

AN ABSTRACT OF THE DISSERTATION OF

Daniel Esler for the degree of Doctor of Philosophy in Wildlife Science presented  
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Prince William Sound, Alaska: Effects of the Exxon Valdez Oil Spill.

*Redacted for Privacy*

Abstract approved: \_\_\_\_\_

Robert L. Jarvis

The 1989 *Exxon Valdez* oil spill was a major perturbation of nearshore habitats of Prince William Sound, a wintering area for harlequin ducks (*Histrionicus histrionicus*). This research was designed to evaluate harlequin duck population recovery from the oil spill from 1995 to 1998, using a demographic approach to assess both the “product” of population changes (e.g., density differences; Chapter 4) and the demographic “processes” affecting population dynamics (e.g., survival; Chapter 3).

Wintering aggregations of harlequin ducks are core population units from a population structure perspective and are largely demographically independent, due to high rates of winter site fidelity, pair formation during winter, and evidence that juveniles follow hens to wintering areas. Therefore, evaluation of population-level effects of the oil spill is appropriately directed at these wintering aggregations. We selected adult female survival as a primary demographic attribute to measure, as population dynamics of animals with life history characteristics like harlequin ducks are particularly sensitive to variation in adult

female survival rates. Also, we speculated that oil spill effects during winter would be manifested as survival reductions.

We found that winter densities of harlequin ducks were lower on oiled study areas than unoiled areas, after accounting for effects of habitat (Chapter 4), indicating that population recovery had not occurred. Also, we determined that adult female survival was lower on oiled areas than unoiled areas (Chapter 3), and speculated that this was related to documented oil exposure of harlequin duck populations in oiled areas coincident with our study. We also confirmed that our survival estimates were not biased by assumptions about effects of radio transmitters or fate of missing radios (Chapter 2). In Chapter 5, we reviewed all data relevant to harlequin duck recovery from the oil spill, including our demographic data, and concluded that population recovery had not occurred by 1998, deleterious effects persisted, and continued oil exposure likely was the primary constraint to full recovery. Although populations of many species may have recovered quickly from the *Exxon Valdez* spill, characteristics of harlequin ducks make their winter populations particularly susceptible, including their habitat associations, diet, life history, and energetics.

Harlequin Duck Demography during Winter in Prince William Sound, Alaska:

Effects of the *Exxon Valdez* Oil Spill

by

Daniel Esler

A DISSERTATION

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## CONTRIBUTION OF AUTHORS

This dissertation resulted from a research program requiring a great deal of cooperation and integration with other investigators, which is reflected in the long list of coauthors who contributed to the core chapters. Each of these coauthors, listed on the chapter heading pages, was involved in study design, data collection, data analysis, interpretation, and manuscript preparation for the chapters upon which their names appear.



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Harlequin Duck Demography during Winter in Prince William Sound, Alaska:  
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CHAPTER 1

GENERAL INTRODUCTION

The *Exxon Valdez* ran aground on 24 March, 1989, spilling nearly 42 million liters of crude oil into Prince William Sound. The immediate effect of the oil spill on individual birds was obvious, as over 30,000 carcasses were recovered (Piatt et al. 1990) and hundreds of thousands of birds were estimated to have died as a result of the spill (Piatt and Ford 1996). The population-level consequences of that mortality and, particularly, longer-term effects of the spill on bird populations have proven to be difficult to determine and controversial. Paine et al. (1996) recommended that measures of demography provide a better measure of population injury and recovery than measures of abundance. We agree, as animal abundance can be highly variable and difficult to interpret without an understanding of the demographic processes underlying population change. Demographic data also lend insight into the mechanisms by which individuals and subsequently populations may be affected by the oil spill.

The research presented in this dissertation was designed to take a demographic approach for evaluating harlequin duck population recovery from the *Exxon Valdez* oil spill. Prince William Sound supports high densities of harlequin ducks during winter (Robertson and Goudie 1999) and, although some breeding occurs in associated watersheds (Crowley 1999), Prince William Sound is primarily nonbreeding habitat. A growing body of literature suggests that winter

harlequin duck aggregations are core units from a population structure perspective. Fidelity to nonbreeding sites is strong, both within and between years (Breault and Savard 1999, Cooke et al. 2000, Robertson et al. 1999, Robertson et al. 2000). Also, pair formation occurs during winter (Gowans et al. 1997, Robertson et al. 1998) and harlequins form interannual pair bonds (Smith et al. 2000). Finally, some evidence suggests that juvenile ducklings accompany their mothers to wintering areas (Smith 2000). These attributes indicate that winter aggregations of harlequin ducks may be demographically independent, suggesting that perturbations specific to particular areas affect a largely distinct population segments. These characteristics make any oil spill effects more detectable and, also, has important implications for recovery processes and time frames. To understand demographic effects of the *Exxon Valdez* oil spill we focused on adult female survival, as population dynamics of animals with life history characteristics like harlequin ducks are particularly sensitive to variation in adult female survival rates. We speculated that oil spill effects during winter would be manifested as survival reductions. Also, the other demographic processes affecting population dynamics during winter (immigration and emigration) are better-documented, as described above, and are less likely to vary in relation to oil spill effects.

Aspects of harlequin duck ecology make their populations particularly susceptible to effects of the *Exxon Valdez* spill. Harlequin ducks life history includes variable and generally low annual productivity, compensated by relatively high adult survival and, thus, long reproductive life spans (Goudie et al. 1994). This type of strategy is particularly sensitive to variation in survival. Also,

harlequin ducks, because of their small body size, are thought to exist near an energetic threshold during winter, with little flexibility for increasing caloric intake or relying on stored reserves (Goudie and Ankney 1986). While this strategy may be tenable under predictable and stable conditions, it does not accommodate perturbations that result in either decreases in energy acquisition or increases in metabolic costs. Finally, strong site fidelity, such as that exhibited by wintering harlequin ducks, does not facilitate movement to undisturbed areas if habitat quality becomes degraded (Cooch et al. 1993).

The core chapters of this dissertation were prepared as journal submissions, each addressing some aspect of harlequin duck winter demography with relevance for understanding population recovery following the *Exxon Valdez* oil spill, based on data collected in oiled and unoled parts of Prince William Sound from 1995-1998. Chapter 2 is methodological, evaluating assumptions that are made during radio telemetry studies of survival but have rarely been tested. Chapter 3 measures adult female survival and compares rates between oiled and unoled areas. Chapter 4 evaluates population status through comparisons of winter densities between areas after accounting for differences in habitat; these results are evaluated in the context of the demographic implications of the survival data presented in Chapter 3. Chapter 5 reviews all available information regarding harlequin duck population injury and recovery following the *Exxon Valdez* spill and evaluates hypotheses about mechanisms constraining full recovery. Chapter 6 offers concluding remarks and broader implications.



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## CHAPTER 2

TESTING ASSUMPTIONS FOR UNBIASED ESTIMATION OF SURVIVAL OF  
RADIOMARKED HARLEQUIN DUCKS

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### Abstract

Unbiased estimates of survival based on individuals outfitted with radiotransmitters require meeting the assumptions that radios do not affect survival, and animals for which the radio signal is lost have the same survival probability as those for which fate is known. In most survival studies, researchers have made these assumptions without testing their validity. We tested these assumptions by comparing interannual recapture rates (and, by inference, survival) between radioed and unradioed adult female harlequin ducks (*Histrionicus histrionicus*) and, for radioed females, between right-censored birds (i.e., those for which the radio signal was lost during the telemetry monitoring period) and birds with known fates. We found that recapture rates of birds equipped with implanted radiotransmitters ( $21.6 \pm 3.0\%$ ;  $\bar{x} \pm \text{SE}$ ) were similar to unradioed birds ( $21.7 \pm 8.6\%$ ), suggesting that radios did not affect survival. Recapture rates also were similar between right-censored ( $20.6 \pm 5.1\%$ ) and known-fate individuals ( $22.1 \pm 3.8\%$ ), suggesting that missing birds were not subject to differential mortality. We also determined that capture and handling resulted in short-term loss of body mass for both radioed and unradioed females and that this effect was more pronounced for radioed birds (the difference between groups was  $15.4 \pm 7.1$  g). However, no difference existed in body mass after recapture 1 year later. Our study suggests that implanted radios are an unbiased method for estimating survival of harlequin ducks and likely other species under similar circumstances.

## Introduction

Radiotelemetry has been used widely in studies of wildlife survival (White and Garrott 1990). Unbiased survival estimation using telemetry requires meeting several critical assumptions (Pollock et al. 1989, Tsai et al. 1999) including (1) radioed animals are representative of the population of interest, (2) survival is independent among individuals, (3) radiomarking does not affect survival during the study period, and (4) censoring of animals for which signals are lost is independent of the fate of those animals (i.e., missing animals are no more or less likely to be dead than animals for which fate is known). The first 2 assumptions often can be met through application of an appropriate experimental design, whereas the latter 2 are under less control by researchers and can not necessarily be assured by a priori planning. In most studies, investigators must make these latter 2 assumptions without being able to test their validity. In this study, we tested assumptions about effects of radios and censored individuals for adult female harlequin ducks implanted with radiotransmitters with external antennas.

A considerable body of literature exists describing effects of radiotransmitters on wildlife species. In birds, deleterious effects of externally mounted transmitters (particularly those attached with backpack harnesses) have been documented in numerous studies, including changes in behavior (Massey et al. 1988, Pietz et al. 1993), reduced reproductive effort (Pietz et al. 1993, Rotella et al. 1993, Paquette et al. 1997, Garrettson and Rohwer 1998), and reductions in survival or return rates (Marks and Marks 1987, Burger et al. 1991, Cotter and Gratto 1995, Ward and Flint 1995, Dzus and Clark 1996). Although not all studies

have shown negative effects of external transmitters (Hines and Zwicker 1985, Foster et al. 1992), the broad occurrence of documented deleterious effects clearly raises concern about generating unbiased survival estimates using externally mounted transmitters. Surgical implantation of transmitters into the abdominal cavity offers a promising alternative (Korschgen et al. 1984, 1996; Olsen et al. 1992; Schulz et al. 1998). In direct comparisons, implanted transmitters cause fewer deleterious effects than externally attached radios (Rotella et al. 1993, Dzus and Clark 1996, Paquette et al. 1997), although no previous studies have contrasted long-term survival of birds with internal radios to unmarked individuals.

Survival estimates from radioed animals are generated based on the assumption that the probability of detecting animals is independent of their mortality status (Bunck et al. 1995, Tsai et al. 1999), an assumption that is critically important for animals for which radio signals are lost and remain undetected through the rest of the monitoring period (i.e., right-censored). Recognizing potential violation of this assumption, some investigators have presented results that include maximum survival estimates, where all right-censored animals are assumed to have lived through the study period, and minimum estimates, where they all are assumed to have died (Conroy et al. 1989). Most investigators produce survival estimates under the assumption that mortality rates of undetected animals are the same as detected animals. We are not aware of any studies that have directly addressed this assumption. Two studies (Miller et al. 1995, Cox et al. 1998) have reported returns of failed radios

from hunter-killed northern pintails (*Anas acuta*), documenting that some right-censored birds were alive and in the study site during telemetry monitoring; however, the proportional frequencies of returns of known fate and right-censored birds were not compared.

Our study offered a unique opportunity to test assumptions of survival estimation of radiomarked animals. Harlequin ducks have high fidelity to molt sites (Robertson 1997), high annual survival (Goudie et al. 1994), and are susceptible to capture during wing molt. These traits, in conjunction with deployment of relatively large numbers of radios, allowed for sufficient sample sizes to compare recapture rates and, by extension, survival differences among groups of birds. To test the assumption of a lack of an effect of radios on survival, we compared recapture rates of radioed and unradioed birds. We also compared recapture rates of radioed birds of known fate with those that were right-censored due to a lost radio signal to test the assumption of similar survival probabilities between these groups. Recapture probability of an individual is the product of between-year fidelity to the study site, capture probability if the bird is on the study site, and survival between capture events. Because site fidelity and capture probability of previously captured birds should not be related to radio status, we assumed that differences in recapture rates among groups of birds would reflect survival differences. We recognize that previously captured birds may exhibit trap shyness; however, because all birds included in this study, irrespective of radio status, were subjected to similar capture methods, handling, and holding time upon their original capture, we assume that the degree of trap shyness would not

vary based on radio status. Also, we examined body mass changes of both radioed and unradioed individuals recaptured within- and between-years to assess potential short- and long-term effects of radiotransmitters on body mass. Body mass has been positively related to survival probability for some waterfowl species (Conroy et al. 1989, Longcore et al. 1991, Bergan and Smith 1993) and, thus, is important to assess as a potential mechanism affecting survival of birds with radiotransmitters.

### Methods

Harlequin ducks were captured in Prince William Sound, Alaska as part of efforts to examine winter survival probabilities in relation to history of contamination by the *Exxon Valdez* oil spill. Captures occurred annually from 1995--97 between 20 August and 17 September, the period of peak wing molt by adult females. Harlequin ducks were captured by using sea kayaks to herd molting, flightless birds into a funnel trap along shore. Once captured, birds were transported by boat to the main vessel for processing. Each bird was leg-banded with a unique U.S. Fish and Wildlife Service aluminum band, which was used to identify recaptured individuals. Sex was identified based on plumage characteristics and age class was estimated by probing bursal depth (Mather and Esler 1999). Body mass ( $\pm 1$  g) was measured on an electronic balance and corrected for estimated mass of radiotransmitters when necessary.

Radiotransmitters were surgically implanted into adult (after-third-year) female harlequin ducks. In 1995, transmitters (ATS, Isanti, Minnesota, USA)



weighed 15 g and were roughly spherical in shape (1.7--2.4 cm diam), due to embedding in resin. In 1996, transmitters (Holohil, Carp, Ontario, Canada) weighed 17.5 g, and were formed as brass cylinders measuring 4.0 cm by 1.5 cm and were coated with a biocompatible compound. All transmitters had wire whip antennas with a dacron-covered silastic sleeve glued to the base of the antenna. To deter birds from breaking antennas, a rubber reinforcement was added to the basal 4 cm of the antennas in 1996, which extended 3 cm outside of the duck's body when implanted. Expected battery life was  $\geq 7$  months for 1995 radios and  $\geq 18$  months for 1996 radios.

A modification of the procedure described by Korschgen et al. (1996) was used to surgically implant transmitters (Mulcahy and Esler 1999). Briefly, anesthesia of the birds was induced and maintained with isoflurane (Aerrane, Ohmeda, Liberty Corner, New Jersey, USA). Following presurgical preparation, a midline incision was made into the abdomen and the right abdominal air sac was breached. The antenna was passed through a trochar inserted from outside the bird and placed as dorsally as possible at the intersection of the right pubic bone and the synsacrum. The transmitter was fitted into the right abdominal air sac and the incision was closed with absorbable sutures. The sole attachment of the transmitter to the body of the duck consisted of a single interrupted suture through the skin, body wall, and the collar at the base of the antenna. Birds recovered from anesthesia for at least 1 hour before being released at the sites of their capture.

Radioed harlequin ducks were monitored approximately weekly from an airplane to determine mortality status, location, and radio signal strength. Monitoring flights began after the first birds were radioed and continued until the last week of March. Transmitters were equipped with mortality sensors that were activated by temperatures  $<27^{\circ}\text{C}$  for 1995 radios and by immobility for  $>12$  hr for 1996 radios. Indicated mortalities were confirmed either by recovery of the radio or location of the radio signal in upland habitats, which harlequin ducks do not use during the nonbreeding season. Monitoring of radios for which signals were lost continued through the end of the monitoring period.

We used a 1-tailed Fisher's Exact Test (Ramsey and Schafer 1997:548) to test the null hypothesis that recapture rates (proportions of birds recaptured) of radioed adult females were not lower than unradioed adult females. Recaptures were defined as the capture of an individual in the year subsequent to previous marking or handling. Variance and standard error of the proportion recaptured from each group were calculated as per Ramsey and Schafer (1997:520). We also estimated the difference in recapture rates between unradioed and radioed birds and the associated standard error after assuring that sample sizes were adequate for the normal approximation (Ramsey and Schafer 1997:521). No unradioed adult females were released in 1995, therefore we compared recapture rates of unradioed birds released in 1996 to both recapture rates of radioed birds from 1995 and 1996 combined, and 1996 only in case there were annual differences in recapture rates of radioed birds that might influence the results. Four birds were captured and radioed in 1995 and not recaptured again until 1997;

these were not included in our analyses, as unradioed birds with comparable capture histories were not available. Animals captured in all 3 years were represented by 2 recapture events. The sample of radioed birds included only those known to have survived the 14-day period following implant surgery, a censor interval designed to eliminate effects of surgery or handling (Mulcahy and Esler 1999).

