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FORAGING PATTERNS AND PREY SELECTION IN AN INCREASING AND EXPANDING SEA OTTER POPULATION

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Focal observations of sea otter (*Enhydra lutris kenyoni*) foraging patterns and prey selection were collected in coastal Washington between 1993 and 1999. Records consisted of 13,847 individual dives from 841 feeding bouts ranging from 1 min to >4 h. Average dive time was 55 s ± 0.9 *SE* and average surface time was 45 s ± 2.3 *SE*, irrespective of dive success. At least 77% of all dives ($n = 10{,}636$) were successful prey captures (dives in low light or of undetermined success were excluded). Prey capture success was significantly lower for subadults (63% ± 5 *SE*) than adults (82% ± 1 *SE*; $P < 0.001$). Sea otters occupying the established population range on the outer coast of Washington fed heavily on bivalves (63%) and had a diverse diet consisting of several prey groups ($n = 10$). In contrast, sea otters occupying new habitat in the Strait of Juan de Fuca had a restricted diet dominated by >60% red urchins (*Strongylocentrotus franciscanus*), with only 2 other prey species comprising >10% of their diet. Prey size and prey category were dominant predictor variables in generalized linear models of dive duration and postdive surface duration on successful dives. Significant increases in areal extent of surface canopy of giant kelp (*Macrocystis integrifolia*) and bull kelp (*Nereocystis leutkeana*) were found both in the outer coast and the Strait of Juan de Fuca (0.4–0.5 km^2 per year, $P < 0.05$) and suggest increasing suitable habitat for a growing population. The growth and expansion of a small and isolated sea otter population provides a unique opportunity to examine the relationship between dietary diversity and population status and explore similarities and differences between trophic paradigms established for sea otter populations at other localities.

Key words: fisheries conflicts, foraging patterns, kelp canopy, sea otter, Washington

Although localized field studies often provide definitive evidence for particular processes, the extent to which these findings can be generalized over broader scales of space and time remains one of ecology's most contentious issues. Ecologists hesitate to make coherent generalizations among communities or systems on the assumption that their uniqueness and complexity makes broad simplifications invalid. Paradoxically, the rejection of general theory comes at a time when robust, general principles in ecology are badly needed (Lawton 1999). The synthesis of accumulated scientific results distilled into general patterns and underlying mechanisms allows for the prediction of certain ecological phenomena, within certain boundaries (Knapp et al. 2004). This information is useful for improving predictive capability in ecology, as well as for identifying limits and contingencies.

Understanding the nature of ecological variation is not possible without replicated studies of similar systems in different places. This is because research tends to be dominated by detailed, short-term studies at a single spatial scale where repeatability is difficult or impossible. The sea otter (*Enhydra lutris*) is an example of a top marine carnivore where strong evidence indicates striking ecosystem-level effects across (at least a majority) all the nearshore marine communities it inhabits (Duggins et al. 1989; Estes 1990; Estes and Duggins 1995; Estes and Palmisano 1974; Garshelis et al. 1986). Sea otters are top predators with a relatively small home range that live close to shore and are easily observed. Thus, they are ideal candidates for comparative foraging studies (Bodkin et al. 2004; Estes et al. 2003) and provide an excellent foundation for making broader generalizations about the top-down influence of mammalian carnivores through repeated observations at different sites.

Sea otters have daily nutritional requirements of up to 30% of their body mass per day (Costa 1978; Riedman and Estes 1990) and consume substantial quantities of benthic invertebrates to maintain such high metabolism. Sea otters tend to quickly remove large, calorically rich, and easily captured prey

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when they move into a new habitat. After these prey are depleted, they expand and diversify their diet into a wider variety of smaller and more energetically expensive prey. Sea otters can forage effectively in a number of different habitat types, ranging from rocky subtidal reefs to sand or mud-bottom estuaries. In rocky habitats, sea otters easily and quickly select large sea urchins or abalones (Kvitek and Oliver 1988) and predation generally leads to a kelp-dominated system under reduced grazing pressure (Estes and Duggins 1995). In soft-bottom substrate, sea otters generally prey on burrowing bivalves and spread foraging effort out over a larger geographical area with less obvious ecosystem modification. Many of the preferred sea otter prey species hold important ecological roles and the removal of these herbivores is known to have cascading effects on ecosystem structure and composition (Estes and Duggins 1995; Estes and Palmisano 1974; Kvitek et al. 1989, 1998). Furthermore, many sea otter prey species have significant economic value; thus predation often leads to conflicts with commercial, tribal, and recreational fisheries (Estes and VanBlaricom 1985; Fanshawe et al. 2003).

In 1969 and 1970, sea otters were successfully reintroduced to Washington State after being extirpated by maritime fur trade hunting in the early 20th century. The population was reestablished by translocations of 59 individuals to the outer coast from Amchitka Island, Alaska (Jameson et al. 1982). The successful reintroduction effort resulted in the rapid growth of Washington's sea otter population (10–20% per year—Jameson et al. 1982, 1986; C. E. Bowlby, B. J. Troutman, and S. J. Jeffries, in litt.), which numbered 814 animals in 2005 (R. J. Jameson and S. J. Jeffries, in litt.). Between the late 1970s and early 1990s, the distribution of sea otters was confined to the outer coast (between Makah Bay and Destruction Island). In this area, the population grew rapidly, apparently reaching equilibrium levels in core parts of the range around the mid-1990s (Laidre et al. 2002). In 1995, sea otters expanded their range north to Cape Flattery and eastward into the Strait of Juan de Fuca. Small numbers of isolated animals were initially sighted in the area and sighting frequency and group sizes increased each successive year after 1995 until 2000, when more than 100 animals were noted in the Strait of Juan de Fuca (east to Pillar Point—United States Geological Survey, in litt.). This range expansion resulted in sea otters occupying new urchin-rich habitat in the Strait of Juan de Fuca for the 1st time since the beginning of the 20th century.

