

Ecology and population status of Northern Fulmars *Fulmarus glacialis* of the North Pacific

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Abstract

In the North Pacific, the breeding distribution of Northern Fulmars *Fulmarus glacialis* includes about equal numbers of very large colonies (50 000–500 000 individuals) and relatively small ones (5–5000 individuals). The almost complete segregation of light and dark colour phases between adjacent colonies in the Bering Sea and Sea of Okhotsk suggests there is little gene flow among the major colonies. Annual productivity averaged 0.42 chicks per breeding pair in 10 years at one colony in the Gulf of Alaska; adult survival was 0.97 per year over five years at the same location. There is no clear indication of population change at either of two large colonies studied, but several small colonies in the western Aleutians and northern Gulf of Alaska have increased since the mid-1970s. Fulmars appear to have low vulnerability to oil pollution and drifting gill nets, but they are relatively heavy consumers of plastic debris. Introduced predators probably reduced fulmar populations in the past. Population monitoring is recommended for one or more of the large Pacific colonies and several of the smaller ones. Small colonies may provide early indications of changing population status.

Résumé

Dans le Pacifique Nord, la distribution géographique des oiseaux nicheurs de l'espèce *Fulmarus glacialis* comprend un nombre presque égal de colonies imposantes (de 50 000 à 500 000 individus) et de colonies relativement petites (de 5 à 5 000 individus). On peut déduire de la ségrégation très nette des phases de couleur claire et foncée, entre colonies voisines dans la mer de Béring et dans la mer d'Okhotsk, que le flux génétique est restreint parmi les principales colonies. La productivité annuelle moyenne, sur une période de 10 ans, s'établit à 0,42 poussin par couple nicheur, dans une colonie du golfe d'Alaska. Au même endroit, on a évalué la survie des adultes à 0,97 an, sur une période de cinq ans. Rien n'indique une modification de la population dans les deux grandes colonies étudiées. Cependant, plusieurs petites colonies ont augmenté en nombre, depuis le milieu des années 1970, dans les îles Aléoutiennes occidentales et dans le nord du golfe d'Alaska. Les fulmars semblent peu vulnérables à la pollution par les hydrocarbures et aux filets maillants dérivants. Ils sont, toutefois, relativement friands de débris de plastique. Les prédateurs non indigènes ont probablement provoqué une diminution des populations de fulmars. L'auteur recommande de surveiller les populations dans au moins une grande colonie et dans plusieurs petites colonies du Pacifique. Les petites

colonies pourraient fournir des renseignements précoces sur l'évolution de la situation démographique du Fulmar boréal.

1. Introduction

In the subarctic Pacific, the Northern Fulmar *Fulmarus glacialis* is the only breeding species of the Procellariidae, a family of tube-nosed birds whose diversity and abundance are greatest in the southern hemisphere. Until recently (Hatch 1979, 1985), information on the breeding biology of Pacific fulmars was virtually nonexistent, although their pelagic distribution and movements were known (Bent 1922; Kuroda 1955, 1960; Gabrielson and Lincoln 1959; Sanger 1970, 1972; Shuntov 1972; Wahl 1975, 1978; Ainley 1976).

An Atlantic subspecies of the Northern Fulmar *F. g. auduboni* has undergone a remarkable expansion of its population size and breeding range over the last 200 years. An extensive literature documents this phenomenon and its possible causes (e.g., Fisher and Waterston 1941; Fisher 1950, 1952a, 1966; Salomonsen 1965; Brown 1970; Crampton et al. 1974). The monograph by Fisher (1952b) is still a standard reference on the breeding of fulmars outside of their Pacific range. Other contributions include reports by Dunnet and his coworkers at the University of Aberdeen (reviewed by Ollason and Dunnet 1988), banding and behavioural studies by Macdonald (1977a, 1977b, 1977c, 1980), and a comparative study of Atlantic fulmars and the Antarctic Fulmar *F. glacialisoides* by Mougou (1967).

The purpose of this review is to summarize information on the natural history and population dynamics of Northern Fulmars in the Pacific. The main topics addressed include geographic variation, distribution and abundance, feeding ecology, breeding biology, and population parameters. I also offer an assessment of potential management problems and recommendations for research.

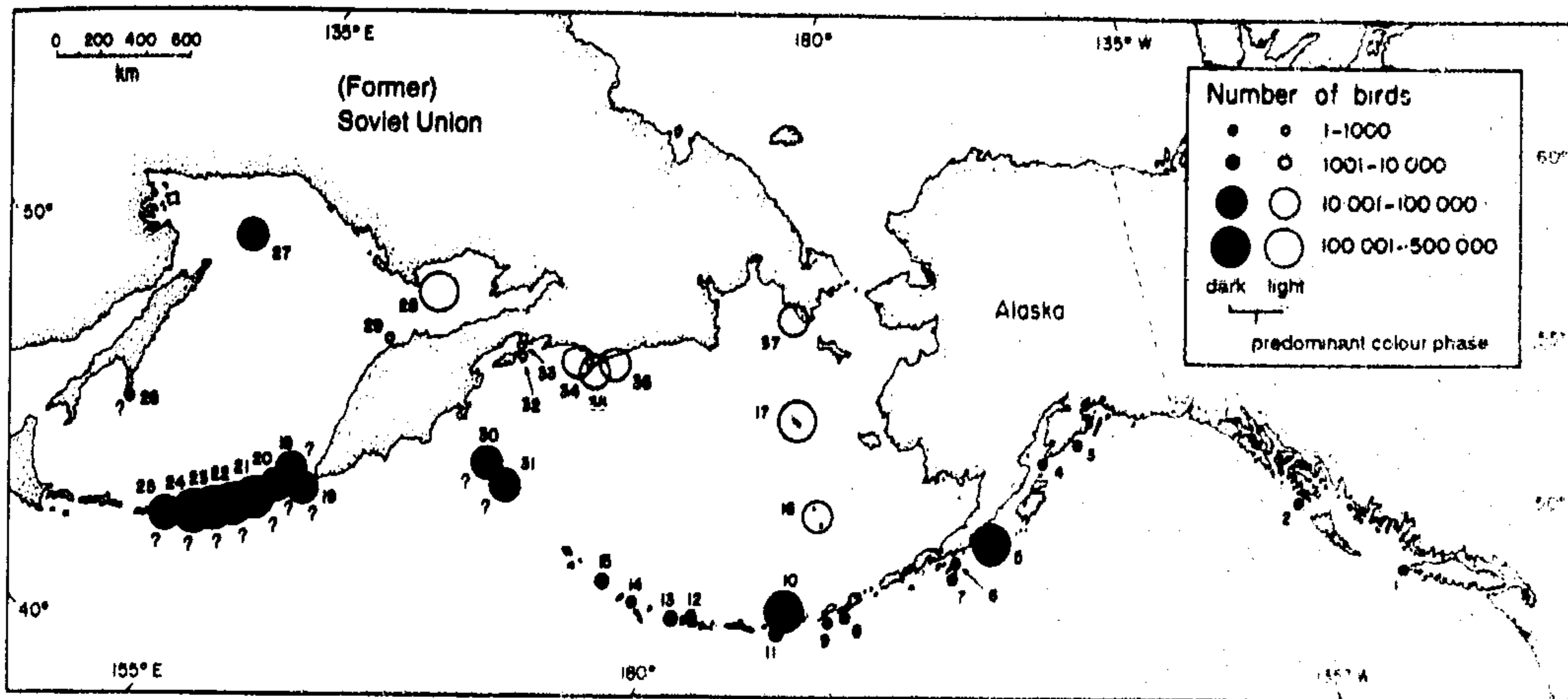
2. Geographic variation

Voous (1949) considered that the Northern Fulmar forms a superspecies with its close austral relative, the Antarctic Fulmar, from which it is probably a Pleistocene descendent. He surmised that fulmars followed cool waters along the west coast of America to colonize the North Pacific, and subsequently entered the North Atlantic through the Arctic Ocean. The two fulmar species remain outwardly similar, although the Northern Fulmar has a comparatively short, broad bill (Voous 1949).

Unlike its southern relative, the Northern Fulmar exhibits plumage polymorphism. Body plumage varies from uniformly dark gray to nearly all-white, individuals of the latter

Figure 1

Distribution and relative sizes of breeding colonies of Northern Fulmars in the North Pacific. Numbers refer to locations listed in Table 1. Question marks indicate uncertainty about relative colony size.



type having at least a small amount of gray feathering on the mantle. The gradation in colour is continuous, although observers have generally employed a classification of two or more discrete types (e.g., Fisher 1939; Francker and Wattel 1982; Hatch 1991).

Three subspecies of the Northern Fulmar are recognized: *F. g. glacialis*, a short-billed, polymorphic form inhabiting arctic regions of the North Atlantic; *F. g. auduboni*, a large-billed, monomorphic (light phase) form characteristic of boreal Atlantic waters; and the Pacific fulmar *F. g. rodgersii*, which is intermediate in bill length and strongly polymorphic (Wynne-Edwards 1952; Salomonsen 1965; Francker and Wattel 1982). The Pacific fulmar has greater extremes of light and dark colour phases than occur anywhere in the Atlantic. The validity of the two Atlantic subspecies has been questioned (Francker and Wattel 1982) because of considerable overlap in morphology.

Geographic variation in body size is less well documented than variation in bill morphology and plumage colour. At the Semidi Islands in Alaska (Fig. 1), males ($n = 47$) averaged 643 ± 7.2 (SE) g and females ($n = 57$) averaged 571 ± 6.2 g in the breeding season, May through August (Hatch, unpubl. data). Boreal Atlantic fulmars are heavier, 30 males and 28 females averaging 863 ± 14.7 g and 705 ± 9.4 g, respectively (Dunnet and Anderson 1961). Atlantic fulmars from the high Arctic may also be heavier than the Semidi birds (means of 725 ± 4.7 g for five males and 577 ± 3.8 g for seven females; Wynne-Edwards 1952; Watson 1957). Thus, Pacific fulmars in the Gulf of Alaska seem to have relatively small body mass. Light-phase fulmars from the northernmost Pacific colonies may bridge the difference, however. Portenko (1981) collected seven males and four females near a colony at Cape Stoletiya, Chukchi Peninsula, that weighed 734 ± 25.8 g and 616 ± 19.1 g, respectively. Portenko collected in May, when fulmars are expected to be leaner than they are in midsummer (Hatch 1990a).

