

THEME SECTION

Nearshore vertebrate predators: constraints to recovery from oil pollution

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Chronic impacts of oil pollution in the sea: risks to vertebrate predators

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Following the 1989 'Exxon Valdez' oil spill in Alaska, several studies of the biological consequences were conducted (e.g. Wells et al. 1995, Rice et al. 1996), targeting especially the vertebrates, whose high diversity, abundance, and importance helps distinguish the coastal ecosystem of the northern Gulf of Alaska. Virtually unique among field programs studying impacts of oil spills has been the availability of support for years after the 'Exxon Valdez' spill for assessment of some of the potential processes of long-term impacts of oil in the marine environment. This Theme Section synthesizes results of the Nearshore Vertebrate Predator project, which was initiated in 1995 to test several hypotheses to explain delays in recovery of some sentinel vertebrates in the coastal ecosystem. The project involved 4 species: 2 marine mammals and 2 marine birds, each of which had demonstrated acute impacts of the spill at the population level and also showed some evidence of delayed recovery (Rice et al. 1996). One bird (harlequin duck: *Histrionicus histrionicus*) and one mammal (sea otter: *Enhydra lutris*) feed largely on benthic invertebrates, plus another bird (pigeon guillemot: *Cephus columba*) and mammal (river otter: *Lontra canadensis*) consume a diet dominated by fish. Parallel studies of each species were conducted to examine: (1) the status of population

recovery 6 to 9 yr after the oil spill; (2) whether food availability constrained the recovery; (3) whether ongoing exposure to oil toxicity delayed recovery; and (4) whether demographic limitations intrinsic to the species and unrelated to food availability or chronic oil toxicity limited the rate of recovery.

The role of acute mortality to marine organisms from exposure to petroleum hydrocarbons can be inferred from well-designed observational sampling over short time intervals. Consequently, a substantial body of information on acute risk has been gathered in nature following oil spills and in the laboratory using protocols of acute toxicity testing (e.g. National Research Council [NRC] 1985). The role of longer-term mortality from oil exposure has proved a much more elusive research target for marine ecologists despite a long-standing recognition of its potential significance (Gray 1982, National Research Council [NRC] 1985, Boesch & Rabalais 1987). Such research is more costly to conduct because it involves time frames of years instead of days and requires simultaneous evaluation of multiple mechanisms of potential impact to biological systems. Unlike acute mortality, which mostly occurs as an immediate narcosis reaction to toxicity (Rice et al. 2001) or some other direct process like physical smothering of rocky-shore invertebrates, long-term consequences of exposure of marine ecosystems to petroleum hydrocarbons can occur via several direct and

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indirect processes mediated through the ecosystem and can be induced at lower pollutant concentrations (National Research Council [NRC] 2002). Among the most important of these potential mechanisms of long-term impacts of petroleum hydrocarbons (Peterson 2001) are: (1) delayed impacts due to impaired survival or reproduction from compromised health or suppressed growth after initially sublethal exposures; (2) impacts that cascade through the population via losses of key individuals important to critical social organization functions; (3) impacts of chronic persistence of toxic components of oil, biological exposures, and resultant population-level responses; and (4) delayed impacts of habitat degradation, prey decline, trophic cascades, and other indirect effects of ecosystem perturbation.

The Theme Section comprises 4 synthesis papers that describe the results of 5 years of research from 1995 to 1999 to follow recovery and test the multiple hypotheses that may help explain any documented delay in the recovery process. The only species for which no synthesis paper is included is the river otter (published elsewhere), which failed to exhibit compelling evidence of long-term impacts or substantially delayed recovery. By contrasting the responses of the 4 consumers, 2 of which feed on benthic invertebrate prey in shallow waters and 2 of which feed largely on fishes, the Nearshore Vertebrate Predator project produced important insight into the risk of long-term impacts of petroleum hydrocarbons to apex vertebrate consumers. When compared with piscivores, vertebrate consumers of benthic invertebrate prey possess a relatively high risk of chronic exposure to residual oil in bottom sediments, physiological responses to that exposure, and elevated mortality for periods of years after an oil spill (Peterson 2001). The inclusion of understanding of how chronic exposure to multi-ringed PAHs sequestered in low concentrations in ground waters of anadromous fish streams induced elevated mortalities of developing pink salmon embryos (Rice et al. 2001) helps reveal the general significance of studies of the 'Exxon Valdez' oil spill to

enhancing appreciation of long-term, chronic, and delayed impacts of oil pollution in the marine environment. Chronic and indirect effects of exposure to petroleum hydrocarbons at low concentrations cannot be ignored in assessments of spill impacts (Wikelski et al. 2002) and in management of chronic sources such as storm water runoff from developed lands into rivers and estuaries (Rice et al. 2001, National Research Council [NRC] 2002). Risk assessment models based solely on acute toxicity underestimate impacts of oil pollution by overlooking the effects of chronic exposures, delayed impacts, and indirect effects driven by ecosystem processes (Kimball & Levin 1985).

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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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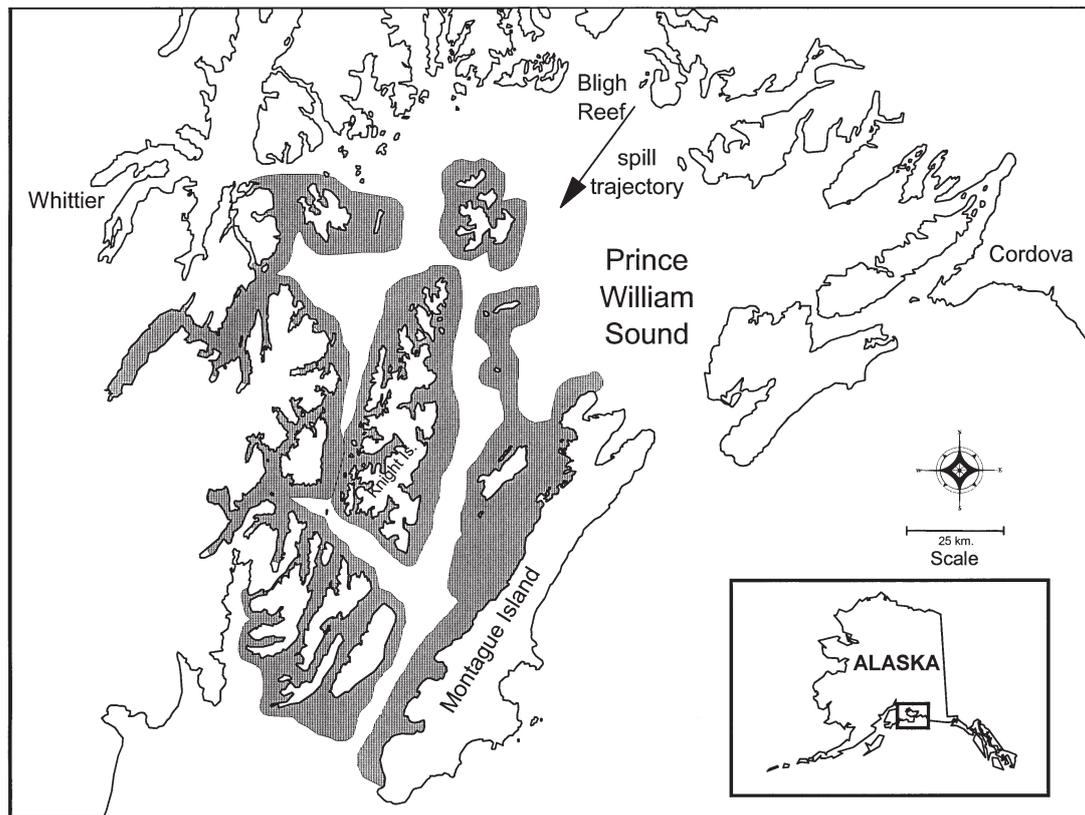


Fig. 1. Western Prince William Sound sea otter survey area (shaded)

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

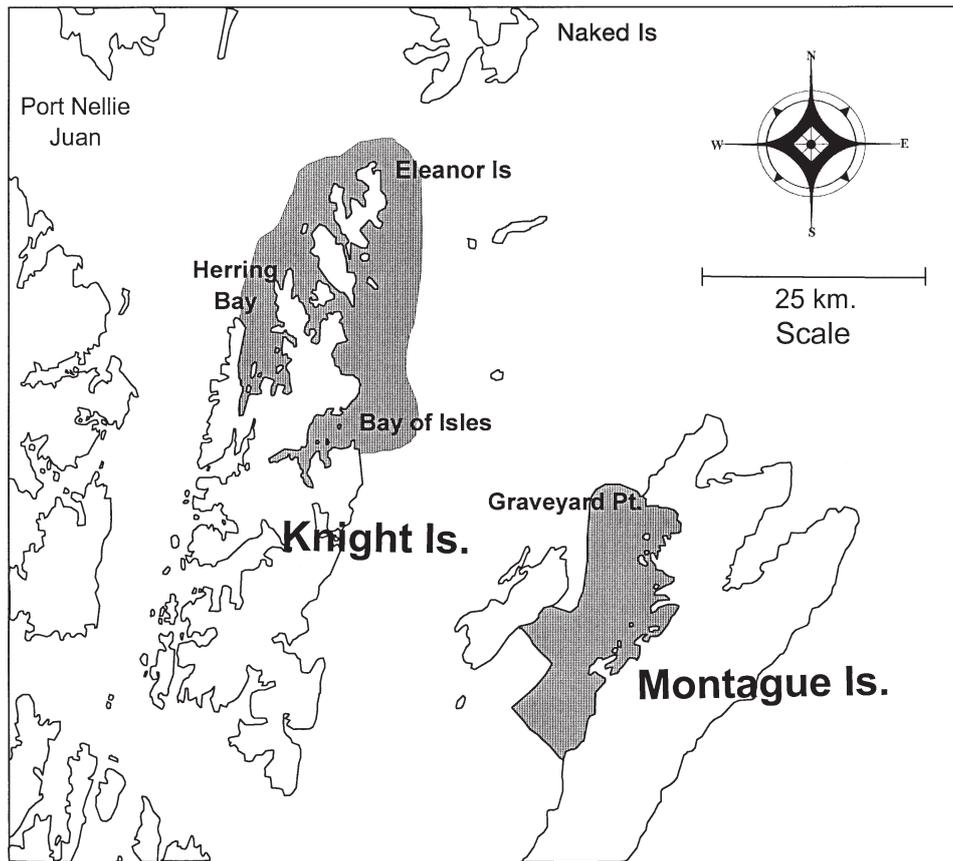


Fig. 2. Intensive sea otter study areas for surveys (shaded), capture, food habits, and prey measures at northern Knight Island (oil-affected) and Montague Island (unoiiled)

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

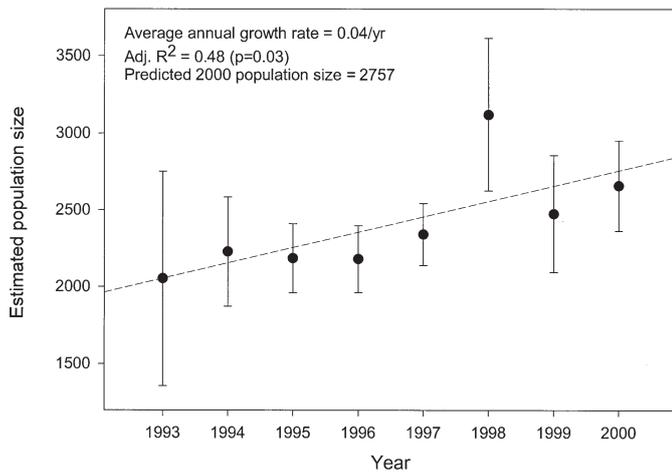


Fig. 3. *Enhydra lutris*. Estimates of abundance (\pm SE) in western Prince William Sound, 1993 to 2000

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.

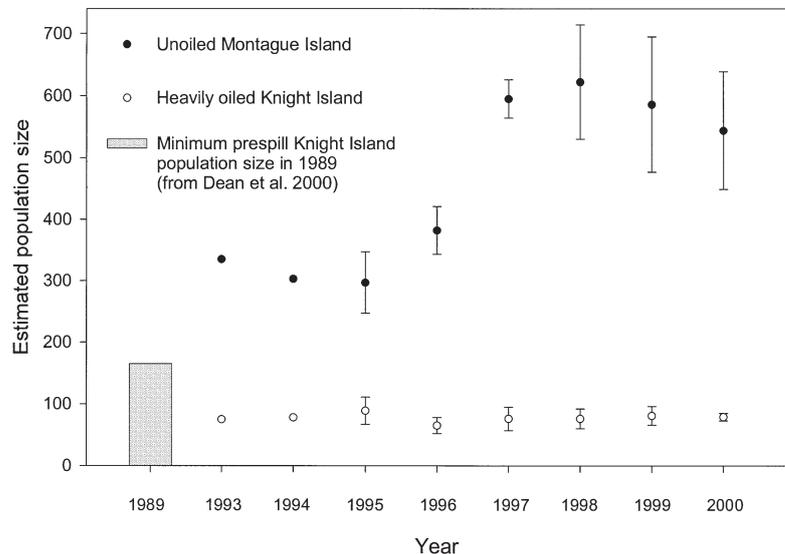


Fig. 4. *Enhydra lutris*. Estimates of abundance (\pm SE) at northern Knight and Montague Island intensive study areas, 1993 to 2000 (no estimates of precision acquired in 1993 to 1994). 1989 pre-spill estimate based on actual and estimated carcasses recovered from the study area and assuming no survivors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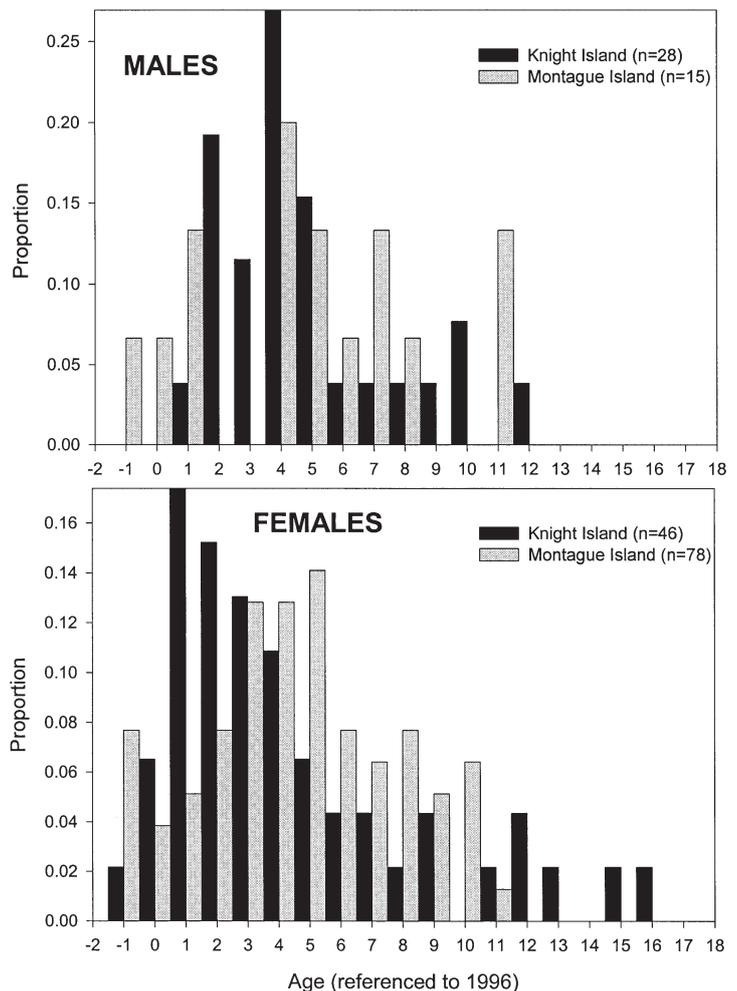


Fig. 5. *Enhydra lutris*. Age distribution of sea otters captured at intensive study areas at northern Knight and Montague Islands, 1996 to 1998

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.

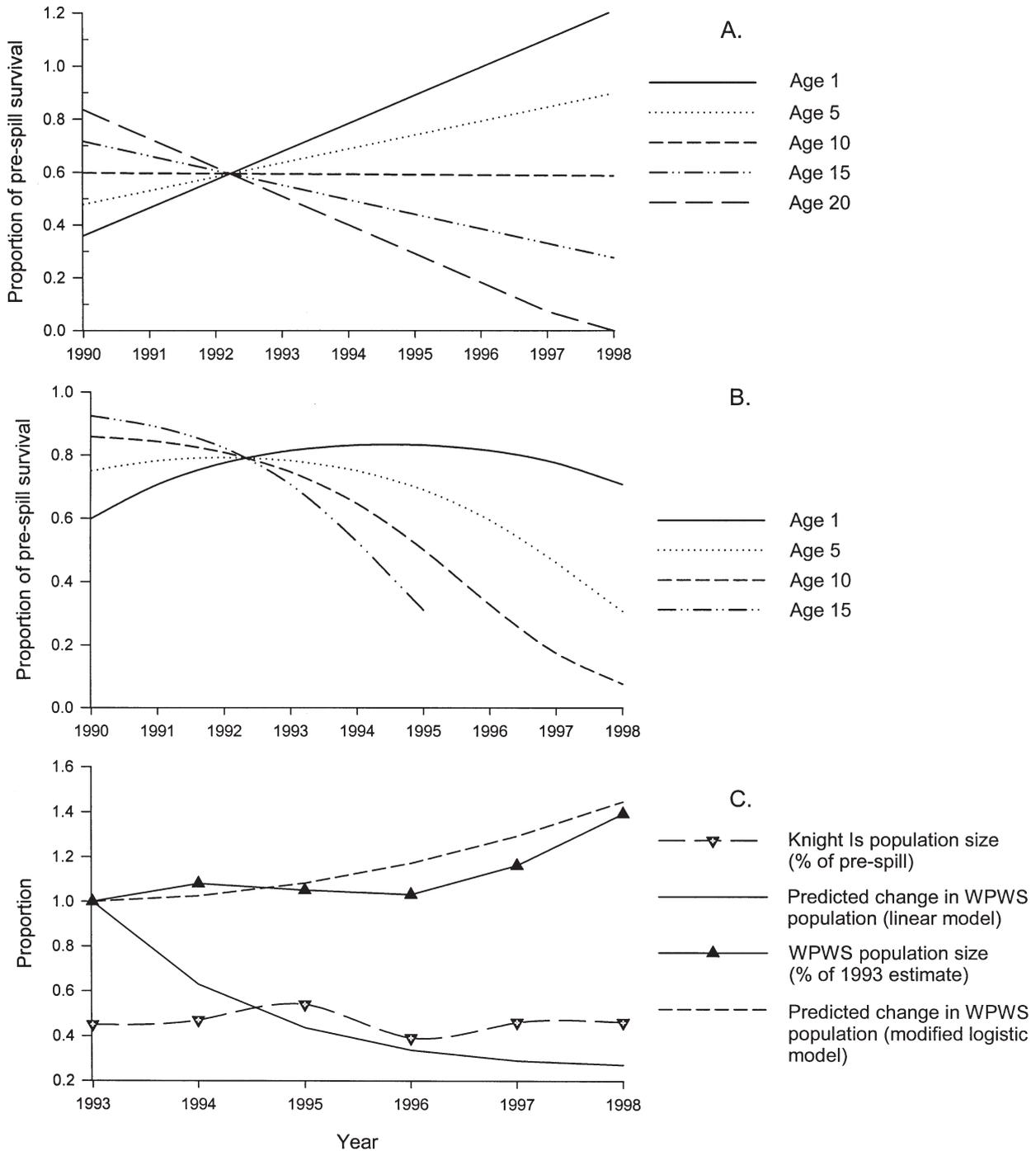


Fig. 6. *Enhydra lutris*. Estimated post-spill effects on age-specific survival rates (linear model; A) and for cohorts of a given age (B) expressed as a proportion of pre-spill survival, and predicted vs observed population trends (C) in western Prince William Sound (from Monson et al. 2000b)

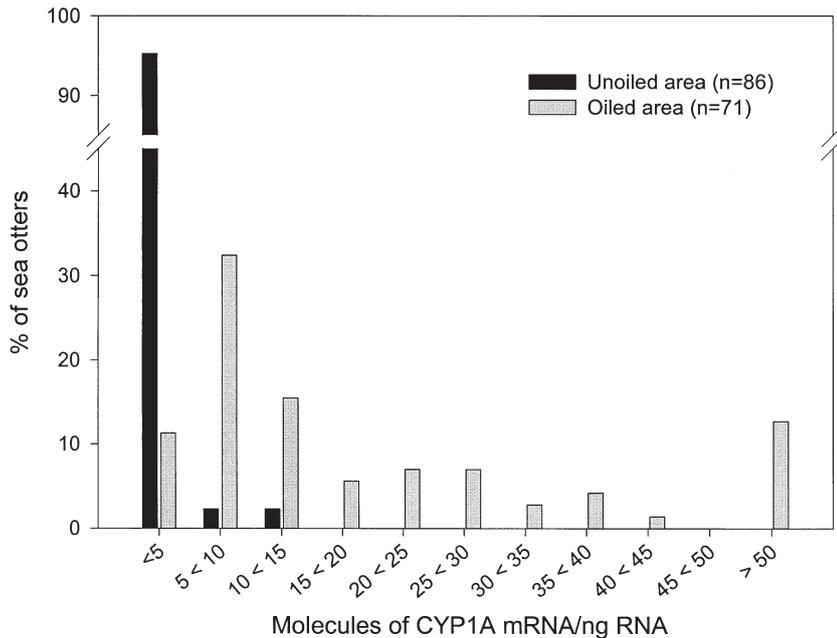


Fig. 7. *Enhydra lutris*. Distribution of Cytochrome P4501A (CYP1A) mRNA values in peripheral blood mononuclear cells collected from sea otters in oiled and unoiled areas of western Prince William Sound (from Ballachey et al. 2000)

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.

Acknowledgements. We thank D. Bohn, D. Bruden, S. Carter, J. DeGroot, D. Douglas, A. Doroff, G. Esslinger, C. Gorbics, S. Haverlack, L. Holland-Bartels, K. Kloecker, P. Kearney, P. Snyder, B. Spies, C. Sterne, L. Thomas, M. Udevitz, and M. Whalen for their contributions to this work. This paper was improved through the thoughtful review of J. A. Estes, E. Knudsen, C. H. Peterson and an anonymous reviewer. Research was supported by the Exxon Valdez Oil Spill Trustee Council and the US Geological Survey.

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Editorial responsibility: Charles Peterson, Morehead City, North Carolina, USA

*Submitted: January 2, 2001; Accepted: April 26, 2002
Proofs received from author(s): August 19, 2002*

Food limitation and the recovery of sea otters following the 'Exxon Valdez' oil spill

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ABSTRACT: We examined the potential role of food limitation in constraining the recovery of sea otters *Enhydra lutris* in Prince William Sound, Alaska, following the 'Exxon Valdez' oil spill. The spill resulted in the removal of a large number of sea otters in 1989, and as of 1998, the portion of the population in the heavily oiled northern Knight Island region had not fully recovered. Between 1996 and 1998, prey consumption rate was higher and the condition of sea otters was better at northern Knight Island than in an unoiled area of the sound (Montague Island). Estimates of prey energy available per unit mass of sea otter were about 4 times higher at Knight than Montague Island, albeit not significantly different between the 2 areas. Over this same period, the number of sea otters remained constant at northern Knight Island but increased at Montague Island. These data suggest that food was at least as abundant at Knight than at Montague Island, and that recovery of sea otters via intrinsic population growth was limited by factors other than food. However, the availability of food, the prey consumption rate, and the condition of sea otters were all much lower at both Knight and Montague Islands than in areas newly occupied by sea otters where the population growth rate was near the theoretical maximum. It is possible that the relatively short supply of food (compared to areas where sea otter population growth rate was high) may have inhibited immigration or interacted with other factors (e.g. oil-induced mortality or predation) to restrict sea otter population growth. Nonetheless, these data suggest that impacts of anthropogenic disturbances on large, often food-limited vertebrate predators can persist in spite of the availability of food resources that are sufficient for intrinsic population growth.

KEY WORDS: Prince William Sound · Alaska · Predator-prey interaction · Prey availability · Prey consumption rate · Condition indices

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INTRODUCTION

The 'Exxon Valdez' ran aground in Prince William Sound (PWS), Alaska, in March 1989, and the estimated 42 million liters of crude oil that were spilled from the tanker had severe adverse impacts on the

nearshore ecosystem (Paine et al. 1996, Spies et al. 1996, Peterson 2001). One effect of the spill was the removal (either via death or for the purposes of rehabilitation and permanent placement in captivity) of a significant proportion of the sea-otter *Enhydra lutris* population in heavily oiled parts of PWS (Garrott et al. 1993, Bodkin & Udevitz 1994, Garshelis 1997, Dean et al. 2000). An estimated 165 sea otters were removed from the heavily oiled area of the western sound

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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. L. Bodkin & D. H. Monson unpubl. data). As of 1998, the sea otter population in this area had not fully recovered (Dean et al. 2000, Bodkin et al. 2002, this issue). From 1993 to 1998, yearly aerial surveys at northern Knight Island found fewer than 90 sea otters, and there was no significant increase in sea otter density over this period. In 1997 and 1998, there were an estimated 76 sea otters, far fewer than the 237 sea otters found in a pre-spill census of the area in 1973, and fewer than half the number of sea otters removed in 1989 following the spill. In contrast, along Montague Island, an area within PWS unaffected by the spill, sea otter density increased between 1993 and 1998, and was 27% higher in 1998 than in 1973.

Models using age-distribution of carcasses collected from beaches indicate that survival of sea otters in oiled areas was lower after the spill than before (Monson et al. 2000a). However, the causes for poorer survival and lack of recovery of sea otters in the northern Knight Island region have not been identified. Determining these causes is important in managing and conserving sea otter populations, evaluating the overall health of the nearshore system during recovery following the oil spill, and predicting patterns and rates of recovery following environmental perturbations of similar scope and type (Bodkin et al. 2002). We hypothesize that the lack of recovery was the result of: (1) a slow rate of increase in sea otter populations, even in the absence of chronic effects of the spill, (2) continued exposure to oil and concomitant effects on survival, immigration, or emigration rates, or (3) a lack of food (resulting from reductions in prey abundance caused by the spill or from natural causes). In this paper, we examine the evidence regarding the food limitation hypothesis by comparing the prey availability, prey consumption rate, and condition of sea otters in an oiled vs unoiled area in PWS.

