Harlequin Duck population injury and recovery dynamics following the 1989 *Exxon Valdez* oil spill

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Abstract. The 1989 *Exxon Valdez* oil spill caused significant injury to wildlife populations in Prince William Sound, Alaska, USA. Harlequin Ducks (*Histrionicus histrionicus*) were particularly vulnerable to the spill and have been studied extensively since, leading to one of the most thorough considerations of the consequences of a major oil spill ever undertaken. We compiled demographic and survey data collected since the spill to evaluate the timing and extent of mortality using a population model. During the immediate aftermath of the spill, we estimated a 25% decrease in Harlequin Duck numbers in oiled areas. Survival rates remained depressed in oiled areas 6–9 years after the spill and did not equal those from unoiled areas until at least 11–14 years later. Despite a high degree of site fidelity to wintering sites, immigration was important for recovery dynamics, as the relatively large number of birds from habitats outside the spill zone provided a pool of individuals to facilitate numerical increases. On the basis of these model inputs and assumptions about fecundity rates for the species, we projected a timeline to recovery of 24 years under the most-likely combination of variables, with a range of 16 to 32 years for the best-case and worst-case scenarios, respectively. Our results corroborate assertions from other studies that the effects of spilled oil on wildlife can be expressed over much longer time frames than previously assumed and that the cumulative mortality associated with chronic exposure to residual oil may actually exceed acute mortality, which has been the primary concern following most oil spills.

Key words: chronic oil exposure; demography; Exxon Valdez; *Harlequin Duck;* Histrionicus histrionicus; *marine birds; oil spill; population dynamics; Prince William Sound, Alaska (USA); wildlife conservation.*

INTRODUCTION

Oil spills can have dramatic effects on wildlife and marine ecosystems. The *Exxon Valdez* oil spill (EVOS), which occurred on 24 March 1989 and resulted in the release of ~42 million liters of crude oil into Prince William Sound, Alaska, USA (Galt et al. 1991, Wolfe et al. 1994; Fig. 1), is among the best known, most damaging, and well-studied oil spills in history (Laughlin 1994, Wells et al. 1995, Paine et al. 1996, Rice et al. 1996, Peterson et al. 2003). In the immediate aftermath of the EVOS most attention by scientists and the public focused on assessing the extent of shoreline contamination and quantifying the magnitude of acute injury to wildlife resources. Indeed, hundreds of thousands of marine bird and mammal deaths were attributed to direct contact with floating oil on the sea surface during the immediate aftermath of the spill (Piatt et al. 1990, Garrott et al. 1993). However, long-term effects also were evident. Residual oil remained trapped in intertidal and subtidal sediment in some areas (Wolfe et al. 1994, Short and Babcock 1996, Hayes and Michel

1999, Short et al. 2004, 2006), and negative physiological and demographic effects were associated with chronic exposure to residual oil by wildlife (Bodkin et al. 2002, Esler et al. 2002, Golet et al. 2002, Bowyer et al. 2003).

Harlequin Ducks (*Histrionicus histrionicus*; see Plate 1) were among the species that experienced significant injury as a result of the EVOS (Esler et al. 2002). Several aspects of Harlequin Duck ecology rendered their population particularly vulnerable to the spill, including the species' close association with marine intertidal habitats (Robertson and Goudie 1999) and a diet that consists primarily of benthic invertebrates in which oil constituents bioaccumulate (Fukuyama et al. 2000, Peterson 2001). Moreover, Prince William Sound is at the northern extent of the species range, where the additive effects of harsh winter weather, coupled with the high metabolic costs of dive-foraging, are thought to reduce their resilience to perturbation (Goudie and Ankney 1986). In addition, Harlequin Duck life histories are characterized by high site fidelity, low annual productivity, and high adult survival (Goudie et al. 1994). These are characteristics that typically evolve in stable environments and can lead to delayed recovery dynamics even after constraints on population growth are removed.

Using data from carcass recoveries (Piatt et al. 1990, Piatt and Ford 1996) and population surveys (Lance et

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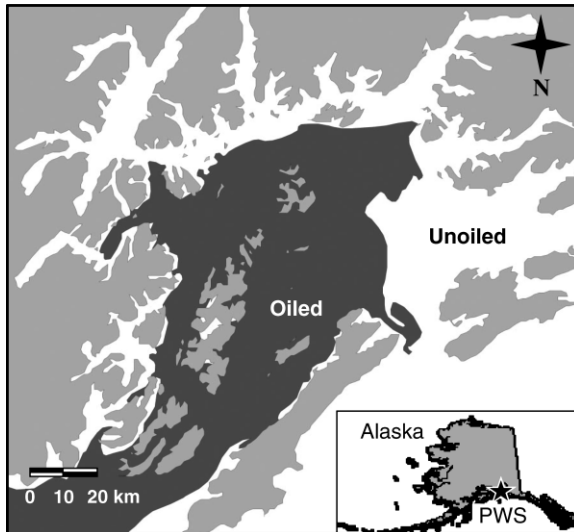[2] Corresponding author. E-mail: desler@sfu.ca

FIG. 1. Map of Prince William Sound (PWS), Alaska, USA, showing areas affected by the 1989 *Exxon Valdez* oil spill.

al. 1999), Esler et al. (2002) estimated that ~7% of the Harlequin Ducks present in Prince William Sound at the time of the spill died as a result of acute exposure to spilled oil. Hydrocarbon metabolites were found in a further 74% of live Harlequin Ducks collected from oiled areas during 1989 and 1990, implying potential for further lethal or sublethal damages (Patten et al. 2000). Monitoring studies initiated during the mid-1990s to measure physiological evidence for exposure to residual oil found elevated cytochrome P450 (CYP1A) induction in Harlequin Ducks from oiled areas compared to unoiled reference sites (Trust et al. 2000), and these findings were corroborated by studies on other near-shore marine vertebrates, including Barrow's Golden-eyes (*Buchephala islandica*; Trust et al. 2000), Pigeon Guillemots (*Cepphus columba*; Golet et al. 2002), river otters (*Lontra canadensis*; Bowyer et al. 2003), masked greenlings (*Hexagrammos octogrammus*; Jewett et al. 2002), and crescent gunnels (*Pholis laeta*; Jewett et al. 2002). Concurrent with this physiological evidence, population surveys indicated numerical declines for Harlequin Ducks in oiled areas (Rosenberg and Petrula 1998), densities that were lower than expected after considering variation in habitat attributes (Esler et al. 2000b), and lower winter survival rates (Esler et al. 2000a). More recent studies suggest that differences in survival between oiled and unoiled areas largely disappeared by the early 2000s (Esler and Iverson 2010); however, residual oil persists in some locations (Short et al. 2006) and CYP1A induction by Harlequin Ducks in oiled areas remains elevated (Esler et al. 2010).

