Coastal feeding ecology of Harlequin Ducks in Prince William Sound, Alaska, during summer

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1. Abstract

Feeding habitat and time allocated to feeding changed from early to late summer among Harlequin Ducks (*Histrionicus histrionicus*) studied in Prince William Sound, Alaska, during summers 1979 and 1980. In early summer, harlequins fed predominantly in the intertidal deltas of small streams, and in the intertidal zones of protected bays, where they consumed a variety of marine invertebrates. Following the arrival of spawning salmon in July, harlequins moved into the lower portions of suitable streams and fed on drifting roe. In May and early June, before incubation began, paired female and male harlequins spent, respectively, about 21 and 13% of their diurnal time (04:00–23:00) feeding (ingesting prey, diving, and dabbling). Following dissolution of pairs in mid June, single females and males spent, respectively, 15 and 12% of their diurnal time (05:00–22:00) feeding.

2. Résumé

Parmi les Canards arlequins (*Histrionicus histrionicus*) étudiés dans le détroit de Prince-William (Alaska) durant les étés de 1979 et de 1980, l'habitat d'alimentation et le temps consacré à l'alimentation changeaient entre le début et la fin de l'été. Ainsi, au début de l'été, les canards se nourrissaient surtout dans les deltas intertidaux des petits cours d'eau et dans les zones intertidales des baies protégées où ils consommaient toute une variété d'invertébrés marins. En juillet, après l'arrivée des saumons en période de frai, les canards se déplacaient vers les parties inférieures des cours d'eau appropriés pour se nourrir des oeufs à la dérive. En mai et au commencement de juin, avant le début de l'incubation, les femelles et les mâles appariés passaient respectivement 21 % et 13 % environ de leur temps diurne (de 4:00 à 23:00) à se nourrir (c'est-à-dire à ingérer leurs proies, à plonger et à barboter). Après la dissolution des couples à la mi-juin, les femelles et les mâles séparés consacraient respectivement 15 % et 12 % de leur temps diurne (de 5:00 à 22:00) à se nourrir.

3. Introduction

The feeding ecology of the Harlequin Duck (*Histrionicus histrionicus*) in North America is poorly known. Along the coast in winter, harlequins apparently feed on a wide variety of foods, but predominantly on crustaceans (mostly crabs and amphipods) and mollusks (especially chitons and gastropods) obtained in shallow and often turbulent water near shore (Bent 1925, Cottam 1939, Kenyon 1961, Palmer 1949, Preble and McAtee 1923, Whitfield 1894). During the summer, along streams located relatively far inland, breeding harlequins feed on blackfly (Simuliidae) larvae, and on aquatic Trichoptera, Chironomidae, and Perlidae (Bengtson 1972, Dement'ev and Gladkov 1952, Gudmundsson 1971). In Iceland during summer, harlequins along inland streams feed in shallow (< 80 cm) rapids near suitable nesting and loafing sites, or they may fly upstream to feed near the outlets of lakes (Bengtson 1972:13). Harlequins use both running and standing water in Montana during summer, and backwater ponds are important there for feeding during high-water periods and during brood rearing (Kuchel 1977:93).

In spring (about April) harlequins migrate from exposed coasts into fiords and bays where they congregate near river mouths before moving inland (Bengtson 1966, Gudmundsson 1971). However, not all harlequins travel far inland; many breed along streams close to the coast (Gabrielson and Lincoln 1959, Palmer 1976, Dzinbal 1982). In addition, most non-breeders remain on the coast during the summer, where they are eventually joined by post-breeding drakes and failed-breeding females (Palmer 1976).

However, little information exists concerning the feeding activity of harlequins or the particular sites they prefer to forage in along the North American coasts during summer. This study was conducted to compare the diurnal feeding activity of harlequins to their habitat use in a small bay in Prince William Sound, Alaska, during the summers of 1979 and 1980. A second objective was to obtain information on their food.

4. Study area

Sawmill Bay, the primary study area, lies in northeast Prince William Sound about 24 km southwest of Valdez, Alaska (Fig. 1). The study area lies within the Coastal Spruce–Hemlock Forest vegetation region (Viereck and Little 1972). The area has a moderate climate characterized by cool, rainy summers and winters with heavy snowfall. Ice fields and glaciers are prominent at higher elevations in the surrounding mountains. The geography, climate, glacial history, and vegetation of Prince William Sound are discussed by Cooper (1942).

