

Sea otter population status and the process of recovery from the 1989 'Exxon Valdez' oil spill

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ABSTRACT: Sea otter *Enhydra lutris* populations were severely affected by the 1989 'Exxon Valdez' oil spill in western Prince William Sound, AK, and had not fully recovered by 2000. Here we present results of population surveys and incorporate findings from related studies to identify current population status and factors affecting recovery. Between 1993 and 2000, the number of sea otters in the spill-area of Prince William Sound increased by about 600 to nearly 2700. However, at Knight Island, where oil exposure and sea otter mortality in 1989 was most severe, no increase has been observed. Sea otter reproduction was not impaired, and the age and sex composition of captured otters are consistent with both intrinsic reproduction and immigration contributing to recovery. However, low resighting rates of marked otters at Knight Island compared to an unoiled reference area, and high proportions of young otters in beach cast carcasses through 1998, suggest that the lack of recovery was caused by relatively poor survival or emigration of potential recruits. Significantly higher levels of cytochrome P4501A (CYP1A), a biomarker of hydrocarbons, were found in sea otters at Knight Island from 1996 to 1998 compared to unoiled Montague Island, implicating oil effects in the lack of recovery at Knight Island. Delayed recovery does not appear to be directly related to food limitation. Although food availability was relatively low at both oiled and unoiled areas, we detected significant increases in sea otter abundance only at Montague Island, a finding inconsistent with food as a principal limiting factor. Persistent oil in habitats and prey provides a source of continued oil exposure and, combined with relatively low prey densities, suggests a potential interaction between oil and food. However, sea otters foraged more successfully at Knight Island and young females were in better condition than those at Montague Island. We conclude that progress toward recovery of sea otters in Prince William Sound is evident, but that in areas where initial oil effects were greatest, recovery may be constrained by residual spill effects, resulting from elevated mortality and emigration. It is evident that internal reproduction and immigration of juveniles has been the primary means of population recovery, as opposed to broad scale redistribution of adults from outside affected areas. The result is a recovery period protracted by long-term spill effects on survival and emigration and intrinsic limits to population growth.

KEY WORDS: Abundance · Biomarker · *Enhydra lutris* · Food · Mortality · P450 · Reproduction · Survival

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INTRODUCTION

Sea otters *Enhydra lutris* are coastal marine carnivores of the North Pacific Ocean (Kenyon 1969) spending their entire life cycle in nearshore habitats (Wild &

Ames 1974, Estes 1980, Riedman & Estes 1990). They utilize both rocky and unconsolidated habitats, and in Prince William Sound (PWS), Alaska, forage primarily on burrowing clams, crabs, and mussels (Calkins 1978, Kvitek & Oliver 1988, Doroff & Bodkin 1994, Dean et al. 2000). Sea otters lack the insulating blubber of other marine mammals, and have instead a dense, water-

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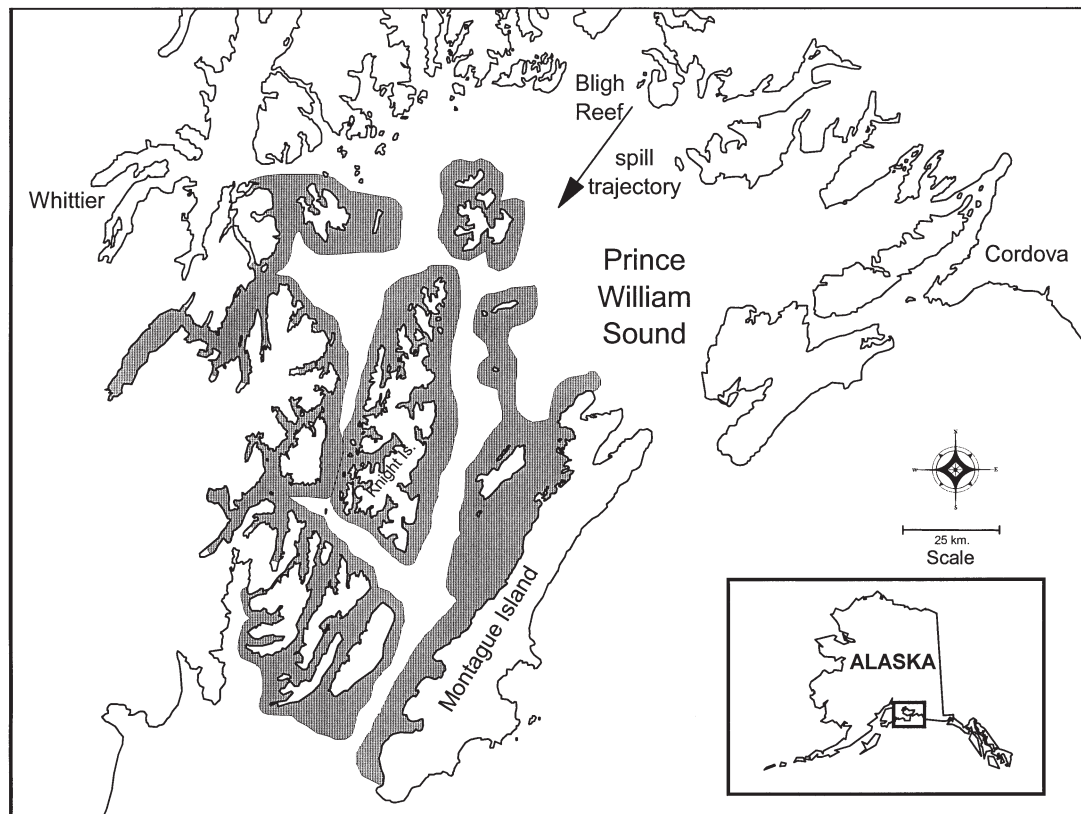


Fig. 1. Western Prince William Sound sea otter survey area (shaded)

resistant pelage and an elevated metabolic rate that enable them to survive in a cold aquatic environment (Kenyon 1969, Costa & Kooyman 1984, Riedman & Estes 1990). Using their mouth and forepaws, they groom their pelage for up to several hours each day to maintain its insulating quality (Estes et al. 1982). Because both the habitat they forage in and the prey they consume serve as repositories for spilled oil, and the fur they rely on for insulation is sensitive to contamination, sea otters are particularly susceptible to the effects of oil spills.

Sea otters are long-lived (Kenyon 1969, Bodkin et al. 1997), with relatively low annual reproductive rates (females produce single offspring) (Siniff & Ralls 1991, Bodkin et al. 1993, Jameson & Johnson 1993, Riedman et al. 1994, Monson & DeGange 1995, Monson et al. 2000a) and high annual adult survival (Siniff & Ralls 1991, Monson & DeGange 1995, Monson et al. 2000a,b). These life history traits resulted in a long-term annual growth rate of about 10% in PWS following the end of the fur harvest in 1911 (Bodkin et al. 1999). Mechanisms ultimately limiting sea otter density are not completely understood, but likely include limits imposed by prey availability and some form(s) of territoriality (Kenyon 1969, Bodkin et al. 2000). Factors

affecting sea otters such as contaminants or predation, that result in either reduced reproduction, increased mortality, or increased emigration, will eventually lead to reduced population growth rates (Riedman & Estes 1990).

The grounding of the TV 'Exxon Valdez' in March 1989 resulted in a spill of approximately 42 million l of crude oil (Spies et al. 1996), with acute mortality among a diverse number of marine organisms (Peterson 2001), including the sea otter (Ballachey et al. 1994). Prolonged effects of the spill on populations have been more difficult to measure but are evident across a wide range of taxa, including invertebrates (Fukuyama et al. 2000), fishes (Jewett et al. 2002), birds (Irons et al. 2000, Esler et al. 2002, Golet et al. 2002), and mammals (Bowyer et al. 1995, Ben-David et al. 2002) and are reviewed in Peterson (2001). To assess the recovery status of the nearshore ecosystem in western Prince William Sound (WPWS), a comprehensive study of nearshore bird and mammal predators, including harlequin ducks *Histrionicus histrionicus*, pigeon guillemots *Cepphus columba*, river otters *Lontra canadensis*, sea otters, and their invertebrate prey, was conducted from 1995 to 1999 (Holland-Bartels 2000). Here we report on the sea otter compo-

ment of that study; results of other components are presented in accompanying papers in this volume (Dean et al. 2002, Esler et al. 2002, and Golet et al. 2002).

