

AN ABSTRACT OF THE THESIS OF

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OF MARINE DIVING BIRDS

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During 1969-1971 I studied patterns of resource allocation and behavioral interaction among Brandt's Cormorants, Pelagic Cormorants, Common Murres and Pigeon Guillemots in the area of a breeding colony on Yaquina Head on the central Oregon coast. Extensive studies of the breeding colony were combined with detailed observations of the distribution, abundance and behavior of these birds at sea.

The nesting areas differed considerably among the four species. Brandt's Cormorants and Common Murres were the most similar, both nesting in colonies on flat or gently sloping, unvegetated surfaces of the same offshore rock. In contrast, Pelagic Cormorants nested on the face of precipitous cliffs on the mainland and offshore rocks, singly or in loose aggregations; Pigeon Guillemots also nested singly or in loose aggregations in nooks, crevices and sometimes burrows on mainland and offshore cliffs.

Breeding phenologies overlapped almost completely, with egg laying beginning in late May and the first young fledging in mid-July. Murres initiated egg laying as early as May 6 and had an abbreviated nestling period. At an age of 2-3 weeks, chicks left the breeding rock, and were accompanied at sea by the adult male. Dispersal from the breeding colony was primarily longshore rather than offshore.

The energetic and competitive advantages of this type of parental care pattern in murres and other alcids are discussed. I suggest that precociality has evolved in some alcids as the result of a gain in subaqueous flight capabilities at the expense of aerial flight. The greater underwater maneuverability permits those species with precocial young to exploit highly mobile midwater fish populations at great distances from the breeding colony. However, their decreased ability to ferry food from the offshore feeding areas to the breeding colony has resulted in selection for early abandonment of the colony by adult and chick.

The four species differed in the average length and range of dive times. The ratio of dive time/rest time, however, was very similar when all dive times or a specific dive time were considered. Pelagic Cormorants had the lowest average dive time, while Brandt's Cormorants, Pigeon Guillemots and Common Murres took increasingly longer dives. The same ranking of species was observed for offshore distribution, with Pelagic Cormorants foraging closest to the beach and Brandt's Cormorants slightly further offshore, followed by Pigeon

Guillemots with Common Murres being the most pelagic in their foraging distribution.

Pigeon Guillemots fed exclusively on bottom-dwelling species while Common Murres took primarily midwater fish. The cormorants fed upon prey occurring in both areas. In addition, both species of cormorants and the murres as well as Western Gulls fed together in mixed-species feeding flocks. These flocks foraged primarily upon schooling fish of the families Engraulidae and Osmeridae, which represent a patchily distributed but locally abundant food source.

The three diving species which participate in mixed species flocks thus differed in their offshore distribution and took slightly different prey items, although overlapping extensively in their utilization of the more abundant species, such as anchovies and juvenile rockfish. This zonation results in less predation pressure per unit area on the less common and more predictably distributed prey species, but allows the entire offshore area to be searched effectively for abundant but patchily distributed fish schools. The behavioral interactions between members of the mixed species flocks allow rapid communication of prey school locations and permit each species to maintain contact with the school for a much longer time. The temporal and spatial overlap in the occurrence of breeding activities may contribute to a more effective coverage of the area surrounding the colony during the time of year at which food supplies are abundant.

Resource Allocation in Four Syntopic Species
of Marine Diving Birds

by

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RESOURCE ALLOCATION IN FOUR SYNTOPIC SPECIES OF MARINE DIVING BIRDS

INTRODUCTION

Marine birds are often the most conspicuous if not the most frequently seen vertebrates in coastal areas. While their populations may number in the millions in areas of coastal upwelling, little effort has been made to assess their numbers or their importance in nutrient cycling, in energy transfer, or as competitors with man for shared resources. Since they are principle components of the biota of many marine ecosystems their role in the system should be ascertained.

Studies of marine birds have concentrated on the feeding and breeding behavior of single species or have reported offshore distribution and abundance based on opportunistic observations at sea (Bailey, 1968, 1971; Sanger, 1970; Kuroda, 1960; King, 1970). Belo polski (1957), Uspenski (1958), Ashmole and Ashmole (1967), and Pearson (1968) studied entire marine bird communities^{1/}, but such investigations are infrequent. Further, most studies of marine bird communities have been confined to breeding colonies, with few,

^{1/}"Community" is used here in the sense of MacArthur (1971) i. e., "any set of organisms that live near each other and about which it is interesting to talk."

if any, observations at sea. This is primarily due, I would suppose, to the difficulties and expense of sea operations, although Bedard (1969a), Uspenski (1958) and Tuck (1961) did make limited observations at sea in conjunction with studies of breeding marine birds.

Marine bird communities present an excellent opportunity to describe the manner in which available resources are allocated among a number of species in a relatively simple marine environment. Such community analyses have been applied to the avian inhabitants of grassland communities by Cody (1968) and Wiens (1969). MacArthur (1969, 1971), Cody (1968) and others have suggested that species may coexist in the same habitat by employing one or more of the following strategies:

- 1) Utilization of different resources,
- 2) Differing in the time of resource utilization,
- 3) Differing in the areas in which resources are obtained.

The second and third of these strategies may or may not result in the utilization of different resources. However, they may frequently result in a reduction in the frequency of agonistic encounters and therefore free more time for other activities, including pursuing and capturing food.

The utilization of different resources is most easily seen in the selection of nesting sites or prey. (Bedard, 1969a, 1969b; Ashmole and Ashmole, 1967). In most breeding marine bird communities,

for example, some species may be found nesting on vertical cliff faces, some on flat surfaces, some burrowing into the substrate, and still others nesting in trees or low shrubs. Similarly, in prey selection some species are uniquely adapted for taking the neuston at the air-water interface (storm petrels) while others take more mobile and larger nektonic species such as herring and anchovy (many of the Alcids).

The effect of differences in the timing of activities such as breeding is more pronounced in tropical situations where seasonal fluctuations in food availability are less than in temperate regions (Ashmole, 1968). The possibilities for year-round breeding by temperate species would seem to be restricted, at least in part, by inclement weather during much of the year. This would restrict the foraging activities of those species which forage in shallow water areas on the open coasts where water visibility is decreased and turbulence increased during the winter months.

Many marine birds rely on individuals of their own or other species to locate food sources which have a patchy distribution in time and space; in such situations temporal differences in foraging might be disadvantageous. On the other hand, differences in the time of day at which foraging occurs in a given area may very well result in completely different types of prey species being taken. This is largely due to the vertical migration of many species of fish

and invertebrates, which results in their being found deep in the water column during the day and at or near the surface at night. This allows surface feeding forms such as albatrosses to take many species at night which are rarely taken during the day.

The spatial division of resources in marine environments thus has both a vertical and a horizontal component. A marine bird may forage at the air-water interface or at a depth of 40 m or more and may do so within 1000 m of the beach or a hundred or more Km out to sea. Both the horizontal and vertical zonations are species specific, at least during the breeding season (Wynne-Edwards, 1935; Bertrand and Scott, unpublished manuscript; Murphy, 1936). The possibilities for vertical zonation are, however, more restricted. The depth of water over the continental shelf may vary from 1 - 200 m, but the maximum depth to which birds characteristically forage is probably considerably less than 200 m. The depth at which species forage may be determined by physiological differences between species (Stonehouse, 1967; Dewar, 1924) while the degree to which the water column is subdivided into different foraging areas by marine birds is undoubtedly dependent upon the complexity of its structure.

Information concerning resource allocation in marine bird communities can be best obtained by combining extensive and continuous examinations of the behavior, abundance, and distribution of

the birds at sea with detailed studies at the breeding colony. This type of approach has not yet been attempted.

A total of 48 species of marine birds occur in Oregon, and nine of these are known to breed in the state (Bertrand and Scott, 1971). Because of the accessibility of many of the breeding colonies, and the availability of suitable vessels for offshore work on a regular basis, Oregon provides an ideal area in which to study Pacific marine bird communities. In addition, many of the accessible colonies have few individuals and species compared to the large breeding colonies of the Arctic or other areas, so that relationships among and within species may be more easily ascertained.

As part of a three-year study of resource subdivision among marine birds, I attempted:

- 1) to develop a standardized technique for censusing marine birds at sea;
- 2) to determine the distribution, abundance, and behavior of these species on a seasonal basis; and
- 3) to study the strategies of habitat utilization adopted by members of a single marine bird community.

The four species involved in this study were Brandt's Cormorant (Phalacrocorax penicillatus), Pelagic Cormorant (P. pelagicus), Common Murre (Uria aalge), and Pigeon Guillemot (Cepphus columba).

STUDY AREA

The focal point of this study was Yaquina Head, an eroded remnant of a Miocene volcano (Snively and MacLeod, 1971), which extends 1.9 km out to sea from the adjacent coastline. The head is 4.5 km north of Newport, Oregon (124° 05'W; 44° 40'N) (Figure 1). The head varies in height from 15 - 30 m above mean low water and encompasses an area of approximately 110 ha, of which less than 20 percent is used by marine birds as nesting sites. A number of offshore stacks, vertical cliff faces and sea caves on the head itself provide the major nesting sites for the birds (Figure 2). The offshore stacks are poorly vegetated, with only widely scattered bunches of grass. However the head itself is covered with vegetation, dominated by salal (Gaultheria shallon).

Six different species of marine birds are known to nest on Yaquina Head. These are Brandt's Cormorant, Pelagic Cormorant, Pigeon Guillemot, Common Murre, Glaucous-winged Gull (Larus glaucescens) and Western Gull (L. occidentalis). Of these, all but the Glaucous-winged Gull nest in fairly large numbers (30 or more pairs) on the head. The Rhinoceros Auklet (Cerorhinca monocerata) and Tufted Puffin (Lunda cirrhata) are also thought to nest on the head, but nests have never been located. In addition, Yaquina Head is a nesting site for one species of shorebird, the Black Oystercatcher

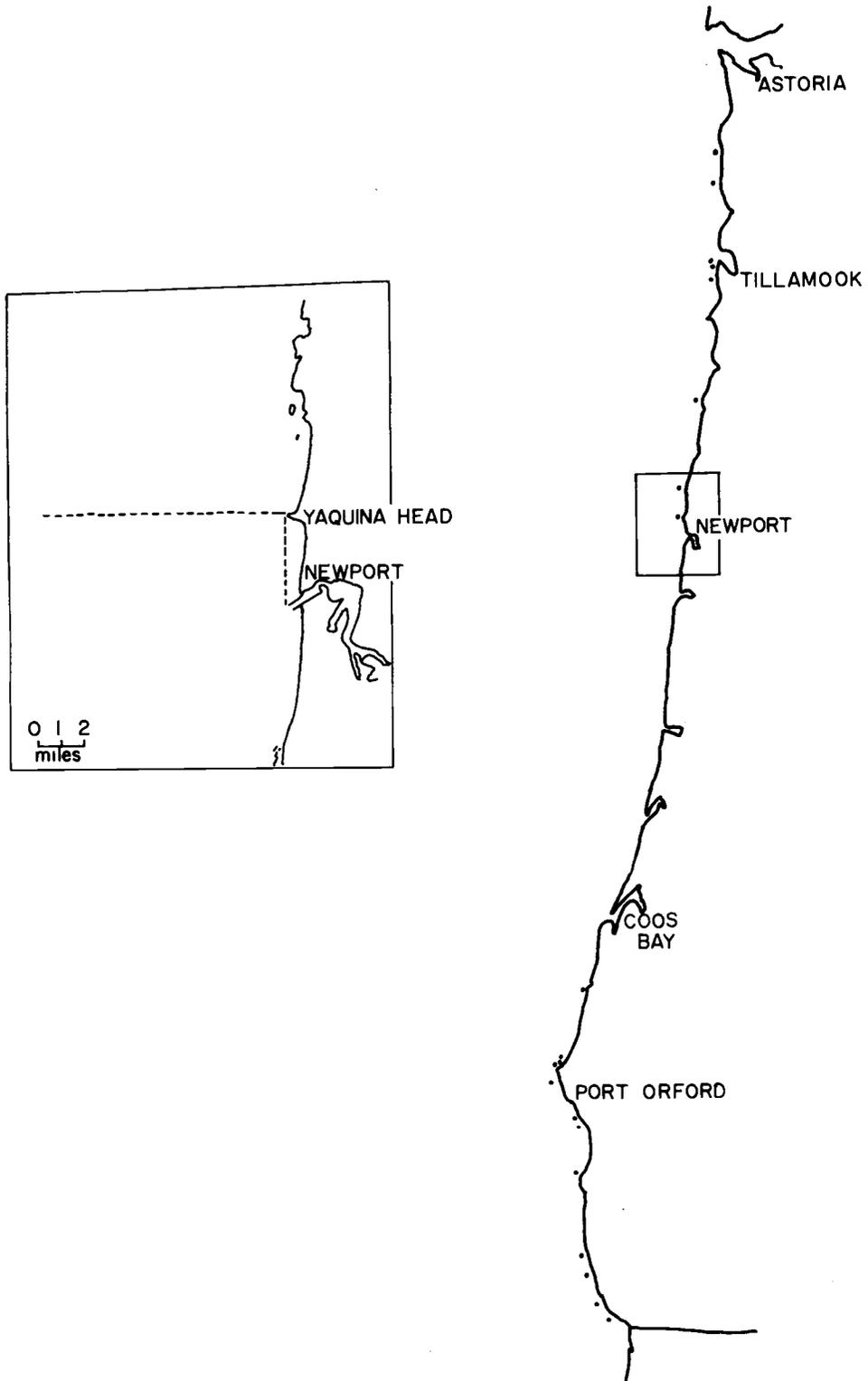


Figure 1. Study area in relation to other major breeding sites for Common Murres in Oregon. The dotted lines in the insert show the two major transect lines. The line running from the north Newport jetty to Yaquina Head is the longshore transect and the one line extending west from Yaquina Head depicts the offshore transect.

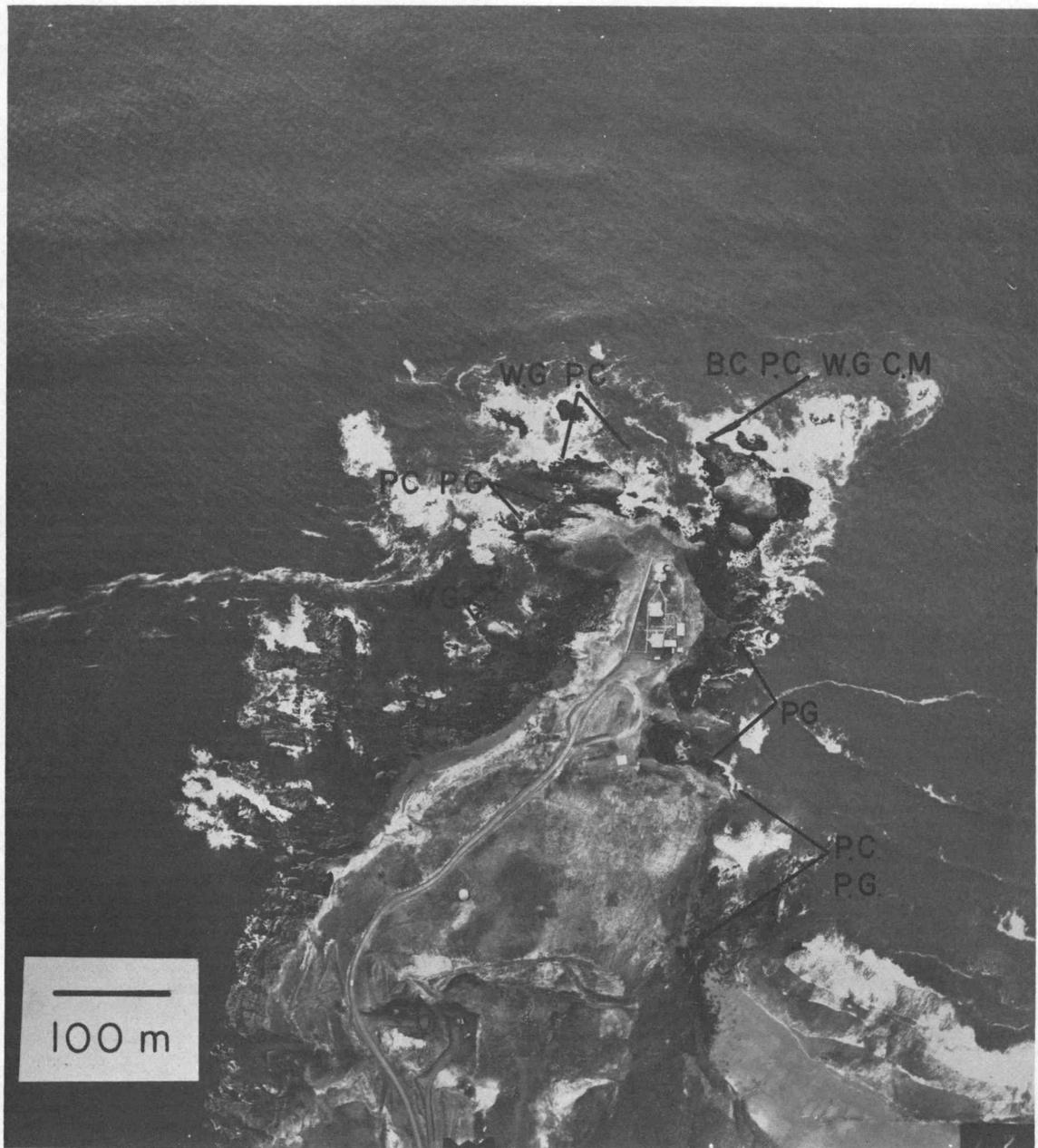


Figure 2. Aerial photograph of Yaquina Head. Breeding sites for the five most abundant species are indicated in the following manner: BC, Brandt's Cormorant; PC, Pelagic Cormorant; CM, Common Murre; PG, Pigeon Guillemot; and WG, Western Gull.

