the region compared to anchovies. Thus, similar to the Peruvian situation, seabird populations have shifted, but patterns also are apparent at smaller timescales depending on interannual changes in spawning areas of the fish. As with all eastern boundary currents, the role of climate in changing pelagic fish populations is being intensively debated.

See also

Benguela Current. California and Alaska Currents. Canary and Portugal Currents. El Niño Southern Oscillation (ENSO). Polynyas. Seabird Foraging Ecology. Sea Ice: Overview. Sea Level Change. Upwelling Ecosystems.

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SEABIRDS AND FISHERIES INTERACTIONS

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Introduction

Of the ~9000 species of birds in the world, only about 350 may be classified as seabirds (**Table 1**). The exact number of species depends on the definition of a 'seabird' and on recent taxonomic conventions. Here, in addition to the four orders that are generally considered as seabirds (all Sphenisciformes, all Pelecaniformes, all Procellariiformes, and some Charadriiformes), also divers or loons (Gaviiformes) and seaducks (members of the much larger order of Anseriformes) are included. Following this selection, it is apparent that only 4% of all species of birds utilize the greater part of the world's surface: the oceans. Seabirds prey upon fish, squid, and other marine organisms and the productivity of the oceans and regional variations in food availability determine the distribution, breeding success, and ultimately the numbers of seabirds on our planet. Most seabirds are largely piscivorous, but, particularly in the penguins, petrels and storm petrels, and northern auks, many species are planktivorous. Some seabirds exploit marine resources only outside the breeding season and shift to terrestrial feeding during nesting. Several species of seaduck exploit shellfish resources in shallow seas and these may shift to fish prey only under exceptional conditions.

Seabirds vary substantially in size and morphology. From the smallest of the storm-petrels (the least petrel *Halocyptena microsoma*, ~20 g) to the largest of the albatrosses (wandering albatross *Diomedea exulans*, up to 11 kg with a wingspan of up to 3.5 m) or penguins (emperor penguin *Aptenodytes forsteri*, 19–46 kg flightless), there is a great variability in capacity for flight, time spent at sea, preferred types of prey, and foraging techniques. Seabirds are wide-ranging organisms and they can be both predators and scavengers of marine

Table 1 Orders and families selected for this review as 'sea birds'[a]

Order	*Selected families*	*Genera*	*Species*	*Taxa*
Sphenisciformes	Penguins	6	17	26
Gaviiformes	Divers (or loons)	1	4	6
Procellariiformes	Albatrosses, petrels, shearwaters, storm-petrels, diving petrels	23	108	175
Pelecaniformes	Tropicbirds, pelicans, gannets and boobies, cormorants, darters, frigatebirds	6	65	117
Anseriformes	Steamer ducks, seaduck, mergansers, and allies	1	22	33
Charadriiformes	Skuas, gulls, terns, skimmers, auks	31	127	261
		68	343	618

[a]The taxonomy follows Del Hogo J, Elliott A and Sargatal J (1992, 1996) *Handbook of the Birds of the World*, vols 1 and 3. Barcelona: Lynx Edition.

prey. Most are essentially surface foragers, obtaining their prey from the top meters of the water column. Penguins, some shearwaters, cormorants, and alcids are exceptions that are known to dive several tens or even hundreds of meters deep. Several species, most notably some gulls, have successfully adapted to humans and exploit new, artificial sources of food such as fishery waste at trawlers, rubbish tips, litter at holiday resorts, etc. Other species, such as the great auk *Penguinis impennis*, the only recent flightless alcid, became overexploited and were driven to extinction.

Seabirds can either be harmed by or benefit from the fishing activities of humans. Direct effects of fisheries involve, for example, the killing of seabirds in fishing gear (by-catch). Indirect effects mostly operate through changes in food supplies of birds. Surface feeders are most vulnerable to baited hooks set in long-line fisheries; pursuit diving seabirds are most likely to suffer from gillnets set on the bottom of coastal seas. Surface feeders, particularly the larger, scavenging species, usually profit most from discarded undersized fish and offal in commercial fisheries. In recent decades, there has been tremendous progress in our quantitative understanding of the processes in marine ecosystems, including the interactions of seabirds and fisheries. Some of the most profound effects of fisheries on seabirds are discussed and illustrated here.

