The status, distribution, and ecology of inshore fish-feeding alcids (*Cepphus* guillemots and *Brachyramphus* murrelets) in the North Pacific

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Abstract

Five species of inshore fish-feeding alcids occur in the North Pacific. The Black Guillemot *Cepphus grylle* frequents the Bering Strait in small numbers but is more numerous in arctic regions. The breeding range of Kittlitz's Murrelet *Brachyramphus brevirostris* extends into the Chukchi Sea but the remaining three species (Pigeon Guillemot *C. columba*, Spectacled Guillemot *C. carbo*, and Marbled Murrelet *B. marmoratus*) are found only in the North Pacific. Censusing of these species is difficult because they tend to breed in dispersed, relatively small colonies, or as isolated pairs, spread over large areas. Consequently, status changes are difficult to assess accurately. However, reliable survey techniques have recently been developed. There are strong indications that populations have declined in some areas due to factors such as introduction of ground predators (guillemots), destruction of old-growth forests (Marbled Murrelet), gillnet fishing, and oil pollution.

Résumé

On a relevé cinq espèces d'Alcidés pêcheurs côtiers dans le Pacifique Nord. Le Guillemot à miroir *Cepphus grylle* fréquente le détroit de Béring, mais les populations des régions arctiques sont plus nombreuses. L'aire de nidification de l'Alque pâle *Brachyramphus brevirostris* s'étend jusque dans la mer de Tchoukotka, mais les trois autres espèces, Guillemot du Pacifique *C. columba*, Guillemot à lunettes *C. carbo* et Alque marbrée *B. marmoratus*, sont confinées dans le Pacifique Nord. Le dénombrement de ces espèces n'est pas aisé, parce qu'elles ont tendance à nicher dans de petites colonies dispersées ou en couples isolés, dans de vastes régions. Par conséquent, les changements de situation sont difficiles à préciser. Cependant, on a récemment mis au point des techniques fiables de relevé, et il y a de bonnes raisons de croire que les populations s'affaiblissent dans certaines régions, en raison de différentes causes, comme l'introduction de prédateurs terrestres (guillemots), la destruction des peuplements mûrs (Alque marbrée), la pêche au filet maillant et la pollution par les hydrocarbures.

1. Introduction

In the North Pacific there are five species of alcids, comprising two genera, which inhabit inshore waters and feed predominantly on fish. Three are guillemots: Black Guillemot *Cepphus grylle*, Pigeon Guillemot *C. columba*, and Spectacled (or Sooty) Guillemot *C. carbo*, and two are murrelets: Marbled Murrelet *Brachyramphus marmoratus* and Kittlitz's Murrelet *B. brevirostris*. These species occupy inshore feeding niches, breeding as scattered pairs or in small groups at regular intervals along coasts and do not normally undergo long-distance movements. This contrasts with the more offshore feeding niches and large breeding colonies of most alcid and other seabird species (Lack 1968).

Until recently our understanding of the distribution and ecology of these species in the Pacific was limited. The Black Guillemot is the only species that occurs elsewhere, and it has been studied intensively in the Canadian Arctic (Cairns 1984), northern Alaska (Divoky et al. 1974; Divoky and Boekelheide 1978), and the northeast Atlantic (Asbirk 1979; Petersen 1981; Ewins 1986). In the North Pacific small numbers have been recorded in Pigeon Guillemot colonies south to St. Lawrence Island, but breeding has not yet been confirmed (Bédard 1966, 1985; Sowls et al. 1978; Konyukhov and Ewins 1992), and there is evidence of some postbreeding movement of birds from higher latitudes into the southern Bering Strait (Kozlova 1957; Gabrielson and Lincoln 1959). However, because Black Guillemots are at the edge of their range here, they are not considered further in this account. In the eastern Pacific we know something of the ecology and distribution of Pigeon Guillemots and Marbled Murrelets, but for the western Pacific information is scarce. The Spectacled Guillemot and Kittlitz's Murrelet are the least studied inshore alcids. The huge lengths of coastline along which these species breed, the absence of reliable census techniques, and the inaccessibility of many nest sites are key reasons for the current gaps in our knowledge of status and ecology.

This paper reviews the available information for these four species and provides recommendations for priority survey and research. The results from such work will facilitate effective conservation action on behalf of these populations.

2. Breeding distribution

For each of the six regions referred to in this paper (Fig. 1) the most recent or reliable census data have been used to obtain the best current estimates of breeding distribution and population size. Table 1 gives the sources of these data. Figure 2 gives the known distribution limits and known or suspected breeding areas of Pigeon Guillemot, Spectacled Guillemot, Marbled Murrelet, and Kittlitz's Murrelet.

Figure 1
Map of the temperate North Pacific showing the boundaries of areas mentioned in the text: 1. Sea of Japan (Pusan – Soviet Harbour), 2. Sea of Okhotsk (– Cape Lopatka, S. Kamchatka), 3. Northeastern Russia (– Chaunskaya Guba), 4. Alaska (Cape Lisburne – Dixon Entrance), 5. British Columbia, 6. Washington, Oregon, and California.

