

Testing the generality of the trophic cascade paradigm for sea otters: a case study with kelp forests in northern Washington, USA

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Received: 6 April 2006 / Revised: 24 August 2006 / Accepted: 15 September 2006 /
Published online: 31 January 2007
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Abstract Trophic cascade hypotheses for biological communities, linking predation by upper trophic levels to major features of ecological structure and dynamics at lower trophic levels, are widely subscribed and may influence conservation policy. Few such hypotheses have been evaluated for temporal or spatial generality. Previous studies of sea otter (*Enhydra lutris*) predation along the outer coast of North America suggest a pattern, often elevated to the status of paradigm, in which sea otter presence leads to reduced sea urchin (*Strongylocentrotus* spp.) biomass and rapid increases in abundance and diversity of annual algal species,

followed by a decline in diversity as one or a few perennial algal species become dominant. Both sea otter predation and commercial sea urchin harvest are ecologically and economically important sources of urchin mortality in nearshore benthic systems in northern Washington marine waters. We recorded changes in density of macroalgae in San Juan Channel, a marine reserve in the physically protected inland waters of northern Washington, resulting from three levels of experimental urchin harvest: (1) simulated sea otter predation (monthly complete harvest of sea urchins), (2) simulated commercial urchin harvest (annual size-selective harvest of sea urchins), and (3) no harvest (control). The two experimental urchin removal treatments did not significantly increase the density of perennial (*Agarum* and *Laminaria*) or annual (*Desmarestia*, *Costaria*, *Alaria* and *Nereocystis*) species of macroalgae after 2 years, despite significant and persistent decreases in urchin densities. Our results suggest that other factors such as grazing by other invertebrates, the presence of dense *Agarum* stands, and recruitment frequency of macroalgae and macroinvertebrates may play a large role in influencing community structure in San Juan Channel and other physically protected marine waters within the range of sea otters.

Handling editor: J. Trexler

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Keywords Apex predator · Sea otter · Sea urchin fishery · Community structure · Benthic ecosystem · Herbivory

Introduction

Predation by top trophic level consumers, or ‘apex predators’ may influence local community structure and dynamics through mechanisms such as trophic cascades (e.g., Paine, 1966; Estes & Palmisano, 1974; Estes & Duggins, 1995; Estes et al., 1998). In the marine ecological literature, two of the most compelling and celebrated cases linking apex predation with community structure and function are studies of sea star predation on rocky intertidal benthic invertebrates for which space is a limiting resource (Paine, 1966, 1974, and related subsequent studies), and studies of sea otter (*Enhydra lutris* [L.]) predation on herbivorous benthic invertebrates that otherwise limit nearshore macrophyte abundance and productivity (Estes & Palmisano, 1974; Estes et al., 1978; Duggins, 1980; Estes & Duggins, 1995 and related studies). Our study focuses on the latter.

Application of trophic cascade models involving sea otters to conservation policy has long been controversial (e.g., Estes & VanBlaricom, 1985; VanBlaricom & Estes, 1988). Controversy results from two categories of problems. First, there is concern that portrayals of trophic cascades involving sea otters and kelp forests oversimplify the realities of kelp forest ecology, inappropriately minimizing consideration of effects of other factors, such as physical disturbance and substratum type, on kelp forest structure and dynamics (e.g., Cowen et al., 1982; Schiel & Foster, 1986; Foster & Schiel, 1988; Foster, 1990). Second, there is concern that uncritical application of trophic cascade hypotheses may facilitate inappropriate conservation and management decisions involving sea otters. For example, sea otters are known to preempt the long-term sustainability of certain shellfish fisheries by virtue of foraging activities, a matter of significant concern to some resource management agencies (e.g., Estes & VanBlaricom, 1985; Wendell et al., 1986; Wendell, 1994, 1996; Fanshawe et al., 2003). However, conservation-oriented initiatives to protect and expand sea otter numbers and distribution are often supported by arguments for the importance of predation by sea otters in restoring trophic cascades said to be natural in the absence of anthropogenic intrusions to marine ecosystems

(e.g., VanBlaricom, 1996; Wendell, 1996). If trophic cascades involving sea otters are afforded credibility without rigorous scrutiny, there is a risk that reasonable shellfish management activities could be inappropriately discarded in favor of unjustified ecological benefits associated with sea otters.

We suggest that there is an inadequate record in the technical literature establishing the generality of trophic cascades driven by sea otter predation across the geographic range of sea otters and productive coastal kelp forest habitats on rocky substrata along the North Pacific Rim (i.e., from northern Japan to the outer coast of Baja California Sur, Mexico). In our view, the applicability of trophic cascade hypotheses driven by sea otter predation has not been established among geographic locations with similar physical settings or among geographically proximate habitats with different physical settings. The most widely cited study of the geographic generality of trophic cascades driven by sea otters (Estes & Duggins, 1995) involves a longitudinally broad region that arguably lacks profound variation in oceanographic or geologic attributes and occurs across a relatively limited latitudinal range compared to the range of sea otters and many types of kelp forest communities in the North Pacific. Thus, we believe there is a need for additional evaluation of the generality of trophic effects of sea otters on kelp forests in the coastal North Pacific.

Here we offer an experimental evaluation of some aspects of kelp forest community structure and dynamics often said to be a general result of sea otter predation in the North Pacific. We also evaluate potential effects of a fishery for sea urchins on nearshore North Pacific coastal ecosystems, recognizing that commercial urchin harvests often mimic effects of sea otters by causing significant reduction in urchin densities.

Sea otter predation and commercial sea urchin (*Strongylocentrotus* spp.) harvest are ecologically and economically important sources of urchin mortality in nearshore benthic systems in northern Washington marine waters. Commercial harvest of sea urchins has occurred in the Strait of Juan de Fuca and the San Juan Islands for nearly four decades and supports several hundred

harvesters and processors statewide (Pfister & Bradbury, 1996; Lai & Bradbury, 1998). During the 1980s and 1990s, the Washington sea otter population grew rapidly and expanded its range into the western Strait of Juan de Fuca, with the rate of numerical and geographic growth slowing somewhat after 2000 (Laidre et al., 2002; Gerber et al., 2004). Both otters and harvesters may substantially reduce urchin biomass (e.g., Estes et al., 1978; Kalvass & Hendrix, 1997), and reduction in urchin densities is known to have important consequences for benthic plant communities in many locations (Lawrence, 1975). As a result, both sea otters and commercial urchin harvesters may significantly impact the structure and composition of nearshore benthic ecosystems.

Observations of the dramatically different communities associated with sea otter presence have prompted various authors to suggest that sea otters are a keystone species (e.g., Estes & Palmisano, 1974; Estes & Duggins, 1995), determining major features of community structure (Paine, 1969). According to the ‘sea otter paradigm’, the presence of sea otters leads to reduced urchin biomass and increased macroalgal biomass, while the absence of otters implies high urchin biomass and very low macroalgal biomass. The paradigm has most recently been applied to the Aleutian Islands, Alaska, where declines in sea otter populations due to killer whale (*Orcinus orca*) predation have been suggested as the cause of increases in sea urchin density and decreases in kelp density (Estes et al., 1998).

Schiel & Foster (1986), Foster & Schiel (1988) and Foster (1990) argue that the sea otter paradigm has been over generalized without adequate supporting research. They found that outer coastal areas in California without sea otters were not consistently characterized by high urchin density and low macroalgal density. Instead, a variety of urchin and macroalgal densities existed in sites across a continuum from zero to ‘abundant’. This suggests that, while sea otters are clearly an important factor determining community structure in nearshore rocky bottom areas, other factors such as storms (Cowen et al., 1982), disease (Pearse & Hines, 1979), other predators (Tegner, 1980), and unpredictable temporal variation in recruitment (e.g., Pearse &

Hines, 1987; Reed, 1990), may also be important in structuring nearshore communities in the absence of otter predation.

Sea otters were exterminated from Washington in the early 1900s due to the largely unmanaged commercial fur trade (Riedman & Estes, 1988). Sea otters were reestablished in the state in 1969 (Jameson et al., 1982), but the population has not yet expanded its range to include the San Juan Islands, the apparent eastern limit of the pre-exploitation sea otter range in Washington (Gerber & VanBlaricom, 1999). Application of the sea-otter paradigm to the San Juan Islands would suggest the presence of high urchin densities and low macroalgal densities. Instead moderate urchin densities coexist with abundant macroalgae, a situation that has apparently persisted across recent decades (e.g., Neushul, 1967; Vadas, 1968, this study). This brings into question the generality of the sea otter paradigm, and suggests that effects of sea otter predation in physically protected areas such as the San Juan Islands may differ from effects of sea otter predation observed in exposed coastal habitats. Recent work in Prince William Sound, Alaska (Dean et al., 2000), is consistent with this hypothesis. Dean and colleagues evaluated changes in kelp communities of Prince William Sound following the drastic reduction in local sea otter densities resulting from the *Exxon Valdez* oil spill of 1989. Despite the presence of a community configuration thought to reflect trophic cascades driven by sea otters, substantial change in kelp forest structure and dynamics did not follow the precipitous reduction in sea otter densities. Prince William Sound is similar to our study area in the San Juan Islands with regard to physical and oceanographic characteristics, and component species of kelp forest communities.

