NOAA Technical Memorandum
NOS MEMD 13

# FORAGING ECOLOGY OF SEABIRDS IN THE GULF OF THE FARALLONES NATIONAL MARINE SANCTUARY

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QH104.N6 no.13
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REPORT TO
NATIONAL OCEANIC AND ATMOSPHERIC ADMINISTRATION
U.S. DEPARTMENT OF COMMERCE

NOAA TECHNICAL MEMORANDA SERIES NOS/MEMD

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NATIONAL OCEANIC AND ATMOSPHERIC ADMINISTRATION
NATIONAL OCEAN SERVICE
OFFICE OF OCEAN AND COASTAL RESOURCE MANAGEMENT
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This work is the result of research sponsored by the U.S. Department of Commerce, National Oceanic and Atmospheric Administration, National Ocean Service, Office of Ocean and Coastal Resource Management, Marine and Estuarine Management Division Under Interagency Agreement Number NA-81-AA-H-CZ151

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PREAMBLE

The following is a report on data gathered 1971 to 1986. It was prepared by D. G. Ainley, L. B. Spear, J. F. Penniman, C. S. Strong and I. Gaffney. The purpose of the report is to fulfill requirements of a cooperative agreement between PRBO and the Marine Sanctuary, namely to gather information on the foraging ecology of Farallon seabirds in 1986 and to merge it with data gathered 1971 to 1985. Information on the foraging habitat of Farallon seabirds in 1985 was gathered in an effort funded by the Minerals Management Service. The work during both years was possible only through the cooperation of the officers and crew of the NOAA Ship David Starr Jordan, and personnel of the Farallon Islands National Wildlife Refuge. The shipboard work involved five cruises in the Gulf of the Farallones, three in 1985 and two in 1986 (more details below in Methods). The April cruises occurred immediately before the onset of egg laying in Farallon seabirds; the June cruises occurred during the height of the nestling period (results in Part II). The cruise made during December 1985, was in the midst of the nonbreeding period (with results contained in Part V).

During the cruises, we attempted to cover as much of the Gulf of the Farallones, as well as waters near Cordell Bank, as time allowed. Cruise tracks are shown on various figures of seabird distributions (see Parts II,V of this report). We also collected Common Murres and Cassin's Auklets on these cruises, as well as on some supplementary trips made in a small fishing boat

at various times of the year (1985 and 1986); these data will be reported at a later time. In conjunction with cruises, observations were made on the prey menus of murre, guillemot and auklet chicks at Southeast Farallon, mainly as a way to index the relative abundance of juvenile rockfish in the diets (Part III). The prevalence of these fish strongly affects the reproductive success of Farallon seabirds (Part IV; Ainley and Boekelheide ms).

## INTRODUCTION

The allocation of two factors, space and food, play pivotal roles in the structuring of animal communities (Diamond 1986, Roughgarden 1986). For Farallon seabirds, we consider the allocation of nesting space in the individual chapters of Ainley and Boekelheide (ms), and here we will consider the way in which Farallon seabirds do or do not differ in their allocation of food resources. The allocation of food, of course, also involves spatial elements.

Coexisting species can divide available trophic resources by a number of means, and each can be considered a separate niche dimension or axis. These include allocation by prey species, by prey size, by foraging behavior and by foraging habitat (or space). Individual species would then reside along these axes, in some cases perhaps overlapping with other species and in others perhaps not. All of these niche dimensions have been investigated many times in studies of seabirds, but, as detailed in the review below, few studies have considered all four dimensions for a particular community or species group.

We have organized this report by niche dimension, rather than by describing the foraging autecology of each species separately. First we consider foraging area and habitat; then foraging behavior, which is divided into prey capture technique, temporal patterns, tendency to feed socially, and foraging effort; then we consider diet composition; and finally, prey size. Our data are largely from the breeding season and, where it was possible, we include between-year variation in these niche dimensions.

Given the large size of the populations involved, it would seem possible that seabirds compete for food in the Gulf of the Farallones and vicinity. Many Farallon species are nonmigratory and reside within or near the Gulf year round. As discussed in Ainley and Boekelheide (ms), these include the Ashy Storm-Petrel and Double-crested Cormorant, as well as, perhaps, Pelagic Cormorant, Common Murre, Cassin's Auklet, and Rhinoceros Auklet. Other species' populations disperse from the area entirely once breeding activities cease. These species include Leach's Storm-Petrel, Pigeon Guillemot, and Tufted Puffin. Finally, some portion of the Brandt's Cormorant and Western Gull populations

remain in the Gulf year round while the remainder disperse along the West Coast. When the breeding populations of all these species are present, from mid-March to August, a minimum of 300,000 individuals are exploiting food resources in the Gulf and are using the Farallones as their base. About 50,000 more breeding individuals from coastal sites can be added to the total (Sowls et al. 1980). In addition, during the breeding season, a large proportion of these species' nonbreeding populations also frequent breeding sites and thus feed in nearby waters. These nonbreeders are more free than adults to exploit food farther afield, but little is known about whether or not they do. In tropical waters, Ashmole (1963) theorized that nonbreeders do feed elsewhere, but in the Ross Sea, Antarctica, Ainley et al. (1984) found that this is not so. Only in the case of the Western Gull is there evidence to indicate that those subadult nonbreeders which make visits to the island feed on a different resource than do adult breeders and nonbreeders (Spear, unpubl. data; see gull section below). Assuming that a significant portion of respective adult nonbreeders also frequent the Gulf during the breeding season, a minimum 400,000 individuals currently reside in, or near to waters of the Gulf of the Farallones during the period of mid-March through mid-August. Before the 1870's, this number was probably a million or more (Ainley and Lewis 1974).

In addition to these breeding species, at least one other seabird is also important in the assemblage of species exploiting trophic resources in the Gulf of the Farallones. This is the Sooty Shearwater *Puffinus griseus*, a southern hemisphere visitor whose numbers in the Gulf probably exceed a million birds during portions of each summer, mainly May through July (Briggs and Chu 1986, Briggs et al. ms). We will consider Sooty Shearwaters in the results presented here because if seabird feeding does affect food availability, thus leading to competition, then certainly Sooty Shearwaters should be involved.

Community-based studies of seabird diet and feeding ecology have been conducted in the Barents Sea (Belopol'skii 1961; diet during three to five breeding seasons depending on species), in the Chukchi Sea (Swartz 1966; diet during one season), at Christmas Island (Ashmole and Ashmole 1967; diet and prey size, two seasons), on the Welsh Coast (Pearson 1968; diet, prey size, feeding range and habitat, one season), at South Georgia (Croxall and Prince 1980; diet and foraging range, one season), at the Pribilof Islands (Hunt et al. 1981a, Schneider and Hunt 1984; diet and habitat during four seasons, but averaged into one season), at Kodiak Island (Sanger 1982; diet and prey size, one season), in the Gulf of Alaska (Baird et al. 1983; diet and behavior, two seasons), at Cousin and Aldabra atolls in the Indian Ocean (Diamond 1983; diet, prey size and foraging range during one averaged season), in the northwestern Hawaiian Islands

(Harrison et al. 1983; diet, one season), and in Varanger, Norway (Furness and Barrett 1985; diet, prey size and foraging range, one season). Studies concerning major portions of breeding communities were conducted on alcids at St. Lawrence Island (Bedard 1969a; diet and prey size, three seasons), on the Welsh coast (Harris 1970; diet and prey size, three seasons), and at the Olympic Peninsula (Cody 1973; diet, prey size and foraging range, one season), on cormorants along the North American West Coast (Ainley et al. 1981; diet and foraging habitat, data for several years averaged), and on more diverse portions of communities in Oregon (Scott 1973, Wiens and Scott 1975; diet, prey size and habitat, one season) and South Africa (Crawford and Shelton 1978; diet, several seasons). Feeding ecology studies of entire seabird communities at sea have been conducted in the high latitude Antarctic by Bierman and Voous (1950; diet, one season) and by Ainley et al. (1984; diet, prey size, behavior and habitat, one season), and of partial communities (auks) by Bradstreet (1979, 1980, 1982; diet, prey size and habitat, several seasons averaged) in the eastern Canadian Arctic.

Among these 20 studies, three characteristics are clear. First, the majority (14) were conducted in high latitude systems of relatively low, constant productivity compared to the high but variable productivity of upwelling-dominated eastern boundary systems. Of the remainder, three involved relatively less productive subtropical and tropical, oceanic systems, and only three involved productive upwelling-based systems (West Coast of North America, Oregon, South Africa). Second, the majority (14) were conducted during only one year, or the data were averaged as if one year; and the majority (13) did not investigate within-year variability. Finally, only three, all high-latitude studies gathered data to relate year-to-year variability in foraging ecology to changes in reproductive success for multiple species (Belopol'skii 1961; Hunt et al. 1981 a,b; Schneider and Hunt 1984; Baird et al. 1983). A number of the latter such studies exist, however, for single species.

A major common finding among the above multi-species studies is that breeding seabirds at a given locality depend on only a few major species of prey, and diet overlap is high (Diamond 1983, Furness and Barrett 1985). The present consensus of opinion is that when segregation occurs it is on the basis of different size classes of common prey or differences in foraging behavior (e.g., range, habitat, or foraging depth). The underlying assumptions in most of the above studies are that breeding seabirds compete for a limited amount of food and that food availability during the breeding season limits reproductive success and population size (Ashmole 1963; Diamond 1978; Hunt et al. 1981 a,b; Hunt et al. 1986; Furness and Birkhead 1984). The contrary opinion to the above assumption has been expressed by Lack (1946, 1966), an opinion which seems lately to be falling

out of favor, that because of a superabundance of a few prey species during the breeding season, seabirds in that situation do not generally compete for food; rather, if competition occurs it should happen during periods when prey are unavailable, namely, the nonbreeding season. Lack went further to hypothesize that food during the nonbreeding season is the factor that limits seabird population size.

The relationship between feeding ecology, breeding success, and population fluctuation remains obscure, except in situations involving total collapse or alteration of food webs (Murphy 1925, 1936, 1981; Crawford and Shelton 1978, Vermeer 1978, Vermeer et al. 1979a, Baird et al. 1983, Schreiber and Schreiber 1984). In addition, Bedard (1969a) noted that the annual breeding effort of auklets on St. Lawrence Island terminated coincident with a diversification of diet during the late summer. This was also observed for other species by Belopol'skii (1961) in the Barent's Sea (see also Pearson 1968, Crawford and Shelton 1978). Such observations support the idea that seabirds undertake breeding coincident with (dependant upon?) the seasonal appearance of super abundant prey (Lack's view). In further support, a number of studies have noted a correspondence between interannual variability in diet and reproductive success (Anderson et al. 1982, Baird et al. 1983, Belopol'skii 1961, Bergman 1978, Harris 1984, Hunt and Butler 1980, Hunt et al. 1981 a,b, Kuletz 1983, MacCall 1986, Schaffner 1982 and Vermeer 1980). In the second and fifth of the latter studies, authors felt that <u>interspecific</u> competition for prey reduced food availability for certain predators, which in turn led to lowered reproductive success (see also Hunt et al. 1986). Birkhead and Furness (1985), however, have expressed a contrary view that interspecific competition for food has little bearing on reproductive success or population size of individual species'. In the other studies, authors ascribed diet and breeding variability to oceanic conditions, independent of interspecific, competitive interaction. Variation in competition and oceanographic factors are not mutually exclusive, but the paucity of studies relating reproductive success of seabirds to food web dynamics makes further discussion difficult.

Given that most seabird community studies were conducted during 1) the breeding season, and 2) on systems relatively less productive than eastern boundary currents, it seems valid to ask whether or not our perceptions of the ultimate factors affecting seabird ecology and populations are not accordingly biased. Or, at the least, to ask how far we can go to generalize these perceptions. Furness and Monaghan (1987) conclude that generalization would be premature at present. Ainley and Boekelheide (ms), however, propose that in productive, upwelling-based systems, seabird populations are not directly limited by food during the breeding season, an opinion already voiced by

Murphy (1981) and Duffy (1983a) for the Peru Current, a system analogous to the California Current. They also propose that for seabirds of the California Current upwelling domain, ecological segregation of food resources is most evident during nonbreeding periods. The implication is that it is likely not valid to generalize patterns of resource segregation, and their relationship to population and breeding biology, among all breeding seabird communities, particularly to upwelling systems.

## METHODS

Foraging areas. During April and June in both 1985 and 1986, we criss-crossed the Gulf of the Farallones and neighboring waters by ship. Cruise dates were 11 to 16 April and 31 May to 19 June 1985, and 14 to 22 April and 4 to 19 June 1986. The first of these years was one of the most productive for Farallon seabirds since our study began with chicks fledged per breeding pair exceeding the 1971-1982 average for all species (Part IV). In contrast, during the second, which was a "warm-water" year, breeding was late in all species except storm-petrels and reproductive success was well below the 1971-1982 average; in fact, Pelagic Cormorants and Pigeon Guillemots failed in their nesting attempts. Thus, we consider 1985 representative more of conditions during the average or better years of seabird reproduction described in Ainley and Boekelheide ms (see also Part IV), and we consider 1986 representative of the warm-water years, such as 1973, 1976, 1978 and 1982-83.

Census methods were the same as those described in Ainley et al. (1984). This work supplemented the information provided by Briggs et al. (1983) who censused seabirds by airplane off the northern California coast during the period 1980 to 1982. Their census lines were perpendicular to the coast and more widely spaced than our cruise tracks.

To construct the 1985 and 1986 maps of foraging areas, we divided the Gulf of the Farallones and vicinity into 3' X 4' latitude X longitude blocks for the April (prebreeding season) and June (breeding season) cruises. Each block was thus about 5 km on a side (ca 27.9 $km^2$). If a census segment (each one half hour or 8.8 km long) intersected a block, then each species' density for that segment was assigned to that block. In cases where more than one segment intersected a block, then values were averaged. When a segment intersected more than one block, its density value was assigned to each. Finally, when an uncensused block was bordered by at least two censused blocks, the uncensused block was given a value equal to the average densities of the bordering blocks. We only considered birds on the water or actively feeding.

We assessed change in the habitat use of species between 1985 and 1986 by comparing blocks occupied in the two years. This was done using Cole's (1949) Coefficient of Association and census blocks common to both years, where

$$C = \frac{(ad - bc)}{(a + b)\ (b + d)},$$

and the variance,

$$s^2 = \frac{(a + c)\ (c + d)}{n\ (a + b)\ (b + d)}.$$

In this formula, a is the number of blocks in which species A (the least abundant of the two being compared) is present in the absence of B, b is the number of blocks in which B is present in the absence of A, c is the number of blocks in which both occur together, and d is the number in which neither occur; n equals the sum of the four variables. Using the same technique we also assessed habitat overlap among the species, and whether overlap changed between the warm and cool year.

We were able to derive a further assessment of between-year variation in foraging areas by censusing seabirds along the supply route between the Golden Gate and Southeast Farallon Island. These censuses were conducted from mid-1972 until early 1981 aboard the small craft that ferried us to and from the island, compliments of the Oceanic Society Farallon Patrol. This census effort proved useful for determing variability in foraging areas only because, as indicated by observations from the island, a significant proportion of Brandt's Cormorants, Western Gulls and Common Murres, on their foraging trips during the breeding season, disappeared toward or appeared from the East or Southeast, the directional axis along which the supply craft traveled. Subsequently, the aerial censuses of Briggs et al. (1983) and the 1985-1986 showed that a major foraging area in the Gulf of the Farallones (especially in warm years) is in those coastal waters from southern Marin to southern San Francisco County, that is East or Southeast from the island. This area is influenced by the plume of waters that flow by tidal action out of San Francisco Bay. Within it, the interface between tidal waters and shelf waters, which is usually a marked, visually observable boundary, is often an area of high bird numbers (see also Storer 1952). In essence, then, by good fortune and the quirks of geography, the Golden Gate to Farallon route provided the means to index the more distant foraging efforts of a large proportion of Farallon cormorants, gulls, and murres.

On all of our trips, only birds that occurred within an estimated 300 m of one side of the boat were counted; observers were usually about 5 m above the sea surface on supply boats and 15 m above on our 1985-86 censuses. Supply boats traveled at 5 to 8 knots, and the vessel used in 1985-86 work traveled at 10 knots. The supply route was partitioned into four units (see Figure 2.2): Area I, Golden Gate Bridge to Point Bonita, the outermost point of the Marin Headlands (a 4.4 km stretch); Area II, Point Bonita to the outermost shipping-channel buoy (6.2 km); Area III, outermost buoy to San Francisco Pilot Buoy (8.7 km); and Area IV, Pilot Buoy to about two kilometers off the Southeast Farallon (24.6 km). When winds were above 25 knots we were unable to census effectively; usually, if winds exceeded that level, supply boat trips were canceled and the larger vessel anchored in the lee of Pt. Reyes headland. During the 8 years of supply run censuses, we were able to make 220 censuses with an exceedingly constant effort of 1-3 censuses per month for April to September.

Feeding behavior. Several previous studies have suggested that much insight into the foraging ecology of seabirds can be gained by measuring dive sequences and characteristics (Dow 1964, Stonehouse 1967, Hobson and Sealy 1985, Cooper 1986). We investigated the diving capabilities of Farallon seabirds by using stopwatches to determine how long birds remained under water and the amount of time between successive dives. As in the above studies, we did not include dives that resulted in known capture of prey, nor the handling of prey at the surface, and we timed ony those pauses terminated by another dive. Thus, measured dives and pauses would not be prematurely ended or unduly prolonged. From the duration of dives and pauses between dives, we calculated the dive-pause (D/P) ratio. All birds were timed within the same 100 square meter area off East Landing at Southeast Farallon; water depth there is about 20 m. All the species observed can certainly dive deeper than 20 m, but we felt it important to compare them in the same habitat.

We also investigated the tendency of species to feed in flocks, including mixed-species flocks, as well as seasonal and year-to-year differences in such tendencies. We recorded the presence of feeding flocks that occurred within 3 km of the South Farallones. The effort from 1972 to 1978 was semi-casual, thus only the large flocks were recorded, but from 1979 to 1983, the effort was more concerted and probably the majority of flocks were noted. We logged time of day, direction from the island, species composition, size of flock and persistence at a given location. To analyze flocking tendencies, we used Cole's (1949) Coefficient of Association with flocks being the unit of comparison rather than the census blocks used above.

We assessed another aspect of foraging behavior--foraging effort---by conducting all-day watches of selected species' nests during the breeding season. We assumed that the time birds spent away from nests, i.e., the interval between successive nest reliefs, was a measure of the ease by which birds located food (Diamond 1983). An all-day watch was conducted every three to five days from blinds. From 1972 to 1978, both cormorants and murres were observed from the blind atop Shubrick Point which overlooked the nests of several species. Samples of about two to five Pelagic nests, 15 Brandt's nests, and 75 murre sites within close (10 m), easy view were identified on colony photos. From 1979 to 1983, Brandt's Cormorant watches were moved to the blind overlooking the large colony at Sea Lion Cove, but murre watches were continued at Shubrick Point. Pelagic Cormorant watches were conducted only during 1973-1977. The sites observed for all three species were among those we followed to assess reproductive effort and success (detailed in Ainley and Boekelheide ms). During watches, we noted the times of arrival and departure of the birds occupying these nests. Biologists spelled one another every hour in order to prevent fatigue; three to five biologists participated in the rotation each day.

We assessed time of day when foraging occurred by combining observations of feeding flocks (above), the all-day watch data just mentioned and information on the daily patterns of attendance of each species (in Ainley and Boekelheide ms).

Seabird diets. We investigated the diet of Farallon seabirds during the nestling period by a variety of means, the method depending on the biology of respective species. As described in Ainley et al. (1981), we collected pellets from Double-crested, Brandt's and Pelagic cormorants just after chicks fledged, 1973 to 1977. During 1977, we were also able to collect Brandt's Cormorant pellets during the nest building period, and this provided the opportunity to compare early- and late-season diet during that year. The qualities of pellets as a means to assess cormorant diet are discussed by Ainley et al. (1981); basically they are quite satisfactory and have been used by a number of workers (e.g., Jordán 1959, Schlatter and Moreno 1976). Within pellets, fish can be identified by their otoliths, and invertebrates by such hard parts as beaks for cephalopods, and carapaces for decapods. A number of studies indicate that respective hard parts may over represent cephalopods and decapods relative to fish (Bradstreet 1980, Ainley et al. 1984, Duffy and Jackson 1986), but in our study the beaks were so tiny and delicate that this may not have been so for cephalopods.

Four different sources of information were used to quantify the diet of Western Gulls:

1. Pellets. The majority of pellets were collected from the concrete water catchment pad on the island's southwest side.

Once per week, weather permitting, biologists walked over the area, broke open all pellets encountered, and recorded the predominant food type in each. Otoliths were collected for identification. This technique was used from March to August 1973 to 1978, and in March-April 1979; a total of 11,490 pellets were inspected.

2. Feces. In the same catchment basin (as above) discrete feces were classified according to major components. Feces identification was done from May to August 1976 to 1978; a total of 1,024 feces samples were inspected.

3. Chick regurgitations. In the course of our annual chick banding effort, during a two-week period in June 1974-1983, we collected food regurgitated by chicks. A total of 325 regurgitations were collected.

4. Adult regurgitations. Observations of courtship feeding or adults feeding chicks were made opportunistically from one of our study blinds in the course of other work. Most identifications required use of a binocular. Information from 1974 was extrapolated from Pierotti (1981), and L. Spear contributed his many observations from 1978 to 1983. A total of 1,468 meals were observed.

In the case of the Common Murre, we determined only the diet (including prey size) fed to chicks during the nestling period (Ainley and Boekelheide ms). As indicated by Scott (1973), Varoujean (unpubl. data), and Bradstreet and Brown (1985), the diet fed to murre chicks differs somewhat from that retained by parents during the period of chick dependence. In general, adults feed their offspring items which can be easily carried length wise in the bill, as well as perhaps those of high caloric value (Harris 1984). These are usually fish or squid from four to 15 cm long. In addition to fish, adults eat small invertebrates such as euphausiids which would be too energetically costly and nutritionally insufficient to carry one by one to the offspring. In 1985 and 1986, when we analyzed diet of adults at sea as well as diet fed to chicks, we found that adults were eating the same species of fish fed to chicks and were not then feeding on invertebrates; whether or not adults ate different sized fish awaits future analysis. During the all-day watches mentioned above, we noted the prey brought to specific pairs, as well as the time of day. Fish were identified to the lowest taxon possible, which for most was to species or species group (in the case of rockfish).

We quantified the diet fed to Pigeon Guillemot chicks in a fashion similar to that used for the murre, although we did not conduct all-day watches. Each day, at about 14:00 h when we made daily rounds of the guillemot study plot (Ainley and Boekelheide ms), we noted prey size and species brought to chicks. As long as we were present, adults refused to enter their burrow with the meal, but instead waited on their roost near the burrow entrance.

Thus, we usually had a good opportunity to observe each prey item. In Black Guillemots C. grylle studied in the high Arctic, the diet of adults differed somewhat from that fed to chicks in much the same way as in murres (Gaston et al. 1985, Bradstreet and Brown 1985).

Observations of prey brought to the chicks of Tufted Puffins were gathered on an opportunistic basis. Several puffin pairs nested in the vicinity of the Shubrick Point blind. When they arrived with prey in their bills, and paused long enough at the burrow entrance, we were able to identify many prey to species. On many occasions, however, they were so quick to enter their burrow that we could only see that the prey was fish rather than squid, or vice versa. During the years when we observed puffin diet, we were unable to collect information on the diet of the Rhinoceros Auklet.

Cassin's Auklets---like cormorants and gulls, but unlike murres, guillemots, or puffins---feed their chicks by regurgitation. Unlike other seabirds that feed their chicks in this way, auklets have gular pouches in which they store the food until they make their once-daily trip to the nest. The food consumed by adults, on the other hand, is swallowed directly into the alimentary tract. Cassin's Auklet adults feed their chicks on the same prey they catch for themselves (data from 1985 and 1986 to be reported later). During the chick rearing periods of 1977 and 1979-1981, we captured weekly samples of adults just as they arrived to feed their chicks and we allowed them to regurgitate into plastic vials (We did the same in 1985 and 1986, but as noted above, results will be reported at a later date). These samples were then analyzed to determine diet.

For most species, we calculated diet diversity by using the Shannon-Weiner formula (Hurtubia 1973):

$$H = - \quad p \ln p,$$

where p is the proportion of the total diet contributed by each prey species.

We also measured the extent of overlap in the diet composition between species and within species between years. To do this we used Morisita's (1959) Index:

$$C = \frac{2 \quad x_i y_i}{x_i^2 + \quad y_i^2},$$

where x and y are the numerical proportions of various prey in the two diets being compared.

Prey size. In order to investigate overlap in prey size, we calculated the lengths of fish prey that were common to several

species' diets. In the case of cormorants, fish standard lengths were determined by regression of otolith diameters. Many of the regressions have been determined by us (PRBO unpubl. data), but a few, especially for commercially important fish such as anchovies and herring, are available in the literature. In the case of murres, guillemots and puffins, fish length was estimated crudely by comparing the fish carried in the bill to bill length. For the more abundant prey species, we were able to convert estimated length to weight using regressions which we had determined or which in a few cases were also available in the literature.

## PART I. ANNUAL VARIATION IN AVAILABILITY OF PREY

The major prey of central California seabirds are juvenile rockfish Sebastes spp., northern anchovy Engraulis mordax, market squid Loligo opalescens, and the euphausiid Thysanoessa spinifera (Manuwal 1974b, Follett and Ainley 1976, Pierotti 1976, Balz and Morejohn 1977, Ainley et al. 1981, Chu 1984). During the winter and early spring, Pacific herring Clupea harengus can also be important to some seabird species, especially gulls and probably cormorants (Spratt 1981a). In addition to these abundant, schooling organisms, California seabirds also feed heavily on a variety of other more dispersed, or more highly localized prey (e.g., Ainley et al. 1981). Unfortunately, for most of the latter species little is known of their biology or abundance because few are of direct commercial importance.

Reviewed here is information on the natural history of the above major prey, particularly aspects of their biology which affect availability to seabirds. Included is information on between-year differences in abundance 1971 to 1985; information for 1986 will not be available until late 1987.

Northern anchovy. The abundance of anchovies in California has been increasing dramatically since the early 1950s. There are three subpopulations; the central subpopulation occurs from northern Baja California, Mexico to about Pt. Reyes, California (Vrooman et al. 1981). Anchovies occur in coastal waters from the shoreline out to those overlying depths of more than 1000 m. Anchovies through one year of age predominate in waters out to 300 m deep, and one- and two-year-olds out to 600 m; older ones predominate in waters overlying deeper depths. In the central subpopulation, individuals enter the second year measuring about 125 mm (Parrish et al. 1985). Almost all anchovies mature by the end of the second year.

Anchovies move offshore and southward during winter, coincident with their major period of spawning (Mais 1974). Some spawning occurs in a number of locations along the coast, including the Gulf of the Farallones, but the major area is off Southern California. Beginning in late summer, anchovies tend to occur in large, dense schools that occur at depths of 180 to 300 m during the day, and which move to the surface and disperse during the night; in the spring and early summer, schools occur near the surface during the day (Frey 1971). During some years, anchovies occur more inshore and in others more offshore (Mais 1974); there is a northward movement of larger anchovies during years of warmer sea surface temperatures (Parrish pers. comm.).

The northern anchovy is one of the most intensively studied creatures in the California Current, if not in the whole world. Much information is available on relative abundance from year to year. Annual abundance estimates are available, and are expressed in terms of spawning biomass (Hewitt 1985, MacCall

1986). Within the central subpopulation, spawning biomass decreased between 1970 and 1972, but recovered to about 1.1 million metric tons by 1975 and 1976 (Figure 1.1). It then entered a period of decline with especially low levels in 1978, 1982 and 1984. Part of the decline in biomass resulted from a reduction in fish size (MacCall 1986). Some recovery occurred in 1986 (MacCall pers. comm.).

It is probable that fluctuations in spawning biomass were partly responses to changes in spawning success and resultant year class strengths, as well as to predation on older fish (Mais 1981). Strong year classes were produced 1970 through 1973, which meant that 0- to 2-year-old anchovies (smaller fish in the size range consumed by birds) were available to seabirds 1971 through 1975. Poor anchovy year classes were produced in 1974, 1975 and 1977, and only a class of mediocre strength was produced in 1976. These poor year classes were, thus, partly responsible for the lower levels of spawning biomass from 1978 on (Figure 1.1). The production of young fish, however, was fairly strong 1978 through 1980, and again in 1982, but was weak in 1981 and 1983 (Mais 1981, Mais <u>in</u> Hewitt 1985). Information on relative year class strengths beyond 1983 are not yet available.

During 1978 and 1982-1984, commercial landings of anchovies were well below allowable takes. This was due to a number of reasons, including fish availability (Calif. Dept. Fish and Game 1985).

<u>Rockfish</u>. In offshore waters of central California the species of rockfish most important to seabirds include blue <u>S. mystinus</u>, boccacio <u>S. paucipinnis</u>, chilipepper <u>S. goodei</u>, shortbelly <u>S. jordani</u>, yellowtail <u>S. flavidus</u>, and widow <u>S. entomelas</u>. Among these, the most important species is the shortbelly (PRBO unpubl. data). Juveniles of all of these species occur in offshore waters of the continental shelf, although abundance is greatest within 15 to 30 km of land. The relative compositon of juveniles in the trawl samples taken by National Marine Fisheries Service in 1985 was 60% <u>S. jordani</u>, 30% <u>S. entomelas</u>, and 10% for the remainder of the above species (Echeverria pers. comm.).

Juvenile rockfish are born alive and at partuition are about 25 to 30 mm in length. Within a few months they grow to about 75 mm long. During this period they occur in schools at mid-depths as well as surface waters; they then settle to depths near the bottom. An exception to this pattern is exhibited by the shortbelly which occurs at mid-depths as an adult (Lenarz 1980, Lenarz and Moreland 1985). Partuition in the above group of species occurs during winter and early spring, with the principle month of partuition being February for all except the blue and chilipepper. For the latter the principle month is January

(MacGregor 1986, Echeverria ms). Partuition in these months, along with a few months of subsequent growth, means that individuals in a size range suitable as prey for smaller seabirds would become available in the period March to April, and for larger seabirds May to July. When they settle to deeper waters beginning late July and August, they become increasingly unavailable to seabirds except for the very deepest diving species. Juvenile rockfish are exceedingly important prey to many marine predators during the spring and early summer, including, other than birds, salmon and marine mammals (Lenarz 1980, Jones 1981).

Pressure to increase the commercial catch of rockfish has grown only in recent years, and juveniles are not targeted by fisheries. Consequently, long time series of information on annual variation in abundance of juvenile rockfish do not exist. Abundance of juveniles has recently been recognized as a good indicator of future year class stength, however, with the result that direct data exist since 1983 (Lenarz and Moreland 1985, Hobson et al. 1986, Lenarz pers. comm.) For prior years, indications of the annual abundance of juveniles can be approximated by the strengths of specific year classes in the fishery (see also MacCall 1986). Unfortunately (or perhaps fortunately for the marine food web), no fishery exists for shortbelly rockfish and thus only the more recent direct data are available.

During the span of the seabird study, exceptionally strong year classes for most of the above commercially important rockfish species occurred in 1971, 1975, 1977 (not chilipepper), 1979 (not widow), and 1985 (1973 and 1978 were strong years for only chilipeppers and widows, respectively); and exceptionally poor year classes occurred in 1972, 1973 (not chilipepper), 1978 (not widows) and 1983 (Hightower and Lenarz 1986, Henry 1986, Hobson et al. 1986, Thomas 1986). For shortbelly rockfish, exceptionally strong years were 1971, 1975, 1977, 1979 and 1985. The record for poor years is much more difficult to reconstruct, but 1972 and 1983 clearly were among such years (MacGregor 1986; Echeverria and Woodbury pers. comm.). These trends are summarized in Figure 1.1, with information after 1979 being less complete because rockfish born since then have not yet entered the fishery.

<u>Pacific Herring</u>. Herring occur in coastal waters throughout central California. They become especially available to seabirds during the winter when they enter shallow coastal bays and lagoons to spawn. Important fisheries exist for herring in Tomales and, particularly, San Francisco bays, November to March. Particularly low spawning biomass in herring occurred in the winters of 1973-74, 1977-78 and 1983-84 (Spratt 1981a, Calif. Dept. of Fish and Game 1983, 1984, 1985).

Market squid. This species of cephalopod moves inshore to spawn in shallow waters (<100m); otherwise it occurs widely in schools in California coastal and offshore waters. Schools remain at depth during the day and approach the surface at night. A major West Coast spawning area is Monterey Bay, but some spawning occurs in the Gulf of the Farallones. The main spawning period occurs in the period April to June but extends to as late as November (Frey 1971, Recksiek and Frey 1978). Market squid reach a maximum size of about 300 mm (including mantle and arms) in two years (Spratt 1981b); thus, the majority eaten by seabirds are probably a year old or less.

No estimates of spawning biomass exist; squid landings in the fishery must suffice to indicate annual differences in availability and to some degree they do at least with regard to periods when the squid are unavailable. The squid fishery in Monterey Bay grew slowly until 1978, when demand began to increase rapidly. Thus, estimates of abundance must be separated by that year (Calif. Dept. of Fish and Game 1982-1986). Squid were notably few in 1973 and 1976 during the early part of the record; and few in number during 1980 and 1983-84 in the later part (Figure 1.1).

Euphausiids. Most of the research on zooplankton in the California Current has dealt with species in offshore waters, thus relatively little is known about *Thysanoessa spinifera* (Smith pers. comm.). The latter species occurs over the continental shelf and slope, and is associated with centers of coastal upwelling. Usually occurring in surface waters over deeper depths is the euphausiid *Euphausia pacifica*, a species for which much more information is available. *E. pacifica* is one of the most abundant and ubiquitous euphausiids off California, except over the shelf; it occurs year round but is most abundant during spring and summer. *T. spinifera*, on the other hand, seems to be abundant in surface waters mainly during the upwelling period (Brinton 1962, 1981). Both species have been observed in swarms at the surface during the day, especially *T. spinifera* (Smith and Adams ms, Harvey ms). Surface swarms in the latter species appear to occur soon after strong northwesterly winds and upwelling events (Ainley pers. obs.).

Little is known about between-year variability in the abundance or availability of these two species. Brinton (1981) observed that *E. pacifica* becomes sparse during the early portion of sea surface warming events. Most recently, this occurred from late 1977 to mid-1978 (Brinton 1981), and also in 1983 (Smith pers. comm.). Even less is known about *T.spinifera* and then only during the 1980s. It was sparse during 1983 as well as during the first half of 1986, but was abundant in 1984 and especially 1985 in the Gulf of the Farallones (Smith pers. comm.).

To summarize these data then, anchovies, in the 0- to 2-year-old year/size classes consumed by seabirds, appeared to be available throughout the period but abundance and fish size declined in the latter part of our study (1980s). Commercial fishermen were unable to find fish in 1978 and from late 1982 to early 1984, and this could well be true for seabirds, too. Juvenile rockfish (particularly shortbelly) were especially abundant in 1971, 1975, 1977, 1979 and 1985, and were relatively unavailable in 1972-73, 1976, possibly 1978, and 1983. Market squid exhibited poor availability in 1973, 1975-1977, 1980 and 1983-84. Herring occurred in low numbers during their winter spawning period, 1973-74, 1977-78 and 1983-84. Little is known about euphausiids, except that warm water affects abundance and distribution: such changes were noted in 1978, 1983 and 1986. Among the above years of note, most frequently mentioned were the warm water years, 1972-73, 1976, 1978, 1982-83 and 1986.

# PART II. FORAGING ECOLOGY OF FARALLON SEABIRDS

## A. Feeding Areas

Overall patterns. As mentioned above, we know that waters along the mainland coast out to the oceanic boundary of the San Francisco Bay plume from southern Marin to southern San Francisco County (Point San Pedro), are exceedingly important. This is apparent in the data of Briggs et al. (1983, ms), who censused seabirds by air within 70 km of the northern and central California coast, monthly in the period 1980 to 1982. Equally important are waters of the continental slope, where the islands are actually positioned. These patterns were confirmed during 1985 and 1986, when we censused sea birds by ship in both April and June. The former month represents the prelaying period and the latter the nestling period for most Farallon seabirds. These data, in addition, provided comparison between productive, cool- (1985) and unproductive, warm-water (1986) years (see above). The data gathered on the Golden Gate-to-Farallon supply run, 1972-1980, were also instructive in providing further perspective on between-year variability.

A general feeling for the location of Farallon species' feeding areas can be derived by comparing the relative frequency with which they were observed on the four segments of the Golden Gate/Farallon track (Table 2.1). Storm-petrels were rarely seen, and then only in deeper waters near the islands. Double-crested Cormorants were seen near San Francisco Bay, flying, rather than feeding. Brandt's Cormorants were quite evenly distributed among the four census segments, but we know that during some years they prefer inshore, and during other years, offshore waters (below). The Pelagic Cormorants encountered in segment IV nest at the Farallones, and those encountered in segments I and II nest near Point Bonita (see Figure 2.2 below). Western Gull and murre distributions resemble that of the Brandt's Cormorant. The remaining four species, all alcids, were encountered only in the deeper waters near the islands.

The above patterns are supported closely by information provided by Briggs et al. (ms), and the 1985-86 censuses. Leach's Storm-Petrels reside mainly in the warmer, blue waters of relatively lower productivity west of the continental slope and of the Gulf of the Farallones (Figure 2.1). These are waters influenced little by coastal upwelling. Ashy Storm-Petrels, on the other hand, occur over the same waters but also nearer the continental shelf break, particularly in the vicinity of Cordell Bank 50 km to the north (Figure 2.1). These are waters influenced strongly by coastal upwelling. At a minimum, then, Leach's Storm-Petrels feed at least 50 km from the Farallones, and the Ashy at least 25 km away. At maximum, individuals of both species probably feed much farther afield, the Leach's more

to the west and the Ashy perhaps more to the north/south of the Farallones. Briggs et al. (ms) report an association between storm-petrels and convergence lines visible at the sea surface. These boundaries along eddies and water-types are generally quite ephemeral in this region.

Based largely on observations of color banded birds, we know that Double-crested Cormorants feed principally in Bolinas Lagoon and the Drake's/Limantour Estero (Figure 2.2). In earlier years, when many thousands of Double-cresteds nested at the Farallones (Ainley and Lewis 1974), large numbers fed in San Francisco Bay (Bartholomew 1943). The extent to which they feed there now is not known, but at times perhaps they do (Table 2.1). Similarly, the extent to which Farallon individuals use Tomales Bay is not known, but we suspect it is an important area. The waters where Double-cresteds feed are no more than 10 m deep, and they overlie flat sand or mud. During the nesting season Double-crested Cormorants feed no closer than 30 km and perhaps more than 80 km from Southeast Farallon.

Early in the spring, Brandt's Cormorants tend to feed within San Francisco Bay, sometimes as far as the Bay's east shore 80 km away, as well as along the coast (Figure 2.3). Later in the season, they feed either near the islands, or in the waters in towards the coast depending on year (Figure 2.4). Waters in the latter area are turbid and are influenced markedly by the outflow from San Francisco Bay. Most of the habitat along the mainland coast is comprised of flat sand or mud bottoms 10-60 m deep; the habitat offshore includes rocky bottoms as well and is up to 120 m deep. Thus, Brandt's Cormorants feed 0-80 km from Southeast Farallon during the breeding season.

Virtually the entire breeding population of the Pelagic Cormorant probably feeds within a few kilometers of the South Farallones (Figure 2.2). In this area are many submerged, rocky reefs, the feeding habitat preferred by this species. Pelagic Cormorants exhibit remarkably little plasticity in this choice of feeding area. We have observed them in waters from the intertidal to those 120 m deep.

The Western Gull probably exploits more of the Gulf of the Farallones and vicinity than any other species (Figures 2.5, 2.6). This is perhaps a function of its confinement to feeding at the surface (see below). During some years gulls feed farther away from the island, especially inshore toward the mainland (1986), while during others (1985) the reverse is true. Their densities, even when concentrated, are usually relatively low compared to some of the other abundant species. The large majority of gulls that are seen departing or arriving at the South Farallones do so in, or from, an easterly to southeasterly direction, that is, towards the Golden Gate. During warm-water

years they exploit garbage dumps 100 km or more away (see below, Diets).

Among those Farallon species for which we have information, the Common Murre appears to vary most in its use of feeding areas. During the early spring, murres frequent deep waters along the edge of the continental shelf near the islands (Figure 2.7). Some individuals range as far north along the slope as the Cordell Banks (about 60 km; Briggs et al. 1983), but if 1985 and 1986 are an indication then most feed much closer. During May and June in cool-water years (1985), the murre feeding range contracts somewhat and they use waters in the vicinity of the islands (Figure 2.8), but in warm years (1986) they spread out especially over the shelf towards the mainland shore. By July in many years, they begin to exploit waters near the outer coasts of Marin and San Francisco counties, although during midsummer of years when rockfish are very abundant (see below) they remain offshore longer. The inshore movement of murres during July and August is evident in the distribution of fledglings accompanied by a parent. Compared to the inshore segments of the Golden Gate/Farallon transect line, few parent/chick groups remain near the island (Segment IV in Figure 2.2). By September, murres apparently spread out; many are then seen, including parents with chicks, along the coast south to Monterey Bay (100 km) and beyond (Briggs et al. 1983).

