AN ANALYSIS OF TEMPORAL AND SPATIAL PATTERNS IN GLOBAL SEABIRD ABUNDANCE DURING THE MODERN INDUSTRIAL ERA, 1950-2010, AND THE RELATIONSHIP BETWEEN GLOBAL SEABIRD DECLINE AND MARINE FISHERIES CATCH

by

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Abstract

Seabird populations worldwide are threatened by anthropogenic activities including hunting, introduced predators, habitat destruction, pollution, and fisheries, yet the cumulative effects of these threats on seabird populations is difficult to assess because seabird population studies are mainly limited to small temporal and spatial scales. The present study used global databases of seabird abundance, seabird distribution, and fisheries catch, to estimate global annual seabird population size, overall and by seabird family, 1950-2010; map observed global seabird population change within the same timeframe; and compare temporal and spatial patterns in seabird decline with fisheries, a major threat for which global temporally and spatially explicit data is available throughout the modern industrial era. The global seabird population was estimated to decline by 25% during the modern industrial era, from 1.023 billion individuals in 1950 to 0.768 billion individuals in 2010, and overall decline was observed in eleven of the fourteen seabird families. Maps of observed seabird population change indicated decline covering 90% of the world's marine surface area, and most severe in the southern temperate and tropical oceans. There was a significant positive relationship between annual seabird decline and annual forage fish catch (a metric of forage fish depletion), as well as between observed seabird decline per spatial cell and year of maximum primary production to support fisheries per marine spatial cell (a metric of the timing of peak ecological footprint of fisheries), both indicating that fisheries presence may play a role in shaping spatial and temporal patterns in global seabird population change. The present study identifies the temporally, taxonomically and spatially pervasive nature of global seabird decline during the modern industrial era and a potentially globally important role of fisheries in this global seabird decline, thus indicating the need for a large-scale and precautionary approach to seabird and marine ecosystem management.

ii

Preface

Vasiliki Karpouzi constructed and compiled a substantial part of the data in the *Sea Around Us* Project seabird database. Edd Hammill and Daniel Pauly made important contributions to the design and execution of the analysis of temporal patterns in seabird abundance and the relationship between seabird decline and fisheries catch. Reg Watson provided data from the *Sea Around Us* database for the fisheries-related analyses.

Table of Contents

Abstractii
Prefaceiii
Table of Contentsiv
List of Tables
List of Figures ix
Acknowledgementsx
Chapter 1 Introduction 1
1.1 Problem statement
1.2 Research questions
1.3 Background and literature review
1.3.1 Definition of the term "seabird"
1.3.2 Seabird diet and foraging
1.3.3 Seabird colonies
1.3.4 Seabird population dynamics
1.3.5 Seabird ecology 12
1.3.6 Anthropogenic activities threatening seabirds 15
1.3.7 Seabird conservation
1.3.8 Seabird population monitoring and status
Chapter 2 Temporal patterns in global seabird abundance, 1950-2010

	2.1 Summary	30
	2.2 Introduction	30
	2.3 Methods	32
	2.3.1 Global database of seabird abundance records, 1950-2010	32
	2.3.2 Estimating annual change in global seabird abundance	34
	2.3.3 Estimating annual global seabird abundance	37
	2.3.4 Breaking the global annual seabird abundance down by seabird family	37
	2.4 Results	38
	2.4.1 Seabird abundance database	38
	2.4.2 Global annual seabird population change	39
	2.4.3 Global annual seabird population size	39
	2.4.4 Global annual seabird population size, by family	39
	2.5 Discussion	46
	2.5.1 Global seabird population change	46
	2.5.2 Global seabird population change, by family	53
C	Chapter 3 Spatial patterns in observed global seabird abundance, 1950-2010	57
	3.1 Summary	57
	3.2 Introduction	57
	3.3 Methods	59
	3.3.1 Global database of range extent maps per seabird species	59

3.3.2 Estimating abundance and change in abundance per seabird species	61
3.3.3 Mapping global seabird density	61
3.3.4 Mapping observed change in global seabird density	62
3.4 Results	62
3.4.1 Estimated abundance and change in abundance, per seabird species	62
3.4.2 Maps of global seabird density	63
3.4.3 Maps of observed change in global seabird density	63
3.5 Discussion	68
3.5.1 Estimated abundance and change in abundance, per seabird species	68
3.5.2 Global maps of seabird density	69
3.5.3 Global maps of observed change in seabird density	70
Chapter 4 Investigating the potential role of industrial marine fisheries in temporal and spatia	ıl
patterns in global seabird population change, 1950-2010	74
4.1 Summary	74
4.2 Introduction	74
4.3 Methods	77
4.3.1 Testing for a relationship between annual global seabird decline and annual global	
forage fish catch	. 77
4.3.2 Testing for a relationship between observed seabird decline and year of maxPPR pe	er
spatial cell	. 77

4.4 Results
4.4.1 Relationship between annual global seabird decline and annual global forage fish
catch
4.4.2 Relationship between observed seabird decline and year of maxPPR in a region 78
4.5 Discussion
4.5.1 Temporal relationship between seabird decline and fisheries catch
4.5.2 Spatial relationship between seabird decline and fisheries catch
Chapter 5 Conclusion
Literature Cited
Appendices
Appendix I. List of all seabird species, their attributes and abundance estimates
Appendix II. Examples of data used to calculate abundance estimates for four species 115
Appendix III. Estimates of global abundance per seabird family in 1950 and 2010

List of Tables

List of Figures

Figure 1.1 Examples of terrestrial breeding areas and marine foraging areas	7
Figure 2.1 Method for estimating annual change in the global seabird population	36
Figure 2.2 Number of seabird populations sampled in the global seabird database, 1950-2010. 4	1
Figure 2.3 Annual relative contribution of each family to the total number of records	12
Figure 2.4 Estimated global annual change in seabird abundance, 1950-2010	13
Figure 2.5 Estimated global annual seabird abundance, 1950-2010 4	14
Figure 2.6 Mean annual global seabird population size, by family, 1950-2010 4	15
Figure 3.1 Examples of range extent polygons	50
Figure 3.2 Map of historical global seabird density	54
Figure 3.3 Map of modern global seabird density6	55
Figure 3.4 Map of absolute change observed in global seabird density	66
Figure 3.5 Map of relative change observed in global seabird density	57

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Chapter 1 Introduction

1.1 Problem statement

Seabirds are are threatened by anthropogenic activities, but the cumulative effects to seabird populations are unclear because seabird population change has not been properly assessed at the global scale.

1.2 Research questions

The purpose of this research is to answer the following questions:

- What is the global annual seabird population size throughout the modern industrial era, overall, as well as by seabird family?
- 2) What is the spatial distribution of observed change in the global seabird population over the modern industrial era?
- 3) Are temporal and spatial patterns in global seabird population change during the modern industrial era related to fisheries?

1.3 Background and literature review

1.3.1 Definition of the term "seabird"

Seabirds are birds that nest colonially on marine islands and coastal cliffs, and travel some distance from shore to feed predominantly on marine prey. Seabirds are notable for their wide ranges and transboundary movements, crossing many ecological and jurisdictional boundaries during their daily foraging trips and seasonal movements (Jodice and Suryan, 2010). For their marine existence, seabirds have a unique set of physical adaptations: salt glands for osmoregulation; black, grey and/or white colouration for attracting conspecifics and/or evading predators at sea; webbed feet for swimming; oily and densely packed feathers for waterproofing and insulation; and wing shapes that maximize efficiency for long distance travel by either flight or swimming.

There are currently 324 seabird species (Appendix I) belonging to 4 orders and 14 families (Table 1.1). The count of seabird species is ever-changing due to discovery of new species and taxonomic revisions as taxonomy transitioned from entirely morphology-based (i.e., nostrils, palate, tarsus, syrinx, and certain muscles and arteries) to including also genetic data after 1990 (Brooke, 2002). For example, morphological and genetic data led to the subdivision of the Wandering albatross (*Diomedea exulans*) into four species, *D. amsterdamensis* (Amsterdam Island), *D. antipodensis* (Campbell, Adams and Antipodes Islands), *D. dabbenena* (Tristan da Cunha Island), and *D. exulans* (Marion and Prince Edward, Crozet, South Georgia and Macquarie Islands) (Rains et al., 2011). As another example, Beck's petrel (*Pseudobulweria becki*) was rediscovered after it was thought to be extinct in the 1920s (Gangloff et al., 2012).

Taxa	Number of species ^a	Foraging technique ^b	Diet items ^c	Marine habitat ^d	Clutch size (avg. # of eggs) ^e
SPHENISCIFORMES					
Spheniscidae (penguins)	17	PD	F/C, S	Ι	1-2
PROCELLARIIFORMES					
Diomedeidae (albatrosses)	22	SS, KL	F/S, C	Ο	1
Procellariidae (petrels, shearwaters)	80	SS, PD, KL, SC	C, F/S	I/O	1
Hydrobatidae (storm-petrels)	20	SS	F/S/C	I/O	1
Pelecanoididae (diving petrels)	4	PD	C, F/S	Ι	1
PELECANIFORMES					
Phaethontidae (tropicbirds)	3	PL	F/S	0	1
Pelecanidae (pelicans)	8	SS, PLD, KL	F	Ι	4
Phalacrocoracidae (cormorants)	38	PD	F, C/S	Ι	2-4
Fregatidae (frigatebirds)	5	KL, SS	F, S	I/O	1
Sulidae (boobies, gannets)	10	PD, PLD	F, S	I/O	1-3
CHARADRIIFORMES					
Stercorariidae (skuas)	7	KL, SS, SC	B/F/C/O	Ι	2
Laridae (gulls, kittiwakes)	47	SS, KL, SC	F/C/B/O	Ι	1-3
Sternidae (terns)	40	PLD, SS, KL	F, S, C	I/O	1-2
Alcidae (auks)	23	PD	F, C, S	Ι	1-2

Table 1.1 Seabird families and their defining ecological attributes.

^a after Peters (1979) ^b PD= pursuit diving, SS= surface seizing, PLD= plunge-diving, KL= kleptoparasitism, SC= scavenging (Shealer, 2002) ^c F= Fish, C= Crustaceans, S= Squid, B= Birds, O= Other, in order of importance (Shealer, 2002) ^d I= Inshore, O= Offshore (Shealer, 2002) ^e after Weimerskirch (2002)

In terms of the global avian community, seabirds are a very small group. Jointly, they cover two thirds of the world's surface area, yet constitute only three percent of the world's avian species diversity and less than one percent of the world's avian abundance, as measured in number of individuals (Gaston and Blackburn, 1997, Brooke, 2004b).

1.3.2 Seabird diet and foraging

Seabirds feed almost exclusively on marine prey. Global annual prey consumption is estimated to consists of 42% marine fish, 38% krill and 20% cephalopods by mass (Karpouzi et al., 2007). The fish consumed by seabirds include "forage fish", small lipid-rich schooling fish that inhabit coastal upwelling ecosystems including sandlance (Ammodytes spp.), herring (Clupea spp.), anchovies (Engraulidae), sardine or pilchard (Sardina spp. and Sardinops spp.), capelin (Mallotus villosus), sprat (Sprattus spp.), and menhaden (Brevoortia spp. and Ethmidium spp.). They also include the egg and juvenile stages of larger fish including perch-like fishes (Perciformes), cods (Gadiformes), needle fishes (Beloniformes), scorpionfishes and flatheads (Scorpaeniformes), flatfishes (Pleuronectiformes), silversides (Atherinidae), jacks and pompanos (Carangidae), crocodile icefishes (Channichthyidae), flyingfishes (Exocoetidae), grenadiers (Macrouridae), lanternfishes (Myctophidae), cod icefishes (Nototheniidae), lizardfishes (Synodontidae), goatfishes (Upeneus spp.), Pacific salmonids (Oncorhynchus spp.), and rockfishes (Sebastes spp.) (Karpouzi et al., 2007). Other prey items may also be seasonally and regionally important in the diets of some gulls, terns, cormorants, pelicans, and skuas, including benthic molluscs, intertidal invertebrates, small terrestrial animals, other seabirds and freshwater fish.

The composition of seabird diets varies between seabird species, age groups, regions, seasons, and years. Most seabird species have a few preferred prey items, although some species have specialized diets, for example the Olrog's gull (*Larus atlanticus*) that eats only crabs and the Dovekie (Alle alle) that eats only copepods (Copepoda), and others have extremely generalist diets, for example most gulls will scavenge on any of the listed seabird prey items. Seabird diet varies based on prey availability as well as energetic gain. For example, the contribution of sandlance to the diet of Common murres varies regionally depending on sandlance availability, between the North Sea, British Columbia, California, and Newfoundland (Wanless et al., 2005, Ainley et al., 1996, Hipfner and Greenwood, 2008, Davoren et al., 2012). Also, the contribution of juvenile rockfish to the diet of several seabird species (i.e., Common murre, *Uria aalge*; Rhinoceros auklet, Cerorhinca monocerata; Pigeon guillemot, Cepphus columba) varies interannually depending on rockfish availability (Sydeman et al., 2001). Most inshore species appear to prefer lipid-rich forage fish when available (Furness, 2003). Forage fish may be especially important during the breeding season, when even some otherwise planktivorous species will provision forage fish to their chicks to increase productivity (e.g., Piatt et al., 2007c).

Seabirds travel some distance from shore to forage for their marine prey, and while different species specialize on feeding in different marine environments (i.e., inshore, coastal, offshore, pelagic, and far distant pelagic), their distribution at sea varies through time and space. Seabird density at sea is generally related to prey availability at large and meso scales (Weimerskirch, 2007). Globally, seabird density, diversity and endemism is highest in the highly productive temperate latitudes and upwelling areas (Karpouzi, 2005, Croxall et al., 2012). Tropical, frontal and pelagic foraging species cover larger areas (e.g., offshore, pelagic) because their prey are

less dense predictably distributed in time and space, while temperate and upwelling region foraging species cover smaller areas (e.g., coastal, inshore) because their prey are more dense and predictably distributed. Most seabirds have a seasonal shift in distribution at sea between the breeding and non-breeding season. During the breeding season (2-11 months long, depending on the species), seabirds forage within a radius around the colonies (i.e., central-place foragers), ranging from kilometres (e.g., most cormorants) to hundreds of kilometres (e.g., most albatrosses). During the non-breeding season, some species remain in the breeding grounds while most (i.e., 220 of the 324 species) disperse or migrate to expand their marine foraging area (e.g., Figure 1.1). Sixty-one species migrate to entirely different latitudinal zones; these include 16 species of Procellariidae, Hydrobatidae, and Stercorariidae that breed in the southern ocean and migrate to the northern hemisphere, and 10 species of Procellariidae, Hydrobatidae, Stercorariidae, Laridae and Sternidae that breed in the northern ocean and migrate to the southern hemisphere (Cox, 2010). The longest seabird migration, incidentally also the longest migration of any animal on earth, is that of the Arctic tern (Sterna paradisaea), which has recently been tracked on its migration from the Arctic (Greenland) breeding grounds to the Antarctic (Weddell Sea) foraging grounds (Egevang et al., 2010).

Seabirds employ a variety of foraging methods to obtain their prey including surface-feeding, kleptoparasitism, scavenging, plunge-diving, and pursuit-diving up to depths of 260 m in the Emperor penguin (*Aptenodytes forsteri*) (see Table 1.1) (Furness and Monaghan, 1987). Many seabirds forage in flocks, and/or alongside other predators such as mammals and large fish (see Section 1.3.5).

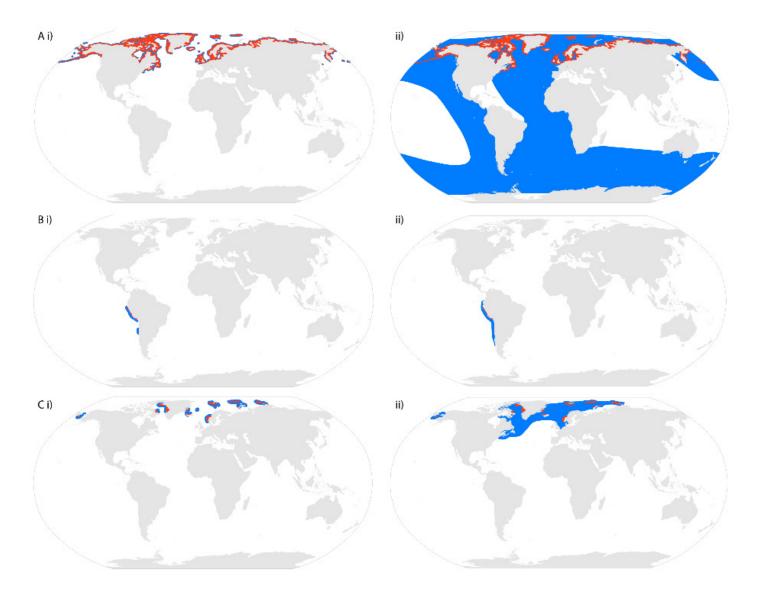


Figure 1.1 Examples of terrestrial breeding areas (red) and marine foraging areas (blue), for three species, (A) Arctic Tern (*Sterna paradisaea*), (B) Peruvian Booby (*Sula variegata*), and (C) Dovekie (*Alle alle*), (i) during the breeding season, and (ii) throughout the entire year (sources: Egevang et al., 2010, Harrison, 1987, Gaston et al., 1998, Poole, 2005).

1.3.3 Seabird colonies

Almost all seabirds (98%) breed in colonies; colonial and synchronized breeding is hypothesized to reduce predation risk and increases social interactions, thereby reducing the costs of breeding. Solitary nesting occurs only in the Kittzlitz's murrelet, Marbled murrelet, all three species of tropicbird, and some large species of gull (Hamer et al., 2002). Colonies may contain tens to millions of breeding pairs, including a single species or multiple species.

Colonies occur on islands and coastal cliffs of continents that are naturally free of terrestrial predators and adjacent to a food supply. Most colonies is situated at the border of land and sea, although a few species commute up to hundreds of kilometres inland to their colonies, including the Marbled murrelet, Kittzlitz's murrelet (*Brachyramphus brevirostris*), and Snow petrel (*Pagodroma nivea*).

Within the colonies, seabirds have a variety of different "nest" types. Small petrels, tropicbirds, 5 species of penguin, and 18 species of Alcidae lay their eggs in a burrow or crevice (Bried and Jouventin, 2001). Albatrosses, large petrels, three species of Alcidae, and most Sphenisciformes, Pelecaniformes, skuas, gulls, and terns lay their egg on the surface, making nests on the ground out of rocks, sticks, mud, guano, or using no nest at all (Bried and Jouventin, 2001). For example, the Emperor penguin holds its egg on its feet, and the Thick-billed murre (*Uria lomvia*) lays its egg on a bare rock cliff (Hamer et al., 2002). Frigatebirds and some boobies, cormorants, and gulls nest in trees (Bried and Jouventin, 2001).

Most seabirds return to their native colony to breed (philopatric), as well as the same site (site tenacious) and sometimes the same mate (monogamous) if successful in previous attempts. In fact some species such as the Cory's shearwater (*Calonectris diomedea*) are so strongly philopatric and site tenacious that they will mate with their own parent (Swatschek et al., 2008).

1.3.4 Seabird population dynamics

Seabirds have the most extremely K-selected life-history strategy of all avian taxa; the Kselected life-history strategy is to maximize lifetime reproductive output by investing in high annual adult survival and low annual reproductive output (Weimerskirch, 2002). Adult annual survival rates can be as high as 98% (Russell, 1999). Adults breed throughout their mature life; the oldest known nesting seabird is a 60+ year old Laysan albatross (*Phoebastria immutabilis*) on Midway Atoll, Northwest Hawaiian Islands (Puckett et al., 2011). Annual reproductive output is low because of high age at maturity (2-9 years, depending on the species) (Hamer et al., 2002); few reproductive events (annual breeding. 30-60% of adults are nonbreeders) (ICES, 2000, Brooke, 2004b); small clutch size (average 1-4 eggs, depending on the species) (Table 1.1); low survival of young (i.e., approximately half of the clutch survives to fledge, and at most half of these will survive to breeding age) (e.g., Vermeer, 1963, Vermeer, 1981, Butler et al., 1980); and high parental care (2-3 months to rear most Charadriiformes to over 12 months to rear some albatrosses) (Hamer et al., 2002).

There is a continuum between extremely K-selected pelagic species (e.g., albatrosses, petrels) and relatively r-selected coastal species (e.g., cormorants, pelicans), which is hypothesized to occur because of the contrasting stability in food supply, from relatively stable through time and widely dispersed in the pelagic environment to highly variable through time and more densely concentrated in the coastal environment. Food supply can be especially variable in upwelling regions such as the Benguela and Humboldt Current ecosystems, where seabirds experience years of low reproductive output and high mortality (e.g., 70% non-breeders in some petrel populations that are affected by ENSO (Weimerskirch, 2002, Chastel et al., 1995); and 90% adult mortality in some Peruvian Booby (*Sula variegata*) populations in El Niño years (Brooke, 2004a)) in contrast with years of rapid population growth.

Seabird populations are limited mainly by availability of food and anthropogenic threats (Section 1.3.6), as well as nesting habitat (Section 1.3.3) and predation (Section 1.3.5) (Weimerskirch, 2002). There is evidence that food is limiting during both the non-breeding season (Lack, 1954) as well as during the breeding season (Ashmole, 1963), and the relative strength of food limitations between seasons varying spatially, temporally, and between seabird species. Cairns (1987) hypothesized that there is an asymptotic relationship between food availability and seabird productivity and/or survival because seabirds can alter their foraging behaviour up to a certain degree to compensate for reduced food availability, and furthermore that the degree to which foraging behaviour can be altered varies between species which have different energetic constraints. Indeed, non-linear relationships have been observed between forage fish abundance and seabird population parameters, for example, the majority of breeding parameters (e.g., chick body condition, foraging trip duration) of Black-legged kittiwake (Rissa tridactyla) and Common murre (Uria aalge) responded to forage fish density in Cook Inlet, Alaska (Piatt et al., 2007b). Also, an asymptotic relationship between forage fish abundance and seabird productivity was recently observed in a global analysis by Cury et al. (2011) including 14 species from seven

ecosystems. Varying sensitivity of seabirds to forage fish depletion have also been observed, for example, kittiwake fledging success was more sensitive than murre fledging success to reduced forage fish density in Alaska, presumably because kittiwakes have less discretionary time in their energy budgets to reallocate to foraging (Piatt et al., 2007b). Furness and Tasker (2000) also demonstrates that the breeding performance of 25 seabird species varies in relation to sandlance densities in the North Sea according to a set of parameters that reflect sensitivity to forage fish depletion (i.e., body size, cost of foraging, foraging range, dive ability, spare time in daily energy budget, and ability to switch diet). However, the global analysis by Cury *et al.* (2011) finds that the asymptote below which seabird productivity declines is consistent across all species, at one third of the long-term maximum biomass or the long-term average biomass. Therefore, further studies are required to better understand if and how the sensitivity of different seabirds to reduced prey availability varies. Overall, food availability plays an important role in regulating seabird populations, and the relationship between prey availability and seabird population parameters is non-linear, with the location of the threshold perhaps varying between species.

Based on existing knowledge of seabird population dynamics, it is expected that undisturbed seabird populations should be relatively stable over long periods of time. The K-selected life-history strategy evolves when populations are regulated around carrying capacity by competition for relatively stable limiting resources. There is little evidence of seabird stability within monitored populations, although the cause of this is difficult to interpret because there are virtually no populations that have been monitored over long timeframes in the absence of anthropogenic threats (Section 1.3.6).

