

Productivity of Harlequin Ducks breeding in Prince William Sound, Alaska

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Abstract

Harlequin Ducks *Histrionicus histrionicus* breeding along coastal streams in Prince William Sound (PWS), Alaska, forage opportunistically on abundant resources of intertidal deltas and salmon spawning beds during summer. In contrast, inland-breeding Harlequin Ducks rely entirely on lotic invertebrates, a shortage of which may reduce breeding propensity (proportion of adult females breeding) during some seasons. Harlequin Ducks breeding in eastern PWS exhibited higher breeding propensity than inland-breeding populations. Twelve of 15 and 20 of 27 adult female Harlequin Ducks captured at stream mouths in PWS were breeding birds in 1991 and 1992, respectively. Of 16 nonbreeding females captured, paired nonbreeders weighed significantly more than unpaired nonbreeders, which I suggest were sexually immature yearlings. Average clutch size for seven nests was 6.1 eggs. Observed duckling mortality from hatching to near fledging age was at least 57%, which was high compared with inland breeding populations. Unusually high mortality of ducklings occurred from three to five weeks of age relative to other populations. Average brood size at fledging age was 2.4 ± 0.8 young. Despite the higher breeding propensity observed in eastern PWS, preliminary estimates of recruitment suggest that coastal-breeding Harlequin Ducks have lower productivity than inland-breeding populations.

Résumé

Les Arlequins plongeurs (*Histrionicus histrionicus*) se reproduisant le long des cours d'eau côtiers dans le golfe du Prince-William, en Alaska, bénéficient des abondantes ressources alimentaires offertes par les deltas intertidaux et les frayères de saumons durant l'été. Par contraste, l'alimentation des Arlequins plongeurs se reproduisant à l'intérieur des terres repose entièrement sur les invertébrés lotiques, dont une pénurie peut réduire la capacité de reproduction de cette espèce (proportion des femelles adultes se reproduisant) en certaines saisons. Les Arlequins plongeurs se reproduisant dans la partie est du golfe du Prince-William présentaient une tendance naturelle de reproduction plus forte que les populations se reproduisant à l'intérieur des terres. Douze des 15, et 20 des 27, Arlequins plongeurs femelles adultes capturés à l'embouchure de cours d'eau dans le golfe du Prince-William étaient des oiseaux

reproducteurs en 1991 et 1992, respectivement. Des 16 femelles non reproductrices capturées, les femelles accouplées pesaient beaucoup plus que les femelles non accouplées, qui étaient probablement des jeunes immatures. La ponte moyenne pour sept nids était de 6,1 œufs. La mortalité, de l'éclosion à un âge approchant la maturité, était d'au moins 57 p. 100, un taux élevé comparativement à celui des populations des terres intérieures. On a observé un taux de mortalité des canetons anormalement élevé entre l'âge de trois à cinq semaines relativement aux autres populations. La taille moyenne des couvées à l'âge de l'envol était de $2,4 \pm 0,8$ petits. Malgré la plus forte propension à se reproduire des oiseaux de l'est du golfe du Prince-William, les premières estimations indiquent que les Arlequins plongeurs se reproduisant sur la côte présentent une productivité moins grande que les populations se reproduisant à l'intérieur des terres.

1.0 Introduction

Harlequin Ducks *Histrionicus histrionicus* exhibit delayed sexual maturity, low annual production, variable breeding propensity, and long lives, typical traits of all sea duck species (Goudie et al. 1994). Population levels are sensitive to adult mortality, particularly when proportionately high losses occur (Goudie et al. 1994). The Exxon Valdez oil spill (March 1989) in Prince William Sound (PWS), Alaska, raised concern over the potential effects of oil on the abundance and productivity of Harlequin Ducks in the spill area. Research on Harlequin Ducks breeding in unperturbed coastal ecosystems was limited to three streams in eastern PWS (Dzinbal 1982; Dzinbal and Jarvis 1984) and nine on the coast of Iceland (Bengtson 1972). To gain more insight into pre-spill productivity, we studied coastal-breeding Harlequin Ducks in eastern PWS, a region that was bypassed by the southwestwardly flowing oil spill (Crowley 1994).

