Checleset Bay
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ECOLOGICAL RESERVES COLLECTION
GOVERNMENT OF BRITISH COLUMBIA
VICTORIA, B.C.
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Sea Otter Foraging, its Effects on Community Structure and Temporal Variability

Report submitted to: Ecological Reserves, B.C. Ministry of Parks, 800 Johnson Street, Victoria, B.C.

Report submitted by: Jane Watson,
P.O. Box 216, Stn. A,
Nanaimo, B.C.
V9R 5K9

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Abstract

This study reports the first direct quantitative observations on the effects of sea otter foraging on nearshore community structure. It also examines temporal variability in species abundance at sites with and without sea otters. On northwestern Vancouver Island, sea otters decrease grazing pressure by requlating sea urchin populations. In this manner sea otters enhance algal growth. At three sites occupied by sea otters between 1987 and 1990 sea urchins disappeared and algae recruited. Temporal variation in algae and sea urchin abundance at sites with and without sea otters was low. The effect of sea otter foraging may differ between geographic areas, both in rate and magnitude of effect. Foraging tactics of sea otters and the behavioral response of sea urchins may create patchy communities. Succession of algae at sites re-occupied by sea otters follows that predicted by the tolerance model of succession.

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Introduction

Sea otters once ranged throughout the northeast Pacific, from northern Japan to central Baja Mexico (Kenyon 1969). Valued for their pelts, sea otters were hunted to near extinction by Russian, European and north American fur hunters. With only 13 remnant populations remaining, sea otters were finally protected by international treaty in 1911 (Kenyon 1969).

In 1967 the Alaskan government offered British Columbia
American sea otters to start a new population in Canadian waters.
From 1969 to 1972 a total of 89 sea otters were translocated from Amchitka Island and Prince William Sound to Checleset Bay, on northwestern Vancouver Island (Bigg and MacAskie 1978). This new population flourished and by 1990 there were about 600 sea otters in British Columbia (Watson 1990), extending from Quatsino Sound to Estevan Point along the northwestern end of Vancouver Island. The population is still classed as endangered (MacAskie 1986). In 1973, Ecological Reserve 109 was established to protect the area then inhabited by the fledgling sea otter population.

The extinction of sea otters in British Columbia had a profound effect on the nearshore ecosystem. Sea otters play an important role in structuring shallow nearshore communities. By feeding on invertebrates, such as sea urchins, sea otters remove major herbivores, reduce grazing pressure and promote the growth of fleshy algae (Palmisano and Estes 1977, Estes and Palmisano 1974). Algae in turn enhances productivity (Duggins, Simenstad and Estes 1989), increases fish populations (Bodkin 1988, Laur et

al 1988) and decreases wave action on shore (Jackson 1984, Jackson and Winant 1983). In general areas occupied by sea otters are characterised by fleshy seaweed and the absence of large invertebrates. In contrast areas without sea otters are dominated by sea urchins and fleshy algae are largely absent.

The role of sea otters in structuring nearshore communities has been well studied but since it is difficult to manipulate sea otter populations, most studies have been inferential, comparing the community structure of areas with sea otters to similar areas without sea otters. Work has been done in California (Foster and Reed 1980, Harrold and Reed 1986, Hines and Pearse 1982), Washington (Kvitek et al 1988), British Columbia (Breen et al 1982 Morris, Ellis and Emerson 1981), Southeast Alaska (Duggins 1980), Prince William Sound (Van Blaricom 1988) and the Aleutian Islands (Estes and Palmisano 1974, Estes et al 1978, Estes et al 1982, Dayton 1975, Duggins, Simenstad and Estes 1989). Some experimental work has simulated the effects of sea otter predation, by removing major herbivores, and examining resulting changes in community composition (Duggins 1980). Only one published paper reports the effects of sea otter foraging. When sea otters started foraging at Hopkin's Marine Reserve in California, McLean (1962) reported a decline in invertebrates and an increase in kelp.

However Foster and Schiel (1988) suggest that other factors may play an important role in regulating the abundance of invertebrates and algae. They point out that species composition

of kelp forest communities can vary significantly without the influence of sea otters. They feel spatial and temporal variation may explain much of the differences attributed to the presence or absence of sea otters.

This study examines the direct effects of sea otter foraging on community structure in shallow rocky communities on northwestern Vancouver Island. Four permanently marked sites were used to document changes in urchin and algae abundance as sea otters occupied the sites over a period of four years. Temporal variability of algae and urchin abundance was monitored at two sites outside of areas occupied by sea otters and two sites in areas which have been occupied by sea otters for 10-20 years. Algae succession at sites recently occupied by sea otters was monitored for three years.

Methods

In 1987 and 1988 eight permanently marked sites were established along 120 nautical miles off the west coast of Vancouver Island (Fig 1). Four sites were established just outside of areas occupied by sea otters. One site was located off of Nootka Island in Nootka Sound the remaining three were established in the southern portion of Checleset Bay, Kyuquot Sound. These sites were established to document the changes in algae and invertebrate abundance created by sea otter foraging. Two sites were established in Barkley Sound in areas without sea otters. These sites were used to document variability in invertebrate and algae abundance in the absence sea otters. Two sites were established within Ecological Reserve 109 in areas occupied by sea otters for 10 - 20 years. These sites were used to document variability in the abundance of algae and invertebrates in the presence of sea otters.