Seabird Feeding Techniques

Seabirds exploit the marine environment in a number of ways: in and from the air, at the water surface, by plunge diving up to a few meters deep and by wing- or foot-propelled pursuit diving, reaching over a 100 m in depth. Several coastal seabirds, such as divers, grebes, cormorants, and seaducks rarely exceed 20 m in depth while foraging over the bottom, while several pelagic seabirds, including, perhaps unexpectedly, some of the generally more aerial shearwaters, reach many tens of meters deep and sometimes well over 100 m (e.g., 180 m by the common guillemot *Uria aalge*). The feeding technique largely determines the sort of conflict or contact that seabirds may have with commercial fisheries. Scavenging at fishing vessels, for example, is typical for large surface feeders. Birds that get caught by baited hooks on long-lines are also mainly large surface feeders, particularly those that scavenge at dead fish, squids or corpses of marine mammals during normal life. Most birds that drown in fish nets (behind trawlers or in gill nets set adrift or set on the bottom) are mainly pursuit diving seabirds, such as auks, cormorants, and seaduck.

Many seabirds are gape-limited, piscivorous species that prey on small shoaling fish in areas where high concentrations of prey occur. Obviously, restricted areas in which large schools of fish are formed are often equally attractive to fishermen. Diving seabirds and fishermen may target the same prey (although possibly different size classes of fish), while commercial fisheries may provide an additional source of food for surface feeders, simply by discarding unwanted material and undersized fish. In practice, it appears the most undersized fish are suitable at least for the largest of scavengers (mollymawk albatrosses and gannets). For the remaining part, the smaller fraction, there is often intense competition among the scavengers, leading to the establishment of complex dominance hierarchies and species-specific feeding success rates. Scavenging seabirds tend to select slightly smaller prey than they can normally handle, thus facilitating a rapid process of picking up and swallowing the food and minimizing the risk of being robbed by competitors.

Diving for prey or flying long distances for food is an energetically expensive way of foraging, requiring very high intake rates. Such high intake rates are impossible under most conditions, so that concentrations of prey are either sought out, or deliberately formed by concerted action of (a group of) predators. Seabirds are famous for exploiting prey concentrated and herded to the surface by cetaceans or large predatory fish such as tuna. Several diving seabirds are known to concentrate the herd prey to the surface, which is in turn, and often through a mechanism of commensalism, exploited by surface feeding birds that are incapable of reaching the prey by other means. High concentrations of prey may also be found 'more naturally' along shelf breaks, in oceanic or coastal fronts, in upwelling areas, and along pack ice or glaciers. The need for concentrated resources of food and the availability of prey in terms of being within reach of the predator, and of suitable size and fat content, is more important than the actual stock. Hence, fishery statistics and stock assessments are usually inadequate to describe or estimate the food resource of individual species of seabirds or other marine predators. A complicating factor is that the availability of prey may be largely determined by the presence and (foraging) activities of another marine predator, so that shifts in the abundance of one species may lead to food shortages and starvation of another, even if the food resource itself is apparently unchanged and sufficiently large.

History

When humans gradually developed and improved fishing techniques through the centuries and finally set out in boats to fish at sea, seabirds were immediately met with in large numbers. It was soon learned that seabirds could be used for navigation at sea and early fishermen successfully followed foraging seabirds as indicators of the presence of fish that were otherwise difficult to find. The peaceful coexistence of seabirds and fishermen did not last long. This was partly because seabirds themselves, or their eggs and offspring, were considered attractive sources of protein, perfectly suitable for human consumption. In addition, seabirds were increasingly considered to be competitors or even pests and were persecuted for that reason. Until the beginning of the twentieth century, many species of seabirds were heavily exploited or persecuted in much of their range and some were nearly driven to extinction.

Human fisheries developed further, and particularly when sailing vessels were gradually replaced by modern purse seiners and powerful trawlers with engines in the nineteenth century, overfishing increasingly caused problems. The interactions between fisheries and marine top-predators such as seabirds now became more complex. In the twentieth century, many species of seabirds have greatly increased in numbers, and have successfully expanded their breeding range. Over the last few decades, the growth in some of these populations has ceased, but seabird numbers are generally at a historically high level. The drastic increase in numbers of seabirds has led to speculation about what might have caused these trends. While the impact of direct exploitation of seabirds in the old days was largely beyond doubt, the effects of overfishing were much less clear-cut. Some seabirds may have benefited from rich, new food supplies made available, first, by offal from whaling and later from commercial fishing vessels. However, even more complex trophic interactions may have occurred, because fisheries are generally directed at much larger prey (marketable fish) than seabirds eat. By cropping large piscivorous predators and cannibals, such fisheries benefit seabirds by increasing the abundance of small fish. As such, even commercial 'overfishing' might have been beneficial for seabirds.

