

Volume 70

An NRC Research
Press Journal

Un journal de
NRC Research
Press

2013

www.nrcresearchpress.com

Canadian Journal of
**Fisheries and
Aquatic Sciences**

Journal canadien des
**sciences halieutiques
et aquatiques**

Impacts of sea otter (*Enhydra lutris*) predation on commercially important sea cucumbers (*Parastichopus californicus*) in southeast Alaska

Sean D. Larson, Zachary N. Hoyt, Ginny L. Eckert, and Verena A. Gill

Abstract: Sea cucumbers (*Parastichopus californicus*), which are an important commercial, subsistence, and ecological resource, are negatively affected by an expanding sea otter (*Enhydra lutris*) population in southeast Alaska. A few hundred sea otters were reintroduced into southeast Alaska in the late 1960s after their extirpation during the 18th and 19th century fur trade. In the ensuing decades after recolonization, the sea otter population grew exponentially in number and distribution, and sea cucumbers declined in density in areas with otters, suggesting an inverse relationship between sea otter numbers and sea cucumber density. We evaluated the interaction and effects of sea otters on sea cucumbers using sea otter foraging observations, sea otter population survey data, and sea cucumber density data. Our results indicate that sea cucumber density declined with and without sea otter presence and that the extent of the decline depends on the duration and magnitude of sea otter presence, with 100% decline in areas occupied by sea otters since 1994. Sea otter predation should be included in sea cucumber fishery management as a step toward ecosystem-based management.

Résumé : Une population de loutres de mer (*Enhydra lutris*) en expansion dans le sud-est de l'Alaska a une incidence négative sur les holothuries (*Parastichopus californicus*), une importante ressource commerciale écologique et de subsistance. Quelques centaines de loutres de mer ont été réintroduites dans le sud-est de l'Alaska à la fin des années 1960 à la suite de leur disparition de cette région durant le commerce des fourrures des 18^e et 19^e siècles. Dans les décennies qui ont suivi leur recolonisation le nombre et la répartition de la population de loutres de mer ont crû de manière exponentielle et la densité des holothuries a diminué dans les secteurs abritant des loutres ce qui semble indiquer une relation inverse entre le nombre de loutres de mer et la densité d'holothuries. Nous avons évalué l'interaction et les effets des loutres de mer sur les holothuries à partir d'observations sur l'alimentation des loutres de données d'évaluation de la population de loutres de mer et de données sur la densité d'holothuries. Nos résultats indiquent que cette densité a diminué en présence ou non de loutres de mer et que l'ampleur de cette diminution dépend de la durée et de la magnitude de la présence des loutres de mer une diminution de 100% étant observée dans les secteurs occupés depuis 1994 par des loutres. La prise en considération de la prédation par les loutres de mer devrait être intégrée à la gestion des pêches d'holothuries dans une optique de gestion écosystémique. [Traduit par la Rédaction]

Introduction

Marine mammal and fishery interactions can be direct, such as in incidental bycatch of marine mammals in fishing gear or depredation, or indirect through competition for fishery resources. Competition between marine mammals and fisheries is often studied from the perspective of how fisheries impact marine mammal populations, particularly for declining marine mammal populations (DeMaster et al. 2001; Dans et al. 2003; Lotze et al. 2011). Identifying how, when, and where marine mammals and fisheries compete is poorly known, because fishery and marine mammal populations fluctuate, have limited data, and observing marine mammal feeding or quantifying diets are usually very difficult. Thus, many studies that investigate this relationship are model-based (Yodzis 1998; Matthiopoulos et al. 2008; Morissette et al. 2012), and empirical examples are limited. The reestablishment of sea otters (*Enhydra lutris*) in southeast Alaska in the late 1960s to areas where they were absent for likely over a century has created a conflict with the sea cucumber (*Parastichopus californicus*) fishery and subsistence resource users. In this study of competition between sea otters and fisheries in southeast Alaska, we provide empirical evidence of marine mammal–fishery competition for resources.

Sea otters were hunted to near extinction across their range during the 18th and 19th century fur trade and were extirpated from southeast Alaska by 1911 (Kenyon 1969). The Alaska Department of Fish and Game (ADF&G) translocated 413 sea otters from Prince William Sound and Amchitka Island to coastal southeast Alaska between 1965 and 1969 (Burris and McKnight 1973). Since then sea otters expanded their distribution and have reached a population size exceeding 25 000 individuals (United States Fish and Wildlife Service 2013). Surveys of the southeast Alaska sea otter population were conducted in 1988 (Pitcher 1989), 1994 (Agler et al. 1995), 1997 (Hodges et al. 2008), 2003 (Esslinger and Bodkin 2009), and 2010 (United States Fish and Wildlife Service 2013) (Fig. 1). We used these surveys to examine the impact of sea otters along a gradient of sea otter occupation, a natural experiment per se, in which we examined the changes resulting from sea otter occupation through a space-for-time substitution.

Owing to high metabolic demands and limited capacity to store energy, sea otters must consume up to 25% of their body mass per day (Estes et al. 2003; Oftedal et al. 2007), and consequently, the abundance and size distribution of their prey can be substantially reduced (Kvitek et al. 1989, 1992; Estes and Duggins 1995). As a result of this strong predator–prey interaction, sea otters are a keystone species that have a great effect on their ecosystem (Steneck et al. 2002). The ecological role of sea otters in kelp