The diet of sea otters in PWS consists mostly of clams, primarily *Saxidomus gigantea*, *Protothaca staminea*, *Humilaria kennerleyi*, *Macoma* spp., and *Mya* spp. (Calkins 1978, Estes et al. 1981, Garshelis et al. 1986, Doroff & Bodkin 1994). Crabs, primarily *Telmessus cheiragonus*, and mussels *Mytilus trossulus* are taken somewhat less frequently, although mussels may be an important food resource for juvenile sea otters (VanBlaricom 1988). Occasional prey in PWS include echinurid and polychaete worms, sea urchins, and sea stars. Densities of some sea-otter prey were reduced at sites adjacent to heavily oiled beaches in PWS following the oil spill in 1989. These included *M. trossulus* (Gilfillan et al. 1995, Highsmith et al. 1996, Houghton et al. 1996), *P. staminea* (Driskell et al. 1996, Trow-

bridge et al. 1998, Fukuyama et al. 2000), and *T. cheiragonus* (Dean et al. 1996). The recovery status of these populations has not been fully evaluated. There is some evidence that communities in the rocky intertidal and rocky subtidal habitats had recovered by 1992 or 1993, 3 to 4 yr after the spill (Coats et al. 1999, Dean & Jewett 2001). However, for *P. staminea*, mortality rates were higher and growth was slower in oiled areas through 1996 (Fukuyama et al. 2000) and adverse impacts of the oil spill to some species of infauna in subtidal, soft-sediment eelgrass habitats persisted through 1995, and perhaps longer (Jewett et al. 1999, Dean & Jewett 2001).

In the 2 decades prior to the oil spill, sea otter densities in our oiled (northern Knight Island) and reference (Montague Island) study areas were relatively stable (reviewed in Bodkin et al. 2000) and further population growth was considered to be limited by food (Garshelis et al. 1986, VanBlaricom 1988). This was based on observations of a relative reduction in several key food items (crabs and mussels) coincident with sea otter expansion and on sea otter feeding observations (Estes et al. 1981, Garshelis et al. 1986). In the early 1980s, sea otters from (or near) our study areas spent approximately twice as long foraging than otters in parts of PWS where the population had only recently expanded (Estes et al. 1981, Garshelis et al. 1986). The fact that the pre-spill population of sea otters was apparently food-limited, coupled with evidence of reductions in sea-otter prey as a result of the spill, suggested that food may be limiting recovery of sea otters.

Over the course of our study (from 1996 through 1998) there was an increase in sea otter density in unoiled portions of western PWS, but no increase in the heavily oiled region around northern Knight Island (Dean et al. 2000). Therefore, demonstration of less food in the oiled area would suggest that food was limiting recovery there. On the other hand, equal or greater abundance of food at the oiled site would indicate that factors other than food were responsible. We relied on both direct and indirect measures of food availability because it is difficult to measure precisely the abundance of the diverse group of sea otter prey, and because prey abundance does not account for factors such as quality of food or the cost to the predator of acquiring its prey. In the absence of other factors that can influence prey abundance, a reduction in the density of food-limited mammalian predators generally leads to an increase in either quantity or quality of food available, and an increase in the condition of the remaining (especially younger) animals (Bobek 1977, Sinclair 1977, Skogland 1983, 1985, Bayliss 1985, Sinclair et al. 1985, Fryxell 1987, Freeland & Choquenot 1990, Choquenot 1991, Messier 1994). Therefore, in addition to prey abundance, we examined prey con-

sumption rate and condition of young sea otters as further indicators of food limitation. Prey consumption rate and condition of animals are often better indicators of food resources than direct measures of prey abundance, especially for large marine mammals (Eberhardt & Siniff 1977).

MATERIALS AND METHODS

Design. As is the case for most large motile predators, it is not practical to test experimentally the food limitation hypothesis (Estes 1996). Instead, we will rely on 3 separate lines of indirect evidence concerning: (1) the availability of food, in terms of both prey energy per unit area and prey energy per unit mass of sea otter, (2) the rate of consumption of food by sea otters, and (3) morphometric characteristics (age-adjusted mass and mass to length ratio) for sea otters that might be expected to be affected by the availability of food. Evaluation of these 3 relatively independent data sets (prey availability, prey consumption rate, and condition of sea otters) provides a more rigorous test of the food limitation hypothesis than evaluation based on any single line of evidence.

For all 3 factors, we compare a heavily oiled area in the vicinity of northern Knight Island with an unoiled area at Montague Island. The Montague site was relatively unaffected by the spill (ADEC 1989, ADNR 1991, Galt et al. 1991, Wolfe et al. 1994, O'Clair et al. 1996, Jewett et al. 1999) and there were no detectable impacts to sea otters (Ballachey et al. 1994) or nearshore benthic communities (Dean et al. 1996, Jewett et al. 1999). Based on the history of sea otter recolonization in PWS following their near extinction in the late 1900s, observations of sea-otter movements, and phenotypic and genotypic characteristics of individuals from throughout PWS, it is clear that sea otters at Knight and Montague Islands are subsets of a larger metapopulation (Gorbics & Bodkin 2001). However, mark-recapture studies indicated little if any movement of sea otters between our Knight and Montague study areas between 1996 and 1999 (Bodkin et al. 2002). Between 1996 and 1998, a total of 66 and 91 sea otters were tagged at northern Knight and Montague Island respectively, and a total of 47 tagged sea otters were observed between 1997 and 1999 in each area. None of the sea otters tagged at Knight Island were observed at Montague Island or vice versa. Population densities of sea otters were likely lower at northern Knight Island than at Montague Island at the time of the spill in 1989 (Dean et al. 2000), but sea otters in both areas were considered food-limited and at or near equilibrium prior to the spill (Estes et al. 1981, Garshe-lis et al. 1986, Bodkin et al. 2002).

For each metric (prey energy per unit area, prey energy per unit mass of sea otter, consumption rate of prey, age-adjusted mass, and mass to length ratio), we tested the hypothesis that there was no difference at northern Knight Island vs Montague Island against the alternative hypothesis that values for these metrics were greater at Knight Island. Equal or higher values at Knight Island would indicate that recovery of sea otters at Knight Island was limited by factors other than food.

When possible, we also compared post-spill values for each metric for the northern Knight and Montague Island with pre-spill PWS values, and with similar data for sea otter populations outside of PWS. Histories of sea otter colonization in these areas are known, and the status of the populations with respect to food limitation is generally acknowledged (Lensink 1962, Kenyon 1969, Estes et al. 1986, Garshelis et al. 1986, Kvitek et al. 1992).

We recognize that this is a pseudoreplicated design in that we primarily rely on comparisons between a single oiled area with a single unoiled reference area (Hurlbert 1984, Stewart-Oaten et al. 1986). Therefore, statistical inference can be made only to those 2 areas and not to other areas within PWS that were impacted by the spill, to spill-impacted areas outside of the sound, or to other oil spills. However, our northern Knight Island study area represents one of the most heavily oiled parts of the sound where sea otters were not recovering, and we were primarily interested in evaluating why recovery of sea otters in this particular area was slow. We did not replicate reference areas (e.g. other unoiled parts of PWS) primarily because of cost constraints. However, the increase in sea otters that we observed in our Montague study area over the course of the study was also observed in other unoiled portions of PWS (Bodkin et al. 2002). Thus, patterns observed at Montague are reflective of sound-wide patterns, at least with respect to this 1 important aspect. We also recognize that our design relies largely on post-spill comparisons (especially with respect to food availability) and that interpretations of results with respect to potential food limitation rest on assumptions regarding food resources and the status of food limitation in sea-otter populations prior to the spill. However, based on the long history of sea-otter occupation in our study areas (Lensink 1962), and the widely recognized impact of sea otters on their food resources (e.g. Kvitek et al. 1992, Estes & Duggins 1995), the assumption that sea otters in both our study areas were food-limited prior to the spill seems reasonable.

Food availability. We used 2 metrics to assess prey availability because of uncertainties as to how sea otters perceive their prey base, uncertainties as to

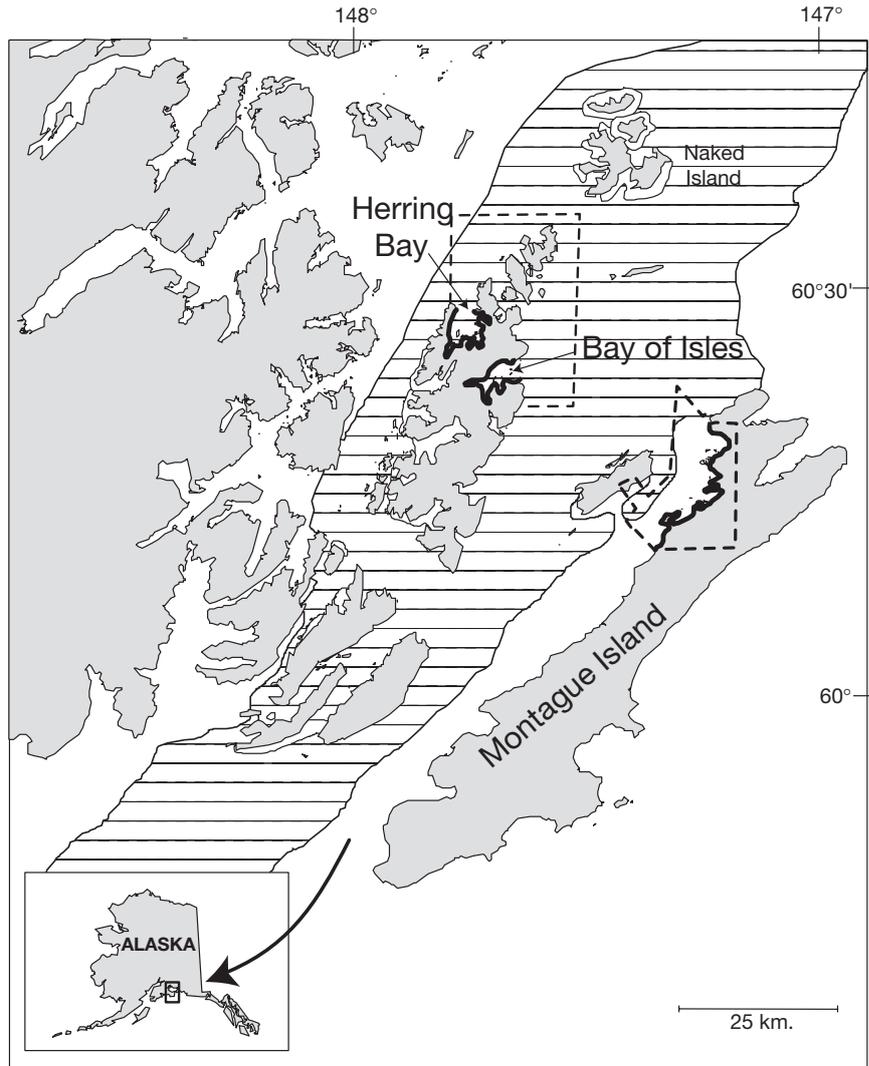


Fig. 1. Location of sampling sites for sea otters and sea otter prey in western Prince William Sound. The cross-hatched area indicates the trajectory of oil from the 'Exxon Valdez' oil spill based on a hind-cast model (Galt et al. 1991) and shoreline oiling surveys (ADEC 1989, ADNR 1991). Areas where sea otters were surveyed are indicated by dotted lines. Thickened lines indicate shoreline areas in Herring Bay and Bay of Isles on Knight Island and Montague Island, where prey were sampled in 1996 through 1998

whether recovery of sea-otter populations may be dependent on immigration or intrinsic growth (i.e. growth resulting from births in the resident population), and known differences between our 2 study areas. First, we examined the energy of prey available per unit area. We assume that immigrating sea otters might assess the suitability of a particular habitat based on the prey that can be obtained in a few foraging sessions, and that the average prey density (i.e. mean prey energy per unit area) is a reasonable index of what an immigrating sea otter might encounter. This especially may be the case for young sea otters that have little knowledge of preferred feeding sites, where prey densities may be higher than average. Younger sea otters (especially young males) are the most likely immigrants (Reidman & Estes 1990).

However, energy available per unit area might not be a reasonable means of assessing the status of a particular area with respect to its carrying capacity and its potential with respect to intrinsic population growth. Our Montague Island study area supported higher densities of sea otters than our northern Knight Island study area prior to the spill, and there are known differences between the 2 study areas that suggest that Montague Island might support a more productive prey base. In a pre-spill census conducted in 1973, densities of sea otters were 5.4 and 1.4 km⁻² at Montague and Knight Island study areas respectively (Dean et al. 2000). The Montague study area is generally shallower and has a higher proportion of soft sediment (Holland-Bartels 1996), suggesting that it may be a more suitable habitat for clams, a preferred sea-otter

prey in PWS. Thus, it is likely that the energy of sea otter prey per unit area was substantially lower at Knight Island than at Montague Island prior to the spill, when food was presumably limiting at both locations. Furthermore, it is possible that prey energy per unit area would remain lower at Knight than at Montague Island, even if the sea otter population at Knight Island was below carrying capacity and food was no longer limiting with respect to the potential for intrinsic population growth. Therefore, we assessed availability of food in terms of energy available per unit mass of sea otter to account for possible differences in carrying capacity of the 2 study areas. We assume that, while prey energy per unit area may differ between the 2 areas when at carrying capacity, the energy available per unit mass of sea otter would be roughly equivalent. Thus, food limitation at northern Knight Island, especially with respect to the potential for intrinsic population growth, would be indicated by lower or equal energy of prey available per unit mass of sea otter.

Prey items evaluated were clams, crabs, mussels and sea urchins. Independent estimates of sea otter diets made both prior to (Calkins 1978, Estes et al. 1981, Garshelis et al. 1986) and subsequent to the oil spill (Doroff & Bodkin 1994 and section on 'Rate of consumption of food by sea otters' below) suggest that these prey comprise the vast majority of food consumed by sea otters in PWS. The density and size distributions of prey were estimated from stratified random sampling within each of 2 study areas: Knight and Montague Islands (Fig. 1). Sampling was stratified by depth and was conducted between 1996 and 1998 (Table 1). We collected prey by hand along intertidal strata sampled at low tide or from subtidal strata using

SCUBA. Subtidal clams were sampled using a diver-operated suction dredge (Fukuyama 2000). Not all species or strata were sampled in each year, and we used combined estimates for all years, ignoring possible year-to-year differences.

The prey energy available per unit area within each study area and depth stratum was calculated based on abundance and size distribution of prey. In most instances, all sampled individuals for a particular prey were measured, and sizes of individuals were converted to energy units using size to dry-tissue mass regressions, and estimates of energy per unit dry-mass. For crabs *Telmessus cheiragonus*, we did not measure sizes but only counted crabs larger than 44 mm carapace length (about 50 mm carapace width), and made conversions from abundance to energy by assuming the average size (carapace width) of crabs was 44 mm. This is a reasonable approximation based on crab size selection in sea otter feeding observations (D. H. Monson pers. obs.).

For all prey, we assumed that sea otters were size-selective predators, and that only prey above a given size were available. This assumption is supported by direct observations of sea-otter foraging, and by comparisons of sizes of prey eaten vs sizes available in a wide variety of sea otter prey, over a range of habitat types (Estes et al. 1978, Simenstad et al. 1978, Ostfeld 1982, Kvitek & Oliver 1988, VanBlaricom 1988, Kvitek et al. 1992, Estes & Duggins 1995). A size cutoff of 20 mm (length) was used for clams and mussels based on the sizes of clams in collections of sea otter-cracked shells (Kvitek et al. 1992, Fukuyama 2000), the sizes of mussels available to otters (VanBlaricom 1988), and direct foraging observations (J. L. Bodkin & D. H. Monson pers. obs.). For crabs, we used a 44 mm carapace

Table 1. Summary of sampling effort for determination of density of sea otter prey at northern Knight Island (KI) and Montague Island (MI). Strata are indicated as: +2.5 to +0.5 m = high intertidal (HI); +0.5 to -0.5 m = low intertidal (LI); -0.5 to -5.0 m = very shallow subtidal (VSS); -5.0 to -10.0 m = shallow subtidal (SS); -10.0 to -20.0 m = deep subtidal (DS). All depths are relative to mean lower-low water

Prey species	Strata sampled	No. sites sampled per area		Years sampled	No. quadrats or transects sampled per site and stratum	Quadrat or transect size (m)
		KI	MI			
<i>Protothaca staminea</i>	LI	75	75	1996, 1997, 1998	5	0.5 × 0.5 × 0.1 deep
	SS	39	37	1996, 1997	3-6 (usually 4)	0.5 × 0.5 × 0.3 deep
	DS	10	10	1998	3-4 (usually 4)	0.5 × 0.5 × 0.3 deep
All other clams	LI	45	45	1997, 1998	5	0.5 × 0.5 × 0.1 deep
	SS	39	37	1996, 1997	3-6 (usually 4)	0.5 × 0.5 × 0.1 deep
	DS	10	10	1998	3-4 (usually 4)	0.5 × 0.5 × 0.1 deep
<i>Telmessus cheiragonus</i>	LI, VSS, SS	60	59	1996, 1997	1	50 × 1
<i>Mytilus trossulus</i>	HI	112	107	1996, 1997	10	0.22 × 0.22
<i>Strongylocentrotus droebachiensis</i>	LI	75	74	1996, 1997, 1998	1	50 × 0.5
	VSS, SS	60	59	1996, 1997	1	50 × 0.5

Table 2. Size to mass and energy to mass relationships for sea otter prey and the source used to quantify these relationships. Sources are as follows: A = our estimate; B = Wacasey & Atkinson (1987); C = Cummins & Wuycheck (1971); D = mean of 43 bivalve species from Cummins & Wuycheck (1971)

Prey Species	Dry mass (mg) vs size (mm)	Source	Energy (J mg ⁻¹ dry mass)	Source
<i>Clinocardium</i> spp.	Mass = 0.000079 × length ^(2.579)	A	18.88	B/C
<i>Diplodonta</i> spp.	Mass = 0.000009 × length ^(3.186)	A	18.85	D
<i>Humilaria kennerleyi</i>	Mass = 0.000018 × length ^(2.920)	A	18.85	D
<i>Macoma</i> spp.	Mass = 0.000006 × length ^(3.147)	A	17.99	B
<i>Mya truncata</i>	Mass = 0.000035 × length ^(2.903)	A	13.90	B
<i>Protothaca staminea</i>	Mass = 0.000098 × length ^(2.432)	A	22.52	A
<i>Saxidomus gigantea</i>	Mass = 0.000100 × length ^(2.555)	A	18.81	A
Other clams	Variable-based on relationships of similar-shaped species	A	18.80–20.2	A,B,C
<i>Telmessus cheiragonus</i>	Mass = 0.000046 × length ^(3.354)	A	11.94	A
<i>Mytilus trossulus</i>	Mass = 0.000011 × length ^(2.843)	A	17.33	A
<i>Strongylocentrotus droebachiensis</i>	Mass = 0.000650 × test diameter ^(2.5187)	A	3.70	A

Table 3. Benthic areas (km²) within depth strata in the study areas at northern Knight Island (KI) and Montague Island (MI)

Depth stratum (m relative to mean lower-low water)	Area (km ²)	
	KI	MI
+ 2.8 to + 0.5	0.59	1.92
+ 0.5 to -0.5	0.39	1.57
-0.5 to -5.0	1.71	7.16
-5.0 to -10.0	2.36	5.88
-10.0 to -20.0	8.27	10.66
-20.0 to -100.0	13.54	46.22
Total	26.86	73.41

length (approximately 50 mm carapace width) lower limit based primarily on feeding observations. A size of 15 mm test diameter was used for sea urchins based on the lower limit of sea urchins, size in sea otter scats (Estes & Duggins 1995).

For the more abundant prey species, we developed dry mass to size relationships, using a subset of animals collected (Table 2). In other cases (all of which were clams) we substituted dry mass to size regressions using similarly shaped species. Energy conversions were based on our calorimetry of a subsample or values reported in the literature.

Weighted mean values for energy of prey per unit area (kJ m⁻²) were computed based on the calculated mean energy of prey per unit area in each stratum in each study area and the size (km²) of each stratum in each study area (Table 3). For strata to a depth of 10 m, the stratum size was determined based on a sampling of distances between stratum boundaries at systematically selected shoreline sites and the total shoreline

length. The area within the 20 to 100 m depth stratum was determined from a GIS analysis of bathymetric charts. The area of the 10 to 20 m depth stratum was determined by subtraction. Not all species were sampled in each depth stratum, either because we had some prior knowledge of the depth distribution of species (e.g. *Mytilus trossulus* occurs almost exclusively in the upper intertidal region in PWS) or because of logistical considerations. None of the species were sampled at depths >20 m because of our inability to safely sample these depths using SCUBA. Extrapolations to depths up to 100 m using data from the 10 to 20 m depth stratum may have introduced bias. There are no quantitative estimates of densities of various sea otter prey at depths greater than 20 m, and we cannot evaluate the direction or extent of these potential biases. Assumptions regarding the abundance estimates for unsampled strata are given in Table 4. It was assumed that otters seldom feed at depths greater than 100 m, as confirmed by feeding observations (J. L. Bodkin & D. H. Monson unpubl. obs.).

Prey energy available per unit mass of sea otter was estimated as:

prey energy per unit mass of sea otter (kJ kg⁻¹ of otter) = (prey energy density [kJ m⁻²] × sea otter sampling area [m²] × the proportion of the sea otter sampling area that is less than 100 m depth) / (sea otter abundance × avg. mass of a sea otter [kg])

Sea otter abundance was the mean of 1996, 1997, and 1998 aerial survey estimates (replicated in each year) at Knight and Montague Islands (Dean et al. 2000). The area over which otters were surveyed (168 and 90 km² at Knight and Montague Islands respectively) was larger than the prey sampling area (27 and

73 km²). We assumed that prey abundance within the smaller prey sampling area was representative of the larger sea otter sampling area. The average mass of a sea otter (22.85 kg) was determined from a sample of 145 individuals captured between 1996 and 1998. This estimate, based on a pooled sample from northern Knight and Montague Islands, was used in the calculation of prey energy available per unit mass of sea otter in each area.

Variances and confidence intervals for both prey energy per unit area and prey energy per unit mass of sea otter were calculated using formulae for estimating the variances of products of an independent variable and a constant, and of ratios of 2 independent means (Goodman 1970). The null hypotheses that prey energy per unit area and prey energy per unit mass of sea otter at Knight Island were equal to those at Montague Island were tested using a 1-tailed z-test (Snedecor & Cochran 1969).

Energy requirements of sea otters at Knight and Montague Islands were determined based on sea otter abundance, the average energy requirement of a sea otter, and the average mass of a sea otter. The energy requirement of 1019 kJ kg⁻¹ d⁻¹ was an average of several published values (Kenyon 1969, Fausett 1976, Costa 1982). Estimates of yearly energy requirements were compared to estimates of yearly production of prey. The latter assumed that the ratio of yearly net production to standing stock (the P:B ratio) for prey was 2.0. This was based on values given for several benthic invertebrates in PWS (Feder & Jewett 1987).

There are no comparable pre-spill estimates of prey availability for PWS, and no estimates for areas outside PWS. However, Kvitek et al. (1992) gave standing stocks (wet meat mass) of bivalves from areas where sea otters were feeding at locations around Kodiak Island with various histories of sea otter colonization. We converted these values to energy units assuming that dry meat mass was 18.7% of wet meat mass (based on the average for clams collected in our study) and an energy density of 18.8 kJ g⁻¹ dry meat mass (based on our data and on values for energy density of

Saxidomus gigantea, the numerically dominant clam). We compared these values to similar estimates of prey energy per unit area from sea otter feeding sites at northern Knight Island (5 sites) and Montague Island (3 sites) sampled in 1997. Sampling and estimation of prey energy per unit area were as described above for systematic sites.

Rate of consumption of food by sea otters. The average prey consumption rate by sea otters in each study area was calculated based on measurements of (1) the time of an average dive plus the time interval between dives, (2) the proportion of dives that were successful in obtaining food, (3) the type, number, and size of prey obtained on each successful dive, and (4) the average energy content of each prey. Numbers 1 to 3 above were based on direct foraging observations made from sites along the shoreline using a 50 to 80× magnification spotting scope while 4 was based on estimates from sea-otter-cracked shells from sea otter foraging sites (see below). Observations were made during daylight hours in June through August 1996, 1997 and 1998. A total of 117 foraging observation sessions were conducted at Knight Island, and 113 were conducted at Montague Island. An average of 8 dives per session was observed in each area. Energy conversions were made based on expressions given in Table 3, or from values given in Cummins & Wuycheck (1971) or Wacasey & Atkinson (1987).

Observers could distinguish prey type (clam, mussel, crab, sea urchin, etc.) and the size class (<4, 4 to 8, or >8 cm in length) of each prey, but could not accurately estimate size or, in the case of clams, species. Therefore, we estimated the species composition of clam prey and average size of each species of clam based on collections of sea-otter-cracked shells from sea otter foraging sites. This method is based on the unique way in which sea otters feed and the ability of divers to distinguish otter-cracked shells from others (Kvitek et al. 1988, 1992, Fukuyama 2000). A total of 33 and 30 foraging sites were sampled at Knight and Montague Islands respectively in summer 1996 and 1997. An average of 11 and 20 otter-cracked clam shells was col-

Table 4. Assumptions regarding sea otter prey densities in unsampled depth strata

Prey species	Assumption
<i>Protothaca staminea</i>	Density = 0 below 20 m depth and above +0.5 m
<i>Telmessus cheiragonus</i> and <i>Strongylocentrotus droebachiensis</i>	Densities at depths below 10 m are equal to densities in the -5 to -10 m depth stratum
<i>Mytilus trossulus</i>	Density = 0 in the +2.8 to 0.5 m depth stratum Density = 0 below the +0.5 m stratum
All others	Densities at depths below 20 m are equal to densities in the -10 to -20 m depth stratum Density = 0 in the +2.8 to 0.5 m depth stratum

lected and measured at each site respectively. Only newly deposited shells (based on color and degree of epifaunal growth) were included.