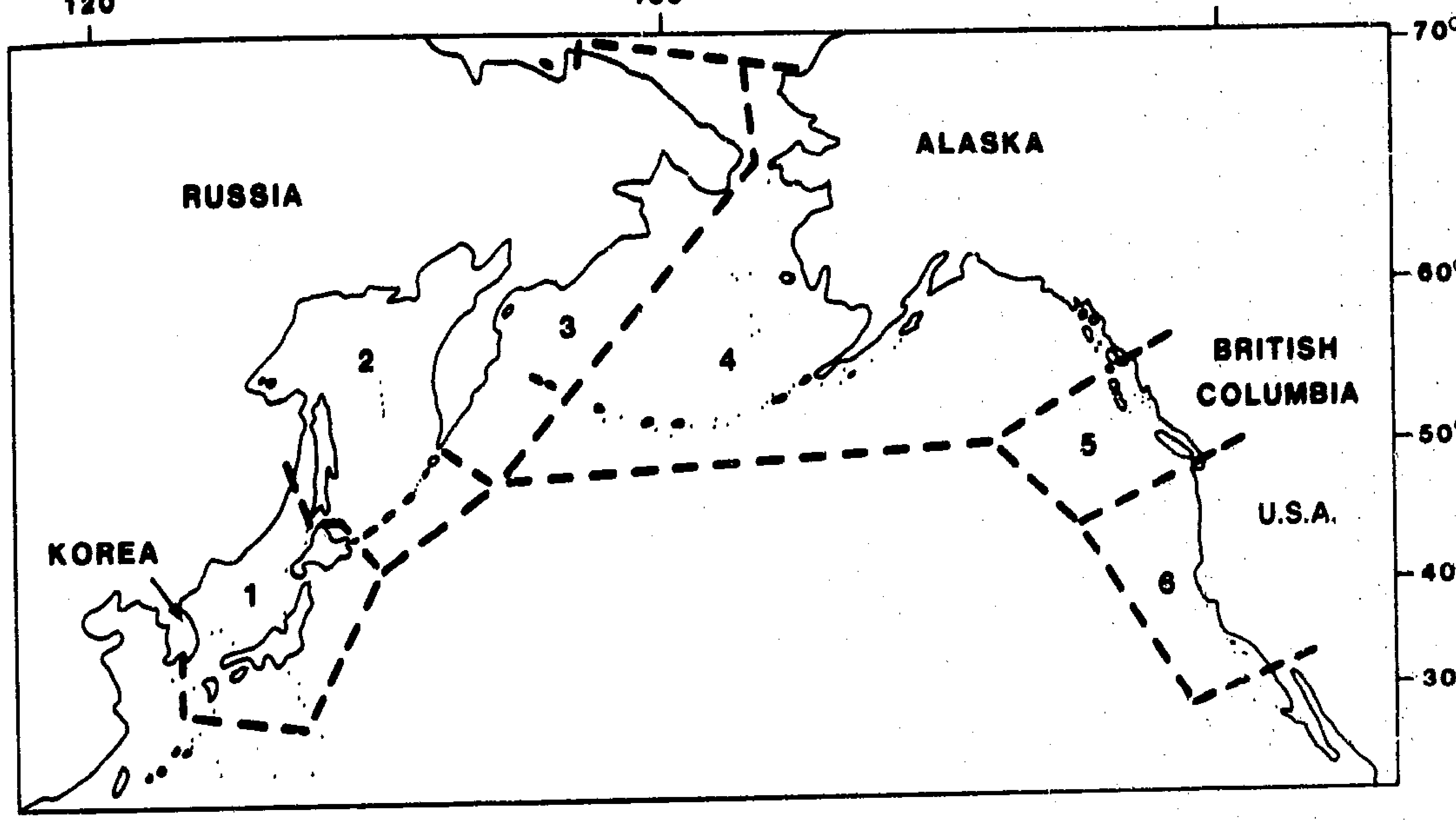


Table 1
Most recently available breeding population counts and estimates for *Cepphus* and *Brachyramphus* alcids in the temperate North Pacific. Count units are as given by the original source authors (in a few cases "pairs" have been converted to "birds" by doubling the count, thereby enabling a regional total to be calculated). Note: Surveys for most regions were incomplete.

Species	Sea of Japan	Sea of Okhotsk	Northeast Russia	U.S.A. (Alaska)	British Columbia	U.S.A. (Washington, Oregon, California)
Pigeon Guillemot *C. columba*	0	5102+ birds	7122 birds	40 000 birds	10 200 birds	22 360 birds
Spectacled Guillemot *C. carbo*	11 400+ birds	63–65 748+ pairs	(4) immatures	0	0	0
Marbled Murrelet *B. marmoratus*	breeds	breeds	probably breeds	250 000–1 million birds	50 000 birds	8050–12 100 birds
Kittlitz's Murrelet *B. brevirostris*	0	1 nest known	breeds	25 000–100 000 birds	0	0

Sources (for counts, estimates, and ranges of populations): Kischinsko 1980; Vermeer et al. 1983, Gerasimov 1986; Vyatkin 1986.
C. columba: Udvardy 1963; Velizhanin 1969, 1977; Portenko 1973; Sowls et al. 1978, 1980; Spendelow and Patton 1988; Speich and Wahl 1989; Vermeer 1989.
Kondratiev et al. 1987; Lobkov and Alexeev 1987; Roslyakov 1986; Shuntov 1986; Vyatkin 1986; Watanuki et al. 1986.
C. carbo: Udvardy 1963; Velizhanin 1975, 1977; Elsukov 1984; Hasegawa 1984; Nechaev 1986;
Lobkov and Alexeev 1987; Shibaev 1987.
B. marmoratus: Kuzyakin 1963; Sowls et al. 1980; Elsukov 1984; Hasegawa 1984; Sealy and Carter 1984; Nechaev 1986; Shuntov 1986, Labzyuk 1987, Vermeer et al. 1987; Carter and Erickson 1988; Watanuki et al. 1988; Speich and Wahl 1989.
B. brevirostris: Kischinskii 1968; Sowls et al. 1978; Forsell and Gould 1981; Gould et al. 1982; Tomkovich and Sorokin 1983; Kondratiev 1986, Johnsgard 1987. A.L. Sowls, unpubl. data.