To test whether survival differed between birds with known fates (i.e., known to have survived or died during the monitoring period) and birds for which radio signals were lost during the monitoring period, we compared recapture rates of these groups following the methods described above for radioed to unradioed comparisons. Our null hypothesis for the 1-tailed Fisher's Exact Test was that the recapture rate of right-censored birds was not lower than that of birds of known fate, which we contrasted with an alternative hypothesis that recapture rates of right-censored birds were lower, which presumably would result from higher mortality rates for missing birds. We also calculated the difference (and standard error of the difference) between recapture rates of birds with known fates and right-censored birds.

To examine differences in body mass between recaptured birds with radios and those without, we first standardized mass to account for seasonal, annual, geographic, and individual variation unrelated to our hypotheses of interest. We used residuals around a general linear model as our measure of standardized body mass. The model was generated from body mass data from molting females captured during our studies ( $n = 607$ ), including all birds used in subsequent

analyses. We used only data for first captures of females within a year to generate the model. The best-fitting model was determined by comparison of Mallow's  $C_p$  values of all possible combinations of main effects in a data-based model selection context (Burnham and Anderson 1998). Main effects included in the model selection process were area (an indicator variable in which unoiled Montague Island = 0 and capture sites in oiled areas = 1), year (1/0 indicator variables for 1996 and 1997, with 1995 set as the reference value), age (1/0 indicator variables for juvenile and subadult age classes, with the adult age class set as the reference value), and ninth primary length (a continuous variable indexing the stage of wing molt). The model with the lowest  $C_p$  value was

$$\text{Mass} = 606.18 - (9.61 \times \text{area}) - (18.64 \times \text{year 1996}) - (15.06 \times \text{juvenile age class}) - (0.19 \times \text{ninth primary length}).$$

Because subadult and adult age classes did not differ in body mass variation during wing molt (i.e., the subadult age class variable was not included in the best-fitting model), we used birds of both age classes for subsequent analyses of changes in body mass. For an individual, the difference in body mass residuals between the original capture and subsequent recapture reflects the relative change in body mass after accounting for variation due to other factors. Differences in body mass residuals could not be calculated for a small number of birds that, at  $\geq 1$  of their captures, had not shed their old primaries and therefore molt stage (ninth primary length) could not be determined.

To examine whether body mass was affected by implanting radios, we compared the average between-year change in residuals between recaptured

birds that were radioed and those that were unradioed using a *t*-test. We also compared the average change in residuals to zero, the expected result under a null hypothesis of no effect.

We assessed the effects of radio status and duration between captures on short-term changes in body mass using a general linear model. The dependent variable was the change in body mass residuals between within-year capture events of individuals and independent variables were radio status and the number of days between capture events. For all tests, we used  $\alpha = 0.05$  as the level of significance and results are presented as  $\bar{x} \pm \text{SE}$ .

## Results

Twenty-three adult female harlequin ducks were captured, banded, and released without radiotransmitters during 1996; of those, 5 ( $21.7 \pm 8.6\%$ ) were recaptured in 1997. Of 185 adult females implanted with radiotransmitters in 1995 and 1996 that survived the 14-day postsurgery period, 40 were recaptured, a rate ( $21.6 \pm 3.0\%$ ) not lower ( $P = 0.585$ ) than unradioed birds. When considering only 1996 radioed birds, 23 of 95 were recaptured, a rate ( $24.2 \pm 4.3\%$ ) comparable to our unradioed sample ( $P = 0.691$ ). The difference in recapture rates (unradioed recapture rate - radioed recapture rate) was  $0.1\% \pm 3.8\%$  when including all radioed birds and was  $-2.5\% \pm 5.1\%$  when considering only 1996 radioed birds; these results further suggest no difference between groups.

Radio signals were permanently lost during the monitoring period (right-censored) for 63 birds transmitted during 1995 and 1996. Thirteen ( $20.6 \pm$

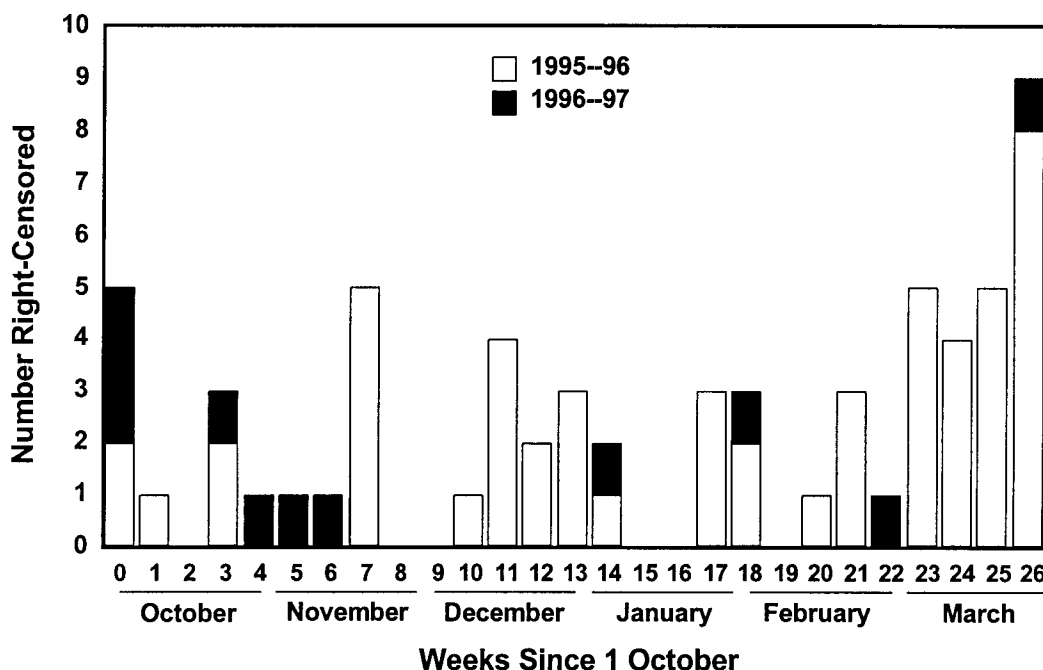


Figure 2.1. Distribution of dates of signal loss (right-censoring) of radiomarked adult female harlequin ducks in Prince William Sound, Alaska.

5.1%) of the right-censored birds were subsequently recaptured, which was similar ( $P = 0.486$ ) to the recapture rate of birds with known fates during the monitoring period (27 of 122;  $22.1 \pm 3.8\%$ ). The difference between recapture rates (known fate - right-censored) was  $1.5\% \pm 5.2\%$ . Dates of right-censoring occurred throughout the monitoring period (Fig. 1). The number of undetected radios increased during the final 4 weeks of the monitoring period, probably due to battery exhaustion of 1995 transmitters. We compared recapture rates of right-censored birds and birds with known fates, excluding those with signals lost during the final 4 weeks, to determine whether mechanisms resulting in signal loss other than battery failure could be related to survival. We found that the recapture rate

(9 of 40;  $22.5 \pm 6.6\%$ ) of birds right-censored during the first 5 months of the monitoring period was not lower ( $P = 0.613$ ) than that for birds with known fates reported above. Also, the difference in recapture rates between groups was  $-0.4\% \pm 6.7\%$ . Most lost signals occurred during the winter following 1995 captures (Fig. 1). Of 17 radioed birds recaptured in 1996, 13 had broken off their antenna at or near the skin surface (Mulcahy et al. 1999), likely explaining some signal loss. However, we also recaptured some individuals with intact antennas that were right-censored, perhaps as a result of other types of radio failure.

Body mass residuals of unradioed adult and subadult females ( $n = 42$ ) averaged  $5.0 \pm 4.3$  g higher in the year of recapture than the previous year, a result not different from zero ( $t_{41} = 1.176$ ,  $P = 0.246$ ). For radioed adult females ( $n = 34$ ), body mass residuals averaged  $7.4 \pm 4.7$  g lower upon their recapture than in the year of their first capture, not different ( $t_{33} = 1.584$ ,  $P = 0.123$ ) from the expected value of zero under a hypothesis of no radio effect. The  $12.5 \pm 6.4$  g difference between groups was not significant ( $t_{74} = 1.961$ ,  $P = 0.054$ ). Taken together, these results do not suggest a strong effect of radios on body mass after a year.

For within-year recaptures, the number of days between capture events did not explain variation in the change in body mass residuals between capture events ( $t_{50} = 0.031$ ,  $P = 0.975$ ) within a general linear model including a radio status term. Also, average number of days between capture events did not differ ( $t_{51} = 0.368$ ,  $P = 0.714$ ) between radioed ( $13.0 \pm 0.9$ ) and unradioed ( $13.3 \pm 0.6$ ) birds. Therefore, the analysis reduced to *t*-test comparisons. Body mass

residuals of unradioed females ( $n = 33$ ) declined an average of  $15.0 \pm 4.3$  g between capture events, a result significantly lower than zero ( $t_{32} = 3.480$ ,  $P = 0.001$ ). Body mass residuals of radioed females ( $n = 20$ ) declined  $30.3 \pm 5.7$  g, also different from zero ( $t_{19} = 5.349$ ,  $P < 0.001$ ). The  $15.4 \pm 7.1$  g difference in changes in body mass residuals between groups was marginally significant ( $t_{51} = 2.178$ ,  $P = 0.034$ ). These results suggest that capture and handling have short-term effects on body mass for both radioed and unradioed birds, but that these effects were greater for those birds receiving radiotransmitters.

## Discussion

We found no evidence to suggest that survival estimation of adult female harlequin ducks was biased by either deleterious effects of implanted radiotransmitters or differential survival between known-fate and right-censored birds. We recognize that we had limited power to detect differences in recapture rates; however, recapture rates invariably were quite similar between groups, building confidence for using these methods to test hypotheses related to survival.

This study is the first to compare interannual survival between birds with implanted radios and unradioed birds. Our finding that recapture rates were not reduced for harlequin ducks with implanted radios suggests that use of implanted radios can result in unbiased survival estimates. In previous comparisons, birds with implanted radiotransmitters had higher survival than others with externally attached transmitters (Dzus and Clark 1996, Paquette et al. 1997). Other studies have documented lower survival or return rates for sharp-tailed grouse



(*Tympanuchus phasianellus*; Marks and Marks 1987), black brant (*Branta bernicla nigricans*; Ward and Flint 1995), and rock ptarmigan (*Lagopus mutus*; Cotter and Gratto 1995) with external transmitters than for unradioed birds. However, no differences in survival were detected between externally transmitted and unradioed spotted owls (*Strix occidentalis*; Foster et al. 1992) and blue grouse (*Dendragapus obscurus*; Hines and Zwickel 1985). We recommend that investigators be aware of potential bias using externally attached transmitters and consider the use of implanted transmitters as an alternative.

Disadvantages of implanting radios include longer handling time and requirement of veterinary support for implant surgeries, although these are relatively minor compared to the desirability of obtaining unbiased estimates of survival and minimizing adverse effects on marked individuals. Schulz et al. (1998) reported elevated heterophil:lymphocyte ratios in captive mourning doves (*Zenaida macroura*) following abdominal implantation of radiotransmitters, although postsurgery body mass and other blood chemistry parameters were not affected. Also, extrusion through the body wall and loss of implanted radio transmitters with external antennas was documented for some of the harlequin ducks in this study (Mulcahy et al. 1999). This could result in bias in survival estimation if extrusion and loss resulted in undetected mortality. However, recapture rates did not differ between a year without known extrusions and a year with documented extrusions, the incidence of extrusion and loss was relatively low, recaptured birds that had lost their radios were apparently healthy, and radio loss occurred after the monitoring period (Mulcahy et al. 1999). Further, our

results from this study show that recapture rates of radioed birds, including birds that lost radios, were similar to those of unradioed birds, corroborating the conclusion of Mulcahy et al. (1999) that extrusions did not affect health of birds. Radio extrusions can be avoided largely through attention to radio design and surgical technique (Mulcahy et al. 1999).

Short-term effects of transmitter implantation in birds have been detected, including reduced nesting effort (Meyers et al. 1998), surgical and postrelease mortality (Mulcahy and Esler 1999), and reductions in body mass documented in this study. However, biases to survival estimation can be avoided by censoring data during the period immediately following implantation when these effects occur. For our studies, 14 days was an appropriate censor interval. Ten mortalities of radioed harlequin ducks (out of 295 radioed and released during 1995--97) were documented during the 14 days following surgery (Mulcahy and Esler 1999), compared to none during the next 14 days. Also, the results from this study show no evidence of differential survival of radioed birds after the 14-day censor interval relative to unradioed birds.

One potential bias resulting from using radiotelemetry to estimate survival is that deaths potentially related to the radiotagging process (i.e., within the censor interval) may not be distributed at random within the sample of captured birds and, thus, the assumption that the radioed birds entering into the monitoring period are representative of the population of interest may be violated. In other words, the small number of deaths associated with radiomarking (Cox and Afton 1998, Mulcahy and Esler 1999) may occur in birds that had a different (presumably

lower) survival probability had they not been captured than birds that survived the censor interval. In this case, one might predict higher recapture rates for radioed birds that survived the censor period than unradioed birds; we did not detect this, although we had little power to detect these presumably subtle effects. We believe that this potential bias had little effect on our survival estimates, as the incidence of deaths within the censor interval was relatively low (Cox and Afton 1998, Mulcahy and Esler 1999) and deaths were related more to procedural attributes than individual variation. We encourage investigators to minimize deaths due to radiomarking by adaptive modifications to capture and radiomarking techniques.

Loss of radio signals, and the subsequent assumption that right-censored individuals have the same survival probability as individuals with known fates, is an issue that has been difficult to address in field studies. In many cases, undetected radios likely result from radio failure (Miller et al. 1995, Cox et al. 1998, this study), but other plausible scenarios of loss of a radio signal exist that are not independent of mortality status (e.g., a predator destroys the antenna or radio during the predation event). We suggest that this bias did not exist for our study of harlequin duck survival. However, due to the paucity of data addressing this bias, we recommend other attempts to test this assumption.

Short-term body mass loss associated with radiomarking has been previously documented (Dugger et al. 1994), and we found short-term reductions in body mass, presumably related to capture and handling in both radioed and unradioed individuals. Body mass loss is a concern when estimating survival

because of the documented relationship between body mass and subsequent mortality in some situations (Conroy et al. 1989, Longcore et al. 1991, Bergan and Smith 1993), although not others (Dugger et al. 1994, Migoya and Baldassarre 1995, Miller et al. 1995, Cox et al. 1998). However, because there were no strong effects of radios on interannual change in body mass and, particularly, because of our finding that interannual recapture rates did not differ between radioed and unradioed birds, we conclude that the short-term mass loss associated with implanting radios does not affect subsequent survival.

### **Management Implications**

Survival is an important demographic parameter for understanding population status and predicting population trends, as well as, for identifying environmental or anthropogenic factors that affect wildlife species. This is particularly true for species with life-history traits similar to harlequin ducks (i.e., long-lived with relatively low investment in annual reproduction; Goudie et al. 1994, Schmutz et al. 1997). Thus, it is critical to use methods for measuring survival that result in unbiased estimates. Our results suggest that use of abdominally implanted radiotransmitters for estimating survival of harlequin ducks does not violate assumptions of no effect of radiotransmitters and no differential survival between right-censored and known-fate individuals. Based on our results, and those of studies contrasting external transmitters with implanted transmitters, we suggest that implanted transmitters likely offer investigators a less biased method. Finally, we recommend that investigators attempt to quantitatively test

assumptions of survival estimation for their particular species of interest and situation. Generation of survival rates in an unbiased manner is critically important for making subsequent management decisions for wildlife populations.

