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Review

Prolonged recovery of sea otters from the *Exxon Valdez* oil spill? A re-examination of the evidence

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ABSTRACT

Sea otters (*Enhydra lutris*) suffered major mortality after the *Exxon Valdez* oil spill in Prince William Sound, Alaska, 1989. We evaluate the contention that their recovery spanned over two decades. A model based on the otter age-at-death distribution suggested a large, spill-related population sink, but this has never been found, and other model predictions failed to match empirical data. Studies focused on a previously-oiled area where otter numbers (~80) stagnated post-spill; nevertheless, post-spill abundance exceeded the most recent pre-spill count, and population trends paralleled an adjacent, unoiled–lightly-oiled area. Some investigators posited that otters suffered chronic effects by digging up buried oil residues while foraging, but an ecological risk assessment indicated that exposure levels via this pathway were well below thresholds for toxicological effects. Significant confounding factors, including killer whale predation, subsistence harvests, human disturbances, and environmental regime shifts made it impossible to judge recovery at such a small scale.

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1. Introduction

When the *Exxon Valdez* ran aground in Prince William Sound, Alaska, on March 24, 1989, it unleashed not only the largest spill of oil into American waters (at the time), but also protracted legal disputes regarding Exxon's (and its successor Exxon Mobil's) liability for damages to natural resources. Both as part of and apart from these legal disputes, studies were initiated to assess immediate damages as well as longer-term effects. Few scientists then would have imagined that their studies would still be ongoing more than 20 years after the spill.

No species affected by the *Exxon Valdez* oil spill (EVOS) attracted more public or scientific attention than the sea otter (*Enhydra lu-*

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tris). The sea otter became, in effect, the "poster species" of this spill: photos of moribund oiled otters hauled out on beaches or collected in boats appeared in many popular magazines and government reports (Batten, 1990). Rice et al. (2007, p. 450) commented that "perhaps our most persistent collective memory of the oil spill is the dead and dying sea otters." A major report summarizing the "legacy of an oil spill 20 years after *Exxon Valdez*" featured sea otters on the cover and used this species as the foremost case study (Exxon Valdez Oil Spill Trustee Council, 2009).

Two reasons for the attention on sea otters stand out: no mammal suffered greater mortality from the spill, and no affected species had greater public appeal. Whereas the value of damaged fishery stocks could be measured in terms of losses to the commercial industry, the value of lost sea otters was more elusive. One valuation was $80,000 per individual, the cost that Exxon expended per oiled otter that was successfully cleaned and rehabilitated shortly after the spill (Estes, 1991). With potentially thousands of otters dying (or not being born) as an immediate or longer-term result of the spill, the significance of this species in terms of possible legal reparations, as well as its ecological role, was enormous.

Sea otters were particularly vulnerable to oil because they rely strictly on their fur for insulation; they float on the water surface when resting, swimming, or consuming food, so were apt to encounter floating oil; they groom their fur meticulously, which provided a pathway to ingestion; they eat primarily bivalve prey, some of which became contaminated; and they spend much of their time digging for prey in nearshore sediments, where some oil residues collected. Thus, otters could suffer effects from immediate contamination of their fur or chronic effects from consuming oiled prey or digging in oiled sediments. This vulnerability was recognized at the time of the spill and set in motion a host of studies to monitor short- and long-term effects of the spill. In the first 4 years after the spill, more than 20 scientists were involved in a wide range of sea otter research, mainly in Prince William Sound (PWS), costing over $3 million (Ballachey et al., 1994). Since then many millions more dollars have been spent to ascertain whether this species has recovered from the initial effects of the spill or is suffering from continued impacts. Notably, no funds were spent on active management aimed at sea otter restoration (e.g., reduced hunting or population augmentation); however, considerable efforts were expended to clean and rehabilitate oiled otters (with disappointing results: Monnett and Rotterman, 1995) and to clean oiled shorelines where otters and their prey reside (Mearns, 1996).

Oil that leaked from the *Exxon Valdez* spread from Bligh Reef in Valdez Arm in northern PWS (Fig. 1), southward through much of

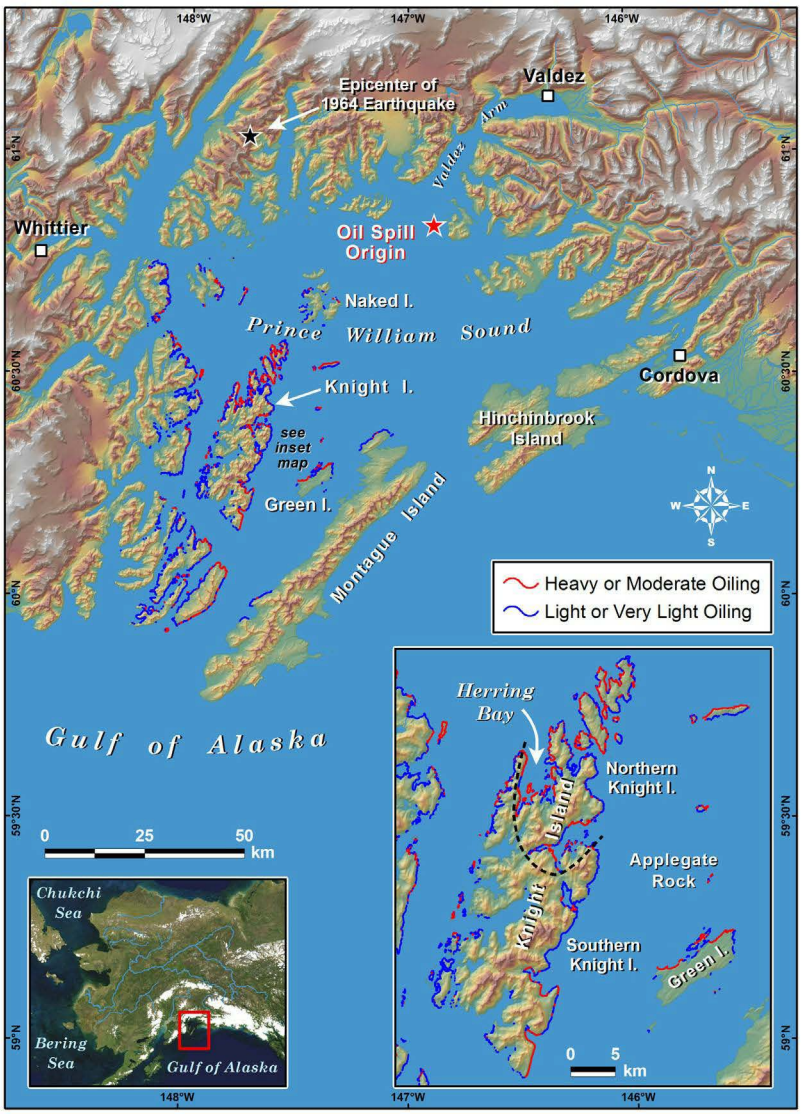

Fig. 1. Principal sea otter study sites and maximum distribution of oil on shorelines in western Prince William Sound, Alaska, following the *Exxon Valdez* oil spill.

western PWS (WPWS) and then, with diminishing intensity, across the outer coast of the Kenai and Alaska peninsulas and Kodiak Island. The extent of oiling in WPWS varied widely among shorelines, from heavy to none (Neff et al., 1995). Several long-term studies were conducted by scientists funded by the *Exxon Valdez* Oil Spill Trustee Council, a body of six governmental agencies that was formed to plan, coordinate, review and support research and restoration efforts, using the funds from the civil settlement with Exxon (Exxon Valdez Oil Spill Trustee Council, 2009). Other studies were conducted by scientists supported by Exxon (subsequently Exxon Mobil). These different groups of scientists often collected different types of data and interpreted data somewhat differently; these varied approaches, which often yielded disparate findings, enhanced scientific rigor, even if it led to less-certain conclusions.

