Status, ecology, and conservation of *Synthliboramphus* murrelets and auklets

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Abstract

The *Synthliboramphus* murrelets and auklets are widely distributed around the rim of the North Pacific Ocean. In general, the murrelets and Cassin's Auklet *Ptychoramphus aleuticus* nest much farther south than the Parakeet *Cyclorrhynchus psittacula* and *Aethia* auklets—three species of murrelets (Xantus' *Synthliboramphus hypoleucus*, Craveri's *S. craveri*, and Japanese *S. wumizusume*) are restricted to subtropical locations, whereas the Ancient Murrelet *S. antiquus* and Cassin's Auklet range from the subtropics to the Subarctic. Although there is some overlap between the groups, the murrelets and Cassin's Auklet are replaced in the Subarctic and Arctic by the Parakeet Auklet and the *Aethia* auklets. The groups also are separated trophically—murrelets and Cassin's Auklets consume a much greater proportion of fishes than do the other, more planktivorous Parakeet and *Aethia* auklets. Estimates of the numbers of most species for most locations are crude. Ancient Murrelets and Cassin's Auklets were decimated throughout the Aleutian Islands and northern Gulf of Alaska by foxes during the fox-farming era. Elsewhere, murrelets and Cassin's Auklets are threatened by introduced rats, cats, raccoons, and people. The Japanese Murrelet is now a critically endangered species. The conservation of subtropical murrelets and the restoration of Ancient Murrelet and Cassin's Auklet populations (and other avifauna) in the Aleutian Islands and Gulf of Alaska by eliminating introduced mammals are high priorities for the immediate future.

Résumé

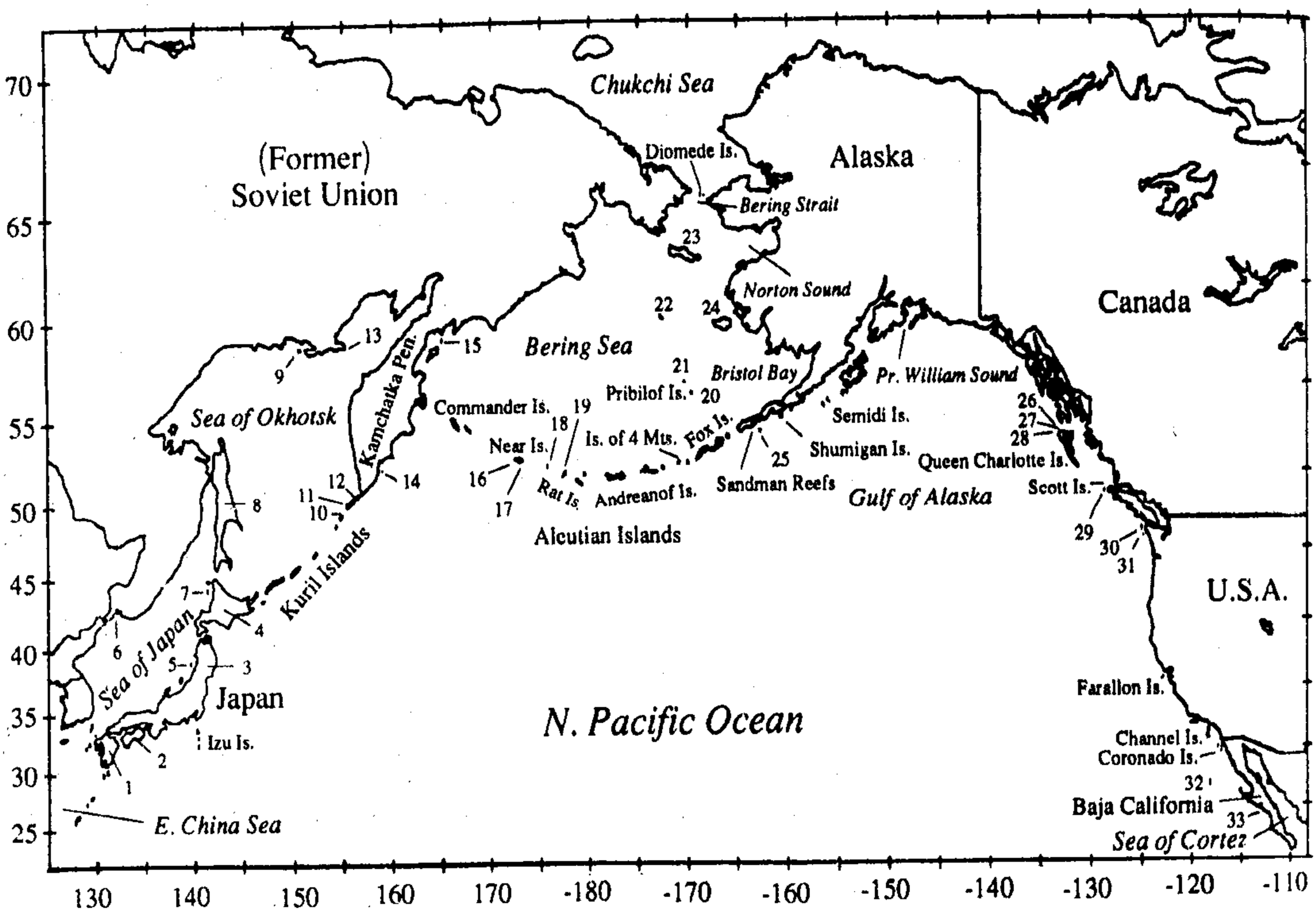
Les alques *Synthliboramphus* sont très répandues le long des côtes du Pacifique Nord. En règle générale, les *Synthliboramphus* et l'Alque de Cassin *Ptychoramphus aleuticus* nichent beaucoup plus au sud que l'Alque perroquet *Cyclorrhynchus psittacula* et que les oiseaux marins du genre *Aethia*. Les alques à dos noir *Synthliboramphus hypoleucus*, de Craveri *S. craveri* et du Japon *S. wumizusume* sont confinées dans les régions subtropicales, tandis que l'Alque à cou blanc *S. antiquus* et l'Alque de Cassin fréquentent autant les régions subtropicales que les régions subarctiques. Malgré un certain chevauchement des espèces, les *Synthliboramphus* et l'Alque de Cassin cèdent les régions subarctiques et arctiques à l'Alque perroquet et aux oiseaux marins du genre *Aethia*. Les groupes affichent aussi des habitudes alimentaires différentes. Le régime des *Synthliboramphus* et de l'Alque de Cassin comprend beaucoup plus de poissons que le régime des autres espèces. L'Alque perroquet et les *Aethia* préfèrent le plancton. Pour la plupart des espèces et la plupart des emplacements, les données de population sont des estimations brutes. L'Alque à cou blanc et l'Alque de Cassin ont été décimées par les renards, partout dans les îles Aléoutiennes et dans le nord du golfe d'Alaska, lorsque l'élevage y était une activité féconde. Ailleurs, les *Synthliboramphus* et l'Alque de Cassin sont menacées par les rats, les chats, les ratons laveurs et les hommes. L'Alque du Japon est maintenant en voie d'extinction. Il faut, le plus vite possible, protéger les alques subtropicales et rétablir les populations d'Alques à cou blanc et d'Alques de Cassin (ainsi que d'autres espèces d'oiseaux) dans les îles Aléoutiennes et dans le golfe d'Alaska, en éliminant les mammifères non indigènes.

1. Introduction

This group of auks includes Xantus', Craveri's, Japanese, and Ancient Murrelets (*Synthliboramphus hypoleucus*, *S. craveri*, *S. wumizusume*, and *S. antiquus*), Cassin's Auklet *Ptychoramphus aleuticus*, Parakeet Auklet *Cyclorrhynchus psittacula*, and Crested, Whiskered, and Least auklets (*Aethia cristatella*, *A. pygmaea*, and *A. pusilla*). Although the overall distributions of each species are well known and span the full rim of the North Pacific Ocean and its marginal seas (East China, Japan, Okhotsk, Bering, Cortez) (Fig. 1), numbers of individuals at numerous locations have not been determined. They all are extremely difficult to count—the murrelets and Cassin's Auklets are active at the colonies at night, and they and the other species nest underground or in other inaccessible locations. Thus, murrelets and Cassin's Auklets, in particular, are known simply to be present or probably absent at many sites, and most colony totals for most species are rough approximations.

In the following status accounts, we have not attempted to identify all of the known nesting locations of any of the species, but show the locations of the greatest known numbers. Information on individual colonies in Alaska and the eastern North Pacific can be found in NOAA/FWS (1991). We have estimated possible "real/pristine" numbers of each species if there is reason to believe that the catalogue total does not fairly represent the numbers that would derive from thorough censuses of all known colonies and if populations had not been reduced by introduced predators. For example, 13 islands in the Sandman Reefs group, Alaska, are known to have Ancient Murrelets, but the number of birds has been estimated for only one of the islands. Yet, even if birds were counted everywhere, the totals would not reflect pristine numbers because the abundances of Ancient Murrelets and Cassin's Auklets today

Figure 1
Landmarks of the North Pacific Ocean. 1–Kyushu I., 2–Shikoku I., 3–Honshu I., 4–Hokkaido I., 5–Tobishima I., 6–Peter the Great Bay, 7–Teuri I., 8–Sakhalin I., 9–Talan I., 10–Shimushir I., 11–Ushishir I., 12–Paramushir I., 13–Jamskie Is., 14–Starichkov I., 15–Verkhoturova I., 16–Attu I., 17–Agattu I., 18–Buldir I., 19–Kiska I., 20–St. George I., 21–St. Paul I., 22–St. Matthew I., 23–St. Lawrence I., 24–Nunivak I., 25–Sanak I., 26–Forrester I., 27–Langara I., 28–Frederick I., 29–Triangle I., 30–Tatoosh I., 31–Alexander I., 32–Guadalupe I., 33–Bahia de Ballenas.



apparently are only fractions of the sizes they were a century ago before foxes (*Vulpes fulva* and/or *Alopex lagopus*) and other terrestrial mammals were introduced to most of the islands where they nest (Bailey 1990; Bailey and Kaiser, this volume). We have based our estimates of possible pristine numbers on (1) reports of early explorers, (2) present numbers on predator-free islands, and (3) the sizes of islands where birds probably would nest in much greater numbers if there were no introduced mammals.

