

# Correlates to survival of juvenile sea otters in Prince William Sound, Alaska, 1992–1993

B.E. Ballachey, J.L. Bodkin, S. Howlin, A.M. Doroff, and A.H. Rebar

**Abstract:** We estimated survival of sea otters (*Enhydra lutris*) for 1 year post weaning during 1992–1993 in Prince William Sound (PWS), location of the 1989 *Exxon Valdez* oil spill. We sampled 38 pups in eastern PWS (EPWS), an unoiled area occupied by sea otters for <15 years, and 33 pups from oiled western PWS (WPWS), occupied for >25 years. We compared survival between areas, sexes, and condition groups. We also examined the relation of blood parameters to survival. Survival was estimated at 0.74 in EPWS and 0.52 in WPWS. Female survival was 0.86 in EPWS and 0.64 in WPWS, whereas male survival was lower, 0.61 in EPWS and 0.44 in WPWS. Sea otters from EPWS were in better condition (mass/length) than WPWS sea otters. Pups in better condition had higher survival in EPWS but not in WPWS. Foraging success was greater in EPWS than in WPWS, consistent with either an effect of length of occupation or the effects of oil on the prey base or a combination of these effects. Area differences in blood parameters suggested liver damage in WPWS sea otters, perhaps resulting from continued exposure to oil. Thus, both length of occupation and oiling history likely influenced juvenile survival in PWS.

**Résumé :** Nous avons estimé la survie des loutres de mer (*Enhydra lutris*) pendant l'année qui a suivi leur sevrage en 1992–1993 dans le détroit du Prince William (PWS), le site du déversement de mazout par l'*Exxon Valdez* en 1989. Nous avons échantillonné 38 petits dans la partie est du détroit (EPWS), une région non affectée par le déversement et habitée par les loutres depuis moins de 15 ans, et 33 petits de la partie ouest (WPWS) où s'est produit le déversement et qui est habitée par les loutres depuis plus de 25 ans. Nous avons examiné la survie en fonction du site, du sexe et de la condition physique, ainsi que la relation entre les paramètres sanguins et la survie. La survie est estimée à 0,74 dans EPWS et à 0,52 dans WPWS, celle des femelles à 0,86 dans EPWS et à 0,64 dans WPWS et celle des mâles à 0,61 dans EPWS et à 0,44 dans WPWS. Les loutres de EPWS sont en meilleure condition (masse/longueur) que celles de WPWS. Les petits en meilleure condition ont aussi une meilleure survie dans EPWS, mais pas dans WPWS. Le succès de la quête de nourriture est supérieur dans EPWS, ce qui s'explique par les effets de la durée de l'occupation du territoire, ou par les effets du déversement sur les proies qui servent de base de l'alimentation, ou alors par une combinaison de ces deux effets. Des différences dans les paramètres sanguins entre les deux localités semblent démontrer l'existence de lésions hépatiques chez les loutres de WPWS, peut-être reliées à l'exposition prolongée au mazout. Ainsi, la durée de l'occupation du territoire et l'incidence du mazoutage influencent vraisemblablement la survie des jeunes loutres dans PWS.

[Traduit par la Rédaction]

## Introduction

In March 1989, the T/V *Exxon Valdez* went aground in Prince William Sound (PWS), Alaska, spilling approximately 42 million litres of crude oil. Over the next few weeks, oil moved south and west through western PWS

(WPWS) and into the Gulf of Alaska, with an estimated 40% of the spilled oil washing onto shorelines of WPWS (Wolfe et al. 1994). The spill had dramatic effects on natural resources of the region, particularly nearshore species, evidenced by direct mortality of marine plants, invertebrates, fishes, birds, and mammals, as well as cascading ecological effects (Spies et al. 1996; Peterson 2001). Sea otters (*Enhydra lutris*) were particularly vulnerable to the oil, with nearly 500 carcasses recovered in WPWS in the months following the spill. Estimates of total acute mortality in WPWS range from 750 to 3000 sea otters (Garrott et al. 1993; Ballachey et al. 1994; Garshelis 1997); because of uncertainties in the data, a single defensible estimate of mortality cannot be attained. Chronic effects of the spill may have influenced survival of sea otters in subsequent years, either through sublethal exposure in 1989, through continued exposure to residual oil, or through alterations in prey populations, resulting from direct oiling or cleaning efforts (Monson et al. 2000a; Bodkin et al. 2002).

Assessment of spill effects on natural resources, as well as monitoring the process of resource recovery, has been ham-

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pered by inadequate prespill data and lack of experimental replication and control (Wiens 1995; Paine et al. 1996; Spies et al. 1996). Despite these constraints, recent studies have documented long-term effects of the spill and protracted periods of recovery of some injured resources. As late as 2001, oil could still be found at the surface and in beach sediments (Hayes and Michel 1999; Irvine et al. 1999; Short et al. 2002). Spill and response activities resulted in reductions in some clam, crab, and mussel populations for at least 2–3 years post spill (Driskell et al. 1996; Dean et al. 1996; Highsmith et al. 1996). Some mussel (*Mytilus trossulus*) beds in WPWS exhibited contamination (Babcock et al. 1996; Harris et al. 1996; Carls et al. 2001) through at least 1995, and the presence of residual oil in the heavily oiled northern Knight Island area resulted in elevated tissue burdens of hydrocarbons in clams (*Protothaca staminea*) that reduced their growth and survival (Fukuyama et al. 2000).

Many of the habitats and invertebrates that were adversely affected by the spill and cleanup events, and that continue to sequester residual oil, are important to nearshore bird and mammal predators such as shorebirds, sea ducks, and otters. Nearshore bird and mammal species that have exhibited long-term effects of the spill and delayed recovery rates include black oystercatchers (*Haematopus bachmani*; Sharp 1996; Andres 1997), harlequin ducks (*Histrionicus histrionicus*; Esler et al. 2000; Esler et al. 2002), river otters (*Lontra canadensis*; Bowyer et al. 1994; Bowyer et al. 1995), and sea otters (Dean et al. 2000; Monson et al. 2000a; Bodkin et al. 2002). Although increases in sea otter abundance in WPWS are evident a decade post spill (Bodkin et al. 2002) and approximate the minimum loss estimates (Garshelis 1997), there has been no evidence of population increase in the area of northern Knight Island (Fig. 1) where oiling was extensive and mortality approached 0.90 (Bodkin and Udevitz 1994; Bodkin et al. 2002). Available data through 1998 identified elevated mortality and possibly emigration as the proximate factors limiting sea otter recovery in WPWS (Monson et al. 2000a; Bodkin et al. 2002). Induction of the biomarker cytochrome P450 1A in sea otters captured from heavily oiled areas of northern Knight Island implicated continued exposure to hydrocarbons in the lack of recovery (Bodkin et al. 2002).

In this study, our objective was to compare survival rates of juvenile sea otters in WPWS (within the spill area) with those in eastern PWS (EPWS, an unoiled area) in 1992–1993. The study was initially implemented to assess potential chronic effects of the spill and measure population recovery. However, in addition to the oiling difference, the eastern and western areas of PWS differed in length of occupation: sea otters had been present in the west at relatively high densities for >25 years, whereas in the east, at the time of our study, they had been present for <15 years. A further potential source of variation between the two study areas was intrinsic differences in quality of the habitat. Thus, our interpretation of area differences in survival necessitated consideration of factors other than oil effects in the western Sound.

Survival of male and female juveniles was estimated for the 1st year immediately following weaning because this is believed to be a period of variable and often high mortality (Kenyon 1969; VanBlaricom 1988). We also assessed sur-

vival relative to the sex and condition of pups and their mothers at capture. Blood was collected from sea otter pups and adults (mothers of pups and adult males) to evaluate (i) juvenile blood parameters as correlates to their subsequent survival and (ii) area differences in hematology and serum chemistry of adults and pups. As an adjunct to the juvenile survival estimates, we estimated prey species composition and sizes and numbers of prey recovered by unmarked sea otters in EPWS and WPWS. Our objective in the blood and forage study components was to gain insight into the causes of potential differences in survival rates between areas.