This paper was motivated by a series of recent reports asserting, definitively, that sea otters in one area of WPWS that was heavily oiled continue to suffer, individually and demographically, from residual effects of the 1989 spill (Bodkin et al., 2011, 2012; Monson et al., 2011; Miles et al., 2012). Here we critically evaluate these and other previous studies that collectively have argued that effects of the spill persisted for more than two decades, thus providing the basis for keeping sea otters on the short list of species that have not yet recovered from EVOS (Exxon Valdez Oil Spill Trustee Council, 2009). Our intent is not to present a comprehensive review of the impacts of the spill on sea otters, but rather to focus on results that have been interpreted as evidence of effects continuing to the present. We do not discredit any of the investigators who reached these conclusions; we simply aim to offer an alternate interpretation of data related to long-term demographic consequences.

2. Evidence for chronic effects

Acute effects of the spill on sea otters were well documented, and the vulnerability of this species to oil contamination confirmed (Bayha and Kormendy, 1990; Lipscomb et al., 1994). Whereas estimates of direct, spill-related mortality varied widely with varying methodological procedures and assumptions (Garrott et al., 1993; DeGange et al., 1994; Garshelis, 1997; Garshelis and Estes, 1997), there was no doubt that a large proportion of otters in WPWS died.

With time, and the continued weathering of the oil residues, it was generally presumed that sea otters would gradually rebound to baseline conditions. In an introductory chapter to a book summarizing a symposium on effects of EVOS, held 4 years after the spill, Spies et al. (1996, p. 11) wrote: "These results do not preclude ongoing toxic effects in highly sensitive species in some areas, but they do support a conclusion that direct effects of the oil in the intertidal zone [where the residual oil settled] were largely over by 1991, when major cleanup activities ceased." Indications that this was not the case for sea otters began to emerge by the mid-1990s, stimulating further studies of recovery of this species (Holland-Bartels et al., 1996). In assessing recovery, the chief variable of interest is abundance, so measures of changing abundance or parameters directly affecting abundance (reproduction and survival) were the primary focus. However, the ability to track recovery, or conversely to discern chronic effects impeding recovery, depend largely on availability of adequate pre-event data and suitable control sites, as well as understanding the extent of natural variability in the system (Wiens and Parker, 1995), all issues that affected long-term investigations of sea otters.

2.1. Reproduction and survival

No study detected any spill-related effects on sea otter reproduction (Garshelis and Johnson, 2001; Bodkin et al., 2002). Previous studies found that reproductive rates tend to be rather fixed among adult sea otters, even with large differences in food supplies (Monson et al., 2000a). However, age of first reproduction appears to be linked to subadult nutrition (von Biela et al., 2009), and Dean et al. (2002) found that subadult otters in one of the most heavily-oiled sites in WPWS had better body condition than those in an unoiled site with a much higher otter density, due to greater food abundance and hence higher consumption rates in the low density area.

Weaning success (survival of dependent pups) in sea otters is sensitive to environmental stressors (Monson et al., 2000a), but appeared to be unaffected by the spill (Johnson and Garshelis, 1995). Two studies (Rotterman and Monnett, 1995; Ballachey et al., 2003) surgically implanted radio transmitters in sea otter pups and monitored their survival for the year immediately post-weaning (weanling survival) 2–4 years after the spill. Results of these studies were equivocal because (1) pre-spill estimates of weanling survival in WPWS were lacking; (2) post-spill comparisons of weanling survival in WPWS versus unoiled EPWS were confounded by differing food conditions in these two areas, due to differences in duration of occupancy by otters (Garshelis et al., 1986); (3) most of the WPWS pups in the two telemetry studies were not from oiled sites; and (4) no observed mortalities were attributable to oil (Ballachey et al., 2003). Moreover, these studies were short term, ending in 1993.

Sea otter carcasses (generally skeletons) collected on beaches during the spring, after the normal winter die-off, provided another means for examining changes in patterns of mortality over time. The age at death of each otter carcass can be judged from growth layers in the teeth. Pre-spill data on the age structure of dead otters were available from systematic carcass collections at Green Island (1976–1985; Johnson, 1987), and since this island was oiled on one side (Fig. 1), this site appeared to be a good choice for testing before-spill versus after-spill effects.

Systematic carcass collections were resumed at Green Island in 1990, the spring after the spill, and expanded to a larger oiled area in 1998 (Monson et al., 2000b). The age structure of these collections changed over time, and modeling was employed to explain this change. Holding reproduction, immigration and emigration constant, age-specific survival was altered in the model to produce results that best matched the observed age composition of dead animals (Monson et al., 2000b). Results indicated that young animals had higher rates of mortality immediately after the spill than before the spill, but this effect quickly dissipated. The model also indicated that, with time, survival improved (relative to pre-spill) for cohorts of otters that were young at the time of the spill, but declined for middle-aged and older otters. These results were interpreted as indicative of a gradual recovery, due to the eventual loss of these older-aged, debilitated cohorts, but with prolonged spill-related impacts on survival even for otters born after the spill (Monson et al., 2000b; Bodkin et al., 2002).

There was a major incongruity, however, between the results of the modeling and numbers of live otters actually observed: the post-spill carcass collection was primarily from Green Island, where counts of otters (~180, excluding dependent pups) were stable or increasing since 1990 and were equal to or greater than pre-spill levels (Johnson and Garshelis, 1995; Garshelis and Johnson, 2001). If survival of adult animals had been declining through time, it must have been compensated for by increased reproduction or immigration in order for total numbers to remain so high. However, such an increase in reproduction or immigration would violate the assumptions of the model; in other words, the model could not explain both the carcass age distribution and the number of otters living at Green Island.

Annual carcass collections were continued over a wide area of WPWS from 1999 to 2008, and the observed age structure contin-

ued to change in a way that suggested prolonged negative effects on survival (Monson et al., 2011). Whereas the proportion of pups among the carcass sample remained fairly stable, the proportion of 2–8 year olds ('prime age') increased while the proportion of older otters declined. In an attempt to explain this seeming depression of survival in prime-age otters in the face of a continuing overall increase in the WPWS population, Monson et al. (2011) developed a more complex source–sink model in which otter numbers in one portion of WPWS could be increasing (as observed), while emigrants from that source area supported a population sink, where otters were purportedly dying at a high rate.

Monson et al.'s model used data from an unoiled site on Montague Island (Fig. 1) as a source population, and a large portion of WPWS, with variable degrees of past oiling (from none to heavy) as the presumed sink. The model predicted an unchanging sink population of about 900 otters during 1990–2009, supported by a continually growing source population. Model results indicated depressed survival among the sink otters for at least two decades post-spill, yielding a cumulative loss over this period of nearly 900 animals beyond what was expected had baseline survival not changed; these purported deaths were considered to be chronic effects of the oil spill (Monson et al., 2011).

Models like that of Monson et al. are designed to help explain complexity, and may appear to do so even if some assumptions or some results do not match reality. Some notable contradictions among the assumptions and predictions of this model and empirical observations of the living sea otters in WPWS include the following:

- The model assumed that emigrating juvenile otters, mainly males, from Montague Island were the source for maintaining numbers in sink populations across WPWS. Although emigration of young males has been observed, there is no evidence from the extensive tagging and telemetry studies that have been conducted in this area of young males from Montague settling elsewhere in WPWS.
- If dispersing male otters from unoiled areas did preferentially settle in previously-oiled areas (e.g., due to lower densities) and lived into adulthood (as the model predicted), the sex ratio and hence reproductive output of the resettled area would change, a violation of model assumptions and counter to observations of the living populations (Bodkin et al., 2002).
- With high rates of male immigration in the modeled sink area, mortality would have to be male-biased to maintain the female-biased sex ratio of otters in WPWS. Thus, most carcasses should have been male. However, the sex of carcasses could not be reliably determined (without genetic analysis), so sexes were lumped together and taken as representative of the distribution of female ages at death.
- The model used population trends at one small heavily-oiled area on northern Knight Island (NKI; discussed in more detail below) to represent the trends in the entire hypothesized sink area, which encompassed >10× the number of otters at NKI and ~25–40% of the WPWS population. However, no other area with the same population trend as NKI (stagnant to very low growth) has been identified, despite over two decades of WPWS-wide surveys.
- The model predicted a continued decline of the sink population, but counts at NKI during 2007–2009 showed a sizeable increase (discussed further below).