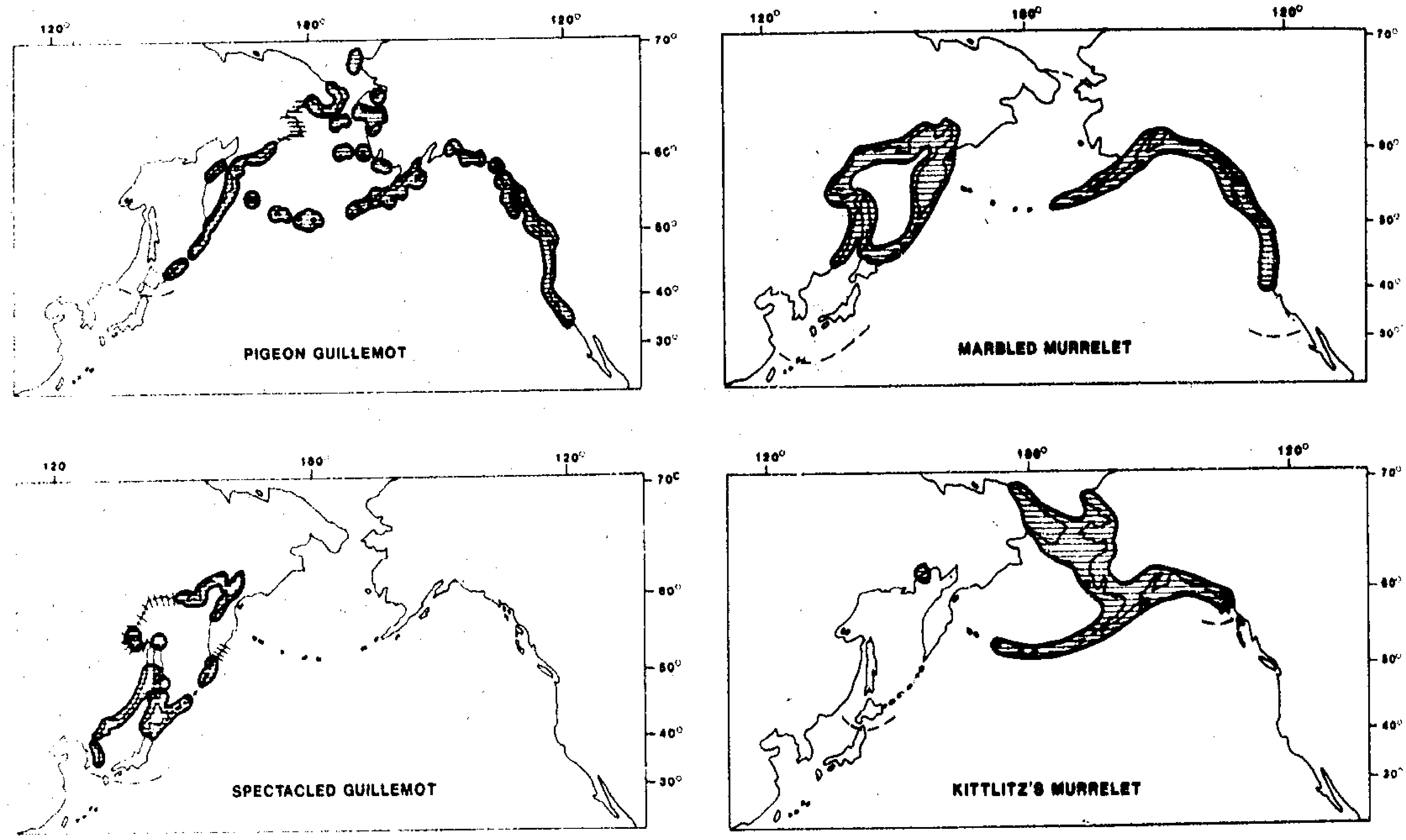
Figure 2
The breeding distribution of *Cepphus* guillemots and *Brachyramphus* murrelets in the temperate North Pacific

Cepphus

known breeding areas
suspected breeding areas

Brachyramphus

probable extent of breeding range
limits of distribution



2.1. Pigeon Guillemot

The Pigeon Guillemot occurs as a widespread breeding species in small colonies along coastlines with suitable breeding sites and shallow foraging areas, between 33°N (Sutil and Santa Barbara islands, southern California) and 69°N (Cape Lisburne, Alaska) (Fig. 2). It is replaced by the Spectacled Guillemot in many western areas. Udvardy (1963) recognizes five distinct subspecies: *columba* (Kamchatka north to Bering Strait coasts), *snowi* (Kuril Islands), *kaiurka* (Commander Islands and west/central Aleutian Islands), *adianta* (eastern Aleutians, Alaska, and south to Washington state), and *eureka* (Oregon and California).

2.2. Spectacled Guillemot

Spectacled Guillemots breed between about 38°N and 62°N, in the Sea of Okhotsk and the Sea of Japan (Fig. 2). Austin (1948) found it to be the third most numerous species in some mixed seabird colonies in Korea, but the present breeding status there is unknown. Numerous small colonies are found along many mainland Russian coasts (Elsukov 1984), but birds are thinly scattered on Sakhalin Island and appear to be absent from the low western coasts of the Kamchatka peninsula. In the Shantarsky archipelago the breeding distribution was found to depend upon the availability of nest sites (Roslyakov 1986).

2.3. Marbled Murrelet

The Marbled Murrelet occurs in each of the six regions and probably breeds between 38°N and 62°N. Because so few confirmed breeding records exist (see Table 2), the breeding distribution map shows the known and suspected summer range of birds in inshore waters off potential nesting habitat (Fig. 2). The eastern Pacific population belongs to the subspecies *marmoratus*, whereas the larger *perdix* subspecies occurs in the western Pacific. All specimens from the northern Bering Sea as far north as Idlidlya Island (northern Chukotka peninsula) have been referred to *marmoratus* (Sealy et al. 1982). The species is not known to breed in this area, but one unconfirmed nest was reported near Nome in 1904 (Bent 1919, 1920), and *perdix* may breed in the Commander Islands (Taczanowski 1893). Between 1979 and 1989 there were 13 records of *perdix* in North America, as far east as the Atlantic Ocean; these vagrants may be related to unusual weather patterns (Sealy et al., in press).

2.4. Kittlitz's Murrelet

Our knowledge of the breeding distribution of Kittlitz's Murrelets is based on the few nests located and summer observations of birds in inshore waters. The breeding range lies between about 52°N and 69°N and probably extends along most of the Bering Sea coasts and north into the Chukchi Sea, with an

Table 2
Changes in numbers of breeding Pigeon and Spectacled guillemots at selected localities

Year	Breeding population size	Source
Pigeon Guillemot: Farallon Islands, California		
1886	c. 2000 birds[a]	Ainley and Lewis 1974
1911	c. 200 birds	Ainley and Lewis 1974
1959	1000 birds	Ainley and Lewis 1974
1972	1000 breeding pairs	Ainley and Boekelheide 1990
1978	500 breeding pairs	Ainley and Boekelheide 1990
1979	1000 breeding pairs	Ainley and Boekelheide 1990
1982	1100 breeding pairs	Ainley and Boekelheide 1990
1983	<50 breeding pairs	Ainley and Boekelheide 1990
1984	750 breeding pairs	Ainley and Boekelheide 1990
1985	650 breeding pairs	Ainley and Boekelheide 1990
1986	625 breeding pairs	Ainley and Boekelheide 1990
1989	c. 2000 birds	W.J. Sydeman, pers. commun.
Spectacled Guillemot: Teuri Island, N. Japan		
1949	7000+ birds[b]	Austin and Kuroda 1953
1963	c. 3000 birds	Kuroda 1963
1981	<400 birds (<200 breeding)	Thoresen 1984
1985	249 birds (60+ occupied sites)	Watanuki et al. 1986
1987	213 birds	Watanuki et al. 1988
Spectacled Guillemot: Furugelm Island, Peter the Great Bay, Russia		
1979	4362 birds	Shibaev 1987
1982	3300 birds	Shibaev 1987
1984	3305 birds	Shibaev, unpubl. data
1989	2040 birds	Shibaev, unpubl. data

[a] Estimated by Ainley and Lewis, based on old accounts describing breeding colonies and general abundance.
[b] Accuracy of this estimate has been questioned by some authors.

outlying nest recorded from Shelekov Bay, in the northern Sea of Okhotsk (Fig. 2). Kittlitz's Murrelets occur along coastlines adjacent to extensive areas of alpine tundra, where they nest on rocky slopes. In Alaska, greatest numbers are usually found in association with glaciers and the summer distribution appears to be more patchy than that of Marbled Murrelets (K. Kuletz, pers. commun.). The breeding range overlaps with that of the Marbled Murrelet in much of southern Alaska and along the Alaska Peninsula. Although no surveys exist for Russia it is likely that the majority of the world population occurs in Alaska.