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## CHAPTER 3

WINTER SURVIVAL OF ADULT FEMALE HARLEQUIN DUCKS IN RELATION  
TO HISTORY OF CONTAMINATION BY THE *EXXON VALDEZ* OIL SPILL

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### Abstract

Harlequin duck (*Histrionicus histrionicus*) life-history characteristics make their populations particularly vulnerable to perturbations during nonbreeding periods. The 1989 *Exxon Valdez* oil spill was a major perturbation to nonbreeding habitats of harlequin ducks in Prince William Sound, Alaska, which resulted in population injury. To assess the status of population recovery from the oil spill and to evaluate factors potentially constraining full recovery, we used radiotelemetry to examine survival of adult female harlequin ducks during winters of 1995--96, 1996--97, and 1997--98. We implanted 294 harlequin ducks (154 and 140 in oiled and unoiled areas, respectively) with transmitters and tracked their signals from aircraft during October through March. We examined variation in survival rates relative to area and season (early, mid, and late winter) through comparisons of models using Akaike's information criterion ( $AIC_c$ ) values. The 3 models best supported by the data indicated that survival of birds in oiled areas was lower than in unoiled areas. Inclusion of standardized body mass during wing molt in the 3 best models did not improve their fit, indicating that body mass during wing molt did not affect subsequent winter survival. In the model that best fit our data, survival was high in early winter for both areas, lower during mid and late winter seasons, and lowest in oiled areas during mid winter. Cumulative winter survival estimated from this model was 78.0% (SE = 3.3%) in oiled areas and 83.7% (SE = 2.9%) in unoiled areas. We determined that area differences in survival were more likely related to oiling history than intrinsic geographic differences. Based on a demographic model, area differences in survival offer a

likely mechanism for observed declines in populations on oiled areas. Concurrent studies indicated that harlequin ducks continued to be exposed to residual *Exxon Valdez* oil as much as 9 years after the spill. We suggest that oil exposure, mortality, and population dynamics were linked and conclude that continued effects of the oil spill likely restricted recovery of harlequin duck populations through at least 1998.

### **Introduction**

Harlequin ducks spend most of their annual cycle in nearshore marine environments, with breeding age birds leaving only for a few summer months to nest and raise broods on fast-moving streams (Robertson and Goudie 1999). Populations of harlequin ducks may be particularly sensitive to perturbations to their nonbreeding habitats. Harlequin ducks, like many sea ducks, exhibit a life history in which variable and generally low annual reproductive effort is compensated by relatively high adult survival and long reproductive life spans (Goudie et al. 1994). This type of life history would be expected to evolve under conditions of predictable and stable nonbreeding environments (Stearns 1992). Further, Goudie and Ankney (1986) described harlequin ducks, which are small-bodied relative to most other sea ducks, as existing near an energetic threshold during winter, with little flexibility for increasing caloric intake or relying on stored reserves. While this strategy may be tenable under predictable and stable conditions, it does not accommodate perturbations that result in either decreases in energy acquisition or increases in metabolic costs.

The release of nearly 42 million liters of crude oil into the waters of Prince William Sound as a result of the March 1989 grounding of the *Exxon Valdez* was a significant perturbation to the nonbreeding habitat of harlequin ducks. As much as 40% of the spilled oil was deposited in intertidal and subtidal zones of Prince William Sound (Galt et al. 1991, Wolfe et al. 1994), the habitats used by harlequin ducks, and some residual oil was still present in these areas during our study (Hayes and Michel 1999). Immediate bird mortality from the *Exxon Valdez* oil spill was high (Piatt et al. 1990) and more than 1,000 harlequin ducks were estimated to have died as a direct result of the spill (J. Piatt, U.S. Geological Survey, personal communication). Further, there are concerns that there may be continued, longer-term effects on harlequin duck populations in oil spill-affected areas (Holland-Bartels 2000).

This study was part of a program to assess population recovery of harlequin ducks from the *Exxon Valdez* oil spill in Prince William Sound. We focused on adult female survival during winter because (1) population dynamics of long-lived waterfowl species are particularly sensitive to changes in adult female survival (Goudie et al. 1994, Schmutz et al. 1997), (2) harlequin duck populations are likely sensitive to perturbations on wintering areas, and (3) Prince William Sound is used primarily by harlequin ducks during nonbreeding life stages. Paine et al. (1996), in a critique of studies immediately following the *Exxon Valdez* oil spill, recommended that demographic measures likely provide a better assessment of injury than species occurrence or abundance. We agree, and suggest that demographic studies not only serve to assess injury or recovery

status, but also can lend insight into the processes and mechanisms underlying any constraints to full recovery.

## **Methods**

As described by Paine et al. (1996), the *Exxon Valdez* oil spill was an imperfect experiment -- a one-time perturbation without replication and, as in the case of wintering harlequin ducks, with little prespill data for comparison. Under these conditions, our approach was to compare oiled and unoiled areas, while attempting to minimize or account for differences between areas that might confound interpretation of oil spill effects (Wiens and Parker 1995). We recognize that our statistical inference is to areas only, and that assessment of oil spill effects is subject to interpretation. We present ancillary data relevant to this interpretation.

### **Data Collection**

This study was conducted in Prince William Sound (60°N, 148°W), the area most affected by the oil spill, during winters of 1995--96, 1996--97, and 1997--98. We used radiotelemetry to estimate survival of adult female harlequin ducks captured throughout the oil spill zone and on nearby unoiled Montague Island (Fig. 1).

Harlequin ducks, unlike most waterfowl, undergo wing molt on their marine wintering areas (Robertson and Goudie 1999). We herded flocks of flightless birds into funnel traps using sea kayaks during 20 August to 17 September, 1995--97, the dates of peak wing molt by adult females. Captured harlequin ducks were

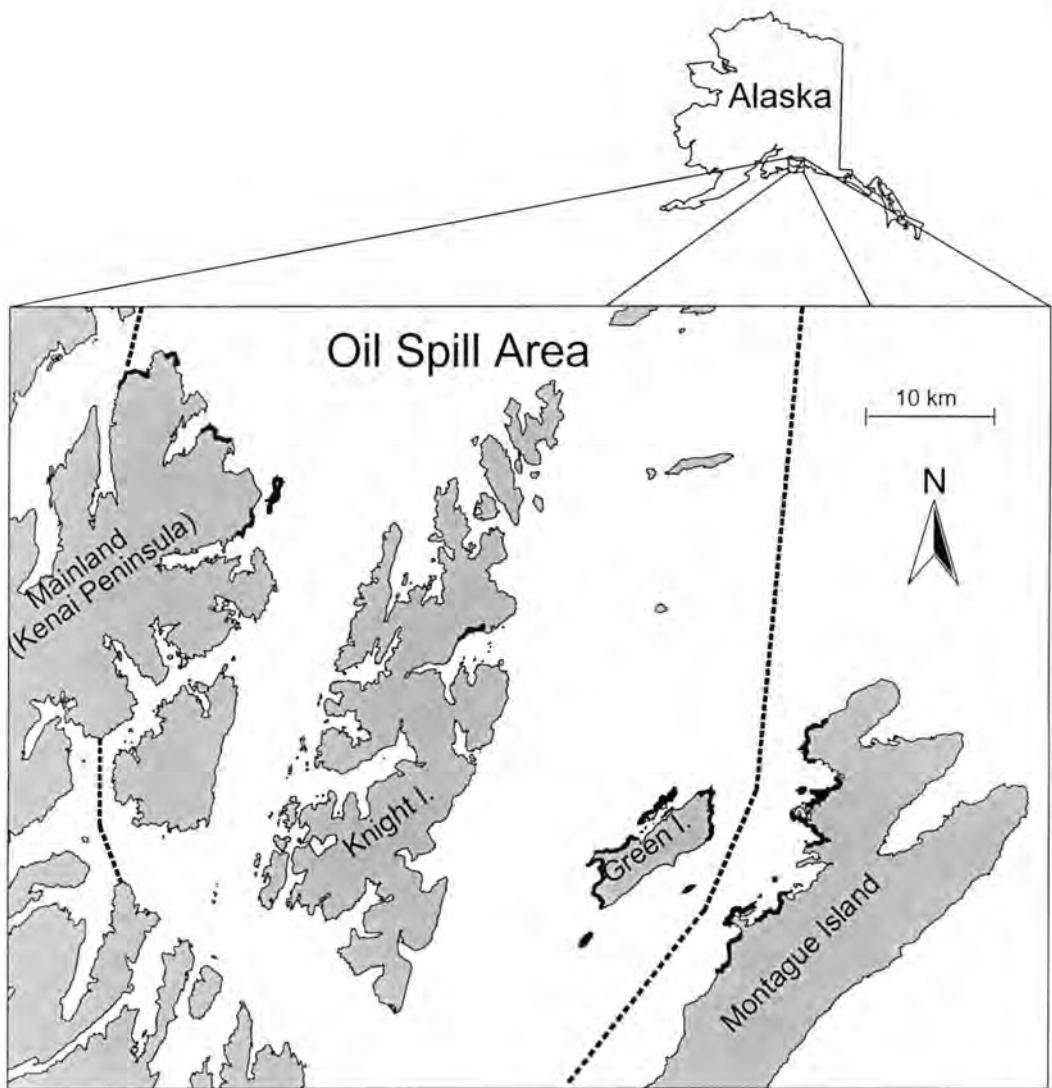


Figure 3.1. Study sites for estimating survival of adult female harlequin ducks in Prince William Sound, Alaska. Shorelines in bold represent capture areas. The oil spill area is bounded by dashed lines.

removed from the trap, placed in holding pens, and transported by skiff to a larger vessel for processing. All birds were banded with unique U.S. Fish and Wildlife Service aluminum bands. We identified sex based on plumage characteristics and estimated age class by probing bursal depth (Mather and Esler 1999). Body mass ( $\pm 1$  g) was measured on an electronic balance.

Radiotransmitters were implanted surgically into adult (after third year) female harlequin ducks using modifications (Mulcahy and Esler 1999) of the procedure described by Korschgen et al. (1996). Surgeries were conducted by veterinarians experienced in avian implant procedures. Implanted transmitters have been used successfully in waterfowl studies (e.g., Olsen et al. 1992, Haramis et al. 1993), and an increasing body of literature suggests that radiotransmitters implanted into wild waterfowl are less disruptive than external methods of attachment (Esler et al. 2000). Transmitters weighed  $\leq 17.5$  g ( $< 3\%$  of average body mass of adult females during wing molt) and had external antennas (Mulcahy and Esler 1999). Birds recovered from anesthesia for at least 1 hr before being released at their capture sites.

Radiomarked harlequin ducks were monitored approximately weekly from an airplane to determine mortality status and location. Monitoring flights began after the first birds were radioed and continued through the last week of March. Transmitters were equipped with mortality sensors that indicated death of a bird by doubling the transmitter pulse rate. Indicated mortalities were confirmed either by recovery of the radio or location of the radiosignal in upland habitats, which

harlequin ducks do not use during the nonbreeding season. When radiosignals were lost, monitoring continued until the end of March.

## **Data Analysis**

Unbiased survival estimation using telemetry requires that several critical assumptions are met (Pollock et al. 1989a, Tsai et al. 1999), including (1) radioed animals are representative of the population of interest, (2) survival is independent among individuals, (3) radiomarking does not affect survival during the study period, and (4) censoring of animals for which signals are lost is independent of the fate of those animals (i.e., missing animals are no more or less likely to be dead than animals for which fate is known). We felt that the first 2 assumptions were met based on our capture technique and marking regime. We perceived little chance of a systematically biased sample based on susceptibility to capture, as we often were able to catch most birds within a given shoreline segment. Also, because we were marking only adult females, we felt that survival among individuals was independent beyond shared area effects (e.g., we were not marking both members of a pair or a mother and her offspring). We explicitly tested assumptions 3 and 4 (Esler et al. 2000) and found that these were met for our sample.

For each week's sample of relocations, we counted mortalities and numbers of harlequin ducks at risk of mortality (i.e., numbers of detected radios), following procedures outlined in Pollock et al. (1989a,b) and Bunck et al. (1995). We used 1 October as the beginning of the data analysis period to ensure that all



birds in the sample had survived a 14-day post-surgery censor period (Mulcahy and Esler 1999) and had completed wing molt. We made an a priori decision to combine data from all years to assure adequate power for detecting biologically meaningful differences between areas. A small number of birds ( $n = 6$ ) moved between oiled and unoled areas during winter; if a bird was detected in a different area for  $\geq 2$  consecutive observations, we included those observations in the at-risk data set for the newly occupied area.

We defined seasons as early winter, mid-winter, and late winter, corresponding to the first 9 weeks of data collection, the middle 8 weeks, and the final 9 weeks. Our most general survival model contained 52 parameters (i.e., 1 for each area and week) and corresponded to the Kaplan-Meier method (Pollock et al. 1989a) of computing binomial estimates of survival. Variance estimates for this model were calculated using Greenwood's formula (Pollock 1989a). We examined the effects of season, area, and several season by area interactions on survival by comparing a series of reduced (fewer parameters) models, in which survival was constrained to be constant among weeks within each season and area combination. We based our inference on the model or models that best fit our data, as determined by comparisons of  $AIC_c$  values (Burnham and Anderson 1998). The  $AIC_c$  indicates the most parsimonious model by balancing the goodness-of-fit of each model (from the maximum likelihood) with the number of parameters to be estimated. Under this approach, the model with the lowest  $AIC_c$  indicates the parameters that are supported by the data, which we interpreted as factors related to variation in survival. Models with  $AIC_c$  values within 2 units of

the  $AIC_c$  of the best-fitting model are substantially supported by the data (Burnham and Anderson 1998), and thus we also considered the inference from those models. We also calculated  $AIC_c$  weights for each model, which is the weight of evidence that the model is the best of the models considered, given the data. The  $AIC_c$  weights for a collection of models sum to 1 and can be used to contrast relative support for each model, and hence the support for the model inference. Survival estimates and variances were calculated by iterative solution of the likelihood using program MARK (White and Burnham 1999). Use of  $AIC_c$  to direct model selection and inference deviates from traditional analyses based on significance testing, but is supported by a growing body of literature describing the pitfalls of statistical hypothesis tests (Johnson 1999), particularly for observational studies.

We also assessed whether body mass during wing molt affected subsequent survival by adding standardized body mass to the best-fitting models as determined above. A reduction in  $AIC_c$  value would indicate that the addition of the body mass term resulted in a more parsimonious model and that body mass during wing molt was related to winter survival. Body mass was standardized to account for annual, geographic, and molt-stage variation unrelated to our hypothesis of interest by using residuals around a general linear model (Esler et al. 2000) as the body mass parameter. Body mass residuals could not be calculated for 12 of the radioed birds, which were excluded from this analysis.

## Results

On 1 October, the beginning of the survival monitoring period, 294 radiomarked adult female harlequin ducks were included in the sample (154 at oiled areas and 140 at unoiled areas). Kaplan-Meier estimates of cumulative winter survival were  $76.6 \pm 4.0\%$  (SE) in oiled areas and  $86.6 \pm 3.2\%$  in unoiled areas (Fig. 2a).