(Haematopus bachmani). Estimates of breeding densities of these species on the Head are given in Table 1.

Table 1. Total number of nesting pairs of marine and shorebirds known to be nesting on Yaquina Head during each of the three years of the study. Figures for the Common Murre and for the two species of Cormorants are from aerial surveys.

Species	Year		
	1969	1970	1971
Black Oystercatcher	1-2	1-2	2
Brandt's Cormorant	NC ^{a/}	41	45
Pelagic Cormorant	46	52	34
Common Murre	1200	2534	1660
Pigeon Guillemot	75-100 ^{b/}	75-100 ^{b/}	75-100 ^{b/}
Glaucous-winged Gull	4 ^{c/}	4 ^{c/}	5 ^{c/}
Western Gull	NC	NC	63

^{a/} No census

^{b/} It was impossible to count the number of Pigeon Guillemot nests, so these figures are estimates.

^{c/} Three of these were mixed pairs, Larus glaucescens x L. occidentalis, in each of the three years. For details, see Scott, 1971.

The area inshore of Yaquina Head is characterized by a relative shallow mixed sand and rock bottom, with the inshore area to the south protected from heavy ocean swells by a shallow intermittent reef which extends south 4 nautical miles to the north jetty of Yaquina Bay. This reef provides a protected inshore area for foraging during

moderately rough weather. The area north of Yaquina Head is also relatively shallow, but no protective reef formations are found there (U. S. Coast and Geodetic Survey Chart #6056). Water depth increases relatively uniformly from the head to the edge of the continental shelf some 25 nautical miles offshore. There is, however, a relatively shallow reefy area (13 - 30 fathoms) some 16 nautical miles southwest of Yaquina Head which might serve as a possible foraging area for birds nesting on the head.

The dominant characteristic of the oceanic area off Oregon is the strong coastal upwelling which occurs annually from May through September (Smith, 1964). The upwelling is not continuous, but is the result of strong northerly winds during the spring and summer months which produce an offshore component in the movement of relatively warm surface water and a subsequent influx of cold, nutrient-laden water from relatively shallow depths (less than 200 m). This upwelling into the photic zone results in high levels of primary production during the summer months (Small, Curl and Glooschenko, 1972). This high production, with the subsequent increases in phytoplankton biomass, provides the food base for large populations of organisms higher in marine food chains, and is largely responsible for the large populations of marine birds which occur in Oregon. Large populations of marine birds and other animals also seem characteristic of other areas of the world with

strong upwelling (Alexander, 1928; Murphy, 1936).

Yaquina Head is relatively isolated from other major marine bird breeding areas along the Oregon coast (United States Fish and Wildlife Service unpublished reports). It is 7.7 km north to the nearest breeding colony of Brandt's Cormorants and Common Murres and 123 km to the nearest Murre colony to the south (Figure 1). Pelagic Cormorants and Pigeon Guillemots may nest at suitable sites less than 20 km to the south, but not in the large colonies characteristic of the first two species.

METHODS

Census Procedures

The density and/or distribution of the four species I studied were determined by censuses taken at Yaquina Head, by censuses of Yaquina Bay, and from longshore and offshore transects.

To assess the inshore feeding patterns of the four species, I stopped at five predetermined spots around the head and, on a field map, recorded observations of all birds actively engaged in feeding within 200 m of the head. I remained at each stop for 5 min or until all birds were mapped. Each bird was observed for 30 sec and its position noted if it initiated a dive or handled food at the surface. Birds which were observed surfacing during an observation period were also counted. Because cormorants dive continuously once a sequence of dives has been initiated and spend very little time on the water for activities other than foraging, I feel confident that all feeding cormorants were mapped. Some of the feeding murrelets and guillemots may not have been tallied because of their propensity to loaf on the water and dive intermittently. In the case of feeding flocks, all of the birds which appeared to be part of that flock were counted as feeding. After the final count, then, I had a spot map of all feeding birds observed during a given time period.

Such censuses were taken at 2-4 hr intervals beginning at dawn and ending at sunset on 9 different days during the summer of 1971. Additional censuses were taken at least weekly during this period. In addition, at least one census a month was taken through the winter of 1971-72 in order to assess seasonal variations in the foraging activities and occurrence of the four species. This type of census allows me to quantify the relative intensity of foraging activities in different areas and at different times. It was not designed to serve as an estimator of populations. Population estimates of birds at Yaquina Head were obtained by direct count of nesting birds (Table 1).

Another census was taken at Yaquina Bay. Here the positions of all individuals of the four species observed between the Marine Science Center small boat dock and the end of the Yaquina Bay jetties (a distance of 4.1 km) were noted on the map of the bay. These birds were observed from the bridge of the R/B PAIUTE while going to and from sea. Non-feeding as well as feeding individuals were included, so this census is not directly comparable to the Yaquina Head census.

The third technique involved the use of standard longshore and offshore transect lines. The longshore transect originated at a point 0.25 mi off the north jetty of Yaquina Bay (all measurements are in nautical miles), and extended north on a straight line to a

point 0.25 mi off Yaquina Head. The total distance covered was 4.0 mi. The depth was relatively shallow and uniform along the transect, at no point exceeding 21 m at mean lower low water. The offshore transect originated at the end point of the longshore transect off Yaquina Head, and ended 10.25 mi off the head on a compass heading of 240° (Figure 1). Depth increased gradually from 20 m at the origin to 82 m at the 10.25 mi point. Occasional transects were run to a point 20.25 mi offshore, but not on a regular basis. Transects were run on a weekly basis during the summer months (May - August) and monthly for the remainder of the year, weather permitting (1969-1971). The first offshore transect during any given day was begun 3 - 4 hours after sunrise.

The 11 m R/ B PAIUTE was used during all transects. I observed from the right side of the flying bridge, 3.5 m above the water line. In each 0.25 mi segment of the transect traversed, all birds observed in a 180° arc while facing the bow of the vessel were counted. Notes on their behavior, direction of flight, group size, and age of each individual or group sighted were recorded on standardized forms. Sea surface temperature, atmospheric visibility, swell height and direction, water clarity, and wind velocity were also recorded at the beginning and end of each offshore transect.

The vessel's engine was run at a constant speed of 2200 RPM during a transect run. This allowed for a speed of 9 knots under

calm sea conditions and no drift. The position of the vessel along the transect was determined by using a stopwatch, allowing 1 min 40 sec for each quarter mile traversed. Compensation for currents, winds and sea conditions was made by adding or subtracting as much as 10 sec to the elapsed time for each 0.25 mi traversed. The accuracy of these position estimates was verified during the long-shore transect by using radar and a fixed reference point on land at the beginning and end of the transect. During the offshore transect a fixed reference point on land and radar were used to establish the position at the beginning of the run, and radar and a fathometer at the end of the run. The reliability of these methods was quite good, with ± 0.25 mi accuracy, or 2.5 percent error, in a 10 mile run. Runs that deviated more than this were few, and were not included in my analysis.

In counting birds along a transect, all individuals which could be identified to genus were included. The distance at which a particular species could be observed varied depending on its behavior (sitting on the water, flying low, flying high, flying alone or in a group, etc.). Additional factors which varied from cruise to cruise (e.g., wind chop, wave height and period, fog, glare, and observer alertness) affected the distance at which a particular species could be seen. These factors have been discussed by King (1970). I attempted to eliminate or minimize the effect of as many of these variables as

possible. Weather and sea conditions (wind velocity, chop, swell height) were held within a minimum range of values by the extremely limited weather conditions under which the vessel could run the transects. The effect of glare and possible effects of time of day on the behavior of the birds were minimized by standardizing the time of day (with respect to sunrise) that the transect was run. Variations in atmospheric visibility were minimized by confining censuses to conditions of at least 200 m visibility. Possible effects of the vessel serving as either an attractant or repellent to birds were minimized by using a relatively small vessel and by using the same vessel for all runs. Moreover, the same individual made observations on all transects, and by confining the observations to a period of just over 1 hr I could give complete attention to the task at hand.

Differences in conspicuousness among the four species of interest and lack of lateral or frontal spatial constraints in the transects make any expression of bird densities on an absolute basis (individuals/unit area) undesirable. King (1970) and Kuroda (1960) discussed the problem of estimating density on a per unit area basis, but neither allowed for behavioral differences within a species, assuming an average sighting distance for each species. This would produce serious biases in density estimates of species which have marked diurnal differences in their behavior, and this problem could be especially acute in continuous transects. These problems are

largely overcome by recording only those birds which occur in a given area to the front and side of the vessel (Cline, Siniff and Erickson, 1969), providing that all the behavioral types of a species are equally conspicuous within that area. Because this type of census technique was not used in this study, all bird densities will be expressed as birds/linear nautical mile only.

The three different census techniques used allowed me to determine the distribution and relative abundance of each of the four species studied from the high tide line to a point 10 mi offshore.

Diving Behavior

The diving behavior of each of the four species was observed over a variety of depths. The time an individual spent submerged and the time spent on the surface during a diving sequence were determined in the following manner. I first located a bird on the water surface which was isolated enough from others of its species so that its diving behavior could be monitored without confusing it with other individuals. These birds were most often diving when first observed or were watched until they did dive. Two stopwatches were used to document the subsequent series of dives and rest periods to the nearest 0.1 sec. A second observer was often used to record the dive and rest periods on standard data sheets.

A timing sequence was always begun with a dive. Whenever the

bird under observation initiated a dive by submerging its head, the first stop-watch was started. It ran until the bird was observed breaking the water surface, whereupon that watch was stopped and the second simultaneously started to record the rest period. The elapsed time of the dive was then recorded on the data sheet and the first watch returned to zero in readiness for the next dive.

If a bird returned to the surface with a prey item in its beak or was obviously engaged in eating after a dive, the dive and rest times were recorded but were not included in my final calculation of dive-rest ratios. Rest periods were also deleted from these calculations if they followed the bird's final dive of a sequence or if the bird was obviously disturbed by other birds, mammals, or man.

The majority of the dive times were obtained by observation from the beach, although a large number of dive times for Common Murres were obtained from the R/B PAIUTE. It was possible while aboard the R/B PAIUTE to approach murres to within 25 - 50 m without noticeably disturbing their foraging activities. In these cases there were always two observers aboard the vessel in order to facilitate tracking of the diving birds. Most of the dive-rest times obtained from the PAIUTE were of adult murres accompanied by a chick.

Food Analysis

Specimens were collected for stomach analysis at infrequent intervals throughout the year. Birds were collected at sea from the R/B PAIUTE with a twelve gauge shotgun. All birds were collected within a 10 mi radius of Yaquina Head and most were shot while they were on the water to reduce cripple loss. Immediately after capture 20cc of formalin was injected into the stomach via the esophagus. Information on the water depth, flock association, and distance offshore was recorded for each specimen. Upon return to the laboratory each bird was weighed and then frozen until it could be dissected.

During dissection, sex, gonad size, and the presence or absence of a brood patch were noted, and a subjective evaluation of the fat deposits was made. The digestive tract from the esophagus to and including the ventriculus was then removed and the contents preserved in 10 percent formalin. The contents of the esophagus, proventriculus and ventriculus were kept separate, and only the first two were used for analysis of food habits. Prior to examination the contents were leached in water for several hours and then placed in 70 percent isopropyl alcohol. Individual food items were identified to species if possible and the number of individuals in each taxon recorded. To determine prey size, fish were measured from the most anterior point to the base of the tail, while euphausiids and other

midwater crustaceans were measured from the front of the rostrum to the bend of the telson. The decapod crustacean widths were measured at the widest part of the cephalothorax. All food items were graded, using the same system as Ashmole and Ashmole (1967, p. 12):

- Grade 1: Items in good condition whose length could be measured accurately,
- Grade 2: Slightly broken or digested items from which fairly accurate measurements of length could be obtained,
- Grade 3: Largely digested items which could nonetheless be assigned a length on the basis of remains present,
- Grade 4: Items which could be identified to class but with no estimate of length possible.

Additional information on food types taken by the four species was obtained from observations of birds (Common Murres and Pigeon Guillemots) returning to the nest site to feed young, or from observations of prey captures at sea.

GENERAL BREEDING BIOLOGY

In order to place the four species studied in perspective with relationship to each other and the study area, a brief outline of the biology and ecology of each species is given below.

Brandt's Cormorant

Brandt's Cormorants with a mean weight of 2459 g (Table 2) and a body length of 88.0 cm (Palmer, 1962) is the largest of the four species studied. It breeds from the coast of northern Washington south to Natividad Island and Gull Rocks, Baja California, with some colonies in the Gulf of California (Wetmore, 1957). The breeding population in Oregon numbers about 15,000 individuals (U. S. Fish and Wildlife Service, unpublished reports).

Table 2. Body weights of the four species of interest based on specimens collected in the study area during the summer of 1970 (s = standard deviation).

Species	N	Weight (g)		
		X	Range	s
Brandt's Cormorant	10	2458.6	2055-2727	62.7
Pelagic Cormorant	5	1626.2	1371-1936	101.6
Common Murre	10	1021.7	867-1195	30.8
Pigeon Guillemot	2	523.0	554- 595	40.5

Brandt's Cormorant breeds in colonies of up to 500 or more individuals in Oregon. It is found nesting on the flat and gently sloping surfaces of offshore stacks and islands, although mainland colonies are known to occur. Normal clutch size is four, with a range from three to six (Palmer, 1962). The nesting habits and breeding behavior of this species have been described by Bent (1922) and Williams (1942).

The colony at Yaquina Head nested exclusively on the relatively flat surface of the largest of the two stacks situated off the tip of the head (Figure 2). The colony consisted of 41 to 45 pairs (Table 1), and was situated amidst the large colony of Common Murres. The nests were constructed of grasses and sea weeds, the latter obtained by diving in the shallow water immediately adjacent to the north side of the head. Brandt's Cormorants were observed with young as early as the last week in June. The breeding chronology for this and the other three species of interest nesting on Yaquina Head is given in Table 3.

Pelagic Cormorant

The smallest of the three species of cormorants found in Oregon have a mean weight of 1626 g (Table 2) and a length of 63.5-73.7 cm (Palmer, 1962). Pelagic Cormorants breed in North America from the northwest coast of Alaska south to Los Coronados

Table 3. Breeding chronology for the four species of interest. Dates given are the first date on which eggs or young were observed and are not necessarily the first date of occurrence.

	First Eggs Observed	First Young Seen	First Young Fledged
Brandt's Cormorant			
1969	----	----	----
1970	6/25/70	7/1/70 - 3 nests with young less than 1 week old	8/9/70 - young fully feathered and ready to fledge
1971	5/29/71 - 29 nests in various stages of construction; eggs in some	6/29/71 - 2 nests had young less than 1 week old	8/9/71 - 70 young completely feathered and ready to fledge
Pelagic Cormorant			
1969	5/28/69 - eggs in 2 of 4 nests under observation	----	----
1970	5/29/70 - single eggs in 2 of 4 nests under observation	7/1/70	8/8/70 - young fully feathered and ready to fledge
1971	5/23/71 - first eggs observed; 6/19, 3 eggs in one nest	7/9/71 - first young seen less than 1 week old	7/30/71
Common Murre			
1969	5/6/69 - 100 eggs observed	----	7/21/69 - first young murre seen at sea
1970	5/21/70	----	6/30/70 - first adult chick pair seen at sea
1971	5/29/71	----	7/5/71 - first adult-chick pair seen at sea
Pigeon Guillemot			
1969	----	----	----
1970	----	----	----
1971	5/22/71	7/3/71	8/17/71

Islands, Baja California (Wetmore, 1957). It is difficult to estimate the Oregon population of this bird because it nests on vertical cliff faces, often singly or in small groups, where it is very difficult for airborne observers to assess its numbers. However, it is probably less numerous than the Brandt's Cormorant. Like Brandt's, the Pelagic Cormorant is a strictly marine bird and is not found inland like the Double-crested Cormorant (Phalacrocorax auritus). Clutch size ranges from three to seven eggs, with four being the modal size (Peterson, 1961).

In Oregon this species nests in isolated pairs and in loose colonies on precipitous cliff faces of the mainland and offshore stacks and islands. The nesting habits and breeding behavior of this species are poorly known, but some information is to be found in Bent (1964) and Van Tets (1965) and a summary of available information is given in Palmer (1962).

On Yaquina Head this species nested at scattered sites on the end and north side of the head itself, with a few individuals nesting on the cliff faces of the two large stacks situated off the tip of the head. Although suitable nest sites seemed available on the southern cliff faces, no Pelagic Cormorants were observed nesting or attempting to nest on these cliffs. Both Brandt's and Pelagic Cormorants, however, used the offshore rocks in this area as roosting sites.

Common Murre

Certainly the most conspicuous marine bird breeding in Oregon, the Common Murre attains an average weight of 1022 g (Table 2) and average length of 36 cm (Cody, 1973). Its breeding range in North America includes the Atlantic, Arctic and Pacific Oceans, and in the last it can be found breeding at sites ranging from Alaska to Central California (Wetmore, 1957). The Oregon breeding population of this species numbers some 200,000 individuals and some colonies number 50,000 or more (U. S. Fish and Wildlife Service, unpublished reports). It lays a single egg each year and in Oregon characteristically breeds on the barren flat or gently sloping unvegetated surfaces of offshore stacks and islands. In addition, there is at least one mainland breeding site where murre nest on relatively wide cliff ledges. The nesting habits and breeding behavior of this species have been described by Johnson (1941) and Storer (1952) and were reviewed by Tuck (1961).

