

THE UNIVERSITY OF MANITOBA

AT-SEA BIOLOGY
OF THE
MARBLED MURRELET (Brachyramphus marmoratus)
IN BARKLEY SOUND, BRITISH COLUMBIA
by

HARRY R. CARTER

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A thesis submitted to the Faculty of Graduate Studies of
the University of Manitoba in partial fulfillment of the requirements
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MASTER OF SCIENCE

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ABSTRACT

The at-sea biology of the Marbled Murrelet (Brachyramphus marmoratus [Gmelin]) was studied in Barkley Sound, on the west coast of Vancouver Island, British Columbia in 1979 and 1980. The number and distribution of murrelets feeding at sea were determined from boat surveys in offshore, inshore and nearshore habitats. The murrelets' breeding phenology and diet were determined mainly by examining stomach contents, brood patches, and molt of collected birds, and identifying fish being held in adults' bills, intended for their young. The feeding ecology and distribution of murrelets at sea during the breeding and molting seasons were related to the distribution and availability of prey, as synthesized from the literature (Chapter 1). Further censuses at sea were used to examine: daily patterns of movements and distribution relative to foraging behavior during the nestling period (Chapter 2); and the dispersion of murrelets relative to foraging and social (flocking) behavior during the nestling period (Chapter 3).

The diet of breeding and molting Marbled Murrelets consisted mainly of larval and juvenile Pacific Herring (Clupea harengus) and Pacific Sandlance (Ammodytes hexapterus). Murrelets aggregated above clumped prey in south Trevor Channel during the nestling period. This aggregation occurs each breeding season probably because the food supply there is abundant and reliable throughout the nestling period. Murrelets flew directly to and aggregated in south Trevor Channel each morning. Birds apparently learned the location of this feeding area and sites within it because large numbers of birds clumped there in the same

pattern each day. Although clumped in the feeding area, murrelets fed solitarily, mainly in singles and flocks of 2 birds, even when they were in high density. In the afternoon and evening, birds foraging for their nestlings left the aggregation and flew to other feeding areas presumably to obtain larger fish (mainly sandlance) which they delivered to nestlings mainly at night.

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GENERAL INTRODUCTION

Recent reviews of the evolution of life-history tactics have suggested that a tactic evolves as a "set of coadapted traits designed, by natural selection, to solve particular ecological problems" (Stearns 1976, 1980). The marine bird family Alcidae has been examined extensively in regard to the diversity of life-history tactics found in it. Since all species in this family are marine, restricted to the Northern Hemisphere, feed individually by capturing single prey organisms underwater (propelled by their wings), lay clutches of 1 or 2 eggs, delay maturity, are long lived, and occupy an ecological zone with few other competitors, alcid tactics have evolved through adaptive radiation related largely to their different means of exploiting marine food sources (Bédard 1969). This radiation has resulted in 22 extant species of 11 genera (A.O.U. 1983). As well, the Great Auk (Pinguinus impennis) became extinct in historical times (Orton 1870) and others have been described from the fossil record (e.g., Howard 1976). The radiation of alcid traits involves a range of body size (90-5000g), bill morphology (plankton and/or fish feeding), molting patterns (gradual to simultaneous), and post-hatching developmental patterns (semi-precocial to precocial development) (Stresemann and Stresemann 1966; Bédard 1969; Sealy 1972, 1973; Birkhead 1976). The comparative approach of examining life-history tactics has been useful for interpreting several diverse breeding adaptations in alcids. Cody (1973) attempted to identify alcid tactics by grouping traits and noted that offshore-feeding alcids tend to be smaller, feed on plankton, nest in burrows, and have 24-72 h nocturnal incubation shifts to provide time for long distance movements while inshore-feeding alcids tend to be larger, feed on fish, nest in

more open locations, and make several trips to the nest during daylight. Offshore feeders, therefore, bring fewer, but larger loads of food in modified bills to slower-growing young, while inshore feeders bring many, smaller packages in less modified bills to faster-growing young. As Bédard (1976) pointed out, however, no clearcut gradation exists for any one trait, let alone foraging distance from shore, and no species has either of these combinations of life-history traits. The use of the comparative approach to examine alcid life-history tactics is further limited by the feasibility of directly studying many aspects of their biologies, especially the relationship between feeding and breeding which underlies the evolution of alcid tactics.

The Marbled Murrelet [Brachyramphus marmoratus (Gmelin)] was singled out by Cody (1973) as an obvious anomaly when patterns of life histories in the Alcidae were considered. It is a small, fish- and plankton-feeding alcid with a 24 h nocturnal incubation shift, yet feeds exclusively inshore. It nests solitarily in trees, on the open ground or in cavities on the mainland and islands (Day et al. 1983; Sealy and Carter, in press; Johnston and Carter, in press), unlike most other alcids which nest colonially on islands in burrows, crevices or on cliff ledges. Although Marbled Murrelets range widely along the coasts of the North Pacific Ocean (Sealy et al. 1982), the first authenticated nest of this species was not found until 1959 in Alaska (Day et al. 1983). Since then, only 7 other nests have been found in Alaska (Simons 1980, Hirsch et al. 1981, Day et al. 1983), California (Binford et al. 1975), Japan (The Ornithological Society of Japan 1975) and the U.S.S.R. (Kuzyakin 1963). Its breeding and feeding biologies hitherto have been examined by the collection and observation of birds at sea (Sealy 1972;

1974; 1975a, b). Because information on Marbled Murrelets at their nest sites is difficult to obtain, it has not been possible to compare most aspects of its breeding biology with other alcids, and its life-history tactic has not been examined in depth. The inshore distribution of Marbled Murrelets, on the other hand, facilitates studying them at sea and provides the opportunity to interrelate more directly their feeding and breeding biologies. The attainment of this objective, however, is hampered by the little knowledge available on its breeding biology.

The aims of this study are three-fold: in Chapter 1, the feeding ecology and distribution of Marbled Murrelets at sea are related to the breeding phenology, marine habitat and distribution of prey in Barkley Sound, British Columbia during the breeding season; in Chapter 2, daily patterns of movements and distribution at sea are related to foraging behavior during the nestling period; and, in Chapter 3, the dispersion of Marbled Murrelets at sea is related to foraging and social (flocking) behavior during the nestling period. With this study, knowledge of the diversity of alcid life-history tactics is furthered. As well, new techniques for and the potential of at-sea studies for interrelating feeding and breeding biologies is explored.

CHAPTER I

FEEDING ECOLOGY OF MARBLED
MURRELETS IN BARKLEY SOUND, BRITISH COLUMBIA

INTRODUCTION

Seabirds are marine animals but most knowledge of their life histories has been obtained at their breeding sites on land (Brown 1980). The few studies that have been conducted at sea have concentrated on seasonal patterns of distribution in relation to general features of the marine habitat over large areas of the ocean. The difficulties of studying birds at sea and the vast areas they inhabit have made interrelating their feeding and breeding biologies a laborious task. Nevertheless, this task is important since many aspects of the diverse breeding biologies of seabirds have been interpreted as adaptations to the marine environments that they exploit while feeding (Ashmole 1971). In particular, prey type, distance travelled to obtain prey and the presumed "patchiness" and/or unpredictability of prey resources have been considered to be the major selective forces in the evolution of seabirds (Lack 1967, 1968; Pearson 1968; Bedard 1969; Ashmole 1971; Sealy 1972, 1973, 1975a; Cody 1973; Diamond 1978; Gaston and Nettleship 1981).

The Marbled Murrelet is distributed in coastal waters within a few km of shore throughout the year (Sealy and Carter, in press). The accessibility of local populations in relatively small areas at sea permits one to study aspects of their at-sea biology more easily than many other alcid species. In this chapter, I examine aspects of the feeding ecology of Marbled Murrelets in Barkley Sound, British Columbia. I focus mainly on the relationship between their diet, at-sea distribution and breeding phenology in this locality.

STUDY AREA

Barkley Sound is an embayment about 25 km wide and 20 km long located on the southwestern coast of Vancouver Island, British Columbia (Fig. 1). The Sound opens onto the Pacific Ocean across a 60-80 km wide portion of the continental shelf (Thomson 1981). The coastlines of the Sound and surrounding lands are heavily forested and mountainous (Sealy and Carter, in press). Several fiords lead into, widen and coalesce to form Barkley Sound which is also continuous with glacially eroded basins on the inner continental shelf (Figs. 1-3). The Broken Group and Deer Group islands divide the Sound into 3 channels, which comprise most of the marine habitat in the Sound. Each channel exhibits the characteristic sill and basin bathymetry of fiords (Matthews and Heimdal 1980): Trevor Channel has the shallowest sill (30-40 m) and the deepest basin (100+ m); Imperial Eagle Channel has the deepest sill (70 m) and a basin of intermediate depth (70-100 m); Loudoun Channel has a sill of intermediate depth (40-50 m) and the shallowest basin (30-50 m) (Fig. 3). The sill in Trevor Channel is the most distinct and unbroken, unlike the sills in Imperial Eagle and Loudoun channels. The sills mark general boundaries between nearshore (channel and inlet) and inshore (inner part of the continental shelf) waters in Barkley Sound. Sills are largely deposits of sand and gravel, while bottom sediments of the channels, fiords and around islands are primarily mud (Fig. 4).

Fig. 1. Location of Barkley Sound relative to major geographic areas in coastal British Columbia. Other localities refer to aggregations of Marbled Murrelets in Table 10.

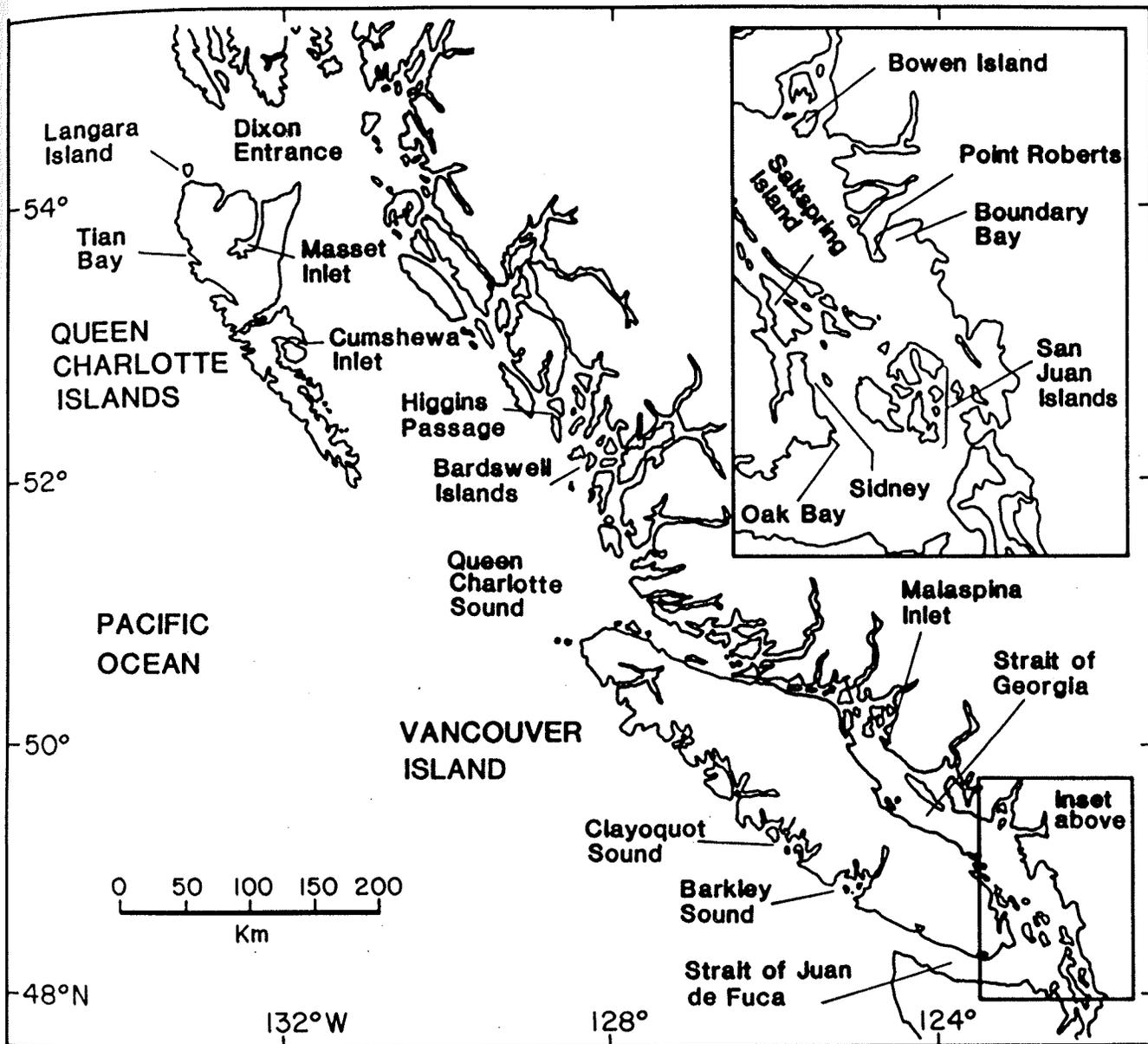


Fig. 2. Place names in Barkley Sound mentioned in the text.

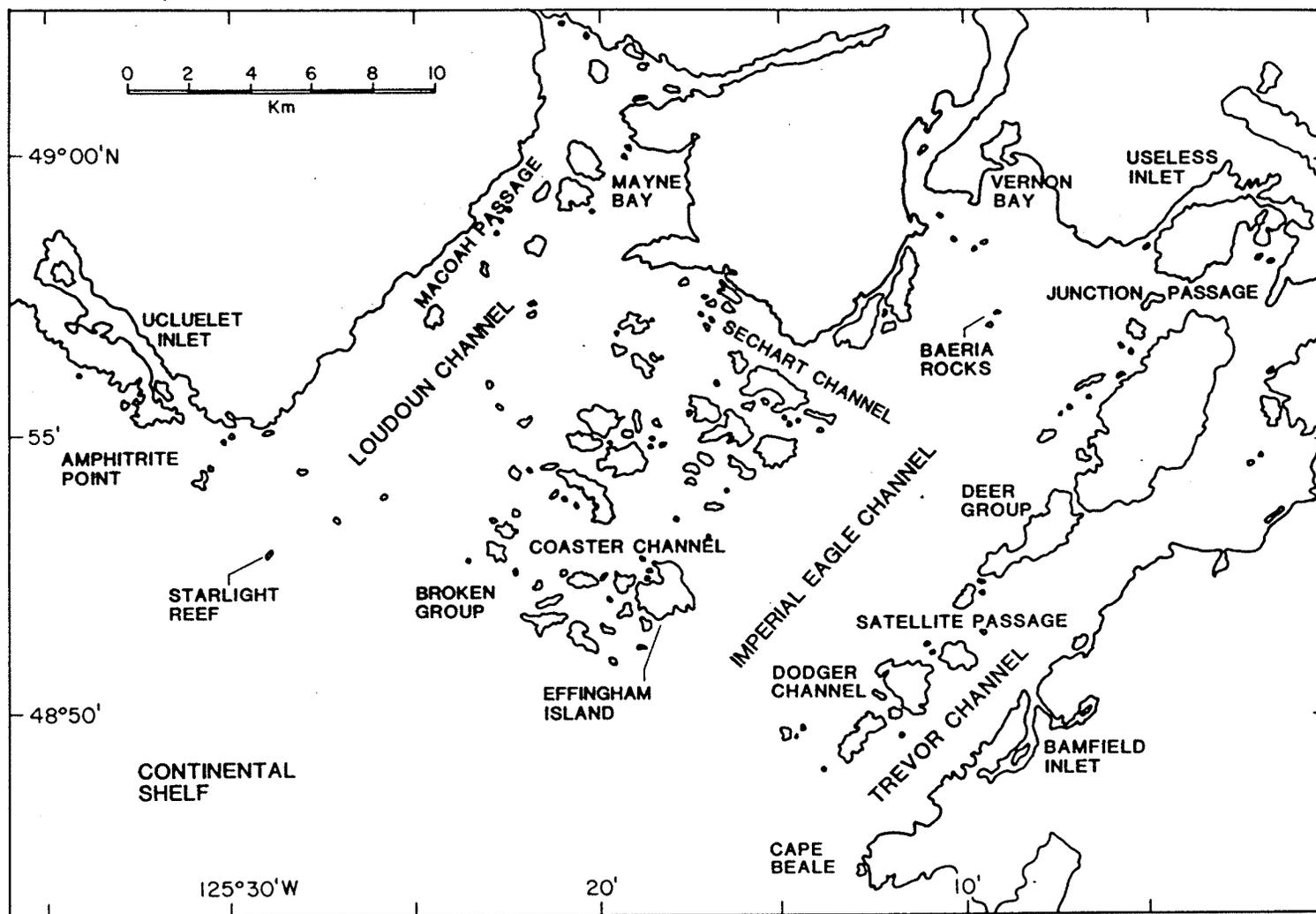


Fig. 3 Major submarine topographic features in Barkley Sound (depths in m). Thick lines indicate bottom contours which show the locations of sills. Dotted areas indicate major passages between Loudoun, Imperial Eagle and Trevor Channels. Striped areas indicate fiords.

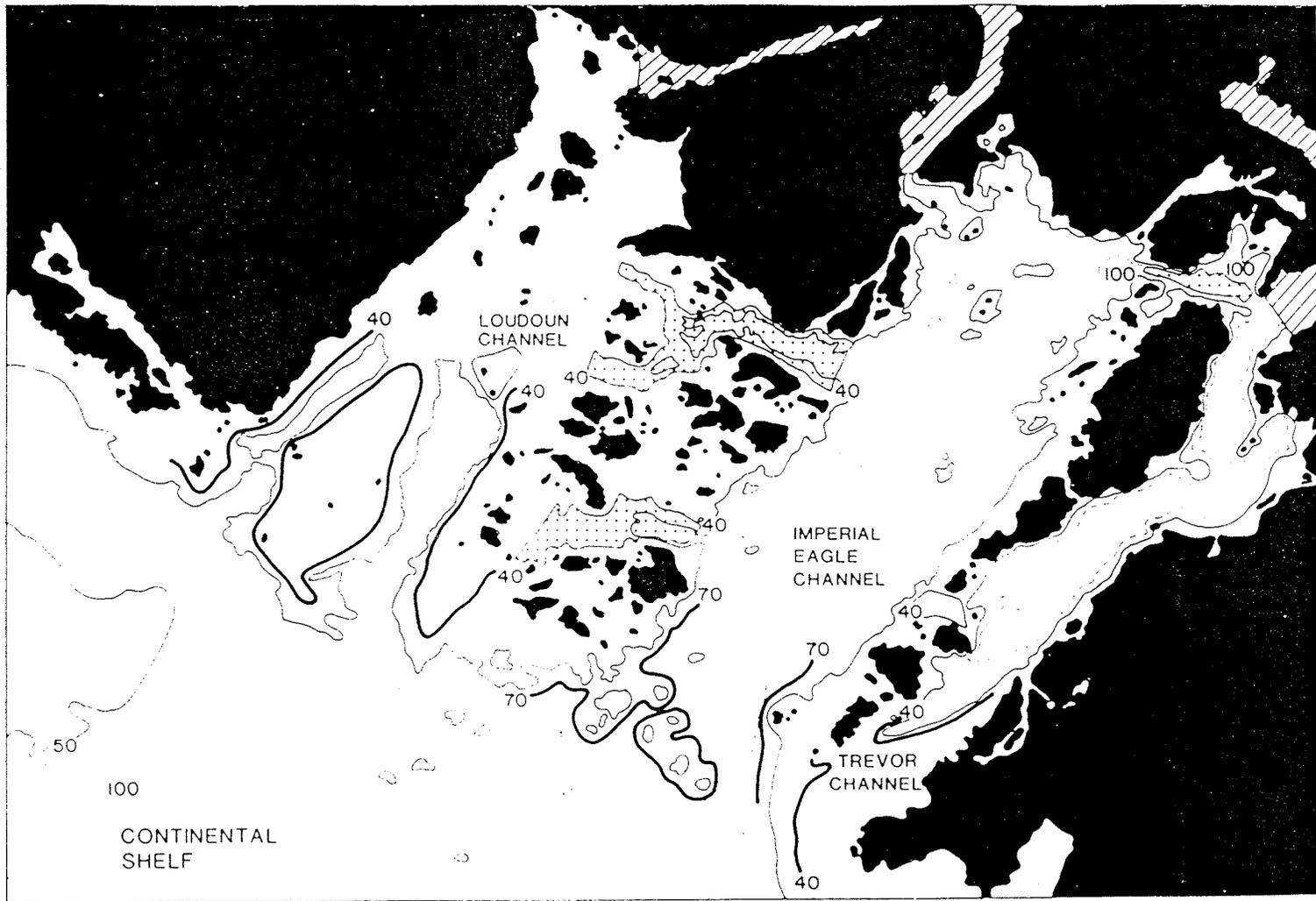
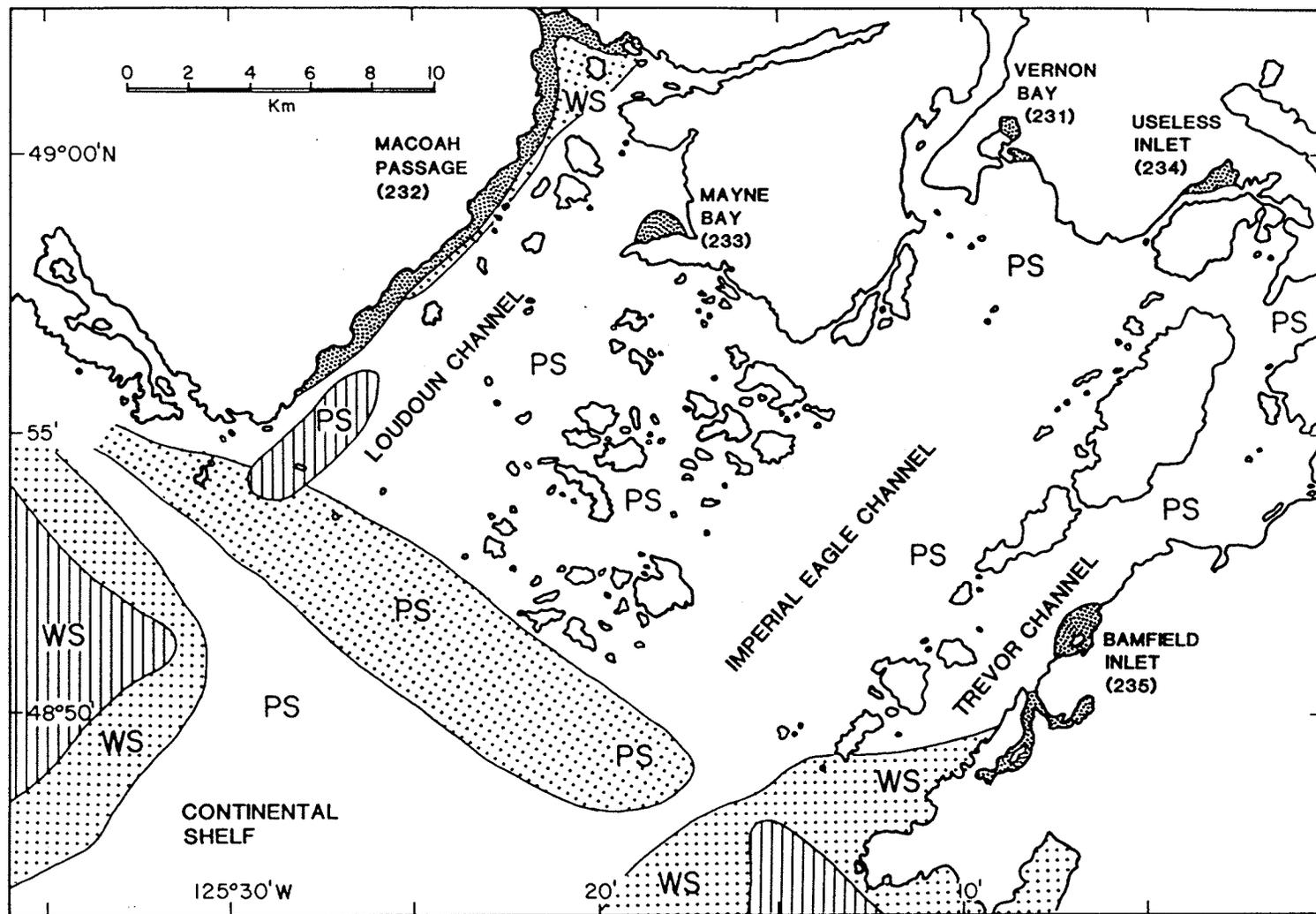


Fig. 4 Distribution of bottom sediments (Carter 1973) and Pacific Herring spawning areas (Hourston 1959a, 1980) in Barkley Sound. Sand, gravel and mud are dotted, striped and unshaded, respectively. PS and WS refer to poorly-sorted and well-sorted sediments, respectively. Spawning areas are heavily stippled and adjacent names and numbers correspond to herring management sections.



METHODS

Breeding phenology

Field work was conducted from 10 May to 7 September 1979 and 8 June to 13 October 1980. Barkley Sound also was visited on 6 and 7 December 1978 and 17 to 20 December 1979. These periods covered the egg-laying, incubation and nestling periods of the breeding season as well as the molting and early winter periods of the non-breeding season.

Because Marbled Murrelet nests are hard to find (see General Introduction), the pattern and timing of the breeding cycle were ascertained using behavioral observations and information on breeding status obtained from birds collected at sea (after Sealy 1974). The timing of egg-laying can be determined to within 1-3 days by the presence of postovulatory follicles, the unshelled egg in the oviduct and mature follicles. The single brood patch is fully developed by the time eggs are laid and apparently does not begin to refeather until after the chick has fledged. Marbled Murrelets carry fish to feed the chick at the nest site. This behavior is readily visible and permits the extent of the nestling period to be delimited. When chicks fledge, they appear with adults and non-breeders (which do not develop a brood patch) at sea in a distinct juvenal plumage (Drent and Guiguet 1961). Murrelets undergo a prebasic molt after breeding which renders them flightless (Stresemann and Stresemann 1966; Sealy 1975a; Carter, unpub. data) and the resultant basic plumage is distinctive through the winter. By integrating this information, the timing of the major events of the breeding cycle can be outlined (Sealy 1974).

Food samples and stomach analysis

Eighty-seven specimens of Marbled Murrelets were obtained in Barkley Sound during this study (see Appendices A,B). In 1979, the esophagus, proventriculus and gizzard of each bird were removed 2-3 hours after collection and stored in 10% buffered formalin. In 1980, each bird was frozen whole 2-3 hours after collection. Birds salvaged from gill nets by fishermen were iced in their boats and 1-2 days later were transferred to a freezer. Frozen birds were subsequently thawed and their digestive tracts were processed as described above. Prey items were examined under a low-power microscope and whole or nearly whole items from the proventriculi were counted, measured and assigned to one of three length classes (fork length for fish and total length for invertebrates): I (0.1-30.0 mm), II (30.1-60.0 mm), and III (60.1-90.0 mm).

Proventricular items, however, were usually in various stages of digestion, and 43.7% of the proventriculi were empty or contained small fragments of unidentified fish. Often, in early summer, only a few prey items could be isolated from moderate amounts of unidentified fish. Fish larvae (size class I) were apparently digested quickly and this size class was therefore under-represented at this time. This bias is related mainly to the percent frequency of size class I in early summer. When total numbers of prey items and percent frequencies per size class were determined, no correction was made for partly filled proventriculi or for the under-represented fish of size class I (see Sealy 1975a).

Food samples of both sexes taken throughout the day in both years were combined for analysis. By assigning each bird to status categories of breeding, molting, hatching-year (HY) and winter, reasonable sample

sizes were obtained for comparing between these major groups but, in doing so, intra-seasonal prey shifts and degree of diet overlap could not be detected (Holmes and Pitelka 1968, Sealy 1975b, Wallace and Ramsey 1983).

Survey methodologies and marine habitat definitions

The distribution and abundance of Marbled Murrelets in relation to marine habitats in the Barkley Sound area were determined using two types of surveys in 1979. Continental shelf surveys sampled offshore (11-35 km from shore) and inshore (5-10 km from shore) habitats. Barkley Sound surveys were used to sample inshore (up to 10 km from shore) and nearshore habitats. Marine habitats used by birds have been defined largely by their distance from shore and the depth of water at these locations (Wynne-Edwards 1935, Lack 1967, see also Brown 1980). In the Barkley Sound area, I defined marine habitats by modifying Kessel's (1979) classification of marine habitats in Alaska. Inshore waters are exposed coastal waters generally within 10 km of shore and less than 100 m deep. These waters occur on the inner portion of the continental shelf and are landward of basins on the shelf. Offshore waters include all marine waters from inshore waters to the edge of the continental shelf. These waters range in depth from 100-200 m and cover banks and basins on the shelf. Nearshore waters are protected coastal waters where the surrounding shoreline is at least 3 times as long as the width of the opening to unprotected, inshore waters. In Barkley Sound, these waters comprise all waters from mouths of channels to the heads of fiords. Since the access of fiords to the open ocean is

restricted, fiords are distinguished from channels which open directly into inshore waters. Waters are generally 50+ m deep.