Pigeon Guillemots, like Pelagic Cormorants, forage near the Farallones (Figure 2.2), but sometimes they frequent waters a little farther away. Like the latter, guillemots are very specific in their foraging habitat preferring to feed in association with rocky substrate. They range up to 15 km from the islands, but usually remain much closer than that.

The remaining three alcids all forage in the deeper waters of the continental slope. They are rarely encountered very far inshore of the islands except to the northeast where the shelf break (=40 fathom, ca. 80 m, depth contour) turns inshore. According to Briggs et al. (1983, ms) and the 1985-86 data, large concentrations of Cassin's Auklets occur over waters of the continental slope deeper than 80 m, between the Cordell Bank 60 km to the north, and as far as 50 km south of the island (Figures 2.10, 2.11). Rhinoceros Auklets (Figures 2.12, 2.13) and Tufted Puffins (Figures 2.14, 2.15) also occur most frequently in these same slope waters.

Sooty Shearwaters can be found throughout the shelf and slope as well as the deeper waters of the Gulf and vicinity (Briggs and Chu 1986). Depending on year, after arriving in late April, they may concentrate more inshore than offshore or vice versa (Figure 2.16). In June 1985, immense numbers occurred around the Farallones, particularly over the deeper waters to the west, but

also over shallow waters to the southeast. The large concentrations of this species near the Farallones in 1985, presumably a response to food availability, indicates that the feeding ranges of Farallon species, also concentrating there, were a function of where the prey were located, rather than being a constrainment due to nesting duties. Conversely, few Sooty Shearwaters were observed in June of the warmer year, 1986, particularly over the continental shelf.

Between-year variation. We have few data to indicate what annual variability might exist in the foraging ranges and habitats of the storm-petrels. Their densities were too low to allow adequate between-year variation. In the case of Double-crested and Pelagic cormorants, and Pigeon Guillemot, the data available (Briggs et al. 1983, ms; our 1985/86 data) indicate little variability at the height of the breeding season (in June) one year to the next. Coefficient of association values between habitat blocks occupied June 1985 compared to June 1986 habitat equaled 1.00 ± 0.01. Similarly, although densities differed dramatically, the habitat occupied by Sooty Shearwaters changed only a little between these two periods, with a slight shift to slope waters (C=0.88 ± 0.01). The habitats of other species, however, shifted much more, 1985 compared to 1986. Between-year C-values for Brandt's Cormorant and Western Gull were 0.74 ± 0.01 and 0.72 ± 0.01, respectively, and were associated with a shift towards the mainland, but these values are artificially high because they do not incorporate the many individuals feeding near the Golden Gate and in San Francisco Bay where our ship could not go (because of heavy vessel traffic). Cassin's Auklets, Tufted Puffins and Rhinoceros Auklets remained in slope waters during the two years, but spread farther from the islands in 1986 (C=0.68, 0.55 and 0.51, respectively; ± 0.01). The largest shift in habitat was exhibited by the murre with its switch from slope waters in 1985 to inshore waters in 1986 (C=0.21 ± 0.01). These habitat changes are discussed more qualitatively in the following paragraphs.

During April in the 1985 nesting season, Common Murres, Cassin's Auklets and Sooty Shearwaters fed in large concentrations within 10 km of the Farallones and Fanny Shoal, 10 km north. Brandt's Cormorants fed inshore near the coast. Habitat occupancy in June exhibited little change, except that cormorants had moved to feed at the islands as well (Figures 2.3 to 2.10). Many cormorants and murres, in fact, fed within several hundred meters of island shores, and our density estimates are accordingly biased downward because the survey vessel could not pass closer than about one kilometer to island. The only cormorants we observed, other than those from mainland nesting colonies feeding near the mainland, were flocks of Double-crested Cormorants in transit to and from Drake's Estero. Similarly, concentrations of murres also occurred around mainland nesting areas. Gulls were "concentrated" within about 15 km of the islands (Figures 2.5, 2.6). Rhinoceros Auklets and puffins were relatively numerous (for them) in slope waters adjacent to the Farallones (Figures 2.12 to 2.15).

During the 1986 nesting season, when warm-water conditions prevailed, the patterns were markedly different. Although in April, murres and Cassin's Auklets concentrated near the North Farallones, by early June murres began to feed in mainland coastal waters and auklets spread more widely along the slope (Figures 2.8 to 2.11). Some Brandt's Cormorants, and a few murres, fed 5 km northwest of Southeast Farallon in a flock that persisted for several days in early June. Otherwise, most Brandt's Cormorants undertook long flights to waters near the mainland coast. Gulls and Rhinoceros Auklets were dispersed in much lower densities all over the Gulf and the deep waters to seaward, respectively. Tufted Puffins also occurred in slope waters, but farther from the islands than in 1985.

These patterns indicate broad overlap of feeding habitat between species in 1985 compared to 1986, with some notable exceptions. Comparing coefficients of association between species by census block, 36 of a possible 45 species combinations showed significantly greater overlap in habitat use during 1985 than they did during 1986; and one combination of extensive overlap, that between the murre and guillemot, did not change (Table 2.2). The other nine species combinations, all of which involved the Sooty Shearwater, Western Gull and/or Rhinoceros Auklet, exhibited the opposite pattern: greater overlap in 1986. The shearwater and gull are known to be attracted to the feeding of other species, and supposedly some species to the gull, but analogous tendencies involving the Rhinoceros Auklet are unknown (see discussion of feeding flocks below). Lower food availability in 1986 must have been involved in some way to affect the closer overlap of these social foragers.

Our Farallon/Golden Gate transects 1972-1980, as well as observations of feeding flocks near the island, reveal the frequency by which the above two sets of conditions may have alternated during the study period. For purposes of the following review, note from Ainley and Boekelheide (ms) that 1973, 1976, 1978, 1982-83, and to a lesser extent 1980 were years of warm water and low marine production. Fish availability patterns were altered in those years as well (see Part I). Large numbers of cormorants fed near the coast (transect segments I and II, Figure 2.17) in early 1971, 1973, 1976, 1978, and to a lesser degree 1980. Cormorant flocks were especially prevalent near the islands in 1973, 1975, 1977, 1979, and to a lesser extent 1981 and 1982. Very few cormorants were observed feeding near the islands in 1983 (Figure 2.18).

Common Murres fed inshore near the coast in late 1971 to early 1972, 1973, late 1975 to 1976, 1978 and 1980 (Figure 2.19). Murre feeding flocks were prevalent near the islands 1974, 1975, 1979, and 1982. Few were seen near Southeast Farallon in 1972, 1973, 1976, 1977, 1978, and 1983 (Figure 2.20).

Gulls were especially prevalent in inshore coastal waters in 1976 and 1978 (Figure 2.21). They fed close to the islands in 1974, early 1975, 1977, 1979 through early 1981 (Figure 2.22).

B. Feeding Behavior

Depth of foraging. Storm-petrels and gulls feed at the surface by dipping, surface seizing, or shallow plunges in which they hardly submerge themselves. They are thus restricted to acquiring prey that occur at the surface. Sooty Shearwaters feed by pursuit plunging to depths up to 10 m (Brown et al. 1981; Baldridge pers. comm.). All of these species are thus capable of exploiting mobile prey and capable of searching a large area. The remaining eight species of Farallon seabirds feed by diving; cormorants propel themselves underwater using their large webbed feet, while alcids propel themselves with their wings. Diving species are more heavy-bodied than the shallow-feeding species above. Thus, only at great energetic cost (relative to the others) can diving species search large areas for food. Rather, they require food that is predictable in occurrence or feeding habitats that are habitually productive (Ainley 1977; Ainley et al. 1984; Crawford and Shelton 1978).

It is intriguing that eight species of diving seabirds can coexist in the same region. As part of our effort to investigate resource partitioning by Farallon seabirds, we compared diving capabilities by timing dives and pauses between dives and by calculating dive-to-pause ratios (Dow 1964, Stonehouse 1967,

Hobson and Sealy 1985). We were able to measure these ratios on birds feeding in the same plot at Southeast Farallon, where depths were shallow (20 m). All the species observed are probably capable of reaching depths of at least 50 m, and most can probably swim deeper (as deep as 180 m in murres; Piatt and Nettleship 1985). Were it possible, it would have been instructive to observe them all feeding in deep waters (180 m, for example). Nevertheless, while our analysis does not prove the maximum capabilities of any of the species, we believe the comparison is instructive.

The Double-crested Cormorant remained submerged the least amount of time at 25 seconds per dive, and the Pigeon Guillemot remained submerged for the greatest amount of time, at 75 seconds per dive (Figure 2.23). Both these extremes were significantly different from the other species, which in terms of amount of time submerged per dive ranged downward as follows: Tufted Puffin, Common Murre, Brandt's Cormorant, Pelagic Cormorant, Cassin's Auklet, Horned Puffin (a nonbreeding species), and Rhinoceros Auklet. Pigeon Guillemots took the most time between successive dives and Tufted Puffins the least (Figure 2.23).

Our measurements of diving times for some species agreed but for others disagreed with those reported in the literature. Among cormorants our values for the Pelagic (mean 45 sec, maximum 70 sec, n=96) exceeded most values summarized by Cooper (1986) and were almost double those derived by Scott (1973); for Brandt's Cormorant (mean 51 sec, max 95 sec, n=39) our values also exceeded Scott's by a wide margin; and for the Double-crested (mean 25 sec, max 35, n=12) our values were similar to those reviewed in Cooper (1986). If diving times are indeed an effective relative indication of diving depths, then Brandt's and Pelagic cormorants are among the deepest divers in the 29 cormorant species addressed by Cooper (1986). Little direct information is available on the actual diving depths of cormorants.

Among auks, information for Atlantic species is reviewed by Bradstreet and Brown (1985); additional information for Pacific alcids is contained in Scott (1973) and Cody (1973). The mean and maximum values determined by us for the murre exceeded Cody's values, but were exceeded in Scott's study (mean 55 versus their 41 and 71 sec; maximum 70 versus their 71 and 140 sec). The mean and maximum values determined for Pigeon Guillemot exceeded both Cody's and Scott's (75 versus their 41 and 36 sec; maximum 110 versus their 68 and 69 sec), although they were similar to the values determined by Bradstreet (1982b) for the Black Guillemot (mean 60, maximum 46 sec). Our values for Cassin's Auklet exceeded that calculated by Cody (mean 43 versus his 10 sec; maximum 70 versus his 24 sec), as did our value for Tufted Puffin (mean 58 versus his 37 sec; maximum 80 versus his 60 sec). No comparison is available for Horned Puffin.

Bradstreet and Brown (1985) concluded that based on dive times, murres and guillemots could dive much deeper than other Atlantic alcids. Their conclusions for the murre were supported by known diving depths (Piatt and Nettleship 1985). The latter authors recorded depths of 50 m for guillemots, but Bradstreet and Brown concluded they could dive in excess of 100 m based on circumstanial evidence (see also Follett and Ainley 1976). In the Pacific, it appears that Tufted Puffin could be added to the deep-diver category, along with Brandt's and Pelagic cormorant. Cooper (1986) and others have stated that diving depth is a function of body size, which may be true within bird families but certainly is not evident comparing alcids and cormorants. The apparently shallow dives of the large-bodied Double-crested Cormorant, as well as the deep dives of the small-bodied Pelagic Cormorant, appear to be rather enigmatic.

In regard to dive time/pause time ratios (D/P), Dewar (1924) and Stonehouse (1967) concluded that the species with higher values are capable of diving deeper, or at least more efficiently, than those with smaller values. A comparison of the D/P ratios we calculated indicates that Tufted Puffins clearly outperformed the other species (Figure 2.24). This means that per unit measure of time submerged, they required the least amount of time for recovery. Among the various species considered here, the D/P values we measured in most cases are similar to those measured by other authors for similar groups (Dewar 1924, Cooper 1986), although those for Pelagic Cormorant were a third again higher than measurements in other studies (e.g., Hobson and Sealy 1985).

The D/P ratio is to some degree a function of water depth (Scott 1973), which in our case was the same for all species. For cormorants, Cooper (1986) noted a direct relationship between D/P ratios and body mass. Might it also be possible that the diving capabilities of a seabird are related to the type of prey it is designed to catch, as well as to water depth? The three Farallon species with highest D/P ratios are those that feed almost exclusively on mid-water, schooling prey (as we shall see later) and the remainder feed a great deal, and in some cases exclusively, on benthic prey. This is logical. A seabird that feeds on mobile prey should spend little time resting on the surface once it locates a school. Otherwise the prey may move away while the bird is recuperating, and this would increase energetic costs by requiring it to relocate the school. On the other hand, seabirds that feed on prey that hide near, on, or in the substrate can afford to rest at the surface, because their quarry is not likely to move off. In the case of the Pelagic Cormorant and Pigeon Guillemot, both being benthic foragers with long dive times and long rest times, it would seem beneficial to maximize time spent under water in order to investigate the nooks and crannies where their prey hide.

Dive times and D/F ratios could also be a function of age, as pointed out by Bradstreet and Brown (1985). Confirming this, diving times and D/F ratios averaged 75 ± 16 sec (n=156) and 2.5 ± 0.8 (n=57) for adult Pigeon Guillemots, compared to 62 ± 14 sec (n=120) and 2.0 ± 0.6 (n=36) for recently fledged juveniles. The Double-crested Cormorants in our sample were also recently fledged and, thus, our values for that species although consistent with other studies (ages not specified) could be an under estimate as well.

To summarize information on diving capabilities, then, we seem to have three groups of species. The deep divers, capable of exceeding 100 m depth, are comprised of Brandt's and Pelagic cormorant, Common Murre, Pigeon Guillemot and Tufted Puffin; intermediate-depth divers, which probably dive 20 to 80 m, are Double-crested Cormorant, Cassin's Auklet, and Rhinoceros Auklet (as well as Horned Puffin); and the only shallow diver is the Sooty Shearwater (to 10 m). The remaining Farallon species feed at the surface.

Tendency to feed socially. Seabirds differed in their tendency to feed socially. The most solitary feeders among Farallon species were the Pelagic Cormorant and the Pigeon Guillemot, which in the period April through August 1979-1983 were seen in only 4 and 41 flocks, respectively (<5% of all flocks; n=738), and some of the guillemot flocks could have been social gatherings (Storer 1952). Both species exhibited a greater frequency of association with multispecies flocks during years of superabundant prey. Otherwise, they fed alone at submerged reefs and hunted for the solitary prey that hide in the rocks (Ainley et al. 1981, Follett and Ainley 1976). Even when in flocks, relatively few individuals were usually involved (Figure 2.25). The Rhinoceros Auklet and Tufted Puffin also tended to feed alone or occasionally in small flocks (unpubl. observations 1985 and 1986; Briggs et al. ms; Sealy 1973, Hoffman et al. 1981, Grover and Olla 1983). Double-crested Cormorants are highly social in their feeding (Bartholomew 1942; Ainley pers. obs.), but as indicated above, they do not feed near the island. The Cassin's Auklet feeds in dense flocks, but not usually in asociation with other species except the Sooty Shearwater (unpubl. observations 1985 and 1986; Briggs et al. ms), and rarely in sight of the island. Farallon species that we most often observed feeding in flocks were the Brandt's Cormorant, Western Gull, and Common Murre, along with the abundant nonbreeding visitor, the Sooty Shearwater (Table 2.3).

Among the latter four species, the cormorant and gull were observed in 63 and 51%, respectively, of the 738 flocks observed April to August 1979-1983. Numbers of cormorants in flocks tended to be much greater than gulls (Figure 2.25). Both were

most often observed feeding in unispecies flocks (i.e. three or more birds together), and their tendency to feed in flocks containing only their own species increased during years of warm oceanic conditions when food was presumably less available. This is consistent with results from diet analyses (presented later), and is also consistent with a lessened tendency to feed in association with other species (Table 2.3). According to several studies on the benefits of feeding in multispecies flocks, or any flocks for that matter, feeding socially should increase an individual bird's chances of finding food (e.g. Sealy 1973, Hoffman et al. 1981, Porter and Sealy 1982, Brown 1986). On the other hand, our observations seem to indicate that abundant food brings individuals of different species together, while conditions of sparse feeding opportunities drive species apart. This is perhaps consistent with the ideas of Hoffman et al. (1981), who observed that when feeding socially, seabird species play different roles: catalysts (gulls, some alcids), divers (shearwaters, cormorants, alcids), kleptoparasites (gulls), and suppressors (shearwaters, cormorants). When food is abundant, species in their various roles accrue benefits from multi-species flocks, but when it is not, the benefits are few. For instance, the patterns we observed, warm-water years versus others (Table 2.3), could be explained largely by some species' avoidance of others that dominate feeding situations by their feeding behavior or success (suppressors). Also, although during warm-water years we observed plenty of gull (catalyst) flocks, other species seemed to "know" that their existence did not necessarily indicate the presence of appropriate food.

Murres and shearwaters were observed in 15 and 5%, respectively, of the flocks we observed. Like cormorants, numbers of murres in flocks tended to be large; shearwaters were quite variable in the numbers participating in flocks (Figure 2.25).

Most feeding flocks we observed (principally gulls and cormorants) in the vicinity of the Farallones occurred in the downstream direction, that is, to the southwest, south, and southeast. The frequency with which feeding flocks occurred was a function of year. Fewest flocks were observed near the island during warm-water years 1973, 1976, 1978, 1983, and, to a lesser extent 1980. This pattern was apparent when we looked at the occurrence of feeding flocks by month as well as by year. For instance, Brandt's Cormorants tended to feed in flocks near the island only early in the 1981 and 1982 breeding seasons (Figure 2.18); in 1977, more flocks occurred late in the season than early; and in 1980, flocks were equally abundant early and late. These changing patterns of feeding, as we shall see, have important effects on feeding effort and breeding success.

As for murres, we saw them in far fewer flocks than cormorants or gulls, but, except for warm-water years, their flocks occurred near the island most consistently during June and July, the chick rearing period (Figure 2.20). We rarely saw murre flocks nearby during April and May, when they tended to feed north of the island (Figure 2.7). Compared tc cormorants, Western Gulls appeared to be less erratic in the frequency with which they fed in flocks near the island (Figure 2.22). Notwithstanding the warm-water years, only during 1981 was a particularly marked difference in the number of gull flocks observed early compared to late in the nesting season.

Foraging effort. We measured foraging effort for Pelagic Cormorants, Brandt's Cormorants and murres by determining the amount of time they spent away from their nest, or the number of trips they made per day between sea and nest site. Our measure of effort included the time required to capture prey as well as that required to fly to and from the feeding area. As an index to "foraging difficulty", our measure is imperfect for a number of reasons. First, a bird could spend as much time gathering prey from an abundant source far away, as from a situation where prey are every where scarce. Second, for cormorants, where we measured the time between nest reliefs, the interval also included the brooding tendencies of the incubating bird---though a mate has returned from feeding at sea, the incubating bird can "elect" to remain on the nest. Thus, in years when food was abundantly available and parents were not hungry, we might still observe as long an interval between nest reliefs as during years when foraging individuals were absent for a long time. Finally, we had to assume that any trip away from the nest site (except for those obviously for bringing back nest material) was for purposes of feeding. This was mostly true, but cormorants also take a swim each day in order to bathe; and murres probably do so as well.

Not surprisingly, the Brandt's Cormorant nest relief interval during incubation (289 $\pm$ 125 min, or about 4.8 hours; n = 1200) was longer than during the nestling period (204 $\pm$ 101 min, or about 3.4 hours; n =1871, t = 20.8, p <.001). Certainly the difference was due to the fact that parents were not pressed to feed chicks during the incubation period, but it may also have been due to seasonal shifts in the location of available prey. As indicated previously, during April and May, large numbers of Brandt's Cormorants feed by the Golden Gate; in fact, many at that time feed within San Francisco Bay itself. Nest relief intervals were usually longest during the early season regardless of whether birds were tending eggs or chicks (Figure 2.26). Feeding that far away, i.e., on the order of 50 to 80 km, early in the breeding season occurred during at least five of the 10 years when we censused birds along the Golden Gate/Farallon transect---1971, 1972, 1973, 1976 and 1978 (Figure 2.17). If

during other years, they were feeding away from our transect line, then we would not have known. This probably was the case in most of the other years, because cormorant feeding flocks were not observed close to the island early in the nesting season, except during 1981 and 1982 (Figure 2.18). We can begin to see, then, that nest relief interval does, in fact, indicate "foraging effort" to some degree.

A comparison of mean nest relief intervals during the incubation phase of nesting (Table 2.4) revealed that intervals were shortest during 1981 and 1982. The longest nest relief intervals during incubation occurred in 1974, 1975, and all the warm-water years (no nesting in 1983): 1976, 1978, 1980 and 1973. What was happening in 1974 and 1975 is not known; Brandt's Cormorants fed neither near the Golden Gate nor to the south or east of the island during the early part of those years (Figures 2.19, 2.20).

During the nestling period, Brandt's Cormorants took longer to return from feeding during all warm-water years except 1978; 1974 and 1975 were again enigmatic in this regard (Table 2.4). The position of 1978 relative to other years could be an artifact of the small sample size and the possibility that the few adults feeding chicks during this especially poor year were atypical, i.e. older, more experienced individuals. The nest relief interval of birds feeding chicks lengthened dramatically late in 1981 (Figure 2.26) which is consistent with the disappearance of cormorant feeding flocks near the island at that time (Figure 2.18). Nest relief intervals during incubation were correlated with those during the chick phase. That is, years with long intervals early tended to have long intervals late (Spearman $r=.6606, t=2.49$, $DF=8$, $p<.05$). Exceptional was 1978 and also 1982 (Table 2.4).

During the nestling period, a close correlation existed between the number of Brandt's feeding trips per day and the nest relief interval (Spearman $r=.9030$, $t=5.94$, $DF=8$, $p<.05$); Table 2.4). Two years, 1977 and 1979, were clearly outstanding in the high frequency of feeding trips during the chick period. These years were also outstanding in the large number of cormorant feeding flocks observed close to the island late in the nesting season (Figure 2.18).

Pelagic Cormorant patterns were similar to those of Brandt's Cormorants. During the egg stage, foraging time was shortest in 1975; during the nestling stage, foraging time was shortest in 1975 and 1977 (Table 2.5). The longer trips early in the 1977 season coincide with the late start to nesting that year (Ainley and Boekelheide ms 6). Longest trip time occurred during the two ENSO/warm-water years, 1973 and 1976, as well as 1974. Pelagic Cormorants made the most frequent feeding trips during 1974, 1975, and 1977, and the fewest during 1973 (and 1976; Table 2.5).

The patterns for murres were similar to those for cormorants, although we did not have data for as many years. The amount of time between arrivals of parents with fish was markedly greater during the two warm-water years, 1976 and 1983 (Table 2.6). Corresponding to the relatively longer feeding absences, fewer fish were brought each day to chicks during those years. Except for 1977, when the second fastest return rate occurred, the ranking of years by the length of time between feeds is consistent with the frequency of feeding flocks containing murres within three kilometers of the island. A comparison of Figure 2.20 and Table 2.6, for example, indicates few murre feeding flocks nearby during June 1976 and 1983, when absences were long, but many flocks nearby in June 1974, 1975 and 1982, when absences were short. In 1977, though few murres were feeding within 3 km, many were doing so within segment IV of our transect corridor or within 15 km of the colony (Figure 2.19). The latter distance is still relatively close.

We have little data with which to compare relative feeding effort among years for other species. Results of the Golden Gate/Farallon censuses indicate that Western Gulls fed close to the Marin coast during the early parts of the warm-water years, 1976 and 1978, and to a lesser extent during early 1974 (Figure 2.21). Late in the nesting season during the cooler-water years of 1977 and 1979, they apparently fed near the island (also evident in Figure 2.22). These patterns are consistent with those of the cormorants and murre. Thus, we would expect a longer duration of feeding trips during the warm-water years.

Temporal patterns of foraging. A mass of circumstantial and direct evidence indicates that most Farallon seabirds are probably diurnal foragers, although feeding activity is greatest during or near to twilight and is least between about 10:00 and 15:00 hours. This evidence includes 1) all-day watches of cormorants, gulls, murres, and puffins [data presented above; Pierotti 1976; Ainley and Boekelheide (ms)]; 2) observations of gulls and cormorants at night using a night-vision scope (Pierotti 1976); 3) direct observations of Rhinoceros Auklet arrivals (Sander ms); 4) electronic monitoring of Ashy Storm-Petrel and Cassin's Auklet arrivals (Ainley and Boekelheide ms); 5) collections of murres and auklets (see Diet below; unpubl. data); and 6) observations to determine temporal patterns of territory occupancy (Ainley and Boekelheide ms).

Only the storm-petrels, which depart their nests and the island in the early morning hours (01:00-03:00; Ainley and Boekelheide ms 4), likely forage extensively at night, and probably in the predawn hours. In the data derived from collections of several storm-petrel species at sea, but not off California, night foraging is clearly indicated (PRBO unpubl.).

Cormorants and gulls definitely roost on the island during the night (Ainley and Boekelheide ms), but members of pairs not incubating eggs or tending small chicks depart at the first twilight of dawn and/or arrive back just at dark. The cormorant diet contains several species that are active in the water column at night and are looking for hiding places in the substrate during the morning twilight (Ainley et al. 1981; Fitch pers. comm.). Murres and guillemots also roost on the island at night, and peak feeding rate of chicks occurs from morning twilight to about 10:00 (Ainley and Boekelheide ms), as well as in the late afternoon and evening. Cassin's Auklets feed at the same time in the morning as these other two alcids, judging from collections of birds at sea (1985-86 data); they spend the night ashore and arrive and depart the island just after dark and just before dawn, respectively (Ainley and Boekelheide ms). Tufted Puffins remain in their burrow at night (Ainley and Boekelheide ms), and usually bring fish to their chicks in the early morning (ca. 08:00-09:00) and just before dark. Finally, Rhinoceros Auklets, which also spend the night on the island, arrive with fresh fish within the twilight hour just after sunset (Sander ms).

## C. Diets of Farallon Seabirds during the Breeding Season

We know little about the diet of the storm-petrels that nest on the Farallones. Presumably, they feed on zooplankton and micronekton that occur near the surface in waters seaward of the continental shelf. Similarly, we know little about the diet of the Farallon Rhinoceros Auklet, except that elsewhere it feeds heavily on zooplankton and feeds fish to the young (Ainley and Sanger 1979; Vermeer 1978, 1980). Collections of items brought to chicks in 1986, indicated a diet that year dominated by three fish species, juvenile rockfish, Pacific saury Cololabis saira, and juvenile black cod Anoplopoma fimbria (Sander ms). Except for Tufted Puffin (see below), no other Farallon seabird, to our knowledge, feeds substantially on the latter two species, both of which occur in waters seaward of the continental shelf. The Rhino diet is thus consistent with the observed pattern in foraging area and habitat.

For the remaining Farallon species, we have amassed a considerable amount of information on the within-season and between-year variability of the diet fed to chicks. In the case of murres and puffins, adult diets, which we did not sample, may differ from those of the chicks (Bradstreet and Brown 1985), but in the case of other species the chick and adult diets are probably similar. Previous work on the trophic relationships of seabirds in the Gulf of the Farallones is restricted to five studies: Ainley et al. (1981) for cormorants; Pierotti (1981) for Western Gulls; Follett and Ainley (1976) for Pigeon Guillemots; and Thoresen (1964) and Manuwal (1974b) for Cassin's Auklets. The information from all these publications will be incorporated into the data discussed below. In the following discussions, we are concerned largely with the period from about late May through August, the nestling period, for each species. We will first consider diets in what Diamond (1983) termed a "level three" analysis, that is, determining diet overlap among years for each species, as well as between species X years, on the basis of numerical composition only. In level three analysis, Diamond used prey categories based on taxonomic families, whereas we use the lowest taxa possible. Many food items in our study could be identified to species, though some could be identified only to family. We also look at dietary overlaps after combining numerical composition with data on prey weight (a function of size). Such a procedure was considered to be a "level one" (size plus lowest possible taxon) or "level two" analysis (size at family level). Our number X size procedure is thus a combination of these two levels. Consistent with Diamond's analysis, we considered an overlap index greater than or equal to .8 (80%) to indicate diet similarity.

### Cormorants

The diet of the Double-crested Cormorant was investigated during four summers, 1974-1977. There was virtually total overlap in the diet composition compared among the four years in a level

three analysis (Table 2.6). This is not surprising given the great stability of estuarine habitat where these birds feed, compared to the upwelling-influenced waters offshore where greater dietary variability might be expected. The major prey was surfperch, particularly the shiner surfperch C. aggregata (Table 2.6). The majority of other prey species consumed are, like the surfperch, typical of quiet, shallow, inshore waters. Most are schooling species that occur above bottoms of flat relief (sand). Prey diversity in the diet was greater during 1976, a warm-water year, than during the other three years. Given the lack of a significant difference in the size of the surfperch eaten among the four years sampled (Table 2.7), an analysis of diet overlap which included prey size did not alter results.

The diet of the Pelagic Cormorant was investigated during three summers, 1975-1977. Diets were virtually identical between 1975 and 1977 but were completely different in 1976 (Table 2.5). Prey were characteristic of submerged, rocky reefs and, in particular, were dominated by organisms that hide in the substrate. Predominating were several species of sculpin (cottids), juvenile rockfish, mostly S. flavidus and S. jordani, and a mysid shrimp, Spirontocaris sp. (Table 2.6). Few of the prey could be considered schooling species. Because most of the prey items fell within the 5-10 cm range in length, otoliths were too tiny to distinguish species within the rockfish or sculpin families. Certainly, the species of scorpaenids and cottids listed by Follett and Ainley (1976) for guillemots included the major species eaten by this cormorant. As with the Double-crested Cormorant, diet diversity based on numerical composition (but not weight) differed, but was lower, in the warm-water year of 1976. That year, there were also fewer items per sample. The lack of any between-year differences in size of prey (Table 2.7) resulted in no change of relative dietary overlaps among years.

The diet of the Brandt's Cormorant was investigated during five summers, 1973-1977. In a comparison of diet overlap among all five summers (excluding the early spring collection from the 1977 sample; see below), diets proved to be largely similar except in 1976 (Table 2.5). The principal prey were rockfish, mainly S. flavidus and S. jordani (Table 2.6). Other important prey were flatfishes (bothids and pleuronectids), tomcod M. proximus, midshipmen P. notatus, and cuskeels O. taylori. On a weight basis, the importance of flatfishes increased dramatically. This assemblage of fishes, except for the juvenile rockfish, is typical of waters near or on the bottom over flat relief (mud, sand). The rockfish and tomcod are schooling species, but the others are not. Diet diversity was exceedingly low during most years as a result of the preponderance of juvenile rockfish; on the other hand, diversity was exceedingly high during 1976 (Table 2.6). The number of prey per sample was

low during 1976 as well. Considering the larger rockfish and sculpins eaten by Brandt's Cormorants during 1976 (probably year 1 instead of year 0 fish; Table 2.7), diet overlap was even lower between that and the other years than Table 2.5 indicates.

During 1977, we were able to collect some Brandt's Cormorant samples just before egg laying for comparison with diet during the chick period (Table 2.8). The early diet was far more diverse than that eaten later, and there was little overlap in species composition. The menu of species was similar to that of 1976, but the contibutions of anchovy, flatfishes, surfperch and cuskeels were quite different.

For each of the three cormorant species, we combined data for those years that proved to have similar diets: all years were the same for the Double-crested; 1976 differed from 1975-plus-1977 for the Pelagic; and 1976 differed from all other years for the Brandt's (Table 2.4-2.6). Judging on the basis of diversity indices, the diet of Brandt's Cormorant was much more complex than that of the other two species. There was little overlap of the Double-crested's diet with the other two species (Table 2.9), except in 1976, when overlap with the Brandt's Cormorant diet was slightly greater. This was likely due to Brandt's Cormorants feeding more inshore (even within estuaries?) that year as discussed in a previous section. In contrast, a remarkable degree of overlap occurred between the diets of Pelagic and Brandt's cormorants during years excluding 1976. This overlap was due largely to the preponderance of juvenile rockfish in both cormorants' diet during those years. Based on weight, the between-year similarity of the Pelagic Cormorant diet increased slightly. Otherwise, overlap indices based on weight were generally lower than numerical overlaps, a tendency also observed by Diamond (1983).

Western Gull

Given the different techniques used to assess the Western Gull diet, it is first necessary to evaluate each method with respect to the others. The various methods have been employed in numerous studies of the diet of gulls, but a comparison of results between methods has not been performed before.

<u>Pellet and feces examination</u>. The two techniques sampled the population of gulls that roosted on the catchment basin during three years, and thus provide a good opportunity for comparison (Table 2.10). Percentage of fish in respective samples were similar, even for 1977 (t-test after arcsin transformation, $p<.5$). Looking only at the marine invertebrates total, the species breakdown reveals different prey compositions: euphausiids did not occur in pellets but did in feces, and barnacles clearly predominated in the pellets (Table 2.11).

Terrestrial invertebrates, primarily tenebrionid beetles, were equally represented in both samples. Bird remains occurred in up to 7% of pellets but not in feces. Garbage was also present in pellets but not feces. These differences were thus likely due to digestive processes. A large percentage of fecal remains was unidentifiable, and these were likely comprised mostly of garbage and bird components. The overall composition of pellets did not change even with a reduced sample and sampling period. This suggests only slight within-season variability in the diet of the gulls that frequent these roosts, a large portion of which are nonbreeders (Spear ms).

Collected versus observed chick regurgitations. These two techniques sampled the prey fed to chicks. Percentage of fish was consistently higher in collections, except during 1983 when the percentages of fish were equal (Table 2.12). These differences may be due to (1) the smaller sample size of collected regurgitations; (2) difficulty in identifying fish at a distance, which was perhaps reflected in the unidentified category; or (3) within-season variability. Collected regurgitations were accumulated during a short period when most chicks were 10 to 20 days old, the age at which maximum food demand begins (Coulter 1973). It may be that improved diet quality (i.e. more fish) is required to meet this demand. In reality, however, the different trends were more likely due to biases in the methods. We could not compare invertebrate's (marine or non-marine) due to different recording methods used for observations in 1978-1982. In 1983, few regurgitations were found (n=5), in spite of increased efforts. Food was not easily available that year, and comparisons using 1983 data are unfortunately difficult. Birds as prey did not appear in collections. This may be due to (1) the relative unimportance of birds in chick diets (1-3%); (2) lower quality items not being present during the chick-banding period, as mentioned above; or (3) high visibility of regurgitations containing birds, which would increase their likelihood of being sighted.

During years with adequate samples (1978, 1979, 1981 and 1982), percentage of garbage was comparable. In the two years with the lowest reproductive success---1978 and 1983 (warm-water years; Ainley and Boekelheide ms 7)---garbage was more prevalent in collected than in observed regurgitations. This difference arose from differences in sampling period; for 1983, only during the chick-banding period, a negligible difference existed in prevalence of garbage (28% in observed versus 24% in collected regurgitations). Thus, sample size, unidentified items, and time of season may all have affected differences in diet estimation using these two techniques.

Pellets and regurgitations. The populations of gulls sampled by pellets and regurgitations may have been exploiting different

resources. Percentage of fish was much higher in regurgitations than in pellets, except in 1976 when percentages were equal (Table 2.13). In 1975 and 1978, the difference increased between pellets and regurgitations sampled at the same time. Pellets then showed an even lower percentage of fish.

Barnacles were not detected in regurgitations, either collected or observed, again suggesting that pellets sampled a different subpopulation of gulls. Euphausiids and squid were also lacking in the pellet samples, but as they are present in the feces, this difference was probably due to the methods employed. The difference in the garbage component between the two methods was greatest during 1975 and 1979. Reproductive success during those years was especially high (Ainley and Boekelheide ms), and not surprisingly a low percentage of garbage occurred in the diet. It is therefore interesting that garbage remained a constant, important feature in the diet of individuals who roosted on the catchment basin, but this is consistent with Spear's (unpubl.) findings that these birds tend to feed more at coastal sites. Similarity in percentage of garbage for all methods in 1976 and 1978 indicates that breeding adults fed more on garbage when fish availability was reduced, and hence exploited the same resource as the roosting, nonbreeding gulls during those years.

Feces and regurgitations. Feces and pellet collections probably sampled the diet of nonbreeders, and thus results should be similar. Indeed they were, with the differences noted above. The presence of euphausiids was quite comparable for the two methods, especially when sampling from the same periods (Table 2.14).

The major fish eaten by gulls were *Sebastes* spp. 39%, *C. taylori* 21%, *Merluccius productus* 12%, and *Porichthys notatus* 11% (Table 2.15). The importance of rockfish is also evident in chick regurgitations where *Sebastes* comprised 47% of fish eaten (Table 2.16). No other fish approached this level of importance. Juvenile rockfish were much smaller than the other fishes prominent in the Western Gull diet, but even on a percent weight basis they remained the major fish prey (Table 2.16); samples containing *Sebastes* had more individual fish than samples without. Hake *M. productus* can be considered "offal" and as such represents garbage foraging, but at sea rather than at land dumps. This fish is frequently discarded by boats fishing for salmon, and up to 1978 a large commercial trawl fishery for hake occurred in waters near the islands.

Overall, fish accounted for 60-80% of the total diet of gull chicks. Marine invertebrates contributed 5-7% of the total mass, although they occurred in 10% of samples. Garbage was certainly supplemental in the diet and it is clear that the Farallon gull breeding population primarily exploits the marine environment.

Although gulls are often considered to be scavengers, this is not the case for the Farallon Western Gull (see also Hunt and Hunt 1975). Breeding individuals apparently feed in surface waters on live marine organisms. This was dramatically evident in 1983, a severe warm-water year when chick production reached an all-time low. If the Farallon population had been able to switch effectively to feeding on garbage, chick production should have been little affected (see Ainley and Boekelheide ms).

Given the variety of methods employed to sample the gull diet, we did not consider it valid to calculate diet diversity or overlaps with other species. Relative to the other seabirds, however, some points are worth noting. First, many of the fish species eaten by gulls generally occur in deeper waters than gulls should be able to exploit. The close association of gulls with cormorants, as discussed in a previous section (Table 2.4), may account for the existence of these species in the gull diet. Either the gulls sometimes parasitize cormorants, or they are scavenging fish that cormorants regurgitate in order to take off (sometimes cormorants eat too much), or the cormorant (or other predators) are driving some of these fishes to the surface. Another source of these fish for gulls would be from trawler spoils and certainly this is so for hake. Second, gull diets appeared to be more diverse during warm-water years, including the increase in use of garbage. During these years---1976, 1978, and 1983---the preponderance of fish was lower as well (Table 2.12, 2.13). Because gulls appear to associate closely with Brandt's Cormorants when feeding (Table 2.4), the high preponderance of juvenile rockfish in the gull diet is not surprising. In all regards, considering terrestrial, intertidal or ocean habitat, gulls can be considered surface feeders.

Alcids

The diet fed to Common Murre chicks was studied during 11 years, 1973-1983 (Tables 2.16, 2.17). Principal prey were juvenile rockfish, anchovies, smelt, and market squid. These are all schooling mid-water species of the shelf and slope. During years when rockfish (S. flavidus and S. jordani) comprised relatively little of the diet, i.e., the warm-water years 1973, 1976, 1978 and 1983, they were replaced by anchovies and diet diversity was high. These years of diverse diet and the high anchovy component were also years when murres fed inshore the most (Figures 2.7, 2.8, 2.19, 2.20). The greater rockfish anomaly in the diet during warm-water years, compared to the anchovy anomaly (Figure 2.27), suggests that anchovies and other species may have been "replacement" prey. A comparison of the diet among all 11 years indicates that 1) diet during 1976 overlapped little with other years, but most with another warm-water year, 1978; 2) diets during the warm-water years, 1973,

1978 and 1983, were similar; and 3) diets in the remaining years were similar largely due to domination by rockfish (Table 2.17). During the atypical warm-water year of 1976 (Ainley and Boekelheide ms), squid and smelt replaced rockfish much more than in the other warm-water years when anchovy was the principal prey.

Murres at larger sanddabs eaten in 1977, and the length of anchovies eaten increased gradually during the study period (Table 2.19). The large size of anchovies relative to rockfish, increased the importance of anchovies slightly considering diet on a weight basis (Table 2.18).

We were able to look at seasonal shifts in the murre diet (Figure 2.28). All years combined, diet diversity increased from .581 during the first 10 days of the nestling period to 1.068 in the seventh and last 10-day period (Spearman $r=.786$, $p<.05$). This trend, however, was largely a function of warm-water years when murre nesting was late. In those years, parents were feeding chicks on the ledges from about 20 June into the first week of August (Ainley and Boekelheide ms), and during that period the contribution of rockfish decreased from about 20% at the start to 13% near the end while the contribution of anchovies changed from 40% to 70%. The prevalence of other species increased as well. In other years, when nestlings were being fed from 10 June to about 19 July, the contributions of rockfish and anchovies remained relatively stable at about 85% and 7%, respectively. The shift to anchovies and smelt late in the chick period is consistent with the inshore movement of murres during that time as discussed previously. In that many parents with chicks eventually move inshore even in years other than warm ones, Figure 2.28 probably illustrates fairly well the gneral trends in the seasonal shift of the murre diet.

