

Stability, resilience, and phase shifts in rocky subtidal communities along the west coast of Vancouver Island, Canada

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Abstract. We used the extirpation, reintroduction, and spread of sea otters (*Enhydra lutris*) along the west coast of Vancouver Island, Canada, to evaluate how the otter–urchin–algae trophic cascade creates variation in rocky reef community structure over space and time. By repeatedly sampling both randomly selected and permanently marked sites in areas where sea otters were continuously present, continuously absent, or became reestablished during a 23-year study period, we found a highly predictable association between community phase states (algae abundant or urchins abundant) and the population status of sea otters. In areas where sea otters were continuously present, urchins were rare and algae dominated, whereas in areas where otters were continuously absent, urchins were abundant and algae were rare. Despite this predictability, the species composition and abundance of algae within otter-dominated sites and the abundance of urchins in otter-free sites were spatially and temporally variable. The transition from the urchin-dominated to algal-dominated phase state, brought about by sea otters preying on sea urchins, was documented; at some sites the transition occurred rapidly, whereas at other sites a short-lived transitional state composed of algal–urchin mosaics occurred. We experimentally demonstrate that this mosaic forms when living urchins flee from the damaged tests of conspecifics that are discarded by foraging sea otters, and kelp recruits into the urchin-free patches. Thus, although the phase state dynamics appeared to be stable and predictable based upon the presence or absence of sea otters, we found that spatial and asynchronous temporal variation in recruitment, mortality demography, succession, and prey behavior led to differences in the abundance and/or composition of species within the two phase states.

Key words: *Desmarestia* spp.; *Enhydra lutris*; kelp demography; *Macrocystis pyrifera* (= *integrifolia*); mosaic structure; phase state; *Pterygophora californica*; resilience; sea otter; sea urchin; *Strongylocentrotus franciscanus*; variation.

INTRODUCTION

Ecosystems do not behave as static and predictable entities but rather as dynamic systems that can be highly unpredictable in time and space (Scheffer and Carpenter 2003, Doak et al. 2008). One of the greatest challenges to understanding the dynamics of such systems is that it requires long-term information. This is because snapshots in time provide a stationary view of ecological processes whereas, in reality, systems are dynamic and characterized by protracted change (Knowlton 2004). A long-term perspective further provides insight into ecological stability, in particular measures of persistence, resilience, and sometimes even the existence of multiple states.

Measuring ecological change requires a baseline or benchmark against which to document natural variation (Dayton et al. 1998). Baselines are usually generated by long-term monitoring (Spellerberg 1991), which allows ecologists to detect rare events as well as slow, subtle,

and intricate ecological processes (Strayer et al. 1986). However, the temporal scale over which these changes are measured depends upon the system (Carpenter et al. 2001) and, in particular, on the longevity and generation time of the important interacting factors. Most ecological studies are too short term to distinguish between demographic inertia and the myriad other processes that influence the structure and dynamics of the system (Thrush et al. 1997). Because of the comparatively short generation times of the dominant autotrophs, some of the best known examples of long-term studies have been conducted in marine ecosystems, especially in kelp forests (Steneck et al. 2002).

Kelp forests, which occur in temperate ecosystems throughout the world's oceans (Dayton 1985, Steneck et al. 2002), are regulated and structured by the interaction of a variety of environmental and biological factors (Dayton 1985, Foster and Schiel 1985, Schiel and Foster 1986, Steneck et al. 2002). Globally, they are known to be highly dynamic communities that can collapse and recover with great speed (Steneck et al. 2002). Changes in kelp abundance can be brought about by physical forcing such as episodic warm-water events that

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facilitate disease outbreaks in grazers (Pearse and Hines 1979, Scheibling et al. 1999) or kill kelps outright (Vasquez et al. 2006), by longer term temperature changes (Dayton et al. 1992, Sutherland 1998), and by biotic factors such as grazing by sea urchins (Lawrence 1975, Foreman 1977, Harrold and Pearse 1987). In the eastern North Pacific Ocean, deforestation is precipitated most often at lower latitudes ($<40^\circ$) by oceanographic events, but the deforested state is usually short lived (Steneck et al. 2002). In contrast, deforestation at higher latitudes ($40\text{--}60^\circ$) is induced usually by urchin grazing, but the deforested condition tends to be persistent and not easily reversed (Estes and Duggins 1995).

Various predators regulate the abundance (Shears and Babcock 2003) or grazing behavior of sea urchins (Vadas and Elnor 2003) and, in doing so, can mediate the abundance and species composition of kelp through a trophic cascade (Paine 1980, Terborgh and Estes 2010). The ecological dynamics of urchins and their predators have been particularly well studied along the Pacific coast of North America (Steneck et al. 2002, Estes et al. 2010). In Alaska (Estes and Duggins 1995), British Columbia (Breen et al. 1982), and Washington (Kvitek et al. 1998), predation by sea otters (*Enhydra lutris*) often limits the size and abundance of urchins. In these areas, most rocky reefs with sea otters have abundant algae and few sea urchins, whereas those without otters generally have abundant urchins and few algae. These differing community configurations have been referred to as alternate stable states (Simenstad et al. 1978) or distinct phase states (Steneck et al. 2002) due to their tendency, once achieved, to be self maintaining (Konar and Estes 2003), and because intermediate or transitional stages are apparently unstable and short lived (Estes and Duggins 1995).

Although alternate stable states have been reported in diverse ecosystems, empirical analyses of this phenomenon are often limited by the lack of historical context: inadequate baselines and a poor understanding of variability over larger scales of space and time. The well-described interaction between sea otters, sea urchins, and algae provides a useful model for observing temporal and spatial variation within a historical context and thus better understanding persistence, resilience, and other aspects of stability in rocky reef communities. Firstly, the components of these communities are, for the most part, easily observed, measured, counted, and manipulated; secondly, the local extinction, recovery, and expansion of sea otter populations makes it possible to document spatial and temporal variation in kelp- and urchin-dominated alternate state communities with known ecological histories, over appropriate scales of space and time.

In this study, based on 23 years of fieldwork, we examined spatial and temporal variation in rocky reef communities in areas with and without sea otters along the outer coast of Vancouver Island, British Columbia, Canada. Our study had three major goals: (1) to

measure variation in species composition and population density within the algal- or urchin-dominated phase states and to determine the degree to which this variation is attributable to spatial differences vs. temporal processes; (2) to document patterns of change that occur with the switch from an urchin- to algal-dominated phase state as sea otters colonized areas; and (3) to measure and understand heterogeneity within these phase states.

The study was designed around the reintroduction and expansion of sea otters into an environment from which they had been historically extirpated. Knowing the distribution and population trends of sea otters at the onset of our field study in the mid-1980s, we used three approaches to achieve our goals. First, we used a random sampling method to compare the abundance and species composition of sea urchins and macroalgae on rocky reefs in areas where (1) sea otters were well established, (2) sea otters were in the process of becoming established, or (3) sea otters had long been absent. This approach produced a largely spatial assessment of variation in the otter-free and otter-dominated phase states. Second, we used permanently marked plots to provide a temporal record of phase state persistence and variation in algae and urchin densities in the same ecological setting: i.e., areas where sea otters were (1) well established, (2) absent, or (3) became reestablished during the study period. This approach provided a detailed view of the temporal dynamics of systems with and without sea otters, and chronicled community changes associated with the return of sea otters. Finally we conducted a manipulative experiment designed to explain the patterns of change that we observed as otters spread and the system switched from the urchin- to algal-dominated phase state. By combining the observations obtained from the two approaches with the experimental results, we describe the patterns and explain the mechanisms of community transition associated with the arrival of sea otters and then document variation, persistence, and resilience in the two-phase-state configurations over time and space.

METHODS

The study area

Our research was conducted from 1987 to 2009 in four general locations on the west coast of Vancouver Island, British Columbia (BC): Checleset Bay ($\sim 50^\circ 02' \text{ N}$, $127^\circ 36' \text{ W}$); Kyuquot Sound ($\sim 49^\circ 53' \text{ N}$, $127^\circ 17' \text{ W}$); Nootka Island ($\sim 49^\circ 34' \text{ N}$, $126^\circ 40' \text{ W}$); and Barkley Sound ($\sim 48^\circ 54' \text{ N}$, $125^\circ 18' \text{ W}$; Fig. 1). This area has a highly convoluted shoreline, with open shores exposed to ocean swell, deep fjords extending inland, large island-filled bays, and shallow reefs. Although much of the coast is rocky, hard substrate is often restricted to a narrow fringe that extends to a water depth of $\sim 12 \text{ m}$, below which rock often gives way to soft sediment deposited from glaciers that melted after the Pleistocene (Cannings and Cannings 1996).

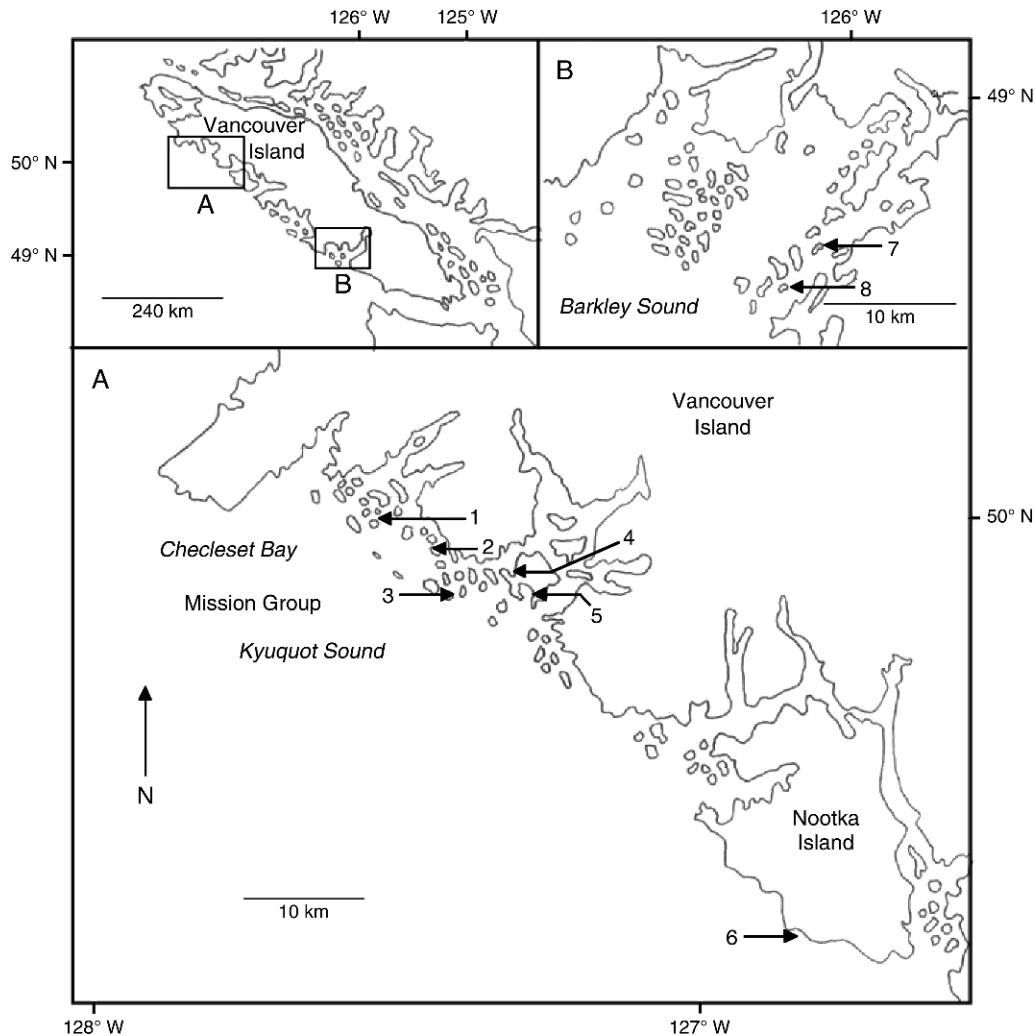


FIG. 1. Vancouver Island, Canada, and the place names mentioned in the text. The numbers shown for (A) Checleset Bay/Kyuquot and (B) Barkley Sounds are the locations of the permanent plots: 1, Gull Island; 2, No Name Island; 3, Kamils Anchorage; 4, Union Island; 5, Kyuquot Bay; 6, Maquinna Point; 7, Wizard Island; 8, Taylor Islet.

The history of British Columbia sea otters

Historically, sea otters were abundant along the BC coast. Estimates and records suggest that up to 55 000 pelts were harvested from this area during the maritime fur trade, which lasted from the late 1700s until 1911 (Rickard 1947, Busch and Gough 1997, Mackie 1997, Gregr et al. 2008). Sea otters were economically and probably ecologically extinct from BC waters by about 1850; the last confirmed record of otters in BC is from 1929 (Cowan and Guiguet 1960). Sea otters were absent from BC until 89 animals were reintroduced to Checleset Bay, on Vancouver Island from 1969 to 1972 (Bigg and MacAskie 1978). At the start of our study in 1987, sea otters occurred in northern Checleset Bay and in a small area off Nootka Island, but were absent from Barkley and Kyuquot Sounds (Fig. 1). By 1990, sea otters had expanded throughout Kyuquot Sound. In

2001, the sea otter population in BC was estimated at 3180 animals, with 2673 of these located off the west coast of Vancouver Island (Nichol et al. 2005). Sea otters were functionally absent from Barkley Sound throughout our study.