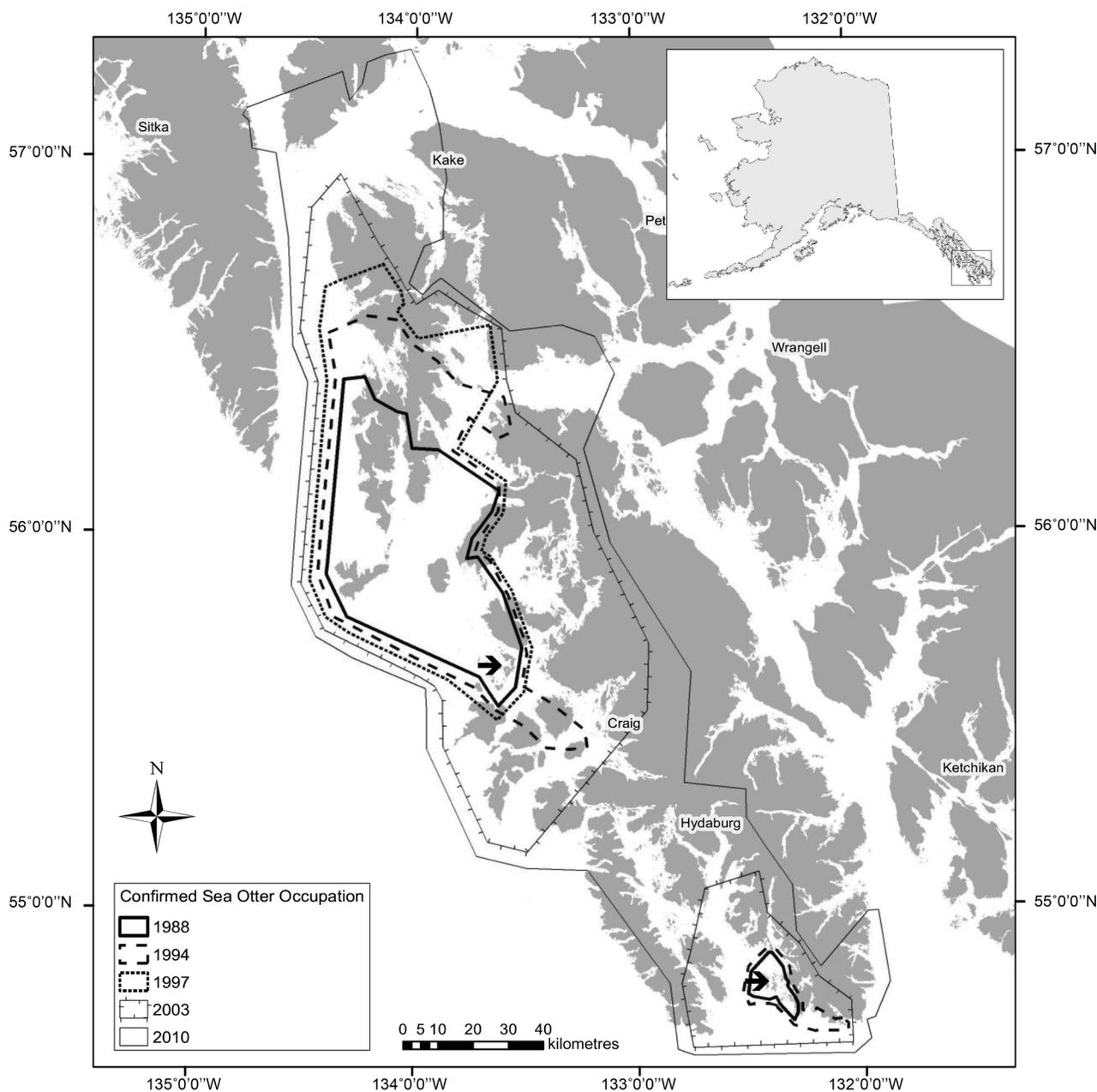
Received 14 January 2013. Accepted 22 July 2013.

Paper handled by Associate Editor Marie-Joëlle Rochet.

S.D. Larson, Z.N. Hoyt, and G.L. Eckert. School of Fisheries and Ocean Sciences, University of Alaska Fairbanks, 17101 Point Lena Loop Road, Juneau, AK 99801-8344, USA.
V.A. Gill. US Fish and Wildlife Service, Marine Mammals Management, 1011 East Tudor Road, MS 341, Anchorage, AK 99503, USA.

Corresponding author: Sean D. Larson (e-mail: sdlarson@alaska.edu).

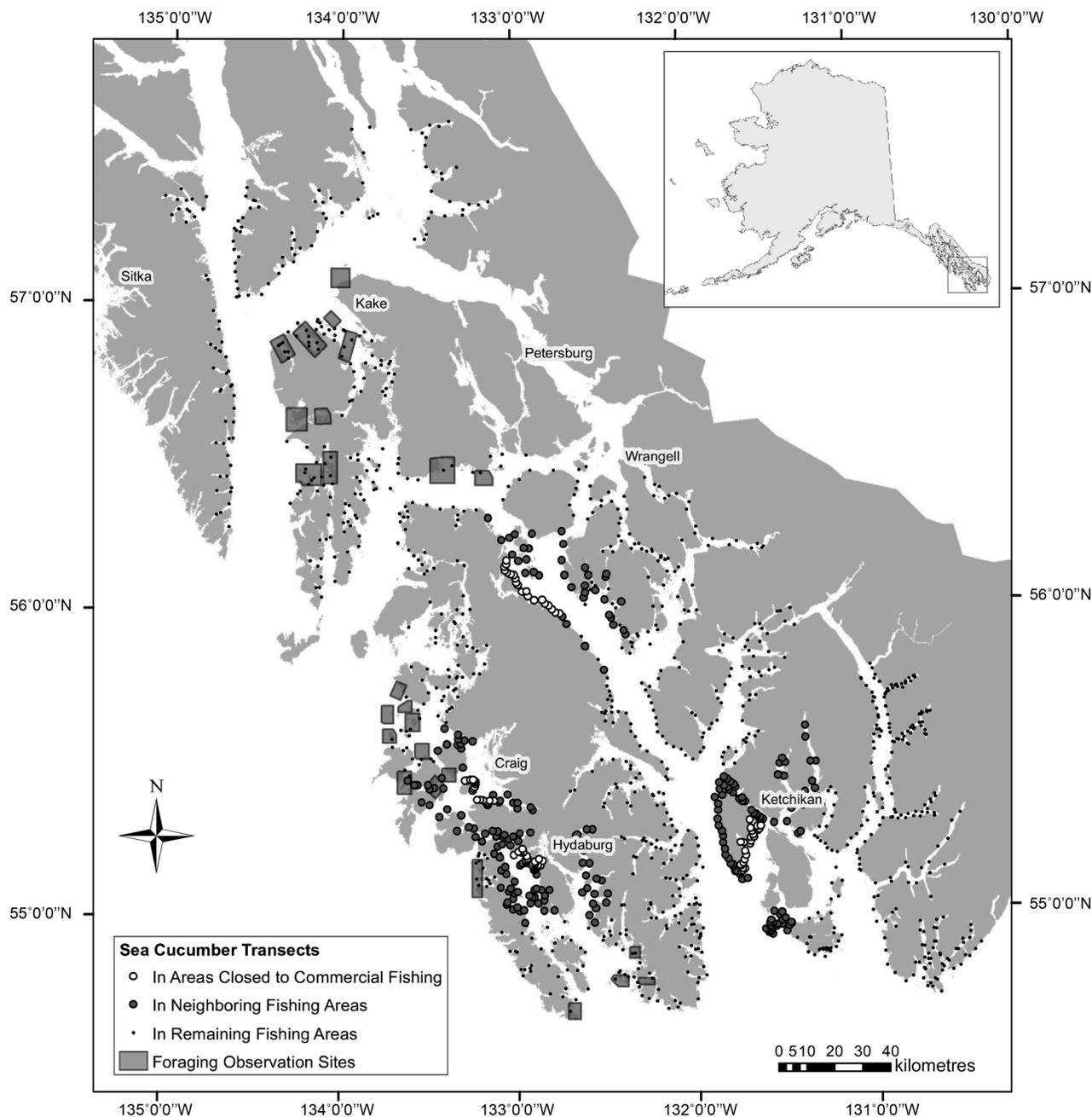
Fig. 1. Southeast Alaska with estimated sea otter distributions in 1988, 1994, 1997, 2003, and 2010 and original translocation sites (arrows) (Pitcher 1989; Agler et al. 1995; Hodges et al. 2008; Esslinger and Bodkin 2009; United States Fish and Wildlife Service 2013).