Despite the fact that a range of population parameters have been estimated for Harlequin Ducks in the wake of the EVOS, these data have never been used to quantify the extent of mortality related to the spill. In this paper,

we compiled demographic and survey data collected during the last 20 years to construct a set of projection matrix population models and explore post-spill recovery dynamics. Similar models have been used in wildlife management decision making (e.g., Hitchcock and Gratto-Trevor 1997, Beissinger and Westphal 1998, Flint et al. 2006) and have the advantage over approaches that rely solely on numerical endpoints in that they allow testable predictions to be made about the factors underlying population growth rates (Gauthier et al. 2007). Our specific objectives were to (1) compare the relative magnitudes of acute vs. chronic oil spill mortality, (2) determine the importance of various demographic constraints on recovery (i.e., reduced survival, low productivity, and low dispersal), (3) assess current recovery status, and (4) project a timeline to recovery for Harlequin Ducks and thereby provide scientific insight into the factors regulating post-spill population dynamics.

METHODS

Modeling approach

We used an age-structured demographic projection matrix model to assess population growth rates (Caswell 2001, Morris and Doak 2002). In our model we evaluated female vital rates because, for waterfowl with male-biased sex ratios, females are the limiting sex from a population growth perspective (Johnson et al. 1992). We employed a birth pulse projection to reflect the synchronous breeding pattern of northern-hemisphere migratory birds and used a post-breeding census formulation for the state transition when individuals advance an age class. We divided the life cycle into juvenile and adult classes, with separate estimates of annual survival for each. We defined the juvenile period as that extending from when young birds first arrive on coastal areas in year t (at the age of ~50 days or ~0.1 years) until the start of the next nonbreeding season in year $t + 1$ (~1.1 years of age). We assumed that only adults breed; thus, the reproduction term in our projection matrix, fecundity (F), represents the number of juvenile females that each adult female in the current census will contribute to the next census. To make such a contribution, the breeding female itself must survive and reproduce; making F the product of adult survival (s_{2+}) and fertility (f; Fig. 2).

The EVOS was a one-time perturbation without replication and for which little pre-spill data are available for comparison (Paine et al. 1996). As such, we relied on several simplifying assumptions, the most important of which was that in the absence of oil spill effects demographic rates should be similar across habitats. This assumption has been subject to interpretation (Wiens and Parker 1995, Wiens et al. 2001); however, it is well supported by the available data within the range of habitats and spatial scales under consideration (Esler et al. 2002). We defined recovery as a return to the long-term average from survey counts and used a
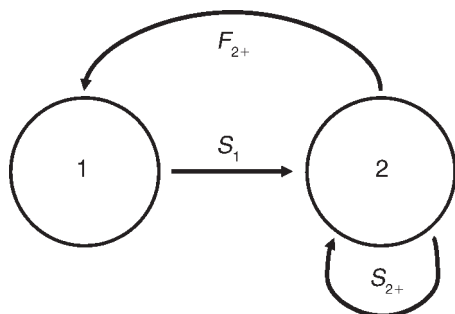
Fig. 2. Life cycle diagram for female Harlequin Ducks (*Histrionicus histrionicus*). Two reproductive stages are denoted, which correspond to juvenile (1) and adult (2+) age classes. In the model, a post-breeding census formulation was used, making fecundity (F_{2+}) the product of adult survival (s_{2+}) and fertility (f).

deterministic formulation because we were not able to assess the effect of environmental variation on recovery rates. Finally, in instances where empirical estimates were not available for certain demographic parameters, we evaluated alternative scenarios using plausible values garnered from the literature to place confidence bounds on estimates.

Data sources

Several studies were relevant for our quantitative assessment of post-spill population dynamics. Our uses of these data are briefly summarized here.

Abundance.—U.S. Fish and Wildlife Service (Agler et al. 1994, Klosiewski and Laing 1994, Agler and Kendall 1997, Lance et al. 1999, Sullivan et al. 2004, McKnight et al. 2006), Alaska Department of Fish and Game (Rosenberg and Petrula 1998, Rosenberg et al. 2005), and Exxon Corporation (Wiens et al. 1996, Day et al. 1997, Murphy et al. 1997) all sponsored and/or collected data to describe trends in marine bird abundance after the EVOS. There has been some disagreement over interpretation of survey results (see Irons et al. 2000, Irons et al. 2001, Wiens et al. 2001), most of which stems from methodological differences and difficulties inherent in separating oil spill effects from natural environmental variation. For our purposes, Alaska Department of Fish and Game estimates of population sex ratios (Rosenberg et al. 2005) and U.S. Fish and Wildlife Service estimates of total abundance (McKnight et al. 2006) were the most useful for parameterizing our model (Table 1).

Survival.—Survival estimates came from several sources. We derived an estimate for acute mortality by converting the estimate for total number of Harlequin Duck mortalities in Prince William Sound (Esler et al. 2002) by the number of individuals at risk within oiled areas. Survival rates during the recovery period were estimated using radio telemetry data collected during two intervals. The first was during the winters of 1995–1996 through 1997–1998 (hereafter 1995 to 1998; Esler

et al. 2000b) and the second during the winters of 2000–2001 through 2002–2003 (hereafter 2000 to 2003; Esler and Iverson 2010). In these studies, female Harlequin Ducks were tracked in previously oiled areas around Green Island, Knight Island, and the Kenai Peninsula, and in unoiled areas around Montague Island. We combined these estimates with survival rates measured during other annual cycle stages, including the breeding season at several locations in the Pacific Flyway (Bond et al. 2009) and during the post-breeding period in Prince William Sound (Iverson and Esler 2007), to infer annual survival (Table 2).

Reproduction.—Breeding parameters were investigated for a small number of Harlequin Ducks using inland habitats adjacent to Prince William Sound during the summers of 1990 and 1991 (Crowley and Patten 1996). However, these data were limited. Therefore, we also consulted published estimates for studies conducted in Alberta during the mid-1990s (Smith et al. 2000) and Iceland (Gardarsson and Einarsson 2008), as well as estimates for other sea duck species evaluated in long-term studies (Swennen 1991, Krementz et al. 1997) to parameterize our model.

Dispersal.—Harlequin Duck movements in Prince William Sound were evaluated using mark–recapture (Iverson et al. 2004) and radio telemetry (Iverson and Esler 2006). We used these estimates to derive transition probabilities between oiled and unoiled areas, as well as the probability of emigration from Prince William Sound as a whole during the 1995–1997 and 2000–2003 monitoring periods (Table 3).