2. Present and historical status

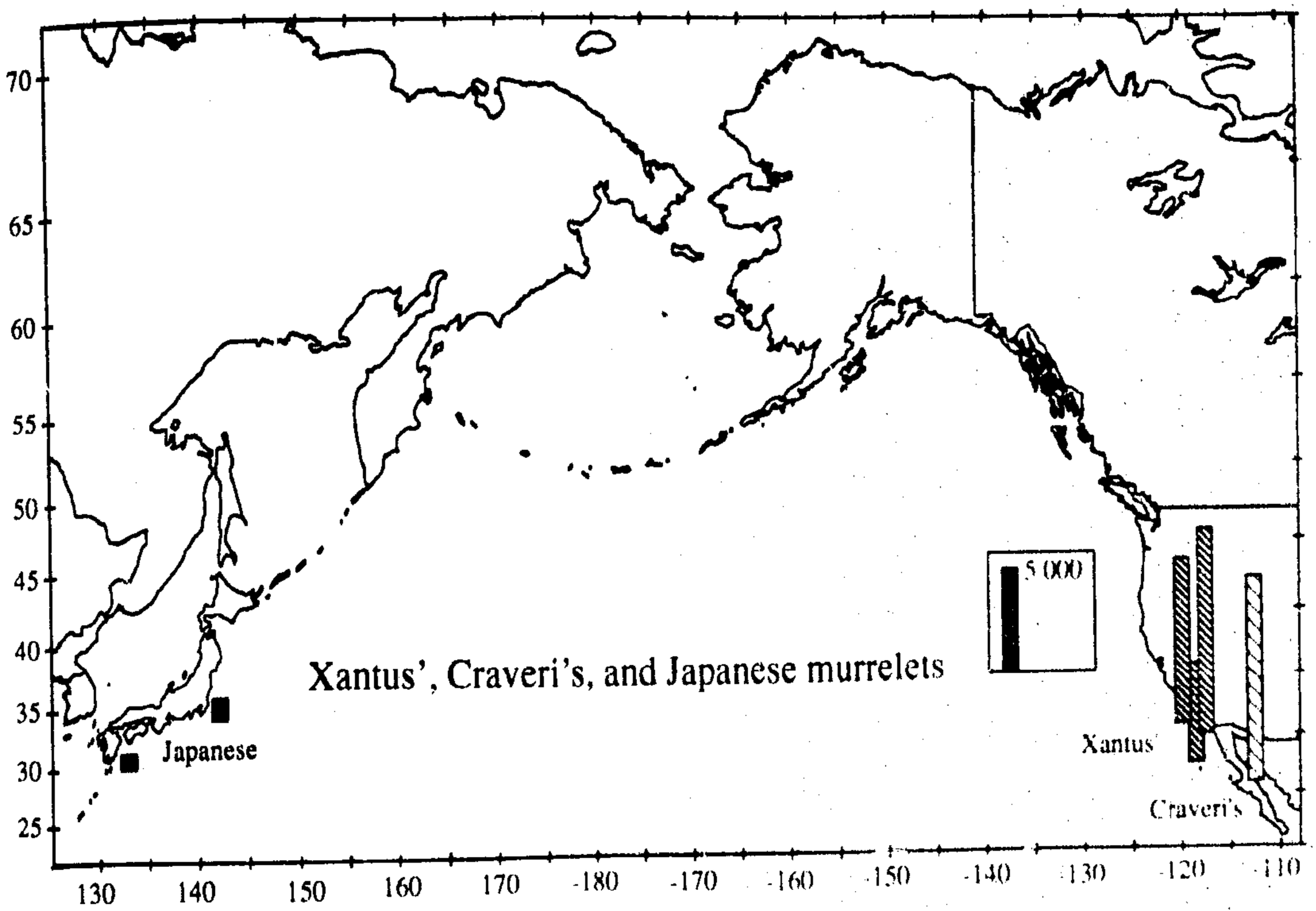
2.1. Xantus' Murrelet

Xantus' Murrelets nest in southern California (United States) and on the outer coast of Baja California (Mexico) (Fig. 2). Two subspecies are recognized, although they differ from each other in size, plumage, and distribution about as much as they do from the closely related Craveri's Murrelet, and the correct taxonomic status of all three has been the subject of a prolonged debate (Jehl and Bond 1975).

Synthliboramphus hypoleucus scrippsi is the more northern of the two forms, and is most abundant on Santa Barbara Island in the Channel Islands, where a population of 6000–10 000 individuals was estimated during the breeding seasons of 1976–1978 (Murray et al. 1983). Fewer than 100–150 pairs nest on any of the other Channel Islands, but as many as 5000 pairs might nest in the Coronado Islands (W. Everett, pers. commun.). Farther south, approximately 4800 individuals (1300 nonbreeding) of *S. h. hypoleucus* were counted on Guadalupe Island (Jehl and Everett 1985). The combined breeding population on islands off the outer coast of Baja California is probably 10 000–20 000 pairs (W. Everett, pers. commun.).

Feral cats *Felis domesticus* reduced or eliminated murrelets on many of the Channel Islands. The murrelet population on Santa Barbara Island, which was nearly destroyed by cats in the early part of this century, recovered quickly by the mid-1970s after the removal of cats (Hunt et al. 1981a). Cats have also killed many murrelets on the Coronado Islands (W. Everett, pers. commun.). The decline of Peregrine Falcons

Figure 2
Centres of abundance of Xantus', Craveri's, and Japanese murrelets



Falco peregrinus from pesticide poisoning during the 1960s and 1970s possibly helped speed the recovery of the murrelet population in the Channel Islands (Hunt et al. 1981a).

2.2. Craveri's Murrelet

Craveri's Murrelet replaces Xantus' Murrelet in the Sea of Cortez (Fig. 2). Pairs have been seen along the outer coast of Baja California during the breeding season (Jehl and Bond 1975), and Jehl saw a pair of adults with two half-grown chicks in Bahia de Ballenas in mid-May (Everett and Anderson 1991), which suggests that nesting of Craveri's Murrelets might not be restricted to the Sea of Cortez. Because the birds are secretive and scattered, it has been difficult to determine their numbers—the best estimate of the size of the population in the Sea of Cortez is about 5000 pairs (Everett and Anderson 1991). There is no evidence that recent historical numbers were appreciably higher than current numbers (W. Everett, pers. commun.).

2.3. Japanese Murrelet

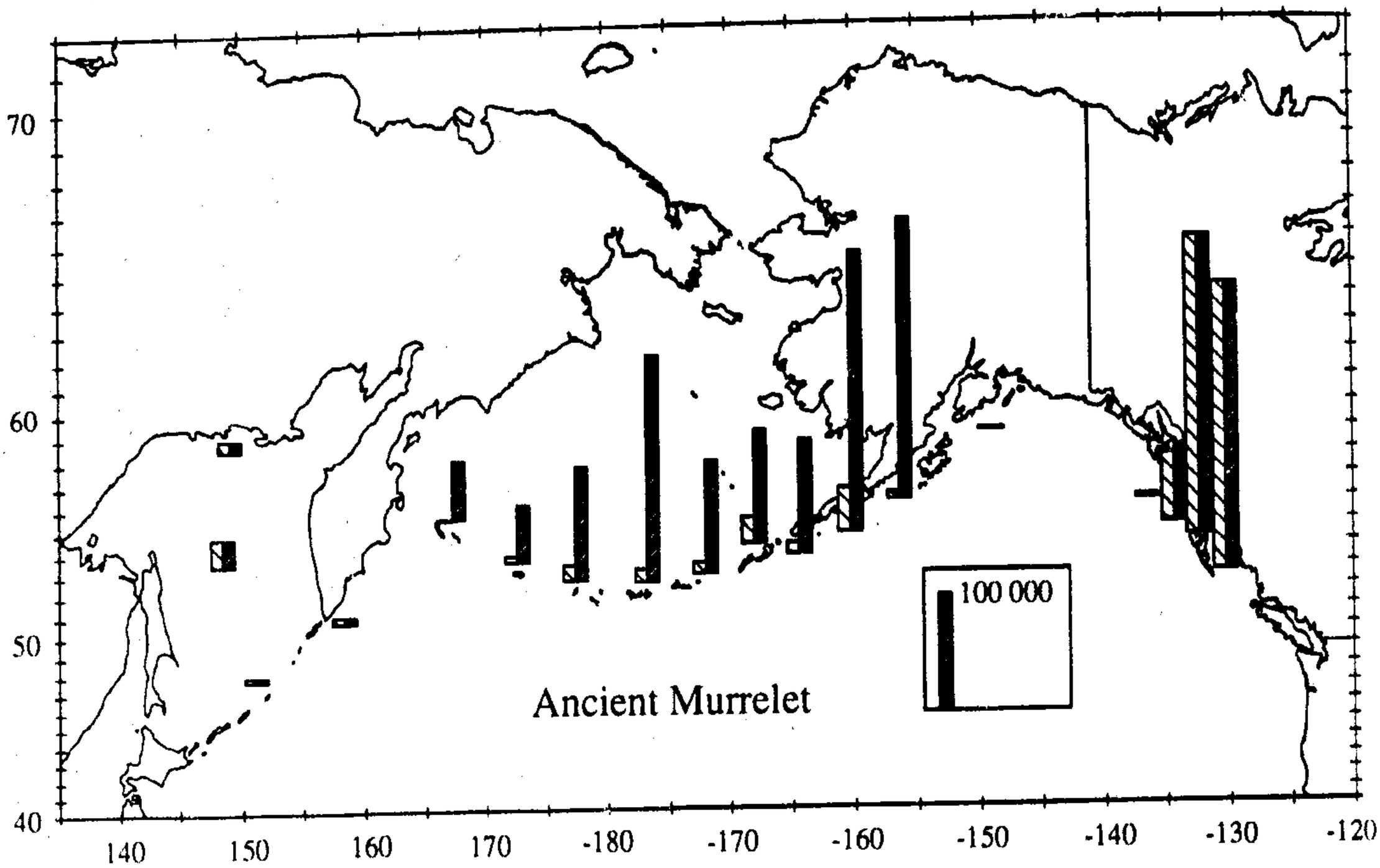
The Japanese Murrelet is the rarest of the alcids, and in Japan is protected by national law and by being designated as a special natural monument (Hasegawa 1984). By the early 1980s the known number of Japanese Murrelets was approximately 1000 in the Izu Islands and 650 on islets off southwest Honshu, Shikoku, and Kyushu (Fig. 2) (Hasegawa 1984) . The number of murrelets on Izu Island was drastically reduced in 1951–52 when the U.S. Air Force used the island for bombing practice (Austin and Kuroda 1972). Japanese Murrelets might also nest in very small numbers in Peter the Great Bay. Nazarov and Shibaev (1987) found an adult female on 28 June 1984, a fledgling female with some down remaining on 8 July 1984, and three other adults on various dates between June and September in other years.