3. Populations

3.1. Guillemot census methods

The term "colony" has been used rather imprecisely for guillemots by some previous authors, to mean anything from a discrete breeding group to the total population inhabiting an island or stretch of coastline. In this paper we use the term to mean an aggregation of breeding birds sufficiently separated from the adjacent group that an observer can pass (either on foot or by boat) between them without disturbing either group (*sensu* Ewins and Tasker 1985). For guillemots at least, many larger islands support a number of colonies.

Because guillemot colony attendance fluctuates markedly both diurnally and seasonally, and also in relation to weather conditions (e.g., Ainley and Lewis 1972; Lehnhausen 1980; Kuletz 1983; Ewins 1985; Nelson 1987; Ainley and Boekelheide 1990), interpretation of census results is difficult. It is generally accepted that the most accurate and repeatable census method for guillemots involves counting adult-plumaged birds associated with potential breeding habitat in the early mornings during the prebreeding season (Ewins 1985; Ewins and Tasker 1985; Emms and Morgan 1989). In areas with very large tidal ranges, guillemot colony attendance can be influenced strongly by tide levels, resulting in reduced early morning attendance in the breeding period when tides are very low (Petersen 1981; Vermeer et al., in press). All guillemot counts for the Pacific were made during the incubation and nestling periods, at various times of day, when often only a small proportion of breeding birds would have been present at a colony. Further, nests are difficult to find. In Scotland prebreeding counts of adult Black Guillemots ranged from three to seven times greater than head counts made during the breeding season (Ewins 1985; Ewins and M.L. Tasker, unpubl. data). Therefore, most guillemot counts used in these analyses are probably underestimates. Also, many suitable coastlines have not been surveyed, particularly in the west Pacific, and so the regional totals given in Table 1 reflect coverage to a large extent. For these reasons it would be inappropriate to present total population estimates for guillemots at this stage.

3.2. Murrelet census methods

Census methods for Marbled Murrelets have only recently been established. Because murrelets forage mostly in inshore waters, counts along transects at sea (covering either an entire grid or sample transect up to 6 km offshore) have been used to estimate population size in some areas (Sealy and Carter 1984). However, in most regions only general indications of breeding numbers and distribution have been obtained, by unsystematic counts at sea (e.g., Sowls et al. 1980; Carter and Erickson 1988). Probable nesting areas can be identified by conducting activity surveys inland using either 10-min. stations along roads, or a series of single stations surveyed throughout the dawn activity period (Paton and Ralph 1988; Nelson 1989; Paton et al. 1991; Hamer and Cummins 1991), and extensive dawn surveys have been conducted in parts of the breeding range in the eastern Pacific. A ground survey technique for finding nests has recently been developed, which facilitated the location of two nests in California in 1989 (Singer et al., in press), and in 1990, two in Oregon (S.K. Nelson, pers. commun.), two in Washington (Hamer et al. 1991), and one in British Columbia (Manley and Kelson 1991). Radiotelemetry continues to be developed but thus far has led to the discovery of only one nest (Quinlan and Hughes 1984, 1990).

No specific census methods have been devised for Kittlitz's Murrelet, but at-sea transects are currently being investigated (K. Kuletz and K. Laing, pers. commun.). General observations at sea provide approximate information on breeding numbers and distribution, but many surveys in Alaskan inshore waters now record only *Brachyramphus* sp., due to the difficulties in distinguishing the two species, other than at short distances, in most light and weather conditions.

3.3. Pigeon Guillemot

Census data from the western Pacific are patchy and actual breeding numbers are undoubtedly much higher than those given in Table 1. We have presented the total numbers recorded by the catalogues, and not the authors' estimates of population sizes. Coverage for Washington, Oregon, and California is probably better than for other regions. The largest breeding concentrations are on the Farallon Islands, California, and at Cape Ulyakhpen (south Chukot Peninsula, Russia) (up to about 2200 birds at each), and over 1000 birds on each of three Alaskan islands.

Population trends are difficult to assess from previous counts, due to the large fluctuations in colony attendance already mentioned; apparent increases are most likely to reflect improved coverage and census techniques (e.g., Sowls et al. 1980). However, there is evidence of a marked population decline or abandonment of breeding colonies in some areas (Table 2). The long-term studies at the Farallon Islands indicate quite large changes in breeding numbers, associated mainly with fluctuations in water temperature and hence prey availability (Ainley and Boekelheide 1990). Palmer (cited in Storer 1952) found this species to be common near Walrus Island, in the Pribilof group in June 1890, but today it is only a winter visitor there. Because both Black and Pigeon guillemots often nest in human-made structures it is likely that numbers have increased locally in areas where such structures have supplemented the shortage of suitable natural sites. Excavations of Indian middens in British Columbia found Pigeon Guillemot bones in deposits up to 4000 years old, but at frequencies suggesting that it was never as numerous in the area as some other seabird species (Vermeer and Sealy 1984; Hobson and Driver 1989).

3.4. Spectacled Guillemot

This species is probably the least numerous inshore fish-feeding alcid in the North Pacific (Table 1). The largest known breeding concentrations (estimates?) are at the Shantarsky Islands (18–20 000 pairs), in Peter the Great Bay (c. 5500 pairs), and on Matykil Island, Yamsky Islands group (4000 pairs). Along the mainland Russian coasts on the Sea of Japan north of Soviet Harbour, Elsukov (1984) found an average of 5.7 pairs per kilometre, in numerous small colonies. However, many coasts have not been surveyed and the total population is undoubtedly larger than is currently known. Marked declines have been noted in northern Japan, with an estimated 10–20% annual reduction in numbers at many colonies around Hokkaido in recent years (Watanuki et al. 1988). At Teuri Island there seems to have been a 93% decline between 1963 and 1987, and numbers had probably been falling since 1949 (Table 2). In Peter the Great Bay breeding numbers have declined by 53% since 1979 on Furugelm Island, for reasons as yet unknown (Table 2).