Seabird populations are especially vulnerable to extinction. Seabird populations are inherently poor at buffering against additional mortality, especially adult mortality; their late age at maturity, low annual fecundity, high percentage of non-breeding individuals, and high adult survival contribute to an inherently low maximum potential population growth rate of 1.03-1.12 for most species under ideal circumstances (Russell, 1999). Additional adult mortality as low as 1-2% can cause population decline in long-lived seabirds such as Procellariiformes (Russell, 1999). The biogeography of seabirds also lends to their relatively high vulnerability to extinction; like all island biota, many seabird species consists of small populations and endemics, and therefore lack other populations to rescue them if they collapse (Freedman et al., 2010). Furthermore, there is also a low probability of the rescue effect among seabirds because seabirds are highly philopatric, with low breeding attempts and/or success outside of their natal colonies (Jones and Kress, 2011). Finally, the wide-ranging and transboundary nature of most seabirds leads to increased probability of exposure to different threats during their lifetimes (Jodice and Suryan, 2010).

1.3.5 Seabird ecology

Most seabirds are top predators, consuming fish, krill and squid. Recent studies indicate that top-down control plays an important role in the structure of marine food webs, and that the removal of marine top predators, such as seabirds, results in major changes (e.g., mesopredator and invertebrate release, mesopredator and invertebrate declines, and trophic cascades) which alter the structure, function, and resilience of marine ecosystems (Baum and Worm, 2009). Some seabirds, mainly gulls, skuas, albatrosses, and giant petrels (*Macronectes* spp.), consume dead marine mammals, squid, other seabirds, and fish discarded by fisheries. These seabirds act

as decomposers in marine ecosystems, facilitating rapid decomposition of carrion, which reduces the rate of disease transfer and recycles nutrients in the marine food web (Sekercioglu et al., 2004).

Seabirds are eaten by a variety of mammal, fish, and bird predators including true seals (Phocidae), fur seals and sea lions (Otariidae), walrus (*Odobeus rosmarus*), Sea otters (*Enhydra lutris*), Killer whales (*Orcinus orca*), Polar bears (*Ursus maratimus*), White sharks (*Carcharondon carcharias*), hawks, falcons and eagles (O. Falconiformes), owls (Strigiformes), giant petrels, rails (Rallidae), Stercorariidae, and sheathbills (*Chionis* spp.) (see Hipfner et al., 2012), as well as a variety of introduced terrestrial predators (see Section 1.1.7).

Many seabirds have symbiotic foraging interactions with other marine predators. The interactions are perhaps most often commensalistic, with surface feeding seabirds benefitting when predators bring food to the surface (Evans et al., 1993). In fact, the majority of tropical seabirds are surface-feeders that may be obligate commensals of tunas (*Thunnus* spp.) and dolphins (Delphinidae) to bring prey fish to the surface (Ballance and Pitman, 1999). On the other hand, marine mammals have been observed to benefit from cooperative feeding from seabirds, perhaps in a commensalistic or mutualistic relationship. For example, in the North Pacific, piscivorous guillemots, razorbills and puffins dive to herd forage fish into bait balls, which increases foraging efficiency of Minke whales (*Balaenoptera acutorostrata*) (Anderwald et al., 2011).

Seabirds also play a keystone role in shaping the plant community in their terrestrial and coastal breeding habitat. Seabirds transport allochthonous nutrients (i.e., fixed nitrogen, phosphorus, and trace elements), mainly via their guano, to seabird colonies (i.e., cross-ecosystem subsidies). They also shape plant communities in their breeding habitat by creating physical disturbance, dispersing seeds, and bioturbating soil with their burrow (Ellis, 2005, Bancroft et al., 2005). These ecosystem services provided by seabirds increase productivity and diversity in terrestrial and coastal ecosystems surrounding seabird colonies (Powell et al., 1991, Bosman et al., 1986, Ellis, 2005, Brimble et al., 2009, Polis et al., 1997). A major demonstration of the importance of seabirds in shaping terrestrial plant communities was the transformation of Aleutian archipelago islands from grassland to tundra after the removal of seabirds by introduced predators (Croll et al., 2005). Although seabird guano accounts for only 2% of the world's fixed nitrogen emissions, it is a globally important because it facilitates hotspots of productivity in remote and otherwise unproductive areas (Riddick et al., 2012).

Overall, seabirds have high intrinsic and utilitarian value in marine ecosystems; seabirds provide ecological services, ecotourism, top-down control of marine food webs, and bottom-up control of productivity in unique island ecosystems (Mulder et al., 2011, Baum and Worm, 2009). They are also an important part of marine biodiversity which supports ecosystem function including productivity, water quality, and ability to recover from perturbations (Worm et al., 2006).

1.3.6 Anthropogenic activities threatening seabirds

There is a long history of anthropogenic activities threatening seabirds, beginning in the age of exploration with the hunting of seabirds and introduction of predators to their colonies, followed by threats of the modern industrial era including habitat destruction, pollution, and fisheries.

Hunting of seabirds for food, fuel, fishing bait and feathers has occurred throughout the history of human existence on coasts. Seabird populations are easily wiped out by hunting because seabirds are not adapted to evade land-based predators, and furthermore they are easily accessible at their colonies. Great auk (Pinguinus impennis) colonies throughout the North Atlantic were wiped out over the course of three centuries of exploitation by cod fishermen and explorers hunting them for food, fuel, fishing bait and feathers (1400-1800). Millions of penguins were killed in the 1800s and 1900s for the production of lamp oil (Boersma et al., 2002). Tens to hundreds of millions of terns, gulls, kittiwakes, and albatrosses were killed annually for the ornamentation of hats during the millinery trade (1869-1922). Hunting played a major role in the extinction of many species, including the Pallas's cormorant (*Phalacrocorax* perspicillatus) in the 1950s, the Great auk in 1844 (Bengston, 1984), both the Small St. Helena petrel (Bulweria bifax) the Large St. Helena petrel (Pterodroma rupinarum) species in 1502 (IUCN, 2011), and at least ten additional seabird species (Millberg and Tyrberg, 1993). Many species also declined dramatically due to hunting, including the Short-tailed albatross (*Phoebastria albatrus*) which had no breeding population in 1949 (Hasegawa and DeGange, 1982). Northern temperate and tropical regions appear to have faced the longest history of seabird hunting, with travel to the Arctic for hunting and fishing beginning in the 1500s (Klein et al., 2010), and exploitation of Antarctic resources beginning only after its discovery in the 1770s

(Antarctic Ocean Alliance, 2012). The intensity of seabird hunting has since declined, although it still affects at least 23 seabird species (Croxall et al., 2012). For example, 13% of the annual New Zealand Sooty shearwater (*Puffinus griseus*) chick production is harvested (Newman et al., 2009), and approximately 2 million adults and countless eggs of several species of Alcidae are harvested per year in the Arctic (Circumpolar Seabird Working Group, 2001).

Introduced predators including rats (Rattus spp.), cats (Felis catus), foxes (Vulpes spp.), pigs (Suss scrofa), mice (Muss spp.), and weasels (Mustela spp.) have been introduced to seabird islands since early exploration, now affecting the majority of seabird islands worldwide (Mulder et al., 2011). Introduced predators are a threat because seabirds have not evolved defences against land-based predators (Igual et al., 2007). The decline in tropical seabirds from a historical population that was 100-1000 times greater than present, is mainly due to hunting and introduced predators (Steadman, 1997). All seabird taxa are affected by introduced predators; small-bodied burrow- and crevice-nesters are especially vulnerable to the most widespread of predators, rats (Jones et al., 2008), while surface nesters are more exposed to surface predators such as cats and foxes (e.g., Byrd et al., 2005). The removal of invasive predators from some seabird islands has benefitted some seabird populations over the past two decades (Croxall et al., 2012, Jones and Kress, 2011). For example, Ancient murrelet (Synthliboramphus antiquus) populations increased on Langara Island after rat eradication (Regehr et al., 2007), and numerous seabird species re-colonized the Aleutian Islands after fox eradication (Bailey, 1993, Byrd et al., 2005). However, recovery rates are often hindered by the presence of other introduced predators and/or threats. For example, five seabird species re-colonized Ascension Island after cats were eradicated, but with low breeding success compared to elsewhere because of remaining rat

predators (Ratcliffe et al., 2009, Madeiros, 2011). Introduced predators continue to be a major threat to seabirds, affecting 75% of IUCN Red Listed seabird species (Croxall et al., 2012).

Habitat degradation and destruction is also a substantial threat to seabirds. One of the first major examples of habitat destruction was the guano harvest. Since at least the Inca Empire (1438-1533), seabird guano was harvested from seabird colonies in the Humboldt Current region for use as fertilizer. This became a major threat to seabird habitat during the Guano Age (1840-1880), when the British harvested 13 million metric tonnes of guano from the Humboldt Current region and 2 million metric tonnes from the Benguela Current region, both important guano regions because they have large seabird colonies that do not receive enough rain to wash away guano. The extraction of guano caused the destruction of nesting habitat, which resulted in seabird population decline and the collapse of the guano industry. However, protection and artificial nesting habitat were implemented in 1909 to serve the Peruvian guano industry, which produced almost 8 million tonnes before its collapse in 1965 (Cushman, 2005). Although remaining guano deposits are relatively depleted (i.e., less than 30 cm, compared to about 50 m thick prior to the guano rush), an industry persists (producing 12-15,000 tonnes per year), because the guano is highly valued in France, Israel and the USA as an organic fertilizer (Romero, 2008). Another major cause of habitat degradation and destruction is coastal development including building resorts, cities, mines and ports of seabird nesting habitat, rerouting rivers and/or altering wetland water levels for hydroelectric power, and building marine oil platforms along seabird flyways. Coastal development may have the greatest effect on seabird populations in the world's most altered shorelines, which are in Europe, South and East Asia, and South and East North America (Harrison and Pearce, 2001). Seabird collisions with

marine oil platforms are difficult to quantify, occurring episodically in low-visibility conditions and probably exacerbated by seabirds' attraction to their bright lights and flares. However, up to tens of thousands of seabirds have been observed in a single collision event (Montevecchi, 2006). Tourism and research in seabird breeding habitat can also degrade the quality of the breeding site, causing stress to seabirds and consequent reproductive failure and population declines (Carney and Sydeman, 1999). Tourism now affects seabird colonies in even the most remote regions of the world, including Antarctica. Overall, increasing human population and coastal development throughout the modern industrial era have probably caused continuous increase and spatial expansion of seabird habitat destruction worldwide.

There are four key fisheries-related threats to seabirds. First, fisheries may compete with seabirds for their prey; seabirds require an estimated 12.1 million tonnes of forage fish annually (Kaschner et al., 2006), while fisheries extract approximately 31.5 million tonnes of forage fish annually in the early 2000's (FAO, 2006); both concentrate their fishing effort in the same highly productive regions of the worlds oceans. These fisheries are not sustainable for many forage fish and the ecosystems in which they play an important role (Pikitch et al., 2012, Fréon et al., 2005). Although it is often difficult to differentiate between environmental and fisheries induced fluctuations in forage fish abundance, there are several clear examples of negative effects of forage fish overexploitation on seabirds around the world. These include the decline in abundance of Peruvian seabirds (Guanay cormorant, *Phalacrocorax bougainvillii*; Peruvian booby, *Sula variegata*; Peruvian pelican, *Pelecanus thagus*in) corresponding with overexploitation of Peruvian anchoveta (*Engraulis ringens*) (Jahncke et al., 2004); decline in abundance and egg size of Atlantic puffins (*Fratercula arctica*) corresponding with collapse of

Atlantic herring (Clupea harengus) off Western Norway (Barrett et al., 1987, Barrett et al., 2012); decline in trophic level of Marbled murrelet (Brachyramphus marmoratus) corresponding with the overexploitation of Pacific sardine (Sardinops sagax) off California (Becker and Beissinger, 2006); decline in abundance of Black-legged kittiwakes (*Rissa tridactyla*) corresponding with overexploitation of sandlance (Ammodytes marinus) in the North Sea (Frederiksen et al., 2004); and decline in abundance of South African seabirds (African penguin, Spheniscus demersus; Cape gannet, Morus capensis; and Cape cormorant Phalacrocorax *capensis*) corresponding with overexploitation of sardine (*Sardinops sagax*) and anchovy (Engraulis encrasicolus) (Crawford, 2007). As a general rule, seabird productivity has been found to decline if prey biomass is reduced below one third of the peak biomass, incidentally also the long-term average biomass (Cury et al., 2011). Forage fish fisheries have occurred for millennia, but grew rapidly since they were industrialized in 1950. Forage fish landings peaked in the 1970s although effort has not subsided since and is expected to grow with increased demand for fish meal and fish oil to fuel agriculture (Alder et al., 2008). Throughout the modern industrial era, regions with important forage fish fishing areas have been the west coast of South America, northern Europe, Alaska, and the east coast of the United States (Alder et al., 2008).

Second, some fisheries also target and reduce abundance of predators in marine ecosystems (i.e., fish, whales, marine mammals), which may affect seabirds in several ways. The reduction of tunas may reduce the productivity and population size of tropical seabirds that are obligate commensals; the effects on seabirds have not yet been quantified (Le Corre and Jaquemet, 2005). On the other hand, the removal of large fish may result in the release of seabird prey (e.g., mesopredator and invertebrates). For example, herring, capelin and sandlance increased after the

collapse of cod in several coastal regions of the North Atlantic, North Sea and Baltic Sea; small fish increased after the collapse of tunas, billfishes and sharks (Chondrichthyes) in the tropical Pacific; squid populations increased after the collapse of Sperm whales (*Physeter* macrocephalus) in the North Pacific (Baum and Worm, 2009). However, there is scarce to nonexistent evidence of resulting seabird population increase. Rather, predator release has been observed to cause increase in different species of small fish and/or increase in abundance of the same species but with lower individual energy density (Baum and Worm, 2009). For seabirds and other predators, these different prey species and/or lower energy density prey are "junkfood", and have been linked with reduced seabird productivity in the North Pacific, North Sea, and Baltic Sea (Osterblom et al., 2008). The history of reduced predator populations in the oceans dates back hundreds to thousands of years (Lotze and Worm, 2009), and some fisheries began a few decades prior to the modern industrial era, for example, the Newfoundland cod (Gadus morhua) fishery, which started in the 1500s (Rose, 2004), and industrial whaling, from 1926 to 1975 (Clark and Lamberson, 1982). However, the most severe global predator depletion affecting seabirds probably occurred within the modern industrial era (i.e., 1950-present).

Third, discards from fisheries provide alternative food for seabirds, thereby altering their foraging ecology. This has mixed effects, benefiting some scavenging seabirds such as gannets, gulls, and skuas (Chapdelaine and Rail, 1997, Garthe et al., 1996, Bunce et al., 2002), but also threatening these scavengers if discards are of lower energetic value (Mullers et al., 2009) and threatening the smaller-bodied seabird species upon which augmented scavenger populations prey (Votier et al., 2004). Fisheries discards appear to have peaked in the 1990s, and are estimated to now be reduced to 25% of the peak tonnage (Zeller and Pauly, 2005). The amount

of discards is highest in the northern hemisphere, particularly the Northeast Atlantic and Northwest Pacific, which jointly account for 40% of global discards (Kelleher, 2005).

Fourth, where fisheries activities and seabird foraging overlap, fisheries gear may entangle and drown seabirds. The two most lethal types of fisheries gear are the baited hooks on pelagic and demersal longlines, which attract large pelagic surface-feeding albatrosses and petrels, as well as demersal diving birds (Brothers et al., 1999), and coastal gillnets and trawls, which entangle seabirds that dive to forage for their prey (Zydelis et al., 2009). Longline bycatch has grown during the modern industrial era, but declined since the 1990s in some key fisheries due to mitigation (Anderson et al., 2011). Gillnet bycatch has probably grown continuously throughout the modern industrial era, as global gillnet-caught fisheries catch has increased (Sea Around Us 2012, *unpublished data*) regardless of the United Nations ban on large-scale (i.e., >2.5 km long) pelagic drift net fishing in international waters in 1991 (FAO, 2001). The current annual seabird mortality is estimated as at least 160,000-320,000 individuals on longlines (Anderson et al., 2011), 100,000-200,000 individuals in gillnets (Zydelis et al., 2009), as well as an undetermined number in trawl gear (Moore and Zydelis, 2008). Overall, industrial scale fishing effort increased throughout the modern industrial era (i.e., 1950-present) (Anticamara et al., 2011), and spatially expanded from the north Atlantic and southwest Pacific epicentres (Swartz et al., 2010).

There are several pollutants threatening seabirds. First, persistent organic pollutants, including polychlorinated biphenyls and persistent pesticides, are hydrophobic and persistent, and therefore become bioconcentrated in marine organisms and biomagnified at higher trophic levels in marine food webs. In seabirds, they attack the endocrine and nervous systems, resulting in various

responses that ultimately cause reduced reproductive success and survival (e.g., Bustnes et al., 2003, Miljeteig et al., 2012). The production of persistent organic pollutants began in the 1940's and have grown since; global pesticide use alone has grown to several million tonnes per year (World Health Organization, 1990). Some seabird-harming pesticides have been banned in recent decades (e.g., DDT), although they still persist at potentially harmful levels in the tissues of arctic seabirds (Braune et al., 2005).

Second, marine oil pollution may foul seabird feathers, causing hypothermia and loss of buoyancy, or become ingested during seabird feeding or preening, causing digestive and osmoregulatory disorders, reproductive failure, reduced immunity, and mutations (Burger and Fry, 1993). Individual oil spills can cause major seabird mortality, for example, the Deepwater Horizon spill of 700,000 tonnes killed several thousand seabirds, and the Exxon Valdez spill of 75,000 tonnes killed 250,000 seabirds (Piatt and Ford, 1996, Safina, 2011). However, chronic oil spills from ships and offshore oil exploration release an additional 600,000 tonnes of oil per year (GESAMP, 2007). Given that oil spills as small as 10 ml can lethally reduce thermoregulation in seabirds (O'Hara and Morandin, 2010), chronic oil spills stand to cause substantial yet unquantified seabird mortality. It is estimated that chronic oil spills cause approximately 300,000 Common murre deaths per year off Newfoundland alone (Wiese and Robertson, 2004).

Third, plastic pollution causes seabird mortality in two ways; either seabirds ingest floating plastic particles that block their digestive tracts, or seabirds become entangled in larger plastic pollution such as "ghost" fishing nets discarded at sea or plastic fibres used as nesting material

(Votier et al., 2011). Plastic pollution is a widespread problem; at least 100 species of seabird have been documented to ingest and/or become entangled in marine plastic pollution (Laist, 1997).

Fourth, greenhouse gas pollution (i.e., CO_2 , CH_4 , CFC_5 , O_3 , N_2O) is the major driver of modern industrial era climate change (Oreskes, 2004), which has several indirect impacts on seabirds. Changes in ocean circulation can drive changes in abundance, phenology, distribution, and lipidcontent of seabird prey, which in turn affects seabird survival and productivity (Gremillet and Boulinier, 2009, Gaston and Woo, 2008). Quantifying the effects of climate change on seabirds is complex, as the strength and direction of effects may vary between seabird species, regions, and over time. For example, El Niño Southern Oscillation (ENSO) events, characterized by warm water and reduced upwelling in the Humboldt Current ecosystem, reduce Peruvian anchoveta available for guano bird populations, Guanay cormorant (Phalacrocorax *bougainvillii*), Peruvian pelican (*Pelecanus thagus*) and Peruvian booby (*Sula variegata*). Meanwhile, warm water regimes in the Okhotsk Sea bring an influx of forage fish, but a decline in the meso-zooplankton upon which planktivorous auklets feed (Kitaysky and Golubova, 2000). Reduced annual sea ice extent and altered sea ice dynamics in the Antarctic is probably a major driver of decline in ice-loving (pagophylic) species, such as the Emperor penguin (Aptenodytes forsteri) and Adelie penguin (Pygoscelis adeliae), and increase in ice-avoiding species, such as the Gentoo penguin (*Pygoscelis papua*) (Barbraud et al., 2012). However, recent studies indicate that change in krill abundance also plays a role in these penguin population changes (Trivelpiece et al., 2011). Increased strength and southward movement of the westerly winds in the Southern Ocean has been linked to increase in Wandering albatross (*Diomedea exulans*) foraging success,

breeding success and body mass (Weimerskirch et al., 2012). Sea level rise reduces availability of nesting habitat in low-lying areas such as atolls and estuaries, causing reduced productivity where nesting habitat is limiting (Baker et al., 2006, Scarton, 2010). Increased frequency and severity of storms and warm weather events cause additional adult and chick mortality (e.g., Mallory et al., 2009). Warmer temperatures permit spread and outbreak of parasites and diseases (Harvell et al., 2002), for example mosquito outbreaks affect Thick-billed murres (Uria lomvia) in Arctic Canada (Gaston et al., 2002) and the worldwide spread of avian cholera (Pasteurella *multicida*) is probably the major cause of decline in Indian yellow-nosed albatross (*Diomedea* carteri) on Amsterdam Island (Weimerskirch, 2004). These effects of climate change on seabird habitat and prey ultimately influence seabird abundance as well as at-sea and colony distribution. For example, the northernmost colonies of the pagophilic (ice-loving) Adelie penguin are declining, and although at-sea data are relatively scarce for Antarctic seabirds, the foraging ranges of several albatross, petrel and penguin species have been observed to change over years or decades in relation to changes in sea surface temperature, ocean currents and sea ice cover (Barbraud et al., 2012). The effects of climate change on seabirds are still not completely understood, thus quantifying and assessing the spatial distribution of the effects of climate change on the global seabird population is virtually impossible. However, there is evidence that range-restricted species, such as polar or endemic seabirds, are at high risk of range contraction and extinction caused by climate change (Parmesan, 2006).

To what extent each threat affects global seabird population change is poorly understood. In their analysis of the percentage of threatened species affected by threat categories, Croxall *et al.* (2012) found that introduced species affected 75%, entanglement in fisheries gear affected 41%,

climate change affected 40%, and each of the other threats (including habitat destruction, pollution, and fisheries-induced prey depletion) each affected less than 31%.

1.3.7 Seabird conservation

Seabird conservation began in the late 1800's, when humans realized that hunting birds (including seabirds) for their feathers, which were used in the millinery trade, had severely negative impacts on seabird populations. This spurred the first national and international organizations, laws, and agreements to protect seabirds including the Audubon Society in the United States (1886), the Royal Society for the Protection of Birds in the United Kingdom (1889), Britain's Seabirds Preservation Act (1869), the United States' Lacey Act (1900), and the USA-Britain Convention for the Protection of Migratory Birds (1916). International agreements are important because almost all seabird species move between multiple countries in their daily movements and seasonal migrations (Nettleship, 1991, Jodice and Suryan, 2010), and most threats disperse from their source country to other countries and/or the internationally "owned" high seas. National law is important because it provides the primary protective regime for most wildlife, including seabirds (Boersma et al., 2002, Jodice and Suryan, 2010). Together, this first wave of national and international agreements was successful in reducing the harvest of birds for the millinery trade.

