SUBMITTED TO CONDOR FEB 1980
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Breeding Biology of the Pelagic Cormorant (*Phalacrocorax pelagicus*) at Cape Peirce, Alaska

by

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The Pelagic Cormorant presently breeds in North America from Cape Lisburne, Alaska (Sowls et al. 1978) south to the Channel Islands, California (J. R. Jehl, pers. comm.). Two subspecies are recognized (Bent 1922, Palmer 1958). The Baird's Cormorant, *P. p. resplendens*, breeds as far north as extreme southern British Columbia. The more robust subspecies *P. p. pelagicus* breeds throughout the remainder of British Columbia, in Alaska, and in northeastern Asia.

The first study of the species in the northeastern Pacific was made by van Tets at Mandarte Island, British Columbia (van Tets 1959, Drent et al. 1964), and further work was done there by Robertson (1971, 1974). Numerous workers have contributed information on the breeding phenology, distribution and migration of the species in Alaska. However, until the present work, no detailed study had been made of the Pelagic Cormorant farther north than southern British Columbia.

DESCRIPTION OF THE STUDY AREA

Cape Peirce ($58^{\circ}33.3'$N,$161^{\circ}46'$W), the southernmost point of the Cape Newenham Wildlife Refuge, forms the tip of the peninsula south and southeast of Nanvak Bay (Figure 1). The terrestrial environment is coastal tundra, both climatically (Hopkins 1959) and vegetationally (Hulten 1968), in an area affected by Pleistocene glaciation and still underlain by discontinuous permafrost (Hoare and Coonrad 1961, Johnson and Hartman 1969).

On the western side of the peninsula are 2.5 km (linear distance) of cliffs ranging from 10 m to 90 m in height and interrupted by slides. On the southern side are 6.8 km of cliffs with a similar height range, but more broken and interspersed with slides and vegetated slopes than those on the west. The longest continuous cliff on the peninsula runs from the cape to a point 1.1 km NNE, and is topped by extensive sea slopes.

The intertidal around the peninsula consists of boulder and cobble beach, solid rock strand, and sheer rock face. In most years Cape Peirce lies within the southern limit of winter pack ice in the Bering Sea. It is adjoined by continental shelf not deeper than 37 m for at least 32 km to sea. Sea temperatures in summer reach 11° C. In summer there is a 1-2 knot along-shore current running south along the barrier beach of Nanvak Bay and counter-clockwise around Cape Peirce peninsula.

Mean maximum air temperatures from June through August range from 10-12° C, mean minumums from 6-8° C. Mean annual precipitation is 89 cm (Temperature and precipitation data are from the Cape Newenham Weather Station, Alaska Climatological Data). From 23 May-27 August 1970, 64 percent of the days had steady wind, and most others had at least intermittent breezes. Wind velocities of 80 km/hr were not uncommon. Prevailing summer winds are from the NE. Fog quite often hangs over the area, though it rarely hampers cliff observations.

Nanvak Bay, adjoining the north side of the peninsula, is a shallow, channeled estuary 7.2 km long by 1.8 km wide, fed by the Slug River at the north end and drained by a narrow mouth at the south. The bay contains extensive beds of eelgrass (*Zostera marina*). It freezes over in winter and begins to break up at the end of April. The southern half is ice free by mid May and the entirety by the end of May.

METHODS

The study periods were 23 May-28 August 1970, 26 April-24 June 1973 and 14 August-27 September 1973. Further seabird research conducted by Petersen and Sigman (1977) contributed information on the Pelagic Cormorant.

Cormorant censuses were taken by skiff on 4 July and 10 August 1970.

Most observations were made from the clifftops. The cormorants became accustomed to an observer sitting in open view of a colony, provided he used a customary spot and approached slowly. Predation pressure was quite low, and certain colonies could be frightened from the cliffs for egg counts without mortality. Sex and individual identification were based on diethic behavior and plumage differences, respectively.

WINTERING, MIGRATION AND ARRIVAL

The Cape Peirce population is migratory, and likely winters in the Aleutians, south of the Alaska Peninsula or in the Gulf of Alaska. There is no conclusive evidence concerning wintering grounds. Brown, first-year immatures, which are only rarely seen at Cape Peirce in summer, are commonly seen in the aforementioned areas all year long. Perhaps first year birds from Cape Peirce remain in the wintering area until their second spring.

Pelagic Cormorants began to return to Cape Peirce in mid April. On 27 April 1973, there were none on the west cliffs, but flocks of them stood on boulders below colony sites. Most of the nesting ledges were still snowbound, though two individuals courted on a loitering area. The next day, several males at a colony on Shaiak Strait displayed and courted females in a driving snowstorm at 0° C, with a 60-80 km/hr wind striking them. Between these activities, the birds assumed storm posture, their heads on their backs.

Colony sites were occupied before the ledges were snow free, and males often displayed while standing in snow. Snow distribution on the cliffs probably influences the timing and distribution of colonies in a given year. In 1973, breeding at one colony in particular was considerably later than in 1970 due to snow buildup.

There is an extensive northward movement of Pelagic Cormorants along the Bering Sea coast from mid April to early May. The Cape Peirce birds form the vanguard, but they are already on the cliffs when the bulk of the migration occurs, and do not mix with the birds headed farther north.

Several staging areas are used during spring migration. King et al. (1974) reported concentrations of cormorants in Unimak Pass on 21 April 1971. King (1966) estimated over 10,000 Pelagic Cormorants in Hagemeister Strait, 50-60 km from Cape Peirce, on 30 April 1964. In an aerial survey from 3-8 May 1972, Bartonek (unpublished data) found the greatest cormorant concentration between Hagemeister Island and Cape Constantine, with scattered birds along the north side of the Alaska Peninsula.

