

1 Stability, resilience, and phase shifts in rocky subtidal communities along the west coast of

2 Vancouver Island, Canada

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ABSTRACT

We used the extirpation, reintroduction, and spread of sea otters 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 re-established 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 was 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 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 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 behaviour led to differences in the abundance and/or composition of species within the two phase states.

Key words: *Enhydra lutris*, kelp demography, *Macrocystis*, mosaic structure, phase state, *Pterygophora*, resilience, sea otter, sea urchin, *Strongylocentrotus*, variation, *Desmarestia*

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INTRODUCTION

42 Ecosystems do not behave as static and predictable entities but rather as dynamic systems
43 that can be highly unpredictable in time and space (Scheffer and Carpenter 2003, Doak et al.
44 2008). One of the greatest challenges to understanding the dynamics of such systems is that it
45 requires long-term information. This is because snapshots in time provide a stationary view of
46 ecological processes whereas in reality systems are dynamic and characterized by protracted
47 change (Knowlton 2004). A long-term perspective further provides insight into ecological
48 stability, in particular measures of persistence, resilience, and sometimes even the existence of
49 multiple states.

50 Measuring ecological change requires a baseline or benchmark against which to
51 document natural variation (Dayton et al. 1998). Baselines are usually generated by long-term
52 monitoring (Spellerberg 1991), which allow ecologists to detect rare events as well as slow,
53 subtle and intricate ecological processes (Strayer et al. 1986). However, the temporal scale over
54 which these changes are measured depends upon the system (Carpenter et al. 2001), depending
55 in particular on the longevity and generation time of the important interactors. Most ecological
56 studies are too short term to distinguish between demographic inertia and the myriad other
57 processes that influence the structure and dynamics of the system (Thrush et al. 1997). Because
58 of the comparatively short generation times of the dominant autotrophs, some of the best known
59 examples of long-term studies have been conducted in marine ecosystems, especially in kelp
60 forests (Steneck et al. 2002).

61 Kelp forests, which occur in temperate ecosystems throughout the world's oceans
62 (Dayton 1985, Steneck et al. 2002), are regulated and structured by the interaction of a variety of
63 environmental and biological factors (Dayton 1985, Foster and Schiel 1985, Schiel and Foster

64 1986, Steneck et al. 2002). Globally, they are known to be highly-dynamic communities that can
65 collapse and recover with great speed (Steneck et al. 2002). Changes in kelp abundance can be
66 brought about by physical forcing such as episodic warm water events that facilitate disease
67 outbreaks in grazers (Pearse and Hines 1979, Scheibling et al. 1999) or kill kelps outright
68 (Vasquez et al. 2006), by longer term temperature changes (Dayton et al. 1992, Sutherland
69 1998), and by biotic factors such as grazing by sea urchins (Lawrence 1975, Foreman 1977,
70 Harrold and Pearse 1987). In the eastern North Pacific Ocean, deforestation is precipitated most
71 often at lower latitudes ($< 40^\circ$) by oceanographic events, but the deforested state is usually short-
72 lived (Steneck et al. 2002). In contrast, deforestation at higher latitudes (40-60°) is induced
73 usually by urchin grazing but the deforested condition tends to be persistent and not easily
74 reversed (Estes and Duggins 1995).

75 A variety of predators regulate the abundance (Shears and Babcock 2003) or grazing
76 behaviour of sea urchins (Vadas and Elner 2003) and in doing so can mediate the abundance
77 species composition of kelp through a trophic cascade (Paine 1980, Terborgh and Estes 2010).
78 The ecological dynamics of urchins and their predators have been particularly well studied along
79 the Pacific coast of North America (Steneck et al. 2002, Estes et al. 2010). In Alaska (Estes and
80 Duggins 1995), British Columbia (Breen et al. 1982), and Washington (Kvitek et al. 1998)
81 predation by sea otters (*Enhydra lutris*) often limits the size and abundance of urchins. In these
82 areas most rocky reefs with sea otters have abundant algae and few sea urchins whereas those
83 without otters generally have abundant urchins and little algae. These differing community
84 configurations have been referred to as alternate stable states (Simenstad et al. 1978) or distinct
85 phase states (Steneck et al. 2002) due to their tendency, once achieved, to be self maintaining

86 (Konar and Estes 2003), and because intermediate or transitional stages are apparently unstable
87 and short-lived (Estes and Duggins 1995).

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

99 In this study, based on 23 years of field work, we examined spatial and temporal
100 variation in rocky reef communities in areas with and without sea otters along the outer coast of
101 Vancouver Island, British Columbia. Our study had three major goals: 1) to measure variation in
102 species composition and population density within the algal or urchin-dominated phase states
103 and determine the degree to which this variation is attributable to spatial differences versus
104 temporal processes; 2) to document patterns of change that occur with the switch from an urchin
105 to algal-dominated phase state as sea otters colonized areas; and 3) to measure and understand
106 heterogeneity within these phase states.

107 The study was designed around the reintroduction and expansion of sea otters into an
108 environment from which they had been historically extirpated. Knowing the distribution and

109 population trends of sea otters at the onset of our field study in the mid-1980s, we used three
110 approaches to achieve our goals. First, we used a random sampling method to compare the
111 abundance and species composition of sea urchins and macroalgae on rocky reefs in areas where
112 1) sea otters were well established, 2) sea otters were in the process of becoming established, or
113 3) sea otters had long been absent. This approach produced a largely spatial assessment of
114 variation in the otter-free and otter-dominated phase states. Second, we used permanently-
115 marked plots to provide a temporal record of phase state persistence and variation in algae and
116 urchin densities in the same ecological setting—i.e., areas where sea otters were 1) well
117 established 2) absent or 3) became re-established during the study period. This approach
118 provided a detailed view of the temporal dynamics of systems with and without sea otters, and
119 chronicled community changes associated with the return of sea otters. Finally we conducted a
120 manipulative experiment designed to explain the patterns of change that we observed as otters
121 spread and the system switched from the urchin to algal-dominated phase state. By combining
122 the observations obtained from the two approaches with the experimental results we describe the
123 patterns and explain the mechanisms of community transition associated with the arrival of sea
124 otters and then document variation, persistence, and resilience in the two phase state
125 configurations over time and space.

126 **METHODS**

127 *The Study Area*

128 Our research was conducted from 1987-2009 in four general locations on the west coast
129 of Vancouver Island, British Columbia (BC): Checleset Bay (~ 50 02° N 127 36° W); Kyuquot
130 Sound (~ 49 53° N 127 17° W); Nootka Island (~ 49 34° N 126 40° W); and Barkley Sound (~
131 48 54° N 125 18° W; Fig. 1). This area has a highly convoluted shoreline with open shores

132 exposed to ocean swell, deep fjords extending inland, large island-filled bays and shallow reefs.
133 Although much of the coast is rocky, hard substrate is often restricted to a narrow fringe that
134 extends to a water depth of ~12 m, below which rock often gives way of soft sediment deposited
135 from glaciers that melted after the Pleistocene (Cannings and Cannings 1996).

136 *The history of British Columbia sea otters*

137 Historically sea otters were abundant along the BC coast. Estimates and records suggest
138 that up to 55,000 pelts were harvested from this area during the maritime fur trade, which lasted
139 from the late 1700s until 1911 (Rickard 1947, Busch and Gough 1997, Mackie 1997, Gregr et al.
140 2008). Sea otters were economically and likely ecologically extinct from BC waters by about
141 1850; the last confirmed record of otters in BC is from 1929 (Cowan and Guiguet 1960). Sea
142 otters were absent from BC until 89 animals were reintroduced to Checleset Bay, on Vancouver
143 Island from 1969-1972 (Bigg and MacAskie 1978). At the start of our study in 1987, sea otters
144 occurred in northern Checleset Bay and in a small area off Nootka Island, but were absent from
145 Barkley and Kyuquot Sounds (Fig. 1). By 1990 sea otters had expanded throughout Kyuquot
146 Sound. In 2001 the sea otter population in BC was estimated at 3,180 animals, with 2,673 of
147 these located off the west coast of Vancouver Island (Nichol et al. 2005). Sea otters were
148 functionally absent from Barkley Sound throughout our study.

149 *Sea otter surveys*

150 Sea otter surveys were done annually from Checleset Bay to Kyuquot Sound between
151 July and September 1987 – 2009 and intermittently off Nootka Island during this period. Surveys
152 were conducted from small boats (~ 5 m) by 3-4 observers using binoculars, when sea conditions
153 were Beaufort 2 or less. Procedures were similar to those used for skiff surveys of sea otters in
154 the Aleutian Islands (Estes 1990, Doroff et al. 2003). The surveys followed a set route, and

155 covered all areas except fjords, which were not systematically surveyed. Multiple surveys were
156 conducted most years but the highest annual count was used to estimate population size.

157 *Subtidal community surveys*

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

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

178 Red urchins were the only common urchin species at our study sites. To estimate biomass
179 density and characterize population structure, red urchin test diameters were measured *in situ*
180 with callipers to the nearest mm. A minimum of 100 individuals or all the red urchins in the
181 quadrats were measured at each site. Red urchin biomass density (g wet mass /m²) was
182 calculated for each site using a regression of wet urchin mass to test diameter (see Table 2).
183 Average red urchin biomass density for each site was calculated from the total biomass of the
184 urchins collected divided by the number of quadrats sampled for urchins.

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

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

206 We established five permanent plots at each of the eight sites. A 25 m main axis was
207 placed parallel to shore 6-12 m below MLW and the five 2x10 m plots were located
208 perpendicular to the main axis on either side at random intervals. The main axis and the ends of
209 each plot were marked with stainless-steel bolts set into holes drilled in the rock substratum. To
210 ensure sites were similar in relief, (topography can affect the abundance, movement, and
211 behavior of sea urchins; Kitching and Ebling 1961) topographic indices (n=5 for each site) were
212 determined by comparing the contour distance along the seabed of each plot to its lineal distance
213 of 10m (Foster et al. 1986). A single-factor ANOVA was used to test for differences in
214 topography among the sites.

215 A Stowaway Tidbit Temperature Logger (Onset Computer Corporation, Pocasset MA)
216 was installed at each site at ~10m below MLW in the summer of 1999. Algal growth and
217 abundance can be limited by nitrate levels and since temperature is inversely related to nitrate
218 concentration, temperature can be used as a proxy for nitrate availability (Tegner et al. 1996). In
219 Southern California water temperatures < 14° C provide adequate nutrients for kelp growth (see
220 Dayton et al. 1999 for a review), whereas at temperatures >16° C nitrate is undetectable. In the
221 euryhaline waters of coastal BC, kelp growth can also be limited by salinity if low salinity co-
222 occurs with warm water (Druehl 1978). However these limiting conditions did not occur at our
223 sites as low salinity occurs in the winter when rainfall is greatest but the water is relatively cool.

224 During summer, when water is warm, salinity is stable at 30-32 ‰ (Druehl 1978). This meant
225 we could use water temperature to reasonably infer if nitrate availability affected kelp abundance
226 / biomass. Water temperature was recorded at 8 h intervals starting at 1200 h. Temperatures from
227 each site were averaged to provide a mean monthly water temperature for each area. To infer
228 water temperatures before 1999, the data collected from the loggers were compared to the long-
229 term SST data collected by the Canadian Department of Fisheries and Oceans at Kains Island
230 Light (50 25.9°N 128 00.3°W; www.pac.dfo-mpo.gc.ca/sci/osap/data).

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

239 To assess population stability (e.g., Dayton et al. 1984), mortality and recruitment in the
240 long-lived kelp *Pterygophora californica* was monitored at the Gull Island and No Name Island
241 permanent plots. From 1988-1998 all individuals of *Pterygophora* on one plot were labeled with
242 a numbered strip of PVC tape fastened loosely about the stipe by a cable tie. Surviving plants
243 were retagged each year. Plants ≤ 0.20 m tall were too small to tag, so recruits were defined as
244 untagged plants ≥ 0.20 m but ≤ 0.50 m (plants that had lost tags therefore were not considered
245 new recruits). From 1988 -1989 fifty *Pterygophora* plants in the shallow sublittoral zone at
246 Wizard Island were double-tagged to estimate tag loss and/or tag-induced mortality.

247 The age structure of *Pterygophora* populations at the Gull Island, No Name Island and
248 Kyuquot Bay permanent plots (where *Pterygophora* was abundant) was estimated by aging the
249 plants (DeWreede 1984). *Pterygophora* plants in 10 randomly selected 0.5 m² quadrats were
250 sampled in areas neighboring the permanent plots. A 0.07 – 0.10 m section was cut from above
251 the holdfast of each plant. Sections were placed in a labeled plastic bag (one / quadrat) and
252 preserved in 1% buffered formalin. Three thin sections were cut ~ 0.04 m from the base of each
253 of the sections, the thin sections were placed on a light table and the dark rings completely
254 encircling the stipe were counted. Plant age was calculated as a mean of the three estimates.

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

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

270 potential mechanisms to explain the mosaic pattern: 1) red urchins fled from the damaged red
271 urchin tests discarded by sea otters, creating urchin free patches, and 2) red urchins were
272 attracted to brown algae recruiting to urchin-free patches, creating urchin aggregations.

