

Modelling and mapping resource overlap between seabirds and fisheries on a global scale: a preliminary assessment

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ABSTRACT: Coexistence of foraging seabirds and operating fisheries may result in interactions such as competition for the same prey resources. We used GIS-based modelling at a scale of $0.5 \times 0.5^\circ$ spatial cells to: (1) map the foraging distribution of seabirds; (2) predict their annual food consumption rates in a spatially explicit manner; and (3) estimate a spatially explicit seabird–fisheries overlap index. Information on population size, diet composition and foraging attributes of 351 seabird species was compiled into a Microsoft Access database. Global annual food consumption by seabirds was estimated to be 96.4 million tonnes (95 % CI: 78.0 to 114.7 million tonnes), compared with a total catch of nearly 120 million tonnes by all marine fisheries. Krill and cephalopods comprised over 58 % of the overall food consumed and fish most of the remainder. The families Procellariidae (albatrosses, petrels, shearwaters) and Spheniscidae (penguins) were responsible for over 54 % of the overall food consumption. Seabird foraging distribution maps revealed that areas around New Zealand, the eastern Australian coast, and the sub-Antarctic islands had high species richness. However, temperate and polar regions supported high seabird densities and most food extracted by seabirds originated there. Furthermore, maps of food consumption rates revealed that most food consumed by seabirds was extracted from offshore rather than nearshore waters and from areas where seabird–fisheries overlap was low. The resource overlap maps identified 'hotspots' of highest potential for conflict between fisheries and seabirds. Thus, this study may provide useful insight when developing management approaches for designing offshore marine conservation areas.

KEY WORDS: Seabird–fisheries interactions · Resource overlap · Foraging distribution · Seabird food consumption

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INTRODUCTION

Fisheries have dramatically expanded in the last few decades (Pauly et al. 2002, 2003, 2005, Myers & Worm 2003) and now extract from the world's oceans well over 120 million tonnes of resources annually (Pauly et al. 2002). Global fishing operations reduce populations of target and non-target species and alter food web function and ecosystem structure (Pauly et al. 1998, Moore & Jennings 2000, Jennings et al. 2001). To quantify these effects, these reductions must be analysed on a large scale and within an ecosystem-based

context. To date fisheries assessment approaches have used time series analyses to study the variability of target species over time. These approaches, however, often fail to detect variability in space. Maps have been proposed as a complementary tool for fisheries science (Pauly et al. 2003, Worm et al. 2003) to help make the necessary transition towards ecosystem-based management.

Moreover, the incorporation of top predators, such as seabirds, into large scale ecosystem approaches has been acknowledged as an integral part of understanding food web structure and ecosystem functions (e.g.

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Cairns 1992, Fowler 1999). Seabirds are abundant, conspicuous and can indicate ecological effects of oceanographic changes (e.g. sea surface temperature anomalies in the Southern Indian Ocean; Weimerskirch et al. 2003). They also may signal changes in the condition and availability of prey stocks (e.g. Barrett & Krasnov 1996, Kitaysky et al. 2000) and serve as indicators of ecosystem change (e.g. Ainley et al. 1995, Weimerskirch et al. 2003).

Several authors have attempted to determine the trophic role of seabirds in marine food webs by estimating the amount of food they consume. These studies have focused on only one (e.g. Lorentsen et al. 1998, Rodhouse et al. 1998, Bunce 2001) or a few seabird species breeding at one location (e.g. Croll & Tershy 1998, Green et al. 1998, Goldsworthy et al. 2001, Barrett et al. 2002). Efforts to estimate food consumption on larger spatial scales (e.g. within a large marine ecosystem or throughout an ocean basin) have been sporadic and have focused on a single species (e.g. Woehler 1995). Brooke (2004) was the first investigator to tackle the issue of seabird food consumption on a global scale; his study included most seabird species. He estimated an annual food consumption of 70 million tonnes for the world's oceans. The present study represents the first attempt to express global food consumption rates by seabirds on a spatial scale. In addition we investigated how the world's seabirds may interact with fisheries and identified areas of highest concern.

Interactions between fisheries and seabirds have also received considerable attention (e.g. Furness 1982, Montevecchi 2002). Some studies have shed light on how entanglement in fishing gear increases seabird mortality and affects seabird populations (e.g. Belda & Sanchez 2001, Tuck et al. 2003). In addition human exploitation of marine resources has provided an increased opportunity for some seabirds to take advantage of prey (as discards) that would otherwise be unavailable to them. This form of interaction results in increases in seabird population sizes (e.g. Furness et al. 1988, Votier et al. 2004); however, seabird populations rely heavily on the fate and future of fisheries (e.g. reduction in discarding by fisheries appears to affect entire seabird communities; Reeves & Furness 2002).

Other forms of interaction between fisheries and seabirds result from sharing the same resource. Resource overlap represents the extent to which 2 consumers overlap in the exploitation of the same resource in the same area and time (Hurlbert 1978). Although resource overlap describes a more neutral form of interaction, it may be regarded as an indicator of potential competition (Hurlbert 1978). In this case competition occurs only when a resource is limited. Mod-

ern fisheries selectively remove large quantities of biomass from marine ecosystems (e.g. Pauly & Christensen 1995). Their vast expansion worldwide in the last few decades has resulted in the collapse of many fish stocks (Pauly et al. 2002), overexploitation of high trophic level prey and a worrisome trend toward fishing down the food web (Pauly et al. 1998). As a result industrialized modern fisheries may negatively affect seabirds through depletion of resources that would otherwise be available as prey (e.g. Wanless et al. 2005). Prey depletion by fisheries may also trigger indirect trophic cascading effects and enhance competition with other top predators that rely on the same prey as seabirds (Verity et al. 2002).