The diet fed to Pigeon Guillemot chicks was investigated for 11 years, 1972-1982. We would have collected observations during 1983, but the species failed to breed that year (Ainley and Boekelheide ms). Primary prey were the same as for the Pelagic Cormorant, i.e., juvenile rockfish and cottids, but guillemots ate more octopus and fewer mysids. When the contribution of rockfish was low during a given year, cottids and other species were more prevalent (Figure 2.29), and diet diversity was much higher (Table 2.18). Curiously, rockfish were also less prevalent in the guillemot diet during years preceding ENSOs. This indicates that rockfish may have been generally less available during these years, and consequently, with their much less variable foraging range, guillemots had a harder time finding them than, for example, murres. A comparison of diet among the 11 years (Table 2.20) produced groupings of years approximately similar to the murre (Table 2.18), but with 1978 being the most unusual. When groupings of years were compared to

those of the murre and the cormorants, little overlap occurred during the warm-water years, but much overlap occurred when rockfish were prevalent in the diet of all seabirds (except Double-crested Cormorant; Table 2.9). During "rockfish years," the diet of the guillemot and Pelagic Cormorant were virtually identical, which is interesting, considering that the two species were both restricted to feeding in the same habitat close to the island. Even on the basis of prey size (weight), overlap was almost complete. During 1978, poor prey availability in the rocky habitat apparently forced the guillemot to feed more on sandy bottoms, probably near to rocky relief (note high incidence of sanddabs that year; Table 2.18). Interestingly, few guillemots attempted to breed during 1978 (Ainley and Boekelheide ms). During the warm-water years, what little diet overlap was evident based on species composition was reduced 50% more on the basis of prey size.

Like the murre, guillemots diversified their diet toward the end of the chick period when rockfish decreased and other species increased in importance (Figure 2.30). Diet diversity changed from .500 early in the nestling period to 1.619 at the end (8 ten-day periods; Spearman $r=.988$, $p<.05$). Unlike the murre, the decrease in importance of rockfish (and increase of other species) occurred in all years. In warm ones, the contribution of rockfish to the diet changed from 50 to 9% and in others it changed from 80 to 50% during the course of the nestling period.

We investigated the diet of Cassin's Auklet during four years, 1977 and 1979-81 (Table 2.21). A lack of data during the warm-water year of 1978 was partly the result of having few breeding auklets available to sample (Ainley and Boekelheide ms 10). Auklet prey are all schooling, mid-water organisms of the outer shelf and slope. Unlike all other Farallon species, auklets fed principally on zooplankton, principally euphausiids of two species, Thysanoessa spinifera and Euphausia pacifica. The principal larval fish in the diet was Sebastes, and its contribution on a weight basis was much higher than by numerical composition. Our results were similar to those of Manuwal (1974b), who studied the diet during 1971, but because most of his data were from late in the nestling period they are not really comparable. The diet shown in Table 2.21 is similar to the diet during April; adult diet is the same diet as that of chicks (unpubl. data 1985-86). We also know that adult murres and puffins, and to some extent Western Gulls, have a diet similar to that of the auklet during March and April (1985-86 data). At that time the cliffs turn reddish from the murres' guano, another indication that they are eating reddish crustaceans.

Among the few years sampled, we detected little year-to-year variability in the auklet diet. Within our sample of years, 1980

was actually somewhat different from the others for auklets because E. pacifica instead of T. spinifera dominated the euphausiids, and amphipods became much more important. During another warm-water year, 1986, this same shift in diet occurred (unpubl. data). As with the two other alcids discussed above, auklet diet diversified toward the end of the chick period, a trend also evident in Manuwal's (1974b) data. The diversity index increased from .551 early in the nestling period to 1.259 at the end (nine periods; Spearman $r=.768$, $p<.05$). The pattern occurred in all years; the late season diet is similar to that of the warmer years.

We were able to collect information on the diet fed to Tufted Puffin chicks during 10 summers, 1973 to 1982. As with the guillemot, we would have gathered data during 1983 had the species bred (Ainley and Boekelheide ms). Unfortunately, we could identify fewer than 50% of the prey, because many times puffins entered burrows too quickly or did so under poor light conditions (see Methods). Because so many prey were not identified we calculated neither diet diversity nor an index of overlap. Among the prey identified, anchovies, rockfish, and squid predominated (Table 2.22). Squid apparently replaced fish during the warm-water years, 1976, 1978 and 1982. The contribution of rockfish was greatest during years when they were especially abundant in the diet of other species, i.e., 1975, 1977, 1979, 1980 and 1981. On a weight basis, however, rockfish were important only in 1979 and 1981. Diet diversified as the nestling period progressed, the diversity index changing from .423 early to 1.153 late (five 10-day periods; Spearman $r=.800$, $p<.05$). This change was largely a function of anchovies decreasing, squid and unidentified fish increasing, and the prevalence of rockfish staying about the same (Figure 2.31). This was just the opposite of the other seabirds. We suspect many of the unidentified fish were Pacific saury, a species of slope and pelagic waters. The puffin pattern with regard to anchovies is intriguing in that it is so different from the murre. Anchovies apparently move inshore during the late season (Ainley and Boekelheide ms; Part I), followed there by murres, and by remaining offshore, the puffin no longer has access to them. The fact that rockfish do not decrease in importance in the puffin diet as the summer progresses can perhaps be accounted for by the deep diving abilities of this seabird. As the juvenile rockfish grow and settle deeper in the water column (Lenarz 1980), the puffin is still able to feed on them. Unlike the pattern exhibited in the anchovies eaten by murres, the generally larger anchovies eaten by puffins did not increase as the study progressed (Table 2.19).

No data are available on the diet of Sooty Shearwaters in the Gulf of the Farallones, but anchovies, squid, euphausiids, and especially juvenile rockfish, are important in their diet in the

southern portion of central California waters during early summer (Chu 1984). On fortuitous occasions in the Gulf, we have observed them feeding in large numbers on these prey, with individuals regurgitating their catch prior to taking wing. According to Chu (1984), Sooty Shearwaters switch from rockfish to anchovies in August. Thus, their diet and the seasonal changes therein appear to be similar to those of several breeding seabird species in the Gulf of the Farallones. Chu felt that the switch to anchovies was a behavior to take advantage of a more energy-rich food source just before the shearwaters' long trans-equatorial migration. The information presented here and in Part I, however, indicate that breeding seabirds switch because rockfish become unavailable when they settle closer to the bottom. Thus, it would appear that Chu's idea requires more data on relative prey availability at the time of the switch to determine whether or not energetic considerations are a part of the story.

D. Prey Size

We used data on fish and squid size in the above analyses to investigate diet composition by weight. We did not make interspecific comparisons, however, to investigate whether trophic segregation by prey size was an important factor in this community. We were able to compare the sizes of six fish species common to the diets of the three cormorants: juvenile rockfish and sculpins were common to the diets of all three cormorants, while sanddabs, anchovies, shiner surfperch and tomcod occurred in the diets of two cormorants, mainly the Double-crested and Brandt's. Among the four years for which data were available, 1974-1977, the smaller-billed Pelagic Cormorant (see Ainley and Boekelheide ms) consistently took smaller Sebastes than the other two cormorants, although differences were rarely statistically significant (Table 2.9). The same was true for cottids. The greatest differences, by far, occurred during the atypical year, 1976. Between the Double-crested Cormorant and Brandt's Cormorant, which has a longer but more slender bill than the former, results were mixed. In four annual comparisons where more than 10 otoliths (and fish sizes) were available, Brandt's Cormorant ate the larger fish in three of them.

Although results from other researchers indicate a direct correlation between predator size and prey size in some seabirds (Ashmole 1968, Bedard 1969a, Harris 1970), the significance of the above findings for cormorants are not so clear. Double-crested Cormorants were clearly exploiting a different prey population---that of estuaries---where in the case of cottids, the large Leptocottus armatus dominated the diet. Brandt's Cormorants also fed mainly on this species of cottid, whereas the Pelagic fed on the wide variety of cottids which inhabit rocky substrates. Among the two species of fish that Harris compared

in the diets of three auks, mean sizes differed by 23 to 50%, which is a much more dramatic result than our findings, i.e. differences less than 20%. Pearson (1968) also found little size difference in the prey eaten by the several seabirds he investigated.

We were also able to compare the sizes of certain prey captured by three auks, where we had sufficient observations for nine summers, 1974 to 1982, and for three prey species, juvenile rockfish, sanddabs and anchovies. Only rockfish were common to all three predators' diets, and again results were mixed (Table 2.21). The longer-billed murre ate larger Sebastes than the smaller puffin in only three of seven years, but compared to the still smaller guillemot it ate larger Sebastes in seven of eight years. So far, results are consistent with expectations. The larger puffin compared to the smaller guillemot, however, took larger Sebastes in only three of seven years. Within years, differences in the size of Sebastes taken by these three predators were actually very small (virtually all in the 5% range).

Expectations were assaulted still further in comparisons for the other two fish species. The larger murre compared to the smaller guillemot took larger sanddabs in only three of seven years, and the larger murre compared to the smaller puffin took smaller anchovies in all years. Again, actual differences in the sanddab comparison were quite small. In the anchovy comparison, differences were large. As with the cottid pattern for cormorants, the difference in anchovy size was likely related to differences in foraging habitat. Larger anchovies occur over deeper waters (Ainley and Boekelheide ms; Part I), and puffins, unlike murres, restrict their foraging to the continental slope or to waters even deeper. Diamond (1983) thought that size differences he observed in the prey of tropical seabirds could well have been due to differing foraging areas; the same was true of Volkman et al. (1980) in assessing size differences in the prey of three penguin species in the Antarctic.

Although we used different techniques to estimate prey length for cormorants (regressions from otolith diamters) and alcids (comparison to bill length), given the extreme range in size between the six species (Ainley and Boekelheide ms), differences in prey size should be evident. Results for rockfish, anchovies and cottids, however, were remarkably close; they all seemed to take the same size fish with the exception of the large anchovies taken by the puffin and Brandt's Cormorant. The sanddabs taken by the larger cormorants were much larger than those taken by the alcids, and are the most clear-cut results thus far relative to expectations based on predator size. At the lengths of these larger sanddabs, fish shape should also have dissuaded any birds but cormorants, which can open their mouths very wide, from taking them (Swennen and Duiven 1977).

It is clear that the summertime natural history of breeding seabirds, and even visitors such as Sooty Shearwater, in the Gulf of the Farallones is based on a "juvenile rockfish economy". When rockfish are available, foraging habitats and behaviors and diets overlap extensively among many of the seabirds. When young rockfish are not available, which usually is the case during years of anomalously warm sea temperatures, then avian predators diverge in their foraging habitats (except for some particularly social species) and diets diverge as well. In so doing, the birds switch to alternate prey, usually anchovies, squid or other species. In all years, as the summer draws to a close, seabirds also switch to these other prey. This is true not only for those species that feed heavily on rockfish, but also for planktivorous species like Cassin's Auklet.

It is not clear whether the foraging of Sooty Shearwaters plays any role in affecting the foraging patterns of the resident species. When rockfish were abundant, shearwaters occurred in great numbers and foraged in the same areas as other species. When rockfish were not abundant, few shearwaters were present, and those that were fed in closer association with some of the other species. Perhaps in the latter situation, the shearwaters had greater impacts on the foraging of some species, playing their role as "supressors" in mixed species flocks (Hoffman et al. 1981). The importance of that role, however, may be diminished when food is superabundant; it may also be diminished when food is much more scarce because so few shearwaters are then present.

The obvious switching from an economy based on one species to another economy that is much more diversified is an important finding. On the one hand, it means that the summertime diet is likely not representative of the entire year, something which seabird researchers have sometimes assumed in trying to summarize or review foraging patterns for large numbers of species (e.g. Ashmole 1971, Harper et al. 1985). Because the diet data available are almost always confined to the height of the chick period, generalizing further must be done with extreme caution. On the other hand, the switching of diet suggest that investigations during the nonbreeding period for a number of years will likely reveal some of the biological factors that affect timing and success of reproduction in the Farallon, as well as other populations. The subject of feeding ecology and relationships to breeding productivity is presented briefly in Part IV, and in detail in Ainley and Boekelheide ms.

FIGURE CAPTIONS PART II

Figure 2.1. Densities of Leach's and Ashy storm-petrels along cruise tracks in April and June 1985-86.

Figure 2.2. Densities of feeding Double-crested and Pelagic cormorants, and Pigeon Guillemots, in the Gulf of the Farallones, June 1985-86; and the segments of the Farallon-to-Golden Gate census track.

Figure 2.3. Densities of feeding Brandt's Cormorants along cruise tracks in April 1985 versus 1986.

Figure 2.4. Densities of feeding Brandt's Cormorants along cruise tracks in June 1985 versus 1986.

Figure 2.5. Densities of feeding Western Gulls along cruise tracks in April 1985 verus 1986.

Figure 2.6. Densities of feeding Western Gulls along cruise tracks in June 1985 versus 1986.

Figure 2.7. Densities of feeding Common Murres along cruise tracks in April 1985 versus 1986.

Figure 2.8. Densities of feeding Common Nurres along cruise tracks in June 1985 versus 1986.

Figure 2.9. Average numbers of murre parent/chick groups seen within the four segments of the Farallon to Golden Gate cruise track by year.

Figure 2.10. Densities of feeding Cassin's Auklets along cruise tracks in April 1985 versus 1986.

Figure 2.11. Densities of feeding Cassin's Auklets along cruise tracks in June 1985 versus 1986.

Figure 2.12. Densities of feeding Rhinoceros Auklets along cruise tracks in April 1985 versus 1986.

Figure 2.13. Densities of feeding Rhinoceros Auklets along cruise tracks in June 1985 versus 1986.

Figure 2.14. Densities of Tufted Puffins along cruise tracks in April 1985 versus 1986.

Figure 2.15 Densities of Tufted Puffins along cruise tracks in June 1985 versus 1986.

Figure 2.16. Densities of feeding Sooty Shearwaters along cruise tracks in June 1985 versus 1986.

Figure 2.17. The mean number of feeding cormorants observed along the Golden Gate to Farallon track, by track segment and year, April to August.

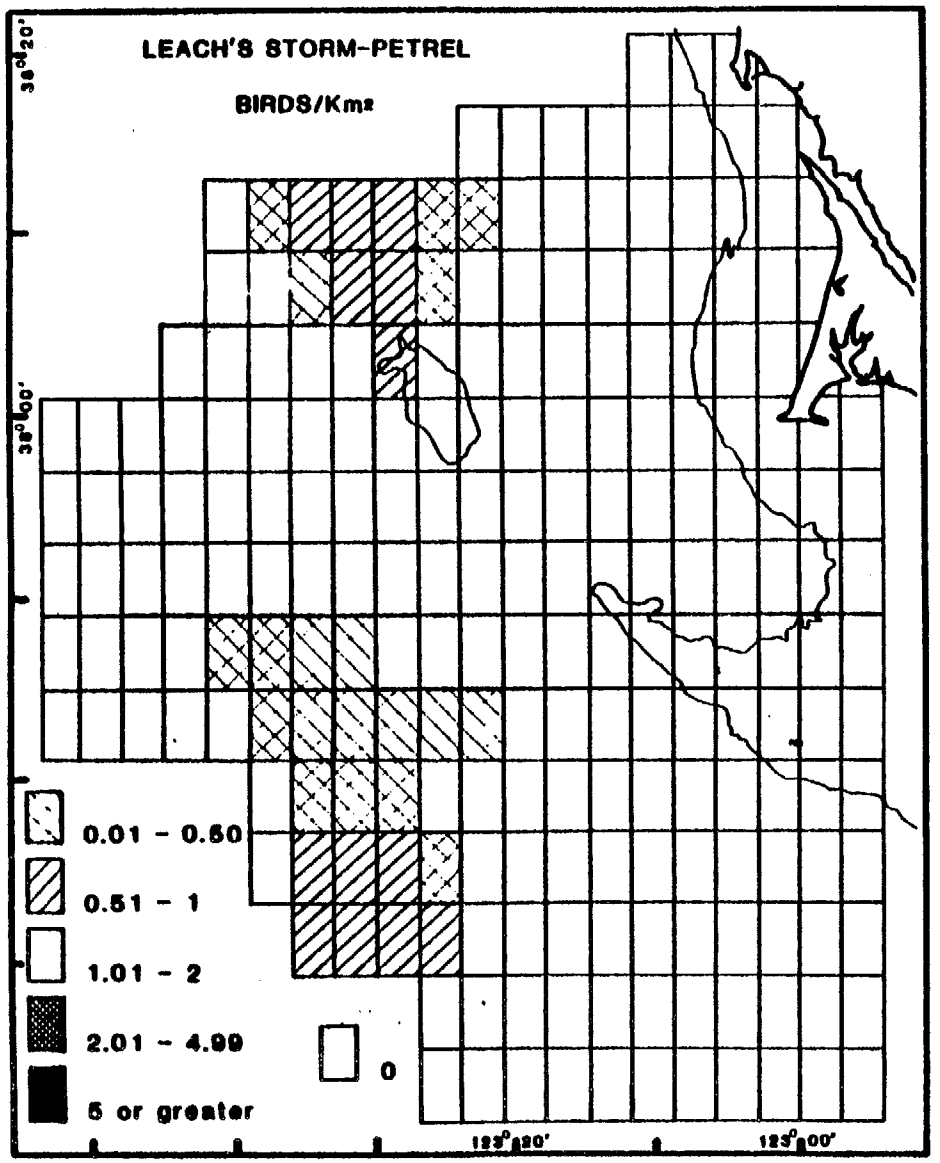
Figure 2.18. The number of cormorant feeding flocks (>200 birds) per month within three kilometers of the island by year.

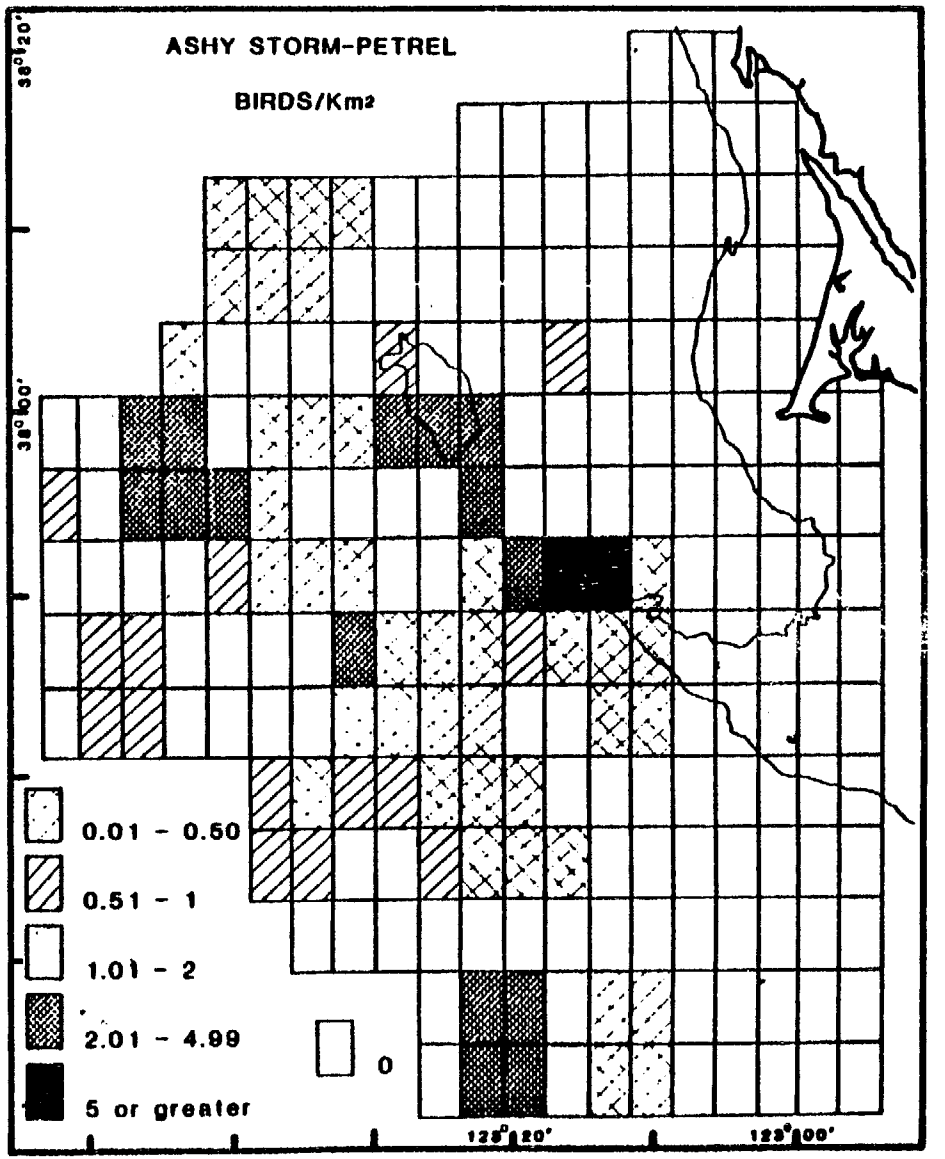
Figure 2.19. The mean number of feeding murres observed along the Golden Gate to Farallon track, by track segment and year, April to August.

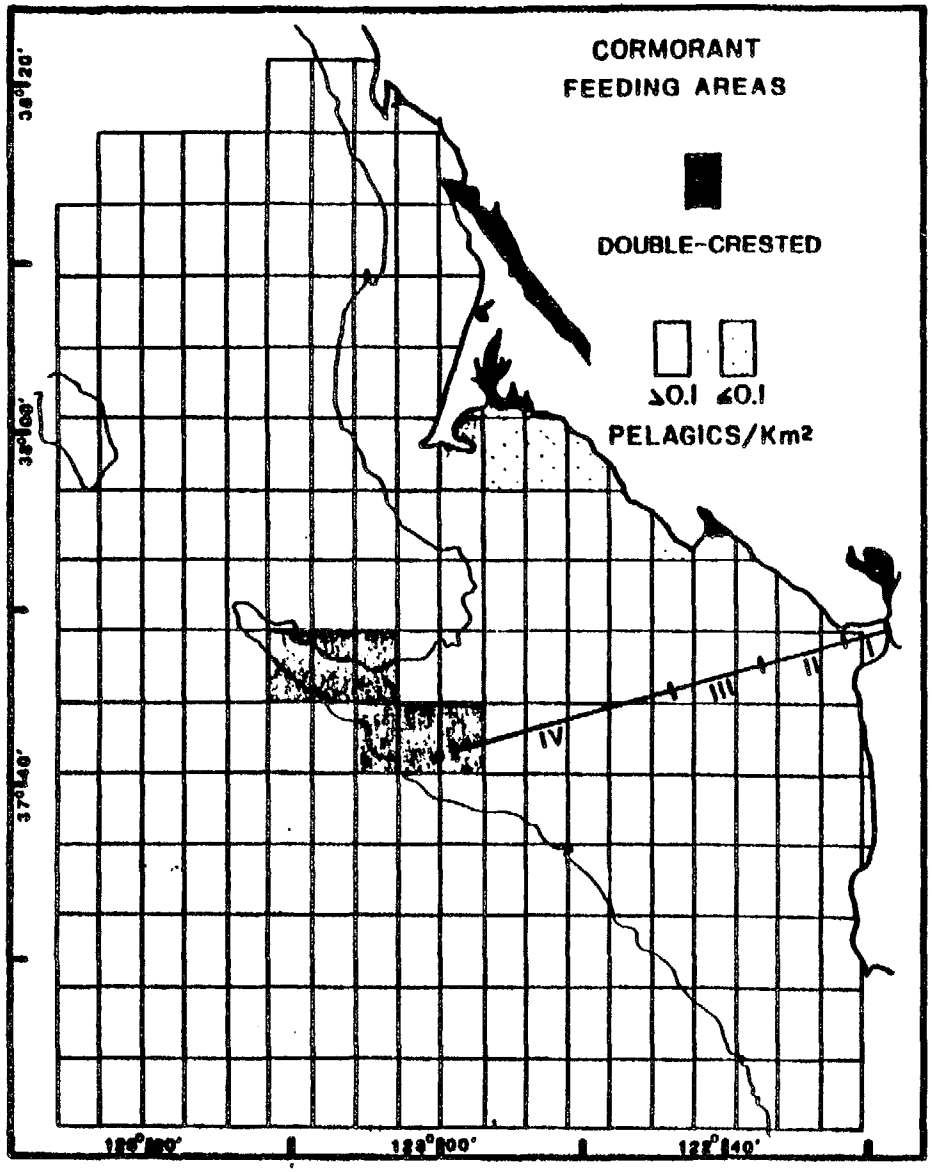
Figure 2.20. The number of murre feeding flocks (>200 birds) per month within three kilometers of the island by year.

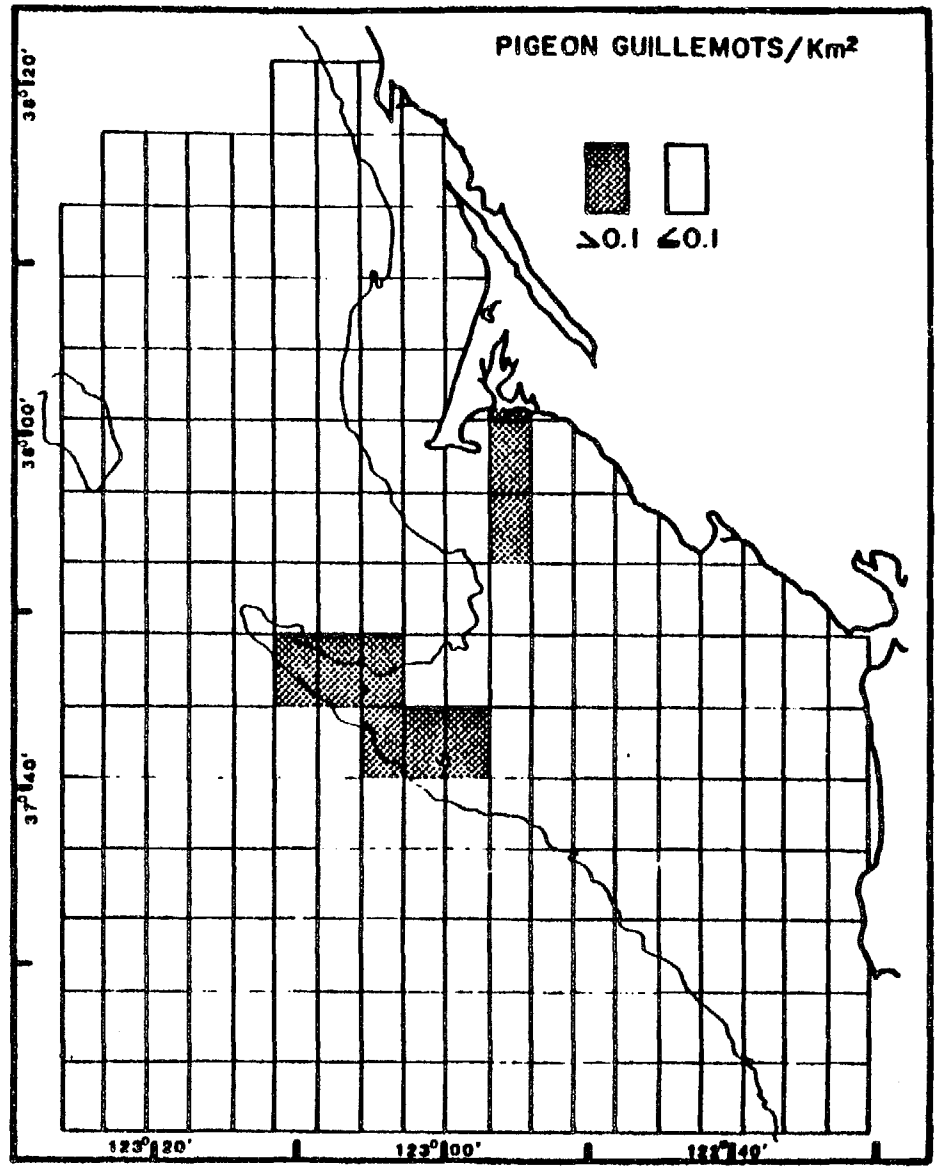
Figure 2.21. The mean number of feeding Western Gulls observed along the Golden Gate to Farallon track, by track

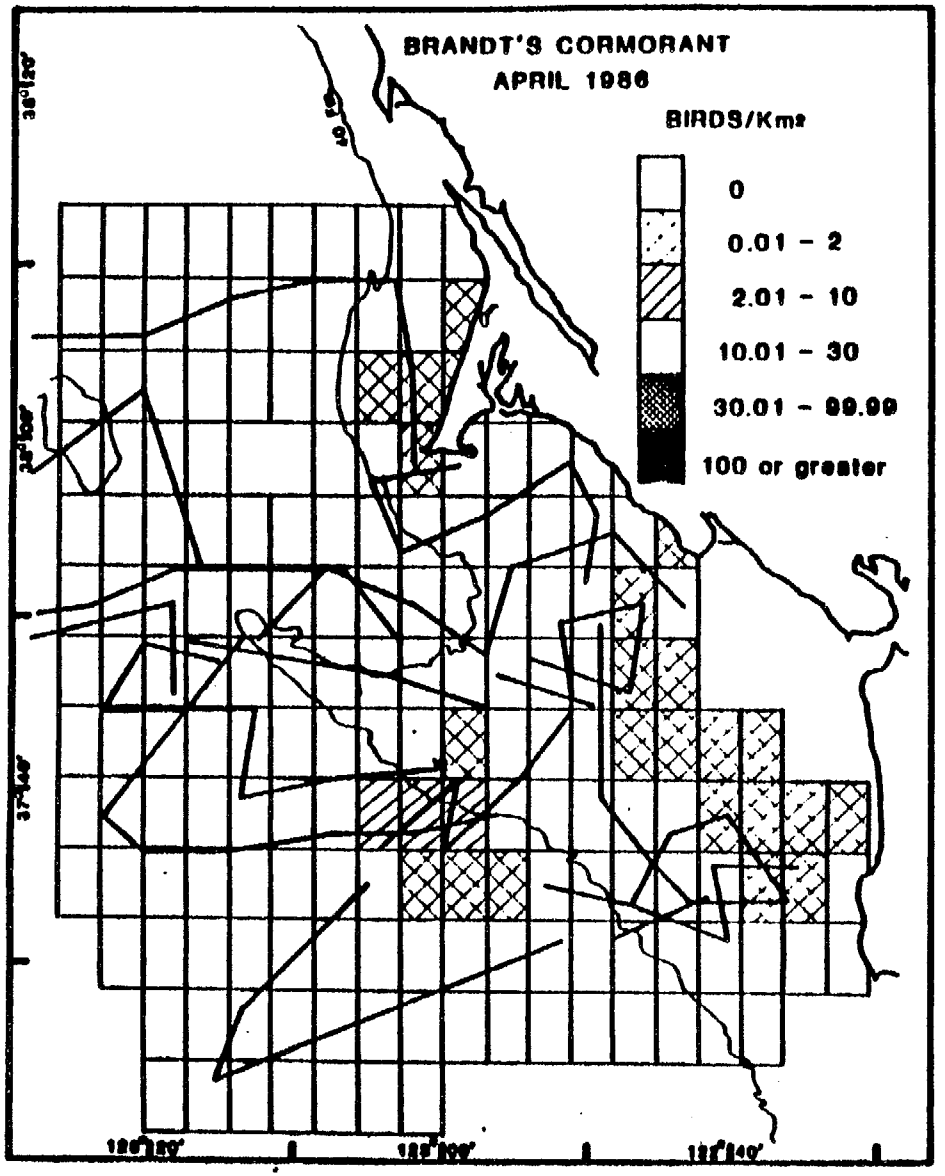
segment and year, April to August.
Figure 2.22. The number of Western Gull feeding flocks (>200 birds) per month within three kilometers of the island by year.
Figure 2.23. The average number of seconds species remained submerged or paused between dives during feeding; horizontal lines at top connect similar diving times (SNK test, p>.05).
Figure 2.24. The average dive-to-pause ratio in the feeding by various species; horizontal lines at top connect similar averages (SNK test, p>.05).
Figure 2.25. Frequency distributions showing number of birds participating in feeding flocks, April to August 1979-1983 (n = 783 total flocks).
Figure 2.26. Within-year variation in the time interval between nest reliefs by Brandt's Cormorants, 1973-1982.
Figure 2.27. The switching between anchovies and juvenile rockfish in diet of murres during different years.
Figure 2.28. Seasonal change in the proportion of principal prey in the murre diet, all years.
Figure 2.29. The switching between rockfish and cottids in the Pigeon Guillemot diet during different years.
Figure 2.30. Seasonal change in the proportions of principal prey in the Pigeon Guillemot diet, all years.
Figure 2.31. Seasonal change in the proportions of principal prey in the Tufted Puffin diet, all years.

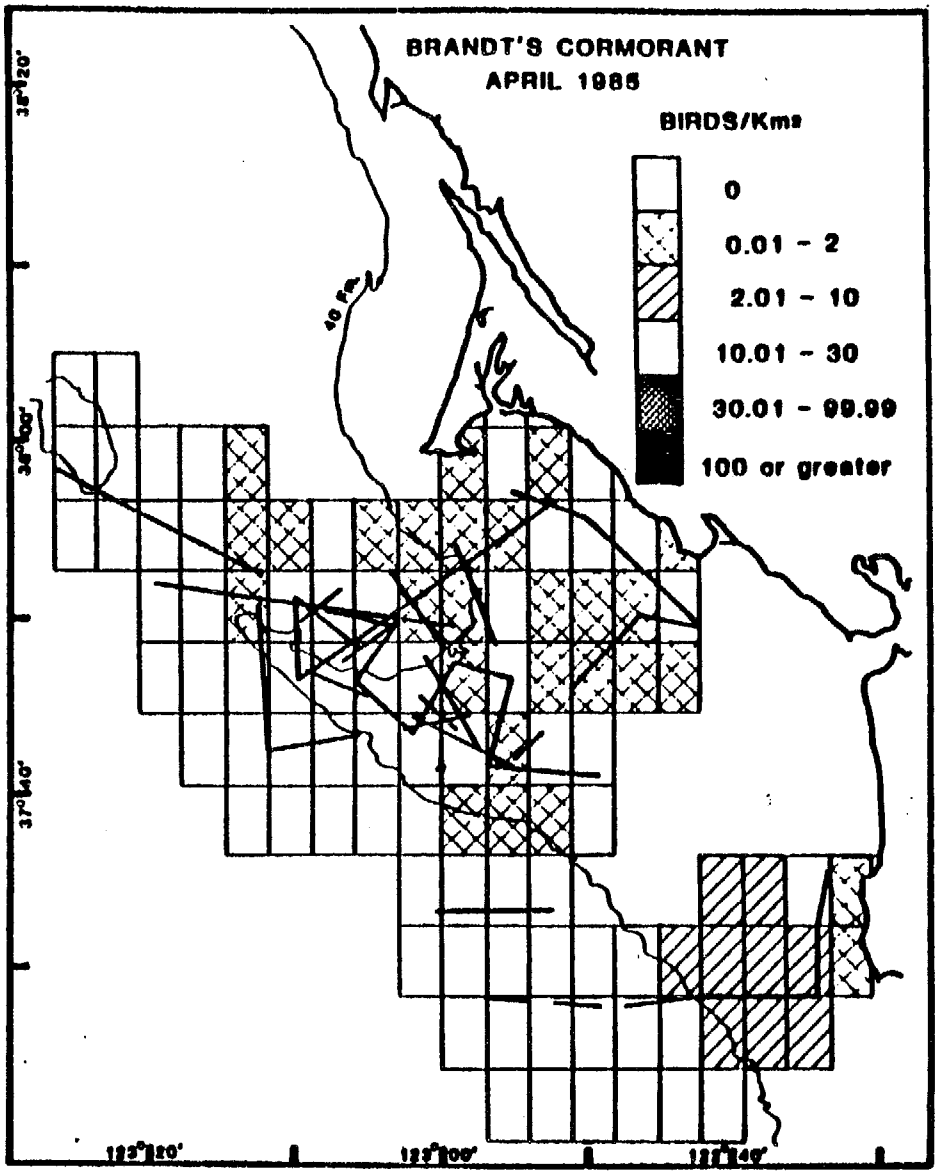

LEACH'S STORM-PETREL
BIRDS/Km²
38°20'
38°00'
0.01 - 0.50
0.51 - 1
1.01 - 2
2.01 - 4.99
5 or greater
0
123°20'
123°00'

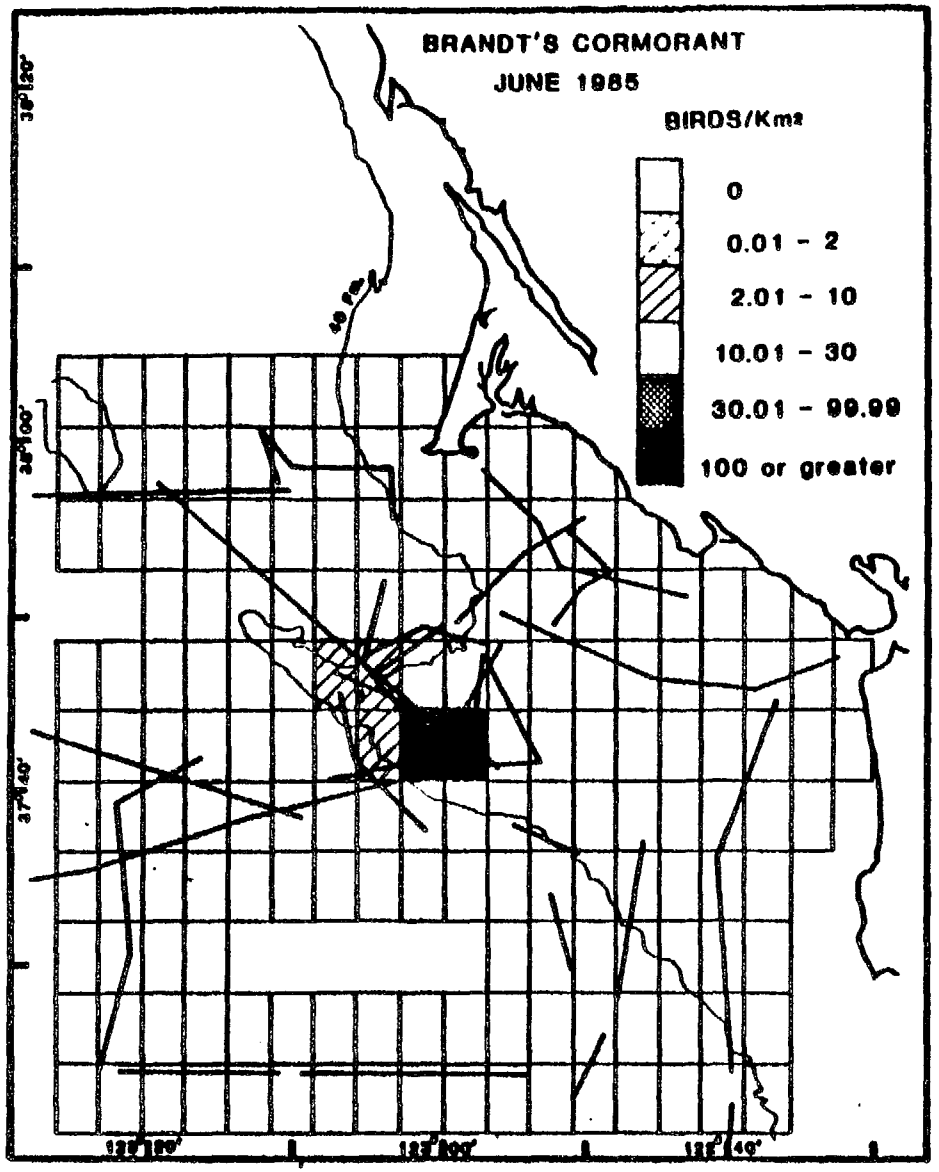

ASHY STORM-PETREL
BIRDS/Km²
38°20'
38°00'
0.01 - 0.50
0.51 - 1
1.01 - 2
2.01 - 4.99
5 or greater
0
123°20'
123°00'