3.5. Marbled Murrelet

In California, only two small populations remain, having probably declined to the present estimated total of 1650–2000 breeding birds due to extensive logging of old-growth forests (Sowls et al. 1980; Carter and Erickson 1988). However, Ralph and Miller (1991) suggested that the Californian population may be as high as 5000 birds, because some boat-based surveys may not have taken full account of sea state and detectability distances. Small populations also occur in Oregon and Washington, but further north the species is more numerous, although survey data are incomplete. Southeastern Alaska probably supports the largest numbers, although the western Pacific status is unknown (Table 1). Surveys in the western Sea of Okhotsk found 0.5–2.0 birds per kilometre of coastline in summer (Babenko and Pojarkov 1987). The extensive logging of old-growth forests has undoubtedly led to substantial population declines, particularly during the 20th century, but there are only a few historical data against which to gauge the scale of declines (Carter and Erickson 1988; Paton and Ralph 1988).

3.6. Kittlitz's Murrelet

In Alaska this species appears to be less numerous than the Marbled Murrelet, but no population counts or estimates are available for the western Pacific (Table 1). In south-central Alaska, surveys during the breeding season have found that Marbled Murrelets outnumber Kittlitz's Murrelets by about 9:1, although there is considerable regional fluctuation in relative abundances (K. Kuletz and K. Laing, pers. commun.). Although Lensink (1984) regarded Alaskan numbers to be relatively stable, this assessment was not based on systematic census data, and more recent survey work has found difficulty in making any meaningful conclusions about population trends. However, considerable numbers were killed in the *Exxon Valdez* oil spill (Piatt et al. 1990; V. Mendenhall, pers. commun.).

4. Nesting habitat

4.1. Pigeon Guillemot

In many areas the breeding distribution is determined mainly by the dispersion and quality of nest cavities. The variety of nesting habitats occupied often reflects local availability to the nesting birds. Sites accessible to ground predators tend to be avoided in infested areas. Cliff crevices and boulder beaches or talus slopes are widely used for breeding. Also used are cliff-edge cavities amongst tree roots (K. Vermeer et al., unpubl. data), abandoned burrows of rabbits *Lepus californicus* (Bowman 1961) or Tufted Puffins *Fratercula cirrhata*, holes excavated in banks by the Pigeon Guillemots themselves (Bent 1919; K. Vermeer et al., unpubl. data), holes under driftwood or in rotten logs (Drent 1965), cavities under wharves or bridges or in disused buildings or navigation aids (Fisk 1978; Speich and Wahl 1989), spent tire casings (Campbell 1977), cavities under vegetation, or open ledges (Thoresen and Booth 1958; Bowman 1961; K. Vermeer et al., unpubl. data). Sites with small entrances are often preferred (Lehnhausen 1980). Most birds breed in small colonies or occasionally as isolated pairs, and in the eastern Pacific 63–96% of breeding aggregations contain fewer than 50 birds.

4.2. Spectacled Guillemot

Spectacled Guillemots breed along rocky coasts, in cliff crevices or caves or amongst boulders on talus slopes, or in more accessible locations on islands lacking mammalian predators. Nazarov and Labzyuk (1972) found many nests amongst boulders 1.5–20 m from the surf line, with fewer in cliff crevices and under bushes and tree roots, up to 120 m from the sea. On Teuri Island, 60% of nests were more than 20 m above sea level (Thoresen 1984). Most birds probably breed in small colonies of 10–20 pairs, but isolated pairs and some colonies of a few hundred pairs are known.

4.3. Marbled Murrelet

This is the only alcid species that nests in trees, although it also nests on open rocky ground in the north of its range. Tree nests are in depressions on broad moss- or lichen-covered branches (usually close to the base of the branch) of various mature Pacific coastal conifer species (for eastern Pacific see Binford et al. 1975; Marshall 1988), or on intertwined smaller branches of larch (*Dahurica* sp.) in the western Pacific (see Kuzyakin 1963; Kondratiev and Nechaev 1989). One Californian nest site was a constructed nest of twigs and foliose lichens, possibly an old nest of Band-tailed Pigeon *Columba fasciata* (Singer et al., in press). Pairs nest solitarily, but loose aggregations may occur in preferred old-growth nesting habitat. Alaskan ground nests occur at about 300 m above sea level on average and, in the area of sympatry with Kittlitz's Murrelet, nearer the sea (mean 6 km for Marbled, versus 11 km for Kittlitz's, see Day et al. 1983). Further south, activity has been recorded in forest stands as far as 55 km inland (exceptionally 75 km), but mostly within 20 km of the ocean (Carter and Sealy

Table 3
Breeding statistics for Pigeon Guillemots in various areas

Location	Year	No. of nests	Mean clutch	% hatching success	% fledging success[a]	No. fledged per nest[b]	Source
California							
SE Farallon I.	1971–82	?	1.8	76	67	1.0	Ainley and Boekelheide 1990
Washington							
Puget Sound	1957	42	1.76	54	86	0.82	Thoresen and Booth 1958
Protection I.	?	31	1.48	91	67	0.89	Leschner and Hirsch 1980
British Columbia							
Mandarte I.	?	58	1.86	62	84	0.96	Aitchison 1972
Mandarte I.	1957–59	111	1.91	62	90	1.08	Drent et al. 1964
Mandarte I.	1960	51	1.90	59	41	0.46	Drent 1965
Mittlenatch I.	1984	91	1.76	69	47	0.57	Emms and Morgan 1989
Mittlenatch I.	1985	106	1.74	45	24	0.19	Emms and Morgan 1989
Alaska							
Fish I.	?	14	1.78	84	81	1.21	Lehnhausen (in Oakley 1981)
Shumagin I.	?	14	1.92	56	33	0.36	Moe and Day 1979
Naked I.	1978	32	1.78	75	96	1.28	Oakley 1981
Naked I.	1979	33	1.82	75	85	1.48	Kuletz 1983
Naked I.	1980	22	1.73	61	63	1.00	Kuletz 1983
Naked I.	1981	26	1.58	73	63	1.00	Kuletz 1983
Russia							
Commander Is.	—	33	1.70				Mikhtaryants, no date

[a] The percentage of chicks that fledged.
[b] Mean number of chicks fledging per breeding attempt made.

1986, 1987). From southern British Columbia to California some birds visit nesting areas and freshwater lakes throughout the year (Carter and Sealy 1986; Hobson 1990).