Model development

We conducted our analyses using the R package popbio (Stubben and Milligan 2007), which is a statistical modeling platform that consists primarily of translated MATLAB code (The MathWorks 2007) for models developed by Caswell (2001) and Morris and Doak (2002). We began with models for which our primary purpose was diagnostic and included the effects

TABLE 1. Harlequin Duck (*Histrionicus histrionicus*) abundance in Prince William Sound, Alaska, USA.

Year	Number (mean ± SE)	
	Oiled areas	Unoiled estimate
1990	2738.6 ± 972.5	7881.0 ± 2320.2
1991	2831.8 ± 987.0	8326.7 ± 2676.1
1993	3315.2 ± 1254.4	15 303.9 ± 7232.2
1994	4418.9 ± 1456.5	14 785.3 ± 4302.9
1996	4954.5 ± 1799.0	12 196.6 ± 3589.4
1998	4016.2 ± 1274.0	10 604.9 ± 3267.1
2000	4934.9 ± 1755.6	9940.9 ± 2807.2

Notes: Abundance was estimated from U.S. Fish and Wildlife Service surveys conducted during 1990–2000, with long-term averages for the proportion female estimated as 1593.7 females in oiled areas and 4629.4 females in unoiled areas.

TABLE 2. Annual cycle stage-specific cumulative survival rate (CSR) estimates for female Harlequin Ducks in Prince William Sound (PWS), Alaska.

Stage and year	Location	Age class	CSR (estimate $\pm$ SE)	Source
Acute exposure phase (24 Mar–14 Aug)				
1989	PWS (oiled)	all	0.748†	1, 2
Post-breeding (15 Aug–6 Oct)				
1995 to 1998	PWS: Green Island, Knight Island, Kenai Peninsula (oiled); Montague Island (unoiled)	adult	0.999 ± 0.002	3
Winter (7 Oct–14 Apr)				
1995 to 1998	PWS: Green Island, Knight Island, Kenai Peninsula (oiled)	adult	0.780 ± 0.033	4
1995 to 1998	PWS: Montague Island (unoiled)	adult	0.837 ± 0.029	4
2000 to 2003	PWS: Green Island, Knight Island, Kenai Peninsula (oiled)	adult	0.834 ± 0.065	5
2000 to 2003	PWS: Montague Island (unoiled)	adult	0.837 ± 0.064	5
2000 to 2003	PWS: Green Island, Knight Island, Kenai Peninsula (oiled)	juvenile	0.766 ± 0.138	5
2000 to 2003	PWS: Montague Island (unoiled)	juvenile	0.758 ± 0.152	5
Breeding (15 Apr–14 Aug)				
1994 to 2004	Cascade Mountains, Oregon, USA; Coast Mountains, British Columbia, Canada	adult	0.885 ± 0.077	6

Note: Sources are: 1, Esler et al. (2002); 2, McKnight et al. (2006); 3, Iverson and Esler (2007); 4, Esler et al. (2000*b*); 5, Esler and Iverson (2010); and 6, Bond et al. (2009).

† Estimated as $1 - d/r$, where d is the estimated number of Harlequin Duck deaths (980) and r is the estimated number of individuals at risk within oiled areas, taken from U.S. Fish and Wildlife Service survey estimates (3887.2).

of reduced survival, variable productivity, and dispersal in a stepwise manner. We then proceeded to evaluate a series of fully parameterized models representing the worst-case, best-case, and most-likely combinations of input data (Table 4).

Null model.—For our most basic modeling formulation we used demographic estimates from unoiled areas to characterize the population. In our null model,

$$\mathbf{n}(t + 1) = \mathbf{A}(t)\mathbf{n}(t) \qquad (1a)$$

population size was included in vector **n** and vital rates in matrix **A**:

$$\mathbf{n}(t) = \begin{bmatrix} n_1 \\ n_{2+} \end{bmatrix}$$

and

$$\mathbf{A}(t) = \begin{bmatrix} 0 & F_{2+} \\ s_1 & s_{2+} \end{bmatrix}. \qquad (1b)$$

We used our null model as a basis for comparison and to determine the stable age distribution of the population (**w**), as well as the sensitivity ($\mathbf{S}_{ij}$) and elasticity ($\mathbf{E}_{ij}$) of the growth rate (λ) to variation in the underlying matrix elements. To parameterize matrix **A**, we used mean survival rates in unoiled areas (SURV$_0$). For juvenile birds, we assumed that survival during the breeding season was proportional to the rate measured during the nonbreeding season (Esler and Iverson 2010). For the fecundity term, we assumed a constant population size ($\lambda = 1$) and calculated the rate that would be necessary to maintain numbers at equilibrium. We defined the corresponding fertility rate as f_{base}, and used it for the null fertility parameterization (FERT$_0$).

We parameterized the population vector using long-term averages from survey counts adjusted for the number of females and projected forward 25 years to assure numerical convergence.

Survival probability in relation to oiling history.—Our next step was to incorporate survival probability in relation to oiling history (SURV$_1$). For modeling simplicity, we began by assuming no immigration and modeled the population growth rate in oiled areas using matrix **B**. We retained the null fertility parameterization (FERT$_0$), making our estimate one of gross mortality (i.e., the total number of deaths in the absence of compensatory reproduction).

To derive estimates for Harlequin Duck survival rates during years in which empirical data were not collected, we fit the available data to an exponential rise to maximum equation using a least squares model fitting approach (SYSTAT Software 2006) for the equation

$$s_t \text{winter}(t) = s_0 \text{winter} + a\left(1 - b^{\text{yr}(t)}\right) \qquad (2)$$

where parameters a and b are constants, and winter

TABLE 3. Probability of dispersal between oiled and unoiled areas of Prince William Sound, Alaska, by female Harlequin Ducks during 1995–1997 and 2000–2003.

Transition	Probability of movement (mean $\pm$ SE)†
Oiled areas to unoiled areas	0.026 ± 0.003
Unoiled areas to oiled areas	0.014 ± 0.002

† On average, >98% of all marked females remained within the 4500-km^2 study area in Prince William Sound.

TABLE 4. Models used to evaluate Harlequin Duck population recovery, including survival in relation to oiling history (SURV), fertility (FERT), and movement probability between oiled and unoiled areas (MOVE).