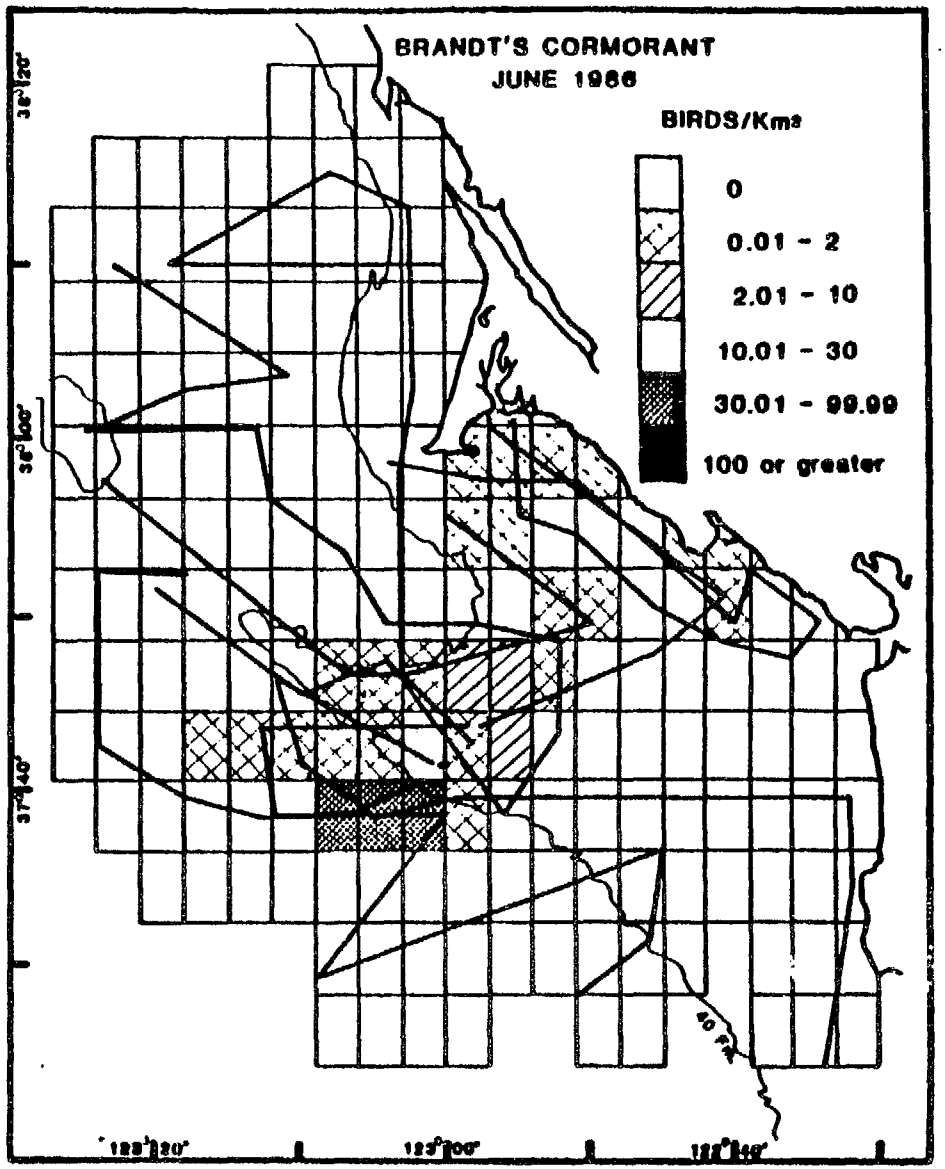

CORMORANT
FEEDING AREAS
DOUBLE-CRESTED
≥0.1 ≤0.1
PELAGICS/Km²
38°20'
38°00'
37°40'
122°40'
IV
III
II
I

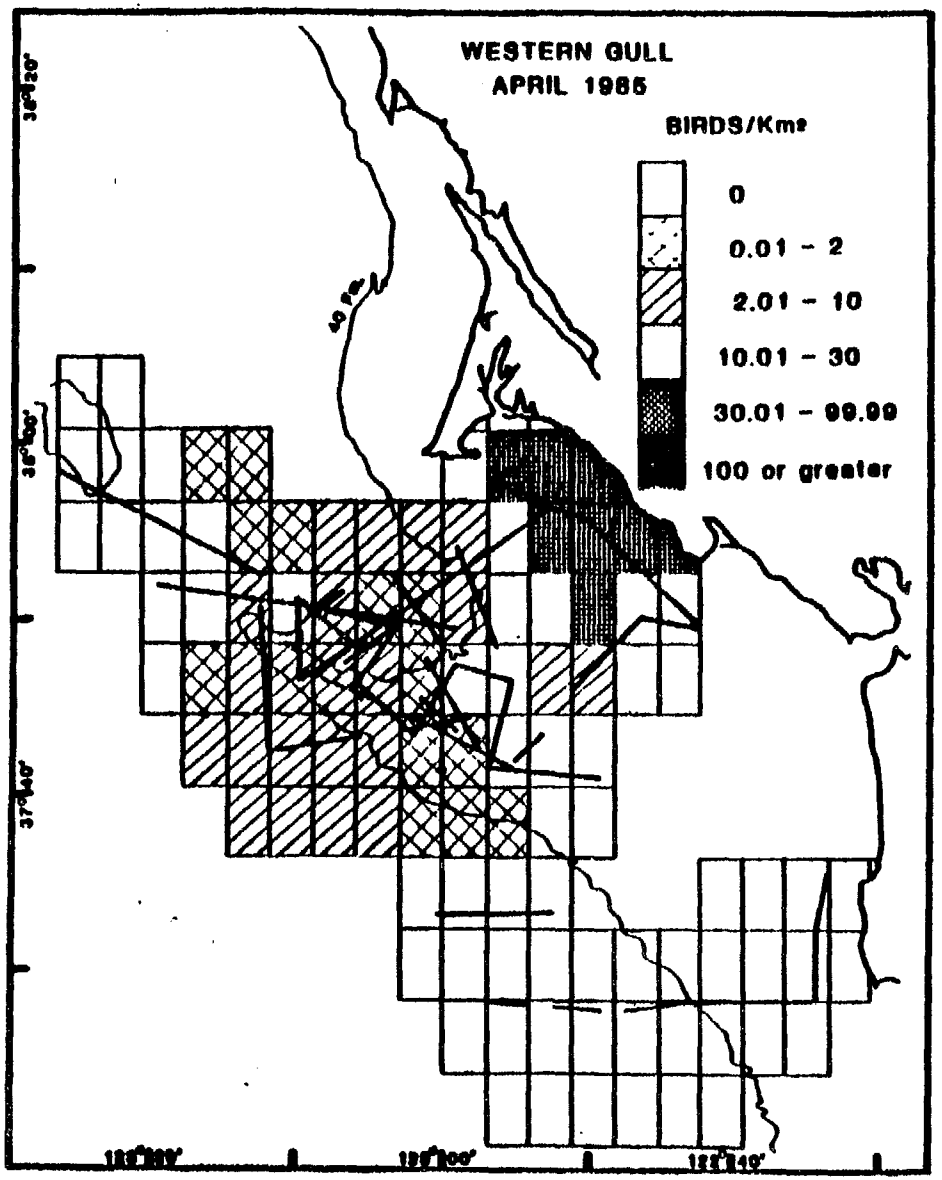

PIGEON GUILLEMOTS/Km²
≥0.1 ≤0.1
38°20'
38°00'
37°40'
123°20'
123°00'
122°40'

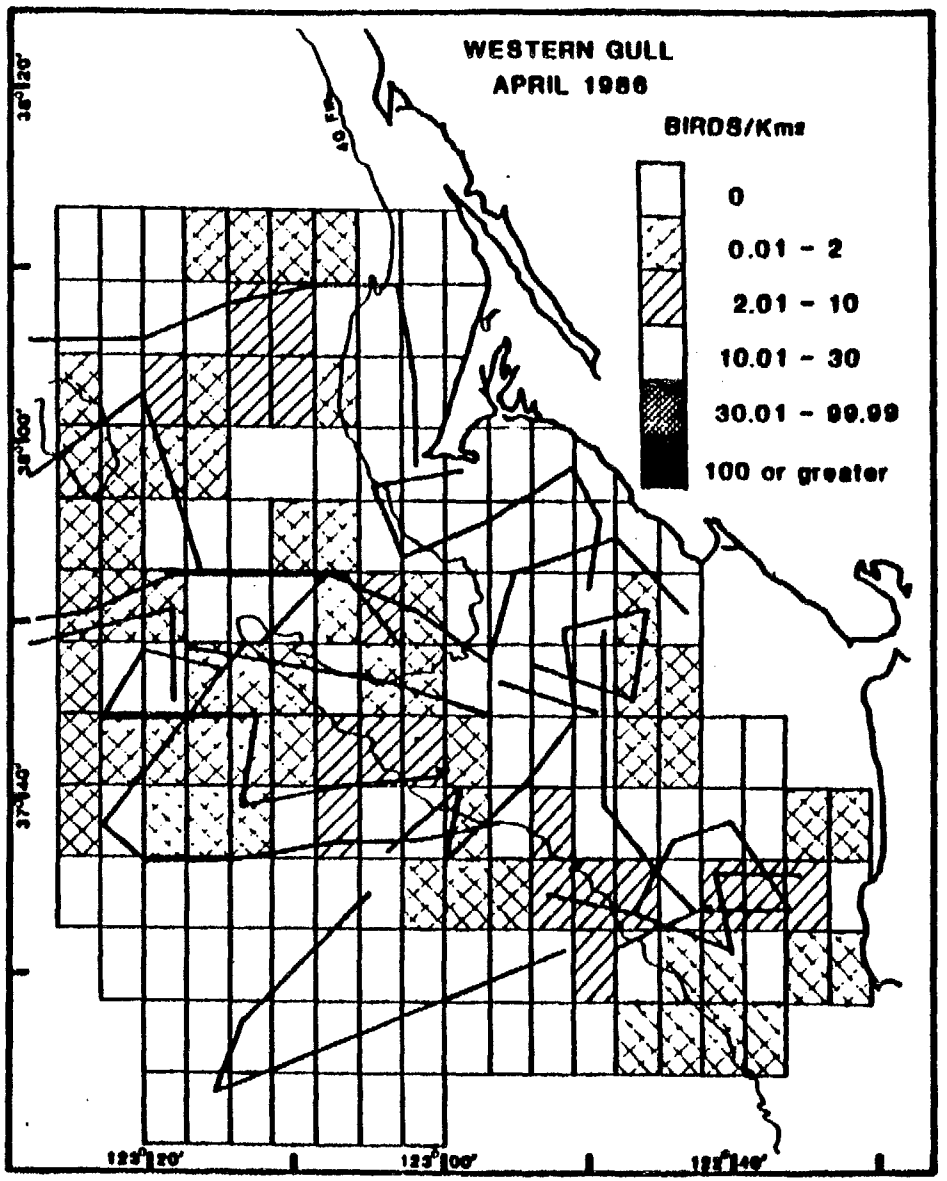

BRANDT'S CORMORANT
APRIL 1986
BIRDS/Km²
0
0.01 - 2
2.01 - 10
10.01 - 30
30.01 - 99.99
100 or greater

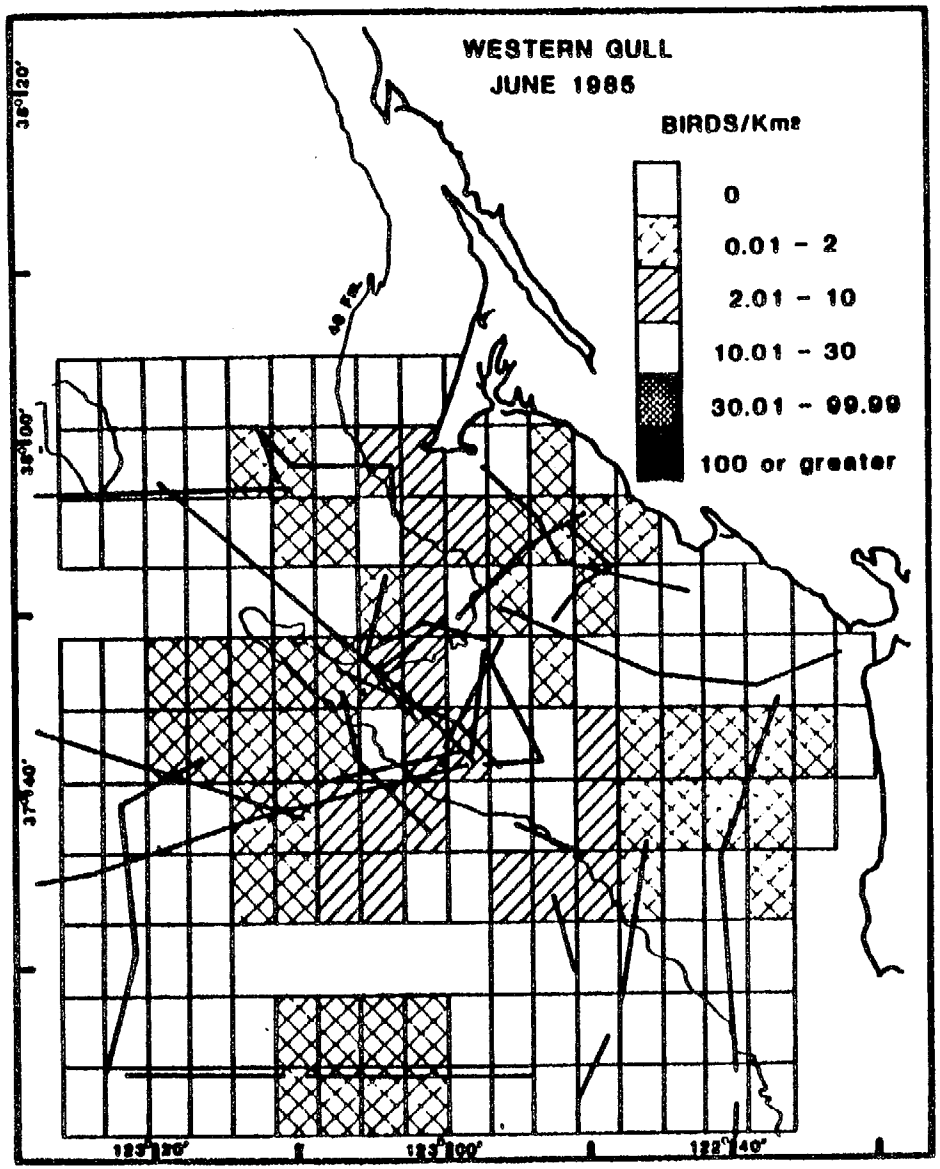

BRANDT'S CORMORANT
APRIL 1985
BIRDS/Km²
0
0.01 - 2
2.01 - 10
10.01 - 30
30.01 - 99.99
100 or greater

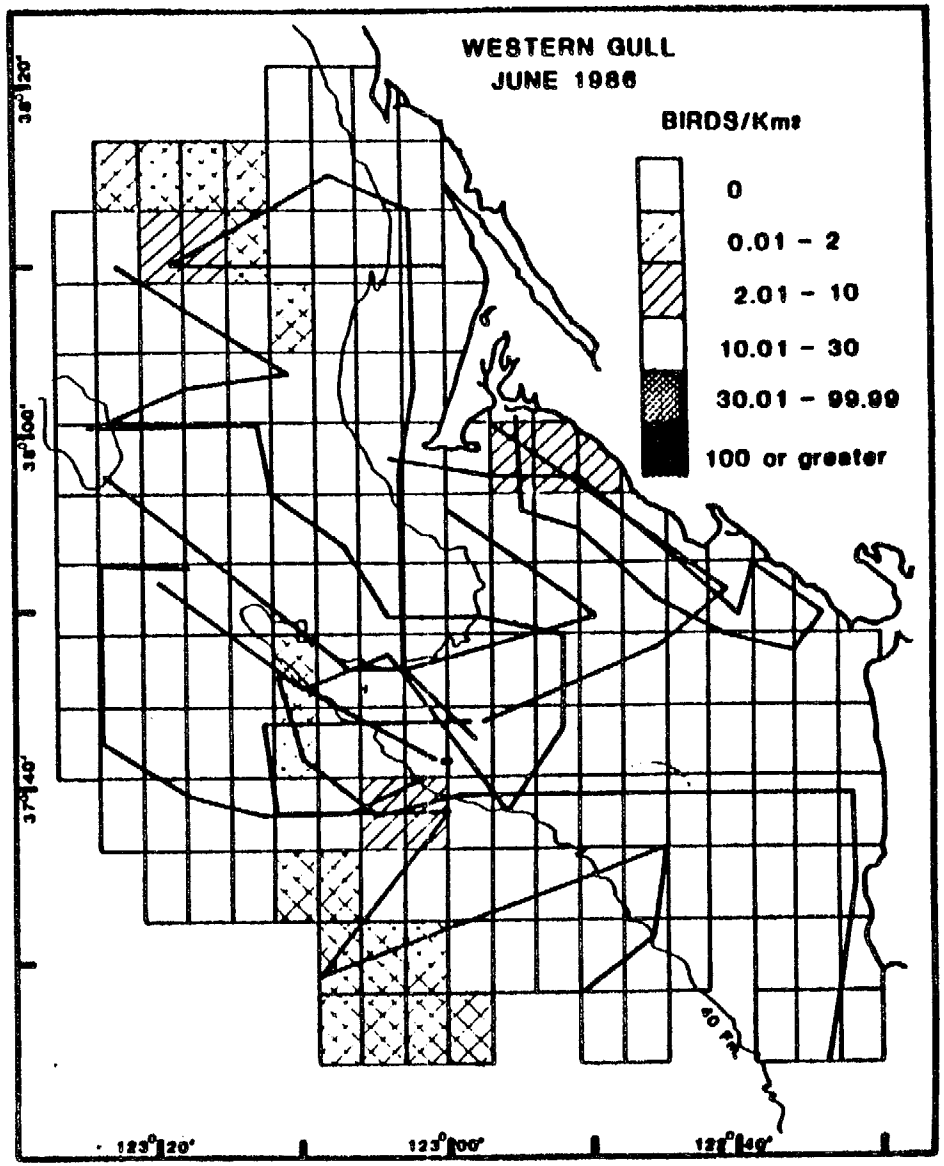

BRANDT'S CORMORANT
JUNE 1985
BIRDS/Km²
0
0.01 - 2
2.01 - 10
10.01 - 30
30.01 - 99.99
100 or greater

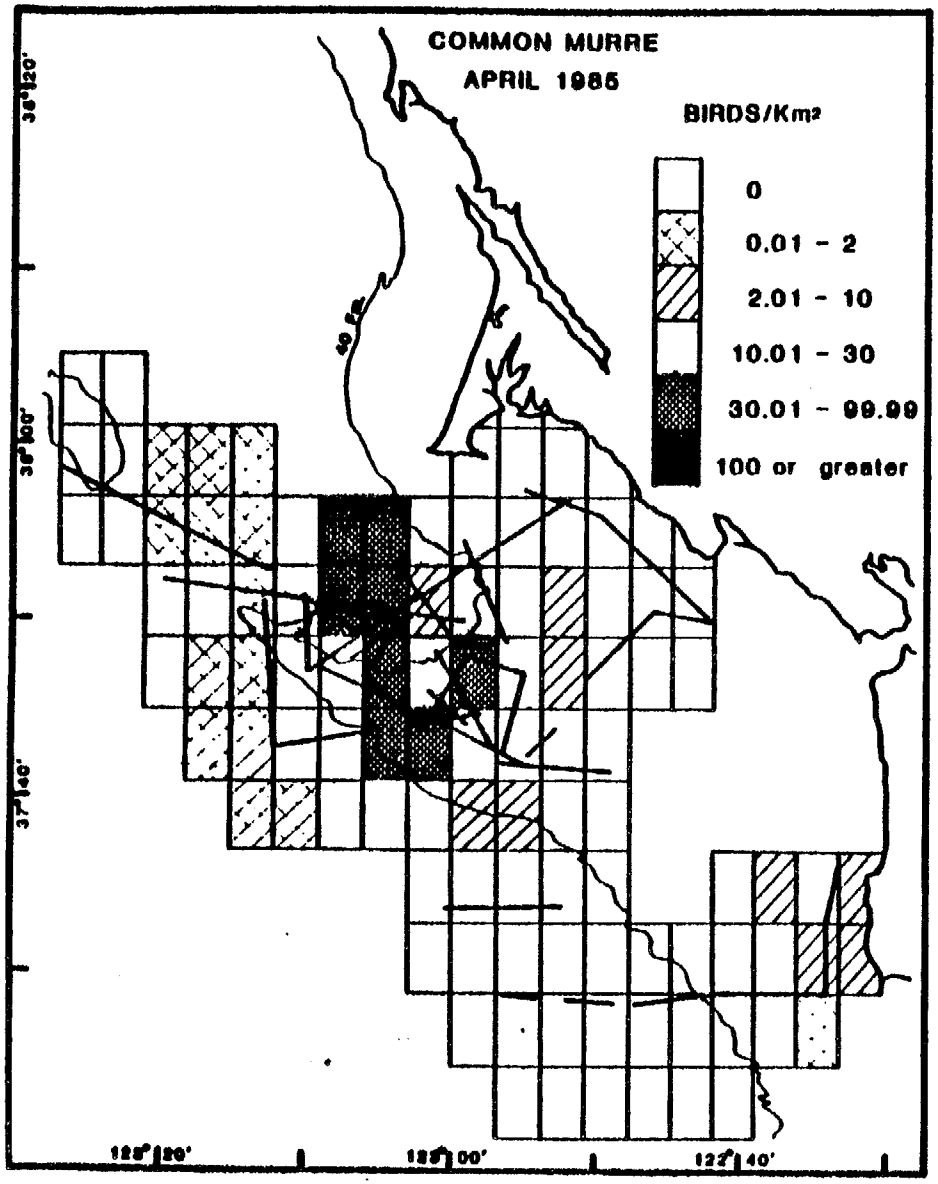

BRANDT'S CORMORANT
JUNE 1986
BIRDS/Km²
0
0.01 - 2
2.01 - 10
10.01 - 30
30.01 - 99.99
100 or greater

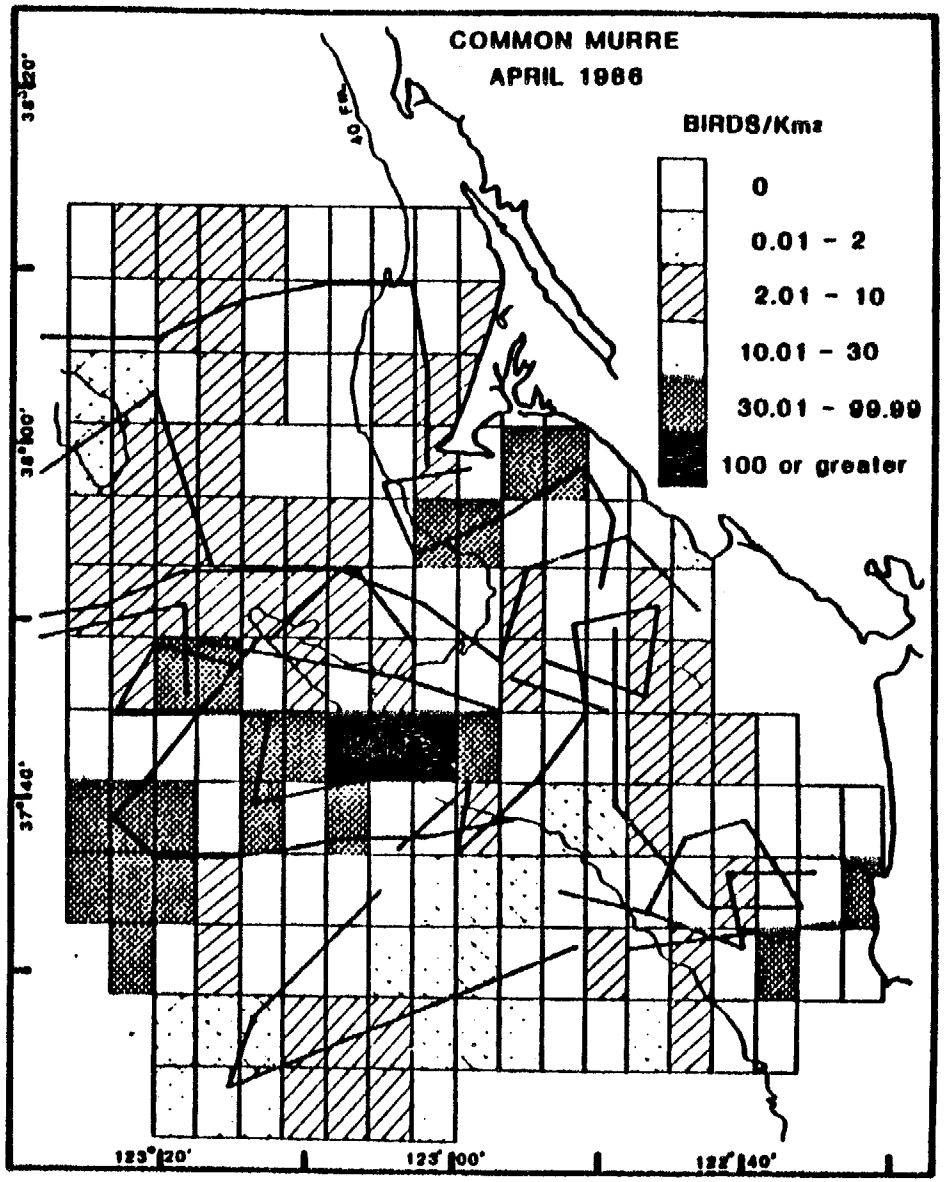

WESTERN GULL
APRIL 1985
BIRDS/Km²
0
0.01 - 2
2.01 - 10
10.01 - 30
30.01 - 99.99
100 or greater

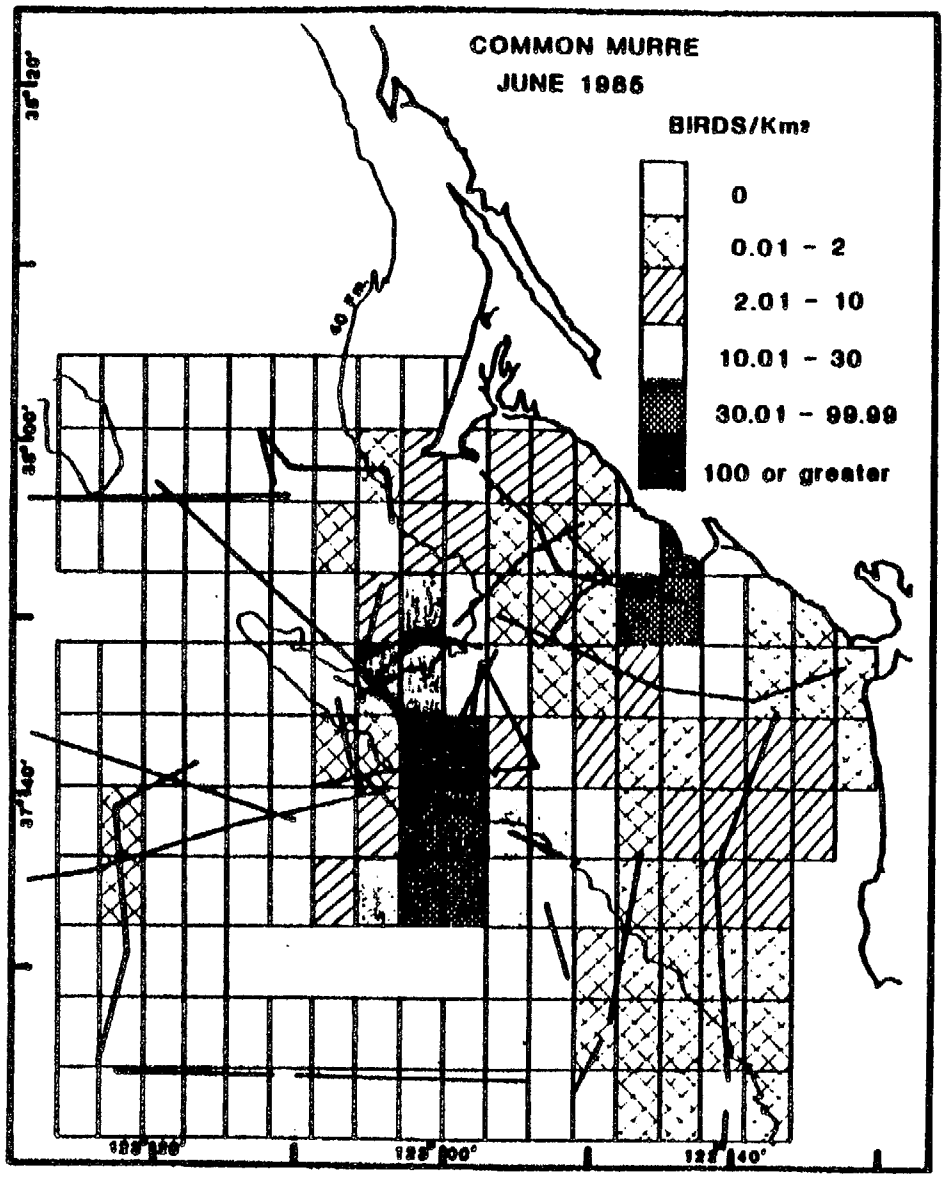

WESTERN GULL
APRIL 1986
BIRDS/Km²
0
0.01 - 2
2.01 - 10
10.01 - 30
30.01 - 99.99
100 or greater

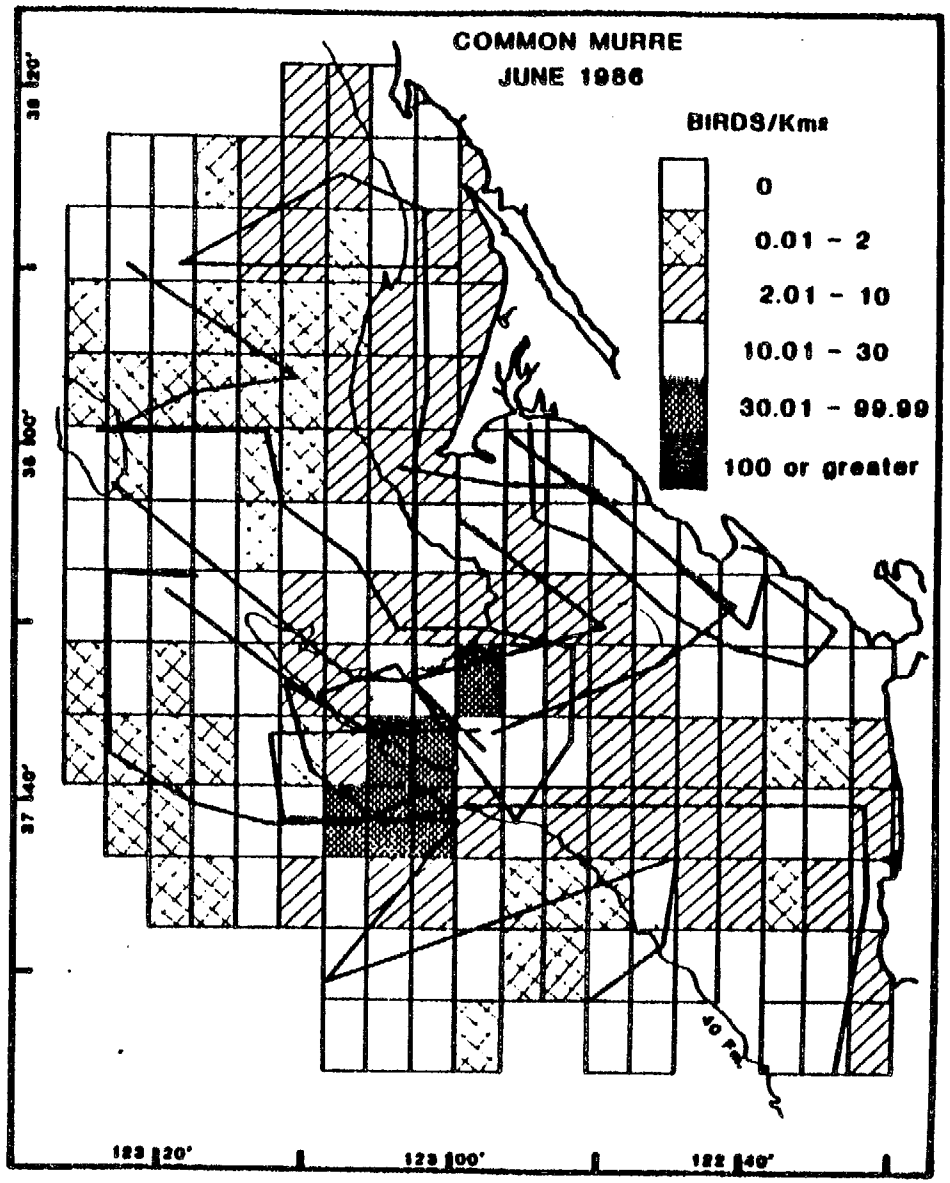

WESTERN GULL
JUNE 1985
BIRDS/Km²
0
0.01 - 2
2.01 - 10
10.01 - 30
30.01 - 99.99
100 or greater
38°20'
38°00'
37°40'
123°20'
123°00'
122°40'

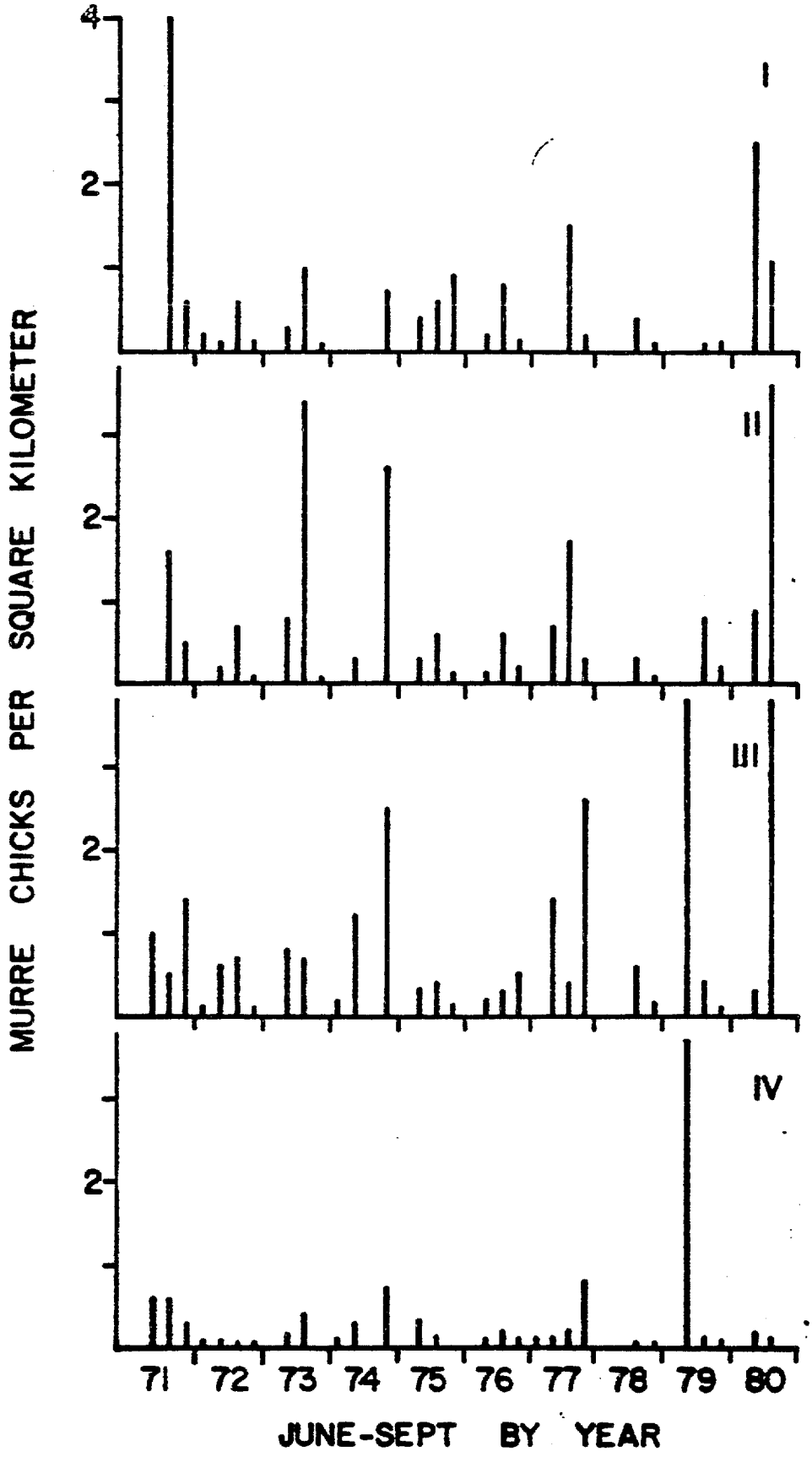

WESTERN GULL
JUNE 1986
BIRDS/Km²
0
0.01 - 2
2.01 - 10
10.01 - 30
30.01 - 99.99
100 or greater
38°20'
38°00'
37°40'
123°20'
123°00'
122°40'

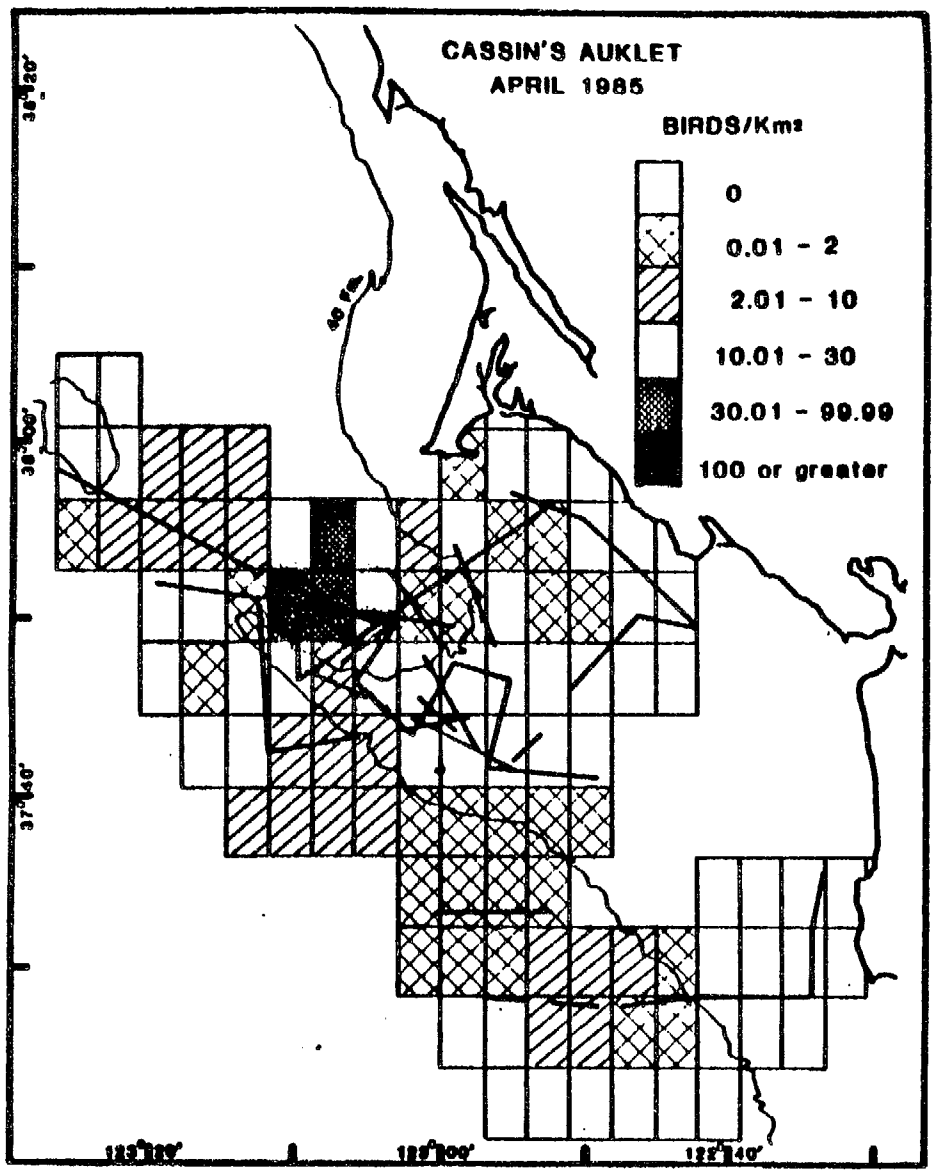

COMMON MURRE
APRIL 1985
BIRDS/Km²
0
0.01 - 2
2.01 - 10
10.01 - 30
30.01 - 99.99
100 or greater
38°20'
38°00'
37°40'
122°40'