Three Continental Shelf surveys were conducted between July and September, 1979. A fixed-width line transect (Franzreb 1981), 165 km long, was used (Fig. 5). Offshore and inshore habitats constituted 77 and 88 km of the transect, respectively. Two observers in July and August and one observer in September recorded all birds observed in a 180° zone from the bow of the ship. Marbled Murrelets were counted out to a maximum of 750 m from the side of the ship. Counts were made from a 3-m high (above sealevel) platform on the M.V. John Strickland which travelled at about 18 km/h.

Thirteen Barkley Sound surveys were conducted between May and September 1979, using a fixed-width line transect 60 km long (Fig. 6). Nearshore and inshore habitats constituted 24.4 and 35.6 km of this transect, respectively. Two observers recorded all birds observed in a 180° zone from the bow of the ship during 7 transects between 10 May and 9 July. One observer recorded all birds during 6 transects between 21 July and 28 September. Marbled Murrelets were counted out to a maximum of 500 m from the side of the ship. Counts were made from a 1-m high (above sealevel) platform on the M.V. Tedmac which travelled at about 9-11 km/h.

Fig. 5 Continental Shelf transect on the southwestern coast of Vancouver Island, British Columbia. Segments are numbered and described in Table 5. Segments 1 and 6-10 are in inshore habitats while segments 2-5 are in offshore habitats.

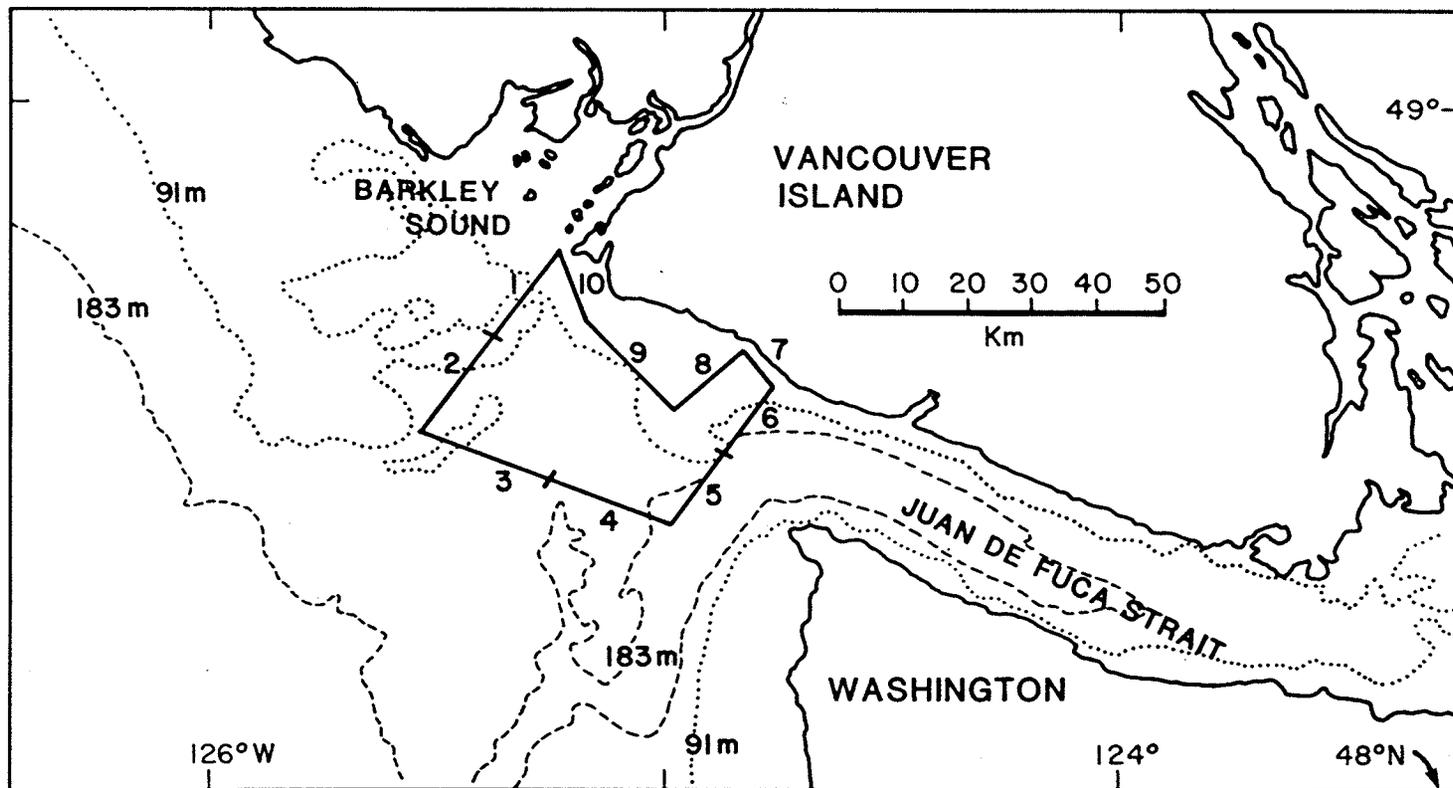
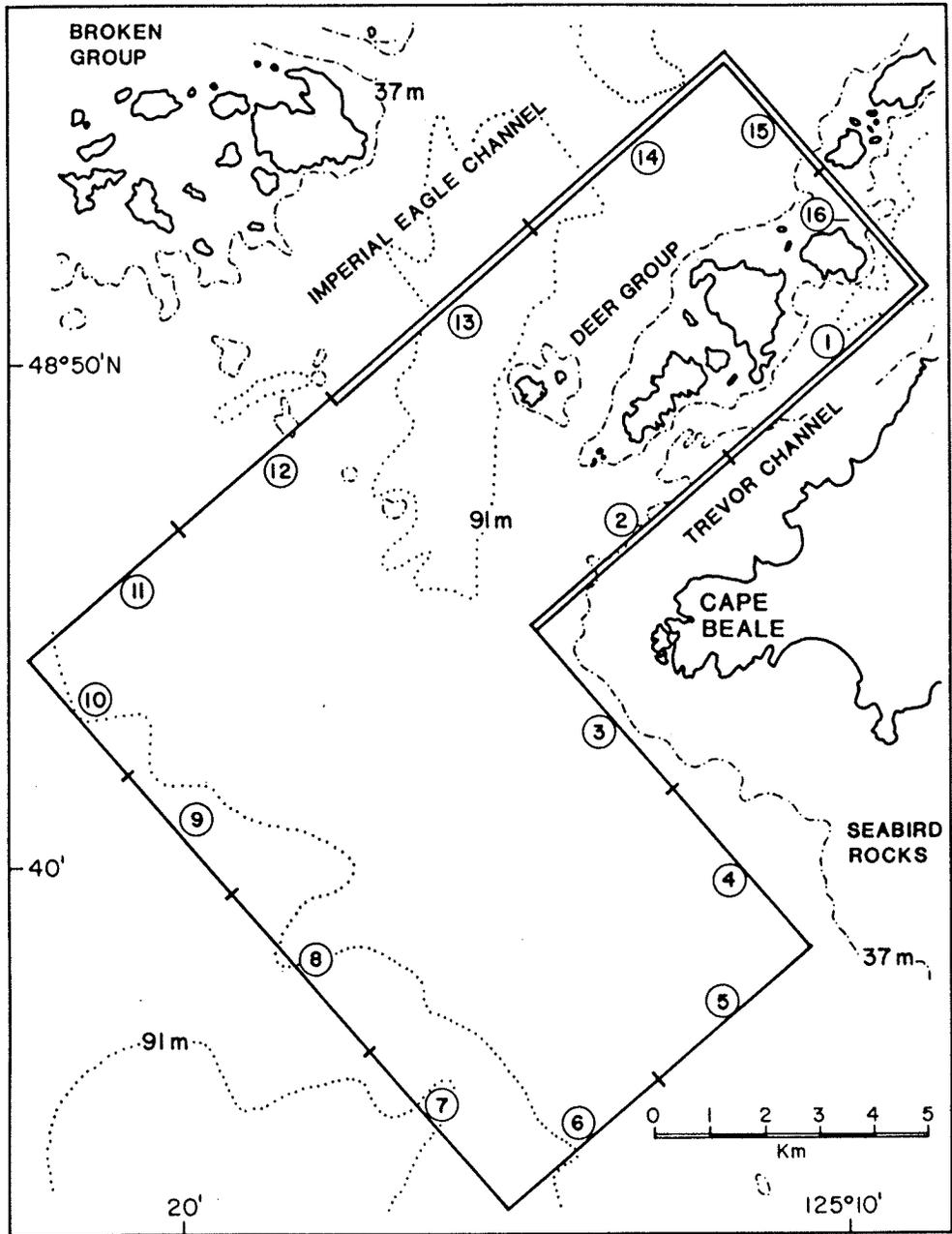


Fig. 6. Location of Barkley Sound transect. The thick portion indicates segments in nearshore habitat and the thin portion to segments in inshore habitat. Segments are numbered and described in Appendix D.



RESULTS

Breeding and molting phenologies

Evidence for the temporal ranges of major events in the breeding and molting of Marbled Murrelets in Barkley Sound in 1979 and 1980 (Fig. 7) is presented below:

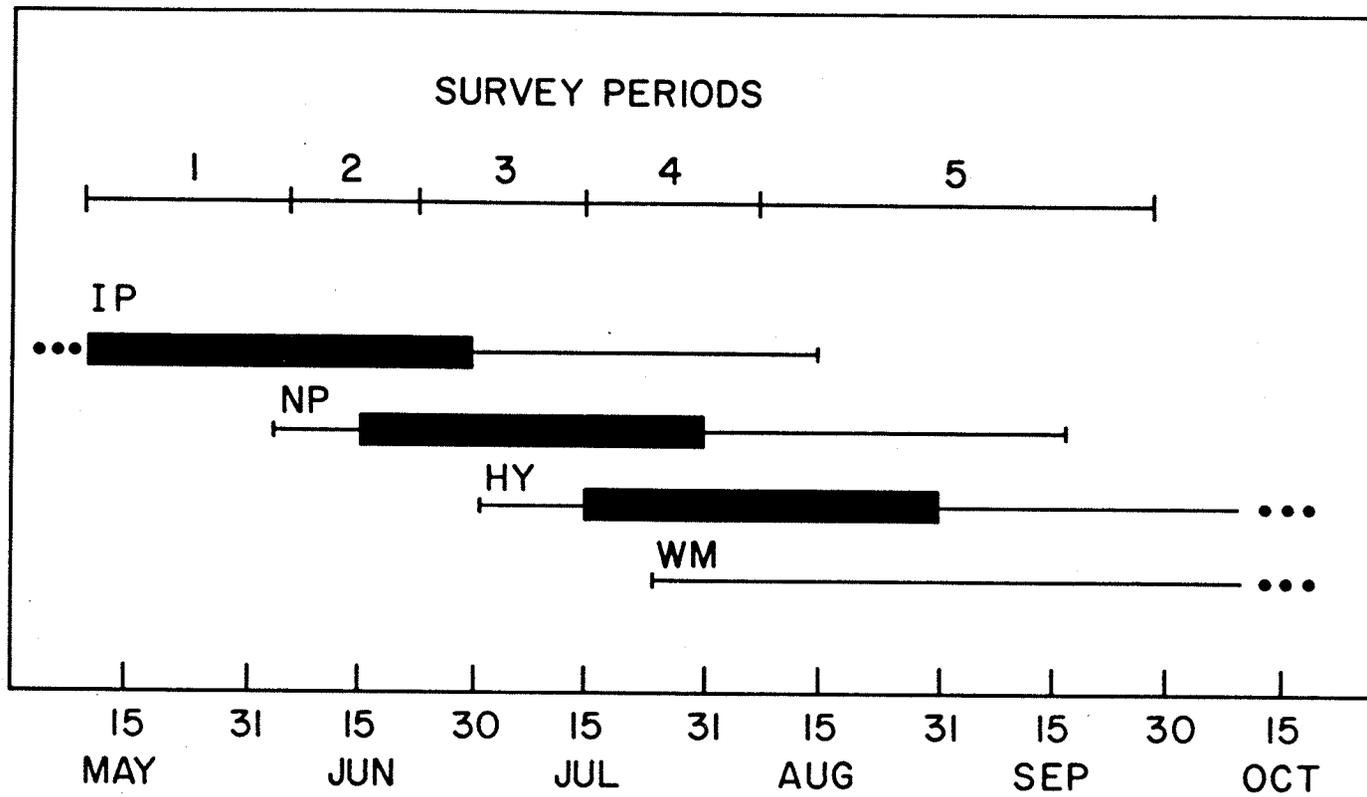
a) egg-laying period. One female Marbled Murrelet collected on 10 May 1979 (University of Manitoba Zoology Museum, UMZM 1127) contained an unshelled ovum (diameter 32.9 mm, 15.8 g).

b) nestling period. On 4 June 1979, the first adult was observed holding a fish in its bill (presumably intended for its young). Fish-holding birds were observed on the first day of observations (8 June) in 1980. These dates marked approximately the start of the nestling period. On 4 July 1979 and 28 June 1980, the first fledged young (HY birds) were observed. These dates marked the first dates observed when some birds had finished breeding successfully. One HY bird with an intact egg tooth was collected on 5 October 1980. This provides an approximate date for the end of the fledging period. Since the last bird seen holding a fish was observed on 17 September 1980, this was indicated as the end of the nestling period in Fig. 7.

c) molting period. The first bird undergoing pre-basic wing molt was collected on 24 July 1980. While some collected birds had completed wing molt by mid-September, others still molting in early October would not have completed molt until November (Carter, unpub. data).

The ranges of the breeding and molting periods of Marbled Murrelets in Barkley Sound are protracted when compared to the known times

Fig. 7. Breeding phenology of the Marbled Murrelet in 1979 and 1980 in relation to Barkley Sound survey periods. Definitions, in part, follow Sealy (1974): IP, incubation period; NP, nestling period; HY, fledged young at sea; WM, wing molt period; and ..., extremes unknown. Thick portions of ranges indicate timing for most of the population (see text). Survey periods are defined by major changes in relative densities of murrelets per transect (see Table 6).



required for individuals to complete these activities. In two nests examined recently in Alaska (Simons 1980, Hirsch et al. 1981), the single egg was incubated for about 30 days while nestlings were fed for about 28 days before fledging from the nests. In Barkley Sound, the incubation and nestling periods based on observations and collected birds, each spanned over 90 days (Fig. 7). The refeathering of brood patches permitted me to determine more specifically when most of the individuals in the population were breeding and molting. Maximal development of brood patches was achieved before mid-June (Table 1); thus, most birds were incubating before this time. Sealy (1974) correlated the start of brood patch regression with the time of the first appearance of HY birds at sea. In Barkley Sound, the same pattern existed. The first birds that were collected with refeathering brood patches and the first HY birds observed at sea both occurred in late June. By August, most birds had brood patches that were completely refeathered (Table 1) which indicated that for most birds, the nestling period lasted from mid-June to late July. Observations of fish-holding birds were also most numerous in this period (see also Hatler et al. 1978) which supports this timing of the nestling period. HY birds were most frequently observed in July and August (see also Guiguet 1971a, Hatler et al. 1978).

A few birds were observed holding fish and a few were collected with incompletely regressed brood patches into mid-September (Table 1). This indicated that some individuals nested later than the main population (Fig. 7). Later breeders possibly included first, second and/or replacement nesting efforts, while nesting stages were fairly synchronized for most of the population (see Manuwal 1979, Gochfeld

Table 1. Brood patch scores of Marbled Murrelets in Barkley Sound, British Columbia^a.

Period	n	Brood patch scores ^b						
		0	1	2	3	4	5	6
1-15 May	3	-	-	-	3	-	-	-
16-31 May	-	-	-	-	-	-	-	-
1-15 Jun	7	1 ^c	-	-	6	-	-	-
16-30 Jun	10	1 ^c	-	-	7	2	-	-
1-15 Jul	18	-	-	-	9	6	3	-
16-31 Jul	4	-	-	-	-	2	1	1 ^d
1-15 Aug	3	-	-	-	-	-	-	3 ^d
16-31 Aug	8	-	-	-	1	-	1	6 ^d
1-15 Sep	12	-	-	-	-	-	1	11 ^d
16-30 Sep	1	-	-	-	-	-	-	1 ^d
1-15 Oct	4	-	-	-	-	-	-	4 ^d
16-31 Dec	5	-	-	-	-	-	-	5 ^d

^a Scores of after-hatching-year birds of both sexes collected in 1979 and 1980 are combined.

^b Scoring scheme after Sealy (1974: 13-14): class 0, no evidence of defeathering, class 1, loss of down and some contour feathers; class 2, almost complete loss of down and most contour feathers with vascularization beginning; class 3, complete loss of feathers with heavy vascularization (maximum development); class 4, regression beginning with down appearing, especially around the edges, and sheaths of new contour feathers appearing; class 5, most of area down-covered, contour feathers beginning to break out of sheaths; class 6, complete regression, appearance as in class 0.

^c Non-breeding birds which do not develop a brood patch.

^d Post-breeding and non-breeding AHY birds cannot be distinguished once the brood patches have regressed completely.

1980). Since molting occurs after breeding, a skewed distribution for molting activities (Carter, unpub. data) resulted from the protracted breeding season.

Diet of the Marbled Murrelet in Barkley Sound

The diets of Marbled Murrelets in Barkley Sound are summarized in Table 2. Breeding adults and subadults fed primarily on small Pacific Herring (Clupea harengus) and Pacific Sandlance (Ammodytes hexapterus) which included larvae (size class I) and juvenile fish (size class II) (Hart 1973). The three adults collected in May had fed exclusively on larval fish. Molting and HY birds also fed primarily on herring and sandlance although four juvenile Northern Anchovy (Engraulis mordax) were found in the stomach of one molting bird. Herring were taken most frequently by molting and HY birds, whereas similar amounts of herring and sandlance were found in the stomachs of breeding birds. Molting and HY birds took larger (size classes II and III) juvenile herring and sandlance than those taken by breeding birds. Breeding birds also took fish of class II that were smaller than those in class II taken by molting and HY birds. Both herring and sandlance were found in 26.3%, 21.1% and 12.5% of stomachs which contained prey in breeding, molting and HY birds, respectively. The five Marbled Murrelets collected in winter had eaten scorpaenid rockfish and squid (Loligo opalescens) as well as large juvenile herring and sandlance.

Prey fed to nestlings

Marbled Murrelets carry fish in their bills to feed their nestlings at the nest (reviews in Drent and Guiguet 1961, Sealy 1975b). Birds

Table 2. Diet of the Marbled Murrelet in Barkley Sound, British Columbia
(n=87 stomachs examined)¹

Prey species	Size class ²	N ³	F(%) ⁴	Status					
				Breeding		Molting		HY	
				N	F(%)	N	F(%)	N	F(%)
Fish									
<u>Clupea harengus</u>	I	35	22.2	-	-	3	0.1	-	-
	II	22	13.9	79	68.7	38	67.9	-	-
	III	-	-	24	20.9	7	12.5	2	20.0
<u>Engraulis mordax</u>	II	-	-	4	3.5	-	-	-	-
<u>Ammodytes hexapterus</u>	I	41	25.9	-	-	-	-	-	-
	II	57	36.1	6	5.2	7	12.5	-	-
	III	2	1.3	2	1.7	-	-	1	10.0
Scorbaenidae	II	1	0.1	-	-	1	<0.1	2	20.0
Invertebrates									
<u>Loligo opalescens</u>	I	-	-	-	-	-	-	5	50.0

¹ Details of dates, sexes and locations of specimens collected are in Appendices A and B.

² Size classes (length): I, 0.1-30.0 mm; II, 30.1-60.0 mm; III, 60.1-90.0 mm; IV, 90.1-120.0 mm.

³ Total number of prey items.

⁴ Percent frequency of all size classes of prey combined.

holding fish were observed from early June to mid-September in Barkley Sound (NP in Fig. 7). During censuses of murrelets in Trevor Channel during the nestling period in 1980 (Chapter 2), fish held in the bill were identified with 8.5 x 30 power binoculars from a close (< 50 m) distance when possible (Table 3). Sandlance was the most frequently identified species although herring and anchovy were sometimes observed. Almost all fish observed were larger than prey items found in the stomachs of breeding birds and ranged between about 60-120 mm in length. The estimated weights of sandlance were the lowest (2-8g); most herring and all anchovy were larger (10-25g). Murrelets held only single fish although smaller fish were held in a different way than larger ones (Carter, unpub. data).

Diurnal feeding activity

Feeding did not occur continually because the stomachs of many birds were empty (or only crushed prey remained in the gizzard). The percentages of empty stomachs varied with time of day (Table 4). Fewer breeding birds had empty stomachs early in the day (25.0%) than later (88.9%) (Z test, $\alpha = .05$), indicating that they fed themselves mainly early in the day. Since most breeding birds were collected during the nestling period, this suggests that adult birds fed themselves early and obtained food for their young later in the day (Chapter 2). These feeding activities may be indeed mutually exclusive since 4 fish-holding birds collected between 1930-2030 h on 7 and 13 June 1979, all had empty stomachs. About 64% of the stomachs of adult birds killed in gill nets at night were empty. At this time, many birds may be foraging to obtain prey for nestlings; however, some birds were also feeding (Carter and

Table 3. Frequencies (%) and sizes of prey held by Marbled Murrelets in their bills while they sat on the water in Trevor Channel, 16 June-6 July 1980 (n=144 fish observed).

	N	F(%)	Size class ¹	Weight (g) ²
<u>Clupea harengus</u>	16	11.1	III, IV	2-25
<u>Engraulis mordax</u>	2	1.4	IV	10-25
<u>Ammodytes hexapterus</u>	70	48.6	IV	2-8
Unidentified fish ³	56	38.9	III, IV	-

¹ See Table 2 for definitions; length was estimated relative to bill length from tip to the commissure (approx. 30 mm; Bédard 1969).

² Ranges of weights are from Appendix C.

³ Included fish that were too far away to identify and 8+ individual fish not of the species listed above.

Table 4. Percentages of Marbled Murrelets with empty stomachs by time of day (n=66 stomachs examined).

Status	Time of day			Total
	Day		Night ¹ 2230-0400h	
	Early 0800-1400h	Late 1401-2030h		
Breeding ²	25.0 (8) ³	88.9 (9)	63.6 (11)	57.8 (45)
Molting	22.2 (18)	25.0 (8)	-	26.9 (26)
HY	50.0 (2)	0.0 (5)	-	27.3 (11)
Winter	50.0 (4)	0.0 (1)	-	40.0 (5)

¹ All birds were killed in gill nets in 1980.

² Excluding subadults.

³ % empty stomachs (n).

Sealy 1984). The percentage of empty stomachs at night did not differ significantly from values early or late in the day. During the molting period, there was no significant difference between early and late day, and these values were similar to values of breeding birds early in the day ($\sim 25\%$).

Availability and behavior of prey

Pacific Herring

Herring spawn in Barkley Sound from January to April with a peak usually in late February and early March (Hourston 1980). Eggs hatch in about 2 weeks and larvae metamorphose into juveniles about 4-8 weeks later (Hourston 1958, Stevenson 1962). Larval herring ($\leq 25-40$ mm) are planktonic and are carried passively by moving water. They occur 5 m from the surface during the day and night (Stevenson 1962). Juveniles are present by May and initially form schools of several hundred fish which remain in the Sound. Juvenile herring actively feed within 5 m of the surface, mainly in the early morning and evening. Where fish are abundant, they are also seen feeding at the surface during the day (Hourston 1959a). When not feeding (usually during mid-day), they may be found slightly deeper (5-15 m). Juveniles probably feed near the surface at night, as well. Juveniles form schools of about 10,000 individuals by mid-July and, by late August, schools may contain over a million individuals (Hourston 1959a). Juveniles remain in Barkley Sound until September or October when most migrate offshore when they are 70-100 mm long (Hourston 1958, Hart 1973).

Pacific Sandlance

The Pacific Sandlance is poorly known in Barkley Sound. They probably spawn there because "young" fish have been noted near herring spawning areas from March to May (Stevenson 1962). Daggett (1981) found sandlance larvae in large numbers from March to May near shorelines in Juan de Fuca Strait (southeast of Barkley Sound), as did Chester et al. (1977) in April. Larvae also occur in southern Georgia Strait (on the eastern side of Vancouver Island) in early summer (Hart 1973). Thus, sandlance spawn in late winter like herring do in this area. Larvae (< 25 mm) are planktonic and are carried away from spawning areas. They occur in surface waters (Hart 1973) and often feed in schools in the day (Covill 1959). Juveniles form large schools when they assume the demersal habit of adults (Macer 1965, 1966). Although "bottom dwellers" as juveniles, sandlance are often found throughout the water column (Meyer et al. 1979). Hourston (1959a) observed sandlance at the surface in Barkley Sound and I often observed schools at the surface during the day in June and July. In general, sandlance are most active during the day and burrow in the sand at night, although this behavior varies with the species and locality (Motoda and Tanaka 1950; Macer 1965, 1966). Hamada (1968) did not discern a diel pattern, but instead found them throughout the water column and in the sand in the day and night.

Distribution and abundance and prey

Pacific Herring

The distribution of larval herring depends largely on where spawning areas are located because they tend to stay near them after hatching (Stevenson 1962). However, being planktonic, they can be

carried a few km from spawning areas by moving water. Stevenson (1962) found that larval herring were present near Macoah Passage, the main spawning area in Barkley Sound (Fig. 4), until May when they migrated across the Sound to their main rearing area in southern Trevor Channel (Hourston 1958, 1959a). In early July, some juveniles were still present in the Broken Group islands but by late July, most were on the southeast side of the Sound. Juvenile fish also move from spawning areas on the northeast side of the Sound to the rearing area in Trevor Channel. Hourston (1953, 1959a) noted that the habitats in which juveniles occur are sheltered with shallow thermoclines and only moderate salinities. Oceanographic data collected in 1979 reveal that these habitat characteristics prevail in south Trevor Channel (Carter, unpub. data).

Juvenile herring comprise the bulk of the small planktivorous, pelagic fish in the Sound (Waldichuk 1956). An estimated 600-700 million juvenile fish occur in Barkley Sound in the summer and the Sound contains one of the largest spawning populations in British Columbia (Tester 1937, Hourston 1959b, Taylor 1964).

Pacific Sandlance

Sandlance probably spawn on sandy bottoms on the continental shelf as well as inshore areas (Macer 1965). Larvae may be carried inshore by onshore water movements in spring (Lane 1963) or juveniles may migrate into inshore areas (Macer 1965, 1966). Larval fish are probably found widely at the mouth of the Sound but they tend to concentrate in areas of tidal currents (Eldridge 1977). Hourston (1959a) found juvenile sandlance in the same habitats as juvenile herring in Barkley Sound;

they are also known to school together (Richards and Kendall 1973). Sandlance, however, occur in a wide range of water temperature and salinities, although in certain localities they have been noted to prefer moderate salinities (Richards et al. 1963). Juvenile sandlance probably become restricted to areas of the Sound with coarse sandy bottoms suitable for burrowing, such as the sills at the mouth of the Sound (Figs. 3,4), and juveniles therefore probably occur mainly in these habitats (Hart 1973).

Availability and behavior of fish fed to nestlings

Pacific Herring and Pacific Sandlance

The sizes of herring (60-120 mm) that I saw Marbled Murrelets holding for their young (Table 3) were larger than most juvenile herring (> 70 mm) available in July (Hourston 1958) and probably represented second-year herring for the most part. Similarly, the sizes of sandlance held by murrelets may have contained both large juvenile and second year fish. Second-year sandlance occur with adults in large schools (Macer 1965).

Northern Anchovy

Anchovy spawn mainly in July and August in Barkley Sound (Hart 1973). All anchovies held by murrelets were second-year fish which by May accompany spawning adults in the Sound (Appendix C). Anchovies are usually deep during the day but come to the surface at night (Baxter 1967). Hourston (1959a), however, observed them near the surface in the day in Barkley Sound (see also Squire 1978).