Accurate and defensible estimates of acute sea otter mortality from the spill, beyond the number of carcasses recovered (nearly 1000 throughout the spill area), could not be made, largely because accurate and recent pre-spill population estimates were not available (Ballachey et al. 1994). While several widely disparate estimates of sea otter mortality resulting from the spill in PWS have been published, all include recognized uncertainties (Garrott et al. 1993, Bodkin & Udevitz 1994, DeGange et al. 1994, Garshelis 1997, Dean et al. 2000). Although acute mortality estimates generated controversy (Eberhardt & Garrott 1997, Garshelis & Estes 1997, Garshelis 1997), it is clear that sea otter mortality was extensive and widespread regardless of the particular estimate.

Oil exposure and acute sea otter mortality were not distributed evenly throughout PWS (Bodkin & Weltz 1990, Bodkin & Udevitz 1994). Generally, shoreline oiling decreased as distance from the spill origin increased. Along the spill trajectory in WPWS, bays and

shores oriented between north and east were subjected to high oil exposure and persistence (Fig. 1), while more distant shores or those with different orientation may have received little or no oiling (Neff et al. 1995). Exposure to oil and sea otter mortality in 1989 were particularly high along the shores of the northern Knight Island archipelago in WPWS (Figs. 1 & 2), where mortality in one large bay was estimated at 0.88 (Bodkin & Udevitz 1994).

Immediate impacts of oil spills on sea otters occur through contamination of pelage, ingestion, and inhalation, and are well understood (Costa & Kooyman 1982, Siniff et al. 1982, Geraci & Williams 1990, Williams et al. 1995), but longer-term effects have not been well documented. Chronic effects of initial oil, continued exposure to persistent oil (through prey or physical contact) and reduction in prey caused by direct oiling all may result in long-term injury. Oil-related damage to liver, kidney, and lung was documented in sea otters that died in 1989 after being exposed to oil (Lipscomb et al. 1993, 1994, Williams et al. 1995). Presumably, the health of otters that survived initial exposure could have been compromised, and

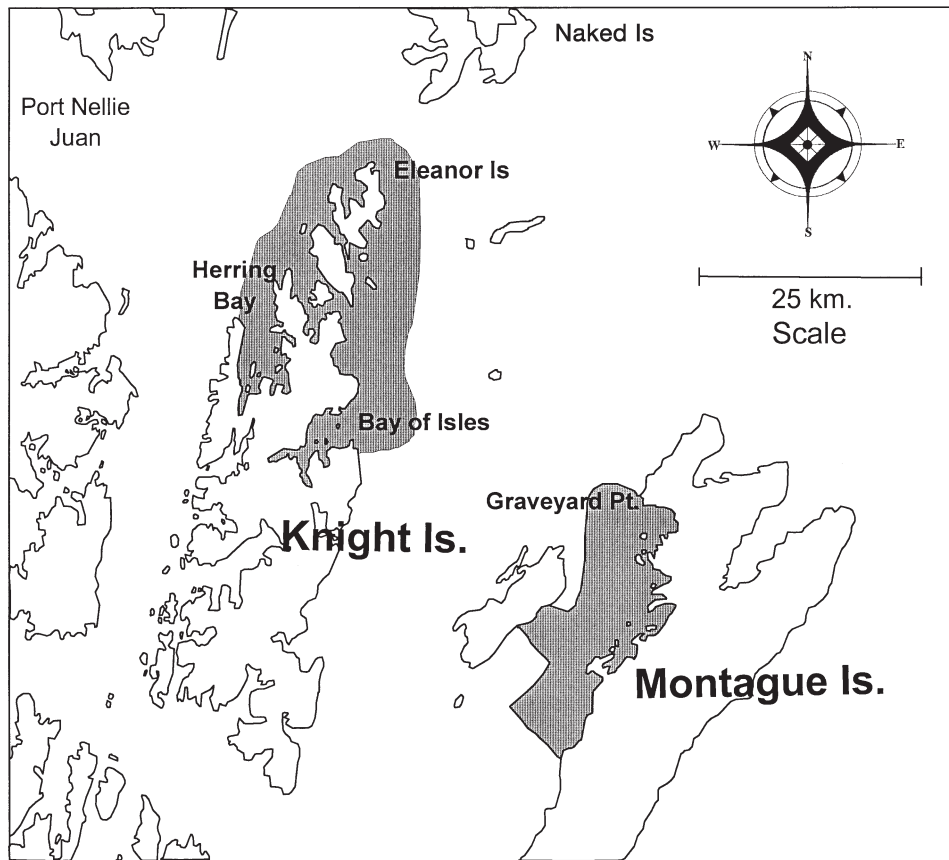


Fig. 2. Intensive sea otter study areas for surveys (shaded), capture, food habits, and prey measures at northern Knight Island (oil-affected) and Montague Island (unshaded)

exposed individuals may exhibit reduced long-term survival (Monson et al. 2000b). Further, sea otters have a high potential to encounter residual oil while excavating infaunal and epifaunal prey such as clams and mussels.

The importance of spill-related effects on sea otter prey populations to sea otter recovery are not well understood. Oil in nearshore habitats persisted through to at least 1997 in WPWS, although at greatly reduced levels from 1989 (Hayes & Michel 1999, Carls et al. 2001) and through 1994 along the Alaska Peninsula (Irvine et al. 1999). Projected recovery times for hydrocarbon levels in mussel beds to return to background range to 30 yr (Carls et al. 2001). The spill and related clean-up activities resulted in reductions in densities of some sea otter prey along oiled shorelines, including intertidal clams (Driskell et al. 1996), mussels (Gilfillan et al. 1995, Highsmith et al. 1996), and the helmet crab *Telmessus cheiragonus* (Dean et al. 1996). Elevated levels of hydrocarbons were found in some surviving sea otter prey populations, including intertidal mussels from 1990 through to at least 1995 (Babcock et al. 1996, Short & Babcock 1996, Carls et al. 2001) and some mollusks from northern Knight Island in 1991 (Armstrong et al. 1995). Residual oil at northern Knight Island through to at least 1996 resulted in elevated tissue burdens of hydrocarbons in clams *Protothaca staminea*, that reduced their growth and survival (Fukuyama et al. 2000). However, in subtidal clams collected from southern Knight Island, where oiling was less, elevated hydrocarbon levels were not detected in 1991 (Doroff & Bodkin 1994).

One measure of recovery after a population decline is simply replacement of the number of animals removed from the affected population. Two independent modeling efforts projected recovery times for spill-affected sea otter populations (Garrott et al. 1993, Udevitz et al. 1996). Both sea otter recovery models implicitly assume that all otters remaining in the area of interest will contribute equally to the replacement of otters removed and that the study population is geographically closed. Garrott et al. (1993) applied an estimated pre-spill annual population growth rate of 1.09 to the entire PWS 1989 post-spill sea otter population of about 13 000 and estimated a minimum recovery time of 3 yr, but recognized that population growth was not evident, based on post-spill surveys through to at least 1991. An age-specific reproductive and survival rate recovery model for only the oiled WPWS population of about 2000, produced by Udevitz et al. (1996), projected recovery times ranging from 10 to 23 yr, dependent on assumptions regarding survival rates. Although Garrott et al. (1993) and Udevitz et al. (1996) calculated similar growth rates (about 1.10 yr^{-1}), recovery times differed primarily because the number

of otters assumed to contribute to recovery differed (13000 vs 2000). However, neither recovery model incorporated long-term spill related effects in projecting recovery times.