4.4. Kittlitz's Murrelet

Kittlitz's Murrelets nest on rocky ground usually high on barren north-facing slopes above the timber line. Nests found thus far have been solitary, but it is possible that loose nesting aggregations could occur in the most favoured areas. The nest depression is usually in a gravelly substrate or in short ground vegetation, and is often situated at the base of a large rock. Day et al. (1983) summarized known nest details, revealing a mean elevation of 570 m above sea level (range 230–1070 m) and a mean distance inland of 16 km (max. 75 km).

5. Breeding biology and mortality

5.1. Pigeon Guillemot

Compared with other inshore Pacific alcids, this species has been relatively well studied. The following summary of breeding biology is drawn from studies carried out in California (Ainley and Lewis 1972, 1974; Osborne 1972; Follett and Ainley 1976; Nelson 1987; Ainley and Boekelheide 1990), Oregon (Scott 1973), Washington (Thoresen and Booth 1958), British Columbia (Drent 1965; Aitchison 1972; Koelink 1972; Emms 1987; Emms and Verbeek 1989; K. Vermeer et al., unpubl. data), Alaska (Lehnhausen 1980; Oakley 1981; Kuletz 1983), and the Commander Islands, Russia (Mikhtaryants, no date).

The timing and success of breeding vary markedly amongst studies (Table 3), due to factors such as weather conditions, food supply, availability of nest sites, and predation. Guillemots are sensitive to human disturbance (e.g., from researchers trapping breeding adults, particularly during the earlier stages of incubation) and this factor may have influenced breeding statistics in some cases (Cairns 1980; Ainley and Boekelheide 1990). There is frequently as much variation in breeding output between years at the same site as there is between sites, so no generalizations can be made from regional comparisons of breeding success. This has been well demonstrated on the Farallons, where average reproductive output varied from zero to 1.6 fledglings per pair in the study years between 1971 and 1982, associated mainly with warm-water events and their effect on the food supply (Ainley and Boekelheide 1990). Birds associate with breeding areas from late March in most of the range, with onshore activity from late April to early September recorded in British Columbia.

In years of food scarcity (such as during El Niño warm-water events) fewer adults make a breeding attempt and starvation may be a major cause of breeding failure and adult mortality (Hodder and Graybill 1985; Ainley and Boekelheide 1990). Flooding of nests close to the splash zone is a regular cause of failure, but predation of eggs and chicks by mammals or birds often causes heavy losses on a local scale (e.g., by mink *Mustela vison*, ermine *M. erminea*, Northwestern Crow *Corvus caurinus*, Raven *C. corax*, Black-billed Magpie *Pica pica*, or Glaucous-winged Gull *Larus glaucescens*). In British Columbia large numbers of small chicks were eaten by garter snakes *Thamnophis elegans* on Mittlenatch Island (Emms and Morgan 1989).

There are no survival estimates for Pigeon Guillemots, but life history parameters are likely similar to those for Black Guillemots (see Asbirk 1979). The oldest banded bird on the Farallon Islands was 14 years old in 1990 (W.J. Sydeman, pers. commun.). The 1982–83 El Niño event caused significant adult mortality (via changes to the food supply) in Oregon (Hodder and Graybill 1985) and at the Farallon Islands (Ainley et al. 1988; Stenzel et al. 1988; Ainley and Boekelheide 1990). Recorded predators of full-grown birds include Bald Eagle *Haliaeetus leucocephalus*, Peregrine Falcon *Falco peregrinus*, giant Pacific octopus *Octopus dofleini martini*, and killer whale *Orcinus orca* (Vermeer et al. 1989; Sharpe et al. 1990; Stacey et al., in press). Substantial gillnet mortality of Pigeon Guillemots was noted in central California from 1979 to 1987 (California Department of Fish and Game 1987), but has not been reported elsewhere. Mortality in oil spillages has undoubtedly been high in some areas, e.g., the Farallon Islands

(Ainley and Lewis 1974). Of the approximately 30 000 carcasses retrieved in the four months following the *Exxon Valdez* spill in southern Alaska (Piatt et al. 1990), 2.2% were Pigeon Guillemots. However, very few oiled Pigeon Guillemots were found after the *Nestucca* oil spill off Grays Harbor, Washington, possibly due to the more offshore distribution of the oil slick in that case (Rodway et al. 1989).

5.2. Spectacled Guillemot

This species remains one of the least known alcids. Various accounts of breeding biology and incidental notes are available for Korea (Austin 1948) and Russia (Dement'ev and Gladkov 1951; Roslyakov 1986), but the only reasonably detailed studies are from Peter the Great Bay (Nazarov and Labzyuk 1972) and Teuri Island, Japan (Thoresen 1984).

Like its congeners, the Spectacled Guillemot has two brood patches and normally lays clutches of two eggs (Nazarov and Labzyuk 1972; Thoresen 1984), contrary to the accounts by Dement'ev and Gladkov (1951) and Kozlova (1957), which indicate clutches of one egg only.

Eggs and small chicks are often taken by Jungle Crows *Corvus macrorhynchos*, Ravens, and Slaty-backed Gulls *Larus schistisagus*, but mammalian ground predators such as fox and sable (e.g., *Martes zibellina, Lamprogale flavigula, Kolnocus sibirica*) can cause abandonment of colonies. Adults are killed by Eagle Owls *Bubo bubo* in Russia. Nazarov and Labzyuk (1972) reported remains of 53 adults at one plucking post, representing 65% of the owl's avian prey. Adults are also taken by Peregrine Falcon (Gizenko 1955), and in some parts of Russia are shot illegally.

5.3. Marbled Murrelet

Breeding success at a limited number of tree nests studied appears to be low, and recent observations have recorded chicks preyed upon by Raven and Steller's Jay *Cyanocitta stelleri* (Singer et al., in press), and probably also Great Horned Owl *Bubo virginianus* (S.K. Nelson, pers. commun.). In Alaska, fully grown Marbled Murrelets were the main prey item found at some Peregrine Falcon eyries on the southern Kenai Peninsula (J. Hughes, unpubl. data), and Bald Eagles can catch Marbled Murrelets on the water (K. Kuletz, pers. commun.). Predation by both these species has also been recorded in British Columbia (Vermeer et al. 1989; Rodway et al., in press). In southern Alaska 2.2% of the carcasses retrieved in the four months following the *Exxon Valdez* oil spill were of *Brachyramphus* species, and local populations of Marbled Murrelets were decimated by the oiling (Piatt et al. 1990).