Model	Notation	Parameterization		
		SURV	FERT	MOVE
Diagnostic models				
Null model	$SURV_0 + FERT_0$	unoiled area	baseline rate	none
Gross mortality	$SURV_1 + FERT_0$	oiled area	base rate	none
Low fertility	$SURV_1 + FERT_1$	oiled area	low	none
Moderate fertility	$SURV_1 + FERT_2$	oiled area	moderate	none
High fertility	$SURV_1 + FERT_3$	oiled area	high	none
Correlated reproduction	$SURV_1 + FERT_{2'}$	oiled area	correlated/moderate	none
Observed movement	$SURV_1 + FERT_2 + MOVE_1$	oiled and unoiled areas	moderate	constant
Avoidance behavior	$SURV_1 + FERT_2 + MOVE_2$	oiled and unoiled areas	moderate	variable
Evaluation models				
Worst-case model	$SURV_1 + FERT_{1'} + MOVE_1$	oiled and unoiled areas	correlated/low	constant
Best-case model	$SURV_1 + FERT_3 + MOVE_2$	oiled and unoiled areas	high	variable
Most likely model	$SURV_1 + FERT_{2'} + MOVE_2$	oiled and unoiled areas	correlated/moderate	variable

survival estimates were input for intervals $t = 1$ (the year that the spill occurred), $t = 8$ (the rate during 1995 to 1998), $t = 13$ (the rate during 2000 to 2003), and $t = 15$ (the baseline rate from unoiled areas; Fig. 3). We then compared projections for the null model [$SURV_0 + FERT_0$] to those made when estimates from oiled areas were used [$SURV_1 + FERT_0$].

Reproduction and population recovery.—To explore the effects of compensatory reproduction on recovery rate we evaluated three scenarios for post-spill productivity: low, moderate, and high fertility. We assumed that, in the absence of perturbation, abundance should be maintained at a maximum level (K), which we set just above the long-term average from U.S. Fish and Wildlife Service survey counts. We assumed that when numbers drop, fertility rates increase; we estimated a value by (1) applying f_{base} in situations where $N_i \geq K$, (2) applying the maximum fertility rate (f_{max}) when $N_i \leq$ minimum from FWS counts, or (3) calculating for

intermediate values using the three-parameter sigmoidal function

$$\exp\left(\left(N_i(t) - N_0\right)/b\right) \qquad (3)$$

where a, b, and N_0 and are constants used to ensure model fit (Fig. 4).

Our low-fertility parameterization ($FERT_1$) assumed that individual productivity could increase by as much as 5% when densities were reduced ($f_{max} = 0.610$ fledgling females per adult female). The moderate-fertility formulation assumed a 10% increase was possible ($FERT_2$; $f_{max} = 0.639$), and the high-fertility formulation assumed a 25% increase ($FERT_3$; $f_{max} = 0.726$). The low and moderate portion of the range were approximated values for Harlequin Ducks in Alaska (0.6–1.1 total fledglings per female; Crowley and Patten 1996), Alberta (1.2 total fledglings per female; Smith et al. 2000) and Iceland (0.8 ± 0.2 total fledglings per female [mean ± SE]; Gardarsson and Einarsson 2008),
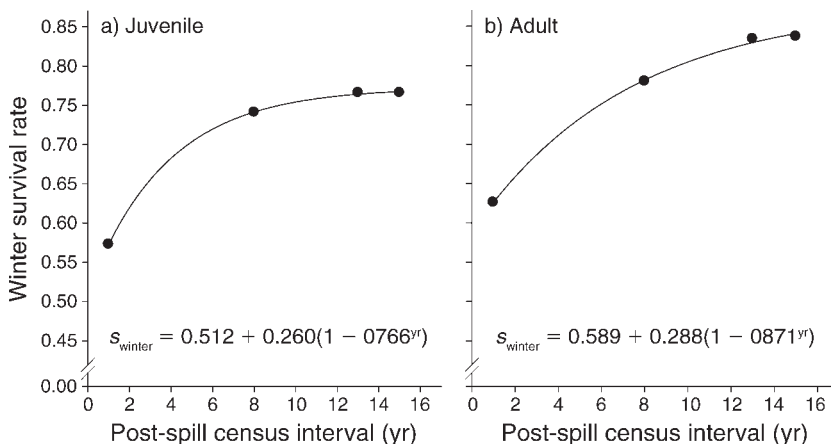

FIG. 3. Estimated winter survival rate of (a) juvenile and (b) adult female Harlequin Ducks inferred from empirical estimates (circles) collected in Prince William Sound, Alaska, in years following the 1989 *Exxon Valdez* oil spill.

while the upper end of the range was covered by estimates for other sea duck species during periods of numerical increase (White-winged Scoter [*Melanitta fusca*]: 0.2–1.6 young per adult in the fall flight, Krementz et al. 1997; Common Eiders [*Somateria mollissima*]: 0.0–1.5 total fledglings per female, Swennen 1991).

We also included in our analysis a formulation to consider the implications of sublethal effects of oil contamination on Harlequin Duck productivity. In this model we allowed the fertility rate to vary as a function of winter survival such that

$$f_i'(t) = f_i(t)\sqrt{\frac{s_{2+}(t)}{\hat{s}_{2+}}} \qquad (4)$$

where f_i' is the correlated fertility rate and $\hat{s}_{2+}$ is the survival rate of adult females in unoiled areas.

Growth projections were then made for three models in which fertility was not correlated with survival and oil exposure: [$SURV_1 + FERT_1$], [$SURV_1 + FERT_2$] and [$SURV_1 + FERT_3$], and a fourth model in which correlated fertility was assumed [$SURV_1 + FERT_{2'}$].

Movement between oiled and unoiled areas.—As a final step in model development, we incorporated dispersal between oiled and unoiled areas. Our interest was to determine the degree to which movement influenced recovery dynamics, including the possibility of demographic rescue by immigrating females. The incorporation of movement required several simplifying assumptions that previous studies indicated were well supported (Iverson and Esler 2006). First, we treated the aggregation of birds wintering in Prince William Sound as a closed population and treated oiled and unoiled areas as discrete population segments. Second, we assumed that when dispersal events did occur, they happened immediately after the post-breeding period. Finally, we assumed that movement probabilities were equivalent for juvenile and adult age classes.

For models that considered movement between areas, we combined matrices **A** and **B** into a single grand matrix **G** (Morris and Doak 2002):

$$\mathbf{n}(t + 1) = \mathbf{G}(t)\mathbf{n}(t) \qquad (5a)$$

where

$$\mathbf{n}(t) = \begin{bmatrix} n_{1A} \\ n_{2+A} \\ n_{1B} \\ n_{2+B} \end{bmatrix}$$

and
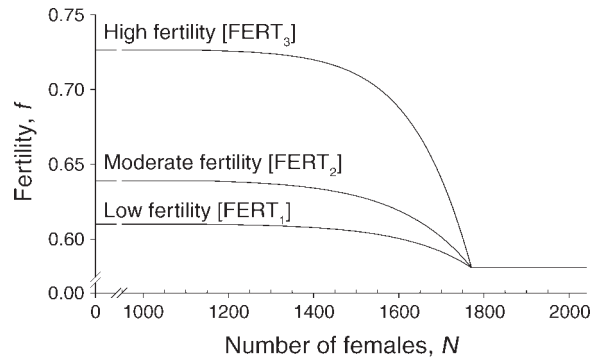
FIG. 4. Fertility estimates (f) used to infer the relationship between population size (N_i) and fecundity (F) in Prince William Sound, Alaska, following the 1989 *Exxon Valdez* oil spill.