We contrasted 11 different models with various area and season combinations (Table 1). In the best-fitting model (Model 1), survival varied by season and area, with estimates higher in early winter than other seasons and lower in oiled than unoiled areas during mid-winter (Table 2). Cumulative winter survival estimated from this model was  $78.0 \pm 3.3\%$  in oiled areas and  $83.7 \pm 2.9\%$  in unoiled areas. Two other models (Models 2 and 3; Table 1) had  $AIC_c$  values  $<2$  units higher than Model 1. In Model 2, survival varied by season and was lower in oiled areas than unoiled during mid-winter (Table 2). In Model 3, survival was high in the fall for both areas, lower and constant during mid and late winter on the unoiled area, and lower on oiled areas than unoiled during mid and late winter, particularly during mid-winter (Table 2). These 3 best models all included an area effect, with survival on oiled areas lower than on unoiled areas (Fig. 2b). The sum of  $AIC_c$  weights for models without an area effect was  $<0.05$ , indicating that area effects were strongly supported by the data. Similarly, seasonal effects were well supported by the data, with survival during early winter consistently higher than in mid and late winter in the 3 best models. Inclusion of standardized body mass increased  $AIC_c$  values of Models 1, 2, and 3 (change in  $AIC_c \geq 0.69$ ),

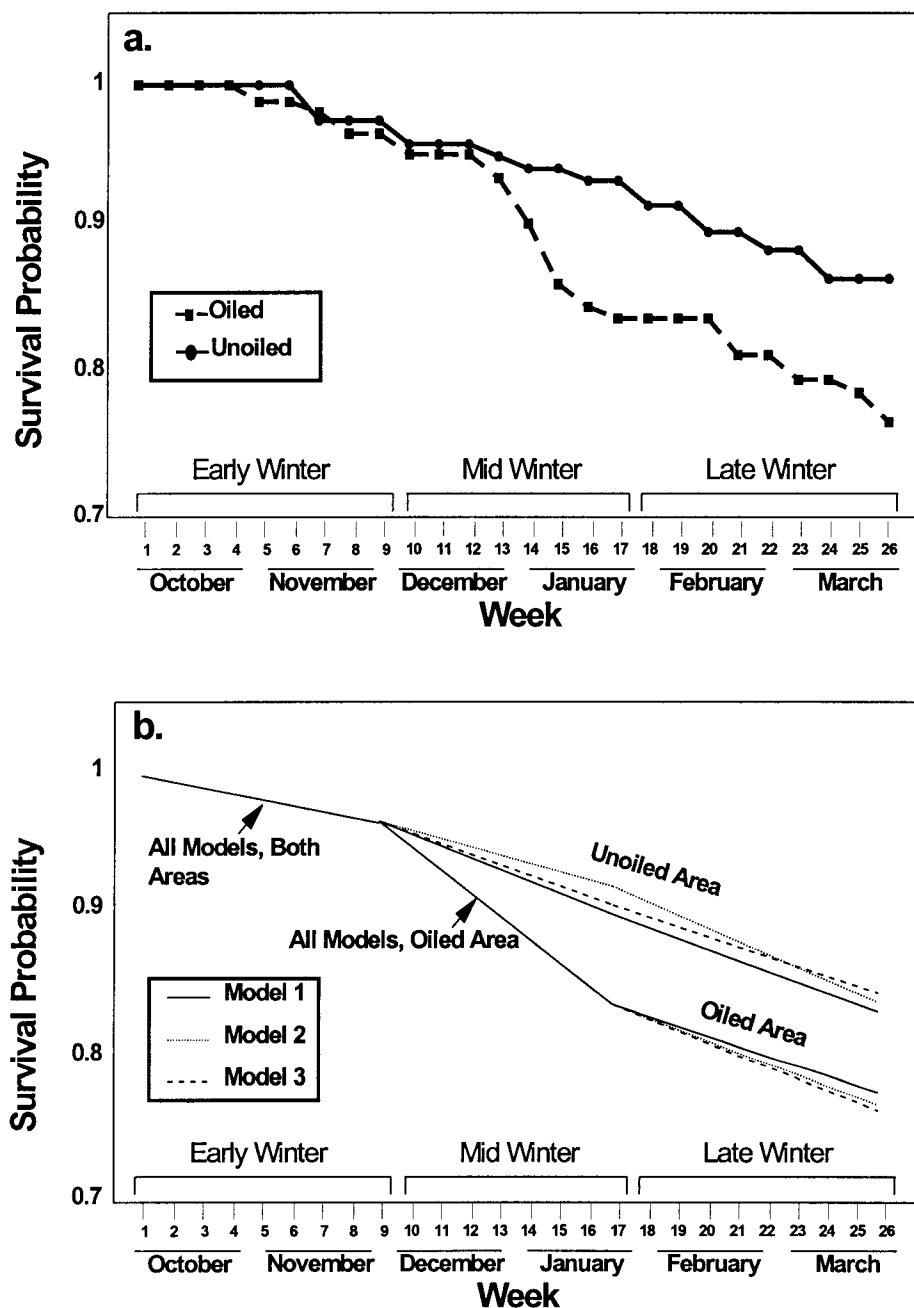


Figure 3.2. Winter survival probabilities for harlequin ducks in Prince William Sound, Alaska, based on (a) Kaplan-Meier estimates and (b) the 3 best-fitting reduced models (see Table 3.1).

indicating that mass during wing molt was not strongly related to subsequent winter survival.

A difficulty inherent in our study design was determining whether survival differences between oiled and unoiled areas were more likely related to intrinsic differences (such as habitat, disease, climate, or predator densities) rather than history of oil contamination. To address this, we looked more closely at data for birds ( $n = 75$ ) from the Green Island area. Although Green Island was in the oil spill area, it was closer to unoiled Montague Island than to other oiled sites (Fig. 1). Also, habitats and harlequin duck densities (D. Esler, unpublished data) were similar to the Montague Island study area. We found that the Kaplan-Meier estimate of cumulative survival of birds captured at Green Island ( $76.8 \pm 5.7\%$ ) was more similar to that for all oiled areas combined than to unoiled Montague Island. We also contrasted a general season by area model (modified Model 8, Table 1; 3 areas = Green Island, other oiled areas, and unoiled Montague Island) to 2 models each with 2 areas (1 model with Green Island pooled with other oiled areas and 1 model with Green Island pooled with Montague Island). The  $AIC_c$  for the model with Green Island pooled with other oiled areas was  $\geq 3.94$  units lower than either of the other 2 models, suggesting that oiling history better explains differences in survival between areas than do intrinsic area differences.

Table 3.1. Models used to estimate winter survival rates of adult female harlequin ducks in Prince William Sound, Alaska, using various combinations of season (early, mid, and late winter) and area (oiled and unoled). The best model is that with the lowest Akaike information criterion, adjusted for small sample size ( $AIC_c$ ; Burnham and Anderson 1998). Support for each model is indicated by differences in  $AIC_c$  values, not their absolute magnitude; therefore, we present  $AIC_c$  values as differences from the best model ( $\Delta AIC_c$ ).

Models	Model description <sup>a</sup>	Number of	$AIC_c$	
		parameters	weight	$\Delta AIC_c$
		in model		
1	EWO=EWU, MWO, MWU=LWO=LWU; survival differs between early winter and other seasons, areas differ during mid-winter	3	0.314	0.0
2	EWO=EWU, MWO, MWU, LWO=LWU; survival differs among all seasons, areas differ during mid-winter	4	0.199	1.0
3	EWO=EWU, MWO, MWU=LWU, LWO; survival differs between early winter and other seasons, areas differ during mid and late winter	4	0.144	1.6
4	EWO=EWU=MWU=LWU, MWO, LWO; survival does not vary seasonally in unoled areas, areas differ during mid and late winter	3	0.100	2.3

Table 3.1 (Continued)

5	EWO=EWU=MWU=LWO=LWU, MWO; survival differs between mid-winter on oiled areas and all other season and area combinations	2	0.088	2.6
6	EW, MW, LW, O<>U; survival differs among seasons, with a constant area difference	4	0.074	2.9
7	EWO=EWU, MWO=MWU, LWO=LWU; survival differs by seasons, with no area differences	3	0.046	3.9
8	EWO, EWU, MWO, MWU, LWO, LWU; survival differs by all season and area combinations	6	0.028	4.9
9	EWO=MWO=LWO, EWU=MWU=LWU; survival differs between areas, with no seasonal differences	2	0.004	8.6
10	EWO=EWU=MWO=MWU=LWO=LWU; survival does not vary by season or area	1	0.003	9.4
11	General model; estimates generated for each week and area	52	0.000	35.4

<sup>a</sup>EWO = early winter in oiled areas, EWU = early winter in unoiled areas, MWO = mid-winter in oiled areas, MWU =

midwinter in unoiled areas, LWO = late winter in oiled areas, and LWU = late winter in unoiled areas.

Table 3.2. Parameter estimates (SE) for the top 3 models describing adult female harlequin duck survival during winter in Prince William Sound, Alaska. See Table 3.1 for model descriptions.

Season <sup>a</sup>	Oiled Areas	Un-oiled Areas
Model 1		
Early winter	0.969 (0.012)	0.969 (0.012)
Mid-winter	0.870 (0.031)	0.934 (0.014)
Late winter	0.925 (0.016)	0.925 (0.016)
Overall	0.780 (0.033)	0.837 (0.029)
Model 2		
Early winter	0.969 (0.012)	0.969 (0.012)
Mid-winter	0.870 (0.031)	0.953 (0.020)
Late winter	0.914 (0.021)	0.914 (0.021)
Overall	0.770 (0.034)	0.843 (0.029)
Model 3		
Early winter	0.969 (0.012)	0.969 (0.012)
Mid-winter	0.870 (0.031)	0.940 (0.017)
Late winter	0.910 (0.030)	0.933 (0.019)
Overall	0.767 (0.039)	0.850 (0.034)

<sup>a</sup>Seasons are of differing lengths (early = 9 weeks, mid = 8 weeks, and late = 9 weeks).



## Discussion

Winter survival of adult female harlequin ducks was lower on oiled areas than unoiled areas, primarily due to poorer survival on oiled areas during the mid-winter period. In both areas, survival during early winter was higher than during mid or late winter. To understand how these estimates of survival might influence population dynamics, we incorporated the overall cumulative winter survival estimates for each area from Model 1 into a harlequin duck population model (Robertson 1997), holding all other parameters constant. The estimate of annual population change ( $\lambda$ ) was 0.9464 for oiled areas (i.e., annual population declines of about 5.4%). For unoiled areas,  $\lambda$  was 1.0054, suggesting a relatively stable population. These estimates are consistent with trends estimated from population surveys conducted during fall 1995--97 (Rosenberg and Petrula 1998). Differences in adult female survival offer a likely mechanism for differences in population trends between areas, and further poor survival on oiled areas may be responsible for population declines.

Our data suggest that area differences in winter survival are more likely due to history of oil contamination than intrinsic area differences. For oiling history to affect survival probabilities and subsequent population trends, there must be some mechanism by which birds from oiled areas are compromised. One potential mechanism is that the immediate effects of the spill or subsequent effects of residual oil resulted in reductions of prey populations. However, during the period of this study, density and abundance of prey were similar between oiled Knight Island and unoiled Montague Island (Holland-Bartels 2000) and winter body

mass of female harlequin ducks was similar between oiled and unoiled areas (Holland-Bartels 2000). This suggested that differential food abundance was not responsible for differences in survival between areas.

Exposure to residual *Exxon Valdez* oil is another potential mechanism by which harlequin duck survival could be affected, as oil exposure is known to have deleterious toxic (Leighton 1993) and metabolic (Jenssen 1994) consequences. To determine if harlequin ducks in Prince William Sound were still being exposed to residual oil, Trust et al. (2000) measured induction of cytochrome P4501A (P450), which can indicate exposure to polycyclic aromatic hydrocarbon constituents of crude oil, in harlequin ducks captured during winter 1998 in both oiled and unoiled areas. Cytochrome P450 induction was much higher in harlequin ducks from oiled areas than those from unoiled areas, and Trust et al. (2000) concluded that this was almost certainly due to exposure to residual *Exxon Valdez* oil, because background hydrocarbon levels were negligible in intertidal areas of Prince William Sound prior to the oil spill (Short and Babcock 1996) and polychlorinated biphenyl (PCB) levels were low and similar between areas (Trust et al. 2000). Further, some residual oil was documented in nearshore habitats contemporary with our study (Hayes and Michel 1999). Finally, P450 results from harlequin ducks are consistent with those from several other nearshore vertebrates from oiled areas (B. Ballachey, U.S. Geological Survey, unpublished data).

Could exposure to residual *Exxon Valdez* oil result in lower survival and concomitant population declines? Most lab studies have shown that mallards

(*Anas platyrhynchos*) are tolerant of ingestion of oil, with acute toxic effects not evident until very high doses. These studies have been used to suggest that harlequin ducks should be unaffected by residual *Exxon Valdez* oil (Stubblefield et al. 1995, Boehm et al. 1996). However, other studies have found that the addition of other stressors such as cold temperatures caused oiled ducks in the lab to suffer considerably higher mortality than unoiled birds (Holmes et al. 1978, 1979). This compounding effect of environmental stress and oil exposure seems to be a more appropriate analog for wild harlequin ducks, which exist under relatively harsh winter conditions with little flexibility for accommodating additive stresses (Goudie and Ankney 1986). Our data indicate that mid and late winter may be stressful periods in the annual cycle of harlequin ducks even under unperturbed conditions, as survival on unoiled areas was lower during these seasons than during early winter.

The divergence of survival probabilities between oiled and unoiled areas during mid-winter (Fig. 2) is consistent with a hypothesis of additive effects of oil in the presence of other stressors. Harlequin ducks are visual foragers, and during mid-winter when day length is shortest, they spend most of their time feeding (Goudie and Ankney 1986, Fischer 1998). Prince William Sound is one of the farthest north-wintering areas for harlequin ducks (Robertson and Goudie 1999), thus daylight available for foraging may be particularly limited. Because harlequin ducks have little flexibility for meeting increased energy demands during winter (Goudie and Ankney 1986), which could result from either ingestion of hydrocarbons or plumage oiling (Jenssen 1994), they may be unable to

accommodate additive effects of the oil spill, even if relatively small. We speculate that differences in survival and population trends are related to documented differences in contaminant exposure (Trust et al. 2000).

### **Management Implications**

Although populations of some animals may be unaffected or recover rapidly from oil spill effects (Bowman et al. 1995, 1997; Wiens et al. 1996), others such as harlequin ducks have characteristics that make them vulnerable to population-level effects of oil spills for years following the event. For harlequin ducks, these characteristics include a life history requiring high adult survival, occurrence in habitats most affected by oil spills (and which may hold residual oil for years), adaptation to stable and predictable marine environments, and high site fidelity. These traits also make harlequin ducks, and similar species, vulnerable to chronic, low-level oil pollution (Clark 1984). In the cases of either oil spills or chronic oil pollution, the primary management recommendation is, of course, prevention; oil that does not go into the water does not threaten marine bird populations. Unfortunately for harlequin ducks in the spill-affected area, there is little direct management action that now can improve winter survival. Hunter harvest of harlequin ducks is negligible in Prince William Sound and bag limits already were reduced following the oil spill. The extent of the *Exxon Valdez* oil spill zone is too large to recommend intensive habitat restoration; also, residual oil may be deeply buried in sediment (Hayes and Michel 1999) and oil removal efforts could result in significant disruption of intertidal habitats. Therefore, recovery of

harlequin duck populations in Prince William Sound will depend largely on natural dispersal and degradation of residual oil and intrinsic population growth.

Wintering aggregations of harlequin ducks are demographically distinct at a relatively fine scale (Cooke et al. 2000). Winter site fidelity of harlequin ducks is high to specific stretches of coastline (Robertson 1997, Cooke et al. 2000) and pair formation occurs on the wintering areas (Gowans et al. 1997, Robertson et al. 1998). Thus, factors that affect survival rates on marine areas can have disproportionate and cumulative effects on these local subpopulations. Fortunately in the case of the *Exxon Valdez* oil spill, levels of dispersal are high enough that subpopulations within the northern Gulf of Alaska were not genetically distinct (Lancot et al. 1999); the oil spill did not threaten a unique, evolutionarily significant unit (Moritz et al. 1995). However, dispersal rates likely are low, and because of demographic isolation, recovery of groups of birds in oiled areas must occur primarily through recruitment specific to that group (i.e., numbers are not enhanced through immigration from other areas). Population recovery will require not only time for demographic processes to operate, but also elimination of continuing deleterious oil spill effects. Our data suggest that deleterious effects of the *Exxon Valdez* oil spill were evident as many as 9 years following the spill. Managers must recognize that, while oil spill effects may be short-lived for some species, full population recovery for species like harlequin ducks may require decades. In a broader context, the characteristics of harlequin ducks that make them vulnerable to oil spill effects also make them susceptible to population level

consequences of other perturbations during nonbreeding periods, including human disturbance, habitat deterioration, and local overharvest.

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## CHAPTER 4

CORRELATES OF HARLEQUIN DUCK DENSITIES DURING WINTER IN  
PRINCE WILLIAM SOUND, ALASKA

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### **Abstract**

We evaluated relationships of Harlequin Duck (*Histrionicus histrionicus*) densities to habitat attributes, history of habitat contamination by the 1989 *Exxon Valdez* oil spill, and prey biomass density and abundance during winters 1995-1997 in Prince William Sound, Alaska. Habitat features that explained variation in duck densities included distance to streams and reefs, degree of exposure to wind and wave action, and dominant substrate type. After accounting for these effects, densities were lower in oiled than unoiled areas, suggesting that population recovery from the oil spill was not complete, due either to lack of recovery from initial oil spill effects or continuing deleterious effects. Prey biomass density and abundance were not strongly related to duck densities after accounting for habitat and area effects. Traits of Harlequin Ducks that reflect their affiliation with naturally predictable winter habitats, such as strong site fidelity and intolerance of increased energy costs, may make their populations particularly vulnerable to chronic oil spill effects and slow to recover from population reductions, which may explain lower densities than expected on oiled areas nearly a decade following the oil spill.

### **Introduction**

Harlequin Ducks (*Histrionicus histrionicus*) are inextricably linked to nearshore marine environments during the nonbreeding portion of the annual cycle throughout their holarctic range. Adults leave coastal areas only for a few summer months when they migrate to fast-moving streams to nest and raise

broods. Despite the importance of nearshore areas for Harlequin Duck populations, fine scale winter habitat associations rarely have been quantified.