Potential competition between seabirds and fisheries for the same prey has been given considerable attention (e.g. Furness 1982, Furness & Birkhead 1984, Montevecchi 2002, Cowx 2003); however, few studies have actually quantified this form of competition. Duffy & Schneider (1994) proposed the use of Horn's (1966) modification of Morisita's (1959) index for the assessment of resource overlap. Resource overlap has been estimated between the penguin population and the krill fisheries in the South Shetland Islands (Ichii et al. 1996, Croll & Tershy 1998). Moreover, Goldsworthy et al. (2001) used a percentage similarity index (% PSI; sensu Schoener 1970) and assessed low overlap between seabird populations and the Patagonian toothfish *Dissostichus eleginoides* fishery around Macquarie Island.

In this study we attempted to express on a spatial scale the amount of food seabirds consume and identify areas where competition between seabirds and fisheries may be possible by addressing 3 goals: (1) to map the foraging distribution of seabirds; (2) to estimate seabird annual food consumption rates per cell; and (3) to obtain an estimate of a seabird–fisheries overlap index per cell by comparing seabird food consumption rates from (2) with the spatially disaggregated fisheries catches database of the Sea Around Us Project (Watson et al. 2004; www.seaaroundus.org).

METHODS

We compiled information for 351 marine bird species (belonging to 4 orders and 14 families) in a Microsoft Access database. Of these species 334 are traditionally considered to be seabirds. The remaining 17 were species of sea ducks that breed inland, but prey upon small fish and invertebrates that occur along the coast. We gathered information using the following databases: (1) Aquatic Sciences and Fisheries Abstracts; (2) Web of Science, Institute for Scientific Information; and (3) BioSciences Informa-

tion Service of Biological Abstracts. These cover peer-reviewed journals and other literature sources. Information was also extracted from the following online databases: (1) Avibase—the world bird database (www.bsc-eoc.org/avibase); (2) the United Nations Environment Programme—World Conservation Monitoring Centre Species Database (<http://www.unep-wcmc.org/species/dbases/about.cfm>); (3) BirdLife International (www.birdlife.net); (4) the National Audubon Society Christmas Bird Count (www.audubon.org/bird/cbc/); (5) Birds of North America Online (<http://bna.birds.cornell.edu/BNA/>); and (6) Wetlands International (www.wetlands.org).

Our database contains information on seabird taxonomy, population dynamics, diet composition and foraging ecology. The above information was used to estimate annual food intake rates of seabirds as well as to map their foraging distribution. Furthermore, spatially explicit food consumption rates were then compared with spatially disaggregated annual fisheries catches to obtain a map of resource overlap between fisheries and the world's seabirds. We used a GIS-based modelling approach and the same spatial grid of $0.5 \times 0.5^\circ$ cells developed by the Sea Around Us Project (Watson et al. 2004) to compare seabird food consumption per cell with fisheries catch.

Food consumption by seabirds. Information necessary to estimate the seabirds' daily food intake (DFI) and, hence, their annual food consumption included: (1) body mass (in g) of seabirds species taken from Dunning (1993) and Schreiber & Burger (2002); (2) basal and field metabolic rates (BMR and FMR, respectively, estimated using order-specific allometric equations from Ellis & Gabrielsen 2002; in kJ d^{-1}). BMR and FMR were used to estimate energy requirements (ER) of seabirds in the non-breeding and breeding season, respectively; (3) a matrix of standardized diet composition; and (4) population sizes of breeding seabirds (see below).

Daily food intake (DFI) was estimated using a bioenergetic model created by the ICES Working Group on Seabird Ecology (ICES 2000):

$$\text{DFI}_i = \frac{\text{ER}_i}{\sum_{j=1}^G \text{DC}_{ij} \times \text{ED}_j} \times \frac{1}{\text{AE}_i} \quad (1)$$

where DFI_i denotes daily food intake for each seabird species i , ER_i is the energy requirements for each i , DC_{ij} is the fraction of food item j in the diet of each i , ED_j is the mean energy density of each prey j (see Table 11 in Karpouzi 2005). ED_j values were available either at the species or the taxon level for prey items (see Table 11 in Karpouzi 2005). AE_i is the mean food assimilation efficiency for each i , and G the total num-

ber of food groups (Table 1) encountered in the diet of each i . AE_i was assumed equal to 75% (Gabrielsen 1994, ICES 2000, Barrett et al. 2002) unless species-specific information was found in the literature.

To estimate seabird species' annual food consumption DFI_i was estimated separately for the breeding and non-breeding season by considering ER_i for the breeding season equal to FMR (ICES 2000) and equal to $2.5 \times \text{BMR}$ for the non-breeding season (ICES 2000). The length of the breeding season was assumed equal to incubation period plus time from hatching to leaving the nest or burrow plus 20 d (Cramp 1985). Following Brooke (2004) we assumed a coefficient of variation of 50% for population size to estimate minimum and maximum confidence intervals for global food consumption rates.

Consumption by seabirds was specified using 25 food groups (see Table 1 for description). Food groups were compiled based on the taxonomic groups represented in the Sea Around Us database (Table 1). Total food consumption was estimated per spatial cell based on the seabird density of each cell (see below).

At-sea distribution of seabirds. Data on seabirds' global breeding distribution and demography were tabulated by species, year and breeding location. Each breeding location was assigned a population size for each breeding species and original census year. Population sizes are usually expressed in the literature as breeding pairs (bp). The following formulae were used to estimate non- and prebreeders present in colonies (1) for single-egg laying species ($\text{bp} \times 0.6$) + ($\text{bp} \times 0.7$); and (2) for multi-egg laying species ($\text{bp} \times 0.6$) + ($\text{bp} \times 1.0$) (ICES 2000). These calculations assume that nonbreeders comprise 30% of the breeding population and that the fledging success of single-egg and multi-egg clutch species is 0.7 and 1.0 chick per pair, respectively (Cairns et al. 1991). The population size table covered the years from 1950 to 2003. For years when population sizes were not available, data were interpolated assuming a linear relationship between the available data points. Data were also extrapolated from the first available data point back to 1950 as well as from the last available data point to 2003 assuming no change in the population size had occurred.

