Status and ecology of kittiwakes (*Rissa tridactyla* and *R. brevirostris*) in the North Pacific

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Abstract

Black-legged Kittiwakes *Rissa tridactyla* are widely distributed in the subarctic North Pacific and adjacent seas, with a total breeding population of about 2.6 million individuals. Red-legged Kittiwakes *R. brevirostris* breed in four locations, and at least 95% of their estimated world population of 230 000 birds nest on one island (St. George, Pribilof Islands). Compared to Black-legged Kittiwakes in Britain, both species in Alaska have exhibited poor productivity since at least the mid-1970s. The situation worsened during the 1980s, with recent (1985–1989) estimates of annual productivity averaging 0.19 young per nest. The frequency of "colony failures" (≤0.1 young per nest) exceeded 50% in Alaska between 1985 and 1989. Low productivity has involved, to varying degrees, the failure of many birds to lay eggs, reduced clutch sizes, low hatching success, and poor chick survival. There is evidence of population declines in some colonies of Black-legged Kittiwakes, but other colonies appear to be stable or increasing. High adult survival may account for the relative stability of Black-legged Kittiwakes, but widespread declines are anticipated unless productivity improves. The evidence suggests that poor productivity results from low surface availability of key prey species.

Résumé

La Mouette tridactyle *Rissa tridactyla* est très répandue dans les eaux subarctiques du Pacifique Nord et dans les mers voisines. On évalue à environ 2,6 millions d'individus la population totale de nicheurs. On sait que la Mouette à pattes rouges *R. brevirostris* se reproduit à quatre endroits différents et qu'au moins 95 % de sa population mondiale, évaluée à 230 000 individus, niche dans l'île St. George de l'archipel Pribilof. Par comparaison avec la Mouette tridactyle de Grande-Bretagne, les deux espèces de l'Alaska affichent une faible productivité depuis le milieu des années 1970, au moins. La situation s'est aggravée dans les années 1980, au point que les estimations récentes (de 1985 à 1989) de la productivité annuelle font état de 0,19 poussin par nid. Entre 1985 et 1989, la fréquence des échecs de renouvellement des colonies (≤ 0,1 poussin par nid) a dépassé 50 %, en Alaska. Selon des degrés variables, la faible productivité se traduit par l'incapacité de pondre, un moins grand nombre d'oeufs par couvée, un faible taux d'éclosion et le faible taux de survie des oisillons. Certaines colonies de Mouettes tridactyles présentent des signes évidents de déclin, mais d'autres semblent stables, sinon en croissance démographique. Le taux élevé de survie des adultes peut expliquer la stabilité relative de la Mouette tridactyle, mai: il faut s'attendre au déclin généralisé de l'espèce, à moins que sa productivité ne s'améliore. Les auteurs attribuent la faible productivité de l'oiseau marin à la diminution des espèces-proies essentielles dans les eaux de surface.

1. Introduction

The genus *Rissa* includes the Black-legged Kittiwake *R. tridactyla*, which has a circumpolar range and two subspecies, and the Red-legged Kittiwake *R. brevirostris*, a monotypic species endemic to the Bering Sea. Few studies of the breeding biology of Red-legged Kittiwakes have been conducted—most have occurred since the mid-1970s. In contrast, detailed information is available on the ecology and population dynamics of Black-legged Kittiwakes in the North Atlantic (e.g., Barrett et al. 1985; Coulson and Thomas 1985; Danchin 1988; Chapdelaine and Brousseau 1989; Wanless and Harris 1989). Since the early 1970s, Black-legged Kittiwakes have received more attention than other seabird species in Alaska because their colonies are numerous and relatively easy to observe.

We review the ecology and population parameters of Pacific kittiwakes, placing special emphasis on the analysis anc interpretation of breeding productivity, which is low and apparently declining. We offer an evaluation of several hypotheses to account for poor productivity in Pacific kittiwakes and make recommendations for further study.

2. Distribution and abundance

Black-legged Kittiwakes breed on islands and mainlanc sites from southeastern Alaska to Cape Lisburne in North America, and from the Kuril Islands to northeastern Siberia along the Asian coast (Fig. 1). More than 260 colony sites have been identified in Alaska (Sowls et al. 1978). Most colonies contain fewer than 10 000 birds, but a few of the larger colonie support 50 000 or more (e.g., Middleton Island, Semidi Islands St. George Island, St. Matthew Island; refer to Fig. 2 for colony locations mentioned in the text). We estimate that there are 2.6 million Black-legged Kittiwakes at colonies in the North Pacifi and adjacent seas (Sowls et al. 1978; Golovkin 1984; Shuntov 1986).

Black-legged Kittiwakes, mostly immatures, are regular summer visitors in the southeastern Beaufort Sea, where there are no colonies (Frame 1973; Johnson and Herter 1989). In winter this species occurs throughout ice-free regions of its summer range, south to the East China Sea and the coasts of

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Figure 1
Breeding distributions and abundance of (a) Black-legged Kittiwakes and (b) Red-legged Kittiwakes 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 x 3° longitude block).

Sources: Sowls et al. (1978), Golovkin (1984), Gerasimov (1986), Kondratyev (1986), Nechaev (1986), Shuntov (1986), and Vyatkin (1986).

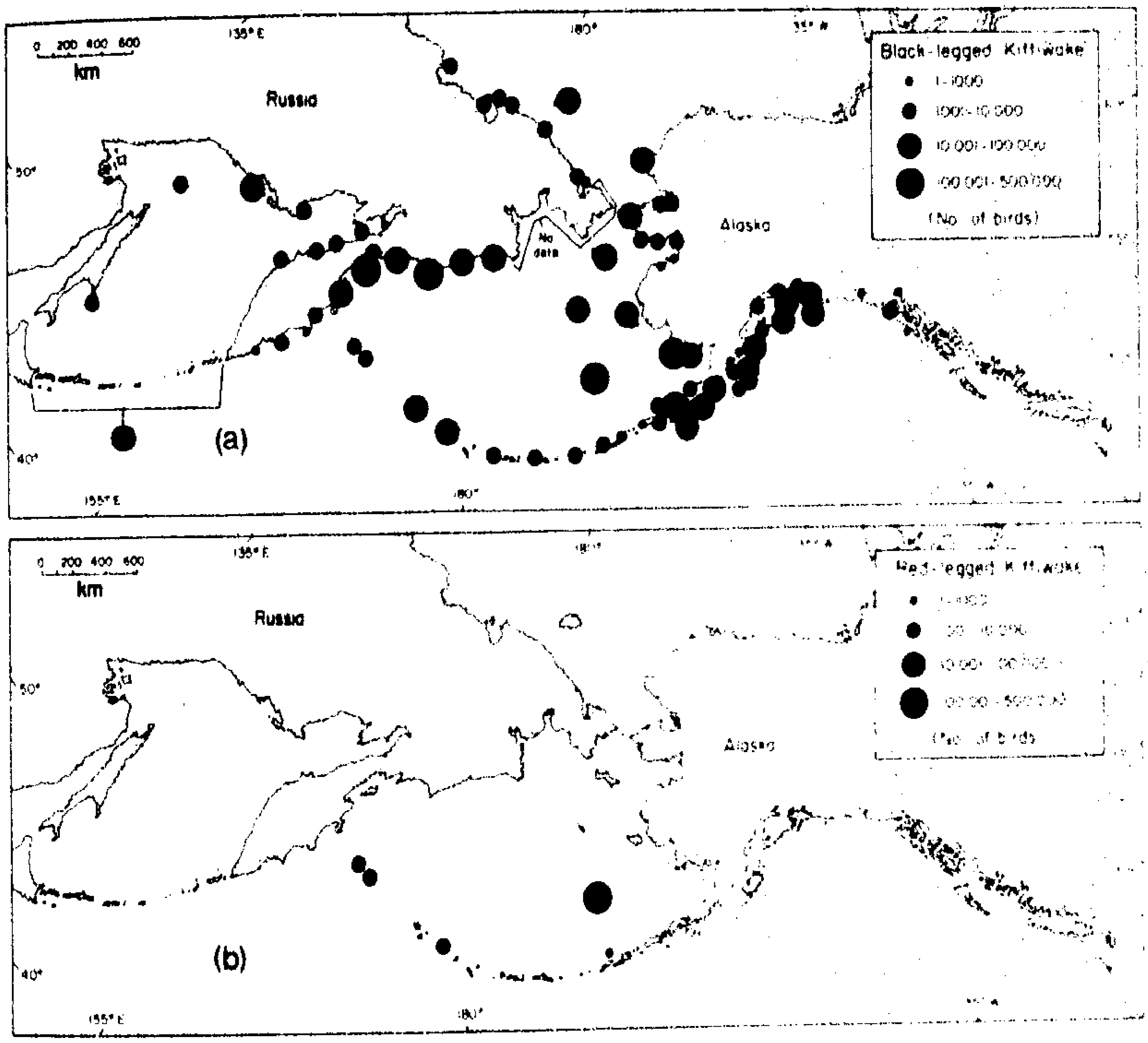


Figure 2
Distribution of sampling sites for Red- and/or Black-legged kittiwake productivity in the North Pacific. Numbers correspond to colonies listed in Table 2.