Harlequin Ducks breeding in PWS nest along short streams flowing seaward from coastal mountains (Dzinbal 1982; Crowley 1994). The number of Harlequin Ducks breeding in PWS is unknown. The total population in PWS during July 1991 was an estimated 8300 ± 3100 Harlequin Ducks (K. Laing, pers. commun.). This estimate, however, was an instantaneous sample of a seasonally fluctuating population (Isleib and Kessel 1973; D.W. Crowley, unpubl. data). Typically, the summer population of Harlequin Ducks begins increasing in late June and July, as postbreeding

males return to moult in PWS from their inland breeding areas (D. Rosenberg, pers. commun.). This increase in abundance continues during August and September as failed-breeding and postbreeding females and broods arrive in PWS (D. Rosenberg, pers. commun.). In addition to locally breeding Harlequin Ducks, most yearlings reared either locally or on inland streams also spend the entire summer along the coast (Salomonsen 1950; Bengtson 1972; Palmer 1976).

Bengtson and Ulfstrand (1971) and Gardarsson and Einarsson (1994) reported that low food resources limited production on interior streams of Iceland, where Harlequin Ducks relied on stream invertebrates (particularly simuliids) for all of their diet. Coastal-breeding Harlequin Ducks, however, are probably not limited by food resources on streams in PWS (Dzinbal and Jarvis 1984). Dzinbal and Jarvis (1984) reported that prior to the arrival of anadromous salmon (pink salmon *Oncorhynchus gorbuscha* and chum salmon *O. keta*), Harlequin Ducks avoided foraging in streams in PWS, feeding almost exclusively on marine invertebrates in the intertidal delta. When salmon returned to spawn in July, Harlequin Ducks moved slightly upstream to forage on salmon roe, usually within 0.5 km of intertidal deltas (Dzinbal and Jarvis 1984). In PWS and coastal Iceland, incubating females flew from upstream nest sites down to spawning beds and deltas to feed (Bengtson 1972; Dzinbal 1982; Crowley 1994). The abundance of forage, combined with relatively high pair density observed by Dzinbal (1982) in PWS, suggested that the productivity of coastal-breeding Harlequin Ducks could be higher than that of populations breeding farther inland.

The primary objectives of the study were to develop indices of abundance and productivity in PWS and to determine habitat use by breeding Harlequin Ducks. In this paper, I calculate indices of productivity of Harlequin Ducks in eastern PWS and compare them with the performance of Harlequin Duck populations breeding in inland regions.

2.0 Study area

PWS is located on the south-central coast of Alaska (see Isleib and Kessel 1973). The study area consisted of shoreline, estuaries, and stream mouths from Cordova to Valdez and the protected leeward shores of Hinchinbrook and Hawkins islands, covering approximately 630 km of coastline and 85 streams. Streams used by Harlequin Ducks breeding in PWS are relatively low in average length (13.2 km), average volume discharge (3.2 m³/s) (Crowley 1994), and invertebrate abundance (Dzinbal and Jarvis 1984). Daily tidal exchange of up to 6 m creates large intertidal deltas at the outflow of streams.

3.0 Methods

Harlequin Ducks were captured in mist nets suspended across streams within 100 m of intertidal deltas. We monitored streams from 21:00 to 01:00 and from 03:00 to 08:00 during June, when ducks were flying to and from upstream reaches while searching for nest sites (Bengtson 1966) and laying eggs (Crowley 1994). Mist nets used (Avinet Inc., #12N-210/2) had a 10-cm mesh and measured 1.8 m in height by 12 m or 18 m in length. Mist nets were most effective when placed in pairs (10–20 m apart) on

bends in the stream channel. This trap configuration 1) took advantage of the characteristic low flight (<1 m off the surface) of Harlequin Ducks closely following the stream channel (Bengtson 1966), 2) was less visible on bends and consequently not often avoided by ducks, 3) caught Harlequin Ducks flying more slowly around sharp bends, resulting in fewer ducks bursting through nets, and 4) usually captured ducks in the second net if the first net was avoided or breached. I assumed that all females using streams had equal probability of capture using this configuration. Streams were kept under surveillance while nets were deployed, allowing immediate removal of captured birds and observation of whether females were paired (accompanied proximally by a male) before striking the net.