We modelled the at-sea distribution of seabirds using information on their distributional range. Primarily, all 351 species were assigned a distributional range defined by the northernmost and southernmost latitude for each species. Distributional ranges were taken from Harrison (2004), the Global Register of Migratory Species (GROMS; www.groms.de) and BirdLife International. The species were divided into 4 groups according to the distance they fly from their colony to feed. The following groups emerged. Group A

Table 1. Food groups used to express standardized diet composition data, calculate annual food consumption rates and assess resource overlap between seabirds and fisheries on a global scale. Food groups were compiled based on the taxonomic groups represented in the Sea Around Us Project database

Food group	Taxa included
Perch-like	Perciformes, Anarhichadidae, Mugilidae, Labridae, Apogonidae, <i>Diplodus</i> spp., <i>Scomber japonicus</i> , <i>S. scombrus</i> , <i>Emmelichthys nitidus nitidus</i> , <i>Seriola brama</i> , <i>Dicentrarchus labrax</i> , <i>Pagellus acarne</i> , <i>Lithognathus mormyrus</i> , <i>Pomatomus saltator</i> , <i>Thyrsites atun</i>
Gadiformes	<i>Boreogadus saida</i> , <i>Gadus morhua</i> , <i>G. macrocephalus</i> , <i>Macruronus novaezelandiae</i> , <i>M. magellanicus</i> , <i>Pseudophycis bachus</i> , <i>Micromesistius poutassou</i> , <i>Micromesistius australis</i> , <i>Pollachius virens</i> , <i>Merluccius</i> spp., <i>Theragra chalcogramma</i> , <i>Eleginus gracilis</i> , <i>Pleurogrammus monoptyerygius</i> , <i>Pleurogrammus azonus</i>
Beloniformes	<i>Belone belone belone</i> , <i>Scomberesox saurus saurus</i> , <i>S. saurus scombroides</i> , <i>Cololabis saira</i>
Scorpaeniformes	Cottidae, <i>Prionotus</i> spp., <i>Trigla</i> spp.
Flatfishes	Pleuronectidae, <i>Reinhardtius hippoglossoides</i> , <i>Solea</i> spp.
Anchovies	<i>Engraulis encrasicolus</i> , <i>E. australis</i> , <i>E. anchoita</i> , <i>E. capensis</i> , <i>E. japonicus</i> , <i>E. mordax</i> , <i>E. ringens</i>
Atherinidae	Silversides
Carangidae	<i>Decapterus</i> spp., <i>Trachurus declivis</i> , <i>T. mediterraneus</i> , <i>T. trachurus</i> , <i>T. symmetricus</i>
Channichthyidae	Crocodile icefishes
Clupeidae	<i>Clupea harengus</i> , <i>C. pallasii</i> , <i>Sardinops sagax</i> , <i>Etrumeus teres</i> , <i>E. whiteheadi</i> , <i>Sardina pilchardus</i> , <i>Sprattus sprattus</i>
Osmeridae	Smelts
Exocoetidae	Flyingfishes
Macrouridae	Grenadiers
Myctophidae	<i>Electrona antarctica</i> , <i>Gymnoscopelus nicholsi</i> , <i>Lampanyctus</i> spp., <i>Lampichthys</i> spp.
Nototheniidae	<i>Notothenia rossii</i> , <i>N. coriiceps</i> , <i>N. nybelini</i> , <i>Gobionotothen gibberifrons</i> , <i>Lepidonotothen squamifrons</i> , <i>Pleuragramma antarcticum</i> , <i>Dissostichus eleginoides</i> , <i>D. mawsoni</i>
Synodontidae	Lizardfishes
Sand lances	<i>Ammodytes hexapterus</i> , <i>A. americanus</i> , <i>A. marinus</i>
Capelin	<i>Mallotus villosus</i>
Goatfishes	<i>Upeneus</i> spp.
Pacific salmonids	<i>Oncorhynchus</i> spp.
Redfishes	<i>Sebastes</i> spp.
Fish	Other taxa, not included in the above food groups
Cephalopods	Teuthida, <i>Kondakovia longimana</i> , <i>Loligo</i> spp., <i>Illex</i> spp.
Decapods	Shrimps, prawns, Brachyura
Krill	<i>Euphausia superba</i> , <i>E. crystallorophias</i> , <i>Meganyctiphanes norvegica</i> , <i>Thysanoessa</i> spp.

was made up of nearshore species that forage within 1 km from shore and included some species of cormorants, gulls, terns, pelicans, seabirds and some alcids. Group B consisted of coastal species that travel up to 10 km from shore to find food and included mainly species of cormorants, gulls, terns and seabirds as well as some alcids. Group C consisted of seabird species of the continental shelf that forage within 200 km from land and contained some storm petrels and shearwaters, some boobies, crested penguins, alcids, and larger-bodied gulls and cormorants. Each breeding population was assumed to disperse evenly from the colony in all directions. The probability of occurrence was assumed to decrease linearly with distance from land, to zero at the maximum reported foraging range. Group D comprised pelagic species that forage in deeper, offshore waters at distances >200 km. This group includes pelagic, deep diving penguins, as well as albatrosses, prions, petrels, gannets, some boobies, some shearwaters and

storm petrels. Group D was further divided into 3 sub-groups: (1) species that travel distances >200 km to feed; however, the probability of occurrence decreases linearly to zero at the maximum reported foraging range; (2) species whose probability of occurrence was described by a trapezoidal probability distribution (i.e. occurrence was assumed to be uniformly highest within a threshold distance from the breeding colony and then to decrease linearly to zero at the maximum reported foraging range); and (3) 12 *Puffinus* species (i.e. *P. assimilis*, *P. bulleri*, *P. carneipes*, *P. creatopus*, *P. gravis*, *P. griseus*, *P. huttoni*, *P. nativitatis*, *P. newelli*, *P. pacificus*, *P. puffinus* and *P. tenuirostris*). These *Puffinus* spp. breed in areas of the Southwest Pacific and South Atlantic oceans. At the end of the breeding season they migrate to feed and winter in the waters of the North Pacific and the North Atlantic oceans (e.g. Guzman & Myres 1983, Camphuysen 1995, Gould et al. 1997, 1998, Spear & Ainley 1999, Ito 2002).