forests is well demonstrated as a trophic cascade, which involves humans, sea otters, sea urchins, and kelp forests in rocky habitats (Estes and Duggins 1995). In the absence of exploitation by humans, and in the presence of sea otters, sea urchin populations are kept in check and kelp communities can thrive. Kelp forest communities are more stable in the presence of this top level predator (Steneck et al. 2002), but the role of sea otters on other species and habitats is not well studied. Incorporating sea otters into sea cucumber fishery management requires a clear understanding of the interaction between the two species to predict changes in the sea cucumber fishery. Sea otter diet in an area can change temporally (Ostfeld 1982; Laidre and Jameson 2006; Tinker et al. 2008); thus, knowing the feeding preference of sea otters for sea cucumbers and how it changes as sea otters colonize can help identify areas most at risk from sea otter predation.

A lucrative commercial sea cucumber fishery began in southeast Alaska in 1981 and by 2010–2011 included 289 active permit holders; 180 of those reported landings for an annual ex-vessel value exceeding \$3,200,000 (Rumble and Hebert 2011). Sea otter predation in southeast Alaska is blamed for the closure of nine sea cucumber fishery subdistricts and a decline in sea cucumber density in others, resulting in a reduction in guideline harvest level for the commercial fishery (Rumble and Hebert 2011). Surprisingly few data exist addressing the impacts of sea otter predation on its prey in southeast Alaska or the relative value of sea cucumbers in the sea otter diet. Fishing has depressed sea cucumber stocks in the United States and abroad (Uthicke and Benzie 2000; Schroeter et al. 2001; Friedman et al. 2011) in areas with high harvest levels and minimal management (Purcell et al. 2013). Fishing mortality was responsible for 33%–83% of stock declines for the congener,

Fig. 2. Southeast Alaska with sea cucumber transects representing sea cucumber density data in areas closed to commercial fishing (open dots), open to commercial fishing and near areas closed to commercial fishing (large solid dots), and open to commercial fishing but not near closed areas (small solid dots). Also shown are data collection sites (rectangles) representing sea otter foraging observations.



Parastichopus parvimensis, in the Channel Islands, California, from 1993 to 1999 (Schroeter et al. 2001), and 58% of sea cucumber fisheries in the Indo-Pacific are either depleted or overexploited (Purcell et al. 2013). In contrast, the sea cucumber fishery in southeast Alaska is conservatively managed using a surplus production model (Woodby et al. 1993) that specifies a harvest rate of no more than 18.6% every 3 years for subdistricts open to commercial harvesting (Clark et al. 2009). Areas of southeast Alaska that are open and closed to fishing occur in areas with and without sea otters, which allows us to identify and separate the roles of sea otter predation and commercial fishing on sea cucumber density.

The objective of this study is to investigate the interaction between sea otters and sea cucumbers to determine the extent

to which sea otters are negatively affecting sea cucumbers in southeast Alaska. Here, we use foraging observations, sea otter population survey data, and sea cucumber density data with a before–after, control–impact (BACI) approach to examine (i) how sea otter diet varies with time since colonization and (ii) changes in sea cucumber density in the presence and absence of sea otters.

Methods

Study area

The study area encompassed the distribution of sea otters in southern southeast Alaska (Fig. 1). We identified areas as a function of time since sea otter recolonization, i.e., sea otter persis-

tence. Persistence levels include areas colonized by sea otters by 1988 (Pitcher 1989), 1994 or 1997 (Agler et al. 1995; Hodges et al. 2008), 2003 (Esslinger and Bodkin 2009), and 2010 (United States Fish and Wildlife Service 2013) (Fig. 1).

Observations of foraging sea otters

We performed field observations of foraging sea otters to create several indices of predation on sea cucumbers. Direct foraging observations and diet studies are possible, unlike for other marine mammals, because sea otters bring their prey to the surface. We took foraging observations from various locations in southeast Alaska ranging from southern Prince of Wales Island to northwestern Kupreanoff Island in June through August of 2010 and 2011 (Fig. 2). Locations were representative of the region and varied in habitat type and sea otter persistence. Our methods were adapted from Kvitek et al. (1993), where researchers used Questar telescopes and binoculars to make observations on individual foraging otters from shore. An individual sea otter was observed until it had either stopped foraging, 20 foraging dives had been observed, or it was lost from view. The date, location, sex, and the presence of a pup were noted for each otter observed. The dive time, surface interval, prey type, number of prey, and prey size were recorded for each foraging dive observed. Prey were identified to species, or next nearest taxonomic group, and prey size was estimated by comparing the prey item to sea otter paw width, or multiple thereof (VanBlaricom 1988); some prey were unidentified and were labeled as such. Prey size was estimated by comparing the prey diameter (mm) to sea otter paw width, assuming an average paw width of 50 mm (VanBlaricom 1988; Kvitek et al. 1993), and converted to total edible biomass using estimates of mean prey biomass-at-size from Glacier Bay, southeast Alaska (Garshelis et al. 1986). An exponential length-mass regression formula was used to calculate edible biomass for sea cucumbers (biomass = $1.14 \times \text{diameter}^{1.83}$; Cone 1989) using length and biomass data from sea cucumber samples collected during 2007 ADF&G dive surveys ($r^2 = 0.54$; $n = 108$; Zac Hoyt, unpublished data). The sizes of sea cucumbers in this reference sample, 90 to 265 mm, encompassed that found in our study. The biomass of unidentified species was determined by size-specific mean values obtained for all identified species. Foraging data were grouped into "sites" based on length of sea otter persistence and location (data within a site were separated by no more than 8 km; Fig. 2).