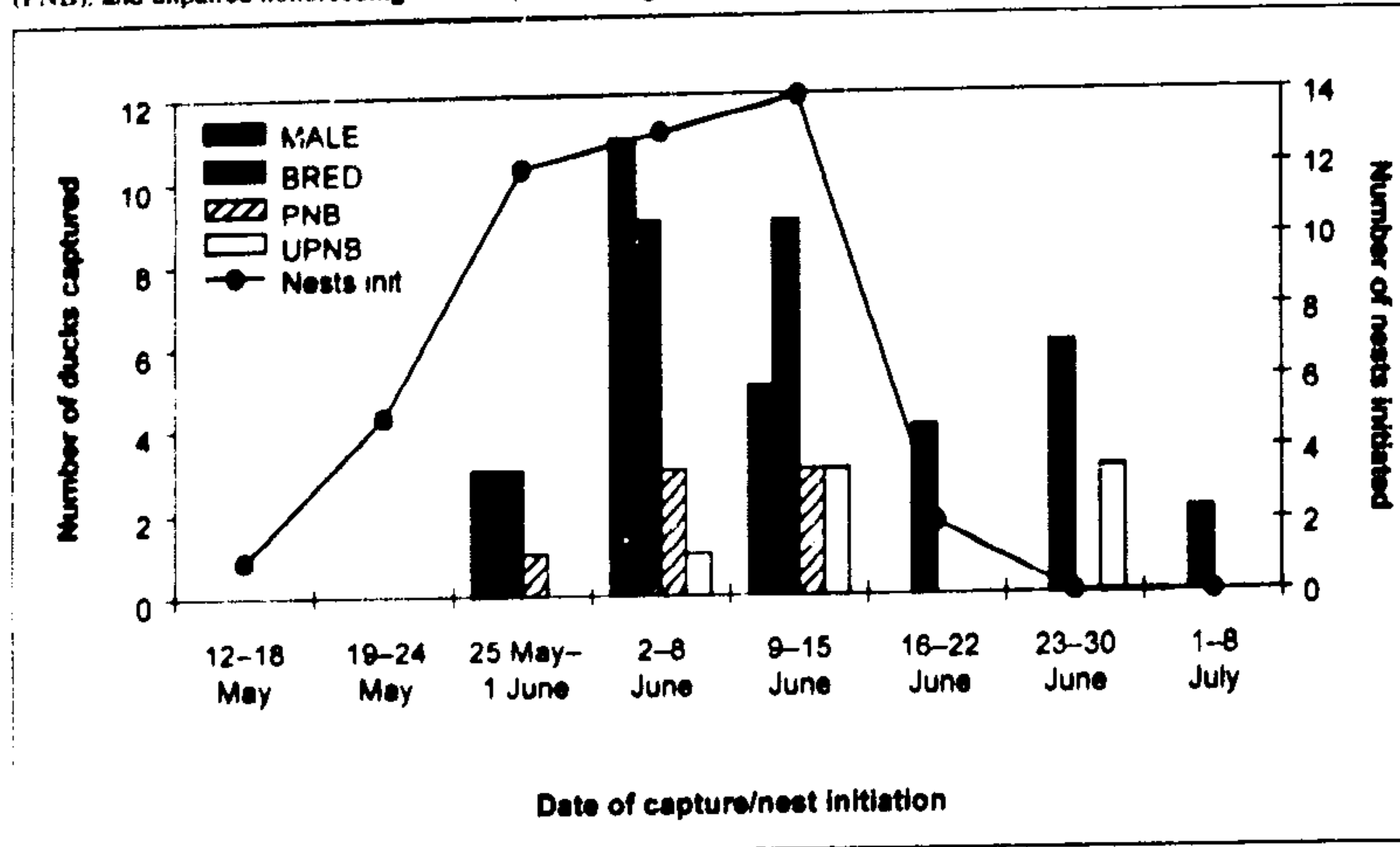
Captured female Harlequin Ducks exhibiting a distended and flaccid cloacal aperture (indicating egg laying) or brood patch (indicating incubation) were considered breeding, and those with neither were nonbreeding. I further classified nonbreeding females as paired or unpaired. To limit a potential low bias in estimating breeding propensity (caused by a change of status from nonbreeding to breeding), we continued trapping streams for three weeks beyond the peak period of nest initiation, which occurred during the first two weeks of June (DWC, unpubl. data). We also trapped again in late June on streams that had been monitored early in the season (May – 7 June). I estimated breeding propensity (percentage of adult females breeding) by dividing the number of breeders captured by the total number of adult females captured.

We measured mass, tarsus, culmen, and wing chord of captured ducks. I compared morphology between sexes and among breeding, paired nonbreeding (PNB), and unpaired nonbreeding (UPNB) females using two-sample testing (Student's *t* and Mann-Whitney-Wilcoxon *Z*) and analysis of variance (ANOVA). We determined age class of captured males (adult or subadult) by plumage characteristics (Dement'ev and Gladkov 1967; Palmer 1976), but there was no similar technique to determine age of nonbreeding females (Bengtson 1972), which therefore remained unknown.