In two hours on 2 May 1973, an estimated 125,000 King Eiders (Somateria spectabilis) and exactly 522 Pelagic Cormorants rounded Cape Peirce from the east, headed north. Forty-four flocks of cormorants ranging in size from one to 75 birds and averaging 12 per flock were recorded. Of these, 38 flocks were pure. Five small groups flew in formation with long lines of King Eiders, and two individuals with Emperor Geese (Philacte canagica). An estimated 625,000 King Eiders and 2,600 Pelagic Cormorants rounded the cape on 2 May. According to a native of Quinhagak, the eiders and cormorants stage in Hagemeister Strait in the presence of a northerly wind, but move north with the first strong southerly breeze in late April or early May. This was the case in 1973.

Brandt (1943) observed Pelagic Cormorants first moving past Dall Point on 7 May in 1924; for the next two weeks, small flocks passed by. The first Pelagics were seen at Cape Thompson on 8 May in 1960 and 21 May in 1961 (Swartz 1966). The most northern populations arrive at their sites five weeks later than the Cape Peirce population.

NESTING HABITAT

Pelagic Cormorants nested exclusively on cliffs at Cape Peirce, more often on open ledges than on those with overhang or in vertical clefts (Table 1). The proportion of utilization of each type was nearly equivalent for the south and west cliffs. Either open ledges were actively selected, or site selection merely reflected the proportions of nest site types available. Nests ranged from 3.5 to 100 m in elevation, with two-thirds of them below 12 m.

Pelagic Cormorants were closely associated with Black-legged Kittiwakes (Rissa tridactyla) and Common Murres (Uria aalge) on the west cliffs and scarcely on the south cliffs (Table 2). When the three species occupied the same cliff, kittiwakes and murres nested both higher and lower than cormorants.

THE COLONY

For the purposes of this study, a colony was defined as a single nest more than 5 m away from any other, or an aggregation of nests each within 5m of at least one other. Although 5 m was the point at which intracolony spacing was distinguished from intercolony separation, colonies were usually well defined and separated by considerably more than 5 m. The colony size frequency distribution for a segment of the west cliffs is shown in Figure 2 . The Pelagic Cormorant is not strictly colonial, but shows a tendency for gregariousness.

Colonies were particularly well defined on the south side of the peninsula. They consisted of usually large, dense groups separated from other groups by wide gaps. On the west side, some of the cliff stretches were occupied by scattered singles and small colonies. The difference between the two areas was due to the structure of the cliffs, mor broken on the south and more continuous on the west.

Between 1970 and 1973, colonies at some sites remained stable in size; at others they increased drastically or decreased. Some sites were utilized one year but not the other. Intracolony synchronization in onset of laying and intercolony differences in timing occurred each year. Certain colonies were occupied by older, more experienced birds during both seasons, and were the first to lay eggs. Others occupied by young, inexperienced birds, some of them with dark flanks, were among the latest colonies to settle and lay eggs. During a given season, nonbreeders returned to the same colony each night to roost. A colony, therefore, is not only a spatial entity which can be plotted on a map, but a biological entity as well, recognized by its members, more or less synchronized, and perhaps changing locality from year to year.

The Cape Peirce population was apparently stable during the time of the study. An estimated 346 pairs were present on the peninsula in 1970; Petersen and Sigman (1971) estimated 350 in 1976.

AGE AT FIRST BREEDING

Stejneger (1885) and van Tets (1959) differ in their accounts of plumage sequence and age at first breeding, and it may be that the populations they considered differ in these characters. Van Tets dealt with a marked population at Mandarte Island, whereas Stejneger's population in the Commander Islands was unmarked. According to van Tets, the Pelagic Cormorant retains the sooty-black juvenile plumage its first winter, but attains the brown first alternate plumage by 10 months of age. By 22 months it attains the iridescent black plumage without white flank patches. At 34 months it attains adult plumage and begins to breed. The birds observed by Stejneger were sooty black in their first basic plumage, and iridescent black without flank patches in their first alternate plumage at 10 months. They attained full adult plumage and began to breed at 23 months. Stejneger made no mention of a brown first alternate plumage.

The absence of brown immatures at Cape Peirce may indicate that that population has the same plumage sequence as Stejneger's, and that first breeding usually occurs at 23 months. Some black, iridescent birds with dark flanks and brown alulas (a character described by van Tets as characteristic of the brown first alternate plumage) bred successfully at Cape Peirce, meaning that some breeding possibly occurs at 11 months of age. Alternatively, Stejnager's population may also be migratory, with the brown subadults remaining in the wintering area.

TERRITORY

Territory size depended on the aggressiveness of the male, the amount of ledge available, and the distance to other pairs. Territory usually extended as far on either side of the nest as the male could reach with his bill, especially when there were nests on both sides of him. Some males defended up to 2.5 m of ledge, and utilized the extra for loitering. Much of each colony was free ground, where both breeders and nonbreeders could loiter. Pairs often had a favorite loitering spot a meter or so above or below the nest, but this was not usually defended.

Some males which failed to obtain mates in May defended territories until August.

GATHERING AND NEST MATERIAL

As van Tets (1965) found, males began gathering nest materials before they were mated, but nest building did not become effective until females were present to guard against theives, which at Cape Peirce included other Pelagics and Black-legged Kittiwakes. Males brought most of the nest material. In 61 observations of gathering, males were involved in 57, one female in three and another in one. Gathering began before 27 April in 1973 and was observed as late as 27 August in 1970. It was engaged in during all daylight hours.