Tests of the sea otter diet

We examined differences in percent diet composed of sea cucumbers, in edible biomass, at each sea otter persistence category. Percent diet composed of sea cucumbers, i.e., the response values, were arcsine-transformed to meet conditions of normality and differences were examined using analysis of variance (ANOVA; generalized linear model), with sea otter persistence as the categorical predictor variable. If ANOVA results were significant, differences among factor levels were assessed with Tukey's honestly significant difference test (Tukey HSD).

Sea cucumber density

ADF&G research divers have surveyed sea cucumbers annually in southeast Alaska since 1990 to assess sea cucumber abundance for fishery management, and up to 500 strip transects were sampled each year (Hebert 2010). Fishery subdistricts, hereafter fished areas, were surveyed once every 3 years, while management control subdistricts, hereafter unfished areas, were surveyed every year (Fig. 2; Hebert 2010). Primary substrate type (rock, gravel, shell, sand, boulder, mud, silt, woody, or cobble), number of sea cucumbers per transect, and average sea cucumber mass were recorded with each survey. Total number of sea cucumbers from a transect pair was divided by total length of shoreline that the transects encompassed (4 m) to get an average number of sea cucumbers per linear metre of shoreline to 15 m depth, hereafter

Table 1. (a) Before–after, control–impact (BACI) ANOVA design and (b) results from BACI ANOVA comparing sea cucumber density among periods (years before sea otter impact, years after sea otter impact), impacts (areas with sea otters, areas without sea otters), and their interaction.

(a) Sea cucumber density data before and after sea otter colonization. ^a					
Year of sea otter impact	"Before" years	<i>n</i>	"After" years	<i>n</i>	
1994	1990–1992	205	2009–2011	192	
2003	1994–1996	181	2009–2011	181	
2010	2004–2005	442	2010–2011	383	
(b) Sea cucumber density among periods, impacts, and their interaction. ^b					
Year of sea otter impact	Source of variation	df	MS	<i>F</i>	<i>p</i>
1994	Period	1	11.29	23.28	<0.001***
	Impact	1	52.03	107.32	<0.001***
	Period × impact	1	19.78	40.80	<0.001***
	Residuals	197	0.49		
2003	Period	1	17.92	43.35	<0.001***
	Impact	1	79.71	192.78	<0.001***
	Period × impact	1	31.52	76.24	<0.001***
	Residuals	272	0.41		
2010	Period	1	5.46	18.56	<0.001***
	Impact	1	31.70	107.88	<0.001***
	Period × impact	1	1.26	4.29	0.039
	Residuals	433	0.29		

^aPeriod compares "before" and "after" while Impact compares sites with and without otters. Sample sizes (*n*) represent the number of sea cucumber density estimates across all transects during that time period.

^bAnalyses were performed for areas with a confirmed sea otter occupation in 1994, 2003, and 2010. Data reported include *p* values, *F* statistics, degrees of freedom (df), and mean squares (MS). Critical *p* values were adjusted using the Bonferroni correction; significance levels are indicated as follows: ***, $p < 0.001$.

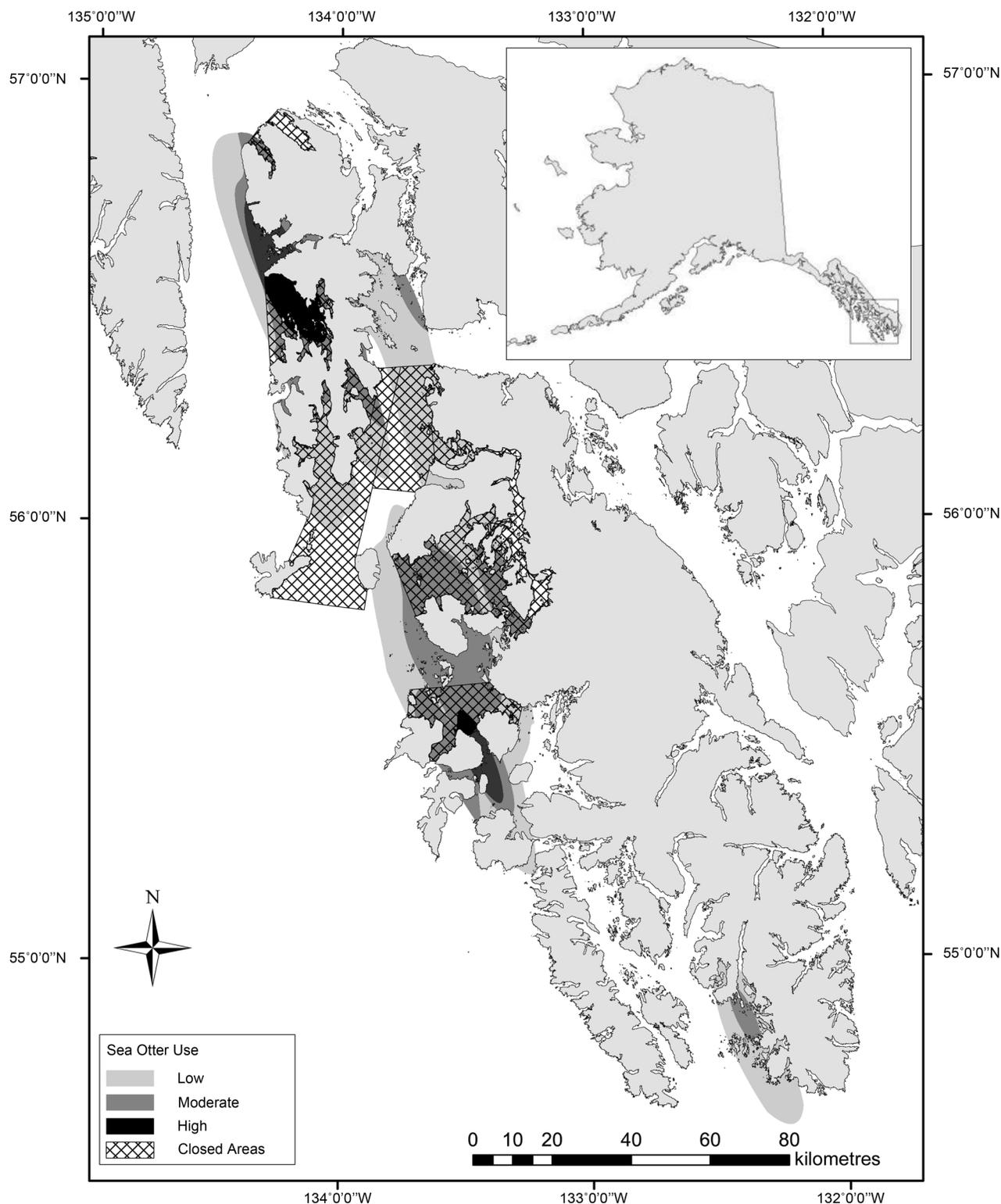
density, to be used for comparison in our study. Sea cucumber densities were calculated using data from 1990 to 2011 from transects south of 57°35'00"N.

