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Abstract approved:

(Robert L. Jarvis, Associate Professor)

Harlequin ducks (Histrionicus histrionicus) were observed during the summers of 1979 and 1980 in Sawmill Bay, northeast Prince William Sound, Alaska. Harlequins were associated with a short, medium gradient, non-glacial stream (Stellar Creek) also used by salmon. Although harlequins nested along Stellar Creek, they apparently did not establish home ranges there during the prenesting period, and both courtship and copulation occurred in the bay. Pairs were most numerous in the bay in mid-late May; 15 pairs were recorded in 1979, and 14 pairs were observed in 1980. Laying occurred from about 26 May - 17 June, and hatching took place from 3-15 July. Females lost weight during the incubation period, but gained weight the remainder of the summer. The non-breeding frequency among females was estimated as 47% in 1979 and 50% in 1980. The application of patagial tags, however, appeared to reduce production. Following nesting, males generally deserted Sawmill Bay for comparatively exposed moulting areas. Females mostly remained in the bay until mid-late August. Use of habitats by harlequins varied with time of day, and activity budgets varied with habitat. Paired harlequins during prenesting and laying (10 May - 21 June) spent about 47% of their time near rocks and headlands, and about 26% of their time each in Stellar Creek and in lee (i.e. protected) waters. Unpaired harlequins (22 June - 15 August) were rare in lee waters (<3%); unpaired males spent about 77% of their time on rocks and about 20% of their time in Stellar Creek, while unpaired females spent about 43% and 55% of their time on rocks and in Stellar Creek, respectively. Harlequins primarily rested on rocks and headlands, while lee waters seemed important mostly for social spacing among pairs. Stellar Creek was the focus of nearly half to practically all of the feeding activity of harlequins. Early in the summer they fed primarily on marine invertebrates in the intertidal delta of the creek, but in July they moved upstream into the spawning beds of the arriving salmon, where they fed predominately on loose, drifting roe. Paired females spent more time feeding (21% *vs* 13%), but less time resting (41% *vs* 46%) and interacting (1% *vs* 3%) than did their mates. Unpaired females spent slightly more time feeding (15% *vs* 13%) and in locomotion (13% *vs* 10%), but less time preening (6% *vs* 8%) than did unpaired males. The large proportion of time harlequins spent resting was tentatively attributed to a strategy of minimizing energy expenditure, versus one of maximizing energy intake.

Ecology of Harlequin Ducks in Prince William Sound, Alaska During Summer

by

Kenneth A. Dzinbal

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Associate Professor of Wildlife Ecology
in charge of major

Redacted for Privacy

Head of Department of Fisheries and Wildlife

Redacted for Privacy

Dean of Graduate School

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ECOLOGY OF HARLEQUIN DUCKS IN PRINCE WILLIAM SOUND, ALASKA DURING SUMMER

I. INTRODUCTION

The harlequin duck (*Histrionicus histrionicus*) is a holarctic anatid (Tribe Mergini) noted for the striking patterns and colors assumed by the adult male in Alternate plumage. *Histrionicus* is a monotypic genus whose affinities appear to lie closest to the long-tailed duck (*Clangula*) and the scoters (*Melanitta*) (Delacour and Mayr 1945; Woolfenden 1961). Delacour and Mayr (1945) considered *Histrionicus* to be near the "core" of the sea ducks, a conclusion also reached by Johnsgard (1960, 1965), based on behavioral patterns, and by Woolfenden (1961), based on skeletal features. The species is, however, unique among northern hemisphere waterfowl for its habit of breeding exclusively along swiftly flowing mountain or tundra streams, and for its disrupted distribution; distinct populations occur in Iceland, Greenland, northeast North America, northwest North America, and northeast Asia (Palmer 1976:331).

Classical accounts of the harlequin duck emphasized its affinity for swift or turbulent water (Kortwright 1942; Delacour 1959). Harlequins winter along the rocky, wave-pounded portions of the sea coast (Bengston 1966; Palmer 1976). Harlequins probably first breed at 2 years of age (Palmer 1976:335; Johnsgard 1975:408) but this has not been definitely established. Bengston (1972:7) and Kuchel (1977:32) reported that adults leave the coasts and arrive on the breeding rivers in late April and May. First year harlequins apparently remain on the coast during the summer, perhaps moving to "summering areas" (Palmer 1976:336).

In Iceland, harlequins preferred to nest on small islands covered by thick willow (Salix spp.) and birch (Betula spp.) (Bengston 1966: 82. The mean density of breeding pairs along 16 Icelandic rivers was 1.3 pairs/km (Bengston 1972:5). Breeding densities in Montana ranged from 0.67 - 0.91 pairs/km (Kuchel 1977:35). Egg laying took place from mid-May through early July in Montana (Kuchel 1977:35) and from late May through mid-July in Iceland (Bengston 1972:9). The mean number of eggs in 77 complete clutches in Iceland was 5.7 (Bengston 1972:10). Bengston (1972:8) noted a strong tendency for individuals to return to the same nest site and loafing area each year.

With the start of incubation, males in Iceland grouped together in feeding areas, and in June or July they left the breeding rivers to moult at sea (Bengston 1972:10). Following hatching, broods were raised in quiet parts of the rivers. Females and young usually did not move to the sea until the young were fledged, but some broods began moving downstream when only a few weeks old (Bengston 1966:81). On Bering Island, broods left the upper rivers in mid-August and appeared at the sea in mid-September (Dementiev and Gladkov 1952:613). Age of young at fledging was about 6 weeks in Iceland (Bengston 1972: 16) and approximately 46 days in Montana (Kuchel 1977:68).

Knowledge of the species in North America is mostly limited to scattered, incidental observations and brief distribution records. Recent accounts of the species (Palmer 1976; Bellrose 1976; Johnsgard 1975, 1978) relied largely upon the Icelandic studies for basic information on harlequin reproduction and ecology (e.g. Bengston 1966, 1972; Bengston and Ulfstrand 1971; Gudmundsson 1961, 1971). To date, the only significant study of breeding harlequin ducks in North America was conducted at the periphery of the species' range on a single stream in Glacier National Park, Montana (Kuchel 1977).

The Icelandic studies, and Kuchel's (1977) investigation in Montana, focused on concentrations of harlequins breeding along interior rivers. In contrast, this study was conducted near short, coastal streams in northeastern Prince William Sound, Alaska. The nearly pristine condition of much of Prince William Sound offered an opportunity to investigate a relatively undisturbed population of harlequins breeding along short, coastal streams. Also, a need for "baseline" data was suggested by the commencement of oil tanker traffic through the Sound following the opening, in 1977, of the Alyeska Pipeline Terminal in Valdez Arm. Initiated in 1979, the objectives of this study were: 1) to document the reproductive chronology and local movements of harlequin ducks breeding along short, coastal streams, 2) to determine patterns of habitat use and activity budgets of those harlequins, 3) to assess the productivity of the harlequin population, and 4) to determine the summer foraging habits of harlequins in northeast Prince William Sound.

Historical records of harlequin ducks in Prince William Sound

Alaska supports a majority of the world population of harlequins (Bellrose 1976; Palmer 1976) with notable concentrations occurring in Southeast Alaska, Prince William Sound and the north Gulf Coast, and (especially during winter) the Aleutian Islands (Gabrielson and Lincoln 1959; Isleib and Kessel 1973). Isleib and Kessel (1973:65) estimated "a few 10,000" harlequins annually use the North Gulf Coast and Prince William Sound.

Early records of harlequin ducks in Prince William Sound include a nest located in 1908 by Dixon on Hinchinbrook Island, and a brood observed by Heller at Montague Island (Grinnel 1910). Grinnel (1910: 371) reported seeing harlequins "throughout the summer in many of the bays and channels of the Sound, where it doubtless regularly breeds;" he specifically mentioned observations at Green Island, Port Nell Juan, Valdez Narrows, and Cordova Bay. A specimen was collected at Cordova Bay from a group of "about twenty (which) frequented a tide flat" (Grinnel 1910:371). Gabrielson saw a brood on 13 August 1945 in College Fiord, and reported the species was common to abundant in the Sound in winter (Gabrielson and Lincoln 1959).

Isleib and Kessel (1973:65) mentioned that harlequins may become "less common...when they move to the mountain streams and up the river systems" to nest. But in July and August, "Isleib has seen scores of broods...along the shorelines," and "outside the breeding season... Isleib has counted pairs and small flocks every few yards along the rocky shores, at times totalling well in excess of a hundred birds per mile of shoreline" (Isleib and Kessel 1973:65). Harlequins were distributed in varying densities throughout most of Prince William Sound during surveys conducted by the U. S. Fish and Wildlife Service during the spring of 1971; in August harlequins were concentrated in larger groups and occurred in fewer areas of the Sound than in the spring (M. Sangster, personal communication). During 1976, 1977, and 1978, Sangster (personal communication) recorded numerous harlequin broods in or near Port Etches on Hinchinbrook Island, and around the Naked Island group, from late July through August.

In northeast Prince William Sound, harlequins were found in "small, scattered groups" and averaged 0.6 individuals per km of shoreline during 5 surveys conducted in the Port Valdez - Valdez Arm area between November 1977 and April 1978 by the U. S. Fish and Wildlife Service (Sangster 1978). During the summer months, M. Jackson (personal communication) observed harlequins and harlequin broods in the mouth of Stellar Creek in Sawmill Bay, and M. E. Isleib (personal communication) observed harlequin broods in Sawmill Bay and in the mouth of Duck River in Galena Bay.

II. STUDY AREA

General description

The topography of Prince William Sound (Fig. 1) is characterized by deep, branched fiords, precipitous mountains, and massive ice fields and glaciers, several of which extend to tidewater. Valdez Arm (Fig. 2), in northeast Prince William Sound, is a typical fiord extending about 40 km into the Chugach Mountains. Sawmill Bay, the primary study area, extends north from Valdez Arm about 24 km southwest of the town of Valdez, Alaska. The bay (Fig. 3) has a water area of about 2.25 km^2, is about 18 m deep at its mouth, and is surrounded by steep mountains of 1000-1370 m elevation. Three streams, Stellar Creek, Fault Creek, and Twin Falls Creek, enter the bay. Tides fluctuate 2-6 m in the bay, and at low tide a large portion of the bay lies exposed. A brief description of Sawmill Bay focusing on the marsh at Twin Falls Creek, the surrounding forest vegetation, and the intertidal zone immediately adjacent to the marsh, was provided by Batten et al. (undated).

The study area lies within the Coastal Spruce-Hemlock Forest vegetation region of Viereck and Little (1972). The area has a moderate climate with cool, rainy summers and winters with heavy snowfall. Climatic data for Valdez, Alaska are summarized in Appendix 1. The geography, climate, glacial history, and vegetation of Prince William Sound were discussed by Cooper (1942).

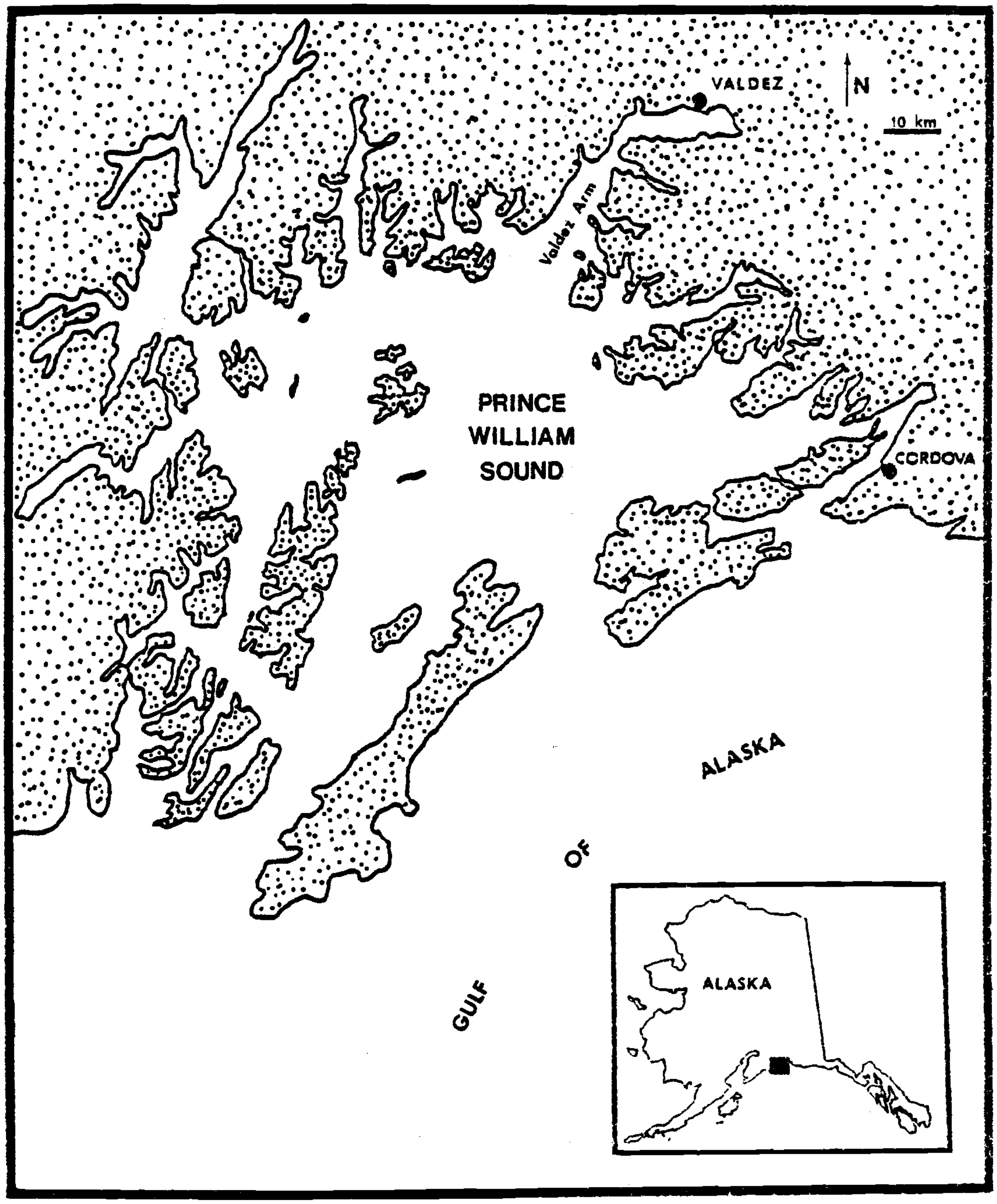


Fig. 1. Prince William Sound, Alaska.

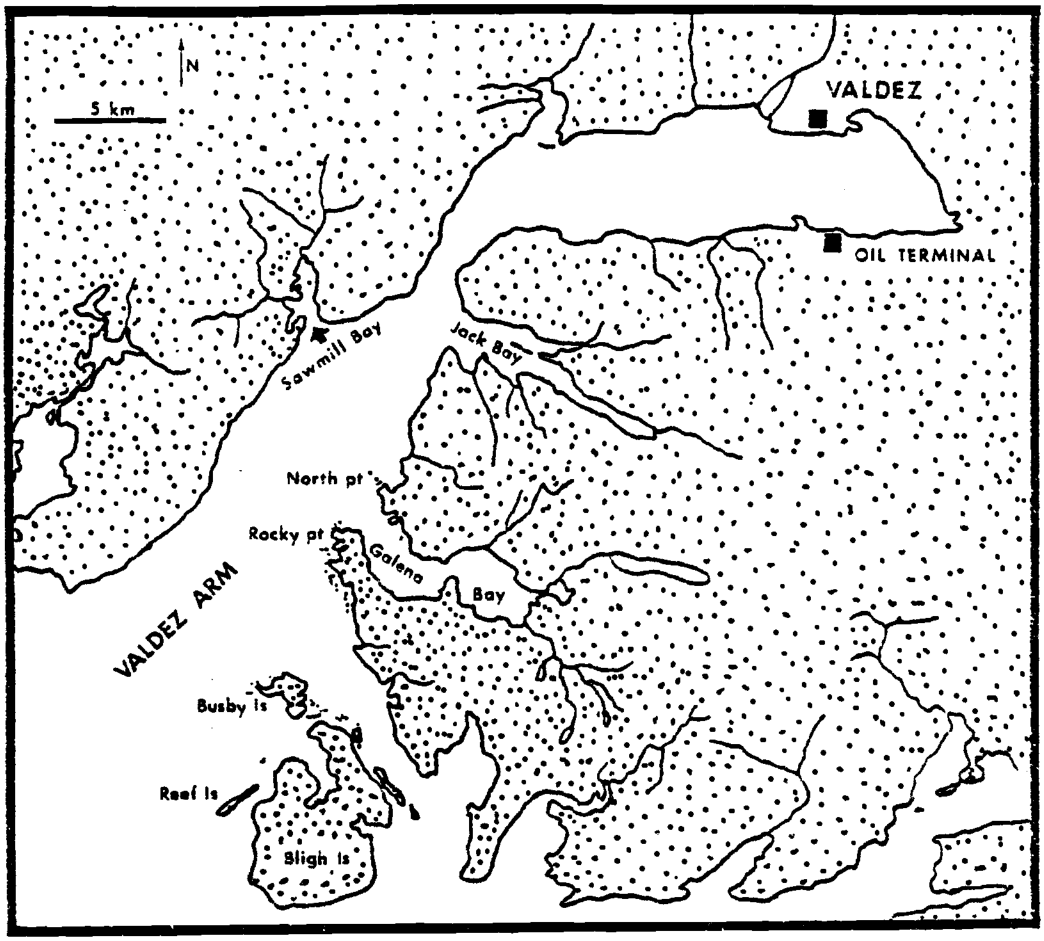


Fig. 2. Valdez Arm, northeast Prince William Sound, Alaska.

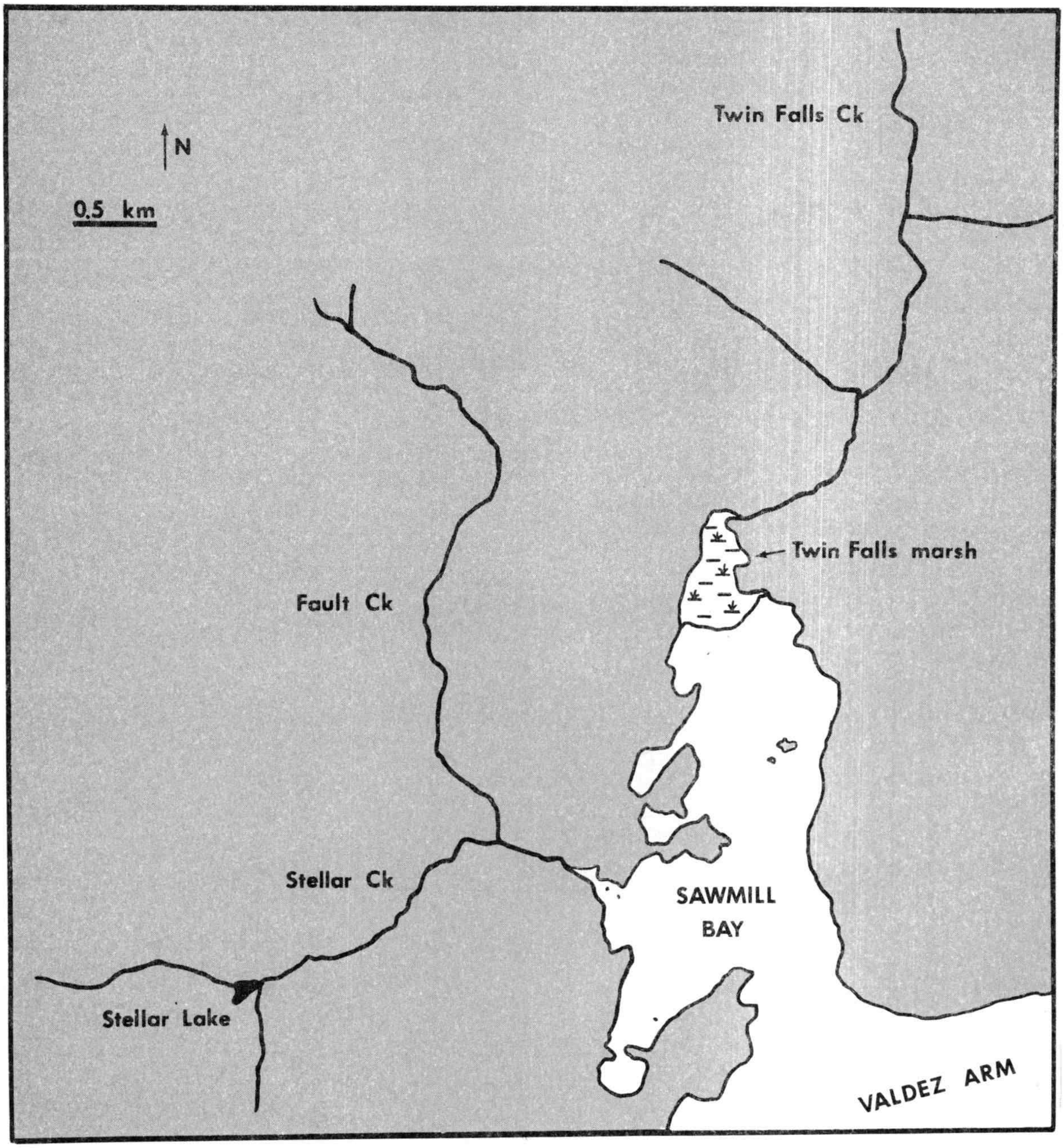


Fig. 3. Sawmill Bay, northeast Prince William Sound, Alaska.