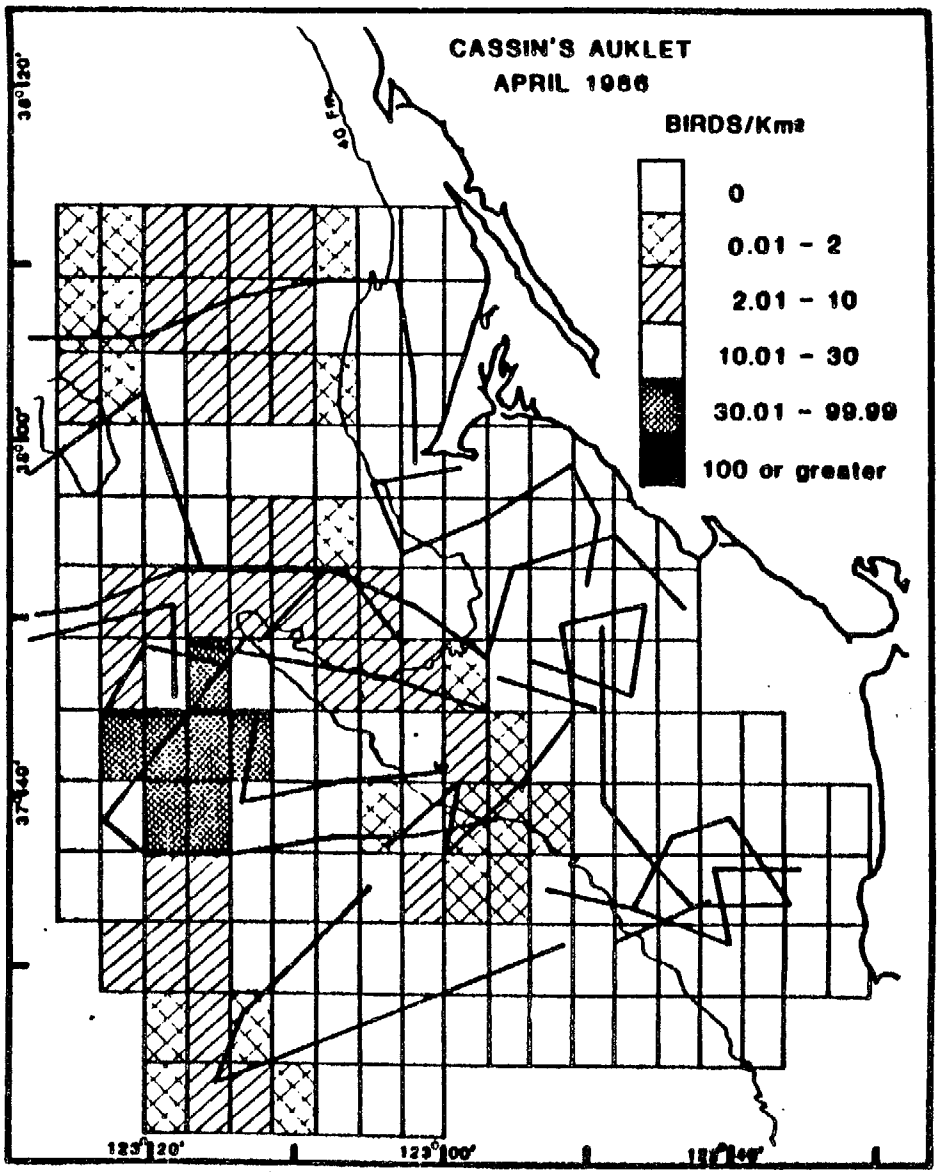

COMMON MURRE
APRIL 1986
BIRDS/Km²
0
0.01 - 2
2.01 - 10
10.01 - 30
30.01 - 99.99
100 or greater
38°20'
38°00'
37°40'
123°20'
123°00'
122°40'

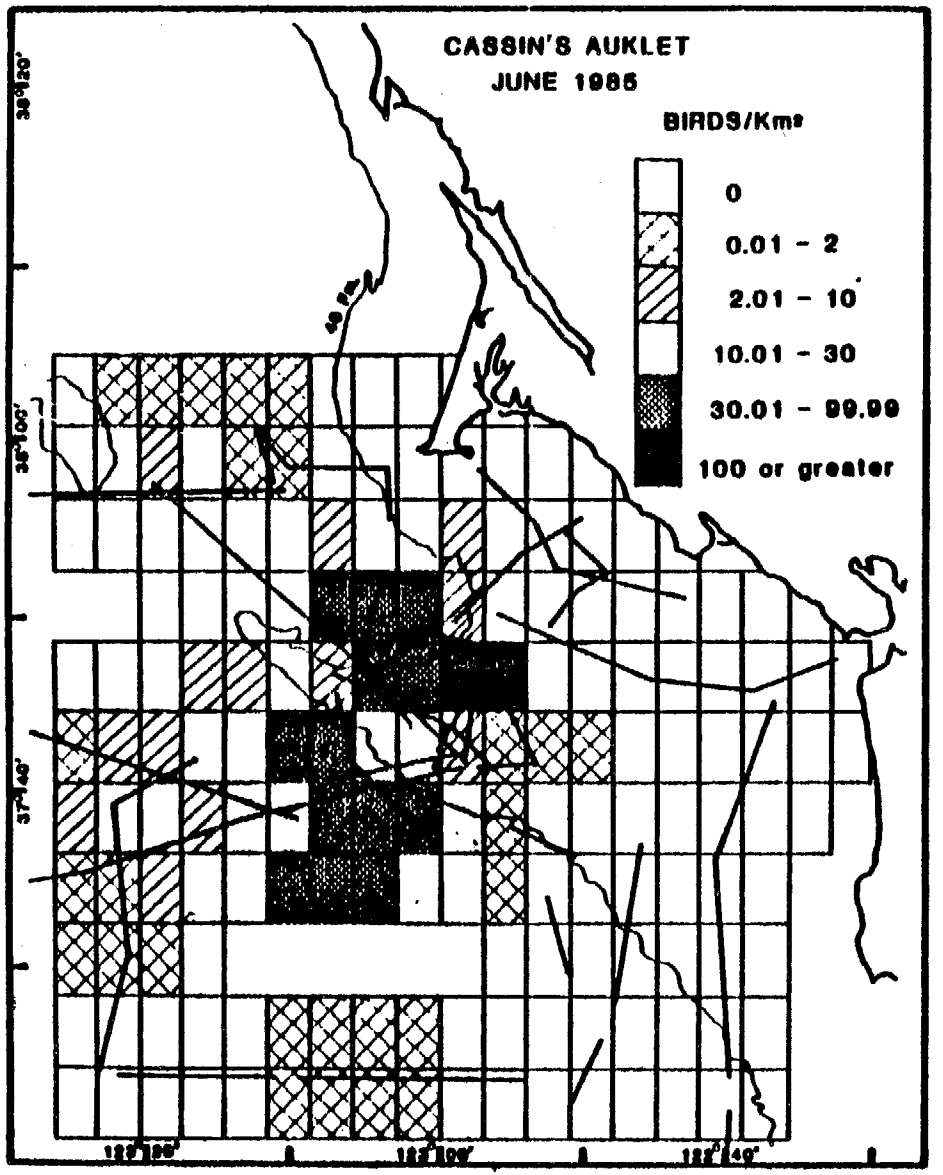

COMMON MURRE
JUNE 1986
BIRDS/Km²
0
0.01 - 2
2.01 - 10
10.01 - 30
30.01 - 99.99
100 or greater
38°20'
38°00'
37°40'
122°40'

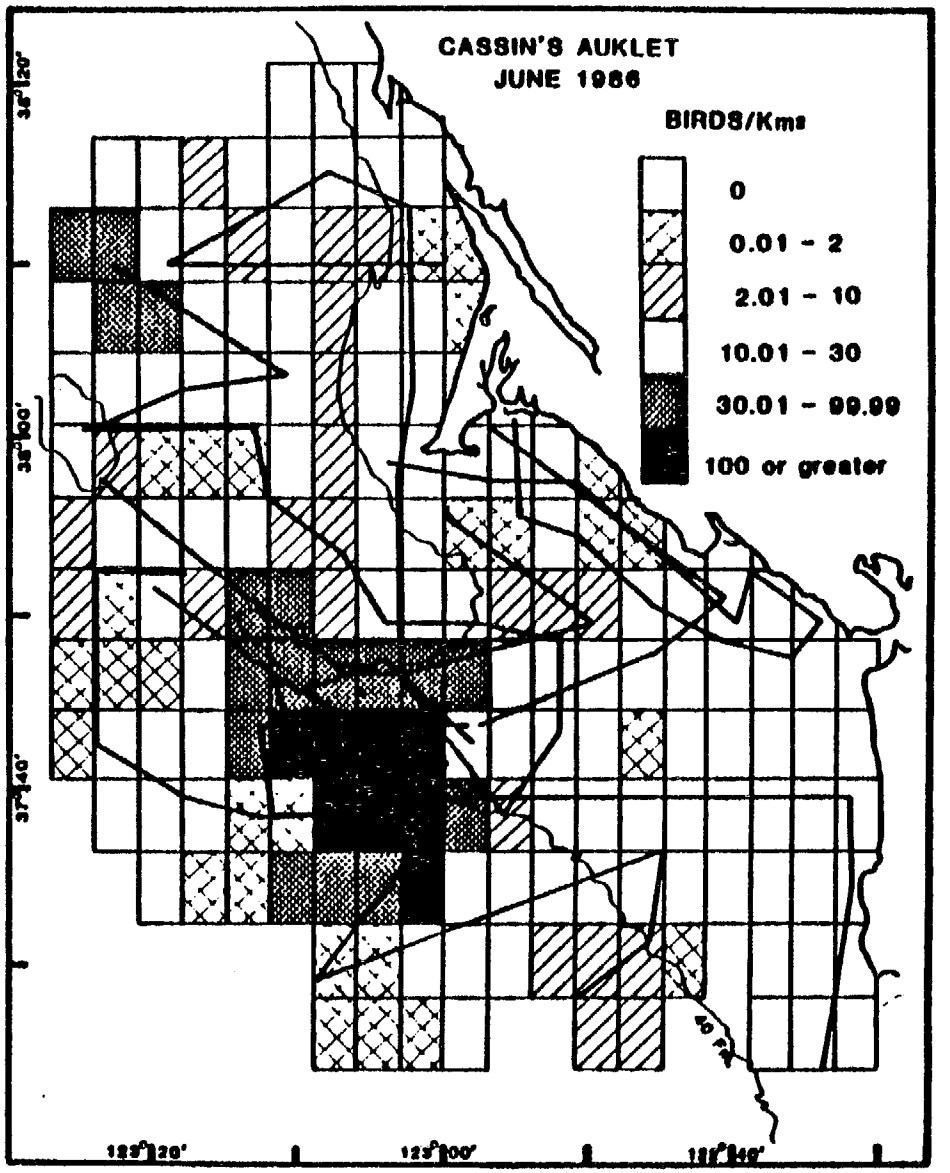

COMMON MURRE
JUNE 1986
BIRDS/Km²
0
0.01 - 2
2.01 - 10
10.01 - 30
30.01 - 99.99
100 or greater
38°20'
38°00'
37°40'
123°20'
123°00'
122°40'

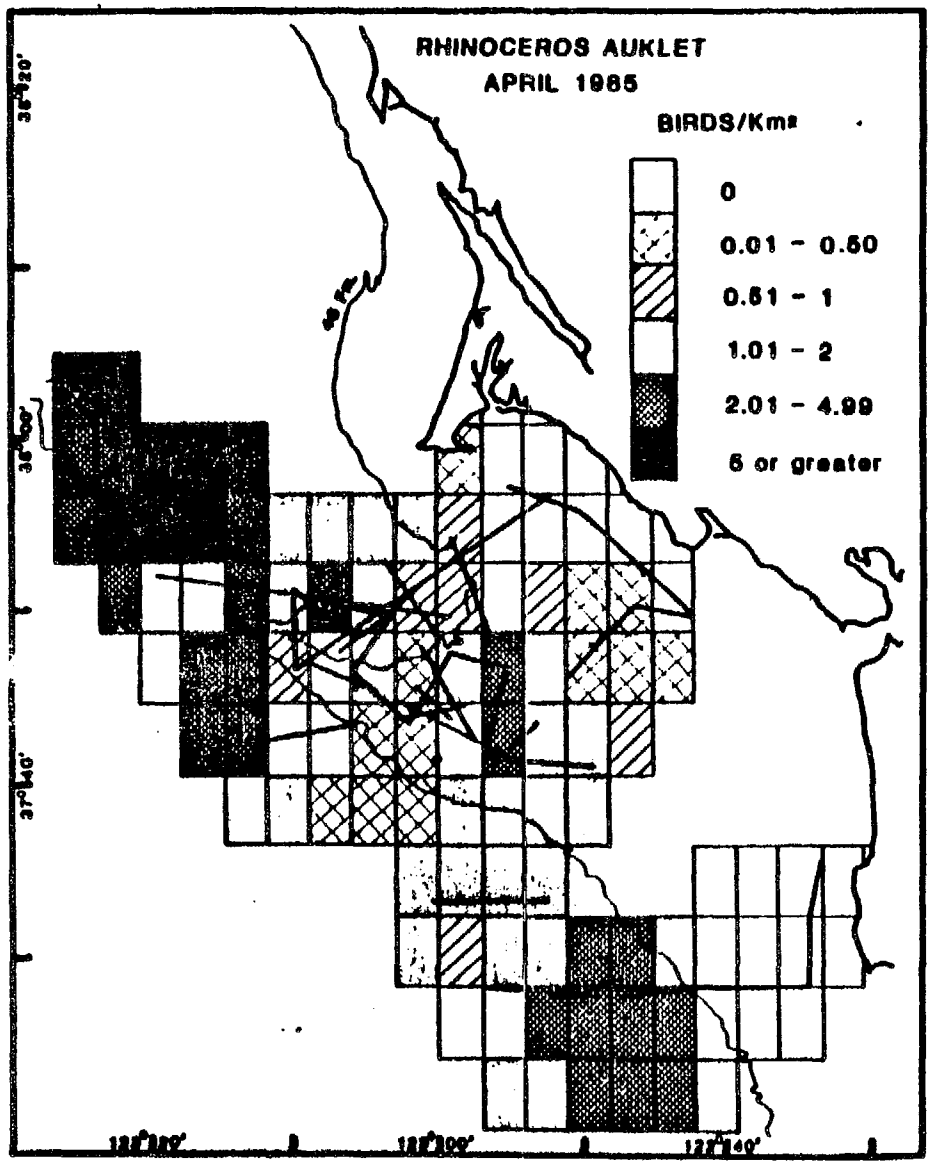

MURRE CHICKS PER SQUARE KILOMETER
4
2
I
II
III
IV
71
72
73
74
75
76
77
78
79
80
JUNE-SEPT BY YEAR

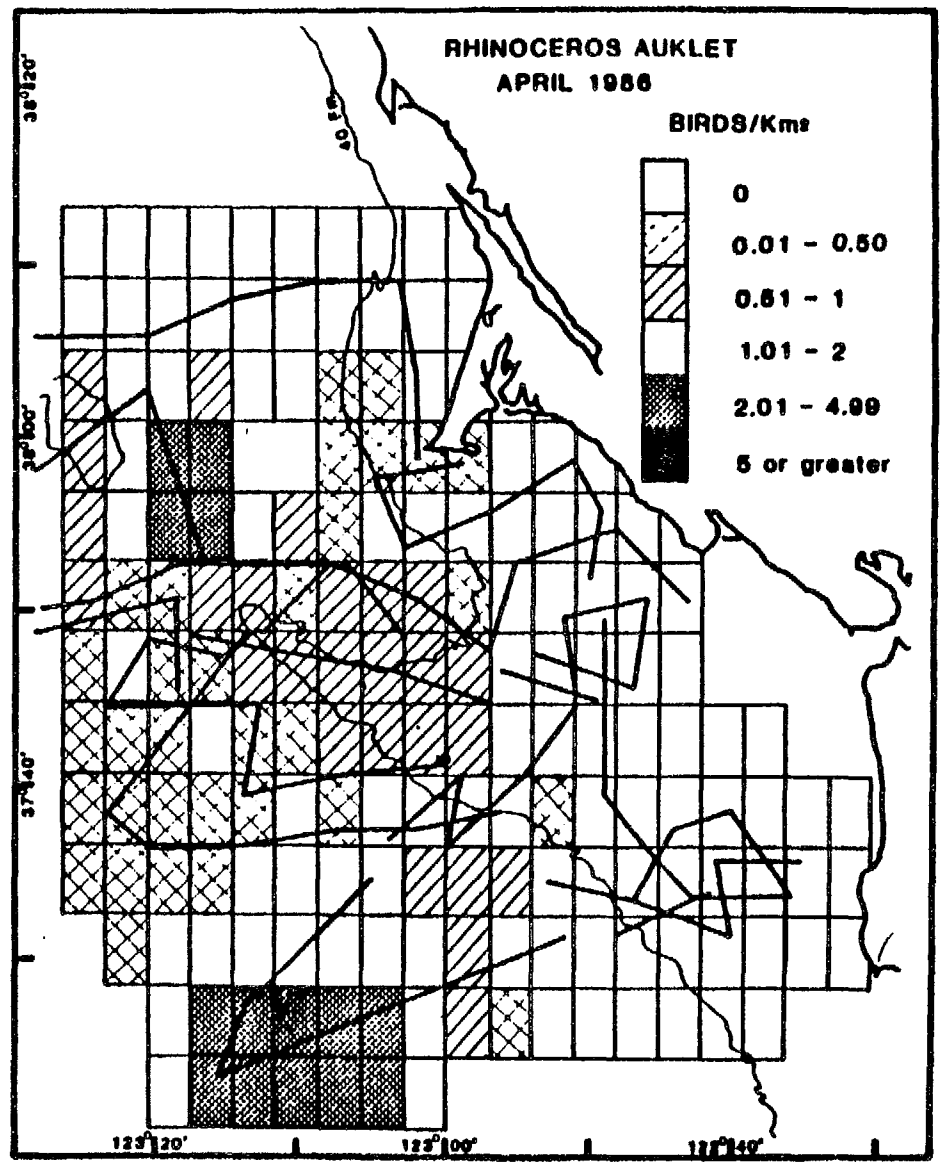

CASSIN'S AUKLET
APRIL 1985
BIRDS/Km²
0
0.01 - 2
2.01 - 10
10.01 - 30
30.01 - 99.99
100 or greater
38°120'
38°100'
37°140'
123°120'
123°100'
122°140'

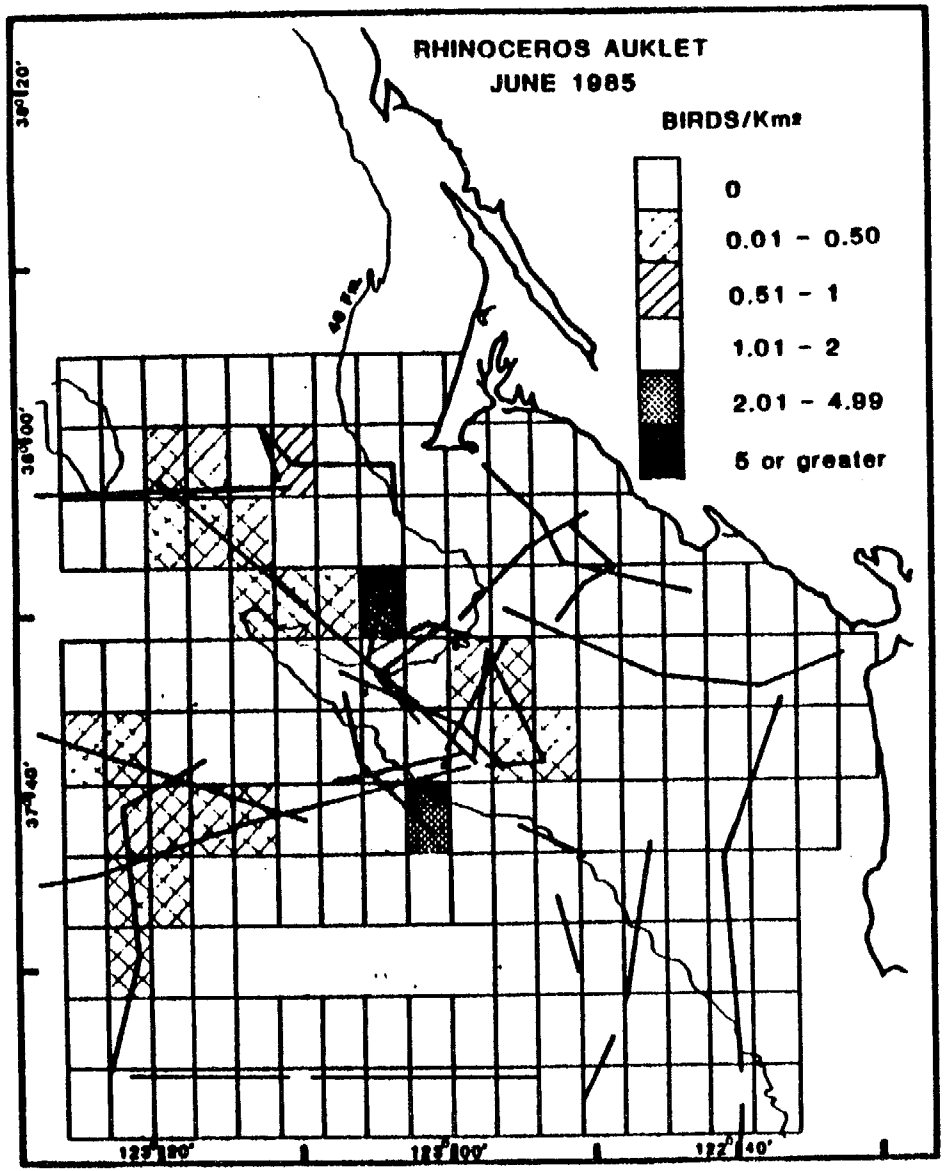

CASSIN'S AUKLET
APRIL 1986
BIRDS/Km²
0
0.01 - 2
2.01 - 10
10.01 - 30
30.01 - 99.99
100 or greater
38°120'
38°100'
37°140'
123°120'
123°100'

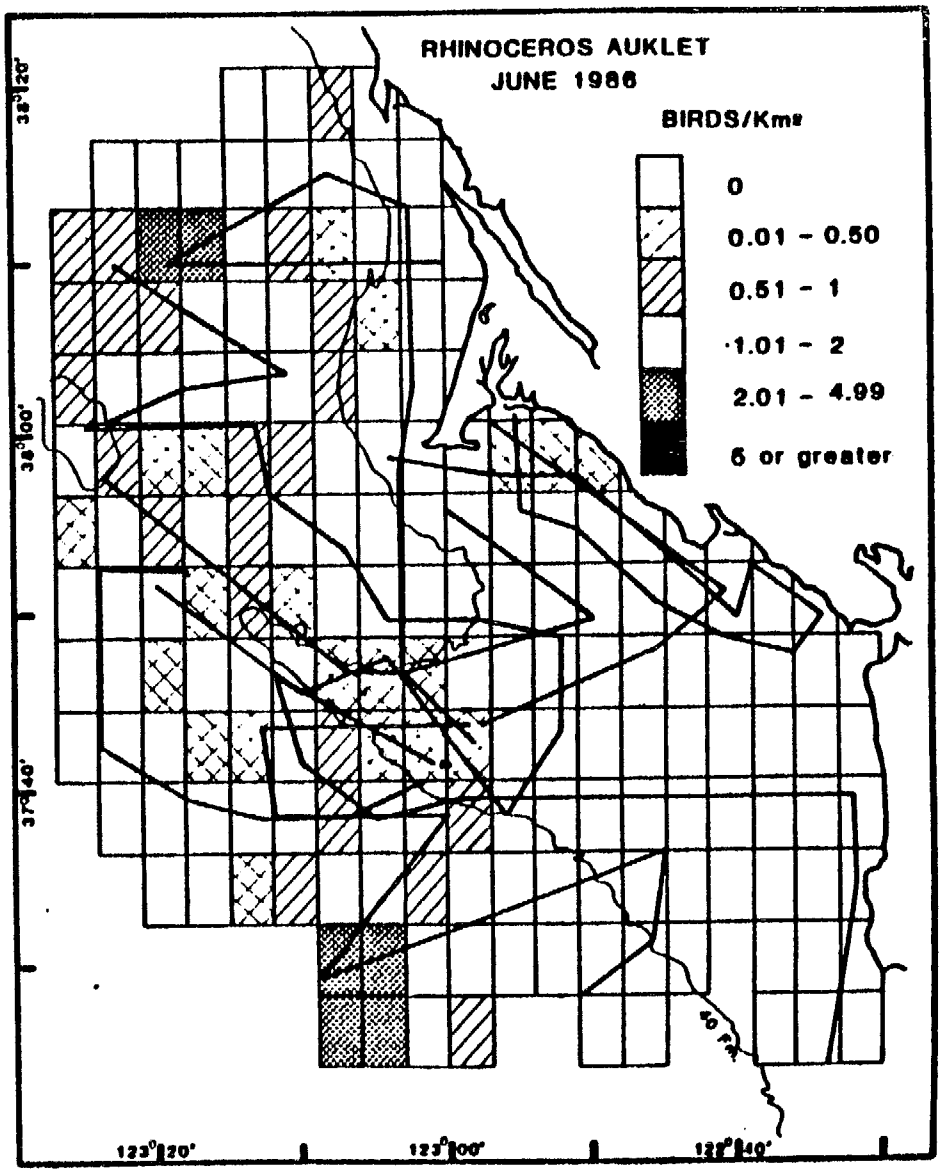

CASSIN'S AUKLET
JUNE 1986
BIRDS/Km²
0
0.01 - 2
2.01 - 10
10.01 - 30
30.01 - 99.99
100 or greater
38°20'
38°00'
37°40'
122°20'
122°00'
121°40'
40 Fm

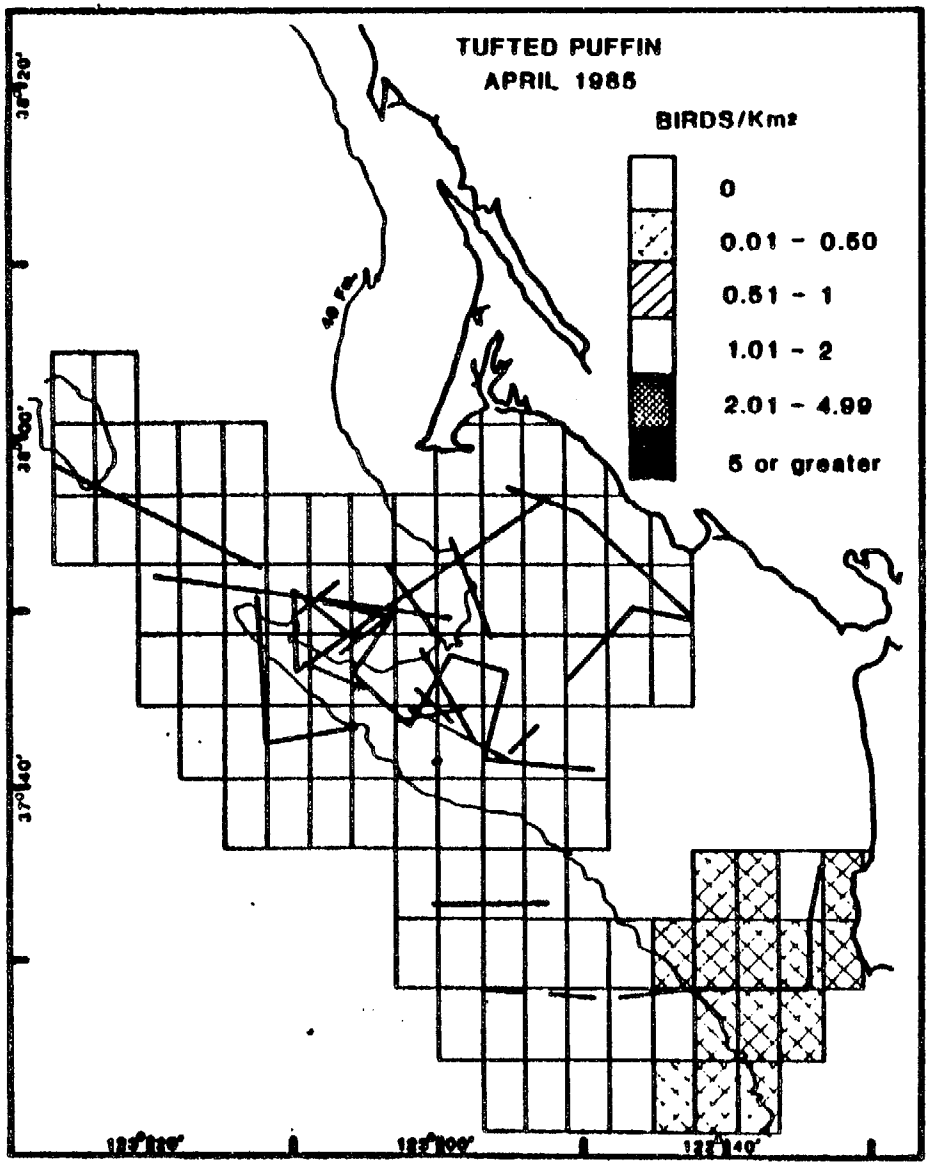

CASSIN'S AUKLET
JUNE 1986
BIRDS/Km²
0
0.01 - 2
2.01 - 10
10.01 - 30
30.01 - 99.99
100 or greater
38°20'
38°00'
37°40'
122°20'
122°00'
121°40'
40 Fm

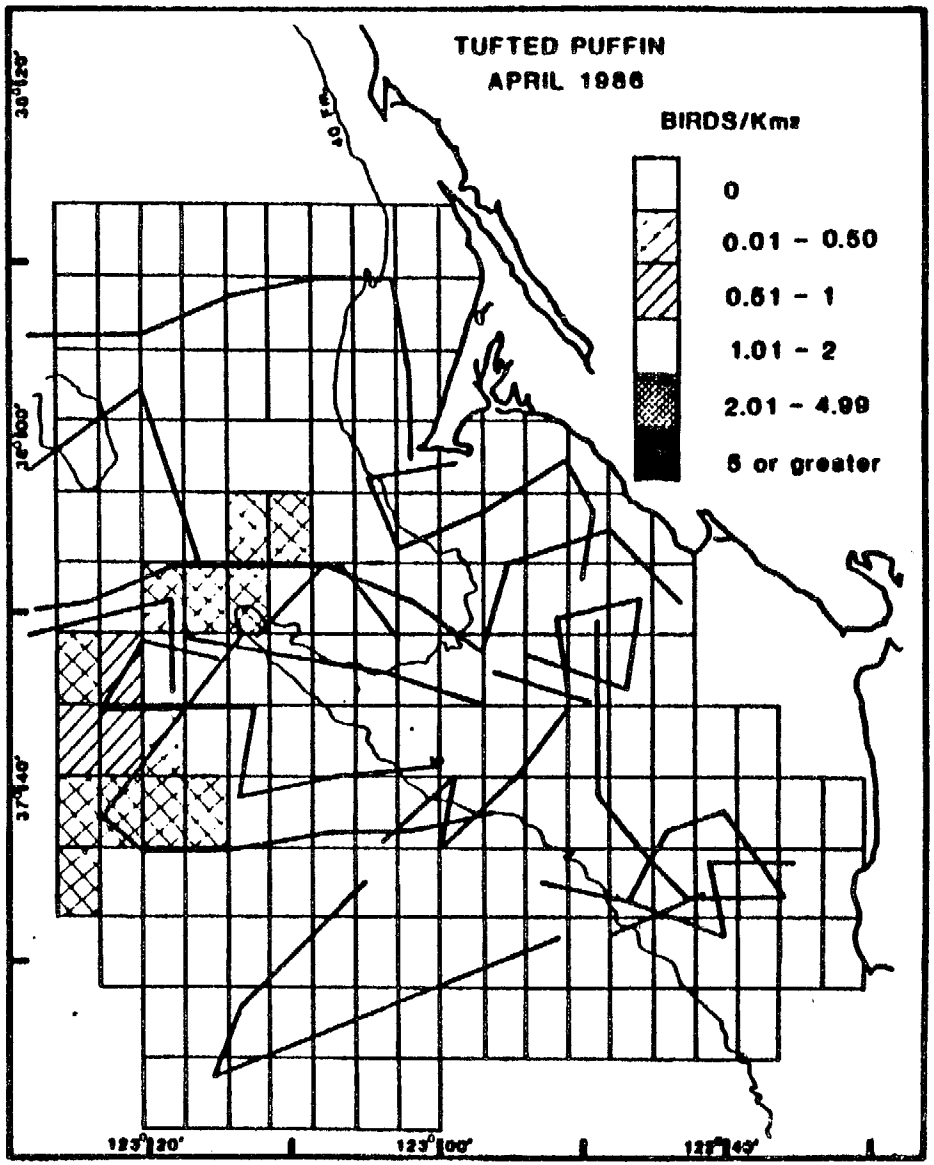

RHINOCEROS AUKLET
APRIL 1985
BIRDS/Km²
0
0.01 - 0.50
0.51 - 1
1.01 - 2
2.01 - 4.99
5 or greater
38°20'
38°00'
37°40'
122°20'
122°00'
121°40'

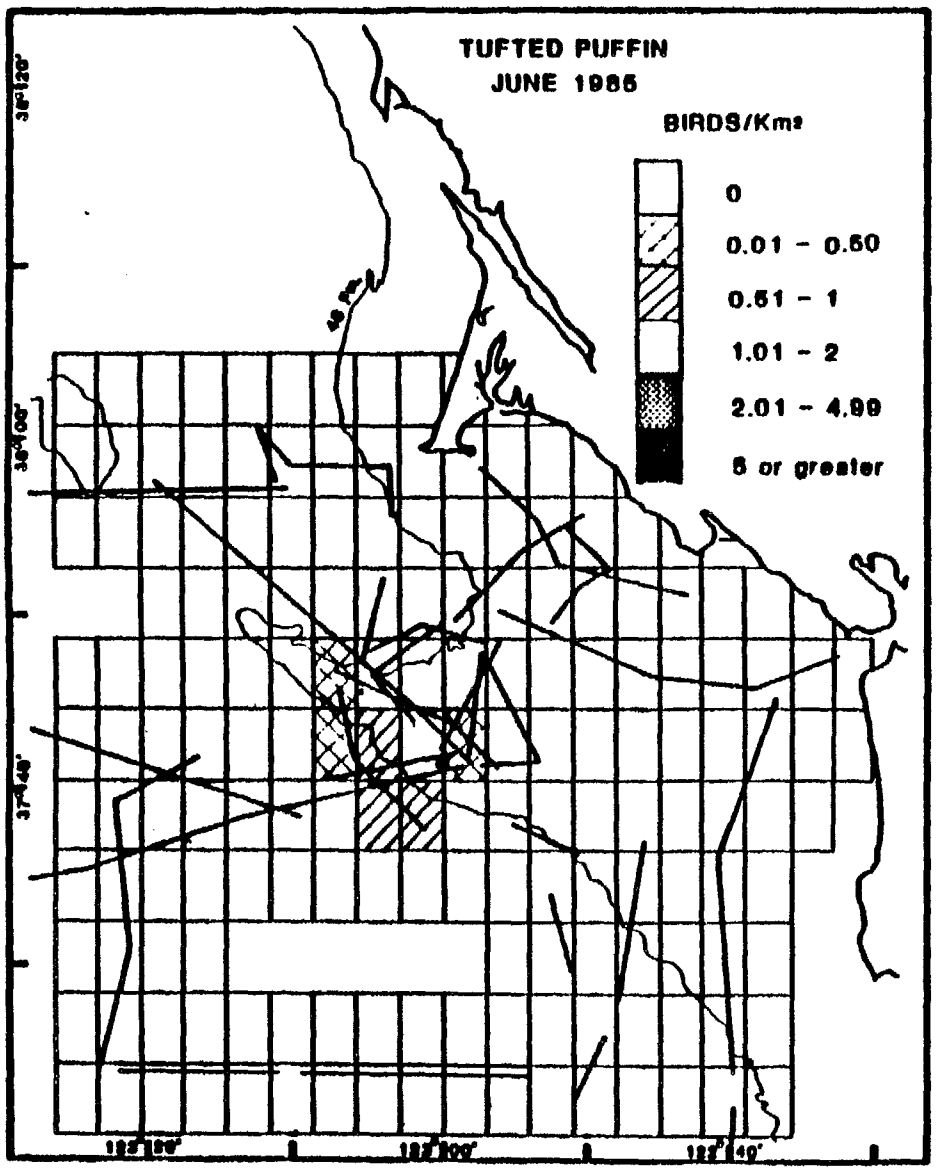

RHINOCEROS AUKLET
APRIL 1986
BIRDS/Km²
0
0.01 - 0.50
0.51 - 1
1.01 - 2
2.01 - 4.99
5 or greater
38°20'
38°00'
37°40'
123°20'
123°00'
122°40'

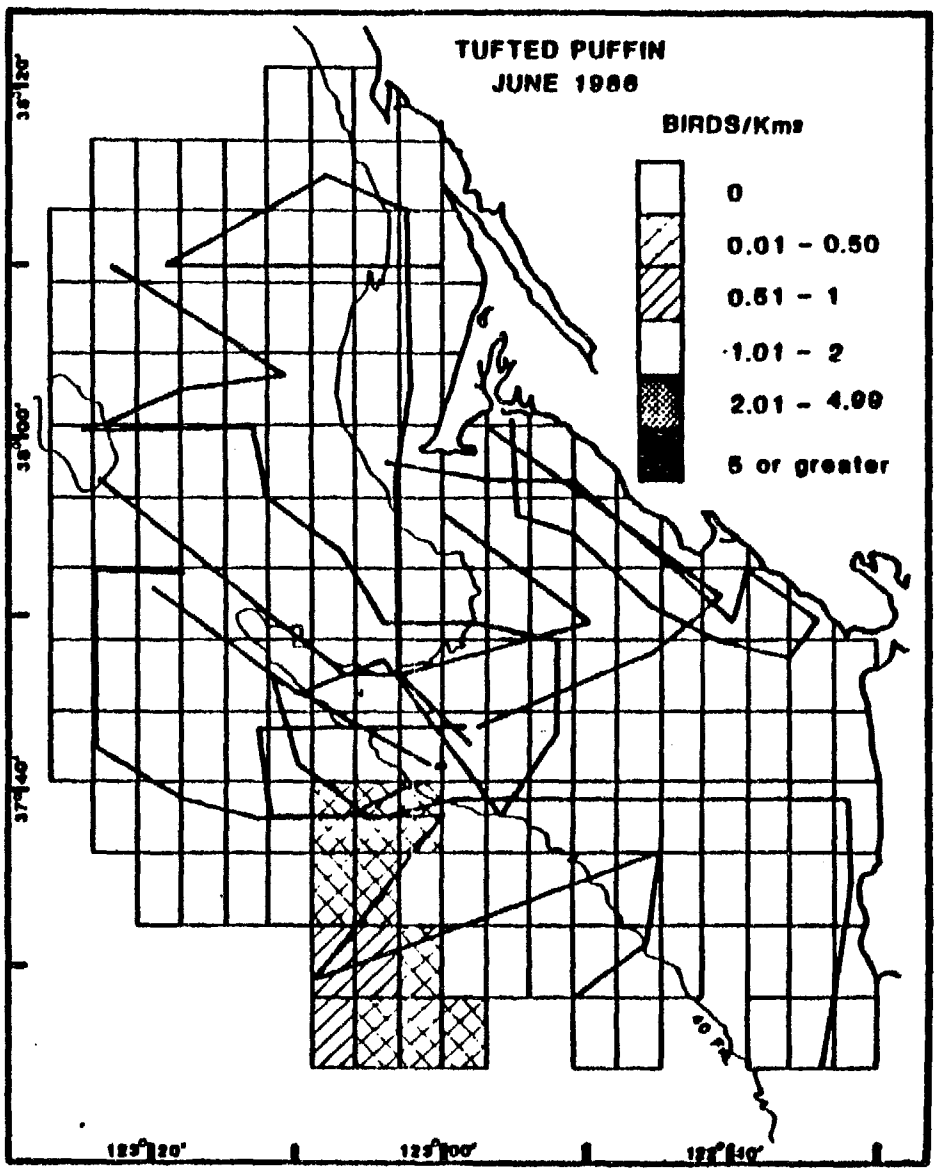

RHINOCEROS AUKLET
JUNE 1985
BIRDS/Km²
0
0.01 - 0.50
0.51 - 1
1.01 - 2
2.01 - 4.99
5 or greater
38°20'
38°00'
37°40'
123°20'
123°00'
122°40'

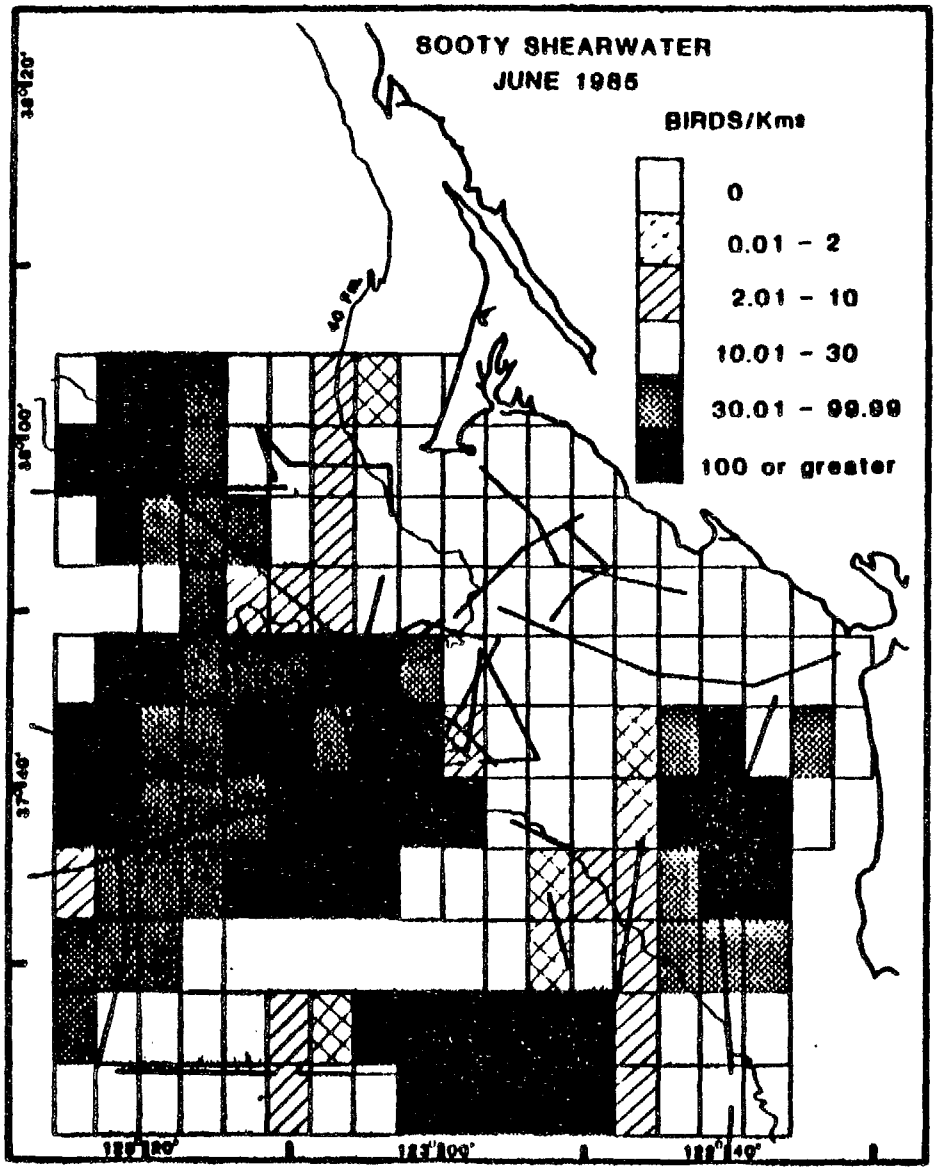

RHINOCEROS AUKLET
JUNE 1986
BIRDS/Km²
0
0.01 - 0.50
0.51 - 1
1.01 - 2
2.01 - 4.99
5 or greater
38°20'
38°00'
37°40'
123°20'
123°00'
122°40'


