Exxon Valdez Oil Spill
State/Federal Natural Resource Damage Assessment Final Report

Breeding Ecology of Harlequin Ducks in Prince William Sound, Alaska

Restoration Study Number 71
Final Report

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Study History: Lack of information on the ecology of harlequin ducks was recognized during planning of oil spill restoration in April 1990. Study of breeding habitat received high priority. Harlequin ducks were observed breeding throughout unoiled eastern Prince William Sound (EPWS) during 1990, providing a focal area for habitat analyses and population studies for comparison with the oil spill area. Restoration Study 71 was initiated in 1991 to describe breeding habitat of harlequin ducks in EPWS for application toward identifying critical habitats in the oil spill region. This final report is composed primarily of the first author's M.S. thesis (Crowley 1994); sections regarding breeding habitat remain mostly unchanged. One exception is the Alternative Breeding Habitat section, which was revised after more extensive review of literature. The thesis manuscript was expanded to include comparisons of streams in eastern EPWS to those monitored in the oil spill area, as well as further analyses of productivity data.

Abstract: Breeding habitat and productivity of harlequin ducks was studied in eastern Prince William Sound (EPWS), Alaska, during 1991 - 1993. Harlequin ducks usually selected the largest anadromous salmon streams available for nesting. Volume discharge of breeding streams averaged 3.2 m^3/s and was the strongest variable distinguishing between streams used and not used by breeding harlequins. Ten nests of harlequins were located on southwest-facing, steeply-sloped banks of first order tributaries near timberline elevations. Nests were associated with woody debris and shrubs, in shallow depressions or cavities, and beneath the canopy of old growth forest. Productivity of harlequin ducks in EPWS was low relative to other breeding populations. Nest density for 7 streams was approximately 0.3 - 0.5 breeding females per km. Estimated breeding propensity of adult females was 86% in 1991 and 74% in 1992. Average clutch size for 8 nests was 6.1 eggs. Duckling mortality was estimated at 59%, occurring mostly during 15 - 35 days of age. Average brood size at fledging was 2.50 and recruitment was estimated at 0.6 - 1.1 per breeding female. Coastline densities of broods during 1991 - 1993, respectively, was 2.3, 0.9, and 1.8 per 100 km.

Key Words: Breeding, habitat, harlequin duck, *Histrionicus histrionicus*, landscape, nesting, Prince William Sound, stream, watershed.

Project Data: *Description of data* - Data collected on harlequin ducks in eastern Prince William Sound include: 1) measurements of streams and watersheds; 2) times, dates, locations and measurements of captured harlequin ducks; 3) locations, dates, ages and sizes of harlequin duck broods; 4) habitat description, location, chronology and clutch size of harlequin duck nests. *Format* - The data are in Lotus 123 (available in Excel for Windows) and Statgraphics. *Custodian* - Contact Dave Crowley, Alaska Department of

Fish and Game, Division of Wildlife Conservation, (907) 267-2205. *Availability* - Data are available upon request.

Citation:

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EXECUTIVE SUMMARY

We studied breeding habitat of harlequin ducks (*Histrionicus histrionicus*) in eastern Prince William Sound (EPWS), Alaska, during 1991 - 1993. Streams in EPWS were surveyed for harlequin ducks and monitored with mist nets. Physical characteristics of 24 Harlequin breeding streams were compared to those of 24 streams not used for breeding using 2-sample and logistic regression analyses. Nests were located using radio-telemetry of marked females. Parameters of productivity were estimated from breeding status and weights of captured females, nest clutches, and brood counts.

We captured 23 harlequin ducks (16 females) in 1991 during 330 hours of mist-netting on streams in EPWS. In 1992, we captured 42 ducks (28 females) during 224 net-hours of effort. Forty females were marked with radio tags during both years combined. Breeding females weighed significantly more than non-breeding females. Weights of paired, non-breeding females were significantly greater than those of unpaired, non-breeding females. Lower weight and absence of mates during nest initiation indicated that unpaired females may have been subadults (1 or 2 years old). Paired non-breeders, similar in weight to breeding females, were likely adult females that had refrained from breeding.

Harlequin ducks breeding in EPWS selected the largest anadromous salmon streams available for nesting. Volume discharge of breeding streams averaged 3.2 m^3/s and was the most important factor in habitat variation between streams used and not used by breeding harlequins. Expansive estuaries and intertidal deltas at the mouths of large streams were important foraging and loafing areas of harlequin ducks. Ten nest sites of harlequin ducks in EPWS were located on southwest-facing, steeply-sloped banks of small, first order tributaries near timberline elevations. Nests were associated with woody debris and shrubs, in shallow depressions or cavities, and were beneath the canopy of old growth forest. Microhabitat used for nest sites was well-drained and exposed to sunlight, favoring early melting of spring snow. Exceptional snow depths and late melting may, however, limit harlequin breeding effort in some years.

Productivity of harlequin ducks in EPWS was low. Nest density for 7 streams was approximately 0.3 - 0.5 breeding females per linear km. Estimated breeding propensity of adult females was 86% in 1991 and 74% in 1992. Average clutch size for 8 nests was 6.1 eggs. Duckling mortality from hatching to fledging was estimated at 59%, occurring mostly during 15 -35 days of age. Average brood size at fledging was 2.67 and recruitment was estimated at 0.6 - 1.1 per breeding female. Coastline densities of broods during 1991 - 1993, respectively, was 2.3, 0.9, and 1.8 per 100 km.

Because of this species' sensitivity to human disturbances, we recommend protection of harlequin duck breeding habitat in riparian zones, with a minimum 50-m streamside buffer strip in watersheds undergoing timber harvest or other development.

INTRODUCTION

The harlequin duck (*Histrionicus histrionicus*) is a small, strikingly marked sea duck renowned for its use of turbulent, rushing streams as breeding habitat. Life history characteristics and habitat use of harlequin ducks in Prince William Sound uniquely link upland forests, riparian ecotones, freshwater streams, estuarine, and marine communities. Breeding harlequins are essentially dependant on each community, either directly for food and cover, or indirectly for the regulatory function that each community or ecotone provides to its adjacent habitat (Petts 1990). Upland forests and riparian ecotones provide woody debris, tree cavities, and shrubs used by harlequin ducks for nesting cover (Bellrose 1980, Cassirer and Groves 1992). Riparian ecotones also regulate and maintain aquatic temperature, nutrients, and structural habitat necessary for invertebrate production (Risser 1990, Gregory et al. 1989, 1991), an important food source for harlequins. Harlequin ducks breeding in eastern Prince William Sound spend most of their lives in intertidal areas of stream deltas, estuaries and rocky coastline (Dzinbal 1982). As intertidal specialists, harlequins use shallow-sloping, boulder-strewn shoals for feeding and resting (Dzinbal 1982).

Invertebrate populations on streams used by inland-breeding harlequin ducks (i.e., those that migrate inland and remain away from the coast during the breeding season) must be adequate to meet nutritional needs for survival and successful reproduction (Bengtson and Ulfstrand 1971). Reduced breeding propensity of adult harlequin females in interior Iceland coincided with decreased populations of aquatic invertebrates, suggesting that harlequin duck populations were limited by food resources on inland breeding areas (Bengtson and Ulfstrand 1971).

Unlike inland-breeding harlequins of Iceland (Bengtson 1972, Inglis et al. 1990), Wyoming (Wallen 1987), Idaho (Cassirer and Groves 1991) and Montana (Kuchel 1977, Diamond and Finnegan 1993), coastal-breeding harlequins of Iceland (Bengtson 1972) and Prince William Sound fly downstream from nest sites to estuaries and adjacent intertidal zones where they forage on small crustaceans, invertebrates and polychaetes (Dzinbal and Jarvis 1982). Late incubation and brood rearing periods of harlequin ducks in Prince William Sound correspond with annual spawning runs of anadromous salmon. Salmon roe provides a substantial increase in available food for breeding hens and ducklings (Dzinbal 1982, Dzinbal and Jarvis 1982). Although estuarine and marine communities inhabited by coastal-breeding harlequin ducks probably produce a more abundant food supply than inland streams used for breeding, productivity of coastal-breeders is similar to that of inland breeders (Bengtson 1966, 1972, Dzinbal 1982, Wallen 1987, Cassirer and Groves 1992).

Throughout their breeding range, most female harlequin ducks presumably do not breed until they are 3 years old, non-breeding proportions of paired females ranges from 31 - 62%, brood size is about 3.0 ducklings at fledgling age, and breeding density is low. Apparent low productivity in Prince William Sound despite rich food sources and diverse food resources indicate that other factors (e.g., habitat availability, predation, and climate) may be limiting productivity of coastal harlequin populations.

Knowledge of factors limiting harlequin duck populations became important on March 24, 1989 when the *T/V Exxon Valdez* ran aground on Bligh Reef and spilled approximately 11 million gallons of crude oil into western Prince William Sound. Rocky intertidal communities were impacted first as oil washed ashore, and again when clean-up crews treated beaches with pressurized hot water and bioremediation compounds which contain chemicals potentially toxic to vertebrates (Patten 1995). Because harlequin ducks inhabit intertidal areas year-round, exposure to crude oil through foraging and preening activities potentially predisposed this species of sea duck to both lethal and sublethal effects of crude oil toxicity (Patten 1995).

Persistent oil contamination on intertidal habitat in western Prince William Sound was considered the probable cause for low productivity (Patten 1995) and population decline of harlequins in that area (Klosiewski and Laing 1994, Patten et al. 1995). In eastern Prince William Sound, presumably an area not impacted by the oil spill, impending timber harvest threatens harlequin duck nesting, foraging, and molting habitat. These disturbances prompted a study of harlequin duck breeding biology, productivity, habitat requirements for breeding and molting, and an inventory of breeding streams in eastern Prince William Sound. The primary objectives of this study were to determine which habitat characteristics, if any, differentiate streams used by breeding harlequin ducks from those not used for breeding in eastern Prince William Sound, to locate and describe habitat used by female harlequin ducks for nesting, and to measure productivity. Comparison of harlequin population densities, productivity, and 1991-1993 trends between the oil spill and control areas are addressed in Patten (1995) and Patten et al. (1995).

OBJECTIVES

A. Locate and inventory streams used for breeding by harlequin ducks in Prince William Sound.

B. Identify and describe habitats used by nesting and brood-rearing harlequins by documenting topographic, hydrologic, and vegetation characteristics at nest sites and brood-rearing areas.

C. Identify other harlequin breeding habitat parameters such as distance from nest to coast, distance from nest to stream, and physical features of nest sites.

D. Construct a model that predicts potential stream use by breeding harlequins with the characteristics identified in objectives B and C.

E. Measure harlequin duck productivity by documenting clutch size, hatching success, and duckling survival to fledging.

F. Document harlequin duck breeding behavior including pair-bonding, nesting, and brood-rearing in eastern PWS for comparison with the harlequin monitoring study in the spill area.

G. Determine width of forested buffer strips necessary to protect harlequin breeding sites from the effects of timber harvest in Prince William Sound.

H. Determine feasibility of stream habitat enhancement by erecting artificial nesting cavities (nest boxes) along known breeding streams and testing for use by harlequins.

STUDY AREA

Prince William Sound is a marine water body on the south-central coast of Alaska nearly enclosed and sheltered by large islands (Figure 1). Prince William Sound is characterized by fjord-like ports and bays with tides of up to 4.5 m (14 ft), and a landscape of steeply rising mountains and large glaciers. A narrow ecologic region of coastal rain forest occurs on the seaward side of coastal mountains of southcentral Alaska (Hultén 1968). Coniferous forest composed of Sitka spruce (*Picea sitchensis*), western hemlock (*Tsuga heterophylla*), and mountain hemlock (*T. mertensiana*) flourishes on mountain slopes and valleys. Regional climate is generally cool, with high precipitation during summer months, and cold with snowfall often exceeding 7.6 m (300 in.) during winter.

The study area of eastern Prince William Sound (EPWS) consisted of all shoreline, small islands, estuaries, and 75 anadromous fish streams along 630 km of coastline from Cordova to Valdez, Alaska and the protected, leeward shores of Hinchinbrook and Hawkins Islands (Figure 2). Hanning and McLeod Creeks of southwest Montague Island (Figure 1), though disjunct from the main study area, were not oiled and were used by breeding harlequin ducks. We included these streams in the habitat analyses to increase sample size. Compared to streams used by inland-breeding harlequins, streams of Prince William Sound are short (averaging less than 15 km), of low volume discharge and low invertebrate productivity (Dzinbal 1982). At the outflow of most streams are small estuaries whose biological communities are influenced by both fresh water from streams and salt water from each rising tide. Estuaries expand downstream into alluvial deltas supporting a diversity of intertidal marine communities. We refer to the entire system from estuary to lower deltas (high to low tide) as an estuary, and to intertidal areas not influenced by stream outflow as intertidal coastline.

Except for the initial spill west of Bligh Island, oil from the *Exxon Valdez* did not reach shorelines of EPWS. Strong winds shortly after the spill propelled most oil south westward. Although it is unknown whether harlequins move between EPWS and the oil spill area of western Prince William Sound (WPWS), we assumed that harlequin ducks of EPWS were not sublethally impacted by oil.

METHODS

Stream and Coastline Surveys

We identified potential breeding streams by the presence of harlequin ducks on estuaries in late May during surveys of the study area. Surveys were conducted from a skiff piloted within 5 - 30 m of shore. Estuaries and lowest reaches of streams were surveyed on foot, if not navigable by boat. Harlequin ducks were counted and classified by sex with 10-power binoculars. When possible, breeding pairs were identified and counted. All other estuaries of anadromous salmon streams (Alaska Department of Fish and Game 1993) within the same basin or bay of the potential breeding stream were surveyed at least 3 more times throughout the season to confirm presence or absence of breeding harlequins. Brood surveys were conducted in late July to mid-August (1991 - 1993); presence of ducklings on an estuary provided further evidence that the stream was used for breeding.

Based on results of survey visits, streams were grouped into 4 categories: (1) harlequin breeding activity observed on stream; (2) no breeding activity observed, but stream supported an anadromous fish run, and of apparently suitable volume and estuary size for breeding (based on known breeding streams); (3) small anadromous fish stream with low discharge (usually < 1.0 m^3/sec), small estuary, and no observed breeding activity by harlequin ducks; (4) large river of glacial origin having heavy siltation, extensive mud flats, and no harlequin activity. Streams of the first 2 categories were given priority for intensive monitoring using mist nets. Streams of category 4 were included in harlequin duck surveys but were not intensively monitored.

Harlequin Duck Capture

Locating harlequin nests and brood-rearing areas necessitated capturing and radio-tagging females. Harlequin ducks were captured in mist nets suspended across streams. To avoid submergence at high tides, nets were placed above the tidally influenced estuaries. Mist nets (Avinet, Inc., #12N-210/2) were heavy-duty, with 10-cm (4-in) mesh and measured 1.8 m (6 ft) in height by 12 m or 18 m (40 or 60 ft) in length. Mist nets were most effective when placed in pairs, 10 - 20 m apart, on bends in the stream channel where low-flying harlequins often slowed to negotiate sharp turns. Streams were kept under surveillance while nets were deployed, allowing immediate removal of captured harlequins, an account of ducks flying up- and downstream, and observation of whether ducks were paired before striking the net.

Harlequin ducks were most active during twilight hours. We therefore monitored streams from 2100 to 0100 and 0300 to 0800 (9 net hours) to determine whether harlequins were present. Breeding by harlequins was confirmed either by actual captures of ducks or by observing flights of harlequins (singly, or in pairs and small flocks) to and from upstream reaches. We trapped streams that were not conspicuously used by breeding harlequins for 1 - 2 trap nights in an effort to determine if limited use of the streams was occurring. Capture rates (ducks caught per hour) were calculated for each year. Captured harlequin females were marked with a 4.5-g radio transmitter (Advanced Telemetry Systems, #357) glued to center tail feathers for tracking to nest sites (Quinlan and Hughes 1990). We weighed captured ducks and measured tarsus, culmen, and wing cord. Morphology was compared between sexes and females of various breeding status using two-sample and ANOVA analyses. Colored nasal disks were placed on 10 males to determine their movements from breeding to molting areas.

Stream Data Collection

Streams were classified as breeding streams if they satisfied one of the following criteria: (1) harlequin duck nests located, (2) breeding females captured, (3) solitary females observed flying upstream, or (4) broods observed upstream. Also classified as breeding streams were those that met two of the following three conditions: (1) harlequin brood(s) observed in the intertidal area of the stream; (2) lone hen observed feeding in estuary; (3) harlequin pairs (assumed to be breeding) observed near stream mouth in the spring. Streams meeting only 1 of the 3 conditions and having apparently suitable breeding habitat were designated as probable breeding streams. Low density and inherent low breeding propensity of adult females resulted in a small sample size of breeding streams compared to streams not used for breeding. Consequently, probable breeding streams and breeding streams were combined in our analysis to increase sample size.

Streams that had no observed breeding activity by harlequin ducks after repeated surveys or trapping were designated as non-breeding streams. We prioritized which non-breeding streams were to be included in the analyses, based first on use by harlequin ducks for activities other than breeding, and secondly on resemblance to breeding streams. Consequently, we included in the analyses two groups of non-breeding streams: (1) those streams whose estuaries had sporadic use by small flocks of post-breeding females and molting harlequins, but that had no perceptible breeding activity; and (2) the larger remaining streams (based on discharge and estuary size), because field observations suggested that harlequins were breeding mostly on larger streams.

Because the structure and dynamics of stream habitat are determined by the surrounding watershed, many researchers (e.g., Lotspeich and Platts 1982, Frissell et al. 1986, Urban et al. 1987, Gregory et al. 1991) have recommended the integration of basin geomorphology, and aquatic and terrestrial characteristics of streams when describing stream habitat. We developed a conceptual model of a watershed in Prince William Sound to determine at which levels of hierarchy we collected data (Figure 3). We selected variables within 3 hierarchical levels: (1) local-level characteristics at each stream mouth, (2) within-basin characteristics of each drainage network, and (3) landscape-level data describing basin morphology.

We collected 10 variables at each stream mouth near the marker of mean higher high water (previously installed by ADFG fisheries workers). Channel width (m) was measured and marked into three segments of equal width. At the measured midpoint of each segment depth was measured and rate of surface flow was estimated by timing progress of a float over a distance of 2.0 m. These data (as well as a friction constant based on substrate smoothness) were used in an equation to estimate volume of discharge (m^3/s) (Robins and Crawford 1954). We defined the riparian zone as the periodically flooded area along the stream having predominantly shrub and grass vegetation and measured its width (m). Channel gradient (%) was measured over 100 m, or as far as visibility permitted, using a compass clinometer. The slopes of the adjacent uplands within 300 m of both banks of the stream mouth were determined using 1:63,360 USGS topographic maps; the 2 slopes were averaged for a measure of sideslope topography (%). Area of estuary (ha) was measured using a computer digitizer and USGS topographic maps. Water turbidity, channel substrate, channel configuration (e.g., straight, curved, or braided), and bank vegetation were described categorically (Cassirer and Groves 1991).

Twelve geomorphic characteristics of each watershed were measured from topographic maps. We collected the following six measurements to describe geomorphology of drainage networks within each basin (Swanston et al. 1977, Verstappen 1983): (1) channel length (km) was estimated by measuring all permanently flowing tributaries within the basin as indicated on topographic maps; if a stream flowed through a lake, straight distance from inlet to outlet were included in the length measurement, (2) stream density (km/km^2) was calculated by dividing channel length by area of the basin, (3) channel frequency was determined by counting all first-order streams in the drainage network (4) channel gradient (%) was calculated from elevation of stream origin divided by length of the main stream channel, (5) the number of lakes (wider than 5 stream channel widths) through which permanent streams flowed were counted. We included only lakes below 460 m (1500 ft) elevation because lakes above this elevation remained frozen and unavailable for harlequin use for most of the summer, (6) bifurcation ratio was calculated as number of first-order streams divided by number of second-order streams.

Basin size and shape were described using the following six variables (Swanston et al. 1977, Verstappen 1983): (1) basin perimeter (km) was drawn by hand along the highest circumference and measured using a map-measure, (2) basin area (km^2) was measured within the same perimeter using a digitizer, (3) basin aspect (degrees from north) was determined by drawing a straight line along the approximate average direction of the main stream channel through the watershed and measuring degrees from north with a compass protractor. If basins were curved, the measurement was taken from the middle to upper part of the watershed because all harlequin duck nests were found in the upper half of basins, (4) basin relief (m) was measured from the highest point of the watershed to the outlet at sea level (5) basin shape was described using the circularity ratio, whose value decreases as shape becomes less circular: $R_c = A_d/A_c$, in which A_d is the basin area and A_c is the area of a circle having the same perimeter as the basin (Verstappen 1983); (6) average basin slope (%) was calculated as the ratio of the difference in elevation between the most distant ridge (determined by map-measure) and watershed outlet at sea level, to the approximate average length of the watershed.

Nesting Habitat

Nest sites of harlequin ducks were located by radio-tracking incubating females, first by fixed-wing aircraft to locate general vicinity within the watershed, then on foot to the nest site. Females were flushed from the nest, and eggs were measured and protected from the weather. Habitat data were collected as listed above for stream mouths. We also estimated percent occurrence of plant species in the overstory (greater than 1 m in height and within 3 m of the nest), understory (less than or equal to 1 m in height and within 1 m of the nest), and cryptic-cover (material or structure concealing the nest bowl).

Analysis of Habitat Data

Habitat data collected in this study are representative of streams potentially used for breeding by harlequin ducks in EPWS and were not randomly selected. Inferences should therefore be limited to EPWS.

Basin and drainage network variables and continuous variables from stream mouths were analyzed by first testing (at $\alpha = 0.05$) for differences between the 2 stream groups (breeding and non-breeding) for each of the individual habitat variables. We used Student's t on normally-distributed data sets, or Mann-Whitney-Wilcoxon Z on nonparametric data. Aspect, collected as compass degrees, was compared using Watson's U^2 test for circular data (Zar 1984). Categorical data collected at stream mouths were compared using Fisher's Exact Test for contingency tables (Ramsey and Schafer 1993). Data were arranged in 2x2 tables whereby the explanatory factors (rows) were the presence or absence of each habitat category, and the binary response variables (columns) were the occurrence of the habitat on breeding or non-breeding streams.

Standardized principal components analysis (based on a correlation matrix) was used to test for combinations of variables that explained the greatest portion of original variance within the data set (Morrison et al. 1992). We used 13 habitat variables in the analysis, including all basin-level variables (except bifurcation ratio) and the continuous variables from stream mouths: discharge, area of estuary, and sideslope gradient.

Logistic regression for binary responses was used to analyze basin, drainage network, and stream mouth variables. Each of the variables were first tested in individual models for their ability to explain breeding vs. non-breeding responses. Those variables not demonstrating a significant ($p \leq 0.05$) effect on responses were eliminated from further modeling. The remaining variables were tested within hierarchical levels (i.e., stream mouth, drainage network, and basin) by modeling the highest-effect variable within each hierarchical level with each of the other remaining variables in that level (limiting models to 2 terms to maximize degrees of freedom).

Finally, the remaining 3 variables were modeled together to determine which of the habitat characteristics most successfully explained the variation between breeding and non-breeding responses.

Discriminant function analysis (DFA), (originally proposed to meet Objective D but replaced by logistic regression in modelling variables) was used to determine which of the landscape variables were most important in discriminating between groups (breeding and non-breeding streams) (Martinka 1972, Anderson and Shugart 1974, Conner and Adkisson 1976, Swanston et al. 1977, Rice et al. 1983, Ramsey and Schafer 1993).

Measurements of compass aspects (degrees) of stream banks and channels at nest sites were tested for goodness of fit using Watson's U^2 test for circular distributions (Zar 1984). The remaining nest site variables were summarized in graphs.

Streams measured in EPWS (both breeding and non-breeding) were compared to streams monitored in WPWS using the parameters width-at-mouth (m) and length of stream channels (km). These data sets were compared using a Mann-Whitney-Wilcoxon Z Test for unpaired data (Statgraphics 5.0, Manugistics, Inc.). This test uses ranked data and so is robust with smaller sample sizes, non-normal distributions, and unequal variance between data sets.

Productivity

We derived measures of productivity from coastline surveys and capture of females. We determined breeding status of female harlequin ducks (a parameter needed to estimate recruitment) by examining cloacal apertures for distention caused by laying eggs and by presence or absence of a brood patch (area on belly plucked clean of feathers). We assumed an average clutch size of 6 eggs, one egg laid every 2 - 3 days, and that incubation began before the last 1 - 2 eggs were laid (Bellrose 1980). We expected distended cloacas to occur with the onset of nest initiation, increasing our ability to detect breeding females by approximately 8 - 15 days prior to incubation, which in turn was indicated by the presence of a brood patch. Females with one or both characteristics were considered breeding (B); those without either were assumed non-breeding.

Non-breeding females were further classified, when possible, as paired or unpaired, determined by whether or not a female was accompanied proximally by a male before flying into a mist net. We assumed that paired, non-breeding (PNB) females were adults that did not breed. Typical of most waterfowl species, a surplus of adult male harlequin ducks occurs in breeding areas (Baldassarre and Bolen 1994, Bengtson 1972). We therefore assumed that un-paired, non-breeding (UPNB) females were subadults (< 3 years old) as yet incapable of breeding (Dow and Fredga 1984). Based on observations in EPWS and other study areas, subadult harlequins are typically less numerous or absent on breeding grounds than adults (Bengtson 1972). Consequently, we assumed that non-breeding females of unknown pair status (NB) were adults. The number of breeding females captured was divided by the estimated total number of adult females captured to give a percentage of adult breeding females.