<u>Stream characteristics</u>

Stellar Creek, Fault Creek, and Twin Falls Creek (Fig. 3) are typical, short (about 5 km), second order (Strahler 1954) coastal streams with discharge rates of about 1.5 - 7.0 m^3/sec. Discharge rates were calculated by Davis' formula (<u>in</u> Hynes 1975:4) using a tennis ball to estimate current velocity. Stream flows generally increased in late May as snow melted; after late June flows tended to parallel local precipitation patterns. Minimum flows occurred about the first week of August in all creeks (Fig. 4).

Differences between the streams primarily reflected differences in their gradients (Fig. 5) and in their water sources. Stellar Creek and Fault Creek were relatively steep, clear, non-glacial streams with substrates composed primarily of large stones, rocks, and boulders. Both streams (but especially Stellar Creek) were used by harlequins and by large numbers of salmon (<u>Onchorhynchus</u> spp.). Conversely, Twin Falls Creek rose only 15 m in its first km (Fig. 5), was glacially fed, and was essentially opaque with glacial sediment after the third week of June. The substrate of Twin Falls Creek consisted mostly of gravel, sand, and small stones, and the creek emptied into Sawmill Bay through an alluvial tidal marsh approximately 25 ha in area. Salmon used only the lowest, tidal portion of Twin Falls Creek. Harlequins used the stream only rarely, although they were occasionally observed feeding in eelgrass (<u>Zostera</u> spp.) beds adjacent to Twin Falls marsh.

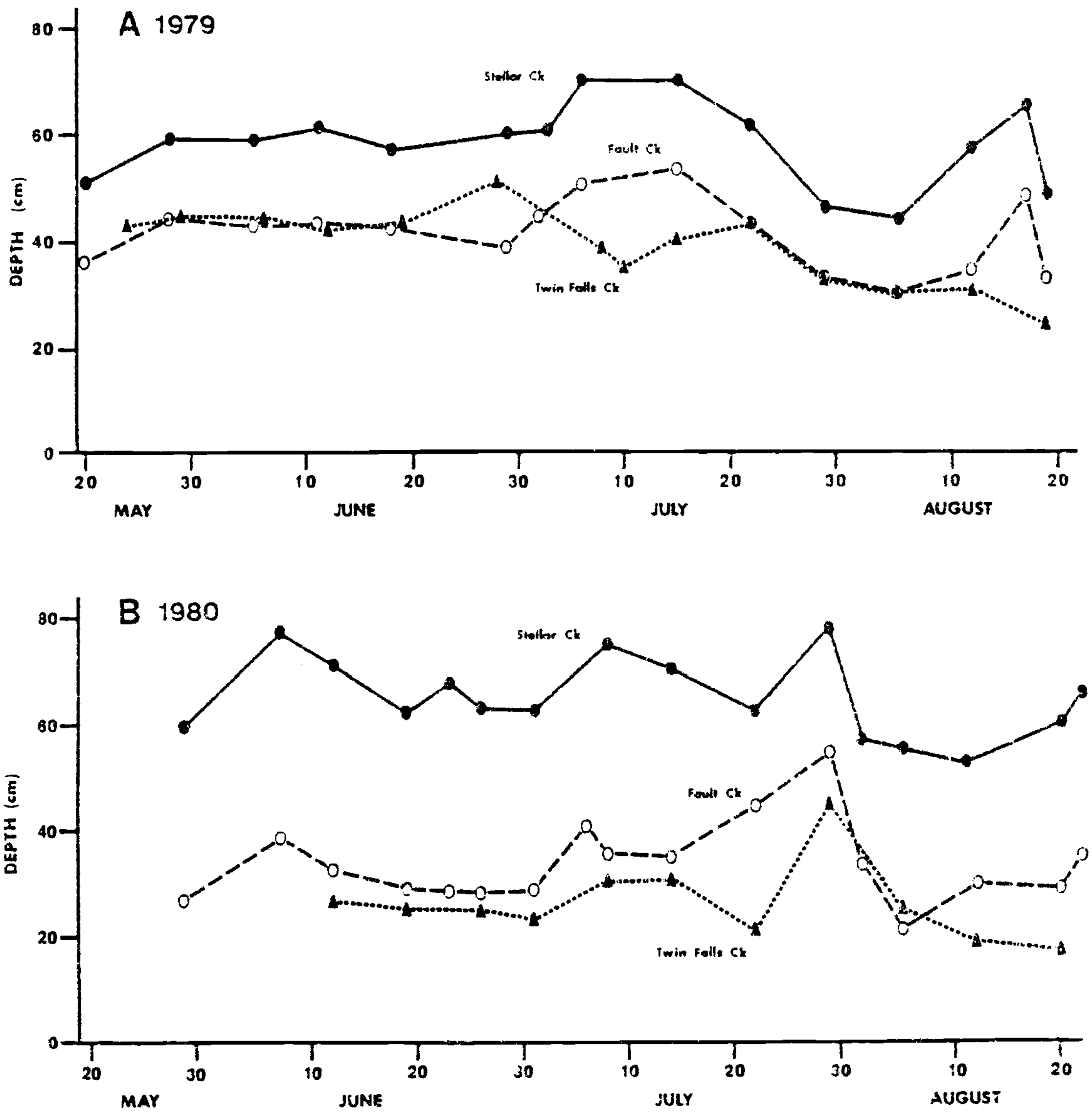


Fig. 4. Depths of Stellar Creek, Fault Creek, and Twin Falls Creek during (A) 1979, and (B) 1980. Measuring stations changed between years.

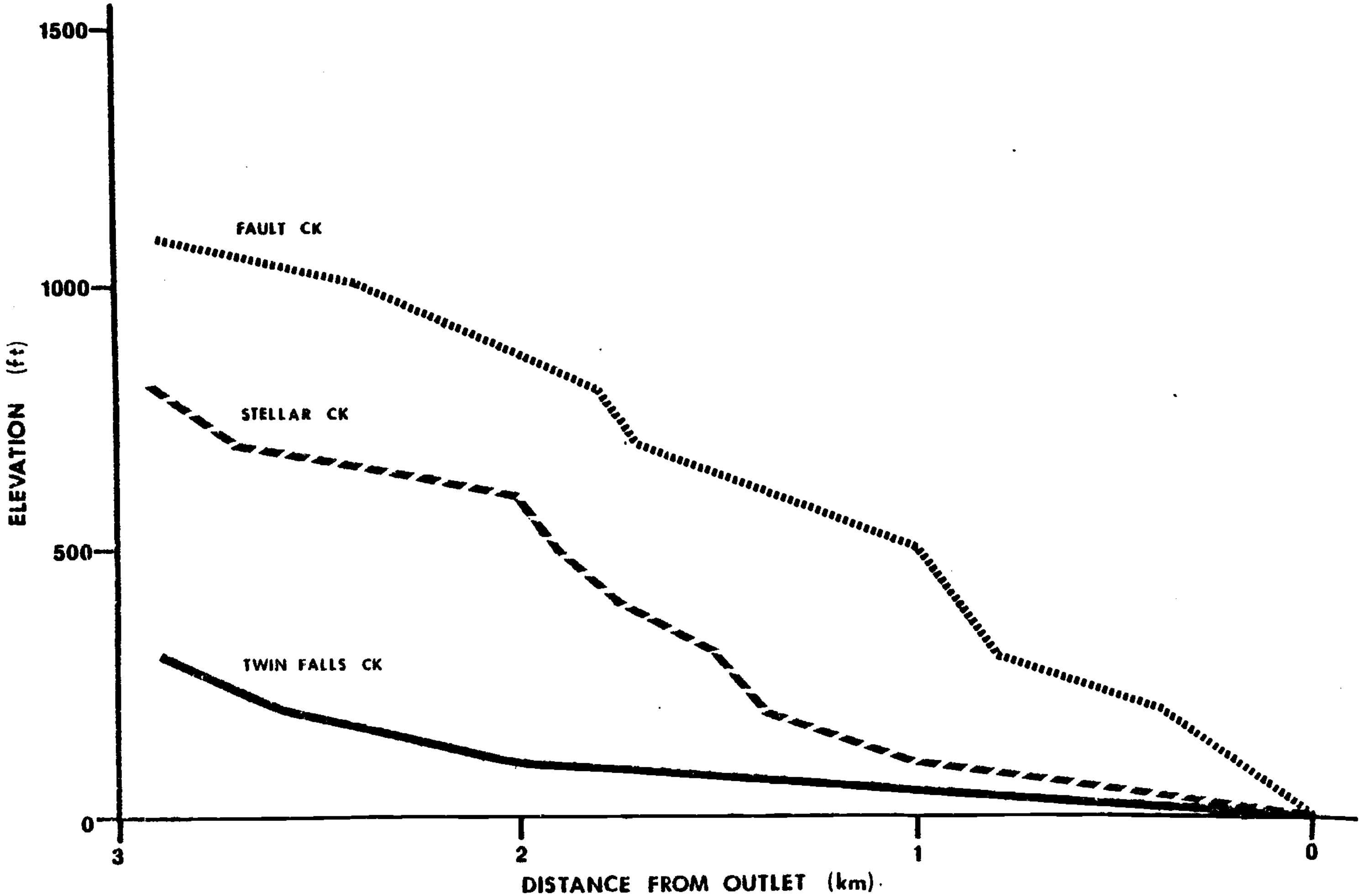


Fig. 5. Gradients of the lower portions of Fault Creek, Stellar Creek, and Twin Falls Creek, northeast Prince William Sound, Alaska.

The extremely rugged terrain and lack of access prevented extensive exploration of the upper creeks. However, above about 3.0 km, the streams were of greatly reduced size and remained mostly under snow cover until at least mid-June.

III. METHODS

Observations and census techniques

Field work was conducted from 8 May - 26 August 1979 and from 25 May - 26 August 1980. Harlequins were observed with 10 X binoculars and with a 40 X spotting scope. Data collected during observations included time of day, behavior, habitat, group size and composition, and associated species. One to five censuses were conducted every 5 days in Sawmill Bay to determine the seasonal changes in the size and composition of the harlequin population. Censuses were also conducted periodically in Valdez Arm from (and including) Jack Bay to the rocky area north of the mouth of Galena Bay (termed "North Point" here), Galena Bay, Rocky Point, the area around Busby Island and north of Bligh Island, and the shoreline extending approximately 5 km northeast and southwest of the entrance to Sawmill Bay (Fig. 2). Censuses were conducted from an inflatable boat travelling 8-20 km/hr approximately 10-20 m offshore with stops on shore at selected vantage points to ensure maximum visual coverage of the census area. The lower portions of Stellar Creek, Fault Creek, and Twin Falls Creek were surveyed at least weekly to document the presence or absence, and the activities, of harlequins and harlequin broods along those creeks.

Banding and tagging

Harlequins were captured in mist nets set across the lower reaches of Stellar Creek. Captured individuals were weighed, measured, and banded. Some harlequins were fitted with numbered, 28 X 75 mm vinyl patagial tags to facilitate individual identification. Re-sightings of tagged birds allowed patterns of local movement to be compared among harlequins whose individual histories and reproductive success were known. Re-sighting rates were similar both years, with 247 re-sightings recorded for 27 (87%) of the 31 harlequins tagged in 1979, and 198 re-sightings recorded for 23 (88%) of the 26 harlequins tagged in 1980. The age and sex of all harlequins tagged and/or banded during the study is given in Appendix 2.

A radio telemetry experiment in 1980 failed when the available transmitters proved too large for the ducks. Consequently, attempts to precisely assess habitat use and movements of individuals, and attempts to track individuals to nest sites, were precluded.

Stream habitat

Water depths were measured once each week at a permanent site in each of the three streams. Habitat differences between the three streams were compared in early July 1979 using a modified stream reach inventory (Phankuch 1975). Each stream was divided into "reaches" of similar appearance, and each reach was evaluated relative to nine parameters (Appendix 3). The inventory provided a basis for judging the stability and character of the streams and their capacities for various geomorphic processes (Phankuch 1975).

Roost sites

Harlequins typically roosted at particular, traditional sites on intertidal rocks, headlands, or shores. Characteristics of eight such roost sites were compared to 50 random sites in Sawmill Bay. At each site a transect was established perpendicular to the water's edge from the 0.0 m tide level to (the lowest boundary of) terrestrial vegetation. At 0.5 m vertical steps, 0.25 m^2 plots were established. Percent cover of attached, sessile species was estimated by setting a clear, flexible plastic sheet marked with 100 random dots over each plot and recording the number of dots which overlaid each species (Menge 1976; Lubchenco and Menge 1978). Percent cover data were normalized with the arcsin $\sqrt{X}$ transformation (Snedecor and Cochran 1980:290) and comparisons of selected species between roosts and random sites were made with unpaired t-tests. The average slope of each site was measured as the Tan^{-1} Δ height / Δ distance (Strahler 1956).

Quantification of habitat use

Three types of habitat used by harlequins in Sawmill Bay were distinguished: Stellar Creek, Rocks and headlands, and "Lee" waters. The number of harlequins present in each habitat was recorded during morning, mid-day, and evening censuses of Sawmill Bay. Visibility of harlequins in the bay was good and censuses were assumed to record essentially all individuals present in the bay. However, harlequins did not always remain in Sawmill Bay proper; consequently, census results reflected only the proportion of time harlequins occurred in each habitat while they were actually present in the bay.

Census results from both years were combined, and chi-square tests of independence (habitats vs time periods) and goodness-of-fit tests among habitats (within time periods) were conducted on census totals. The 90% family of confidence intervals for the proportions of harlequins observed in all habitat and time categories was estimated with the normal approximation (Steel and Torrie 1980:479; Neu et al. 1974).

Estimates of habitat use were based on censuses which tallied all harlequins present and were not limited to records of marked individuals (as were analyses of local movements). Thus habitat use could not strictly be compared between successful and unsuccessful (or non-breeding) individuals. Rather, it was assessed for paired males and females during the prenesting and laying period from 10 May - 21 June (thus mostly before breeding success was determined), and for unpaired males and females from 22 June - 15 August (unpaired males included both successful and unsuccessful breeders; unpaired females were mostly failed or non-breeders). Patterns of habitat use were not determined for yearling harlequins (which were rare), for unpaired males during the prenesting and laying season (which were common but sporadic and unpredictable in number), nor for successful (i.e. incubating or brooding) females, which were secretive and impossible to monitor regularly.

Activity budgets

Activity budgets were constructed for harlequin pairs (10 May - 21 June) and for unpaired males and females (22 June - 15 August) for each of the three habitats (Stellar Ck, Rocks, Lee). Activity budgets were prepared in a manner similar to that described by Wiens et al. (1970) by recording, every 60 seconds, the behavior of both the male and the female of randomly selected pairs, or of randomly selected unpaired individuals. Only harlequins observed for a minimum of 10 minutes were included in analyses.

For activity budgets, harlequin behaviors were grouped into the following categories: resting, feeding, locomotion (swimming, walking, and flying), preening, alert, and interactions (agonistic, appeasement, and sexual). Only the actual time spent underwater when diving, or when actually ingesting food, dabbling, or tipping-up was recorded as feeding. Locomotion or other behaviors between dives or other feeding acts were not included with feeding behavior.

Activity budget observations from both years were combined, and chi-square tests of independence (activity *vs* habitat, activity *vs* sex, and activity *vs* season) were conducted on the number of observations recorded for each activity in the relevant categories. Comparisons between activities (within habitat, sex, and season) were made by constructing the 95% family of confidence intervals for the proportions of observations recorded for each activity (Steel and Torrie 1980:479; Neu et al. 1974). Values having non-overlapping confidence intervals were considered significantly different.

The activities of harlequins, and their occurrence in habitats, varied with time of day. In some cases, however, activity budget samples were too small to partition into morning, mid-day, and evening periods. Therefore, observations were pooled from as wide a range of daylight hours as possible (mean = 13.7 hr). Total, diurnal activity budgets of harlequins were then calculated by expanding their (pooled) habitat-specific activity budgets by the (pooled) proportion of time they occurred in each habitat. Where sample sizes did permit partitioned analyses (i.e. morning, mid-day, and evening habitat-specific activity budgets X morning, mid-day, and evening occurrence values) results differed from the pooled analyses by an average of only 0.5%, and in no case did a partitioned analysis result in conclusions different from the comparable pooled analysis.

Stellar Creek salmon index and stream drift

In 1979 a general correspondance was noted between the feeding activity of harlequins and the abundance of salmon in Stellar Creek. In 1980 counts were made of harlequins feeding outside the mouth of Stellar Creek (i.e. in the intertidal delta of the creek) and of harlequins feeding in the creek (generally the area around the confluence of Fault Creek). Indices of salmon abundance in the creek and stream drift samples were collected concurrently.

Salmon (*Onchorhynchus gorbuscha*, *O. keta*) and anadramous dolly varden (*Salvelinus malma*) density 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 salmon present in a 1 m wide transect across the stream. Drift samples were collected at intervals from 3 June - 13 August 1980 at two stations in lower Stellar Creek to measure the rate of export of loose, drifting salmon roe and invertebrates. Each drift sampler consisted of a bag of aquatic netting (40 meshes/cm) 50 cm deep supported inside an aluminum frame to maintain a square mouth (25 X 25 cm). Drift 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 drift samples included Chloroperlidae, Baetidae (Heterocloeon, and others), Heptageniidae (Heptagenia, Rithrogena, and others), and Oligochaeta. However, the selectivity of neither the harlequins nor the drift samplers for specific invertebrates was known. Consequently, invertebrates in the drift samples were treated as a single, unified group and were not sorted taxonomically.

The density of loose, uncovered salmon eggs in Stellar Creek was estimated by counting the number of eggs visible within a 0.25 m^2 aluminum frame carefully placed on the stream bed at successive 1 m intervals along a transect across the stream channel.