The second major wave of seabird conservation began after the 1970's and 1980's, when the impacts of modern industrial era threats became apparent. Several international agreements were made, aiming to protect nesting habitat, reduce pollutants, reduce fisheries-related threats, and protect migratory and threatened species. These include the Ramsar Convention on Wetlands of

International Importance (1975), the Stockholm Convention (2004), the Convention for the Prohibition of Fishing with Long Driftnets in the South Pacific (1989), the United Nations Convention on the Law of the Sea (1982), the Code of Conduct for Responsible Fisheries (1995), the United Nations International Plan for Action for Reducing Incidental Catch of Seabirds in Longline Fisheries (1998), some Regional Fisheries Management Organizations (RFMOs), the Convention on the Conservation of Migratory Species of Wild Animals (1979), the Convention of Biological Diversity (1993), and the Agreement for the Conservation of Albatrosses and Petrels (2001). Some of these have been effective in mitigating seabird threats, for example, one RFMO, the Commission of the Conservation of Antarctic Marine Living Resources (CCAMLR) was effective in reducing albatross bycatch by over 99% in the fisheries surrounding South Georgia (Croxall and Nicol, 2004). This action most likely contributed to the recovery of some species threatened by entanglement in fishing gear in the southern ocean including the Amsterdam albatross (Diomedea amsterdamensis), Short-tailed albatross, and Bermuda petrel (Pterodroma cahow) (IUCN, 2011). Other successful conservation efforts of modern seabird conservation include eradication of introduced predators and habitat restoration projects, pioneered in the 1970s and more widely applied after the 1990s (Jones and Kress, 2011, Croxall et al., 2012); and protection of approximately one third of the world's currently identified Important Bird Areas (IBAs) in recent decades (Croxall et al., 2012). However, existing legislation and agreements are not adequate; international agreements fail to address some of the major threats to seabirds such as oil pollution and fisheries-induced prey depletion. Furthermore, many international agreements remain to be signed and ratified by all countries. Habitat protection and conservation effort is mainly limited to nesting habitat, and occurs predominately in Australasian and European countries; increased habitat protection and conservation is

required in the marine habitat and in North America, the Caribbean, Taiwan and North Korea (Croxall et al., 2012). A recent review of global seabird status, threats, and priority actions indicates that seabird conservation is not currently adequate, with need for increased control of invasive species, habitat protection, legislation and enforcement, education, fisheries harvest management, and reintroduction of extirpated seabirds (Croxall et al., 2012).

1.3.8 Seabird population monitoring and status

Seabird populations are relatively easy to monitor compared to other marine organisms because of their terrestrial colonial breeding, and therefore have been monitored in some capacity for centuries. Early population estimates consisted of opportunistic counts of seabirds present at a given colony, often in references to the quantity available for harvest, and typically reported to the nearest order of magnitude. For example, the now extinct Great auk was reported to be so abundant in the early 1500s on Funk Island, Newfoundland, that "in one half and hour at least 4-5 tonnes were taken by two visiting vessels" (Grieve, 1885). The development of science and technology after the industrial revolution enabled more systematic seabird population monitoring including more frequent visits to seabird colonies, visits targeting the breeding season, surveys covering larger areas, and development of methods to account for undetected burrow-nesters as well as non-breeders. Overall, seabird population monitoring has increased through time, with quantitative data mainly confined to the modern industrial era.

Monitoring data is useful for assessing the status of seabirds, which is inherently important and also indicative of the status of marine ecosystems. Seabird population change and other demographic, behavioural and physiological parameters can be a good indicator of marine

ecosystem change because seabirds are relatively well-monitored and have qualities that enable their populations to track long-term and large-scale changes in marine food webs including long life spans, large ranges, and feeding at a range of trophic levels (Piatt et al., 2007a). For example, seabird breeding failures preceded the collapse of several globally important forage fish stocks including Peruvian anchoveta (*Engraulis ringens*), Norwegian herring (*Clupea harengus*), Barents Sea capelin (*Mallotus villosus*), and North Sea sandlance (*Ammodytes* spp.) (Piatt et al., 2007a), and a global relationship was found between seabird productivity and forage fish abundance (Cury et al., 2011). Seabirds are also useful indicators of pollutant levels including oil, mercury and organochlorides (Furness and Camphuysen, 1997).

The majority of seabird population monitoring is limited to relatively small temporal and spatial scales. Although long-term seabird population monitoring is underway at select seabird colonies, in some cases spanning back to the 1950s (Wooller et al., 1992), most existing seabird population monitoring was initiated after 1970. Some seabird populations and/or species lack population monitoring altogether, resulting in unknown population trends for 53 seabird species on the IUCN Red List (IUCN, 2011). Furthermore, seabird population monitoring typically occurs at small spatial scales such as colonies or islands. For example, a relatively large spatial scale study would be the assessment of population trends in all Canadian seabirds since 1970 (Gaston et al., 2009). There have been some attempts to summarize seabird population change at larger scales, including a compilation of accounts of the status of seabirds in all major seabird-supporting regions of the world (Croxall et al., 1984) and assessment of the probability of extinction for all seabird species (IUCN, 2011). The former described qualitatively historical and modern declines in seabird abundance across many of the regions of the world due to

anthropogenic threats, while the latter designated one third of all seabird species as threatened with extinction, establishing seabirds as the most threatened of all similarly sized groups of birds in the world (Croxall et al., 2012).

There is currently no reliable quantitative assessment of the status of the global seabird population. The only assessment of global seabird population change over any period of time was made by Karpouzi (2005), estimating that the global seabird population declined by 14%, from 1.076 billion individuals in 1950 to 0.922 billion individuals in 2003. However, this estimate is only preliminary as Karpouzi calculated cumulative observed change in seabird abundance, the majority of which is sampled over only a subset of the time series and therefore does not capture the total population change. A reliable estimate of global seabird population change is needed to quantitatively demonstrate the status of seabirds. Global studies are essential in understanding and communicating the magnitude of anthropogenic threats to wildlife. For example, the Sea Around Us Project, led by Pauly (2007), summarized fisheries catch and its impact marine ecosystems, thus reframing various fisheries-related issues that had previously only been viewed from a small-scale myopic perspective. A global scale approach is particularly important in seabird conservation; seabirds and their threats are wide-ranging and cross many jurisdictional and ecological boundaries, so it is especially necessary for conservation initiatives to occur at large scales in order to be effective (Jodice and Suryan, 2010).

Chapter 2 Temporal patterns in global seabird abundance, 1950-2010

2.1 Summary

Seabirds face a variety of modern industrial threats, and their populations appear to be declining as a result. One third of all seabird species are IUCN Red Listed (IUCN, 2011), and a preliminary analysis reveals that the global seabird population has declined within the modern industrial era (Karpouzi, 2005). A reliable estimate of global seabird population change is required however, to assess and communicate the status of the global seabird population. The present study estimates global annual seabird population size throughout the modern industrial era, by calculating global average annual change and anchoring it on a fixed year global population estimate (i.e., using a method established and widely used by climate scientists to estimate global average annual temperature change). The estimate was also subdivided by seabird family. The global seabird population was estimated to decline by 25% over the modern industrial era, from 1.023 billion individuals in 1950 to 0.768 billion individuals in 2010. Overall decline was observed in 11 of the 14 seabird families, and maximum decline per family was one order of magnitude greater than maximum increase per family. These results highlight the urgent need for global seabird conservation, addressing threats faced by all seabird families.

2.2 Introduction

One third of the world's seabird species are IUCN Red Listed (Croxall et al., 2012), mainly because of threatening anthropogenic activities including hunting, introduced predators, habitat destruction, pollution, and fisheries. There is no previous analysis of global seabird population

change by seabird family, and only one preliminary analysis of global seabird population change, which estimated that the global seabird population has declined throughout the modern industrial era by at least 14% (Karpouzi, 2005). However, this preliminary study does not capture all seabird population change occurring within the modern industrial era because it only accounts for cumulative observed change of all seabird populations, most of which are derived from monitoring populations over relatively short timeframes within the modern industrial era. The present study seeks to provide a more reliable estimate of global annual seabird population size throughout the modern industrial era, overall, as well as by seabird family.

The present study estimates global annual seabird abundance using a method established by climate scientists to calculate global annual temperature change based on a similarly opportunistic dataset. The challenge in estimating both global annual temperature change and global annual seabird population change is that the data consist of time-series collected over different spans of time at each station or colony respectively. Climate scientists overcame this problem by calculating global annual temperature as the average annual observed temperature change anchored on global average temperature in a reliably estimated year (Hansen et al., 2006). Likewise, the present study will estimate global annual seabird population size in a reliably estimated year. Family-specific annual abundance estimates are also made by calculating family-specific average annual seabird population change, anchoring them on an absolute estimate of abundance, then scaling all annual family-specific abundance estimates to fit under the previously calculated global annual seabird abundance curve.

It is expected that the estimate of global seabird population change may reveal greater global seabird decline than the preliminary estimate, given that the present method will account for seabird population change over the entire modern industrial era instead of only counting the change observed within monitored years for all populations. One might also expect families to decline at different rates, although the relative decline of families is difficult to predict because families vary in their exposure and sensitivity to various threats.

2.3 Methods

2.3.1 Global database of seabird abundance records, 1950-2010

A global database of seabird abundance records, 1950-2003, was initially constructed by Vasiliki Karpouzi for her M.Sc. research (Karpouzi, 2005); The abundance records therein were augmented and updated to 2010. Examples of abundance data in the database are provided for four numerically important but otherwise randomly selected seabird species (Appendix II).

The database included breeding population estimates for all 324 seabird species in the world (Appendix I), at 358 *coastal stretches*, 1950-present. Coastal stretches, are here defined by subdividing the world's coastline into units in which seabird abundance data were most commonly and/or likely to be aggregated for reporting. Coastal stretches were typically countries, unless the coastline of a country was large and/or discrete (e.g., USA), in which case it was divided into multiple stretches (e.g., Oregon, Washington, Aleutian Islands, Gulf of Alaska, etc.). The seabirds of a single species breeding within a coastal stretch represents a *population*.

Seabird abundance records were collected for the breeding populations (i.e., rather than wintering population) for two reasons. First, seabird abundance estimates are most commonly made by counting breeding populations (e.g., nests, apparently occupied nests, breeding pairs, or occupied burrows). Second, seabirds are philopatric and reproduce annually, so the global abundance can be estimated as the sum of all breeding populations in a given year, plus nonbreeders. For the few species that breed also at inland colonies, for example, the Herring gull (Larus argentatus), only coastal breeding locations were included in the database. If abundance was reported as a range, the geometric mean of the minimum and maximum population was used as the population size; here, the geometric mean is the square root of the product of a pair of values, used to approximate the central tendency (Freedman et al., 2010). Although less common, some estimates were reported as the entire population size (i.e., including breeders and non-breeders). In order to be able to use population estimates reported in both breeding pairs and population size, the present study assumed that non-breeders accounted for 30% of the total population, a value that is commonly used as the global average (e.g., Riddick et al., 2012, Brooke, 2004b, Karpouzi, 2005).

Data were collected from a variety of sources, including books, journal articles, and online databases (e.g., that of Birdlife International). Regional seabird population biologists were consulted to verify database contents in six selected ecosystems supporting large seabird populations (i.e., North Sea, Norwegian Sea, New Zealand, Benguela Current, Gulf of Alaska, and California Current).

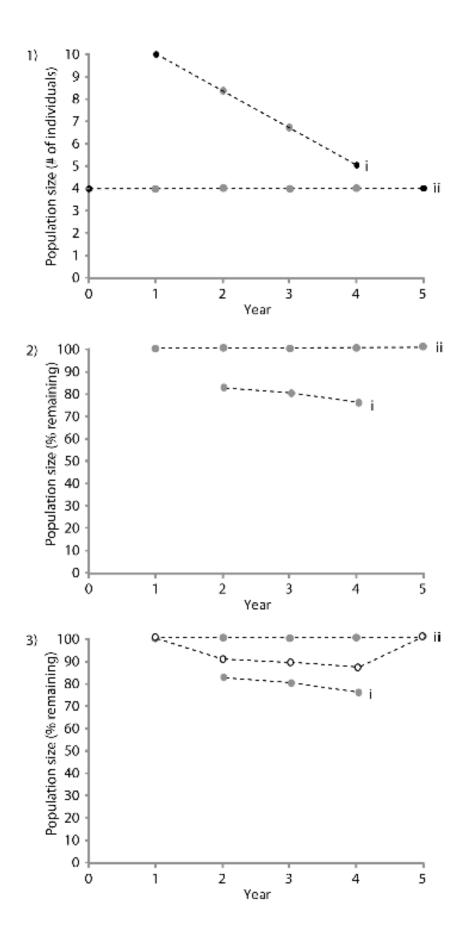
2.3.2 Estimating annual change in global seabird abundance

Annual change in global seabird abundance was estimated following three steps (Figure 2.1, panels 1- 3):

Step 1: For all populations with more than one record, calculate annual abundance using linear interpolation between the first and last data points. No abundance data was included in years before the first and after the last abundance record for a given population, and therefore no assumptions were made regarding change in abundance of a population in years outside of available abundance records.

Step 2: For all populations, calculate annual percent change in abundance.

Step 3: Calculate the annual average of percent change in abundance across all populations (from Step 2), weighted by population size so that the influence of a population on global annual change in abundance is proportional to its size.



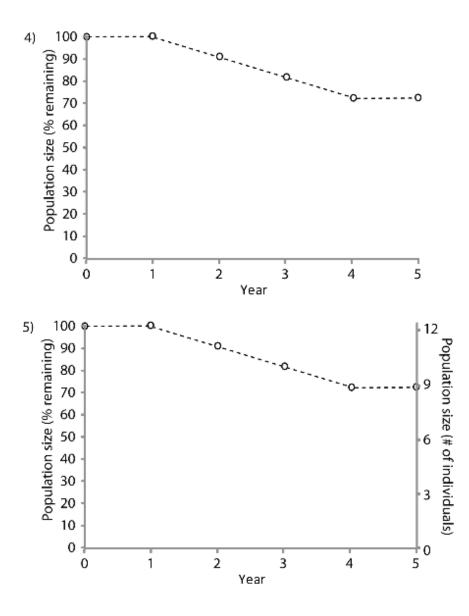


Figure 2.1 Method for estimating annual change in abundance then absolute abundance of the global seabird population, based on two hypothetical populations (i and ii) monitored over six years. There are five steps: (1) calculate annual abundance (grey dots) based on linear interpolation between data points (black dots) for all populations, (2) convert annual abundance to annual percent change in abundance for all populations, (3) calculate the annual average percent change in abundance across all populations (white dots), weighted by population size, which is assumed equal for this example, (4) convert this to cumulative annual population change, and (5) estimate annual population size, by anchoring the cumulative annual population change on an estimate of abundance in 1950.

2.3.3 Estimating annual global seabird abundance

Global annual seabird abundance was estimated following two additional steps after those described above in Section 2.3.2 (Figure 2.1, panels 4-5):

Step 4: Express the global annual average percent change in cumulative terms. In other words, 100% abundance was assumed in 1950, and the percent of seabirds remaining in each subsequent year was calculated as the product of the percent remaining in that particular year and the cumulative percent remaining in the preceding year.

Step 5: Anchor this global cumulative annual percent change curve on an absolute global abundance estimate. The absolute global abundance estimate was calculated as the sum of abundance estimates for all populations, taken from records closest to the year 2010, which allowed the use of all of the most recent seabird abundance estimates available. The global cumulative annual percent change curve was then anchored on this estimate of abundance in 2010, by first using the ratio of cumulative percent abundance remaining in 1950 to 2010 to estimate the abundance in 1950 (i.e., the product of this ratio multiplied by the estimate of abundance in 2010), then second multiplying this estimate of abundance in 1950 by the cumulative annual percent change in each given year.

2.3.4 Breaking the global annual seabird abundance down by seabird family

Global annual seabird abundance was subdivided by family using two steps. First, annual population size of each of the 14 seabird families was calculated following the methods

described in Section 2.2.2-2.2.3. If the global annual abundance had been calculated as the sum of these family-specific estimates, it would expectedly vary slightly from the global estimate, with the global estimate being more accurate because of the large sample size. Thus as the second step, the sum of these family-specific annual population sizes were fitted under the more accurate global curve; this was done by dividing the annual global population size by the relative abundance of each family in the respective year.

2.4 Results

2.4.1 Seabird abundance database

The global seabird abundance database contains 9920 records for 3231 populations between the years 1950 and 2010 (Figure 2.2). Seabird abundance data are most abundant in the later decades; the decade of most abundant records was the 1990s, and the decade of least abundant records was the 1950s. It appears that most or all seabird populations have been sampled at least once by the end of the timeframe, as indicated by the levelling of the accumulation curve in the final decade (Figure 2.2). The number of records per population ranged from one to fifty-one, averaging three. Two thirds of the populations were sampled more than once, and this fraction of the population accounted for 86% of the global seabird population size. Populations sampled more than once were monitored over an average duration of 20 years. The relative number of records per family was consistent through time (Figure 2.3).

2.4.2 Global annual seabird population change

The estimated annual change in global seabird abundance ranged from -3.1% to +2.7%, and averaged -0.5% of abundance in the previous year. Decline was observed in 80% of all years (Figure 2.4).

2.4.3 Global annual seabird population size

The cumulative annual change in global seabird abundance during the modern industrial era was estimated to be -25% (Figure 2.5). Cumulative decline occurred over five of the six decades, with most dramatic decline in the 1970's (i.e., -13% in the 1970s, compared to -1% in the 1960s, -4% in the 1980s, -4% in the 1990s, and -3% in the 2000s), and no population change in the remaining decade (i.e., 0% in the 1950s). There was no statistically significant decline until after 1970, after which the standard deviation no longer overlapped consistently with the baseline global seabird population size. The anchor point of global seabird abundance was estimated to be 0.768 billion seabirds for the year 2010. The global seabird population was estimated to have declined from 1.023 billion individuals in 1950 to 0.768 billion individuals (Figure 2.5).

2.4.4 Global annual seabird population size, by family

Annual abundance of all seabird families was estimated (Figure 2.6) using calculated anchor points of family-specific abundance in 2010 (Appendix III). Eleven of the fourteen seabird families declined in abundance while three increased in abundance (Figure 2.6). In absolute terms, extreme decline (i.e., decline of more than 100 million individuals) occurred in two

families (Procellariidae, 116 million; Sternidae, 115 million), moderate decline (i.e., decline of 10-100 million individuals) occurred in three families, and smaller decline (i.e., decline of less than 10 million individuals) occurred in six families. Small increase (i.e., increase of less than 10 million individuals) occurred in one family, and moderate increase (i.e., increase by 10-100 million individuals) occurred in two families (Alcidae, 22 million; Hydrobatidae 18 million). In relation to their baseline abundance in 1950, three families declined dramatically to 29-36% (Phalacrocoracidae, Sternidae, and Fregatidae), while eight declined to 71-94%, two increased to 104-112%, and one increased to 164% (Hydrobatidae).

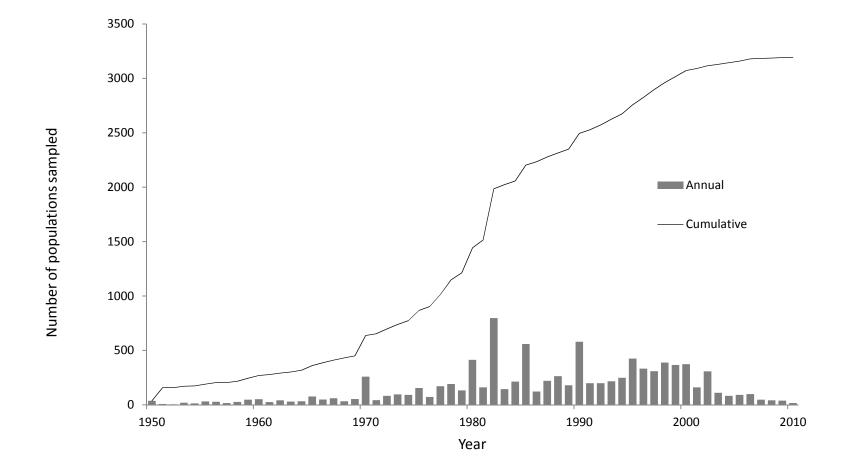


Figure 2.2 Number of seabird populations sampled in the global seabird database, 1950-2010.

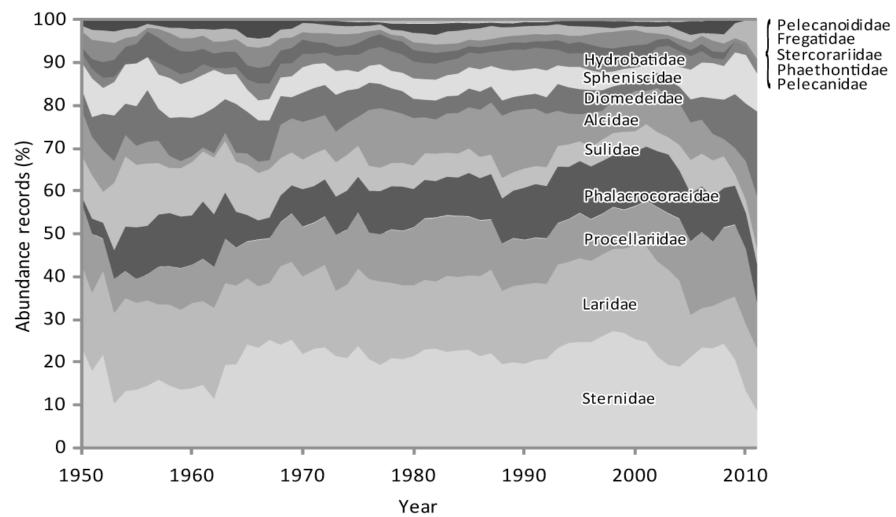


Figure 2.3 Annual relative contribution of each family to the total number of records (5-year running average), 1950-2010; families are ordered by overall contribution.

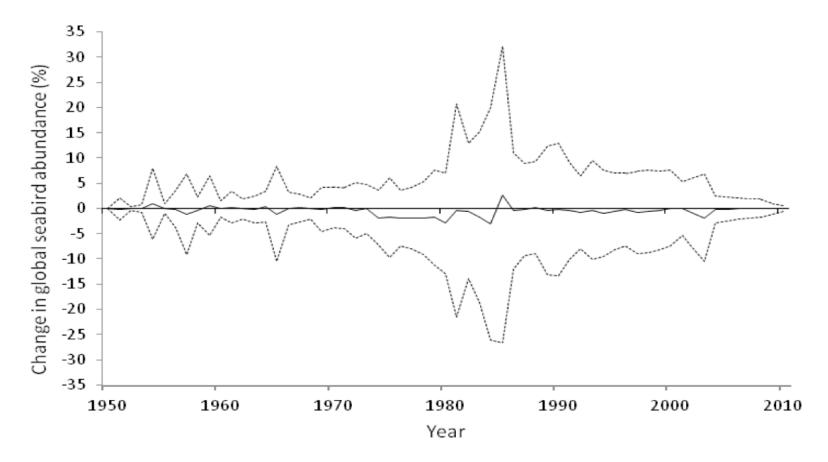


Figure 2.4 Estimated global annual change in seabird abundance, expressed as percent of abundance in the previous year (solid line), and standard deviation (dotted line), 1950-2010.

