea otter foraging on rocky nearshore community structure of northwestern Vancouver Island is the topic of the following chapters.

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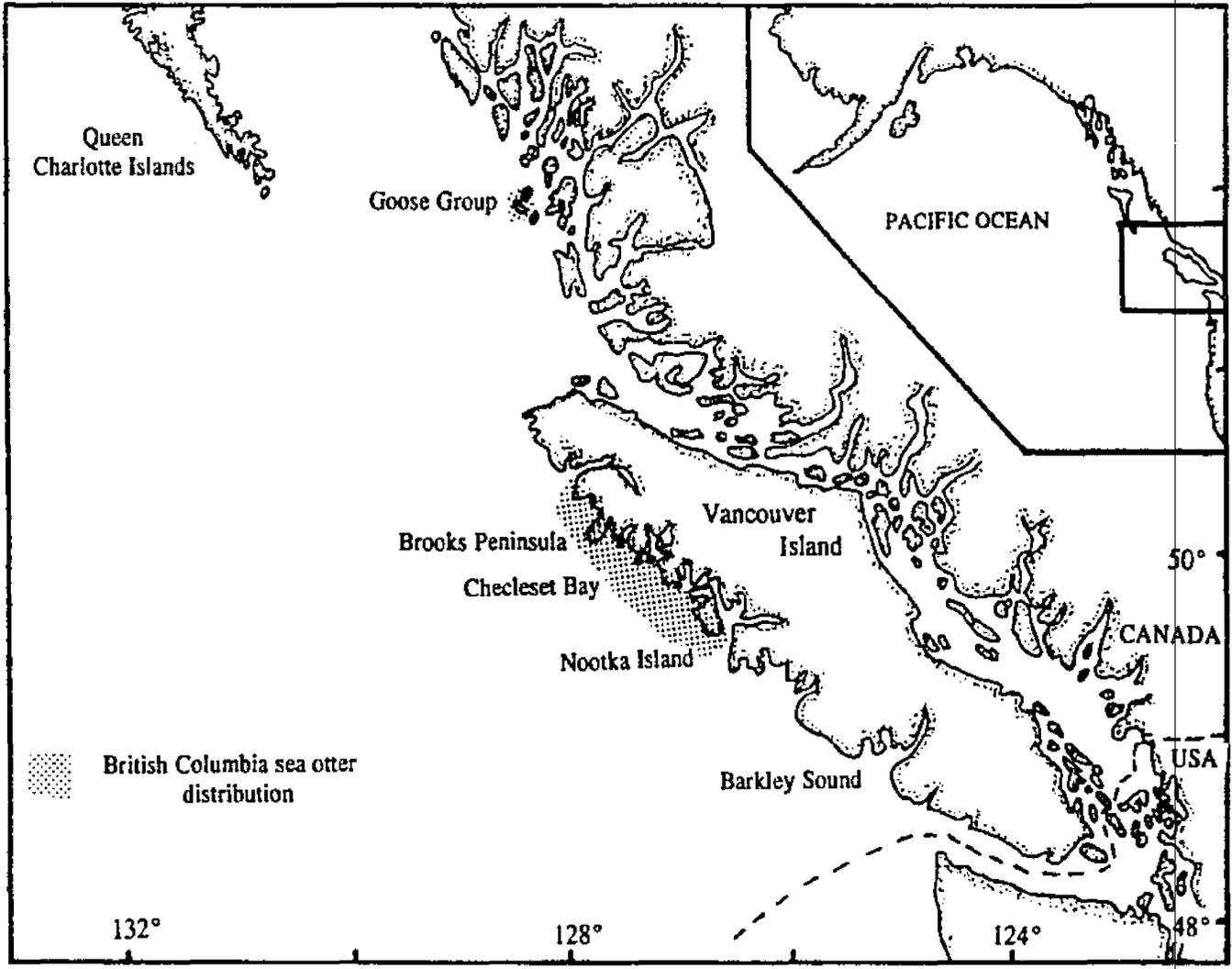


FIGURE 2.1 Location of the British Columbia sea otter population.

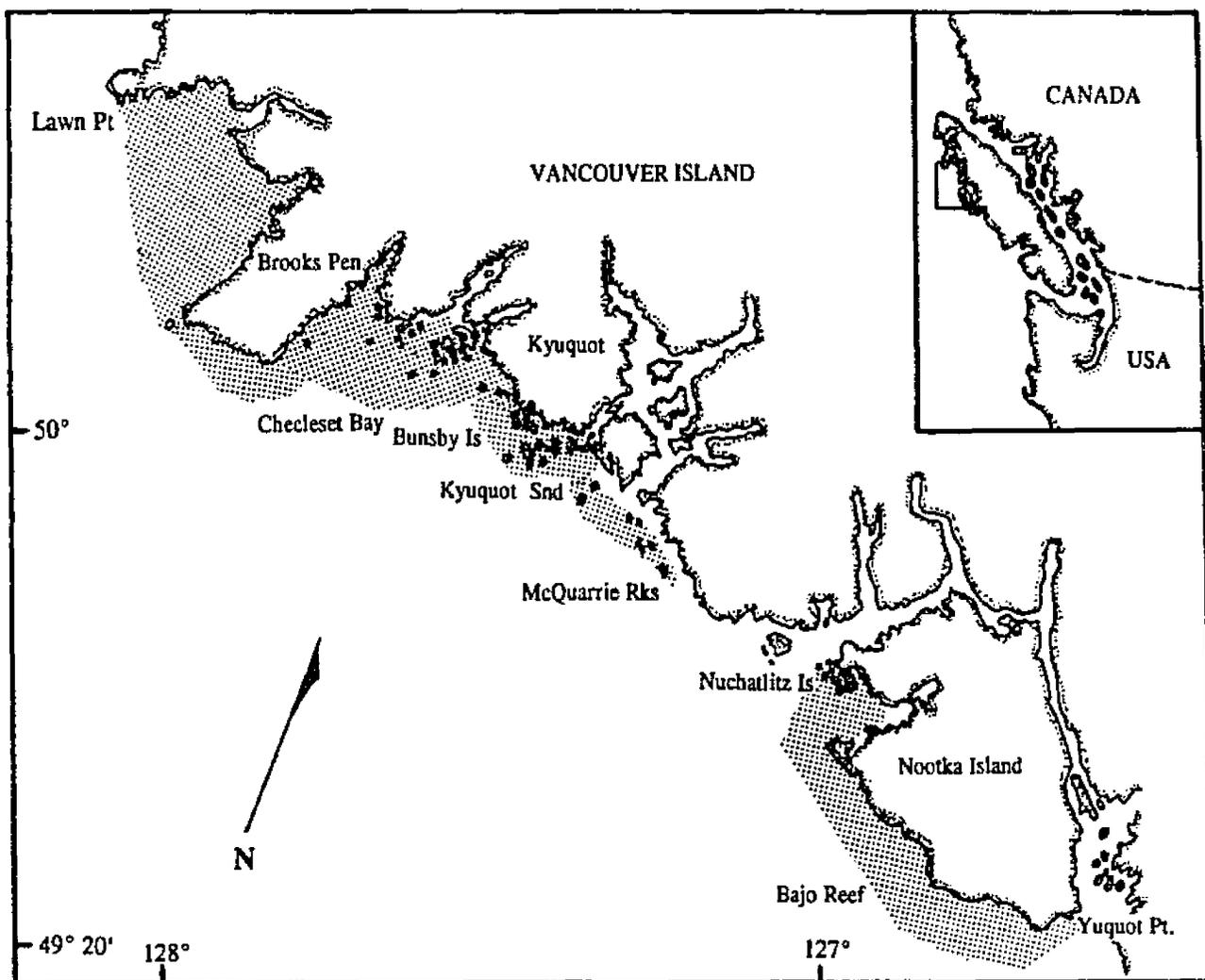
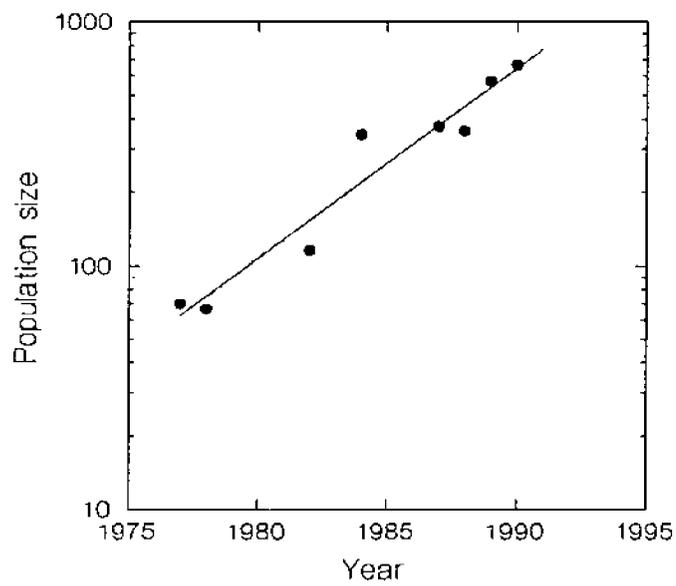
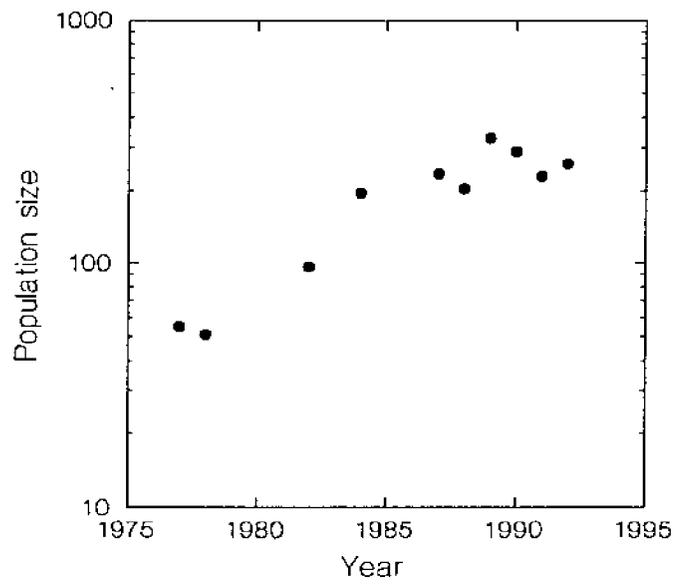


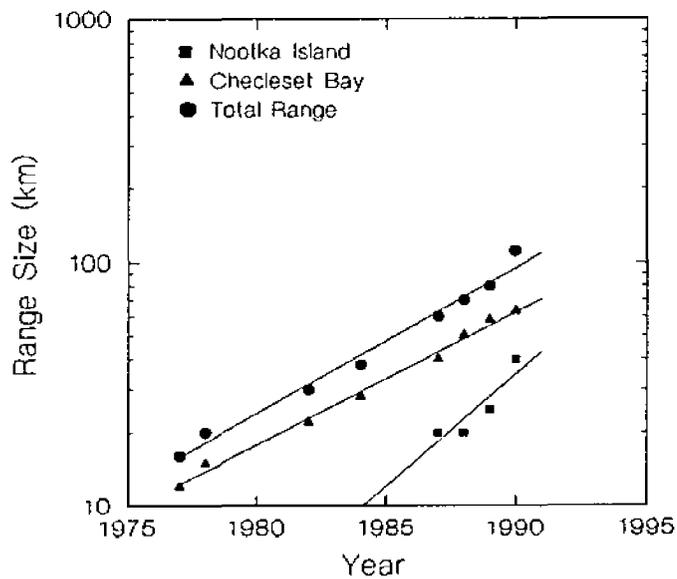
Figure 2.2 Extent of the Vancouver Island sea otter population



**FIGURE 2.3** Growth of the Vancouver Island sea otter population from 1977-1990. The population increased exponentially at a rate of  $19.2\% \text{ yr}^{-1}$  ( $r^2=0.937$ ).



**FIGURE 2.4** Estimate of the number of sea otters in Checleset Bay, 1977-1992.



**FIGURE 2.5** Geographic expansion of the Vancouver Island sea otter population. The overall increase together with the increase in Checleset Bay and Nootka Island is shown. Range increase (regression of  $\ln(\text{km})$  vs. time) were  $15.4\% \text{ yr}^{-1}$  ( $r^2=0.986$ ) for the entire Vancouver Island population,  $13.1\% \text{ yr}^{-1}$  ( $r^2=0.992$ ) for the western group in Checleset Bay and  $17.8\% \text{ yr}^{-1}$  ( $r^2=0.977$ ) for the eastern group off Nootka Island.

TABLE 2.1. Maximum size estimates of the British Columbia sea otter population from aerial and boat surveys conducted from 1977-1991. The population is broken up into groups including Checleset Bay, Kyuquot Sound, Nootka Island, east of Checleset Bay (Brooks Peninsula and Quatsino Sound), and Goose Island. Conditions did not permit a complete survey in 1991.

Year	Total Vancouver Island	Checleset Bay	Kyuquot Sound	Nootka Island	Brooks Penin.	Quatsino Sound	Goose Island	Source:
1977	70	55		15				Bigg & MacAskie 1977
1978	67	51		16				Morris et al. 1981
1982	116	97		19				Bigg unpub.
1984	345	196		149				MacAskie 1987
1987	373	234		139				Bigg and Olesiuk unpub.
1988	357	204		153				This study.
1989	571	328	18	213		12		This study.
1990	612	288	173	143		8	56	This study, Powers unpub.
1991		229	86		80		104	This study

TABLE 2.2 Variability in estimates of sea otter abundance in Checleset Bay and Kyuquot Sound from boat surveys conducted in 1988-1990.

Date	Checleset Bay	Kyuquot Sound
August 7, 1988	176	
August 13, 1988	111	
August 22, 1988	146	
August 27, 1988	163	
Sept. 3, 1988	213	
Sept. 10, 1988	159	
July 26, 1989	328	
July 27, 1989		18
August 3, 1989	169	
August 5, 1989	177	
August 12, 1989	214	
August 24, 1989	149	
Sept. 1, 1989	262	
Sept. 7, 1989	199	
Sept. 9, 1989	270	
August 3, 1990	183	173
August 8, 1990	91	109
August 27, 1990	229	
August 28, 1990		100
August 29, 1990	288	
August 31, 1990		123
Sept. 2, 1990	170	

### CHAPTER 3

## **The Community Structure of Shallow Rocky Reefs off Northwestern Vancouver Island: Sea Otter Foraging and Spatial Variation**

### ABSTRACT

The effects of sea-otter foraging on community composition were inferred by comparing hard-substrate communities 8-10 m below MLW in areas with and without sea otters off western Vancouver Island. Twenty randomly selected sites were examined in each of three areas, two without sea otters (Barkley and Kyuquot Sounds) and one with sea otters (Checleset Bay). Two community configurations were observed, areas without sea otters were dominated by sea urchins and brown algae were rare, whereas areas with sea otters were dominated by brown algae and sea urchins were rare. There was little overlap in these community configurations except at sites which had been recently occupied by sea otters, where algal density was high despite high densities of urchins. Areas with patchily distributed urchins and algae appeared to represent a short-lived transitional stage between the otter-free and otter-dominated configurations. The species composition of algal assemblages within sea-otter dominated areas varied possibly reflecting the length of time individual sites had been occupied by sea otters.

### INTRODUCTION

The importance of predation in structuring communities has been a central controversy in ecology (e.g. Hairston et al. 1960, Paine 1974, Menge and Sutherland 1976, Fretwell 1977, Sih et al. 1985, Schoener 1989, Hunter and Price 1992). The role of sea

otters in structuring rocky nearshore communities provides one widely cited example of a predator-controlled system. Predation by sea otters has been shown to regulate herbivore abundance and biomass, reduce grazing pressure and promote the growth of fleshy algae (Estes and Palmisano 1974, Duggins 1980, Breen et al. 1982). Recently, the geographical generality of the importance of otters in regulating grazing pressure, and thus community structure, has been questioned (Foster and Schiel 1988, Foster 1990). While the debate ostensibly centers on the importance of sea otter predation, it really concerns how herbivore populations are controlled and whether herbivore populations regulate plant biomass.

Sea otters were once abundant throughout the northeast Pacific Ocean, ranging from the Northern Japan, through the Aleutian Islands to Baja, California (Kenyon 1969, Riedman and Estes 1990). An intensive fur hunt commencing in the 1740s resulted in the near extinction of sea otters. In 1911 when otters were finally protected under provisions of the International Fur Seal Treaty, less than 2000 animals remained (Riedman and Estes 1990). Sea otters were declared extinct in Canada in 1929 (Cowan and Guiguet 1960) but were re-introduced to northwest Vancouver Island from 1969-1972 (Bigg and MacAskie 1978, Jameson et al. 1982). Despite the potential impact of these animals on commercial shellfish stocks (Estes and VanBlaricom 1985), only two qualitative studies, conducted in late 1970's, have examined the effects of sea otter foraging on community composition in British Columbia (Morris et al. 1981, Breen et al. 1982). Both studies compared the species composition of areas with and without sea otters and obtained results consistent with those from other geographic regions (McLean 1962, Estes and Palmisano 1974, Palmisano and Estes 1977, Estes et al. 1978, Simenstad et al. 1978).

The results of such comparative studies are not proof of cause, because they lack appropriate controls for temporal and spatial variation (Estes and Harrold 1988). However if such "natural experiments" or comparisons (Diamond 1986) are conducted in a rigorous and unbiased manner over a wide geographic range, the general importance of sea otter predation can be assessed (Estes and Harrold 1988, Estes and Duggins in prep., but see Foster and Schiel 1988). Such studies are underway or have been recently completed at San Nicolas Island, California (Estes and Harrold 1988), Cape Flattery, Washington State (Kvitek et al. 1989), the Aleutian Islands and southeast Alaska (Estes and Duggins in prep.), and western Vancouver Island, British Columbia (this study).

In this chapter I compare the community composition of 60 randomly selected sites located in areas with and without sea otters off the west coast of Vancouver Island, British Columbia. Forty sites in two areas without sea otters, were quantitatively compared to 20 sites located in an area with sea otters. The results of this study suggest that while there is considerable variation in species abundance within otter-free and otter-dominated communities. However, sea urchins appear to strongly influence algal abundance and species composition (reviewed in Harrold and Pearse 1987), by regulating urchins, sea otters predictably alter the composition of rocky nearshore communities off Vancouver Island.

## METHODS

My research was conducted along the west coast of Vancouver Island from July to September of 1988 and 1989. Twenty sites in each of two areas without sea otters (Barkley Sound and Kyuquot Sound) and twenty sites in one area with sea otters (Checleset Bay) were sampled (Fig 3.1). Logistic constraints meant only one area with

sea otters could be sampled. The sites were randomly located in semi-exposed areas, open to oceanic swell, and situated on rocky substrate. This was done by placing a numbered grid over a hydrographic chart of the study area. The extent of each area was determined by the limits of safe boat travel or the geographic range of the sea-otter population. Random numbers were drawn until 20 sites, determined by the intersection of the grid lines with the shoreline or offshore reefs, were selected. Sites with soft or unstable substrate were not sampled and new sites were redrawn as needed.

At each site divers sampled twenty 0.7 by 0.7 m quadrats (0.5m<sup>2</sup>), at depths 8-10 m below mean low water (MLW). The depth regime was selected to avoid sampling shallow wave-washed and disturbed areas, and because hard substrata rarely extended below 12 m. Divers swam a predetermined random number of kicks and dropped the quadrat to the substrate, pushing it through the epibenthic-kelp canopy when required. In each quadrat divers counted the number of each species of brown algae and each of a selected list invertebrate species (Table 3.1). Brown algae were divided into perennial and annual species. Annual species included *Costaria costata* (Turner), *Desmarestia* spp., and *Nereocystis luetkeana* ((Mertens) Postels and Ruprecht). Perennial algae included *Pterygophora californica* (Ruprecht), *Laminaria setchellii* (Silva), *Macrocystis integrifolia* (Bory) and *Pleurophycus gardneri* (Setchell and Saunders). Total algae included all of the above, and juvenile laminariales which were kelp sporophytes too small to identify to species. The percent cover of coralline algae, encrusting red algae and encrusting invertebrates was visually estimated.

The test diameters of red urchins, *Strongylocentrotus franciscanus* (Agassiz), within the randomly selected quadrats, were measured *in situ* to the nearest millimeter with vernier calipers. Urchin sampling was terminated when 100 red urchins or 20 quadrats had been sampled at each site. Urchin biomass per 0.5m<sup>2</sup> was calculated for

each site by using the size frequency distribution and red urchin density at that site and a linear regression of  $\ln(\text{mass})$  versus  $\ln(\text{test diameter})$ . The regression was calculated from 600 sea urchins collected from randomly placed quadrats at three sites in Barkley Sound in July 1989.

Four of the sea otter-free sites were re-visited in September 1992, shortly after sea otters had inhabited them. These sites were sampled using the same protocol as in 1988. Sites were examined for changes in sea urchin size distribution brought about by sea otter foraging and to see if sea otter foraging had affected the spatial distribution of urchins.

## RESULTS

Sites with sea otters were characterized by the presence of brown algae and the absence of sea urchins, whereas sites without sea otters were characterized by the absence of brown algae and the presence of sea urchins (Fig. 3.2).

### Sea urchins

Sea urchin density differed significantly between all three areas (Table 3.2). Mean urchin density ranged from 1.15 to 11.2 urchins  $0.5\text{m}^{-2}$  at sites in otter-free areas ( $n=800$  quadrats). Fourteen percent of the quadrats (114/800) did not have urchins in them. In contrast sea urchins were largely absent from sites within the otter-dominated area, four percent of the quadrats (16/400) had urchins in them. Mean urchin density at individual sites ranged from 0 to 0.85 urchins  $0.5\text{m}^{-2}$  ( $n=400$  quadrats).

Urchin size distributions were highly variable between sites, largely because recent recruits were present at some sites but not at others. However, the overall urchin-size distributions in the two otter-free areas were not significantly different (Kolmogorov

Smirnov goodness of fit,  $D=25$ ,  $P=0.484$ , Fig. 3.3). Urchin biomass was calculated from the density and size distribution of sea urchins at each site using the regression equation  $\ln(\text{mass}) = -7.046 + 2.807 \ln(\text{test diameter})$  ( $r^2=0.984$ ). Sea urchin biomass varied significantly among the three areas (Table 3.2). A Tukey multiple comparison test showed that urchin biomass in the otter-dominated area and the two otter-free sites differed significantly but the two otter-free sites did not differ (Table 3.2). Urchin biomass ranged from 874 to 3424 gms  $0.5\text{m}^{-2}$  at individual sites without sea otters, but was negligible at sites with sea otters because urchins were both small and rare.

### Algae

The abundance of annual, perennial and total brown algae varied significantly among the areas (Table 3.2). A Tukey multiple comparison test showed that brown algal density in any category (perennial, annual or total) did not differ between the two otter-free areas but both otter-free areas differed from the area with sea otters. Eighty-four percent (676/800) of the quadrats sampled in the otter-free areas lacked brown algae of any type whereas only 1.8% (7/400) of the quadrats in the otter-occupied area were without brown algae.

Algal density also varied among sites with sea otters (Fig. 3.4). Sites located near the edge of the sea otter's range were dominated by annual brown algae whereas those near the original release site were dominated by perennial kelps (see Chapter 6). At sites with sea otters annual brown algae ranged from a mean of 0.75 to 12.25 plants  $0.5 \text{ m}^{-2}$  and perennial brown algae ranged from a mean of 0.05 to 8.15 plants  $0.5\text{m}^{-2}$ . Both groups of algae occurred at all 20 sites, although perennials were rare ( $< 1$  plant  $\text{m}^{-2}$ ) at three of the sites (Fig. 3.4) .

### Sea urchin and algal abundance

Despite significant variation in the density of red urchins among areas, there was little overlap in the abundance of urchins and kelp, especially among sites with a longer history of being either otter-dominated or otter-free (Fig 3.2). Three sites, located in areas classed as otter-free, but on the periphery of the sea otters' range and thus recently recolonized, were characterized by the presence of both urchins and algae. The communities in these areas were mosaics of kelp-dominated, urchin-free patches and dense aggregations of sea urchins (up to 70 urchins  $0.5\text{m}^2$ ). The sea urchin-free patches were littered with broken urchin tests. Sea otters were later observed foraging at all three sites suggesting that the patchy distribution of urchins and algae represented the transition from urchin-dominated to algal-dominated.

That the observed mosaic of urchins and algae was a transitional stage was supported in 1992, when four of the otter-free sites sampled in 1988 were revisited. All of the sites had been invaded by sea otters in the preceding 12 months. Between 1988 and 1992 urchin abundance increased significantly from 4.5 to 19.25 urchins  $0.5\text{ m}^{-2}$  at one site but did not change significantly at the other three. Algal abundance increased at all the sites (Fig 3.5). Furthermore, at each site, algae were present in urchin-free patches that were littered with broken urchin tests while dense patches of sea urchins occurred in nearby areas. Urchin test diameters were measured at three of the four sites and compared to the 1988 distributions. In two of the three sites the size distributions were not different, but at the third, larger size classes present in 1988 were missing in 1992, and the distribution differed significantly (Kolmogorov Smirnov goodness of fit,  $D=30$ ,  $P=0.018$ , Fig. 3.6).

### **Encrusting algae and invertebrates**

The percent cover of encrusting coralline and non-coralline algae did not differ significantly between areas (Table 3.2). In contrast, the percent cover of encrusting invertebrates was significantly different among areas (Table 3.2). A Tukey multiple comparison test showed that percent cover of encrusting invertebrates in the sea-otter free area in Kyuquot Sound and the otter-occupied area in Checleset Bay were not significantly different in percent cover although both differed significantly from Barkley Sound.

## **DISCUSSION**

The study of community ecology broadly seeks to explain patterns of distribution and abundance in animal and plant populations (Krebs 1978). "Natural experiments", which compare communities with and without some biotic or abiotic variable are often used to this end, allowing ecologists to sample natural variation amongst real communities over wide temporal and spatial scales (Diamond 1986). "Natural experiments" further permit the study of populations that cannot be manipulated. The weakness of this method lies in the facts that 1) cause is not observed directly and effect must therefore be inferred and 2) one must assume that places or times being compared differ only in the selected factor (Connell 1972, Underwood 1984, Miller 1986, McGuinness 1988). However, natural "experiments" have become a widely used and accepted ecological tool because the results of such comparisons can be compelling if sampling is done in an unbiased and rigorous manner over large areas (e.g. Yeaton and Cody 1974, Schoener 1974, Toft et al. 1982, Duggins et al. 1989). This method provides one means of assessing the effects of sea otter foraging (Estes and Duggins in prep.).

In contrast to many previous studies, my results are based on rigorous probability sampling, with sites randomly selected from three areas spanning 175 km of coastline. Such a design ensures unbiased, quantitative estimates of community composition in areas with and without sea otters. My findings were similar to those of earlier studies conducted in Alaska, British Columbia and Washington State (Estes and Palmisano 1974, Palmisano and Estes 1977, Estes et al. 1978, Morris et al. 1981, Breen et al. 1982, Kvitek et al. 1989), areas occupied by sea otters were characterized by fleshy algae and an absence of sea urchins, whereas areas without sea otters were typically dominated by sea urchins and fleshy algae were rare.

For the most part the quantitative configuration of algal-dominated and urchin-dominated communities were mutually exclusive and respectively associated with the presence or absence of sea otters. However, three of the sites located in an "otter-free" area, and the four sites revisited in 1992, were the exception, characterized by high densities of both urchins and algae. Sea otters were later observed foraging at all three sites suggesting that the observed mosaic of urchins and algae represented a transitional state between the urchin-dominated and algal-dominated configuration. Observations and experiments subsequently indicated that the transitional state is probably caused by a behavioral response in red urchins brought about by sea otter foraging (Chapter 5). Red urchins avoid damaged conspecifics, consequently, broken red urchin tests dropped by foraging sea otters may evoke an avoidance response in nearby urchins. As red urchins move away from the damaged conspecifics urchin-free patches are created and urchins accumulate at increased densities in nearby areas. Algae may eventually recruit to the urchin-free areas (Chapter 5).

Simenstad et al. (1978) first characterized urchin-dominated and algal-dominated community configurations as alternate stable states (Holling 1973, Sutherland 1974,

1981), with community configuration being determined by the presence or absence of sea otters. Duggins and Estes (in prep.) suggest that the two community configurations, urchin barrens and kelp forests are more properly considered boundary points, because a species (the sea otter) is removed or added to the system (Lewontin 1969). In their model, urchin-dominated and algal-dominated community configurations represent the stable end points of an ecological continuum. Thus transitional or intermediate states, representing the shift between the two boundary configurations, are short-lived, rare and probably unstable. The mosaics of urchins and algae I observed in areas recently occupied by sea otters appear to represent this transition, occurring as the community switches from urchin to algal-dominated. Foster and Schiel (1988), suggest that communities in California do not alternate between stable states, but vary continuously over a "dynamic range", where deforested areas and dense macroalgal cover represent only the extreme conditions. In their model mosaics of urchins and algae not associated with sea otter foraging (e.g. Harrold and Reed 1985, Watanabe and Harrold 1991) represent one of many possible configurations of kelp forest communities.