273 In 1990 we conducted experiments in Kyuquot Sound to evaluate these hypotheses. Six,
274 5x5 m plots were situated at least 25 m apart at 10–12 m below MLW in a semi-exposed bay
275 (49° 59.2 N, 127° 17.7W). The site was selected because urchins were abundant and a large
276 expanse of flat rocky substrate allowed us to replicate the treatments without the potentially
277 confounding effects of variation in substrate relief. Each quadrat was delineated by 1.2 m rebar
278 pins set in the substrate at 1m intervals and a grid of twenty-five 1m² subplots was created by
279 stringing nylon cord around the tops of the pins 1.0 m above the substrate. We used this grid to
280 map the position of red urchins and sea stars within each quadrat.

281 The plots were subjected to one of four treatments. In each experiment divers mapped the
282 red urchins in the 1m² subplots before treatment and then at 2 h intervals during daylight for
283 varying lengths of time (depending on the observed changes) thereafter. In the first treatment,
284 divers mapped urchin positions to determine if urchin abundance and spatial distribution was
285 affected by monitoring activities. Monitoring was conducted at 2 h intervals for 48 h. In the
286 second treatment the pneumatocyst and blades of bull kelp (*Nereocystis luetkeana*) were added
287 to the center of the quadrats to see how the spatial distribution of urchins changed in response to
288 kelp. The kelp was weighted down by a pushing a rebar pin through the pneumatocyst and
289 urchins were mapped for 48 h and intermittently for 5 days after adding the kelp. In the third
290 treatment 10-12 uninjured red urchins were placed in the center of the quadrats to determine how
291 urchins responded to the addition of living and undamaged conspecifics. In the fourth treatment
292 we mimicked otter predation by breaking the oral surface of the urchins and scooping out the

293 viscera. We placed 10-12 eviscerated red urchin tests in the centers of plots to see how red
294 urchins responded to the addition of damaged conspecifics. Urchins were mapped for 48 h and
295 intermittently for 15 days thereafter.

296 Each treatment was applied to three of the six quadrats. Two experiments were run
297 simultaneously starting with the addition of living urchins, and the addition of kelp. A period of
298 7 days elapsed between the end of the first set of experiments and the start of the second set of
299 experiments (effects of mapping urchins; eviscerated urchin addition). We analyzed the data
300 from each experiment separately and used two tailed t-tests to determine if urchin density varied
301 significantly before vs. 24 h after the treatments.

302 **RESULTS**

303 *Sea otter surveys*

304 At the start of our study, in 1987, otters occurred in northwestern Checleset Bay and off
305 Nootka Island but were absent from Barkley and Kyuquot sounds. Population density and range
306 both increased in the ensuing 23 years. In 1987, we counted 234 sea otters in central and
307 northwestern Checleset Bay (Fig. 2). That number had increased to about 600 in 1995 and 950 in
308 2007. The number of otters counted at Nootka Island remained roughly constant at about 150
309 animals from 1987 through 1997 (Fig. 2), when we stopped surveying this area for logistical
310 reasons. We first saw sea otters in the Mission Islands in 1987, shortly after we started working
311 in the area. Our counts in this area remained at four or less until 1992, increased to 40 in 1996,
312 and to 256 in 2009 (Fig. 2). Otters were not seen in Kyuquot Sound until 1988 when up to four
313 solitary individuals were observed. The count reached 25 the following year and increased
314 steadily to 1996 before levelling off at about 400 individuals where it remained until 2006 when

315 a sudden increase to 900 was observed. Other than occasional individuals, sea otters were absent
316 from Barkley Sound throughout the study.

317 *Random site surveys*

318 Barkley Sound (sea otters continuously absent) – Brown algae were generally rare (range
319 0 - 9.1 /m²) and red urchins abundant (range 2.2 – 22.1/m²) over the study period (Fig. 3A).
320 Despite this overall pattern, overall brown algal abundance differed significantly among the three
321 sampling periods (Kruskal Wallis $H = 11.9$, $P = 0.002$) from 1.1 plants /m² in 1988, to 0.2
322 plants/m² in 1994, to 1.3 plants/m² in 2007 (Table 2). In 1988 and 2007, about 33% of the
323 individual brown algae were perennial species whereas in 1994 nearly all of the few plants found
324 were annuals (Table 2).

325 Although red urchins were ubiquitous, variation in urchin density among sites was high
326 (1988 CV = 39%, 1994 CV = 38%, 2007 CV = 47%; Fig. 3A), with variance among years being
327 significantly different (Cochran's C test $C_{2,19} = 0.49$, $P \leq 0.05$). At least in part because of this
328 variation, urchin biomass and density could not be shown to vary significantly among years
329 (Single factor ANOVAs; biomass: $F_{2,57} = 2.4$, $P = 0.12$, density square root transformed:
330 $F_{2,57} = 2.7$, $P = 0.08$; Table 2). However, mean test diameter varied significantly among years
331 (Single factor ANOVA $F_{2,57} = 13.3$, $P = 0.000$; Table 2) due to a recruitment event in 1994, after
332 which about 33% of the animals sampled were ≤ 50 mm test diameter (Fig. 4A-C). Although
333 these recruits reduced mean test diameter, they contributed little to biomass (Table 2).

334 Checleset Bay (sea otters continuously present) -- In contrast with Barkley Sound, sea
335 urchins were small (≤ 50 mm TD) and rare (range: 0 – 2.2/m²) and brown algae were abundant
336 (range: 7.3 - 32.1/m²; Fig. 3A) in Checleset Bay throughout the study period. The algal species
337 composition differed across sites and among years--about 50% of the brown algae were annuals

338 in 1988 and in 2007 (predominantly *Desmarestia*) whereas only 10% were annuals in 1994
339 (Table 2). Brown algal density could not be shown to vary significantly among years (Kruskal
340 Wallis $H = 6.1$ $df = 2$, $P = 0.06$; Table 2), due in part to high across site variation (1988 CV =
341 28%, 1994 CV = 31%, 2007 CV = 53%; Fig. 3A, with variances about the three means being
342 significantly different $C_{2,19} = 0.61$, $P \leq 0.05$).

343 Urchin density varied significantly among years in Checleset Bay (Kruskal Wallis $H =$
344 7.8 , $df = 2$, 19 , $P = 0.02$; Table 2). As was the case in Barkley Sound, this variation resulted from
345 episodic recruitment although in Checleset Bay these events occurred in different years and
346 varied more substantially in intensity among sites than they did in Barkley Sound. Red urchins
347 recruited to two sites in Checleset Bay in 1995, 1998 and 2007. At one of these sites (McLean
348 Island, the other was not as frequently monitored) urchin population density increased from zero
349 in 1994 to $7.9 \pm 1.7 /m^2$ in 1995, at which time the mean TD was 35.7 ± 0.9 mm ($n = 100$) (Fig
350 5A-B). Recruitment in Checleset Bay was invariably followed by size-specific mortality as these
351 animals apparently were eaten by sea otters after reaching ~ 50 mm TD (Fig. 5B-D).

352 Kyuquot Sound (reinvaded by sea otters) –The arrival of sea otters to Kyuquot Sound
353 was followed by a reduction in urchin biomass and density and an increase in brown algae (Fig.
354 3B, Table 2). Red urchin biomass dropped significantly from 2.9 kg/m^2 in 1988, to 0.7 kg/m^2 in
355 1994, to near zero in 2007 (Single Factor ANOVA $F_{2,57} = 29.37$ $P = 0.00$; Table 2), this
356 reduction in biomass was caused by a decline in urchin density after 1988 (Single Factor
357 ANOVA $F_{2,57} = 22.10$ $P = 0.00$; Table 2) because mean urchin test diameter did not differ
358 significantly between 1988 and 1994 ($t = 0.47$ $P = 0.64$; Table 2; Fig. 4D-E). Between 1988 and
359 1994 overall brown algal density changed significantly increasing from $1.7/m^2$ to $25.5/m^2$, but
360 declining to $10.4/m^2$ by 2007 (Kruskal Wallis $H = 45.08$, $P = 0.00$; Table 2). In 1988 and 1994

384 average warmest monthly water temperature occurred in August. Average SST at Kains Island
385 exceeded 16° C only once from 1987-2009, reaching 16.2° in August 1994 (Fig. 7A). Average
386 water temperatures at 10m below MLW never exceeded 16° C during the 1999-2009
387 measurement period (Fig. 7B-C) and only surpassed 13° C twice--in August 1999 and 2004 (Fig.
388 7B-C), however daily water temperatures at sites in Checleset Bay and Kyuquot Sound regularly
389 exceeded 14 ° C, and occasionally 16° in late July, August and early September, particularly in
390 2007.

391 Permanent plots continuously without sea otters: Wizard Island and Taylor Islet. -- These
392 were mostly urchin-dominated throughout the 23 year study period (Fig. 8A&B). However, the
393 density and size structure of the urchin population changed through time. Red urchins recruited
394 to both sites in 1994 and 1996 and urchin density varied significantly among years at both sites,
395 ranging from 4.9/m² in 1991 to 9.3/m² in 1997 at Wizard Island (Repeated measures ANOVA
396 $F_{4,22} = 1.94, P = 0.02$; Fig. 9A), and from 3.0/m² in 1987 to 6.2/m² in 1994 at Taylor Islet
397 (Repeated measures ANOVA $F_{4,21} = 3.34, P=0.00$ Fig. 9A). Algae recruited regularly to the
398 shoreward ends of plots at both sites, when urchins were excluded periodically by wave-induced
399 surge. Overall brown algal densities thus varied from 0.5/m² in 1988 to 3.8/m² in 2004 at Wizard
400 Island (Repeated measures ANOVA $F_{4,22} = 1.56, P=0.08$; Fig. 9A, 10A) and from 0 /m² in 1992
401 to 1.2/m² in 1993 at Taylor Islet (Repeated measures ANOVA, $F_{4,21} = 2.16, P = 0.007$; Fig. 9A,
402 10A).

403 Permanent plots continuously with otters: Gull and No Name islands – In contrast, these
404 sites were dominated by brown algae throughout the study (Figs. 8C&D), but although the phase
405 state remained unchanged, the species composition, population structure and density of algae
406 varied over time.

407 Total brown algal abundance at Gull Island changed little between 1988 and 1997, but
408 increased sharply in 1998 (Fig. 9B) with the recruitment of *Desmarestia* following declines in
409 *Pterygophora* and *Laminaria setchelli* (from 7.0/m² in 1988 to 0.6/m² in 1999; Fig. 10B). There
410 was little *Pterygophora* recruitment to the permanent plots at Gull Island (Table 4), except in
411 1990 (when 20 new plants were tagged) and 1995 (when there were 23 plants too small to tag).
412 The number of adult (tagged) plants declined from 87 to 23 individuals between 1989 and 1998.
413 Furthermore, in 1989, the *Pterygophora* population at Gull Island was dominated by older plants
414 with the modal age of 13-14 years, there were no plants younger than 7 years and 73% of the
415 population was ≥ 12 years old (Fig. 11A). Tag-induced mortality and tag loss were considered
416 negligible because only one of the 50 *Pterygophora* plants that were double-tagged in the
417 sublittoral zone at Wizard Island was missing after one year and none of the plants lost their tags.

418 In 1992, ninety-four dead *Pterygophora* plants were found on the Gull Island permanent
419 plots, the average age of which was 12.1 ± 0.2 yrs (range = 8 – 18, mode = 13-14 yrs, Fig. 11D).
420 *Desmarestia* spp. recruited at Gull Island following the decline of *Pterygophora* and from 1996
421 onward *Desmarestia* was the most common brown algal species at the Gull Island site (Fig.
422 10B). *Nereocystis luetkeana* formed a surface canopy in 2006 when it recruited at a density of
423 6.8/m² (Fig. 10B) but was absent in 2007.

424 The species composition and abundance of brown algae at No Name Island (which in
425 contrast with Gull Island contained a *Macrocystis* surface canopy) also varied through time (Fig.
426 9B & 10B). As at Gull Island, overall stipitate kelp density declined during the first half of the
427 study, from 11.2/m² in 1988 to 1.5/m² in 1995 (Fig. 10B). The number of adult (tagged)
428 *Pterygophora* plants increased from 76 in 1988 to 139 in 1990 but then declined to 18 in 1998

429 (Table 5). In 1989 all of the plants aged were younger than 10 years. There was no clear modal
430 age and 81% of the population was between 3 and 7 years old (Fig. 11B).

431 Recruitment, as indicated by the presence of small untagged *Pterygophora* plants,
432 occurred but few of these new recruits survived to be tagged (Table 5). There was a distinct
433 recruitment of various brown algal species at No Name Island in 1996 followed by a pulse of
434 *Desmarestia* in 1998. In contrast with Gull Island, *Desmarestia* did not persist at No Name
435 Island. Stipitate kelps increased to $7.8/\text{m}^2$ after the 1996 recruitment event, declining to $2.2/\text{m}^2$
436 by 2007 (Fig. 10B). *Macrocystis* whole-plant density increased to $8.2/\text{m}^2$ following the 1996
437 recruitment event, with the stipes/plant declining from 9.7 in 1995 to 2.7 in 1996 because the
438 newly-recruited plants had few stipes compared to the older ones. *Macrocystis* stipe density (no.
439 / m^2) varied significantly over the 23 year monitoring period (Repeated measures ANOVA $F_{4,21} =$
440 4.3, $P=0.00$; Fig 12A), due to the 1996 recruitment event (Tukey Kramer Multiple Comparison
441 Test $P < 0.05$). The number of stipes/plant increased from 2.9 in 1996 to 23.2 in 1999 as the
442 plants matured, but fluctuated from 5.8 – 19.8 stipes/plant from 2000 to 2009 as older plants
443 were lost and new ones recruited (Fig. 12A).