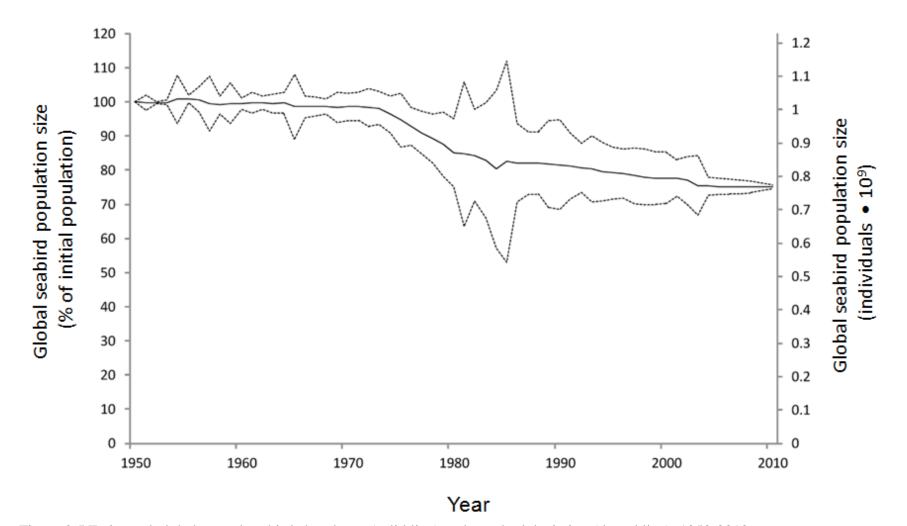


Figure 2.5 Estimated global annual seabird abundance (solid line) and standard deviation (dotted line), 1950-2010.

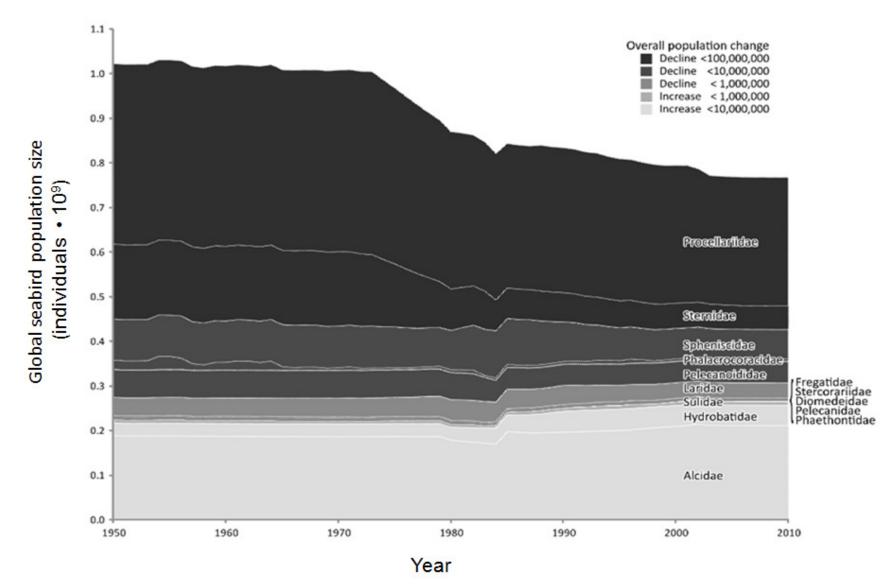


Figure 2.6 Mean annual global seabird population size, by family, 1950-2010. Families are ordered by absolute change in abundance (see legend).

2.5 Discussion

2.5.1 Global seabird population change

The present study estimated global seabird abundance to be 0.768 billion individuals in 2010; this estimate is comparable with previous estimates of seabird abundance at a stationary point in time, including 0.7 billion individuals (Brooke, 2004b) and 1.18 billion individuals (Riddick et al., 2012). The variation between estimates is attributable to the fact that Riddick et al. included inland populations of seabirds and therefore had a higher estimate. Also, each estimate was derived from data collected at different spatial resolutions; data for the present study were collected at the population scale, data for the study of Brooke were collected at the species scale, and data for the study of Riddick et al. were collected at the colony scale. Assumptions about the percentage of non-breeders in the population did not contribute to the difference between estimates, as all three studies assumed 30-33% non-breeders. While the present estimate of global seabird abundance in 2010 is in line with previous estimates, and is therefore a reliable anchor point for the global seabird population change curve, no global annual estimate of seabird abundance can be perfectly accurate because there is no single year in which all seabird populations are counted. However, recent decades have considerably more seabird population monitoring and therefore an estimate of abundance made by summing all abundance estimates closest to 2010 is more reliable than an estimate of abundance made by summing all abundance estimates in an earlier year such as 1950 when fewer records were available.

The present study also provides a first reliable analysis of global annual seabird abundance, and estimates that the global seabird population declined by 25% over the modern industrial era,

from 1.023 billion individuals in 1950 to 0.768 billion individuals in 2010; net decline occurred in all decades and the greatest decline occurred in the 1970s. The overall decline was expected, given that seabird populations around the world are threatened by anthropogenic activities and one third of all seabird species are designated threatened with extinction by the IUCN Red List (IUCN, 2011, Croxall et al., 2012). It was also greater than the preliminary estimate of 14% decline in the global seabird population change during the modern industrial era (Karpouzi, 2005). This more severe decline than the preliminary estimate was also expected because the preliminary estimate accounts for only the observed population change within the modern industrial era whereas the present estimate accounts for unobserved population change that occurred in years when populations were not monitored.

The present estimate of global annual seabird abundance assumes that the unmonitored segment of the population is changing at the same rate as the monitored segment of the population, i.e., that there is no sampling error. Sampling error is inevitable in scientific research, but is reduced by using a randomly selected and large sub-sample of the population. Because the sample size and randomness of the samples varies inter-annually throughout the timeframe of the present study, so too will sampling error. The sample size is greatest in the recent decades (especially the 1970s, 1980s and 1990s), resulting in potentially more reliable estimates in these years. There is evidence that most of the global seabird population is monitored over at least some timeframe, as indicated by the fact that the accumulation of new populations levels off in the final decade (Figure 2.2). Although the annual samples are not random, there is no evidence that increasing or declining populations were monitored more than others, overall or over part of the timeframe. For example, declining populations may be sampled more than others if funding for

monitoring threatened populations is easier to obtain and/or if accessibility for monitoring is correlated with population decline. However, a bias towards intentionally sampling threatened populations is unlikely to affect assessment of population trends over the modern industrial era because this would require that seabird biologists establishing early population monitoring had advanced knowledge of which populations would increase or decline later in the modern industrial era. On the other hand, there is reason to believe that unthreatened populations may be more heavily sampled, since larger populations are often sampled because of their numerical importance, but also less prone to decline/extinction than small populations. For example, Mallory (2006) points out that only the most numerically important seabird in the Canadian Arctic, the Thick-billed murre (Uria lomvia), has been monitored over significant temporal and spatial scales. As a general rule, large populations are less prone to decline/extinction than smaller populations (Pimm et al., 1988). Thus, it is possible that disproportionately high sampling of larger populations exists, and that this may result in some underestimation of global seabird decline if larger populations indeed decline less than smaller populations as predicted by Pimm *et al.*. Evidence of randomly distributed sampling exists in the fact that seabird families are adequately and consistently represented in the sample through time (Figure 2.3). Overall, there is no evidence of sampling error being a major concern, nor changing through time, and therefore there is no reason to believe that it would have a major effect on the estimate of global seabird population change, nor in the inter-annual variation in rates of change.

The present estimate of global annual seabird abundance also assumes that the data accurately depict the change in the monitored segment of the population, i.e., that there is no observational error. Observational error is introduced at the data collection level if inaccurate population

estimates are made. Accurate population estimates can be difficult to achieve for burrow and crevice nesting species because these can be difficult to detect and furthermore are not all occupied (e.g., Lawton et al., 2006). Accuracy of population estimates may also be influenced by variation in the percentage of non-breeders in the population; approximately 30% of the population remains at sea and does not breed in a given year, although this percentage may vary inter-annually for a given population. For example, some populations may consist of 70% nonbreeders in El Niño affected areas (Weimerskirch, 2002, Chastel et al., 1995). This may lead to short-term exaggeration of population increases or declines in response to oceanographic conditions. Accuracy of population estimates may also be influenced by varying sampling effort through time. For example, the most recent observer of the northern Greenland coastal stretch used higher sampling effort than previous observers and found previously undocumented Ivory gull (Pagophila eburnean) colonies (Gilg et al., 2009). This detection of new colonies within the study period creates erroneously increasing population trends; Although the prevalence of this source of observational error is unknown, it may be common in large and remote stretches (e.g., Aleutian Islands, Antarctic Peninsula), creating a bias towards population increase in the global trend. Observational error was also introduced in the methods; by assuming linear change between first and last available record, the study does not account for the relatively small but common inter-annual variation that exists in seabird populations. This may result in erroneous population trends, but with no directional bias, thus adding non-directional variation in average annual change. Although observational error inevitably contributes to erroneous estimates of population change for a subset of the populations included in this global study, there is general consensus among seabird biologists that the methods used to collect seabird abundance data have not changed directionally within the modern industrial era. Thus, there is no reason to suspect

that observational error drives the observed change in global seabird abundance, but rather it probably contributes to noise which is observed as increased standard deviation around the mean annual population change.

Anthropogenic threats are probably a major driver of estimated global annual seabird population change, which includes no change over the 1950s, decline over all other decades, rapid decline in the 1970s, and greatest variation in change during the 1980s. Low rates of seabird population change in early decades may occur because modern industrial threats were still relatively low. The main modern threats (i.e., fisheries, pollution and habitat destruction) have grown monotonically over the modern industrial era. In addition to this, some seabird populations are rebounding from historical depletion; laws protecting seabirds were instigated in the late 1800s after hunting for seabirds during the age of exploration (1400s-1600s) and the millinery trade (1850-1950) had depleted seabird populations. For example, the Short-tailed albatross was heavily hunted during the millinery trade, depleting the species to near extinction in 1949. Since hunting ceased in 1949, the population has grown to approximately 2,300 individuals (incidentally, this is only 2% of the historical baseline of the population, probably in part because Short-tailed albatross continue to be threatened by entanglement in longline fishing gear) (IUCN, 2011, Hasegawa and DeGange, 1982, Piatt et al., 2006). Such population increases due to cessation of hunting and/or removal of historically introduced predators have occurred during the modern industrial era, and would contribute to apparent stability in the global seabird population. The severe decline of seabirds worldwide in the 1970s coincided with an unprecedented rates and accumulation of modern industrial threats; pollution, fisheries and habitat destruction were virtually unrestrained. The decades of most severe decline in the global seabird population

(1960s-1980s) did coincide with the time of unprecedented rates of anthropogenic threats to seabirds. Following this (1990s-2000s), seabird populations continued to decline but at a reduced rate, perhaps in part due to the reduction of fisheries by catch in some regions (Moore and Zydelis, 2008) and some persistent organic pollutants (e.g., Stemmler and Lammel, 2009), but also due to restoration and predator eradication (Howald et al., 2007, Jones and Kress, 2011). Relatively high standard deviation in seabird population change in the 1980s may be related to the relatively high data availability in these years, or perhaps at this time there was a large variation between seabirds threatened by anthropogenic threats and seabirds benefitting from fisheries discards and modern conservation. Although many threats continue to have severe negative effects on seabirds (Croxall et al., 2012), some seabirds have benefitted from improved fisheries management, while others have benefitted from breeding habitat restoration, pioneered in the 1970s and currently underway at 143 sites worldwide, potentially affecting 47 seabird species (Jones and Kress, 2011). Low rates of population change in recent decades may be in part attributable to conservation initiatives and/or the possibility that remaining seabirds have higher resilience to anthropogenic threats. For example, Furness and Tasker (2000) demonstrate that there is a range of sensitivity of seabirds to reduced prey availability, and it has been widely observed that some large scavenging seabirds such as gulls and skuas are increasing in abundance due to increased availability of fisheries discards (e.g., Votier et al., 2004, e.g., Lisnizer et al., 2011).

Natural climate cycles may drive seabird population changes because they alter quantity, quality and availability of seabird prey in marine ecosystems, which limits seabird carrying capacity. There is evidence of long-term declines in predators caused by natural climate cycles, such as the Steller sea lion (*Eumetopias jubatus*) population in the Aleutian Islands and Gulf of Alaska (Trites et al., 2007), and this may also be the case for seabirds in the region. Indeed, in the present study, the decade of most rapid global seabird decline (1970s) did coincide with a lowproductivity regime in the Pacific, causing reduced anchovy abundance in Japan, California, Peru, and Chile, as well as reduced seabird abundance in California and Peru (Chavez et al., 2003). However, the regime switched back to high productivity in the late 1990s and there was no corresponding increase in seabird abundance in California, Peru, or worldwide. This indicates that either another factor was driving the global seabird decline in the 1970s, or seabird populations declined at least in part because of the regime shift in the 1970s, but were not able to recover when the regime shifted back in the late 1990s because other threats reduced survival and/or reproduction. There is circumstantial evidence of the latter, fisheries-induced prey depletion reducing the growth rate of the seabird population, and therefore its ability to recover, in both Peru and California (Goya and Garica-Godos, 2002, Ainley and Hyrenbach, 2010). Given the inherently stable nature of seabird populations due to their K-selected life-history strategy, natural climate cycles may play a role in global seabird population change, although it is highly improbable that they are the sole driver of global seabird decline.

Although the present study provides the most robust possible method of estimating global seabird population change within the modern industrial era, anecdotal evidence suggests severe historical seabird depletion due to hunting and introduced species. Thus, the present analysis of global seabird population change to the modern industrial era may be victim to Pauly's "shifting baselines syndrome" (1995), whereby the observer is unaware that the baseline of abundance is shifted downwards between generations, or in this case between the historical era and the

modern industrial era. Quantifying historical depletion would be a useful addition to the present study because it would further increase our understanding of anthropogenic activities on the global seabird population, but was not undertaken because it would require inclusion of historical data which are generally more qualitative or anecdotal in nature. Recent work by Al-Abdulrazzak *et al.* (2012) establishes the reliability of encoding anecdotal data to acquire quantitative historical abundance data, but this technique has only seen limited application to assessing historical seabird population changes to date (e.g., Palomares et al., 2006). Future research may involve the development of a method for encoding historical seabird abundance anecdotes to acquire quantitative data in order to extend the present analysis of global annual seabird abundance further back in time.

2.5.2 Global seabird population change, by family

The present study provides a summary of abundance estimates per seabird family. Only one previous study had analyzed seabird abundance by seabird family; Karpouzi (2005) presented relative abundance of seabird families in 1950s compared to 1990s. The estimates in the present study rank seabird families by population change during the modern industrial era in generally the same order, but use updated data to estimate absolute seabird abundance per family in 2010, and a new method to estimate annual seabird abundance per family dating back to 1950. Besides this, there are no previous estimates of annual seabird abundance per family. The only measure with which one could potentially compare estimates of population change per family is the percentage of IUCN Red Listed species per family, which Croxall *et al.* (2012) summarize for the seven most numerically important seabird families. However, the IUCN Red List status is not necessarily indicative of the overall decline of a family because it is based on other criteria in

addition to population change (e.g., number of individuals remaining, amount and quality of habitat remaining, threats, range size, and/or calculated probability of extinction in the wild (IUCN, 2011). Nonetheless, there is general agreement between ranking of families by absolute decline and the ranking of families IUCN Red List status. One exception existed; it was estimated that the family Diomedeidae declined by 10%, yet it is the seabird family with the highest percentage of species on the IUCN Red List (i.e., 17 of 22 species) (Croxall et al., 2012). This could be because albatross decline was most severe prior to the modern industrial era due to hunting and introduced predators, although albatross decline caused by entanglement in longline fishing gear during the modern industrial era may not have been adequately quantified due to sampling error (e.g., the average span of monitoring for an albatross population is 30 years). On the other hand, albatross populations may be relatively highly Red Listed in comparison to other declining species at least in part because of their inherently small population sizes, which trigger the IUCN Red List criteria (IUCN, 2011).

As expected, the seabird families did face varying degrees of population change over the modern industrial era. Interpreting the causes of relative population change among seabird families is challenging to impossible because each family may face different exposure and sensitivity to threats, as well as different sources of error. There may be a pattern of greater decline among families with high exposure and/or sensitivity to fisheries-related threats; Procellariidae are highly threatened by entanglement in longline fishing gear, Phalacrocoracidae and Sternidae are threatened by forage fish depletion, and Fregatidae are threatened by depletion of tuna which facilitate their foraging opportunities. Furthermore, the two increasing seabird families, Hydrobatidae and Alcidae, contain many planktivorous species, which probably have reduced

exposure and sensitivity to fisheries-related threats. However, this is not to say that fisheries interactions are the main driver of population change across seabird families. Sulidae did not decline despite the known threat of fisheries-induced prey depletion, perhaps in part because some benefit from increased availability of fisheries discards, and also because their physical and ecological attributes such as large body size and ability to switch between prey lend them to reduce their sensitivity to reduced prey abundance (Furness and Tasker, 2000). Families affected by climate change also appear to decline substantially. Spheniscidae are among the most severely impacted by climate change driven changes in sea ice and krill (Barbraud et al., 2012, Trivelpiece et al., 2011), while Procellariidae and Sternidae, containing most of the world's inter-regional migrants, are negatively affected by climate change driven mismatch between seabird phenology and prey availability (Cox, 2010, Walther et al., 2002). Conservation initiatives may be related to the increase in Alcidae, given that Alcidae are among the most targeted and most successful families in global seabird restoration projects (Jones and Kress, 2011). Procellariidae and Sternidae are also relatively highly targeted and successful in restoration projects, and although they did not increase overall during the modern industrial era, their rate of decline was reduced in recent decades coinciding with restoration. Historical depletion may also influence the relative population change observed in seabird families. For example, albatrosses and gulls were heavily persecuted during the millinery trade, and therefore their observed decline may be relatively small despite exposure to modern industrial threats because some populations are rebounding from historical decline. Meanwhile, storm-petrels are perhaps most severely threatened by introduced rats (Jones et al., 2008), so although their population appears stable or increasing based on the assessment of population change during the modern industrial era, their populations probably declined prior to the modern industrial era.

The difference in change between families may also be influenced by sampling and observational error. Sampling error may be greatest in families with relatively small fractions of the population are monitored due to lower interest and/or accessibility (e.g., Laridae and Procellariiformes, respectively). However, data were available throughout the entire timeframe for all families, except there were no data for Pelecanoididae in the first 3 years. Observational error may be greatest in families that are more difficult to quantify such as sub-surface and noncolonial nesters (e.g., most small petrels and Marbled murrelet, respectively). Assessing population change in crevice and burrow nesting seabirds is notably challenging (e.g., Harding et al., 2005). Overall, assessing why some seabird families changed more than others is challenging because all families are influenced by different historical threats, modern threats, conservation, sampling error and observational error. Thus, to improve our understanding of population change in each seabird family, further research should seek to extend the temporal scale of abundance estimates per seabird families further back in time. Further studies may also seek to investigate the causes of observed change by dividing families into functional groups. For example, given that fisheries-affected families may decline more than other families, one might test the hypothesis that piscivorous species decline more than planktivorous species. This may be informative to answering the cause of decline in some cases, because families often encompass a variety of functional groups. For example, the family Alcidae contains both piscivorous and planktivorous species.

Chapter 3 Spatial patterns in observed global seabird abundance, 1950-2010

3.1 Summary

The global seabird population has declined substantially during the modern industrial era (Chapter 2), but the spatial distribution of global seabird decline is poorly understood. The present study mapped observed change in global seabird abundance over the modern industrial era (1950-present), based on available seabird abundance data and species-specific range extent maps. The global seabird population was observed to decline across 90% of the global marine surface area during the modern industrial era, with increase restricted to the northern hemisphere and severe decline observed in the Humboldt Current and tropical and southern temperate regions, where major threats to seabirds include, respectively, the forage fish fishery and the combination of entanglement in longline fisheries and climate change. The present study highlights hotspots of seabird threat within the span of seabird population monitoring, and moreover the need for spatially extensive seabird conservation.

3.2 Introduction

The previous chapter in this thesis highlights the global seabird population decline, and consequent urgent need for large-scale seabird conservation. Understanding global patterns in seabird density and population change may facilitate the large-scale approach to seabird conservation by (i) demonstrating the spatial scale at which seabird population decline is occurring, and (ii) highlighting areas of greatest seabird density and decline where conservation is most urgently required.

The spatial distribution of global seabird density and change in density are hitherto poorly understood. The only existing map of global seabird density was the preliminary estimate made by Karpouzi *et al.* (2007) which was based on estimated breeding season ranges for an average year in the 1990s, and there is no existing map of change in global seabird density. The present study aims to provide an improved and more robust map of global seabird density, as well as a global map of observed change in seabird density. These maps of seabird density and change in seabird density will be made using species-specific range maps and abundance estimates. Incidentally, the present study also provides abundance estimates for all seabird species, which are in some cases more reliable than previously available estimates.

It is expected that the spatial distribution of seabird density will be more spread than that of Karpouzi (2007) because entire range extent is considered here rather than only breeding season ranges. It is also expected that the spatial distribution of the global seabird population change will include widespread decline, since decline was observed across the majority of seabird families (Chapter 2). Given that only observed population change is mapped, which extends over 20 years on average, and are biased towards the latter half of the modern industrial era (see Chapter 2), it is also expected that decline will be greatest in regions where threats were severe during the latter half of the modern industrial era. Thus, we might expect to observe greatest decline in the southern ocean, where many seabird populations faced peak threats (e.g., pollution, fisheries, climate change) in the latter half of the modern industrial era.

3.3 Methods

3.3.1 Global database of range extent maps per seabird species

A spatial database containing each species' marine range extent was constructed. Range extents were derived from the most up-to-date global range extent map for a given species; namely the Bird Families of the World series, which covered Procellariiformes (Brooke, 2004a), Sphenisciformes (Williams, 1997), Pelecaniformes (Nelson, 2005), and most Charadriiformes (Gaston et al., 1998, Olsen and Larsson, 1997), as well as the only global field guide, Seabirds of the World (Harrison, 1987). Global maps were augmented with finer scale updates when relevant and available (e.g., the global range extent of the Herring Gull was extracted from Harrison (1987) and refined in the North American region using a regional map from the Birds of North America online database). Maps were digitized in ArcGIS by importing and georeferencing to a standard global map then tracing the outline of the range extent using the polygon tool. Resulting species range extent polygons (e.g., Figure 3.1) were linked to estimates of abundance and observed change in abundance per species, described in Section 3.3.2.

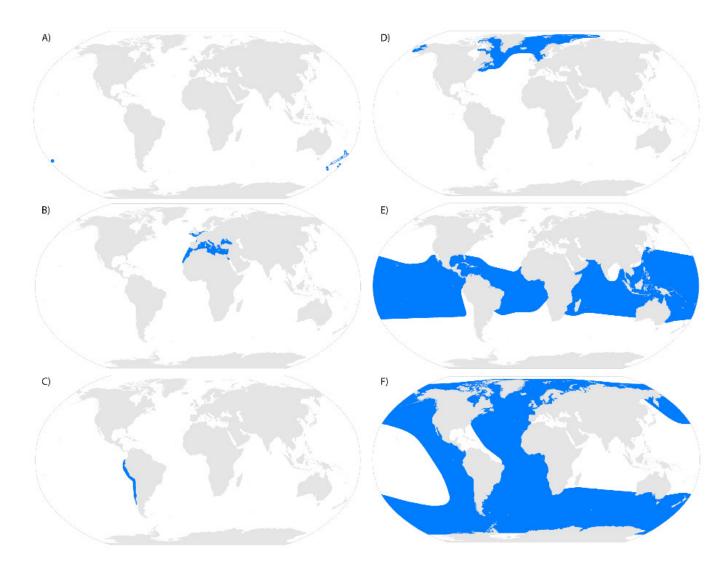


Figure 3.1 Examples of range extent polygons (blue), for six seabird species: (A) Red-billed gull (*Larus scopulinus*) (Source: del Hoyo et al., 1996); (B) Mediterranean Gull (*Larus melanocephalus*) (Source: Harrison, 1987); (C) Peruvian Booby (*Sula variegate*) (Source: Nelson, 2005); (D) Dovekie (*Alle alle*) (Source: Gaston et al., 1998); (E) Sooty Tern (*Sterna fuscata*) (Source: Harrison, 1987); and (F) Arctic Tern (*Sterna vittata*) (Source: Harrison, 1987).