In the Aleutian Islands high densities of small sea urchins (*S. polycanthus*) often persist, despite the presence of sea otters. Sea otters, apparently constrained by the energetic costs of feeding on small urchins, forage selectively on urchins >20 mm test diameter (Estes et al. 1989). This creates a population of urchins too small to be sea otter prey, yet capable of both maintaining "urchin barrens" (*sensu* Lawrence 1975) and reproducing. Green urchin populations are sustained by regular or periodically heavy recruitment, possibly caused by oceanographic processes or larval entrainment around the islands (Estes and Duggins in prep.). Consequently sea otter foraging results in a gradual decline in the biomass (not necessarily abundance) of sea urchins while the continued

grazing of small and numerous sea urchins results in a slow change from a deforested to algal-dominated community (Estes et al. 1989, Estes and Duggins in prep.).

In contrast, I found red urchins (of any size) to be rare at sites occupied by sea otters. Red urchins under 30 mm test diameter constituted <5 % of the sea urchin population in otter-free areas, a pattern found in many red urchin populations (Bernard and Miller 1973, Tegner and Dayton 1977, 1981, Breen 1984, Kato and Schroeter 1985, Sloan et al. 1987, Pearse and Hines 1979, 1987). Red urchins first reproduce at 50 mm test diameter (Bernard and Miller 1973), which is 20 mm larger than the smallest green urchins preyed on by otters in the Aleutian Islands (Estes et al. 1989, Estes and Duggins in prep.). Thus urchin populations in British Columbia and southeast Alaska differ from the Aleutian Islands in several ways; 1) small urchins are rare and there is little need for otters to select large urchins, 2) the 50 mm size at first reproduction in red urchins means that all reproductive individuals within the population are preyed upon by sea otters and 3) red urchin recruitment is rare (Pearse and Hines 1987, Sloan et al. 1987). These differences mean that foraging sea otters remove almost all the urchin population and the few remaining urchins are too small to reproduce and too rare to maintain the urchin-dominated community configuration. Community changes are consequently rapid and complete (Estes and Duggins in prep., Chapter 4).

Sea urchins are generalist grazers that feed on algae and animals alike (Breen 1980, Duggins 1981, Sebens 1986, Harrold and Pearse 1987). Urchins are known to structure turf communities, reducing encrusting invertebrates and benefitting coralline algae by removing fouling organisms (Vance 1979, Steneck 1983, 1986, Sebens 1986). Consequently, I expected less coralline algae and more encrusting invertebrates in the otter-occupied area than in the otter-free areas. While the cover of coralline algae was not significantly different between areas, mean cover was slightly lower (49.9%) at the

otter-occupied sites than at the otter-free sites (60.4 - 63.5%). However, encrusting invertebrate abundance in Kyuquot Sound (otter-free) and Checleset Bay (otter-dominated) was not significantly different. The visual estimates used in this study may have been inaccurate, because more precise measures of percent cover (Chapter 6) suggest that coralline-algal cover declines and encrusting invertebrate cover increases in the absence of urchin grazing .

Most natural communities, including kelp forests, are patchy (Sousa 1984, Dayton et al. 1984, Connell 1987, Johnson and Mann 1989, Tegner and Dayton 1991, Dayton et al. 1992). Algal abundance and species composition in the otter-occupied area was variable, probably because the area encompassed sites that were in different successional states, having been occupied by sea otters for varying lengths (Chapter 6). Sites dominated by annual brown algae appeared most variable in species composition and algal density. Such sites may have been recently occupied by sea otters and undergoing rapid successional changes (Chapter 4) or alternatively subject to regular physical disturbance (VanBlaricom 1984). Sites dominated by perennial brown algae varied less in algal density and species composition (see Chapter 6).

The results of this study suggest that the effect of sea otter foraging is predictable off northwestern Vancouver Island, where sea urchins often regulate algal abundance (Pace 1975, 1981, Druehl 1978, 1979) and sea otters can regulate urchin biomass (Breen 1980). Evidence suggests that although the rate of community change brought about by sea otter foraging may vary, the direction of change is predictable; sea otter foraging causes a decline in urchin biomass and an increase in fleshy algae (Chapter 4). Similar roles for sea otters have been proposed for the outer Washington coast (Kvitek et al. 1989) and parts of Alaska (Estes and Duggins in prep.). However the importance of

sea otters in California is less clear (Harrold and Pearse 1987, Foster and Schiel 1988, Foster 1990) and will only be resolved by further study.

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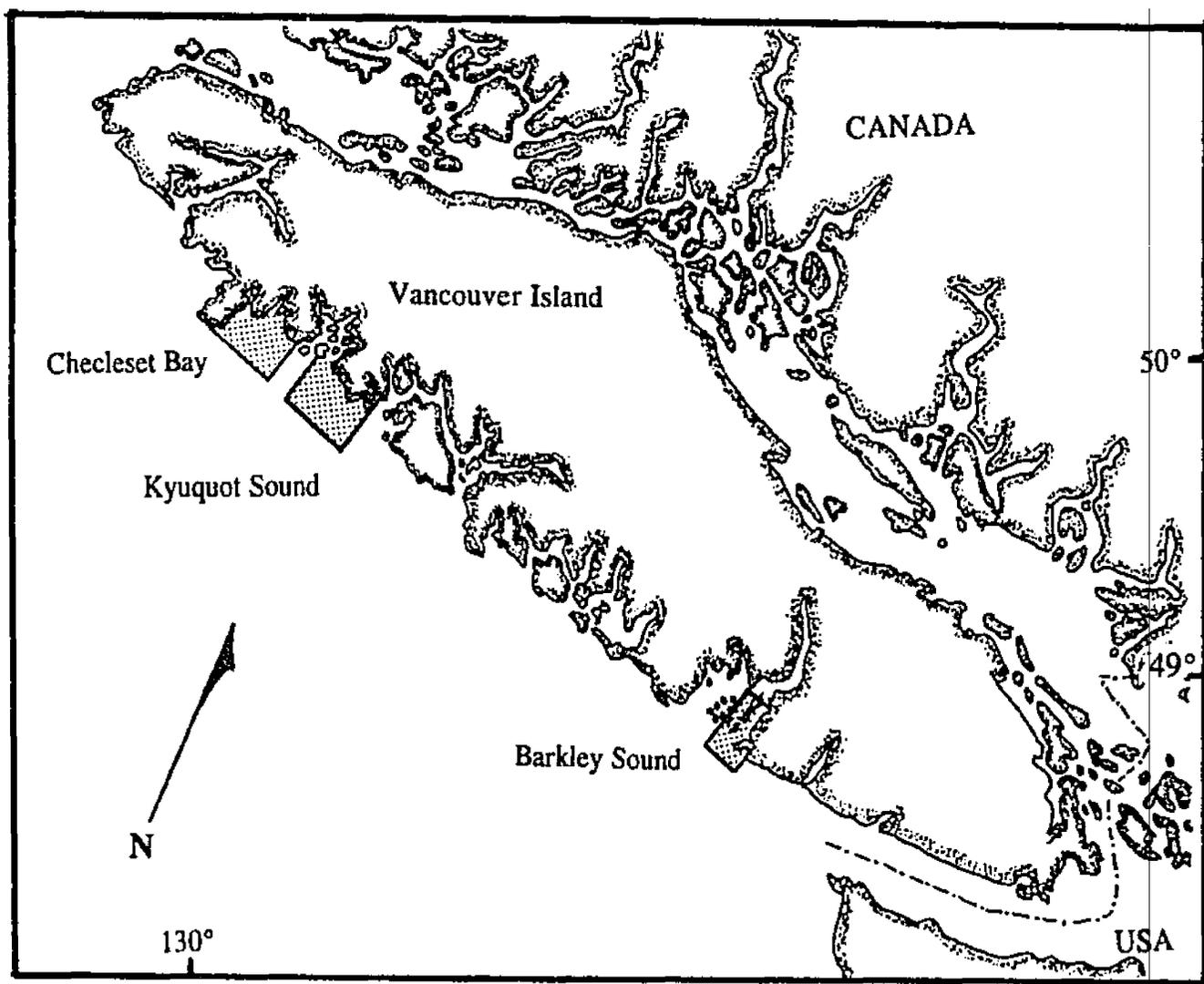


FIGURE 3.1 Location of the three study areas

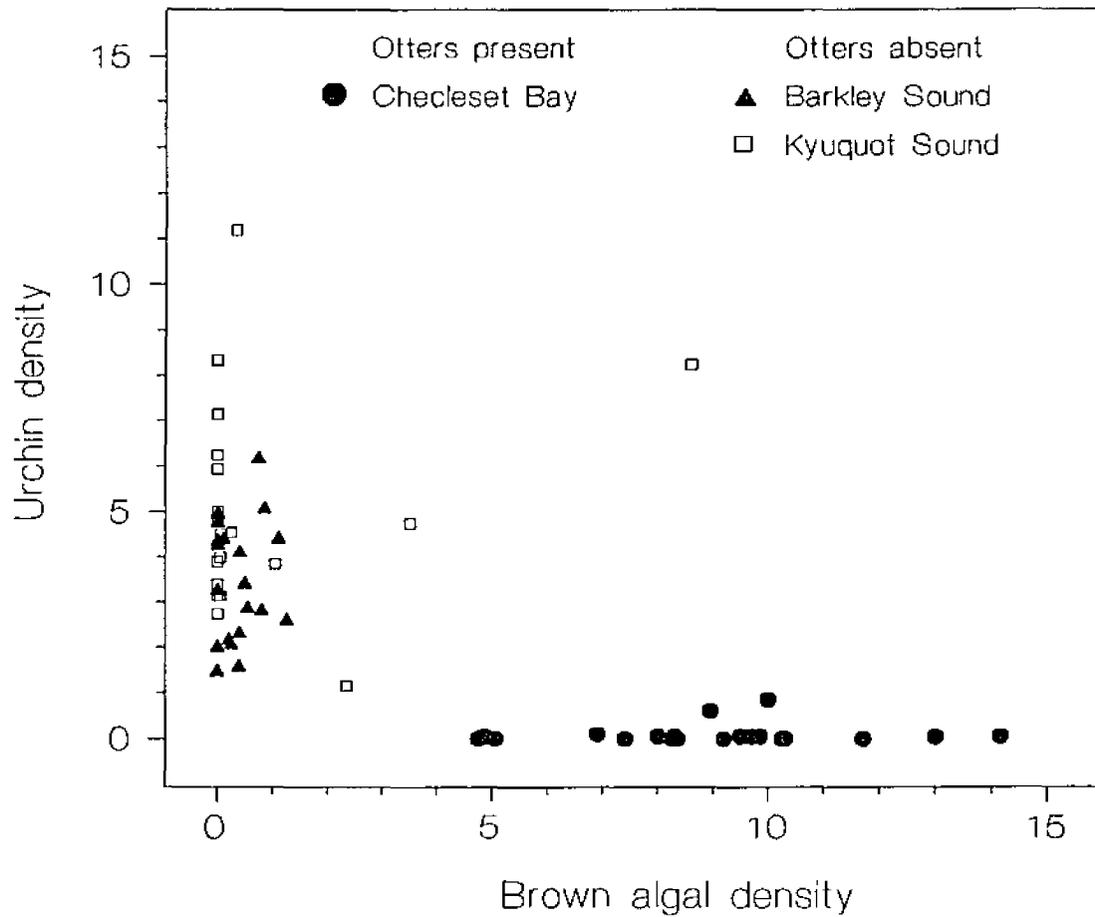
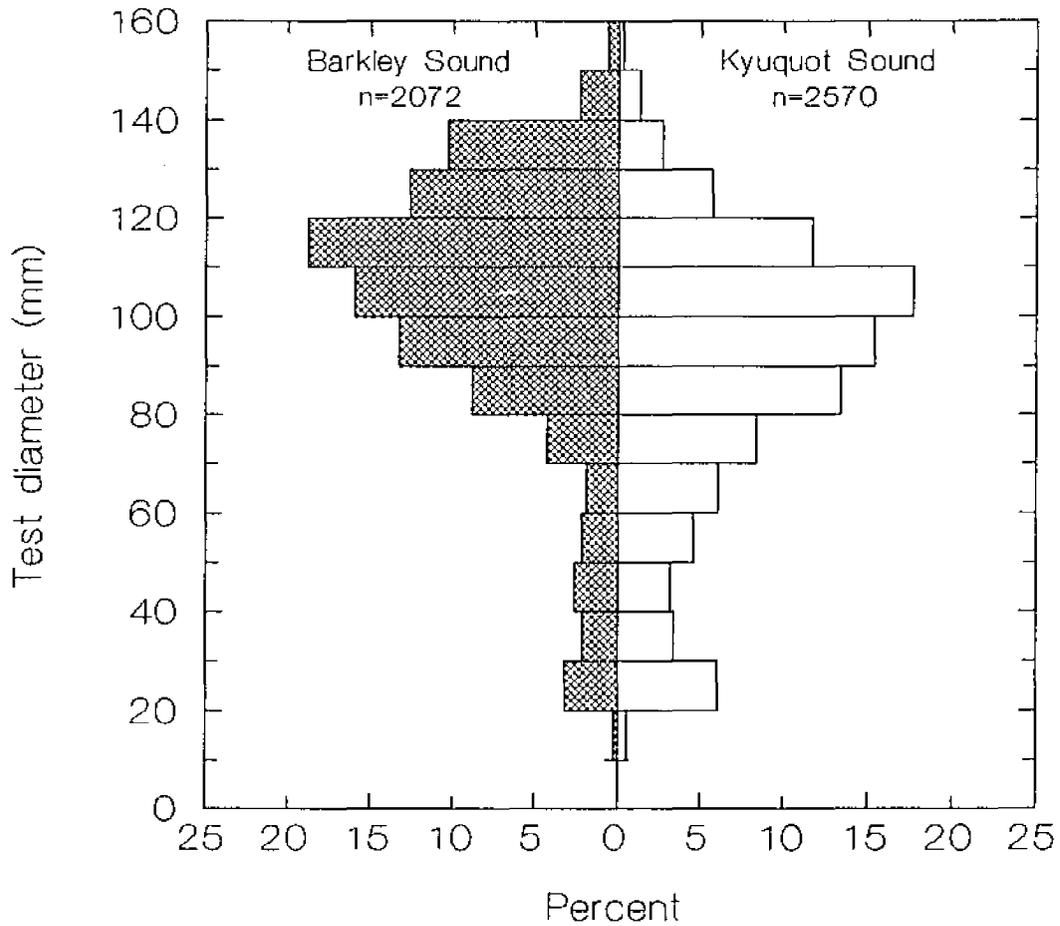
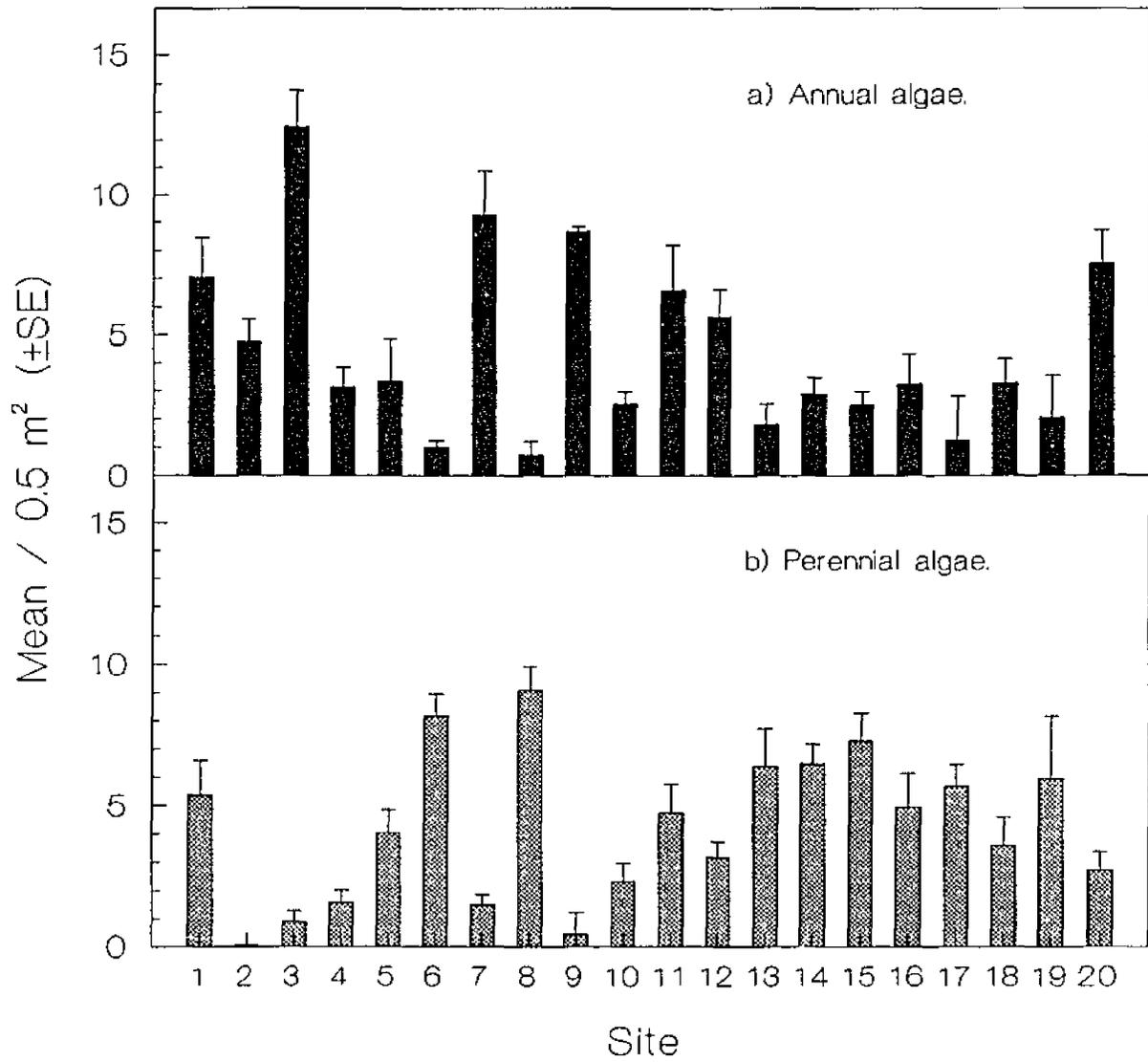


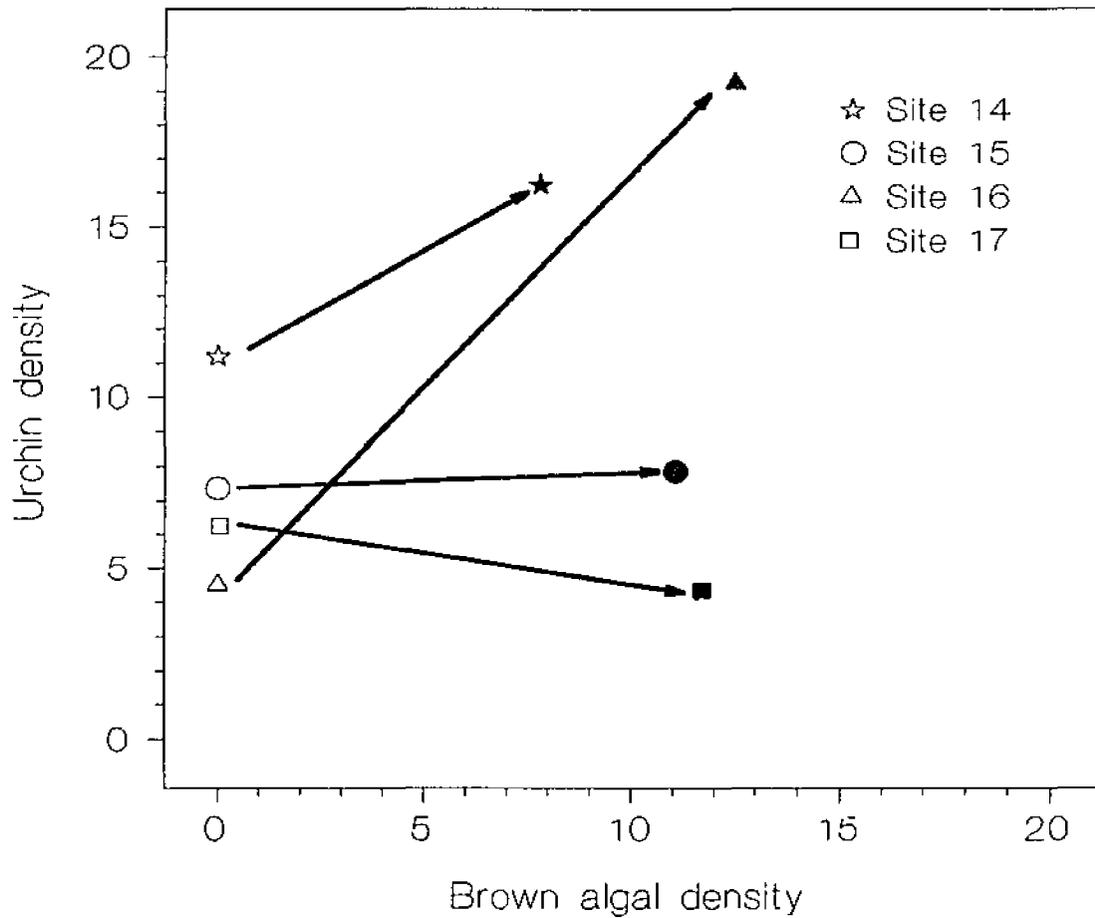
FIGURE 3.2 Kelp density plotted against sea urchin density (no.  $0.5\text{m}^{-2}$ ) for the 60 sites along the west coast of Vancouver Island. Points represent means for each site ( $n=20$ ).



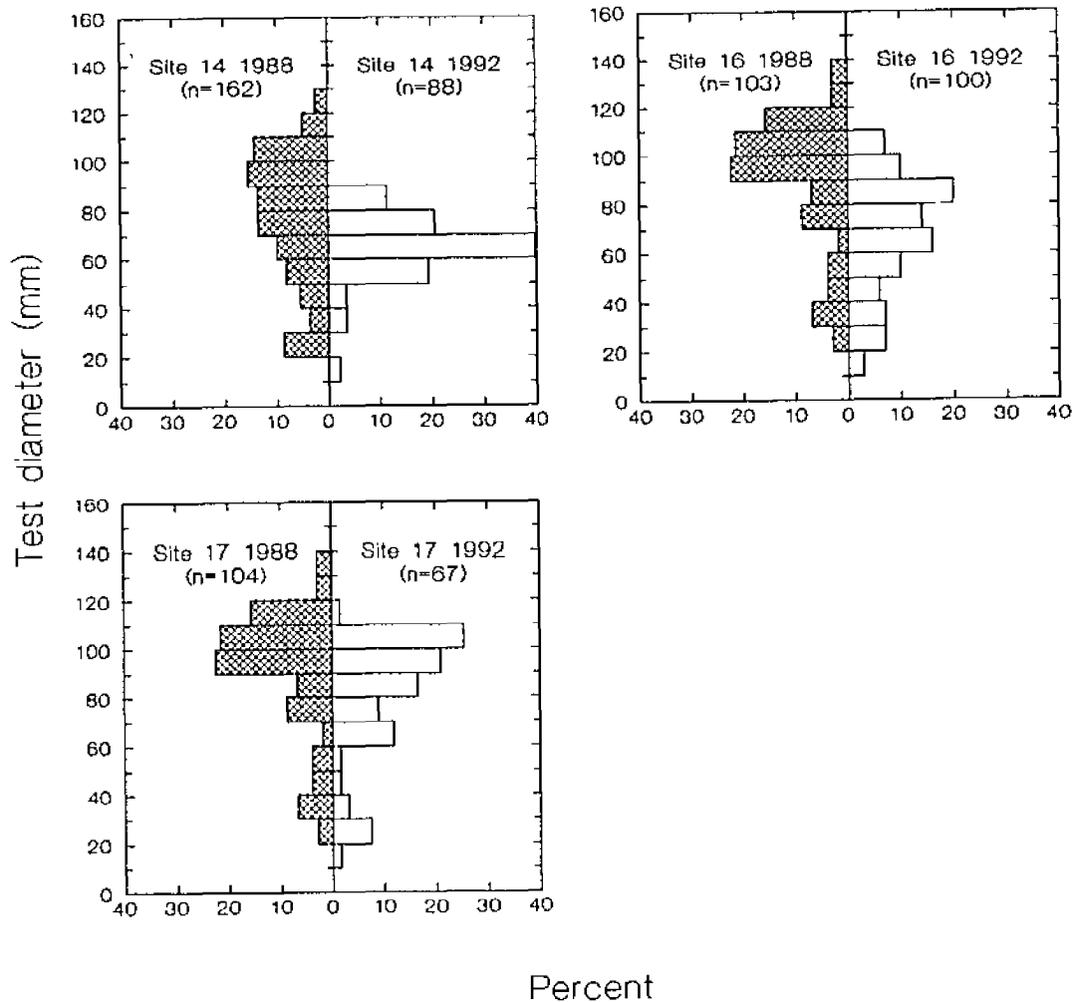
**FIGURE 3.3** Size frequency distribution of sea urchin test diameters measured at sites in the otter-free areas. The distributions are the pooled frequencies of all the sites in each area. The distributions were not significantly different (Kolmogorov Smirnov goodness of fit  $D= 25, P=0.484$ ).



**FIGURE 3.4** Mean abundance  $0.5 \text{ m}^{-2} \pm \text{SE}$  ( $n=20$ ) of **a)** annual brown algae and **b)** perennial brown algae at the 20 sites in Checleset Bay an area with sea otters.



**FIGURE 3.5** Changes in the density of urchins and algae at three sites occupied by sea otters. Open symbols are sea urchin and algal density in 1988, before the arrival of sea otters and solid symbols are urchin and algal density in 1992, soon after sea otters had occupied the sites. Changes in algal abundance are all significant (t test  $P < 0.01$ ). Only the change in urchin abundance at site 15 is significant ( $t_{(2,19)} = 2.92$ ,  $P < 0.01$ ).



**FIGURE 3.6** Size frequency distribution of sea urchin test diameters at three sites visited in 1988 and 1992. Sites were otter-free in 1988 but were invaded by sea otters in 1992. The size frequency distributions at site 16 and 17 were not significantly different (Kolmogorov Smirnov goodness of fit test  $P > 0.523$ ), the distributions at site 14 were significantly different between 1988 and 1992 (Kolmogorov Smirnov goodness of fit test  $D = 30.0$ ,  $P = 0.018$ ).

TABLE 3.1 List of species and categories of organisms enumerated in community surveys.

Group or Order	Description
Annual brown algae	<i>Desmarestia</i> spp., <i>Nereocystis luetkeana</i> , <i>Costaria costata</i>
Perennial brown algae	<i>Pterygophora californica</i> , <i>Laminaria</i> spp., <i>Macrocystis integrifolia</i> , <i>Pleurophycus gardneri</i>
Other algae	Young laminariales
Sea stars	<i>Dermasterias imbricata</i> , <i>Pycnopodia</i> <i>helianthoides</i> , <i>Henricia</i> spp.
Other macro-invertebrates	<i>Haliotis kamtschatkana</i> , <i>Strongylocentrotus franciscanus</i> , <i>S.</i> <i>purpuratus</i> , <i>S. droebachiensis</i> , <i>Cucumaria miniata</i> , <i>Parastichopus</i> <i>californicus</i>
Coralline algae	<i>Corallina</i> spp., <i>Lithothamnion</i> spp.
Red algae	<i>Petrocelis</i> and unidentified spp.
Encrusting invertebrates	Includes many species of Bryozoa, Ascidia, Polychaeta, Porifera, and Hydrozoa.

TABLE 3.2 Summary statistics from community surveys conducted in areas with and without sea otters off Vancouver Island. Density and biomass measurements are per  $0.5\text{m}^2$ . Similarities among locations were tested with a one-way ANOVA using areas, Kyuquot Sound (no otters), Barkley Sound (no otters) and Checleset Bay (otters) as treatments and the sites means ( $n=20$ ) within areas as replicates. A Tukey multiple comparison test was used to identify significant differences between pairs when  $H_0$  was rejected. Analysis of percent cover data was done on Arcsin transformed data (Zar 1984).

