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

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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 30-min spatial cells to: (a) map the foraging distribution of seabirds; (b) predict their annual food consumption rates in a spatially-explicit manner; and (c) 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 to a total catch of nearly 120 million tonnes by all marine fisheries. Krill and cephalopods comprised over 58% of the overall food consumed and fishes most of the remainder. The families Procellariidae (albatrosses, petrels, shearwaters, etc.) 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

Introduction
Fisheries have dramatically expanded in the last few decades (Pauly *et al.*, 2002, 2003, 2005; Myers and 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 and Jennings, 2000; Jennings *et al.*, 2001). In order to quantify these impacts, these processes must be analyzed at 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. This is why maps have been proposed as a complementary tool for fisheries science (Pauly *et al.*, 2003). They help to make the necessary transition towards ecosystem-based management.

Moreover, the consideration 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. Cairns, 1992; Fowler, 1999). Marine ornithological research has broadened its spectrum in order to understand the key role seabirds play in marine food webs. Seabirds are abundant, conspicuous and can indicate ecological impacts 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. Montevecchi, 1993; Barrett and Krasnov, 1996; Kitaysky *et al.*, 2000), and serve as indicators of ecosystem change (e.g. Cairns, 1987; Montevecchi, 1993; Cherel and Weimerskirch, 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. Williams, 1991; Lorentsen *et al.*, 1998; Rodhouse *et al.*, 1998; Bunce, 2001) or a few seabird species breeding at one location (e.g. Croxall and Prince, 1987; Woehler and Green, 1992; Guinet *et al.*, 1996; Croll and Tershy, 1998; Green *et al.*, 1998; Goldsworthy *et al.*, 2001; Barrett *et al.*, 2002; Huettmann, 2003). 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 author to tackle the issue of seabird food consumption on a global scale; his study includes most seabird species. He estimated an annual food consumption of 70 million tonnes for the world's oceans.

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. Klaer and Polacheck, 1997; Belda and Sanchez, 2001; Tuck *et al.*, 2003). In addition, it has been shown how 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 impact entire seabird communities; Reeves and Furness, 2002).

Other forms of interaction between fisheries and seabirds result from sharing the same resource. Resource overlap represents the extent to which two consumers overlap in the exploitation of the same resource in the same area (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. Modern fisheries selectively remove large quantities of biomass from marine ecosystems (e.g. Pauly and Christensen, 1995). Their vast expansion worldwide in the last decades has resulted in collapses 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 impact seabirds, because they deplete resources that would otherwise be available as food to them (e.g. Wanless *et al.*, 2005). Prey depletion by fisheries may also trigger indirect trophic cascading effects and enhance competition with other top predator 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 and Birkhead, 1984; Montevecchi, 2002; Cowx, 2003); however, few studies have actually quantified this form of competition. Duffy and 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 and Tershy, 1998). Moreover, Goldsworthy *et al.* (2001) used a percentage similarity index (% PSI; Schoener, 1970) and assessed low overlap between seabird populations and the Patagonian toothfish fishery around Macquarie Island (Goldsworthy *et al.*, 2001).

In the present study, we attempted to express on a spatial scale the amount of food seabirds consume, and finally identify areas where competition between seabirds and fisheries may be possible. We used a GIS-based modelling approach and the spatial grid of 30-min cells developed by the *Sea Around Us* Project (Watson *et al.*, 2004; www.seaaroundus.org), in order to address three goals; to: (a) map the foraging distribution of seabirds; (b) estimate seabird annual food consumption rates per cell; and (c) compare the latter with the spatially disaggregated fisheries catches database of the *Sea Around Us* Project, to obtain an estimate of a seabird – fisheries overlap index per cell.

Methods
We compiled information for 351 marine bird species (belonging to four 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, which consist of birds that breed inland, but which prey upon small fish and invertebrates that occur along the coast. Information was gathered using the following databases: (a) Aquatic Sciences and Fisheries Abstracts (ASFA); (b) Web of Science, Institute for Scientific Information

(ISI); and (c) BioSciences Information Service (BIOSIS) of Biological Abstracts. These cover peer-reviewed journals and grey literature sources. Information was also extracted from the following online databases: (a) Avibase – the world bird database (http://www. bsceoc.org/avibase/avibase.jsp?pg=homeandlang=EN); (b) the United Nations Environment Programme (UNEP) – World Conservation Monitoring Centre Species Database (http://www.unep-wcmc.org/right.htm); (c) BirdLife International (www. birdlife.net); (d) the National Audubon Society (www.audubon.org) Christmas Bird Count (http://www.audubon.org/bird/cbc/index.html); (e) the Birds of North America Online (http://bna.birds.cornell.edu/BNA/); and (d) Wetlands International (www. wetlands.org).