We tested the hypothesis of no difference in consumption rate between Knight and Montague Islands using a Monte Carlo re-sampling method (Manly 1991). We used the mean and variance estimate for each of the observable foraging attributes used in the calculation of consumption rates (dive times, number and size of prey, etc.) to estimate a statistical distribution for each attribute. Initially data from both study sites were combined to represent a null distribution of no difference between populations at Knight and Montague Islands. A sample size of 117 (Knight) and 113 (Montague) was randomly selected (representing the number of foraging sessions observed in each area) from the distribution of each attribute, the averages of these were computed, a consumption rate calculated for each area, and a difference in consumption rate found. This process was repeated 1000 times to create a Monte Carlo simulation of the null distribution of differences. The observed difference in consumption rates was estimated using the site-specific mean values for each attribute to derive 1 consumption rate for each area. The statistical significance of the difference in consumption rate was estimated by the proportion of the null distribution of differences that was greater than the observed difference. This can essentially be interpreted in the same manner as the probability associated with a *t*-statistic testing the hypothesis of no difference between means. We also calculated 95% Monte Carlo confidence intervals for consumption rates. The Monte Carlo procedure included drawing a random sample from the site-specific distribution for each attribute of sample size 117 and 113, for Knight and Montague respectively. We again calculated the mean values to estimate the new consumption rate and

repeated the process 1000 times for each area. Confidence limits were estimated by the 2.5 and 97.5% points in the Monte Carlo distribution of consumption rates.

The consumption rates for sea otters at Knight and Montague Islands in 1996 to 1998 were contrasted with comparable data from other PWS sites (Garshelis et al. 1986) and from Kodiak Island collected prior to the spill. Means and 95% confidence intervals were estimated for consumption rates at Kodiak largely using published data from these sites as inputs. Calculations were made in the same manner described above for Knight and Montague Islands. Foraging data for Kodiak Island (Doroff & DeGange 1994, A. R. DeGange unpubl. data) were collected in a manner similar to those described for PWS. Size distributions of clams at Kodiak Island were based on shell litter collections (Kvitek et al. 1992).

Morphometrics. Age-adjusted body mass and mass to length ratios were compared between sea otters captured from northern Knight, Montague, and Kodiak Islands. Animals at Knight and Montague Islands were captured in 1996, 1997, and 1998 using either tangle nets or diver-operated modified Wilson traps (Bodkin et al. 2002). The sex, mass, and body length (from the tip of the nose to the tip of the tailbone) of each animal was determined and a tooth (pre-molar) of each animal was determined and a tooth (pre-molar) was extracted prior to the animal's release. Each tooth was analyzed to estimate the age of the sea otter based on the number of cementum layers (Garshelis 1984, Bodkin et al. 1997). This analysis provides ages accurate to ± 1 yr on average. The Kodiak data were collected in 1986 and 1987 using methods similar to those described above (Monson et al. 2000b, Monson & DeGange 1995). The Kodiak site was recently occupied by sea otters (within 5 to 15 yr prior to sampling) and there was abundant food.

Table 5. Mean energy per unit area (kJ m^{-2}) for sea otter prey at northern Knight and Montague Islands, 1996–1998. CI: confidence interval

Taxa	Knight Island		Montague Island		z	p
	Mean	95% CI	Mean	95% CI		
<i>Humilaria kennerleyi</i>	31.66	± 67.27	16.76	± 39.00	0.38	0.35
<i>Mya truncata</i>	15.82	± 49.09	31.47	± 97.36	-0.28	0.61
Other clams	6.73	± 26.01	31.09	± 57.60	-0.76	0.78
<i>Mytilus trossulus</i>	6.44	± 0.83	14.62	± 1.48	-9.43	<0.01
<i>Saxidomus gigantea</i>	4.40	± 22.88	22.04	± 41.68	-0.73	0.77
<i>Protothaca staminea</i>	3.99	± 14.13	0.99	± 4.04	0.40	0.34
<i>Telmessus cheiragonus</i>	1.62	± 3.89	0.34	± 1.10	0.33	0.37
<i>Clinocardium</i> spp.	1.89	± 4.53	7.66	± 23.83	-0.47	0.68
<i>Macoma</i> spp.	1.29	± 3.65	23.34	± 63.76	-0.68	0.75
<i>Diplodonta</i> spp.	0.32	± 1.33	0.96	± 5.62	-0.22	0.59
<i>Strongylocentrotus droebachiensis</i>	0.03	± 0.23	0.03	± 0.23	0.01	0.50
Total	74.20	± 91.58	149.30	± 144.01	-0.86	0.81

Analyses were conducted for females from 1 to 4 yr of age that did not have dependent pups with them at the time of capture. We restricted the analyses to females because there were too few males captured for the purpose of comparison. Older females were excluded because of possible confounding effects of having a large number of pregnant females among older individuals, and because the effects of a limited food supply were expected to have their greatest impact on younger animals that are generally poorer competitors. Higher starvation-caused mortality in young animals has been suggested for sea otters (Kenyon 1969) and demonstrated for other large mammals (Choquenot 1990, Virgil & Messier 1997). Variation in survival of immature individuals accounts for most of the variation in rates of population increase for marine mammals (Eberhardt & Siniff 1977).

We tested the null hypotheses of no difference between age-adjusted mass and mass to length ratio using an analysis of covariance. Age classes used were 1, 2, 3, and 4 yr. Areas were contrasted using pairwise comparisons of least-square means.

RESULTS

Food availability

The mean energy content of sea-otter prey per unit area was nearly twice as high at Montague as at Knight Island (Table 5). This was primarily the result of higher energy per unit area for *Macoma* spp., *Mya truncata*, *Saxidomus gigantea*, *Mytilus trossulus*, and 'other clams' at Montague Island. However, among individual species, only the energy per unit area of *M. trossulus* differed significantly between areas ($p < 0.01$), and there was no significant difference between areas for the energy per unit areas summed over all sea otter prey ($p = 0.81$).

The relative proportions of total energy contributed by each species differed between areas (Table 5). At Knight Island, the majority of energy available was from *Humilaria kennerleyi* (43%) and *Mya truncata* (21%). At Montague Island, 'other clams', *M. truncata*, and *Macoma* spp. contributed 21, 20, and 16% respectively.

The prey energy per unit mass of sea otter was 4.8 times higher at Knight than at Montague Island (Table 6). However, we failed to reject the null hypothesis that energy per unit mass of sea otter was equal within the 2 areas ($z = 1.19$, $p = 0.12$). The estimated annual production of prey energy at Knight Island (1.6×10^{10} kJ yr⁻¹) was about 26 times higher than that required to support the sea-otter population there (6.1×10^8 kJ yr⁻¹). At Montague Island, the estimate of

Table 6. *Enhydra lutris*. Means ($\pm 95\%$ CI) of 1996–1998 values for sea-otter prey energy per unit area, sea otter abundance, prey energy per unit mass of sea otter, yearly production of sea otter prey, and yearly prey production required to support the average number of sea otters within each study area. Yearly production of prey was calculated as the mean prey energy per unit area \times the potential foraging area (i.e. area < 100 m depth) \times an estimated production to biomass ratio of 2. The yearly production required to support sea otters was calculated as the number of sea otters \times average mass of a sea otter \times the energy of prey required by sea otters daily (1019 kJ kg d⁻¹) $\times 365$ d yr⁻¹

Study Area	Prey energy per unit area (kJ km ⁻²)	Sea-otter abundance	Potential foraging area (km ²)	Average mass of a sea otter (kg)	Prey energy per unit mass of sea otter (kJ kg ⁻¹)	Yearly production of sea otter prey (kJ yr ⁻¹)	Yearly production of prey required to support sea otter population (kJ yr ⁻¹)	Ratio of prey energy available per year: prey energy required
Knight Island	74×10^6 ($\pm 92 \times 10^6$)	72 (± 12)	106	22.85	4.8×10^6 ($\pm 6.0 \times 10^6$)	1.6×10^{10} ($\pm 1.9 \times 10^{10}$)	6.1×10^8 ($\pm 1.1 \times 10^8$)	26.2
Montague Island	149×10^6 ($\pm 144 \times 10^6$)	533 (± 202)	89	22.85	1.1×10^6 ($\pm 1.2 \times 10^6$)	2.7×10^{10} ($\pm 2.6 \times 10^{10}$)	4.5×10^9 ($\pm 2.2 \times 10^9$)	6.0

Table 7. Comparisons of clam densities (kJ m^{-2}) at sea otter feeding sites at Kodiak, Knight, and Montague Islands. Kodiak Island data are from Kvitek et al. (1992). Data for otter-free sites Kodiak Island are from randomly selected sampling areas. PWS: Prince William Sound

Region	Areas within region	Year	Sea otter population status	Clam energy per unit area (kJ m^{-2})	Dominant clam species
Kodiak	6 otter-free sites	1987–88	None	12958	<i>Saxidomus gigantea</i>
Kodiak	6 frontal sites	1986–88	Newly occupied	8384	<i>Saxidomus gigantea</i>
Kodiak	5 intermediate sites	1986–87	Occupied 5–15 yr	4008	<i>Saxidomus gigantea</i>
Kodiak	2 long occupied sites	1987	Occupied >25 yr	591	<i>Saxidomus gigantea</i>
PWS	Montague Island	1996–98	Occupied >25 yr	228	<i>Mya truncata</i>
PWS	Knight Island	1996–98	Long occupied, reduced in 1989	85	<i>Humilaria kenneleyi</i>

Table 8. *Enhydra lutris*. Means (± 1 SD) for feeding data for sea otters at northern Knight and Montague Islands, 1996–1997. A total of 117 and 113 sessions were observed at Knight and Montague Islands respectively, with an average of 8 dives observed in each session within both areas

Variable	Units	Knight Island	Montague Island
Success rate	% of dives in which prey were captured		
Clam-mussel dives		90.3	88.3
Non-clam-mussel dives		80.7	78.8
Time per dive (dive time + surface time)	s	162 (± 66)	121 (± 48)
Successful		111 (± 43)	87 (± 35)
Unsuccessful			
Prey composition	% of successful dives		
Clams		72	80
Mussels		14	9
Crabs		3	4
Other		11	7
Number of individuals per successful dive	No. ind.		
Clams		2.43 (± 0.77)	2.12 (± 0.30)
Mussels		11.25 (± 4.25)	8.14 (± 2.13)
Crabs		1.28 (± 0.33)	1.04 (± 0.07)
Other		2.90 (± 1.66)	2.48 (± 2.44)
Energy per prey item	kJ		
Clams		51 (± 16.2)	36 (± 17.6)
Mussels		5 (± 0.8)	5 (± 0.8)
Crabs		505 (± 50.7)	274 (± 27.2)
Other		17 (± 1.7)	17 (± 1.7)

Table 9. Percentage of clams by species, mean size of each species (± 1 SD), and percentage of total available prey energy contributed by each prey species in sea-otter-cracked shells from sea otter foraging sites at northern Knight (KI; $n = 33$) and Montague Islands (MI; $n = 30$). An average of 11 and 20 recently cracked clam shells per site were collected at Knight and Montague respectively

Clam species	% (by no. ind.)		Mean size (mm)		% (by energy)	
	KI	MI	KI	MI	KI	MI
<i>Saxidomus gigantea</i>	46.2	12.9	61.6 (7.1)	56.8 (9.8)	58.7	23.7
<i>Protothaca staminea</i>	8.4	4.1	49.6 (8.6)	38.2 (8.1)	5.3	2.1
<i>Macoma</i> spp.	11.2	5.6	45.3 (9.7)	42.0 (11.7)	3.3	2.4
<i>Clinocardium</i> spp.	3.6	18.3	42.8 (16.2)	39.5 (5.9)	2.2	8.7
<i>Humilaria kenneleyi</i>	10.9	11.1	47.3 (12.2)	44.3 (5.6)	6.3	8.3
<i>Mya truncata</i>	10.6	33.1	52.6 (10.3)	48.8 (5.0)	9.7	38.2
<i>Serripes groenlandicus</i>	5.3	2.5	64.7 (20.2)	53.9 (13.7)	11.0	4.8
Others	3.8	12.4	62.5 (13.0)	49.5 (4.9)	3.5	11.8

Table 10. *Enhydra lutris*. Estimates of prey consumption and hours spent feeding by independent adult female sea otters (upper and lower 95% CI). Data from Green Island, Nelson Bay and Orca Inlet are from Garshelis et al. (1986). Feeding data from Kodiak are from Doroff & DeGange (1994) and A. R. DeGange (unpubl.). Shell length and mass-to-length conversions for Kodiak are from Kvitek et al. (1992) and mass-to-energy conversions were from Kenyon (1969), Cummins & Wuycheck (1971), and Wacasey & Atkinson (1987). PWS: Prince William Sound

Region	Area	Year	Sea otter population status	Prey consumption rate (kJ hr ⁻¹)	Feeding time required (h d ⁻¹)
PWS	Orca Inlet	1980–81	Occupied <2 yr	6134	5.0 ^b
Kodiak	Kupreanof Strait	1986–87	Occupied <15 yr	5100 (4230–6230)	4.4 ^b (3.6–5.3)
Kodiak	Afognak Island	1986–87	Occupied >25 yr	2340 (1482–3337)	10.0 ^b (6.7–15.1)
PWS	Knight Island	1996–98	Occupied >25 yr, reduced 1989–1998	2260 (1980–2570)	9.9 ^b (8.7–11.3)
PWS	Nelson Bay	1980–81	Occupied 2 to 3 yr	2187	8.8 ^a (7.7–9.9)
PWS	Montague Island	1996–98	Occupied >25 yr	1900 (1630–2180)	11.8 ^b (10.3–13.7)
PWS	Green Island	1980–81	Occupied >25 yr	1274	11.3 ^a (10.7–11.9)

^aBased on observations of activity from telemetry
^bEstimate based on hours required to obtain energy needed for maintenance (1019 kJ kg⁻¹ d⁻¹), given the measured prey consumption rate. For Montague and Knight Islands the average sea otter was 22.5 kg, at Orca Inlet most animals were males and an average size of 30 kg was assumed

the mean energy available (2.7×10^{10} kJ yr⁻¹) was only about 6 times that required (4.5×10^9 kJ yr⁻¹).

Within sea otter foraging areas, the average clam energy per unit area was substantially higher at Kodiak Island sites sampled by Kvitek et al. (1992) than at either Knight or Montague Islands (Table 7). This was especially true for those Kodiak Island sites where sea otters had only recently become re-established. Frontal areas at Kodiak Island had over 36 times higher densities of clams (in terms of energy per unit area) than Montague Island and over 98 times higher prey energy per unit area than Knight Island. Kodiak sites that were long occupied by sea otters and were considered food-limited had approximately 3 times more kJ m⁻² of clams than Montague, and about 7 times more than Knight Island sites. The dominant clam species (in terms of energy per unit area within sea otter foraging sites) at Knight and Montague Islands were *Saxidomus gigantea* and *Mya truncata* respectively. *S. gigantea* dominated at all Kodiak Island sites.

Rate of consumption

Clams comprised the majority of the prey energy consumed by sea otters at both Knight and Montague Islands (Table 8). Sea-otter-cracked shell collections indicated that at Knight Island *Saxidomus gigantea* were the most often taken prey and had the majority of prey energy (Table 9). The species composition in the

sea-otter-cracked shell litter at Montague Island was more varied. Most of the prey energy was supplied by *Mya truncata* and *S. gigantea*. Mean sizes for all species of clams were slightly larger at Knight than at Montague Island.

Sea otters at Knight Island had a slightly higher proportion of successful dives and took prey that were, on average, of higher energy (Table 8). An average of 90.3% of dives was successful in obtaining clams or mussels at Knight Island compared to 88.3% at Montague Island. The average energy provided per prey item was higher at Knight Island for both clams and crabs. At Knight Island, the average clam taken supplied an estimated 51 kJ compared to 36 kJ for those taken at Montague Island. Crabs taken had 505 kJ at Knight Island vs 274 kJ at Montague Island. For all prey items, sea otters at Knight Island also took more individuals per dive. Factors advantageous to a higher rate of consumption at Knight Island were offset to an extent by a higher average dive time at Knight Island. Dive time plus surface time of successful dives were 33% longer, and unsuccessful dives were 28% longer at Knight than at Montague Island. Also, there was a slightly higher proportion of low energy prey (mussels and 'other') taken at Knight Island.

The resulting average consumption rate for sea otters at Knight Island was 2260 kJ h⁻¹, about 18.9% higher than at Montague Island (1900 kJ h⁻¹; Table 10) and differed significantly between areas ($p = 0.001$,

1-tailed randomization test). Using these consumption rates, we estimate that the average size female sea otter at Knight Island fed an average of 9.9 h d^{-1} to obtain energy required for maintenance ($1019 \text{ kJ kg}^{-1} \text{ d}^{-1}$). This is lower than the 11.8 h needed at Montague Island.

The prey consumption rate for sea otters at Montague Island (1900 kJ h^{-1}) was slightly higher than that observed at nearby Green Island, PWS, prior to the oil spill (1300 kJ h^{-1} , Garshelis et al. 1986) (Table 10). Sea otters had occupied the Green Island site for many years and were considered food-limited. The rate for Knight Island was similar to that observed at Nelson Bay, PWS (Garshelis et al. 1986), an area that was occupied by sea otters for only 2 to 3 yr prior to the surveys of consumption and likely not food-limited. Both Knight Island (sampled post-spill) and Nelson Bay sea otters had consumption rates that were higher than at Green Island and Montague Islands. Consumption rates were much higher at Orca Inlet in 1980-81, and Kuperanof Strait (Kodiak region) sites in 1986-87 than at all other sites. The Orca Inlet and Kuperanof sites were surveyed only several years after colonization by sea otters, and sea otters there were clearly not food-limited. However, sea otters at a long-occupied site at Afognak Island (Kodiak region) had a consumption rate in the same range as animals from Knight and Montague Islands (Table 10).

Morphometrics

The age-adjusted body mass and mass to length ratio of 1 to 4 yr old female sea otters (without pups) captured at Knight Island were both significantly higher than for otters from Montague Island in 1996 to 1998 (Table 11). Body mass was 8.7% higher at Knight, and the mass:length ratio was 6.3% higher. The difference in the mass to length ratio translates to 1.1 kg difference for the average young sea otter (113 cm in length). Body mass and mass to length ratio were significantly higher at Kodiak Island sites that were only recently colonized by sea otters than at either Knight or Montague Islands. Body mass to length ratio at Kodiak was about 6.5% higher than at Knight Island and 13.1% higher than at Montague Island.

DISCUSSION

The availability of food resources for sea otters was the same, if not greater, at northern Knight as at Mon-

Table 11. *Enhydra lutris*. Age-adjusted mean body length (cm), mass (kg), and mass to length ratio for 1 to 4 yr old female sea otters from recently colonized Kodiak Island sites, northern Knight Island, and Montague Island. Results of ANCOVA, and contrasts between sea otters from different areas are given. Means of groups with like letters did not differ significantly at $p < 0.05$. Probabilities of equality among areas with respect to age-adjusted means are given. Age effects were significant ($p < 0.001$) in all cases

Area	N	Length		Mass		Mass:Length	
		Mean	Group	Mean	Group	Mean	Group
Kodiak	26	123.63	A	22.46	A	0.181	A
Knight	22	113.88	B	19.43	B	0.170	B
Montague	28	111.09	B	17.88	C	0.160	C
ANCOVA		<0.0001		<0.0001		<0.0001	
(p-values for area effect)							

tagne Island over the period from 1996 to 1998. The rate of consumption of food was significantly higher and the condition of young female sea otters was significantly better at northern Knight than at Montague Island. Furthermore, the mean prey energy per unit area did not differ significantly between areas, and the prey energy available per kg of sea otter, while not significantly different between the 2 areas, averaged about 4 times higher at Knight Island. Based on the assumption that sea otters were better samplers of their available food supply than we were, and based on the relative lack of precision in estimation of food availability (see discussion below), we suspect that food resources were in fact more available at Knight Island.

Our estimation of food available to sea otters, both in terms of energy of prey per unit area and energy per unit mass of sea otter, were dependent on a number of assumptions. In particular, inaccuracies may have resulted if (1) densities of prey in unsampled habitats (e.g. at depths greater than 20 m) were different than we assumed, (2) our sampling missed some widely dispersed, high-density patches of prey, (3) summer sampling misrepresented the average yearly energy density of prey, or (4) there were seasonal movements of sea otters (especially winter decreases in the more exposed Montague Island site) that were undetected by our summer sampling. While the estimates of prey per unit area are clearly imprecise and the estimates of the absolute quantity of prey available may be inaccurate, we have no good reason to suspect that there were biases that may have affected the relative measures of food available at our Knight and Montague Island study sites. Therefore, we feel that they provide a reasonable index of the relative abundance of prey at northern Knight and Montague Islands. There is some evidence that sea otters may move from more exposed areas (like our Montague Island site) in winter (Garshelis et al. 1986) and a winter survey of sea otters at Montague Island conducted in March 1998 (J. L.

Bodkin unpubl. data) counted ~44% fewer sea otters than in July 1998. However, low light levels during winter resulted in poor precision, and density estimates did not differ significantly between March and July surveys.

Although food was at least as abundant at northern Knight Island as at Montague Island, there was no increase in sea otter population at northern Knight Island between 1993 and 1998, but a significant increase at Montague Island over the same period (Dean et al. 2000). The number of sea otters at Montague Island increased from 335 in 1993 to 623 in 1998, a rate of about 15% yr⁻¹, but remained almost constant (from 77 in 1993 to 76 in 1998) at northern Knight Island. These data provide evidence that the population of sea otters at northern Knight Island was below its carrying capacity with respect to food resources, and that the lack of growth of the sea otter population at northern Knight Island was due to factors other than the availability of food resources necessary for intrinsic population growth.

There is also demographic evidence that suggests that food was not limiting intrinsic population growth of sea otters at northern Knight Island. The growth of food-limited populations is often constrained because of lower juvenile survival (Choquenot 1991). In the several years after the oil spill, survival rates of juvenile sea otters were lower than pre-spill rates (Monson et al. 2000a) and lower weanling survival was noted in oil impacted vs unimpacted areas (Ballachey et al. 1994). However, in more recent years (including the years 1996 to 1998 in which our study was conducted) survival rates for juveniles returned to pre-spill levels (Monson et al. 2000a). This is consistent with what would be expected under non-food limiting conditions. Also, birth rates of sea otters did not differ between oiled and unoiled portions of PWS (Johnson & Garshelis 1995, Bodkin et al. 2000). Survival rates of older sea otters decreased with time after the spill (Monson et al. 2000a), but given the better condition of sea otters in northern Knight Island, it is unlikely that the lower survival of older animals was caused by a lack of food.

While there was apparently sufficient food to allow for intrinsic growth of the existing segment of the population at northern Knight Island in 1996 to 1998, there is some question as to whether there was sufficient food to allow for successful immigration. Food appeared at least equally abundant at northern Knight Island compared to Montague Island, but food resources were still substantially lower at both Knight and Montague Islands than in areas recently reoccupied by sea otters (after decades of absence) where food was clearly not limiting. The relative lack of food at Knight and Montague Islands was probably largely the result of predation by sea otters that occupied these

sites for several decades prior to the oil spill (Garshelis et al. 1986, Bodkin et al. 2000), but may have been exacerbated at Knight Island due to impacts of the spill on the prey (reviewed in Peterson 2001). Sufficient food resources are a requisite for successful immigration (Estes et al. 1986), and higher densities of food might be required for successful immigration than are required for growth within resident populations. This may especially be the case because food resources are patchy, and new immigrants may not be as efficient at utilizing food resources as resident adult sea otters or pups that learn feeding behavior from their mothers. Thus, it is possible that there may have been sufficient food at northern Knight Island for intrinsic growth, but insufficient food to induce potential immigrants to establish residency. However, age-distribution models suggest that there must have been some net immigration to the northern Knight Island area in order to offset losses due to mortality and maintain the current population density (Monson et al. 2000a). Therefore, while the relative short supply of food at Knight Island (compared to areas unoccupied by sea otters for decades) may have been sufficient to curtail net immigration, it apparently did not altogether prevent immigration and does not appear to be a primary cause for the lack of sea otter recovery.

While food resources at northern Knight Island appear sufficient to allow for population growth, they do not appear sufficient to allow for maximum potential population growth as observed in some sea otter populations in newly occupied areas. Sea otter populations that inhabit areas unoccupied by sea otters for several decades prior, and that have unlimited food supplies, can increase at the rate of 25% yr⁻¹ (Estes 1990, Bodkin et al. 1999). Food resources at both northern Knight and Montague Islands were much lower than in these newly occupied sites, and were likely insufficient to allow for population growth rates near the maximum. Nonetheless, there was clearly sufficient food at both locations for some sea otter population growth, yet we observed growth at Montague Island, but not at northern Knight Island.

It is also possible that the relatively short supply of food at northern Knight Island (again compared to areas unoccupied by sea otters) may have interacted with other factors (e.g. oil-induced mortality or predation) to constrain sea otter population growth, and therefore sea otter recovery. Higher sea otter mortality rates were observed in oil-affected areas of PWS through 1998, perhaps as a result of exposure to oil (Ballachey et al. 2000, Monson et al. 2000a). Furthermore, predation by killer whales (Estes et al. 1998, Hatfield et al. 1998, Garshelis & Johnson 1999) and other hunters (Bodkin et al. 2001) may have contributed to the lack of recovery. Populations occupying

habitats with low-potential food supplies are more prone to being regulated at low densities by predation (Messier 1994) or possibly by oil-induced mortality. However, there is little evidence that predation pressure was higher at northern Knight than at Montague Island. Thus, the relative differences in sea otter population growth at northern Knight vs Montague Island, and the lack of recovery of sea otter populations at northern Knight Island were unlikely the result of higher predation rates there.

Based on the equal if not greater availability of prey energy per otter at northern Knight Island than at Montague Island, and based on the increasing population density of sea otters at Montague Island but not at northern Knight Island, we conclude that factors other than food were primarily responsible for lack of recovery of sea otters in the heavily oiled northern Knight Island portion of PWS following the 'Exxon Valdez' oil spill. Evidence presented elsewhere (Ballachey et al. 2000, Monson et al. 2000a, Bodkin et al. 2002) suggests that the recovery was primarily constrained by high rates of mortality and emigration that were linked to continued exposure to oil or persistent sublethal effects of oiling. However, it was also apparent that the potential population growth rate for sea otters at both Knight and Montague Islands was food-limited and the relatively short supply of food may have restricted immigration or interacted with other factors (e.g. predation or oil-induced mortality or emigration) to constrain sea otter recovery at northern Knight Island. Nonetheless, our data suggest that impacts of anthropogenic disturbances on large, often food-limited vertebrate predators may persist in spite of the availability of food resources that is generally sufficient for intrinsic population growth.