Parameter	Location			F	DF	P	Tukey test
	1. Barkley Sound	2. Kyuquot Sound	3. Checleset Bay				
Urchin density (no. $0.5\text{m}^{-2}$ )	3.44	4.90	0.98	51.00	2,57	0.0001	1 2 3
Urchin biomass (gm $0.5\text{m}^{-2}$ )	1698.0	1453.0	0.04	51.50	2,57	0.0001	1=2 3
Total algae (no. $0.5\text{m}^{-2}$ )	0.48	1.53	8.90	58.85	2,57	0.0001	1=2 3
Annual algae (no. $0.5\text{m}^{-2}$ )	0.12	0.95	4.49	17.13	2,57	0.0001	1=2 3
Perennial algae (no. $0.5\text{m}^{-2}$ )	0.19	0.41	4.20	37.82	2,57	0.0001	1=2 3
Encrusting filter feeders (% cover $0.5\text{m}^{-2}$ )	15.48	29.32	26.37	3.26	2,57	0.05	1 2=3
Encrusting Coralline algae (% cover $0.5\text{m}^{-2}$ )	63.45	60.46	49.94	1.96	2,57	0.07	1=2=3
Encrusting Red algae (% cover $0.5\text{m}^{-2}$ )	6.25	4.26	11.04	2.72	2,57	0.074	1=2=3

**CHAPTER 4****The Community Structure of Shallow Rocky Reefs off Northwestern Vancouver Island: Sea Otter Foraging and Temporal Variation.****ABSTRACT**

The effect of sea otter foraging on the structure of subtidal rocky communities was examined off northwest Vancouver Island from 1987-1991 by measuring changes in species composition and abundance at four sites before and after the arrival of sea otters. Temporal variability in community composition was monitored concurrently at two sites in areas without sea otters and at two sites in areas with sea otters. The two sites without sea otters were dominated by sea urchins. Sea urchin abundance varied little and fleshy algae were rare. The two sites with sea otters were dominated by *Pterygophora californica* (Ruprecht) and *Laminaria setchellii* (Silva). At one of these sites, occupied by sea otters for at least 15 yrs, *P. californica* abundance remained almost constant because mortality and recruitment were low. At the second site where sea otters had foraged for 7-9 yrs *P. californica* abundance declined because mortality was high and recruitment was low. With the onset of sea otter foraging, sea urchin abundance declined and brown algal abundance increased. The rate and pattern of community change was influenced by the frequency, intensity and season of sea otter foraging. Sites where sea otters foraged intermittently changed gradually because although urchin abundance declined slightly, the spatial distribution of sea urchins changed and algae recruited to urchin-free patches. A patchy algal assemblage composed of plants of different ages and successional stages resulted. Where sea otter foraging was intense, urchin-dominated

communities became algal-dominated within a year. When the onset of sea otter foraging occurred in the summer, annual species of algae were most abundant in the following year, but were replaced by perennial stipitate kelps. When the onset of sea otter foraging occurred during the winter, stipitate kelps (*P. californica* and *L. setchellii*) recruited first and remained dominant. These results suggest that algal assemblages within the sea otter's range on Vancouver Island are a patchwork of different successional assemblages, whose state is determined by the length of time sea otters have inhabited the area.

## INTRODUCTION

Sea otter predation on sea urchins can significantly reduce urchin grazing and promote the growth of fleshy algae (Estes and Palmisano 1974, Estes et al. 1978, Duggins 1980, Breen et al. 1982, Estes et al. 1989, Kvitek et al. 1989). Consequently, communities in areas occupied by sea otters often support abundant fleshy algae, few sea urchins, and are structured largely by competitive interactions among algal species (Dayton 1975). In contrast, communities without sea otters are often dominated by sea urchins and structured by grazer/plant interactions (Estes and Steinberg 1988). Such communities, often called "urchin barrens" (Lawrence 1975), are dominated by sea urchins and grazer-resistant crustose algae. Fleshy algae are rare and restricted to areas where water motion or unstable substrate excludes sea urchins (Dayton 1975, Palmisano and Estes 1977, Estes et al. 1978, Duggins 1980, 1983, Breen et al. 1982, VanBlaricom and Estes 1988).

There has been considerable discussion in the ecological literature on the generality of ecological processes (e.g. Dayton 1984, Underwood and Denley 1984, Paine et al. 1985). The general importance of sea otters in structuring nearshore communities

has been questioned, largely because sea otter populations are difficult to manipulate and studies examining the effects of sea otter foraging have been indirect, lacking appropriate controls for spatial and temporal variation (Foster and Schiel 1988, Estes and Harrold 1988, Foster 1990). Some authors have inferred the effects of sea otter foraging by comparing communities with and without sea otters (Estes and Palmisano 1974, Palmisano and Estes 1977, Morris et al. 1981, Breen et al. 1982, Foster and Schiel 1988, Kvitek et al. 1989, Duggins et al. 1989), others have simulated sea otter foraging by removing major herbivores (Paine and Vadas 1969, Pace 1975, 1981, Pearse and Hines 1979, Duggins 1980, Cowen et al. 1982), while only a few studies examine the effects of otter foraging by comparing areas before and after the arrival of sea otters (McLean 1962, Simenstad et al. 1978, VanBlaricom 1984, Laur et al. 1988).

The geographic and temporal generality of ecological paradigms, such as ecological importance of the sea otter, can be addressed by asking similar questions in different geographic areas. Such studies are presently underway in California, (Estes and Harrold 1988), Washington state (Kvitek et al. 1989), Alaska (Estes and Duggins in prep.) and British Columbia (this study).

In this chapter I report the effects of sea otter foraging on shallow rocky reef communities off northwestern Vancouver Island from 1987-1991. My work was done by comparing the community composition of four permanently marked sites before and after sea otters arrived. Four additional sites, two located in areas with sea otters and two in areas without sea otters were monitored annually to document natural variation in species abundance. All the sites colonized by sea otters during the study changed from urchin-dominated communities to those dominated by fleshy algae, although the rate and pattern of change varied among sites. In contrast, communities at sites in areas continu-

ously with or without sea otters varied somewhat from year to year but without any obvious trend.

## METHODS

### Site selection and description

Eight permanently marked sites were established along 240 km of semi-exposed, rocky coastline off northwestern Vancouver Island in 1987 and 1988 (Fig. 4.1). To facilitate comparison with other studies, sampling procedures similar to those of Estes and Harrold (1988) and Kvitek et al. (1989) were used. Each site was situated 6-12 m below MLW and marked with a 25 m main axis placed parallel to shore. Five permanently marked, 2X10 m swaths projected at random intervals from the right or left side (Fig. 4.2). Each swath was marked with a stainless steel anchor bolt labelled with PVC tape. The topography of the eight sites was compared by measuring the actual distance along the sea floor and dividing by the linear distance of 10 m (Foster et al. 1986).

The effects of sea otter foraging were documented as sea otters re-colonized four sites that were located just outside the populations' range in 1988. Two sites located 200 km south of the sea otter range (Fig. 4.1) were used to document concurrent temporal variation in areas without sea otters while two sites located in areas occupied by sea otters (Fig. 4.1) were used to document temporal variability in communities with sea otters. Sites were monitored annually by counting the abundance of selected species of algae and invertebrates in all five swaths (Table 4.1). Kelp sporophytes too small to identify to species were classed as juvenile Laminariales and each stipe of *Macrocystis integrifolia* (Bory) was scored as one plant because individual plants were often difficult to distinguish.

Mortality and recruitment in *Pterygophora californica* (Ruprecht) was monitored to determine how stable (*sensu* Dayton et al. 1984) the *P. californica* dominated algal assemblages were at sites continuously inhabited by sea otters. All *P. californica* plants on one swath were labelled with a strip of PVC tape that was attached to a cable tie and fastened loosely about the stipe. Surviving plants were re-tagged each year. Plants < 0.20 m tall were too small to tag, so recruits were defined as untagged plants  $\geq 0.20$  m but < 0.50 m (so that plants which had lost their tags were not considered new recruits). A double-tagging study was conducted at Wizard Islet from 1988-1989. Fifty *P. californica* plants in the shallow sublittoral were double tagged to estimate tag loss and/or tag-induced mortality.

### Data analysis

The use of permanently marked sites minimized spatial variability inherent in random sampling but made formal statistical comparisons between years inappropriate because annual observations were not independent. Thus, mean annual abundance per swath (2 X 10 m, n=5) was plotted; algae were combined as brown algae which included both perennial species (*Macrocystis integrifolia*, *Laminaria* spp., and *Pterygophora californica*) and annual species (*Nereocystis luetkeana* ((Mertens) Postels and Ruprecht), *Costaria costata* (Turner) and *Desmarestia* spp.). *P. californica* recruitment and mortality was calculated from the number of newly tagged and missing plants per year. The pattern and rate of change in community composition was compared by plotting the relative densities ( $\text{m}^{-2} \text{yr}^{-1}$ ) of red urchins (*Strongylocentrotus franciscanus* Agassiz) and brown algae in trajectory diagrams (*after* Holling 1973).

In this study a community is defined as all the species monitored at each site and an assemblage is a subset of species within the community. I use the terms community

composition and community structure to describe interacting species within the community. Configuration refers to the state of the community, either urchin or algal-dominated.

## RESULTS

### Site topography

The topography or relief at the eight sites did not vary significantly ( $\chi^2_7 = 0.703$ ,  $P > 0.999$ ), which reduced concern that between site differences in topography affected community structure and development.

### Sites continuously without sea otters

Sites without sea otters were used to examine temporal variation in sea urchin-dominated communities. Over a five year period both sites were dominated by red urchins. Species abundance varied slightly but unpredictably and community configuration did not change (Fig 4.3a)

### Wizard Islet

The mean abundance of red sea urchins varied from 108.4 individuals/swath in 1987 to 97.0 individuals/swath in 1991 (Fig. 4.4a, Appendix 1.1). Algae recruited to the shallow ends of the shoreward swaths where water motion periodically excluded sea urchins. For example, *Pterygophora californica* abundance increased from 3.0 individuals/swath in 1987 to 22.8 individuals/swath in 1991 (Appendix 1.1). The abundance of macro-invertebrates (Table 4.1) remained fairly constant except for the turban snail *Astraea gibberosa* (Dillwyn) which recruited and increased 10-fold in 1989 (Appendix 1.1).

### **Taylor Islet**

Taylor Islet was similar to Wizard Islet in that the configuration of the community remained unchanged during the study. Mean red urchin abundance increased from 60.6 individuals/swath in 1987 to a maximum of 90.8 individuals/swath in 1990 and algae remained almost absent from the site (Fig. 4.4a, Appendix 1.2). The abundance of other macro-invertebrates (Table 4.1) remained constant during the study (Appendix 1.2).

### **Sites continuously with sea otters**

Two sites with sea otters were used to document natural temporal variation in communities dominated by fleshy algae. There was more variation in species composition and abundance within these sites than within the urchin-dominated sites, although both sites remained dominated by fleshy algae throughout the study and did not change configuration (Fig. 4.3a).

### **Gull Island**

Mean brown algal density varied from a maximum of 218 individuals/swath in 1989 to a minimum of 135 individuals/swath in 1991 (Fig 4.4b, Appendix 1.3). Most of this variation was caused by changes in the abundance of *Desmarestia* spp. which recruited opportunistically to small disturbed areas and ranged from a mean of 78.4 individuals/swath in 1989 to a mean of 12.8 individuals/swath in 1991. The abundance of perennial species was remarkably constant (Fig. 4.5a, Table 3). The mean abundance of *L. setchellii* ranged from 58.0 individuals/swath in 1989 to 41.2 individuals/swath in 1991. Mean *P. californica* abundance ranged from 93.6 individuals/swath in 1988 to 79.6 individuals/swath in 1990 (Appendix 1.3). Large invertebrates (Table 4.1) except for sea stars were rare ( $< 1 \text{ m}^{-2}$ ).

Only one of the fifty double-tagged plants at Wizard Island was missing after one year. While some tags were difficult to read none were lost, thus tag-induced mortality and tag loss were considered negligible. *P. californica* tagged at Gull Island were persistent and had low mortality and recruitment. In 1988 all the plants on the swath were large enough to tag. From 1988-1991 annual survivorship was 84% and only five recruits (plants  $\geq 0.20$  < 0.50 m) were tagged (Table 4.2).

### **No Name Island**

Community configuration did not change at No Name Island even though the abundance of brown algae, especially perennial species, was highly variable (Figs. 4.3a, 4.4a). *M. integrifolia* density increased from a mean of 63.0 individuals/swath in 1988 to 98.6 individuals/swath in 1991. Mean *L. setchellii* abundance increased from 22.1 individuals/swath in 1988 to 68.4 individuals/swath in 1989, but declined to 14.0 individuals/swath in 1991. *P. californica* density declined from a mean of 202.6 individuals/swath in 1988 to 103.2 individuals/swath in 1991 (Appendix 1.4). Results of the tagging study indicated that *P. californica* mortality rate was highest in plants < 0.20 m tall, however mortality rates in this size class could not be directly calculated because the plants were not tagged. Annual survival of tagged *P. californica* between 1988 and 1991 was 95%. Plants at No Name Island were small and young; in 1988 only 55% of the *P. californica* plants were large enough to tag but by 1991, 97% of the plants were tagged (Table 4.3).

### **Sites occupied by sea otters during the study period.**

Four sites established just outside the range of sea otters in 1988 and 1989 were used to document changes in community composition associated with the arrival of sea

otters. With the onset of sea otter foraging three of the four sites changed from urchin-dominated communities to communities dominated by fleshy algae (Fig. 4.3b)

### **Kamils Anchorage**

The site was established in early September and sea otters were first observed shortly afterwards in early October. Sea otters foraged intermittently at the site and the change from urchin-dominated to algal-dominated took two years. Algal abundance increased despite a small decline in overall sea urchin abundance. A transitional stage composed of patches of fleshy algae and sea urchins resulted (Fig 4.3b).

Red urchin abundance declined slightly from 1987-1988, but algal abundance increased substantially following a change in the spatial distribution of sea urchins (Fig 4.4c). In 1987, red urchins were evenly distributed over all five swaths but by 1988 sea urchin abundance had declined to zero on two swaths, had increased on two swaths, and was unchanged on the fifth (Table 4.4). Algae subsequently recruited to the swaths without sea urchins. Sea urchins were rare in all swaths in 1989 and absent in 1990 and 1991 (Table 4.4, Appendix 1.5). Algal abundance declined in 1988 as annual species (*N. luetkeana*, *C. costata* and *Desmarestia* spp.) were replaced by less abundant perennial species, (*M. integrifolia*, *Laminaria* spp. and *P. californica*) (Fig. 4.5b, Appendix 1.5). Other species, including globulose red alga (*Colpomenia* sp. or *Leathesia* sp.), *Ulva* spp., and *Dictyota binghamiae* (Lamouroux) were abundant (but not counted) in 1988 but had disappeared by 1990.

The abundance of macro-invertebrates (Table 4.1), other than urchins, remained unchanged from 1987-1991. However the turban snail *Astraea gibberosa* increased six-fold from 6.6 individuals/swath in 1988 to 40.4 individuals/swath in 1989. *A. gibberosa* declined to 3.4 individuals/swath in 1990 but recruited again in 1991 (Appendix 1.5).

### Union Island

Sea otters were absent when the site was established in 1988, but by the summer of 1990 a raft of up to 120 sea otters was regularly observed in the general vicinity of the permanent site. Intense foraging by large numbers of sea otters was accompanied by a rapid change in community configuration (Fig. 4.3b).

Red urchins increased slightly from 110.2 individuals/swath in 1988 to 143.4 individuals/swath in summer 1989. Brown algae were rare in 1989 but by the following summer, annual algae (*N. luetkeana*, *C. costata*, and *Desmarestia* spp.) had increased 200 fold to 209.4 individuals/swath whereas red sea urchins, sea cucumbers (*Parastichopus californicus* Stimpson) and abalone (*Haliotis kamtschatkana* Jonas) were almost absent (Appendix 1.6). The mean density of perennial algae, (*M. integrifolia*, *P. californica* and *L. setchellii*) was 47.2 individuals/swath in 1990 but increased to 92.8 individuals/swath by 1991. Algal abundance had declined by 1991 as perennials apparently out-competed annual species (Fig. 4.5b, Appendix 1.6).

### Maquinna Point

The permanent site at Maquinna Pt. was established in an urchin-dominated area in 1987. Sea otters were first seen at the site in January 1989. The change from an urchin-dominated to algal-dominated community occurred in under six months (Fig. 4.3b).

Prior to the arrival of sea otters, red sea urchin abundance increased slightly from 182.8 individuals/swath in 1987 to 256.0 individuals/swath in October 1988 (Fig. 4.4c, Appendix 1.7). However, by May 1989 urchins were virtually absent and algae, especially the perennial stipitate kelps *L. setchellii* and *P. californica* were abundant (Fig. 4.5b). *N. luetkeana* abundance declined from 42.0 individuals/swath in 1989 to 31.4 in-

individuals/swath in 1990 and was nearly zero in 1991. The abundance of *L. setchellii* and *P. californica* increased 600-fold to 609.0 individuals/swath in 1990 and was at 606.0 individuals/swath in 1991.

### **Kyuquot Bay**

The permanent site at Kyuquot Bay was established in 1988. Sea otters were first observed at the permanent site in November 1988 (J. Short pers. comm.). A small decline in urchin abundance and a change in the spatial distribution of sea urchins was accompanied by an increase in algal abundance (Fig. 4.3b). The mean abundance of red urchins varied from 275.2 individuals/swath in 1989 to a low of 269.6 urchins in 1989 and up to 275.6 individuals/swath in 1990, however the spatial distribution of sea urchins changed, as indicated by the increased standard error (Table 4.5, Fig. 4.4c). Mean algal abundance increased from 1.8 individuals/swath in 1988 to 219.6 individuals/swath in 1991 (Fig. 4.5b, Appendix 1.8). The abundance of annual algae (*Desmarestia* spp., *N. luetkeana* and *C. costata*) increased from near zero in 1988 to 100.6 individuals/swath in 1991. By 1991 perennial algae (*P. californica* and *L. setchellii*) had increased to 119.0 individuals/swath. The abundance of *Cucumaria miniata* (Brandt) declined, presumably due to otter predation, from 35 individuals/swath in 1988 to zero in 1991 (Appendix 1.8). The community remained in a transitional stage (a mosaic of sea urchins and algae) in 1991 although the presence of broken sea urchin tests provided indirect evidence that sea otters continued to visit the site sporadically (Appendix 1.8).

## DISCUSSION

The effects of sea otter foraging offer the opportunity to examine models of predation, disturbance and succession in marine communities. The effect of sea otters on community structure off northwest Vancouver Island has been inferred by comparing areas with and without sea otters (Morris et al. 1981, Stewart et al. 1981, Breen et al. 1982, Chapter 3). While such studies allow a "snapshot" look at the ecological consequences of sea otters, they do not consider the importance of temporal and spatial variability (Foster and Schiel 1988, Estes and Harrold 1988). In my study the changes associated with sea otter foraging are viewed in the context of both temporal and spatial variation.

At three out of four sites the arrival of sea otters at the permanently marked sites was followed by a decline in sea urchins and an increase in fleshy algae, at the fourth site, Kyuquot Bay, intermittent foraging resulted in the formation of a patchy mosaic of urchins and algae. Although the direction of these changes was predictable, the rate and pattern varied, reflecting differences in the periodicity, intensity and seasonality of sea otter foraging. In contrast to the large and directional changes seen at sites that were invaded by sea otters, the community configuration of sites located in areas continuously with and without sea otters did not change. Even though the abundance of invertebrates and algae varied slightly at these sites the changes were small and inconsistent.

### **Sea otters or random variation?**

The role of physical and biological factors other than sea otters in structuring marine communities cannot be ignored. Physical disturbance caused by storms, for example, has been shown to change sea urchin feeding behavior by altering the abundance of algal drift. When drift is not available sea urchins switch from passive sedentary drift

feeding to aggressive highly mobile grazing which can lead to deforestation (Ebeling et al. 1985, Harrold and Reed 1985, Laur et al. 1988). Large scale changes in climatic patterns such as the El Niño Southern Oscillation event caused enormous declines in kelp abundance in southern California in 1983-1984, and had long term effects on the composition of kelp forest communities (Dayton and Tegner 1984, Tegner and Dayton 1991, Dayton et al. 1992). Outbreaks of urchin pathogens have lowered urchin density and increased algal biomass off the California and Atlantic coasts (Pearse and Hines 1979, Scheibling 1986). Even local effects such as alternative food resources, patchy predation, or heavy urchin recruitment can affect the intensity of sea urchin grazing and alter the abundance of algae (Duggins 1981, 1983, Ebert and Russell 1988, Watanabe and Harrold 1991).

It has been suggested that the importance of these and perhaps other effects on variation in community structure has been underestimated, while the role of sea otters has been over-emphasized and generalized (Foster and Schiel 1988). In a review of the literature Foster and Schiel (1988) concluded that in California, contrary to expectations, sea-urchin-dominated communities were not characteristic of areas without sea otters. They suggested that if, in California, "urchin barrens" are not characteristic of otter-free sites, then urchins may not necessarily regulate algal abundance and sea otters may not necessarily determine community configuration (Foster and Schiel 1988, Foster 1990). Other authors (Estes and Harrold 1988, Estes and Duggins in prep.) point out that sea otters have been shown to be important over much of their geographic range, reducing urchin grazing and increasing algal biomass, despite geographic differences in species composition (Estes and Harrold 1988, Estes and Duggins in prep.).

Many rocky subtidal areas described in British Columbia are urchin-dominated (for coast-wide, multi-depth descriptions: Breen and Adkins 1979, 1980, 1981, 1982),

with sea urchins often limiting the abundance and distribution of fleshy algae (Pace 1975, 1981, Druehl 1978, 1979, Breen 1980, Breen et al. 1982). The patterns seen at the two sites without sea otters, small variation in urchin and algal abundance with no overall change in community configuration (Fig 4.3), are thus consistent with descriptions of many study sites off Vancouver Island (e.g. Pace 1975, 1981, Low 1975, Druehl 1979, Sloan et al. 1987, Stewart et al. 1981, Breen et al. 1982). I could find only two recorded examples of environmentally-mediated switches between kelp-forest communities and urchin-dominated communities. Coon (1982) reported the decline of a *Nereocystis luetkeana* bed off Porcher Island on the north coast of British Columbia and Foreman (1977) reported a local change in kelp abundance caused by an episodic recruitment of sea urchins in Georgia Strait. However, relative to California, there have been few longitudinal studies conducted in British Columbia.

Geographic differences in the importance of predators or "strongly-linked species" on community structure have also been recognized (Paine 1980, Paine et al. 1985, Dethier and Duggins 1988). For example, if sea urchins regulate the abundance and distribution of fleshy algae, then sea otters should exert more influence on community structure in areas where urchin populations are largely unregulated by biotic or abiotic factors than in areas where they are regulated (Pearse et al. 1977, Cowen 1983, Dayton and Tegner 1984, Harrold and Pearse 1987). In British Columbia, for example, sea otters are apparently the only non-human predator capable of regulating urchin abundance and consequently have a strong influence on community structure (Breen 1980, Breen et al. 1982).

The effects of sea otter foraging may also differ geographically with the biological characteristics of different urchin species. In the Aleutian Islands, sea otters prey selectively on large urchins. Frequent or occasionally heavy recruitment apparently

sustains and creates urchin populations composed of individuals too small to be sea otter prey, but large enough to reproduce and maintain urchin barrens (Estes et al. 1989). In British Columbia urchin recruitment is irregular (Breen 1980, Sloan et al. 1987) and sea otter foraging is apparently not size selective, possibly because the sea urchins are generally large (Chapter 3). These two factors result in sea otters completely reducing urchin populations and dramatically influencing community structure.

### **Disturbance and succession; the effects of sea otter foraging**

Much like other kinds of disturbance (Sousa 1979, 1984), both the intensity and frequency of sea otter foraging appeared to affect the rate of community change. Frequent foraging by one or two otters (Maquinna Pt.) and intense otter foraging by large numbers of sea otters (Union Island) changed the community configuration from urchin-dominated to algal-dominated in less than a year. In contrast, intermittent foraging, resulted in more gradual and patchy changes. At Kamils Anchorage and Kyuquot Bay intermittent otter foraging caused an insignificant decline in urchin abundance, but more importantly altered the spatial distribution of sea urchins. This likely occurred because injured red urchins elicit an avoidance response in neighboring conspecifics (Chapter 5). The remains of sea urchins, dropped by foraging sea otters, apparently evoked an avoidance response in the surviving urchins which created urchin-free patches around the discarded urchin tests. As algae recruited to the urchin-free patches, algal abundance increased despite the small decline in overall urchin abundance. Patchy algal assemblages resulted because algal recruitment was spatially and temporally variable. Duggins (1983) reported a similar mosaic of algal patches in Torch Bay, Alaska, where the sunflower star (*P. helianthoides*) elicited an escape in sea urchins

creating urchin-free patches that resulted in spatially and temporally variable algal recruitment.

The seasonality of disturbance also can affect patterns of algal recolonization in that the recruiting species are determined by what propagules are available when space is created (Foster 1975, Sousa 1979, 1984, e.g. Konar and Foster 1992). Off northwest Vancouver Island, refugial algal populations, in the shallow sublittoral fringe were likely the nearest source of algal propagules (e.g. Keats 1991). Dayton et al. (1984) found that the species which recruited after a disturbance were determined by those that were fertile at the time. *L. setchellii* and *P. californica* were the most abundant colonists at Maquinna Point where sea otters removed sea urchins during the winter, when spores from these algae are most abundant (McPeak 1981). Reed and Foster (1984) found that annual species recruited more abundantly to cleared patches during the spring. In my study *Desmarestia* spp. and *N. luetkeana* were the predominant colonists at Union Island and Kamils Anchorage, suggesting sea otters removed urchins in the spring or summer when the propagules of these species were abundant.

Patterns of algal succession have been well studied. In temperate subtidal regions macro-algal succession usually leads to the establishment of long-lived perennial species (Johnson and Mann 1988). Available space is often colonized by "opportunistic" species which are eventually replaced by perennial species (Jones and Kain 1967, Paine and Vadas 1969, Kain 1975, Foreman 1977, Pearse and Hines 1979, Pace 1981, Himmelman et al. 1983, Scheibling 1986). On the Pacific coast of North America, algal succession is described as unpredictable, while on the Atlantic coast, algal succession is considered more predictable, leading to dominance by one or two species of *Laminaria* (Johnson and Mann 1988, Chapman and Johnson 1990). Algal succession may be most predictable where species diversity is low (i.e. the Atlantic) and competition has fewer possible out-

comes (Johnson and Mann 1988, Farrell 1991). At my sites I found algal succession to be fairly predictable in outcome, even though patterns of recruitment and rate of change varied. Although the exact composition of the assemblages could not be predicted, seemingly opportunistic species (*Desmarestia* spp., *N. luetkeana* and *D. binghamiae*) were usually the initial colonists, but were eventually replaced by perennial species (*L. setchellii*, *P. californica* and occasionally *M. integrifolia*) which appeared to be the successional dominants. Similar results were obtained by Paine and Vadas (1969) who excluded urchins from subtidal boulders at Friday Harbor, Washington and Duggins (1980) who removed urchins from rocky reefs in southeast Alaska. Pace (1981) excluded sea urchins at a site near Bamfield, British Columbia and found that annual species such as *Desmarestia* spp. and *N. luetkeana* dominated in the first year but were replaced by *P. californica* and *M. integrifolia* in the following spring.

Algal assemblages within the sea otter range on Vancouver Island are probably a patchwork of successional assemblages, whose state may be determined by the length of time sea otters have inhabited the area (Chapter 6). Since *P. californica* and *L. setchellii* can live in excess of 18 yrs (Reed and Foster 1984, DeWreede 1984, 1986, Klinger and DeWreede 1988, Hymanson et al. 1990) the oldest subtidal populations of these algae may date back to the re-introduction of sea otters (Chapter 6). Despite similar exposure and depth, the dynamics of the *P. californica* populations at Gull and No Name Island differed from each other and may represent different successional states. Sea otters have foraged at Gull Island for at least 15 years (Morris et al. 1981, Chapter 6) and an established *P. californica* forest has been present there since at least 1979 (Breen et al. 1982). *P. californica* abundance at Gull Island remained almost constant throughout my study because individual plants were persistent and mortality and recruitment were low. In contrast sea otters have been present at No Name Island for 7-9 years (Chapter 6). *P.*

*californica* abundance at No Name Island was twice that at Gull Island but declined from 1988-1991 as recruitment decreased and mortality in small plants was high. The decline in small plants at No Name Island may have occurred because larger individuals reduced light available to the smaller ones below (Reed and Foster 1984, Dayton et al. 1984).

The results of this study suggest that sea otter foraging off northwest Vancouver Island results in highly predictable and directional changes in community configuration. However, the pattern and rate of change varies with the intensity, frequency and season of sea otter foraging. These differences can result in the formation of a mosaic of varied algal assemblages which may influence subsequent community development and long-term successional processes.