On occasion shearwaters form flocks and feed with surface-schooling tunas (Au & Pitman 1988, Au 1991). These seabirds benefit when tunas drive prey closer to the surface where they can be reached by surface divers. Such foraging behaviour has been documented, for instance, for Wedge-tailed shearwaters that feed with yellowfin tuna *Thunnus albacares* and less frequently with Skipjack tuna *Katsuwonus pelamis* in the eastern tropical Pacific Ocean (Au & Pitman 1988, Au 1991). The same habit is also shown by Greater shearwaters that feed with tunas in the Atlantic Ocean (Clua & Grosvalet 2001). Hence, to map the foraging distribution of the abovementioned 12 species of shearwaters we assumed that their distribution matched that of 3 species of schooling tunas (yellowfin tuna, southern bluefin tuna *T. maccoyii* and northern bluefin tuna *T. thynnus*; available online at www.seararoundus.org).

For all 4 groups seabird distribution was further constrained by the distribution of prey that occurs in the diet of the avian predators. Prey distribution maps are available from the Sea Around Us Project.

Seabirds–fisheries resource overlap. To assess interactions between seabirds and fisheries we estimated a resource overlap index, a , that uses the amounts of prey taken jointly by seabirds and fisheries. We used the indices of Morisita (1959) and Horn (1966) as modified by Kaschner (2004). Kaschner (2004) applied a weighting factor to measure the importance of spatial cell of either very low seabird food consumption rates, or very low fisheries catches or both. Thus, the resource overlap index was as follows:

$$a = \frac{2 \times \sum_{i=1}^G p_{ij} \times p_{fj}}{\sum_{i=1}^G p_{ij}^2 + \sum_{f=1}^H p_{fj}^2} \times (pQ_i \times pC_f) \quad (2)$$

where a takes values from 0 to 1, with 0 indicating no overlap and 1 complete overlap; p_{ij} is the proportion of a food group j to the total amount of food taken by a seabird i ; p_{fj} is the proportion of j in the catch of the fishery f ; G denotes the number of food groups taken by i , and H the number in the catch of the fishery f ; pQ_i and pC_f denote the proportion of food taken by i and the proportion of food caught by f at each cell. The resource overlap index, a , was quantified on a global scale and allocated to each spatial cell using seabird densities for each cell and the disaggregated fisheries catches from the Sea Around Us Project (Watson et al. 2004).

We also calculated the proportion of seabird food consumption by areas of overlap with fisheries. Logarithmic transformation of the y -axis was required, because the proportion of food consumed in cells with overlap >0.3 was very close to 0.

RESULTS

At-sea distribution of seabirds

Fig. 1 shows the predicted foraging distribution of all seabird species combined and seabird density (i.e. number of individuals km^{-2}). Areas along the coast of New Zealand, the eastern, southeastern coast of Australia, the sub-Antarctic islands and the Patagonian Shelf are characterized by the highest number of foraging seabird species in the world (Fig. 1a). In addition, Hawaii, the Caribbean Sea, the California current system and the waters around and north of the Galápagos Islands are the only areas north of the equator with high numbers of foraging species (Fig. 1a). Temperate and polar regions of the northern hemisphere have the lowest number of foraging species (Fig. 1a); however, these areas are characterized by high seabird densities (Fig. 1b).

Total annual food consumption by seabirds

The estimated annual global food consumption of all seabird species combined was 96.4 million tonnes (95% CI: 78.0–114.7 million tonnes). Krill and cephalopods comprised more than 58% of the overall food consumption (krill, 37.8%; cephalopods, 20.5%, Fig. 2). Fish, for which no catch is reported, and myctophids were the 3rd and 4th ranked prey, respectively, consumed by seabirds (Fig. 2). The families Procellariidae and Spheniscidae were responsible for more than 54% of the overall food consumption.

Mapping food consumption rates of all seabirds combined (Fig. 3) revealed that a considerable amount of food is consumed by seabirds over the continental shelves (e.g. along the western and eastern coasts of South America, the northwestern Pacific Ocean [Okhotsk Sea and the Sea of Japan] and the continental shelves of the North Atlantic Ocean, Fig. 3). However, most of the food is taken from offshore areas (e.g. offshore waters of the southwestern Pacific Ocean and the Southern Ocean, Fig. 3) particularly from the cold temperate and polar waters of the world (Fig. 3) where seabirds forage in high densities.

Spatially explicit resource overlap between seabirds and fisheries

Mapping the overlap between all seabirds and fisheries on a global scale revealed that, for the 1990s, overlap mostly occurred in the cold temperate waters of the northern hemisphere (Fig. 4). In the North Atlantic Ocean 'hotspots' of high overlap were present