## Methods

### Study areas and the sea otter population

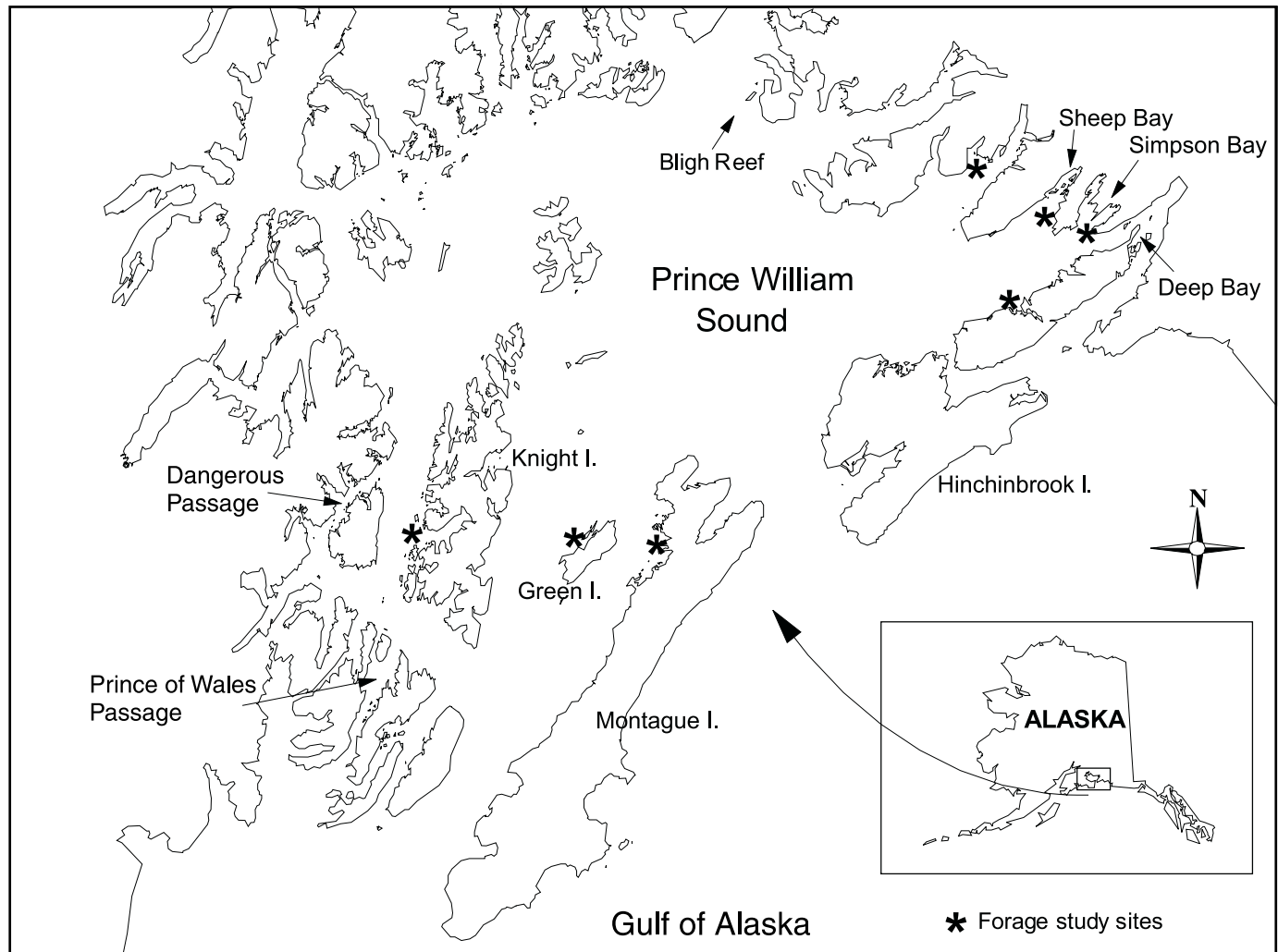
As a result of the harvest for their fur during the eighteenth and nineteenth centuries, sea otters were extirpated from most of the North Pacific (Kenyon 1969). However, a remnant population of about 50 sea otters persisted in the southwest corner of PWS, near northern Montague Island (Lensink 1962) (Fig. 1). Recolonization of PWS apparently resulted from growth and range expansion of the remnant population. In the 1970s, sea otters were present in the northwest Sound and were beginning to occupy the eastern Sound. By 1980, sea otters had reoccupied all major regions of PWS (Garshelis and Garshelis 1984; Garshelis et al. 1984), and in 1985, the population size was estimated to be about 10 000 sea otters (Irons et al. 1988).

We estimated juvenile sea otter survival rates in the western and eastern regions of PWS (Fig. 1). In WPWS, sea otters were captured in the vicinities of Green Island, Dangerous Passage, and Prince of Wales Passage and on the west side of Knight Island, all of which were within the path of the oil spill. However, the extent of shoreline oiling that these areas received was variable (Neff et al. 1995). In EPWS, sea otters were captured in Deep, Simpson, and Sheep bays, areas that were east of the path of the spill and were not oiled.

### Sea otter capture, sampling, and data collection

Sea otters (adult females with pups and adult males) were captured in 1992 from 8 August to 9 September in EPWS and from 22 August to 4 September in WPWS using primarily tangle nets supplemented by dip nets (Ames et al. 1986). Captured sea otters were anesthetized with a combination of fentanyl citrate and diazepam, and anesthesia was reversed with naloxone or naltrexone (Monson et al. 2001). Mass (kilograms) and length (centimetres, measured dorsally from tip of tail to nose) were recorded and a premolar tooth was collected from mothers for aging (Bodkin et al. 1997). Adults and pups were tagged with color-number coded plastic tags (Temple Tags, Temple, Tex.) in the interdigital space on the hind flipper (Ames et al. 1983). Pups that weighed >8.2 kg were surgically implanted with radio transmitters equipped with temperature-sensitive mortality switches (Advanced Telemetry Systems, Isanti, Minn.) in the peritoneal cavities (Ralls et al. 1989). Pups were released with their mothers and, with the exception of two pups that were judged to be independent at capture, were observed to have reunited with their mothers post release. Total holding time

**Fig. 1.** Study areas in Prince William Sound, Alaska. Sea otters (*Enhydra lutris*) from WPWS were caught in the vicinities of Dangerous Passage, Prince of Wales Passage, and Green Island. Sea otters from EPWS were caught in Sheep, Simpson, and Deep bays.



for mother–pup pairs averaged about 2 h. Capture and handling of sea otters were authorized under a permit from the U.S. Fish and Wildlife Service and were conducted in accordance with the guidelines of the Canadian Council on Animal Care.

Approximately 20 mL of blood was collected from each sea otter by jugular venipuncture, with about 3 mL drawn into an ethylenediaminetetraacetic acid (EDTA) tube and refrigerated pending shipment to the clinical laboratory and the remainder drawn into one or two glass tubes and allowed to clot for at least 30 min before centrifuging to separate serum, which was then frozen. Two blood smears on glass slides were made from the whole blood. Whole blood in the EDTA tube and smears were shipped to Quest Laboratories (formerly Corning Clinical Laboratory, and prior to that, Physicians Medlab Laboratories), Portland, Oreg., as soon as possible after collection for analysis of hematologic parameters. Only samples that arrived at the laboratory within 72 h of collection were used in the data analyses. Serum samples were maintained in frozen storage (–20 °C) until fieldwork

was complete and then submitted as a batch to Quest Laboratories for serum chemistry analyses.

Radio-marked sea otter pups were monitored from boats and fixed-wing aircraft equipped with Yagi antennas and programmable scanning receivers. From September 1992 through May 1993, relocation of pups in the intensive study area was attempted at least once per week, and missing animal surveys (flights to locate missing animals that included the intensive study area and adjacent areas) were conducted at least once per month. From June 1993 through January 1994, relocation of pups in the intensive study areas was attempted at 3-week intervals, and three missing animal surveys were conducted. Four surveys of the entire PWS and adjacent areas (Gulf of Alaska from Cape Suckling to Gore Point) were conducted by aircraft during September 1992 through January 1994. For each sea otter relocation, we recorded identification, date, time, association with tagged adult (yes, no, or unknown), location (by global positioning system or plotted directly on topographic maps), status (dead or live), and activity (resting, feeding, traveling, evading, or

unknown). We attempted to recover carcasses as soon as possible after receiving mortality signals. If carcasses were in adequate condition at recovery, gross necropsies were conducted by veterinarians.

Data on foraging sea otters were collected using focal animal sampling (Altmann 1974) in areas with sufficient sea otter densities and varying degrees of shoreline oiling. In WPWS, data were collected during April through July 1991 and were previously reported by Doroff and Bodkin (1994). High-resolution 10–80× telescopes (Questar Corporation, New Hope, Pa.) and 10 × 40 binoculars were used to observe sea otters. An individual diving for prey was selected as a focal animal and observed until visual contact with the animal was lost, distance or obstruction prevented accurate data collection, or feeding ceased. A foraging bout was defined as a continuous record of dives with breaks not exceeding 10 min for one sea otter. Data recorded for each dive of a foraging bout were success, prey type, and number and size class of prey (by prey type). Dives were successful if one or more prey items were captured and unsuccessful if no prey item was captured. Dives with unknown success were not included in the analyses. The same methods were applied in April through June 1994, when foraging data were collected in EPWS, primarily on surrogate (nontagged) animals in areas used by the radio-tagged juvenile sea otters in this study. In EPWS, we used five observation sites that provided unobstructed views of feeding locations within the areas used by the radio-tagged juveniles. In both areas, data on prey retrieved per dive and the size class of the prey were enumerated. Prey were identified to species where possible and classified in the database as clams, mussels, crabs, other, or unknown (for a species list see Doroff and Bodkin 1994). Size classes of prey were estimated relative to forepaw width and skull size (Kvitek et al. 1993) and categorized as 1 (<5 cm), 2 (>5 cm and <9 cm), 3 (>9 cm and <13 cm), or 4 (>13 cm). A foraging bout of an individual animal was used as the sampling unit and individual dives were a replicate within each sample (Doroff and DeGange 1994; Doroff and Bodkin 1994).