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### **Personal Communications**

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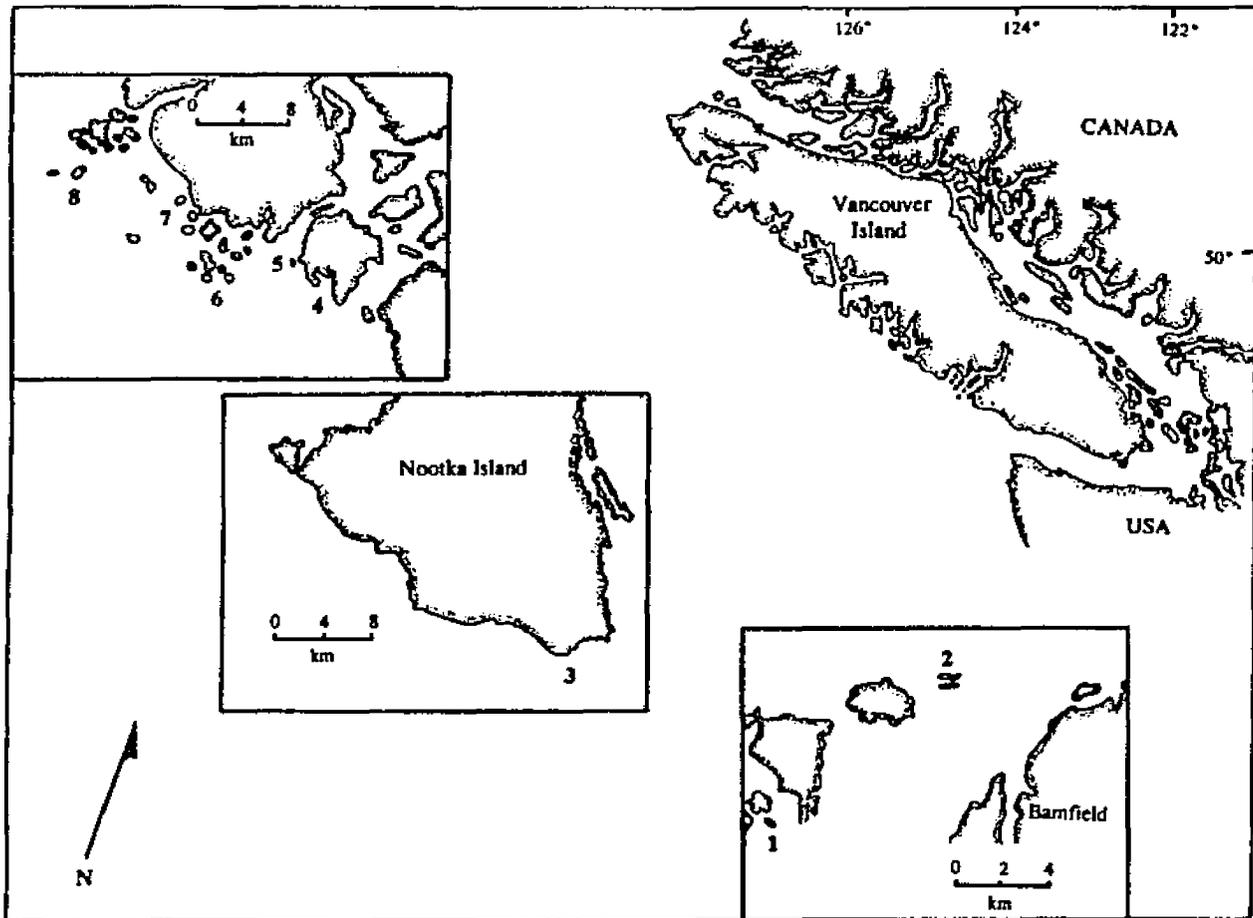


FIGURE 4.1 Location of sites. Sites continuously without sea otters: 1) Wizard Islet ( $48^{\circ}53.0'N, 125^{\circ}9.2'W$ ) 2) Taylor Islet ( $48^{\circ}49.0'N, 125^{\circ}13.2'W$ ). Sites occupied by sea otters during the study: 3) Maquinna Point ( $49^{\circ}34.8'N, 126^{\circ}40.5'W$ ) 4) Kyuquot Bay ( $49^{\circ}58.5'N, 127^{\circ}17.5'W$ ) 5) Union Island ( $50^{\circ}N, 127^{\circ}19'W$ ) 6) Kamils Anchorage ( $49^{\circ}57.5'N, 127^{\circ}22.5'W$ ). Sites continuously with sea otters: 7) No Name Island ( $50^{\circ}0.5'N, 127^{\circ}27.8'W$ ) 8) Gull Island ( $50^{\circ}5.0'N, 127^{\circ}32.5'$ ).

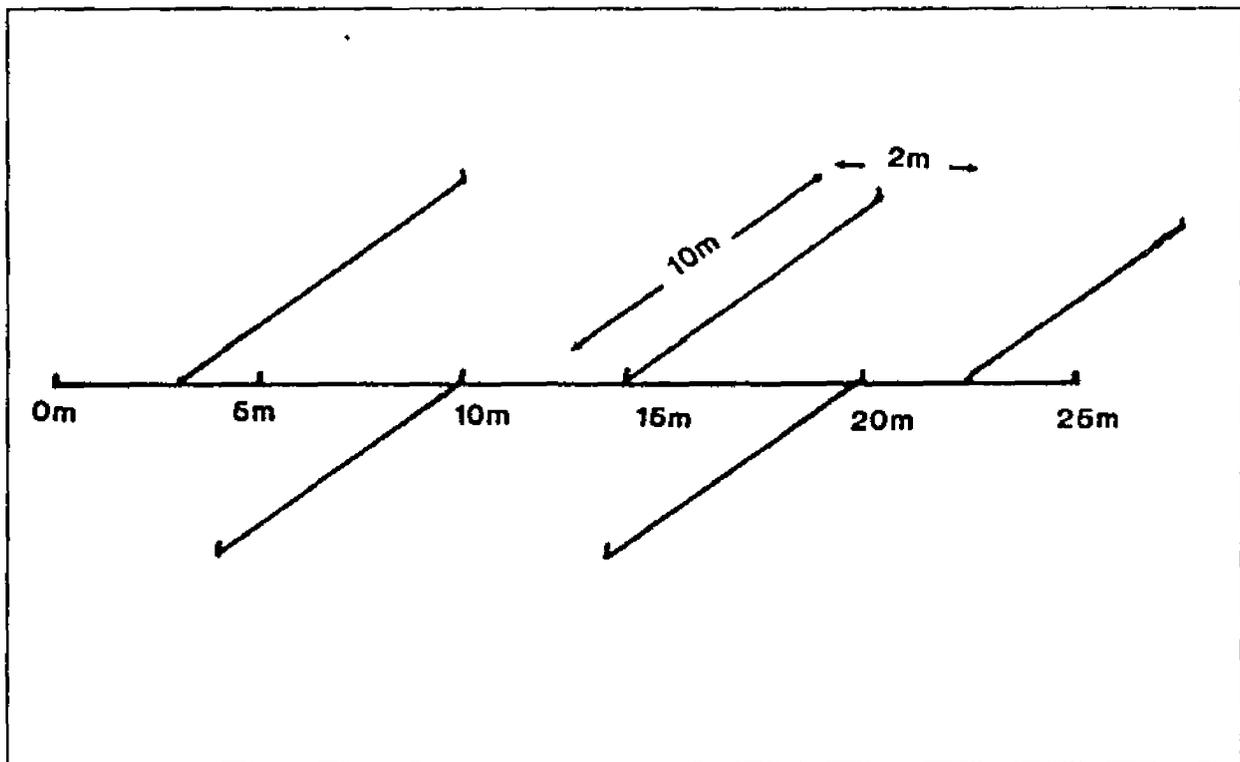
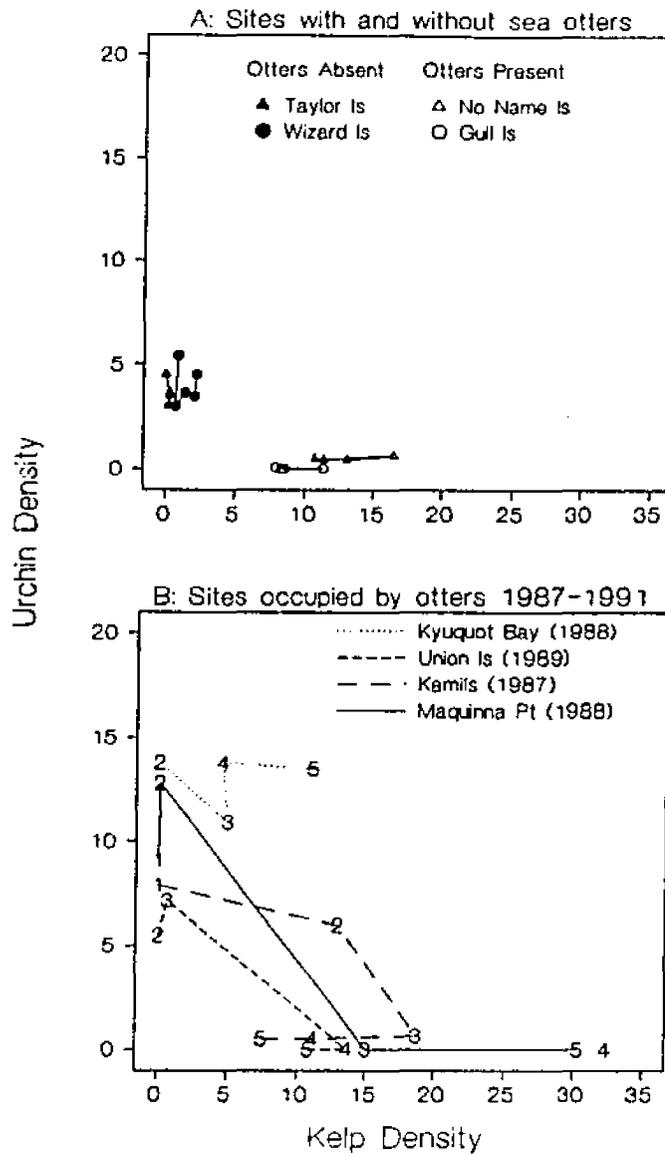


FIGURE 4.2 Configuration of the permanently marked sites.



**FIGURE 4.3** Changes over time in the relative abundance of red urchins and brown algae ( $m^{-2}$ ) at sites without sea otters, sites with sea otters, and sites re-inhabited by sea otter during the study a) urchin-dominated sites in areas continuously without sea otters and algal-dominated sites in areas continuously with sea otters. b) sites in areas re-inhabited by sea otters during the study. Numbers are the year (1)=1987, (2)=1988, (3)=1989, (4)=1990, (5)=1991. (Year) is the year sea otters occupied that site.

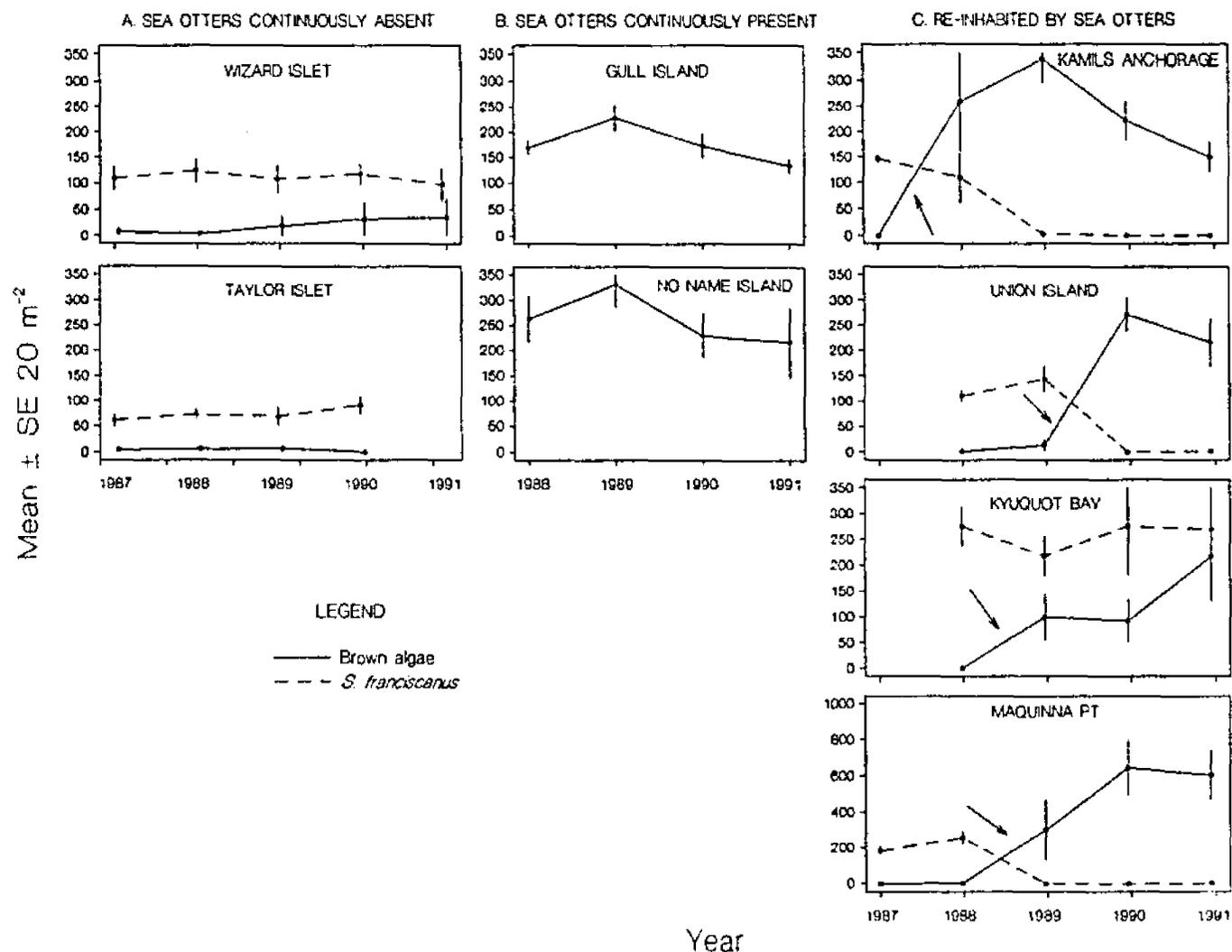


Figure 4.4 Mean density  $\pm$  SE 20 m<sup>-2</sup> (n=5) of red urchins and brown algae at a) sites where sea otters were continuously present, b) sites where sea otters were continuously present c) sites which were re-inhabited by sea otters during the study. Arrows indicate the approximate arrival of sea otters. Note the different Y axis scale on the Maquinna Point panel

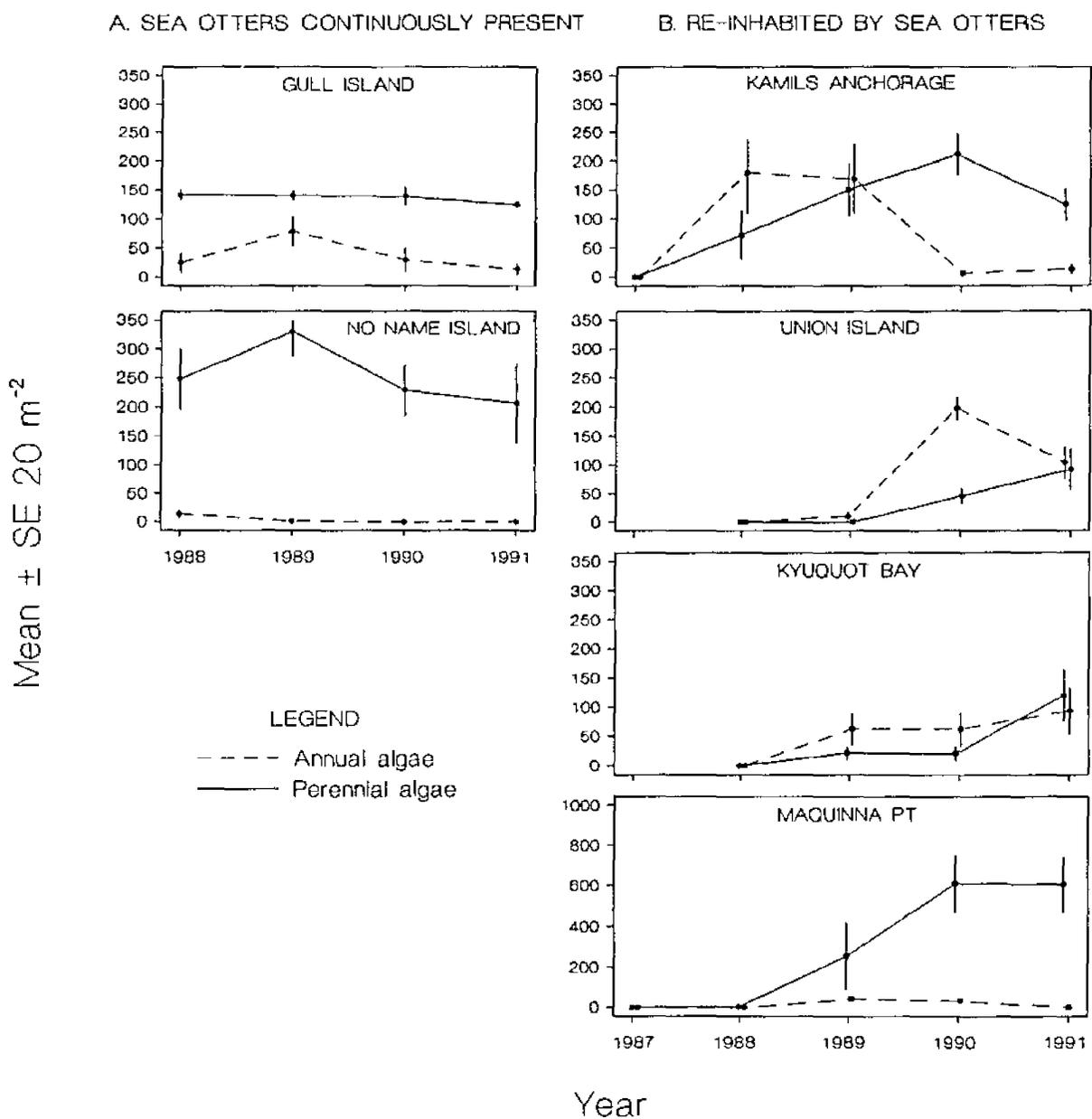


FIGURE 4.5 Mean density  $\pm$  SE 20 m<sup>-2</sup> (n=5) of perennial and annual algae at a) sites which were continuously occupied by sea otters and b) sites which were re-inhabited by sea otters during the study.

TABLE 4.1 Species of invertebrates and algae counted at permanent sites.

Group or Order	Description
Annual algae	<i>Desmarestia</i> spp., <i>Nereocystis luetkeana</i> , <i>Costaria costata</i>
Perennial algae	<i>Pterygophora californica</i> , <i>Laminaria</i> spp., <i>Macrocystis integrifolia</i> ,
Other algae	Young laminariales
Sea stars	<i>Dermasterias imbricata</i> , <i>Pycnopodia</i> <i>helianthoides</i> , <i>Henricia</i> spp.
Other macro-invertebrates	<i>Haliotis kamtschatkana</i> , <i>Strongylocentrotus franciscanus</i> , <i>S. purpuratus</i> , <i>S. droebachiensis</i> , <i>Cucumaria miniata</i> , <i>Parastichopus</i> <i>californicus</i> , <i>Astraea gibberosa</i>

TABLE 4.2 *Pterygophora californica* plants tagged at Gull Island. Bracketed values are plants tagged for the first time. Unbracketed values are plants that were tagged and survived, or surviving plants that had lost their tags. Plants too small to tag were <0.20 m tall.

Year Tagged	No. of tagged plants re-located			
	1988	1989	1990	1991
1988	(86)	73	57	56
1989	x	8	6	5
1990	x	x	17(4)	16
1991	x	x	x	1(1)
Total tagged plants	86	81	84	79
Small untagged plants	0	0	6	4
Total plants on swath	86	81	90	83

TABLE 4.3 *Pterygophora californica* plants tagged at No Name Island. Bracketed values are plants tagged for the first time. Unbracketed values are plants that were tagged and survived, or surviving plants which had lost their tags. Plants too small to tag were <0.20 m tall.

Year Tagged	No. of tagged plants re-located			
	1988	1989	1990	1991
1988	(76)	76	75	72
1989	x	(20)	20	18
1990	x	x	(43)	25
1991	x	x	x	8
Total tagged plants	76	96	138	123
Small untagged plants	62	116	38	4
Total plants on swath	138	212	176	127

TABLE 4.4 Red urchin and brown algal abundance by swath and year at Kamils Anchorage. No red urchins were observed on any swaths in 1990 and 1991.

Swath	1987		1988		1989	
	Urchins	Kelp	Urchins	Kelp	Urchins	Kelp
1	175	1	0	512	3	336
2	154	0	141	115	12	300
3	149	0	173	452	1	320
4	129	0	235	0	0	685
5	127	0	0	227	0	61

TABLE 4.5 Red urchin and brown algal abundance by swath and year at Kyuquot Bay.

Swath	1988		1989		1990		1991	
	Urchins	Kelp	Urchins	Kelp	Urchins	Kelp	Urchins	Kelp
1	416	8	351	243	478	116	329	241
2	244	0	196	0	458	0	448	22
3	281	0	251	0	326	0	410	18
4	210	0	150	119	109	274	43	395
5	223	0	143	155	7	208	118	408

## CHAPTER 5

### **Movements and Distribution of Red Sea Urchins, *Strongylocentrotus franciscanus* in Response to Damaged Conspecifics and Kelp.**

#### **ABSTRACT**

Experiments were conducted to explain changes in the distribution of red sea urchins *Strongylocentrotus franciscanus* (Agassiz) observed in areas which had been recently invaded by sea otters off northwest Vancouver Island, British Columbia, Canada. Urchin-free patches were observed around broken red urchin tests, dropped by foraging sea otters, while urchin density in adjacent areas was twice that previously observed. When eviscerated red urchins were added to the center of three 5 by 5 m quadrats nearby urchins moved away and urchin density declined significantly within 24 hrs. Urchin density remained below pre-treatment levels in two of three quadrats for 16 days. When *Nereocystis luetkeana* ((Mertens) Postels and Ruprecht) was added to three 5 by 5 m quadrats, short-lived aggregations of sea urchins formed around the kelp 24 hrs after it was added, but overall urchin density did not change. Urchin density and distribution did not change in untreated quadrats or in quadrats to which undamaged urchins were added. When sea otters drop the remains of red urchins the reported avoidance response may be elicited and create urchin-free patches which allows patchy algal recruitment.

#### **INTRODUCTION**

Although studies of behavior and community ecology are often pursued independently, animal behavior often has important community-level consequences. Herbivores,

for example, play an important role in determining the structure of many terrestrial and aquatic communities. Consequently, factors which modify grazing behavior can affect community structure (Halligan 1974, Vine 1974, Cumming 1982). The effect of sea urchin grazing on the distribution and abundance of marine plants provides one such example.

Sea urchins are generalist grazers that feed on drift and attached algae as well as diatoms and encrusting animals (Leighton 1971, Mottett 1976, Breen 1980, Sebens 1986). Sea urchin grazing can denude large areas of fleshy algae, and create what have been termed "urchin barrens" (Lawrence 1975). This phenomena of urchin "over-grazing" is widespread in temperate marine ecosystems (reviewed in Lawrence 1975, Harrold and Pearse 1987). While the abundance or density of sea urchins has been thought to regulate plant biomass (Breen and Mann 1976, Ebert 1977), an increasing body of evidence suggests that grazing intensity is often independent of sea urchin density. Recent studies suggest that grazing intensity is often strongly linked to urchin behavior, which changes in response to food availability (Lees 1970, Mattison et al. 1977, Russo 1979, Duggins 1981a, Dean et al. 1984, Mann 1985, Harrold and Reed 1985, Vadas et al. 1986) or the presence of predators (Snyder and Snyder 1970, Bernstein et al. 1981, 1983, Schroeter et al. 1983, Duggins 1981b, 1983, Mann et al. 1984, Mann 1985, Breen et. al 1985, Dayton 1985, Parker and Shulman 1986, Scheibling and Hamm 1991).

On the Atlantic coast of North America aggregations of green urchins, *Strongylocentrotus droebachiensis* (Müller), have been blamed for the reduction of algal biomass (Scheibling 1986). Green urchins may be passive detritivores, aggressive herbivores or browsers, depending on such factors as population density, kelp availability and the presence of predators (Garnick 1978, Mann 1985). Some authors have suggested that

urchins aggregate in response to predators (Mann et al. 1984, Bernstein et al. 1983), while others argue that they flee predators and aggregate around food (Vadas et al. 1986).

On the Pacific coast of North America, changes in feeding behavior of the red sea urchin, *Strongylocentrotus franciscanus* (Agassiz), may cause switches in community configuration (Harrold and Reed 1985, Ebeling et al. 1985). In areas where algal drift is rare, red sea urchins become highly mobile and graze aggressively, often denuding the substratum of macroalgae. When drift algae is abundant, they are sedentary, feed passively on the drift and have little effect on the abundance of attached algae (Lees 1970, Russo 1979, Dean et al. 1984, Harrold and Reed 1985, Ebeling et al. 1985).

Red urchins further exhibit a variety of behavioral responses to predators. They form aggregations that exclude predators (Tegner and Levin 1983), flatten their spines against the substrate to prevent dislodgement (Tegner and Levin 1983), fend off predators with their spines (Moitsozoa and Phillips 1979), occupy refugia (Lowry and Pearse 1973) or move away (Duggins 1983).

Off northwest Vancouver Island sea otters (*Enhydra lutris* Linn.) are the only predator apparently capable of regulating red urchin populations (Breen 1980). By preying on sea urchins sea otters reduce grazing pressure and enhance the growth of fleshy algae (Estes and Palmisano 1974, Breen et al. 1982, Chapter 4). The effect of sea otter predation on urchin abundance is so great that small scale effects are easily overlooked. While diving in areas recently invaded by sea otters, it became apparent that although the eventual outcome of sea otter foraging was to decimate urchin populations, the initial effect altered the spatial distribution of sea urchins. Urchin-free patches were observed around broken urchin tests dropped by foraging sea otters, while urchin density in adjacent areas (without broken tests) was almost twice that previously observed

(Chapters 3 & 4). In many cases algae had recruited to the urchin-free patches. At least two hypotheses explained this pattern. First, red sea urchins move away from conspecific remains discarded by sea otters creating urchin-free patches around the broken urchin tests. As urchins move from the tests they accumulate at increased densities in adjacent areas. Second, sea otters remove sea urchins from patches to which algae recruit and attract urchins.

In this chapter I report the results of experiments conducted to determine if the presence of damaged red sea urchins or kelp best explain the patchy distribution of red sea urchins observed in areas recently reinvaded by sea otters.

## METHODS

The study was conducted in a semi-exposed bay located at 49°59.2'N, 127°18.2'W, on northwestern Vancouver Island (Fig. 5.1). Six 5 by 5 m quadrats were haphazardly situated, at least 25 m apart, on low-relief, rocky substrate, 10-12 m below mean low water. Each quadrat was subdivided into 25 one meter plots, allowing divers to map the location of individual urchins. Four treatments were used to investigate how the presence of eviscerated conspecifics or kelp affected the density and distribution of red urchins.

The response of red urchins to the presence of damaged conspecifics was investigated by adding 10-12 (-2.5 kg whole weight) eviscerated sea urchin tests to the center of three quadrats. Sea urchins were eviscerated by breaking their oral surface and scooping out the viscera. This roughly mimicked sea otter predation. Divers plotted the location of the urchins in each quadrat before adding the eviscerated urchins and then afterwards at 2 hr intervals for 48 hrs during daylight. Monitoring continued intermittently until the experiment was terminated at 396 hrs (16.5 days).

The response of red urchins to kelp was investigated by adding the pneumatocysts and sporophylls of *Nereocystis luetkeana* ((Mertens) Postels and Ruprecht) to three quadrats. Kelp was anchored in the centers of the quadrats (3 pneumatocysts/quadrat, -4 kg.). Divers plotted the location of urchins before adding kelp and afterwards at 2 hr intervals during daylight for 48 hrs. Monitoring was continued intermittently until the experiment was terminated at 96 hrs (4 days).

Natural variation in sea urchin density (= no treatment) was monitored by plotting the location of sea urchins in three quadrats at 2 hr intervals during daylight for 48 hrs. The potential response of sea urchins to the addition of undamaged sea urchins (a control for treatment effects) was investigated by adding 10-12 uninjured red urchins (-2.5 kg/quadrat) to the center of three 5 by 5 m quadrats. Divers plotted the location of sea urchins before adding undamaged urchins and then afterwards at 2 hr intervals for 48 hrs during daylight.

Since time and resources permitted establishing only six quadrats each treatment was randomly assigned to three of the six quadrats. The no treatment and eviscerated urchin treatment trials were randomly selected to run simultaneously, and the undamaged urchins and kelp trials were started seven days after the initial trials concluded. While the four treatments were not run concurrently there were no obvious effects of time.