There are relatively few data available to evaluate how a sea otter population may recover from the removal of a proportion of its population, but except for human-aided translocations only 2 mechanisms are possible. One is intrinsic growth, resulting from births that exceed deaths and emigration from within the affected population. The second is successful immigration of surplus otters from outside the affected area. The latter assumes an increased survival probability of individuals that immigrate (relative to the area they came from), and not simply a large-scale redistribution of the population. As the potential source of replacements into a reduced population increases beyond the area of reduction, recovery time will decrease if growth rates are held constant. The relative contribution of intrinsic growth and immigration to recovery of depleted sea otter populations is unknown. The reduction in sea otter abundance resulting from the spill provides a unique opportunity to observe and describe the processes contributing to replacement of lost individuals.

The primary purpose of this work is to assess the status of the oil-affected sea otter population in PWS, and if the population is not recovering, determine if growth is constrained by toxicological effects of oiling, indirect effects of food limitation, or remnant demographic consequences from the spill (e.g. changes in age and sex composition). We present results of population surveys conducted between 1993 and 2000 in WPWS that identify the current status of the affected population. Additionally, we review related studies on sea otter exposure to residual oil and on sea otter prey populations available to support recovery, and integrate the results of those studies with the population studies to provide a synthesis of the state of sea otter recovery and factors apparently affecting recovery. We also discuss our findings relative to the conservation and recovery of other reduced or depleted sea otter populations.

Because the 1989 spill was accidental, it was not replicated, making it difficult to disassociate the potentially confounding effects of the area from those of the spill. Much of the work we report on here was designed to contrast a single oil-affected area and an unoiled reference area. We recognize the limits imposed by the sampling design (lack of replication of the oil spill treatment and selected study areas) relative to assigning cause to observed differences and extrapolating beyond study area boundaries. However, we make no inference to areas outside our intensive study areas, except where we have direct observations, such as the WPWS survey area. Because of

limits imposed by study design we recognize that our findings relative to potential spill effects and constraints to sea otter recovery are subject to interpretation.

STUDY AREA

The WPWS study area includes all shorelines within the PWS spill area that were oiled, and some areas along the boundary of the spill area that may not have been oiled (Fig. 1). The area included approximately 2358 km² of sea otter habitat (defined by the area between the shoreline and the 100 m depth contour or 0.4 km from shore, whichever is greater).

For comparison between oiled and unoiled habitats, we selected 2 intensive study areas within WPWS. The oiled site was in the area of northern Knight Island, including 198 km of shoreline from the northwest Pt. of Herring Bay to the southeast Pt. of Bay of Isles, including the smaller islands in the northern archipelago (Fig. 2). This area received heavy oiling, and sea otter mortality approached 90% (Bodkin & Udevitz 1994). An estimated 165 sea otters were removed from the heavily oiled area around northern Knight Island as a result of the spill (Dean et al. 2000) and few if any sea otters remained there following the spill in summer 1989 (Bodkin & Udevitz 1994, J. Bodkin & D. Monson unpubl. data). Oil persisted for at least 6 yr in some nearshore sediments and in some invertebrate populations (Babcock et al. 1996, Boehm et al. 1996, Fukuyama et al. 2000, Carls et al. 2001). Our unoiled reference area included 72 km of shoreline along Montague Island southwest from Graveyard Pt. and extended to Green Island (Fig. 2). Our 2 study areas were separated by a minimum of 24 km of open water and we observed no movement of marked animals between areas.

RECOVERY STATUS

Aerial survey methods

Aerial survey methods follow those described in detail in Bodkin & Udevitz (1999) and consisted of 2 components: (1) strip transects and (2) intensive search units to estimate the probability of detection of otters along strips. Sea otter habitat was sampled in 2 strata, a stratum characterized by high sea otter densities between the shore and 40 m depth contour, and a deeper water stratum offshore between the 40 and 100 m depth contours, where sea otter densities are usually lower. Survey effort was allocated proportional to expected sea otter abundance by systematically

adjusting spacing of transects within each stratum. Transects 400 m wide were surveyed by a single observer at an air speed of 65 miles h⁻¹ (29 m s⁻¹) and an altitude of 300 ft (91 m). Strip transect data included location, group size, and group activity (diving or not diving). A group was defined as 1 or more otters separated by less than 4 m. Transect end points were identified by latitude/longitude coordinates in ARC INFO and displayed visually in the aircraft GPS. Intensive searches, made by flying five 400 m diameter circles within the strip transects, were conducted systematically to estimate the proportion of otters not detected during strip counts. Population estimates were generated by adjusting strip counts for areas not surveyed and for otters not observed using the intensive searches within strips.

From 1993 to 2000, we conducted an annual summer survey of WPWS (Fig. 1). The area surveyed included approximately 1003 km² in the nearshore stratum and 1355 km² in the offshore stratum.

From 1995 to 2000, we surveyed our northern Knight and Montague study areas (Fig. 2). Because those areas are relatively small, precision in individual estimates was limited by the number of transects in each area (sample sizes). Therefore, we replicated the surveys in each study area up to 6 times within each year, within a 2 wk period in mid-summer. In 1993 and 1994, only a single estimate was obtained for our Knight and Montague study areas, using strip transect and intensive search unit data collected in our larger WPWS survey area. The Knight and Montague Island area we surveyed for sea otters was larger than, but encompassed all of the area sampled for their prey (Dean et al. 2002).

Trends in population estimates over time were calculated by regressing the natural logs of survey counts ($\ln [x]$) over time. The slope of the line was back-transformed by the antilog to yield a discrete growth rate. Because of apparent non-linearity in population estimates at Montague Island, we did not calculate an average annual growth rate, but simply report annual population number and proportional change.

Aerial survey results and discussion

Between 1993 and 2000, there was a significant increase ($p = 0.03$) of about 600 sea otters in WPWS (Fig. 3). The population appeared generally stable from 1993 to 1996, with most of the increase apparently occurring after 1996. The minimum estimate was 2054 (SE = 698) in 1993 and the maximum was 3119 (SE = 494) in 1998. The annual growth rate was estimated at 0.04, and the rate from 1996 to 2000 was 0.05 (Fig. 3). The observed rate of increase in WPWS is

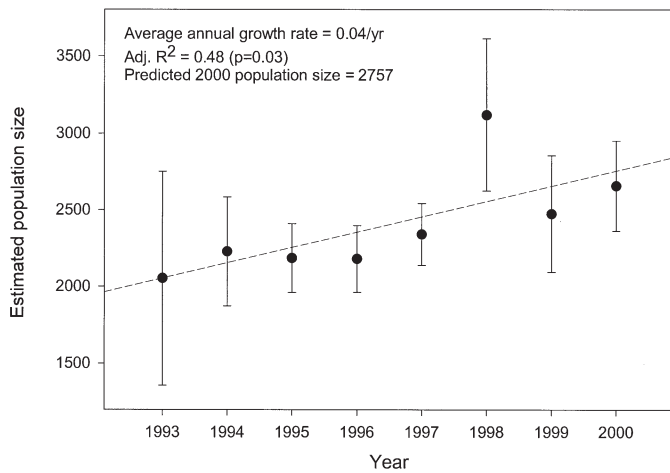


Fig. 3. *Enhydra lutris*. Estimates of abundance (\pm SE) in western Prince William Sound, 1993 to 2000

about half the predicted rate used in recovery models (Garrott et al. 1993, Udevitz et al. 1996) and half the long-term rate during recovery of the PWS sea otter population during much of the 20th century (i.e. something is constraining the rate of recovery).