## Data analyses

### *Survival analyses*

We defined an instrumented juvenile sea otter as independent when it was first observed without an adult female in the field. We estimated the date of independence as the midpoint between the last observation of the sea otter with its mother and the first observation of the otter without its mother. Independence dates spanned from 16 August 1992 to 28 January 1993. Mean independence date was 11 October 1992 and median independence date was 29 September 1992.

We calculated Kaplan–Meier survival estimates for the year following the weaning date of juvenile sea otters in our study. The analysis estimated survival throughout the study based on the number of sea otters at risk and the number of sea otters that died during each time period (Kaplan and Meier 1958). The time origin for the survival analysis was when the first sea otters were tagged, and sea otters entered the analysis when they became independent. Consequently, the staggered entry modification to the Kaplan–Meier esti-

mates (Pollock et al. 1989a) was used. The time intervals were approximately equal to the length of time between sea otter relocations.

We compared differences in survival between levels of the discrete covariates gender, area, and condition index, including their interactions. The condition index of each individual was defined as the mass (grams) divided by the length (centimetres), and sea otters were divided into two groups based on condition index greater or less than the median value (“more fit” and “less fit”).

We present the Kaplan–Meier estimates of survival on 12 October 1993 as the postweaning annual survival estimates; 12 October 1993 was the relocation date closest to 1 year after the average independence date. We tested for differences in the 1-year postweaning estimates of survival between levels of the discrete covariates using Greenwood’s formula for variance and an approximately normal test (Pollock et al. 1989a).

We also analyzed the radio-relocation data in a medical survival analysis context to discern the effect of blood and body condition covariates on survival (Pollock et al. 1989b). We used the Cox proportional hazards model in which the hazard function is nonparametrically modeled based on the distribution of the survival times of individuals. The model allows for the incorporation of continuous covariates through a linear function of the log of the hazard ratio. All of the covariates were measured when the sea otters first entered the study and their effects on postweaning survival were modeled as multiplicative influences on the hazard function (Collett 1994). The parameter estimates from the models can be interpreted as changes in the hazard rate as a result of changes in the covariate(s) in the model while holding values of the other covariates constant.

Initially, univariate models were run for each covariate individually (covariates included blood values and also pup and maternal masses, lengths, and condition indices), and those with a *P* value <0.15 were selected for further analysis in multivariate models. In addition, we ran two a priori models: one to examine the effects of covariates associated with liver function, including aspartate aminotransferase, alanine aminotransferase, low-density lipoproteins,  $\gamma$ -glutamyltransferase, alkaline phosphatase, albumin, as well as sex, area, and the sex × area interaction, and a second to examine the effects of covariates associated with kidney function, including uric acid, blood urea nitrogen, creatinine, as well as sex, area, and the sex × area interaction. The date of independence of a sea otter pup from its mother was the time origin for the proportional hazards analyses. The study ended on 12 October 1993, 1 year after the average independence date and near the end of the life expectancy of the radio transmitters. Because we started the analysis at each sea otter’s independence date, the analysis was synchronized at this life stage enabling survival from the time origin to represent postweaning survival. Because the sea otters are synchronized in this manner, seasonal effects on survival are not incorporated into the Cox analysis.

The Cox analysis assumes that the sea otters in the study were a random sample of animals with independent survival times. The model also assumes that censoring was independent of survival. In this study, a sea otter was censored if it was still being followed at the end of the study. A sea otter

was also censored if its fate was unknown at the end of the study for any reason (e.g., lost to follow-up, radio failure). The Kaplan–Meier analysis assumes that censoring occurs uniformly throughout the time intervals. Both analyses assumed that the exact time of death was known and that the radio tags do not affect an animal's survival. The latter assumption was accommodated by using postweaning information, which effectively gives a conditioning period for sea otters to become accustomed to the radio tags (Pollock et al. 1989a).

### Body size and blood analyses

To examine area differences in body size (mass, length, and condition index) and blood parameters (9 hematology and 18 serum chemistry parameters<sup>2</sup>), we conducted a model selection process. The ranks of the values were used as the responses to control for nonnormality. We included covariates of area, sex, and age (pup versus adult). For each parameter, we fit 10 models, ranging from univariate models of each covariate alone to the fullest model with all three covariates and all interactions. The best model for each parameter was selected based on Akaike's Information Criterion (AIC) (Burnham and Anderson 1998).

### Foraging analyses

Forage success, number of prey retrieved per dive, and size of prey were used as indicators of foraging efficiency. Null hypotheses were that diet composition, number of prey captured per dive, and prey size did not differ between areas. A foraging bout of an individual sea otter was the experimental unit for tests of differences in foraging parameters. We tested the effects of area on the proportion of prey in each type (MANOVA, PROC GLM; SAS Institute Inc. 1990) and on the mean number of prey retrieved per dive and the proportion of prey in the smallest size class (<5 cm in diameter) within prey types (PROC GLM for unbalanced ANOVA; SAS Institute Inc. 1990). Data expressed as proportions were arcsine transformed prior to analyses. Means were weighted by number of dives observed per bout to enable us to include bouts with few dives in the analyses.

## Results

Our sample of instrumented sea otter pups used to estimate survival consisted of 38 individuals from EPWS (19 females and 19 males) and 33 individuals from WPWS (17 females and 16 males). An additional 1 female and 2 male pups from EPWS and 1 female and 4 male pups from WPWS were sampled for condition, hematology, and serum chemistry, resulting in a potential data set of 79 sea otter pups for comparisons between EPWS and WPWS and between sexes. We also collected age, condition, hematology, and serum chemistry data from 67 adult females (33 in EPWS and 31 in WPWS), including 66 mothers of the pups

that we sampled, and we sampled age, condition, hematology, and serum chemistry from 22 adult males (17 in EPWS and 5 in WPWS). All measurements were not obtained for all individuals captured, resulting in slight differences in sample size for the different variables. From August 1992 through January 1994, the average period between relocations of radio-marked sea otter pups was 10.6 ( $\pm 10.2$ ) days in EPWS and 11.7 ( $\pm 10.4$ ) days in WPWS.

### Condition

The sea otters captured in EPWS were generally in better condition (they weighed more per unit length) than the animals captured in WPWS (Table 1). Sea otters captured in EPWS were significantly heavier than those captured in WPWS ( $P = 0.0004$ ). The area effect on the length variable depended on the age of the sea otters, as the pups from EPWS were longer but the adults were not different (interaction,  $P < 0.0114$ ). The condition index (mass/length) was significantly greater in animals from EPWS than those from WPWS ( $P = 0.0002$ ). Female sea otter pups from EPWS weighed, on average, 141.1 g/cm compared with 116.8 g/cm in those from WPWS, and male pups from EPWS weighed 133.5 g/cm and those from WPWS weighed 124.5 g/cm. In EPWS, the relation between a pup's and a mother's condition was positive but weak ( $R^2 = 0.29$ ,  $P = 0.10$ ), whereas in WPWS, there was essentially no relation ( $R^2 = 0.17$ ,  $P = 0.40$ ). Mean ages of mothers of instrumented pups were 7.8 and 7.1 years in EPWS and WPWS, respectively.

### Pup survival

Survival of sea otter pups to 1 year post weaning was significantly related to area, sex (Table 2), and condition. Survival was greater in EPWS than in WPWS for the sexes combined (0.74 versus 0.52, respectively,  $P = 0.05$ ) (Fig. 2a), and female pups had greater survival than males for areas combined (0.75 versus 0.54, respectively,  $P = 0.05$ ). Within each area, female pup survival was greater than that of males: in EPWS, the rate was 0.86 versus 0.61 and in WPWS was 0.64 versus 0.44 for females and males, respectively (Figs. 2b and 2c). Within both sexes, survival in EPWS exceeded that in WPWS (Table 2).

We further examined survival of pups based on their condition at capture by categorizing them as either "more fit" (mass/length ratio  $> 125.7$  g/cm) or "less fit" (mass/length ratio  $< 125.7$  g/cm). The relative survival of the two groups varied by area. In EPWS, better condition conferred an advantage, with survival of 0.86 for more fit pups compared with 0.49 for the less fit group (Fig. 2d). In contrast, there was little or no condition advantage in WPWS, as survival of more fit pups, 0.53, was only slightly higher than that of less fit pups, 0.44 (Fig. 2e).