In March 1989, the *Exxon Valdez* ran aground, spilling nearly 42 million L of oil into Prince William Sound, a wintering area for approximately 14,000 Harlequin Ducks. As much as 40% of the spilled oil was deposited in intertidal and shallow subtidal zones of Prince William Sound (Wolfe et al. 1994), the areas used by Harlequin Ducks. Although much of the oil degraded and dissipated within a few years of the spill, some residual oil was still present in these areas through at least 1997 (Hayes and Michel 1999). Immediate bird mortality from the *Exxon Valdez* oil spill was high (Piatt et al. 1990) and more than 1,000 Harlequin Ducks were estimated to have died as an immediate and direct result of the spill (J. Piatt, U.S. Geological Survey, pers. comm.). Furthermore, there have been concerns about continued effects of the *Exxon Valdez* oil spill on Harlequin Duck populations and lack of full population recovery (Esler et al. 2000).

We studied Harlequin Duck habitat associations in Prince William Sound during winter to identify environmental variables that relate to Harlequin Duck densities and to assess the status of Harlequin Duck populations following the *Exxon Valdez* oil spill. Evaluation of Harlequin Duck population recovery from the oil spill has been constrained by a paucity of prespill data from winter, the season of highest abundance of Harlequin Ducks in Prince William Sound and likely the period of formation of core subpopulations from a population structure perspective (Cooke et al. 2000). For this study, we adopted a control-impact study design to assess potential oil spill effects, in which we compared densities of Harlequin

Ducks between oiled and unoled areas, recognizing the need to control for intrinsic area differences (Wiens and Parker 1995). Lower densities than expected on oiled areas (after accounting for other environmental factors) could result from either failure to recover from immediate population impacts or from continuing deleterious effects of the spill; either case would lead to an interpretation of lack of full population recovery.

## **Methods**

### **Study Area**

Study locations were within oiled and unoled areas of Prince William Sound, Alaska. The oiled study area included 75.7 km of shoreline within two bays on Knight Island, Herring Bay and Bay of Isles, which were heavily oiled by the *Exxon Valdez* spill. The unoled area was 74.1 km of shoreline in the Stockdale Harbor and Port Chalmers region of northwestern Montague Island, selected because of the close proximity to the oil spill zone.

Analyses of habitat associations were based on measurement of habitat attributes and Harlequin Duck densities at sampling sites within each study area. To select sites, the shoreline of each study area was divided into contiguous 200-m sections. From randomly selected start points, 216 sections (113 on Knight Island and 103 on Montague Island) were then systematically selected as sampling sites, resulting in coverage throughout each study area.

## Harlequin Duck Surveys

We surveyed Harlequin Duck numbers and distribution during 4-12 December 1995, 12-24 February 1996, 4-14 December 1996, and 14-23 February 1997, completing five replicates on Knight Island and seven on Montague Island. Surveys were conducted by boat with a two- or three-person team consisting of an operator/observer and at least one observer/data recorder. For all Harlequin Ducks observed within 200 m of the study area shoreline, we recorded flock sizes and mapped locations on mylar overlays of 1:15,000 aerial photos.

To estimate Harlequin Duck densities associated with each sampling site, we calculated the number of ducks detected during shoreline censuses within 200-m linear shoreline distance of the midpoint of each sampling site. Duck densities were expressed as the average number of birds associated with the sampling site over all replicate surveys. Harlequin Duck numbers were consistent across surveys (CV = 4.1% on Montague Island and 8.0% on Knight Island) and Harlequin Duck site fidelity is high (Robertson et al. 1999, Cooke et al. 2000), suggesting that average densities should be a robust indicator of Harlequin Duck use of each site. Replication and duration of surveys resulted in data collection over a range of tidal states and weather conditions in both areas, and thus any variation potentially related to these factors should not influence inter-area comparisons.

### **Habitat Attributes**

At each site, we measured several habitat variables, including: exposure - a description of wind and wave action, categorized as full exposure, partial exposure, and not exposed; dominant substrate - categorized as rocky (bedrock and boulder areas) and mixed (unconsolidated, i.e., various mixtures of sand, pebbles, and cobble); distance to stream mouth - straight line distance from the midpoint of the sampling site to nearest stream mouth categorized as < 200 m, 200-500 m, 500-1,000 m, and > 1,000 m; distance to reef - straight line distance from the midpoint of the sampling site to the nearest offshore reef (defined as covered at high tide but exposed at lower tides) categorized as 200-500 m, 500-1,000 m, and > 1,000 m; and intertidal slope - the average slope (in degrees) of the mussel zone. Observations with missing data for a habitat variable were excluded from habitat association models that included that variable.

### **Habitat Association Models**

We conducted general linear model analyses to assess relationships of habitat attributes (explanatory variables) to average Harlequin Duck densities (the response variable), using each sampling site as an observation. Scatterplots of Harlequin Duck densities by habitat and food variables indicated that distributions violated the assumption of linearity; square-root transformation of Harlequin Duck densities resolved this problem. Categorical variables were included as a set of indicator variables, with one level of each variable designated as the reference



level and, thus, not included in model selection procedures (Ramsey and Schafer 1997).

To select the model from which we drew inference, we used Mallows's  $C_p$  values to contrast all possible combinations of explanatory variables. Explanatory variables included all habitat parameters, their interactions with area, and an area (oiling history) term. This method of model selection uses the principle of parsimony to determine which model is best fit by the data (Burnham and Anderson 1998), avoiding assumptions and biases of traditional stepping (i.e., forward, backward, and stepwise) model selection procedures (Flack and Chang 1987). Using this approach to model selection, the model with the lowest  $C_p$  value is the one best supported by the data and, thus, provides the strongest inference. We interpreted inclusion of a given parameter in a selected model as evidence that the parameter was related to Harlequin Duck densities, after accounting for effects of other included parameters. Inclusion of the area term in the best-fitting model would suggest that oiling history was related to Harlequin Duck densities after accounting for any effects of habitat attributes and differences in effects of habitat attributes between areas.

### **The Role of Food**

Harlequin Ducks in marine areas eat intertidal and shallow subtidal benthic invertebrates, particularly amphipods, limpets, snails, chitons, and mussels (Goudie and Ankney 1986). We sampled Harlequin Duck prey in each area at a systematically selected subset of 15 of the sampling sites. Because of generally

low densities of Harlequin Ducks on Knight Island, four additional sites with relatively higher Harlequin Duck densities were selected to ensure that sampling represented the full range of Harlequin Duck densities. Similarly, four sites with moderate to low duck densities were added on Montague Island.

To sample intertidal blue mussels (*Mytilus trossulus*), we removed all mussels from within 10 500-cm<sup>2</sup> quadrats placed in the mussel zone of each site. Ash-free dry mass of each mussel 5-25 mm in length was estimated based on predictive equations of biomass by length (Holland-Bartels 2000). Samples of other invertebrate prey (limpets, chitons, lacunid snails, littorine snails, other snails, amphipods, and other crustaceans) were obtained at six intertidal and shallow subtidal locations within each prey sampling site. All epifauna were removed from a 0.25-m<sup>2</sup> quadrat at each location. Ash-free dry weights of each prey item < 25 mm in length were determined using a muffle furnace.

For data analyses, prey data were included in four forms: total food biomass density - the combined average biomass densities (g per 100 m<sup>2</sup>) of mussels and other prey items; total food abundance - an estimate of the biomass (kg ash-free dry mass) of all food types within the 200-m sampling site, based on expansion of food biomass densities to the prey sampling areas; food biomass density without mussels - we also used biomass density estimates excluding mussels because biomass estimates of mussels were considerably higher (usually more than an order of magnitude) than other prey types, yet they constitute a relatively small part of the diet of Harlequin Ducks; and food abundance without mussels - similarly, we used prey abundance estimates excluding mussels.

To examine effects of prey on Harlequin Duck distributions, we assessed additional variation in duck densities related to food variables after accounting for habitat and area effects. We regressed residuals (observed Harlequin Duck densities - predicted densities) from the best-fitting habitat association model against the four measures of prey abundance and density.

## **Results**

Harlequin Duck densities were considerably higher at unoiled Montague Island ( $3.0 \pm 0.2$ ; average ducks per 400 m shoreline  $\pm$  SE) than at oiled Knight Island ( $0.6 \pm 0.1$ ). Some aspects of the habitat were distinctly different between Montague and Knight Islands, including intertidal slope ( $5.8 \pm 0.4$  and  $25.5 \pm 1.7$  degrees, respectively) and dominant substrate (37.9% and 73.5% rocky, respectively). On both areas, Harlequin Ducks were almost always observed in intertidal and shallow subtidal habitats very close to shore.

### **Habitat Association Models**

In the best-fitting model (Table 1), Harlequin Duck densities were positively related with having an offshore reef within 500 m, a stream within 200 m, and full exposure. The main effect of mixed substrate also had a positive parameter estimate, although there was a larger negative interaction of area by mixed substrate, suggesting that Harlequin Duck densities were positively associated with mixed substrate on Montague Island and negatively associated on Knight Island (Table 1). The rest of the top five models (those with the next four lowest

Table 4.1. Results of general linear model analyses to evaluate relationships of Harlequin Duck densities (square-root transformed) in Prince William Sound, Alaska, winters 1995-1997, with habitat attributes and history of oil contamination by the 1989 *Exxon Valdez* oil spill. The parameter estimates ( $\pm$ SE) are from the best-fitting model, based on comparisons of all possible combinations of habitat attribute variables, habitat by area interactions, and an area (history of oil contamination) term.

Response variable	$R^2$	Explanatory variable	Parameter estimate
Ducks per 400 m	0.45	Intercept	$1.17 \pm 0.12$
		Reef 200-500 m <sup>a</sup>	$0.51 \pm 0.15$
		Stream 0-200 m <sup>a</sup>	$0.34 \pm 0.14$
		Full exposure <sup>a</sup>	$0.45 \pm 0.12$
		Mixed substrate <sup>a</sup>	$0.32 \pm 0.14$
		Mixed substrate $\times$ Area <sup>b</sup>	$-0.48 \pm 0.18$
		Area <sup>b</sup>	$-0.69 \pm 0.12$

<sup>a</sup>Parameter estimate is in relation to all other levels of the categorical variable.

<sup>b</sup>Reference value for area is unoiled Montague Island; parameter estimates are interpreted as effects on oiled Knight Island.

Mallow's  $C_p$  values) also included the terms from the best-fitting model, indicating their importance for explaining variation in Harlequin Duck densities.

### **Effects of History of Oil Contamination**

The area term was included in the best-fitting model and had a large, negative parameter estimate (Table 1). In other words, duck densities were lower on oiled Knight Island than unoiled Montague Island (the reference level for the area term) after accounting for effects of habitat attributes and differences in these attributes between areas, which we interpret as evidence that history of oil contamination was related to Harlequin Duck densities. All of the top five models included the area term. Also, a more complicated analysis of our data, in which the area term was added after selection of models including only habitat variables, found an exactly concordant result - oiling history was strongly and negatively related to Harlequin Duck densities (Holland-Bartels 2000).

### **The Role of Food**

Duck density residuals were not related to total food abundance ( $R^2 < 0.01$ ,  $F_{1,30} = 0.02$ ,  $P = 0.89$ ), total food biomass density ( $R^2 < 0.01$ ,  $F_{1,31} = 0.03$ ,  $P = 0.87$ ), or food abundance without mussels ( $R^2 = 0.04$ ,  $F_{1,36} = 1.52$ ,  $P = 0.23$ ). Food biomass density without mussels was positively correlated with duck density residuals ( $R^2 = 0.17$ ,  $F_{1,37} = 7.83$ ,  $P = 0.01$ ). However, the amount of variation explained was low and the relationship was highly influenced by a single observation (Fig. 1), a site on oiled Knight Island that was nonsystematically selected to represent high duck densities and which also had high densities of

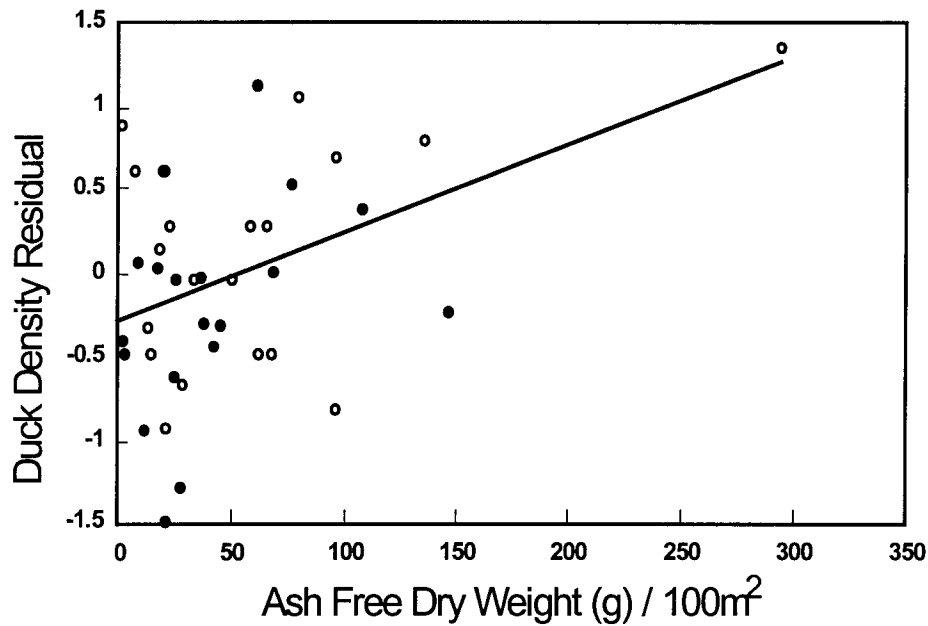


Figure 4.1. Linear relationship of residuals of Harlequin Duck densities (ducks/400 m shoreline; square-root transformed) from a general linear model of habitat associations against prey biomass density. Open circles represent Knight Island (oiled) study sites and closed circles represent Montague Island (un-oiled) sites.

subtidal foods (especially snails and amphipods); without this observation, the relationship was nonsignificant ( $R^2 = 0.07$ ,  $F_{1,36} = 2.62$ ,  $P = 0.11$ ). Taken together, these analyses suggest that variation in food explained little variation in duck densities beyond that explained by habitat attributes.

## Discussion

### Habitat Relations to Harlequin Duck Winter Densities

We assume that habitat associations of Harlequin Ducks that we observed were related to habitat profitability and reflected, to some degree, solutions to the optimization process of balancing benefits of habitats against detrimental aspects (Abrahams and Dill 1989, Guillemette et al. 1993). This balance is influenced by ecological characteristics of the species (Hilden 1965), which in the case of Harlequin Ducks include a life history requirement for high winter survival and high levels of winter philopatry.

Few other studies have quantified winter Harlequin Duck habitat associations. Goudie and Ankney (1988) documented that Harlequin Ducks were closer to shore and used reefs more than other sea duck species in Newfoundland. Harlequin Duck winter habitats have been qualitatively characterized and consistently described as being very close to shore and in a varied mix of substrates (Vermeer 1983), in agreement with our findings. We found strong positive relationships between Harlequin Duck densities and full exposure, occurrence of nearby streams, and occurrence of nearby reefs. Presence of a stream may influence prey distribution and provide fresh water to reduce osmotic stress for birds that ingest salts while feeding on marine invertebrates (Nyström and Pehrsson 1988). Reefs likely serve as safe resting sites and also offer intertidal foraging opportunities.

Harlequin Duck habitat use and life history are inextricably linked. Among ducks, Harlequin Ducks are relatively long-lived and have low and variable annual productivity (Goudie et al. 1994), a life history that requires high survival. High survival, in turn, depends on selection of stable and predictable habitats. On a broad scale, coastal habitats are thought to offer more stable wintering environments for waterfowl than inland sites (Diefenbach et al. 1988). Within coastal habitats, Harlequin Ducks occupy the productive intertidal and shallow subtidal zones. Goudie and Ankney (1986) described Harlequin Ducks as living near an energetic threshold as a result of their small body size and relatively harsh wintering environments. Consequently, Harlequin Ducks must forage nearly continuously during daylight hours of winter (Goudie and Ankney 1986). The habitat associations that we documented are consistent with this foraging strategy. Use of shallow water reduces dive and search times for more efficient foraging (Guillemette et al. 1993). Use of areas near streams and reefs may reduce energetic costs and time of transit between foraging areas and other resources (e.g., fresher water, roost sites). In summary, Harlequin Ducks must use habitats that predictably allow them to meet daily energy costs within their time-limited foraging regime, while minimizing risk of mortality in concordance with their life history requirement for high survival probabilities.

### **Effects of History of Oil Contamination**

We found that after accounting for effects of habitat attributes, history of oil contamination from the *Exxon Valdez* spill was related to Harlequin Duck



densities, with densities lower on oiled Knight Island than would be predicted based on the habitat attributes that we measured. Our data were consistent with a hypothesis that Harlequin Duck populations were not fully recovered from the oil spill.