Thus, our first study objective is to evaluate to what extent community level effects of sea otter predation observed in outer coastal habitats may be similar to effects observed in the physically protected waters of San Juan Channel (SJC). There are important similarities and differences between our study site, SJC, and previously studied areas on the outer coast of North America, particularly the Aleutian Islands where most of the definitive work on trophic cascades driven

by sea otters has been done. The predominant benthic organisms at our study sites were similar to those typically found on rocky nearshore substrata of the Aleutian Islands. In both regions the predominant grazing invertebrates are sea urchins of the genus *Strongylocentrotus*. Dominant urchin species in both regions (*S. polyacanthus* and *S. droebachiensis* in the Aleutian Islands, and *S. franciscanus* in the San Juan Islands) are known to be capable of profound effects on algal species composition, diversity, density, and physical structure when urchin densities are high (e.g., Estes & Palmisano, 1974; Pearse & Hines, 1979; Duggins, 1980; Harrold & Reed, 1985; Watanabe & Harrold, 1991). Kelp forest structure is also similar between regions. In both cases, dominant understory kelps include species of *Laminara* and *Agarum* (Dayton, 1975; Estes & Duggins, 1995). In both cases, the dominant surface canopy kelps (*Alaria fistulosa* in the Aleutian Islands, *Nereocystis luetkeana* in the San Juan Islands) are annual species with canopies forming in late spring and persisting through summer, typically experiencing high mortalities by storms of autumn and winter.

Both the San Juan and Aleutian regions are characterized by strong and frequent water movement, with local waters known for low temperatures and high nutrient concentrations, supporting high levels of primary productivity. Clearly, the Aleutian region is subject to far greater influence from open oceanic conditions, including large swell. In addition, percentage cover of benthic substrata by coralline algae is substantially greater in the Aleutian region (e.g., Lebednik et al., 1971) as compared to the San Juan Island region. These and other differences in biotic and abiotic factors between outer coastal and inland habitats suggest that effects of sea otter predation on nearshore communities may differ in physically protected marine waters.

Direct effects of sea otters and sea urchin harvesters differ in timing, duration and size-selectivity of urchin mortality. Commercial harvest is size selective (legal size limits are 102–140 mm test diameter), is concentrated during the winter, and typically occurs only once each season in any given location (Pfister & Bradbury, 1996, Alex Bradbury, Washington Department of Fish and

Wildlife, personal communication). In contrast, sea otters consume all exposed urchins above approximately 20 mm (Estes & Duggins, 1995), and predation is effectively continuous once otters become established. Commercial red sea urchin (*S. franciscanus*) harvest in northern Washington significantly decreases urchin density and alters the size distribution of urchin populations (Carter & VanBlaricom, 2002). Studies of the indirect effects of urchin mortality from other sources (e.g. sea otters, disease, storms; Estes & Palmisano, 1974; Pearse & Hines, 1979; Harrold & Reed, 1985) suggest that urchin mortality from commercial harvest may also impact non-target species. However, the differences in timing, duration, species-, size- and microhabitat selectivity of urchin removal from these different sources of urchin mortality suggest that the effects of commercial harvest on non-target organisms may also be different. Community level effects of commercial red sea urchin harvest remain largely unstudied. Qualitative observations suggest that algal abundance may increase in some areas, and may remain unchanged in others (Breen et al., 1976, 1978; Rogers-Bennett et al., 1998). Thus, our second objective is to assess indirect effects of commercial sea urchin harvest and clarify whether differences in the timing, duration and size-selectivity of direct effects of sea otter predation and commercial sea urchin harvest lead to differences in indirect effects on the macroalgal community.

We suggest that results of our study can also be useful in evaluating potential ecosystem-level impacts of a recolonization by sea otters of SJC and other northern Washington marine waters. Sea otters in Washington are expanding in both numbers and range extent (Fig. 1; Jameson et al., 1982; Jameson, 1998; Kvittek et al., 1998). Seasonal inhabitation of the western Strait of Juan de Fuca (SJDF) was observed from 1995 through 2000 (Gerber & VanBlaricom, 1999; Laidre et al., 2002; Gerber et al., 2004). This pattern, along with sightings of sea otters farther east in SJDF, in the Gulf and San Juan Islands, and in Puget Sound (Jameson et al., 1997) suggest that sea otters may soon expand their range farther into SJDF and possibly north into the San Juan Islands.

Finally, our study results also permit evaluation of implications of recent management changes in the commercial urchin fishery for nearshore ecosystems (including existing marine

preserves) in northern Washington. Management of the urchin fishery underwent significant change in 1995 in response to a US federal court ruling on shellfishery harvests in Washington

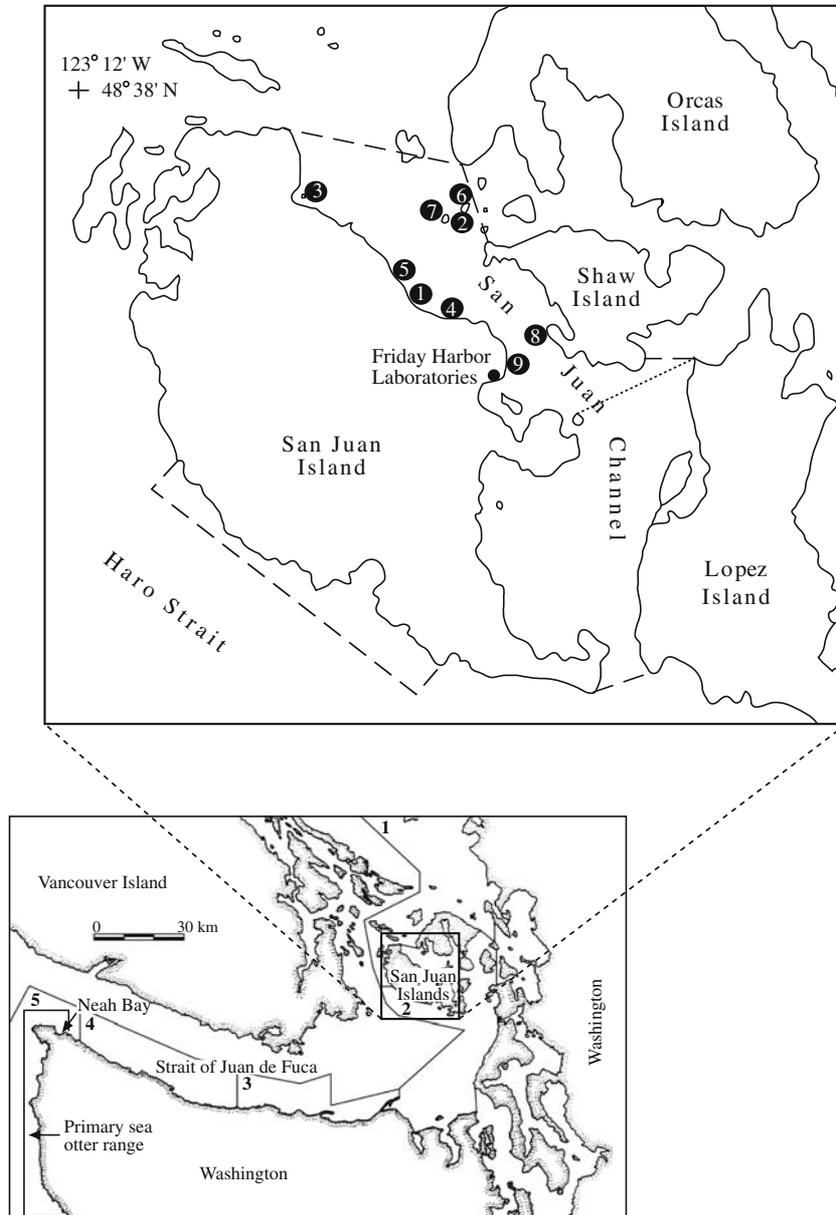


Fig. 1 The primary sea otter range and commercial sea urchin harvesting districts in Washington (after Kvitek et al., 1998, Lai and Bradbury 1998), and the locations of study sites in San Juan Channel. Harvest district numbers are shown in the upper left corner of each district. Sites 1–3 are simulated sea otter predation sites, sites 4–6 are simulated commercial fishery sites, and sites 7–9 are

control sites. Dashed lines represent the boundary of the areas on the west coast of San Juan Island and in San Juan Channel closed to commercial urchin harvest through fall 1998. The dotted line represents the modified southern boundary of the reserve area in San Juan Channel established in fall 1998

