Status, ecology, and conservation of shags and cormorants of the temperate North Pacific

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Abstract

Excluding species confined to continental and freshwater habitats, there are six common species of shags and cormorants in north temperate coastal regions. Temminck's *Phalacrocorax capillatus* and Great *P. carbo* cormorants are found primarily in Asia, but only Temminck's Cormorant is exclusively marine. Double-crested *P. auritus* and Brandt's *P. penicillatus* cormorants are confined to the New World. Pacific coastal populations of Double-crested Cormorants extend from the Mexican border north to Bristol Bay, Alaska, and have their greatest abundances in the central part of the range. Brandt's Cormorants have the most circumscribed distribution of the three and are most abundant along the central California coast. Red-faced *P. urile* and Pelagic *P. pelagicus* shags bridge the gap between the species discussed above and breed throughout the northern North Pacific basin and Beringia. The ecology and behaviour of shags and cormorants are different: shags generally prefer to nest on steep cliffs and are opportunistic feeders on nonschooling prey over shallow rocky bottoms; cormorants usually nest on flat, level areas on offshore rocks and islets and prefer feeding on a broad range of demersal schooling fish in neritic waters. Both species are found close to shore and are sensitive to colony disturbances. For reasons still unknown, shifts in colony sites are common and complicate accurate assessment of numbers.

Résumé

Sans tenir compte des espèces confinées dans les habitats continentaux et dulçaquicoles, on compte six espèces courantes de cormorans dans les zones tempérées côtières du Pacifique Nord. Le Cormoran de Temminck *Phalacrocorax capillatus* et le Grand cormoran *P. carbo* se retrouvent surtout en Asie, le premier étant exclusivement marin. Le Cormoran à aigrettes *P. auritus* et le Cormoran de Brandt *P. penicillatus* sont confinés dans les Amériques. Les populations de Cormorans à aigrettes fréquentent les côtes du Pacifique, de la frontière du Mexique à la baie Bristol, en Alaska. On les retrouve en plus grand nombre au centre de cette grande région. Le Cormoran de Brandt est l'espèce la moins dispersée, son habitat privilégié étant la région côtière du centre de la Californie. Le Cormoran à face rouge *P. urile* et le Cormoran pélagique *P. pelagicus* comblent les vides entre les espèces susmentionnées et se reproduisent dans tout le bassin nord du Pacifique Nord et dans toute la Béringie. Les diverses familles de cormorans présentent une écologie et un comportement différents. En règle générale, les Leucocarboninés (qui comptent notamment les Cormorans à face rouge et les Cormorans pélagiques) préfèrent nicher dans les falaises abruptes et sont des prédateurs opportunistes, se nourrissant des proies isolées qu'ils trouvent sur les fonds rocheux peu profonds. Les Phalacrocarinés, eux, préfèrent nicher sur les rochers et les îlots plats du large et se nourrir de poissons démersaux qui se rassemblent en bancs dans les zones néritiques. Tous les cormorans se tiennent près du rivage et sont vulnérables aux perturbations de leurs colonies. Pour des raisons encore inconnues, il arrive souvent que les cormorans changent de colonie, ce qui complique l'exercice de dénombrement.

1. Introduction

Cormorants and shags (Phalacrocoracidae) are the most successful family of pelecaniform birds, comprising at least 35 species worldwide. Birds of this family are generally in coastal and neritic waters, and are common dwellers in marine and freshwater littoral habitats. They are restricted from more oceanic habitats chiefly because of their unique wettable plumage, a feature well-suited for underwater pursuit of shallow demersal fish, but one that requires perching sites for drying and thermoregulation. Consequently, members of this group are found along most of the productive coastlines worldwide (except in polar regions) and often far inland following major freshwater drainages.

Phalacrocoracidae have been considered to be a homogeneous group. Recent systematic study revealed instead that there are two well-defined clades in the family: cormorants and shags (Siegel-Causey 1988). Cormorants can be generalized as heavy-bodied, deep-feeding neritic foragers, flat- and tree-nesting pelecaniforms with indifferent or laboured flight. By contrast, shags characteristically are compact, pelagic foragers, flat- and cliff-nesting birds with fair flight abilities. Excluding species confined to continental and freshwater habitats, there are six common species of shags and cormorants in the temperate North Pacific: Temminck's *Phalacrocorax capillatus*, Great *P. carbo*, Double-crested *P. auritus*, and Brandt's *P. penicillatus* cormorants; Red-faced *P. urile* and Pelagic *P. pelagicus* shags. In addition, there are two other little-known species identified from this region. Pallas's Cormorant *Compsohalieus perspicillatus*, now extinct, was known to breed on the Commander Islands (Stejneger 1884), which are the far-western component of the Aleutian Islands. Finally, the existence of a small, recently described shag closely related to Pelagic and Red-faced shags (Kenyon's Shag *Stictocarbo kenyoni*) was discovered on Amchitka Island (Siegel-Causey 1991; Siegel-Causey et al. 1991).

Table 1
Estimates of breeding numbers of six cormorants and shags in the temperate North Pacific

Region	Brandt's Cormorant	Double-crested Cormorant[n]	Pelagic Shag	Red-faced Shag	Temminck's Cormorant	Great Cormorant[n]
California[a]	65 (00)	2 (00)	16 (00)			
Oregon[b]	16 (00)	1 700	7 (00)			
Washington[c]	600	4 (00)	5 (00)			
British Columbia[d]	152	4 (00)	8 400			
Southeast[e]		100	1 100			
Kenai[e]		3 (00)	14 (00)	20 (00)		
Aleutian Is.[e]		1 200	5 (00)	21 (00)		
Pribilof Is.[e]			[illegible]	8 (00)		
Bristol Bay[e]		2 (00)	16 (00)	3 500		
NE Bering[e]			6 (00)			
Chukchi Sea[e,f]			3 (00)			
Anadyr Gulf[g]			10 (00)			
Karaginskii[h]			40 (00)	30 (00)		
Kamchatkan[i]			56 (00)	15 (00)		
Okhotsk Sea[j]			[illegible] 2 (00)	[illegible] 5 (00)	[illegible] 5 (00)	[illegible] 500
Kuril Is.[k]			200 (00)	50 (00)	8 (00)	
Primorye[l]			1 (00)	500	3 (00)	[illegible] 100
Japan Sea[m]			1 (00)	[illegible] 300	1 (00)	[illegible] 200
Total	82 (00)	18 (00)	400 (00)	155 (00)	[illegible] (00)	11 (00)