### **Statistical analysis**

The pairwise differences in sea urchin density before and 24 hrs after treatment were used as replicates (n=3) in each treatment. A single-factor ANOVA was used to compare sea urchin density in each of the treatments. Bartlett's test was used to test the data for homogeneity of variance (Zar 1984). When the ANOVA indicated significant

treatment effects a Tukey's multiple comparison test was used for specific treatment comparisons (Zar 1984).

## RESULTS

Sea urchin density differed significantly among treatments (ANOVA,  $P=0.002$ , Table 5.1). Urchin density in the "no treatment", "whole urchins" and the "kelp treatments" did not differ significantly from each other, but urchin density in the eviscerated sea urchin treatment differed (declined) significantly from all others (Tukey test,  $P \leq 0.02$ , Table 5.2).

### Response of red sea urchins to damaged conspecifics

Sea urchin density declined from a pre-treatment mean of 1.7 - 2.6 urchins to 0.08 - 0.2 urchins  $m^{-2}$  within 24 hours of adding eviscerated conspecifics (Figs. 5.2c & 5.3c). Sea urchins responded immediately by moving away from the eviscerated urchins and out of the quadrats at speeds of up to 1  $m \text{ min}^{-1}$ . Sea urchin density remained well below pretreatment densities in two of the three quadrats when the experiment was terminated at 396 hrs, but approached pre-treatment density in the third (Fig. 5.3c).

Sea stars, including the sunflower star (*Pycnopodia helianthoides* Brandt) and the leather star, (*Dermasterias imbricata* Grube) entered the quadrats 24 hrs after adding the sea urchin tests. A maximum of four *Pycnopodia* and one *Dermasterias* per quadrat were observed. Sea stars fed on the tests for up to six days before leaving the quadrats. The effect of sea stars on sea urchin density was unknown, because there were few sea urchins in the quadrats when the sea stars entered, sea stars however, can evoke avoidance responses in sea urchins (Duggins 1983).

### **The response of red sea urchins to added kelp.**

Sea urchins aggregated around the kelp, but overall urchin density did not change (Figs 5.2d & 5.3d). The number of sea urchins in the center of the 5 by 5 m quadrats increased from a mean of 5.7 urchins m<sup>-2</sup> (range = 0-9) before kelp was added to 15.3 urchins m<sup>-2</sup> (range = 6-26) after kelp was added. Sea urchin aggregations were not apparent after 72 hrs although some of the kelp remained.

### **No treatment and the addition of whole urchins**

Sea urchin density varied slightly, but non-directionally, in the quadrats used to monitor natural variation in sea urchin density (Figs 5.2a & 5.3a). The addition of undamaged sea urchins had no effect on density (Figs. 5.2b & 5.3b). Adding 10-12 urchins to the quadrats represented a 11-18% increase in sea urchin abundance.

## **DISCUSSION**

Sea urchins show a variety of responses to predators or cues indicating predation (i.e. crushed conspecifics, Snyder and Snyder 1970). The literature offers a variable and confusing picture of escape responses in red urchins. In contrast to my results, where sea urchins avoided damaged conspecifics, Tegner and Levin (1983) found that red urchins in southern California flattened their spines against the substratum and remained stationary in response to broken conspecifics, but formed defensive aggregations when exposed to rock lobsters (*Panulirus interruptus* Randall). Red urchins in very wave exposed areas off western Vancouver Island respond to the presence of damaged conspecifics by flattening their spines against the substrate, instead of moving away (J. Watson, M. Sewell pers. obs.). Moitsozoa and Phillips (1979) reported that red urchins in central California generally "fought off" attacks by *Pycnopodia* and fled only as a last resort. In Puget

Sound Mauzey et al. (1968) found that *Pycnopodia* fed on red urchins up to 15 cm in diameter but first had to "chase down" their prey. In southeast Alaska Duggins (1983) found *Pycnopodia* preyed primarily on red and green urchins but not on red urchins > 8 cm test diameter. Furthermore red urchins < 8 cm moved away from *Pycnopodia* while the larger ones did not (Duggins 1983). In areas inhabited by sea otters, red urchins are found mostly in crevices, which are inaccessible to sea otters (Lowry and Pearse 1973, Pearse and Hines 1987).

The variety of results obtained suggest that the response of red urchins to predators is modified by such factors as the mobility of the predator species, water motion, the size of the urchin, the presence of more desirable prey or the availability of physical refugia and in some cases may be experimental artifacts (Snyder and Snyder 1970, Vadas et al. 1986). In fact the only consistent result that emerges is that red urchins often respond to predators. Selection should favour the development of such responses if 1) they decrease the chance of a successful attack, 2) the predator can be detected and 3) the predator has been encountered frequently over evolutionary time (Parker and Shulman 1986). Consequently the adaptive significance of the escape responses is often difficult to assess because the observed escape responses undoubtedly arose in a variety of environmental conditions in response to a suite of predators. Running from a damaged conspecific, for example, is only adaptive if the predator can be outrun, or a refuge reached. Likewise aggregating, reduces risk of predation only if an aggregation swamps the predator's ability to catch prey (Calvert et al. 1979), reduces the probability of an individual being caught (Brock and Riffenbergh 1960), excludes the predator (Tegner and Levin 1983) or confuses the predator and reduces predation success (Landeau and Terborough 1986).

Predators often create temporal or spatial refuges from grazing by altering the distribution of herbivores (Paine and Vadas 1969, Menge and Sutherland 1976). Duggins (1983), for example, found that a patchy assemblage of algae resulted when the sea star *Pycnopodia helianthoides* elicited an escape response in green and purple urchins and created temporary, localized clearings that were rapidly colonized by kelps. Patches of annual algae occurred in areas which were temporarily free of urchins, while perennials occurred in patches which had not been grazed for longer periods (Duggins 1983). Schroeter et al. (1983) likewise suggested that the sea star *Asterina miniata* (Brandt) (= *Patira miniata*) determined the distribution of the sea urchin *Lytechinus anamesus* (Clark) and thereby influenced the distribution and abundance of kelp.

Sea otters are generally thought to have an "all or none" impact on sea urchin abundance (Harrold and Pearse 1987), ultimately decimating red urchin populations (Chapter 3). However, when otter foraging is periodic and urchins are removed intermittently, the decline in abundance appears gradual (Chapter 4). Under these circumstances, urchin tests dropped by sea otters may alter the distribution of nearby sea urchins, and create urchin-free patches. Thus the observed avoidance response offers a plausible mechanism for the formation of urchin-free patches and dense aggregations of urchins seen in areas recently re-inhabited by sea otters. If sea otters forage intermittently in an area, "randomly scattering" damaged urchin tests, the small-scale spatial distribution of sea urchins may change as red urchins move away from the damaged tests and accumulate in areas without damaged urchin tests. Algae may recruit to the urchin-free patches, resulting in the observed pattern of dense aggregations of urchins, urchin-free patches and algae. The alternative hypothesis that urchin-free patches resulted because sea otters fed patchily seems improbable on two counts; it is

unlikely that sea otters would return repeatedly to the same patch to prey on an abundant species, and it fails to explain why the urchin-free patches persist.

The avoidance response elicited by eviscerated sea urchin tests created urchin-free patches that lasted for at least 16 days. These patches offer refuge from urchin grazing. Under ideal conditions some species of kelp (*Macrocystis integrifolia* (Bory), *Nereocystis luetkeana*, *Pterygophora californica* (Ruprecht), and *Egregia menziesii* ((Turner) Ares.)) require 14-28 days to settle, undergo gametogenesis and develop a minute sporophyte (Vadas 1972, Lüning and Neushul 1978, Druehl 1980), consequently urchin-free patches that form around sea urchin remains persist long enough for kelp to recruit.

If urchin-free patches formed in response to the presence of damaged conspecifics the accompanying dense patches of urchins may have resulted as urchins aggregated around recruiting kelp or as red urchins moved away from broken urchin tests into adjoining areas. The aggregations that formed around experimentally added kelp were short-lived and did not affect urchin density significantly. Red urchins are known to aggregate in response to predators (Tegner and Levin 1983), but the difference between moving away from a predator or into an aggregation can be difficult to distinguish, particularly if the end result and not the actual response is documented (Bernstein et al. 1983, Vadas et al. 1986, Chapter 3). As urchins move away from a predator (or cue), urchin density will increase in adjacent areas. The dense patches of sea urchins observed in areas recently occupied by sea otters may have formed in this manner.

The results of the present study emphasize the importance of examining both small and large-scale ecological events. While sea otter foraging will ultimately result in widespread increases in algal biomass, the avoidance response I observed may affect what type of algal assemblages result. If changes in sea urchin distribution result in tem-

porally and spatially variable algal recruitment a patchy assemblage may develop. Seasonal differences in availability of algal propagules, for example, can result in the formation of mixed stands of perennial and annual algae (Chapter 4). Such heterogeneity may have important effects on ecological processes such as succession, within the kelp forest community (e.g. Duggins 1983, Tegner and Dayton 1991, Dayton et al. 1992).

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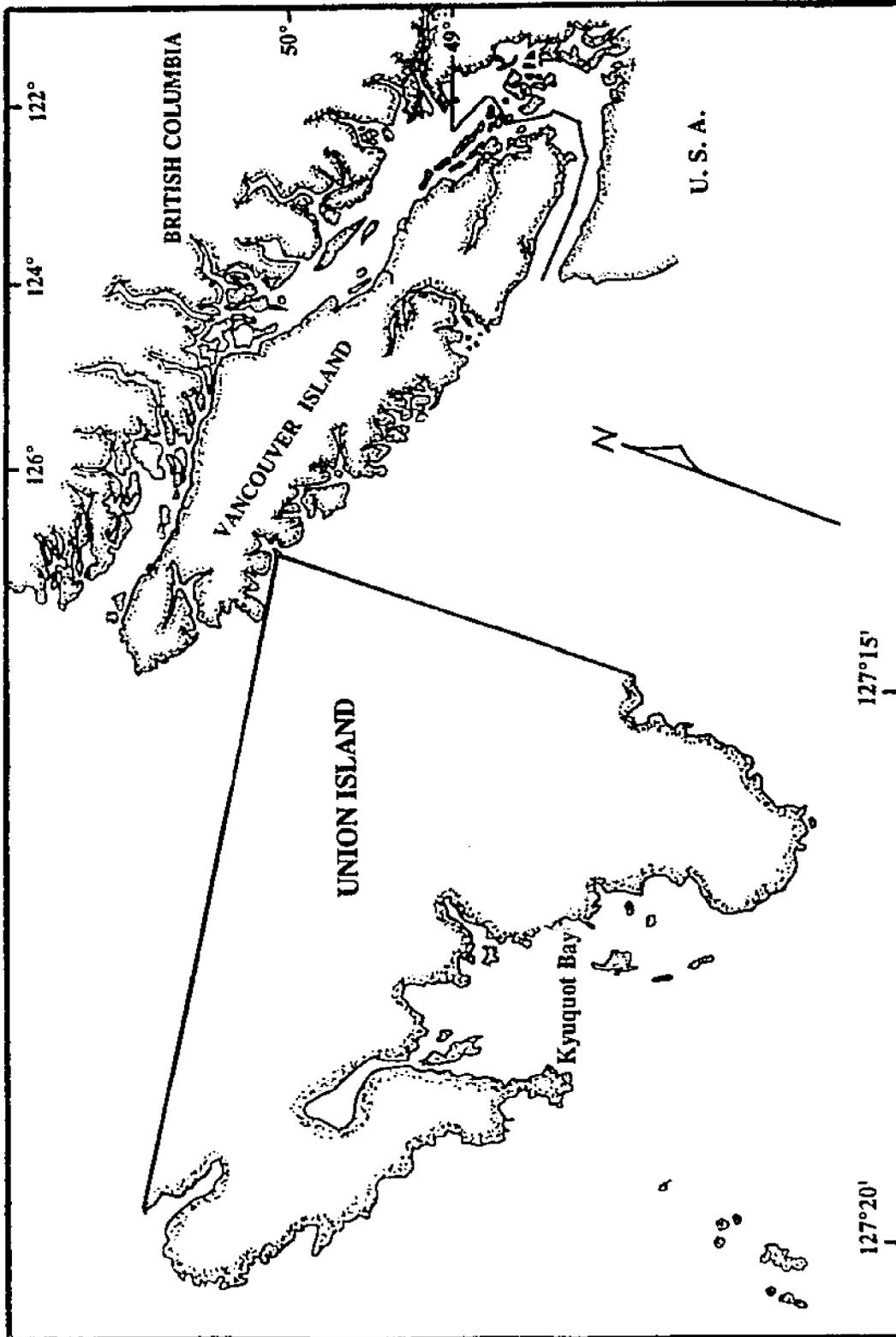
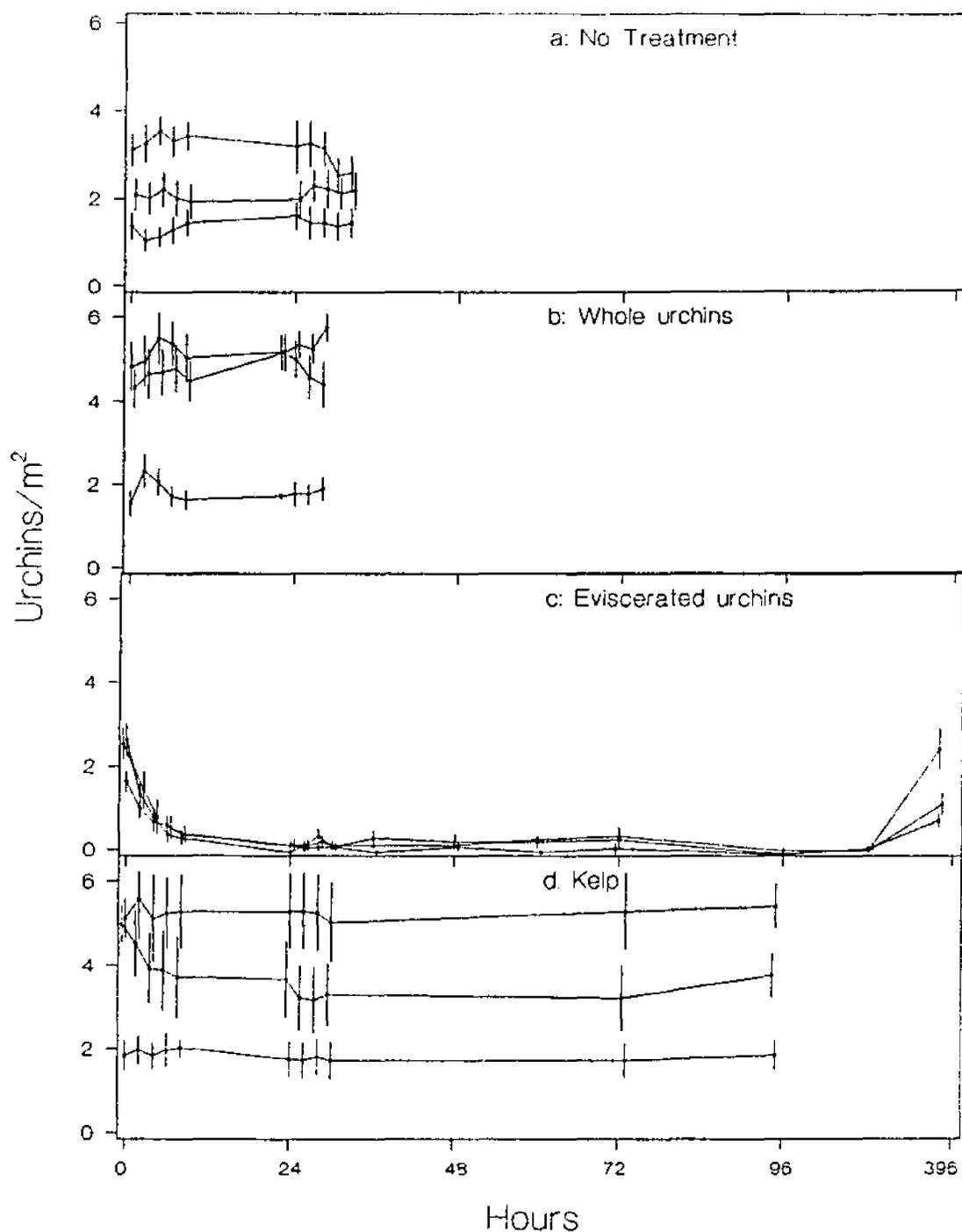
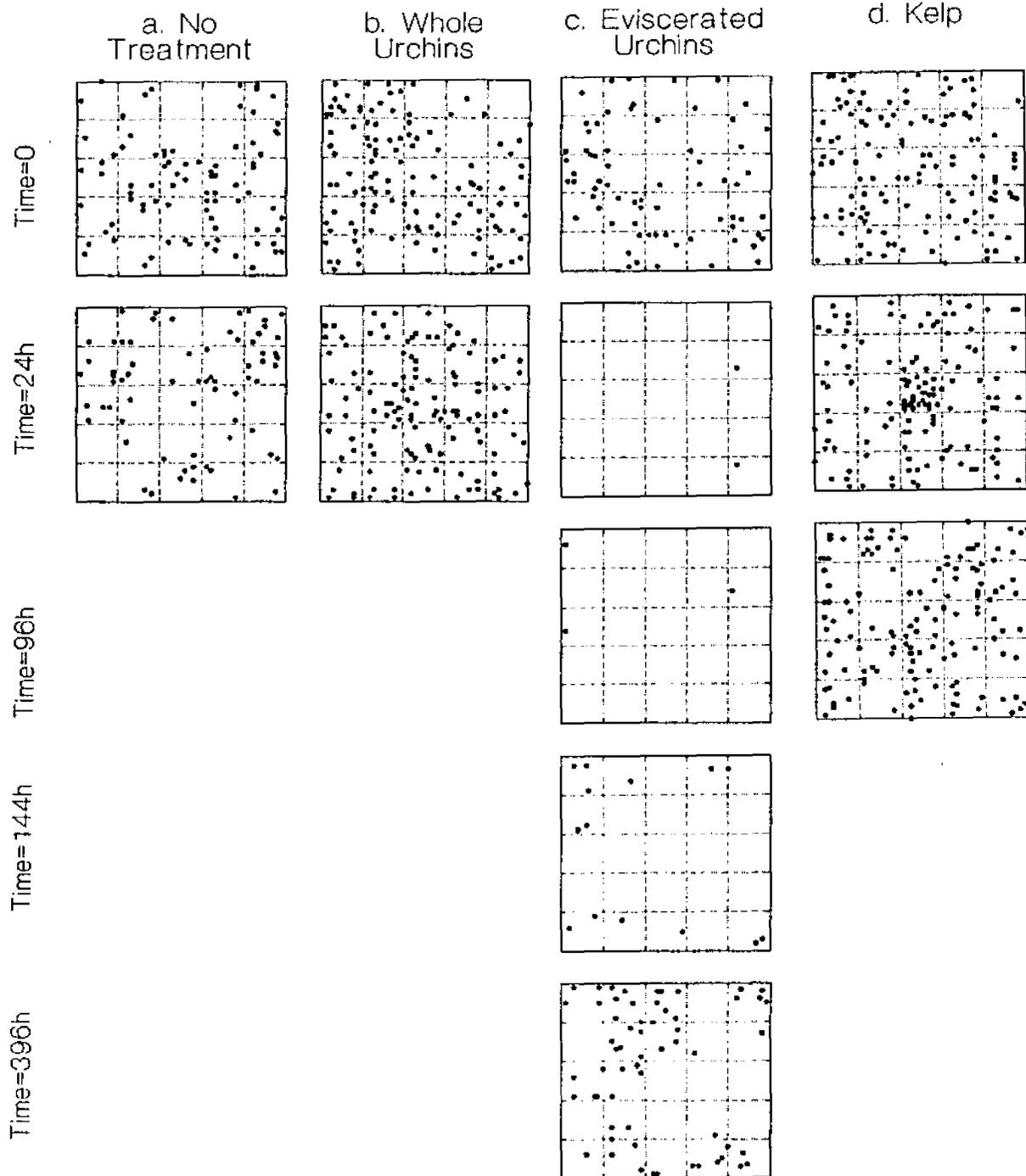


FIGURE 5.1 Location of the study site



**FIGURE 5.2** Mean density ( $\text{m}^{-2} \pm \text{SE}$ ,  $n=25$ ) of urchins in response to **a)** no treatment **b)** undamaged red sea urchins (added immediately after  $t=0$ ). **c)** eviscerated red sea urchins (added immediately after  $t=0$ ). Note the break in the X axis. **d)** kelp (added immediately after  $t=0$ ).



**FIGURE 5.3** Examples of treatment responses **a)** no treatment. **b)** uninjured red urchins **c)** eviscerated red sea urchins. (urchin density is not significantly different from pre-treatment density at 396 hrs) **d)** adding kelp.

TABLE 5.1 Summary of the single factor analysis of variance. Bartlett test for homogeneity of variance,  $\chi^2_{(0.05,3)}=3.128$ ,  $P=0.463$ .

Source of Variation	SS	DF	MS	F	P
Groups	11.905	3	3.968		
Error	2.393	8	0.299	13.270	0.002

TABLE 5.2 Summary of the Tukey multiple comparison test. Matrix of pairwise probabilities (\* = significant).

Treatment	No treatment	Whole urchins	Kelp	Eviscerated. urchins
No Treatment	1.00			
Whole urchins	0.762	1.00		
Kelp	0.730	0.254	1.00	
Evisc. urchins	0.005*	0.002*	0.020*	1.00

**CHAPTER 6****Spatio-temporal Variation in Kelp Forest Communities: Using *Pterygophora californica* to Estimate Time of Recovery of Algal Assemblages in Sea Otter Dominated Areas off Northwest Vancouver Island****ABSTRACT**

Long-term succession in kelp forest communities was inferred at 12 sites located off northwest Vancouver Island. The age of algal assemblages was estimated by assuming that the modal age of *Pterygophora californica* (Turner) coincided with the onset of sea otter foraging at each site. The species composition, density and biomass of algal assemblages and percent cover of encrusting assemblages were examined. The age-frequency distributions of *P. californica* samples collected from 8-10 m below MLW were compared to age-frequency distributions of samples collected 3-5 m below MLW at each site. This helped ensure that refugial *P. californica* populations in the sublittoral fringe had not been sampled inadvertently. Age distributions in the deep and shallow samples were significantly different at all but one site. Based on annual brown algal density, perennial brown algal density and brown algal biomass a hierarchical cluster analysis roughly grouped samples from the deep sites into three groups of similar ages. Algal assemblages at sites occupied by sea otters for 3-4 yrs were highly variable in species composition, algal density, and biomass. Algal assemblages at sites occupied by sea otters for 7-9 years were dominated by stipitate kelps and were similar in terms of algal density although biomass and median *P. californica* height were more variable.

Brown algal assemblages at sites occupied by sea otters for > 11 yrs were dominated by stipitate kelps, but had lower algal density than younger algal assemblages. A hierarchical cluster analysis of the shallow samples resulted in clusters that did not resemble the deep clusters, suggesting that the deep samples had grouped by age and not by site specific factors. The percent cover of coralline algae declined with the length of time sea otters had occupied a site while the abundance of encrusting invertebrates increased. The results of this study suggest that stipitate kelps dominate algal assemblages in semi-exposed areas occupied by sea otters off Vancouver Island. Furthermore early differences in species composition, algal density and biomass appear to have little affect on the eventual composition of algal assemblages.

## INTRODUCTION

Traditional models of succession (e.g. Clements 1916) that predicted an orderly sequence of successional events to a predictable "climax", have largely been replaced by models that recognize the role of disturbance in interrupting long-term successional processes (Horn 1974, Pickett 1976, Connell and Slatyer 1977, Christensen and Peet 1984, Dayton et al. 1984, Dayton and Tegner 1984, Foster and Sousa 1986). The structure of most communities is now thought to be a product of historical events as well as physical and biological processes (Miles 1987, Dayton et al. 1992). Short-term succession in kelp forest communities has been well studied (reviewed in Foster and Schiel 1985, Dayton 1985, Schiel and Foster 1986, Johnson and Mann 1988), whereas patterns of long-term succession are less clearly understood (but see Tegner and Dayton 1991, Dayton et al. 1992).

In terrestrial ecology, successional processes often exceed the life span of ecologists and must be inferred from the structure and composition of present communities.

Annual rings in trees, for example, are used to estimate community age and infer events that occurred long before the onset of the study (Harper 1977). Such techniques have potential application in the study of kelp forests (e.g. Dayton et al. 1984, Reed and Foster 1984). The stipitate kelps *Pterygophora californica* (Turner) and *Laminaria setchellii* (Silva) are long-lived successional dominants that have annual rings in their 'woody' stipes that can be used to estimate plant age (DeWreede 1984, 1986, Reed and Foster 1984, Klinger and DeWreede 1988, Hymanson et al. 1990). DeWreede (1984, 1986) demonstrated that one dark ring (slow growth) and one light ring (rapid growth) form in *Pterygophora californica* each year. Hymanson et al. (1990) assessed the usefulness of various morphological features for determining *P. californica* age and concluded that although single plants could not always be reliably aged, cortical rings could be used to age populations.

Along northwest Vancouver Island, British Columbia, grazing by sea urchins, restricts fleshy algae such as *P. californica* and *L. setchellii* to areas where water motion or unstable substrate provide a refuge from urchin-grazing (Druehl 1978, 1979, Pace 1975, 1981, Breen et al. 1982), consequently algae are often restricted to a narrow wave-washed band in the shallow sublittoral (Breen 1980, Black 1981). The lower extent of these "refugial" (Keats 1991) or "fringing" (Black 1981) kelp beds varies, but is sharply demarcated by sea urchins whose upward extent may be limited by water motion (Pace 1975, Low 1975), the availability of stable substrate and salinity in sheltered areas (Pace 1975, Breen 1980). These refugial algal populations, composed of perennial and annual species, are probably the source of algal propagules for algal colonization following the removal of sea urchins (e.g. Keats 1991).

In British Columbia, sea otters (*Enhydra lutris* Linn.) appear to be the only predator capable of regulating urchin populations (Breen 1980). By reducing urchin

biomass, sea otters can increase the abundance and distribution of fleshy algae, and affect the structure of rocky nearshore communities (Estes and Palmisano 1974, Pace 1975, 1981, Morris et al. 1981, Breen et al. 1982). Sea otters were hunted to extinction in British Columbia, but were reintroduced to Checleset Bay, Vancouver Island from 1969-1972 (Bigg and MacAskie 1978, Jameson et al. 1982). Since their re-introduction the sea otter population has expanded north-west and south-east along Vancouver Island (Morris et al. 1981, Breen et al. 1982, Chapter 2).

*Pterygophora californica* recruits in the wake of sea otter foraging (Chapter 4). Rings in the stipe of *P. californica* suggest it lives up to 18 yrs (Reed and Foster 1984, DeWreede 1986). Thus the age of *P. californica* populations within the sea otter range off Vancouver Island should provide an estimate of the onset of otter foraging as well as the "age" of the current algal assemblage. Furthermore, successional processes can be inferred by comparing the species composition of plant assemblages of known ages (see Harper 1977). In this study long-term successional processes were examined by comparing the composition, density and biomass of brown algae and encrusting assemblages at sites where the modal age of *P. californica* populations was used to estimate algal assemblage age.

## METHODS

### Site selection and sampling

Twelve sites located in semi-exposed, rocky subtidal areas located within the sea otter range off northwestern Vancouver Island were sampled in 1989 and 1990 (Fig. 6.1, Table 6.1). Sites were selected in a randomly-stratified manner to ensure that communities of varying age were sampled. Sites with unstable or soft substrate were

rejected. At each site thirty 0.7 by 0.7 m (0.5m<sup>2</sup>) quadrats were sampled 8-10 m below mean low water (MLW) and then at 3-5 m below MLW. *Pterygophora californica* populations and the algal assemblage at 3-5 m were sampled for two reasons; 1) the shallow and deep age distributions of *P. californica* were compared to ensure the deep *P. californica* sample was not inadvertently taken from the shallow "refugial" population and 2) to control for among site differences, not attributable to the age of the algal assemblage (see later explanation and Green 1979).

Divers swam a random number of kicks, dropped the quadrat and pushed it through the epibenthic kelp canopy to the substrate. In each quadrat individuals of selected species of algae were counted. Algal biomass was measured in the last 10 of the 30 randomly selected quadrats. *Pterygophora californica* and *Laminaria setchellii* plants in each quadrat were harvested, taken to the surface, drained, sorted by species and weighed to the nearest 100 gms. Individual *P. californica* plants were measured to the nearest cm, from immediately above the holdfast to the bottom of the apical meristem, a light colored region near the top of the stipe. Although *P. Californica* plants from within a quadrat could not be considered independent, they were considered representative of the population.