Sea otter population growth, range expansion, and associated dietary changes have been well documented in other areas (Estes 1990; Garshelis et al. 1986) and have been the foundation for established ecological paradigms (Estes and Duggins 1995; Estes and Palmisano 1974). Changes in benthic communities in Washington State have been suggested in response to the growing sea otter population (Kvitek et al. 1989, 1998) and we examined if direct links could be made through studies of sea otter foraging behavior and prey selection. The growth and expansion of the small and isolated Washington sea otter population provides a unique opportunity to contrast population status and diet diversity over a 7-year period and examine if the Washington population epitomizes traditional paradigms. Furthermore, the population along the Washington coast provides a dynamic opportunity for examining what the similarities and differences are between foraging behavior of sea otters in other areas, such as the Aleutian Islands, south-central Alaska, southeastern Alaska, and California.

MATERIALS AND METHODS

Study site.—The study was conducted on the coastline of Washington from Destruction Island (on the outer coast at 47°N, 124°28′W) north to Cape Flattery and east into the Strait of Juan de Fuca, south of Vancouver Island (Fig. 1). Coastal Washington has a typical eastern Pacific maritime climate, with average annual temperatures ranging from 2°C to 16°C, and average monthly precipitation ranging from 8 to 36 cm.

Data collection.—Focal studies on sea otters were conducted between 1993 and 1999. Visual observations were systematically collected both from known individuals (tagged during radiotelemetry studies) and unknown individuals using standard protocols established and used in studies of sea otters throughout their range in North America (Estes et al. 2003; Ralls et al. 1995; Tinker 2004). Sea otters were monitored with a 50–80× high-quality Questar (New Hope, Pennsylvania) spotting scope 10–500 m from shore. Protocol called for all focal animals to be observed as long as possible, until they left the area or disappeared from sight. At this time, if another sea otter was sighted, a new observation period was initiated. Sequential observations of unbroken feeding are referred to as foraging bouts and vary in duration. On subsequent days, several sea otters were monitored and unless the animal was tagged, it was not possible to distinguish if the sea otter was a new individual from previous observations. Research on sea otters was maintained in accordance with guidelines of the American Society of Mammalogists (Animal Care and Use Committee 1998) and was approved by the Animal Care Committee (United States Geological Survey).

The recorded information included date and time, location of the animal (determined by triangulation or estimated from nautical charts), dive time, postdive surface time, and dive success (i.e., if prey was captured). Dive time was defined as the time (in s) from the beginning of a dive to the next surfacing. Postdive surface time was defined as the time (in s) from a surfacing to next dive, including activity normally associated with consuming food (such as manipulating a food item, eating, grooming, tending a pup, and short interactions with other animals). On all successful dives, prey species, prey size, and number of prey items taken by the sea otter were recorded.

All prey species observed were identified to the lowest taxonomic unit possible, generally genus or species. For purposes of analysis, prey items were pooled into 1 of 11 general categories. Prey size was determined based on comparison with the sea otter's forepaw. Small prey items were <4 cm or less than the size of forepaw, medium prey items were between 4 and 10 cm or up to 3 forepaw widths, and large prey items were >10 cm or >3 forepaw widths.

Data analysis.—Each foraging bout was considered an independent sample and the smallest sampling unit for statistical analysis. Dietary composition was measured as the percentage occurrence of each prey type on successful foraging bouts. Frequencies of occurrence were averaged by prey type across individual sea otters for habitat-, age-, or sex-based comparisons. Differences in prey capture success, prey choice, and prey size were examined with respect to the established sea otter habitat on the outer coast (south of Cape Flattery to Destruction Island) and newly reoccupied habitat in the Strait of Juan de Fuca (east of Cape Flattery to Bullman Creek; Fig. 1). Relative

