Status and ecology of offshore fish-feeding alcids (murres and puffins) in the North Pacific

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Abstract

The Common Murre *Uria aalge*, Thick-billed Murre *U. lomvia*, Rhinoceros Auklet *Cerorhinca monocerata*, Tufted Puffin *Fratercula cirrhata*, and Horned Puffin *F. corniculata* comprise a guild of offshore fish-feeding seabirds that numbers approximately 17 million breeders in the North Pacific Ocean. It appears murres have declined in the eastern Bering Sea and in portions of the west coast of the continental United States within the past 15–20 years, but stable or increasing populations have been noted along the arctic coast of North America and Asia, in the western Gulf of Alaska, and in the western Aleutian Islands. Rhinoceros Auklets seem to be increasing recently in several areas, but the quality of monitoring data is poor. There are few data for judging widespread trends in Tufted and Horned puffins.

Reproductive success for all species varies among years from nearly total failure to over 70% of the eggs producing fledglings, but no temporal trends have been detected. In the majority of years roughly 40–60% of the nesting pairs of murres and puffins fledge young. Egg predation and scarcity of food near colonies are the factors most frequently listed as causes of reduced success.

Résumé

La Marmette de Troïl *Uria aalge*, la Marmette de Brünnich *U. lomvia*, le Macareux rhinocéros *Cerorhinca monocerata*, le Macareux huppé *Fratercula cirrhata* et le Macareux cornu *F. corniculata* forment une grande confrérie d'oiseaux marins, qui pêchent au large et qui comptent environ 17 millions de nicheurs dans le Pacifique Nord. Il semble que le nombre de marmettes ait diminué, au cours des 15 à 20 dernières années, dans la partie est de la mer de Béring et dans certaines régions de la côte ouest des États-Unis. Le long du littoral arctique de l'Amérique du Nord et de l'Asie, dans la partie ouest du golfe d'Alaska et dans la partie ouest des îles Aléoutiennes, les populations sont stables ou en expansion. Les populations de Macareux rhinocéros semblent augmenter dans plusieurs régions, mais les données de surveillance ne sont pas de bonne qualité. Pour ce qui est des Macareux huppés et des Macareux cornus, on ne dispose pas d'une information suffisante pour établir des tendances valables.

Pour toutes les espèces, la réussite de la reproduction est variable d'une année à l'autre. On observe tantôt un échec presque complet et tantôt un taux d'éclosion de plus de 70 % des oeufs, sans jamais pouvoir établir de tendances temporelles. En règle générale, de 40 à 60 % des couples nicheurs de marmettes et de macareux produisent des oisillons. Pour expliquer l'échec relatif de la reproduction, les causes les plus souvent mentionnées sont la prédation vis-à-vis des oeufs et la rareté de la nourriture près des colonies.

1. Introduction

The offshore fish-feeding alcids include five species in the North Pacific area: Common Murre *Uria aalge*, Thick-billed Murre *U. lomvia*, Rhinoceros Auklet *Cerorhinca monocerata*, Tufted Puffin *Fratercula cirrhata*, and Horned Puffin *F. corniculata*. The murres (tribe Alcini) and the puffins (tribe Fraterculini), including Rhinoceros Auklet, represent two distinct and widely separated phylogenetic lineages (Strauch 1985). However, these species comprise a single ecological guild that preys primarily on fish by pursuit diving (Ashmole 1971), often at relatively great distances from breeding colonies (Schneider and Hunt 1984). Murres and puffins have delayed maturity, are relatively long-lived with high adult survival rates (Hudson 1985), and nest colonially in large concentrations. In all five species mating systems are monogamous, and females lay a single egg that is incubated alternately by both parents. The male and female coordinate their brooding and provisioning of the chicks so that one parent is always present at the nest site until the chick is ready to depart (Ydenberg 1989).

Alcids are vulnerable to local perturbations because they tend to be concentrated at breeding colonies and foraging areas. These species include open-ledge nesters (murres) and crevice nesters (puffins), species that are active at breeding colonies primarily during darkness (Rhinoceros Auklet) and those that are active throughout the day (murres).

Although offshore fish-feeding alcid populations are large in the North Pacific, they are subject to substantial losses from gill nets (DeGange et al., this volume), oil (Burger and Fry, this volume), predation by exotic predators (Bailey and Kaiser, this volume), and reduction in food sources caused by overharvesting of marine resources (V. Vader, unpubl. data) as well as natural environmental perturbations (Vermeer et al. 1979).

A great deal has been learned about alcids in the North Pacific region in the past 15 years. It is likely that most large breeding colonies have been identified, particularly on the eastern side of the region (e.g., Sowls et al. 1978), and this information has been used to place the majority of important nesting areas under some form of protection. General aspects of the breeding ecology of most species have been described (e.g., Hunt et al. 1981), although much of the detailed information

Table 1
Estimates[a] of numbers of breeding murres and puffins in the temperate North Pacific (expressed in thousands, rounded to nearest thousand)

Region	Species[b]						
	COMU	TBMU	UNMU	TOMU[c]	RHAU	TUPU	HOPU
California	363	0	—	363	<2	<1	0
Oregon	426	0	—	426	1	5	0
Washington	31	0	—	31	61	23	0
British Columbia	6	<1	—	6	446	77	<1
Southeastern Alaska	10	2	—	12	110	97	<1
South-central Alaska	80	<1	—	80	6	98	16
Alaska Peninsula	334	40	1257	1631	2	1008	762
Aleutian Is.	43	109	93	245	<1	1332	92
Alaska Bering Sea	1323	1611	1603	4537	0	99	58
Siberian Bering Sea			1200	1200	0	59	40
Arctic Ocean	110	290	562	962	0	4	48
Sea of Okhotsk	600	300	—	900	3	500	200
Kuril Is.			350	350	10	200	4
Sea of Japan/ Hokkaido	1			1	334	<1	0
Totals	3327	2352	5065	10 744	973	3502	1220

[a] References: California (Sowls et al. 1980; H. Carter, pers. commun.), Oregon (R. Lowe, pers. commun.), Washington (Speich and Wahl 1989), British Columbia (Campbell et al. 1990; Kaiser, pers. commun.), all parts of Alaska (U.S. Fish and Wildlife Service Seabird Colony data base), Siberia (Kondratyev, pers. commun.), and Shibaev (pers. commun.), Kuril Islands and Sea of Japan (Golovkin 1984; Shuntov 1986), Hokkaido (Hasegawa 1984; Fujimaki 1986).
[b] COMU=Common Murre, TBMU=Thick-billed Murre, UNMU=unidentified murre, TOMU=total murres, RHAU=Rhinoceros Auklet, TUPU=Tufted Puffin, HOPU=Horned Puffin.
[c] Sum of the first three columns.

remains unpublished. Monitoring programs have begun which are designed to provide information about long-term trends in populations and reproductive performance. This information will be used to identify problems so that research can be focused on factors causing changes (Byrd 1989).