2.4. Ancient Murrelet

The Ancient Murrelet is the only species in the genus *Synthliboramphus* with a broad breeding distribution. It nests from China to Washington, with the greatest current concentration in British Columbia (Fig. 3). The number of Ancient Murrelets on most islands in the Gulf of Alaska and the Aleutian Islands is not known, and the actual numbers in Alaska are likely much larger than those reported in the colony catalogue (Sowls et al. 1978).

In the extreme southwest of their range, Ancient Murrelets are rare breeders along the northwestern coast of the East China Sea (Tso-hsin 1987). They have been seen on the water during the breeding season near Tobishima Island, suggesting that they nest there (Hasegawa 1984). Ancient Murrelets formerly nested in the southwest of Teuri Island, where about 500 were estimated in 1956. However, only a few birds were present in 1963, and none has been seen since (Hasegawa 1984; Fujimaki 1986). There are also a few colonies on the continental coast of the Sea of Japan (North Korea) from De-Kastry Bay to the border with Russia (Schrenk 1860;

Figure 3
Centres of abundance of Ancient Murrelets. Dark bars are possible real/pristine numbers, light bars are present estimates.



Labzyuk 1975; Elsukov 1984). Ancient Murrelets nest on 4–5 islands in Peter the Great Bay, with the greatest numbers, about 500 pairs in 1976, on Verkhovsky Island (Shibaev 1987) and about 100 pairs on Karamzin Island (Labzyuk et al. 1971).

Ancient Murrelets nest in "small" numbers on Sakhalin Island (Nechaev 1986). Approximately 3000 individuals are estimated to inhabit all the Kuril Islands (Velizhanin 1972) and about 6500 pairs nest on Starichkov Island (Vyatkin 1986). Additional pairs possibly nest on several islands along the western coast of the Kamchatka Peninsula (Vyatkin 1986). They nest at a minimum of 18 colonies in the Sea of Okhotsk with a total nominal population of 25 000 birds (Kondratyev and A. Kitesky, unpubl. data). The largest colony, about 10 000 birds, is on Talan Island.

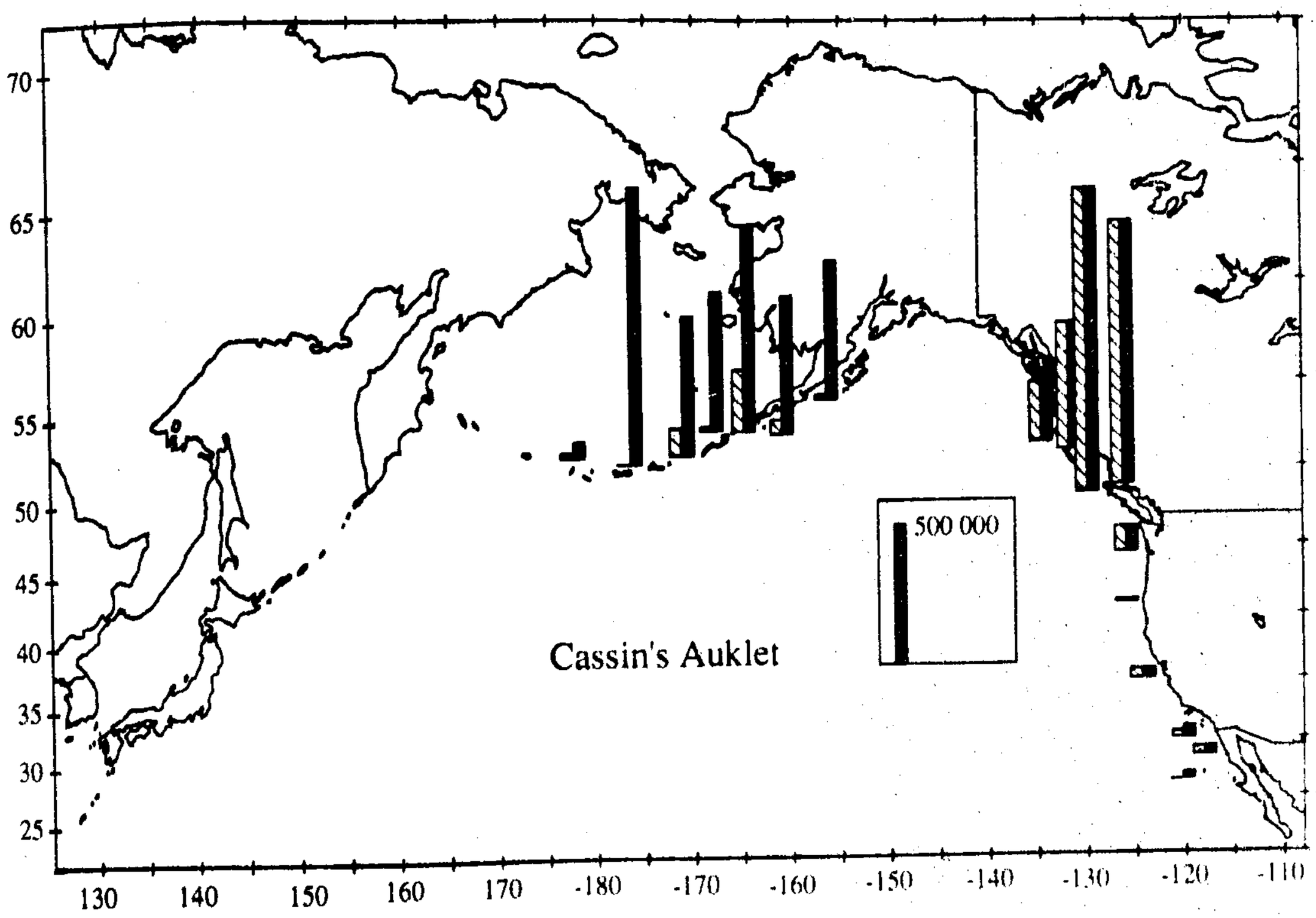
Stejneger (1885) found Ancient Murrelets breeding in small numbers on both of the Commander Islands, where they might never have been numerous because foxes apparently are native there (Bailey 1990). It is now perhaps the rarest of the breeding alcids on the Commanders (Kartashov 1961; Marakov 1972).

Turner (1885) claimed that Ancient Murrelets were "abundant" in the Near Islands. Clark (1910) found them to be "very common" throughout the Aleutian Islands, particularly around Atka, Attu, and especially Agattu, "rather common" around the Commander Islands, and "a few" along the eastern Kamchatka coast and Kuril Islands as far south as Simushir Island. The high relative numbers around Agattu compared to Attu in the Near Islands at that time might have been because Agattu was then fox-free, but Attu had had foxes since 1750 when Russians brought them from the Commanders (Bailey 1990).

Elsewhere in the Gulf of Alaska and throughout much of the Aleutian chain, introduced foxes probably decimated Ancient Murrelets (Murie 1959; Bailey 1990). For example, approximately 5000 pairs nest on Buldir Island, a small, fox-free island just east of the Near Islands (Byrd and Day 1986). Likewise, approximately 5000 pairs nest on fox-free Koniuji Island (Andreanof Islands) and 2500 pairs nest on Chagulak Island (Islands of Four Mountains). In contrast to what Clark (1910) observed, murrelets are now uncommon in the Near Islands group following the addition of foxes to Agattu and Nizke-Alaid islands earlier this century. Foxes were removed from Nizke-Alaid in 1976 and since then the numbers of Ancient Murrelets and numerous other species of marine and terrestrial birds have been rapidly increasing (Zeillemaker and Trapp 1986; Byrd and Bailey 1990). In the Gulf of Alaska, Castle Rock (Shumigan Islands) remained fox-free and has substantial numbers of Ancient Murrelets (30 000) and other burrow nesters, compared to other islands in that group where foxes were introduced and where murrelets are now absent.

Ancient Murrelets in the southern Gulf of Alaska and in British Columbia have fared much better—approximately 523 000 birds nest in the Queen Charlotte Islands, and another 60 000 nearby on Forrester Island (Alaska). But on Langara Island, the number of murrelets has declined from an estimated 50 000–90 000 pairs 20 years ago (Nelson and Myres 1976; Vermeer et al. 1984) to about 20 000–25 000 pairs in the 1980s,

Figure 4
Centres of abundance of Cassin's Auklets. Dark bars are possible real/pristine numbers, light bars are present estimates.



apparently because of predation by black rats *Rattus rattus* (Bertram 1989).

Indigenous peoples also probably have had an adverse effect on numbers of Ancient Murrelets on at least two islands. Littlejohn (in Bendire 1895) speculated that on Sanak Island in the western Gulf of Alaska, Ancient Murrelets "...certainly number several thousand and if left unmolested by man the island would soon become too small to accommodate their natural increase, but such is not the case. The native Aleuts know, almost to a day, when the first ones will arrive, and every bird, Auklet or Murrelet, that is overtaken is promptly clubbed to death and thrown into a sack carried for this purpose. At each of these raids hundreds of these birds are killed, and as they are made frequently and throughout the entire season, it is astonishing that any remain. But this is not all; as soon as day dawns, the entire crew sets out to make a systematic search for eggs ... each one striving to get more than his mates...." Murie (1959) did not find any Ancient Murrelets on Sanak Island in 1937, but by then foxes had been there for many years. Apparently they are still absent (NOAA/FWS 1991).