3.3.2 Estimating abundance and change in abundance per seabird species

Given that the spatial database of range extent maps was constructed at the species-scale, it was necessary to calculate seabird abundance and change in abundance per species in order to link maps to abundance data. However, it is not possible to estimate species-specific annual abundance using the methods applied to the global and family-specific population in Chapter 2 because not all species were represented in the data throughout the entire timeframe, and therefore the calculation of average annual change would not be possible in the early years for many species. Instead, an estimated species-specific abundance was made by summing abundance estimates for all populations within a species, where *historical abundance* was the sum of all records closest to the year 1950 and *modern abundance* was the sum of all records for a given species is the *observed change*. Examples of data used to calculate historical and modern abundance are provided for four numerically important but otherwise randomly selected seabird species (Appendix II).

3.3.3 Mapping global seabird density

A global map of modern global seabird density was constructed by distributing each species' modern abundance evenly across its range extent, then summing the seabird density per square kilometre across all species' layers. Likewise, a global map of historical global seabird density was constructed by distributing each species' historical abundance evenly across its range extent, then summing the seabird density per square kilometre of all species' layers.

3.3.4 Mapping observed change in global seabird density

A map of observed change in global seabird density was constructed by distributing the difference between historical and modern abundance evenly across each species' range extent, then summing all species layers. This change in density per square kilometre was then expressed in absolute terms as well as relative terms.

3.4 Results

3.4.1 Estimated abundance and change in abundance, per seabird species

Historical and modern abundance were estimated per seabird species (Appendix I). Speciesspecific modern abundance estimates ranged from less than 100 individuals per species (i.e., Chinese crested tern (*Sterna bernsteini*), Beck's petrel (*Pseudobulweria becki*), Fiji petrel (*Pseudobulweria macgillivrayi*), Jamaica petrel (*Pterodroma caribbaea*), Indian yellow-nosed albatross (*Thalassarche carteri*)) to over 100 million individuals for one species (i.e., Dovekie (*Alle alle*)). Observed population change ranged from decline of more than 100 million individuals in the Sooty tern (*Sterna fuscata*) to increase of over 10 million individuals in the Dovekie (*Alle alle*), and the average observed population change was a decline by 0.9 million individuals. Net decline was observed in 50% of species, no change in 10% of species, and increase in 40% of species.

3.4.2 Maps of global seabird density

Historical seabird density ranges from 0-30,000 seabirds/km², while modern seabird density ranged from 0-15,000 seabirds/km². Seabird density is highest in tropical upwelling and temperate regions and lowest in the tropical and polar regions (Figures 3.2 & 3.3).

3.4.3 Maps of observed change in global seabird density

Population decline was more ubiquitous than population increase, covering 90% of the world's marine area, and occurring in both pelagic and coastal habitats (Figures 3.4 & 3.5). Greatest absolute decline occurred off the west coast of Peru, and greatest relative decline occurred in the southern tropics. Population increase was limited to the Northern temperate region, where it occurred in both pelagic and coastal regions. Maximum absolute decline was more than six times larger than maximum absolute increase.

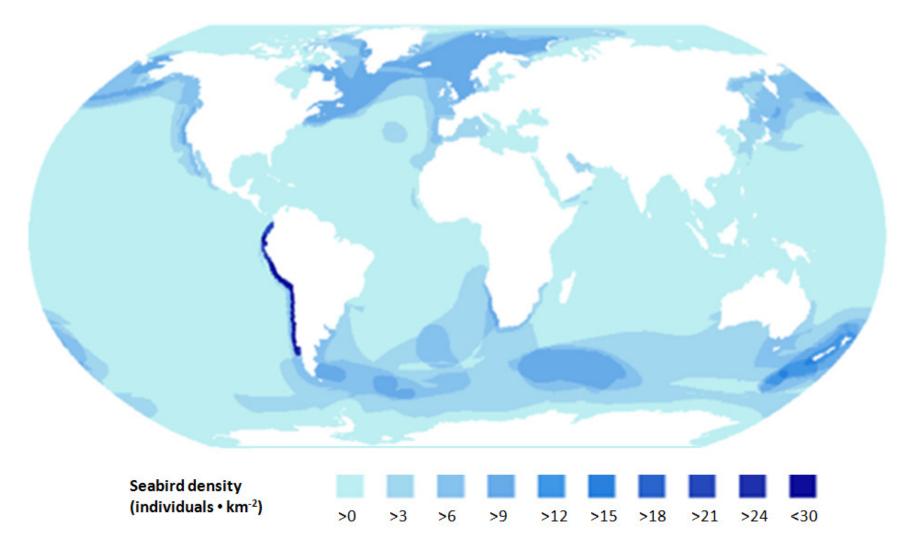


Figure 3.2 Historical global seabird density, mapped as the accumulation of all species' most historical abundance estimates (mostly <1980) distributed within their range extent.

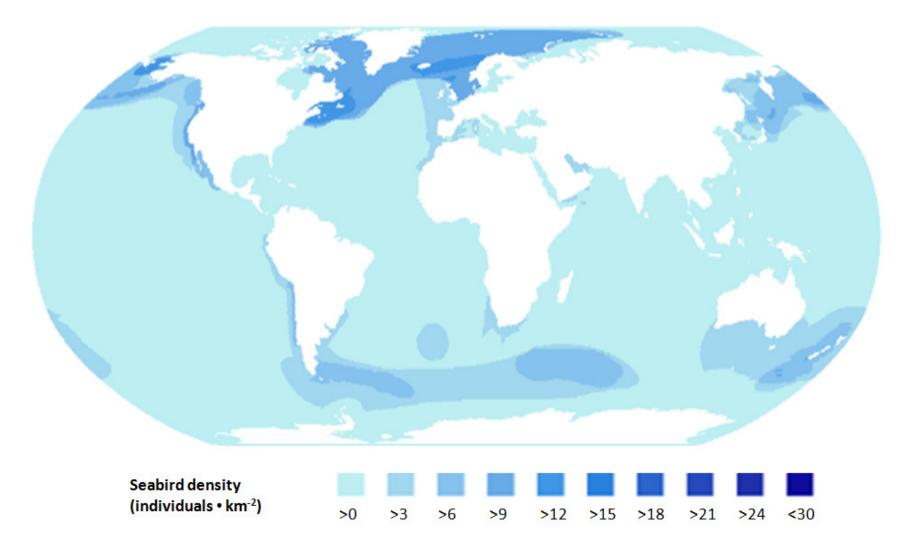


Figure 3.3 Modern global seabird density, mapped as the accumulation of all species' most modern abundances estimates (mostly >1990) distributed within their range extent.

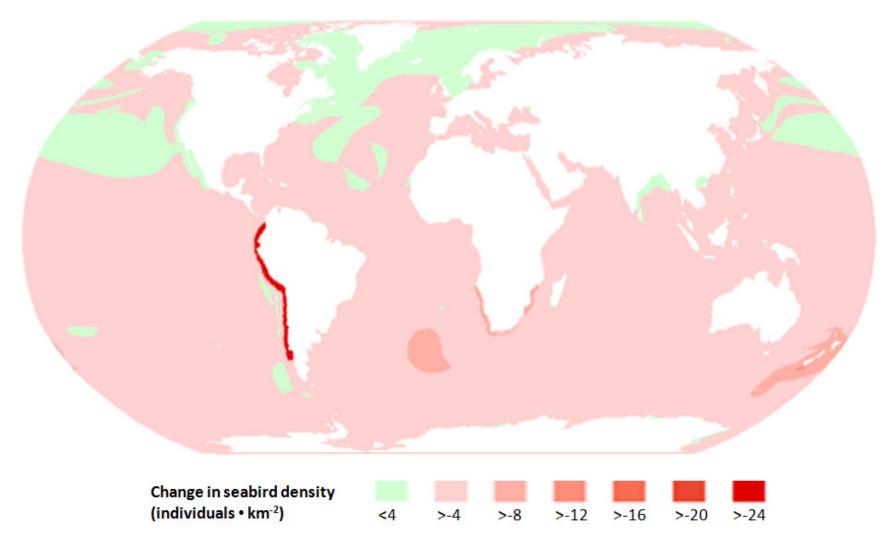


Figure 3.4 Absolute observed change in global seabird density, 1950-2010, mapped as the cumulative observed population change of all species distributed evenly within their range extents. Red represents regions of net decline in seabird density while green represent regions of stable or net increase in seabird density.

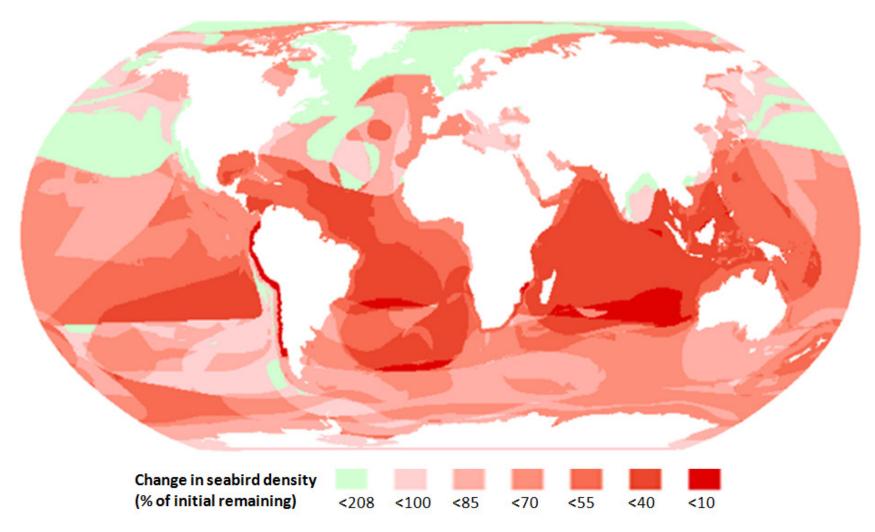


Figure 3.5 Relative observed change in global seabird density, 1950-2010, mapped as the relative observed population change of all species distributed evenly within their range extents. Red represents regions of net decline in seabird density while green represent regions of stable or net increase in seabird density.

3.5 Discussion

3.5.1 Estimated abundance and change in abundance, per seabird species

The present study yields estimates of abundance (modern and historical) and observed change in abundance for all seabird species. Depending on the species, the present estimates may be more or less accurate than pre-existing estimates. They will be less accurate than well-studied species, especially endemics where the global annual abundance is easy to enumerate in any given year. For example, it is relatively easy to estimate the annual abundance of the Juan Fernandez Petrel (Pterodroma externa) which nests only on one island in the Juan Fernandez Island archipelago, Chile. On the other hand, the present species-specific abundance estimates may be more accurate than previously available estimates for some poorly studied and/or wide-ranging species. For example, there is no single year in which the entire nesting habitat of the Dovekie (Alle alle) is surveyed, as it nests on numerous islands throughout the high arctic (i.e., Greenland, Iceland, Novaya Zemlya, Spitsbergen, and Franz Josef Land). In the latter case, the present estimates of change in abundance may serve as the most accurate and up to date global abundance estimates for several species. This is demonstrated by four examples of numerically important seabird species for which precise global abundance estimates were previously unavailable, the Blue petrel (Halobaena caerulea), Antarctic prion Pachyptila desolata), Sooty tern, and Dovekie (see Appendix II).

3.5.2 Global maps of seabird density

The present maps of global seabird density depict seabird density to be highest in temperate and upwelling regions of the world, and more widely dispersed from their breeding season foraging ranges than predicted in the preliminary maps by Karpouzi et al. (2007). This is because the present maps assume that individuals of a species were distributed evenly within their expertderived year-round species range extent maps. This assumption is perhaps a simplified view of seabird distribution in the marine environment, which is known to vary spatially and temporally in relation to prey availability, which itself is influenced by oceanographic and ecological processes. In general, seabird prey and foraging areas are predictable at large spatial scales, but not at small and meso scales (Weimerskirch, 2007) and furthermore may vary through time, as has been increasingly observed with climate change (Barbraud et al., 2012). This is why the present study uses range extent maps to define the boundaries of the large scale foraging area, then assume that seabirds are distributed evenly through time and space within these ranges. Seabirds may spend more time overall in certain areas of their at-sea range extents, such as areas surrounding colonies or important feeding areas (e.g., Le Corre et al., 2012, Egevang et al., 2010). Consequently, the maps presented in this study may underestimate seabird density in some areas, such as those near seabird colonies. However, given that widespread seabird tracking is relatively new because of recent miniaturization and increased memory of tracking devices (Burger and Shaffer, 2008), data-derived density maps do not presently exist for seabird species but may in the future. Thus, the present method will provide reasonably accurate maps, which are accurate for identifying the large-scale patterns and therefore adequate for meeting the immediate needs of global seabird conservation. Future studies may be able to refine global seabird density maps by using new knowledge of seabird distribution at sea, derived from recent

tracking studies. For example, BirdLife International has currently compiled almost 7000 at-sea tracking datasets for 41 Procellariiformes species to date, which can potentially be used to generate species density distribution maps (BirdLife International, 2004, BirdLife International, 2012). Using tracking data to map seabird density may also enable mapping of colonies or populations rather than entire species, which would further refine the maps.

Ground-truthing the maps against available data on seabird density is challenging because average annual (or change in average annual) seabird density data are only very rarely reported. Existing data do agree with the maps produced herein, for example, the average annual density is estimated at 3-22 seabirds/km² near Vancouver Island, Canada (Robertson, 1977) and 8 seabirds/km² across the Peru Current (Spear and Ainley, 2007). As expected, there are regions surrounding seabird colonies that experience much higher seabird densities than predicted in the maps herein, at least during the breeding season, for example, Northern gannets (*Morus bassanus*) alone reach densities of over 2500 individuals/km² surrounding their colony on Bass Rock, Scotland, during the breeding season (Camphuysen et al., In press). This may demonstrate the error associated with assuming equal distribution within range extents, but the lack of annual average data makes it difficult to interpret the extent of this error, especially in terms of assessing global patterns.

3.5.3 Global maps of observed change in seabird density

The present study provides the first maps of observed change in the global seabird population. Greatest seabird decline was observed in the southern ocean and Humboldt Current ecosystem. In the southern ocean, two major threats have peaked in intensity within the recent 20-30 years that are best covered by seabird monitoring effort: entanglement of seabirds in pelagic longline fishing gear and climate change (Barbraud et al., 2012). In the Humboldt Current ecosystem, seabirds face severe and ongoing competition for prey with the world's largest forage fish fishery, Peruvian anchoveta (Jahncke et al., 2004). Decline was also observed throughout the tropical oceans, where the major threat is perhaps the pelagic longline fishing for tuna and swordfish (Lewison et al., 2004), which threatens seabirds by removing the tuna and dolphins with which they forage cooperatively (Ballance and Pitman, 1999). Seabird increase was restricted to the northern hemisphere, perhaps because of large amounts of fisheries discards (i.e., 40% of the world's discards occur in the North Atlantic (Kelleher, 2005), and some scavenging seabirds are increasing as a result (Furness, 2003); higher numbers of restoration projects (Jones and Kress, 2011); and an earlier peak in intensity of seabird threats in the northern hemisphere, for example, forage fish collapsed off California in the 1940s (Becker and Beissinger, 2006) but not off Peru until the 1970s (Jahncke et al., 2004).

While these maps of observed change in seabird density are an important step in understanding the global scope and spatial distribution of global seabird population change, bias and limitations influence the patterns observed. First, the assumption of equal distribution of seabird species' change in abundance across its' range extent may result in regional population change being spread across large spatial scales for cosmopolitan species. For example, increase in the Falkland Island Black-browed albatross (*Thalassarche melanophris*) population would be pooled with all of the observed population change and spread evenly across its Antarctic circumpolar range. Future research may overcome this bias by mapping population change per population rather than species, as suggested in Section 3.5.1. Second, the present study is limited to

mapping only observed population change which occurred over different timeframes, because total change throughout the entire modern industrial era could not be estimated at the species level, and range maps were not available at the population level. As a result, the present maps do not demonstrate all of the seabird population change that occurred during the modern industrial era. Presumably seabird decline spread southward and seaward from the northern hemisphere during the modern industrial era, following the spatial expansion of fisheries and other anthropogenic threats. Seabird monitoring effort is biased towards the most recent decades, so seabird population decline in the northern hemisphere probably went largely undocumented, much like the historical decline caused by hunting and introduced predators. How could we map total seabird population change over the modern industrial era? Mapping modern industrial era change in abundance by seabird family (as estimated in Chapter 2), linked to family range extent maps, may provide a general picture of the spatial distribution of the total seabird population change over the modern industrial era. This would require the assumption that individuals are distributed across their family range extent, most of which are extremely large and/or global in nature, resulting in a rather non-informative map. Thus, although the present maps of observed seabird population change are useful because they depict the available data with minimal assumptions, further maps that may be helpful in assessing the spatial distribution of seabird population change would be (i) a map of the average annual change in seabird density, or (ii) a map of the number of threatened or declining species per spatial cell, as per the marine mammal map of Pompa et al. (2011).

It is impossible to ground-truth these maps because other data summarizing total or observed change in average annual seabird density do not exist. However, seabird biologists from six ecosystems supporting large seabird populations (i.e., North Sea, Norwegian Sea, New Zealand, Benguela Current, Gulf of Alaska, and California Current) were consulted to verify that overall trends in seabird abundance in their ecosystem were indeed in line with observed patterns in seabird population data within their ecosystem. Chapter 4 Investigating the potential role of industrial marine fisheries in temporal and spatial patterns in global seabird population change, 1950-2010

4.1 Summary

Fisheries-related threats are known to affect seabird populations worldwide and they are the only threat for which data are available at temporal and spatial scales appropriate for comparison with temporal and spatial patterns observed in global seabird population change (Chapters 2 & 3). Thus, the present study seeks to determine if there are significant temporal and spatial relationships between seabird population change and marine fisheries. A significant positive relationship was observed between global annual seabird decline and global annual forage fish catch, as well as between observed seabird decline and total ecological footprint of fisheries per marine spatial cell. These results indicate that fisheries may indeed play a role in shaping temporal and spatial patterns in global seabird abundance.

4.2 Introduction

Fisheries are among the most serious threats to seabirds of the modern industrial era, depleting abundance and availability of seabird prey, driving changes in quality of seabird prey, and entangling seabirds in fishing gear. These fisheries-related threats have been observed to have a population-level effect on seabirds at regional and species scales (Wagner and Boersma, 2011, Furness, 2003, Tasker et al., 2000). However, the cumulative impacts of fisheries-related threats on seabird populations are often difficult to assess given the many factors that may be affecting seabird populations and corresponding seabird-fisheries data. Global fisheries data are available from the *Sea Around Us* Project at the appropriate temporal and spatial scales for comparison with global temporal and spatial patterns in seabird population change. Therefore, the present study seeks to determine if there is a global relationship between temporal and spatial patterns in seabird decline during the modern industrial era (Chapters 2 & 3) and fisheries.

Temporal patterns in global seabird decline suggest that there may be a relationship between seabird decline and overexploitation of forage fish. Monotonic seabird decline throughout the modern industrial era (Chapter 2) may be related to an increase in forage fish fishing effort throughout the modern industrial era (Anticamara et al., 2011), including rapid seabird decline corresponding with peak forage fish catch in the 1970s (Alder et al., 2008). There is evidence that the abundance and availability of forage fish may play a key role in regulating global seabird abundance. Forage fish biomass has been linked to seabird productivity and/or abundance in multiple regional scale studies including Peru, Norwegian Sea, Barents Sea, western Norway, North Sea, South Africa (Tasker et al., 2000, Furness, 2003), and a globally consistent long-term relationship between forage fish biomass and seabird productivity has recently been observed (Cury et al., 2011). However, the role of forage fish fisheries in these relationships can be unclear due to the natural variation in forage fish biomass caused by climate oscillations (e.g., Frederiksen et al., 2004). Thus, the present study seeks to determine if there was a significant relationship between global seabird decline and overexploitation of forage fish. A rank correlation was performed between global annual seabird decline and global annual forage fish catch. Forage fish catch is a good measure for inverse forage fish biomass because trends in fisheries catch data are found to be consistent with trends in biomass data (Froese et al., 2012). Although the relationship may be more noisy for forage fish because their biomass fluctuates

naturally in relation to climactic cycles in the upwelling ecosystems in which they occur, their biomass too is nonetheless influenced by fisheries catches (Cury et al., 2000).

Spatial patterns in observed global seabird population change suggest that there may be a relationship between seabird decline per spatial cell and intensity and duration of fisheries presence. Greatest observed seabird decline appears to occur in regions where fisheries have reached their maximum ecological footprint within the timeframe of seabird population monitoring (i.e., in the tropical and southern oceans, and in the pelagic realm). Thus, the present study seeks to determine if there is a significant relationship between observed seabird decline and year of maximum ecological footprint of fisheries per spatial cell. A regression was performed between observed seabird decline per marine spatial cell and year of maximum primary production required to support fisheries (hereafter year of maxPPR) per spatial cell. Year of maxPPR is a good metric for year of maximum ecological footprint of fisheries are overexploited. Thus, if year of maxPPR is more recent then fisheries have been present for a shorter period of time and one would be more likely to observe the total effects of fisheries on the seabird population in that region.

4.3 Methods

4.3.1 Testing for a relationship between annual global seabird decline and annual global forage fish catch

To test the hypothesis that global annual seabird decline is related to global annual fisheries catch of forage fish, a rank correlation was performed between global annual fisheries catch and global annual seabird decline (cumulative percent remaining, as calculated in Chapter 2, Figure 2.5). Global annual forage fish catch data were extracted from the *Sea Around Us* Project database (www.seaaroundus.org). Forage fish include Atlantic herring (*Clupea harengus*), Atlantic menhaden (*Brevoortia tyrannus*), chub mackerel (*Scomber japonicas*), European sprat, capelin, blue whiting (*Micromesistius poutassou*), Pacific menhaden (*Ethmidium maculatum*), anchovies, Inca scad (*Trachurus murphyi*), South American pilchard (*Sardinops sagax*), European pilchard (*Sardinops pilchardus*), Atlantic mackerel (*Scomber scombrus*), and sandlances. Rank correlation was chosen because the data were not normally distributed.

4.3.2 Testing for a relationship between observed seabird decline and year of maxPPR per spatial cell

To test the hypothesis that seabird decline in a given region was related to the year of maxPPR (a proxy for the duration of fisheries presence), a regression was performed between percent seabirds remaining per 0.5° by 0.5° marine spatial cell (there are ~180,000 such cells in the world) and year of maxPPR in that cell. Year of maxPPR data were extracted from the *Sea*

Around Us Project database (www.seaaroundus.org), and percent seabirds remaining per spatial cell were calculated in Chapter 3 (Figure 3.5).

4.4 Results

4.4.1 Relationship between annual global seabird decline and annual global forage fish catch

Annual global seabird population decline was correlated to annual global catch of forage fish (Figure 4.1).

4.4.2 Relationship between observed seabird decline and year of maxPPR in a region

There was a significant relationship between seabird decline per spatial cell (percent of the seabird population remaining) and year of maxPPR (Figure 4.2).

