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JELLYFICATION OF MARINE ECOSYSTEMS AS A LIKELY CONSEQUENCE OF OVERFISHING SMALL PELAGIC FISHES: LESSONS FROM THE BENGUELA

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ABSTRACT

Changes in two contrasting ecosystems of the Benguela upwelling region, one dominated at mid-trophic level by jellyfishes (Namibia, northern Benguela ecosystem, where small pelagic fish abundance has been severely depleted) and one still dominated by small pelagic fishes (South Africa, southern Benguela) were compared in an effort to determine ecosystem trajectories under different exploitation regimes. The role of small pelagic fishes (clupeoids) was highlighted in the context of their importance in maintaining interactions in marine ecosystems. In particular, we examined trophic cascades and possible irreversible changes that promote the proliferation of jellyfishes in marine systems. We found that the presence of large populations of small pelagic fishes has a fundamental role in preserving beneficial trophic interactions in these marine ecosystems. The implications of trophic cascades, such as those observed in the northern Benguela, for ecosystem-based management were apparent. In addition, this comparison provides contrasting case studies to inform the development of management scenarios that avoid ecosystem shifts that affect predators and reduce the value of fisheries production.

Considerable attention has been given in the last decade to the perceived increases in jellyfish populations and frequency of jellyfish outbreaks worldwide, and their potential causes (Arai 2001, Brodeur et al. 2002, Parsons and Lalli 2002, Attrill et al. 2007, Purcell et al. 2007, Richardson et al. 2009, Brotz et al. 2012). Because these outbreaks have negative impacts on many human activities and can affect the functioning of marine ecosystems (Purcell et al. 2007, Richardson et al. 2009), identifying and mitigating the effects of the potential human causes of increased jellyfish abundance (Hay 2006, Richardson et al. 2009) has become a research focus with important management implications. Of the many possible such causes (ranging from global climate change to coastal developments), those linked to the trophic impacts of overfishing are of particular concern, as most marine ecosystems have been profoundly modified by fishing (see e.g., Pauly et al. 1998). As attempts are made to implement an ecosystem approach to fisheries to improve the sustainability of world fisheries (FAO 2001, 2003, Pauly et al. 2002, Pikitch et al. 2004), and jellyfishes are now often viewed as a threat to fishing, the potential linkages between fisheries and jellyfish populations are increasingly relevant.

The northern Benguela (NB) ecosystem is often highlighted as an example of a system where increased jellyfish abundance may have resulted from overfishing (Bakun and Weeks 2006, Lynam et al. 2006, Richardson et al. 2009, Utne-Palm et al. 2010, Jensen et al. 2012). Although the southern Benguela (SB) has also been

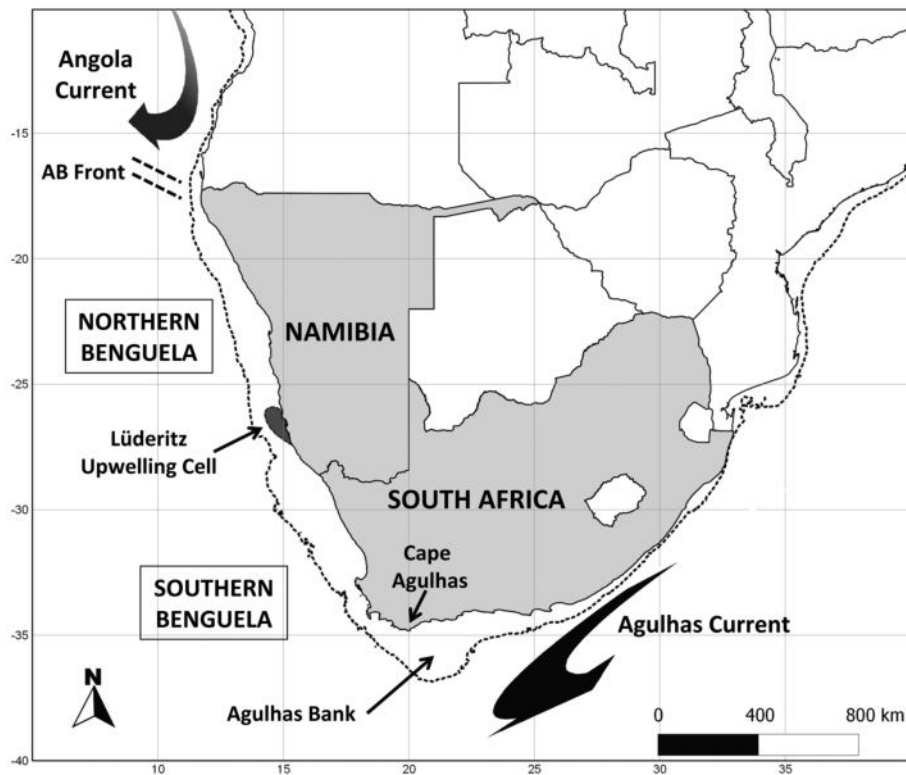


Figure 1. Map of the Benguela Current region bordering Namibia and South Africa, showing the 500-m depth contour (dashed line) and the approximate locations of the Angola Current, the Angola/Benguela (AB) Front, the Lüderitz upwelling cell (which separates the northern and southern Benguela subsystems), and the Agulhas Current.

substantially fished over the past six decades, jellyfish have not increased there. The ecosystem structures and catch histories of both the northern and southern parts of the Benguela Current ecosystem have been relatively well studied, and a comparison of these systems provides an excellent opportunity to determine how the effects of fishing might have caused the present state of jellyfishes dominance in the northern part.

The Benguela Current system is one of the world's four major eastern boundary upwelling ecosystems and, as is typical of these systems, is highly dynamic and characterized by wind-driven coastal upwelling and resultant high productivity (Fréon et al. 2009). Located off the southwestern coast of Africa (Fig. 1), it lies between the warm, temperate Agulhas Current in the south and the warm, subtropical Angola Current in the north and is divided into southern and northern subsystems by a permanent, and the world's strongest (Bakun 1996), upwelling cell at Lüderitz (about 27°S). The SB off South Africa is further divided into a coastal upwelling system off the west coast, characterized by seasonal, wind-driven upwelling at discrete centers and moderate to high productivity, as well as a temperate shallow shelf system (the Agulhas Bank) off the south coast that shows seasonal stratification and mixing, coastal, shelf-edge and dynamic upwelling, moderate productivity, and a well-oxygenated shelf (Hutchings et al. 2009a). The NB (Namibian) shelf is a typical coastal

upwelling system characterized by almost continuous upwelling and high productivity, but subject to widespread oxygen depletion and occasional hydrogen-sulphide eruptions (Bakun and Weeks 2004), arising from both local and remote forcing. Reviews of important processes and characteristics of the Benguela Current ecosystem can be found in Shannon et al. (2006).

Also typical of eastern boundary upwelling ecosystems, the Benguela is (or was; see below) characterized by large populations of a few small pelagic fish species [Pacific sardine, *Sardinops sagax* (Jenyns, 1842); European anchovy, *Engraulis encrasicolus* (Linnaeus, 1758); and to a lesser extent Whitehead's round herring, *Etrumeus whiteheadi* Wongratana, 1983]. These species provide the crucial link between lower and upper trophic levels and are the forage for a variety of top predators in the ecosystem, including seabirds [e.g., African Penguin, *Spheniscus demersus* (Linnaeus, 1758), and Cape Gannet, *Morus capensis* (Lichtenstein, 1823)], marine mammals [e.g., Cape fur seal, *Arctocephalus pusillus pusillus* (Schreber, 1775)], and piscivorous fishes (Cury et al. 2000). Small pelagic fishes are also the target of commercial industrial fisheries in the NB and SB, as are other species such as Cape hake, *Merluccius capensis* Castelnau, 1861; deepwater hake, *Merluccius paradoxus* Franca, 1960; and Cape horse mackerel or maasbanker, *Trachurus capensis* Castelnau, 1861. A variety of other fish species, and crustaceans such as Cape rock lobster [*Jasus lalandii* (H. Milne-Edwards, 1837)], are also exploited in the two regions.

Fisheries for small pelagics, hakes, and Cape horse mackerel have been established in the SB since before 1950, and although purse-seining for small pelagics in the NB also started over 60 yrs ago, demersal and midwater trawling for the other species only started there in the mid- to late 1960s (Boyer and Hampton 2001, van der Lingen et al. 2006). Whereas annual catches and the relative species composition of these three groups in the SB have been relatively stable through time, however, those for the NB have not (Fig. 2).

Small pelagic fishes have almost completely disappeared from the NB, and their removal has had substantial, and possibly irreversible, impacts on the structure and functioning of that ecosystem (Cury and Shannon 2004, Bakun and Weeks 2006), including an increase in jellyfishes and bearded or pelagic goby, *Sufflogobius bibarbatus* (von Bonde, 1923), and possibly Cape horse mackerel.

In this paper we first review our current knowledge of jellyfishes in the Benguela and evidence of their increase and its timing in the NB. We then compare the faunal trajectories of the main fisheries resources as well as some top predators since the establishment of the industrial fisheries in the Southern and Northern Benguela subsystems. We further compare updated time series of trophodynamic indicators estimated for the two systems and highlight the differences. We then examine trophic interactions between some predators and their prey base and highlight the effects that overfishing small pelagic fishes have had on high trophic levels. We review the results of trophic (food web) models with respect to the role of small pelagic fishes in the Benguela food web and the possible effect of overfishing and links with jellyfishes to assess how the removal of small pelagic fishes from the NB may have affected trophic function and productivity patterns. Finally we conclude by suggesting that a conservative approach to management of small pelagic fisheries should be considered in order to avoid such a detrimental ecosystem shift in other regions.

