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Comparison of assemblages and some life-history traits of seabirds in the Humboldt and Benguela systems

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There are 21 and 15 species of seabirds that breed in the Humboldt and Benguela upwelling systems respectively. Only two species of gull are common to both systems, one as an endemic subspecies to the Benguela system. Eleven species and two subspecies are endemic (or nearly so) to the Humboldt system; seven species and one subspecies to the Benguela system. Each system has an endemic penguin, sulid, cormorant and tern that feed mainly on anchovy *Engraulis* spp., sardine *Sardinops sagax* or both these fish. The Peruvian pelican *Pelecanus thagus* also feeds primarily on these prey items. A plentiful availability of food has resulted in many of these seabirds attaining high levels of abundance. For the four pairs of species that feed on anchovy and sardine, those in the Humboldt system all have a biology that enables them to increase more rapidly than their Benguela counterparts. This reflects the higher frequency of environmental perturbations that depress seabird populations in the Humboldt system. In addition, both systems have a small endemic cormorant that feeds near the coast and a small endemic tern that breeds in the adjacent mainland desert and feeds at the sea surface. Several seabirds endemic to a system have no obvious ecological equivalent in the other system: the pelican, a diving-petrel, four storm-petrels and a gull in the Humboldt system; a cormorant and a gull in the Benguela system. Some species with tropical or subantarctic affinities breed at the boundaries of the systems. Others breed also in freshwater systems. The grey gull *Larus modestus*, which feeds in the Humboldt system, breeds in montane deserts.

Keywords: anchovy, Benguela, demographic parameter, environmental perturbation, Humboldt, sardine, seabird assemblage

Introduction

The Humboldt and Benguela upwelling ecosystems off the coasts of western South America and western southern Africa respectively are those of the world's four major eastern boundary current systems that are located in the Southern Hemisphere (Parrish *et al*. 1983). The faunas of the two systems are similar in many respects. Their fish assemblages include anchovy *Engraulis ringens* and *E. encrasicolus*, sardine *Sardinops sagax*, horse (jack) mackerels *Trachurus murphyi* and *T. trachurus*, chub mackerel *Scomber japonicus* and hakes *Merluccius* spp. (Crawford 1987, 1991). There are also similarities in the seabirds found in the two systems (Hutchinson 1950, Crawford and Jahncke 1999).

It is thought that comparative studies of ecosystems in which anchovy and sardine are abundant may elucidate their functioning and hence assist in their management (Parrish *et al*. 1983, Schwartzlose *et al*. 1999). The conservation of marine ecosystems is an objective of South Africa's Marine Living Resources Act of 1998 (Crawford 2004). An ecosystem approach to fisheries management has been advocated by the World Summit on Sustainable Development and other agreements (FAO 2003). In this paper, we compare the seabird assemblages of the Humboldt and Benguela systems and some life-history traits of some of their dominant seabirds, in an attempt to gain insight into similarities and differences in the functioning of the two systems. The Humboldt system is assumed here as extending from the north of Peru to about 42°S and the Benguela system as extending from southern Angola to Algoa Bay on South Africa's south coast (Schwartzlose *et al*. 1999). The investigation has been based on a survey of the literature, as well as on some unpublished information for seabirds in the Humboldt system.

Assemblages of Breeding Seabirds

There are 21 species of seabird that breed in the Humboldt upwelling system and 15 that breed in the Benguela system.

These are listed in Table 1, which shows those species that are endemic (or nearly so) to each system, or that occur more widely, and those that may or may not be regarded as ecologically equivalent in the two systems. There is some subjectivity in assigning a species as nearly endemic. We did not use any quantitative measure of ecological equivalence but the based classification on the relative abundances, breeding and feeding habits of the various species. This approach also has an element of subjectivity. In instances, body size or mass were compared. Several other characters could also be used to compare species, including bill length, size of prey eaten, seasonal pattern of breeding, breeding habitat and colony size, but for this preliminary consideration we did not collate information on these aspects.