Each site was 25m by 20m, with the long axis running parallel to shore. Sites were established in 6-12 m of water on rocky substrate. Stainless steel pins, labelled with Flexon handle bar tape, marked 5m intervals along the main axis. Five randomly placed swaths extended perpendicularly, right or left of the main line. Each 10m by 2m swath was marked at each end with stainless steel pins and vinyl tape (Fig 2). Divers counted selected invertebrates and algae within each swath annually.

Permanently marked sites were used to remove the variability created by examining slightly different locations each year, the

use of permanently marked sites, meant that annual observations were not independent and inferential statistics could not be used. Therefore, results were plotted as changes in abundance of the selected species over time. Similar species were combined in categories and reported as the mean abundance across all five swathes for that year. In this report the brown algae category includes the following five species of brown algae; Desmarestia ligulata, Nereocystis luetkeana, Macrocystis integrifolia, Pterygophora californica, and Laminaria spp.. In this report the only invertebrate considered is the red sea urchin, Strongylocentrotus franciscanus.

Results

Three of the four sites established just outside of the existing sea otter range were occupied by sea otters between 1987 and 1990. At all three sites urchin abundance declined and algal abundance increased. There was little change in the abundance of urchins or algae at the sites in areas without sea otters or at the sites in areas already occupied by sea otters.

Changes at sites occupied by sea otters.

The Kamils Anchorage site (Fig 1) was established in 1987.

Sea otters started foraging in this area in the autumn of 1987.

Brown algae was absent from the site before sea otters arrived (Fig 3). By 1988 brown algae occurred in mean densities of 261.2 plants per swath (Table 1). Brown algae abundance increased until 1990 and then declined. Meanwhile mean urchin density dropped from 146 urchins per swath in 1987 to 109 urchins per swath in 1988. By 1990 urchin density had declined to zero (Fig 3).

The sharp increase in algal abundance and comparatively small decrease in urchin density which occurred between 1987 and 1989 is a result of patchy urchin distribution and algal recruitment. Between 1987 and 1989 urchin density declined on three of the five swaths (Table 2) and increased on the remaining two swaths. Algal abundance increased on four of the five swaths, but not on the fifth swath where urchin abundance had doubled. Experimental work suggests the patchy distribution of sea urchins and algae is the combined product of intermittent sea otter foraging and sea urchin behaviour (Watson in prep.)

The decline in algae abundance in 1990 reflected a change in species composition. The brown algae category was divided into annual species including Nereocystsis and Desmarestia and perennial species including Laminaria, Pterygophora and Macrocystis. Perennial and annual species were plotted separately (Fig 4). Annual species of algae were most abundant early on and declined in abundance, possibly out competed by perennial species. The Nootka Island site was established in 1987 (Fig 1), sea otters occupied the site between 1988 and 1989. By summer 1989 urchin densities declined to zero and brown algae abundance increased to 258 plants per swath (Fig 5, Table 1). As at Kamils Anchorage, annual species were largely replaced by perennial species by 1990 (Fig 6, Table 3).

The Union Island Site (Fig 1) was established in 1988 and occupied by sea otters between 1989 and 1990. In one year urchin densities declined to zero and brown algae abundance increased (Fig 7, Table 1). Primarily annual species recruited to this site.

The fourth site at Kyuquot Bay (Fig 1), established in 1988, was not occupied by sea otters during the study. Both algae and sea urchin abundances fluctuated moderately throughout the study (Fig 8, Table 1).

Sites without sea otters

The site at Wizard Islet (Fig 1) was established in 1987. Brown algae and sea urchin abundances were fairly constant between 1987 and 1990 (Fig 9). Mean urchin densities varied

between 108 and 123 urchins per swath (Table 1). Brown algae abundance fluctuated between means of 4 and 31 plants per swath (Table 1). Variation in algae abundance was highest on the swaths which ended in the shallow portion of the site, where wave action periodically excluded sea urchins, and allowed algae recruitment.

The site at Taylor Island (Fig 1) was established in 1987.

Mean abundance of brown algae and sea urchins was fairly constant (Fig 10). Mean abundance of sea urchins varied between 61 and 90 urchins per swath (Table 1). Brown algae abundance varied between mean abundances of 0.2 and 5.9 plants per swath (Table 1).

Sites already occupied by sea otters

The permanent site at Gull Island (Fig 1) was established in 1988. Sea otters have been observed at this site since 1974 (Morris et al 1981). There were no sea urchins at this site.

Annual abundance of brown algae varied from means of 168 to 228 plants per swath (Fig 11, Table 1). Fluctuation in algal abundance at this sites was due to changes in the abundance of annual species of algae. From 1987 to 1990 the mean abundance of annual species varied between 25 and 79 plants per swath (Fig 12, Table 3). During the same period, the mean abundance of perennial algae, primarily Pterygophora sp. varied between 139 and 143 plants per swath (Table 3).

The site at No Name Island (Fig 1) was established in 1988. This area has been occupied by sea otters for about 10 years (Watson, Saville and Peterson Unpub report). From 1988 to 1990 abundance of brown algae varied from means of 262 to 330 plants

per swath (Fig 13, Table 1)). As at Gull Island sea urchins were absent. Unlike the Gull Island site most of the variation in brown algae abundance is due to variation in the abundance of perennial algae which fluctuated between 228 and 330 plants per swath from 1988 to 1990 (Fig 14, Table 3).