Tests of the effects of sea otters

We examined differences in sea cucumber density before and after sea otter colonization at control transects without sea otters and impact transects with sea otters using a BACI design (Smith 2002) with two-way ANOVA and interactions; significance in the interaction would imply that sea otters are having an effect (Green 1979). Primary substrate type and a unique transect identifier (to account for spatial correlation) were included in the model. Separate analyses, each with a single before–after comparison, were performed at three different levels of sea otter persistence. Before–after periods include 3 years of sea cucumber density estimates that were taken prior to or after sea otter colonization (except the most recent, which only has 2 years; Table 1a). Bonferroni corrections were applied to each analysis. ADF&G discontinued surveys at some transects, and new transects were added to the survey; thus, only transects with survey data before and after sea otter arrival and within fished areas were included. To meet assumptions of BACI analyses, sea cucumber densities were log-transformed (Stewart-Oaten et al. 1986). We compared differences in mean sea cucumber density across levels of sea otter persistence with ANOVA and Tukey HSD.

We calculated sea otter population ranges in 2003 and 2010 using sea otter distribution and abundance surveys (Esslinger and Bodkin 2009; United States Fish and Wildlife Service 2013) and kernel density estimation (Worton 1989). Kernel density estimation was used to create probability density functions for sea otter counts in 2003 and 2010, and then isopleth lines were used to

Fig. 3. Southeast Alaska with fished areas that were closed because of low biomass (hatched polygons) (Rumble and Hebert 2011) and areas with low (light gray), moderate (dark gray), and high sea otter use (black). Sea otter use categories were derived from combined kernel density estimates for sea otter counts in 2003 and 2010 (Esslinger and Bodkin 2009; United States Fish and Wildlife Service 2013).



delineate total ranges and core areas, i.e., areas containing 95% and 50% of the probability density functions, respectively. Kernel density estimation was performed with a Gaussian kernel (Sheather 2004), a grid resolution of 100 m, and a bandwidth estimated using the least squares cross-validation algorithm (Worton 1989). Sea

otter ranges for 2003 and 2010 were combined into three sea otter use categories: areas of high use were core areas during both 2003 and 2010 sea otter surveys, areas of moderate use were core areas during one survey, and areas with low use were in the total range during one or both surveys (Fig. 3). We examined differences in

Table 2. ANOVAs comparing percent sea otter diet consisting of sea cucumbers and mean sea cucumber density (sea cucumbers per metre of shoreline) among sea otter persistence (confirmed sea otter occupation since 1988, 1994 or 1997, 2003, and 2010).

Response	Source of variation	df	MS	F	p
% Sea cucumbers	Persistence	3	0.01	2.24	0.115
	Residuals	20	0.01		
Sea cucumber density	Persistence	3	68.63	215.42	<0.001***
	Residuals	843	0.32		

Note: Data reported include *p* values, *F* statistics, degrees of freedom (df), and mean squares (MS). Significance levels are indicated as follows: ***, *p* < 0.001.

sea cucumber density before and after sea otter colonization in areas with high, moderate, and low use by sea otters using a two-way ANOVA with an interaction between sea otter use category and before or after periods.

Tests of the effects of fishing

To identify the effect of fishing on sea cucumbers, we compared changes in sea cucumber density through time and overall sea cucumber density in unfished areas with changes and overall density in their neighboring fished areas, i.e., areas within 10 km of an unfished area, using two-way repeated measures ANOVA. Model factors included area type (fished or unfished), survey year of sea cucumber density estimates, and their interaction, with individual transect ID as the error term. The four areas were labeled, for simplicity, after the community with the closest proximity, separate analyses were performed for each area, and Bonferroni corrections were applied to each. Significance in the interaction would imply that the trend in sea cucumber density through time differed between unfished and fished areas.

R version 2.15.2 was used for all statistical analyses and figures; ArcGIS 10 was used to manipulate and code data and to create maps; and Geospatial Modeling Environment (Spatial Ecology LLC) was used for kernel density estimation. All statistical tests were performed with a statistical significance of *p* = 0.05.

Results

Observations of foraging sea otters

Researchers recorded foraging observations for 336 sea otters and 3404 successful foraging dives. Sea otters consumed a total of 58 sea cucumbers; the minimum and maximum sized sea cucumber consumed had a calculated edible biomass of 14 and 332 g, respectively, with a mean \pm SD biomass of 147 ± 60 g. Mean \pm SD percent of the diet, by edible biomass, consisting of sea cucumbers was $5\% \pm 8\%$ at all sites and $13\% \pm 8\%$ for sites where sea cucumbers were observed in the sea otter diet. Sea otters foraged on 58 prey species, and apart from sea cucumbers, the sea otter diet consisted primarily of red sea urchins (*Strongylocentrotus franciscanus*), clams, including geoducks (*Panopea generosa*), and crabs. About 2% of the sea otter diet, in mass, was from unidentified prey. The percent diet consisting of sea cucumbers did not differ significantly among sea otter persistence categories (Table 2) and was $5\% \pm 9\%$ in areas occupied since 1988, $2\% \pm 4\%$ in areas occupied since 1994 or 1997, $3\% \pm 4\%$ in areas occupied since 2003, and $11\% \pm 12\%$ in areas occupied since 2010.

Sea cucumber density

Sea otters negatively impact sea cucumber density in southeast Alaska (Table 1b; Fig. 4). Sea cucumber density decreased 100.0% after being colonized by sea otters in 1994 compared with a 19.6% decline at control transects without sea otters over this time period (Fig. 4a). Sea cucumber density decreased 80.1% after being colonized by sea otters in 2003 compared with a 19.1% decline at control transects over this time period (Fig. 4b). Sea cucumber density decreased 25.8% after being colonized by sea otters in

2010, while sea cucumber density at control transects decreased 15.4% over this time period (Fig. 4c).