This model has been promoted as the chief evidence of continuing elevated mortality of otters attributable to the spill (Bodkin et al., 2012). Like any model, however, the output is largely dependent on the assumptions, and in this case there appear to be significant discrepancies between assumed conditions, predicted outcomes, and observations of the living populations.

2.2. Population trends

Before–after studies of otter numbers in oiled areas were hindered by limited pre-spill data and the patchy distribution of the oil. Pre-spill counts of otters were centered at Green Island, where surveys were conducted from small boats 1–4 times per year during 1977–1985 (Johnson, 1987). During these same years, multiple boat-based counts were also conducted along a portion of Montague Island and Applegate Rock (a tiny island and shoal west of Green Island, Fig. 1). Additionally, one complete boat-based survey of all of PWS (although restricted mainly to the swath within 200 m of the shoreline) was conducted during 1984–1985 (Irons et al., 1988). A general pattern of population stability was perceived for WPWS during the late 1970s–mid-1980s (Johnson, 1987).

Effects of oiling were judged by comparing counts of otters before the spill to counts made afterwards, using the same methodology, at sites that were impacted to different degrees (Burn, 1994; Johnson and Garshelis, 1995). Green Island, Knight Island, and the Naked Island group were oiled only along north and northwest facing shorelines, whereas Montague Island was not oiled (Fig. 1). Applegate Rock was completely engulfed with oil, and presumably all otters that were at this site at the time of the spill died. One year after the spill, otter numbers at this site were lower than pre-spill, but they recovered by the following year (Johnson and Garshelis, 1995). At Green Island, Naked Island, and even heavily-oiled Knight Island, most counts made 1–7 years after the spill were equal to or higher than pre-spill (Johnson and Garshelis, 1995; Garshelis and Johnson, 2001; Fig. 2). Numbers at Montague Island, which served as a control site for some studies, were also higher post-spill than in pre-spill surveys (Fig. 2). Likewise, a boat

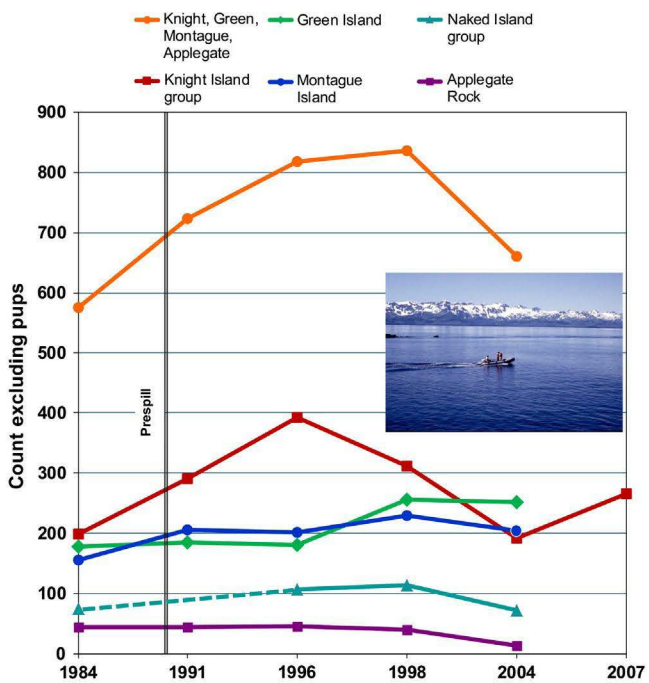

Fig. 2. Counts of sea otters, excluding dependent pups, obtained during boat surveys of portions of WPWS (site locations shown in Fig. 1). Pre-spill data are from Johnson (1987) and Irons et al. (1988), and post-spill data from Garshelis and Johnson (2001, unpublished data). Post-spill survey methods (shown in inset photo) followed those of pre-spill investigators. Yearly points are the means of 1–8 surveys per site. Only years with survey data at Knight Island are shown on *X*-axis.

survey in the summer of 1989, just months after the spill, tallied 12% more otters throughout WPWS than the most recent pre-spill survey, in 1984 (Burn, 1994; reanalyzed by Garshelis and Johnson, 2001).

That otter numbers at oiled sites in WPWS were higher shortly after the spill than before was an obvious paradox. One explanation is that the spill-caused mortality was masked by an increase in otter numbers that occurred during the 5-year interval between the last pre-spill counts and the spill (Garshelis and Johnson, 2001). Previously, it was thought that all of WPWS had been at carrying capacity, so increases in otter numbers were not expected. However, even at carrying capacity, otter numbers could increase if the food base increased. Garshelis and Johnson (2001) found that otters retrieved more and larger clams (their primary food in PWS) after the spill than they had at the same sites in the early 1980s and also spent less time foraging, suggesting that food resources had increased.

Two studies, using different methodologies, indicated that otter numbers in WPWS continued to increase for several years after the spill. Boat surveys conducted in a portion of WPWS that included both oiled and unoiled areas indicated an annual population growth rate of 2.5% per year during 1991–1996 (Garshelis and Johnson, 2001; Fig. 2). Aerial surveys conducted across a broader area of WPWS during 1993–2009 indicated that numbers continued to grow at an average of 2.6% per year over this longer period; in fact, the population in this region virtually doubled, increasing by nearly 2000 otters (Bodkin et al., 2011).

Population changes in WPWS after the spill differed by site, with no clear association between rates of change and previous extent of oiling (Johnson and Garshelis, 1995). For example, among three oiled sites, otter numbers increased rapidly at Knight Island but remained stable at Green Island and Applegate Rock during the early 1990s (Fig. 2). During the late 1990s, numbers declined at Knight Island, increased at Green Island, and stayed stable at Applegate Rock (but then declined after 1998) (Garshelis and Johnson, 2001). At the neighboring unoiled site, Montague Island, boat surveys showed no trend in otter numbers, whereas aerial surveys indicated a sudden rise in 1997 (Fig. 3a). This discrepancy may have been due to the inclusion of a portion of Green Island in the aerial counts of Montague; this portion of Green Island contained a large kelp bed where sizeable but variable numbers of otters often rested.

The delineation of study-site boundaries became a significant factor in the assessment of population trends and evaluation of potential effects of the spill (see Garshelis and Estes, 1997). In a study of oil-spill effects on harlequin ducks (*Histrionicus histrionicus*) (Esler et al., 2002; Esler and Iverson, 2010) that was conducted under the same program as the sea otters (Holland-Bartels et al., 1996), all of Knight and Green Islands were considered part of the oiled (treatment) area, including the portion of Green that was pooled with Montague as a reference area for sea otter counts (Bodkin et al., 2002, 2011). Esler and Iverson (2010) reported that spill effects on this benthic-feeding sea duck persisted for about a decade in this combined area. Ironically, had the sea otter studies also