Discussion

The results of this study suggest that on northwestern Vancouver Island sea otter foraging can structure nearshore communities in shallow rocky areas. Areas without sea otters are usually dominated by sea urchins, which graze fleshy algae away, areas with sea otters are characterised by fleshy algae and the abundance of large invertebrates.

In British Columbia, with the exception of sea otters, the red sea urchin, S. franciscanus has few predators. The sunflower star (Pycnopodia helianthoides) and the wolf eel (Anarrichthys ocellatus) prey on sea urchins but do not regulate populations (Breen 1979a 1979b). In the absence of sea otters sea urchin populations probably approach carrying capacity (Breen 1979a). In British Columbia sea otters act as "keystone species" (sensu Paine 1969) By controlling sea urchin populations, sea otters reduce herbivory and dramatic changes in community structure result.

While sea otters function as "keystone" predators in the waters off of northwestern Vancouver Island their importance as a predator may vary geographically. The magnitude of effect and rate of community change caused by sea otter foraging may vary geographically.

In more complex communities sea urchins are preyed upon by a number of predators. In southern California, for example,

Sheephead wrasse (Semicophyssus pulcher) and Panularid lobsters

(Panularis interuptus) prey on sea urchin recruits (Cowen 1983,

Tegner and Dayton 1982) and regulate sea urchin populations. In southern California, enormous kelp beds occur in areas without sea otters. Since other predators exert an influence on sea urchin populations, the addition of sea otters to this system, might not cause in the same dramatic changes in community structure seen in British Columbia. In a system with multiple urchin predators, sea otter foraging is less important and sea otters may not be "keystone predators".

The rate of change in community structure caused by sea otter foraging may vary in different areas. In the Aleutians sea otters forage on S. polycanthus, a small species of sea urchin. The small size of the sea urchin makes it energetically impractical for sea otters to eat sea urchins below a certain size (Estes, Duggins and Rathbun 1989). This selective foraging means small urchins are left in the system. Small urchins may not have the grazing impact of larger urchins but their presence might inhibit algae recruitment and slow the rate of community change. Because red sea urchins are much larger, sea otters in British Columbia quickly remove all urchins and community changes are rapid.

On Vancouver Island the length of time it takes a community to change, from urchin barrens to kelp forest can be affected by the foraging tactics of the sea otter and red urchin behaviour. At Union and Nootka Islands, sea otters removed almost all sea urchins less than a year, while at the Kamils Anchorage site, it took two years for sea otters to remove all the sea urchins. Sea

otters appeared to forage intermittently at the site throughout the winter of 1987 - 1988.

An experiment conducted this past summer, demonstrated that red sea urchins move away from the tests of recently killed conspecifics. The addition of ten freshly killed, empty urchin tests, cleared sea urchins out of an area 5m by 5m, in less than 24 hours. Urchins did not return to the area for seven days and had still not returned to pre-treatment densities after 13 days (Watson in prep.).

By foraging in an area intermittently and dropping the empty urchin tests, sea otters may create urchin free patches. Algae may recruit to these patches, but the overall abundance of sea urchins may decline slowly. This mosaic of algae and sea urchins may create a community composed of a patchwork of different successional stages. Duggins (1983) found a similar situation in Torch Bay, Alaska, where predatory seastars were able to create urchin free patches to which algae could recruit.

The effects foraging were remarkably predictable. Algae recruited almost immediatley to the three sites occupied by sea otters. As sea urchin abundance declined both annual and perennial algae recruited. Annual algae were initially more abundant but were replaced by perennial species. This pattern follows the "tolerance model" of succession proposed by Connell and Slatyer (1977). In the tolerance model early and late successional species recruit and competition determines the eventual community composition.

Annual algae were almost absent from the Gull Island site, which has been occupied by sea otter for about 20 years (Morris et el 1981). This suggests that perennial species will eventually dominate the three sites occupied by sea otters between 1987 and 1990. Duggins (1980) found similar results in Torch Bay, Alaska. He experimentally removed sea urchins from plots and monitored algal recruitment. Both annual and perennial species recruited but annuals were replaced in the second year by the perennial species Laminaria.

The species composition of a site may represent the successional stage the community is at. This would be determined by how long sea otters have foraged at the site and may explain differences between Gull Island and No Name Island. At Gull Island the abundance of perennial algae remained almost constant throughout the study. The dominant algae at Gull Island was Pterygophora californica, a perennial stipitate kelp which can live up to 24 years (Dewreede 1984). The very constant abundance of perennial algae at Gull Island may represent an old or fairly stable (sensu Sutherland 1974) climax community. Annual algae varied more than perennial species. Annual algae may recruit opportunistically to patches created in the Pterygophora forest by disturbance. Since patches are unpredictable in time and space the abundance of annual algae would be expected to vary.

Variation in algae abundance was much greater at No Name Island. Most of this variation was due to fluctuations in the abundance of perennial algae. Macrocystis contributed to much of

this variation. Since it is difficult to distinguish individual plants of Macrocystis integrifolia, individual fronds were counted. As a result Macrocystis contributed disproportionately to the abundance of perennial algae. The abundance of Laminaria and Pterygophora also varied. Since sea otters have occupied this site for about 10 years, it is possible that the constant community seen at Gull Island had not yet been reached at No Name Island. The variation in algal abundance and species composition at No Name Island may be due to successional development.

Physical environmental factors may also affect species composition and abundance in a community. Macrocystis cannot tolerate wave exposure, and is generally found in more sheltered environments. It is easily out competed by stipitate kelps in exposed areas (Dayton 1985) but will out compete the same plants in a more sheltered environment. As a result successional events and community composition can be moderated by the effects of the physical environment.