Ancient Murrelets on Langara Island were abundant through the early part of this century, but might have been even more so had it not been for a heavy harvest by native people. Green (1916) said "...the whole island is a warren of Ancient Murrelets, and there are colonies of other sea-fowl at particular points and on adjacent islets, but the Ancient Murrelets predominate, and are killed by hundreds by the Falcons [peregrines] and by the thousands by Indians, who visit the island from May to August and destroy the birds and eggs *simply* for food " (emphasis added).

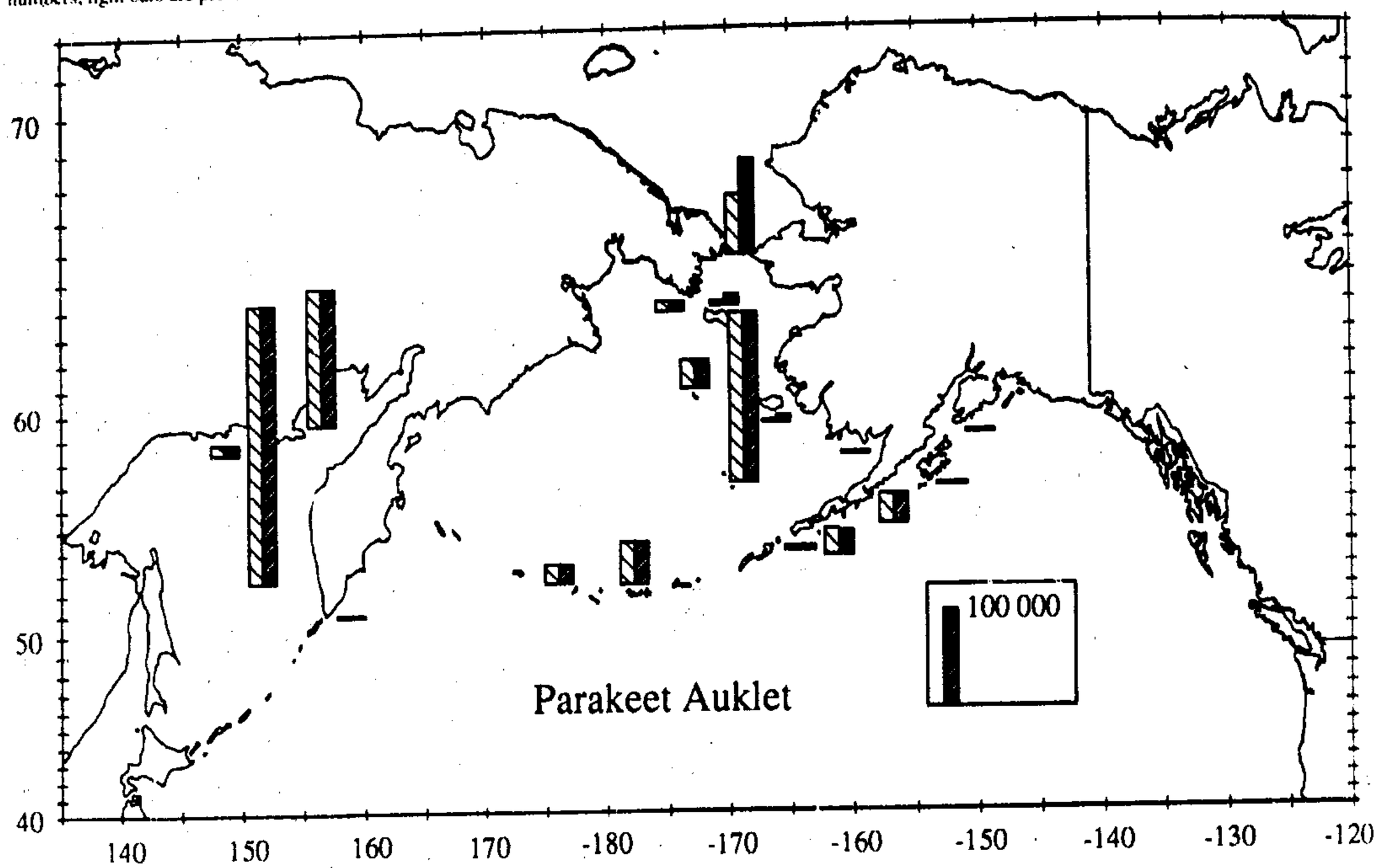
2.5. Cassin's Auklet

Cassin's Auklets nest from the western Aleutian Islands to Baja California, with their centre of abundance in British Columbia (Fig. 4). However, the distribution and numbers in Alaska are poorly known because of the difficulty of censusing them, and, like Ancient Murrelets, the population is undoubtedly larger than the current information indicates.

The western extent of the breeding range of Cassin's Auklets ends abruptly at Buldir Island, where about 200 pairs nest (Byrd and Day 1986). They formerly occurred in small numbers around the Near Islands (Clark 1910), but were not reported from the Commander Islands or west of there by Stejneger (1885, 1899) or Hartert (1920).

Cassin's Auklets in the Aleutian Islands and Gulf of Alaska also suffered greatly as a result of the fox-farming industry, and numbers now throughout that region are probably much lower than in the past. For example, Murie (1959) was told by residents of Atka that two huge colonies, "millions" each, on small islands near Amlia (Andreanof Is.) had been decimated by arctic foxes that swam out from Amlia. However, nearby on fox-free Chagulak Island (Islands of Four

Figure 5
Centres of abundance of Parakeet Auklets. Dark bars are possible real/pristine numbers, light bars are present estimates.



Mountains) there are currently in the order of 100 000 Cassin's Auklets. They are gone, along with Ancient Murrelets, from Sanak Island, but number in the order of 100 000 on each of two fox-free islands nearby in the Sandman Reefs, and 50 000 on Castle Rock in the Shumigan Islands.

The greatest number of Cassin's Auklets is in British Columbia, where approximately 2 782 500 nest (NOAA/FWS 1991). The single largest colony is on Triangle Island, which has in the order of 1.1 million birds. Cassin's Auklets once were also abundant on Langara Island but no longer nest there, probably because of predation by rats (Vermeer et al. 1984; Bertram 1989).

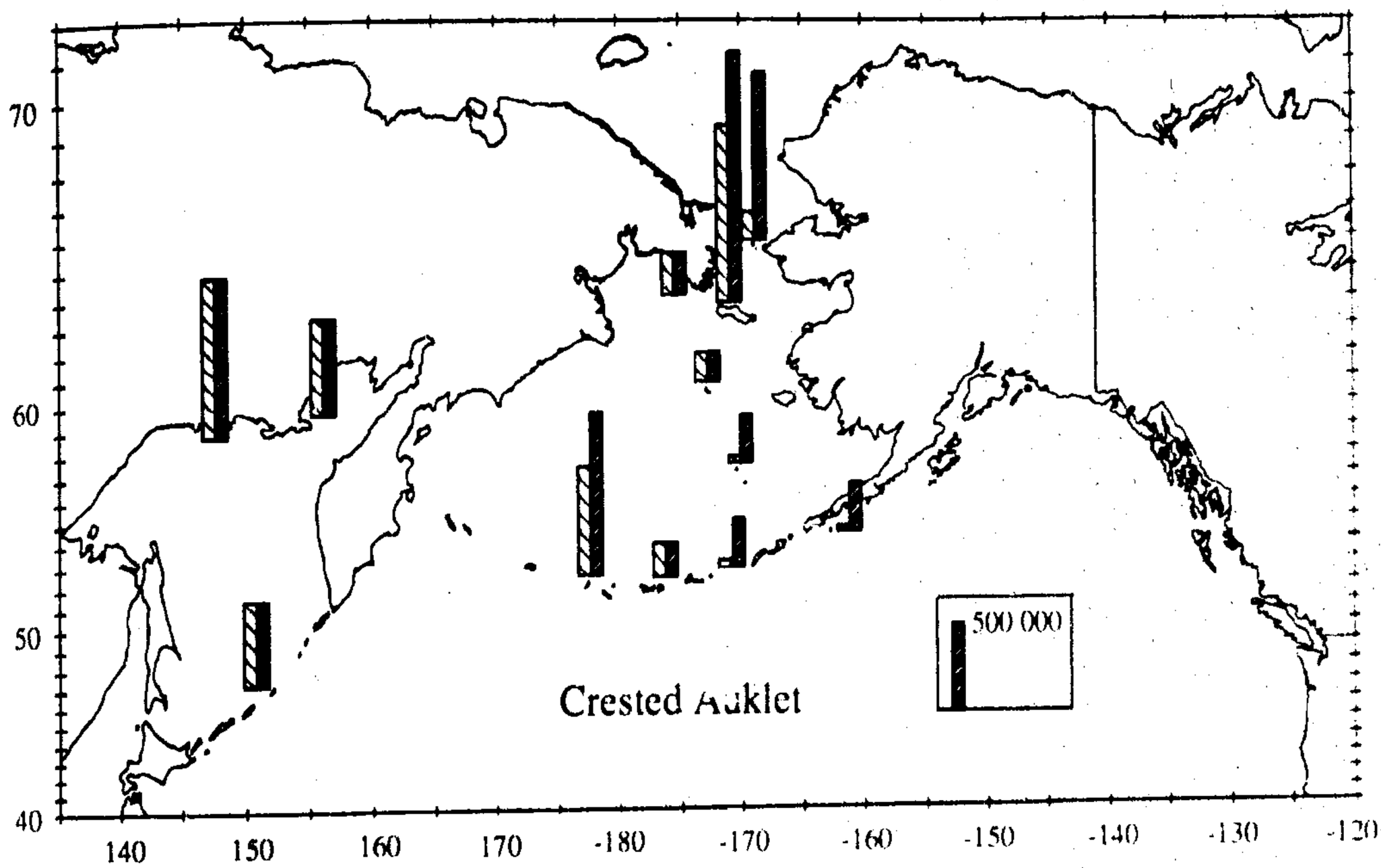
The largest colony of Cassin's Auklets south of British Columbia is on Alexander Island in northern Washington, which has about 55 000 birds. The number on the South Farallon Islands (California) was long considered to be between 105 000 and 171 000 (Manuwal 1974; Ainley and Boekelheide 1990), but has since been revised downward to about 36 000 because of errors in early estimation methods (Carter et al. 1990). At the extreme south of their range, roughly 23 000 nest on the Channel Islands, primarily San Miguel Island, in southern California (NOAA/FWS 1991). They are abundant on several islands along the outer coast of Baja California (San Geronimo, San Benitos, San Roque, and Asuncion) (Everett and Anderson 1991), and the total population is probably somewhere between 20 000 and 40 000 birds (W. Everett, pers. commun.).