3. Distribution and abundance

The breeding distribution of fulmars in the North Pacific includes about equal numbers of very large colonies and relatively small ones (Fig. 1, Table 1). In Alaska, more than 99% of the population breeds in colonies containing over 50 000 birds, and egg-laying has not been verified at some of the small colonies (e.g., numbers 1, 2, 3, 6, 7, 8, and 9, Fig. 1). Colony 26 (Terpenie Cape) may no longer exist. It was reported in 1955 by Gizenko (in Nechaev 1986), but no fulmars were seen there during a June 1981 visit (Nechaev 1986).

A reasonable estimate of total population size for the North Pacific is 3-3.5 million birds, excluding age groups that do not return to land in summer. However, most large colonies are in need of improved censusing. In particular, present information provides only a general picture of distribution and abundance in the Kuril Islands, possibly the most heavily populated area of the species' range in the North Pacific.

The distribution of colour phases in Pacific colonies is well established (Table 1). Over the North Pacific as a whole, dark-phase fulmars are predominant, comprising perhaps 80% of total numbers. Except for the Semidi Islands, large colonies tend to be monomorphic, or nearly so. Light-phase fulmars are largely confined to breeding sites in the Bering Sea and northern Sea of Okhotsk (Fig. 1). All colonies of predominantly light-phase fulmars are located on mainland sites or portions of the continental shelves that were ice-covered or landlocked during glacial periods of the Pleistocene (Hopkins 1976). Potentially, then, most dark-phase colonies have existed at their present sites longer than have light-phase colonies.

Fulmars regularly occur in winter as far south as 30° N on the Asian and American coasts and to the subtropical front in the central Pacific (Gould and Piatt, this volume). Individuals occasionally venture into the tropics (Shuntov 1972). The northern limit of the winter range includes ice-edge habitats and open water areas of the Bering Sea and Sea of Okhotsk (Trukhin and Kosygin 1986, 1987). Light and dark phases

Table 1
Breeding sites, colony sizes, and colour phases of Pacific Northern Fulmars

Location ^a	Population (individuals)	Proportion dark phase (%)	Source(s)
1. Triangle I.	4	75	Vermeer et al. 1976
2. Petrel I.	150	>90	DeGange et al. 1977
3. Chiswell Is.	40	"most"	Bailey 1977
4. Barren Is.	120	ca. 85	Bailey 1976; Manuwal 1980; Hatch, pers. obs.
5. Semidi Is.	440 000	85	Hatch and Hatch 1983
6. Castle Rock	20	100	E.P. Bailey, pers. commun.
7. Bird I.	20	100	E.P. Bailey, pers. commun.
8. Cape Izigan Is.	6	80	Nysewander et al. 1982
9. Ogchul I.	4	75	Nysewander et al. 1982
10. Chagulak I.	500 000	99	Bailey and Trapp 1986; Hatch, pers. obs.
11. Amukta I.	3 000	99	Bailey and Trapp 1986
12. Bobrot I.	180	100	Sowls et al. 1978; Day et al. 1978
13. Gareloi I.	5 920	"great majority"	Day et al. 1978
14. Davidof I.	20	100	J.L. Trapp, pers. commun.
15. Buldir I.	1 240	>99	Byrd 1978; Byrd and Day 1986
16. Pribilof Is.	79 700	0.2	Craighead and Oppenheim 1985
17. St. Matthew I.	450 000	0	DeGange and Sowls 1978
Subtotal, B.C. and Alaska	1 480 424		
18. Paramushiro I.	"breeding"	100	Yamashina (in Fisher 1952b)
19. Torishima I.	"plentiful"	100	Snow (in Fisher 1952b)
20. Shiranki I.	"breeding"	100	Yamashina (in Fisher 1952b)
21. Moshuro I.	"great numbers"	100	Yamashina (in Fisher 1952b)
22. Rakoko I.	"great numbers"	100	Yamashina (in Fisher 1952b)
23. Matsuwa I.	"large colony"	100	Bergman (in Fisher 1952b)
24. I-shishiro I.	"hundreds of thousands"	100	Snow (in Fisher 1952b)
25. Chiriboi I.	"very plentiful"	100	Snow (in Fisher 1952b)
Subtotal, Kuril Is.	1 500 000	100	Golovkin 1984; Shuntov 1986a
26. Terpenie Cape	<100 ^b	95	Gizenko 1955 (in Nechaev 1986)
27. Iona I.	70 000	99	Golovkin 1984; Shuntov 1986a
28. Matykol I.	50 000	0	Golovkin 1984; Shuntov 1986a
29. Skala I.	<100	0	E. Lobkov, pers. commun.
30. Bering I.	"large colonies"	99	Stejneger (in Fisher 1952b)
31. Medni I.	"large colonies"	99	Stejneger (in Fisher 1952b)
32. Karaginski I.	36	0	Gerasimov 1986; Shuntov 1986a
33. Verkhoturova I.	20	0	Vyatkin 1986; Shuntov 1986a
34. Iren Cape	34 000	0	P.S. Vyatkin, pers. commun.
35. Olutorsky Cape	36 000	0	P.S. Vyatkin, pers. commun.
36. Skalistiy Cape	40 000	ca. 0	P.S. Vyatkin, pers. commun.
37. Cape Stoletiya ^c	80 000	0	N. Konyukov, pers. commun.
Subtotal, Russia	1 960 000 (plus Bering and Medni islands)		
Grand total	ca. 3.0-3.5 million		

^a Colony numbers correspond to locations identified in Figure 1.

^b Gizenko (in Nechaev 1986) reported small numbers breeding in 1948; could not be confirmed by Nechaev in 1981.

^c Includes 14 "colonies" clustered in two portions of the coast between Cape Stoletiya and Cape Enmelyan (N. Konyukov, pers. commun.).

occur throughout the pelagic range, although light-phase fulmars predominate in northern waters during fall and winter (Shuntov 1986b, 1988a, 1988b).

In summer, the pelagic distribution moves generally northwards, but fulmars continue to occur regularly off northern Japan and central California (Shuntov 1972). Birds are also encountered well north of their northernmost breeding sites in summer. Fisher (1952b) provided records of occurrence up to 500 miles (800 km) north of Bering Strait, although fulmars are uncommon in the Chukchi Sea south of Cape Lisburne (Swartz 1967; Piatt et al. 1991) and they rarely enter the Beaufort Sea (Divoky 1983; Johnson and Herter 1989). Portenko (1981) reported that fulmars occur in small numbers near Wrangel Island, western Chukchi Sea, in summer.

4. Feeding ecology

4.1. Diet

Analysis of stomach contents indicates that fulmars are omnivorous, taking crustaceans and other zooplankton, fish, cephalopods, and offal in varying amounts (Table 2). The major component of the diet on the Pribilof Islands has been reported

variously as fish, squid, and offal, suggesting possible annual or long-term changes in food habits there. At least 10 families of squids and octopods have been identified in the diets of Pacific fulmars (Hills and Fiscus 1988). Squids are reported in most studies, and they appear to be the main food type off the Pacific coast of North America in winter. The importance of cephalopods may be exaggerated because of the relatively long retention times of beaks in the gut (Furness et al. 1984).

Fishes commonly identified in fulmar stomachs from Alaska include Pacific sand lance *Ammodytes hexapterus*, capelin *Mallotus villosus*, walleye pollock *Theragra chalcogramma*, and lanternfishes Myctophidae (Hunt et al. 1981a; Sanger 1987; Hatch, unpubl. data). Crustacean prey reported from Pacific sites include amphipods, decapods, copepods, and euphausiids (Bradstreet 1985; Sanger 1986, 1987). Fulmars are avid consumers of jellyfish, especially large, brown-rayed types such as *Chrysaora* species (Preble and McAtee 1923; Hunt et al. 1981a). At the Semidi Islands, some meals delivered to chicks consisted entirely of jellyfish (Hatch, pers. obs.).

As natural scavengers of food sources such as the floating carcasses of birds and mammals, fulmars were

Table 2
Summary of Northern Fulmar diet information from various locations in the North Pacific

Location	Sampling period	Prey use ^a					Source(s)
		Fish	Cephalopods	Crustaceans	Carion/offal	Other	
Pribilof Is.	breeding season		+++				Preble and McAtee 1923
Pribilof Is.	breeding season	+++	++	+	++?		Hunt et al. 1981a
Pribilof Is.	July	+	++	+	+++?	+ ^b	Bradstreet 1985
Kodiak I./Gulf of Alaska	spring-fall	+	+++	+		+ ^c	Sanger 1986
Semidi Is.	Jul.-Aug.	+++	++	++		+ ^d	Hatch, unpubl. data
Washington	Feb.-Mar.	+	+++			+ ^e	Harrington-Tweit 1979; Hills and Fiscus 1988
Monterey Bay, Calif.	Sep.-Apr.	+	+++				Baltz and Morejohn 1977

^a +++ major use; ++ moderate use; + minor use; blank, no reported use. Qualitative assessments based on reported frequencies of occurrence or percentage of total weight or volume of stomach contents.

^b Unidentified gastropods.

^c Nereid polychaetes, unidentified bivalves.

^d Unidentified jellyfish.

^e Unidentifiable invertebrate remains.

preadapted for taking the byproducts of fishing and whaling operations (Fisher 1952b). In the North Pacific, however, the importance of offal in the diet of fulmars is largely undocumented, except by the observation of fulmars associated with fishing vessels in the southeastern Bering Sea (Hunt et al. 1981c) and off the Washington coast (Wahl and Heinemann 1979). Several fulmar stomachs from the Pribilof Islands contained large chunks of fish flesh assumed to be offal (Bradstreet 1985), whereas none of the fish remains I found in more than 200 regurgitations of adults and young on the Semidi Islands appeared to be offal (Hatch, unpubl. data).