Both the Humboldt and Benguela systems have an endemic penguin (Humboldt penguin *Spheniscus humboldti*, African penguin *S. demersus*), sulid (Peruvian booby *Sula variegata*, Cape gannet *Morus capensis*) and cormorant (guanay cormorant *Phalacrocorax bougainvillii*, Cape cormorant *P. capensis*) that were previously, or are still, abundant and that feed mainly on anchovy and sardine (Matthews 1961, Berry 1976, Crawford and Shelton 1978, Duffy 1983, Hays 1986, Berruti *et al*. 1993, Crawford and Dyer 1995, Jahncke and Goya 1997a, 1998b, Adams and Klages 1999, Zavalaga and Paredes 1999) — equivalents are listed first for the Humboldt system and then for the Benguela system. Additionally, both systems have an endemic tern that also feeds mainly on anchovy or sardine (Inca tern *Larosterna inca*, swift tern *Sterna bergii bergii*, which is endemic as a subspecies to southern Africa) (Walter *et al*. 1987, Cooper *et al*. 1990, Crawford and Dyer 1995, del Hoyo *et al*. 1996, Zavalaga 1997). The guanay cormorant (71–76cm) is larger than the Cape cormorant (61–64cm), whereas the Peruvian booby (71–76cm) is smaller than the Cape gannet (81–90cm) (del Hoyo *et al*. 1992) and the Inca tern (180–210g) is smaller than the swift tern (320–400g) (del Hoyo *et al*. 1996). The Inca tern breeds in crevices (Velando and Márquez 2002), whereas the swift tern breeds in colonies on the ground (Cooper *et al*. 1990).

In both systems there is an endemic (or nearly so) cormorant that is not abundant, breeds in small colonies and feeds mainly on fish in intertidal and shallow (<10m) water, especially on benthic prey (red-legged cormorant *P. gaimardi*, which extends into Argentina, and crowned cormorant *P. coronatus*) (Williams and Cooper 1983, del Hoyo *et al*. 1992, Johnsgard 1993, Zavalaga *et al*. 2002, Gandini *et al*. 2005). The red-legged cormorant (71–76cm) is larger than the crowned cormorant (54cm). Both systems also have an endemic small tern that feeds inshore near the sea surface mainly on small fish, including anchovy, and breeds mostly in the adjoining mainland desert (Peruvian tern *S. lorata*, Damara tern *S. balaenarum*) (Clinning 1978, Simmons and Braine 1994, del Hoyo *et al*. 1996, Simmons *et al.* 1998, Vilina 1998).

Species that are endemic (or nearly so) to the Humboldt system (del Hoyo *et al*. 1992, 1996, Garciá-Godos *et al*. 2002) but that have no obvious counterparts in the Benguela system include the Peruvian diving-petrel *Pelecanoides garnotii*, Markham's storm-petrel *Oceanodroma markhami*, Hornby's storm-petrel *O. hornbyi*, Peruvian pelican *Pelecanus thagus* and band-tailed (Belcher's) gull *Larus belcheri*. Additionally, subspecies of Elliot's storm-petrel *O. gracilis gracilis* and wedge-rumped storm-petrel *O. tethys kelsalli* are endemic to the Humboldt system (Schlatter and Marin 1983, Ayala *et al*. 2004).

Table 1: Seabirds that breed in the Humboldt and Benguela systems (based on information in Cooper *et al*. 1984, Duffy *et al*. 1984, Schlatter 1984). Those endemic, or nearly so, are indicated, as well as those thought to be ecologically equivalent in the two systems