In this report we have tried to assemble available information on populations and reproductive performances of murres and puffins in the North Pacific and provide a basis for directing future studies to fill obvious gaps.

2. Breeding distribution and population levels

It is estimated that roughly 17 million murres and puffins breed in the North Pacific region (Table 1). The murres are circumpolar with slightly higher populations in the North Atlantic than in the North Pacific (Nettleship and Evans 1985). The Rhinoceros Auklet, Tufted Puffin, and Horned Puffin are confined to the North Pacific (American Ornithologists' Union 1983).

2.1. Murres

About 11 million murres nest in the North Pacific region (Table 1, Fig. 1). Common Murres tend to range farther south than Thick-billed Murres. Common Murres prevail in warmer, more coastal locations whereas Thick-billed Murres are restricted to colder waters (Tuck 1961).

Within the North Pacific region, the largest numbers of breeding murres are found in the Bering Sea (Table 1), and the highest concentrations exceed one million individuals (e.g., the Pribilof Islands, Hickey and Craighead 1977). Colonies extend as far north in the region as 71°N (Wrangel Island, Kondratyev 1986) and as far south as 36°N (northern part of the Big Sur coast of California, Sowls et al. 1980).

2.2. Rhinoceros Auklet

Estimates of breeding birds in the North Pacific region approach one million (Table 1). The greatest concentrations are in a band of latitude between 44°N and 55°N (Fig. 2). The largest single colony is on Teuri Island, Japan, where nearly 350 000 birds occur (Watanuki 1987). The largest North American concentration is on Storm and Pine islands in British Columbia where about 280 000 birds breed (Bertram and Kaiser 1988). The northernmost colony of Rhinoceros Auklets on the eastern side of the Pacific is on Middleton Island, just south of 60°N latitude, and a small group is becoming reestablished in the Farallon Islands, about 47°N (Sowls et al 1980). That is the southernmost colony in North America. In eastern Asia, the species breeds at least as far north as central Sakhalin (49°N) and as far south as the Vladivostok area (43°N) (Shibaev 1987).

2.3. Tufted Puffin

Nearly 3.5 million Tufted Puffins breed in the North Pacific region (Table 1). The Alaska Peninsula and Aleutian Islands contain the highest concentrations (Fig. 3). Several colonies exceed 100 000 birds (e.g., Egg Island, in the eastern Aleutians, Nysewander et al. 1982). Relatively few Tufted Puffins nest in the regions of the Bering Sea and Arctic Ocean (Table 1) or south of Triangle Island, British Columbia (Vermeer 1979a). Nevertheless, small groups and solitary nests have been found as far south as Big Sur, California (Sowls et al. 1980), and the species breeds as far south in Asia as Kojima Island near the south tip of Hokkaido (Fujimaki 1986).

2.4. Horned Puffin

The breeding population of Horned Puffins in the North Pacific is estimated at over 1.2 million (Table 1). This species has a more northerly distribution than its congener (Fig. 4), although the centre of abundance is similar (i.e., the Alaska Peninsula). The largest single colony, Suklik Island, in the Semidis, contains 250 000 birds (Sowls et al. 1978). The species has attempted to breed as far north as Cooper Island in the Beaufort Sea (over 71°N) (G.J. Divoky, pers. commun.). Horned Puffins breed as far south as the central Aleutians (52°N) in Alaska, northwestern Vancouver Island (50°N) in British Columbia, and Cape Terpenie (49°N), Sakhalin Island, in Asia (Nechaev 1986).

3. Population trends

3.1. Murres

Most data sets that may be used to assess trends in numbers of murres at various sites in the North Pacific date back only as far as the mid-1970s (Table 2). One exception is for the Farallon Islands, California, where information dates back to the 1850s. Common Murres there have changed in response to human disturbance. From 1850 to 1950 murre populations declined from roughly 400 000 to 6000 (Ainley and Boekelheide 1990). Following protection and removal of introduced predators, populations increased to over 80 000 by the early 1980s. Since then numbers have again declined probably due to gillnet mortality (Carter et al. 1990; Takekawa et al., in press). The recent declines documented in the Farallons have not been seen in northern California, Oregon, or British Columbia, but apparently Common Murres at most colonies in Washington have declined within the past decade (Table 2).

In Alaska, no trends are evident at Middleton Island or in the Semidi Islands in the Gulf of Alaska region, but in the

Figure 1
Breeding distribution and abundance of Thick-billed and Common murres in the North Pacific. Abundances in North America plotted relative to 1:500 000-scale map areas, with approximately equal resolution on the Asian coast (one dot per 1° latitude × 3° longitude block).

Sources: Campbell et al. (1990), Fujimaki (1986), Gerasimov (1986), Johansen (1961), Kondratyev (1986), R. Lowe (pers. commun.), Nechaev (1986), Shuntov (1986), Sowls et al. (1978, 1980), and Vyatkin (1986).