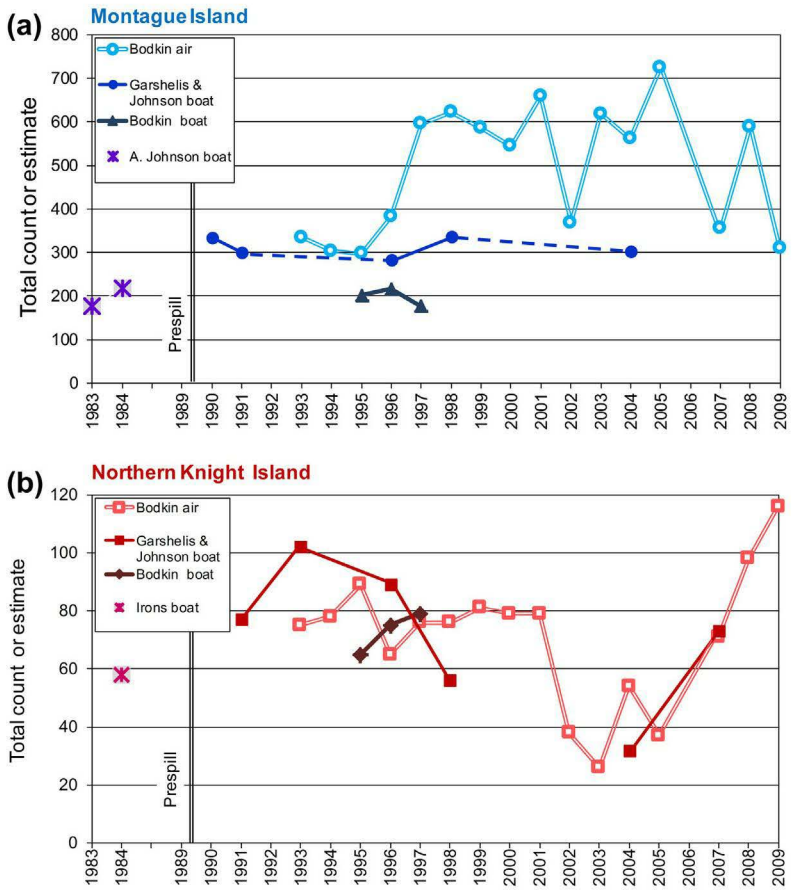

Fig. 3. (a) Trends in total sea-otter numbers at northwestern Montague Island and (b) Northern Knight Island, Prince William Sound, Alaska. Boat surveys were counts along the complete shoreline, unadjusted for detection rate. Post-spill counting methods from boats followed pre-spill methods at each site. Aerial counts were made along sample transects, corrected for varying detection (Bodkin and Udevitz, 1999) and extrapolated to the entire shoreline. Aerial counts at Montague Island included a portion of Green Island, so were higher and more variable than boat counts. Pups could not be differentiated during aerial surveys, so all data include dependent pups. Dashed lines denote significant gaps (>3 years) between boat surveys at Montague. Indicated data sources: Johnson (1987), Irons et al. (1988), Garshelis and Johnson (2001, unpublished data) and Bodkin et al. (2002, 2011).

Table 1
Counts of sea otters made 16–5 years before the *Exxon Valdez* oil spill (1973–1984) at Southern Knight Island (SKI), Northern Knight Island (NKI), and Herring Bay (part of NKI), Prince William Sound, Alaska, compared to counts made 2 years post-spill (1991) and more recently (2007) using the same survey methodology as used in 1984.

Survey			Count[a]				
Year[b]	Month	Platform[c]	SKI	NKI	% Knight Is. otters in NKI	Herring Bay	% NKI otters in Herring Bay
1973	June	Helicopter	103	105	50	22	21
1974	March	Helicopter	50	27	35	9	33
1984	June–August	Boat	200	58	22	7	12
1991	June–August	Boat	345	77	18	11	15
2007	June	Boat	299	73	20	15	21

[a] All counts include pups; pups were distinguished during boat-based counts, but not during helicopter counts. Counts are not adjusted for imperfect detection.
[b] Surveys in 1973 and 1974 were conducted by Pitcher (1975), 1984 survey by Irons et al. (1988), and 1991 and 2007 surveys by Garshelis and Johnson (unpublished data).
[c] Although counts from different survey platforms are not directly comparable, the counts highlight changes in otter distribution around Knight Island over time.

combined Knight and Green Island, the downward population trend observed in the mid–late 1990s for NKI alone (Fig. 3b), which was reported as a spill effect (Bodkin et al., 2002), would not have existed (Fig. 2).

2.3. Focus on Northern Knight Island

Over time, concerns regarding sea otter recovery from EVOS narrowed to a smaller and smaller portion of WPWS. Eventually, most attention centered on the northern half of Knight Island (including Disk, Ingot, and Eleanor Islands; Fig. 1). One of the first major landings of oil following the grounding of the *Exxon Valdez* was on the north-facing shorelines of this island group. Thus, NKI became the focal point not only of extensive clean-up efforts, but also of post-spill studies of recovery for a host of species.

Some studies reported that sea otters at NKI had not recovered for nearly two decades after the spill, based on lower abundance than pre-spill estimates (Rice et al., 2007; Bodkin et al., 2012). There was considerable uncertainty and disagreement, however, as to the number of otters that occupied NKI before the spill.

Dean et al. (2000, 2002) derived an estimate of pre-spill abundance at NKI from a count made by Pitcher (1975) 16 years before the spill. Pitcher surveyed all of PWS from a helicopter during June 1973 and again in March 1974. At NKI, these two counts varied nearly four-fold (Table 1). To assess the proportion of otters missed, Pitcher compared the March helicopter counts to counts made by boat. Overall, Pitcher's boat counts were 73% higher than helicopter counts, although at Knight Island the difference was 205%. Applying this range of correction factors to the March 1974 helicopter count at NKI yielded estimates of 47–82 otters. Pitcher did not compare helicopter to boat counts during summer. However, because of better lighting (higher sun angle), summer aerial counts tend to be more accurate than in winter. Given that the uncorrected summer helicopter count at NKI (105 otters) was higher than the corrected winter count, it seems reasonable to assume that significantly fewer otters were missed during the summer. Unexplainably, Dean et al. (2000, 2002) apparently applied a correction factor of 230% to Pitcher's summer count to derive their estimate (237) for the number of otters present at NKI just before the spill in 1989.

Dean et al. (2000) also used another approach to estimate pre-spill numbers of otters at NKI. They reasoned that the number of dead and moribund otters collected shortly after the spill provided a minimum estimate of the number of otters that must have lived there when the spill occurred. Adjusting for carcasses that were not recovered (per Garshelis, 1997), they estimated 165 otters at NKI at the time of the spill. In deriving this estimate, they "assumed that the number of carcasses drifting out of the study area equaled the number drifting in" (Dean et al., 2000, p. 284). This assumption is unlikely to be true because prevailing currents flowed into this area from the origin of the spill (Fig. 1). Moreover, shortly after the spill, PWS was struck by a large storm with northerly winds that pushed the floating oil southward, explaining why the north-facing shorelines were most heavily oiled (Galt and Payton, 1990). As otters died in the path of the spill, they either drifted out to sea and eventually sank or washed up on beaches. Oil landed disproportionately at NKI (Fig. 1), so it follows that dead and moribund otters drifted on a similar course (Hill et al., 1990). With these currents and wind conditions, the number of sea otter carcasses collected at NKI could have been substantially higher than the number living there at the time of the spill.

Counts made at NKI in 1984, just 5 years before the spill, provide a better indication of the number of otters living there at the time of the spill. Irons et al. (1988) counted 2.5 times more otters than did Pitcher for the whole of PWS, but saw only 58 otters at NKI, suggesting that the NKI population had declined since the early 1970s and that both of the Dean et al. (2000) pre-spill estimates were too high.

Herring Bay on NKI (Fig. 1) captured large amounts of oil, and thus attracted disproportionate cleaning efforts and later research work. At the height of the spill response, nearly 1000 people worked in this bay (Hooten and Highsmith, 1996). Anecdotal reports indicate that clean-up boats herded oil, floating debris, and some wildlife carcasses into this area in order to contain them. Some scientists have drawn particular attention to the 38 sea otter carcasses known or estimated to have come from Herring Bay (Rice et al., 2007), suggesting this as a minimum baseline number of otters present in that bay at the time of the spill. This value, though, is more than five times higher than the seven otters that Irons et al. (1988) counted in this bay during the summer of 1984. Either otter numbers in Herring Bay had increased dramatically between 1984 and 1989 or, more likely, the number of carcasses found in this bay in the months following the spill represented an accumulation of individuals that died in the expanse of water to the north. Depending on which pre-spill values are used, otter numbers in Herring Bay and other parts of NKI could have been above the pre-spill baseline as early as 1991, or could have been below baseline for two decades post-spill (Table 1 and Fig. 3b).