Humboldt system	Benguela system
Endemic or nearly endemic	
Ecologically equivalent	
Spheniscus humboldti	*Spheniscus demersus*
Sula variegata	*Morus capensis*
Phalacrocorax bougainvillii	*Phalacrocorax capensis*
Phalacrocorax gaimardi	*Phalacrocorax coronatus*
Larosterna inca	*Sterna bergii bergii*
Sterna lorata	*Sterna balaenarum*
Not ecologically equivalent	
Pelecanoides garnotii	
Oceanodroma markhami	
Oceanodroma hornbyi	
Oceanodroma gracilis gracilis	
Oceanodroma tethys kelsalli	
Pelecanus thagus	
	Phalacrocorax neglectus
Larus belcheri	
	Larus hartlaubii
Not nearly endemic	
Ecologically equivalent	
Phalacrocorax olivaceous	*Phalacrocorax lucidus*
Larus dominicanus	*Larus dominicanus*
Larus cirrocephalus	*Larus cirrocephalus*
Not ecologically equivalent	
Spheniscus magellanicus	
	Oceanodroma leucorhoa
	Pelecanus onocrotalus
Sula nebouxi	
Sula granti	
Larus modestus	
Sterna hirundinacea	
	Sterna caspia
	Sterna dougallii

The Peruvian diving-petrel's main colonies are located at two islands in central Peru with a maximum population of 13 000 pairs (Jahncke and Goya 1998a). About 1 700 pairs breed at three islands in north-central Chile (Simeone *et al*. 2003). It is observed close to the coast (Brown 1981), where it feeds during the day, primarily on zooplankton or small larval fish (Jahncke and Goya 1999). It can dive to 83m but for most dives the maximum depth attained is from 10m to 50m (Zavalaga and Jahncke 1997).

Markam's storm-petrel breeds on the Paracas Peninsula and at islands off the central Peruvian coast (Jahncke 1993). It feeds on small fish, including anchovy and myctophids, cephalopods and crustaceans, mainly the swarming

planktonic pelagic squat lobster *Pleuroncodes monodon* (Garciá-Godos *et al*. 2002). Dietary information suggests feeding both inshore and offshore, including nocturnal foraging on fish that migrate to the surface at night. It may scavenge dead cephalopods floating on the surface and from carcasses of southern sea lions *Otaria byronia* (Garciá-Godos *et al*. 2002). Some 90% of individuals seen at sea are beyond the continental shelf, up to 360km offshore (Garciá-Godos *et al*. 2002).

The localities where Hornby's storm-petrel breeds are unknown. It may breed in coastal desert, possibly well inland (del Hoyo *et al*. 1992). No nest of this species has been found in Peru or Chile. However, several fledglings that could fly but still retained down on the belly were seen at Punta San Juan, Peru (CBZ pers. obs.). The species normally occurs in warmer water away from the coast (Brown 1981) and feeds mostly on the wing, by pattering, dipping and snatching prey from the surface (del Hoyo *et al*. 1992). It has been observed scavenging from carcasses of southern sea lions (Garciá-Godos *et al*. 2002).

Elliot's storm-petrel breeds in Chile (Schlatter and Marin 1983, Hertel and Torres-Mura 2003) and may breed in Peru. The nominate race is distributed from southern Ecuador to central Chile, over the continental shelf and inshore when breeding but in pelagic waters after breeding. It follows trawlers and associates with cetaceans and probably feeds on small fish and crustaceans (del Hoyo *et al*. 1992). The wedge-rumped storm-petrel breeds at several islands off Peru (Ayala *et al*. 2004) and one off north-central Chile (Simeone *et al*. 2003). It occurs in warmer water offshore (Brown 1981) and ranges south to Chile and north as far as USA (Ayala *et al*. 2004). It feeds on neuston by surface-seizing (del Hoyo *et al*. 1996, Ribic *et al*. 1997).

The Peruvian pelican is abundant in the Humboldt system (Crawford and Jahncke 1999). Anchovy and sardine form a major component of its diet (Jordán and Fuentes 1966). It feeds by plunge-diving (Johnsgard 1993). It also encircles shoals of anchovy in bays along the Peruvian coast in places where the water depth is <c. 5m (M Niquen, Instituto del Mar del Peru, pers. comm.). It takes fish discarded by trawlers and by artisanal fishers and may feed at night (EG pers. obs.).