Sawmill Bay has a water area of 2.25 km^2 (Fig. 1), is about 18 m deep at its mouth, and is enclosed by steep mountains rising 1000–1370 m. Tides fluctuate 2–6 m in the bay, and at low tide a large portion of the bay lies exposed. Three short (about 5 km) streams with discharge

rates of about 1.5–7.0 m^3/s enter the bay (Dzinbal 1982). Only Stellar Creek, a moderately steep, clear, non-glacial stream, received appreciable use by harlequins, mostly below the confluence of Fault Creek (Fig. 1). Only incubating and brooding females regularly occurred farther upstream.

About 50 harlequins (including 14–15 pairs) were present in Sawmill Bay at the peak of the breeding season in late May each year. In 1979 and 1980, respectively, 11 and 8 of the pairs observed in late May were thought to have attempted nesting along Stellar Creek (Dzinbal 1982). The other 3–7 pairs either nested on streams outside of the Sawmill Bay drainage or failed to nest.

5. Methods

Three habitats used by Harlequin Ducks in Sawmill Bay were distinguished: creek (Stellar Creek including the intertidal delta), rocks (offshore rocks, headlands, and small islands, including their immediately adjacent waters), and lee waters (quiet coves or areas in the lee of islands or peninsulas that were sheltered from all but the most violent storms).

Occurrence and feeding activity in the three habitats were assessed (1) for paired male and female harlequins during the pre-nesting and laying period (10 May – 21 June), and (2) for single males and females during the post-laying period (22 June – 15 August). Single males included both successful and unsuccessful breeders; single females were mostly failed or non-breeders (Dzinbal 1982). Data were not gathered for incubating or brooding females, which were secretive and difficult to monitor.

Harlequins appear to be daytime feeders only (Johnsgard 1975:411, Dzinbal 1982), and diurnal hours of study extended from 04:00–23:00 (Alaska DT) during the pre-nesting–laying period, and from 05:00–22:00 during the post-laying period.

Forty-three censuses were conducted during the pre-nesting–laying period and 37 during the post-laying period. Censuses lasted about 1 h each, and were conducted from an inflatable boat travelling at 8–20 km/h, 10–20 m off shore; stops were made on shore at selected vantage points to ensure maximum visual coverage of the study area. Visibility of harlequins in Sawmill Bay was good, and censuses were assumed to record virtually all harlequins present. Observations were conducted from a distance with 10X binoculars to minimize disturbance, and each group was observed long enough to insure all individuals were counted. The proportion of time harlequins occurred in each habitat was estimated from pooled morning, midday, and evening censuses of the study area. Results were similar each year and, consequently, data from both years were combined. Chi-square goodness-of-fit tests among treatments (habitats) were conducted on census totals.