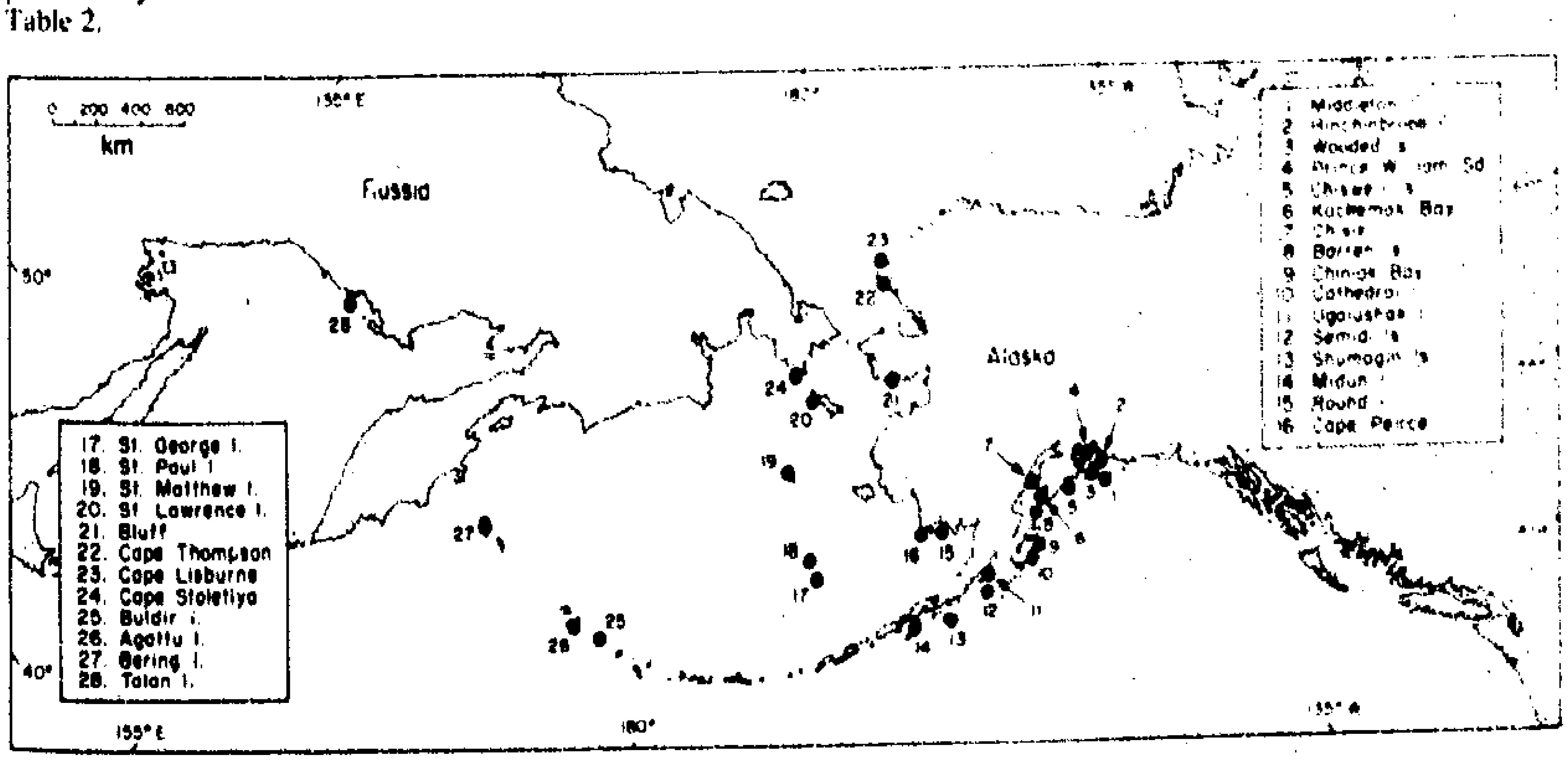


Table 1
Locations and sizes of breeding colonies of Red-legged Kittiwakes

Location	Estimated population (individuals)	Year of estimate	Reference
St. Paul I.	2 200	1976	Hickey and Craighead 1977
St. George I.	220 000	1976	Hickey and Craighead 1977
Otter I.	230[a]	1984	Byrd 1984
Walrus I.	0	1987	Byrd, unpubl. data
Pribilof subtotal	222 430		
Bogoslof I.	200	1973	Byrd 1978
Buldir I.	4 400	1976	Byrd and Day 1986
Arri Kamen I.	1 600	1969–1973	Firsova 1978
Bering and Medni Is.	2 400–3 400	1969–1973	Firsova 1978
Commander subtotal	4 000–5 000		
Grand total	231 030–232 030		

[a] Counted 230 individuals and the species was "present" at two other subcolonies.

southern California and Mexico (Kenyon 1949; Shuntov 1972; Harrington 1975; Briggs et al. 1987; Morgan et al. 1991). In Alaska and British Columbia, wintering birds are most frequently encountered over outer shelf and deep ocean habitats (Gould et al. 1982; Zweifelhofer and Forsell 1989; Morgan et al. 1991).

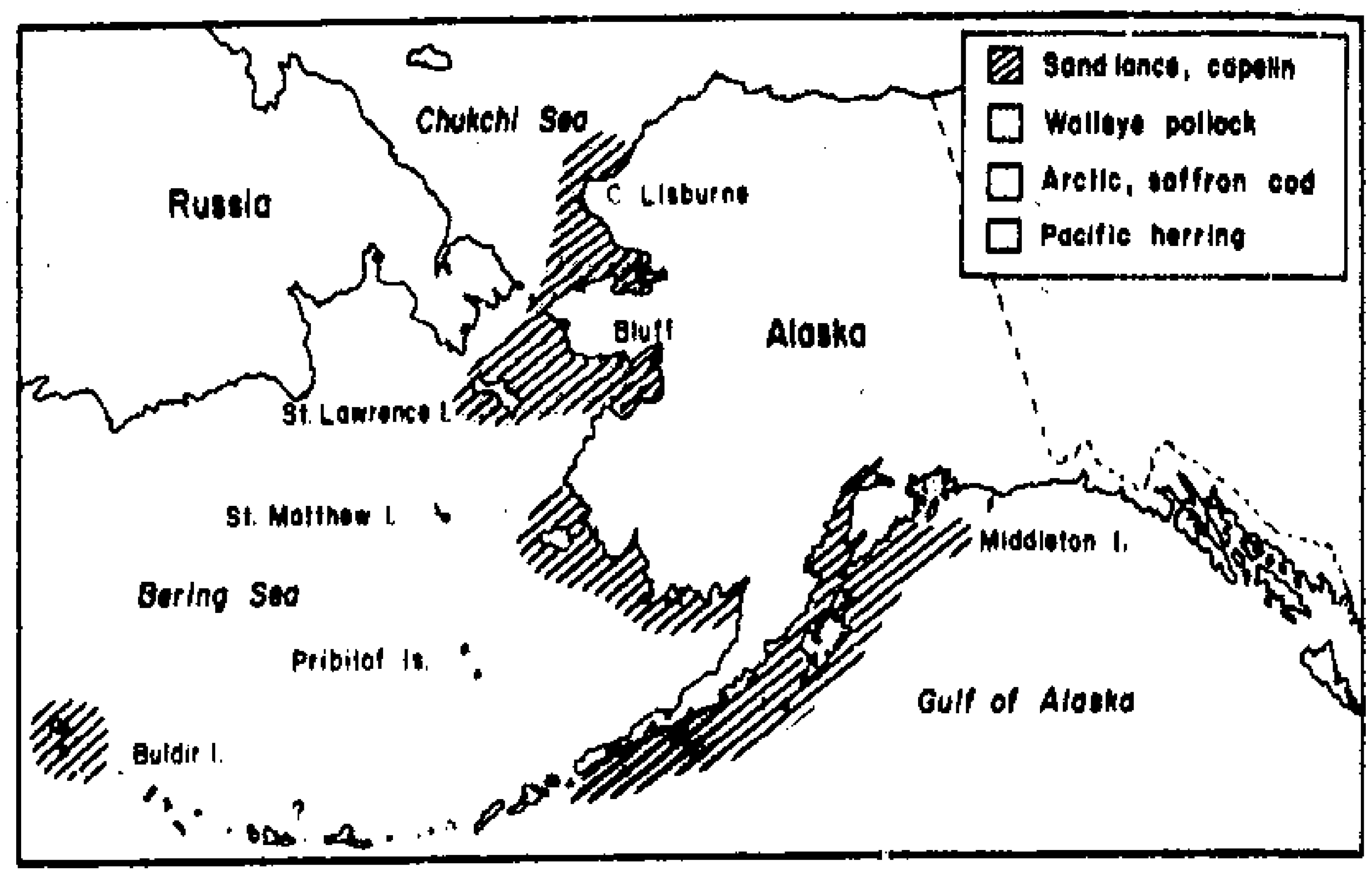
Red-legged Kittiwakes are known to breed on eight islands at five locations in the Bering Sea (Fig. 1). Ninety-six percent of an estimated population of 230 000 adults breed on St. George Island in the Pribilofs (Table 1). There are few records of wintering Red-legged Kittiwakes—most are of scattered individuals in the northern Gulf of Alaska (Kessel and Gibson 1978). Shuntov (1972) concluded that most Red-legged Kittiwakes leave the Bering Sea in winter, and Firsova (1978) stated that their fall migration from colonies on the Commander Islands is mainly toward the southeast to a wintering area in the northeastern Pacific. There is one September record of Red-legged Kittiwakes feeding at a salmon stream on Admiralty Island, southeast Alaska (Siegel-Causey and Meehan 1981).