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

448 *Union Island* – Sea otters were absent from Union Island in 1988, but about 120 animals
449 had occupied this area by July 1990. The arrival of otters was followed by a rapid shift from the
450 urchin to algal-dominated phase state (Fig. 8E). Red urchin density declined from 5.5 and $7.2/\text{m}^2$
451 in 1988 and 1989 respectively to $0.03/\text{m}^2$ in 1990, whereas brown algal density increased from

452 0.1 to 0.7/m² in 1988 and 1989 (respectively) to 13.6/m² in 1990. The initial algal colonists were
453 mostly annual species (Fig. 9C). By 1992 these annuals had been replaced primarily by stipitate
454 kelps (Fig. 10C), which increased from 2.2/m² in 1990 to 5.9/m² in 1993 but declined to 1.1/m²
455 in 2007. *Macrocystis* stipe density varied significantly through time (Repeated measures
456 ANOVA $F_{4,21} = 2.41, P=0.003$; Fig. 12B) increasing after 2007 to become the numerically
457 dominant (based on stipe counts) brown algal species (Fig. 10C).

458 *Kamils Anchorage* – The first known sea otter in Kamils Anchorage was a single animal
459 seen in mid October of 1987 feeding near the permanent plots. In the summer of 1987, red
460 urchins were abundant and brown algae were rare (Fig. 8F). By 1988 brown algal density had
461 increased, from 0 to 13.3/m² (Repeated measures ANOVA, $F_{1,8} = 7.2, P=0.05$; Fig. 9C).
462 Although red urchin abundance had not declined significantly at this time (Repeated measures
463 ANOVA, $F_{1,8} = 0.60, P=0.5$; Fig. 9C), their spatial distribution across the plots changed
464 noticeably, from a relatively even distribution before otters arrived in 1987 (CV urchin density =
465 13.5%) to a highly aggregated distribution after their arrival in 1988 (CV urchin density =
466 96.3%; Cochran's C test, $C_{2,4} = 0.94, P=0.051$). During the same time brown algae recruited to
467 four of the five plots. By 1989 red urchins were largely absent and brown algae occurred in all
468 the plots. The first algae to recruit to Kamils Anchorage after otters arrived were primarily
469 annual species, *Nereocystis* in 1988 and *Desmarestia* spp. in 1989 (Fig. 10C). By 1990 these
470 species had been largely replaced by perennials (Fig. 9C). Stipitate kelps declined from 6.0/m² in
471 1990 to 0.9/m² in 2007. *Macrocystis* stipe density increased with the arrival of sea otters but
472 fluctuated over time (Fig. 12C).

473 *Kyuquot Bay* - The first sea otter was reported in Kyuquot Bay in November 1988 and
474 although broken urchin tests on the sea floor indicated sea otters were foraging occasionally in

475 the area, they were rarely seen until 1993 when one or two animals were consistently present. In
476 contrast with the other three permanent plots, the phase shift from an urchin to algal-dominated
477 state in Kyuquot Bay occurred slowly (Fig. 8G). Red urchin density did not change significantly
478 between 1988 and 1993 (Repeated measures ANOVA $F_{4,5} = 0.26$, $P = 0.96$), ranging from 10.9
479 /m² in 1989 to 14.3/m² in 1992 whereas brown algal density increased significantly over this
480 same period (Repeated measures ANOVA $F_{4,5} = 6.26$, $P = 0.001$) from 0.1/m² to 12.2/m² (Fig.
481 8G). As at Kamils Anchorage, urchins and algae occurred in an algal/urchin mosaic caused by a
482 change in the spatial distribution of red urchins. Urchins occurred on all five plots in 1988 and
483 1989 (CV urchin density = 32.6 and 39.4%, respectively) but by 1993 they had disappeared from
484 three of these (CV urchin density = 134%; Cochran's C test $C_{6,4} = 0.35$, $P \leq 0.05$). By 1994,
485 urchins were absent from all of the plots and brown algae occurred as a mix of annual and
486 perennial species (Fig 9C). By 1995 annual algae had declined and stipitate kelps dominated
487 (Fig. 10C). Stipitate kelp (mostly *Pterygophora*) abundance peaked in 1996 at 14.6/m², declining
488 to 0.9/m² by 2008. In 1990 the age structure of *Pterygophora* was composed of plants 3-5 years
489 old (Fig. 11C). *Desmarestia* settled in 1999 and abundance peaked at 12.5/m² in 2006 (Fig.
490 10C).

491 *Maquinna Point* – Sea otters were first seen at Maquinna Point in January 1989 when a
492 single animal was observed eating red urchins over the permanent plots. Red urchin density
493 declined from 12.8/m² in 1988 to 0.01/m² in 1989 whereas brown algae, which were absent in
494 1988 increased sharply (Fig. 8H). Although the rapid change from an urchin to algal-dominated
495 phase state following the arrival of sea otters was similar to that seen at Union Island (Fig. 8E),
496 the patterns of algal recruitment differed. Perennial stipitate kelps were the initial colonists at

497 Maquinna Point and remained as the dominate species until we stopped monitoring this site in
498 1992 (Fig. 9C & 10C).

499 *Transitional Dynamics*

500 The density of red urchins did not change significantly in response to divers mapping
501 them ($t = 0.10$, $df = 2$, $P = 0.97$; Fig. 13) or in response to adding undamaged conspecifics ($t = -$
502 0.31 , $df = 2$, $P = 0.77$; Fig. 13). Likewise, adding kelp did not affect overall urchin density ($t =$
503 0.39 , $df = 2$, $P = 0.71$; Fig. 13), although distribution within the quadrats changed as urchins
504 aggregated around the kelp. Before adding kelp the mean CV of urchin density within the 3
505 quadrats was 58.5% ($n=3$) whereas 24 hours after adding kelp it had increased to 102.9% (Fig.
506 13), and by 196 hours the CV had declined to 62.4%. Urchin density changed significantly in
507 response to the addition of eviscerated conspecifics ($t = 7.1$, $df = 2$, $P = 0.002$). The living urchins
508 immediately fled these quadrats and after 24 hours few remained (Fig. 13). Urchin densities
509 remained significantly below pre-treatment levels for 228 h ($t = 2.9$, $df = 2$, $P=0.04$). Sunflower
510 stars (*Pycnopodia helianthoides*) scavenged on the eviscerated tests 24-48 h after the experiment
511 started, which may have deterred urchins from returning (e.g. Dayton 1975a, Duggins 1983).
512 Urchin density was $\sim 0 /m^2$ when the sea stars arrived.

513 **DISCUSSION**

514 To capture the influences of long-term processes in natural systems, ecologists often use
515 broad-scale spatial sampling as “space-for-time-substitutions” (Pickett 1989). However, it is hard
516 to know whether the heterogeneity seen in such samples is due to spatial variation in physical
517 habitat or differing site-specific histories (Rees et al. 2001). In contrast long-term studies, which
518 reduce spatial variation and control for historical differences among sites, provide a less
519 representative picture of the larger area but a more detailed account of temporal change (Pickett

543 in abundance (see Harrold and Pearse 1987 for a review). Our findings accord well with this
544 view. Sea urchins persist at high densities over large spatial and temporal scales along the west
545 coast of Vancouver Island, but only where sea otters are absent. This urchin-dominated phase
546 state is characterized by considerable small-scale temporal variation. For example, sea urchins
547 recruited twice (in 1994 and 1996) to our permanent plots in Barkley Sound. The resulting
548 changes in urchin density potentially accounted for 51% of the spatial variation documented in
549 the random site surveys of Barkley Sound. At urchin-dominated sites algae were restricted
550 primarily to the sublittoral fringe, where wave action reduced urchin grazing (e.g., Keats 1991),
551 and although macroalgae were sometimes present on the shoreward ends of the permanent plots
552 at Wizard Island and Taylor Islet, these algae were frequently mowed down by foraging urchins
553 (Fig. 9A), thus maintaining the deforested state.

554 Kelp forest systems have long been viewed as a mosaic of continuously changing patches
555 that reflect the different histories and responses of particular areas to small and large scale
556 environmental events (Dayton et al. 1984, Dayton et al. 1992). This mosaic structure, first
557 described in terrestrial systems (Tansley 1920), is now broadly recognized as an emergent
558 property of kelp forest communities in South Africa (Velimirov and Griffiths 1979), New
559 Zealand (Schiel 1990), Chile (Vasquez et al. 2006), Australia (Andrew and Jones 1990),
560 Southeast Alaska (Duggins 1983) and the Atlantic coast of North America (Steneck et al. 2002).
561 In our study much of this patchiness, which appears as spatial heterogeneity at any instant in
562 time, is caused by differences among sites in algal recruitment, succession and demography,
563 variation probably driven largely by exposure, proximity to source populations, and when sea
564 otters first arrived. For example, brown algal densities in the permanent plots at both Gull and
565 No Name islands (sites continuously occupied by sea otters) varied by an order of magnitude

566 (6.1 - 57.5/m² and 6.2 – 48.7/m² respectively Figs. 8C&D) over the course of our study, which
567 exceeded the maximum spatial variation in algal abundance (7.3 – 32.1/m²) documented in the
568 2007 random site survey of Checleset Bay (Fig. 3A).

569 Much of the variation in macroalgal abundance in kelp forest communities results not
570 only from disturbance but also from propagule availability. This contention is supported by the
571 fact that the initial algal colonists at three of the four permanent plots that were recolonized by
572 otters during our study (Union Island, Kamils Anchorage, and Kyuquot Bay) were
573 predominantly annuals--*Nereocystis* and *Desmarestia*--whereas at Maquinna Point the first algal
574 recruits were perennials--primarily *Pterygophora* and *Laminaria*. Various studies have shown
575 that seasonal differences in propagule availability can affect succession (Foster 1975, Dayton et
576 al. 1984, Dayton et al. 1992, Reed et al. 1997), which probably explains why the initial recruits
577 and subsequent successional patterns varied among our permanent plots. Sea otters were first
578 seen at Maquinna Point in December suggesting urchins were removed from this area during
579 winter when the stipitate perennials *L. setchelli* and *P. californica* produce zoospores (McPeak
580 1981, DeWreede and Klinger 1987). Conversely, sea otters began foraging at Kamils Anchorage
581 and Union Island in the early fall and summer respectively, when annual species such as
582 *Nereocystis* and *Desmarestia* spp. produce zoospores (Amsler and Neushul 1989, Edwards
583 2000). At Kyuquot Bay, where an algal/urchin mosaic persisted for 5 years after sea otters
584 initially colonized the area, a mix of annual and perennial algae occurred, probably reflecting
585 seasonally-variable recruitment to urchin-free patches.

586 The patterns of succession we saw were similar to those reported in other studies of the
587 cool-temperate northeast Pacific Ocean. Duggins (1980) followed algal succession after
588 removing urchins from the outer coast of Glacier Bay, Alaska and found that within 2 years the

589 initial annual colonist *Nereocystis* was replaced by the perennial *Saccharina bongardiana*
590 (= *Laminaria groenlandica*). Off Vancouver Island, Pace (1981) removed red urchins and
591 reported that *Nereocystis* and *Desmarestia* were initially most abundant but were replaced by
592 *Pterygophora*. Annual brown algae are also out-competed by perennials in central and southern
593 California, with *Macrocystis* generally becoming dominant in sheltered areas and stipitate kelps
594 in exposed areas (Dayton et al. 1984, Reed and Foster 1984). Similar patterns were seen during
595 our study. The annual algae that recruited to plots invaded by otters were soon outnumbered by
596 perennial species. This pattern was reflected in the 1988 and 1994 random site surveys of
597 Checleset Bay and Kyuquot Sound. However, as perennial algae senesced at the Gull Island and
598 Kyuquot Bay permanent plots they were replaced by opportunistic annual species, a pattern
599 mirrored in the 2007 random site surveys of Checleset Bay.