We recorded clutch size for each nest located by telemetry and calculated average clutch size. We candled eggs to estimate incubation stage (Weller 1956), assuming a 30-day incubation period (Bellrose 1980). Hatching success was determined by observing the hatch underway, revisiting nests after hatching, and by locating intact nests from previous seasons. We counted shell membranes and addled (unhatched) eggs in revisited and previous-season nests.

Linear density of breeding females was calculated by dividing estimated number of breeding females by channel length. On those streams most intensively studied, we estimated the number of hens actually breeding along the stream, in addition to those we captured. This estimate was derived from observations of unmarked females flying to and from upstream reaches during the incubation period and from the size of female flocks observed on lower stream reaches.

Indices of brood density, duckling mortality, and recruitment of harlequin ducks were calculated using data from coastal surveys during mid-late summer. Harlequin broods observed during 1991 - 1993 were assigned to one of seven age classes, using Wallen's (1987) application of Gollop and Marshall's (1954) stages of plumage development of ducklings (see Bellrose 1980). Assuming that ducklings fledged at 42 days (Wallen 1987, Bengtson 1972), approximate age of harlequin ducklings classified by plumage development were: Ia = 1-5, Ib = 6-9, Ic = 10-14, IIa = 15-21, IIb = 22-27, IIc = 28-35, and III = 36-42 days (Wallen 1987). Average brood size and 95% confidence intervals were calculated for each age class using an analysis of variance (multifactor ANOVA, Statgraphics 5.0; Manugistics, Inc.). Mortality was indicated by the percent decrease in brood size from one age class to the next older, beginning with average clutch size as the baseline. We assumed in estimating mortality that all pre-fledged, class III ducklings survived to fledging. Linear brood density (broods observed per 100 km of coastline) was calculated as an index to compare productivity in EPWS to that of WPWS.

Recruitment, the number of fledged harlequin ducklings produced per adult female and per breeding female, was modelled to gain insight into relative productivity, rather as than an accurate estimate (which would require further study of assumptions on which calculations are based). Recruitment was calculated by dividing the number of ducklings observed during brood surveys by the number of adult females observed during mid-summer surveys of molting harlequins. Because recruitment in this paper represents survival to fledging age, the observed sizes of broods in classes I-IIa and IIb were reduced by a mortality factor (estimated from observed brood size decline) to decrease them to average brood size of class III ducklings. We assumed in calculating the recruitment index that ducklings of both classes IIc and III survived to fledging. Adult females could not be reliably differentiated from subadults (i.e. 1 and 2 years old) by plumage characteristics. We therefore assumed, speculatively, that flight-capable females occurring in small flocks in estuaries, streams, and along nearby coastline were adults (known to molt later after brood-rearing) and that flightless females in predominantly male molting flocks were subadults. The number of breeding females was estimated as the product of total adult females observed on surveys and percentage of breeding females.

Chronology of nest initiation, onset of incubation, hatching, and fledging was estimated by determining incubation stage for nests and age-class for broods, then forward- or back-dating. Assumptions included: average of 6 eggs per clutch for unknown clutch sizes (Prince William Sound average was 6.1 eggs/clutch); 1 egg laid every 2 days (Bengtson 1966, 1972); incubation began after the entire clutch was laid and lasted 30 days, including the day of hatch and drying of downy young (Bellrose 1980); and age at fledging was 42 days (Wallen 1987). Because of the 2-3 day uncertainty in estimating incubation stage and duckling age, a range of 4-6 days resulted in estimating date of occurrence. Using the mid-point dates of each nest and brood in each of the 4 events, frequency of occurrence was plotted against an axis composed of the breeding season broken into 7-day blocks.

Habitat Enhancement

We investigated feasibility of habitat enhancement in 1992 by designing and constructing nest boxes based on dimensions of cavities used by nesting harlequin ducks in Washington and Idaho (Cassirer et al. 1993), and on nest boxes used by captive harlequins (C. Pilling, pers. comm.). Prior to onset of nesting, disassembled nest boxes were backpacked to upstream sites, assembled, and lined with moss and leaf litter. Boxes were revisited throughout the nesting season to determine use by harlequin ducks.

RESULTS

Stream and Coastline Surveys

Spring surveys for harlequin ducks (Table 1, Figure 4) produced a 2-year average of 1.23 ducks/km in May, which increased during brood/molt surveys to a 3-year average of 2.00/km in August (Table 2). Molt/brood surveys only were conducted in 1993, covering most of the shoreline surveyed in previous years (Table 1, Figure 5). Surveys during 1991 to 1993 included approximately 75, 90 and 80 estuaries, respectively. Harlequin ducks often occurred in small flocks making positive identification of pairs difficult. Densities of molting harlequin ducks were relatively stable during the 3 years of study (Table 2).

Harlequins were observed along rocky or gravel beaches of shallow sloping bathymetry, where substrate consisted of emergent and intertidal rocks, islands, reefs, and bedrock outcroppings. Because nest searching, courtship, and feeding activities of harlequin ducks occurred on estuaries in May and early June, it was usually obvious during spring surveys whether or not a stream was used for breeding. Although low numbers of harlequin females and molting males were sporadically observed foraging in estuaries of smaller salmon streams (categories 2 and 3) during mid- to late summer, these streams were either not used for breeding or used too infrequently (i.e. not every year) for detection.

Harlequin Capture

We captured 23 harlequin ducks (16 females) in 1991 streams during 330 net-hours on 5 of 15 streams trapped in PWS (Appendix A). In 1992, we captured 42 ducks (32 females) on 10 of 16 streams trapped during 224 net-hours of effort. Capture rate increased from 14.3 net-hours per duck in 1991 to 5.3 hours per duck in 1992, probably resulting from improved efficiency (i.e., knowledge gained in 1991 of location, time and technique to best capture ducks). Forty females were marked with radio tags in both years combined. A nesting female captured in 1991 showed no evidence of breeding when recaptured on the same stream in late June 1992. A PNB female captured in 1991 bred in 1992. Four other recaptured females nested during both years on the same streams. The only 2 males caught both years were also on the same stream. We captured 6 of 7 UPNB females during mid- to late June, by which time most breeding females had begun incubating (Crowley, unpubl. data). Four of 7 UPNB females were captured while males were still present on streams. Pair status of 2 non-breeding (NB) females was unknown and were assumed adults. We captured 17 males total, all of which were in adult breeding plumage. Our capture effort extended from late May to early July.

Weights, Sex and Age.-- Male harlequin ducks had significantly greater average body weight (by 8.2%, $P < 0.001$, Table 3) and lengths of tarsus (6.7%, $P < 0.001$), culmen (6.3%, $P < 0.001$) and wing cord (1992 data only, 4.3%, $P = 0.004$) than those of captured females. Weights of PNB females were significantly greater than those of UPNB females ($P = 0.008$, Figure 6), although other body measurements did not differ significantly. Breeding females did not differ in weight from PNB females ($P = 0.7$), but were significantly heavier than UPNB females ($P = 0.003$, Figure 6). Two breeding females recaptured as the season progressed indicated a tendency to lose weight (by 17% and 11.5% over 1 month). However, breeders captured after June 13 ($n=12$) still weighed significantly more ($P = 0.006$) than UPNB females captured during the same period ($n=5$).

Six of 10 male harlequin ducks marked with nasal disks were resighted. Five of the males and one radio-marked female were known to have moved an average of 23 km shoreline distance from breeding streams to molting sites (Table 4).

Stream Habitat

Two-sample Tests.--We identified and measured 22 harlequin duck breeding streams, 2 probable breeding streams, and 24 streams not used for breeding in EPWS and western Montague Island (Appendix B). Transformation of data to their natural logs was necessary to normalize distributions to meet assumptions of statistical tests. Two-sample testing of variables measured at stream mouths indicated that harlequin breeding streams had significantly greater values for volume discharge ($p < 0.001$), area of estuary ($p = 0.003$), stream width ($p < 0.01$), and width of riparian zone ($p = 0.046$), than did non-breeding streams (Table 5). No significant differences were detected between breeding and non-breeding streams with respect to channel slope, sideslope topography, and aspects of stream mouths (Table 5, Figure 7).

Fisher's exact test for homogeneity of the categorical variables collected at mouths of streams indicated no statistically significant differences between harlequin duck breeding and non-breeding streams, except that deep slow water (pools) was more common on breeding streams, and shallow slow water was more prevalent on non-breeding streams (Table 6). There were no apparent differences in the composition of vegetation types on stream banks (Table 7).

Seven of 12 geomorphic variables measured were transformed to their natural logs, and average channel gradient to the logit scale, to normalize distributions. Two-sample tests of area, perimeter, relief, average slope, bifurcation ratio, channel frequency, and length indicated significant differences ($p < 0.05$) between the stream groups (Table 8). All of these variables were greater on harlequin breeding streams, except average basin slope, which was higher on non-breeding streams. These data indicate that number of stream channels available and basin size were positively related to use of streams by breeding harlequin ducks.

Most of the streams used by breeding harlequins were of non-glacial origin. The two exceptions were streams having some tributaries of glacial origin, but whose silt burden was low enough to allow salmon to spawn in gravel beds.

Multivariate analyses.--Principal components analysis indicated that most variation among streams was explained in measurements of stream size and gradient. We interpreted the first component (PC1), which explained 50% of the variation in the data, as representative of overall stream size because PC1 was primarily correlated with basin area (correlation coefficient = 0.98, $p < 0.0001$), perimeter (0.94, $p < 0.0001$), discharge (0.88, $p < 0.0001$), channel length (0.90, $p <0.0001$) and channel frequency (0.78, $p < 0.0001$). PC1 was negatively correlated with the index of basin shape (-0.87, $p < 0.0001$) because the larger watersheds were generally long and narrow resulting in a lower shape index value (less circular).

The second component (PC2) explained an additional 15% of the variation in the data set. We interpreted PC2 as representative of stream gradient because it was correlated primarily with various measurements of gradient: overall channel gradient (correlation coefficient = 0.94, $p < 0.0001$), mean sideslope at stream mouths (0.79, $p < 0.0001$), and mean sideslope of basins (0.61, $p < 0.0001$). A scatterplot of the values from PC1 against those of PC2 separated most harlequin duck breeding streams from non-breeding streams along PC1. Mean PC1 and PC2 values were tested by stream group using an analysis of variance and plotted with 95% confidence ellipses (Figure 8). The mean of PC1 values for breeding streams was significantly larger than mean PC1 values for non-breeding streams (F-ratio = 26.12, $p < 0.0001$). We detected no significant difference between mean PC2 values of breeding and non-breeding streams (F-ratio = 0.496, $p = 0.4925$).

Single-factor logistic regression eliminated 6 variables which did not significantly account for the binary responses of harlequin breeding or non-breeding streams (Table 9). The second step, modeling variables within each hierarchical level, eliminated 9 more variables, leaving basin area, channel length, and discharge representing each spatial scale. Final modeling determined that discharge was the single most important variable, and local stream mouth the most important level, in explaining the difference in response (Chi-square from maximum likelihood ANOVA = 11.74, $p = 0.0006$, Table 10).

Large basins in Prince William Sound had both long channel lengths (area vs. channel length) and higher frequency of first order tributaries (area vs. channel frequency, Figure 9). Channel length vs. frequency of tributaries were also related (corr. coeff. = 0.73, $p < 0.0001$); long streams tended to have many first order tributaries flowing into them. The greater number of tributaries present in drainage networks of larger basins provided more stream banks suitable for nesting. Of 10 harlequin duck nests found, 8 were on first-order tributaries or at the confluence of a first-order tributary and main stream channel (usually second order) just below timberline elevation.

Results of discriminant function analysis (DFA) are in Appendix C.

Nesting Habitat

We found 10 harlequin duck nests on streams of Prince William Sound by tracking telemetered females to nest sites (Table 11). Five nests, 2 active and 3 inactive nests (containing eggs or egg remains from previous breeding seasons), were found within a 40-m stretch of stream bank on a small, first order tributary of Beartrap River (Figure 2). Nests from previous seasons were found incidentally while crawling under deadfalls in search of radio-marked nesting females. The 2 active nests (1 found each year) were made by the same harlequin female that was captured and radio-tagged both years (Appendix A). One nest was found on Hanning Creek (Figure 1) outside of the oil spill zone.

Nests were located from 0.6 to 3.0 km upstream from the coast, in old-growth forest (trees greater than 75 cm diameter at breast height), and 25 m or less from streams (Tables 11 and 12). All stream banks used for nesting were southwest-facing (218° - 241°), regardless of channel, stream mouth, or basin aspect (Figure 10). A one-sample Watson's U^2 test indicated that aspects of nest banks differed significantly from a random distribution ($p < 0.001$ with all 5 Beartrap River nests included; $p < 0.01$ with only 1 Beartrap entry included to eliminate dependent sites) (Table 13). Stream channel aspects at nest sites differed from a random distribution with the full data set ($p < 0.001$), but not when using only 1 Beartrap entry.

Stream banks on which harlequin nests were located were steep or vertical, allowing females to launch into flight directly from most nests. At stream level, banks used for nesting (Figure 11c) were composed of bedrock (six of 10), cobble and boulder (two), and grass/forbes (two of 10). At mid-level, stream banks were composed of tree/shrub mosaic (six of 10) or shrubs (four). On the upper level of stream banks, composition was of old growth trees (10 of 10).

Averages for estimated percent cover contributed to the overstory by plant species were: western hemlock (87%), followed by Sitka spruce (11%), and alder (2%) (Figure 11a). The understory composition was primarily *Vaccinium* with an estimated average cover of 62%, followed by fern (11%, usually *Athyrium filix-femina*), and hemlock seedlings (9%). Woody debris concealed 8 of 10 nests; of these, 7 nests were situated beneath deadfalls and 1 was in a shallow cavity atop a rotting stump 2 m in height. One nest was in a shallow cavity at the base of a hemlock tree, and 1 was in a moss-lined rock crevice. Nest substrate was either conifer needles, moss, or both (Figure 11b), and all nests were lined with down. (See also Appendix D).

EPWS and WPWS Stream Comparisons

We consider the following results to be preliminary because only stream width at mouth and length of main channel were collected for streams in WPWS. Mann-Whitney-Wilcoxon *Z* testing indicated that there was no difference in width between streams of EPWS and WPWS study areas ($U = 0.91$, 2-tailed $p = 0.36$, Figure 12b). There was a difference in stream lengths between study areas ($U = -2.45$, $p = 0.014$; Figure 13b). Streams in the eastern area were on average 2.6 km longer than streams in WPWS. There was much overlap, however, between range of lengths used by breeding harlequin ducks in EPWS (2.0 - 9.5 km, Figure 13a) and those streams available for breeding in WPWS (0.2 - 10.8 km, Figure 13b).

Productivity

Breeding propensity among all female harlequin ducks captured (Table 14) was higher in 1991 and than 1992. Breeding propensity of adult females was higher with 7 subadults removed from the sample (Table 2). Average number of eggs in 8 clutches of known size was 6.13 (SD = 0.92), all of 7 active nests produced hatchlings, and known hatching success for 32 eggs in 5 nests was 97.2% (Table 15). We estimated that average linear density of breeding females was 0.5/km stream channel in 1991 (based on 6 streams) and 0.3/km in 1992 (based on 7 streams, Table 116).

Duckling Mortality.--We observed 32 broods in EPWS; 16 in 1991 (linear density of 2.28/100 km), 5 in 1992 (0.94/100 km), and 11 in 1993 (1.77/100 km) (Appendix E). There was no significant difference between brood sizes in EPWS vs. WPWS (Mann-Whitney-Wilcoxon $Z = 1.67$, $p = 0.09$). Therefore, 8 known-age broods in WPWS were combined with EPWS broods to calculate average brood sizes. Three broods observed at hatching and 2 from nests of known hatch success (Table 15) were assumed to have survived 1 day and were combined with 7 broods of ages Ia - IIa to increase sample size of younger broods to 12. A total of 45 known-age broods were used to calculate mortality between age classes (Table 17). Average brood size decreased with increase in age (ANOVA F-ratio = 8.912, $p < 0.0001$) (Table 17, Figure 14a). Mortality of ducklings from laying to fledging was 59%. This is likely an underestimation of mortality because loss of entire broods was not detectable; only those broods with 1 or more ducklings remaining were included in the calculation. Mortality rate was highest between the ages of IIb and IIc (33%) and became negligible after class IIc (Figure 14b).

Recruitment.--The number of ducklings in hatchling to IIa age classes were reduced by 51%, and those of age IIb by 33% to simulate mortality observed in Figure 14. Recruitment of fledged young by harlequin ducks was relatively low in EPWS, estimated at 1.0 young/breeding female over the entire study area in 1992 (Table 18). Recruitment for 1991 could not be estimated because few females were captured, and we did not differentiate between most flight-capable and molting females (indicating breeding status) during the molt survey. Estimation of breeding females and recruitment was not possible in 1993 because many second-year females were flight-capable by the time of the mid-August survey.

Breeding Chronology.--Chronology of breeding activities was estimated from capture rates of harlequin ducks, and estimated ages of 7 nests (Table 19) and 42 broods of known age class (Appendix E). Pairs were first observed flying along streams during the last week of May. Pair activity in streams peaked during the second week of June, after which males began to depart (Figure 15a). Capture rate of breeding females on streams peaked during the third week of June, while capture rate of non-breeding females remained stable from late May through late June (Figure 15b). Nest initiations occurred from 15 May through 20 June, with the majority (39 of 49) occurring during the three weeks from 24 May to 15 June. Incubation was initiated from 2 through 28 June, and hatches occurred from 2 through 27 July (Figure 16a). Fledging occurred from 11 August through 9 September, and peaked during the last week of August (Figure 16b).

Peak capture rate of breeding females occurred when most females had finished laying and were in early incubation. After hatching began in late June, females flew along streams less often (and became adept at avoiding mist nets) and we stopped trapping when capture efficiency dropped.

Habitat Enhancement

Because of effort and time required to transport nest boxes to upper stream reaches, we were able to deploy only 3 boxes prior to nest initiation. Two boxes were set on Beartrap River and 1 on Sheep River (northeast Sheep Bay). None of the boxes were used by harlequins.

DISCUSSION

Stream and Coastline Surveys

Harlequins were predictably present in areas of suitable habitat along the coast and consistently absent in others, reflecting their use of shallow-sloping intertidal areas strewn with emergent boulders and rich in invertebrate prey. Shoreline density of total harlequin ducks remained relatively stable in EPWS during the 3 summer molt surveys. An average of 30% of known-age molters counted on surveys and 35% (11 of 31) of the molting harlequins captured (by drive-trapping) in WPWS (Patten 1995) were females. Females in molting flocks were probably second- and third year (1 and 2 years old) ducks spending their first summer along the coast with molting males (Salomonsen 1950, Dzinbal 1982).

Harlequin Capture

Site Fidelity.--Harlequin ducks exhibited fidelity to nest sites and streams in EPWS. Site fidelity by harlequins was also observed in Idaho (Wallen and Groves 1989, Cassirer and Groves 1991, 1992), Wyoming (Wallen 1987), Montana (Kuchel 1977) and Iceland (Bengtson 1966, 1972). All 9 harlequin ducks recaptured in EPWS during 1992 were using the same streams on which they were captured in 1991. One female in 1992 nested within 5 meters of her nest site from 1991, and 3 other nest bowls were found within a 30 m diameter of the first nest. Female common goldeneyes (*Bucephala clangula*) exhibiting site fidelity tended to produce larger clutches, more young, and began laying earlier than if they nested elsewhere (Dow and Fredga 1983).

We could not determine breeding status of females based only on weight as was suggested by Wallen (1987) for inland-breeding harlequins. Heavier females tended to be paired regardless of breeding status. We propose that UPNB females were yearlings not yet sexually mature, indicated by lower weight and absence of mate during the laying period. Goldeneyes (*Bucephala clangula* and *B. islandica*) and buffleheads (*B. albeola*), captured while prospecting nest cavities after the laying period, weighed significantly less than nesting adults and were evidently yearlings (Eadie and Gauthier 1987). Visiting a future breeding stream (perhaps a natal stream) in PWS prior to the molt would provide yearling females with familiarity of potential nest sites, foraging areas, and predators (Lack 1966), without the disadvantages of undergoing migration. Use of coastal streams by yearling females hatched on inland streams and summering in PWS might provide a mechanism for dispersal from inland breeding areas.

We believe that PNB females were likely sexually mature adults including 2-year-olds that paired but did not produce clutches. Historical literature indicates that harlequin ducks begin breeding when they are 2 years old (Bent 1962). Two-year-old female harlequins captured during fall in PWS were similar in molt chronology to older females (Dan Essler, National Biological Service, pers. comm.). Kuchel (1977) observed 2 female harlequins return to natal streams at 2 years of age. They arrived paired and established home ranges 2 - 3 weeks later than nesting females, and apparently did not produce broods. Spending a season or two on the breeding grounds may increase success of first breeding attempt for female common goldeneyes (Dow and Fredga 1983) which on average breed at 3 years of age (Dow and Fredga 1984).

Two-year-old females resident in PWS may be more likely to attempt nesting than inland-breeding harlequin ducks because no energetically-costly migration is necessary, and food resources are abundant in intertidal deltas (Dzinbal and Jarvis 1982). The maritime climate remains relatively mild into September, allowing later nest initiation for first-time breeders. Nest initiation in PWS occured from late May through late June in PWS (Figure 16). Two-year old females might also be more likely to attempt nesting if they had spent the previous season on the breeding stream as yearlings (Eadie and Gauthier 1987). Therefore, we believe that breeding females captured in PWS included some component of 2-year-olds that attempted nesting. Pairing, nesting attempts, and prospecting by 2-year-old females might explain the high breeding propensity in PWS relative to inland-breeding harlequins.

Selection of a breeding stream by an individual harlequin duck may be proximately influenced by where that individual was reared. The habitat differences we observed between harlequin duck breeding streams and non-breeding streams, however, suggests that habitat characteristics influence some aspect of population dynamics (such as probability of survival, productivity, or density of breeding ducks on a stream), and hence ultimately regulate use of streams by a population of harlequin ducks.

Stream Habitat

Estuaries.--We selected the stream mouth for local-level habitat study for several reasons, both biological and practical. First, harlequin ducks demonstrated an ecological dependency on the intertidal area where the streams met the sea. Feeding, courtship, resting, and brood-rearing activities on streams were concentrated at or near the stream mouth, and absent elsewhere on the stream (Dzinbal 1982). Before salmon arrived to spawn, we observed harlequins feeding on rising tides at or just below the confluence of tide and stream, following the tideline to the highest point and, unless suitable loafing sites were available (i.e., mid-stream boulders or open, trampled banks), retreating to the lower estuary or coastal rocks with the outgoing tide. During the salmon run, harlequins sometimes fed above the tideline in spawning beds, but generally within 50 m of the high tide area.

Second, the area where the stream meets the tide is unique from the entire remaining length of the stream and therefore provided a standard location for measurements at each stream.

Finally, because it appears that the short, coastal streams in Prince William Sound are principally a travel conduit for harlequin ducks between upper elevation nesting areas and the ecologically important area of the estuary, we believe that differences in breeding and non-breeding streams over their entire length are adequately described using basin geomorphology and drainage network measurements.

Use of Larger Streams.--Analyses of basin geomorphology and drainage network data all indicated that streams used by breeding harlequin ducks were larger than those streams not used for breeding. Basin area was correlated with higher elevations (corr. coeff.= 0.73, $p < 0.0001$). Larger, higher basins retain more melting snow through the summer, and capture more precipitation than lower elevation, smaller basins, thus providing a more stable source of water flow (Verstrappen 1983). Large basins may also buffer against sudden flooding caused by heavy precipitation (Verstappen 1983). Flooding probably reduces brood survival of harlequin ducks (Kuchel 1977, Diamond and Finnegan 1993, Wallen 1987).

Habitat variables collected at stream mouths also indicated that harlequin ducks used larger streams for breeding. Discharge accounted for most variation, probably because it was strongly linked both to basin area, to which it is exponentially related (Verstappen 1983), and to length of drainage networks. Furthermore, stream discharge described a local habitat feature (depth, expanse and velocity of flow) that is of ecological importance to foraging harlequins. There was greater frequency of deep pools along harlequin breeding streams than in non-breeding streams, where a greater frequency of shallow slow water occurred.

Estuary size and width of riparian zone, functions of stream size (Verstappen 1983), were also greater on breeding streams (Table 5). Grassy riparian areas were large, and braided channels were more common, at the mouths of harlequin breeding streams, whereas the mouths of smaller streams were often closed in by dense riparian or forest vegetation. Riparian meadows of grass and shrubs, prevalent on larger streams, were heavily used by brown bears (*Ursus arctos*) for travel and feeding along spawning beds. Once grass was trampled flat by bears, groups of harlequin females used exposed banks for loafing between feeding bouts. Loafing areas were occupied by females sitting side by side, often in physical contact. The same behavior occurred along gravel spits on braided channels, and on large boulders both mid-channel and intertidal. Perhaps wider and more open stream mouths, generally found on larger streams, provided better loafing areas with good visibility to avoid potential predators.