4.2. Feeding behaviour

Fulmars obtain food by dipping, surface seizing, surface plunging, scavenging, and pursuit diving (Ashmole 1971; Prince and Morgan 1987). By suspending baits at known depths, Hobson and Welch (in press) found that fulmars can dive to 3 m, but this feeding method seems to be rarely used (Wahl 1984).

Fulmars probably rely to some degree on olfactory cues for locating food. They have a well-developed olfactory bulb (Bang 1966) and show a positive attraction to food-related odours at sea in controlled experiments (Hutchinson and Wenzel 1980; Hutchinson et al. 1984). It is also likely that fulmars do much of their foraging at night, when mesopelagic fish and cephalopods are available at the surface (Hills and Fiscus 1988). Attendance patterns at breeding sites suggested nocturnal feeding at a Scottish colony (Furness and Todd 1984) and also at the Semidi Islands (Hatch, unpubl. data). In British Columbia, fulmars were observed feeding at night on Pacific sauries *Cololabis saira* that were attracted to the lights of a stationary vessel. Fish were obtained primarily by surface seizing and, to a lesser extent, by surface plunging (Vermeer et al. 1989). P.J. Gould (pers. commun.) observed fulmars surface plunging for undetermined prey at night near the Pribilof Islands.

4.3. Foraging habitats and range

Ship and aerial surveys in the southeastern Bering Sea indicate that fulmars are most numerous over the shelf break from the Aleutian Islands to the Chukchi Peninsula (Shuntov 1972; Hunt et al. 1981c). In the Gulf of Alaska, they occurred at roughly similar densities in continental shelf, shelf break, and oceanic habitats but were more uniformly distributed in the latter two zones than over the continental shelf (Gould et al. 1982). Concentrations encountered over the shelf and shelf

break may be associated with nearby breeding sites or the presence of fishing fleets (Hunt et al. 1981c; Gould et al. 1982). During spring and late fall, fulmars were most abundant along the seaward edge of the shelf break off the coast of British Columbia (Morgan et al. 1991). They moved inshore in late summer, apparently attracted to the abundant offal discharged from foreign factory ships (Vermeer et al. 1987).

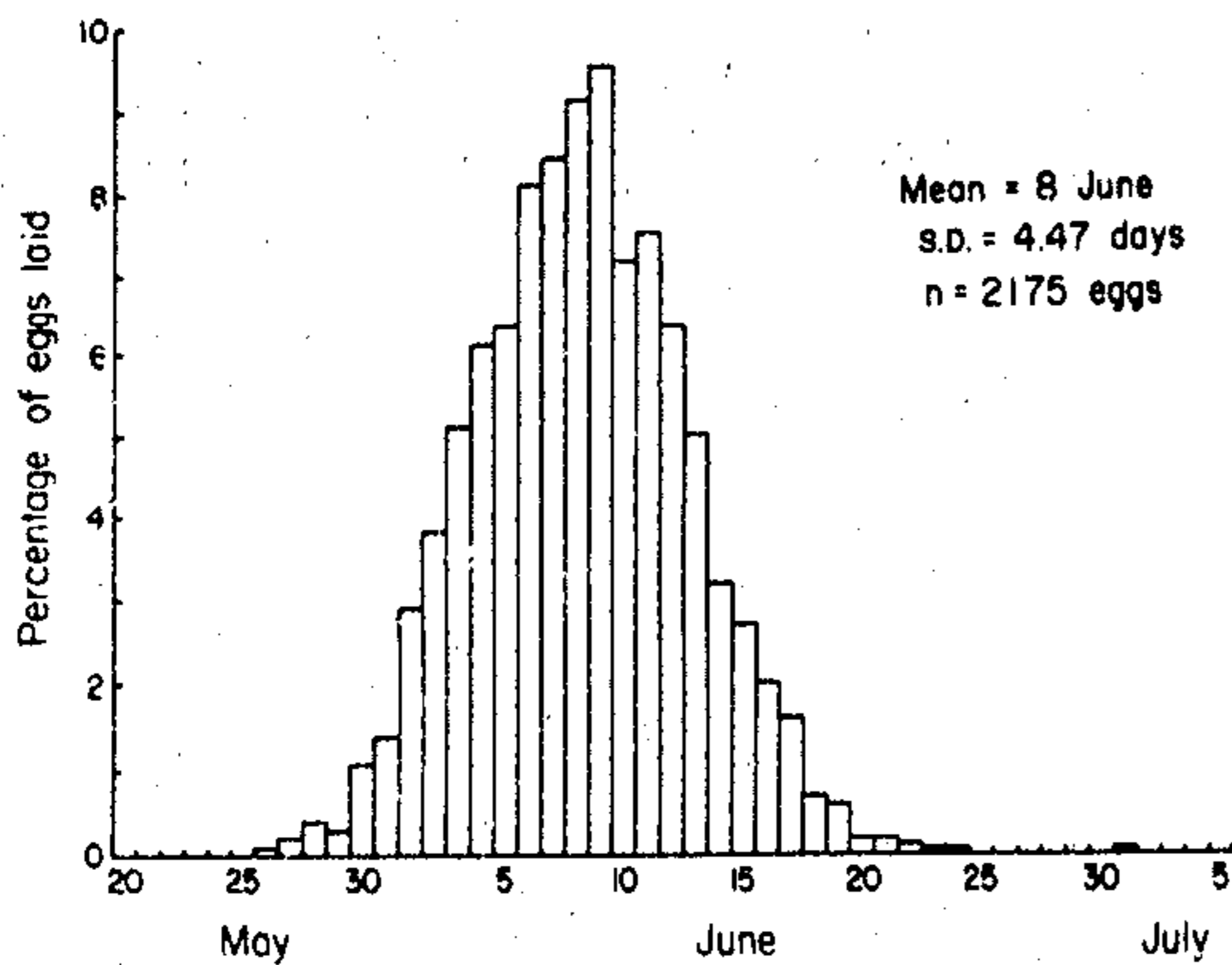
At the northern limits of their winter range, fulmars show a strong affinity for ice-edge habitats. They were absent in dense ice areas and were uncommon over ice-free deep water areas of the Sea of Okhotsk and western Bering Sea (Trukhin and Kosygin 1986, 1987). On a small spatial scale, Haney (1989) observed intensive feeding by fulmars in a tidal eddy off the northwest cape of St. Lawrence Island in May.

The potential foraging range of breeding fulmars is large because adults are often away from their breeding sites for a week or longer (Hatch 1990b) and the average ground speed of a fulmar in flight is 47 km/h (Pennycuik 1987). There is, however, little direct information on foraging range. Macdonald (1977c) noted band recoveries of adult fulmars in summer up to 800 km from known breeding sites. Such data must be interpreted cautiously because band recoveries can include failed breeders or birds that did not breed during the year of recovery. However, one breeding fulmar whose chick eventually fledged was live-trapped at sea and released about 460 km from its breeding site in Orkney (Dunnert and Ollason 1982). Observations of dye-marked adults and daily activity patterns suggested most foraging during chick rearing occurred within 100 km of another colony in Scotland (Furness and Todd 1984).

5. Nesting habitat and phenology

The Northern Fulmar is primarily a cliff-nesting species and all colonies in Alaska are on islands with rugged and precipitous cliffs. At the Semidi Islands, the nesting habitat of fulmars rarely overlaps with that of murre, kittiwake, or cormorants. These other cliff nesters use mainly bare ledges of bedrock, whereas fulmars dominate the higher, vegetated portions of cliffs. In contrast, fulmars on St. George Island in the Pribilofs use mainly the lower strata of high cliffs (Hickey and Craighead 1977), possibly because arctic foxes *Alopex lagopus* have access to the higher ledges. Most nest sites at the Semidi Islands have a soil substrate and a lush plant cover, but some eggs are laid on bare ledges or in areas of unconsolidated

Figure 2
Distribution of egg-laying dates in Northern Fulmars on the Semidi Islands during six years, 1976–81



sand and rubble (Hatch 1985). Wherever the base material is friable, the birds scratch out a simple nest cup.

The timing of egg-laying varies little from year to year and is fairly synchronous within years at the Semidi Islands. Ninety percent of the eggs laid in six years appeared in the interval from 1 to 16 June (Fig. 2). The prelaying period of colony occupation (first landing to first eggs) was about seven weeks in one year at the Semidis (Hatch and Hatch 1990a). Attendance during that period was intermittent and highly synchronized (Hatch 1989). Similar to other petrels (Warham 1964), individual fulmars stay at sea for two to three weeks immediately before laying (Hatch 1990a). Copulation occurs at the nest site before the prelaying absence (Hatch 1987a), and sperm are stored in the oviduct for fertilization of the egg while the female is away (Hatch 1983). The breeding cycle from laying to fledging averages about 102 days, including 49 days for incubation (Hatch 1979) and 53 days for chick rearing (Mougin 1967).

6. Population parameters

6.1. Productivity

Breeding success (chicks fledged per egg laid) averaged 42% in 10 years on the Semidi Islands (Table 3). In addition to annual variability (range 7–72%), individual variation in breeding success was substantial—some pairs tended consistently to raise young while others repeatedly failed (Hatch 1988). Pairs that laid early had lower success than those that laid in the middle or late portions of the period for nest initiation (Hatch 1990c).

Five years' data indicate that 75% of pre fledging mortality occurs during the egg stage, the remainder after hatching. A plot of daily egg and chick survivorship shows that egg losses were especially high during the first two weeks after laying (Fig. 3). The mortality of chicks from four to six weeks old was very low, suggesting most would survive to fledge about eight weeks after hatching.

Hatching success was highly variable from year to year and was the key factor accounting for annual variation in overall productivity (Hatch and Hatch 1990b). A relatively constant proportion (87%) of potential breeding sites were

occupied by fulmar pairs at the Semidis, and about 85% of the site-holding pairs produced eggs each year (Table 3). Because neither parameter exhibited much annual variation, neither was responsible for much of the annual variation in breeding success.

