

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-

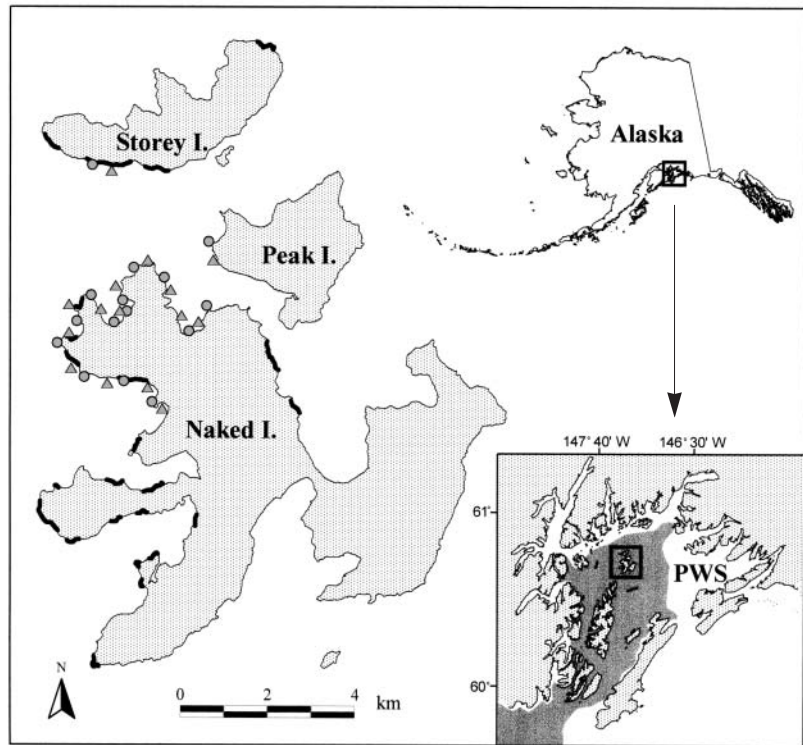


Fig. 1. Map of the oiled study site. Study areas of pigeon guillemot *Cepphus columba* colonies are depicted by thickened shoreline. Dive transect locations are shown as circles (1996 sites) or triangles (1997 sites). Inset map shows the locations of the oiled colonies (inside box) and the oiled area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

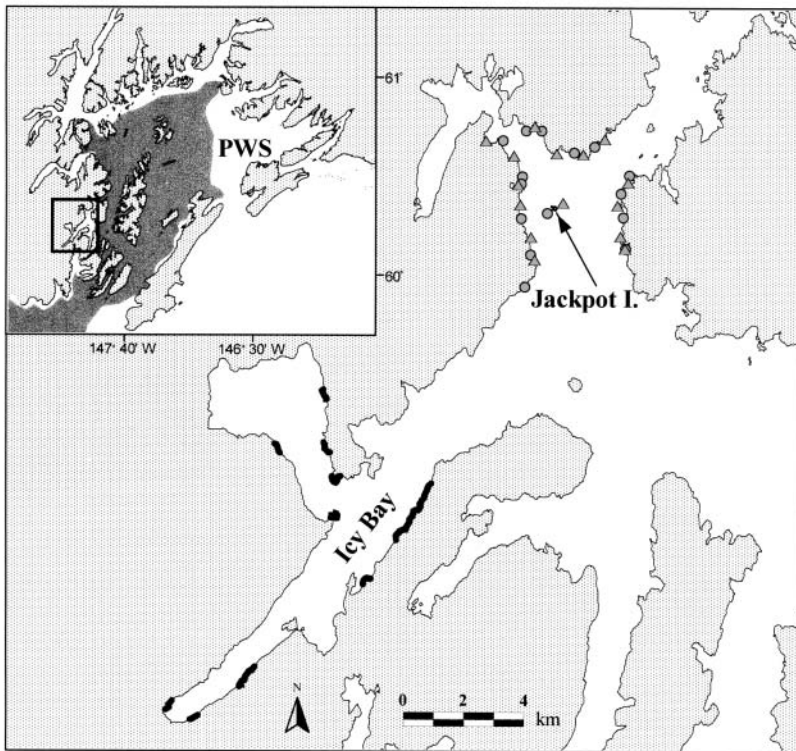


Fig. 2. Map of the unoiled study site. Study areas of pigeon guillemot *Cepphus columba* colonies are depicted by thickened shoreline. Dive transect locations are shown as circles (1996 sites) or triangles (1997 sites). Inset map shows locations of the unoiled colonies (inside box) and the oiled area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