Sea otter surveys

Sea otter surveys were done annually from Checleset Bay to Kyuquot Sound between July and September 1987–2009, and intermittently off Nootka Island during this period. Surveys were conducted from small boats (~5 m long) by 3–4 observers using binoculars, when sea conditions were Beaufort 2 or less. Procedures were similar to those used for skiff surveys of sea otters in the Aleutian Islands (Estes 1990, Doroff et al. 2003). The surveys followed a set route and covered all areas except fjords, which were not systematically surveyed. Multiple

TABLE 1. The categories of algae monitored in random-site surveys and at permanent plots in rocky intertidal communities of the west coast of Vancouver Island, Canada.

Category and species	Common name
Annual brown algae	
<i>Nereocystis luetkeana</i> (Mertens) Postels and Ruprecht	bull kelp
<i>Costaria costata</i> (C. Agardh) Saunders	five-lined kelp
<i>Desmarestia</i> spp.	acid weed
Perennial brown algae	
<i>Pterygophora californica</i> Ruprecht	tree kelp
<i>Eisenia arborea</i> Areschoug	
<i>Laminaria setchellii</i> Silva	
<i>Macrocystis pyrifera</i> (= <i>integrifolia</i>) (Linnaeus) C. Agardh	giant kelp
Other brown algae	
Young Laminariales	

surveys were conducted in most years, but the highest annual count was used to estimate population size.

Subtidal community surveys

We used two approaches to assess spatial and temporal variation in community structure in areas with and without sea otters and to document community changes associated with the expansion of the otter population. Randomly selected sites were used to examine spatial variation on a large scale, whereas annually sampled, permanently marked plots were used to obtain a detailed view of temporal variation. All sampling was done between July and September.

Random sites.—We sampled 20 sites in two areas where sea otters were absent (Barkley and Kyuquot Sounds; the latter was occupied by otters during the study) and 20 sites in one area where sea otters were present (Checleset Bay) in 1988, 1994, and 2007. The sites were selected initially by placing a grid over a chart of the study area. Grid intersections with the shore or offshore islands were numbered sequentially, and the numbers were sampled randomly until 20 sites had been selected. Sites with soft substrate, which could not support kelp, were not sampled, and additional sites were drawn as needed. At each site, divers sampled 20–30 0.5-m² quadrats (0.7 × 0.7 m) at 8–10 m below mean low water (MLW). The depth regime was selected to avoid shallow, wave-swept areas and soft substrate, which often occurred below 12 m depth. Quadrats were placed on the sea floor using a predetermined random number of kicks from the anchor or the previous quadrat position. In each quadrat, the number of red urchins (*Strongylocentrotus franciscanus*) and brown algae (including kelp sporophytes too small to identify to species) were counted (Table 1). This protocol is similar to that used by Estes and Duggins (1995) in the Aleutian Islands and southeast Alaska.

Red urchins were the only common urchin species at our study sites. To estimate biomass density and characterize population structure, red urchin test diameters were measured in situ with calipers to the nearest millimeter. A minimum of 100 individuals or all the red urchins in the quadrats were measured at each site. Red

urchin biomass density (grams wet mass per square meter) was calculated for each site using a regression of wet urchin mass to test diameter (see Table 2). Average red urchin biomass density for each site was calculated from the total biomass of the urchins collected divided by the number of quadrats sampled for urchins.

To assess changes over time in community structure, mean urchin test diameter, urchin biomass density, and algal density (of annual, perennial, and total algae; Table 1) were calculated for each site and compared between years within areas (but not between areas, because we were unable to replicate the area with sea otters [Checleset Bay]). In 1988, Nootka Island was the only other area in BC besides Checleset Bay with sea otters (Fig. 1), and the otters at this island occurred along a small, exposed stretch of coast that could not be sampled easily. Mean abundance or biomass (in the case of urchins) for each of the variables was calculated for each of the 20 sites within each of the three areas. Data were tested for normality (Shapiro-Wilk test) and equality of variances (Cochran's *C* or modified Lavene equal-variance tests). We tested for differences among years in urchin density and size (diameter and biomass) and algal density within the three types of sites (i.e., otters established, otters absent, otters becoming established), using a single-factor ANOVA if the data met parametric assumptions or a nonparametric Kruskal-Wallis test, SYSTAT (Wilkinson 1999) or NCSS (Hintze 2007), when parametric assumptions were violated and could not be met by data transformation. Phase-state plots (i.e., mean algal density vs. urchin density among sample sites) were used to characterize community configurations for each area and time sampled.

Permanent plots.—Permanently marked plots were established at eight sites (Fig. 1). Four of these sites, initially outside the otters' range in Kyuquot Sound and off Nootka Island, were occupied by sea otters during the study. The four other sites were in areas where the status of sea otters did not change: two in Checleset Bay where otters were continuously present, and two in Barkley Sound where otters were continuously absent.

We established five permanent plots at each of the eight sites. A 25-m main axis was placed parallel to shore

6–12 m below MLW and the five 2×10 m plots were located perpendicular to the main axis on either side at random intervals. The main axis and the ends of each plot were marked with stainless-steel bolts set into holes drilled in the rock substratum. To ensure that sites were similar in relief (topography can affect the abundance, movement, and behavior of sea urchins; Kitching and Ebling 1961), topographic indices ($n = 5$ for each site) were determined by comparing the contour distance along the seabed of each plot to its lineal distance of 10 m (Foster et al. 1986). A single-factor ANOVA was used to test for differences in topography among the sites.

A Stowaway Tidbit Temperature Logger (Onset Computer Corporation, Pocasset, Massachusetts, USA) was installed at each site at ~ 10 m below MLW in the summer of 1999. Algal growth and abundance can be limited by nitrate levels and because temperature is inversely related to nitrate concentration, temperature can be used as a proxy for nitrate availability (Tegner et al. 1996). In southern California, water temperatures $< 14^\circ\text{C}$ provide adequate nutrients for kelp growth (for a review, see Dayton et al. 1999), whereas at temperatures $> 16^\circ\text{C}$, nitrate is undetectable. In the euryhaline waters of coastal BC, kelp growth can also be limited by salinity if low salinity co-occurs with warm water (Druehl 1978). However, these limiting conditions did not occur at our sites, as low salinity occurs in the winter when rainfall is greatest but the water is relatively cool. During summer, when water is warm, salinity is stable at 30–32‰ (Druehl 1978). This meant that we could use water temperature to reasonably infer whether nitrate availability affected kelp abundance or biomass. Water temperature was recorded at 8-h intervals starting at 12:00 hours. Temperatures from each site were averaged to provide a mean monthly water temperature for each area. To infer water temperatures before 1999, the data collected from the loggers were compared to the long-term SST (sea surface temperature) data collected by the Canadian Department of Fisheries and Oceans at Kains Island Light ($50^\circ 25.9' \text{N}$ $128^\circ 00.3' \text{W}$; *available online*).⁴

Red urchins and brown algal species (Table 1) were counted annually in each plot. Individual stipes and plants of *Macrocystis pyrifera* (= *integrifolia*) were counted, but unless noted, stipe density is reported (see Druehl and Wheeler 1986). Total brown algae, which included kelp sporophytes too small to identify to species, were grouped as perennials or annuals (Table 1) and identified to the lowest possible taxon. To test for significant temporal variation in the abundance of algae or urchins within the plots ($n = 5$) among years ($n = 23$), we used a single-factor, within-subjects (plots), repeated-measures ANOVA with fixed effects (Wilkinson 1999, Hintze 2007). These analyses were conducted independently for each of the eight sites.

To assess population stability (e.g., Dayton et al. 1984), mortality and recruitment in the long-lived kelp

Pterygophora californica were monitored at the Gull Island and No Name Island permanent plots. From 1988 to 1998, all individuals of *Pterygophora* on one plot were labeled with a numbered strip of PVC tape fastened loosely about the stipe by a cable tie. Surviving plants were retagged each year. Plants ≤ 0.20 m tall were too small to tag, so recruits were defined as untagged plants ≥ 0.20 m but ≤ 0.50 m (plants that had lost tags therefore were not considered new recruits). From 1988 to 1989, 50 *Pterygophora* plants in the shallow sublittoral zone at Wizard Island were double-tagged to estimate tag loss and tag-induced mortality.

In 1989 and 1990, the age structure of *Pterygophora* populations at the Gull Island, No Name Island, and Kyuquot Bay permanent plots (where *Pterygophora* was abundant) was estimated by aging the plants (DeWreede 1984). *Pterygophora* plants in 10 randomly selected 0.5-m^2 quadrats were sampled in areas neighboring the permanent plots. A $0.07\text{--}0.10$ m section was cut from above the holdfast of each plant. Sections were placed in a labeled plastic bag (one per quadrat) and preserved in 1% buffered formalin. Three thin sections were cut ~ 0.04 m from the base of each of the sections; the thin sections were placed on a light table and the dark rings completely encircling the stipe were counted. Plant age was calculated as a mean of the three estimates.

Large numbers of dead *Pterygophora* plants were found at the Gull Island permanent plots in Checleset Bay beginning in 1992. It seemed likely that this mortality resulted from senescence (aging). To determine age at death, these plants were collected and aged using the previously described methods. Dead plants were observed until 1998, but were sampled only in 1992.

Transitional dynamics.—A phase shift from urchin barrens to kelp forest occurred when sea otters spread into the permanent plots in Kyuquot Sound and off Nootka Island. The transition from urchin barrens to kelp forests did not occur uniformly at each of the sites. At some sites the transition was rapid, whereas at other sites it involved the development of urchin-free and or algal-dominated patches. This transition was observed most closely in Kyuquot Sound, where urchin-free patches (3–8 m across) often occurred around red urchin tests that had been cracked open and dropped to the sea floor by the colonizing otters. In many cases, brown algae had recruited to the urchin-free patches. It seemed unlikely that the patches had been created directly by sea otters removing urchins, because overall urchin density remained high and urchins in areas adjoining the urchin-free patches were aggregated. Based on other studies of urchin behavior and urchin–algal interactions (Russo 1979, Duggins 1983), we envisioned two potential mechanisms to explain the mosaic pattern: (1) red urchins fled from the damaged red urchin tests discarded by sea otters, creating urchin-free patches, and (2) red urchins were attracted to brown

⁴ <http://www.pac.dfo-mpo.gc.ca/sci/osap/data>

TABLE 2. A summary of survey results in rocky intertidal communities of the west coast of Vancouver Island, Canada; values are means \pm SE.

Parameter	Barkley Sound, otters absent			Checleset Bay, otters present		
	1988	1994	2007	1988	1994	2007
Sea otters						
Max. no. otters	0	0	0	201	413	949
Red urchins						
Mean TD (mm)	93.3 \pm 1.9	71.0 \pm 4.3	87.9 \pm 2.5	NA	NA	NA
Density, no./m ²	6.7 \pm 0.5	8.8 \pm 0.8	8.9 \pm 0.9	0.2 \pm 0.1	0.1 \pm 0.0	0.3 \pm 0.1
Mass, kg/m ²	3.4 \pm 0.2	3.3 \pm 0.3	2.8 \pm 9.5	NA	NA	NA
Brown algae						
Total, no./m ²	1.1 \pm 0.4	0.2 \pm 0.1	1.3 \pm 0.4	17.8 \pm 0.1	13.7 \pm 0.9	15.3 \pm 1.8
Annuals, no./m ²	0.4 \pm 0.1	0.1 \pm 0.1	0.4 \pm 0.1	8.2 \pm 1.4	1.3 \pm 0.4	7.3 \pm 1.3
Perennials, no./m ²	0.4 \pm 0.2	0	0.4 \pm 0.2	9.1 \pm 1.2	12.3 \pm 0.9	7.4 \pm 0.8
<i>Nereocystis</i>	0.03 \pm 0.02	0.01 \pm 0.01	0.1 \pm 0.02	1.3 \pm 0.4	0.03 \pm 0.02	0.2 \pm 0.1
<i>Desmarestia</i>	0.2 \pm 0.1	0.1 \pm 0.1	0.8 \pm 0.4	2.5 \pm 0.8	1.4 \pm 0.5	6.8 \pm 1.2
<i>Macrocystis</i>	0.1 \pm 0.1	0	1.5 \pm 0.8	1.7 \pm 0.8	1.6 \pm 0.7	1.6 \pm 0.4
<i>Laminaria</i> spp.	0.1 \pm 0.0	0	0.2 \pm 0.2	1.6 \pm 0.4	3.6 \pm 0.8	0.6 \pm 0.2
<i>Pterygophora</i>	0.1 \pm 0.04	0	0.2 \pm 0.2	4.2 \pm 1.1	6.4 \pm 0.8	4.5 \pm 0.7

Notes: Sea otter (*Enhydra lutris*) abundance is the maximum annual count of sea otters in each of the three main areas in 1988, 1994, and 2007. Sample sizes for urchin and brown algal density are $n = 20$ quadrats (each 0.5-m²) for 1988 and 1994 and $n = 30$ quadrats (each 0.5-m²) for 2007. Red urchin (*Strongylocentrotus franciscanus*) biomass was based on test diameter (TD) from the equation $\ln(\text{biomass}) = -7.046 + 2.807 \ln(\text{test diameter})$, which was calculated from 600 red urchins collected from three sites in Barkley Sound in 1989. Total algae include kelp sporophytes too small to classify as either perennial or annual species.

algae recruiting to urchin-free patches, creating urchin aggregations.