3. Feeding ecology

Kittiwakes obtain food at the ocean's surface by dipping, surface-seizing, or plunge-diving (Ashmole 1971). In summer, both species feed primarily on fish. The most common prey in Alaskan waters are Pacific sand lance *Ammodytes hexapterus*, capelin *Mallotus villosus*, cods (Gadidae), and lanternfishes (Myctophidae) (Hunt et al. 1981a; Springer et al. 1984, 1986, 1987; Sanger 1986, 1987). Myctophids were the major prey of Red-legged Kittiwakes at the Pribilof Islands in the 1970s (Hunt et al. 1981a) and at Buldir Island in 1988 and 1989 (J.F. Piatt and A.M. Springer, unpubl. data). At the Pribilofs, Red-legged Kittiwakes also preyed heavily on walleye pollock *Theragra chalcogramma*, the predominant prey of Black- legged Kittiwakes there. Black-legged Kittiwakes took myctophids at Buldir, but fed on other species of fish more often than did Red-legged Kittiwakes. In general, there appears to be substantial overlap in kittiwake diets in areas of sympatry, although Red-legged Kittiwakes may rely more heavily on myctophids.

Sand lance are important prey of Black-legged Kittiwakes at many colonies in the Gulf of Alaska (Sanger 1986) and also at Bluff and St. Lawrence Island (Springer et al. 1987), Cape Peirce (Lloyd 1985), and Agattu Island (A.M. Springer and J.F. Piatt, unpubl. data) (Fig. 3). Capelin were the dominant prey in nearshore waters of Kodiak Island in 1977–78

Figure 3
Major fish prey of Black-legged Kittiwakes during the breeding season in coastal areas of Alaska (modified from Springer and Byrd 1988)



(Krasnow and Sanger 1986). Pollock are the major gadid prey at colonies in the southeastern Bering Sea, whereas arctic cod *Boreogadus saida* and saffron cod *Eleginus gracilis* are taken in Norton Sound and waters north of the Bering Strait (Springer et al. 1984, 1986, 1987; Fadely et al. 1989). Black-legged Kittiwakes have been observed feeding on Pacific herring *Clupea harengus* at Cape Thompson (Fadely et al. 1989) and in Prince William Sound (G.A. Sanger, pers. commun.; Irons, unpubl. data).

Invertebrate prey such as squid and euphausiids are taken frequently by Red- and Black-legged kittiwakes at Buldir Island (J.F. Piatt and A.M. Springer, unpubl. data) and have also been noted in some years at the Pribilof Islands (Preble and McAtee 1923; Hunt et al. 1981b). Euphausiids and polychaetes were prominent in the diet of Black-legged Kittiwakes on St. Matthew Island in 1982 (Springer et al. 1986), as were euphausiids on Middleton Island in 1978 and 1989 (Hatch et al. 1979; B.S. Fadely and Hatch, unpubl. data). Black-legged Kittiwakes obtain some epibenthic and benthic prey by foraging in association with diving species such as murres *Uria* spp. (Hunt et al. 1988) and gray whales *Eschictius robustus* (Obst and Hunt 1990).

Most information on kittiwake diets in Alaska pertains to the chick-rearing period (July–August). There are few data on diets earlier in the breeding cycle or in winter, but it appears that Black-legged Kittiwakes rely more heavily then on invertebrate prey, especially squid (Baltz and Morejohn 1977; Krasnow and Sanger 1986).

The two kittiwake species forage both in daylight and at night, when vertically migrating myctophids and squid are available near the surface. Differences in eye structure suggest Red-legged Kittiwakes are the more specialized of the two for nocturnal foraging (Storer 1987). Both species have been observed to fly south from colonies in the Pribilof Islands toward the continental slope in evening, where they remain until daybreak, apparently foraging on myctophids (Hunt et al. 1981b). Black-legged Kittiwakes exhibited similar behaviour at the Semidi Islands in April and May 1981 (Hatch, unpubl. data).

Foraging ranges of 55 km and 27 km were calculated for Black-legged Kittiwakes at two colonies in the northeastern Atlantic (Pearson 1968; Furness and Barrett 1985), and adults are known to travel up to 95 km from their nests at one colony in Prince William Sound (Irons, unpubl. data). Substantial differences appear between colonies and possibly between species in this respect. At the Pribilof Islands, Red-legged Kittiwakes showed a strong preference for waters at or beyond the shelf break 60–110 km southeast of their breeding sites, whereas Black-legged Kittiwakes foraged more over shallow waters to the northeast (Schneider and Hunt 1984).

4. Breeding productivity

4.1. Means and variability

We assembled 162 estimates of annual productivity in Black-legged Kittiwakes, representing 28 colony sites (Fig. 2, Table 2). Each value is an estimate of young fledged per nest started, including the empty nests built by nonbreeding pairs. Data range in quality from detailed, season-long studies to short-term observations made at varying stages during chick-rearing. Most estimates pertain to a single colony, but in some instances (Prince William Sound, Kachemak Bay, Chiniak Bay, Shumagin Islands) they are averages of two or more colonies.

An important feature of these data is the frequency of total or near-total breeding failures, particularly in recent years. We define a colony failure as an overall productivity of ≤0.1 young per nest. There were 63 (39%) failures in 162 observations between 1960 and 1989. Productivity averaged 0.4–0.5 young per nest in the 1960s and 1970s, but declined in the 1980s to less than 0.2 young per nest. Colony failure increased in frequency during each of three five-year periods beginning in 1975, approaching 50% in 71 observations since 1985. Overall, productivity in the Pacific region (0.31 young per nest) is markedly lower than productivity in Britain, where Black-legged Kittiwakes commonly rear more than one chick per nest (Coulson and Thomas 1985; Harris and Wanless 1990).

Colony failure is not a new phenomenon in Alaska—it was reported from Chisik Island as early as 1970. The recent record of failure at some colonies, however, is impressive. For example, few or no young were raised in five of seven consecutive years (1983–1989) at Middleton Island, the Semidi Islands, or Chiniak Bay (Gulf of Alaska), and the colony on Round Island (Bristol Bay) had only moderate success in one of eight years from 1982 to 1989. Few, if any, colonies are exempt from occasional breeding failure, but the northernmost sites (Bluff, Cape Thompson, Cape Lisburne) seem to fare better than others. There are also some small colonies in Kachemak Bay and Prince William Sound that often produce above- average numbers of young.

Information on the productivity of Red-legged Kittiwakes is limited to four locations (Table 3). Mean productivity of this species was 0.23 young per nest in 28 colony-years, and nine (32%) of the breeding attempts were failures (≤0.1 young per nest). At St. George Island, data for 14 consecutive years (1976–1989) indicate that success was lower after 1980 than in previous years ($\chi^2 = 66.4$, $P < 0.01$). Mean productivity was only 0.14 young per nest from 1981 to 1989 compared to 0.30 young per nest from 1976 to 1980 (Table 3).