The band-tailed gull (48–52cm) is smaller than the kelp gull *L. dominicanus* (54–65cm) but larger than Hartlaub's *L. hartlaubii* (37–39 cm) and grey-headed *L. cirrocephalus* gulls (38–43cm) (del Hoyo *et al*. 1996). It feeds on anchovy, invertebrates, pelagic squat lobster and on the eggs and chicks of other seabirds (Johnsgard 1993, Williams 1995, del Hoyo *et al*. 1996). In central Peru it is more abundant than the kelp gull, but it is considerably less common than the latter species in Chile (del Hoyo *et al*. 1996).

Two seabirds endemic to the Benguela region have no obvious equivalents in the Humboldt system: bank cormorant *Phalacrocorax neglectus* and Hartlaub's gull. Most bank cormorants breed at two islands in southern Namibia, where pelagic goby *Sufflogobius bibarbatus* forms the major portion of their diet (Cooper 1981, Crawford *et al*. 1985). In regions where pelagic goby is not plentiful, colonies of bank cormorants are smaller and the species feeds on Cape rock lobster *Jasus lalandii*, molluscs and fish taken near the seabed (Rand 1960, Avery 1983).

The Hartlaub's gull is a small gull that feeds on small fish, zooplankton and intertidal invertebrates, especially those associated with kelp *Ecklonia maxima*. Recently, food made available by human activities has become increasingly important in its diet (Ryan 1987, Steele 1992).

Kelp gulls and grey-headed gulls are common to the two systems. In the Benguela system, the former is endemic as a subspecies (Hockey *et al*. 2005). Grey-headed gulls breed only in small numbers in Peru and the Benguela system (Brooke *et al*. 1999, CBZ pers. obs.). Both the Humboldt and Benguela systems also have a cormorant that feeds in freshwater and in the inshore marine environment (olivaceous or Neotropical cormorant *P. olivaceous*, white-breasted cormorant *P. [carbo] lucidus*) (Rand 1960, Whitfield and Blaber 1979, Johnsgard 1993, Randall *et al*. 2002).

In its north, the Humboldt system additionally supports two boobies (blue-footed *Sula nebouxi* and Nazca *S. granti*) with tropical affinities (Duffy *et al*. 1984, Jahncke and Goya 1997b, Figueroa 2004). Male greater frigatebirds *Fregata magnificens* were seen displaying at Tumbes in northern Peru (Duffy *et al*. 1984), but breeding has not been confirmed. The Magellanic penguin *Spheniscus magellanicus* breeds in southern Chile (Schlatter 1984). The South American tern *Sterna hirundinacea* bred at Isla Santa Rosa and Isla La Vieja, central Peru. Human disturbance led to the extinction of the latter colony after 1996 (CBZ pers. obs.).

The grey (or gray) gull *Larus modestus* breeds 35–100km inland in barren montane deserts, which it crosses to feed on crabs, fish, worms and offal along the littoral zone of sandy coastal beaches (Howell 1982, Ryan *et al.* 1987, Guerra *et al*. 1988a, del Hoyo *et al*. 1996). In Chile, grey gulls did not breed following the 1982/83 El Niño, thought to be a result of decreased availability of anchovy in coastal waters (Guerra *et al*. 1988b). The inland-breeding Andean gull *L. serranus* rarely visits the coast (del Hoyo *et al*. 1996) and is not regarded as marine. Similarly, black skimmers *Rinchops níger*, which breed in Peru in the tropical rainforest and in the Andes, are not regarded as marine, although they are common along the coast in summer.

The Benguela system supports small numbers of breeding Leach's storm-petrel *O. leucorhoa* (c. 25 pairs), a species that is not known to breed elsewhere in the Southern Hemisphere but is abundant in the Northern Hemisphere, great white pelicans *Pelecanus onocrotalus*, Caspian terns *Sterna caspia* and roseate terns *S. dougallii* (Crawford *et al*. 1981, 1991, 1995a, Underhill *et al*. 2002). Larger numbers of Leach's storm-petrel visit the Benguela system in the austral summer, occurring in highest densities offshore (Underhill *et al*. 2002). They feed at the surface on small fish, squid and crustaceans by surface-seizing and dipping. Feeding takes place by day and night (del Hoyo *et al*. 1996, Hockey *et al*. 2005).