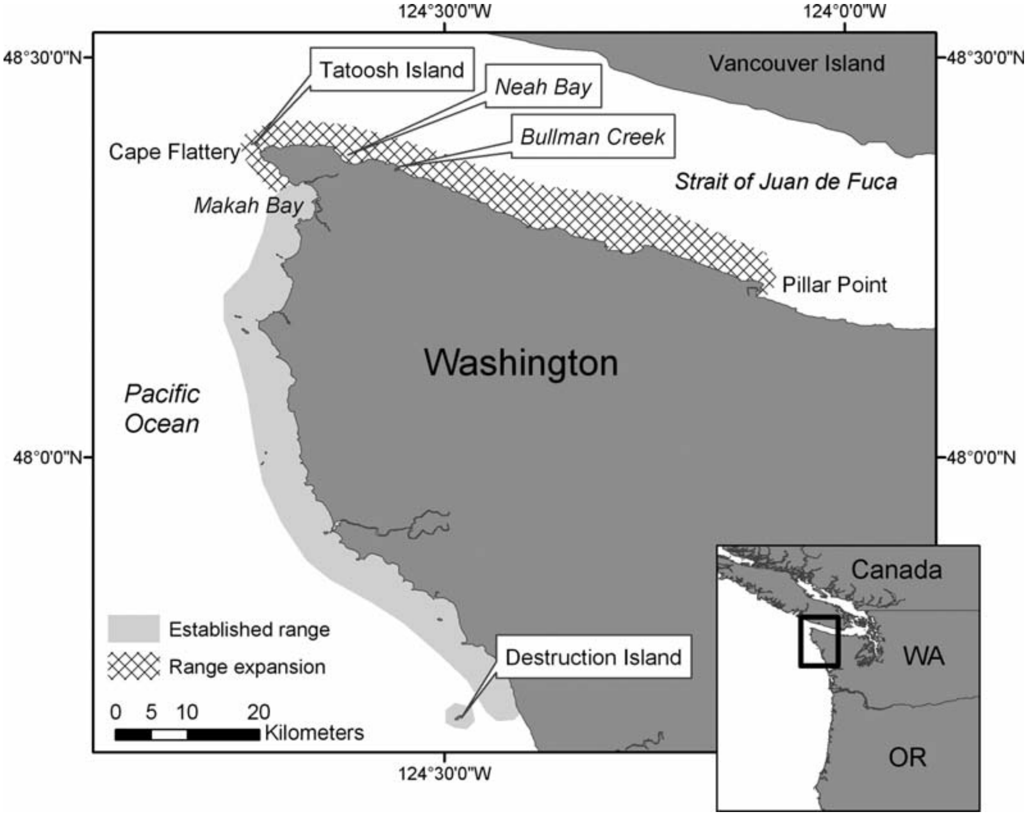

FIG. 1.—Map of localities studied, the established population range (outer coast of Washington), and the newly occupied habitat (Strait of Juan de Fuca) for *Enhydra lutris kenyoni*. Sea otter foraging records in the Strait of Juan de Fuca were collected between Makah Bay and Bullman Creek. WA = Washington, OR = Oregon.

frequency of occurrence of each prey type was calculated to provide a measure of the likelihood of observing a particular prey species and used to quantify spatial and temporal differences in diet at the population level. Dive data and frequency distribution of prey types and size were examined with standard statistics using *t*-tests, analysis of variance (ANOVA), and Tukey post hoc tests with a significance level of 0.05. Chi-square contingency analyses were used to examine if prey type varied by year and habitat along the coast.

A general linear model was built for response variables dive duration (on successful dives) and surface time (post–successful dive) as a function of main effects or interactions between age, sex, year, prey category, prey size, and region (Strait of Juan de Fuca or outer coast) to explore significant influences on dive variables upon prey capture. Only dives where all potential independent variables were available were used. The best model was determined using a forward stepwise procedure with a Gaussian model structure using maximum likelihood, where main fixed effects were added to the model from the pool of potential independent variables based on the lowest Akaike's information criterion (AIC) value (Akaike 1973). Thus, the most significant variables entered the model 1st. Main effects and interactions were continuously added at each stepwise increment until the AIC of the model no longer decreased.

Structural changes in sea otter habitat were examined through trends in bull kelp (*Nereocystis leutkeana*) and giant kelp (*Macrocystis integrifolia*) canopies (area in km^2) based on digital kelp data from the Nearshore Habitat Program, Washington State Department of Natural Resources. Annual kelp canopy coverage was estimated from color-infared aerial photographic surveys between 1989 and 2000. Areal extent of kelp canopy was converted into a global information system polygon coverage using standardized geoprocessing methods developed by the Washington State Department of Natural Resources. Surface canopy area (bull and giant kelp combined) was calculated along the outer coast (between Destruction Island and Cape Flattery) and in the Strait of Juan de Fuca (between Cape Flattery and Pillar Point). Trends in the proportion of kelp cover were calculated for each year between 1989 and 2000 using standard regression models and slopes were evaluated at a significance level of 0.05. Values throughout the text are presented as mean ± *SE* except for sizes of kelp canopy, which are presented as mean ± *SD*.

RESULTS

Foraging records consisted of 13,847 individual dives from 841 feeding bouts collected between 20 September 1993 and 5 April 1999. Female sea otters were observed on 492 individual feeding bouts (433 from adult animals, 26 from subadults, and 33 from unidentified-age females), male sea otters were observed on 258 feeding bouts (215 from adults, 31 subadults, and 12 unidentified-age males), and 91 feeding bouts were observed from sea otters of unknown sex (30 adults, 4 subadults, and 57 unknown age). Average feeding bout duration was 55 ± 1.5 min and feeding bouts ranged from 1 min to 4 h and 46 min.

Dive and surfacing behavior.—Average dive time across all feeding bouts irrespective of dive success was 55 ± 1 s ranging from 3 to 300 s. Average surface time across feeding bouts was 45 ± 2 s ranging from 1 s to 32 min. Average dive time was not significantly different for positively identified males (54 ± 2 s) and females (55 ± 1 s) and did not vary significantly

Table 1.—Prey items captured by *Enhydra lutris kenyoni* on successful foraging dives along the outer coast of Washington and in the Strait of Juan de Fuca, reported as frequency of occurrence. Data were summarized from successful dives between 1993 and 1999.