4.2. Components of productivity

In Alaskan colonies, only 65% of nest-building Black-legged Kittiwakes produce eggs in an average year (Table 4). Those that lay have an average clutch of 1.5 eggs and hatch 57% of their eggs. Fifty percent of the chicks are fledged, resulting in an overall productivity ($\propto$) of 0.32 young per nest. In poor years ($\propto \leq 0.1$), fewer than half of the nest-building pairs lay eggs, clutch sizes are smaller, and only 6% of the eggs laid result in fledged chicks. There have been instances of nearly complete failure to produce eggs in a colony—for example, at St. Lawrence Island in 1976 (Searing 1977) and at St. George Island in 1989 (Dragoo et al. 1991).

To identify the stage or stages of breeding at which failure is most prevalent it is useful to calculate the maximum productivity of which Alaskan kittiwakes are theoretically capable. This "maximum potential productivity" (1.92 young per nest) would occur if 97% of the pairs in a colony produced eggs (the highest proportion observed in any study), their clutches averaged 1.98 eggs (the largest mean clutch size observed), and every egg laid resulted in a fledged chick (100% hatching and fledging success). Relative to that standard, egg production (or the absence of it) accounts for half of the unrealized potential for fledged young in a typical year (Table 5). When colonies fail ($\propto \leq 0.1$), two-thirds of their potential productivity is removed by a combination of non-breeding and reduced clutch sizes. Even during the most productive years ($\propto \geq 0.4$), the loss of potential production from the failure to produce eggs is about equal to the number of chicks fledged. It is clear that kittiwake productivity in Alaska is limited primarily by the inability of many pairs to achieve breeding condition, and secondarily by their poor success at hatching eggs and rearing chicks.

The above statements describe the mean effects on overall productivity of failure to lay, clutch size, hatching success, and fledging success, but it is also important to consider the relative variability of each component. For example, there is an 18% difference between mean clutch sizes recorded during "good" years ($\propto \geq 0.4$, 1.63 eggs per clutch) and "bad" years ($\propto \leq 0.1$, 1.33 eggs per clutch). The ratio of breeding to nonbreeding pairs declines 40% in bad years, whereas hatching success and fledging success decline 65% and 70%, respectively. Thus the failure to produce eggs takes the largest toll on average, but later stages of breeding are more variable in outcome from year to year. The same conclusion is evident in comparing coefficients of variation computed for each component across all colonies and years (Table 4).

Few data are available on the components of productivity in Red-legged Kittiwakes, but the tendency of this species to lay a single-egg clutch is well documented (Firsova 1978; Hunt et al. 1981c; Byrd and Douglas 1989). Curiously, Elliot (1882) stated that Red-legged Kittiwakes on the Pribilof Islands laid two eggs per clutch most commonly, and sometimes three. Byrd and Day (1986) observed several nests containing two eggs at Buldir Island in the mid-1970s, but there are no recent observations of two-egg clutches in Red-legged Kittiwakes.

4.3. Geographic and species concordance

Although breeding failure was reported for at least one locality in nearly every year from 1976 to 1989 (Table 2), it was more widespread in some years than others. The patterns in some years suggest regional differences between the Gulf of Alaska and waters to the north. In 1978, for instance, most colonies failed in the Gulf of Alaska, whereas those observed in the Bering and Chukchi seas were relatively productive (Fig. 4). The opposite was true in 1984. A rare example of moderate to good production of Black-legged Kittiwakes throughout Alaska occurred in 1988. In the following year there was breeding failure at most of the same colonies.

When kittiwakes do poorly, do other species breeding in the same locations also fail? We examined this question with reference to piscivorous diving birds—Common and Thick-billed murres (*Uria aalge* and *U. lomvia*), Tufted and Horned puffins (*Fratercula cirrhata* and *F. corniculata*), and Pelagic

Table 2
Productivity (number of young per nest) of Black-legged Kittiwakes at North Pacific colonies from 1960 through 1989[a]

Location	1960	1961	1970	1971	1973	1975	1976	1977	1978	1979	1980	1981	1982	1983	1984	1985	1986	1987	1988	1989	Mean	n (yrs)
	Year																					
Gulf of Alaska[b]																						
1. Middleton I.[c]	—	—	—	—	—	—	—	—	0.14	—	—	≥0.47	0.30	0.03	0.76	0.04	0.05	0	0.21	0.02	0.20	10
2. Hinchinbrook I.[d]	—	—	—	—	—	—	≤0.03	≤0.51	≤0.04	—	—	—	—	—	0.28	—	—	—	—	—	0.22	4
3. Wooded Is.	—	—	—	—	—	—	0.33	0.63	—	—	—	—	—	—	—	—	—	—	—	—	0.48	2
4. Prince Wm. Sound[d]	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0.35	0.25	0.31	0.34	0.33	0.34	0.32	6
5. Chiswell Is.[e]	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0	—	—	0	1
6. Kachemak Bay[f]	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0.78	0.22	0.55	0.02	0.61	0.29	0.41	6
7. Chisik I.[g]	—	—	0	0	1.50	—	—	—	0.01	0.32	—	—	—	0	—	—	0.25	0	—	—	0.26	8
8. Barren Is.[h]	—	—	—	—	—	—	—	0.90	0.13	0.13	—	—	—	—	—	0	—	—	—	0	0.23	5
9. Chiniak Bay[i]	—	—	—	—	—	—	—	1.23	0.77	—	—	—	—	0	0.42	0	0	0	0.26	0.09	0.31	9
10. Cathedral I.	—	—	—	—	—	—	—	0.74	0.17	—	—	—	—	—	—	—	—	—	—	—	0.46	2
11. Ugaiushak I.	—	—	—	—	—	—	0.07	0.77	—	—	—	—	—	—	—	—	—	—	—	—	0.42	2
12. Semidi Is.[j]	—	—	—	—	—	—	0.29	0.62	0	0.36	0.30	1.04	—	0	—	0	0	0	0	0	0.24	11
13. Shumagin Is.[k]	—	—	—	—	—	—	0.19	—	—	—	—		—	—	—	0	0.18	—	—	—	0.12	3
14. Midun I.[l]	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0	0.26	—	—	0.13	2
Bering/Chukchi seas																						
15. Round I.[m]	—	—	—	—	—	—	—	—	—	—	—	—	0	0	0	0	0	0.08	0.54	0.08	0.09	8
16. Cape Peirce[n]	—	—	0.15	—	0.09	—	0.16	0	—	—	—	0.16	—	—	0.01	0.01	0	0.02	0.16	0.06	0.08	11
17. St. George I.[o]	—	—	—	—	—	—	0.62	0.45	0.22	0.40	0.38	0.07	0.01	0.01	0.14	0.12	0.26	0	0.40	0	0.22	14
18. St. Paul I.[p]	—	—	—	—	—	0.44	0.52	0.43	0.36	0.54	—	—	—	—	0.06	0.27	0.31	0.24	0.53	0.04	0.34	11
19. St. Matthew I.[q]	—	—	—	—	—	—	—	—	—	—	—	—	0	0	—	0.19	0.19	—	—	—	0.10	4
20. St. Lawrence I.[r]	—	—	—	—	—	—	0	—	—	—	—	0.86	—	—	—	—	—	0.09	—	—	0.32	3
21. Bluff[s]	—	—	—	—	—	0.40	0.04	0.11	0.82	1.07	≤0.94	≤0.70	—	0.27	0	0	≤0.38	0.65	0.61	0	0.43	14
22. Cape Thompson[t]	1.10	0.65	—	—	—	—	0	0.64	0.50	1.10	1.15	—	—	—	—	—	—	—	0.15	—	0.66	8
23. Cape Lisburne[u]	—	—	—	—	—	—	0.14	0.61	0.78	1.70	1.53	1.36	—	0.61	0	0.20	0.90	—	—	—	0.78	10
24. Cape Stoletiya[v]	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0	0	1
W. Aleutians/Commander Is.																						
25. Buldir I.[w]	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0.27	0.05	0.16	2
26. Agattu I.[w]	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0.30	0.28	0.29	2
27. Bering I.[x]	—	—	—	0.56	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0.56	1
Sea of Okhotsk																						
28. Talan I.[v]	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0.61	1.00	0.81	2
Mean	1.10	0.65	0.08	0.28	0.80	0.42	0.20	0.59	0.33	0.70	0.86	0.67	0.08	0.10	0.26	0.09	0.23	0.12	0.38	0.15	0.31	
n (colonies)	1	1	2	2	2	2	12	13	12	8	5	7	4	9	11	14	15	14	12	15		162
Five-year means																						Overall:
n (colony years)			8					47					36					71				63 failures/162
Colony failures			3 (38%)					9 (19%)					16 (44%)					35 (49%)				colony-years
Productivity			0.51					0.44					0.36					0.19				= 39%