Between August 1995 and July 2000, we completed 4 to 6 replicate sea otter surveys at our Knight and Montague Island intensive study areas each year (Fig. 4). We also estimated abundance (without estimated precision) within our intensive study areas in 1993 and 1994, using data from the WPWS surveys. At Knight Island, the mean population size over the 8 yr was estimated to be 77 (SE = 2.4), and there was no significant trend in sea otter abundance. In 2000 we estimated the Knight Island study area population to be 79 (SE = 6). This estimate remains slightly less than half of a minimum pre-spill estimate in this same area of 165, based on the number of carcasses recovered (Dean et al. 2000; Fig. 4) and about a third of a 1973 estimated population size of 237 (Dean et al. 2000). In contrast, at Montague Island, sea otter abundance appeared relatively stable between 1993 (n = 335) and 1995 (n = 297) but increased by about 300 otters between 1995 and 1998 (n = 622; Fig. 4).

The primary conclusion from 8 yr of population surveys is that sea otter recovery in most of WPWS is under way, although at a rate less than expected, with an increase of about 600 sea otters between 1993 and 2000. However, we

found no comparable increases in sea otter abundance at our northern Knight Island study area, where oil exposure and persistence were high and sea otter mortality approached 90% immediately after the spill. The estimated number of sea otters at northern Knight Island from 1993 to 2000 remains about half the number removed from our study area because of the spill in 1989 (77 vs 165) (Dean et al. 2000; Fig. 4).

Reproductive survey methods

Indices of annual reproduction, as indicated by ratios of dependent (pups) to independent (non-pup) sea otters, were obtained in each of our intensive study areas (Fig. 2) from small boat surveys in August 1995, 1996, and 1997. Sample units corresponded to coast-line transects, 200 m long with widths extending offshore out to the 100 m depth contour or $\frac{1}{2}$ the distance to the opposing shoreline, whichever was less. The entire coastline of each study area was surveyed. The survey vessel maneuvered about 200 to 300 m offshore and out to the offshore boundary in an attempt to observe all otters within each sample unit. Two observers used high-resolution 10 \times binoculars to classify and record otters as either dependent or independent. Proportions of dependent sea otters were calculated for each group of otters within an area, and the proportions within areas were compared using continuity adjusted chi-squared analysis.



Fig. 4. *Enhydra lutris*. Estimates of abundance (\pm SE) at northern Knight and Montague Island intensive study areas, 1993 to 2000 (no estimates of precision acquired in 1993 to 1994). 1989 pre-spill estimate based on actual and estimated carcasses recovered from the study area and assuming no survivors (from Dean et al. 2000)

Table 1. *Enhydra lutris*. Ratio of independent to dependent sea otters at Knight and Montague study areas, 1995 to 1997, Prince William Sound, Alaska

Area	Year	No. independents	No. dependents	Independents/dependents
Knight	1995	44	21	0.48
Knight ^a	1996	78	23	0.29
Knight (w/o 26 males)	1996	53	22	0.42
Knight	1997	55	24	0.44
Montague	1995	134	68	0.52
Montague	1996	158	58	0.37
Montague	1997	126	50	0.40

^aIncludes a group of 26 young males near SE Eleanor Island in 1996

Reproductive survey results and discussion

Ratios of dependent pups to independent animals ranged from 0.29 to 0.48 at Knight Island and from 0.37 to 0.51 at Montague Island (Table 1), with mean ratios of 0.38 (Knight) and 0.42 (Montague). There were no differences among years or between areas ($p > 0.1$). In 1996 we observed a group of 26 young independent male sea otters at Knight Island (see next 2 subsections) that resulted in a relatively low independent:dependent ratio of 0.29. This group was not observed after 1996, despite intensive searches around northern Knight Island.

The equivalent and high ratios of dependent to independent sea otters at our study sites suggest several biological processes relevant to sea otter population recovery. First, similar rates of pup production in the oiled and unoiled areas indicate no reproductive impairment. Second, reproduction as indexed by this ratio equaled or exceeded values reported for sea otters elsewhere in Alaska and Russia (Riedman & Estes 1990, Johnson & Garshelis 1995, Bodkin et al. 2000). Third, although we noted differences in female age composition (higher proportion of females age 0 to 3 yr captured at Knight, see next 2 subsections; Fig. 5), the equivalent ratios suggest that a relatively large proportion of females age 3 are successfully raising pups at Knight Island. This observation is consistent with sea otters at Knight being in good physical condition (Bodkin et al. 1993, Monson et al. 2000a).

It is possible that immigration of sea otters from unoiled to oiled areas could contribute to recovery of depleted populations (but only to the extent that immigrant survival increased as a consequence of immigration, as otherwise

there would be no overall net gain). Immigrants would likely consist of dispersing juveniles of both sexes and older males, as adult females are the most sedentary component of the population, with the smallest home ranges (Garshelis & Garshelis 1984, Riedman & Estes 1990). If immigration were widespread, we would expect a lower dependent:independent ratio in the oiled area than in unoiled areas. However, similar dependent:independent ratios between oiled and unoiled areas were observed shortly after the spill (0.46 at Knight and 0.47 at Montague in 1991; Johnson & Garshelis 1995) and during our study (with the exception of 1996, when the group of young males was observed at Knight Island). These results are inconsistent with widespread immigration

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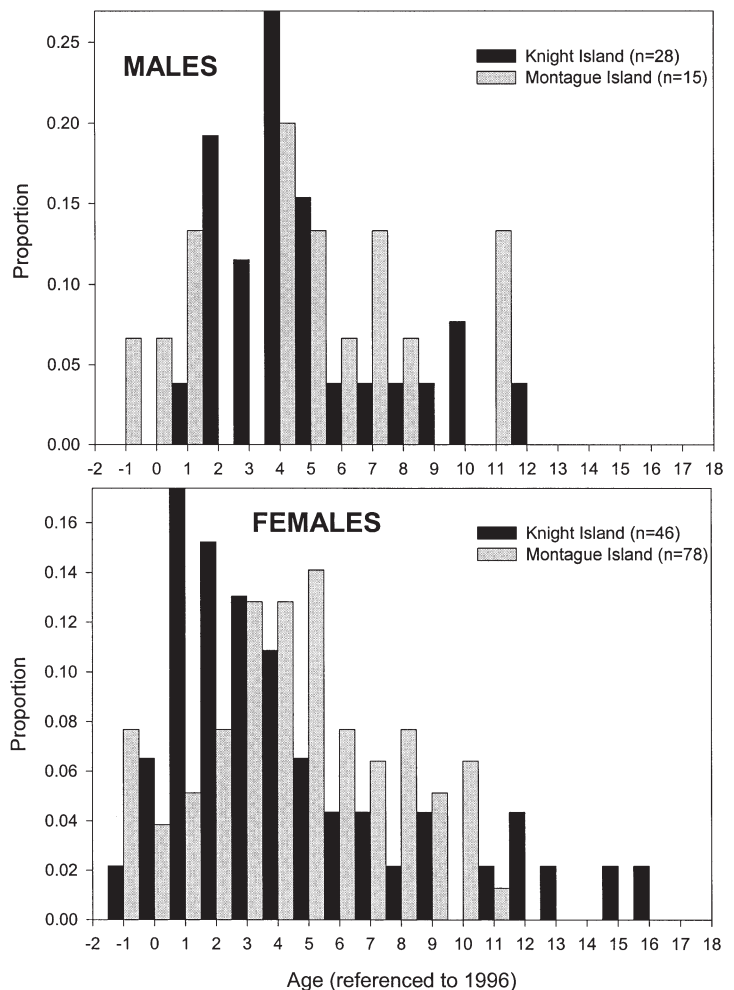


Fig. 5. *Enhydra lutris*. Age distribution of sea otters captured at intensive study areas at northern Knight and Montague Islands, 1996 to 1998

of sea otters as a principal means of recovery. Further, the high ratio of dependents to independents at Montague Island is consistent with the observed growth being supported, at least in part, through intrinsic reproduction. However, at our oiled area, similar reproduction did not result in population increases and apparently was offset by either increased post-weaning mortality or emigration, evidenced in part by the absence after 1996 of the young male immigrants that we marked at Knight in 1996 (see 'Capture-recapture results and discussion').