IV. RESULTS

Numbers using study area

Census results were similar in 1979 and 1980, with a maximum population of about 50 harlequins present in Sawmill Bay in late May of each year (Tables 1,2). Fifteen pairs were present in the bay in 1979, and 14 pairs were observed there in 1980.

Mid-summer (late June - early August) censuses of Sawmill Bay, North Point, and Rocky Point averaged about 55 harlequins both years. During July and August of both years about 35 moulting males were present at North Point. Late August censuses, which included the area around Busby and Bligh Islands and, in 1980, also Jack Bay, averaged about 110 harlequins each year.

Sex ratios

During 1980 the proportion of males observed in the harlequin population increased from 68% on 6 June to 85% on 4 July, and then decreased to 56% on 19 August (Table 2). This pattern closely corresponded to the estimated periods of incubation and brood rearing by females, when, of course, they would be least visible. The true population sex ratio was best estimated in late August, when males and females were approximately equally visible (because females were no longer incubating, and a large proportion of males were in the female-like Basic plumage) but while broods remained intact (eliminating the confusion of classifying Juvenal plumage males as

Table 1. Population counts of harlequin ducks during the 1979 study period.

		SAWMILL BAY							NORTH PT, ROCKY PT BUSBY IS. & BLIGH IS.							TOTAL		
		Pairs	Unpaired males	Unpaired females	Females w/ broods	Total censused	Total classified	Percent males	Pairs	Unpaired males	Unpaired females	Females w/ broods	Total censused	Total classified	Percent males	Total censused	Total classified	Percent males
May	6-10	?	?	?		22	0	?										
	11-15	9	5			23	23	61										
	16-20	11	4			26	26	58										
	21-25	15	6			36	36	58										
	26-31	14	17	1		46	46	67										
June	1-5	13	9			35	35	63										
	6-10	6	12	2		26	26	69										
	11-15	5	21			31	31	84										
	16-20	3	6	1		27	13	69		58	4		60	60	93	87	73	88
	21-25	2	17	3		24	24	79										
	26-30		13	4		17	17	76		23	4		43	27	85	60	44	82
July	1-5		3	10		13	13	23										
	6-10		2	7		9	9	22										
	11-15		1	11		12	12	8										
	16-20			10		10	10	0		16	5		37	21	76	47	31	52
	21-25		3	11	1	15	15	20										
	26-31			12	1	13	13	0										
August	1-5			19	2	21	21	0										
	6-10			11	2	13	13	0										
	11-15			3	4	7	7	0										
	16-20		1	4	5	10	10	10		83	18		101	101	82	111	111	76
	21-25		1	3	5	9	9	11										

Table 2. Population counts of harlequin ducks during the 1980 study period.

		SAWMILL BAY						NORTH PT, ROCKY PT BUSBY IS. & BLIGH IS.						JACK BAY						TOTAL	
		Pairs	Unpaired males	Unpaired females	Females w/ broods	Total	Percent males	Pairs	Unpaired males	Unpaired females	Females w/ broods	Total	Percent males	Pairs	Unpaired males	Unpaired females	Females w/ broods	Total	Percent males	Total censused	Percent males
May	21-25	13	28			54	76														
	26-31	14	23			51	73														
June	1-5	11	17			39	72														
	6-10	9	21	4		43	70	6	7	1		20	65							63	68
	11-15	7	15	1		30	73														
	16-20	6	11	4		27	63	1	15			17	94							44	75
	21-25	5	6	2		18	61														
	26-30	1	6	8		16	44														
July	1-5		3	8		11	27	1	51	1		54	96							65	85
	6-10		4	4		8	50														
	11-15		3	6		9	33														
	16-20		2	6		8	25		38	6		44	86							52	77
	21-25			7		7	0														
	26-31		1	16	1	18	6														
August	1-5			10	1	11	0		38	11		49	78							60	63
	6-10			16	2	18	0														
	11-15		3	17	2	22	14		32	7		39	82							61	57
	16-20		2	14	2	18	11		44	21		65	68		18	12	1	31	58	114	56
	21-25		1	4	2	7	14		51	29		80	64		18	5	1	24	75	110	64

females). Censuses including Sawmill Bay, Jack Bay, North Point, Rocky Point, and the area around Busby and Bligh Islands conducted on 19 and 22 August 1980 averaged 60% males (Table 2). A similar census (excluding Jack Bay) on 18 August 1979 tallied 76% males (Table 1). Bengston (1072:6) reported a grand mean of 125 males per 100 females (56% males) during spring censuses of interior "breeding grounds;" his censuses did not include harlequins which remained on the coast.

Chronology

The general reproductive chronology observed among harlequins in Sawmill Bay was similar both years (Fig. 6). Formation of pairs was not observed in Sawmill Bay, but observations in Resurrection Bay on 14 April 1979 and in Valdez Harbor from 1-7 May 1979 indicated harlequins were already paired by those dates. Thus the increase of pairs in Sawmill Bay during May (Tables 1,2) was attributed to the arrival of already established pairs.

Copulatory behavior appeared to range about 10 days later in 1980 than in 1979 (Fig. 7a). However, our later arrival on the study area (25 May in 1980 vs 9 May in 1979) precluded observations in 1980 comparably early to those of 1979. Further, a 3 day absence (2-4 June) in 1979 prevented observations during that period. Noting the same considerations, the period during which harlequins engaged in sexual behavior was similar both years (Fig. 7b).

Counts of unpaired males in Sawmill Bay were highest in late May and early June (Tables 1,2). The erratic nature of those counts can be accounted for by the gradual dissolution of pair bonds through

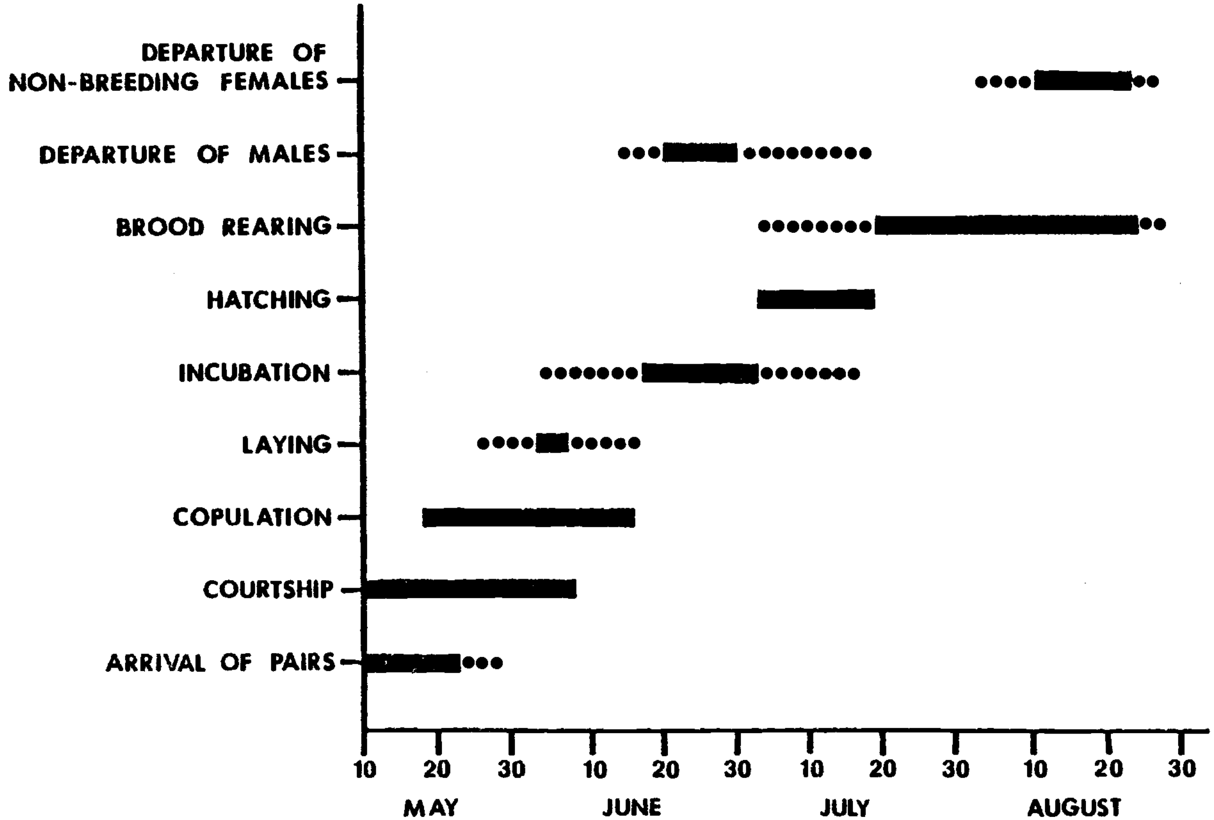


Fig. 6. General chronology of harlequin ducks observed in Sawmill Bay, Alaska during 1979 and 1980.

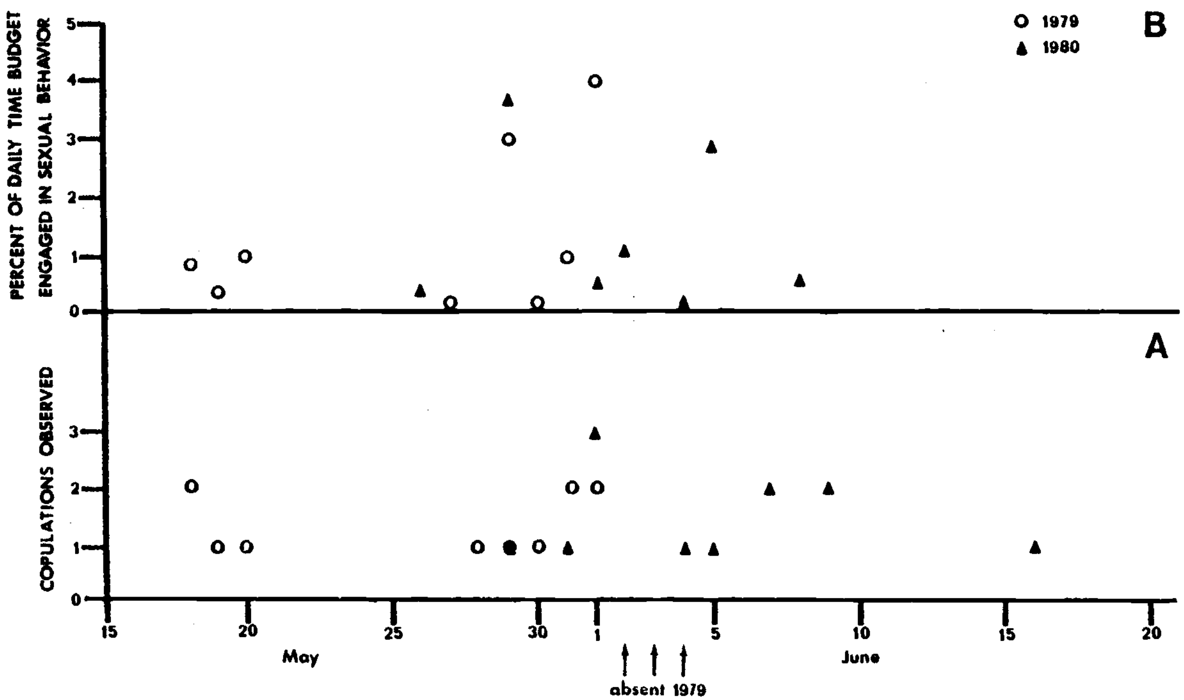


Fig. 7. (A) The number of copulations observed, and (B) the percent of daily time that harlequins engaged in sexual behavior, during 1979-1980. Sexual behavior includes, but is not limited to, copulations. Investigator arrived in study area on 9 May 1979 and on 25 May 1980. Investigator was absent from 2-4 June 1979.

June, thus augmenting the "pool" of unpaired males, and by the daily influxes and exoduses of small bands of unpaired males observed throughout that period.

Broods were first observed in Sawmill Bay in late July. Hatching (back-dated from six broods in 1979 and from two broods in 1980) occurred from 3-15 July. Given a 28 day incubation period (Bengston 1972:10), incubation was initiated from 5-17 June. Thus, assuming an average clutch size of six eggs and a laying interval of 2 days between eggs (Bengston 1972:10), laying occurred from 26 May - 17 June.

The breakdown of pair bonds through June coincided with the initiation of incubation by females, and from mid-June through mid-July the number of males in Sawmill Bay decreased. Concommittantly, the number of males increased in almost exact proportion at North Point. Males began acquiring Basic ("eclipse") plumage in late June and early July, became flightless in mid-late July, and began regaining flight and Alternate plumage by mid-August (Fig. 8).

The number of females in Sawmill Bay increased through June and July probably due to the influx of both failed-breeding and non-breeding individuals. Groups of 3-12 unpaired females were regularly observed feeding or resting in lower Stellar Creek, or loafing at roost sites in Sawmill Bay, throughout July and early August. Three (33%) of nine females examined on 2-3 August 1979, and three (43%) of seven females examined from 5-14 August 1980 had initiated body moult.

The number of females in Sawmill Bay declined after mid-August; Conversely, the number of females at North Point increased. Most females with broods remained in the bay through the end of the study

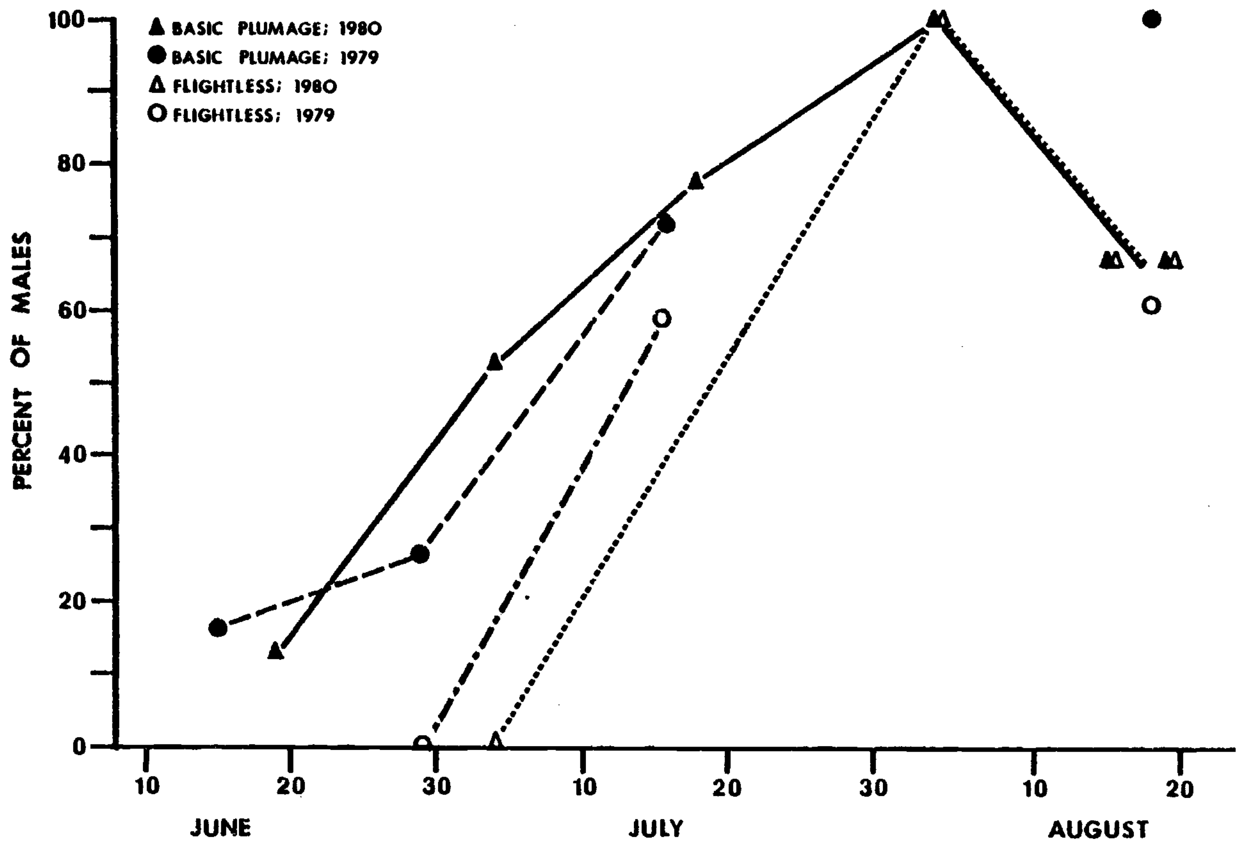


Fig. 8. Percent of all males censused in 1979 and 1980 (see Tables 1, 2) that were in Basic plumage, and the percent that were (also) flightless.

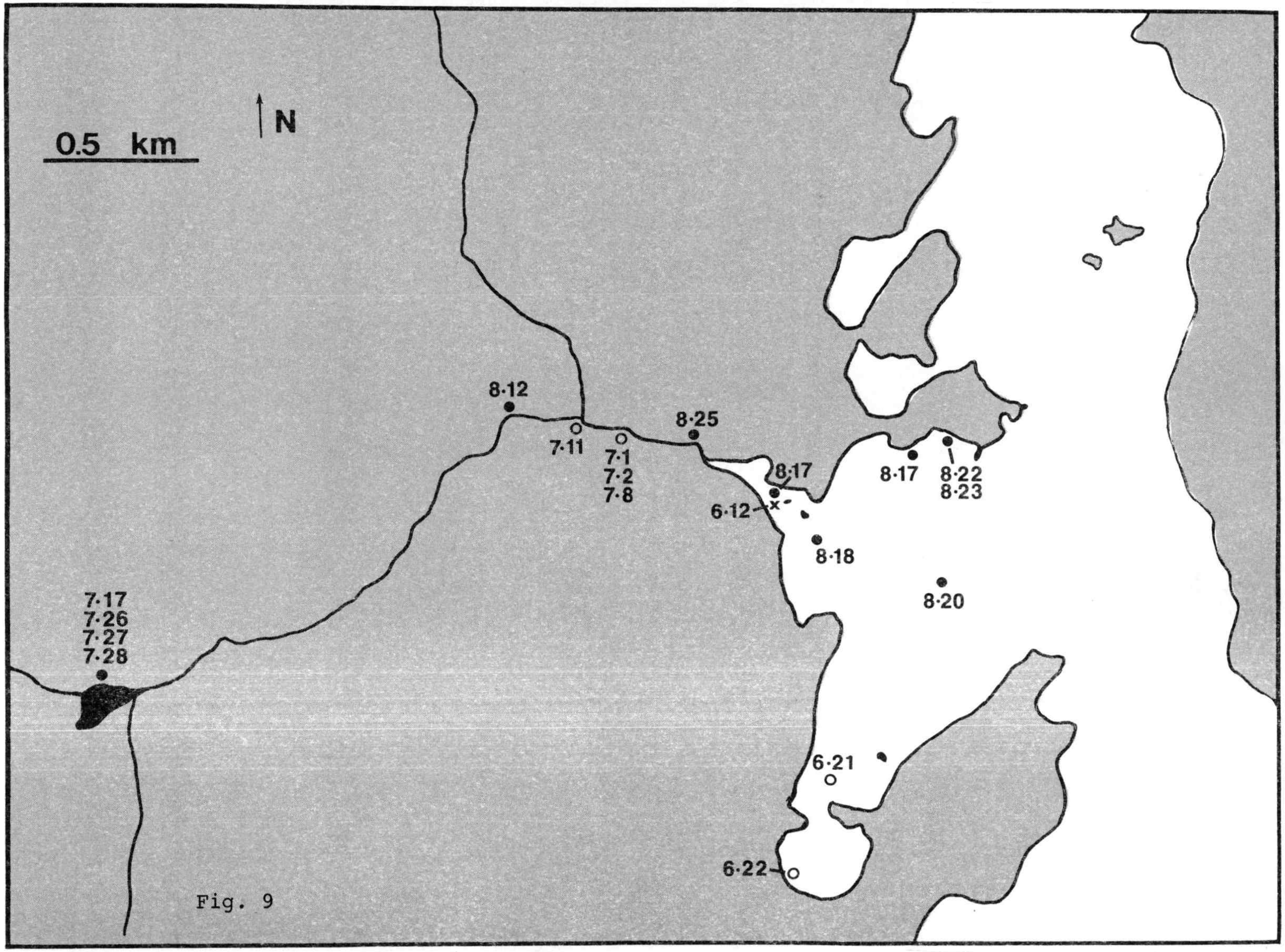
both summers, even though young were fledged by the third week of August each year. However, one brood was thought to have departed the bay about 23 August 1979, and on 25 August 1980 a marked brood flew a short distance into Valdez Arm when flushed from the mouth of Stellar Creek.