(*Shellfish Subproceedings of United States vs. State of Washington*, 873 F. Supp. 1422, 1994, known commonly as the “Rafeedie Decision”) that allotted one half of all harvestable shellfish to native tribes. As a result, a 3 year rotational harvest strategy, which had been employed for nearly two decades, was discontinued and replaced by annual harvest, to ensure that all tribes have equal access to their usual and accustomed fishing areas during each year. Carter & VanBlaricom (2002) provide experimental evidence that annual urchin harvests within a given location may not be sustainable in the region. The closure of the Neah Bay harvesting district in 1995 due to the movement of sea otters into the bay (Alex Bradbury, Washington Department of Fish and Wildlife, personal communication) in combination with declining catches in recent years (Hoiner, 1998) has resulted in some former marine preserve areas, including part of SJC, being opened to commercial harvest (Fig. 1).

We tested the null hypothesis that the presence of sea otters and commercial sea urchin harvesters do not affect the density of macroalgal species present in SJC by experimentally manipulating red urchin density to simulate sea otter predation and commercial red urchin harvest, and monitoring effects of the manipulation on macroalgae for 18 months. High urchin density despite urchin removal treatments, rapid recolonization of sites by urchins following treatment, a lack of kelp recruitment, or fluctuations in macroalgae too small or short-lived to be detected by our

sampling scheme might all lead to this result. Alternatively, short term fluctuations or sustained changes in the algal community over time may be observed in one or both treatments.

Methods

We established nine study sites in SJC, a marine preserve closed to commercial harvest of sea urchins, in November 1996–March 1997 (Fig. 1). Site selection was based on high red urchin density ($\geq 1.5/\text{m}^2$ in preliminary surveys), substrate (primarily large cobble or bedrock, see Table 1) and safety considerations. Sites were 6–10 m in depth and approximately 10 m \times 40 m, with the long axis of each site running parallel to the shoreline along the depth contour. Urchins were sampled in eight permanently marked circular sampling areas (each 7.07 m²) located along the midline of each site along the depth contour. Density of macroalgal species was monitored as an indicator of community change (Table 2). We define density as the number of algal holdfasts per unit area. Algal density is easily sampled for large, individually distinguishable plant species using standard scuba methods (e.g., Estes & Harrold, 1988), and has been used successfully by many authors as an indicator of change in nearshore benthic communities (e.g., Duggins, 1980; Cowen et al., 1982; Dayton et al., 1984; Watson, 1993; Estes & Duggins, 1995; Dean et al., 2000; Foster & VanBlaricom, 2001).

Table 1 Average depth (meters below mean lower low water) and substrate cover of San Juan Channel study sites

Site	Abbreviation	Treatment	Depth (m)	Substrate (%)		
				Sand	Cobble	Rock
1. Mid San Juan Island	Mid SJI _{Otter}	Otter	6.6	16.3	50.0	33.8
2. South McConnell Island	South McConnell _{Otter}	Otter	10.4	10.6	30.6	58.8
3. O’Neal Island	O’Neal _{Otter}	Otter	5.8	7.5	11.3	81.3
4. Point Caution, San Juan Island	Point Caution _{Fishery}	Fishery	7.5	23.8	27.5	48.8
5. Upper San Juan Island	Upper SJI _{Fishery}	Fishery	9.1	21.9	60.0	18.1
6. North McConnell Island	North McConnell _{Fishery}	Fishery	9.1	28.8	33.1	38.1
7. Yellow Island	Yellow _{Control}	Control	6.9	20.0	35.6	44.4
8. Point George, Shaw Island	Point George _{Control}	Control	7.5	24.1	13.8	62.1
9. Shady Cove, San Juan Island	Shady Cove _{Control}	Control	10.2	8.8	25.6	65.6

Substrate is based on visual estimates of percent cover in each permanently marked circular sampling area. In most cases cover was estimated at least twice in each circle, and the average value for all circles within each site is presented. Site numbers are those shown in Fig. 1

Table 2 Macroalgae sampled in permanently marked wedges in San Juan Channel study sites

Group/name	Order	Average density (number/m ²)	Standard deviation
Total macroalgae ^a		21.88	12.88
Agarum ^a		19.33	12.77
<i>Agarum fimbriatum</i> (primarily), <i>A. cribrosum</i>	Laminariales		
<i>Laminaria</i> ^a		0.77	1.29
<i>Laminaria groenlandica</i> (= <i>bongardiana</i>), <i>L. complanata</i> , <i>L. saccharina</i>	Laminariales		
Annual brown algae ^a		1.44	3.84
<i>Costaria costata</i> ^a	Laminariales	0.12	0.24
<i>Nereocystis luetkeana</i> ^a	Laminariales	0.01	0.04
<i>Alaria marginata</i>	Laminariales	0.02	0.07
<i>Desmarestia ligulata</i> ^a	Desmarestiales	1.29	3.58
Unknown macroalgae		0.35	0.60

^a Indicates the group or species was analyzed statistically. Values are averages of control sites over the duration of the study. Total macroalgae includes *Agarum*, *Laminaria*, annual brown algae and unknown macroalgae

Macroalgae were sampled in one permanently marked wedge (0.80 m²) within each circular sampling area. In our study areas, red algae were a minor component of cover on rocky substrata. However, we observed dense patches of both foliose and coralline red algae at shoaler depths adjacent to our study areas.

We applied one of three harvest treatments to each site. 'Otter predation' simulated the continuous presence of sea otters, and consisted of removal of all urchins present in March 1997, and at monthly intervals thereafter through September 1998. 'Commercial harvest' simulated annual commercial harvest of a bed of red urchins in the San Juan Islands according to current regulations (Pfister & Bradbury, 1996), and consisted of annual removal of all legal-sized urchins (102–140 mm test diameter) each winter (March of 1997 and 1998). Urchin densities were not manipulated in the 'control' treatment. Because of logistical constraints, control sites were located in smaller preserve areas within the larger SJC preserve where harvest of all invertebrates and fish is prohibited. Harvest treatments were randomly assigned to the remaining six sites. We did not simulate a combined otter and urchin harvest treatment, as sea otter presence in an area quickly reduces the density of large, exposed sea urchins to a level too low to support commercial harvest (Estes & VanBlaricom, 1985).

We removed only red urchins to simulate sea otter presence for several reasons. First, red

urchins are a favored prey item of sea otters (Riedman & Estes, 1990). Second, sea otters primarily consume urchins in newly occupied areas, switching to less preferred prey only after urchin density declines (Estes et al., 1978, 1982; Ostfeld, 1982). Third, prior to treatment, red urchins were the most abundant of known sea otter prey species in SJC (Table 3). While sea otters will consume sea cucumbers (the next most abundant group of invertebrates in our study sites), they are not a preferred species and will only be eaten in quantity after densities of urchins are greatly reduced. Green sea urchins (*S. droebachiensis*), a preferred prey item of sea otters in other areas along the west coast were present in only very low densities in our study sites (Table 3) and in diameters smaller than sea otters are known to consume. The few green sea urchins that were observed over the course of the study (26 vs. 3,700 red sea urchins) were tiny (2–12 mm test diameter) and often in cryptic or concealed microhabitats such as on cobble, kelp blades or in algal holdfasts (Carter, 1999). Thus green sea urchins did not represent an important grazing presence or food source for sea otters in our study sites.