Great white pelicans scavenge food along the shoreline and at farms, feed at inland water bodies and eat eggs and nestlings of other seabirds (Berry and Berry 1975, Berry 1976, Guillet and Crowe 1983, Crawford *et al*. 1995a). Caspian terns feed in sheltered bays and estuaries (Velasquez *et al*. 1990, Hockey *et al*. 2005). Great white pelicans and Caspian terns also breed at inland water bodies in southern Africa and farther north, as do white-breasted

cormorants and grey-headed gulls (Cooper *et al*. 1992, Hockey *et al*. 2005). The roseate tern breeds at three localities in the southern Benguela system, which are influenced by the warm Agulhas Current (Tree and Klages 2003).

Life-history Traits

Age at first breeding, clutch size and the maximum number of successful broods pairs can raise each year are compared in Table 2 for the four pairs of seabirds in the Humboldt and Benguela systems that are thought to be ecologically equivalent, and for which anchovy or sardine form a major portion of the diet.

These parameters are similar for the penguins and cormorants, although African penguins may defer first breeding until an age of six years (Whittington 2002). The Peruvian booby has a lower age at first breeding and larger clutch than the Cape gannet. It produces 1.75 fledged chicks per pair per year, compared with 0.80 for the Cape gannet (Jarvis 1974, Nelson 1978, 2002). The Inca tern has a larger clutch than the swift tern and is able to produce two broods per year, compared with one for the swift tern (Dunlop 1985, Higgins and Davies 1996, Velando and Márquez 2002).

Discussion

In all, nine pairs of seabird are thought to be ecologically equivalent in the Humboldt and Benguela systems, including four pairs (endemic penguins, sulids, cormorants and terns) that feed predominately on small shoaling epipelagic fish species such as anchovy and sardine; a pair of endemic small cormorants; a pair of endemic small terns; a pair of larger, more widespread cormorants that are able also to feed in freshwater; and kelp and grey-headed gulls, which are the only species that breed in both systems.

Although some species, such as Humboldt and African penguins, have suffered major declines in abundance (Hays 1986, Crawford *et al*. 1995b), in terms of numbers, those seabirds that feed mainly on the abundant anchovy and sardine continue to dominate the avifaunas of the two systems (Duffy *et al*. 1984, Crawford *et al*. 1991). These birds have sustained substantial guano harvests over periods of more than a century (Hutchinson 1950, Crawford and Jahncke 1999). This reflects the abundant food source that is provided by the anchovy and sardine. The Humboldt and Benguela systems also have similar niches for some less abundant seabirds, e.g. for the red-legged and crowned cormorants, which are intertidal and shallow-water feeders, and the Peruvian and Damara terns, which are desert-breeding surface feeders.

The 12 species of seabird that breed in the Humboldt system, for which no obvious equivalent exists in the Benguela system, include a penguin that is found in the south, an endemic diving-petrel, four storm-petrels (two endemic as species, two as subspecies), an endemic pelican, two tropical pelecaniform birds that occur in the north, an endemic medium-sized gull, a desert-nesting gull, and a tern.

The six seabirds that breed in the Benguela system but that do not have a counterpart in the Humboldt system include a storm-petrel that is abundant in the northern hemisphere, an endemic cormorant, an endemic small gull, a small tern that breeds at three localities influenced by the warmer Agulhas Current, and the great white pelican and Caspian tern that also breed and feed to the east and north in freshwater environments.

If species that occur at the extremities of the systems (blue-footed and Nazca boobies and Magellanic penguin in the Humboldt system; roseate tern in the Benguela system) or that also breed and feed in adjacent freshwater systems (great white pelican and Caspian tern in the Benguela system) are discounted, there remain nine species in the Humboldt system and three in the Benguela system for which no obvious equivalents exist in the other system.