When building was at its peak, males made consecutive trips for nest material. The most observed were 11 trips in 30 minutes (2.7 min/trip); the fastest, 9 trips in 12 minutes (1.3 min/trip). The mean time of 44 trips from six instances of consecutive gathering was 2.2 minutes. Males did most of their gathering within 200 m of the nest.

Nest material consisted almost entirely of dry strands of beach rye (Elymus arenarius) which the birds pulled from steep slopes by bracing themselves with their tails. Other materials occasionally used included crowberry (Empetrum nigrum), dwarf willow (Salix sp.), moss, lichen, herbaceous cliff plants and dried twigs. Pelagic Cormorants occasionally bathed or dived with nest material before taking it to the nest, or surfaced with subtidal algae, a nest material commonly used by the Red-faced Cormorant.

Four or five days before laying, both members of a pair began "waddling", or shifting from foot to foot on the nest while turning various directions, thus packing the nest. Three days before laying they began to assume the "goose posture", standing nearly horizontally while waddling at the center of the nest. This shaped the cup.

COPULATION, LAYING AND INCUBATION

Data on clutch commencement are shown in Figure 3 .

Pairs began to copulate successfully 6-9 days before laying. An unsuccessful attempt was observed 14 days, and reverse mounting by a female 10-11 days, before laying. Copulation peaked within 3 days of, and was attempted for up to 1 week after, the onset of laying. It was commonly successful with a partial clutch present. Copulation was initiated by the male, but its success depended upon the receptiveness of the female, who became unreeptive as the clutch approached completion.

Nest relief began up to five days before laying commenced, and both members of a pair began sitting in incubating posture two or three days before laying. The mean laying interval was 1.7 days.

With a later spring, more rain and more frequent storms, 1970 was a harsher season than 1973. In 1970, laying commenced later, and no five egg clutches were observed. Mean clutch size was 3.1 to 3.2 during three seasons. Relaying of lost clutches was not observed in 1970. In 1973, four nests were relaid between 6 and 24 June. Petersen and Sigman (1977) found relays as late as 7 July.

Table 3 indicates that incubation was not effective from the first egg. Either this was the case, or each successive egg had a slightly shorter incubation period. Egg measurements were taken on one clutch of four where order of laying could be determined; the widths remained constant, but the lengths decreased progressively from the first to the last. Decreasing volume could shorten the incubation period.

Mean incubation period ~~is~~ was 29 days if incubation ~~is~~ was effective from the first egg, and 28 days if effective from the second.

Clutch size frequency is shown in Figure 4.

HATCHING AND BROODING

Fifteen hatching intervals in 1970 had a mean of 1.0 days. This asynchronous hatching results in the death by starvation of one or more chicks in most nests during harsh years, since adults tend to feed older, more vocal chicks more readily than younger, weaker ones. The mortality generally occurred within two weeks after hatching.

Following is a summary of the amount of parental care given as the brooding period progressed.

Days after hatching	Degree of parental care
1-14	Chicks were brooded closely. By the end of the second week, they became so large that adults stood nearly erect with their wings lax.
15-21	The chicks became too large to shelter all at once. By the end of the third week, adults stood erect at the nest edge.
22-28	Brooding ceased, though parents continued to take turns guarding the nest.
29-35	Adults began to leave the nest totally unguarded, returning at intervals to feed chicks or roost.
36-45+	Adults returned to the nest primarily to feed chicks, and spent most of their time away from the colony at communal loitering areas or perched at spots near the nest where the chicks could not reach them.

NEST SANITATION

Adults removed from the nest anything they recognized as foreign, including lichens brought as nest material, feces from small chicks, bits of food, egg shells and dead chicks. Both chicks and adults ate food which had been dropped into the nest during feeding. Fresh material was added continually to the nest during the nestling period, and often dead chicks were covered up with it.

One female swallowed whole a dead, 2-3 day old chick that had been lying in the nest for several days.

THE CHICK

Chicks began to beg and be fed 2-3 days after hatching, before their eyes were open. At first they took macerated fish from the mandibular groove of the adult, but at 4-5 days began to eat solid bits of fish. When both adults were present, both fed, thus disregarding the distinction between "in" and "out". The first chick to hatch was the first fed, and obtained a head start in growth over the rest of the brood which it maintained until fledging.

At four weeks chicks began to follow their parents out of the nest to beg, and at five weeks were fed at abandoned nests, perching spots and communal loitering areas. In the three weeks prior to fledging, chicks begged neighboring adults from a distance if they could not reach them, or joined foreign broods if they could. Adults never fed chicks other than their own.

Chicks recognized their parents by sight from at least 6 m away, and by voice as the latter landed on the colony. Parents recognized the begging calls of their chicks, even when they could not see them. Chicks recognized their siblings by sight and probably by voice. Large chicks which had wandered from the nest took precedence over territory. Adults left the nest to feed them, but did not regard them as a floating territory, as they did not defend the area around them.

FLEDGING AND POST-FLEDGING

Two chicks in 1970 fledged at 49-50 days; this is within the range of 42-51 days at Mandarte Island (Drent et al. 1964). Age at fledging was difficult to determine, since chicks left the nest before they could fly and returned to it sporadically, especially at night, for up to 3.5 weeks after fledging. ~~The frequency distributions and averages of~~ Brood size at fledging is ~~are~~ shown in Table 4 .

On 27 August 1970 all colonies but three had completely fledged. In 1973 all young on the cape were fledged by 15 September, and most by the last week in August. In 1976, five percent of the nests still had unfledged young on 3 September.