The birds at Yaquina Head nested exclusively on the relatively flat surface of the largest of the two stacks situated off the tip of the Head. Although the rock immediately to the south would seem to be equally appropriate, its top served as a nesting site for Western Gulls only. Common Murres were the earliest nesters of the four species studied and also had the shortest nestling period (Table 3).

The nestling period was shortened considerably by the chick leaving the nest and going to sea at only 1/4 of the adult weight (Tuck, 1961). Each chick was accompanied out to sea by a single adult which provided food for the chick for an undetermined period of time, probably in the neighborhood of three to four weeks.

Pigeon Guillemot

The Pigeon Guillemot is the smallest of the four species studied, with a weight of 523 g (Table 2) and an average length of 27 cm (Cody, 1973). It breeds in both Asia and North America, and in the latter it ranges from Alaska south to Santa Barbara Island off southern California (Wetmore, 1957). The Oregon population of this species has not been estimated.

Pigeon Guillemots nest singly or in loose assemblages of several dozen pairs in crevices and crannies of cliff faces on the mainland and on offshore stacks and islands. They lay from one to two eggs and, unlike the murre, the young are completely independent after leaving the nest site. Like the murre, the Pigeon Guillemot constructs no nest. The nesting habits and breeding behavior of this species have been described by Drent (1965), Storer (1952), and Thoresen and Booth (1958).

The birds on Yaquina Head were found nesting at scattered sites on the cliff faces of the Head itself, on the offshore stacks, and in the

sea caves under the Head (Figure 2). No estimate of the total number breeding on the Head was possible, but it was probably between 75 and 100 pairs.

OFFSHORE DISTRIBUTION

The four species varied in the areas and the distances offshore in which they characteristically foraged (Figure 3). During the breeding season the differences in the occurrence of the four species within vs. beyond 50 m of Yaquina Head was highly significant ($X^2 = 31.5$, $p < .005$). Pelagic Cormorants foraged most frequently within 50 m of the head (Table 4), while Brandt's Cormorants and Common Murres foraged more frequently at distances greater than 50 m from the beach, and Pigeon Guillemots were evenly divided between the two areas. The area within 50 m of the head was quite shallow and the water's surface was often broken by rocks and stacks, especially at low tide. The area beyond 50 m was deeper, and had an uninterrupted surface. Taking into consideration the differences in population numbers, the four species can be ranked according to their propensity to forage within 200 m of Yaquina Head as follows: Pelagic Cormorant, Brandt's Cormorant, Pigeon Guillemot, and Common Murre (Figure 4).

Highly significant differences were also observed in the occurrence of these species in the inner and outer sections of Yaquina Bay ($X^2 = 27.4$, $p < .005$). The dividing line between the two areas was the Newport Bay Bridge, which marked the dividing line between the bay proper and the entrance channel. Common Murres and

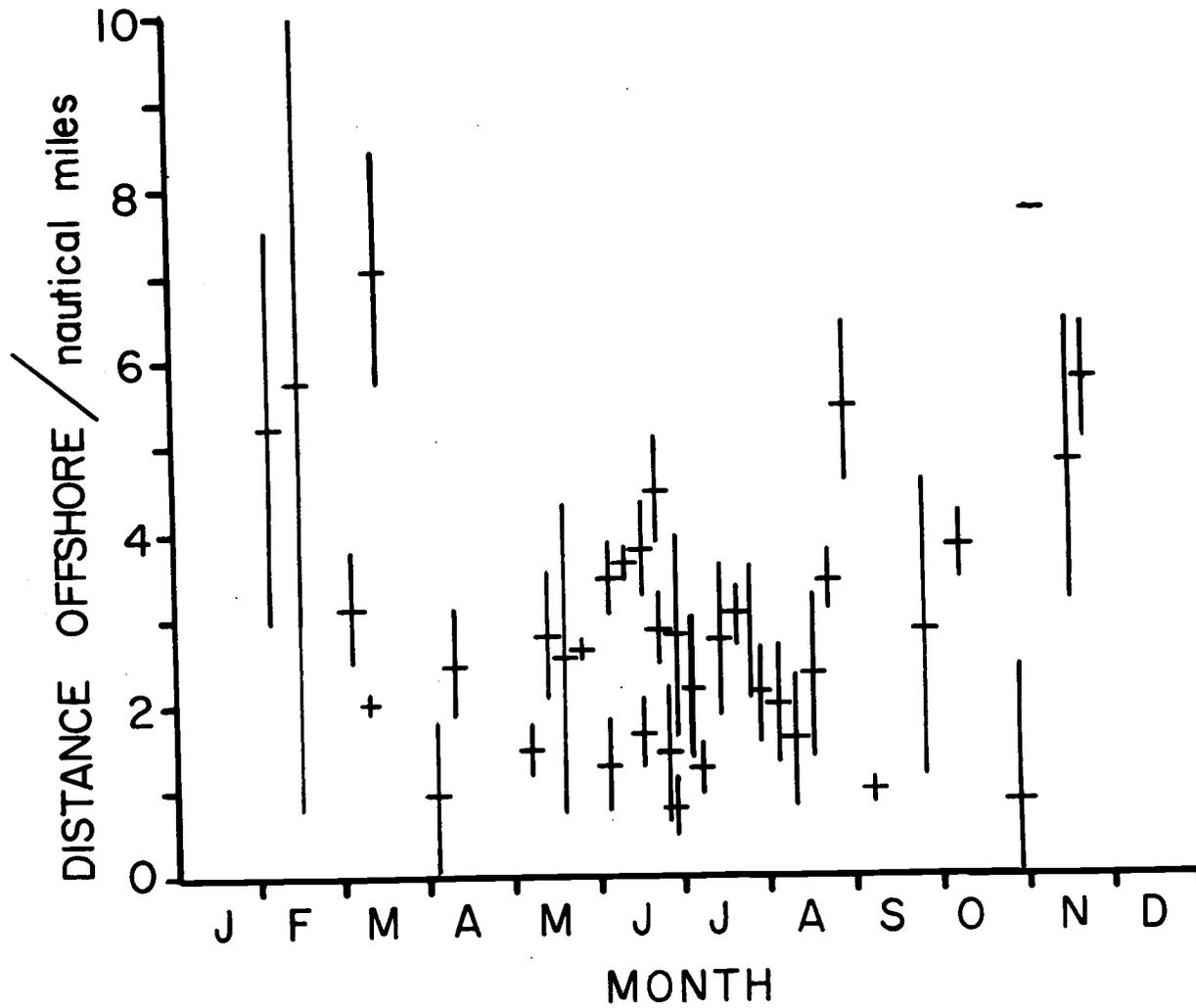


Figure 3. Mean distance offshore and two standard errors for Common Murres observed on offshore transects which were run within four hours of sunrise during the study period.

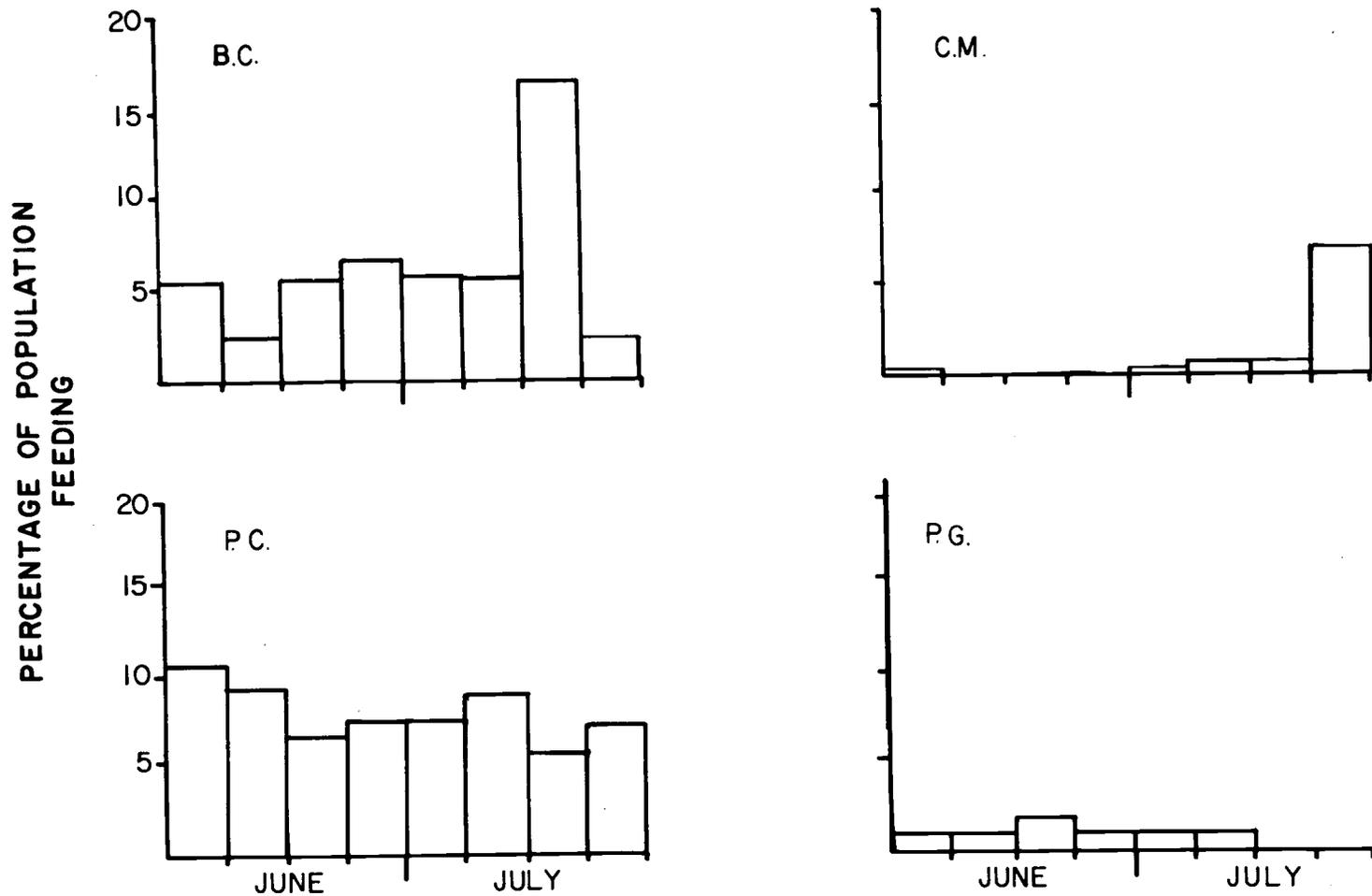


Figure 4. Percentage of breeding birds of Yaquina Head observed foraging within 200 m of the head during the 1971 breeding season (June-July). Brandt's Cormorant = B.C. , Pelagic Cormorant = P.C. , Common Murre = C.M. , and Pigeon Guillemot = P.G. These same abbreviations are used in the remainder of the figures.

Pelagic Cormorants foraged more frequently in the entrance channel while Pigeon Guillemots and Brandt's Cormorants were evenly divided between the two areas (Table 5).

Pelagic Cormorants were found most frequently during the breeding season foraging singly within 25 m of the beach, often over the intertidal zone at high tide, near wave-swept rocks offshore or immediately adjacent to the rip-rap or pilings in Yaquina Bay. They were observed less frequently in mixed-species feeding flocks.

Of the four species, only Common Murres were seen frequently enough (more than 20 times) on offshore transects to characterize their offshore distribution (Figure 3). The mean distance offshore was calculated as:

$$\frac{\sum n_i D}{4N}$$

Where D = distance offshore (in 0.25 mi segments)

n_i = number of individuals observed within the i^{th} quarter mile segment

N = the total number of individuals observed on a given transect (i. e. $\sum n_i$)

The mean distance offshore at which Common Murres were observed varied considerably during the breeding season prior to the observation of the first adult-chick group at sea (Figure 3). However, the majority of birds seen during this period occurred

Table 4. Total number of each species observed feeding within and outside of 50 m off Yaquina Head for the period October 1970 to May 1971. The number in parentheses is the total for the four-month period when all four species are breeding (May - August).

Species	Inside	Outside
Brandt's Cormorant	49 (48)	108 (108)
Pelagic Cormorant	89 (82)	55 (54)
Common Murre	75 (71)	113 (113)
Pigeon Guillemot	25 (25)	19 (18)

Table 5. Total number of each species observed feeding inside and outside the Yaquina Bay bridge. This is the total for all censuses, May 1971 to May 1972. The number in parentheses is the total for the four-month period when the four species of interest are breeding (May - August).

Species	Inside	Outside
Brandt's Cormorant	27 (5)	25 (8)
Pelagic Cormorant	8 (2)	32 (7)
Common Murre	53 (53)	187 (187)
Pigeon Guillemot	44 (44)	40 (40)

within 5 mi of the beach. During the winter murre were found less frequently within 5 mi of the beach and the mean distance offshore increased (Figure 3). This change in distribution is perhaps best depicted in Figure 5.

The within season variation in the offshore distributional pattern of Common Murres (Figure 3) is undoubtedly due to the nature of the food resource that these birds are exploiting. Schooling fish are patchily distributed on a horizontal plane radiating away from the breeding colony. The distance from the colony at which murre feed is a function of the availability of these schools within a given area. This distance may vary as much in a season as it does between seasons (Figure 3). If the first birds out in the morning locate a large school of fish or several schools within a mile of the colony and are able to maintain contact throughout the day then later foraging birds will be found in this area and any transects run through that area will show a strong inshore bias. A strong offshore bias might be shown if the same conditions occurred 5 miles offshore. Seasonal patterns in the offshore occurrence of murre are best depicted as averages in which daily trends are averaged (Figure 5).

Brandt's Cormorants foraged singly or in very compact single-species feeding flocks which were most frequently seen in late summer. They were also found foraging in mixed-species feeding flocks. They were generally seen feeding farther offshore than Pelagic

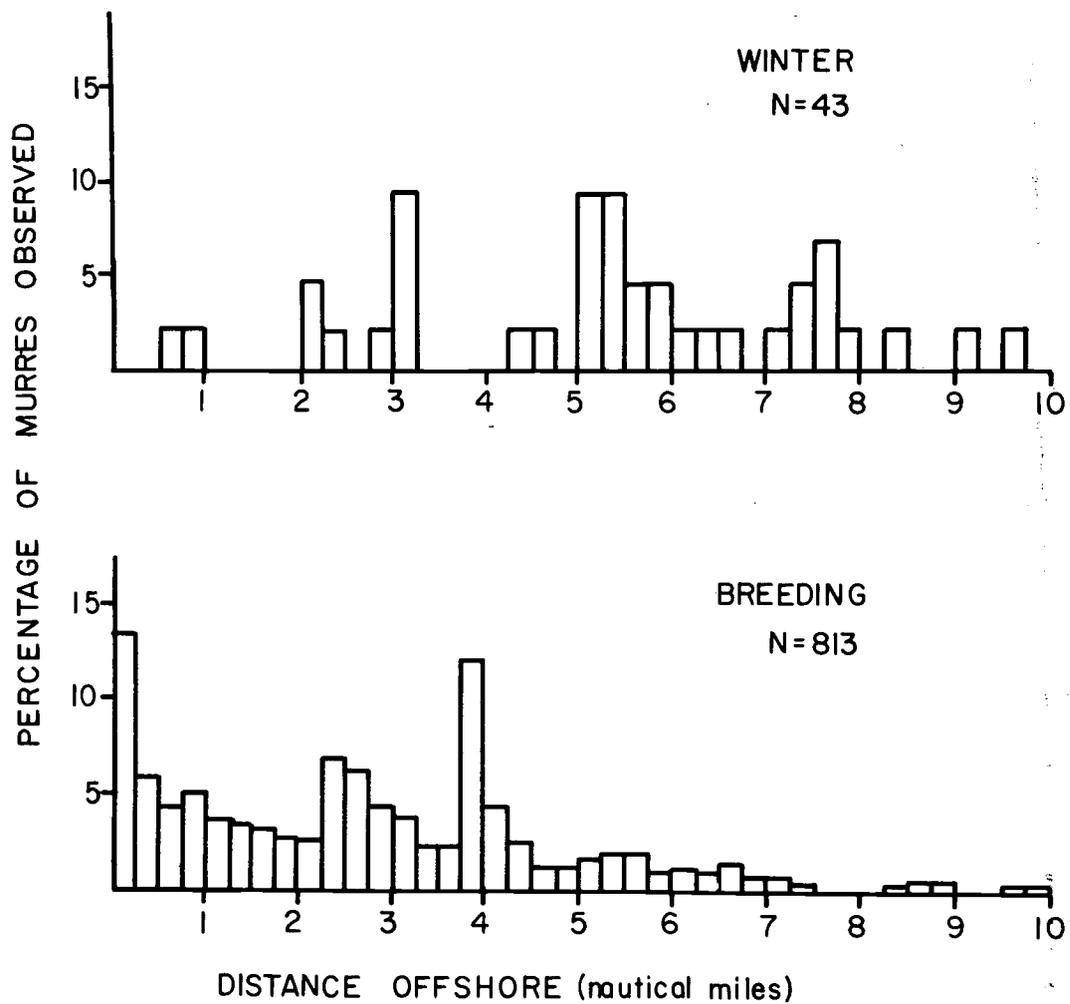


Figure 5. The offshore distribution of Common Murres observed on the water's surface. This is the average offshore distribution based on 60 nautical mi of transects for the winter (October - March) and 150 mi during the breeding season (May - June) prior to the departure of the young from the breeding rocks.