In 1990 we conducted experiments in Kyuquot Sound to evaluate these hypotheses. Six 5 \times 5 m plots were situated at least 25 m apart at 10–12 m below MLW in a semi-exposed bay (49°59.2' N, 127°17.7' W). The site was selected because urchins were abundant and a large expanse of flat rocky substrate allowed us to replicate the treatments without the potentially confounding effects of variation in substrate relief. Each quadrat was delineated by 1.2-m rebar pins set in the substrate at 1-m intervals and a grid of 25 1-m² subplots was created by stringing nylon cord around the tops of the pins 1.0 m above the substrate. We used this grid to map the position of red urchins and sea stars within each quadrat.

The plots were subjected to one of four treatments. In each experiment, divers mapped the red urchins in the 1-m² subplots before treatment and then at 2-h intervals during daylight for varying lengths of time (depending on the observed changes) thereafter. In the first treatment, divers mapped urchin positions to determine if urchin abundance and spatial distribution was affected by monitoring activities. Monitoring was conducted at 2-h intervals for 48 h. In the second treatment, the pneumatocyst and blades of bull kelp (*Nereocystis luetkeana*) were added to the center of the quadrats to see how the spatial distribution of urchins changed in response to kelp. The kelp was weighted down by pushing a rebar pin through the pneumatocyst, and urchins were mapped for 48 h and intermittently for 5 days after adding the kelp. In the third treatment, 10–

12 uninjured red urchins were placed in the center of the quadrats to determine how urchins responded to the addition of living and undamaged conspecifics. In the fourth treatment, we mimicked otter predation by breaking the oral surface of the urchins and scooping out the viscera. We placed 10–12 eviscerated red urchin tests in the centers of plots to see how red urchins responded to the addition of damaged conspecifics. Urchins were mapped for 48 h and intermittently for 15 days thereafter.

Each treatment was applied to three of the six quadrats. Two experiments were run simultaneously, starting with the addition of living urchins and the addition of kelp. A period of 7 days elapsed between the end of the first set of experiments and the start of the second set of experiments (effects of mapping urchins; eviscerated urchin addition). We analyzed the data from each experiment separately and used two-tailed *t* tests to determine if urchin density varied significantly before vs. 24 h after the treatments.

RESULTS

Sea otter surveys

At the start of our study in 1987, otters occurred in northwestern Checleset Bay and off Nootka Island, but were absent from Barkley and Kyuquot Sounds. Population density and range both increased in the ensuing 23 years. In 1987, we counted 234 sea otters in central and northwestern Checleset Bay (Fig. 2). That number had increased to about 600 in 1995 and 950 in 2007. The number of otters counted at Nootka Island remained roughly constant at ~150 animals from 1987

TABLE 2. Extended.

Kyuquot Sound, otters		
Absent	Present	Present
1988	1994	2007
3	397	566
79.2 ± 2.5	72.5 ± 2.0	NA
9.5 ± 1.0	2.8 ± 1.2	0.1 ± 0
2.9 ± 0.2	0.7 ± 0.4	NA
1.7 ± 0.7	25.5 ± 1.6	10.4 ± 1.5
1.0 ± 0.5	9.3 ± 1.9	2.3 ± 0.9
0.4 ± 0.2	15.9 ± 1.6	7.4 ± 1.2
0.2 ± 0.1	2.3 ± 0.6	0.5 ± 0.2
0.9 ± 0.5	5.8 ± 1.5	1.7 ± 0.7
0	1.0 ± 0.8	0.7 ± 0.4
0.4 ± 0.3	8.3 ± 1.4	4.5 ± 1.4
0.2 ± 0.2	5.7 ± 1.0	3.9 ± 0.9

through 1997 (Fig. 2), when we stopped surveying this area for logistical reasons. We first saw sea otters in the Mission Islands in 1987, shortly after we started working in the area. Our counts in this area remained at four or less until 1992, increased to 40 in 1996, and to 256 in 2009 (Fig. 2). Otters were not seen in Kyuquot Sound until 1988, when up to four solitary individuals were observed. The count reached 25 in the following year and increased steadily to 1996 before leveling off at ~400 individuals, where it remained until 2006, when a sudden increase to 900 was observed. Other than occasional individuals, sea otters were absent from Barkley Sound throughout the study.

Random-site surveys

Barkley Sound (sea otters continuously absent).—Brown algae were generally rare (range 0–9.1 plants/m²) and red urchins abundant (range 2.2–22.1 urchins/m²) over the study period (Fig. 3A). Despite this overall pattern, brown algal abundance differed significantly among the three sampling periods (Kruskal-Wallis $H = 11.93$, $df = 2$, $P = 0.002$) from 1.1 plants/m² in 1988, to 0.2 plants/m² in 1994, to 1.3 plants/m² in 2007 (Table 2). In 1988 and 2007, ~33% of the individual brown algae were perennial species, whereas in 1994 nearly all of the few plants found were annuals (Table 2).

Although red urchins were ubiquitous, variation in urchin density among sites was high (1988 CV = 39%, 1994 CV = 38%, 2007 CV = 47%; Fig. 3A), with variance among years being significantly different (Cochran's C test, $C_{2,19} = 0.49$, $P \leq 0.05$). At least in part because of this variation, urchin biomass and density could not be shown to vary significantly among years (single-factor ANOVAs: for biomass, $F_{2,57} = 2.4$, $P = 0.12$; for square-root-transformed density, $F_{2,57} = 2.7$, $P = 0.08$; Table 2). However, mean test diameter varied significantly among

years (single-factor ANOVA, $F_{2,57} = 13.3$, $P < 0.0001$; Table 2) due to a recruitment event in 1994, after which ~33% of the animals sampled had test diameters ≤ 50 mm (Fig. 4A–C). Although these recruits reduced mean test diameter, they contributed little to biomass (Table 2).

Checleset Bay (sea otters continuously present).—In contrast with Barkley Sound, sea urchins were small (≤ 50 mm TD) and rare (range 0–2.2 urchins/m²) and brown algae were abundant (range 7.3–32.1 plants/m²; Fig. 3A) in Checleset Bay throughout the study period. The algal species composition differed across sites and among years; ~50% of the brown algae were annuals in 1988 and in 2007 (predominantly *Desmarestia*), whereas only 10% were annuals in 1994 (Table 2). Brown algal density could not be shown to vary significantly among years (Kruskal-Wallis $H = 6.1$, $df = 2$, $P = 0.06$; Table 2), due in part to high across-site variation (1988 CV = 28%, 1994 CV = 31%, 2007 CV = 53%; Fig. 3A), with variances about the three means being significantly different ($C_{2,19} = 0.61$, $P \leq 0.05$).

Urchin density varied significantly among years in Checleset Bay (Kruskal-Wallis $H = 7.8$, $df = 2$, $P = 0.06$; Table 2). As was the case in Barkley Sound, this variation resulted from episodic recruitment, although in Checleset Bay these events occurred in different years and varied more substantially in intensity among sites than they did in Barkley Sound. Red urchins recruited to two sites in Checleset Bay in 1995, 1998, and 2007. At one of these sites (McLean Island; the other was not as frequently monitored), urchin population density increased from zero in 1994 to 7.9 ± 1.7 urchins/m² in 1995, at which time the mean TD was 35.7 ± 0.9 mm ($n = 100$); values are means \pm SE (see Fig. 5A, B).

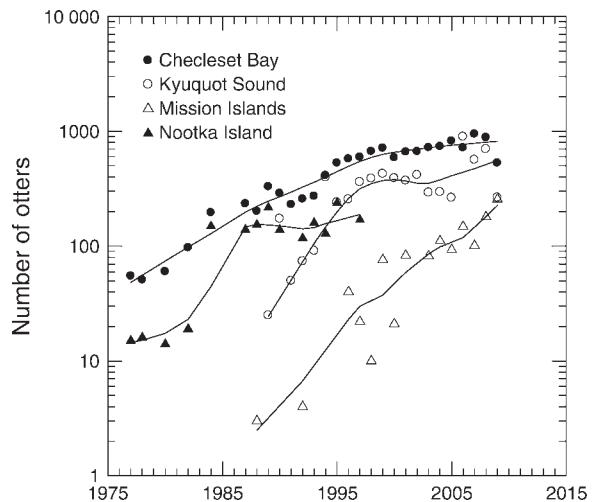


FIG. 2. Changes in sea otter (*Enhydra lutris*) abundance between 1977 and 2009; abundance estimates are the highest annual count for each area. Lines are Lowess smoothing function (Wilkinson 1999). Additional sources of data are: for 1977, Bigg and MacAskie (1978); for 1978, Morris et al. (1981); for 1982, M. A. Bigg (unpublished data); for 1984, MacAskie (1987).

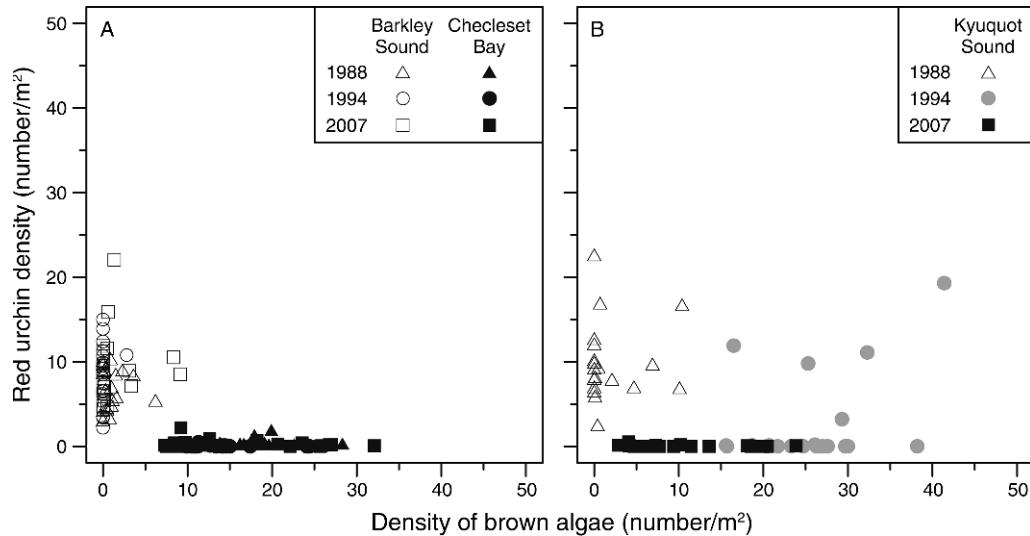


FIG. 3. Densities of red sea urchins (*Strongylocentrotus franciscanus*) vs. brown algae from random-site surveys (A) in Barkley Sound (sea otters absent) and Checleset Bay (sea otters abundant) and (B) in Kyuquot Sound. The surveys were first conducted in 1988 (triangles) and were repeated in 1994 (circles) and 2007 (squares). Sea otters were absent from Kyuquot Sound in 1988 (open triangles), present but in the early stage of reinvasion in 1994 (gray circles), and well established in 2007 (black squares).

Recruitment in Checleset Bay was invariably followed by size-specific mortality as these animals apparently were eaten by sea otters after reaching ~50 mm TD (Fig. 5B–D).

Kyuquot Sound (reinvaded by sea otters).—The arrival of sea otters to Kyuquot Sound was followed by a reduction in urchin biomass and density and an increase in brown algae (Fig. 3B, Table 2). Red urchin biomass

dropped significantly from 2.9 kg/m² in 1988, to 0.7 kg/m² in 1994, to near zero in 2007 (single-factor ANOVA, $F_{2,57} = 29.37$, $P < 0.0001$; Table 2). This reduction in biomass was caused by a decline in urchin density after 1988 (single-factor ANOVA, $F_{2,57} = 22.10$, $P < 0.0001$; Table 2), because urchin test diameter did not change significantly between 1988 and 1994 ($t = 0.47$, $P = 0.64$; Table 2; Fig. 4D, E). Between 1988 and 1994 overall

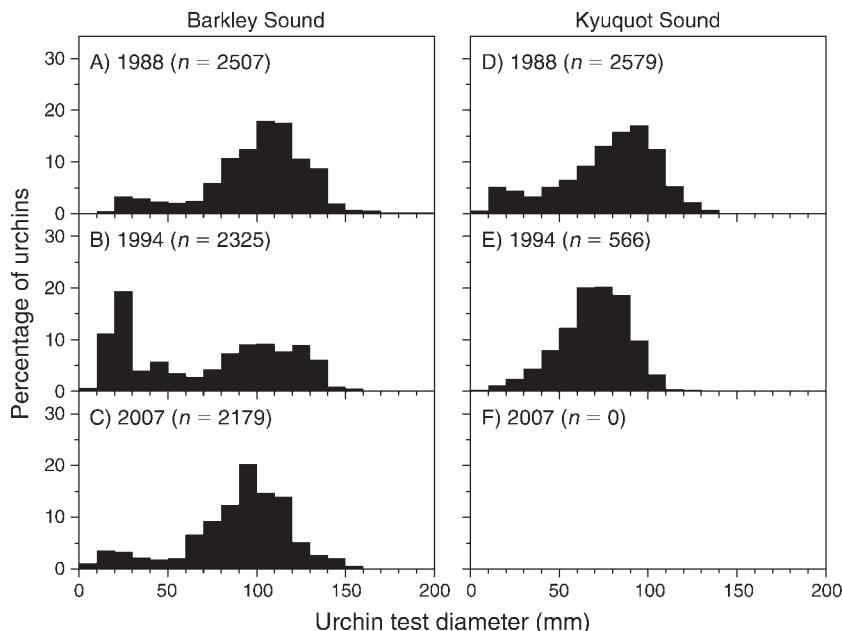


FIG. 4. Size frequency histogram of red urchin test diameters (TD) from the random-site surveys conducted in (A–C) Barkley Sound in 1988, 1994, and 2007 (otters absent throughout) and (D–F) Kyuquot Sound (otters absent in 1988, in early stages of reinvasion in 1994, and well established in 2007). Note that both population density and maximum size of red urchins had declined in Kyuquot Sound by 1994 and that urchin density had declined to near zero in 2007.