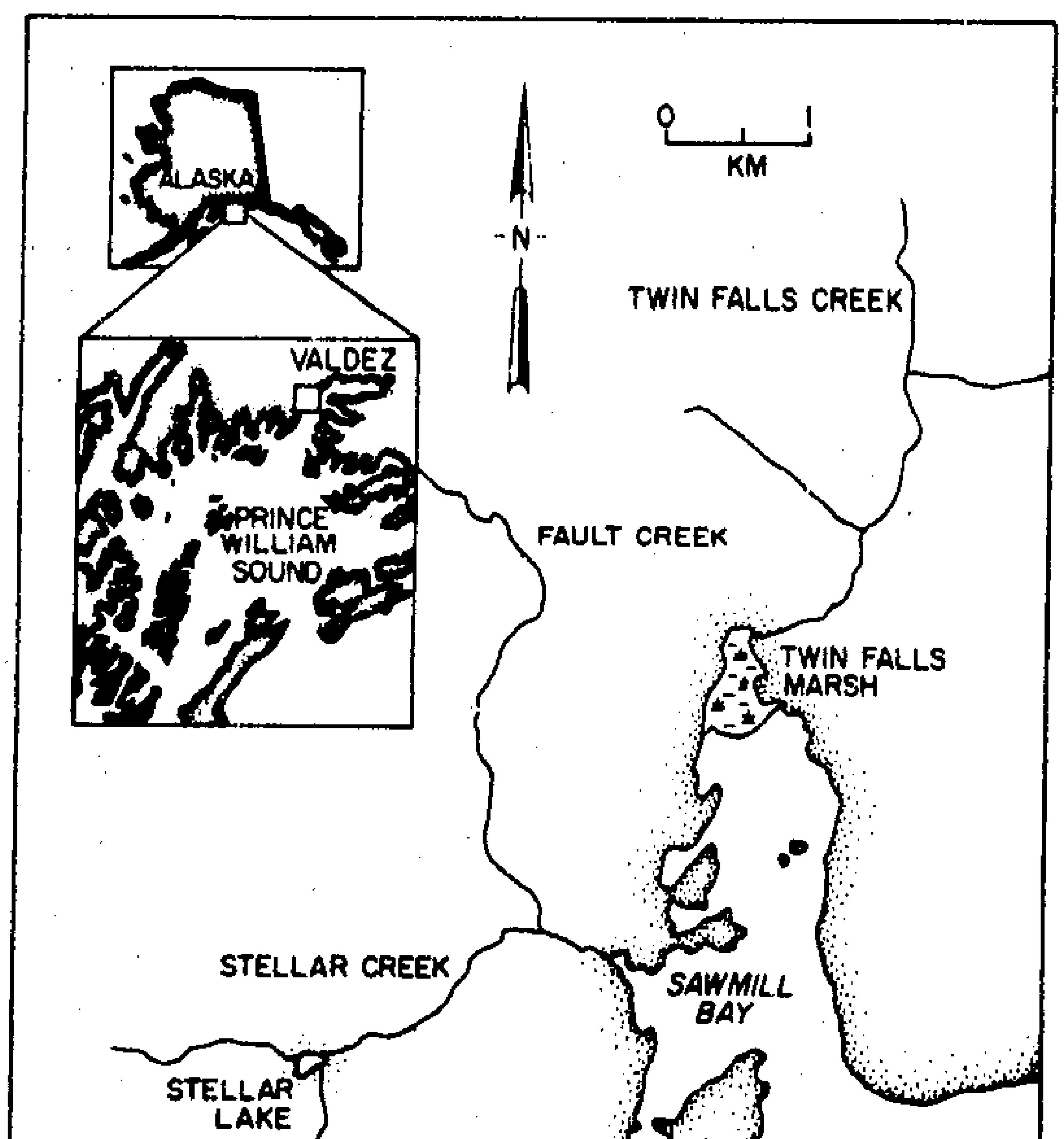
Diurnal feeding activity was determined in each habitat by recording, every 60 s, the behaviour of both the male and the female of randomly selected pairs, or of randomly selected single individuals. Censuses and observations of activities were conducted at separate times. Only those pairs or individuals watched continually for at least 10 min were included in analyses. Observations were obtained throughout all daylight hours but were pooled for analyses. Feeding behaviour, as used here, included only the actual time spent under water when diving, or time actually engaged in ingesting food, dabbling, or tipping-up. Time spent in locomotion, "peering" (i.e. inserting the bill and eyes vertically into the water), or other behaviour between feeding acts was not considered feeding behaviour. Comparisons of feeding rates (sex *vs* habitat and season) were made with chi-square tests of independence using a tabular χ^2 value corrected for multiple comparisons (cf. Neu *et al.* 1974).

Aggregate density of pink salmon (*Onchorhynchus gorbuscha*), chum salmon (*O. keta*), and anadromous Dolly Varden (*Salvelinus malma*) was indexed once every 7–10 days from 1 July – 20 August 1980 at five stations in lower Stellar Creek, below Fault Creek, by counting the number of stationary individuals present in a 1-m wide transect across the creek.