General category	Common name	Latin name	% of diet
Crustaceans	Dungeness crabs	*Cancer magister*	0.3
	Red crabs	*Cancer productus*	1.1
	Shield-backed kelp crabs	*Pugettia producta*	2.2
	Unidentified *Cancer* species		1.6
	Unidentified crustacean		7.9
Bivalves	Butter clams	*Saxidomus giganteus*	3.8
	Gaper clams	*Tresus nuttalli*	0.9
	Littleneck clams	*Protothaca staminea*	17.0
	Razor clams	*Siliqua patula*	<0.01
	Bent-nose clams	*Macoma nasuta*	0.1
	Rock scallops	*Crassadoma gigantea*	0.1
	California mussels	*Mytilus californianus*	1.2
	Unidentified mussels		9.0
	Unidentified clams		18.0
	Unidentified barnacles		0.1
Snails	Turban snails	*Tegula* species	5.7
Echinoderms	Red urchins	*Strongylocentrotus franciscanus*	22.5
	Purple urchins	*Strongylocentrotus purpuratus*	3.8
	Ochre sea stars	*Pisaster ochraceus*	0.6
	Sunflower stars	*Pycnopodia helianthoides*	<0.1
	Red sea cucumbers	*Cucumaria miniata*	<0.1
	Unidentified urchins		0.5
	Unidentified sea stars		0.3
	Unidentified sea cucumbers		0.3
Other	Unidentified *Octopus* species		0.1
	Giant Pacific chitons	*Cryptochiton stelleri*	1.6
	Unidentified chitons		<0.1
	Peanut worms	*Phascolosoma agassizii*	0.1
	Unidentified worms		0.9
	Egg masses (from lingcod)	*Ophiodon elongatus*	0.2

between adult and subadult age classes (positively identified adults 56 ± 1 s and subadults 52 ± 3 s).

Average surface time was not significantly different for males and females, 50 ± 3 s and 43 ± 2 s, respectively; however, average surface time varied significantly with age ($P = 0.04$). Adult sea otters had, on average, significantly longer periods at the surface (47 ± 3 s) than did subadult sea otters (34 ± 4 s; $P < 0.05$).

Surface time was significantly correlated with dive time ($P < 0.001$). Average dive time across foraging bouts was not statistically different for dives that were successful (54 ± 1.9 s) and nonsuccessful (55 ± 2.9 s). However, average postdive surface time on foraging bouts was significantly higher after a successful dive (49 ± 1.7 s) than a nonsuccessful dive (22 ± 1.3 s; $P < 0.001$).

Prey capture success.—Out of 13,847 individual foraging dives, 77% ($n = 10{,}636$) were successful prey captures (excluding dives in hours of low light or that were undetermined). Average rates of success for prey capture on foraging bouts were not different for males and females when all ages were pooled, with an 80% ± 1.2% success rate for females and 82% ± 1.6% success rate for males. However, average prey capture success rates on foraging bouts were significantly lower for subadult sea otters (63% ± 5%) than for adult sea otters (82% ± 1%; $P < 0.001$).

Table 2.—Mean (± 1 *SD*) number of each sea otter prey caught per dive on the outer coast of Washington and in the Strait of Juan de Fuca. Unidentified species (clams, crabs, and mussels) are not enumerated.

Prey type	$\bar{X} \pm SE$	Range
Crabs of the genus *Cancer*	1.1 ± 0.03	1–7
Chitons	1.0 ± 0.02	1–2
Bivalves	2.3 ± 0.03	1–30
Kelp crabs	1.3 ± 0.04	1–4
Other prey species	1.3 ± 0.07	1–7
Purple urchin	1.2 ± 0.07	1–10
Red urchin	1.0 ± 0.01	1–5
Sea star	1.0 ± 0.01	1–2
Turban snails	6.3 ± 0.25	1–34

Prey selection.—Sea otters in this study preyed upon at least 19 identified species on 7,888 successful foraging dives where prey was identified (Table 1). Prey species were pooled into 11 groups: bivalves, including butter clams (*Saxidomus giganteus*), gaper clams (*Tresus nuttalli*), littleneck clams (*Protothaca staminea*), razor clams (*Siliqua patula*), bent-nose clams (*Macoma nasuta*), rock scallops (*Crassadoma gigantea*), California mussels (*Mytilus californianus*), and unidentified mussels, clams, or barnacles; chitons (*Cryptochiton stelleri* and other species); crabs of the genus *Cancer*, including *Cancer magister*, *Cancer productus*, and unidentified *Cancer* species; kelp crabs (*Pugettia producta*); sea stars (*Pisaster* and *Pycnopodia* species); red urchins (*Strongylocentrotus franciscanus*); purple urchins (*Strongylocentrotus purpuratus*); unidentified urchins; turban snails (*Tegula* species); unidentified crustaceans; and other prey (including egg masses, octopuses, sea cucumbers, and worms). When prey selection was examined irrespective of habitat or region, dominant prey species in the diet of sea otters were clams (unidentified or littleneck clams), red urchins, and turban snails (Table 1). No predation on fish species or abalone (*Haliotis* species) was observed.