Capture-recapture methods

In 1996, 1997 and 1998, we captured and tagged sea otters in our intensive study areas. The primary method of capture was tangle nets, supplemented by diver-operated Wilson traps (Ames et al. 1986). Measurements taken from sedated sea otters (Monson et al. 2001) included mass (to the nearest 0.5 lb [230 g], 100 lb spring scale) and total length (dorsal, from tip of tail bone to nose in supine position, measured to the nearest cm). A pre-molar was collected from independent animals for aging (Bodkin et al. 1997). Adults and juveniles were tagged with color-coded plastic ear tags (Temple Tag, Temple, Texas) in the inter-digital webbing of the hind flipper (Ames et al. 1983). Different colors and tag locations allowed individual identification of all marked animals. Up to 35 cm³ of blood was collected for blood chemistries and bioindicator analyses (Ballachey et al. 2000). We directed our capture efforts to areas where sea otters were most abundant based on prior skiff, shore, and aerial surveys. We assume that the 2 capture methods resulted in random samples of the populations.

We used the SAS GENMOD procedure and the chi-square statistic to make comparisons of the age and sex composition of sea otters we captured between areas and among years. Each otter captured was assigned to 1 of 36 categories based on year, capture location, sex and age. Age categories were 0 to 3 yr (juvenile), 4 to 9 yr (adult), and >9 yr (aged) (Bodkin et al. 2000). We assumed that capture of individual sea otters was independent of age and sex.

In 1999, we conducted 2 comprehensive visual surveys of our intensive study areas to search for otters marked between 1996 and 1998. Surveys were conducted in both April and July. During these surveys, teams of 2 observers systematically searched the entire study areas, attempting to locate and observe as many otters as possible. Observations were made from shore vantage points that were accessed by small (3 or 4 m) skiffs. High resolution 50 to 80× Questar telescopes were used to identify each sea otter observed as either

marked or unmarked. Each otter was observed until both rear flippers were determined to be with or without tags. Occasionally, otter activity or distance from observer precluded certainty in determining the presence or absence of tags. In those cases, the otter was not included in the analysis. We used estimated population sizes, the expected number of marked otters in the population and the observed number of marked and unmarked otters to estimate retention or survival of marked otters in our 2 study areas. We assumed that re-sighting followed a binomial distribution with re-sighting probability equaling:

$$\hat{P} = \frac{(m_{96}s_{96}s_{97}s_{98}) + (m_{97}s_{97}s_{98}) + (m_{98}s_{98})}{\hat{N}} \quad (\text{Eq. 1})$$

where m_i is the number marked in year i , \hat{N} is total population size in 1999 (aerial survey estimate) and s_i is survival rate for year i to $i + 1$.

The survival rate estimates were based on age-specific survival rates for the PWS sea otter population (Udevitz & Ballachey 1998). Age-specific female survival rates were 0.92 for ages 2 to 4, 1.00 for ages 5 to 9, 0.81 for ages 9 to 15 and 0.00 for ages 16 to 20. Male survival rates were estimated as the female rate minus 0.05 to account for the generally lower survivorship of males (Siniff & Ralls 1991, Monson & DeGange 1995). Survival of post-weaning juveniles, ages 0 to 1, was estimated at 0.75.

The tag retention rate was calculated as:

$$\hat{R} = \frac{r\hat{N}}{n(m_{96}s_{96}s_{97}s_{98} + m_{97}s_{97}s_{98} + m_{98}s_{98})} \quad (\text{Eq. 2})$$

where n is the total number of otters sighted in 1999 and r is the number of tags re-sighted in 1999

The variance of the tag retention rate was estimated using a combined bootstrap/Monte Carlo routine. We bootstrapped the 1999 replicate population counts from each study area to estimate a new \hat{N} , and used Monte Carlo simulation to provide new estimates of s_i in the calculation of retention rates. We do not derive an estimate of tag retention from recapture rates from our study sites in 1997 and 1998 because of potential biases against recapturing previously handled sea otters.

Capture-recapture results and discussion

During July and August 1996 to 1998, we captured 180 sea otters, with approximately equal numbers captured each year (Table 2). In both areas, most otters were caught with tangle nets (137 of 180, including 68% at Knight Island and 83% at Montague Island). Females were captured at a much higher frequency in all years and in both areas (Table 2), except in 1996 at Knight Island, when the number of males and females

Table 2. *Enhydra lutris*. Age class composition and sex ratios of sea otters captured at Knight^a and Montague Islands, 1996 to 1998

Year	Area (N)	Age class			# F: # M
		0–3 yr (%)	4–7 yr (%)	≥8 yr (%)	
1996	Knight (30)	17 (0.57)	7 (0.23)	6 (0.20)	15:15
	Montague (31)	5 (0.16)	17 (0.55)	9 (0.29)	24:7
1997	Knight (19)	8 (0.42)	8 (0.42)	3 (0.16)	15:4
	Montague (29)	4 (0.14)	16 (0.55)	9 (0.31)	22:7
1998	Knight (22)	8 (0.36)	7 (0.32)	7 (0.32)	18:4
	Montague (35)	12 (0.36)	12 (0.36)	11 (0.28)	33:2
1996–1998	Knight (71)	33 (0.46)	22 (0.31)	16 (0.23)	48:23
	Montague (95)	21 (0.22)	45 (0.47)	29 (0.31)	79:16

^aExcludes 9 animals captured at Naked Island (8 in 1997 and 1 in 1998)

Table 3. *Enhydra lutris*. Retention rates at Knight and Montague Islands, based on visual resighting of marked individuals

Area & time	Population size ^a	No. observed	No. expected ^b	No. re-sighted	'Retention' (R)	95 % CI of R
Knight						
April 1999	81	32	20	14	0.71	0.49–0.92
July 1999	81	31	19	9	0.47	0.33–0.62
Montague						
April 1999	586	120	16	26	1.66	1.17–2.26
July 1999	586	71	9	19	2.05	1.43–2.73

^aPopulation size estimates from aerial surveys
^bBased on estimated survival of marked animals and the number of animals observed (Eq. 1)

captured were equal. We captured males at a higher frequency at Knight Island, compared to Montague Island, each year (Table 1), and the sex ratio of captured animals differed between areas and among years ($\chi^2_{area} = 6.75$, $p = 0.0094$, $\chi^2_{year} = 10.49$, $p = 0.0053$).

Because sex composition differed between areas and among years, we examined age composition by sex. For female sea otters captured at our 2 study sites, the age class distributions were similar among years but differed significantly between areas ($\chi^2_{area} = 4.58$, $p = 0.03$, $\chi^2_{year} = 0.09$, $p = 0.96$) (Fig. 5). At Knight, we caught a higher proportion of young females aged 0 to 3 yr (0.48 at Knight vs 0.22 at Montague), whereas at Montague we caught more adult females (0.35 at Knight vs 0.66 at Montague). Nearly equal proportions of older females, >9 yr, were caught at both areas (0.16 at Knight vs 0.13 at Montague). There was no difference in the age class distributions of captured males between areas or years ($\chi^2_{area} = 0.64$, $p = 0.42$, $\chi^2_{year} = 1.02$, $p = 0.60$). In 1996, we captured a relatively large number of young male sea otters from a male group observed at Knight Island. However, this male group was not present at Knight Island during later years and primarily older males, presumably holding territories, were captured in both areas at all other times.

In April 1999, we visually re-sighted 14 marked otters at Knight Island and 26 at Montague Island (Table 3), and, in July, we observed 9 marked otters at Knight Island and 19 marked otters at Montague Island. Average retention rate estimates of marked otters from visual recaptures were 3 times higher at Montague Island (1.86) than at Knight Island (0.59), with broad, but non-overlapping confidence intervals (Table 3). No otter tagged at one of our study areas was recaptured or re-sighted at the other study area, but movements of otters within areas could affect retention estimates.