TUFTED PUFFIN
APRIL 1985
BIRDS/Km²
0
0.01 - 0.50
0.51 - 1
1.01 - 2
2.01 - 4.99
5 or greater
40 Fm
38°20'
38°00'
37°40'
123°20'
123°00'
122°40'


TUFTED PUFFIN
APRIL 1986
BIRDS/Km²
0
0.01 - 0.50
0.51 - 1
1.01 - 2
2.01 - 4.99
5 or greater
40 Fm
38°20'
38°00'
37°40'
123°20'
123°00'
122°40'


TUFTED PUFFIN
JUNE 1985
BIRDS/Km²
0
0.01 - 0.50
0.51 - 1
1.01 - 2
2.01 - 4.99
5 or greater


TUFTED PUFFIN
JUNE 1986
BIRDS/Km²
0
0.01 - 0.50
0.51 - 1
1.01 - 2
2.01 - 4.99
5 or greater


SOOTY SHEARWATER
JUNE 1985
BIRDS/Kms
0
0.01 - 2
2.01 - 10
10.01 - 30
30.01 - 99.99
100 or greater
40 Fm
38°20'
38°00'
37°40'
123°20'
123°00'
122°40'

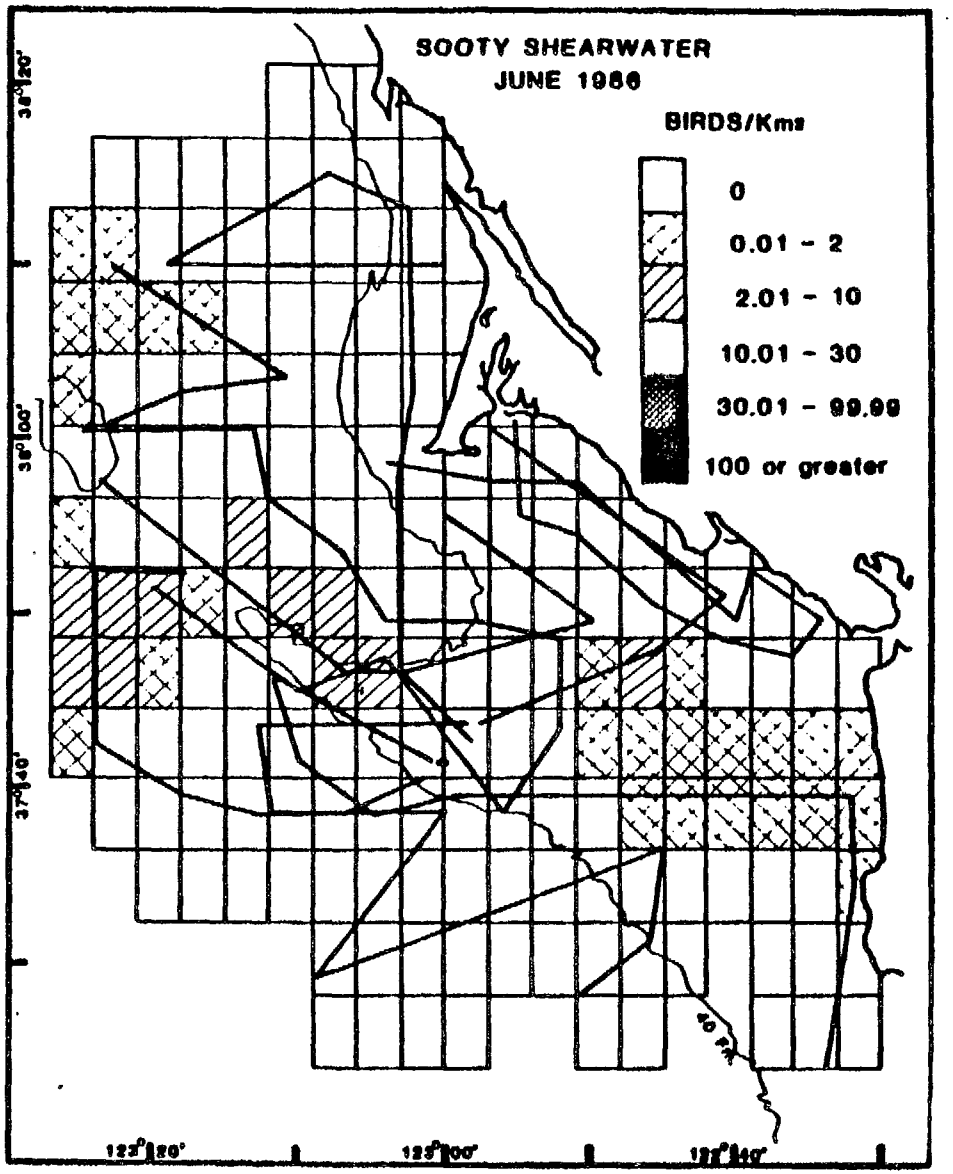
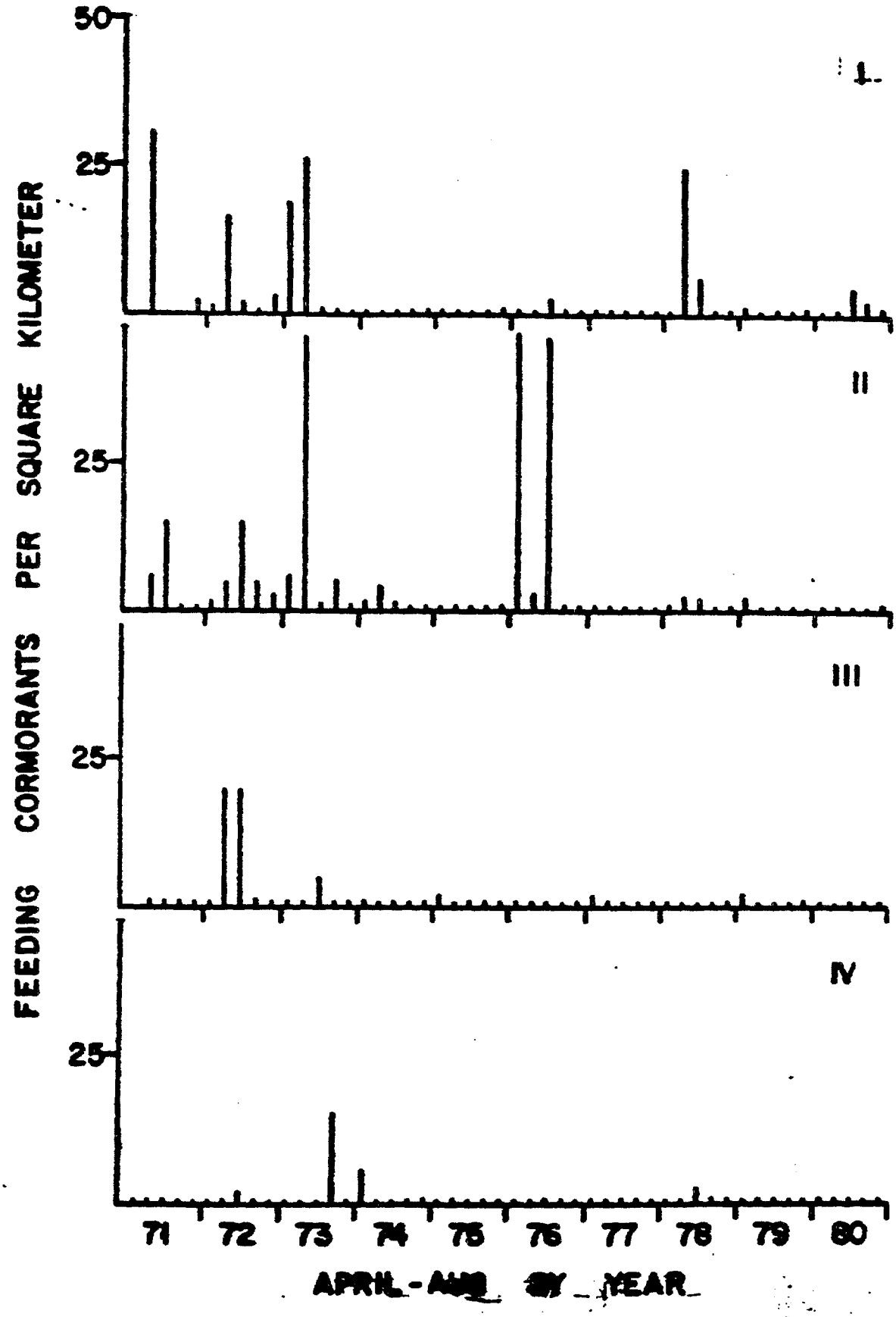
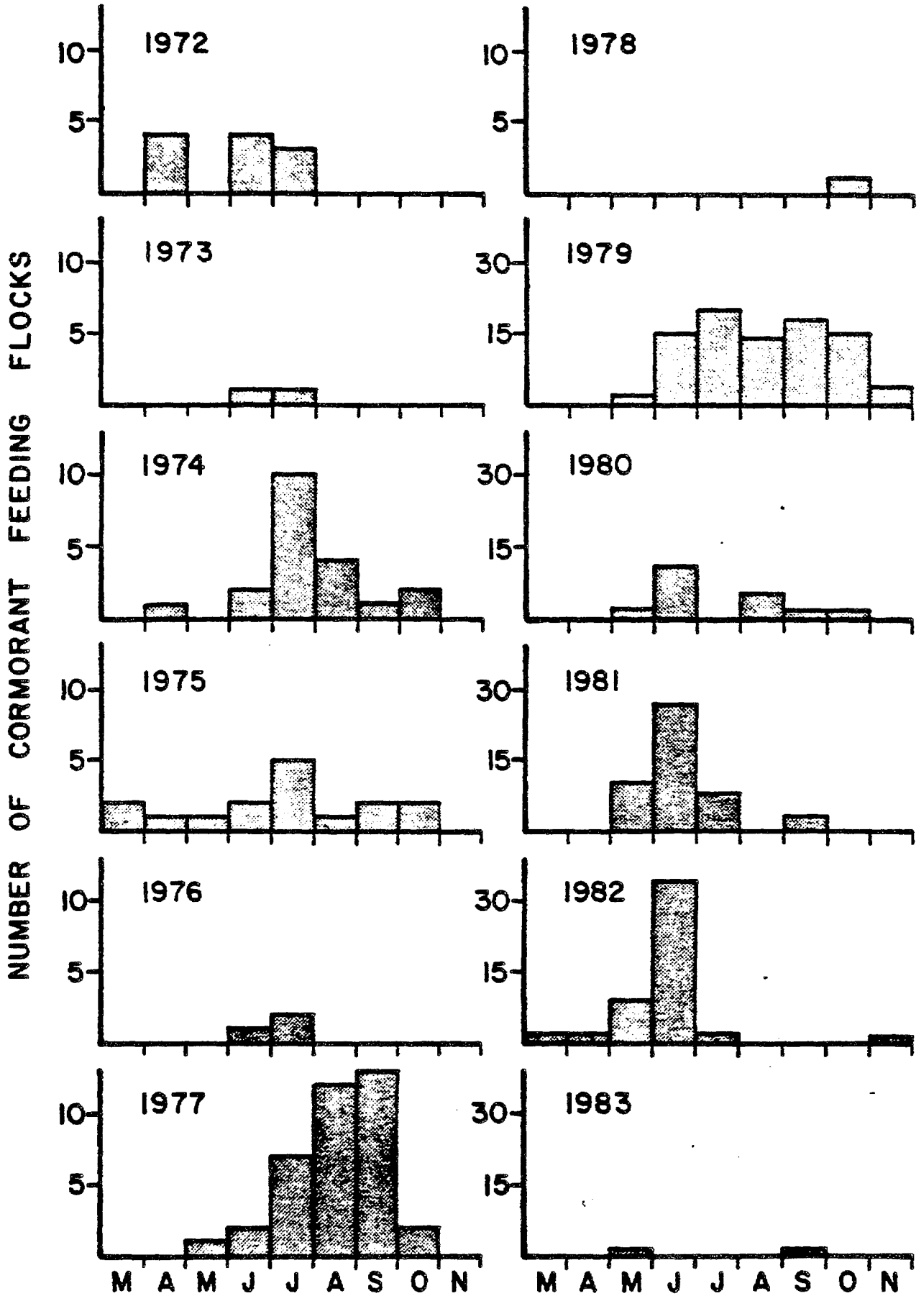
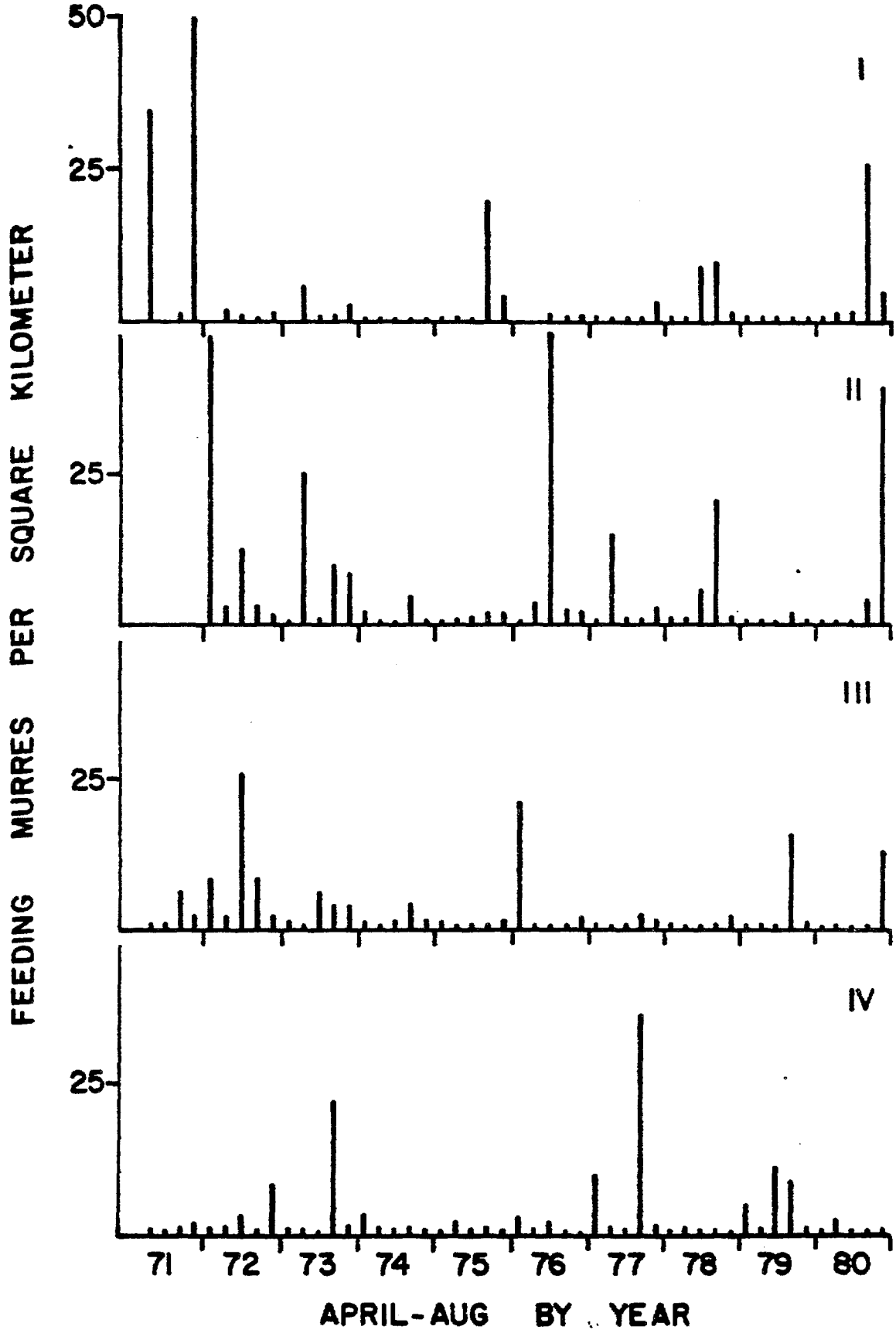
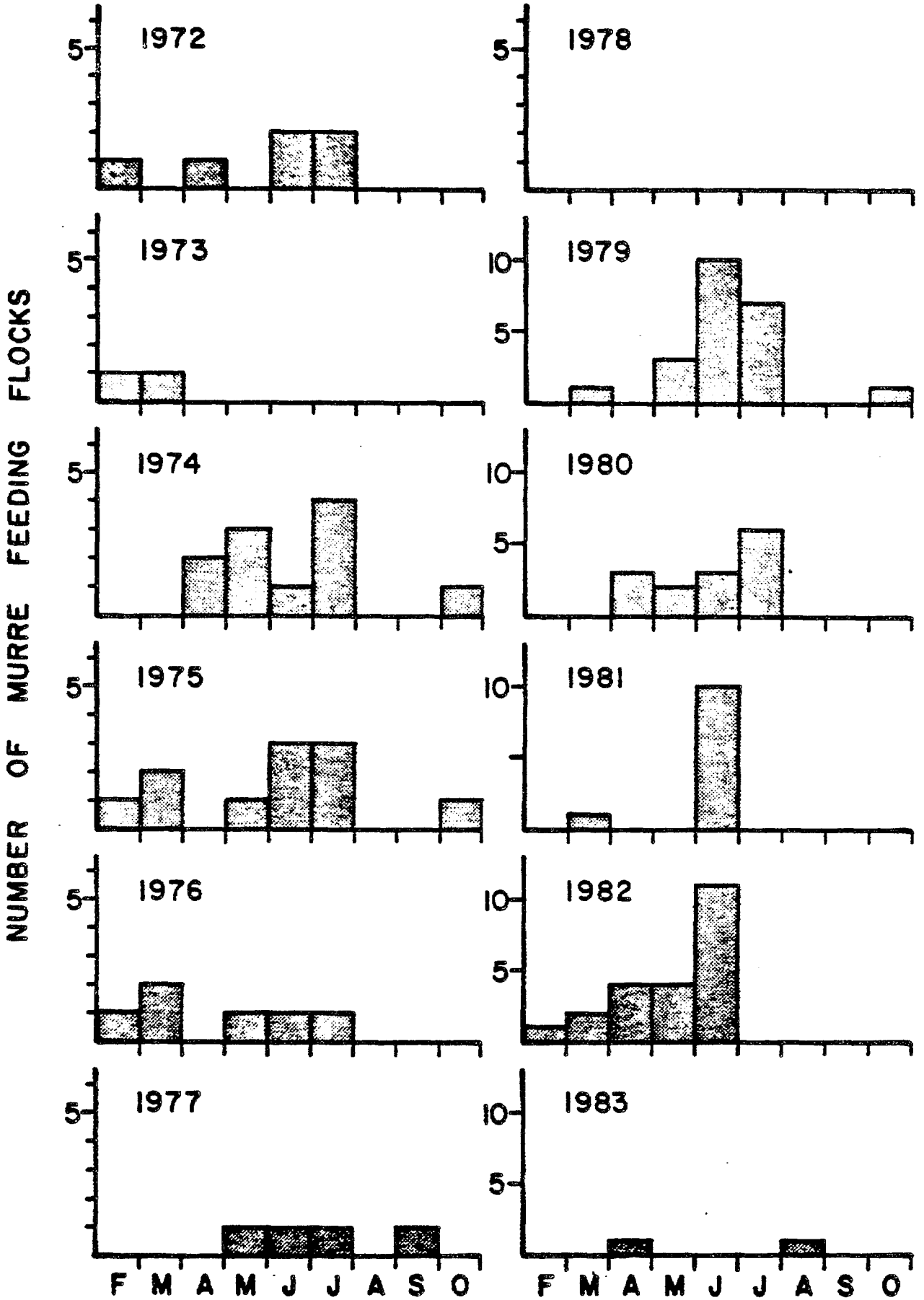

SOOTY SHEARWATER
JUNE 1986
BIRDS/Kms
0
0.01 - 2
2.01 - 10
10.01 - 30
30.01 - 99.99
100 or greater
40 Fm
38°20'
38°00'
37°40'
123°20'
123°00'
122°40'

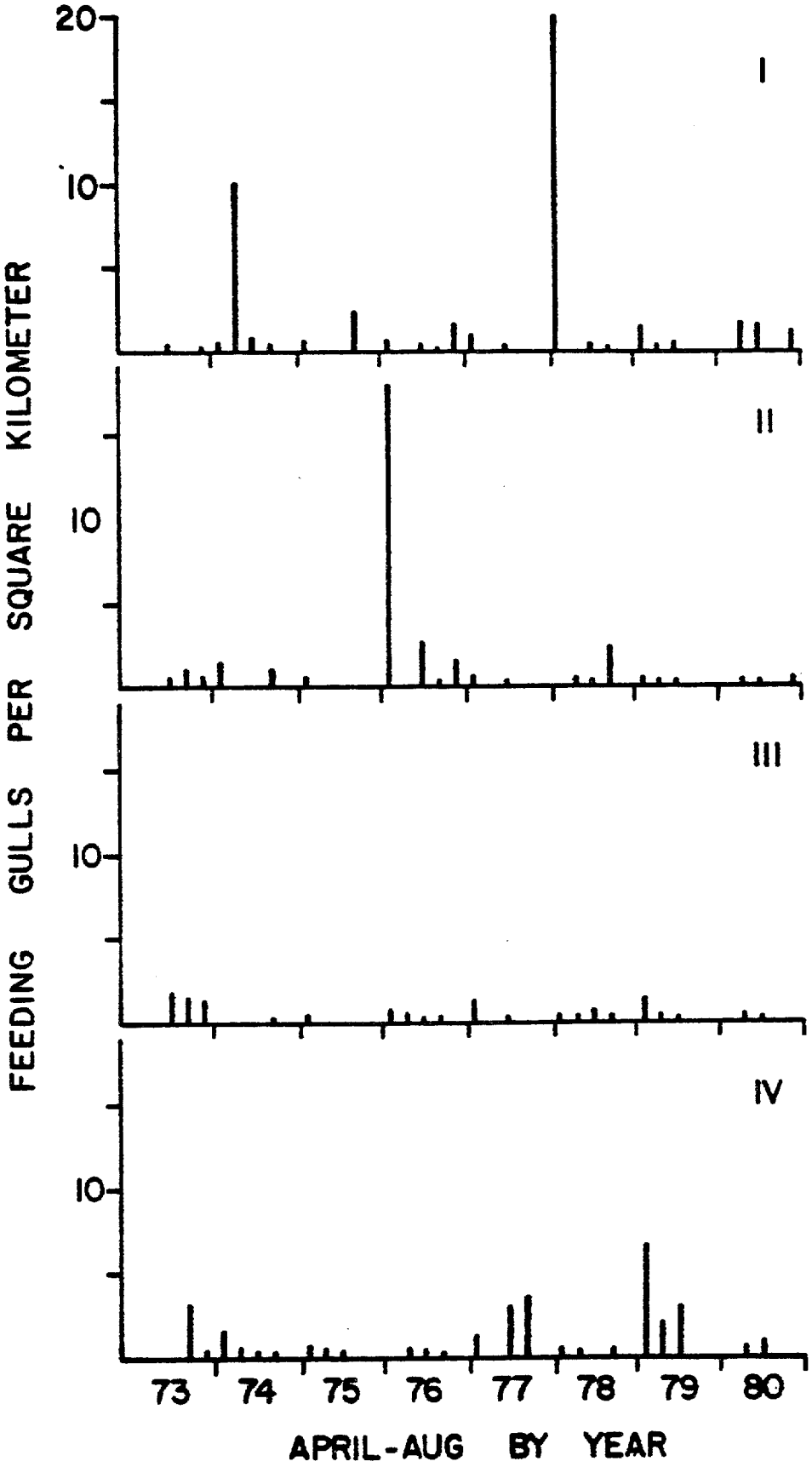
FIG 3B

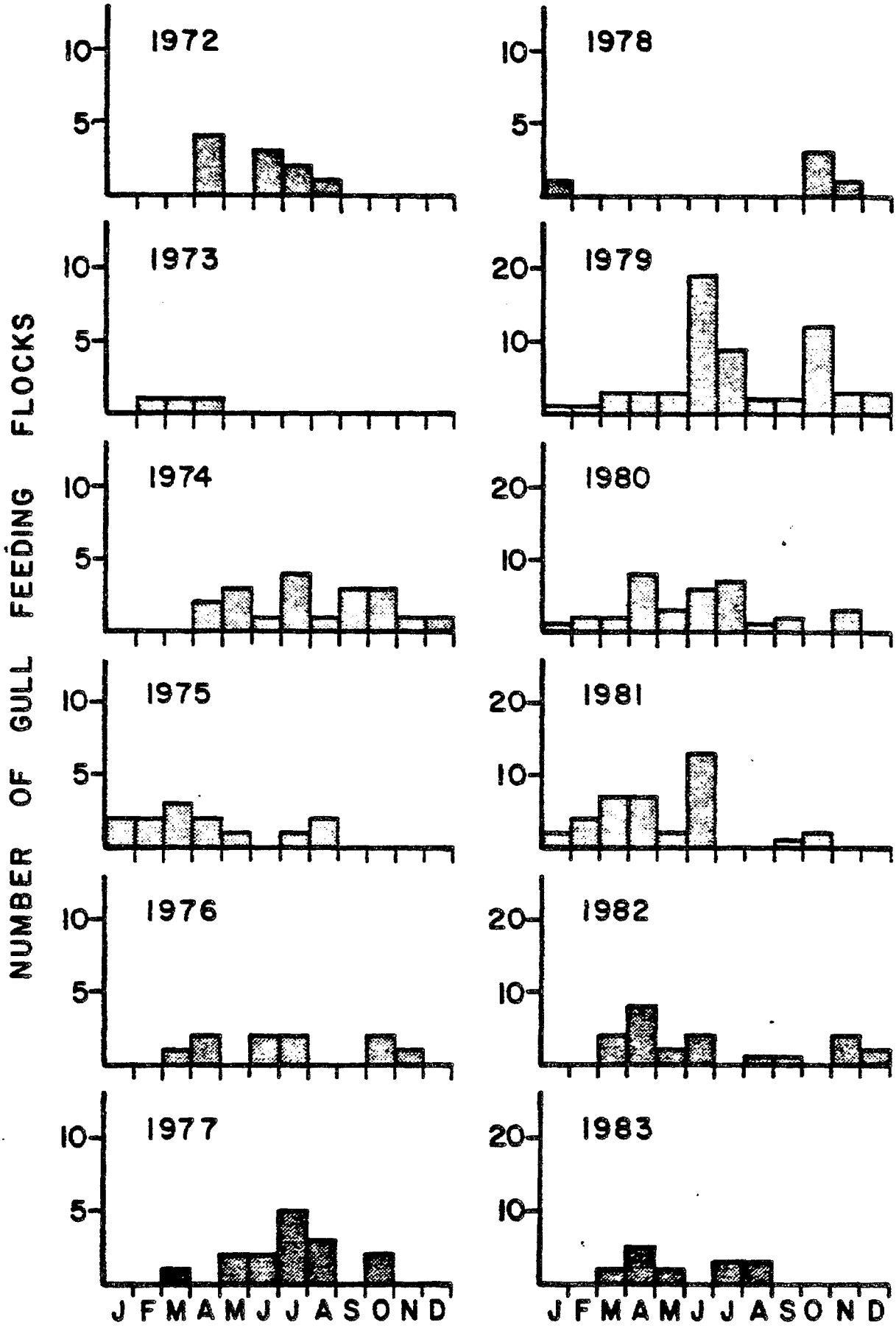

FEEDING CORMORANTS PER SQUARE KILOMETER
50
25
I
II
III
IV
71
72
73
74
75
76
77
78
79
80
APRIL-AUG BY YEAR

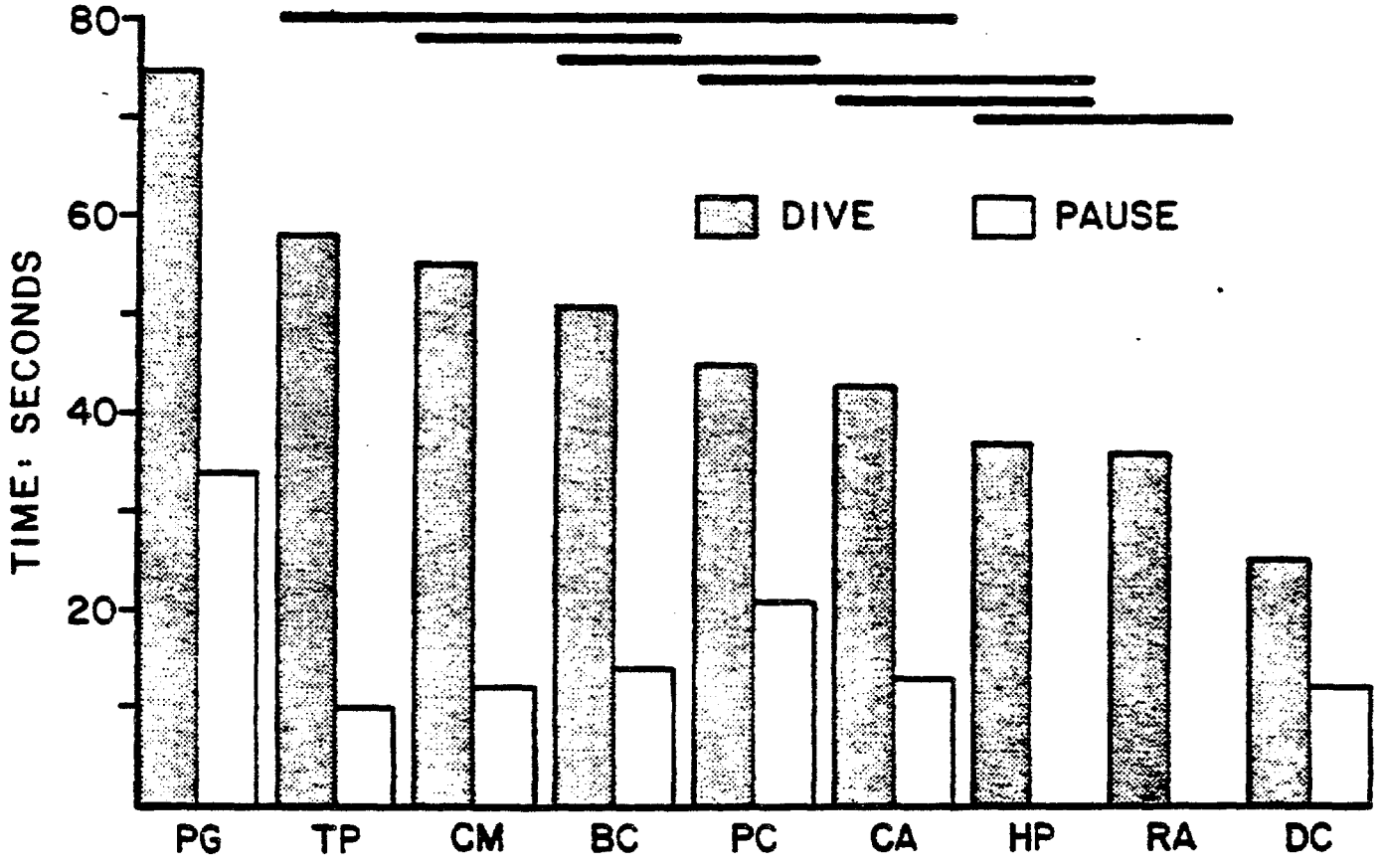

NUMBER OF CORMORANT FEEDING FLOCKS
1972
1973
1974
1975
1976
1977
1978
1979
1980
1981
1982
1983
10
5
30
15
M A M J J A S O N

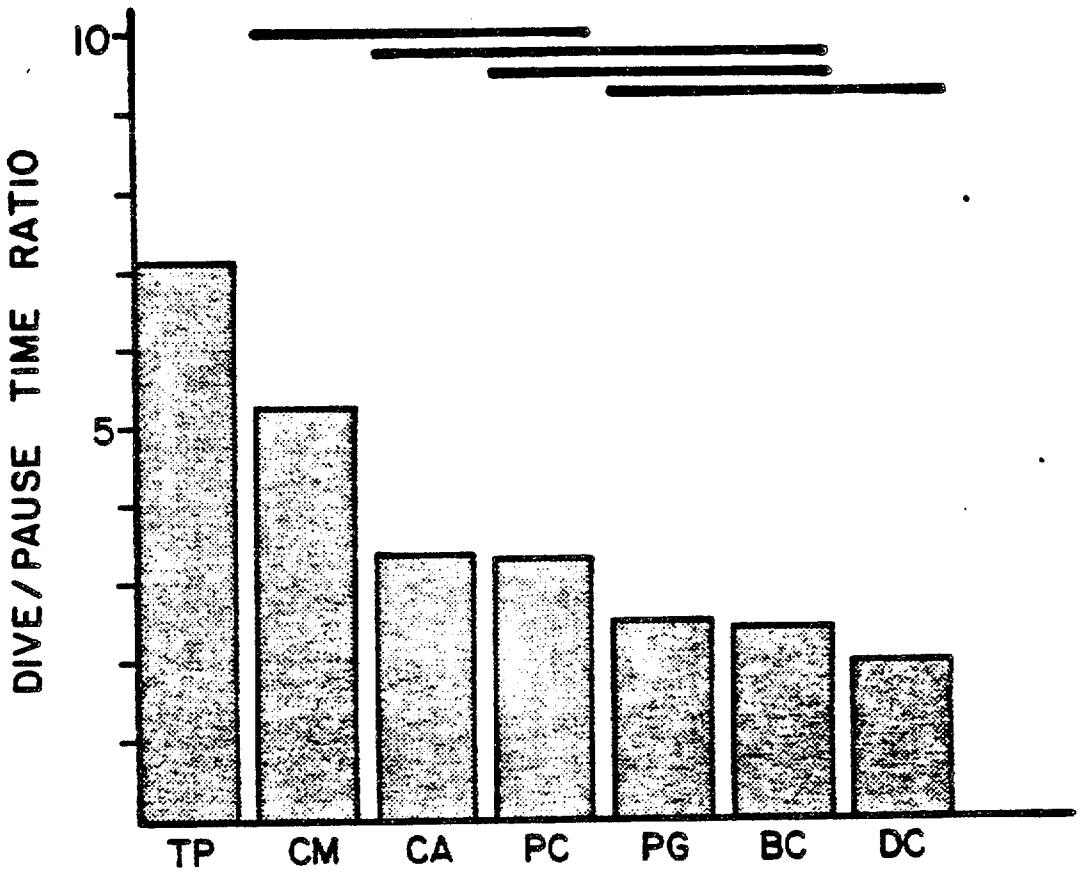

FEEDING MURRES PER SQUARE KILOMETER
50
25
I
25
II
25
III
25
IV
71
72
73
74
75
76
77
78
79
80
APRIL-AUG BY YEAR

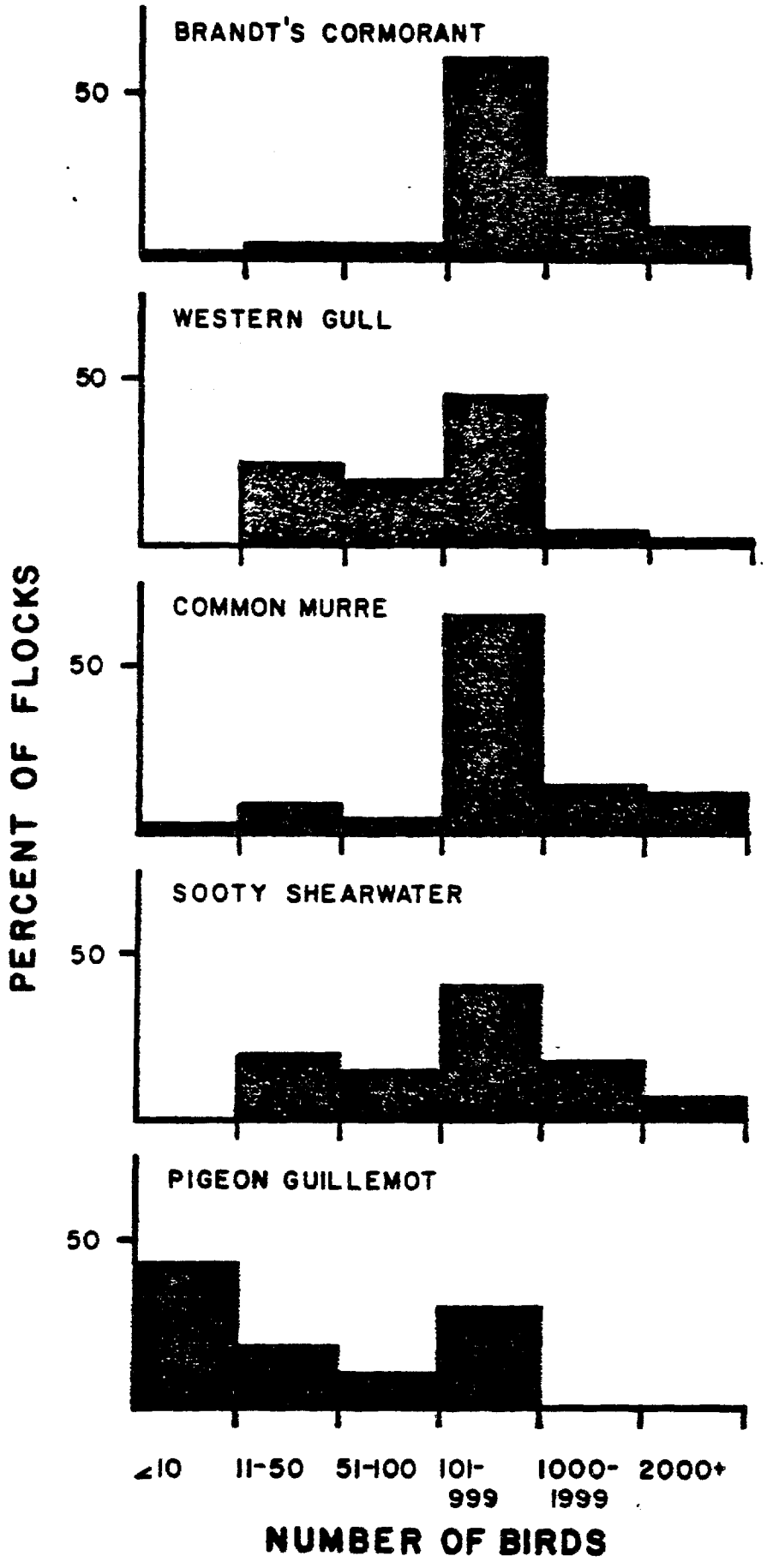

NUMBER OF MURRE FEEDING FLOCKS
1972
1973
1974
1975
1976
1977
1978
1979
1980
1981
1982
1983
5
10
F M A M J J A S O

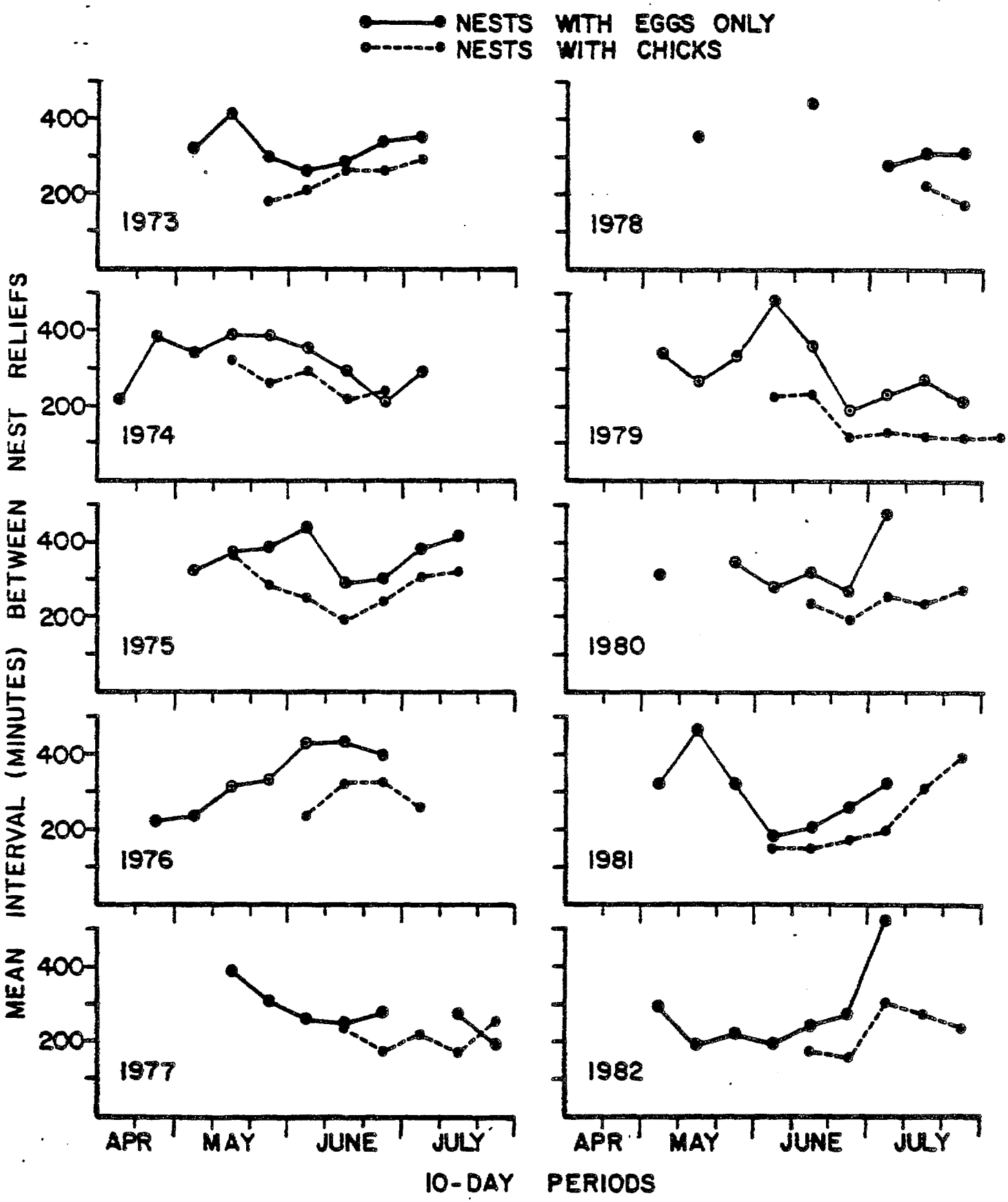

FEEDING GULLS PER SQUARE KILOMETER
20
10
I
10
II
10
III
10
IV
73
74
75
76
77
78
79
80
APRIL-AUG BY YEAR

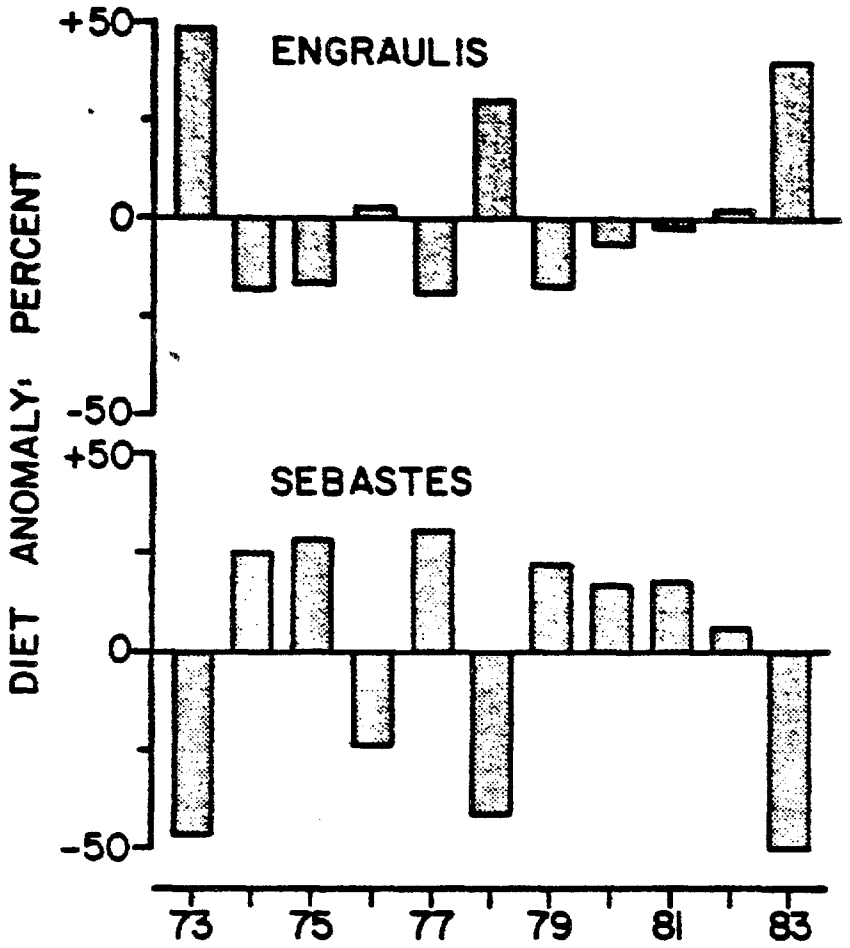

NUMBER OF GULL FEEDING FLOCKS
1972
1973
1974
1975
1976
1977
1978
1979
1980
1981
1982
1983
10
5
20
J F M A M J J A S O N D