Comparable data from other Pacific colonies are unavailable. Hunt et al. (1981b) expressed fulmar productivity as the number of chicks fledged divided by the mean number of adults counted on study plots at the Pribilof Islands. The estimates from three years on St. Paul (1976–78) were 0.15, 0.30, and 0.27 chicks per adult. Two estimates from St. George (1977–78) were 0.34 and 0.29 chicks per adult. Byrd (1986) obtained comparable estimates of 0.39 chicks per adult on St. George and 0.38 chicks per adult on St. Paul in 1986. Productivity has also been assessed as chicks fledged per active site, the latter being defined as sites occupied by one or two adults on $\geq 50\%$ of visits to a study plot. By that measure, breeding success on St. Matthew Island was 0.45 in 1985 and 0.37 in 1986 (Murphy et al. 1987).

6.2. Postfledging survival

The mean annual survival of adults at the Semidi Islands was 0.969, with no detectable difference between the sexes (Hatch 1987b). I estimated that 90% of adult mortality occurred outside of the breeding season, and the overwinter mortality of failed breeders was substantially higher than that of successful breeders (Hatch 1987b).

Mortality is probably high in the first few weeks after fledging. Recoveries of fulmars banded in Britain in the first month after they fledged comprised nearly 30% of all recoveries obtained through four years of age (Macdonald 1977c). Presumably, mortality at this stage depends on weather conditions and food availability as young fulmars make the transition to self-feeding.

The 0.969 value for adult survival corresponds to a mean adult life span of 31.8 years. Survival and longevity may be overestimated if the years of study (1977–81) did not include the occasional year of exceptionally high winter mortality, as occurred, for example, off the Pacific west coast in 1976 (Harrington-Tweit 1979). Other episodes of elevated mortality occurred during late summer and fall in at least two years since 1981 (Nysewander and Trapp 1984; Lobkov 1986; Piatt et al. 1990).

6.3. Age structure

The age of first breeding is unknown for Pacific fulmars, but it is probably similar to the modal age of eight years reported for Atlantic fulmars (Ollason and Dunnet 1988). An estimated 30% of the birds on or near the Semidi Islands in 1981 were of prebreeding age (Hatch 1987b).

6.4. Population trends

Mean attendance of fulmars on study plots at the Semidi Islands increased between 1976 and 1981 and was also high in 1989 (Fig. 4). Fulmars with eggs spend more time at their breeding sites than failed breeders, and egg losses were lower in the later years of the 1976–81 study period. Furthermore, failed breeders and nonbreeders spend more time at the colony in years when breeding success is high (Hatch 1990a). The combination of those factors produced a positive correlation between mean plot counts and the percentage of nests still active at the end of the census period in six years (Fig. 4; $r = 0.76$, $P < 0.04$). Breeding success was above average in 1989 (0.47 chicks per egg; Baggot et al. 1989) and the mean plot count that year was not significantly greater than the 1981 mean

Table 3
Components of productivity in Northern Fulmars breeding on the Semidi Islands^a

Parameter	N (years)	n (sites or pairs)	Mean \pm SE ^b	Range	CV
(1) Occupied sites (pairs)/site ^c	5	1913	0.866 \pm 0.0061	0.853-0.889	1.58
(2) Breeding pairs/occupied site	5	1658	0.848 \pm 0.0146	0.802-0.873	3.84
(3) Eggs hatched/eggs laid	5	1778	0.631 \pm 0.1036	0.226-0.790	36.70
(4) Chicks fledged/eggs hatched	5	1196	0.809 \pm 0.0469	0.660-0.907	12.98
(5) Chicks fledged/eggs laid ^d	10	3517	0.418 \pm 0.0700	0.066-0.716	52.92
(6) Chicks fledged/occupied site ^e	5	2545	0.451 \pm 0.0896	0.119-0.625	44.42

^a Data from Hatch (1987b) and Baggot et al. (1989).

^b Unweighted means of annual estimates.

^c Sample of potential breeding sites includes all sites regularly occupied by a single fulmar or pair in at least one season of a five-year study.

^d Includes data for years with assumed numbers of eggs laid.

^e Computed as the product of (2) and (5), which were based on different samples in each of five years.

Figure 3
Average daily survivorship of fulmar eggs and nestlings over five years on the Semidi Islands

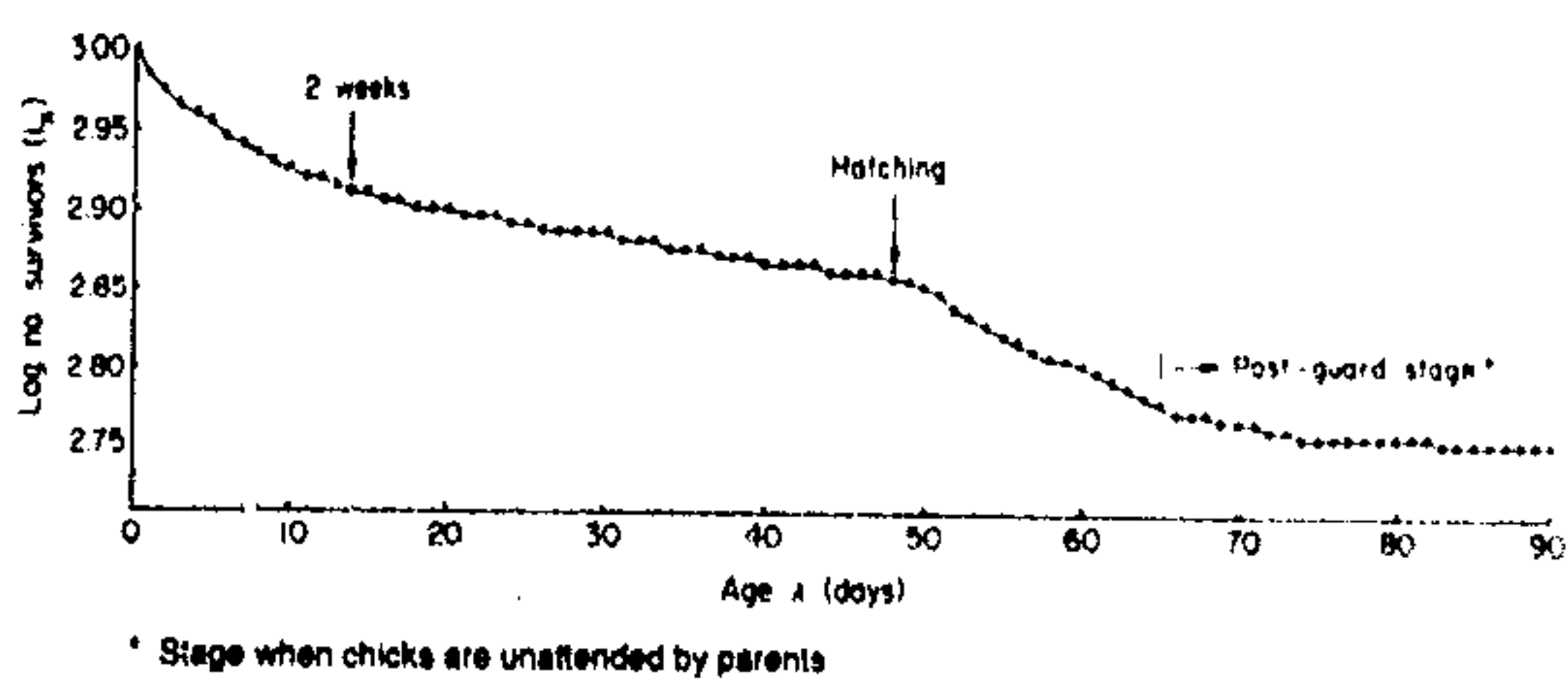
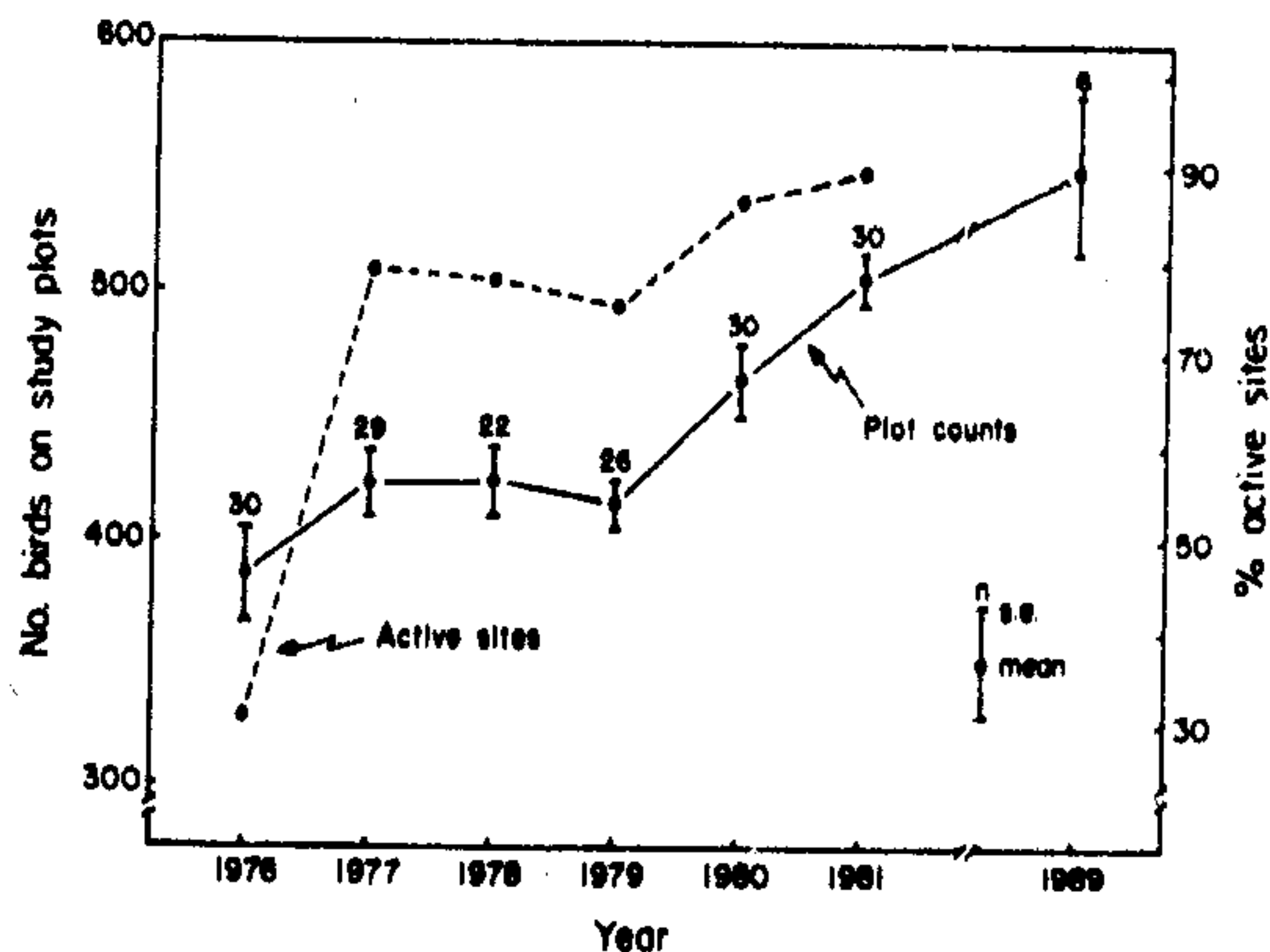