Evidence from other studies supports a hypothesis that Harlequin Duck populations experienced continued effects of the *Exxon Valdez* oil spill during the course of this study. Trust et al. (2000) concluded that Harlequin Ducks and the ecologically similar Barrow's Goldeneye (*Bucephala islandica*) continued to be exposed to oil through 1998, as indicated by higher induction of cytochrome P450 1A in oiled areas than unoiled areas. Also, Harlequin Duck adult female survival during winters 1995-1998 was lower on oiled areas than unoiled areas (Esler et al. 2000), and laboratory studies support logical links between reduced survival rates and oil exposure (Holmes et al. 1979). Because population dynamics of birds with life histories like Harlequin Ducks are particularly sensitive to variation in adult female survival (Goudie et al. 1994, Schmutz et al. 1997), lower survival on oiled areas may have led to population declines (Rosenberg and Petrula 1998) and hence lower densities on oiled areas than predicted, as found in this study. Harlequin Duck populations have relatively low intrinsic growth rates (Goudie et al. 1994), so full recovery (i.e., duck densities at levels predicted from intrinsic habitat attributes) likely will not occur until long after deleterious effects of the oil spill have ceased.

Day et al. (1997) studied habitat use by birds in Prince William Sound during the period immediately following the *Exxon Valdez* spill (1989-1991) and

found no oil spill effects on Harlequin Ducks during winter. Why were our results different from those of Day et al. (1997)? First, because deleterious effects of the oil spill continued through the period of our study and until at least 1998 (Rosenberg and Petrula 1998, Esler et al. 2000, Trust et al. 2000), differences in Harlequin Duck abundance relative to oil contamination may have been more pronounced during our study than during the studies of Day et al. (1997). Also, Day et al. (1997) used bays as sampling units and characterized habitats at the scale of the entire bay, presumably by necessity due to their broader study question to look at all marine birds over a wider geographic area. Our study demonstrated that Harlequin Ducks respond to much smaller scale variations in habitat attributes. Harlequin Ducks exhibit high fidelity to specific shoreline segments (Robertson et al. 1999, Cooke et al. 2000), therefore, we were able to account for differences in environmental attributes at the scale that Harlequin Ducks select habitats before testing for relationships to history of oil contamination, allowing for a finer scale and presumably more powerful test.

### **The Role of Food**

Food may influence the distribution and abundance of some sea ducks (Nilsson 1972, Guillemette et al. 1993). In the context of the *Exxon Valdez*, strong relationships between Harlequin Duck densities and food would indicate food limitation as a possible mechanism for lack of population recovery. However, we found that food explained little variation in duck densities beyond habitat attributes and area effects.

Foraging characteristics of Harlequin Ducks suggest that they may be more time-limited than food-limited. Energetic requirements of this small-bodied sea duck necessitate nearly continuous feeding during daylight hours of winter and a generalist diet that includes many common benthic invertebrates (Goudie and Ankney 1986). This foraging strategy, particularly in association with high levels of winter site fidelity (see below), suggests that food may be predictably abundant, and the crux for Harlequin Ducks is to maximize energy intake during a short daily foraging period. Other authors (Nilsson 1972) have found that food exploitation by some wintering diving ducks was small relative to standing crop; we suggest that this is likely the case for Harlequin Ducks.

### **Significance of Philopatry**

A growing body of data suggests that Harlequin Ducks exhibit high philopatry throughout their annual cycle (Cooke et al. 2000, Robertson et al. 2000). Harlequin Duck winter habitat use is likely influenced by strong philopatry (Cooke et al. 2000), which reflects high stability of nearshore environments coupled with advantages of philopatry, including site familiarity and interannual pair reunion (Robertson and Cooke 1999, Smith et al. 2000).

From the perspective of oil spill recovery, high winter philopatry suggests that if residual oil spill damages exist, birds from oiled areas are vulnerable to chronic and cumulative spill effects as they return to those areas each year. Also, if dispersal and movements among areas are limited, recovery of groups of birds in oiled areas must occur largely through production and recruitment specific to

that group and numbers are not bolstered through immigration. Lower densities than expected on oiled areas detected in this study may be a result of one or both of these processes.

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## CHAPTER 5

HARLEQUIN DUCK POPULATION RECOVERY FOLLOWING THE *EXXON*  
*VALDEZ* OIL SPILL: PROGRESS, PROCESS, AND CONSTRAINTS

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### Abstract

As part of restoration programs following the 1989 *Exxon Valdez* oil spill in Prince William Sound, Alaska, we assessed the status of recovery of harlequin duck (*Histrionicus histrionicus*) populations during 1995-1998 and evaluated potential constraints to full recovery, including exposure to residual oil, food limitation, and intrinsic limitations on population recovery rates unrelated to the oil spill. In this paper, we synthesize the findings from our studies 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 were not fully recovered and, further, continued to show deleterious effects of the oil spill as much as 9 years after the spill, in contrast to the conventional paradigm that oil spill effects on bird populations are short-lived. Our conclusion was based on the findings that, through at least 1998: (1) elevated cytochrome P450 induction on oiled areas indicated continued exposure to oil, (2) adult female winter survival was lower on oiled than unoiled areas, (3) fall population surveys indicated declines in oiled areas, and (4) densities were lower than expected on oiled areas, after accounting for habitat effects. Based on hypothesized links between oil contamination and population demography, we suggest that harlequin duck population recovery may be constrained by continued oil exposure and also conclude that full recovery likely will be further delayed by the time necessary for intrinsic population growth to allow return to pre-spill numbers following cessation of residual oil spill effects. Although many wildlife species may have been



unaffected by the *Exxon Valdez* oil spill, or recovered quickly from any effects, harlequin duck life history characteristics make them susceptible to both initial and long-term oil spill effects. In a broader context, these results suggest that populations of harlequin ducks, and other birds with similar life history traits, are vulnerable to both long-term effects of catastrophic oil spills and effects of chronic, low-level oil pollution.

### Introduction

Harlequin ducks (*Histrionicus histrionicus*), like most sea ducks (tribe Mergini), are well-adapted to existence in northern marine systems. Harlequin ducks spend most of the year in marine habitats (Robertson and Goudie 1999), where they are inextricably linked to the nearshore environment, occurring in intertidal and shallow subtidal zones where they forage on benthic invertebrates (Goudie and Ankney 1986).

Aspects of harlequin duck ecology make their populations particularly susceptible to perturbations of their wintering environment. Harlequin ducks, like many sea ducks, employ a life history in which variable and generally low annual productivity is compensated by relatively high adult survival and, thus, long reproductive life spans (Goudie et al. 1994). This type of strategy evolves under conditions of predictable and stable nonbreeding environments, which are required to ensure adult survival (Stearns 1992). Also, harlequin ducks, because of their small body size, are thought to exist near an energetic threshold during winter, with little flexibility for increasing caloric intake or relying on stored reserves

(Goudie and Ankney 1986). While this strategy may be tenable under predictable and stable conditions, it does not accommodate perturbations that result in either decreases in energy acquisition or increases in metabolic costs. Finally, strong site fidelity, such as that exhibited by wintering harlequin ducks, evolves in predictable and stable habitats (Johnson and Gaines 1990, Robertson and Cooke 1999, Cooke et al. 2000) and does not facilitate movement to undisturbed areas if habitat quality becomes degraded (Hilden 1965, Cooch et al. 1993). Coastal habitats offer relatively stable and predictable habitats for wintering waterfowl (Diefenbach et al. 1988) and harlequin ducks (and most other sea ducks) have evolved life histories based on predictable, although somewhat harsh, conditions on their wintering areas. While adaptive under natural conditions, these life histories lead to vulnerability to anthropogenic perturbations of wintering habitats.

The release of approximately 42 million liters of crude oil into Prince William Sound by the 1989 *Exxon Valdez* oil spill (EVOS) represented a significant perturbation to harlequin duck nonbreeding habitat. As much as 40% of the spilled oil was deposited in intertidal and subtidal zones of Prince William Sound (Galt et al. 1991, Wolfe et al. 1994), the habitats used by harlequin ducks, and some residual oil persisted in these areas more than 8 years after the oil was spilled (Hayes and Michel 1999). Vulnerability to oil spill effects is exacerbated by the harlequin duck's diet, which consists of a variety of intertidal and shallow subtidal benthic invertebrates (Vermeer 1983, Goudie and Ankney 1986, Gaines and Fitzner 1987, Goudie and Ryan 1991, Patten et al. 1998). Oil constituents accumulate in bottom sediments and subsequently, benthic invertebrates (Woodin

et al. 1997), suggesting that food could be a potential route of oil contamination of harlequin ducks. Studies have documented hydrocarbons in harlequin duck prey from immediately post-spill through 1995 (Babcock et al. 1996, Boehm et al 1995, Patten et al. 1998, Short and Babcock 1996, Wolfe et al. 1996).

In this paper, we examine effects of the EVOS on harlequin duck populations and consider potential constraints to full population recovery. We recognize that populations of other bird species may respond differently to perturbations generally, and the EVOS in particular (Bowman et al. 1995, 1997), and we do not intend this work to be interpreted as a typical bird response to oil spill impacts. We focus explicitly on harlequin duck populations because of concern generated by their vulnerability.

This paper is a synthesis document, with the goal of assessing harlequin duck population recovery from the EVOS. The first objective of this paper is to review data that provide insight into population injury and recovery status. The second objective is to evaluate mechanisms potentially constraining full recovery including (1) intrinsic limitations on population growth rates precluding return to prespill numbers despite lack of continuing oil spill effects, (2) continued oil exposure at levels that have population consequences, and (3) food limitation due to oil spill-related reductions in prey that either lowers carrying capacity or reduces health and survival of individuals.

Data incorporated in this synthesis of harlequin duck population recovery from the EVOS were gathered from journal publications and *Exxon Valdez* Oil Spill Trustee Council reports, both from our own studies conducted from 1995-1998

and from other research and monitoring programs that collected post-spill harlequin duck data in PWS. We also reviewed published studies of harlequin duck ecology conducted throughout their range and considered implications of these results for understanding constraints to full recovery from the EVOS. Primary sources cited herein should be consulted for detail; our intent is to provide an overview of harlequin duck population recovery based on a summary of available information.

The EVOS was a one-time perturbation without replication and, as in the case of wintering harlequin ducks, with few prespill data to compare. Much of the harlequin duck research following the EVOS, including our studies, was designed to contrast impact and reference areas, while attempting to minimize or account for differences between areas that might confound interpretation of impact effects (Wiens and Parker 1995).

This paper focuses on harlequin duck populations in Prince William Sound (PWS), the area most affected by the EVOS. PWS is prime harlequin duck nonbreeding habitat, supporting approximately 14,000 birds (Lance et al. 1999), although it is one of the farthest north wintering areas within the species' range (Robertson and Goudie 1999). Although some reproduction occurs in streams feeding into PWS (Crowley 1999), the bulk of reproduction by harlequin ducks that winter in PWS occurs outside of PWS, although breeding locations have not been determined and could conceivably be throughout the vast breeding range in Alaska and the Yukon Territories (Robertson and Goudie 1999). Therefore, we concentrated our review on the nonbreeding portion of the annual cycle when, as

described above, harlequin duck populations are particularly vulnerable and EVOS effects are most likely to occur.

### **Injury and Recovery Status**

In this section, we review a broad range of studies conducted following the EVOS that lend insight into harlequin duck population injury and defining recovery status. We have categorized these as studies of population status, adult female survival, body mass variation, and serum chemistry variation. Implications of these studies for evaluating hypotheses about mechanisms constraining recovery are considered in succeeding sections.

#### **Population Status**

A number of studies are relevant for evaluating harlequin duck population status, most of which were conducted outside of our own research program. These measured a range of population parameters, including direct mortalities, abundance, trends, densities, age and sex ratios, and habitat use. The rationale of these studies was that measures of population status are indicative of population health (although see Paine et al. [1996], who suggested that demographic parameters may be better indicators of injury and recovery status). Following this rationale, we would predict that measures of population status would be comparable between oiled and unoiled areas once full population recovery had occurred.

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 large

proportion of dead birds that were not recovered (Piatt and Ford 1996).

Immediately following the EVOS, 212 harlequin duck carcasses were recovered, mostly in PWS; the estimate of total harlequin mortality due to immediate effects of the EVOS was 1298 (J. Piatt, pers. comm.). This estimate indicates immediate population injury, but does not reflect any subsequent, longer-term effects of the EVOS.

The Alaska Department of Fish and Game (Patten et al. 1998) conducted damage assessment studies immediately following the EVOS, focusing on abundance and contaminant exposure. Patten et al. (1998) found hydrocarbon metabolites in some harlequin ducks collected from oiled areas in 1989 and 1990, consistent with potential for injurious effects of oil exposure. Also, numbers of adults and broods were lower in oiled areas of PWS than in unoiled areas (Patten et al. 1998); however, these studies did not account for intrinsic area effects, which may explain observed differences. For example, lower numbers of broods in oiled areas do not necessarily indicate that harlequin productivity was affected by the EVOS because (1) most of the core wintering population migrates outside of PWS to breed (Esler, unpubl. data), (2) within PWS, breeding habitats used by harlequin ducks (Crowley 1994) are found primarily in eastern, unoiled areas (Rosenberg and Petrula 1998), and (3) prepill records of broods in oiled areas could have been misidentified, flightless birds during wing molt (Rosenberg and Petrula 1998). However, no data have been collected to explicitly examine reproductive effort of harlequin duck subpopulations from oiled areas, so we can

not preclude the possibility that the EVOS had, or continues to have, deleterious effects on harlequin duck reproduction.

The U. S. Fish and Wildlife Service has conducted marine bird surveys in PWS since 1989 (Lance et al. 1999) during summer and winter. While these were not designed to estimate harlequin duck numbers or trends specifically, they do provide a long-term assessment of population status. For this paper, we consider only winter data from these surveys. Also, from 1995 to 1997, the Alaska Department of Fish and Game conducted surveys designed specifically to assess harlequin duck population status (Rosenberg and Petrula 1998). They surveyed during spring and fall and measured numbers, pair status, sex ratios, age composition, and molt chronology in oiled and unoled areas. These surveys have more power for estimating abundance and trends than U. S. Fish and Wildlife Service surveys (Rosenberg and Petrula 1998), and we feel that their fall data provided the best estimates of population trends for nonbreeding populations during the course of our research (1995 - 1998). Winter U. S. Fish and Wildlife Service surveys (Lance et al. 1999) conducted through 1998 found that winter harlequin duck population trends did not differ ( $P = 0.77$ ) between oiled and unoled areas of PWS. Lance et al. (1999) interpreted this result as evidence of lack of recovery, under the premise that an EVOS-injured population should have a higher growth rate than reference populations for recovery to be occurring. However, their data indicated that harlequin duck populations were growing at approximately 5% annually on oiled areas ( $P = 0.08$ ), a finding consistent with ongoing recovery. Alaska Department of Fish and Game surveys (Rosenberg and

Petrula 1998) indicated that fall numbers declined ( $P = 0.023$ ) on oiled areas from 1995 through 1997, whereas numbers were stable on unoiled areas, consistent with a hypothesis of continued EVOS injury. Measures of other population attributes (age ratios, sex ratios, and phenology) did not differ between oiled and unoiled areas (Rosenberg and Petrula 1998).

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 across a range of oil contamination levels. While designed to examine all marine birds, these studies draw 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 populations showed negative relationships with oiling intensity during 1989 and 1990, but not in 1991, and Murphy et al. (1997) concluded that summer abundance did not differ from prespill numbers.