The database contains information on seabirds' taxonomy, population dynamics, diet composition, and foraging ecology of seabirds. The above information was used to estimate annual food intake rates of seabirds, as well as map their foraging distribution. Furthermore, spatially-explicit food consumption rates were then compared to spatially disaggregated annual fisheries catches, in order 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 30-min cells developed by the *Sea Around Us* Project (Watson *et al.*, 2004; www.seaaroundus.org).

Food consumption by seabirds
Information necessary to estimate the seabirds' daily food intake (DFI), and hence their annual food consumption, included: (a) body mass (m; in g) of seabirds species taken from Dunning (1993) and Schreiber and Burger (2002). (b) Basal and Field Metabolic Rates [BMR and FMR respectively, estimated using order-specific allometric equations from Ellis and Gabrielsen (2002); in kJ/day]. BMR and FMR were used to estimate energy requirements (ER) of seabirds in the non-breeding and breeding season respectively. (c) A matrix of standardized diet composition; and (d) 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):

$$DFI_i = \frac{ER_i}{\sum_{j=1}^{G} DC_{ij} * ED_j} * \frac{1}{AE_i} \quad \dots 1)$$

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 number 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.

In order to estimate seabird species' annual food consumption, DFI_i was estimated

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

separately for the breeding and non-breeding season, by considering ER_i for the breeding season equal to FMR (ICES, 2000), for the non-breeding season, equal to $2.5 \times BMR$

(ICES, 2000). The length of the breeding season was assumed equal to incubation period + time from hatching to leaving the nest or burrow + 20 days (Cramp, 1985).

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 per 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 equations were used to account for non- and pre-breeders present in colonies: (a) for single-egg laying species (bp×0.6)+(bp×0.7); and (b) for multi-egg laying species (bp×0.6)+(bp×1.0) (ICES, 2000). These calculations assume that non-breeders 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 chicks/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 datapoints. Data were also extrapolated from the first available datapoint back to 1950, as well as from the last available datapoint to 2003, assuming no change in the population size.

We modelled the at-sea distribution of seabirds using information on their foraging behaviour. 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 (www.birdlife.net). Furthermore, the species were divided into four groups, according to the distance they fly from their colony to feed. The following groups emerged: (a) Nearshore species that forage within 1 km from shore. The group comprises of some species of cormorants, gulls, terns, pelicans, seaducks, and some alcids; (b) Coastal species that fly up to 10 km from shore to find food. This group includes mainly species of cormorants, gulls, terns and seaducks, as well as some alcids; (c) Seabirds species of the continental shelf that forage within 200 km from land. This group contains some storm petrels and shearwaters, 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 of 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, some shearwaters, and storm petrels. Group d was further divided into three sub-groups: (i) species that fly to distances >200 km to feed. However, the probability of occurrence decreases linearly to zero at the maximum reported foraging range. (ii) 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). (iii) Twelve species of the genus *Puffinus* (i.e. Little, Buller's, Flesh-footed, Pink-footed, Greater, Sooty, Hutton's, Christmas, Newell's, Wedge-tailed, Manx and Short-tailed shearwaters). These species 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. Ogi *et al.*, 1980; Guzman and Myres, 1983; Briggs and Chu, 1986; Camphuysen, 1995; Spear and Ainley, 1999; Gould *et al.*, 1997, 1998; Ito, 2002).

On occasion, shearwaters form flocks and feed with surface-schooling tunas (Ashmole and Ashmole, 1967; Au and Pitman, 1986, 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 (*Thunnus albacares*) and less frequently with Skipjack tunas (*Katsuwonus pelamis*) in the Eastern Tropical Pacific Ocean (Au and Pitman, 1986, 1988; Au, 1991). The same habit is also shown by Greater shearwaters that feed with tunas in the Atlantic Ocean (Clua and Grosvalet, 2001). Hence, in order to map the foraging distribution of the above-mentioned twelve species of shearwaters, we assumed that their distribution matched that of three species of schooling tuna (Yellowfin, *Thunnus albacares*; Southern bluefin, *Thunnus maccoyii*; and Northern bluefin, *Thunnus thynnus*; available online at www.seaaroundus.org).

For all four 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 by the *Sea Around Us* Project (www.seaaroundus.org).

