The food consumption of the world's seabirds

M. de L. Brooke

Department of Zoology, University of Cambridge, Downing Street, Cambridge CB2 3EJ, UK (mb10005@cus.cam.ac.uk)

Improving knowledge of the population sizes of all the world's seabirds allows this provisional estimate of their annual food consumption. Knowing the body mass and energy density of prey it is possible to employ standard metabolic equations to estimate daily and hence annual consumption of a seabird. Using this approach, and assuming that, at the least, there are three individuals alive for every recorded breeding pair, the annual food consumption of all the world's seabirds is 70 million tonnes (Mt: 95% CI 55.9–83.7 Mt). The total obviously increases if more liberal assumptions are made about the number of individuals alive per breeding pair. The principal consumers are mostly high-latitude, often pelagic species—penguins, petrels and auks. The total is similar to the global fisheries landings, currently *ca.* 80 Mt.

Keywords: penguins; petrels; auks; fishery landings

1. INTRODUCTION

As global marine fisheries landings, which are currently *ca.* 80 million tonnes (Mt) per year, have begun to decline (Pauly *et al.* 2002), it is pertinent to ask how humanity's catch compares with that of other higher vertebrates exploiting the sea. I present calculations of the quantity of prey taken from the sea each year by the world's seabirds, and discuss the degree to which the roughly similar take by birds and fishermen implies competition.

2. METHODS

To establish the global populations of all the world's species, I used recent global estimates of the number of breeding pairs for most of the major seabird groups: penguins (Williams 1995), petrels and albatrosses (Brooke 2004), auks (Gaston & Jones 1998), pelicans, cormorants, gulls, terns and skimmers (Delany & Scott 2002). The estimates are of varying reliability but there is no reason to suspect systematic bias. Populations of the remaining seabird groups (tropicbirds, frigatebirds, gannets, boobies and skuas) were extracted from Del Hoyo *et al.* (1992, 1996).

More problematical is converting breeding populations to numbers of free-living individuals. Following Meininger *et al.* (1995) and Hashmi (2002), I multiplied breeding pair totals by three, equivalent to one male, one female and one non-breeder per pair, to generate the estimate of individuals needed for what I term the base estimate of food consumption. At-sea surveys have produced estimates of the number of free-living individuals for a small minority of species (e.g. some albatrosses and petrels: Robertson & Gales 1998; BirdLife International 2000); these estimates were used, when available, in preference to a value of three times the number of breeding pairs.

Using the three-times multiplier could lead to a significant underestimate of the populations of free-living birds. Consider a species where a single egg is laid. Breeding success is 60%, first breeding is at age six, immature mortality—particularly in the year immediately after fledging—is at least as great as the annual adult mortality of 10%, and 20% of breeders do not breed in any one year. Simple

calculations show that, in a stable population of a seabird with such a life history (which is typical of many petrels; Ricklefs 2000; Brooke 2004), the number of individuals is approximately five times the number of breeding pairs. Therefore, in the liberal estimate of consumption, I multiplied the number of breeding pairs by five for longer-lived seabirds (procellariiforms except diving petrels, penguins and auks), and by four for other groups, while retaining the at-sea estimates where available.

Where species breed inland and overwinter at sea (e.g. certain gulls), I assumed that half of the annual food consumed was taken from the sea. While crude, this assumption hardly affects the overall calculation because the food consumption of gulls is far lower than that of more pelagic species (see § 3). Inland species (e.g. some terns and cormorants) are excluded.

For penguins, the daily food consumption of six species is known (Williams 1995) and can be used to generate an allometric equation that allows estimation of the daily, and hence annual consumption of the remaining species.

For all other species, namely procellariiforms, pelecaniforms, auks, gulls, terns, skimmers and skuas, body mass data (Schreiber & Burger 2002) were combined with allometric equations for field metabolic rate (Ellis & Gabrielsen 2002) to estimate the daily and annual food requirements of free-living birds, assuming a typical energy density of prey of 5.5 kJ g^{-1} (Clarke & Prince 1980) and an assimilation efficiency of 75% (Jackson 1986). Knowing the annual food consumption both of an individual and of total populations, the food consumption by the species is readily calculated.

For the base estimate, the equation of Ellis & Gabrielsen (2002) for all seabirds, field metabolic rate (kJ d^{-1}) = 16.69 mass (g)$^{0.651}$, was used. The impact of instead using their order-specific equations for the three volant orders, Procellariiformes, Pelecaniformes and Charadriiformes, was checked.