Acknowledgements. We thank all of those participants in the Nearshore Vertebrate Predator Project for their enthusiasm, support, and stimulating comments throughout this study. In particular, we thank our project leader, Leslie Holland-Bartels, and co-investigators Brenda Ballachey, Terry Bowyer, Dan Esler, Greg Golet, Dave McGuire, and Lyman McDonald. Invaluable statistical assistance was obtained from John Kern. We also thank all of those who supplied technical support, and especially those who assisted in collecting the data under rigorous field conditions. The work was supported by the Alaska Biological Science Center, Biological Resources Division, US Geological Survey, the Alaska Department of Fish and Game, and the Exxon Valdez Oil Spill Trustee Council. The findings and conclusions presented by the authors, however, are their own and do not necessarily reflect the views or opinions of the supporting organizations.

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Editorial responsibility: Charles Peterson (Contributing Editor), Morehead City, North Carolina, USA

*Submitted: April 14, 2000; Accepted: April 26, 2002
Proofs received from author(s): September 10, 2002*

Harlequin duck population recovery following the 'Exxon Valdez' oil spill: progress, process and constraints

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ABSTRACT: Following the 1989 'Exxon Valdez' oil spill in Prince William Sound, Alaska, we studied the status of recovery of harlequin duck *Histrionicus histrionicus* populations during 1995 to 1998. We evaluated potential constraints on full recovery, including (1) exposure to residual oil; (2) food limitation; and (3) intrinsic demographic limitations on population growth rates. In this paper, we synthesize the findings from our work and incorporate information from other harlequin duck research and monitoring programs to provide a comprehensive evaluation of the response of this species to the 'Exxon Valdez' spill. We conclude that harlequin duck populations had not fully recovered by 1998. Furthermore, adverse effects continued as many as 9 yr after the oil spill, in contrast to the conventional paradigm that oil spill effects on bird populations are short-lived. These conclusions are based on the findings that (1) elevated cytochrome P450 (CYP1A) induction on oiled areas indicated continued exposure to oil in 1998; (2) adult female winter survival was lower on oiled than unoiled areas during 1995 to 1998; (3) fall population surveys by the Alaska Department of Fish and Game indicated numerical declines in oiled areas during 1995 to 1997; and (4) densities on oiled areas in 1996 and 1997 were lower than expected using models that accounted for effects of habitat attributes. Based on hypothesized links between oil contamination and demography, we suggest that harlequin duck population recovery was constrained primarily by continued oil exposure. Full population recovery will also be delayed by the time necessary for intrinsic population growth to allow return to pre-spill numbers following cessation of residual oil spill effects. Although not all wildlife species were affected by the 'Exxon Valdez' oil spill, and some others may have recovered quickly from any effects, harlequin duck life history characteristics and benthic, nearshore feeding habits make them susceptible to both initial and long-term oil spill effects.

KEY WORDS: Demography · 'Exxon Valdez' · Harlequin duck · *Histrionicus histrionicus* · Marine birds · Oil contamination · Population recovery

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INTRODUCTION

Harlequin ducks *Histrionicus histrionicus* spend most of the year in nearshore marine habitats (Robert-

son & Goudie 1999), where they feed on benthic invertebrates (Goudie & Ankney 1986) in intertidal and shallow subtidal zones. Aspects of harlequin duck ecology make their populations particularly suscepti-

ble to perturbations of their wintering environment. Harlequin ducks, like many sea ducks, have a life history in which variable and generally low annual productivity is compensated by relatively high adult survival and long reproductive life spans (Goudie et al. 1994). This type of strategy evolves under conditions of predictable and stable nonbreeding environments, which are required to ensure adult survival (Stearns 1992). Also, harlequin ducks, because of their small body size, are thought to exist near an energetic threshold during winter, with little flexibility for increasing caloric intake or relying on stored reserves (Goudie & Ankney 1986). While this strategy may be tenable under predictable and stable conditions, it does not readily accommodate perturbations that result in either decreases in energy acquisition or increases in metabolic costs. Finally, strong site fidelity, such as that exhibited by wintering harlequin ducks, evolves in predictable and stable habitats (Johnson & Gaines 1990, Robertson & Cooke 1999, Cooke et al. 2000) and does not facilitate movement to undisturbed areas if local habitat quality becomes degraded (Hilden 1965, Cooch et al. 1993).

The release of approximately 42 million l of crude oil into Prince William Sound (PWS) by the 1989 'Exxon Valdez' oil spill (EVOS) was a significant perturbation to harlequin duck nonbreeding habitat. As much as 40% of the spilled oil was deposited in intertidal and subtidal zones of PWS (Galt et al. 1991, Wolfe et al. 1994) and oil persisted in these areas more than 8 yr after the oil was spilled (Hayes & Michel 1999). Vulnerability of harlequin ducks to oil spill effects is exacerbated by their diet of intertidal and shallow subtidal benthic invertebrates (Vermeer 1983, Goudie & Ankney 1986, Gaines & Fitzner 1987, Goudie & Ryan 1991, Patten et al. 2000) as oil constituents can accumulate in bottom sediments and subsequently, in benthic invertebrates (Fukuyama et al. 2000, Peterson 2001). Petroleum hydrocarbons occurred in harlequin duck prey from immediately after the spill through at least 1995 (Boehm et al. 1995, Babcock et al. 1996, Short & Babcock 1996, Wolfe et al. 1996, Patten et al. 2000).

In this paper, we examine effects of the EVOS on harlequin duck populations in PWS and consider potential constraints on full population recovery. The first objective is to review data that provide insight into population injury and recovery status. The second objective is to evaluate mechanisms potentially constraining full recovery, including (1) intrinsic demographic limitations on population growth rates that delay return to prespill numbers despite lack of continuing oil spill effects; (2) health effects of continued oil exposure at levels that have population consequences; and (3) food limitation due to oil spill-related reduc-

tions in prey that either lowers carrying capacity or reduces health and survival of individual ducks.

Data used in this synthesis were gathered from journal publications and Exxon Valdez Oil Spill Trustee Council reports, both from our own studies conducted during 1995 to 1998 and from other research and monitoring programs in PWS after the spill. We also reviewed published studies of harlequin duck ecology conducted throughout their range and their implications for understanding constraints on full recovery from the EVOS.

PWS is prime nonbreeding habitat for harlequin ducks. It supports about 14 000 birds during winter (Lance et al. 1999), although it is one of the northernmost wintering areas within the species' range (Robertson & Goudie 1999). Some reproduction occurs in streams feeding into PWS (Crowley 1999), but most harlequin ducks that winter in PWS nest outside of the area. Breeding locations have not been determined and could extend throughout the vast breeding range in Alaska and the Yukon Territories (Robertson & Goudie 1999).

INJURY AND RECOVERY STATUS

We reviewed studies conducted after the EVOS that lend insight into harlequin duck population injury and recovery. We categorized these as studies of population status, adult female survival and body mass variation.

Population status

Several studies are relevant for evaluating harlequin duck population status, most of which were conducted outside of our own research program. These measured a range of population parameters, including direct mortalities, abundance, numerical trends, densities, age and sex ratios, and habitat use. Generally, we would predict that these population parameters (excluding initial mortalities) would be similar in oiled and unoiled areas once full population recovery had occurred. However, this prediction rests on a suite of assumptions and is subject to a number of problems (Wiens & Parker 1995). For example, lack of comprehensive prespill data for many parameters (e.g. winter densities, habitat use, age and sex ratios) precluded use of a before-after-control-impact (BACI) design, which can be used to distinguish effects of an environmental perturbation from natural spatial and temporal variation. Also, comparisons between affected and control areas, without preperturbation data, often assume that natural attributes of the areas are similar

(Wiens & Parker 1995); for harlequin duck population parameters, sometimes that assumption could be addressed, but not always. Finally, changes in demographic endpoints such as numbers, trends or densities do not address underlying demographic processes and thus can not indicate mechanisms leading to population change. However, despite these limitations and assumptions, convergence of population densities, trends, and age and sex distributions in oiled and unoiled areas would be consistent with population recovery.

Estimates of direct mortality of birds due to the EVOS were based on recovery of carcasses (Piatt et al. 1990), expanded to account for the proportions of dead birds that were not recovered (Piatt & Ford 1996). The true fraction of all dead birds retrieved after the EVOS is difficult to determine, even with data from experimental carcass drift and recovery studies (Piatt & Ford 1996). The associated uncertainty has led to controversy about the numbers of birds killed by acute effects of the EVOS (Parrish & Boersma 1995, Piatt & Ford 1996), although Piatt & Ford (1996) convincingly argue that despite uncertainty, incorporation of estimated recovery rates is appropriate and realistic. In the case of the EVOS, even when using a variety of recovery rates, estimates of the magnitude of total bird mortality were similar (Piatt & Ford 1996). Immediately following the EVOS, 212 harlequin duck carcasses were recovered, including 147 in PWS; using a recovery rate of 15% (Piatt & Ford 1996), the estimate of total harlequin mortality due to immediate effects of the EVOS was 1413, with 980 of those in PWS (J. Piatt pers. comm.). This mortality estimate represents roughly 7% of the harlequin ducks wintering throughout PWS, and a much higher proportion of those wintering in oiled areas of PWS. Sea ducks were quite vulnerable to immediate effects of the oil spill; numbers of oiled sea duck carcasses recovered in PWS exceeded those of any other taxa (Piatt et al. 1990). Mortality estimates from carcasses retrieved just after the spill indicate immediate population injury, but do not address any subsequent, longer-term effects of the EVOS.

Patten et al. (2000) conducted damage assessment studies immediately following the EVOS, focusing on contaminant exposure and abundance. They found hydrocarbon metabolites in 74% of live harlequin ducks collected from oiled areas in 1989 and 1990, consistent with exposure to oil and implying potential for injurious effects. Also, numbers of adults and broods were lower in oiled areas of PWS than in unoiled areas (Patten et al. 2000); however, this study did not account for potential geographic variation from natural causes, which may contribute to or explain observed differences. For example, lower numbers of broods in oiled areas do not necessarily indicate that harlequin pro-

ductivity was affected by the EVOS because (1) most of the wintering population migrates outside of PWS to breed; (2) within PWS, breeding habitats used by harlequin ducks (Crowley 1994) are found primarily in eastern, unoiled areas (Rosenberg & Petrula 1998); and (3) pre-spill records of broods in oiled areas could have been flightless birds during wing molt that were misclassified (Rosenberg & Petrula 1998). However, no data have been collected to explicitly examine reproductive effort of harlequin duck subpopulations from oiled areas, so we cannot eliminate the possibility that the EVOS had deleterious effects on harlequin duck reproduction.

The US Fish and Wildlife Service has conducted marine bird surveys during summer (July) and winter (March) in PWS since 1989 (Lance et al. 1999). While these were not explicitly designed to estimate harlequin duck numbers or population trends, they do provide a long-term assessment of population status. Pre-spill survey data exist for PWS from summers 1984 and 1985, which have been used for comparison to post-spill data (Irons et al. 2000). Unfortunately, pre-spill survey data for PWS in winter, the period of high and stable harlequin duck numbers, are not adequate for before-after comparisons, although post-spill data can be used to compare winter trends between oiled and unoiled areas (Lance et al. 2001). Also, from 1995 to 1997, the Alaska Department of Fish and Game conducted surveys designed specifically to assess harlequin duck population status (Rosenberg & Petrula 1998). They surveyed during spring (May and June) and fall (late July to September) and measured numbers, pair status (paired versus unpaired), sex ratios, age composition and molt chronology in oiled and unoiled areas (over more than 250 km shoreline in each area). These surveys have more statistical power for estimating abundance and trends than US Fish and Wildlife Service surveys (Rosenberg & Petrula 1998), and their fall data provide the best estimates of population trends for nonbreeding populations during the course of our research (1995 to 1998).

Using a BACI design, Irons et al. (2000) found that harlequin duck densities were lower than expected in oiled areas of PWS during the summers of 1990 and 1991, based on comparison to observed changes in reference areas. This effect was not evident in subsequent years. Lance et al. (2001) reported stable densities of harlequin ducks in oiled areas of PWS during summer, and increasing densities during winter from 1989 through 1998; the increasing trend during winter could be interpreted as evidence of recovery of winter numbers. However, trends in oiled areas did not differ from those in unoiled areas (during summer or winter). Lance et al. (1999) interpreted this result as evidence of lack of recovery, under the premise that an EVOS-injured population

should have a higher growth rate than reference populations for convergence and thus recovery to be occurring. Alaska Department of Fish and Game surveys (Rosenberg & Petrula 1998) indicated that fall numbers significantly declined on oiled areas from 1995 through 1997, whereas numbers were stable on unoiled areas, consistent with a hypothesis that continued, negative effects of the EVOS were occurring during the time of their survey. Measures of other population attributes (age ratios, sex ratios and phenology) did not differ between oiled and unoiled areas (Rosenberg & Petrula 1998). Results of the US Fish and Wildlife Service and Alaska Department of Fish and Game support the general conclusions that harlequin duck populations were reduced in the years immediately after the spill, that populations were not increasing more quickly in oiled areas through at least 1998, and that the most powerful monitoring study indicated declines in wintering numbers in oiled areas through 1997, consistent with continuing negative effects of the EVOS.

Exxon Corporation sponsored studies to assess effects of the EVOS on marine birds (Wiens et al. 1996, Day et al. 1997, Murphy et al. 1997). These studies relied on data collected following the EVOS (1989 through 1991) in 10 bays in western PWS across a range of oil contamination levels. While designed to examine all marine birds, these studies also drew conclusions relevant to assessment of harlequin duck population status. Authors of these studies concluded that oil spill effects were short-lived for most bird species based on their response parameters of species richness (Wiens et al. 1996), habitat use (Day et al. 1997) and

summer abundance relative to prespill data (Murphy et al. 1997). In the studies that present results for harlequin ducks explicitly, Day et al. (1997) concluded that harlequin duck densities showed negative relationships with oiling intensity during 1989 and 1990, but not in 1991, and Murphy et al. (1997) concluded that summer abundance in western PWS did not differ from prespill numbers. Generally, these studies imply initial population injury and recovery within 2 yr; these results are contrasted with US Fish and Wildlife and Alaska Department of Fish and Game studies in our 'Discussion'.

As part of our research, we examined correlates of harlequin duck densities within oiled (Bay of Isles and Herring Bay on Knight Island) and unoiled (Montague Island) study areas (Fig. 1). We formally evaluated variation in duck densities in relation to habitat characteristics including substrate, exposure to wind and waves, distance to stream mouths and offshore reefs, intertidal slope, prey biomass and history of contamination by the EVOS (Esler et al. 2000a). Habitats within PWS are diverse, making it necessary to segregate effects of oil contamination from other naturally varying environmental factors (Wiens & Parker 1995). Persisting lower densities than expected on oiled areas (after accounting for other factors) could result from either failure of the population to recover from the immediate impact or from ongoing, longer-term negative effects of the EVOS; in either case, this result would be consistent with a lack of full population recovery. During 1995 to 1997, we surveyed densities of wintering harlequin ducks and measured habitat

attributes at 216 shoreline segments (113 on oiled Knight Island and 103 on unoiled Montague Island; Fig. 1). We used general linear models to evaluate variation in harlequin duck densities in relation to habitat attributes and history of oiling, using information-theoretic methods for model selection (Burnham & Anderson 1998). We found (Esler et al. 2000a) that harlequin duck densities during winter were related to several habitat attributes, including substrate type, distance to offshore reefs, distance to stream mouths, and exposure to wind and wave action (Table 1). After accounting for these habitat relationships and their interactions with area, oiling history was negatively related to harlequin duck densities (Table 1). These data are consistent with a hypothesis of lack of complete population recovery from the EVOS.

Table 1. *Histrionicus histrionicus*. Results of general linear model analyses to evaluate relationships of harlequin duck densities (square-root transformed) in Prince William Sound, Alaska, during winters 1995 to 1997, with habitat attributes and history of oil contamination by the 1989 'Exxon Valdez' oil spill. The parameter estimates (\pm SE) are from the best-fitting model, based on comparisons of all possible combinations of habitat attribute variables, habitat by area interactions and an area (history of oil contamination) term. From Esler et al. (2000a)

Response variable R^2	Explanatory variable	Parameter estimate
Ducks per 400 m 0.45	Intercept	1.17 \pm 0.12
	Reef 200–500 m ^a	0.51 \pm 0.15
	Stream 0–200 m ^a	0.34 \pm 0.14
	Full exposure to wind/waves ^a	0.45 \pm 0.12
	Mixed substrate ^a	0.32 \pm 0.14
	Mixed substrate \times Area ^b	–0.48 \pm 0.18
	Area ^b	–0.69 \pm 0.12
^a Parameter estimate value is the difference in duck density in relation to all other levels of the explanatory variable		
^b Reference value for area is unoiled Montague Island; parameter estimates are interpreted as effects on oiled Knight Island		

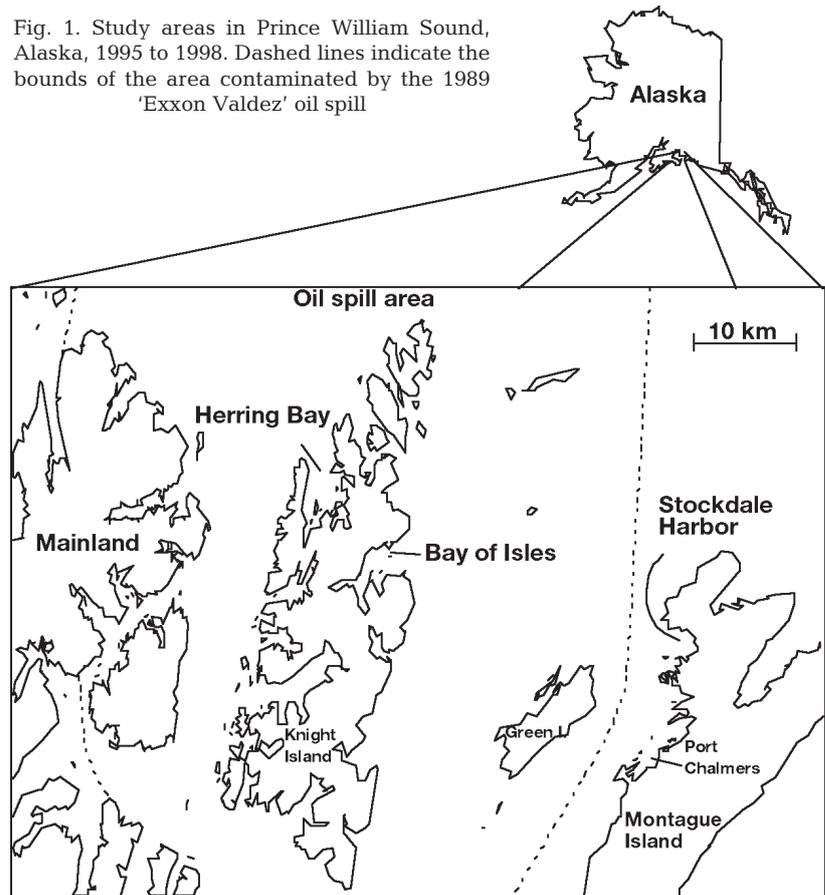
Adult female survival during winter

Within our research program, we used radio telemetry to measure adult female survival during winter (Esler et al. 2000b), because (1) population dynamics of species with a life history like harlequin ducks are particularly sensitive to adult female survival (Goudie et al. 1994, Schmutz et al. 1997); and (2), as described above, harlequin duck populations are sensitive to perturbations on wintering areas, which could result in reductions in survival. As an assessment of recovery status, we would predict similar harlequin duck winter survival between oiled and unoled areas in the absence of continuing EVOS effects. We also would predict survival rates that result in stable or increasing numbers on oiled areas if there were no lingering effects of the EVOS.

During autumns of 1995 through 1997, we captured adult females during wing molt throughout the oil spill zone and on nearby Montague Island (Fig. 1) and surgically implanted conventional radio transmitters. Radio signals ($n = 294$ over the 3 winters) were monitored by air approximately weekly from October through March. We used an information-theoretic approach for data analysis (Burnham & Anderson 1998, White & Burnham 1999), in which we contrasted the fit of our data to 11 models with various combinations of season and area (history of oil contamination) parameters.

The data strongly supported the inference that survival was lower in oiled areas than unoled areas (Esler et al. 2000b). The top 3 models, i.e. those with the best fit to the data, all included a difference in survival between areas. Further, models without an area term had very little support, emphasizing the importance of including a term for an area effect. Winter survival rates from the best-fitting model were 78.0% (SE = 3.3%) on oiled areas and 83.7% (SE = 2.9%) on unoled areas, due primarily to a divergence between areas during mid-winter (Fig. 2). We also determined that survival differences between oiled and unoled areas were more likely related to the history of oil contamination than intrinsic differences (such as habitat, disease, climate, social influences or predator densities); this was based on a closer evaluation of survival rates of birds from oiled Green Island, which is very close to Montague Island (Fig. 1) and is similar in most

Fig. 1. Study areas in Prince William Sound, Alaska, 1995 to 1998. Dashed lines indicate the bounds of the area contaminated by the 1989 'Exxon Valdez' oil spill



attributes. Survival of Green Island birds was much more similar to that of all oiled area birds combined than to Montague Island birds. Finally, we incorporated survival estimates into a pre-existing harlequin duck population model (Robertson 1997), holding all other parameters constant, to evaluate the effect of differences in survival on population dynamics. The estimate of annual population change (λ) was 0.9464 for oiled areas (i.e. annual population declines of about 5.4%). For unoled areas, $\lambda = 1.0054$, suggesting an approximately stable population. These estimates were consistent with the Alaska Department of Fish and Game (Rosenberg & Petrula 1998) fall survey results, showing declining numbers from 1995 to 1997 on oiled areas and stable numbers on unoled areas.

Variation in body mass and composition

Body mass and body composition (relative amounts of lipid and lean mass) are often used as indicators of individual and population health under the assumption that fitness increases with increases in mass and

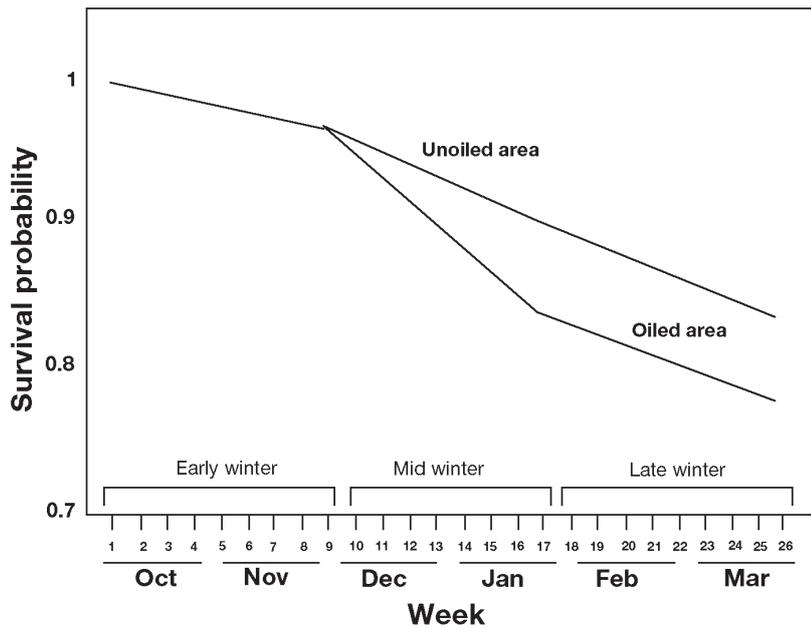


Fig. 2. *Histrionicus histrionicus*. Winter survival probabilities for adult females in Prince William Sound, Alaska based on radio telemetry data combined over winters 1995–1996 through 1997–1998 (Esler et al. 2000b)

energy reserves. This assumption is most likely to be untrue in a number of situations (King & Murphy 1985), i.e. optimal body mass may not be the maximum, particularly for birds. However, in our situation, in which we were comparing populations of harlequin ducks experiencing similar extrinsic environmental conditions with the exception of oiling history (and

Table 2. *Histrionicus histrionicus*. Effect sizes ($g \pm SE$) of body mass and composition comparisons between oiled and unoiled areas of Prince William Sound, Alaska. These are parameter estimates for an area term from multiple regression analyses and represent differences in body mass or composition between areas after accounting for the other explanatory variables in the bestfitting model. The reference value for the area term was unoiled areas and hence, the parameter estimates represent the difference in body mass or composition on oiled areas

Sex	Response variable	Season	
		Wing molt	Winter
Female			
	Body mass	-9.6 (± 2.6)	0.00 (± 0.0) ^a
	Lipid mass	-2.5 (± 0.7)	- ^b
	Lean mass	-7.0 (± 2.0)	- ^b
Male			
	Body mass	13.4 (± 4.5)	-21.5 (± 8.7)

^aThe area term was not included in the best-fitting model
^bLipid and lean mass were not estimated for females during winter

thus presumably similar body mass optima), differences in body mass between areas could reflect continuing effects of the EVOS. Thus, we would predict that EVOS effects related to changes in prey abundance or sub-lethal effects of oil exposure could result in lower body mass and smaller lipid reserves on oiled areas than unoiled.

We compared body mass between oiled and unoiled areas during wing molt (late summer and early fall) 1995 to 1997 and winter 1997–1998 as part of our research program, using general linear models to determine factors explaining variation in harlequin duck body mass and to evaluate any area differences after accounting for other explanatory variables. We used separate models for wing molt and winter and, within each season, separate models for each sex. To select the model from which we drew inference, we used Mallows's C_p values to contrast all possible combinations of explanatory variables (Burnham & Anderson 1998). Explanatory variables in wing molt models included year, age, 9th primary length (as a measure of stage of molt) and area. For winter, explanatory variables included age, season (December vs March and April) and area. We also compared estimated lipid and lean (lipid-free) masses of female harlequin ducks captured during wing molt based on condition indices created from a sample of collected harlequin duck females collected during wing molt for which composition was measured using laboratory analysis.

During wing molt, variation in female harlequin duck body mass was related to stage of wing molt, age and year. After accounting for effects of these variables, females averaged 9.6 g lighter on oiled areas than unoiled (Table 2). This represents 1.6% of average body mass of molting females on unoiled Montague Island. Similarly, estimated body lipid and lean averaged 2.5 and 7.0 g lower, respectively, in oiled areas than in unoiled areas. Like females, male body mass was related to stage of wing molt. After accounting for molt stage, average body mass differed by area, although unlike females, male body mass averaged 13.4 g higher in oiled areas than unoiled, a 2.0% increase over average body mass on unoiled areas.