600 Demographic processes also contribute to temporal variability in plant communities
601 (Harper 1977, Dayton et al. 1984, Dayton et al. 1999). *Pterygophora* plants can live up to 18
602 years (Reed and Foster 1984), often forming persistent stands on the shallow subtidal reefs of
603 southern and central California (Dayton et al. 1984, Foster and Schiel 1985, Schiel and Foster
604 1986). *Pterygophora* was abundant off Vancouver Island, recruiting to all of the sites within 2
605 years of sea otters removing urchins. This pulsed recruitment created *Pterygophora* populations
606 with a narrow range of age classes (Fig 11A-C; Watson 1993). Shading by adult plants appeared
607 to prevent further algal recruitment so that younger age classes of plants did not become
608 established and the entire stand senesced, opening the system to massive algal recruitment. This
609 interaction between initial recruitment, longevity, senescence, and renewed macroalgal
610 recruitment was tracked in the permanent plots at Gull and No Name Islands. Gull Island was
611 occupied by sea otters in the mid 1970s (Morris et al. 1981). By 1989, the *Pterygophora*

612 population was dominated by older plants (73% of the population was ≥ 12 years and no plants
613 were younger than 7 years, Fig. 11A, Watson 1993). There was little recruitment and
614 *Pterygophora* remained relatively constant in abundance until about 1993 (Table 4). However, in
615 1992 *Pterygophora* started to senesce and density declined until 1998, when *Desmarestia*
616 recruited heavily to the plots (Fig. 10B). The resulting blanket of *Desmarestia* dominated the
617 plots until 2009 and may have inhibited further kelp recruitment, as it does in California (Reed
618 and Foster 1984, Dayton et al. 1984, 1999, Clark et al. 2005). *Desmarestia* increased until 2005,
619 when it started to decline. *Pterygophora*, *Laminaria* and *Eisenia arborea* had begun to recruit to
620 these sites by 2007.

621 A different series of events occurred at No Name Island, which was invaded by sea otters
622 in the early 1980s. Although the oldest *Pterygophora* plants in 1989 were 9 years, 89% of the
623 population was 2-7 years (Fig. 11B; Watson 1993). *Pterygophora* mortality and recruitment
624 appeared more variable at No Name Island (Table 5), and the failure of a few strong cohorts to
625 dominate at No Name Island was likely caused by a dense *Macrocystis* surface canopy, which
626 shaded the understory (e.g., Dayton et al. 1984). *Desmarestia*, which recruited to these plots in
627 1996 and 1997, also disappeared fairly quickly, possibly because light levels beneath the
628 *Macrocystis* canopy were too low (Dayton et al. 1984, Reed and Foster 1984, Edwards 1998).
629 Even at Kyuquot Bay, where prolonged and patchy recruitment should have broadened the
630 *Pterygophora* age distribution (Fig. 10C), *Pterygophora* eventually declined and was replaced by
631 *Desmarestia* (Fig. 10C).

632 These data suggest that the mosaic structure of algal assemblages along the west coast of
633 Vancouver Island is at least in part a consequence of pulsed recruitment and succession
634 following the removal of urchins by sea otters. Furthermore it appears that the year and season

635 that otters arrive can set the starting point of succession and affect algal demography in a way
636 that could remain apparent for decades into the future. On a small scale these *Pterygophora*
637 stands, with their even-aged distributions, may resemble severely-burned terrestrial or
638 silvicultural forests, whose demographic structure makes them increasingly susceptible to
639 subsequent disturbance (Lecompte et al. 2005, Drever et al. 2006).

640 Physical forcing from oceanographic change also can strongly influence kelp forest
641 ecosystems in the North Pacific Ocean, especially in southern California and Mexico. El Niño
642 Southern Oscillation Events (ENSO) and the Pacific Decadal Oscillation (PDO) are two such
643 processes that have been shown to affect kelp forests on a variety of scales (Dayton and Tegner
644 1984, Tegner et al. 1996, Edwards 2004, Edwards and Estes 2006). For example during the
645 strong 1997/98 ENSO event, the southern range limit of *Macrocystis* along the Pacific coast of
646 Baja California, Mexico shifted 100 km northwards, the return of which was delayed when dense
647 stands of *Eisenia arborea* recruited into these habitats (Ladah et al. 1999, Edwards 2004).
648 Although the effects of ENSO events on kelp forests off Vancouver Island are less well known
649 (but see Germann 1988, Milligan et al. 1999) we did not detect signs of synchronous
650 environmental forcing during the ENSO events of 1991/92 or 1997/98. Long-term water
651 temperature records from Kains Island and the shorter-term records from our permanent sites
652 (Fig. 7A-C) suggest nitrate generally was not limiting during our study. In California
653 *Macrocystis* stipe density is used as an index of environmental carrying capacity (Dayton et al.
654 1992, Tegner et al. 1996). *Macrocystis* stipe density, measured on the three of our permanent
655 plot sites where it occurred, did not vary significantly during ENSO event years (Fig. 12A-C),
656 further suggesting that carrying capacity did not change appreciably in response to the same
657 oceanographic events that strongly impacted kelp forests further to the south. The Pacific decadal

658 Oscillation, which affects coastal water temperatures on roughly 30 year cycle, shifted to a
659 warmer less productive phase in 1977 (Ware and Thomson 2005). The effects of PDO on kelp
660 are not well known but may be large. *Macrocystis* biomass off Pt Loma, California declined by
661 66% from 1957-1994 (Tegner et al. 1997). In BC, Sutherland (1998) reported that kelp canopy
662 biomass declined by 50% from 1976 – 1996, and a widescale decline of *Nereocystis* was
663 detected off Vancouver Island in the early 1980s (Foreman 1984). Our study conducted mainly
664 during the warm phase of the PDO is too short to detect the effects of such a low frequency
665 event.

666 *Phase State Transitions*

667 Although there are numerous examples of systems with multiple stable states (Knowlton
668 2004, Schröder et al. 2005, Beisner et al. 2003), studies of the transition between phase states are
669 rare, largely because the interceding equilibria are unstable, and because the shifts are infrequent,
670 and occur rapidly and unexpectedly (Konar and Estes 2003, Carpenter and Brock 2006, Scheffer
671 2009). Although we encountered the algal and urchin-dominated states associated with the
672 presence and absence of otters, as expected, we also found mosaics of urchins and algae in areas
673 being invaded by sea otters, including the permanent plots. This mix of urchin-free patches,
674 algae, and aggregations of urchins, appeared to represent a transitional state between urchin
675 barrens and kelp forests. Our experimental results suggest that the mosaics formed when sea
676 urchins responded behaviourally to the risk of predation rather than from sea otters removing
677 urchins directly. As urchins fled from the damaged tests used to mimic those dropped by
678 foraging otters they created urchin-free patches within the deforested landscape. The urchin-free
679 patches remained for ~10 days and were still visible 17 days later, which is sufficient time for
680 algal recruitment, suggesting that algae could recruit (to the urchin-free patches) even when

681 overall urchin abundance had not declined appreciably (e.g., Fig 6A-D). Eventually however, sea
682 urchin abundance was reduced by sea otter predation and the system became entirely algal-
683 dominated.

684 A number of urchin species are known to flee from injured conspecifics (Parker and
685 Schulman 1986, Vadas and Elner 2003) and their invertebrate predators (Dayton 1975a, Moitzo
686 and Philips 1979, Tegner and Levin 1983, Duggins 1983, Freeman 2006). The influence of these
687 trait-mediated effects on herbivory can equal or exceed those of direct mortality (Lima and Dill
688 1990, Schmitz et al. 1997, Dill et al. 2003). Strongylocentrotid urchins, for example, are known
689 to “stampede” from the seastar *Pycnopodia* creating urchin free patches to which algae may
690 recruit (Dayton 1975a, 1975b, Duggins 1983). Although a behavioural response likely explained
691 both urchin-free patches and aggregations (which formed as urchins fled), foraging urchins also
692 are attracted to and aggregate around kelp (Lees 1970, Russo 1979, Konar and Estes 2003).
693 However, the urchin aggregations that formed around the experimentally-introduced kelp in our
694 study were short lived and did not alter urchin population density appreciably.

695 Variation in the abundance and foraging behaviour of sea otters probably explain why the
696 transitional pathways from urchin- to algal-dominated phase states differed among our study
697 sites. Algal/urchin mosaics most likely formed where otters foraged intermittently and removed a
698 few urchins each time they fed, whereas rapid and extensive phase shifts probably occurred
699 where otters (a few or many) foraged intensely and removed all the urchins in short order. For
700 example although sea otters had expanded past the Kyuquot Bay plots by 1989, it was 5 years
701 before they were seen regularly in this area, and the algal-urchin mosaic persisted throughout this
702 period. In contrast, at Union Island and Maquinna Point the change from urchin barrens to kelp
703 forest following the influx of otters occurred in less than a year.

704 Mosaics may be a common feature of many communities exhibiting alternate states
705 (Rietkerk et al. 2004) and could contribute to the increased variability in thresholds of regime
706 shifts among these various systems (see Carpenter and Brock 2006). Algal/urchin mosaics are a
707 global phenomenon. In the Aleutian Islands and South Africa urchins and patches of kelp coexist
708 when the sweeping motion of algal blades prevent urchins from entering kelp stands (Velimirov
709 and Griffiths 1979, Konar 2000, Konar and Estes 2003). In the Mediterranean (Sala et al. 1998,
710 Bulleri and Benedetti-Cecchi 2006), the United Kingdom (Kitching and Ebling 1961), the
711 Caribbean (Carpenter 1984) and South Australia (Andrew 1993) stable mosaics of urchins and
712 algae occur where high relief substrate provides refuge from predators. Finally, in the North
713 Atlantic and southern California, urchins feed on detritus and graze less actively when algal drift
714 is abundant, thereby maintaining the borders between kelp beds and urchin barrens (Harrold and
715 Reed 1985, Steneck et al. 2002). The kelp/urchin mosaics we observed on the west coast of
716 Vancouver Island were highly transitory elements of the phase shift from the urchin to algal-
717 dominated phase states. This relatively rapid transition following sea otter reinvasion, which has
718 also been described in southeast Alaska (Estes and Duggins 1995) and the outer coast of
719 Washington State (Kvitek et al. 1998), is strikingly different from the Aleutian Islands where the
720 shift from an urchin barrens to the algal-dominated state can take decades (Estes and Duggins
721 1995).

722 *Persistence, resilience and stability*

723 Ecosystem stability encompasses two related phenomena- ecological resilience, the
724 degree to which systems are capable of recovering from perturbations and persistence, how
725 constant a system remains through time (Holling 1973). Suggestions that heterogeneous natural
726 systems are more resilient (and thus more stable) than homogenous ones, has refocused attention

727 on the role that natural variation plays in ecological stability (McCann 2000, Elmqvist et al.
728 2003). Our long-term chronicle of variation in urchin and algal-dominated systems off the west
729 coast of Vancouver Island provides new insights into the stability of these two community types.

730 When viewed from the perspective of phase states, the algal and urchin-dominated
731 systems both appear to be highly resilient. Except in areas reinvaded by sea otters, the phase
732 states at all of our permanent plots remained unchanged during the 23 years over which they
733 were monitored. This is very much in contrast with Ebeling et al.'s' (1985) findings from Naples
734 Reef in southern California where periodic storms drove the system back and forth between the
735 urchin- and algal-dominated phase states over several year intervals. These differing patterns
736 suggest that the phase states documented off Vancouver Island system are globally-stable basins
737 of attraction (*sensu* Lewontin 1969) and the phase state shifts that followed sea otter range
738 expansion along the west coast of Vancouver Island are technically boundary points (changes
739 with the addition or loss of a species) rather than strict alternate stable states (*sensu* Lewontin
740 1969). In contrast, the southern California system is characterized by regularly alternating stable
741 states.

742 Stable states are often more broadly defined as predictable self-maintaining systems
743 (Holling 1973), with species composition and abundance fluctuating within the limits defined by
744 the basin of attraction (Gunderson 2000). A more detailed look within the phase states at the
745 permanent plots provides insight into just how broad these basins of attraction can be (Fig 3A-
746 B). The composition of species and the abundance and structure of populations changed within
747 all of our permanent plots. This was especially true for the algal-dominated phase state where the
748 species composition and demographic structure of the algal assemblage at any place and time
749 was dictated by the vagaries of history, longevity, propagule availability, and the season of

750 disturbance. Resilient communities need not simply tend towards an equilibrium state, but can
751 cycle over time (Holling and Gunderson 2002). In our system, lags between succession, periods
752 of stability, collapse and renewed succession created the mosaic of kelp-forest patches which
753 defined the entire basin of attraction (e.g., Gunderson 2000). Thus, while persistent and
754 predictable on one scale, the algal phase state was highly dynamic and unpredictable at another.
755 Dayton et al's. (1999) long-term records from the Pt. Loma kelp forest in southern California
756 suggest similar patterns and processes.

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

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1055 **Table 1.** The categories of algae monitored in the random site surveys and at the permanent
 1056 plots.

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

1057 **Table 2.** A summary of survey results. Sea otter abundance is the maximum annual count of sea
 1058 otters in each of the three main areas in 1988, 1994 and 2007. Red urchin and brown algal
 1059 density is mean abundance \pm SE (1988, 1994: n=20 2007: n=30). Red urchin biomass was
 1060 calculated from the equation $\ln(\text{biomass}) = -7.046 + 2.807 \ln(\text{test diameter})$, which was
 1061 calculated from 600 red urchins collected from three sites in Barkley Sound in 1989. Total algae
 1062 includes kelp sporophytes too small to class as either perennial or annual species.