Seabirds – Fisheries resource overlap
In order 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). She applied a weighting factor, to measure the importance of spatial cell of either very low seabird food consumption rates and/or very low fisheries catches. Thus, the resource overlap index was as follows:

$$a = \frac{2 * \sum_{i=1}^{G} p_{ij} * p_{fj}}{\sum_{i=1}^{G} p_{ij}^2 + \sum_{f=1}^{H} p_{fj}^2} * \left(pQ_i * pC_f\right) \qquad \ldots 2)$$

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 and H denote the number of food groups taken by i, and comprise the catch of the fishery f respectively; pQ_i and pC_f denote the proportion of food taken by i and the proportion of food caught by f at each cell. *a* was quantified on a global scale and was 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; www.seaaroundus.org).

Results

At-sea distribution of seabirds

Figure 1 shows: (a) the predicted foraging distribution of all seabirds species combined, and (b) seabird density (i.e. number of seabird individuals per 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 (Figure 1a). In addition, Hawaii, the Caribbean, the California
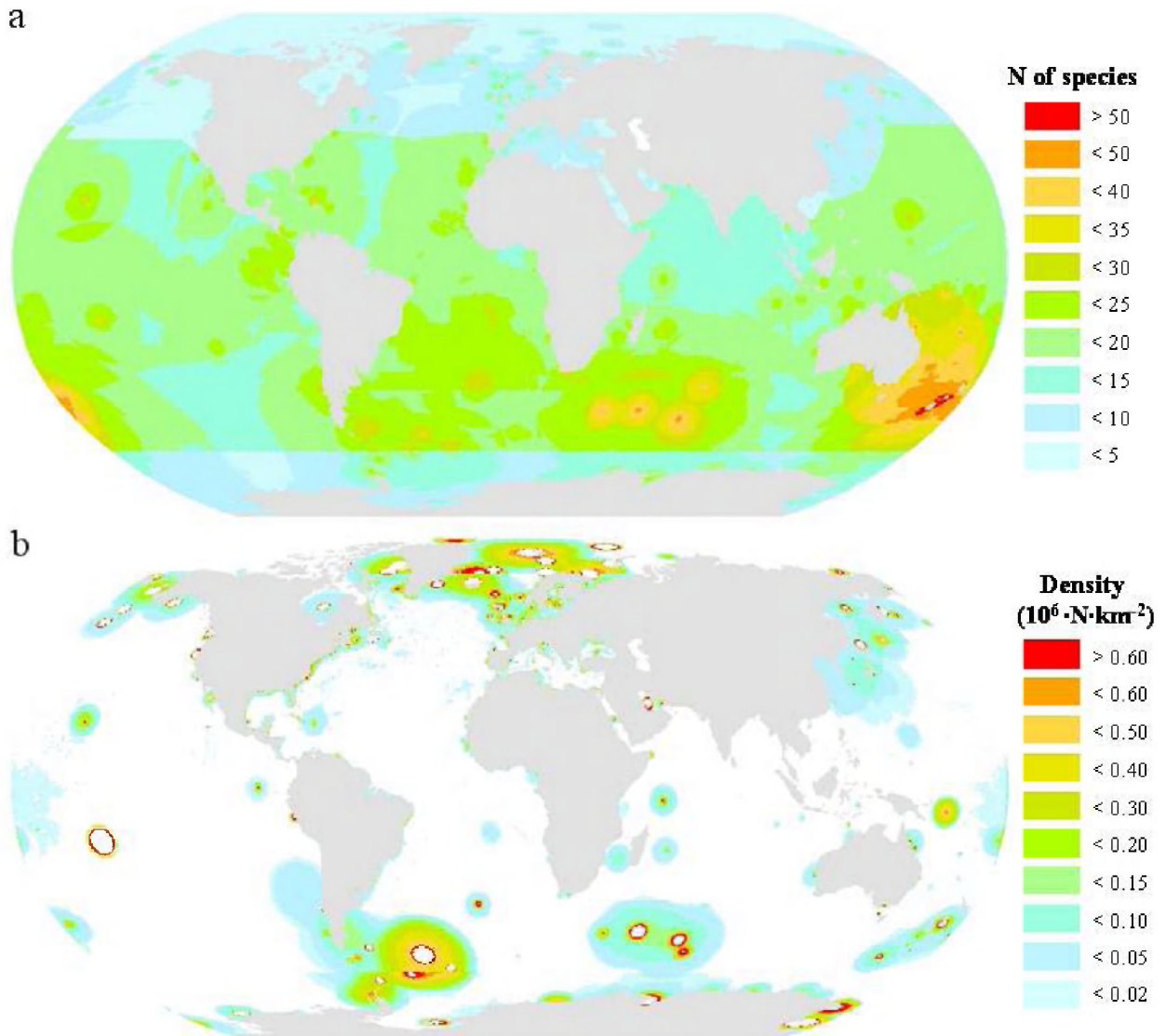
a

b

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

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 (Figure 1a). Temperate and polar regions of the northern hemisphere have the lowest number of foraging species (Figure 1a); however, these areas are characterized by high seabird densities (Figure 1b).