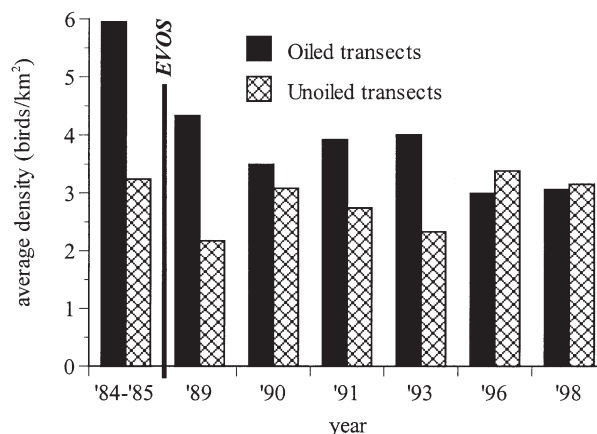


Fig 3. *Cephus columba*. Densities along oiled and unoiled shorelines before and after the 'Exxon Valdez' oil spill. Densities were determined by surveys conducted during June and July. Survey transects ($n = 123$) were selected by stratified-random sampling to account for differences in marine habitat. 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;

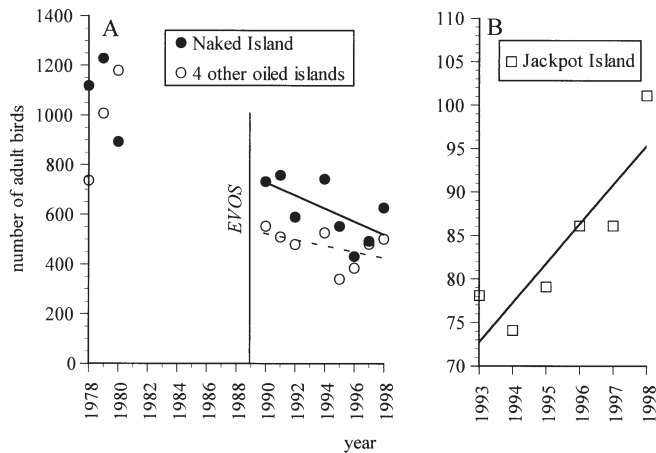


Fig. 4. *Cepheus columba*. Population trends at oiled (A) and unoiled (B) study colonies in Prince William Sound, Alaska, before and after the 'Exxon Valdez' oil spill. Post-spill trends at oiled colonies are similar when considering Naked Island ($y = -27.1x + 54\,589$, $n = 8$ yr, $r^2 = 0.42$, $p = 0.084$; 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-

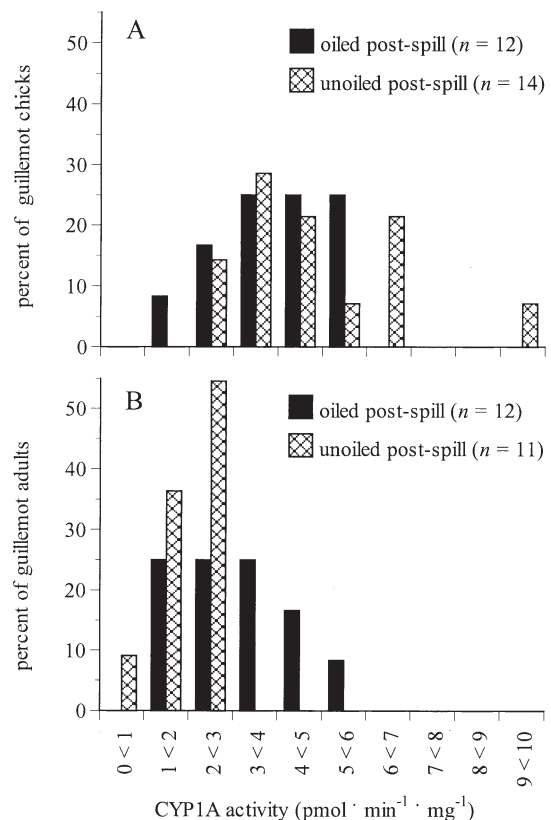


Fig. 5. *Cepheus columba*. Frequency histogram of CYP1A for chicks in 1998 (A), and adults in 1999 (B), at oiled (Naked and Storey Islands) and unoiled (Jackpot Island and Icy Bay) colonies in Prince William Sound, Alaska, after the 'Exxon Valdez' oil spill