#### **Aging *Pterygophora californica***

A 7-10 cm section was cut from above the holdfast of each *P. californica* plant. Sections were placed in a labelled plastic bag (one/quadrat) and preserved in 1% buffered formalin (Although *Laminaria setchellii* has cortical rings that can be used to estimate plant age (Klinger and DeWreede 1988), it was not sufficiently abundant at all sites for use in this study.). Three thin sections were cut approximately 4 cm from the base of each *P. californica* segment, the cross sections were placed on a light table and

the dark rings completely encircling the stipe were counted. Plant age was calculated as the mean of the three estimates. Age distributions were constructed for the deep and shallow samples at all sites. The age distributions of shallow and deep *P. californica* samples at each site were compared to ensure that plants in the deep sample had likely recruited when sea otters removed sea urchins and had not been collected from kelp populations at the sublittoral fringe.

The repeatability of age estimates was assessed by having a second person age three of *P. californica* samples and comparing the age frequencies. The modal age of *P. californica* from each deep sample was used as the estimate of when sea otter foraging started at that site (Fig. 6.2). The assumption that *Pterygophora californica* age provided a reasonable estimate of "otter arrival" was tested by regressing the modal age of *P. californica* samples at sites where the year sea otters had arrived was known against the known time of arrival. However senescence in plants older than 14 yrs may have meant that older plants were under-represented in the population, making the modal age of *P. californica* a poor indicator of algal assemblage age at sites occupied by sea otters for > 14 yrs.

### Community composition

A hierarchical cluster analysis was used to group the samples. The deep and shallow samples were analyzed independently. Euclidean distance was chosen as the similarity measure and a single linkage method was used (Green 1979, Wilkinson 1990). Algae were clustered by mean density of annual brown algae, perennial brown algae, and perennial brown algal biomass per 0.5 m<sup>2</sup>. Annual algae included *Nereocystis luetkeana* ((Mertens) Postels and Ruprecht), *Desmarestia* spp., and *Costaria costata* ((Turner) Saund.). Perennial algae included *Laminaria setchellii*, *Pterygophora*

*californica*, *Pleurophycus gardneri* (Setch. and Saund.) and *Macrocystis integrifolia* (Bory). Each stipe of *M. integrifolia* was scored as one plant because individual plants were difficult to distinguish. The results of the shallow and deep cluster analysis were compared. It was assumed that the deep and shallow sites would group identically if site specific factors, other than assemblage age, were responsible for the clustering of deep samples. A discriminant function analysis (Green 1979) was used to assess the separation of the clustered deep samples, by drawing 95% confidence limits around the group centroids and examining group overlap (Matthews 1979).

### **Encrusting assemblages**

Eight of the twelve sites and five additional sites, located outside the sea otter range, were randomly selected and sampled to examine encrusting assemblages at sites with and without sea otters (Table 6.1). Fifty random point intercepts in ten 0.5m<sup>2</sup> quadrats were used to determine the percent cover of encrusting flora and fauna. Encrusting invertebrates and algae were identified to the lowest possible taxon and later pooled in the categories encrusting flora or fauna (Table 6.2). Percent cover data were arcsin square root transformed before analysis (Sokal and Rolf 1981).

## **RESULTS**

### ***Pterygophora californica* age distributions**

The age distributions of the shallow and deep samples of *P. californica* were significantly different at all but one site (Kolmogorov Smirnov test  $P < 0.001$ , Fig. 6.2). At Thomas Island the shallow and deep *P. californica* samples were not significantly different ( $P > 0.50$ , Fig. 6.2). Shallow samples were not collected from Clara Islets because surge made diving difficult.

The independent age assessments of the three samples were not significantly different (Kolmogorov Smirnov test  $P > 0.05$ ) indicating that repeatable *P. californica* age estimates could be obtained. Although the age frequency distributions did not vary, estimates of individual plant age, as noted by Hymanson et al. (1990), occasionally differed by up to two years.

The regression of *P. californica* modal age against known (or expected) age (Fig. 6.3) confirmed that the modal age of *P. californica* samples appeared to provide a reasonable estimate of the onset of sea otter foraging ( $r^2 = 0.882$ , reject  $H_0: P = 0$ ,  $t_{(0.05, 2, 6)} = 5.56$ ,  $P < 0.005$ ). The age distributions of the *P. californica* samples from Gull Island and Clara Islets, located near where the sea otters were re-introduced from 1969-1972 (Bigg and MacAskie 1978) suggested that sea otters arrived at these sites 11 and 14 yrs ago respectively (Fig. 6.2). The deep *P. californica* samples from Kyuquot Bay, Moos Islets and Polygon Island, at the edge of the sea otter range, had modal ages of 3-4 yrs (Fig. 6.2). The modal age of the deep *P. californica* sample from No Name and Canoe Islands was 7 yrs, the mode at Thomas Island, McLean Island, Nasparti Inlet, and Aktis Island was 8 yrs while the mode at Acous Peninsula was 9 yrs (Fig. 6.2).

The modal age of *P. californica* sampled in autumn 1991 at Maquinna Point, 100 km west of the study area, was 3-4 years and agreed with the observed arrival of sea otters at that site in late 1988 (Fig. 6.4, Chapter 4). The modal age of the deep *P. californica* sample collected from Thomas in 1989 indicated most of the *P. californica* had recruited 7-8 yrs earlier (Fig. 6.2) and agreed with the first report of sea otters foraging at Thomas Island in 1980 (Foreman unpub.). The modal ages of the *P. californica* sample from Acous Peninsula collected in 1989 indicated that sea otters had started to forage 9-10 yrs earlier, shortly after Breen et al. (1982) surveyed it in 1979. A similar comparison was made for Canoe Island (Breen et al. 1982). Sea urchins were abundant

at Gull Island in 1972 (Bernard and Miller 1973) but absent in 1978 (Morris et al. 1981), and sea otters were observed at Gull Island in 1977 (Bigg and MacAskie 1978). The modal age of the *P. californica* sample collected from Gull Island in 1989 was 14 yrs (Fig. 6.2), but senescence in plants older than 14 yrs may mean that old plants are under-represented in the population making the modal age of *Pterygophora californica* a poor indicator of assemblage age at "older" sites.

### **Community composition**

#### **Deep samples**

Algal assemblages at sites occupied by sea otters for 3-4 yrs were highly variable in species composition, algal density and biomass. Sites occupied by sea otters for 7-9 yrs were dominated by stipitate perennial kelp and were similar in terms of brown algal density and species composition. Algal assemblages at sites occupied by sea otters for >11 yrs were dominated by stipitate kelps but had a lower algal density than younger sites.

Annual brown algae, especially *Nereocystis luetkeana* and *Desmarestia* spp. were most abundant at sites occupied by sea otters for 3-4 yrs (Polygon Island, Kyuquot Bay and Moos Islets). Annual brown algae ranged in abundance from a mean of 4.7 plants  $0.5\text{m}^{-2}$  at Polygon Island to 8.9 plants  $0.5\text{m}^{-2}$  at Kyuquot Bay (Table 6.3). Annual algae were least abundant at sites occupied by sea otters for 7-9 yrs and ranged from 0.3 plants  $0.5\text{m}^{-2}$  at Aktis Island to 2.6 plants  $0.5\text{m}^{-2}$  at Acous Peninsula (Fig. 6.5, Table 6.3 ).

Perennial algae were generally less abundant in algal assemblages 3-4 yrs old and ranged from a mean of 5.5 plants  $0.5\text{m}^{-2}$  at Moos Islets to 11.0 plants  $0.5\text{m}^{-2}$  at Kyuquot Bay. The density of perennial algae in assemblages 7-9 yrs old was surprisingly

similar and ranged from 11.3 plants  $0.5 \text{ m}^{-2}$  at Thomas Island to 12.5 plants  $0.5 \text{ m}^{-2}$  at Nasperti Inlet Island. The density of perennial algae in algal assemblages 11-14 yrs old was lower than in assemblages 7-9 yrs old. There were 6.1 plants  $0.5 \text{ m}^{-2}$  at Clara Islets and 5.3 plants  $0.5 \text{ m}^{-2}$  at Gull Island (Fig. 6.5, Table 6.3).

The size and weight of algae in monospecific stands are known to vary with both stand density and plant age (Schiel and Choat 1980, Schiel 1985, Hymanson et al. 1990). Algal assemblages in this study were composed of mixed species and ages. Young *Pterygophora californica* plants at sites occupied by sea otters for 3-4 yrs were smaller than at older sites such as Gull Island, where *P. californica* plants were largest (Fig. 6.6). Algal biomass was lowest in sites 3-4 yrs old, but variable at older sites (Table 6.4). The biomass of stipitate kelps in 3-4 yr old assemblages was low ranging from 0.34 kg  $0.5 \text{ m}^{-2}$  at Moos Islets to 0.74 kg  $0.5 \text{ m}^{-2}$  at Kyuquot Bay (Table 6.4). The median height of *P. californica* plants in algal assemblages 3-4 yrs old ranged from 0.19 m at Polygon Island to 0.26 m at Kyuquot Bay (Fig. 6.6). The biomass of other algal species was low and unmeasured. The biomass of stipitate kelps in 7-9 yr old assemblages ranged from 2.42 kg  $0.5 \text{ m}^{-2}$  at No Name Island to 5.42 kg  $0.5 \text{ m}^{-2}$  at Aktis Island (Fig. 6.6, Table 6.4) while median height of *P. californica* plants ranged from 0.48 m at Nasperti Inlet to 1.10 m at Aktis Island (Fig 6.6). Mean stipitate kelp biomass was 2.99 kg  $0.5 \text{ m}^{-2}$  at Clara Islets and 5.05 kg  $0.5 \text{ m}^{-2}$  at Gull Island (Table 6.4) and median *P. californica* height was 1.11 m and 1.60 m respectively (Fig. 6.6).

### **Shallow samples**

In shallow samples the mean density of annual algae, predominantly *Desmarestia* spp. ranged from no plants at Moos Islets and No Name Island to 3.8 plants  $0.5 \text{ m}^{-2}$  at Gull Island (Table 6.5). The density of perennial species ranged from 8.1 plants  $0.5 \text{ m}^{-2}$

at Gull Island to 17.4 plants  $0.5\text{m}^{-2}$  at Polygon Island (Table 6.5). *Laminaria setchellii* was generally more abundant in shallow than deep samples. *Pleurophycus gardneri* and *Eisenia arborea* (Areschoug) were present in shallow assemblages but not in deep assemblages. Median *P. californica* height ranged from 0.64 m at Acous Peninsula to 1.20 m at No Name Island (Fig. 6.6), while perennial biomass ranged from 2.74 kg  $0.5\text{m}^{-2}$  at Acous Peninsula to 9.94 kg  $0.5\text{m}^{-2}$  at Aktis Island (Table 6.6).

### Cluster analysis

The hierarchical cluster analysis grouped the deep samples into three groups: the three sites aged 3-4 yrs (Polygon Island, Moos Islets and Kyuquot Bay which is a separate group, but most similar to the Polygon and Moos), the seven sites aged 7-9 yrs (No Name Island, Thomas Island, Nasparti Inlet McLean Island Canoe Island, Aktis Island and Acous Peninsula), and the two sites  $>11$  yrs, (Clara Islets and Gull Island; Fig. 6.7a). The shallow samples grouped differently than the deep samples, with no apparent pattern (Fig. 6.7b), suggesting that the deep samples had grouped by assemblage age and not site characteristics.

The results of the discriminant function analysis showed the abundance of annual brown algae, perennial brown algae and mean biomass/quadrat were highly variable in algal assemblages at sites occupied by sea otters for 3-4 yrs; the 95% confidence limits encompassed all other clusters (Fig 6.8). The 95% confidence limits around the cluster of 7-9 yr old sites encompassed 5/7 sites, and did not include members of any other cluster (Fig. 6.8). Confidence limits could not be drawn around the cluster composed of the two older sites (Clara Islet. and Gull Island.)

### Encrusting assemblages

The percent cover of coralline algae differed significantly among sites (1-way ANOVA,  $F_{(13,126)}=17.36$ ,  $P<0.001$ ). A multiple comparison test indicated that the sites could be divided into two groups. Group one was composed of sites without sea otters and sites which sea otters had been present at for 3-4 yrs (Polygon Island, Moos Islets, Kyuquot Bay). Group one differed significantly ( $P<0.05$ ) from the second group, composed of sites that had been occupied by sea otters for  $>7$  yrs (except for Nasparti Inlet; Table 6.7). Crustose coralline algal cover (primarily *Lithothamnion* spp.), at sites without sea otters ranged from a mean of 59.0% at Kapoose Point to 89.5% at Union Island. Coralline algal cover, at sites occupied by otters for  $>7$  yrs ranged from a mean of 24.5% at McLean Island to 54.8% at Nasparti Inlet (Fig 6.9).

The percent cover of encrusting invertebrates also varied significantly among sites (1-way ANOVA,  $F_{(13,126)}=30.9$ ,  $P<0.0001$ ). A multiple comparison test indicated that, except for Nasparti Inlet, sites which had been occupied by sea otters for  $>7$  yrs did not differ significantly from each other (Table 6.8). Sites without sea otters, or those occupied by sea otters for 3-4 yrs varied from each other unpredictably but all differed significantly from sites occupied by sea otters for  $>7$  yrs (Table 6.8). In general, encrusting invertebrates were scarcer at sites without sea otters and ranged from a mean cover of 2.5% at Brecciated Point and McQuarrie Rocks to 16.2% at Raccoon Point (Fig 6.9). Polychaetes, primarily *Dodecaceria* sp., living within the coralline algal crusts accounted for most of this cover (Fig 6.9). The cover of encrusting fauna including Bryozoa, Ascidia, Porifera, Cnidaria, and Polychaeta increased with the length of time otters had been present (Fig. 6.9). Bryozoa, primarily *Heteropora* spp., were the most abundant order ranging from a cover of 6.9% at Moos Islets (3 yrs) to 33.8% at McLean Island (8 yrs) (Fig 6.9).

## DISCUSSION

### **Inferring succession in algal assemblages**

Debates over succession have played a pivotal role in the development of ecology as a science (McIntosh 1981, Miles 1987). There was an extreme dichotomy in early views; namely vegetative succession was thought to either converge on a regional climax (Clements 1916) or be largely unpredictable and stochastic (Gleason 1927). Present views suggest the truth lies between these two extremes (e.g. Horn 1976, Foster and Sousa 1986, Leps 1991, Dayton et al. 1992). Over the years a plethora of studies have demonstrated that vegetative change sometimes converges on a regional climax, sometimes diverges from a regional climax, and is often unpredictable (e.g. Matthews 1979, Christensen and Peet 1984, McCune and Allen 1984, Inouye and Tilman 1988). The reason for these varied results may be the large time scale over which most successional changes occur (Connell 1987).

The longevity of many plant communities means that successional processes must often be inferred. This is usually done by assuming that communities of different ages represent time-sequences of succession (Brown 1992). However the importance of chance events (past events) are difficult to assess because they often leave little or no record, making it difficult, if not impossible, to rule out variation in community composition due solely to long-past events (McCune and Allen 1985). Thus spatial variation is rarely addressed, even though variation within an area where successional age is known may be greater than variation between areas of different ages (Brown 1992).

In temperate subtidal regions, macro-algal succession often leads to the establishment of assemblages composed of long-lived species of kelp (Foster and Schiel 1985, Dayton 1985, Schiel and Foster 1986, Chapman 1986, Johnson and Mann 1988, Dayton

et al. 1992). Following a disturbance, available space is usually colonized opportunistically, often by annual species which are eventually replaced by perennial algae (Jones and Kain 1967, Paine and Vadas 1969, Kain 1975, 1979, Foreman 1977, Pearse and Hines 1979, Pace 1975, 1981, Himmelman et al. 1983, Scheibling 1986). My results were consistent with the prediction that community composition becomes more predictable as succession proceeds (Margalef 1968). Algal assemblages at sites estimated occupied by sea otters for 3-4 yrs were characterized by a mixture of perennial and annual brown algae and were highly variable (thus unpredictable) in terms of species composition and algal density. In contrast brown algal assemblages at sites which had been occupied by sea otters for 7-9 yrs were dominated by stipitate kelps, and were similar (thus predictable) in algal density and species composition. The two sites > 11 yrs had lower densities of perennial brown algae than younger sites, suggesting that thinning may occur. These results suggest that chance events affect the composition of early successional assemblages but are less important with increasing successional age. Competitive interactions between algal species apparently determine the eventual composition of algal assemblages and make the outcome of long-term succession (> 7 yrs) predictable at least at the sites studied.

Chance events, such as time of year the space is created (Foster 1975a, McPeak 1981, Dayton et al. 1984, Dayton et al. 1992), the intensity and frequency of disturbance (Sousa 1979) or the proximity of the source of spores (Fager 1971, Kennelly 1983, Sousa 1984, Scheibling 1986, Reed et al. 1988) may account for much of the variability in species composition found at sites occupied by sea otters for 3-4 yrs. While annual species often dominate early successional stages (Paine and Vadas 1969, Pearse and Hines 1979, Duggins 1980, Pace 1981, VanBlaricom 1984, Reed and Foster 1984) the seasonality of disturbance determines what propagules are available and thus what

species recruit (Foster 1975a, Sousa 1984, Reed et al. 1988). For instance, annual species such as *Desmarestia* spp. and *Nereocystis luetkeana* recruit principally in the spring and summer, whereas perennial species such as *Pterygophora californica* and *Laminaria setchellii* tend to recruit during the fall and winter (McPeak 1981, Dayton et al. 1984, Chapter 4).

Competition also plays a role in structuring subtidal algal assemblages, especially in the absence of herbivory (Dayton 1975, Kain 1975, Foster 1975b, Duggins 1980, Reed and Foster 1984). Scheibling (1986) compared algal assemblages at different sites after the mass mortality of sea urchins off the Atlantic coast of North America, and found that species composition was variable in the year following the urchin die-off, but similar four years later. Pearse and Hines (1979) found that competition between four species of kelp eventually resulted in a nearly monospecific stand of *Macrocystis pyrifera* (Aghard.) after a mass die-off of red urchins in central California. VanBlaricom (1984) suggested that in California *M. pyrifera* usually outcompetes stipitate kelps and dominates many algal assemblages. In contrast stipitate kelps are often the competitive dominants off Vancouver Island (Low 1975, Pace 1975, 1981, Foreman 1977), with *M. integrifolia* dominating sheltered high salinity areas (Druehl, 1978, Coon 1982). In fact the dynamics of algal assemblages along much of northwest Vancouver Island may more closely resemble the stipitate kelp assemblages described in southeast Alaska (Duggins 1980, 1981, 1983) and the Aleutian Islands (Estes and Duggins in prep.) than the generally canopy-dominated kelp beds of southern California (Tegner and Dayton 1991, Dayton and Tegner 1992).

Successional processes occurring over a time span of > 11 yrs were difficult to infer, largely because algal assemblages older than 11 yrs appeared to be rare within the study area. Kelp density in the two assemblages estimated to be 11 and 14 yrs old was

lower than in 7-9 yr old assemblages, suggesting that a gradual thinning may occur as plants are lost but not replaced. Even as plants are lost, substrate light levels beneath the canopy may inhibit the growth of new recruits (Kain 1979, Santelices et al. 1980, Cowen et al. 1982, Reed and Foster 1984, Santelices and Ojeda 1984, Dayton et al. 1984). Inhibition of recruitment may result in age distributions that lack young age classes (e.g. Gull Island). However as thinning continues substrate light levels should eventually increase, allowing a new cohort of algae to become established (Reed and Foster 1984).

The major causes of mortality in *Pterygophora californica* are grazing and water motion (DeWreede 1986, Biedka et al. 1987). Within the study area large grazers (urchins) are absent and water motion is undoubtedly the principle source of mortality. Thus plants growing in deep water may have lower mortality rates than individuals in turbulent shallow water (e.g. Dayton et al. 1992). *P. californica* plants in the shallow samples generally had irregular age distributions, probably caused by patchy plant loss and recruitment (Chapman 1986). In contrast *P. californica* from the deep samples were often restricted to a smaller range of age classes, or were sharply truncated at an older age class. Such age distributions may arise when sea urchins are removed by sea otters and *P. californica* and *L. setchellii* recruit, dominating subtidal algal assemblages with populations whose modal age coincides with the arrival of sea otters.

### **Encrusting assemblages**

The percent cover of encrusting invertebrates appeared to increase with the length of time sea otters were estimated to have been present at a site. In contrast the cover of coralline algae generally declined. The removal of urchins by sea otters may have been responsible for this change. While the sites could be *roughly* divided into two

groups, 1) sites without sea otters and those recently occupied by sea otters and 2) sites occupied by sea otters for >7 yrs, there was considerable variation both between sites and within the two groups. Nasparti Inlet for example, (estimated occupied by sea otters for 8 yrs) was in many cases more similar to otter-free sites than otter-occupied sites, at least in terms of encrusting coralline and invertebrate cover.

Sea urchins are known to influence the composition of epifaunal or encrusting assemblages (Karlson 1978, Vance 1979, Sebens 1986, reviewed in Harrold and Pearse 1987). As generalist grazers sea urchins can reduce the abundance of both fleshy algae and sessile epifauna (Sebens 1985, Karlson 1978). Crustose coralline algae often dominate areas where herbivores are abundant, in part because coralline algae require regular biological or physical disturbance to remain free of fouling organisms, and herbivores provide this disturbance (Steneck 1986). In the presence of urchin grazing horizontal rocky substrate is often dominated by encrusting coralline algae (*Lithothamnion* spp.). In the absence of urchin grazing, epifauna (or algae) often recruit to available substrate and may over-grow coralline crusts (Sebens 1986, Karlson 1978, Steneck 1986).

The percent cover of encrusting invertebrates appears to be a poor indicator of how long sea otters have occupied a site. This may be because kelp canopies can affect encrusting invertebrates in several ways. Since encrusting invertebrates can consume kelp-derived particulate matter increased kelp abundance may increase the growth rates of encrusting invertebrates (Duggins et al. 1989). Furthermore low light levels, beneath algal canopies may inhibit the growth of algae and favor bryozoan-dominated assemblages (Foster 1975b). Filter-feeders may further inhibit algal recruitment by preempting space and ingesting settling propagules (Foster 1975b). However, by reducing water motion understory kelps can increase sedimentation and diminish invertebrate

recruitment (Duggins 1988, Eckman et al. 1989, Duggins et al. 1990, Eckman and Duggins 1991), making the interaction between kelp and encrusting invertebrates difficult to predict.

### **Summary**

In this study the ages of different algal assemblages were determined. Their composition was compared and successional processes inferred. Algal assemblages were assumed to be a product of age, and site specific variation was controlled for by sampling and comparing shallow sublittoral assemblages at the same sites. The results suggest that in semi-exposed sites along northwestern Vancouver Island, chance events are most important in the early stages of algal succession, and that predictable algal assemblages appear to develop after a maximum of 7 yrs. Thus differences in the seasonality, frequency and intensity of sea otter foraging (Chapter 4) and avoidance responses in red urchins (Chapter 5) may have little effect on the long-term development of kelp forest communities in Checleset Bay.

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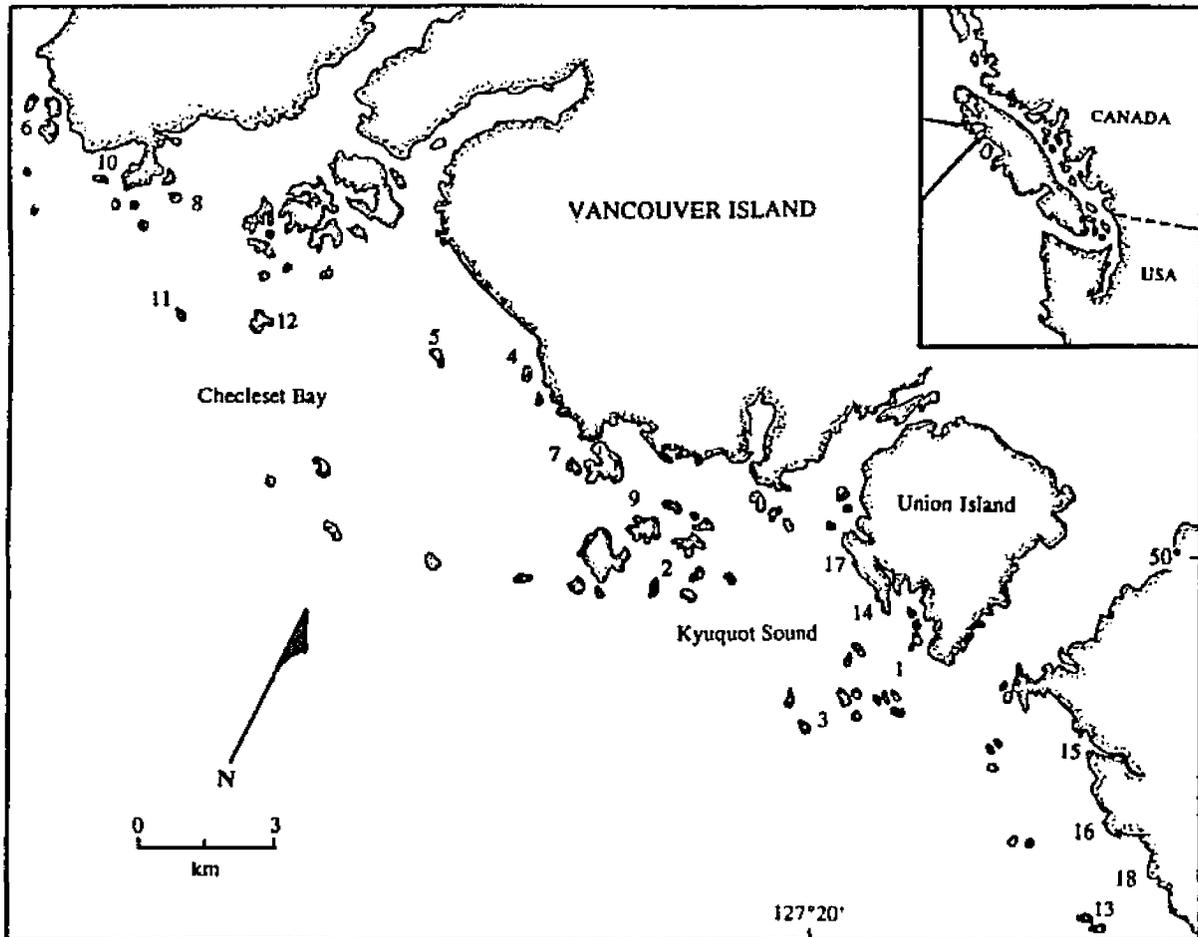
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**FIGURE 6.1** Map of Vancouver Island (inset) with expanded area showing the 18 study sites. Sites 3-4 yrs old: 1) Kyuquot Bay; 2) Polygon Is; 3) Moos Its. Sites 7-9 yrs old: 4) No Name Is; 5) Thomas Is; 6) Naspardi Inlet; 7) McLean Is; 8) Canoe Is; 9) Aktis Is; 10) Acous Pen. Sites 11-14+ yrs old: 11) Clara Its; 12) Gull Is. Sites without sea otters: 13) McQuarrie Its; 14) Raccoon Pt; 15) Kapoose Pt; 16) Brecciated Pt; 17) Union Is; 18) Gregoire Pt.