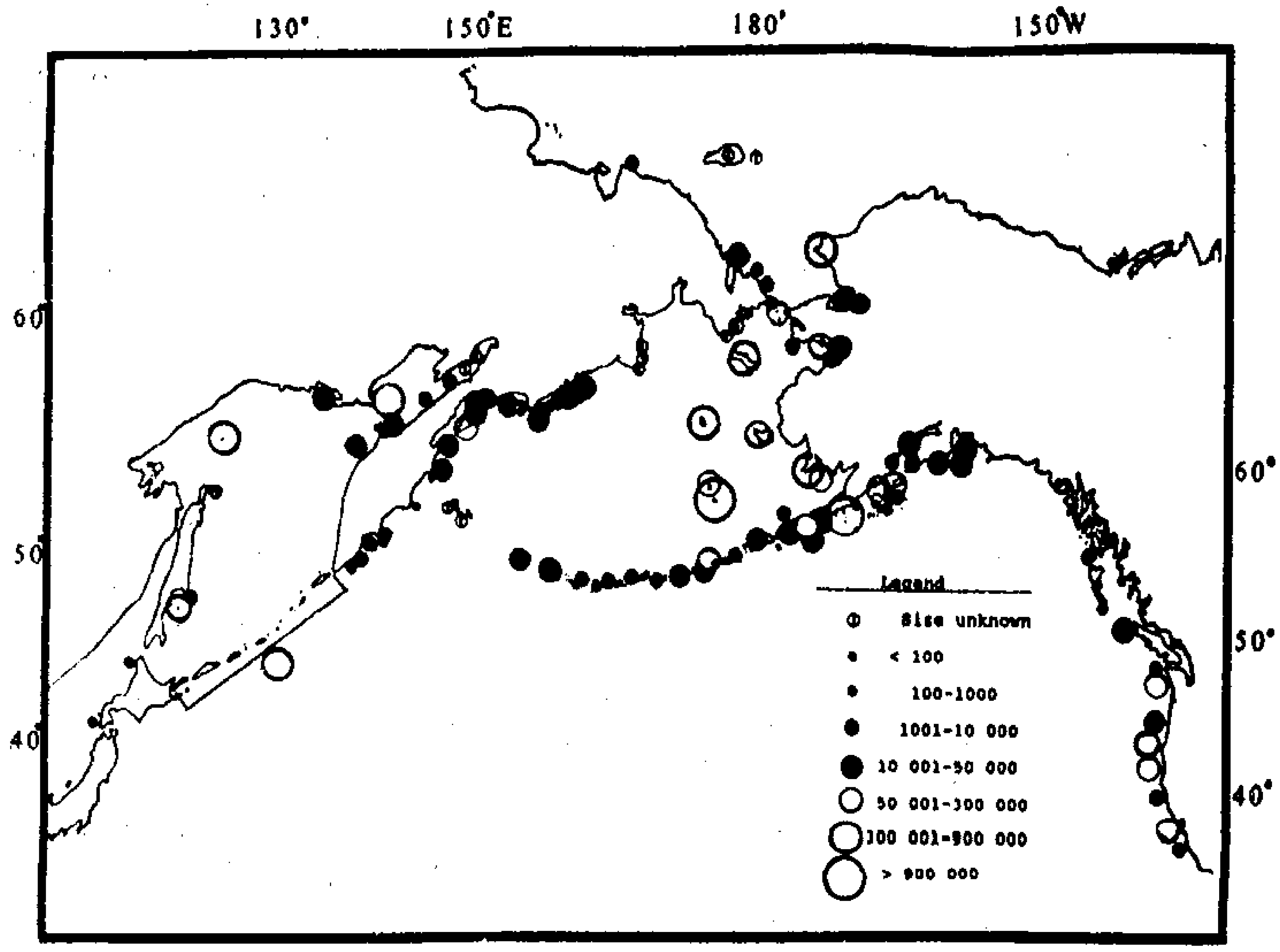

Figure 2
Breeding distribution and abundance of Rhinoceros Auklets in the North Pacific. Abundances in North America plotted relative to 1:500 000-scale map areas, with approximately equal resolution on the Asian coast (one dot per 1° latitude × 3° longitude block).

Sources: Campbell et al. (1990), Fujimaki (1986), R. Lowe (pers. commun.), Shibaev (1987, pers. commun.), Sowls et al. (1978, 1980), and Watanuki (1987).

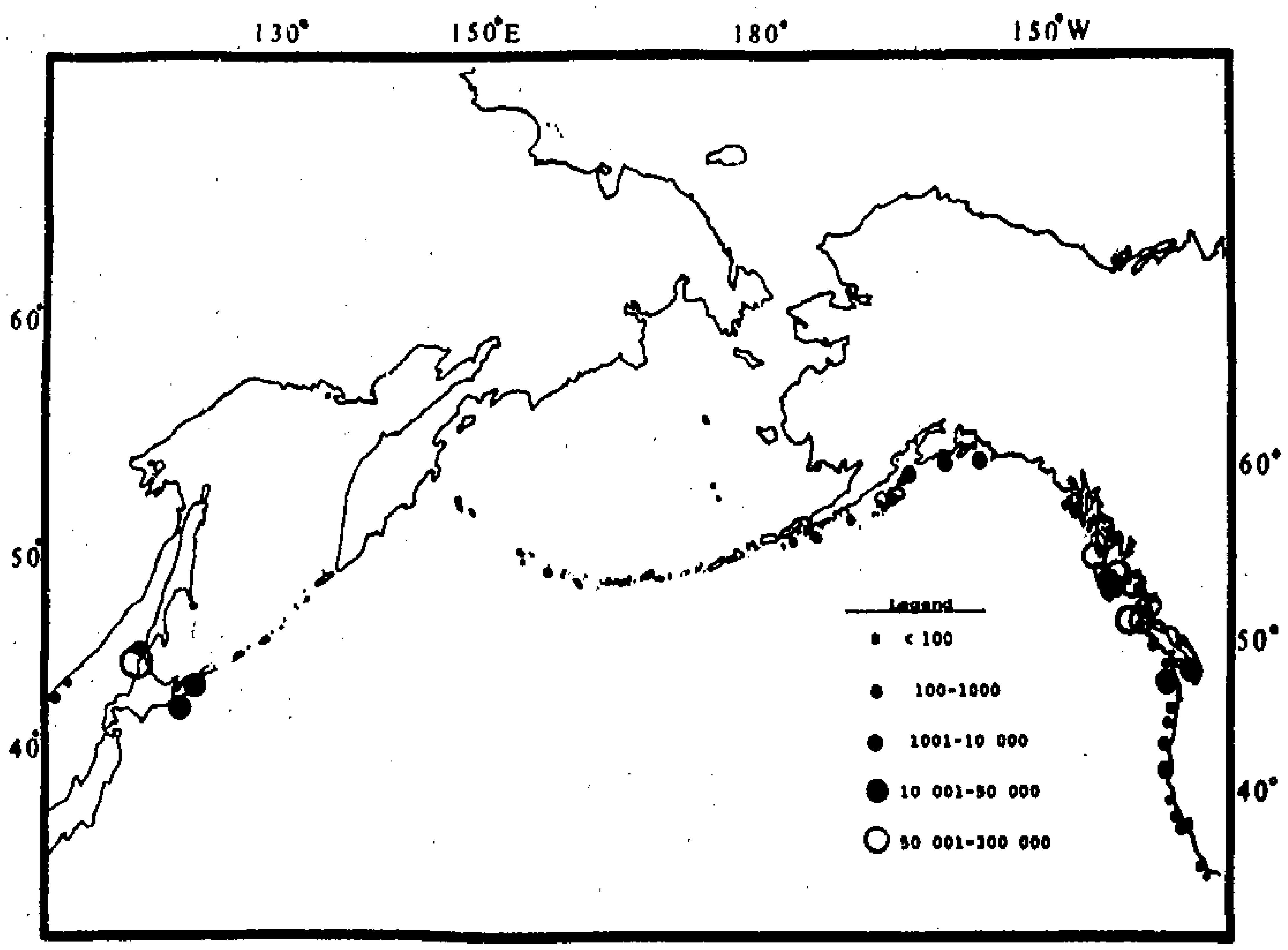

Figure 3
Breeding distribution and abundance of Tufted Puffins in the North Pacific. Abundances in North America plotted relative to 1:500 000-scale map areas, with approximately equal resolution on the Asian coast (one dot per 1° latitude × 3° longitude block).