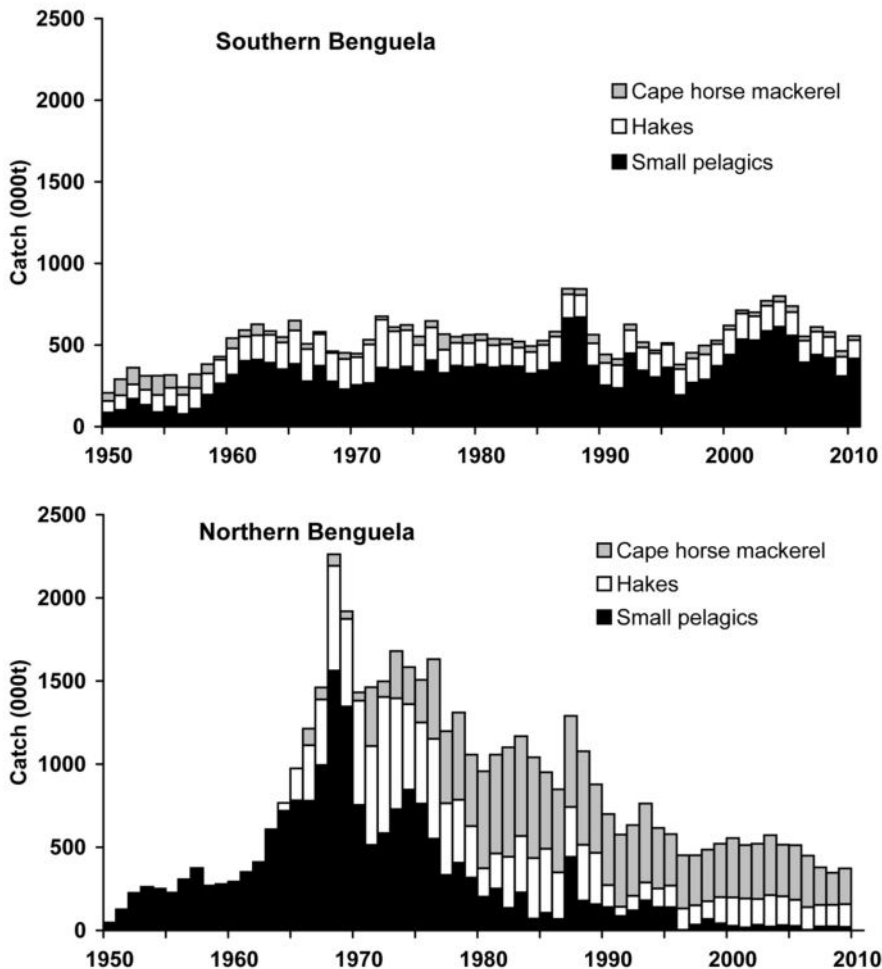


Figure 2. Annual combined catches of small pelagic fish, Cape hakes, and Cape horse mackerel in the southern and northern Benguela ecosystems, 1950–2010, in thousands of metric tons.

JELLYFISHES IN THE BENGUELA

The jellyfishes we refer to here, in the context of the Benguela, are two large medusae (Cnidaria, Medusozoa), *Aequorea forskalea* Péron and Lesueur, 1810, in the class Hydrozoa, and *Chrysaora fulgida* (Reynaud, 1830), in the class Scyphozoa. Traditionally the term also includes ctenophores, but the latter are relatively uncommon in the region. Although *A. forskalea* and *C. fulgida* belong to different classes, they both have metagenic life histories; i.e., their generations alternate between a large, conspicuous and pelagic medusa phase that is responsible for sexual reproduction and dispersal and a minute, cryptic, and benthic polyp phase that produces new medusae by asexual reproduction.

Medusae are planktivorous carnivores that feed nonvisually and will effectively ingest anything that is stung by the nematocysts on their tentacles and/or oral arms

and cannot subsequently escape. Even though they are largely planktivorous, they will also consume benthic organisms that move up into the water column, thereby increasing benthic-pelagic coupling (Gibbons et al. 1999, Flynn and Gibbons 2007). Although selective predation has been demonstrated for some medusae (Fulton and Wear 1985, Purcell and Mills 1988, Han et al. 2009), most are treated as fairly unselective predators and will consume anything from protists to chordates (Arai 1997, Malej et al. 2007). Laboratory experiments have indicated that jellyfish rarely reach satiation at natural prey densities (Arai 1997), so they are effective predators of zooplankton, including fish eggs and larvae.

Perhaps because medusae are approximately 96% water and lack complex, high-maintenance tissues, they can shrink in size when food is scarce, then resume normal growth and reproduction within days of feeding (Hamner and Jenssen 1974). They and their polyps can also tolerate hypoxia (Arai 2001, Grove and Breitbart 2005, Thuesen et al. 2005). In many senses, the polyps can be considered immortal (Galliot and Schmid 2002), being able to encyst for prolonged periods of time (as can planulae) under adverse conditions (Arai 2009) and to regrow from fragments if damaged (Arai 1997). Under certain circumstances, they can also proliferate, for example by budding (Willcox et al. 2007, Liu et al. 2009, Han and Uye 2010).

Although small jellyfishes may be subject to predation by a range of species, large individuals have few predators other than sunfish and sea turtles (Purcell and Arai 2001, Arai 2005), which are themselves rare. Although polyps are subject to predation by nudibranchs (see e.g., Hernroth and Grondahl 1985), other predators are considered to be few. Perhaps the greatest predators of jellyfishes are their congeners (Purcell 1991, Titelman et al. 2007).

Although *A. forskalea* and *C. fulgida* may have been present in the Benguela ecosystem for a long time, their absence from reports of otherwise comprehensive studies before the 1970s (e.g., Hart and Currie 1960, Stander and De Decker 1969, reviewed in Flynn et al. 2012) suggests that they were not a major component of the system at that time (Fearon et al. 1992). Significant quantities of jellyfishes in the region were first noted in the early 1970s (together with large biomass of juvenile horse mackerel and bearded goby), and by the 1980s they had reached a very high biomass, estimated at more than 40 Mt by Fearon et al. (1992) from bongo-net surveys. Venter (1988) wrote, "The abundant occurrence and wide distribution of jellyfish off the coast of South West Africa (Namibia) is a well known phenomenon, *especially after the dramatic decrease in pelagic fishing in 1972*" (emphasis added), highlighting the temporal coincidence of the collapse of the small pelagic fish resources and the increase in jellyfish abundance. As noted by Venter (1988), the high biomass of jellyfishes in the late 1970s had become a nuisance to fishermen and interfered with fishing operations in the region by clogging and damaging nets. More recently acoustic techniques were developed for assessment of the biomass of jellyfishes in the region (Brierley et al. 2001) without the potential biases introduced by bongo-net surveys. In August 2003, one acoustic survey of the NB shelf yielded an estimated biomass of 12.2 Mt (Lynam et al. 2006). Possibly more important than this result itself is that it represented nearly 2.4 times the estimated combined biomass of the main commercial fish stocks (horse mackerel, hakes, and small pelagic fishes) during the same survey (and more than 15 times that of the clupeoids alone). Although the ecological role of jellyfishes in ecosystems is still poorly understood (see e.g., Pauly et al. 2009),

jellyfishes probably have become major zooplankton consumers in the NB since the collapse of the sardine and subsequent decline in other small pelagic fishes.

Both *A. forskalea* and *C. fulgida* are also part of the jellyfish assemblages of the SB (Pagès et al. 1992, Buecher and Gibbons 2000) but have not been observed at high densities, and no indication is apparent of a temporal trend in abundance like that in the NB. No jellyfish species has been exploited commercially in the Benguela region.

FAUNAL TRAJECTORIES IN THE SOUTHERN BENGUELA

SMALL PELAGIC FISHES.—The sardine was initially the primary target of South Africa's small pelagic fishery, and landings of this species increased during the 1950s, peaking at 410,000 t in 1962, but then rapidly declined (Fig. 3) after increased effort, a southward expansion of the fishery, and variable recruitment (Beckley and van der Lingen 1999). By 1970 sardine catches were <100,000 t per annum, and landings remained low (except in 1972 and 1976) until the early 1990s. Catches increased during the 1990s and early 2000s to a high of 374,000 t in 2004 before again rapidly declining to present levels of around 100,000 t. Sardine catches over the past 60 yrs have matched population biomass estimates, derived (before 1982) by virtual population analysis and subsequently (after 1984) from annual acoustic surveys (see fig. 9.3b of Barange et al. 2009). Peak biomass in the first "boom" period was estimated at 1.7 Mt (in 1959) and that during the second period at 4.1 Mt (in 2002), although estimates from the two methods are not directly comparable. Recently (end of 2010), the SB sardine population was estimated at around 500,000 t (Department of Agriculture, Forestry and Fisheries unpubl data).

After the mid-1960s collapse of the SB sardine population, purse seiners switched to using smaller-meshed nets to pursue the anchovy, which became the mainstay of the fishery with average annual landings of 250,000 t between the mid-1960s and the mid-1990s (Fig. 3). Peak anchovy catches of almost 600,000 t were made in 1987 and 1988, and after some years of low catches (approximately 50,000 t) in the mid-1990s, annual landings returned to levels of about 200,000 t thereafter (Fig. 3). Fluctuations in anchovy catches did not closely match those in biomass estimates. Such estimates derived from acoustic surveys conducted since 1984 averaged 1.4 Mt over the period 1984–1999, whereas from 2000 to 2010 biomass averaged 3.5 Mt (updated from Coetzee et al. 2008a). Nevertheless, anchovy catches over the past decade have been the same as, or less than, those made over the previous 16 yrs despite a doubling in biomass. A third small pelagic species in the SB, Whitehead's round herring, is less heavily fished, and although annual catches have never exceeded 100,000 t, they have steadily increased from the mid-1970s to the present. Biomass estimates for this species have ranged between 1 and 2 Mt over the past decade (Department of Agriculture, Forestry and Fisheries unpubl data).