Wave action can exclude sea urchins from shallow areas.

Algae was largely absent from the two otter-free sites in Barkley Sound, but occurred in the shallower portions of the site at Wizard Rocks. Wave action may have seasonally excluded urchins from shallow areas and allowed some algal recruitment. Variation in abundance of algae between years may be caused by differences in wave action.

Sea urchin abundances at the two sites without sea otters was fairly constant throughout the study. At Taylor Islet, algae

abundance varied slightly in an inverse relationship to the abundance of sea urchins. Communities without sea otters appear to be quite constant in species composition and abundance.

On northwestern Vancouver Island sea otter foraging has an enormous effect on species abundance and composition in shallow rocky areas. The rate of change and magnitude of these effects may vary geographically. The communities created by sea otter foraging can vary temporally and spatially. Most of this apparent variation may be caused by the successional stage, of the community, the forging tactics of the sea otter and the environmental regime. These factors must be considered when generalizing the effects of sea otter foraging over a wide spatial or temporal scale.

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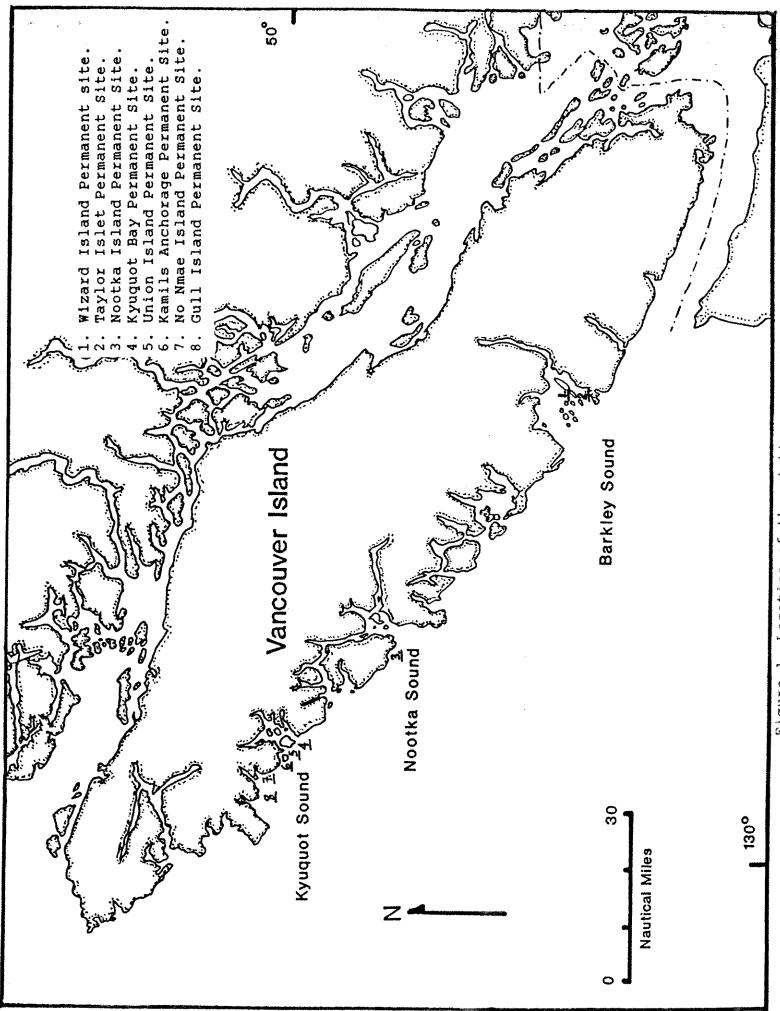


Figure 1. Location of the eight normanant sites

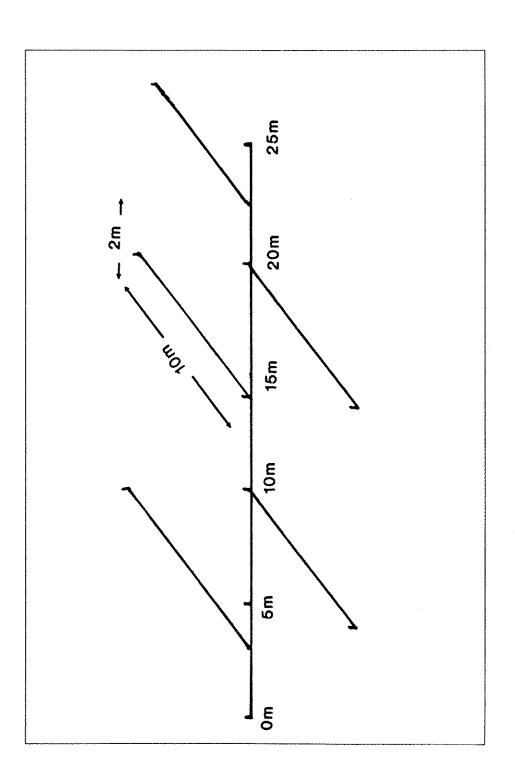


Figure 2. Configuration of the permanent sites.