Captured female Harlequin Ducks were tagged with a 4.5-g radio transmitter (Advanced Telemetry Systems, model #357) glued to the centre tail feathers. I located the general vicinity of nesting females by radiotelemetry from fixed-wing aircraft, then hiked up streams to search for nests. I determined clutch size and hatching success (eggs hatched, eggs laid) by observing eggs pipping or ducklings drying in the nest and by counting shell membranes and added eggs in nests that I revisited.

I assessed duckling mortality using data from coastal surveys from July and August, 1991–1993 and 1995–1996. Surveys were conducted from a skiff piloted within 5–30 m of shore. Deltas and approximately 100 m of streams were surveyed on foot if not navigable by boat. Harlequin Duck broods were counted and classified by age based on plumage development (Gollop and Marshall 1954). Assuming that juveniles fledged at 42 days (Bengtson 1972; Wallen 1987), approximate ages (days) of ducklings classified by plumage development were as follows: 1a = 1–5, 1b = 6–9, 1c = 10–14, 2a = 15–21, 2b = 22–27, 2c = 28–35, and 3 = 36–42 (Wallen 1987). I did not attempt to follow individual broods through time. Consequently, mortality was indicated by the

Figure 1
Chronology and numbers of Harlequin Ducks captured and nests initiated on breeding streams in Prince William Sound, Alaska, 1991-1992. Sex and breeding status include adult males, breeding females (BRED), paired nonbreeding females (PNB), and unpaired nonbreeding females (UPNB). Age of most PNB and all UPNB females was unknown.



change in average brood size from one age class to the next, analyzed using ANOVA and Mann-Whitney-Wilcoxon tests.

4.0 Results

4.1 Breeding status of captured ducks

We captured 23 Harlequin Ducks (16 females) in 1991 during 330 net-hours of trapping effort and 42 ducks (32 females) in 1992 during 224 net-hours (Fig. 1). We captured Harlequin Ducks on 10 of 23 streams trapped. I assumed that PNB females were adults that did not breed, a status that characteristically applies to 15-60% of adult female Harlequin Ducks on breeding streams (Bengtson and Ulfstrand 1971; Bengtson 1972; Dzinbal 1982; Wallen 1987). Because there was typically a surplus of unpaired adult males using streams (Bengtson 1972; Kuchel 1977; Dzinbal 1982; DWC, pers. obs.), I assumed that UPNB females were subadults as yet incapable of breeding or forming pair bonds. We captured six of seven UPNB females during mid- to late June (Fig. 1), by which time most breeding females had begun incubating. Four of seven UPNB females were captured while males were still present on streams (Fig. 1). Pair status of two nonbreeding females was unknown; they were assumed to be adults. Of six females captured in both 1991 and 1992, two PNB females in 1991 became breeders in 1992, three females bred in both years, and one breeder in 1991 was a nonbreeding female in 1992. Although we discontinued trapping after 7 July, we regularly observed flocks of 5-15 non- and failed-breeding females (with few or no males present) at stream mouths during surveys.

All 17 male Harlequin Ducks captured were in adult breeding plumage. Males were more likely than females to break through or avoid mist nets. No males were captured or observed flying up streams after 15 June, indicating that pair bonds had dissolved for both breeding and nonbreeding

females. Male Harlequin Ducks shifted use from stream mouths to exposed coastline to moult after females began incubating.

Male Harlequin Ducks had significantly greater average body weight ($F = 9.25, P = 0.0001$) (Fig. 2) and lengths of tarsus ($t = 3.97, df = 2,59, P < 0.001$), culmen ($t = 4.23, df = 2,59, P < 0.001$), and wing chord (1992 data only, $t = 3.08, df = 2,35, P = 0.004$) than those of captured females. Weights of PNB females were significantly greater than those of UPNB females ($F = 9.25, P = 0.0001$) (Fig. 2), although other body measurements did not differ significantly. Breeding females did not differ in weight from PNB females but were significantly heavier than UPNB females ($F = 9.25, P = 0.0001$) (Fig. 2). Two breeding females recaptured as the nesting season progressed indicated a tendency to lose weight (by 17% and 12% over one month). However, breeding females captured after 13 June ($n = 12$) still weighed significantly more ($Z = 2.74, P = 0.006$) than UPNB females ($n = 5$) captured after 13 June.

4.2 Productivity

Breeding propensity of adult females was higher in 1991 than in 1992, averaging 80% (Table 1). Nest initiations, calculated by back-dating from seven nests and 40 broods of known age class (1991-1992, combined), occurred from 15 May through 18 June, with 45 of 47 occurring by 15 June. Average number of eggs in seven clutches of known size was 6.13 ± 0.92 (SD). Low density and difficulty in locating Harlequin Duck nests resulted in a sample size too small to estimate nest success (proportion of nests producing broods). At least five of seven nests produced hatchlings, and known hatching success for 32 eggs in five nests was 97.2%.