3. RESULTS

On the conservative approach of one breeding pair representing three free-flying individuals, the annual global consumption of all 0.7 billion individuals of 309 seabird species is 69.8 Mt annually, the totals for the principal groups being as follows (in Mt): procellariiforms 24.1, penguins 23.6, auks 11.2, terns and skimmers 3.9, gulls and skuas 3.7, cormorants 1.5, boobies, gannets, tropicbirds and frigatebirds 1.2 and pelicans 0.5. These totals represent the base estimates. The penguin total agrees moderately well with an earlier and more complicated assessment of penguin consumption (18.1 Mt) that was, however, restricted geographically to the Southern Ocean Ecosystem (Woehler 1995), which is home to more than 90% of all penguins.

Ninety-five per cent of the 69.8 Mt consumption is due to the leading 81 species, and the top 20 species are responsible for 71% of the total consumption (figure 1). With the exception of the tropical sooty tern *Sterna fuscata* and the partial exception of three migrant shearwater species (*Puffinus griseus*, *P. tenuirostris* and *P. gravis*), which may feed in the tropics for approximately one month on their north- and southbound migrations each year, the top 20 species consume prey at high latitudes (more than 30°). The 20 species are also mostly pelagic.

The estimates presented show limited sensitivity to the metabolic equations used. If the order-specific equations of Ellis & Gabrielsen (2002) are used instead of the general seabird equation (see § 2), then the estimated consumption by the three volant orders becomes: Procellariiformes 22.3 Mt (cf. 24.1 above), Pelecaniformes 3.9 (cf. 3.2), Charadriiformes 19.6 (cf. 18.8).

If the liberal estimate of the number of free-living individuals, namely four to five times the number of breeding pairs (see § 2), is used, then overall consumption is estimated at 110.3 Mt annually.
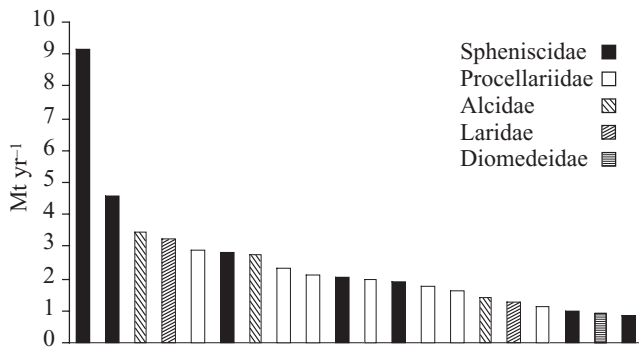
Figure 1. The global annual food consumption of the 20 seabird species whose populations consume the most prey. The penguins (Spheniscidae) are confined to higher latitudes (see Appendix A) of the Southern Hemisphere and the auks (Alcidae) to the Northern Hemisphere, whereas the procellariids include species that are confined to one or other hemisphere (e.g. Antarctic petrel *Thalassoica antarctica*, northern fulmar *Fulmarus glacialis*) and others (migratory shearwaters *Puffinus* spp.) that travel between the hemispheres. The two larids are sooty tern *Sterna fuscata* (higher consumption) and black-legged kittiwake *Rissa tridactyla*. The only albatross (Diomedeidae) is the black-browed *Thalassarche melanophrys*.

4. DISCUSSION

The principal finding of this study is that seabirds and fisheries landings remove comparable quantities of biomass from the world's oceans. The seabird take therefore exceeds the aggregate tonnage of discarded catch and illegal, unreported and unregulated catches (Pauly *et al.* 2002). However, these results need not imply that birds and fishermen are in competition for prey everywhere. Rather, at the broad scale, competition is anticipated only if both birds and fishermen are active in the same oceanic areas, and if they are catching similar prey at similar trophic levels.

The seabirds responsible for taking the greatest quantities of prey are generally pelagic species (figure 1), many living in areas where fishing is relatively limited. This is certainly true of the dominant penguin species of the Southern Ocean. There, the annual fishery take of krill *Euphausia superba* is *ca.* 0.1 Mt (see http://www.ccamlr.org), a total completely dwarfed by the 9.2 Mt removed by krill-eating macaroni penguins *Eudyptes chrysolophus*, the leading consumer in figure 1.

Globally, only *ca.* 4% of the fishery catch currently comes from the open ocean (Pauly & Christensen 1995), thus the offshore feeding habits of the most abundant seabirds may restrict resource competition between birds and fisheries. However, those habits do not protect some bird species from certain fishing practices, for example long-lining (Robertson & Gales 1998).