[a] Missing values indicate no data.
[b] Data for Gulf of Alaska colonies in 1976–1978 in Nysewander (1986). Other sources as noted below.
[c] Nysewander et al. (1986); Hatch, B.D. Roberts, and B.S. Fadely (unpubl. data).
[d] Irons et al. (1987); Irons (unpubl. data).
[e] L. Catlin (pers. commun.).
[f] Nishimoto and Beringer (1989, 1990).
[g] Snarski (1974); Nishimoto et al. (1987); Beringer and Nishimoto (1988).
[h] Hatch (unpubl. data); D.R. Nysewander (pers. commun.).
[i] Krasnow et al. (1983); D.R. Nysewander (pers. commun.); D. Zwiefelhofer (pers. commun.).
[j] Hatch and Hatch (1990); Hatch (unpubl. data); Baggot et al. (1989).
[k] Moe and Day (1979); E.P. Bailey (pers. commun.); Hatch (unpubl. data).
[l] Hatch (unpubl. data).
[m] C. Zabel (pers. commun.); Sherburne (1988); K. Taylor (pers. commun.).
[n] Haggblom and Mendenhall (1991).
[o] Dragoo et al. (1991).
[p] Dragoo et al. (1989); D. Dragoo (pers. commun.).
[q] Springer et al. (1985a); Murphy et al. (1987).
[r] Searing (1977); Springer et al. (1985b); Piatt et al. (1988).
[s] Drury et al. (1981); Murphy et al. (1991).
[t] Swartz (1966); Springer et al. (1985c); Fadely et al. (1989). Young fledged per nest with eggs (Swartz 1966) adjusted to young fledged per nest built assuming 0.9 egg-laying pairs per nest built.
[u] Springer et al. (1985b); Byrd (1986a).
[v] Kondratyev (1990).
[w] Byrd and Climo (1988); Byrd and Douglas (1989).
[x] Firsova (1978). Reported valued is a composite estimate of productivity in four years between 1969 and 1973.

Table 3
Productivity (number of young per nest) of Red-legged Kittiwakes at North Pacific colonies[a]

Year	Location	No. nests	Young fledged/nest
1969–1973	Commander Is.	54	0.39
1975	St. Paul	50	0.34
1976	St. Paul	76	0.63
	St. George	88	0.38
1977	St. Paul	78	0.54
	St. George	240	0.54
1978	St. Paul	112	0.10
	St. George	235	0.13
1979	St. Paul	56	0.34
	St. George	52	0.18
1980	St. George	123	0.27
1981	St. George	79	0.11
1982	St. George	—[b]	0.01
1983	St. George	—[b]	0.01
1984	St. Paul	39	0.09
	St. George	149	0.13
1985	St. Paul	70	0.18
	St. George	259	0.07
1986	St. Paul	67	0.25
	St. George	256	0.29
1987	St. Paul	61	0
	St. George	250	0.13
1988	St. Paul	38	0.42
	St. George	230	0.54
	Buldir	144	0.35
1989	St. Paul	—[b]	0
	St. George	190	0
	Buldir	233	0.10
Unweighted mean (n = 28 years)	—	—	0.23

[a] Sources: 1969–1973 (Firsova 1978); 1975–1979 (Hunt et al. 1981b); 1980–1982 (Lloyd 1985); 1983 (L. Merculief, pers. commun.); 1984 (Johnson and Baker 1985); 1985 (Byrd et al. 1985); 1986 (Byrd 1986b); 1987 (Byrd 1989); 1988 (Pribilofs: Dragoo et al. 1989; Buldir: Byrd and Climo 1988), 1989 (Pribilofs: D. Dragoo, pers. commun.; Buldir: Byrd and Douglas 1989).
[b] Nearly all nests were empty at a stage when chicks should have been present.

and Red-faced cormorants (*Phalacrocorax pelagicus* and *P. urile*). The available data are summarized in Table 6, which compares the performance of these species during years when kittiwakes failed with their performance during years when kittiwakes did relatively well. Individually, some of the species examined have done worse when kittiwakes fail, others have done better, but none of the species shows significant variation in productivity corresponding to that of Black-legged Kittiwakes. Apparently, these diving species are largely unaffected by the factors causing breeding failure in kittiwakes.

Concordance between Red- and Black-legged kittiwakes is high. Data from three locations (St. Paul Island, St. George Island, and Buldir) constitute 24 colony-years of paired observations (Tables 2 and 3). The Spearman rank correlation is 0.81 ($P < 0.001$; $r_s = 0.84$, $P < 0.001$, $n = 15$ colony-years with data from St. George and St. Paul islands combined before analysis) and the mean productivities of Red- and Black-legged kittiwakes do not differ significantly (Wilcoxon signed ranks test; $P = 0.21$). Data are also available to examine the relation between kittiwake productivity and that of another surface feeder on macroplankton and nekton, the Northern Fulmar *Fulmarus glacialis*. The productivities of Black-legged Kittiwakes and fulmars were positively correlated ($r_s = 0.70$, $P < 0.01$, one-tailed test) over 11 years in which both species were observed at the Semidi Islands (Hatch 1987a; Baggot et al. 1989).

5. Postfledging mortality

Estimates of annual survival of adult Black-legged Kittiwakes are available from studies conducted on Middleton Island (Hatch et al., in press). In four years (1988–1991), the mean annual survival of breeding males (n = 473 bird-years) was 0.928, and survival of breeding females (n = 395 bird-years) averaged 0.937. Survival rates did not differ significantly between the sexes; the combined estimate of annual survival in four years was 0.925.

It appears that under normal conditions most mortality in adult kittiwakes occurs during the winter months, yet large-scale mortality of Black-legged Kittiwakes occurred in the period from mid-July through late September in at least three years during the 1980s—1981, 1983, and 1989. In 1981, the die-off was reported only from the Kamchatka coast (Lobkov 1986). The 1983 event was probably the most severe. Beginning in mid-July, large numbers of kittiwakes were found dead or dying, apparently from starvation, on beaches from the northern Gulf of Alaska (Middleton Island), west to the Kamchatka coast and Sakhalin Island (Sea of Okhotsk), and north to Kotzebue Sound (Chukchi Sea). Tens or hundreds of thousands of birds may have been involved (Nysewander and Trapp 1984). Recently fledged young were included in a die off during late August and September 1989 (D.R. Nysewander, pers. commun.), and starvation was again identified as the most likely cause of death (Piatt et al. 1990). The 1989 event encompassed at least the area from Middleton Island to the central Alaska Peninsula.

6. Population trends in Black-legged Kittiwakes

Information on annual and longer-term variation in numbers of Black-legged Kittiwakes is now available from a few colonies in Alaska (Fig. 5). The interpretation of temporal patterns depends partly on the quality of data available and the methods used at different sites.

6.1. Middleton Island

Rausch (1958) reported there were "several thousand" Black-legged Kittiwakes on Middleton Island in 1956, an estimate he later refined to 10 000–15 000 birds (R. Rausch, pers. commun.). Between 1956 and 1974, this colony increased to more than 70 000 nests (140 000 birds); it stayed at approximately that level through 1982, but a decline in the 1980s removed about half of the earlier gains by 1989 (Nysewander et al. 1986; Hatch, unpubl. data).

6.2. Prince William Sound

Twenty-four colonies, most containing fewer than 1000 nests, were censused annually in Prince William Sound from 1984 to 1989. In the aggregate, there was much annual variation in the number of nests built but no apparent change from the 1972 level. There is circumstantial evidence, however, of large interannual movements of breeding adults among colonies in the sound (Irons, unpubl. data).

6.3. Chiniak Bay

As in Prince William Sound, nest counts in Chiniak Bay include a number of island and mainland sites. The census total for 20 colonies increased markedly between the late 1970s and mid-1980s and has remained at the higher level through 1989 (Nysewander 1986, pers. commun.).