Sampling occurred from March 1997 through September 1998. All sites were sampled five times per year: early March, mid March, April, June, and September. The early March 1997 sampling period occurred prior to any urchin removal. The sampling periods represent pre-harvest and 5, 30,

Table 3 Average density (number/m²) of invertebrates in San Juan Channel study sites in March 1997 (pre-harvest)

Common name of species or group of species	Latin name(s)	Density
Red sea urchin _H *	<i>Strongylocentrotus franciscanus</i>	1.35
Green sea urchin _H *	<i>Strongylocentrotus droebachiensis</i>	0.01
Sea urchins		1.36
California sea cucumber _D *	<i>Parastichopus californicus</i>	0.29
Orange sea cucumber _F	<i>Cucumaria miniata</i>	0.60
Slipper sea cucumber _F	<i>Psolus chitonoides</i>	0.05
Sea cucumbers	Includes species <i>Parastichopus californicus</i> , <i>Cucumaria miniata</i> , <i>Eupentacta quinquesemita</i> , <i>Cucumaria piperata</i> _F , <i>Psolus chitonoides</i>	0.94
Sea stars	Includes species <i>Henricia leviuscula</i> _C *, <i>Evasterias troschelii</i> _C *, <i>Dermasterias imbricata</i> _C , <i>Pycnopodia helianthoides</i> _C *, <i>Solaster dawsoni</i> _C , <i>Solaster stimpsoni</i> _C , <i>Stylasterias forreri</i> _C , <i>Leptasterias hexactis</i> _C , <i>Pteraster tessellatus</i> _C	0.12
Crabs	Includes species <i>Scyra acutifrons</i> _H , <i>Oregonia gracilis</i> _H , <i>Pugettia gracilis</i> _H *, <i>Pugettia producta</i> _H *, <i>Cancer productus</i> _C *, <i>Cancer oregonensis</i> _C *, <i>Telmessus cheiragonus</i> *, <i>Cryptolithoides</i> sp.*	0.10
Large snails	<i>Cerastostoma foliatum</i> _C , <i>Nucella lamellosa</i> _C *, <i>Fusitriton oregonensis</i> _C	0.12
Pinto abalone _H	<i>Haliotis kamtschatkana</i> *	0.002
Scallops	Includes <i>Hinnites giganteus</i> _F *, <i>Chlamys</i> sp. _F	0.01
Clams _F *		0
Gumboot chiton _H *	<i>Cryptochiton stelleri</i>	0.01
Nudibranchs _C	e.g., <i>Archidoris</i> spp., <i>Dirona</i> spp.	0.04
Solitary tunicate _F	<i>Cnemidocarpa finsmarkiensis</i>	0.19
Anemones _F *		0.004
Brachiopod _F	<i>Terebratalia transversa</i>	0.04

Species which are primarily herbivores (H), detritivores (D), filter feeders (F), and carnivores (C) are indicated. Known prey items of sea otters (Riedman & Estes, 1990) are indicated by an asterisk (*). Species with low densities (<0.2/m²) were grouped in the table; densities of individual species can be found in Carter (1999)

90 and 180 days post-harvest in each year for the commercial harvest treatment. The sampling dates were chosen to detect both short term and seasonal variation in abundance of kelps. The duration of the study (1.5 years of sampling after initial treatment) has proven adequate to detect changes in abundance and diversity of kelps in comparable studies in California, Washington and Alaska (Vadas, 1968; Paine & Vadas, 1969; Duggins, 1980; Laur et al., 1988; Watson, 1993).

Data were analyzed using analysis of variance or repeated measures analysis of variance. We first analyzed site depths using a one-way analysis of variance to determine if significant differences in depth existed between treatment groups. One way analyses of variance were also conducted on densities of red sea urchins and algal groups to determine if significant differences in density between treatments existed prior to the initial treatment of sites (i.e., using data from the early March 1997 time period). Abundance data for red sea urchins and macroalgae were log transformed

for analyses to improve the variance structure, using log ($x + 1$) which is the specific transformation recommended by Zar (1984) when some of the observed values are small numbers (particularly zero).

We conducted a repeated measures analysis of variance on the density of sea urchins and algal groups over time to detect potential changes in these variables as a result of our treatments. Data from all ten sampling periods are presented graphically. To decrease temporal correlation of the data, only data collected in April, June, and September of each year were analyzed statistically. The three sampling periods were modeled as three unevenly spaced dates (hereafter seasons) within each of 2 years. We used Mauchley's test to assess the sphericity of our data. Sphericity refers to the condition in which the variances of the differences between values of the variable of interest over time are the same for all treatments (Quinn & Keough, 2002). If the sphericity condition is not met and the degrees of freedom are not

adjusted, the type I error rate will be greater than expected. When the sphericity condition was not met, we adjusted the degrees of freedom for significance tests for within subjects effects by the Huynh-Feldt epsilon (SPSS, 1996). Site was considered a random factor and treatment a fixed factor in the repeated measures analyses of variance. Site was nested within treatment for analyses. Kelp abundance is well known to vary on a local scale with substrate type because individuals cannot effectively attach to sand or small cobble substrates. We included a substrate covariate (estimated percent cover of sand, rock or cobble) in the model if it explained a significant amount of the variability within or between sites. The percent cover of substrate in sampling units was arcsin transformed for analyses to improve the variance structure (Zar, 1984). We include the full repeated measures analysis of variance table for the dominant species of algae (*Agarum*) as an example of the repeated measures analysis of variance performed for all macroalgae. Repeated measures analysis of variance results are summarized in Table 4.

In the repeated measures analysis of variance, effects of the experimental treatments may be detected as a significant treatment effect, or as a significant interaction between treatment and season, year, or season and year. A significant treatment effect may or may not represent an actual effect of the urchin removal treatment, dependent upon whether the treatment means were significantly different prior to treatment, the speed with which a treatment effect occurred, and the duration of a treatment effect. Significant interactions involving treatment and year or

season indicate that the effect of treatment varied over time, and also may indicate significant impacts of the urchin removal treatments over time. When significant interactions between treatment and time were detected, results were interpreted based on graphs of the data.

One-way analyses of variance were also performed on algal density data collected at the end of the second summer (September 1998, the final sampling period) to determine if urchin removal treatments conducted over a period of two full growing seasons had resulted in significant differences in algal density between treatments. We did a post-hoc power calculation (Quinn & Keough, 2002) to assess the power of this analysis to detect differences. Minimum detectable differences for the one way analyses of variance conducted on the September 1998 algal data were calculated using $\alpha = 0.05$ and $\beta = 0.20$ (i.e., power of 0.80). We used the formula $\delta = \sqrt{((2ks^2\phi^2)/n)}$, where k is the number of experimental groups (here 3), s^2 is the estimate of variance within algal groups from the analysis of variance, n is the number of sampling units in each treatment (here 3), and ϕ is an intermediate parameter necessary to calculate the minimum detectable difference and is related to the noncentrality parameter (Zar, 1984). The level of significance for all tests was $\alpha = 0.05$.

Results

Though the initial density of urchins did not differ between treatments ($P = 0.65$), direct effects of the harvest treatments emerged quickly and persisted throughout the study. Direct effects of

Table 4 Summary of repeated measures analysis of variance results for sea urchins and macroalgae

Species group	Year	Season	Year * treatment	Season * treatment	Year * Season * treatment	Treatment	Substrate
Sea urchins (<i>S. franciscanus</i>)	0.72	0.59	0.75	0.16	0.45	0.003	
Total algae	0.92	0.34	0.48	0.47	0.68	0.29	Rock
<i>Agarum</i>	0.97	0.02	0.62	0.02	0.81	0.53	Rock
<i>Laminaria</i>	0.09	0.11	0.06	0.78	0.46	0.60	Sand
Annual algae	0.26	0.02	0.75	0.95	0.78	0.81	Sand
<i>Desmarestia</i>	0.09	0.02	0.64	0.90	0.76	0.80	Sand
<i>Costaria</i>	0.75	0.09	0.86	0.61	0.91	0.50	Sand
<i>Nereocystis</i>	0.60	0.14	0.31	0.43	0.28	0.42	Sand

P values are given for each effect. If a measure of substrate was included in the model, it is listed in the final column

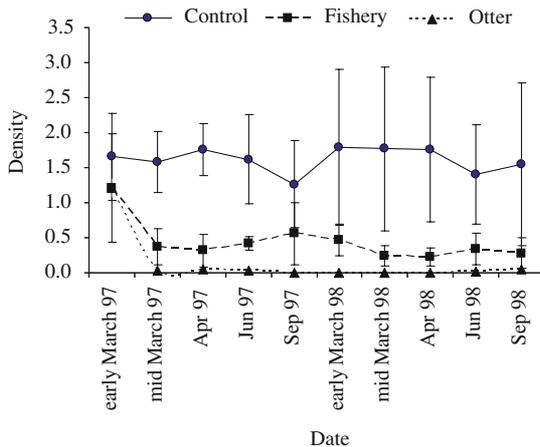


Fig. 2 Average density (no/m² ±SD) of sea urchins in control, fishery, and otter treatments in San Juan Channel. The early March 1997 sampling period occurred prior to any urchin removal, and the early March 1998 sampling period occurred immediately prior to the second annual harvest in the fishery treatment sites

the harvest treatments on urchin densities were significant ($P < 0.003$, Fig. 2, Table 4). Simulated sea otter predation reduced urchin density by 98% initially. Urchin density remained low for the duration of the study ($<0.04/\text{m}^2$), confirming that monthly removal of urchins was adequate to simulate continuous sea otter presence. Simulated commercial urchin harvest reduced urchin density by 70% initially. Urchin density in fishery sites remained lower than in control sites throughout the study (Fig. 2).