According to Howell (1917), Cassin's Auklets on the Channel Islands were "A most abundant resident, breeding in all suitable localities that are free from cats and foxes." By the time of his visit in 1908, however, auklets had been eliminated from Santa Barbara Island by cats that were introduced sometime after 1897. From at least the mid-1800s through the end of the century, auklets had been abundant on the island, "...where they had undermined almost every part of the soft, earthy surface with their burrows." Cassin's Auklets probably nested in large numbers on Guadalupe Island also, but now are restricted to Islote Negro, a very small islet near the southern end of the island, where about 200 pairs nest (Jehl and Everett 1985). Most of the nesting habitat on Guadalupe Island was destroyed by goats that were introduced first in the 18th century and again in the 1870s, by which time they numbered in the tens of thousands (Jehl and Everett 1985). Domestic cats were introduced as well and possibly also had a role in reducing seabird populations.

2.6. Parakeet Auklet

The Parakeet Auklet is primarily a northern and western species (Fig. 5) compared to the murrelets and Cassin's Auklet. They nest from the Kuril Islands (Stejneger 1899; Austin and Kuroda 1972) to Prince William Sound in the Gulf of Alaska, and north to Bering Strait, but numbers in the Kuril Islands and Gulf of Alaska are small compared to the Sea of Okhotsk and Bering Sea (NOAA/FWS 1991; Kondratyev, unpubl. data). There are 15 known colonies of Parakeet Auklets in the Sea of Okhotsk with a total population in the order of 300 000, half of which nest on Matykil Island (Jamskie Islands) (Kondratyev, unpubl. data). The other major concentration is on the Pribilof Islands, principally St. George Island, where about 180 000 nest (Hickey and Craighead 1977). It is the only species of this

Figure 6
Centres of abundance of Crested Auklets. Dark bars are possible real/pristine numbers, light bars are present estimates.



group that commonly nests in inner shelf regions such as Bristol Bay (3000 birds), Nunivak Island (5000 birds), and Norton Sound (200 birds) in the eastern Bering Sea and in the central and eastern Gulf of Alaska, including Prince William Sound (1200 birds).

There is little evidence that numbers of Parakeet Auklets were greatly affected by foxes, because none of the early accounts of seabirds in Alaska mentions large numbers of them at locations where now they are few.

2.7. Crested Auklet

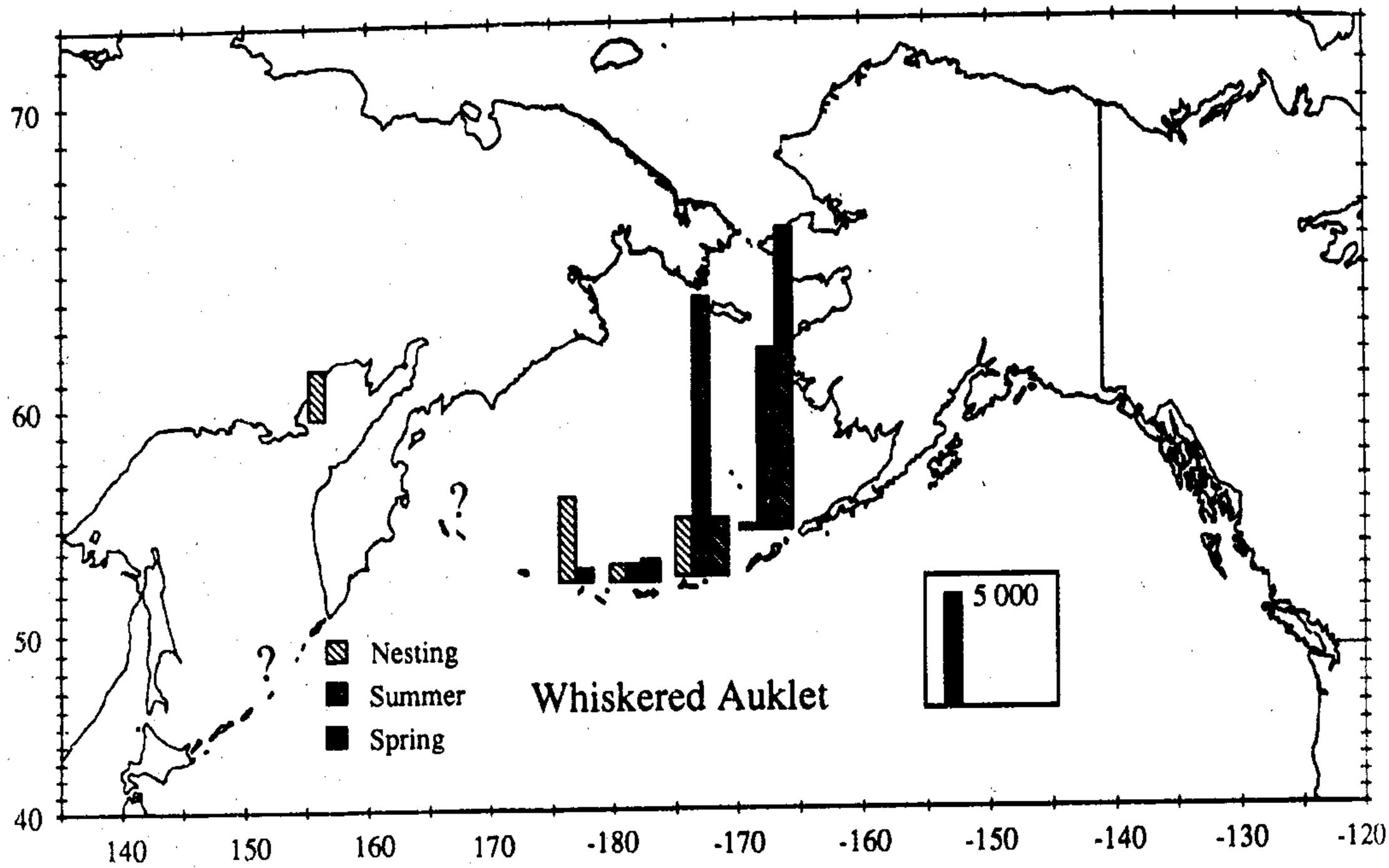
The distribution of Crested Auklets is even more western than that of Parakeet Auklets, as there is only one nesting area east of the Bering Sea (Fig. 6). In the west, Crested Auklets nest as far south as Sakhalin Island, where colonies are known from Cape Terpenie (800–1000 pairs) and the Shmidt Peninsula (Nechaev 1986). Numbers once were, and may still be, "immense" in Crater Bay at south Ushishir Island (Stejneger 1899). They were concentrated on the water southeast and southwest of Paramushir Island (northern Kurils) in August–September 1990 (Ogi, unpubl. data), which suggests that they might nest somewhere in that region. There are 8–10 known colonies in the Sea of Okhotsk, with about 1 million birds on Talan Island and 600 000 on Matykil Island (Jamskie Islands) (Kondratyev and A. Kitesky, unpubl. data).

The greatest numbers in the Bering Sea are found in the western and central Aleutian Islands and the Bering Strait region. The catalogue totals, however, probably underestimate numbers at Kiska Island and Little Diomede Island (pers. obs.) and at St. Lawrence Island considering recent increases there (see below). No estimates of numbers of seabirds on Big Diomede Island are available, but residents of Little Diomede claim that there are many more auklets on the large island than on the small island.

Crested Auklets nest in the Gulf of Alaska only in the Shumigan Islands. The present total number is about 25 000, with about 10 000 nesting at Yukon Harbor on Big Koniuji Island (E. Bailey, unpubl. data). However, this is only a small fraction of the number there before foxes were introduced. Townsend (1914) believed that the "myriad" Crested Auklets at Yukon Harbor were more abundant than Least Auklets on the Pribilofs. Their former number is estimated to have been as high as 300 000, but by the mid-1970s only about 30 000 remained. Numbers continued to fall to a low of about 6000, and now might have recovered to around 10 000 (E. Bailey, unpubl. data). Foxes were introduced to Big Koniuji Island in 1916 (red foxes) and 1925 (arctic foxes) and were removed in 1985–86 (Bailey 1990).

In the Aleutian Islands, an "enormous" colony on Kagamil Island (Islands of Four Mountains) (Gabrielson 1940) apparently was eliminated by foxes, and possibly other colonies in the Aleutians also were affected (Bailey 1990). However, Crested Auklets (and Parakeet, Whiskered, and Least auklets) nest under talus and boulders and in crevices on cliffs and in general appear to be less susceptible to foxes than the burrow-nesting Ancient Murrelets and Cassin's Auklets. Crested Auklet colonies are large on Talus Island (Andreanof Islands) (ca. 200 000) and Segula Island (Rat Islands) (ca. 50 000), and

Figure 7
Centres of abundance of Whiskered Auklets



foxes were introduced there in 1925 and 1927, respectively (Bailey 1990). Likewise, Crested Auklets have persisted in large numbers on all of the offshore islands in the Bering Sea (e.g., Pribilof Islands, St. Matthew Island, and St. Lawrence Island) where foxes are native.

2.8. Whiskered Auklet

Whiskered Auklets have the most restricted distribution of all the auklets (Fig. 7), but have not been censused well at most colonies. Apparently they nest only in the Sea of Okhotsk and on the Kuril and Aleutian islands. Golovkin (1984) indicated that in the order of 1000 pairs of Whiskered Auklets nest on the Jamskie Islands. Clark (1910) said they were common in the Kurils, and Austin and Kuroda (1972) found them breeding on Urup, Shimushir, and Raikoke islands in the Kurils. In the Commander Islands, Stejneger (1885) said they were "rather common" breeders on Copper Island, but rare on Bering Island.