The Exploitation and Culling of Seabirds

Seabirds have been exploited as food for as long as humans have established coastal communities. At some archaeological sites it appeared that such communities were often entirely reliant on seabirds and fish for their protein intake. Fishermen killed seabirds at sea or visited seabird colonies to obtain flesh with which to bait their hooks on a large scale, at least until the late nineteenth century. As an example, the harvest of the northern gannets in the Gulf of St. Lawrence is likely to have reduced the local population from over 100 000 pairs in the early 1800s to below 750 pairs by the turn of the century, when bird protection laws were enacted. Today, seabirds are still harvested by local fishermen in areas like Indonesia, and boobies are probably still killed to be used as bait in lobster traps off Brazil.

Fish-eating birds, particularly those capable of eating relatively large fish, have always been blamed by fishermen for depleting local fish stocks and were often held responsible for declining catches. This has led to mass killing or culls, even if no evidence was provided to support the impact of the birds or to show that the birds had negatively affected the fish populations concerned. For that reason, both in Europe (great cormorant *Phalacrocorax carbo*) and in the New World (double-crested cormorant *Phalacrocorax auritus*), cormorants were at least regionally nearly driven to extinction. So far there is no scientific evidence that a cull of any marine predator has enhanced any commercial fishery.

Recognition of the need to conserve nature rather than to relentlessly exploit its resources developed largely during the twentieth century. As a result, the mass slaughter of birds, even of species that were generally considered as pests, largely came to a halt. Yet, for example, the rise and fall of herring gull populations in The Netherlands during the twentieth century closely followed trends in levels of persecution. When breeding colonies became protected, around the 1920s, all populations increased. This increase ceased when culling was introduced to 'manage' gull numbers for the protection of other birds and to maintain the population at 'acceptable levels.' Culling in the late 1960s was not so intense that populations declined, but when full protection measures were taken in the 1970s, populations exploded to unprecedented levels and peaked in the 1980s.

By-catches of Seabirds in Commercial Fisheries

Seabird populations are negatively affected by the extra mortality induced by commercial fisheries all over the world: any net or line set with baited hooks carries the risk of catching seabirds as a bycatch. Many surface-foraging seabirds commonly scavenge on dead or moribund prey and such birds are likely to try to steal bait from longline hooks during line setting. Large numbers of seabirds become hooked and subsequently drown as the longline sinks below the sea surface, a problem only fully appreciated in the last few decades. Pelagic long-lining in tropical and temperate seas concentrates mainly on tuna, swordfish, and sharks. Demersal long-lining in cold temperate waters of the continental shelves of the Atlantic and the Pacific, and in the Southern Ocean mainly concentrates on bottom-dwelling fish such as large gadoids and flatfish. Both types of longline fisheries use baited hooks. Procellariiform birds (mainly albatrosses and petrels) are the principal by-catch in longline fisheries all over the globe (**Table 2**). The by-catch of long-liners operating in the north-east Atlantic is known to have killed as many as 1.75 birds per 1000 hooks (95% of which were northern fulmars). At night, mortality rates are substantially lower (0.02 birds/1000 hooks). When these figures are multiplied by the nearly 500 million hooks set in one year by the Norwegian autoline fleet alone, the annual mortality of seabirds must be very large. In the Pacific demersal and pelagic longline fisheries, an estimated 'several thousand' black-footed and Laysan albatrosses are killed annually. Catch rates of seabirds by

Table 2 Review of longline fisheries in the world and the principal sea bird bycatch[a]

Region	*Countries mainly involved*	*Target fish*	*Principal by-catch*
North-east Atlantic longline fisheries	Norway, Iceland, Faeroes	Demersal fish (e.g., cod)	Northern fulmar
North Pacific longline fisheries; Bering Sea, Sea of Okhotsk and the Gulf of Alaska	USA, Canada, Russia	Demersal fish (e.g., cod, halibut)	Albatrosses, northern fulmar
North Pacific longline fisheries; international waters	USA, Japan, Korea, Taiwan	Pelagic fish (e.g., swordfish)	Albatrosses
Southern continental shelf demersal longline fisheries; Pacific and Atlantic coasts of South America	Chile, Argentina, Uruguay and Brazil	Hakes, ling	Albatrosses and petrels
Southern continental shelf demersal longline fisheries	Atlantic coast of southern Africa (South Africa, Namibia)	Hakes, ling	Albatrosses and petrels
Southern continental shelf demersal longline fisheries	Australia, New Zealand	Hakes, ling	Albatrosses and petrels
Southern Ocean Patagonian toothfish longline fishery; sub-Antarctic islands and seamounts of the Southern Ocean		Patagonian toothfish	Mollymawk albatrosses, wandering albatrosses, white-chinned petrel, giant petrels
Southern Ocean bluefin tuna longline fishery	Australia, Japan, New Zealand, Korea, Taiwan	Bluefin tuna	Albatrosses, petrels

[a]From Tasker *et al.* (1999).