Local movements

The patterns of local movement among harlequins varied with the season and with the sex and reproductive status of the individuals. In general, successfully-breeding females were secretive and were observed only occasionally when they left their nest to feed in Sawmill Bay or lower Stellar Creek, or when (later in the summer) they were seen leading their brood. Conversely, unsuccessful (and non-breeding) females remained in lower Stellar Creek or near roost sites in the bay and were easily observed throughout the summer. Males, following the dissolution of pair bonds, remained near roost sites in the bay or were found feeding outside the mouth of Stellar Creek until their departure to moulting areas in June and early July.

Successful females. Typical of successfully-breeding females was L6, who was captured on 12 June 1979 (Fig. 9). On 21 June she spent at least 3.25 hr (1935-2250) feeding and loafing in a quiet cove. She was in the same cove the following evening, and exactly 25 days later she was discovered leading four class 1a (Gollop and Marshall 1954) chicks in Stellar Lake. Her mate (male L6) was seen among the males moulting at North Point on 29-30 June, and on 17 July he was flightless and in Basic plumage.

Fig. 9. Re-sightings (month·day) of harlequin female L6 during 1979. Open circles = female sighted alone. Closed circles = female sighted with brood. x = capture site.



0.5 km
N
8·12
7·11
7·1
7·2
7·8
8·25
8·17
6·12
8·17
8·22
8·23
8·18
8·20
7·17
7·26
7·27
7·28
6·21
6·22

Fig. 9

From 1-11 July (when she must surely have been incubating), female L6 was observed on four different occasions feeding and resting near the confluence of Fault and Stellar Creeks with 5-11 other harlequins (almost all females). On 1 July she spent at least 1.5 hr away from her nest (2140-2305), and the next evening she spent 2 hr off her nest (2045-2250). From 26-28 July she was observed on Stellar Lake with her brood, on 12 August she was first seen with her brood in lower Stellar Creek, and from mid-late August she was seen with her brood (then class 2c-3) in Sawmill Bay and the tidal portion of Stellar Creek. She apparently remained in or near the bay throughout the fall, and on 12 November 1979 she was shot by a waterfowl hunter near the mouth of Stellar Creek.

Unsuccessful females. Female U3 was typical of unsuccessfully-breeding females. She was captured in early June of 1979 and 1980 and was paired with the same male each year. She exhibited a brood patch (but was not tending young) when recaptured later each summer, indicating she had attempted to breed but failed both years. Re-sightings of U3 during 1979 in the mouth of Stellar Creek, half-way to the junction of Fault Creek, and at Fault Creek display sets of increasingly later dates at each station (Fig. 10). As in 1979, U3 was not observed in the non-tidal portion of Stellar Creek until mid-summer of 1980 (Fig. 11). These re-sightings corresponded to a general pattern observed among all female harlequins in Sawmill Bay to feed further up Stellar Creek as the summer progressed. This chronological "ascent" by females of the lower portion of Stellar

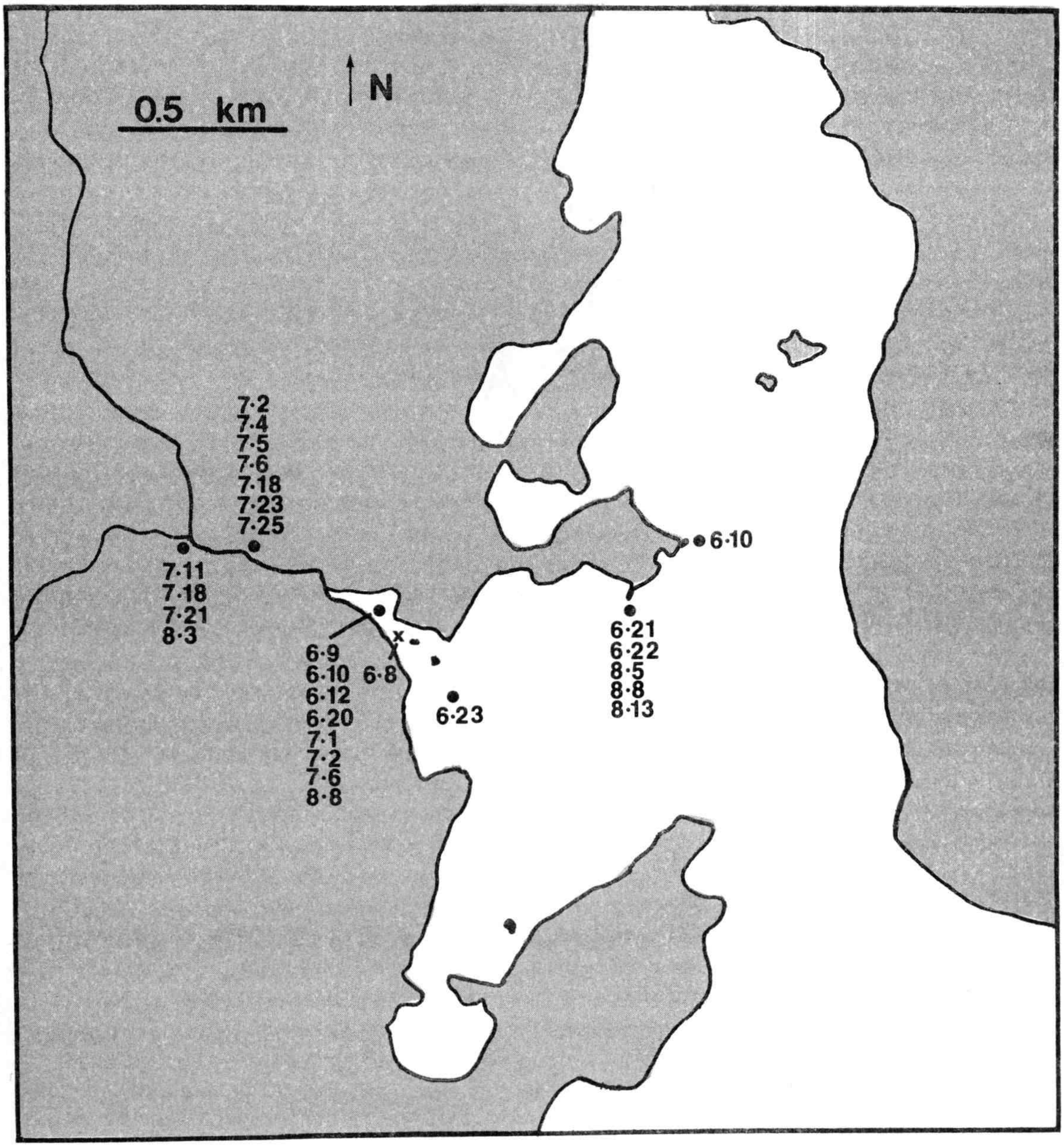


Fig. 10. Re-sightings (month·day) of harlequin female U3 during 1979. x = capture site.

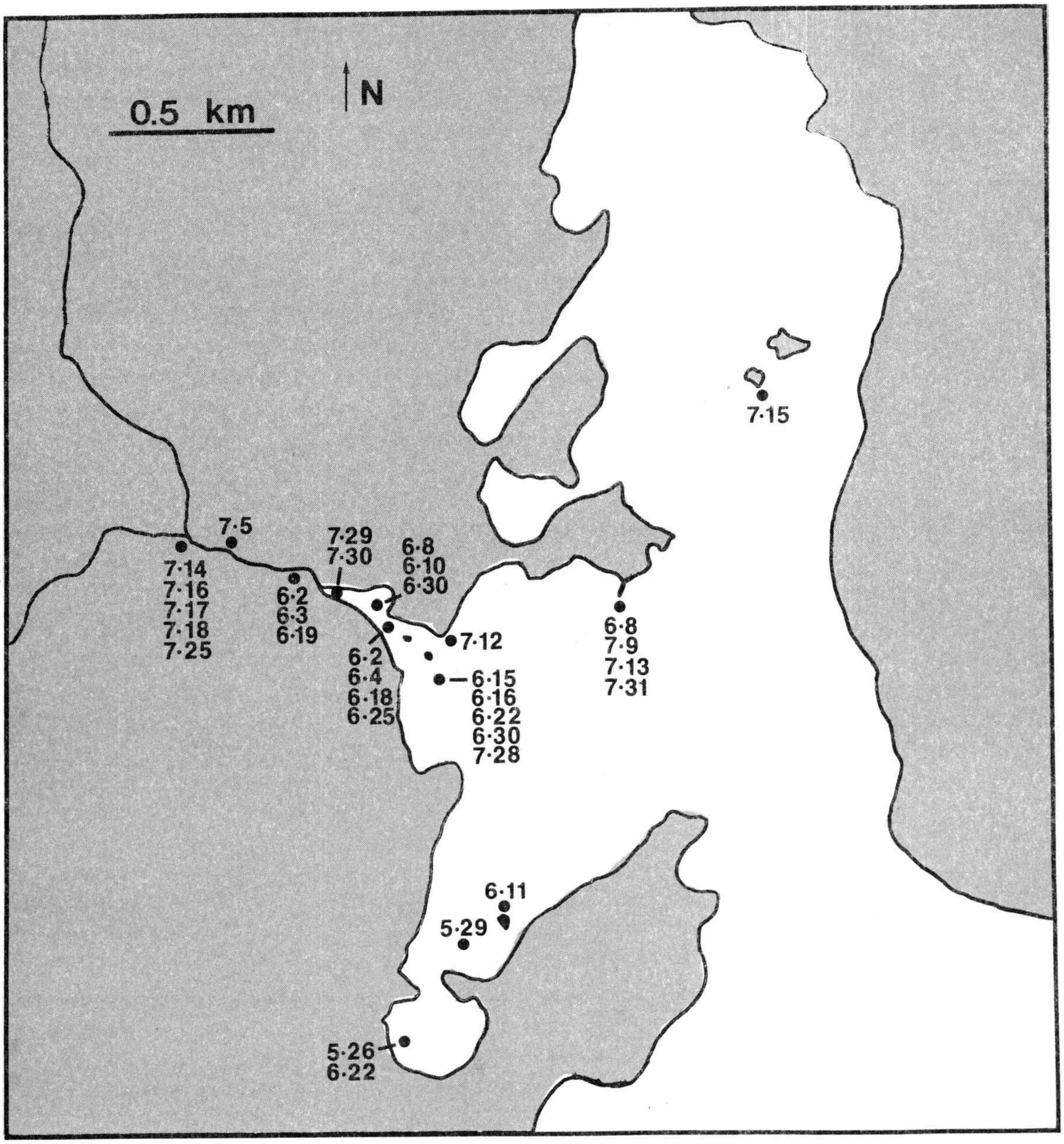


Fig. 11. Re-sightings (month·day) of harlequin female U3 during 1980.

Creek coincided with the general progression of salmon up the creek and was a focus of investigation in 1980 (see "Foraging relationships" - page 52).

Males. Following the dissolution of pair bonds in June, males were seen only infrequently in Stellar Creek, and they did not exhibit an ascending pattern of stream use similar to that of females. Re-sightings during 1979 of male L3 (Fig. 12) were typical of males in Sawmill Bay following the break-down of their pair bond (about mid-June for L3). During this period males tended to remain near rocks and headlands, although they often moved to the mouth of Stellar Creek to feed.

Movements outside Sawmill Bay. Harlequins leaving Sawmill Bay apparently moved southeast across Valdez Arm. Seven re-sightings of tagged harlequins (representing five individuals) were obtained in 1979 from North Point and Rocky Point. Seventeen re-sightings (representing five individuals) were obtained from the same area in 1980 (Fig. 13). Tag loss, however, resulted in under-estimation of the number of individuals from Sawmill Bay present among harlequins observed during surveys of Valdez Arm. For example, in a group of 22 males observed at North Point on 18 July 1980, three (of five examined) were banded but had lost their tags.

Females at North Point early in the summer may not have been so restricted to the area as were the moulting males. For example, female Z2 was seen in Sawmill Bay on 12 June 1980 with her mate, male H7. Both Z2 and H7 were observed at North Point on 19 June, but from

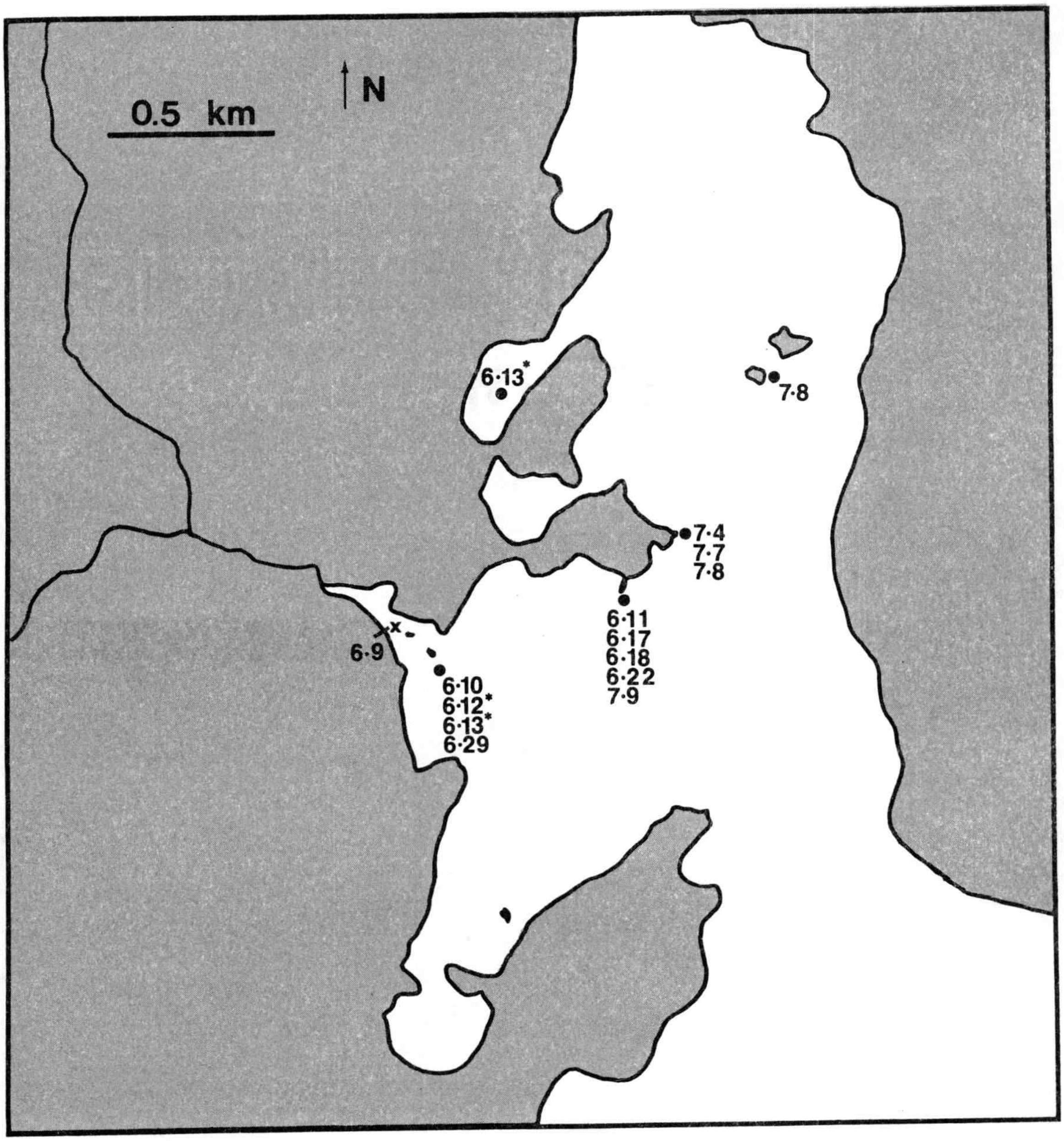


Fig. 12. Re-sightings (month·day) of harlequin male L3 during 1979.

x = capture site. * = sighted with mate.

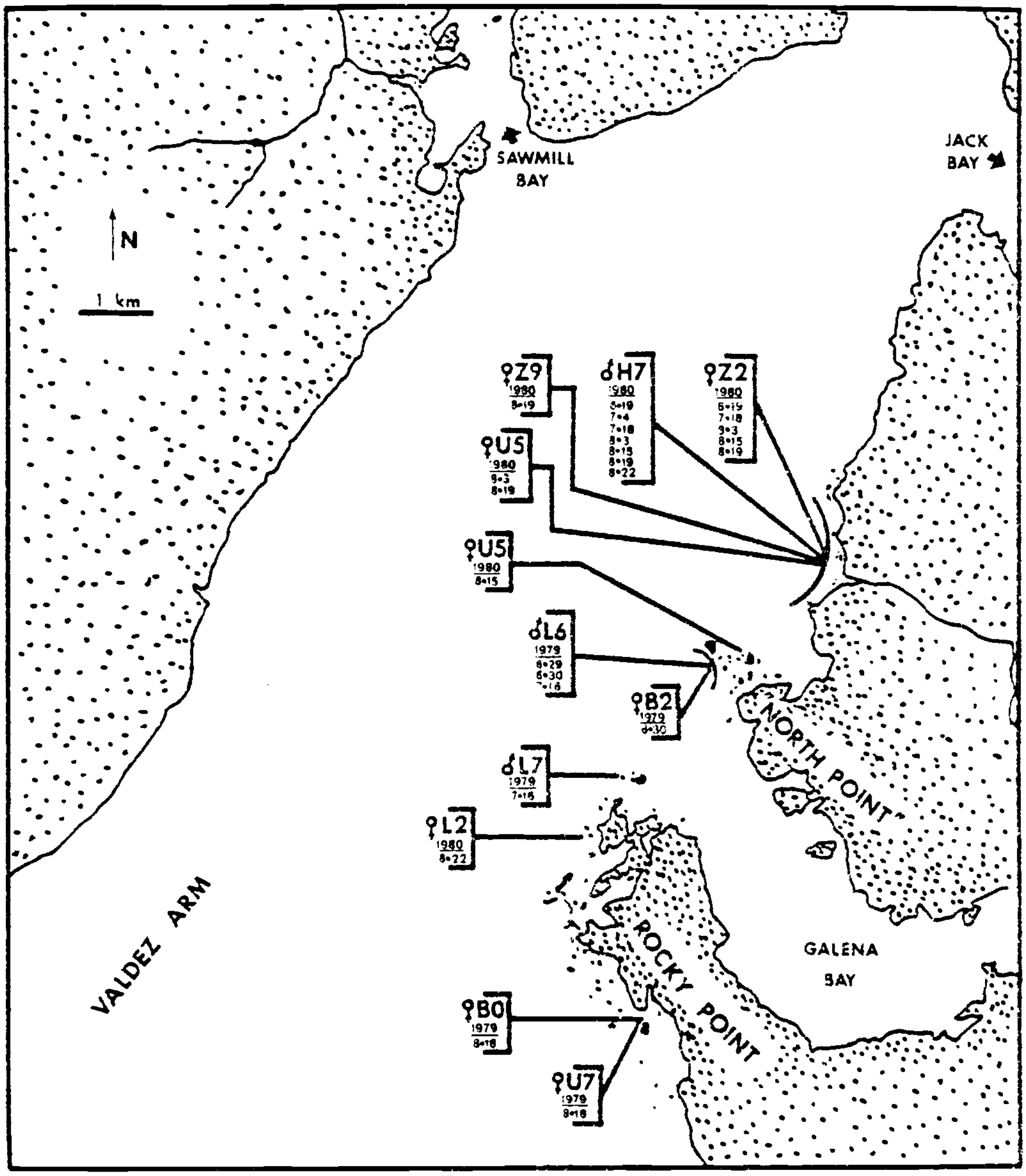


Fig. 13. Dates and locations of tagged harlequin ducks re-sighted outside Sawmill Bay during 1979-1980. All individuals were originally captured in Sawmill Bay.