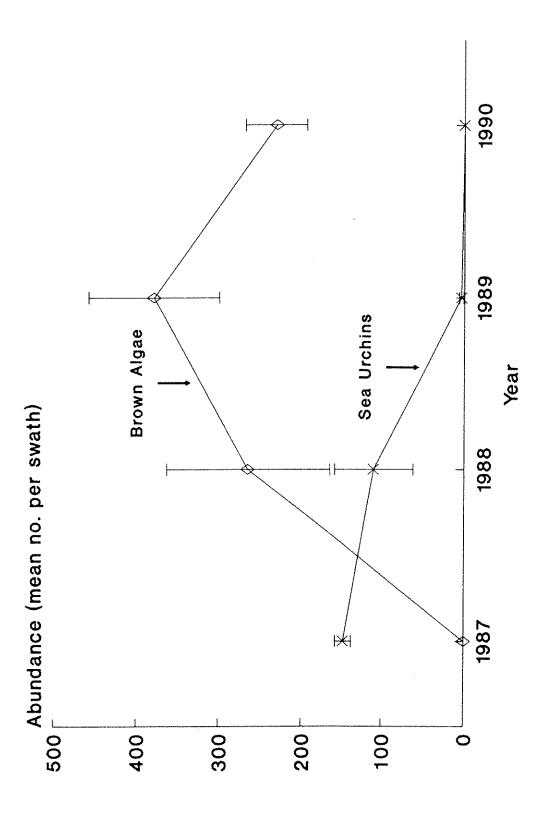


Figure 3. Changes due to sea otter foraging at Kamils Anchorage permanent site.

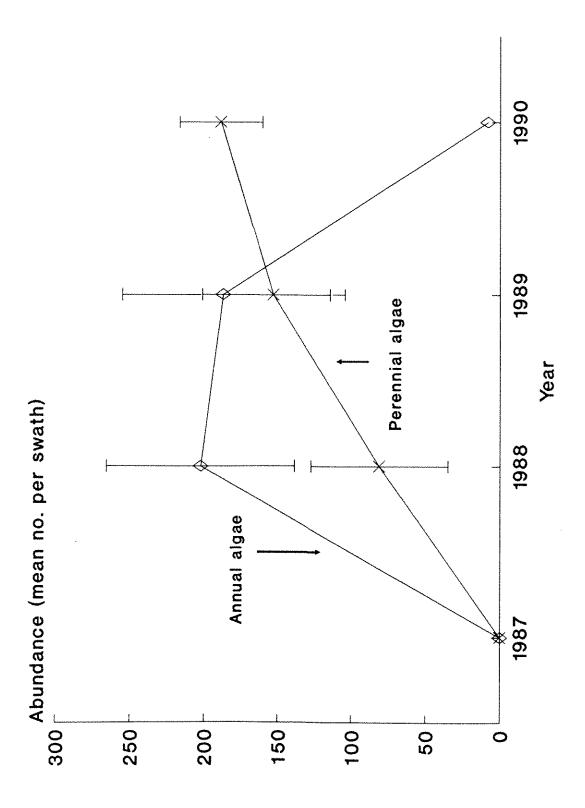


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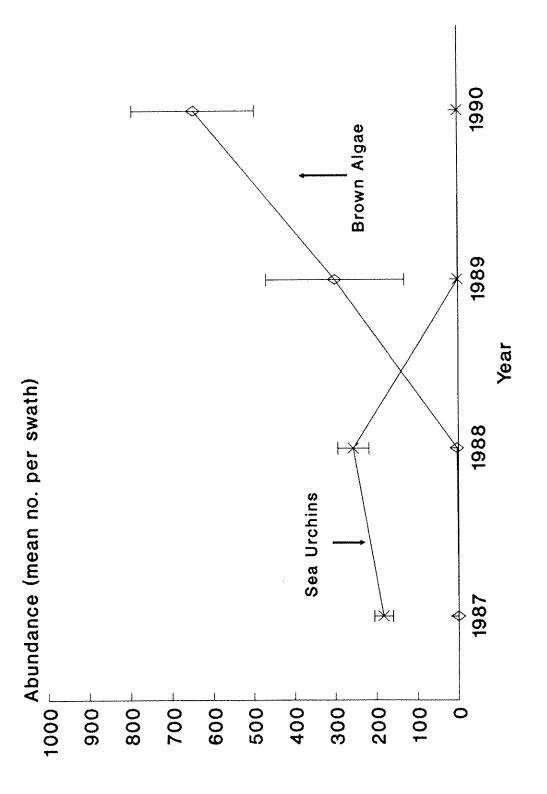
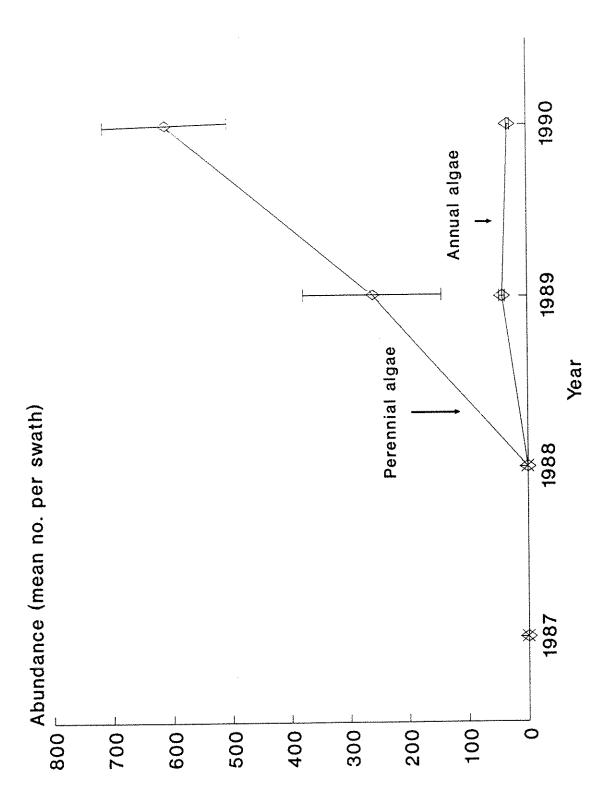


Figure 5. Changes due to sea otter foraging at Nootka Island permanent site.