Sea cucumber density was significantly lower where sea otters have persisted for longer times (Table 2; Fig. 5a). Sea cucumber density (mean \pm SD) in areas that sea otters have colonized since 1988 was 0.1 ± 0.4 , density in areas with sea otters since 1994 or 1997 was 3.9 ± 6.0 , density in areas with sea otters since 2003 was 6.6 ± 7.5 , and density in areas with sea otters since 2010 was 10.6 ± 16.6 (Fig. 5a). Sea cucumber density in areas with sea otters since 1988 was not significantly different from areas with sea otters since 1994 or 1997 (*p* = 0.941; Fig. 5a), while all other areas had sea cucumber densities that were significantly different from one another (*p* < 0.001; Fig. 5a).

Declines in sea cucumber density after sea otter occupation were greater in areas with higher sea otter use as determined by kernel density estimation (Table 3; Fig. 5b). Sea cucumber density declined 44.3%, 88.1%, and 99.8% in low, moderate, and high sea otter use areas, respectively (Fig. 5b).

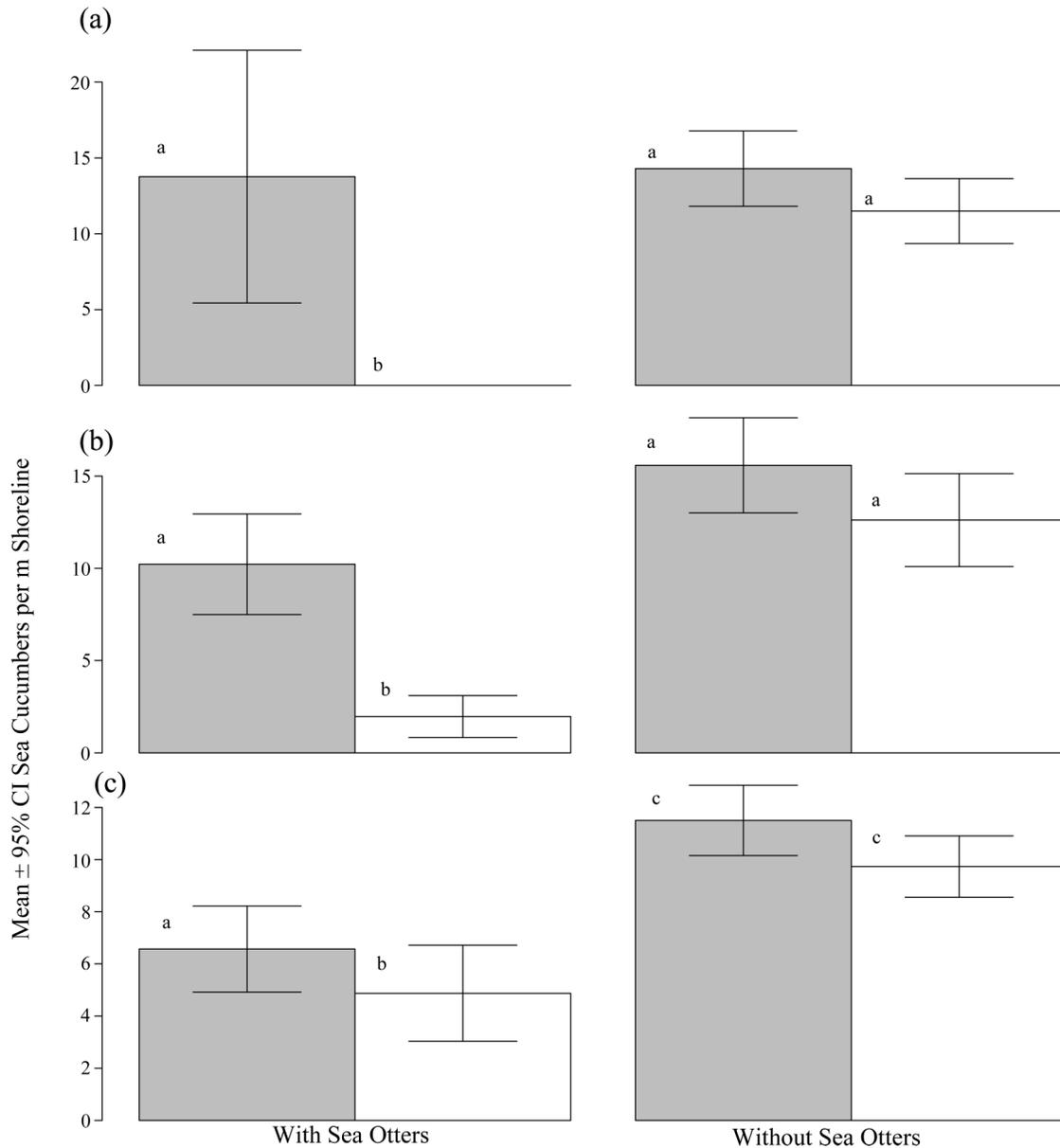
Sea cucumber density declined in all areas (Hydaburg, Craig, Ketchikan, Wrangell) (Table 4; Fig. 5c). Trends in sea cucumber density through time were similar between unfished and fished areas in areas without sea otters. In areas with sea otters (Hydaburg and Craig), the result differed. In Hydaburg, declines in sea cucumber density were significantly lower than at its neighboring fished areas. In Craig, the overall mean sea cucumber density was significantly lower at the unfished area than at its neighboring fished areas.

Discussion

Sea otters in southeast Alaska are an interesting case study of marine mammal–fishery interactions, in which a recovering marine mammal population negatively impacts a commercial fished species. Sea otters deplete sea cucumbers in southeast Alaska, well below levels needed to sustain a fishery, the extent of which depends on the duration and magnitude of sea otter presence. Areas within core sea otter ranges since 2003 or earlier have sea cucumber densities near zero. While sea cucumber density declined at transects with and without sea otters, declines in areas where sea otters have existed since at least 1994 were four times greater than those at the control transects without sea otters, declines in areas where sea otters have existed since at least 2003 were five times greater than those at the control transects without sea otters, and declines in areas where sea otters have existed since at least 2010 were two times greater than those at the control transects without sea otters. The weak effect of sea otters on sea cucumbers in recently occupied areas (2010) suggests that the effects of sea otters on sea cucumber populations are delayed, accumulate over time, and may require multiple years of survey data to detect. Other studies have found that sea otters significantly reduced the biomass of items in their diet, including Dungeness crab (*Cancer magister*) biomass in Prince William Sound (Garshelis et al. 1986), sea urchin biomass in Washington (Laidre and Jameson 2006), and sea cucumber (*Cucumaria miniata*) biomass along the outer coast of Washington (Kvitek et al. 1989).