Cormorants and in more open expanses of water, often over sandy bottoms and in the bay. As was true of Pelagic Cormorants, Brandt's were seldom observed more than 2 mi offshore.

Pigeon Guillemots foraged singly, with seldom more than two or three foraging in the same area and never as a flock. They were found further offshore than the cormorants, but never more than 5 mi. They were, however, occasionally seen foraging extensively in water less than 0.5 m deep inside Yaquina Bay. Pigeon Guillemots were observed feeding in the bay more frequently than any of the other species and were the only species studied which did not join in the foraging activities of the mixed-species feeding flocks. The observation of Pigeon Guillemots foraging very close to shore in my study area contrasts with the complete lack of inshore feeding activities by Pigeon Guillemots in central California as reported by Storer (1952). This suggests that Pigeon Guillemots are very plastic in their choice of foraging areas, responding to local environmental conditions.

Common Murres were the most pelagic of the four species studied. They were frequently observed feeding in single and mixed-species flocks as far as 10 mi offshore and were seldom found foraging within 200 m of the beach.

SEASONAL SHIFTS IN DISTRIBUTION AND ABUNDANCE

Common Murres and both species of cormorants are found throughout the year in Oregon, while Pigeon Guillemots are absent during the winter months, with only scattered individuals being found from late October to the middle of March (Gabrielson and Jewett, 1940). These differences in the seasonal occurrence of the four species are shown clearly in Figures 5, 6, 7, 8 and 9.

Brandt's and Pelagic Cormorants had similar seasonal patterns during the period of my study. Following the end of the breeding season in August, there was a reduction in the number of birds observed within 200 m of Yaquina Head (Figure 7). The same general pattern was observed in the longshore transects (Figure 8), although the number of birds observed was never great. The number of both cormorant species observed on offshore transects was so small that meaningful seasonal comparisons could not be made.

In contrast to the reduced number of Pelagic and Brandt's Cormorants seen about Yaquina Head and in the waters immediately offshore, abundance in the protected waters of Yaquina Bay showed a sharp increase during the non-breeding season (Figure 9). The number of both species found in the bay represented about 50 percent of the breeding population of Yaquina Head. This, combined with the reduction in numbers at the breeding rocks, suggests dispersal and

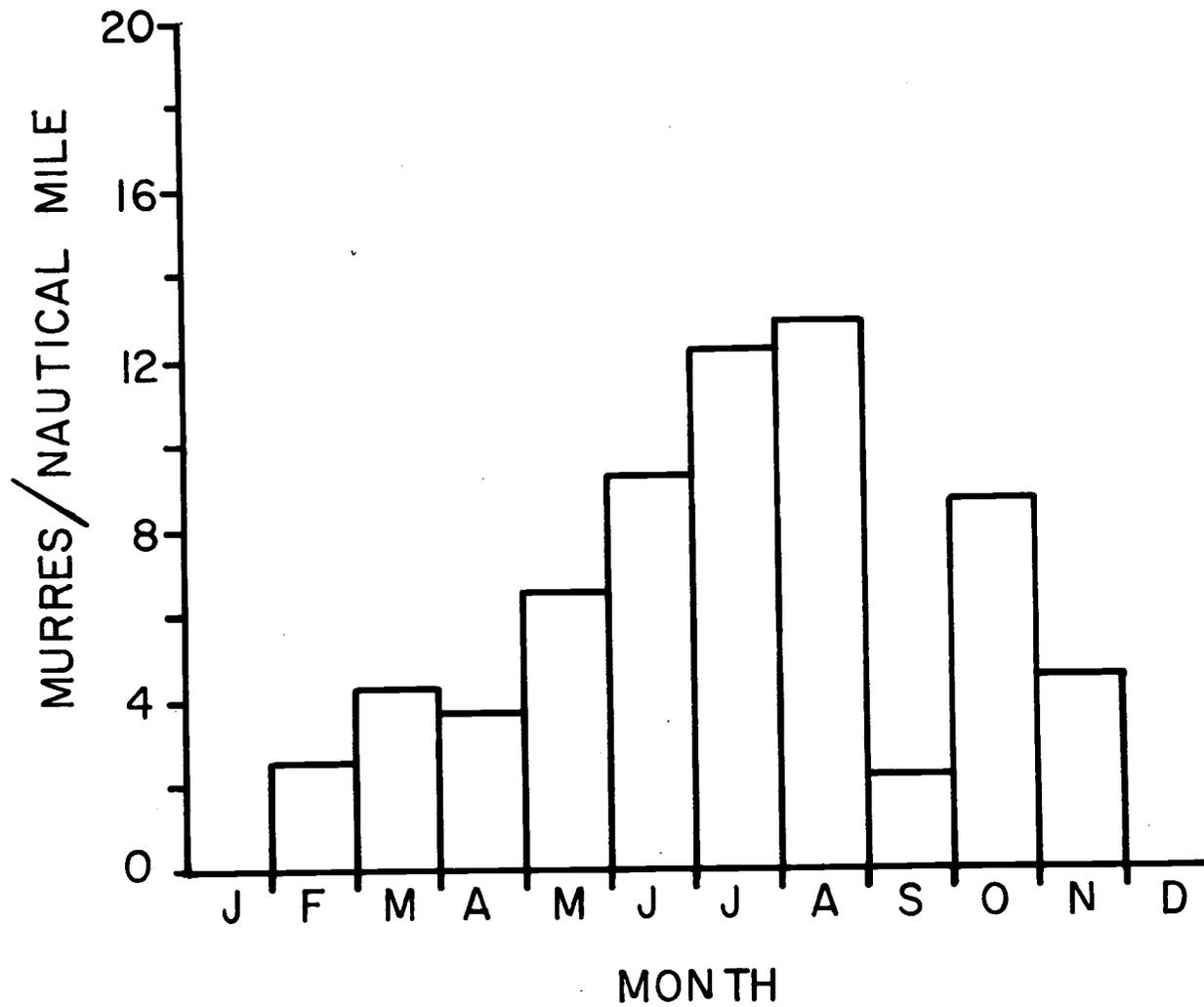


Figure 6. Average number of Common Murres observed per nautical mile during offshore transects from June 1969 - September 1971.

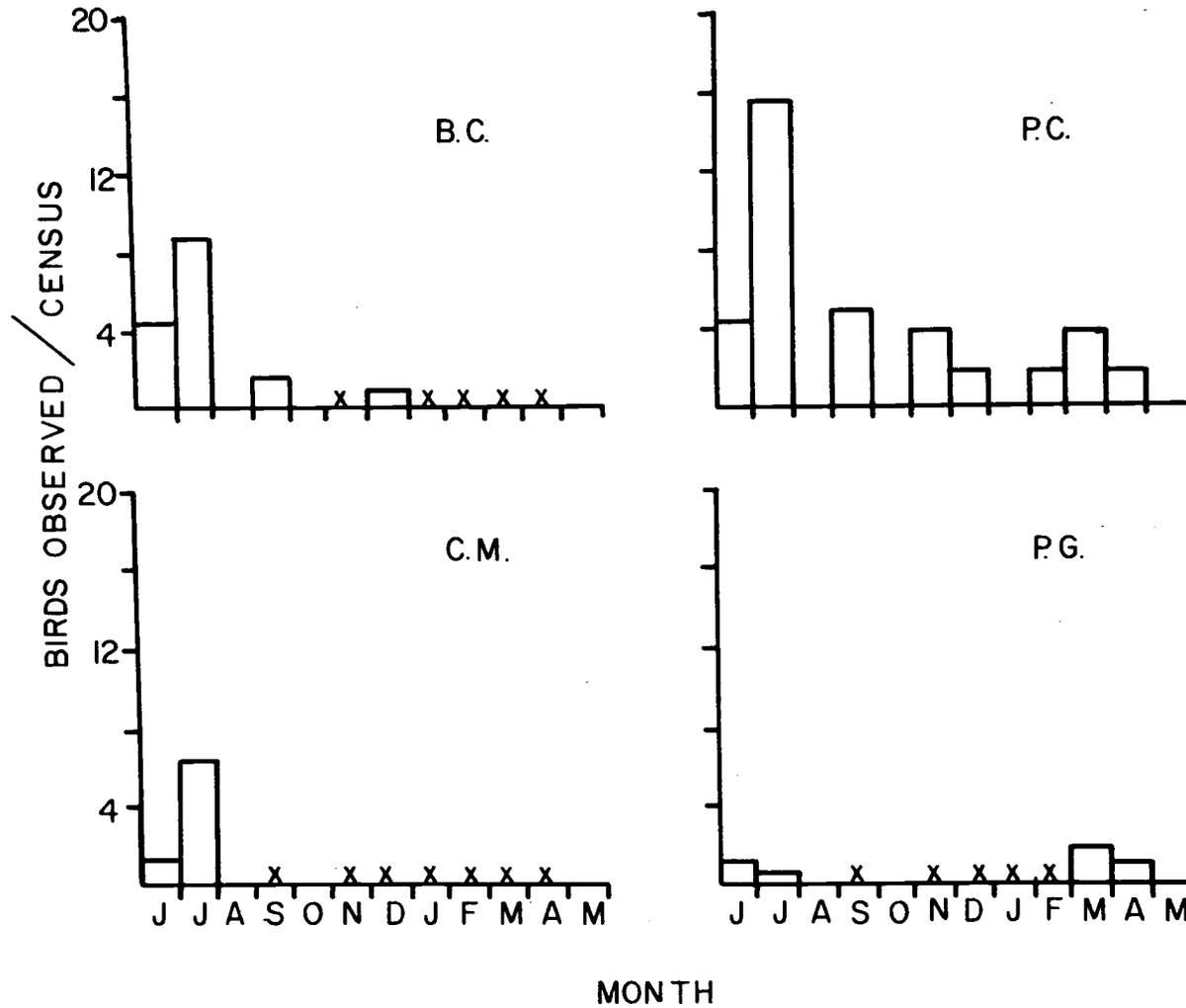


Figure 7. Average number of birds of the four species of interest observed feeding during censuses of Yaquina Head. Censuses were made within two hours of noon. X indicates census made but no birds observed.

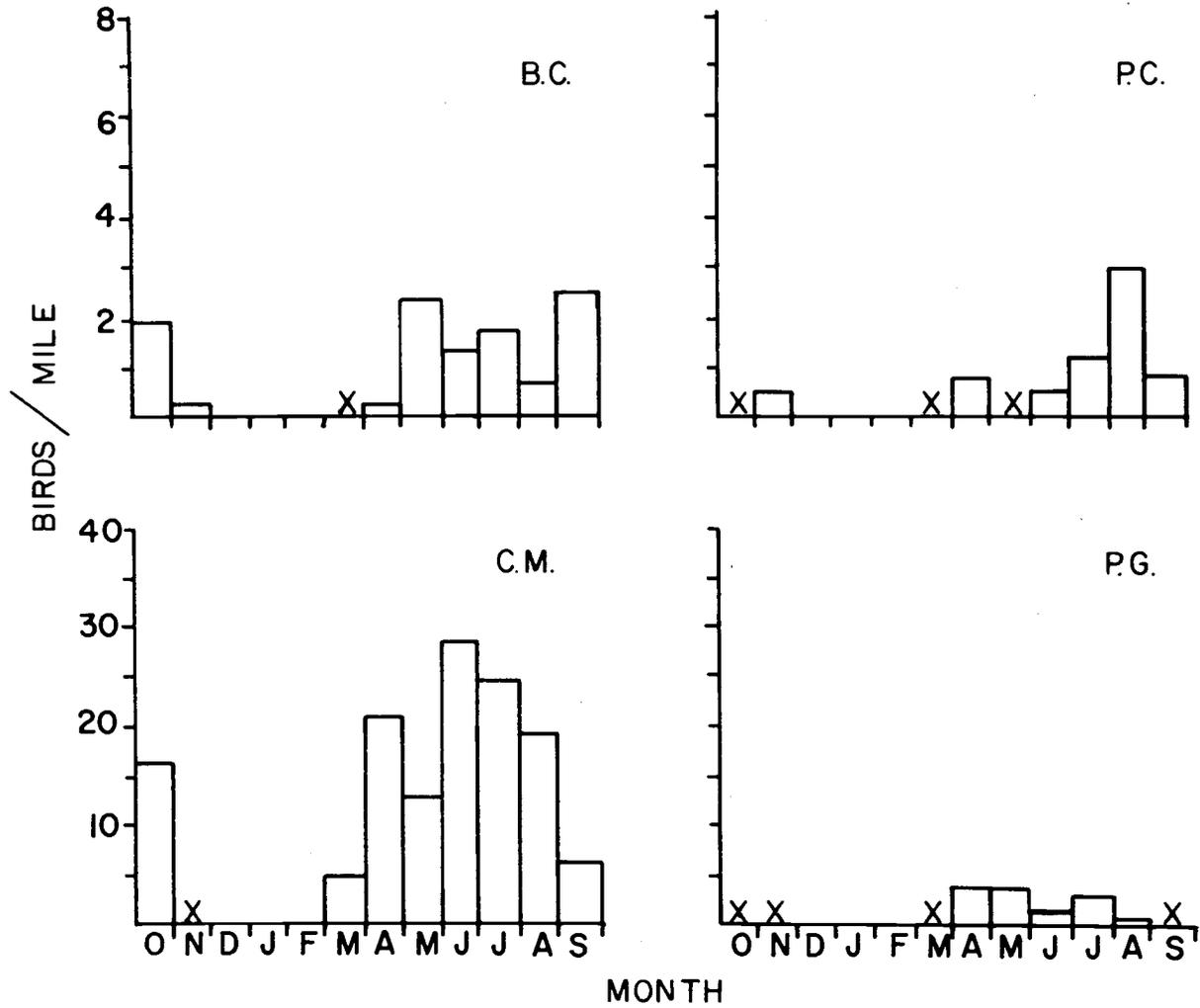


Figure 8. Mean number of birds of the four species of interest observed per nautical mile during longshore transects, October 1970 - September 1971. X indicates census made but no birds observed.

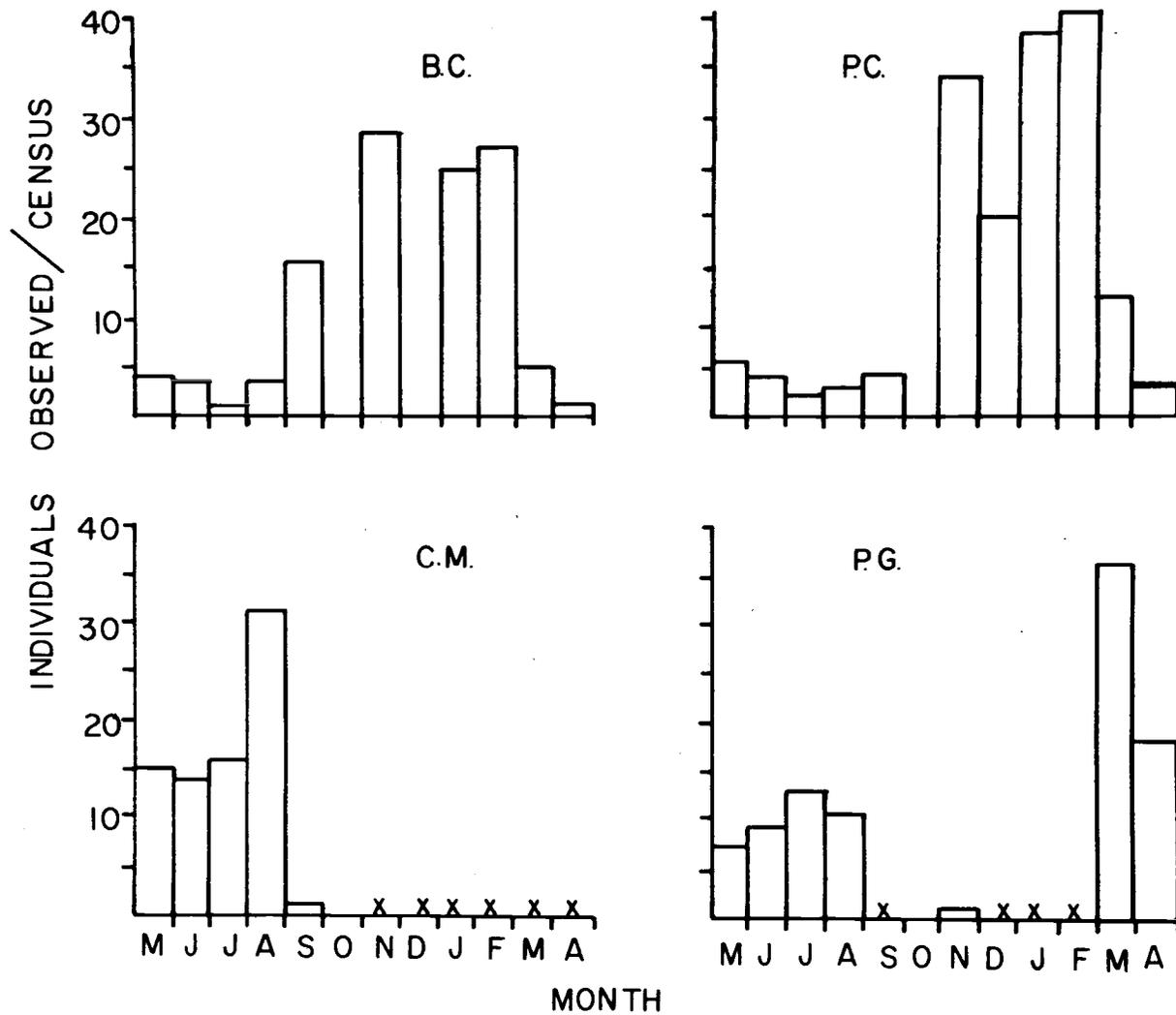


Figure 9. Average number of the four species of interest observed on the water in censuses of Yaquina Bay. Censuses were made during the early morning hours, 0630-1000, May 1971 - April 1972. X indicates census made but no birds observed.

migration out of the area. The large flocks of adult Brandt's Cormorants observed immediately offshore in late July and August probably represented birds from more southerly populations that had completed their breeding activities.