[a] Data from Sowls et al. (1980).
[b] Data from Varoujean (1979).
[c] Data from Speich and Wahl (1989).
[d] Data from Vermeer (1989).
[e] Data from Sowls et al. (1978).
[f] Data from Kondratiev (1986). Colonies on Wrangel, Gerald (Herald), Diomede islands and all smaller offshore islands are included.
[g] Data from Kischinskii (1980), Vyatkin (1986). This region is defined as the coastline between Bering Strait and Khatyr.
[h] Data from Kischinskii (1980), Vyatkin (1986), and Marakov (1975). This region is defined as the area between Khatyr and the Kamchatka peninsula including Commander, Vyatarskii, and all offshore islands.
[i] Data from Vyatkin (1986). This region is the Pacific coast of Kamchatka and all offshore islands.
[j] Data from V.P. Shuntov (unpubl. data). This region includes the west coast of Kamchatka, Sakhalin Island, and all offshore islands.
[k] Data from V.A. Nechaev (unpubl. data).
[l] Data from Shibaev (1987). This region includes all of Soviet territory in the Sea of Japan.
[m] Data from Fujimaki (1986), Lebedev (1986), and Hashimoto (1987). This region includes the Japan Islands and all offshore islands in the Sea of Japan.
[n] Estimates are for coastal populations only in the region. Freshwater populations and extralimital colonies were excluded.

In the species accounts that follow, we will stress detail from Asian species or populations because little information has been published previously for them in English. Orthography of non-English place names uses standard transliteration practices. Table 1 gives the abundance estimates for each cormorant species dealt with.

2. Species accounts

2.1. Great Cormorant

The distribution of this species is chiefly continental throughout Europe and Asia. Marine populations in the North Pacific basin are small and isolated and restricted entirely to the northern Sea of Japan, in the Primorye and Japan (Fig. 1). This cormorant is a common breeding species of the mainland, however, and there are several colonies located on river inlets throughout the Primorye, e.g., Ussuri and Amur rivers. The main colonies are located on Furugelm and Butakov islands, Peter the Great Bay in the far northeastern Sea of Japan. This species was first observed here in 1979 (Shibaev 1987); about 10 pairs nested on one of the cliffs on Butakov Islet. In 1982 this group of Great Cormorants moved to nearby Furugelm Island, where a new colony of 15 nests was established. Both colony sites were adjacent to nesting Temminck's Cormorants. The colony doubled in size each year (33 pairs in 1983, 70 in 1984; Shibaev 1987). Furugelm Island is within the limits of the Far East State Marine Reserve and is a protected site. Several coastal colonies exist in Japan; the largest is at Unoyama, Ise Bay, central Honshu. There are undoubtedly other colonies to the south, but information is lacking.

2.2. Temminck's Cormorant

2.2.1. *Breeding distribution*

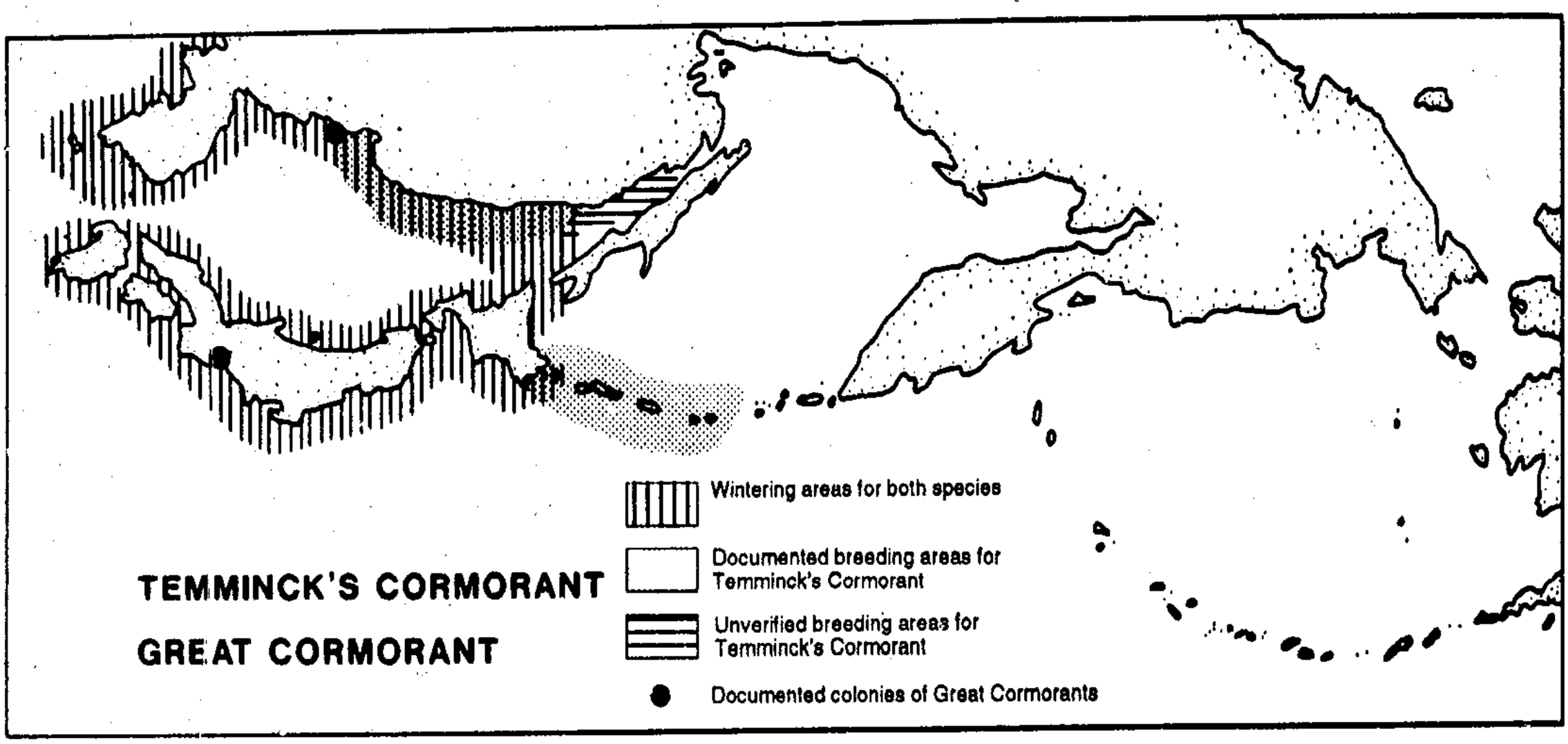
This species nests in Japan, along coastlines in the Sea of Japan, Primorye, Sea of Okhotsk, and Kuril Islands. The highest numbers in Russia are found in the Tartar Strait, Sakhalin Island, and southern Kurils (Fig. 1). In Japan, nesting colonies exist on cliffs and offshore islets in temperate and subarctic waters (Hasegawa 1984). Numbers decrease abruptly to the south, perhaps in direct response to higher sea surface temperatures. The most southern colony (20 nests) is on Okinoshima Island, northern Kyushu.