Changes in abundance of annual and perennial algae at Nootka Island permanent site. Figure 6.

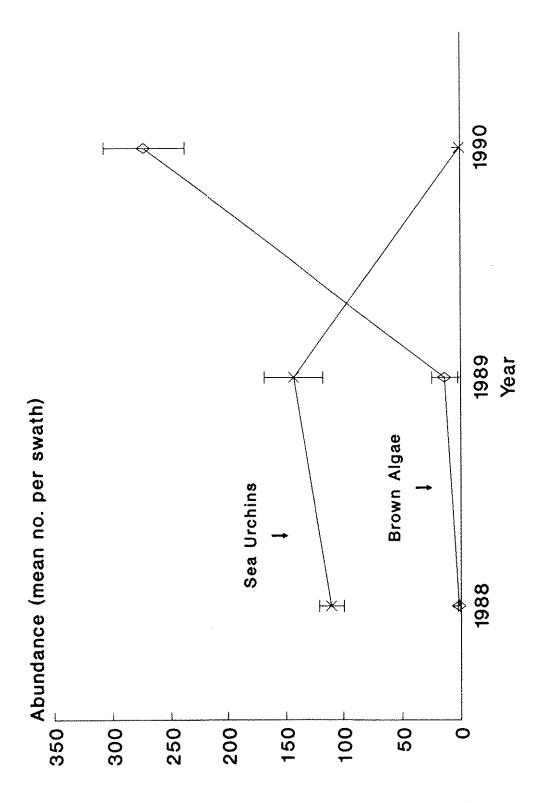


Figure 7. Changes due to sea otter foraging at Union Island permanent site.

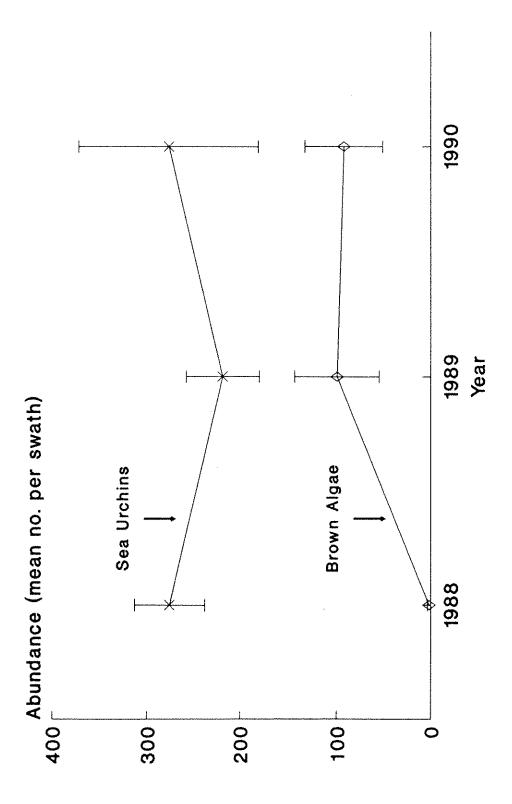


Figure 8. Changes in abundance of brown algae and sea urchins at Kyuquot Bay permanent site.

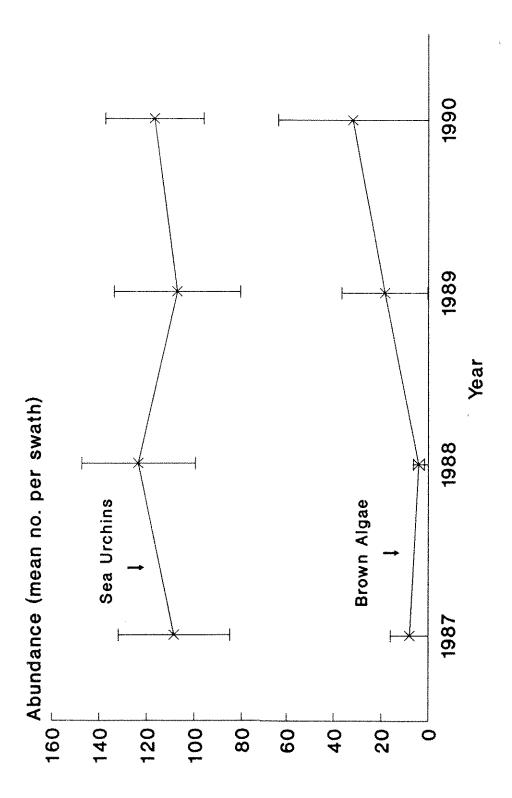


Figure 9. Changes in brown algae and sea urchin abundances at Wizard Island permanent site. No sea otters.