Juveniles depended wholly or partly upon adults for food for at least two weeks after fledging. Up to three of them at a time would chase an adult in the air or on the water, begging, and they were fed both on the water and on shore rocks. This post-fledging dependence period performed an educational function. Begging juveniles followed adults to sea until lost to binocular view, or underwater when the latter tried to elude them by diving. This behavior perhaps helped juveniles orient the colony on the coastline, showed them preferred feeding areas, and aided them in learning to fish.

NESTING SUCCESS AND MORTALITY

Nesting success and mortality rates at Cape Peirce were determined only in 1970, primarily from several south cliff colonies. These are compared with results from Mandarte Island in Table 5 . Mortality rates were calculated using Ricklefs'

(1969) formula $\underline{m = -(\log_e P)/t}$ where $\underline{m}$ is average daily mortality rate in percent and $\underline{P}$ is the proportion of nests, eggs or individuals which survive any portion $\underline{t}$ (measured in days) of the nesting period.

Success and mortality have been calculated for the whole cape using the 1970 boat survey data. Some nest mortality occurred prior to the first survey on 4 July, which was 6 weeks after the onset of laying. Nest mortalities at five colonies from both sides of the cape ranged from 0 to 33 percent, with a mean of 16 percent. From the mean was derived a correction factor of 1.19 which, when multiplied by the number of nests active on 4 July, gave the number present at the end of the laying period. The corrected values for the number of nests, multiplied by the average clutch size of 3.1, gave the total number of eggs on the peninsula just after laying. The number of young fledged or about to fledge were counted on the 10 August survey. Mortality during fledging was negligable. Table 6 shows corrected nesting success and mortality rates.

Mortality data such as those presented in Tables 5 and 6 can be compared only with extreme caution, in a general way, and are sometimes misused. They often represent non-random samples of small size, differences in calculation of the duration of portions of the nesting period, investigator-induced mortality, or too few seasons' data. In 1970, mean brood size at fledging was much lower than in 1976, indicating a greater success the latter year. The differences were due to the weather. The different mortality rates between the south and west cliffs in 1970 demonstrates the inadequacy of a small, non-random sample.

Robertson (1971) found a much higher fledging success during two seasons at Mandarte Island than van Tets (Drent et al. 1964), though the latter figure was used by Ricklefs (1969) in making broad comparisons between species.

Egg mortality occurred at a lower rate than nestling mortality at Cape Peirce. Predation pressure, which affects breeding primarily during the egg period, was low; hence, desertion must have been responsible for most cases of total nest failure, 37 percent in 1970. Causes of desertion include death or injury of one member of a pair, inability of adults to feed both themselves and chicks, and weakening of the adults due to exposure.

The weather, more important during the nestling period, was harsh, and starvation due to asynchronous hatching was the most significant mortality factor. In 1970 one or more chicks died in 82 percent of the successful nests.

INTERSPECIFIC RELATIONS

Predation pressure was low, considering the hundreds of Glaucous-winged Gulls (*Larus glaucescens*) which constantly patrolled the cliffs. Some nests remained unguarded for up to 20 minutes during egg counts, but no predation occurred. One pair repeatedly left their eggs alone for up to 12 minutes during routine nest relief, and still fledged two young. One nest, when abandoned, remained untouched for 4 hours, though gulls and ravens flew by it. Not once in two seasons was a gull seen to predate a cormorant nest, though they attempted to frighten adults from nests. Several times ravens drove cormorants from nests, but only once was an egg present. Had the clutches been full, it is unlikely the cormorants would have flushed.

The Black-legged Kittiwake was the major competitor with the Pelagic Cormorant. Nest site requirements overlapped considerably, and competition for nest sites would have been intense if the cormorants had not begun courting 1-2 weeks before the kittiwakes arrived on the cliffs and 3-5 weeks before they began gathering nest material. In 1973, 80 percent of the cormorants had commenced laying before the kittiwakes began gathering. The display spots of late males were plundered as fast as their owners could bring grass; this undoubtedly interfered with pairing. Established kittiwake pairs successfully drove away cormorants attempting to land at their spots. The sites of unsuccessful cormorant pairs were frequently taken over by kittiwakes. Aggressive interaction between the two species ranged from threat to pecking intention to attack and chasing, the cormorants being more aggressive than the kittiwakes.

There was feeding overlap between the two species. From late May to mid June, aggregations of hundreds of kittiwakes feeding on schooling fish off the west cliffs and in Nanvak Bay attracted tens of cormorants. The latter were more effective predators. Upon surfacing, they were beset by up to three kittiwakes at once trying to steal their catch.

Kittiwakes nested within 6 m of cormorants 17 times as frequently on the west cliffs as on the south in 1970. Egg success to fledging and overall nest success were half as great on the west cliffs as on the south. This suggests that the density of kittiwakes on the west was in some way connected with higher cormorant mortality there, though other factors such as prevailing winds from the northwest may have been responsible. In 1973, there were over twice as many cormorant pairs on the south cliffs as on the west, whereas in 1970 the two stretches supported nearly equal numbers.

FEEDING

Pelagic Cormorants fed extensively in Nanvak Bay. They dived in open leads during spring breakup, and joined large feeding assemblages composed mostly of anseriforms at the ice edge in early May. When the ice had gone, they preferred the deeper water of channels, though they used the entire bay. Daily during nesting there was a steady stream of singles and small flocks from the west cliffs to and from the bay. Pelagic Cormorants commonly dived in the shoal waters around the peninsula ~~cape~~, within a hundred meters of the cliffs. They travelled tens of kilometers to sea as well, though how much feeding took place there is unknown.