Drift samples of 2-h duration were continuously collected for a 24-h period, at 1–2-week intervals, to measure the rate of export of loose, drifting roe and invertebrates. Samples were collected from 3 June – 13 August 1980 at each of two stations in Stellar Creek (below Fault Creek). Each drift sampler consisted of a bag of aquatic netting (40 meshes per cm, 50 cm deep) supported inside an aluminum frame to maintain a square mouth of 25 × 25 cm. Samplers were placed at the foot of shallow riffles and, except occasionally during storm spates, they sampled the entire vertical water column. Salmon eggs and invertebrates were sorted from preserved samples and dried to constant weight at 45°C. Major invertebrate taxa collected in samples included Chloroperlidae, Baetidae, Heptageniidae, and Oligochaeta. However, neither the selectivity of the harlequins nor that of the drift samplers for specific invertebrates was known. Consequently, invertebrates in the drift samples were, for quantitative purposes, treated as a single, unified group and were not sorted taxonomically.

Five harlequins (two from Sawmill Bay and three from similar areas in Valdez Arm) were collected for food

Figure 1
Sawmill Bay study area, northeast Prince William Sound, Alaska



analyses after they had been observed feeding for a minimum of 10 min. Upon collection, 70% ethanol was injected into the esophagus, and the esophagus, proventriculus, and gizzard were removed and stored in 70% ethanol. Esophageal contents were analysed separately from those of the proventriculus and gizzard.

6. Results

Harlequin Ducks feeding at Stellar Creek remained almost exclusively in the intertidal zone outside the mouth of the creek until the first week of July (Fig. 2*A*). They fed most actively in the morning at all tide stages (Dzinbal 1982), but feeding was most intense when ebb and low tides occurred in the morning, a pattern similar to feeding activity of Common Eiders (*Somateria mollissima*) in Scotland (Campbell 1978). Harlequins feeding outside Stellar Creek most often dabbled or tipped-up at the edge of tidewater. They usually gleaned algae or probed in and sifted substrate sediments. Harlequins seemed to be opportunistic feeders, and were observed ingesting small crabs, snails, and worms while foraging in the delta of Stellar Creek. Stomachs of five harlequins contained mostly crabs (Decapoda), *Littorina* snails, and, in one case, starfish (Asteroidea) (Table 1).

After the first week of July, harlequins began feeding in the lower 1 km of Stellar Creek, and essentially ceased feeding in the intertidal area outside the mouth of the creek (Fig. 2*A*). The shift in feeding areas by harlequins coincided with a marked increase in both the abundance of salmon in the stream (Fig. 2*B*) and in the rate of drift of invertebrates and salmon eggs (Fig. 2*C*). Salmon eggs were abundant in stream drift samples from late July through early August, primarily because of the disruption of stream gravels and established salmon beds by late-arriving salmon and by storm freshets. The same processes probably caused the increased drift of invertebrates. Biomass of salmon eggs in late July and August was about one-third to one-half again as great as the biomass of invertebrates, but the difference was not significant (t = 0.58; P>0.10). However, relatively few salmon eggs comprised the total egg biomass ($\bar{x}$ = 15.7 eggs/sample h from 31 July – 13 August), whereas several hundred or more individual invertebrates were captured per hour in the same samples. Harlequins, as well as hundreds of Glaucous-winged Gulls (*Larus glaucescens*), were observed feeding upon these waste eggs as they drifted downstream or where they collected in eddies or lodged behind debris obstacles.

The amount of time harlequins spent in each habitat varied. Harlequin pairs during pre-nesting and laying spent more time around rocks than at Stellar Creek or in lee waters (χ^2 = 28.2, 2 df; P<0.005) (Table 2). Single males during the post-laying period spent more time around rocks than at Stellar Creek (χ^2 = 38.2, 1 df; P<0.005), but single females divided their time equally between Stellar Creek and rocks (χ^2 = 3.8, 1 df; P>0.05) (Table 2).