We observed 60 broods during five years of surveys in PWS. Six of seven broods of class 1a were in or near nests at time of observation; all other broods were seen near stream mouths and along the coast. The average number of

Figure 2
Body weight of Harlequin Ducks captured on streams in Prince William Sound, Alaska, 1991-1992. Sex and breeding status include adult males, breeding females, paired nonbreeding females (PNB), and unpaired nonbreeding females (UPNB). Age of most PNB and all UPNB females was unknown. UPNB females weighed significantly less than other females ($P < 0.001$). Error bars represent 95% confidence interval; numbers above bars are sample sizes.

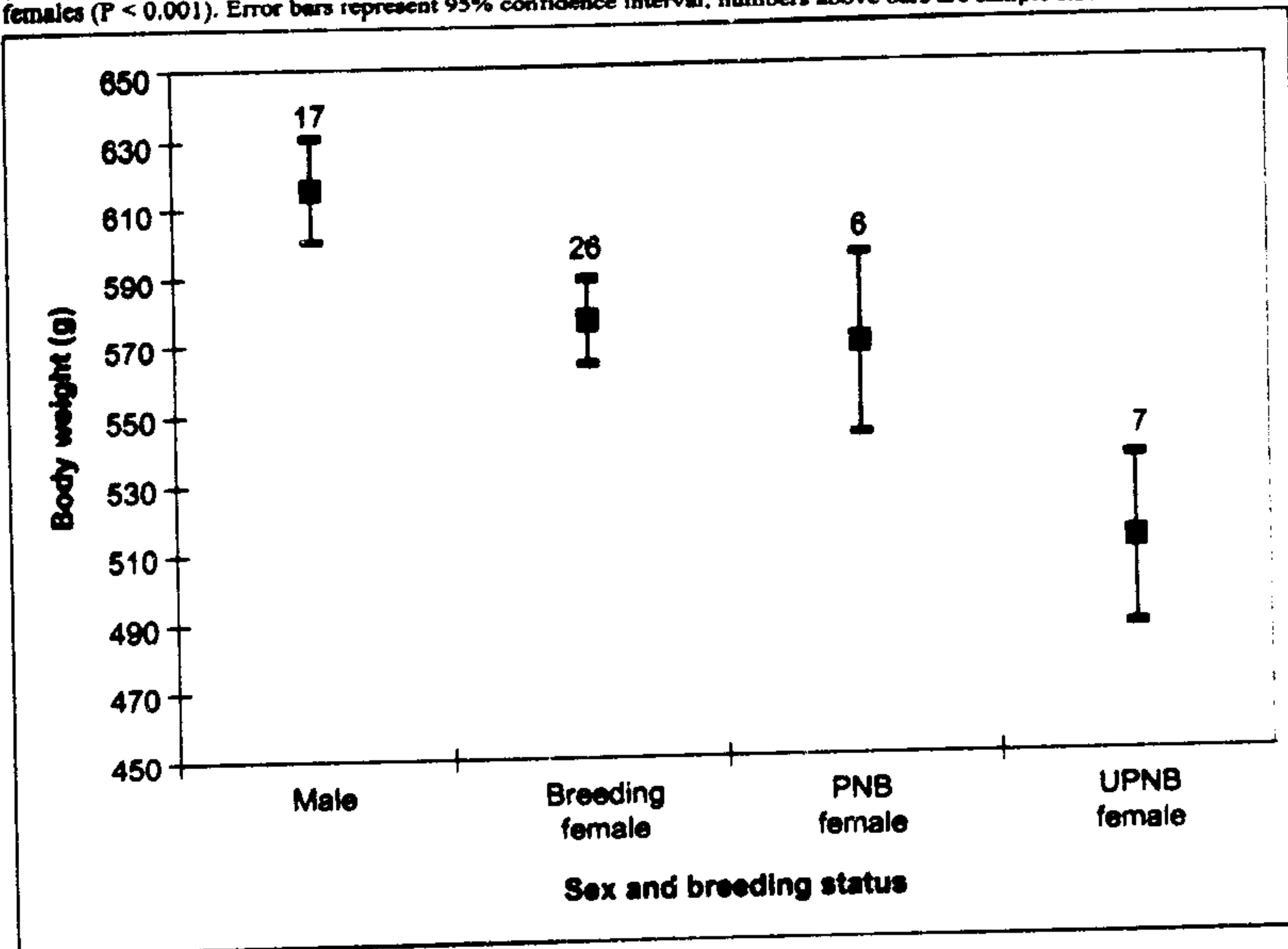


Table 1
Estimated breeding^a propensity of female Harlequin Ducks captured near stream mouths in Prince William Sound, Alaska, 1991-1992