Dive time on successful dives was significantly different for prey species category (1-way ANOVA, $F = 49.95$, $d.f. = 10, 7{,}139$, $P < 0.001$). Dive time was highest for the "other" prey category (57 ± 2 s) and lowest for purple urchins (30 ± 1 s), although these 2 categories were based on relatively small samples sizes of 132 and 237 dives, respectively. Postdive surface time on successful dives also was significantly different for prey species category (1-way ANOVA, $F = 22.93$, $d.f. = 10, 7{,}185$, $P < 0.001$). Postdive surface time was highest for "other" prey (92 ± 4 s) and sea stars (80 ± 6 s), and lowest for purple urchins (36 ± 3 s). Sea otters generally returned to the surface after successful foraging dives with 1 or 2 prey items, with the exception of bivalves and turban snails (Table 2).

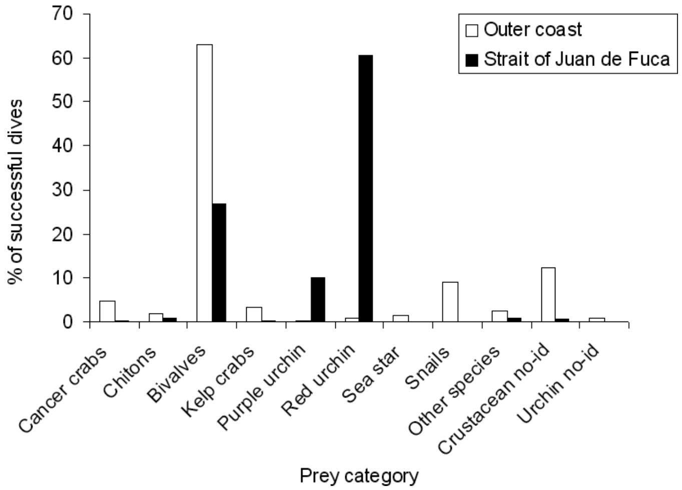

Fig. 2.—Distribution of prey species or prey groups taken by *Enhydra lutris kenyoni* on successful foraging dives between 1993 and 1999 in each of 2 areas: the outer coast of Washington ($n = 4{,}974$ dives) and the Strait of Juan de Fuca ($n = 2{,}873$ dives). Data are summarized based on frequency of occurrence.

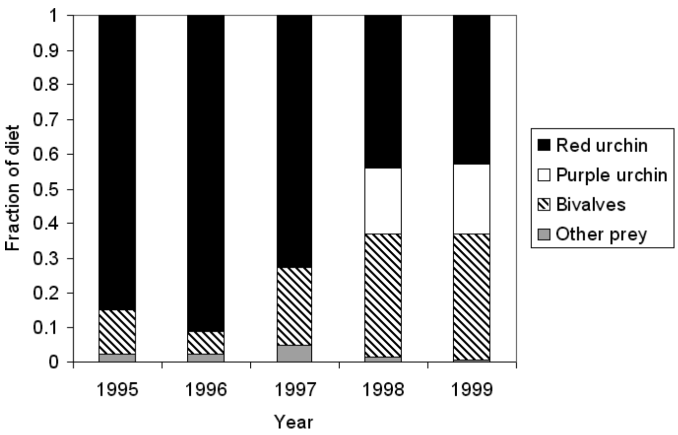

Fig. 3.—Distribution of prey species selected by *Enhydra lutris kenyoni* in the Strait of Juan de Fuca. The 1st foraging records were collected in 1995. The "other" prey category includes crabs of the genus *Cancer*, kelp crabs, chitons, sea stars, all "other" prey species, and unidentified crustaceans.

Regional differences in prey choice, prey size, and success rates.—Prey selection was contrasted between the outer coast, which consisted of 461 foraging bouts ($n = 4{,}974$ dives), and the Strait of Juan de Fuca, which consisted of 373 foraging bouts ($n = 2{,}873$ dives; Figs. 1 and 2). Sea otter diet on the outer coast was disproportionably weighted toward bivalves (63%) yet had a high prey species diversity ($n = 10$ prey species or groups). On the outer coast, predation on red or purple urchins was negligible and they composed no more than 1% of the total diet. In stark contrast, 60% of sea otter diet in the Strait of Juan de Fuca comprised red urchins. No predation on crab species, sea stars, or snails was observed and prey species diversity was low; only 2 other prey groups (purple urchins and bivalves) made up >10% of the diet (all other prey categories were ≤1%; Fig. 2). Bivalves were of secondary importance in the diet of sea otters in the Strait of Juan de Fuca (27%).

Significant differences were detected in the proportion of prey in different categories over the period observations were collected in the Strait of Juan de Fuca ($\chi^2 = 744$, $d.f. = 32$, $P < 0.001$). A time series of prey selection in the Strait of Juan de Fuca suggested that sea otters fed almost exclusively on red urchins upon arrival in 1995–1996 (85–90%; Fig. 3). However, as sea otters occupied the Strait of Juan de Fuca for longer periods, the proportion of red urchins in the diet decreased (50–70%) while bivalves and purple urchins proportionally increased (1998–1999; Fig. 3).

Success rates of dives on the outer coast and in the Strait of Juan de Fuca significantly differed. Sea otters were more frequently successful on foraging dives in the Strait of Juan de Fuca (88% ± 0.9% of the time) than on the outer coast (76% ± 1.4% of the time; *t*-test, $P < 0.001$). Furthermore, larger prey items were taken in nearly all prey categories in the Strait of Juan de Fuca than on the outer coast (e.g., >98% of red urchins taken by sea otters in the Strait of Juan de Fuca [$n = 1{,}706$] were classified as large yet <60% were such on the outer coast [$n = 37$]). Similarly, 32% of bivalves taken by sea otters in the Strait of Juan de Fuca were classified as large prey ($n = 252$), and there were no observations of predation on small bivalves. In contrast only 5% of bivalves taken by sea otters were classified as large ($n = 170$) on the outer coast, and >50% were classified as small ($n = 1{,}596$).