Patagonian toothfish long-liners were estimated at 145 000 birds killed during the 1996/97 season alone, mainly mollymawk albatrosses and the white-chinned petrel, with smaller numbers of wandering albatrosses and giant petrels. For some of these species, population decreases have been recorded at their breeding grounds that are thought to be due to longline-induced mortality.

Perhaps even larger numbers of seabirds drown in gill nets (set nets and drift nets combined), whether these are still in commercial exploitation and set by fishermen or have been lost and have established themselves on the seafloor as 'ghost nets' (continuing their catches). Surface gill nets are mainly used for squid, salmon, and small tunalike bonitos; bottom nets are used for demersal fish such as cod and various species of flatfish (**Table 3**). Much of the mortality in these nets will go unnoticed, as fishermen are known to 'hide' the casualties by sinking them, and most certainly are very reluctant to report any seabird kills. Serious problems with gill nets are reported from Newfoundland (inshore capelin fisheries, offshore salmon fisheries), Greenland (offshore salmon fisheries), the North Pacific (offshore, salmon), northern Norway (offshore and nearshore, cod and salmon), the Baltic (shallow waters, demersal fish such as flatfish and cod), and around Britain and Ireland (mainly nearshore, salmon and bass). It is mainly pursuit diving alcids, shearwaters, and seaducks (Baltic) that are known to drown in vast numbers (**Table 3**). For example, prior to the 1992 moratorium on high-seas drift nets in the North Pacific, $\sim$ 500 000 seabirds were drowned annually (mainly shearwaters). More recent data showed that approximately 50 000 seaducks drown annually in an area as small as the IJsselmeer area in The Netherlands, including 1100, or 4.5% of the world population, of smew *Mergus albellus*.

A less serious but unnecessary threat to seabirds is that seabirds pick up floating debris, including netting, nylon line and ropes, from the sea surface to use as nesting material instead of seaweed, or simply by accident. As a result, the birds become entangled and die from starvation. The northern gannet *Morus bassanus* and great cormorant ranked highest among 90 species of stranded marine birds of which 140 000 corpses were checked for entanglements as cause of death in the southern North Sea. Some 5% of all beached northern gannets checked ($n = 1395$) were entangled in ropes or fishing gear, while 2% of all great cormorants ($n = 310$) had suffered a similar fate. Inspection of northern gannet nests on the Shetland Islands in Britain revealed that 92% of all nests contained at least some plastics, while 50% contained virtually nothing else. Both chicks and adult birds are seen to become entangled in the colony and most of these casualties die from starvation. While the mortality associated with this type of pollution may be quite low, the amount of debris floating around at sea has increased substantially in recent decades and sightings of gannets carrying around nets, plastics, and ropes are now very common, particularly at the main fishing grounds.

Discards and Offal as Food for Scavenging Seabirds

Albatrosses, petrels, shearwaters, gannets, and most gulls are common scavengers at fishing vessels. Away from fishing vessels, most of these birds are

Table 3 Review of gill-net fisheries in the northern hemisphere and principal sea bird by-catch[a]

Region	*Countries mainly involved*	*Area, target fish*	*Principal by-catch*
NW Atlantic	Newfoundland (Canada)	Inshore, spawning capelin Offshore, salmon	Common guillemot, Atlantic puffin, black guillemot, Brünnich's guillemot, great shearwater, northern gannet
NW Atlantic	Greenland	Offshore, salmon	Brünnich's guillemot
N Pacific	Japan	High-seas drift-netting, salmon	Sooty and short-tailed shearwater, black-footed albatross, tufted puffin, horned puffin
		Offshore, squid	Japanese murrelet
		Inshore, salmon	Ancient murrelet, marbled murrelet
Pacific	California	Near-shore	Common guillemot
NE Atlantic	Norway	Near-shore, cod, salmon	Common and Brünnichs guillemot
Baltic	Poland, Sweden, Germany	Inshore, flatfish, cod	Common eider, common scoter, common guillemot, razorbill, long-tailed duck
North Sea	IJsselmeer, The Netherlands	Inshore, eel, freshwater fish	Red-breasted merganser, goosander, smew, scaup, tufted duck
NE Atlantic	Britain and Ireland	Inshore, bass, salmon	Common guillemot, razorbill