Common Murres showed a somewhat different pattern than that described for the cormorants. There were no murres observed feeding within 200 m of Yaquina Head during the non-breeding season, and abundance in Yaquina Bay showed a similar decline (Figures 7 and 9). The greatest number of birds were observed in the offshore and longshore transects during the breeding season. However, the greatest number observed on any single census was in March. This was the result of the occurrence immediately offshore of Yaquina Head of what was apparently the entire breeding colony. The return of the entire colony to the nesting rock occurs at infrequent intervals and for brief periods during winter, becoming more frequent during the spring (Tuck, 1961; American Birds, 1970). The difference in the number of murres observed in the offshore transects (Figure 6) during the breeding and non-breeding seasons was highly significant (Mann-Whitney U test: $t = 170$, $p < .005$).

Pigeon Guillemots were absent from the census area from October to mid-March, when they returned to Yaquina Bay and the waters within 3 mi of the beach (Figures 7, 8 and 9). Storer (1952) and Bent (1963) have suggested that Pigeon Guillemots winter at

distances further offshore than they are commonly found during the breeding season. No Pigeon Guillemots were observed during the winter months on any of the regular offshore transects, nor on several transects which extended as far as 100 mi out to sea. In addition Pigeon Guillemots are regularly found during the winter months in the protected waters of Puget Sound and the inland passage (Cruickshank, 1970; Crowell and Nehls, 1972). I suggest that California, Oregon and open coast Washington populations of Pigeon Guillemots are to be found during the winter months in the previously mentioned protected waters which provide more foraging opportunities during rough weather than would the unprotected outer coasts from Point Conception north.

COMMON MURRE ADULT-CHICK INTERACTION

The chick of the Common Murre leaves the nesting rock 2 to 3 weeks after hatching (Tuck, 1961). At sea, three different patterns of adult-chick association may be observed:

- 1) a single chick unaccompanied by any adult
- 2) a single adult accompanying a single chick
- 3) two adults accompanying a single chick.

The first two categories probably represent the same adult-chick grouping. Thus in my observations at Newport it was likely that in the first case the accompanying adult was submerged at the time of observation. When groupings of two adults with one chick were followed for periods of up to 15 min it became apparent that one of the adults was only temporarily associated with the chick. In addition, single adult-chick pairs which were under observation were occasionally joined by a second adult whose path they crossed. This third bird then accompanied the pair for up to 5 min before separation from the pair. Therefore, I suspect that most of the two adult-single chick groupings I observed actually represented a single adult-single chick association. However, in the analysis of adult-chick groups all two adult-one chick associations are considered as such.

To analyze patterns of adult-chick association, I divided into four 2-week periods the time from the observation of the first

adult-chick group at sea until no adult-chick groups were observed. There was no variation during the three-year study period in the nature of the adult-chick groups, nor were there major differences in the time that they were first seen at sea. Data from all 3 years were combined and the number of observations of each type of association totalled for each time period (Table 6). Most groups observed were of single adults with single chicks. No variation in the type of grouping was observed as the season progressed. Further, I observed 15 different adult-chick groups going to sea from Yaquina Head, and each of these groups consisted of a single adult and a single chick. This lack of variation contrasts with that reported by Storer (1952) for central California populations of the same subspecies. However, more recently he has indicated (personal communication) that he in fact observed only single adult-single chick groups, and that his earlier statements were in error.

There was an increase in both the number and percentage of murres on the water which were part of adult-chick groupings following the observation of the first adult-chick groups at sea (Table 6). At the same time, the number of murres observed on the water, per nautical mile, remained relatively constant through the first two week periods, decreasing after that. The number of adults unaccompanied by chicks declined during this same time period. This suggests that there is a real reduction in the number of adult

Table 6. Composition and occurrence of adult-chick groups for the four 2 week periods following the observation of the first adult-chick group at sea. Data for all three years are combined for the offshore transects.

	June 30-July 14	July 15-29	July 30-Aug 12	Aug 13-26
Nautical miles censused	30	60	60	35
Adult-chick groups observed	46	239	142	202
Percent of groups having 1 adult and 1 chick	97.7	96.9	99.1	95.3
Total adults observed on the water	304	616	343	284
Percent of adults associated with chick	15.1	38.8	41.4	71.1
Adults/transect/mile	10.1	10.3	5.7	8.1
Unaccompanied adults per mile	8.7	6.3	3.4	2.3

murres which are foraging in the immediate area of Yaquina Head. This is the result of a dispersal out of the area of females which were successful in rearing young as well as unsuccessful females and males not accompanied by chicks.

Adults accompanied by a chick occurred significantly farther offshore ($\bar{X} = 3.88$ mi, S. D. = 2.72, N = 551) than unaccompanied adults ($\bar{X} = 2.91$ mi, S. D. = 2.48, N = 453). Comparing 1 mi intervals for the first four mi of longshore and offshore transects which were run within 1 hr of each other, there was no significant difference in the dispersal patterns of adults accompanied by chicks south vs. west of the breeding colony (signed rank test, $n = 16$, $\Sigma R = 43.5$ $p > .20$). This suggests that the dispersal away from the breeding colony within 4.0 mi of the beach is not primarily a movement offshore as has been suggested by Cody (1973). Several additional transects to assess the extent of the offshore dispersal of adult-chick pairs extended as far as 200 mi out to sea, and all but 5 of 56 pairs seen were found within 10 mi of the beach, with one pair being observed 35 mi at sea (Figure 10).

Adult-chick groups have been observed in Alsea Bay and in Siuslaw Bay, 28.6 km and 73.7 km south of the nearest murre colony and 145.4 km and 103.2 km, respectively, north of the nearest murre colony to the south. Likewise, adult-chick groups have been observed in large numbers in Monterey Bay, California, 80.5 km south of the

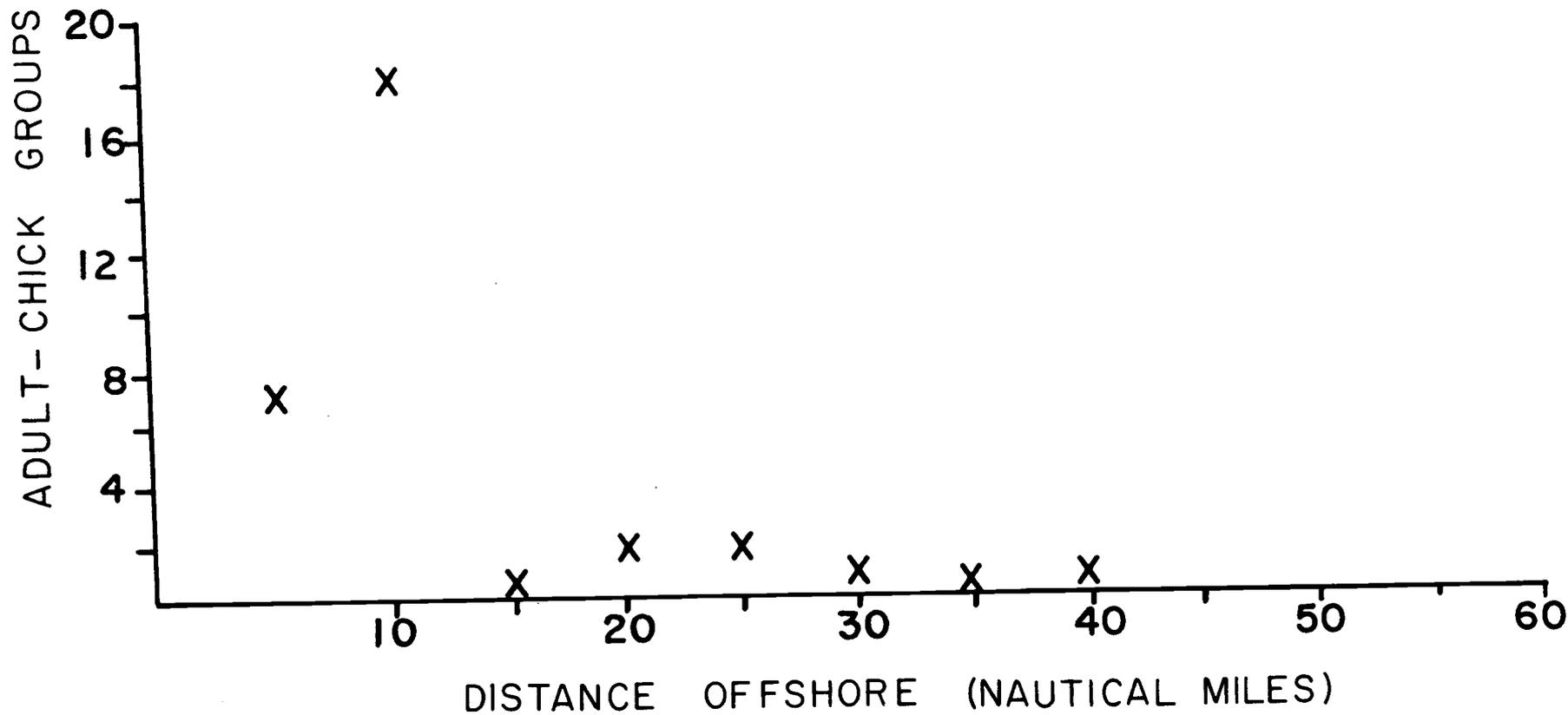


Figure 10. Number and distribution of adult-chick pairs observed during a 55 mile transect run from the Newport Jetty at Newport, Oregon, due west.

nearest breeding colony from which the prevailing currents and winds flow (Chadnik and Baldrige, 1967, 1969). This is further evidence that dispersal from the breeding rocks is primarily longshore and confined to inshore waters. This is also the area where feeding opportunities might be expected to be the greatest. Schooling fishes are found in large numbers in shallow inshore waters, and in addition the water is shallow enough so that the murrelets can feed on fish living on or immediately above the bottom, something they might not be able to do regularly in water deeper than 100 m. Further, the deeper the water the greater the volume in which a school of fish can hide, and in deep water a school of fish might escape predation by swimming to depths beyond the diving capability of the birds.

Eighteen adult-chick groups were collected at sea. Seventeen of these were composed of a single adult and a single chick, while the other contained two adults and one chick. A special effort was made in the collection of adult-chick groups to pick isolated pairs in order to avoid confusion as to which adult was accompanying which chick. In all but the last group the adult was a male, and in the last case only one of the two adults, a female, was collected. These findings contradict the report by Tuck (1961) and others that either sex may accompany the chick out to sea. However, Tuck (personal communication) has recently indicated that of the 20 adults that he collected accompanying chicks, 16 or 17 were males. The only

females collected were taken toward the end of the sea-going period and were accompanying late-fledging young. This would suggest that under normal circumstances it is the male that accompanies the young to sea and only when the male is unable to do so will the female take over. However, Uspenski (1958) suggested that two adults accompany chicks of the Thick-billed (Uria lomvia) and Common Murres, but gave no details.

DIVING BEHAVIOR

The four species differed in the duration of the dives that they made (Figure 11) and were ranked according to the mean time (in sec) that they remained submerged, as follows: Common Murre ($\bar{X} = 71.3$, S. D. = 38.7, $n = 228$); Pigeon Guillemot ($\bar{X} = 36.2$, S. D. = 26.6, $n = 259$); Brandt's Cormorant ($\bar{X} = 30.45$, S. D. = 13.2, $n = 193$) and Pelagic Cormorant ($\bar{X} = 28.8$, S. D. = 7.7, $n = 586$).

For all species the duration of the dive was closely related to the depth of water in which the bird was diving, the shortest dives being in quite shallow water and the longest in deep water. The relationship between depth of dive and duration of dive has been explored in great detail by DeWar (1924). I made no attempt to substantiate his conclusions, although the relationship between depth and duration of dive was confirmed for each of the four species (Table 6).

The depth to which these birds dive was not determined directly. However, Pigeon Guillemots commonly brought benthic fish up from areas inside Yaquina Bay where the water was at least 10 m deep. A Common Murre accompanied by a chick was observed surfacing with a flatfish in water 31.7 m deep after a dive of 88 sec. This was in an area where the water is relatively uniform in depth. Other dives by this same bird averaged 88.7 sec. A second murre (also

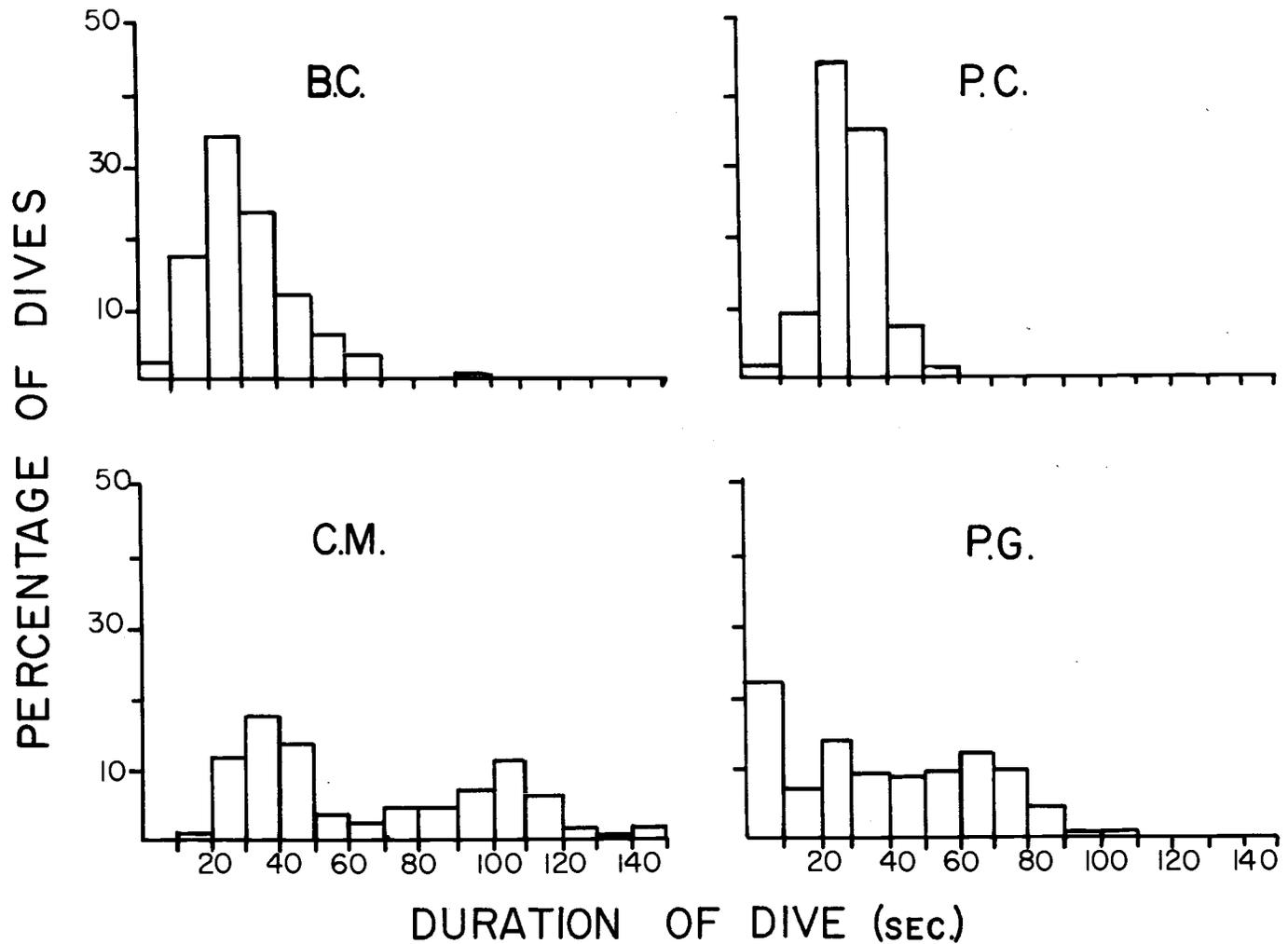


Figure 11. Number of dives of different durations observed in each species. All dives in which a bird handled prey at the surface, was disturbed in any way, or for which no rest time was obtained are excluded.

accompanied by a chick) was observed surfacing with a flatfish in water 60.4 m deep.

I was unable to make observations of similar detail for the two species of cormorants in water exceeding 10 m in depth. However, if one assumes DeWar's formulation of 20 sec for the first fathom and 10 sec for each additional fathom to be a good minimum estimate of the maximum depth attained, then the estimated maximum depths reached by the four species are: Common Murre, 26.0 m; Pigeon Guillemot, 18.1 m; Brandt's Cormorant, 12.9 m; and Pelagic Cormorant, 7.8 m. DeWar indicated that this relationship might be conservative at depths greater than 3 fathoms, and this is further suggested by the dive which resulted in capture of a bottom fish in 31.7 m of water by the Common Murre. Using DeWar's formulation, the calculated depth was 15.8 m, half the actual depth.