29 June - 15 July, Z2 was recorded in Sawmill Bay seven times (without H7). On 18 July, Z2 was once again with H7 at North Point, where she then apparently remained.

Most female harlequins left Sawmill Bay about mid-August. In 1979, two females captured in Sawmill Bay in early August were re-sighted south of Rocky Point on 18 August. In 1980, three tagged females observed in Sawmill Bay until late July or early August were later re-sighted at North Point or Rocky Point in mid-August (Fig. 13).

Patterns of habitat use

Habitat descriptions

Stellar Creek. Stellar Creek emptied into Sawmill Bay through a 0.7 km long tidal "gorge" which varied from 25-75 m wide and which was bordered by steep, forested banks. Fault Creek joined Stellar Creek as a tributary at the upper end of this gorge, slightly above the point of highest tidal influence on Stellar Creek. The 0.7 km tidal portion of Stellar Creek, the next 0.6 km of the creek, and the first 0.2 km of Fault Creek formed a unit of broadly similar habitat which supported large numbers of salmon and much harlequin activity. This unit of similar habitat, together with the intertidal delta of Stellar Creek, was referred to in this study as the habitat type "Stellar Creek."

Rocks and headlands. Harlequins frequented particular, traditional off-shore rocks, rocky headlands, and small islands. Harlequins used these sites primarily for roosts, but often fed in the adjacent waters. Eight such roost sites were identified in

Sawmill Bay, and they accounted for 82% of all harlequins observed resting on land during 14 censuses of the bay from 28 May - 16 August 1980.

The eight roosts were compared to 50 randomly selected sites in Sawmill Bay. Roosts were characterized by their relative geographic isolation and by their predominately boulder or broken rock substrates. The average slope of roosts (22°) was greater ($P<0.001$) than that of random sites (10°). Also, the intertidal biota of the roosts was generally richer than that of random sites. Mean percent cover of barnacles (*Balanus* spp.), mussels (*Mytilus* spp.), *Fucus* spp., and *Laminaria* spp. was greater on roosts than on random sites at almost all tide levels (Fig. 14, 15).

Lee waters. The habitat type "lee waters" refers to quiet coves or areas in the lee of islands or peninsulas which were sheltered from all but the most violent storms. In Sawmill Bay, lee waters included (only) the three coves extending southwest from the main body of the bay, and the protected area fanning northeast behind the two small islands in the bay.

Occurrence in habitats

The amount of time harlequins spent in each habitat (Stellar, Rocks, Lee) varied with the season, sex (among unpaired harlequins), and time of day. Generally, the quantitative patterns of habitat use reflected the qualitative patterns of local movements.

Harlequin pairs used the three habitats equally during the morning ($P>0.10$), but they occurred most frequently on rocks during

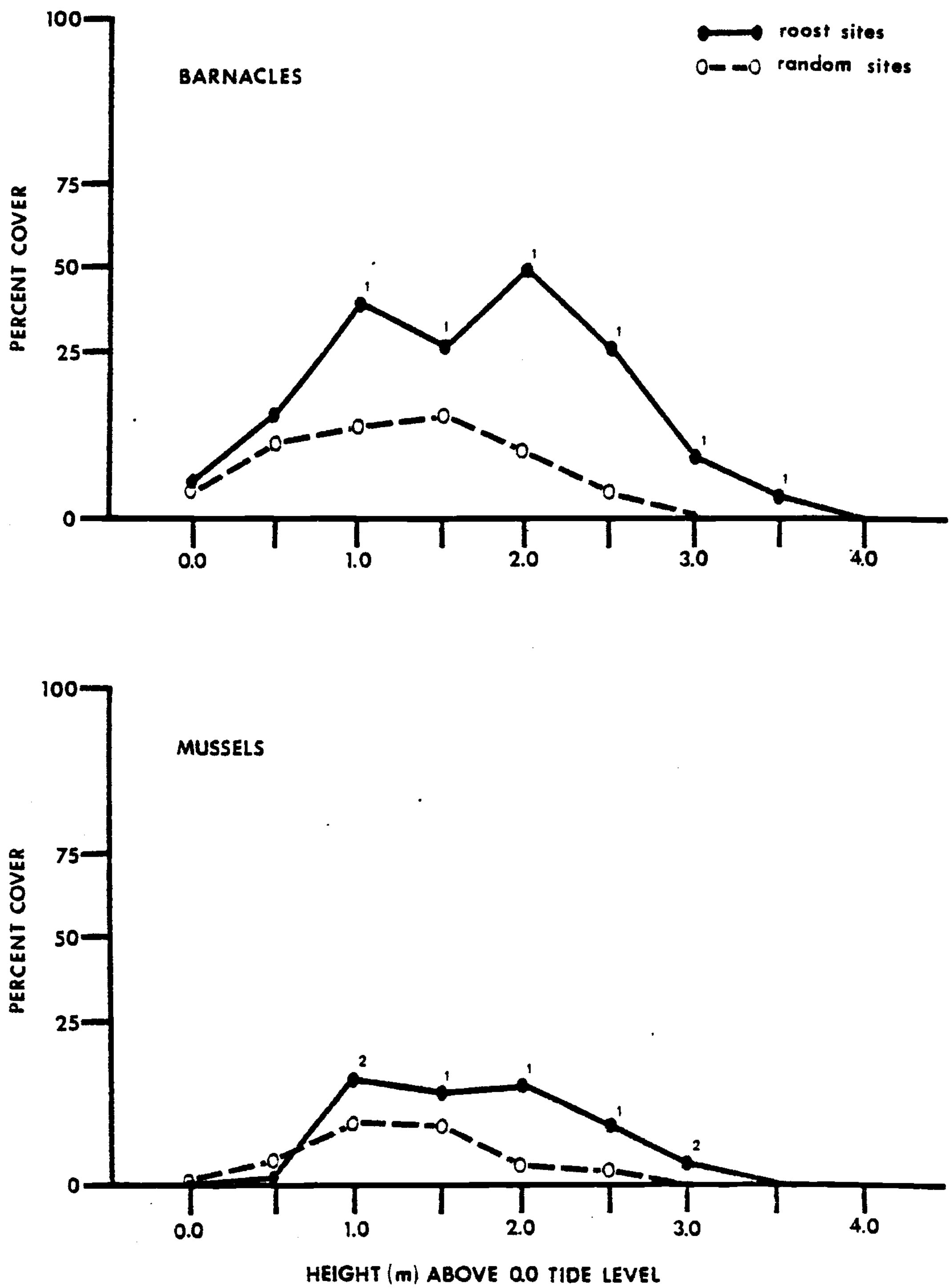


Fig. 14. Percent cover of barnacles and mussels at eight roost sites used by harlequin ducks and at 50 random sites in Sawmill Bay. Data are transformed and plotted in degrees (see Methods). The ordinate is back-transformed for ease of interpretation.

[1] Corresponding points are significantly different ($P<0.05$).

[2] Corresponding points are significantly different ($P<0.01$).

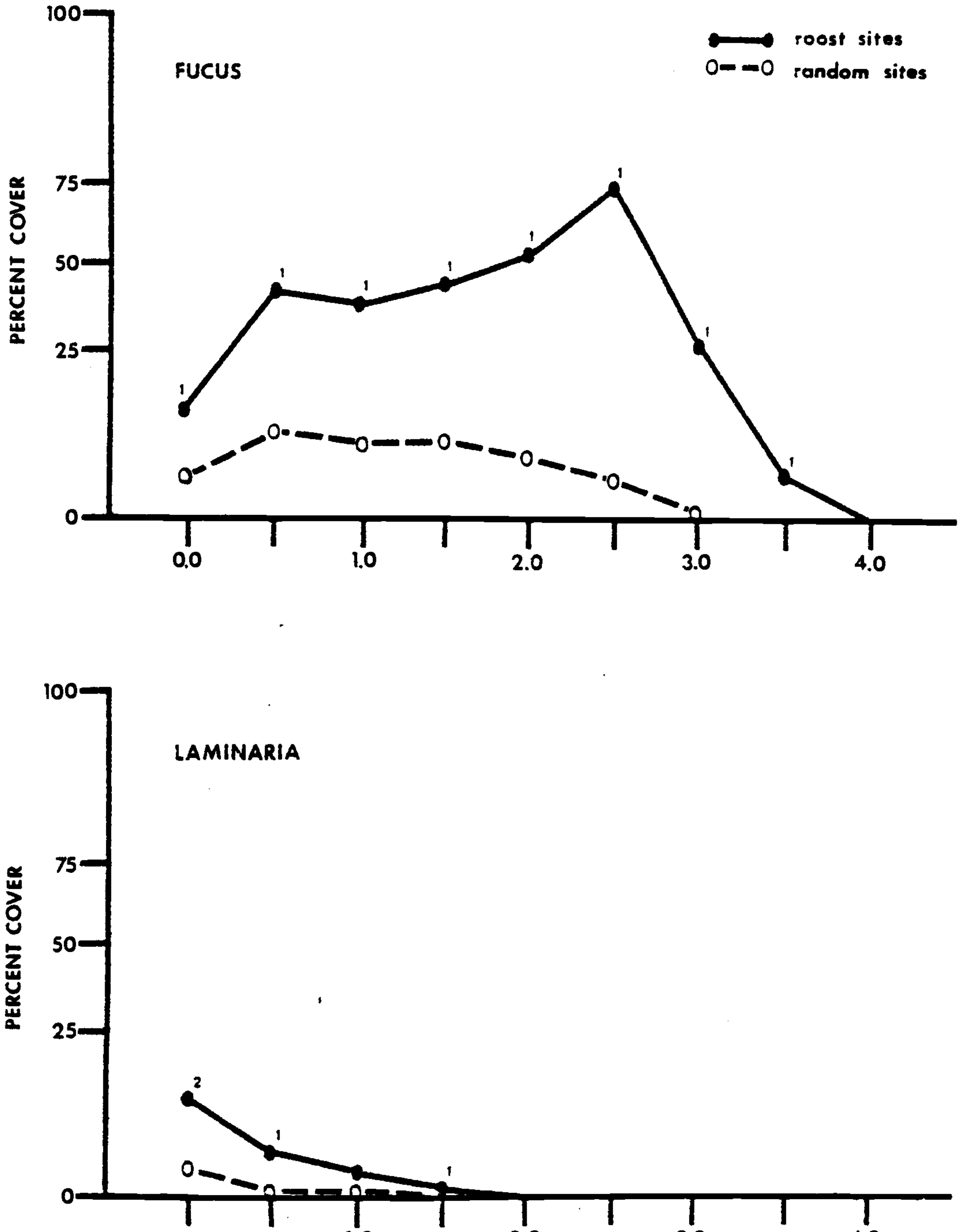


Fig. 15. Percent cover of *Fucus* and *Laminaria* at eight roost sites used by harlequin ducks and at 50 random sites in Sawmill Bay. Data are transformed and plotted in degrees (see Methods). The ordinate is back-transformed for ease of interpretation.

[1] Corresponding points are significantly different ($P<0.05$).

[2] Corresponding points are significantly different ($P<0.01$).

mid-day ($P<0.005$) and evening ($P<0.005$) (Fig. 16). Unpaired males occurred in Stellar Creek and on rocks equally during the morning ($P>0.10$), but they occurred most often on rocks during mid-day ($P<0.005$) and evening ($P<0.005$) (Fig. 17a). Unpaired females occurred most frequently in Stellar Creek during the morning ($P<0.01$), but they occurred in Stellar Creek and on rocks equally during mid-day ($P>0.10$) and evening ($P>0.10$) (Fig. 17b).

The total (diurnal) proportion of time harlequins occurred in each habitat was determined by pooling censuses over all daylight hours. Harlequin pairs during prenesting and laying spent nearly half their time around rocks and headlands, and a fourth of their time each in Stellar Creek and lee waters ($P<0.005$) (Table 3). Unpaired harlequins were rare in lee waters (Table 3), and the few recorded there appeared merely transient or possibly seeking shelter from unseasonally powerful storms. Comparing only Stellar Creek and rocks, unpaired males spent about three-fourths of their time around rocks and headlands ($P<0.005$), while unpaired females spent slightly more than half their time in Stellar Creek ($P<0.10$) Table 3).

Activity budgets

Resting, feeding, locomotion, and preening comprised 95-98% of the diurnal activity budget of harlequins. However, resting and feeding behavior alone accounted for about 60% of the diurnal activity budget of harlequin pairs and about 75% of the diurnal

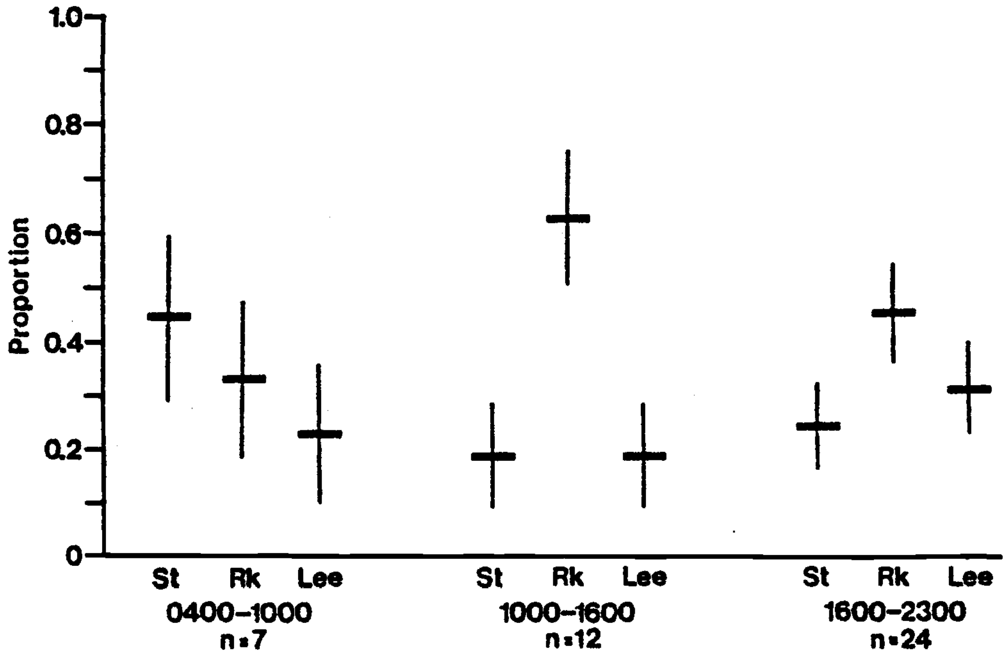
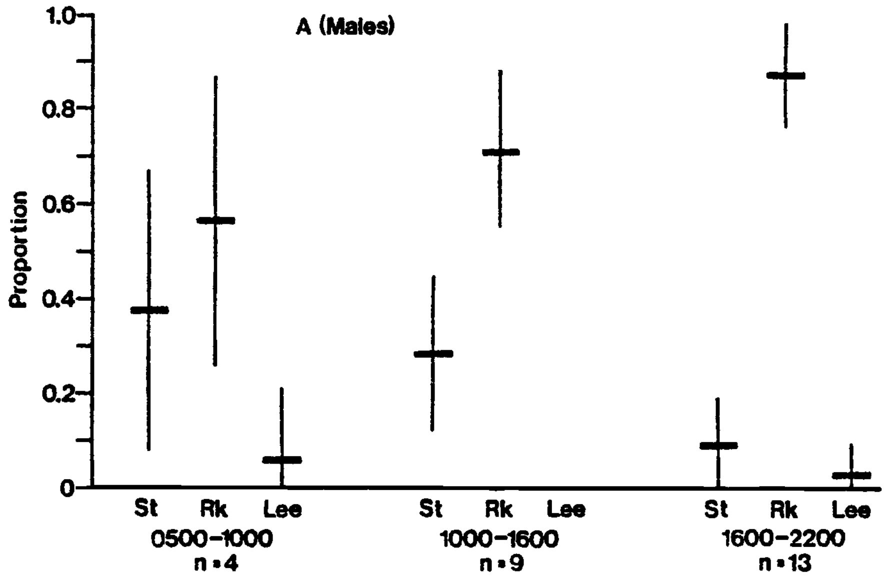


Fig. 16. Proportion (mean + 90% C.I.) of harlequin pairs observed in Stellar Ck (St), rocks (Rk), and lee waters (Lee) during morning (0400-1000), mid-day (1000-1600), and evening (1600-2300) censuses of Sawmill Bay from 10 May - 21 June 1979-1980. Sample size (n) = the number of censuses conducted.



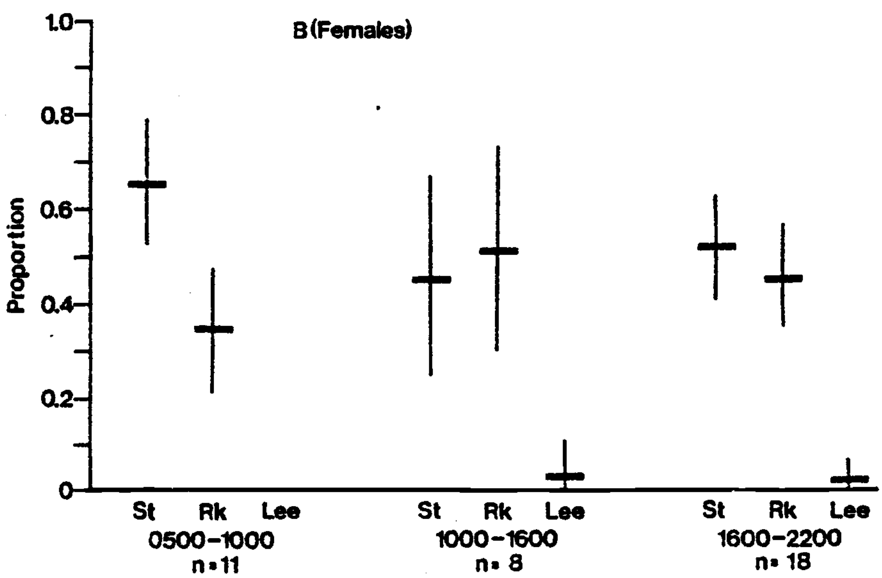


Fig. 17. Proportion (mean + 90% C.I.) of (A) unpaired male, and (B) unpaired female harlequins observed in Stellar Ck (St), rocks (Rk), and lee waters (Lee) during morning (0500-1000), mid-day (1000-1600), and evening (1600-2200) censuses of Sawmill Bay from 22 June - 15 August 1979-1980. Sample size (n) = the number of censuses conducted.