The largest known number in the Bering Sea is on Buldir Island, where about 1000–1500 pairs nest (Byrd and Day 1986). However, there are numerous colonies throughout the Andreanof Islands, Islands of Four Mountains, and Fox Islands (NOAA/FWS 1991), and if the birds were censused more thoroughly the totals probably would be considerably higher.

Whiskered Auklets are common in the eastern Aleutians year-round. High numbers were found during spring and summer cruises by Byrd and Gibson (1980) and during fall, winter, and spring cruises by Troy (1989) (Fig. 7), indicating that the centre of abundance of Whiskered Auklets is in the eastern Aleutians.

2.9. Least Auklet

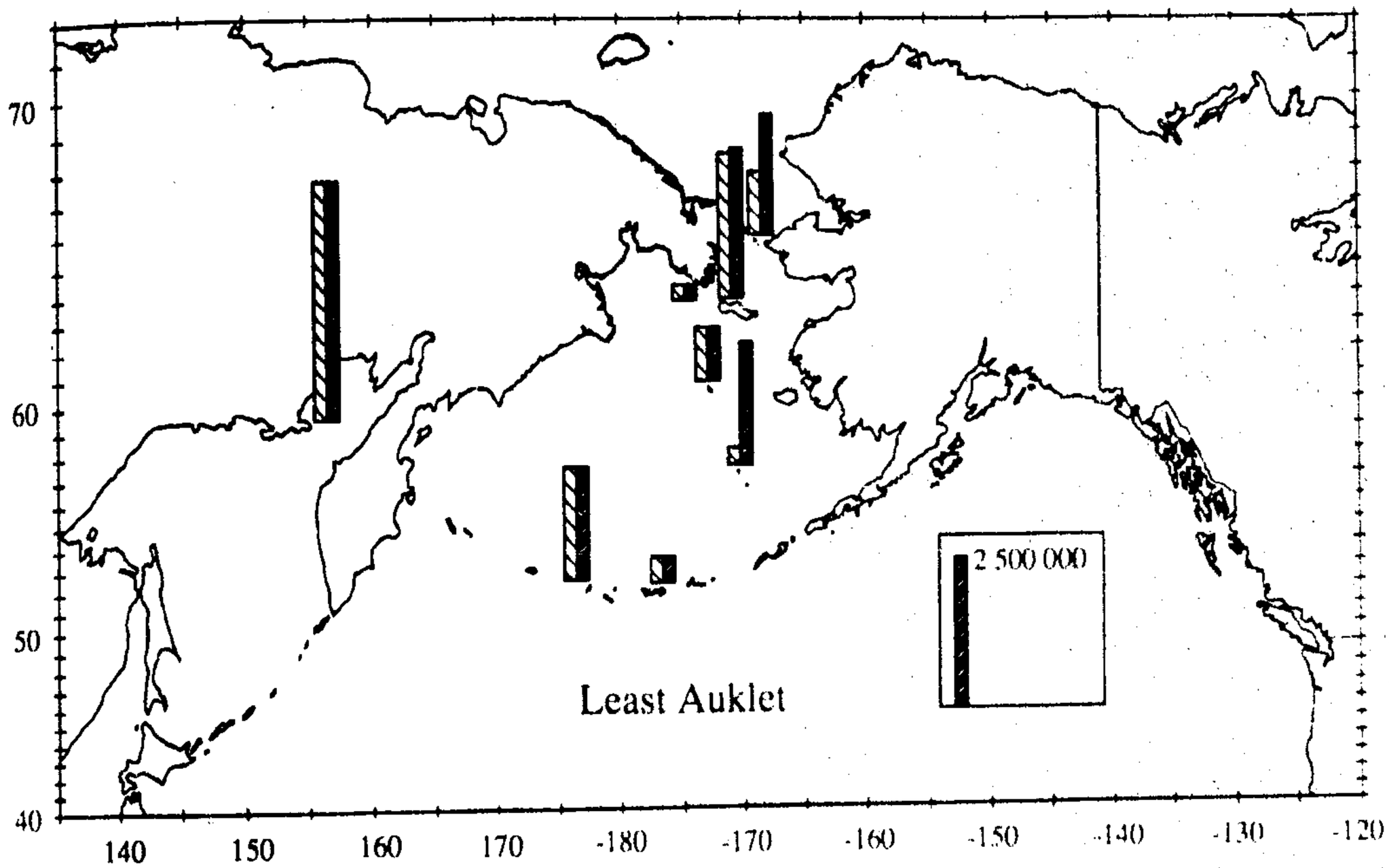
Least Auklets are undoubtedly the most abundant of the auklets, and are possibly the most abundant breeding species of seabird in the Bering Sea (NOAA/FWS 1991) and in the Sea of Okhotsk (Kondratyev and A. Kitesky, unpubl. data). The bulk of the breeding population is concentrated in a few enormous colonies. There are six known colonies in the Sea of Okhotsk with a total population in the order of 5.5 million birds, 4 million of which nest on Matykil Island (Fig. 8). The total number in the Bering Sea is estimated to be in the order of 6 million, with colonies on the two Diomede Islands, St. Lawrence Island, St. Matthew–Hall islands, and Kiska Island having 1–2 million birds each (NOAA/FWS 1991; pers. obs.). The easternmost known colony is on Chowiet Island (Semidi Islands), where about 20 birds possibly nest (Hatch and Hatch 1983).

Least Auklets apparently have been affected little by introduced predators. One notable exception is on Verkhoturov Island, where Least Auklets were eliminated by ermine *Mustela erminea* following their arrival on the island (Gerasimov 1986). Another possible exception is on Bobrof Island (Andreanof Islands)—Murie (1959) was told by Aleuts that Least Auklets formerly were abundant there but that they had been nearly eliminated by foxes. Apparently Least Auklets do not nest there now (Day et al. 1978).

3. Population trends not related to introduced mammals

Because the abundances of these species have been so poorly recorded at most colonies, it is not surprising that little is known about numerical changes other than the great extirpations caused by foxes and other predators during this and past

Figure 8
Centres of abundance of Least Auklets. Dark bars are possible real/pristine numbers, light bars are present estimates.



centuries. However, a few other documented or suspected changes in abundance have been seen at some locations, and they indicate additional, more natural, factors that are important in the population dynamics of certain species.

One of the most spectacular cases of a major change in numbers unrelated to predation is that of Cassin's Auklets on the Farallon Islands. Cassin's Auklets are today one of the most abundant breeding species of seabirds there, but in the 1850s and 1860s they were absent except in winter, when they were rare (Ainley and Lewis 1974). Between the 1870s and the first decade of the 1900s their numbers rose rapidly to approximately the present level. The dramatic increase coincided with the end of a prolonged intrusion of warm tropical water from the south that began at least as early as 1853. A return to typical cold subarctic water and upwelling conditions began in the 1870s, which coincided with the initial recovery of the Cassin's Auklet population. The effect of anomalous warm oceanographic conditions on the fauna of the coast of northern California is well described, and it is likely that decreases in prey availability or changes in prey type brought on by the warm water event led to the loss of Cassin's Auklets on the Farallons during the mid-1800s (Ainley and Lewis 1974).

Loss of nesting habitat during this century apparently has reduced the abundance of Least Auklets on St. George Island in the Pribilofs by as much as an order of magnitude (Roby and Brink 1986a). Early impressions of the number of Least Auklets on St. George Island were consistently in the order of "millions." However, the area of the Ulakaia Hill colony, where the majority of the birds nest, has been steadily shrinking. It formerly covered over 700 ha but currently is less than 15 ha because it is being overgrown by mosses and vascular plants. Roby and Brink (1986a) concluded that primary plant succession and resultant soil formation is an important limiting factor of Least Auklet populations in the southern Bering Sea and Aleutian Islands. It appears to be less of a problem farther north at St. Lawrence Island and the Diomede Islands and in the Sea of Okhotsk, where the harsher arctic environment retards rates of succession.

Auklets have been systematically censused at few colonies in Alaska, and at only two locations is there any precise information on quantitative changes in numbers. Bedard (1969a) counted Parakeet, Crested, and Least auklets on census plots on St. Lawrence Island in 1964. This was repeated in 1976 by Searing (1977) and in 1987 by Piatt et al. (1990) using similar methods and plots. During that time, Least Auklets apparently increased by about 250% at the Kongkok Bay colony and by 150% at the Owahl Mountain colony, and Crested Auklets increased by 140% and 170%, respectively. A less compelling, but similar, trend of increasing numbers of Crested and Least auklets was reported by Craighead and Oppenheim (1985) on St. George Island between 1976 and 1982, during which time numbers of both species approximately doubled in size. A third census in 1984 (Johnson 1985) failed to indicate additional increases, but the time interval since the previous count was short and the method was not entirely comparable to the earlier two.

Two hypotheses have been advanced to account for increasing auklet populations on St. Lawrence Island. One is

that modern, efficient methods of hunting and trapping reduced the abundance of foxes on the island and a decline in the importance of auklets in the subsistence economies of the residents combined to lower the overall predation pressure sufficiently that the auklet populations grew (Piatt et al. 1990). However, the practice of living in the colonies in summer to collect large numbers of auklets ended early in the 1900s and by mid-century the reliance on birds was low, and the seasonal pattern of fox harvests on St. Lawrence Island does not support the notion of an overall reduction in fox numbers (Fay and Cade 1959; F. Fay, pers. commun.). Alternatively, an increase in prey biomass caused by declines in the abundance of trophic competitors, such as walleye pollock *Theragra chalcogramma*, other fishes, or whales, might have led to higher natality or lower mortality and subsequent growth in numbers (Springer 1991, 1992). Such an effect could explain the possible recent increase on the Pribilof Islands also.