There may be some equivalence in the feeding strategies of the storm-petrels in the two systems, but the diversity and numbers of breeding birds are clearly much lower in the Benguela than in the Humboldt system. All four storm-petrels in the Humboldt system forage offshore, Markham's storm-petrel also feeding inshore. In the Benguela system, Leach's storm-petrel also feeds mainly offshore (Underhill *et al*. 2002). In the Humboldt system, there is a wide shelf at Chimbote with strong offshore Ekman transport and

Table 2: Comparison of some demographic parameters for the four pairs of seabirds in the Humboldt and Benguela systems that feed to a large extent on anchovy and sardine

Species	Age at first breeding (year)	Usual clutch size	Maximum number of successful broods per year
Spheniscus humboldti	3–4[a]	2[b]	2[c]
S. demersus	3–6[d,e,f]	2[g]	2[e,h]
Sula variegata	2[i]–3	3[i]	1[j]
Morus capensis	3–4[k]	1[l]	1[l]
Phalacrocorax bougainvillii	2[m]	3[m]	2[m]
P. capensis	2[n]	3[o]	2[p]
Larosterna inca		2[q]	2[r]
Sterna bergii	3–6[s]	1[s]	1[t]

[a] Guerra and Oyarzo (1992) cited by Ellis *et al*. (1998)
[b] Williams (1995)
[c] Paredes *et al*. (2002)
[d] Randall (1983)
[e] Crawford *et al*. (1999)
[f] Whittington (2002)
[g] Williams and Cooper (1984)
[h] Randall and Randall (1981)
[i] Nelson (1978)
[j] Nelson (2002)
[k] Crawford (1999)
[l] Jarvis (1974)
[m] Johnsgaard (1993)
[n] Crawford *et al*. (2001)
[o] Berry (1976)
[p] RJMC (unpublished information)
[q] del Hoyo *et al*. (1996)
[r] Velando and Márquez (2002)
[s] Crawford *et al*. (2002)
[t] Dunlop (1985)

upwelling (Parrish *et al*. 1983). The four endemic storm-petrels are abundant at the edge of this shelf (Brown 1981).

The Peruvian pelican (c. 3.5kg, del Hoyo *et al*. 1992) feeds mainly on anchovy and sardine. Hence, the Humboldt system has five species of seabird that subsist mainly on these fish, compared with four in the Benguela system. The biomass and purse-seine harvests of anchovy and sardine have been substantially higher in the Humboldt system than in the Benguela system (Schwartzlose *et al*. 1999). The larger size of the great white pelican (9–15kg, del Hoyo *et al*. 1992), a marginal species in the Benguela system, does not permit it to feed by plunge-diving, as does the Peruvian pelican, and consequently it has not been able to exploit anchovy and sardine to any great extent.

The Peruvian diving-petrel and the bank cormorant are both able to feed at some depth in the water column. The pelagic goby, which is the main prey of much of the bank cormorant population, occurs in an area of intense upwelling between the Benguela's northern and southern stocks of anchovy and sardine (Crawford *et al*. 1985) and has no equivalent in the Humboldt system. The world has four species of diving-petrel, of which three are found at subantarctic latitudes (del Hoyo *et al.* 1992). The extension of the South American continent to subantarctic latitudes may have enabled the Peruvian diving-petrel to colonise the Humboldt system. The African continent does not extend as far south.

The Humboldt system has two gulls (band-tailed, grey) and one tern (South American) without obvious equivalents in the Benguela system. The grey gull breeds in a desert environment, similarly to the Peruvian and Damara terns. The Benguela system has one gull (Hartlaub's) that has no distinct equivalent in the Humboldt system. However, the grey gull feeds on similar prey along the coastline.

In the Humboldt system, El Niños cause a greatly reduced availability of anchovy and sardine to seabirds. Those seabirds feeding on these fish species respond by changing their diet, terminating breeding and dispersing to the south or north. Nests may be flooded and there may be substantial mortality through starvation (Schreiber 2002, Simeone *et al*. 2002). In the Benguela system, Benguela Niños have a similar impact on food fish off Namibia (Boyer and Hampton 2001). The El Niños of the Humboldt system occur at a much greater frequency than the Benguela Niños. In the former, there were 54 El Niños between 1726 and 1998 (Schreiber 2002), so that these events occurred on average every five years. By contrast, there were four Benguela Niños between 1963 and 1995, at intervals of about 10 years (Binet *et al.* 2001).