Parameter	Otters Absent			Otters Present			Otters		
	Barkley Sound			Checleset Bay			Absent	Present	Present
	1988	1994	2007	1988	1994	2007	1988	1994	2007
Sea otters									
Max # otters	0	0	0	201	413	949	3	397	566
Red Urchins									
Mean TD	93.3 \pm 1.9	71.0 \pm 4.3	87.9 \pm 2.5	NA	NA	NA	79.2 \pm 2.5	72.5 \pm 2.0	NA
Density /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	9.5 \pm 1.0	2.8 \pm 1.2	0.1 \pm 0
Mass kg/m ²	3.4 \pm 0.2	3.3 \pm 0.3	2.8 \pm 9.5	N/A	N/A	N/A	2.9 \pm 0.2	0.7 \pm 0.4	NA
Brown Algae									
Total /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	1.7 \pm 0.7	25.5 \pm 1.6	10.4 \pm 1.5
Annuals /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	1.0 \pm 0.5	9.3 \pm 1.9	2.3 \pm 0.9
Perennials /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	0.4 \pm 0.2	15.9 \pm 1.6	7.4 \pm 1.2
<i>Nereocystis</i>	0.03 \pm .02	0.01 \pm .01	0.1 \pm 0.02	1.3 \pm 0.4	0.03 \pm .02	0.2 \pm 0.1	0.2 \pm 0.1	2.3 \pm 0.6	0.5 \pm 0.2
<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	0.9 \pm 0.5	5.8 \pm 1.5	1.7 \pm 0.7
<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	0	1.0 \pm 0.8	0.7 \pm 0.4
<i>Laminaria spp</i>	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	0.4 \pm 0.3	8.3 \pm 1.4	4.5 \pm 1.4
<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	0.2 \pm 0.2	5.7 \pm 1.0	3.9 \pm 0.9

1063 **Table 3.** The mean length of the 2X10m plots at each of the permanent plot sites. The relief of
 1064 the plots was not significantly different among sites (see text).

Permanent Plot	Length (m) ($\bar{X} \pm \text{SE}$)	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

1065 **Table 4.** The number of *Pterygophora* plants newly tagged each year (bracketed numbers) and
 1066 the tagged plants that were relocated each year in the Gull Island permanent plot. Untagged
 1067 plants were those plants too small to be tagged (<0.20m).

Year	1988	1989	1990	1991	1992	1993	1994	1995	1996	1997	1998
Tagged											
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

1068 **Table 5.** The number of *Pterygophora* plants newly tagged each year (bracketed numbers) and
 1069 the tagged plants that were relocated each year in the No Name Island permanent plot. Untagged
 1070 plants were those plants too small to be tagged (< 0.20m).

Year	1988	1989	1990	1991	1992	1993	1994	1995	1996	1997	1998
Tagged											
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

1071

FIGURES AND TABLES

1072 **Figure 1.** Vancouver Island and the place names mentioned in the text. The numbers shown for

1073 **A.** Checleset Bay / Kyuquot and **B.** Barkley Sounds are the locations of the permanent plots - 1.

1074 Gull Island, 2. No Name Island, 3. Kamils Anchorage, 4. Union Island, 5. Kyuquot Bay, 6.

1075 Maquinna Point, 7. Wizard Island, 8. Taylor Islet.

1076 **Figure 2.** Changes in sea otter abundance between 1977 and 2009, abundance estimates are the

1077 highest annual count for each area. Lines are Lowess smoothing function (Wilkinson 1999).

1078 Additional sources of Data: 1977 - Bigg and MacAskie (1978); 1978 – Morris et al. (1981); 1982

1079 - Bigg (unpub): 1984 – MacAskie (1987).

1080 **Figure 3.** Densities of red sea urchins vs. kelps from random site surveys in **A.** Barkley Sound

1081 (sea otters absent) and Checleset Bay (sea otters abundant), and **B.** Kyuquot Sound. The surveys

1082 were first conducted in 1988 (triangles) and repeated in 1994 (circles) and 2007 (squares). Sea

1083 otters were absent from Kyuquot Sound in 1988 (open triangles), present but in the early stage of

1084 reinvasion in 1994 (grey circles), and well established in 2007 (black squares).

1085 **Figure 4.** Size frequency histogram of red urchin test diameters (TD) from the random site

1086 surveys conducted in Barkley Sound in 1988, 1994 and 2007 (otters absent throughout, left

1087 panel) and Kyuquot Sound (otters absent in 1988, early stages of reinvasion in 1994, well

1088 established in 2007. Right panel). Note that both population density and maximum size of red

1089 urchins had declined in Kyuquot Sound by 1994 and that urchin density had declined to near

1090 zero in 2007.

1091 **Figure 5. A.** Abundance of red urchins at MacLean Island between 1988 and 2009 (not all years
1092 were sampled) **B.** Size frequency of red urchins in 1995 **C.** Size frequency of red urchins in 1998
1093 **D.** Size frequency of red urchins in 2009 (see text for details).

1094 **Figure 6 A-D.** Mean red urchin abundance (\pm SE, $n = 20$) plotted against mean brown algal
1095 abundance (\pm SE, $n = 20$) at four of the random sites in 1988, 1992, and 1994. Patchy mosaics of
1096 urchins and algae formed at all of these sites when sea otters arrived. **E-H.** Red-urchin size
1097 frequencies at four random sites in Kyuquot Sound sampled in 1988, 1992, and 1994.

1098 **Figure 7. A.** Sea surface temperature at Kains Island Light Station from 1986-2009 (DFO – see
1099 text for web site). **B.** Mean monthly water temperatures at \sim 10m in Checleset Bay and Kyuquot
1100 Sound from 1999-2009. **C.** Mean water temperature at \sim 10m in Barkley Sound from 1999-2009.

1101 **Figure 8.** Phase state transitions at the permanent plots shown by plotting annual mean red
1102 urchin density ($n=5$) plotted against brown algal density ($n=5$) between 1987/88 - 2009. **A-B.**
1103 Permanent plots in areas continuously without sea otters. **C-D.** Permanent plots in areas
1104 continuously with sea otters. **E-H.** Permanent plots in areas that were occupied by sea otters
1105 during the study.

1106 **Figure 9.** Mean annual abundance (\pm SE, $n=5$) of annual (grey bars), perennial (black bars), and
1107 total brown algae (open circles) and red urchins (filled circles) at the permanent plot sites **A.** that
1108 were continuously without sea otters, **B.** that were continuously with sea otters and **C.** that were
1109 occupied by sea otters during the study. Standard error bars are omitted from histograms for
1110 clarity. Graphs are all on the same scale.

1111 **Figure 10.** Mean annual abundance (\pm SE, $n=5$) of *Nereocystis* (black circles), *Macrocystis* (grey
1112 squares), *Desmarestia* (open circles) and stipitate kelps (*Pterygophora* and *Laminaria* (black
1113 triangles) at the permanent plot sites in **A.** areas continuously without sea otters, **B.** areas

1114 continuously with sea otters and **C.** areas which were occupied by sea otters during the study.

1115 Graphs are all on the same scale.

1116 **Figure 11. A.** Age frequency of *Pterygophora* in 1989 near the Gull Island Permanent plots **B.**

1117 Age frequency of *Pterygophora* in 1989 near the No Name Island Permanent plots **C.** Age

1118 frequency of *Pterygophora* in 1990 near the Kyuquot Bay Permanent plots **D.** Age frequency of

1119 dead *Pterygophora* collected in 1992 at the Gull Island Permanent plots.

1120 **Figure 12.** The mean density (n=5) of *Macrocystis* plants, stipes and stipes /plant at **A.** No Name

1121 Island (continuously with otters) **B.** Kamils Anchorage (occupied by otters during the study) and

1122 **C.** Union Island (Occupied by otters during the study). Permanent plots not listed did not have

1123 *Macrocystis*.

1124 **Figure 13.** The mean density of red urchins /m² (\pm SE, n=3) in each of the four urchin

1125 experiments at time = 0 (black) and 24 hours after (grey) each experimental treatment.