Sources: Campbell et al. (1990), Fujimaki (1986), Kondratyev (1986), R. Lowe (pers. commun.), Mikhtaryantz (1986), Nechaev (1986), Rosiyakov (1986), Shuntov (1986), Sowls et al. (1978, 1980), Speich and Wahl (1989), and Vyatkin (1986).

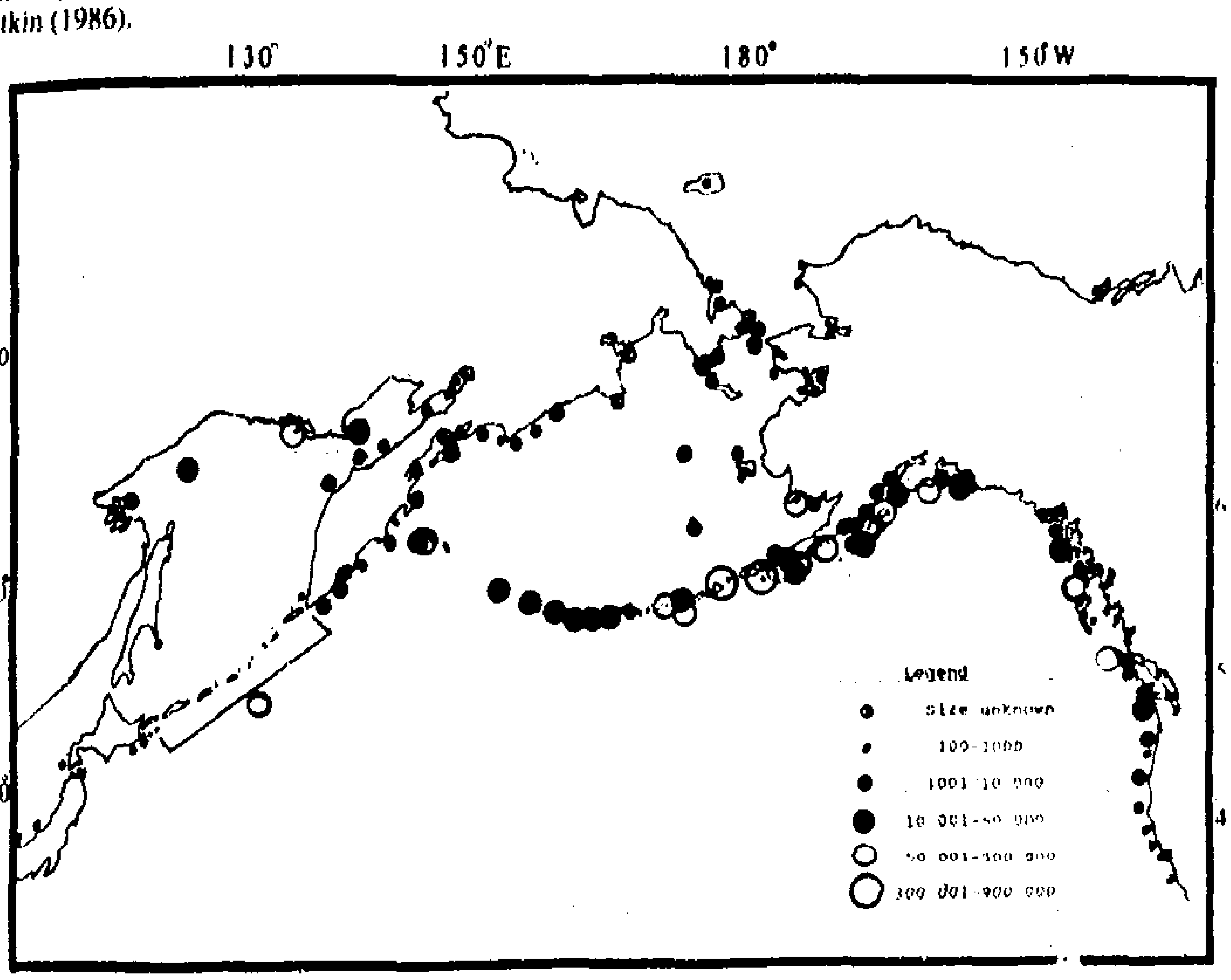

Figure 4
Breeding distribution and abundance of Horned Puffins in the North Pacific. Abundances in North America plotted relative to 1:500 000-scale map areas, with approximately equal resolution on the Asian coast (one dot per 1° latitude × 3° longitude block).

Sources: Campbell et al. (1990), Gerasimov (1986), Johansen (1961), Kondratyev (1986), R. Lowe (pers. commun.), Nechaev (1986), Roslyakov (1986), Shuntov (1986), Sowls et al. (1978, 1980), Speich and Wahl (1989), and Vyatkin (1986).