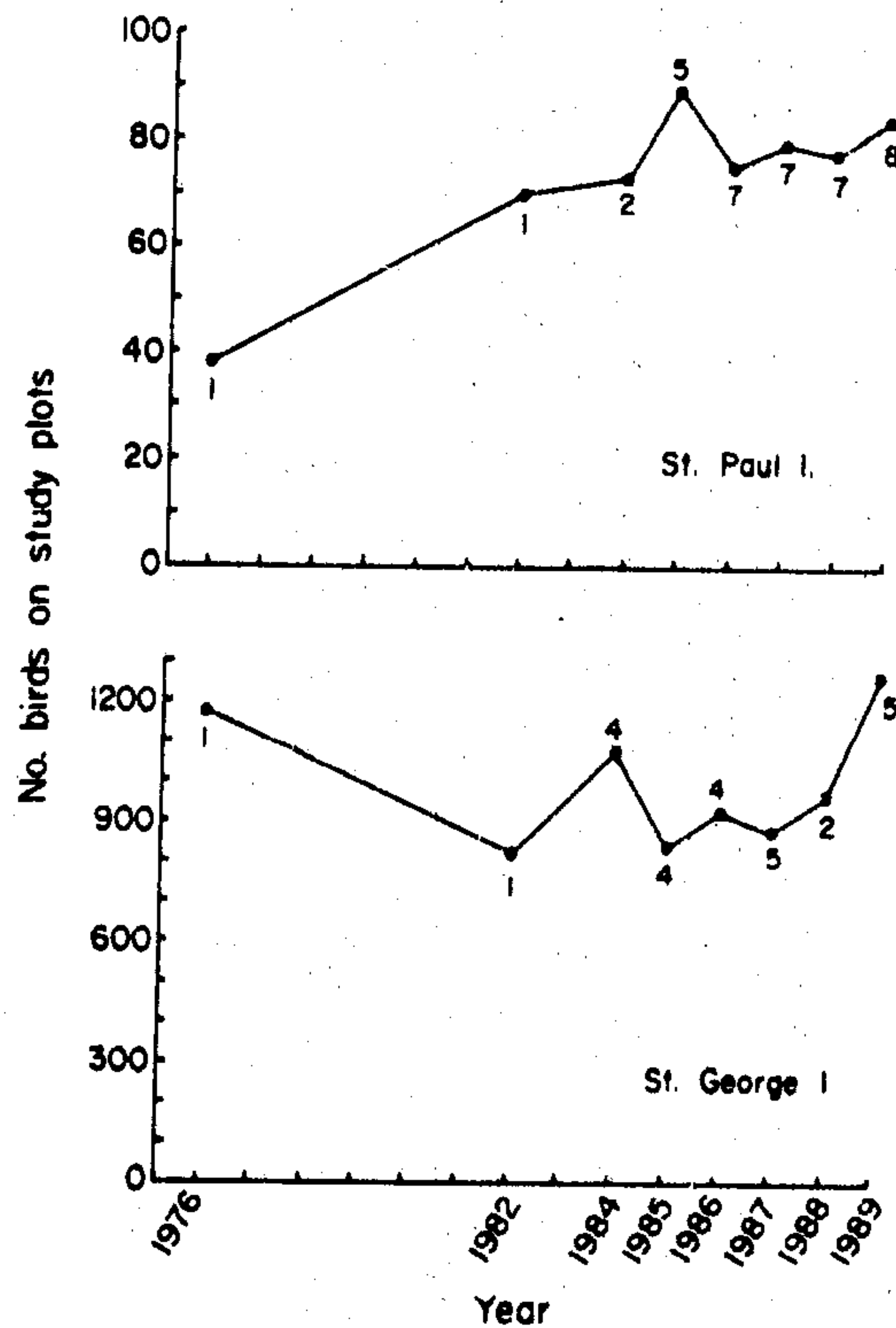
Figure 4
Mean numbers of fulmars counted on study plots at the Semidi Islands in seven years. The census period included dates from 11 to 40 days after egg-laying began. The plot of active sites is the percentage of eggs laid still surviving on the last day of the census period.



($t = 1.65$, 34 df, $P = 0.11$). Thus, although the unqualified census results suggest an upward trend in fulmar numbers, there is as yet no definite evidence of population growth at the Semidis.

Plot counts from several years are also available for each of the two large islands in the Pribilofs (Dragoo et al. 1989, 1991). The data suggest an increase in numbers on St. Paul and a decline on St. George between 1976 and 1982, followed by irregular annual variation through 1989 (Fig. 5). The 1976 and 1982 totals are based on single counts and are subject to errors associated with daily variation in attendance

Figure 5
Mean numbers of fulmars counted on study plots in eight years at the Pribilof Islands. Numbers of replicate counts per year are indicated



(Hatch 1989), as well as possible differences between years in breeding effort and attendance. There is thus no reliable evidence of changing populations on the Pribilofs.

Recent observations at Buldir Island (colony 15, Fig. 1) provide a clear indication of population growth in this small colony. Observers estimated there were at least 1200 fulmars on Buldir in 1979, compared to 100-200 in 1972 (Byrd and Day 1986). By 1988, the area used for nesting had expanded on Buldir since the 1970s (Byrd and Climo 1988) and continued expansion was evident in 1989 (G.V. Byrd, pers. commun.). The density of fulmars was also up within the core nesting area

on Buldir's northeast cape in 1989, although no recent estimates of total colony size are available (G.V. Byrd, pers. commun.).

There are indications that a small colony on East Amatuli in the Barren Islands (colony 4, Fig. 1) is also growing. D.G. Roseneau (pers. commun.) saw no fulmars nesting on East Amatuli during a five-week visit in 1965. Bailey (1976) discovered a small population (estimated at 10 pairs) in 1975, and Manuwal (1980) noted an increase from 15–25 pairs in 1977 to 60 pairs in 1978. In 1979, a small group (13 pairs) was breeding at a new location about 1.5 km from the previously used site on East Amatuli (Manuwal 1980).

Two small colonies were recently established in the Shumagin Islands. About 10 pairs of dark-phase fulmars were noted on cliffs at Bird Island (colony 7, Fig. 1) in 1984, where none were present in the mid-1970s (E.P. Bailey, pers. commun.). Similarly, in 1990 Bailey (pers. commun.) saw about 10 pairs of dark-phase birds at Castle Rock (colony 6, Fig. 1), where fulmars were not in evidence during thorough surveys conducted in 1984. Egg-laying has not yet been confirmed for either colony in the Shumagins.

To summarize, at least four small colonies of Pacific fulmars may be recently established and growing, but the data from two large colonies are inconclusive with respect to changes in population size. Trends are easier to detect in small colonies, where even qualitative observations are often adequate to document growth or decline. We cannot, however, reject the possibility of population stasis in the North Pacific without clear evidence to the contrary from the major colonies.

6.5. Life table analysis

With a mean breeding success of 0.418 chicks per year and an annual survival rate of 0.969 (see above), a pair of fulmars would fledge 13.3 young in a lifetime. Two of those offspring (15.0%) would survive to breed in a population at equilibrium. Given a mean age at first breeding of eight years (Ollason and Dunnet 1988), the calculated annual survival rate of prebreeders is 0.782. On the assumption that juvenile survival after the first year approximates that of adults (Lack 1966; Nelson 1966; Potts et al. 1980), survival from fledging to age one would be 0.188. Juvenile survival exceeding those levels should result in population growth.

7. Conservation problems

Oil pollution, plastic debris, entanglement in fishing gear, introduced predators, and human disturbance at colonies are potential threats to the well-being of Pacific fulmar populations (Lensink 1984). Because most fulmars breed in a few large colonies, the possibility exists for serious damage to result from a single adverse event. For example, a catastrophic oil spill near one of the major colonies could conceivably kill or impair the breeding of a large fraction of the population in a region such as the Gulf of Alaska or Aleutian Islands. There has been no critical test of that possibility—the closest approach to date was the *Exxon Valdez* spill in Alaska, which extended to within 100 km of the Semidi Islands in April and May 1989 (Piatt et al. 1990). Fulmars constituted only a small part of total seabird mortality, however, and they had one of the lowest mortalities of any species relative to the number of birds considered to be at risk. Aerial foraging probably reduces the vulnerability of fulmars to oil slicks; the birds may also be able to detect petroleum by smell and avoid it (Hutchinson and Wenzel 1980).

Ingestion of plastics by seabirds is a growing concern, and fulmars are among the heaviest consumers of plastic debris in Alaska (Day 1980; Day et al. 1985). A high incidence of plastics in fulmar stomachs is also reported from both industrialized and remote regions of the North Atlantic (Franeker 1985). Day et al. (1985) found a 54% mean frequency of plastics in seven studies of Atlantic and Pacific fulmars, including 58% occurrence in Alaska ($n = 38$ individuals). They attributed high ingestion rates in fulmars and other planktivorous seabirds to the resemblance of floating plastic particles to some of the birds' natural prey. The effects of plastics are largely unknown, although Bourne (1976) described ulcerations of the stomach mucosa in fulmars resulting from ingested plastics. In general, the quantity of plastic consumed by fulmars seems minor compared with indigestible prey parts such as cephalopod beaks, but plastic particles may be more resistant to abrasion and therefore have a longer residence time in the gut.