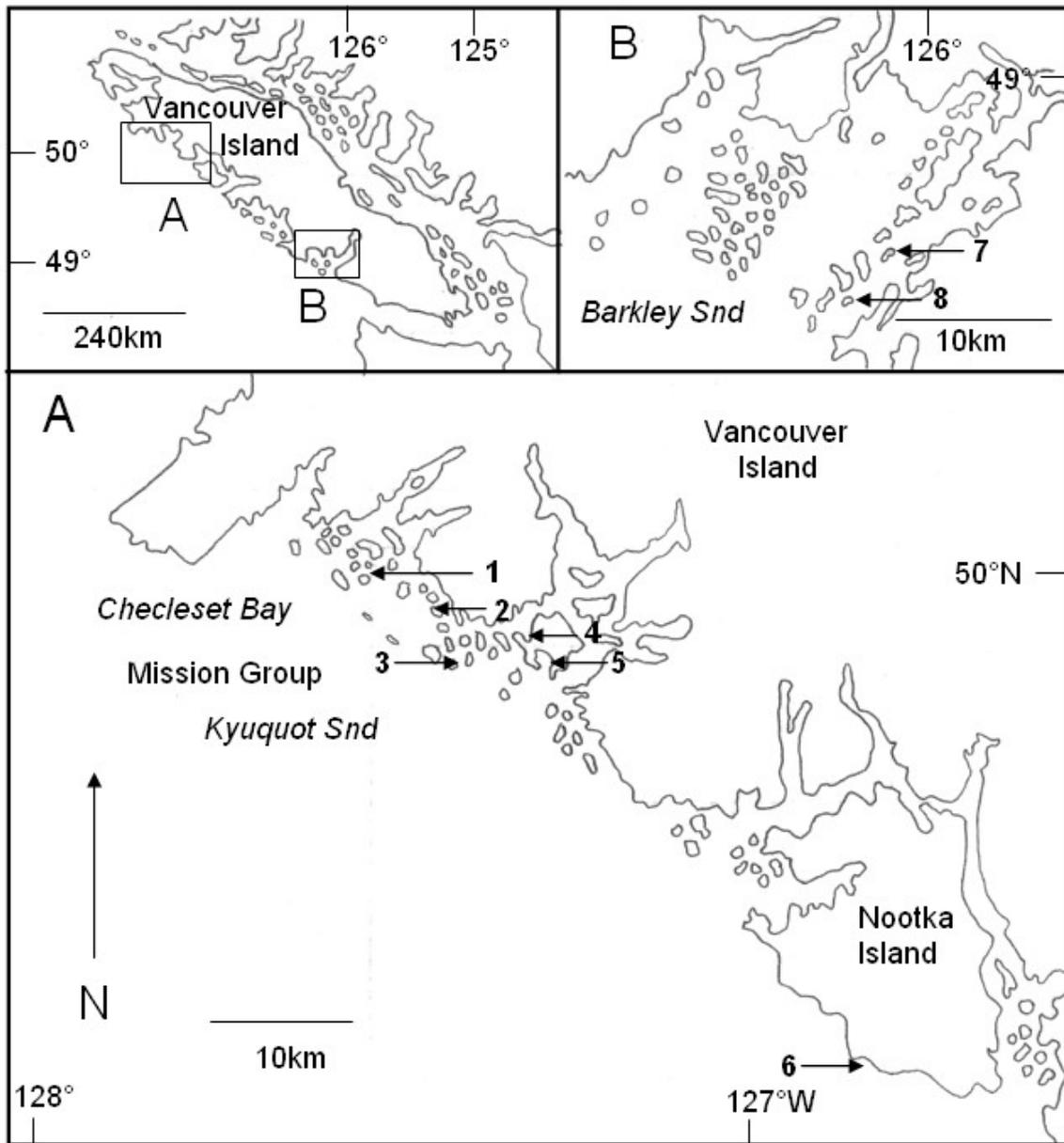


Figure 1

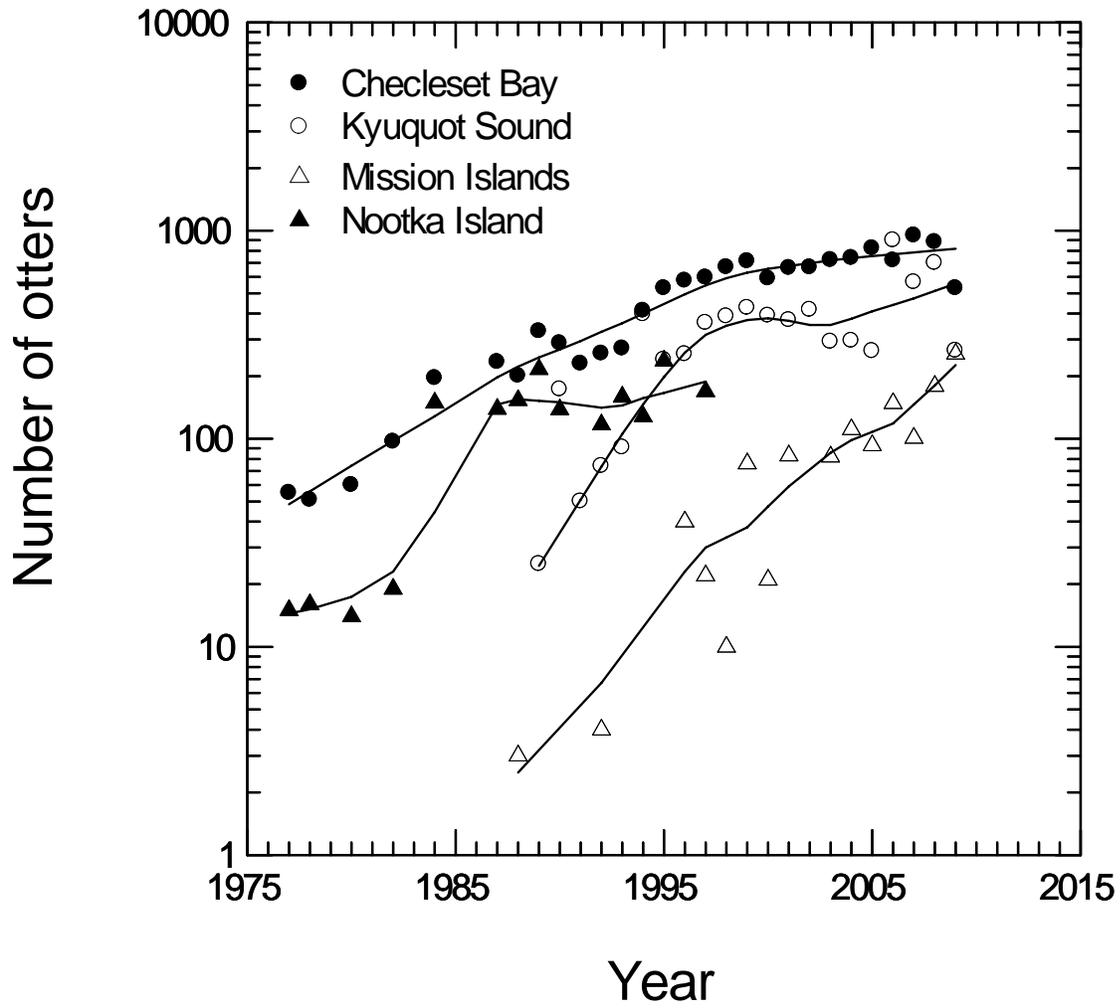


Figure 2

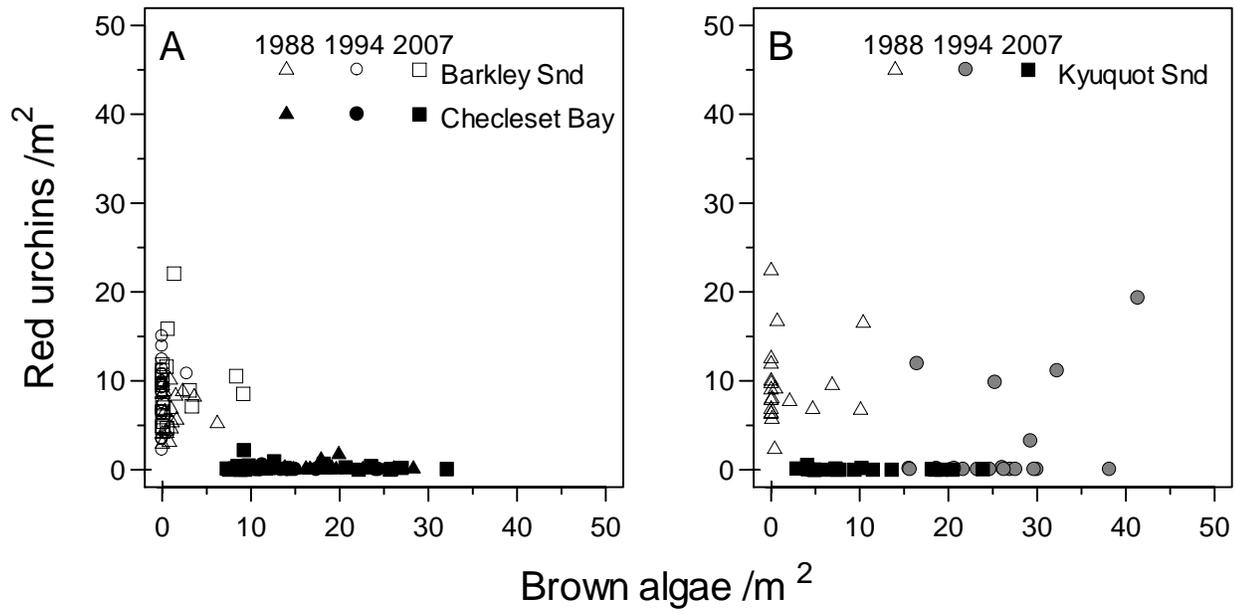


Figure 3

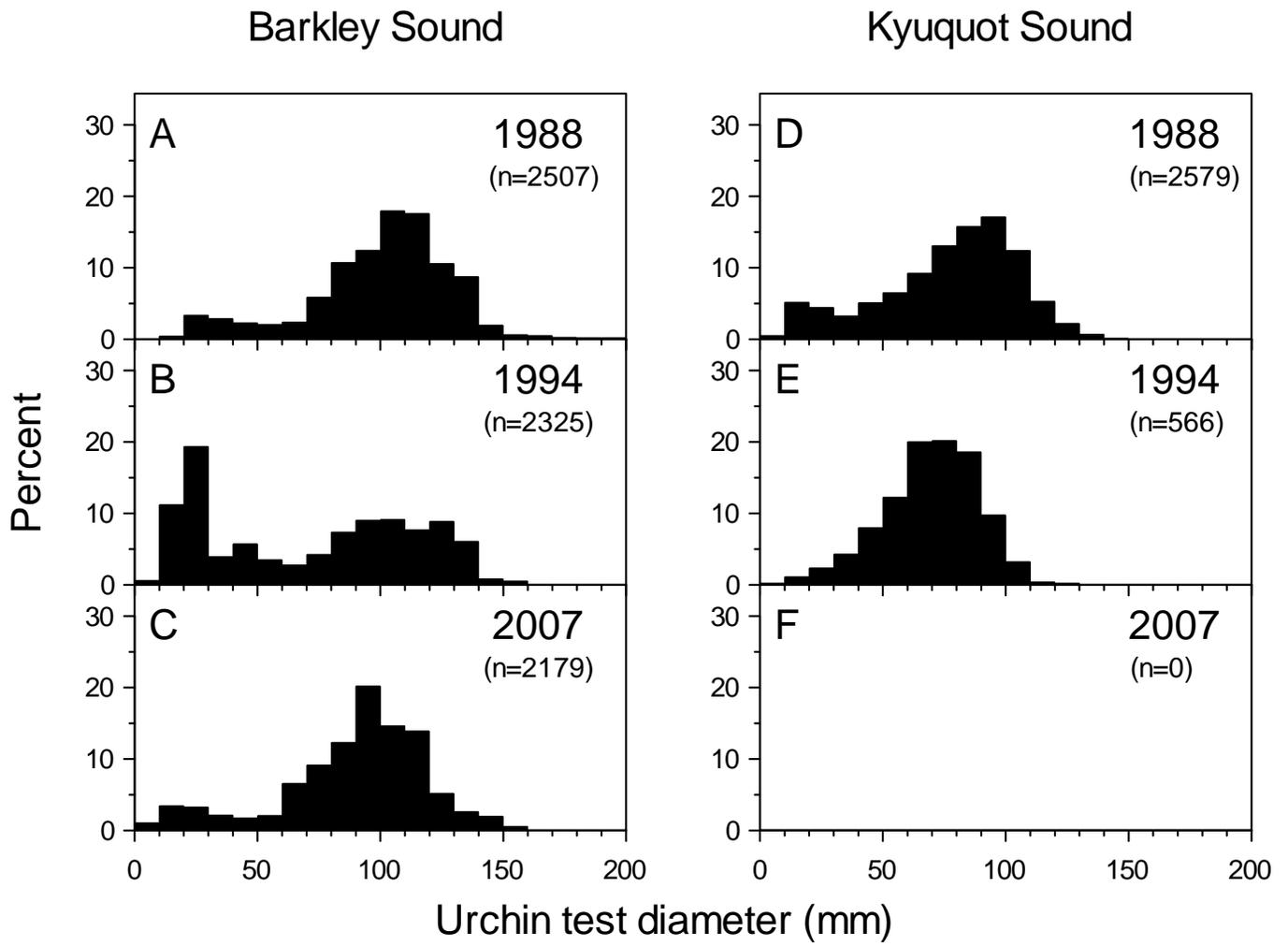


Figure 4