During winter, female body mass varied with season (mid- vs late winter) and age; however, no area effect was detected (Table 2). Body mass of males also varied seasonally during winter and averaged 21.6 g lower in

oiled areas than unoiled areas, which corresponds to 3.3% of average body mass on unoiled areas.

Most of the body mass and composition data were consistent with a hypothesis of no continuing effects of the EVOS. Area differences during wing molt were small and were in different directions for males and females; the high statistical power due to the large sample size of captured birds allowed statistically significant detection of small differences of little biological meaning. The 21.6 g body mass difference between areas for male harlequin ducks during winter suggests potential residual EVOS effects; however, because the effect is relatively small and because females captured during the same time on the same areas did not show a similar effect, this does not constitute strong evidence of an EVOS effect.

We also tested whether body mass of wintering harlequin ducks was related to induction of cytochrome P4501A (CYP1A) (Trust et al. 1998), an indicator of exposure to oil (see 'Continued exposure to oil'). For birds captured during March and April 1998 on both oiled and unoiled areas, we used a regression approach to measure the effect of CYP1A on body mass after accounting for body mass variation due to sex. We found that sex-corrected body mass was negatively related (-0.11 ± 0.05 ; $\text{g pmol}^{-1} \text{min}^{-1} \text{mg}^{-1} \pm \text{SE}$) to 7-ethoxyresorufin-O-deethylase (EROD) activity (Fig. 3). These data suggest physiological consequences of oil exposure, with potential demographic consequences. Survival of some wintering ducks has been demonstrated to vary with body mass (Conroy et al. 1989, Longcore et al. 1991, Bergan & Smith 1993), indicating a mechanism linking contaminant exposure and reductions in survival.

Intrinsic limitations on population growth rates

Full recovery of harlequin duck populations could be delayed by the time needed for intrinsic population growth to replace birds removed by initial or early oil spill effects. In other words, even if negative effects related to the EVOS (mortality and emigration) had ended, the time required for demographic effects (recruitment and immigration) to rebuild populations to prespill conditions could be considered a constraint on full recovery. In this section, we review data on harlequin duck demography and population structure that lend insight into this possible mechanism constraining recovery.

Population models, based on demographic data collected from throughout the range of the harlequin duck (Goudie et al. 1994, Robertson 1997), provide an indication of population growth potential. Goudie et al. (1994) concluded that the potential growth rate of

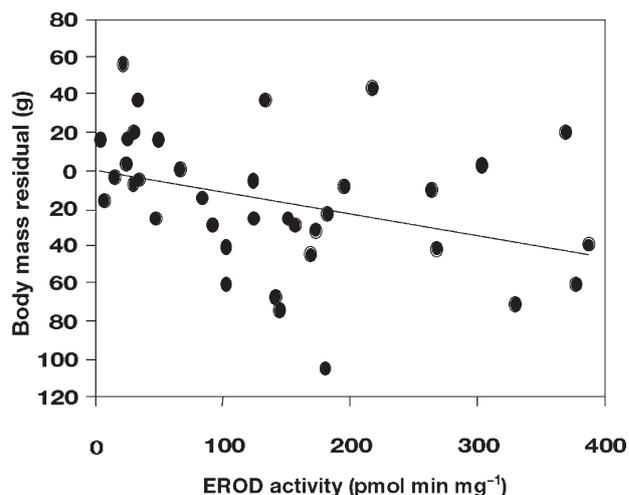


Fig. 3. *Histrionicus histrionicus*. Relationship of body mass residuals (i.e. accounting for mass differences between sexes) with CYP1A induction, as measured by liver 7-ethoxyresorufin-O-deethylase (EROD) activity, an indicator of exposure to polycyclic aromatic hydrocarbons (PAHs)

harlequin duck populations is low relative to most other ducks because of their life history strategy favoring high survival and long lifespans over high annual productivity. Other waterfowl with similar life histories also have low population growth rates (Schmutz et al. 1997). These data suggest that full recovery of harlequin duck populations could be delayed by the relatively long time frames needed for recruitment to replace birds removed as a result of EVOS effects, even if those effects were no longer operating.

Local wintering aggregations could constitute demographically independent subpopulations if site fidelity is high and dispersal among areas low (Cooke et al. 2000). We reviewed published studies addressing harlequin duck site fidelity and movements in coastal British Columbia; these studies consistently indicated high molt and winter site fidelity and low dispersal (Breault & Savard 1999, Robertson et al. 1999, 2000, Cooke et al. 2000). Also, Regehr et al. (2001) reported evidence that juvenile harlequin ducks accompany their mothers to wintering areas, which further indicates that local wintering groups represent aggregations that are largely independent.

We also examined data collected during our own studies to assess molt site fidelity based on recapture locations. We conducted captures of flightless (due to wing molt) birds along discrete, non-overlapping stretches of shoreline that were 1 to 3 km in length during falls of 1995 through 1997. These captures occurred throughout the oil spill zone and along Montague Island. For individuals that we captured in more

than 1 year, we summarized recaptures in relation to the distance from the original capture. Of 151 harlequin ducks recaptured during wing molt, 135 (89.5%) were in the same shoreline segment as their original capture, 10 (6.6%) were in an immediately adjacent shoreline segment (i.e. a segment within 1 km of the original capture segment) and 6 (4.0%) had moved to a molting area >1 km from their original capture location. Also, of the birds recaptured at a different shoreline segment, none was >20 km from its original capture location. Larger-scale movements may have occurred, but we would have detected them if they were common, given that we sampled broadly and intensively throughout western PWS. These data, and the results from other studies, indicate that groups of wintering harlequin ducks are largely demographically independent and that local subpopulation recovery would have to occur largely by recruitment rather than by immigration. Without positive inputs by immigration, local population recovery from the EVOS is more likely to be constrained.

Lancot et al. (1999) used genetic data to evaluate whether harlequin duck aggregations within the EVOS zone were demographically isolated. DNA was obtained from blood samples of molting harlequin ducks from oiled and unoiled areas of PWS, the Kodiak Archipelago and the Alaska Peninsula, which are separated at the scale of 100s of km. With this approach, significant differences in nuclear DNA allele frequencies or mtDNA haplotype frequencies among areas would be strong evidence that aggregations are demographically independent (e.g. Slatkin 1995) and, thus, that intrinsic limitations on population growth rates

could constrain population recovery. However, Lancot et al. (1999) found that molting aggregations in PWS, the Kodiak Archipelago and the Alaska Peninsula did not have different allele or haplotype frequencies. Lack of genetic differentiation does not necessarily imply demographic panmixia; genetic panmixia also could occur from historical gene flow or from low levels of immigration (Wright 1931) that have little effect on local demography.

Continued exposure to oil

Exposure to oil has been documented to have a suite of deleterious toxic (Leighton 1993) and energetic (Jenssen 1994) consequences for birds. To determine if harlequin ducks in PWS were still being exposed to residual oil, we (Trust et al. 2000) measured induction of CYP1A in harlequin ducks captured during March and April 1998 in both oiled and unoiled areas. CYP1A is induced upon exposure to polycyclic aromatic hydrocarbon (PAH) constituents of crude oil and has proven to be a sensitive and fairly specific indicator of oil exposure (e.g. Woodin et al. 1997). In addition to oil-derived PAHs, certain polychlorinated biphenyl (PCB) congeners can induce CYP1A systems (Rattner et al. 1994). Therefore, we also measured congener-specific PCB concentrations in plasma from harlequin ducks wintering in PWS to contrast with CYP1A enzyme activity. Evidence of exposure to oil would not necessarily imply that exposure had adverse physiological or demographic consequences. However, evidence of exposure would be consistent with potential for these deleterious consequences, and could be interpreted in light of other available data as a possible mechanism constraining full population recovery.

Liver EROD activity (\pm SE) is an indicator of CYP1A induction. EROD activity in wintering harlequin ducks was higher in oiled areas (204.6 ± 20.3 pmol min^{-1} mg protein $^{-1}$, $n = 19$) than on unoiled Montague Island (70.7 ± 21.5 pmol min^{-1} mg protein $^{-1}$, $n = 18$, $p < 0.001$; Fig. 4; Trust et al. 2000). This is strong evidence of continued exposure to 'Exxon Valdez' oil, given that background PAH concentrations in intertidal sediments and mussel tissues were negligible in PWS immediately prior to the EVOS (Short & Babcock 1996). Area differences in CYP1A induction could not be explained by differences in PCB exposure (Trust et al. 2000); congener-specific PCB concentrations were low and did not differ between areas. These data suggest that continued oil exposure could be limiting population recovery if there were physiological and population consequences of this exposure.

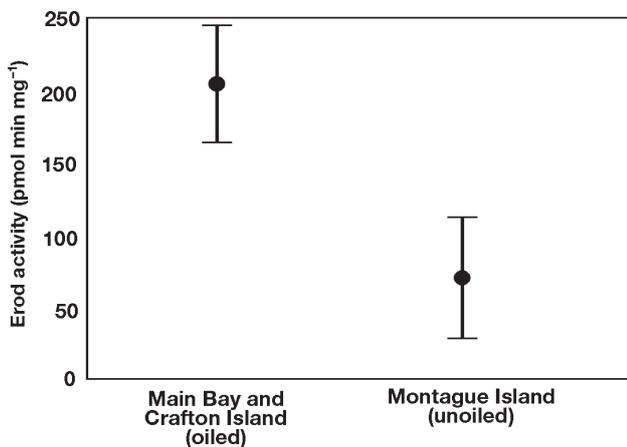


Fig. 4. *Histrionicus histrionicus*. Comparisons of average (\pm 95% confidence intervals) liver 7-ethoxyresorufin-O-deethylase (EROD) activity, as a measure of CYP1A induction, of harlequin ducks captured from oiled and unoiled areas of Prince William Sound, Alaska in March and April 1998 (Trust et al. 2000)

Food limitation

Food limitation could constrain population recovery if the EVOS resulted in reduction in abundance of harlequin duck prey. This could occur from either direct effects (e.g. acute toxicity or habitat destruction during cleanup activities) or indirect effects (e.g. changes in food web structure; Peterson 2001). In turn, prey reductions could lead to increased intraspecific competition or reduced health of individuals, either of which could have population-level consequences.

During winter, the diet of harlequin ducks consists of a broad array of benthic marine invertebrates, especially amphipods, limpets, other snails, chitons and mussels (Vermeer 1983, Goudie & Ankney 1986, Gaines & Fitzner 1987, Goudie & Ryan 1991, Patten et al. 2000). Goudie & Ankney (1986) hypothesized that harlequin ducks are trophic generalists because they must feed continuously to meet metabolic needs during winter; high energy prey (e.g. amphipods) are consumed when encountered, but lower quality prey are consumed when high energy prey are not available.

Effects of the EVOS on populations of several important harlequin duck prey were evaluated by sampling at multiple pairs of oiled and unoiled sites in intertidal and nearshore subtidal habitats shortly after the spill (Highsmith et al. 1996, Jewett et al. 1999). Numerically dominant taxa within several important harlequin duck prey groups (limpets, other snails, mussels and amphipods) were reduced in density by the oil spill. At oiled sites, numbers of *Mytilus trossulus* (mussels), *Tectura persona* (limpets) and *Littorina sitkana* (littorine snails), were reduced in the years following the EVOS (Highsmith et al. 1996). Similarly, several numerically dominant amphipod taxa were reduced at oiled sites in the nearshore subtidal zone (Jewett et al. 1999). Many of these differences in mean abundance at oiled and reference sites were no longer evident in 1993 (Hooten & Highsmith 1996, Houghton et al. 1996), suggesting that recovery of the intertidal and nearshore subtidal community was well underway. However, the last reported values suggest that there continued to be fewer individuals of some important prey at selected oiled sites, at least through 1993 in the intertidal (Hooten & Highsmith 1996, Houghton et al. 1996) and through 1995 in the subtidal (Jewett et al. 1999) sites. Reduced prey densities at oiled sites can be largely attributed to the direct toxic effects of oil and impacts associated with cleanup procedures (Boehm et al. 1995, Houghton et al. 1996, Wolfe et al. 1996, Jewett et al. 1999). These results are consistent with food limitation of harlequin duck population recovery, at least within the few years immediately following the EVOS.

We estimated availability of harlequin duck prey items (Esler et al. 2000a) on oiled Knight Island (Bay of

Isles and Herring Bay) and unoiled Montague Island study areas (Fig. 1) in summer 1997. Although prey availability may vary seasonally, we assumed that relative differences between study areas in summer would also reflect relative winter prey abundance because these invertebrates, as a rule, do not experience multiple generations within the year. To sample intertidal blue mussels *Mytilus trossulus*, we removed all mussels from within 10 500 cm² quadrats placed in the mussel zone of each site. Ash-free dry mass of each mussel 5 to 25 mm in length (the size range appropriate for consumption by ducks) was estimated based on predictive equations of biomass by length. Samples of other invertebrate prey (limpets, chitons, lacunid snails, littorine snails, other snails, amphipods and other crustaceans) were obtained at 6 intertidal and shallow subtidal locations within each prey sampling site. All epifauna were removed from a 0.25 m² quadrat at each location. Ash-free dry weights of each prey item <25 mm in length were determined using a muffle furnace. We compared 2 metrics of food availability between areas: food biomass density and total food biomass relative to harlequin duck abundance. Food biomass density was defined as average g ash-free dry weight per 100 m²; we used *t*-tests to compare food biomass densities between areas. Total food biomass was estimated as density expanded to the area of potential foraging for each sampling site (a 200 m shoreline segment by the width of the intertidal zone). Average total food biomass across sampling sites was divided by average number of harlequin ducks per sampling site to generate the metric describing food availability per duck; variance was calculated for a ratio of 2 independent estimates (Seber 1973) and 2-tailed Z-scores were calculated to compare areas (Snedecor & Cochran 1980). Biomass density and total food biomass comparisons were conducted for all food items combined and also with mussels excluded because mussel abundance was much higher than for other prey species, yet they constitute a relatively minor part of the diet. Higher food densities or more food per duck on oiled than unoiled areas would imply that food limitation does not constrain recovery. Similar densities or quantities of food per duck between areas would be somewhat equivocal. Higher food densities or more food per duck on unoiled areas than oiled would be consistent with food limitation to population recovery. In 1997, food biomass densities were similar between oiled Knight Island and unoiled Montague Island study areas (Esler et al. 2000a; Table 3). Also, on a per duck basis, total food biomass was similar between areas (Table 3). These data were highly variable, but generally consistent with a hypothesis of no food limitation to population recovery.

Food variables were also incorporated into habitat association models to determine whether harlequin

duck densities were related to food biomass density or total food biomass (Esler et al. 2000a). Strong relationships between food density or abundance and duck densities would suggest that harlequin ducks may be susceptible to food limitation. Biomass density and total biomass of harlequin duck prey items did not explain additional variation in harlequin duck densities beyond effects of habitat and history of oil contamination (Esler et al. 2000a). However, when data for mussels were excluded, prey biomass density was slightly, positively related to harlequin duck density, although this was strongly influenced by a single observation, without which there was no relationship.

Finally, body mass (see above) should provide strong evidence for the potential for food limitation. We would expect body mass to be lower in oiled than unoiled areas if food were limiting recovery, although other factors also could cause body mass differences. Body mass (see above) did not differ dramatically between areas, suggesting that food limitation was not occurring.

DISCUSSION

Injury and recovery status

Our harlequin duck studies, and this review, were focused on effects of the EVOS at the level of the population. We agree with Underwood & Peterson (1988), who described population-level evaluation as a link between the physiological mechanisms that affect individuals, subsequent effects on demography, and potential impacts on community and ecosystem processes. In this light, we summarize the findings of our review in terms of level of biological organization (Table 4) and discuss the implications for population injury and recovery.

The evidence from postspill harlequin duck research and monitoring supports the conclusions that (1) harlequin duck populations were reduced by the EVOS; (2) these populations had not fully recovered by 1998; and (3) continued, direct effects of the EVOS were still

occurring for as long as 9 yr after the EVOS. Key data (Table 4) leading to these conclusions include evidence of acute harlequin duck mortality immediately following the spill (J. Piatt pers. comm.), continued exposure of harlequin ducks to oil through at least 1998 (Trust et al. 2000), differing fall population trends in oiled and unoiled areas from 1995–1997 (Rosenberg & Petrula 1998), lower densities than expected on oiled areas during winters 1995–1996 and 1996–1997 (Esler et al. 2000a) and differences in adult female survival between oiled and unoiled areas during winters 1995–1996 through 1997–1998 (Esler et al. 2000b). These results are internally consistent, i.e. predictions from each study are confirmed in the others. Differences in adult female survival offer a likely mechanism for divergence in population trends between areas. Under conditions of low survival, population declines and high site fidelity, densities would be expected to be depressed in the oiled area, which we observed. The adult female survival analysis is particularly important for our interpretation; it demonstrates continued EVOS effects and describes the demographic mechanism that would lead to persistent population declines. Missing from these studies (Table 4) is a clear link between exposure and subsequent variation in survival; changes in physiology and metabolism presumably result from oil exposure (Leighton 1993, Jenssen 1994), although such responses are difficult to detect under field conditions. Laboratory experiments addressing these mechanisms would be exceedingly useful. The negative relationship between CYP1A induction and body mass suggests that such a mechanism may have been operating. Also, there are no data that address changes in community structure or ecosystem processes that may have resulted from lack of recovery of harlequin duck populations (Table 4); hence, it is impossible to evaluate indirect effects on other system components or processes.

Not all studies of harlequin duck population status and trends give consistent conclusions. US Fish and Wildlife marine bird survey data (Lance et al. 1999) suggest increasing numbers on oiled areas during winter through 1998, consistent with ongoing population

Table 3. Biomass density and total biomass of harlequin duck prey (amphipods, chitons, limpets, other snails and mussels <25 mm) at oiled and unoiled study areas within Prince William Sound, Alaska, 1997 (mean \pm SE)

Parameter	Montague Island (unoiled)	Knight Island (oiled)	p
Biomass density (g AFDW ^a per 100 m ²)	2030.8 (\pm 555.2)	1964.1 (\pm 638.9)	0.94 (t = 0.08)
Total biomass (kg AFDW per duck)	51.8 (\pm 16.4)	100.5 (\pm 52.0)	0.81 (Z = 0.24)
Biomass density without mussels (g AFDW per 100 m ²)	45.9 (\pm 10.1)	42.8 (\pm 7.3)	0.80 (t = 0.251)
Total biomass without mussels (kg AFDW per duck)	3.9 (\pm 1.2)	3.2 (\pm 1.5)	0.94 (Z = 0.08)

^aAsh free dry weight

Table 4. *Histrionicus histrionicus*. Summary of findings from studies relevant for understanding harlequin duck population injury, status of population recovery and constraints on full recovery in Prince William Sound (PWS), Alaska, following the 1989 'Exxon Valdez' oil spill. Findings are arranged by level of biological organization and interpreted in terms of population processes

Parameter	Findings	Source
Individual		
Oil exposure	Hydrocarbon metabolites in 1989 to 1990 Elevated CYP1A through 1998 on oiled areas	Patten et al. (2000) Trust et al. (2000)
Mass variation	No consistent, strong population-level differences between areas Negative relationship between mass and CYP1A induction in late winter	This document This document
Population demography		
Initial mortalities	Approximately 1000	Piatt et al. (1990), J. Piatt pers. comm.
Adult female survival	Lower in oiled areas than unoiled areas	Esler et al. (2000b)
Dispersal	Generally low in the species; molt site fidelity high in PWS	Breault & Savard 1999, Robertson et al. (1999), Cooke et al. (2000), This document
Reproduction/recruitment	Similar age ratios between areas; most breeding outside PWS	Rosenberg & Petrula (1998)
Population status		
Abundance/densities	Lower densities on oiled areas during summers 1990 and 1991 Summer abundance 1989 to 1991 unchanged from pre-spill Stable summer and increasing winter densities in oiled areas 1989 to 1998 Similar summer and winter trends in density 1989 to 1998 Numerical declines during fall of 1995 to 1997 on oiled areas, stable on unoiled Densities lower than expected on oiled areas, winter 1995 to 1997 Densities related to oiling intensity 1989 to 1990, not 1991 Population model predicts declines on oiled areas, stable on unoiled	Irons et al. (2000) Murphy et al. (1997) Lance et al. (2001) Lance et al. (2001) Rosenberg & Petrula (1998) Esler et al. (2000a) Day et al. (1997) Esler et al. (2000b)

recovery, although these surveys are statistically less powerful than those of the Alaska Department of Fish and Game (Rosenberg & Petrula 1998) that described declining numbers on oiled areas. However, lack of differences in population trends between oiled and unoiled areas based on the US Fish and Wildlife Service surveys was interpreted as evidence of lack of recovery (Lance et al. 1999).

Wiens et al. (1996) reported rapid recovery of bird communities following the EVOS based on measures of species richness and diversity. These parameters are derived from measures of presence or absence of a species within the study areas. For understanding recovery of populations, occurrence in oiled habitats is an incomplete measure. For example, occurrence of harlequin ducks in oiled areas most likely reflects high site fidelity (Cooke et al. 2000) despite deleterious changes in habitat quality (Hilden 1965, Cooch et al. 1993) and declines in abundance. Occurrence in an area does not indicate a recovered population; populations could, in fact, be declining or a demographic 'sink' (Pulliam 1988). We agree with Paine et al. (1996) that measures of demographic processes are more

powerful measures of injury and recovery than occurrence or abundance.

The habitat use studies of Day et al. (1997) indicated no EVOS effects on harlequin ducks during winter 1989 to 1991, in contrast to our findings of lower densities on oiled than unoiled areas (Esler et al. 2000a). This inconsistency may be a consequence of accumulating deleterious effects of the spill that extended beyond the study period of Day et al. (1997) and through at least our study period (Rosenberg & Petrula 1998, Esler et al. 2000, Trust et al. 2000). Thus, density differences may have been larger and more detectable during our study in 1995 to 1997 than in 1989 to 1991. Also, we collected harlequin duck abundance and habitat data at the scale that harlequin ducks use wintering sites (i.e. 100s of m reflecting specific shoreline segments; Robertson et al. 1999, Cooke et al. 2000) rather than at the scale of entire bays used by Day et al. (1997); our approach presumably results in greater resolution and power to determine habitat affiliations and evaluate oil spill effects.

Because most harlequin ducks wintering in PWS breed elsewhere, results of pre- and postspill compar-

isons of summer abundance by Murphy et al. (1997) have limited relevance for understanding dynamics of wintering populations, which we consider to be the core, demographically distinct population segments. Also, although Murphy et al. (1997) had high power for detecting a 50% postspill population decline, they did not report power for detecting smaller but biologically meaningful reductions (e.g. 10%). In fact, they estimated 13.5, 6.4 and 11.9% reductions in harlequin duck numbers from prespill counts in 1989, 1990 and 1991, respectively, although these were not statistically significant. In contrast, Irons et al. (2000) detected significant negative effects for summer harlequin duck numbers in 1990 and 1991.

Body mass comparisons between oiled and unoled areas did not indicate a mechanism for the observed lack of recovery. However, differences in body mass that are demographically relevant may be difficult to detect in wild populations, as significant mass declines may precede death by only a short period, particularly for animals naturally existing near a metabolic threshold (Goudie & Ankney 1986). For example, body mass declines in captive, oiled mallards faced with other environmental stressors were detectable only within 2 wk of death (Holmes et al. 1979). Because dead animals are not available to sample, detecting population-level differences in body mass or condition of field-captured ducks may be unlikely. The subtle but significant body mass decline with increasing CYP1A induction (Fig. 3) suggests that oil exposure may have been directly linked to changes in physiology of individuals.

Our conclusion of lack of full population recovery is supported by those data sets and approaches that are most powerful for assessing population status. Below we consider the potential mechanisms involved in lack of full population recovery.

Intrinsic limitations on population growth rates

Aggregations of harlequin ducks on wintering areas constitute demographically independent subpopulations from a population structure standpoint (Cooke et al. 2000). Winter site fidelity of harlequin ducks is high (Robertson 1997, Cooke et al. 2000) and pair formation occurs on the wintering areas (Gowans et al. 1997, Robertson et al. 1998). Because dispersal from wintering areas is limited, recovery of groups of birds in oiled areas must occur primarily through recruitment specific to that group (i.e. immigration from other areas does not contribute much to population change). Thus, factors that affect wintering aggregations are influencing subpopulations that are largely distinct demographic units, suggesting that harlequin ducks may be

susceptible to constraints on population recovery due to intrinsic demographic limits to population growth rates.

However, demographic limitations on population growth rate cannot be invoked as the primary constraint to harlequin duck population recovery until lingering effects of the EVOS on survival are gone and the population in the oil spill zone can achieve positive growth. This was not the case through 1998, and the time frame for cessation of EVOS effects is unknown. However, once freed from other constraints to recovery (see below), recovery of populations will then be limited by the time necessary for intrinsic rates of increase to operate (Goudie et al. 1994). Because it is not clear what naturally regulates harlequin duck populations, nor the life stage where regulation or limitation occurs, it is difficult to predict recovery times of an injured winter harlequin duck subpopulation.

Results from genetic studies offer some good news for harlequin duck populations. Levels of dispersal, either historical or contemporary, have resulted in subpopulations within the oil spill zone that are not genetically distinct (Lanctot et al. 1999), i.e. the EVOS does not threaten a unique genetic resource. Also, these results may reflect low levels of juvenile dispersal that we were unable to detect; if this is the case, population recovery could be enhanced by some immigration.

Continued exposure to oil

A growing body of evidence indicates that PAHs from residual 'Exxon Valdez' oil were responsible for the observed CYP1A induction in oiled areas of PWS in sea ducks (Trust et al. 2000) and several other vertebrates (Marty et al. 1997, Woodin et al. 1997, Bodkin et al. 2002, Jewett et al. 2002). However, exposure does not necessarily indicate effects on individuals or populations (Underwood & Peterson 1988). A critical question is whether oil exposure could cause physiological challenges that affect demographic properties which, in turn, have population-level consequences.

As described above, our data on adult female winter survival offer a likely explanation for continued injury to harlequin duck populations and, hence, lack of recovery. Although the survival differences between oiled and unoled areas may appear small, harlequin duck population dynamics are particularly sensitive to changes in adult female survival (Goudie et al. 1994) because their life history is oriented toward long reproductive lifespans (Stearns 1992). Oil exposure (Leighton 1993, Jenssen 1994) could negatively affect harlequin duck health and subsequent survival. Continued oil exposure was the most likely mechanism constraining full population recovery through at least 1998.