Fulmars are captured incidentally in drift gill nets, but their method of surface feeding reduces their risk relative to that of diving seabirds. DeGange et al. (1985) estimated that about 2000 fulmars were killed annually in the Japanese salmon mothership fishery between 1981 and 1984; a roughly similar number may be taken in the land-based gillnet fishery (DeGange and Day 1991). Those levels constitute less than 2% of the total seabird kill in each instance, and fulmars are greatly underrepresented relative to their at-sea densities in the fishing areas (DeGange et al. 1985).

By using only inaccessible sites, fulmars coexist with mammalian predators on some islands (e.g., St. Matthew Island and the Pribilofs). However, introduced foxes may have reduced or eliminated fulmars at other Pacific colonies in the late 1800s and early 1900s. Murie (1959) mentions three possible instances of this in the Aleutian Islands (Gareloi, Unalga, and Agattu islands), and there is little doubt that colonies on the Semidi Islands were also affected. Free-ranging arctic foxes and red foxes *Vulpes vulpes* were introduced to several of the Semidi Islands beginning in 1885 and supported a successful fur-ranching business there until about 1914 (Bower and Aller 1917). Foxes apparently died out naturally after caretaking was discontinued in 1907. Today, extensive use of accessible nesting habitat on the Semidis suggests a full recovery from what was possibly a much reduced population during the era of fox-ranching.

Incubating fulmars that are unaccustomed to low-flying aircraft or the approach of human observers on foot often leave their nests temporarily unattended, risking egg loss to aerial predators (Ollason and Dunnet 1980; Hatch, pers. obs.). Habituation plays an important role in reducing such losses (Dunnet 1977). In Alaska, at least, most fulmars breed on remote islands that rarely receive human visitors or air traffic (the Pribilofs being a notable exception), and disturbance does not seem to pose a significant threat to any colony.

All known colonies of fulmars in Alaska are included in the Alaska Maritime National Wildlife Refuge, and a system of regulatory laws and nature preserves for the protection of fulmars and other seabirds exists in Russia (Golovkin 1984). This, combined with the low vulnerability of fulmars to most identifiable threats in the North Pacific, encourages optimism that healthy populations will persist for the foreseeable future.

8. Recommendations for research

It seems likely that the locations of all fulmar colonies in the North Pacific are currently known. Sample plots for monitoring population trends have not been established in most areas, however, and estimates of population size for many of the largest colonies are crude. Thus, major changes in population may go undetected or may be erroneously inferred on the basis of future censuses. This is especially true of the large colonies on Chagulak Island and in the Kurils, for which better estimates of population size are desirable.

Unlike fulmars in the boreal Atlantic, Pacific fulmars have not as yet exhibited profound changes in distribution and abundance. Nevertheless, observations on productivity, adult survival, and age structure at one colony (the Semidi Islands) suggest potential, if not current, population growth in the Pacific. Changes in the Pacific population may be easiest to detect at small, possibly recently established colonies such as Buldir, the Barren Islands, the Shumagin Islands, or the Chiswells. At these sites, a complete and accurate annual census of the breeding population is possible. Regular sampling is also advisable to monitor population trends and breeding productivity in at least one of the major Pacific colonies; the Semidi Islands probably offer the most amenable study sites.

Life table calculations for Pacific fulmars may be wrong if the assumption of equilibrium is incorrect. Indeed, if juvenile survival after one year is equivalent to adult survival, it can be shown that only 17% of the birds in a stable colony should be prebreeders (Hatch 1987b). Thus, the estimate of 30% prebreeders at the Semidi Islands suggests a growing population. The importance of age structure to life table calculations and the low precision of the only existing information underscore the need for closer study of prebreeding survival and behaviour.

Where nesting habitat is easily accessible, as on the Semidi Islands and Chagulak, it is feasible to mark thousands of young annually, using unique combinations of coloured leg bands for each colony and cohort. Fulmars are easily attracted to stationary vessels at sea, and the presence of leg bands on swimming birds can be readily observed at close range. A coordinated program of cohort banding at selected colonies and resighting at sea could provide detailed information on age- and site-specific patterns of migration and mortality during the juvenile period.

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Literature cited

- Ainley, D.G. 1976. The occurrence of seabirds in the coastal region of California. *West. Birds* 7:33-68.
- Ashmole, N.P. 1971. Seabird ecology and the marine environment. Pages 223-286 in Farner, D.S.; King, J.R. (eds.), *Avian biology*. Vol. 1. Academic Press, New York and London.
- Baggot, C.M.; Bain, B.K.; Nysewander, D.R. 1989. Changes in colony size and reproductive success of seabirds at the Semidi Islands, Alaska, 1977-1989. Unpublished report. U.S. Fish and Wildlife Service, Homer, AK.
- Bulley, E.P. 1976. Breeding bird distribution and abundance in the Barren Islands, Alaska. *Murrelet* 57:2-12.
- Bulley, E.P. 1977. Distribution and abundance of marine birds and mammals along the south side of the Kenai Peninsula, Alaska. *Murrelet* 58:58-72.
- Bulley, E.P.; Trapp, J.L. 1986. A reconnaissance of breeding marine birds and mammals in the east-central Aleutian Islands—Kasatochi to the Islands of Four Mountains—summer 1982, with notes on other species. Unpublished report U.S. Fish and Wildlife Service, Anchorage, AK.
- Baltz, D.M.; Morejohn, G.V. 1977. Food habits and niche overlap of seabirds wintering on Monterey Bay, California. *Auk* 94:526-543.
- Bang, B.G. 1966. The olfactory apparatus of tubenosed birds. *Acta Anat* 65:391-415.
- Bent, A.C. 1922. Life histories of North American petrels and pelicans and their allies. U.S. Natl. Mus. Bull. No. 121.
- Bourne, W.R.P. 1976. Seabirds and pollution. Pages 403-502 in Johnston, R. (ed.), *Marine pollution*. Academic Press, New York.
- Bower, W.T.; Aller, H.D. 1917. Alaskan fisheries and fur industries in 1915. U.S. Dep. Commer., Bur. Fish., Washington, DC.
- Bradstreet, M.S.W. 1985. Feeding studies. Pages 257-306 in Johnson, S.R. (ed.), *Population estimation, productivity, and food habits of nesting seabirds at Cape Peirce and the Pribilof Islands, Bering Sea*. U.S. Minerals Management Service, OCS Study MMS 85-0068, Anchorage, AK.
- Brown, R.G.B. 1970. Fulmar distribution: a Canadian perspective. *Ibis* 112:44-51.
- Byrd, G.V. 1978. Birds of Buldir Island, Alaska with notes on abundance and nesting chronology. Unpublished report. U.S. Fish and Wildlife Service, Anchorage, AK.
- Byrd, G.V. 1986. Results of seabird monitoring in the Pribilof Islands in 1986. Unpublished report. U.S. Fish and Wildlife Service, Homer, AK.
- Byrd, G.V.; Climo, L.A. 1988. The status of ledge-nesting seabirds in the western Aleutian Islands, Alaska in summer 1988. Unpublished report. U.S. Fish and Wildlife Service, Homer, AK.
- Byrd, G.V.; Day, R.H. 1986. The avifauna of Buldir Island, Aleutian Islands, Alaska. *Arctic* 39:109-113.
- Craighead, F.L.; Oppenheim, J. 1985. Population estimates and temporal trends of Pribilof Island seabirds. U.S. Dep. Commer., NOAA, OCS AP Final Rep. 30, 307-356.
- Cramp, S.; Bourne, W.R.P.; Saunders, D. 1974. *The seabirds of Britain and Ireland*. Taplinger Publ. Co., New York.
- Day, R.H. 1980. The occurrence and characteristics of plastic pollution in Alaska's marine birds. MSc thesis, Univ. of Alaska, Fairbanks.
- Day, R.H.; Early, T.J.; Knudtson, E.P. 1978. A bird and mammal survey of the west-central Aleutians, summer, 1977. Unpublished report. U.S. Fish and Wildlife Service, Anchorage, AK.
- Day, R.H.; Wehle, D.H.S.; Coleman, F.C. 1985. Ingestion of plastic pollutants by marine birds. Pages 344-386 in Shimura, R.S.; Yoshida, H.O. (eds.), *Proceedings of the workshop on the fate and impact of marine debris*. U.S. Dep. Commer., NOAA Tech. Memo. NOAA-TM-NMFS-SWFC-54.
- DeGange, A.R.; Day, R.H. 1991. Mortality of seabirds in the Japanese land-based gill-net fishery for salmon. *Condor* 93:251-258.
- DeGange, A.R.; SOWLS, A.L. 1978. A faunal reconnaissance of the Bering Sea National Wildlife Refuge. Unpublished report. U.S. Fish and Wildlife Service, Anchorage, AK.