Despite their predominant occurrence around rocks, harlequins fed most actively at Stellar Creek, and least actively at rocks (Table 3). Paired females at Stellar Creek fed more actively during pre-nesting–laying (13%) than did single females there during the post-laying period

Figure 2
(*A*) Mean maximum daily count of Harlequin Ducks in the intertidal delta of Stellar Creek (intertidal) and in the non-tidal, lower portion of Stellar Creek proper (Stellar Creek) from May to September 1980; (*B*) Mean and 95% confidence intervals of the index to salmonid (*Oncorhynchus* spp. and *Salvelinus malma*) abundance in lower Stellar Creek during 1980; (*C*) Dry weight biomass (mean and 95% confidence intervals) of invertebrates and salmon eggs collected (per hour) in drift samples from lower Stellar Creek during 1980

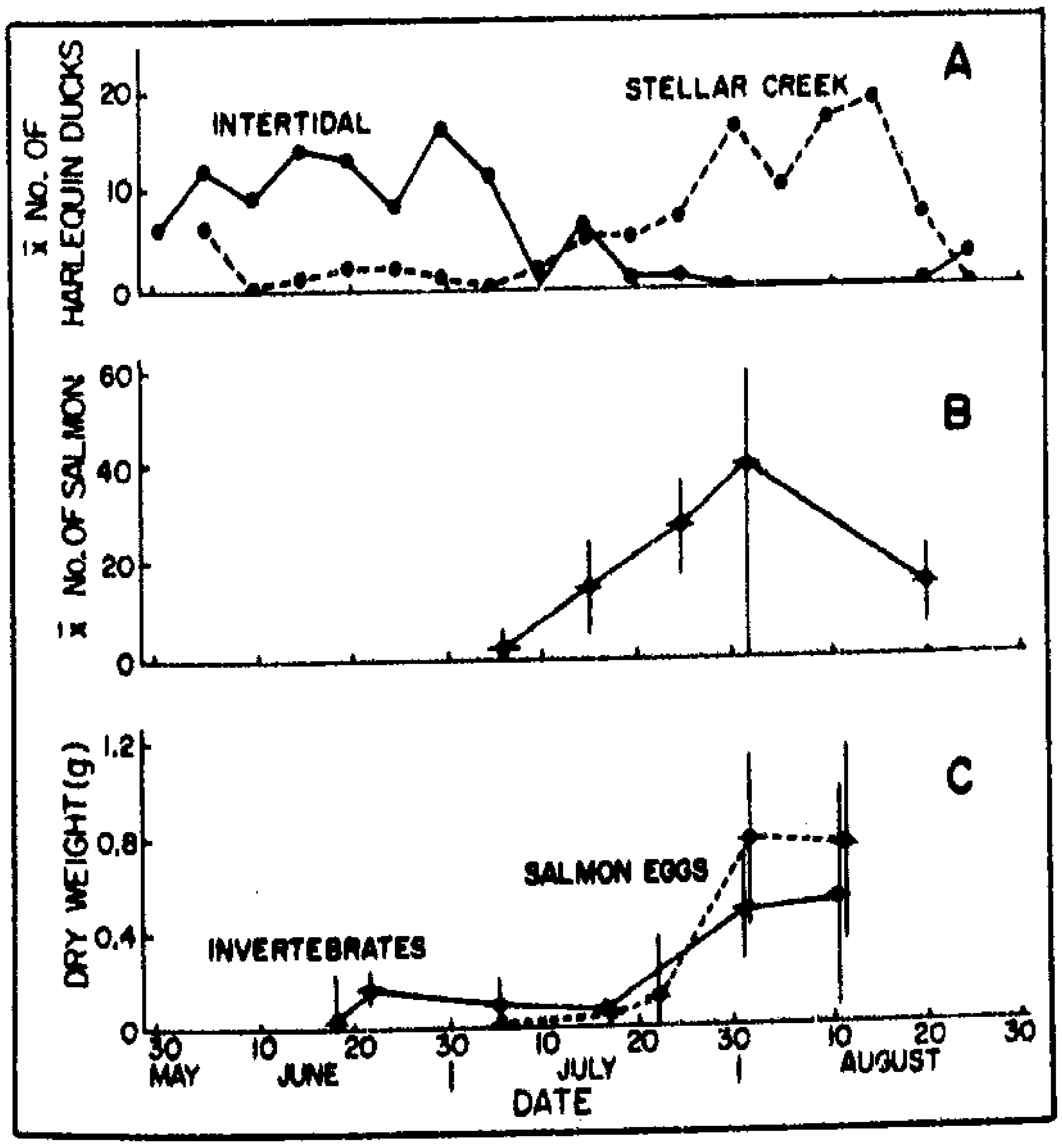


Table 1
Esophageal and stomach contents of two Harlequin Ducks collected from Sawmill Bay (specimens 1 and 2)* and three from Valdez Arm (specimens 3–5)†, summer 1980. Values are percent of total food volume (wet)