Trends in otter abundance in the NKI area have also been subject to debate. Counts of otters sharply declined across a broad region of WPWS, including unoiled Montague Island, from 2001 to 2002 (Fig. 3a; Bodkin et al., 2011). At NKI, numbers did not fully rebound until 2007 (Fig. 3b). No other areas have been investigated as intensely as NKI, so it is not known whether the more prolonged dip in numbers there was an anomaly or part of a broader trend.

Eight boat-based surveys conducted during 1991–2007 around Knight Island found a strikingly parallel trend in otter numbers between the northern and southern halves of the island (Fig. 4a), even though Southern Knight Island (SKI) was much less impacted by oil than NKI (Table 2), and reproduction (measured as the pro-

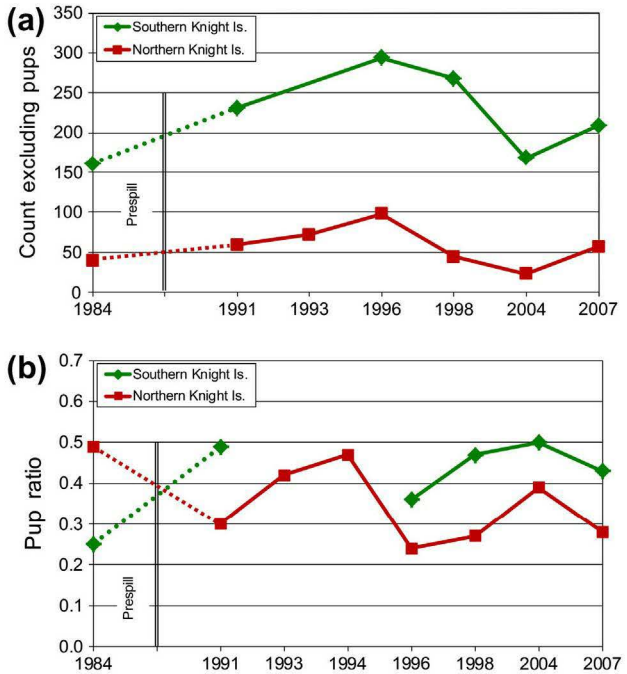

Fig. 4. (a) Counts of sea otters (excluding dependent pups) and (b) ratios of dependent pups:independent otters tallied during boat-based surveys conducted during 1991–2007 (some years missing) along the northern and southern halves of Knight Island, Prince William Sound (Johnson and Garshelis, 1995; Garshelis and Johnson, 2001, unpublished data) versus results from a single pre-spill survey using the same technique (Irons et al., 1988). Only years with survey data are shown on X-axis.

portion of otters with pups) was consistently higher at SKI after the spill (Fig. 4b). Notably, a change in distribution of otters around Knight Island was evident prior to the spill: otter numbers declined precipitously at NKI from 1973 to 1984 while increasing at SKI (Table 1). Although it is not wise to infer trends from only two points in time, that is all that was available in this case, and the counts changed markedly over this 11-year period. If this pattern continued after 1984, then numbers may have been decreasing at NKI while increasing at SKI at the time of the spill. Uncorrected counts from different platforms (Table 1) are difficult to compare, but changes in the proportion of otters counted within the northern versus southern halves of this island should nevertheless be reflective of real changes in distribution. These apparent spatial dynamics in the sea otter population complicated interpretations of population recovery, although parallelism between similar sites with differing impacts is one measure of recovery (Skalski et al., 2001; Parker and Wiens, 2005).

3. Explanations for observed trends in abundance

3.1. Misunderstood population dynamics

A host of demographic circumstances has been posed to explain the lack of growth of the NKI otter population during an extended period post-spill. These included higher mortality and emigration from NKI (Bodkin et al., 2002); higher rates of loss despite immigration from source populations (Monson et al., 2011); and immigration of otters from EPWS to WPWS but avoiding NKI (Rice et al., 2007). The variety of these conjectures reflects the lack of direct evidence that mortality, immigration, or emigration were aberrant at this site. Moreover, other sites that were less oiled also showed no noticeable population increase (Fig. 2).

Although a population increase was expected across WPWS as otters recovered from the spill, such an increase was not expected for unoiled sites such as Montague Island, which was the primary control site for several comparative studies. Historically, numbers of otters at Montague have varied widely, but no trend was apparent in counts ($n = 9$) made during 1959–1984 (Lensink, 1962; Pitcher, 1975; Johnson, 1987). A post-spill surge in otters at this site (doubling from 1995 to 1997, based on aerial counts but not boat-based counts), followed by sudden sporadic declines (nearly 50% in 2002, 2007, and 2009, returning to the mid-90s levels; Fig. 3a), were as anomalous as the lack of an increase at some other sites. Up-and-down swings in otter populations at various sites in PWS predated the spill (Johnson, 1987; Garshelis and Garshelis, 1984), but are still not well understood.

Peterson et al. (2003, p. 2083) proposed that the 4% increase (occurring at the time) in otter numbers in WPWS observed after the spill was "far short of the 10% expected from earlier population recovery after termination of trade in sea otter pelts." The two situations, however, are not analogous. Recovery from the fur trade followed decades of virtual absence of sea otters in PWS, enabling their food resources to flourish and otter numbers to grow rapidly when hunting ceased (Lensink, 1962; Bodkin et al., 1999). In contrast, following the spill, otter numbers in WPWS were equivalent to what they had been in the early 1980s, with no areas totally free of the sea otter predation that constrains food resources (Johnson and Garshelis, 1995; Garshelis and Johnson, 2001).

Overall, there is little empirical or conceptual basis for claims about what the trajectory in otter numbers at individual sites in WPWS should have been in the period since the oil spill, especially since they were assumed to have been at carrying capacity – an issue that seems to have been lost in discussions related to assessment of otter recovery. No concerns would have been raised had there been no spill and these same population changes occurred over the past 20 years, as they were easily within the range of previously observed variability. Thus, one explanation for the population trends observed at various sites across WPWS is that they were due to normal vagaries of sea otter population dynamics. Be-

Table 2
Extent of shoreline area along the northern and southern portions of Knight Island (Fig. 1), Prince William Sound, Alaska, that was covered by three categories of oil, recorded during two time periods.

Portion of Knight Island	Date[a]	Percent of shoreline in oiling category[b]			
		Heavy (%)	Moderate (%)	Light (%)	No impact (%)
Northern	Summer 1989	29	21	27	24
	Fall 1989	29	21	39	10
Southern	Summer 1989	8	5	7	80
	Fall 1989	9	5	28	58

[a] Data for summer represent the cumulative extent of oiling from the date of the spill in late March through 21 August, before cleanup operations were completed. Some areas that were not directly impacted became lightly oiled by fall (September–November) 1989 from cleanup operations that dispersed some of the oil.
[b] Digital data were obtained from the Alaska Department of Natural Resources (1996a,b) and analyzed using ArcMap 9.1. Oiling categories are described by Neff et al. (1995). Total shoreline lengths were 136 km and 299 km at northern and southern portions of the island, respectively. Oil distribution was patchy (Fig. 1).

low we discuss other potential explanations for the observed trends in numbers, specifically at NKI.

3.2. Remnant oil

Conceivably otters could have been exposed to oil persisting in the environment. Whereas potential exposure through contaminated food was examined and discounted (Neff et al., 2011), direct physical contact with oil residues has been raised as a plausible exposure pathway. Oil residues still exist below the surface of some shorelines in WPWS, most notably at NKI (Short et al., 2006). It has been suggested by a number of authors (Bodkin et al., 2002, 2012; Peterson et al., 2003; Rice et al., 2007) that by digging for clams, sea otters at NKI may continue to contact and become contaminated by this buried oil.