We also evaluated condition of the mother as an influence on pup survival. Overall, sea otter pups with mothers in

<sup>2</sup>Hematology parameters: WBC, white blood cells ( $10^3$  cells/mm<sup>3</sup>); RBC, red blood cells ( $10^6$  cells/mm<sup>3</sup>); HGB, hemoglobin (g/dL); HCT, hematocrit (%); MCV, mean corpuscular volume (fL); MCH, mean corpuscular hemoglobin (pg); MCHC, mean corpuscular hemoglobin concentration (g/dL); RDW, red cell distribution width (%); EOS, eosinophils ( $10^3$  cells/mm<sup>3</sup>). Serum chemistry parameters: glucose (mg/dL); BUN, blood urea nitrogen (mg/dL); creatinine (mg/dL); uric acid (mg/dL); sodium (mequiv./L); potassium (mequiv./L); chloride (mequiv./L); calcium (mg/dL); phosphorus (mg/dL); albumin (g/dL); globulin (g/dL); total bilirubin (mg/dL); direct bilirubin (mg/dL);  $\gamma$ GT,  $\gamma$ -glutamyltransferase (1 U/L  $\approx 16.67$  nkat/L); AP, alkaline phosphatase (1 U/L  $\approx 16.67$  nkat/L); LDH, lactic dehydrogenase (1 U/L  $\approx 16.67$  nkat/L); AST, aspartate aminotransferase (1 U/L  $\approx 16.67$  nkat/L); ALT, alanine aminotransferase (1 U/L  $\approx 16.67$  nkat/L).

**Table 1.** Total mass, length, and condition index (mass/length) of sea otters (*Enhydra lutris*) sampled in 1992 in eastern and western Prince William Sound, Alaska, by sex, age class, and area.

Variable	Best model*		Pups (mean ± SD)							
	Main effect (P)	Interaction (P)†	Adults (mean ± SD)			Pups (mean ± SD)				
			EPWS females (n = 36)	WPWS females (n = 31)	EPWS males (n = 17)	WPWS males (n = 5)	EPWS females (n = 20)	WPWS females (n = 18)	EPWS males (n = 21)	WPWS males (n = 20)
Mass (kg)	Sex (0.0001) Age (0.0001) Area (0.0004)	Sex × age (0.0001) Sex × area (0.20) Age × area (0.25)	24.2 ± 2.1	22.9 ± 2.1	34.8 ± 2.9	31.6 ± 2.5	14.1 ± 2.8	11.0 ± 2.1	13.2 ± 3.2	11.9 ± 2.7
Length (cm)	Sex (0.0001) Age (0.0001)	Sex × age (0.0001) Sex × area (0.66)	122.1 ± 3.6	122.2 ± 4.5	133.0 ± 4.1	132.4 ± 4.0	99.4 ± 5.2	94.1 ± 5.4	97.9 ± 6.9	94.6 ± 5.7
Mass/length (g/cm)	Sex (0.0001) Age (0.0001) Area (0.0002)	Sex × age (0.0001) Sex × area (0.11) Age × area (0.48)	198.2 ± 13.7	186.9 ± 14.7	261.2 ± 17.8	238.3 ± 14.6	141.1 ± 22.0	116.8 ± 16.1	133.5 ± 26.1	124.5 ± 21.7

\*Based on ranking of all possible models, with sex, age, and area and interactions among them as potential effects.

†The sex × age × area interaction was nonsignificant in the best model for all three variables.

better condition at capture (>194.7 g/cm) had a mean survival rate of 0.65 (95% CI: ±0.20) compared with a survival rate of 0.60 (95% CI: ±0.20) for pups with mothers in poorer condition (<194.7 g/cm). However, within area, the relationship differed, with maternal condition positively related to survival in EPWS but not in WPWS. In EPWS, pups from mothers in better condition had a survival rate of 0.77 (±0.20) compared with 0.56 (±0.33) for pups from mothers in poorer condition ( $P \leq 0.14$ ), whereas in WPWS, pups from mothers in better condition had a survival rate of 0.22 (±0.38) compared with 0.63 (±0.27) for their counterparts from less fit mothers ( $P \leq 0.04$ ).

### Cox proportional hazard model

The univariate analysis on blood and body condition variables identified 11 variables for which  $P < 0.15$  was obtained (Table 3), including six hematology and three chemistry variables, maternal body length (Mlength), and sex. Of these, WBC had the strongest relation with survival ( $P \leq 0.01$ ), with higher numbers of WBC associated with decreased survival. When the 11 variables plus area were entered into a multivariate model-selection procedure, two models were identified as best, with equivalent AIC values (Table 3): a five-parameter model including EOS, AST, Mlength, RDW, and HCT and a four-parameter model including WBC, RDW, sex, and the WBC × sex interaction. Neither of the two a priori models (including variables associated with liver function or with kidney function) identified a significant relation between variables in the model and subsequent survival of juvenile sea otters.

### Causes of mortality

Nine pups were recovered as intact carcasses on which gross necropsies were performed, two pups were recovered as skeletal remains only, seven transmitters were recovered alone, and mortality signals provided the only evidence of death for five pups. Factors contributing to death based on necropsies were similar between EPWS and WPWS and included malnutrition, mauling (probably by other sea otters), and trauma of unknown cause. Seven of the nine pups recovered as intact carcasses were male, and all but one showed evidence of fighting (i.e., bite wounds to the forepaws or head) and (or) severe trauma, possibly due to fighting with another sea otter. No evidence of intraspecific aggression was evident in two female pups necropsied. Because tissues were not collected for histopathology, we were only able to evaluate causes of death that were evident on physical examination of the carcass.

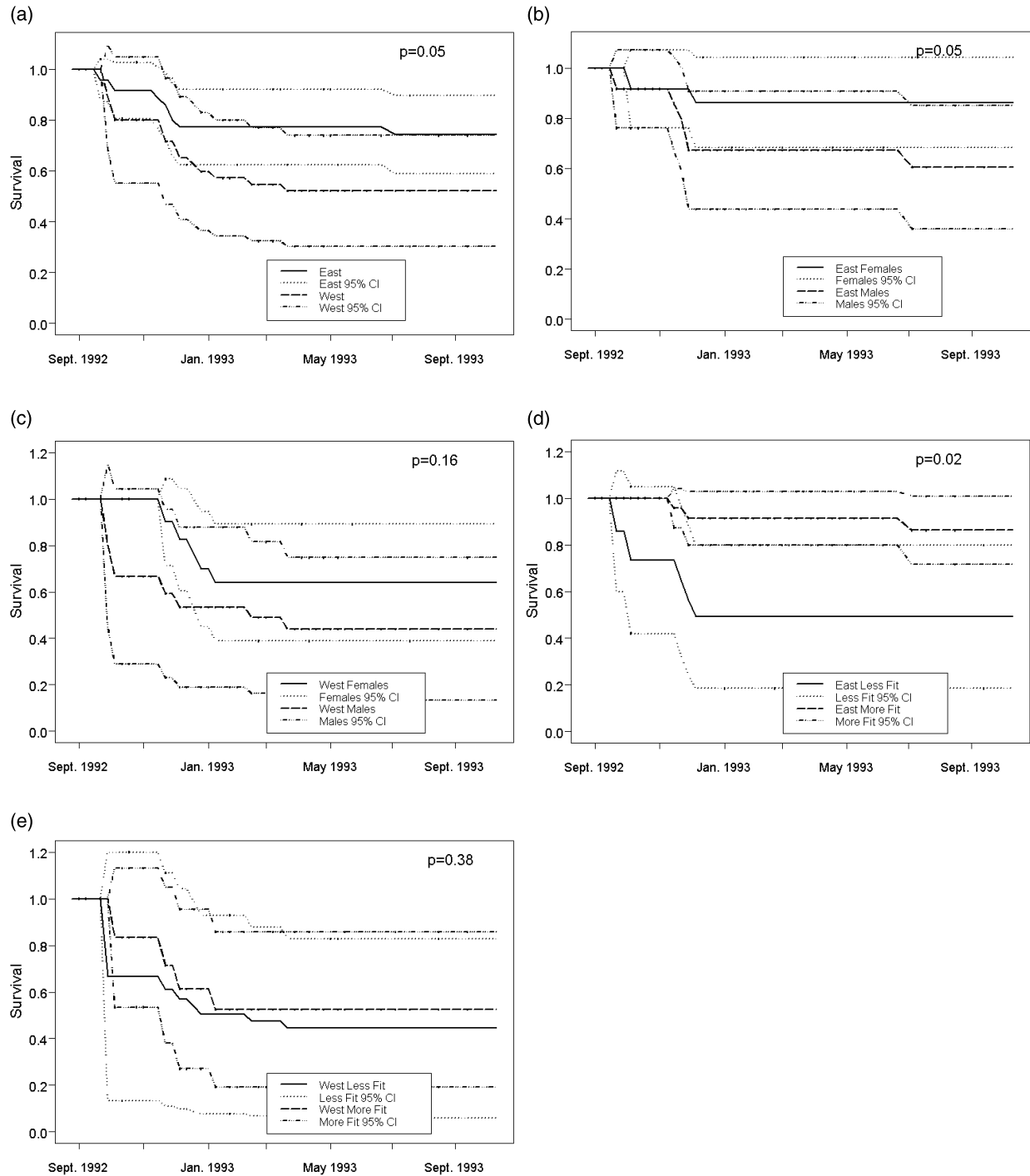
### Hematology and serum chemistry

Six hematology variables differed ( $P \leq 0.05$ ) between sea otters in WPWS and EPWS (Table 4), including WBC and EOS (which were elevated in the west); HGB, MCH, and MCHC (which were lower in the west); and HCT (which was lower in pups from the west but higher in adult sea otters). Differences were also found in chemistry variables, including serum enzymes  $\gamma$ GT, AP, and ALT (which were elevated in the west); and creatinine, sodium, and chloride (which were lower in the west) (Table 5). Blood glucose was also slightly lower in western sea otters ( $P \leq 0.06$ ) (Table 5). Variation among hematology and chemistry values was also