2.2.2. *Abundance*

On mainland Russia there are about 8000 breeding Temminck's Cormorants. Approximately 3000 nest on islands (15 colonies) in Peter the Great Bay; the largest colony is on Furugelm Island where 726 pairs were counted in 1989. The other colonies (38–40 breeding sites) located on the coastline of the Primorye are small, generally no more than 10–20 pairs (Elsukov 1984; Shibaev 1987).

The most recent census estimated about 7000 Temminck's Cormorants in the Kuril Islands with colonies noted from Kunashir Island north to Simushir Island (Velizhanin 1978). Only a single colony on Sakhalin Island has been found; in 1980, 100–120 pairs were seen nesting on Cape Aniva (Nechaev 1986). A small colony has persisted on Moneron Island, but the numbers have fluctuated over the years from 20–30 pairs in 1948 to 5–6 pairs in 1973 (Gisenko 1955; Nechaev 1975). The total number of Temminck's Cormorants

Figure 1
Distribution of Temminck's and Great cormorants. See text for discussion of other possible breeding sites for both species.



nesting in Russia is estimated to be no more than 16 000 individuals. About 1000 birds are known to breed in Japan. Little is known about abundances further south or west.

2.2.3. Population trends

The number of Temminck's Cormorants has varied in Peter the Great Bay for the last 50 years. On Furugelm Island the colony was completely annihilated by arctic foxes *Alopex lagopus* that had been introduced in 1929–30. The cormorants returned later and by the 1950s their numbers increased, but in 1967, most of them died for unknown reasons (Labzyuk 1975). From 1977, the number of individuals increased and by 1985 the colony had increased 10-fold. This probably was due to favourable conditions created in the late 1970s with the creation of the Peter the Great Bay Marine State Reserve in 1978 and the occurrence of abundant food, Pacific sardine *Sardinops sagax* (Shibaev 1987).

2.2.4. Reproduction

First successful breeding occurs at three years of age. Nonbreeding birds are present in colonies during the entire breeding period, but never exceed 20% of the total numbers. In the Primorye, egg-laying begins in late May and is at its peak by early June. Incubation lasts about 30 days. The fledging period is approximately 40 days, but this depends upon food supply and weather.

2.2.5. Nesting habitat

Temminck's Cormorants are strictly colonial and rarely breed as isolated pairs. Most colonies are small (20–30 nests), although larger ones do occur; for example, the colony on Furugelm Island in 1989 comprised 1500 nesting birds. Nest sites are broad ledges and shelves on open cliff faces, and often in mixed colonies with Common Murres *Uria aalge* and Black-tailed Gulls *Larus crassirostris*.

2.2.6. Wintering

Small numbers of this species winter in southern far-eastern Russia. Based on banding data, young birds forage along the Primorye after leaving colonies in Peter the Great Bay and remain until late October, some until December. Most of the first-year Temminck's Cormorants from this region migrate southwest, however, and winter in the Korean Straits, as do most adults coming from all along the far-eastern coast.

Temminck's Cormorants from Hokkaido colonies disperse southwards along the coasts of Japan. Birds from the eastern colonies primarily move along the Pacific coast and those from the western colonies move along the coast of the Sea of Japan.