[a]From Tasker *et al.* (1999).

surface feeders, specialized in catching zooplankton, squid, or small fish or as scavengers on carrion. Some of the gulls also have terrestrial feeding modes; the gannets and boobies are deep plunge diving seabirds; while most shearwaters naturally feed by pursuit plunging (reaching considerable depth). Pursuit diving piscivorous seabirds, such as cormorants and larger auks, are occasionally observed in association with fishing vessels, but, even if these birds benefit from human fisheries, they have very different feeding techniques from the 'ordinary' scavengers at trawlers.

Consumption rates of scavenging seabirds have been measured onboard fishing vessels during sessions of experimental discarding. Overall consumption rates vary greatly in different parts of the world but are generally highest for offal (liver and guts of gutted fish), and discarded roundfish (usually undersize roundfish and nontarget species), and considerably lower for discarded flatfish and benthic invertebrates. In the North Sea, consumption rates (proportion of prey items taken by seabirds of all discards and fishery waste produced) of the most common forms of fishery waste ranged from $< 10\%$ in benthic invertebrates to 25% of the flatfish, over 80% of all roundfish, and 92% of all offal (**Table 4**). In several studies it was shown that consumption rates in winter were particularly high. Seabirds tend to select prey that is easy to handle and to swallow, which appeared to be more important than its energetic equivalent. Several species demonstrated strong preferences for certain types of prey (whether or not forced by competitors). For example, most spiny grey gurnards were picked up by lesser black-backed gulls *Larus graellsii*, while smooth and slender whitings, offered simultaneously, were often ignored. The consumption of both flatfish and benthic invertebrates, less preferred food for most scavenging seabirds, increases when competition is high, but is often negligible when the number of scavengers was low in proportion to the amount of discards supplied.

Although discards and offal are an important additional source of food for scavenging seabirds, the reproductive output of individuals that take nearly only fishery waste is not usually very high. For example, the chick growth index of great skuas *Stercorarius skua* breeding on the Shetland Islands declined considerably when more than 50% of the prey delivered by the parents comprised of discards and offal. Similarly, the reproductive output of lesser black-backed gulls in the southern North Sea was high in years when clupeoid fish dominated chick diets, but low when chicks were mainly provisioned with fishery waste. In the northern fulmar *Fulmarus glacialis*, one of the commoner scavengers behind fishing vessels in the North Sea, no correlation was found between numbers of fishing vessels or the amount of discards produced per km^2 in a given area and the numbers of fulmars at sea, suggesting that commercial fisheries were not the prime determinant of their distribution at sea.

Seaduck, Aquacultures and Fisheries for Clams

Several seaduck, such as common eider *Somateria mollissima* and common scoter *Melanitta nigra*, feed on bivalves during most of the winter. In aquacultures in coastal, shallow seas, these duck are often considered and treated as pests and are disturbed, shot, or otherwise scared away. In so-called mussel farms, where mussels are manipulated to grow on ropes or other structures, a single eider duck can do considerable damage by stripping off hundreds of shells to obtain a single specimen or perhaps a few to eat. In areas as the Wadden Sea in The Netherlands, where musselseed is harvested in one place, to be dumped to grow to marketable size in certain licensed, cultivated parts of that sea area, eiders tend to be attracted in vast numbers, and fishermen scare these birds away by establishing small teams of people with speed boats that enter the mussel cultures at regular intervals. In the presence of alternative feeding sites, such activities cause little or no problems to the seaduck. However, most (natural) shellfish occur in dense banks that grow for a number of years and die off at times. For example, in the southern North Sea, large concentrations of up to 160 000 common scoters along with smaller numbers of velvet scoters *Melanitta fusca* winter over banks holding stocks of the bivalve *Spisula subtruncata* within approximately 10 km of the coast. These seaduck are easily disturbed and the appearance of fishing vessels in the recently established *Spisula* fishery has led to both disturbance and local depletion of food stocks. With these banks of shellfish now being exploited, and usually overexploited, and although the future of the bivalves itself is not set at risk, the local feeding conditions of seaduck deteriorate to such levels that mass mortality due to starvation or departure are the only alternatives. To complicate the interactions between seaduck and fisheries in the Wadden Sea even further, the natural resources of eider duck within the Wadden Sea (old, established mussel banks on the mudflats) were removed in the early 1990s and have still not recovered, so that the wintering population of nearly 200 000 eiders, seeking alternative prey in the coastal waters, is now in direct competition with