There was usually a sharp increase in the rest period between dives with increasing dive time for each species. Dive-rest ratios were very similar for all four species, with mean values of 3.11 and 2.7 for the Common Murre and Pigeon Guillemot respectively, compared with 2.5 for Brandt's Cormorant and 2.7 for the Pelagic Cormorants. The differences between the average dive-rest ratios were not significant (Figure 12). Differences in the mean values of both dive-rest ratios and the length of the rest period were observed between the four species for each of the dive intervals, but they were

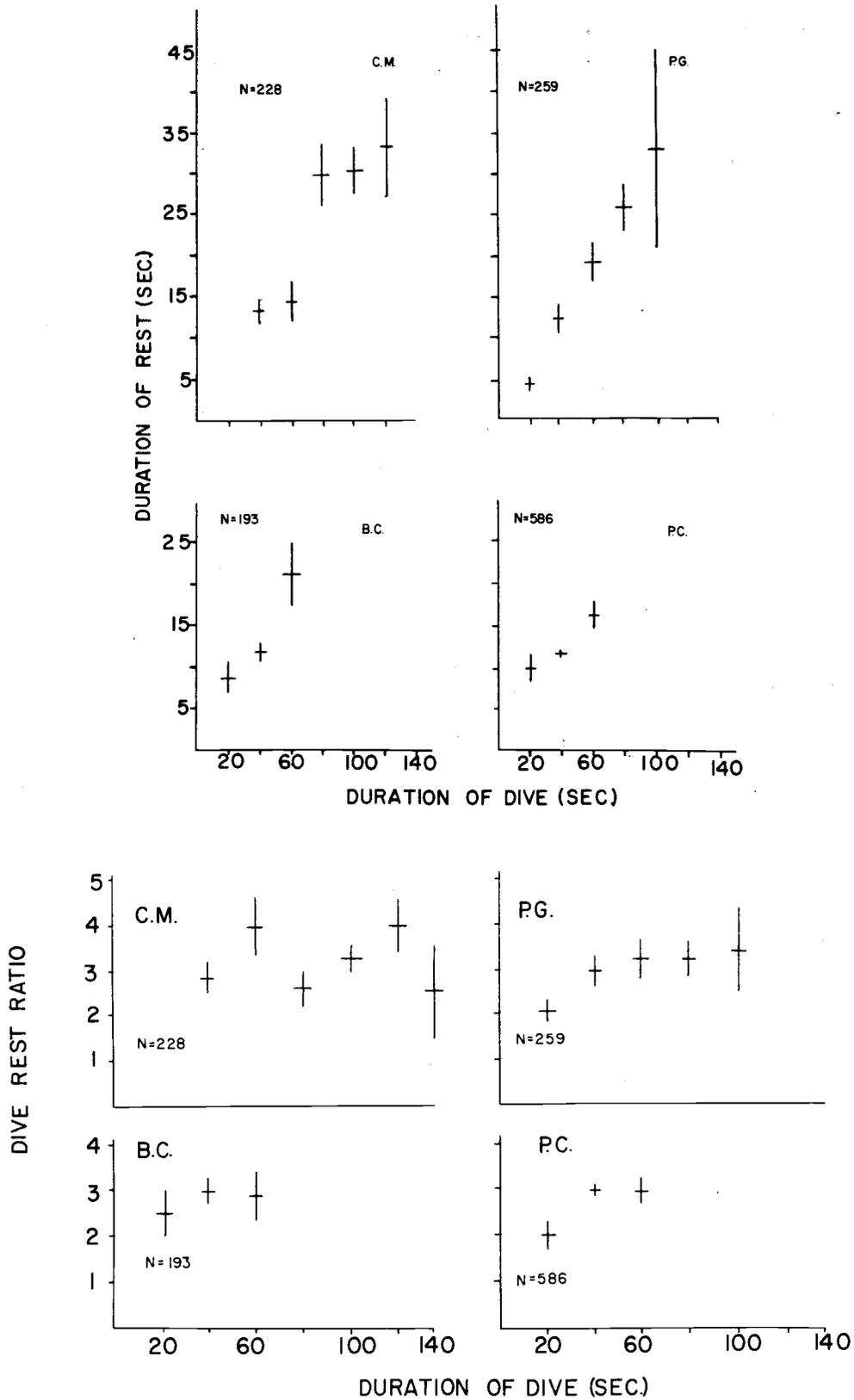


Figure 12. Rest periods and dive rest ratios depicted as a function of dive time. The mean values are indicated by the horizontal line and two standard errors of the mean by the vertical lines.

significantly different only between the Common Murre and Brandt's Cormorant in the 40 - 59.9 sec dive interval (Figure 12). The dive-rest ratio increased as the dive time increased, reaching a plateau in all species except the Common Murre (Figure 12). In the murre, the dive-rest ratio varied considerably and decreased sharply only at a dive period of 120 - 129.9 sec. The murre was the only species which showed a decrease in its dive-rest ratio but it was not a significant one. The longer dive times for Common Murres were obtained from adults which were accompanied by chicks, suggesting that perhaps these individuals are closer to their limits than non-accompanied adults. That there was no decrease in the dive-rest ratios of the other birds indicates that they are perhaps operating well within their physiological limits for duration of dive and presumably, for depth of dive, and that these limits have to be established in the laboratory and not in the field. Stonehouse (1967) nevertheless indicated physiological differences in diving ability between four species of Phalacrocoracidae without giving statistical differences between the dive-rest ratios either within or between species.

A second way to ascertain the physiological limits of a species would be to obtain dive times for dive sequences of 1 hr or longer duration and compare the first ten dives with the last ten. This was done for the Pelagic Cormorant. Dive-rest ratios for dives of 20 - 39.9 seconds duration were compared for the first and last ten dives

in sequences of 50 or more dives. The dives from the end of the sequence had a larger (but not significantly so) dive-rest ratio (2.63 vs. 2.53 at the beginning). This would seem to indicate again that these birds are diving well within their limitations at this dive time interval.

Yet another means for estimating maximum diving capabilities has been suggested by Cody (1973) who forced a series of dives by repeatedly approaching the birds with a boat and timed these, obtaining what he called the mean maximum dive. The value he obtained for Pigeon Guillemots, 68 sec, is very close to the maximum dive time I observed (68.8 sec) for this same species. However, the 71.1 sec he obtained for Common Murres is less than half the value I observed (152.2 sec).

A final way to get at maximum or relative diving abilities of diving birds would be to take them into the laboratory and subject them to dive times and rest periods comparable to the maximum times observed in the field. If this were done over a prolonged period and the duration and intensity of bradycardia compared between species, relative diving abilities could be determined.

FOOD

Common Murre

Common Murres have been characterized as feeding primarily on midwater fishes (Uspenski, 1958; Belopolski, 1957; and Bedard, 1969b). In general my studies substantiated this finding (Table 7), although during July and August of 1969 euphausiids, mysids and other planktonic crustaceans constituted 86.2 percent of the diet volume. This dietary shift was apparently due to the lack of midwater schooling fishes and juvenile Sebastes sp. in the area (Scott, Wiens and Claeys, m. s.). The species of midwater fish taken by murres varied from year to year with eulachons (Thaleichthys pacificus) being the most abundant in 1969 and northern anchovies (Engraulis mordax) dominating the diet in 1970 and 1971 (Table 8). These yearly differences may reflect annual variation in the availability of the prey species. If we ignore 1969 as an abnormal year, the 1970-71 data indicate that in July and August, after the chicks left the breeding rocks, juvenile Scorpaenidae, primarily Sebastes sp., became a major constituent of the diet (Table 7). These fish are found in large aggregations around kelp beds and submerged reefs (Jim Washburn, personal communication). That they are easily available is also suggested by the fact that large numbers of murre stomachs contained

Table 7. Seasonal variation in food items taken by Common Murres collected during 1969-71 (n = 140, 50 percent empty stomachs).

Prey Item	May-June			July-August			September-April		
	% N	% Vol	% Occ	% N	% Vol	% Occ	% N	% Vol	% Occ
<u>Crustacea</u>									
Euphausiidae	.4	.1	3.1	68.0	13.3	18.2			
Other	12.7	.1	12.5	4.0	23.6	27.3			
<u>Mollusca</u>									
Loli ginidae	.8	1.8	6.3						
<u>Osteichthyes</u>									
Clupeidae	1.5	8.8	6.3	.2	.9	4.5	12.5	49.2	50.0
Engraulidae	31.5	52.2	56.3	.7	21.3	27.3			
Osmeridae	35.8	23.2	43.8	.1	.1	4.5	37.5	16.4	100.0
Gadidae	.8	5.7	6.3	.1	5.3	4.5	12.5	19.7	50.0
Scorpaenidae (except <u>Sebastes</u>)	4.6	1.5	9.4	2.0	12.3	18.2	25.0	11.5	50.0
<u>Sebastes</u>	6.9	2.3	21.9	4.6	24.4	31.8			
Cottidae	.4	1.3	3.1				12.5	3.3	50.0
Bathymasteridae	.8	.1	3.1						
Ammodytidae				.2	.7	9.1			
Bothidae/ Pleuronectidae	.4	.1	3.1						
Unidentified Fish	3.5	2.8	28.1	.6	17.6	45.5			

Table 8. Yearly variation in food items taken by Common Murres collected during May-August, 1969-71 (N = 120, 43.3 percent empty stomachs).

Taxa	1969		1970		1971	
	% N	% Vol	% N	% Vol	% N	% Vol
<u>Crustacea</u>						
Euphausiidae	67.0	6.9	58.6	6.0		
Other	28.1	3.7	15.4	1.9		
<u>Mollusca</u>						
Loliginidae	.1	1.5			.9	2.4
<u>Osteichthyes</u>						
Clupeidae	.2	1.5	.8	16.5		
Engraulidae	1.5	24.3	2.1	23.0	60.0	78.7
Osmeridae	8.0	44.4	1.4	3.7	13.6	.8
Gadidae						
Scorpaenidae						
(except <u>Sebastes</u>)	.1	1.1	7.0	11.6		
<u>Sebastes</u>	.1	.3	12.8	22.3	5.5	.5
Cottidae			.2	2.6		
Bathymasteridae	.2	.7				
Ammodytidae			.6	.9		
Bathidae/ Pleuronectidae						
Unidentified Fish	.2	15.6		11.6		2.4

only these fish. The same was true for eulachons and northern anchovies, both schooling fish.

The number of Common Murre stomachs collected during the winter months was quite limited (N = 20, 90 percent of which were empty). Information from stomachs which had distinguishable remains suggests that murrees may take different prey at this time. Murrees were observed on several occasions from October to April in large flocks feeding on schooling fishes. On 26 February, 1972, for example, a flock of 900-1200 birds was observed feeding in 40 fathoms of water 9 mi off Yaquina Head on two large schools of eulachons. The distribution offshore of schooling fishes varies seasonally. Northern anchovies are abundant in the shallow inshore waters during the summer months but move offshore and south during the winter (Blaxter, 1967). The offshore movement of murrees during the winter may be in response to this offshore movement of midwater schooling fishes (e. g. *Osmeridae*).

Comparison of food items taken by adult murrees accompanying chicks and those unaccompanied by chicks shows that anchovies comprised a greater proportion of the diet of accompanied adults (38.6 percent by volume) than unaccompanied adults (27.5 percent) (Table 9). Both groups utilized Sebastes sp. extensively; 51.6 percent by volume for unaccompanied vs. 38.6 percent for accompanied adults. Whether these differences reflect selection on the part of

Table 9. Comparison of prey items taken by juvenile murrelets accompanying adults and adult murrelets unaccompanied by juveniles collected at the same time. Birds were collected during July and August of 1970, 1971, and 1972. (N = 48, 45.8 percent empty stomachs).

Prey Item	Adults			Juveniles			Unaccompanied adult		
	% N	% Vol (N = 7)	% Occ	% N	% Vol (N = 9)	% Occ	% N	% Vol (N = 11)	% Occ
Crustaceans				12.2	1.5	14.3			
Fish									
Engraulidae	14.3	38.6	42.9	30.6	57.7	71.4	4.8	27.5	50.0
Osmeridae	4.8	2.2	14.3	--	--	--			
Scorpaenidae (except <u>Sebastes</u>)	21.4	14.4	42.9	6.1	4.7	28.6	15.9	10.9	16.7
<u>Sebastes</u>	42.9	38.6	57.1	36.7	24.5	42.9	76.2	51.6	4.2
Ammodytidae	4.8	2.2	14.3				1.6	9.5	50.0
Anoplomidae				5.9	3.1	7.0			
Unidentified fishes	11.9	4.0	14.3	12.2	12.6	42.9	1.6	.6	16.7

accompanied adults for the larger, energetically more valuable anchovies or are simply a sampling bias is uncertain.

Anchovies were the most important dietary component of murre chicks collected at sea with adults. Scorpaenidae, primarily Sebastes sp., were the next most important prey taxon (Table 9). The prey items taken did not differ significantly in size from those taken by their accompanying adults although young murre did consume 19.1 percent (by volume) more anchovies than did the adult birds. Dietary similarity between young murre and their accompanying adults, as gauged by Horn's (1966) Similarity Index, was less ($c_s = .90$) than between accompanied and unaccompanied adults ($c_s = .94$)^{2/}. These differences are small and largely accounted for by the greater volume of anchovies taken by the young. This may reflect a propensity on the part of the adults to feed the larger anchovies to their young. Observation of food items brought to chicks at the nesting rock indicated that midwater schooling fishes (e. g. Osmeridae and Engraulidae) made up over 99 percent of the prey items delivered. In contrast to this, the much smaller juvenile Sebastes and other Scorpaenidae constituted 29.2 percent by volume of diet at sea and were then the most frequently taken prey species (71.5 percent).

^{2/} The similarity index (c_s) will vary from 0 when paired samples share no taxa in common to 1.0 when all taxa occur in both samples in equal proportion.

Comparison of the diets of murrees collected in 12 fathoms of water within 1 mi of the beach and those collected in 37 fathoms of water 4 mi offshore on the same date, within 2 hr of each other, revealed that the offshore murrees took fewer Scorpaenidae and more anchovies. This may reflect less frequent foraging near the bottom, and suggests that the principal prey species, E. mordax and Sebastes sp., are distributed throughout the inshore area over water of varying depths. Dietary similarity ($c\hat{\lambda}$) between the two samples was 0.82.

If it were possible to take dietary samples on a daily basis variation similar to the seasonal variation might be found within a season. In an attempt to evaluate within season variation I collected murrees in the same area and at the same time of day on three successive days in June 1971. On each of the three days northern anchovies were the major food item taken, while the importance of other prey species varied (Table 10) (mean $c\hat{\lambda}$ = .857).

Brandt's Cormorant

Brandt's Cormorants were collected on four occasions at the same time as Common Murrees (Table 11). The wariness of these birds on the water made it all but impossible to collect them at sea. All but two of the specimens were collected from roosting rocks. The specific areas in which the birds were foraging is therefore

Table 10. Daily variation in food items taken by Common Murres collected on three successive days in June, 1971 in the same area off Newport, Oregon (N = 30, 43.3 percent empty stomachs).

Prey Item	June 26			June 27			June 28		
	% N	% Vol (N = 10)	% Occ	% N	% Vol (N = 10)	% Occ	% N	% Vol (N = 10)	% Occ
Mollusca									
Loliginidae	3.3	6.8	14.3						
Pisces									
Engraulidae	36.7	51.6	57.1	100	100	100	68.4	69.4	83.3
Osmeridae	26.7	28.1	42.8				15.8	8.5	33.3
Scorpaenidae	13.3	1.3	57.1				7.9	.6	16.7
Gadidae	3.3	11.6	14.3				2.6	20.2	16.7
Bothidae/Pleuronectidae							2.6	.1	16.7
Unidentified fish	16.7	.7	42.8				2.6	1.3	16.7

Table 11. Occurrence of food items taken by Brandt's Cormorants, Pelagic Cormorants, and Common Murres collected at the same time off Yaquina Head on four occasions (20 June, 1969, 10 August, 1969, 4 August 1970 and 16 August, 1970).

	Brandt's Cormorant			Pelagic Cormorant			Common Murre		
	% N	% Vol (N = 29)	% Occ	% N	% Vol (N = 12)	% Occ	% N	% Vol (N = 30)	% Occ
Crustaceans							.4	.5	5.6
Euphausiacea							50.5	2.9	11.2
Mysidacea							23.1	1.6	28.0
Fish									
Clupeidae							.6	3.0	5.6
Engraulidae	24.3	25.0	10.0				1.5	20.9	22.4
Osmeridae	7.1	3.6	10.0				6.3	7.6	39.2
Scorpaenidae	10.7	2.9					4.9	13.6	39.2
(except <u>Sebastes</u>)	37.9	13.5	10.0						
<u>Sebastes</u>							10.7	27.8	56.0
Gadidae							.1	2.8	5.6
Cottidae	3.6	16.2	10.0	57.1	57.0	100			
Hexagrammidae	2.1	12.0	15.0						
Bathymasteridae							.2	.3	5.6
Ammodytioea							.5	.7	11.2
Flatfish	10.0	4.8	20.0						
Unidentified fish	10.0	4.8	35.0	42.9	42.9	100	1.3	18.4	50.4

unknown. This was not true in the case of the murrens.