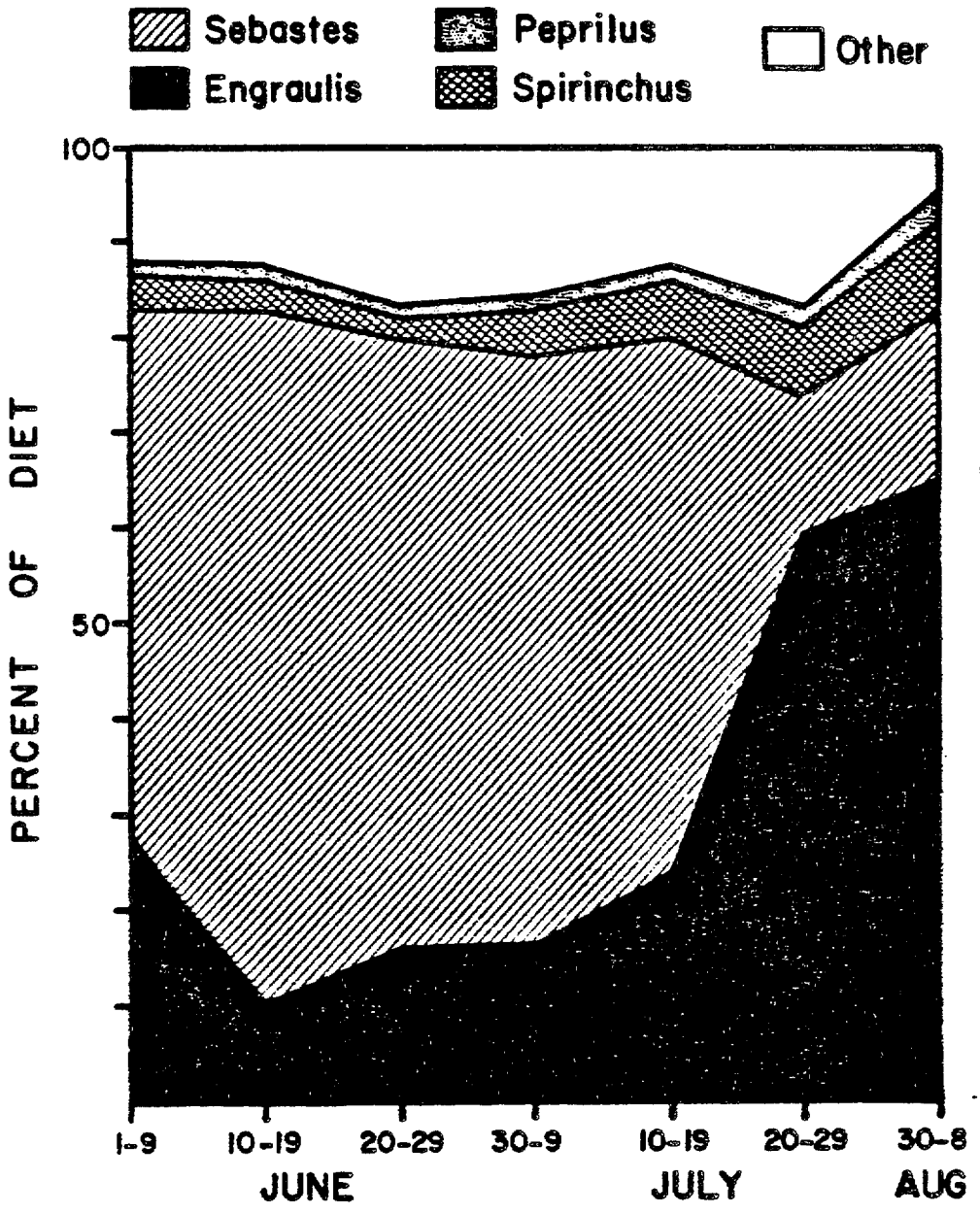

80
60
40
20
TIME: SECONDS
DIVE
PAUSE
PG
TP
CM
BC
PC
CA
HP
RA
DC

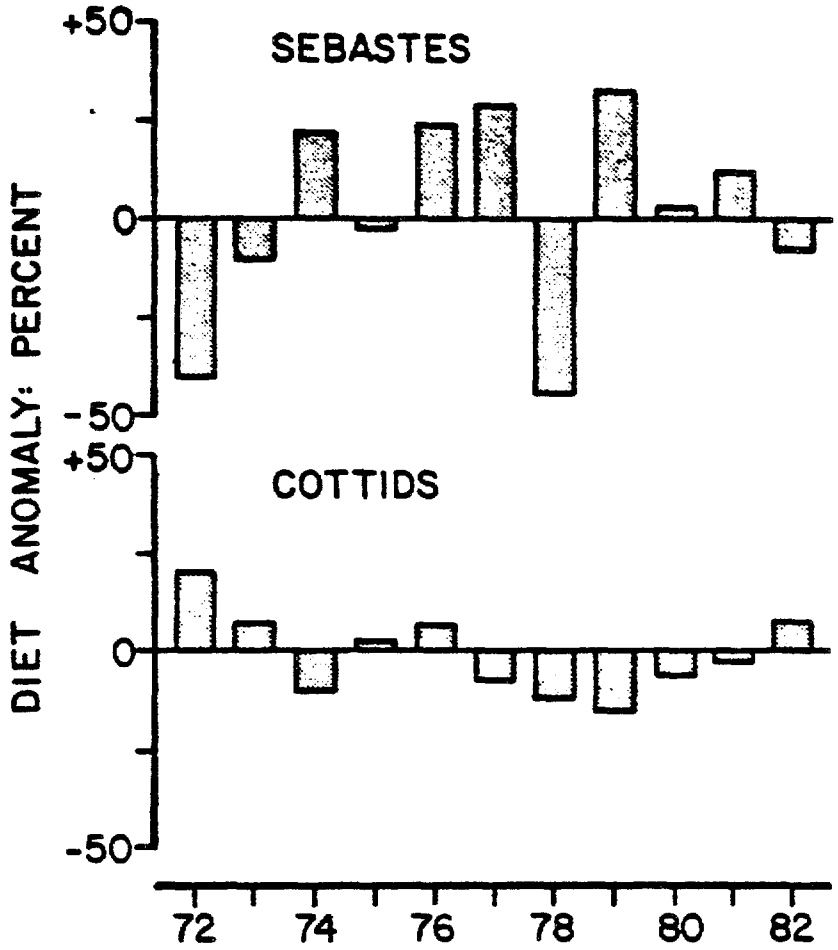

10
5
DIVE/PAUSE TIME RATIO
TP
CM
CA
PC
PG
BC
DC

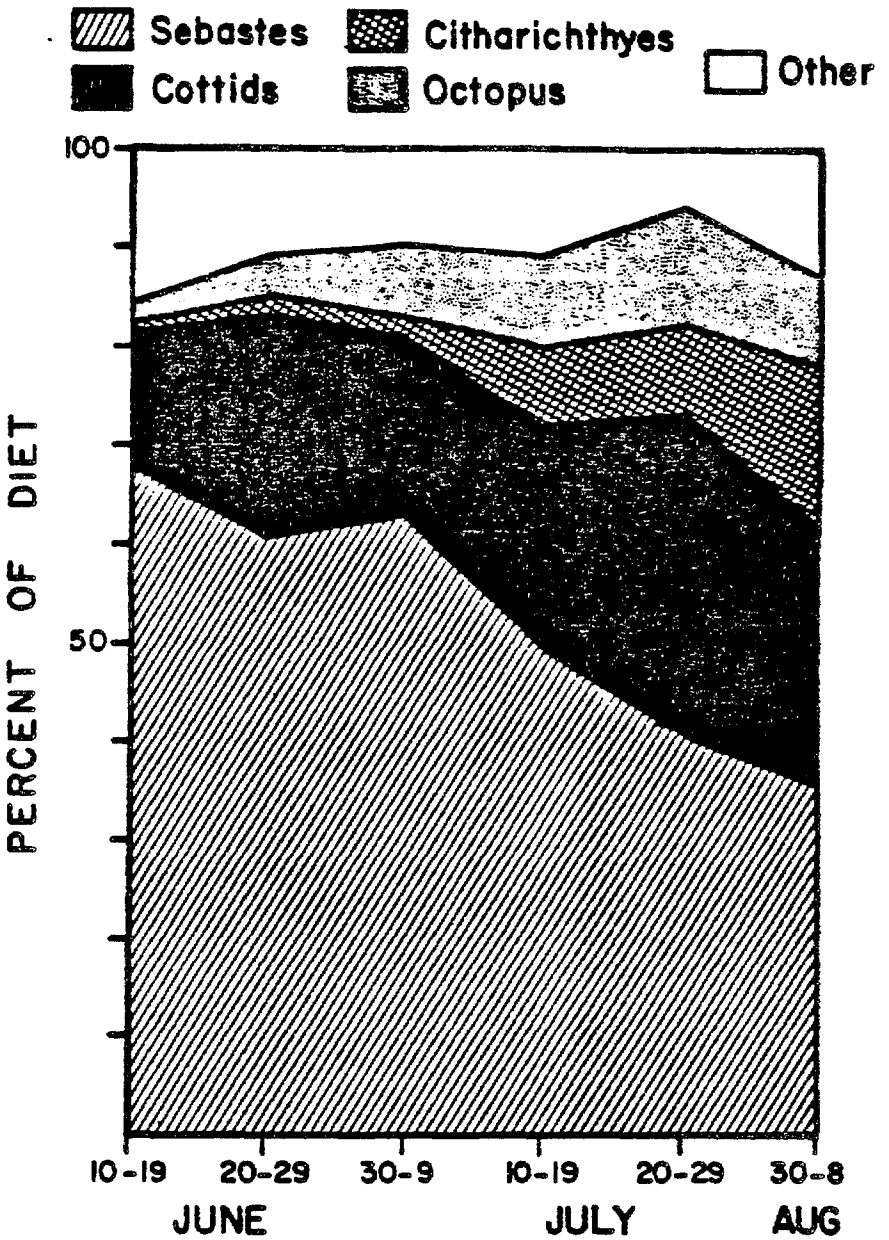

BRANDT'S CORMORANT
WESTERN GULL
COMMON MURRE
SOOTY SHEARWATER
PIGEON GUILLEMOT
50
PERCENT OF FLOCKS
<10
11-50
51-100
101-999
1000-1999
2000+
NUMBER OF BIRDS


NESTS WITH EGGS ONLY
NESTS WITH CHICKS
MEAN INTERVAL (MINUTES) BETWEEN NEST RELIEFS
400
200
1973
1974
1975
1976
1977
1978
1979
1980
1981
1982
APR
MAY
JUNE
JULY
10-DAY PERIODS


ENGRAULIS
SEBASTES
DIET ANOMALY: PERCENT
+50
0
-50
+50
0
-50
73
75
77
79
81
83


Sebastes
Engraulis
Peprilus
Spirinchus
Other
100
50
PERCENT OF DIET
1-9
10-19
20-29
30-9
10-19
20-29
30-8
JUNE
JULY
AUG


SEBASTES
COTTIDS
DIET ANOMALY: PERCENT
+50
0
-50
+50
0
-50
72
74
76
78
80
82


Sebastes
Citharichthyes
Cottids
Octopus
Other
100
50
PERCENT OF DIET
10-19
20-29
30-9
10-19
20-29
30-8
JUNE
JULY
AUG

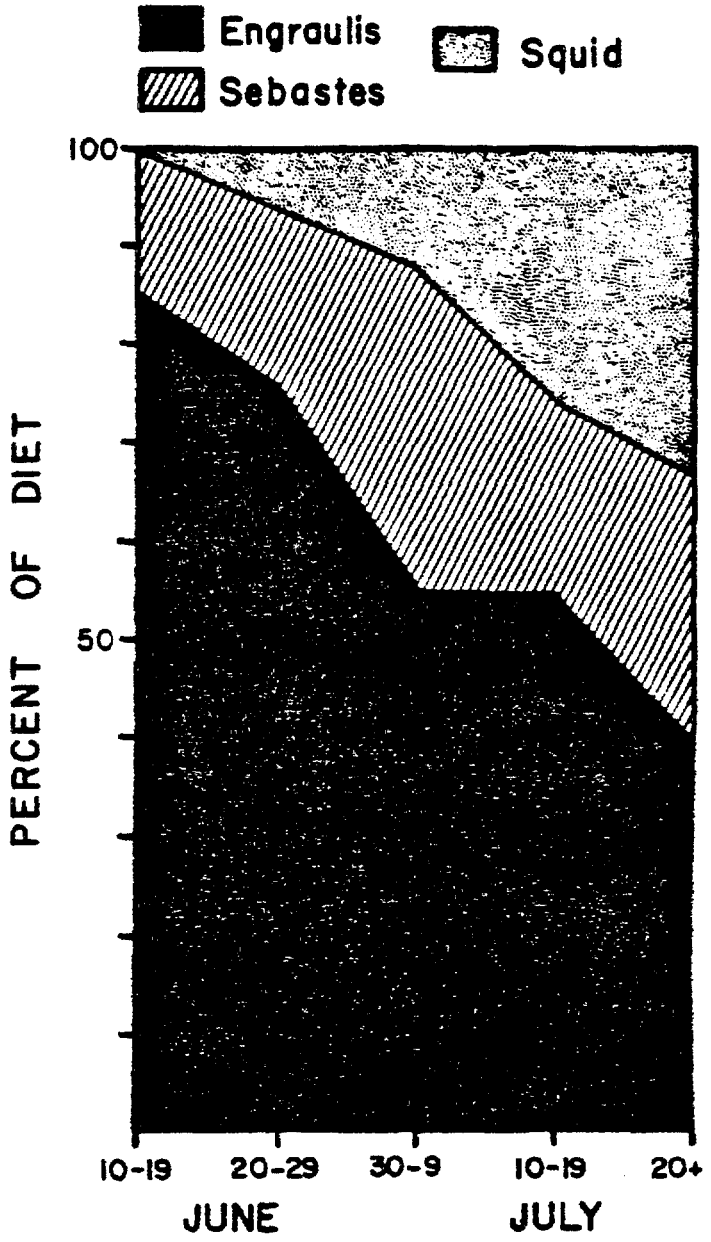

Engraulis
Sebastes
Squid
100
50
PERCENT OF DIET
10-19
20-29
30-9
10-19
20+
JUNE
JULY

Table 2.1. The number of transects in which each species was seen, by zone, along the Golden Gate-to-Farallon census track

| Species | Zone[a] | | | |
|---|---|---|---|---|
| | I | II | III | IV |
| Leach's Storm-Petrel | 0 | 0 | 0 | 1 |
| Ashy Storm-Petrel | 0 | 0 | 1 | 3 |
| Double-crested Cormorant | 19 | 6 | 5 | 9 |
| Brandt's Cormorant | 169 | 183 | 196 | 217 |
| Pelagic Cormorant | 27 | 14 | 7 | 26 |
| Western Gull | 127 | 134 | 147 | 147 |
| Common Murre | 145 | 184 | 216 | 222 |
| Pigeon Guillemot | 6 | 12 | 14 | 43 |
| Cassin's Auklet | 1 | 0 | 2 | 74 |
| Tufted Puffin | 0 | 0 | 1 | 36 |
| Rhinoceros Auklet | 0 | 0 | 2 | 47 |

a Zone I is near the coast, zone IV near the islands; Figure 2.2.

Table 2.2. Coefficients of association between species by census blocks in the Gulf of the Farallones, compared during June 1985 and June 1986

| | | 1[a] | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 |
|---|---|---|---|---|---|---|---|---|---|---|
| | | | | | | 1985 | | | | |
| Sooty Shearwater | (1) | — | | | | | | | | |
| Ashy Storm-Petrel | (2) | 1.000 | — | | | | | | | |
| Brandt's Cormorant | (3) | 1.000 | .734 | — | | | | | | |
| Pelagic Cormorant | (4) | 1.000 | .612 | 1.000 | — | | | | | |
| Western Gull | (5) | .076 | .921 | .941 | .971 | — | | | | |
| Common Murre | (6) | .130 | .085 | .975 | .969 | .347 | — | | | |
| Pigeon Guillemot | (7) | 1.000 | .612 | 1.000 | 1.000 | .971 | .969 | — | | |
| Cassin's Auklet | (8) | .596 | .939 | 1.000 | 1.000 | .491 | .283 | 1.000 | — | |
| Rhinoceros Auklet | (9) | .514 | .972 | 1.000 | 1.000 | .706 | .246 | 1.000 | .662 | — |
| Tufted Puffin | (10) | 1.000 | .685 | .734 | .738 | .942 | .967 | .738 | 1.000 | 1.000 |
| | | | | | | 1986 | | | | |
| Sooty Shearwater | | — | | | | | | | | |
| Ashy Storm-Petrel | | .107 | — | | | | | | | |
| Brandt's Cormorant | | .552 | .000 | — | | | | | | |
| Pelagic Cormorant | | .595 | .000 | .719 | — | | | | | |
| Western Gull | | .519 | .000 | .415 | .759 | — | | | | |
| Common Murre | | .779 | .000 | .768 | .938 | .665 | — | | | |

Table 2.2 (cont'd)

| | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| Pigeon Guillemot | .576 | .000 | .787 | .647 | .705 | .968 | -- | | |
| Cassin's Auklet | .823 | .103 | .517 | .908 | .665 | .200 | .938 | -- | |
| Rhinoceros Auklet | .760 | .167 | .488 | .889 | .668 | .405 | .924 | .704 | -- |
| Tufted Puffin | .469 | .000 | .610 | .564 | .820 | .804 | .598 | .873 | 1.000 |

a Numbers correspond to those following respective species; underlining indicates values which were greater in 1986.

Table 2.3. A comparison among abundant species, which forage within three kilometers of the island, in their tendencies to form mixed-species foraging flocks; warm-water years as opposed to others

| Species | No. flocks | Proportion flocks alone | Cole's Coefficient: Brandt's Cormorant | Western Gull | Common Murre |
|---|---|---|---|---|---|
| | Cool years: all except 1973, 1976, 1978, 1980 & 1983 | | | | |
| Brandt's Cormorant | 391 | 0.37 [a] | — | | |
| Western Gull | 227 | 0.21 [a] | 0.84 [a,b] | — | |
| Common Murre | 99 | 0.08 | 0.28 [a,b] | 0.19 [a,b] | — |
| Sooty Shearwater | 15 | 0.20 | 0.03 | 0.02 | -0.04 [a] |
| | Warm years: 1973, 1976, 1978, 1980, 1983 | | | | |
| Brandt's Cormorant | 139 | 0.50 [b] | — | | |
| Western Gull | 126 | 0.54 [b] | 0.34 [b] | — | |
| Common Murre | 28 | 0.07 | 0.12 | 0.11 | — |
| Sooty Shearwater | 12 | 0.00 | 0.01 | 0.06 | 0.23 [b] |

Table 23 (cont'd)

a Comparison of species' percentages for the two groups of years show statistical signficance ($p<.05$, paired t-test).

b These are statistically significant values ($p<.05$).

Table 24. Comparison of the mean time interval between nest reliefs by Brandt's Cormorants incubating eggs or attending chicks and of the number of feeding trips per day, 1973-1982[a]

| | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| Minutes between reliefs, birds with eggs: | 1975 | 1974 | 1976 | 1978 | 1980 | 1973 | 1977 | 1979 | 1981 | 1982 |
| | 355 | 340 | 334 | 329 | 322 | 297 | 277 | 260 | 248 | 233 |
| Minutes between reliefs, birds with chicks: | 1976 | 1975 | 1974 | 1973 | 1980 | 1982 | 1977 | 1982 | 1978 | 1979 |
| | 303 | 258 | 241 | 244 | 231 | 201 | 193 | 188 | 182 | 132 |
| Visits per nest per day:[b] | 1976 | 1973 | 1975 | 1974 | 1982 | 1980 | 1978 | 1981 | 1977 | 1979 |
| | 2.6 | 3.5 | 3.8 | 4.0 | 4.3 | 4.6 | 5.2 | 5.9 | 6.7 | 8.6 |

a Means connected by lines are similar; SNK test, $p > .05$.

b Includes nests only with chick between 11-35 days old.

Table 2.5. Comparison of the mean time interval away from nests, and number feeding trips per day by Pelagic Cormorants, 1973-1977[a]

| | Nests with eggs | | | | | Nests with chicks | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| Minutes away: | | | | | | | | | | |
| | 1976 | 1977 | 1974 | 1973 | 1975 | 1976 | 1974 | 1973 | 1975 | 1977 |
| | 248 | 201 | 191 | 179 | 123 | | 191 | 134 | 96 | 91 |
| | | | | | | No | | | | |
| | | | | | | chicks | | | | |
| Trips per day per nest: | | | | | | | | | | |
| | 1976 | 1973 | 1977 | 1974 | 1975 | 1976 | 1974 | 1973 | 1977 | 1975 |
| | 3.3 | 3.6 | 3.6 | 4.6 | 5.4 | | 5.0 | 6.4 | 7.9 | 8.6 |
| | Not | | | | | No | | | | |
| | compared | | | | | chicks | | | | |

a Means connected by lines are similar; SNK test, $p > .05$.

Table 2.6. Comparison of the mean time interval between feeds and number of feeds per day for Common Murre chicks, 1973-1982[a]

Minutes between feeds:

| 1982 | 1977 | 1974 | 1975 | 1976 | 1983 |
|---|---|---|---|---|---|
| 141.2 | 142.6 | 147.4 | 151.6 | 194.4 | 217.9 |

Feeds per day:

| 1977 | 1982 | 1975 | 1974 | 1976 | 1983 | 1973 |
|---|---|---|---|---|---|---|
| 5.0 | 4.8 | 4.6 | 3.8 | 3.0 | 2.8 | 2.2 |

a Similar means underlined; SNK test, $p > .05$.

Table 2.7. Extent of overlap between years in the numerical composition of diet of Double-crested, Pelagic and Brandt's cormorants using Morisita's Index[a]

| Year | 1974 | 1975 | 1976 | 1977 |
|---|---|---|---|---|
| | | Double-crested Cormorant | | |
| 1974 | | .999 | .999 | .999 |
| 1975 | | — | .999 | .999 |
| 1976 | | | — | .999 |
| | | Pelagic Cormorant | | |
| 1975 | | — | .637 | .982 |
| 1976 | | | — | .521 |
| | | Brandt's Cormorant | | |
| 1973 | .914 | .882 | .616 | .561 |
| 1974 | — | .990 | .405 | .768 |
| 1975 | | — | .402 | .853 |
| 1976 | | | — | .107 |

a 1 = complete overlap, 0 = none; similar diets indicated by underlining.

Table 2.8. Percent diet composition by number (n) and weight (w) compared among three cormorant species, with years grouped according to overlaps identified in Table 2.7

| | Double-crested | | Pelagic | | | | Brandt's | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | 1974-77 | | 1975/77 | | 1976 | | 1973-75/77 | | 1976 | |
| Prey[a] | n | w | n | w | n | w | n | w | n | w |
| *Porichthys notatus* | | | | | | | 2 | 1 | 6 | 1 |
| *Citharichthys sordidus* | 1 | | | | | | 2 | 13 | 14 | 25 |
| *C. stigmaeus* | | | | | | | | | 1 | 2 |
| *Clupea pallasi* | | | | | | | | | 1 | 1 |
| *Cottids* | 3 | 1 | 27 | 24 | 78 | 61 | 3 | 1 | 12 | 4 |
| *Cymatogaster aggregata* | 91 | 8 | | | | | 1 | 1 | 10 | 19 |
| *Phanerodon furcatus* | 1 | | | | | | | | | |
| *Engraulis mordax* | | | | | | | 1 | 4 | 14 | 10 |
| *Microgadus proximus* | 1 | | | | | | 21 | 22 | 8 | 2 |
| *Acanthogobius flavimanus* | | | | | | | | | 1 | 1 |
| *Coryphopterus nicholsii* | | | 1 | 1 | 1 | 1 | | | | |
| *Chilara taylori* | | | 1 | 1 | | | 3 | 6 | 6 | 3 |
| *Glyptocephalus zachirus* | | | | | | | | 1 | 1 | 2 |
| *Parophrys vetulus* | | | | | | | 1 | 8 | 10 | 20 |
| *Sebastes* spp. | 1 | | 65 | 72 | 20 | 37 | 66 | 42 | 13 | 10 |
| *Spirontocaris* spp. | | | 5 | 2 | | | | | | |

Table 28 (cont'd)

| Loligo opalescens | | | | | 2 3 |
|---|---|---|---|---|---|
| Total items | 2815 | 5673 | 1166 | 10125 | 1065 |
| Total weight, gm | 104394 | 11832 | 2517 | 54644 | 21950 |
| Mean diversity, n | .359±.153 | .830±.077 | .462 | 1.013±.597 | 2.379 |
| diversity, w | .066±.121 | .749±.063 | .715 | 1.647±.439 | 2.157 |
| Prey/sample | 16.5±2 | 40.5±1 | 20 | 44±20 | 14 |

a Only species contributing to the diet by at least 1% of the total are shown.

Table 2.9. Approximate mean sizes of fish eaten by cormorants (standard length, ±SD, n)

| Year | Pelagic (48)[a] | Double-crested (55) | Brandt's (67) | Difference, t-test |
|---|---|---|---|---|
| | *Sebastes* spp. | | | |
| 1974 | 69.4± 9.6, 48 | 80.5±26.2, 4 | 71.0± 7.2, 48 | ns |
| 1975 | 56.3±17.3, 48 | 69.2±34.8, 5 | 61.2±14.3, 48 | ns |
| 1976 | 70.6±28.8, 48[b] | | 107.8±14.3, 8 | p<.05 |
| 1977 | 59.8± 7.5, 48 | 62.0±17.7, 22 | 65.4±11.6, 48 | ns |
| | *Citharichthys* spp. | | | |
| 1974 | | 165.4, 1 | 182.7±12, 2 | ns |
| 1975 | 202.8±5.0, 2 | | 134.2±54.0, 48 | ns |
| 1976 | | | | |
| 1977 | | 114.6±81.5, 9[b] | 188.9±47.5, 6 | p<.05 |
| | *Engraulis mordax* | | | |
| 1974 | | 103,1 | 98.9±17.4, 3 | ns |
| 1975 | | 106.7±13.4, 16 | 118.2± 9.4, 7 | ns |
| 1976 | | | 114.1±12.9, 24 | |
| | Cottids[d] | | | |
| 1975 | 60.0±24.0, 48 | 103.0±15.3, 35[c] | 65.0±23.8, 48 | DC:p<.05 |
| 1976 | 45.6±11.5, 48 | 97.0±22.4, 6 | 143.0±29.9, 21 | ns |
| 1977 | 46.1± 9.2, 37 | 44.0± 5.6, 2 | 49.0±10.5, 14 | ns |

Table 2.9 (cont'd)

| | | | |
|---|---|---|---|
| | *Cymatogaster aggregata* | | |
| 1975 | 74.4±12.4, 48 | 78.4±8.4, 5 | ns |
| 1976 | 66.4±12.4, 48 | 70.4±6.4, 48 | ns |
| | *Microgadus proximus*[e] | | |
| 1975 | 4.2±1.1, 48 | 4.4±0.9, 5 | ns |
| 1976 | 3.8±1.1, 48 | 4.0±0.8, 48 | ns |

a Bill size (mm) in parenthesis

b Smaller, $p<.05$.

c Larger, $p<.05$.

d The estimated mean total length of cottids eaten by guillemots during 1975, 1976, and 1977, was 50.1±8.1 (n=12), 68.8±14.6 (n=88), and 67.0±15.0 (n=50) mm, respectively.

e These are otolith diameters; regression with fish size and weight not available.

Table 2.10. Percent numerical composition of Brandt's Cormorant diet compared between samples gathered early and late in the 1977 nesting season

| Prey | Mar-Apr | Jul-Aug |
|---|---|---|
| *Ammodytes hexapterus* | 1 | |
| *Atherinopsis californiensis* | 1 | |
| *Porichthys notatus* | 3 | |
| *Citharichthys stigmaeus* | 2 | |
| *Hemilepidotus* spp. | 10 | |
| *Leptocottus armatus* | 2 | |
| *Phanerodon furcatus* | 6 | |
| *Engraulis mordax* | 29 | |
| *Microgadus proximus* | | |
| *Merluccius productus* | | |
| *Chilara taylori* | 25 | |
| *Iopsetta isolepis* | 2 | |
| *Parophrys vetulus* | 8 | |
| *Sebastes* spp. | 12 | 99 |
| *Loligo opalescens* | | 1 |
| Total items | 105 | 2811 |
| Diversity | 1.993 | .056 |

Table 2.11. On the basis of numerical (top) and weight (bottom) composition, comparison of diet overlap between years and between Double-crested (DCC), Pelagic (PC) and Brandt's cormorants (BC), Common Murres (CM) and Pigeon Guillemots (PG) using Morisita's Index[a]

| | | PC | | BC | | CM | | | PG | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | | 1975, 1977 | 1976 | 1973, 1975 | 1976 | 1973, 78,83 | 1976 | 1974,77, 75,79-82 | 1972, 1976 | 1978 | 1973-75, 77,79-82 |
| DCC | 1974-77 | .022 | .034 | .015 | .210 | .004 | .006 | .011 | .028 | .030 | .018 |
| | | .003 | .008 | .016 | .331 | .000 | .000 | .000 | .004 | .004 | .001 |
| PC | 1975,77 | -- | .594 | .892 | .318 | .266 | .513 | .896 | .517 | .337 | .975 |
| | | | .761 | .736 | .222 | .052 | .154 | .865 | .252 | .159 | .980 |
| | 1976 | | -- | .254 | .318 | .070 | .130 | .246 | .763 | .566 | .444 |
| | | | | .021 | .183 | .029 | .085 | .475 | .434 | .307 | .505 |
| BC | 1973-75 | | | -- | .453 | .290 | .540 | .923 | .272 | .170 | .933 |
| | | | | | .496 | .116 | .167 | .762 | .204 | .293 | .788 |

Table 2.11 (cont'd)

| | | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| | 1976 | -- | .438 | .464 | .298 | .415 | .507 | .343 |
| | | | .052 | .186 | .296 | .247 | .673 | .527 |
| | 1973,78,83 | | — | .662 | .386 | .089 | .086 | .282 |
| | | | | .426 | .436 | .016 | .030 | .056 |
| CM | 1976 | | | -- | .560 | .161 | .093 | .525 |
| | | | | | .390 | .029 | .027 | .017 |
| | 1974,75,77,79-82 | | | | -- | .224 | .131 | .963 |
| | | | | | | .134 | .079 | .894 |
| PG | 1972,76 | | | | | -- | .738 | .411 |
| | | | | | | | .415 | .239 |
| | 1978 | | | | | | -- | .284 |
| | | | | | | | | .208 |

a Years grouped as in Tables 2.8 and 2.20; similar diets (>.7) indicated by underlining.

Table 2.12. Percent composition of gull diets, comparing feces (F) and pellets (P)[a]

| | 1976 | | | 1977 | | 1978 | | |
|---|---|---|---|---|---|---|---|---|
| Prey | F | P | P-all | F | P | F | P | P-all |
| Fish | 63 | 65 | 61 | 55 | 39 | 27 | 31 | 30 |
| Euphausiids[b] | (10) | | (<1) | (14) | (<1) | (4) | (<1) | (<1) |
| Invertebrates | | | | | | | | |
| Marine[b] | 10 | 7 | 6 | 15 | 13 | 8 | 17 | 18 |
| Other[c] | 1 | 1 | 5 | <1 | <1 | | <1 | <1 |
| Birds | | 4 | 4 | | 7 | <1 | 5 | 5 |
| Garbage | 5 | 23 | 28 | 1 | 41 | 10 | 46 | 47 |
| Unidentified | 21 | -- | -- | 28 | | 55 | <1 | <1 |
| Total items | 354 | 2350 | 3189 | 354 | 2025 | 359 | 2589 | 2877 |

a Pellets column, P, uses data only from time period also covered by feces data; "P-all" uses all pellets.

b Euphausiids also included within marine invertebrate totals.

c Includes tenebrionid beetles.

Table 2.13. Percent composition of marine invertebrates in Western Gull pellets (P) and feces (F)

| | 1975 | 1976 | | 1977 | | 1978 | |
|---|---|---|---|---|---|---|---|
| Prey [a] | P | P | F | P | F | P | F |
| Cnidarid | | | | | | | |
| *V. velella* | 1 | | | | | | |
| Actinarid | 1 | | | | | | |
| Arthropods | | | | | | 1 | |
| *Lepas* sp. | 72 | 82 | 3 | 89 | 6 | 91 | 50 |
| Mysid | | | 6 | | | | |
| Isopod | | 1 | | | | | |
| Euphausiid | | 1 | 91 | 1 | 94 | | 50 |
| Decapoda | 3 | 3 | | 5 | | | |
| Molluscs | | | | | | | |
| Octopods | | | | 4 | | | |
| Squid | 6 | 3 | | | | | |
| Acmaeid [b] | 5 | 3 | | | | 1 | |
| *Mytilus* sp. | 8 | 2 | | | | 2 | |
| Heterodont | 2 | 4 | | | | 3 | |
| Unidentified | 2 | 1 | | | | 1 | |
| Total items | 151 | 209 | 35 | 256 | 53 | 509 | 28 |

Table 2.13 (cont'd)

a Only items contributing at least 1% included.

b Species of limpets identified in pellets: *Collisella digitalis*, *C. pelta*, *C. scabra* and *Lothia gigantea*. *Collisella pelta* accounted for 79% of those identified (n=28).

Table 2.14. Percent composition of gull diet comparing collected (CR) and observed (OB) chick regurgitations

| | 1974 | | 1978 | | 1979 | | 1980 | | 1981 | | 1982 | | 1983 | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Prey[a] | CR | OB | CR | OB | CR | OB | CR | OB | CR | OB | CR | OB | CR | OB |
| Fish | 86 | 74 | 58 | 51 | 93 | 78 | 62 | 58 | 87 | 64 | 78 | 73 | 57 | 57 |
| Euphausiid | 8 | 12 | | | <1 | | 24 | | 2 | | 3 | | | 4 |
| Invertebrate | | | | | | | | | | | | | | |
| Marine[b] | 12 | 13 | 2 | | 2 | | 38 | | 3 | | 9 | | | 9 |
| Other[c] | | | 1 | | <1 | | | | | | | | | |
| Bird | | 2 | | 3 | | 1 | | 1 | | 2 | | 2 | | 2 |
| Garbage | 1 | | 39 | 28 | 4 | 6 | | 24 | 10 | 16 | 13 | 15 | 43 | 24 |
| Unidentified | | | | 9 | | 5 | | 10 | | 8 | | 6 | | 7 |
| Total items | 7 | 805 | 112 | 43 | 59 | 184 | 17 | 68 | 62 | 83 | 19 | 53 | 5 | 232 |

Table 2.14 (cont'd)

a All observations (OB) in 1974 are extrapolated from Pierotti (1981); observations (OB) 1978 to 1982 from Spear (unpubl. data).

b Euphausiids also included in marine invertebrate totals.

c Includes tenebrionid beetles.