	1991	1992
Total females captured (TOT)	16	32
Total breeders (B)	12	20
Paired breeders (PB)	4	2
Unpaired breeders (UPB)	0	10
Other breeders ^b	8	8
Total nonbreeders	4	12
Paired nonbreeders (PNB)	1	6
Unpaired nonbreeders (UPNB)	2	5
Other nonbreeders (NB) ^b	1	1
% females breeding (B/TOT)	75	63
Adult females (B+PNB+NB)	14	27
Subadult females (UPNB)	2	5
% adults [(B+PNB+NB)/TOT]	88	84
% adults breeding [B/(B+PNB+NB)]	86	74

^a Breeding was indicated by the presence of distended cloacal aperture and brood patch.

^b Pair status unknown.

ducklings in broods decreased with an increase in age class ($F = 3.91$, $P = 0.0042$) (Fig. 3). Under this model, broods of age class 1a were significantly larger than those of age classes 2b, 2c, and 3, but not age class 1c. Harlequin Duck broods decreased in size by 27% from age class 2b to 2c ($Z = 1.94$, $P = 0.052$), when most broods first appeared near stream mouths, then dropped by 9% from 2c to 3 (Fig. 3).

The observed cumulative mortality of ducklings from age class 1a to fledging was approximately 57%. This was likely an underestimation of mortality, because loss of entire broods was not detectable using this method. The average brood size at fledging age was 2.4 ± 0.82 (SD), assuming that pre-fledged class 3 ducklings survived to fledging.