Prior to the initial harvest in March 1997, macroalgae were abundant in all study sites and the total abundance of macroalgae did not vary significantly by treatment ($P = 0.86$). Depth of sites, a well-known factor influencing algal abundance, did not differ between treatments ($P = 0.81$). Harvest treatment did not significantly affect the total abundance of macroalgae sampled over time (Table 4, Fig. 3a). Macroalgae were not significantly more abundant in treatment sites than in control sites in September of 1998 (i.e., after 1.5 years of urchin removal treatment, Table 5).

Agarum spp., perennial understory kelps, dominated kelp communities in SJC study sites (Table 2). Prior to the initial harvest in March 1997, density of *Agarum* did not vary significantly

by treatment ($P = 0.71$). The urchin removal treatments did not significantly affect the mean density of *Agarum* averaged over time (i.e., a treatment effect, Tables 4 and 6). The significant interaction between treatment and season indicates that the effect of treatment varied with time. Close inspection of Fig. 3c indicates that this interaction is due to the fact that *Agarum* density increased more in control sites than in treatment sites between June and September of each year, although the effect is not consistent among control sites (Fig. 3d). The density of *Agarum* did not differ between treatments in September 1998 (Table 5).

Laminaria was the only other perennial understory kelp present in SJC study sites. Prior to the initial harvest in March 1997, density of *Laminaria* did not vary significantly between treatments ($P = 0.61$). Urchin removal did not significantly affect the mean density of *Laminaria* (Table 4, Fig. 3e). Density of *Laminaria* was not significantly higher in either harvest treatment versus the control treatment in September 1998 (Table 5).

Annual species of macroalgae sampled in SJC were generally less common (Table 2). The pronounced annual cycle of spring recruitment, summer growth, and nearly complete winter die-off/removal by storms is reflected in the significant effect of season on the group (Table 4, Fig. 3g). Prior to the initial harvest in March 1997, no annual algae were present in any of the study sites. Treatment did not significantly affect the density of all annual species combined or of individual species (Table 4). Density of annual species of algae was not significantly higher in either harvest treatment versus the control treatment in September 1998 (Table 5).

Discussion

In previous studies of simulated or actual sea otter predation at selected sites in Alaska, British Columbia, and Washington, a reduction in urchin density led to rapid and dramatic changes in the macroalgal community. Abundance and diversity of annual species increased rapidly, followed by a

decline in diversity as one or a few species became dominant (Paine & Vadas, 1969; Duggins, 1980; Pace, 1981; Watson, 1993). The process of succession from urchin-dominated barren grounds to kelp forests generally began within a few months of simulated or actual sea otter predation, and was largely complete within 1 year (rarely 2 years). Similar changes in algal communities have been observed on the east coast of North America following experimental urchin removal (Breen & Mann, 1976; Chapman, 1981;

Himmelman et al., 1983; Witman, 1987; Johnson & Mann, 1988; Keats et al., 1990).

Effects of simulated sea otter predation in SJC differed substantially from this well-known pattern. We detected only one significant effect in our analyses of macroalgae. The effect of treatment on abundance of *Agarum* differed by season. However, graphical examination of the data reveal that the interaction is due to larger increases in the density of *Agarum* in control sites than in treatment sites between June and

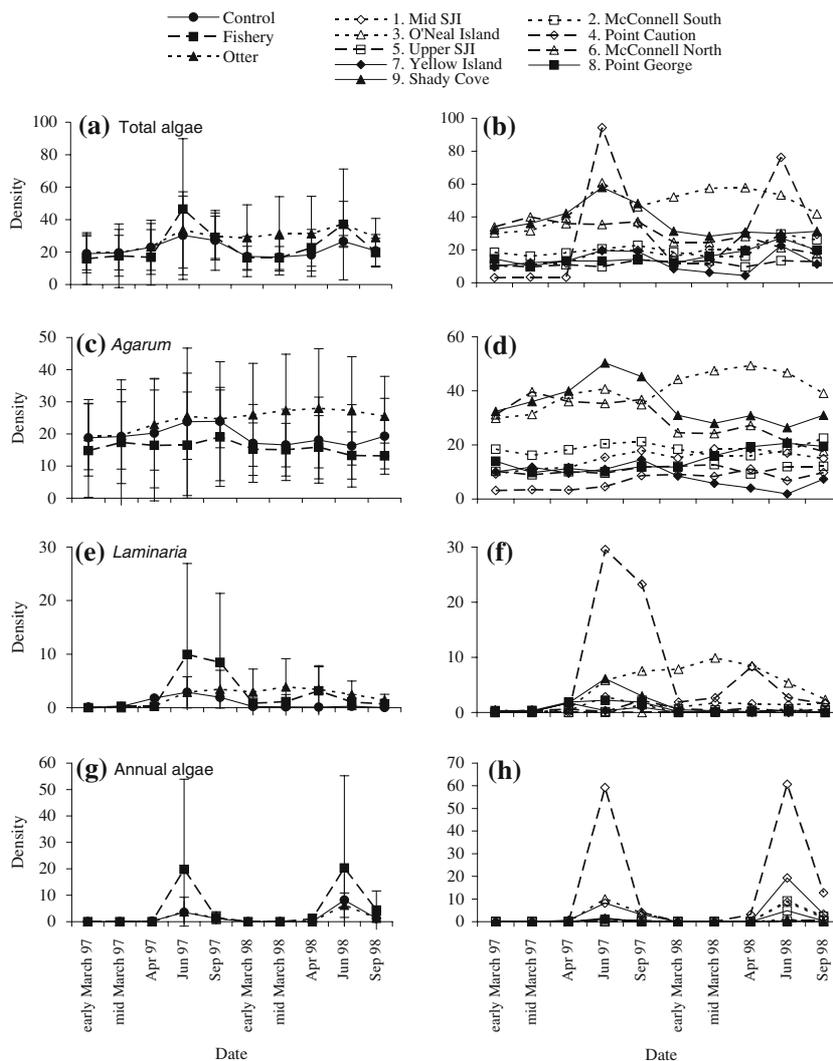


Fig. 3 Average density (no/m² ± SD) of total macroalgae (a–b), *Agarum* (c–d), *Laminaria* (e–f), and annual brown algae (g–h) in control, fishery, and otter treatments (first column) and individual study sites (second column) in San Juan Channel. Sites 1–3 are otter sites, sites 4–6 are fishery

sites, and sites 7–9 are control sites. The early March 1997 sampling period occurred prior to any urchin removal, and the early March 1998 sampling period occurred immediately prior to the second annual harvest in the fishery treatment sites

Table 5 Summary of one-way analysis of variance results for density of macroalgae sampled in September 1998

Algal group	<i>P</i> value	δ (number/m ²)
Total algae	0.46	33.89
<i>Agarum</i>	0.42	33.70
<i>Laminaria</i>	0.13	2.54
Annual algae	0.74	14.54
<i>Desmarestia</i>	0.96	6.72
<i>Costaria</i>	0.52	4.31
<i>Nereocystis</i>	0.42	4.00

The *P* value and a post hoc calculation of the minimum detectable difference for each test (δ) are presented. Minimum detectable differences in algal density (number/m²) shown are based on $\alpha = 0.05$ and $\beta = 0.20$

September of each year, an effect unlikely to be related to our urchin removal treatments which significantly decreased grazing pressure in treatment sites compared to control sites. In addition, after 18 months of simulated sea otter predation (~98% reduction in urchin density), density of *Agarum* in otter predation sites was not significantly greater than in control sites. Similarly, densities of *Laminaria* and all annual species of algae were also not significantly higher in treatment compared to control sites after two seasons of simulated otter predation. Our results suggest

that a potential future range expansion of the Washington sea otter population into SJC would not be accompanied by the dramatic changes in nearshore benthic communities typically seen when sea otters recolonize outer coastal areas.