In matrix **G** the population is divided into four categories based on movement history: females that remained site-faithful to unoiled areas (upper left: $1 - m_{AB}$), females that immigrated to oiled areas from unoiled areas (upper right: m_{AB}), females that immigrated to unoiled areas from oiled areas (lower left: m_{BA}), and females that remained site-faithful to the oiled areas (lower right: $1 - m_{BA}$).

We parameterized matrix **G** using two alternative formulations. The first assumed that the movement rates we documented during the 1995 to 1998 and 2000 to 2003 study periods were constant over time ($MOVE_1$). Under this formulation the dispersal rate was higher for females moving from oiled to unoiled areas than in the reverse ($m_{AB} = 0.014$; $m_{BA} = 0.026$; Table 3); however, because the total number of ducks was larger in unoiled areas, this parameterization resulted in a net flow of females from unoiled to oiled areas over time. The second formulation ($MOVE_2$) explored the possibility of an adaptive behavioral response by individuals during the immediate aftermath of the EVOS (and before telemetry studies were initiated). For this scenario we assumed that a higher proportion of females moved out of oiled areas during the first winter after the spill when the habitat was most disturbed and cleanup efforts were most intense ($m_{AB} = 0.005$; $m_{BA} = 0.150$).

For the models that considered movement, we applied a cap to immigration when matrix projections indicated that $N_i \geq K$, and we compared two formulations [$SURV_1 + FERT_2 + MOVE_1$] and [$SURV_1 + FERT_2 + MOVE_2$].

Evaluation models.—To assess the full suite of interacting variables that influence population dynamics, we compared the results of three models representing

$$\mathbf{G}(t) = \begin{bmatrix} 0 & F_{2+A} & 0 & F_{2+B} \\ s_{1A}(1 - m_{AB}) & s_{2+A}(1 - m_{AB}) & s_{1B}m_{AB} & s_{2+B}m_{AB} \\ 0 & F_{2+A} & 0 & F_{2+B} \\ s_{1A}m_{BA} & s_{2+A}m_{BA} & s_{1B}(1 - m_{BA}) & s_{2+B}(1 - m_{BA}) \end{bmatrix}. \qquad (5b)$$

the worst-case, best-case, and what we believed to be the most likely case scenarios of model input data. In our worst-case scenario model [$SURV_1$ + $FERT_{1'}$ + $MOVE_1$], we assumed a low potential for population growth through increased fertility, fertility rates that were negatively correlated with oil exposure, and constant movement rates over time. In our best-case scenario model [$SURV_1$ + $FERT_3$ + $MOVE_2$], we assumed a high capacity for increased fertility, no correlation between survival and fertility, and avoidance behavior during the first winter in the spill zone. These models were used to generate confidence bounds around estimates for our most likely recovery scenario: [$SURV_1$ + $FERT_{2'}$ + $MOVE_2$], in which we assumed a moderate capacity for population increase though reproduction, a negative relationship between oil exposure and fertility, and avoidance behavior immediately after the spill. We based these assumptions on our knowledge of the reproductive ecology of Harlequin Ducks, documented reductions in breeding performance by other marine bird species affected by the EVOS in Prince William Sound (Golet et al. 2002), and the considerable disturbance created by cleanup efforts.

Results

Null model

For the null model [$SURV_0$ + $FERT_0$], matrix **A** was parameterized using the estimates

$$\mathbf{A}(t) = \begin{bmatrix} 0 & 0.430 \\ 0.605 & 0.740 \end{bmatrix}$$

where F_{2+} was a calculated term representing the productivity necessary to maintain a stable population. This rate of productivity corresponds to a baseline fertility rate of $f_{base} = 0.581$, which was used to calculate subsequent fertility scenarios. Matrix calculations indicated that at the stable age distribution (**w**) the population was composed of 30% juvenile and 70% adult females. The damping ratio was estimated at 3.8, which suggests that equilibrium is attained fairly rapidly compared to species in which reproduction is more tightly regulated by age class.

As expected, our sensitivity and elasticity analysis indicated that λ was most responsive to changes adult female survival rates. The sensitivity matrix was estimated as

$$[\mathbf{S}_{ij}] = \begin{bmatrix} - & 0.480 \\ 0.341 & 0.794 \end{bmatrix}$$

and the elasticity matrix, which gives the sensitivity measured in terms of proportional changes, as

$$[\mathbf{E}_{ij}] = \begin{bmatrix} - & 0.206 \\ 0.206 & 0.587 \end{bmatrix}.$$

Thus, adult female survival exerted ~2–3 times the effect on λ as the other variables under consideration.
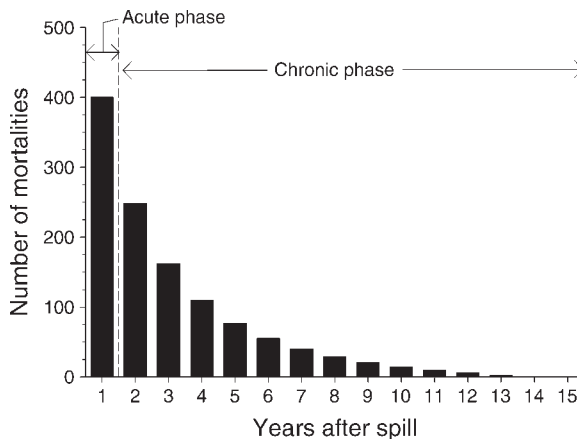

FIG. 5. Projected mortality of female Harlequin Ducks in the absence of compensatory reproduction in Prince William Sound, Alaska, following the 1989 *Exxon Valdez* oil spill. Mortality is divided into that occurring during the acute (1989) and chronic (1990–2004) phases of oil exposure.

Survival probability in relation to oiling history

Under the model [$SURV_1$ + $FERT_0$], we estimated a gross decline in female Harlequin Duck numbers within oiled areas of 25.0% during the acute phase of exposure. This corresponded to ~400 female deaths (Fig. 5). A further loss of 772 females was indicated during the chronic exposure phase. Thus, a total of 1173 female deaths (or 73.4% of the starting population) was estimated as a direct result of the EVOS. After rescaling to include males, our model projected 2860 total mortalities.