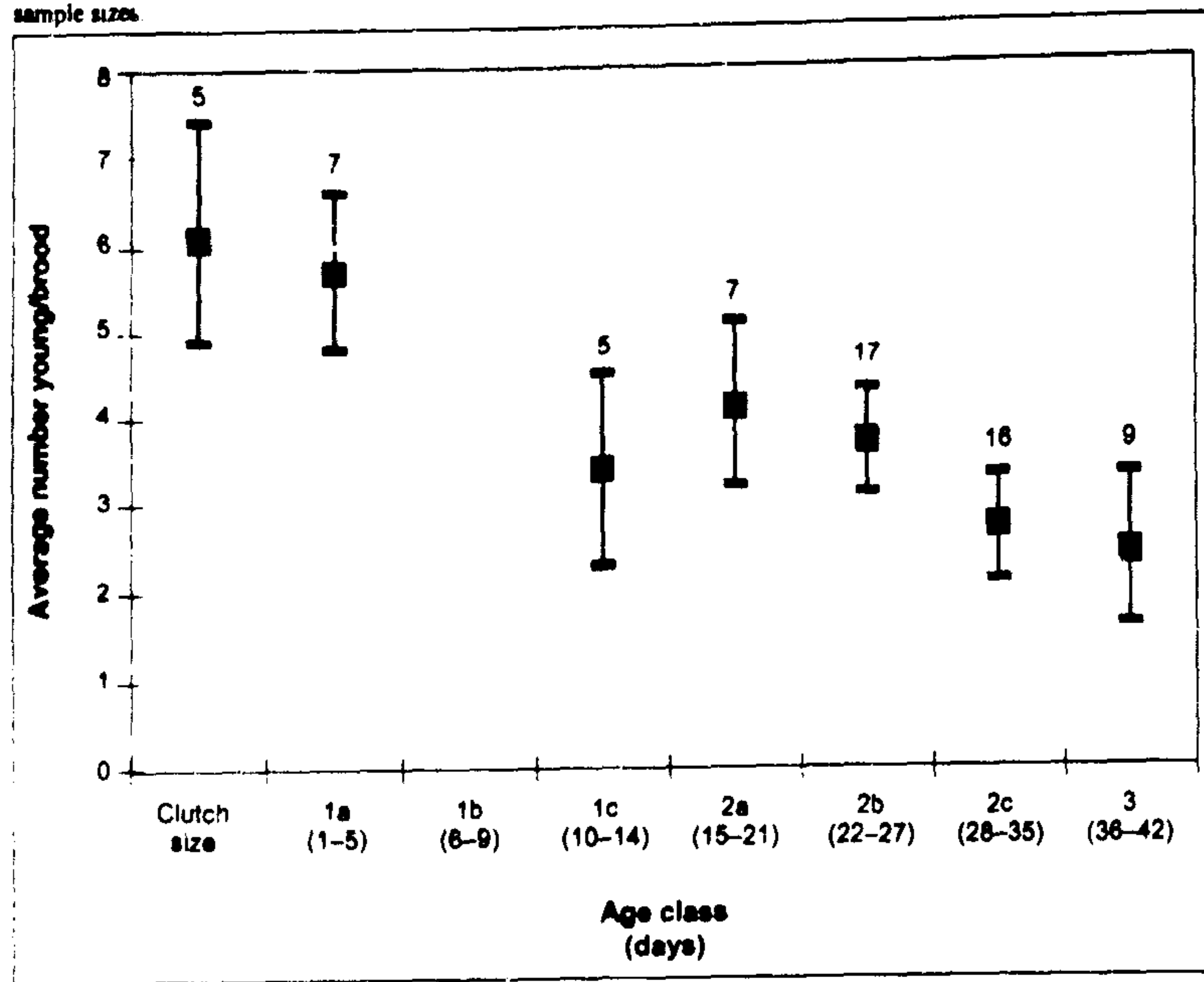
5.0 Discussion

5.1 Breeding status of captured ducks

The coastal-breeding population of PWS Harlequin Ducks exhibited characteristics similar to those of inland-breeding populations in Iceland and western North America, including the presence of nonbreeding adult females and the absence or scarcity of yearling males (Bengtson and Ulfstrand 1971; Bengtson 1972; Kuchel 1977; Dzinbal 1982; Wallen 1987). Bengtson and Ulfstrand (1971) also determined by cloacal examination and necropsy that yearling females were absent from their inland study streams of Iceland. In contrast, the presence of yearlings could be expected on streams in PWS, because most yearlings apparently spend their first summer on the coast (Salomonsen 1950; Bengtson 1972; Palmer 1976), and stream mouths are preferred feeding areas for Harlequin Ducks during summer (Dzinbal 1982). Dzinbal (1982) captured two yearling males on several streams in PWS but did not determine age of captured females.

Harlequin Ducks do not begin breeding until they are at least two years of age (Bent 1925; Dement'ev and Gladkov 1967), and age at first breeding often varies for sea

Figure 3
Mortality of juvenile Harlequin Ducks hatched on streams in Prince William Sound, Alaska, 1991-1992, indicated by decreasing number of ducklings per brood with increasing age. Most broods first appeared at stream mouths at age 2a-2c, during which high mortality occurred. Error bars represent 95% confidence interval; numbers above bars are sample sizes.



ducks (Bellrose 1980). First breeding for Common Goldeneyes *Bucephala clangula*, for example, occurs from two to six years of age and averages 3.2 years (Dow and Fredga 1984). The presence of yearlings and the fact that sexual maturity can be delayed for a variable number of years suggest that the following classes of females were captured at our study site: 1) experienced adults, either breeding or nonbreeding (three or more years of age), 2) those breeding for the first time (two years and older), and 3) sexually immature subadults not yet attempting to breed (yearlings and older).

Brooding females captured in PWS probably included some proportion of two-year-olds that had initiated nests. Kuchel (1977) observed two female Harlequin Ducks returning to natal streams at two years of age. They were paired and established home ranges but arrived 2-3 weeks later than nesting females and apparently did not produce broods (Kuchel 1977). 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 the maritime climate remains relatively mild into September, allowing later nest initiation. Eadie and Gauthier (1985) reported that two-year-old female goldeneyes might be more likely to attempt nesting if they had spent the previous season on the breeding grounds as yearlings.

PNB females in PWS were similar to nonbreeding females on inland streams recorded in Iceland that arrived paired, did not nest, parted from mates by mid-June, and

were observed in small flocks on breeding streams during the rest of the summer (Bengtson and Ulfstrand 1971). There was no obvious reason why PNB Harlequin Ducks in PWS did not nest. Availability of nest sites limited by spring snow (Wallen 1987; Crowley 1994) or lack of suitable nesting habitat (Bengtson 1972) could be environmental or density-dependent effects (respectively) that preclude some adult females from nesting but not from pairing. Alternatively, some PNB females may have been young adults that lacked nesting experience.