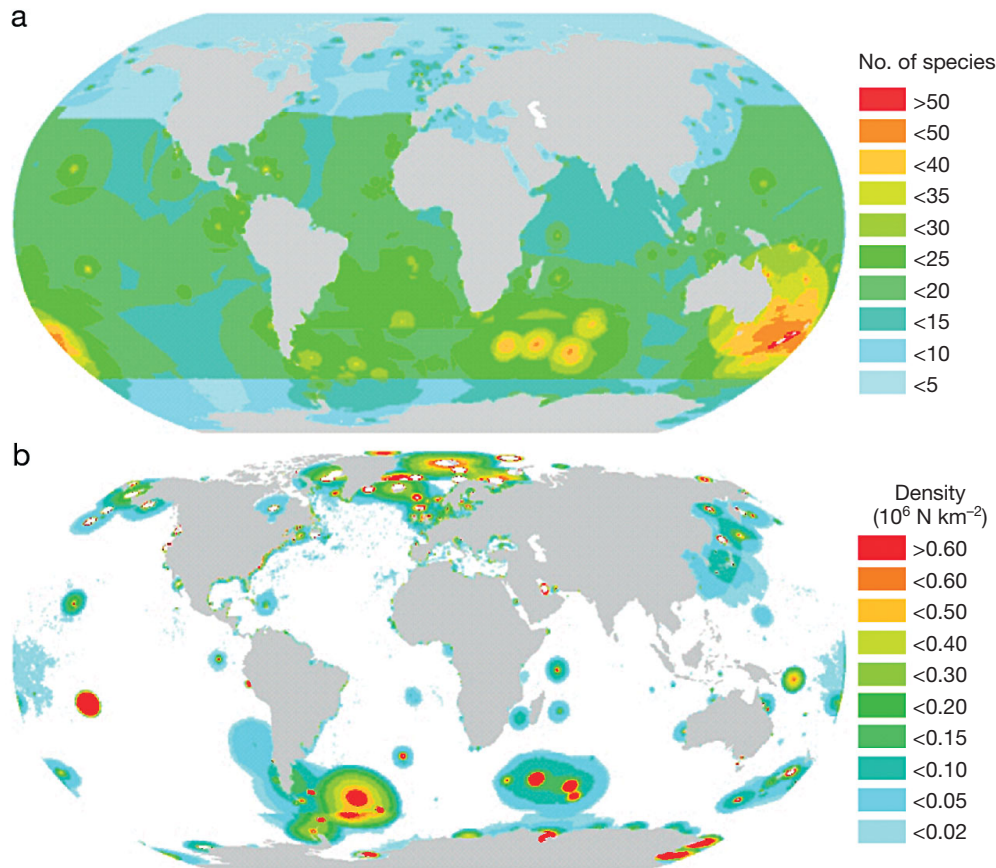


Fig. 1. Predicted foraging distribution of seabird species during an average year in the 1990s, expressed in (a) number of seabird species per spatial cell, and (b) number (N) of individuals per km²

throughout the shelf areas of Europe and along the coast and shelf areas of eastern Canada. In the North Pacific Ocean high overlap was estimated for the Asian shelves and the eastern Bering Sea (Fig. 4).

In the southern hemisphere resource overlap between seabirds and fisheries was high in the productive waters of the Humboldt and Benguela currents (Fig. 4). The waters around New Zealand were also characterized by very high overlap (Fig. 4). Lastly, the Patagonian Shelf and the areas around the Antarctic Peninsula were both of high relative importance (Fig. 4).

In the 1990s, <1% of all food taken by seabirds was consumed in areas of high spatial overlap with commercial fisheries (Fig. 5). In other words, most of the food consumed by seabirds originated from areas where resource overlap was very low (Fig. 5).

DISCUSSION

The first major step of this work was the creation of a database to incorporate and computerize information on the biology, ecology and demography of the world's

seabird species. Only recently has the need been expressed for transforming published information on marine biodiversity into a digital, more interactive and

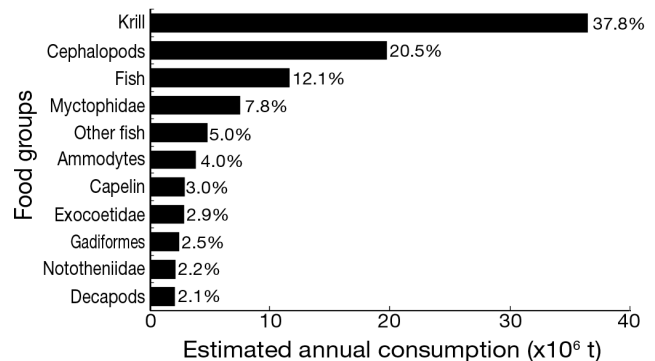


Fig. 2. Percentage contribution of food groups (see Table 1) in the estimated annual global food consumption of all seabird species combined. 'Other fish': anchovies (1.4%), Clupeidae (1.1%), *Sebastes* spp. (0.7%), Carangidae (0.5%), goatfishes (0.4%), perch-like fishes (0.2%), flatfishes (0.2%), Belontiiformes (0.1%), Scorpaeniformes (0.1%), Channichthyidae (0.1%), Osmeridae, Atherinidae, Synodontidae, *Oncorhynchus* spp. and Macrouridae (<0.05% each)

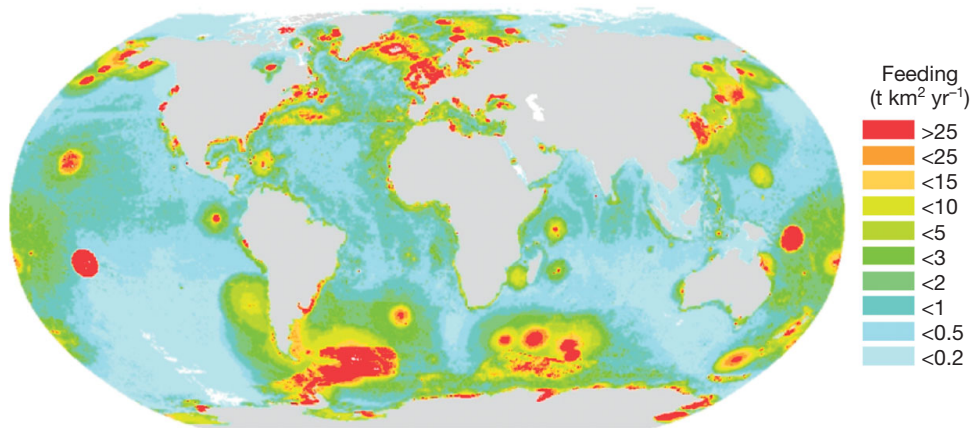


Fig. 3. Predicted global food consumption rate (in tonnes $\text{km}^{-2} \text{year}^{-1}$) of all sea-birds combined for an average year in the 1990s