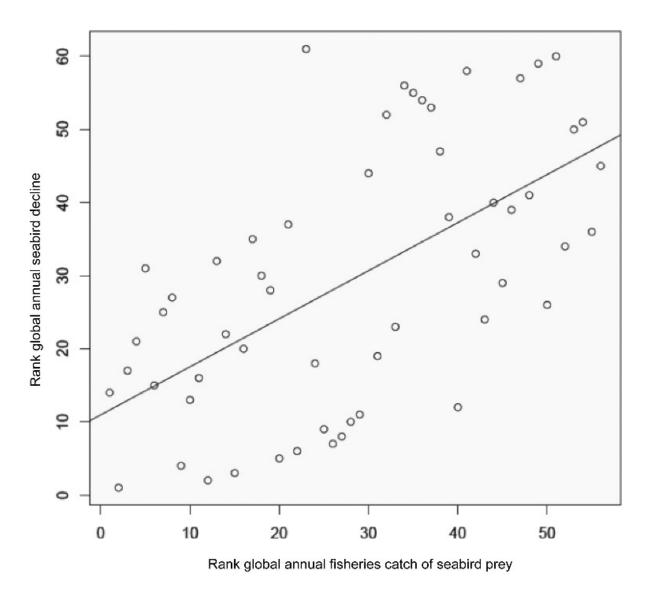


Figure 4.1 Spearman's rank correlation of annual global seabird population decline as a function of annual global fisheries catch of forage fish (S = 11696, p < 0.001).

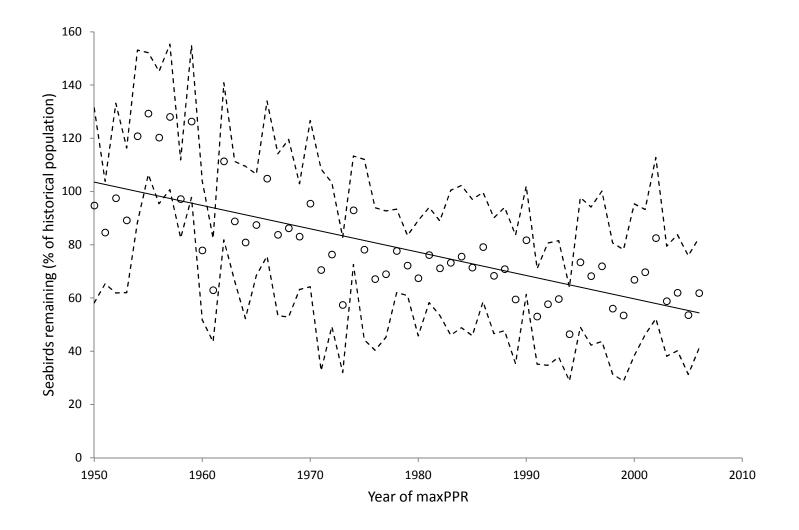


Figure 4.2 Regression (solid line) and standard deviation (dotted line) of percent seabirds remaining per spatial cell as a function of year of maxPPR ($R^2 = 0.10$, p < .001; pseudoreplicates are depicted as binned for this figure, but not for statistics). Data for percent seabirds remaining originated from the map of global seabird population change observed within the modern industrial era (Figure 3.5) and data for year of maxPPR were derived from the *Sea Around Us* Project global fisheries catch database.

4.5 Discussion

4.5.1 Temporal relationship between seabird decline and fisheries catch

Global annual seabird decline was correlated with global annual forage fish catch. This relationship was expected given the established effect of forage fish catch on forage fish biomass (Cury et al., 2000, Froese et al., 2012) and also of forage fish biomass on seabird productivity and/or population size (Cury et al., 2011, Furness, 2003, Tasker et al., 2000). This finding is important because it identifies that a relationship observed repeatedly at smaller scales is also seen at the global scale, indicating the potentially important role of forage fish fisheries in global seabird decline.

The observed correlation between seabird decline and forage fish catch does not infer causation; other factors correlated with forage fish catch may be driving the observed decline. These may include bycatch in fishing gear, habitat destruction, climate change, and a variety of other pollutants (e.g., oil, plastic, persistent organic pollutants). Further studies may attempt to isolate the impacts of fisheries on global seabird population change by assessing the population trajectory of piscivorous versus non-piscivorous seabirds in relation to fisheries catch data, perhaps subdividing piscivorous seabirds into groups based on predicted sensitivity to reduced prey. If piscivores (especially the most sensitive groups) decline more than non-piscivores, this would indicate that the relationship observed in the present study is causative. The previously mentioned factors (i.e., bycatch in fishing gear, habitat destruction, climate change, and a variety of other pollutants), in addition to natural climate oscillation, rebounding from historical threats, and positive effects of conservation initiatives, have all been identified as factors affecting

seabird population change to some extent. Therefore, they probably contribute to some of the observed variation in the relationship. While it is important to further investigate the causativeness of the observed relationship, it is highly probable based on the repeated observation of a causative relationship at smaller scales (i.e., fisheries reduce biomass and seabirds decline) that the significant relationship observed at the global scale is at least in part causative.

Variation may occur in the relationship because the relationship between global forage fish catch and global forage fish biomass is not entirely consistent through time. In the beginning of the modern industrial era there is an inverse relationship between forage fish catch and forage fish biomass, but in later years as forage fish stocks collapse, years of simultaneously low forage fish catch and biomass will occur. An alternative assessment of forage fish biomass might have been forage fish stock status. Stock status is a recently developed measure of fish abundance that accounts for the difference between pre- and post-overexploitation low-catch years (Kleisner and Pauly, 2011). Further studies may seek to refine the assessment of this relationship by comparing global annual seabird decline with global annual stock status of forage fish.

Variation may also occur in the relationship if forage fish biomass does not have a linear effect on seabird abundance. The occurrence of a non-linear relationship is quite probable, as seabird productivity and/or abundance has been observed to respond asymptotically to prey depletion in nature (Piatt et al., 2007b, Cury et al., 2011). This is because seabirds can generally buffer their survival and reproduction against prey depletion by increasing foraging effort, up to a certain point. At the global scale, rapid seabird decline in the 1970s may coincide with the

overexploitation of forage fish stocks. On the other hand, the variation in the relationship between seabird decline and fisheries catch may be related to the sequential overexploitation of forage fish stocks and expansion of fisheries to include new stocks; Herring, sardine, menhaden were among the first stocks targeted, followed by an increasing range of species (Alder et al., 2008).

Variation may also occur in the relationship due to unaccounted for lag between fisheries catch and the effect on change in seabird abundance. In the present analysis, fisheries catch was compared to seabird decline in the same year, which would capture any immediate impacts on the breeding population in that year (e.g., number of seabirds attempting to breed is related to prey abundance). However, it may take 2-9 years for the effects of fisheries catch to be measured in seabird population size, because this is the average amount of time that it takes seabirds to recruit to the population, depending on the family (Weimerskirch, 2002). This lag was not considered in the present study because it varies between families. Unfortunately, it probably introduces variation into the global relationship between forage fish and seabird abundance.

Finally, noise may occur in the relationship because the global nature of the analysis does not allow for fine resolution of the seabird population change and forage fish catch data. Catch of all forage fish species are included when perhaps the catch of some species is more influential to seabird populations than others. For example, both anchovy and sardine are fished off Peru, but change in anchovy biomass has a far greater influence on seabird productivity and abundance than sardine biomass (Jahncke et al., 2004). Furthermore, catch of all size classes of forage fish

are considered although not all size classes are eaten by seabirds. This is because intuitively the overexploitation of any given stock reduces the abundance of all size classes. Finally, the analysis is not spatially restricted because there is complete overlap between cumulative seabird range extent maps and regions where forage fish are caught. Although the present study investigates seabird fishery relationships at a coarse scale that will include noise, this is necessary when assessing global relationships.

4.5.2 Spatial relationship between seabird decline and fisheries catch

There was a significant relationship between percent of seabirds remaining and year of maxPPR per spatial cell. In other words, the extent of observed seabird decline in a spatial cell is related to the amount of time since peak ecological footprint of fisheries. Thus, if fisheries occurred more recently, then more seabird population change was observed. This is probably because the majority of seabird population change observations were made over recent decades, so regions that were historically affected by fisheries and other threats and currently experiencing seabird population rebounds. However, this relationship may also be at least in part driven by another factor that co-varies with year of maxPPR per spatial cell, such as strong effects of climate change in the southern oceans (Barbraud et al., 2012). Thus, although the pattern of observed seabird decline bears striking resemblance to the spatial pattern of fisheries expansion during the modern industrial era (Swartz et al., 2010), the present analysis does infer causation.

The variation in duration over which seabird population change was observed for the maps makes this analysis difficult to interpret. The average duration of seabird population monitoring per spatial cell is 20 years, but some some cells have data for up 60 years. If data were available for the entire timeframe in all cells (i.e., all actually occurring seabird population change was observed, rather than a subset), the expected result would be drastically different: seabird decline may be more closely related to the intensity of the ecological footprint than the year of maximum ecological footprint. In fact, seabird population decline would be expectedly less in regions where year of maximum ecological footprint was more recent if population change was observed over the entire modern industrial era.

Variation may also be introduced into the relationship because seabirds in all cells are not equally related to the "ecological footprint" of fisheries. For example, ecological footprint fisheries in a pelagic cell with moderate tuna fisheries may be higher than the ecological footprint of fisheries in a coastal cell with high forage fish fisheries, but the impacts on seabirds may be greater in the coastal cell.

The observed relationship between seabird decline and duration of fisheries presence per spatial cell is important because it identifies the potential role of fisheries in shaping global patterns in seabird population change. It may also suggest the extent to which undocumented fisheries-related global seabird decline occurred in the northern hemisphere before seabird population monitoring began. Furthermore, the increase in seabird abundance in regions where peak ecological footprint of fisheries occurred long ago may indicate the ability of seabird populations to bounce back from historical fisheries-related threats if fishing intensity is reduced.

Chapter 5 Conclusion

This study provides (i) a robust estimate of global annual seabird population throughout the modern industrial era, demonstrating a 25% decline in the global seabird population across 11 or the 14 seabird families during the modern industrial era; (ii) a reliable map of observed change in global seabird density during the modern industrial era, demonstrating decline across 90% of the worlds marine surface area; and (iii) an analysis of the temporal and spatial patterns in observed global seabird decline in relation to global marine fisheries, demonstrating significant relationships between global annual seabird decline and global annual forage fish catch, as well as between seabird decline per spatial cell and year of maxPPR per spatial cell.

These results are important because they depict the temporally, taxonomically and spatially pervasive nature of the global seabird population decline and highlight the potentially important role of marine fisheries in global seabird decline, a threat that is repeatedly noted at regional scales but difficult to quantify. As such, they have important implications for the management and preservation of seabirds and marine ecosystems. The temporal, taxonomic, and spatial pervasiveness of seabird decline lends support to the call for a large-scale approach to seabird conservation (Jodice and Suryan, 2010, Croxall et al., 2012). The observed global seabird decline also demonstrates the cumulative impacts that fisheries and other threats have, but are often overlooked or unmanaged at small spatial scales, thus identifying the need for increased use of the precautionary approach to marine ecosystem management. The precautionary approach is an essential and useful method of managing wildlife such as seabirds with uncertain population trends and uncertain and/or uncontrollable threats (Lauck et al., 1998). Part of the precautionary approach may involve designation of marine no-take zones in important seabird

foraging areas to minimize threats and maintain sufficient prey for seabird population growth. Large-scale commitment to seabird conservation and use of the precautionary approach is increasingly important as most threats could increase with the growing human population (e.g., forage fish fisheries, pollution, climate change, habitat destruction).

Estimates of seabird population change are inevitably limited by data availability; the present study overcame limitations as much as possible by relying on the rate of change in the sampled population to estimate the change observed in the global seabird population, and mapping observed population change rather than actual population change during the modern industrial era. However, future research may seek to assess total anthropogenic impacts on the global seabird population by incorporating these historical abundance estimates, or to create maps that better depict the spatial distribution of seabird population change throughout the entire modern industrial era. However, the present studies have perhaps sufficiently demonstrated global patterns in seabird population change that indicate a need for large-scale and precautionary seabird conservation. Thus, future research may be most effective in conserving seabirds by aiming to develop methods for implementing large-scale and precautionary seabird conservation initiatives.

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Appendices

Appendix I. List of all seabird species considered in the present study, along with attributes from the *Sea Around Us* Project global seabird database. References are available upon request.

Taxa ^a	Common name	Mass (g) ^b	Culmen; tarsus; wing (cm) ^b	Clutch (# of eggs)	Incub.; fledging; breeding (days)	Marine habitat ^c	Main forage method d	Dive ability ^e	Discards in diet ^f	Fish in diet ^g	Historical pop.; modern pop. (10 ³ individuals) ^h	Avg. pop. data time- series (years between records) ⁱ
SPHENISCIFORMES												
Spheniscidae												
Aptenodytes forsteri	Emperor penguin	33360		One	64; 190; 274	Р	PD	0	0	2	741; 706	30
Aptenodytes patagonicus	King penguin	12654		One	53; 335; 408	Р	PD	0	0	2	1831; 5197	31
Eudyptes chrysocome	Rockhopper penguin	2812	43; 19;	Multi	35; 68; 123	0	PD	0	0	1	26317; 5140	22
Eudyptes chrysolophus	Macaroni penguin	4601	58; 26;	Multi	39; 60; 119	0	PD	0	0	1	26828; 30911	22
Eudyptes pachyrhynchus	Fiordland penguin	3400	48; 24;	Multi	36; 75; 131	Ι	PD	0	0	1	26; 10	8
Eudyptes robustus	Snares penguin	2800	55; 26;	Multi	37; 75; 132	Ι	PD	0	0	1	80; 119	8
Eudyptes schlegeli	Royal penguin	5700	62; 31;	Multi	37; 40; 97	0	PD	0	0	2	3600; 1697	27
Eudyptes sclateri	Erect-crested penguin	5400	56; 24;	Multi	35; 75; 130	0	PD	0	0	1	829; 292	18
Eudyptula minor	Blue penguin	2100		Multi	50; 63; 133	Ι	PD	0	0	2	599; 550	15
Megadyptes antipodes	Yellow-eyed penguin	5500		One	44; 35; 99	Ι	PD	0	0	2	9; 9	6
Pygoscelis adeliae	Adelie penguin	4470		Multi	34; 54; 108	0	PD	0	0	1	9848; 8135	14
Pygoscelis antarctica	Chinstrap penguin	4354		Multi	35; 53; 108	0	PD	0	0	0	23921; 8454	21
Pygoscelis papua	Gentoo penguin	6121		Multi	36; 29; 85	Ι	PD	0	0	1	1115; 1102	26
Spheniscus demersus	Jackass penguin	3100		Multi	38; 80; 138	Ι	PD	0	0	2	1528; 91	56
Spheniscus humboldti	Humboldt penguin	4500		Multi	41; 60; 121	Ι	PD	0	0	2	31; 37	20
Spheniscus magellanicus	Magellanic penguin	4100		Multi	40; 60; 120	0	PD	0	1	2	5091; 2832	15
Spheniscus mendiculus	Galapagos penguin	2500		Multi	39; 63; 122	С	PD	0	0	2	3; 1	40
PROCELLARIIFORMES												
Diomedeidae												
Diomedea amsterdamensis	Amsterdam albatross	8000	144; 113; 640	One	79; 235; 334	F	SS	4	0	1	<0.1; <0.1	26
Diomedea antipodensis	Antipodean albatross	7350	;;640	One	79; 271; 370	F	SS	4	0	1	40; 26	29
Diomedea dabbenena	Tristan albatross	6900		One	79; 271; 370	F	SS	4	0	1	7;6	52
Diomedea epomophora	Southern Royal albatross	8900	; 126; 682	One	79; 241; 340	F	SS	4	1	1	8; 26	29

Diomedea exulans	Wandering albatross	8810	166; 151; 683	One	79; 271; 370	F	SS	4	1	1	38; 21	41
Diomedea gibsoni	Gibson's albatross	6800	148; 116; 647	One	79; 271; 370	F	SS	4	0	1	25; 19	45
Diomedea sanfordi	Northern Royal albatross	6670	; ; 640	One	79; 240; 339	F	SS	4	1	1	17; 23	1
Phoebastria albatrus	Short-tailed albatross	4000	;;213	One	49; 180; 249	F	SS	4	1	1	300; 3	36
Phoebastria immutabilis	Laysan albatross	2850	; ; 203	One	65; 165; 250	F	SS	4	1	1	297; 1380	29
Phoebastria irrorata	Waved albatross	2300	146; ; 219	One	60; 150; 230	F	SS	4	1	1	10; 35	28
Phoebastria nigripes	Black-footed albatross	3000	127; 97; 213	One	65; 146; 231	F	SS	4	1	2	27; 196	32
Phoebetria fusca	Sooty albatross	2600	111; 81; 518	One	67; 152; 239	F	SS	4	0	1	44; 58	25
Phoebetria palpebrata	Light-mantled albatross	3016	106; 84; 551	One	67; 152; 239	F	SS	3	0	1	71; 78	28
Thalassarche bulleri	Buller's albatross	2700	; ; 515	One	72; 167; 259	F	SS	4	1	2	51; 105	17
Thalassarche carteri	Indian yellow-nosed albatross	2520	; ; 475	One	71; 115; 206	F	SS	4	0	2	87; 97	20
Thalassarche cauta	Shy albatross	4000	128; 93; 563	One	75; 120; 215	F	SS	3	1	2	245; 189	21
Thalassarche chlororhynchos	Yellow-nosed albatross	2060	116; 77; 476	One	71; 115; 206	F	SS	4	0	2	44; 121	43
Thalassarche chrysostoma	Grey-headed albatross	3553	112; 87; 520	One	73; 141; 234	F	SS	3	0	1	213; 284	27
Thalassarche eremita	Chatham albatross	3770	; ; 565	One	68; 165; 253	F	SS	4	0	2	12; 13	28
Thalassarche impavida	Campbell albatross	3100	; ; 515	One	68; 125; 213	F	SS	4	1	2	103; 74	37
Thalassarche melanophris	Black-browed albatross	3755	119; 88; 522	One	68; 125; 213	F	SS	3	1	2	3604; 2298	28
Thalassarche salvini	Salvin's albatross	4000	; ; 575	One	72; 120; 212	F	SS	4	1	2	254; 117	17
Procellariidae												
Bulweria bulwerii	Bulwer's petrel	990	22; 28; 204	One	44; 62; 126	F	SS	3	0	2	714; 406	16
Bulweria fallax	Jouanin's petrel			One	44; 62; 126	F	SS	4	0	0	5; 5	0
Calonectris diomedea	Cory's shearwater	600	54; 53; 351	One	51; 91; 162	F	SS	3	1	1	2094; 1191	15
Calonectris edwardsii	Cape Verde shearwater		43; 48; 313	One	42; 80; 142	F	SS	4	0	2	33; 33	3
Calonectris leucomelas	Streaked shearwater	550		One	64; 80; 164	F	SS	4	1	2	9142; 9109	13
Daption capense	Cape petrel	441	16; 18; 260	One	45; 47; 112	F	SS	4	1	1	1021; 703	13
Fulmarus glacialis	Northern fulmar	580	55; 51; 330	One	48; 53; 121	F	SS	4	1	2	25859; 20008	28
Fulmarus glacialoides	Southern fulmar	784	41; 52; 328	One	45; 52; 117	F	SS	4	1	2	5402; 1117	16
Halobaena caerulea	Blue petrel	197	27; 33; 194	One	46; 43; 109	F	SS	3	0	1	3056; 6159	12
Lugensa brevirostris	Kerguelen petrel	324	27; 40; 260	One	49; 61; 130	F	PLD	3	1	1	33347; 692	17
Macronectes giganteus	Southern Giant petrel	4735	33; 27; 535	One	61; 122; 203	F	SC	4	1	1	158; 160	24
Macronectes halli	Northern Giant petrel	4541	;;514	One	59; 122; 201	F	SC	4	1	1	41; 35	23
Pachyptila belcheri	Thin-billed prion	137	25; 34; 181	One	47; 50; 117	F	SS	3	0	1	9361; 9361	20
Pachyptila crassirostris	Fulmar prion	126	;;173	One	47; 50; 117	Р	SS	4	0	1	301; 147	11
Pachyptila desolata	Antarctic prion	156	27; 34; 187	One	45; 51; 116	F	SS	4	0	1	86876; 83512	9
Pachyptila salvini	Salvin's prion	166	32; 34; 190	One	49; 61; 131	F	SS	4	0	1	17852; 17522	13
Pachyptila turtur	Fairy prion	140	22; 33; 181	One	47; 48; 115	Р	SS	4	0	1	3687; 3966	10
Pachyptila vittata	Broad-billed prion	240	; ; 203	One	56; 53; 129	Р	SS	4	0	1	36300; 9075	21
Pagodroma nivea	Snow petrel	294	21; 35; 276	One	43; 48; 111	Р	PLD	3	0	2	2204; 265	13
Procellaria aequinoctialis	White-chinned petrel	1254	; ; 385	One	59; 96; 175	F	PLD	2	1	2	9326; 3494	27
Procellaria cinerea	Grey petrel	1090	47; 61; 344	One	61; 147; 228	F	PLD	3	1	1	1883; 228	28