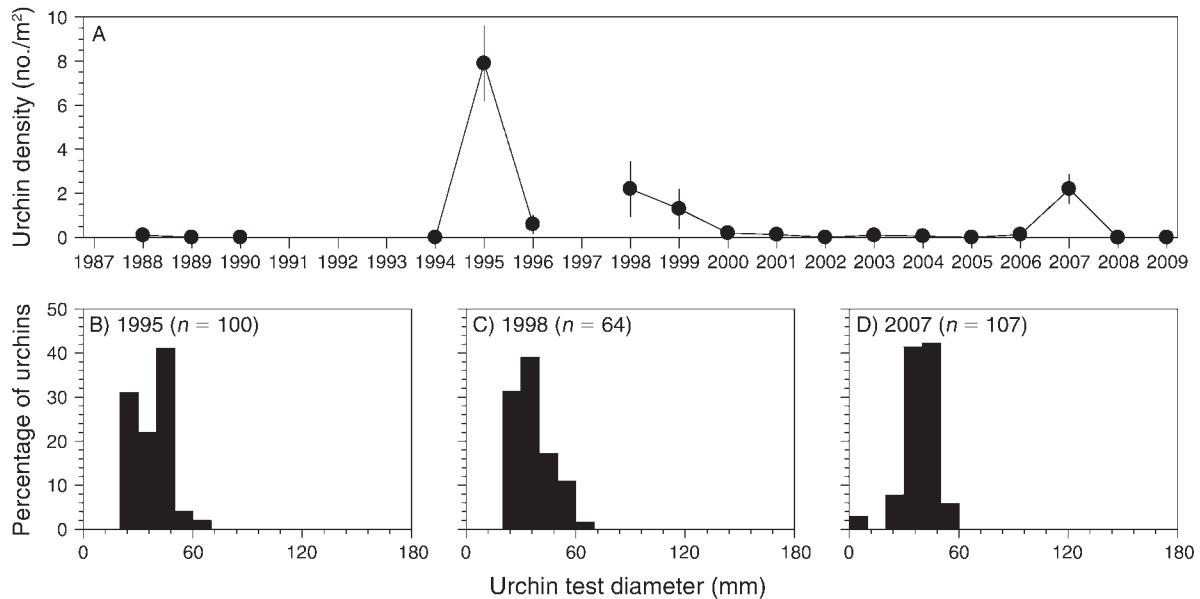


FIG. 5. (A) Density (mean \pm SE; $n = 30$ quadrats, each 0.5 m^2) of red urchins that recruited episodically at McLean Island between 1988 and 2009 (not all years were sampled), and size frequency of red urchins in (B) 1995, (C) 1998, and (D) 2007. Recruitment of urchins at this site, where otters were continuously present, was followed by size selective mortality in the urchin recruits.

brown algal density changed significantly increasing from $1.7/\text{m}^2$ to $25.5/\text{m}^2$, but declining to $10.4/\text{m}^2$ by 2007 (Kruskal-Wallis $H = 45.08$, $df = 2$, $P < 0.0001$; Table 2). In 1988 and 1994, the algae were mostly annuals (predominantly *Desmarestia*; Table 2), whereas in 2007 the algae were mainly perennial species (predominantly stipitate kelps; Table 2).

These community changes were characterized by extreme spatial variation and temporal asynchrony. For example, brown algae, which ranged in abundance from 0 to $10.4 \text{ plants}/\text{m}^2$ among the 20 sample sites in 1988, were rare or absent at 15 of the sites; urchins, with density ranging from 2.3 to $22.4 \text{ urchins}/\text{m}^2$ (Fig. 3B), were abundant at all sites. By 1994, sea otters occurred throughout Kyuquot Sound and brown algae were abundant at all sites (range $15.7\text{--}41.4 \text{ plants}/\text{m}^2$), whereas urchins had become rare or absent at 15 sites (Fig. 3B) and their overall density had declined to $2.8 \text{ urchins}/\text{m}^2$ (Table 2). Recently invaded sites were often characterized by an algal/urchin mosaic (e.g., Duggins 1983) composed of urchin-free areas or patches of brown algae (3–8 m diameter) interspersed among dense aggregations of urchins (up to $140 \text{ urchins}/\text{m}^2$).

In 1988, algal/urchin mosaics occurred at four of the 20 sites in Kyuquot Sound. Sea otters were seen at each of these sites and freshly broken urchin tests provided evidence of otter foraging. In 1992, otters were observed at an additional four sites (sites 14, 16, 17, and 19; Fig. 6), all of which had changed from urchin barrens to algal/urchin mosaics. By 1994, urchins were absent from sites 16 and 17, urchin density had declined at site 14, but remained unchanged at site 19 (Fig. 6A–D). From

1988 to 1992, the size distribution of urchins shifted significantly as the largest urchins disappeared from sites 14, 16, and 19 (Fig. 6E, G, H; $P < 0.0001$, Kolmogorov-Smirnov tests for each). Brown algal densities had increased at all sites by 1994 (Fig. 6A–D), and by 2007 red urchins were rare or absent throughout Kyuquot Sound (Table 2).

Permanent plots

Physical measurements.—The topographic indices of the permanent plots did not differ significantly among the eight sites (single-factor ANOVA, $F_{7,32} = 1.6$, $P = 0.16$; Table 3). The average warmest monthly water temperature occurred in August. Average SST at Kains Island exceeded 16°C only once from 1987 to 2009, reaching 16.2°C in August 1994 (Fig. 7A). Average water temperatures at 10 m below MLW never exceeded 16°C during the 1999–2009 measurement period (Fig. 7B, C) and only surpassed 13°C twice: in August 1999 and 2004 (Fig. 7B, C). However, daily water temperatures at sites in Checleset Bay and Kyuquot Sound regularly exceeded 14°C , and occasionally 16°C in late July, August, and early September, particularly in 2007.

Permanent plots continuously without sea otters: Wizard Island and Taylor Islet.—These were mostly urchin-dominated throughout the 23-year study period (Fig. 8A, B). However, the density and size structure of the urchin population changed through time. Red urchins recruited to both sites in 1994 and urchin density varied significantly among years at both sites, ranging from $4.9 \text{ urchins}/\text{m}^2$ in 1991 to $9.3 \text{ urchins}/\text{m}^2$ in 1997 at Wizard Island (repeated-measures

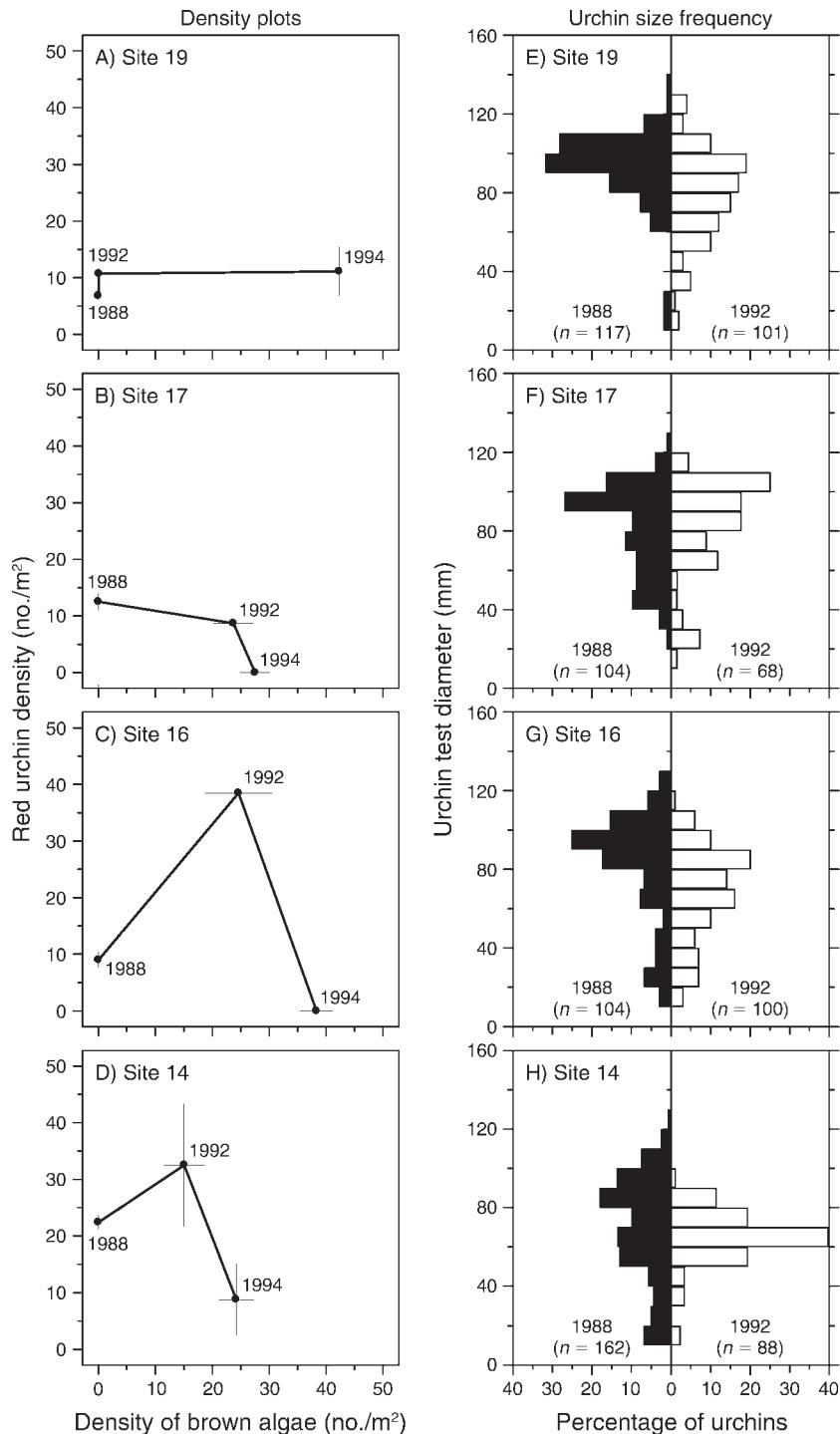


FIG. 6. (A–D) Red urchin density (mean \pm SE; $n = 20$) plotted against brown algal density (mean \pm SE; $n = 20$ quadrats, each 0.5 m^2) at four of the random sites in 1988, 1992, and 1994. Patchy mosaics of urchins and algae formed at all of these sites when sea otters arrived. (E–H) Red urchin size frequencies at four random sites in Kyuquot Sound sampled in 1988 and 1992; sample sizes are the number of urchins measured.

ANOVA, $F_{4,22} = 1.94$, $P = 0.02$; Fig. 9A), and from 3.0 urchins/m² in 1987 to 6.2 urchins/m² in 1994 at Taylor Islet (repeated-measures ANOVA, $F_{4,21} = 3.34$, $P < 0.001$; Fig. 9A). Algae recruited regularly to the

shoreward ends of plots at both sites, when urchins were excluded periodically by wave-induced surge. Overall brown algal densities thus varied from 0.5 plants/m² in 1988 to 3.8 plants/m² in 2004 at Wizard

TABLE 3. Length (mean \pm SE) of the 2×10 m plots at each of the permanent plot sites.

Permanent plot	Length (m)	CV (%)
Wizard Island	10.54 \pm 0.07	1.43
Taylor Islet	10.56 \pm 0.16	1.52
Gull Island	11.26 \pm 0.39	7.83
No Name Island	10.92 \pm 0.26	5.39
Union Island	10.98 \pm 0.23	4.71
Maquinna Point	11.38 \pm 0.38	7.62
Kamils Anchorage	11.52 \pm 0.39	7.56
Kyuquot Bay	11.24 \pm 0.20	4.00

Notes: Relief was measured by comparing the contour distance along the seabed to the lineal distance of 10 m. The relief of the plots was not significantly different among sites (single-factor ANOVA, $F_{7,32} = 1.6$, $P = 0.16$).

Island (repeated-measures ANOVA, $F_{4,22} = 1.56$, $P = 0.08$; Figs. 9A and 10A) and from 0 plants/m² in 1992 to 1.2 plants/m² in 1993 at Taylor Islet (repeated-measures ANOVA, $F_{4,21} = 2.16$, $P = 0.007$; Figs. 9A and 10A).

Permanent plots continuously with otters: Gull and No Name islands.—In contrast, sites at Gull and No Name Islands were dominated by brown algae throughout the study (Fig. 8C, D), but although the phase state

remained unchanged, the species composition, population structure, and density of algae varied over time.