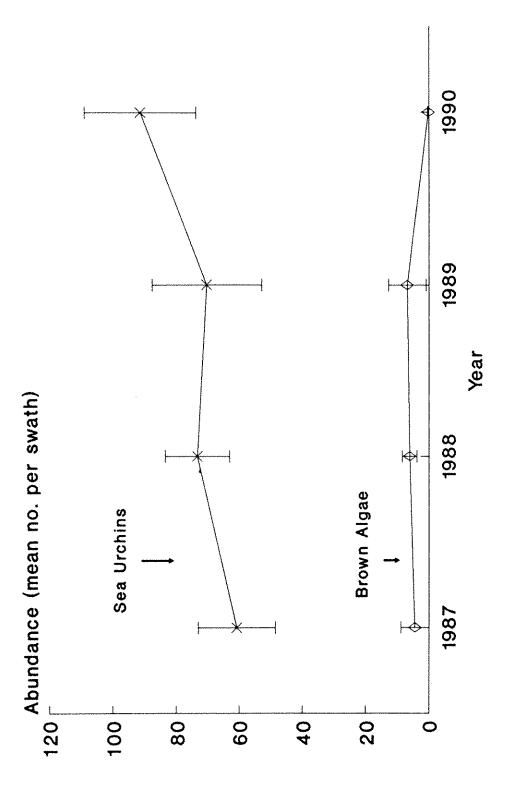


Figure 10. Changes in brown algae and sea urchin abundances at Taylor Islet permanent site. No sea otters.

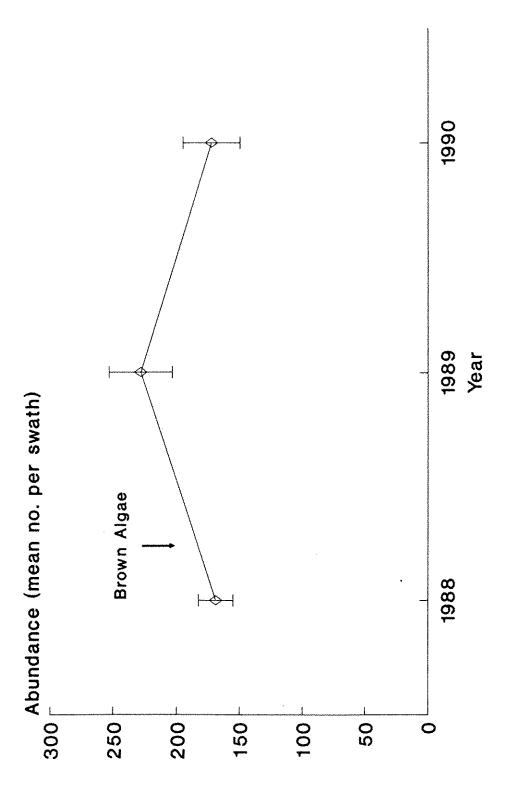


Figure 11. Changes in brown algae abundance at Gull Island permanent site. Sea otters present for 20 years.

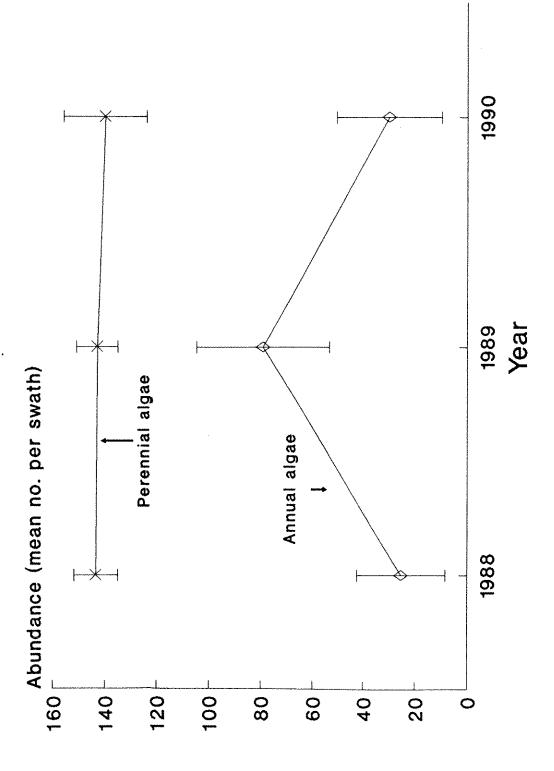


Figure 12. Changes in abundance of perennial and annual algae at Gull Island permanent site.

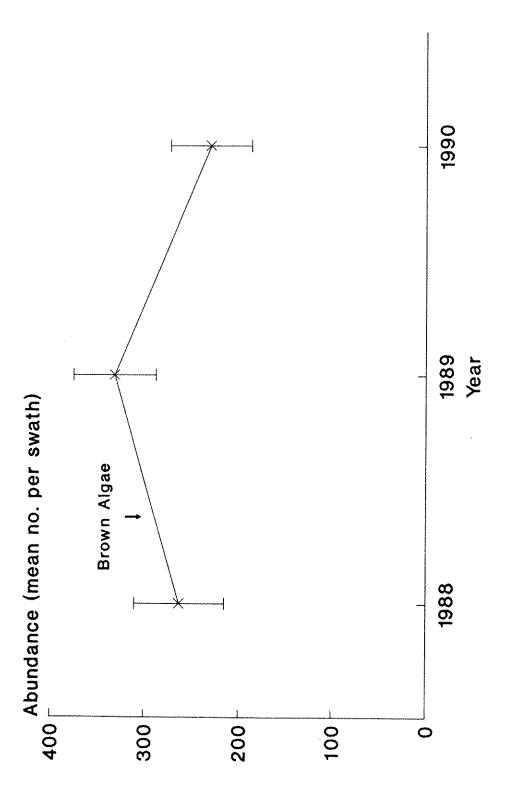


Figure 13. Changes in abundance of brown algae at No Name Island permanent site. Sea otters present for 10 years.