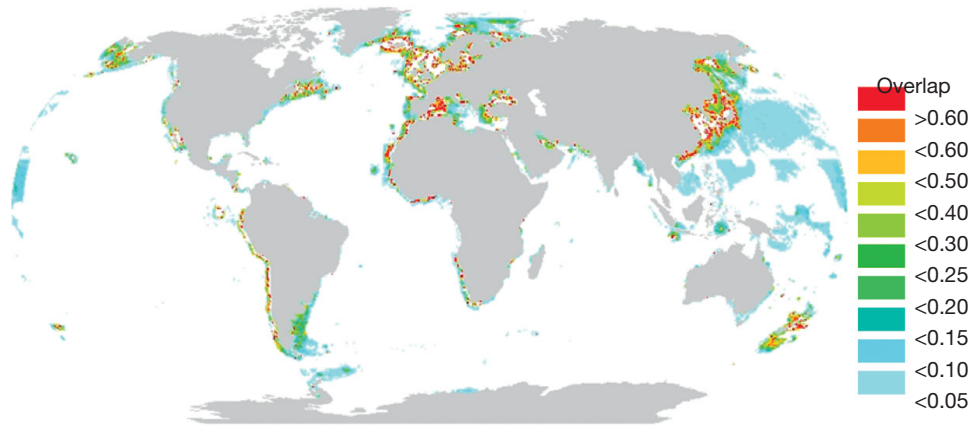


Fig. 4. Estimated resource overlap between all seabirds and fisheries for an average year in the 1990s

readily accessible form (Bisby 2000, Costello et al. 2006 and references therein). Our efforts primarily focused on the extraction of data on seabird population sizes, habitat, and feeding preferences from over 3000 scientific articles published from the early 1900s to the present. Then data were transformed into computerized

information that was further analysed to explore population trends, seabird foraging distribution patterns and interactions with fisheries.

Global estimates of total annual food consumption by seabirds

Our maps of food consumption rates for all seabirds of the world were a first attempt to quantify and express where nesting seabirds extract their food from the world's oceans. Previous publications have quantified regional food consumption by seabirds (e.g. North Atlantic Ocean: Cairns et al. 1991, Lilliendahl & Solmundsson 1997, Barrett et al. 2002, 2006; South Pacific Ocean: Muck & Pauly 1987; Southern Ocean: Adams et al. 1993, Cooper & Woehler 1994). Brooke (2004) was the first to provide a global estimate of food consumption by seabirds. Our estimate of worldwide consumption was about 30% higher (96.4 million tonnes) than Brooke's (2004) estimate of 69.8 million tonnes. This is probably because we considered more seabird species (351) than Brooke (2004) did (309). Moreover, Brooke

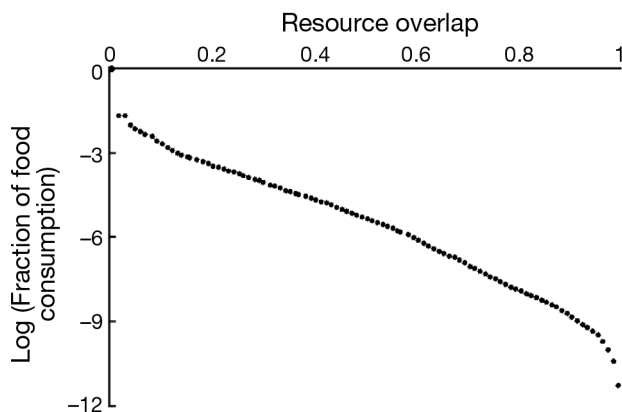


Fig. 5. Fraction of food consumed by seabirds in the 1990s by areas of overlap with fisheries

(2004) assumed, conservatively, that one non-breeder exists for every breeding pair to estimate global population size. As a result, his estimate of population size was 0.7 billion individuals, versus 0.9 billion individuals in our estimate. However, Brooke (2004) agreed that a 'liberal' global population estimate (i.e. breeding pairs multiplied by 5 for longer-lived species and by 4 for other groups) is plausible. Our global food consumption estimate was, thus, similar to Brooke's (2004) 'liberal' estimate.

Uncertainty associated with the parameters of the bioenergetic model used for estimating food consumption by seabirds may affect the model's outputs. Error can be associated with both the metabolic parameters (e.g. Furness 1978) as well as the population size estimates (Goldsworthy et al. 2001, Brooke 2004). Indeed, bioenergetic models are primarily sensitive to changes in the demographic parameters such as the population size estimates. In our case very few population time series that spanned from the early 1950s to the present were available to us. Three examples here are the Guanay cormorant *Phalacrocorax bougainvillii*, the Peruvian booby *Sula variegata*, and the Peruvian pelican *Pelecanus thagus* breeding in Peru; population sizes for all 3 species were available from 1953 to 2000 (Jahncke 1998, Crawford & Jahncke 1999, Sueyoshi 2000). However, for 97% of seabird populations, population size estimates used before 1970 were based on backward extrapolation (i.e. we assumed no change in population size). More data on seabird population sizes then became available and the percentage of interpolated population estimates decreased to 86%. Thus, uncertainty in the model estimates increases both with the lack of population size data and due to the assumption of no trend when extrapolating population sizes. When we assumed a coefficient of variation of 50% in the population sizes as Brooke (2004) did, 95% confidence intervals provided food consumption estimates that ranged from 78.0 to 114.7 million tonnes. Although these confidence intervals are large they suggest that seabirds around the world consume significant quantities of marine resources that are 70 to 95% of the total fisheries catch (i.e. ca. 120 million tonnes of resources annually if account is taken of fish illegally caught and not reported and of fish that are discarded; Pauly et al. 2002).

Energy requirements of seabirds fluctuate seasonally because the energetic costs of various stages in the life cycle of mature seabirds differ (e.g. Furness 1978, Koteja 1991, Ellis & Gabrielsen 2002). Therefore, energy demands of seabirds were estimated here using BMR and FMR for the breeding and the non-breeding season, respectively. However, BMR and FMR values were estimated using allometric equations (see 'Methods' and Ellis & Gabrielsen 2002), which

may entail bias and may affect the model's predictions. Good empirical measurements of FMRs (e.g. with the use of doubly-labelled water [DLW]; Uttley et al. 1994, Golet et al. 2000) measure energy consumption of free-living animals and give estimates with an accuracy of $\pm 7\%$ (Nagy 1989, Nagy et al. 1999). However, such measurements are available for only a small number of seabird species. Thus, sensitivity analysis that compares how metabolic parameters derived from either equations or empirical DLW experiments drive the bioenergetic model outputs could not be undertaken.