Distribution and abundance of fish fed to nestlings

Second-year herring occasionally do not move offshore like adults (Taylor 1964, Clemens et al. 1936). Schweigert and Hourston (1980) estimated that between .09 and 32.8 million fish occurred in the Sound each year between 1972 and 1979. These figures correspond to about 0.01 to 5.1% of the estimated number of juvenile fish in the Sound. Second-year herring are therefore much less abundant than juveniles.

Second-year sandlance and anchovy probably occur in even lower numbers than second-year herring because these species are less abundant to begin with than herring in the Sound (Waldichuk 1956, Tillman 1976). However, sandlance are probably restricted to areas where sandy substrates predominate near the sills (see Winters 1983) and anchovies are more abundant in Trevor Channel than other parts of the Sound (Taylor 1983).

Abundance and distribution of Marbled Murrelets in the Barkley Sound area

Continental Shelf surveys

Very few Marbled Murrelets were seen on shelf surveys (Table 5), although only the July transect was conducted during the breeding season in Barkley Sound (Fig. 7). In July, the few murrelets observed were all found in inshore habitats. Segment 10 contained the largest numbers of birds and was located off Cape Beale and Seabird Rocks, adjacent to the Barkley Sound survey area. The small number of birds overall in offshore habitats in July supports the findings of Cody (1973), Sealy (1975b), Vermeer et al. (1983), and Sealy and Carter (in

Table 5. Relative densities (individuals/km) of Marbled Murrelets by transect segment and habitat type on 3 Continental Shelf surveys in 1979.

Transect date	Inshore habitat						Offshore habitat				Total
	1 ^a	6	7	8	9	10	2	3	4	5	
	19 ^b	14	8	16	20	11	19	23	21	14	165
26-27 July	0 (0.3)	0	0.3 ^c (0.8)	0.4 (0.4)	0.1 (0.1)	2.9 (0.9)	0	0	0	0	0.3 (0.2)
22 August	0	0	0 (0.1)	0	0.1	0.7	0	0 (<0.1)	0	0.1 (0.1)	0.1 (<0.1)
27 September	0	0	0	0	0	0	0	0	0	0	0

^a Transect segment number from Fig. 5. Inshore and offshore segments were 2.4-9.9 and 15.3-36.9 km from shore, respectively. Distances were measured from the centers of the segments. See text for descriptions of the habitats.

^b Length (km) of transect segments.

^c Number of birds/km on the water. Parenthesized numbers underneath refer to the number of flying birds/km.

press) which indicated that murrelets occur primarily within a few km of shore during the breeding season.

Even fewer birds were observed in August on shelf surveys although once again most were present in segment 10. A few birds were observed in offshore segments in August. No birds were observed on the September transect. Since many individuals are molting at this time (Fig. 7) in nearshore habitats, it appears that murrelets do not molt in offshore and inshore habitats (Carter, unpub. data).

Barkley Sound surveys

Barkley Sound surveys were conducted throughout the breeding and molting periods (Fig. 7). These transects were divided into 5 periods by major changes in relative densities (birds/km) of murrelets per transect (see Table 6): period 1, 10 May-5 June (3 transects); period 2, 6-22 June (2 transects); period 3, 23 June-15 July (2 transects); period 4, 16 July- 7 August (2 transects); and period 5, 8 August-28 September (4 transects). The relative densities of murrelets per transect increased from 0.1-1.8 in period 1 to 2.1-2.5 in period 2, peaked at 5.9-6.3 in period 3, then decreased to 1.6-2.3 in period 4, and 0-0.6 in period 5 (Table 6). The increase in relative densities from periods 1-3 correlates with the progression of most breeding birds from the incubation to the nestling period (Fig. 7). During the incubation period, one mate remains at the nest during the day while its mate is feeding at sea; birds exchange incubating and feeding tasks at night (Sealy 1974, 1975b). During the nestling period, the single chick is left unattended in the nest during the day and is fed primarily at night (Simons 1980, Hirsch et al. 1981); thus, more breeding birds are found at sea during this period (Sealy and Carter, in press). The decrease in

Table 6. Relative densities (individuals/km) of Marbled Murrelets by marine habitat on Barkley Sound transects in 1979.

Transect No.	Date	Marine habitats ¹			Total	n ²	Pe
		Nearshore	Inshore -a	Inshore -b			
1 ⁶	10 May	2.4 ⁴ (48.0) ⁵	2.1 (42.0)	0.5 (10.0)	1.8	88	
2 ⁷	22 May	0.1 (100.0)	0	0	0.1	3	
3	2 Jun	0.5 (26.3)	1.4 (73.7)	0	0.5	32	
4	9 Jun	3.9 (55.7)	1.6 (22.9)	1.5 (21.4)	2.5	150	
5	17 Jun	3.2 (53.3)	2.8 (46.7)	0	2.1	119	
6	29 Jun	12.8 (78.0)	3.5 (21.3)	0.1 (<0.1)	6.3	367	
7	9 Jul	11.4 (70.4)	4.1 (25.3)	0.7 (<0.1)	5.9	353	
8	21 Jul	3.7 (94.9)	0	0.2 (5.1)	1.6	95	
9	31 Jul	5.7 (98.3)	0.1 (1.7)	0	2.3	140	
10	13 Aug	1.4 (93.3)	0.1 (6.7)	0	0.6	36	
11	29 Aug	0.7 (100.0)	0	0	0.3	17	
12	5 Sep	0.1 (100.0)	0	0	<0.1	2	
13	28 Sep	0	0	0	0	0	

¹ Nearshore and inshore segments were 0.5-2.5 and 1.0-9.5 km from shore respectively. Inshore-a segments were 1.0-5.5 km from shore (segments 3,4,5, and 12) inshore-b segments were 6.0-9.5 km from shore (segments 6-11) (see Fig. 6). Distances were measured from the centers of the segments. Nearshore, inshore-a and inshore-b segments were 24.4, and 20.6 km long, respectively. See text for descriptions of habitats.

² Total number of Marbled Murrelets observed on the water/transect.

³ Period defined by major changes in the total relative densities of murrelets per transect (see text).

⁴ Relative density of murrelets (birds/km) on the water.

⁵ Percentage of the sum of the relative densities of murrelets from all habitats.

⁶ Segments in inshore-a and inshore-b habitats were 11.4 and 13.1 km long, respectively.

⁷ Segments in nearshore, inshore-a and inshore-b habitats were 18.8, 3.6 and 9.2 km long, respectively.

relative densities from periods 3 to 5 correlates with many birds finishing nesting in periods 3 and 4 as indicated by the presence of HY birds at sea. The addition of HY birds to the numbers of birds at sea would be expected to increase further the total numbers observed. The sharp decrease in numbers indicates that many birds leave the transect area once their nesting is over. By late September, no birds were observed on the transect. However, some individuals were observed in other parts of the Sound during period 5 and in the winter (Carter, unpub. data). Hatler et al. (1978) also noted that numbers of Marbled Murrelets declined from July to October in Loudoun Channel on the west side of Barkley Sound (Fig. 2). Porter (1981) concurrently conducted transects in 1979 around the Deer Group islands (adjacent to the transect area) and also found that numbers of Marbled Murrelets declined during the same period.

More birds were seen on nearshore segments than inshore segments on all transects conducted during the study period (Table 6, Appendix D). Inshore-a segments, however, contained larger numbers than inshore-b segments (Table 6). Within nearshore segments, Trevor Channel and Satellite Passage contained more birds than did Imperial Eagle Channel (Table 7). Within inshore-a segments, Cape Beale segments had more birds than Outer segments. There were no apparent concentrations of birds in inshore-b segments.

Changes in distribution during the breeding season, disproportionately affected the numbers of birds within and between habitats. In period 1, the fewer birds were distributed widely in nearshore and inshore-a habitats (Table 7, Appendix D). As numbers increased in periods 2 and 3, a disproportionately greater increase in

Table 7. Relative densities (individuals/km) of Marbled Murrelets in some marine habitats in Barkley Sound in 1979.

Transect No.	Period ^b	Marine Habitats ^a			
		Nearshore		Inshore-a	
		Trevor Channel	Imperial Eagle Channel	Cape Beale	Outer Segments
1	1	2.7 ^c (56.9) ^d	2.0 ^c (43.1) ^d	2.7 ^c (77.1) ^e	0.8 ^c (22.9) ^e
2	1	0	0.3 (100.0)	- f	0
3	1	0.9 (100.0)	0	2.7 (100.0)	0
4	2	5.0 (63.5)	2.9 (36.5)	1.0 (31.3)	2.2 (68.7)
5	2	6.1 (97.4)	0.2 (2.6)	5.1 (94.4)	0.3 (5.6)
6	3	25.7 (100.0)	0	6.3 (94.0)	0.4 (6.0)
7	3	16.8 (73.7)	6.0 (26.3)	4.0 (48.8)	4.2 (51.2)
8	4	2.5 (33.3)	4.9 (66.7)	0	0
9	4	11.0 (96.4)	0.4 (3.6)	0.1 (100.0)	0
10	5	2.7 (97.1)	0.1 (2.9)	0.3 (100.0)	0
11	5	1.3 (94.1)	0.1 (5.9)	0	0
12	5	0	0.2 (100.0)	0	0
13	5	0	0	0	0

^a Trevor Channel segments (1, 2, 16; 12.2 km); Imperial Eagle Channel segments (13 - 15; 12.2 km); Cape Beale segments (3, 4; 7.8 km); Outer segments (5, 12; 7.2 km). See Fig. 6 for segment locations.

^b See Table 6.

^c Number of birds/km on the water.

^d Percentage of the sum of relative densities of murrelets in nearshore habitat.

^e Percentage of the sum of relative densities of murrelets in inshore-a habitat.

^f Segments not covered in transect.

nearshore segments occurred such that, by period 3, over 70% of the birds observed were found in nearshore habitats (Table 6). Within the nearshore habitat, on the other hand between 63.5% to 100% of the birds observed were found in Trevor Channel and Satellite Passage (Table 7). Alternatively, Imperial Eagle Channel, experienced little increase in numbers over period 1 and was used more sporadically (see Appendix D). Within inshore-a habitat, a slight increase in numbers of birds occurred in periods 2 and 3 (Table 6), most in Cape Beale segments while the Outer segments were used more variably. In period 3, up to 94% of the birds in inshore-a habitats were found in Cape Beale segments (Table 7), but in period 4, a rapid decrease in numbers occurred in inshore habitats such that almost no birds were observed there by period 5 (Tables 6,7). Although numbers of birds also decreased in nearshore habitats at this time, over 90% of the remaining birds occurred there (Table 6). Imperial Eagle Channel segments, however, followed the same rapid decrease as did inshore segments (Table 7). Trevor Channel and Satellite Passage segments accounted for over 95% of birds observed in nearshore habitats in periods 4 and 5. By mid-September (period 5), only a small number of birds remained in the transect area.

Most of the increase in relative densities of murrelets per transect that occurred in periods 2 and 3 resulted from the sharp increase in numbers in Trevor Channel and Satellite Passage nearshore segments. This increase did not result from a shift in habitat by birds within the transect area but rather from a disproportionate allotment of additional numbers of birds that occurred during periods 2 and 3. While the total numbers of birds increased by about five fold, the numbers in Trevor Channel increased by about ten to twenty fold (Tables 5,7). The

five-fold increase in total numbers, however, was much greater than the maximum two-fold increase that could be expected once most birds had entered the nestling period, in period 3 (Fig. 7). Since about 15% of the population are non-breeders (Sealy 1975b; Sealy and Carter, in press), a less than two-fold increase is expected. The additional birds that accounted for this five-fold increase probably shifted into the transect area primarily from areas outside of it.

Although numbers of murrelets declined in periods 4 and 5, smaller numbers persisted longer in Trevor Channel and Satellite Passage (Tables 6,7). Observations in other parts of the Sound indicated that the remaining birds were found within 500 m of shore and by mid-August most of these were HY and molting AHY birds (Carter, unpub. data). Therefore, although numbers declined because many birds left the transect area, numbers also declined because of a shift to shoreline habitats which were not censused effectively by Barkley Sound transects. Porter's (1981) data did not suggest as great a decline in numbers of Marbled Murrelets during this period in her shoreline transects around the Deer Group Islands; in fact, she found that birds persisted in moderate numbers until October there. Although many HY birds were observed in August, their numbers did not appear to account for the numbers of young that could have been produced relative to the size of the breeding population. Hatching-year birds were seldom seen on Barkley Sound transects, although the difficulty of distinguishing birds in juvenal plumage from AHY birds that were molting or in basic plumage meant that HY birds were almost certainly under-estimated. Porter (1981, unpub. data), however, noted that only 12.1% of the birds observed on Deer Group transects in August were HY birds. By late August, she also found

it difficult to distinguish the juvenal plumage from molting AHY birds such that ratios of HY: AHY birds were not determined later.

DISCUSSION

Diet

Sandlance and euphausiids are the principal prey groups in summer of Marbled Murrelets in British Columbia and Alaska (Table 8). In Barkley Sound, however, herring and sandlance were the major prey species. Herring has not been found to be a major component of the diet of murrelets elsewhere. Sealy (1975b) found that murrelets fed on euphausiids for about a month after arrival in late April at Langara Island, British Columbia. Later, their diet consisted mainly of sandlance and to a lesser extent Shiner Perch (Cymatogaster aggregata). Euphausiids were not found in the stomachs of murrelets in Barkley Sound although most birds were collected more than a month after arrival (see Appendices A). Herring were also important in the diet of molting and HY birds in Barkley Sound; they were also found in the diets of murrelets during the winter unlike other areas (Table 8).

The importance of herring in the diet of the Marbled Murrelet in Barkley Sound correlates with the local abundance and availability of juvenile herring there. This suggests that murrelets feed opportunistically on available prey. Juvenile herring, however, are abundant only in localized areas near spawning grounds (Hourston 1958; 1959 a,b). The diet of murrelets has not been studied in other areas where juvenile herring are abundant. In Alaska and at Langara Island, B.C., sandlance and euphausiids are probably more abundant and available leading to their importance in the diet there (Sealy 1975b; A.K.

Table 8. Prey of AHY Marbled Murrelets in British Columbia and Alaska in summer (April - September) and winter (October-March)¹. Major and minor prey items are indicated by X and 0, respectively.

	Crustacean			Squid		Fish										Source			
	Amphipod	Decapod	Euphausiid	Gammarid	Mysid	Schizopod	Loligo	Ammodytes	Clupea	Cymatogaster	Engraulis	Mallotus	Theragra	Trichodon	Osmerid		Scorpaenid	Stichaeid	Unid. larvae
Summer																			
Langara Island, BC	0	0	X				0	X	X						0	0	0		Sealy (1975a)
Barkley Sound, BC								X	X		0					0			This study
Gulf of Alaska, AK			X		0			X			0								A.K. Fukuyama (unpub. data)
Kodiak Island, AK			X					X			X	0	0						A.K. Fukuyama (unpub. data)
British Columbia			X					X											Guiguet (1956, 1971b)
Winter																			
Nanaimo, BC					X	0				X								X	Munro and Clemens (1931)
Barkley Sound, BC							X	0	X						X				This study
Kodiak Island, AK		0	X	0	X						X	0		X					A.K. Fukuyama (unpub. data)
Kachemak Bay, AK			X	0	X			0			X	0							A.K. Fukuyama (unpub. data)

¹ Grinnell (1897) noted small fish and molluscs in the diets of murrelets in Alaska and Jewett et al. (1953) noted that small fish were taken in Washington State.

Fukuyama, unpub. data). In Barkley Sound, juvenile herring and sandlance commonly were found together in stomachs suggesting that these prey were obtained in the same areas (see Hourston 1959a, Richards and Kendall 1973) since digestion is rapid. Molting and HY birds fed on larger juvenile herring and sandlance probably because larger size classes are more available by August and September as juvenile fish grow rapidly in length.

Fish fed to nestlings

Sandlance is the principal species of fish that murrelets feed to nestlings throughout their range (Table 9). While herring and anchovy were also carried in the bill in Barkley Sound, herring only has been identified elsewhere in British Columbia by Guiguet (1950) and anchovy have been observed only in Washington, while Capelin (Mallotus sp.) have been reported carried by murrelets in Alaska.

Marbled Murrelets have been reported carrying from 1-6 fish in their bills at one time (Savile 1972, Cody 1973). Murrelets were observed carrying only single fish in Barkley Sound. One anchovy that was obtained from a fish-holding bird weighed 12.4 g (UMZM). Simons (1980) observed only a single 8-g capelin brought to the nest but estimated the weights of 2 other food loads at 15 and 20 g. Hirsch et al. (1981) determined the weights of 2 food loads in another year at 5 and 13 g. The range of these weights falls within estimated range of second-year fish (2-25g) held in Barkley Sound (Table 3). Based on bill morphology (Bédard 1969) and methods of holding fish, murrelets probably carry single fish to the nest most of the time (Carter, unpub. data).

Table 9. Species of fish held in the bill by Marbled Murrelets in Washington, British Columbia and Alaska.

	Species				Source
	<u>Ammodytes</u>	<u>Clupea</u>	<u>Engraulis</u>	<u>Mallotus</u>	
Olympic Peninsula, WA	X		X		Cody (1973)
San Juan Islands, WA			X		M.L. Cody (<u>in litt.</u> , 1979)
Langara Island, BC	X				Sealy (1974, 1975b, 1978)
Queen Charlotte Islands, BC	X	X			Guiguet (1950, 1956)
Barkley Sound, BC	X	X	X		This study
East Amatuli Island, AK ¹				X	Simons (1980)

¹Fish observed being delivered to chick in nest.

Second-year herring fed to nestlings are much less abundant than the juvenile herring that murrelets ate themselves (Schweigert and Hourston 1980). Second-year sandlance and anchovy also are not very abundant in the Sound. This suggests that murrelets select larger prey to carry to nestlings even though they are less abundant. The predominance of sandlance in fish fed to nestlings probably resulted from this species being more available near the surface during the day than herring or anchovy (Meyer et al. 1979).

The different sizes of fish that Marbled Murrelets carried in Barkley Sound may reflect the age of the nestling at the time. Gaston and Nettleship (1981) and Slater and Slater (1972) noted that adult Thick-billed Murres (Uria lomvia) and Black Guillemots (Cephus grylle), brought larger fish to older (and larger) young, respectively. Species in these genera are primarily single-prey loaders, like the Marbled Murrelet (Carter, unpub. data).

Diurnal feeding activity

Only 12.8% of the stomachs of adult and subadult Marbled Murrelets Sealy (1975b) examined at Langara Island were empty and this did not change with time of day (S.G. Sealy, pers. comm.). Similarly, only 5.7% of stomachs examined from the Gulf of Alaska in the summer of 1976 were empty (A.K. Fukuyama, unpub. data). In contrast, 57.8% of the stomachs of breeding birds in Barkley Sound were empty (Table 4). Fewer stomachs were empty there earlier in the day which suggests that most birds fed early in the day. However, more birds held fish later in the day (Chapter 2). Murrelets probably feed themselves early in the day because juvenile herring and sandlance are closer to the surface at this

time (Hourston 1959a). This behavior probably reduces the time and effort adult murrelets spend searching for and capturing prey which they eat. Fish that they obtain, hold, and later deliver to nestlings are less abundant and distributed more widely in the Sound. These larger fish also migrate vertically (Hourston 1959a; Macer 1965, 1966; Baxter 1967) and would be expected to be less accessible near the surface in the day. Efficient feeding early in the day may permit greater time and effort to search for and obtain prey for nestlings later in the day (Chapter 2).

About 64% of the stomachs of adult murrelets killed at night in gill nets were empty (Table 4); thus, although some birds were feeding, others probably were foraging for prey to take to nestlings. Juvenile herring and sandlance occur near the surface at night and would be accessible for night feeding. Bailey (1977) also suspected that murrelets fed at night in Alaska. Observations of birds in other areas flying inland (to their nests) at all times of the night suggest that night foraging may occur regularly, at this time at least during the nestling period (Carter and Sealy 1983). Foraging for fish for nestlings at night could allow birds to obtain fish when they have been unsuccessful during the day or provide the opportunity for multiple feeding trips to the nest. Simons (1980) suggested that 1, 2 or more feeding trips were made to the nest at night. Larger fish for nestlings are more abundant near the surface at night and therefore should be easier to obtain than during the day.

Timing of the breeding season

Sealy (1975b: 430) concluded that the timing of the breeding season

of the Marbled Murrelet at Langara Island may be controlled ultimately by the "cycles of abundance of fishes near shore, especially Ammodytes, which are taken in great quantities by them and for their young in this region". The breeding season should be timed such that the period of maximal abundance of suitable prey occurs during the nestling period when food demand is maximal (Chapters 2,3). In Barkley Sound, the main nestling period indeed coincides with the period when juvenile herring and sandlance are abundant and larger fish for nestlings are available in the Sound. Juvenile herring are also abundant when newly-fledged young occur at sea (Fig. 7). Median herring spawning in the two main spawning areas in the Sound (Macoah Passage and Mayne Bay) predictably occurs 55-60% of the time in early and mid-March (Hourston 1980), such that juvenile fish are regularly abundant by mid-May. In this respect, 1979 was an average year and similar to the timing of spawning observed by Hourston (1958, 1959a,b) and Stevenson (1962).

Egg laying is initiated about 10 days earlier than it is about 700 km north on Langara Island (Sealy 1974). Hourston (1980) indicated that the median spawning dates of herring are about one month later in northern British Columbia. The difference in the timing of breeding seasons partly results from differences in the timing of prey abundance from a general difference in the seasonality of the two environments (Lane 1963, Crean 1967, Favorite et al. 1976, Thomson 1981) even though prey species are somewhat different in the two areas. Marbled Murrelets, however, may arrive later at Langara Island and do not occur there in late winter (Sealy 1974, 1975a) unlike Barkley Sound (Hatler et al. 1978; Carter, unpub. data). Protraction of the breeding season in

Barkley Sound likely results from the lengthy period from May to October when food is abundant in the Sound. This may also lead to a portion of the population undergoing wing molt in the Sound after breeding (Fig. 7) instead of molting on the wintering grounds (Stresemann and Stresemann 1966).

Seasonal distribution and abundance of Marbled Murrelets in Barkley Sound

Sealy (1975a,b) found that adult and subadult Marbled Murrelets were distributed in well-defined feeding areas within 500 m of shore throughout the breeding season at Langara Island. He noted, however, that their distribution changed early in the nestling period when birds were then found where they were scarce earlier in the breeding season. In Barkley Sound, the distribution of murrelets changed by mid-June, also early in the nestling period. Murrelets were distributed widely in inshore and nearshore habitats early in the breeding season; after the young had begun to hatch until most nestlings had fledged, individuals aggregated in a well-defined nearshore area in south Trevor Channel (Table 7). This change in distribution may be influenced by a change in the distribution of prey. Murrelets feed on larval and juvenile herring and sandlance early in the breeding season which are distributed widely at this time. By late June, herring are concentrated in their rearing area in Trevor Channel, and, at about the same time, juvenile sandlance would be expected to become restricted to the mouth of the Sound (which includes the south end of Trevor Channel) where suitable burrowing substrates occur. Marbled Murrelets therefore aggregate in a restricted area where food is abundant.

This clumping of the food source is also associated with the seasonal development of an oceanographic front over the sill in south Trevor Channel (Carter, unpub. data). This area provides a sheltered, nearshore environment with moderate salinities (27-30 ‰) and a shallow thermocline. This habitat type is preferred by juvenile herring and to a lesser extent by sandlance (Hourston 1953, 1959a; Richards et al. 1963). The turbulence and associated mixing that occurs at or near the front and over the sill, also acts to increase productivity in this area (Appendix E) and probably brings prey organisms nearer to the surface (see Brown 1980). During the nestling period, Trevor Channel is probably the most productive area in Barkley Sound (Waldichuk 1956). Prey are available, however, in other parts of the Sound as indicated by the occurrence of other aggregations of murrelets in June, 1982 (Sealy and Carter, in press). Most other areas of the Sound contain smaller numbers of murrelets which are scattered mainly in small channels. Such smaller feeding areas may develop where small pockets of fish that do not migrate to Trevor Channel occur (Hourston 1958). The continued use of alternate feeding areas during the nestling season may also be related to the obtaining of prey for nestlings (Chapter 2).

Small scale fronts, such as found in Trevor Channel, are well known to attract feeding seabirds (Brown 1980). Uspenski (1958) found that Thick-billed Murres occurred at fronts that formed where fresh water met oceanic water in fiords in Novaya Zemlya, U.S.S.R.. Similarly, Brown et al. (1975a) observed concentrations of shags (Phalacrocorax atriceps and P. albiventer) at the boundary between clear and silty water and in channels where surface temperature and salinity changed abruptly in Chilean fiords. Fronts commonly prevail over sills at the mouths of

inlets and fiords along the west coast of Vancouver Island and aggregations of seabirds have been observed near them (Martin and Myres 1969). Sill areas often support large populations of small, planktivorous fish (Matthews and Heimdal 1980). As shown in Trevor Channel, Marbled Murrelets aggregate to feed on a clumped and abundant fish food source that is associated with a front at the sill. The low silt content of fresh water in Vancouver Island fiords (Pickard 1963, Pickard and Stanton 1980) may also enhance foraging conditions for murrelets in these areas (see Robertson 1977).

The aggregation of murrelets during the nestling period in Trevor Channel resulted when a five-fold increase in the numbers of birds in the study area occurred and most were attracted to this small portion of the Sound. The decline in the numbers of murrelets in Trevor Channel through August reflected the fact that many birds had finished nesting and were leaving the Sound, as well as another change in distribution by remaining birds when they shifted to shoreline habitats. This decline also correlated with a change in the nature of the marine environment in south Trevor Channel by the intrusion of high salinity water over the sill in August (Carter, unpub. data). This change may have rendered prey for murrelets less available. The presence of herring in Dodger Channel, Satellite Passage and Loudoun Channel (Hourston 1958) may provide sufficient prey for smaller numbers of molting and HY birds. Molting and HY birds fed almost exclusively on herring (Table 2) and were found very close to shore usually in or near smaller channels in August to October (Carter, unpub. data). The decline in numbers of murrelets in periods 4 and 5 was further enhanced by wide dispersal of HY birds in shoreline areas. Sealy (1975a,b) also observed HY birds

feeding near kelp beds, close to shore at Langara Island. HY birds also occur in mixed flocks with molting AHY birds from August to October (Guiguet 1971a, in litt.; Carter, unpub. data).

Annual aggregations of Marbled Murrelets in Trevor Channel.

Marbled Murrelets apparently aggregate each breeding season in Trevor Channel. Guiguet (1971a) first reported this behavior when he observed large numbers there in June and July 1970, as well as in August of 1964, and each year between 1967 and 1970. Large numbers were also found there in July 1972 (Robertson 1974, in litt.), June and July 1980 (Chapters 2 and 3) and in June 1982 (Sealy and Carter, in press). Large numbers of murrelets aggregate in Trevor Channel each year probably because the food supply during the nestling period is reliable. At this time, juvenile herring are abundant because each year adult herring spawn at about the same time and use traditional spawning areas in the Sound (Hourston 1980). Although the abundance of spawn (and thus juvenile fish) varies from year to year, the immensity of the spawning in Barkley Sound (over 70% of the Lower West Coast population [Taylor 1964]) ensures that juvenile herring will be abundant each year. The clumping of this abundant prey resource in Trevor Channel each year is related to the traditional use of this location as a rearing area by juvenile herring. The denatant migration of juvenile fish to the rearing area is a regular feature of herring stocks in British Columbia (Taylor 1964) and elsewhere (Harden-Jones 1968, Horwood and Cushing 1978), and it occurs each year in Barkley Sound irrespective of yearly conditions (Hourston 1958, 1959a). Although similar information is not available for sandlance, it is probable that they are also abundant in

Trevor Channel each year due to their preference for sandy bottoms and channels, as well as their use of traditional spawning areas (Cushing 1981).

Other aggregations

The aggregation of Marbled Murrelets in Trevor Channel during the nestling period each year is not a peculiarity of this local environment. Although murrelets are often noted as common and widely distributed in the breeding season, they have also been referred to as locally abundant (Jewett et al. 1953, Gabrielson and Lincoln 1959, Martin and Myres 1969). Aggregations probably are a widespread feature of their distribution at sea but their existence has been documented poorly with existing techniques (Isleib and Kessel 1973, Bailey 1977, SOWLS et al. 1980, Wahl et al. 1981, Gould et al. 1982, Vermeer et al. 1983). Sealy and Carter (in press), alternatively, identified 9 large aggregations in Clayoquot and Barkley sounds on the west coast of Vancouver Island. These aggregations contained larger numbers of birds and consisted of many more flocks over a larger area than the aggregation of 55 birds observed by Sealy (1975a) in a small portion of Pillar Bay, near Langara Island. Observations elsewhere in British Columbia also indicate that large aggregations occur in many locations along the coast (Table 10).