**Table 2.** One-year postweaning survival estimates (from Kaplan–Meier analysis) and 95% confidence intervals for juvenile sea otters in Prince William Sound, Alaska.

Sex	EPWS	WPWS	Both areas
Females	0.863 (0.683, 1.042)	0.640 (0.388, 0.892)	0.753 (0.591, 0.916)
Males	0.605 (0.359, 0.851)	0.440 (0.133, 0.747)	0.546 (0.358, 0.735)
Both sexes	0.743 (0.589, 0.897)	0.521 (0.303, 0.739)	

**Fig. 2.** Kaplan–Meier first year postweaning survival curves for sea otters in Prince William Sound, Alaska. (a) EPWS and WPWS, sexes combined. (b) EPWS, males and females. (c) WPWS, males and females. (d) EPWS, “less fit” and “more fit”. (e) WPWS, “less fit” and “more fit”.



**Table 3.** Models from the Cox proportional hazards analysis of survival of juvenile sea otters in Prince William Sound, Alaska.

	Parameter*	Coefficient <sup>†</sup>	Exp (coefficient)	SE (coefficient)	P	Influence on survival (as parameter increases)	Likelihood ratio test for model
Univariate model							
1	WBC	0.171	1.190	0.063	0.01	↓	
2	Albumin	-2.410	0.090	1.260	0.06	↑	
3	EOS	0.270	1.310	0.148	0.07	↓	
4	AST	0.002	1.000	0.001	0.08	↓	
5	Mlength	-0.127	0.881	0.075	0.09	↑	
6	Uric acid	-0.849	0.428	0.520	0.10	↑	
7	RBC	-0.771	0.462	0.493	0.12	↑	
8	RDW	-0.603	0.547	0.384	0.12	↑	
9	Sex	0.730	2.080	0.469	0.12	↓ (from females to males)	
10	HCT	-0.066	0.936	0.044	0.13	↑	
11	HGB	-0.183	0.833	0.124	0.14	↑	
12	Area	0.418	1.520	0.450	0.35	↓ (from EPWS to WPWS)	
Multivariate model							
13	EOS	0.787	2.197	0.258	0.002		24.1, df = 5, P = 0.0002
	AST	0.003	1.003	0.001	0.035		
	Mlength	-0.261	0.770	0.118	0.027		
	RDW	-1.327	0.265	0.541	0.014		
	HCT	-0.282	0.754	0.086	0.001		
14	WBC	0.989	2.687	0.423	0.019		21.4, df = 4, P = 0.0003
	RDW	-0.787	0.455	0.392	0.045		
	Sex	9.840	18774	4.945	0.047		
	WBC × sex	-0.834	0.434	0.433	0.054		

\*WBC, white blood cells ( $10^3$  cells/mm<sup>3</sup>); albumin (g/dL); EOS, eosinophils ( $10^3$  cells/mm<sup>3</sup>); AST, aspartate aminotransferase (1 U/L  $\approx$  16.67 nkat/L); Mlength, maternal length (cm); uric acid (mg/dL); RBC, red blood cells ( $10^6$  cells/mm<sup>3</sup>); RDW, red cell distribution width (%); HCT, hematocrit (%); HGB, hemoglobin (g/dL).

<sup>†</sup>If the coefficient is positive, survival decreased as the parameter increased; if the coefficient is negative, survival increased as the parameter increased.

frequently associated with both sex and age, with 7 hematology and 14 chemistry variables differing between adults and pups and 3 hematology and 7 chemistry variables differing between sexes ( $P \leq 0.05$ ) (Tables 4 and 5).

### Foraging efficiency

On average, sea otters captured prey on a greater proportion of dives per bout in EPWS (93%) than in WPWS (90%) ( $F_{[1,277]} = 6.64$ ,  $P = 0.010$ ). Diet composition was similar between EPWS and WPWS ( $F_{[4,276]} = 0.712$ ,  $P = 0.615$ ) (Table 6). Clams (family Veneridae, primarily *Saxidomus gigantea*, *Protothaca staminea*, *Mya truncata*, *Clinocardium* spp., and *Macoma* spp.) or mussels (*Mytilus trossolus*) were captured most frequently (74% of dives per bout in EPWS and 60% of dives per bout in WPWS, on average). Crabs (Crustacea) and other prey, including fleshy prey such as fat innkeepers (*Urechis caupo*), sea peaches (*Halocynthia aurantium*), and less common shelled prey such as rock jingles (*Pododesmus macroschisma*), scallops (*Chlamys* spp.), gastropods (*Notoacmea* spp.), and barnacles (*Balanus* spp.), were captured, on average, during <20% of dives per bout in both areas.

Proportionately more small clams (<5 cm in diameter) and fewer clams per dive were retrieved in WPWS per bout

than in EPWS (Table 6). Mussels captured in both study areas were small, nearly all <5 cm; however, more mussels were retrieved per dive in EPWS than in WPWS (Table 6). Proportionately more prey items retrieved by sea otters that could not be identified to taxon were <5 cm in size in WPWS than in EPWS (Table 6).

### Discussion

When we initially developed this study, an important assumption of our study design was that EPWS and WPWS differed in no way other than the oiling treatment. However, a remnant sea otter population persisted in southwest PWS, and sea otters were established throughout our WPWS area by 1950 (Lensink 1962), whereas the first observations of sea otters reoccupying our EPWS study sites occurred between 1975 and 1980 (Garshelis and Garshelis 1984; Garshelis et al. 1984). Differences in the length of occupation by sea otters potentially could be a factor contributing to differences in survival between our study areas. Greater foraging efficiency has been observed in areas recently occupied by sea otters than in areas with long-established populations in Alaska and California (Estes et al. 1981), within PWS (Garshelis et al. 1986), and within the Kodiak Archipelago, Alaska (Kvitek et al. 1992; Doroff and DeGange



**Table 4.** Hematology variables of sea otters sampled in 1992 from eastern and western Prince William Sound, Alaska, by sex and age class.