Quantitative diet composition data were available for 50% of the 351 seabird species. As a result additional uncertainty in the food consumption estimates may have resulted from our assumption that the diet composition for 177 of seabird species was the same as that for another congeneric species. Other sources of error may include differences in the energy density of prey attributed to differences in the relative status (i.e. size, age and reproductive state), or seasonal or geographical differences and influences. Mårtensson et al. (1996) determined that revision of prey calorific density used to estimate the food consumption of minke whales *Balaenoptera acutorostrata* in the northeastern Atlantic Ocean resulted in food consumption estimates that vary by 10 to 15% (translating to ca. 300 000 tonnes of food). Therefore, accurate measures of prey energy density for a range of species are important in generating more accurate model predictions (Tierney et al. 2002).

At-sea distribution of seabirds

This was a first preliminary attempt to construct a GIS-based model that allows mapping the at-sea distribution of all seabird species of the world. A previous attempt to explore global patterns of species richness was carried out by Chown et al. (1998) who compiled data on the breeding locations and foraging-wintering distributions of 108 Procellariiform species. Their analysis revealed that the waters around New Zealand, the sub-Antarctic islands of the Southern Ocean and Hawaii hold the largest number of Procellariiform species (Chown et al. 1988). The same distribution patterns were also found when we considered all seabird species (Fig. 1a). These areas of high species richness comprised biodiversity 'hotspots'. In addition maps of seabird foraging densities showed that the polar waters of the globe hold the highest seabird densities (Fig. 1b). They also represented areas where the most food is taken by seabirds (Fig. 3). In the southern hemisphere these areas coincided with areas where prey, such as the Antarctic krill, squid and the mesopelagic fishes of the families Nototheniidae and Myctophidae,

were abundant (e.g. Rodhouse et al. 1996, Lascara et al. 1999, Duhamel et al. 2000). In the northern hemisphere most feeding occurred in areas that depicted the distributions of prey, such as capelin *Mallotus villosus*, sand lance *Ammodytes* spp. and herring *Clupea harengus* (e.g. the waters of the North Atlantic Ocean; Fig. 3).

Our efforts to model the at-sea distribution of seabirds focused primarily on expressing in a quantitative manner what is already known from the literature about seabird biology and biogeography. The first 3 modelling steps dealt with areas where seabirds breed, the latitudinal range within which they occur and the distance they fly away from shore in search of prey. This is a rather crude, probably simplistic modelling approach and associated uncertainty may stem from the assumption that the probability of occurrence for a seabird species declines linearly with distance from shore. Such a unimodal response curve is likely inadequate to describe the occurrence of seabird species in marine foraging habitats and future work will focus on refining this assumption.

At-sea foraging distributions of seabirds were further refined based on prey distributions available from the Sea Around Us Project. Although the underlying assumption is that seabirds feed where prey occurs, diet for nearly half of the seabird species is not known and therefore was assumed to be similar to that of a congeneric species, adding more uncertainty to our model's output. Lastly, the use of tuna distributions to depict the distribution of 12 migratory shearwater species must be viewed as a stopgap. Associations between shearwaters and feeding surface-schooling tunas have been documented for tropical waters only (Au & Pitman 1988, Au 1991, Clua & Grosvalet 2001). However, the same is not true for temperate waters where shearwaters also occur (e.g. Guzman & Myres 1983). Thus, we may have underestimated the number of seabird species and failed to predict the occurrence of shearwater species in certain cold temperate areas (e.g. the Gulf of Alaska; Fig. 1). Certainly, this feature of the distribution maps will have to be improved.

Several variables that define pelagic foraging habitats and the at-sea distribution of far-ranging seabirds have been used in the literature (e.g. Rodhouse et al. 1996, Hyrenbach et al. 2002, 2006, Ainley et al. 2005); these are sea surface temperature, sea surface salinity, seafloor depth, and chl *a* concentration. Moreover, Nel et al. (2001) recently correlated satellite-tracked grey-headed albatross movements with weekly satellite-derived sea surface height anomaly (SSHA) data. Indeed, positive and negative SSHA (i.e. warm and cold eddies) may contain elevated stocks of potential prey that attract far-ranging pelagic seabirds (Nel et al. 2001). In the future, our efforts will focus on determin-

ing how environmental and oceanographic factors affect the distribution of seabirds at sea. Our ultimate goal will be to build global species- or family-specific predictive models of preferred habitat for foraging seabirds.

Resource overlap between fisheries and seabirds

Our assessment of resource overlap between fisheries and seabirds showed that seabirds extract most food from offshore areas where overlap with fisheries is low (Fig. 5). Our maps of spatial resource overlap identified that 'hotspot' areas occur mainly on or along the continental shelves (Fig. 4). This is not surprising because fisheries that target demersal, benthic and benthic-pelagic organisms cover the shelves surrounding continents and islands, whereas fisheries operating in the open ocean target mainly tuna, billfishes, and other large pelagic species (Pauly et al. 2003), which are not prey items in the diet of seabird species.

The study of seabird food consumption has often served as the means of investigating the potential for competition between seabirds and fisheries (e.g. Croll & Tershy 1998, Green et al. 1998, Bunce 2001, Goldsworthy et al. 2001, Furness 2002). Indeed, fisheries and foraging seabirds inevitably interact in a number of ways (review by Montevecchi 2002). Three main effects of fisheries on seabirds are: (1) consumption of and dependence on fisheries discards (e.g. Votier et al. 2004); (2) increased mortality from entanglement in fishing gear (e.g. Melvin & Parrish 2001); and (3) competition for the same prey targeted by the fisheries for human consumption (e.g. Furness 2002).