Table 3. Number (n), proportion (p), and 90% C.I. of harlequins observed in each habitat type during (pooled) morning, mid-day, and evening censuses of Sawmill Bay, 1979-1980.

	n	p	90% C.I.
Pairs[1]			
Stellar Ck	83	0.264	0.204 - 0.324
Rocks	149	0.475	0.408 - 0.542
Lee	82	0.261	0.202 - 0.320
Total	314	1.000	
Unpaired males[2]			
Stellar Ck	24	0.205	0.114 - 0.296
Rocks	90	0.769	0.674 - 0.864
Lee	3	0.026	-0.010 - 0.062
Total	117	1.000	
Unpaired females[2]			
Stellar Ck	133	0.554	0.475 - 0.633
Rocks	103	0.429	0.351 - 0.507
Lee	4	0.017	-0.003 - 0.037
Total	240	1.000	

[1] 10 May - 21 June.

[2] 22 June - 15 August.

activity budget of unpaired harlequins.

The amount of time harlequins devoted to each activity varied with habitat (Tables 4, 5; Appendix 4), and, within habitats, with sex and season (Tables 4, 5; Appendix 5). The only habitat-specific activity budgets of harlequins that were closely similar were those of paired males and females on rocks and headlands (Appendix 5).

The total, diurnal activity budgets that were calculated indicated that paired females (10 May - 21 June) devoted more time to feeding (21.1% vs 12.6%), but less time to resting (40.9% vs 46.3%) and to interactive behavior (1.3% vs 3.4%) than did their mates (Table 6). Unpaired males and females (22 June - 15 August) spent similar amounts of time in most activities (Table 7). However, unpaired males spent more time preening (8.0% vs 5.8%) and less time in locomotion (10.2% vs 12.5%) than did unpaired females, probably reflecting the onset of the male moult. Although unpaired females appeared to spend more time feeding than did unpaired males (15.3% vs 11.8%), this might have resulted from high rates of feeding among occasional, individual females recovering from nest failure, or possibly it reflected the average rate obtained over a long period of gradually decreasing feeding following the prenesting feeding peak.

For each habitat, the time harlequins devoted to each activity was compared to the proportion of time they spent in that habitat (Tables 8. 9). Paired harlequins used Stellar Creek disproportionately for feeding, locomotion, and interactive behavior. Conversely, rocks

Table 4. Habitat-specific activity budgets for paired harlequins in Sawmill Bay from 10 May - 21 June 1979-1980. Values are the proportion of observations (n) recorded in each activity category.

	Stellar Ck		Rocks		Lee	
	male	female	male	female	male	female
n =	744	744	974	937	2982	3184
Activity						
Resting	0.335[a][1]	0.164	0.568	0.582	0.402	0.346
Feeding	0.198	0.433	0.073	0.082	0.150	0.224
Locomotion	0.339[a]	0.308	0.179[a]	0.166[a]	0.315	0.297
Preening	0.054[b]	0.063[a]	0.147[a]	0.153[a]	0.102	0.115
Alert	0.007	0.004	0.014[b]	0.013[b]	0.005	0.003
Interaction	0.068[b]	0.028[a]	0.020[b]	0.004[b]	0.026	0.015
Total	1.001	1.000	1.001	1.000	1.000	1.000

[1] Values within a column having different (or no) superscripts have non-overlapping 95% confidence intervals.

Table 5. Habitat-specific activity budgets for unpaired harlequins in Sawmill Bay from 22 June - 15 August 1979-1980. Values are the proportion of observations (n) recorded in each activity category.

	Stellar Ck		Rocks		Lee[2]	
	male	female	male	female	male	female
n =	771	2691	2571	2082	0	0
Activity						
Resting	0.113[a][1]	0.430	0.829	0.918	-	-
Feeding	0.507	0.273	0.019[a]	0.005[a]	-	-
Locomotion	0.297	0.200	0.053	0.033[b]	-	-
Preening	0.075[a]	0.076	0.085	0.037[b]	-	-
Alert	0.004[b]	0.021	0.013[a]	0.007[a]	-	-
Interaction	0.004[b]	tr	0.001	tr	-	-
Total	1.000	1.000	1.000	1.000	-	-

[1] Values within a column having different (or no) superscripts have non-overlapping 95% confidence intervals.

[2] Unpaired harlequins occurred in lee waters only rarely (Table 3) and activity budgets were not obtained for them there.

Table 6. Total, diurnal (0400-2300) activity budgets for paired harlequins in Sawmill Bay from 10 May - 21 June 1979-1980. Values are the calculated proportion of time harlequins engaged in each activity, and were obtained by multiplying the habitat-specific activity budgets (Table 4) by the proportion of occurrence in each habitat (Table 3).

	Activity						
	Rest	Feed	Locom	Preen	Alert	Inter	Row sum
Paired males							
Stellar Ck	0.088[1]	0.052	0.089	0.014	0.002	0.018	
Rocks	0.270	0.035	0.085	0.070	0.007	0.009	
Lee	0.105	0.039	0.082	0.026	0.001	0.007	
Total	0.463	0.126	0.256	0.110	0.110	0.010	0.999
Paired females							
Stellar Ck	0.043	0.114	0.081	0.017	0.001	0.007	
Rocks	0.276	0.039	0.079	0.073	0.006	0.002	
Lee	0.090	0.058	0.078	0.030	0.001	0.004	
Total	0.409	0.211	0.238	0.120	0.008	0.013	0.999

[1] Values are the product of comparable entries from Tables 3 and 4. e.g. for paired males resting in Stellar Creek: 0.264 X 0.335 = 0.088.

Table 7. Total, diurnal (0500-2200) activity budgets for unpaired harlequins in Sawmill Bay from 22 June - 15 August 1979-1980. Values are the calculated proportion of time harlequins engaged in each activity, and were obtained by multiplying the habitat-specific activity budgets (Table 5) by the proportion of occurrence in each habitat (Table 3).

	Activity						
	Rest	Feed	Locom	Preen	Alert	Inter	Row sum
Unpaired males							
Stellar Ck	0.023[1]	0.104	0.061	0.015	0.001	0.001	
Rocks	0.637	0.014	0.041	0.065	0.010	0.001	
Lee	-	-	-	-	-	-	
Total	0.660	0.118	0.102	0.080	0.011	0.002	0.973[2]
Unpaired females							
Stellar Ck	0.238	0.151	0.111	0.042	0.012	tr	
Rocks	0.394	0.002	0.014	0.016	0.003	tr	
Lee	-	-	-	-	-	-	
Total	0.632	0.153	0.125	0.058	0.015	tr	0.983[2]

[1] Values are the product of comparable entries from Tables 3 and 5. e.g. for unpaired males resting in Stellar Creek: 0.205 X 0.113 = 0.023.

[2] Row sum <1.000 because activity budgets were not obtained for lee waters.

Table 8. Comparison of the proportion of time paired harlequins (10 May - 21 June) occurred in each habitat, with the proportion, of the total (diurnal) time they devoted to each activity, that they allocated to each habitat.

		Activity					
	Occurrence[1]	Rest	Feed	Locom	Preen	Alert	Inter
Paired males							
Stellar Ck	0.264	0.191[2]	0.414	0.349	0.129	0.182	0.529
Rocks	0.475	0.582	0.275	0.331	0.631	0.687	0.272
Lee	0.261	0.227	0.311	0.320	0.240	0.131	0.199
Total	1.000	1.000	1.000	1.000	1.000	1.000	1.000
Paired females							
Stellar Ck	0.264	0.106	0.540	0.342	0.140	0.139	0.556
Rocks	0.475	0.674	0.184	0.332	0.608	0.772	0.150
Lee	0.261	0.220	0.276	0.326	0.252	0.089	0.293
Total	1.000	1.000	1.000	1.000	1.000	1.000	1.000

[1] Repeated from Table 3 for ease of comparison.

[2] Values derived from Table 6. e.g. for paired males: 0.088 (resting in Stellar Ck) ÷ 0.463 (total resting) = 0.191 (proportion of total resting time allocated to Stellar Ck).

Table 9. Comparison of the proportion of time unpaired harlequins (22 June - 15 August) occurred in each habitat, with the proportion, of the total (diurnal) time they devoted to each activity, that they allocated to each habitat.

	Occurrence[1]	Activity: Rest	Feed	Locom	Preen	Alert	Inter
Unpaired males							
Stellar Ck	0.205	0.035[2]	0.878	0.598	0.191	0.073	0.471
Rocks	0.769	0.965	0.122	0.402	0.809	0.927	0.529
Lee	0.026	-	-	-	-	-	-
Total	1.000	1.000	1.000	1.000	1.000	1.000	1.000
Unpaired females							
Stellar Ck	0.554	0.377	0.986	0.888	0.725	0.791	0.500
Rocks	0.429	0.623	0.014	0.112	0.275	0.209	0.500
Lee	0.017	-	-	-	-	-	-
Total	1.000	1.000	1.000	1.000	1.000	1.000	1.000

[1] Repeated from Table 3 for ease of comparison.

[2] Values derived from Table 7. e.g. for unpaired males: 0.023 (resting in Stellar Ck) ÷ 0.660 (total resting) = 0.035 (proportion of total resting time allocated to Stellar Ck).

were used mostly for resting, preening, and alert behavior, while lee waters were used disproportionately only for locomotion. Unpaired males and females used Stellar Creek and rocks in a pattern similar to that of pairs. Interactive behavior, however, was reduced among unpaired harlequins in late summer.

Foraging relationships

Harlequins fed most actively in the morning, and in early summer they usually began arriving in the intertidal delta of Stellar Creek (a favored feeding area) around 0330, increasing in number to about 0700 (Fig. 18). Although the diurnal rhythm of harlequins seemed to be the predominate factor influencing the number of harlequins feeding outside Stellar Creek, the stage of the tide cycle was also important and may have affected the intensity of feeding in a manner much like that described for eiders (*Somateria mollisima*) in Scotland (Campbell 1978).

Along the coast harlequins apparently feed predominately on crustaceans (mostly crabs and amphipods) and mollusks (especially chitons and various gastropods), with a wide variety of other animals (isopods, hydroids, pycnognids, echinoderms, sea urchins, nereid worms, sand dollars) and plants (kelp, algaes) also consumed (Bent 1925; Cottam 1939; Grinnel 1909; Kenyon 1961; Preble and McAtee 1923; Palmer 1949; Whitfield 1894). Harlequins feeding in the delta of Stellar Creek most often dabbled or tipped-up at the edge of tidewater, where they appeared to glean algae and probe in or sift substrate sediments. Harlequins foraging in the delta were observed

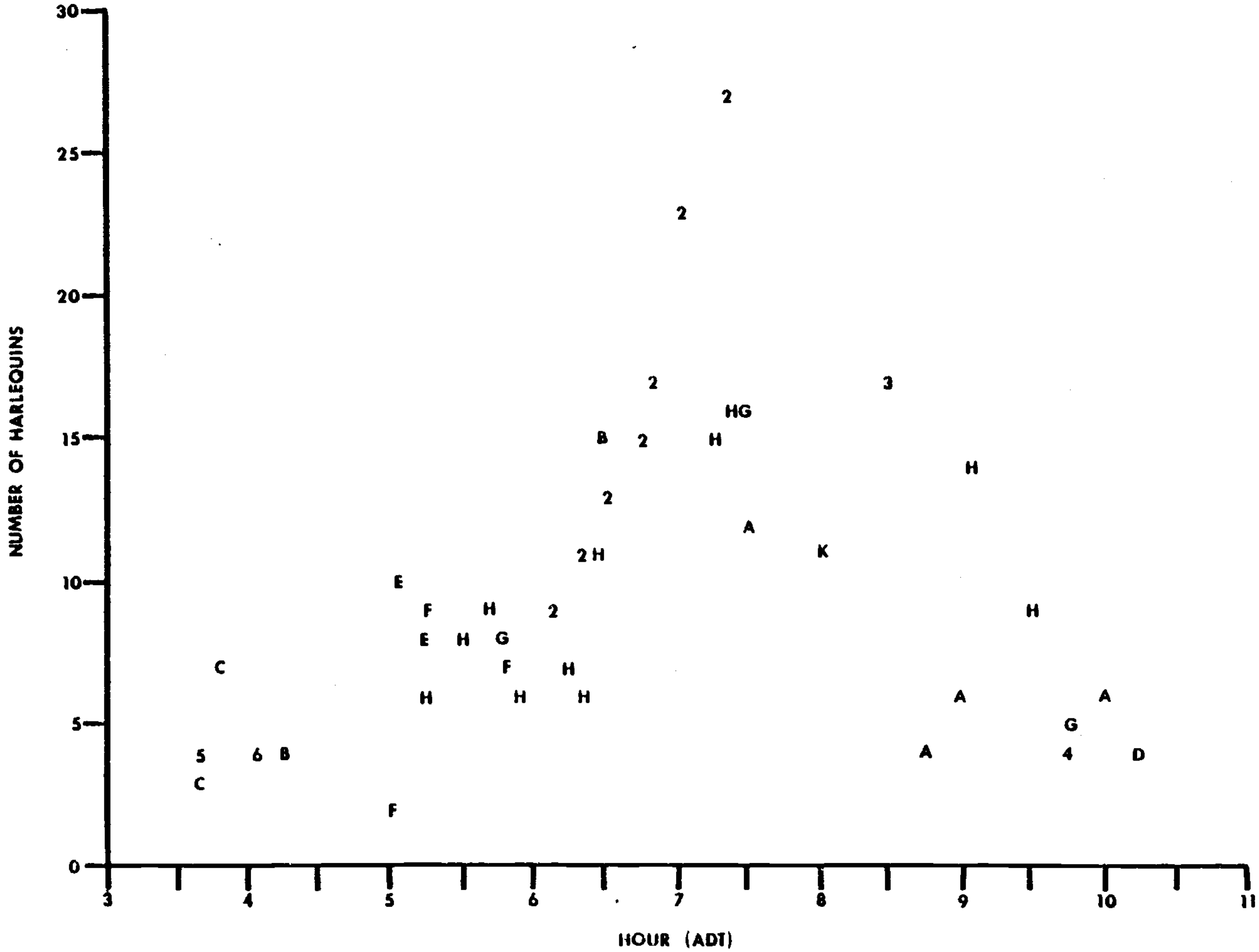


Fig. 18. Number of harlequins present, by hour, in the intertidal delta of Stellar Creek from 20 May - 1 July. Each symbol represents observations on the same day. Numbers denote 1979 observations, letters denote 1980 observations.

ingesting small crabs, snails, and worms. Two harlequin stomachs collected from Sawmill Bay, and three collected from similar areas in Valdez Arm, contained mostly crabs (Pleocyemata), *Littorina* snails, and (in one case) starfish (Table 10).

Harlequins feeding in Stellar Creek remained almost exclusively in the intertidal delta outside the mouth of the creek until the first week of July. After that time an obvious shift occurred to feeding areas in lower Stellar Creek, and the area outside the mouth of the creek was essentially abandoned (Fig. 19a). Coincident with the shift by harlequins in feeding areas was a marked increase in both the abundance of salmon in the stream (Fig. 19b) and in the rate of drift of invertebrates and loose, unburied salmon eggs (Fig. 19c). Salmon eggs, abundant in stream drift samples from late July through early August, resulted primarily from disruption of stream gravels and established salmon redds by late arriving salmon and by storm freshets. The same processes probably resulted in the increased drift of invertebrates. Although biomass of salmon eggs was greater in late July and August samples than was the biomass of invertebrates, the difference was not significant (t-test; $P>0.10$). However, relatively few salmon eggs comprised the total egg biomass ($\overline{X} = 15.7$ eggs/sample hr from 31 July - 13 August), whereas several hundred or more individual invertebrates were captured per hour in the same samples. Thus drifting salmon eggs represented a more efficiently exploited food source for harlequins than did invertebrates.

The mean number of loose, uncovered salmon eggs visible along 8 transects in Stellar Creek (from 0.25 km below, to 0.50 km above,

Table 10. Stomach contents of harlequin ducks collected from Sawmill Bay (#1-2)[1] and from Valdez Arm (#3-5)[2], summer 1980. Values are volume percent of total food.

	esophagus			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
Food item	%	%	%	%	%	%	%	%
Insect								
Diptera			30.0	4.9				
Echinoderm								
Asteroidea (Leptasterias ?)	95.7							
Crustacean								
Decapoda (Pleocyemata)								
Anomura (Paguroidea)					53.1	71.4	25.0	17.2
Brachyura (Brachyrhyncha)					2.8	19.4		
Unidentified Pleocyemata		33.3	60.0					
Isopoda								1.7
Mollusk								
Littorina	2.5	37.8	10.0	90.2	44.1	9.2	43.0	77.6
Mytilus edulis	0.8						26.9	
Macoma balthica		1.1						
Macoma calcarea		3.3						0.9
Unidentified _Macoma_	0.3							
Turbellaria ?	0.7			3.3				
Plants								
Zostera		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

[1] # 1 collected 21 June; # 2 collected 2 July.

[2] # 3-5 collected 22 August.

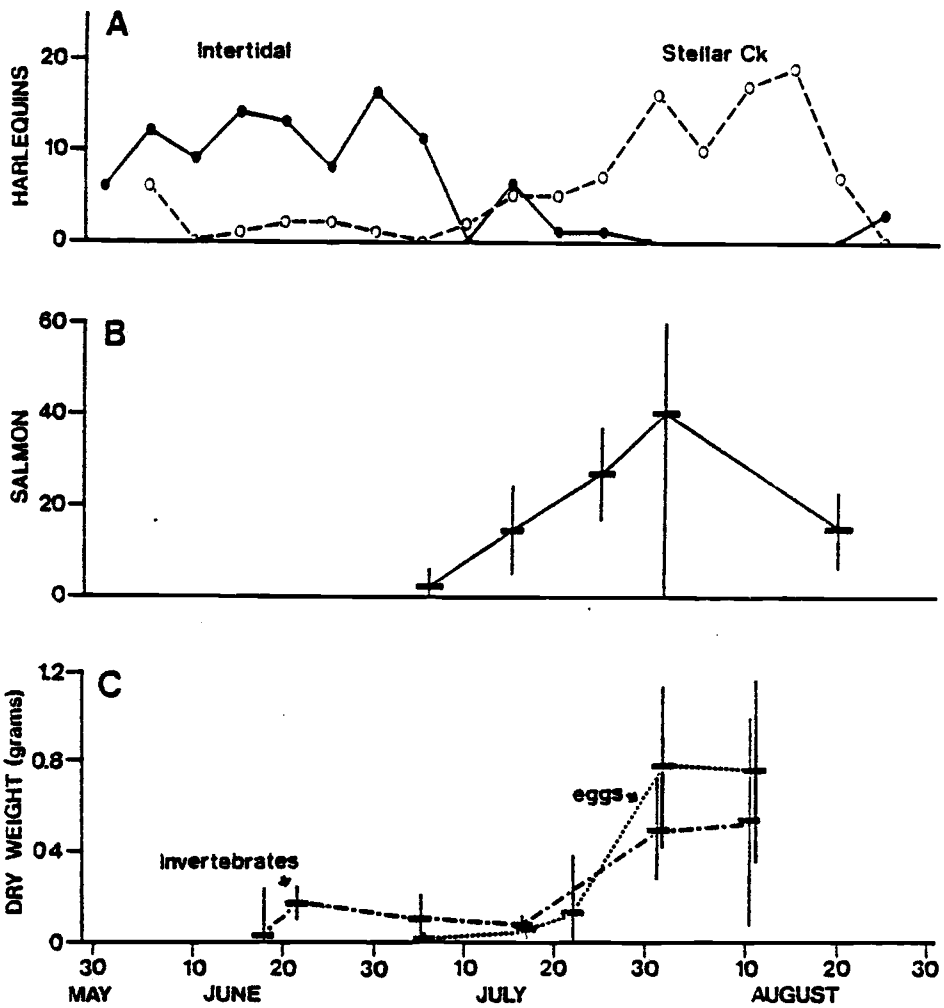


Fig. 19. (A) Peak daily counts of harlequin ducks feeding outside the mouth of Stellar Creek (Intertidal) and in the non-tidal, lower portion of Stellar Creek (Stellar Ck) during 1980.