	Esophagus			Proventriculus and gizzard				
Specimen number	1	2	3	1	2	3	4	5
Total food volume, ml.	7.9	0.5	0.1	0.6	1.5	3.7	2.1	1.2
Echinodermata								
Asteroidea (*Leptasterias*)	95.7							
Insecta								
Diptera			30.0	1.9				
Crustacea								
Isopoda								1.7
Decapoda								
Brachyura (Brachyrhyncha)		2.8	19.4					
Anomura (Paguroidea)					54.1	71.1	25.0	17.2
Unidentified Decapoda		33.3	60.0					
Mollusca								
Macoma balthica		1.1						0.9
Macoma calcarea		3.3						
Unidentified *Macoma*	0.3							
Mytilus edulis	0.8						26.9	
Littorina spp.	2.5	37.8	10.0	90.2	44.1	9.2	43.0	77.6
Turbellaria?	0.7			3.3				
Plant								
Zostera marina		24.4						
Unidentified algae				1.6			5.2	2.6
Total	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0

*Specimen 1 collected 21 June; specimen 2 collected 2 July
†Collected 22 August.

Table 2
Total number and percent of Harlequin Ducks censused in three habitats during pre-nesting–laying (10 May – 21 June), and during post-laying (22 June – 15 August) in Sawmill Bay, Alaska, 1979–1980

	Pre-nesting–laying		Post-laying			
	Pairs		Single males		Single females	
Habitat	*N*	%	*N*	%	*N*	%
Stellar Creek	83	26.4	24	20.5	133	55.4
Rocks	149	47.5	90	76.9	103	42.9
Lee waters	82	26.1	3	2.6	4	1.7
Total	314	100.0	117	100.0	240	100.0

Table 3
Average percent of diurnal time individual Harlequin Ducks spent feeding while in each habitat in Sawmill Bay, Alaska, during pre-nesting- laying (10 May – 21 June), and during post-laying (22 June – 15 August), 1979–80

Period	Habitat	No. of observations	Percent*
Pre-nesting–laying			
Paired males	Stellar Creek	744	19.8[1,2]
	Rocks	974	7.3[3]
	Lee waters	2982	15.0[1]
Paired females	Stellar Creek	744	43.3[4]
	Rocks	937	8.2[3]
	Lee waters	3183	22.4[2]
Post-laying			
Single males	Stellar	771	50.7[4]
	Rocks	2571	1.8
	Lee waters†	—	—
Single females	Stellar	2691	27.3
	Rocks	2082	0.5
	Lee waters†	—	—

*All values are significantly different from each other ($P<0.05$) except those with identical superscripts.
†Single Harlequin Ducks occurred in lee waters only rarely, and feeding rates were not determined for them there.

Table 4
Calculated absolute (and relative) percentages of total diurnal time spent feeding in three habitats by Harlequin Ducks in Sawmill Bay, Alaska, during pre-nesting–laying (10 May – 21 June) and during post-laying (22 June – 15 August), 1979–80

	Pre-nesting–laying				Post-laying			
Habitat	Paired males		Paired females		Single males		Single females	
Stellar Creek	5.2*	(41.6)	11.4	(54.0)	10.4	(88.1)	15.1	(98.7)
Rocks	3.4	(27.2)	3.9	(18.5)	1.4	(11.9)	0.2	(1.3)
Lee waters	3.9	(31.2)	5.8	(27.5)	—	—	—	—
Totals	12.5	(100.0)	21.1	(100.0)	11.8	(100.0)	15.3	(100.0)

*Calculated as percent of time spent feeding in each habitat (Table 3) × percent of occurrence of ducks in each habitat (Table 2); e.g. for paired males: $\frac{19.8\% \times 26.4\%}{100} = 5.2\%$.

(27%). However, paired and single males at Stellar Creek exhibited just the opposite pattern (20% *vs* 51%, respectively) (Table 3).