Table 4 Consumption rates of common forms of discards and other forms of fishery waste (fraction consumed by sea birds of all prey offered) by North Sea seabirds from sessions of experimental discarding at sea and the estimated energetic equivalents ($kJ\,g^{-1}$) of discarded organisms (where known). Shown are total numbers offered, numbers swallowed (consumed) or pecked on (usually to reach and feed on intestines) and the number that sink, the fraction consumed (swallowed or pecked on), and the general body shape of fish

	Consumed	*Pecked on*	*Sunk*	*Total*	*Percentage consumed*	*Body shape*	*Energetic equivalent ($kJ\,g^{-1}$)*
Swimming crab	46		160	206	22.3		3.5
Common starfish	265		1558	1823	14.5		2.0
Hermit crab	7		158	165	4.2		3.5
Sea-mouse	1		124	125	0.8		2.0
Unidentified starfish	2		662	664	0.3		2.0
Brittlestar			450	450	0.0		2.0
Masked crab			246	246	0.0		3.5
All benthic invertebrates	375	4	3779	4158	9.1		
Shrimps	34	1	84	119	29.4		3.5
Cephalopods	62	1	72	135	46.7		
Sole	54	1	104	159	34.6	Slender, supple	
Long rough dab	242	17	527	786	33.0	Rough, slender	
Dab	1102	11	3170	4283	26.0	Stiff, rather wide	
Lemon sole	43	7	162	212	23.6	Smooth, slender	
Plaice	46	1	681	728	6.5	Stiff, rather wide	
All flatfish	1578	41	4850	6469	25.0		4.0
Offal	7533		650	8183	92.1		9.0
Bib	1038		42	1080	96.1	Smooth, slender	4.0
Poor cod	403		22	425	94.8	Smooth, slender	4.0
Blue whiting	98	3	6	107	94.4	Smooth, slender	4.0
Norway pout	5571	21	336	5928	94.3	Smooth, slender	4.0
Lesser Argentine	311		26	337	92.3	Smooth, slender	4.0
Herring or sprat	125		19	144	86.8	Smooth, slender	6.5
Whiting	8420	383	1610	10 413	84.5	Smooth, slender	4.0
Herring	6595	97	1512	8204	81.6	Smooth, slender	6.5
Haddock	4213	194	1080	5487	80.3	Smooth, slender	4.0
Sand eel	1145		345	1490	76.8	Smooth, slender	5.0
Sprat	2824	1	917	3742	75.5	Smooth, slender	6.5
Greater sand eel	203		69	272	74.6	Smooth, slender	5.0
Tub gurnard	126	2	47	175	73.1	Spiny, hooked	4.0
Grey gurnard	1242	92	521	1855	71.9	Spiny, hooked	4.0
Cod	1473	63	653	2189	70.2	Smooth, slender	4.0
Mackerel	583	21	318	922	65.5	Smooth, slender	6.5
Hooknose	109		103	212	51.4	Hooked	
Scad	263	12	304	579	47.5	Rather smooth, slender	4.0
Dragonet	145		186	331	43.8	Spiny	
All roundfish	35 273	895	8258	44 426	81.4		4.0

over 100 000 scoters. Subsequent overfishing of these coastal stocks in 1999 resulted in unprecedented mass mortality of eiders in winter 1999/2000.

The Effects of Overfishing

Stock Depletion

Most piscivorous seabirds specialize on small shoaling fish, such as herring, sardines, anchovy, capelin, or sand eels. Small fatty fish are particularly important prey in the breeding season, when the energetic requirements of the chick(s) are to be met. Competition between fisheries and seabirds for prey resources has been documented for several areas, including the North Pacific (Mexico–Oregon, anchovy), Californian waters (sardine), Peru (anchovy), the North Sea (sand eels), northern Norway (herring), and the Barents Sea (capelin). Major fish stock collapses occurred in each of these areas and, although in most cases recruitment failures, El Niño events, severe winters, or other natural factors were suggested to have caused the crashes, there were poorly managed industrial fisheries running that were not stopped in time to avoid havoc. In all these cases, mass mortality of seabirds, or at least major disruptions in breeding success, occurred. In one of the more famous examples, Atlantic puffins, facing structural food shortages after the depletion of herring stocks off the Lofoten Islands in Norway, suffered from 22 consecutive years with virtually total chick mortality due to insufficient provisioning rates. A recent collapse in sand eel stocks around Shetland and Orkney had the most severe effects on surface feeding seabirds, while deep pursuit diving species maintained high reproductive success. In this event, the foraging mechanisms rather than the fish stocks themselves were apparently damaged (surface swarming sand eels disappeared), but also the local industrial fisheries for sand eels had very low catch rates. The collapse of the Peruvian anchoveta in the early 1970s, coinciding with an El Niño event but in which the stocks were heavily overfished at first, led to exceptionally high mortality rates in local breeding seabirds (boobies and cormorants, or guano birds). The capelin crash in the Barents Sea led to mass mortality of common guillemots (highly specialized on this type of prey), but only to minor reductions in stocks of Brünnich's guillemots (with a more diverse prey spectrum).