Variable*	Main effect (P)	Interaction (P)	Adults (mean $\pm$ SD)						Pups (mean $\pm$ SD)					
			EPWS females (n = 33)	WPWS females (n = 30)	EPWS males (n = 16)	WPWS males (n = 5)	EPWS females (n = 19)	WPWS females (n = 18)	EPWS males (n = 20)	WPWS males (n = 17)				
WBC	Sex (0.001) Area (0.01)		9.45 $\pm$ 2.14	10.27 $\pm$ 1.65	7.59 $\pm$ 1.78	8.18 $\pm$ 9.76	8.33 $\pm$ 2.11	9.61 $\pm$ 2.97	8.55 $\pm$ 2.98	8.99 $\pm$ 3.76				
RBC	Age (0.0001) Area (0.37)	Age $\times$ area (0.06)	5.1 $\pm$ 0.3	5.1 $\pm$ 0.3	5.0 $\pm$ 0.3	5.3 $\pm$ 0.4	5.1 $\pm$ 0.4	4.7 $\pm$ 0.4	4.7 $\pm$ 0.5	4.7 $\pm$ 0.5				
HGB	Sex (0.02) Age (0.0001)		20.8 $\pm$ 1.2	20.5 $\pm$ 0.9	20.2 $\pm$ 0.9	20.7 $\pm$ 1.0	19.2 $\pm$ 1.5	18.1 $\pm$ 1.3	18.4 $\pm$ 1.7	17.4 $\pm$ 1.7				
HCT	Age (0.0001) Area (0.73)	Age $\times$ area (0.0007)	59.8 $\pm$ 3.7	60.6 $\pm$ 2.3	58.2 $\pm$ 3.0	61.6 $\pm$ 2.8	56.4 $\pm$ 4.1	54.1 $\pm$ 4.2	53.3 $\pm$ 4.9	52.6 $\pm$ 5.1				
MCV	Sex (0.07) Age (0.0001)		117.6 $\pm$ 4.3	119.5 $\pm$ 5.8	116.8 $\pm$ 4.7	116.8 $\pm$ 5.1	112.1 $\pm$ 4.5	115.2 $\pm$ 5.6	112.9 $\pm$ 3.9	111.9 $\pm$ 4.3				
MCH	Sex (0.06) Age (0.0001) Area (0.008)	Sex $\times$ age (0.30) Sex $\times$ area (0.01) Age $\times$ area (0.72) Sex $\times$ age $\times$ area (0.22)	40.8 $\pm$ 1.4	40.5 $\pm$ 1.9	40.6 $\pm$ 2.0	39.4 $\pm$ 2.7	38.0 $\pm$ 1.7	38.5 $\pm$ 2.0	38.9 $\pm$ 1.5	37.0 $\pm$ 1.3				
MCHC	Age (0.0004) Area (0.0001)		34.7 $\pm$ 1.0	33.9 $\pm$ 0.8	34.7 $\pm$ 0.8	33.6 $\pm$ 1.0	34.0 $\pm$ 1.1	33.5 $\pm$ 0.6	34.5 $\pm$ 0.9	33.1 $\pm$ 0.6				
RDW	Age (0.0001)		12.9 $\pm$ 0.5	12.8 $\pm$ 0.6	12.7 $\pm$ 0.7	12.4 $\pm$ 0.3	13.8 $\pm$ 0.6	13.9 $\pm$ 0.6	14.0 $\pm$ 0.9	14.0 $\pm$ 0.7				
EOS	Sex (0.05) Area (0.0001)		0.39 $\pm$ 0.39	1.14 $\pm$ 0.66	0.44 $\pm$ 0.38	1.20 $\pm$ 0.49	0.45 $\pm$ 0.32	1.14 $\pm$ 0.86	0.25 $\pm$ 0.40	1.12 $\pm$ 1.60				

\*WBC, white blood cells ( $10^6$  cells/mm<sup>3</sup>); RBC, red blood cells ( $10^6$  cells/mm<sup>3</sup>); HGB, hemoglobin (g/dL); HCT, hematocrit (%); MCV, mean corpuscular volume (fL); MCH, mean corpuscular hemoglobin (pg); MCHC, mean corpuscular hemoglobin concentration (g/dL); RDW, red cell distribution width (%); EOS, eosinophils ( $10^3$  cells/mm<sup>3</sup>).

<sup>†</sup>Based on ranking of all possible models, with sex, age, and area and interactions among them as potential effects.

**Table 5.** Serum chemistry variables of sea otters sampled in 1992 from eastern and western Prince William Sound (EPWS and WPWS, respectively), Alaska, by sex and age class.

Variable*	Best model†	Adults (mean ± SD)			Pups (mean ± SD)					
		EPWS females		WPWS females		EPWS males		WPWS males		WPWS males (n = 18)
		(n = 36)	(n = 31)	(n = 31)	(n = 17)	(n = 5)	(n = 20)	(n = 17)	(n = 21)	
Glucose	Sex (0.0001) Age (0.0001) Area (0.06) Age (0.0001)	154.5±34.6	142.7±30.0	131.3±19.5	121.0±22.2	198.9±49.0	179.1±29.7	167.4±37.0	159.8±29.2	
BUN	Sex (0.0001) Age (0.0001)	49.7±10.7	52.3±10.9	51.2±7.2	50.4±11.3	37.5±7.4	34.0±8.8	31.6±8.8	38.6±11.1	
Creatinine	Sex × age (0.0001) Sex × area (0.14) Age × area (0.89) Sex × age × area (0.57)	0.73±0.09	0.64±0.10	0.98±0.21	0.86±0.11	0.46±0.07	0.39±0.08	0.46±0.06	0.42±0.08	
Uric acid	Age (0.07)	2.45±0.47	2.57±0.66	2.74±1.03	2.46±0.46	2.43±0.43	2.33±0.49	2.50±0.56	2.22±0.33	
Sodium	Age (0.0001) Area (0.0001)	153.9±1.5	152.8±1.8	155.0±1.7	154.0±2.5	151.7±1.0	151.6±1.7	151.7±1.5	150.4±1.7	
Potassium	Sex (0.0001) Age (0.51)	4.02±0.30	4.06±0.35	4.49±0.32	4.42±0.28	4.20±0.43	4.19±0.26	4.39±0.39	4.48±0.45	
Chloride	Age (0.0001) Area (0.032)	118.8±2.0	118.0±3.0	118.2±2.9	120.0±3.7	115.1±2.3	115.0±1.7	115.2±2.6	113.6±1.6	
Calcium	Age (0.0001)	8.68±0.40	8.90±0.81	8.83±0.48	8.52±0.24	9.98±0.49	10.19±0.42	10.09±0.55	10.12±0.39	
Phosphorus	Age (0.0001)	4.22±1.38	4.50±1.69	4.42±1.06	3.50±0.54	7.29±1.43	8.33±1.28	8.06±1.47	8.20±0.89	
Albumin	Age (0.0002)	2.91±0.17	2.89±0.24	2.93±0.17	2.84±0.20	3.03±0.19	3.02±0.13	3.03±0.20	2.98±0.21	
Globulin	Sex (0.03) Age (0.0001)	3.83±0.44	3.87±0.48	3.98±0.44	4.04±0.50	2.58±0.37	2.43±0.32	2.68±0.43	2.74±0.87	
Total bilirubin	Sex (0.0005) Age (0.0001)	0.43±0.14	0.61±0.73	0.34±0.12	0.32±0.08	0.47±0.07	0.56±0.21	0.46±0.16	0.53±0.20	
Direct bilirubin	Area (0.37)	0.01±0.03	0.02±0.04	0±0	0±0	0.02±0.04	0.01±0.02	0.01±0.04	0.02±0.04	
γGT	Area (0.0001)	14.9±3.2	30.9±26.2	17.4±4.6	17.8±4.1	16.6±9.9	53.1±62.9	15.2±4.6	50.4±85.6	
AP	Sex (0.01) Age (0.0001) Area (0.024)	87.6±26.4	97.9±29.2	74.0±18.7	65.6±19.3	237.6±85.6	335.9±179.5	240.4±75.7	313.3±299.7	
LDH	Sex × age (0.043)	573.8±273.7	505.2±325.5	432.3±162.8	342.6±133.0	523.2±199.4	473.4±131.3	574.7±341.1	502.2±170.8	
AST	Sex × age (0.004)	333.1±175.2	363.8±163.7	237.1±104.8	221.4±63.2	211.6±134.4	244.4±142.1	211.5±157.6	310.2±203.7	
ALT	Sex × age (0.0001) Sex × area (0.92) Age × area (0.35)	261.9±63.3	339.9±82.0	181.1±63.1	208.8±49.4	217.3±180.3	369.3±360.4	178.9±69.1	307.1±180.1	

\*Glucose (mg/dL); BUN; blood urea nitrogen (mg/dL); creatinine (mg/dL); uric acid (mg/dL); sodium (mequiv/L); potassium (mequiv/L); chloride (mequiv/dL); calcium (mg/dL); phosphorus (mg/dL); albumin (g/dL); globulin (g/dL); total bilirubin (mg/dL); direct bilirubin (mg/dL); γGT; γ-glutamyltransferase (1 U/L ≈ 16.67 nkat/L); AP; alkaline phosphatase (1 U/L ≈ 16.67 nkat/L); LDH; lactic dehydrogenase (1 U/L ≈ 16.67 nkat/L); AST; aspartate aminotransferase (1 U/L ≈ 16.67 nkat/L); ALT; alanine aminotransferase (1 U/L ≈ 16.67 nkat/L).

†Based on ranking of all possible models, with sex, age, and area and interactions among them as potential effects.

**Table 6.** Mean proportion of dives per bout during which individual prey types were retrieved, mean number of prey retrieved per dive by bout, and mean proportions of prey <5 cm in diameter captured per bout by sea otters in western Prince William Sound (WPWS), April–July 1991, and in eastern Prince William Sound (EPWS), April–June 1994.