FALL DISPERSAL

From fledging onward, juveniles outnumbered adults at most colonies, especially during the day. From the third week in August until they departed, many adults perched at night at communal roosting areas not utilized during the nesting period, whereas l.c. Most juveniles returned to the colonies. ~~at night.~~ The effect of this fall age segregation ~~by age~~ on the migration and wintering of the two groups is unknown.

Fall dispersal was gradual. Some adults left the cape when their nests failed; others left when their young had fledged. In 1973 there was a steady decline in numbers throughout August and

September, until on 25 September there were only 11 birds along the west and half the south cliffs. The population was probably entirely gone by 1 October.

Bartonek (pers. comm) has seen some exceptionally large cormorant concentrations in Unimak Pass in September. These coincide with the departure of most cormorants from Cape Perice. At Cape Thompson, adults were present in near maximum numbers until at least 27 September 1960 (Swartz 1966). Many departed during a storm between 28 September and 5 October, and the last on 17 October. The Cape Peirce cormorants leave before the most northern populations pass by.

COMPARISON OF CAPE PEIRCE AND MANDARTE ISLAND POPULATIONS

Cape Peirce (CP) and Mandarte Island (MI) are separated by ten degrees of latitude. The former environment is subarctic, the latter boreal-temperate. Two subspecies are represented, *P. p. pelagicus* at CP and *P. p. resplendens* at MI. The following differences in the two populations were noted, using Drent et al. (1964) and Robertson (1971) for information on Mandarte.

1. The CP population is migratory; that at MI is resident.
2. Laying at CP commences 1 week *before* and peaks 2 weeks *before* that at MI. At CP, the overall laying period is nearly 2 weeks shorter.
3. Modal clutch size at CP is one egg less, and mean clutch size 0.6-0.7 eggs less than at MI.
4. Relaying is uncommon at CP and does not occur in harsh seasons. It is common at MI. At CP, all laying is completed by 7 July; at MI, relays occur until the first week in August.

5. Incubation period is 2-3 days shorter at CP. Hatching to fledging intervals at CP fall within the range of those at MI.

6. Modal brood size at fledging at CP is two in harsh years and three in mild years. A few broods of four fledge in mild years. At MI modal brood size is three. Four is the maximum number to fledge, though five may have hatched.

7. At CP mortality is higher during the nestling period than the egg period. The reverse is the case at MI. The major mortality factors at CP are weather and starvation. At MI predation is the major factor.

8. Either immatures from CP spend their first summer on the wintering grounds, or the CP population entirely lacks the brown immature phase, indicating that breeding maturity is reached at one or two years of age. In either case, it is different from the MI population where brown, first year immatures summer in the breeding area and breeding maturity is reached at three years.

DISCUSSION

The Cape Peirce population undergoes the rigors of migration before and after a shorter, more severe season than obtains at Mandarte Island, and the nesting strategy reflects these differences. The Cape Peirce birds begin courting as soon as they arrive, even with snow on the ledges. Low clutch size not only reduces energy output for egg formation, but also compresses the laying period. The incubation period is shorter at Cape Peirce, but the nestling period is as long or longer, indicating that growth rates are slower. The overall nesting periods seem to be equivalent.

There are two breeding strategies at Cape Peirce, one operating in mild years and one in harsh years, and the difference between them is as great as if two different populations were involved. In harsh years, modal clutch size, range in clutch size, modal brood size at fledging and range in brood size are reduced by one. The laying period is compressed, and relaying is eliminated from the strategy.

Asynchronous hatching, which results in mortality by starvation in harsh years, reduces the strain on the adults and potentially further reduces the nesting period, since a smaller brood requires fewer feeding trips and grows faster (Robertson 1971).

Egg laying commences one or two weeks before that at Mandarte Island, ten degrees of latitude farther south, and three weeks before that at Cape Thompson, ten degrees farther north (Swartz 1966). The reason for this early shift in laying is unknown. It is possibly an adaptation which allows the cormorants to nest before kittiwakes arrive to compete for nesting space and material. It may be that the Cape Peirce population is a remnant one which once represented the northernmost limit of the range of the Pelagic Cormorant. When the range expanded, birds from more southern populations were involved. There is evidence for this in migration, when the Cape Peirce population both arrives in spring and departs in fall before the more northern birds pass by. It is also possible that the early shift is related to summer food availability.

ACKNOWLEDGMENTS

This study was funded by the Cape Newenham National Wildlife Refuge, U.S. Fish and Wildlife Service. Dr. Brina Kessel gave encouragement and advice in the initial stages of the project. Dr. Calvin Lensink supported the study from its conception. Jerry Hout contributed observations and photographic work. Captain Emil Squazzo, Commander of the Cape Newenham Air Force Site in 1973, provided substantial assistance. Dr. James Bartonek and George Divokey gave freely of their data pertaining to the study. Linda Schandelmeier assisted in every phase of the work through May 1973. This paper is dedicated to the late Dr. Lyndon Lane Hargrave of Prescott, Arizona.

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Table 1. Site types of 105 successful Pelagic Cormorant nests in 1970.

	West Cliffs	South Cliffs
Total number of nests	48	57
Percent of nests in:		
Vertical clefts	8	14
Ledges with overhang	29	26
Open ledges	65	61

Table 2. Proximity of Pelagic Cormorant nests to Black-legged Kittiwake and Common Murre pairs in 1970.

	West Cliffs	South Cliffs
Number of kittiwake pairs[1]	20,500	435
Number of murres[1]	27,000	770
Number of cormorant nests	142	149
Percent within the following distances of kittiwakes		
1.0 m	47	<1
1.5 m	76	5
3.0 m	83	5
6.0 m	85	5
Percent within the following distances of murres		
1.0 m	26	<1
1.5 m	37	2
3.0 m	45	3
6.0 m	46	3

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[1] Estimates by Bartonek and Divokey, 1973.