The abundance of seabirds in small colonies can increase or decrease dramatically as a result of changes in the number of natural predators. The population of Cassin's Auklets on Tatoosh Island, Washington (about 300 in the late 1970s), apparently has been declining steadily during the past 10 years as the number of Peregrine Falcons has been increasing (Paine et al. 1990). The effect of peregrine predation has not been confined to Cassin's Auklets, but has been felt directly or indirectly by nearly all of the other species of seabirds nesting on Tatoosh Island. Peregrines also feed on Rhinoceros Auklets *Cerorhinca monocerata*, which appear to be declining also. In contrast, the abundance of Pelagic Cormorants *Phalacrocorax pelagicus* and Common Murres *Uria aalge* has been increasing rapidly, a likely result of reduced numbers of Northwestern Crows *Corax caurinus*, an important predator of murre and cormorant eggs and also an important prey item of peregrines.

Likewise, the long-term abundance of Xantus' Murrelets is probably regulated in large measure by Peregrine Falcons, island foxes *Urocyon littoralis*, and deer mice *Peromyscus maniculatus* that are native to the Channel Islands. The primary cause of mortality of murrelet eggs on Santa Barbara Island (at least 57%) was predation by deer mice (Hunt et al. 1981a). Peregrine Falcons and Barn Owls *Tyto alba* are the main natural predators of adult Craveri's Murrelets and are probably important regulators of the size of the population (DeWeese and Anderson 1976).

4. Breeding biology

All of the *Synthliboramphus* murrelets are nocturnal, lay two eggs in normal to good years (one or none in poor years), and raise precocial young that leave the nest site at about two days of age (DeWeese and Anderson 1976; Sealy 1976; Higuchi 1979; Murray et al. 1983). Xantus' and Craveri's murrelets nest primarily in crevices, in caves, under rocks or debris, and in shallow holes (DeWeese and Anderson 1976; Murray et al. 1983). Japanese Murrelets nest in crevices and under debris also, as well as in hollows around the roots of grass or in the sand, in old nests of other species, and in holes they have dug into the ground (Higuchi 1979). Ancient Murrelets nest primarily in holes they dig into soil, but occasionally also in rock crevices, between boulders, and in burrows excavated by other species (Sealy 1976; Shibaev, unpubl. data). Chicks of all four species are fed at sea by the parents, one food item at a time.

Cassin's Auklet bridges the gap between the murrelets and the other auklets. Like the murrelets, it is nocturnal, it usually excavates burrows in soil for nesting, and its distribution is distinctly southern and eastern. But, like the auklets, it lays just one egg, raises its chick to adult size in the nest, and has a gular pouch to transport relatively large amounts of food to the chicks (Howell 1917; Manuwal 1974; Speich and Manuwal 1974).

Parakeet Auklets nest mainly under boulders and in crevices in cliffs, whereas the *Aethia* species nest primarily under rocks in talus fields (Bédard 1969a; Sealy and Bédard 1973; Knudtson and Byrd 1982; Roby and Brink 1986b). They all lay only one egg, raise their chicks in the nests, and have gular pouches.

Many of these characteristics might have arisen in response to predation. Natural mammalian predators undoubtedly restricted the nesting locations to islands and inaccessible capes on the mainland, and because of their small sizes, avian predators forced all of them underground and forced some of them into the dark. Gulls *Larus* spp., peregrines, owls (e.g., *Tyto alba* and *Bubo bubo*), and corvids *Corvus* spp. are the principal avian predators in the overall range.

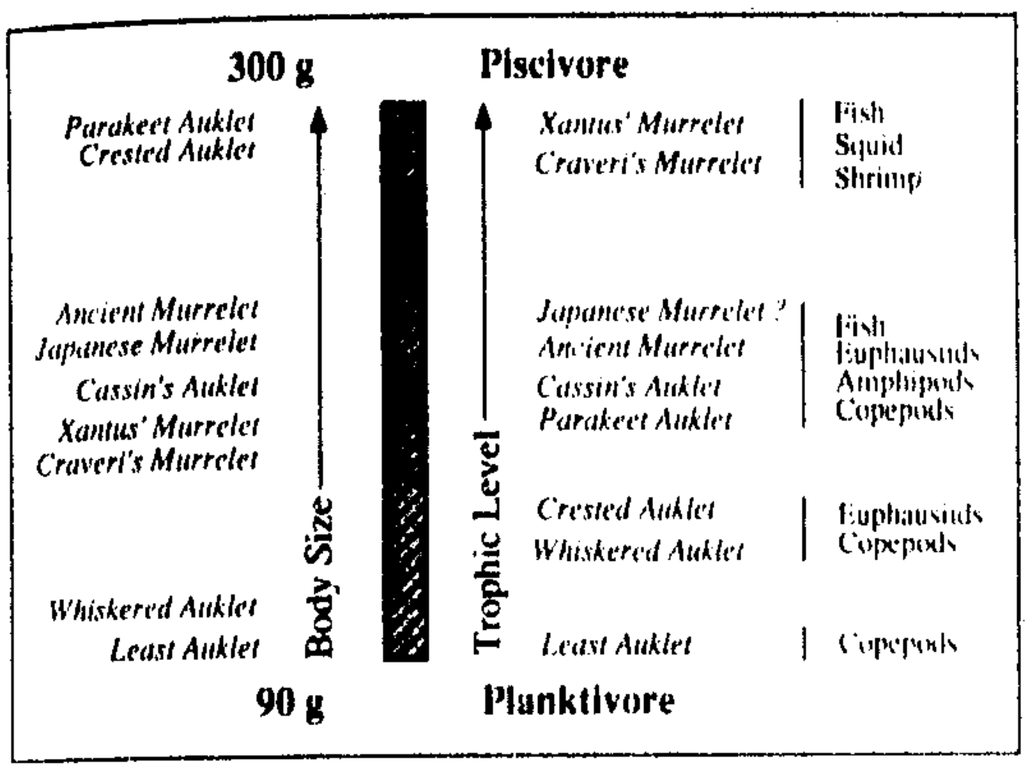
The distribution of nesting habitats and the distribution of summer darkness might now be important in maintaining the geographic separation of the two groups of species. That is, talus is most common on islands in the Bering Sea and Sea of Okhotsk, where soil formation generally is slow due to the harsh environment, whereas soft, deep soils are more common in and south of the Aleutian Islands; and daylight does not entirely fail at night throughout much of summer north of the Aleutian Islands and Gulf of Alaska. The greatest overlap occurs in the Aleutian Islands and Sea of Okhotsk, where talus fields and soft soils allow both groups to nest. Darkness falls in summer in the Aleutians, and two other small, nocturnal species also nest there—Leach's and Fork-tailed storm-petrels (*Oceanodroma leucorhoa* and *O. furcata*). In contrast, soils and talus both are found on the Pribilof Islands, but night is not dark in summer and storm-petrels do not nest there. However, Ancient Murrelets nest in the northern Sea of Okhotsk at a latitude higher than that of the Pribilofs, which casts some doubt on the darkness hypothesis.

5. Diets

The murrelets and auklets have diets in summer that range from essentially all zooplankton to all fish (Fig. 9). There is no definitive relationship between body size and diet, except that the two smallest species, Whiskered and Least auklets, are almost exclusively planktivorous. Much less is known about diets during the nonbreeding season.

Very few Xantus' and Craveri's murrelets have been collected for diet studies, but judging from those samples, both species are predominantly piscivorous. Xantus' Murrelets apparently feed primarily on larval northern anchovies *Engraulis mordax*, but also on Pacific saury *Cololabis saira* and rockfishes *Sebastes* spp. in substantially lesser amounts (Hunt et al. 1981a). At Santa Barbara Island, they typically feed over oceanic water rather than in coastal water (Hunt et al. 1981a). Craveri's Murrelets apparently eat mainly larval rockfishes *Sebastes* spp., larval herrings (Clupeidae), and small adult lanternfish *Benthosema panamense*, as well as some squid and shrimp (DeWeese and Anderson 1976). These diets indicate that Craveri's Murrelets also forage over deep oceanic water.

Figure 9
Trophic relationships of the *Synthliboramphus* murrelets and auklets



Diets of Ancient Murrelets in summer have been described in detail for British Columbia, where the birds feed on variable, but more or less equal, proportions of euphausiids (mostly *Thysanoessa spinifera* with lesser numbers of *T. pacifica*) and fish (sand lance *Ammodytes hexapterus*, shiner perch *Cymatogaster aggregata*, and rockfishes *Sebastes* spp.) (Sealy 1975; Vermeer et al. 1985). They forage most commonly over the shelf break, but occasionally over the shelf (Vermeer et al. 1984). Diets are similar in the Gulf of Alaska, with *T. inermis* replacing the two other species of euphausiids (Sanger 1987). Adult Ancient Murrelets in the Sea of Okhotsk feed on fishes, including sand lance, rainbow smelt *Osmerus mordax*, sculpins *Triglops* spp., and the crangonid shrimps *Sabinea* spp. and *Sclerocrangon* spp. (Kondratyev and A. Kitesky, unpubl. data). Chicks in the Sea of Japan (Peter the Great Bay) are fed Pacific herring *Clupea harengus*, Pacific saury, *Hypoptychus dybowskii*, and small cancroids (Litvinenko and Shibaev 1987).

Like the murrelets, Cassin's Auklets generally forage over deeper water (Howell 1917) at the shelf break (Vermeer et al. 1985) or off the shelf (Briggs et al. 1987). On the Farallon Islands, Cassin's Auklets eat mostly the euphausiid *Thysanoessa spinifera* and the amphipod *Phromena* spp., as well as a few squids and fishes (Manuwal 1974). On Triangle Island and Frederick Island, Cassin's Auklets have a diverse diet, feeding on varying proportions of *Neocalanus cristatus*, the largest of the local calanoid copepods, euphausiids (*T. spinifera* and *T. longipes*), caridea larvae, and fish (sand lance and a sculpin, *Hemilepidotus* spp.) (Vermeer 1984; Vermeer et al. 1985). The somewhat smaller, but much more abundant, copepods *N. plumchrus* and *Eucalanus bungii* apparently are not eaten. A small sample of birds from the Gulf of Alaska contained mostly unidentified calanoid copepods, but also shrimps and unidentified fishes, squids, euphausiids, and gammarid amphipods (Sanger 1987).