Reproduction and population recovery

Even under the most optimistic of scenarios for fecundity, our models projected a prolonged recovery period through in situ reproduction alone (Fig. 6). Our low-fertility model [$SURV_1$ + $FERT_1$] projected a timeline of >100 years, compared to projections of 63 years under the moderate fertility model [$SURV_1$ + $FERT_2$] and 27 years under the high-fertility model [$SURV_1$ + $FERT_3$]. Models assuming lower fertility also predicted deeper reductions in numbers and longer intervals before declining trends could be reversed and for numerical recovery to began. With respect to potential sublethal effects on productivity, the model [$SURV_1$ + $FERT_{2'}$] projected a 70-year timeline to recovery or ~10% longer than the similarly parameterized uncorrelated fertility model [$SURV_1$ + $FERT_2$].

Movement between sites

In our model [$SURV_1$ + $FERT_2$ + $MOVE_1$], we assumed that the rates of movement between oiled and unoiled reference areas were constant and projected a timeline to recovery of 21 years for Prince William Sound as a whole and 24 years within oiled areas (Fig. 7). Projections for the adaptive movement model
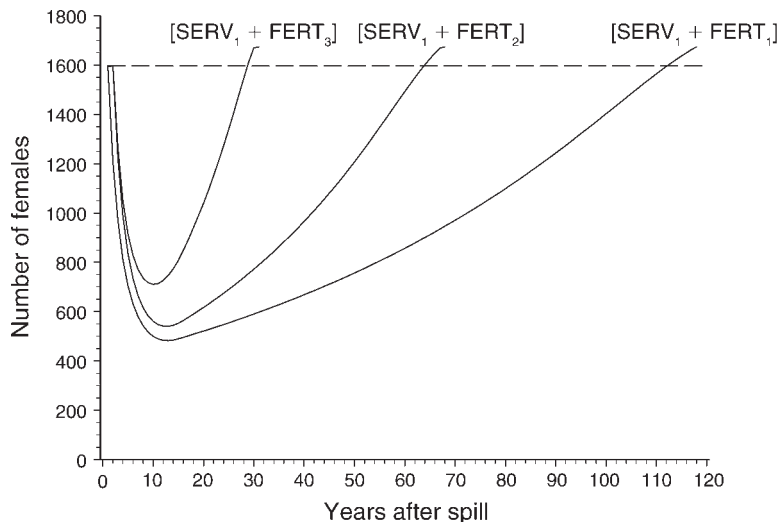
FIG. 6. Projected recovery rate for Harlequin Ducks under low-fertility [$SURV_1$ + $FERT_1$], moderate-fertility [$SURV_1$ + $FERT_2$], and high-fertility [$SURV_1$ + $FERT_3$] scenarios when assuming no immigration. The dashed line indicates the pre-spill parameterization for the population and the level at which recovery is considered complete.

[$SURV_1$ + $FERT_2$ + $MOVE_2$] were nearly identical, estimated at 22 years for Prince William Sound as a whole and 25 years within oiled areas. The primary differences between the projections of the two models was that in the adaptive movement model lower numbers were expected in oiled areas immediately after the spill as a result of emigration. However, the key finding was that under both models the projected recovery timeline was approximately one-third as long as when no movement was assumed.

Evaluation models

After combining variables into a worst-case, best-case, and most likely case scenario, we projected a 5.6% reduction (range: 4.2–6.5%) in female Harlequin Duck numbers during the acute phase of oil exposure for Prince William Sound as a whole and a 24.9% reduction (range: 25.5–32.4%) within oiled areas (Fig. 8). A declining population trend was predicted to persist for 6 years [range: 5–8 years] after the spill across Prince William Sound as a whole, with a mean population growth rate of $\lambda = 0.976$ during this period. At their lowest point, female numbers were predicted to be reduced 14.7% below the pre-spill abundance and by 55.3% below pre-spill abundance in oiled areas. Once the declining trend was reversed, a population growth rate of 1.008 was estimated with numeric recovery predicted in 24 years [range: 16–32 years].

DISCUSSION

A primary objective of our modeling exercise was to evaluate the relative magnitudes of acute and chronic injury to Harlequin Duck populations resulting from the *Exxon Valdez* spill. Contrary to assertions that negative effects on wildlife were short lived (Wiens et al. 1996,
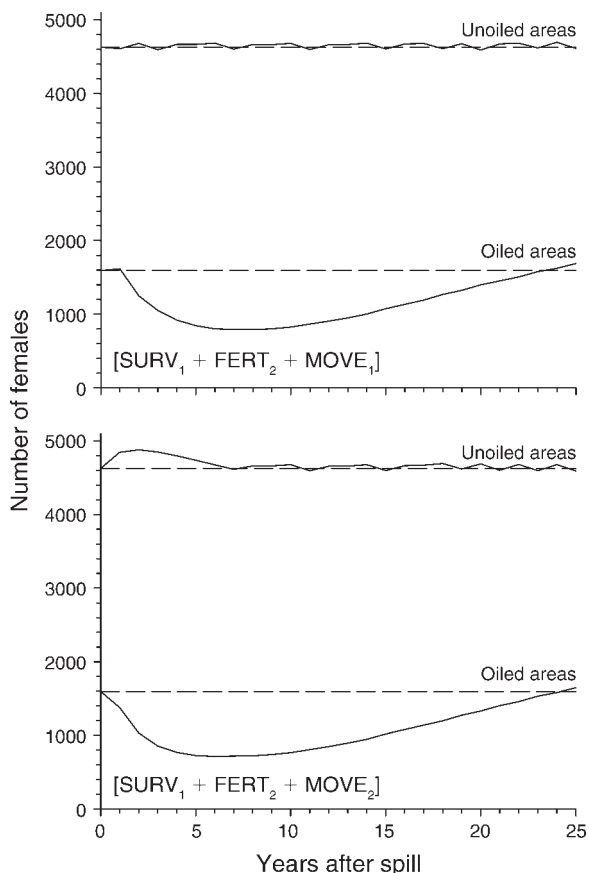