Most laboratory studies have shown that mallards *Anas platyrhynchos* do not suffer acute toxic effects of oil ingestion until very high doses. These studies have been used to infer that harlequin ducks also should not suffer deleterious physiological responses to residual 'Exxon Valdez' oil (Stubblefield et al. 1995, Boehm et al. 1996). However, these lab studies have been conducted under relatively benign conditions. Other lab studies have found that, with addition of other stressors such as cold temperatures, ducks that ingested oil suffered higher mortality than unoiled birds (Holmes et al. 1978, 1979). This is a more appropriate analog for wild harlequin ducks, which exist under winter conditions with cold temperatures and limited foraging time and, hence, little flexibility for accommodating additive stresses (Goudie & Ankney 1986).

The divergence of survival probabilities between oiled and unoiled areas during midwinter (Fig. 2) is consistent with the hypothesis that effects of oil are exacerbated by other stressors. Midwinter is presumably the most stressful period for harlequin ducks under natural conditions. Harlequin ducks feed by sight and during midwinter, when day length is shortest, they spend most of their day time foraging (Fischer 1998, Goudie & Ankney 1986). PWS is one of the northernmost wintering areas for harlequin ducks (Robertson & Goudie 1999); thus, daylight available for foraging is particularly limited. We therefore suggest that observed differences in winter survival and population trends are linked to observed differences in contaminant exposure.

Oil exposure could occur through consumption of contaminated prey. In the marine environment, oil constituents can accumulate in bottom sediments and benthic, filter-feeding invertebrates (Fukuyama et al. 2000, Peterson 2001). Studies have documented hydrocarbons in harlequin duck prey from immediately post-spill through 1995 (Boehm et al. 1995, Babcock et al. 1996, Short & Babcock 1996, Wolfe et al. 1996, Patten et al. 2000). Also, contamination could occur through external contact with residual oil; surface sheening was observed in nearshore areas of PWS during the same period as our studies (Hayes & Michel 1999), suggesting that this also could be a potential route of exposure. Metabolic consequences of external oiling are well documented (Jenssen 1994) and could result in increased mortality.

Food limitation

Available evidence suggests that food availability or quality is not limiting harlequin duck population recovery. Recovery of most duck prey, lack of a strong relationship between harlequin duck densities and

food biomass density or abundance, similar food biomass density and abundance per duck between areas, and similar body masses between areas all support this conclusion.

Interpretation of food data is hampered by a lack of understanding of harlequin duck foraging strategies and the role of winter food abundance, density or quality in harlequin duck population regulation or limitation. Furthermore, we have no data to test causal, mechanistic relationships between winter food supply and carrying capacity. Thus, body mass data provide perhaps the strongest evidence against food limitation. Because harlequin duck body masses across seasons, sexes and ages did not show a consistent difference between oiled and unoiled areas, we conclude that food is unlikely to be a primary constraint to recovery of populations from oiled areas.

CONCLUSIONS AND RECOMMENDATIONS

We conclude that, as of 1998, harlequin duck population recovery had not occurred, that continued oil exposure may be the primary mechanism constraining recovery and that lack of full recovery most likely will be further delayed after deleterious EVOS effects are gone due to intrinsic demographic limits to population growth rates. Our findings are concordant with studies of other nearshore vertebrates. For example, sea otters *Enhydra lutris* had elevated CYP1A (B. Ballachey unpubl. data), increased mortality in oiled areas through at least 1998 (Monson et al. 2000) and lack of return to pre-spill numbers in the most heavily oiled areas of PWS (Bodkin et al. 2002). Like harlequin ducks, food limitation did not appear to limit sea otter population recovery (Dean et al. 2000, 2002). However, sea otters and harlequin ducks both rely on benthic invertebrate prey that can accumulate hydrocarbons, which may explain the parallel findings.

Response of bird populations to the EVOS varied considerably. Populations of some bird species were apparently not reduced by the EVOS or recovered quickly (Bowman et al. 1995, 1997, Wiens et al. 1996). Black oystercatcher *Haematopus bachmani* breeding was depressed in 1989 to 1990 but nearly recovered by 1991 (Andres 1997). Direct effects of oil exposure and indirect effects of prey reduced by the EVOS were indicated as constraints to full recovery of injured pigeon guillemot *Cephus columba* populations in PWS for at least a decade (Golet et al. 2002). Harlequin duck populations have an unfortunate combination of characteristics that make them particularly vulnerable to effects of the oil spill during nonbreeding parts of the annual cycle. These characteristics include a life history requiring high adult survival, occurrence in

nearshore habitats that are strongly affected by oil spills and that may hold residual oil for years, adaptation to stable and predictable marine environments, high site fidelity and a diet of benthic invertebrates. The traits of harlequin ducks that make them (and other wildlife species sharing these traits) vulnerable to catastrophic oil spill effects also render them susceptible to effects of chronic, low-level pollution. Sensitive species like harlequin ducks, sea otters and pigeon guillemots appear to suffer deleterious effects of oil pollution at lower levels and for longer time periods than other species. The duration of the population level effects far exceeds the few years that have conventionally been assumed to represent recovery times for wildlife populations injured by oil pollution.

Acknowledgements. This work was funded primarily by the *Exxon Valdez* Oil Spill Trustee Council; the findings and conclusions are those of the authors and do not necessarily reflect the views or position of the Trustee Council. Administrative and financial support was also provided by the US Geological Survey and the US Fish and Wildlife Service. Duck data collection was assisted by: Brian Baetsle, Rick Ballas, Jeb Benson, Brad Benter, Katherine Brenner, Kathy Burek, Paul Cotter, Jennifer DeGroot, Bob Jarvis, Aaron Johnson, Jeffrey Mason, Danielle Mather, Dan Monson, Julie Morse, Dan Mulcahy, April Nielson, Jennifer Pratt, Dan Ruthrauff, Dorcas Schaeffer, Ted Spencer, Mike Stattleman and Michael Stoskopf. Field assistance for prey sampling included Christine Brodersen, Mary Drew, Daniel Fremgen, Patricia Harris, Max Hoberg, Dennis Jung, Erica Leder, Mandy Lindeberg, Bruce March, Anita Martin, Joshua Millstein, Jon Moreland, Jerry Phillips, Jeffrey Reglin, Michelle Sleeter, Justin Stekoll, Robert Thomas and Noele Weemes. Lab analysis of invertebrate prey was conducted by Mary Drew, Max Hoberg, Mandy Lindeberg, David Love, Bruce March, Joshua Millstein and Justin Stekoll. We thank the captains and crews of the vessels 'Auklet', 'Discovery', 'Julia Breeze', 'Kittiwake II' and 'Waters' for vessel support, and the staff of Fishing and Flying for aerial support and telemetry data collection. We thank Bob Jarvis, Bruce Menge, Cliff Pereira, Pete Peterson, Greg Robertson and Dan Roby for comments on earlier drafts of this manuscript.

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Editorial responsibility: Charles Peterson (Contributing Editor), Morehead City, North Carolina, USA

Submitted: January 3, 2001; Accepted: April 26, 2002
Proofs received from author(s): September 10, 2002

Long-term direct and indirect effects of the 'Exxon Valdez' oil spill on pigeon guillemots in Prince William Sound, Alaska

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ABSTRACT: We conducted a study to determine mechanisms constraining population recovery of pigeon guillemots *Cephus columba* following the 1989 'Exxon Valdez' oil spill. We asked whether recovery was limited by continuing exposure to residual oil, reduced prey availability, or other causes. Our approach was to compare demographic, physiological, and behavioral parameters between an oiled site pre- and post-spill, and between the oiled site and an unoiled site post-spill. Adult mass, body condition, and nestling survival were significantly lower at the oiled site post-spill compared to pre-spill. After the spill, guillemots increased in number at the unoiled site and chicks fledged at significantly heavier weights than at the oiled site, where populations remained depressed. Elevated hepatic cytochrome P4501A (CYP1A), aspartate aminotransferase (AST), and lactate dehydrogenase (LDH) enzyme activities detected in adult guillemots a decade after the spill at the oiled site suggest that continued exposure to residual oil may have limited population recovery, although reduced availability of sand lance, a preferred forage fish, may have also played a role. Previous studies conducted at the oiled site demonstrated that guillemot chick growth and reproductive success were positively related to the percentage of high-lipid forage fishes, such as sand lance, in the chick diet. Aspects of sand lance life history and the pattern of 'Exxon Valdez' oil deposition strongly suggest that sand lance were impacted by the spill, although we lack direct evidence of this, and reductions in this species' abundance may have also resulted from natural causes. Our study suggests that the recovery of a top-level generalist predator may be constrained by both direct effects (continued exposure to residual oil) and indirect effects (reduced availability of a key prey species) following a large-scale perturbation. Furthermore, it demonstrates that recovery following oil spills may take considerably longer for certain species than the few years that have been proposed as typical for marine birds.

KEY WORDS: 'Exxon Valdez' · Oil spills · Marine birds · *Cephus columba* · Pigeon guillemot · Prince William Sound · Blood parameters · Reproductive performance

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INTRODUCTION

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It is well recognized that oil spills can have immediate adverse effects on wildlife populations because

organisms are often killed outright and en masse following exposure (Bourne et al. 1967, Dunnet 1982). Nonetheless, quantifying population-level impacts can be very difficult. Pre-spill population estimates are often unavailable, and initial impact mortalities due to oiling are typically hard to quantify (Parrish & Boersma 1995, Piatt & Ford 1996). Estimating the duration of sustained injury and identifying mechanisms that constrain population recovery following initial impacts is more challenging still, as this requires that both pre-perturbation and current population status be known.

When pre-spill population estimates are available, they are often not comprehensive estimates. For marine birds and mammals, for example, pre-spill population estimates are typically based on counts of breeding adults at their colonies. Assessing injury based upon these counts may underestimate impacts, however, as mortalities of subadults and non-breeders may not be accounted for, and mortalities of breeders may be masked when non-breeders fill vacancies at the colony. Non-breeder replacement may explain why colony-based studies typically identified oil-spill effects on seabirds as short-lived (Birkhead & Hudson 1977, Stowe 1982, Boersma et al. 1995), even though the projections of empirical population models suggest that effects should be longer lasting (Samuels & Lanfear 1982). Empirical support for the notion that colony-based studies in themselves present inadequate estimations of population injury comes from east Britain, where the death of 30 000 auks in late winter had no detectable effects on nearby breeding populations in the subsequent spring (Harris & Wanless 1984).

A better approach for assessing injury to marine bird populations involves comparing geographically broad-based population surveys made before and after a perturbation. Surveys of this type were conducted for marine birds in Prince William Sound (PWS) before and after the 1989 'Exxon Valdez' oil spill (hereafter EVOS). Using a before-after-control-impact design with paired sampling (Osenberg et al. 1994), Murphy et al. (1997) compared pre- and post-spill (through 1991) densities of birds along oiled and unoiled shorelines in PWS. Their analysis revealed that of all marine birds in PWS, the impacts of the spill on abundance and distribution were most pronounced for pigeon guillemots *Cephus columba*. Murphy et al. (1997) stated, 'The Pigeon Guillemot was the one species that...showed persistent declines in overall abundance relative to pre-spill baseline, (and further was the marine bird species that) showed the greatest negative impacts and the fewest signs of recovery'. Irons et al. (2000) performed analyses similar to those of Murphy et al. (1997), but based on surveys that covered a wider geographic area, over a longer time span. The results corroborated those of Murphy et al.

(1997) but further demonstrated that spill effects continued through 1998, 9 yr after the oiling event.

Given clear evidence that guillemot populations in oiled areas of PWS were negatively impacted and not recovering, we initiated a study to determine whether recovery was limited by continuing exposure to residual oil, prey availability, or other causes. Our approach was to compare demographic, behavioral, physiological, and dietary parameters between an oiled site pre- and post-spill, and between the oiled site and an unoiled site post-spill. Our study subsumes data previously collected and analyzed by Oakley & Kuletz (1996). Oakley & Kuletz assessed the effects of EVOS on pigeon guillemots by comparing components of reproductive success measured at an oiled site in the 2 yr immediately following the spill with measures drawn from the same site a decade prior. They found that overall productivity was significantly lower after the spill, but did not attribute the difference to an oil spill effect. Instead, increased post-spill predation on guillemot nests was suggested as the cause (Oakley & Kuletz 1996). Their study did, however, show that chick growth rates tended to be lower following the spill, leaving open the possibility that residual oil continued to affect the birds.

In this paper we suggest that the recovery of a top-level generalist predator may be constrained by both direct effects (continued exposure to residual oil) and indirect effects (reduced availability of a key prey species) following a large-scale perturbation, and further, that recovery following oil spills may take considerably longer for certain species than the few years that have been proposed as typical for marine birds.

Our study fits into a larger context of work that reports on effects of EVOS on a wide assemblage of marine organisms (reviewed by Peterson 2001) including invertebrates (Fukuyama et al. 2000), fishes (Jewett et al. 2002), mammals (Bowyer et al. 1995, Ben-David et al. 2001, Bodkin et al. 2002, Dean et al. 2002) and birds (Irons et al. 2000, Esler et al. 2002).

BACKGROUND

Following the grounding of the supertanker 'Exxon Valdez' on Bligh Reef on the morning of 24 March 1989, $\sim 4.1 \times 10^7$ l of North Slope crude oil spilled into the waters of PWS. Although approximately 20% of the spilled oil volatilized, and a further 20% left the Sound, 60% of the spilled oil was retained in PWS, either sinking or coating shorelines (Wolfe et al. 1994). Oil spread from the spill site southwest across PWS, first hitting the central island groups (Naked & Knight Islands), and then mainland shorelines and adjacent islands (Galt et al. 1991, Neff et al. 1995) (see inset map

of Fig.1). The 'Exxon Valdez' spill differed from other large spills (e.g. the TV 'Braer' spill) because it occurred in an area protected from large seas by barrier islands, and because the bulk of the spilled oil formed a slick that did not disperse into the water column (Kingston 1995). Although oil concentrations declined rapidly in the first few years following the spill (Neff et al. 1995, O'Clair et al. 1996), as recently as 1997, residual oil from EVOS was still found in many intertidal and subtidal zones of the Sound (Hayes & Michel 1999).

An estimated 250 000 seabirds were killed outright by EVOS (Piatt & Ford 1996). Of approximately 30 000 oiled carcasses that were recovered following the spill, ~12% were collected in PWS, with alcids (32%, primarily murrets *Uria aalge*), sea ducks (26%), and cormorants (16%) dominating the carcass recoveries (Piatt et al. 1990). Various aspects of their life history may make alcids, and guillemots in particular, especially vulnerable to oil spills (King & Sanger 1979). Guillemots typically forage in nearshore benthic environments, which can be significant repositories for spilled oil. They spend large portions of their time resting on surface waters and roosting on intertidal rocks, and because they have restricted foraging ranges (Ewins 1993), they may be less able to avoid oiled habitat than seabirds that forage more widely.

MATERIALS AND METHODS

Study sites. Our oiled study site was the Naked Island group, which includes Naked, Peak and Storey Islands, located in central PWS (Fig. 1). We studied guillemots *Cepphus columba* there for 5 yr prior to the spill (1978 to 1981, and 1984), and 8 yr post-spill (1989 to 1990, and 1994 to 1999). Naked Island is located approximately 30 km from Bligh Reef, and was the first land mass hit by oil spilled by the 'Exxon Valdez'. The near-shore habitat of the Naked Island group includes many bays and passages with a shallow (<30 m) shelf habitat radiating about 1 km from shore. The islands are forested to their summits (<400 m), mostly with sitka spruce *Picea sitchensis* and western hemlock *Tsuga heterophylla*. Guillemots nest semi-colonially along the island's rocky shore-

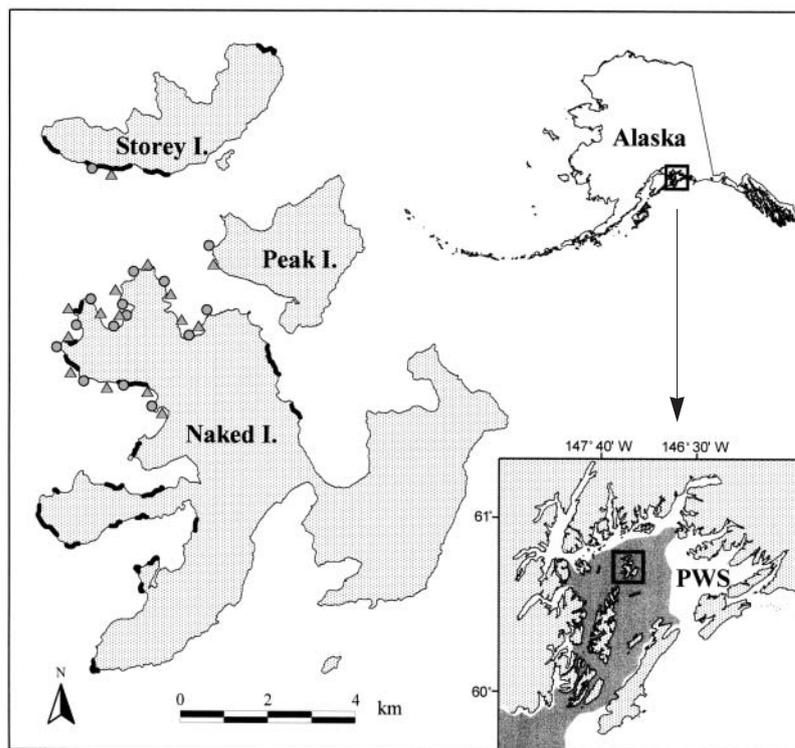


Fig. 1. Map of the oiled study site. Study areas of pigeon guillemot *Cepphus columba* colonies are depicted by thickened shoreline. Dive transect locations are shown as circles (1996 sites) or triangles (1997 sites). Inset map shows the locations of the oiled colonies (inside box) and the oiled area (dark shading) within Prince William Sound, Alaska

lines in cavities beneath tree roots overhanging crumbling cliffs, in rock crevices, and among boulders on talus slopes. Other members of the Alcidae breeding on these islands include marbled murrelets *Brachyramphus marmoratus*, parakeet auklets *Cyclorhynchus psittacula*, tufted puffins *Fratercula cirrhata*, and horned puffins *F. corniculata*. Populations of all these species have declined appreciably in PWS since the 1970s, presumably due to large-scale changes in forage fish abundance in the region (Agler et al. 1999).

Our unoiled study site was located in PWS (Fig. 2). Most of our work was conducted on Jackpot Island, a small low-elevation island with a shoreline of low (<25 m) cliffs and 1 small bay. We studied guillemots there from 1993 to 1998. A sound-wide survey conducted in 1993 showed that Jackpot Island had the highest density of guillemots in all of PWS (Sanger & Cody 1994). Horned puffins also nest on the island. In 1998 and 1999, guillemots breeding at Icy Bay were captured for liver biopsies and blood collection. Icy Bay is situated 7.4 km south of Jackpot Island, and was also unoiled.

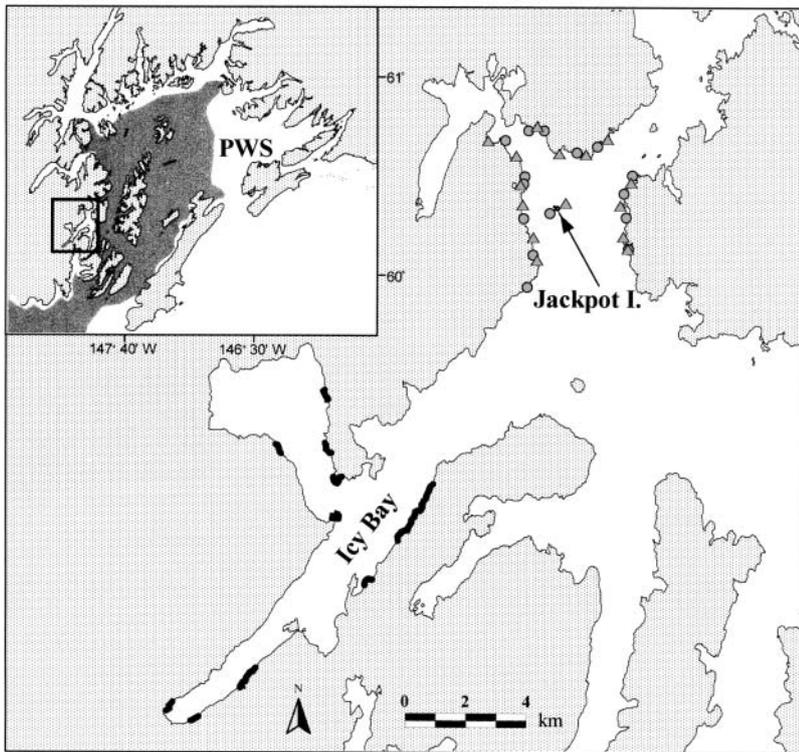


Fig. 2. Map of the unoiled study site. Study areas of pigeon guillemot *Cepphus columba* colonies are depicted by thickened shoreline. Dive transect locations are shown as circles (1996 sites) or triangles (1997 sites). Inset map shows locations of the unoiled colonies (inside box) and the oiled area (dark shading) within Prince William Sound, Alaska

Population assessment

Guillemot populations were assessed before and after EVOS by (1) conducting shoreline surveys as part of a US Fish and Wildlife Service monitoring program designed to estimate the densities of marine birds over the entire PWS, and (2) conducting whole-island censuses to estimate populations of guillemots at locations where this species was known to concentrate during breeding.

Sound-wide surveys were conducted during June and July over 8 yr (see Fig. 3). Transects were selected by stratified-random sampling to account for differences in marine habitat. Surveys were conducted from 8 m boats piloted 100 m offshore. One observer scanned continuously with binoculars from each side of the boat, counting all guillemots observed within a sampling window that extended 100 m to either side of, in front of, and above the survey vessel. Intertidal rocks, beaches, and uplands were also scanned for guillemots. In total, 123 transects were sampled. Transects varied in length, but were typically several km long. For analysis, transects were grouped into 23 oiled

and 22 unoiled clusters. (See Irons et al. [2000] for further details on this survey methodology.)

We conducted whole-island censuses of guillemots along the shores of Naked, Peak, Storey, Smith, Little Smith, and Jackpot Islands in late May and early June. The specific dates of the surveys varied by year, and were set to coincide with early-morning high tides, when guillemot attendance peaks (Vermeer et al. 1993). Years in which counts were made are indicated on Fig. 4. Censuses were conducted in a manner identical to that described above for Sound-wide surveys.

Continuing exposure to oil. To determine if guillemots faced continued exposure to residual 'Exxon Valdez' oil, we assayed hepatic cytochrome P4501A (CYP1A), a liver enzyme that is rapidly induced in many vertebrate species following exposure to polycyclic aromatic hydrocarbons (PAHs) (Collier & Varanasi 1991). PAHs are a refractory class of petroleum hydrocarbons that have a high potential for exerting toxicity in birds (Leighton 1993). Elevated levels of CYP1A are transient following exposure to rapidly metabolized compounds such as PAHs, and thus are indicative of recent exposure to contaminants (J. Stegeman pers. comm.).

CYP1A was assayed following liver biopsies of 26 chicks (14 from the oiled colonies [on Naked and Storey Islands] and 12 from unoiled colonies [on Jackpot Island and in Icy Bay]) that were 18 to 24 d old, and 24 adult guillemots (13 from oiled colonies [on Naked and Storey Islands] and 11 from unoiled colonies [in Icy Bay]). The surgeries were performed by an avian veterinarian in a field laboratory during 20 to 26 July 1998 (chicks) and 15 to 23 June 1999 (adults). Details of the anesthesia and surgery procedures are provided in Degernes et al. (2002).

Blood biomarkers. To determine whether guillemots were adversely affected by continued exposure to residual oil, we assessed blood parameters of adult birds at the oiled and unoiled sites. Blood samples were collected from adult guillemots at the oiled site (Naked and Storey Islands) during 14 June to 12 July 1998, and during 15 to 18 June 1999. At the unoiled site, samples were collected from Jackpot Island during 10 July to 5 August 1998, and at Icy Bay during 21

to 23 June 1999. This investigation complemented the work of Seiser et al. (2000), who studied blood parameters in 1997 and found no obvious oil-induced effects on chicks, but recommended that adults be examined further. Seiser et al.'s recommendation was based largely on the finding that aspartate aminotransferase (AST) was significantly elevated in breeding guillemots at the oiled site relative to the unoiled site. Elevations of AST, as well as elevations of lactate dehydrogenase (LDH), are symptomatic of liver damage, which commonly results from oil exposure (Campbell 1986). These blood parameters may also become elevated following damage to other tissues, however, including kidney, lung, myocardium, or skeletal muscle (Franson 1981). A recent study of mink *Mustela vison* demonstrated that chronic low-level ingestion of food contaminated with Alaska North Slope crude oil resulted in long-term increased LDH activity (Mazet et al. 2000), further suggesting the usefulness of this enzyme for assessing oil exposure. In addition to assaying activity levels of AST and LDH, we assayed creatine kinase and alkaline phosphatase. Serum was analyzed for concentrations of bile and uric acids, corticosterone (1998 samples only), sodium (Na), potassium (K), chloride (Cl), calcium (Ca), phosphorus (P), total CO₂, glucose, total protein, albumin, blood urea nitrogen, and cholesterol. Anion gap, albumin:globulin ratio (A:G ratio), and globulin concentration were calculated. Previous studies of guillemots (Peakall et al. 1980) and other seabirds (Fry & Lowenstine 1985, Leighton 1985, 1993, Khan & Ryan 1991, Peakall and Shugart 1993, Rattner et al. 1996, Newman et al. 2000) suggested that oil exposure might affect these blood parameters.

Approximately 2.0 ml of blood was aseptically obtained from the metatarsal vein using a 23 gauge hypodermic or butterfly needle and 3 ml syringe. Blood was immediately transferred into Microtainer™ serum separator tubes (Becton-Dickinson) and stored in coolers for <3 h prior to centrifugation. Samples were centrifuged in a Triac Centrifuge™ (Clay Adams) for 15 min at 3500 rpm. Sera was transferred with disposable polyethylene pipettes into 1.5 ml plastic microcryovials (Out Patient Services), which were subsequently stored frozen until analyses at the Veterinary Medical Teaching Hospital (University of California Davis).