Table 2.15. Percent composition of gull diet, comparing pellets (P) and collected (CR) and observed (OB) regurgitations

| | 1975 | | | 1976 | | | 1978 | | | | 1979 | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Prey[a] | P-all | P | CR | P-all | P | CR | P-all | P | CR | OB | P | CR | OB |
| Fish | 51 | 40 | 77 | 61 | 61 | 61 | 30 | 26 | 58 | 51 | 24 | 93 | 78 |
| Euphausiid | | | (2) | (<1) | | (4) | (<1) | | | | | (<1) | |
| Invertebrate | | | | | | | | | | | | | |
| Marine[b] | 6 | 12 | 19 | 6 | 10 | 11 | 18 | 30 | 2 | | 12 | 2 | |
| Other[c] | 1 | 1 | | <1 | <1 | | <1 | <1 | 1 | | | | |
| Bird | 7 | 14 | | 4 | 4 | | 5 | 5 | | 3 | 1 | <1 | 1 |
| Garbage | 34 | 33 | 4 | 28 | 24 | 28 | 47 | 43 | 39 | 28 | 62 | 3.5 | 6 |
| Unidentified | | | | — | | | <1 | | | 9 | | | 5 |
| Total items | 2245 | 434 | 26 | 3189 | 615 | 19 | 2877 | 277 | 112 | 43 | 525 | 59 | 184 |

a "Pellet" column uses samples only from periods covered by regurgitations; "P-all" = all pellets.

b Euphausiids also included in marine invertebrates totals.

c Includes tenebrionid beetles.

Table 2.16. Percent composition of gull diet, comparing feces (F) and collected (CR) or observed (OB) regurgitations

| | 1976 | | | 1978 | | | |
|---|---|---|---|---|---|---|---|
| Prey [a] | F-all | F | CR | F-all | F | CR | OB |
| Fish | 63 | 64 | 61 | 27 | 43 | 58 | 51 |
| Euphausiid | (10) | (4) | (4) | (4) | | | |
| Invertebrate | | | | | | | |
| Marine | 10 | 6 | 11 | 8 | | 2 | |
| Other | 1 | 3 | | | | | |
| Bird | | | | <1 | | 1 | 3 |
| Garbage | 5 | 4 | 28 | 10 | 4 | 39 | 28 |
| Unidentified | 21 | 23 | | 55 | 53 | | 9 |
| Total items | 354 | 112 | 19 | 359 | 47 | 112 | 43 |

a See footnotes to Table 2.12.

Table 2.17. Percent composition of fish identified by otoliths in Western Gull pellets

| Prey[a] | 1973 | 1974 | 1975 | Total |
|---|---|---|---|---|
| *Atherinopsis californiensis* | 4 | 1 | 5 | 1 |
| *Porichthys notatus* | 29 | 13 | 9 | 11 |
| *Citharichthys sordidus* | 4 | 3 | 3 | 3 |
| *Brosmophycis marginata* | | 1 | | 2 |
| *Cymatogaster aggregata* | | | 1 | 1 |
| *Zalembius rosaceus* | 6 | 2 | 1 | 2 |
| *Engraulis mordax* | 6 | 2 | | 1 |
| *Microgadus proximus* | | 2 | 3 | 3 |
| *Merluccius productus* | 8 | 9 | 13 | 12 |
| *Chilara taylori* | 17 | 21 | 22 | 21 |
| *Glyptocephalus zachirus* | 1 | 2 | 1 | 1 |
| *Microstomus pacificus* | | 1 | | |
| *Genyonemus lineatus* | 4 | 6 | 4 | 5 |
| *Sebastes* spp. | 21 | 36 | 40 | 39 |
| Total fish | 72 | 533 | 1513 | 2118 |
| Diversity | .855 | .852 | .773 | .956 |

a *Clupea pallasi*, *Hemilepidotus* sp., *Leptocottas armatus*, *Hexagrammus decagrammus*, *Lyopsetta exiles* and *Parophrys vetulus* represented by <1%.

Table 2.18. Composition of Western Gull regurgitations, 1978-1982

| Prey[a] | Mean | | | Percent diet composition by: | | | |
|---|---|---|---|---|---|---|---|
| | No./ sample | Wgt./ sample | Wgt./ item[b] | Freq. | No. | Mass | Mass[c] |
| PISCES | | | | | | | |
| *Porichthys notatus* | 1 | 15 | 13 | 4 | 3 | 10 | |
| *Engraulis mordax* | 1 | 12 | 8 | 6 | 4 | 10 | |
| *Sebastes* spp. | 3 | 10 | 3 | 24 | 37 | 25 | |
| Unidentifiable fish | 1 | 9 | 8 | 54 | 35 | 33 | |
| Fish subtotal | 2 | 12 | 5 | 77 | 79 | 70 | 78 |
| INVERTEBRATE | | | | | | | |
| Euphausiid[d] | 27 | 4 | <1 | 6 | 3 | 2 | 3 |
| Octopod | 2 | 14 | 10 | 1 | 1 | 1 | 1 |
| Teuthoid | 1 | 11 | 11 | 4 | 2 | 3 | 4 |
| Marine invertebrate subtotal | — | 7 | — | 10 | 5 | 7 | 8 |
| Beetles | 2 | <1 | <1 | 1 | 1 | — | |
| GARBAGE | — | 19 | — | 25 | 13 | 22 | 14 |

a Only species contributing at least 1% included; 269 regurgitations, 475 prey items.

Table 218 (cont'd)

b Mass calculations for individual and "unidentified" based on 1981 and 1982.

c Percent mass recalculated minus one garbage sample of three hot dogs, (215 gm).

d Each euphausiid occurrence is treated as one item except in calculation of mean number items/sample.

Table 2.19. Extent of overlap between years in the diet of Common Murres, 1973-1983, using Morisita's Index[a]

| Year | 1973 | 1974 | 1975 | 1976 | 1977 | 1978 | 1979 | 1980 | 1981 | 1982 | 1983 |
|---|---|---|---|---|---|---|---|---|---|---|---|
| 1973 | -- | .284 | .278 | .697 | .278 | .912 | .193 | .370 | .356 | .492 | .802 |
| 1974 | | -- | .963 | .555 | .962 | .397 | .951 | .972 | .957 | .907 | .308 |
| 1975 | | | -- | .558 | .999 | .384 | .990 | .983 | .988 | .930 | .285 |
| 1976 | | | | -- | .549 | .796 | .483 | .633 | .607 | .681 | .544 |
| 1977 | | | | | -- | .381 | .991 | .980 | .986 | .926 | .284 |
| 1978 | | | | | | -- | .306 | .497 | .480 | .623 | .893 |
| 1979 | | | | | | | -- | .954 | .963 | .885 | .211 |
| 1980 | | | | | | | | -- | .999 | .981 | .413 |
| 1981 | | | | | | | | | -- | .975 | .422 |
| 1982 | | | | | | | | | | -- | .564 |

a 1 = complete overlap, 0 = none; particularly extensive overlap indicated by underlining; numerical data only.

Table 2.20. Percent diet composition by number (n) and weight (w) in two large alcids, with years grouped according to overlaps identified in Tables 2.19 and 2.22

| | Common Murre | | | | | | Pigeon Guillemot | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | 1973, 78,83 | | 1976 | | 1974,75, 77,79-82 | | 1972,76 | | 1973 | | 1978 | | 1974-75, 77,79-82 | |
| Prey | n | w | n | w | n | w | n | w | n | w | n | w | n | w |
| *Porichthys notatus* | | | 1 | 1 | | | | | | | | | | |
| *Citharichthys sordidus* | 4 | 2 | 1 | 1 | 1 | 1 | 15 | 16 | 4 | 8 | 49 | 66 | 3 | 6 |
| Clinids | | | | | | | 2 | 1 | 3 | 3 | | | 1 | 1 |
| Cottids | | | | | | | 41 | 24 | 26 | 22 | 35 | 22 | 15 | 13 |
| *Engraulis mordax* | 62 | 71 | 22 | 20 | 10 | 26 | | | | | | | | |
| *Spirinchus starksi* | 8 | 7 | 20 | 14 | 2 | 3 | | | | | | | | |
| Pholids | | | | | | | 6 | 4 | 9 | 8 | 8 | 6 | 2 | 2 |
| Salmonids | 1 | 1 | | | | | | | | | | | | |
| *Cololabis saira* | 1 | 1 | | | | | | | | | | | | |
| *Sebastes* spp. | 19 | 4 | 28 | 10 | 86 | 63 | 13 | 8 | 54 | 46 | 8 | 5 | 77 | 70 |

Table 2.20 (cont'd)

| | | | | | | | |
|---|---|---|---|---|---|---|---|
| Stichaeids | | | | 1 1 | | | |
| *Peprilus simillimus* | 3 9 | | | | | | |
| *Loligo opalescens* | 3 6 | 21 54 | 1 8 | | | | |
| *Octopus rubescens* | | | | 22 46 | 4 12 | | 2 |
| Total items | 3672 | 2033 | 14722 | 766 | 192 | 26 | 1602 |
| weight, gm | 30224 | 19822 | 70393 | 2537 | 446 | 80 | 3475 |
| Mean diversity, n | 1.105±.109 | 1.281 | .531±.249 | 1.646±.006 | 1.467 | .371 | .938±.302 |
| diversity, w | 1.068±.209 | 1.298 | .995±.416 | 1.416±.005 | 1.454 | .926 | .994±.330 |

Table 2.21. Estimated approximate mean total lengths of fish eaten by three alcids

| Year | Pigeon Guillemot (37)[a] | Common Murre (77) | Tufted Puffin (49) |
|---|---|---|---|
| | *Sebastes* spp. | | |
| 1974 | 74.7± 8.1; 96 | 76.1± 0.3; 2270 | 72.9±10.0; 25 |
| 1975 | 60.0± 9.2; 37[b] | 76.7± 5.5; 3532 | 72.4± 6.8; 37 |
| 1976 | 64.1±10.6; 65 | 66.9±12.8; 706 | 69.4± 4.9; 13 |
| 1977 | 80.9± 8.8; 378 | 80.1± 7.9; 2777 | 69.0±14.6; 18[b] |
| 1978 | 64.2± 7.7; 20 | 65.9± 5.8; 248 | 73.8±20.2; 18[c] |
| 1979 | 73.9± 7.7; 127[b] | 88.2± 5.3; 856 | — |
| 1980 | 73.2±11.3; 121 | 75.2± 1.1; 1187 | 67.5± 7.3; 24 |
| 1981 | 74.4± 5.8; 210 | 77.9± 2.1; 1015 | 66.0± 9.3; 11[d] |
| 1982 | 74.7± 5.8; 91 | 79.2± 1.2; 456 | 74.3± 6.8; 14 |
| | *Citharichthys* spp. | | |
| 1974 | 80.5±20.4; 3 | 84.1±19.5; 17 | |
| 1975 | | 71.0±12.5; 20 | |
| 1976 | 80.5±16.8; 34 | 79.5±18.8; 23 | |
| 1977 | | 102.1±23.1; 11 | |
| 1978 | 83.0±14.6; 13 | 84.7± 5.7; 12 | |
| 1979 | 79.1±12.8; 8 | 83.5±14.6; 3 | |
| 1980 | 83.8± 7.3; 14 | 82.2±10.9; 11 | |
| 1981 | 86.4±14.3; 16 | 85.6±10.5; 13 | |
| 1982 | 76.5± 9.5; 8 | 74.1± 7.5; 2 | |

Table 2.21 (cont'd)

| | *Engraulis mordax* |
|---|---|
| 1974 | 125.6±22.0; 30 |
| 1975 | 132.0±12.7; 25 |
| 1976 | 140.8±39.1; 31 |
| 1977 | 126.6±20.5; 14 |
| 1978 | 130.6±18.6; 10 |
| 1979 | -- |
| 1980 | 122.2±18.6; 10 |
| 1981 | -- |
| 1982 | 136.9± 9.8; 2 |

a Bill size (mm) in parenthes

b Smaller; t-test, $p<.05$.

c Larger; t-test, $p<.05$.

d Smaller than for murre; t-te

[illegible]lap between years in the diet of Pigeon

[illegible]ng Horisita's Index[a]

| [illegible] | [illegible] | 1976 | 1977 | 1978 | 1979 | 1980 | 1981 | 1982 |
|---|---|---|---|---|---|---|---|---|
| [illegible]04 | [illegible] | .921 | .203 | .696 | .184 | .383 | .412 | .395 |
| [illegible] | [illegible] | .763 | .931 | .433 | .848 | .961 | .960 | .970 |
| — | [illegible] | .481 | .997 | .145 | .995 | .947 | .948 | .937 |
| | — | .588 | .954 | .286 | .965 | .989 | .979 | .978 |
| | | — | .470 | .591 | .458 | .643 | .666 | .656 |
| | | | — | .140 | .993 | .942 | .948 | .936 |
| | | | | — | .188 | .349 | .333 | .306 |
| | | | | | — | .936 | .945 | .936 |
| | | | | | | — | .993 | .991 |
| | | | | | | | — | .994 |

[illegible] = none; particularly extensive overlaps

[illegible]ing; numerical data only.

Table 223. Percent composition of Cassin's Auklet diet by num weight (w)

| Prey | 1971[a] | 1977 | | 1979 | | 1980 | |
|---|---|---|---|---|---|---|---|
| | n | n | w | n | w | n | w |
| PISCES[b] | 1 | 1 | 2 | 6 | 16 | 3 | 21 |
| AMPHIPOD | | | | | | | |
| Gammarids | | | | | | 11 | [illegible] |
| Hyperids | | | | 19 | 6 | 38 | [illegible] |
| Subtotal | 74 | | | 19 | | 50 | |
| DECAPOD | | | | | | | |
| Cyprids | | | | 4 | 1 | | |
| Mysids | | | | 1 | 1 | | |
| Euphausiids[c] | 22 | 99 | 98 | 66 | 74 | 46 | 72 |
| Squid | | | | 9 | 1 | 2 | [illegible] |
| Total number | 8083 | 966 | | 10907 | | 7031 | |
| Total weight, gm | | 271 | | 2963 | | 1337 | |
| Diversity, n | | .0980 | | .1012 | | 1.151 | |
| Diversity, w | | .0560 | | .8230 | | .7937 | |

a Data from Manuwal (1974); most samples from latter third of [illegible] period.

b Almost all fish were Sebastes spp.; a few larval Citharichthys

c Percent contribution of T. spinifera, by year = 85, 68, 6 and [illegible] respectively, 1977-1981.

Table 2.24. Percent composition of Tufted Puffin diet by number (n) and weight (w)

| | 1973 | | 1974 | | 1975 | | 1976 | | 1977 | | 1978 | | 1979 | | 1980 | | 1981 | | 1982 | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Prey | n | w | n | w | n | w | n | w | n | w | n | w | n | w | n | w | n | w | n | w |
| *Engraulis mordax* | 94 | 87 | 79 | 94 | 41 | 71 | 55 | 71 | 44 | 83 | 30 | 46 | | | 22 | 48 | 15 | 56 | 4 | 3 |
| *Cololabis saira* | | | | | 3 | 3 | 4 | 2 | | | 3 | 2 | | | | | | | | |
| *Sebastes* spp. | | | 11 | 4 | 22 | 19 | 30 | 4 | 56 | 17 | | | 100 | 100 | 73 | 27 | 85 | 44 | 48 | 6 |
| *Peprilus simillimus* | | | | | | | | | | | 1 | 2 | | | | | | | | |
| *Loligo opalescens* | 6 | 13 | 1 | 2 | 1 | 7 | 11 | 23 | | | 4 | 39 | | | 4 | 25 | | | 48 | 91 |
| Decopod | | | | | 9 | – | | | | | | | | | | | | | | |
| Total items | 285 | | 124 | | 76 | | 56 | | 32 | | 34 | | 7 | | 45 | | 13 | | 56 | |
| Total weight, gm | 4888 | | 1653 | | 554 | | 976 | | 267 | | 324 | | 18 | | 307 | | 64 | | 1135 | |
| Unidentified items[a] | 5 | | 14 | | 525 | | 52 | | 156 | | 236 | | 6 | | 3 | | 4 | | 49 | |

[a] Not included in percent composition calculations.

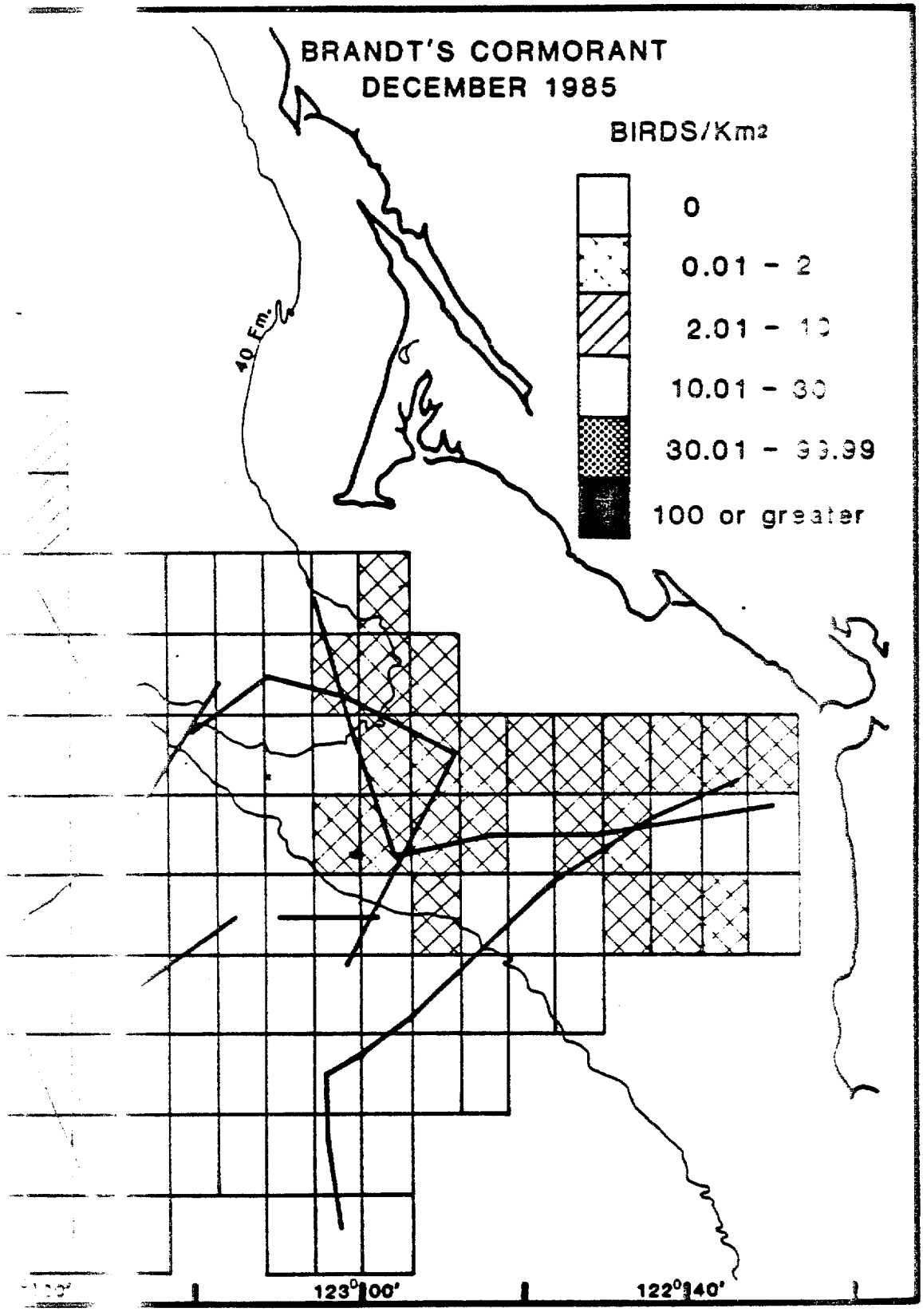
PART III (A). The following table gives percent composition of the diet fed to murre and guillemot chicks at Southeast Farallon during 1984-86, and updates Table 2.20 in Part II; the data were collected in the same way as in previous years. The low prevalence of rockfish in the diet during the warm water year of 1986 is evident.

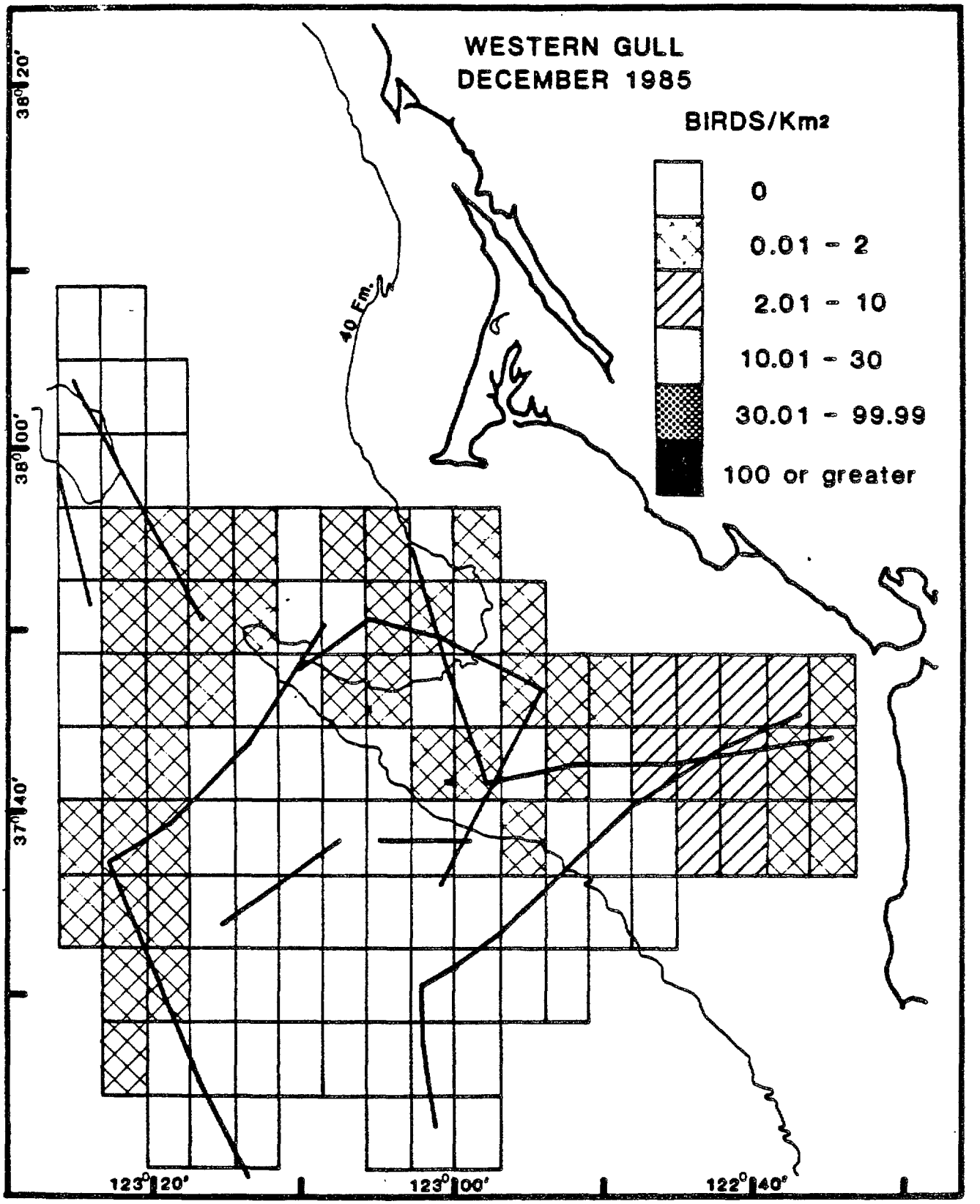
| | Common Murre | | | Pigeon Guillemot | | |
|---|---|---|---|---|---|---|
| | 1984 | 1985 | 1986 | 1984 | 1985 | 1986 |
| *Porichthys notatus* | | | | | | 3 |
| *Citharichthys sordidus* | | | 2 | 10 | 5 | 15 |
| Clinids | | | | 1 | | |
| Cottids | | | | 3 | 16 | 15 |
| *Clupea pallasi* | 1 | | | | | |
| *Engraulis mordax* | 24 | 19 | 47 | | | |
| *Spirinchus starksi* | 1 | 1 | 3 | | | |
| *Oxyjulis californica* | | 4 | | | | |
| *Chilara taylori* | | | | | | 6 |
| Pholids | | | | 7 | 12 | 3 |
| Salmonid | 2 | | 2 | | | |
| *Cololabis saira* | 1 | 1 | | | | |
| *Sebastes* spp | 69 | 74 | 42 | 72 | 65 | 36 |
| Stichaeids | | | | | | 3 |
| *Loligo opalescens* | | 1 | 3 | | | |
| *Octopus rufescens* | | | | 6 | 2 | 3 |
| Total items | 1156 | 1185 | 223 | 270 | 213 | 33 |

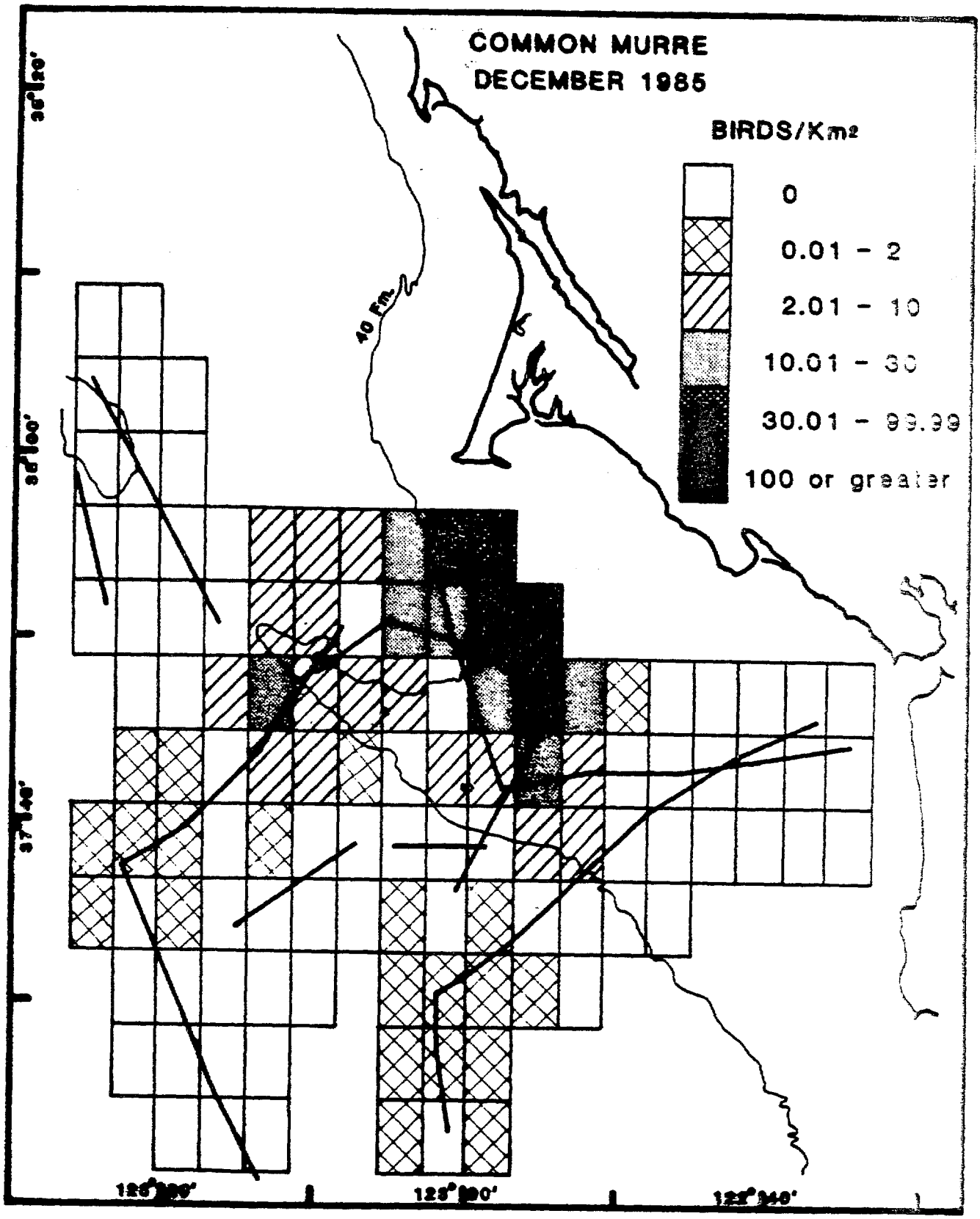
PART IV. The point was emphasized in Part II that Farallon seabirds depend on a rockfish economy. This is demonstrated here with rank correlations between the percentage of rockfish in the diet and the number of chicks fledged per pair for several breeding species; the analysis is treated in much more detail in Ainley and Boekelheide (ms).

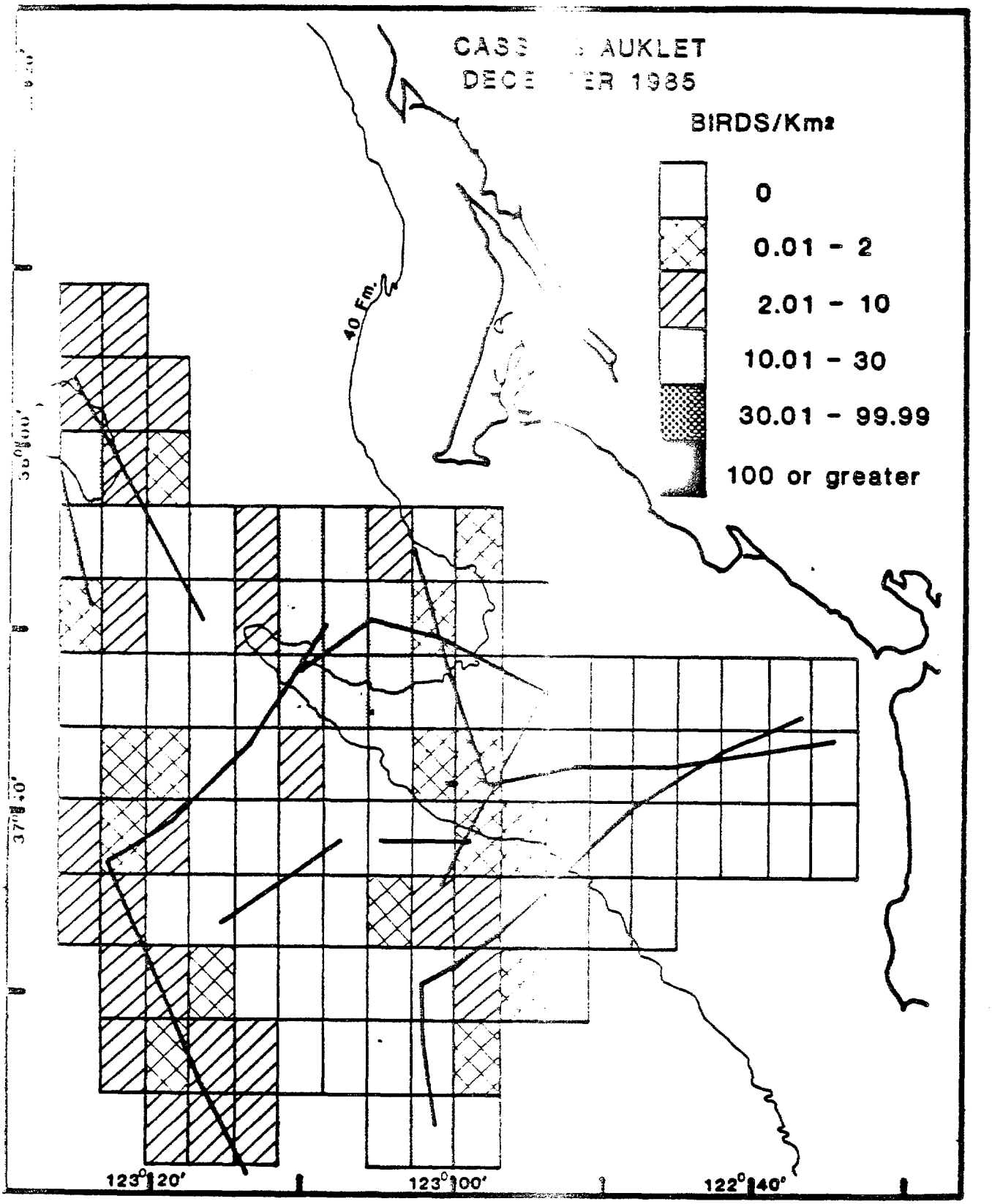
| | Period | No. years | Rank correlation coefficient* |
|---|---|---|---|
| Brandt's Cormorant | 1973-77 | 5 | .98 |
| Pelagic Cormorant | 1975-77 | 3 | 1.00 |
| Western Gull | 1975-79 | 4 | .74 |
| Common Murre | 1973-86 | 14 | .52 |
| Pigeon Guillemot | 1972-86 | 15 | .80 |

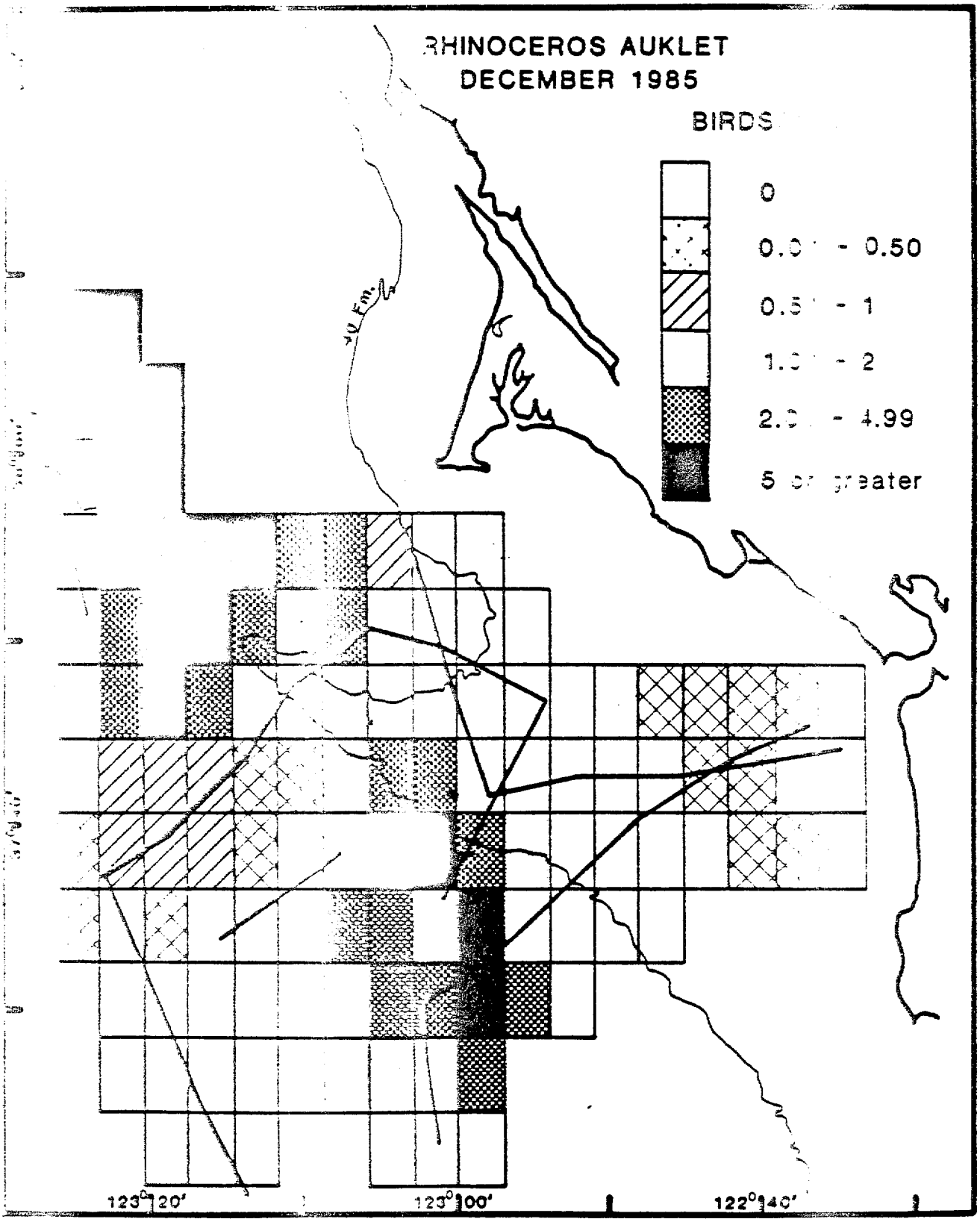
*All r* values are significant ($p<.05$), except for that of murres which lay but one egg, and thus exhibit low variability in breeding success ($p=.06$).

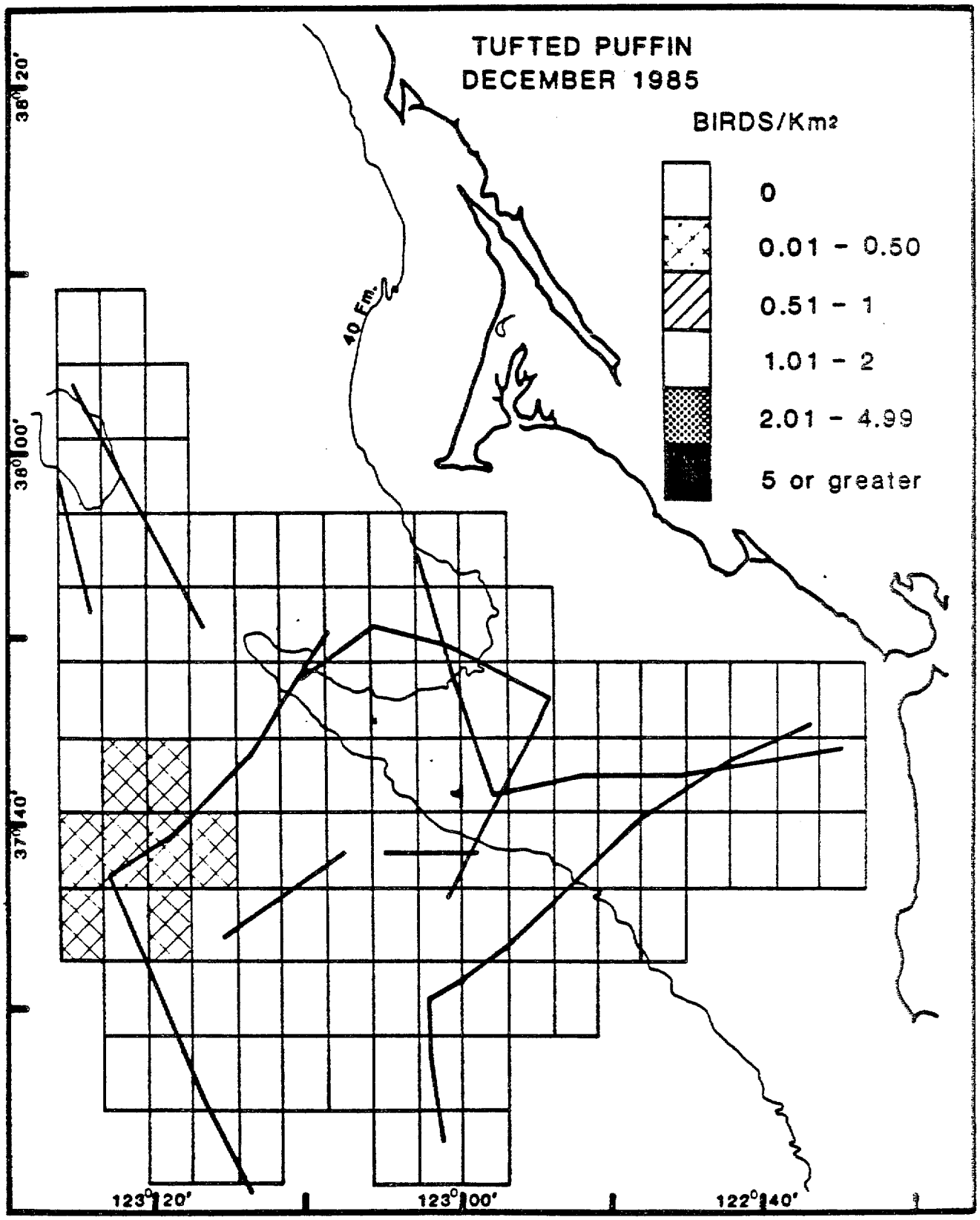

BRANDT'S CORMORANT
DECEMBER 1985
BIRDS/Km2
0
0.01 - 2
2.01 - 10
10.01 - 30
30.01 - 99.99
100 or greater
40 Fm.
123°00'
122°40'


WESTERN GULL
DECEMBER 1985
BIRDS/Km2
0
0.01 - 2
2.01 - 10
10.01 - 30
30.01 - 99.99
100 or greater
40 Fm.
38° 20'
38° 00'
37° 40'
123° 20'
123° 00'
122° 40'


COMMON MURRE
DECEMBER 1985
BIRDS/Km2
0
0.01 - 2
2.01 - 10
10.01 - 30
30.01 - 99.99
100 or greater
40 Fm.


CASS AUKLET
DECE ER 1985
BIRDS/Km²
0
0.01 - 2
2.01 - 10
10.01 - 30
30.01 - 99.99
100 or greater
40 Fm.
123°20'
123°00'
122°40'


RHINOCEROS AUKLET
DECEMBER 1985
BIRDS
0
0.0 - 0.50
0.5 - 1
1.0 - 2
2.0 - 4.99
5 or greater
123°20'
123°00'
122°40'


TUFTED PUFFIN
DECEMBER 1985
BIRDS/Km²
0
0.01 - 0.50
0.51 - 1
1.01 - 2
2.01 - 4.99
5 or greater
40 Fm.
38°20'
38°00'
37°40'
123°20'
123°00'
122°40'

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