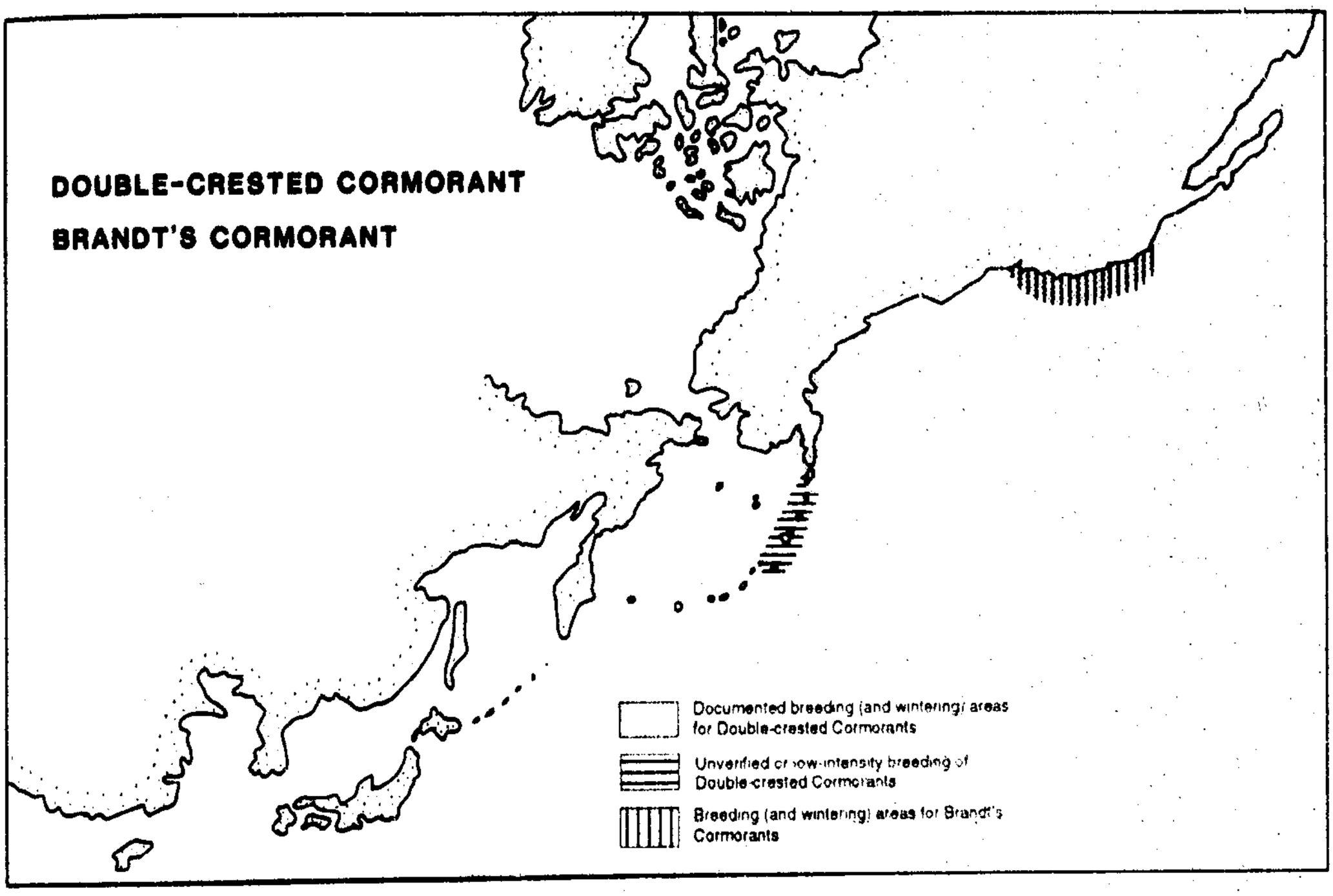
2.2.7. Diet

Temminck's Cormorants feed either separately or in small flocks in coastal and estuarine waters, often in association with large flocks of gulls. Food samples regurgitated by chicks in colonies from Peter the Great Bay contained small bottom-dwelling fish (e.g., Cottidae, Stichaeidae, Pholidae, Clupeidae, Gadidae, Hemirhamphidae).

2.2.8. Mortality

The main predators of Temminck's Cormorants are Black-tailed Gulls, Carrion Crow *Corvus corone*, and Jungle Crow *C. macrorhynchos*. The majority of depredations were on eggs and small chicks and occurred when parents were disturbed from the nests. A few cases are known of attacks by Steller's Sea Eagle *Haliaeetus albicilla* on incubating adults, and there is a report (Labzyuk 1975) of some nests having been destroyed by bears *Ursus tibetanus*. The main threat to this species, however, is human disturbance. On Sakhalin, Moneron, and southern Kuril Islands, crews of fishing boats over many years have systematically destroyed most colonies through egging and target shooting (Gisenko 1955; Benkovskii 1968).

Figure 2
Distributions of Double-crested and Brandt's cormorants



2.3. Brandt's Cormorant

2.3.1. Breeding distribution and abundance

Brandt's Cormorants breed from Baja California north, possibly to the Gulf of Alaska (Fig. 2). Small numbers of Brandt's Cormorants (<50 birds) have been noted from Alaska, but their population status is still unknown. In 1989, 56 nests were found at two colonies west and north of Barkley Sound, Vancouver Island (K. Vermeer and K.H. Morgan, unpubl. data), and a small number of cormorants (20–40 pairs) have been found nesting on Sartine Island, at the northwestern tip of Vancouver Island (Vermeer et al. 1976). In Washington, Brandt's Cormorants are more numerous (about 300 pairs), with the greatest nesting on cliffs at Cape Disappointment and Willoughby Island (Speich and Wahl 1989). Abundance increases further south, with about 16 000 birds nesting along the Oregon coast (Varoujean 1979).

The greatest numbers are found along the California coast and account for the majority of the breeding population. The largest single colony is located on Southeast Farallon Island, where about 40% of the entire species nest (Sowls et al. 1978; Ainley and Boekelheide 1990).

2.3.2. Population trends

The population of Brandt's Cormorants has varied in California since they were first studied around the turn of the century. Colony sizes have been decreasing since then, but exact causes are unknown. It is clear that early human disturbance by exploitation and harassment and later by pesticide effects was the main reason for this decline (Sowls et al. 1978; Hunt et al. 1979; Ainley and Boekelheide 1990). Colony sizes are largely associated with oceanographic conditions, and changes in the number of breeding adults often follow changes in local upwelling or large-scale events like El Niño.

2.3.3. Reproduction

In the southern part of the range (southern California), adults are present all year round, but clutch initiation occurs by the middle of March. Mass hatching occurs in early May, and most chicks have fledged by the end of August (Sowls et al. 1980). Hatching success varies widely among sites, but the average rate of about 45% observed in the Farallon Islands is representative. Fledging success, as in most cormorants, is high (75%) (Ainley and Boekelheide 1990). In Washington, breeding adults arrive by the end of April and mass laying begins by the first week of May. The majority of chicks hatch in the first week of July and most fledge by late September (Speich and Wahl 1989). Full details of reproduction on Southeast Farallon Island are given by Ainley and Boekelheide (1990).

2.3.4. Nesting habitat

Brandt's Cormorants are entirely colonial and rarely are found in small nesting groups. This species is typical of marine cormorants, in that broad level areas of offshore islands are preferred for nesting, but gently sloping bluffs and cliff ledges are often used. Furthermore, Brandt's Cormorants prefer to feed in upwelling regions and choose nest sites that are adjacent to such water. Ainley and Boekelheide (1990) discuss nest site selection by this species on Southeast Farallon Island.