FIG. 7. Projected recovery rate for Harlequin Ducks under observed [$SURV_1$ + $FERT_2$ + $MOVE_1$] and adaptive [$SURV_1$ + $FERT_2$ + $MOVE_2$] movement scenarios in oiled and unoiled areas. The dashed line indicates the pre-spill abundance in the respective habitats and the level at which recovery was considered complete.
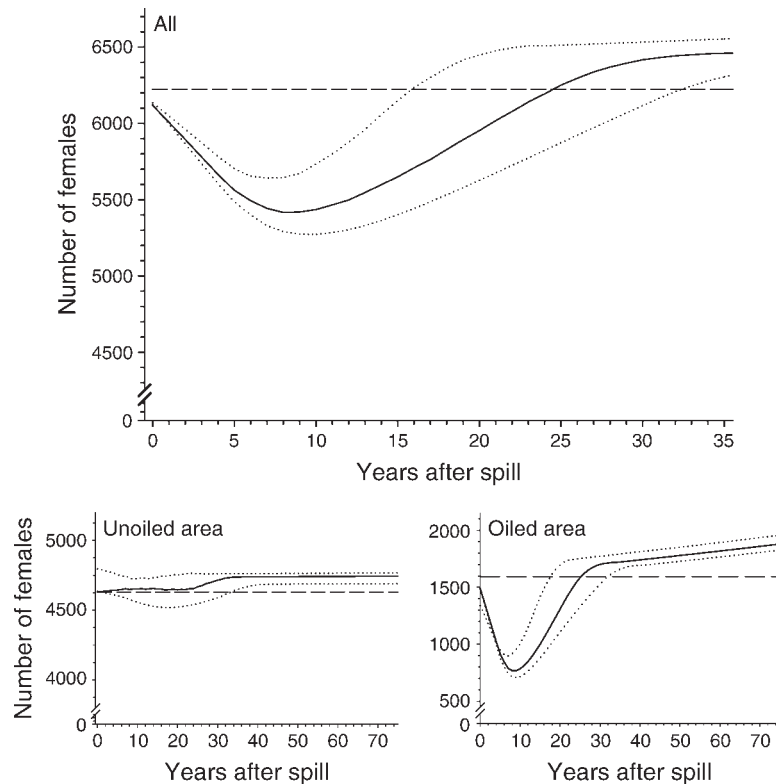
Fig. 8. Projected recovery rate for Harlequin Ducks in Prince William Sound, Alaska, following the 1989 *Exxon Valdez* oil spill. Estimates were derived using the most likely combination of model inputs (solid line) with confidence intervals derived using worst- and best-case scenario models (dotted lines).

Day et al. 1997, Murphy et al. 1997), model projections from demographic data for Harlequin Ducks suggest long-term impact with mortality resulting from chronic exposure to residual oil exceeding acute-phase mortality. This finding rests on empirical estimates of reduced survival nearly a decade after the spill (Esler et al. 2000b, Esler and Iverson 2010) and supports a growing body of evidence that major spills like the EVOS can have significant long-term consequences for marine vertebrate populations (Peterson et al. 2003). Another related objective of our analyses was to compare the effects of various demographic constraints on population recovery. Our sensitivity analyses confirmed that adult-female survival exerts the greatest influence on Harlequin Duck population growth rates and even under the most optimistic assumptions about fecundity, declining population trends were projected to persist in oiled areas for several years after the spill. Moreover, complete recovery was projected to be delayed until after survival rates in oiled areas converged with those in unoiled areas. Prolonged reductions in adult survival within oiled areas were the primary driver of these projections and the most important predictor of recovery rate.

Unfortunately, empirical estimates of fecundity were not available with that same specificity as those for survival and dispersal and probably never will be given the difficulties of working with nesting birds and

applying information from breeding grounds to a wintering population. Although the estimates that we used in our model were in line with those from long-term studies (Swennen 1991, Krementz et al. 1997, Gardarsson and Einarsson 2008), their correspondence to the actual rates realized by Harlequin Ducks in Prince William Sound after the EVOS cannot be known. This is an important issue because assumptions about the capacity for compensatory reproduction strongly influenced confidence bounds around our estimates for recovery. All models indicated a prolonged period would be necessary, but our best- and worst-case scenarios ranged from 16 to 32 years. Also uncertain was the extent to which oil contamination indirectly affected Harlequin Duck productivity after the spill. Delays in egg laying, reductions in the proportion of adults laying eggs, lower hatching success, lower fledging success, and lower return rates of adults to breeding locations have all been documented for marine bird species exposed to petroleum hydrocarbons (Ainley et al. 1981, Fry et al. 1986, Butler et al. 1988, Walton et al. 1997). Although it is not possible to relate oil exposure by Harlequin Ducks to their breeding performance, Rizzolo (2004) determined that Harlequin Ducks dosed externally with oil had increased energy intake, increased oxygen consumption, and decreased body mass in comparison to control birds in a laboratory setting.

PLATE 1.   Harlequin Ducks captured in a mist net in Prince William Sound, Alaska, USA. Photo credit: D. Esler.

This observation, combined with observations by Regehr (2003) that young accompany their mothers to nonbreeding areas, would suggest a potential mechanism for localized effects similar to that identified by Golet et al. (2002) for Pigeon Guillemots.

With respect to dispersal, previous studies have indicated high site fidelity by Harlequin Ducks to nonbreeding areas in Prince William Sound (Iverson et al. 2004, Iverson and Esler 2006) and elsewhere in their Pacific coast range (Cooke et al. 2000, Robertson et al. 2000, Regehr 2003). On this basis we expected recovery of local population segments to occur largely by recruitment (Esler et al. 2002); however, our model projections emphasized the importance of dispersal on recovery even when site fidelity exceeded 95% in both oiled and unoiled areas. This dynamic was a result of the comparatively large number of birds from outside the spill zone available to facilitate numerical increases within oiled areas and was projected to occur despite higher dispersal rates from oiled areas to unoiled areas in telemetry studies conducted during the mid-1990s and early 2000s.

Concordance between our projections and estimates derived from survey counts was strong during the first decade after the EVOS, when the effects were most pronounced; however, some discrepancies were evident. Among the various surveys, U.S. Fish and Wildlife Service counts have been the longest term, most geographically extensive, and most useful for inferring trends (Lance et al. 2001). These surveys were initiated immediately after the spill and are conducted during late winter, which is a period when Harlequin Ducks are present in large numbers on nonbreeding areas. Although the confidence intervals associated U.S. Fish

and Wildlife Service survey estimates for Harlequin Ducks preclude fine-scale comparison, they indicate a substantial and prolonged period of increases in oiled areas from 1990 to 2000 (McKnight et al. 2006). Unlike our projections, in which a low point in numbers was predicted to occur several years after the EVOS, the survey data suggest the population bottomed out immediately after the spill during the winter of 1990. Surveys conducted after 2000 suggest a leveling off or slight decrease in numbers in oiled areas, whereas our population model projected sustained growth. One prediction from our model was that numbers were projected to increase in unoiled areas of Prince William Sound during the years immediately after the spill as a result of emigration from oil contaminated areas and then decrease as dispersal patterns favored the repopulation of previously oiled areas. This prediction appeared borne out by U.S. Fish and Wildlife Service data, in which numbers in unoiled areas peaked during 1993 and 1994 and gradually declined thereafter.