Parakeet Auklets have by far the most varied diet of all the species in this group. Among their important prey are hyperiid amphipods (*Parathemisto libellula* and *P. pacifica*), polychaetes *Nereis* spp., euphausiids *Thysanoessa* spp., copepods *Neocalanus cristatus*, decapod larvae, gelatinous zooplankton (Ctenophora and Scyphomedusae), and juvenile fishes including sand lance and walleye pollock (Bédard 1969b; Hunt et al. 1981b; Day and Byrd 1989; Harrison 1990; Kondratyev and A. Kitesky, unpubl. data). Parakeet Auklets also consume large numbers of plastic particles, which accumulate in their stomachs (Day 1980; J.F. Piatt et al., unpubl. data). Most particles are spherical and about 2–5 mm in diameter, suggesting that the birds perhaps mistake them for fish eggs. The utilization of large amounts of fish eggs and juveniles for food could explain why Parakeet Auklets are so abundant on the Pribilof Islands, which lie near the centre of the spawning distribution of the huge stock of pollock in the southeastern Bering Sea (Wespestad 1989). Their utilization of a broad food base might allow them to occupy shallow inner shelf and coastal regions where primary productivity and zooplankton biomass typically are low.

Crested Auklets feed on a similarly diverse suite of invertebrate species, but rarely take fish. Adult diets in summer consist of euphausiids, hyperiid, and gammarid amphipods, and mysids (Bédard 1969b; Day and Byrd 1989). Chicks are fed primarily euphausiids, as well as some hyperiid amphipods and large copepods (Hunt et al. 1981b; Piatt et al. 1988; Kondratyev and A. Kitesky, unpubl. data; A.M. Springer et al., unpubl. data). During the nonbreeding season in the eastern Aleutians and western Gulf of Alaska, Crested Auklets feed almost exclusively on euphausiids (Sanger 1987; Troy 1989).

Whiskered Auklets nesting on Buldir Island feed chiefly on *Neocalanus plumchrus* (Day and Byrd 1989; J.F. Piatt et al., unpubl. data). However, they also consume other invertebrates during summer as indicated by specimens collected from various locations in the Aleutians by Cottam and Knappen (1939). In a sample of six birds, one was empty; three contained only "*Xanthocalanus*" (probably *N. plumchrus*); one contained unidentified copepods, amphipods, isopods, and a fish; and one contained 10% crustaceans and 90% possible mollusk eggs. In fall, winter, and spring, Whiskered Auklets in the Fox Islands region feed mainly on euphausiids (mainly *T. inermis*), which constituted 93–99% of the diets (Troy 1989).

Least Auklets, the smallest of the group, eat the copepods *Neocalanus plumchrus*, *N. cristatus*, and *Calanus marshallae* during the breeding season (Bedard 1969b; Hunt et al. 1981b; Roby and Brink 1986b; Piatt et al. 1988; Day and Byrd 1989) in proportions occurring in the environment (Springer and Roseneau 1985; Hunt and Harrison 1990). They supplement this diet with other small crustaceans such as euphausiids, crab and shrimp larvae, and hyperiid amphipods (primarily *Parathemisto* spp.). In contrast, in winter Least Auklets off the coast of Hokkaido (Japan) apparently feed primarily on "*Euphausia*" (Austin and Kuroda 1972).

Like the murrelets and Cassin's Auklet, all of the *Aethia* auklets nest in proximity to deep water where they feed on typically large, oceanic prey species, or in shallower areas if they have access to sufficient prey. Thus, Crested and Least auklets can nest on most islands on the shallow inner shelf of the northern Bering Sea because a strong current carries a huge biomass of oceanic zooplankton there that originate over the outer continental shelf, slope, and basin of the Bering Sea (Springer and Roseneau 1985; Springer et al. 1989). Least Auklets can nest on St. Matthew Island, which is isolated in the middle shelf, because they can feed on *Calanus marshallae*, the large copepod of the middle and inner shelf that replaces the oceanic species eaten elsewhere (Cooney 1981; Springer and Roseneau 1985). Unlike the Parakeet Auklet, none of the *Aethia* auklets nests on islands in the coastal zone, probably because of a lack of suitable prey.

6. Conservation concerns

Introduced mammals have undoubtedly had the greatest recent effect on population sizes of these species, particularly the burrow- and crevice-nesters—e.g., the devastation of Ancient Murrelet and Cassin's Auklet populations by foxes released on islands in the Aleutian chain and Gulf of Alaska and of Xantus' Murrelets and Cassin's Auklets by cats on islands in southern California and Baja California. Foxes and cats remain on many islands and until they are exterminated will continue to keep numbers of burrow-nesting seabirds at low levels. Furthermore, as described by Bailey (1990) and Bailey and Kaiser (this volume), microtine rodents and ground squirrels also were introduced to many islands in Alaska to supplement the food of foxes and they have had an additional adverse impact on seabirds. Eradication of voles and squirrels probably will be impossible, and, if foxes are removed, rodent numbers might rise to such levels that their effect could quantitatively replace that of foxes.

Next to foxes and cats, rats (*Rattus rattus* and *R. norvegicus*) are probably the most serious threat to murrelets and auklets, and the spread of rats to additional islands is of great concern. Langara Island has lost not only a large proportion of its Ancient Murrelets to rats, but all of its Cassin's Auklets and other burrow-nesting species—Fork-tailed and Leach's storm-petrels, Rhinoceros Auklets, and Tufted Puffins *Fratercula cirrhata*. The number and distribution of Ancient Murrelets on Moneron Island (western Sea of Japan) are undoubtedly regulated by rats (Shibaev, unpubl. data).

Japanese Murrelets also are endangered by rats. In 1987, rats apparently killed about 270 adults on Koyashima Islet and no breeding pairs were found (Takeishi 1987). This might have been most of the colony, because there were only about 140 pairs counted in 1974 and 204 pairs in 1976, and it was perhaps 10% of the entire population of the species.

Ancient Murrelets, and other ground-nesting birds, in the Queen Charlotte Islands may not long escape the ravages of introduced predators, as raccoons are now widespread (A.J. Gaston, unpubl. data). The disappearance of Ancient Murrelets from four islands in recent years can be linked to raccoons, and if raccoons spread they will likely have a disastrous effect on bird populations.

Auklets and murrelets in large colonies have been able to withstand significant directed mortality from indigenous people in the North Pacific, and have been important in subsistence economies of villagers at several places. In addition to the former use of Ancient Murrelets by people on Langara Island and Sanak Island, Crested and Least auklets were consumed in large numbers by residents of numerous islands in the Bering Sea. On St. Lawrence Island, for example, summer dwellings were maintained in the colonies where people would live while they collected auklets for consumption then and during the winter (Fay and Cade 1959).

Such resistance is not the case for Japanese Murrelets, and the direct impact of people is now a serious problem for the small, remnant population of this endangered species. The birds formerly were protected because of the isolation of the islands where they nest, but in recent years people have begun to visit those islands to fish. The fishermen have trampled eggs and chicks on Koya Island, and recent destructions on Mikomoto Island also probably resulted from fishermen (Higuchi 1979).

The ingestion of plastic particles by Parakeet Auklets is a potential concern for this species, but little is known about the long-term effect on the health of individuals of plastics in the gut (Day 1980). The abundance of small plastic particles in the North Pacific increased significantly between 1976 and 1985 (Day and Shaw 1987).

7. Conclusions

Synthliboramphus murrelets are distributed around the rim of the North Pacific Ocean from the the East China Sea to the Sea of Cortez. The three subtropical species, Xantus', Craveri's, and Japanese, have restricted ranges and small numbers, whereas the range of Ancient Murrelets is broad and the population is large. The centre of abundance of Ancient Murrelets is in the temperate northeast Pacific. Cassin's Auklets also have a wide distribution from the western Aleutian Islands to the Sea of Cortez. Their centre of abundance is similar to that of Ancient Murrelets.

The general pattern of eastern and southern distribution of the murrelets and Cassin's Auklet contrasts with the distinctly western and northern (subarctic–arctic) distribution of Parakeet Auklets and the *Aethia* auklets. All four of these species nest predominantly in the Sea of Okhotsk and Bering Sea, and overlap with murrelets and Cassin's Auklets to only a limited extent.

All of the murrelets and auklets nest only on islands and inaccessible mainland capes, probably to escape terrestrial mammals. Also, they all nest underground to escape avian predators. These strategies proved successful until terrestrial mammals were introduced to many of the islands. Ancient Murrelets and Cassin's Auklets are particularly susceptible because they nest in burrows excavated in soft soils that are easily dug out by foxes. Thus, the present numbers of these two species are densely clustered on a few fox-free and cat-free islands in the northeastern Pacific Ocean. Before the fox-farming era in the Aleutian Islands and Gulf of Alaska, total numbers of Ancient Murrelets and Cassin's Auklets were undoubtedly much greater than today, and the numerical distribution was likely more uniform over much of the range. Parakeet Auklets and *Aethia* auklets have been more resistant to foxes since they nest under boulders and rocks in talus fields, and indeed coexist with foxes in many locations.

Diets of the murrelets range from mostly fish (Xantus' and Craveri's murrelets) to a combination of fish and invertebrates (Ancient and probably Japanese murrelets), particularly euphausiids and copepods. Cassin's Auklets and Parakeet Auklets also eat a combination of fishes and invertebrates, but the *Aethia* auklets are almost completely planktivorous. All species feed on oceanic/outer shelf and middle shelf species, and only the Parakeet Auklet nests in shallow coastal areas without access to such prey.

Little is known about the dynamics of undisturbed populations. The few documented or suspected changes in numbers suggest that loss of nesting habitat through primary plant succession and soil formation, changes in food abundance, and changes in predation can have important effects on the regional abundance of some species.

Introduced mammals are the most serious concern for the future of all species in this group, but particularly the murrelets and Cassin's Auklet. The devastating effects of foxes, rats, cats, and goats have been well documented, and continue to threaten birds in several places. Also, raccoons are now considered to be potentially a major threat to Ancient Murrelets in British Columbia and people a major threat to Japanese Murrelets, which are highly endangered and may be on the brink of extinction. Attempts to eliminate introduced mammals

from infected islands and to prevent their spread to others should be given the highest priority by agencies charged with preserving and restoring the natural biota.

Acknowledgements

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