2.3.5. *Diet*

The most detailed sources for the diet of Brandt's Cormorants is Ainley et al. (1981) and Ainley and Boekelheide (1990); the most prevalent food items in the diet were *Engraulis*, *Sebastes*, *Oxyjulis*, and *Chromis*.

2.4. Double-crested Cormorant

2.4.1. *Breeding distribution*

Double-crested Cormorants are found from Labrador to the Caribbean, the midwestern U.S. and Canada, west coast of North America (including Mexico and Canada), and southeastern Alaska. The Pacific coastal populations of Double-crested Cormorants are distinguished by white nuptial plumes on the sides of the head and are considered a distinct subspecies (i.e., *P. auritus albociliatus*). This species nests in colonies ranging from a few nests to hundreds of nests; most aggregations are less than 200 pairs (Ainley and Boekelheide 1990). Moderate-sized colonies (less than 200 pairs) occur along the California, Oregon, and Washington shorelines; largest colonies are located chiefly on protected offshore rocks and islands (Fig. 2).

Double-crested Cormorants are rarely encountered north of the Strait of Georgia in southwestern British Columbia and do not nest in any significant numbers until the northern Gulf of Alaska (Sowls et al. 1978; Vermeer 1989). Small aggregations have been found north into Bristol Bay and west along the Alaska Peninsula. This species does not nest further west into the Aleutians than Unalaska Island (Sowls et al. 1978), although transients may range throughout the archipelago (Siegel-Causey et al. 1991).

2.4.2. *Abundance and population trends*

Double-crested Cormorants are the least abundant of all coastal breeding cormorants and shags in the temperate North Pacific (Table 1). In the southern part of the range, populations have decreased since the beginning of the century, where on the Farallons they were once the second most abundant cormorant (Ainley and Lewis 1974). Commercial egg collectors and other exploitation may have started the decline that was accelerated by the disappearance of the Pacific sardine from the California Current. Numbers appear to be increasing in central and southern California (Sowls et al. 1980), but they may actually only reflect improved census methodology. In Washington and Oregon, coastal breeding Double-crested Cormorants also seem to be increasing in numbers, but colony shifts and desertions are commonplace (Speich and Wahl 1989). On the British Columbia coast, Double-crested Cormorants breed only in the Strait of Georgia, where the population increased from 203 nesting pairs in 1960 to 1981 pairs in 1987 (Vermeer et al. 1989).

2.4.3. *Reproduction*

In the southern part of the range, adults are present year-round, but clutch initiation does not begin until about the middle of April. Mass hatching begins in late May and most birds fledge by the middle of August. In Washington, adults arrive in early April, mass laying begins in early May, and chicks are fledged by late September. Nesting chronology is about two to three weeks later in the northern part of the range. Full details on breeding are given in Ainley and Boekelheide (1990).

2.4.4. *Nesting habitat*

Double-crested Cormorants prefer level sites in protected habitats and often will select broad ledges on the shoulders and upper portions of cliff faces (Siegel-Causey 1988; Vermeer et al. 1989). Where conditions are dry enough, nests are reused year after year and often exceed 2 m in height. Double-crested Cormorants also nest in trees in both marine and freshwater habitats (Vermeer et al. 1989).

2.4.5. *Diet*

Coastal breeding Double-crested Cormorants have rather narrow food preferences and seem to specialize on small demersal fish schooling near the bottom (Ainley et al. 1981). Atherinids, embiotocids, engraulids, and sciaenids were among the most common foods found in the southern populations. Food samples taken from Alaskan birds showed essentially the same pattern, but with the addition of decapods (*Crangon* spp.) (Sanger 1986).

2.5. Pelagic Shag

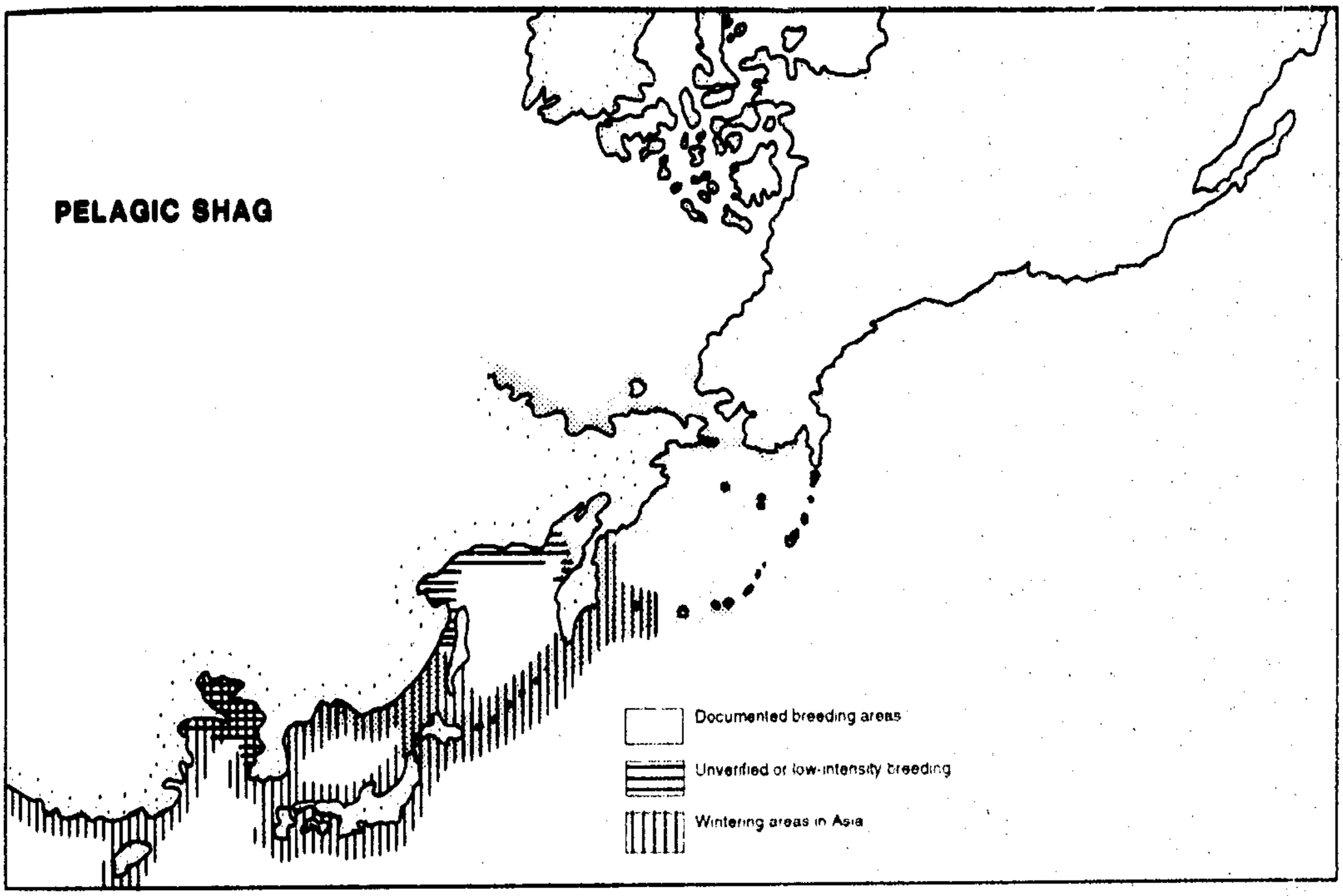
2.5.1. *Breeding distribution (western shores)*