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

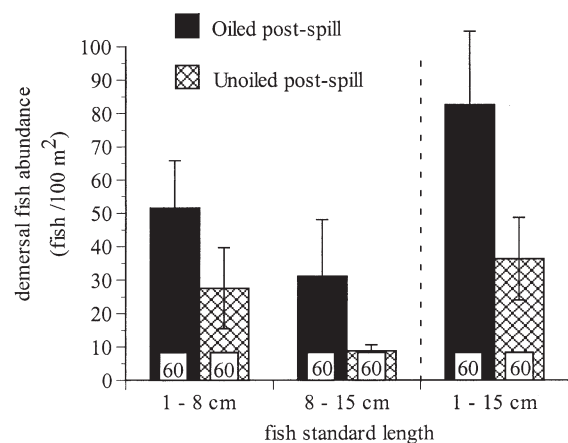


Fig. 6. *Cephus columba*. Demersal fish abundance in foraging areas near oiled (Naked, Peak and Storey Islands) and unoiled colonies in Prince William Sound, Alaska, 1996 and 1997. Data from the 2 years were pooled because the difference in fish densities between years was not statistically significant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

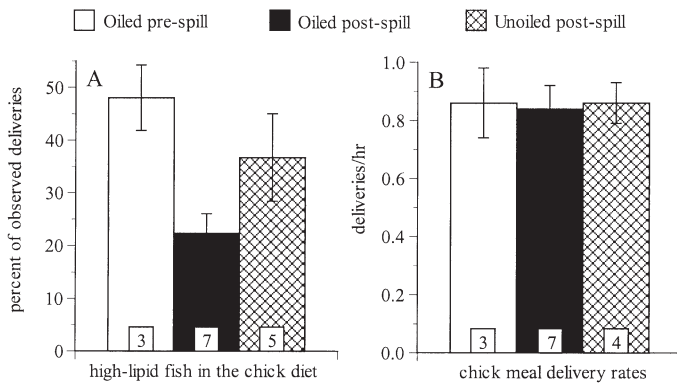


Fig. 7. *Cephus columba*. Percent high-lipid fishes in chick diet (A), and chick meal-delivery rates (B), at oiled (Naked Island) and unoiled (Jackpot Island) colonies in Prince William Sound, Alaska, before and after the 'Exxon Valdez' oil spill. Values are grand means (± 1 SE) of individual year means.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

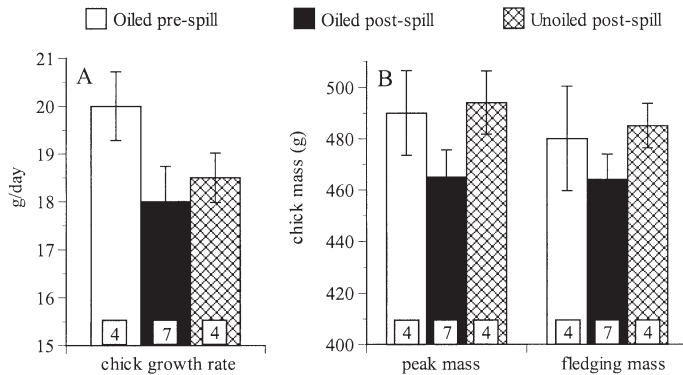


Fig. 8. *Cephus columba*. Chick growth rates (A), and peak and fledging masses (B), at oiled (Naked Island) and unoiled (Jackpot Island) colonies in Prince William Sound, Alaska, before and after the 'Exxon Valdez' oil spill. Values are grand means (± 1 SE) of individual year means. Sample sizes are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

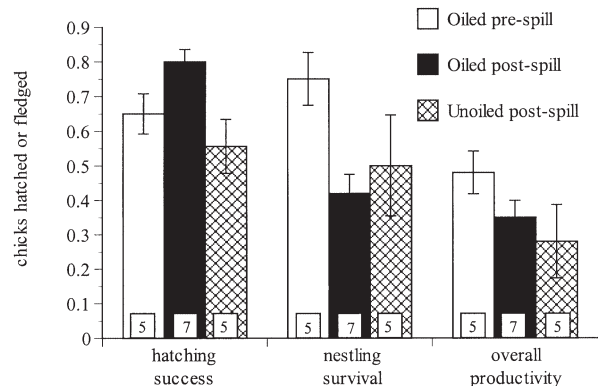


Fig. 9. *Cephus columba*. Reproductive success at oiled (Naked Island) and unoiled (Jackpot Island) colonies in Prince William Sound, Alaska, before and after the 'Exxon Valdez' oil spill. Values are grand means (± 1 SE) of individual year means. Sample sizes are indicated at the bases of the bars

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 fledgling 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)	Nestling 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 (unoilied 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)	Nestling 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

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