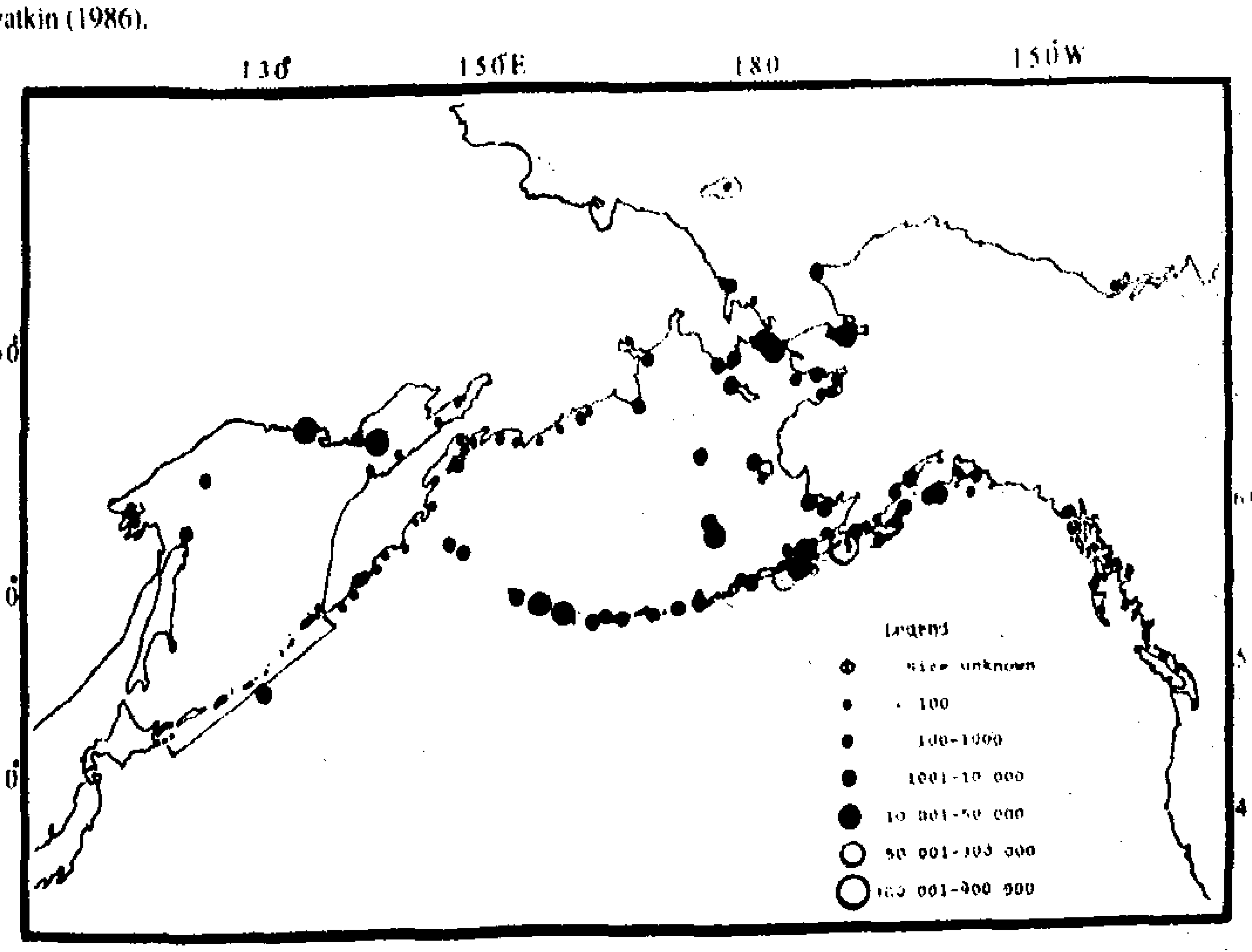

Table 2
Trends in murre populations in various North Pacific locations

Location	Range of years[a]	Trend	Reference
California			
Farallon Is.	1850–1950	Decrease	Ainley and Boekelheide 1990
	1950–1982	Increase	Ainley and Boekelheide 1990
	1982–1991	Decrease	Takekawa et al., in press
N. Calif.	1900–1980	Increase	Sowls et al. 1980
	1980–1989	Increase	Carter et al. 1990
Oregon			
Entire coast		Insufficient data	R. Lowe, pers. commun.
Washington			
Tatoosh I.	1956–1979	Stable	Paine et al. 1990
	1979–1989	Increase	Paine et al. 1990
Other islands[b]	1979–1989	Decrease	Speich and Wahl 1989; U. Wilson, pers. commun.
British Columbia			
Triangle I.	1979–1989	Fluctuations but no trend	Rodway 1990
Other areas		No obvious trends	Campbell et al. 1990
Gulf of Alaska			
Middleton I.	1974–1990	Stable	Dragoo and Bain 1990
Bering Sea			
Cape Peirce	1985–1989	Decrease	Haggblom and Mendenhall 1990
St. George I.	1976–1989	TBMU[c] decline, COMU stable	Dragoo et al. 1990
St. Paul I.	1976–1988	Decrease	Byrd 1989; A. Sowls, pers. commun.
Bluff[d]	1975–1981	Decrease	Murphy et al. 1986
	1982–1989	Stable	Murphy, unpubl. data
Chukchi Sea			
Cape Thompson	1960–1979	Decrease	Fadely et al. 1989
	1980–1988	Stable	Fadely et al. 1989
Cape Lisburne	1976–1987	Increase	
Aleutians			
Buldir I.	1976–1990	Increase	Hipfner et al. 1991
Agattu I.	1979–1990	Increase	Hipfner et al. 1991
Siberia			
Arctic coast	1933–1985	Increase[e]	Kondratyev 1986
Tyulenii I.	1950–1960	Decrease	Shuntov 1986
	1960–1989	Stable	Shuntov 1986

[a] Inexact references like mid-1970s are recorded as 1975, late 1980s as 1989, etc.
[b] Most major colonies on the coast.
[c] TBMU = Thick-billed Murre, COMU = Common Murre.
[d] Near St. Paul in the Pribilofs.
[e] Apparently murres have "widened" their range in "recent time."

Bering Sea numbers of murres have been lower at most colonies in recent years than in the mid-1970s (Table 2). Further, at Cape Thompson in the Chukchi Sea, a large decline apparently occurred between 1960 and 1976, but numbers have remained relatively stable since about 1982. A slight increase has been recorded in the past 15 years at Cape Lisburne in the Chukchi region, and murres have increased in the western Aleutian Islands since the 1970s (Table 2).

On the arctic coast of Russia, the distribution of both species apparently has extended further north and west in recent years. Since 1974, Kondratyev (1986) has recorded murres at colonies along the northeastern Chukotka Peninsula where no birds were found in the 1930s. In addition, Common Murres were absent on Koluchin Island in 1972–1974 but present in 1984–85, and Thick-billed Murres apparently first bred on Shalauro Island in the late 1970s (Kondratyev 1986).

For Tyulenii Island in the Sea of Okhotsk, Shuntov (1986) reported that human disturbance caused a large decline in murres. Roughly 650 000 murres were present at Tyulenii in the late 1940s. Apparently there was a concerted effort to commercially exploit the large murre colony including hunting, egging, and destruction of cliffs. By 1960, when the planned exploitation stopped, only 140 000 murres remained. The population has remained at approximately 150 000 since that time. This example, along with the Farallon experience, demonstrates that murres are vulnerable to direct disturbance such as oil spills and gillnetting, but it is less clear how populations are affected by more indirect human influences like modifications to food webs by commercial fishing, marine pollution, and the cumulative effects of human activities near colonies. Furthermore, natural perturbations in the environment (e.g., El Niño southern oscillations) obviously affect populations of murres at least temporarily, and more subtle shifts in temperature, current, or other oceanographic characteristics may affect food availability and therefore reproductive performance and ultimately populations. It is unclear what has caused recent declines in murres at study colonies in the Bering Sea.

3.2. Puffins

Generally, historic data on populations of puffins at most locations in the temperate North Pacific are insufficient to determine trends. Nevertheless, available data suggest several recent patterns of change.