	Prey type											
	Clam		Mussel		Crab		Other		Unknown			
	<i>n</i>	Mean ± SD	<i>n</i>	Mean ± SD	<i>n</i>	Mean ± SD	<i>n</i>	Mean ± SD	<i>n</i>	Mean ± SD	<i>n</i>	Mean ± SD
<b>Proportion of dives</b>												
EPWS	94	0.47 ± 1.30	94	0.27 ± 1.50	94	0.04 ± 0.35	94	0.08 ± 0.70	94	0.13 ± 0.58		
WPWS	190	0.46 ± 1.29	190	0.14 ± 0.91	190	0.08 ± 0.62	190	0.08 ± 0.51	190	0.22 ± 0.96		
<b>Number per dive</b>												
EPWS	74	1.60 ± 1.56 A	28	6.65 ± 9.99 A	28	1.00 ± 0.00 A	30	1.30 ± 0.73 A	36	2.05 ± 2.67 A		
WPWS	116	1.33 ± 1.28 B	30	2.69 ± 4.07 B	56	1.10 ± 0.31 B	81	1.29 ± 0.88 A	116	1.17 ± 1.03 B		
<b>Proportion &lt;5 cm</b>												
EPWS	75	0.56 ± 0.98 C	36	1.00 ± 0.04 C	28	0.19 ± 0.48 C	31	0.27 ± 0.73 C	41	0.87 ± 0.44 C		
WPWS	134	0.64 ± 0.93 D	43	1.00 ± 0.00 C	57	0.31 ± 0.71 C	80	0.25 ± 0.63 C	108	0.92 ± 0.40 D		

Note: *n* is the number of foraging bouts of sea otters. Means are weighted by the number of dives observed per bout. Means that differ ( $P < 0.01$ ) between areas are followed by different letters; means that do not differ between areas ( $P > 0.10$ ) are followed by the same letter ( $F$  test for unbalanced ANOVA, PROC GLM; SAS Institute Inc. 1990; tests on differences in proportions of prey <5 cm in diameter were performed on ranks of proportions).

1994). Prey size and abundance were greater (Kvitek et al. 1992) and foraging efficiency of sea otters was better (Doroff and DeGange 1994) in areas occupied for 5–15 years than in sites occupied for >25 years at Kodiak Island where substrate and prey composition were similar to those of our study areas.

In our study, observed differences between areas in survival of juveniles may be related to length of occupancy by sea otters and differences in prey populations resulting from persistent sea otter predation. Alternatively, reduced survival in WPWS could result from adverse effects on health associated with exposure of sea otters to residual oil in the environment. Although we believe the two areas to be largely comparable, further variation in survival rates may arise from intrinsic differences between the areas in quality of habitat. The potential confounding of these several factors precludes assigning a single cause to observed differences in survival and illustrates the difficulty in designing a study to measure biological effects of an unanticipated catastrophic event. We collected additional data, including foraging success, body condition, hematology, and serum chemistry of adults and pups in an attempt to help distinguish factors contributing to observed differences in survival.

We also assumed that our sample of sea otters from WPWS represented the spill-affected population, but because of the relative scarcity of sea otters in the most heavily affected areas of WPWS following the spill, it is unlikely that this assumption was met. Shoreline oiling, oil persistence, and sea otter mortality were not distributed evenly in WPWS (Neff et al. 1995; Bodkin and Weltz 1990). Sea otter mortality was particularly high along the shores of the northern Knight Island archipelago, approaching 90% in at least one large bay (Bodkin and Udevitz 1994). The lack of sea otters in the most severely affected habitats forced us to capture sea otters in habitats that were not heavily oiled and where acute mortality of sea otters was less than that observed in the most severely affected areas. The effect of this sampling bias would be to dilute our ability to detect differences related to the oil spill, but there should be no bias related to length of occupation.

Previous radio-tracking studies have indicated that movements of sea otters between the eastern and western areas of the Sound may occur but are infrequent (Garshelis et al. 1984; Monnett et al. 1995). During the period of our study, no juveniles were observed to move from one study area to the other.

### Foraging success

The observed differences in foraging success of sea otters between EPWS and WPWS may have contributed to higher survival of pups in EPWS than in WPWS, particularly as pups in better condition had better survival in EPWS. Sea otters captured more clams and mussels per dive and larger clams in EPWS than in WPWS. Garshelis (1983) and VanBlaricom (1988) suggested that mussels may be important prey for juvenile sea otters because mussels are abundant in very shallow water and are more easily captured than other prey types. Juvenile sea otters typically forage more in shallow water than do adults (Estes et al. 1981; Garshelis and Garshelis 1984) and may consume proportionately more mussels than adults (Garshelis 1983; Doroff and

Bodkin 1994; Doroff and DeGange 1994). Our finding of different foraging success between EPWS and WPWS is suggestive of differences in prey populations, supporting the alternative that length of occupation explains the observed differences in survival. However, we cannot discount the possibility that spill-related reductions in prey contributed to the observed foraging differences. Both mussel and clam populations in WPWS were reduced as a direct result of oiling and spill-cleanup activities, with reductions persisting throughout the period of this study (Highsmith et al. 1996). Additionally, in at least some WPWS locations, sediments that sea otters excavate and the clam and mussel populations that they consume continued to contain residual oil (Babcock et al. 1996; Harris et al. 1996; Hayes and Michel 1999; Fukuyama et al. 2000), providing a potential route of exposure to oil and possible adverse effects on their health. A further factor complicating interpretation of spill effects on prey availability is the reduction in sea otter densities in the oiled area, which may have acted to counter the effects on the population from reductions in prey abundance.

Differences in foraging habits have been observed among different age and sex classes of sea otters (Riedman and Estes 1990; Doroff and Bodkin 1994; Doroff and DeGange 1994). Our sample of foraging sea otters in both study areas was unmarked and potentially varied in age and sex structure between areas, and we cannot rule out differences in the age and sex composition of the observed animals as a factor contributing to our finding of different foraging success between areas. Consistency in dietary composition in PWS during the 1970s, 1980s, and 1990s (Calkins 1978; Garshelis et al. 1986; Doroff and Bodkin 1994; Garshelis and Johnson 2001; Dean et al. 2002) leads us to conclude that interannual variation in diet likely did not contribute to the foraging differences observed between areas.

### Body condition

A positive correlation between body condition and survival has been demonstrated in sea otters (Monson et al. 2000b), as well as in many other animal species (e.g., Choquenot 1991; Williams et al. 1993; Singer et al. 1997; Schmutz and Ely 1999; Hall et al. 2001). We found both adult and juvenile sea otters in EPWS to be significantly heavier and in better condition than their counterparts in WPWS. Total lengths of adults (females and males) were equal between areas, while EPWS pups were significantly longer. The effect of condition of mother on pup survival differed between EPWS and WPWS (pups with mothers in better condition survived better in EPWS but not in WPWS), possibly because the association between maternal and pup condition was stronger in EPWS than in WPWS, and heavier pups survived better in EPWS but not in WPWS. In WPWS, pups of mothers in better condition actually had lower survival (0.22) than did those of mothers in poorer condition (0.63); however, the number of pups ( $n = 9$ ) in WPWS with less fit mothers was relatively small and included three males, all of which died.

Differences in masses and lengths of sea otter pups between EPWS and WPWS could be attributed to differences in birth date, capture date, or growth rates. Although the pupping period is extended in sea otters, a peak of pupping occurs in late May in PWS (Garshelis et al. 1984; Monnett

et al. 1991; Johnson and Garshelis 1995). In 1990–1991, Johnson and Garshelis (1995) found that timing of pup production was similar at oiled and unoiled sites in PWS. In our study, pups in EPWS were captured only 4 days earlier, on average, than pups in WPWS; therefore, the difference in size of pups between areas (about 2 kg higher in EPWS, on average) likely was not due to growth during the capture period. Greater growth rates of pups in EPWS than in WPWS are a more likely explanation for differences in pup mass between areas. Alternatively, pups in WPWS may have been slightly younger, on average, at capture, resulting in lower body masses.

The better condition (mass and mass/length ratio) that we found in adults and pups from EPWS is consistent with the length of occupation alternative to explain higher survival. However, the similar body lengths between areas for sea otters that attained adulthood prior to the spill suggest that food resources were approximately equivalent between areas in the years prior to the spill. Poorer condition of adult females sea otters caught in WPWS in 1989–1990, relative to their counterparts in EPWS, also was reported by Rotterman and Monnett (2002).

Body-mass and condition-index differences in PWS may have been influenced by the oil spill. Possible mechanisms for a spill-related effect include reductions in prey as a direct result of the spill and increased metabolic costs or toxic effects due to exposure to lingering oil. Rotterman and Monnett (2002) attributed differences in condition of adult females between EPWS and WPWS in 1989–1990 to spill-related effects. Continuing studies (1996–1998) identified ongoing exposure of sea otters in WPWS to hydrocarbons (Bodkin et al. 2002), and residual oil was still found on beaches through 2001 (Hayes and Michel 1999; Short et al. 2002). Presumably, in 1992–1993, sea otters would have been subject to lingering oil from ingestion of contaminated prey or through grooming of contaminated fur. River otters had lower body mass in oiled areas of PWS (Duffy et al. 1993), and a study of captive river otters showed that low levels of petroleum hydrocarbons in the diet were associated with anemia and increased metabolic costs (Ben-David et al. 2000). Similar mechanisms may be acting in sea otters in the wild, with negative effects on ability to forage, growth, and, consequently, survival.