Sealy and Carter (in press) noted that aggregations of Marbled Murrelets along the west coast of Vancouver Island were restricted to the mouths of inlets and channels at the boundary between nearshore and inshore waters, as well as inshore waters with sandy bottoms. Aggregations elsewhere in British Columbia also have been found in these

Table 10. Aggregations of 200+ Marbled Murrelets recorded in British Columbia outside of Trevor Channel. Sources include field notes of C.J. Guiguet (CJG) housed in the British Columbia Provincial Museum, Victoria, British Columbia. Locations of aggregations are indicated in Fig. 1.

Date	Locality	Numbers and comments	Source
<u>Summer records</u>			
Summer 1946	Masset Inlet	200 birds	Guiguet(1956)
7 Jul 1947	Tian Bay	120-200 birds, 3 HY (probably referred to as Frederick I. in Guiguet (1956))	CJG field notes
24 Jul 1947	Cumshewa Inlet	400+ AHY birds	CJG field notes
26 Jul 1947	Masset Inlet	200 birds (near to but not exactly the same area as in 1946)	CJG field notes
2 Jul 1948	Higgins Passage	300 birds, 5 HY	Guiguet(1953)
Summer 1948	Bardswell Is.	"concentration" (similar to those in Massett and Cumshewa inlets and Tian Bay)	Guiguet(1956)
25 Aug 1952	Sidney	150-200 birds, 3 HY	CJG field notes
3 Jun 1959	Cumshewa Inlet	200-400 birds (in same area as in 1947)	CJG field notes
30 May 1963	Oak Bay	200-300 birds during the past month	CJG field notes
21 Jul 1971	Langara Island	400 AHY, 35 HY birds (only 50 birds on 27 June 1971)	Sealy(1975b)
Jun 1982	Estevan Point to Cape Beale	6 aggregations (408, 422, 515, 417, 622, 3197 birds - includes Trevor Channel)	Sealy and Carter (in press)
<u>Winter records</u>			
6 Feb 1921	Bowen/Gambier Is.	300 birds	Munro (1921)
1 Oct 1953	Saltspring I.	several hundred (HY+AHY)	CJG field notes
10 Dec 1972	Point Roberts	450 birds	Campbell <i>et al.</i> (1974)
25 Dec 1972	Point Roberts	237 birds	Campbell <i>et al.</i> (1974)
Winter 1978/79	Point Roberts	100-500 birds	Wahl <i>et al.</i> (1981)
Winter 1978/79	Boundary Bay	100-500 birds	Wahl <i>et al.</i> (1981)
12 Nov 1981	Malaspina Inlet	300+ birds	G. Kaiser <i>in litt.</i>
12 Jan 1982	Mission Pt.	200+ birds	G. Kaiser <i>in litt.</i>

habitats primarily during the nestling period. Breeding murrelets apparently aggregate around local prey concentrations in these habitats as shown in Trevor Channel. Many of these localities occur near herring spawning areas (Hourston 1980) and juvenile herring may be an important prey resource in these areas. It is interesting that the aggregation observed by Sealy (1975a) at Langara Island (Cloak Bay) is not located near a herring spawning area and that sandlance is the main prey resource in that area (Sealy 1975b).

Whether other aggregations persist elsewhere from year to year, as they appear to in Trevor Channel, is not known. Guiguet's (1950) observations suggested that birds did not aggregate in the same locality in successive years. However, upon examination of his unpublished field notes, it is evident that aggregations did occur in or near the same locality in Masset and Cumshewa inlets in different years as shown in Table 10 (see also Guiguet 1971b). Aggregations of murrelets also have been reported in winter in British Columbia (Table 10) and other parts of their range (Jewett et al. 1953, Forsell and Gould 1981). Interestingly in British Columbia, although these localities are not known to have aggregations of breeding murrelets, winter aggregations tend to occur in similar habitat types and possibly also are responses to concentrations of prey at that time.

CHAPTER 2
DISTRIBUTION AND FLIGHTS
OF MARBLED MURRELETS AT SEA DURING THE
NESTLING PERIOD

INTRODUCTION

Several workers have censused seabirds at sea to determine the sizes of populations and their distributions in relation to general features of the marine environment (e.g., King 1970; Brown et al. 1975a, b; Nettleship and Gaston 1978; Bradstreet 1979; Pocklington 1979; Harrison 1981; Wahl et al. 1981; Gould et al. 1982; Vermeer et al. 1983). Some of these workers examined inter-seasonal and inter-year differences but variation in distribution and numbers of birds at sea throughout the day have not been examined. Such variation is influenced by the movements the birds make while they are foraging at sea and when they move to and from nesting and roosting areas.

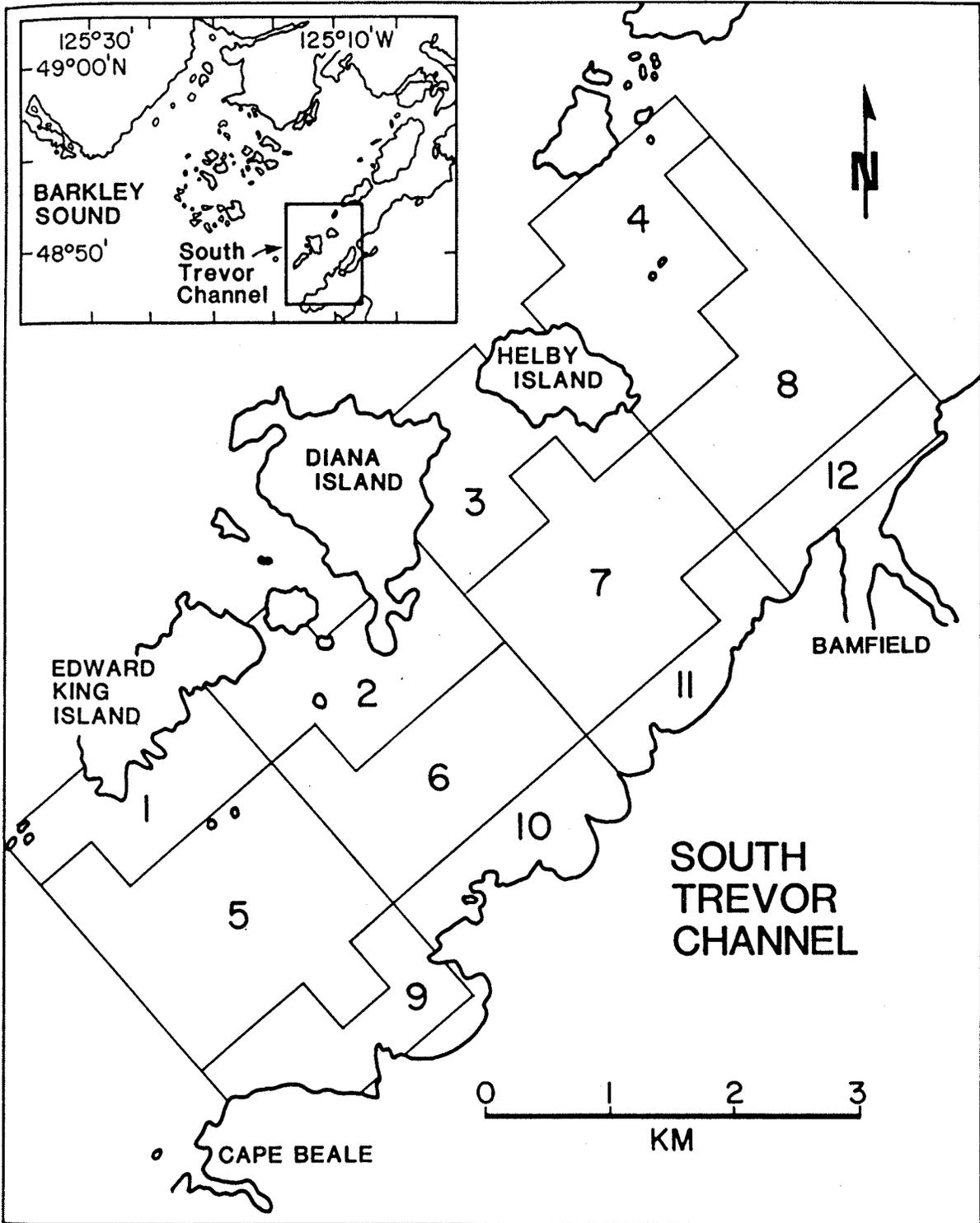
Marbled Murrelets (Brachyramphus marmoratus) use inshore and nearshore waters in summer and winter, apparently throughout their range, and often aggregate in well-defined feeding areas (Sealy 1975a; Sealy and Carter, in press; Chapter 1). The accessible and concentrated nature of their aggregations at sea provides a focal point for an analysis of temporal and spatial patterns of their distribution and movements at sea. Marbled Murrelets are most aggregated during the nestling period (Chapter 1) when most birds have left their single young unattended at the nest (Simons 1980, Hirsch et al. 1981) and are feeding at sea during the day. Birds should forage most efficiently when raising young, and thus temporal and spatial patterns of distribution at sea that are influenced by their foraging behavior should be detectable at this time (Norberg 1977). I use patterns of the distribution and movements of Marbled Murrelets at sea to construct a descriptive model of daily foraging behavior during the nestling period.

METHODS

Marbled Murrelets were censused 37 times, between 16 June and 6 July 1980 (see Chapter 3), in Trevor Channel, British Columbia. A contiguous quadrat grid was established such that all of the south Trevor Channel and Satellite Passage was censused where large numbers of murrelets had aggregated during the nestling period the previous year (Chapter 1). The grid was composed of 96 quadrats (each quadrat = 0.25 km² in area) and encompassed an area of 23.7 km² of nearshore waters (see Chapter 3 for a complete description of the grid). The number and size of all flocks of Marbled Murrelets that were sitting on the water or flying were recorded in each quadrat on each census. Each census was conducted from a pneumatic boat, powered by an outboard motor, as the boat passed through the center of each quadrat. Murrelets were observed up to a distance of 250 m on both sides of the boat. During censuses, it was not possible to distinguish the age, sex, or breeding status of after-hatching-year (AHY) birds. Marbled Murrelets observed on the water and flying were analyzed separately, but flocks that were observed landing or taking off were lumped with birds sitting on the water. Censuses were conducted at 4 times of day (PDT): dawn (0500 h, n=6 censuses); morning (1000 h, n=10 censuses); afternoon (1500 h, n=9 censuses); and dusk (2000 h, n=12 censuses). Each census took 2.0±0.3 (mean±SD) hours of censusing over 2.0-2.5 hours in the area. Dawn, morning, and afternoon censuses required similar mean lengths of time (2.1, 2.1 and 2.2 hours, respectively) while dusk censuses were shorter (1.7 hours).

The grid in south Trevor Channel was divided into 12 regions (Fig. 8) to facilitate the detection of patterns of use by Marbled Murrelets sitting on the water in different parts of the grid. Three

Fig. 8. Twelve regions used to describe the distribution of Marbled Murrelets in south Trevor Channel (see text for method of delineating regions). Regions are described in Table 11.

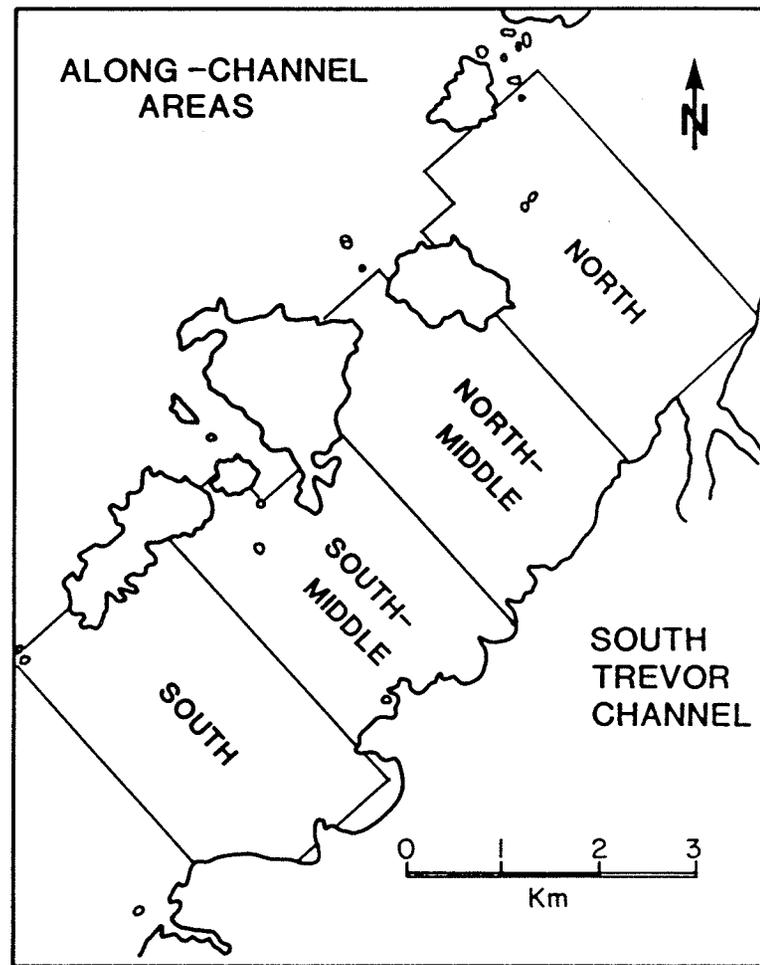
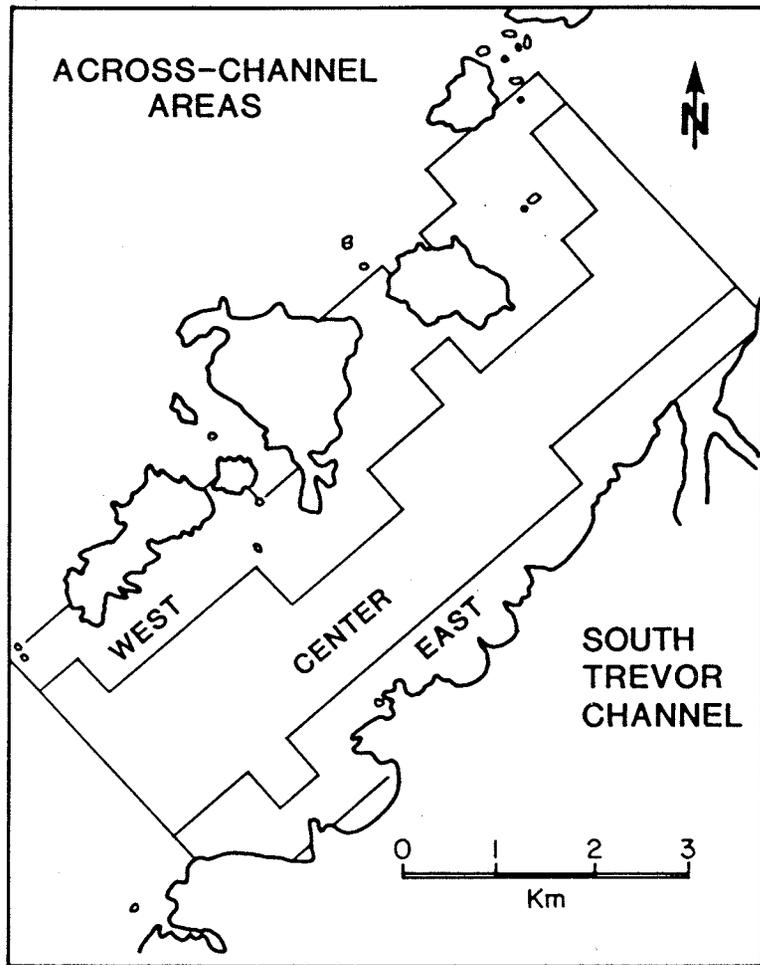


considerations were basic for establishing the regions so as to represent habitats and feeding sites of murrelets: 1) the system of regions should be simple; 2) the quadrats within a region should be similar so as to promote homogeneity within regions; 3) regions should be compact (i.e., only contiguous quadrats should be combined and they should be closely knit rather than forming a long string) (see Cliff *et al.* 1975). Murrelets clumped in areas of ≤ 0.25 , 1.5 and 6.0 km² which corresponded largely with coastline and sill habitats in the grid (Chapters 1,3). Regions varied from 1.0-3.5 km² (Fig. 8) and therefore their sizes approximated the area of 1.5 km² clumps of murrelets. Boundaries between regions were established so they they did not bisect clumps of birds in the grid, and quadrats in coastline regions were 500 m from shore (measured from the center of the quadrat). The different sized regions reflected the different water surfaces in these locations and each region formed a geographic unit.

Within the grid, regions were grouped into areas along and across the channel (Fig. 9) so that flights and fish-holding behavior of birds on the water could be analyzed. Murrelets usually flew in straight lines in the grid and along one of the two major axes of the channel. Birds flew in small flocks below the tops of the forested coastlines such that all birds that flew over each quadrat were detected. The direction of a bird's or flock's flight was recorded when the bird or flock was first observed; thus, changes in direction within the grid were not detected.

The number of birds that were observed flying depended mainly on how much time was spent in a quadrat while counting birds on the water. This time was proportional to the size of the area and hence different

Fig. 9. Across- and along-channel areas used to describe flights of Marbled Murrelets in south Trevor Channel (areas were formed by combining regions in Fig. 8).
Across-channel areas: west (regions 1-4; 7.3 km^2), center (regions 5-8; 11.8 km^2), east (regions 9-12; 4.6 km^2).
Along-channel areas: south (regions 1, 5 and 9; 6.4 km^2) south-middle (regions 2, 6 and 10; 5.1 km^2), north-middle (regions 3, 7 and 11; 5.6 km^2), north (regions 4, 8 and 12; 6.6 km^2).



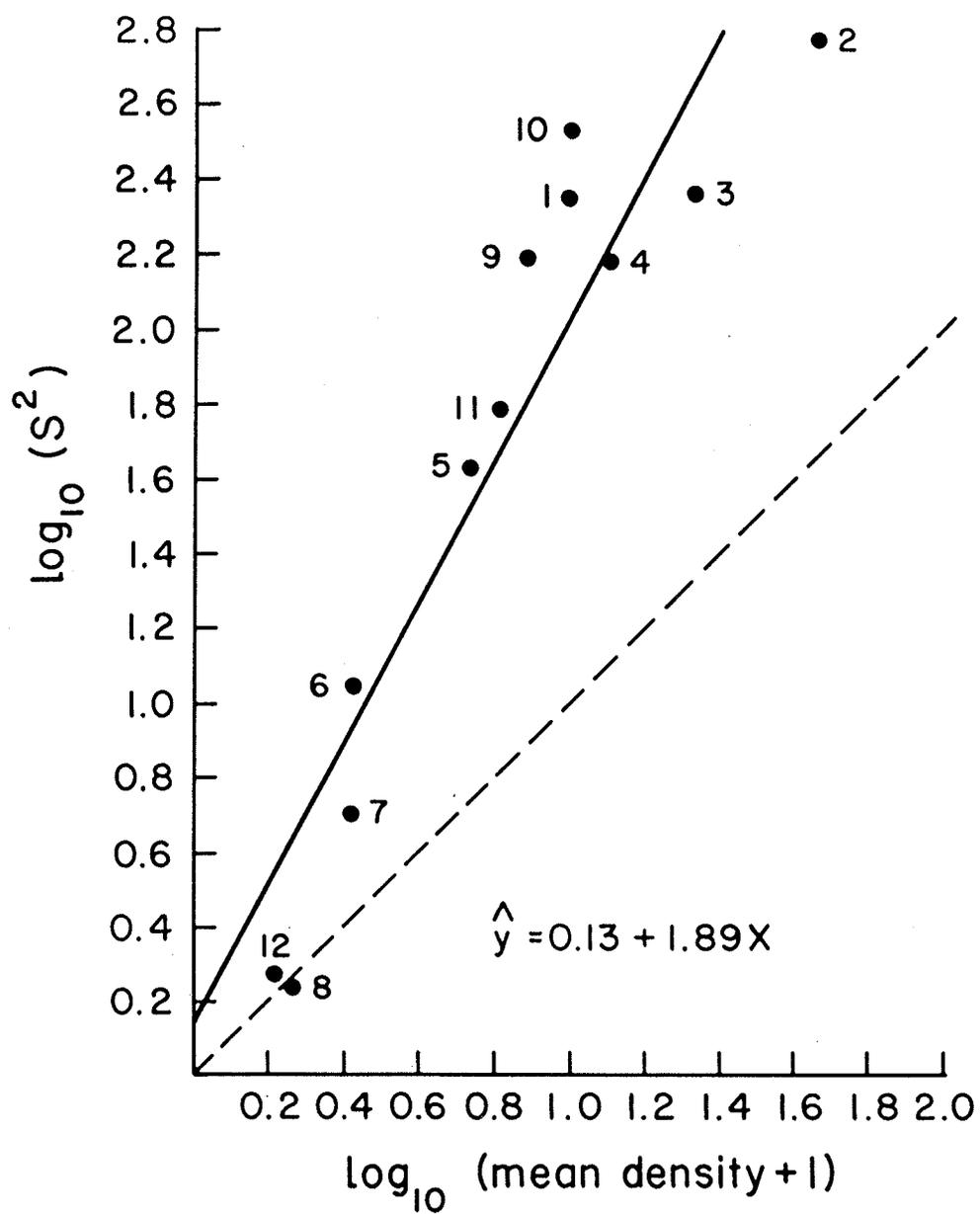
times were spent in different areas of the grid: 0.5, 0.4, 0.5, and 0.6 mean hours were spent in south, south-middle, north-middle and north areas, respectively, while 0.6, 1.0, and 0.4 mean hours were spent in west, center and east areas, respectively. A relative index of flights (number of birds flying/census hour) was used to examine flights over different areas of the grid.

Although I focused on the relationship of time and area to abundance (May 1975), tide and weather were also examined because they are known to influence the number and distribution of birds at sea. (e.g., Bradstreet 1979). Tide state was determined indirectly for the time of the census midpoint using Canadian Tide and Current Tables (Fisheries and Oceans Canada 1980) adjusted for the secondary port of Bamfield which is adjacent to the grid. Tide state was described by tide direction and current indices. The tide direction index was divided into 3 stages: 1) flood or incoming tide (n=17 censuses); 2) ebb or outflowing tide (n=17 censuses); 3) slack (high or low) tides (n =3 censuses). The tide current index was the rate of change in water level between slack tides. The tide current index was divided into 4 levels: 1) low (0-0.25 m/h, n=7 censuses); 2) medium-low (0.26-0.35 m/h, n=12 censuses); 3) medium-high (0.36-0.45 m/h, n=10 censuses); and 4) high (0.46-0.55 m/h, n=8 censuses). Tide indices, although rough measures of tide state, were deemed appropriate in the grid where tidal water movements occur primarily along the channel (R.E. Thomson, pers. comm.). Information on weather was obtained from the Cape Beale lighthouse just south of the grid (Fig. 8) and included sky, visibility, rain/fog and sea state conditions as well as the speed and direction of the wind.

The numbers of murrelets sitting on the water in the regions were expressed as densities (birds/km²) to preclude differences caused by the different sizes of regions. Before statistical analyses, densities and the numbers of birds flying/hour were transformed logarithmically [$\log_{10}(x + 1)$] because sample variances were greater than sample means and 1 was added to each count because some regions and areas did not contain any birds. This general transformation is often used for small samples from contagious distributions because it normalizes the frequency distribution of counts, eliminates the dependence of the variance on the mean, and ensures that the components of the variance are additive which is required for analysis of variance and other parametric tests (Elliot 1971, Neter and Wasserman 1974). Post-hoc comparison tests [Sheffé's S test and Games-Howell procedure (Kirk 1982)] were used to identify pair-wise differences between means after one-way analysis of variance tests had indicated that differences existed.

To justify using changes in mean density (regardless of variation around the mean) to indicate regional and grid use by murrelets, the $\log_{10}(\text{mean density} + 1)$ of Marbled Murrelets was plotted against $\log(S^2 \text{ or variance})$ for each region in Trevor Channel (Fig. 10). Variance is here used as a measure of stability of local population density in a region. The power law (Taylor 1961) states that the variance of a population is proportional to a fractional power of the arithmetic mean: $\sigma^2 = a \mu^b$ and therefore $\log \sigma^2 = \log a + b \log \mu$ (Elliot 1971). The linear regression, $\hat{y} = 0.13 + 1.89 x$ (Fig. 10), indicated that the log transformation was appropriate since the slope was approximately equal to 2. Williams (1937) noted that changes in population density are proportional and hence logarithmic rather than arithmetic. The

Fig. 10. Regression of $\log_{10} (S^2)$ on $\log_{10} (\text{mean density} + 1)$ for the 12 regions (numbered as in Fig. 8) in south Trevor Channel. The dashed line indicates a random dispersion.



regression was linear and mean density accounted for 87% of the variance of the log variances. Marbled Murrelets, therefore, have a fixed, non-linear, functional relationship between temporal stability and mean density: $S^2 = 0.13 \times 1.89$; this relationship is presumably intrinsically controlled (Taylor and Woivod 1980). The unexplained variance is probably related to environmental stability in each region (see Chesson 1981). Environmental effects are then considered to act primarily on mean density which controls temporal stability through movements (Taylor and Woivod 1980); however, spatial stability could be governed by environmental patterns with no systematically correlated temporal sequence.

RESULTS

Patterns of densities of Marbled Murrelets

Numbers and thus densities of Marbled Murrelets on the water varied among the censuses, but large numbers of murrelets were always present compared to other areas outside the grid (i.e., murrelets were "numerically persistent" [Maynard Smith 1974] in the grid). Numbers of birds in the grid ranged from 74-518 birds/census while densities were between 3.1 and 21.9 birds/km². The high variances of the mean (\pm SD) number of 265.8 \pm 118.3 birds/census and mean (\pm SD) density of 11.3 \pm 5.0 birds/km² (Table 11) indicated that there was little tendency for numbers of birds in the grid to remain near an equilibrium point; thus, the population existed in a "quasi-equilibrium" state (Orians 1974, Maynard Smith 1974, Berryman 1981).

Mean densities of Marbled Murrelets in the grid (Table 12) were higher in dawn and morning censuses (14.4 and 13.9 birds/km²,

Table 11. Characteristics of the 12 regions in Trevor Channel and their use by Marbled Murrelets, 1980 (n = 37 censuses).

Region	Coastline (km)	Area (km ²)	Depth (m)	Mean No. (Birds) ± SD	Mean Density (Birds/km ² ± SD)
1	3.2	1.4	0-40	20.3±21.4	14.2±14.9
2	4.1	1.8	0-70	87.3±42.2	50.0±24.2
3	3.1	1.6	0-70	40.3±25.1	24.6±15.2
4	3.5	2.5	0-100	39.4±30.7	15.7±12.3
5	0	3.5	25-35	23.1±23.1	6.3± 6.5
6	0	2.3	20-70	7.1± 8.5	2.6± 3.4
7	0	3.0	30-100	7.4± 7.4	2.2± 2.2
8	0	3.0	70-120	3.9± 5.7	1.1± 1.3
9	3.7	1.4	0-25	15.7±17.7	11.0±12.4
10	4.0	1.1	0-20	16.5±16.6	16.1±18.3
11	2.7	1.0	0-50	8.9± 9.1	8.5± 7.8
12	1.6	1.1	0-60	1.1± 1.5	0.9± 1.4
Total	25.9	23.7	0-120	265.8±118.3	11.3± 5.0

Table 12. Mean densities (birds/km²) and mean log densities ($\log_{10} [\text{density} + 1]$) of Marbled Murrelets in the grid in relation to time of day, region and state of tide. Mean log densities that are not significantly different are underscored by a line (Sheffé's S Test for all pair-wise comparisons, $\alpha=.05$) or are indicated by NS (One-way ANOVA, $\alpha=.05$).

Variable		Ranked mean log densities											
Time of day ¹		1	2	3	4								
	\bar{X} density	14.4	13.9	11.0	7.7								
	\bar{X} log density	1.17	1.15	1.06	0.90								
Region ²		2	3	4	10	1	9	11	5	6	7	8	12
	X density	50.0	24.6	15.7	16.1	14.2	11.0	8.5	6.3	2.6	2.2	1.1	0.9
	X log density	1.66	1.33	1.10	1.00	0.99	0.88	0.81	0.73	0.42	0.42	0.26	0.21
Tide direction index ³		3	2	1									
	\bar{X} log density	1.14	1.08	1.00									
		NS											
Tide current index ⁴		1	2	4	3								
	\bar{X} log density	1.14	1.05	1.04	0.98								
		NS											

¹ Time of day: 1, dawn; 2, morning; 3, afternoon; 4, dusk (see methods).