Total annual food consumption by seabirds
The estimated annual global food consumption of all seabird species combined was 96.4 million tonnes. Krill and cephalopods comprised more than 58% of the overall food consumption (krill: 37.8%, cephalopods: 20.5%; Figure 2). Fish, for which no catch is reported, and myctophids were the third and fourth ranked prey consumed by seabirds (Figure 2). Following Brooke (2004), we assumed a coefficient of variation of 50% for population size; global food consumption then ranged from 78.0 to 114.7 million t. The most abundant Procellariidae and Spheniscidae were responsible for more than 54% of the overall food consumption.

Mapping of food consumption rates of all seabirds combined (Figure 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 Northwest Pacific Ocean –
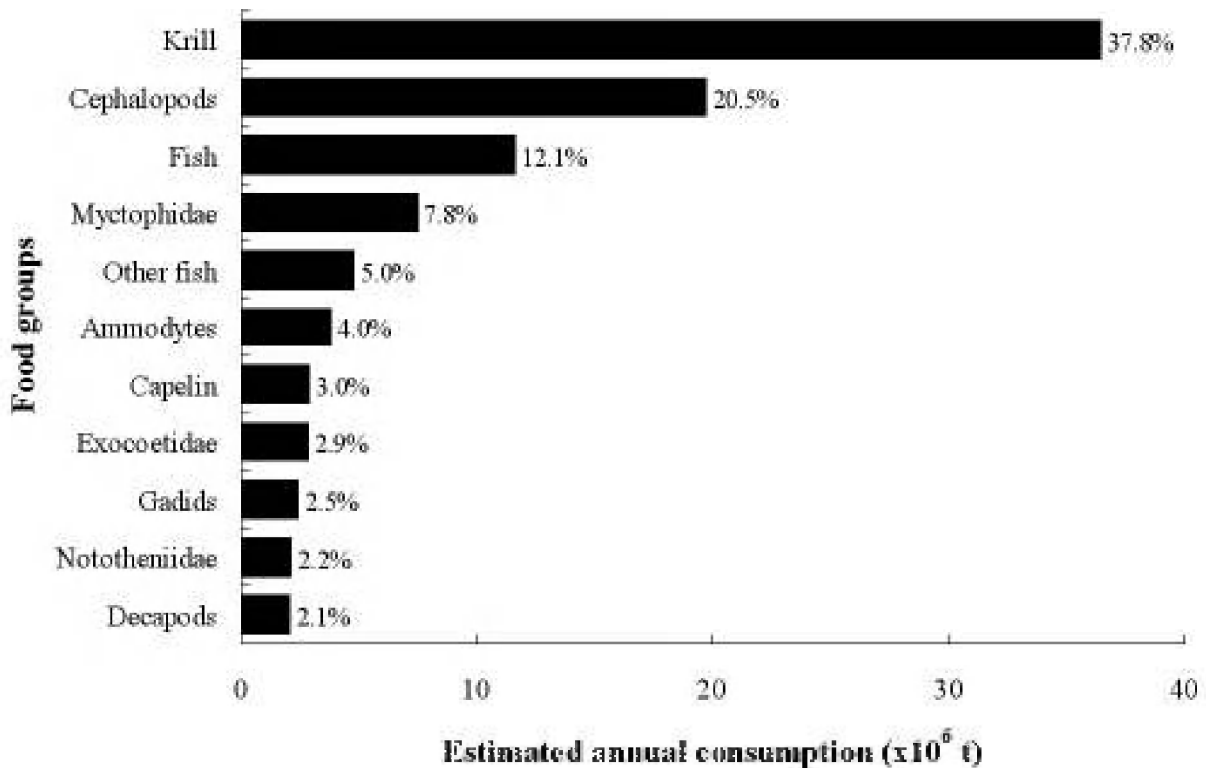

Figure 2. Percentage contribution of food groups in the estimated annual global food consumption of all seabird species combined. Other fish: contains Anchovies (1.4%), Clupeidae (1.1%), *Sebastes* spp. (0.7%), Carangidae (0.5%), Goatfish (0.4%), Perch-like (0.2%), Flatfish (0.2%), Beloniformes (0.1%), Scorpaeniformes (0.1), Channichthyidae (0.1%), Osmeridae, Atherinidae, Synodontidae, *Oncorhynchus* spp. and Macrouridae (<0.05% each).