Total brown algal abundance at Gull Island changed little between 1988 and 1997, but increased sharply in 1998 (Fig. 9B) with the recruitment of *Desmarestia* following declines in *Pterygophora* and *Laminaria setchelli* (from 7.0 plants/m² in 1988 to 0.6 plants/m² in 1999; Fig. 10B). There was little *Pterygophora* recruitment to the permanent plots at Gull Island (Table 4), except in 1990 (when 20 new plants were tagged) and 1995 (when there were 23 plants too small to tag). The number of adult (tagged) plants declined from 87 to 23 individuals between 1988 and 1998. Furthermore, in 1989, the *Pterygophora* population at Gull Island was dominated by older plants with the modal age of 13–14 years; there were no plants younger than 7 years old, and 73% of the population was ≥ 12 years old (Fig. 11A). Tag-induced mortality and tag loss were considered negligible because only one of the 50 *Pterygophora* plants that were double-tagged in the sublittoral zone at Wizard Island was missing after one year and none of the plants lost their tags.

In 1992, 94 dead *Pterygophora* plants were found on the Gull Island permanent plots, the average age of

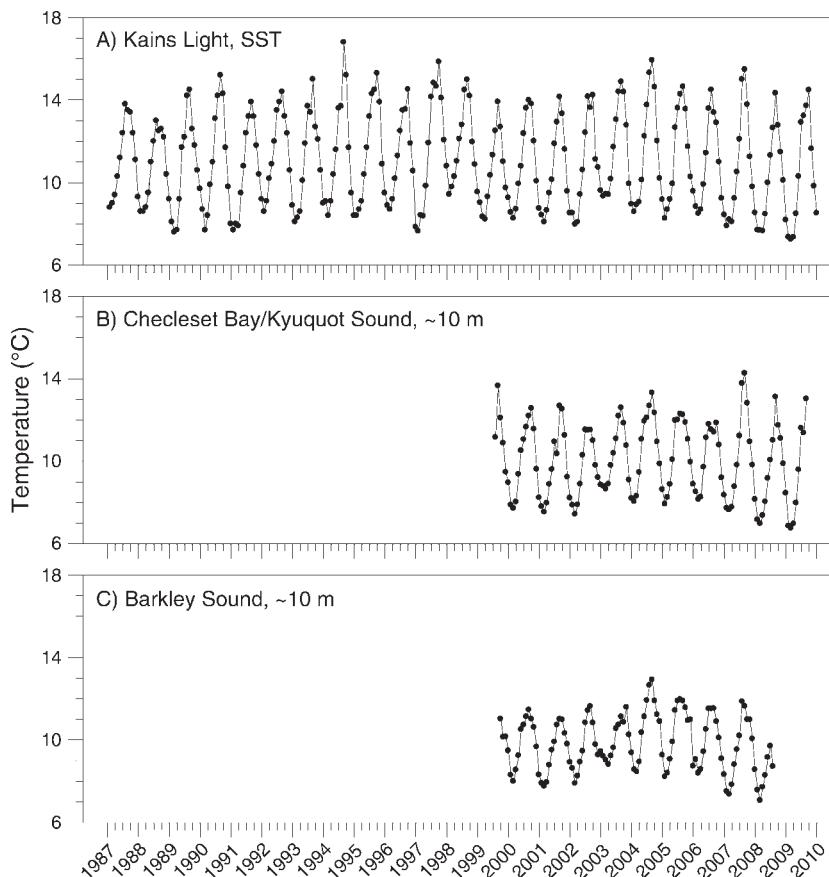


FIG. 7. (A) Sea surface temperature at Kains Island Light Station from 1986 to 2009 (available from Fisheries and Oceans Canada (<http://www.pac.dfo-mpo.gc.ca/sci/osap/data>)). (B) Mean monthly water temperatures at ~ 10 m depth in Checleset Bay and Kyuquot Sound from 1999 to 2009. (C) Mean water temperature at ~ 10 m in Barkley Sound from 1999 to 2009.

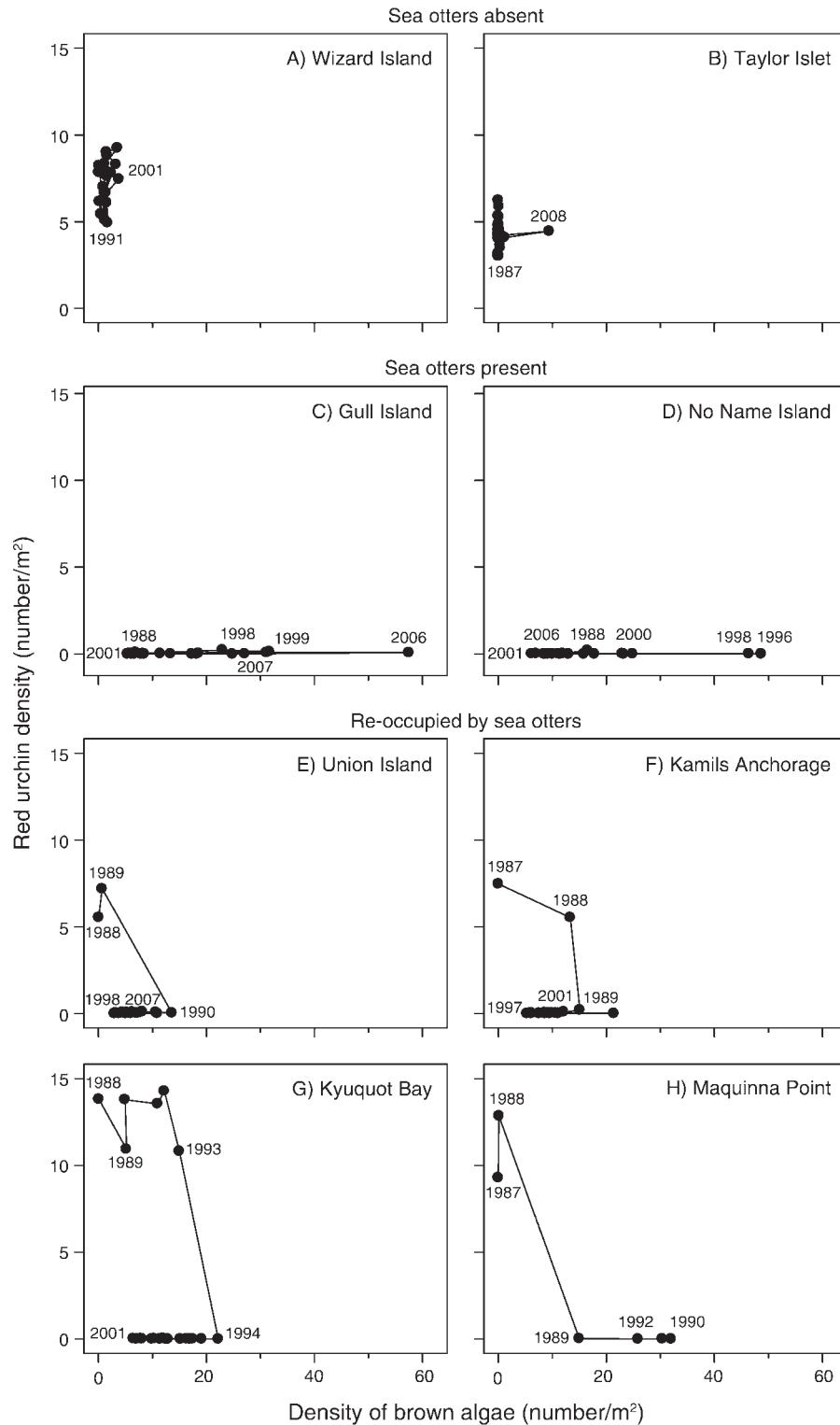


FIG. 8. Phase state transitions at the permanent plots shown by plotting annual mean red urchin density ($n = 5$ plots, 2×10 m each) against brown algal density ($n = 5$ plots, 2×10 m each) between 1987/1988 and 2009. (A, B) Permanent plots in areas continuously without sea otters. (C, D) Permanent plots in areas continuously with sea otters. (E–H) Permanent plots in areas that were occupied by sea otters during the study.

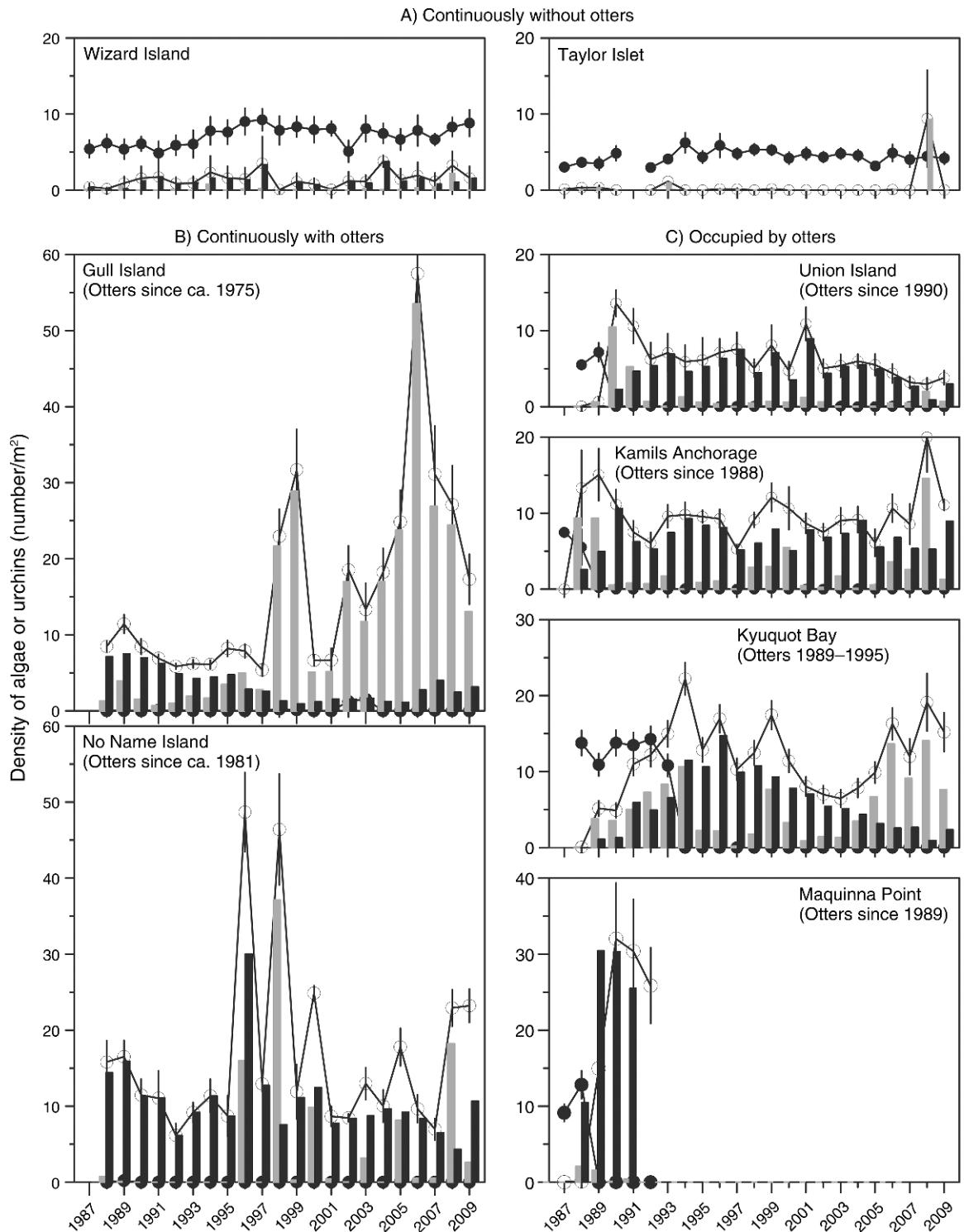


FIG. 9. Mean density ($n = 5$ plots, 2×10 m each), by year, of annual brown algae (gray bars), perennial brown algae (black bars), and total brown algae (open circles), and density of red urchins (solid circles) at the permanent plot sites (A) that were continuously without sea otters, (B) that were continuously with sea otters, and (C) that were occupied by sea otters during the study. Error bars are omitted from histograms for clarity; error bars for circles indicate \pm SE. Graphs are all on the same scale.