² Regions are numbered 1-12 as in Fig. 8.

³ Tide direction index: 1, flood; 2, ebb; 3, slack (see methods).

⁴ Tide current index: 1, low; 2, medium-low; 3, medium-high; 4, high (see methods).

respectively) but decreased through the afternoon (11.0 birds/km²) to dusk (7.7 birds/km²). This decrease in mean densities is caused by "removal" of birds from the grid. Tide state did not affect mean densities in the entire grid (Table 12) or in any of the 12 regions tested alone (Table 13). Since the weather was fairly calm throughout (Fig. 11), its influence on mean density seemed unimportant. On 5 days where 4 censuses were conducted in one day, the highest numbers were counted at dawn (n=2 censuses), morning (n=2 censuses) or afternoon (n=1 census), but numbers were always lowest at dusk, when only $37.1 \pm 16.7\%$ (range 17.5-51.6%) of the highest number that day remained in the grid. On 11 days when more than 1 census was conducted, the mean densities decreased in 7 through the day, while on 4 days increases prevailed in morning or afternoon; on only 1 day, the numbers at dusk were higher than at other times of day (see also Carter and Sealy 1984). The amount of removal and time of day when it occurred varied, but generally mean density decreased from dawn to dusk. Since densities were higher again by the following dawn, the population is "cyclically stable" (Orians 1974) which contributes to its numerical persistence over time.

The population of Marbled Murrelets was distributed widely in the grid but nevertheless aggregated in certain regions (Tables 11,12) as also indicated by a Taylor's slope dispersion parameter greater than 1 in Figure 10 (Taylor 1961, Elliot 1971). The highest mean densities of birds were in regions 2 and 3 (50.0 and 24.6 birds/km², respectively). Regions along the west coastline of the channel contained higher mean densities than on the east; this pattern partly reflects the greater coastline habitat on the west (7.3 km²) compared to east (4.6 km²) side (Fig. 8, Table 11). Mid-channel regions generally supported lower mean

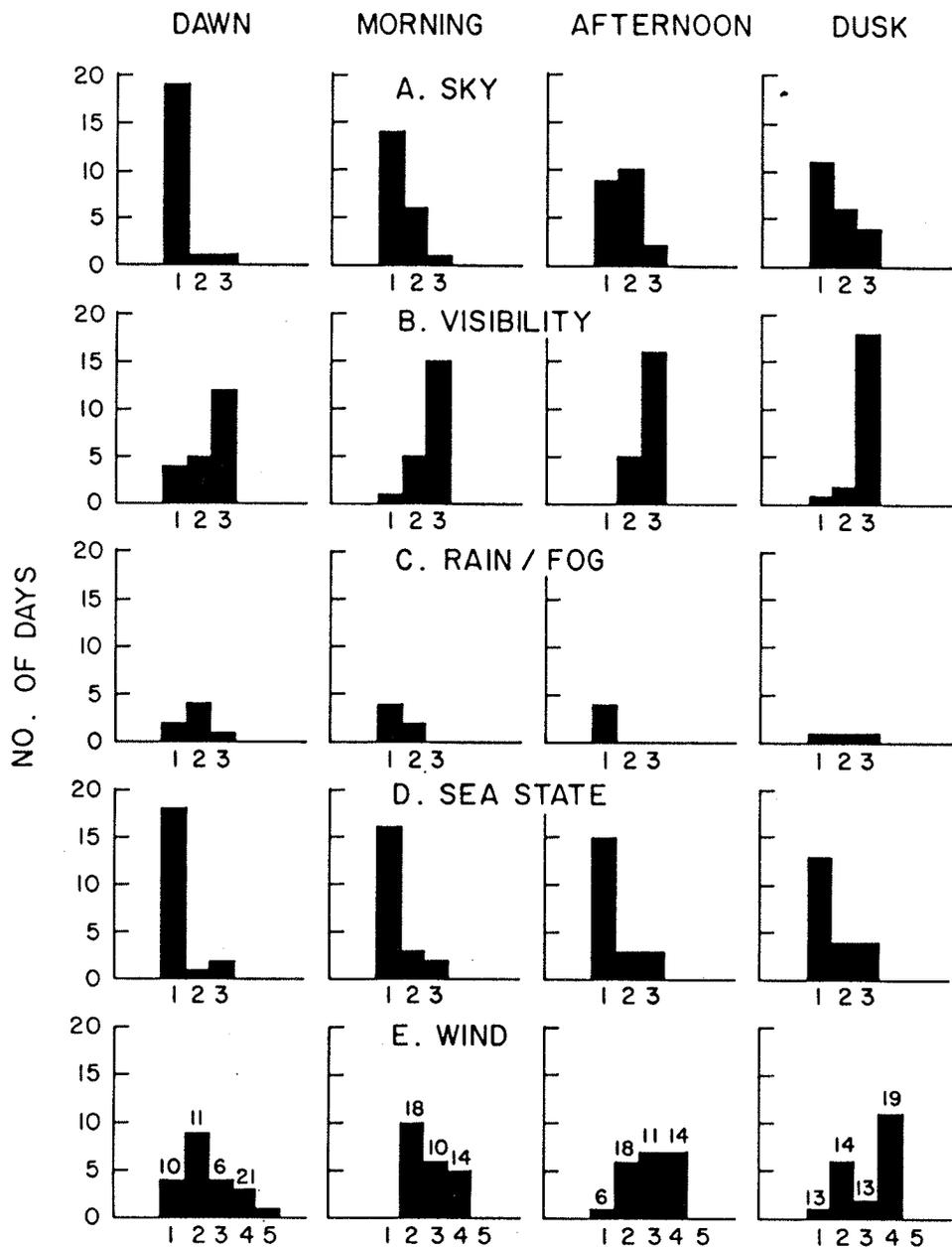
Table 13. One-way analyses of variance of transformed densities ($\log_{10} [\text{density} + 1]$) of Marbled Murrelets in south Trevor Channel, B.C., in 1980 ($n = 37$ censuses).

Region ¹	Variables			Mean density
	Time of day	Tide indices		
		direction	current	
2	2.0 NS ²	2.1 NS	0.6 NS	50.0
3	0.5 NS	0.8 NS	0.5 NS	24.6
10	7.7 ***	0.1 NS	2.0 NS	16.1
4	2.3 NS	1.0 NS	0.9 NS	15.7
1	15.1 ***	0.4 NS	1.3 NS	14.2
9	18.6 ***	<0.1 NS	0.4 NS	11.0
11	4.3 *	1.7 NS	2.0 NS	8.5
5	5.8 **	0.3 NS	1.7 NS	6.3
6	2.2 NS	0.4 NS	1.4 NS	2.6
7	0.7 NS	7.1 *	6.6 **	2.2
8	1.5 NS	0.2 NS	1.3 NS	1.1
12	0.9 NS	2.0 NS	0.5 NS	0.9
Total	5.5 **	1.3 NS	0.9 NS	11.3

¹ Regions 1 to 12 are ranked from highest to lowest mean density of Marbled Murrelets.

² F-ratio (ratio of the factor mean square to the residual mean square). The F-ratio is a measure of the significance of a factor. Significance is noted * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$; NS indicates no significant differences between variable levels.

Fig. 11. Weather variables by time of day during the 21-day study period. Times of day approximate times of censuses (dawn, 0630 h; morning, 1130 h; afternoon, 1445 h; dusk, 1930 h [PDT]). Weather variables are coded from 1 to 3: sky (overcast, partly cloudy, clear), visibility (0-8, 9-16, 17-24 km), rain/fog (rain, fog, both) and sea state (rippled, light chop, choppy). Mean wind speed is indicated per wind directions coded 1 to 5 (N-NE, E-SE, S-SW, W-NW, calm, respectively). A low south-westerly swell occurred throughout the study.

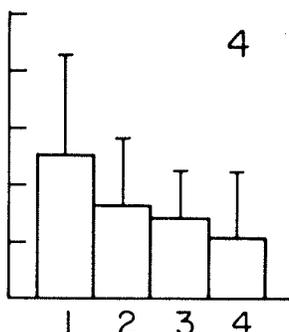
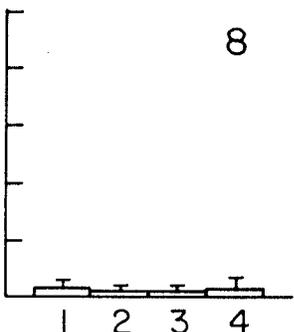
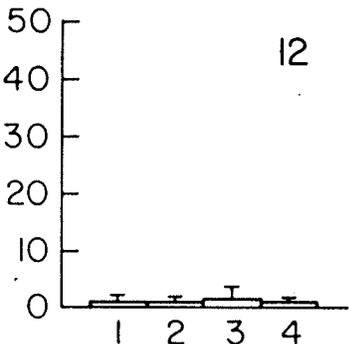
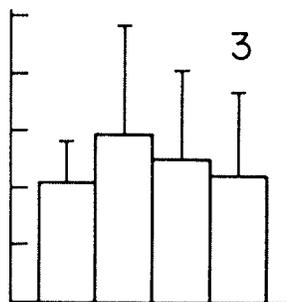
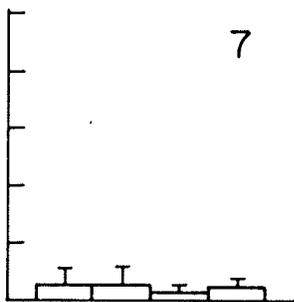
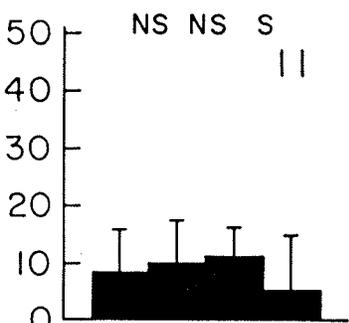
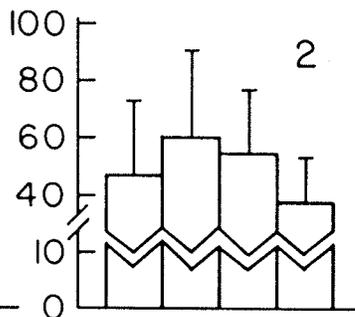
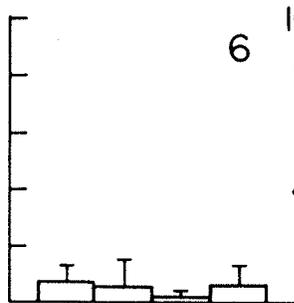
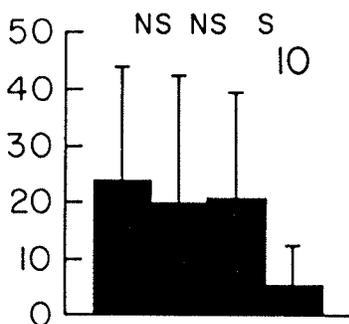
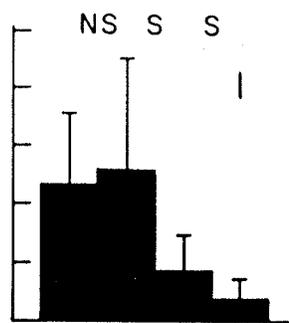
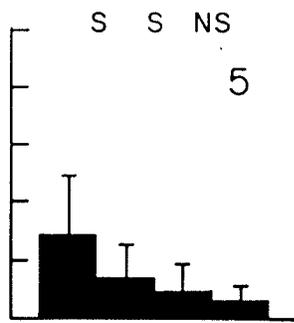
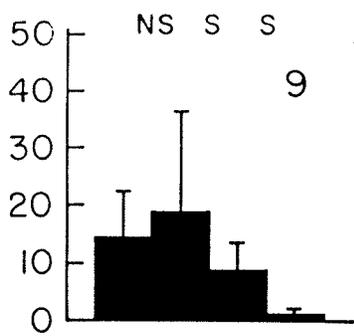


densities than did coastal regions, despite being the largest areas (2.3-3.5 km²). Since the areas of coastline and mid-channel habitats in the grid were about the same (11.9 and 11.8 km², respectively), coastal habitats were "preferred" (Wiens 1977). Region 5, over the sill where the water is shallower, had the highest mid-channel mean density (6.3 birds/km²) (Table 11, Fig. 8). In general, regions near or over the sill in south Trevor Channel (regions 1, 2, 5, 6, 9 and 10) had the highest mean densities.

All regions did not differ significantly in mean density over the day although mean densities decreased progressively in most regions from dawn/morning to dusk (Fig. 12, Table 13). Five regions that did differ significantly between times of day showed decreasing densities through the day (Table 12, 14). These regions were located across the sill (regions 1, 5 and 9) and along the east side of the channel (regions 10 and 11) where shallow waters extend inwards from the sill (Table 11). Regions that did not differ significantly with time of day were located mainly in the deeper mid-channel areas and along the west side of the channel by the Deer Group islands. The densities of birds in these regions differed (Table 12) and were classified as low-density regions (regions 6, 7, 8 and 12) and high-density regions (regions 2, 3 and 4). Regions that differed significantly with time of day were of intermediate mean densities (Table 13). In those regions, mean densities were comparable with high-density regions in dawn and morning censuses while, in afternoon and dusk censuses, they were comparable with low-density regions (Fig. 12, Table 14). Regions have different responses by murrelets during the day which is related to different mean densities in regions.

Fig. 12. Mean densities (birds/km²±SD) of Marbled Murrelets at different times of the day in 12 regions of south Trevor Channel. Time of day is coded: 1, dawn; 2, morning; 3, afternoon; 4, dusk. Significant differences between adjacent mean log densities (+1) are indicated by S; nonsignificant differences are indicated by NS (Sheffé's S Test, $\alpha = .05$). Regions with solid bars have significant differences between times of day while regions with open bars do not (Table 13).

MEAN DENSITY (BIRDS/km²)



TIME OF DAY

Table 14. Mean densities (individuals/km²) of Marbled Murrelets in each region of south Trevor Channel, B.C., by time of day, 1980 (n = 37 censuses).

Region	Time of day				Differences between ranked (transformed) means ²
	Dawn (DN)	Morning (M)	Afternoon (A)	Dusk (DK)	
1	23.4+12.4 ¹	26.0+19.3	8.7+ 6.1	3.9+ 3.3	M DN A DK
2	47.6+26.2	61.2+29.4	55.6+21.1	37.5+16.2	NS
3	21.0+ 7.2	29.3+19.3	25.1+15.5	22.2+14.7	NS
4	25.7+17.1	16.9+11.3	14.2+ 8.2	10.9+11.2	NS
5	14.2+10.2	7.0+ 5.5	4.6+ 4.5	3.1+ 2.3	DN M A DK
6	3.8+ 2.9	2.8+ 4.6	0.8+ 1.0	3.1+ 3.4	NS
7	2.7+ 2.9	2.7+ 3.1	1.3+ 1.2	2.3+ 1.6	NS
8	1.2+ 1.1	0.6+ 1.0	1.1+ 0.9	1.6+ 1.8	NS
9	14.2+ 8.0	18.4+17.7	8.4+ 4.9	0.8+ 0.8	M DN A D
10	23.9+20.1	20.1+22.7	20.5+18.8	5.5+ 7.1	DN A M D
11	8.7+ 7.1	10.0+ 7.3	11.2+ 5.0	5.1+ 9.8	A M DN DK
12	0.6+ 1.1	0.6+ 0.9	1.7+ 2.3	0.9+ 0.8	NS
Differences between ranked (transformed) means ²	2	2	2	2	
	4	3	3	3	
	3	1	10	4	
	1	10	4	1	
	10	4	11	5	
	9	9	9	10	
	5	11	1	11	
	11	5	5	6	
	6	7	12	7	
	7	6	7	8	
	8	8	8	12	
	12	12	6	9	

¹ Mean density (±SD) of birds on the water.

² Means that are not significantly different are underscored by a line (Sheffé's S Test for all pairwise comparisons, $\alpha=.05$) or are indicated by NS (One-way ANOVA, $\alpha=.05$).

Densities of murrelets in high-density regions varied less through the day than did those in intermediate-density regions because the rate of change of mean densities was lower (Orians 1974, Taylor and Woivod 1980). Densities of murrelets in low-density regions varied little because these regions were seldom used and thus constituted less suitable habitat in general. Differences in daily variation between high- and intermediate-density regions resulted from proportionately greater numbers of murrelets moving out of intermediate-density regions (Fig. 12). This resulted in more distinct differences in mean densities between regions at dusk (see Chapter 3). The mean densities in five coastal regions (regions 1, 2, 3, 9 and 11) increased from dawn to morning (Fig. 12), and corresponded to the decreased mean density in the adjacent region 5 (Fig. 12, Table 14). This probably indicated some within-grid movement at this time.

Flights of Marbled Murrelets

The total numbers of flying birds and the number of birds flying/hour varied considerably from one census to the next. In the grid, numbers of flying birds ranged from 7 to 163 birds/census while the numbers of birds flying/hour varied between 3.0 and 64.7 birds/hour. The high variance of the mean (\pm SD) number of 33.7 ± 29.5 flying birds/census and mean (\pm SD) number of 16.3 ± 12.7 birds flying/hour (Table 15) indicated that flights did not occur at a constant rate. More birds flew/hour at dawn (37.4 birds/hour) than morning, afternoon and dusk (11.1, 9.3 and 15.2 birds/hour, respectively) which did not differ significantly (Table 15). Most flights occurred at dawn when the most birds were on the water in the grid. Most flights were north and south

Table 15. Mean numbers of Marbled Murrelets flying/hour by time of day and direction of flight in Trevor Channel, B.C., in 1980 (n = 37 censuses).

Flying direction	Total	Time of day				Differences between ranked (transformed) means ¹			
		Dawn (DN)	Morning (M)	Afternoon (A)	Dusk (DK)	DN	DK	M	A
North (N)	6.0 _± 5.2 ²	14.1 _± 6.6	4.3 _± 2.6	2.4 _± 2.0	6.1 _± 3.4	DN	DK	M	A
South (S)	6.3 _± 5.9	14.6 _± 9.8	3.6 _± 2.1	3.6 _± 2.1	6.3 _± 3.7	DN	DK	A	M
West (W)	2.7 _± 2.4	6.6 _± 3.0	2.0 _± 1.5	1.5 _± 1.0	2.4 _± 1.6	DN	DK	M	A
East (E)	1.6 _± 2.5	2.2 _± 1.2	1.3 _± 1.5	1.9 _± 4.5	1.2 _± 1.6	NS			
Differences between ranked (transformed) means ¹	S N W E	N S W E	N S W E	S N W E	N S W E				
Total	16.3 _± 12.7	37.4 _± 16.6	11.1 _± 5.2	9.3 _± 4.0	15.2 _± 7.5	DN	DK	M	A
Total with fish	0.4 _± 0.8	0.1 _± 0.2	0.1 _± 0.2	0.3 _± 0.2	1.0 _± 1.2	DK	A	M	DN

¹ Means that are not significantly different are connected by a line (Sheffé's S test for all pair-wise comparisons, $\alpha=.05$) or are indicated by NS (One-way ANOVA, $\alpha=.05$).

² Mean (\pm SD) number of Marbled Murrelets flying/hour.

and accounted for 75.5% of the daily movements while east-west movements accounted for only 24.6% (Table 15).

Marbled Murrelets did not fly randomly in the grid. Most movement across the channel occurred generally over the west and center areas with fewer flights in the east area (Table 16). Most movement along the channel occurred over the south area of the grid whereas similar numbers of flights were recorded in other areas. (Table 16). Areas where greater movements occurred, generally were associated with regions with intermediate and high densities of birds on the water. The high numbers of birds flying/hour in the center area which generally had low at-sea densities is related largely to the greater number of flights in the south area where region 5 is located (the only mid-channel area with an intermediate mean density) (Fig. 8, Table 11). More flights to the north and south occurred in south and south-middle areas. West movements were greatest in north and south areas and most of the east movements occurred in the south area (Table 16).

Dawn movements. At dawn, more birds flew north (into the grid) than south in the south area and more birds flew south (into the grid) than north in the north area of the grid (Fig. 13). There was no difference between north and south movements in south and north-middle areas at dawn. Some birds apparently flew through the north area of the grid (Satellite Passage) from north of the grid to other feeding areas in Imperial Eagle Channel without travelling through most of the grid (Figs. 8, 13). The few eastward flights through Satellite Passage at dawn suggest little reciprocal exchange through the Passage (Fig. 13). There also was more movement to the north and south in the west and center areas, which indicated directional flying movements across the

Table 16. Mean numbers of Marbled Murrelets flying/hour by area and direction of flight in south Trevor Channel, 1980 (n = 37 censuses).

Flying direction	Across-Channel Areas			Differences between ranked (transformed) means	Along-Channel Areas				Differences between ranked (transformed) means ¹	
	Total	West (WT)	Centre (CR)		East (ET)	South (SH)	South Middle (SM)	North Middle (NM)		North (NH)
North (N)	6.0 _± 5.2 ²	6.9 _± 7.5	7.2 _± 7.5	1.5 _± 4.7	CR WT ET	11.3 _± 13.9	9.5 _± 12.5	3.6 _± 4.4	2.6 _± 3.5	SH SM NM NH
South (S)	6.3 _± 5.9	9.3 _± 8.8	6.1 _± 7.7	1.7 _± 2.4	WT CR ET	5.6 _± 6.2	8.1 _± 7.6	0.5 _± 1.9	1.3 _± 3.2	SH SM NH NM
West (W)	2.7 _± 2.4	5.9 _± 6.7	1.7 _± 1.8	0.2 _± 0.7	WT CR ET	3.8 _± 4.1	4.0 _± 4.5	0.7 _± 1.9	1.9 _± 9.5	NH SH NM SM
East (E)	1.6 _± 2.5	2.0 _± 3.1	1.9 _± 4.7	0.2 _± 0.9	WT CR ET	3.2 _± 5.3	3.0 _± 5.5	5.8 _± 6.7	0.6 _± 1.7	SH SM NH NM
Differences between ranked (transformed) means ¹	S N W E	S N W E	N S W E	S N W E		N S W E	N S W E	S N W E	W N S E	
Total	16.3 _± 12.7	23.8 _± 19.2	16.4 _± 16.4	3.5 _± 6.9	WT CR ET	26.6 _± 29.7	14.8 _± 14.3	9.9 _± 10.8	12.4 _± 13.6	SH SM NH NM
Total with fish	0.4 _± 0.8	0.6 _± 1.3	0.4 _± 1.0	0.1 _± 0.5	WT CR ET	0.3 _± 0.7	0.7 _± 1.9	0.5 _± 1.2	0.2 _± 0.8	NS

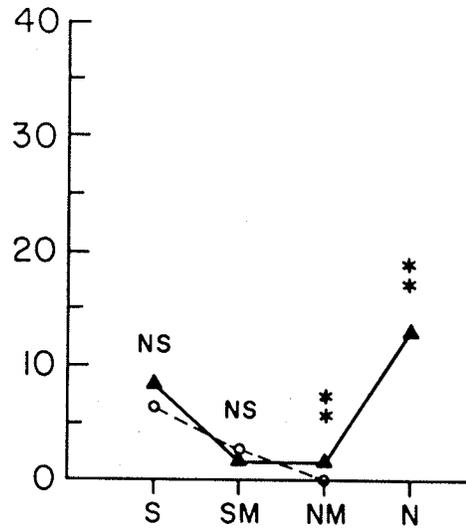
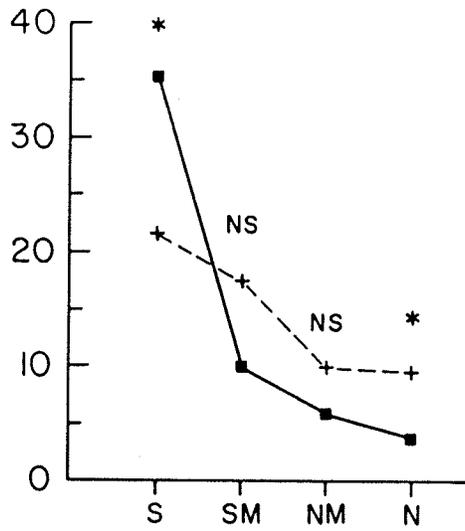
¹ means that are not significantly different are connected by a line (Sheffé's S Test for all pair-wise comparisons, $\alpha=.05$) or are indicated by NS (One-way ANOVA, $\alpha=.05$).

² mean (\pm SD) number of Marbled Murrelets flying/hour.

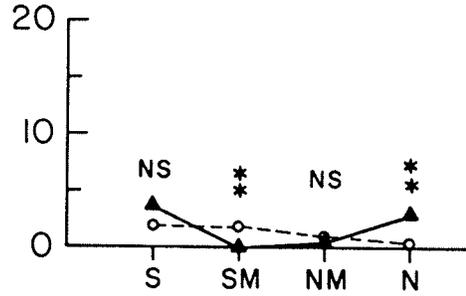
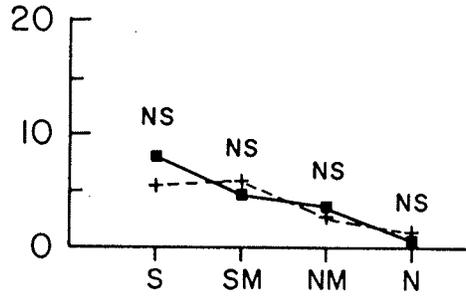
Fig. 13. Mean numbers of Marbled Murrelets flying/hour by time of day, along-channel area and flying direction. In the left column of the figure, the numbers of birds flying north (solid line) are compared to those flying south (dashed line); in the right column, birds flying west (solid line) are compared to those flying east (dashed line). Along-channel areas are coded: S, south; SM, south-middle; NM, north-middle; N, north area (see Fig. 10). Significant differences between directions of flight in each area are indicated by * ($\alpha = .10$) and ** ($\alpha = .05$); nonsignificant differences are indicated by NS (One-tailed t-test).