(B) Mean and 95% C.I. of the index to salmon abundance in lower Stellar Creek during 1980.

(C) Dry weight biomass (mean + 95% C.I.) of invertebrates and salmon eggs collected (per hour) in drift samples from lower Stellar Creek in 1980.

Fault Creek) was 1.33 (SD = 1.48) per 0.25 m^2 on 1 August, and 0.46 (SD = 0.55) per 0.25 m^2 on 11 August. Along two transects through a favored feeding area on 17 August an average of 3.56 (SD = 3.12) eggs were visible per 0.25 m^2 of stream bottom. Harlequins, as well as hundreds of gulls (mostly Larus glaucescens) fed upon these waste eggs as they drifted downstream or where they collected in eddies or lodged behind debris obstacles.

Production

Six different broods were observed a total of 59 times in Sawmill Bay in 1979, while two broods were observed a total of 21 times in 1980. An additional brood of five, class 2c-3 young were observed in Jack Bay on 19 August 1980. Average brood size at fledging in Sawmill Bay was 2.67 (range 1-4) in 1979 and 2.50 (range 1-4) in 1980 (Fig. 20).

Recruitment (young per breeding female, young per known pair, and young per adult female in the population) was estimated as 1.5, 1.1, and 0.8, respectively, in 1979, and only 0.6, 0.4, and 0.3, respectively, in 1980 (Table 11). However, differential reproductive success of marked and unmarked individuals suggested the application of patagial tags may have negatively affected production. For both years combined, 15 paired females were banded and tagged in early spring while 13 pairs were neither banded nor tagged. From these females (which comprised all known, paired females in spring) one tagged (7%) and seven untagged (55%) females were eventually observed with broods. This difference was significant (χ^2 = $P<0.05$; Fisher's

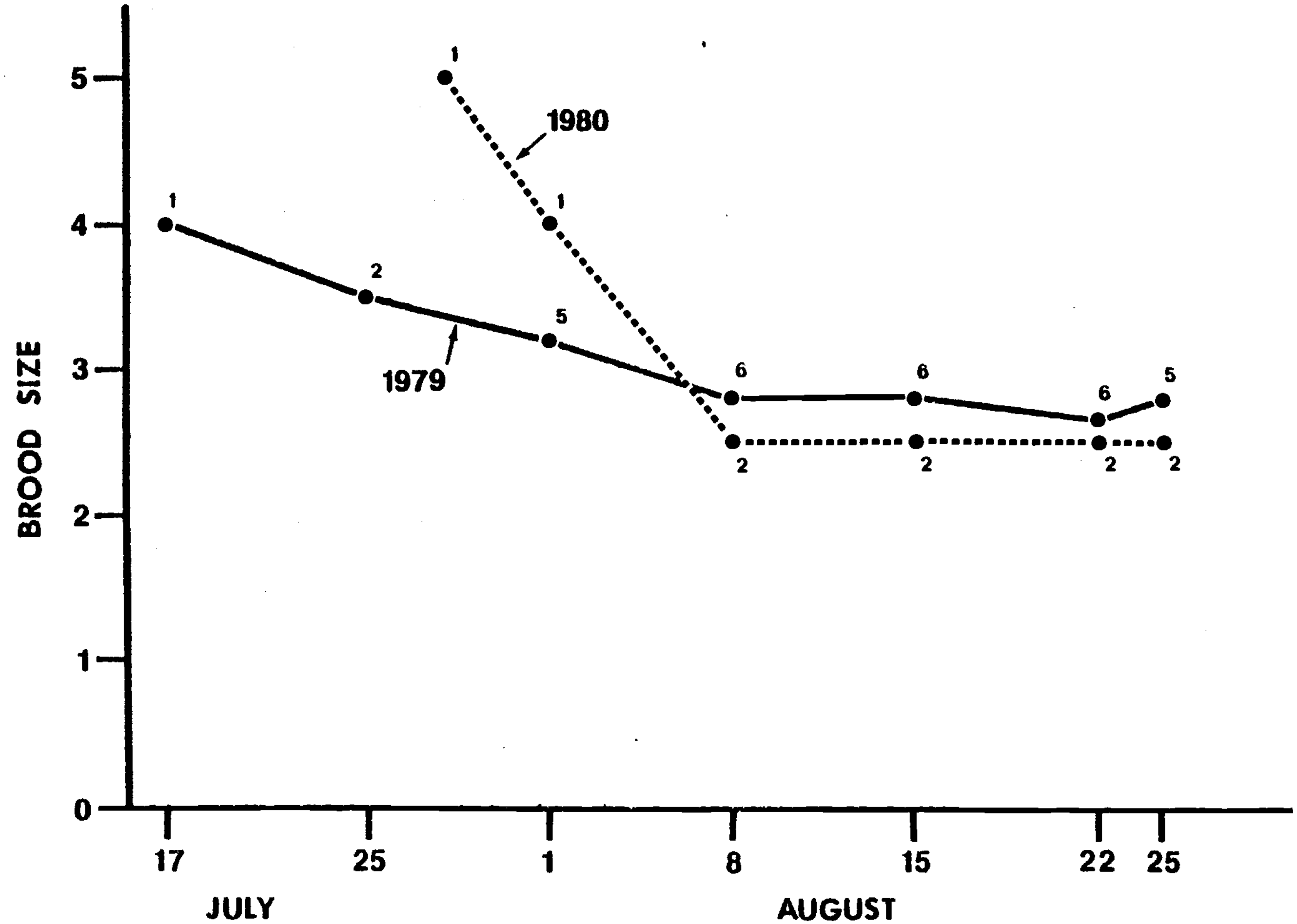


Fig. 20. Average size of all harlequin broods observed in Sawmill Bay during 1979-1980. Numbers indicate the number of different broods observed.

Table 11. Estimation of reproductive success among harlequin ducks in Sawmill Bay, 1979-1980.

		1979	1980
A.	Known pairs (late May early June)	15	14
B.	Post-breeding females[1]	14	14
C.	Post-breeding females with brood patches	33%[2]	43%[3]
D.	Failed-breeding females (B × C)	4.6	6
E.	Females with broods	6	2
F.	Attempted breeders (D + E)	10.6	8
G.	Total young fledged	16	5
	Recruitment		
H.	Young per breeding female (G / F)	1.5	0.6
I.	Young per known pair (G / A)	1.1	0.4
J.	Young per adult female (G / B + E)	0.8	0.3
	Non-breeding frequency		
K.	Non-breeding females (B + E - F / B + E)	47%	50%

[1] The average number of females not tending broods (26 July - 10 August).

[2] 3 of 9 females examined from 2-3 August 1979.

[3] 3 of 7 females examined from 5-14 August 1980.

exact test P = 0.0375). Thus the estimate of recruitment may be biased, and the depressed values (especially in 1980) may be due in part to the cumulative effects of tagging.

The non-breeding frequency among females was estimated as 47% in 1979 and 50% in 1980 (Table 11). However, estimates were based on the assumptions that all failed-breeding females exhibited a brood patch and remained in Sawmill Bay, and that averages of post-breeding censuses accurately reflected the net number of non-breeding females in Sawmill Bay. The non-breeding frequency for 1965-1970 calculated from data reported by Bengston and Ulfstrand (1971:238) from four sites in Iceland was 27.7% (SD = 10.6).

Weights

Mean weights of all male and of all female harlequins captured in early June were similar between years (P>0.10). Mean weights of females captured in July and in early August were also similar between years (P>0.10). Likewise, individual weights of five females and of three males captured on similar dates each year did not differ significantly between years (paired t-test; P>0.10). Consequently, data from both years were combined.

Weights of females changed through the course of each summer (Fig. 21). The mean weight of females was greatest in early June (591 g), approximately corresponding to the initiation of incubation, but was less than the mean weight of males in early June (632 g; P<0.02). Females lost weight through June and reached their minimum weight in July, approximately corresponding to the completion of

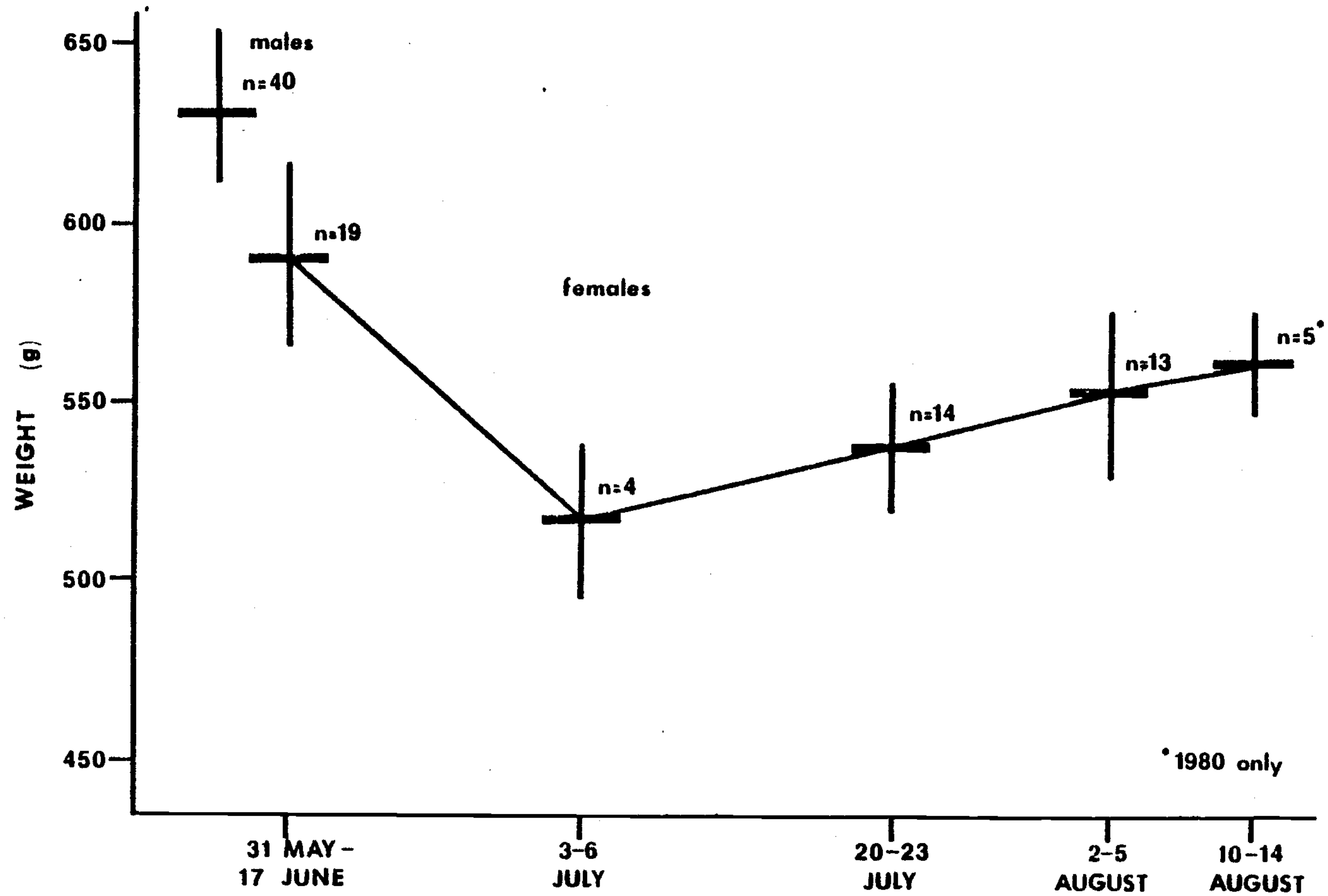


Fig. 21. Weight (mean + 95% C.I.) of all adult male and adult female harlequins captured in Sawmill Bay 1979-1980.

incubation. Female weights increased steadily throughout the remainder of the summer (Fig. 21).

The mean weight of five juvenile males (552 g) captured on 23 August 1979 was about 96% of the mean weight of three adult females tending broods on the same date. The mean weight of two juvenile females (481 g) was 93% of the mean weight of two juvenile males captured simultaneously from the same brood on 10 August 1980. The mean weight of the two juvenile females and of the two juvenile males was, respectively, 85% of (and different from; $P<0.001$) and 91% of (and different from: $P<0.01$) the mean weight of six adult females (568 g) captured between 10-14 August 1980. Standard measurements of all harlequins captured during 1979 and 1980 are given in Appendix 6.

Return rates

Only two individuals were seen in Sawmill Bay in 1980 with patagial tags lasting from 1979. Although nine of 11 birds recaptured in 1980 from 1979 had originally been tagged, only one, a female, retained a tag (on one wing only). Another female (not recaptured in 1980) was last seen on 19 August 1980 still wearing a tag retained from 1979. The large number of banded but untagged ducks in Sawmill Bay in 1980, and the proportion of recaptured individuals which had lost both 1979 tags (89%) clearly indicated that tag loss, and not poor survival, accounted for the paucity of 1979 tags seen in 1980.

The return rate between years was probably fairly high. Eight (30%) of the adult females, and three (30%) of the adult males captured in 1979 were recaptured in 1980. Two of the recaptured males were paired to the same female each year; the mate of the third male escaped capture and was not identified. Two of the eight recaptured females were those paired with the recaptured males. Two others (whose mates were not captured in 1979) were paired with unbanded males in 1980, and the remaining four females were captured following pair break-up both years and hence their mates were never determined. Bengston (1972) and Kuchel (1977) found about half the individuals marked in one year were observed the following year, and they both noted a tendency for some pairs to remain intact between years.

V. DISCUSSION

Use of coastal streams

This study differed from previous investigations of harlequin ducks chiefly in its focus on a population breeding close to the coast. Harlequins nesting along short, coastal streams need not migrate long distances inland, and during the breeding season they face an environment probably different (at least in its proximity to salt water) from that faced by interior nesting harlequins. Consequently, habitat use, feeding strategies, and even limiting factors of coastal breeding harlequins might vary from those of interior breeding harlequins.

Short, coastal streams probably contribute substantially to the annual global production of harlequins. In Alaska, harlequins breed primarily along the coast from southeast Alaska to the Alaskan peninsula (Johnsgard 1975:405), and breeding records from the interior of Alaska are comparatively uncommon (Gabrielson and Lincoln 1959:208). In this study, a relatively large population of harlequins (13-14 spring pairs; 8-11 attempted breeders annually) was associated with Stellar and Fault Creeks, which had a combined, effective length of only about 6 km (1.3 - 1.8 breeders per km). Similarly, harlequins bred on 4 of 9 short, coastal streams surveyed in northwest Iceland (Bengston 1972). And of 19 "breeding concentrations" in Iceland known to Gudmundsson (1971:15, 89), eight (42%) were located on first or second order streams within about 5 km of the coast, while four

(21%) were located between approximately 5-25 km from the coast.

The activity of harlequins along Stellar and Fault Creeks was largely cryptic and pointed out the ease with which the presence of harlequins could be overlooked or their numbers substantially underestimated. For example, harlequin pairs apparently did not establish home ranges along Stellar or Fault Creek (prior to nesting) in a manner typical of harlequins along inland streams (see Kuchel 1977). Rather, pairs remained active in Sawmill Bay until (presumably) females began incubating, and both courtship and copulation were observed in the bay. Also, harlequins moving up or down the streams usually did so by flying low along the water at night. Fully 46% of all harlequins captured on Stellar Creek from 31 May - 23 July (the period corresponding to laying and incubation) of both years were caught between 2100 and 0500, even though far less effort was extended towards mist-netting during those hours than during any other period. An additional 39% of all captures occurred between 0500 and 0800, while only 13% of all captures occurred between 0800 and 2100, although the latter period accounted for the majority of trapping effort.

Harlequins in this study depended on Stellar Creek for nearly half to practically all of their feeding activity. Early in the summer harlequins fed largely on marine invertebrates in the intertidal delta of the creek, while later in the summer they moved slightly upstream into the spawning beds of the arriving salmon, where they fed primarily on waste, drifting roe. Incubating females also flew downstream (at least occasionally) to feed in the lowest reaches of Stellar Creek, the intertidal stream delta, or even the coastal bays

(Fig. 9). This pattern was not unique to Sawmill Bay. Six medium gradient, non-glacial salmon streams surveyed in Valdez Arm also had small contingents of harlequins feeding in their outflows or lower reaches, and male harlequins moulting at North Point regularly fed at the outflow of one of those streams. Harlequins at Kanatak and Cold Bay during the summer "frequently...visit the mouths of small streams or ascend them for considerable distances" (Osgood 1904:58). And harlequins breeding along short, coastal streams in northwest Iceland also tended to fly downstream to feed in the stream deltas (Bengston 1972:14).

Bengston (1972:18) suggested harlequin populations "are regulated by the quantity of food available on the breeding grounds." Harlequins breeding along interior streams often concentrate below the outlets of lakes, where detrital output may enhance stream productivity (Gudmundsson 1971:89). Values obtained for (especially) angularity, brightness, and aquatic vegetation in the stream reach inventory indicated that, of the three streams entering Sawmill Bay, Stellar Creek (the stream most used by harlequins) was also the most stable and productive stream, while Twin Falls Creek (least used by harlequins) was the least stable and productive (Appendix 7). However, this result is difficult to interpret as the streams also differed in their gradients (Fig. 5), character of available islands, topography of their outlets, and use by salmon. Furthermore, none of the streams was outstandingly productive; repeated "kick" samples (after Frost et al. 1971) in each of the streams both years produced negligible amounts of invertebrates (generally <0.001 g dry weight of invertebrates per sample). The small lake located on Stellar Creek did not attract harlequins below its outlet; rather, harlequins seemed attracted to the lake itself, probably for its dense willow and alder "mangrove" border, which offered cover and (perhaps) nesting habitat. Harlequins were several times observed loafing on the lake, and in 1979 a tagged female successfully raised a brood on the lake. Similarly, harlequins along McDonald Creek in Montana selected oxbow ponds for brood-rearing, and for foraging during periods of high run-off (Kuchel 1977:55).

Harlequin nesting grounds in Iceland often coincide with Atlantic salmon (Salmo salar) spawning grounds, and Gudmundsson (1971: 89) suggested that harlequin ducklings and salmon fry may depend upon similar prey. Unlike Atlantic salmon, however, the fry of pink and chum salmon (prevalent in this study) usually do not feed in freshwater streams as short as Stellar Creek, but move to the sea the first night following emergence (Scott and Crossman 1973). Undoubtedly, the primary attraction of the salmon spawning grounds for the harlequins in this study was the loose, drifting roe they consumed, rather than the endogenous invertebrates. Thus the low productivity typical of coastal streams may be offset for harlequins by the seasonal influx of anadramous fish, and (or) where they have the capacity to make daily feeding flights to the sea, by the relative abundance of food in the intertidal stream deltas. Although this study neither supports nor refutes Bengston's (1972) suggestion that harlequins are limited by food during the breeding season, it does point out that the manner of that limitation might be very different in coastal *vs* interior streams.

Production

Harlequins examined during both summers appeared to be in excellent condition. The change in body weight through the summer exhibited by females (Fig. 21) probably reflected only normal changes in body composition and nutrient reserves through the reproductive cycle, and was similar to patterns found in Canada geese (*Branta canadensis minima*) (Raveling 1979), American eiders (*S. m. dresseri*) (Korschgen 1977), and mallards (*Anas platyrhynchos*) (Krapu 1981).