Several generalities relative to movements of sea otters are required to provide a framework for evaluating the sex and age differences that we observed among sea otters in our study areas. Adult sea otter home ranges are relatively small and stable, commonly including a few to 10s of km of coastline (Jameson 1989, Ralls et al. 1996). Generally, male sea otters exhibit greater movements than females, and juveniles exhibit greater movements than adults and are more likely to disperse from natal areas (Riedman & Estes 1990, Ralls et al. 1996). If population recovery resulted from reproductive recruitment from within the affected population, the sex ratio in the recovering

population should favor females, because young males exhibit greater movements and are more likely to be excluded from reproductive areas by territorial males. Alternatively, if recovery resulted from immigration, the sex ratio in the recovering population should favor males, for the same reasons. At Knight Island, we observed consistently higher proportions of male sea otters in our annual samples, compared to Montague Island, particularly in 1996 when the sex ratio was 1:1 (Table 2). The 1996 sex ratio resulted in part from a group of 26 young males (sex assumed based on 12 captures) found near Knight Island (southeast of Eleanor Island; Fig. 2). Because male groups are commonly associated with the initial recolonization of habitat (Riedman & Estes 1990), this finding is consistent with an immigration pathway of recovery. However, this male group was not observed in subsequent ground, skiff, or aerial surveys of northern Knight Island, through 2000. The higher proportion of young animals of both sexes that we captured at Knight Island, compared to Montague Island, remains consistent with recovery through either reproductive recruitment within the area or immigration of young otters of both sexes from outside the study area.

Our aerial survey data describe a population increasing in abundance throughout much of the spill-affected areas of WPWS, although no increase is evident in the northern Knight Island area, where oil was persistent and mortality had been high (Bodkin & Udevitz 1994, Dean et al. 2000). The high proportion of pups, the large proportion of young females, and the presence of a large group of young males at Knight Island suggest potential population growth could result from both intrinsic reproduction and immigration. However, the lack of population growth observed at northern Knight Island suggests that losses (due to high mortality, emigration or both) were equivalent to the birth plus immigration rate at Knight Island, thus constraining population recovery. The difference in retention rates estimated from the re-sighting of marked individuals from our study areas is consistent with this conclusion.

Mortality and population trend

Between 1976 and 1985, and 1989 and 1998, beach-cast sea otter carcasses were systematically collected from the shores of WPWS each spring (Monson et al. 2000b). Ages of individuals dying each year were estimated from teeth collected. Collections prior to the spill, during the spill in 1989, and after the spill provide an annual description of the age distribution of dying otters. Monson et al. (2000b) used time-varying population models in combination with maximum-likeli-

hood methods to evaluate hypotheses about changes in sea otter survival rates in the years following the spill that would result in the observed age distributions after the spill. The model best fitting the data indicates sea otter survival after the spill was generally lower than before the spill (Fig. 6A,B) and survival declined rather than increased after the spill, particularly for older otters. Furthermore, the data indicate that otters born after the spill also exhibited reduced survival. The effects of the spill on survival and population abundance appear to be moderated largely by time as those otters affected by the spill eventually die (Fig. 6B,C). The divergent population trends at heavily oiled Knight Island, compared to the larger WPWS (Fig. 6C) suggest that effects of the spill on survival reported by Monson et al. (2000b) may persist longest where initial oil impacts were greatest.

Predation-related mortality is likely to contribute to the observed population patterns at our 2 study areas, although the specific predators and magnitude of the effect is largely unknown. At least some losses can be attributed to killer whales and subsistence harvest. There were 9 reported cases of killer whale *Orcinus orca* predation on sea otters between 1992 and 1996. Of these, 3 were at Knight Island, including 2 in our northern Knight Island study area (Hatfield et al. 1998). Another possible attack by a killer whale was reported from Montague Island in 1998 (C. Gorbics & J. DeGroot pers. comm.). One human subsistence harvest of a sea otter was reported from our Knight Island study area in 1995, although an additional 25 sea otters were reported as harvested elsewhere at Knight Island and 11 were reported from Naked Island (NE of Knight Island) between 1992 and 1998 (US Fish and Wildlife Service, Anchorage, AK, unpubl. data). During this same period, 11 sea otters were reported as subsistence harvested from Montague Island.

Killer whales have been proposed as agents of decline in Aleutian Islands sea otter populations during the 1990s (Estes et al. 1998). Given the increase in sea otter abundance in WPWS and at Montague Island since 1993, any effect of predation must be localized to the northern Knight Island area, which is inconsistent with the nature of widespread declines attributed to killer whale predation in the Aleutian Islands. In addition, predation events should not result in beach-cast carcasses. The estimates of increased mortality are based on beach-cast carcasses (Monson et al. 2000b), suggesting that predation would be additive to estimates of decreased survival, rather than explaining it. However, any predation occurring in the northern Knight Island area may be expected to have a comparatively large effect because of the relatively small sea otter population

existing there. For example, given the population size of 77 at northern Knight Island, an annual loss of 3 additional otters would offset the expected growth increment of 0.04, the growth rate observed elsewhere in WPWS since 1993. In contrast, an increase

in annual mortality of 3 otters at Montague Island would result in only a slight reduction in annual population growth from 52 to 49 otters per year, assuming a similar growth rate of 0.04, and a population size of 586.