Generalized linear model selection for dive duration resulted in prey category as the most significant main effect, followed by region, and prey size (Table 3). The model for postdive surface duration was best explained by prey size, prey category, and then region (Table 4). Sex, age, and sex–age interactions were not important predictor variables for either dependent variable. Dive durations were lowest when sea otters selected for red or purple urchins and crabs (Table 3) and dive duration was inversely correlated with prey size, although overall differences in duration were low. Sea otters spent about 74 ± 1.5 s at the surface consuming prey after a successful dive when large prey items were taken, and surface duration was reduced by 9–13 s when prey items were classified as small or medium (Table 4). Furthermore, prey categories such as red or purple urchins and chitons required 9–12 s less to consume at the surface, where as kelp crabs and "other" prey required approximately an additional 5 s for consumption (Table 4). Region entered both models and dive and surface durations were lower for sea otters foraging on the outer coast than in the Strait of Juan de Fuca.

Kelp canopy habitat.—Between 1989 and 2000 the average areal extent of surface kelp canopy was 6.5 ± 2.3 km^2 on the outer coast and 8.8 ± 2.2 km^2 in the Strait of Juan de Fuca. Over the 10-year period when kelp canopy species was identified (1990–2000), kelp on the outer coast was dominated by *M. integrifolia* and kelp in the Strait of Juan de Fuca was dominated by *N. leutkeana*. Approximately 60% of the canopy on the outer coast was *M. integrifolia* (3.4 ± 0.7 km^2), 36% was *N. leutkeana* (2.4 ± 1.8 km^2), and 2% was classified as mixed (0.2 ± 0.2 km^2). In the Strait of Juan de Fuca,

TABLE 3.—Parameter estimates for generalized linear model for the average dive duration on successful dives (dives where prey items were brought to the surface for consumption), for *Enhydra lutris kenyoni* in coastal Washington. AIC = Akaike's information criterion value.

Main effect	Dive duration	*SE*	*t* value	*P* (> |*t*|)	Model AIC
Intercept	54.47	0.66	83.16	<0.0001	
Prey category					58,086.22
Crabs of the genus *Cancer*	0				
Chitons	−0.15	1.39	−0.11	0.9163	
Bivalves	0.74	0.50	1.48	0.1383	
Kelp crabs	−1.99	0.50	−4.03	0.0001	
Other prey species	1.08	0.42	2.59	0.0096	
Purple urchin	−6.08	0.32	−19.09	<0.0001	
Red urchin	−1.27	0.19	−6.88	<0.0001	
Sea star	−0.17	0.36	−0.47	0.6401	
Turban snails	−0.32	0.15	−2.06	0.0398	
Unidentified crustacean	0.96	0.12	8.14	<0.0001	
Unidentified urchin	2.34	0.37	−2.06	0.0398	
Region					57,853.11
Strait of Juan de Fuca	0				
Outer coast	−7.60	0.51	−14.87	<0.0001	
Prey size					57,851.85
Large	0				
Medium	0.10	0.57	0.18	0.8569	
Small	0.58	0.29	2.21	0.0428	

TABLE 4.—Parameter estimates for generalized linear model for the average post–successful dive surface duration (in s), for *Enhydra lutris kenyoni* in coastal Washington. AIC = Akaike's information criterion value.

Main effect	Surface time	*SE*	*t* value	*P* (> |*t*|)	Model AIC
Intercept	74.045	1.46	50.676	<0.0001	
Prey size					69,311.6
Large	0				
Medium	−13.96	1.27	−11.009	<0.0001	
Small	−9.15	0.64	−14.273	<0.0001	
Prey category					68,850.0
Crabs of the genus *Cancer*	0				
Chitons	−10.99	3.17	−3.467	0.0005	
Bivalves	−0.22	1.13	−0.191	0.8487	
Kelp crabs	4.73	1.11	4.270	<0.0001	
Other prey species	4.60	0.93	4.975	<0.0001	
Purple urchin	−12.79	0.70	−18.465	<0.0001	
Red urchin	−9.20	0.41	−22.365	<0.0001	
Sea star	2.27	0.81	2.791	0.0052	
Turban snails	2.75	0.35	7.979	<0.0001	
Unidentified crustacean	0.50	0.26	1.900	0.0575	
Unidentified urchin	1.42	0.83	1.703	0.0886	
Region					68,390.29
Strait of Juan de Fuca	0				
Outer coast	−24.65	1.13	−21.854	<0.0001	

approximately 37% of the canopy was *M. integrifolia* (3.2 ± 1.1 km^2), 57% was *N. leutkeana* (5.0 ± 1.6 km^2), and 9% was classified as mixed (0.8 ± 0.5 km^2). Trends in kelp cover on the outer coast resulted in significantly increasing areal extent of kelp cover (0.4 km^2 per year; $F = 6.9$, $d.f. = 1, 9$, $P < 0.05$) between 1989 and 2000. Similarly over that same period in the Strait of Juan de Fuca, significantly increasing and slightly higher trends in areal extent of kelp cover were detected (0.5 km^2 per year; $F = 15.2$, $d.f. = 1, 9$, $P < 0.01$; Fig. 4). In both areas, canopy of *N. leutkeana* increased nearly 30% faster than that of *M. integrifolia*.