Foraging Habitat.--Gravel beds used by spawning salmon and intertidal areas were generally larger on breeding streams. Habitat selection theory suggests that larger or richer foraging patches promote selection of those patches (Rosenzweig 1985). Foraging patches within the selected intertidal areas are probably used opportunistically, i.e. in proportion to occurrence of prey items within a patch (Rosenzweig 1985). We observed harlequins diving, dabbling, skimming, wading and gleaning prey items from the water's surface to the bottom, from marine coastline to freshwater spawning beds, consuming a variety of invertebrates, alevins and roe (Dzinbal 1982).

Although harlequin ducks are not territorial (Bengtson 1972), we saw individual females defending small (1-m diameter) feeding areas directly above redds of spawning salmon, which they located after much swimming about and peering under water. Defense of feeding areas is perhaps a mechanism limiting numbers of foraging harlequins on any one stream. Larger streams, such as Beartrap River, had up to 30 harlequin ducks present at their mouths. Smaller streams, such as Control Creek in Port Gravina, generally had late-summer hen flocks of 7 or less.

Brood Rearing Habitat.--None of the 30 harlequin duck broods we saw on or near regularly-surveyed streams in EPWS from 1991 - 1993 appeared with adult harlequins in estuaries until the age of two weeks or older. We suspect that avoidance of the estuary reduced chances of brood mortality on the predator-rich spawning beds (pers. obs.). Despite the possible avoidance of predators during the first 2 weeks of life, brood size at fledging averaged 2.7 ducklings over 3 years, whereas clutch size at hatching averaged 5.9 eggs. Though brood-rearing occurred somewhere upstream, telemetric observations indicated that during the first several weeks of brood-rearing, females occasionally flew to the stream mouth area to forage. Overall invertebrate abundance of coastal streams is low (Dzinbal 1982); possibly harlequin ducklings fed on adult flying insects which were abundant along streams. Bengtson (1972) found a relatively high proportion of adult insects in the diets of harlequin ducklings.

Alternately, harlequin ducklings less than 2 weeks of age may have fed on locally abundant aquatic invertebrates within specific microhabitats. Because of a young harlequin duckling's diminutive size, high buoyancy, and inexperience, foraging may be more energy efficient in slow water than in turbulent, fast-flowing water (Kuchel 1977). Regardless of invertebrate abundance, invertebrates may be less available to foraging ducklings in high energy water. Dzinbal (1982) reported that a harlequin brood was reared on a lake near the origin of Stellar Creek (Valdez Arm), Prince William Sound. Harlequin ducklings were also reared on small beaver ponds in Montana (Kuchel 1977). Larger streams in EPWS provide more slow-water areas in upstream reaches than do the steep, small streams (pers. obs.).

We saw only one harlequin brood upstream of an estuary. It was on a stepwise series of fast, turbulent runs and calm pools of Sheep River in Sheep Bay. Water depth was 0.25 - 1.0 m deep with a substrate of cobbles and boulders, approximately 1.5 km downstream of the nesting area. Although dense alder lined both banks, there was little vegetation overhanging the stream and the south-facing channel was exposed to sunlight. A series of small beaver ponds was adjacent to the stream.

Nesting Habitat

Harlequin females exhibited site fidelity, delayed sexual maturity, and what appeared to be prospecting behavior typical of other hole-nesting ducks (Eadie and Gauthier 1985). A hole as perceived by a female harlequin duck, however, may be a tree cavity (Cassirer et al. 1993); depression or cavity on an elevated stream bank, stump, or root wad (Jewett 1931; Latta 1993); crevice in a cliff face (Flint et al. 1983); space beneath a deadfall; a cave within a rock pile; or, for captive-raised harlequins, a large nest box (Charles Pilling, pers. comm.). Woody debris, both as snags and blowdowns, were important to nesting harlequins in Prince William Sound and throughout the Pacific Northwest (Cassirer et al. 1993, Latta 1993). Harlequin females in Iceland searched for nest sites by carefully examining every crevice, bush, and rock along stretches of stream bank (Bengtson 1966).

Aspect was an important component of nesting habitat. Nests were consistently located on southwest-facing, sunny and well-drained stream banks. Harlequin nest sites on stumps, root wads, cliffs, and in tree cavities probably function similarly to elevated stream banks by providing relatively dry sites that are protected from heavy snow and floods, and provide security from predators.

Nests of harlequin ducks in EPWS were generally positioned under the canopy of old-growth forest (which may provide a snow shadow) up to 25 m from the stream, but close enough to canopy gaps caused by stream channels to allow penetration of sunlight. During 1991, nest sites at 220 m elevation on Beartrap River were exposed in late May, while much of the area still snow-covered. Because harlequins nest in mid- to timberline elevations in a region of heavy snowfall (often greater than 7.6 m annually), snow-covered stream banks may delay or limit nesting on any particular stream. Wallen (1987) suggested that snow and lack of leaves on shrubs (nest cover) discouraged early nesting by harlequins at upper elevations of Grand Teton National Park.

To determine whether snow cover had an effect on breeding by harlequin ducks in EPWS, we compared snow depth during the early nest initiation period to indices of harlequin breeding activity by year. In 1992 the spring thaw in Prince William Sound was delayed by cool weather, consequently most basins had snow cover near sea-level elevation in late May. Snow depth at 180 m (mean elevation of harlequin nests was 167 m) near Valdez, Alaska in early May was 56 cm in 1991, 104 cm in 1992, and 58 cm in 1993 (National Weather Service, unpub. data). The number of females captured per hour peaked one week later, and males remained on streams two weeks later, in 1992 than in 1991 (Figure 17). Breeding propensity of captured females and linear brood density decreased in 1992. Five streams on which harlequin broods were observed during surveys in 1991 were absent of broods in 1992.

In contrast, spring of 1993 was similar to 1991, linear brood density increased (Figure 18) and we observed broods on five streams that had no breeding activity in the previous 2 years. While these data are limited, they do indicate a possible extrinsic constraint by weather on harlequin productivity, i.e., increasing snow depth in the spring may decrease nesting attempts.

Nesting by harlequin ducks at higher elevations may improve nest success, despite possible limitations of snow depth during the nest initiation period. Glaucous-winged gulls (*Larus glaucescens*), northwestern crows (*Corvus caurinus*), bald eagles (*Haliaeetus leucocephalus*), mink (*Mustela vison*), river otters (*Lutra canadensis*), and coyotes (*Canis latrans*) were abundant at stream mouths in late June through September, but were not encountered upstream (pers. obs.) In Iceland, harlequins nesting on mid-channel islands on the River Laxa began nesting several km up small tributaries following the spread of mink into the region (Bengtson 1966).

Alternative Breeding Streams

Larger streams had a higher probability of being selected for breeding by harlequin ducks in EPWS. There were exceptions, however, indicating that small streams were used in lower densities. For example, Cloudman Creek on Bligh Island (Figure 2) has a discharge of only 0.53 m^3/s and is 4 m wide at the mouth, yet a harlequin duck brood was present at the outflow of the stream's small intertidal lagoon. This was the largest stream for several km of coastline. We saw two other broods along the coast of western Bligh Island where streams were very small and steep. The nearest anadromous salmon stream was over 10 km distant (ADFG 1993). One brood was observed off Squire Island (60°15', 148°') (Patten 1995), a small island of low elevation, and lacking the larger, anadromous streams typically used by breeding harlequin ducks in EPWS.

The largest streams in EPWS, glacially fed rivers, were apparently not used by harlequin ducks. Our investigation of these rivers, however, were limited to boat surveys. Breeding harlequins used two smaller rivers that were partially of glacial origin but of adequately low silt burden to allow salmon to spawn on gravel beds. One radio-tagged hen was tracked up Beartrap River, over the pass and, unexpectedly, into the next valley of a silty, glacial river. The hen, which we had assumed was laying (indicated by a distended cloaca), had pulled off the radio and dropped it in the river, and no nest was located. Broods have been observed on glacial streams and lakes in British Columbia (Campbell et al. 1990, Breault and Savard 1991).

There are historical accounts of harlequin ducks breeding on small rocky islands along the coast. Salomonsen (1950) reported pairs of harlequins (but not nesting) in late spring on offshore skerries (isolated bedrock islands, sometimes grass-covered, jutting out of the sea) in Greenland. Bengtson (1966) apparently misinterpreted Salomonsen's (1950) account and reported that harlequins breed on skerries in Greenland. Nesting by harlequin ducks was reported on a rocky island in Peter the Great Bay of coastal Siberia (Dement'ev and Gladkov 1967), but the island is similar in size to Bligh Island in EPWS (Times Books Limited 1985), which has at least 1 breeding stream.

While we have evidence of harlequin ducks using relatively small streams on small islands for nesting, we suspect that harlequin ducks do not nest on offshore rocks, islets, or similar habitat in EPWS for several reasons: (1) such sites were usually occupied by glaucous-winged gulls, crows or bald eagles, potential predators of eggs or nesting females; (2) we searched for nests (using experienced, nest-sniffing dogs) on several spits and islets occupied by harlequin ducks in the summer and did not find nests; (3) we observed no downy broods (class Ia-b) on salt or brackish water, indicating that nesting did not occur at the coast; and (4) small, cohesive flocks of molting harlequins in transitional plumage along rocky islets can be easily mistaken for older broods at distances beyond 30 m, leading to the false assumption that the area was used for nesting.

EPWS and WPWS Stream Comparisons

Streams in EPWS appeared to be of similar width at the mouth, but of longer length than those in the WPWS oil spill area. Watershed sizes in WPWS were smaller because of smaller land masses of major islands, multiple fiords, and mountain ranges of lower elevations. Stream lengths appeared to be affected by smaller watersheds in WPWS, while stream widths did not. Volume discharge, which described most variation between breeding and non-breeding streams in EPWS, was not measured on streams in WPWS.

Productivity

Although my estimate of breeding propensity for all females was higher than that of Dzinbal (1982) -- possibly due to scale differences in study areas -- both indicated higher breeding propensity in PWS than on inland rivers of Idaho (Cassirer and Groves 1992, Cassirer 1992), Montana (Genter 1993), and Wyoming (Wallen 1987) (Table 20). Unlike most inland regions, nesting areas in PWS were not subject human disturbance, which may contribute to lower breeding propensity (Kuchel 1977, Wallen 1987).

My estimate of breeding propensity for adult females in PWS was similar to that of Bengtson and Ulfstrand (1971) for 2 inland rivers in Iceland (Table 20). Flocks of 5 - 15 females were common on streams of both PWS (Crowley unpbl. data) and Iceland (Bengtson and Ulfstrand 1971) from June through August, but no subadult females were detected on the Icelandic steams. Estimates of adult breeding propensity are likely more useful for assessing annual breeding potential in the population.

We could not determine why PNB females in PWS did not nest. Bengtson and Ulfstrand (1971) linked lower breeding propensity to limited food resources, which we do not believe was an important factor in PWS (Dzinbal and Jarvis 1982). Limited availability of nest sites by snow (Wallen 1987) or by habitat type (Bengtson 1972) could result in lower breeding propensity of harlequin ducks.

Estimates of breeding density for streams in PWS were relatively low. We adjusted Dzinbal's (1982) calculation of breeding density with our measurement of length of

Stellar Creek (Figure 1). The resulting density of 0.9 - 1.3 breeding hens per km in 1979 and 1980 was higher than in 1991 - 1992. This apparent decline in the number of breeders, and overall decline in numbers of harlequins using the area (Crowley unpbl. data) since 1980, may be a result of the *Exxon Valdez* oil spill (Patten 1995), which occurred 24 km south. Pair densities varied in other regions (Table 20) probably reflecting varying food resources, availability of nesting habitat (Bengtson and Ulfstrand 1971, Bengtson 1972) and methods used in calculating density. The latter factor suggests problems in using density to assess productivity within and between regions.

Observed mortality of harlequin ducklings in PWS was highest from age class IIb to IIc, the age at which most broods first appeared near stream mouths. Potential predators attracted to lower stream reaches during the salmon spawn may have contributed to observed increase in duckling mortality (Dzinbal 1982). Mortality of ducklings was generally lower in inland regions (Table 20), with unusually high mortality ascribed to flooding on inland streams (Kuchel 1977, Wallen 1987, Diamond and Finnegan 1993). We believe flooding is a less important factor than predation for coastal streams in PWS. Broods were generally hatched after high spring water and reared during receding water levels (Dzinbal 1982). Furthermore, potential effects of flooding are probably negligible once broods begin using intertidal areas for foraging.

Average brood size of fledged harlequins, 1991- 1993, combined, was similar to that of the Stellar Creek area from 1979 to 1980 (Dzinbal 1982; Table 5). Our speculative assessment of recruitment provided a value comparable to that of Dzinbal (1982) for 1979 (Table 20). This just exceeded half of the lowest rate reported over five years on interior streams of Iceland (Bengtson 1972). Estimates of both brood size and recruitment of fledged young in PWS were lower than for inland regions (Table 5) except during years of flooding (Kuchel 1977, Wallen 1987, Diamond and Finnegan 1993).

Our estimates of breeding propensity and recruitment (subject to violations of our assumptions differentiating female breeders from non-breeders, and adults from subadults) can be generalized as follows: (1) if any adult females were misidentified as subadults (e.g., a non-breeding adult was captured without a mate in attendance), then our estimates of breeding propensity and recruitment are high and density low (or vice versa); (2) if breeding females were misidentified as adult non-breeders (e.g., a non-breeder was captured early and began laying late) then the estimate of breeding propensity is low and recruitment (young per breeder) is slightly high (or vice versa); (3) if females incapable of flight (assumed subadults) in predominantly male molting flocks include some adult females, then our estimate of recruitment is high. Despite potential violation of assumptions and corresponding adjustment to estimates, the evidence suggests productivity in EPWS was low relative to other studies (Table 20).

Limiting Factors.-- Environmental cues and physiological responses causing deferred breeding in harlequin ducks are not well known. Female harlequin ducks in PWS were probably not limited in food resources on streams because of their use of intertidal foraging habitat before and during the nesting period. Snow may limit availability of nesting habitat during some years, causing delayed or curtailed breeding. The innate low productivity of harlequin ducks (delayed sexual maturity, small clutch size, and deferred breeding) appears to be an important factor in limiting annual recruitment. Bengtson (1972) suggested that these characteristics were adaptations for survival in less-productive, subalpine to arctic communities. Charnov and Krebs (1974) proposed that because demands of breeding decrease chances of survival, clutch size in birds is probably a compromise between producing maximum young and survival of the female to breed again. Dow and Fredga (1984) found evidence that common goldeneye females producing fewer young per year had higher reproductive output over their lifetime than those producing large clutches, suggesting a reproductive strategy used by long-lived sea duck species. Predation of ducklings may have also been an important limiting factor.

STATUS OF RESTORATION

Current Restoration Activity

Restoration of harlequin ducks is being pursued through strategies that protect habitats and reduce exposure to residual oil in the spill area. Habitat protection throughout Prince William Sound by land acquisition and land use regulation has the greatest potential to promote natural recovery of breeding birds and annual production. Production in EPWS must sustain regional harlequin duck population, and is the most likely source of pioneers to the spill area. Careful management of timber harvest in vital nesting stream habitat is the primary challenge to maintain harlequin duck production in the east and ensure optimum habitat conditions for breeding birds in the spill region. Ongoing research in cleaning blue mussel beds in WPWS could aid in restoring harlequin ducks by removing sources of continued oil exposure that may be affecting reproductive success.

Management Recommendations

Locating coastal streams used by breeding Harlequin ducks can be accomplished efficiently by conducting surveys in late May and early June, when breeding pairs are readily observed at or near stream mouths. Brood surveys conducted when young are approximately 2 - 3 weeks of age (presumably earlier with decreasing latitude) when broods begin appearing at the coast can help confirm or provide additional breeding streams. Modelling watersheds characteristics, particularly those pertaining to size and gradient, of breeding streams within the study area using topographic maps or a geographic information system can provide evidence of probable breeding streams (on which harlequins were not directly observed) for further investigation.

Stream-side buffer strips for structural and visual isolation should be provided on those watersheds where timber will be harvested. Petts (1990) stated that the most important parameter for effective management of land-water ecotones is the minimum size (i.e. width) required to sustain riparian habitat and its function as a flow regulator between ecosystems. Petterjohn and Correll (1984) reported that 50 m of riparian forest habitat removed most of the excess nutrients and pollutants from overland and throughflow water in an agricultural watershed. Cassirer and Groves (1990) observed harlequin broods more often on undisturbed streams away from roads and human activity in National Forests of northern Idaho. They also recommended a 50 m undisturbed riparian corridor, visual isolation, and limited human activity during the breeding season to minimize impacts of timber harvest.

Eight of the 10 harlequin nests we found were on small, steep tributaries of large streams that had discharges of less than 0.5 m^3/s and were less than 3 m wide. All nests were far above stream reaches used by spawning salmon. State guidelines regarding forest practices on private timberlands require leaving forested buffer strips of 30.5 m (100 ft) only on stream reaches used by spawning salmon (Alaska Department of Natural Resources as ammended 1990) which would not protect tributaries used by nesting harlequin ducks. If timber harvest extends into the upper reaches of basins, forested buffers along first and second order streams will be necessary to protect nest sites of harlequin ducks. We believe that siltation of breeding streams and human and machinery disturbances associated with logging would be a much more serious hindrance to reproducing harlequins than local reductions in nesting habitat. Harlequin ducks in Iceland, Greenland, Siberia, and western and northern Alaska do not nest in old growth forest (Bellrose 1980), but do require adequate streamside vegetation ranging from dwarf birch (*Betula nana*) to *Salix* spp. (Bengtson 1972).

Human activities near intertidal stream deltas, estuaries, and coastline where harlequin ducks forage, molt, and rest must be managed to minimize disturbance. Aquaculture, residential development, motorized watercraft and camping near important breeding and molting areas could potentially displace harlequins into less favorable habitat. For example, the small cove of Gregorioff Creek in Jack Bay of Valdez Arm consistently has the highest concentration of breeding pairs in spring, had the highest nesting density of any stream in 1991, and is the only concentration of Harlequins within approximately 25 km of coastline. This area is slated for residential development by the city of Valdez. Because of the patchiness of harlequin distribution, development of Gregorioff Creek area will likely reduce productivity in the entire Jack Bay region.

Monitoring of harlequin duck populations should continue throughout Prince William Sound. Monitoring would provide more conclusive information on factors affecting annual breeding and production by harlequin ducks, as well as evidence of successful restoration in WPWS, where continued population decline has been apparent (Patten

1995). Continued monitoring would also provide insight into long term effects of oil exposure on a species sensitive to habitat disturbance.

CONCLUSIONS

Breeding Stream Selection.--Harlequin ducks breeding in EPWS selected the largest anadromous salmon streams available for nesting. Volume discharge of breeding streams averaged 3.2 m^3/s and was the most important factor in habitat variation between streams used and not used by breeding harlequins. While large streams had a higher probability of being selected for breeding by harlequins, there is evidence that small, steep streams may be used for nesting by some coastal-breeding harlequins where large streams are not available. The largest streams in Prince William Sound, silt-laden, glacially fed rivers, were not apparently used by breeding harlequins.

Nest Site Selection.--Harlequin ducks in EPWS nested on southwest facing, steeply sloping banks of small, first order tributaries near timberline elevation. Nests were associated with woody debris and shrubs, in shallow depressions or cavities, and were beneath the canopy of old growth forest.

Productivity.--Except for breeding propensity, indices of productivity of harlequin ducks in EPWS was low relative to other breeding populations. Food resources are probably not a limiting factor. Inherent low breeding propensity of female harlequins, predation on ducklings, and late snow pack at nesting elevations probably limit productivity in EPWS.

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Table 1. Location, length and dates of shoreline surveyed (☒) by boat for harlequin ducks during spring and summer in eastern Prince William Sound, Alaska, 1991 - 1993.

	Spring		Molt/brood		
	1991	1992	1991	1992	1993
Survey shoreline (km)	5/22- 5/30	5/16- 5/22	7/23- 8/09	7/28- 8/20	8/09- 8/18
Port Gravina (99.8)	☒	☒	☒	☒	☒
Sheep Bay (38.8)	☒	☒	☒	☒	☒
Simpson Bay (42.6)	☒	☒	☒	☒	☒
Nelson Bay (20.4)		☒			☒
Orca Inlet (17.1)		☒			☒
Red-Knowles, Goose (24.5)	☒	☒			
Port Fidalgo S&W (148.2)	☒	☒	☒	☒	☒
Fidalgo NE & Lagoon (18.0)				☒	☒
Tatitlek/Bligh/Busby (53.8)	☒	☒	☒	☒	☒
Valdez Arm & Bays (161.7)	☒	☒	☒		☒
Heather Bay (19.6)			☒	☒	☒
Hinchinbrook (N and W) (30.0)		☒	☒		
Port Etches (51.5)			☒	☒	
Hawkins Is. (N side) (28.1)	☒	☒			
Total survey length (km):	544.9	635.0	698.6	410.9	620.0

Table 2. Spring and summer near-shore boat surveys for pairs, molting flocks and broods of harlequin ducks in eastern Prince William Sound, Alaska, 1991-1993.

	Spring Survey		Molt/brood survey		
	1991	1992	1991	1992	1993
Survey dates	5/22- 5/30	5/16- 5/22	7/23- 8/09	7/28- 8/20	8/09- 8/18
Survey length (km)	545	635	700	410	620
Total ducks	474	1000	1396	743	1373
Ducks/km	0.87	1.58	1.99	1.81	2.20
Average ducks/km		1.23			2.00
Standard deviation		0.36			0.16
Pairs (n)	49	116			
Males (n)	53	318	491	359	644
Females (n)	54	239	181	129	385
% males (of total known)	49	57	73	74	63
Sex unknown	367	443	724	255	344
Broods (n)			16	5	11
Broods/100 km			2.28	0.94[a]	1.77
Average broods/100k					1.66
Standard deviation					0.55

[a] Includes an additional 120 km surveyed only for broods.

Table 3. Averages and standard deviations of morphologic measurements of harlequin ducks captured in Prince William Sound, Alaska, 1991-1992 combined.

	Weight (g)	Tarsus (mm)	Culmen (mm)	Wing (mm)
All males	615.2	37.87	27.98	159.4
SD[a]	40.1	2.29	1.46	7.8
n	17	19	19	12
All females (♀♀)	561.3	35.33	26.33	152.5
SD	51.6	2.33	1.53	5.6
n	41	42	42	25
Breeding ♀♀[b]	576.0	35.49	26.20	152.9
SD	51.9	2.34	1.34	6.8
n	26	26	26	13
Nonbreeding ♀♀	543.2	35.07	26.24	152.1
SD	39.6	2034	1.84	4.2
n	15	16	16	12
Paired nonbreeding ♀♀[c]	568.5			
SD	41.9			
n	6			
Unpaired nonbreeding ♀♀	505.0	36.12	27.31	152.0
SD	21.8	0.79	2.09	6.2
n	7	5	5	4

[a] Standard deviation.

[b] Breeding determined by presence of brood patch or distended cloacal aperature from egg-laying.

[c] Paired status based on whether female was accompanied by a male before striking mist net.

Table 4. Distances between capture and molting sites for individually marked harlequin ducks captured on breeding streams in eastern Prince William Sound, Alaska, 1991 - 1992.

Sex	Age[a]	Date captured	Capture stream	Date observed	Molt location	Moved (km)
M	ATY	01Jun92	Beartrap	29Jul92	Sheep Bay Islands	40
M	ATY	04Jun92	Sheep	29Jul92	Sheep Bay Islands	5
M	ATY	04Jun92	Sheep	10Jul92	W Olsen Headlands	35
M	ATY	07Jun92	Beartrap	28Jul92	W Olsen Headlands	13
F	ASY	21Jun92	Stellar	08Aug92	Point Freemantle	19
M	ATY	03Jun92	Sheep	11Aug93	SE Port Gravina	29
					Average:	23
					SD[b]:	13

[a] ATY = after third year, ASY = after second year.

[b] SD = standard deviation.

Table 5. Comparison of characteristics at the mouths of streams used and not used by harlequin ducks breeding in Prince William Sound, Alaska, 1991 - 1993.

	Breeding		Non-breeding					P-
Variable	Mean	SD[a]	Mean	SD	Unit	Transf.	Test[b]	value
Volume discharge	3.18	2.11	0.80	0.58	m^3/s	Log	t	< 0.001
Stream width	16.56	9.82	9.58	4.08	m	Log	t	< 0.010
Riparian width	116.10	135.70	44.65	44.64	m	Log	t	0.046
Area of estuary	50.29	63.76	17.33	37.73	km^2	Log	Z	0.003
Channel aspect[c]	210-240		300-330		°	Ranks	U^2	0.50
Channel slope	2.85	1.81	5.53	12.92	%	Log	Z	0.23
Mean sideslope	13	8	14	12	%	Log	t	0.86

[a] Standard deviation.

[b] Student's t, Mann-Whitney-Wilcoxon Z, and Watson's U^2 at α-level ≤ 0.05.

[c] Reported values are most frequent occurrence (mode) in 30° category.

Table 6. Comparison of categorical variables measured at the mouths of streams used and not used by harlequin ducks breeding in Prince William Sound, Alaska, 1991 -1993. Reported P-values are 1-tailed, n = 24 per sample.