The low production estimates obtained each year (especially considering possible tagging effects: pg 57) may be characteristic of harlequin populations. Both Kuchel (1977:73) and Bengston (1972: 12) reported average brood sizes at fledging larger than those found in this study. However, for 20 August 1974 and 1975, Kuchel (1977:75) indicated the mean brood size of all known broods was approximately 3.0 and 2.0, respectively. And Bengston (1972:12) reported an average brood size of slightly less than 3.0 among broods of "half-grown to large" ducklings from 1966-1970; he attributed increased brood size in older broods to the abandonment of young by some females and their consequent adoption into other broods, a phenomena he had earlier discounted (Bengston 1966:93), that Kuchel (1977) refuted, and which I never observed.

Along McDonald Creek in Montana, late run-off and high water was correlated with low production of young, possibly through nest washout and juvenile mortality (Kuchel 1977). In this study, precipitation and stream discharge was greater in 1980 than in 1979, and may have contributed (along with tagging effects: pg 57) to the reduced production recorded in 1980 vs 1979. Generally, however, hatching in Sawmill Bay coincided with high water levels, and brood-rearing occurred through the late summer period of decreasing (albeit fluctuating) water levels. Broods were first observed in lower Stellar Creek about the time water levels dropped substantially and the influx of spawning salmon had occurred.

Predation on ducklings was insignificant in Iceland (Bengston 1972:11), and Kuchel (1977) had no data regarding predation in Montana. Data regarding predation are also lacking in this study; however, mink (*Mustela vison*) and river otter (*Lutra canadensis*) were abundant along Stellar, Fault, and Twin Falls Creeks and could potentially have been important predators of harlequins. Bald eagles (*Haliaeetus leucocephalus*) were numerous in Sawmill Bay and along the creeks but often fed on salmon in immediate proximity to harlequins without evoking any response from the ducks. In fact, one roost site regularly used by harlequins was adjacent to (<50 m from) an eagle nest active both years. Twice in 1980, however, 2-3 year old bald eagles elicited escape responses from harlequins when they unsuccessfully stooped on individuals feeding in the intertidal delta of Stellar Creek.

Patterns of habitat use

Harlequins in Sawmill Bay spent most of their time near small islands and off-shore rocks or in the intertidal portions and lower reaches of Stellar Creek. The upper reaches of the stream were used significantly only by incubating females, although males occasionally accompanied females into the upper creeks for periods of several minutes or hours early in the nesting season. Lee waters, used primarily by pairs during the prenesting and laying period, appeared to serve mostly social functions of spacing, and avoidance (by pairs) of pursuit by bands of unpaired males. Lee waters were not noticeably selected for either feeding or resting.

Following nesting, males from Sawmill Bay generally retreated to comparatively exposed moulting areas (off-shore rocks, broken islands, and isolated boulder beaches) in Valdez Arm. Moulting males at North Point and in Jack Bay fed mostly at the outflow of nearby, relatively unsheltered salmon streams.

Females, which retained their ability to fly throughout July and most of August, tended to band together near sheltered streams (e.g. Stellar Creek) where drifting roe was abundant. However, after mid-August, females (which were then approaching flightlessness) also deserted the sheltered bays and streams for more exposed sites in Valdez Arm. Possibly, exposed sites offered greater security to moulting harlequins than did sheltered sites. In fact, exposed sites appeared to be preferred in general except where sheltered sites offered nesting or unusually good feeding opportunities.

A possible bias was introduced in this study because harlequins not present in Sawmill Bay or along the lower portions of the streams could not ordinarily be accounted for during habitat use censuses or during activity budget observations. Harlequins not observed in the bay might have been in the upper portions of the creeks (which were not regularly censused) or in other coastal locations outside Sawmill Bay (e.g. Valdez Arm, Galena Bay, etc.). But only incubating females frequented the upper streams (and neither habitat use nor activity budgets were determined for them). Further, harlequins outside Sawmill Bay were consistently found in areas where a medium gradient, non-glacial salmon stream (or alternatively a shallow, reefy area supporting extensive kelp beds) was adjacent to or near a group of small islands or isolated off-shore rocks. Thus the habitat elements of greatest importance to harlequins in Sawmill Bay were common to most sites outside the bay where harlequins occurred, and their activities and patterns of habitat use appeared subjectively to correspond to those found in Sawmill Bay.

Activity budgets

The seasonal and sexual differences in activity budgets of harlequins probably corresponded to changing energetic requirements of reproduction, maintenance, and moulting. Female ducks may compensate for the demands of egg production during prelaying and laying by altering the composition of their diet (Krapu and Swanson 1975) and by increasing their time spent feeding (Dwyer 1975; Dwyer and Janke 1979). Meanwhile, males may facilitate their mate's increased foraging through territorial defense (primarily alert and interactive behavior) while reducing their own feeding and resting time (Ashcroft 1976). The activity patterns exhibited by harlequins in this study can be interpreted similarly.

Compared to some other species of waterfowl (Afton 1979; Dwyer 1975; Miller 1976; Ryan and Dinsmore 1976; Siegfried 1974), harlequins spent a relatively small portion of their day feeding. This difference can be partly explained by definitions used for the term "feeding," which here was applied more restrictively than is often the case. For example, harlequins frequently searched for food (presumably) by swimming and "peering" (i.e. inserting the bill and eyes vertically into the water). In this study, peering was considered a form of locomotion and was thus distinguished from feeding. Also, only 62-76% of pairs attempted to breed (Table 11). But because observations were randomly obtained, it was inevitable that some non-breeders were included in the activity budgets for pairs. If non-breeding pairs actually fed less intensively than did pairs attempting to breed, then the feeding rates obtained here would be lower than actually occurred among breeding pairs, and conversely, resting rates would be somewhat inflated.

Whereas some prairie nesting dabbling ducks feed actively at night (Swanson and Sargeant 1972), harlequins, like eiders (see Peterson 1980:105) apparently do not (Johnsgard 1975:411). Nighttime darkness extended only from about 2300-0400 during early summer in Prince William Sound, and individually tagged harlequins were often observed leaving the same roost site in the morning as they had occupied the previous evening (suggesting no nighttime activity had occurred). Assuming that during nighttime harlequins only rested, then paired males and females, respectively, spent about 13.8 and 12.8 hr/day resting, while they spent, respectively, 2.4 and 4.0 hr/day feeding. Unpaired males and females rested for 18.2 and 17.7 hr/day, respectively, and spent 2.0 and 2.6 hr/day feeding, respectively.

Ettinger and King (1980) argued that the reduced time spent foraging (<5% of daily time) by willow flycatchers (*Empidonax traillii*) was a result of selection for survival during periods of "stringency." The large proportion of time willow flycatchers devoted to loafing acted as a buffer which minimized variations in daily energy expenditure between phases of the breeding cycle. 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 large proportion of time which harlequins spent resting would be one expected result of such a strategy.

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VII. APPENDIX

Appendix 1. Climatic data for Valdez, Alaska. From Ancn. (1979) and Anon. (1980).

AVG. TEMPERATURE (°F)

Year	Jan	Feb	Mar	Apr	May	June	July	Aug	Sept	Oct	Nov	Dec	Annual
1972	12.0	19.0	20.7	28.8	41.6	49.3	58.8	58.0			28.4	19.2	
1973	13.5	21.2	31.0	38.2	44.0	50.2	53.9	51.3	45.9	36.8	22.8	23.1	36.0
1974	14.6	21.1	26.9	37.5	47.2	52.5	54.7	55.2	49.5	38.1	33.3	25.1	37.7
1975	19.6	21.1	27.6	35.3	44.0	50.2	55.3	54.5	46.5	37.3	23.4	19.7	36.2
1976	22.3	19.4	29.0	36.5	43.6	52.8	55.6	53.6	46.2	36.7	33.7	28.2	38.1
1977	30.5	32.0	30.1	36.2	42.9	51.3	55.7	54.9	48.3	40.9	24.4	19.0	38.9
1978	26.7	28.8	31.9	39.7	46.2	50.5	52.8	55.3	48.4	38.3	29.4	24.7	39.4
1979	25.1	15.5	31.8	38.4	46.2	51.3	55.6	54.4	49.8	41.5	33.1	19.3	38.6
1980	21.1	29.8	31.5	39.5	44.9	51.3	54.6	51.9					
Mean	20.6	23.1	28.9	36.7	44.5	51.0	55.2	54.4	47.8	38.5	28.2	22.3	37.5

PRECIPITATION (in.)

Year	Jan	Feb	Mar	Apr	May	June	July	Aug	Sept	Oct	Nov	Dec	Annual
1972	1.76	2.66	3.61		4.35	2.78	1.44	3.19			6.85	1.52	
1973	4.63	3.07	3.43	3.75	2.51	3.22	1.68	9.35	2.78	4.35	2.43	3.35	44.55
1974	0.01	5.21	1.55	5.93	0.79	2.08	2.34	4.22	7.59	12.90	9.78	6.42	58.82
1975	5.24	3.98	2.00	5.42	1.95	2.74	4.30	3.41	12.83	5.51	0.42	6.36	54.16
1976	7.00	2.27	3.80	5.47	2.53	1.00	1.87	3.03	12.58	9.53	20.59	8.29	77.96
1977	11.76	7.95	3.45	8.11	2.89	1.81	2.24	2.50	12.53	5.81	0.70	2.66	62.41
1978	4.18	6.18	2.14	1.25	2.14	3.28	3.81	2.17	4.94	15.38	3.27	6.07	54.81
1979	2.66	1.00	9.99	1.09	1.09	2.91	6.04	6.20	8.05	15.43	13.32	5.14	73.42
1980	8.56	9.64	3.27	2.90	3.32	3.22	7.70	6.72					
Mean	5.09	4.66	3.70	4.24	2.40	2.56	3.50	4.53	8.76	9.84	7.23	4.98	59.68

SNOWFALL (in.)

Season	July	Aug	Sept	Oct	Nov	Dec	Jan	Feb	Mar	Apr	May	June	Total
1972-73	0.00	0.00			64.6	25.4	83.2	48.7	46.6	10.1	T	0.0	278.6
1973-74	0.00	0.00	0.00		26.7	40.3	T	77.8	22.4	15.0	0.0	0.0	182.2
1974-75	0.00	0.00	0.00	10.8	38.2	90.6	90.3	65.8	37.4	29.0	1.8	0.0	363.9
1975-76	0.00	0.00	0.00	14.7	6.8	84.1	96.1	33.2	75.5	40.6	T	0.0	351.0
1976-77	0.00	0.00	0.00	25.8	44.7	101.5	54.0	26.2	52.9	71.4	2.8	0.0	379.3
1977-78	0.00	0.00	0.00	0.6	17.5	41.2	32.4	75.9	27.8	0.7	0.0	0.0	196.1
1978-79	0.00	0.00	0.00	19.8	28.0	82.2	45.6	12.1	112.6	12.0	T	0.0	312.3
1979-80	0.00	0.00	0.00	T	31.8	105.5	37.3	86.5	36.4	3.9	0.0	0.0	301.4
Mean	0.00	0.00	0.00	12.0	32.3	71.4	54.9	53.3	51.4	22.8	0.6	0.0	295.6

Weather type	1979				1980			
# of days of:	May	June	July	Aug	May	June	July	Aug
Precip. >0.01 in.	17	15	23	14	22	17	17	22
light fog	6	9	13	12	7	8	10	14
heavy fog	0	0	8	9	0	0	5	6
Clear	2	5	3	6	1	2	3	4
Partly cloudy	8	3	5	5	2	4	5	3
Cloudy	21	22	23	20	28	24	23	19

Appendix 2. Number of adult (Ad), yearling (Yr), and juvenile (Juv) harlequin ducks captured and marked in Sawmill Bay, 1979-1980.

	Males			Females		
	Ad	Yr	Juv	Ad[1]	Juv	Total
Number captured in 1979	10	1	5	27	1	44
New captures in 1980	10	1	2	15	2	30
Sub-total	20	2	7	42	3	74
1979 recaptures in 1980	3	—	—	8	—	11
Total	23	2	7	50	3	85
Number marked in 1979	10	1		20		31
Number marked in 1980	13[2]	1		11		25
Total	23	2		31		56

[1] Includes yearlings.

[2] Exceeds the number of new individuals captured in 1980 because the three males recaptured from 1979 were re-tagged.

Appendix 3. Parameters used in the stream reach inventory (taken or modified from Phankuch (1975).

Flow type: Still water, riffles, rapids, or waterfalls.

Islands: The number of islands in each reach.

Rocks: The number of rocks (per 10 m) suitable for loafing sites.

Angularity: The "roundness" of substrate rocks, on a scale of 1-4. 1 = rocks with sharp edges and corners and with rough plane surfaces. 4 = smooth, well-rounded rocks. Roundness indicates a dynamic, moving substrate.

Brightness: The "polish" of substrate rocks, on a scale of 1-4. 1 = darkened or stained substrate denoting algal growth or organic stains. 4 = >85% of the substrate was bright, suggesting substrate tumbling or scouring.

Aquatic vegetation: The abundance of aquatic vegetation, on a scale of 1-4. 1 = abundant, perennial growths even in fast water. 4 = scarce or absent perennial growths and only short-term, yellow-green blooms.

Slope: Percent slope of adjacent streambanks in four categories: 1 = <30%; 2 = 30-40%; 3 = 40-60%; 4 = >60%.

Vegetation density: The density of streamside vegetation, on a scale of 1-4. 1 = >90% of soil covered with vegetation showing vigor, variety, and a deep root mass. 4 = <50% of ground covered with vegetation of low vigor and only a shallow root mass.

Appendix 4. Chi-square comparisons of activity budget observations recorded for harlequins in Sawmill Bay, Alaska, summer 1979-1980. Refer to Tables 4-5 in text. The larger of the two means is indicated ($P<0.005$). - = the means were not significantly different.

	Activity					
	Rest	Feed	Locom	Preen	Alert	Inter
Paired males						
St vs Rk[1]	Rk	St	St	Rk	-	St
St vs Lee	Lee	St	-	Lee	-	St
Rk vs Lee	Rk	Lee	Lee	Rk	Rk	-
Paired females						
St vs Rk	Rk	St	St	Rk	-	St
St vs Lee	Lee	St	-	Lee	-	-
Rk vs Lee	Rk	Lee	Lee	Rk	Rk	-
Unpaired males						
St vs Rk	Rk	St	St	-	Rk	-
Unpaired females						
St vs Rk	Rk	St	St	St	St	-

[1] St = Stellar Creek; Rk = Rocks and headlands; Lee = Lee waters.

Appendix 5. Chi-square comparisons of activity budget observations recorded for harlequins in Sawmill Bay, Alaska, summer 1979-1980. Refer to Tables 4-5 in text. The larger of the two means is indicated (P<0.005). - = the means were not significantly different.

	Activity					
	Rest	Feed	Locom	Preen	Alert	Inter
Stellar Creek						
PM vs PF[1]	PM	PF	-	-	-	PM
UM vs UF	UF	UM	UM	-	UF	-
Rocks						
PM vs UF	-	-	-	-	-	PM
UM vs UF	UF	UM	UM	UM	-	-
Lee						
PM vs PF	PM	PF	-	-	-	-
Stellar Creek						
PM vs UM	PM	UM	-	-	-	PM
PF vs UF	UF	PF	PF	-	UF	PF
Rocks						
PM vs UM	UM	PM	PM	PM	-	PM
PF vs UF	UF	PF	PF	PF	-	-

[1] PM = paired male; PF = paired female; UM = unpaired male; UF = unpaired female.

Appendix 6. Measurements of harlequin ducks captured in Sawmill Bay, 1979-1980.

		Culmen (mm)	Wing Chord (cm)	Total Tarsus (mm)
Adult male	n	21	17	21
	$\bar{X}$	27.7	27.4	45.8
	Range	26.3 - 29.7	23.9 - 28.7	41.2 - 49.0
	SD	1.10	1.08	1.54
Adult female	n	42	34	37
	$\bar{X}$	26.3	26.4	44.2
	Range	21.9 - 28.0	25.3 - 27.7	38.6 - 47.2
	SD	1.29	0.73	1.46
Yearling male	n	2	2	2
	$\bar{X}$	27.6	25.5	45.8
	Range	26.7 - 28.5	25.4 - 25.5	43.9 - 47.7
	SD	1.31	0.07	2.65
Juvenile male (10 Aug. 1980)	n	2	2	2
	$\bar{X}$	25.4	24.0	44.4
	Range	25.3 - 25.5	23.4 - 24.6	42.5 - 46.3
	SD	0.14	0.85	2.65
Juvenile female (10 Aug. 1980)	n	2	1	2
	$\bar{X}$	24.7	23.0	43.7
	Range	24.1 - 25.3	-	43.6 - 43.9
	SD	0.81	-	0.21
Juvenile male (23 Aug. 1979)	n	5	-	-
	$\bar{X}$	26.0	-	-
	Range	25.7 - 26.4	-	-
	SD	0.30	-	-

Appendix 7. Results of the stream reach inventory conducted along Stellar, Fault, and Twin Falls Creeks during July, 1979. Parameters are described in Appendix 3.

Stellar Creek

Reach (km)	Flow	Is	Rock	Ang	Brt	Ag Veg	Slope	Veg Dens
0.15	rif	0	0.5	3.00	3.00	3.00	1	2.00
0.15	rif	3	0.5	3.25	3.00	2.00	1	2.25
0.05	rif	1	3	2.50	3.00	2.00	1	1.75
0.10	rap	1	4	3.00	2.00	2.00	4	3.00
0.10	rif	0	2	2.50	3.00	2.00	4	2.50
0.10	rap	0	6	3.00	2.50	2.00	3	2.50
0.10	rap	0	8	3.00	3.50	3.00	4	3.25
0.15	rap	0	5	3.00	2.00	2.00	4	3.00
0.05	fall	5	8	3.00	4.00	3.50	4	2.50
0.10	fall	0	15	3.00	3.00	2.50	4	3.38
0.20	fall	many	5	2.00	2.00	2.00	3	2.00
0.10	rif	0	0	2.00	1.50	2.00	3	2.25
0.05	lake	0	0	-	2.00	2.50	4	2.50
0.45	rif	0	0	2.00	2.50	2.50	1	2.50
Total: 1.85								
Weighted mean:			3.2	2.57	2.56	2.34		2.50

Appendix 7. (continued)

Fault Creek

Reach (km)	Flow	Is	Rock	Ang	Brt	Ag veg	Slope	Veg Dens
0.20	rif	0	5	3.00	3.00	2.00	1	2.00
0.50	fall	0	4	2.50	3.50	3.00	4	3.00
0.20	rap	1	3	3.00	3.50	2.50	4	4.00
0.30	fall	1	10	3.00	3.50	4.00	4	3.50
0.40	fall	0	12	3.00	4.00	4.00	4	3.50
0.20	rif	0	4	3.00	2.50	1.75	3	2.75
0.30	rap	4	6	3.00	3.00	2.00	2	2.00
Total: 2.10								
Weighted mean:			6.7	2.88	3.38	2.93		3.00

Appendix 7. (continued)

Twin Falls Creek

	Reach (km)	Flow	Is	Rock	Ang	Brt	Aq Veg	Slope	Veg Dens
	0.15	rif	2[1]	0	3.50	4.00	4.00	1	2.50
	0.15	rif	0	0	3.50	4.00	4.00	1	2.00
	0.40	rif	0	0	3.50	4.00	4.00	3	2.50
	0.20	rif	0	0	3.50	4.00	4.00	1	2.25
	0.15	rap	0	0	3.50	4.00	4.00	1	2.00
	0.05	rif	1[1]	0	3.50	4.00	4.00	1	2.25
	0.10	rif	1[1]	0	3.50	4.00	4.00	2	2.25
	0.40	rap	0	0	3.00	4.00	4.00	1	2.50
	0.05	rap	0	2	3.00	3.00	2.50	4	2.25
	0.55	fall	0	5	3.00	3.50	3.00	4	4.00
Total:	2.20								
Weighted mean:				1.3	3.27	3.85	3.72		3.72

[1]gravel, sparsely vegetated islands.