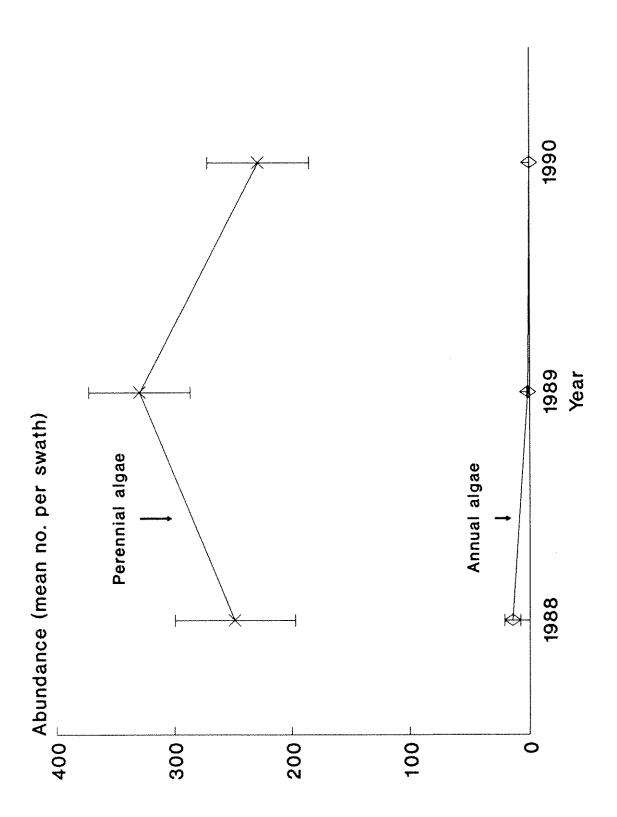


Figure 14. Changes in abundance of perennial and annual algae at $_{\mbox{\scriptsize No}}$ No Name Island permanent site.

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Sites changed by sea otters

	198		1988		1989		1990							
Kamils Anchorage	Mean	SE	Mean	SE	Mean	SE	Mean	SE						
Brown Algae Red Urchins	0 147	0 10	261 110	99 48	374 3	79 3	222 0	38						
Maskles Talumi														
Nootka Island Brown Algae	0	0	2	2	300	169	645	150						
Red Urchins	183	23	256	37	. 2	. 2	ő	0						
Union Island														
Brown Algae	X	X	1	1	14	11	272	35						
Red Urchins	X	X	110	11	143	26	. 6	. 5						
	Kyuquot Bay (no sea otters)													
Brown Algae	Χ	X	2	2	99	45	92	41						
Red Urchins	Х	X	275	38	218	39	276	96						
Sites with sea otters														
	1987		1988		1989		1990							
, mig. *1: *2: 330 *1 *1	Mean	SE	Mean	SE	Mean	SE	Mean	SE						
Gull Island	35	**	3.60	+5 A	000		4 7 0							
Brown Algae Red Urchins	X X	X X	169 0	14 0	228	25	172	23						
Ked Offillip	^	Λ.	Ų	U	0	0	0	0						
No Name Island			•											
Brown Algae	X	Х	263	48	331	44	229	43						
Sea Urchins	Х	X	0	0	0	0	0	0						
Sites without sea		S												
	1987 Mean	SE	Mean	SE	Mann	O.T.	\$ # m .m .m	and deep						
Wizard Rocks	nean	ಶಿಥಿ	nean	ðE.	Mean	SE	Mean	SE						
Brown Algae	8	8	4	2	18	18	32	32						
Red Urchins	108	24	123	24	107	27	116	21						
Taylor Islet														
Brown Algae	4	4	6	2	7	6	. 2	. 2						
Red Urchins	61	12	73	10	70	18	91	18						

Table 1. Abundance of brown algae and sea urchins at all sites from 1987 - 1990. (mean of 5 swaths and standard error)

Swath 1	1987	1988	1989	1990
Brown algae	175	0	3	0
Red urchins	1	512	336	304
Swath 2				
Brown algae	154	141	12	1
Red urchins	0	115	300	158
Swath 3				
Brown algae	149	173	1	0
Red urchins	0	452	320	308
Swath 4				
Brown algae	129	235	0	0
Red urchins	0	0	679	225
Swath 5				
Brown algae	127	0	0	0
Red urchins	0	227	61	122

Table 2. The abundance of sea urchins and brown algae per swath at Kamils Anchorage permanent site from 1987-1990

	1987 Mean	SE	1988 Mean	SE	1989 Mean	SE	1990 Mean	SE
Gull Island Perennial Algae Annual Algae	X X	X X	143 25	8 17	142 79	8 25	139 30	16 20
No Name Island Perennial Algae Annual Algae	X X	x x	248 14	51 7	330 1	4 3	227 0	4 3
Kamils Anchorage Perennial Algae Annual Algae	0 0	0 0	81 202	46 64	152 187	48 68	188 8	28 6
Nootka Island Perennial Algae Annual Algae	0 0	0	0 0	0	258 42	170 47	613 31	148

Table 3. Abundance of perennial and annual algae at Gull Island, No Name Island, Kamils Anchorage and Nootka Island. Mean of 5 swaths and standard error