### Sex

Male sea otters generally exhibit lower survival rates than females (Kenyon 1969; Udevitz et al. 1996; Bodkin et al. 2000), and similar gender differences have been observed in many other mammalian species (Ralls et al. 1980; Hastings et al. 1999; Hall et al. 2001). In both our PWS study areas, juvenile male sea otters exhibited lower survival than females. Graphs of survival over time (Fig. 2) indicate that all losses of juvenile females occurred in early to midwinter, within a few months of weaning, whereas losses of juvenile males extended over a longer period (Fig. 2). Based on necropsies of recovered carcasses, we speculate that higher risk to males from aggressive older males may contribute to this pattern. Juvenile males also may tend to disperse more widely, which could entail greater risk for survival. The differences that we observed in survival between the sexes do

not appear to be explained preferentially by either the length of occupancy or the oil-spill alternative.

### Hematology and serum chemistry

We detected numerous differences in hematologies and serum chemistries between ages, sexes, and areas. However, few of these showed any relation to subsequent survival of juveniles. Significant age effects were noted for almost every variable measured and generally are consistent with age-related changes recognized for mammalian species (Duncan et al. 1994). Given that we had a marked contrast in age (young pups versus mature adults) and our sample sizes were relatively large, it is not surprising that we detected differences. An effect of sex on blood variables was less prevalent but still noted for a number of variables, and again, differences were consistent with expectations based on other mammalian species (Duncan et al. 1994).

The hematology and clinical chemistry data were collected primarily to evaluate health of individual sea otters and, by comparing animals in oiled and unoled areas, to assess potential toxic effects of oil. Changes in both hematology and chemistry parameters had been seen in 1989 for oiled sea otters in rehabilitation centers (Rebar et al. 1995; Thomas 1995; Williams et al. 1995), in 1990 for wild-caught sea otters in PWS (Rebar et al. 1996), and in 1991 for wild-caught river otters in PWS (Duffy et al. 1994). Based on these findings, we anticipated that sea otters in our study might be subject to residual oil in quantities sufficient to cause toxic effects. We observed that sea otters in WPWS, relative to their counterparts in EPWS, exhibited elevated serum enzymes  $\gamma$ GT, AP, and ALT, elevated WBC counts (primarily owing to an eosinophilia), decreased HGB content and, for pups, lower HCT values. The serum enzyme differences indicate hepatocellular leakage and cholestasis, perhaps associated with exposure to oil. However, interpretation of the hematology values is less clear, particularly as the differences are thought to be of little significance physiologically.

Two captive studies lend support to toxic effects of oil causing area differences in blood values. Mazet et al. (2000) evaluated hematology and serum chemistry values of mink fed petroleum hydrocarbons (crude oil or bunker C fuel oil) in their diet at levels thought to be similar to those experienced by sea otters in the wild post spill. After 6 months of exposure,  $\gamma$ GT, AP, and AST were elevated, indicating toxic effects on the liver, and RBC counts were decreased. Ben-David et al. (2000) exposed river otters in captivity to crude oil, also at concentrations intended to simulate exposure of animals in PWS post spill. They observed lower HGB levels and altered foraging behavior in exposed animals and hypothesized that increased energetic costs and impaired diving ability may have affected wild river otters following the spill.

Although the differences observed between study areas in blood parameters are consistent with oil toxicity, in general, we did not find significant relations between blood variables and subsequent survival of juveniles based on univariate analyses. When we looked specifically at parameters that would change with damage to liver or kidney, we did not find strong evidence of a relation between organ function

and survival, although  $P$  values for  $\gamma$ GT and AP were marginally significant ( $P \leq 0.09$ ) in the multivariate liver-function model. In the univariate models, only WBC had  $P < 0.05$ . Higher WBC counts were associated with greater juvenile mortality; however, the elevations seen in WBC counts resulted largely from the eosinophilia observed in WPWS sea otters. Eosinophilia is associated with systemic parasitic infections, and although we have no data to support this (from gross necropsies in the present study or from other necropsies of sea otters from PWS), there may have been differences in parasite loads, which contributed to individual health and survival. Eosinophilia also may indicate systemic hypersensitivity reactions in affected individuals. The top multivariate models included WBC, EOS, AST, RDW, and HCT. For WBC, EOS and AST, higher values related to poorer survival, whereas for RDW and HCT, lower values related to poorer survival. Both WBC and EOS were higher in WPWS sea otters, but neither differed by age. For HCT, we observed an age  $\times$  area interaction, with lower mean values in pups than in adults and higher mean values in EPWS pups than in those from WPWS, but differences between areas were small. Neither AST nor RDW varied by area, but both varied by age, with higher mean RDW values and lower mean HCT values in pups than in adults. We can speculate that increased HCT as animals mature would be associated with improved diving capacity, which may explain the positive relation between HCT values and pup survival. The relation of increased RDW to survival is unclear.

It is perhaps not surprising that blood samples taken prior to weaning are of limited value for prediction of individual survival over the subsequent year, particularly in consideration of the multiple factors that can contribute to survival outcome. However, our analyses of blood parameters suggest that further investigations of (i) age-related changes, particularly in hematological variables, and (ii) consistency of oiled vs. unoled area differences over time may enhance our understanding of factors influencing juvenile sea otter survival.

### Conclusion

Conclusively demonstrating cause of observed differences in juvenile survival is impossible without an appropriate experimental design. The immediate effects of the *Exxon Valdez* oil spill were documented through the collection of carcasses, primarily of sea otters and seabirds. The removal of a large number of top predators would in itself cause changes in the abundance and species composition of the region's marine flora and fauna; further change may have resulted from direct effects of the oil on lower level intertidal and subtidal species (Peterson 2001). Because of a lack of appropriate controls and minimal baseline data on the composition and natural variability among potentially affected natural resources, documenting chronic effects of the spill has been a difficult process.

Our purpose in conducting this study was to gain insight into the process of sea otter population recovery following the removal of a large proportion of the WPWS sea otter population in 1989. Assuming that the population was resource limited in 1989, factors limiting population growth presumably would have been moderated by the removal of

sea otters that died during the spill, resulting in an increase in food and space resources available to the remaining animals and leading to increased reproduction and survival, with eventual population recovery. However, Udevitz et al. (1996) concluded that the survival rates that we observed in this study from WPWS would be inadequate for recovery of the affected sea otter population to its pre-spill abundance. Notwithstanding the potential for confounding differences between our study areas, our results do not suggest that the WPWS sea otter population was increasing in 1992–1993. Subsequently, aerial surveys have demonstrated a lack of population growth in heavily oiled areas through 2000 and relatively low growth (0.04/year) in less heavily oiled WPWS (Dean et al. 2000; Bodkin et al. 2002).

Our finding that juvenile sea otter survival rates differ between EPWS and WPWS is consistent with a treatment effect, either length of occupation or a spill-related effect. Differences in condition of adults and pups as well as in foraging success are consistent with the hypothesis that prey are more available in EPWS than in WPWS and support the length of occupation alternative to explain survival differences. Differences in survival corresponding to condition were evident in EPWS but not in WPWS, suggesting that factors other than body condition are important in WPWS and are affecting pup survival. In addition, our findings of differences in hematology and serum chemistry between areas may be explained by chronic oil exposure, and subsequent findings of elevated exposure to hydrocarbons in WPWS (Bodkin et al. 2002) are consistent with an oil-spill effect in explaining observed differences. Monson et al. (2000a), using ages at death before and after the spill in WPWS, detected elevated levels of sea otter mortality through at least 1998, a finding consistent with a spill-effect explanation for the differences that we observed in this study. Further, Monson et al. (2000a) found that, in the years immediately post spill, juvenile sea otters exhibited the greatest relative decline in survival.

Because of the potential of more than a single treatment (oil and length of occupation) or intrinsic habitat differences, we are precluded from assigning cause to the differences in survival that we found. Through investigating how the correlates of body condition, foraging success, hematology, and serum chemistry vary in relation to area, we conclude that both length of occupation and oiling history contributed to the differences in juvenile sea otter survival that we observed between EPWS and WPWS. Although both length of occupation and oiling history appear to be important determinants of survival, the relative contribution of each factor remains unknown. We suggest that it is likely that the relief of density-dependent mechanisms in WPWS resulting from spill mortality is in the opposing direction of any chronic oil-exposure effects on sea otter survival and thus reduces our power to detect the effects of chronic oil exposure.

Our study exemplifies the difficulty in the assessment of environmental impacts and the value of appropriate controls in experimental design. It is unlikely that major environmental perturbations can be predicted. Therefore, it will remain unlikely that appropriate experimental designs can be employed to assess impacts. Our study also exemplifies the assets of correlates as an aid to inferring cause when rigorous

experimental control is not feasible. We suggest that knowledge of processes that structure populations and the variability within those processes will provide improved ability to infer cause to observed differences in cases of unpredictable environmental perturbations.

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