This species is the most numerous and broadly distributed of all cormorants in the temperate North Pacific (Table 1, Fig. 3). In Russia, it nests along the shores of the Chukotsk, Bering, Okhotsk, and Japan seas, from Chaun Inlet and Wrangel Island in the north to Peter the Great Bay in the south. Until recently, the northernmost nesting of this species occurred at Cape Schmidt (Portenko 1972). In 1984, however, nesting pairs of Pelagic Shags were noted in Chaun Inlet (Kondratiev 1986), extending considerably the northern limit of this species' breeding range. Further to the east, there are small colonies (<10 pairs) along the Chukchi Sea coast.

Pelagic Shags nest everywhere along the east and southeastern shores of the Chukotsk peninsula from Cape Dezhneva to Krest Gulf and are common nesting birds far to the west from Krest Gulf to the Anadyr Lagoon (Uspenskii et al. 1963; Velizhanin 1965; Portenko 1972; Golovkin and Flint 1975; Krechmar et al. 1978; Kondratiev 1986). Pelagic Shags nest on the shores of the Koryak uplands and are found on all suitable cliffs which abound on the coast (Kischinskii 1980). The majority of the nesting colonies are small from here south to the tip of Kamchatka, comprising less than 20 pairs each. Large colonies are absent or rare on shores of the gulfs of Kronotskii, Kamchatskii, and Karaginskii (Lobkov 1986; Vyatkin 1986) and the largest colonies are found on Karaginskii, Verkhotyrova, and the Commander Islands (Vyatkin 1975, 1986; Gerasimov 1986).

The western part of the Sea of Okhotsk from Okhotsk City to Sakhalin Gulf is one of the least studied regions of the Far East. Pelagic Shags have been noted on Nansikan Island, Iona Island (Nechaev and Timofeeva 1973; Velizhanin 1978), and Shantarskii Islands (Yakhontov 1977). There are several small colonies on the eastern side of Sakhalin Island: Cape Terpen, the eastern bank of the Aniv peninsula, and the northeastern shores of the Shmidt peninsula (Gisenko 1955; Nechaev 1986). They have also been observed in the south from the north of the Amur River to Peter the Great Bay, but, as a rule, in very small numbers (Labzyuk 1975; Elsukov 1984).

Figure 3
Distribution of Pelagic Shags. Wintering areas in North America are similar to the breeding range.



2.5.2. Breeding distribution (eastern shores)

The northernmost North American colonies apparently are those on Cape Lisburne (68°50′N), near Point Hope, Alaska. Scattered colony sites occur throughout the Bering Strait regions and Norton Sound, but numbers are relatively low. Pelagic Shags breed in a single small colony on St. Lawrence Island, and in several colony sites on St. Matthew and Hall islands (Sowls et al. 1978). This species is found nesting only in small groups south along the eastern Bering Sea coastline until the Cape Peirce–Walrus Islands area, where high cliffs and numerous offshore rocks and islets provide safe nesting. The abundance of Pelagic Shags here equals that of the entire Gulf of Alaska ("Kenai" region in Table 1) population. Small colonies of Pelagic Shags are found throughout the eastern Aleutians and southeastern Alaska, but never in colonies as large as found in Bristol Bay.

British Columbia, Washington, and Oregon colonies are small and dispersed, and are located on offshore rocks, islands, and sometimes human-made structures. The largest single colony (537 nests in 1987) in this region is on Mandarte Island in the Strait of Georgia, British Columbia (Vermeer et al. 1989). Pelagic Shags nest along the California coastline, about half of the population on offshore rocks and islets and half on coastal cliffs. South of San Francisco, this species occurs in decreasing numbers and more dispersed colonies until the Channel Islands, which are at the southern limit of nesting (about 34°N) (Sowls et al. 1980).

2.5.3. Wintering

During winter, Pelagic Shags are found over a vast region, distributed along the shores of the Asiatic continent from the eastern shores of Kamchatka to Hong Kong. Within these limits they are found everywhere there is no shelf ice. Pelagic Shags winter on the southern shores of Kamchatka and along its eastern shores in limited numbers, but seldom are found to the north (Lobkov 1986).