Alaska Department of Fish and Game also conducted surveys in Prince William Sound during 1995 to 2005 (Rosenberg and Petrula 1998, Rosenberg et al. 2005). These surveys focused exclusively on coastal waterfowl and yielded very precise estimates of abundance, as well as sex and age ratios for the Harlequin Duck population. They also had very high degree of spatial and temporal correspondence to the studies in which we estimated demographic rates. Similar to our model projections, the Alaska Department of Fish and Game surveys indicated delayed population declines in oiled areas through 1997. Statistically significant trends were not apparent from 2000 to 2005 in oiled areas, nor were they apparent during the study period as a whole in

unoiled areas. Finally, our projections showed little correspondence to estimates described in Exxon Corporation sponsored studies (Wiens et al. 1996, Day et al. 1997, Murphy et al. 1997). The Exxon sponsored studies used data collected across a range of oil contamination levels and concluded that the negative effects associated with the EVOS were short lived (<2.5 years) for most wildlife species. These conclusions were based on estimates of species richness, habitat use, and summer abundance. Unfortunately, the data are of limited utility for evaluating Harlequin Duck population trends because of their timing (nearly all adult Harlequin Ducks migrate to inland breeding areas during the summer) and their duration (the surveys were conducted from 1989 to 1991 only).

A persistent point of contention concerning interpretation of post-EVOS survey data has been the difficulty in discerning oil spill effects from environmental variation. This is exacerbated by the paucity of pre-spill data with which to judge post-spill dynamics. These topics have received considerable attention in the scientific literature (Irons et al. 2001, Lance et al. 2001, Wiens et al. 2001, 2004) and although our analyses cannot resolve these disagreements, they do provide new insights into the processes regulating population dynamics. A growing body of evidence suggests that exposure to residual *Exxon Valdez* oil has been responsible for physiological challenges affecting the demographic properties of Harlequin Ducks (Trust et al. 2000, Esler et al. 2002) and other marine vertebrate species (Bodkin et al. 2002, Jewett et al. 2002, Bowyer et al. 2003). Although exposure does not necessarily imply negative effects on individuals or populations (Underwood and Peterson 1988), our research is unique in that demographic rates were empirically estimated in relation to oiling history allowing consideration of population-level effects.

As with any model, the strength of our conclusions is highly dependent on the validity of the underlying assumptions and when developing our model, we made several important assumptions that require consideration. First, we assumed that in the absence of oil spill effects, Harlequin Duck demographic rates should be similar across habitats within Prince William Sound. Supporting this assumption for Harlequin Ducks was the finding that winter survival rates in unoiled areas remained constant over time (Esler and Iverson 2010); whereas survival in oiled areas was depressed after the spill (Esler et al. 2000a, 2002), but eventually increased and converged to the level documented in unoiled areas over time (Esler and Iverson 2010). This is not to suggest habitat-related differences do not exist. Esler et al. 2000b evaluated Harlequin 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. After accounting for habitat relationships it was concluded that oiling history

was negatively related to Harlequin Duck densities; however, densities within unoiled habitats tended to be higher overall, particularly in relation to intertidal slope and distance to stream mouths and offshore reefs. Similarly, the extent of oil contamination and rate of dissipation within the spill zone has not been uniform over time. Some areas were more heavily oiled than others, and fine-scale population dynamics are almost certainly more complex than described in our models.

A second assumption of our model was that the aggregation of Harlequin Ducks wintering in Prince William Sound could be modeled as two discrete population segments. Previous studies have demonstrated that fewer than 2% of female Harlequin Ducks marked with radio transmitters disperse from Prince William Sound each year (Iverson and Esler 2006) and that annual return rates exceed 95% (Iverson et al. 2004). Within Prince William Sound, movements between oiled and unoiled areas were studied in detail during the chronic phase of oil exposure, but it is possible that dispersal patterns differed during the years immediately after the spill and from 2004 onward, when no measurements were taken. We evaluated a scenario for adaptive movements away from oiled areas during the first winter when contamination was most severe and cleanup efforts most intense, but this scenario was not empirically derived. Nonetheless, the projected timeline to recovery differed little between models that assumed constant rates of movement and those in which it varied during the immediate post-spill period.

We also assumed that environmental variation did not affect Harlequin Duck demographic rates and that the fecundity of individual females was density dependent. These assumptions were made for practical reasons and we acknowledge that they are a simplification of biological reality. The effect of environmental stochasticity on wildlife population dynamics is an important topic that has received considerable attention in the literature. As was evident from survey data in Prince William Sound (Rosenberg et al. 2005, McKnight et al. 2006), annual variations in Harlequin Duck numbers were significant and at times obscured population trends. Because our projections were based on demographic rates averaged over a multiple years they tended to smooth predictions about change over time. With respect to density-dependent population regulation, fecundity of female Harlequin Ducks likely operates through complex interactions on reproductive output and/or post-fledging juvenile survival rates. Our model accommodates these mechanisms the same way, so which of those that is operating is not necessary to know. Available data suggest that feeding by pre-laying female Harlequin Ducks is limited (Goudie and Jones 2005), implying that they are not nutrient limited in producing clutches. Moreover, the species nests at such low densities there would appear to be little density-related regulation of nesting success or hatching rates. Evidence for density-dependent breeding propensity

and/or post-fledging survival has been suggested for other sea ducks (Mehl 2004) and may operate for Harlequin Ducks.

It has been suggested that structured waterfowl populations are often characterized by nonlinear dynamics following perturbation such that they exhibit significant momentum before population trends can be reversed (Hauser et al. 2006). Our findings confirm assertions that effects of oil spills on wildlife populations are expressed over much longer time frames than previously assumed and that chronic exposure to spilled oil can have far reaching population-level consequences. Our study also defines the duration over which reduced demographic performance may be expected in areas contaminated during a major oil spill. This understanding of duration and mechanism is critical when applying management following large spills; for example, considering the costs and benefits of removal of residual oil, and when applying risk assessment under scenarios of catastrophic contaminant releases. It also demonstrates the sensitivity of benthic-foraging vertebrates to residual oil sequestered in sediments and indicates that species with natural-history and life-history traits similar to those of Harlequin Ducks might be particularly vulnerable. We recommend continued monitoring of Harlequin Duck survival and movement rates in Prince William Sound to accompany ongoing survey and habitat monitoring efforts. We believe that it is only through a multifaceted approach that relies on different sources of data, including the physiological and mechanistic factors influencing individual survival and behavior, that a complete picture of the population recovery process can be attained.

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