Since the 1960s collapse, before which no catch limits were set, management measures for small pelagic fishes have been progressively introduced, first with a global pelagic quota in 1971, followed by species-specific quotas in 1984 and management procedures in the early 1990s (De Oliveira and Butterworth 2004, Moloney et al. 2004, Barange et al. 2009). In particular, a conservative management strategy was applied to the sardine in an attempt to rebuild the stock (Cochrane et al. 1998). This strategy was based on the increasing understanding of the ecology and dynamics of pelagic fish stocks and prevented their gross overfishing. In addition to providing

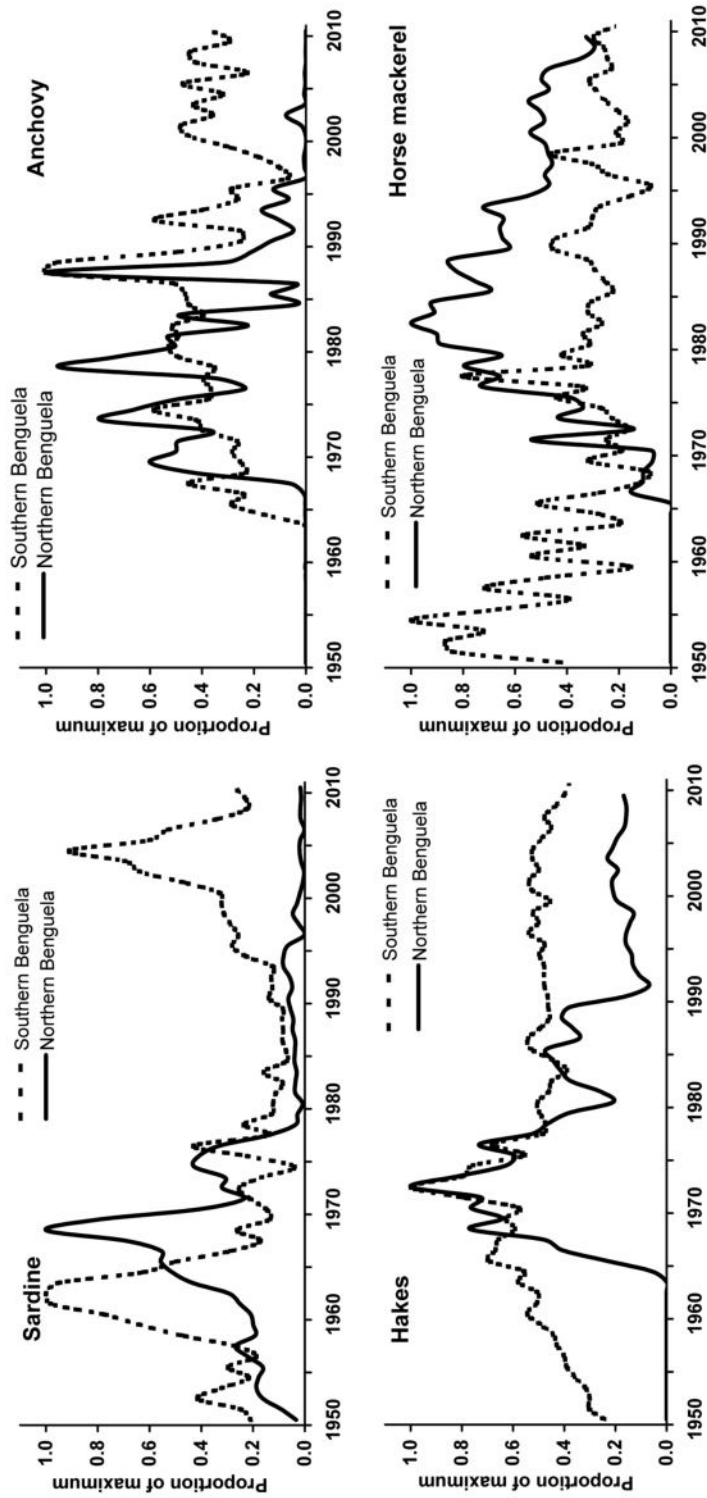


Figure 3. Time series of relative catch (scaled to proportion of maximum catch) for the main commercial stocks in the study areas.

biomass estimates from the mid-1980s onwards, acoustic surveys have also revealed changes in anchovy and sardine distribution patterns in the SB. In the mid-1990s, anchovy spawners showed an abrupt eastward shift in the relative distribution of their biomass, from being located predominantly (>50% of biomass) to the west of Cape Agulhas (see Fig. 1) during 1984–1995 to being located predominantly to the east of Cape Agulhas from 1996 through 2010. Synchronous changes in temperature gradients across the Agulhas Bank suggested that this shift was environmentally mediated (Roy et al. 2007). Sardines have also shown an eastward shift in their relative distribution, albeit a more gradual one. From 1984 to 1998 over half (generally >65%) of the sardine biomass was located west of Cape Agulhas, but from 1999 to 2005 this value decreased to <10%, and the bulk of the stock was located off the south coast (Coetzee et al. 2008b). This shift has had negative implications both for the purse-seine fishery and for predator species off the west coast for which sardines were an important dietary component, but the shift appears to be reversing in recent years; some sardines were found off the west coast in 2009 and 2010 (Department of Agriculture, Forestry and Fisheries unpubl data).

HAKES AND CAPE HORSE MACKEREL.—Fishing for hake off South Africa started early in the 20th century but only became intensive during the 1950s, and the 1960s and early 1970s saw increasing effort from international fleets until the declaration of South Africa's exclusive economic zone in 1977 (Hutchings et al. 2009b). Both species of hake are primarily taken by demersal trawling; Cape hake dominates catches made over the Agulhas Bank, and deepwater hake dominates those made off the west coast (Payne and Punt 1995) and overall hake catches (Atkinson et al. 2011). Combined annual landings of the two species increased from <100,000 t in the early 1950s to a peak of 295,000 t in 1972, but declined rapidly thereafter, after the introduction of a variety of management measures, including the exclusion of foreign vessels (Atkinson et al. 2011). Subsequently, annual hake catches have remained stable at around 150,000 t (approximately 50% of maximum; see Fig. 3), albeit with a slight decline in recent years.

Adult Cape horse mackerel were a major component of purse-seine catches off South Africa's west coast during the initial development of the pelagic fishery; around 100,000 t per annum were taken in the early 1950s, but catches declined to <5000 t by 1970 (Crawford 1995). Subsequently, smaller (generally <10,000 t yr⁻¹) amounts of predominantly juvenile horse mackerel have been taken as a bycatch by the pelagic fishery. Adult horse mackerel were the target of local and foreign demersal trawlers off South Africa's south coast during the 1960s (Barange et al. 1998), and by the mid-1990s this species was considered to have the potential to support the largest fishery on the Agulhas Bank (Japp et al. 1994). Although still taken as a bycatch in demersal trawls, horse mackerel have been the target of a midwater trawl fishery since the 1990s. Overall annual landings of this species have been fairly stable since 1980 at around 30,000 t (30% of maximum; see Fig. 3).

PREDATORS (CAPE FUR SEALS, AFRICAN PENGUINS, AND CAPE GANNETS).—Breeding colonies of Cape fur seals occur at several island and some mainland locations along the south and west coasts of southern Africa. Overexploitation of seals between the 17th and 19th centuries reduced their numbers substantially and caused the extinction of many island colonies. Under controlled harvesting from the beginning of the 20th century, the population increased from <100,000 to around 2

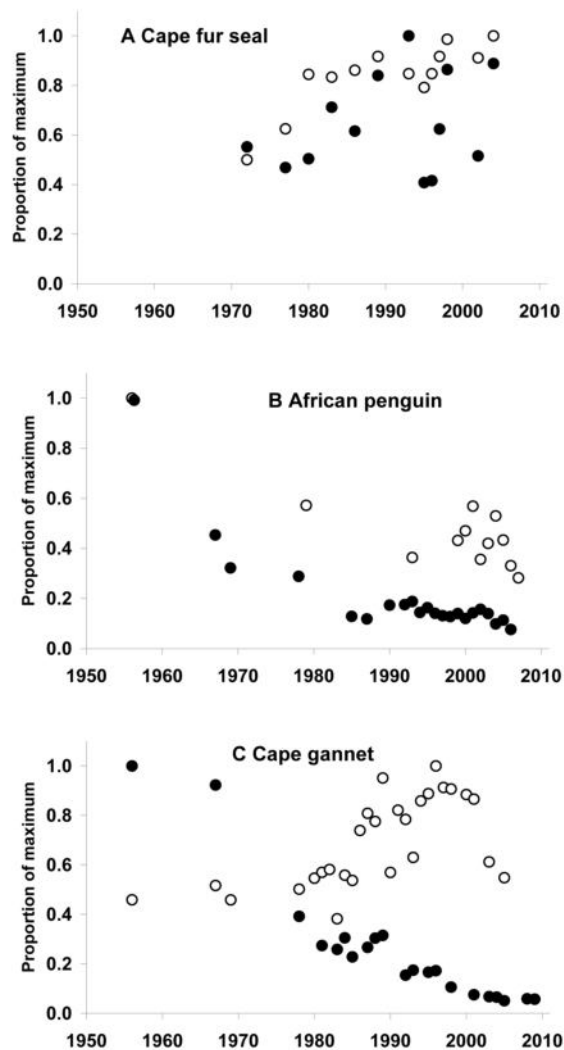


Figure 4. Time-series of relative abundance (scaled to proportion of maximum) for some top predators in the northern (filled circles) and southern (open circles) Benguela ecosystems. (A) Numbers of seal pups from aerial photographic censuses. (B) Numbers of breeding pairs of African Penguin. (C) Cape Gannet breeding populations (numbers of breeding pairs from aerial surveys in the northern Benguela and area occupied by breeding colonies in the southern Benguela).

million individuals overall between 1920 and the late-1990s, distributed throughout the SB and NB (Butterworth et al. 1995). Sealing stopped in South Africa in 1990 (Wickens et al. 1991), but is still practiced in Namibia, at three mainland colonies (Kirkman and Lavigne 2010). Since the early 1970s, abundance trends have been estimated from series of aerial, photographic censuses of pups at breeding colonies in both the SB and NB. Analysis of trends in pup production as a proxy for total population trend showed that in the SB the fur-seal population grew consistently from the 1970s to the mid-1990s (Fig. 4A) and stabilized thereafter (Kirkman et al. 2007c).

The numbers of breeding pairs of African Penguins in the SB underwent a substantial decline from about 100,000 in 1956 to 36,000 in 1993, mostly driven by overexploitation of eggs until 1967 (Shelton et al. 1984, Shannon and Crawford 1999). After a partial recovery (Crawford et al. 2001) numbers collapsed from 56,000 breeding pairs in 2001 to 21,000 in 2009 (Fig. 4B), a decline of >60% (Crawford et al. 2011). This decrease, together with the continued decline of the penguin population in the NB (Fig. 4B), led to a change in classification from Vulnerable to Endangered (IUCN 2011) and has been attributed to the reduced availability of their primary prey species, anchovies and sardines (Crawford et al. 2011), as a result of both the decrease in sardine biomass and the eastward shifts in relative distribution of adults of both species. Numbers of penguins off South Africa have declined in their western (Western Cape) and eastern (Algoa Bay) breeding localities, the latter somewhat surprisingly given the relatively high anchovy biomass in that area that has persisted for the past decade.

The Cape Gannet, also a species endemic to the Benguela, is classified as Vulnerable (IUCN 2011). From the 1950s to the late-1990s, it exhibited a steady increase in the area occupied by breeding birds (a proxy for the number of breeding birds) at two colonies (Lamberts Bay and Malgas Island) off South Africa's west coast. Subsequently, the breeding area rapidly declined to around half of maximum values by 2005 and 2006 (Fig. 4C), coincident with the reduced availability of sardines in particular (Pichegru et al. 2007, 2010), although a slight increase has occurred in recent years.