As part of our research, we examined correlates of harlequin duck densities within oiled (Bay of Isles and Herring Bay) and unoiled (Montague Island) study areas (Fig. 5.1), including habitat characteristics and history of contamination by the EVOS (Esler et al. 2000a). Habitats within PWS are diverse,



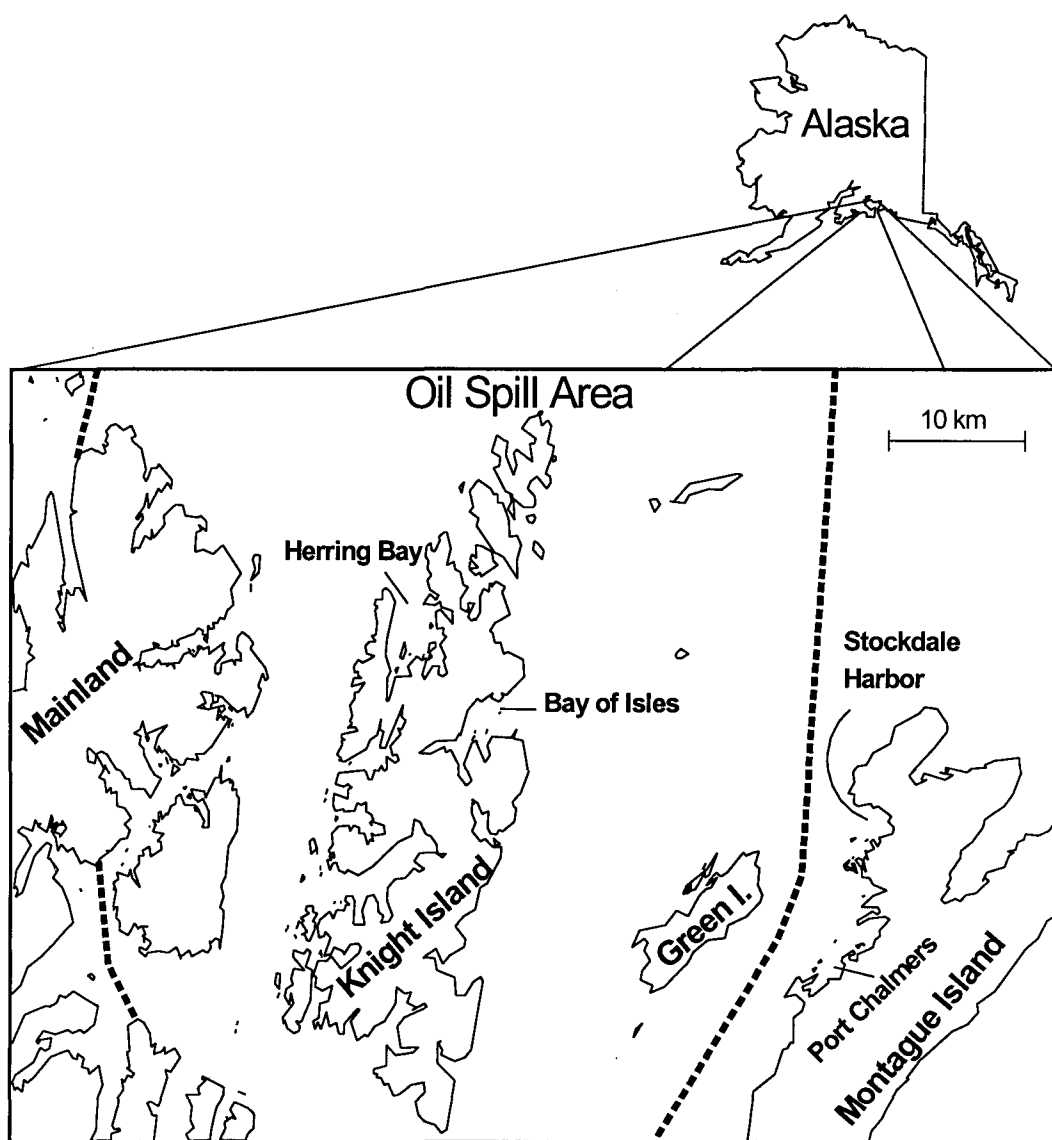


Figure 5.1. Study areas for the authors' harlequin duck studies in Prince William Sound, Alaska, 1995-1998.

making it necessary to segregate effects of oil contamination from other environmental factors (Wiens and Parker 1995). Lower densities than expected on oiled areas (after accounting for other factors) could result from either failure to

recover from the immediate population impact or from continuing deleterious effects of the EVOS; in either case, this result would be consistent with a lack of full population recovery. 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. After accounting for these habitat relationships and their interactions with area, oiling history was significantly ( $P = 0.001$ ) and negatively related to harlequin duck densities. These data are consistent with a hypothesis of lack of population recovery from the EVOS.

### **Adult Female Survival during Winter**

Within our research, we used radio telemetry to measure adult female survival during winter (Esler et al. 2000b), because (1) population dynamics of species with life history traits 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 likely sensitive to perturbations on wintering areas, which could be manifested as 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 found that the data strongly supported the inference that survival was lower in oiled areas than unoiled areas (Esler et al. 2000b). Kaplan-Meier estimates of winter survival were 76.6% (SE = 4.0) on oiled areas and 86.6% (SE = 3.2) on unoiled (Fig. 5.2a) and we estimated survival rates of 78.0% (SE =

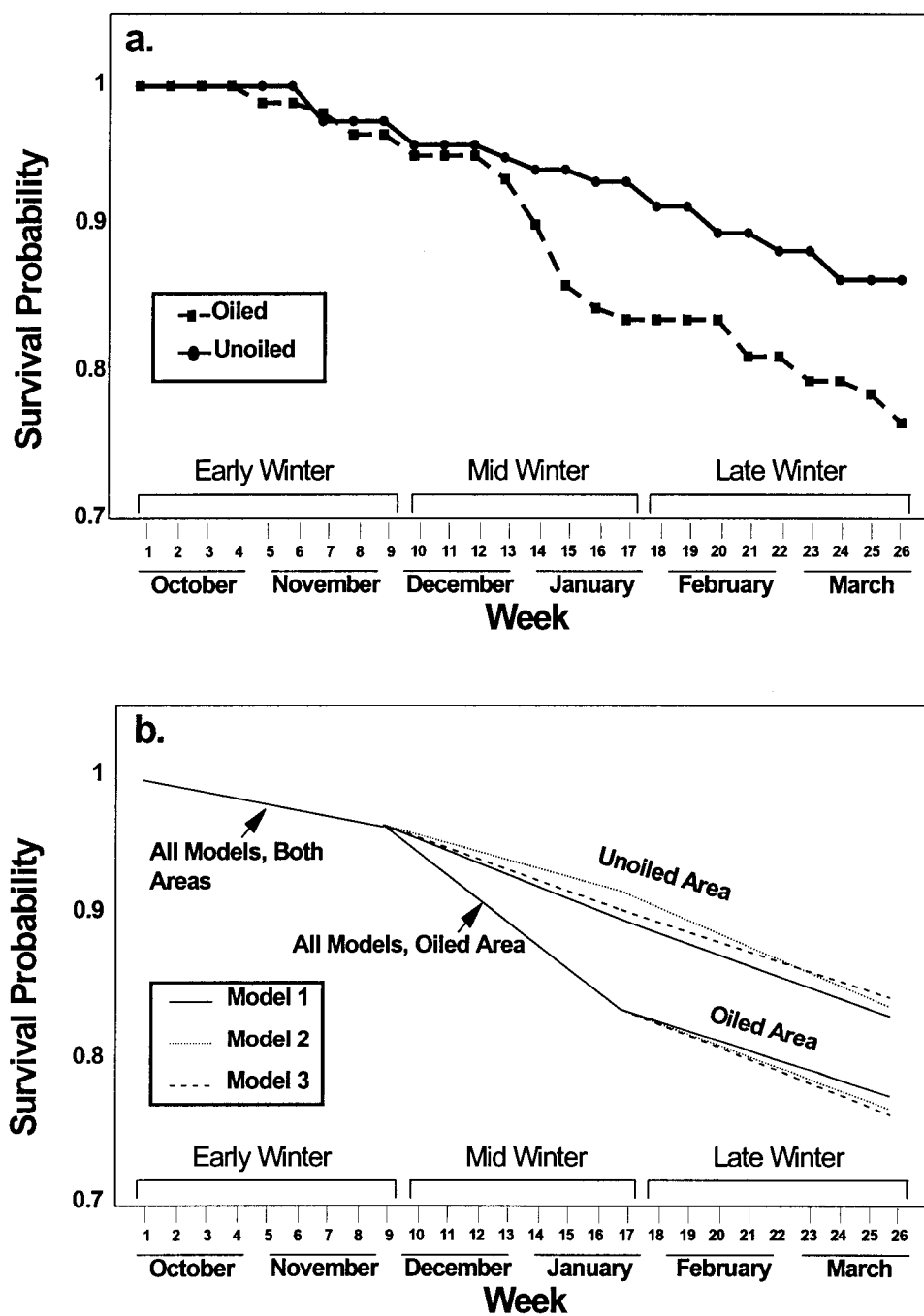


Figure 5.2. Winter survival probabilities for adult female harlequin ducks in Prince William Sound, Alaska, based on Kaplan-Meier estimates (top) and the 3 best-fitting reduced models (bottom). [from Esler et al. 2000b]

3.3%) and 83.7% (SE = 2.9%), respectively (Fig. 5.2b), using analyses based on information-theoretic methods (Burnham and Anderson 1998, White and Burnham 1999). We also determined that survival differences between oiled and unoled areas were more likely related to history of oil contamination than intrinsic differences (such as habitat, disease, climate, social influences, or predator densities). We incorporated survival estimates into a harlequin duck population model (Robertson 1997), holding all other parameters constant, to evaluate the effect of differences in survival on population dynamics. The estimate of annual population change ( $\lambda$ ) was 0.9464 for oiled areas (i.e., annual population declines of about 5.4%). For unoled areas,  $\lambda = 1.0054$ , suggesting an approximately stable population. These estimates were consistent with the Alaska Department of Fish and Game fall survey results (Rosenberg and Petrula 1998).

### **Body Mass and Composition Variation**

Body mass and composition often are used as indicators of individual and population health under the assumption that fitness increases with increases in energy reserves (with the corollary that animals are always striving to maximize their energy reserves). This assumption is likely untrue in a number of situations (King and Murphy 1985), i.e., optimal body mass may not be the maximum. 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 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 toxic 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 and winter as part of our research program (Holland-Bartels 2000) using general linear models to determine factors explaining variation in harlequin duck body mass and to evaluate any area differences after accounting for other significant explanatory variables. We used separate models for wing molt and winter and, within each season, separate models for each sex. We also compared estimated lipid and lean masses of female harlequin ducks captured during wing molt based on condition indices created from a sample of harlequin duck females collected during wing molt for which composition was measured using proximate analysis.

During wing molt, variation in female harlequin duck body mass was related to stage of wing molt, age, and year (Holland-Bartels 2000). After accounting for effects of these variables, females averaged ( $\pm$  SE) 9.6 g ( $\pm$  2.6 g) lighter on oiled areas than unoiled. Similarly, estimated body lipid averaged 2.5 g ( $\pm$  0.7 g) lower in oiled areas than unoiled. Like females, male body mass declined during wing molt. Average body mass differed by area, although unlike females, male body mass averaged 13.4 g ( $\pm$  4.5 g) higher in oiled areas than unoiled.

During winter, female body mass varied with season (mid versus late winter) and age (Holland-Bartels 2000); however, no area effect was detected.

Body mass of males also varied seasonally during winter and averaged 21.6 g ( $\pm$  8.7 g) higher in unoiled areas than oiled areas, consistent with a health effect of the EVOS.

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; we believe that this reflects high statistical power due to the large sample size of captured birds and has little biological meaning. The 21 g body mass difference between areas for male harlequin ducks during winter suggests potential residual EVOS effects; because the effect is relatively small (approximately 3% of average body mass) and because females captured during the same time on the same areas did not show a similar effect, we conclude that this is not strong evidence of an EVOS effect. However, see the section below regarding oil exposure for results of an analysis of body mass relationships to cytochrome P450 1A induction.

### **Serum Chemistry**

Like body mass, serum chemistry parameters may be useful for assessing differences in population health between areas. As part of our studies, we contrasted hematology and serum chemistry from adult female harlequin ducks captured during wing molt between oiled and unoiled areas (Holland-Bartels 2000) and found significant differences in total red blood cell count, sodium, and glucose. Although red blood cell count was significantly lower in birds in the oiled areas of Prince William Sound, there was no report of Heinz body anemia, as may occur

during acute exposure to oil (Leighton et al. 1983, Yamato et al. 1996). Also, packed cell volume and red blood cell indices (mean corpuscular volume, hemoglobin, and mean corpuscular hemoglobin concentration) did not differ. Sodium and glucose concentrations were significantly but moderately higher in birds from the oiled areas. Sodium and glucose levels could reflect a higher level of stress in birds living in oiled areas, but also could be a result of different durations of capture chases, handling times, or effects of recent adverse weather prior to capture. We conclude that these data are generally consistent with a hypothesis of no residual health effects of the EVOS.

### **Intrinsic Limitations on Population Growth Rates**

Harlequin Duck population recovery could be constrained under a scenario in which deleterious effects of the EVOS have ceased, yet populations have not yet fully recovered from initial oil spill population reductions due to the time necessary for intrinsic population processes to operate. 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 including relatively low annual productivity and long reproductive lifespans. Other waterfowl species with these

life history characteristics also have low population growth rates (Schmutz et al. 1997). These data suggest that harlequin ducks are susceptible to intrinsic growth rate limits to population recovery following cessation of any effects of the EVOS.

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 and these consistently indicated high molt and winter site fidelity and low dispersal (Breault and Savard 1999, Cooke et al. 2000, Robertson et al. 1999, Robertson et al. 2000). Also, Smith (2000) reported evidence that juvenile harlequin ducks accompany their mothers to wintering areas. These data indicate that groups of wintering harlequin ducks are largely demographically independent and that population recovery would occur largely by recruitment and would not be enhanced by immigration and, thus, would make population recovery from the EVOS more likely to be constrained by intrinsic limits to growth rates. We also examined data collected during our studies (Holland-Bartels 2000) to assess molt site fidelity based on recapture locations. Of 151 harlequin ducks recaptured during wing molt, 135 (89.5%) were in the same shoreline segment as during their original capture, 10 (6.6%) were in an immediately adjacent shoreline 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 were > 20 km from their original capture location. Larger scale movements may have occurred, but we feel that these were rare or we would have detected them, as we sampled broadly and intensively throughout western PWS. This body of data on



harlequin duck site fidelity and movements strongly suggests that their populations could be limited by low intrinsic recovery rates.

Lanctot et al. (1999) used genetic data to evaluate whether harlequin duck aggregations within the EVOS zone were demographically independent. DNA was obtained from blood samples of molting harlequin ducks from oiled and unoiled areas of PWS, the Kodiak Archipelago, and the Alaska Peninsula. Under this approach, differences in nuclear DNA allele frequencies or mtDNA haplotype frequencies among areas would be strong evidence that aggregations are demographically independent and, thus, intrinsic limitations on population growth rates could constrain population recovery. However, Lanctot et al. (1999) found that molting aggregations in PWS, 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 metabolic (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 cytochrome P450 1A (P450), which can indicate exposure to polycyclic aromatic hydrocarbon (PAH) constituents of crude oil, in harlequin ducks captured during winter 1998 in both oiled and unoiled areas.

In addition to oil-derived PAHs, certain polychlorinated biphenyl (PCB) congeners can induce cytochrome P450 systems. Therefore, we also measured congener-specific PCB concentrations in plasma from harlequin ducks wintering in PWS to contrast with P450 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 would be interpreted in light of other available data as a possible mechanism constraining full population recovery.

Liver 7-ethoxyresorufin-O-deethylase (EROD) activity of wintering harlequin ducks was higher in oiled areas (204.6 pmol/min/mg protein;  $n = 19$ ) than on unoiled Montague Island (70.7 pmol/min/mg protein;  $n = 18$ ;  $P < 0.001$ ; Fig. 5.3; Trust et al., 2000). This is strong evidence of continued exposure to *Exxon Valdez* oil, as background PAH concentrations in intertidal sediments and mussel tissues were negligible in PWS immediately prior to the EVOS (Short and Babcock 1996). Area differences in P450 induction were not explicable 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 are physiological and population consequences of this exposure.

We found that body mass of harlequin ducks during late winter was negatively related to EROD activity (Holland-Bartels 2000), suggesting potential physiological consequences of oil exposure. Waterfowl body condition has been shown to be affected by other contaminants, such as lead (Hohman et al. 1990).