Procellaria consipicillata	Spectacled petrel		; ; 383	One	57; 110; 187	F	PLD	3	1	1	<0.1; 31	54
Procellaria parkinsoni	Parkinson's petrel	680	; ; 343	One	56; 122; 198	F	PLD	3	0	0	3; 8	16
Procellaria westlandica	Westland petrel	1200	; ; 381	One	68; 130; 218	F	PLD	2	1	2	6; 7	41
Pseudobulweria aterrima	Mascarene petrel	216	28; 39; 244	One	55; 95; 170	Р	SS	4	0	1	1; <0.1	9
Pseudobulweria becki	Beck's petrel	143		One	55; 95; 170	Р	SS	4	0	1	<0.1; <0.1	0
Pseudobulweria macgillivrayi	Fiji petrel	143		One	55; 95; 170	Р	SS	4	0	1	<0.1; <0.1	0
Pseudobulweria rostrata	Tahiti petrel	442	37; 50; 302	One	55; 95; 170	Р	SS	4	0	1	37; 37	0
Pterodroma alba	Phoenix petrel	270		One	53; 93; 166	F	PLD	3	0	1	106; 31	27
Pterodroma arminjoniana	Trindade petrel	460	; ; 268	One	50; 90; 160	F	SS	4	0	1	4; 4	0
Pterodroma atrata	Henderson petrel			One	50; 90; 160	Р	SS	4	0	1	53; 70	12
Pterodroma axillaris	Chatham Island petrel	200	24; 31; 219	One	47; 85; 152	Р	SS	4	0	1	3; <0.1	27
Pterodroma baraui	Barau's petrel	434	34; 39; 295	One	55; 110; 185	F	SS	4	1	2	5; 17	26
Pterodroma brevipes	Collared petrel	136		One	50; 95; 165	Р	SS	4	0	1	30; 30	0
Pterodroma cahow	Bermuda petrel	246		One	52; 92; 164	Р	SS	4	0	1	<0.1; <0.1	57
Pterodroma caribbaea	Jamaica petrel			One	50; 95; 165	Р	SS	4	0	1	<0.1; <0.1	0
Pterodroma cervicalis	White-necked petrel	540		One	50; 115; 185	F	PLD	3	0	1	33; 165	18
Pterodroma cookii	Cook's petrel	200	;;234	One	47; 87; 154	F	SS	4	0	1	74; 1300	27
Pterodroma defilippiana	De Filippi's petrel	159	;;235	One	50; 95; 165	F	SS	4	0	1	11; 11	15
Pterodroma externa	Juan Fernandez petrel	430	38; 41; 318	One	50; 95; 165	F	PD	2	0	1	3283; 3000	18
Pterodroma feae	Cape Verde petrel	311		One	50; 95; 165	F	SS	4	0	1	1; 3	37
Pterodroma hasitata	Black-capped petrel	278		One	54; 100; 174	F	SS	4	1	1	23; 4	29
Pterodroma heraldica	Herald petrel	320		One	50; 90; 160	Р	SS	4	0	1	104; 27	24
Pterodroma hypoleuca	Bonin petrel	240		One	49; 82; 151	F	SS	4	0	2	1093; 1093	10
Pterodroma incerta	Atlantic petrel	520	;;324	One	50; 90; 160	F	SS	4	0	1	3301; 5940	30
Pterodroma inexpectata	Mottled petrel	323	;;257	One	50; 105; 175	F	SS	4	0	1	132; 1188	23
Pterodroma lessonii	White-headed petrel	732	39; 47; 313	One	61; 107; 188	F	SS	4	0	1	791; 792	21
Pterodroma leucoptera	Gould's petrel	220	;;226	One	49; 84; 153	F	SS	4	0	0	12; 14	35
Pterodroma longirostris	Stejneger's petrel	170	25; 29; 220	One	53; 90; 163	F	SS	4	0	1	430; 430	0
Pterodroma macroptera	Great-winged petrel	576	37; 43; 318	One	56; 118; 194	Р	SS	4	0	1	6506; 2026	17
Pterodroma madeira	Madeira petrel	312		One	52; 92; 164	Р	SS	4	0	1	<0.1; <0.1	23
Pterodroma magentae	Magenta petrel	510	33; 41; 305	One	52; 90; 162	F	SS	4	0	1	3; <0.1	27
Pterodroma mollis	Soft-plumaged petrel	291	29; 36; 254	One	50; 91; 161	F	SS	4	1	0	33129; 1501	13
Pterodroma neglecta	Kermadec petrel	590		One	52; 130; 202	F	SS	4	1	1	635; 36	23
Pterodroma nigripennis	Black-winged petrel	200	24; 29; 227	One	45; 85; 150	F	SS	4	0	0	1050; 8741	15
Pterodroma phaeopygia	Galapagos petrel	410		One	52; 90; 162	F	PD	2	0	2	33; 15	33
Pterodroma pycrofti	Pycroft's petrel	200	;;218	One	45; 80; 145	F	SS	4	0	1	7; 14	16
Pterodroma sandwichensis	Hawaiian Dark-rumped petrel	450		One	55; 119; 194	F	SS	4	0	1	2; 24	36
Pterodroma solandri	Providence petrel	430		One	56; 100; 176	F	SS	4	1	2	3630; 100	18
Pterodroma ultima	Murphy's petrel	360	31; 40; 278	One	50; 90; 160	F	SS	4	0	1	877; 877	11
Puffinus assimilis	Little shearwater	238	27; 43; 196	One	58; 75; 153	F	PLD	3	0	1	3930; 1693	14
Puffinus auricularis	Townsend's shearwater	400		One	51; 100; 171	Р	PLD	3	0	2	3; <0.1	27
											,	

Puffinus bulleri	Buller's shearwater	410	41; 50; 287	One	51; 100; 171	F	SS	4	0	2	2500; 2500	0
Puffinus carneipes	Flesh-footed shearwater	750	; 56; 325	One	60; 92; 172	F	PLD	3	1	2	2712; 522	27
Puffinus creatopus	Pink-footed shearwater	720		One	52; 90; 162	F	PLD	3	0	2	76; 74	11
Puffinus gavia	Fluttering shearwater	420	; ; 201	One	52; 90; 162	Р	PLD	3	0	2	2333; 330	27
Puffinus gravis	Greater shearwater	950	70; 57; 336	One	57; 105; 182	F	PLD	3	1	2	16830; 3234	22
Puffinus griseus	Sooty shearwater	869	41; 57; 300	One	53; 97; 170	F	PLD	1	1	2	12674; 20452	20
Puffinus heinrothi	Heinroth's shearwater			One	52; 90; 162	Р	PLD	3	0	2	1; 1	0
Puffinus huttoni	Hutton's shearwater	370	;;218	One	50; 84; 154	F	PLD	3	0	2	74; 325	24
Puffinus lherminieri	Audubon's shearwater	230	29; 42; 208	One	51; 75; 146	Р	SS	2	1	1	313; 285	15
Puffinus mauretanicus	Balearic shearwater	502	38; 50; 251	One	50; 72; 142	F	PLD	2	1	2	17; 6	20
Puffinus nativitatis	Christmas shearwater	340	32; 49; 262	One	52; 96; 168	F	PLD	3	0	2	139; 27	24
Puffinus newelli	Newell's shearwater	390		One	66; 110; 196	F	PLD	3	0	2	20; 36	32
Puffinus opisthomelas	Black-vented shearwater	410		One	50; 69; 139	Р	PLD	2	0	2	26; 250	24
Puffinus pacificus	Wedge-tailed shearwater	570	40; 51; 310	One	53; 115; 188	F	PLD	2	0	2	9334; 10839	21
Puffinus puffinus	Manx shearwater	580	35; 46; 244	One	51; 69; 140	Р	PLD	2	0	2	834; 1227	22
Puffinus tenuirostris	Short-tailed shearwater	543	47; 50; 278	One	55; 94; 169	F	PLD	1	0	2	27572; 44639	6
Puffinus yelkouan	Levantine shearwater	420		One	52; 72; 144	F	PLD	3	0	2	91; 47	17
Thalassoica antarctica	Antarctic petrel	695	;;312	One	46; 45; 111	Р	PLD	3	0	1	6812; 6668	14
Hydrobatidae												
Fregetta grallaria	White-bellied storm petrel	60	; ; 167	One	40; 68; 128	Р	SS	4	0	0	48; 140	17
Fregetta tropica	Black-bellied storm petrel	52	16; 43; 171	One	38; 69; 127	Р	SS	4	0	2	435; 442	8
Garrodia nereis	Grey-backed storm petrel	33	13; 32; 127	One	45; 75; 140	Р	SS	4	0	0	161; 175	11
Halocyptena microsoma	Least storm petrel	20		One	41; 66; 127	Р	SS	4	0	0	334; 300	22
Hydrobates pelagicus	European storm petrel	30	12; 22; 124	One	41; 66; 127	Р	SS	3	1	2	1687; 2252	20
Nesofregetta fuliginosa	White-throated storm petrel	115		One	45; 70; 135	Р	SS	4	0	2	12; 2	21
Oceanites gracilis	White-vented storm petrel	30		One	45; 70; 135	Р	SS	4	1	1	3; 3	22
Oceanites oceanicus	Wilson's storm petrel	38	12; 35; 143	One	50; 127; 197	Р	SS	4	1	2	11139; 10457	8
Oceanodroma castro	Madeiran storm petrel	40	15; 24; 158	One	42; 65; 127	Р	SS	4	0	1	154; 98	16
Oceanodroma furcata	Forked-tailed storm petrel	60		One	40; 58; 118	Р	SS	4	0	2	4136; 3894	12
Oceanodroma homochroa	Ashy storm petrel	39		One	45; 84; 149	Р	SS	4	0	2	10; 24	32
Oceanodroma hornbyi	Hornby's storm petrel	50		One	43; 55; 118	Р	SS	4	0	1	14; 14	0
Oceanodroma leucorhoa	Leach's storm petrel	50	16; 25; 154	One	43; 79; 142	Р	SS	3	0	2	10572; 24019	16
Oceanodroma markhami	Markham's storm petrel	60		One	45; 75; 140	Р	SS	4	0	2	<0.1;11	2
Oceanodroma matsudairae	Matsudaira's storm petrel	62		One	45; 75; 140	Р	SS	4	1	1	20; 20	0
Oceanodroma melania	Black storm petrel	59	;;172	One	50; 80; 150	Р	SS	4	1	1	14; 14	18
Oceanodroma monorhis	Swinhoe's storm petrel	40	15; 24; 152	One	45; 75; 140	Р	SS	4	0	1	66; 57	22
Oceanodroma tethys	Wedge-rumped storm petrel	20		One	42; 70; 132	Р	SS	4	1	1	201; 661	16
Oceanodroma tristrami	Tristram's storm petrel	84	19; 30; 110	One	45; 75; 140	Р	SS	4	0	1	25; 25	10
Pelagodroma marina	White-faced storm petrel	70	17; 44; 161	One	59; 67; 146	Р	SS	4	0	1	3670; 3460	19

Pelecanoididae

Pelecanoides garnotii	Peruvian diving petrel	202		One	55; 50; 125	0	PD	1	0	2	1322; 49	18
Pelecanoides georgicus	South Georgia diving petrel	124	;;117	One	47; 49; 116	0	PD	1	0	1	24931; 18086	8
Pelecanoides magellani	Magellanic diving petrel	160	; ; 126.5	One	55; 50; 125	0	PD	1	0	1	32; 32	0
Pelecanoides urinatrix	Common diving petrel	147	;;124.5	One	54; 54; 127	0	PD	1	0	0	34669; 29767	10
PELECANIFORMES												
Phaethontidae												
Phaethon aethereus	Red-billed tropicbird	700	62; 30; 310	One	44; 90; 154	Р	PLD	3	0	2	22; 18	19
Phaethon lepturus	White-tailed tropicbird	320	64; 47; 286	One	42; 85; 147	Р	SS	3	0	2	68; 61	19
Phaethon rubricauda	Red-tailed tropicbird	850	62; 28; 219	One	43; 85; 148	Р	PLD	3	0	2	138; 135	17
Pelecanidae												
Pelecanus conspicillatus	Australian pelican	6800		Multi	35; 90; 145	С	SS	4	0	2	3; 3	11
Pelecanus crispus	Dalmatian pelican	10000	437; 131; 716	Multi	34; 85; 139	С	SS	4	0	2	8;5	9
Pelecanus erythrorhynchos	American White pelican	5900	381; 119; 622	Multi	30; 60; 110	Ι	SS	4	0	2	1; 54	21
Pelecanus occidentalis	Brown pelican	3200	289; 80; 514	Multi	30; 80; 130	I	PLD	3	1	2	264; 173	18
Pelecanus thagus	Peruvian pelican	3200		Multi	30; 80; 130	Ι	SS	3	0	2	356; 165	34
Pelecanus onocrotalus	Great White pelican	9000	330; 102; 610	Multi	31; 70; 121	С	SS	4	0	2	87; 94	19
Pelecanus philippensis	Spot-billed pelican	4650		Multi	31; 120; 171	С	SS	4	0	2	4;6	24
Pelecanus rufescens	Pink-backed pelican	6200	330; 93; 595	Multi	35; 75; 130	С	SS	4	0	2	7; 8	19
Phalacrocoracidae												
Compsohalieus harrisi	Flightless cormorant	3390		Multi	35; 55; 110	С	PD	2	0	2	9; 9	36
Compsohalieus neglectus	Bank cormorant	1800		Multi	30; 50; 100	С	PD	2	0	2	2; 2	29
Compsohalieus penicillatus	Brandt's cormorant	2300		Multi	29; 49; 98	С	PD	2	0	2	32; 9	14
Euleucocarbo carunculatus	New Zealand King shag	2500	66; 75; 301	Multi	30; 50; 100	С	PD	2	0	2	202; 285	18
Euleucocarbo chalconotus	Stewart Island shag	3880		Multi	30; 50; 100	С	PD	2	0	2	4; <0.1	23
Euleucocarbo colensoi	Auckland Island shag		; ; 267	Multi	32; 52; 104	С	PD	2	0	2	8;6	20
Euleucocarbo onslowi	Chatham Island shag	1790	;;277	Multi	30; 50; 100	С	PD	2	0	2	4; 2	26
Euleucocarbo ranfurlyi	Bounty Island shag	2900	; ; 286	Multi	30; 50; 100	С	PD	2	0	2	4; 1	27
Hypoleucos auritus	Double-crested cormorant	2600		Multi	28; 56; 104	С	PLD	2	0	2	2; 1	21
Hypoleucos brasiliensis	Neotropic cormorant	1070		Multi	25; 63; 108	С	PLD	2	0	2	343; 588	2
Hypoleucos fuscicollis	Indian cormorant	790		Multi	30; 50; 100	С	PLD	2	0	2	187; 172	4
Hypoleucos sulcirostris	Little Black cormorant	1200		Multi	30; 50; 100	С	PD	2	0	2	9; 10	10
Hypoleucos varius	Pied cormorant	1900		Multi	53; 60; 133	С	PD	2	1	2	32; 27	22
Leucocarbo bougainvillii	Guanay cormorant	1800		Multi	30; 50; 100	Ι	PD	2	0	2	30; 45	30

Leucocarbo capensis	Cape cormorant	1310		Multi	28; 49; 97	Ι	PD	2	0	2	13821; 801	44
Leucocarbo nigrogularis	Socotra cormorant		71; 74; 292	Multi	28; 48; 96	Ι	PLD	2	0	2	117; 292	10
Microcarbo africanus	Long-tailed cormorant	600	31; 36; 210	Multi	25; 35; 80	С	PD	2	0	2	1008; 706	40
Microcarbo coronatus	Crowned cormorant	780		Multi	23; 35; 78	С	PD	2	0	2	7; 5	28
Microcarbo melanoleucos	Little Pied cormorant	900	;;233	Multi	30; 50; 100	С	PD	2	0	2	12; 6	2
Microcarbo niger	Little cormorant	530		Multi	30; 50; 100	С	PD	2	0	2	77; 77	4
Microcarbo pygmaeus	Pygmy cormorant	640	30; 38; 204	Multi	30; 70; 120	С	PD	2	0	2	4; 42	16
Nesocarbo campbelli	Campbell shag	2000	;;270	Multi	31; 49; 100	С	PD	2	0	2	46; 68	25
Notocarbo atriceps	Imperial shag	2841	;;273	Multi	31; 49; 100	С	PD	1	1	2	4; 8	4
Notocarbo bransfieldensis	Antarctic shag	3022	; ; 325	Multi	31; 45; 96	С	PD	0	0	2	202; 202	24
Notocarbo georgianus	South Georgia shag	2883	;;287	Multi	29; 65; 114	С	PD	0	0	2	39; 36	23
Notocarbo verrucosus	Kerguelen shag	2630	55; 67; 286	Multi	31; 49; 100	С	PD	0	0	2	28; 23	5
Phalacrocorax albiventer	King cormorant	2910	61; 67; 295	Multi	31; 49; 100	С	PD	2	0	2	23; 35	14
Phalacrocorax capillatus	Japanese cormorant	3100		Multi	34; 40; 94	С	PD	2	0	2	7; 302	11
Phalacrocorax carbo	Great cormorant	2500	70; 74; 357	Multi	30; 53; 103	С	PD	0	0	2	13; 24	22
Phalacrocorax purpurascens	Macquarie shag	2910	57; 65; 302	Multi	33; 49; 102	С	PD	2	0	2	485; 1038	20
Strictocarbo aristotelis	European shag	1600	57; 63; 265	Multi	34; 53; 107	С	PD	0	0	2	3; 2	19
Strictocarbo featherstoni	Pitt Island shag	1330	;;315	Multi	30; 50; 100	С	PD	1	0	2	275; 306	21
Strictocarbo gaimardi	Red-legged cormorant	1300		Multi	36; 56; 112	С	PD	1	0	2	4; 1	12
Strictocarbo magellanicus	Rock cormorant		53; 55; 253	Multi	30; 50; 100	С	PD	2	0	2	19; 22	9
Strictocarbo pelagicus	Pelagic cormorant	1868		Multi	30; 45; 95	С	PD	1	0	2	33; 244	13
Strictocarbo punctatus	Spotted shag	1600		Multi	32; 62; 114	Ι	PD	1	0	2	343; 352	19
Strictocarbo urile	Red-faced cormorant	2050		Multi	33; 59; 112	С	PD	1	0	2	342; 216	23
Fregatidae												
Fregata andrewsi	Christmas Island frigatebird	1550		One	54; 177; 251	0	SS	4	0	2	2; 2	23
Fregata aquila	Ascension frigatebird	1250		One	51; 180; 251	0	SS	4	0	2	12; 19	57
Fregata ariel	Lesser frigatebird	1110		One	50; 179; 249	0	SS	4	1	2	435; 146	24
Fregata magnificens	Magnificent frigatebird	1670	142; 76; 635	One	59; 165; 244	0	SS	4	1	2	259; 251	17
Fregata minor	Great frigatebird	1890	104; 85; 555	One	55; 169; 244	0	SS	4	1	1	329; 116	14
Sulidae												
Morus serrator	Australasian gannet	2300	89; ; 463	One	44; 102; 166	0	PLD	2	0	2	78; 279	39
Morus bassanus	Northern gannet	3070	100; 55; 435	One	44; 91; 155	0	PLD	2	1	2	324; 1335	32
Morus capensis	Cape gannet	2700	93; ; 479	One	44; 97; 161	0	PLD	2	1	2	634; 455	52
Sula abbotti	Abbott's booby	1460	113; 41; 455	One	57; 168; 245	0	PLD	2	0	2	2;6	29
Sula dactylatra	Masked booby	2100	108; 62; 444	Multi	43; 130; 193	0	PLD	2	0	2	443; 493	20
Sula granti	Nazca booby	1750		Multi	43; 120; 183	0	PLD	2	0	2	125; 125	12
Sula leucogaster	Brown booby	1800	127; 42; 419	Multi	43; 95; 158	0	PLD	2	1	2	817; 806	17
Sula nebouxii	Blue-footed booby	1800	110; ; 445	Multi	41; 102; 163	0	PLD	2	0	2	812; 846	20

Sula sula	Red-footed booby	1500	85; 35; 407	One	46; 102; 168	0	PLD	2	0	2	1272; 1299	17
Sula variegata	Peruvian booby	1300	97; ; 408	Multi	42; 78; 140	0	PLD	2	0	2	2058; 1306	25
CHARADRIIFORMES												
Stercorariidae												
		1054	57 70 404	N 14	20 (0 110	G	66		1	0	76.62	14
Catharacta antarctica	Brown skua	1854	57; 79; 424	Multi	30; 60; 110	C C	SS	4	1	0	76; 63	14 0
Catharacta chilensis	Chilean skua	1350	;; 393	Multi	30; 60; 110		PLD		0	-	6; 6	
Catharacta maccormicki	South Polar skua	1260	;;396	Multi	28; 53; 101	I	SS	4	0	2 0	27; 42	17
Catharacta pomarinus	Pomarine jaeger	694	64; 53; 356	Multi	25; 31; 76	С	KL		1		866; 866	0
Catharacta skua	Great skua	1418	20 42 204	Multi	29; 46; 95	I	SC	4	1	2	37; 51	24
Stercorarius longicaudus	Long-tailed jaeger	297	28; 43; 294	Multi	25; 25; 70	I	KL	4	0	1	126; 114	17
Stercorarius parasiticus	Parasitic jaeger	465	32; 46; 320	Multi	26; 31; 77	Ι	KL	4	0	2	144; 83	20
Laridae												
Creagrus furcatus	Swallow-tailed gull	740		One	32; 70; 122	Ι	SC	4	0	2	50; 50	15
Larus argentatus	Herring gull	1135	51; 57; 412	Multi	28; 40; 88	С	SC	4	1	1	4456; 4200	23
Larus armenicus	Armenian gull	1050		Multi	25; 40; 85	С	SC	4	1	1	10; 10	0
Larus atlanticus	Olrog's gull	960		Multi	25; 40; 85	С	SC	4	0	0	13; 13	8
Larus atricilla	Laughing gull	289	40; 51; 321	Multi	25; 43; 87	С	SC	3	1	1	1167; 1205	17
Larus audouini	Audouin's gull	770	47; ; 400	Multi	33; 40; 93	I	SC	4	1	2	20; 69	21
Larus belcheri	Band-tailed gull	600		Multi	25; 40; 85	С	SC	4	1	1	7; 7	0
Larus bulleri	Black-billed gull	270	; ; 292	Multi	25; 40; 85	С	SC	4	1	1	1138; 96	21
Larus cachinnans	Yellow-legged gull	1500	54; 65; 438	Multi	29; 49; 98	Ι	SC	3	1	1	879; 962	14
Larus californicus	California gull	607	50; ; 399	Multi	26; 35; 81	Ι	SC	4	0	0	0; 21	23
Larus canus	Common gull	404	35; ; 351	Multi	23; 35; 78	Ι	SC	4	1	1	2985; 2168	26
Larus cirrocephalus	Grey-headed gull	330		Multi	25; 40; 85	С	SC	3	1	2	31; 37	28
Larus crassirostris	Black-tailed gull	640		Multi	25; 40; 85	С	SC	4	1	2	46; 205	8
Larus delawarensis	Ring-billed gull	471	42; 51; 377	Multi	26; 40; 86	Ι	SC	4	1	1	2; <0.1	16
Larus dominicanus	Kelp gull	1051	; ; 397	Multi	28; 61; 109	С	SC	4	1	1	403; 570	16
Larus fuliginosus	Lava gull			Multi	32; 45; 97	С	SC	4	1	1	1; 1	33
Larus fuscus	Lesser Black-backed gull	830	51; ; 427	Multi	28; 40; 88	Ι	SC	4	1	1	774; 1279	24
Larus genei	Slender-Billed gull	350	46; ; 320	Multi	22; 37; 79	С	SC	4	0	2	184; 255	17
Larus glaucescens	Glaucous-winged gull	1010	58; ; 423	Multi	28; 53; 101	С	SC	4	1	1	608; 387	18
Larus glaucoides	Iceland gull	863	43; 64; 412	Multi	25; 40; 85	С	SC	4	1	2	45; 124	20
Larus thayeri	Thayer's gull	996	52; ; 418	Multi	28; 45; 93	С	SC	4	1	1	15; 15	0
Larus hartlaubii	Hartlaub's gull	340		Multi	25; 40; 85	С	SC	4	1	1	13; 18	27
Larus heermanni	Heermann's gull	640	44; ; 347	Multi	28; 45; 93	С	SC	3	0	2	1008; 2970	25
Larus hemprichi	Sooty gull	510		Multi	25; 40; 85	С	SC	4	1	1	34; 44	11
Larus hyperboreus	Glaucous gull	1413	63; 74; 459	Multi	30; 49; 99	I	SC	4	1	1	234; 244	21
Larus ichthyaetus	Great Black-headed gull	2000		Multi	25; 40; 85	Ι	SC	4	1	1	8; 3	8