FAUNAL TRAJECTORIES IN THE NORTHERN BENGUELA

SMALL PELAGIC FISHES.—The species composition of the pelagic stocks in the NB is the same as that in the SB, but these stocks are considered discrete because of the environmental barrier presented by the Lüderitz upwelling cell in southern Namibia (Shannon 1985, Agenbag and Shannon 1988). Scale deposits in sediments seem to show that the dominant small pelagic fishes in the NB was the sardine, which, during periods of low abundance, was only partially replaced by a mix of anchovy and horse mackerel (Shackleton 1987). The purse-seine industrial fishery for small pelagic fishes was established after World War II in the NB; its primary target was the sardine. Fishing effort increased rapidly during the 1960s, and catches peaked in 1968 at a reported 1.4 Mt (the actual catch is likely to have been considerably higher). The sardine biomass has been estimated to have varied between 4 and 11 Mt between 1952 and 1964. A 10-fold decline in biomass was noted between 1964 and 1971 (the period of peak catches), and after a slight recovery due to one strong year class in 1972, the stock and the fishery collapsed. As the sardine stock started declining, the fishery introduced a smaller mesh size in 1968, and directed catches of anchovies and juvenile horse mackerel increased (as did the bycatch of juvenile sardines). Although eight of 11 sardine canneries closed between 1974 and 1980, fish-meal production increased, and high fishing pressure was maintained on anchovies and juvenile horse mackerel, both regarded as potential competitors of sardines (Butterworth 1983, Shelton 1992, Bakun and Weeks 2006). The result was a rapid crash of the anchovy but not a recovery of the sardine (Fig. 3). In the early 1980s, despite calls by scientists for a moratorium on sardine fishing to promote stock recovery, the authorities decided to continue fishing at low levels to maintain the canning activities (Armstrong and Thomas 1995, Boyer et al. 2001). Average annual sardine landings dropped from

around 750,000 t in the 1960s to <70,000 t in the 1980s and 1990s. Since the beginning of the 21st century, sardine catches have averaged <20,000 t yr⁻¹, about 1.4% of the peak catch of 1968.

Anchovy catches dominated the pelagic landings for only a few years in the late 1970s and early 1980s (averaging 200,000 t yr⁻¹) and were high for 2 yrs in the late 1980s, possibly because of an exceptional influx of recruits from the SB (Boyer and Hampton 2001), before dropping to insignificant levels (averaging less than 5000 t yr⁻¹) in the last 15 yrs. Although Whitehead's round herring is present in Namibian waters, the population there is thought to be small (Boyer and Hampton 2001) and this species has never significantly contributed to pelagic catches. Consequently the small pelagic fish stocks in the NB have been virtually removed from the ecosystem, declining from several million tons in the 1950s and 1960s to possibly less than 200,000 t at present.

HAKES AND CAPE HORSE MACKEREL.—The hake trawl fishery started in the mid-1960s and developed rapidly as a long-distance fishery operated by various nationalities benefiting from the lack of control in preindependence Namibia. Catches increased to a peak of >800,000 t in 1972, but started declining rapidly soon thereafter (Fig. 3), and at the time of Namibia's independence in 1990, the stocks were severely depleted. After independence, Namibia claimed its authority over a 200-nmi exclusive economic zone, curbed illegal fishing, developed its own trawl industry, and implemented management measures to rebuild the depleted hake stocks (van der Westhuizen 2001). Since 1990, hake catches have averaged around 135,000 t annually, but despite the conservative management measures in place, the stocks have not shown the expected rebuilding and remain at approximately 1990 levels (C Kirchner unpubl data).

Juvenile horse mackerel were rarely recorded as a bycatch of the purse-seine fishery until the early 1970s, after the collapse of the sardine stock. In 1971, 140,000 t were caught (Boyer and Hampton 2001), and catches have been quite erratic since then. The catches of the midwater trawl fishery for adult horse mackerel rose rapidly from 50,000 t in the early 1970s to nearly 600,000 t yr⁻¹ in the early 1980s (Fig. 3). This expansion was partially triggered by a change of target species from hake to horse mackerel by a portion of the fleet (mainly Eastern bloc vessels) as the hake stocks started declining (Boyer and Hampton 2001), as well as a possible increase in the horse mackerel biomass after the collapse of the sardine (Vaske et al. 1989, Roux and Shannon 2004). Since the peak of the catches in the early 1980s, annual horse-mackerel landings have progressively declined to below 400,000 t a decade later and to an average of 260,000 t annually from the mid-1990s. Overall, horse-mackerel catches have dominated Namibian landings for the past three decades (Fig. 2).

BEARDED GOBY.—The bearded goby has never been the target of a commercial fishery but was first noted as a bycatch of the purse-seine fishery in the early 1970s. By the late 1970s substantial stocks were found between Walvis Bay and Lüderitz, and the extension of the species range was documented (Cruickshank et al. 1980). Since then, the bearded goby has become one of the major prey items of most top predators feeding on the shelf in the NB, from seabirds (Crawford et al. 1985, Ludynia et al. 2010) to marine mammals (Mecenero et al. 2006a, b) and predatory fishes such as juvenile hake (Traut 1996) and snoek, *Thyrsites atun* (Euphrasen, 1791) (Ministry of Fisheries and Marine Resources, Namibia, unpubl data). The goby stock increased

rapidly after collapse of the small pelagic stocks (Cruickshank et al. 1980), but recent studies (Utne-Palm et al. 2010) have demonstrated that the trophic position of the bearded goby is very different from that of a clupeoid. This species is not a filter feeder and has exceptional physiological adaptations (Salvanes et al. 2011) allowing it to feed within the anoxic layer on the benthos and anoxic mud rich in detritus, including sedimented diatoms and anaerobic bacterial mats. Gobies can also feed directly on jellyfishes (van der Bank et al. 2011).

PREDATORS (CAPE FUR SEALS, AFRICAN PENGUINS, AND CAPE GANNETS).—The Cape fur seal population in the NB has showed trends similar to those seen in the SB in which the population recovered from past overexploitation. Pup production increased from around 100,000 in the early 1970s to around 250,000 (Fig. 4A). After the late 1980s, large fluctuations in the numbers of pups occurred and were related to poor feeding conditions linked to environmental perturbations (Gammelsrød et al. 1998, Hutchings et al. 2009a) affecting the prey quantity and distribution, which resulted in mass starvation events and low-pregnancy years (Guinet et al. 1998, Roux 1998, Kirkman et al. 2007c). In addition the relative distribution of the fur-seal population has changed as new colonies have been established in northern Namibia since the mid-1990s, whereas colonies in southern Namibia have declined. These changes are attributed to a decline in prey availability in the south (Kirkman et al. 2007c).

The population of African Penguins in the NB (even in the absence of egg exploitation) has decreased by 77% since the mid-1950s (Fig. 4B); the decline was steeper until 1985 (Kemper et al. 2001, 2007). Initially colonies differed in the rate and timing of this decline, which was earlier and steeper for the southern colonies, probably because of the geographical contraction to the north of the declining small pelagic fish stocks (Crawford and Shelton 1981, Crawford et al. 2001). Since the mid-1990s, the decline has affected northern colonies as well (Kemper 2007, in press a). The penguin population has declined at an average exponential rate of $-2.55\% \text{ yr}^{-1}$ (based on counts of molting birds, updated from Kemper 2007), and the species is classified as Endangered (Kemper et al. 2007). The main reason cited for this trend is the low availability of energy-rich small pelagic fishes (Ludynia et al. 2010).

The Cape Gannet population in the NB was estimated at around 190,000 pairs at the time of the sardine collapse in the late 1960s (Fig. 4C). Since then, the population has sharply declined at an annual exponential rate of $-6.9\% \text{ yr}^{-1}$ to reach 11,000 breeding pairs in recent years, a decline of more than 94% since the mid-1950s (Crawford et al. 2007, Kemper 2007, in press b). The collapse of the small pelagic fish stocks was found to be the main cause for this dramatic decline (Crawford et al. 2007) and remains the principal threat to this species now at serious risk of extinction in the NB (Kemper in press b).

TROPHODYNAMIC INDICATORS

A suite of trophodynamic indicators was estimated for both the SB and the NB, and their usefulness in detecting the development of the fisheries and associated ecosystem changes was evaluated by Cury et al. (2005), who also analyzed their trends since 1950. The trophic level of the catch as defined by Pauly et al. (1998) is the mean of the trophic levels of each group caught by the fisheries weighted by their landed mass. A modified form of the marine trophic index (MTI; Pauly and Watson

2005) was calculated as the trophic level of the catch, excluding all three commercial small pelagic fish species (sardine, anchovy, and Whitehead's round herring). The fishing-in-balance index (FiB), as defined by Pauly et al. (2000), is a dimensionless indicator tracking the ecological consistency of fisheries yield with the trophic level being fished, given an estimate of the transfer efficiency between trophic levels. By 1970, most of the fisheries were fully developed in both ecosystems, and Figure 5 illustrates the changes in some of these indicators since then for both ecosystems.

The trophic level of the catch in the SB (Fig. 5A) has remained fairly constant (mean trophic level = 3.64, SD 0.07) with no trend for the past four decades. The slight decline apparent between 2000 and 2004 was due to an increase in sardine landings. In the NB on the other hand (Fig. 5B), the trophic level has significantly increased in the last four decades, from around 3.66 to 3.90 ($P = 0.0034$) because of the still diminishing contribution of small pelagic fish to the landings. The fairly tight grouping of points in the plot of trophic level against catches for the SB (Fig. 5C) illustrates the relative stability in this ecosystem, whereas the spread of points between the beginning and the end of the series for the NB (Fig. 5D) reveals the large scale of changes in both catch and trophic levels over these four decades.

The modified MTI in the SB (Fig. 5E) fluctuated slightly in the first two decades of the series around a mean value of 3.99 after which it increased very slightly to 4.13 in the mid 1990s and stabilized thereafter just above 4.0. In the NB it decreased sharply in the 1970s from around 4.5 to reach a plateau during the 1980s at around 3.98. During this period the hake stocks were overfished and in sharp decline, and catches of the lower-trophic-level horse mackerel were increasing. Some changes in the Namibian fishing industry at the time of independence in 1990 (and particularly the withdrawal of the foreign hake vessels) probably contributed to the rapid decline in this index between 1989 and 1991. This drop was followed by a partial recovery corresponding to the establishment of a local hake trawl fishery during the following decade and the general decline in horse mackerel catches, but the overall trend of the MTI in the NB is a large decline (mainly during the 1970s) and stabilization thereafter (Fig. 5F). The main driver behind this trend was the overexploitation of the high-trophic-level hake stocks in the 1970s and early 1980s and their subsequent lack of recovery.