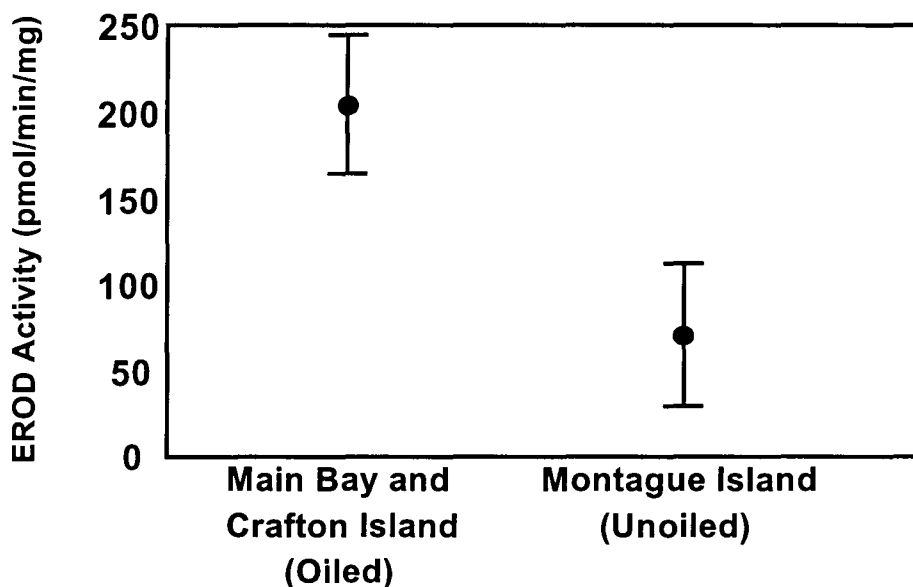


Figure 5.3. Comparisons of average ( $\pm$  95% confidence intervals) liver EROD activity of harlequin ducks captured from oiled and unoiled areas of Prince William Sound, Alaska, March and April 1998. [from Trust et al. 2000].

Further, survival of some wintering ducks has been demonstrated to vary with body condition (Conroy et al. 1989, Longcore et al. 1991, Bergan and Smith 1993), suggesting a link between contaminant exposure and reductions in survival.

### 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 2000). In turn, prey

reductions could lead to increased intra-specific 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, snails, chitons, and mussels (Vermeer 1983, Goudie and Ankney 1986, Gaines and Fitzner 1987, Goudie and Ryan 1991, Patten et al. 1998). Goudie and Ankney (1986) hypothesized that harlequin ducks consume a generalist diet 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 paired oiled and unoiled sites in intertidal and nearshore subtidal habitats shortly after the spill (Highsmith et al. 1996, Jewett et al. 1999). Numerically dominant taxa within several important harlequin duck prey groups (snails, limpets, mussels, and amphipods) were adversely affected by the oil spill. At oiled sites within a number of intertidal habitats in PWS, numbers of *Mytilus trossulus* (mussels), *Tectura persona* (limpets), and *Littorina sitkana* (snails), were reduced in the years following the EVOS (Highsmith et al. 1996). Similarly, several numerically dominant amphipod taxa (including Ischcryoceridae) were reduced at oiled sites in the nearshore subtidal zone (Jewett et al. 1999). Many of these differences in mean abundance at oiled and reference sites were no longer evident in 1993, suggesting that recovery of the intertidal and nearshore subtidal community was underway. However, the last reported values suggest

that there continued to be fewer individuals of some important prey at selected oiled sites at least through 1993 in the intertidal (Hooten and Highsmith 1996, Houghton et al. 1996) and through 1995 in the subtidal (Jewett et al. 1999). Reduced prey densities at oiled sites can be largely attributed to the direct toxic effects of oil or impacts associated with cleanup procedures (Boehm et al 1995, Wolfe et al 1996, Houghton et al 1996, Jewett et al. 1999). These results are consistent with food limitation of harlequin duck population recovery, at least within the few years immediately following the EVOS.

We estimated availability of harlequin duck prey items (Esler et al. 2000a) on oiled Knight Island (Bay of Isles and Herring Bay) and unoiled Montague Island study areas (Fig. 5.1) in summer 1997. Although prey availability may vary seasonally, we assumed that relative differences between study areas in summer would index relative winter prey abundance. We compared two metrics of food availability between areas: food biomass density and food abundance relative to duck abundance. Food biomass density was defined as average g ash-free dry weight per 100 m<sup>2</sup>; we used t-tests to compare food biomass densities between areas. Food abundance was estimated as density expanded to the area of the potential foraging area for each site. Average food abundance across sampling sites was divided by average number of harlequin ducks per sampling site to generate the metric describing food availability relative to duck abundance; variance was calculated for a ratio of two independent estimates (Seber 1973) and 2-tailed Z scores were calculated to compare areas (Snedecor and Cochran 1980). Biomass density and abundance comparisons were conducted for all food

Table 5.1. Average ( $\pm$  SD) biomass density and abundance of harlequin duck prey (amphipods, chitons, limpets, snails, and mussels < 25mm) at sites within Prince William Sound, Alaska, 1997.

Parameter	Montague Island	Knight Island	<i>P</i>
	(Unoiled)	(Oiled)	
Biomass density (g AFDW <sup>a</sup> /100 m <sup>2</sup> )	2030.76 ( $\pm$ 2077.18)	1964.13 ( $\pm$ 2474.37)	0.94 ( $t$ = 0.08)
Abundance (kg AFDW/duck)	51.75 ( $\pm$ 61.43)	100.48 ( $\pm$ 194.71)	0.81 ( $Z$ = 0.24)
Biomass density w/o mussels (g AFDW/100 m <sup>2</sup> )	45.89 ( $\pm$ 39.14)	42.80 ( $\pm$ 29.22)	0.80 ( $t$ = 0.251)
Abundance w/o mussels (kg AFDW/duck)	3.84 ( $\pm$ 4.71)	3.23 ( $\pm$ 5.72)	0.94 ( $Z$ = 0.08)

<sup>a</sup>Ash free dry weight.

items combined and also with mussels excluded because mussel abundance was much higher than for other prey species, yet they constitute a relatively minor part of the diet. Higher food densities or more food per duck on oiled areas than unoiled would be consistent with no evidence of food limitation. Comparable densities or quantities of food per duck between areas would be somewhat equivocal. Higher food densities or more food per duck on unoiled areas than oiled would be consistent with food limitation to population recovery. In 1997, food biomass densities were similar between oiled Knight Island and unoiled Montague Island study areas (Table 5.1). Also, on a per duck basis, food abundance was comparable between areas (Table 5.1). These data are somewhat equivocal, but generally consistent with a hypothesis of no food limitation to population recovery.

Also, food variables were incorporated into habitat association models to determine whether food biomass density or abundance were related to harlequin duck densities (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 abundance 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 predict that body mass would be lower in oiled

than unoiled areas if food was limiting recovery, although other factors also could cause body mass differences. Body mass data (see above) did not differ dramatically between areas, which would be predicted under conditions of food limitation.

## **Discussion**

### **Injury and Recovery Status**

We feel that the weight of evidence from post-spill harlequin duck research and monitoring supports the conclusions that: (1) harlequin duck populations were injured by the EVOS, (2) these populations have not fully recovered, and (3) deleterious effects of the EVOS were still evident as much as 9 years later. These conclusions are supported by differing fall population trends in oiled and unoiled areas (Rosenberg and Petrula 1998), lower densities than expected on oiled areas (Esler et al. 2000a), and differences in adult female survival between oiled and unoiled areas (Esler et al. 2000b). These results are internally consistent, i.e., predictions from each study are confirmed in the others. Differences in adult female survival offer a likely mechanism for differences in population trends between areas. Under these conditions (especially in light of high site fidelity), densities would be predicted to be lower in the oiled area where population declines were occurring. The adult female survival analysis is particularly important for our interpretation; it demonstrates not only potential for continued injury, but describes a mechanism that would lead to population declines and lack of full population recovery.



Not all studies fully support our conclusions. U. S. Fish and Wildlife marine bird survey data (Lance et al. 1999) suggested increasing numbers on oiled areas, consistent with ongoing population recovery, although these are statistically less powerful than Alaska Department of Fish and Game surveys (Rosenberg and Petrula 1998). Further, lack of differences in population trends between oiled and unoiled areas 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 a weak and uninformative measure. For example, occurrence of harlequin ducks in oiled areas likely reflects high site fidelity (Cooke et al. 2000) despite deleterious changes in habitat quality (Hilden 1965, Cooch et al. 1993). Occurrence in an area does not indicate a recovered population; populations could, in fact, be declining or a “sink” (Pulliam 1988). We agree with Paine et al. (1996) that measures of population 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 1989-1991, in contrast to our findings of lower densities on oiled areas than unoiled (Esler et al. 2000a). We speculate that this may be because deleterious effects of the spill occurred beyond the study period of Day et al. (1997) through at least our study period (Rosenberg and Petrula 1998, Esler et al. 2000b, Trust et al. 2000), thus density differences may have

been larger and more detectable during our study. Also, we collected harlequin duck abundance and habitat data at the scale that harlequin ducks use wintering sites (i.e., hundreds of meters reflecting specific shoreline segments; Robertson et al. 1999, Cooke et al. 2000) rather than at the scale of entire bays used by Day et al. (1997), which we presume would result in greater resolution and power to evaluate oil spill effects.

Results of pre- and postspill comparisons of summer abundance by Murphy et al. (1997) have limited inference for understanding dynamics of core wintering populations. Also, although they had high power for detecting a 50% postspill population decline, they did not report power of detecting smaller but biologically meaningful reductions (e.g., 10%). In fact, they reported estimates of 13.5%, 6.4%, and 11.9% reductions in harlequin duck numbers from prespill counts to 1989, 1990, and 1991, respectively, although these were not statistically significant.

Data regarding health and condition of captured birds did not suggest lack of recovery (with the exception of the relationship between P450 induction and winter body mass). However, differences in these parameters may be difficult to detect in wild populations, as significant changes may precede death by only a short period, particularly for animals in harsh environments. For example, body mass declines in oiled mallards faced with other environmental stressors were detectable only within 2 weeks prior to death (Holmes et al. 1979). Because dead animals are not available to sample, detectable differences in health parameters may be unlikely (A. Rebar, pers. comm.; Holland-Bartels 2000).

We believe that our conclusion of lack of full population recovery is supported by the data that are most powerful for assessing population status. Below we consider the potential mechanisms involved in lack of full population recovery.

### **Intrinsic Limitations on Population Growth Rates**

Aggregations on wintering areas constitute core subpopulations from a population structure standpoint (Cooke et al. 2000). Winter site fidelity of harlequin ducks is high (Robertson 1997, Cooke et al. 2000) and pair formation occurs on the wintering areas (Gowans et al. 1997, Robertson et al. 1998). Because dispersal is limited, recovery of groups of birds in oiled areas must occur primarily through recruitment specific to that group (i.e., immigration from other areas does not contribute much to population change). Thus, factors that affect wintering aggregations likely are impacting subpopulations that are largely distinct demographic units, suggesting that harlequin ducks are susceptible to constraints to population recovery due to intrinsic limits to population growth rates.

However, limitations on population growth rate, as we have defined it can not be invoked as the primary constraint to harlequin duck population recovery until lingering effects of the EVOS are gone and the population in the oil spill zone can achieve positive growth; this does not appear to be the case through 1998. However, once freed from other constraints to recovery (see below), recovery of populations likely will be limited by the time necessary for intrinsic rates of increase to operate (Goudie et al. 1994). Because it is not clear what naturally

regulates harlequin duck populations, nor the life stage where regulation or limitation occurs, it is difficult to predict recovery times of an injured core winter population.

Results from genetic studies offer some good news for harlequin duck populations. Levels of dispersal, either historical or contemporary, have resulted in subpopulations within the oil spill zone that are not genetically distinct (Lancot et al. 1999), i.e., the EVOS does not threaten a unique genetic resource. Also, these results may reflect low levels of juvenile dispersal that we were unable to detect; if this is the case, population recovery could be enhanced by some immigration.

### **Continued Exposure to Oil**

A growing body of evidence indicates that PAHs from residual *Exxon Valdez* oil were likely responsible for the observed P450 induction in oiled areas of PWS in sea ducks (Trust et al. 2000) and several other vertebrates (Marty et al. 1997, Woodin et al. 1997, Holland-Bartels 2000). A critical question is whether oil exposure could cause physiological challenges that affect demographic properties which, in turn, have population level consequences.

As described above, our data on adult female winter survival offer a likely mechanism for lack of population recovery. Although the survival differences between oiled and unoled areas may appear small, harlequin duck population dynamics are particularly sensitive to changes in adult female survival (Goudie et al. 1994) as their life history strategy is oriented towards long reproductive life spans (Stearns 1992). We speculate that deleterious effects of oil exposure

(Leighton 1993, Jenssen 1994) could affect harlequin duck health and subsequent survival and, in fact, suggest that continued oil exposure is likely the primary mechanism constraining full population recovery.

Most lab studies have shown that ducks, at least 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 seems to be a more appropriate analog for wild harlequin ducks, which exist under relatively harsh winter conditions with little flexibility for accommodating additive stresses (Goudie and Ankney 1986).

The divergence of survival probabilities between oiled and unoiled areas during midwinter (Fig. 5.2) is consistent with a 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 time foraging (Fischer 1998, Goudie and Ankney 1986 ). PWS is one of the farthest north wintering areas for harlequin ducks (Robertson and Goudie 1999); thus, daylight available for foraging is particularly limited. Thus, we suggest that

observed differences in survival and populations trends may be linked to observed differences in contaminant exposure.

Oil exposure could occur through consumption of contaminated prey. In the marine environment, oil constituents accumulate in bottom sediments and subsequently, benthic invertebrates (Woodin et al. 1997). Studies have documented hydrocarbons in harlequin duck prey from immediately post-spill through 1995 (Babcock et al. 1996, Boehm et al 1995, Patten et al. 1998, Short and Babcock 1996, Wolfe et al. 1996). Also, contamination could occur through external contact with residual oil; surface sheening was observed in some areas of PWS during the same period as our studies (Hayes and Michel 1999), suggesting that this also could be a potential route of exposure. Metabolic consequences of external oiling are well documented (Jenssen 1994) and could certainly result in increased mortality.

### **Food Limitation**

Most evidence suggests that food availability or quality is not limiting harlequin duck population recovery. Recovery of many components of benthic invertebrate communities, lack of a strong relationship between harlequin duck densities and food biomass density or abundance, comparable food biomass density and abundance per duck between areas, and similar body masses between areas generally support this conclusion.

Interpretation of food data is hampered by a lack of understanding of harlequin duck foraging strategies and the role of winter food abundance, density,

or quality in harlequin duck population regulation or limitation. Further, we have no evidence documenting causal, mechanistic relationships between winter food and carrying capacity. Thus, body mass data provide perhaps the strongest evidence against food limitation. Because harlequin duck body masses across seasons, sexes, and ages did not show a consistent difference between oiled and unoiled areas, we conclude that food is unlikely to be a primary constraint to recovery of populations from oiled areas.

## Conclusions

We conclude that recovery has not occurred, continued oil exposure may be the primary mechanism constraining recovery, and lack of full recovery likely will be further delayed long after deleterious EVOS effects are gone due to intrinsic limits to population growth rates. Our findings are concordant with studies of other nearshore vertebrates. For example, sea otters (*Enhydra lutris*) had elevated P450 (Holland-Bartels 2000), increased mortality in oiled areas through at least 1998 (Monson et al. 2000), and lack of return to pre-spill numbers in the most heavily oiled areas of PWS (Holland-Bartels 2000).

Populations of some bird species likely were not injured by the EVOS, or recovered quickly (Wiens et al. 1996). Harlequin duck populations, however, have an unfortunate combination of characteristics that make them particularly vulnerable to effects from the oil spill during nonbreeding parts of the annual cycle. These characteristics include a life history requiring high adult survival, occurrence in habitats most affected by oil spills and which may hold residual oil for years,

adaptation to stable and predictable marine environments, and high site fidelity.

The traits of harlequin ducks that make them (and bird 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 appear to suffer deleterious effects of oil pollution at lower levels and for longer time periods than other species.

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## CHAPTER 6

## SUMMARY

The results from this dissertation indicate that demography of harlequin ducks in Prince William Sound was related to history of oil contamination by the *Exxon Valdez* oil through at least 1998, 9 years after the spill event. Densities of birds were lower than expected on oiled areas compared to unoiled and differences in survival rates between areas were a likely mechanism explaining reduced densities on oiled areas. We speculate that continued exposure to oil affected individual physiology and, subsequently, survival. Despite a conventional paradigm that effects of oil spills on birds tend to be short-lived, these results indicate that this is not an appropriate assumption for all species, particularly those for which life history or natural history traits lead to increased vulnerability. Harlequin duck populations apparently were sensitive to effects of the spill. Sensitivity to oil spill effects, and presumably other forms of anthropogenic perturbation, makes harlequin ducks an appropriate sentinel species for monitoring effects of perturbations and evaluating recovery. We recommend using demographic characteristics of populations, such as survival rates, as research and monitoring tools, as they provide not only a sensitive measure of population status but also lend insight into mechanisms underlying population change.

This work has implications not only for understanding longer-term effects of catastrophic spills like the *Exxon Valdez* but also chronic, low-level oil pollution



that occurs on coastlines throughout the world. Harlequin ducks, and other sensitive species, presumably would exhibit demographic responses to chronic oiling in a manner similar to that in response to residual effects from large spills.

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