In this study we quantified the potential for competition that resulted from seabirds feeding on fish and other aquatic organisms and fisheries targeting the same resources (Type 3 interactions) by measuring a resource overlap index. However, for seabird populations that rely heavily on discards (e.g. Votier et al. 2004) discards found in the diet of seabirds were not included in the consumption rate and overlap calculations. Therefore, in areas of the world where seabirds rely on discards for food (e.g. the North Sea: Garthe et al. 1996; the Mediterranean Sea: Oro & Ruiz 1997) we believe that overlap was underestimated.

Entanglement of seabirds in fishing gear was also not taken into account in our modelling approach. Mortality of seabirds due to entanglement in fishing gear usually results from seabirds being hooked or dragged underwater and drowned while trying to feed on bait or on fish caught by long-line gear. In net fisheries birds are caught and drowned in the nets while diving in pursuit of their prey (Moore & Jennings 2000). Such interactions cannot be quantified as out-

lined in the methodology section here. Thus, in areas where such interactions are prevalent we believe that competition between seabirds and fisheries was underestimated. For instance, mortality from fishing gear has been blamed for population declines in several endangered seabird species in the waters of the Southern Ocean (e.g. wandering albatross *Diomedea exulans*, Cherel & Weimerskirch 1996; white-chinned petrel *Procellaria aequinoctialis*, Weimerskirch et al. 1999; grey-headed albatross *Thalassarche chrysotoma*, Nel et al. 2000; Tristan albatross *Diomedea dabbenena*, Cuthbert et al. 2005). Indeed, in these areas where long-lining is a dominant fishing method very low or no resource overlap was predicted in our study (Fig. 4). However, the expansion of the Sea Around Us catch database to allow for the inclusion of information on fishing gear worldwide will allow the development of maps that reveal what types of gears are used in different areas (Watson et al. 2006). Overlay of gear maps with seabird distribution maps will also allow us to explore spatial overlap between seabirds and fisheries that are attributed to entanglement in fishing gear (Watson et al. 2006).

Regardless of all the biases and limitations of our modelling approach we believe that even a simple model may provide useful insights on how different seabird species distribute their foraging efforts on a large spatial scale. In addition, our maps of resource overlap identified areas of the world that may present the potential for competition between seabirds and fisheries. Resource overlap between fisheries and top predators has only recently been quantified spatially at a global scale for marine mammals (Kaschner 2004, Kaschner & Pauly 2004, Kaschner et al. 2006). Kaschner (2004) and Kaschner et al. (2006) have developed maps of marine mammal distributions and quantified spatial overlap. Overall, the overlap between marine mammals and fisheries is low; however, in certain shelf areas of the world overlap is highest (Kaschner & Pauly 2004). Likewise, only a small amount of food consumed by seabirds comes from areas where fisheries operate (Figs. 4 & 5). In other words, most catches are taken from waters where only a small fraction of the world's seabird population forages.

Our maps of resource overlap identified 'hotspot' areas that have been previously noted in the literature to hold the potential for competition between seabirds and fisheries. These areas have either high seabird densities (e.g. the North Atlantic; Fig. 1b), or a large number of abundant seabird species (e.g. the Patagonian shelf and the Campbell Plateau; Fig. 1a). In particular, in the North Atlantic Ocean, fisheries of capelin and sand eel *Ammodytes marinus* are expanding to provide raw material for agricultural and aquaculture

feed (Carscadden et al. 2002, Huntington et al. 2004). Capelin and sand eel dominate the diet of many seabird populations breeding in the North Atlantic (Carscadden et al. 2002, Davoren & Montevecchi 2003). As a result, depletion of stocks may lead to conflict between seabirds and fisheries. Similarly on the Patagonian shelf, squid stocks have been maximally exploited and probably overfished (Boyle & Rodhouse 2005). Published maps of the distribution of effort for squid fisheries (Rodhouse et al. 2000), as well as maps produced for this study (Fig. 4), show substantial apparent overlap with the seabirds that forage in the area (Gremillet et al. 2000, Rodhouse et al. 2000, Croxall & Wood 2002).

The scientific community is currently undertaking the major task of development of new tools and approaches to conservation and management. Some of the most important issues of global concern include loss of biodiversity, destruction of habitat, sustainable use of resources and governance and management of the high seas. The open oceans are poorly studied, though intensively exploited (e.g. Myers & Worm 2003, Pauly et al. 2003, 2005). They are a challenge to those interested in protecting marine biodiversity. It is now widely recognized that the establishment of marine reserves in the high seas can generate a wide range of benefits (e.g. protect ecosystem structure and function, reduce overfishing and preserve critical habitat; Gjerke & Breide 2003, Worm et al. 2003, Pauly et al. 2005). In addition, it is a key mechanism for promoting ecosystem-based management and conservation on larger geographical scales.

For seabirds, a broad consensus exists that the identification of marine important bird areas (IBAs) will make a vital contribution to global initiatives for protection and sustainable management of the oceans, including valuable input to the development of marine reserves in the high seas (BirdLife International 2004). BirdLife International has pioneered IBAs for terrestrial and freshwater ecosystems since the 1980s (www.birdlife.org.uk/action/science/sites). However, the criteria currently in use need to be adapted and applied to marine ecosystems. Our maps identified areas of high conservation concern by revealing where species richness and seabird density are high and where the potential for competition for the same resources between seabirds and fisheries may be prevalent. Thus, spatial modelling of seabird distributions may serve as a useful tool in the effort of identifying and developing standardised global criteria for the establishment of marine IBAs to conserve marine biodiversity and critical habitat and promote ecosystem-based management (Gjerke & Breide 2003, BirdLife International 2004, Cheung et al. 2005).

General summary

The maps developed from this analysis are useful in understanding distribution patterns of seabirds at sea and how their consumption of prey resources is allocated in the waters around the globe. These maps are also an important step in identifying which areas of the world present the potential for competition between seabirds and fisheries when sharing the same prey resources between these 2 marine ecosystem components is considered. Spatial modelling of seabird distribution may prove an essential tool for establishing criteria when designing offshore marine protected areas for conserving biodiversity and critical habitat. Meanwhile, maps of interactions between seabirds and fisheries may help concentrate conservation efforts primarily on those areas of highest concern.

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