In California, a decline in Tufted Puffins has occurred since 1900 (Sowls et al. 1980). Apparently the Farallon Island population in particular was much larger historically than it is today (Ainley and Lewis 1974). A similar pattern also occurred on Alaskan islands where Tufted Puffins were extirpated by introduced arctic foxes *Alopex lagopus* by the late 1930s (Bailey and Kaiser, this volume). In contrast, Tufted Puffins have begun to nest again on several islands following removal of foxes (e.g., Agattu Island, Byrd and Douglas 1990).

Horned Puffins may also have declined as a result of predation by introduced mammals on Alaskan islands. However, no standard method exists for estimating numbers of this crevice-nesting species, and counts, especially at larger colonies, may underestimate the actual number of birds associated with colonies.

Rhinoceros Auklets may have increased in California (Sowls et al. 1980; Carter et al. 1990), Oregon (R. Lowe, pers. commun.), and British Columbia (Campbell et al. 1990). Monitoring for this nocturnal species is crude, but baseline data are available in British Columbia (e.g., Rodway et al. 1990). In the Soviet Far East, a drastic reduction (14 000 to 1500 birds) in numbers of Rhinoceros Auklets was reported between 1938 and 1949, and the population has remained at low levels since (Takahasi 1939; Gizenko 1955; Nechaev 1975). Fujimaki (1986) suggests increases in Rhinoceros Auklets at Teuri Island, Japan, between 1951 and the 1970s.

4. Breeding biology

4.1. Breeding habitat

4.1.1. *Murres*

Common and Thick-billed murres nest on flat horizontal ledges. Where the species are sympatric, Common Murres tend to nest on relatively broad ledges and flat-top islets and Thick-billed Murres nest on relatively narrow ledges (Swartz 1966; Squibb and Hunt 1983). In allopatry, both species use a wide range of nest sites (e.g., Uspenski 1958; Williams 1974). Harris and Birkhead (1985) point out that differences in nest

Table 3
Reproductive success of Common Murres

Location[a]	Numbers of: Years	Plots	Nest sites	First eggs: Hatch (%)	Fledge (%)	Replacement eggs[c]: n	%	Hatch (%)	Fledge (%)	Site[b] success (%)
SE Farallon I., CA	12	1	41–173	81±16	89±23	1–11	34±21	61±36	63±42	[illegible]±23
Choweit I., AK	3	6	103–119	69±5	82±6	2–5	15±7	47±50	17±29	5[illegible]±8
Agattu I., AK	2	16–17	451–452	76±8[c]	88±10					[illegible]8±16
St. George I., AK	7	≤5	10–114	75±9	77±20					60±19
St. Paul I., AK	6	8–10	16–310	76±4	80±6					61±6
St. Matthew I., AK	2	13	117–194	55±13	<86±4					<47±13
St. Lawrence I., AK	1	2	71	68[c]	94	7	30	57	50	66
Cape Peirce, AK	5	5?	42–290	34±32	68±45					27±21
Bluff, AK	3	7	382–407	53±7	91±7	64–92	43±7	65±9	83±10	60±13
Cape Thompson, AK	1	?	25	<80	<76					
Talan I., Siberia	2	?	80–210	54±18	67±6					37±15

[a] References: SE Farallon (Ainley and Boekelheide 1990), Choweit (Hatch and Hatch, in press), Agattu I. (Byrd and Douglas 1989), St. George (Dragoo et al. 1990), St. Paul (Byrd 1989; Dragoo et al. 1989), St. Matthew (Murphy et al. 1987), St. Lawrence (Piatt et al. 1988), Cape Peirce (Haggblom and Mendenhall 1990), Bluff (J.H. Schauer and Murphy, unpubl. data), Cape Thompson (Fadely et al. 1989), Talan I. (Kondratyev, unpubl. data).
[b] Overall reproductive success (i.e., % of nest sites where an egg was laid from which a chick fledged)
[c] In cases where no data for replacement eggs were recorded, data listed under "first eggs" include both first and replacement eggs

Table 4
Reproductive success of Thick-billed Murres

Location[a]	Numbers of: Years	Plots	Nest sites	First eggs: Hatch (%)	Fledge (%)	Replacement eggs[c]: n	%	Hatch (%)	Fledge (%)	Site[b] success (%)
Choweit I., AK	3	6	138–146	65±4	77±96	2–10	21±11	39±13	40±4	52±9
Buldir I., AK	2	12	337–545	81±1[c]	89±7					[illegible]±4
St. George I., AK	9	≤15	51–388	72±5	73±23					51±[illegible]
St. Paul I., AK	7	≤27	27–792	66±29	75±11					[illegible]±13
St. Matthew I., AK	2	21	216–342	47±8	<77±4					36±7
St. Lawrence I., AK	1	2	123	57	91	10	19	80	50	[illegible]5
Cape Thompson, AK	1	?	84	<70[d]	<77[d]					<61[b]
Talan I., Siberia	2	?	47–70	58±18	72±0					[illegible]±13

[a] References: Choweit (Hatch and Hatch, in press), Buldir (Byrd and Climo 1988; Byrd and Douglas 1989), St. George (Dragoo et al. 1990), St. Paul (Byrd 1989), St. Matthew (Murphy et al. 1986), St. Lawrence (Piatt et al. 1988), Cape Thompson (Fadely et al. 1989), Talan (Kondratyev, unpubl. data)
[b] Overall reproductive success (i.e., % of nest sites where an egg was laid from which a chick fledged)
[c] In cases where no data for replacement eggs were recorded, data listed under "first eggs" include both first and replacement eggs
[d] Fieldwork ended during chick period.

site preferences probably relate to anatomical differences between the species (Spring 1971).

4.1.2. *Puffins*

The majority of Rhinoceros Auklets and Tufted Puffins breed in earthen burrows, generally on slopes steep enough for birds to quickly take flight and land (Vermeer 1979a; Wehle 1980). Occasionally Tufted Puffins use rock crevices (Drent and Guiguet 1961), and many Rhinoceros Auklets nest on relatively level ground on forested islands (Vermeer 1979a). The opposite pattern is true for Horned Puffins: i.e., they primarily use rock crevices, but at a few colonies use earthen burrows (Sealy 1973; Wehle 1980; Byrd and Day 1986). Once adult puffins have established breeding sites, they apparently exhibit high nest site fidelity (e.g., Wehle 1980).

4.2. Reproductive success

4.2.1. *Murres*

The single study plot on SE Farallon Island provides the longest-term data on reproduction of murres in the North Pacific. Typically both hatching and fledging success of the first egg are high, and about a third of the eggs lost during incubation are replaced at this plot (Table 3). Reproductive success declines through the season, and success of replacement eggs is much lower than that of first eggs. Although sample sizes are small, available data suggest 15–40% of lost first eggs are replaced at other study areas (Table 3). The highest recorded replacement rate has been at Bluff, Alaska, where up to 40% of lost first eggs are replaced, and where, even in years of late breeding, some of the lost replacement eggs are replaced (J.H. Schauer and Murphy, unpubl. data).