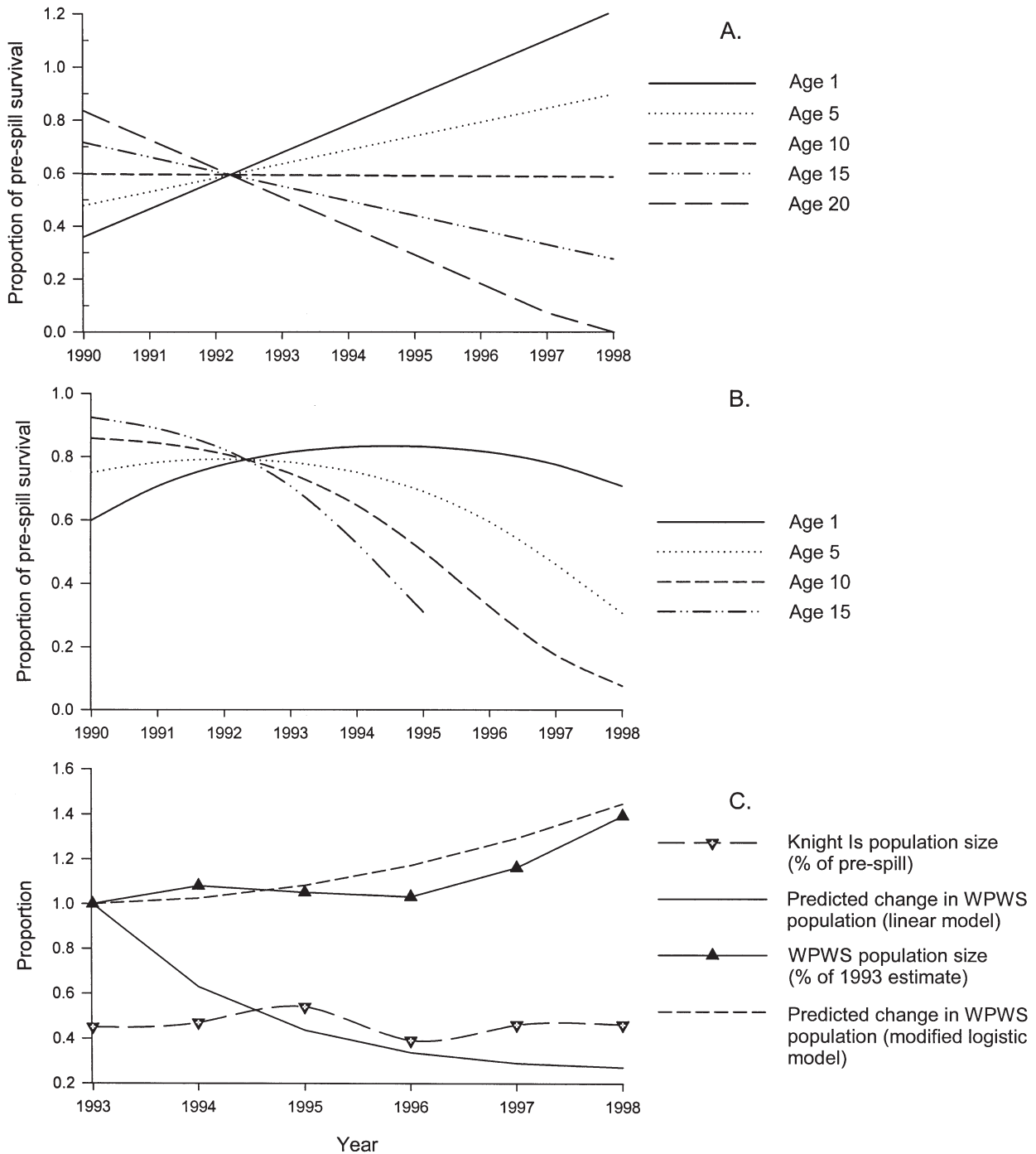


Fig. 6. *Enhydra lutris*. Estimated post-spill effects on age-specific survival rates (linear model; A) and for cohorts of a given age (B) expressed as a proportion of pre-spill survival, and predicted vs observed population trends (C) in western Prince William Sound (from Monson et al. 2000b)

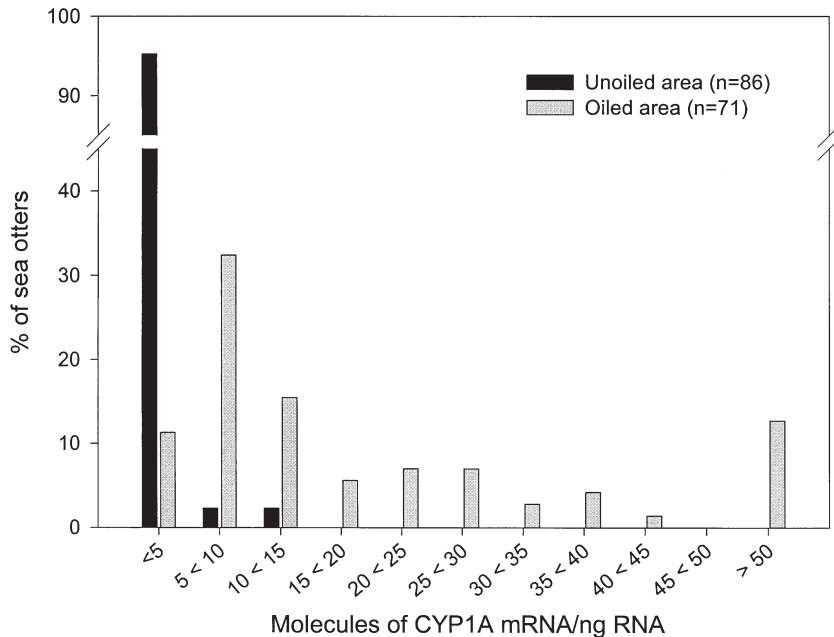


Fig. 7. *Enhydra lutris*. Distribution of Cytochrome P4501A (CYP1A) mRNA values in peripheral blood mononuclear cells collected from sea otters in oiled and unoiled areas of western Prince William Sound (from Ballachey et al. 2000)

CONTINUED EXPOSURE TO OIL

It is possible that residual effects of spilled oil could be limiting recovery of sea otter populations. Exposure to oil following the spill in 1989 resulted in organ damage among lethally exposed animals (Lipscomb et al. 1993, 1994). Presumably, sub-lethal exposure also causes similar pathologies among surviving otters, eventually contributing to long-term reduced survival rates such as reported by Monson et al. (2000b). Additionally, residual oil sequestered in near-shore habitats may become available through disturbances such as storms and excavation by foraging animals such as sea otters. From 1996 to 1998, 157 of the 180 sea otters captured were tested for exposure to oil, hematology, serum chemistries and body condition (Ballachey et al. 2000). Cytochrome P450 1A (CYP1A) is a protein involved in the metabolism of aromatic hydrocarbons.

Using a reverse transcriptase polymerase chain reaction (RT-PCR) to quantify mRNA for CYP1A production (Vanden Heuvel et al. 1993), Ballachey et al. (2000) measured mRNA for CYP1A in peripheral blood mononuclear cells, and found significantly higher levels in sea otters at Knight Island compared to Montague Island (Fig. 7). Mean CYP1A values at Knight were 27.3×10^6 vs 1.5×10^6 at unoiled Montague. Ballachey et al. (2000) also report higher CYP1A findings at Knight Island for other species that are residents of nearshore communities, including the harlequin duck, pigeon guillemot, Barrow's goldeneye *Bucephala islandica*, and the masked greenling *Hexagrammos octogrammus*. One common feature of these species is a strong behavioral or trophic link to the nearshore marine habitats that were repositories for residual oil. Ballachey et al. (2000) found greater differences in CYP1A levels between oiled and unoiled areas in consumers of near-

shore invertebrates (i.e. sea otters and sea ducks), as compared to consumers of fish (i.e. river otters and pigeon guillemots). Because invertebrates do not metabolize hydrocarbons as vertebrates do (Vandermeulen & Penrose 1978), they are capable of accumulating hydrocarbon burdens (Roesijadi et al. 1978, Pruell et al. 1986, Short & Harris 1996).

Many of the nearshore invertebrates that sea otters prey on (e.g. clams and mussels) occur in habitats that serve as repositories for residual oil, and they accumulate hydrocarbons in their tissues. Because sea otters consume invertebrates that sequester hydrocarbons and they excavate large volumes of sediments to recover prey (Hines & Loughlin 1980, Kvittek & Oliver 1988), they are potentially exposed to residual oil through 2 pathways (i.e. in sediments and in prey). Although the levels of exposure that lead to the differences in CYP1A among areas reported by Ballachey et

Table 4. *Enhydra lutris*. Summary of energy availability, energy consumption, foraging time and young female condition at Knight and Montague Islands (95% confidence interval) (from Dean et al. 2000a). n.s. = not significant

Metric	Knight Is.	Montague Is.	Significance at 0.05
Energy area ⁻¹ (kJ m ⁻¹)	74.2 (±91.6)	149.3 (±144.0)	n.s.
Energy otter ⁻¹	4.8×10^6 (± 6.0×10^6)	1.1×10^6 (± 1.2×10^6)	n.s.
Prey consumption (kJ h ⁻¹)	2260 (± 280)	1900 (±270)	Significant
Foraging (h d ⁻¹) foraging	9.9 ± (1.2)	11.8 (±1.5)	Significant
Wt/total length (g cm ⁻¹)	170	160	Significant

al. (2000) are unknown, the elevated CYP1A levels occurred in the same regions where reduced survival was observed among sea otters (Monson et al. 2000b) and harlequin ducks (Esler et al. 2002) and where sea otter populations have not increased (Figs. 3 & 4). In addition to CYP1A, significantly higher levels of the serum enzyme GGT, associated with liver disease or injury, were found in sea otters from Knight Island from 1996 to 1998 compared to Montague Island (Ballachey et al. 2000). Elevated GGT levels are consistent with the liver pathologies observed during the spill (Lipscomb et al. 1993, 1994) and with observations of captive mink *Mustela vison* exposed to oil (Mazet et al. 2000). However, high variation in CYP1A and GGT levels led Ballachey et al. (2000) to speculate that residual oil sufficient to cause toxicity is patchily distributed. The GGT values from oiled and unoled areas converged between 1992 and 1998, likely reflecting mortality among individuals with chronic organ damage and their removal from the population being sampled. Their conclusion is consistent with the independent results of Monson et al. (2000b) indicating the convergence of survival estimates to pre-spill values largely as a result of mortality within spill-affected cohorts.