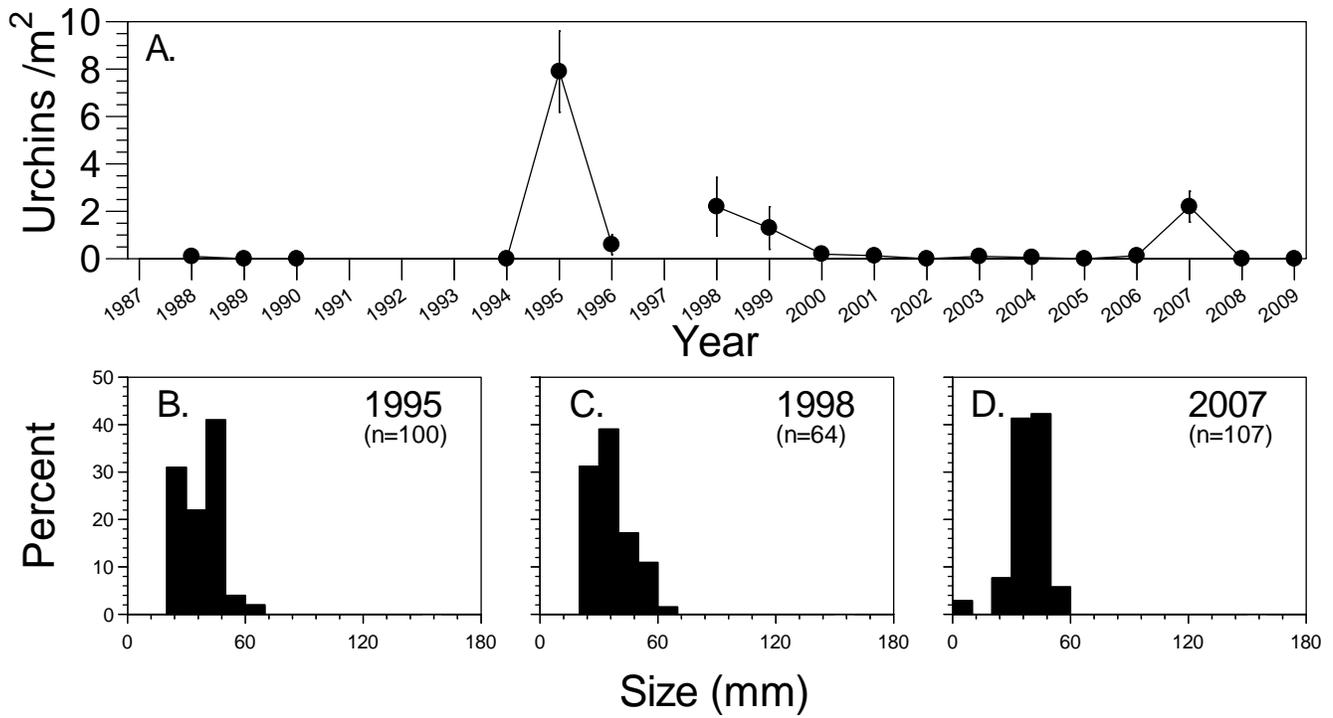


Figure 5

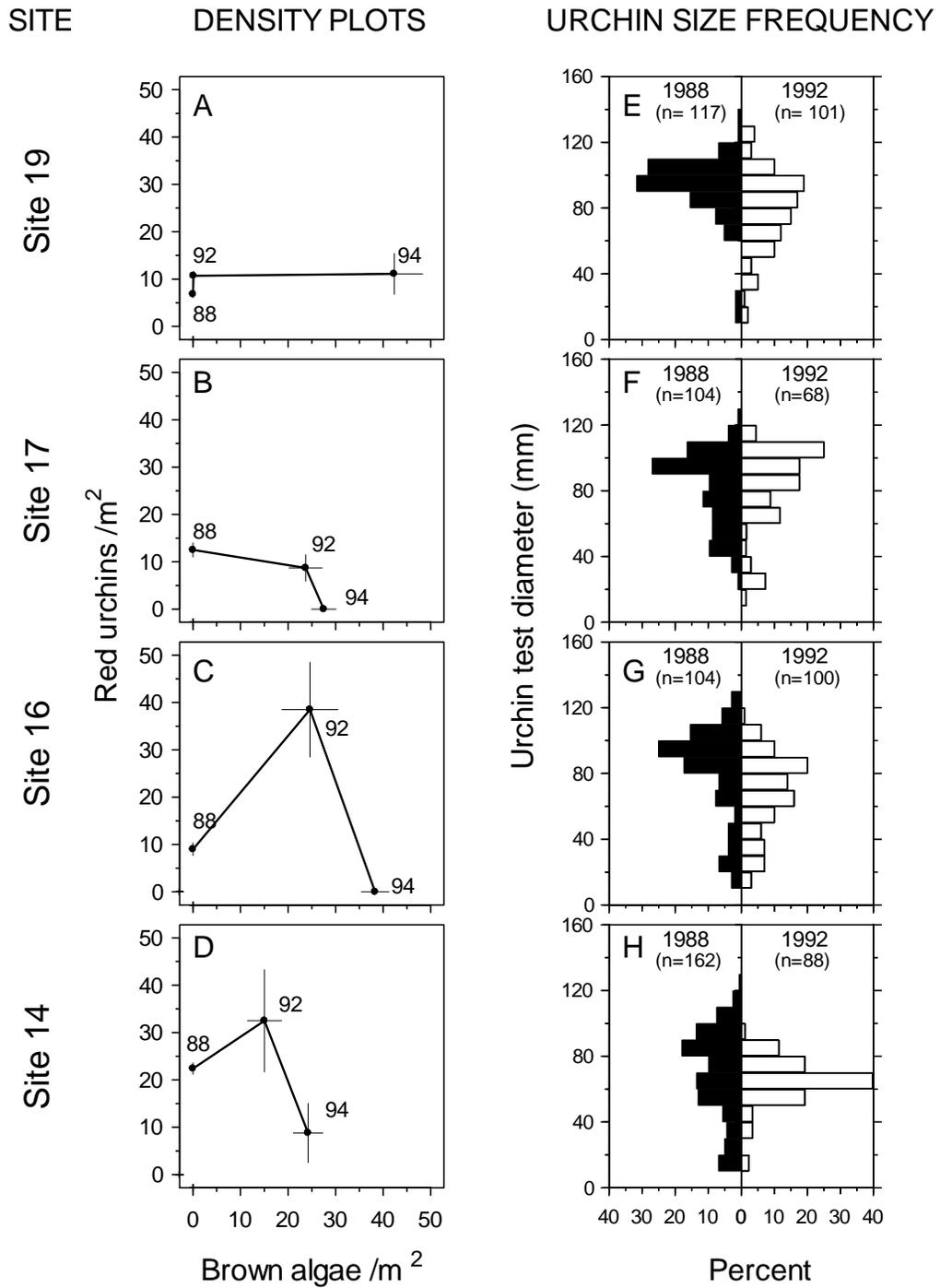


Figure 6

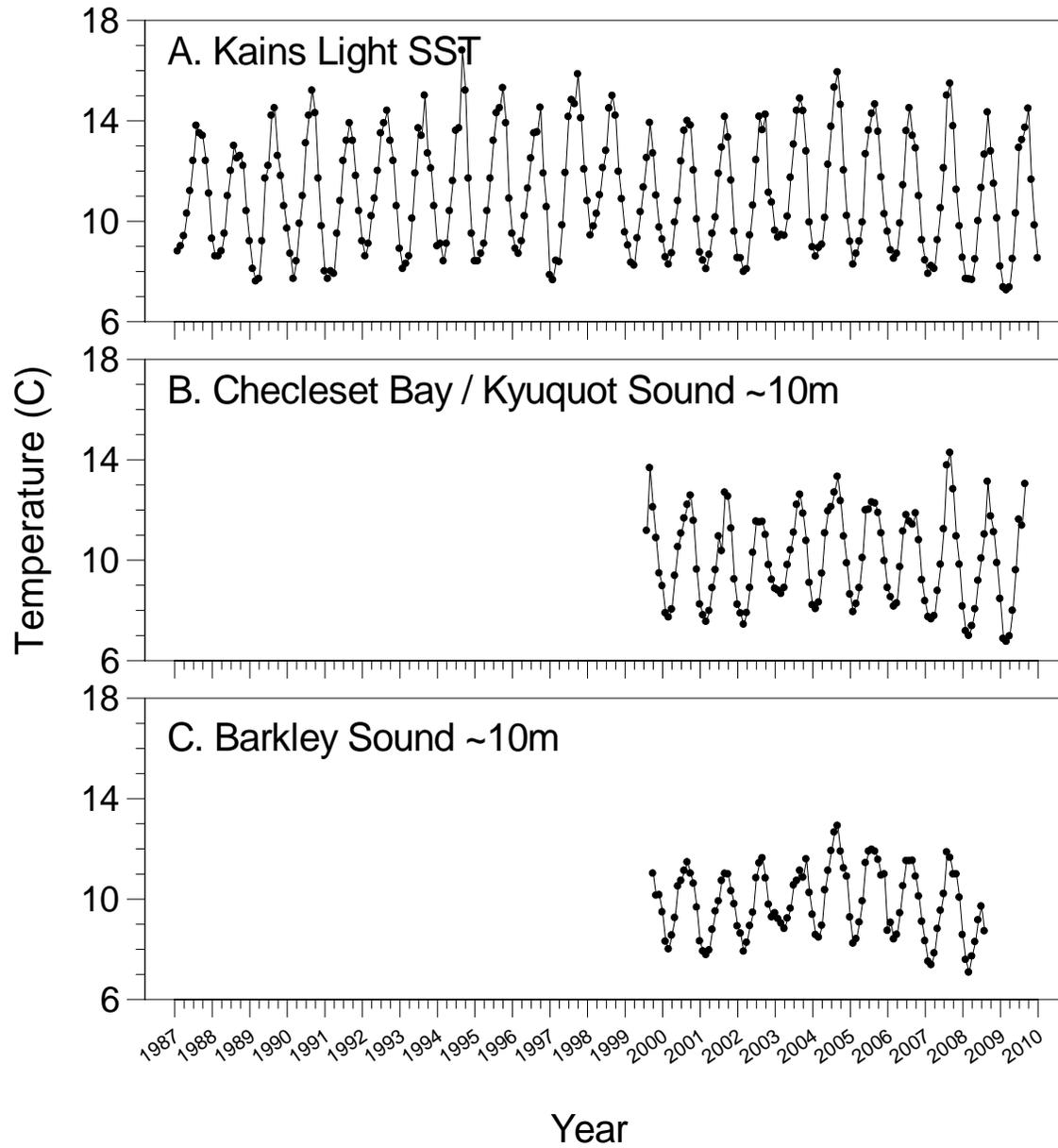


Figure 7

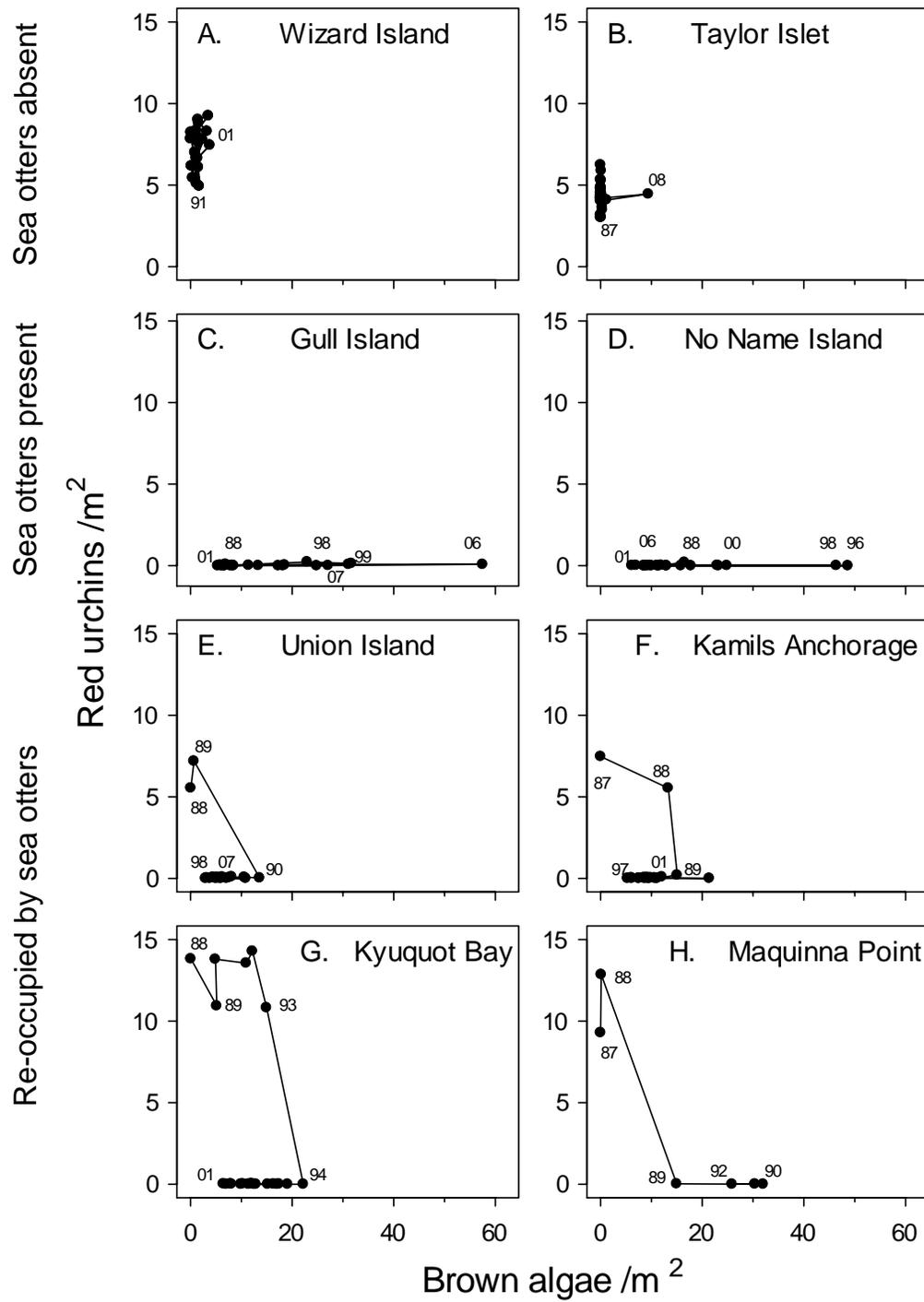


Figure 8

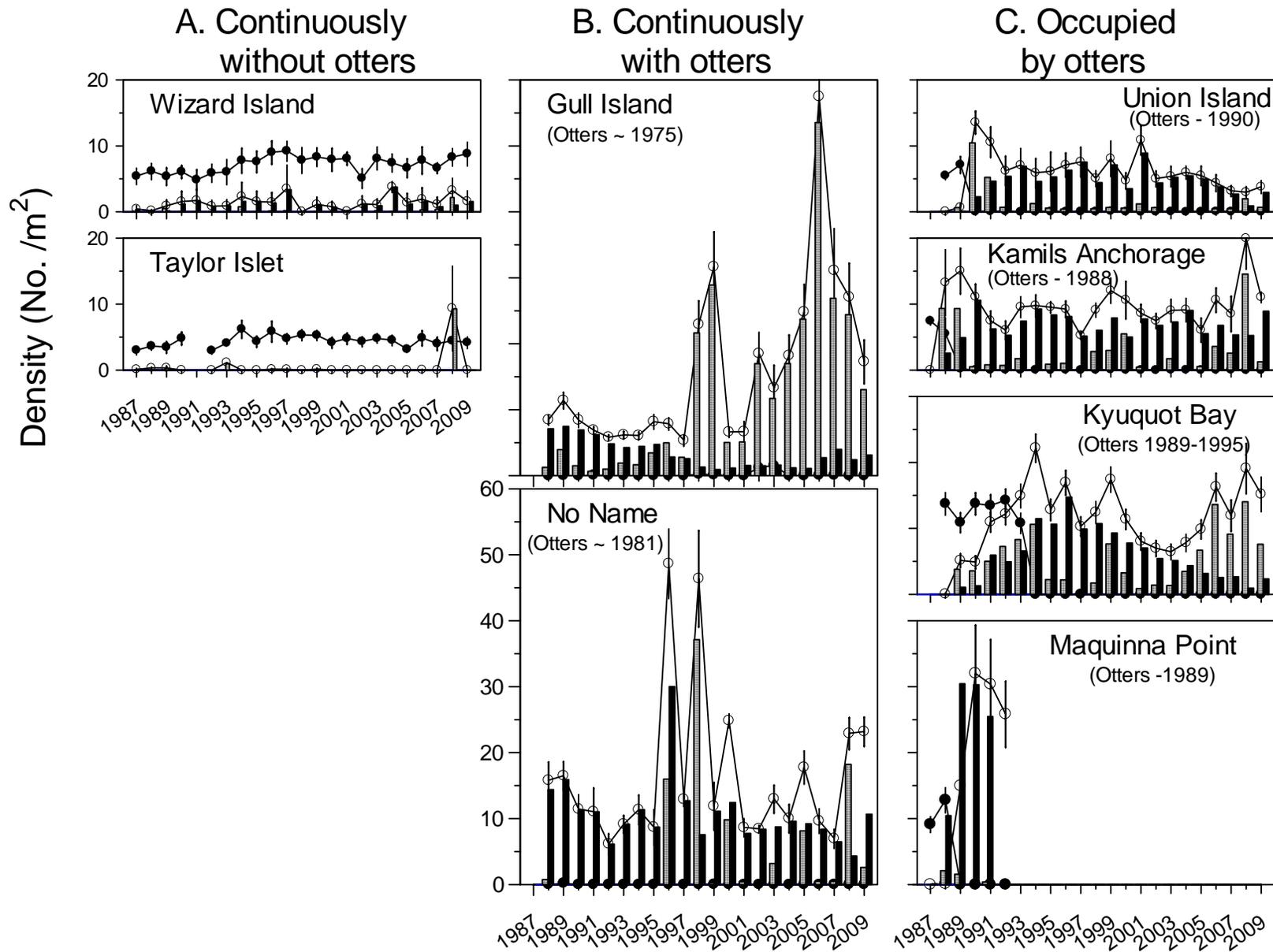