Previous studies of effects of commercial urchin harvest on macroalgal communities are limited, but suggest a possible increase in algal density over time. Commercial harvest of red urchins on the west coast of Vancouver Island appeared to increase *Nereocystis* and *Pterygophora* density in some sites, but other sites showed no change (Breen et al., 1976, 1978). Experimental harvest of adult (>89 mm) red urchins in shallow sites (5 m) in northern California resulted in a general but unquantified increase in macroalgae within several years (Rogers-Bennett et al., 1998). Harvest of *Loxechinus albus* on the southwest coast of South America appeared to result in widespread recruitment of juvenile kelps (Dayton, 1985b). Simulated commercial fishing (~65% reduction in urchin density) in SJC had little effect on abundance of the algae studied over 2 years. As explained in the previous paragraph, the significant interaction between treatment and time for *Agarum* is unlikely to be due to our urchin

Table 6 Summary of repeated measures analysis of variance results for *Agarum*

In cases where the degrees of freedom for the tests of significance for the within subjects effects were adjusted by the Huynh–Feldt epsilon, the unadjusted degrees of freedom are given in parentheses. Asterisks in column five indicate factors significant at the $\alpha = 0.05$ level

Source	Degrees of freedom	Mean square	F ratio	<i>P</i> value
Within subjects effects				
Year	1	0.00120	0.002	0.966
Year * rock	1	0.0127	0.063	0.803
Year * treatment	2	0.324	0.528	0.615
Year * site (treatment)	6	0.614		
Error (year)	62	0.203		
Season	1.896 (2)	0.406	6.059	0.017*
Season * rock	1.896 (2)	0.0350	0.742	0.472
Season * treatment	3.792 (4)	0.288	4.298	0.025*
Season * site (treatment)	11.377 (12)	0.0670		
Error (season)	117.558 (124)	0.0471		
Year * season	1.954 (2)	0.118	1.190	0.338
Year * season * rock	1.954 (2)	0.0485	1.156	0.317
Year * season * treatment	3.908 (4)	0.0390	0.394	0.809
Year * season * site (treatment)	11.723 (12)	0.0991		
Error (year * season)	121.135 (124)	0.0419		
Between subjects effects				
Intercept	1	113.795	249.161	0.000
Rock	1	2.527	5.533	0.022*
Treatment	2	2.476	0.702	0.532
Site (treatment)	6	3.526		
Error	62	0.457		

removal treatments, and density of all algal groups was not significantly higher in the fishery treatment than in the control treatment after two seasons of simulated commercial red urchin harvest. Thus while annual harvest of red sea urchins under current management regulations does significantly impact urchin populations in SJC (Carter & VanBlaricom, 2002, this study), our results do not suggest that annual commercial urchin harvest would elicit large changes in algal communities in SJC in the near term.

The lack of significantly higher densities of algae in the second year of urchin removal confirms that there was a substantial difference in effects of urchin removal in SJC versus outer coastal habitats studied previously. Activity of urchins, the presence of dense stands of *Agarum*, and grazing by microinvertebrates may explain the difference. Urchin movement in SJC appeared to be low (Carter & VanBlaricom, 2002) and urchin fronts were never observed, suggesting little active grazing on attached macroalgae (Mattison et al., 1977; Dean et al., 1984). The understory bed of *Agarum* present in all SJC sites may have inhibited effects commonly associated with urchin removal in several ways. *Agarum* is less susceptible to urchin grazing than *Laminaria*, *Nereocystis*, *Alaria* and *Costaria* (Vadas, 1968, 1977; Himmelman & Nédélec, 1990), probably due to higher tissue concentrations of phlorotannins (Van Alstyne et al., 1999). In addition, because of the dominance and abundance of *Agarum* in SJC, reproductively mature individuals of other species (particularly annual species) are relatively rare and may have limited recruitment potential for a variety of reasons, including spacing of adult plants and effects of shading, sedimentation, physical scouring, and heavy spore settlement by *Agarum* (Vadas, 1968, 1972; Dayton et al., 1984; Reed et al., 1988; Reed, 1990). Finally, invertebrate grazers other than urchins present in SJC sites, such as chitons, abalone, spider crabs, limpets, gastropods (e.g., *Lacuna*, *Calliostoma*, *Margarites*), various filter feeders, amphipods, isopods and polychaetes, all likely consume algal spores, gametophytes or sporophytes, potentially contributing to low algal recruitment (Dayton et al., 1984; Dayton, 1985a).

Based on consideration of our data and relevant published studies in more exposed, outer coast locations, we offer the following set of related general hypotheses to explain why trophic cascades driven by sea otter predation may be less prominent in kelp forests in physically protected locations than in exposed outer coast locations. First, *Agarum* is able to form a dense canopy in relatively shallow waters in physically protected locations. The same does not occur in exposed locations because *Agarum* cannot tolerate persistent accelerations associated with large oceanic waves. We note that Dayton (1975) found that *Agarum* was abundant at Amchitka Island in the Aleutian region, but only below threshold depths at which wave-associated accelerations apparently do not exceed a critical maximum. Second, in the presence of dense *Agarum* stands in protected locations, recruitment of other algae and possibly of invertebrates is greatly restricted by the combined effects of shading, abrasion, and possibly negative chemical effects of *Agarum* blades. Recruitment of benthic organisms, including urchins and other invertebrates as well as other algae, may also be limited by processes independent of *Agarum* density. Conversely, in the absence of dense *Agarum* beds in exposed locations, other kelps are able to recruit, grow, and reproduce more successfully. Successful kelps in such habitats are highly flexible and elastic, thereby reducing potentially damaging effects of frequent accelerations associated with large waves. In the North Pacific, kelps able to survive in outer coast habitats are, coincidentally, generally lacking in the chemical defenses necessary to minimize or resist grazing by urchins. Third, during episodes of relative calm, urchins on outer coasts are able to move about efficiently, locate kelps that lack significant chemical defenses, and graze actively on these kelps such that kelp densities are reduced. Consequently, urchins have significant ecological roles as grazers in outer coast habitats, although effects of urchins can be mitigated episodically by intensive wave action. The addition of sea otters to nearshore systems through, for example, recolonization of historically occupied areas, has very different effects on outer coast habitats compared to protected locations. In the outer coast case, sea otters

eliminate episodic grazing by sea urchins and facilitate larger, more productive, and more diverse kelp forests as has been observed in selected sites in California, British Columbia and Alaska. In the physically protected case, urchin predation and the subsequent loss of urchin grazing has minimal effects on the algal community because urchin grazing cannot influence density and canopy structure of the chemically defended *Agarum*.

Low statistical power to detect treatment effects is a common problem in ecological studies, particularly in those conducted in subtidal habitats (Schroeter et al., 1993). To our knowledge, no previous studies of effects of sea otter predation or urchin removal on algal abundance have reported power (Cowen et al., 1982; Watson, 1993; Estes & Duggins, 1995). Schroeter et al. (1993) suggest that effects of disturbances on nearshore subtidal organisms should be interpreted considering the consistency of effects on various organisms and evidence of reasonable mechanisms, as well as the confidence in the statistical analyses. Many previous studies have established potential mechanisms for effects of reductions in urchin density on algae (e.g., Lawrence, 1975). We analyzed a variety of species of macroalgae, and results were consistent both within and among groups. In this study, we used large sites to more accurately simulate trophic effects of sea otters and anthropogenic effects of commercial sea urchin harvesters. Consequently, the number of replicate sites within treatments was low for logistical reasons. The high variability in density of organisms within and between sites (see Fig. 3) also contributed to the low statistical power. However, effects of urchin removal on algal populations have typically been dramatic, and minimum detectable differences in algal density for the more abundant species of algae in our study (see Table 5) were substantially smaller than actual changes observed as a result of urchin removals in other studies in the region (e.g., total kelp density increased by $\sim 47/\text{m}^2$ after 2 years of sea otter occupation in southeast Alaska (Estes & Duggins, 1995) and densities of *Laminaria* were 0 vs. $\sim 100/\text{m}^2$ in control versus urchin removal sites after 2 years of treatment in southeast Alaska (Duggins, 1980).

Are sea otters keystone predators?

Sea otters have long been absent from SJC, yet urchins are only moderately abundant ($\sim 1/\text{m}^2$, this study). Low density and a size distribution strongly skewed toward large individuals suggest that red urchin populations in SJC are effectively regulated by recruitment frequency (Carter, 1999; Carter & VanBlaricom, 2002). This observation lends support to assertions of Foster & Schiel (1988) and Foster (1990) that sea otters are only one of several factors that may regulate urchin populations in nearshore waters. Two years of simulated sea otter predation did not result in significantly higher densities of macroalgae in this study, suggesting that other factors such as grazing by other invertebrates, the presence of dense stands of *Agarum*, and recruitment frequency of macroalgae and macroinvertebrates may play a large role in influencing community structure in SJC and other physically protected marine waters.