FOOD LIMITATION

Sea otter population size at equilibrium density is generally considered to be limited by available food resources. Sea otter prey populations were reduced directly by oiling and shoreline treatments, including physical modifications to habitats through the removal of fine sediments that persisted for years (Lees et al. 1996). The initial perturbation caused by the spill and subsequent clean-up efforts resulted in cascading effects through shoreline habitats (Peterson 2001). Both direct spill-related reductions in prey and cascading community effects would likely delay recovery of affected sea otter populations through limiting food availability. Further evidence suggests that some biological components of the nearshore community, including some important sea otter prey, had not fully recovered several years after the spill (Jewett et al. 1999, Fukuyama et al. 2000, Dean & Jewett 2001, Peterson 2001), leading Dean et al. (2002) to evaluate in a comprehensive fashion the potential role of food limitation in constraining sea otter recovery at Knight Island. Because of difficulty in directly measuring the diverse array of sea otter prey, uncertainty in energy content and the cost to sea otters in recovering different prey, both direct (energy/area and energy/otter) and indirect (foraging efficiency and body condition) measures of food availability were made at northern

Knight Island and at the Montague site (Fig. 2). Dean et al. (2002) found prey availability to be variable, relatively low, but approximately equivalent between areas, while foraging efficiency and young female sea otter condition were significantly greater at Knight Island (Table 4). Dean et al. (2000) also found increasing densities and sizes of sea urchins at Knight Island between 1996 and 1998, where sea otter densities had been reduced since 1989. These findings are consistent with at least a partial relaxation of the predation pressures sea otters are known to exert on their preferred prey (Estes & Palmisano 1974, Estes & Duggins 1995), and suggestive of prey resources sufficient to support some level of sea otter population growth at Knight Island. Although all prey did not demonstrate consistent responses to reduced sea otter densities, preferred clam species, *Protothaca staminea* and *Saxidomus gigantea*, were larger in size at Knight Island (VanBlaricom et al. 2001). During the course of this study, we found significant increases in sea otter abundance at Montague Island that apparently were supported by prey availability that was approximately equivalent to prey availability at Knight Island. Therefore, we concur with the conclusion of Dean et al. (2002) that prey populations at Knight Island were capable of supporting a growth rate approximately equal to that observed at Montague Island, and that food limitation may be acting to constrain growth only above those rates observed at Montague Island.

While we do not have strong evidence to suggest that food availability is limiting recovery at Knight Island, it is possible there are important interactions between food availability, chronic exposure to oil contamination, and sources of sea otter mortality that contribute to the lack of recovery we have observed (Fig. 4). Annual population growth rates in PWS averaged about 0.10 throughout much of the 20th century, a level well below the 0.21 observed in some other recovering sea otter populations (Bodkin et al. 1999). Causes for differences in growth rates among recovering populations are unclear but may be explained, at least in part, by potential differences in food availability as well as human sources of mortality (Bodkin et al. 1999). In the decade following the spill in PWS, the surviving sea otter population at Knight Island encountered food resources that were negatively influenced by spill effects, i.e. population reductions and persistent oil (Jewett et al. 1999, Fukuyama et al. 2000, Dean & Jewett 2001, Peterson 2001). During this same period some prey populations were experiencing the positive effects of reduced sea otter densities (i.e. increasing densities and mean sizes) (Dean et al. 2000, 2002). However, residual oil in their food and environment may lead to additional metabolic costs and reduced foraging efficiency for sea otters (Davis et al. 1988,

Ben-David et al. 2000), potentially offsetting benefits gained through increasing prey densities or sizes. Our results support the hypothesis that long-term spill effects may be dominating the process of sea otter recovery, and despite equal or higher levels of prey, otters at Knight Island may be more susceptible to other stresses (e.g. environmental conditions) than otters that do not encounter similar contamination. This interaction may contribute to the elevated levels of mortality observed after the spill (Monson et al. 2000b).

CONCLUSION

Sea otter populations declined precipitously following the TV 'Exxon Valdez' oil spill of 1989. While populations are recovering throughout much of WPWS, in the area most heavily impacted by the spill, we found no evidence of population growth through 2000, and recovery remains incomplete. Accumulating data from sediments and across a broad suite of taxa (including sea otters) that occupy and utilize nearshore habitats indicate that residual oil persists and has been transferred through the nearshore food web for up to a decade after the spill. Elevated mortality in, and emigration from, the oiled area appear to be contributing to the lack of population growth. It appears likely that continued exposure to residual oil or persistent sub-lethal effects are linked to mortality and emigration. However, our study design precludes assigning cause to effect. While spill-related reductions in prey populations may be limiting growth below maximum, estimated prey availability at Knight Island should be capable of supporting some level of growth, as indicated by population growth at Montague Island, where prey resources are comparable, and elsewhere in WPWS. Based on our findings from Knight Island, recovery of the WPWS sea otter population apparently resulted from intrinsic reproduction and immigration of juveniles as opposed to broad-scale redistribution of adults. The limited reproductive potential of sea otters, coupled with apparent chronic spill related effects on survival, has resulted in a protracted period of recovery, particularly where oiling was extensive and persistent and mortality was greatest.

CONSERVATION AND MANAGEMENT IMPLICATIONS

Our view of sea otters during this century has been one of widespread recovery of both remnant and reintroduced populations. This view has provided unique opportunities to study the community-level consequences of a 'keystone' predator recolonizing habitat

after long (decades to a century) periods of absence, during which time the community changed dramatically, generally including large increases in sea otter prey populations (Estes & Palmisano 1974, Estes & Duggins 1995). Our understanding of sea otter population dynamics and influences on community ecology has been strongly influenced by this situation of recovering populations with largely unexploited prey resources to support growth rates that reached their theoretical maximum (Estes 1990, Bodkin et al. 1999, 2000). As sea otters increased their range and abundance, we are afforded a very different view, one where populations may achieve a dynamic equilibrium (long-term growth $\cong 1.00$) with their prey resources and exist in a state that may be more representative of their pre-exploitation status in nearshore marine communities. However, as sea otter populations return to their pre-exploitation status, they face increasing threats that may result in population reductions. The 1989 oil spill in PWS provides an opportunity to address new issues relating to recovery processes following large declines in sea otter abundance, but where community structure and prey populations do not have the long periods of relaxed predation that were characteristic of earlier periods of sea otter recovery. It may be unrealistic to expect growth rates to approach the theoretical maximum in cases where prey populations experience only a partial relaxation of the effects of sea otter predation. Further, it is necessary to consider how recovery may be constrained by effects other than simply the reduction in abundance. In the case of oil spills, the potential biological consequences of sub-lethal initial oil exposure, exposure to residual oil over a longer period, and effects of prey reductions are demonstrated in a recovery period extending more than a decade following the TV 'Exxon Valdez' spill. The potential role of predation (both human and other) in constraining recovery of depleted populations also warrants consideration. Additional knowledge of relations between sea otter social organization and behavior and depleted populations may be important in understanding processes regulating population recovery.

Our results identify several issues relevant to the conservation and recovery of species reduced or depleted by similar catastrophic events. First, how large is the pool of survivors that will contribute to recovery within the depleted area, and how will intrinsic growth and immigration contribute? Second, is there potential for residual effects of the event on critical life history attributes such as fecundity and survival, and will residual effects influence emigration and immigration? Third, are there direct or indirect effects of the event on critical resources required for recovery, such as food? And finally, are there sources of mortality that

can be reduced to facilitate recovery? Answers to these questions will benefit from a thorough knowledge of the natural history of the species and ecosystem in question.

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