If population numbers at NKI have been depressed due to individuals contacting oil residues, then the following population patterns would be predicted: (1) otters at NKI should exhibit lower reproduction and/or higher mortality than otters elsewhere; (2) SKI, which has little residual oil, should show a different population trajectory than NKI; and (3) effects at NKI should have waned over time as oil residues declined (from natural decomposition and otters digging them up [i.e., bioturbation]). The available evidence does not support these predictions. Reproductive output, measured in terms of pups per independent otter, was consistently lower at NKI than at SKI (Fig. 4b), apparently due to a lower proportion of adult females in this area (Bodkin et al., 2002). Although many otters from NKI have been radio-tagged since the spill, no studies have reported unusually high mortality there, and since the months after the spill, no dead otters have been recovered for which mortality was attributed directly or indirectly to oil contamination. Secondly, SKI and NKI showed parallel population dynamics despite dramatically different oiling levels (Fig. 4a). Thirdly, instead of slowly recovering over time, otter numbers at NKI dropped sharply after 2001 (Fig. 3b), coinciding with an abrupt decline in numbers at unoiled Montague Island (Fig. 3a). That same year investigators discovered more buried oil persisting on shorelines of WPWS than was previously thought (Short et al., 2004), suggesting a possible pathway for continued contamination of otters digging in the intertidal zone, but no explanation for why otter numbers would decline so suddenly (along both oiled and unoiled shorelines) 12 years after the spill.

Short et al. (2006, p. 3728), who investigated the distribution of subsurface oil residues on shorelines at NKI, suggested that otters digging for clams in this region would "encounter lingering *Exxon Valdez* oil repeatedly during the course of a year," perhaps at least once every 2 months, and concluded that this frequency of encounter would be sufficient to affect their health and thus hamper population growth. Neff et al. (2011) pointed out, however, that Short's estimate assumed that otters dig for clams everywhere along the shoreline and that oil residues occur evenly across all shoreline substrates – neither of which is correct. Otters dig for clams in perpetually-wet sandy or gravel beaches in the lower intertidal zone, whereas remaining oil residues are sequestered in small pockets in mid- and upper tide zones behind boulders or under cobble, protected from wave and storm action (Neff et al., 2011). Indeed, the protection afforded by this substrate is the very reason that some oil remained in the environment. Clams are generally not found in this type of habitat, and otters do not (and cannot) dig there.

When otters dig for clams, they leave pits in the substrate, which may last for many months and are readily visible along shorelines at low tide. Boehm et al. (2007, 2011) and Neff et al. (2011) found that foraging pits along NKI shorelines in 2006 were distinctly separated by habitat and tidal zone from pockets of subsurface oil residues that existed within the intertidal zone, suggesting that foraging otters would rarely encounter oil. These results spurred a further investigation by Bodkin et al. (2012), who searched soft-sediment beaches in 2008 and found more otter pits in the mid-intertidal zone than Boehm et al. did along all shoreline types in NKI. Bodkin et al. also found traces of oil in or near some otter pits. Using time–depth recorders implanted in otters to estimate their rate of pit-digging in the intertidal zone, Bodkin et al. estimated a higher rate of potential encounter with oil residues than projected by Boehm et al. (2007, 2011), and concluded that these results provided evidence of long-term effects of the spill on sea otters at NKI.

The relevant question is whether the disparities between the findings of Bodkin et al. (2012) and Boehm et al. (2007, 2011) regarding the extent of overlap between foraging otters and subsurface oil residues at NKI is likely to have had real consequences for the health of otters living there. As Harwell and Gentile (in press) pointed out, a potential pathway of exposure is not sufficient evidence of toxicological effects from remnant oil. Harwell et al. (2010a) agreed that a pathway of exposure to subsurface oil was present at NKI, so they developed a model to examine the ecological risks to otters from various degrees of exposure. The model included a range of oil-encounter frequencies that exceeded the higher estimates of Bodkin et al. (2012). Model results indicated that oil-encounter rates for these maximally-exposed individuals would have to be >30 times higher than predicted to reach the minimum dose to cause chronic effects. Sensitivity analyses conducted using the risk-assessment model (Harwell et al., 2010a, 2012) indicated that, for toxicological effects to occur, maximally-exposed otters would need to dig 4–10 pits into residual oil each day over several months; for a discernible population-level effect, the average otter would need to encounter oil at least 60 times per day. Much lower exposure values were realized using Bodkin et al.'s (2012) oil-encounter rate of 2–24 pits per year estimated from telemetered otters. The conclusion from this modeling, which included >1 billion simulated sea otter-hours, was that no plausible toxicological risk from remnant oil existed for even extreme individuals, much less for the population of "average" otters at NKI.

Harwell et al.'s modeling results initially seemed counter to two studies of biomarkers that purportedly showed direct evidence of exposure-related biological effects. NKI otters were reported to have higher levels of CYP1A, an enzyme system involved in metabolism of hydrocarbons, in their blood and tissues than otters from unoiled Montague Island (Ballachey et al., 2002). Bodkin et al. (2002) concluded that this difference between levels of CYP1A at NKI versus Montague directly implicated oil in retarding the recovery of NKI otters. Recently, however, it was learned that these blood and tissue studies did not actually measure CYP1A (Hook et al., 2008), so these data are not relevant for assessing a linkage between otter health and residual *Exxon Valdez* oil. Moreover, CYP1A can be induced by a very low exposure to oil residues, so even if it had been correctly measured and found to be elevated among otters at NKI, that would not necessarily indicate an effect on otter health or demography (Anderson and Lee, 2006). Harlequin ducks in WPWS had normal survival despite elevated CYP1A (Esler and Iverson, 2010).

A later study by Miles et al. (2012) used gene transcript analysis of blood leukocytes to identify possible genomic responses of sea otters to environmental stresses in WPWS. Altered gene transcripts may be a sign of health impairment. Bowen et al. (2012) reported "reference values" for a group of immune-function genes, based on captive otters and seemingly healthy wild otters from the Alaska Peninsula (although otter numbers were declining there; Burn and Doroff, 2005). Miles et al. found that otters captured in WPWS in 2008 had noticeably different transcript patterns than the reference otters. The profiles of the WPWS otters suggested to Miles et al. (2012, p. 201) that these otters may have suffered from "tu-

mor formation, cell death, organic exposure, inflammation, and viral exposure indicating possible recent and chronic exposure to organic contaminants." A major problem with this conclusion, though, is that the sample of WPWS otters used in this study were not only from previously oiled sites – portions of Knight Island (whether NKI or SKI, not specified) and Prince of Wales Passage – but also from unoiled Montague Island, and no significant differences were found between these areas. Montague had been treated as an oil-free site based on post-spill shoreline assessments (Neff et al., 1995), and had been used as a reference area in all previous sea otter studies, including the companion study by Bodkin et al. (2011). However, in view of their results, Miles et al. (2012) considered the presumed oiling effects to have been as strong at Montague as at Knight Island; this contrasts sharply with Bodkin et al.'s (2011, p. 12) view of Montague: "The trend toward increasing [sea otter] abundance at Montague Island is consistent with the increasing trend observed in the larger spill area of WPWS, although at a reduced rate. The trend also is consistent in representing a population that was not affected by the 1989 oil spill, and thus not expected to attain the magnitude of increase observed in the neighboring spill area where mortality estimates were high and recovery was expected." Perhaps the apparently anomalous genetic results for WPWS were related more to the fact that this population had been subjected to an extended bottleneck of fewer than 20 animals <60 years before the spill (Bodkin et al., 1999).

Miles et al. (2012) did not actually detect tumors or other severe health issues that they suggested could be associated with the gene transcript profiles; however, they reported "clinically significant anomalies" in a number of otters in their sample, including dental disease, signs of infections, and nasal mites, which although not specifically linked to gene transcription at the individual level, were more common among WPWS otters than those from the Alaska Peninsula. However, again, there was no indication that Knight Island otters had more ailments than those from Montague Island. Moreover, at least some of these ailments are age-related in otters (e.g., dental disease, Kenyon, 1969); thus, it is not surprising that they were more common in the WPWS sample, where 22% were old-age (9 + years) (31% of the Knight Island sample), than the sample from the Alaska Peninsula, where only 8% were old. Likewise, studies of other species have shown that gene expression can change dramatically in older age; in particular, inflammation/immune response genes become overexpressed as the body becomes more frail (Ershler and Keller, 2000; de Magalhães et al., 2009). This aging process may be speeded up from the stresses of a harsh environment. Additionally, facial wounds from mating and fighting have been shown to be a major contribution to infection (and subsequent mortality) in wild sea otters (Kreuder et al., 2003). In these respects, the captive otters were probably not a fair reference group for free-ranging WPWS otters.