The FiB indices for the two ecosystems were calculated as by Cury et al. (2005) with 1950 as the reference year and a 10% transfer efficiency between trophic levels for both ecosystems. Because the absolute value of this index depends on the state of the fishery during the reference year (Pauly et al. 2000), and because fisheries were more developed in the SB than in the NB in 1950, the FiB values for the two ecosystems are not directly comparable, but their temporal trends are.

The time series of FiB index for the SB (Fig. 5G) displays a remarkable temporal stability and no apparent trend during the period. The slightly domed shape (slight increase to the late 1980s and slight decrease since the early 1990s) tracks the increasing catches of anchovies during the first part of the period and the increasing contribution of sardines since the 1990s (Cury et al. 2005). In contrast, the FiB index in the NB has declined significantly (Fig. 5H) over the last four decades ($P < 10^{-5}$). Although an increase in FiB could denote an expansion of the fishery or an increase in productivity of the system, a decrease in this index is observed if the fishery is contracting or if the productivity of the ecosystem is declining (Cury et al. 2005, Pauly and Watson 2005). The sharp drop of the value of the FiB between 1989 and 1991 can

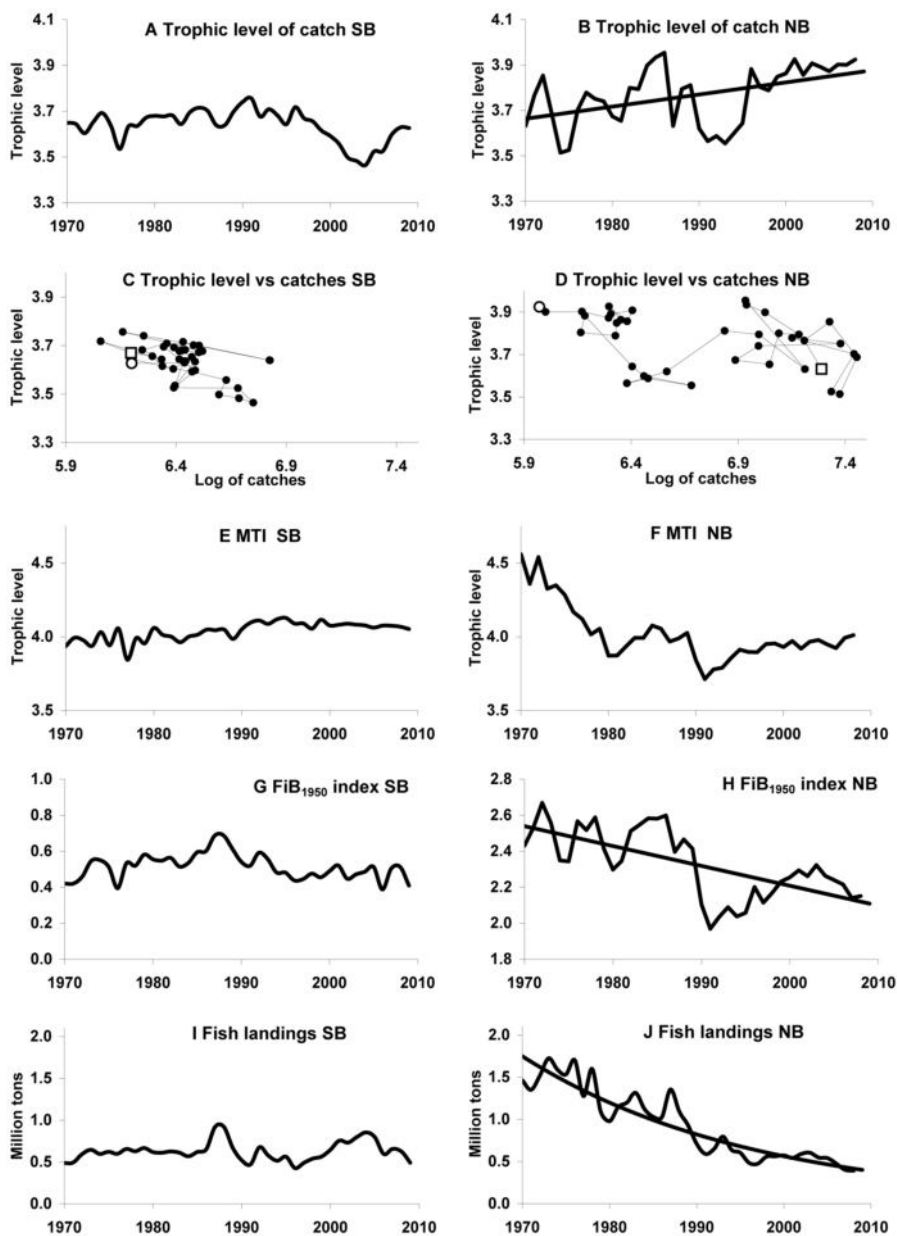


Figure 5. Comparison of some trophodynamic and fisheries indicators in the southern Benguela (SB) and northern Benguela (NB) from 1970 to the present. Open squares denote 1970 and open circles 2009. MTI, marine trophic index, calculated as the mean trophic level excluding small pelagic fishes. FiB, fishing-in-balance index.

be attributed, at least in part, to the temporary decline in the hake fishery triggered by policy changes at the time of Namibia's independence, but its subsequent recovery was only partial, and the declining trend resumed after 2003, suggesting that overall the productivity of the NB ecosystem has indeed been declining since the 1970s.

Total fish landings (including all the fish species used in the calculations of trophic level and MTI) have been relatively stable in the SB since 1970 (Fig. 5I), averaging around 628,000 t annually (SD 114,000 t) with no apparent trend. The relative composition of landings has not varied markedly over time; small pelagic fish represent 68.6% (SD 6.0%) of the total catches. In contrast, fish landings in the NB (Fig. 5J) have declined precipitously from more than 1.5 Mt to less than 500,000 t in recent years at an average exponential rate of $-3.76\% \text{ yr}^{-1}$ ($P = 10^{-18}$) since 1970. The small pelagic fishes that dominated landings in the early part of this time series represented on average only 5.3% of the total fish landings in the last decade.

Overall these indices highlight the relative stability of the SB ecosystem during the last four decades, despite the change in relative abundance of small pelagic species from a period of anchovy dominance (1970 to the mid-1990s) to a period of roughly equal dominance by anchovies and sardines (mid-1990s to mid-2000s) and then back to an anchovy-dominated system after 2005. The very large changes apparent in the NB (besides the collapse of the small pelagic stocks) are all consistent with a large-scale decline in productivity of all the main commercial fish stocks and an altered functioning of the underlying food web since the 1970s.

TROPHIC INTERACTIONS BETWEEN PREDATORS AND THEIR PREY

Sardines were the major component of the diet of most top predators in the NB until the late 1960s. Since the decline in small pelagic fish in that system, bearded goby has become an important prey species for most predators, together with a suite of species occurring over the shelf, including horse mackerel (mostly in the northern part of the system), juvenile Cape hake, lantern fish (Myctophidae), squid, etc. In the SB most predators switched between sardines and anchovies in response to the fluctuations of these two pelagic stocks, but they could not in the NB after the almost complete removal of these species in the late 1960s and early 1970s. To illustrate the energetic implications of the shift in predator diets we have reanalyzed, from an energetic point of view, studies from the SB and NB systems before and after the collapse of the sardine (Fig. 6). The energetic values of the different prey taxa were determined by bomb calorimetry (Balmelli and Wickens 1994, K Ludynia unpubl data), and the diet energy density (in kJ g^{-1}) of the different predators was calculated by the methods of Ludynia et al. (2010).

African Penguin diet was studied in the 1950s in the SB by Davies (cited by Crawford and Shelton 1978) and Rand (1960) and in the central NB by Matthews (1961). Sardines were the dominant prey in both regions. Since the late 1970s bearded goby has dominated penguin diet in the NB (Crawford et al. 1985, Ludynia et al. 2010), and as a result the energy density of the diet has declined from more than 6 kJ g^{-1} in the 1950s to 3.50 in the 1980s and 4.11 kJ g^{-1} since the mid-1990s (a decline of between 35% and 45% from values from early studies of both ecosystems; Fig. 6A).

The diet of the Cape Gannet was quantified during the 1950s in the SB by Davies (cited by Crawford and Shelton 1978) and in the central NB by Matthews (1961) and Matthews and Berruti (1983). More recent data on gannet diet were collected in the

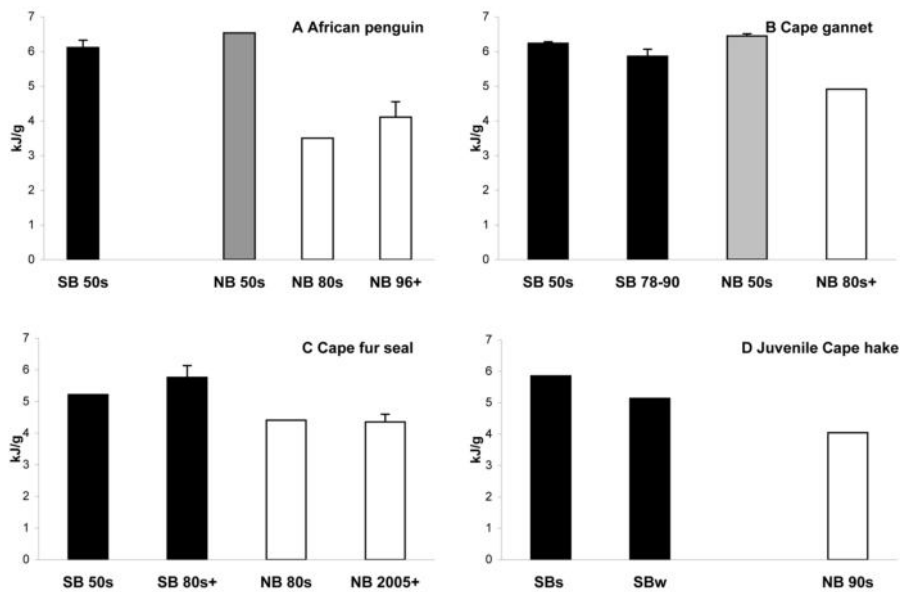


Figure 6. Energy density of the diets of some predators in the Benguela ecosystem, contrasting the southern Benguela (SB, solid bars) and northern Benguela (NB) before (gray bars) and after (open bars) the sardine crash. Error bars depict standard deviations when appropriate. SBs and SBw refer to juvenile hake diets in the 1990s on the south coast and west coast of South Africa, respectively.