Table 3. Laying to hatching intervals by clutch position for 11 Pelagic Cormorant eggs in 1970.

	Number of Eggs		
	First Laid	Second Laid	Last Laid
Interval (days)			
27			2
28		2	
29	1		
30	2		
31	4		

Table 4. Size of Pelagic Cormorant broods at fledging during two seasons.

	No. of Young Per Nest					
	1	2	3	4	Average	Total
Number of Broods						
1970	41	56	11	0	1.7	108
1976[1]	14	38	48	3	2.4	103

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[1] 1976 data from Petersen and Sigman (1977)

Table 5. Nesting success and mortality rates at Cape Peirce and Mandarte Island.

Locality	Cape Peirce	Mandarte I.[1]	Mandarte I.[1]
Year(s)	1970	1957	1958-59
Total nests	27	37	39
Total eggs	82	141	--
Chicks[2]			
Total	64	70	101
% hatching	*78 (0.8)	*50 (2.0)	--
Per nest	*2.4	*1.9	**2.6
Young fledged[3]			
Total	36	--	77
% fledging	*56 (1.2)	--	*76 (0.6)
Per nest	1.3	--	**2.0
Egg success[4] to fledging in %	44 (1.0)	--	--
No. of nests fledged	17	--	--
Nest success[4] in %	63 (0.6)	--	--

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[1] Figures combined from Drent et.al. (1964, Table 7) and Ricklefs (1969, Table 15).

[2] Average daily mortality rates of eggs to hatching are in parentheses, based on egg periods of 33 days at Cape Peirce and 35 days at Mandarte Island.

[3] Average daily mortality rates of chicks to fledging are in parentheses, based on nestling periods of 49 days at Cape Peirce and 45 days at Mandarte Island.

(continued)

Table 5 (continued)

[4] Average daily mortality rate in parentheses is based on a nesting period of 82 days.

*Indicates the figures from the two localities are comparable.

**Indicates the figures from the two localities are not comparable.

Table 6. Corrected nesting success and morality rates at Cape Peirce based on boat survey data, 1970.

Area	West Cliffs	South Cliffs	Whole Cape
Total nests			
July 4	142	149	291
Corrected[1]	169	177	346
Total eggs[1]	524	549	1,073
Young fledged	85	171	256
Egg success[2] to fledging in %	16 (2.2)	32 (1.4)	24 (1.7)
Young fledged per nest	0.5	1.0	0.8
Total nests fledged	48	100	148
Nest success[2] in %	28 (1.6)	57 (0.7)	43 (1.1)

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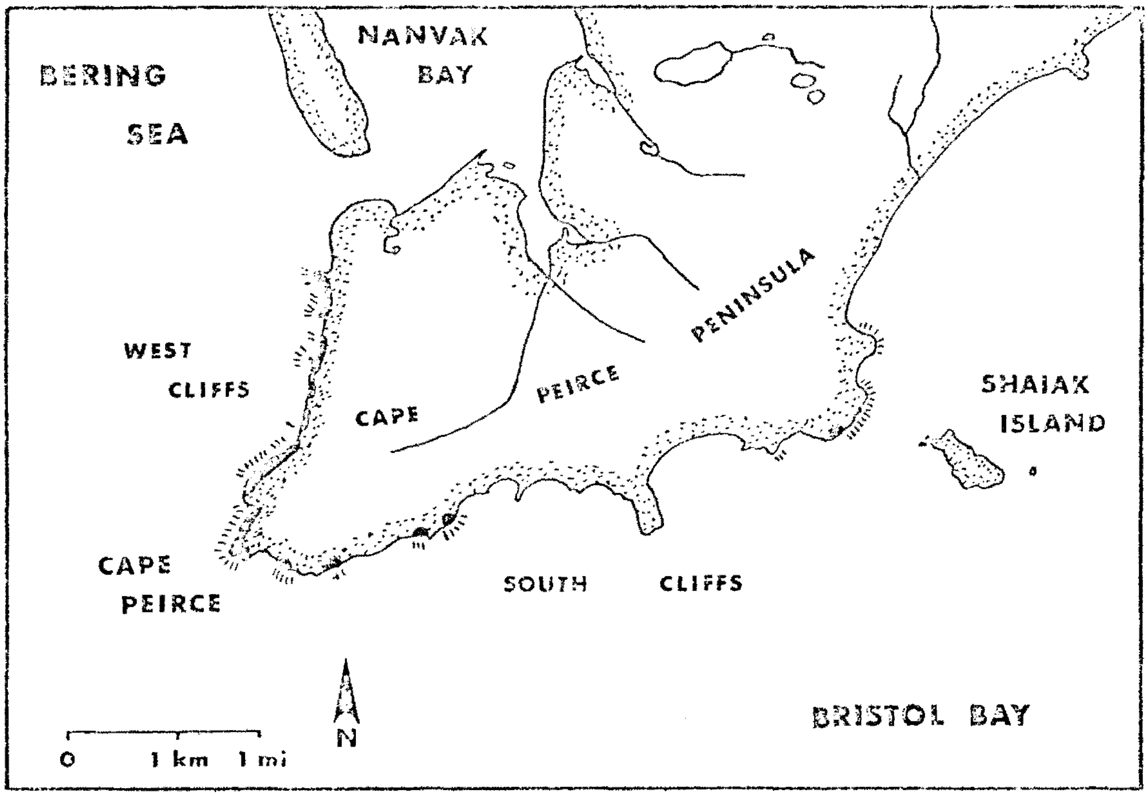
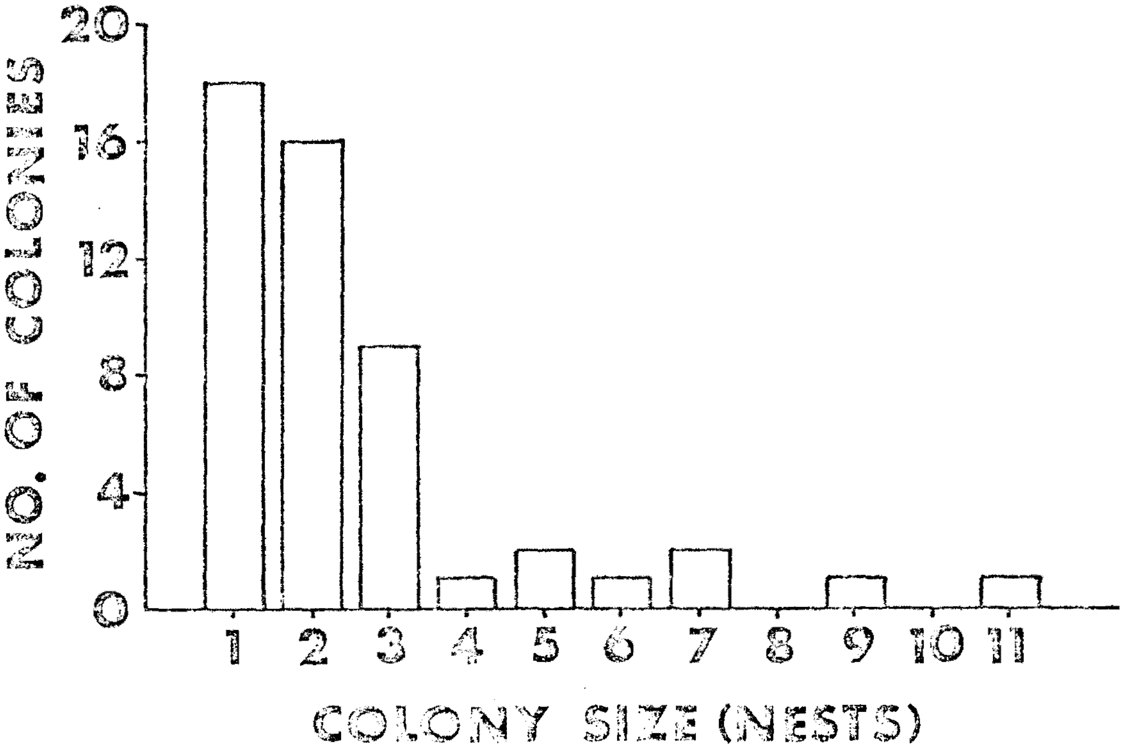
[1] See text for explanation.