Maybe the most interesting result of Miles et al.'s (2012) study was that the purportedly unusual gene signatures were considered sub-lethal, as none of the captured otters appeared to be fatally ill. Similarly, the radio-instrumented individuals studied by Bodkin et al. (2012), some of which were estimated to have encountered residual patches of submerged oil up to 24 times per year, all survived. If the NKI population is suffering long-term demographic consequences from continued exposure to oil, then reproduction or survival must be affected, yet in these studies, the individuals exhibiting the most extreme levels of exposure were not found to have reduced survival or declining fecundity.

Bodkin et al. (2012) asserted that two elements are required to attribute delayed recovery to the spill: evidence of some demographic anomaly, and evidence of continuing exposure to oil. They claimed that "this exposure pathway provides a *logical* [our emphasis] explanation for why the northern-Knight Island subpopulation ... had such a protracted recovery [if indeed that occurred]" (Bodkin et al., 2012, p. 284). We argue that to attribute causation, one must observe a linkage between the exposure pathway and the effect, or at least a dose adequate to cause an effect; the mere existence of the exposure pathway is not sufficient, given that there is no evidence that otters could have been exposed to enough oil to have produced toxicological effects. Ecological risk assessment, as adopted by the U.S. Federal Government, demands much more than demonstrating the existence of an exposure pathway (U.S. Environmental Protection Agency, 1998). Sea otters were also exposed to various other factors that could have affected their demography at NKI (discussed next).

3.3. Killer whale predation

Following the 1989 oil spill, sea otter numbers began to plummet in the western Aleutian Islands, even though *Exxon Valdez* oil never reached the Aleutians and was never implicated in the otter decline there. Based on several lines of evidence, Estes et al. (1998) concluded that killer whale (*Orcinus orca*) predation was the most parsimonious explanation for this decline. Garshelis and Johnson (1999) commented that equally compelling evidence for killer whale predation on otters existed for Knight Island. Common to both Knight Island and the Aleutians, there was no indication of reduced birthing or pup survival, few dead otters washed ashore (as they would in cases of disease, malnutrition, winter mortality, or contamination), and body condition of otters indicated that food supplies were adequate (Dean et al., 2000, 2002; Laidre et al., 2006).

In the Aleutians, only six killer whale attacks have been observed, and among these only three of the otters died (Hatfield et al., 1998). However, given the low probability of actually witnessing such brief events in this huge area, the three confirmed mortalities were extrapolated to an estimated 40,000 otters consumed by killer whales (Estes et al., 1998). It is now widely believed that killer whale predation reduced the Aleutian Islands' otter population by more than 95% (Estes et al., 2005). Doroff et al. (2003, p. 55) called it "one of the most widespread and precipitous population declines for a mammalian carnivore in recorded history." Despite the rather scant observational evidence of the cause for this decline, when southwestern Alaska sea otters were proposed as a threatened population under the U.S. Endangered Species Act, killer whale predation was considered the most probable cause, with little support for other alternatives (U.S. Federal Register, 2004).

Although intensive studies of both otters and killer whales have been conducted in PWS since the early 1980s, the first attack was not witnessed until 1992 – by coincidence, shortly after the spill. All three observed killer whale attacks since then occurred at Knight Island, two of which were in Herring Bay, NKI (Hatfield et al., 1998). Additionally, in 2003, a killer whale was found dead in LaTouche Passage, south of Knight Island, with five sea otters in its stomach. This whale was identified as part of a pod whose range was centered in the Knight Island area (Vos et al., 2006). Killer whales could not only consume several otters per day at Knight Island, but the risk of predation could drive otters to move to safer areas.

Many scientists have moved beyond the question of whether killer whales began preying heavily on sea otters to why they did. Leading theories suggest that those killer whales that preferentially prey on marine mammals (rather than fish) have been forced to switch from diminishing stocks of harbor seals (*Phoca vitulina*) and Steller sea lions (*Eumetopias jubatus*) to much smaller, less-preferred sea otters. Although harbor seals are a preferred prey of most marine-mammal eating killer whales, in PWS whales prey equally on Dall's porpoise (*Phocoenoides dalli*). Data on harbor seal abundance in PWS showed a steady decline since the mid-

1980s (Frost et al., 1999; ver Hoef and Frost, 2003). Saulitis et al. (2000, p. 102) commented that "low harbor seal numbers may account for the fact that Prince William Sound transients [mammal-eating killer whales] consistently prey on a species [Dall's porpoise] more difficult to capture than harbor seals." Matkin (2004: 3) added: "harbor seals are a known major prey item of transient killer whales and we are concerned that sea otters could also become an important prey due to the severe decline and lack of recovery of harbor seals in the region [southwestern PWS]."

Bodkin et al. (2002) noted that, with an average of 77 otters at NKI, an extrinsic factor that caused an added annual loss of only three otters would offset the population growth of 4% per year ($0.04 \times 77 = 3$) observed elsewhere in WPWS at the time. One killer whale could easily consume this number of otters in just 1 day (and still not satisfy its daily caloric requirements; Williams et al., 2004). Accordingly, it seems that killer whale predation should be considered a potential factor affecting population trends of sea otters at Knight Island.

3.4. Subsistence harvest

Alaska natives legally harvest sea otters for subsistence or handicrafts, and these harvests may have affected population trends in WPWS. In parts of southeast Alaska, the rate of reported harvest (averaging up to 8% per year) has apparently been sufficient to limit or depress otter numbers (Esslinger and Bodkin, 2009). The same may be true for parts of WPWS. After the *Exxon Valdez* spill, at least 139 otters were harvested throughout the oil spill area of WPWS (U.S. Fish and Wildlife Service, unpublished data, 1990–2009), potentially confounding the assessment of population recovery. Harvests were especially high at Knight Island: in 2000 and 2003, natives took 5–10% of the 200–300 otters living there (data were inadequate to trace losses to the northern or southern halves of the island). That these harvests exceeded the highest population growth rate observed in other portions of WPWS suggests that they could have caused a population decline at Knight Island. By contrast, since 1998 only two otters were harvested from Montague Island, which harbors a larger sea otter population than Knight Island (Fig. 3a reflects only a portion of Montague).

Only two sea otters were reported harvested at Knight Island during 2005–2009. This coincides with the increase in otter numbers at NKI (Fig. 3b). Whereas the effects of subsistence harvests on otter numbers at NKI remain equivocal, they cannot be discounted as a factor that has affected the dynamics of the otter population in this area.

3.5. Disturbance from human activity

Ironically, one of the largest impacts to PWS following the *Exxon Valdez* spill – aside from the oil itself – was the substantial increase in human activity directed at assessing impacts in the most heavily-oiled areas. NKI was not only the target of extensive cleanup operations, but also of numerous post-spill studies of shoreline chemistry, kelp, invertebrates, fish, birds, and otters (river and sea otters) (Holland-Bartels et al., 1996; Hooten and Highsmith, 1996; Dean et al., 2000; Bodkin et al., 2002; Huggett et al., 2003; Short et al., 2006; Esler and Iverson, 2010). Investigators established campsites and ran boats in and out of this area for two decades. In other parts of PWS, otters tended to leave areas with high boat traffic (Garshelis and Garshelis, 1984). Bodkin et al. (2011) suggested that the disturbance from a new fishery contributed to many otters leaving the Montague Island survey areas in 2009 (Fig. 3a). Notably, the various post-spill sea otter studies involved capturing, immobilizing, and surgically implanting radio-transmitters in over 200 individuals at NKI (out of a population averaging less than 80 individuals, but with substantial individual turnover), adding more disturbance (and direct stress) to sea otters in the study site.