Adult body condition. We compared adult body condition at the oiled and unoiled sites because previous studies have shown that oiling adversely affects this parameter in seabirds (Culik et al. 1991, Fowler et al. 1995). Adult guillemot body condition was determined by scaling body mass by body size. Two techniques were used. For the pre- versus post-spill comparison, we calculated body condition with a simple ratio index (body mass:wingcord³) (Moeller 1987). We used this

analysis method because few morphometric measurements were taken on individual birds in pre-spill years. Additional morphometric parameters were assessed in post-spill years, enabling us to compare body condition between sites with a more sophisticated method, a principle components residual index (Reid 1987, Golet & Irons 1999). Calculating post-spill body condition involved: (1) establishing an index of body size from measurements of captured adults, (2) developing regression equations between the index of body size and body mass for the study population at large, and (3) applying measurements of our study animals to these equations and using residuals to generate individual body-condition estimates. This method of estimating body condition is recommended over other techniques because the metric is independent of an individual's linear size (Piersma 1984, Piersma & Davidson 1991, Jakob et al. 1996).

To establish the body size index, we performed a principle components analysis (PCA) (SYSTAT 1997) on measurements of 24 adults (13 from Naked Island and 11 from Icy Bay) captured during 15 to 23 June 1999. We weighed and individually color-marked each bird, and measured the tarsus, head-plus-bill, and wingcord lengths. With PCA, we generated weighting coefficients that described positive covariance among the linear measurements. These coefficients had variable loadings (tarsus 0.57, head-plus-bill 0.29, and wingcord 0.53), and the first principle component accounted for 48% of the variance in the original measures. Standardized measurements were multiplied by these coefficients and added together to produce a PCA factor score (our body-size index). By regressing body mass (grams) on the body-size index, we developed a least-squares regression ($y = 478.3 + 11.5x$, $n = 24$, $r^2 = 0.19$, $p = 0.034$) that allowed us to predict the mass of a bird given its size. Although this equation has relatively low predictive power, it serves as a useful benchmark for comparing mean levels of condition in groups of individuals.

We calculated the body condition of experimental birds by subtracting the predicted weight of each bird (based on the regression equation) from its actual weight, dividing this difference by the predicted weight, and then multiplying the resulting quotient by 100. This value (our body-condition index) represents the percent by which a bird's measured weight differs from what it was expected to weigh, given its size, thus providing a rough estimate of each bird's level of nutrient reserves.

Prey availability. To determine if the recovery of oil-impacted populations was constrained by prey availability, we performed dive transects at guillemot foraging areas near the study colonies. Demersal fish population densities were estimated in 1996 and 1997. A total of 60 sites were surveyed (15 sites area⁻¹ yr⁻¹).

Sites were systematically selected within a 4 km radius of major guillemot nesting areas (Figs. 1 & 2). At each site, we counted demersal fishes along 2 transects running perpendicular to shore. Transects extended 30 m from shore, or in cases where the shoreline was steep, until a depth of 15 m was attained. The 2 transects originated 10 m to either side of the shoreline midpoint at each site. Demersal fishes were counted along a 1 m wide swath on each transect while moving aside algae and other vegetation. All fish <15 cm were identified to the family level, and classified as 1 of 2 size classes (1 to 8 cm and 8 to 15 cm). For comparison purposes, we calculated the average density of fishes (number observed per 100 m²) at each site.

Chick diet. We studied chick diet to determine if recovery of oil-impacted populations was constrained by food availability. Chick diet composition and delivery rates were determined by observing prey items held crosswise in the bills of adult guillemots as they provisioned their young in the nest. Feeding observations were made with binoculars and spotting scopes from land-based blinds at the oiled site (Naked Island) before and after the spill, and at the unoiled site (Jackpot Island) after the spill. Years in which chick diet and delivery rates were determined are indicated in Appendixes 1 & 2. We watched from each blind for an average of 4 full days, alternating our observation points to ensure that the diet of chicks aged 8 to 30 d was well documented. Because guillemots often pause on the water or on rocks in front of their nests before making deliveries to their chicks, we were usually able to identify the prey items they carried in their bills. During our blind watches, prey items were identified to the lowest possible taxon, but for the purposes of this paper, observed prey items were divided into 1 of 2 categories based on lipid content. High-lipid fishes included Pacific sand lance *Ammodytes hexapterus*, Pacific herring *Clupea pallasii* and smelt (Osmeridae), whereas low-lipid fishes included gadids *Gadidae* spp., sculpins *Cottidae* spp., blennies *Stichaeidae* and *Pholidae* spp., and other demersal fishes. We report the percent high-lipid fishes in the chick diet because this parameter is positively related to guillemot chick growth and reproductive success (Golet et al. 2000). High-lipid fishes probably confer reproductive advantages to guillemot chicks because they have high energy densities (kJ g⁻¹ fresh mass) (Barrett et al. 1987, Hislop et al. 1991, Van Pelt et al. 1997, Anthony et al. 2000), high metabolizable energy coefficients (Massias & Becker 1990, Brekke & Gabrielsen 1994), and are not lacking in other nutrients because lipids tend to replace water and not protein (Harris & Hislop 1978, Anthony et al. 2000).

Chick growth and reproductive success. Previous studies have demonstrated that oil exposure can lead

to reductions in egg laying (Ainley et al. 1981), chick growth rates (Miller et al. 1978, Butler & Lukasiewicz 1979, Andres 1999), hatching success, and nestling survival (Trivelpiece et al. 1984, Fry et al. 1986). To test for such effects, we measured chick growth and reproductive success at the oiled site (Naked and Storey Islands) pre- and post-spill, and at the unoiled site (Jackpot Island) post-spill. Years in which chick growth and reproductive success were determined are indicated in Appendixes 1 & 2. We visited all known nests at least once every 5 d from the egg-laying stage until the chick(s) fledged. At hatching we marked the web of the foot of alpha (the first to hatch, or larger chick, of 2-chick broods), and beta (the second to hatch, or smaller chick, of 2-chick broods) chicks to distinguish them from one another until they were old enough for banding. Chicks were weighed and measured to determine growth rates, calculated as the slope of the regression of mass on age for chicks between 8 and 18 d post-hatch, the linear phase of the growth cycle (Emms & Verbeek 1991, Ewins 1993). Because this growth measure is not influenced by the particular asymptote that individual chicks attain (Hussel 1972, Gaston 1985), it is independent of peak and fledging mass, which we also report. We define peak mass as the highest mass measured, and fledging mass as the last mass measured prior to fledging. Peak and fledging mass have been shown to affect fledging success and subsequent survival (Perrins et al. 1973).

Based on observations made during nest visits we determined reproductive success parameters, including clutch size, hatching success (eggs hatched per egg laid), nestling survival (chicks fledged per egg hatched), overall productivity (chicks fledged per egg laid), and brood size at fledging. We calculated predation rate as the percent of total nests observed that showed evidence of predation (e.g. egg shell fragments, blood stains, dead chicks).

Statistics. For most post-spill comparisons, we used general linear models (GLMs) to test for 'site' (oiled vs unoiled) effects. We included 'year' and 'chick type' (separate categories designated for alpha, beta, and single chicks) as categorical random factors in our GLMs when appropriate. For binomially-distributed data we compared multiple logistic regression models, and tested for significance by assessing the deviance (expressed as a likelihood ratio statistic) of saturated models and models lacking particular effects (Agresti 1990). For pre- versus post-spill comparisons, we used individual year means as our sample units. We used the Lilliefors test to assess normality with variables having continuous frequency distributions. In some instances we performed transformations to satisfy assumptions of parametric tests; otherwise we used

non-parametric tests (Kruskal-Wallis or Mann-Whitney U). For all t -tests we assumed unequal variance. Data on fish abundance were log-transformed ($\log[\text{density} + 0.1]$) prior to analyses. For contingency-table analyses, log-likelihood ratio tests (G -tests) were used (Fienberg 1970, Bishop et al. 1975). For G -tests involving only 2 classes, the Williams correction was applied to reduce the likelihood of Type I errors (Sokal & Rohlf 1995). All tests are 2-tailed, and statistical significance was assigned at $p < 0.05$. We report mean values ± 1 SE.

RESULTS

Table 1 summarizes the results of pre- versus post-spill comparisons at the oiled site and post-spill comparisons between the oiled and unoiled sites.

Guillemot populations

Cephus columba populations were negatively affected by EVOS and, as of 1998, had not recovered to pre-spill levels (see Fig. 3 and Irons et al. 2000). In the first few yr following the spill (1989 to 1993), guillemot

Table 1. *Cephus columba*. Significance of difference between parameters examined pre- vs post-spill at the oiled site, and post-spill at oiled vs unoiled sites. When differences were detected, '>' and '<' indicate directionality relative to column headings. na: data not available; -: no significant difference or trend; * $p < 0.10$ (trend); ** $p < 0.05$; *** $p < 0.01$

Parameter	Pre- vs. post-spill at oiled site	Post-spill at oiled vs. unoiled sites
Population growth rate (λ)	na	< ^a
% high-lipid fishes in diet	>**	<***
Demersal prey-fish availability	na	>***
Meal delivery rate (h^{-1})	-	<***
Clutch size (eggs)	-	<**
Hatching success	<**	>***
Chick growth rate (g^{-1})	>*	-
Peak mass of chicks (g)	>*	<***
Fledging mass of chicks (g)	-	<***
Nestling survival	>***	-
Nest predation rate (%)	<***	>***
Overall productivity	>*	-
Adult body size	na	<***
Adult body mass	>***	-
Adult body condition	>***	-
CYP1A of adults	na	>**
Blood biomarkers of adults	na	> ^b
CYP1A of chicks	na	-
Blood biomarkers of chicks	na	-

^aSignificant increase in population at unoiled site, nonsignificant trend at oiled site (see 'Results').
^bSignificance level varied by biomarker (see Table 2)

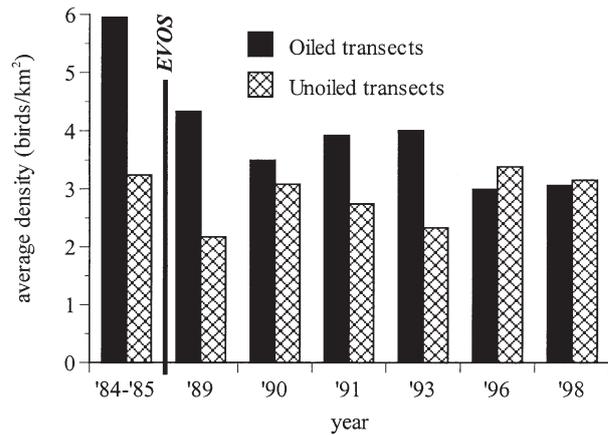


Fig 3. *Cephus columba*. Densities along oiled and unoiled shorelines before and after the 'Exxon Valdez' oil spill. Densities were determined by surveys conducted during June and July. Survey transects ($n = 123$) were selected by stratified-random sampling to account for differences in marine habitat. Surveys were conducted from 8 m boats piloted 100 m offshore. All guillemots observed within a sampling window that extended 100 m to either side of, in front of, and above the survey vessel were counted. Intertidal rocks, beaches, and nearshore uplands were also scanned for guillemots

densities appeared depressed relative to pre-spill levels along both the oiled and unoiled transects; however, the magnitude of the decline was greater along oiled transects. In more recent years (1996 and 1998), guillemot densities along oiled shorelines continued to decline, and for the first time fell below what was observed along unoiled coastlines, further suggesting that recovery had not taken place.

Whole-island censuses indicate that guillemots at the oiled and unoiled study sites exhibited divergent population trends following EVOS (Fig. 4). The population at the unoiled site increased significantly during 1993 to 1998, while no significant post-spill trend was observed at the oiled site. The population multiplication rate (λ) was 1.05 at the unoiled site (Fig. 4B), and 0.98 at the oiled site (Fig. 4A).

Continuing exposure to oil

Ten years after the spill, adults from the oiled site had significantly higher CYP1A activity in the liver than adults from the unoiled site (oiled: 3.1 ± 0.4 pmol min^{-1} mg^{-1} , $n = 12$ birds;

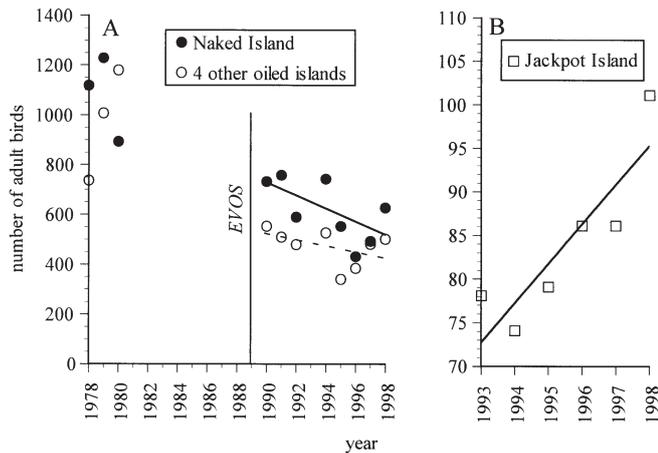


Fig. 4. *Cephus columba*. Population trends at oiled (A) and unoiled (B) study colonies in Prince William Sound, Alaska, before and after the 'Exxon Valdez' oil spill. Post-spill trends at oiled colonies are similar when considering Naked Island ($y = -27.1x + 54\,589$, $n = 8$ yr, $r^2 = 0.42$, $p = 0.084$; solid regression line), or 4 other oiled islands (Storey, Peak, Smith, and Little Smith) for which comparable census data were collected ($y = -10.4x + 22\,252$, $n = 8$ yr, $r^2 = 0.17$, $p = 0.31$; dashed regression line). The population of guillemots at Jackpot Island, the unoiled colony, increased significantly post-spill ($y = 4.5x - 8924$, $n = 6$ yr, $r^2 = 0.78$, $p = 0.020$)

unoiled: 1.9 ± 0.2 pmol min^{-1} mg^{-1} , $n = 11$ birds, $t = 2.1$, $p = 0.020$; Fig. 5B). Nestlings measured 1 yr earlier, however, did not show a statistically significant difference in this parameter between the 2 sites (oiled: 4.1 ± 0.4 pmol min^{-1} mg^{-1} , $n = 12$ birds; unoiled 4.7 ± 0.5 pmol min^{-1} mg^{-1} , $n = 14$ birds, $t = 2.06$, $p = 0.38$; Fig. 5A). These results suggest that adults, but not chicks, were exposed to residual petroleum hydrocarbons at the oiled site a decade after the spill. Although CYP1A activity was elevated at the oiled site, absolute CYP1A activities were low, suggesting that oil exposure was low-level. CYP1A activities were variable among individuals at the oiled site, indicating different levels of oil exposure. This finding matches expectations, given that guillemots have strong foraging-site fidelity (Golet unpubl. data) and 'Exxon Valdez' oil was patchily distributed at the oiled site (Neff et al. 1995, O'Clair et al. 1996, Wolfe et al. 1996).

Elevated CYP1A activity at the oiled site could have been caused by exposure to contaminants that did not originate with EVOS; however, we know of no other contaminant sources in PWS that are likely to explain this result. That EVOS hydrocarbons were the cause of observed differences in CYP1A activities (and blood biomarkers) is further suggested by a recent report that found no differences in marine vessel traffic between our oiled and unoiled sites (Murphy et al. 1999).

Blood biomarkers

Significant differences were detected in blood parameters of adult guillemots from the 2 sites post-spill (see Table 2). In 1998, adult guillemots at the oiled site had lower concentrations of Na, Ca, and P, higher concentrations of K, total CO_2 , glucose, and corticosterone, and higher activities of LDH than guillemots sampled at the unoiled site. In 1999, adult guillemots at the oiled site again had higher glucose concentrations and LDH activity than birds at the unoiled site. An additional difference apparent in 1999 was elevated AST activity among birds at the oiled site.

The most noteworthy differences between sites from the perspective of assessment of injury from the oil spill were the elevated AST and LDH enzyme activities found at the oiled site. Among adults sampled in 1999, significant correlations were found between both AST and LDH activities (Pearson correlation coefficient = 0.79, Bonferroni probability < 0.001), and CYP1A and AST activities (Pearson correlation coefficient = 0.43, Bonferroni probability = 0.047). Simultaneous eleva-

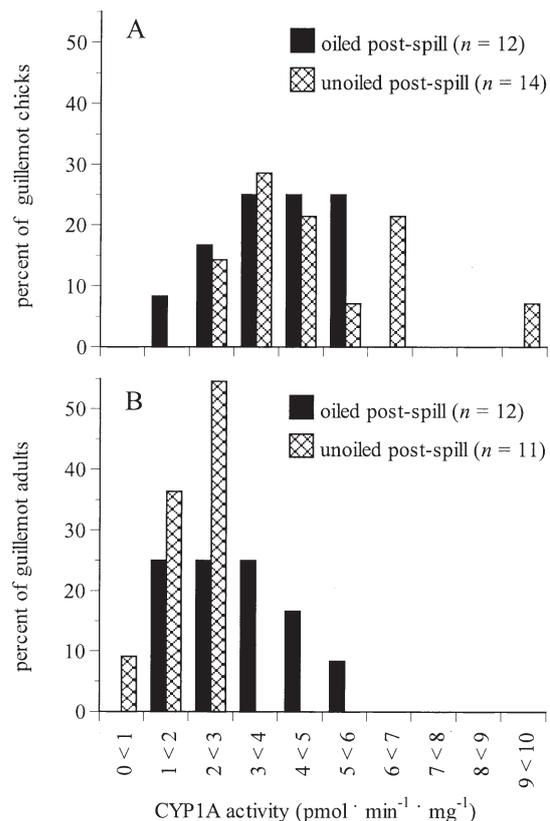


Fig. 5. *Cephus columba*. Frequency histogram of CYP1A for chicks in 1998 (A), and adults in 1999 (B), at oiled (Naked and Storey Islands) and unoiled (Jackpot Island and Icy Bay) colonies in Prince William Sound, Alaska, after the 'Exxon Valdez' oil spill

Table 2. *Cephus columba*. Comparisons of adult pigeon guillemot blood parameters from oiled and unoiled sites 9 and 10 yr after the 'Exxon Valdez' oil spill in Prince William Sound, Alaska. Only those parameters for which there were differences at the $p < 0.1$ level are listed; for a complete list of parameters compared between sites see 'Materials and methods'. Values presented are means \pm SE

Parameter	1998			1999		
	Oiled (n = 9)	Unoiled (n = 9)	p-value	Oiled (n = 13)	Unoiled (n = 11)	p-value
Aspartate aminotransferase (IU l ⁻¹)	359 \pm 44	279 \pm 28	0.35	526 \pm 42	413 \pm 42	0.05
Bile acid (umol l ⁻¹)	12 \pm 1	18 \pm 2	0.07	14 \pm 1	14.4 \pm 1 ^b	0.45
Calcium (mg dl ⁻¹)	7.1 \pm 0.5	8.6 \pm 0.2	0.02	9.0 \pm 0.5	8.8 \pm 0.2	0.62
Chloride (mmol l ⁻¹)	114 \pm 1	115 \pm 2	0.37	118 \pm 1	115 \pm 1 ^b	0.06
Corticosterone (ng ml ⁻¹)	67 \pm 9 ^a	24 \pm 5	0.003	No data	No data	No data
Glucose (mg dl ⁻¹)	433 \pm 22	333 \pm 23	0.004	469 \pm 14	436 \pm 30	0.04
Lactate dehydrogenase (ul l ⁻¹)	1029 \pm 168	470 \pm 43	0.01	931 \pm 82	627 \pm 48	0.006
Phosphorus (mg dl ⁻¹)	1.0 \pm 0.2	2.6 \pm 0.5	0.03	5.4 \pm 0.8	6.8 \pm 0.5	0.20
Potassium (mmol l ⁻¹)	2.9 \pm 0.2	2.3 \pm 0.5	0.03	4.1 \pm 0.2	4.2 \pm 0.3 ^b	0.71
Sodium (mmol l ⁻¹)	155 \pm 1	157 \pm 0.3	0.02	158 \pm 1	157 \pm 1 ^b	0.21
Total CO ₂ (mmol l ⁻¹)	23 \pm 1	19 \pm 1	0.01	39 \pm 1	41 \pm 1	0.55
Uric Acid (mg dl ⁻¹)	8.9 \pm 1	14 \pm 2	0.06	3.4 \pm 1	3.5 \pm 0.5	0.10

^an = 6 birds; ^bn = 10 birds

tions of these parameters are strongly indicative of a toxicological response, and support the notion that adult guillemots at the oiled site were exposed to residual oil 9 and 10 yr post-spill. Some caution must be exercised in interpreting these results, however, as AST was significantly elevated in only 1 of the 2 years.

Adult body condition

Among adult guillemots studied at the oiled site, both body mass (pre-spill: 502 \pm 3 g, n = 3 yr; post-spill: 478 \pm 2 g, n = 4 yr; $t = 6.1$, $p = 0.002$) and body condition (pre-spill: 9.2 \pm 0.1 g mm⁻³, n = 3 yr; post-spill: 7.9 \pm 0.1 g mm⁻³; n = 4 yr, $t = 7.7$, $p = 0.002$) were significantly higher pre-spill than post-spill. Following the spill, however, there were no statistically significant differences in either of these parameters between oiled and unoiled sites (body mass: $F_{1,44} = 0.32$, $p = 0.58$; body condition: $F_{1,44} = 1.2$, $p = 0.28$).

Prey availability and chick diet

Demersal prey fish availability, as determined by dive transects near guillemot colonies post-spill, was significantly greater overall at the oiled site than at the unoiled site (n = 60 transects, $t = 2.87$, $p = 0.006$; Fig. 6). When broken down by size class, the difference was statistically significant for fishes of 1 to 8 cm (n = 60 transects, $t = 3.12$, $p = 0.003$), but not for fishes of 8 to 15 cm (n = 60, $t = 1.82$, $p = 0.075$), although the oiled site tended to have higher densities of fishes of the

larger size class as well. ANOVA analyses of log-transformed fish densities revealed no significant year ($F_{1,56} = 0.02$, $p = 0.90$) or year \times site interaction ($F_{1,56} = 1.09$, $p = 0.30$) effects. These results suggest that availability of demersal prey fishes was not lower at the oiled site relative to the unoiled site 7 to 8 yr after EVOS.

The percent high-lipid schooling fishes (sand lance, herring, smelt) in chick diets was reduced at the oiled site following EVOS. Significantly fewer high-lipid

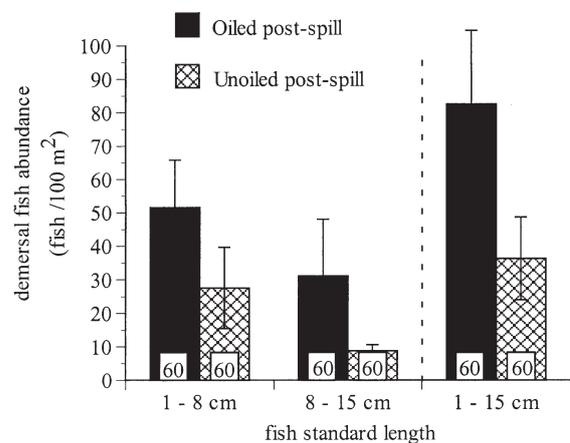


Fig. 6. *Cephus columba*. Demersal fish abundance in foraging areas near oiled (Naked, Peak and Storey Islands) and unoiled colonies in Prince William Sound, Alaska, 1996 and 1997. Data from the 2 years were pooled because the difference in fish densities between years was not statistically significant (see 'Results'). Mean values (\pm 1 SE) are presented, and sample sizes are indicated at the bases of the bars

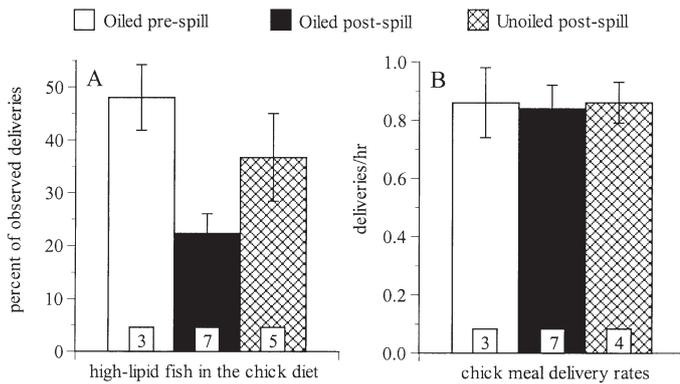


Fig. 7. *Cephus columba*. Percent high-lipid fishes in chick diet (A), and chick meal-delivery rates (B), at oiled (Naked Island) and unoiled (Jackpot Island) colonies in Prince William Sound, Alaska, before and after the 'Exxon Valdez' oil spill. Values are grand means (± 1 SE) of individual year means. Sample sizes are indicated at the bases of the bars

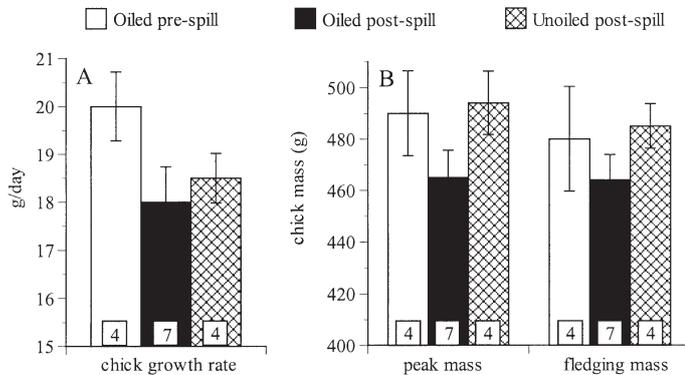


Fig. 8. *Cephus columba*. Chick growth rates (A), and peak and fledging masses (B), at oiled (Naked Island) and unoiled (Jackpot Island) colonies in Prince William Sound, Alaska, before and after the 'Exxon Valdez' oil spill. Values are grand means (± 1 SE) of individual year means. Sample sizes are indicated at the bases of the bars

prey were delivered to chicks at the oiled site post-spill compared to pre-spill ($U = 0.0$, $p = 0.016$; Fig. 7A), and compared to the unoiled site post-spill ($n = 4619$ identified prey items, $G = 71$, $p < 0.001$; Fig. 7A). Although the availability of high-lipid schooling fishes appeared reduced at the oiled site following EVOS, this did not appear to affect meal delivery rates. There were no significant differences in the rate at which chick meals were delivered to the nests at the oiled site pre- versus post-spill ($U = 9$, $p = 0.73$; Fig. 7B). Chick meal deliveries were significantly less frequent (when controlling for effects of 'year' and 'number of chicks in the nest'), however, at the oiled site post-spill compared to the unoiled site ($F_{1,82} = 7.7$, $p = 0.007$; Fig. 7B). The post-spill difference in delivery rates between sites is not evident in

Fig. 7B because the values presented are yearly as opposed to least-squares means. In other words, the post-spill 'site' effect is masked in Fig. 7B by the effects of 'year' and 'number of chicks in the nest'.