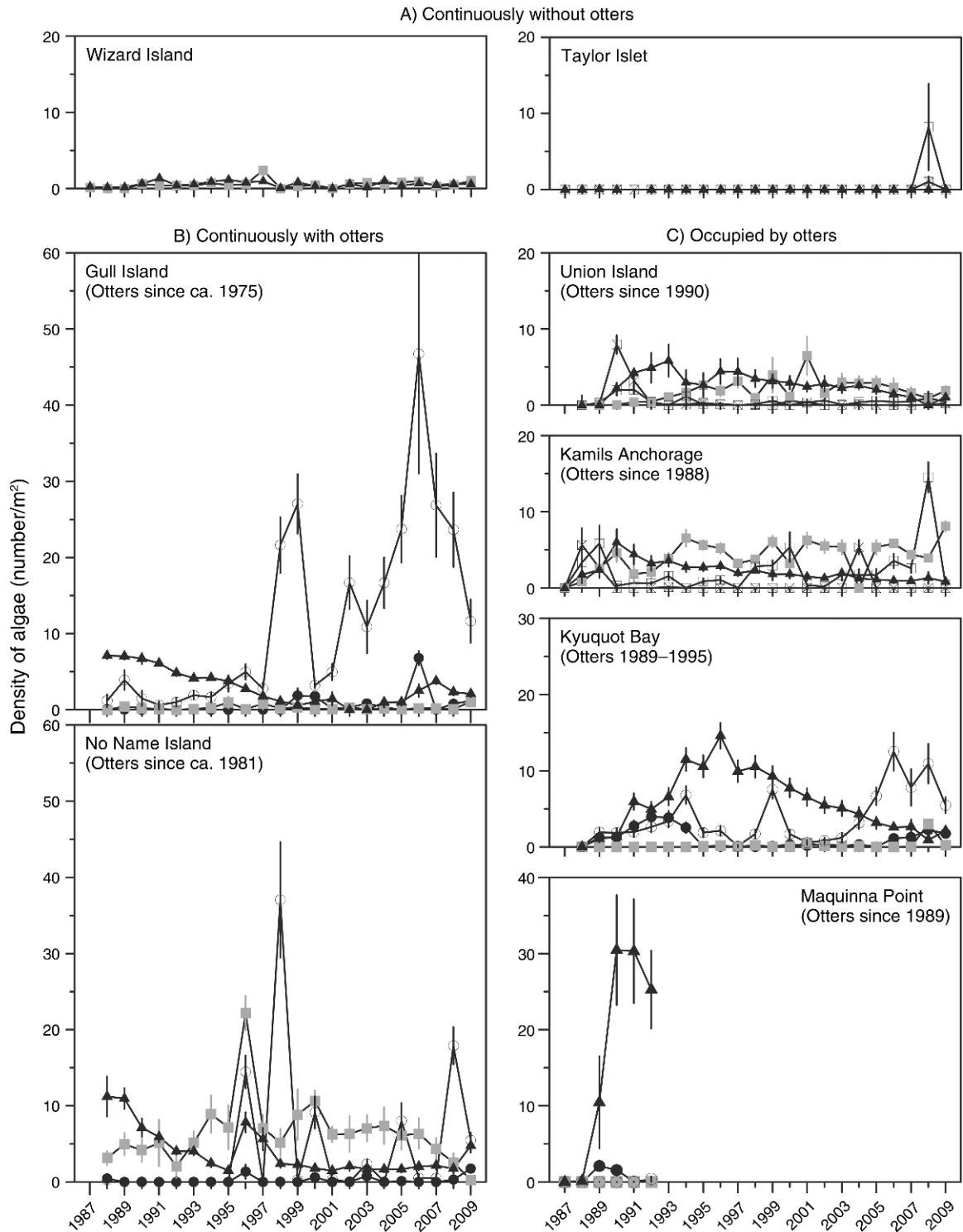


FIG. 10. Density (mean \pm SE; $n = 5$ plots, 2×10 m each) of *Nereocystis* (black circles), *Macrocyctis* (gray squares), *Desmarestia* (open circles), and stipitate kelps (*Pterygophora* and *Laminaria*; black triangles) at the permanent plot sites in (A) areas continuously without sea otters, (B) areas continuously with sea otters, and (C) areas that were occupied by sea otters during the study. Graphs are all on the same scale.

TABLE 4. The number of *Pterygophora* plants newly tagged each year (in parentheses) and the tagged plants that were relocated each year in the Gull Island permanent plot.

Year tagged	Year relocated										
	1988	1989	1990	1991	1992	1993	1994	1995	1996	1997	1998
1988	(87)	74	61	60	59	56	51	36	35	25	19
1989		(6)	6	6	6	4	3	1	1	1	0
1990			(20)	18	13	9	7	4	4	3	1
1991				(2)	1	1	1	1	0	0	0
1992					0	0	0	0	0	0	0
1993						(7)	7	3	2	2	2
1994							(1)	1	1	1	1
1995								0	0	0	0
1996									0	0	0
1997										0	0
Tagged	87	80	87	86	79	77	70	46	43	33	23
Untagged	1	0	3	0	0	0	1	23	9	5	0
Total	88	80	90	86	79	77	71	69	52	38	23

Note: Untagged plants were those plants too small to be tagged (<0.20 m).

which was 12.1 ± 0.2 years, mean \pm SE (range 8–18 years, mode = 13–14 years; Fig. 11D). *Desmarestia* spp. recruited at Gull Island following the decline of *Pterygophora*, and from 1996 onward, *Desmarestia* was the most common brown algal species at the Gull Island site (Fig. 10B). *Nereocystis luetkeana* formed a surface canopy in 2006, when it recruited at a density of 6.8 plants/m² (Fig. 10B), but was absent in 2007.

The species composition and abundance of brown algae at No Name Island (which in contrast with Gull Island contained a *Macrocystis* surface canopy) also varied through time (Figs. 9B and 10B). As at Gull Island, overall stipitate kelp density declined during the first half of the study, from 11.2 plants/m² in 1988 to 1.5 plants/m² in 1995 (Fig. 10B). The number of adult (tagged) *Pterygophora* plants increased from 76 in 1988 to 139 in 1990, but then declined to 18 in 1998 (Table 5). In 1989, all of the plants aged were younger than 10 years. There was no clear modal age and 81% of the population was between 3 and 7 years old (Fig. 11B).

Recruitment occurred, as indicated by the presence of small, untagged *Pterygophora* plants, but few of these new recruits survived to be tagged (Table 5). There was a distinct recruitment of various brown algal species at No Name Island in 1996, followed by a pulse of *Desmarestia* in 1998. In contrast with Gull Island, *Desmarestia* did not persist at No Name Island. Stipitate kelps increased to 7.8 plants/m² after the 1996 recruitment event, declining to 2.2 plants/m² by 2007 (Fig. 10B). *Macrocystis* whole-plant density increased to 8.2 plants/m² following the 1996 recruitment event, with stipes declining from 9.7 stipes/plant in 1995 to 2.7 stipes/plant in 1996, because the newly-recruited plants had few stipes compared to the older ones. *Macrocystis* stipe density (number of plants per square meter) varied significantly over the 23 year monitoring period (repeated-measures ANOVA, $F_{4,21} = 4.32$, $P = 0.0001$; Fig. 12A), due to the 1996 recruitment event (Tukey-Kramer multiple comparison test, $P < 0.05$). The number of stipes increased from 2.9 stipes/plant in

1996 to 23.2 stipes/plant in 1999 as the plants matured, but fluctuated from 5.8 to 19.8 stipes/plant from 2000 to 2009 as older plants were lost and new ones recruited (Fig. 12A).

Plots occupied by sea otters during the study: Union Island, Kamils Anchorage, Kyuquot Bay, Maquinna Point.—The arrival of sea otters led to shifts from urchin- to algal-dominated phase states in all permanent plots at each of the four sites. However, the timing and pattern of change differed among the sites.

1. *Union Island.*—Sea otters were absent from Union Island in 1988, but ~120 animals had occupied this area by July 1990. The arrival of otters was followed by a rapid shift from the urchin- to algal-dominated phase state (Fig. 8E). Red urchin density declined from 5.5 and 7.2 urchins/m² in 1988 and 1989, respectively, to 0.03 urchins/m² in 1990, whereas brown algal density increased from 0.1 to 0.7 plants/m² in 1988 and 1989 (respectively) to 13.6 plants/m² in 1990. The initial algal colonists were mostly annual species (Fig. 9C). By 1992, these annuals had been replaced primarily by stipitate kelps (Fig. 10C), which increased from 2.2 plants/m² in 1990 to 5.9 plants/m² in 1993, but declined to 1.1 plants/m² in 2007. *Macrocystis* stipe density varied significantly through time (repeated-measures ANOVA, $F_{4,21} = 2.41$, $P = 0.003$; Fig. 12B), increasing after 2007 to become the numerically dominant (based on stipe counts) brown algal species (Fig. 10C).

2. *Kamils Anchorage.*—The first known sea otter in Kamils Anchorage was a single animal seen in mid-October of 1987 feeding near the permanent plots. In the summer of 1987, red urchins were abundant and brown algae were rare (Fig. 8F). By 1988, brown algal density had increased from 0 to 13.3 plants/m² (repeated-measures ANOVA, $F_{1,8} = 7.2$, $P = 0.05$; Fig. 9C). Although abundance of red urchins had not declined significantly at this time (repeated-measures ANOVA, $F_{1,8} = 0.60$, $P = 0.5$; Fig. 9C), their spatial distribution across the plots changed noticeably, from a relatively even distribution before otters arrived in 1987 (CV

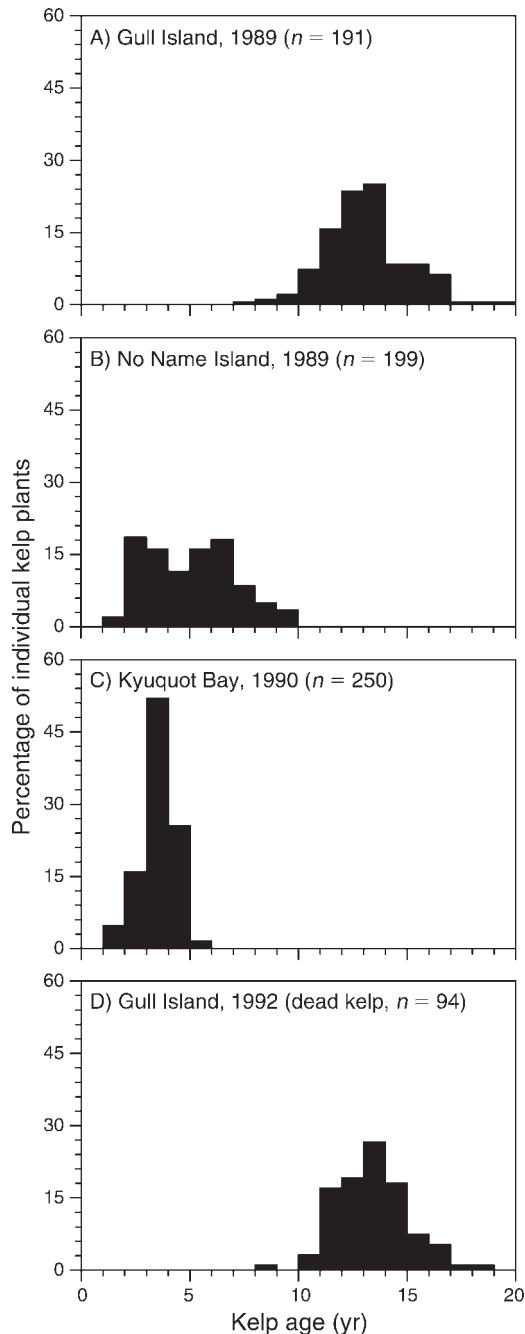


FIG. 11. To examine demographic variation in *Pterygophora californica* (tree kelp) populations, the age structure of kelp plants near three of the permanent plot sites was estimated by counting annuli in the stipes: (A) Gull Island in 1989, (B) No Name Island in 1989, and (C) Kyuquot Bay in 1990. The narrow age structure represents pulsed recruitment following the arrival of sea otters at each site. (D) Age frequency of dead *P. californica* plants found at Gull Island in 1992; the age of the plants suggested that mortality was due to senescence. For details, see *Discussion: Variation within phase states*.

urchin density = 13.5%) to a highly aggregated distribution after their arrival in 1988 (CV urchin density = 96.3%; Cochran's C test, $C_{2,4} = 0.94$, $P = 0.051$). During the same time, brown algae recruited to four of the five plots. By 1989, red urchins were largely absent and brown algae occurred in all of the plots. The first algae to recruit to Kamils Anchorage after otters arrived were primarily annual species: *Nereocystis* in 1988 and *Desmarestia* spp. in 1989 (Fig. 10C). By 1990, these species had been largely replaced by perennials (Fig. 9C). Stipitate kelps declined from 6.0 plants/m² in 1990 to 0.9 plants/m² in 2007. *Macrocystis* stipe density increased with the arrival of sea otters but fluctuated over time (Fig. 12C).

3. *Kyuquot Bay*.—The first sea otter was reported in Kyuquot Bay in November 1988, and although broken urchin tests on the sea floor indicated that sea otters were foraging occasionally in the area, they were rarely seen until 1993, when one or two animals were consistently present. In contrast with the other three permanent plots, the phase shift from an urchin- to algal-dominated state in Kyuquot Bay occurred slowly (Fig. 8G). Red urchin density did not change significantly between 1988 and 1993 (repeated-measures ANOVA, $F_{4,5} = 0.26$, $P = 0.96$), ranging from 10.9 urchins/m² in 1989 to 14.3 urchins/m² in 1992, whereas brown algal density increased significantly over this same period (repeated-measures ANOVA, $F_{4,5} = 6.26$, $P = 0.001$) from 0.1 plants/m² to 12.2 plants/m² (Fig. 8G). As at Kamils Anchorage, urchins and algae occurred in an algal/urchin mosaic caused by a change in the spatial distribution of red urchins. Urchins occurred on all five plots in 1988 and 1989 (CV urchin density = 32.6% and 39.4%, respectively), but by 1993 they had disappeared from three of these (CV urchin density = 134%; Cochran's C test, $C_{6,4} = 0.35$, $P \leq 0.05$). By 1994, urchins were absent from all of the plots and brown algae occurred as a mix of annual and perennial species (Fig. 9C). By 1995, annual algae had declined and stipitate kelps dominated (Fig. 10C). Stipitate kelp (mostly *Pterygophora*) abundance peaked in 1996 at 14.6 plants/m², declining to 0.9 plants/m² by 2008. In 1990, the age structure of *Pterygophora* was composed of plants 3–5 years old (Fig. 11C). *Desmarestia* settled in 1999 and abundance peaked at 12.5 plants/m² in 2006 (Fig. 10C).