The sea cucumber *P. californicus* represented a relatively high proportion of the sea otter diet (13% at sites where sea cucumbers were observed in the diet), which is surprising, considering that sea cucumbers contain only $1744 \text{ cal}\cdot\text{g}^{-1}$ (1 calorie = 4.186 J) compared with $3905 \text{ cal}\cdot\text{g}^{-1}$ for a butter clam (*Saxidomus gigantea*) (Ofstedal et al. 2007). Sea cucumbers may be selected as sea otter prey because they require no energetically costly excavation effort, are often found on accessible shallow-water habitats, are void of any hard calcareous protection, and do not have any potentially harmful defense mechanisms such as claws or spines. Sea otters selected a wide size range of sea cucumbers with a small mean \pm SD size of 146 ± 60 g in relation to ADF&G estimates of mean size ranging from 134 to 289 g (Hebert 2010); thus, sea otters

Fig. 4. Mean sea cucumber density and 95% confidence intervals before (grey) and after (open) the presence of sea otters at transects with sea otters and control transects without sea otters during the same time period. Comparisons were broken down to areas with a confirmed sea otter occupation in 1994 (a), 2003 (b), and 2010 (c); letters indicate significant differences.



likely select sea cucumbers opportunistically, i.e., they select sea cucumbers as they see them and do not focus on large individuals; however, a true test of selectivity would require in situ studies of available prey sizes. The sea cucumber *P. californicus* has been observed in the sea otter diet at Amchitka Island, Alaska (Watt et al. 2000), Glacier Bay, Alaska (Bodkin et al. 2006), and Washington (Laidre and Jameson 2006). *Cucumaria miniata* represented less than 0.1% of the sea otter diet along the outer coast of Washington and in the Strait of Juan de Fuca between 1993 and 1999 (Laidre and Jameson 2006). The low incidence of *C. miniata* in the sea otter diet along the coast of Washington may be because, unlike *P. californicus*, they are often found wedged between rocks (Lambert 1997) and may be difficult to extract, or alternatively, they may be less abundant.

Sea cucumbers represented roughly the same percentage of the sea otter diet at all levels of sea otter persistence. Intriguingly, sea cucumbers were observed in the sea otter diet in areas that expe-

rienced 100% declines in sea cucumber density, indicating that sea otters are able to find and eat sea cucumbers even where ADF&G surveys did not find them. Surveys may not be able to find sea cucumbers in those areas because sea cucumbers could become more cryptic in the presence of sea otter predators or sea otters may forage deeper than ADF&G surveys. It is possible that sea cucumbers have a depth refuge and therefore are not driven locally extinct by sea otters. Sea otters generally forage in water shallower than 30 m (Bodkin et al. 2004), but *P. californicus* can be found at depths exceeding 249 m (Lambert 1997).

Our results suggest that observed declines in sea cucumber density from commercial fishing are within the natural range of variation for this species; therefore, fishing contributes little, if at all, to the decline in sea cucumber density in southeast Alaska. These results agree with Clark et al. (2009), who found that decreases in sea cucumber density in unfished areas averaged 5.8% per year compared with an average of 5.0% per year in fished areas. De-

Fig. 5. Mean sea cucumber density and 95% confidence intervals at (a) each sea otter persistence category, including no persistence; (b) before (gray) and after (open) sea otter impact at each sea otter area use category; and (c) at the four unfished areas (open) and their neighboring fished areas (gray). Sea otters impact areas near Hydaburg and Craig. Density estimates in panels (a) and (c) and the after period in panel (b) were based on ADF&G sea cucumber survey data from 2006 through 2011; letters indicate significant differences.

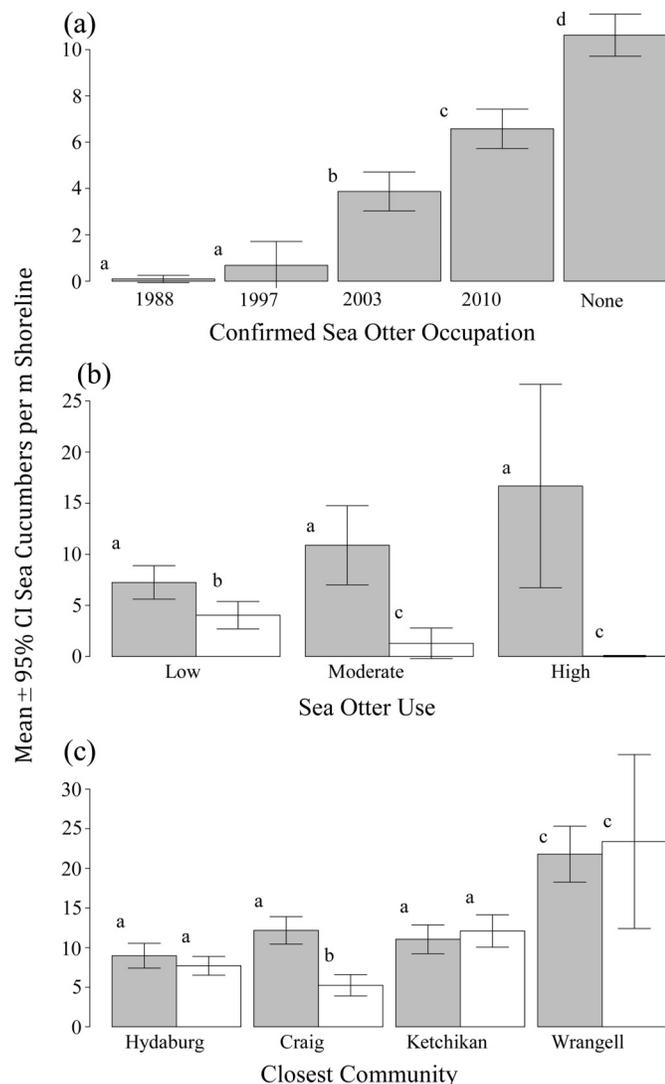


Table 3. Results from ANOVA comparing sea cucumber density among periods (years before sea otter impact, years after sea otter impact), sea otter use (low use, moderate use, high use), and their interaction.