The Seabird Paradox

The paradox is, however, that overfishing can also be beneficial for seabirds. There is a general belief that stocks of immature fish in the North Sea have increased, largely thanks to the overfishing of large (predatory) fish. Similarly, congruent shifts in sand eel abundance in the North Atlantic ecosystems were explained by the relative scarcity of large predatory fish as a result of overfishing. At present, the heavily exploited North Sea is a pool of young (immature) fish rather than a balanced ecosystem. A much larger proportion of young fish survives in the absence of mature conspecifics and other (fish) predators than previously, many of which become available to seabirds as discards during commercial trawling operations. The drastic overfishing of mackerel has led to a major increase of sand eels stocks, but the fraction previously taken by this predatory fish (a summer visitor) is now removed by rapidly developing Danish and Norwegian industrial fisheries. The increased food supply (in terms of a greater proportion of fish of suitable size for seabirds) is thought to have been beneficial for seabirds and is suspected to have caused the dramatic expansion and growth of most populations of seabirds in the NE Atlantic over the last hundred years or so. Substantial increases have been recorded in breeding populations of a variety of seabirds, including surface feeders, scavengers, plunge divers, and pursuit diving birds (**Table 5**). Although it is now generally accepted that most of these birds have profited from the overfishing of large predatory fish (as piscivorous competitors), part of the increase will have been caused by the relaxation of persecution and exploitation of these species. As far as known, there has not been a large increase in populations of molluskivorous seaduck, nor in the more coastal piscivorous divers wintering in these waters, while the increase in the breeding population of the equally coastal and nonmigratory European shags *Stictocarbo aristotelis* has been modest.

Discussion and Conclusions

Fisheries and seabirds compete for the same resources and, although some aspects of human fisheries are beneficial for seabirds, several of the side-effects do great harm to birds. Some piscivorous seabirds are persecuted by fishermen because they are thought to deplete local fish stocks. However, fisheries probably always have greater effects on seabirds than vice versa and there are no examples of fish stock recoveries after an avian predator has been removed from an ecosystem. The annual losses of seabirds, most notably albatrosses, petrels, and several species of auks in longline fisheries and in drifting or bottom-set gill nets are immense. It has been suggested that the gross overfishing of large predatory fish over the last century has led to increases in the survival and stocks of young fish. There is circumstantial evidence, though there are few factual data, that seabirds have profited from this newly established and abundant food resource. There is little doubt that the production of discards (unwanted by-catch of small fish, unmarketable species of fish and benthic invertebrates) and offal (discarded waste of gutted marketable fish) in commercial fisheries is of great significance for some species of seabirds. Discards and offal benefit a group of 'scavenging' seabirds, by 'offering' prey that would otherwise be unavailable and out of reach for these birds. Catches by industrial fisheries, usually targeting the staple foods of marine predators such as seabirds, cetaceans, and seals, have increased dramatically over the last 40 years. Major crashes in (local) fish stocks are not usually attributed to industrial fisheries with certainty, but few of these fisheries are adequately managed such that havoc can actually be prevented. Several case