[2] Average daily mortality rates in parentheses, based on 78 days, the nesting period exclusive of laying.

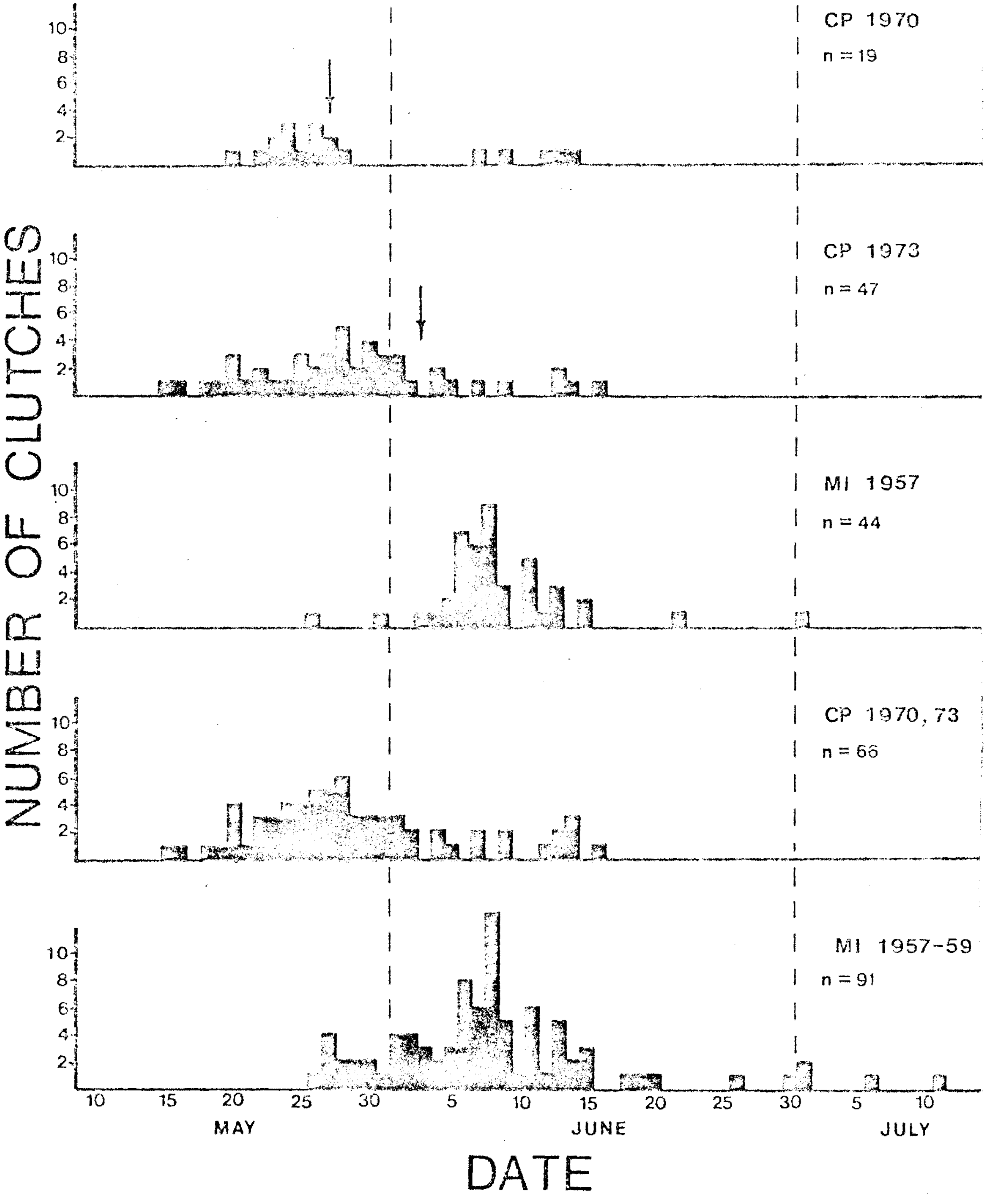
List of Figures



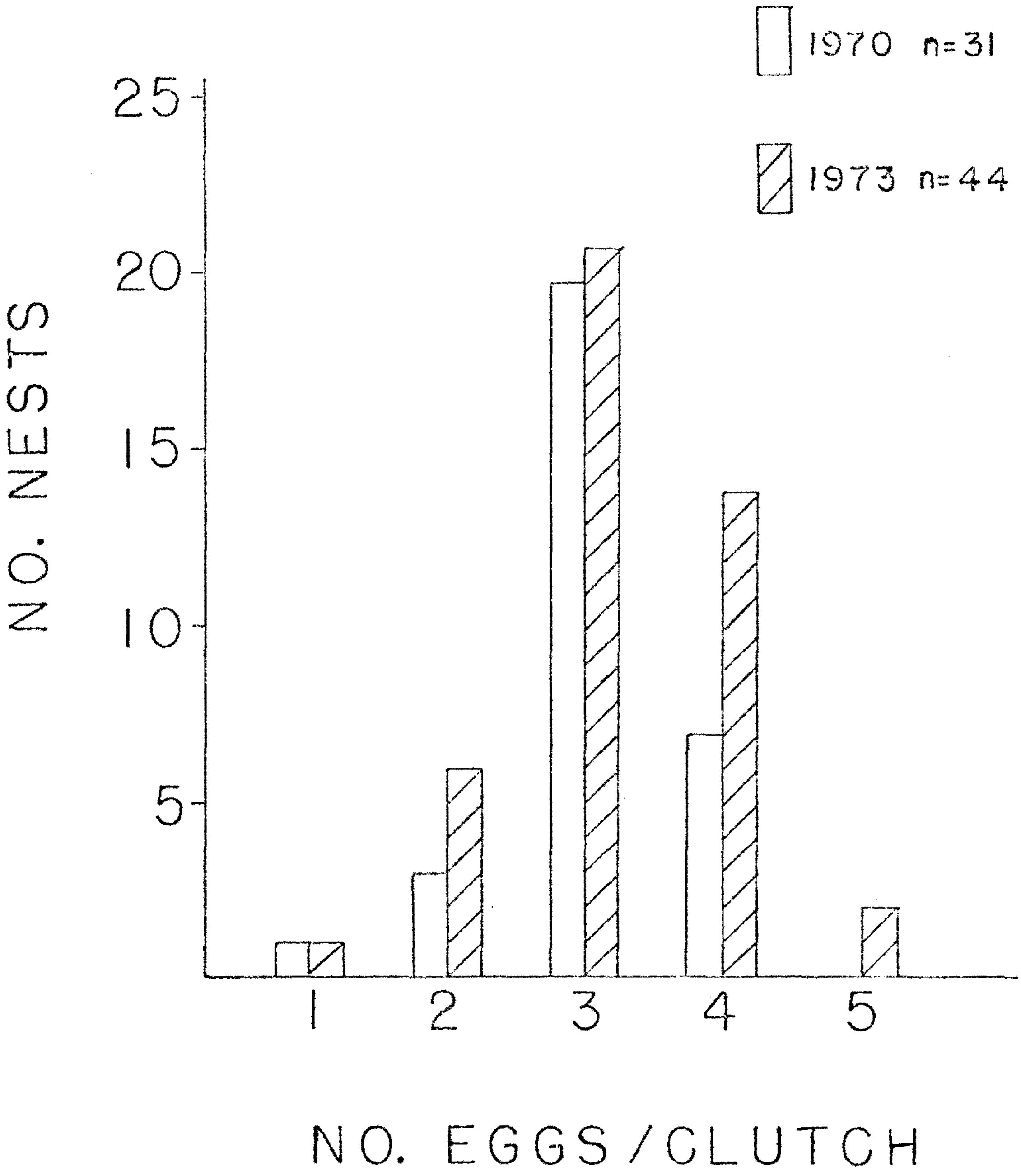
1. Map of the study area. Black shading on shoreline indicates Black-legged Kittiwake nesting areas; hatchures indicate Pelagic Cormorant nesting areas.



2. Size frequency of Pelagic Cormorant colonies on the southern west cliffs of Cape Peirce.



3. Clutch commencement of the Pelagic Cormorant at Cape Peirce and Mandarte Island (figures adapted from Drent et al. 1964). Arrows indicate onset of nest material gathering by Black-legged Kittiwakes.



4. Clutch size frequency of the Pelagic Cormorant for two seasons at Cape Peirce.