	Occurrence (%)				Occurrence (%)		
Variable	Used	Not used	P - value[a]	Variable	Used	Not used	P - value[a]
Hydrology				Substrate			
Deep fast	7	0	<0.01	Gravel	20	35	0.24
Shallow slow	10	45	<0.01	Cobble	11	12	0.50
Shallow fast	50	50	0.50	Boulder	4	1	0.05
Deep slow	1	0	0.50	Sand	1	0	0.50
Falls	0	1	0.50	Bedrock	0	0	no test
Boulder run	0	0	no test[b]				
Pocket water	0	0	no test				
Channel type				Sideslopes			
Straight	10	20	0.33	Enclosing	15	20	0.50
Slight curve	36	65	0.06	Moderate	30	40	0.37
Curve	30	10	0.12	Distant	55	40	0.26
Braided	25	5	0.09				

[a] Fishers Exact Test for Homogeneity at α-level ≤ 0.05.

[b] Not tested because of identical parameters in response categories.

Table 7. Comparison of bank composition at mouths of streams used and not used by harlequin ducks breeding in Prince William Sound, Alaska, 1991 - 1993. There were no significant differences between variables at $\alpha \leq 0.05$. Reported P-values are 1-tailed, n = 24 per group.

	% OCCURRENCE		Fisher's Exact Test for Homogeneity
	Breeding	Non-breed	P-value
Lower bank habitat:			
Grass/forbes	48	60	0.185
Gravel	33	25	0.500
Shrubs	3	0	0.500
Tree/shrub mosaic	10	8	0.500
Trees	3	3	0.500
Bedrock	5	5	0.692
Forest debris	0	3	0.500
Sand	5	0	0.247
Mid-bank habitat:			
Grass/forbes	23	18	0.390
Gravel	0	0	no test[a]
Shrubs	43	35	0.323
Tree/shrub mosaic	20	13	0.378
Trees	15	30	0.090
Bedrock	0	5	0.247
Forest debris	0	5	0.500
Sand	0	0	no test
Upper bank habitat:			
Grass/forbes	0	0	no test
Gravel	5	0	0.247
Shrubs	25	20	0.395
Tree/shrub mosaic	5	10	0.338
Trees	65	70	0.635
Bedrock	0	0	no test
Forest debris	0	0	no test
Sand	0	0	no test

[a] Not tested because of identical parameters in response categories.

Table 8. Comparison of characteristics of basins and drainage networks from streams used and not used by harlequin ducks breeding in Prince William Sound, Alaska, 1991 -1993.

	Breeding		Non-breeding					
Variable	Mean	SD	Mean	SD	Unit	Transf.	Test[a]	P-value
Basin area	23.52	19.01	7.09	5.25	km^2	Log	t	<0.0001
Basin perimeter	19.55	10.17	10.71	4.45	km	Log	t	<0.0001
Basin relief	1141	388	810	225	m	none	Z	0.0017
Average basin slope	15.51	5.34	21.73	10.18	%	Log	Z	0.02
Channels length	13.20	9.44	4.64	2.99	km	Log	Z	<0.0001
Bifurcation ratio	4.01	1.73	2.67	1.34		Log	Z	<0.0001
Channel frequency	5.38	4.16	2.33	1.81		Log	Z	0.0004
Basin aspect[b]	210-240		270-299		°	Ranks	U^2	>0.30
Channel slope	7.95	3.97	11.71	7.52	%	Logit	t	0.10
Stream density	0.67	0.26	0.73	0.32	$^{km}/km^2$	none	t	0.49
Basin shape	2.15	1.07	4.04	2.22		none	t	0.50
Number of lakes	0.67	1.05	0.75	1.19		Log	t	0.68

[a] Student's *t*, Mann-Whitney-Wilcoxon *Z*, and Watson's U^2 at α-level ≤ 0.05.
[b] Reported values are most frequent occurrence (mode) in 30° categories.

Table 9. Single- followed by multi-factor logistic regression analyses of habitat variables from streams used and not used by harlequin ducks breeding in Prince William Sound, Alaska, 1991 - 1993.

	Single-factor logistic regression			Multi-factor logistic regression			
		Maximum likelihood			Maximum likelihood		Likeli. ratio
Hierarchy level	Variables	Chi^2	P-value	Remaining variables	Chi^2	Pvalue	Pvalue
	Basin area	10.93	<0.01				
	Perimeter	9.53	<0.01	Area[*]	4.13	0.04	
Basin	Relief	8.66	<0.01	Perimeter	0.73	0.39	0.48
	Shape	8.41	<0.01	Relief	0.64	0.43	0.50
	Mean sideslopes	4.35	0.04	Shape	0.02	0.88	0.46
	Aspect	1.31	0.25	Sideslope	0.47	0.49	0.48
	Channel length	10.67	<0.01				
	Channel frequency	10.01	<0.01	Length[*]	4.59	0.03	
Drainage density	Gradient	3.86	0.05	Frequency	0.14	0.71	0.51
	Stream density	0.50	0.48	Gradient	0.52	0.47	0.42
	Bifurcat. ratio	7.62	<0.01	Bifurcat.	2.54	0.11	0.50
	Number of lakes	0.18	0.67				
	Discharge	11.74	<0.01	Discharge[*]	10.18	<0.01	
	Stream width	6.36	0.01	Estuary	6.95	0.33	0.90
Stream Mouth	Riparian width	3.71	0.05	Stream width	0.14	0.74	0.68
	Estuary area	7.65	<0.01				
	Mean sideslopes	0.03	0.86				
	Channel gradient	0.02	0.89				

[*] The indicated variable remaining within each hierarchical level formed a reduced model that adequately explained a significant difference between stream groups at $\alpha \leq 0.05$..

Table 10. Logistic regression modeling of basin area, channel length and volume discharge; a reduced model where only the discharge term adequately explained variation between streams used and not used by harlequin ducks breeding in Prince William Sound, Alaska, 1991 - 1993.

Hierarchical level	Models tested	Maximum likelihood Chi^2	Maximum likelihood P-value	Likelihood ratio P-value
Basin	Area*	2.14	0.1431	
	Length	0.65	0.4185	0.4914
Drainage density	Length*	0.05	0.8267	
	Discharge	7.28	0.0070	0.8714
Stream mouth	Discharge*	6.14	0.0132	
	Area	0.35	0.5519	0.8796
	Discharge	6.13	0.0133	
Combined	Area	0.90	0.3426	0.8796
	Length	0.60	0.0133	

*Variables remaining within each hierarchical level from initial analyses.

Table 11. Locations of 10 harlequin duck nests on coastal, mountain streams in old growth forests of Prince William Sound, Alaska, 1991 and 1992.

Year	Stream name	Location	Alaska Stream Catalog number	Latitude Longitude	Elevation (m)
1991 1992	Beartrap[a]	Beartrap Bay Port Gravina	221-30-10480	60°46'30" 146°28'00"	220 225
1991	Gregorioff	Jack Bay Valdez Arm	221-50-11230	61°00'30" 146°34'45"	46
1991	Gregorioff	Jack Bay Valdez Arm	221-50-11230	61°00'15" 146°34'15"	122
1991	Nuchek	Port Etches Hinchinbrook Island	228-60-18120	60°15'30" 146°28'00"	150
1992	South Fork Constantine	Hinchinbrook Island	288-60-18150	60°22'45" 146°31'30"	90
1992	Hanning	Montague	277-10-17110	59°59'05" 147°35'30"	150

[a] Five nests were found, 2 and 3 during 1991 and 1992, respectively.

Table 12. Characteristics of habitat at 10 nest sites of harlequin ducks in Prince William Sound, Alaska, 1991 - 1992.

Location	Volume Discharge m^3/s	Stream Width m	Riparian Width m	Channel Slope %	Nest Bank Slope %	Stream Channel Aspect °	Nest Bank Aspect °	Dist. to Stream m	Dist. to Forest m	Dist. to Coast km
Beartrap	0.26	1.5	9.0	30	45	321	238	7.1	0	1.8
Beartrap	0.27	3.0	8.0	30	50	321	238	5.0	3	1.8
Beartrap	0.26	1.5	9.0	30	45	321	238	25.0	0	1.8
Beartrap	0.27	2.5	8.0	30	45	321	238	8.0	0	1.8
Beartrap	0.27	3.0	8.0	30	45	321	238	12.0	0	1.8
Gregorioff	1.24	6.0	1.0	7	90	320	228	1.0	0	0.6
Gregorioff	0.83	4.0	6.5	17	80	320	222	1.5	5	1.5
Nuchek	0.13	3.5	5.0	5	35	178	229	22.0	0	0.9
Hanning	3.59	7.6	12.0	5	75	242	218	4.0	3	3.0
Constant	0.55	3.5	7.0	10	20	332	241	12.0	0	3.0
Mean	0.76	3.6	7.4	5.4	53	320[a]	238[a]	9.8	1	1.8
SD	1.05	1.9	2.9	18.1	22			8.2	1.8	0.8

[a] Mode is measure of central tendency.

Table 13. Four groups of directional aspects from streams used for nesting by harlequin ducks in Prince William Sound, Alaska, with the full data set (n = 10) and without 4 redundant nest sites on Beartrap River.

	Full data set		Partial data set	
Variable	U^2 [a]	P-value[b]	U^2	P-value
Nest Bank	0.728	<0.001	0.427	<0.01
Nest Channel	0.464	<0.001	0.206	$0.05<p<0.10$
Mouth Channel			0.223	$0.02<p<0.05$
Basin			0.244	$0.02<p<0.05$

[a] Watson's U^2 test for circular distributions (Zar 1984).

[b] A P-value of ≤ 0.05 indicates a significant difference from a randomly distributed sample.

Table 14. Breeding status of female harlequin ducks captured on streams in Prince William Sound, Alaska, 1991 - 1992. Breeders were determined by presence of distended cloacal aperture and brood patch.

	1991	1992
Total females (♀♀)	16	32
Total breeders (B)	12	20
Paired breeders (PB)	4	2
Unpaired breeders (UPB)	0	10
Other breeders*	8	8
Total non-breeders	4	12
Paired nonbreeders (PNB)	1	6
Unpaired nonbreeders (UPNB)	2	5
Other nonbreeders (NB)*	1	1
% Females breeding (B/♀♀)	75	62.5
Adult females (B+PNB+NB)	14	27
Subadult females (UPNB)	2	5
% Adults (adults/♀♀)	87.5	84
% Adults breeding (B/adults)	86	74

* Pair status unknown.

Table 15. Status and fate of harlequin duck nests found on streams in eastern Prince William Sound, Alaska, 1991 - 1992.

Location	Date located	Nest status	Incubation stage	Eggs present	Eggs hatched	Addled eggs	Shell membranes
Beartrap*	06Jul91	active	hatched,dry	7	7	0	7
Beartrap*	28Jun91	active	12 days	6	6	0	6
Beartrap	06Jul91	inactive	hatched	7	6	1	6
Beartrap	28May92	inactive	unknown	3	unknown	0	0
Beartrap	15Jul92	inactive	unknown	1	unknown	1	0
Gregorioff*	27Jun91	active	15 days	4	unknown	0	unknown
Gregorioff	27Jun91	active	20-25 days	7	unknown	0	unknown
Nuchek*	03Jul91	active	12 days	6	6	0	unknown
Hanning	01Jul92	active	29 pipped	6	6	0	unknown
Constantine	01Jul92	active	15 days	6	unknown	0	unknown
Revisited nests			Date revisited				
Beartrap	06Jul91	hatched	09Jul91		7	0	7
Beartrap	28Jun91	pipping	15Jul92	6	6	0	6
Gregorioff	27Jun91	inactive	29Jul93			0	0
Nuchek	03Jul91	inactive	16Jul92		6	0	6

Average clutch size: 6.125 (n = 8 known)

* Revisited nests

Table 16. Density (linear km) of adult female harlequin ducks breeding along streams in eastern Prince William Sound, Alaska, 1991-1992.

Stream	AWC#[a]	Breeders caught/observed 1991	Breeders caught/observed 1992	Estimated total breeders 1991	Estimated total breeders 1992	Stream length (km)	Breeding density (/km) 1991	Breeding density (/km) 1992
Beartrap	221-30-10480	3	5	6	6	10.6	0.6	0.6
Sheep	221-20-10360	2	5	6	6	14.5	0.4	0.4
Stellar	221-50-11530	2	0	4	2	8.7	0.5	0.2
Constantine	228-60-18150		4		6	14.3		0.4
Fish	221-40-10950	2	1	3	1	11.4	0.3	0.1
Gregorioff	221-50-11230	3	0	3	1	2.7	1.1	0.4
Nuchek	228-60-18120	1	0	2	1	8.5	0.2	0.3
						Average:	0.5	0.3
						SD:	0.3	0.2

[a] AWC = Catalog of Waters Important for Spawning, Rearing or Migration of Anadromous Fishes, Alaska Department of Fish and Game, Habitat Division.

Table 17. Age classes and mortality of known-age harlequin duck broods observed in eastern Prince William Sound (EPWS) and the oil spill area (WPWS), Alaska, 1991 - 1993.

		Number of Broods Observed						
		1991		1992		1993		Total
Age class	Age (days)	EPWS	WPWS	EPWS	WPWS	EPWS	WPWS	no.
Hatch[a]	< 1	3	0	2	0			5
Ia - IIa	1-21	5	0	0	1	1	0	7
IIb	22-27	2	3	1	0	3	2	11
IIc	28-35	6	0	4	0	3	1	14
III	36-42	3	1	0	0	4	0	8
Known-age		19	4	7	1	11	3	45
Unknown age		0	1	0	2	0	0	3
	Totals:	19	5	7	3	11	3	48

Brood age class	Average brood size	SD	Homogeneous groups (⊗)[b] $P > 0.05$	Percent mortality between ages	Cumulative percent mortality
Clutch[c]	6.13	0.93	⊗		
Hatch - IIa	5.17	2.25	⊗⊗	16	16
IIb	3.82	1.53	⊗⊗	26	38
IIc	2.57	1.54	⊗	33	58
III	2.50	1.22	⊗	3	59
Unknown	3.13	1.20			

---

[a] Broods from 5 nests of known hatch success added to class Ia.

[b] Brood age classes having the symbol ⊗ in the same column are not significantly different from one another (ANOVA multiple range analysis at $\alpha \leq 0.05$). Age class IIc, for example, is not significantly different in size than IIb and III, but is signifcantly lower than clutch size and class Hatch-IIa.

[c] Average clutch size ($n = 8$) used as baseline brood size.

Table 18. Estimated recruitment of harlequin duck fledglings in eastern Prince William Sound (EPWS), Alaska. Percentages of adults and breeders estimated from 1992 captures and molt surveys (Table 14).

	EPWS 1992
a. Total young observed	23
b. Estimated fledglings[a]	18
c. Flight-capable ♀♀ (adults)	28
d. % adults	84
e. Adult ♀♀ (c*d)	23.5
f. % breeding	74
g. Breeding ♀♀ (e*f)	17.4
Fledged young/adult (b/e)	0.8
Fledged young/breeder (b/g)	1.0

[a] Number of Class I-IIb young reduced to simulate pre-fledging mortality (Table 17).

Table 19. Chronology of 7 active nests of harlequin ducks breeding in Prince William Sound, Alaska, 1991 - 1992.

		Approximate dates (± 2 days)			
Location	Date located	Nest initiation	Began incubation	Hatching	Fledging
Beartrap	06Jul91	22May	05Jun	05Jul*	15Aug
Beartrap	28Jun91	04Jun	16Jun	16Jul*	27Aug
Gregorioff	27Jun91	04Jun	12Jun	12Jul	23Aug
Gregorioff	27Jun91	26May	09Jun	09Jul	21Aug
Nuchek	03Jul91	09Jun	21Jun	21Jul	01Sep
Hanning	01Jul92	21May	02Jun	02Jul*	13Aug
Constantine	01Jul92	04Jun	16Jun	16Jul	27Aug

* Hatch dates known to within 1 day.

Table 20. Productivity of harlequin ducks in Prince William Sound (PWS), Alaska, compared to inland breeding regions.

Region	Adult % breeding propensity	Breeding density (No./km)	Fledged brood size	Duckling mortality (%)	Fledged young/ female	Breeding success (%)
PWS 1991-1993	74-86	0.3-0.5	2.5	59	0.8	
PWS 1979-1980[a]	50-53*	1.3-1.8	2.5-2.7	33-50	0.3-0.8	57-67
Idaho[b]	33-36*	0.06-1.3	3.3	27-55	1.2	33-36
Wyoming[c]	38*	0.89	4.5		1.9	
Montana	41*[d]	0.05-1.2[de]	3.5-3.9[e]	25-82[e]	0.3-1.44[e]	41[d]
Iceland[f]	70-85	0.2-7.1	2.9	44	1.5-2.2	87

* Assumes all females were adults (usually paired).

[a] Dzinbal (1982).

[b] Cassirer (1992), Cassirer and Groves (1990, 1992, 1994).

[c] Wallen (1987).

[d] Genter (1992).

[e] Kuchel (1977), Diamond and Finnegan (1993).

[f] Bengtson (1972).

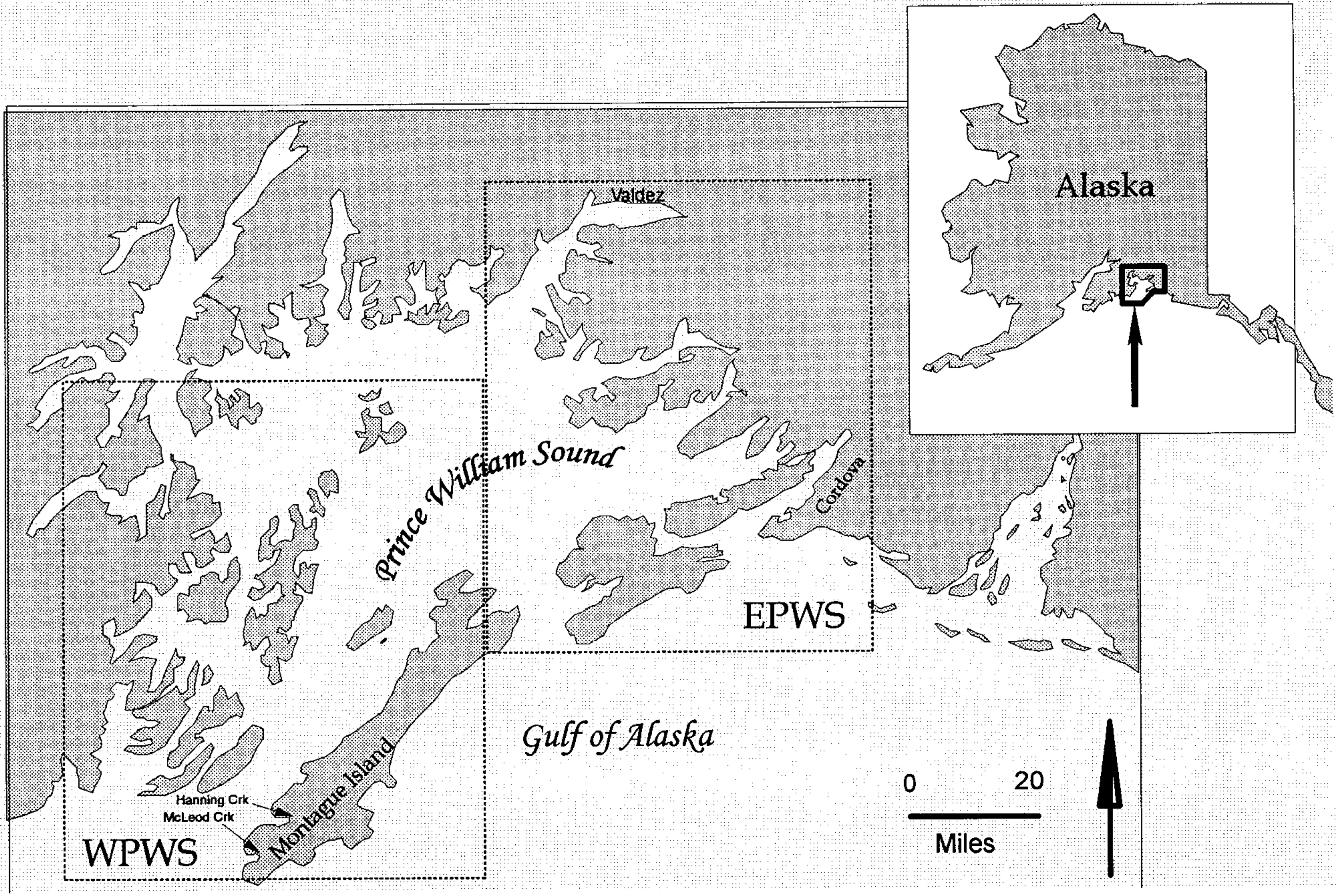


Figure 1. Oil spill study area (WPWS) and breeding habitat study area (EPWS) in Prince William Sound, Alaska.

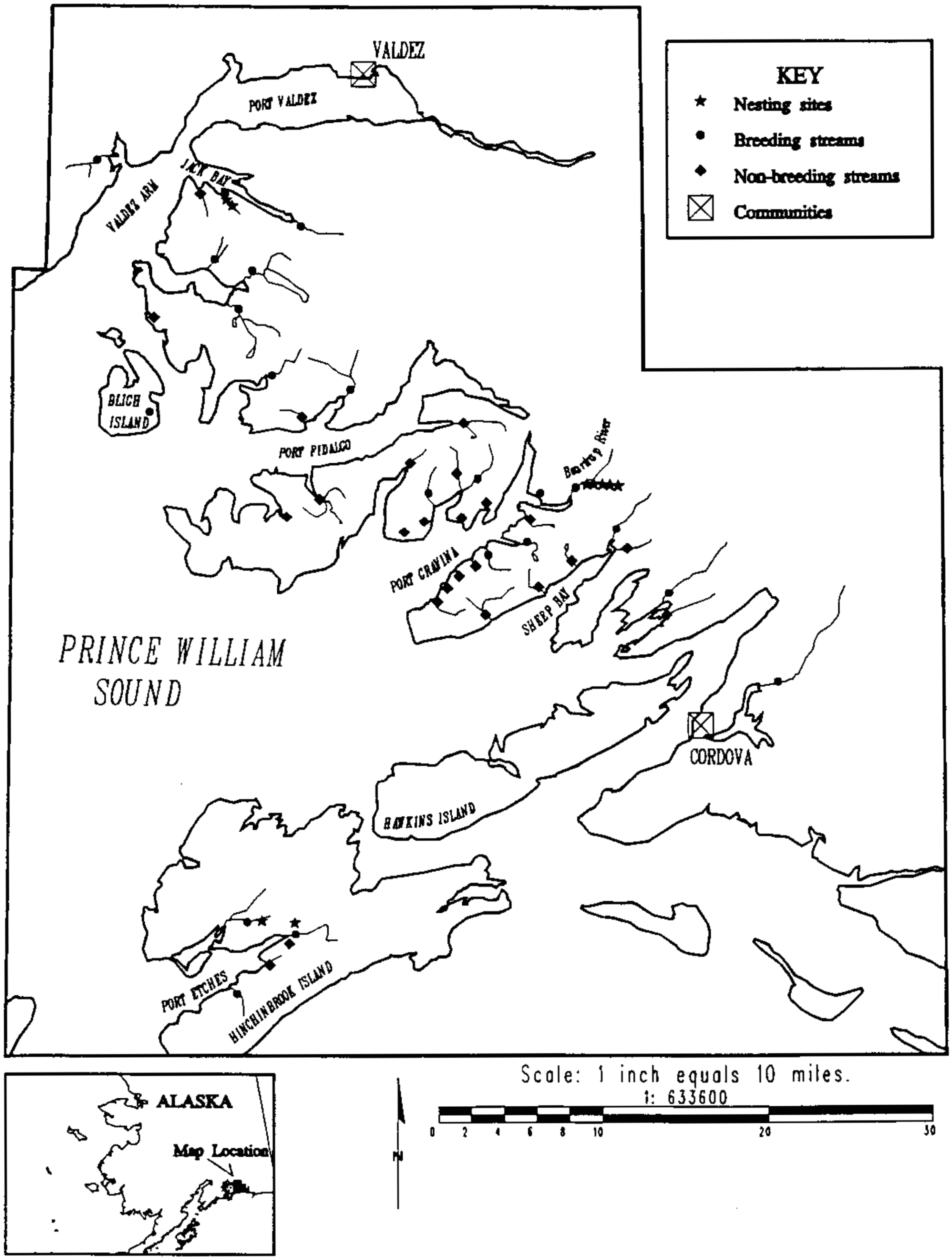
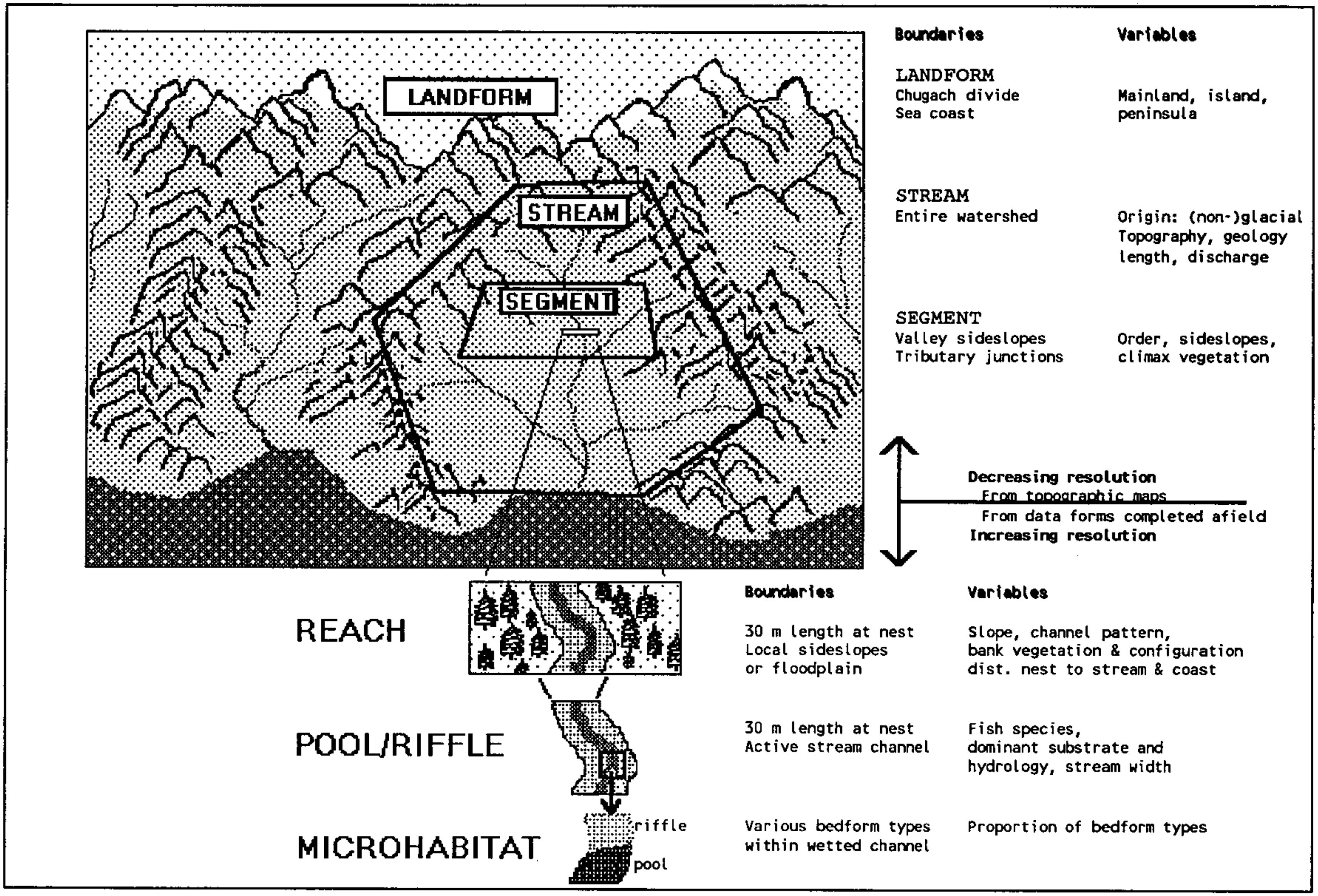


Figure 2. Study area for harlequin ducks breeding in Prince William Sound, Alaska, 1991 - 1993.