Figure 9

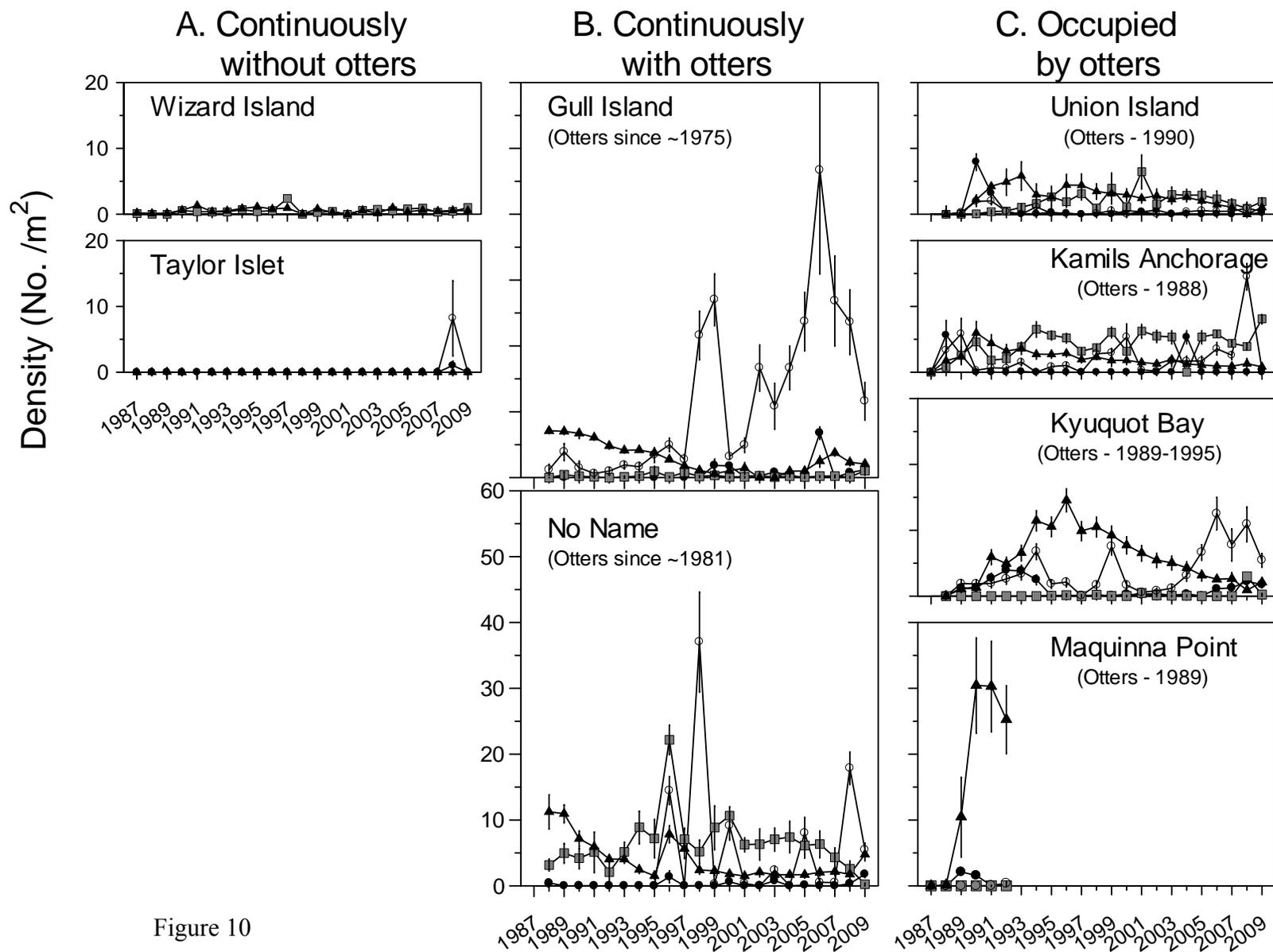


Figure 10

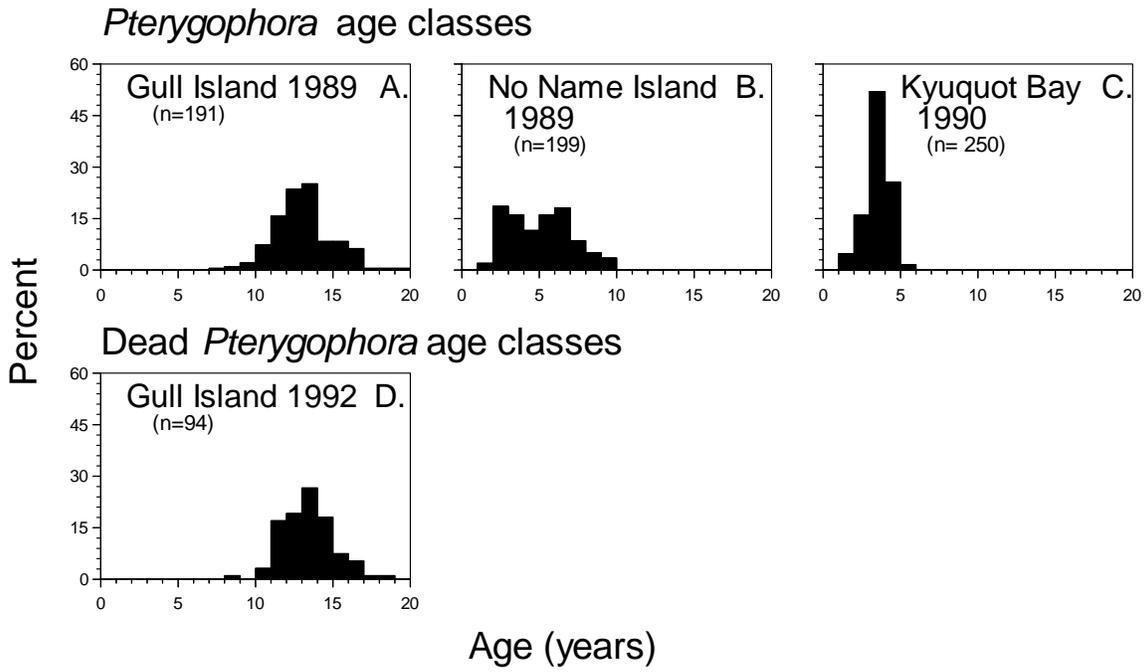


Figure 11

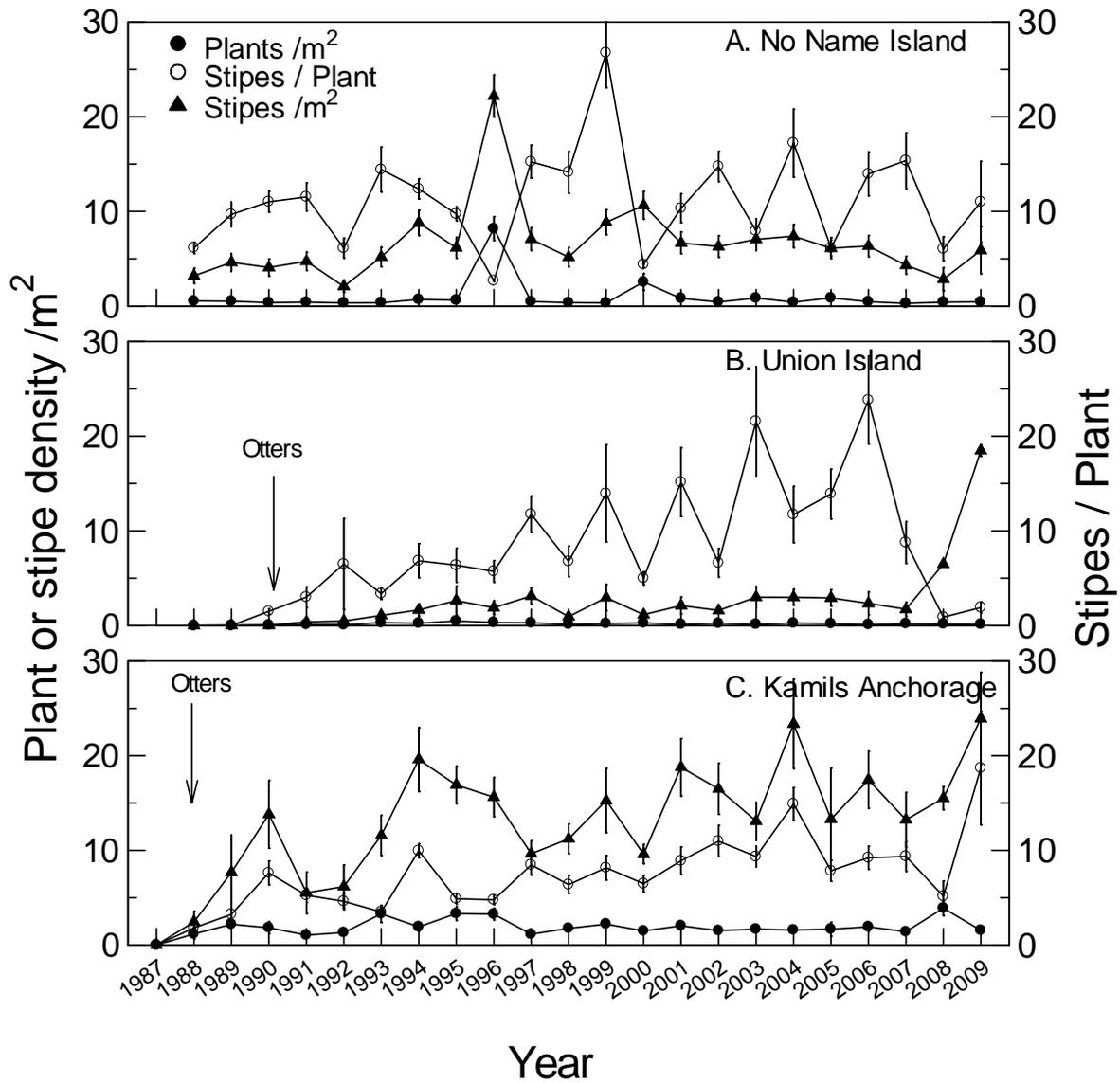


Figure 12

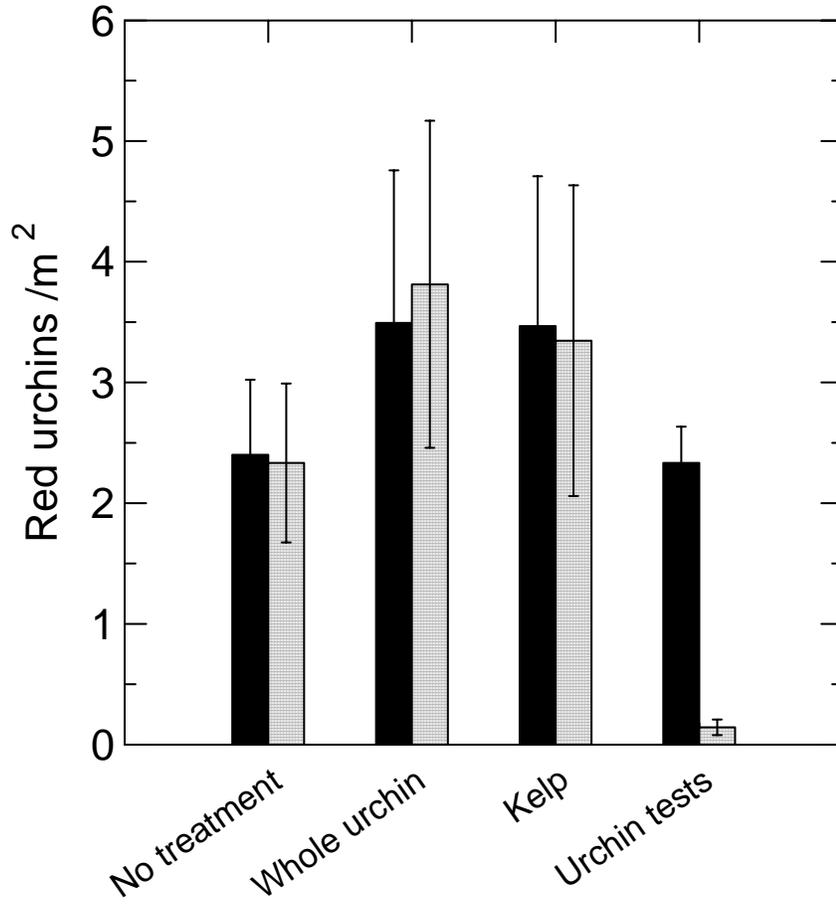


Figure 13