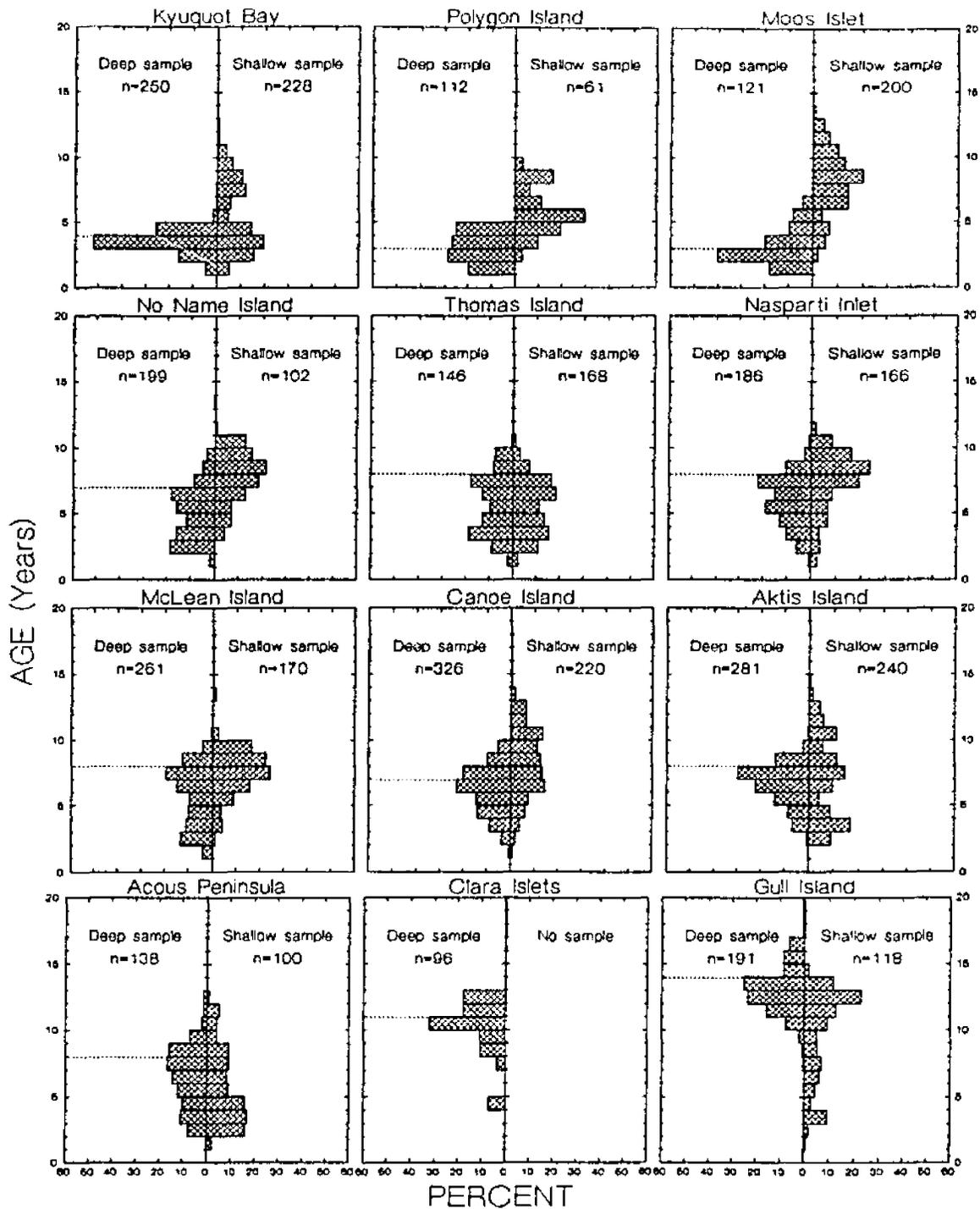
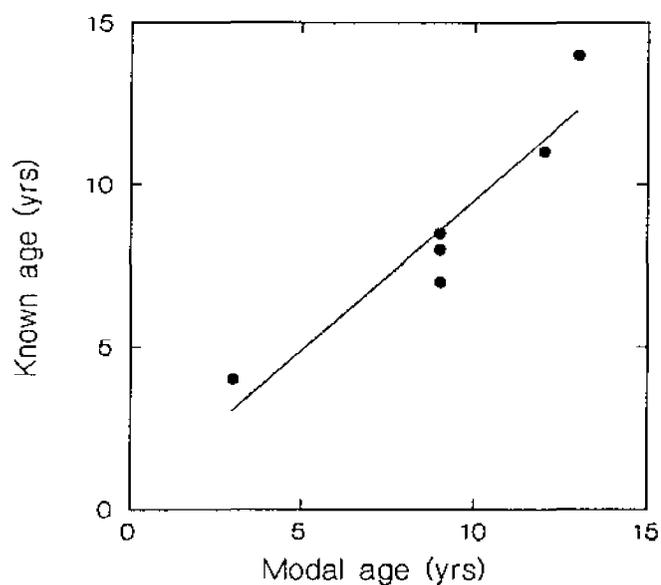
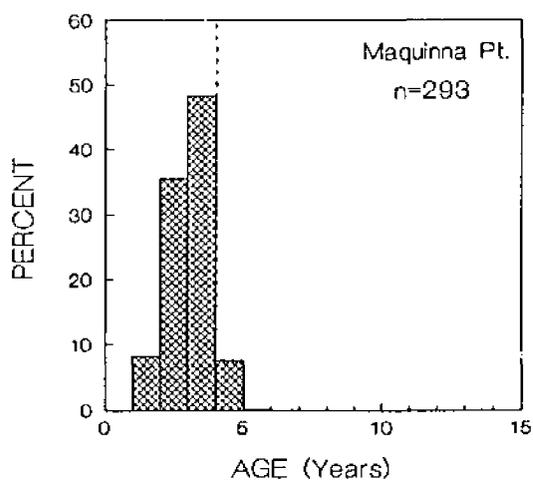


FIGURE 6.2 Age-frequency distributions of *P. californica* samples. Dotted line is the modal age of *P. californica* and estimated onset of sea otter foraging. Shallow and deep age distributions were significantly different at all sites (Kolmogorov Smirnov test  $P=0.001$ ), except Thomas Is. ( $P \geq 0.50$ ).



**FIGURE 6.3** Regression of expected age against modal age of *Pterygophora californica* at sites where the approximate time of arrival for sea otters is known ( $r^2=0.882$ , reject  $H_0: P=0$ ,  $t_{(0.05,2,6)}=5.56$ ,  $P<0.005$ ).



**FIGURE 6.4** Age-frequency distribution of *Pterygophora californica* at Maquinna Pt. in 1991. The site was occupied by sea otters in late 1988. Dotted line represents the onset of sea otter foraging as estimated by the modal age of *P. californica*.

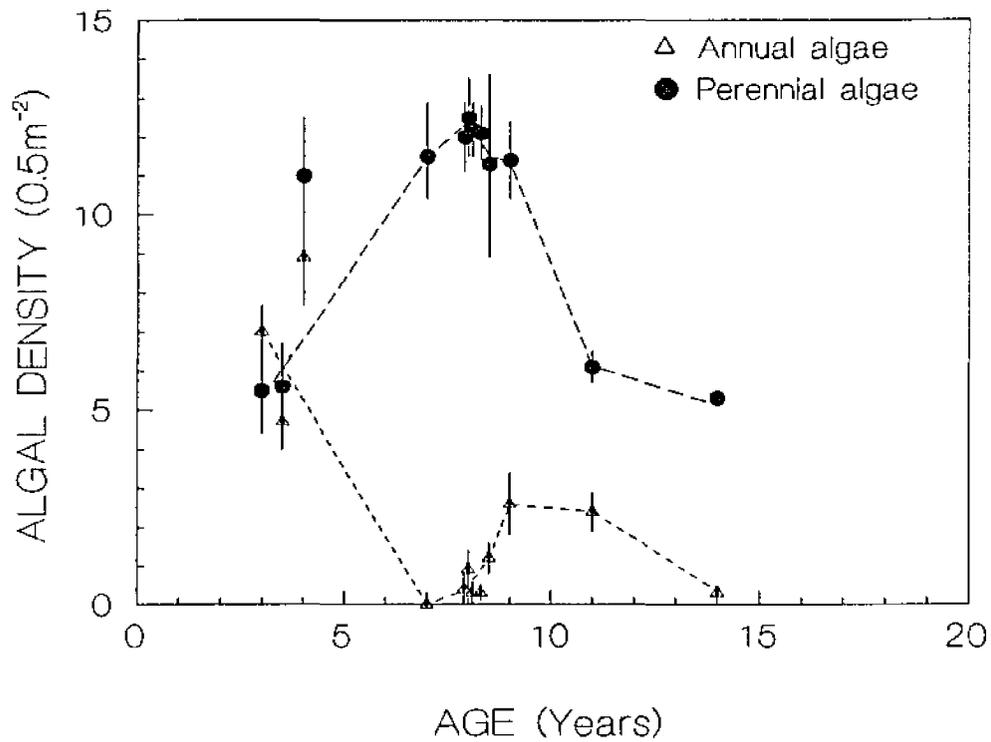


FIGURE 6.5 Mean algal density ( $\pm$  SE,  $n=30$ ) at 12 sites. The age of the site is the length of time the site has been occupied by sea otters as estimated from the modal age of the *P. californica* sample collected at that site. Line is a lowess best fit (Chambers et al. 1983). Points have been jittered to prevent overlap.

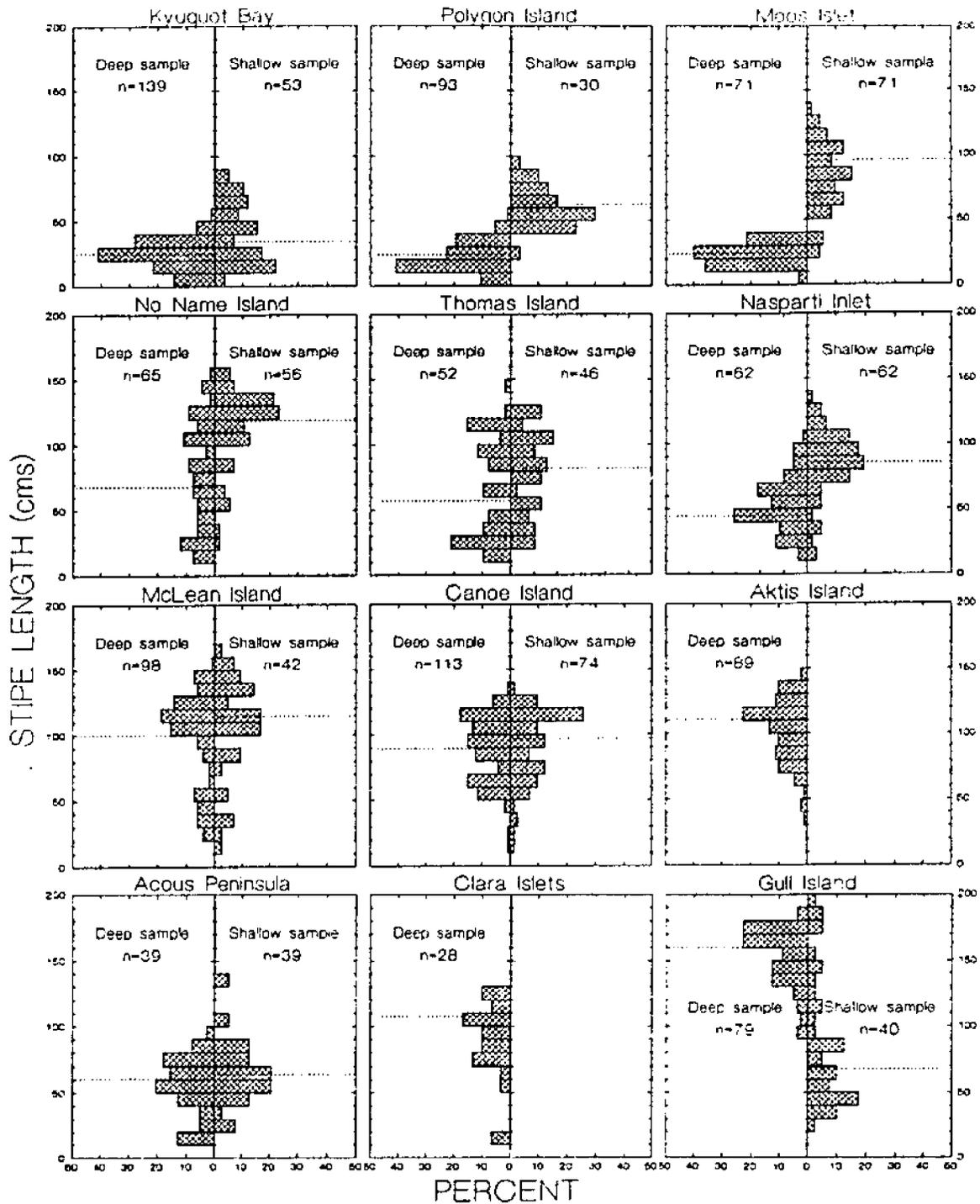
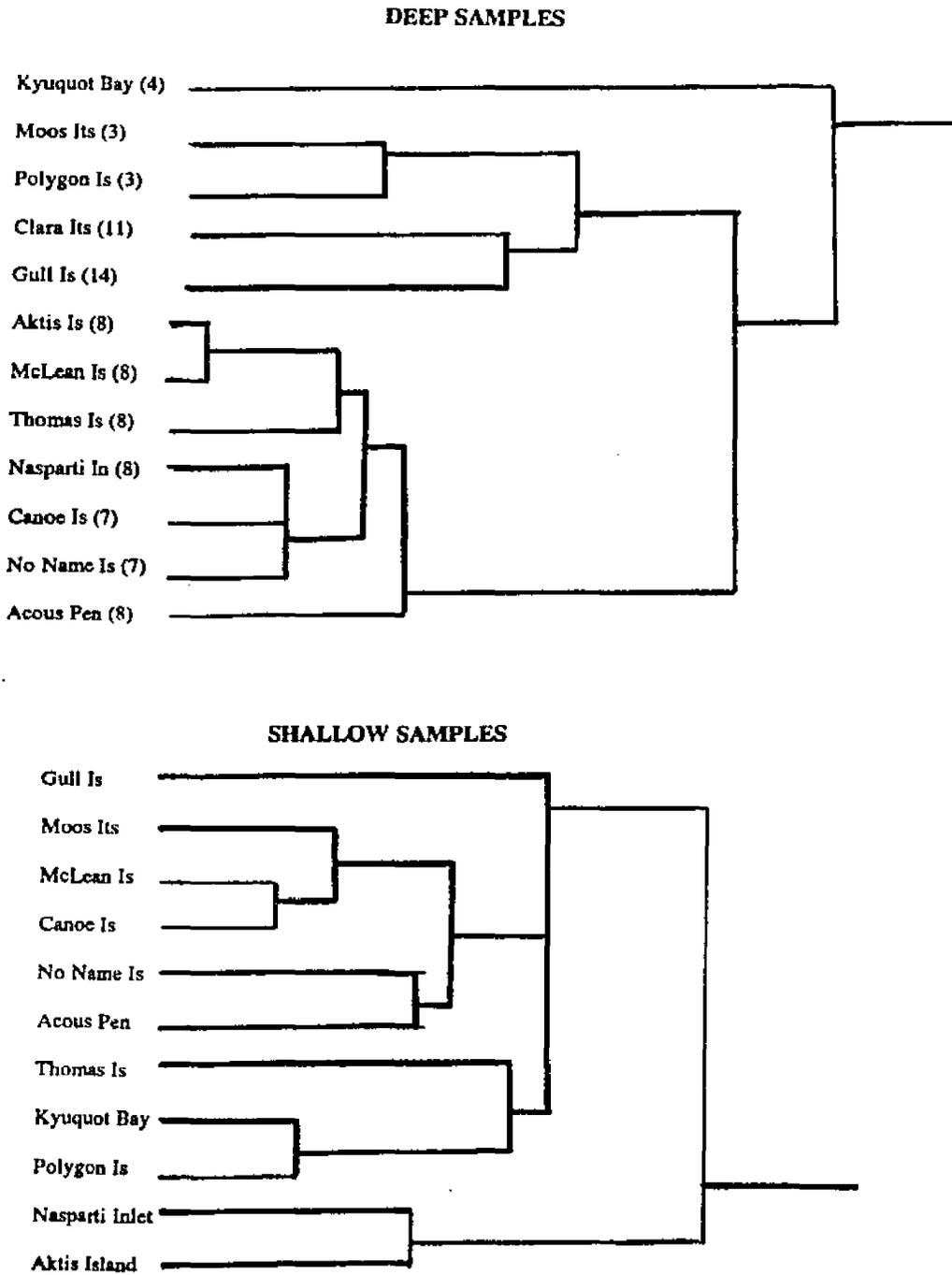
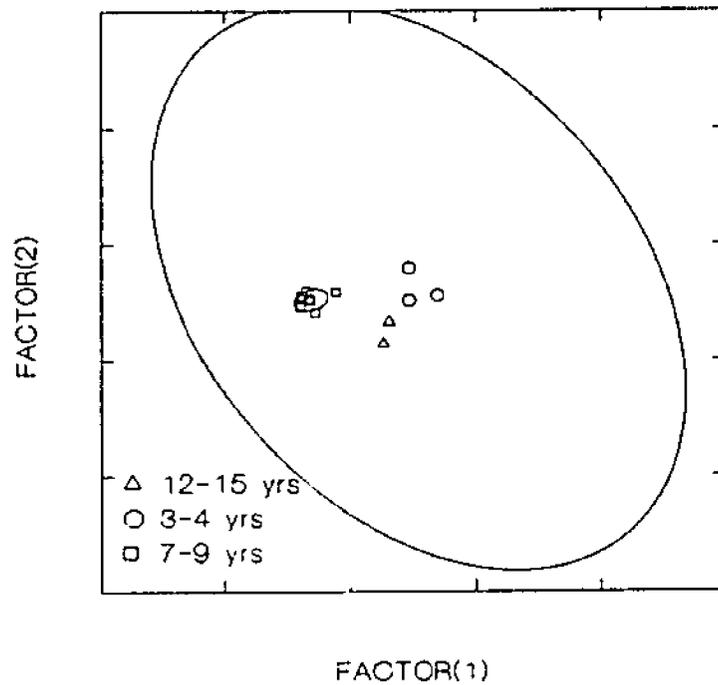


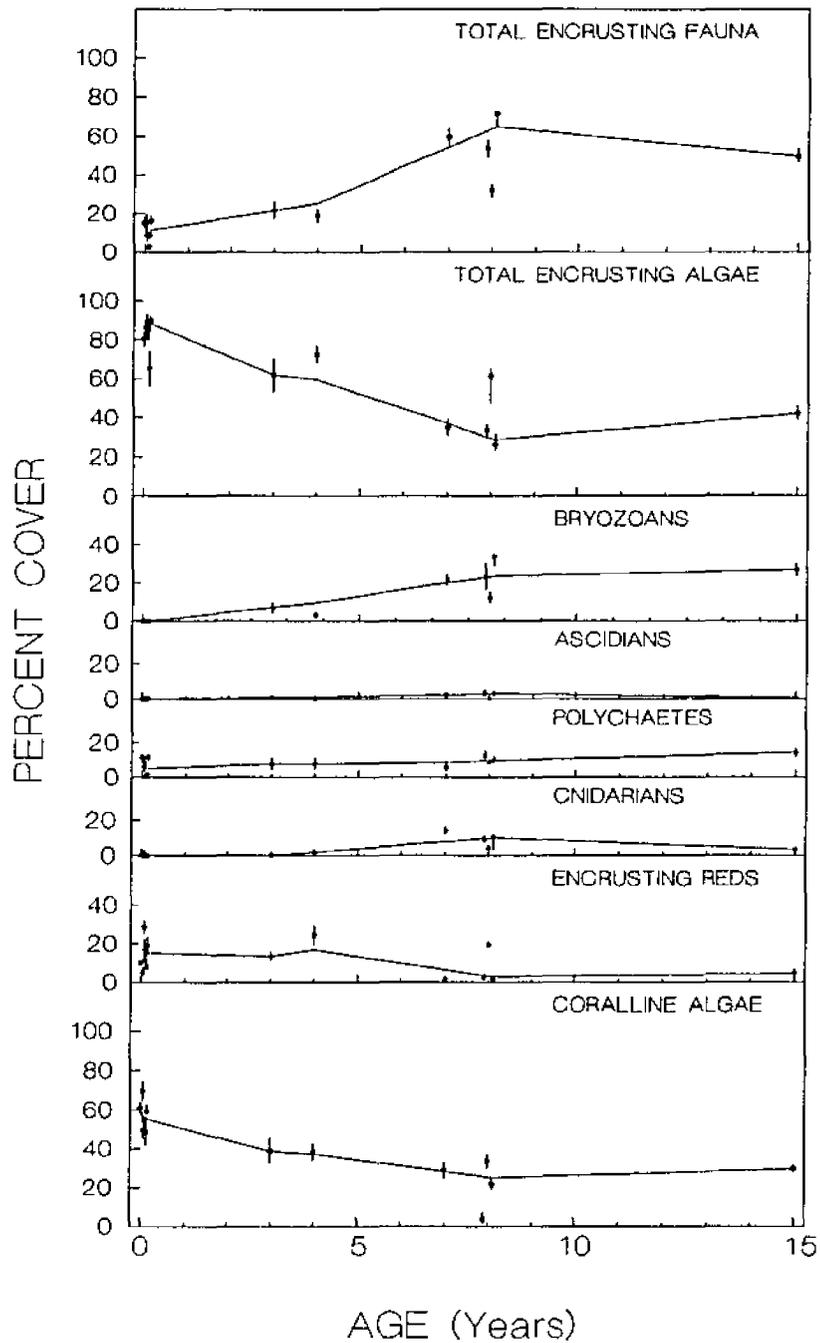
FIGURE 6.6 Stipe length frequency distributions of *Pterygophora californica* samples (n=10 quadrats). Dotted lines represent the median length.



**FIGURE 6.7** Cluster diagram of a) samples collected from 8-10 m below MLW b) samples collected from 3-5 m below MLW. Cluster is single linkage, Euclidean distance, according to perennial brown algal density, annual brown algal density and perennial biomass.



**FIGURE 6.8** Separation of the three deep sample groups defined by the cluster analysis, on the first two discriminant axes. Ellipses are 95% confidence limits, around the clusters.



**FIGURE 6.9** Mean percent cover of encrusting organisms by site age, the length of time sea otters have been present. Mean percent cover and SE ( $n=10$ ) were calculated on arcsin transformed data. Line is a lowess best fit (Chambers et al. 1983).

TABLE 6.1 Location of the sites where algal communities and/or encrusting assemblages were sampled.

Site No.	Site	Location	Otters	Sampling type
1	Kyuquot Bay	49° 58.1' N 127° 17.0' W	yes	algal assemblage
2	Polygon Is	49° 59.8' N 127° 23.9' W	yes	algal and encrusting assemblages
3	Moos Its	49° 57.4' N 127° 19.2' W	yes	algal assemblage
4	No Name Is	50° 03.6' N 127° 26.4' W	yes	algal and encrusting assemblages
5	Thomas Is	50° 03.8' N 127° 29.8' W	yes	algal assemblage
6	Nasparti Inlet	50° 06.9' N 127° 37.8' W	yes	algal and encrusting assemblages
7	McLean Is	50° 01.6' N 127° 26.0' W	yes	algal and encrusting assemblages
8	Canoe Is	50° 01.7' N 127° 34.9' W	yes	algal and encrusting assemblages
9	Aktis Is	50° 00.8' N 127° 24.0' W	yes	algal and encrusting assemblages
10	Acous Pen	50° 06.7' N 127° 37.2' W	yes	algal and encrusting assemblages
11	Clara Its	50° 04.2' N 127° 35.1' W	yes	algal assemblages
12	Gull Is	50° 04.0' N 127° 33.4' W	yes	algal and encrusting assemblages
13	McQuarrie Its	49° 55.0' N 127° 13.1' W	no	encrusting assemblage
14	Raccoon Pt	49° 59.8' N 127° 18.5' W	no	encrusting assemblage
15	Kapoose Pt	50° 55.6' N 127° 13.0' W	no	encrusting assemblage
16	Brecciated Pt	49° 59.8' N 127° 12.4' W	no	encrusting assemblage
17	Union Is	50° 00.0' N 127° 19.1' W	no	encrusting assemblage
18	Gregoire Pt	49° 58.2' N 127° 11.9' W	no	encrusting assemblage

TABLE 6.2 Categories, groups and orders used in the study of encrusting assemblages.

Category	Group or Order	Description
Encrusting invertebrates	Bryozoans	<i>Crisia</i> spp., <i>Heteropora</i> spp., <i>Dendrobeatia</i> spp., <i>Hippodiplosia</i> spp., <i>Costazia</i> spp., <i>Schizoporella</i> spp., <i>Bugula</i> spp., <i>Phidolopora labiata</i> , others.
Encrusting invertebrates	Ascidians	<i>Distaplia</i> spp., <i>Didemnum</i> spp., <i>Aplidium</i> spp., <i>Cystodytes lobatus</i> , <i>Pycnoclavella stanleyi</i> , <i>Styela</i> spp., others.
Encrusting invertebrates	Polychaetes	<i>Salmacina tribranchiata</i> , <i>Serpula vermicularis</i> , <i>Dodecaceria concharum</i> , others.
Encrusting invertebrates	Porifera	<i>Lissodendoryx</i> spp., <i>Halichondria</i> spp., <i>Haliclona</i> spp., others.
Encrusting invertebrates	Cnidarians	<i>Aglaophenia</i> spp., <i>Tubularia</i> spp., <i>Gersemia rubiformis</i> , <i>Obelia</i> spp., many others.
Encrusting algae	Encrusting algae; Corallines and encrusting reds	<i>Lithothamnion</i> spp., <i>Petrocelis</i> many others.
	Foliose algae	<i>Desmarestia</i> spp., "fuzzy" red algae, <i>Laurencia spectabilis</i> , others
	Substratum	Rock, cobble, sand

TABLE 6.3 Mean density  $\pm$  SE (n=30) of algal species 0.5m<sup>-2</sup> in samples collected 8-10 m below MLW. Age is the number of years sea otters have been present at the site as determined by the modal age of *Pterygophora californica* at that site.

Site	Age Yrs	<i>Desmarestia</i> spp.	<i>Nereocystis luetkeana</i>	<i>Costaria costata</i>	<i>Laminaria setchellii</i>	<i>Pterygophora californica</i>	<i>Macrocystis integrifolia</i>	Young Laminariales	Total annuals	Total perennials	Total algae
Kyuquot Bay	4	0.7 $\pm$ 0.2	7.4 $\pm$ 1.1	0.8 $\pm$ 0.2	2.1 $\pm$ 0.3	8.9 $\pm$ 1.4	0	0.1 $\pm$ 0.1	8.9 $\pm$ 1.2	11.0 $\pm$ 1.5	20.0 $\pm$ 1.5
Polygon Is.	3	3.0 $\pm$ 0.6	1.4 $\pm$ 0.4	0.3 $\pm$ 0.1	1.7 $\pm$ 0.3	3.8 $\pm$ 1.0	0.1 $\pm$ 0.0	0.6 $\pm$ 0.2	4.7 $\pm$ 0.7	5.6 $\pm$ 1.1	10.9 $\pm$ 2.0
Moos Its.	3	6.7 $\pm$ 0.7	0.3 $\pm$ 0.1	0	1.1 $\pm$ 0.2	4.4 $\pm$ 1.0	0	1.1 $\pm$ 0.5	7.0 $\pm$ 0.7	5.5 $\pm$ 1.1	13.6 $\pm$ 2.0
No Name Is.	7	0	0	0	2.2 $\pm$ 0.5	6.6 $\pm$ 0.6	2.7 $\pm$ 0.4	0.2 $\pm$ 0.1	0	11.5 $\pm$ 1.4	11.7 $\pm$ 1.4
Thomas Is.	8	1.1 $\pm$ 0.4	0	0.1 $\pm$ 0.1	5.6 $\pm$ 2.1	5.7 $\pm$ 0.8	0	0.5 $\pm$ 0.5	1.2 $\pm$ 0.4	11.3 $\pm$ 2.4	13.0 $\pm$ 0.8
Nasparti Inlet	8	0.9 $\pm$ 0.4	0	0	6.1 $\pm$ 0.8	6.4 $\pm$ 0.3	0	0.4 $\pm$ 0.2	0.9 $\pm$ 0.5	12.5 $\pm$ 1.0	13.8 $\pm$ 1.0
McLean Isl.	8	0.2 $\pm$ 0.2	0	0.1 $\pm$ 0.5	2.6 $\pm$ 0.5	9.6 $\pm$ 0.6	0	0.8 $\pm$ 0.2	0.3 $\pm$ 0.3	12.2 $\pm$ 0.7	13.3 $\pm$ 0.8
Canoe Is.	8	0.2 $\pm$ 0.1	0.1 $\pm$ 0.1	0.1 $\pm$ 0.1	0.7 $\pm$ 0.2	10.8 $\pm$ 0.8	0.5 $\pm$ 0.4	0.7 $\pm$ 0.3	0.4 $\pm$ 0.4	12.0 $\pm$ 0.9	13.1 $\pm$ 0.9
Aktis Is.	8	0.2 $\pm$ 0.2	0.1 $\pm$ 0.1	0	2.6 $\pm$ 0.4	9.3 $\pm$ 0.7	0.2 $\pm$ 0.1	1.3 $\pm$ 1.3	0.3 $\pm$ 0.2	12.1 $\pm$ 0.7	13.7 $\pm$ 1.6
Acous Pen.	9	2.4 $\pm$ 0.7	0	0.2 $\pm$ 0.1	6.4 $\pm$ 0.8	4.9 $\pm$ 0.6	0.1 $\pm$ 0.1	0.6 $\pm$ 0.5	2.6 $\pm$ 0.8	11.4 $\pm$ 1.0	14.6 $\pm$ 1.3
Clara Its	11	2.1 $\pm$ 0.5	0.2 $\pm$ 0.1	0.1 $\pm$ 0.1	4.5 $\pm$ 0.4	1.6 $\pm$ 0.2	0	0	2.4 $\pm$ 0.5	6.1 $\pm$ 0.4	8.5 $\pm$ 0.6
Gull Is.	14+	0.3 $\pm$ 0.2	0	0	0.1 $\pm$ 0.0	5.2 $\pm$ 0.2	0	0	0.3 $\pm$ 0.1	5.3 $\pm$ 0.2	5.6 $\pm$ 0.3

TABLE 6.4 Mean biomass (n=10)  $\pm$  SE (kg 0.5m<sup>-2</sup>) of perennial algae in samples collected 8-10 below MLW.