Our data show by counterexample that the sea otter-trophic cascade paradigm is not universally applicable across locations or habitat types. Despite an experimental design with a time line greater than previous experimental or descriptive studies, and with adequate statistical power to detect community-level changes smaller than those seen in other studies, we did not duplicate the results of previously published work. Our results reinforce our concern that charismatic linkages between foraging by apex predators and biodiversity at the community level should be allowed to influence conservation and management policy only to the extent that reproducibility has been empirically confirmed within the geographic and habitat context of the specific issues and questions under consideration.

Acknowledgments This work was conducted as part of the requirements for a Master of Science degree for S.K. Carter in the School of Aquatic and Fishery Sciences at the University of Washington. Drs. D.O. Duggins, T. Klinger, C.J. Foote, and K.K. Chew provided helpful suggestions and guidance on many aspects of the project. S. Sublett, J.M. Grassley, and many others assisted with data collection. Dr. A.O.D. Willows and the staff and faculty at Friday Harbor Laboratories provided logistical support and use of the facilities and equipment. A.H. Fayram facilitated completion of the project and final manuscript,

and P. Rasmussen assisted with statistical analysis and interpretation. Funding for the project was provided by the U.S. Geological Survey-Biological Resources Division, the Washington Department of Fish and Wildlife, the North Pacific Universities Marine Mammal Research Consortium, the Washington Cooperative Fish and Wildlife Research Unit, the H. Mason Keeler Endowment for Excellence, the Egtvedt Endowment Scholarship, the John N. Cobb Scholarship and the School of Aquatic and Fishery Sciences, University of Washington. We offer sincere thanks to all.

References

- Breen, P. A. & K. H. Mann, 1976. Destructive grazing of kelp by sea urchins in eastern Canada. *Journal of the Fisheries Research Board of Canada* 33: 1278–1283.
- Breen, P. A., B. E. Adkins & D. C. Miller, 1978. Recovery rate in three exploited sea urchin populations from 1972 to 1977. *Fisheries and Marine Services Manuscript Report* 1446: 1–27.
- Breen, P. A., D. C. Miller & B. E. Adkins, 1976. An examination of harvested sea urchin populations in the Tofino area. *Fisheries Research Board of Canada Manuscript Report Series* 1401: 1–23.
- Carter, S. K., 1999. Ecosystem effects of simulated sea otter predation and commercial sea urchin harvest on nearshore benthic communities in northern Washington. M. S. Thesis. University of Washington, Seattle.
- Carter, S. K. & G. R. VanBlaricom, 2002. Effects of experimental harvest on red sea urchins, *Strongylocentrotus franciscanus*, in northern Washington. *Fisheries Bulletin* 100: 662–673.
- Chapman, A. R. O., 1981. Stability of sea urchin dominated barren grounds following destructive grazing of kelp in St Margaret's Bay, eastern Canada. *Marine Biology* 62: 307–311.
- Cowen, R. K., C. R. Agegian & M. S. Foster, 1982. The maintenance of community structure in a central California giant kelp forest. *Journal of Experimental Marine Biology and Ecology* 64: 189–201.
- Dayton, P. K., 1975. Experimental studies of algal canopy interactions in a sea otter-dominated kelp community at Amchitka Island, Alaska. *Fishery Bulletin* 73: 230–238.
- Dayton, P. K., 1985a. Ecology of kelp communities. *Annual Review of Ecology and Systematics* 16: 215–245.
- Dayton, P. K., 1985b. The structure and regulation of some South American kelp communities. *Ecological Monographs* 55: 447–468.
- Dayton, P. K., V. Currie, T. Gerrodette, B. D. Keller, R. Rosenthal & D. Ven Tresca, 1984. Patch dynamics and stability of some California kelp communities. *Ecological Monographs* 54: 253–289.
- Dean, T. A., S. C. Schroeter & J. D. Dixon, 1984. Effects of grazing by two species of sea urchins (*Strongylocentrotus franciscanus* and *Lytechinus anamesus*) on recruitment and survival of two species of kelp (*Macrocystis pyrifera* and *Pterygophora californica*). *Marine Biology* 78: 301–313.
- Dean, T. A., J. L. Bodkin, S. C. Jewett, D. H. Monson & D. Jung, 2000. Changes in sea urchins and kelp following a reduction in sea otter density as a result of the *Exxon Valdez* oil spill. *Marine Ecology Progress Series* 199: 281–291.
- Duggins, D. O., 1980. Kelp beds and sea otters: an experimental approach. *Ecology* 61: 447–453.
- Estes, J. A. & D. O. Duggins, 1995. Sea otters and kelp forests in Alaska: generality and variation in a community ecological paradigm. *Ecological Monographs* 65: 75–100.
- Estes, J. A. & C. Harrold, 1988. Sea otters, sea urchins, and kelp beds: some questions of scale. In VanBlaricom, G. R. & J. A. Estes (eds), *The Community Ecology of Sea Otters*. Springer-Verlag, Berlin, 116–150.
- Estes, J. A. & J. F. Palmisano, 1974. Sea otters: their role in structuring nearshore communities. *Science* 185: 1058–1060.
- Estes, J. A. & G. R. VanBlaricom, 1985. Sea-otters and shellfisheries. In Beddington, J. R., R. J. H. Beverton & D. M. Lavigne (eds), *Marine Mammals and Fisheries*. George Allen and Unwin, London, UK, 187–235.
- Estes, J. A., R. J. Jameson & E. B. Rhode, 1982. Activity and prey election in the sea otter: influence of population status on community structure. *American Naturalist* 120: 242–258.
- Estes, J. A., N. S. Smith & J. F. Palmisano, 1978. Sea otter predation and community organization in the western Aleutian Islands, Alaska. *Ecology* 59: 822–833.
- Estes, J. A., M. T. Tinker, T. M. Williams & D. F. Doak, 1998. Killer whale predation on sea otters linking oceanic and nearshore ecosystems. *Science* 282: 473–476.
- Fanshawe, S., G. R. VanBlaricom & A. A. Shelly, 2003. Restored top carnivores as detriments to the performance of marine protected areas intended for fishery sustainability: a case study with red abalones and sea otters. *Conservation Biology* 17: 273–283.
- Foster, M. S., 1990. Organization of macroalgal assemblages in the Northeast Pacific: the assumption of homogeneity and the illusion of generality. *Hydrobiologia* 192: 21–33.
- Foster, M. S. & D. R. Schiel, 1988. Kelp communities and sea otters: keystone species or just another brick in the wall? In VanBlaricom, G. R. & J. A. Estes (eds), *The Community Ecology of Sea Otters*. Springer-Verlag, Berlin, 92–115.
- Foster, M. S. & G. R. VanBlaricom, 2001. Spatial variation in kelp forest communities along the Big Sur coast of central California, USA. *Cryptogamie et Algologie* 22: 173–186.
- Gerber, L. R. & G. R. VanBlaricom, 1999. Potential fishery conflicts involving sea otters (*Enhydra lutris* [L.]) in Washington state waters. Final report, contract T30917202. Marine Mammal Commission, Washington, DC.
- Gerber, L. R., K. E. Buenau & G. R. VanBlaricom, 2004. Density dependence and risk of extinction in a small population of sea otters. *Biodiversity and Conservation* 13: 2741–2757.
- Harrold, C. & D. C. Reed, 1985. Food availability, sea urchin grazing, and kelp forest community structure. *Ecology* 66: 1160–1169.