To determine the absolute proportion of total diurnal time that the various segments of the harlequin population spent feeding (Table 4), the habitat-specific feeding rates (Table 3) were multiplied by the proportion of harlequins that occurred in each habitat (Table 2). For all habitats combined, paired females during pre-nesting–laying spent more total time feeding (about 21%) than did paired males during the same period (13%) or than single males and females did during post-laying (12 and 15%, respectively) (Table 4).

Comparing the relative percent of time harlequins spent feeding in each habitat (in parentheses on Table 4) with the percent occurrence of ducks in each habitat (Table 2) we concluded the following:

1. Relative to the amount of time they spent there, harlequins allocated a disproportionately large fraction of their total feeding time to Stellar Creek.
2. Conversely, rocks were under-used for feeding in proportion to the amount of time harlequins spent there.
3. Among paired harlequins, lee waters were used for feeding in about the same proportion as the amount of time they spent in that habitat.

7. Discussion

Harlequins in this study depended on Stellar Creek for nearly half to practically all of their feeding activity. Early in the summer, harlequins fed primarily on marine invertebrates in the intertidal delta of the creek. Later in the summer they moved slightly upstream into the spawning beds of the arriving salmon, where they fed largely on waste, drifting roe. Incubating females flew downstream, at least occasionally, to forage in the outflow or lower portions of the creek (Dzinbal 1982).

This pattern was not unique to Stellar Creek or to Sawmill Bay. Although harlequins hardly used Twin Falls Creek in early summer, after salmon arrived they occasionally foraged along the same few channels used by the salmon. Also, six medium-gradient, non-glacial salmon streams in Valdez Arm had small contingents of harlequins feeding in their outflows or lower reaches, and male harlequins at a moulting site in Valdez Arm regularly fed at the outflow of one such stream (Dzinbal 1982). Osgood (1904) observed that harlequins during summer at Kanatak and Cold Bay on the Alaskan Peninsula "frequently . . . visit the mouths of small streams or . . . ascend them for considerable distances." Also, Bengtson (1972:14) found that harlequins breeding along short, coastal streams in northwest Iceland tended to fly downstream to feed in the river deltas.

Gudmundsson (1971:89) noted that harlequin nesting grounds in Iceland often coincide with Atlantic salmon (*Salmo salar*) spawning grounds, and he suggested that harlequin ducklings and salmon fry may depend upon similar foods. Unlike Atlantic salmon, however, the fry of pink and chum salmon (prevalent in this study) usually do not feed in streams as short as Stellar Creek, but move to the sea the first night following their emergence (Scott and Crossman 1973). Because of their larger size, drifting salmon eggs probably represented a more efficiently exploited food source for harlequins than did invertebrates. Thus, the most likely attraction of the salmon spawning beds for the harlequins in this study was the drifting roe available there. Possibly the low productivity typical of many coastal streams may be offset for harlequins by the seasonal influx of anadromous fish, and by the relative abundance of food in the intertidal stream deltas.

During spring and summer, Harlequin Ducks spent little time feeding, but paired females during pre-nesting and laying fed more often (21%) than other harlequins (12–15%). However, paired female harlequins spent much less time feeding than paired females of six species of dabbling ducks (45–70%; Dwyer 1975, Afton 1979,

Kaminski and Prince 1981). Subtle differences in definition of feeding behaviour may account for some of the reported differences between harlequins and other ducks in the proportion of time spent feeding. Nevertheless, harlequins spent much of their time loafing and preening (~53–74%; Dzinbal 1982) and devoted a relatively small amount of time to searching for and acquiring food. Similarly, Pool (1962:127) only rarely observed harlequins feeding, and noted their "favourite occupation . . . consisted of just sitting around doing nothing."

Ettinger and King (1980) suggested that the large proportion of time Willow Flycatchers (*Empidonax traillii*) devoted to loafing minimized variations in daily energy expenditure between phases of the breeding cycle, and acted as a buffer against periods of stringency (see Wilson [1975:142] for a discussion of stringency). Harlequin Ducks undoubtedly face unpredictable periods of stringency in their storm-prone environment, and possibly their activity patterns have evolved to minimize their energy expenditure rather than to maximize their energy intake. The relatively small proportion of daily time that harlequins spent feeding would be one expected result of such a strategy.

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