6. Distribution at sea

6.1. Pigeon Guillemot

Young Pigeon Guillemots are usually fed fish caught within 7 km of the nest, but breeding and nonbreeding adults may forage for themselves further from the colony (Thoresen and Booth 1958; Drent 1965; Oakley 1981; Nelson 1987).

In winter, Pigeon Guillemots are widely dispersed and favour sheltered, inshore waters, probably due to heavy seas and prey shortages along more exposed coastlines in winter (Scott 1973; Oakley 1981; Trapp 1985). Adults and immatures from the Farallons move to mainland coasts after the breeding season, with at least 30% of the winter band recoveries of immatures in Washington and British Columbia, where substantial areas of sheltered coastline exist (Ainley and Boekelheide 1990). Analyses of Christmas Bird Counts and other partial censuses in the eastern Pacific revealed that winter densities were highest in southern Alaska and Washington, with relatively few birds elsewhere (Trapp 1985; Krasnow and Sanger 1986). Pigeon Guillemots are rarely seen more than a few kilometres from land, or in waters more than 50 m deep, but small numbers do occur in mixed-species feeding flocks out to the continental shelf break (Sanger 1987; Vermeer et al. 1987). Although ice forces more northerly birds south in winter, small groups occur up ice leads and at holes in the ice, even off ice-bound St. Matthew Island, 2° north of the ice edge (Storer 1952; Kozlova 1957; Irving et al. 1970).

6.2. Spectacled Guillemot

During the breeding season adults forage up to 6 km from the nest, in shallow water (15–20 m depth recorded), or in tidal races. A wide range of benthic fish species as well as sardines (*Sardinops* sp.), herring, and a few invertebrates are fed to chicks. As with Pigeon Guillemots, the distribution of foraging birds probably reflects the availability of these prey items in suitable areas of vegetated or rocky benthos.

In Peter the Great Bay there is a distinct movement of birds away from breeding areas in August and September, presumably to moulting areas. Most birds breeding in the Sea of Okhotsk are forced south by ice, which is usually well formed by early December. This large exodus may account for the influxes to the Sea of Japan in early September (Vyshkvartsev and Lebedev 1986). Birds breeding elsewhere appear to be more sedentary, although there is some southerly movement in winter along the coasts of Japan, probably mostly of immatures. However, very little is known of the distribution of this species outside the breeding season.

6.3. Marbled Murrelet

Marbled Murrelets generally forage in sheltered inshore waters, usually shallower than 50–100 m and within 5 km of the shore. They probably feed throughout the water column in shallow areas. In winter and early spring, adults feed on a variety of midwater fish (mainly capelin, Pacific sand lance, and herring), and invertebrates (mainly euphausiids and mysids, e.g., *Thysanoessa spinifera, T. inermis, T. raschii, Acanthomysis* sp., *Neomysis* sp.). These species of fish form the bulk of the diet in summer, for both chicks and adults (Sealy 1975b; Simons 1980; Carter 1984; Sanger 1987). Concentrations of foraging birds are regularly noted in areas favoured by these prey species. During the nestling period in Barkley Sound birds aggregated at dawn at specific and traditional rich feeding areas (Carter 1984; Carter and Sealy 1990). Fish for chicks were obtained elsewhere, later in the day. Such feeding aggregations of a few hundred birds are found in many parts of the breeding range, but single, or pairs of, feeding birds are also regular. Unlike other alcids, Marbled Murrelets sometimes forage in freshwater lakes, up to 75 km inland (Kozlova 1957; Vyatkin 1981; Carter and Sealy 1986; Nechaev 1986). Hobson (1990) provided isotopic evidence that for some individuals freshwater prey may be very important for parts of the year.

In southern parts of the range, nesting areas are visited by some birds year-round, mostly around dawn (Carter and Erickson 1988). In California there appears to be some southerly postbreeding dispersal as far south as San Diego; influxes occasionally occur, presumably of birds from further north (Garrett and Dunn 1981). In British Columbia most birds vacate breeding areas on the outer coasts in late summer, and only arrive back in April (Sealy 1974, 1975a, 1975b; Carter 1984); many probably winter in inshore waters (Rodway et al.

1992). In Alaska, murrelets winter in large numbers in the Kodiak Island area (Forsell and Gould 1981) and in south-eastern Alaska (based on Christmas Bird Counts). However, only approximately 25% of the Prince William Sound summer population is present in winter months there (K. Kuletz, pers. commun.). Much of the Alaskan range remains ice-free in winter, whereas in the Sea of Okhotsk and northern Kamchatka many birds are forced south by the extensive winter ice cover.

6.4. Kittlitz's Murrelet

During the summer in southern Alaska, adults forage closer inshore (in bays and fjords), concentrating at glacier outfalls (Gabrielson and Lincoln 1959), and feed primarily on sand lance, postlarval capelin, herring, smelt, and Pacific sandfish (Sanger 1986). However, Kittlitz's Murrelet also eats euphausiids and gammarid amphipods, and these appear to be more important in its diet than they are in the diet of the Marbled Murrelet (Sanger 1986, 1987). Outside the breeding season, Kittlitz's Murrelets occur in flocks of up to 500 birds (Dement'ev and Gladkov 1951). Kozlova (1957) documented southerly movements in winter along the coasts of Kamchatka and the Kuril Islands. Although such movements have not been reported in the Bering Sea or eastern Pacific, some southerly movement from ice-bound areas is assumed. Distribution in winter is poorly known, although some birds remain in Alaskan waters. A few stragglers have been noted south to California.

7. Threats and conservation measures

7.1. Pigeon Guillemot

The introduction and spread of mammalian predators to many islands have probably greatly reduced breeding numbers of Pigeon Guillemots in some areas of the North Pacific, although actual data are scarce. Such effects have been documented for other alcid species in the North Pacific (Byrd et al. 1990; Springer et al. 1990).

Inshore gillnet fisheries probably cause significant local mortality of Pigeon Guillemots, but the only available data are from the central Californian gillnet fishery: between 1983 and 1986, 85 Pigeon Guillemots were reported in nets, but as for other species entangled the actual mortality was undoubtedly much higher, and the scale of this seabird mortality eventually led to the closure of the fishery in 1987 (Takekawa et al. 1990). On the Farallons, interspecific competition for nest cavities is probably causing progressive declines in the Pigeon Guillemot population, as numbers of Rhinoceros Auklets *Cerorhinca monocerata* and Tufted Puffins increase (Ainley and Boekelheide 1990).