4. *Maquinna Point*.—Sea otters were first seen at Maquinna Point in January 1989, when a single animal was observed eating red urchins over the permanent plots. Red urchin density declined from 12.8 urchins/m² in 1988 to 0.01 urchin/m² in 1989, whereas brown algae, which were absent in 1988 increased sharply (Fig. 8H). Although the rapid change from an urchin- to algal-dominated phase state following the arrival of sea otters was similar to that seen at Union Island (Fig. 8E), the patterns of algal recruitment differed. Perennial stipitate kelps were the initial colonists at Maquinna Point and

TABLE 5. The number of *Pterygophora* plants newly tagged each year (in parentheses) and the tagged plants that were relocated each year in the No Name Island permanent plot.

Year tagged	Year relocated										
	1988	1989	1990	1991	1992	1993	1994	1995	1996	1997	1998
1988	(76)	76	75	73	71	62	56	36	31	26	12
1989		(21)	21	20	19	16	12	7	8	7	4
1990			(43)	31	15	8	6	2	1	1	0
1991				(8)	5	1	1	0	0	0	0
1992					0	0	0	0	0	0	0
1993						(7)	7	2	1	0	0
1994							(2)	2	0	0	0
1995								(2)	0	0	0
1996									(1)	1	1
1997										(1)	1
Tagged	76	97	139	132	110	94	84	51	42	35	18
Untagged	62	115	37	0	0	10	0	0	126	25	1
Total	138	212	176	132	110	104	84	51	168	61	19

Note: Untagged plants were those plants too small to be tagged (<0.20 m).

remained as the dominate species until we stopped monitoring this site in 1992 (Figs. 9C and 10C).

Transitional dynamics

The density of red urchins did not change significantly in response to divers mapping them ($t = 0.10$, $df = 2$, $P =$

0.97; Fig. 13) or in response to adding undamaged conspecifics ($t = -0.31$, $df = 2$, $P = 0.77$; Fig. 13). Likewise, adding kelp did not affect overall urchin density ($t = 0.39$, $df = 2$, $P = 0.71$; Fig. 13), although distribution within the quadrats changed as urchins aggregated around the kelp. Before adding kelp, the

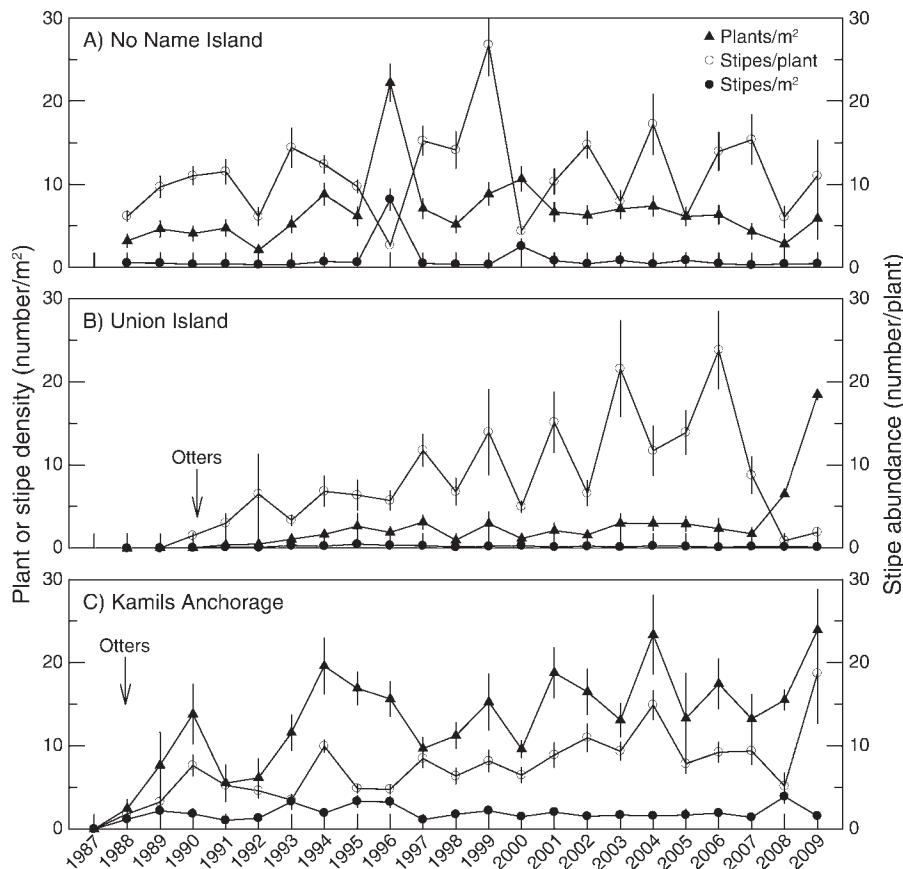


FIG. 12. Density (mean \pm SE; $n = 5$ plots, 2×10 m each) of *Macrocystis* plants and stipes, and the number of stipes per plant (mean \pm SE) at (A) No Name Island (continuously with otters), (B) Kamils Anchorage (occupied by otters during the study), and (C) Union Island (occupied by otters during the study). Permanent plots not listed did not have *Macrocystis*.

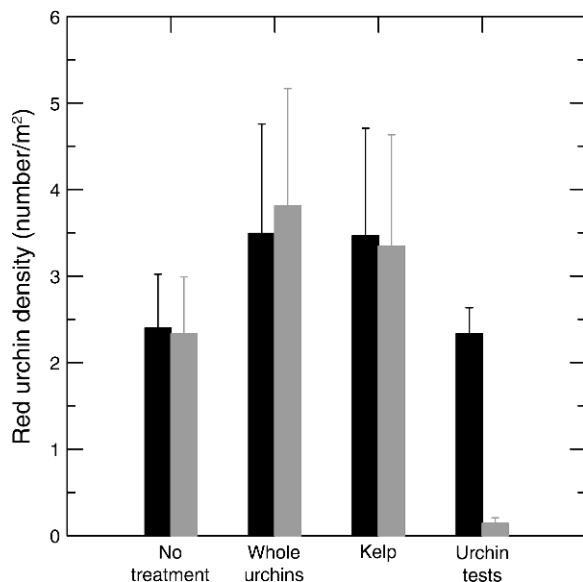


FIG. 13. Density of red urchins (mean \pm SE; $n = 3$ quadrats, each 5×5 m) in each of the four urchin experiments at time 0 (black) and 24 hours after (gray) each experimental treatment. Treatments, designed to examine the role that red urchin behavior played in creating algal/urchin mosaics, measured the response of urchins to: (1) no treatment, a control for the effects of divers mapping urchin position in each quadrat; (2) whole urchins, a control for treatment effects, in which 10–12 red urchins were added to the center of each quadrat; (3) kelp, in which the bulb and sporophylls of a *Nereocystis luetkeana* plant were skewered with a steel rod and placed in the center of each quadrat; and (4) urchin tests, in which 10–12 urchins were eviscerated (to mimic sea urchins preyed upon by sea otters) and added to the center of each quadrat.

mean CV of urchin density within the three quadrats was 58.5% ($n = 3$), whereas 24 h after adding kelp, it had increased to 102.9% (Fig. 13), and by 196 h, the CV had declined to 62.4%. Urchin density changed significantly in response to the addition of eviscerated conspecifics ($t = 7.1$, $df = 2$, $P = 0.002$). The living urchins immediately fled these quadrats and after 24 h, few remained (Fig. 13). Urchin densities remained significantly below pretreatment levels for 228 h ($t = 2.9$, $df = 2$, $P = 0.04$). Sunflower stars (*Pycnopodia helianthoides*) scavenged on the eviscerated tests 24–48 h after the experiment started, which may have deterred urchins from returning (e.g., Dayton 1975a, Duggins 1983). Urchin density was ~ 0 urchins/m² when the sea stars arrived.

DISCUSSION

To capture the influences of long-term processes in natural systems, ecologists often use broadscale spatial sampling as “space-for-time-substitutions” (Pickett 1989). However, it is hard to know whether the heterogeneity seen in such samples is due to spatial variation in physical habitat or differing site-specific histories (Rees et al. 2001). In contrast, long-term studies, which reduce spatial variation and control for

historical differences among sites, provide a less representative picture of the larger area but a more detailed account of temporal change (Pickett and McDonnell 1989). Most long-term studies of kelp forests have been conducted in California and Mexico, where researchers, with relatively easy access to their study sites, have been able to document both spatial and temporal variation at a variety of scales (e.g., Dayton et al. 1999, Edwards 2004). In other regions, where kelp forests are less accessible, researchers have instead sampled intermittently over broad geographic areas to infer temporal processes and document spatial variation (e.g., Breen et al. 1982, Dayton 1985, Estes and Duggins 1995). These sampling approaches, which operate on different scales, can produce different impressions of community dynamics and may have contributed to some of the debate over what types of forcing are most important in structuring and regulating kelp forest communities (e.g., Foster 1990, Halpern et al. 2006).

In this study we used both broadscale random sampling and long-term monitoring to examine variation in the urchin- and kelp-dominated phase states created by the presence and absence of sea otters. Our overall findings are similar to those of Estes and Duggins (1995) in Alaska; i.e., these systems occur as either algal- or urchin-dominated phase states that are predictable in space and time based on the presence or absence of sea otters. There is, however, considerable variation in the composition of species and the demography of populations within these phase states. Further, we have shown that much of this variation, the time course and pattern of change between phase states, is explained by small-scale differences in recruitment, demography, succession, prey behavior, and the apparent vagaries of foraging sea otters.

Variation within phase states

In temperate subtidal systems, sea urchin grazing can create deforested landscapes (Lawrence 1975; see Plate 1). On a global scale, urchin populations are regulated by a range of invertebrate and vertebrate predators as well as physical factors, all of which can cause episodic fluctuations in abundance (for a review, see Harrold and Pearse 1987). Our findings accord well with this view. Sea urchins persist at high densities over large spatial and temporal scales along the west coast of Vancouver Island, but only where sea otters are absent. This urchin-dominated phase state is characterized by considerable small-scale temporal variation. For example, sea urchins recruited twice (in 1994 and 1996) to our permanent plots in Barkley Sound. The resulting changes in urchin density potentially accounted for 51% of the spatial variation documented in the random-site surveys of Barkley Sound. At urchin-dominated sites, algae were restricted primarily to the sublittoral fringe, where wave action reduced urchin grazing (e.g., Keats 1991); although macroalgae were sometimes present on the shoreward ends of the permanent plots at Wizard Island



PLATE 1. Along rocky shores on the west coast of Vancouver Island, Canada, grazing by urchins (in this case primarily *Strongylocentrotus. franciscanus*) can create deforested landscapes such as pictured here. Photo credit: Lynn Lee.

and Taylor Islet, these algae were frequently mowed down by foraging urchins (Fig. 9A), thus maintaining the deforested state.

Kelp forest systems have long been viewed as a mosaic of continuously changing patches that reflect the different histories and responses of particular areas to small- and large-scale environmental events (Dayton et al. 1984, Dayton et al. 1992). This mosaic structure, first described in terrestrial systems (Tansley 1920), is now broadly recognized as an emergent property of kelp forest communities in South Africa (Velimirov and Griffiths 1979), New Zealand (Schiel 1990), Chile (Vasquez et al. 2006), Australia (Andrew and Jones 1990), southeast Alaska (Duggins 1983), and the Atlantic coast of North America (Steneck et al. 2002). In our study, much of this patchiness, which appears as spatial heterogeneity at any instant in time, is caused by differences among sites in algal recruitment, succession, and demography, variation probably driven largely by exposure, proximity to source populations, and the time when sea otters first arrived. For example, brown algal densities in the permanent plots at both Gull and No Name islands (sites continuously occupied by sea otters) varied by an order of magnitude (6.1–57.5 plants/m² and 6.2–48.7 plants/m², respectively; Fig. 8C, D) over the course of our study, which exceeded the maximum spatial variation in algal abundance (7.3–32.1 plants/m²)

documented in the 2007 random-site survey of Checleset Bay (Fig. 3A).

Much of the variation in macroalgal abundance in kelp forest communities results not only from disturbance but also from propagule availability. This contention is supported by the fact that the initial algal colonists at three of the four permanent plots that were recolonized by otters during our study (Union Island, Kamils Anchorage, and Kyuquot Bay) were predominantly annuals (*Nereocystis* and *Desmarestia*), whereas at Maquinna Point the first algal recruits were perennials (primarily *Pterygophora* and *Laminaria*). Various studies have shown that seasonal differences in propagule availability can affect succession (Foster 1975, Dayton et al. 1984, 1992, Reed et al. 1997), which probably explains why the initial recruits and subsequent successional patterns varied among our permanent plots. Sea otters were first seen at Maquinna Point in December, suggesting that urchins were removed from this area during winter when the stipitate perennials *L. setchelli* and *P. californica* produce zoospores (McPeak 1981, DeWreede and Klinger 1987). Conversely, sea otters began foraging at Kamils Anchorage and Union Island in the early fall and summer, respectively, when annual species such as *Nereocystis* and *Desmarestia* spp. produce zoospores (Amsler and Neushul 1989, Edwards 2000). At Kyuquot Bay, where an algal/urchin mosaic persisted for 5 years

after sea otters initially colonized the area, a mix of annual and perennial algae occurred, probably reflecting seasonally variable recruitment to urchin-free patches.