DISCUSSION

Sea otter diving.—Diving and surface times recorded for sea otters in Washington were similar to those reported for other populations. Mean dive durations for sea otters in Washington (55 s) followed well with means in California and Alaska (Bodkin et al. 2004; Ralls et al. 1995); however maximum values recorded (300 s) were slightly above those reported in other areas (Bodkin et al. 2004; Estes et al. 1981; Loughlin 1979; Ralls et al. 1995). Surface time on unsuccessful dives was approximately one-half that of successful dives (22.3 s versus 49.2 s).

Although adult and subadult sea otters spent about the same time underwater searching for prey, capture success was significantly higher and postdive surfacing time was significantly longer for adults. Longer surfacing times for adults likely reflect time spent consuming prey items at the surface after successful dives, whereas juveniles probably return for air and depart quickly for the next attempt. Alternatively, success during foraging bouts may result in more time available for resting.

Dive duration and postdive surface duration on successful dives were best explained by prey category and prey size (Tables 3 and 4). Sea otters must make energy-maximizing decisions to support their high caloric needs, and therefore bioenergetic and physiological trade-offs exist when selecting prey. At some point, the increased energy invested on a long dive for high-quality prey equalizes the energy conserved by making several shorter dives taking lower-quality prey. Thus, the influence of prey species and size on dive behavior in this study suggest that there are clear and quantifiable relationships between energy expended and prey obtained on a dive (see also Estes et al. 2003; Tinker 2004). Interestingly, age and sex did not play important roles when all potential explanatory variables were combined in a single model. Although region entered both models it was more important in explaining dive duration (Table 3). Along the outer coast, sea otters had shorter dive durations and postdive surface durations than in the Strait of Juan de Fuca (Tables 3 and 4). Higher prey densities, increased availability of preferred prey, and larger prey sizes likely all contribute to more time spent at the surface in the Strait of Juan de Fuca. The contrast in parameter estimates was much larger for postdive surface durations than dive durations, suggesting that dive duration may not be as variable (likely because of aerobic limits). This lack of contrast, and the relative consistency in mean dive time irrespective of capture

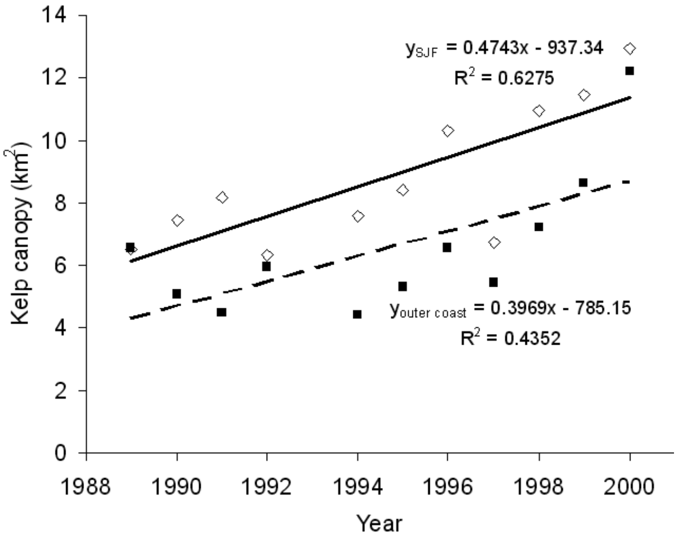

Fig. 4.—Trends in areal extent of kelp canopy within the range of *Enhydra lutris kenyoni* in Washington examined for the outer coast (i.e., between Destruction Island and Cape Flattery) and in the Strait of Juan de Fuca (subscript SJF; i.e., between Cape Flattery and Pillar Point). Giant kelp (*Macrocystis integrifolia*) and bull kelp (*Nereocystis leutkeana*) are combined. The outer coast trend is shown with a dashed line and closed symbols and the Strait of Juan de Fuca trend is shown with a solid line and open symbols.

success suggests that sea otters in Washington spend a relatively fixed duration below the surface (~55 s) searching for prey.

Sea otter predation.—The results of this study provide clear evidence that as Washington sea otters expanded their range, they targeted and depleted preferred and economically valuable prey species such as large red sea urchins. Urchin predation made up the majority of the sea otter diet in the Strait of Juan de Fuca (60%), whereas on the outer coast evidence of urchin predation was negligible (1%). Instead sea otters had a diverse diet including a large proportion of bivalves.

The dramatic differences in diet for sea otters on outer coast habitat (occupied for 25 years) and the Strait of Juan de Fuca habitat (occupied for <4 years) has important implications for both ecosystem structure and fishery conflicts in Washington. Examination of available data from habitat surveys suggests that as sea otters in Washington expanded, they significantly altered benthic prey communities (Kvitek et al. 1989, 1998). Benthic surveys were conducted on the outer coast in 1987 and 1995 in areas with and without otters. Results suggested marked changes in urchin densities and algal coverage, changes proportional to sea otter abundance and most pronounced where sea otters had been present the longest.