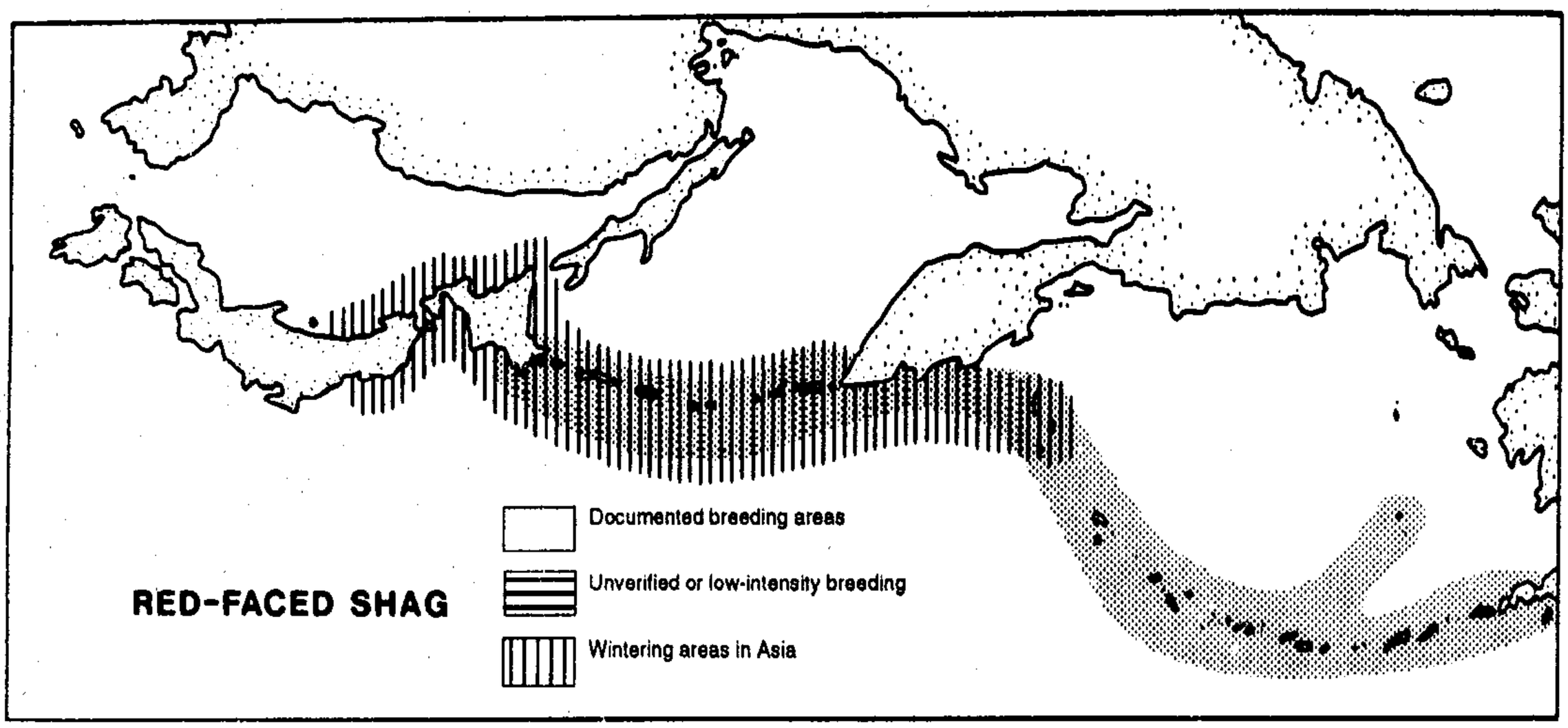
The Kuril Islands serve as wintering grounds for the majority of the eastern population, and Pelagic Shags make up 6% of the wintering seabirds (Shuntov 1972). They are encountered along the entire island chain; seasonal movements are connected apparently with the presence of ice and changing food stocks (Gisenko 1955).

2.5.4. Abundance

Throughout its range the numbers of Pelagic Shags are fairly stable. In a great part of the range, Pelagic Shags prefer to nest in medium-sized colonies from several pairs to several hundred birds. The largest groups aggregate on separate islands or archipelagos. In regions close to the northern and southern limits of the range, the numbers are much smaller. Thus, along the entire coastline of the Chukchi Sea, where because of climate and less productive waters seabird colonies are small and dispersed, Pelagic Shags nest infrequently and in small groups. On the eastern shores of the Chukotsk peninsula, the number of Pelagic Shags is somewhat greater. Colonies do not exceed more than 100 birds and usually contain around 20–30 birds.

The number of nesting birds on the greater part of the northern shore of the Okhotsk Sea is unknown. Estimates give the distribution of Pelagic Shags as about 1 pair/km of shoreline (Kischinskii 1968).

Figure 4
Distribution of Red-faced Shags



2.5.5. *Reproduction*

Nests are situated on ledges or cornices of precipitous rocks generally inaccessible to terrestrial predators. Nests in the Strait of Georgia, British Columbia, are constructed primarily from grass, kelp, and eelgrass (Vermeer et al. 1989).

Basic information on nest and egg dimensions and variation in clutch sizes is given in Palmer (1962), Portenko (1972), and Lobkov (1986). Clutch initiation in the north of the Chukotsk peninsula proceeds from the beginning of June (Portenko 1972). In the southern Primorye (Peter the Great Bay), egg-laying begins in the first part of May.

The period of incubation is approximately 25–26 days; hatching success is about 50%, but varies widely among sites (Robertson 1974; Ainley and Boekelheide 1990). Chicks remain in the nest for about two months and fledging success is high (75%). On the northern Chukotsk peninsula, fledging proceeds from the end of August to the beginning of October.

2.5.6. *Diet*

Small fish predominate in food samples collected in summer from Wrangel Island (Portenko 1972). A similar pattern was observed in Pelagic Shags on the west coast. At all sites, from British Columbia to the Gulf of California, this species preferred nonschooling fish of rocky reefs and bottoms (Ainley et al. 1981), and fed primarily in inshore and neritic waters. Diet diversities were large at all localities and suggested that Pelagic Shags select a particular habitat to feed in, rather than specializing in a small number of prey.

2.6. Red-faced Shag

2.6.1. *Breeding distribution*

Red-faced Shags breed in a narrow latitudinally compressed band from the northern Sea of Japan, along the Kuril and Aleutian island chain, and far east into the southeastern Gulf of Alaska (Fig. 4). In Russia, this species nests on the Commander Islands: Bering, Mednii, Ari Kamen' (Marakov 1975), most of the Kuril Islands (Velizhanin 1977), and in the southern part of the Kamchatka peninsula (on the eastern shores from the mouth of the Zhupanova River to Cape Lopatka and on the western shores to Cape Sibuchii) (Lobkov 1986; Vyatkin 1986). Colonies on the shores of Kamchatka are the only ones known on the Asian continent.