King and Sanger (1979) ascribed a relatively high index of oil vulnerability for this species, and indeed for all guillemot and murrelet species. In California, breeding numbers declined on the Farallon Islands with the increase in oil-related shipping in the early 20th century, but improved oil pollution controls and protection of the islands as a National Wildlife Refuge have allowed the population to recover (Table 2). In southern Alaska over 600 oiled Pigeon Guillemots were found in the aftermath of the *Exxon Valdez* oil spill in late March 1989, but possibly only 10–30% of the birds affected were thought to have been retrieved (Piatt et al. 1990). Many of the Pigeon Guillemots affected would probably have been local breeders, so it is likely that the oil spill caused substantial declines in the breeding population. Similarly, in Shetland many breeding areas of Black Guillemots which were within the area affected by the *Esso Bernicia* oil spill in winter 1978–79 were not occupied for a number of years afterwards (Ewins and Tasker 1985). Oil spill contingency plans should incorporate maps of known concentrations of guillemots (for all times of year, but especially during the breeding season and postnuptial moult period), thereby increasing the chances of effective conservation of these populations.

7.2. Spectacled Guillemot

Reductions in forage fish stocks near Teuri Island may have contributed to the declines in breeding numbers of Spectacled Guillemots there, but the status of mammalian predators on the island is unknown. As with the previous species, the introduction of fur-bearing mammals to offshore islands in the North Pacific has constituted a major threat to breeding populations of Spectacled Guillemots along Russian coasts. Small numbers of the Spectacled Guillemot are shot in Russia, even though it is not a designated hunting species. Human disturbance at some Russian colonies is thought to be a relatively insignificant threat, but development of the oil industry in the Sea of Okhotsk clearly poses a more major threat. The species breeds within five large state reserves along the Russian coast, but no other conservation measures are known.

7.3. Marbled Murrelet

From southeastern Alaska to California and in the Sea of Okhotsk Marbled Murrelets appear to nest only in old-growth forests. The continued removal of large areas of this habitat poses a serious threat to the future of many Marbled Murrelet populations – undoubtedly many major declines have already occurred (Sealy and Carter 1984; Carter and Erickson 1988; Marshall 1988; Paton and Ralph 1988). Further, in the south of the breeding range, some of the oldest stands of suitable nesting trees are within state parks and other protected areas. Although this ensures the conservation of the trees, corvid populations may well be elevated because of the often large numbers of tourists, thereby increasing the likelihood of predation of murrelet nests (Singer et al., in press).

Significant mortality has been reported in nearshore commercial gillnet fisheries in Alaska and British Columbia (Carter and Sealy 1984; Sealy and Carter 1984), and in California (Carter and Erickson 1988). Mariculture operations may kill murrelets in nets or cages, as well as affect prey species locally (Rodway et al. 1992). Like guillemots, inshore murrelets are regarded as particularly vulnerable to oil pollution (King and Sanger 1979). Relatively small numbers have been recovered after oil spills, but small alcids are greatly underestimated in such incidents. In California and British Columbia such mortality was probably significant to local populations (Carter and Erickson 1988; Page et al. 1990). Mortality from the *Exxon Valdez* oil spill has been the worst noted to date and affected the core of the world population of this species (Piatt et al. 1990; Mendenhall, in press).

7.4. Kittlitz's Murrelet

In the absence of specific data on population changes or mortality causes, it is difficult to assess potential threats to Kittlitz's Murrelet populations. However, the threats at sea are probably the same as those for Marbled Murrelets, with oil pollution currently the most serious concern (King and Sanger 1979; Piatt et al. 1990; V. Mendenhall, pers. commun.).

8. Conclusions

The need for specialized census techniques and the relatively small number of long-term ecological studies and surveys available preclude definitive conclusions about the status and ecology of these inshore alcids in the North Pacific. They occupy inshore feeding niches and are widely dispersed along rocky coastlines but never occur in such large concentrations as many other North Pacific seabirds. Guillemots usually breed in small colonies, reflecting the clumped distribution of rocky cavities, whereas murrelets may nest more solitarily. The young of both genera are semi-precocial, and are fed mostly with fish. Young guillemots leave the nest at near adult weight, whereas young murrelets probably do so at about two-thirds of adult weight. Guillemots breed within a few metres of the sea and usually forage within 7 km of the colony, and can often raise two young. Murrelets regularly breed further inland, frequently up to 30 km from the sea and lay only single-egg clutches. Presumably the single-egg clutch is better suited than a two-egg clutch to this strategy, because a pair of adult murrelets would be unable to provide sufficient food at nests so far from foraging areas to raise two chicks, particularly when most provisioning has to be done in the hours of darkness (thereby reducing the risk of predation on adults and nests). Limited movements southwards, or to more sheltered inshore waters, occur in winter, but these species are relatively sedentary compared to other Pacific seabirds. Food supply and the availability of suitable nest sites are the key determinants of breeding distributions.

Loss of breeding habitat via introduction of mammalian ground predators or logging of old-growth forests (Marbled Murrelet only) has almost certainly caused population declines. Similarly, oil pollution, some fisheries, and oceanographic fluctuations have caused local mortality. These four species of inshore alcid are endemic to the North Pacific (with the exception of small populations of Pigeon Guillemots and Kittlitz's Murrelets along the southern coasts of the Chukchi Sea), and so such threats must be evaluated in relation to the survival of the various populations. However, despite their high vulnerability to oiling, these species have widespread overall distributions, which may render them less susceptible to major losses than more aggregated seabird species. Clearly, the exception is those Marbled Murrelet populations that depend upon mature stands of trees for suitable nesting habitat; continued removal of this habitat will reduce population sizes even further.

9. Recommendations

(1) Refine and apply census techniques for guillemots and murrelets. Investigate nest-site attendance patterns for all species in regions not previously studied.

(2) Conduct systematic surveys of guillemots (prebreeding) and murrelets (summer) along west Pacific coasts to assess the magnitude of breeding populations.

(3) Survey fall moult concentrations and "hot spots" of flightless birds.

(4) Research the ecology of Kittlitz's Murrelet and Spectacled Guillemot.

(5) Continue with investigations on Marbled Murrelet distribution and ecology in the eastern Pacific. Develop means to measure life-history parameters to evaluate impact of mortalities and loss of nesting habitat.

(6) Design and establish monitoring programs for all species in representative areas.

(7) Review progress on North Pacific inshore alcid research, survey work, and conservation at regular intervals. The reviews should integrate work on other groups of seabirds and involve cooperation amongst all countries bordering the North Pacific.

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