Average estimates of hatching success for Common Murres have ranged from 34 to 81% (Table 3), and from 47 to 81% for Thick-billed Murres at different sites in the North Pacific (Table 4). Fledging success (of eggs that hatched) generally has been higher than hatching success, ranging from 67 to 91% for both species of murres (Tables 3 and 4). There have been no obvious differences between species or among locations in rates of success.

Overall average reproductive rates for Common Murres have ranged from 27 to 77%. The two estimates below 45% are Cape Peirce, Alaska, and Talan Island, Russia. In both cases predation by birds (Common Ravens *Corvus corax* and Slaty-backed Gulls *Larus schistisagus*, respectively) was implicated as the cause of reduced productivity (Haggblom and Mendenhall 1990; Kondratyev, unpubl. data, respectively). Thick-billed Murres have similar rates of success as Common Murres (Table 4).

Complete reproductive failures of murres appear to be infrequent throughout the breeding range (Tables 3 and 4). The only known failure at SE Farallon Island followed the 1982–83 El Niño. Reproductive success there was negatively correlated with water temperatures in spring and positively correlated with an upwelling index and abundance of juvenile rockfish (Ainley and Boekelheide 1990). At Bluff, Alaska, reproductive success has been highest following moderately warm springs and lowest following extremely cold springs (e.g., Murphy et al.

Table 5
Reproductive success of Rhinoceros Auklets

Location	Source[a]	Year	Total eggs	Hatching success	Fledging success
Destruction I., WA	1	1974	70	0.76	0.74
	1	1975	79	0.75	0.84
Protection I., WA	1	1975	65	0.82	0.93
	1	1976	62	0.92	0.97
Triangle I., B.C.	2	1975	50	0.80	0.73
	2	1976	47	0.94	0.34
	2	1977	68	0.91	0.65
	2	1978	47	0.83	0.83
Teuri I., Japan	3	1984	40	0.65	0.27
	3	1985	45	0.71	0.56

[a] Codes for sources of information: 1 = Wilson and Manuwal 1986, 2 = Vermeer et al. 1979, 3 = Watanuki 1987.

1986); again food availability is probably the primary factor. At Koluchin Island, Siberia, early build-up of ice can preclude successful "fledging" of chicks (Kondratyev et al. 1987).

In conjunction with an extended foraging range and ability to feed throughout the water column, murres probably have damped variability in reproductive success relative to species with smaller foraging zones (e.g., Black-legged Kittiwakes *Rissa tridactyla*).

4.2.2. Rhinoceros Auklet

Data from four study sites for a total of 10 seasons suggest that overall productivity can vary from less than 20% to nearly 90% of the active nest sites producing a fledgling (Table 5). Apparently there is less variation in hatching success than in chick survival, and food availability is probably responsible for the relatively high chick loss in some years. Fledging success was 65% or greater in seven of the 10 cases for which we had data.

4.2.3. Tufted and Horned puffins

Wehle (1980) reviewed available data and concluded that typically about 50–60% of the Tufted Puffin burrows at a given colony have eggs present in a particular year. Nevertheless, occupancy rates as high as 75% have been found (Lemon et al. 1983).

Recorded productivity for Tufted Puffins (Table 6) has ranged from nearly complete failure to complete success (i.e., all laying pairs producing a fledgling). The average of 25 data sets was approximately 46% (SD = 23%). High rates of reproductive failure have been recorded at both the egg (1976) and chick stage (1977) on Triangle Island (Vermeer 1979b). In the 27 cases for which we found data, hatching success averaged 63% (SD = 22%), and fledging success in 26 cases averaged 71% (SD = 23%) (Table 6).

For Horned Puffins overall productivity ranged from complete failure to 77% in 18 cases, with an average of 57% (SD = 19%) (Table 7). Hatching success averaged 76% (SD = 21%), and fledging success averaged 71% (SD = 23%) (Table 7).

Disturbance by investigators accounted for reduced success in some cases, and Wehle (1980) concluded that natural hatching success for Tufted Puffins might be as high as 75–90%. Horned Puffins may be less subject to desertion because their rock crevice nests can be examined with less disturbance.

5. Research needs

Monitoring needs to continue for fish-feeding alcids because these birds provide an indication of the stability of the marine food web. Fairly standard indices are being used for tracking changes in populations of murres (e.g., Hatch and Hatch 1989; Byrd 1989) and burrow-nesting puffins (e.g., Nettleship 1976; Harris and Murray 1981; Rodway et al. 1990). Nevertheless, there are currently no standard methods for determining changes in populations of crevice-nesting Horned Puffins, and these need to be developed. Besides tracking population trends, it is necessary to monitor reproductive success and other measures of food web productivity to understand demographic and ecological processes affecting population change.

In much of the range of murres and puffins, little is known about their at-sea distribution or food habits, especially in winter. These data gaps need to be filled to understand the potential impacts that human activities such as commercial fishing and oil development might have on offshore fish-feeding alcids.

6. Summary and conclusions

Five species of seabirds in the family Alcidae comprise a guild of offshore fish-feeders that breed on islands and coastal fringes in the North Pacific Ocean. Common and Thick-billed murres are the most abundant species in this guild with approximately 11 million breeders in the North Pacific. Next in abundance are Tufted Puffins with an estimated 3.5 million breeders in the region. Least common are Rhinoceros Auklets and Horned Puffins, each with about one million breeders in the North Pacific.

Of the five species in the guild, the Rhinoceros Auklet is the only species that is active primarily during darkness at nesting colonies. This auklet also has the most southerly distribution of any of the species, the greatest concentrations being south of 52°N. Common Murres and Tufted Puffins extend farther south than their congeners, but in the northern parts of their ranges there is extensive overlap.

Few long-term studies of murres are available from which to judge population trends. Nevertheless, data from the past 15–20 years suggest some patterns. There have been declines in central California and Washington, but no data are available for Oregon to determine whether a similar decline has occurred there. No clear trends are evident in British Columbia either. In Alaska, data from the western Gulf of Alaska suggest no significant trends have occurred in populations over the past 15 years, but there have been declines recently at most monitoring sites in the Bering Sea and at Cape Thompson in the Chukchi Sea. In contrast, recent increases in murre populations have been recorded at Cape Lisburne in the Chukchi Sea, along the arctic coast of Siberia, and in the western Aleutian Islands.