SB between 1978 and 1990 (R Crawford unpubl data) and in the NB between 1980 and 2006 (Ministry of Fisheries and Marine Resources, Namibia, unpubl data and R Crawford unpubl data). In the 1950s the energy density of the Cape Gannet diet was $>6 \text{ kJ g}^{-1}$ in both ecosystems (Fig. 6B) and was estimated at 5.86 kJ g^{-1} in the SB in the more recent period, whereas it was slightly less than 5 kJ g^{-1} in the NB (between 21% and 24% less than in the other studies). The Cape Gannet is probably the most specialized predator considered here, consistently deriving the largest portion of its diet from pelagic fishes (Berruti et al. 1993), but also able to scavenge offal behind vessels fishing for hake (Lewis et al. 2006, Pichegru et al. 2010). Of the predator species discussed here, the Cape Gannet also has the largest potential feeding range. As a result, although its food in the SB is entirely dominated by anchovies and sardines when they are available, in the NB, the sardine that dominated gannet diet in the 1950s has not been replaced by the low-energy bearded goby, which on average contributed $<4\%$ to the diet. Instead, gannets in the NB make longer feeding trips (Lewis et al. 2006) and derive a higher percentage of their diet from trawler offal. Recently, Cape Gannets off South Africa's west coast have also turned to feeding on lower-energy discards from the hake fishery after the eastward shift in relative distribution of sardines and anchovies and have not been able to sustain breeding at the levels they achieved when more anchovies and sardines were available (Pichegru et al. 2007).

The diet of Cape fur seals has been determined from stomach contents of animals shot at sea (Rand 1959, David 1987, Kirkman et al. 2007b) and, since the mid-1990s, in the NB through analysis of hard prey remains in seal scats (De Bruyn et al. 2003, 2005, Mecenero et al. 2006a, Kirkman et al. 2007a). For the SB we have used diet composition estimates from the west coast in the 1950s (Rand 1959) and, since 1980, data

reanalyzed and updated by Kirkman et al. (2007b). For the NB in the 1980s, we used results from stomach contents collected between 1980 and 1984 (David 1987) and estimates from scat analysis calculated independently for four different subregions (J-P Roux unpubl data) and then weighted those estimates according to estimates derived from aerial surveys of fur-seal populations breeding in each subregion (Kirkman et al. 2007c). In the SB, estimates of Cape fur seal diet energy density ranged between 5.22 kJ g^{-1} in the 1950s and 5.76 kJ g^{-1} in the more recent period (Fig. 6C). In the NB, estimates were similar between the 1980s and since 2005 at about 4.38 kJ g^{-1} (between 16% and 24% less than in the SB since the 1950s). Those differences between the two ecosystems could be attributed to the scarcity of sardines and anchovies (the two most energy-dense prey species in the Benguela) and the abundance of bearded goby (one of the least energy-dense prey) in the diet in the NB. Although no data for that system were available for the earlier period, the diet of Cape fur seals in the NB before the sardine collapse was also dominated by sardines (Rand 1959, Matthews 1961); we can therefore assume that the energy density of their diet has declined by approximately 20% since the collapse of this stock.

The diet of Cape hake has been regularly monitored off South Africa during bottom trawl surveys (Pillar and Wilkinson 1995, Punt and Leslie 1995), whereas few studies have been published for the NB (Roel and Macpherson 1988, Traut 1996). We compared the energetic values of the diets of juvenile Cape hake (up to 30 cm in the SB and up to 35 cm in the NB), as these size classes are distributed over the shelf and interact readily with pelagic fishes. For the NB, we used data from two studies done in 1994 (Traut 1996) and 1999 (J-P Roux unpubl data), as Roel and Macpherson (1988) presented a detailed analysis of the diet of these size classes only in terms of frequency of occurrence of prey categories. Up to the mid-1990s the energy density of juvenile Cape hake was highest along the south coast of South Africa, at 5.86 kJ g^{-1} , and the lowest in the NB, at 4.05 kJ g^{-1} (Fig. 6D). This difference mainly was due to the high incidence of energy-rich anchovy in the diet of small hake in the SB and the virtual absence of clupeoids in the NB, where the energy-poor bearded goby and juvenile hake were the dominant prey and where hake cannibalism was between 4.9 and 7.2 times higher (as a proportion of the diet in mass); both results contributed to the lower productivity of the NB Cape hake stock than of its SB counterpart.

Snoek is an abundant and important large pelagic fish species off South Africa that is a highly mobile and opportunistic predator (Griffiths 2002). McQueen and Griffiths (2004) have shown that snoek consume anchovies, sardines, hake, horse mackerel, and lanternfish in quantities relative to their spatial and temporal abundances. In the NB, the diet of snoek has been dominated by goby since the late 1980s (J-P Roux unpubl data).

Overall, the effect of the collapse of sardines and anchovies in the NB and subsequent changes in the food-web was to lower the energy density of the predator diets by between 16% and 45%, whereas SB predators were apparently able to maintain an energy-rich diet by switching between the most dominant small pelagic fishes available during the fluctuations in sardine and anchovy relative abundance. In addition the diet changes of predatory fish over the NB continental shelf may have contributed to lowering the recruitment potential of hake through an increase in predation and cannibalism on prerecruits.

THE ROLE OF SMALL PELAGIC FISHES AND WHAT CAN BE LEARNED FROM FOOD-WEB MODELS

Small pelagic fishes are now recognized to play a structuring role in most marine food webs (and in upwelling ecosystems in particular) through trophic controls exerted on both their planktonic prey and their predators (Cury et al. 2000, 2003). In particular these species constitute the principal link allowing efficient and direct transfer of energy between planktonic organisms and high-trophic-level species such as piscivorous fishes, seabirds, and most marine mammals (Cury et al. 2000, 2011, Smith et al. 2011), though their importance differs somewhat in different ecosystems.

Although the SB and NB ecosystems were historically similar in their structure, species communities, and functions, the virtual removal of the small pelagic fishes from the NB was akin to conducting an “accidental” experiment to clarify the role of small pelagic fishes (by default) in these ecosystems. Whereas the SB (at least the west-coast portion thereof) continues to function as a “classic” upwelling ecosystem, the NB has undergone profound structural changes since the collapse of the sardine population there (Cury and Shannon 2004, Bakun and Weeks 2006, van der Lingen et al. 2006) and now stands out as the only eastern boundary upwelling ecosystem with few small pelagic fishes and with a very high jellyfish biomass (see e.g., Moloney et al. 2005).

Several ecosystem models have been constructed for the Benguela region to characterize the trophic structure of these ecosystems and explore the effects of fishing (Shannon and Jarre-Teichmann 1999, Shannon et al. 2000, Roux and Shannon 2004). Food-web models using the Ecopath with Ecosim approach (Christensen and Walters 2004) were also used in the region for describing within-system structural changes over time (Heymans et al. 2004, Shannon et al. 2004, Watermeyer et al. 2008a,b) or for comparisons with other ecosystems (Jarre-Teichmann et al. 1998, Moloney et al. 2005, Shannon et al. 2008, 2009). These modeling studies (e.g., Shannon et al. 2009) have suggested that the energy flows within ecosystems can be disrupted by changes in the abundance of small pelagic fishes. In particular, they suggest that flows to detritus are likely to increase when small pelagic fishes are less abundant and therefore consume less plankton and that this increased flow of energy to detrital groups causes the demersal part of the food web to become more important, possibly strengthening the pelagic-demersal coupling of food webs (Shannon et al. 2009). This certainly appears to be the case for the NB (see e.g., Watermeyer et al. 2008b).

What can we learn from a set of exploratory model simulations with respect to possible trophic cascades in the Benguela? Trophic model simulations highlight some of the important trophic interactions that drive the functioning of the SB ecosystem and provide the necessary context for postulating and considering the potential for trophic cascades in the Benguela, given that the NB and SB originally had very similar structures. They also pose plausible explanations as to how these cascades might differ from those observed in the NB ecosystem, where small pelagic fish have collapsed and evidence points to concurrent and/or subsequent large increases in the biomass of jellyfishes and bearded gobies. In general, when small pelagic fishes (anchovies, sardines, Whitehead’s round herrings, juvenile horse mackerel, or mesopelagic fishes, together termed forage fishes because they are common prey for predators) were more heavily fished in depletion-model simulations of the SB (see Appendix 1 for details), most other forage-fish groups competing with the group

under examination showed increases in biomass. In contrast, predators relying heavily on the forage-fish group in question often showed noticeable declines.

When the Shannon et al. (2008) trophic model for the SB was employed with a recent version of Ecopath with Ecosim (see Appendix 1 for details), some exceptions to the expected patterns were noted, particularly with respect to sardines. Model sardine biomass declined when anchovy or Whitehead's round herring biomass was reduced by fishing, whereas other groups of forage fish competing with anchovies or herring for zooplankton prey benefited. The unexpected decline in sardines is possibly related to a shift in diet composition of predators from anchovies or herring to sardines in the modeled scenarios. In contrast, model simulations suggest that heavier fishing on juvenile horse mackerel may result in an increase in the sardine, whereas very small impacts were felt by the anchovy, herring, and hake (Fig. 7). Deepwater hake and pelagic-feeding demersal fishes are predators that increased when modeled anchovies declined or showed only small declines when modeled sardines were depleted, suggesting that these opportunistic predators are able to take advantage of increases in anchovy/sardine competitors that serve as alternate forage.

Model fishing on mesopelagics had diverse effects on other ecosystem components. Zooplankton groups responded very differently to the cases where fishing on anchovies, sardines, or herring were modeled. About a quarter (23%) of modeled groups, mostly fished groups, substantially benefited (increasing by >20%) from a reduction of mesopelagic fishes to 40% of their estimated unfished level. This result suggests that, despite a severe decline in an important forage-fish species such as mesopelagic fishes, many predators benefited as a result of increased abundances of competing forage-fish species such as clupeoids that compete for planktonic food.

Model simulations of the SB suggested that sardines and horse mackerel have an inverse relationship, the one increasing to some extent if the other collapses, although the amplitude of the model increases appeared dampened in comparison to what has been observed in reality in the NB, where Whitehead's round herring is virtually absent and anchovy biomass is very low. In simulations where mesopelagic fished and juvenile horse mackerel collapsed, model gelatinous zooplankton declined, whereas jellyfishes appeared likely to increase in abundance when any of the three main small pelagic fishes underwent dramatic declines (Fig. 7). Notably, modeled impacts on jellyfish [presented here and generated by a slightly modified version of the Shannon et al. (2008) model; see Appendix 1] are well within the magnitude of impacts on other ecosystem components.