Boundaries	Variables
LANDFORM Chugach divide Sea coast	Mainland, island, peninsula
STREAM Entire watershed	Origin: (non-)glacial Topography, geology length, discharge
SEGMENT Valley sideslopes Tributary junctions	Order, sideslopes, climax vegetation

	Boundaries	Variables
REACH	30 m length at nest Local sideslopes or floodplain	Slope, channel pattern, bank vegetation & configuration dist. nest to stream & coast
POOL/RIFFLE	30 m length at nest Active stream channel	Fish species, dominant substrate and hydrology, stream width
MICROHABITAT	Various bedform types within wetted channel	Proportion of bedform types

Figure 3. Conceptual diagram of a hierarchical system used to describe and classify stream habitat in Prince William Sound.

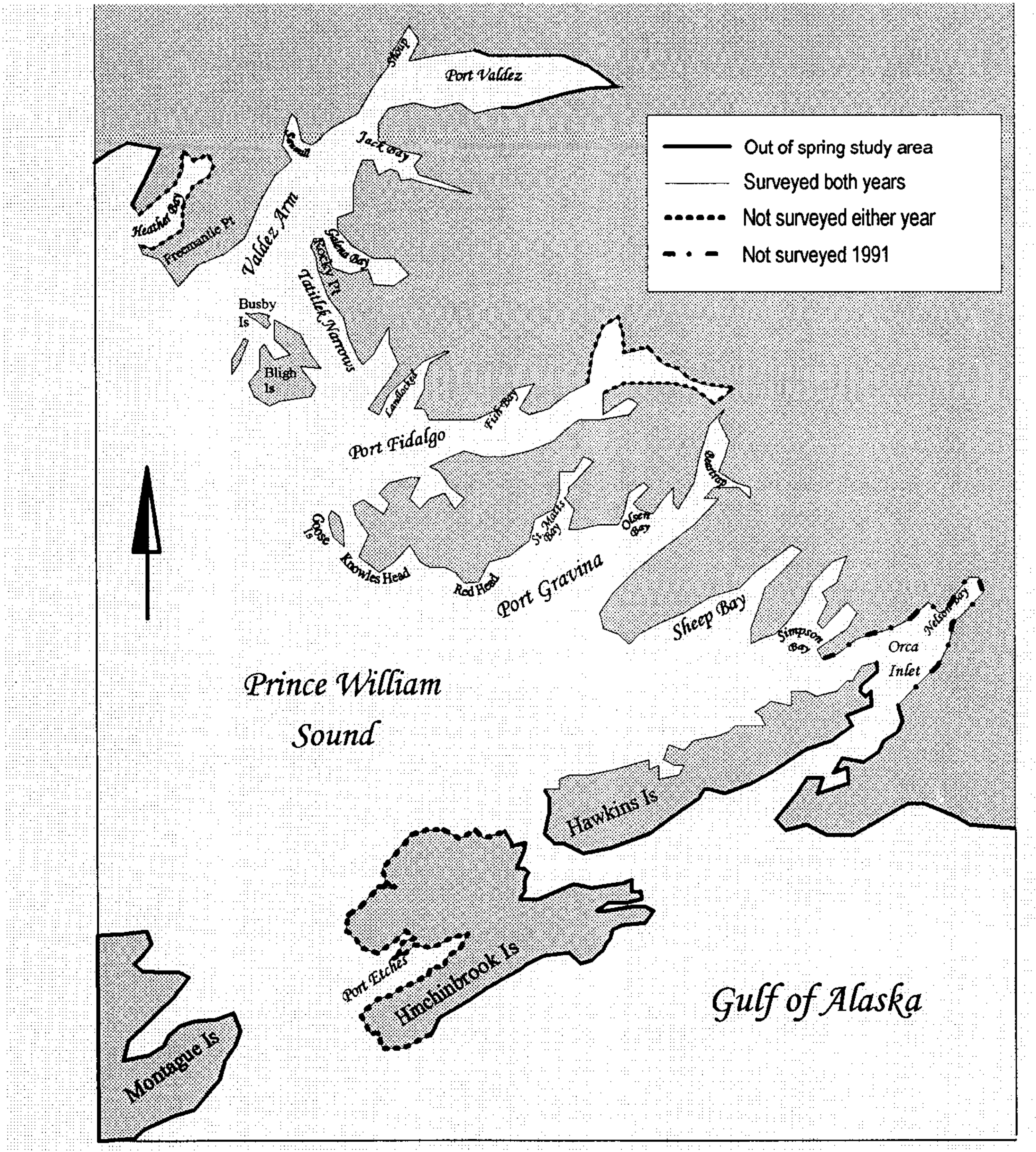


Figure 4. Spring surveys for harlequin ducks in Prince William Sound, Alaska, 1991 - 1992.

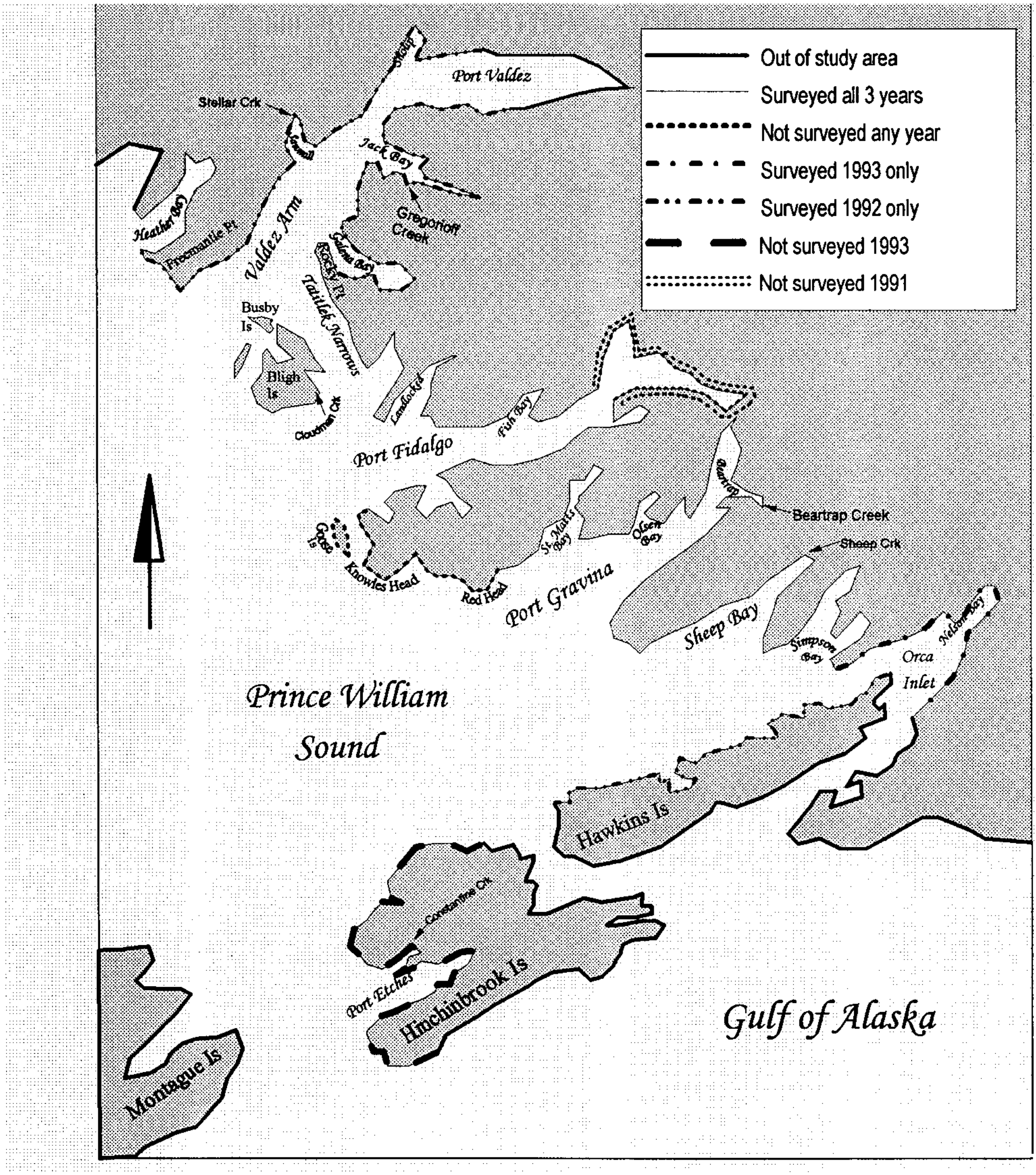


Figure 5. Molt and brood surveys for harlequin ducks in Prince William Sound, Alaska, 1991 - 1993.

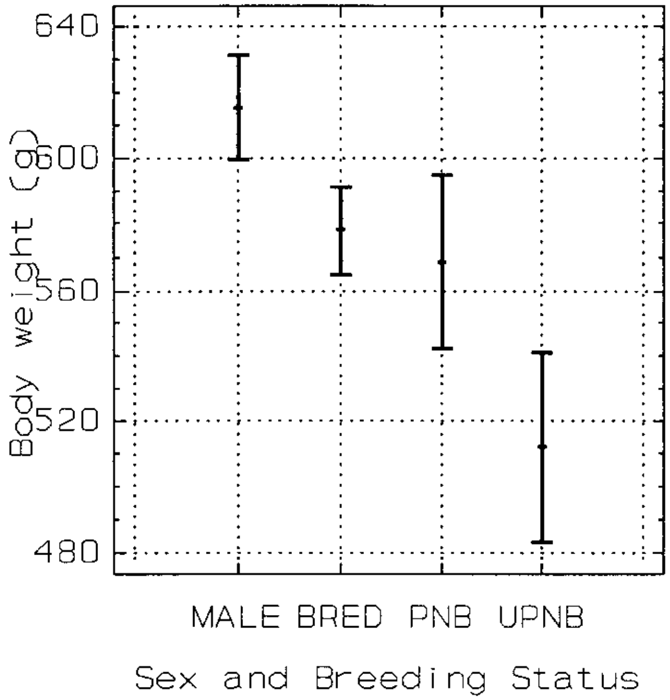


Figure 6. Mean weights and 95% confidence intervals (ANOVA, $p < 0.05$) of harlequin ducks captured during June, 1991 and 1992 in Prince William Sound, Alaska. Males were adult, breeding status of females was: breeding adults (BRED); paired, non-breeding adults (PNB); and unpaired, non-breeding subadults (UPNB).

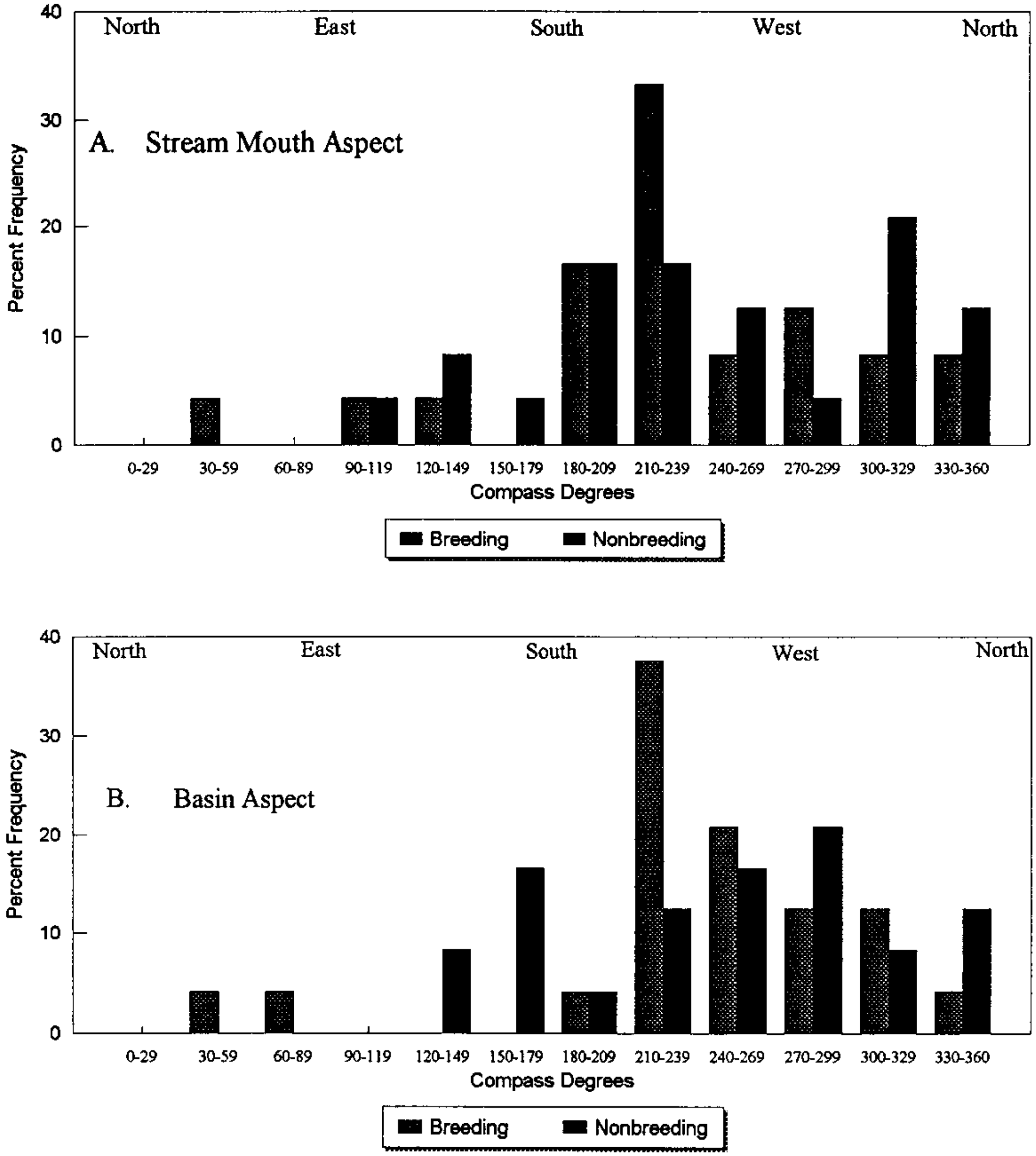


Figure 7. Aspects of stream mouths (A) and basins (B) of streams used by breeding harlequin ducks compared to those not used (Nonbreeding) in Prince William Sound, Alaska, 1991 - 1992.

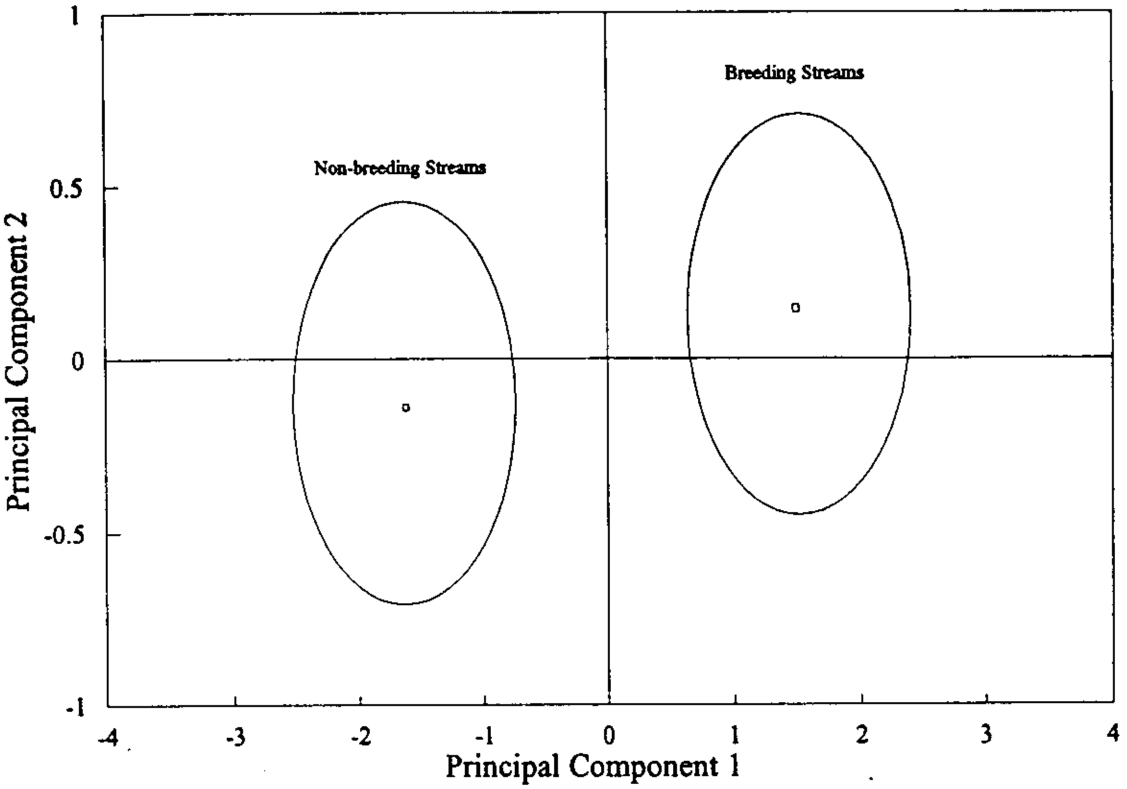
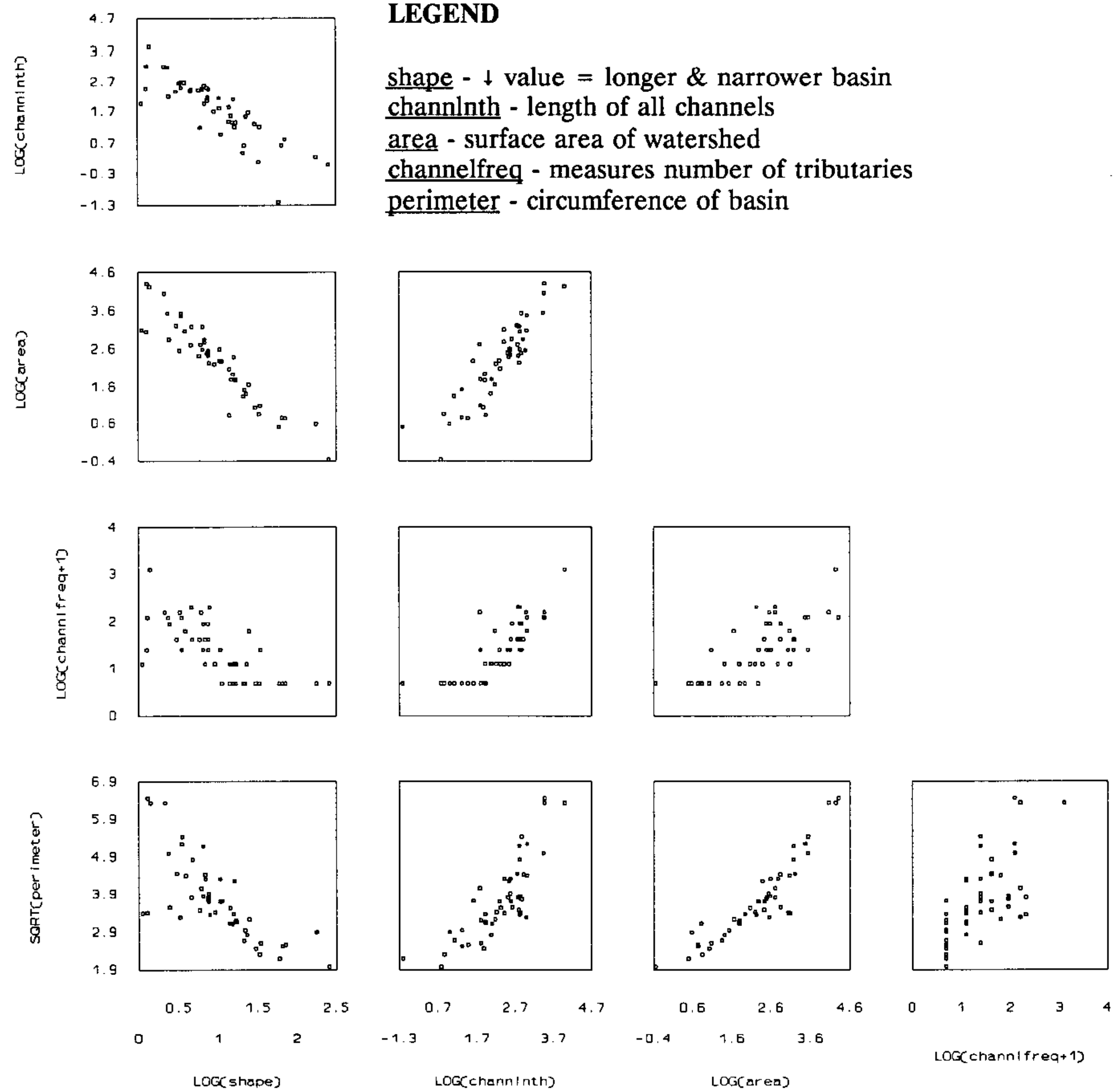


Figure 8. Means and 95% confidence ellipses indicating a significant difference in PC1 (composed of stream size variables, ANOVA $P < 0.0001$) of streams used and not used by breeding harlequins in Prince William Sound, Alaska, 1991 - 1993. Stream groups did not differ significantly along PC2, which is composed of gradient variables (ANOVA $P = 0.49$).



LEGEND

shape - ↓ value = longer & narrower basin
channlnth - length of all channels
area - surface area of watershed
channelfreq - measures number of tributaries
perimeter - circumference of basin

Figure 9. Correlation among 5 geomorphic variables important in discriminating between streams used and not used by harlequin ducks breeding in Prince William Sound, Alaska, 1991 - 1993.