Larus leucophthalmus	White-eyed gull	410		Multi	25; 40; 85	I	SC	3	1	1	31; 40	11
Larus livens	Yellow-footed gull	1320		Multi	28; 37; 85	С	SC	4	1	1	72; 60	21
Larus maculipennis	Brown-hooded gull	360	; ; 291	Multi	25; 40; 85	С	SC	4	0	1	9; 9	0
Larus marinus	Great Black-backed gull	1488	65; 80; 481	Multi	32; 55; 107	Ι	SC	4	1	1	938; 726	25
Larus melanocephalus	Mediterranean gull	390	37; ; 318	Multi	26; 40; 86	С	SC	3	1	1	1513; 699	17
Larus minutus	Little gull	118	23; ; 221	Multi	22; 28; 70	С	SC	4	0	1	126; 88	7
Larus modestus	Gray gull	400		Multi	31; 40; 91	С	SC	4	1	1	36; 36	0
Larus novaehollandiae	Silver gull	350	; ; 294	Multi	27; 28; 75	С	SC	4	1	1	241; 227	13
Larus occidentalis	Western gull	1010	56; 72; 412	Multi	32; 48; 100	Ι	SC	4	0	1	276; 213	19
Larus pacificus	Pacific gull	1180		Multi	26; 42; 88	С	SC	4	1	1	2; 11	19
Larus philadelphia	Bonaparte's gull	212	30; 32; 263	Multi	25; 40; 85	Ι	SC	4	0	1	30; 30	0
Larus ridibundus	Common Black-headed gull	320	37; 47; 315	Multi	26; 35; 81	Ι	SC	4	1	1	5295; 5035	24
Larus saundersi	Saunder's gull			Multi	25; 40; 85	С	SC	4	0	1	30; 30	0
Larus schistisagus	Slaty-backed gull	1327	56; 68; 431	Multi	30; 45; 95	С	SC	4	1	1	401; 370	13
Larus scopulinus	Red-billed gull	280	;;276	Multi	24; 42; 86	I	SC	4	0	0	145; 101	29
Larus scoresbii	Dolphin gull	520	;;323	Multi	27; 45; 92	С	SC	4	1	1	7; 25	9
Pagophila eburnea	Ivory gull	616	36; 40; 338	Multi	26; 35; 81	I	SC	4	0	1	27; 25	20
Rhodostethia rosea	Ross's gull	187	19; 28; 255	Multi	21; 21; 62	I	SC	4	0	1	50; 50	0
Rissa brevirostris	Red-legged kittiwake	382	29; ; 305	Multi	30; 50; 100	0	SS	4	1	1	466; 161	16
Rissa tridactyla	Black-legged kittiwake	407	36; 40; 319	Multi	26; 42; 88	0	SS	4	1	1	16146; 11925	27
Xema sabini	Sabine's gull	998	26; 36; 267	Multi	25; 65; 110	Ι	SC	4	0	2	53; 29	18
Sternidae												
Anous minutus	Black noddy	144	37; 25; 235	Multi	34; 60; 114	Р	SS	4	0	2	694; 954	20
Anous tenuirostris	Lesser noddy	120		One	15; 55; 90	Р	SS	4	0	2	1696; 1050	25
Anous stolidus	Brown noddy	167	42; 57; 281	Multi	35; 45; 100	Р	SS	4	1	2	3742; 2388	18
Chlidonias albostriata	Black-fronted tern			One	23; 25; 68	С	SS	3	0	2	8;6	21
Chlidonias niger	Black tern	65	27; 17; 214	Multi	21; 22; 63	С	SS	3	0	2	398; 421	12
Gygis alba	White tern	160	32; 14; 252	Multi	36; 49; 105	Р	SS	3	0	2	284; 278	21
Gygis microrhyncha	Lesser White tern			One	35; 48; 103	Р	SS	3	0	2	24; 16	22
Larosterna inca	Inca tern	189		Multi	25; 28; 73	С	PLD	3	0	2	7; 180	19
Procelsterna albivitta	Gray noddy		29; 25; 208	One	25; 45; 90	Р	SS	3	0	1	79; 99	21
Procelsterna cerulea	Blue noddy	45	25; ; 205	One	25; 40; 85	Р	SS	3	0	1	47; 62	15
Sterna acuticauda	Black-bellied tern			Multi	25; 25; 70	С	SS	3	0	2	<0.1; <0.1	3
Sterna albifrons	Little tern	60	32; ; 180	Multi	24; 24; 68	С	PD	3	0	2	186; 181	14
Sterna aleutica	Aleutian tern	120		Multi	23; 28; 71	С	SS	3	0	2	62; 55	17
Sterna anaethetus	Bridled tern	131	43; 23; 271	One	29; 60; 109	С	SS	3	0	2	2510; 1563	18
Sterna antillarum	Least tern	57	36; 15; 176	Multi	22; 35; 77	С	PD	3	0	1	115; 117	14
Sterna balaenarum	Damara tern	46		One	22; 20; 62	С	SS	3	0	2	1; 2	22
Sterna bengalensis	Lesser Crested tern	240	528; 26; 286	One	26; 35; 81	С	PLD	3	1	2	248; 288	16
Sterna bergii	Crested tern	400	62; ; 345	Multi	30; 41; 91	С	PLD	3	1	2	323; 374	17

Sterna bernsteini	Chinese Crested tern			Multi	30; 41; 91	С	PLD	3	0	2	<0.1; <0.1	7
Sterna caspia	Caspian tern	662	69; ; 400	Multi	27; 40; 87	С	PLD	3	0	2	99; 111	19
Sterna dougallii	Roseate tern	110	39; 20; 233	Multi	23; 26; 69	С	PLD	3	1	2	236; 156	20
Sterna elegans	Elegant tern	260		One	26; 35; 81	С	PLD	3	0	2	50; 269	24
Sterna forsteri	Forster's tern	190	59; 24; 271	Multi	26; 35; 81	С	SS	3	0	2	130; 75	17
Sterna fuscata	Sooty tern	180	45; 25; 305	One	29; 60; 109	Р	SS	4	0	2	118096; 39766	18
Sterna hirundinacea	South American tern	190	; ; 300	Multi	23; 27; 70	С	SS	3	1	2	216; 147	9
Sterna hirundo	Common tern	120	38; 21; 280	Multi	24; 26; 70	С	SS	3	0	2	1319; 1242	19
Sterna lorata	Peruvian tern			Multi	23; 27; 70	С	SS	3	0	2	2; 2	26
Sterna lunata	Gray-backed tern	140	;;280	One	30; 49; 99	С	SS	3	0	2	392; 199	18
Sterna maxima	Royal tern	500	49; 80; 381	One	31; 30; 81	С	SS	3	1	2	459; 539	20
Sterna nereis	Fairy tern	57		Multi	25; 30; 75	С	SS	3	0	2	12;9	24
Sterna nilotica	Gull-billed tern	290	41; 23; 330	Multi	23; 32; 74	С	SS	3	0	1	51; 36	24
Sterna paradisaea	Arctic tern	110	34; 17; 270	Multi	22; 25; 67	С	SS	3	0	2	4498; 2119	23
Sterna repressa	White-cheeked tern	142		Multi	25; 30; 75	С	PLD	3	0	2	1259; 390	7
Sterna sandvicensis	Sandwich tern	300	58; 25; 325	One	24; 28; 72	С	PLD	3	1	2	794; 445	22
Sterna eurygnatha	Cayenne tern	300	55; 27; 250	One	29; 28; 77	С	PLD	3	1	2	70; 99	14
Sterna saundersi	Saunder's tern	50		Multi	25; 30; 75	С	PLD	3	0	2	2; 3	6
Sterna striata	White-fronted tern		;;274	Multi	25; 35; 80	С	PLD	3	0	2	1140; 50	13
Sterna sumatrana	Black-naped tern	110	35; ; 222	Multi	23; 24; 67	С	SS	3	1	2	23; 29	13
Sterna virgata	Kerguelen tern	125	; ; 259	Multi	24; 39; 83	С	SS	3	0	2	7; 7	21
Sterna vittata	Antarctic tern	143	; ; 263	One	25; 25; 70	С	SS	3	0	2	153; 69	14
Alcidae												
Aethia cristatella	Crested auklet	264	16; 29; 171	One	34; 33; 87	0	PD	1	0	0	6132; 4964	21
Aethia pusilla	Least auklet	84	15; 19; 102	One	30; 29; 79	0	PD	1	0	0	7384; 15899	21
Aethia pygmaea	Whiskered auklet	121	10; 22; 110	One	36; 41; 96	Ι	PD	1	0	0	76; 180	15
Alca torda	Razorbill	719	35; 30; 211	One	35; 23; 78	0	PD	1	0	2	4181; 1998	19
Alle alle	Dovekie	163	13; 21; 115	One	29; 28; 77	0	PD	1	0	1	56313; 117312	19
Brachyramphus brevirostris	Kittlitz's murrelet	296	20; 18; 140	One	30; 24; 74	Ι	PD	1	0	2	16; 15	13
Brachyramphus marmoratus	Marbled murrelet	203	16; 16; 127	One	29; 34; 83	Ι	PD	1	0	2	394; 307	16
Brachyramphus perdix	Long-billed murrelet	293	20; 18; 141	One	29; 40; 89	Ι	PD	1	0	2	11; 11	0
Cepphus carbo	Spectacled guillemot	490	41; 37;	Multi	30; 40; 90	Ι	PD	1	0	2	248; 136	12
Cepphus columba	Pigeon guillemot	487	44; ; 188	Multi	29; 40; 89	I	PD	1	0	2	1031; 880	18
Cepphus grylle	Black guillemot	405	33; 39; 137	Multi	29; 37; 86	С	PD	1	0	2	1041; 706	18
Cerorhinca monocerata	Rhinoceros auklet	520	35; 30; 152	One	45; 60; 125	0	PD	1	0	2	2622; 2976	13
Cyclorrhynchus psittacula	Parakeet auklet	258	16; 30; 152	One	35; 35; 90	Ι	PD	1	0	1	1089; 1191	21
Endomychura craveri	Craveri's murrelet	150		Multi	34; 2; 56	0	PD	1	0	2	18; 25	17
Endomychura hypoleuca	Xantus' murrelet	170	18; 24; 120	Multi	34; 2; 56	0	PD	1	0	2	15; 23	11
Fratercula arctica	Atlantic puffin	381	46; 29; 172	One	42; 39; 101	0	PD	2	0	2	44804; 19142	20
Fratercula cirrhata	Tufted puffin	779	58; 36; 201	One	44; 55; 119	0	PD	1	0	2	6799; 2676	21
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Fratercula corniculata	Horned puffin	619	48; 31; 190	One	40; 38; 98	0	PD	1	0	2	1946; 1110	17
Ptychoramphus aleuticus	Cassin's auklet	188	19; 27; 148	One	39; 46; 105	0	PD	1	0	1	5584; 5076	14
Synthliboramphus antiquus	Ancient murrelet	206	30; 32; 146	Multi	33; 2; 55	0	PD	1	0	1	2935; 1245	20
Synthliboramphus wumizusume	Japanese murrelet	296	20; 18; 144	Multi	33; 2; 55	Ι	PD	1	0	1	6; 8	17
Uria aalge	Common murre	993	48; 38; 203	One	33; 22; 75	0	PD	0	0	2	19316; 16098	22
Uria lomvia	Thick-billed murre	964	43; 48; 224	One	33; 23; 76	0	PD	0	0	2	34826; 20079	21

^a Classification follows Peters (1979).

^b Average of available records for adults.

^c C=close to shore (within 10km), I=inshore (within 50km), O=offshore (within 150km), P=pelagic (within 750km), F=far distant pelagic (>750km).

^d PD= pursuit diving, SS= surface seizing, PLD= plunge-diving, KL= kleptoparasitism, SC= scavenging.

^e 0=regularly dive to 60m, 1=regularly dive to 30m, 2=regularly dive to 10m, 3=upper 1m of water column, 4=surface feeders.

^f 0= have not been observed in diet, 1= have been observed in diet.

^g 0= fish occur only in diet only rarely if at all, 1=fish present but not the most important prey item, <30% of weight, 2=fish are the most important/predominate or only prey item, or one of two most important prey items (e.g., fish & squid).

^h after the present study (see Section 2.1.2).

ⁱ average length (years) of datasets for all populations of the species with more than one record.

Appendix II. Examples of data used to calculate abundance estimates for four numerically important seabird species. Complete references available upon request.

Species	Coastal stretch	Year	Number of individuals ^a	Reference
Blue Petrel (<i>Halobaena caerulea</i>)	Crozet Islands	1982	207900	Jouventin et al. 1984
(1984	294015	www.birdlife.net/datazone
	Diego Ramirez Islands	1982	2000000	Fugler et al. 1987
	-	2002	3105000	Lawton et al 2006
	Kerguelen Islands	1985	466690	Weimerskirch et al. 1989
	-	1989	495000	www.birdlife.net/datazone
		2002	1866762	Barbraud & Delord 2006
	Macquarie Island	1979	1980	Rounsevell& Brothers 1984
	1	1984	1815	Brooke 2004
	Prince Edward Islands	1977	99000	Williams et al. 1979
		1982	99000	Williams 1984
		1990	1815000	Cooper & Brown 1990
		1997	660000	www.birdlife.net/datazone
	South Georgia	1980	231000	Croxall et al. 1985
	5	1982	231000	Croxall et al. 1984
	Global		"at least 3,000,000"	(Brooke, 2004a)
			6,159,000	Modern abundance
Antarctic Prion (<i>Pachyptila</i> lesolata)	Auckland Island	1980	2333452	Robertson & Bell 1984
· · · · · · · · · · · · · · · · · · ·	Crozet Islands	1982	330	Jouventin et al. 1984
	Kerguelen Islands	1985	8083316	Weimerskirch & Jouventin 1989
	Macquarie Island	1979	161370	Rounsevell & Brothers 1984
		1985	161700	Garnett & Crowley 2000
		1999	97800	Goldsworthy et al. 2001
	McDonald Islands	1987	33330	Woehler 1991
		1990	33033	Marchant & Higgins 1990
	South Georgia	1980	72600000	Croxall et al. 1985
	-	1982	72600000	Croxall et al. 1984
	South Orkney Islands	1982	330000	Croxall et al. 1984
	South Sandwich Islands	1982	33000	Croxall et al. 1984
	South Shetland Islands	1982	1452	Croxall et al. 1984
	Global		"approx. 50,000,000"	(Brooke, 2004a)
			83,512,000	Modern abundance
Sooty Tern (<i>Sterna fuscata</i>)	Amsterdam Island	1972	3	Bourne & David 1995
		1982	3	Jouventin et al. 1984
		1985	3	Bourne & David 1995
• • • • •				
	Anguilla	1996	3	www.birdlife.net/datazone
• • • •	Anguilla Antigua Barbuda	1996 1999	3 7753	www.birdlife.net/datazone Saliva 2000
• • • •	Antigua Barbuda	1996 1999 1982	3 7753 3300	www.birdlife.net/datazone Saliva 2000 Halewyn & Norton 1984
• • • •	•	1996 1999 1982 1982	3 7753 3300 1320	www.birdlife.net/datazone Saliva 2000 Halewyn & Norton 1984 Halewyn & Norton 1985
• • • •	Antigua Barbuda	1996 1999 1982 1982 1984	3 7753 3300 1320 1208	www.birdlife.net/datazone Saliva 2000 Halewyn & Norton 1984 Halewyn & Norton 1985 Gochfeld et al. 1994
	Antigua Barbuda	1996 1999 1982 1982	3 7753 3300 1320	www.birdlife.net/datazone Saliva 2000 Halewyn & Norton 1984 Halewyn & Norton 1985

	1988	7260	Gochfeld et al. 1998
	1989	6600	Gochfeld et al. 1999
	1990	10560	Gochfeld et al. 2000
Ascension Island	1942	1000000	Ashmole 1963
	1959	750000	Ashmole 1964
	1962	104355	Williams 1984
	1997	640200	www.birdlife.net/datazone
	2002	906200	Ratcliffe et al. 2010
	2007	420000	Hulsman et al. 2008
Ashmore Reef	1998	6900	Milton 1999
Bahamas	1981	139071	Sprunt 1984
	1999	18668	Saliva 2000
Baja California	1983	250	Pitman 1985
Banda Sea	1987	3300	De Korte & Silvius 1994
Belize	2006	1414	Miller & Miller 2006
Br Virgin Islands	1982	660	Halewyn & Norton 1984
	1999	330	Saliva 2000
Caroline Islands	1995	200	Bunden 1996
Chagos	1970	1147907	Feare 1984
	1996	240900	McGowan et al. 2008
	2006	271286	McGowan et al. 2008
Cocos Islands	1983	116	Stokes et al. 1984
Cuba	1982	9900	Halewyn & Norton 1984
	1999	161666	Saliva 2000
Dominica	1982	3300	Halewyn & Norton 1984
Dominican Republic	1982	330000	Halewyn & Norton 1984
1	1999	168300	Saliva 2000
Europa Island	1974	150000	Le Corre & Jouventin 1997
. I	1996	3000000	Le Corre & Jouventin 1997
	2000	2475000	www.birdlife.net/datazone
	2003	2508000	Jaquemet et al. 2005
Fiji	1980	1043	Garnett 1984
Florida	1982	132000	Halewyn & Norton 1984
French Polynesia	1973	55044000	Holyoak & Thibault 1984
r tenen r orynesia	1980	11479067	Garnett 1984
Gambia	1975	7	Cooper et al. 1984
Glorieuses	2003	, 891000	Le Corre & Jouventin 2005
Great Barrier Reef	1989	910200	Fuller & Burbidge 1992
Great Darner Reer	1990	862100	Fuller & Burbidge 1992
	1995	88800	Hulsman et al. 1997
Guadeloupe	1995	88800 990	Halewyn & Norton 1984
Guadeloupe	1992	990 16167	Saliva 2000
Gulf of Mexico		10107	
Guil of Mexico	1977		Clapp & Buckley 1984
TT!!	1982	231	Halewyn & Norton 1984 Harrison et al. 1984
Hawaii	1975	5182650	Harrison & Seki 1987
	1980	4852650	
TT	1985	4918650	Harrison 1990
Houtman Abrolhos	1993	859056	Fuller et al. 1994
Indonesian Sea	1963	1650	Wells 1991
Islands off Mexico	1990	990	Everett & Anderson 1991
Jamaica	1982	7379	Halewyn & Norton 1984
	1999	266709	Saliva 2000
Johnston Atoll	1923	5500	Saliva 2000
	1973	600000	Saliva 2000
	1999	295161	Saliva 2000

T 1 XT	2002	<<00000	L G 0 L 0005
Juan de Nova	2003	6600000	Le Corre & Jaquemet 2005
Kenya Kenya	1980	16500	Cooper et al. 1984 Veitch et al. 2004
Kermadec	1967	328515	
	1994	7983	Veitch et al. 2004
	1995	8913	Veitch et al. 2004 Veitch et al. 2004
Line Islands	1997	6683	
Line Islands	1970	18960000	Perry 1980 Garnett 1984
	1980 1983	13530000	Schreiber & Schreiber 1986
	1985	11431535 40000	Schreiber & Schreiber 1986
	1984	40000 621047	Kepler et al. 1994
Lord Howe Island	1988	3300000	•
Lord Howe Island	1970	397650	Fullagar & Disney 1975 van Tets & Fullagar 1984
Madagagaga		23100	•
Madagascar	1980 1998	6600	Cooper et al. 1984 www.birdlife.net/datazone
	2000	6930	
Moriana Islanda		924000	Le Corre & Jaquemet 2005
Mariana Islands	1995		Stinson 1995
Marshall Islands	1966	16000	Carpenter et al. 1968
Mantiniana	1967	16000	Carpenter et al. 1968
Martinique	1982	1650	Halewyn & Norton 1984
Mauritious	1975	1864500	Feare 1984
Maria Caribban	1998	1303995	www.birdlife.net/datazone
Mexico Caribbean Mexico Gulf	1982	363	Halewyn & Norton 1984
	1982	7379	Halewyn & Norton 1984
Mexico West	1998	700	Chipley 1999
Mozambique	1997	6600 104255	Kromer 1998
Nauru	1980	104355	Garnett 1984
Netherlands Antilles	1982	46669	Halewyn & Norton 1984
New Caledonia	1995	33000	Robinet et al. 1997
	1996	990	Benoit & Bretagnolle 2002
	1997	660 50	Benoit & Bretagnolle 2002
Norfolly Jaland	1998	30 181500	Benoit & Bretagnolle 2002
Norfolk Island	1970	5610	Taylor 2000 De Luca et al. 2006
Noronha Archipelago Oman	2006 1981	33	Gallagher et al. 1984
Panama Pacific			www.birdlife.net/datazone
Phoenix Islands	2004	10435516	Garnett 1984
Phoenix Islands	1980		Pierce et al. 2006
Puerto Rico	2006	2036100	Furniss 1983
rucito Rico	1971 1980	551100 99000	Furniss 1983
			Furniss 1983
	1981	59400	Furniss 1984
	1982 1999	99000 98759	Saliva 2000
Queensland	1999	296862	King 1993
Rio Grande do Norte	1990	99000	Williams 1984
KIO Ofalide do Norte	1980	5558	Neto 1998
Ryuku Islands	1994	21120	Abe et al. 1986
Kyuku Islalius			
	1982	13530	Abe et al. 1986
Colore Comerciale	1983	10230	Kohno et al. 1986
Sala y Gomez Islands	1985	330	Harrison & Jehl 1988
	1986	165	Harrison & Jehl 1989
Salvaga-	1997	637	Vilina & Gazitua 1999
Salvages	1980	3	Le Grand et al. 1984
Sao Tome Principe	2000	330000	www.birdlife.net/datazone
Seychelles	1976	7475490	Feare 1984

	Global		"16,000,000-36,000,000" 117,312,000	(del Hoyo et al., 1996) Modern abundance
		1994	3300000	Anker-Nilssen et al. 2000
		1993	3300000	Isaksen & Bakken 1995
		1989	3300000	Mehlum & Bakken 1994
		1985	5346000	Evans 1986
		1982	5280000	Evans 1984
	Svalbard	1978	4950000	Kempf & Sittler 1987
		1996	102300	www.birdlife.net/datazone
		1992	73790	Anker-Nilssen et al. 2000
		1967	73790	Golovkin 1984
	Novaya Zemlya	1950	16500	Joiris et al. 1996
	Norwegian Shelf SW	1993	705000	www.birdlife.net/datazone
		1986	330000	www.birdlife.net/datazone
		1984	330000	Barrett & Mehlum 1989
	Jan Mayen Island	1982	165000	Evans 1984
	Iceland	1979	33	Evans 1984
		2002	108900000	ICES 2003
		1985	82669930	Evans 1986
	Greenland West	1980	49501650	Evans 1984
		1989	3300000	www.birdlife.net/datazone
		1985	193070	Evans 1986
	Greenland East	1980	115500	Evans 1984
		1985	507514	Evans 1986
	Franz Josef Land	1950	825000	Golovkin 1984
	East Bering Sea	1997	20	U.S. Fish and Wildlife Service 200
	Chukchi Sea	1985	90	U.S. Fish and Wildlife Service 200
		1985	165000	www.birdlife.net/datazone
		1984	165000	Barrett & Mehlum 1989
(1110 (1110))	Bear Island	1982	33000	Evans 1984
Dovekie (Alle alle)	Baffin Bay	2002	1650	ICES 2003
			39,766,000	Modern abundance
	Global		``21,000,000-22,000,000'	(Delany and Scott, 2006)
	W Australia	1986	247500	Burbidge & Fuller 1989
	Venezuela	1982	165000	Halewyn & Norton 1984
	-	1999	115457	Saliva 2000
	US Virgin Islands	1982	104355	Halewyn & Norton 1984
		1982	14850	Halewyn & Norton 1984
	Trinidad	1980	16500	Williams 1984
		2005	14553	Crawford et al. 2006
		1989	29580	Crawford et al. 2006
	Tanzania	1972	73790	Cooper et al. 1984
		1980	3300	Williams 1984
	St Helena	1950	3300	Williams 1984

Family	Estimated abundance in 1950 $(10^6 \text{ individuals})$	Estimated abundance in 2010 $(10^6 \text{ individuals})$
Spheniscidae	92	65
Diomedeidae	5	5
Procellariidae	404	288
Hydrobatidae	28	46
Pelecanoididae	63	48
Phaethontidae	<1	<1
Pelecanidae	1	1
Phalacrocoracidae	21	6
Fregatidae	1	1
Sulidae	7	7
Stercorariidae	2	1
Laridae	41	35
Sternidae	168	54
Alcidae	190	212
Total	1023	768

Appendix III. Estimates of global abundance per seabird family in 1950 and 2010, as per Section 2.4.4.