Table 4
Components of productivity in Black-legged Kittiwakes during years with varying levels of breeding success[a]

Component of productivity[b]	Overall productivity (∝) Low (∝ ≤ 0.1)	Intermediate (0.1 < ∝ < 0.4)	High (∝ ≥ 0.4)	Average
Clutches/nest (A)				
Mean	0.484	0.682	0.801	0.648
n (colony-years)	27	27	23	77
Std. error	0.0377	0.0380	0.0254	0.0249
Range	0.04–0.81	0.24–0.96	0.54–0.97	0.04–0.97
Coeff. of var.	—	—	—	33.8
Clutch size (B)				
Mean	1.326	1.515	1.625	1.486
n (colony-years)	32	28	31	91
Std. error	0.0400	0.0477	0.0367	0.0271
Range	1.00–1.79	1.00–1.94	1.18–1.98	1.00–1.98
Coeff. of var.	—	—	—	17.4
Eggs hatched/eggs laid (C)				
Mean	0.269	0.596	0.763	0.569
n (colony-years)	19	18	27	64
Std. error	0.0526	0.0432	0.0224	0.0338
Range	0–0.64	0.24–0.81	0.37–0.94	0–0.94
Coeff. of var.	—	—	—	47.6
Chicks fledged/eggs hatched (D)[b]				
Mean	0.217	0.446	0.711	0.499
n (colony-years)	16	19	26	61
Std. error	0.0553	0.0550	0.0253	0.0357
Range	0–0.71	0.10–0.92	0.47–0.95	0–0.95
Coeff. of var.	—	—	—	55.9
Chicks fledged/nest (∝)				
Mean	0.023	0.235	0.715	0.323
n (colony-years)	34	31	33	98
Std. error	0.0051	0.0140	0.0404	0.0329
Range	0–0.09	0.11–0.36	0.40–1.23	0–1.23
Coeff. of var.	—	—	—	101.0
A x B x C x D[c]	0.037	0.275	0.706	0.273

[a] Data from colonies 1–4, 7–13, 15–23, and 25–26. See Table 3 for references.
[b] Calculation excludes colony-years for which component C (eggs hatched/eggs laid) was zero.
[c] The product A x B x C x D should equal overall productivity (∝). Discrepancies arise because of incomplete data, i.e., not all components were measured at every colony in all years.

Table 5
Factors limiting the productivity of Black-legged Kittiwakes: relative contributions (% reduction of potential productivity) at three levels of breeding success[a]

	Productivity High (∝ ≥ 0.4)	Low (∝ ≤ 0.1)	Average
Limiting factors			
Eggs not laid[b]	32.2	66.6	49.9
Nonbreeding pairs[c]	(15.9)	(44.7)	(29.9)
Reduced clutch sizes[d]	(16.3)	(21.9)	(20.0)
Eggs not hatched	16.1	24.4	21.6
Chicks not fledged	14.9	7.0	14.3
Chicks fledged	36.8	2.0	14.2
Total potential productivity	100.0	100.0	100.0

[a] Percentages express the loss of potential productivity attributed to each factor. See text for definition of maximum potential productivity.
[b] Potential eggs not laid (%) calculated as $100\,[1 - (B_oC_o/B_mC_m)]$, where B_o = observed proportion of pairs laying eggs, C_o = observed clutch size, B_m = maximum proportion of pairs laying eggs (0.97), C_m = maximum clutch size (1.98).
[c] Contribution to eggs not laid attributed to nonbreeding calculated as $[(B_m - B_o)C_o]/[(C_m - C_o)B_o + (B_m - B_o)C_o]$. Symbols defined as in footnote b.
[d] Contribution to eggs not laid attributed to reduced clutch sizes calculated as $[(C_m - C_o)B_o]/[(C_m - C_o)B_o + (B_m - B_o)C_o]$. Symbols defined as in footnote b.

6.4. Semidi Islands

A five-year study from 1977 to 1981 documented changes in the mean attendance of kittiwakes on study plots (up to 20% in consecutive years) but no sustained trend (Hatch and Hatch 1988). Recent data indicate no change between 1981 and 1989 (Baggot et al. 1989).

6.5. Pribilof Islands

Patterns observed on the two main islands, St. George and St. Paul, suggest downward trends in both kittiwake species between 1976 and 1989 (Dragoo et al. 1991). Caution is dictated, however, because the trends are largely defined by early, nonreplicated counts of adults (Hickey and Craighead 1977; Craighead and Oppenheim 1985). Such counts are subject to the sampling error associated with daily variation in attendance (Hatch and Hatch 1988).

6.6. Cape Peirce

Recent counts (1985–1989) of birds at Cape Peirce display considerable annual variation but no apparent trend (Haggblom and Mendenhall 1991). There is no definite change in population size since the colony was first censused in 1976 (M.R. Petersen, unpubl. data).

6.7. Bluff

Between 1975 and 1989, annual counts of nests showed wide variation on five study plots at Bluff (Murphy et al. 1991). The highest count (in 1988) followed the lowest (18% of the maximum) by only three years, which suggests the data may track variation in breeding effort more closely than they track adult population size.

6.8. Cape Thompson

The first quantitative data for any Alaskan colony were obtained at Cape Thompson in 1960 and 1961 (Swartz 1966). Later observers recensused many of Swartz's plots, but data

Figure 4
Geographic concordance of breeding failure and success of Black-legged Kittiwakes at North Pacific colonies

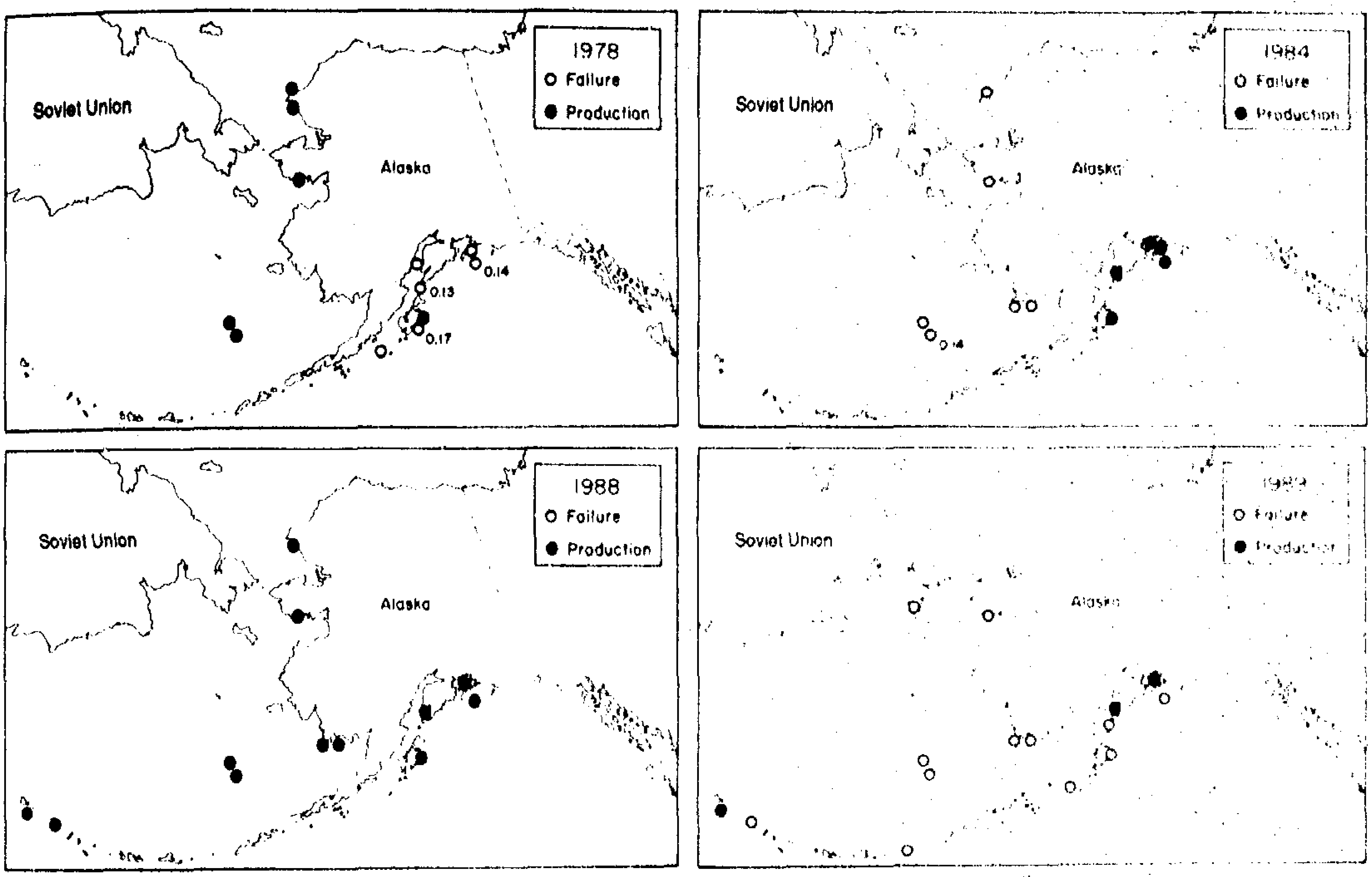


Table 6
Productivity of piscivorous diving seabirds associated with breeding failure and success in Black-legged Kittiwakes[a]