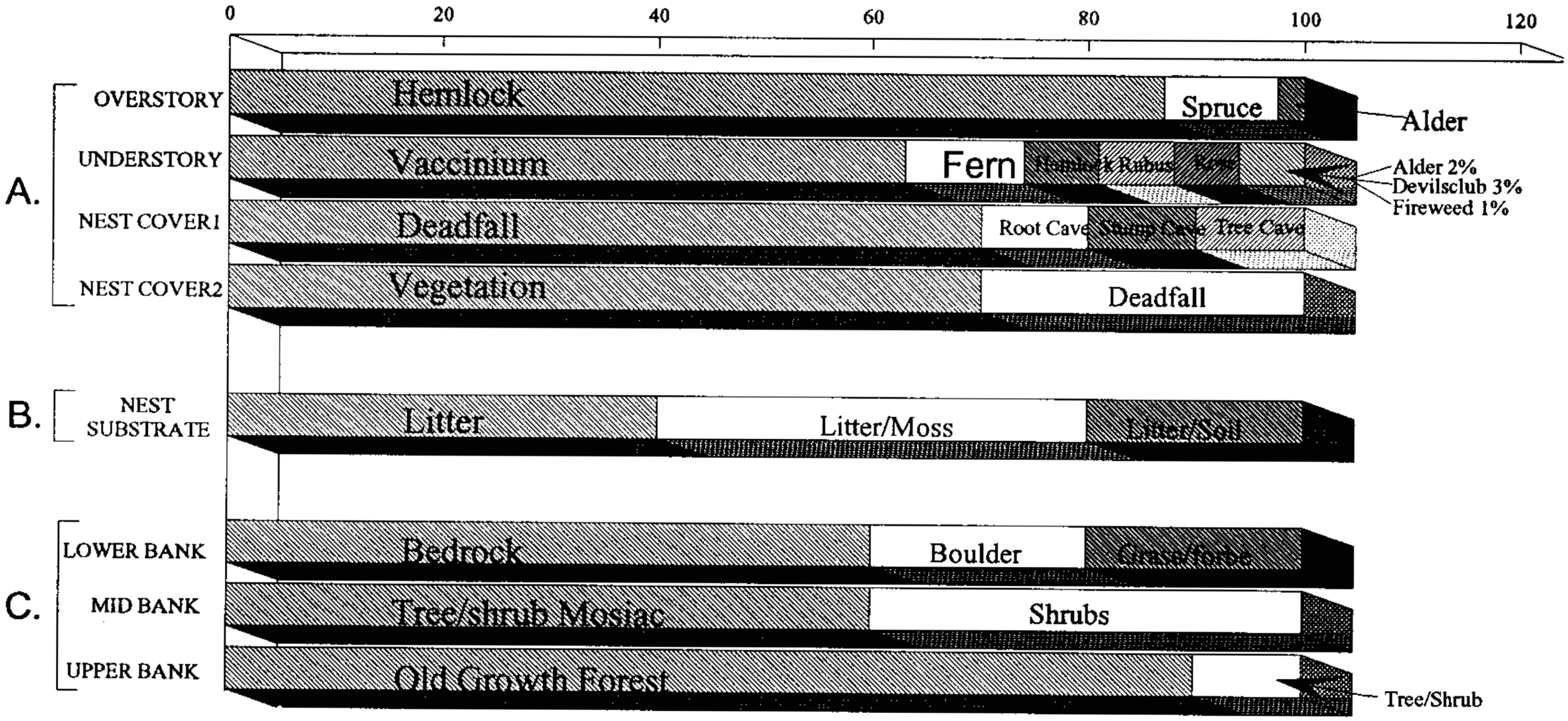


Figure 11. Vegetation (A), substrate (B) and stream bank composition (C) at 10 harlequin duck nests in Prince William Sound, Alaska, 1991 - 1992. Units of measure are average percent occurrence.

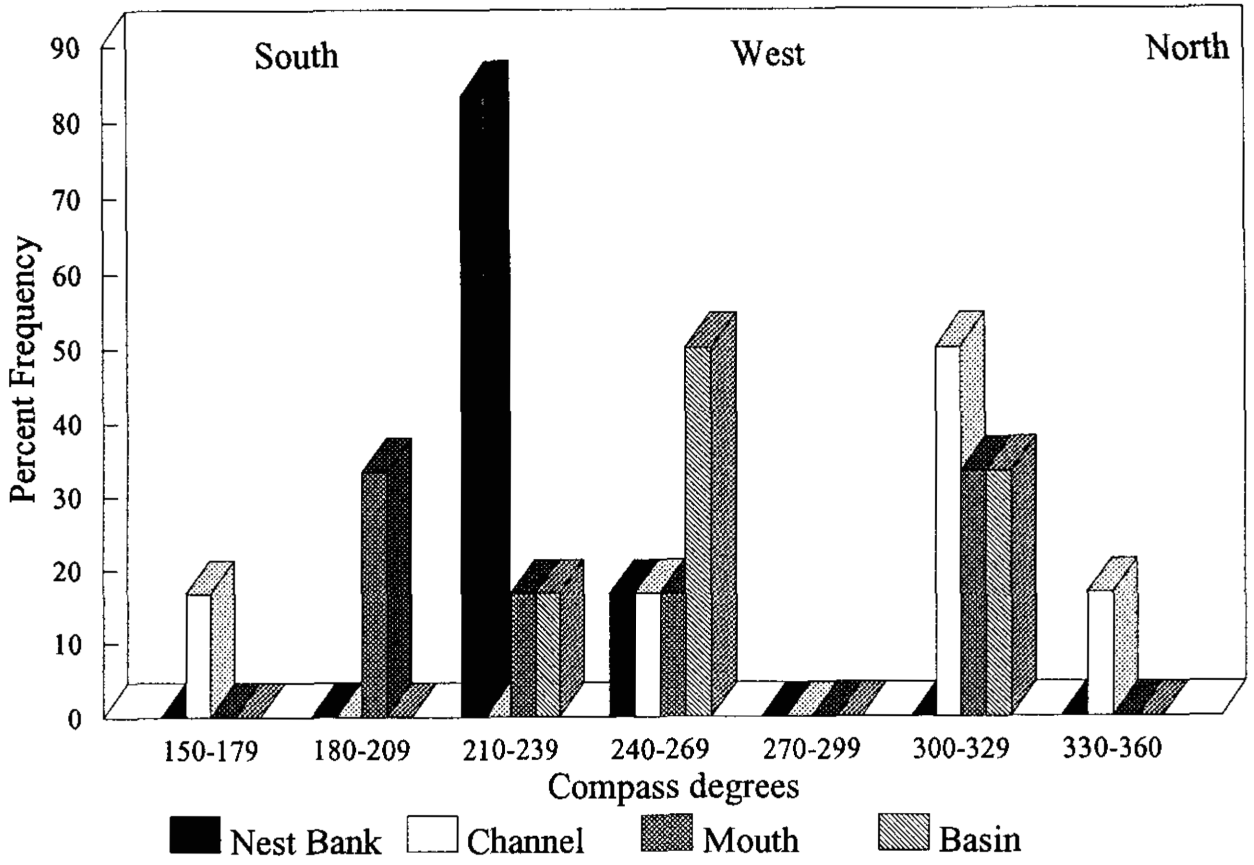
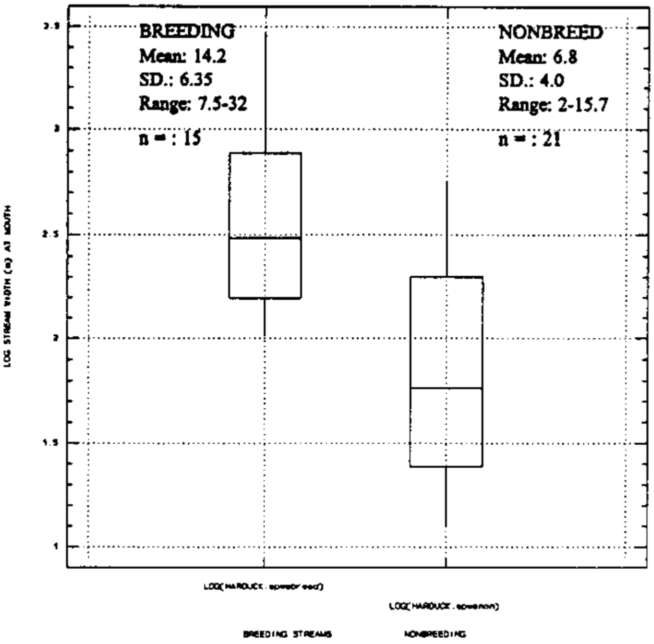
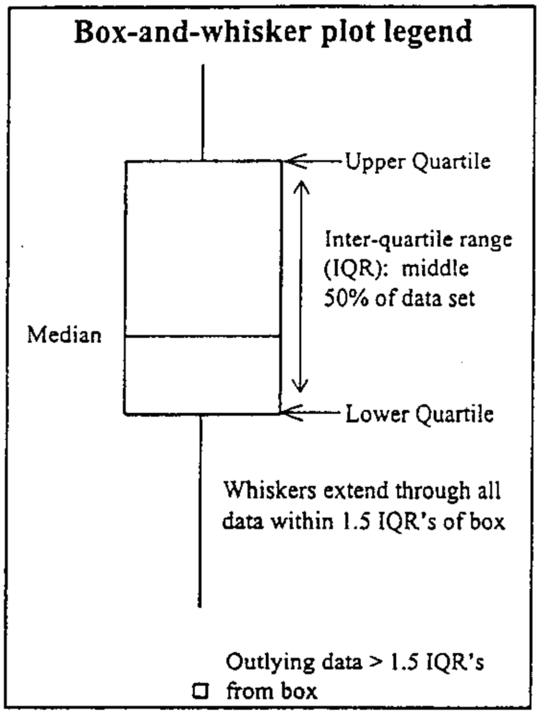


Figure 10. Distribution of 4 directional aspects: nest bank, channel adjacent to nest site, stream mouth, and basin, from 10 nest sites of harlequin ducks in Prince William Sound, Alaska, 1991-1992. All nest bank aspects occur between 218 and 241°.

A. Breeding & nonbreeding stream widths.





B. Widths of eastern & oil spill streams.

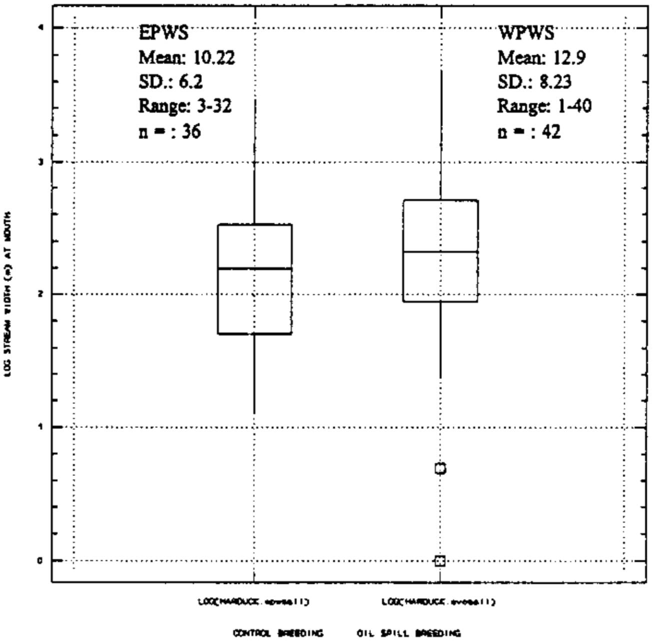
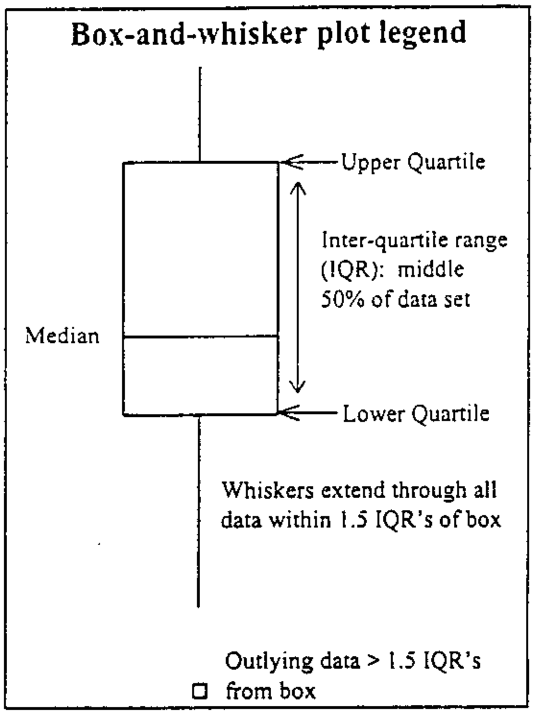
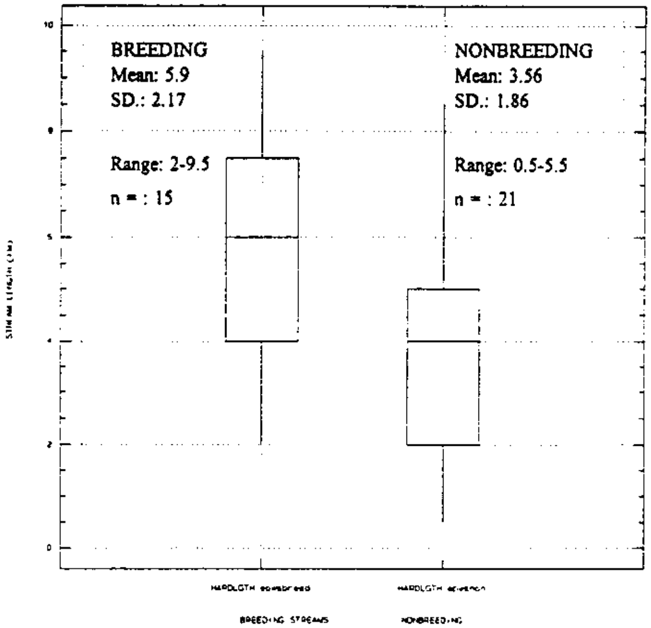


Figure 12. Comparison of widths of (A) harlequin breeding and nonbreeding streams in eastern area; (B) eastern (EPWS) and western (WPWS) streams in Prince William Sound, Alaska.



A. Eastern breeding & nonbreeding streams.



B. Lengths of eastern and oil spill streams.

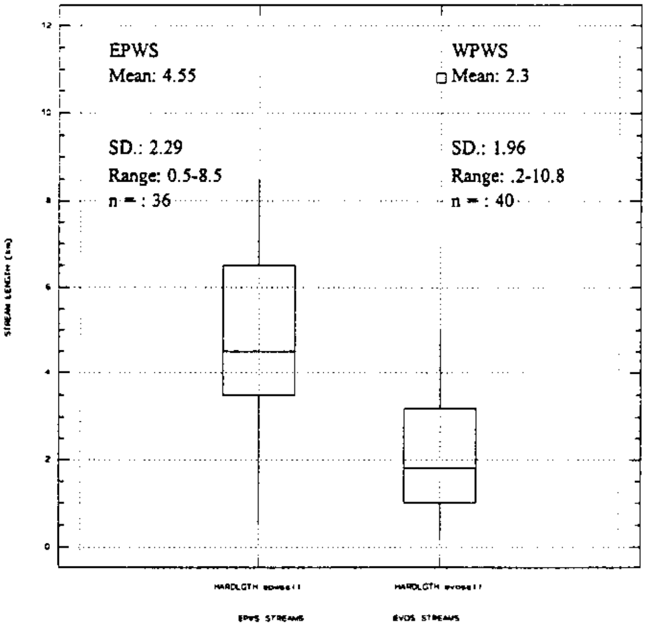


Figure 13. Comparison of main channel lengths of (A) eastern breeding and non-breeding streams; (B) all eastern (EPWS) and western (WPWS) streams in Prince William Sound, Alaska.

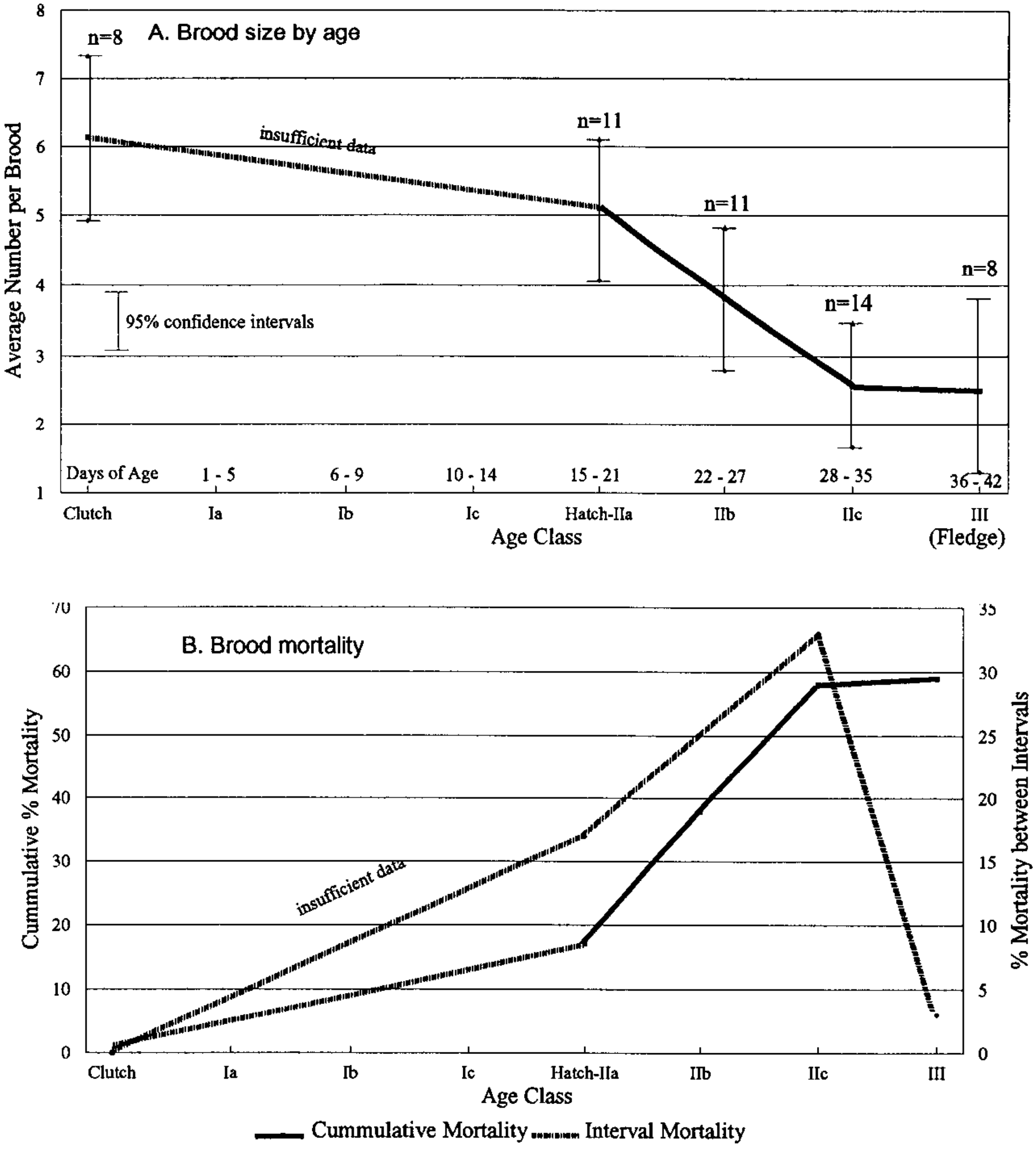


Figure 14. Brood sizes and ages (A) and mortality (B) of harlequin ducklings in Prince William Sound, Alaska, 1991 - 1993.

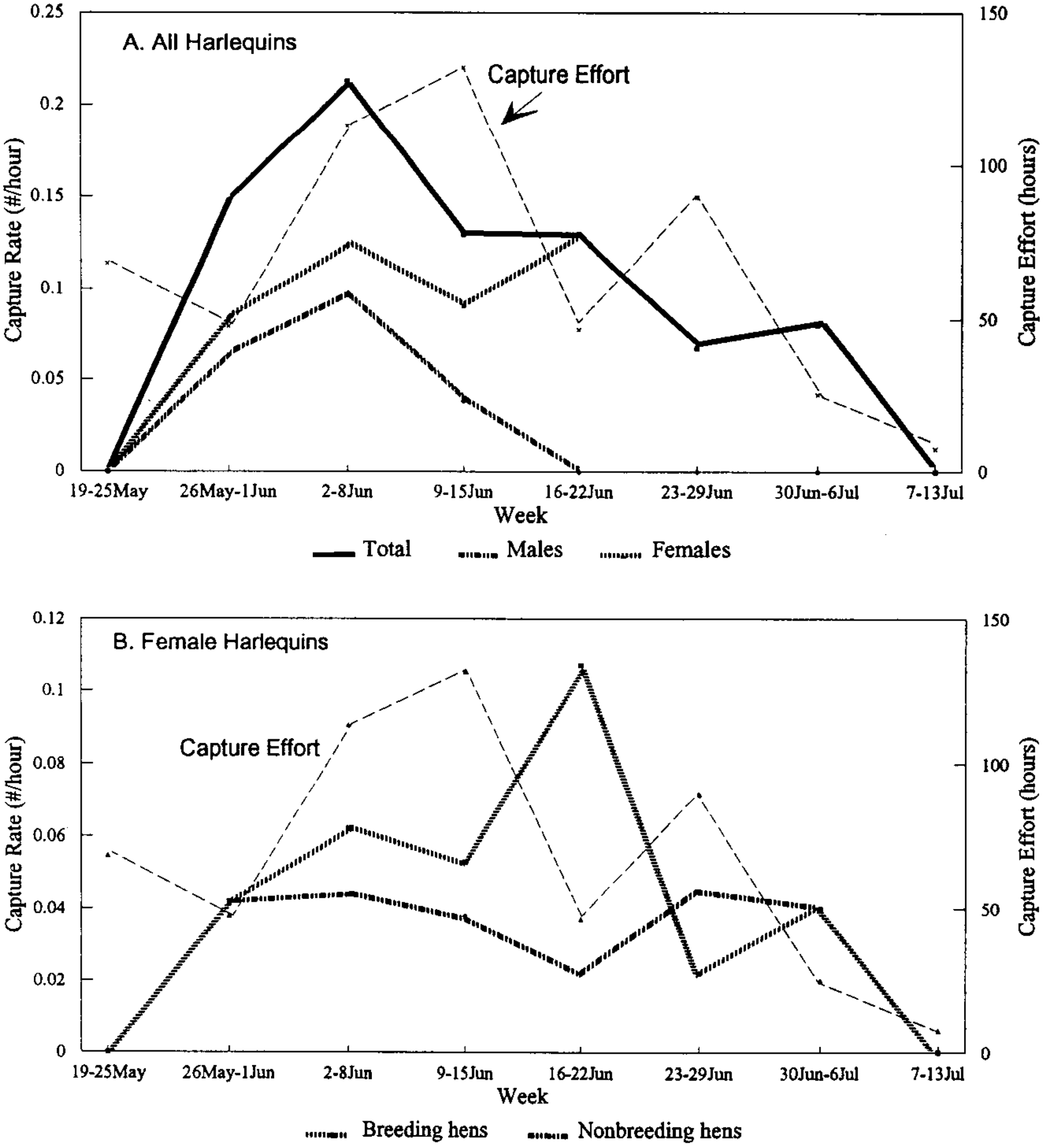


Figure 15. Capture rates of all harlequins (A) and females only (B) during the breeding season on streams in eastern Prince William Sound, Alaska, 1991 - 1992 combined.

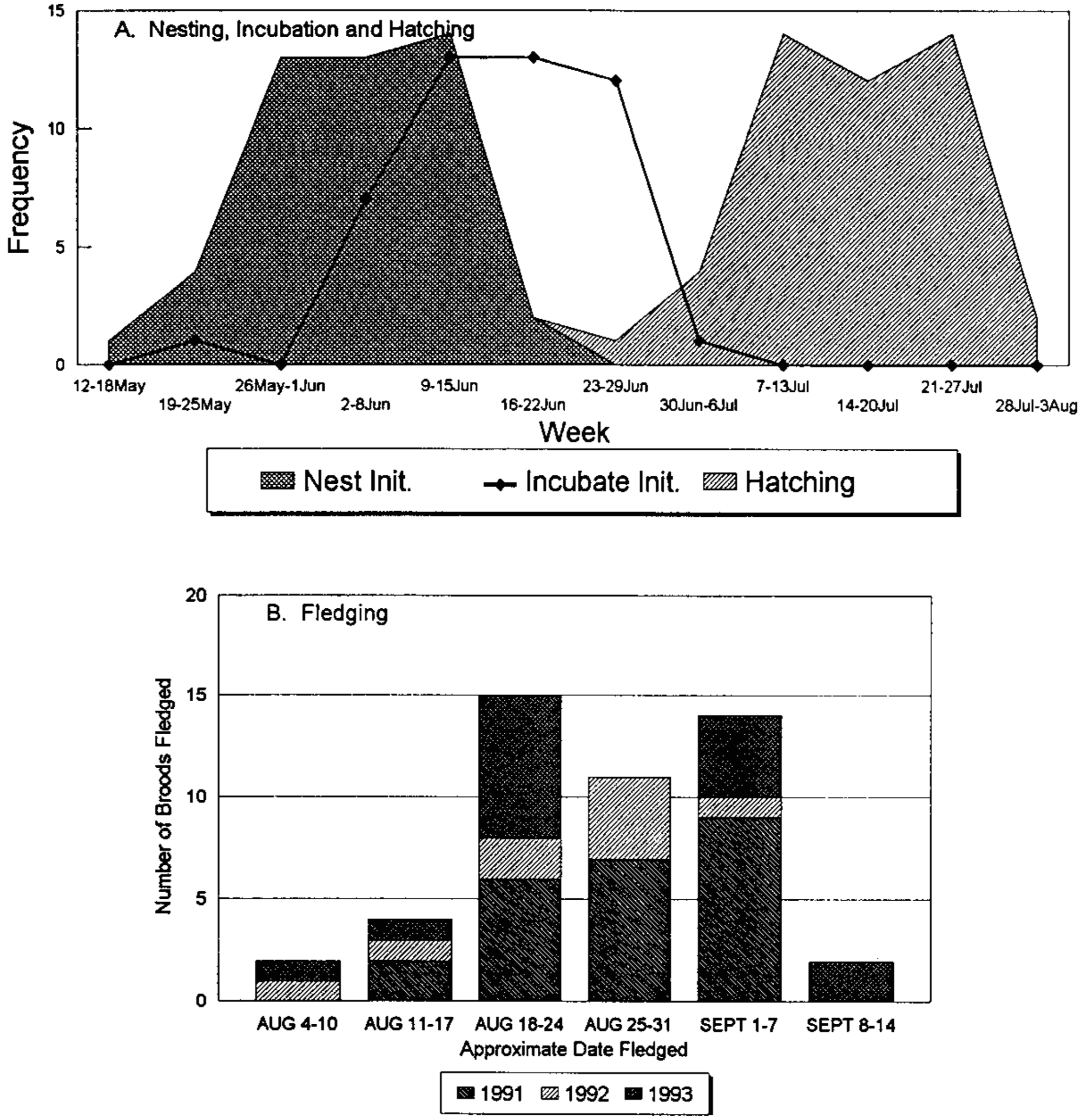


Figure 16. Chronology of laying, incubation and hatching (A) and fledging (B) of harlequin ducks in Prince William Sound, Alaska, 1991 - 1993, estimated from 42 broods and 7 nests.