Members of the family Cottidae (e. g. Scorpaenichthys marmoratus), juvenile Scorpaenidae (e. g. Sebastes sp.), and Hexagrammidae were the most important groups taken by Brandt's Cormorants (Table 11) although when collected in mixed-species feeding flocks anchovies dominated the diet. In addition to these items, Brandt's Cormorants were observed on more than 100 occasions during the summer months (May-August) feeding in mixed-species feeding flocks on anchovies and smelt, and several birds were observed surfacing with large (300-500 g) Scorpaenichthys sp. as well as smaller surf perch (Embiotocidae) in their beaks. The dietary composition of the cormorants was moderately similar ($c_{\lambda}^{\wedge} = 0.681$) so that the murrens and the two species took similar size of prey in the major taxa represented in common (Table 12).

Several other studies of the feeding habits of Brandt's Cormorants (see Palmer, 1962, for a review) indicated that the birds feed primarily on species occurring at or near the bottom, although one stomach collected in British Columbia contained only herring (Clupea harengus). Of two stomachs collected in Oregon, one contained 75 percent cabezon (Scorpaenichthys marmoratus) and 25 percent crustaceans, while the other had 99 percent benthic shrimp (Spirontocaris sp.) and 1 percent cottids. Martini (1966) as cited by Hubbs, Kelly and Limbaugh (1970) found that in southern California

Table 12. Size (in centimeters) of the three commonst prey categories by Brandt's Cormorants and Common Murres. Sizes are based on measurements of only those prey items whose entire length could be measured.

	Brandt's Cormorant	Common Murre
<u>Engraulis mordax</u>		
\bar{X}	10.6	10.1
Range	7 - 12.6	5 - 15.0
95% C. I.	10.1 - 11.1	9.8 - 10.4
S. D.	1.9	2.2
N	18	65
<u>Scorpaenidae</u>		
\bar{X}	5.9	5.4
Range	4 - 18.0	4 - 8.0
95% C. I.	3.0 - 8.8	5.2 - 5.6
S. D.	7.6	1.0
N	7	26
<u>Sebastes sp.</u>		
\bar{X}	5.5	5.1
Range	3 - 11.0	3 - 10.0
95% C. I.	5.3 - 5.7	4.9 - 5.3
S. D.	1.2	1.5
N	52	73

the five most important prey taxa, ranked in order of importance, were Embiotocidae (Phanerodon furcatus and Embiotoca sp.), Engraulidae (Engraulis mordax), Batrachoididae (Porichthys notatus), and Ophidiidae (Otophidium scrippsi). With the exception of E. mordax all occur at or immediately above the ocean bottom.

Direct examination of stomachs taken over a period of years by Hubbs, Kelly and Limbaugh (1970) gave the following rankings for the four most important prey species: flatfish (Bothidae and Pleuronectidae), Pomacentridae (Chromis punctipinnis), and Labridae (Oxyjulis californica). With the exception of E. mordax and O. californica, these also occur at or immediately above the bottom.

Hubbs et al.(1970) analysis of prey items taken from birds presumed to be foraging in different habitat types (e. g. kelp beds, sandy bottoms and rocky bottom areas), indicated that they foraged on the most available species, and are generalists in their foraging activities. Based on the nature of the prey species taken compared with what was available, Brandt's Cormorants rely primarily on vision and feed primarily on fishes in motion.

Pelagic Cormorant

Pelagic Cormorants taken during the course of this study had been feeding extensively on members of the family Cottidae (Table 11), although other individuals were also observed feeding on anchovies

and smelt in large mixed-species feeding flocks. In addition, single birds were observed feeding on benthic crustaceans immediately adjacent to Yaquina Head. A single bird collected in December at Netarts, Oregon (Gabrielson and Jewett, 1940) contained 92 percent Cottus sp., 1 percent sculpin, 2 percent Myoxocephalus sp., and 5 percent invertebrates. Examination of 31 stomachs collected in Alaska (Palmer, 1962) indicated that Pelagic Cormorants fed primarily on bottom fish of the families Cottidae, Hexagrammidae, Pholidae, Agonidae, and Pleuronectidae. Midwater fishes such as herring (Clupeidae), and tomcod (Gadidae) were also taken. In addition the stomachs contained various benthic crustaceans.

Pigeon Guillemot

Immature Pigeon Guillemots have been the subject of two feeding studies (Thoresen and Booth, 1958; Drent, 1965). Drent (1965) found that the commonest species delivered to nestlings in order of abundance were blennies, flatfish and sculpins. These accounted for 81 percent of the total identified food items. Thoresen and Booth (1958) listed sand lance (Ammodytes), smelt (Hypomesus sp.), black blenny eels (Epigeichthys), snake eels (Lumpenus) and small soles as items fed to nestling Pigeon Guillemots. They did not give any indication of their numbers or even relative importance. In my own observations of prey items carried to nestlings, the importance

of various prey groups was similar to that given by Drent (1965).

In contrast to the studies of food items fed to the young, there are few observations of adult prey. Gabrielson and Jewett (1940, p. 314) indicated that "Pigeon Guillemots could be commonly found on the Oregon coast feeding on the great schools of small fish that abound on the coast." They did not state what species they were, but presumably they were anchovies, or smelt.

Fourteen of 16 prey items observed being consumed by adult Pigeon Guillemots were flatfish (Bothidae or Pleuronectidae), the remainder blennies. All of the flatfish were taken in Yaquina Bay over a sandy bottom, while the blennies were taken in water less than 0.5 m deep over rocky areas in the bay. Two adults collected at sea contained the remains of a single flatfish (Pleuronectidae), eight planktonic crustaceans and two decapod crabs.

MIXED-SPECIES FEEDING FLOCKS

Three of the four species I studied were often found foraging in mixed-species feeding flocks, numbering from only a few to several thousand birds. In addition to Common Murres, Brandt's and Pelagic cormorants, these flocks included Arctic Loons (Gavia arctica), Sooty Shearwaters (Puffinus griseus), Glaucous-winged Gulls, Western Gulls, California Gulls (L. californicus), Bonaparte's Gulls (L. philadelphia), Black-legged Kittiwakes (Rissa tridactyla), and Tufted Puffins, although no single flock contained all these species. These flocks were dominated by Western Gulls, Common Murres, Brandt's Cormorants and Pelagic Cormorants.

Pigeon Guillemots were not observed feeding in these flocks. The other species were found in flocks most frequently during the spring and fall when they passed through the area as migrants. Birds in these flocks were almost always feeding on schooling fish of the families Engraulidae, Osmeridae or Clupeidae (personal observation). Such flocks occurred throughout the year, but were most numerous from June through August.

Mixed-species feeding flocks developed quite rapidly, with a flock of several hundred birds being formed in less than 15 min and persisting from 10 min to an entire day. A flock of 1500 or more birds was found on successive days at the same location on the north

side of Yaquina Head during August, 1971. Flocks were observed in the early stages of development on more than 20 occasions, and developed in several different contexts. For example, a single Common Murre was observed diving in Yaquina Bay 11 July 1971. The school of bait fish it was feeding upon broke the water surface with a flurry and attracted the attention of a single Western Gull, which also began to forage. Within 2 min several other Western Gulls, Glaucous-winged Gulls, and unidentified gulls joined the flock. They were subsequently joined by a Brandt's Cormorant which had been foraging nearby. Within 10 min there formed a flock of 75-100 birds, primarily Western Gulls but with several Brandt's Cormorants and Common Murres, all actively feeding on the fish school. As the school moved out the channel and beyond the end of the jetty the flock followed. What began, then, as a single murre feeding on a school of fish ended up as a flock of 75-100 actively feeding birds.

On three separate occasions sea lions (Zalophus californianus and/or Eumetopias jubata) were observed at the water surface tearing at and tossing around relatively large fish (Sebastes sp. or Raja sp.). On one occasion this occurred within 200 m of the murre colony on Yaquina Head. Shortly after the feeding activities of the sea lion began, several Western and Glaucous-winged gulls vocalized loudly and flew directly to the sea lion from the Head and the immediately adjacent area. They were quickly joined by Brandt's and Pelagic

Cormorants and Common Murres, which flew from the breeding colony and set down on the water near the sea lion. However, there was no ensuing feeding activity by these birds and the flock quickly dissipated when the reinforcing stimuli (food items) did not become available. Apparently the murrees and cormorants responded to the actions of the gulls and not directly to the sea lions.

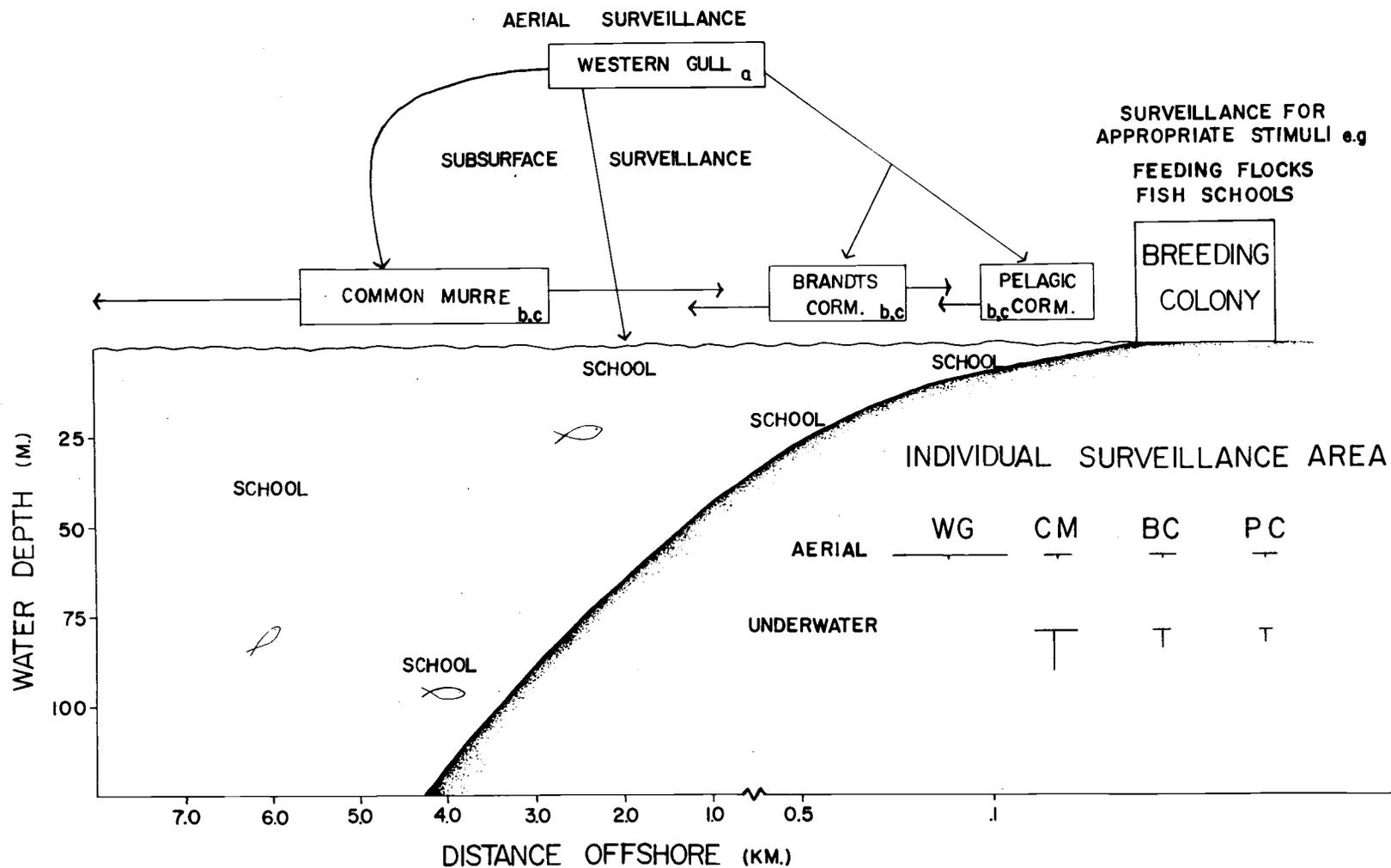
On numerous occasions during this study large numbers of Brandt's and Pelagic Cormorants and Glaucous-winged and Western gulls were observed leaving Yaquina Head within seconds of each other and flying in a single direction. I followed their direction of flight and invariably found a mixed-species flock already well developed and actively feeding at the water's surface, presumably on bait fish. The stimuli to which the birds were responding were as far as 2-3 mi from the Head. I observed mixed-species feeding flocks as far as 4 mi offshore with the aid of a 20-power spotting scope. The gulls were the most conspicuous members of these flocks with their high, circling flight and light coloration (Armstrong, 1970; Frings et al., 1955). Pat Gould (personal communication) has observed similar flocks of aerial foragers in the central Pacific. In this case, too, changes in behavioral patterns signal the presence of food to individuals of the same and different species.

More than 20 mixed-species flocks were watched for continuous periods of up to three hours and their movements and structure

observed. In one instance a large flock of gulls was feeding inside the surf line on a school of fish which appeared as a dark ball in the clear, shallow water. On several instances feeding had stopped and the gulls were sitting on the water or flying overhead when one or two gulls commenced feeding again some distance to the north. The entire flock then moved to the new spot and began feeding. This shift in feeding activities occurred several times in response to shifts in the position of the fish schools. In each case the gulls relocated the school and renewed their feeding activities. This same type of mobility has been observed in mixed-species flocks composed of diving birds (e. g. cormorants, murre, loons) and gulls. Gulls flying above the flock would locate the bait school at the surface or immediately below it and begin to feed. If their activities continued for several minutes or more, additional gulls and diving birds would leave the main flock and fly or swim to the new center of activity.

From these observations one may conceptualize the various means by which the water surface and depths are searched for schooling fishes (Figure 13). Fish schools may be located at the water's surface to depths exceeding 100 m. They may be visible to birds in the air or only those underwater. The probability of detection of these schools in a given area is increased by having complete coverage of the area and rapid communication of the location of the school. In most seabird communities there are a number of species which

SPECIES SURVEILLANCE AREA



differ in the foraging areas and methods. Thus, each species may forage upon a different basic set of prey species while simultaneously surveying the area for the large schools of bait fish which are utilized in common by all the species. The individual, thereby, may expend no more energy than it would if it were searching only for its own preferred set of prey species.

I believe that Western Gulls are the key species in discovering these fish schools, because they forage at the greatest heights and therefore survey the greatest area. Aerial surveillance of the other species is limited, as they generally fly very close to the surface. While gulls are more efficient in locating surface schools of fish, the diving birds are capable of locating subsurface schools too deep in the water column to be seen by gulls. The large mixed-species feeding flocks are thus three-dimensional in form, with gulls circling overhead and plunging into the water to take fish at or immediately below the air-water interface or harassing diving birds or other gulls for fish already captured. While the diving birds are actively foraging below the surface they occasionally drive sections of the bait school to the surface where the fish are fed upon by the gulls.

Flock development can stop at any point, ranging from a single bird feeding on a school of fish to a large flock of several species.

Whether or not a flock develops, and the speed with which it does so is dependent upon

- (1) the abundance and availability and dispersal of the prey species;
- (2) the conspicuousness and abundance of the birds, fish or mammals and their feeding behaviors;
- (3) the number of potential mixed-species flock members in the area;
- (4) hunger level of the birds; and
- (5) atmospheric visibility.

DISCUSSION

The efficiency of food procurement and energy demands per unit area for the species studied were affected to a great extent by three events documented during the course of this study. These events were the 1) seasonal variations in the abundance of the species studied, 2) dispersal away from the breeding colony by adult-chick groups of Common Murres, and 3) participation in mixed species feeding flocks by all but one of the species studied. Theoretical aspects and the possible evolutionary significance of each of these is discussed in the following pages.

Determinants and Effects of Abundance Patterns

The seasonal patterns in abundance of the four species I studied may result from an actual reduction in the number of birds occurring in the immediate area of the breeding rocks due to long distance migration, from dispersal of the resident birds over a much greater area than they occupied during the breeding season, or from elements of both.

During the breeding season, individuals are restricted in their distribution by the necessity to return to their nest regularly. The distance a bird travels from its nest site to a foraging area is determined for each species by: 1) the energy demands of the young;

2) the energy demands of the adult; 3) the availability of food as determined by the abundance and distribution of prey species; 4) the nature of food delivery to the young (i. e. single item, multiple item, or regurgitation); 5) the flying speed of adults, and 6) the size and nutritional value of food items delivered to the young. The distance that an individual forages from the nest site may be increased by a decreased growth rate in the young so that they require less food per unit time (Lack, 1968), by increasing its flying speed so that it can travel a greater distance in the same or less time, by feeding the young a greater volume of food or more nutritious food at each feeding, enabling them to endure longer periods between feedings, or by taking the young with them into foraging areas. This last tactic will be discussed in some detail with reference to Common Murres in a later section.

During the non-breeding season the travel constraints placed on an individual by the necessity of returning to the nest site are removed and the birds may disperse over a much wider area or migrate to areas which are seasonally more desirable during the non-breeding season. The locations of the nesting areas of both Common Murres and Brandt's Cormorants in Oregon are well enough known to allow a more detailed discussion of this matter.