In two of four comparisons of seabirds that feed predominately on anchovy and sardine, the life-history parameters of species in the Humboldt system (Peruvian booby, Inca tern) provide an ability to increase more rapidly than their counterparts in the Benguela system (Cape gannet, swift tern). Although the Humboldt penguin and African penguin have similar life-history parameters, it appears that the Humboldt penguin double broods more frequently than does the African penguin when feeding conditions are favourable (Crawford *et al*. 1999, Paredes *et al*. 2002, 2003, Simeone *et al*. 2003). Similarly, the guanay cormorant, unlike the Cape cormorant (Berry 1976), will often raise two broods in a season (Johnsgaard 1993), although Nelson (2005) states that, while this may be possible, no firm evidence for raising two broods in a year exists. Therefore, in all four comparisons, the Humboldt species has the potential to increase more rapidly than its Benguela equivalent. This is necessary given the more frequent occurrence in the Humboldt system of unfavourable environmental perturbations, which depress the seabird populations there. The ability to increase rapidly has permitted some stability in the Humboldt seabird populations (Duffy and Siegfried 1987). Should an altered climate or fishing increase the frequency of troughs in the abundance of food in the Benguela system, its seabirds would not have the same ability to recover and may decrease in the long-term.

The Cape cormorant is, to a large extent, dependent on anchovy (Crawford *et al*. 1992b), which, similarly to anchovy in the Humboldt system, has a highly variable abundance (Schwartzlose *et al*. 1999). As does the guanay cormorant when food is scarce (Hutchinson 1950), the Cape cormorant may abandon breeding colonies *en masse* (Crawford *et al*. 1992b, Crawford and Jahncke 1999). Stress, such as that caused by food scarcity, may lead to heavy mortality of Cape cormorants from disease (Crawford *et al*. 1992a). Guanay cormorants also suffer high mortality during food scarcity (Tovar *et al*. 1987, Jahncke 1998).

Age-at-maturity and mean size of clutches are similar for Peruvian booby and guanay cormorant. However, the guanay cormorant is able to produce more broods per year (Table 2). It also breeds in bigger colonies than the Peruvian booby. This may lead to a higher reproductive success, through reduced loss of eggs and chicks to predators (Hutchinson 1950), and an ability to dominate when anchovy is available in large quantities, as it was before the introduction of the purse-seine fishery. Guanay cormorants feed in immense flocks that are generally larger than those of Peruvian boobies (Hutchinson 1950, Johnsgard 1993). Since the commencement of the purse-seine fishery, the catch of anchovy has negatively impacted the numbers of guanay cormorants (Crawford and Jahncke 1999). The Peruvian booby has had a more stable population since the introduction of the purse-seine fishery on anchovy and sardine (Crawford and Jahncke 1999).

Although the Humboldt and Benguela systems have many similarities in their seabird faunas, especially in the abundant species that feed on the plentiful anchovy and sardine, and also amongst some less numerous species, there are some noticeable differences. Humboldt seabirds feeding on anchovy and sardine generally have a demography that enables them to recover more rapidly from population decreases that are caused by the frequent El Niño perturbations. The Humboldt system has a group of endemic storm-petrels that feed offshore in surface waters, a diving-petrel and a pelican that eats shoaling pelagic fish, for which no equivalents exist in the Benguela system. Conversely, the Benguela system has the bank cormorant, which feeds in midwater as well as on the seabed, and for which there is no counterpart in the Humboldt system. Some gulls occur in both systems, but there are differences among those that do not. Several seabirds enter both systems at their boundaries.

More comparative studies, e.g. on demographic parameters of other species, prey eaten, foraging distributions and breeding patterns, can be expected to provide further insights into the functioning of the two systems. However, it is clear that Humboldt seabirds are adapted to a variable environment and to exploit the abundant epipelagic food resources of that system, which may extend far offshore. Benguela seabirds are suited to a more stable supply of food. Therefore, management of their prey should aim to avoid increasing variability in their food supply.

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