MEAN NO. MARBLED MURRELETS FLYING/HOUR

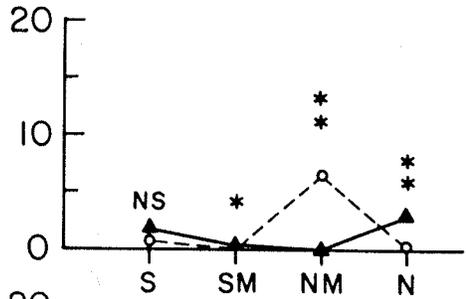
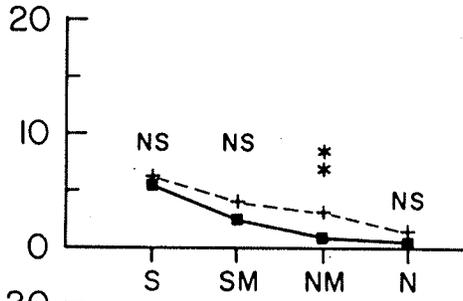
DAWN



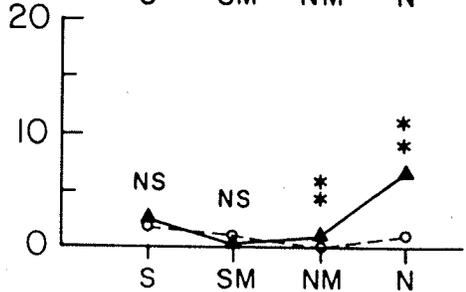
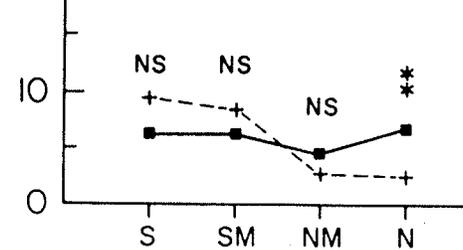
MORNING



AFTERNOON



DUSK



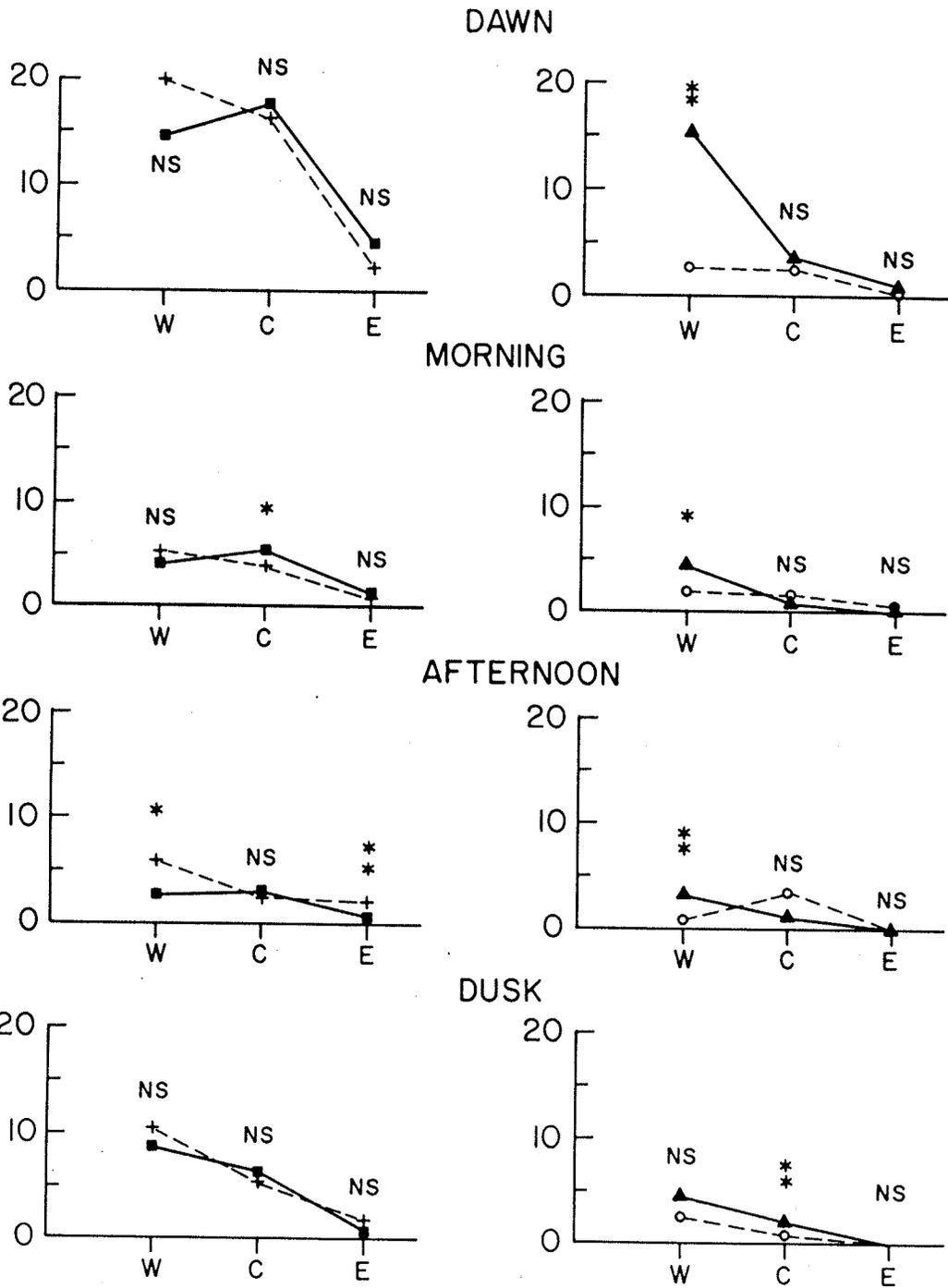
channel (Fig. 14). Along the channel, movement was highest over the sill (south and south-middle areas). On the sill, more birds flew north than south, while inside the sill (north and north-middle areas) more birds flew south than north (Fig. 13). Thus, it appeared that many birds flew directly towards the sill and the west coastal areas of the grid.

Morning and afternoon movements. After dawn, slightly more movement occurred near the sill than in other areas (Fig. 13) when densities decreased in sill regions (Fig. 12, Table 14). In general, however, there was little difference between along- or across-channel areas in the numbers of birds flying/hour or in the directions of their flight (Figs. 13, 14). The little movement in morning and afternoon represent low amounts of within-channel movement and removal from the grid.

Dusk movements. At dusk, murrelets would be expected to move towards their nesting sites (Simons 1980, Hirsch et al. 1981). Although the total number of flights at dusk did not differ significantly from morning and afternoon (Table 15), the number of birds in the grid was lowest. Therefore, increased movement probably occurred relative to the proportion of flying birds that originated from sitting birds in the grid. More birds flew south (out of the grid) than north in the south area and more birds flew north (out of the grid) than south in the north area of the grid at dusk (Fig. 13). The direction of flight changed near the sill where more birds flew north than south inside the sill while more birds flew south than north over the sill (Fig. 13). Most movement occurred in west and center areas as found at dawn (Fig. 14). Therefore, the directions of flight were the reverse of that at dawn,

Fig. 14. Mean numbers of Marbled Murrelets flying/hour by time of day, across-channel area and flying direction. Across-channel areas are coded: W, west; C, center; and E, east (see Fig. 9). Other symbols and tests as in Fig. 13.

MEAN NO. MARBLED MURRELETS FLYING / HOUR



suggesting that birds probably were returning to the nesting sites from whence they came at dawn. Still more birds flew west than east through Satellite Passage at dusk, as at all other times of day (Fig. 13); therefore, some movement between feeding areas at sea also occurred at dusk.

Patterns of Marbled Murrelets holding fish

In the grid, numbers of birds holding fish (while on the water) ranged between 0 and 26 birds/census while densities ranged between 0 and 1.0 birds/km². The mean (\pm SD) number of 3.9 ± 4.9 birds/census and mean (\pm SD) density of 0.17 ± 0.21 birds/km² indicated that birds holding fish were observed infrequently and occurred in low numbers during the study (Table 17). Similarly, few birds holding fish as they flew were counted (range 0 and 5 birds/census) while the numbers of fish-holding birds flying/hour ranged between 0 and 3.3 birds/hour. The mean (\pm SD) number of 0.8 ± 1.3 birds/census and the mean (\pm SD) number of 0.4 ± 0.8 birds/hour also indicated that fish-holding behavior occurred infrequently and in low numbers while flying (Tables 15, 16). At least one bird, however, was observed holding a fish on 86.5% of the 37 censuses conducted over the study period. Although fish-holding was a persistent behavior during the nestling period, the mean density of fish-holding birds on the water accounted for only 1.5% of the total mean density of birds on the water. The mean number of fish-holding birds flying/hour similarly accounted for only 2.5% of the total mean number of birds flying/hour.

The highest densities of fish-holding birds and the highest numbers of fish-holding birds flying/hour were recorded at dusk (0.27 birds/km²

and 1.0 birds/h, respectively (Tables 15,17). These values were only slightly higher than those at other times of day, however, such that significant differences were found only between the censuses at dawn and dusk. (Tables 15, 17). Since at-sea densities and movements decreased from dawn to dusk, the proportions of fish-holding birds increased from 0.2% of the mean density at dawn to 3.5% at dusk and 0.3% of the mean number of birds flying/hour at dawn to 6.6% at dusk.

The densities of birds holding fish did not differ significantly between the regions, due largely to the low frequency of this behavior in the grid. To examine more general trends, regions were grouped into the same areas that also were used for the analyses of flying patterns. There were no significant differences between across-channel areas at any time of day (Table 17). There was also no within-day differences in the densities of birds holding fish in west and east areas. In the center area, however, densities of fish-holding birds were significantly higher at dusk than dawn (Table 17). This trend contrasted with the general pattern of at-sea densities in mid-channel, where densities were lowest at dusk, even though most regions in this area contained low densities of birds throughout the day (Fig. 12). There were no significant differences between along-channel areas at each time of day but, overall, mean densities of fish-holding birds were higher in the south-middle area than in the north area (Table 17). Only the north-middle area had within-day differences in densities of fish-holding birds, probably due to the proportionately greater increase at dusk compared to other along-channel areas. There were no significant differences between the numbers of fish-holding birds flying/hour in along-channel areas at each time of day, although

Table 17. Mean densities (individuals/km²) of Marbled Murrelets holding fish by time of day and area in south Trevor Channel, 1980 (n = 37 censuses).

Channel Areas	Total	Time of day				Differences between ranked means ¹
		Dawn (DN)	Morning (M)	Afternoon (A)	Dusk (DK)	
West (W)	0.13±0.20 ²	0.05±0.11	0.18±0.30	0.18±0.23	0.08±0.09	NS*
Center (C)	0.17±0.32	0.01±0.03	0.08±0.09	0.11±0.13	0.35±0.51	DK A M DN
East (E)	0.11±0.19	0.04±0.09	0.04±0.09	0.12±0.16	0.18±0.29	NS*
Differences between ranked means ¹	NS	NS	NS*	NS	NS*	
South (S)	0.14±0.22	0	0.20±0.31	0.19±0.25	0.10±0.15	NS
South middle (SM)	0.27±0.34	0.13±0.20	0.16±0.20	0.28±0.28	0.42±0.48	NS
North middle (NM)	0.11±0.22	0	0.04±0.07	0.06±0.13	0.27±0.33	DK A M DN
North (N)	0.07±0.20	0	0.02±0.05	0.03±0.10	0.19±0.31	NS*
Differences between ranked means ¹	SM S NM N	NS	NS*	NS	NS	
Total	0.17±0.21	0.03±0.04	0.10±0.12	0.19±0.17	0.27±0.28	DK A M DN

¹ Transformed means [$\log_{10}(\text{density} + 1)$] that are not significantly different are connected by a line (Games-Howell procedure for all pairwise comparisons, $\alpha = .05$) or are indicated by NS (One-way ANOVA, $\alpha = .05$). An asterisk indicates heterogeneous variances and test results were verified using the Games-Howell procedure.

² Mean (\pm SD) density (birds/km²) of Marbled Murrelets holding fish.

overall, more fish-holding birds flew in west compared to east areas (Table 16).

DISCUSSION

The synthesis of temporal and spatial patterns of at-sea distribution, flights and fish-holding behavior of Marbled Murrelets in Trevor Channel permits a descriptive model of daily foraging behavior during the nestling period to be developed (see Wiegert 1979). The understanding of foraging behavior in the general contexts of how patches are selected and when and how frequently they are used permits the evaluation of daily variation in the distribution and numbers of Marbled Murrelets in feeding areas at sea. Foraging and patterns of movement, however, would be expected to differ between adults that are feeding nestlings, adults that are still incubating, non-breeders and failed breeders. Birds that are feeding a nestling at a nest site must also feed themselves, and as such are central-place foragers (Orians and Pearson 1979). Incubating Marbled Murrelets spend about 24 hours on the nest, followed by about 24 hours at sea feeding themselves before returning again to the nest (Sealy 1974, 1975 a, b). Non-breeding birds spend time at sea feeding only themselves. These groups would also be expected to occur in different proportions in Trevor Channel during the study period. Although murrelets were censused during the nestling period, undoubtedly some birds were still incubating (Carter and Sealy 1984, see also Chapter 1). Non-breeders feed at sea along with breeders during the breeding season and constitute approximately 15% of Marbled Murrelet populations during this time (Sealy 1975 a, b).

Daily patterns of foraging

The highest mean density and highest mean number of birds flying/hour were recorded in the grid at dawn (Tables 12, 15). Since more birds moved into the grid than out (Fig. 13), this behavior suggests that breeding birds were returning directly from their nest sites. However, because many birds already were present in the grid by this time, many individuals must have flown to the grid at night or simply remained there all night. Large numbers of Marbled Murrelets returned directly to the grid each day suggesting further that murrelets have learned the location of the feeding area and that it provides a reliable source of food (Chapter 1). If birds searched randomly, they would be expected to accumulate over the day instead of occurring in the highest numbers at dawn. Within the grid, the clumped distribution of birds probably reflects birds aggregating over smaller patches of prey within the grid, especially along coastlines and over the sill. The major prey species, the Pacific Herring (Clupea harengus) and Pacific Sandlance (Ammodytes hexapterus), are probably more abundant in these habitats (Chapter 1). Non-random flights by birds at dawn (where more birds fly over intermediate- and high-density regions) suggests that birds learn the whereabouts of specific feeding sites and simply return to them or that they are attracted to certain areas, perhaps by the continual presence of other birds on the water, an example of foraging by "local enhancement" (Thorpe 1963). The re-establishment of a similar distributional configuration at sea each day indicates that prey are spatially stable in the grid at dawn which provides the basis for feeding-site selection largely through learned associations with habitat or habitat-birds in the habitat (Chapter 3).

In the morning and afternoon, mean densities varied in the grid but generally decreased (Fig. 12); also fewer flights occurred at these times (Table 15). Less movement and a similar distribution pattern at dawn suggest that birds stayed within certain regions in the overall feeding area (see Chapter 3). This behavior promoted the relationship between mean density and stability (Fig. 10) and explained why densities of murrelets in high-density regions varied less throughout the day than those in intermediate-density regions (Fig. 12). Movements resulted in a decreased number of birds in the grid because more birds left the grid than came to it, and presumably flew to other feeding areas. Some within-channel movements also occur, particularly over the sill (regions 1, 5, 9) where numbers declined more rapidly. This may indicate that the availability of prey here changes somewhat at this time, with a concomitant movement of birds to coastal regions. Some coastal regions indeed experienced an increase in the number of murrelets from dawn to morning. By dusk, most birds had left the grid and the lowest mean density of birds on the water prevailed. Substantial numbers (37%) of birds, however, were still present on the water in the grid at dusk (Table 14, Fig. 12). These birds may have spent the night in the grid or flown to the nest later at night.

Foraging by birds feeding nestlings

Observations of birds holding fish tell much about the foraging behavior of adult Marbled Murrelets that are feeding nestlings. Marbled Murrelets are mainly "single prey loaders" (Orians and Pearson 1979; Chapter 1; Carter, unpub. data) and capturing and holding prey for nestlings precludes capturing more prey or feeding themselves. It appears to be disadvantageous to capture and hold prey destined for nestlings early in the day, at the expense of not feeding themselves until after they visit the nest at night. Thus, an a priori expectation would be that birds would hold fish only near dusk, just before flying to the nest.

Few birds held fish when compared to the total numbers of birds in the grid. A greater proportion of birds, however, indeed held fish towards dusk (Table 17) which suggests that birds mainly feed nestlings at dusk and during the night, as has been suggested previously (Cody 1973; Sealy 1974, 1975a, b; Simons 1980; K.V. Hirsch, in litt.) A few birds, however, were observed holding fish at dawn and in the morning while on the water or flying. Marbled Murrelets have been also observed flying inland and holding fish in the morning during the nestling period in other areas (Summers 1974; Carter and Sealy 1983; Sealy and Carter, in press), which suggests that at least some birds feed nestlings during the day in Barkley Sound. Since very few birds held fish at dawn or in the morning, only a small proportion of the population (that are feeding nestlings) may feed young during the day. S.G. Sealy (pers. comm.) did not observe birds holding fish in the earlier part of the day at Langara Island, B.C.

Although more birds held fish at dusk on the water as well as while flying, these birds were still a small proportion of the total numbers of the birds on the water and flying, respectively. This low incidence of fish-holding behavior probably indicates that nestling prey are less available in Trevor Channel in the day than the prey birds consume themselves (see Chapter 1). This contrasts with what Guiguet (1956) found in Masset Inlet, B.C. in July 1946 where all murrelets in an aggregation of 200 birds were "packing feed" towards dusk. Birds in Trevor Channel did not hold fish more often in one region than another and only slightly more birds held fish over the sill (Table 17). This suggests that nestling prey are not clumped or abundant in Trevor Channel during the day. The increase in fish-holding birds from dawn to dusk, however, is matched by a decrease in overall numbers of birds in the grid. The proportion of birds (about 63%) that had left the grid by dusk corresponds roughly to the expected proportion of the population that are feeding nestlings. Since few birds in the grid were observed holding fish, movements of birds out of the grid during the day probably represent birds moving to other feeding areas to obtain prey for their nestlings. Variation in the amount of time spent in the grid by birds feeding nestlings may be due to feeding performance in a feeding site (Krebs 1978, 1979) and probably contributes to variation in densities in the grid in the morning and afternoon periods. By dusk, however, birds that still have not captured prey in the grid probably have moved to alternate feeding areas. Movements out of the grid become more advantageous as the day progresses because time spent fruitlessly in the grid reduces searching time at other possibly rewarding sites which previously yielded nestling food (see Schoener 1974, Norberg 1977).

Marbled Murrelets should choose their nestling food carefully, since they usually carry only one, large fish per trip to the nest which may be a considerable distance from where they captured the prey (Chapter I). More time and effort probably are required to procure the less available fish for young in Barkley Sound (Chapter I). The need to obtain at least one fish each day is great to maintain the relatively fast growth rate of the young (Simons 1980, Hirsch et al. 1981). Movements to alternate feeding areas occur before dusk to allow time to find nestling prey which also probably involves a change in food-searching behavior. Alternate feeding areas are widely distributed in Barkley Sound but are generally smaller and along coastlines and were used by smaller numbers of birds (see Sealy and Carter, in press). Alternate sites may also be learned since birds were observed consistently in small, well-defined areas in several parts of Barkley Sound. Since birds need to capture only a single fish, they can afford to move to and search in areas of lower prey densities even if this consumes more energy (Norberg 1977).

Descriptive model of daily foraging behavior

A general synthesis of movements between nesting areas, the feeding area in Trevor Channel, and to other feeding areas is presented in Table 18. Marbled Murrelets aggregate in Trevor Channel before and at dawn by flying directly from nesting areas to the feeding area whose location they have learned. Aggregation behavior results partly from the presence of abundant and reliable prey resources in the grid which provides the basis for "feedback control" (i.e. positive reinforcement) of this behavior (Maynard Smith 1974, Wiegert 1979). Birds feeding

Table 18. Synthesis of movements of breeding Marbled Murrelets between nesting areas, Trevor Channel and alternate feeding areas.

Time of day ¹	Relative amounts of movements ²	Comments ³
Dawn		Higher flying activity. Many birds (I + N) moving from nest to sea. A few birds (N) flying to nest to feed young.
Morning		Lower flying activity. A few birds (N) flying to the nests to feed young.
Afternoon		Lower flying activity. Some birds (N) flying to alternate feeding areas to find fish for young and a few flying to nests to feed young.
Dusk		Higher flying activity. Many birds (I + N) flying to nests; some (N) still moving to alternate feeding areas.
Night		Higher flying activity. Some birds (I) flying to nest and mate returning; many others (N) visiting nest (perhaps several times) (Carter and Sealy 1984, Chapter I).

¹ Night (2230-0500h).

² NA (nesting areas), TC (Trevor Channel), AFA (alternate feeding areas); thick, thin and dashed arrows refer to high, medium and low flying activity, respectively.

³ I (incubating adults), N (adults feeding nestlings); non-breeding birds are assumed not to be moving around at sea or to nests (regularly) and are not included.

nestlings, however, spend less time in the grid and move to alternate feeding areas to find fish for nestlings before returning to the nest.

The foraging behavior of Marbled Murrelets feeding nestlings is similar to that of a "time minimizer" (Schoener 1969, 1974; Norberg 1977) where maximal amounts of time are allocated to obtaining a fish for the young. By flying directly to Trevor Channel early in the day, birds "minimize" the amount of flying movement and search time (once on the water) required to feed themselves. Thus, birds apparently forage efficiently for themselves by specializing on the abundant and easily found resources early in the day in Trevor Channel. This behavior increases the time (and effort) available for searching for less abundant and more difficult-to-locate fish for the young later in the day in other areas (see Maynard Smith 1974, Norberg 1977). This strategy of foraging is enhanced by the timing of the nestling period which presumably occurs at the period when prey for adults is most abundant (Perrins 1970, Norberg 1977) as well as most aggregated in Trevor Channel (Chapter 1). The persistence of numbers of murrelets in the grid through the day is augmented by incubating and non-breeding birds. These birds probably stay at feeding sites in the grid throughout the day and thus reduce their movement and searching costs (Norberg 1977, Chapter 3).

CHAPTER 3
DISPERSION OF MARBLED MURRELETS AT SEA
DURING THE NESTLING PERIOD

INTRODUCTION

The dispersion of mobile animals in space and time results, in a proximate sense, from the direct response of individuals to features of their environment and to the presence or absence of other individuals of the same species (Brown and Orians 1970, Levin 1976, Pulliam 1978, Waser and Wiley 1979). Dispersion therefore plays an important role in the evolution of population structure and behavior (Cliff et al. 1975; Emlen and Oring 1977; Sokal and Oden 1978a, b; Baker and Marler 1980).

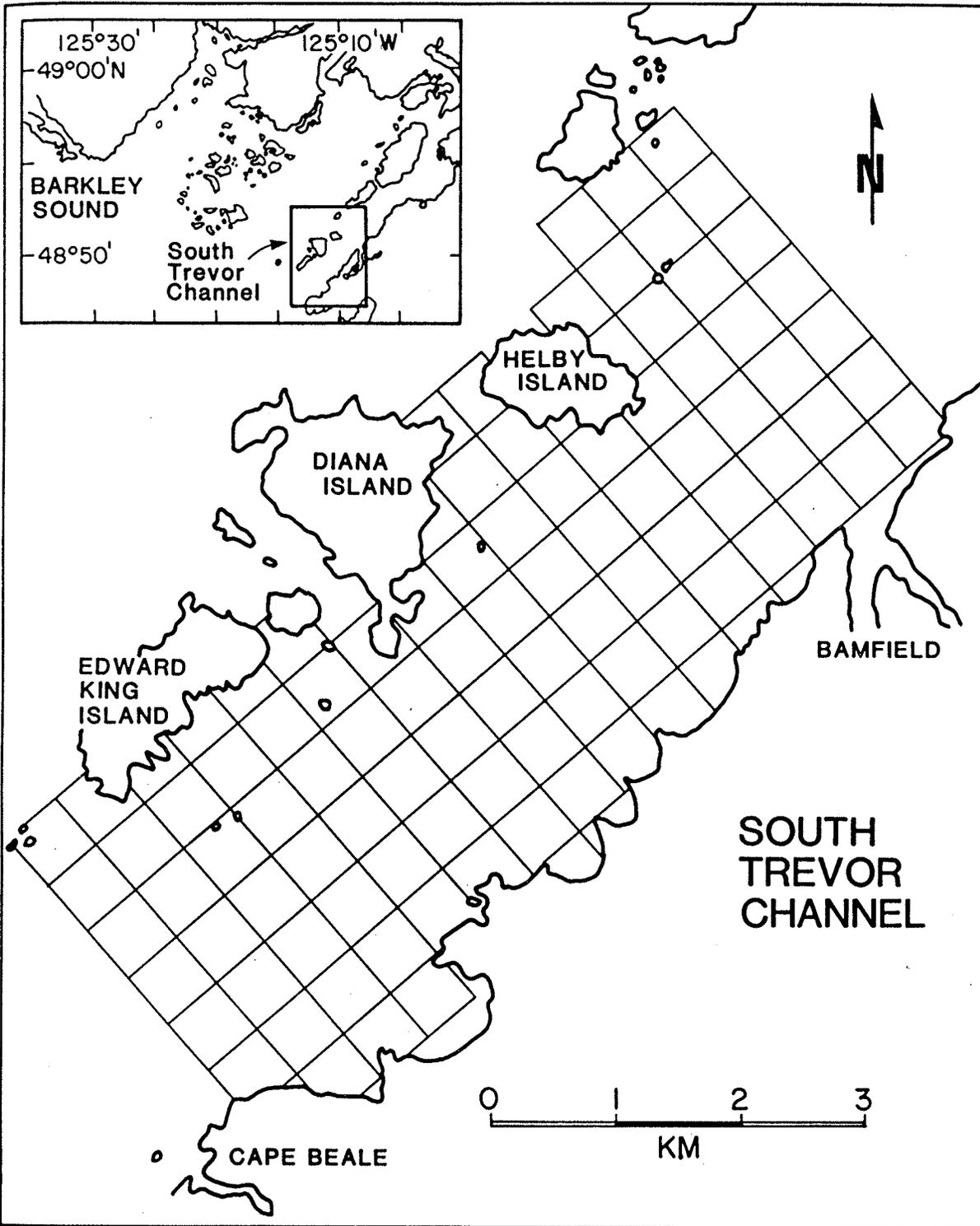
Marbled Murrelets (Brachyramphus marmoratus) nest solitarily (Sealy and Carter, in press) but many birds feed at sea in small geographically well-defined areas while breeding (Sealy 1975a, b; Chapters 1, 2). In this chapter, I determined the pattern of dispersion and sizes of flocks of Marbled Murrelets on a feeding area in Barkley Sound, British Columbia. Spatial patterns were examined in the context of "foraging strategies" (Schoener 1971, Krebs 1979) that they employ during the nestling period. While breeding, the largest numbers of Marbled Murrelets occur in feeding areas during the nestling period, because the single chick is left unattended at the nest during the day (Simons 1980, Hirsch et al. 1981) while both parents are at sea (Sealy 1975b; Sealy and Carter, in press). The parents return to the nest to feed the young only at night (see Chapters 1, 2). At this time in the breeding season, birds should be more efficient foragers when the population exerts maximal demand on local prey resources (Waser and Wiley 1979, Zach and Smith 1981). During this "sensitive period" (Bateson 1979, Mason 1979), behavioral skills involved in efficient foraging should be most evident (Chapter 2).

METHODS

Marbled Murrelets were censused 37 times between 16 June and 6 July 1980 in south Trevor Channel, Barkley Sound, British Columbia. A contiguous quadrat grid was used (Fig. 15) and the number and size of all flocks of murrelets on the water were recorded in each quadrat on each census. Flocks of flying birds also were recorded but were not included in quadrat totals. Censuses were started at 4 times (PDT) of the day: 0500h (dawn, n=6); 1000h (morning, n=10); 1500h (afternoon, n=9); and 2000h (dusk, n=12). Censuses were conducted by one observer from a pneumatic boat powered by an outboard engine and required 2.0 - 2.5 hours to complete (Chapter 2). One to four censuses were conducted each day and no censuses occurred on 8 days of the 21-day period (see Carter and Sealy 1984). The census period generally coincided with the nestling period of Marbled Murrelets in this area (Chapter 1).

The grid was established where large numbers of murrelets regularly had occurred the previous year in south Trevor Channel (see Chapter 1). The size of the grid encompassed all of south Trevor channel. The smallest possible quadrat size was used to maximize the number of quadrats in the grid to gain as fine a picture of murrelet dispersion as possible. It was feasible to use a 0.25 km² quadrat because of the narrow width (2-3 km) of the channel. Boundaries of quadrats were determined by eye using features of the topography of the coastlines and a compass. Near coastlines, some partial quadrats resulted which were combined to keep quadrat size and shape constant. The shape of the channel promoted the rectangular shape of the grid, arranged in 9 rows along the channel and 16 columns across the channel. Column boundaries

Fig. 15. Contiguous grid of 96 quadrats in south Trevor Channel,
British Columbia.



matched channel constrictions for ease of quadrat boundary determinations. The grid therefore consisted of 96 quadrats and covered 23.7 km² of the water's surface.

The Marbled Murrelet is a good species in which to measure at-sea dispersion. Although murrelets are small and sometimes difficult to see especially at long distances, they nevertheless can be censused easily. The total numbers of murrelets are sufficiently small and concentrated to permit the study of a large fraction of the individuals of the local nesting population (see Sealy and Carter, in press). The two-dimensional structure of their environment facilitates quantitative analyses of dispersion patterns (Hurlbert and Keith 1979).