Table 5 General trends in sea bird populations in the North Sea

	Population	*Principal prey*	*Habitat*	*Trend*
Divers (or loons)	Winter	Fish	Coastal	Stable or decline
	Breeding	Fish	Inland	Decline
Northern fulmar	Breeding	Plankton, squid, fish, offal	Pelagic	Increase
Manx shearwater	Breeding	Fish, squid	Pelagic	Stable
European storm-petrel	Breeding	Plankton, nekton, small fish	Pelagic	Stable
Leach's storm-petrel	Breeding	Plankton, nekton, small fish	Pelagic	Stable or increase
Northern gannet	Breeding	Shoaling fish	Offshore	Increase
Great cormorant	Breeding	Fish	Coastal	Increase
European shag	Breeding	Fish	Coastal	Increase
Common eider	Breeding/winter	Mollusks	Coastal	Stable/slow increase
Common scoter	Winter	Mollusks	Coastal	Stable?
Velvet scoter	Winter	Mollusks	Coastal	Stable?
Arctic skua	Breeding	Robbing birds (fish)	Coastal	Stable or Increase
Great skua	Breeding	Fish, birds, discards	Offshore	Increase
Common gull	Breeding	Largely terrestrial	Coastal/land	Stable or increase
Herring gull	Breeding	Fish, mollusks, benthic inv., discards	Coastal	Increase, recent decline
Lesser black-backed gull	Breeding	Fish, discards	Offshore	Increase
Great black-backed gull	Breeding	Fish, birds, discards	Offshore	Stable
Black-legged kittiwake	Breeding	Fish	Pelagic	Increase
Sandwich tern	Breeding	Fish	Coastal	Slow increase
Common tern	Breeding	Fish	Coastal/land	Stable
Arctic tern	Breeding	Fish	Coastal/offshore	Increase
Common guillemot	Breeding	Fish	Offshore	Increase
Razorbill	Breeding	Fish	Offshore	Increase
Black guillemot	Breeding	Fish	Coastal	Stable?
Atlantic puffin	Breeding	Fish	Offshore	Gradual increase

studies have indicated that poor reproductive output in seabirds, mass mortalities due to starvation, or complete breeding failures in some breeding seasons could be attributed to fish stock depletion and probably to overfishing.

See also

El Niño Southern Oscillation (ENSO). El Niño Southern Oscillation (ENSO) Models. Fisheries: Multispecies Dynamics. Seabird Foraging Ecology.

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SEABIRDS AS INDICATORS OF OCEAN POLLUTION

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Background

As wide-ranging, upper and multi-trophic level consumers, marine birds can provide useful indication of ocean pollutants. Seabirds are the most visible marine animals, and individuals, chicks, and eggs are relatively easily sampled, often nonlethally, over wide oceanographic regions. Birds also appeal to the general public who often go to great lengths to protect them. Hence, there is opportunity to help preserve marine ecosystems by monitoring and protecting sea birds and the habitats and prey on which they depend.

Pollutants are assayed to measure levels or rates of change of environmental pollution and to assess biological effects including those on humans. Both nominal and ordinal (qualitative) and interval and ratio (quantitative) measurements are possible. However, physiological, behavioral, taxomonic, and seasonal variations can limit the usefulness of different avian assays in reflecting variation in environmental levels of ocean pollution. Quantitative assays can be problematic because pollutants and other environmental stresses frequently occur in combination in indicator organisms, so it is often difficult or impossible to delineate the effects of a specific pollutant. The problem is complicated when different pollutants have synergistic or additive effects. Hence, determining the most appropriate assay for a pollutant to be monitored and then calibrating the assay are critical problems in all bio-monitoring programs.

Pelagic seabirds such as albatrosses and petrels can provide information on oceanic food webs, whereas coastal and littoral species such as auks and terns can provide information on inshore trophic interactions. Birds that feed at different trophic levels, such as gannets on large pelagic fishes, cormorants on benthic fishes, and sea ducks on bivalves, can be targeted to address different monitoring questions.

Many problems associated with pollution in the ocean are the result of nontarget organisms being affected by chemical management tools. Agricultural and forestry practices have been major sources of organochlorine and of other pesticide and herbicide treatments that affect birds and other nontarget organisms. Assays using marine birds also yield information about industrial chemicals, heavy metals and radionuclides. Pollutant levels reflect toxin sources in regional as well as local environments and are frequently high in estuaries and adjacent waters. Moreover, many chemical and metal pollutants are transported atmospherically, as well as aquatically, over great distances from contact zones – often to pristine polar regions. The movements of contaminated animals can also carry pollutants from source interactions to distant sites. Marine oil pollution is a global problem that results from both highly publicized spills and more extensively from long-term chronic low levels of illegal discharges. In both of these situations, research with seabirds has provided scientists with a means of studying and quantifying biological effects and of raising public awareness and concern about ocean health. Discarded and lost fishing gear and plastics are relatively recent and highly persistent sources of marine pollution that are increasing with expanding global use.

History

Widespread uses of synthetic chemicals following World War II rapidly created environmental