The range of Red-faced Shags extends throughout the Aleutian Islands and Pribilof Islands; colonies are generally small and dispersed (Sowls et al. 1978). There are a large number of colony sites on the Alaska mainland centred around the Gulf of Alaska, but none is large. The furthest east this species breeds is apparently on Middleton Island (146°30'W).

2.6.2. *Abundance*

The abundance of Red-faced Shags on the Commander Islands was estimated in 1972 at approximately 24 000 individuals, significantly more than were counted two decades earlier (Marakov 1975). About the same number of birds (20 000–30 000) were noted in 1963 on the Kurils (Velizhanin 1977). On Kamchatka, more than 11 000 birds were noted in 1983.

2.6.3. *Population trends*

The past 50–60 years have seen significant broadening of the nesting area of Red-faced Shags. On the Commander Islands, expansion of this species has occurred quickly: since 1953, the number of Red-faced Shags has increased fivefold. At the turn of the century, Red-faced Shags were known only from Mednii Island, in 1958 they were noted on Bering Island, and by 1969 they populated all suitable sites on these islands (Marakov 1975).

Apparently this growth period occurred also in the Kuril Islands. Early in this century this species was noted only in small numbers here, but at present they represent about one-third the total number of shags and cormorants (Gizenko 1955; Velizhanin 1977). This increase began somewhat later in Kamchatka: from 1980 to 1983, the number of Red-faced Shags nesting in the southern part of the peninsula trebled from approximately 3000–4000 birds to about 11 000 (Vyatkin

1986). Pelagic Shags which nested here earlier in large numbers have in several places been fully replaced by Red-faced Shags.

Numbers are small in Japan (Hasegawa 1984). Small colonies are known from eastern Hokkaido, but their status and numbers are unknown.

2.6.4. *Reproduction*

Nesting is on projections of high cliffs. On Kamchatka, Red-faced Shags are found on islands and rocks as well as on coastal cliffs. On the Commander Islands in colonies of Red-faced Shags and Pelagic Shags, Red-faced Shags occupy the higher parts of the cliffs and force out Pelagic Shags. As a result, Pelagic Shag colonies often shift to new sites (Marakov 1975).

Nest construction on the Commander Islands begins in March, first eggs may appear the second half of April, but most clutches are completed by the beginning of June. On the Kuril Islands, egg-laying is initiated by late May. As in other shags, the period of egg-laying is quite protracted; on Mednii Island, the difference in clutch initiation is about 20–30 days (Marakov 1975). Chicks leave the nests by the last half of July.

The nest is cone-shaped with a broad base and is utilized several years in a row. The nests are constructed of dry stems of grass and small tundra plants (Marakov 1975) in the Commander Islands; in the Kuril Islands nests were constructed from seaweeds and stems of *Elymus* spp. (Velizhanin 1977).

2.6.5. *Wintering*

Few leave the limits of the nesting area; most remain on the Commander Islands, southern Kurils, and in the northern part of the Japan Islands (Iogansen 1934; Marakov 1975; Velizhanin 1977). The most southerly distribution of Red-faced Shags in winter was noted north of Honshu Island and in northeast China: on Lyaodunskii peninsula and in Manchuria (Cheng 1976).

On the Commander Islands more than half of the Red-faced and Pelagic shags move to the south with the approach of fall storms; the others winter around the sites where they were observed nesting (Marakov 1972).

2.6.6. *Diet*

Red-faced Shags on the Pribilofs feed within 20 km of land (Schneider and Hunt 1984). This species showed no diet specialization and over 50 types of food were recorded, although benthic fish (Cottidae and other scorpaeniform fish) and crustaceans predominated. Diets and feeding behaviour of birds on the Commander Islands were similar.

3. Conclusions

Several aspects of the history of cormorants and shags make them particularly vulnerable to disturbance. As with other colonial species, breeding in a colony has disadvantages. The close proximity of neighbours in a colony can help to intensify aggression among breeding pairs. Because the young are nidicolous, all nest defence is by adults until the chicks fledge. The appearance of natural predators near or within a colony often causes the sudden mass departure of adults from nests; if the departure is violent enough, eggs and chicks are displaced out of the nest and exposed to predation or weather. Gulls and crows move into the colony area as soon as the adults leave and take eggs and chicks. Mass departures seem more easily induced at the beginning of the reproductive season than at other times, but can occur at any time, especially if the colony is subject to repeated disturbance. At critical times during the breeding season (i.e., late egg incubation, first weeks of hatchlings), these desertions can destroy an entire colony's reproductive output (Kharitonov and Siegel-Causey 1987). At other times, the effects are localized in the area where the predator hunted.

By contrast, the effects of passive human disturbance seem more intensive and pervasive than those of natural predators (Ellison and Cleary 1978). As mentioned above, the birds generally eat bottom-feeding fish of no economic importance. Misinformation, the ubiquity of large feeding aggregations, and declining fishing yields have led to intense persecution by humans, with most of the effort focused on breeding colonies. The direct effects of shooting adults and egging are obvious and devastating. The passive effects, however, are equally effective in reducing numbers.

More birds are likely to leave when humans enter a colony and adults remain away from the colony longer than they do when they are frightened by a natural terrestrial predator (Kharitonov and Siegel-Causey 1987). Compared to cliff-nesting species like shags, flat-nesting cormorants are much more vulnerable to the secondary effects of human disturbance. Population sizes of Brandt's Cormorants on the Farallon Islands were depressed for decades after intense egging in the late 19th century (Ainley and Boekelheide 1990). In spite of this, cormorants and shags are able to withstand the effects of disturbance considerably better than other seabirds for several reasons. Cormorants and shags breed at an early age and clutches are large (up to six eggs). Consequently, their reproductive potential is high, and this tends to buffer them against irreversible, widespread population declines (Ainley and Boekelheide 1990).

Cormorants and shags are generally shy, and disturbance of colonies (especially at the beginning of the nesting season) can be disastrous. In high latitudes, second broods usually are not possible because of the truncated breeding season. Although isolated or heavily impacted populations can recover from exploitation or human disturbance, they cannot come back from extirpation. Therefore, small populations must be protected from all contact until numbers regain former levels.

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