- DeGange, A.R.; Prossardt, E.E.; Frazer, D.A. 1977. The breeding biology of seabirds on the Forrester Island National Wildlife Refuge, 15 May to 1 September 1976. Unpublished report. U.S. Fish and Wildlife Service, Anchorage, AK.
- DeGange, A.R.; Forsell, D.J.; Jones, L.L. 1985. Mortality of seabirds in the high-seas Japanese salmon mothership fishery, 1981-1984. Unpublished report. U.S. Fish and Wildlife Service, Anchorage, AK.
- Divoky, G.J. 1983. The pelagic and nearshore birds of the Alaskan Beaufort Sea. U.S. Dep. Commer., NOAA, OCSEAP Final Rep. 23: 397-513.
- Dragoo, D.E.; Bain, B.K.; Sows, A.L.; Chaundy, R.F. 1989. The status of cliff nesting seabirds in the Pribilof Islands, Alaska, 1976-1988: a summary. Unpublished report. U.S. Fish and Wildlife Service, Homer, AK.
- Dragoo, D.E.; Schulmeister, S.D.; Bain, B.K.; Mendenhall, V.M. 1991. St. George Island. Pages 12-39 in Mendenhall, V.M. (ed.), Monitoring of populations and productivity of seabirds at St. George Island, Cape Peirce, and Bluff, Alaska. U.S. Minerals Management Service, OCS Study MMS 90-0049, Anchorage, AK.
- Dunnet, G.M. 1977. Observations on the effects of low-flying aircraft at seabird colonies on the coast of Aberdeenshire, Scotland. *Biol. Conserv.* 12: 55-63.
- Dunnet, G.M.; Anderson, A. 1961. A method for sexing living Fulmars in the hand. *Bird Study* 8:119-126.
- Dunnet, G.M.; Ollason, J.C. 1982. The feeding dispersal of Fulmars *Fulmarus glacialis* in the breeding season. *Ibis* 124:359-361.
- Fisher, J. 1939. Distribution of the colour phases of the Fulmar *Fulmarus glacialis*. *Nature* 144:941.
- Fisher, J. 1950. The changes in the distribution of the Fulmar *Fulmarus glacialis*. *Proc. Int. Ornithol. Congr.* 10:449-461.
- Fisher, J. 1952a. A history of the Fulmar *Fulmarus glacialis* and its population problems. *Ibis* 94:334-354.
- Fisher, J. 1952b. *The Fulmar*. Collins, London.
- Fisher, J. 1966. The Fulmar population of Britain and Ireland, 1959. *Bird Study* 13:5-76.
- Fisher, J.; Waterston, G. 1941. The breeding distribution, history and population of the Fulmar *Fulmarus glacialis* in the British Isles. *J. Anim. Ecol.* 10:204-272.
- Franeker, J.A. van. 1985. Plastic ingestion in the North Atlantic Fulmar. *Mar. Pollut. Bull.* 16:367-369.
- Franeker, J.A. van; Wattel, J. 1982. Geographical variation of the Fulmar *Fulmarus glacialis* in the North Atlantic. *Ardea* 70:31-44.
- Furness, B.L.; Laugksch, R.C.; Duffy, D.C. 1984. Cephalopod beaks and studies of seabird diets. *Auk* 101:619-620.
- Furness, R.W.; Todd, C.M. 1984. Diets and feeding of Fulmars *Fulmarus glacialis* during the breeding season: a comparison between St. Kilda and Shetland colonies. *Ibis* 126:379-387.
- Gabrielson, I.N.; Lincoln, F.C. 1959. *Birds of Alaska*. Wildl. Manage. Inst., Washington, DC.
- Gerasimov, N.N. 1986. Colonial seabirds on Karaginskii Island. Pages 94-113 in Litvinenko, N.M. (ed.), *Seabirds of the Far East: collection of scientific papers*. Far East Science Center, U.S.S.R. Academy of Sciences, Vladivostok. Translated from Russian by Can. Wildl. Serv. (1988).
- Golovkin, A.N. 1984. Seabirds nesting in the U.S.S.R.: the status and protection of populations. Pages 473-486 in Croxall, J.P.; Evans, P.G.H.; Schreiber, R.W. (eds.), *Status and conservation of the world's seabirds*. Int. Counc. Bird Preserv. Tech. Publ. 2, Cambridge, U.K.
- Gould, P.J.; Forsell, D.J.; Lensink, C.J. 1982. Pelagic distribution and abundance of seabirds in the Gulf of Alaska and eastern Bering Sea. U.S. Fish Wildl. Serv. FWS/OBS-82/48.
- Haney, J.C. 1989. Foraging by Northern Fulmars (*Fulmarus glacialis*) at a nearshore anticyclonic tidal eddy in the northern Bering Sea, Alaska. *Colon. Waterbirds* 11:318-321.
- Harrington-Twelt, B. 1979. A seabird die-off on the Washington coast in mid-winter 1976. *West. Birds* 10:49-56.
- Hatch, S.A. 1979. Breeding and population ecology of Northern Fulmars (*Fulmarus glacialis*) at Semidi Islands, Alaska. MSc thesis, Univ. of Alaska, Fairbanks.
- Hatch, S.A. 1983. Mechanism and ecological significance of sperm storage in the Northern Fulmar with reference to its occurrence in other birds. *Auk* 100:593-600.
- Hatch, S.A. 1985. Population dynamics, breeding ecology, and social behavior of the Northern Fulmar (*Fulmarus glacialis*). PhD thesis, Univ. of California, Berkeley.
- Hatch, S.A. 1987a. Copulation and mate guarding in the Northern Fulmar. *Auk* 104:450-461.
- Hatch, S.A. 1987b. Adult survival and productivity of Northern Fulmars in Alaska. *Condor* 89:685-696.
- Hatch, S.A. 1988. Testing for individual variation in breeding success. *Auk* 105:193-194.
- Hatch, S.A. 1989. Diurnal and seasonal patterns of colony attendance in the Northern Fulmar, *Fulmarus glacialis*, in Alaska. *Can. Field-Nat.* 103:248-260.
- Hatch, S.A. 1990a. Time allocation by Northern Fulmars *Fulmarus glacialis* during the breeding season. *Ornis Scand.* 21:89-98.
- Hatch, S.A. 1990b. Incubation rhythm in the Fulmar *Fulmarus glacialis*: annual variation and sex roles. *Ibis* 132:515-524.
- Hatch, S.A. 1990c. Individual variation in behavior and breeding success of Northern Fulmars. *Auk* 107:750-755.
- Hatch, S.A. 1991. Evidence for color phase effects on the breeding and life history of Northern Fulmars. *Condor* 93:409-417.
- Hatch, S.A.; Hatch, M.A. 1983. Populations and habitat use of marine birds in the Semidi Islands, Alaska. *Murrelet* 64:39-46.
- Hatch, S.A.; Hatch, M.A. 1990a. Breeding seasons of oceanic birds in a subarctic colony. *Can. J. Zool.* 68:1664-1679.
- Hatch, S.A.; Hatch, M.A. 1990b. Components of breeding productivity in a marine bird community: key factors and concordance. *Can. J. Zool.* 68:1680-1690.
- Hickey, J.J.; Craighead, F.L. 1977. A census of seabirds on the Pribilof Islands. U.S. Dep. Commer., NOAA, OCSEAP Annu. Rep. 2:96-195.
- Hills, S.; Fiscus, C.H. 1988. Cephalopod beaks from the stomachs of Northern Fulmars (*Fulmarus glacialis*) found dead on the Washington coast. *Murrelet* 69:15-20.
- Hobson, K.A.; Welch, H.E. In press. Observations of foraging Northern Fulmars (*Fulmarus glacialis*) in the Canadian high Arctic. Arctic.
- Hopkins, D.M. 1976. Sea-level history in Beringia during the past 25,000 years. Pages 3-29 in Kontrimavichus, V.L. (ed.), *Beringia in the Cenozoic era*. U.S. Dep. Commer., Natl. Tech. Inf. Serv., Springfield, VA. Translated from Russian (1984).
- Hunt, G.L. Jr.; Burgeson, B.; Sanger, G.A. 1981a. Feeding ecology of seabirds in the eastern Bering Sea. Pages 629-647 in Hood, D.W.; Calder, J.A. (eds.), *The eastern Bering Sea shelf: oceanography and resources*. Univ. of Washington Press, Seattle.
- Hunt, G.L. Jr.; Eppley, Z.; Drury, W.H. 1981b. Breeding distribution and reproductive biology of marine birds in the eastern Bering Sea. Pages 649-687 in Hood, D.W.; Calder, J.A. (eds.), *The eastern Bering Sea shelf: oceanography and resources*. Univ. of Washington Press, Seattle.