In a different set of model simulations, increases in small pelagic fish biomass were considered by means of hypothetical closure of fisheries, and collapses of small pelagic fish stocks were modeled in four different ecosystems (Shannon et al. 2009). Results across the ecosystems suggest that gelatinous zooplankton biomass tends to increase when small pelagic fish stocks collapse and to decline when small pelagic fish biomass is increased (Shannon et al. 2009). These trends are in agreement with the findings of Roux and Shannon (2004), who modeled the hypothetical removal of half of the jellyfish biomass off Namibia and found that model anchovies and predatory fishes responded by increasing in abundance. Nevertheless, all these model simulations should be treated with some degree of caution because model parameterization of jellyfishes is surrounded by uncertainty, resulting in a large range in jellyfish parameter values across ecosystem models (Pauly et al. 2009).

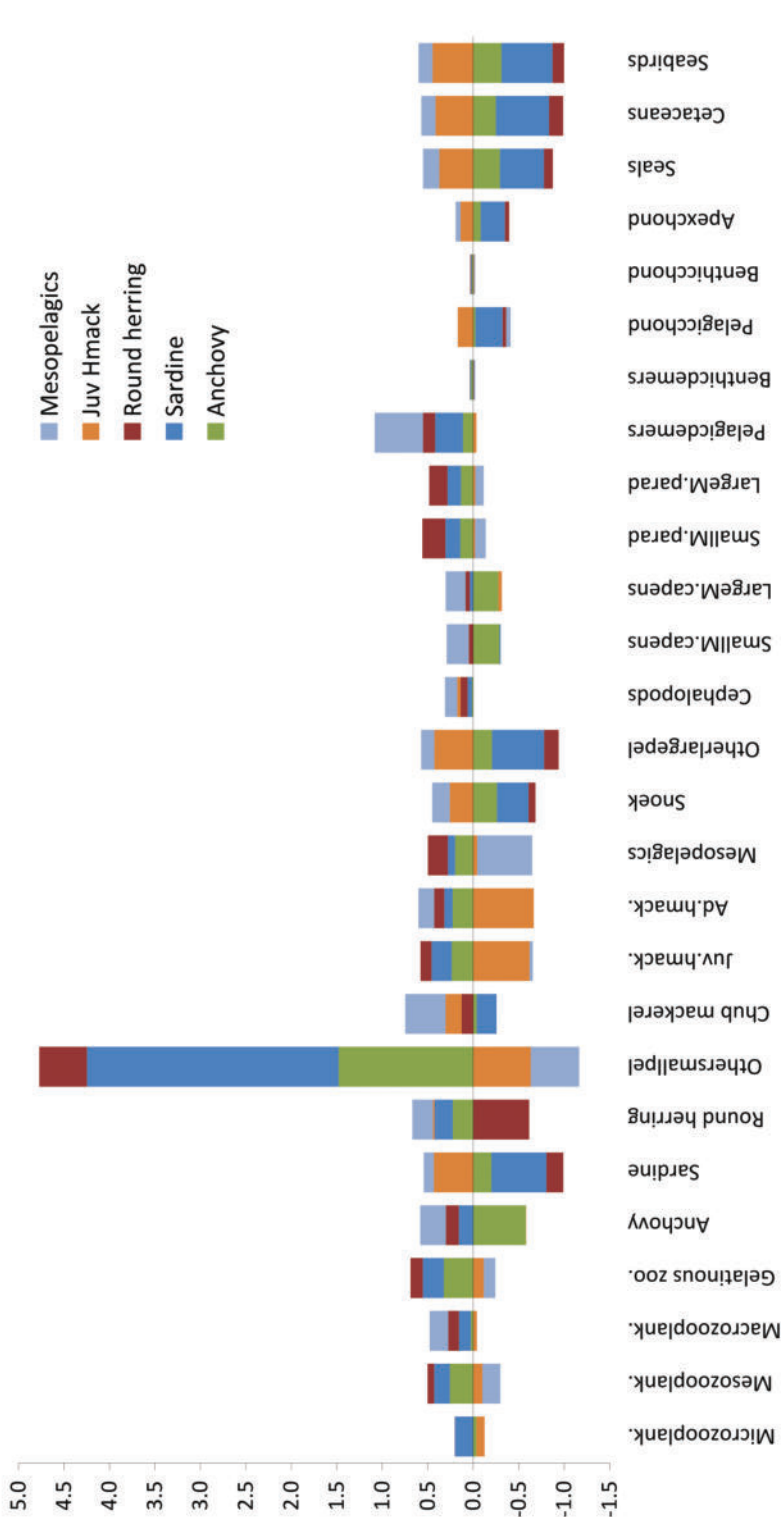


Figure 7. Southern Benguela trophic model results: relative change in end biomass (year 2061) of all model groups when each of the five forage-fish groups (anchovy, sardine, herring, mesopelagic fishes and juvenile horse mackerel) is independently adjusted (fishing is simulated) so that their biomass at the end of the projection period (2011–2061) reaches 40% of virgin biomass (around F_{msy} levels; equivalent to 60% depletion levels; Smith et al. 2011). Cumulative impacts are plotted, separated into impacts per forage-fish scenario.

In summary, the SB may be more resilient than the NB to declines in a single forage-fish species, because the former ecosystem comprises multiple forage-fish stocks that can increase in abundance to take mutual advantage of any vacated part of the forage-fish niche. This multiplicity of the forage-fish base, with a range of responses across ecosystem components (Fig. 7), may make the SB less likely to experience major trophic cascades if only one of its forage-fish species undergoes a collapse. In the NB on the other hand, Whitehead's round herring plays a minor role, and both sardines and anchovies were depleted within a few decades of fishing; all clupeoids were virtually eliminated from the food web.

THE NORTHERN BENGUELA: POSSIBLE BELLWETHER FOR OVERFISHED ECOSYSTEMS?

In contrast to the SB where catches, species composition, and ecosystem structure have remained remarkably stable over the past six decades, the NB ecosystem has undergone spectacular and sustained changes that have affected virtually all trophic levels after the removal of small pelagic fish by fisheries more than four decades ago. Ecosystem function there has been profoundly altered, as indicated by trends in the various trophodynamic indices. Fisheries yields have plummeted despite the implementation in the last two decades of classical fisheries-management measures, including quotas (derived from stock assessments based on resource surveys), gear limitations, and surveillance. Most of the economically important fish stocks have either continued to decline or have not recovered as expected from previous overexploitation.

The human-induced collapse of small pelagic fish stocks off Namibia caused most predators to switch diet toward less suitable prey species. The Namibian population of Cape Gannet, the least opportunistic predator considered here, declined rapidly by more than 94% in four decades despite an increased intake of fisheries offal. Similarly, the African Penguin population in the NB declined drastically (by about 77%) and is still decreasing despite a partial dietary switch to the less energetically valuable bearded goby. Both these seabird species are now at serious risk of extinction in Namibia. The Cape fur seal, one of the most opportunistic predators, also preys massively on the low-energy bearded goby, and in the last two decades its population has displayed some signs of stress, including mass starvation events, population displacements, and lack of recovery in the south of Namibia. The Cape hake, probably the principal high-trophic-level consumer on the Namibian shelf and one of the most valuable fisheries resources, has almost certainly had its recruitment potential reduced through a lack of energy-rich prey and an increase in intercohort cannibalism affecting juveniles in their neritic phase.

Overfishing of planktivorous filter-feeding pelagic fish stocks and their subsequent collapses seems to be linked with major jellyfish outbreaks (Bakun and Weeks 2006, Richardson et al. 2009). As reviewed by Purcell and Arai (2001), the documented direct interactions between fishes and cnidarians are competition for zooplanktonic prey and predation on small or young cnidarians by fish, as well as on fish eggs and larvae by large cnidarians. Although the phenomenon is relatively poorly documented, many fish species have been found to consume jellyfishes (Arai 2005, Pauly et al. 2009), mostly the small stages including ephyrae, which are thought to be particularly at risk of predation by zooplanktivores and filter-feeding fishes (Purcell and Arai

2001, Arai 2005, Richardson et al. 2009). Large jellyfishes themselves have very few predators. Historically, a stock of >10 Mt of filter-feeding sardines in the NB probably had some significant and direct top-down effect on jellyfish recruitment through predation on ephyrae and small juvenile medusae (Purcell and Arai 2001, Arai 2005, Richardson et al. 2009). Strong evidence indicates that jellyfish, in the form of two main species of large medusae (*A. forskalea* and *C. fulgida*), have dramatically increased on the Namibian shelf and are now probably the dominant consumers of zooplankton in the NB ecosystem. Evidence also indicates that the bearded goby has increased in abundance and broadened its distribution.

Despite the lack of direct information on jellyfish diet in the Benguela region, considerable evidence now suggests that the diets of many small pelagic fish species in other ecosystems overlap significantly with those of jellyfishes (see e.g., Purcell and Sturdevant 2001, Brodeur et al. 2008, Shoji et al. 2009), indicating the potential for competition between the two groups. Studies of trophic interaction between jellyfishes and pelagic fishes in the northern California Current ecosystem have documented the dietary overlap between jellyfishes and fishes, including sardines, anchovies, saury, and herring (Brodeur et al. 2002, 2008), as well as the ecological consequences of the competition between those two groups (Ruzicka et al. 2007, Brodeur et al. 2011). Modeling studies of that system highlighted that an increase of flows to jellyfishes most negatively affected the planktivorous fishes and the seabirds, and to a lesser extent other predators such as piscivorous fishes, marine mammals, and fisheries (Brodeur et al. 2011), and that jellyfishes constituted an alternate energy pathway (Ruzicka et al. 2012) resulting in loss of production, a pattern that has been observed in the NB. Until the late 1960s, the sardine must have represented a formidable competitor for zooplanktonic prey even in a system as productive as the NB. These direct interactions between pelagic fishes and jellyfishes came to an abrupt end in the early 1970s as a consequence of the collapse of small pelagic stocks caused by overfishing and could easily have caused the large increase in jellyfish biomass (together with increased flows to detritus) in the NB at that time. This situation has not arisen in the SB because of the persistence of a large biomass of clupeoids (alternately dominated by sardines and anchovies but including a significant biomass of lightly exploited Whitehead's round herring).

Because medusae can consume fish eggs and larvae, they have been shown to exert, at high densities, a top-down effect on pelagic fish recruitment through direct predation as well as competition for zooplankton (Möller 1984, Lynam et al. 2005). In the NB, the main spawning area for sardines on the shelf in the north central part of the ecosystem (Kreiner et al. 2011) overlaps considerably with the region of highest jellyfish abundance, between 20°S and 24°S (Flynn et al. 2012). This overlap highlights the potential for a negative feedback effect of the establishment of a large biomass of jellyfishes on recruitment and recovery potential of the NB sardine stock (Bakun and Weeks 2006). This feedback mechanism is akin to the "cultivation/depensation" effect described by Walters and Kitchell (2001), albeit between two groups of species occupying the same trophic level and operating through the interaction of the adults of one group and juvenile stages of the other.