Several quadrat-count indices of spatial pattern have been developed (Patil and Stiteler 1974). Few indices, however, are applicable for the analysis of contiguous grids (Greig-Smith 1952, Morisita 1959). I chose a comprehensive method for analyzing spatial patterns that was developed on the basis of the relation of Lloyd's (1967) mean crowding index (\underline{m}^*) to mean density (\underline{m}) (Iwao 1968, 1972; Iwao and Kuno 1971). This method is applicable to contiguous grids. Mean crowding is defined as "the mean number per individual of other individuals in the same quadrat" (Lloyd 1967). This index acts as an absolute measure of the concentration of individuals but does not measure "crowding" as its name implies in the context of this paper (Iwao 1977). The $\underline{m}^*/\underline{m}$ ratio is called "patchiness" (Lloyd 1967) and measures concentration relatively. Often, \underline{m}^* is linearly related with \underline{m} . The intercept (α) is the "index of basic contagion" and indicates whether a single individual or a group of individuals is the basic component of the distribution. The slope (β) is the

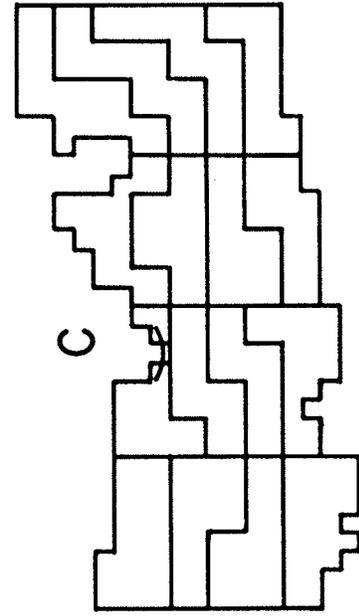
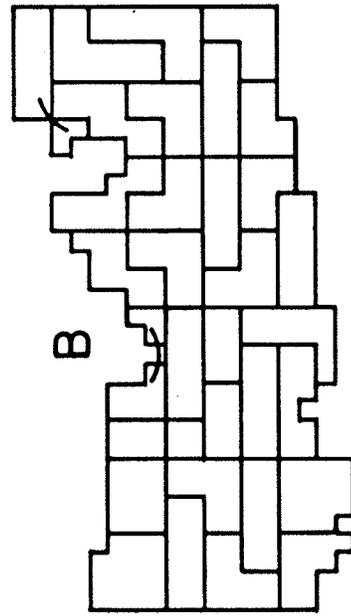
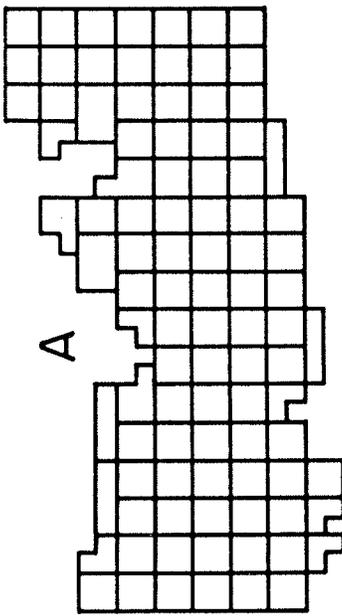
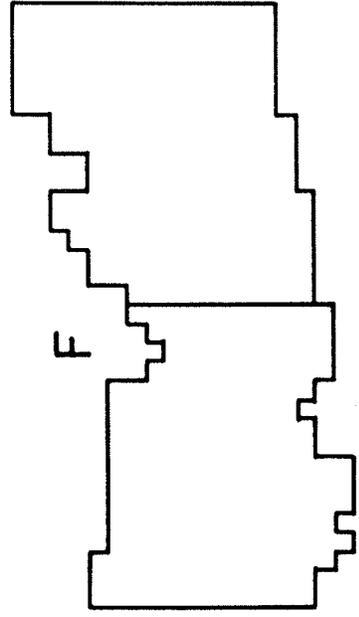
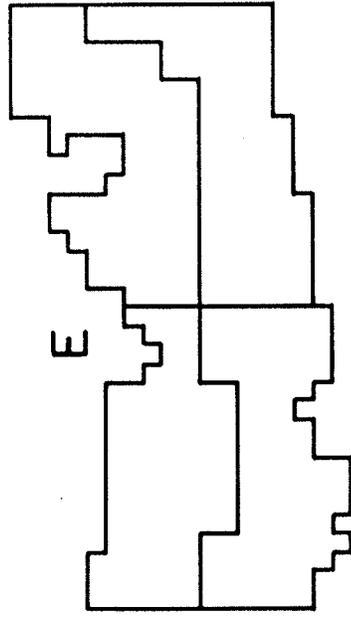
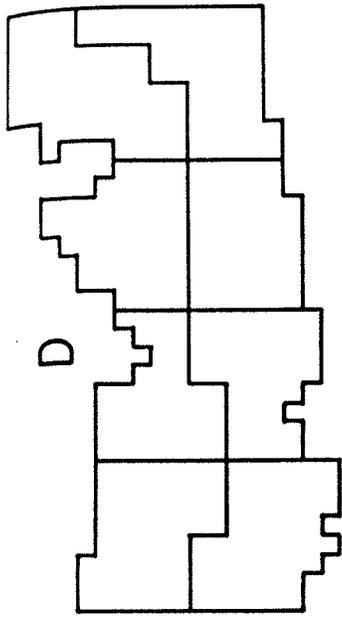
"density-contagiousness coefficient" and indicates how the basic components distribute themselves over the habitat (Iwao 1968).

The ρ index, which is obtained by successive changes in the \underline{m}^* to \underline{m} relationship with quadrat size, provides information about the spatial structure of the population (Iwao 1972).

Quadrat-count indices are often criticized because the choice of quadrat size is arbitrary (Patil and Stiteler 1974). To obtain quadrats of different sizes, I combined adjacent quadrats following a modified version of Greig-Smith's (1952) method for contiguous grids. In order to use the entire grid, 3 quadrats were combined first and then quadrat size was increased by a factor of 2 (see Fig. 16). This method produced 6 quadrat sizes (q): 0.25, 0.75, 1.5, 3.0, 6.0 and 12.0 km². There was some variability in quadrat sizes and shapes because the grid did not form a perfect rectangle.

In this chapter, the grid area is referred to as the feeding area which forms part of the potential "foraging habitat" (Orians 1981). A clump of murrelets is defined as a concentration of individuals within the feeding area resulting from aggregation due to environmental heterogeneity or patchiness, congregation due to intrinsic or social factors, or a combination of both (modified from terms and concepts in Moynihan 1960; Lloyd 1967; Iwao 1972; Wiens 1976; Morse 1970, 1977). The "operational" definition (Christensen 1980) of a sitting flock used to record flock size during censuses was a group of two or more birds sitting together on the water when observed (modified from Bertram 1978). Sitting flocks were perceptually discrete with each bird ≤ 1 m from another bird. Sitting flocks were often arranged in linear formations although large flocks were sometimes in compound-line

Fig. 16. Method of obtaining larger quadrat sizes in the grid. Diagrams are oriented west-to-east (top to bottom) and south-to-north (left to right). A through F refer to quadrat (q) sizes: (mean \pm SD): A ($0.25 \pm 0.03 \text{ km}^2/\text{q}$, $n=96\text{q}$); B ($0.75 \pm 0.12 \text{ km}^2/\text{q}$, $n=32\text{q}$); C ($1.50 \pm 0.18 \text{ km}^2/\text{q}$, $n = 16\text{q}$); D ($3.01 \pm 0.33 \text{ km}^2/\text{q}$, $n=8\text{q}$); E ($6.02 \pm 0.64 \text{ km}^2/\text{q}$, $n=4\text{q}$); F ($12.03 \pm 0.75 \text{ km}^2/\text{q}$, $n=2\text{q}$).



formations and were less discrete (see Heppner 1974 for descriptions of formations). A flying flock was a group of two or more flying birds that appeared to be coordinated when observed (modified from Heppner 1974). Flying flocks were usually coordinated in flight velocity and direction, with 5 m between individuals. Birds varied in vertical alignment and were visually less discrete than sitting flocks. Flying flocks were generally observed less than 10-15 m above the water. Single individuals were treated as a type of flock for ease of presenting the data. Flocks landing or taking off when observed were classified as sitting flocks.

It was not necessary to evaluate the effect of the presence of other species on the spatial distribution of Marbled Murrelets in south Trevor Channel. The mean density of Marbled Murrelets (11.26 birds/km^2) was much higher than other alcid species during censuses; Pigeon Guillemots (Cepphus columba), Common Murres (Uria aalge) and Rhinoceros Auklets (Cerorhinca monocerata) occurred in low mean densities (0.19 , 0.06 , and 0.02 birds/km^2 respectively) (Carter and Sealy 1984). Glaucous-winged Gulls (Larus glaucescens), California Gulls (L. californicus) and Pelagic Cormorants (Phalacrocorax pelagicus) were also present in low numbers. During 18 of the 37 censuses, gill-net fishing boats were present and averaged 2.0 boats/km^2 . Some murrelets were apparently attracted to gill nets but there was no apparent affect on their distribution (Carter and Sealy 1984). During censuses, I avoided disrupting birds on the water as much as possible.

RESULTS

Quadrat use

The frequency distribution of the number of birds/quadrat (0.25 km^2) was positively skewed with a mean (\pm SD) of 2.78 ± 7.89 and ranged from 0 to 161 birds/quadrat (Fig. 17a). This distribution suggested that the birds were clumped within the grid (χ^2 variance to mean ratio test, $d=310.6$, $p < .01$). Also, 61.1% of the quadrats censused ($n=3462$ q [90q omitted due to poor observing conditions]) contained no birds. Similarly, the frequency distribution of the mean numbers of birds/quadrat was positively skewed with a mean (\pm SD) of 2.88 ± 5.83 and ranged from 0 to 43.24 ± 28.50 birds/quadrat (Fig. 17b). This distribution suggested that birds were often clumped in certain quadrats (χ^2 variance to mean ratio test, $d=33.6$, $p < .01$); however, only in one quadrat were no birds ever recorded, indicating widespread use of the grid.

Occupied quadrats ($n=1347$) were arbitrarily divided into 4 classes with respect to density of birds: quadrats of low, medium-low, medium-high and high density contained 1-10, 11-30, 31-50 and 50+ birds, respectively (Table 19). Most occupied quadrats (82.2%) were low-density quadrats; medium-low, medium-high and high-density quadrats represented 13.4%, 2.7% and 1.7%, respectively. However, 38.7% of the total number of birds observed ($n=9626$) occurred in low-density quadrats; medium-low, medium-high and high-density quadrats represented 32.3%, 13.8% and 15.3%, respectively. Thus, although Marbled Murrelets were clumped, much of the population nevertheless occurred in low-density areas.

Fig. 17. Frequency distributions: A, the number of birds per quadrat ($n=3462$ q, from 37 censuses of 96 q); and B, the mean number of birds per quadrat ($n=96$ q, each censused 37 times).

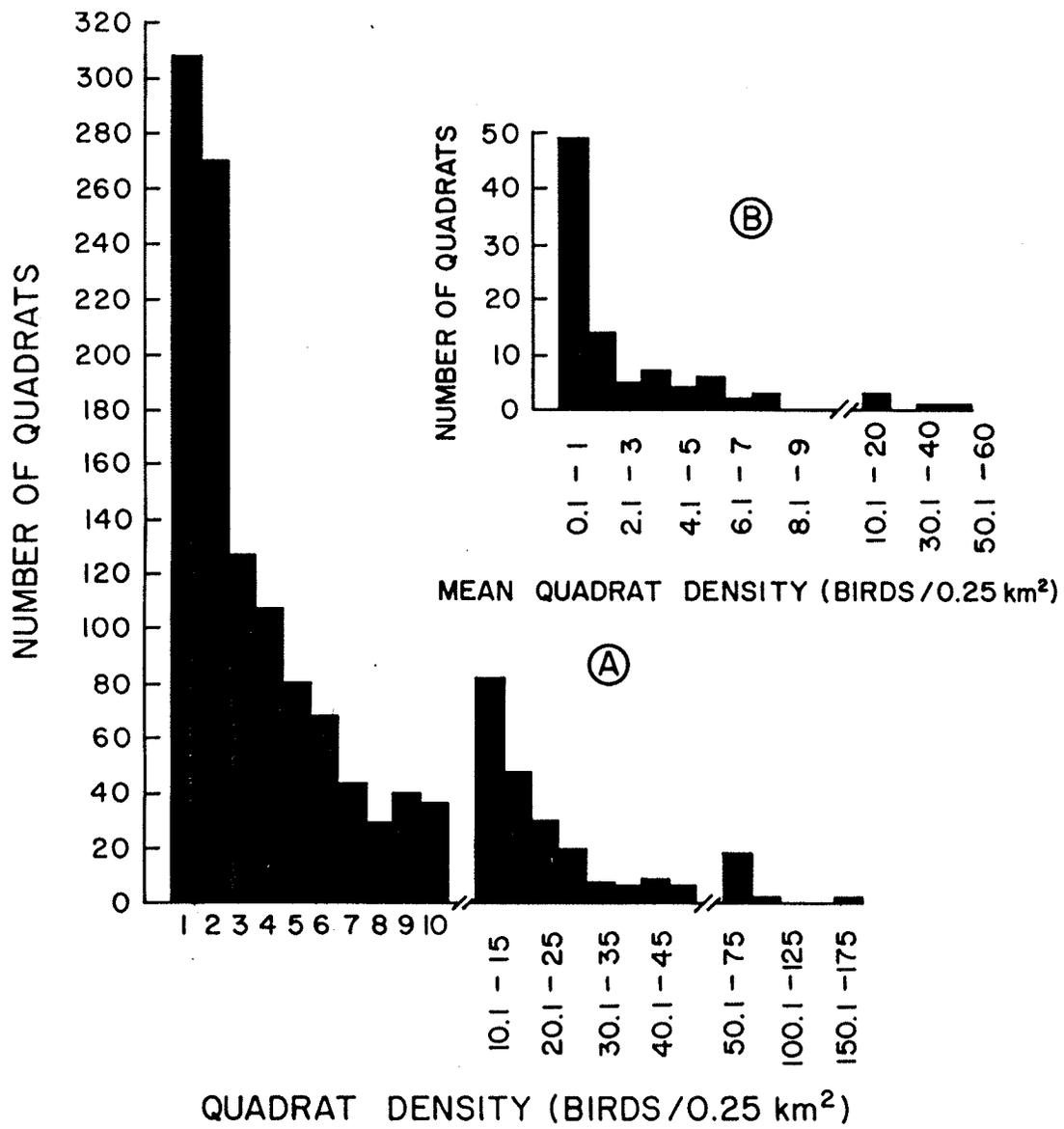


Table 19. Number of quadrats per density class by time of day in the grid in south Trevor Channel, 1980.

Time of day	No. of censuses	Quadrat density ¹					Total
		empty	low	medium-low	medium-high	high	
dawn	6	317	201	47	9	2	576
morning	10	577	300	61	12	10	960
afternoon	9	538	274	37	8	7	864
dusk	12	683	332	36	7	4	1062
total	37	2115	1107	181	36	23	3462

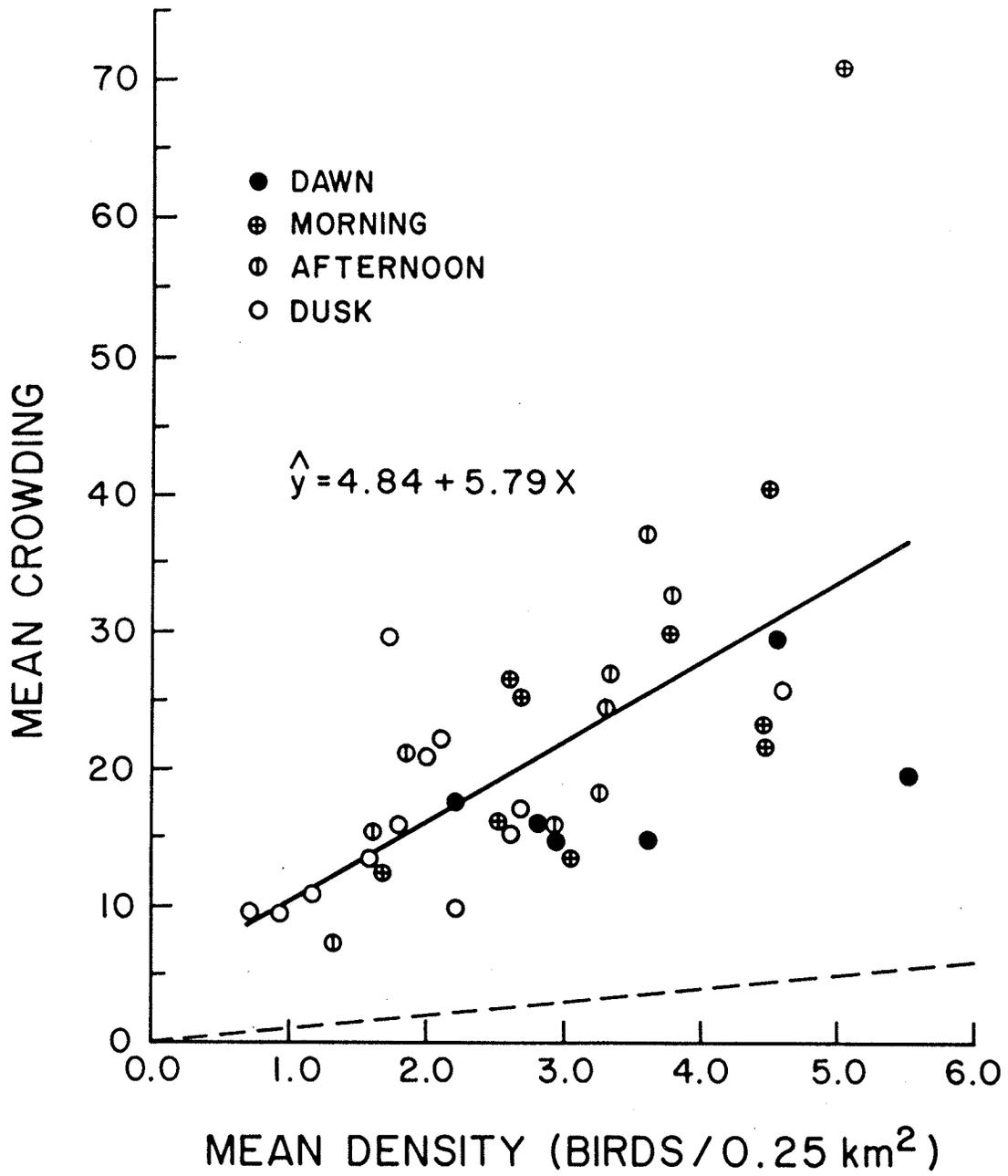
¹ See text for definitions of quadrat density.

Dispersion pattern

The regression of mean crowding (\underline{m}^*) on mean density (\underline{m}) (Fig. 18) was linear: $\underline{m}^* = 4.84 + 5.79 \underline{m}$ ($F=21.2$, $p < .001$, $r^2=0.38$). The fit of the data to a linear model indicated that the birds were dispersed in a definite pattern over a range of mean densities. Thus, the spatial pattern observed was density-independent using quadrats 0.25 km^2 in size. Scatter around the regression line could be caused by sampling errors, stochastic variation and biological reasons (Iwao 1977). However, residual plots did not indicate any curvilinear relationship (see Neter and Wasserman 1974). A distinct outlier occurred at high mean density suggesting that variation may occur at higher densities. High mean densities occurred infrequently during the study and did not create heterogeneity of variance around the line.

Separate regression lines for each time of day were not significantly different (ANOVA, $F=1.8$, $p > .05$). At dawn, however, there was a tendency to deviate from the overall regression line. The dawn line (with highest mean densities) fell below other times of day indicating a less clumped distribution. Also, the number of empty quadrats (55.0%) was lower at dawn than morning, afternoon and dusk (60.1%, 62.3%, and 64.3%, respectively). This factor increased the scatter around the overall regression line (Fig. 18). The non-zero intercept or index of basic contagion indicated that a small number of individuals/quadrat was the basic component of the distribution. Similarly, the mean number of birds/occupied quadrat indicated that on average 7.18 birds occur together in each quadrat. The slope or density-contagiousness coefficient was significantly greater than 1 ($t=$

Fig. 18. Linear regression of mean crowding on mean density.
The dashed line indicates the random dispersion
of basic components composed of single individuals.



28.8, $p < .05$). Thus, the dispersion of the basic components was non-random, being clumped in some quadrats.

Spatial structure: different quadrat sizes

In Table 20, \bar{m}^* on \bar{m} regression line components are presented for each of the 6 quadrat sizes obtained by combining adjacent quadrats. All regressions were fitted by linear models although the degree of fit increased with increasing quadrat size. The lines were significantly different (ANOVA, $F=17.8$, $p < .001$), including differing slopes (ANCOVA, $F=11.9$, $p < .001$) and adjusted means (ANCOVA, $F=18.9$, $p < .001$). All slopes were significantly greater than 1 (except $q=12.0 \text{ km}^2$) indicating clumped dispersions in all but the largest quadrat size. Separate regressions for each time of day within each quadrat size did not differ significantly.

Since the regression lines are not parallel and the slopes approach 1 as the quadrats get larger, clumps are loosely formed. Therefore, clumps vary in density or number in the grid. If the intercepts did not differ but the slopes did, this type of change with quadrat size would indicate an increase of clump density in high-density grid situations. If the slopes did not differ but the intercepts did, this would indicate an increase in clump size (and number) as density increases. The former case often occurs when clumps result from local habitat differences. The latter case often results from the intrinsic properties of the species affecting the dispersion. Since both the slopes and intercepts differ significantly, both of these clumping processes affect the dispersion pattern of Marbled Murrelets in the grid.

Table 20. Regressions of mean crowding on mean density by quadrat size (n=37 censuses). All regressions are significant ($p < .001$).

Quadrat size (km ²)	Intercept	Slope	r ²	F
0.25	4.84	5.79	0.38	21.2
0.75	7.61	2.96	0.58	48.3
1.5	7.44	2.49	0.69	78.9
3.0	6.09	1.65	0.82	161.5
6.0	-1.33	1.54	0.86	223.1
12.0	-3.59	1.13	0.93	462.4

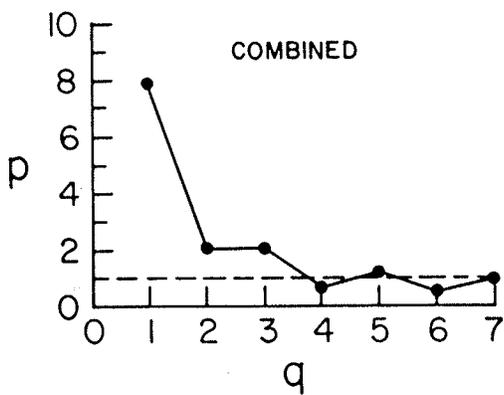
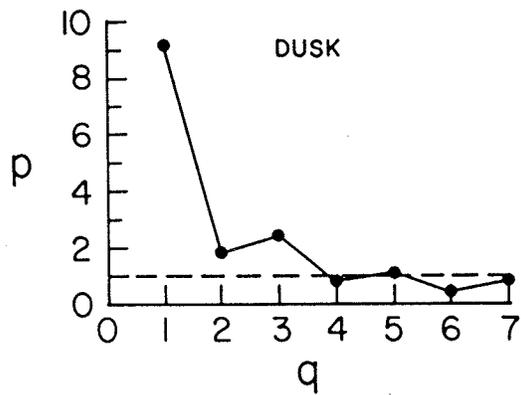
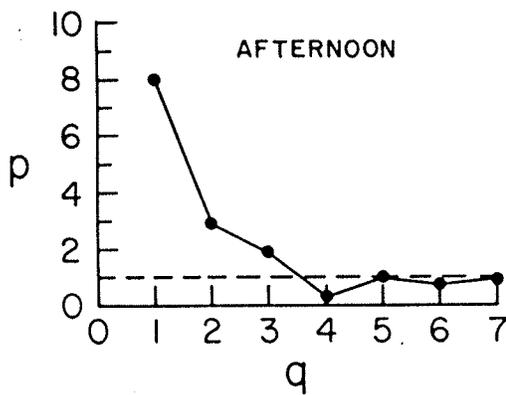
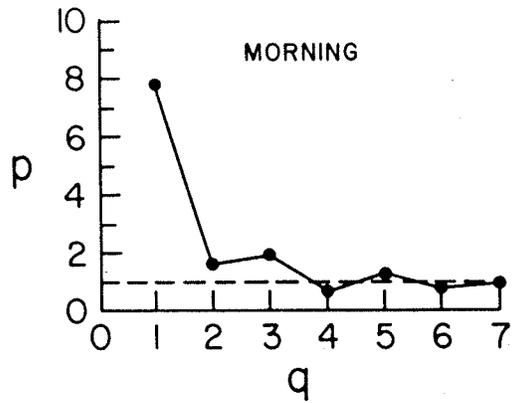
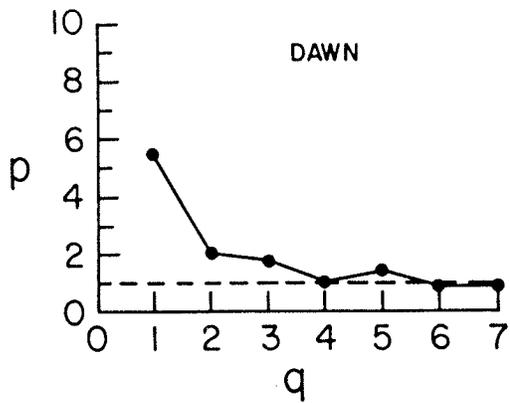
Spatial structure: habitat use

In Fig. 19, the ρ index is graphed by quadrat size for each time of day. This index detects spatial correlation between adjacent quadrats. It equals 1 when there is no correlation and is greater or lesser than 1 when positive or negative correlations exist, respectively. In all graphs, positive correlations occurred between adjacent quadrats. Large values occurred at smaller quadrat sizes while values fluctuated around 1 at larger quadrat sizes. The general shape of the ρ -graph indicates that basic components (> 1 individual) are clumped and that in large quadrats, the quadrat size becomes larger than the area occupied by all clumps. Therefore, the size of the grid used facilitated the detection of various levels of clumping.

Peaks in the ρ -graphs indicate that clumping occurred at several quadrat sizes. In Fig. 19, clumping occurred at 3 main spatial levels:

0.25, 1.5 and 6.0 km². The upward trend of values at $q=12.0$ km² may indicate that clumps also occur at larger quadrat sizes. Clumps appeared at regular quadrat intervals. A triple-clump structure existed with small (≤ 0.25 km²) clumps occurring in regularly-spaced medium (1.5 km²) clumps and medium clumps occurring within regularly-spaced large (6.0 km²) clumps. Some variation on this spatial pattern was observed with time of day. Small and large clumps existed at all times of day while medium clumps were most evident in the morning and at dusk. This variation resulted from medium clumps varying between 0.75 and 1.5 km² quadrat sizes. At the smallest quadrat size ($q = 0.25$ km²), the ρ index equals the $\underline{m^*}/\underline{m}$ ratio or Lloyd's "patchiness" index. There was a tendency for patchiness to increase from dawn to dusk. This further supports the trend that birds were less clumped at dawn but became more

Fig. 19. Mean ρ -index values by quadrat size category (q) for each time of day and combined times of day. Sizes of quadrats are ordered from 1 ($q=0.25 \text{ km}^2$) to 7 ($q=24.0 \text{ km}^2$) as indicated in Fig. 16.



clumped towards dusk. As noted earlier, this trend was not exposed using regression analysis.

The regular spacing of medium and large clumps was emphasized by the technique of obtaining larger quadrat sizes in the grid (see methods). Birds occurred primarily in coastal areas of the grid (Chapter 2). When quadrat sizes were formed by grouping the quadrats along coastlines ($q = 0.75, 1.5$ and 6.0 km^2), medium and large clumps resulted because of the regular dispersion of coastline areas in the grid (Fig. 15). However, small clumps of birds still occurred more often along certain coastlines than others, especially near the sill of the channel. Birds also occurred more often in mid-channel areas in the sill region (Chapter 2). The triple-clump structure indicates 3 regions of habitat use: sill ($q = 6.0 \text{ km}^2$), coasts ($q = 0.75$ and 1.5 km^2), and certain quadrats in coastal areas ($q = 0.25 \text{ km}^2$).

Flock sizes

The smallest quadrats ($q = 0.25 \text{ km}^2$) used in this study were still very large with the respect to the size of individual birds. Flocks are the smallest possible type of clump and were examined relative to the spacing of birds within the quadrats. Since flocks were discrete (i.e. the distance between flock individuals is small compared with distances to other flocks [Clark and Evans 1955]), they were not directly comparable to larger clumps. Also, Marbled Murrelets only occurred in single species flocks.

The frequency distribution of the number of sitting flocks per size of flock was positively skewed with a mean (\pm SD) of 2.03 ± 1.87 and ranged from 1-55 birds/sitting flock (Fig. 20). This distribution indicated

that sitting flocks were seldom large. The most frequent flock sizes were single birds (43.7%) or 2 birds (39.0%) (n=4880 flocks). In terms of the total number of birds observed (n=9626), flocks of 2 birds were most important (40.7%) followed by single birds (22.5%). The frequency distribution of the number of flying flocks per size of flock was also positively skewed with a mean (\pm SD) of 1.41 ± 1.03 and a range of 1-25 birds/flying flock (Fig. 20). Flying flocks most frequently contained single birds (68.8%), although flocks of 2 were common (25.5%) (n=885 flocks). Single flying birds were most important (48.8%), followed by flocks of 2 (36.2%) (n=1248).

Sizes of flocks sitting on the water did not vary with time of day but sizes of flocks increased with increasing quadrat (0.25 km^2) density ($\chi^2=42.6$, $p < .01$) (Table 21). Flocks in low-density quadrats were excluded from the latter analysis since low numbers alone would limit the formation of larger flocks. In fact, the preponderance of low density quadrats (82.2% of occupied quadrats) partly accounts for the large proportion of small flock sizes (90.9% of singles and flocks of 2). Medium-low, medium-high and high-density quadrats also contained large proportions of singles and flocks of 2 birds (77.7%, 75.7% and 67.9%, respectively). However, flock sizes increased with increasing quadrat density only in morning censuses ($\chi^2=32.4$, $p < .05$). Flying flock sizes were larger at dawn ($\chi^2=18.9$, $p < .05$).