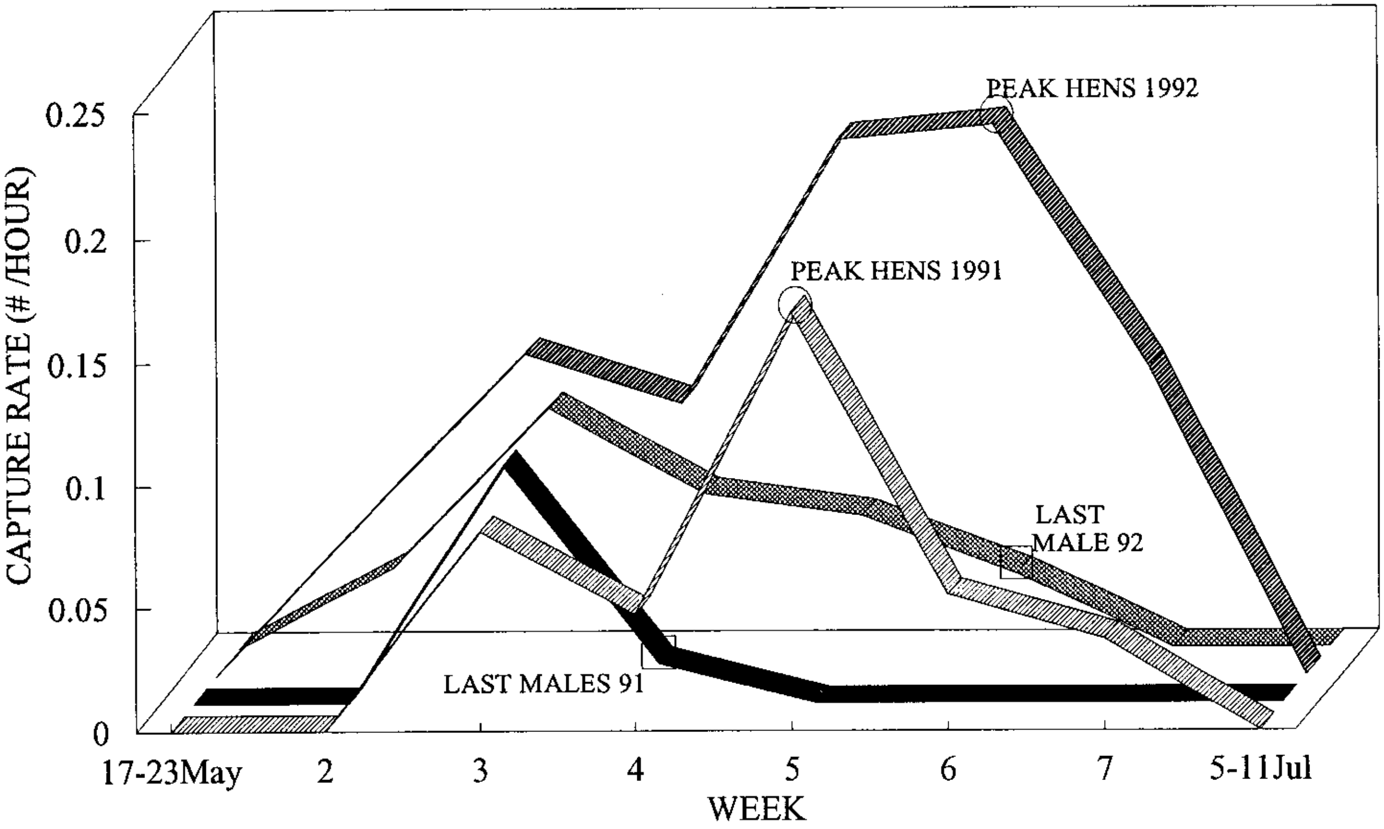


Figure 17. Weekly capture rates (no. harlequin ducks caught per hour) during 1991 and 1992 in Prince William Sound, Alaska.

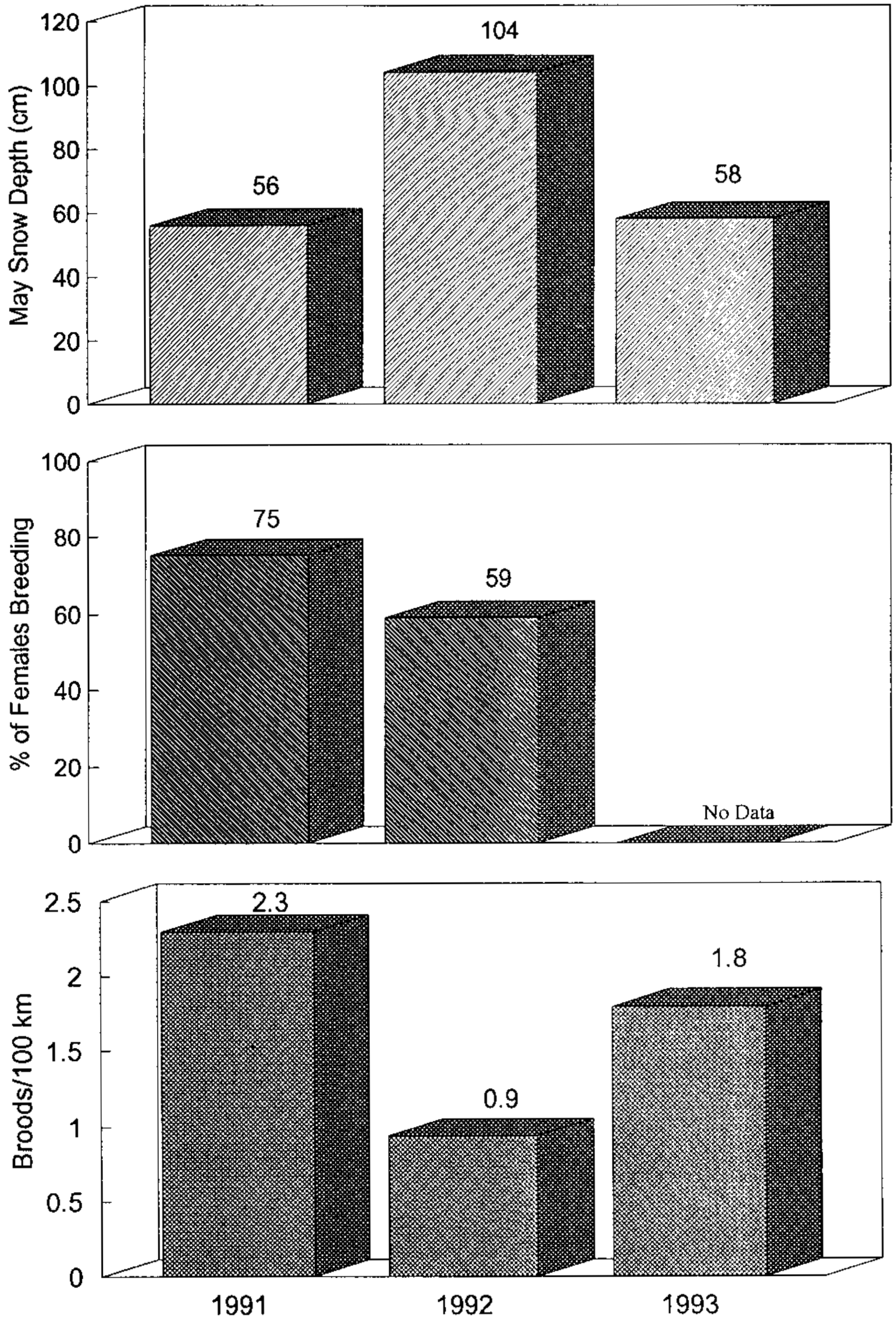


Figure 18. Relation of increased breeding propensity and production index of harlequin ducks, to snow depth in May in Prince William Sound, Alaska, 1991 - 1993.

APPENDIX A. Breeding status and measurements of harlequin ducks captured on streams in eastern Prince William Sound, Alaska, 1991 and 1992.

Table 1. Harlequin ducks captured in 1991.

USFWS band #	Sex	Age	Cloaca distend	Brood patch	Stream name	Date	Weight (g)	Tarsus (mm)	Culmen (mm)	Wing (mm)
805-08601	F	AHY	No		Beartrap	02Jun	540	35.00	27.00	200
805-08602	M	ATY			Beartrap	03Jun	640	36.30	29.65	
805-08603	M	ATY			Beartrap	03Jun	625	36.70	27.50	
805-08604*	M	ATY			Beartrap	04Jun	600	37.65	27.40	195
805-08605	F	ASY	Yes	No	Beartrap	05Jun	580	35.80	25.50	194
805-08606	M	ATY			Beartrap	05Jun	570	35.00	28.60	185
805-08607*	M	ATY			Beartrap	05Jun	615	36.40	27.75	193
805-08608*	F	ASY		Yes	Beartrap	05Jun	600	35.20	27.00	191
805-08609*	F	ASY	Yes	Yes	Beartrap	06Jun	585	35.50	26.65	198
805-08610*	F	AHY	No	No	Beartrap	06Jun	540	34.55	26.35	180
805-08611	M	ATY			Beartrap	06Jun	598	42.80	28.00	204
805-08612	M	ATY			Sheep	11Jun	610	37.00	27.00	191
805-08613*	F	ASY		Yes	Sheep	11Jun	526	33.00	27.00	192
805-08614	F	AHY		No	Sheep	11Jun	520	36.00	28.00	180
805-08615*	F	ASY		Yes	Sheep	12Jun	480	39.80	26.95	179
805-08630	F	ASY		Yes	Stellar	19Jun	560	31.55	22.35	194
805-08631	F	AHY	No	No	Stellar	20Jun	552	31.40	24.00	183
no band	F	ASY	Yes	Yes	Stellar	21Jun	535	35.70	29.00	197
mortality	F	ASY		Yes	Stellar	21Jun		35.00	26.00	185
805-08616	F	ASY	Yes	No	Gregorioff	20Jun		37.00	26.00	193
805-08632*	F	ASY	No	Yes	Gregorioff	24Jun	605	34.35	26.60	186
mortality	F				Gregorioff	25Jun				
805-08617	F	ASY	Yes	Yes	Nuchek	02Jul	540	36.20	25.80	182
				Female Average:		551	35.1	26.3	188.9	
				SD:			34.9	2.1	1.6	7.2
				Male Average:			608.3	37.4	28	193.6
				SD:			22.3	2.5	0.9	7.6
			Student's *t* Test: (compare 1991 measures to 1992)							
				p-value FEMALES			0.24	0.6	0.84	<0.01
				p-value MALES			0.57	0.52	0.99	<0.01

* Captured both years

APPENDIX A. (cont.)
Table 2. Harlequin ducks captured in 1992.

USFWS band #	Sex	Age	Cloac disten	Brd ptch	Pair	Stream name	Date	Weight (g)	Tarsus (mm)	Culmen (mm)	Wing (mm)
805-08623	F	AHY	Yes	No		Beartrap	27May	585	33.10	25.35	
805-08651	F	AHY	Yes	No		Beartrap	30May	645	35.80	25.50	
805-08652	M	ATY			Yes	Beartrap	30May	695	37.00	29.75	161
805-08607*	M	AFY			Yes	Beartrap	01Jun	625	37.25	29.00	167
805-08653	F	AHY	No	No	Yes	Beartrap	01Jun	540	34.35	26.35	155
805-08654	M	ATY			Yes	Beartrap	01Jun	645	43.00	27.95	149
805-08624	F	ASY	Yes	Yes		Beartrap	01Jun	540	36.40	26.35	152
805-08655	F	ASY	Yes	Yes	Yes	Sheep	03Jun	655	33.65	24.70	150
805-08656	F	ASY	Yes	Yes	No	Sheep	03Jun	650	34.20	25.15	158
805-08657	M	ATY			Yes	Sheep	03Jun		36.75	28.15	166
805-08615*	F	ATY	Yes	Yes	No	Sheep	03Jun	580	34.80	26.40	149
805-08658	F	AHY	No	No	Yes	Sheep	04Jun	555	35.23	24.50	150
805-08659	M	ATY			Yes	Sheep	04Jun	610	37.90	27.55	154
805-08660	F	AHY	No	No	Yes	Sheep	04Jun	575	34.80	26.35	154
805-08661	M	ATY			Yes	Sheep	04Jun	670	36.50	27.45	160
805-08613*	F	ATY	Yes	Yes	Yes	Sheep	04Jun	615	33.05	25.15	150
805-08662	M	ATY			Yes	Sheep	04Jun	580	35.45	26.00	160
805-08609*	F	ATY	Yes	Yes	No	Beartrap	07Jun	550	38.95	27.85	163
805-08604*	M	ATY				Beartrap	07Jun	640	38.10	27.30	142
805-08667	F	ASY	No	No		Sheep	07Jun	530	42.50	25.40	140
695-81125	F	AHY	No	No	Yes	Constantin	12Jun	650	29.00	22.00	146
695-81124	M	ATY			Yes	Constantin	12Jun	531	38.85	31.60	166
695-81101	F	AHY	No	No	Yes	Constantin	13Jun		33.65	26.45	156
695-81102	F	AHY	No	No	Yes	Constantin	13Jun	551	38.50	26.65	149
695-81103	M	ATY			Yes	Constantin	13Jun	565	42.00	26.85	157
695-81104	M	ATY			Yes	Constantin	13Jun	640	37.45	29.15	164
695-81126	F	ASY	Yes	Yes	No	Constantin	13Jun	590	33.90	29.10	148
695-81127	F	ASY	No	Yes	No	Constantin	14Jun	510	37.50	25.25	148
695-81105	F	AHY	No	Yes	No	Constantin	14Jun	520	36.45	25.60	144
695-81128	F	ASY	No	Yes	No	Constantin	14Jun	705	35.05	27.00	153
695-81129	F	ASY	No	Yes	No	Constantin	15Jun	540	35.65	26.00	153
695-81106	M	ATY				Constantin	15Jun		37.40	25.00	167
805-08663	F	ASY	Yes	Yes	No	Fish	13Jun	545	36.10	26.60	160
805-08632*	F	ATY	No	No	No	Gregorioff	25Jun	525	35.55	30.60	159
805-08664	F	AHY	No	No	No	Stellar	26Jun	495	35.30	26.80	153
805-08665	F	AHY	No	No	No	Stellar	26Jun	500	37.30	25.55	152
695-81130	F	ASY	Yes	Yes	No	Duck River	27Jun	620	33.00	26.65	164
805-08665	F	AHY	No	No		Stellar	28Jun	500	37.90	26.70	153
805-08608*	F	ASY		Yes	No	Beartrap	27Jun				
805-08610*	F	ASY		Yes	No	Beartrap	27Jun				
805-08625	F	ASY		Yes	No	Beartrap	27Jun				
805-08666	F	AHY	No	Yes	No	Comfort	01Jul	585	36.10	26.90	154
805-8633	F	ASY	Yes	Yes		Hanning	13Jun				
805-08634	F	AHY	No	No		Hanning	14Jun				
						FemaleAverage:		571.4	35.5	26.2	152.5
						SD:		56.1	2.5	1.5	5.6
						Male Average:		620.1	38.1	27.7	159.4
						SD:		41.0	2.2	1.7	7.8

* Captured both years

APPENDIX B. Habitat data collected on streams used and not used by harlequin ducks breeding in Prince William Sound, Alaska, 1991 - 1993.

Table 1. Variables collected at the landscape-level scale on breeding streams.

Stream name	ASC number	km^2 Area of drainage	% Mean sideslope	km channels length	Shape index	km/km^2 drainage density	% Bifurcation ratio	km Channel gradient	m Basin perimeter	Basin relief	Channel frequency	o No. lakes	Basin orientation
Little Bear	2213010490	4.58	29.8	1.9	0.27	0.83	NA	11	14.5	1296	1	0	236
Beartrap	2213010480	24.61	18.5	10.6	0.76	0.43	4	5.8	20.11	1234	4	0	230
Constintine	2286018150	21.44	11.1	14.3	0.72	0.67	4	4.3	19.3	877	5	1	260
Duck	2215011160	68.89	12.4	47	0.53	0.68	4.2	13	40.1	1794	21	2	280
Gregorioff	2215011230	9.7	19.5	2.7	0.64	0.28	NA	5.6	13.8	1158	1	0	322
Namorov	2215011231	74.3	12.7	25.1	0.53	0.34	3.5	8.7	41.7	1747	7	0	310
FishBay	2214010950	23.78	15.9	11.4	0.61	0.72	2	11	22.2	1706	4	0	210
Nuchek	2286018120	13.3	5.4	8.5	0.49	0.64	3	3.4	18.5	518	3	2	250
Rain	2213010450	9.25	12.4	11.4	0.78	1.23	9	6.1	11.3	658	9	0	295
Sheep	2212010360	32.1	16.2	14.5	0.54	0.45	3.5	4.9	27.4	1470	7	2	220
Stellar	2215011530	11.36	20.1	8.7	0.76	0.77	4	9	13.7	1219	4	2	68
EastOlsen	2213010516	12.86	12.7	14	0.64	1.09	8	8.2	15.9	1133	8	0	226
Comfort	2213010460	13.15	21.1	11.6	0.75	0.88	3	16	14.8	1094	6	1	280
Indian	2215011170	14.95	22.7	10.9	0.89	0.73	4.5	15.5	14.5	1231	9	0	216
Hanning	2271017110	20.83	14	11.7	0.71	0.56	3	3.4	19.15	812	3	0	256
McLeod	2271017060	21.84	11.7	7.1	0.79	0.33	2	3.9	18.5	814	2	0	250
Coghill	2233013220	34.24	13	12.1	0.5	0.35	3	2.5	29.45	1687	3	1	237
Eyak/power	2121010050	57.82	10.5	24.9	0.45	0.43	4	3.6	40.1	1420	8	1	220
Control	2213010520	12.08	18.3	7.9	0.72	0.65	3	13	14.5	1133	3	0	185
Raging	2212010230	23.84	7	11.3	0.42	0.47	3	6.7	26.8	1289	3	0	240
Cloudman	2214011080	2.09	15.1	1.9	0.64	0.91	NA	6.3	6.4	396	1	0	58
Lagoon	2214010990	11.95	21.4	12.1	0.74	1.01	6	12	14.2	914	6	0	220
Millard	2215011150	34.34	14.2	24.1	0.7	0.7	3.5	6.7	24.9	1176	7	4	320
Etches	2286018060	11.23	16.6	11.1	0.96	0.99	4	10.2	12.1	610	4	0	338

APPENDIX B. (cont.)

Table 2. Variables collected at the landscape-level scale on non-breeding streams.

Stream name	ASC number	km^2 Area of drainage	% Mean sideslope	km channels length	Shape index	km/km^2 drainage density	% Bifurcation ratio	km Channel gradient	m Basin perimeter	Basin relief	Channel frequency	o No. lakes	Basin orientation
St.Mathews	2213010560	6	24.3	4.8	0.8	0.8	2	13.3	9.7	1133	2	0	220
GravnRock	2213010410	9	5.7	5.5	0.83	0.61	2	1.8	11.7	487	2	1	282
Ganzer	2213010430	2.79	27.1	3.7	0.94	1.33	NA	8.2	6.1	655	1	1	325
RottnHump	2213010440	2.93	21.3	3.4	0.8	1.16	2	16.2	6.8	609	3	2	334
StMatt Seep	2213010540	2.26	21.4	4	0.3	0.64	NA	12.1	9.8	878	1	0	190
Native	2213010470	6.07	26.8	3.4	0.72	0.56	NA	6.3	10.3	1094	1	1	275
2Moon	2214010735	4.11	15.7	4.7	0.81	1.14	2	1.7	8	552	2	0	320
Irish	2214010760	17.08	11.2	12.9	0.56	0.76	2	5.1	19.6	684	4	3	240
Whalen	2214010800	17.19	11.3	9	0.67	0.52	3	7	17.9	1133	6	1	270
Close Sheep	2212010370	5.89	15.6	3.9	0.74	0.66	2	18.9	10	768	2	1	170
Sahlin Falls	none	6.93	26.7	3.9	0.67	0.56	2	18.1	11.4	1073	1	1	178
Koppen	2212010350	16.02	13.3	7.1	0.59	0.44	2	14.5	18.5	1155	2	1	252
Levshakoff	2214011212	7.93	15.1	6.3	0.64	0.79	2	10	12.5	731	2	0	345
Sth Nuchek	2286018110	9.81	8.7	6.1	0.66	0.62	3	5.7	13.7	670	3	0	290
W.FrkOlsen	2213010517	12.71	17	8.5	0.68	0.67	3	6.7	15.3	1133	3	0	175
Little Shark	2213010420	1.63	31	0.3	0.89	0.18	NA	11.4	4.8	655	1	0	340
Little Ole	2213010513	0.7	28.4	1	0.58	1.43	NA	31.5	3.9	488	1	0	210
Olsen West	2213010530	1.77	51	1.3	0.31	0.73	NA	28.4	8.4	770	1	0	128
Garden	2286018100	3.84	32	1.5	0.93	0.39	NA	10.5	7.2	651	1	0	248
Surf	2212010380	15	15.1	3.3	0.7	0.22	7	9.8	16.4	768	8	1	175
Black	2215011070	2.07	34.1	2.3	0.6	1.11	NA	18.9	6.6	853	1	0	275
Parshas	2213010510	2.32	32.7	1.1	0.87	0.47	NA	5.4	5.79	579	1	0	226
Rogue	2212010200	10.84	17.5	8.2	0.42	0.76	2	5.6	18	1097	2	0	248
Small Fish	2214010950	5.23	18.4	5.3	0.6	1.01	4	14	10.5	823	5	5	120

APPENDIX B. (cont.)

Table 3. Variables collected at stream mouths (local-level scale) on breeding streams. Codes are defined after Table 4.

