

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

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

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

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## INTRODUCTION

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

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

ble to perturbations of their wintering environment.

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

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

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

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

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

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

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

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

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

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

Response variable R <sup>2</sup>	Explanatory variable	Parameter estimate
Ducks per 400 m 0.45	Intercept Reef 200–500 m <sup>a</sup> Stream 0–200 m <sup>term nega-</sup>	1.17 ± 0.12 0.51 ± 0.15

### Adult female survival during winter

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

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

The data strongly supported the inference that survival was lower in oiled areas than unoiled areas (Esler et al. 2000b). The top 3 models, i.e. those with the best fit to the data, all included a difference in survival between areas. Further, models without an area term had very little support, emphasizing the importance of including a term for an area effect. Winter survival rates from the best-fitting model were 78.0% (SE = 3.3%) on oiled areas and 83.7% (SE = 2.9%) on unoiled areas, due primarily to a divergence between areas during mid-winter (Fig. 2). We also determined

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

We compared body mass between oiled and unoiled areas during wing molt (late summer and early fall) 1995 to 1997 and winter 1997–1998 as part of our research program, using general linear models to determine factors explaining variation in harlequin duck body mass and to evaluate any area differences after accounting for other explanatory variables. We used separate models for wing molt and winter and, within each season, separate models for each sex. To select the model from which we drew inference, we used Mallow's  $C_p$

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

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

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

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

### **Intrinsic limitations on population growth rates**

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

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

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

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

We also examined data collected during our own studies to assess molt site fidelity based on recapture locations. We conducted captures of flightless (due to wing molt) birds along discrete, non-overlapping stretches of shoreline that were 1 to 3 km in length during falls of 1995 through 1997. These captures



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

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

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

### Continued exposure to oil

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

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

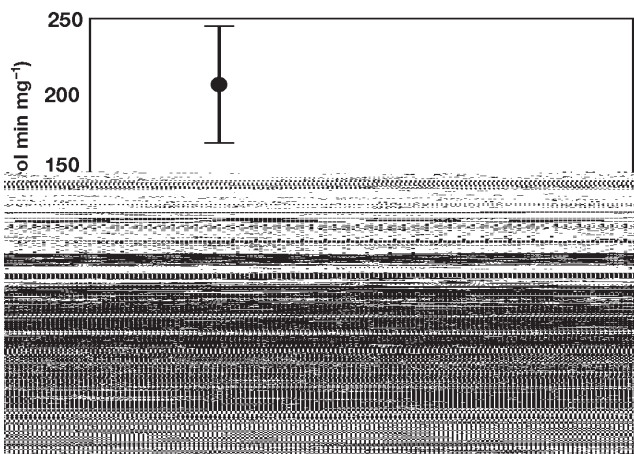


Fig. 4. *Histrionicus histrionicus*. Comparisons of average ( $\pm$ 95% confidence intervals) liver 7-ethoxyresorufin-O-deethylase (EROD) activity, as a measure of CYP1A induction, of harlequin ducks captured from oiled and unoiled areas of Prince William Sound, Alaska in March and April 1998 (Trust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



### **Food limitation**

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

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

Effects of the EVOS on populations of several important harlequin duck prey were evaluated by sampling at multiple pairs of oiled and unoled sites in intertidal

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

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

## **DISCUSSION**

### **Injury and recovery status**

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

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

powerful measures of injury and recovery than occurrence or abundance.

The habitat use studies of Day et al. (1997) indicated no EVOS effects on harlequin ducks during winter 1989 to 1991, in contrast to our findings of lower densities on oiled than unoiled areas (Esler et al. 2000a). This inconsistency may be a consequence of accumulating deleterious effects of the spill that extended

isons of summer abundance by Murphy et al. (1997) have limited relevance for understanding dynamics of wintering populations, which we consider to be the

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

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

Oil exposure could occur through consumption of contaminated prey. In the marine environment, oil constituents can accumulate in bottom sediments and benthic, filter-feeding invertebrates (Fukuyama et al. 2000, Peterson 2001). Studies have documented hydrocarbons in harlequin duck prey from immediately post-spill through 1995 (Boehm et al. 1995, Babcock et al. 1996, Short & Babcock 1996, Wolfe et al. 1996, Patten et al. 1996).

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

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