Okhotsk Sea and the Sea of Japan; and the continental shelves of the North Atlantic Ocean; Figure 3). However, most of the food is taken from offshore areas (e.g. offshore waters of the Southwest Pacific and the Southern Ocean; Figure 3), and particularly, from the cold temperate and polar waters of the world (Figure 3), where seabirds forage in greater densities. In the southern hemisphere, these areas coincide with areas where prey, such as the Antarctic krill, squid, and the mesopelagic fish of the families Nototheniidae and Myctophidae, are abundant (e.g. Rodhouse *et al.*, 1996; Lascara *et al.*, 1999; Duhamel *et al.*, 2000). In the northern hemisphere, most feeding occurs in areas that depict the distributions of prey, such as capelin, sand lance, and herring (e.g. the waters of the North Atlantic; Figure 3).

Spatially explicit resource overlap between seabirds and fisheries
Mapping of the overlap between all seabirds and fisheries on a global scale revealed that, for the 1990s, it mostly occurred in the cold temperate waters of the northern hemisphere (Figure 4). In the North Atlantic, 'hotspots' of high overlap were present throughout the shelf areas of Europe, and along the coast and shelf areas of Eastern Canada. In the North Pacific, high overlap was estimated for the Asian shelves and the Eastern Bering Sea, with regards to overlap estimates (Figure 4).

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

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
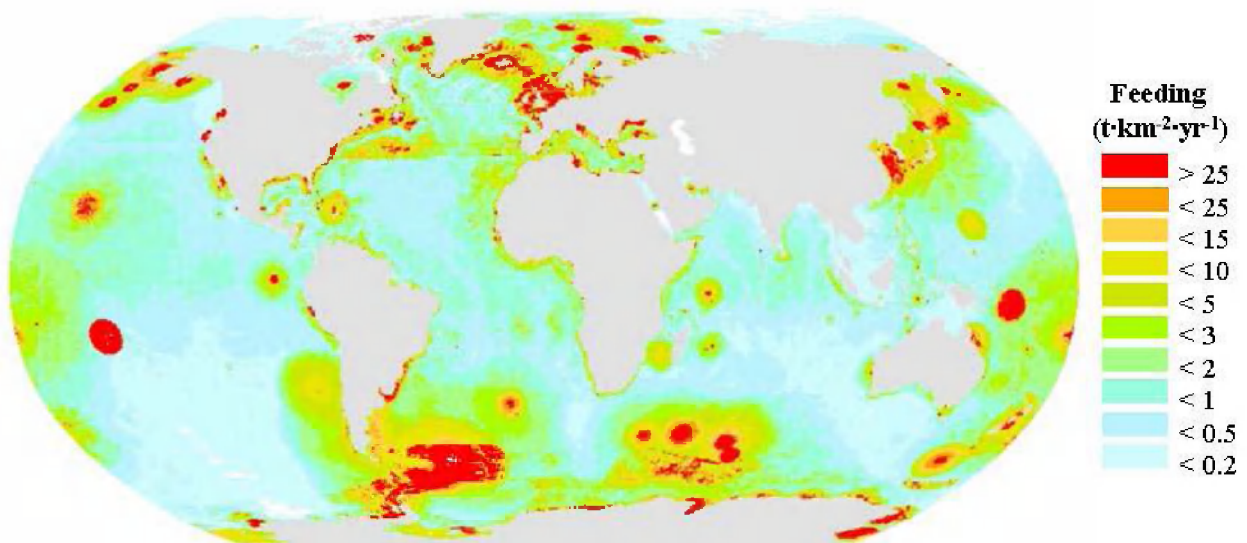

Figure 3. Map of predicted global food consumption rate (in tonnes·km^{-2}·year^{-1}) of all seabirds combined for an average year in the 1990s.