Almost nothing is known about population trends in puffins. There is a general feeling among biologists in the Pacific Northwest (e.g., R. Lowe, pers. commun.) that Rhinoceros Auklets are currently increasing, and an increase was recorded between 1950 and 1970 at Teuri Island, Japan. A major decline was reported in northeastern Siberia prior to 1950, and the population has remained low thereafter. Rhinoceros Auklets probably also decreased following the introduction of arctic foxes to many islands in Alaska and north of Japan prior to 1930. Tufted Puffins have declined since 1900 in California, and this species along with its congener was

Table 6
Reproductive success of Tufted Puffins

Location	Source[a]	Year	Total eggs	Hatching[b] success	Fledging[c] success	Productivity[d]
Goat I., OR	1	1981	20	—	—	0.42
		1982	26	—	—	0.35
Destruction I., WA	2	1975	11	1.00	1.00	1.00
Triangle I., B.C.	3	1975	77	0.81	0.57	0.46
		1976	70	0.04	0.33	0.01
		1977	111	0.53	0.02	0.01
		1978	42	0.74	0.74	0.55
Barren Is., AK	4	1976	40	0.40	0.69	0.28
	5	1977	56	0.50	0.79	0.39
	5	1978	50	0.54	0.78	0.42
	5	1979	56	0.52	0.72	0.37
Sitkalidak I., AK	6	1977	67	0.61	0.88	0.54
	7	1978	69	—	0.69	—
Cliff I., AK	8	1977	25	0.89	0.90	0.80
	7	1978	46	0.85	0.90	0.76
	7	1983	67	—	0.46	—
Semidi Is., AK	9	1976	38	0.42	0.56	0.24
Ugaiushak I., AK	10	1976	52	0.60	0.83[e]	0.50
		1977	99	0.83	0.76[e]	0.63
Hall I., AK	11	1976	51	0.63	0.83	0.52
Buldir I., AK	10	1975	26	0.19	1.00	0.19
	12	1988	27	0.78	0.36	0.25
	13	1989	45	0.73	0.81	0.59
	14	1990	42	0.83	0.43	0.36
Kohl I., AK	13	1989	17	0.82	0.86	0.71
	14	1990	34	0.73	0.91	0.66
Talan I., Siberia	15	1988	34	0.78	0.75	0.59
	15	1989	37	0.59	0.80	—
Commander Is., Siberia	16	1973	18	0.66	—	—
	16	1974	26	0.54	—	—
	16	1975	30	0.47	—	—

[a] Codes for sources of information: 1 = Boone 1985, 2 = G. Burrell, pers. commun., *in* Wehle 1980, 3 = Vermeer et al. 1979, 4 = Amaral 1977, 5 = Manuwal 1980 (disturbed and undisturbed nest sites included), 6 = Baird and Moe 1978, 7 = S. Hatch, pers. commun., 8 = Nysewander and Hoberg 1978, 9 = Leshner and Burrell 1977, 10 = Wehle 1980, 11 = Moe and Day 1979, 12 = Byrd et al. 1989, 13 = Byrd and Douglas 1990, 14 = Byrd et al. 1990, 15 = Kondratyev, unpubl. data, 16 = Mikhtaryantz 1986 (eggs of known fate used for calculations).
[b] Proportion of eggs that hatched.
[c] Proportion of chicks that fledged.
[d] Proportion of eggs that produced fledglings.
[e] Mid-points of reported ranges were used.

Table 7
Reproductive success of Horned Puffins

Location	Source[a]	Year	Total eggs	Hatching[b] success	Fledging[c] success	Productivity[d]
Barren Is., AK	1	1976	14	0.79	0.36	0.29
	2	1977	14	0.93	0.69	0.64
	3	1978	18	0.89	0.81	0.72
Chisik I., AK	3	1978	24	0.75	0.89	0.67
Semidi Is., AK	4	1976	42	0.76	0.59	0.45
		1979	58	0.83	0.83	0.69
		1980	56	0.64	0.75	0.48
		1981	59	0.85	0.86	0.73
		1983	100			0.77
Ugaiushak I., AK	5	1977	68	0.76	0.91	0.69
Big Koniuji I., AK	6	1976	20	0.80	0.72	0.58
Hall I., AK	6	1976	12	0.83	0.83	0.69
Pribilof Is., AK	7	1976	25	0.56	0.79	0.44
		1977	10	0.90	0.83[e]	0.75[e]
Buldir I., AK	5	1975	—[f]	0.00	0.00	0.00
	8	1988	42	0.86	0.63	0.46
	9	1989	69	0.84	—	—
	10	1990	56	0.82	0.74	0.57
Talen I., Siberia	11	1989	?	0.84	0.79	0.66

[a] Codes for sources of information: 1 = Amaral 1977, 2 = Manuwal and Boersma 1978, 3 = S. Hatch, pers. commun., 4 = Hatch and Hatch, in press, 5 = Wehle 1980, 6 = Moe and Day 1979, 7 = Hunt et al. 1981, 8 = Byrd et al. 1989, 9 = Byrd and Douglas 1990, 10 = Byrd et al. 1990, 11 = Kondratyev, unpubl. data.
[b] Proportion of eggs that hatched.
[c] Proportion of chicks that fledged.
[d] Proportion of eggs that produced fledglings.
[e] Mid-points of reported ranges were used.
[f] Reported as having nearly a complete reproductive failure in 1975.

probably decimated by introduced foxes over a major portion of its range.

In most cases for which we found data, reproductive success for murres ranged from 45 to 77% of eggs producing fledglings. Lower success was reported in two cases where egg predation was particularly high and in one case where an El Niño temporarily changed the environment drastically.

The few data sets available on productivity of Rhinoceros Auklets suggest that reproductive success is highly variable among years, ranging from 20 to 90% of the eggs producing fledglings. Food limitations in some years have been the reported cause of poor success. Apparently, Tufted and Horned puffins also experience variable success based upon food availability. For 21 Tufted Puffin data sets, nearly 50% of eggs produced fledglings on average. The average for Horned Puffins was slightly higher, 57% in 18 cases. For all three species of puffins, chick mortality rates tended to be more variable than egg survival rates.

The effective management of murres and puffins requires accurate information about trends in populations, fluctuations in reproductive output, and the reasons for observed changes. For murres, Rhinoceros Auklets, and Tufted Puffins, monitoring methods have been devised that are adequate to detect trends, but there currently is no standard method that could be expected to reliably reflect changes in Horned Puffin populations. Furthermore, little is known about the winter ecology of any of these species. The most obvious recent threats to these seabirds are direct mortality in gill nets, oil spills, predation by introduced predators on nesting areas, and failure to produce young due to food shortages resulting from fluctuations in the marine environment and possibly competition with commercial fisheries.

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