		Dschrg	Channel:					Ripar	Area	Mean	Substrate code			Stream flow code			Left bank			Right bank			Age	Harvst	Side		Chnl
Stream	ASC #	m^3/sec		lgth	wth	freq	slope	aspect	width	estuary	sides		S1	S2	S3	W1	W2	W3	L1	L2	L3	R1	R2	R3	forest		
status	dist	Turbid	type																								
Little Bear	2213010490	0.95	1.9	7.5	1	4	236	10	3.2	0.15	CO	BO	GR	SF	SS		GF	SH	TR	GF	SH	TR	OG	UN	EN	CL	SC
Beartrap	2213010480	3.96	10.6	20	4	2	185	75	14.9	0.19	CO	GR		SF	DF	DS	GF	TS	TR	GR	GF		MA	UN	MO	CL	SC
Constintine	2286018150	5.5	14.3	18	5	2	188	100	98.3	0.03	BO	CO		DF	SF		GR	GF	SH	BE	GF	TR	MA	UN	DI	CL	CU
Duck	2215011160	8.6	47	42	21	4	214	75	68.2	0.21	BO	CO		DF	SF		GF	SH	TR				MA	UN	DI	ST	BR
Gregorioff	2215011230	1.24	2.7	7.5	1	2.5	320	75	11.5	0.27	GR	CO		SF			GR	SH	TR	GR	GF	SH	MA	UN	MO	CL	SC
Namorov	2215011231	6.72	25.1	12	7	2	314	500	55.2	0.25	GR			DF			GR	SH					OG	UN	DI	ST	CU
FishBay	2214010950	2.71	11.4	11.5	4	2	226	50	49.8	0.1	GR	CO		SF			GR	GF	SH	GR	GF	TR	IM	UN	DI	CL	SC
Nuchek	2286018120	1.5	8.5	18	3	2	253	300	189.7	0.06	CO	GR		SF	SS		GF	TS	TR				MA	UN	DI	CL	BR
Rain	2213010450	1.87	11.4	9	9	3	330	12	6.1	0.11	BO	GR	CO	DF	PW		SH	TR	TR				MA	UN	MO	CL	ST
Sheep	2212010360	6.08	14.5	18.5	7	2	191	100	6.1	0.27	CO	BO		DF	SS		GR	GF	SH				MA	UN	MO	CL	CU
Stellar	2215011530	1.89	8.7	12	4	2	90	50	18.3	0.27	CO	GR		SS			BE	SH	TR	GR	GF	TR	MA	UN	EN	CL	ST
EastOlsen	2213010516	1.76	14	8.5	8	2.5	224	10	14.4	0.06	CO	GR		SF			GF	SH	GR			OG	UN	DI	CL	SC	
Comfort	2213010460	3.39	11.6	10	6	3	290	60	23.8	0.1	BO	SA		DF	BR	PW	GF	SH	TR				MA	UN	DI	CL	CU
Indian	2215011170	2.44	10.9	14	9	3	228	100	9.3	0.14	CO	GR		SF	DF		GF	SH	TR	GF	TS	TR	OG	UN	MO	CL	BR
Hanning	2271017110	2.5	11.7	30	3	2	274	200	13.4	0.04	SA	CO		SF	DS		SA	De	TS	SA	DE	TS	IM	SG	DI	CL	BR
McLeod	2271017060	2.31	7.1		2		230		19	0.05	CO	GR		SF	DF		GR	TS	TS	GR	TS	TS	IM	OH	MO	CL	BR
Coghill	2233013220	4.06	12.1		3		244		225.3	0.09																	
Eyak/powr	2121010050	6.08	24.9		8		229		186	0.03																	
Control	2213010520	1.11	7.9	15.7	3	2	122	5	72.5	0.13	CO	GR		SF	DS		GF	SH	TR	GF	SH	TR	OG	UN	DI	CL	CU
Raging	2212010230	1.73	11.3	35	3	2	183	400	7.7	0.11	GR	SI		DF	SF		GF	SH	SH	GF	SH	SH	OG	UN	DI	TU	BR
Cloudman	2214011080	0.53	1.9	4	1	3	58	20	63.8	0.02	CO	BO	GR	SF	SS		TS	TR	TR	TS	TR	TR	MA	UN	DI	CL	SC
Lagoon	2214010990	3.61	12.1	12.9	6	2	228	150	3.1	0.14	CO	GR		DS	DF		GF	TS	TR	GF	TS	TR	OG	UN	MO	CL	SC
Millard	2215011150	4.34	24.1	25	7	10	331	30	36.3	0.15	CO	GR	BE	DF	SS	FA	TS	TR	TR	TS	TR	TR	OG	UN	MO	CL	SC
Etches	2286018060	1.47	11.1		4		277		11	0.11														UN			

APPENDIX B. (cont.)

Table 4. Variables collected at stream mouths (local-level scale) on non-breeding streams. Codes are defined on following page.

Stream status	ASC # dist	Dschrg m^3/sec Turbid	type	Channel: lgth	wth	freq	slope	Ripar aspect	Area width	Mean estuary	Substrate code sides		S1	Stream flow code S2	S3	W1	Left bank W2	W3	L1	Right bank L2	L3	R1	Age R2	Harvst R3	Side forest		Chnl
St.Mathews	2213010560	1.27	4.8	13.9	2	2	228	8	30.3	0.12	CO	BO	GR	SF	SS		GF	TS	TR	GF	TS	TR	OG	UN	MO	CL	ST
GrvnaRock	2213010410	0.48	5.5	10.9	1	4	355	5	4.8	0.06	CO	GR	BO	SF	SS		GF	TR	TR	GF	TR	TR	MA	UN	DI	CL	ST
'Ganzer	2213010430	0.32	3.7		3		326		6.6	0.27														UN			
RottnHmp	2213010440	0.53	3.4	5	1	4	314	10	4	0.08	CO	BO		SF	SS		GR	SH	TR	GR	SH	TR	MA	UN	MO	CL	SC
StMatSeep	2213010540	0.51	4	5.4	1	2	185	60	5.1	0.04	CO	GR		SF	SS		GR	TR	TS	GF	TR	TS	OG	UN	MO	CL	CU
Native	2213010470	1.39	3.4	10	2	2	303	20	4.1	0.13	CO	BO		SF	SS		GR	GF	SH	GR	GF		MA	UN	EN	CL	SC
2Moon	2214010735	0.21	4.7	6.7	4	3	322	10	2.4	0.06	CO	BO		SS	SF		BE	GF	TR	BE	GF	TR	MA	UN	DI	CL	ST
Irish	2214010760	1.06	12.9	15	6	1	300	50	17.9	0.05	CO	BO		SS	SF		GF	TR	TR	GF	TR	TR	MA	UN	DI	ST	SC
Whalen	2214010800	2.27	9	10.5	2	2	267	60	12.6	0.09	CO	BO	GR	SS	SF		GF	TR	TR	GF	TR	TR	OG	UN	DI	CL	SC
ClosSheep	2212010370	0.5	3.9	15	1	4	158	50	11.4	0.11	CO	GR	BO	SF	SS		GF	SH	TS	GF	TS	TR	OG	UN	MO	CL	CU
SahlinFalls	none	1.24	3.9	13	2	60	143	15	4.4	0.19	BO	BE	GR	FA	SF		GF	TS	TR	GF	TS	TR	MA	UN	EN	CL	ST
Koppen	2212010350	1.31	7.1	16	2	1	264	200	3.3	0.13	GR	CO		SS	SF		GF	SH	SH	GF	SH	SH	OG	UN	MO	CL	SC
Levshakoff	2214011212	0.66	6.3	7	3	2	346	60	11.8	0.11	GR	CO	BO	SF	SS		GR	SH	TR	GR	GF	SH	MA	UN	MO	CL	SC
SthNuchek	2286018110	0.22	6.1	5.6	3	2	215	50	12	0.04	GR	CO		SS	SF		GR	GF	SH	GF	SH	TR	MA	UN	DI	CL	SC
W.FrkOlsn	2213010517	1.6	8.5	13	1	2.5	182	75	189.7	0.08	GR	CO		SF	SS		GF	SH	TR	GF	SH	TR	OG	UN	DI	CL	BR
LittleShark	2213010420	0.2	0.3		1		340		23.8	0.3														UN			
LittleOle	2213010513	0.2	1		1		210		3.1	0.11														UN			
OlsenWest	2213010530	0.2	1.3		1		102		2.7	0.06														UN			
Garden	2286018100	0.93	1.5	4.2	8	2	246	10	33.7	0.53	GR	CO	BO	SF	SS	FA	GF	TR	TR	GR	GF	SH	MA	UN	MO	CL	SC
Surf	2212010380	1.86	3.3	14	1	8	142	30	8.9	0.09	GR	BO	CO	SS	DS		TS	TR	TR	TS	TR	TR	OG	UN	EN	CL	SC
Black	2215011070	0.46	2.3	4	1	4	295	75	3	0.32	CO	GR	BO	SS	FA		DE	SH	TR	TS	TR	TR	MA	UN	MO	CL	SC
Parshas	2213010510	0.24	1.1	5	2	3	196	25	3.7	0.27	CO	BO	GR	SS	SF		GF	SH	TR	GF	SH	SH	OG	UN	EN	CL	SC
Rogue	2212010200	0.74	8.2	8.4	5	1	230	75	12.4	0.05	GR	CO		SF	SS		GF	SH	SH	GF	SH	TR	OG	UN	DI	CL	SC
SmallFish	2214010950	0.46	5.3	9		1	188	5	4.2	0.05	CO	GR		SS	SF		GR	BE	BE	GR	BE		MA	UN	DI	CL	SC

APPENDIX B. (Continued) Definitions of habitat codes on standard form used to collect data on streams.

HARLEQUIN DUCK HABITAT DATA FORM

Harlequin Duck Restoration Study, Prince William Sound, Alaska

DATE:
LOCATION:
GPS POSITION:
Mark location on map

BROOD SIZE:
FREQ:
PHOTO #:

ACTIVITY	**SUBSTRATE**	**STREAM HABITAT**	**MARINE HABITAT**
SW Swimming	BE Bedrock	SS Shallow slow	ES Estuary
RO Roosting	BO Boulder (>30cm)	SF Shallow fast	BA Protected Bay
DI Diving	CO Cobble (8-30cm)	DS Deep slow	OS Open sound
PR Preening	GR Gravel (.2-8cm)	DF Deep fast	GU Gulf
CT Courtship	SA Sand	BR Boulder run	Type: 1 2 3
FD Fled dive	SI Silt	PW Pocketwater	4 5
FF Flushed	VE Vegetation	BW Backwater	Water depth:____
		FA Falls	

BANK OR BEACH COMPOSITION	**FOREST AGE CLASS**	**HARVEST STATUS**
TR Trees	OG Old-growth	UN Unharvested
SH Shrub	MA Mature	RH Recect (< 10 yr)
TS Tree/shrub mosaic	IM Immature	OH Old harvest (>10 yr)
GF Grass/forbs	PO Pole	SG Second growth
BE Bedrock	SA Sapling	BU Buffer, width:____
SA Sand	SE Seedling	CL Clearcut
GR Gravel,cobble,boulder		
DE Debris/deadfalls		
RO Roots	Width of riparian zone:_______m	
Left	Right bank	

TOPOGRAPHY	**TURBIDITY**	**HYDROLOGY**
Altitude:_______	CL Clear	Stream length:________km
Channel Slope:_________	ST Slightly turbid	Dist. to estuary:______
Channel Aspect:_________	TU Turbid	Width at activity:______m
Sideslopes: Enclosing	Color, if any:_______	Width at mouth:________m
Moderate Distant		Discharge at mouth:______

CHANNEL TYPE	**SPAWNING STATUS**	**HARLEQUIN FLOCK**
ST Straight	Salmon present: Y N	# Males:________
SC Slight curve <45°	Species:________________	Adult______Juv_______
CU Curved 45 - 90°	Spawning: Y N	# Females:_______
BR Braided		Breed_____Nonbred____

APPENDIX C. Discriminant function analysis of geomorphic variables.

Discriminant function analysis (DFA) was used to determine which of the landscape variables were most important in discriminating between groups (Martinka 1972, Anderson and Shugart 1974, Conner and Adkisson 1976, Swanston et al. 1977, Rice et al. 1983, Ramsey and Schafer 1993).

Discriminant function analysis of landscape variables indicated that numerous stream channels and the contribution of basin area to the number of stream channels was important determinants of breeding habitat. A discriminant function (DF) containing all twelve variables classified 79.2% (19 of 24) of non-breeding streams and 83.3% (20 of 24) of breeding streams correctly at $p = 0.002$ (Figure 1). By using DFA in a stepwise procedure, we determined that perimeter, area, channel length, channel frequency and discharge were most important in discriminating between stream groups. There was much intercorrelation occurring among variables. The DF most successful in separating stream groups contained perimeter and stream density: Crimcord = 1.131 (perimeter) + 0.411 (stream density), $p = 0.00003$. Although a t-test indicated that stream density was not significantly different between stream groups (Table 8), the linear combination formed by perimeter and stream density correctly classified 79.2% of non-breeding streams and 91.7% (22 of 24) of breeding streams (Appendix Figure 2).

This discriminant function should be used with caution to predict streams used and not used by breeding harlequin ducks because the formulation and testing of the DF was done with the same, small data set. Classification rates are likely overestimated and could be much lower when used on an independent data set.

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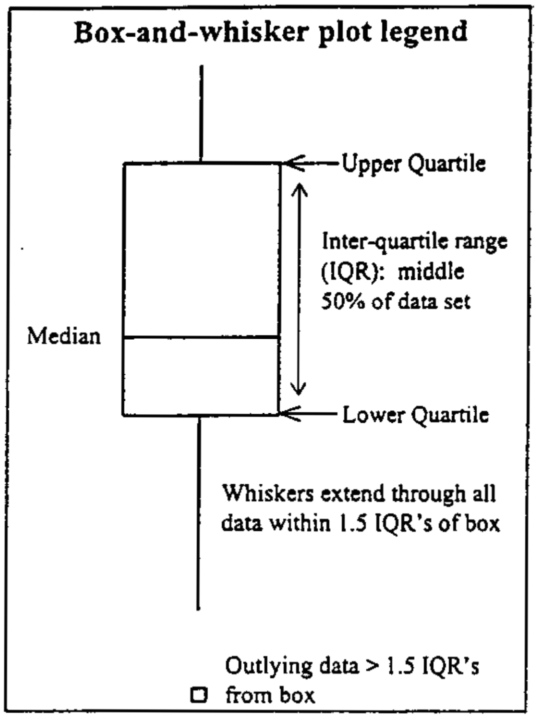

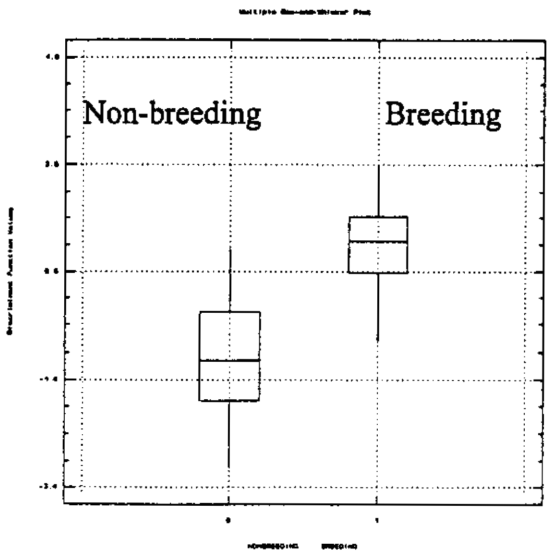

Figure 1. Discrimination between harlequin duck breeding and non-breeding streams in Prince William Sound, Alaska, 1991 - 1993, using a function (y-axis) with all geomorphic variables included.

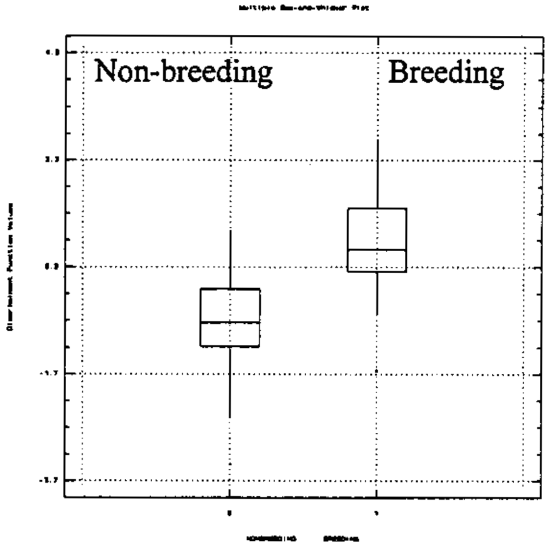

Figure 2. Discrimination, using a function (y-axis) with basin perimeter and stream density, between streams used and not used by harlequin ducks breeding in Prince William Sound, Alaska, 1991 - 1993.

APPENDIX D. Composition of habitat from 10 nests of harlequin ducks breeding in Prince William Sound, Alaska, 1991 -1992. Abbreviations are listed on following page.

	Nest substrate		Nest bowl material		Cryptic nest cover		UNDERSTORY: estimated percent coverage							
Stream	Subs1	Subs2	Mat1	Mat2	Cover1	Cover2	Vaccinium	Fern	Fireweed	Hemlock seedling	Devels club	Salmon berry	Alder	Rel. density
Beartrap91A	LI		down	VEGE	deadfall		0	20	70	0	0	0	10	heavy
Beartrap92A	LI	SI	down	VEGE	deadfall		90	0	0	0	0	0	10	sparse
Beartrap91I	LI		down	LI	deadfall		90	10	0	0	0	0	0	heavy
Beartrap 92I1	LI		down	LI	deadfall	VEGE	80	10	0	10	0	0	0	sparse
Beartrap92I2	LI	MO	down	LI	deadfall	VEGE	100	0	0	0	0	0	0	heavy
Gregorioff low	LI		down	LI	treebase	VEGE	100	0	0	0	0	0	0	moderate
Gregorioff up	MO	LI	down	VEGE	root cavity	VEGE	60	39	1	0	0	0	0	moderate
Nuchek	MO	LI	down	LI	stump bowl	VEGE	85	0	0	15	0	0	0	moderate
Hanning	LI	SI	down	LI	deadfall	VEGE	20	0	0	60	0	20	0	heavy
Constantine	LI	MO	down		deadfall	VEGE	0	30	0	0	30	40	0	heavy

		Nest bank composition			OVERSTORY: estimated percent coverage			
	Forest age	lower	middle	upper	Spruce	Hemlock	Alder	Relative Density
Beartrap91A	OLD	bedrock	tree/shrub	tree	0	100	0	heavy
Beartrap92A	OLD	bedrock	tree/shrub	tree	0	100	0	sparse
Beartrap91I	OLD	bedrock	shrub	tree	0	100	0	heavy
Beartrap 92I1	OLD	bedrock	tree/shrub	tree	0	100	0	sparse
Beartrap92I2	OLD	bedrock	shrub	tree	0	100	0	heavy
Gregorioff up	OLD	bedrock	shrub	tree	60	40	0	moderate
Gregorioff Low	OLD	gravel	tree/shrub	tree/shrub	20	75	5	moderate
Nuchek	OLD	gras/forb	tree/shrub	tree	0	100	0	moderate
Hanning	OLD	bedrock	tree/shrub	tree	25	75	0	sparse
Constantine	OLD	gras/forb	shrub	tree	0	80	20	sparse

APPEDNIX D (cont.)

HARLEQUIN DUCK NESTING HABITAT: TERRESTRIAL DATA FORM

Harlequin Restoration Project, Prince William Sound, Alaska

DATE:
TIME:
LOCATION:
Mark location on map

BROOD SIZE:
HEN I.D.#:
FREQ:

NEST SITE HABITAT: Complete for 10 m plot.

NEST SUBSTRATE

BE	Bedrock
BO	Boulder (>30cm)
CO	Cobble (8-30cm)
GR	Gravel (.2-8cm)
SA	Sand
SI	Silt
LI	Litter/vegetation

LANDFORM

MN	Mainland
IS	Island
PE	Peninsula
SB	Streambank
	UN Undercut
	VE Verticle
	SL Sloping
FL	Floodplain

NEST BOWL MATERIAL

GS	Grasses
DO	Down
VE	Vegetation

UNDERSTORY (ht<1m)

Sp1:________%____
Sp2:________%____
Sp3:________%____
Veg Density: HE MOD SP

OVERSTORY (ht>1m)

Sp1:________%____
Sp2:________%____
Sp3:________%____
HEV MOD SPARSE

CRYPTIC NEST COVER

RO	Rock crevice
TR	Tree cavity
DF	Deadfall
VE	Vegetation
	% Species:

Measure Distance To:

STREAM:______
FOREST:______
HARVEST:______

AREA HABITAT

SPRUCE-HEMLOCK FOREST

(specify if not S-H)

OG	Old growth
MA	Mature
IM	Immature
PO	Pole
SA	Sapling
SE	Seedling

HARVEST STATUS

UN	Unharvested
RH	Recent (<10 yr)
OH	Old harvest (>10yr)
SG	Second growth
BU	Buffer width:
CL	Clear-cut no buffer

BANK COMPOSITION

(list species and % on back)

TR	Trees
SH	Shrubs
TS	Tree/shrub mosaic
GF	Grass/forb
DE	Debris
SA	Sand
SI	Silt
GR	
BE	Bedrock
RO	Roots

TOPOGRAPHY: Altitude:____ Slope:____ Aspect:_____
Gravl/cobbl/bould

APPENDIX E. Location, size, age and chronology of harlequin duck broods observed in Prince William Sound, Alaska, 1991 - 1993.

						Age Range		Estimated Dates: +/- 1-3 days			
Area	Location	Year	Date	# Young	Age Class	Low	High	Nest Initiation Midpt	Incubation Initiation Midpt	Hatching Midpt	Fledging Midpt
EPWS	Sheep Riv	1991	10-Jul	2	1a	1	5	26-May	07-Jun	07-Jul	18-Aug
EPWS	Beartrap Riv	1991	07-Jul	7	1a	1	5	23-May	04-Jun	04-Jul	15-Aug
EPWS	Duck Riv	1991	04-Aug	1	1c	10	14	11-Jun	23-Jun	23-Jul	03-Sep
EPWS	Constantine Crk	1991	07-Aug	8	2a	15	21	08-Jun	20-Jun	20-Jul	31-Aug
EPWS	Beartrap Riv	1991	14-Aug	2	2a	15	21	15-Jun	27-Jun	27-Jul	07-Sep
EPWS	Stellar Crk	1991	20-Aug	5	2b	22	27	14-Jun	26-Jun	26-Jul	06-Sep
EPWS	Gregorioff	1991	20-Aug	6	2b	22	27	14-Jun	26-Jun	26-Jul	06-Sep
EPWS	Beartrap Riv	1991	18-Aug	1	2c	28	35	05-Jun	17-Jun	17-Jul	28-Aug
EPWS	Sheep Riv	1991	15-Aug	3	2c	28	35	02-Jun	14-Jun	14-Jul	25-Aug
EPWS	Stellar Crk	1991	20-Aug	2	2c	28	35	07-Jun	19-Jun	19-Jul	30-Aug
EPWS	Rain Crk	1991	22-Aug	1	2c	28	35	09-Jun	21-Jun	21-Jul	01-Sep
EPWS	Gregorioff	1991	20-Aug	4	2c	28	35	07-Jun	19-Jun	19-Jul	30-Aug
EPWS	Fish Bay	1991	19-Aug	2	2c	28	35	06-Jun	18-Jun	18-Jul	29-Aug
EPWS	Fish Bay	1991	19-Aug	4	3	36	42	30-May	11-Jun	11-Jul	22-Aug
EPWS	Sheep Riv	1991	15-Aug	4	3	36	42	26-May	07-Jun	07-Jul	18-Aug
EPWS	Rain Crk	1991	22-Aug	2	3	36	42	02-Jun	14-Jun	14-Jul	25-Aug
WPWS	Bay of Isles	1991	05-Sep	3	unknown						
WPWS	Hanning Bay	1991	21-Aug	3	2b	22	27	15-Jun	27-Jun	27-Jul	07-Sep
WPWS	Johnson Bay	1991	18-Aug	3	2b	22	27	12-Jun	24-Jun	24-Jul	04-Sep
WPWS	Hanning Bay	1991	21-Aug	4	2b	22	27	15-Jun	27-Jun	27-Jul	07-Sep
WPWS	Whale Bay	1991	19-Aug	4	3	36	42	30-May	11-Jun	11-Jul	22-Aug
EPWS	Stellar Crk	1992	20-Aug	5	2b	22	27	14-Jun	26-Jun	26-Jul	06-Sep
EPWS	Indian Riv.	1992	20-Aug	2	2c	28	35	07-Jun	19-Jun	19-Jul	30-Aug
EPWS	Constantine Crk	1992	18-Aug	5	2c	28	35	05-Jun	17-Jun	17-Jul	28-Aug
EPWS	Constantine Crk	1992	18-Aug	1	2c	28	35	05-Jun	17-Jun	17-Jul	28-Aug
EPWS	Fish Bay	1992	25-Jul	4	2c	28	35	12-May	24-May	23-Jun	04-Aug
WPWS	Hanning Bay	1992	31-Jul	3	unknown						
WPWS	Macleod Hbr	1992	31-Jul	2	unknown						
WPWS	Squire Is	1992	16-Jul	6	1	1	14	27-May	08-Jun	08-Jul	19-Aug
EPWS	Stellar Crk	1993	16-Aug	5	2a	15	21	17-Jun	29-Jun	29-Jul	09-Sep
EPWS	Gregorioff	1993	16-Aug	3	2b	22	27	10-Jun	22-Jun	22-Jul	02-Sep
EPWS	West Bligh Is.	1993	17-Aug	1	2b	22	27	11-Jun	23-Jun	23-Jul	03-Sep
EPWS	Namorov Riv.	1993	16-Aug	4	2b	22	27	10-Jun	22-Jun	22-Jul	02-Sep
EPWS	Sheep Riv.	1993	11-Aug	2	2c	28	35	29-May	10-Jun	10-Jul	21-Aug
EPWS	Beartrap Bay	1993	11-Aug	1	2c	28	35	29-May	10-Jun	10-Jul	21-Aug
EPWS	Control Crk	1993	10-Aug	2	2c	28	35	28-May	09-Jun	09-Jul	20-Aug
EPWS	Graveyard Pt.	1993	17-Aug	1	3	36	42	28-May	09-Jun	09-Jul	20-Aug
EPWS	LandlockedBay	1993	17-Aug	2	3	36	42	28-May	09-Jun	09-Jul	20-Aug
EPWS	Cloudman'sBay	1993	17-Aug	1	3	36	42	28-May	09-Jun	09-Jul	20-Aug
EPWS	Raging Crk	1993	12-Aug	2	3	36	42	23-May	04-Jun	04-Jul	15-Aug
WPWS	WestTwinPerry	1993	24-Aug	2	2b	22	27	18-Jun	30-Jun	30-Jul	10-Sep
WPWS	Hanning Bay	1993	05-Aug	6	2b	22	27	30-May	11-Jun	11-Jul	22-Aug
WPWS	Jackpot/Ewan	1993	26-Aug	6	2c	28	35	13-Jun	25-Jun	25-Jul	05-Sep