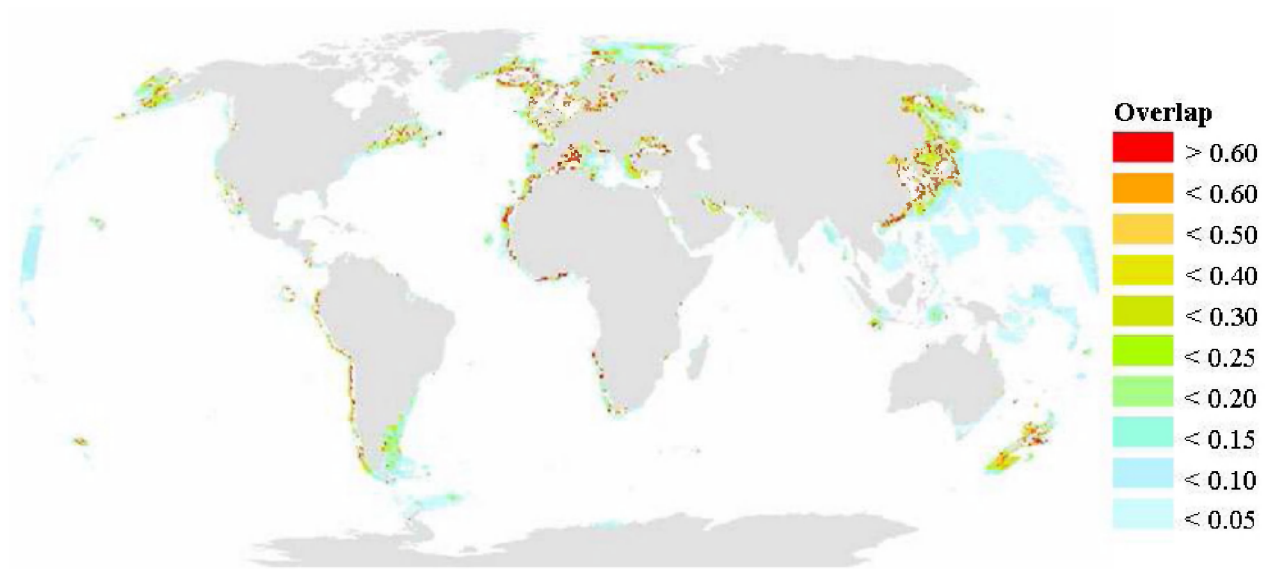| Overlap	
■ (red)	> 0.60
■ (orange)	< 0.60
■ (light orange)	< 0.50
■ (yellow)	< 0.40
■ (yellow-green)	< 0.30
■ (green)	< 0.25
■ (light green)	< 0.20
■ (teal)	< 0.15
■ (light blue)	< 0.10
■ (pale blue)	< 0.05

Figure 4. Map of estimated trophic overlap between all seabirds and fisheries for an average year in the 1990s.

of food consumed in cells with overlap > 0.3 was very close to 0. In the 1990s, < 1% of all food taken by seabirds was consumed in areas of high spatial overlap with commercial fisheries (Figure 5). In other words, most of the food consumed by seabirds originated from areas where resource overlap was very low (Figure 5).
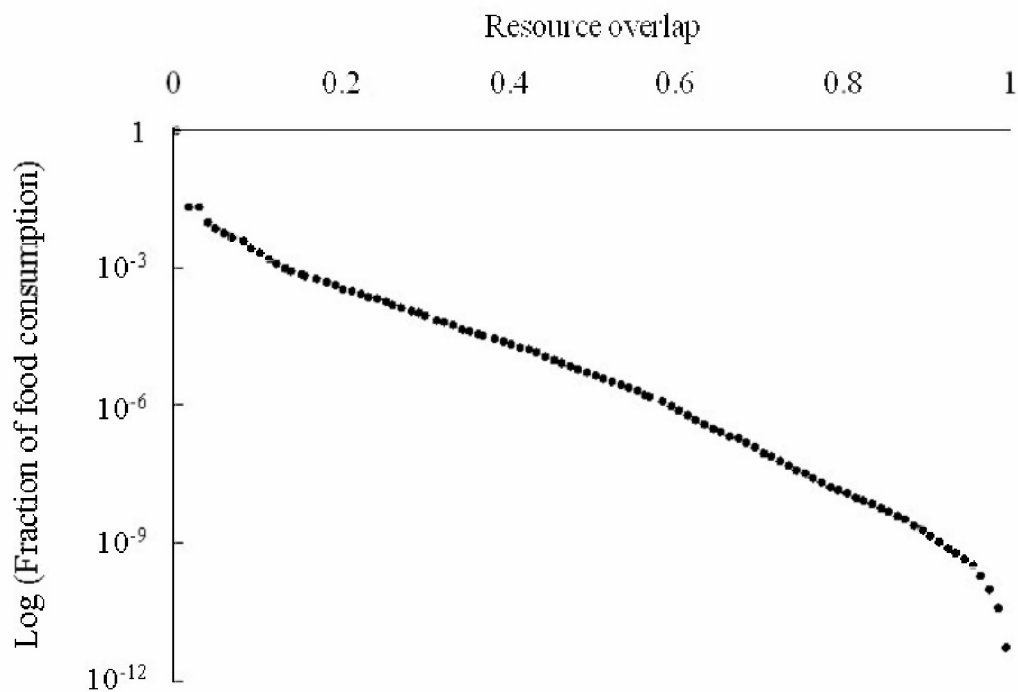

Figure 5. Fraction of food consumed by seabirds in the 1990s by areas of overlap with fisheries.