Chick growth and reproductive success

Linear growth rates of chick mass tended to be higher at the oiled site pre- versus post-spill ($U = 5$, $p = 0.089$; Fig. 8A), although no difference was observed post-spill between study sites ($F_{1,173} = 0.32$, $p = 0.57$; Fig. 8A). Differences in peak and fledging masses were not significantly different pre- versus post-spill (peak mass: $U = 5.5$, $p = 0.10$; fledging mass: $U = 9$, $p = 0.34$; Fig. 8B), although these parameters were both significantly lower post-spill at the oiled site compared to the unoiled site (peak mass: $F_{1,142} = 8.7$, $p = 0.004$; fledging mass: $F_{1,137} = 11.4$, $p = 0.001$; Fig. 8B).

Differences in chick growth appear to have contributed to differences in reproductive success pre- versus post-spill at the oiled site. Guillemot productivity tended to be higher before EVOS than after ($U = 7$, $p = 0.088$; Fig. 9). The trend of higher pre-spill productivity at the oiled site was the result of significantly higher nestling survival pre-spill compared to post-spill ($U = 0.0$, $p = 0.004$; Fig. 9), as hatching success was actually lower at the oiled site before the spill than after the spill ($U = 32$, $p = 0.018$; Fig. 9). Contributing to the lower post-spill productivity was a significantly higher rate of predation of guillemot eggs and chicks after EVOS ($40 \pm 9\%$ of nests depredated, $n = 7$ yr) compared to before EVOS ($6 \pm 2\%$ of nests depredated \times nests with eggs $^{-1}$, $n = 5$ yr, $U = 35$, $p = 0.004$). When considering pre- and post-spill

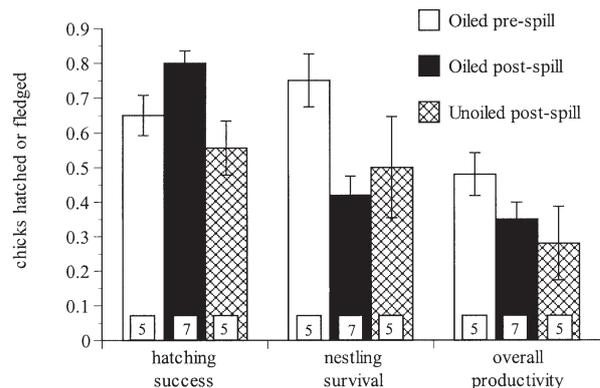


Fig. 9. *Cephus columba*. Reproductive success at oiled (Naked Island) and unoiled (Jackpot Island) colonies in Prince William Sound, Alaska, before and after the 'Exxon Valdez' oil spill. Values are grand means (± 1 SE) of individual year means. Sample sizes are indicated at the bases of the bars

years collectively at the oiled site, productivity was found to be significantly related to predation rate ($y = -0.47x + 0.57$, $n = 12$ yr, $r^2 = 0.57$, $p = 0.004$). No difference was observed in clutch size between the oiled site pre- (1.7 ± 0.03 eggs nest⁻¹, $n = 5$ yr) versus post-spill (1.7 ± 0.03 eggs nest⁻¹, $n = 7$ yr, $U = 14.5$, $p = 0.81$).

Although chicks attained higher peak and fledging masses post-spill at the unoiled site than the oiled site, no difference was observed in overall productivity ($n = 596$ eggs, $G = 0.14$, $p = 0.71$; Fig. 9). Predation of guillemot eggs and chicks was significantly higher at the oiled site post-spill than at the unoiled site (23 ± 16 % of nests depredated nests with eggs⁻¹, $n = 367$ nests, $G = 12.9$, $p < 0.001$); however, nestling survival was not significantly different post-spill between sites ($n = 369$ chicks, $G = 0.26$, $p = 0.65$; Fig. 9). Clutch size was significantly lower post-spill at the oiled site than the unoiled site (1.8 ± 0.03 eggs nest⁻¹, $n = 363$ nests, $G = 6.0$, $p = 0.015$), although post-spill hatching success was higher at the oiled site ($n = 609$ eggs, $G = 40.9$, $p < 0.001$; Fig. 9).

DISCUSSION

In the decade following EVOS, guillemot populations in oiled areas did not show any signs of recovery. Ten years is, however, a sufficient amount of time for this species to increase in number (given its reproductive rate, age at first breeding, etc.) if conditions are sufficiently favorable (Samuels & Lanfear 1982). That impacted populations have not rebounded indicates that some mechanism(s) other than intrinsic demographic constraints limited post-spill population growth of guillemots in oiled areas. Our analyses suggest 2 such mechanisms: a direct effect whereby continued exposure to residual oil reduced adult survival, and an indirect effect whereby the oil spill impacted an important forage fish species, thereby reducing fledging mass and subsequent survival.

Continuing exposure to oil

In 1997, adult guillemots at the oiled site had elevated AST activities relative to the unoiled site, suggesting possible liver injury (Seiser et al. 2000). Because the 1997 study had a small sample size, however, these results were considered preliminary. Analysis of the samples we collected over the next 2 yr corroborated the 1997 results. Elevated CYP1A suggests that adult guillemots at the oiled site were exposed to residual oil, and a significant positive correlation between CYP1A and AST activity among

individual birds strongly suggests that petroleum hydrocarbon exposure caused organ damage. Collectively, these results suggest that continued exposure to residual oil may have directly limited recovery of guillemots by reducing survival of adult birds. Indeed, a relatively small increase in adult mortality is sufficient to explain a lack of recovery (see below). The suggestion that oil exposure may have reduced the survival of adult guillemots inhabiting oiled areas of PWS is made more plausible given findings of concurrent studies conducted on other nearshore vertebrate predators in PWS. Elevated CYP1A activities, suggestive of continued exposure to residual oil, have been detected for Barrow's goldeneyes *Bucephala islandica*, harlequin ducks *Histrionicus histrionicus* (Trust et al. 2000), sea otters *Enhydra lutris* (Bodkin et al. 2002), river otters *Lutra canadensis* (Ballachey et al. 2000), and masked greenling *Hexagrammos octogrammus* (Jewett et al. 2002). Most noteworthy, in the 2 species in which adult survival was studied (harlequin ducks and sea otters), significant reductions in over-winter survival were found for populations inhabiting oiled sites (Esler et al. 2000, Monson et al. 2000). Reduced survival in these studies was observed through at least 1998, suggesting relatively long-term mortality effects associated with the 1989 spill.

That adult guillemots, but not chicks, at the oiled site had elevated CYP1A suggests that differences in diet or habitat use resulted in differential exposure to oil. Because chicks are sheltered in nest cavities, their only opportunities for oil exposure are through their food (almost exclusively fishes [Golet et al. 2000]) or physical contact with their parents. Adults have greater opportunities for exposure because they have wider dietary breadth, consuming both fishes and invertebrates, (Eldridge & Kuletz: unpubl. report to US Fish and Wildlife Service 1980), and inhabit nearshore areas that were heavily contaminated with 'Exxon Valdez' oil. Invertebrate feeders are more likely to ingest toxins than piscivorous species, as invertebrates typically sequester and accumulate toxins while fishes metabolize them (Roesijadi et al. 1978, Varanasi et al. 1989).

Although CYP1A was significantly elevated among adults at the oiled site relative to the unoiled site, levels were low at both sites. Absolute levels of CYP1A expression are difficult to interpret, however, because it is not known what level of exposure is needed to elicit a response of the magnitude observed. Also, because CYP1A values were determined only from breeding birds, they may underestimate exposure levels of the oiled population at large. Higher exposure levels may have existed among non-breeders, as oiling has been shown to reduce egg laying in other alcid

(e.g. Cassin's auklet *Ptychoramphus aleuticus*: Ainley et al. 1981).

High corticosterone and glucose concentrations among adult guillemots at the oiled site are suggestive of active mobilization of energy substrates (Wingfield 1994), which can occur following exposure to oil. Studies of both externally-oiled penguins (Fowler et al. 1995) and oil-fed nestling seabirds (Peakall et al. 1981) demonstrated elevated levels of corticosterone relative to unoiled controls. Experimental studies in mallards *Anas platyrhynchos*, however, showed that ingested oil suppressed adrenocortical function (Gorsline & Holmes 1982). Because oil exposure affects birds through multiple pathways (e.g. thermoregulatory and physiological), variable adrenocortical responses may be expected. Additional research is needed to better understand under what circumstances oil exposure leads to increased versus decreased levels of circulating corticosterone.

Our assessment of effects of oiling on reproductive performance is incomplete (and conservative), as we were unable to determine whether or not exposure to residual oil resulted in greater instances of non-breeding at the oiled colony. Comparisons of breeders are nonetheless informative, as oil exposure can affect factors other than breeding propensity in birds (Leighton 1993). Chick growth and reproductive success patterns observed at the oiled and unoiled sites pre- and post-spill suggest that the level of oil exposure experienced among breeding adults at Naked Island was insufficient to cause reproductive impairment. Although guillemot chick growth rates were higher at the oiled site pre- versus post-spill, growth rates at the oiled site after EVOS compare favorably with values reported in the literature (Drent 1965, Ainley et al. 1990, Emms & Verbeek 1991, Vermeer et al. 1993). Indeed, the difference in chick growth at the oiled site between these 2 periods appears not to be a function of depressed rates of growth after the spill, but rather the result of exceptionally high growth rates pre-spill (Golet et al. 2000). Our finding that chick growth rates did not differ post-spill between oiled and unoiled sites provides additional evidence that residual oil exposure was not affecting chicks. Peak and fledging masses of the chicks were significantly lower following the spill at the oiled site than at the unoiled site; however, it is unlikely that this was a direct result of oil exposure. Oil effects on chick development are more typically manifested when chicks are young (Leighton 1993). Productivity was significantly higher at the oiled site pre-versus post-spill due to differences in nestling survival; however, the weight of evidence does not suggest that this resulted from oiling effects. Lower nestling survival following the spill was more likely to have been the result of reduced availability of high-lipid forage

fishes (see below), although high levels of predation on guillemot nestlings post-spill also contributed.

Forage-fish availability

By examining population trajectories, chick diet, chick growth, and reproductive success between the oiled and unoiled colonies pre- and post-spill, insight can be gained into the mechanistic role that availability of high-lipid forage fishes may have played in limiting the recovery of guillemot populations in PWS following EVOS.

Chick diet data suggest that availability of high-lipid forage fishes was lower at the oiled site following the spill than at both the oiled site pre-spill and the unoiled site post-spill. Although we did not directly assess high-lipid forage fish availability, recent work has shown that the diet of nestling pigeon guillemots reflects the spatial and temporal abundance of these prey in the environment (Litzow et al. 2000). High-lipid fishes are clearly important to guillemots, as the percent of this prey type in the chick diet has been positively related to chick growth rates, nestling survival, and overall productivity (Golet et al. 2000).

In the present study, a decrease in the percent of high-lipid forage fishes in the chick diet at the oiled site after the spill was associated with a decrease in post-spill reproductive performance, suggesting that reduced availability of this prey type may have constrained the recovery of impacted guillemot populations following the oil spill. Compared to pre-spill, post-spill nestling survival at the oiled site was significantly lower, and chick growth and overall productivity also tended to be lower.

A comparison of chick diet and reproductive performance between oiled and unoiled sites after EVOS further suggests that availability of high-lipid forage fishes may have affected recovery. Following the spill, high-lipid fishes formed a higher percentage of the chick diet at the unoiled site than the oiled site, and once again the more lipid-rich diet appeared to confer reproductive benefits. The unoiled site is situated adjacent to several bays that are nursery areas for Pacific herring *Clupea pallasii* (Norcross et al. 1996), a high-lipid forage fish that typically comprised about 45% of the chick diet of guillemots at this site (Appendix 2), and that presumably offset the lower demersal forage-fish availability (as determined by dive surveys) in this area. Chicks at the unoiled site had significantly higher peak and fledging masses (by 29 and 31 g, respectively) than chicks at the oiled site, and recent work on captive seabirds suggests that the benefits of a high-lipid diets to nestlings may be greater than are appreciated by comparisons of body mass alone.

Romano (2000) found that at fledging, chicks fed high-lipid fishes had double the fat reserves of chicks fed isocaloric low-lipid diets, although there were no significant differences between the 2 groups in fledging masses. Larger body masses and greater fat reserves are thought to enhance fledgling survival probabilities in birds (especially in species such as guillemots, where chicks receive no parental care after leaving the nest), presumably because they buffer the young from periods of low caloric intake that may follow fledging (Perrins et al. 1973, Jarvis 1974, Gaston 1997).

Using a Leslie population-projection matrix (Leslie 1945, Krebs 1994), we calculated the reduction in fledgling survival that was required at the oiled site to explain the divergent population trajectories observed at the 2 sites post-spill. The matrix reduced to:

$$P_F = ([N_x \times \lambda] - [N_x \times P_A]) / (F_x \times P_A^2)$$

In this equation, fledgling survival (P_F) is calculated from the population size (N_x), the population multiplication rate (λ), and the number of offspring (F_x) produced at each site (F_x was calculated from measures of clutch size and productivity, see Appendixes 1 and 2). The model assumes stable age distributions, sex ratios of adults and offspring equal to 0.5, that 10% of the population is nonbreeding, and an age-constant adult (>1 yr) survival (P_A) of 0.90. Although this model is simplistic, it is informative, as it suggests that fledgling survival must be 41% lower at the oiled than the unoiled site (0.37 vs 0.81) to explain the population trends. Although we cannot be certain that the observed difference in mean fledging weights translated into a difference in fledgling survival, this analysis presents us with a plausible mechanism to explain the lack of recovery of guillemots at the oiled colonies.

A lack of recovery may also have been caused by increased levels of adult mortality at the oiled site after the spill (a direct oil-spill effect, see above). If we apply the same analysis technique, but this time hold fledgling survival constant (at 0.75), we can calculate what difference in adult survival is necessary to explain the divergent population trends. A reduction in survival of 7% (from 0.91 to 0.84) at the oiled site is sufficient to explain the observed rate of population growth at the oiled site.

High levels of predation of guillemot eggs and chicks at the oiled site following the spill also appear to have played a role in limiting recovery, but it is unlikely that this was the sole explanation for the lack of population growth at the oiled colonies post-spill. Instances of egg and chick predation are incorporated into productivity parameters, and overall productivity did not differ significantly between the oiled and unoiled sites post-spill. Our finding that the population at the unoiled site increased even though its post-spill reproductive suc-

cess was not higher than that observed at the oiled colony suggests that factors other than nest predation limited population recovery of oil-impacted colonies. Predation could have limited recovery, however, if more adult birds were killed by predators at the oiled site post-spill.

Although we lack pre-spill data on sand lance abundance, it is likely that this high-quality forage-fish species was negatively affected by the spill. Sand lance depend on fine gravel or sandy beaches, habitats that were contaminated extensively by 'Exxon Valdez' oil (O'Clair et al. 1996) and that typically retain toxic fractions of crude oil (PAHs) longer than other habitat types (Conan 1982). Sand lance burrow in beach sediments to gain refuge from predators, and seasonally spawn (in a manner that leaves scoured pits) in the same habitat (Robards et al. 1999). Both activities present obvious avenues of oil exposure. Experimental work has shown that sand lance avoid oiled substrates (Pinto et al. 1984) and spend significantly more time in the water column, thereby exposed to predators, when beach sediments are contaminated (Pearson et al. 1984). Furthermore, Stagg & McIntosh (1996) found a significant relationship between petroleum hydrocarbon concentration in the water and CYP1A in *Ammodytes marinus* (the ecological counterpart of *A. hexapterus* in the Atlantic Ocean), suggesting that *Ammodytes* spp. are exposed to oil when their habitat is contaminated. Low concentrations of Prudhoe Bay crude oil are toxic to these fishes, and significant histological damage results when water-suspended oil droplets pass over their gills (Anderson 1985). Also, because sand lance exhibit strong site-fidelity (Hobson 1986), it may take several yr for an impacted population to recover, even in the absence of continuing oil spill effects. Observations that sand lance abundance increased from 1995 to 1999 at the oiled site (E. Brown unpubl. data) are consistent with the notion that local populations were reduced by EVOS.

Reduced availability of high-quality fishes at the unoiled site following the spill could also have resulted from a natural shift in prey communities, as a large-scale regime shift in forage-fish species took place in the northern Gulf of Alaska during the late 1970s and early 1980s (Anderson & Piatt 1999). An examination of seabird diets in the Gulf of Alaska does not, however, support the notion that sand lance declined during this period. Indeed, piscivorous seabirds in the northern Gulf of Alaska shifted from a diet that was dominated by capelin in the early years to one that was primarily sand lance in the late 1980s (Piatt & Anderson 1996). Further evidence that sand lance did not decline in abundance during the regime shift comes from studies conducted in Kachemak Bay, Alaska. Robards et al.

(1999) analyzed beach seine data collected in 1976, 1995 and 1996, and found no decline over this interval in sand lance catch per unit effort or percent occurrence.

Recovery of seabird populations following oil spills

Dunnet (1982) concluded that, in general, oil spills do not represent much of a threat to seabird populations. His conclusion, however, was based upon a comparison of natural levels of mortality and oil-induced mortality, with the former being an order of magnitude greater than the latter. Also, the seabirds in the region studied were experiencing a 'particularly favourable general environment' with nearly all populations increasing. If, as Dunnet acknowledged, oil-induced mortalities were greater, or if conditions were less favorable for seabirds, then mortalities due to oil pollution could have been much more significant in terms of population dynamics. For guillemots in PWS, oil-induced impacts appeared to have significant and lingering effects on populations.

Our study demonstrates that seabird populations cannot always be expected to rebound to pre-perturbation levels in the short term following a mass-mortality event. Furthermore, it suggests that recovery times following oil spills may be considerably longer for certain species than a few yr, which was proposed as typical for marine birds (Wiens et al. 1996, Day et al. 1997). For recovery to occur, impacted populations must not only replace individuals that are lost due to normal levels of attrition, but they must also replace individuals that were lost in the perturbation event. In the case of pigeon guillemots and EVOS, recovery of oiled populations did not take place in the decade following the spill, and this may be due to effects that were both direct (continued exposure of adults to lingering oil) and indirect (oil-spill impacts on an important prey species).

To better understand how oil spills impact seabird populations, future research should more closely examine the physiological effects of oil on both seabirds and their prey (i.e. key forage fish species such as Pacific sand lance). Dose-response studies have the potential to increase our understanding of the level of oil exposure required to manifest enzymatic responses such as those observed in this study, and histopathological investigations may permit better assessments of the long-term consequences of such exposures. Advances along these lines as well as in our understanding of how natural environmental variability influences fundamental demographic characteristics will improve our ability to identify mechanisms that constrain the recovery of seabird populations impacted by oil spills.

Appendix 1. *Cepphus columba*. Chick diet, chick growth and productivity parameters at Naked and Storey Islands (oiled sites), Prince William Sound, Alaska, before and after the 'Exxon Valdez' oil spill (EVOS). na: data not available

Year	% high-lipid fishes in diet	Meal delivery rate (del h ⁻¹)	Clutch size (eggs)	Hatching success	Chick growth rate (g d ⁻¹)	Peak mass (g)	Fledging mass (g)	Nesting survival	Nest predation rate (%)	Overall productivity
1978	na	na	1.5 ± 0.1	0.58 ± 0.11	19.7 ± 1.4	484 ± 10	467 ± 9	1.0 ± 0.0	0 ± 0	0.56 ± 0.1
n			13	19	15	29	29	10	32	18
1979	60 ± 2	1.1 ± 0.1	1.9 ± 0.1	0.73 ± 0.06	22.1 ± 1.0	511 ± 12	506 ± 12	0.85 ± 0.06	10 ± 6	0.61 ± 0.07
n	525	25	33	59	16	17	17	41	30	57
1980	40 ± 2	0.9 ± 0.1	1.8 ± 0.1	0.46 ± 0.07	19.0 ± 0.0	518 ± 52	518 ± 52	0.61 ± 0.12	11 ± 7	0.26 ± 0.07
n	622	30	27	46	1	2	2	18	19	43
1981	44 ± 2	0.7 ± 0.1	1.6 ± 0.1	0.73 ± 0.08	19.2 ± 1.9	445 ± 25	428 ± 29	0.61 ± .10	9 ± 6	0.44 ± 0.09
n	431	37	22	33	11	13	13	23	22	32
1984	na	na	1.9 ± 0.1	0.77 ± 0.15	na	na	na	0.70 ± 0.15	0 ± 0	0.54 ± 0.14
n			7	13				10	7	13
EVOS										
1989	40 ± 2	1.0 ± 0.1	1.6 ± 0.2	0.91 ± 0.09	18.1 ± 2.5	511 ± 16	507 ± 17	0.38 ± 0.18	33 ± 13	0.33 ± 0.17
n	508	21	7	11	5	10	10	8	15	9
1990	14 ± 1	1.2 ± 0.1	1.8 ± 0.1	0.78 ± 0.06	16.7 ± 1.2	442 ± 17	438 ± 17	0.44 ± 0.09	18 ± 6	0.40 ± 0.07
n	646	18	27	51	12	13	13	32	38	47

Appendix 1 (continued)

Year	% high-lipid fishes in diet	Meal delivery rate (del h ⁻¹)	Clutch size (eggs)	Hatching success	Chick growth rate (g d ⁻¹)	Peak mass (g)	Fledging mass (g)	Nesting survival	Nest predation rate (%)	Overall productivity
1994	12 ± 1	0.9 ± 0.2	1.7 ± 0.1	0.90 ± 0.05	15.7 ± 2.1	469 ± 12	464 ± 12	0.51 ± 0.09	39 ± 10	0.46 ± 0.08
n	927	6	23	39	10	18	17	35	23	36
1995	22 ± 1	0.6 ± 0.1	1.8 ± 0.1	0.80 ± 0.05	19.5 ± 1.4	480 ± 14	455 ± 16	0.54 ± 0.07	31 ± 8	0.43 ± 0.06
n	689	9	39	69	13	22	22	55	39	69
1996	21 ± 1	0.6 ± 0.1	1.8 ± 0.1	0.82 ± 0.04	20.9 ± 1.1	482 ± 18	455 ± 15	0.49 ± 0.06	41 ± 8	0.41 ± 0.08
n	645	18	41	74	20	15	15	61	41	41
1997	30 ± 2	0.8 ± 0.1	1.7 ± 0.1	0.79 ± 0.04	18.9 ± 0.8	440 ± 8	431 ± 9	0.47 ± 0.06	34 ± 6	0.35 ± 0.05
n	541	16	56	89	42	59	57	70	56	96
1998	17 ± 3	0.8 ± 0.1	1.6 ± 0.1	0.63 ± 0.05	15.9 ± 1.6	434 ± 15	431 ± 14	0.11 ± 0.04	82 ± 5	0.08 ± 0.03
n	149	7	74	102	18	6	6	64	66	116

Appendix 2. *Cepphus columba*. Chick diet, chick growth and productivity parameters at Jackpot Island (unooiled site), Prince William Sound, Alaska, 1994 to 1998. na: data not available

Year	% high-lipid fishes in diet	Meal delivery rate (del h ⁻¹)	Clutch size (eggs)	Hatching success	Chick growth rate (g d ⁻¹)	Peak mass (g)	Fledging mass (g)	Nesting survival	Nest predation rate (%)	Overall productivity
1994	46 ± 3	1.1 ± 0.2	1.9 ± 0.1	0.80 ± 0.06	20.3 ± 1.4	520 ± 14	509 ± 11	0.86 ± 0.06	0 ± 0	0.65 ± 0.07
n	291	4	24	46	6	8	11	35	21	46
1995	41 ± 2	0.9 ± 0.1	1.9 ± 0.1	0.57 ± 0.07	17.1 ± 0.7	471 ± 12	467 ± 12	0.43 ± 0.10	22 ± 9	0.25 ± 0.06
n	628	23	29	53	16	12	12	28	23	55
1996	44 ± 6	na	1.8 ± 0.1	0.61 ± 0.08	18.3 ± 1.3	na	na	0 ± 0	84 ± 6	0 ± 0
n	70		20	36	8	0	0	22	37	36
1997	4 ± 3	0.8 ± 0.1	1.7 ± 0.1	0.47 ± 0.07	18.8 ± 1.7	474 ± 12	482 ± 9	0.70 ± 0.10	6 ± 4	0.31 ± 0.06
n	484	16	30	53	16	14	13	23	33	52
1998	48 ± 4	0.8 ± 0.1	1.8 ± 0.1	0.33 ± 0.07	18.2 ± 1.0	509 ± 16	483 ± 13	0.53 ± 0.13	4 ± 4	0.18 ± 0.06
n	195	7	27	48	16	9	10	15	28	49

Acknowledgements. We thank L. Ballock, G. Blundell, M. Cody, B. Duggan, A. Gall, C. Geissler, A. Hahn, J. Hamon, D. L. Hayes, P. Joy, C. Kuntzsch, K. Lenington, M. Luanglue, D. Malefant, J. Maniscalco, A. McKnight, A. Palmer, C. Restrepo, M. Russell, S. Shaffer, B. Short, T. Spencer, O. Sternicki, K. Sullivan, D. Tessler, E. Vorisek, M. Walgren, and D. Ziel for valuable field assistance. L. Degernes performed liver biopsy surgeries, while C. Harms and K. Trust administered anesthesia. This manuscript was improved thanks to insightful discussions with B. Ballachey, M. Litzow, K. Oakley, and M. Robards. Dr. M. Christopher (University of California Davis School of Veterinary Medicine) provided helpful interpretations of the blood data. T. Gotthardt produced the study site figures. We are grateful to G. Spencer for critically reviewing an earlier draft of this manuscript. This study was supported by the US Fish and Wildlife Service, the Exxon Valdez Oil Spill Trustees Council, and grant no. BAA-52ABNF400104 from NOAA to D.D.R. This study was a component of, but does not necessarily reflect the views of, the EVOS Trustee Council-funded Alaska Predator Ecosystem Experiment (APEX) and Nearshore Vertebrate Predator Project during 1994 to 1999. Permission to work on Naked and Jackpot Islands was granted by the US Forest Service.

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