I believe that at least some proportion of UPNB females were yearlings. Although samples of UPNB females were small, they had lower weights, did not have mates, and continued to make visits upstream during the incubation period (Fig. 1). These characteristics were similar to those reported by Eadie and Gauthier (1985) for yearling female Barrow's Goldeneye *Bucephala islandica* and Buffleheads *B. albeola* that, when captured while prospecting nest cavities during incubation and hatching, weighed significantly less than nesting adults. Visiting a future breeding stream (perhaps a natal stream) in PWS prior to the moult would provide yearling females familiarity with potential nest sites, foraging areas, and predators (Lack 1966). Dow and Fredga (1983) suggested that Common Goldeneyes may increase their chance of success during first breeding attempt by spending a season or two on the breeding grounds as subadults.

Table 2
Indices of productivity of Harlequin Ducks breeding on coastal streams of eastern Prince William Sound (PWS), Alaska, compared with populations breeding on inland streams

Region	% adult breeding propensity	Breeding density (no./km)	Fledged brood size	Duckling mortality (%)	Fledged young/female	Breeding success (%)
PWS, 1991-1993	74-86		2.4	57		
PWS, 1979-1980 ^a	50-53 ^b	1.3-1.8	2.5-2.7	33-50	0.8	57-67
Idaho ^c	33-36 ^b	0.06-1.3	3.3	27-55	0.8-1.2	33-36
Wyoming ^d	38 ^b	0.89	4.5		1.9	
Montana	41 ^{b,e}	0.05-1.2 ^f	3.5-3.9 ^g	25-82 ^g	0.3-1.44 ^g	41
Iceland ^h	70-85	0.2-7.1	2.9	44	1.5-2.2	87

^a Dzinbal (1982).

^b Assumes all females were adults, which is probably valid for paired females only. This assumption was not valid for PWS, where unpaired yearling females are probably present. Whether yearlings visit inland breeding areas in North America is unknown.

^c Summary of productivity in Idaho from 1990 to 1996 (F. Cassirer, pers. commun.).

^d Wallen (1987).

^e D. Genter (pers. commun.).

^f Seasons of low productivity in Montana were caused by flooding (Kuchel 1977; P. Finnegan, pers. commun.).

^g Bengtson (1972).

5.2 Productivity

Estimated breeding propensity in PWS was similar to that of two interior rivers in Iceland (Table 2) (Bengtson and Ulfstrand 1971). Dzinbal (1982) estimated breeding propensity in PWS using mature and subadult females combined (Table 2). Although my estimate of the same parameter for PWS was higher (B/TOT in Table 1), both indicated higher breeding propensity in PWS than on inland rivers of Idaho (F. Cassirer, pers. commun.), Montana (D. Genter, pers. commun.), and Wyoming (Wallen 1987) (Table 2). Unlike most inland regions, nesting areas in PWS were not subject to human disturbance, which may contribute to lower breeding propensity (Kuchel 1977; Wallen 1987). Breeding and wintering in the same area might also contribute to higher breeding propensity along the coast, by allowing young females to gain familiarity with breeding streams and eliminating the need to migrate.

The first 2-3 weeks of brood rearing usually occurred far upstream of areas observable during boat surveys (Crowley 1994). Consequently, broods younger than age class 2a had low probability of being observed, which was implicit in small samples of age classes 1a-1c. I suspect that those 1c broods observed near stream mouths were more exposed to predation than 1c broods that remained upstream, resulting in the low average of that age class (Fig. 3), although stochastic variation is also a likely explanation.

The high level of mortality observed from age 2b to 2c (4-5 weeks) was unusual for Harlequin Ducks (Bengtson 1972) and other duck species, which typically have progressively decreasing mortality after the first two weeks of life (Baldassarre and Bolen 1994). Potential predators (e.g., mink *Mustela vison*, river otters *Lutra canadensis*, Glaucous-winged Gulls *Larus glaucescens*, and Bald Eagles *Haliaeetus leucocephalus*) attracted to lower stream reaches during the salmon spawn may have contributed to the observed increase in duckling mortality (Dzinbal 1982). Indices of brood size at fledging and recruitment in PWS (Dzinbal 1982) compared with indices for inland regions (Table 2) suggest that the relatively high breeding propensity and pair density may be offset by higher duckling mortality.

Unusually high mortality of Harlequin Duck broods on inland streams has been ascribed to flooding (Kuchel 1977; Wallen 1987; P. Finnegan, pers. commun.). Flooding appeared less important than predation for coastal streams in

PWS. Broods were hatched after high spring water and reared during receding water levels (Dzinbal 1982). Furthermore, potential effects of flooding are probably minimized once broods begin using intertidal areas for foraging.

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