4. Outlook for recovery

The initial recovery target for sea otters, developed by the Exxon Valdez Oil Spill Trustee Council (1994: 52) was defined as "when population abundance and distribution are comparable to pre-spill abundance and distribution, and when all ages appear healthy." They also added this caveat: "Exactly what population increases would constitute recovery is very uncertain, as there are no population data from 1986 to 1989, and the population may have been increasing in Eastern Prince William Sound during that time." The recovery goal has since been modified to "a return to conditions that would have existed had the spill not occurred" (Exxon Valdez Oil Spill Trustee Council, 2006: 4). This is even more difficult to assess, as it requires knowledge of pre-spill conditions as well as the ability to predict what would have occurred over the next several decades in terms of otter abundance and distribution with changing conditions but absent the spill. We contend that such predictions are unreasonable in complex biological systems like this, which are subject to numerous confounding variables, most of which are not quantifiable, except in a relative sense (Harwell et al., 2010b).

Confounding variables are the nemesis of any study investigating the effects of an environmental event on wildlife populations (Wiens and Parker, 1995). Limited data were available for sea otters in PWS before the oil spill, and no truly valid control sites existed after the spill. Compared to a selected reference site at Montague Island, the Knight Island area has much less kelp (preferred otter resting habitat), deeper nearshore waters (and therefore less feeding habitat for pups), higher human subsistence harvests, more killer whales (due to the deeper waters), and direct evidence of recent predation on otters by these whales. Moreover, whereas some studies concluded that otters moved between the reference and treatment areas (e.g., source–sink model; Monson et al., 2011), others based their analyses on the assumption that no such interchange existed (e.g., prey and body condition studies, Dean et al., 2002; biomarker studies, Ballachey et al., 2002; Miles et al., 2012).

Survey data from throughout WPWS indicated a widespread decline in numbers in 2002 (Bodkin et al., 2011). The reasons for this decline are unknown, but it appears that numbers returned to previous levels the following year at most sites other than NKI. NKI may have taken longer to recover (Fig. 3b) because the regrowth of the small population there was limited by losses to killer whales or subsistence harvests, or disturbance from the many scientists conducting studies in this area. Alternately (or additionally), population growth might have been restricted by relatively low pup survival due to limited shallow-water feeding habitat, even though food for adult otters is relatively plentiful (Dean et al., 2000, 2002). Population growth at NKI might also have been constrained by diminished pup production (pup ratio, Fig. 4b). This could have arisen as a result of an altered sex ratio: a large group of males was observed in this area in 1996 (Garshelis and Johnson, 2001; Bodkin et al., 2002), some of which may have taken up residence there. Such a slight perturbation in population composition could shift the dynamics of the small population in this area and render comparisons of population growth rates and pre- versus post-spill population sizes meaningless. Shifts in population composition might or might not have occurred as a result of the spill; such events have been documented in WPWS before the spill (Garshelis et al., 1984; Johnson, 1987).

The biggest problem in weighing competing hypotheses to explain varying population trends in WPWS is that, despite many

years of study, sea otter population dynamics are still poorly understood, even in the absence of major environmental perturbations. This is partly due to an incomplete understanding of otter behavior and partly due to the complexity of the ecosystem in which they live (Estes, 1990; Bodkin et al., 2000; Harwell et al., 2010b). Additionally, significant environmental changes have occurred in the Gulf of Alaska and PWS since sea otter research was initiated there in earnest in the early 1970s (Johnson, 1987). In 1964 the area was struck by the largest recorded earthquake in North America (Fig. 1), severely affecting (and possibly still affecting) habitat and food availability for sea otters (Garshelis and Johnson, 2001). Beginning in the mid-1970s, abrupt, large-scale changes in atmospheric conditions and ocean currents caused increased water temperatures in the northern Gulf of Alaska (including PWS), which altered the physical and biological processes of this region on a massive scale (Mundy, 2005; Spies, 2007). This "regime shift" has been linked to marked changes in abundance of a number of marine species since that time (Anderson and Piatt, 1999; Benson and Trites, 2002; Trites et al., 2007), including species affected by the oil spill in PWS (Agler et al., 1999). Changes in oceanic conditions are still taking place, including a minor regime shift in 1989 (the year of the spill), which nonetheless had noticeable effects on various biota in the region (Hare and Mantua, 2000). In the face of all this ecosystem "noise," it is probably impossible to discern an unambiguous signal from an oil spill that occurred more than two decades in the past, in an area with less than 100 sea otters.

5. Concluding remarks

The sea otter's susceptibility to oil contamination was well known before the spill (Costa and Kooyman, 1982; Davis et al., 1988) and accordingly, dire forecasts had been made in the event of an oil spill within the range of this species (VanBlaricom and Jameson, 1982). Shortly after completion of the Trans-Alaska oil pipeline, with the threat of a future spill near the terminus in PWS, studies were conducted on potential oiling effects on sea otters; this work concluded that otters could survive only light contamination of their pelage (Siniff et al., 1982). At the time, consideration was not given to potential longer-term effects of remnant oil buried in the substrate, altered otter demography, or even what to study in the years after a spill.

An event of the nature and magnitude of EVOS will inevitably lead to disagreements about the eventual short and long-term effects. In this case, scientists with differing perspectives posed questions differently, designed studies differently, and interpreted data differently, resulting in different conclusions. In part, these differences arose from different approaches to examining the situation. One approach was to closely investigate otter abundance in relatively small but heavily-oiled sites like NKI and Herring Bay, looking for discrepancies from either a reference site or a time in the past. An alternate approach was to examine variation across a broader spatial and temporal scale, attempting to discern whether outliers corresponded with places that had significant oiling. The first approach creates more Type I errors (detecting oiling effects that are not real), whereas the latter is more prone to Type II errors (not finding oiling effects that are present). Post-spill studies of sea otters were made more difficult by the fact that potential reference sites were not only ecologically different from oiled sites, but otter numbers at reference sites were changing (unexpectedly).

Ecological catastrophes are messy not only in a literal sense, but also in terms of the complexity of confounding factors and difficulties in study designs (Wiens and Parker, 1995). With large background variation, control-impact studies require too many replicates to be feasible, because each site must be sufficiently large to contain a demographically meaningful population. Likewise, if the pre-event dynamics are not well understood, before–after study designs will not yield reliable results. Thus, unless the signal from the impact is particularly strong, long-term effects are likely to be disputed by scientists looking at different data, or the same data through different lenses. Consequently, the scientific literature is likely to remain conflicted.

We prefer not to make any bold statements about the state of recovery of sea otters from the *Exxon Valdez* spill, except to say that other such claims appear misguided. Various arguments could be made as to what pre-spill abundance data to use, and what control site trend data to use post-spill. As such, these data were probably poor measures of recovery.

Recent dramatic increases in numbers of otters at NKI (Fig. 3b) (Bodkin et al., 2011) are probably more enigmatic than the previous static trend observed there. It is hard to conceive how this increase in otters could have been related to the sudden release of effects of a spill that occurred more than 20 years before. Ironically, after two decades of intensively studying this small population, the explanation for this dramatic and abrupt surge in numbers remains elusive. This highlights the volatile nature of the demographics of these animals and underscores the fallacy of trying to assess recovery in terms of returning the population to conditions that would have existed had the spill not occurred. Those original conditions are unknown and the eventual distribution and abundance of otters stemming from those conditions too unpredictable.

In western PWS, a catastrophic oil spill caused hundreds (to possibly over 2,000) sea otters to die – a large loss that was unmistakable, although not easily quantifiable. Conversely, claims of non-recovery center around only three otters, the apparent missing incremental annual increase at NKI (that would have produced the same population trajectory exhibited by WPWS as a whole; Bodkin et al., 2002); these three 'missing otters' were within a total, robust population of about 12,000 in PWS (U.S. Fish and Wildlife Service, 2008). This small deviation, insignificant in terms of the overall demographics of sea otters in PWS, still spawns myriad new studies and papers, and continuing controversies. If NKI had not been oiled in one of the most infamous spills in recent history, we suspect that no one today would have considered anything there amiss.

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