Flock behavior

Sitting flocks were significantly larger than flying flocks ($\chi^2=201.8$, $p < .01$). Since most birds flew to and from the study area in small flocks, larger sitting flocks were formed mainly through flocks

Fig. 20. Percent frequency distributions per size of flock of: A, the number of sitting flocks (n=4880), B, the number of flying flocks (n=885), C, the number of sitting birds (n= 9626); D, the number of flying birds (n=1248).

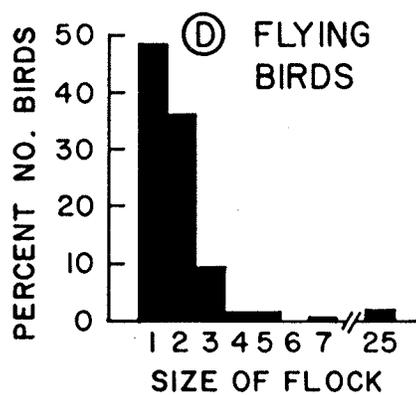
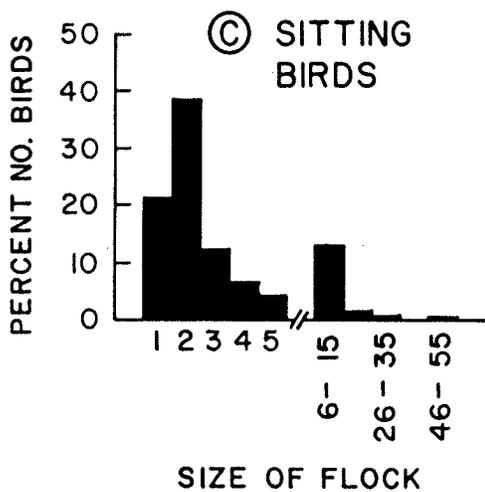
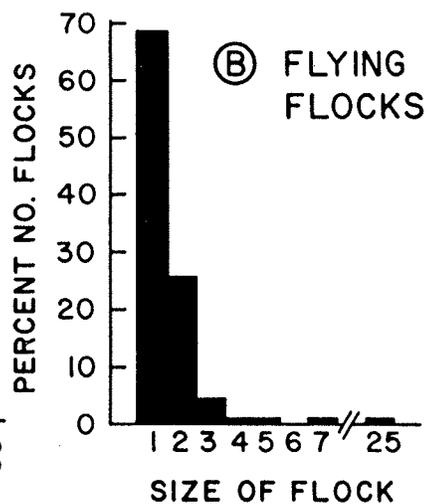
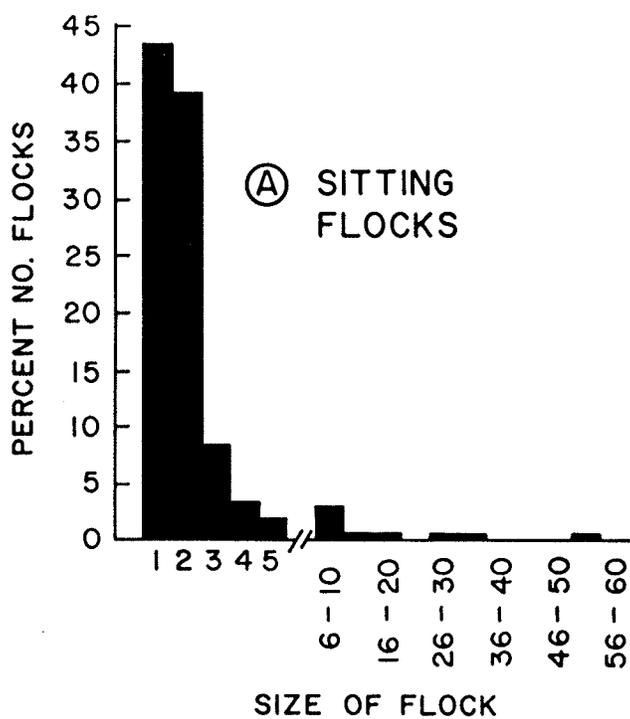


Table 21. Number of flocks in relation to quadrat density and flock size class by time of day (n=4880 flocks).

Time of day	Flock size class	Quadrat density ¹				Total
		low	medium-low	medium-high	high	
dawn	1	204	156	82	18	477
	2	187	154	54	12	436
	3	23	43	15	2	87
	4+	13	33	17	6	73
morning	1	322	166	76	49	613
	2	266	192	68	74	600
	3	36	51	23	27	137
	4+	30	54	29	51	164
afternoon	1	308	99	49	51	509
	2	224	99	62	63	448
	3	45	26	12	18	101
	4+	21	24	19	31	104
dusk	1	398	91	26	19	534
	2	245	108	42	23	418
	3	27	33	13	4	83
	4+	23	42	19	7	97

¹ Definitions as in Table 19.

merging with other flocks on the water. Qualitative observations during censuses provided additional information on the formation of flocks. Single birds sometimes joined other individuals or flocks in flight, particularly at dawn. At this time, more birds were flying (Chapter 2) and this probably accounted for the larger flying flocks observed at that time. Flocks of 2 birds often landed and took off together. Larger flying flocks invariably broke apart as birds landed and other flock members flew on or landed nearby. Only single birds were observed to land beside and form a sitting flock with another individual. Single sitting birds often took off and flew out of observation range. It appeared that small flying flocks generally landed alone and were transposed into small sitting flocks. While on the water, larger sitting flocks may form temporarily but the members of such flocks usually do not leave together. The largest flying flock (25 birds) was observed flying low, in cluster formation (Heppner 1974), but it is not known whether all individuals took off together.

Only flocks of 2 and single birds were observed diving during censuses. In flocks of 2 birds, birds were seen swimming on the surface towards one another before diving again (Carter, unpub. data). Thus, flocks of 2 birds may have been underestimated during censuses if birds were apart or if one was under water at the time. Individuals in sitting flocks of 3 or more birds were never observed diving together. They often occurred in frontal linear formations which suggested that they were not actively feeding. Larger flocks sometimes included birds that were holding fish in their bills, but these birds probably were not feeding at the time (Chapter 1). Most birds that held fish did so singly (80.0%) or in flocks of 2 (9.6%). However, these flocks

comprised only 2.8% of the total number of sitting flocks (see Chapter 2).

DISCUSSION

Clumps and habitat use

Marbled Murrelets were distributed non-randomly within the feeding area (Fig. 18). Individuals were clumped in certain quadrats (Fig. 18) which indicated that these areas, or patches, were "preferred" (Wiens 1976) and were selected among recognized alternatives. However, not all birds were clumped. Many quadrats ($q=0.25 \text{ km}^2$) contained low numbers of birds and even high-density quadrats contained few birds relative to their size (Table 19, Fig. 17). Clumps were then evident largely due to the large proportion of empty quadrats. Since many birds occurred in low-density quadrats, many birds also chose not to occur in the implied habitat patches (Wiens 1976).

The dispersion of Marbled Murrelets within the feeding area is not influenced by the proximity of the nest site. Although breeding murrelets make foraging trips from a "central place" (Hamilton and Watt 1970, Ward and Zahavi 1973), they spend the day at sea presumably far from the nest and visit the nest at night (Chapter 2). Thus, birds are not constrained by the demands of travel when deciding where to feed in the feeding area. Thus, birds would be expected to be dispersed in relation to their prey, manifested by the interaction between individuals near the food supply (Goss-Custard 1970, Krebs 1979, Waser and Wiley 1979). Marbled Murrelets are clumped in south Trevor Channel apparently because their prey are also clumped. However, proof of this

relationship is difficult to obtain. Murrelets are distributed in 2 dimensions on the water surface while the prey are distributed in 3 dimensions in the adjacent underwater habitat. Within this limitation, only a limited understanding of the relation between the dispersions of murrelets and their prey can be achieved.

The triple-clump structure of the dispersion pattern of Marbled Murrelets (Fig. 19) suggests that birds responded to and clumped in 3 (sill, coastline, and intra-coastline) habitat regions. These regions are inter-connected, and occur at different spatial scales. The principal prey species (Ammodytes, Clupea) are probably more abundant over the sill and along the coastlines during the nestling period (Chapters 1, 2). Murrelets apparently aggregated above clumped prey since most birds occurred in these habitat regions; but, since birds may be clumped or in low numbers within these regions and occur widely in the feeding area, this behavior must not be influenced solely by food. Further information on the local dynamics of prey dispersion are required before the relationship between the dispersions of murrelets and their prey can be understood.

Choice of feeding site

The regular use of the feeding area and certain habitats and sites within it suggests that the choice of a feeding site involves previous experience. Marbled Murrelets appear to fly directly to the feeding area at night or around dawn (Chapter 2). Murrelets consequently restrict foraging to occur within a familiar "home patch" of the potential foraging habitat (Wiens 1976, Orians 1981). Fidelity to a feeding area would be expected to reduce searching effort between

various alternative areas (Alexander 1974). It would be an efficient foraging strategy to return to a previously used place only if prey were clumped and comparatively stable, available and non-depletable (Slater 1978), as apparently is the case in south Trevor Channel (Chapter 1).

Such a "win-stay" strategy (Olton et al. 1981) is of limited value to Marbled Murrelets when choosing a particular feeding site. I assume that murrelets usually do not detect their "concealed" prey (Dawkins 1971, Pietrewicz and Kamil 1981) from the air. The inability to evaluate local prey differences results in a less-specific response to feeding site. Birds appear to choose a feeding site within a particular habitat type and this produced the observed triple-clump dispersion. The regular use of certain sites within the feeding area suggests that murrelets have a memorized "correlation" between feeding sites, habitat and feeding benefits (Wiens 1976). Murrelets, therefore, feed in "profitable" areas (Royama 1970) by "niche" or "patch" hunting (MacArthur and Pianka 1966, Krebs 1978). Within each habitat region, however, birds may be clumped or not clumped. Thus, the choice of where to feed at dawn is affected by the presence of other individuals. Otherwise, all birds would occur only in certain habitats rather than being widely distributed in the feeding area (Goss-Custard 1970, Alexander 1974). The tendency for murrelets not to feed in habitat patches increases with the number of birds in the clump producing the skewed distribution of birds/quadrat (Fig. 17) but a constant dispersion pattern (Figs. 18, 19). This response does not imply that other sites are suboptimal but rather that the benefits of feeding in less dense quadrats (e.g., less interference and competition) outweigh the benefits of feeding in a clump (e.g., increased feeding efficiency) for certain

individuals at higher densities. This best possible spacing mechanism (Baker and Marler 1980), where an individual could occur in a clump or not depending on the circumstance, would account for the regular spacing of birds in coastline regions (Fig. 19) and the wide use of the feeding area (see Chapter 2). The differences between prey resources in clump and non-clump habitats must not be great since a large proportion of birds occur in low-density quadrats (Fig. 17). Thus, clumping behavior may be less relevant from the point of view of feeding performance (Slater 1978).

Daily spatial patterns

The triple-clump dispersion of murrelets was generated at dawn when the birds settle on the feeding area. The greatest mean density of birds was present there at that time (Fig. 18, Chapter 2) when birds were most widely distributed (i.e. least clumped). This suggests that murrelets tend to space out at higher densities. That the pattern of dispersion was maintained to some degree throughout the day (Figs. 17, 18), suggests that murrelets feed at chosen feeding sites for periods of time (Chapter 2). Since murrelets cannot detect local differences in prey, the best average strategy would seem to be to exercise "area-restricted" search (Smith 1974, Zach and Falls 1977, Krebs 1978) at the feeding site.

From morning to dusk, the numbers of birds on the feeding area decreased indicating that birds were leaving the feeding area, for the most part, because movement within it would have changed the spatial pattern (Chapter 2). The clumping response of birds to the sill region was most evident at dawn while the response to coastline regions was

less evident (Fig. 18). Later, the sill response waned while the coastline response increased. Thus, birds appeared to leave the feeding area non-randomly. The measurement of dispersion, however, affects this interpretation. "Patchiness" increased towards dusk because, while the number of empty quadrats increased (Table 19), the relative importance of clumps increased regardless of their decreasing size. This result occurs because the mean crowding index ignores empty quadrats (Lloyd 1967). Thus, although the regression (Fig. 18) indicates that birds leave randomly (inferred from the use of a linear model), when quadrat size is changed (Table 20) both the number and size of clumps vary. The decision of when to leave the feeding site and area evidently is influenced by both temporal differences in local habitats that relate to feeding success and temporal changes in intrinsic behavioral properties (Krebs 1978, 1979). Birds may leave to monitor other alternate feeding sites (Zach and Falls 1977) and/or to obtain different food for the young which is more available elsewhere (Chapters 1, 2). Alternatively, food could be cyclically available but since some birds remain throughout the day, this is unlikely.

Flock compositions

Since the age and sex of AHY Marbled Murrelets were not determined, it was not possible to determine directly the compositions of flocks during censuses. Hatching-year (HY) birds, however, have a distinct juvenal plumage (Drent and Guiguet 1961) although none was observed during censuses. Even though censuses were conducted during the earlier part of the population nestling period, individual nesting pairs varied greatly with respect to timing of breeding (Chapter 1).

Therefore, the murrelets present in the feeding area consisted of subadults and breeding birds at various stages in the nesting period (Chapters 1, 2).

The most frequent flock sizes of Marbled Murrelets in south Trevor Channel were singles and flocks of 2 birds (Fig. 20). Marbled Murrelets have often been noted to occur primarily in these flock sizes in summer and winter (Grinnell 1897; Shortt 1939; Sealy 1975 a, b; Hatler et al. 1978). Sealy (1975b) concluded that flocks of 2 birds were primarily mated pairs. Pairs formed a large proportion of the flocks and individuals observed (Table 19, Figs. 17, 20) and probably represented pairs that had rejoined after being separated during the incubation period (see Sealy 1975b). Single birds were also common and may have been subadults or mated adults (with the mate elsewhere at sea or incubating).

Murrelets were also observed landing, taking off and flying mainly in singles and pairs (Fig. 20) (also see Grinnell 1897, Dawson and Bowles 1909, Jewett et al. 1953, Gabrielson and Lincoln 1959). Therefore, larger sitting flocks were formed after the birds had landed on the water. Flocks up to 50 individuals have also been recorded by several observers (Willett 1926, Jewett 1942, Jewett et al. 1953, Sealy 1974, Kessel and Gibson 1978), however, none of these authors defined a "flock". Sealy (1975b) found that subadults and adults occurred in flocks containing 4-11 individuals during the nestling period. Near the end of the nestling period, HY birds also have been seen in these larger flocks (Guiguet 1971a, Sealy 1975b).

Flock activities

Marbled Murrelets appear to be "solitary" feeders as only singles and pairs were observed diving and presumably feeding during censuses (and see Grinnell 1897, Laing 1925, Sealy 1975b). Although individuals in pairs may dive together, this is probably related to synchronized activities within the pair. Synchronized feeding promotes the maintenance of pair bonds rather than increasing feeding performance (Sealy 1975b). Synchronous diving also appears to play a part in courtship (Byrd et al. 1974). Individuals in larger flocks were not observed diving, but rather were probably loafing groups that formed after birds had finished feeding. Since murrelets apparently loaf at feeding sites, the dispersion pattern described here also includes the distribution of feeding and non-feeding birds.

Since murrelets feed solitarily even in high density quadrats (Tables 19, 21), this further suggests that murrelets are solitary and "highly individualistic" feeders. Marbled Murrelets also maintain a distance from other birds. A "time-plan" dispersion pattern (Leyhausen and Wolff 1959, Waser and Wiley 1979) is produced while feeding where at any instant an individual (or pair) is unlikely to encounter other individuals. Feeding birds were not associated with other birds and occurred as discrete entities. This behavior reflects some type of "individual distance" (Conder 1949) or "activity field" (Waser and Wiley 1979) without topographic reference that is maintained by mutual avoidance behavior (Leyhausen 1965, Coss-Custard 1970). Since the prey resource is not "defendable" (Brown 1964, Waser and Wiley 1979), aggression would unlikely account for the regular spacing of feeding flocks. Mutual avoidance behavior could prevent possible interference by other birds with individualized feeding methods; thus, group feeding

is apparently unfeasible (Rubenstein 1978, Slater 1978). This also suggests that prey resources are not highly localized since birds were widely distributed in the various habitat regions.

If individuals gained solely from the clumped nature of the prey and not from the presence of other individuals, birds should aggregate but otherwise avoid other individuals (Alexander 1974). Since murrelets form larger flocks when not feeding, a relaxation of mutual avoidance behavior apparently occurs. This change in behavioral state could allow birds to come into close contact temporarily in a random fashion. However, the large sizes of certain flocks (up to 55 birds), flock sizes relative to quadrat density (Table 21), and their cohesive formations on the water suggests that flocks form from positive attractions between individual flock members. Since flock sizes increased with quadrat density in morning and afternoon censuses, fewer murrelets may be feeding at these times (also see Chapter 1). This implies partial feeding periodicity in the population that may result in many birds not feeding at the same time. This would allow the larger flocks to form and remain together for periods of time. Larger flock sizes, however, occurred frequently in higher-density quadrats regardless of time of day (Table 21).

The importance of social interaction to the individual may also influence the choice of feeding site. Certain individuals may be more prone to "local enhancement" (Thorpe 1963) relative to expected feeding and/or social benefits. Although larger flocks may be quite temporary, this is the only situation where social interaction can occur because murrelets nest solitarily and have no other central localities where birds can congregate. The clumped dispersion of Marbled Murrelets,

therefore, may be affected proximally by social attractions between "solitary" birds (Leyhausen 1965, Rohlf 1969).

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Appendix A. Details of 87 specimens of Marbled Murrelets obtained in Barkley Sound, British Columbia in 1979 and 1980.¹

Year	Sex	Status ²														
		Breeding						HY			Molting			Winter		
		Adults			Subadults			G	S	C	G	S	C	G	S	C
		G ³	S	C	G	S	C	G	S	C	G	S	C	G	S	C
1979	♂	3	-	7	-	1	-	-	-	4	-	-	4	-	-	3
	♀	3	-	6	-	-	1	-	1	-	-	-	1	-	-	2
1980	♂	10	-	2	-	-	-	1	-	5	-	-	12	-	-	-
	♀	9	1	2	-	-	-	-	-	-	-	-	9	-	-	-
Total		25	1	17	-	1	1	1	1	9	-	-	26	-	-	5

¹ Specimens deposited in the University of Manitoba Zoology Museum (UMZM).

² Adults (with a brood patch (10 May-28 August); subadults (without a brood patch during the breeding season [2 June, 29 June]); HY (or hatching-year birds (4 July-5 October); molting birds (without a brood patch and undergoing body and/or wing molt (22 July-5 October); winter birds (in basic plumage [18-19 December 1979]).

³ Methods by which specimens were obtained: G, birds killed in gillnets and salvaged by fishermen and fisheries officers (see Carter and Sealy 1984); S, birds found dead on the water; C, birds collected by shooting.

APPENDIX B. Localities in Barkley Sound where 87 specimens of
Marbled Murrelets were obtained in 1979 and 1980.

Status ¹	Locality		
	Trevor Channel ²	Imperial Eagle Channel ³	Sechart Channel
Breeding	37 (25) ⁴	8 (1)	-
Molting	11	13	2
HY	7 (2)	4	-
Winter	4	1	-

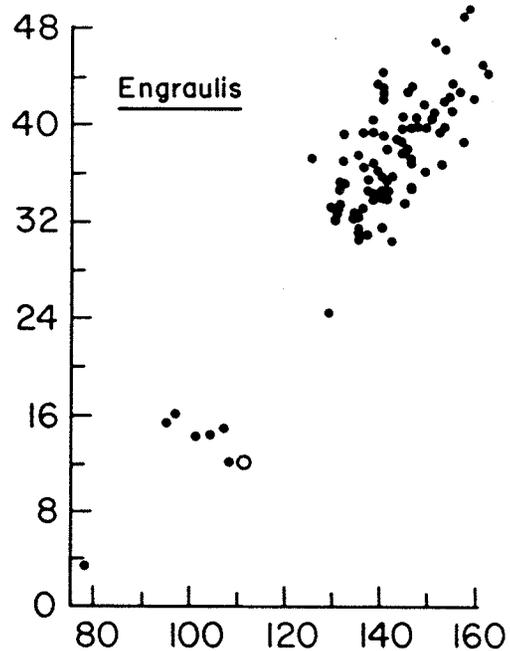
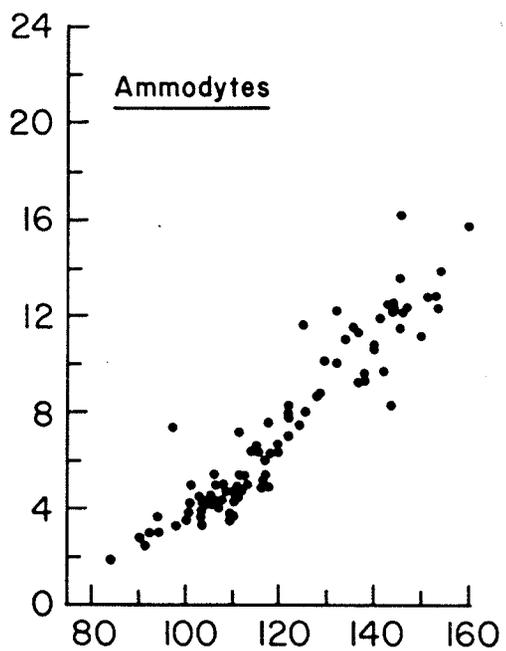
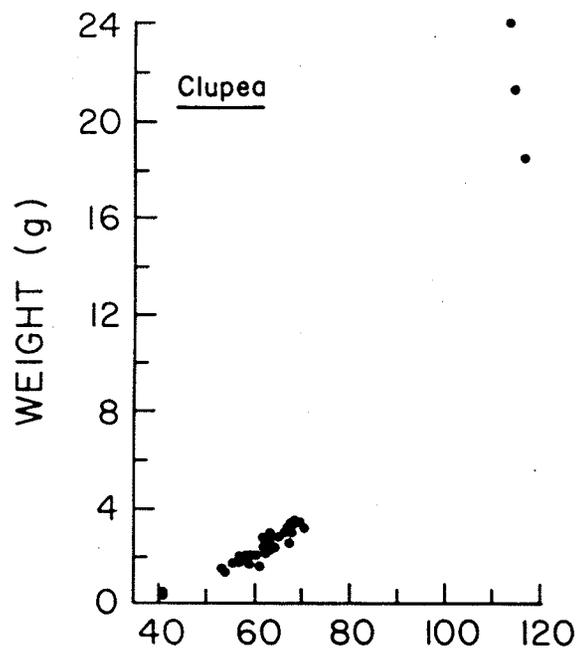
¹ Defined in Appendix A.

² Includes Satellite Passage and waters off Cape Beale.

³ Includes Dodger Channel.

⁴ Numbers in parentheses indicate salvaged and gill-netted birds.
(see Carter and Sealy 1984).

APPENDIX C. Lengths and weights of Clupea harengus,
Ammodytes hexapterus, and Engraulis mordax
from Barkley Sound, British Columbia, Clupea
specimens (n=35) were collected in Bamfield
Inlet and Trevor Channel, between 4 June and
4 September 1979. Ammodytes specimens (n=101)
were obtained from regurgitations of Brandt's
Cormorants (Phalacrocorax penicillatus on
Starlight Reef, 5-12 September 1980. Engraulis
specimens (n=93) were collected in Bamfield
Inlet, between 28 May and 7 June 1979; the
single open dot represents a fish held in the
bill by a Marbled Murrelet on 7 June 1979
(UMZM). Voucher specimens of each species
of fish have been deposited in the University
of Manitoba Fish Museum, Winnipeg, Manitoba.



Appendix D. Relative densities (individuals/km) of Marbled Murrelets by transect segment and habitat type on Parkley Sound surveys (May - September 1979).

TRANSECT	DATE	NEARSHORE ^a						INSHORE (A)					INSHORE (B)				TOTAL	
		1 ^b	2	13	14	15	16	3	4	5	12	6	7	8	9	10		11
		4.7 ^c	4.7	4.7	4.7	2.8	2.8	3.9	3.9	3.6	3.6	3.6	3.9	3.9	2.8	2.8	3.6	60.2
1	10 May	0.4 ^d (0.8)	0.2 (0.4)	1.9 (0.8)	2.3 (0.6)	1.8 -	10.8 (0.4)	3.3 (2.0)	2.0 (0.8)	0 0	0.8 -	0 0	0 0	- -	- -	- -	1.7 -	1.8 (0.5)
2	22 May	- (1.1)	- (1.7)	- -	0.6 (0.2)	0 0	0 0	0 0	0 0	0 0	0 (0.2)	0 0	0 0	0 0	- -	- -	- -	0.1 (0.5)
3	2 Jun	- -	0.8 (1.1)	- -	- -	- -	2.5 (5.0)	4.1 (0.5)	1.3 (0.5)	- -	- -	- -	- -	- -	- -	- (1.1)	- -	(0.5) (0.4)
4	9 Jun	0.2 (0.4)	2.1 (4.7)	3.2 (4.5)	- (1.7)	7.2 (1.4)	18.0 (7.6)	0.8 (0.8)	1.3 (2.8)	0.6 -	3.9 (2.8)	- (0.6)	5.1 (2.5)	1.3 (1.0)	0.7 -	1.1 (2.2)	- (4.1)	2.5 (2.2)
5	17 Jun	2.1 (4.9)	11.3 (1.1)	0.2 -	- (0.4)	0.4 (0.4)	4.3 (2.5)	7.1 (4.3)	3.0 (3.3)	0.6 (0.8)	- -	- (0.3)	- -	- -	- -	- -	- -	2.1 (1.2)
6	29 Jun	20.4 (21.7)	38.8 (7.6)	- (0.2)	- (0.6)	- (0.7)	12.6 (2.5)	0.3 (1.3)	12.4 (7.4)	0.8 (1.9)	- -	0.3 -	- (0.5)	- -	0.4 -	- (0.4)	- (3.3)	6.3 (3.4)
7	9 Jul	15.1 (23.6)	16.3 (5.3)	3.0 (1.1)	10.6 (0.4)	3.2 (1.4)	20.5 (1.4)	5.3 (0.3)	2.5 (4.3)	- -	8.3 (1.9)	- (0.6)	- (0.8)	- -	- -	- (0.4)	4.4 (0.7)	5.9 (3.9)
8	21 Jul	3.4 (2.8)	1.9 (0.8)	0.8 (1.3)	4.7 (0.4)	12.2 (0.7)	1.8 -	- -	- (0.5)	- (0.6)	- (0.8)	- -	0.5 -	0.3 -	0.7 -	- (0.7)	- (0.3)	1.6 (0.6)
9	31 Jul	5.7 (4.2)	19.3 (2.3)	0.6 (0.8)	- (0.2)	0.7 (1.4)	5.8 -	0.3 (0.8)	- (0.3)	- -	- (0.6)	- -	- -	- -	- -	- (0.7)	- (0.4)	2.3 (0.8)
10	13 Aug	0.2 (0.6)	0.6 (0.8)	- -	- -	0.4 -	10.4 (0.4)	0.4 (0.2)	- (0.4)	- -	- -	- -	- -	- -	- -	- -	- -	0.6 (0.2)
11	29 Aug	0.2 -	- -	- -	0.2 (0.2)	- (0.4)	5.4 (0.7)	- -	- -	- -	- -	- -	- -	- -	- -	- -	- -	0.3 (0.1)
12	5 Sep	- -	- -	- -	(0.4) (0.2)	- -	- -	- -	- -	- -	- -	- -	- -	- -	- -	- -	- -	<0.1 <0.1
13	29 Sep	- -	- -	- -	- -	- -	- -	- -	- -	- -	- -	- -	- -	- -	- -	- -	- -	- -

^aNames of marine habitats after Kessel (1979).

^bTransect segment number from Fig. 6. Nearshore, inshore(a) and inshore(b) segments were 0.9-2.8, 1.3-5.6 and 6.5 - 9.4 km from shore respectively. Distances were measured from the center of the segment.

^cLength (km) of transect segment.

^dNumber of birds on the water per km. Numbers in parentheses are the number of flying birds per km.

Dashes indicate that no birds were observed; slashed zeros indicate that the segment was not censused.

APPENDIX E. Changes in surface salinity ($^{\circ}/\text{oo}$), surface temperature ($^{\circ}\text{C}$), and relative Chlorophyll a with changing depth at Trevor Channel, 8 July 1980 (T.R. Parsons, unpub. data). The channel runs from north (left) to south (right). The grid (see Chapters 2,3) is located between the vertical lines and the sill area of the Channel is hatched.