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. It is only recently that the need has been expressed for transforming information on marine biodiversity already published on paper into a digital, more interactive, and readily accessible form (Bisby, 2000; Zeller and Pauly, 2004; Costello *et al.*, 2006, and publications therein). Our efforts primarily focused on the extraction of data on seabird population sizes, habitat, as well as feeding preferences from over 3,000 scientific articles, whose year of publication spanned from the early 1900s, to the present. Then data were transformed into computerized information that was further analyzed 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: Cairns *et al.*, 1991; Lilliendahl and Solmundsson, 1997; Barrett *et al.*, 2002, 2006; South Pacific: Muck and Pauly, 1987; Southern Ocean: Adams *et al.*, 1993; Cooper and Woehler, 1994; Woehler, 1997). Brooke (2004) was the first to give a global estimate of food consumption by seabirds. Our estimate of worldwide consumption was about 30% higher (96.4 million t) than Brooke's (2004; 69.8 million t). This is probably because we considered more seabird species (351) than Brooke did (309). Moreover, Brooke (2004) assumes conservatively one non-breeder per breeding pair to estimate global population size. As a result, his estimate of population size was 0.7 billion individuals vs. 0.9 billion individuals estimated here. However, Brooke (2004) agrees that a 'liberal' global population estimate (i.e. breeding pairs multiplied by five for longer-lived species and by four 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 impact 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, the Peruvian booby, and the Peruvian pelican breeding in Peru; population sizes for all three species were available from 1953 to 2000 (Jahncke, 1998; Crawford and Jahncke, 1999; Sueyoshi, 2000). However, for the majority of seabird populations, more than 95% of population estimates used before 1970 was 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 t. Although these confidence intervals are large, they suggest that seabirds around the world consume significant quantities of marine resources that are 70 – 95 % of to the total fisheries catch (i.e. nearly over 120 million t of resources annually if account is taken of fish illegally caught and not reported, and of fish that is 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 and Gabrielsen, 2002). To tackle this issue, 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 and 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; Davis *et al.*, 1989; Uttley *et al.*, 1994; Golet *et al.*, 2000) measure energy consumption of free-living animals and give estimates with an accuracy of ± 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 nearly half 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) and/or seasonal or geographical differences and influences. Mårtensson *et al.*, (1996) determine that revision of prey calorific density used to estimate the food consumption of minke whales in the Northeast Atlantic result in food consumption estimates that vary by 10-15% (translating to c. 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 is that of 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 applied when we considered all seabird species (Figure 1a). These areas of high species richness comprise biodiversity 'hotspots'. In addition, maps of seabird foraging densities showed that the polar waters of the globe hold the highest seabird densities (Figure 1b). They also represent areas where the most food is taken by seabirds (Figure 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 seabirds' biology and biogeography. The first three 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, likely 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 unimodal response curve is more likely inadequate to describe the occurrence of seabird species in marine foraging habitats and future work will focus on improving such assumption.

At-sea foraging distributions of seabirds were further refined based on prey distributions available by the *Sea Around Us* Project (www.seaaroundus.org). Although the underlying assumption is that seabirds feed where prey occurs, diet for nearly half of the seabird species was not known, and thus assumed 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 twelve migratory shearwater species may be viewed as too much of a stopgap. Associations between shearwaters and feeding surface-schooling tunas have been documented for tropical waters only (Au and Pitman, 1986, 1988; Au, 1991; Clua and Grosvalet, 2001). However, the same is not true for waters in temperate regions, where shearwaters also occur (e.g. Guzman and Myers, 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; Figure 1). Certainly, this feature on the distribution maps will have to be improved upon.