Source of variation	df	MS	F	p
Period	1	63.19	104.17	<0.001***
Sea otter use	2	2.10	3.46	0.035*
Period × sea otter use	2	8.50	14.01	<0.001***
Residuals	118	0.61		

Note: Data reported include *p* values, *F* statistics, degrees of freedoms (df), and mean squares (MS). Significance levels are indicated as follows: *, *p* < 0.05; ***, *p* < 0.001.

clines in sea cucumber density may be similar in areas open and closed to fishing because sea cucumbers have very long larval planktonic stages, up to 120 days (Cameron and Fankboner 1989), and populations may be interconnected through this larval stage.

Table 4. Results from two-way repeated measures ANOVAs comparing sea cucumber density among area type (unfished area, neighboring fishing areas), year, and their interaction.

Area	Source of variation	df	MS	F	p
Hydaburg ^a	Type	1	472.82	1.85	0.176
	Year	17	155.61	4.14	<0.001***
	Type × year	5	158.88	4.23	<0.001***
	Residuals	491	37.58		
Craig ^b	Type	1	5858.50	20.87	<0.001***
	Year	17	166.75	4.22	<0.001***
	Type × year	6	40.83	1.03	0.402
	Residuals	410	39.48		
Ketchikan ^c	Type	1	0.58	0.00	0.983
	Year	19	414.91	3.10	<0.001***
	Type × year	12	215.44	1.61	0.084
	Residuals	568	133.77		
Wrangell ^d	Type	1	100.40	0.03	0.867
	Year	15	682.09	2.66	0.001***
	Type × year	8	297.42	1.16	0.321
	Residuals	423	256.05		

Note: Analyses were performed for two areas with sea otters, near Hydaburg and Craig, and two areas without sea otters, near Ketchikan and Wrangell. Only years with survey data in fished and unfished areas were used. Data reported include *p* values, *F* statistics, degrees of freedom (df), and mean squares (MS). Critical *p* values were adjusted using the Bonferroni correction; significance levels are indicated as follows: ***, *p* < 0.001.

^a*n* (fished) = 129, *n* (unfished) = 133.

^b*n* (fished) = 76, *n* (unfished) = 120.

^c*n* (fished) = 152, *n* (unfished) = 120.

^d*n* (fished) = 73, *n* (unfished) = 100.

Low population density is particularly problematic for broadcast spawning sea cucumbers, because fertilization rates can decline exponentially with decreasing densities (Uthicke and Benzie 2000). Therefore, the net decline of sea cucumbers throughout southeast Alaska may lead to reduced larval supply and recruitment across the region. Another possibility is that subsistence fishing can occur in areas closed to commercial fishing; therefore, these areas are not truly “unfished”. Communities on Prince of Wales Island have a long history of sea cucumber subsistence use by Alaska Natives (Mathews et al. 1990). Data on subsistence harvest is limited, but in 1997–1998, an estimated 19 840 lbs (1 pound = 0.453 kg) of sea cucumbers were collected for subsistence from 10 communities on Prince of Wales Island (Alaska Department of Fish and Game, Division of Subsistence, Juneau, Alaska, unpublished data, 2012).

This study has assumptions that address variation in sea cucumber data collection and spatial and temporal differences between impacted and control transects. First, researchers measured sea cucumber density and sea otter foraging behavior with varying degrees of sampling precision and sampling error. Second, we assumed a dynamic equilibrium, i.e., we recognize that impact and control transects have spatial and temporal variation and we assume that natural changes in mean sea cucumber density through time at impact transects will mimic changes at control transects, and vice versa. Finally, we assume that the sea otter surveys used for kernel density estimation accurately represented sea otter abundance and distribution, and any missing data within the surveys are inconsequential.

Sea cucumber densities in areas of southeast Alaska without sea otters will likely decrease if and when sea otters colonize; therefore, more fishery closures should be expected if the sea otter population continues to expand. Management could be improved with knowledge of this species interaction and efforts to balance economic, socio-cultural, and environmental values and priorities; large-scale removal of sea otters is impractical, and focusing only on the ecological side as a basis for management decisions is

equally undesirable (Folke et al. 2005). Ecosystem-based management and adaptive governance consider the biological, physical, and socio-economic components of an ecosystem (Kappel and Martone 2006) while encouraging collaboration among scientists, communities, government agencies, and other stakeholders (Hughes et al. 2007) and could be used to manage uncertainty and change in the sea cucumber fishery. The long-term sustainability of sea cucumbers in southeast Alaska and sea otters are not necessarily mutually exclusive; however, current single species management at different agencies does not take this interaction into account. These entities could share knowledge concerning sea otters and fisheries to develop a capacity to predict, prepare for, and address changes to resources and fisheries. Predation could be incorporated into the surplus production fishery management model for sea cucumbers to account for removals by sea otters. Failing to account for predation mortality in surplus production models can lead to underestimates of stock biomass and overestimates of fishery surplus production (Moustahfid et al. 2009). Information on sea otter distribution and abundance could offer a fine-scale understanding of predator impacts and valuable information for fishery managers to predict areas most at risk from sea otter predation. Low sea cucumber densities result in reduced reproductive success (Purcell et al. 2013), which could prevent sea cucumber recovery even after closing fishing; therefore, areas with sea otters may need to have more conservative sea cucumber density thresholds for fishery closures to protect spawning stock biomass. To make appropriate management decisions, agencies and stakeholders could work together to develop multiple potential management strategies, evaluate the benefits and risks associated with each, and develop performance metrics to ensure goals are met (Kappel and Martone 2006).

Acknowledgements

We gratefully thank the United States Fish and Wildlife Service for providing sea otter distribution and abundance data and the Alaska Department of Fish and Game for providing sea cucumber survey and fishery data. We thank Gordon Kruse and Doug Woodby for their valuable comments on our manuscript; Tory Wilson, Bonnie Greenwood, Marlene Wagner, Sharon Tsetong, Stena Troyer, and Christina Buck, who helped with data collection; and Sunny Rice, who helped with data collection and was a key player in securing funding for this project. This research was supported by Alaska Sea Grant and by the National Science Foundation (NSF) Marine Ecosystem Sustainability in the Arctic and Subarctic (MESAS) IGERT (Award DGE-0801720) and NSF Science Master's Program: Ecosystem Approaches to Fishery Management (Award DGE-1011707). The findings and conclusions in this article are those of the authors and do not necessarily represent the views of the US Fish and Wildlife Service.

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