	Kittiwake failure[b] (≤ 0.1 young/pair)			Kittiwake success[b] (≥ 0.4 young/pair)				
Species	n (colony-years)	$\bar{X} \pm SE$	Range	n (colony-years)	$\bar{X} \pm SE$	Range	P[c]	Colonies[d]
Pelagic Cormorant	16	1.02 ± 0.154	0.11–1.87	13	0.86 ± 0.201	0–2.08	0.780	1, 3, 6, 8, 9, 11, 13, 15, 16, 20
Red-faced Cormorant	6	0.48 ± 0.215	0.05–1.23	11	0.86 ± 0.183	0–1.46	0.291	9, 11, 13, 17, 18
Common Murre	7	0.49 ± 0.073	0.08–0.66	5	0.56 ± 0.070	0.31–0.71	0.372	11, 12, 16, 18, 20, 21
Thick-billed Murre	9	0.44 ± 0.066	0.15–0.68	7	0.51 ± 0.059	0.24–0.72	0.427	11, 12, 17, 18, 20, 21, 28
Tufted Puffin	3	0.59 ± 0.146	0.30–0.78	5	0.51 ± 0.073	0.32–0.69	0.655	2, 9, 10, 12, 13
Horned Puffin	5	0.71 ± 0.023	0.63–0.77	5	0.61 ± 0.076	0.41–0.74	0.916	7, 8, 12, 18

[a] Productivity of cormorants and puffins expressed as number of young per nest or burrow; productivity of murres expressed as number of young per egg laying pair
[b] Mean kittiwake productivity for colony-years included in this analysis: failures, 0.03 young/pair (n = 32); successes, 0.65 young/pair (n = 23)
[c] Significance of Mann-Whitney U test of the difference between group means.
[d] Colonies from which data are included in the analysis are identified by number in Figure 2; see Table 3 for references

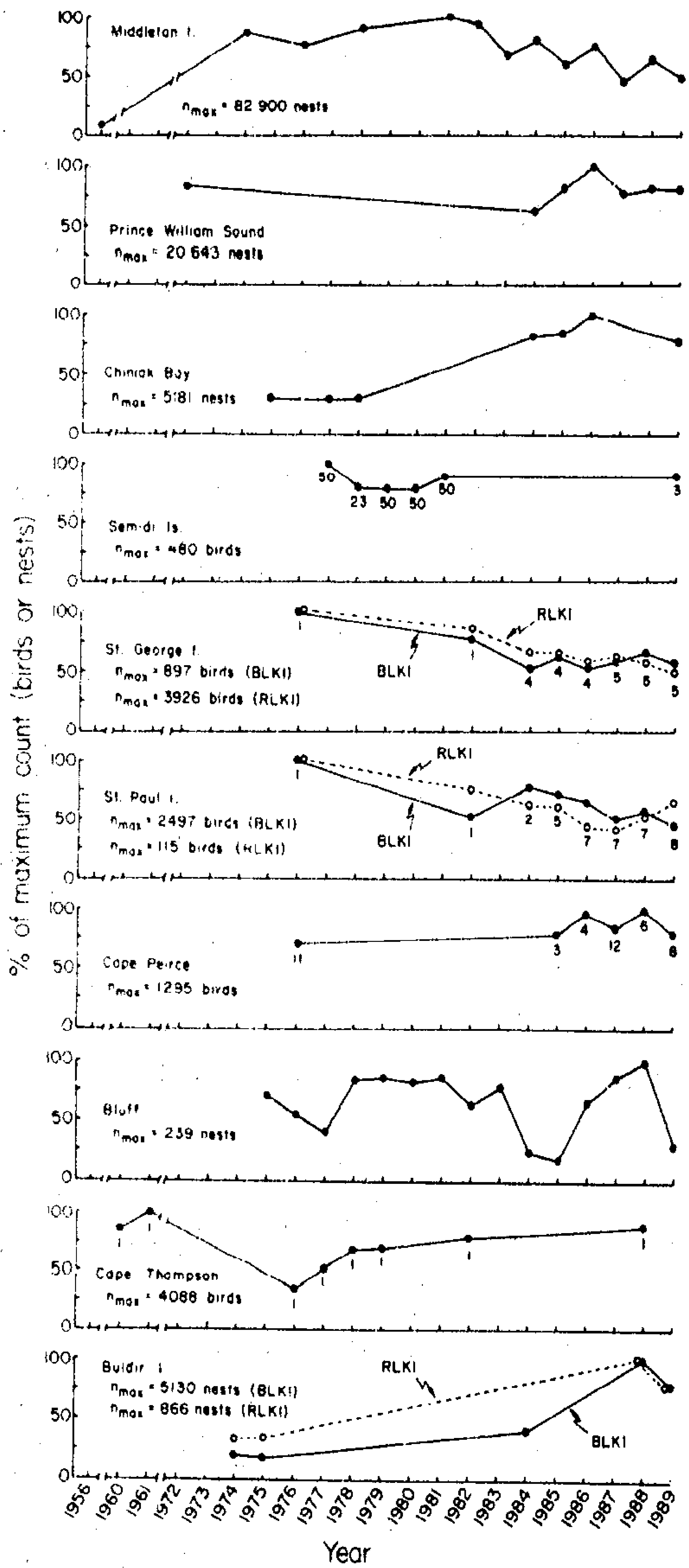
available for comparison consist of nonreplicated counts of birds from boats offshore. Census totals are highly variable because of differences in breeding effort and daily variation in attendance. There is no evidence of a long-term trend.

6.9. Buldir Island

There was a large increase in nesting Black-legged Kittiwakes at Buldir between the mid-1970s and late 1980s (Byrd and Day 1986; Byrd and Climo 1988; Byrd and Douglas 1989).

In summary, the evidence for population trends in Black-legged Kittiwakes is equivocal. It appears that a large decline has occurred on Middleton Island and possibly on the Pribilofs, but there are examples of population growth elsewhere (Chiniak Bay, Buldir Island). Most colonies exhibit substantial annual variation in nest-building and attendance, which increases the difficulty of tracking population sizes (Hatch and Hatch 1988).

Figure 5
Population trends of Red- and Black-legged kittiwakes at selected colonies in the North Pacific. Sample sizes (number of counts) are indicated for sites where birds were the counting units. Data refer to Black-legged Kittiwake only except where noted. BLKI = Black-legged Kittiwake, RLKI = Red-legged Kittiwake.



7. Population trends in Red-legged Kittiwakes

Historical accounts suggest there has been a substantial reduction in numbers and distribution of Red-legged Kittiwakes in the past 100 years. In the late 1800s this species was considered an abundant breeder in the Near Island group of the Aleutians, where it outnumbered Black-legged Kittiwakes (Turner 1885, 1886). Similarly, Prentiss (in Preble and McAtee 1923) indicated that Red-legged Kittiwakes accounted for half the kittiwakes nesting along the west side of St. Paul Island in 1895, and he also noted the species nesting on other parts of the island. In the 1980s few Red-legged Kittiwakes nested anywhere on St. Paul except along the west cliffs, where they were much less common than Black-legged Kittiwakes (Byrd, unpubl. data).

In the late 1800s Red-legged Kittiwakes bred at Akutan and possibly Sanak in the eastern Aleutians, and were considered common west of there (Turner 1886). Apparently they were once the predominant kittiwake species on the southern end of Bering Island (Stejneger 1885), but they were scarce there by the mid-1970s (Firsova 1978). Firsova (1978) also reported the establishment of a new colony near the north end of Bering Island, which she thought became occupied in the 1940s or 1950s. It is unclear whether there was a net change in overall abundance on Bering Island.

Where Red-legged Kittiwakes have been recently monitored, they show patterns similar to Black-legged Kittiwakes. In 1989 their population was down by 50% at the Pribilofs but they were more numerous at Buldir than in the mid-1970s (Fig. 5).

8. Life table analysis

A life table can be constructed for Black-legged Kittiwakes using productivity data (Table 2) and estimates of adult survival from Middleton Island. We assume a mean age at first breeding of 4.9 years as reported from Britain (Wooller and Coulson 1977), because there are no data from the Pacific. Our current estimate of annual survival (0.926) predicts a mean reproductive life of 13.0 years. This estimate assumes a stable age distribution or age-constant mortality. Because neither condition may be true for Pacific kittiwakes, the following analysis must be viewed as an approximation.

Given the productivity observed during the most recent five-year interval (0.19 young/pair/year), a pair of kittiwakes would be expected to fledge 2.47 young in a lifetime. Two offspring (81.0%) would have to reach maturity in a stable population (net replacement rate equal to 1.0). Thus, the mean annual survival of juveniles (fledging to age five) would be 0.957. Under the assumption that juvenile survival from ages one to five approximates the adult rate, survival in the first year after fledging would have to exceed 1.0, which is impossible. We therefore conclude that recent levels of productivity are inadequate to maintain the population. It should be noted, however, that a sustained productivity of 0.31 young per pair (the grand mean from Table 2) predicts, at equilibrium, a mean juvenile survival rate of 0.869 and a minimum first-year survival of 0.674. Those values are arguably within the expected range—Coulson and White (1959) estimated first-year survival to be 79% in one British colony. Thus, the near-term future of Pacific kittiwake populations may hinge on whether recent conditions (1985–1989) persist or improve.