The patterns of succession that we saw were similar to those reported in other studies of the cool-temperate northeast Pacific Ocean. Duggins (1980) followed algal succession after removing urchins from the outer coast of Glacier Bay, Alaska and found that within two years the initial annual colonist *Nereocystis* was replaced by the perennial *Saccharina bongardiana* (= *Laminaria groenlandica*). Off Vancouver Island, Pace (1981) removed red urchins and reported that *Nereocystis* and *Desmarestia* were initially most abundant but were replaced by *Pterygophora*. Annual brown algae are also outcompeted by perennials in central and southern California, with *Macrocystis* generally becoming dominant in sheltered areas and stipitate kelps dominant in exposed areas (Dayton et al. 1984, Reed and Foster 1984). Similar patterns were seen during our study. The annual algae that recruited to plots invaded by otters were soon outnumbered by perennial species. This pattern was reflected in the 1988 and 1994 random-site surveys of Checleset Bay and Kyuquot Sound. However, as perennial algae senesced at the Gull Island and Kyuquot Bay permanent plots, they were replaced by opportunistic annual species, a pattern mirrored in the 2007 random-site surveys of Checleset Bay.

Demographic processes also contribute to temporal variability in plant communities (Harper 1977, Dayton et al. 1984, 1999). *Pterygophora* plants can live up to 18 years (Reed and Foster 1984), often forming persistent stands on the shallow subtidal reefs of southern and central California (Dayton et al. 1984, Foster and Schiel 1985, Schiel and Foster 1986). *Pterygophora* was abundant off Vancouver Island, recruiting to all of the sites within two years of the removal of urchins by sea otters. This pulsed recruitment created *Pterygophora* populations with a narrow range of age classes (Fig. 11A–C; Watson 1993). Shading by adult plants appeared to prevent further algal recruitment, so that younger age classes of plants did not become established and the entire stand senesced, opening the system to massive algal recruitment. This interaction between initial recruitment, longevity, senescence, and renewed macroalgal recruitment was tracked in the permanent plots at Gull and No Name Islands. Gull Island was occupied by sea otters in the mid 1970s (Morris et al. 1981). By 1989, the *Pterygophora* population was dominated by older plants (73% of the population was ≥ 12 years old and no plants were younger than 7 years old; Fig. 11A; see Watson 1993). There was little recruitment and *Pterygophora* remained relatively constant in abundance until about 1993 (Table 4). However, in 1992 *Pterygophora* started to senesce and density declined until 1998, when *Desmarestia* recruited heavily to the plots (Fig. 10B). The resulting blanket of *Desmarestia* dominated the plots until 2009 and may have inhibited further kelp recruitment, as it does in

California (Dayton et al. 1984, 1999, Reed and Foster 1984, Clark et al. 2005). *Desmarestia* increased until 2005, when it started to decline. *Pterygophora*, *Laminaria*, and *Eisenia arborea* had begun to recruit to these sites by 2007.

A different series of events occurred at No Name Island, which was invaded by sea otters in the early 1980s. Although the oldest *Pterygophora* plants in 1989 were 9 years old, 89% of the population was 2–7 years old (Fig. 11B; Watson 1993). *Pterygophora* mortality and recruitment appeared more variable at No Name Island (Table 5), and the failure of a few strong cohorts to dominate at No Name Island was probably caused by a dense *Macrocystis* surface canopy, which shaded the understory (e.g., Dayton et al. 1984). *Desmarestia*, which recruited to these plots in 1996 and 1997, also disappeared fairly quickly, possibly because light levels beneath the *Macrocystis* canopy were too low (Dayton et al. 1984, Reed and Foster 1984, Edwards 1998). Even at Kyuquot Bay, where prolonged and patchy recruitment should have broadened the *Pterygophora* age distribution (Fig. 10C), *Pterygophora* eventually declined and was replaced by *Desmarestia* (Fig. 10C).

These data suggest that the mosaic structure of algal assemblages along the west coast of Vancouver Island is, at least in part, a consequence of pulsed recruitment and succession following the removal of urchins by sea otters. Furthermore it appears that the year and season that otters arrive can set the starting point of succession and affect algal demography in a way that could remain apparent for decades into the future. On a small scale these *Pterygophora* stands, with their even-aged distributions, may resemble severely burned terrestrial or silvicultural forests, whose demographic structure makes them increasingly susceptible to subsequent disturbance (Lecompte et al. 2005, Drever et al. 2006).

Physical forcing from oceanographic change also can strongly influence kelp forest ecosystems in the North Pacific Ocean, especially in southern California and Mexico. El Niño Southern Oscillation Events (ENSO) and the Pacific Decadal Oscillation (PDO) are two such processes that have been shown to affect kelp forests on a variety of scales (Dayton and Tegner 1984, Tegner et al. 1996, Edwards 2004, Edwards and Estes 2006). For example, during the strong 1997/1998 ENSO event, the southern range limit of *Macrocystis* along the Pacific coast of Baja California, Mexico shifted 100 km northward, the return of which was delayed when dense stands of *Eisenia arborea* recruited into these habitats (Ladah et al. 1999, Edwards 2004). Although the effects of ENSO events on kelp forests off Vancouver Island are less well known (but see Germann 1988, Milligan et al. 1999), we did not detect signs of synchronous environmental forcing during the ENSO events of 1991/1992 or 1997/1998. Long-term water temperature records from Kains Island and the shorter-term records from our permanent sites (Fig. 7A–C) suggest that nitrate generally was not limiting during our study. In

California, *Macrocystis* stipe density is used as an index of environmental carrying capacity (Dayton et al. 1992, Tegner et al. 1996). *Macrocystis* stipe density, measured on the three of our permanent plot sites where it occurred, did not vary significantly during ENSO event years (Fig. 12A–C), further suggesting that carrying capacity did not change appreciably in response to the same oceanographic events that strongly impacted kelp forests farther to the south. The Pacific Decadal Oscillation, which affects coastal water temperatures on a roughly 30-year cycle, shifted to a warmer, less productive phase in 1977 (Ware and Thomson 2005). The effects of PDO on kelp are not well known but may be large. *Macrocystis* biomass off Point Loma, California declined by 66% from 1957 to 1994 (Tegner et al. 1997). In British Columbia, Sutherland (1998) reported that kelp canopy biomass declined by 50% from 1976 to 1996, and a wide-scale decline of *Nereocystis* was detected off Vancouver Island in the early 1980s (Foreman 1984). Our study, conducted mainly during the warm phase of the PDO, is too short to detect the effects of such a low-frequency event.

Phase state transitions

Although there are numerous examples of systems with multiple stable states (Beisner et al. 2003, Knowlton 2004, Schröder et al. 2005), studies of the transition between phase states are rare, largely because the interceding equilibria are unstable, and because the shifts are infrequent and occur rapidly and unexpectedly (Konar and Estes 2003, Carpenter and Brock 2006, Scheffer 2009). Although we encountered the algal- and urchin-dominated states associated with the presence and absence of otters, as expected, we also found mosaics of urchins and algae in areas being invaded by sea otters, including the permanent plots. This mix of urchin-free patches, algae, and aggregations of urchins appeared to represent a transitional state between urchin barrens and kelp forests. Our experimental results suggest that the mosaics formed when sea urchins responded behaviorally to the risk of predation, rather than from sea otters removing urchins directly. As urchins fled from the damaged tests used to mimic those dropped by foraging otters, they created urchin-free patches within the deforested landscape. The urchin-free patches remained for ~10 days and were still visible 17 days later, which is sufficient time for algal recruitment, suggesting that algae could recruit (to the urchin-free patches) even when overall urchin abundance had not declined appreciably (e.g., Fig. 6A–D). Eventually, however, sea urchin abundance was reduced by sea otter predation and the system became entirely dominated by algae.

A number of urchin species are known to flee from injured conspecifics (Parker and Schulman 1986, Vadas and Elnor 2003) and their invertebrate predators (Dayton 1975a, Moitza and Philips 1979, Duggins 1983, Tegner and Levin 1983, Freeman 2006). The influence of

these trait-mediated effects on herbivory can equal or exceed those of direct mortality (Lima and Dill 1990, Schmitz et al. 1997, Dill et al. 2003). Stronglylocentrotid urchins, for example, are known to “stampede” from the sea star *Pycnopodia*, creating urchin-free patches to which algae may recruit (Dayton 1975a, b, Duggins 1983). Although a behavioral response probably explained both urchin-free patches and aggregations (which formed as urchins fled), foraging urchins also are attracted to and aggregate around kelp (Lees 1970, Russo 1979, Konar and Estes 2003). However, the urchin aggregations that formed around the experimentally introduced kelp in our study were short lived and did not alter urchin population density appreciably.

Variation in the abundance and foraging behavior of sea otters probably explains why the transitional pathways from urchin- to algal-dominated phase states differed among our study sites. Algal/urchin mosaics most likely formed where otters foraged intermittently and removed a few urchins each time they fed, whereas rapid and extensive phase shifts probably occurred where otters (a few or many) foraged intensely and removed all of the urchins in short order. For example, although sea otters had expanded past the Kyuquot Bay plots by 1989, it was five years before they were seen regularly in this area, and the algal/urchin mosaic persisted throughout this period. In contrast, at Union Island and Maquinna Point, the change from urchin barrens to kelp forest following the influx of otters occurred in less than a year.

Mosaics may be a common feature of many communities exhibiting alternate states (Rietkerk et al. 2004) and could contribute to the increased variability in thresholds of regime shifts among these various systems (see Carpenter and Brock 2006). Algal/urchin mosaics are a global phenomenon. In the Aleutian Islands and South Africa, urchins and patches of kelp coexist when the sweeping motion of algal blades prevent urchins from entering kelp stands (Velimirov and Griffiths 1979, Konar 2000, Konar and Estes 2003). In the Mediterranean (Sala et al. 1998, Bulleri and Benedetti-Cecchi 2006), the United Kingdom (Kitching and Ebling 1961), the Caribbean (Carpenter 1984), and South Australia (Andrew 1993), stable mosaics of urchins and algae occur where high-relief substrate provides refuge from predators. Finally, in the North Atlantic and southern California, urchins feed on detritus and graze less actively when algal drift is abundant, thereby maintaining the borders between kelp beds and urchin barrens (Harrold and Reed 1985, Steneck et al. 2002). The kelp/urchin mosaics that we observed on the west coast of Vancouver Island were highly transitory elements of the phase shift from the urchin- to algal-dominated phase states. This relatively rapid transition following sea otter reinvasion, which has also been described in southeast Alaska (Estes and Duggins 1995) and the outer coast of Washington State (Kvitek et al. 1998), is strikingly different from the Aleutian Islands, where the shift from

an urchin barrens to the algal-dominated state can take decades (Estes and Duggins 1995).

Persistence, resilience, and stability

Ecosystem stability encompasses two related phenomena: ecological resilience, the degree to which systems are capable of recovering from perturbations, and ecological persistence, which refers to how constant a system remains through time (Holling 1973). Suggestions that heterogeneous natural systems are more resilient (and thus more stable) than homogenous ones has refocused attention on the role that natural variation plays in ecological stability (McCann 2000, Elmquist et al. 2003). Our long-term chronicle of variation in urchin- and algal-dominated systems off the west coast of Vancouver Island provides new insights into the stability of these two community types.

When viewed from the perspective of phase states, the algal- and urchin-dominated systems both appear to be highly resilient. Except in areas reinvaded by sea otters, the phase states at all of our permanent plots remained unchanged during the 23 years over which they were monitored. This is very much in contrast with the findings of Ebeling et al. (1985) from Naples Reef in southern California, where periodic storms drove the system back and forth between the urchin- and algal-dominated phase states over several-year intervals. These differing patterns suggest that the phase states documented off Vancouver Island are globally stable basins of attraction (sensu Lewontin 1969), and that the phase state shifts that followed sea otter range expansion along the west coast of Vancouver Island are technically boundary points (changes with the addition or loss of a species) rather than strict alternate stable states (sensu Lewontin 1969). In contrast, the southern California system is characterized by regularly alternating stable states.

Stable states are often more broadly defined as predictable self-maintaining systems (Holling 1973), with species composition and abundance fluctuating within the limits defined by the basin of attraction (Gunderson 2000). A more detailed look within the phase states at the permanent plots provides insight into just how broad these basins of attraction can be (Fig. 3A, B). The composition of species and the abundance and structure of populations changed within all of our permanent plots. This was especially true for the algal-dominated phase state, where the species composition and demographic structure of the algal assemblage at any place and time was dictated by the vagaries of history, longevity, propagule availability, and the season of disturbance. Resilient communities need not simply tend toward an equilibrium state, but can cycle over time (Holling and Gunderson 2002). In our system, lags between succession, periods of stability, collapse, and renewed succession, created the mosaic of kelp-forest patches that defined the entire basin of attraction (e.g., Gunderson 2000). Thus, although persistent and pre-

dictable on one scale, the algal phase state was highly dynamic and unpredictable at another. Long-term records (Dayton et al. 1999) from the Point Loma kelp forest in southern California suggest similar patterns and processes.

The 23-year chronicle on which our analysis is based provides an unprecedented view of the structure and dynamics of rocky subtidal ecosystems in this largely unstudied area, especially when considered next to the patterns of covariation in abundance of sea otters, which are arguably the system's keystone predator. A longer time record may provide a different view of persistence, resilience, and variation, especially in the context of low-frequency environmental events. However, our perceptions and interpretations of the working of this system are based on real-time data that span the majority of a person's professional lifetime. A very much longer record will require the retrospective analysis of historical records or the piecing together of future time series by multiple generations of investigators.

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