In the absence of sea otters for most of the 20th century, potential prey populations in the Strait of Juan de Fuca increased in densities and size in response to reduced predation pressure. Sea urchin harvests between Cape Flattery and Neah Bay peaked in 1987–1988 at 1.6 million pounds (Kvitek et al. 1989). Yet after 1995, the year sea otters arrived, surveys at 9 out of 10 standard urchin monitoring stations (monitored since 1984) demonstrated a 71% decline in sea urchins over 1 year, and by 1997, and so few sea urchins remained in the vicinity of Neah Bay that the fishery district was closed to commercial harvest by Tribal–State harvest agreement (A. Bradbury and M. Ulrich, Washington Department of Fish and Wildlife, pers. comm.). Illegal fishing, changes in survey methods, and disease were all ruled out as explanations for the sea urchin decline, although the decline was never formally attributed to sea otter predation.

The coevolution of sea otters and shellfish in coastal Washington before extirpation by maritime fur trade likely supported a different equilibrium in invertebrate population densities and size classes. Thus, the development of potentially sustainable fishery in Washington was probably the result of the timely removal of sea otters from the system. It is well documented that sustainable sea urchin fisheries are nearly impossible with the combination of sea otter predation and low urchin recruitment (Estes and VanBlaricom 1985; L. R. Gerber and G. R. VanBlaricom, in litt.), and the case in Washington provides further support for this generality.

Kelp canopy.—In general, the Washington coast has high year-to-year variability in kelp canopy extent (J. Shaffer, in litt.; H. Berry, A. Sewell, and B. Van Wagenen, in litt.). In this study, trend analysis was conducted within the known sea otter range (between Destruction Island and Pillar Point) but divided into 2 regions based on length of occupation. The significant increasing trends detected in areal extent of the kelp canopy on the outer coast and in the Strait of Juan de Fuca (Fig. 4) may be related to the increasing sea otter population, reduced grazing pressure, or facilitated macroalgal growth (Estes and Duggins 1995); however, a cause–effect relationship is not possible to determine. Alternative explanations for the increase are available, such as the intense sea urchin harvest beginning in 1988 in the Strait of Juan de Fuca. This harvest could partially or entirely explain increasing trends in kelp in the Strait, although this explanation would not apply to the outer coast (where no harvest was conducted and similar increasing trends were observed). Alternate covariates influencing kelp growth (not examined here) include shifts in algal communities, substrate type, exposure, local oceanography, and influences of climate (Pacific Decadal Oscillation). Regardless of the drivers of the trends, observations of increasing suitable sea otter habitat are critical to predications of population expansion and estimates of carrying capacity, which have varied in their assumptions about habitat availability (Gerber et al. 2004; Laidre et al. 2002).

Future expansion and impact.—This study documents foraging patterns of an expanding population of sea otters in Washington between 1993 and 1999. After this study was terminated, sea otters expanded even farther east in the Strait of Juan de Fuca to Pillar Point (Fig. 1; R. Jameson, in litt.), yet sighting rates declined in the Strait of Juan de Fuca after 2001 (Lance et al. 2004). Although direct records of sea otter foraging are not available after 1999, the fishery district east of Neah Bay demonstrated similar declines in sea urchin abundance between 1998 and 2003 (~11%) and the total allowable catch in the area was subsequently reduced (M. Urlich, pers. comm.).

There is broad and differing speculation on the degree and the extent to which the sea otter population in Washington will expand (Gerber et al. 2004; Laidre et al. 2002). It is unclear to what degree newly occupied habitat in the Strait of Juan de Fuca will be permanently used by sea otters. This is dependent on a number of factors including habitat suitability, prey availability, continued population growth, anthropogenic habitat alteration, and immigration or emigration between this population and the population in British Columbia (Laidre et al. 2002; Lance et al. 2004). The documentation of large and significant increases in the kelp canopy suggest that suitable habitat is available, if not increasing; thus, estimates of carrying capacity assuming expansion into new habitat are perhaps more realistic (Laidre et al. 2002). Sea otters in Washington have demonstrated patterns of foraging and prey reduction similar to that of other expanding sea otter populations, and anticipated anthropogenic conflicts (L. R. Gerber and G. R. VanBlaricom, in litt.) are likely to shape management needs in the coming years.

It is well documented that as sea otters move into new areas they initially select optimal prey species such as urchins (Estes et al. 1981; Ostfeld 1982; Wild and Ames 1974). General theory suggests that as sea otter densities approach equilibrium, diet diversifies and stabilizes to include less profitable prey species because optimal prey have been depleted. The preference for, and consequent depletion of, high-quality prey species essentially limits invertebrate populations and has important consequences for community structure. The relationship between population status and diet diversity is clearly demonstrated by the results of this study.

The results presented here follow well with the literature on sea otter foraging in other localities (Duggins et al. 1989; Estes 1990; Estes and Duggins 1995; Estes and Palmisano 1974; Garshelis et al. 1986) and fit well with the concept of the sea otter as a keystone species. Although these results are not surprising, these paradigms are well documented in only a few places and evidence from Washington provides further support.

A general perception is that ecological systems are idiosyncratic and have limited predictability. Yet the identification of key drivers in communities and ecosystems is critical for threading multiple systems. Results from foraging studies of an apex mammalian carnivore at several sites throughout its range can ultimately be combined to distill coherent generalities useful for identifying constraints on ecological communities. In the case of the sea otter, these threads are valuable in forecasting the impact of growing populations and identifying or predicting anthropogenic conflicts.

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