Several parameters to define pelagic foraging habitats and the at-sea distribution of far-ranging seabirds have been used in the literature (e.g. Rodhouse, 1989; Rodhouse *et al.*, 1996; Hyrenbach *et al.*, 2002, 2006; Ainley *et al.*, 2005); these are sea surface temperature, sea surface salinity, seafloor depth, and chlorophyll concentration (Chl a). 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 determining how environmental and oceanographic parameters 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 (Figure 5). Our maps of spatial resource overlap identified that 'hotspot' areas occur mainly on, or along the continental shelves (Figure 4). This is not surprising because fisheries, which target demersal, benthic, and bentho-pelagic organisms cover the shelves surrounding continents and islands, whereas fisheries operating in the open ocean, target mainly tuna, billfishes, and other large pelagics (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. Furness, 1982, 2002; Furness and Ainley, 1984; Wright, 1996; Croll and Tershy, 1998; Green *et al.*, 1998; Bunce, 2001; Goldsworthy *et al.*, 2001). Indeed, fisheries and foraging seabirds inevitably interact in a number of ways (review by Montevecchi, 2002). Three main effects of fisheries on seabirds are (Moore and Jennings, 2000): (a) consumption of and dependence on fisheries discards (e.g. Votier *et al.*, 2004); (b) increased mortality from entanglement in fishing gear (e.g. Melvin and Parrish, 2001); and (c) 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 results from seabirds feeding on and fisheries targeting the same resources (type *c* interactions), by measuring a resource overlap index (review by Krebs, 1999). However, for seabird populations, which 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. Other indirect competition for food (e.g. cascading effects) was also not taken into account. Therefore, in areas of the world where type *a* interactions between seabirds and fisheries are frequent (e.g. the North Sea; Garthe *et al.*, 1996; the Mediterranean Sea; Oro and Ruiz, 1997), we believe that overlap was underestimated.

Type *b* interactions were also not taken into account in our modelling approach. Mortality of seabirds due to entanglement in fishing gear usually results from seabirds being hooked, dragged underwater and drowned while trying to feed on bait or on fish caught by longline gear. In net fisheries, birds are caught and drowned in the nets while diving in pursuit of their prey (Moore and Jennings, 2000). Such interactions cannot be quantified as outlined in the methodology section here. Thus, we believe that competition between seabirds and fisheries was underestimated in areas where type *b* interactions are prevalent. 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; Cherel and Weimerskirch, 1996; Croxall and Prince, 1996; White-chinned petrel; Weimerskirch *et al.*, 1999; Grey-headed albatross; Nel *et al.*, 2000; Tristan albatross; Cuthbert *et al.*, 2005). Indeed, in these areas where long-lining is a dominant fishing method, very low or no trophic overlap was predicted in our study (Figure 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 at different areas (Watson *et al.*, 2006). Overlay of gear maps with seabird distribution maps will also allow explore spatial overlap between seabirds and fisheries that are attributed to type *b* interactions (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

been only recently quantified spatially at a global scale and for the case of marine mammals (Kaschner, 2004; Kaschner and Pauly, 2004; Watson *et al.*, 2004). 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 and Pauly, 2004). Likewise with seabirds, only a small amount of food consumed by them comes from areas where fisheries operate (Figures 4 and 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; Figure 1b), or a large number of abundant seabird species (e.g. the Patagonian shelf and the Campbell Plateau; Figure 1a.). In particular, in the North Atlantic fisheries of capelin and sand eel are expanding to provide raw material for agricultural and aquaculture feed (Carscadden *et al.*, 2001; 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 and 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 (Csirke, 1987). Published maps of the distribution of effort for squid fisheries (Rodhouse *et al.*, 2000), as well as maps produced for this study (Figure 4) show substantial apparent overlap with the seabirds that forage in the area (Gremillet *et al.*, 2000; Rodhouse *et al.*, 2000; Croxall and Wood, 2002).

The scientific community is currently undertaking a major task, which involves the development of new tools and approaches to conservation and management. The open oceans are poorly known, though intensively exploited (e.g. Myers and Worm, 2003; Pauly *et al.*, 2003, 2005). They are a challenge to those interested in protecting marine biodiversity. There is broad consensus that existing global criteria for identifying Important Bird Areas (IBAs) can be adapted and applied to marine ecosystems. BirdLife International pioneered IBAs for terrestrial ecosystems since the 1980s (http://www.birdlife.org.uk/ action/science/ sites/). However, there is a need to establish marine IBAs primarily for seabird species listed on the IUCN Red List (BirdLife International, 2004). Our maps identified areas of high conservation concern, by revealing where species richness and seabird density are high. In addition, the food consumption and trophic overlap maps shown here may shed light to a threat to seabird populations worldwide, that being the potential for competition for the same resources between seabirds and fisheries. Thus, spatial modelling of seabird distributions may serve as a useful tool in the effort of identifying criteria for the establishment of marine IBAs and of High Seas Marine Protected Areas for conserving biodiversity and critical habitat (Gjerke and Breide, 2003; BirdLife International, 2004; Cheung *et al.*, 2005).

Summary
The maps presented here 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 considering sharing the same prey resources between these two marine ecosystem components. 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 to those areas of highest concern.

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