- Hunt, G.L. Jr.; Gould, P.J.; Forsell, D.J.; Peterson, H. Jr. 1981c. Pelagic distribution of marine birds in the eastern Bering Sea. Pages 689-718 in Hood, D.W.; Calder, J.A. (eds.), The eastern Bering Sea shelf: oceanography and resources. Univ. of Washington Press, Seattle.
- Hutchinson, L.V.; Wenzel, B.M. 1980. Olfactory guidance in foraging by procellariiforms. *Condor* 82:314-319.
- Hutchinson, L.V.; Wenzel, B.M.; Stager, K.E.; Tedford, B.L. 1984. Further evidence for olfactory foraging by Sooty Shearwaters and Northern Fulmars. Pages 72-77 in Nettleship, D.N.; Sanger, G.A.; Springer, P.F. (eds.), Marine birds: their feeding ecology and commercial fisheries relationships. Can. Wildl. Serv. Spec. Publ., Ottawa.
- Johnson, S.R.; Herter, D.R. 1989. The birds of the Beaufort Sea. BP Exploration (Alaska) Inc., Anchorage, AK.
- Kuroda, N. 1955. Observations of pelagic birds of the northwest Pacific. *Condor* 57:290-300.
- Kuroda, N. 1960. Analysis of seabird distribution in the northwest Pacific Ocean. *Pac. Sci.* 14:55-67.
- Lack, D. 1966. Population studies of birds. Oxford Univ. Press, London and New York.
- Lensink, C.J. 1984. The status and conservation of seabirds in Alaska. Pages 13-27 in Croxall, J.P.; Evans, P.G.H.; Schreiber, R.W. (eds.), Status and conservation of the world's seabirds. Int. Coun. Bird Preserv. Tech. Publ. 2. Cambridge, U.K.
- Lobkov, E.G. 1986. The large-scale death of seabirds on the Kamchatka coast in the summer. Pages 166-189 in Litvinenko, N.M. (ed.), Seabirds of the Far East: collection of scientific papers. Far East Science Center, U.S.S.R. Academy of Sciences, Vladivostok. Translated from Russian by Can. Wildl. Serv. (1988).
- Macdonald, M.A. 1977a. The prelaying exodus of the Fulmar *Fulmarus glacialis* (L.). *Ornis Scand.* 8:33-37.
- Macdonald, M.A. 1977b. Adult mortality and fidelity to mate and nest-site in a group of marked Fulmars. *Bird Study* 24:165-168.
- Macdonald, M.A. 1977c. An analysis of the recoveries of British-ringed Fulmars. *Bird Study* 24:208-214.
- Macdonald, M.A. 1980. The winter attendance of Fulmars at land in NE Scotland. *Ornis Scand.* 11:23-29.
- Manuwal, D.A. 1980. Breeding biology of seabirds on the Barren Islands, Alaska. Unpublished report. U.S. Fish and Wildlife Service, Anchorage, AK.
- Morgan, K.H.; Vermeer, K.; McKelvey, R.W. 1991. Atlas of pelagic birds of western Canada. Can. Wildl. Serv. Occas. Pap. No. 72, Ottawa.
- Mougin, J.-L. 1967. Étude écologique des deux espèces des fulmars: le fulmar atlantique *Fulmarus glacialis* et le fulmar antarctique *Fulmarus glacialisoides*. *Oiseau Rev. Fr. Ornithol.* 37:57-103.
- Murle, O.J. 1959. Fauna of the Aleutian Islands and Alaska Peninsula. North Am. Fauna No. 66.
- Murphy, E.C.; Cooper, B.A.; Martin, P.D.; Johnson, C.B.; Lawhead, B.E.; Springer, A.M.; Thomas, D.L. 1987. The population status of seabirds on St. Matthew and Hall islands, 1985 and 1986. U.S. Minerals Management Service, OCS Study MMS 87-0043, Anchorage, AK.
- Nechaev, V.A. 1986. New data about seabirds on Sakhalin Island. Pages 124-151 in Litvinenko, N.M. (ed.), Seabirds of the Far East: collection of scientific papers. Far East Science Center, U.S.S.R. Academy of Sciences, Vladivostok. Translated from Russian by Can. Wildl. Serv. (1988).
- Nelson, J.B. 1966. Population dynamics of the Gannet *Sula bassana* at the Bass Rock, with comparative information from other Sulidae. *J. Anim. Ecol.* 35:443-470.
- Nysegwander, D.R.; Trapp, J.L. 1984. Widespread mortality of adult seabirds in Alaska, August-September 1983. Unpublished report. U.S. Fish and Wildlife Service, Anchorage, AK.
- Nysegwander, D.R.; Forsell, D.J.; Baird, P.A.; Shields, D.J.; Weller, G.J.; Kogan, J.H. 1982. Marine bird and mammal survey of the eastern Aleutian Islands, summers of 1980-81. Unpublished report. U.S. Fish and Wildlife Service, Anchorage, AK.
- Ollason, J.C.; Dunnet, G.M. 1980. Nest failures in the Fulmar: the effect of observers. *J. Field Ornithol.* 51:39-54.
- Ollason, J.C.; Dunnet, G.M. 1988. Variation in breeding success in Fulmars. Pages 263-278 in Clutton-Brock, T.H. (ed.), Reproductive success: studies of individual variation in contrasting breeding systems. Univ. of Chicago Press, Chicago, IL.
- Pennycuik, C.J. 1987. Flight of auks (Alcidae) and other northern seabirds compared with southern Procellariiformes: ornithodolite observations. *J. Exp. Biol.* 128:335-347.
- Platt, J.F.; Lensink, C.J.; Butler, W.; Kendziorek, M.; Nysegwander, D.R. 1990. Immediate impact of the "Exxon Valdez" oil spill on marine birds. *Auk* 107:387-397.
- Platt, J.F.; Wells, J.L.; MacCharles, A.; Fadely, B.S. 1991. The distribution of seabirds and fish in relation to ocean currents in the southeastern Chukchi Sea. Pages 21-31 in Montevecchi, W.A.; Gaston, A.J. (eds.), Studies of high-latitude seabirds. I. Behavioural, energetic, and oceanographic aspects of seabird feeding ecology. Can. Wildl. Serv. Occas. Pap. No. 68, Ottawa.
- Portenko, L.A. 1981. Birds of the Chukchi Peninsula and Wrangel Island. Vol. 1. Amerind Publ. Co. Pvt. Ltd., New Delhi. Translated from Russian.
- Potts, G.R.; Coulson, J.C.; Deans, I.R. 1980. Population dynamics and breeding success of the Shag, *Phalacrocorax aristotelis*, on the Farne Islands, Northumberland. *J. Anim. Ecol.* 49:465-484.
- Preble, E.A.; McAtee, W.L. 1923. A biological survey of the Pribilof Islands, Alaska. Part I. Birds and mammals. *North Am. Fauna* No. 46.
- Prince, P.A.; Morgan, R.A. 1987. Diet and feeding ecology of Procellariiformes. Pages 135-171 in Croxall, J.P. (ed.), Seabirds: feeding ecology and role in marine ecosystems. Cambridge Univ. Press, Cambridge, U.K.
- Salomonsen, F. 1965. The geographical variation of the Fulmar (*Fulmarus glacialis*) and the zones of the marine environment in the North Atlantic. *Auk* 82:327-355.
- Sanger, G.A. 1970. The seasonal distribution of some seabirds off Washington and Oregon, with notes on their ecology and behavior. *Condor* 72:339-357.
- Sanger, G.A. 1972. Preliminary standing stock and biomass estimates of seabirds in the subarctic Pacific region. Pages 589-611 in Takenouchi, A.Y. (ed.), Biological oceanography of the northern North Pacific Ocean. Idemitsu Shoten, Tokyo.
- Sanger, G.A. 1986. Diets and food web relationships of seabirds in the Gulf of Alaska and adjacent marine regions. U.S. Dep. Commer., NOAA, OCSLAP Final Rep. 45/631-771.
- Sanger, G.A. 1987. Trophic levels and trophic relationships of seabirds in the Gulf of Alaska. Pages 229-257 in Croxall, J.P. (ed.), Seabirds: feeding ecology and role in marine ecosystems. Cambridge Univ. Press, Cambridge, U.K.
- Shuntov, V.P. 1972. Sea birds and the biological structure of the ocean. Far-Eastern Publishing House, Vladivostok. Translated from Russian by I. Allardt (1974) (NTIS-TT-74-550-32).
- Shuntov, V.P. 1986a. Seabirds in the Sea of Okhotsk. Pages 1-58 in Litvinenko, N.M. (ed.), Seabirds of the Far East: collection of scientific papers. Far East Science Center, U.S.S.R. Academy of Sciences, Vladivostok. Translated from Russian by Can. Wildl. Serv. (1988).
- Shuntov, V.P. 1986b. Numbers and patterns of distribution of seabirds in the Sea of Okhotsk in autumn. *Zool. Zh.* 65:1362-1372. Translated from Russian by M.O. Pierson.
- Shuntov, V.P. 1988a. Abundance and distribution of seabirds in the eastern part of the U.S.S.R. far east economic zone in autumn. I. Seabirds of the western Bering Sea. *Zool. Zh.* 67:1538-1548. Translated from Russian by M.O. Pierson.

Shuntov, V.P. 1988b. Abundance and distribution of seabirds in the eastern part of the U.S.S.R. far east economic zone in autumn. II. Seabirds of the Pacific waters of Kamchatka and the Kuril Islands. *Zool. Zh.* 67:1680-1688. Translated from Russian by M.O. Pierson.

Sowls, A.L.; Hatch, S.A.; Lensink, C.J. 1978. Catalog of Alaskan seabird colonies. U.S. Fish Wildl. Serv. FWS/OBS-78/78.

Swartz, L.G. 1967. Distribution and movements of birds in the Bering and Chukchi seas. *Pac. Sci.* 21:332-347.

Trukhin, A.M.; Kosygin, G.M. 1986. Distribution of seabirds in the ice of the Okhotsk Sea in winter. Pages 76-93 in Litvinenko, N.M. (ed.), *Seabirds of the Far East: collection of scientific papers.* Far East Science Center, U.S.S.R. Academy of Sciences, Vladivostok. Translated from Russian by Can. Wildl. Serv. (1988).

Trukhin, A.M.; Kosygin, G.M. 1987. Distribution of seabirds in the ice in the western portion of the Bering and Chukotsk Seas. Pages 4-40 in Litvinenko, N.M. (ed.), *Distribution and biology of seabirds of the Far East.* Far East Science Center, U.S.S.R. Academy of Sciences, Vladivostok. Translated from Russian by Can. Wildl. Serv. (1989).

Vermeer, K.; Summers, K.R.; Bingham, D.S. 1976. Birds observed at Triangle Island, British Columbia, 1974 and 1975. *Murrelet* 57:35-42.

Vermeer, K.; Hay, R.; Rankin, I. 1987. Pelagic seabird populations off southwestern Vancouver Island. *Can. Tech. Rep. Hydrogr. Ocean Sci.* 87, Sidney, B.C.

Vermeer, K.; Morgan, K.H.; Smith, G.E.J.; Hay, R. 1989. Fall distribution of pelagic birds over the shelf off SW Vancouver Island. *Colon. Waterbirds* 12:207-214.

Voous, K.H. 1949. The morphological, anatomical, and distributional relationship of the arctic and antarctic fulmars. *Ardea* 37:113-122.

Vyatkin, P.S. 1986. Nesting cadastres of colonial birds in the Kamchatka region. Pages 36-50 in Litvinenko, N.M. (ed.), *Seabirds of the Far East: collection of scientific papers.* Far East Science Center, U.S.S.R. Academy of Sciences, Vladivostok. Translated from Russian by Can. Wildl. Serv. (1988).

Wahl, T.R. 1975. Seabirds in Washington's offshore zone. *West. Birds* 6:117-134.

Wahl, T.R. 1978. Seabirds in the northwestern Pacific Ocean and south central Bering Sea in June 1975. *West. Birds* 9:45-66.

Wahl, T.R. 1984. Observations on the diving behavior of the Northern Fulmar. *West. Birds* 15:131-133.

Wahl, T.R.; Heinemann, D. 1979. Seabirds and fishing vessels: co-occurrence and attraction. *Condor* 81:390-396.

Warham, J. 1964. Breeding behaviour in Procellariiformes. Pages 389-394 in Carrick, R.; Holgate, M.; Prevost, J. (eds.), *Biologie Antarctique Symp. 1.* Hermann, Paris.

Watson, A. 1957. Birds in Cumberland Peninsula, Baffin Island. *Can. Field-Nat.* 71:87-109.

Wynne-Edwards, V.C. 1952. Geographic variation in the bill of the Fulmar *Fulmarus glacialis*. *Scot. Nat.* 64:84-101.