Competition is far more likely in heavily fished coastal and upwelling systems, particularly where seabirds and fishermen are taking prey at similar trophic levels. Studies of seabird communities in the Gulf of Alaska indicate a mean trophic level of seabird prey of 3.0 (Sanger 1987), similar to the trophic level (*ca.* 3.1) of the current global marine fisheries catch (Pauly *et al.* 1998, 2002). This concordance of trophic level is arguably more likely where the trophic level of the fisheries has declined because past

fishing has removed top predators at higher trophic levels (Pauly *et al.* 1998). One obvious potential outcome of such competition is that the fishery reduces the stock of prey for seabirds, leading to a decrease in the seabird population (Duffy 1994). However, the range of possible interactions is great (Duffy & Schneider 1994) and can sometimes, counter-intuitively, benefit seabirds. For example, in the North Sea, following removal of predatory fishes by the fishery, sandeel stocks have expanded. This has supported the growth of seabird populations, despite the fact that the fishery now targets sandeels (Furness 2002).

The calculations of seabird consumption ignore the extra food (and energy) required to raise young because this is not a large fraction of the year's consumption (Boyd 2002). Incubation is not energetically costly for seabirds (Thomson *et al.* 1998). Rearing chicks is more demanding but nevertheless requires only a small proportion of a year's annual food consumption. For example, Brown (1988) calculated the quantity of food that was delivered to the fledged chicks of three petrel species. These amounts constituted from 1.6% to 3.6% of the annual consumption of each of the chick's two parents, as calculated in my spreadsheet.

Certain current seabird populations, notably of tropical and sub-tropical species, represent only a small (less than 5%) percentage of those that existed in the past (Iredale 1914; Warham 1990; Duffy 1994; BirdLife International 2000). While it is ecologically plausible that these declines may have allowed compensating population increases in sympatric seabird species, the historical data are insufficient to allow comment on this possibility. By contrast, some of the most abundant and important of today's seabird consumers are species known to have increased in number in the past 200 years, for example the macaroni penguin and northern fulmar (Fisher 1952; Croxall *et al.* 1984). Thus there is no strong reason to suppose that the overall consumption by the world's seabirds has changed greatly in recent times.

The consumption estimates presented above are sensitive to the parameter values used. Figures for the energy density of prey and assimilation efficiency are probably correct to ± 20%. In § 3, I demonstrate that using alternative metabolic equations has limited impact on the overall consumption estimates for volant orders. More significant uncertainties relate to the population size estimates (Boyd 2002). These errors are unknown but let us assume that the coefficient of variation in the population estimate is 50% for every species. For some well-known species, the 50% estimate is probably unduly large, and so the assumption errs on the side of caution. With this assumption and assuming also that errors are independent across species, the 95% confidence interval attached to the 69.8 Mt base estimate is calculated as 55.9–83.7 Mt.

Not only does uncertainty attach to many breeding population estimates, but the ratio of breeders to non-breeders is also poorly known. While the base estimate was deliberately conservative in assuming three birds for every pair censused, more liberal, but nonetheless reasonable, assumptions of 4–5 birds per pair led to an increased estimate of 110 Mt. Applying the same assumptions as used in the previous paragraph for population errors, the 95% confidence interval is 87.3–133.2 Mt. Although these

confidence intervals are not small, they do not undermine the principal conclusion, that seabirds take a similar amount of prey to human fisheries.

Finally, if fisheries, removing some 80 Mt, are supported by 8% of marine primary productivity (Pauly & Christensen 1995), and birds, removing 70 Mt, by a pro rata amount of 7%, it would be intriguing to extend these simple global calculations to include pinnipeds and cetaceans, the other higher vertebrates of the sea.

APPENDIX A

The 20 seabird species whose total populations consume most prey by weight, ranked from highest to lowest.

macaroni penguin *Eudyptes chrysolophus*
chinstrap penguin *Pygoscelis antarctica*
Brunnich's guillemot *Uria lomvia*
sooty tern *Sterna fuscata*
short-tailed shearwater *Puffinus tenuirostris*
king penguin *Aptenodytes patagonicus*
common guillemot *Uria aalge*
sooty shearwater *Puffinus griseus*
northern fulmar *Fulmarus glacialis*
Adelie penguin *Pygoscelis adeliae*
Antarctic prion *Pachyptila desolata*
rockhopper penguin *Eudyptes chrysocome*
great shearwater *Puffinus gravis*
Antarctic petrel *Thalassoica antarctica*
horned puffin *Fratercula corniculata*
black-legged kittiwake *Rissa tridactyla*
white-chinned petrel *Procellaria aequinoctialis*
emperor penguin *Aptenodytes forsteri*
black-browed albatross *Thalassarche melanophrys*
magellanic penguin *Spheniscus magellanicus*

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