Site	Age	<i>Pterygophora</i> Biomass	<i>Laminaria</i> Biomass	Total stipitate biomass
Kyuquot Bay	4	0.72 $\pm$ 0.15	0	0.72 $\pm$ 0.02
Polygon Island	4	0.34 $\pm$ 0.11	0	0.34 $\pm$ 0.11
Moos Islets	3	0.10 $\pm$ 0.05	0.23 $\pm$ 0.01	0.35 $\pm$ 0.03
No Name Island	7	2.37 $\pm$ 0.65	0.05 $\pm$ 0.03	2.42 $\pm$ 0.67
Thomas Island	8	2.64 $\pm$ 0.29	2.07 $\pm$ 0.42	4.71 $\pm$ 0.52
Nasparti Inlet	8	2.30 $\pm$ 0.25	0.24 $\pm$ 0.01	2.54 $\pm$ 0.26
McLean Island	8	5.23 $\pm$ 0.88	0.19 $\pm$ 0.01	5.42 $\pm$ 0.86
Canoe Island	8	3.22 $\pm$ 0.47	0	3.22 $\pm$ 0.47
Aktis Island	8	5.55 $\pm$ 0.76	0.07 $\pm$ 0.003	5.62 $\pm$ 0.58
Acous Peninsula	9	1.85 $\pm$ 0.36	0.71 $\pm$ 0.22	2.56 $\pm$ 0.38
Clara Islets	12	1.91 $\pm$ 0.55	1.08 $\pm$ 0.19	2.99 $\pm$ 0.47
Gull Island	15+	5.05 $\pm$ 0.34	0	5.05 $\pm$ 0.58

TABLE 6.5 Mean algal density  $\pm$  SE (n=30) 0.5m<sup>-2</sup> in samples collected 3-5 m below MLW.

Site	<i>Desmarestia</i> sp.	<i>Nereocystis</i> <i>luetkeana</i>	<i>Costaria</i> <i>costata</i>	<i>Pleurophycus</i> <i>gardnerii</i>	<i>Eisenia</i> <i>arborea</i>	<i>Laminaria</i> <i>setchellii</i>	<i>Pterygophora</i> <i>californica</i>	<i>Macrocystis</i> <i>integrifolia</i>	Young Laminariales	Total annuals	Total perennials	Total algae
Kyuquot B	0.2 $\pm$ 0.1	0.3 $\pm$ 0.3	0.1 $\pm$ 0.1	0.1 $\pm$ 0.1	0	7.5 $\pm$ 0.8	8.9 $\pm$ 1.2	0	0	0.6 $\pm$ 0.3	16.5 $\pm$ 1.3	17.1 $\pm$ 1.4
Polygon Is.	0.2 $\pm$ 0.1	0.1 $\pm$ 0.1	0.6 $\pm$ 0.5	0	0	15.1 $\pm$ 1.3	2.3 $\pm$ 0.4	0	0	0.9 $\pm$ 0.3	17.4 $\pm$ 3.2	18.5 $\pm$ 1.3
Moos Its.	0	0	0	0	0	3.6 $\pm$ 0.6	6.5 $\pm$ 0.6	0	0	0	10.1 $\pm$ 0.7	10.1 $\pm$ 0.7
No Name	0	0	0	0	0	6.6 $\pm$ 1.0	3.4 $\pm$ 0.2	0	0	0	10.0 $\pm$ 0.8	10.0 $\pm$ 0.8
Thomas Is.	0.9 $\pm$ 0.3	0.1 $\pm$ 0.1	0	0	0	8.7 $\pm$ 0.6	5.4 $\pm$ 0.4	0	0	1.0 $\pm$ 0.3	14.1 $\pm$ 0.6	15.1 $\pm$ 0.7
Nasparti In	1.6 $\pm$ 0.8	0.1 $\pm$ 0.1	0	0	1.5 $\pm$ 0.5	4.5 $\pm$ 0.7	5.5 $\pm$ 0.5	2.4 $\pm$ 0.7	0	1.6 $\pm$ 0.8	15.9 $\pm$ 0.6	17.6 $\pm$ 1.0
McLean Is.	0.6 $\pm$ 0.3	0	0	0	0	4.0 $\pm$ 0.7	5.5 $\pm$ 0.6	0	0	0.6 $\pm$ 0.3	9.5 $\pm$ 0.7	10.1 $\pm$ 0.6
Canoe Is.	1.1 $\pm$ 0.4	0	0	0	0	1.5 $\pm$ 0.3	7.3 $\pm$ 0.6	0	0	1.1 $\pm$ 0.4	8.8 $\pm$ 0.6	9.9 $\pm$ 0.7
Aktis Is.	0.3 $\pm$ 0.2	0	0	0.3 $\pm$ 0.1	0	6.0 $\pm$ 0.8	8.0 $\pm$ 1.3	0	0.1 $\pm$ 0.1	0.3 $\pm$ 0.2	14.3 $\pm$ 1.3	14.7 $\pm$ 1.2
Acous Pen.	1.1 $\pm$ 0.5	0	0	0	0	7.7 $\pm$ 1.0	3.3 $\pm$ 0.3	0.6 $\pm$ 0.5	0	1.1 $\pm$ 0.5	11.6 $\pm$ 1.0	12.7 $\pm$ 1.2
Clara Its	NA	NA	NA	NA	0	NA	NA	NA	NA	NA	NA	NA
Gull Is.	3.8 $\pm$ 1.3	0	0	0.4 $\pm$ 0.2	1.1 $\pm$ 0.3	2.7 $\pm$ 0.4	3.8 $\pm$ 0.4	0	0	3.8 $\pm$ 1.3	8.1 $\pm$ 0.5	11.9 $\pm$ 1.4

TABLE 6.6 Mean biomass (n=10)  $\pm$  SE (kg 0.5m<sup>-2</sup>) of perennial algae in samples collected sites 3-5 below MLW.

Site	<i>Pterygophora</i> Biomass	<i>Laminaria</i> Biomass	Total stipitate biomass
Kyuquot Bay	1.90 $\pm$ 0.61	1.24 $\pm$ 1.13	3.13 $\pm$ 0.20
Polygon Island	1.91 $\pm$ 0.94	1.71 $\pm$ 0.79	3.62 $\pm$ 0.99
Moos Islets	5.71 $\pm$ 2.67	1.50 $\pm$ 1.06	7.21 $\pm$ 2.36
No Name Island	3.23 $\pm$ 1.45	0.37 $\pm$ 0.55	3.60 $\pm$ 1.45
Thomas Island	3.16 $\pm$ 1.63	2.09 $\pm$ 1.09	5.25 $\pm$ 2.01
Nasparti Inlet	7.37 $\pm$ 3.01	1.92 $\pm$ 1.26	9.29 $\pm$ 3.32
McLean Island	4.43 $\pm$ 3.43	1.19 $\pm$ 1.04	6.05 $\pm$ 3.41
Canoe Island	6.30 $\pm$ 2.23	0.22 $\pm$ 0.26	6.53 $\pm$ 2.07
Aktis Island	8.45 $\pm$ 3.62	1.49 $\pm$ 1.21	9.94 $\pm$ 3.65
Acous Peninsula	2.18 $\pm$ 1.82	0.56 $\pm$ 0.34	2.74 $\pm$ 2.01
Clara Islets	NA	NA	NA
Gull Island	3.52 $\pm$ 1.54	0.50 $\pm$ 0.73	4.32 $\pm$ 2.25

TABLE 6.7. Summary of Tukey multiple comparison test of encrusting coralline algae cover. Matrix of pairwise probabilities. Asterix are sites that are notably different, and did not fit apriori expectations.

Age	Site	8 McLean	8 Canoe	15 Gull	8 Nasparti	7 NoName	4 Polygon	3 Moos	3 Kyuquot	0 Kapoose	0 Brecciated	0 McQuarrie	0 Raccoon	0 Union A.
8	McLean	1.00												
8	Canoe	0.69	1.00											
15	Gull	1.00	0.99	1.00										
8	Nasparti	0.00	0.49	0.05*	1.00									
7	No Name	1.00	0.99	1.00	0.05*	1.00								
4	Polygon	0	0.01	0	0.96	0.03	1.00							
3	Moos Its	0	0.04	0.02	1.00	0	0.98	1.00						
4	Kyuquot	0	0	0	0.30	0.01	0.99	0.36	1.00					
0	Kapoose	0	0.04	0.00	1.00	0	1.00	1.00	0.72	1.00				
0	Brecciated	0	0.00	0	0.87*	0	1.00	0.91	1.00	0.99	1.00			
0	McQuarrie	0	0	0	0.05	0	0.87	0.06	1.00	0.23	0.95	1.00		
0	Raccoon	0	0	0	0.00	0	0.40	0.06	0.98	0.03*	0.58	1.00	1.00	
0	Union A	0	0	0	0.01	0	0.51	0.01*	0.99	0.06	0.70	1.00	1.00	1.00
0	Union B	0	0	0	0.10*	0	0.95	0.13	1.00	0.37	0.98	1.00	1.00	1.00

TABLE 6.8 Summary of Tukey multiple comparison test of encrusting invertebrate cover. Matrix of pairwise probabilities.

Age	Site	8 McLean	8 Canoe	15 Gull	8 Nasparti	7 NoName	4 Polygon	3 Moos	3 Kyuquot	0 Kapoose	0 Brecciated	0 McQuarrie	0 Raccoon	0 Union A.
8	McLean	1.00												
8	Canoe	0.20	1.00											
15	Gull	0.47	1.00	1.00										
8	Nasparti	0	0.09	0.06	1.00									
7	No Name	0.97	0.98	1.00	0	1.00								
4	Polygon	0	0	0	0.47	0	1.00							
3	Moos Its	0	0	0	0.85	0	1.00	1.00						
4	Kyuquot	0	0	0	0.08	0	1.00	0.98	1.00					
0	Kapoose	0	0	0	0	0	0.45	0.13	0.93	1.00				
0	Brecciated	0	0	0	0.99	0	0.99	1.00	0.74	0.02	1.00			
0	McQuarrie	0	0	0	0	0	1.00	1.00	0.01	0.61	0	1.00		
0	Raccoon	0	0	0	0.17	0	1.00	0.99	1.00	0.82	0.89	0.03	1.00	
0	Union A	0	0	0	0	0	0.48	0.15	0.90	1.00	0.02	0.58	0.84	1.00
0	Union B	0	0	0	0.06	0	1.00	0.98	1.00	0.95	0.7	0.01	1.00	0.96

APPENDIX 1.1. Wizard Islet. Mean density 20 m<sup>-2</sup> ± SE (n=5) of algae and invertebrate species.

	Mean / 20 m <sup>2</sup> ± SE				
	1987	1988	1989	1990	1991
<i>Pterygophora californica</i>	3.0 ± 3.0	2.6 ± 2.6	1.2 ± 1.2	9.0 ± 8.9	22.8 ± 22.8
<i>Laminaria</i> spp.	1.3 ± 1.3	0	4.8 ± 4.8	3.2 ± 3.2	2.8 ± 2.8
<i>Desmarestia</i> spp.	0	0	0	0	0
<i>Macrocystis integrifolia</i>	2.4 ± 2.4	0	11.2 ± 11.2	11.2 ± 11.2	7.8 ± 3.5
<i>Nereocystis luetkeana</i>	0	1.0 ± 0.8	6.8 ± 6.8	0	0
<i>Costaria costata</i>	0	0	0	0	0
Young Laminariales	0	0	4.8 ± 4.8	6.1 ± 2.7	0
<i>Dermasterias imbricata</i>	0.4 ± 0.2	0.8 ± 1.0	1.0 ± 0.8	5.6 ± 1.6	0.8 ± 0.6
<i>Pycnopodia helianthoides</i>	1.0 ± 0.6	0.2 ± 0.2	2.4 ± 1.1	2.8 ± 0.7	1.6 ± 0.8
<i>Henricia</i> spp.	0.6 ± 0.2	0.4 ± 0.2	0.8 ± 0.4	2.4 ± 0.7	3.0 ± 0.9
<i>Astraea gibberosa</i>	3.6 ± 2.0	11.6 ± 7.6	18.2 ± 6.7	33.2 ± 7.7	18.8 ± 4.7
<i>Haliotis kamtschatkana</i>	0.2 ± 0.2	0.4 ± 0.2	0.4 ± 0.2	1.8 ± 0.8	1.2 ± 0.6
<i>Strongylocentrotus franciscanus</i>	108.4 ± 23.1	123.4 ± 23.4	107.0 ± 26.2	116.4 ± 20.3	97.0 ± 30.8
<i>Parastichopus californicus</i>	3.2 ± 1.7	3.0 ± 1.5	7.0 ± 1.7	6.0 ± 2.8	8.8 ± 2.2
<i>Cucumaria miniata</i>	0	0	0	0	0

APPENDIX 1.2 Taylor Islet Permanent Site. Mean density 20 m<sup>-2</sup> ± SE (n=5) of algae and invertebrate species.

	Mean / 20 m <sup>2</sup> ± SE				
	1987	1988	1989	1990	1991
<i>Pterygophora californica</i>	0	0	1.0 ± 1.0	0	x
<i>Laminaria</i> spp.	0	0	0	0	x
<i>Desmarestia</i> spp.	1.0 ± 1.0	0	0.8 ± 0.8	0	x
<i>Macrocystis integrifolia</i>	0	0	0	0	x
<i>Nereocystis luetkeana</i>	0.6 ± 0.6	0.8 ± 3.7	4.6 ± 4.16	0	x
<i>Costaria costata</i>	0	0	0	0.2 ± 0.1	x
Young Laminariales	0.8 ± 0.8	5.6 ± 2.5	0	0	x
<i>Dermasterias imbricata</i>	0.8 ± 0.5	1.0 ± 0.4	0.6 ± 0.4	0.2 ± 0.2	x
<i>Pycnopodia helianthoides</i>	0.6 ± 0.4	0	0.2 ± 0.2	0	x
<i>Henricia</i> spp.	0	0	0.6 ± 0.4	0	x
<i>Astraea gibberosa</i>	3.6 ± 2.0	2.6 ± 1.3	1.0 ± 0.4	6.0 ± 2.4	x
<i>Haliotis kamtschatkana</i>	4.0 ± 0.9	4.6 ± 2.4	5.4 ± 2.0	3.4 ± 1.5	x
<i>Strongylocentrotus franciscanus</i>	60.6 ± 12.0	73.0 ± 10.1	69.8 ± 17.3	90.8 ± 17.5	x
<i>Parastichopus californicus</i>	0.2 ± 0.2	0.2 ± 0.2	0.6 ± 0.2	1.2 ± 0.4	x
<i>Cucumaria miniata</i>	0	0	0	0	x

APPENDIX 1.3 Gull Island Permanent Site. Mean density  $20 \text{ m}^{-2} \pm \text{SE}$  (n=5) of algae and invertebrate species.

	Mean / $20 \text{ m}^2 \pm \text{SE}$			
	1988	1989	1990	1991
<i>Pterygophora californica</i>	93.6 $\pm$ 4.5	82.8 $\pm$ 2.1	79.6 $\pm$ 3.3	81.0 $\pm$ 3.7
<i>Laminaria</i> spp.	47.8 $\pm$ 9.6	58.0 $\pm$ 8.1	55.2 $\pm$ 15.7	41.2 $\pm$ 9.4
<i>Desmarestia</i> spp.	24.0 $\pm$ 16.7	78.8 $\pm$ 25.4	30.0 $\pm$ 20.0	12.8 $\pm$ 9.3
<i>Macrocystis integrifolia</i>	0	0	0	0
Young Laminariales	0	0	0	0
<i>Dermasterias imbricata</i>	1.2 $\pm$ 0.6	1.0 $\pm$ 0.6	3.4 $\pm$ 1.2	4.2 $\pm$ 0.6
<i>Pycnopodia helianthoides</i>	1.6 $\pm$ 0.6	2.2 $\pm$ 0.6	2.2 $\pm$ 0.7	2.4 $\pm$ 1.0
<i>Henricia</i> spp.	8.8 $\pm$ 1.0	7.6 $\pm$ 2.9	8.7 $\pm$ 1.7	4.2 $\pm$ 1.2
<i>Astraea gibberosa</i>	0.2 $\pm$ 0.2	0	3.4 $\pm$ 0.8	2.0 $\pm$ 1.5
<i>Strongylocentrotus franciscanus</i>	0.2 $\pm$ 0.5	0.6 $\pm$ 0.4	0	1.8 $\pm$ 0.6

APPENDIX 1.4. No Name Island Permanent Site. Mean density  $\pm$  SE 20 m<sup>2</sup> (n=5) of algae and invertebrate species.

	Mean / 20 m <sup>2</sup> $\pm$ SE			
	1988	1989	1990	1991
<i>Pterygophora californica</i>	202.6 $\pm$ 58.1	151.6 $\pm$ 27.2	125.4 $\pm$ 25.2	103.2 $\pm$ 15.0
<i>Laminaria</i> spp.	22.1 $\pm$ 17.6	68.4 $\pm$ 23.5	17.6 $\pm$ 2.2	14.0 $\pm$ 5.6
<i>Desmarestia</i> spp.	5.2 $\pm$ 4.5	1.4 $\pm$ 1.0	0.4 $\pm$ 0.4	0
<i>Macrocystis integrifolia</i>	63.0 $\pm$ 18.2	99.0 $\pm$ 29.1	83.6 $\pm$ 30.4	98.6 $\pm$ 58.1
Young Laminariales	13.6 $\pm$ 4.2	10.6 $\pm$ 5.2	2.0 $\pm$ 0.2	0
<i>Dermasterias imbricata</i>	1.2 $\pm$ 0.7	3.2 $\pm$ 1.7	1.0 $\pm$ 0.6	1.8 $\pm$ 0.4
<i>Pycnopodia helianthoides</i>	1.2 $\pm$ 0.5	1.0 $\pm$ 0.3	3.0 $\pm$ 1.5	1.4 $\pm$ 0.7
<i>Henricia</i> spp.	6.2 $\pm$ 1.6	4.8 $\pm$ 1.2	5.4 $\pm$ 0.7	4.2 $\pm$ 1.8
<i>Astraea gibberosa</i>	2.6 $\pm$ 1.3	7.6 $\pm$ 2.2	9.0 $\pm$ 4.2	10.8 $\pm$ 6.7
<i>Strongylocentrotus franciscanus</i>	0	4.2 $\pm$ 0.6	0	0.2 $\pm$ 0.1

APPENDIX 1.5. Kamils Anchorage Permanent Site. Mean density  $\pm$  SE 20 m<sup>2</sup> (n=5) of algae and invertebrate species.

	Mean / 20 m <sup>2</sup> $\pm$ SE				
	1987	1988	1989	1990	1991
<i>Pterygophora californica</i>	0	5.2 $\pm$ 4.2	16.8 $\pm$ 8.2	24.4 $\pm$ 11.0	23.6 $\pm$ 8.2
<i>Laminaria</i> spp.	0	30.0 $\pm$ 18.1	68.6 $\pm$ 39.0	95.6 $\pm$ 25.3	66.8 $\pm$ 23.1
<i>Desmarestia</i> spp.	0	84.2 $\pm$ 32.3	116.8 $\pm$ 47.2	5.8 $\pm$ 4.4	13.4 $\pm$ 8.4
<i>Macrocystis integrifolia</i>	0	16.4 $\pm$ 7.3	51.2 $\pm$ 26.2	92.0 $\pm$ 23.8	38.8 $\pm$ 14.2
<i>Nereocystis luetkeana</i>	0.2 $\pm$ 0.2	113.0 $\pm$ 44.4	52.8 $\pm$ 14.0	0.8 $\pm$ 0.6	0
<i>Costaria costata</i>	0	7.0 $\pm$ 4.6	17.2 $\pm$ 7.3	4.6 $\pm$ 3.0	2.8 $\pm$ 1.3
Young Laminariales	0	27.4 $\pm$ 20.5	15.8 $\pm$ 52.7	0.4 $\pm$ 0.2	9.0 $\pm$ 5.5
<i>Dermasterias imbricata</i>	0	0	0.6 $\pm$ 0.4	0	0.8 $\pm$ 0.6
<i>Pycnopodia helianthoides</i>	0.8 $\pm$ 0.6	0.4 $\pm$ 0.2	0.4 $\pm$ 0.4	0.6 $\pm$ 0.4	1.4 $\pm$ 0.4
<i>Henricia</i> spp.	0.6 $\pm$ 0.4	1.4 $\pm$ 0.4	1.6 $\pm$ 0.4	1.4 $\pm$ 0.8	2.0 $\pm$ 0.7
<i>Astraea gibberosa</i>	6.6 $\pm$ 5.1	34.6 $\pm$ 14.4	40.4 $\pm$ 33.4	3.4 $\pm$ 1.5	17.2 $\pm$ 9.3
<i>Haliotis kamtschatkana</i>	0.8 $\pm$ 0.3	0	0.2 $\pm$ 0.2	0.2 $\pm$ 0.2	0.6 $\pm$ 0.4
<i>Strongylocentrotus franciscanus</i>	146.8 $\pm$ 7.6	109.8 $\pm$ 47.2	3.2 $\pm$ 2.3	0.2 $\pm$ 0.2	0.2 $\pm$ 0.2
<i>Parastichopus californicus</i>	0.6 $\pm$ 0.5	0	0.2 $\pm$ 0.2	0	0.6 $\pm$ 0.4
<i>Cucumaria miniata</i>	0	0	0	0	0

APPENDIX 1.6. Union Island Permanent Site. Mean density  $\pm$  SE 20 m<sup>-2</sup> (n=5) of algae and invertebrate species.

	Mean / 20 m <sup>2</sup> $\pm$ SE			
	1988	1989	1990	1991
<i>Pterygophora californica</i>	0	0	14.0 $\pm$ 6.3	52.8 $\pm$ 22.1
<i>Laminaria</i> spp.	0	0.2 $\pm$ 0.2	32.0 $\pm$ 14.3	32.2 $\pm$ 13.7
<i>Desmarestia</i> spp.	1.4 $\pm$ 1.0	6.4 $\pm$ 4.8	39.6 $\pm$ 2.2	40.6 $\pm$ 10.5
<i>Macrocystis integrifolia</i>	0	0.8 $\pm$ 1.2	1.2 $\pm$ 0.6	7.8 $\pm$ 5.1
<i>Nereocystis luetkeana</i>	0	4.2 $\pm$ 3.3	159.4 $\pm$ 24.2	64.2 $\pm$ 18.3
<i>Costaria costata</i>	0	2.0 $\pm$ 2.0	10.4 $\pm$ 8.2	0
Young Laminariales	0	0.4 $\pm$ 0.4	17.0 $\pm$ 6.2	6.4 $\pm$ 5.9
<i>Dermasterias imbricata</i>	0	0	0	0
<i>Pycnopodia helianthoides</i>	0.8 $\pm$ 0.4	0.4 $\pm$ 0.2	0.4 $\pm$ 0.2	0.2 $\pm$ 0.2
<i>Henricia</i> spp.	2.6 $\pm$ 0.9	1.2 $\pm$ 0.6	1.0 $\pm$ 0.5	1.4 $\pm$ 0.8
<i>Astraea gibberosa</i>	20.2 $\pm$ 9.0	26.6 $\pm$ 8.0	4.4 $\pm$ 2.4	15.4 $\pm$ 4.8
<i>Haliotis kamtschatkana</i>	1.4 $\pm$ 0.6	0.4 $\pm$ 0.2	0.2 $\pm$ 0.2	0.8 $\pm$ 0.4
<i>Strongylocentrotus franciscanus</i>	110.2 $\pm$ 10.5	143.4 $\pm$ 25.0	0.6 $\pm$ 0.4	1.4 $\pm$ 0.5
<i>Parastichopus californicus</i>	0.8 $\pm$ 0.4	1.2 $\pm$ 0.4	0	0
<i>Cucumaria miniata</i>	0	0	0	0

APPENDIX 1.7. Maquinna Point Permanent Site. Mean density  $\pm$  SE 20 m<sup>-2</sup> (n=5) of algae and invertebrate species.

	Mean / 20 m <sup>2</sup> $\pm$ SE				
	1987	1988	1989	1990	1991
<i>Pterygophora californica</i>	0	0	197.6 $\pm$ 119.8	370.2 $\pm$ 87.6	320.8 $\pm$ 94.0
<i>Laminaria</i> spp.	0	2.4 $\pm$ 2.4	12.6 $\pm$ 8.1	238.8 $\pm$ 77.0	285.2 $\pm$ 47.5
<i>Desmarestia</i> spp.	0	0	0	0	0
<i>Macrocystis integrifolia</i>	0	0	0	0	0
<i>Nereocystis luetkeana</i>	0	0	42.0 $\pm$ 4.6	31.4 $\pm$ 3.8	1.0 $\pm$ 0.4
<i>Costaria costata</i>	0	0	0	0	0
Young Laminariales	0	0	48.2 $\pm$ 46.2	0	0
<i>Dermasterias imbricata</i>	0.2 $\pm$ 0.2	0	0	0.2 $\pm$ 0.2	0.6 $\pm$ 0.4
<i>Pycnopodia helianthoides</i>	2.4 $\pm$ 0.2	4.8 $\pm$ 1.0	1.6 $\pm$ 0.4	3.0 $\pm$ 0.3	1.4 $\pm$ 0.5
<i>Henricia</i> spp.	3.2 $\pm$ 1.1	7.2 $\pm$ 2.2	3.2 $\pm$ 1.4	2.0 $\pm$ 0.6	2.8 $\pm$ 0.8
<i>Astraea gibberosa</i>	1.4 $\pm$ 0.4	0	0	0	0.2 $\pm$ 0.2
<i>Haliotis kamtschatkana</i>	1.2 $\pm$ 0.6	0.2 $\pm$ 0.2	0	0	0
<i>Strongylocentrotus franciscanus</i>	182.8 $\pm$ 22.3	256.0 $\pm$ 36.8	0.2 $\pm$ 0.2	0	0
<i>Parastichopus californicus</i>	1.4 $\pm$ 0.6	0.2 $\pm$ 0.2	0	0	0
<i>Cucumaria miniata</i>	0	0	0	0	0

APPENDIX 1.8. Kyuquot Bay Permanent Site. Mean density  $\pm$  SE 20 m<sup>2</sup> (n=5) of algae and invertebrate species.

	Mean / 20 m <sup>2</sup> $\pm$ SE			
	1988	1989	1990	1991
<i>Pterygophora californica</i>	0	18.0 $\pm$ 8.7	14.4 $\pm$ 11.5	97.6 $\pm$ 42.4
<i>Laminaria</i> spp.	0.4 $\pm$ 0.4	2.2 $\pm$ 2.0	5.8 $\pm$ 3.0	21.4 $\pm$ 13.9
<i>Desmarestia</i> spp.	0	36.2 $\pm$ 15.1	37.2 $\pm$ 22.8	39.0 $\pm$ 21.7
<i>Macrocystis integrifolia</i>	0	0	0	0
<i>Nereocystis luetkeana</i>	0.6 $\pm$ 0.6	24.6 $\pm$ 10.7	25.4 $\pm$ 13.2	54.8 $\pm$ 26.4
<i>Costaria costata</i>	0.8 $\pm$ 0.8	13.4 $\pm$ 8.1	8.8 $\pm$ 4.6	6.8 $\pm$ 4.2
Young Laminariales	0	5.2 $\pm$ 3.5	0	0
<i>Dermasterias imbricata</i>	3.0 $\pm$ 2.1	0.6 $\pm$ 0.2	0.6 $\pm$ 0.4	0.2 $\pm$ 0.2
<i>Pycnopodia helianthoides</i>	1.0 $\pm$ 0.3	0.2 $\pm$ 0.2	0.4 $\pm$ 0.2	0.4 $\pm$ 0.3
<i>Henricia</i> spp.	6.0 $\pm$ 1.4	3.4 $\pm$ 0.7	3.2 $\pm$ 0.6	2.2 $\pm$ 0.5
<i>Astraea gibberosa</i>	8.0 $\pm$ 2.8	42.0 $\pm$ 1.5	0	0.8 $\pm$ 0.6
<i>Haliotis kamschatkana</i>	19.4 $\pm$ 5.0	7.2 $\pm$ 2.5	4.4 $\pm$ 1.0	11.8 $\pm$ 1.5
<i>Strongylocentrotus franciscanus</i>	275.4 $\pm$ 37.1	218.2 $\pm$ 38.4	275.6 $\pm$ 94.0	269.6 $\pm$ 80.4
<i>Parastichopus californicus</i>	0.6 $\pm$ 0.4	0.6 $\pm$ 0.2	0.2 $\pm$ 0.2	0
<i>Cucumaria miniata</i>	35.0 $\pm$ 18.9	14.8 $\pm$ 7.4	11.8 $\pm$ 5.6	0