- Himmelman, J. H., A. Cardinal & E. Bourget, 1983. Community development following removal of urchins, *Strongylocentrotus droebachiensis*, from the rocky subtidal zone of the St Lawrence Estuary, eastern Canada. *Oecologia* 59: 27–39.
- Himmelman, J. H. & H. Nédélec, 1990. Urchin foraging and algal survival strategies in intensely grazed communities in eastern Canada. *Canadian Journal of Fisheries and Aquatic Sciences* 47: 1011–1026.
- Hoines, L., 1998. 1995 Fisheries statistical report. Washington State Department of Fish and Wildlife, Olympia.
- Jameson, R. J., 1998. Translocated sea otter populations off the Oregon and Washington coasts. In Mac, M. J., P. A. Opler, C. E. Puckett-Haecker & P. D. Doran (eds), *Status and Trends of the Nation's Biological Resources*, Vol. 2. U.S. Geological Survey, Washington, DC, 684–686.
- Jameson, R. J., S. Jeffries & K. W. Kenyon, 1997. Status and trends of the Washington translocated sea otter population. Presentation at the Sixth Joint US-Russia Sea Otter Workshop, November 9–15, 1997, Forks, Washington.
- Jameson, R. J., K. W. Kenyon, A. M. Johnson & H. N. Wight, 1982. History and status of translocated sea otter populations in North America. *Wildlife Society Bulletin* 10: 100–107.
- Johnson, C. R. & K. H. Mann, 1988. Diversity, patterns of adaptation, and stability of Nova Scotian kelp beds. *Ecological Monographs* 58: 129–154.
- Kalvass, P. E. & J. M. Hendrix, 1997. The California red sea urchin, *Strongylocentrotus franciscanus*, fishery: catch, effort, and management trends. *Marine Fisheries Review* 59(2): 1–17.
- Keats, D. W., G. R. South & D. H. Steele, 1990. Effects of an experimental reduction in grazing by green sea urchins on a benthic macroalgal community in eastern Newfoundland. *Marine Ecology Progress Series* 68: 181–193.
- Kvitek, R. G., P. J. Iampietro & C. E. Bowlby, 1998. Sea otters and benthic prey communities: a direct test of the sea otter as keystone predator in Washington state. *Marine Mammal Science* 14: 895–902.
- Lai, H. L. & A. Bradbury, 1998. A modified catch-at-size analysis model for a red sea urchin (*Strongylocentrotus franciscanus*) population. In Jamieson, G. S. & A. Campbell (eds), *Proceedings of the North Pacific Symposium on Invertebrate Stock Assessment and Management*. Canadian Special Publications in Fisheries and Aquatic Sciences 125: 85–96.
- Laidre, K. L., R. J. Jameson, S. J. Jeffries, R. C. Hobbs, C. E. Bowlby & G. R. VanBlaricom, 2002. Estimates of carrying capacity for sea otters in Washington State. *Wildlife Society Bulletin* 30: 1172–1181.
- Laur, D. R., A. W. Ebeling & D. A. Coon, 1988. Effects of sea otter foraging on subtidal reef communities off central California. In VanBlaricom, G. R. & J. A. Estes (eds), *The Community Ecology of Sea Otters*. Springer-Verlag, Berlin, 151–168.
- Lawrence, J. M., 1975. On the relationships between marine plants and sea urchins. *Oceanogr Marine Biology Annual Review* 13: 213–286.
- Lebednik, P. A., F. C. Weinmann & R. E. Norris, 1971. Spatial and seasonal distributions of marine algal communities at Amchitka Island, Alaska. *Bioscience* 21: 656–660.
- Mattison, J. E., J. D. Trent, A. L. Shanks, T. B. Akin & J. S. Pearse, 1977. Movement and feeding activity of red sea urchins (*Strongylocentrotus franciscanus*) adjacent to a kelp forest. *Marine Biology* 39: 25–30.
- Neushul, M., 1967. Studies of subtidal marine vegetation in western Washington. *Ecology* 48: 83–94.
- Ostfeld, R. S., 1982. Foraging strategies and prey switching in the California sea otter. *Oecologia* 53: 170–178.
- Pace, D., 1981. Kelp community development in Barkley Sound, British Columbia following sea urchin removal. In Fogg, G. E. & W. E. Jones (eds), *Proceedings of the Eighth International Seaweed Symposium*, 18–23 August, 1974. Bangor, North Wales, The Marine Science Laboratories, Menai Bridge, United Kingdom, 457–463.
- Paine, R. T., 1966. Food web complexity and species diversity. *American Naturalist* 100: 65–75.
- Paine, R. T., 1974. Intertidal community structure: experimental studies on the relationship between a dominant competitor and its principal predator. *Oecologia* 15: 93–120.
- Paine, R. T., 1969. A note on trophic complexity and community stability. *American Naturalist* 103: 91–93.
- Paine, R. T. & R. L. Vadas, 1969. The effects of grazing by sea urchins, *Strongylocentrotus* spp., on benthic algal populations. *Limnology and Oceanography* 14: 710–719.
- Pearse, J. S. & A. H. Hines, 1979. Expansion of a central California kelp forest following the mass mortality of sea urchins. *Marine Biology* 51: 83–91.
- Pearse, J. S. & A. H. Hines, 1987. Long-term population dynamics of sea urchins in a central California kelp forest: rare recruitment and rapid decline. *Marine Ecology Progress Series* 39: 275–283.
- Pfister, C. A. & A. Bradbury, 1996. Harvesting red sea urchins: recent effects and future predictions. *Ecological Applications* 6: 298–310.
- Quinn, G. P. & M. J. Keough, 2002. *Experimental Design and Data Analysis for Biologists*. University Press Cambridge, United Kingdom.
- Reed, D. C., 1990. The effects of variable settlement and early competition on patterns of kelp recruitment. *Ecology* 71: 776–787.
- Reed, D. C., D. R. Laur & A. W. Ebeling, 1988. Variation in algal dispersal and recruitment: the importance of episodic events. *Ecological Monographs* 58: 321–335.
- Riedman, M. L. & J. A. Estes, 1988. A review of the history, distribution and foraging ecology of sea otters. In VanBlaricom, G. R. & J. A. Estes (eds), *The Community Ecology of Sea Otters*. Springer-Verlag, Berlin, 4–21.
- Riedman, M. L. & J. A. Estes, 1990. The sea otter (*Enhydra lutris*): behavior, ecology, and natural history US Fish and Wildlife Service. *Biological Report* 90(14): 1–126.
- Rogers-Bennett, L., H. C. Fastenau & C. M. Dewees, 1998. Recovery of red sea urchin beds following experimental harvest. In Mooi, R. & M. Telford (eds),

- Echinoderms: San Francisco, Proceedings of the Ninth International Echinoderm Conference, August 5–9, 1996. San Francisco, California, 805–809.
- Schroeter, S. C., J. D. Dixon, J. Kastendiek, R. O. Smith & J. R. Bence, 1993. Detecting the ecological effects of environmental impacts: a case study of kelp forest invertebrates. *Ecological Applications* 3: 331–350.
- Schiel, D. R. & M. S. Foster, 1986. The structure of subtidal algal stands in temperate waters. *Oceanography and Marine Biology Annual Reviews* 24: 265–307.
- SPSS, 1996. SPSS® Base 7.5 for Windows™. User's guide. Prentice-Hall, Paramus.
- Tegner, M. J., 1980. Multispecies consideration of resource management in southern California kelp beds. In Pringle, J. D., G. J. Sharp & J. F. Caddy (eds), Proceedings of the Workshop on the Relationship between Sea Urchin Grazing and Commercial Plant/animal Harvesting. Canadian Technical Reports of Fisheries and Aquatic Sciences 954: 125–143.
- Vadas, R. L., 1968. The Ecology of Agarum and the Kelp Bed Community. PhD dissertation, University of Washington, Seattle.
- Vadas R. L., 1972. Ecological implications of culture studies on *Nereocystis luetkeana*. *Journal of Phycology* 8: 196–203.
- Vadas, R. L., 1977. Preferential feeding: an optimization strategy in sea urchins *Ecological Monographs* 47: 337–371.
- Van Alstyne, K. L., J. J. McCarthy, C. L. Hustead & D. O. Duggins, 1999. Geographic variation in polyphenolic levels of Northeastern Pacific kelps and rockweeds. *Marine Biology* 133: 371–379.
- VanBlaricom, G. R., 1996. Saving the sea otter population in California: contemporary problems and future pitfalls. *Endangered Species UPDATE* 13(12): 85–91.
- VanBlaricom, G. R. & J. A. Estes (eds), 1988. The Community Ecology of Sea Otters. *Ecological Studies*. Springer-Verlag, Heidelberg, Germany.
- Watanabe, J. M. & C. Harrold, 1991. Destructive grazing by sea urchins *Strongylocentrotis* spp in a central California kelp forest: potential roles of depth, recruitment, and predation. *Marine Ecology Progress Series* 71: 125–141.
- Watson, J. C., 1993. The effects of sea otter (*Enhydra lutris*) foraging on shallow rocky communities off northwestern Vancouver Island, British Columbia. PhD Dissertation, University of California, Santa Cruz.
- Wendell, F. E., 1994. Relationship between sea otter range expansion and red abalone abundance and size distribution in central California. *California Fish and Game* 80: 45–56.
- Wendell, F. E., 1996. The State of California's role in the conservation of sea otters and other aquatic resources. *Endangered Species UPDATE* 13(12): 82–84.
- Wendell, F. E., R. Hardy, J. Ames & R. Burge, 1986. Temporal and spatial patterns in sea otter, *Enhydra lutris*, range expansion and in the loss of Pismo clam fisheries. *California Fish and Game* 72: 197–212.
- Witman, J. D., 1987. Subtidal coexistence: storms, grazing, mutualism, and the zonation of kelps and mussels. *Ecological Monographs* 57: 167–187.
- Zar, J. H., 1984. *Biostatistical Analysis*, 2nd edn. Prentice Hall, Englewood Cliffs, New Jersey.