9. Possible explanations of breeding failure in Pacific kittiwakes

There is no generally accepted explanation for the repeated and widespread failure of kittiwakes to raise young in Pacific colonies. Primary or contributing causes could include disease, contaminants, predation, or an inadequate food supply.

Some of the symptoms of kittiwake breeding failure (e.g., failure to lay, depressed clutch sizes) suggest the possibility of pathogens, notably avian influenza virus (AIV), which in domestic turkeys tends to lower breeding potential but not the survival of infected individuals (Easterday and Hinshaw 1990). Tracheal and cloacal swabs were obtained from adults and downy chicks on Middleton Island in 1988, a year of poor productivity (0.21 young per nest island-wide, zero in the sampled areas). Laboratory analysis failed to find any evidence of infection with AIV, other myxo viruses, or paramyxo viruses (V.S. Hinshaw et al., unpubl. data). Similarly, necropsies of dead or dying Black-legged Kittiwakes (three adults and four chicks) on St. Paul Island in 1987 revealed no evidence for disease as a cause of death (T. Spraker and Byrd, unpubl. data). These limited investigations reduce but do not eliminate the likelihood of disease as a contributing factor in kittiwake breeding failure.

Ohlendorf et al. (1982) reported generally low concentrations of organochlorines in seabird eggs from Alaska, including 62 eggs of Black-legged Kittiwakes collected in 1973–1976 from eight colonies in the Gulf of Alaska, Aleutian Islands, Bering Sea, and Norton Sound. Residues in kittiwakes were among the lowest in 19 species examined. Concentrations of DDE and PCBs in eggs of Black-legged Kittiwakes were considerably higher along the British coast (Parslow in Ohlendorf et al. 1982) than in Alaskan eggs, as were egg, liver, and muscle loads in kittiwakes from other locations in the North Atlantic (Nettleship and Peakall 1987). Thus, it appears unlikely that contaminants have seriously affected kittiwake reproduction in Alaska.

Avian predators such as gulls, raptors, and corvids annually remove a large share of kittiwake eggs and young in many Alaskan colonies (Bonfield 1986; Nysewander 1986; Irons 1988). Where predation is prevalent, however, it is important to distinguish whether it is opportunistic or forcible (Hatch and Hatch 1990). Opportunistic predation occurs when incubating or brooding kittiwakes leave their nests unattended. For example, nest-leaving during incubation was seen commonly at the Semidi Islands in 1978, a year that ended in complete breeding failure for Black-legged Kittiwakes (Hatch and Hatch 1990). Poor incubation behaviour—birds standing over rather than sitting on their eggs—has been noted in some colonies (Hatch, B.D. Roberts, and B.S. Fadely, unpubl. data). The contents of the affected nests are usually lost within a few days after the appearance of such behaviour, presumably due to opportunistic predation.

There is no doubt that *Larus* gulls are also forcible predators on kittiwakes, capable of displacing unwilling adults from attended nests (Bonfield 1986; Roberts 1988). However, kittiwake breeding performance is not noticeably improved where predators are scarce. For instance, few gulls or other egg predators are active on the Pribilof Islands, yet kittiwake productivity was generally poor there during the 1980s. Many egg losses on the Pribilofs result from adults rolling their own eggs out of the nest (A.L. Sowls, pers. commun.).

Indirect evidence supports the view that kittiwake productivity is limited primarily by the inability of adults to obtain sufficient food for successful breeding. Apparently, food shortages occur at various stages of the breeding cycle from pre-nesting through chick-rearing. The largest share of potential productivity is lost due to the failure to lay eggs, and birds that lay may provide inadequate parental care. The second-hatched chick in broods of two usually disappears in the first or second week after hatching (Braun and Hunt 1983; Roberts 1988; Fadely et al. 1989; Hatch and Hatch 1990). This appears to result from competition for parental care and siblicide (Braun and Hunt 1983; Roberts 1988). The late summer die-offs of adults observed in the 1980s suggest that at times food is sufficiently scarce that kittiwakes not only are unable to raise young, but are also unable even to meet their own maintenance requirements.

Low productivity on the Pribilof Islands during the 1980s was correlated with declining abundance of juvenile pollock (Lloyd 1985; Springer et al. 1986). However, depressed breeding performance has not occurred in other pollock consumers such as murres, cormorants, or puffins, and kittiwake breeding failures have not been limited to areas where pollock is the most important component of the summer diet. The lack of concordant productivity in diving and surface-feeding seabirds suggests the problem is not the abundance but the availability at the surface of key prey species.

Prey availability to kittiwakes is probably determined by numerous oceanographic variables, both physical and biological (Wooster 1983). It is useful to examine temperature anomalies, because temperature affects the food uptake and growth (i.e., biomass) of pollock, capelin, and other pelagic fish (Laevastu 1984) as well as their vertical distribution (e.g., Methven and Piatt 1991). Lloyd (1985) found that kittiwakes at St. George Island exhibited improved breeding performance during years with colder summer surface temperatures. The opposite effect is reported for Cape Lisburne, where kittiwake productivity was positively correlated with mid-July surface temperatures in 11 years (Springer and Byrd 1988). In the Gulf of Alaska, a qualitative analysis revealed no consistent relation between productivity and summer (May–August) surface temperatures recorded near Kodiak (Hatch 1987b). Clearly, our understanding of environmental controls on prey abundance and availability in kittiwakes is incomplete.

10. Conservation problems and recommended research

Significant threats to northern seabirds include oil pollution, commercial fisheries, and introduced mammalian predators on islands (Lensink 1984). Fortunately, kittiwakes may be little affected by at least two of these problems. Kittiwakes are relatively invulnerable to floating oil, as shown by their underrepresentation in the toll of marine birds resulting from the *Exxon Valdez* spill in 1989 (Piatt et al. 1990). Their response to long-term exposure to petroleum hydrocarbons is unknown (Ohlendorf et al. 1978). Unlike some upland nesting species (Jones and Byrd 1979), kittiwakes have largely escaped impact from introduced mammals by nesting mainly on inaccessible cliffs. In Alaska, most nesting habitat of both kittiwake species is now protected by inclusion in the National Wildlife Refuge System (Lensink 1984).

Few of the known prey species of Pacific kittiwakes are currently targeted by commercial fisheries. The notable exception is walleye pollock, but because kittiwakes feed only on juvenile pollock, which are not harvested, no negative effects of fishing are expected unless spawning stocks are severely depleted in the future. Because adult pollock are important predators on juvenile pollock (Dwyer et al. 1987) and also take other kittiwake prey such as capelin and sand lance (Straty and Haight 1979), the fishery could theoretically benefit kittiwakes by reducing competition for available food.

Although there is no evidence that fishing, pollution, or other anthropogenic changes have substantially degraded the environment for kittiwakes in Alaska, the causes and possible consequences of persistent breeding failure are not understood. There is no indication to date of an overall population decline in Black-legged Kittiwakes, but downward trends can be expected if recent levels of productivity do not improve. Red-legged Kittiwakes appear to be declining on the Pribilof Islands, and because most of this species' world population breeds on St. George Island, its status there is of special concern.

Present knowledge of population dynamics in Pacific kittiwakes is based on the combined efforts of numerous observers to document productivity and population trends over a large area. These observations should continue, as we do not yet know whether the poor performance of recent years is a normal, transitory phenomenon or a serious problem for kittiwake populations. In addition to this broad-scale approach, we recommend that studies be initiated or intensified in the following areas:

(1) Additional banding and resighting studies are needed to establish whether adult survival is directly related to breeding success in individual kittiwakes and whether survival estimates from Middleton Island are representative. We expect less geographic variation in survival than in productivity because most adult mortality occurs outside of the breeding season and kittiwakes from different colonies probably share common wintering areas. This assumption will remain untested, however, until the effort to monitor kittiwake survival rates is expanded geographically.

(2) Food abundance and distribution near selected colonies should be measured directly using hydroacoustics or other methods to test the hypothesis that kittiwake foraging success is limited by the vertical distribution of prey.

(3) Comparative studies of food habits, energetics, and activity patterns in failing and productive colonies may help to reveal the factors limiting breeding success.

(4) Wherever possible, observers of kittiwake breeding performance should also report on diving species such as murres, puffins, and cormorants. There is much to be learned from the comparative approach.

(5) Controlled studies are needed to separate predation and food supply as factors affecting breeding success.

In general, investigations are needed that go beyond the assessment of overall productivity to identify the specific causes of breeding failure. Because existing information on the status and ecology of Pacific kittiwakes raises substantial questions about their population dynamics, the opportunity for significant ecological research is clear.

Acknowledgements

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