Common Murres are found breeding at 46 different sites and 26 different colony areas (a colony area being two or more colonies

separated by 0.5 km or less) in Oregon. The distribution of these colonies was tested for randomness using Hazen's (1966) line transect method (Figure 14). The breeding colonies were not randomly distributed ($\chi^2 = 10.6$, $p < .005$) and were concentrated in the northern and southern extremes of the state. Assuming that the foraging area of the individuals within each of these colonies is a half circle with a radius of 16.1 km (Tuck, 1961; and personal observation), then of the 445.4 km of coastline lying between the limits of the foraging range of the southernmost and northernmost murre colonies, 144.7 km (32.5 percent) is utilized by breeding birds. The total area falling within the 16.1 km foraging range of one or more colonies is 4980 km². I have estimated the Oregon breeding population of murre to be 200,029 individuals, based on aerial and land censuses. During the breeding season, then, the average density in the calculated foraging area would be 40.2 murre/km². During the winter months, when the birds are no longer restricted to the breeding rocks, they move offshore and occupy the entire coastline from 3-18 mi offshore, an area of 11,640 km². The expected density of murre, assuming an increase in the population of 9.2 percent (Leslie, 1966) is 18.8/km². This is a reduction in average density of over 53 percent with an increase in population size. During the offshore transects 18.3 murre/km² were actually observed, assuming a sighting distance of 0.25 km for flying birds and 0.125 km for birds sitting on

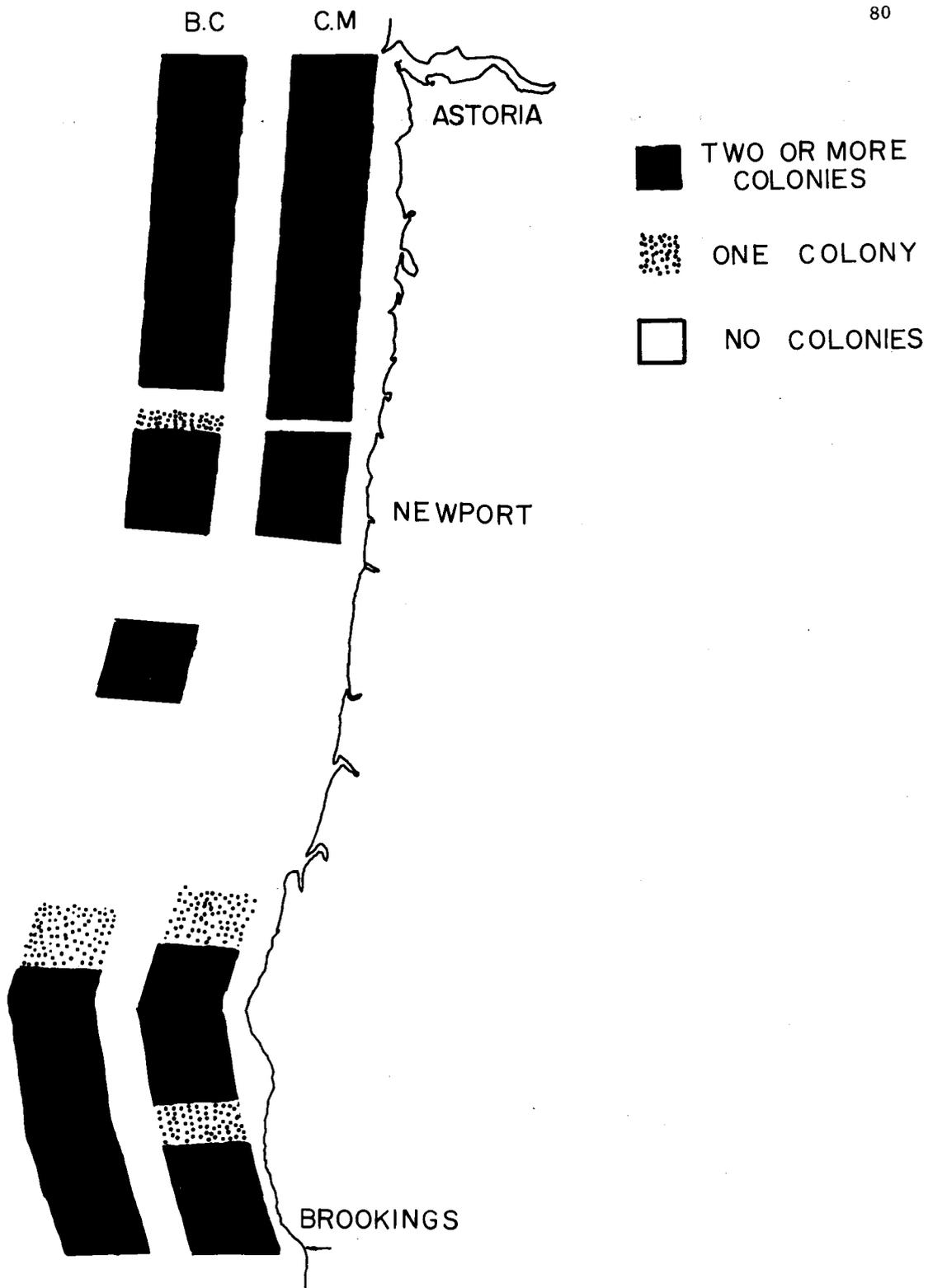


Figure 14. Distribution of breeding colonies of Brandt's Cormorants (B. C.) and Common Murres (C. M.) along the Oregon coast. The depicted distribution includes a 16.1 km foraging radius in the form of a half circle for murres and a rectangle extending 3.2 km to sea and 16.1 km north and south of the colony in the case of Brandt's Cormorants.

the water. The observed density fits very closely the predicted density, suggesting that the reduced densities are the result of dispersal through a larger area rather than an actual reduction in number of birds. This interpretation also agrees with the observation of large numbers of murrelets on the breeding colonies during the middle of winter, which would require that the birds be wintering within a relatively short distance of the breeding rock. This raises the possibility of traditional wintering areas for adult populations from a single breeding rock, a question worthy of further study.

The seasonal changes in bird densities dramatically affect the energetic demands placed on a given area. Wiens, Scott and Innis (In prep.) have estimated that the average energy demands for Common Murrelets in Oregon ranged from 8.8 to 19.9×10^3 kcal/km²/day during the winter (November-March). The bioenergetics of the common marine birds in Oregon and their possible impact on specific prey species are discussed in detail by Wiens, Scott and Innis (In prep.).

Brandt's Cormorants are found breeding at 62 different colonies and 40 different colony areas in Oregon. These colonies are not randomly distributed along the coast ($X^2 = 58.6$, $p < .005$; Hazen, 1966), also being concentrated in the northern and southern extremes of the state (Figure 14). Assuming that the foraging area of the individuals within each of the colonies is a rectangle 3.2 km wide and

32.2 km long, with the colony situated at the mid-point of the landward side of the rectangle, then of the 478 km of coastline found between the foraging limits of the northernmost and southernmost colonies, 180.3 km (37.7 percent) lies beyond the foraging range of breeding birds.

Assuming a breeding population of Brandt's Cormorants of 14,217 (U.S. Fish and Wildlife Service, Unpublished data) uniformly distributed throughout the available area, then the average density in the state would be 36.0 birds/km^2 . During the winter months when the birds are no longer restricted to the breeding rocks, the potential dispersal area is 966 km^2 and the expected density, assuming a 15.7 percent population increase due to reproduction, would be 17.0 birds/km^2 , a density reduction of 52.8 percent with no migration.

The energy requirements of Brandt's Cormorants on a km^2/day basis were very similar to those of murre, ranging from $10.3\text{-}18.8 \times 10^3 \text{ kcal/km}^2/\text{day}$ during the breeding season and only $1.3 \times 10^3 \text{ kcal/km}^2/\text{day}$ during the winter. These energy demands are very similar to those of Common Murres despite smaller population sizes and reflect larger body sizes and smaller foraging area. However, the total energy demands of murre's during a year are $45.4 \times 10^9 \text{ kcal}$, compared to $2.1 \times 10^9 \text{ kcal}$ for cormorants. There is a migration out of Oregon by a sizeable but undertermined percentage of the Brandt's Cormorants which breed in the state. The remaining birds

seem to be concentrated in the protected bays and estuaries of the state rather than being found on the breeding rocks or dispersing uniformly throughout the available area as was the case with Common Murres. Thus concentrating the energy demands even more per unit area.

Adaptive Significance of Precociality

It has been tentatively suggested by Lack (1968) that precocial birds such as the murre are far from rich feeding grounds, partly due to reduction of food resources around the colony by feeding birds. Hence it is energetically more efficient for the parents to take the young to the foraging area rather than commute between feeding areas and the colony. There are, in addition, other advantages which accrue to an individual which takes its young out to sea:

- 1) It makes practical, on an energetic balance basis, the procurement of smaller energy packages for the young and more frequent feedings;
- 2) The pair can go to areas which were beyond the effective foraging range of the adult when the chick was confined to the breeding colony;
- 3) It allows the reduction of population density in a given area by at least 1/3;
- 4) The chick can learn to forage while still dependent upon the

adult for food. Assuming that the chick is gradually fledged from the adult, this would make it possible for the chick to provide at least a part of its energy requirements during the latter stages of the adult-chick association, thereby reducing energy procurement demands on the adult.

At the breeding rocks nestling murrelets were fed large midwater bait fishes almost exclusively (Tuck, 1961, and personal observation). A much wider variety of sizes and types of food items was fed the chicks at sea. Among these were crustaceans (presumably euphausiids), midwater bait fishes of less than 5 cm in length, larger bait fishes and an occasional flatfish (e.g. Pleuronectidae and/or Bothidae).

There is at least one disadvantage to this tactic, however. The adult-chick pair is less able to participate in mixed-species feeding flocks because of the elusive nature of the prey species and the fact that a murre on the water (adults don't fly while accompanying chicks at sea) has a very limited area which can be visually scanned to locate these flocks and their attendant food.

Cody (1973) has presented a model for reproductive strategies in alcids. He suggests that inshore feeders have evolved precocial young as a means of reducing energetic expenditures of foraging adults as well as reducing intra- and interspecific competition for food in the immediate vicinity of the breeding colony. In fact, of the

species he discussed, only Pigeon Guillemots, Marbled Murrelets (Brachyramphus marmoratum) and, to a lesser extent, Common Murres, can be classified as inshore feeders. Of these, only the Common Murre has precocial young. The information available for young of Marbled Murrelets is inconclusive (Bent, 1963; Gabrielson and Lincoln, 1959). Cody cited Ancient Murrelets as an example of an inshore feeder with precocial young. In fact, Ancient Murrelets feed well offshore during the breeding season and take their young as far as 400-500 mi to sea (Bent, 1963). The Ancient Murrelets he reported immediately offshore of the Queen Charlotte Islands were, undoubtedly, immature birds loafing in the vicinity of the breeding grounds (Spencer Sealy, personal communication). Furthermore, of the other four species of alcids with precocial young found in the eastern Pacific, Thick-billed Murres and Xantus' Murrelet (Endomychura hypoleuca) feed well out to sea during the breeding season (Howell, 1917). Little is known about the distribution of Craveri's Murrelet (E. craveri).

Preliminary information on the six species of alcids known to have precocial young indicates a number of shared characteristics:

- 1) They forage some distance greater than 3 km offshore of the breeding colony;
- 2) They seem to be best adapted to foraging for pelagic fishes

(Bedard, 1970), prey species which require considerable speed and maneuverability to capture;

3) They have a higher wing loading (wing surface area/body weight) than do those species which lack precocial young (for example, Common Murre: 2.4 g/cm^2 , vs. Pigeon Guillemots 1.4 g/cm^2);

4) Of the six, those species which are known to forage closest to the beach (Common Murre, Thick-billed Murre and Razor-billed Auk, Alca torda) are also those species in which the young don't leave the nesting rock until 2-3 weeks of age.

Although much additional information is needed (studies are presently underway), I suggest that precociality has evolved in alcids as the result of a gain in subaqueous flight capabilities at the expense of aerial flight, allowing these species to exploit populations of mid-water fishes at great distances from shore but decreasing their ability to fly long distances to deliver food to their young. This necessitated taking the young to sea, with the advantages already discussed.

Common Murres carry but a single prey item at a time to their young. Assuming that only one parent at a time forages for the young at a mean distance of 5 mi from the colony, with a flight speed of 35 mph (Tuck, 1961) and that an average prey item weighs 9.8 g (based on measurements of 65 northern anchovies, Engraulis mordax, taken from murres, (Table 12) then a 250 g chick would require 71.4 g of

food a day, necessitating 7.8 foraging trips by the adult (the calculated energy requirements are a function of body weight, ambient temperature and other factors; Wiens and Innis, In prep.). If there were 15 daylight hours, these trips would have to average no more than 116 min each, 19.7 min of which (17 percent) would be taken up by going to and from the colony. At this weight (250 g) the chick normally goes to sea (Tuck, 1961; Belopolski, 1957; and Uspenski, 1958). If the chick were to stay on the nesting rock until it reached a weight of 1000 g it would require 16.5 foraging trips a day by the adult, averaging no more than 55 min each, and 36.5 percent of that time would be taken up by traveling to and from the nest site. If it is impossible to increase the size of the food package carried to the young or its caloric content, efficiency would be increased by taking the young to the food. Even if the figures given are reduced by 50 percent, assuming both adults are always foraging, as might be the case in some instances, a 1000 g bird would still require 8.4 trips a day on the part of each adult. These trips would be limited to an average of 107 min.

There are several possible reasons why it is usually the male which accompanies the chick to sea. The adult male averages 3-5 percent heavier than the female during the breeding season and averages slightly larger in body measurements (Storer, 1952). This may allow the males to provide for the combined energy demands of

themselves and their young with less strain than could the females, because of the greater swimming abilities and perhaps diving abilities resulting from their somewhat larger size. In addition, the female, by being more mobile and having to provide for only her own energy demands, may be able to put on more weight and fat stores. This may allow her to survive the winter in relatively better condition than had she been obliged to meet the combined energy demands of herself and the chick. This would place her in a better condition for the energy demands of the next year's nesting, since a female must produce a 111.7 g egg (Uspenski, 1958), which represents 10.6 percent of her body weight.

Mixed-Species Foraging Flocks

Midwater bait fishes are patchily distributed in time and space on both a horizontal and a vertical plane, and occur in schools that may exceed 100,000 individuals and 10 tons in weight (Clark and Phillips, 1952). These schools may occur at the surface to depths exceeding 100 m. The nature of the distribution and occurrence of a school is such that it is an undefendable but locally abundant resource. Species which feed on patchily distributed but locally abundant food types often nest in large colonies and feed by "local enhancement", defined as "an increased tendency to respond to part of the environment as a consequence of the response of another

individual to it" (Hinde, 1966). This insures not only a greater area surveyed for food but identification of food sources by a significant portion of the population when they are located.

There are a total of 56 major marine bird breeding sites in Oregon. Brandt's Cormorants and Common Murres breed in only one colony in the absence of Western Gulls and in that one case there is a colony of Western Gulls within 0.5 km. Pelagic Cormorants nested singly or in single-species aggregations in four locations. This may be related to this species' greater dependence on prey species other than mid-water schooling fishes. A partial explanation of the co-occurrence of these species as well as many other marine birds is that they utilize the same types of nesting areas which are limited in number. The availability of nest sites is a related, but distinct, question. The almost complete overlap in the breeding activities (Table 3) of these birds is probably a common response to increased food availability at this time of year.

The three diving species I studied which participate in mixed-species flocks differ in their offshore distribution and as a result of this zonation in their distribution take slightly different prey items, overlapping extensively only in the more abundant species such as anchovies, smelt and juvenile rockfish. The observed zonation results in less pressure being placed per unit area on the less common and more predictably distributed prey species, but

allows the entire offshore area to be searched very effectively for the patchily distributed but locally abundant prey species. The behavioral interactions described result in rapid communication of the location of these locally abundant prey resources and permit each species to maintain contact with the school for a much longer period of time. I would emphasize that this system works only because there is a superabundant prey resource being exploited. The temporal and spatial overlap in the occurrence of breeding activities contributed to a more effective coverage of the area surrounding the colony as the result of more searchers over a larger area. The high productivity at this time of year, as well as the clumped distributional pattern of nesting sites also contribute to the observed breeding patterns.

The pattern of community organization observed among the marine birds breeding on Yaquina Head, Oregon is very similar to that seen among related species in almost every high latitude marine bird community studied to date (Uspenski, 1958; Bolopolski, 1957; Pearson, 1968). This pattern of organization includes, specifically, co-occurrence on the same breeding rock, nest site segregation, feeding area segregation, extensive temporal overlap in breeding activities, extensive overlap in principle prey species taken and occurrence in mixed-species foraging flocks. The exceptions to this pattern (e.g. Fork-tailed Petrels, Leach's Petrels, and

Double-crested Cormorants) would be interesting subjects for future work.

Tropical marine bird communities differ in some respects from the generalizations given for high latitude communities. There is less overlap in the timing of breeding activities between species and a longer nesting period for individual species (Ashmole and Ashmole, 1967; Schreiber and Ashmole, 1970). These differences have been attributed, in part at least, to the temporal uniformity of productivity in the tropics (Ashmole, 1972). In addition, if tropical marine birds rely extensively on tuna schools to make prey available to them (Ashmole and Ashmole, 1967) there may be competitive interference for access to the limited area above and around a tuna school where prey is available. If this is the case one might expect additional dispersion, both temporally and spatially, e. g. an extended breeding season and greater offshore dispersal. In fact, a greater percentage of species and individuals among the tropical birds seem to be found offshore relative to the comparatively narrow coastal zonation of high latitude species.

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