A dense population of jellyfishes in an aquatic ecosystem also results in a "carbon shunt" away from fish production (Condon et al. 2011). Through their heavy predation on zooplankton, large quantities of carbon are sequestered into gelatinous biomass, resulting in a high release of dissolved organic matter, which is metabolized

by bacterioplankton toward respiration rather than production (Condon et al. 2011). In addition, because large medusae have few predators, much of the organic matter fixed by jellyfishes ultimately results in an increased flux to the benthos and detritus (Yamamoto et al. 2008), diverting more production away from the pelagos and increasing pelagic-benthic coupling. As found in Norwegian fjords (Sweetman and Chapman 2011), these jelly-falls result in an increased sedimentation of carbon and nitrogen and increased subsidies to the benthic and demersal fauna. In the NB both these effects would promote hypoxia, which is detrimental to sardines (Kreiner et al. 2009) while benefiting the hypoxia-resistant and detritivorous bearded goby (Utne-Palm et al. 2010).

Overall, the NB food web apparently has been profoundly altered from its original state, in which small pelagic fishes constituted the main link between producers and higher trophic levels (Fig. 8). Now, a large proportion of the energy flow is diverted away from higher-trophic-level production toward detritus through the jellyfishes, benefiting mostly the bearded goby, which has become the new (but less efficient) main trophic link in the NB food web (Fig. 8). This scenario is consistent with the currently observed differences between the NB and the SB ecosystems and points to the overfishing of small pelagic fishes as being the trigger of a chain of events resulting in the rise of jellyfishes and goby and their maintenance in the system for the last four decades. Moreover, several negative feedback mechanisms (both direct and indirect) between jellyfishes and small pelagic fishes could contribute to "locking" the NB ecosystem into an alternative (and less productive) stable state (Bakun and Weeks 2006, Jensen et al. 2012).

Realization is growing that overfishing may result in possibly irreversible changes to the structure and functioning of marine ecosystems. Many studies have shown that overexploitation of predatory fish stocks in particular has affected marine ecosystems across the world (Pauly et al. 1998, Jackson et al. 2001, Pitcher 2001, Baum et al. 2003, Myers and Worm 2003, 2005, Scheffer et al. 2005, Baum and Worm 2009). We have shown that the collapse of the low-trophic-level planktivorous species has resulted in drastic changes in a productive upwelling ecosystem, leading to a possible alternate stable state that has affected the entire food web and is characterized by a high biomass of jellyfishes and loss of productivity of the higher trophic levels, including endangered top predators and commercially important predatory fish stocks. Similar ecosystem changes favoring gelatinous zooplankton have been described in other regions, particularly in coastal areas of the Far East and in the Black Sea with ctenophores (Daskalov 2002, Daskalov et al. 2007), although those cases involved eutrophication as one of the triggers, in addition to overfishing.

Additional research is urgently needed in the Benguela region with particular emphasis on jellyfish feeding ecology and diet and the trophic interactions between small pelagic fishes, bearded goby, jellyfishes, and their zooplankton prey. Results and understanding gained from such studies, incorporated into ecosystem models and the exploration of ecosystem trajectories, would allow elucidation of the mechanisms that have led to the jellyfication of the NB and examination of possible conditions that may allow a reversal of this situation (Pauly et al. 2009, Richardson et al. 2009).

Marine ecosystems worldwide are increasingly subjected to a suite of human-caused stressors in addition to fishing, including global climate change, eutrophication, intensification of mariculture, and coastal developments. Evidence in the

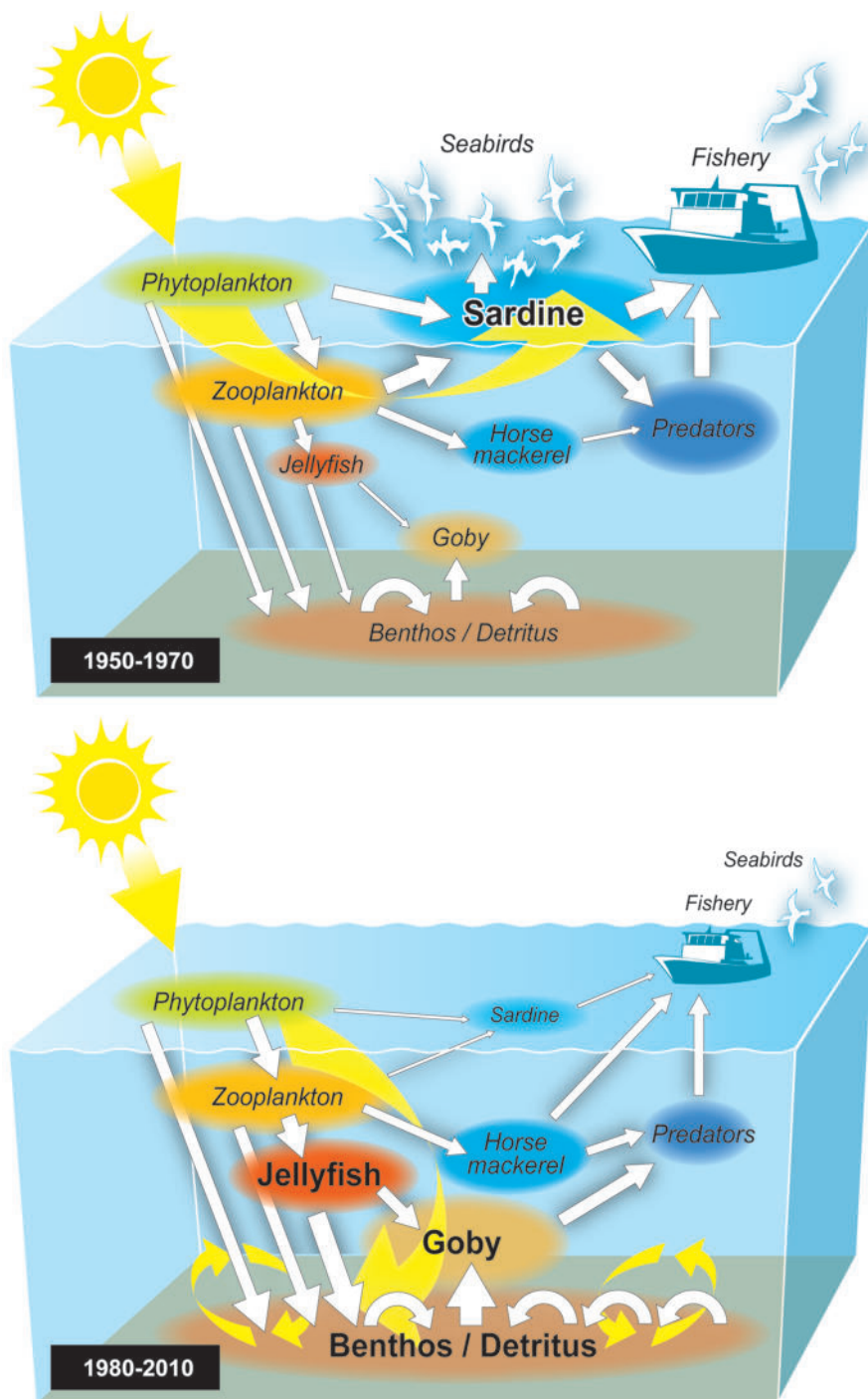


Figure 8. Conceptual sketch of the main energy flows toward fish production and fisheries in the northern Benguela. The sardine was the main link between primary and secondary producers and fish, fisheries, and predators in the early period (top); after the sardine collapse in the early 1970s most of the energy flow (yellow arrows) was diverted away from the pelagos through jellyfish, detritus, benthic recycling, and bearded goby (bottom).

literature indicates that these pressures can act synergistically and seem to favor jellyfish outbreaks. Other productive marine ecosystems might be at an increased risk of the type of long-lasting changes that have affected the NB in the last four decades.

Because such changes are mediated by nonlinear feedback mechanisms leading to abrupt instabilities, they are inherently difficult to predict and perhaps impossible to reverse. This comparison of the NB and SB ecosystems highlights the important role of small pelagic fishes in maintaining the integrity and stability of such ecosystems and the necessity for a conservative approach in managing small pelagic fish stocks (Cury et al. 2011, Smith et al. 2011) to preserve biodiversity, productivity, and the main functions and services of marine ecosystems. Failure to do so might result in sudden degradations and collapses of other productive marine systems.

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APPENDIX 1

DETAILS OF MODEL SIMULATIONS OF DEPLETION OF FORAGE FISHES

For purposes of our study, model experiments on depletion of the various small pelagic fishes species in the southern Benguela were run with a slightly modified version of the Shannon et al. (2008) Ecopath with Ecosim model that was fitted to time series of abundance and catch for the period 1978–2003. The aim of including these simulations is primarily to demonstrate the vital role played by small pelagics in sustaining ecosystem function, which is eroded when these stocks collapse, as appears to be the case in the northern Benguela, where jellyfishes and goby are now strong ecosystem components. The original trophic model fitted to time series and used to explore ecosystem drivers (Shannon et al. 2008), was reconfigured in Ecopath with Ecosim version 6 so that the dynamics of small and large horse mackerel and shallow- and deepwater Cape hake were represented as multistanza groups (one group growing into another) as opposed to simple linked model groups. Total mortality rates for the juvenile stanzas of the three species were estimated to retain biomass levels per model group as close as possible to those in the previous model version. The model was then refitted to time-series data by the procedure previously adopted and reported in Shannon et al. (2008). First, a search was run for vulnerability values describing the 25 most sensitive predator/prey interactions in the model. Second, a hypothetical forcing function that improved model fits to available time-series data was fitted to interactions between anchovy and its predators. Third, a hypothetical forcing function was fitted to sardine-predator interactions. Finally, a small hypothetical forcing function was applied to primary productivity to optimize the fit of the model. Dynamic trajectories of model groups were consistent with published trajectories (Shannon et al. 2008). Simulations from this refitted model were run with Ecopath with Ecosim 6 (version 1.0.0.0, the latest publicly available model build for mid-February 2010).

SIMULATED DEPLETION OF FORAGE FISHES IN THE SOUTHERN BENGUELA

We examined the trophic effects of depleting one forage-fish group at a time: anchovy, sardine, Whitehead's round herring, juvenile horse mackerel, and mesopelagic fishes. The model ran from 1978 through 2003. Thereafter annual fishing mortality (F) per fished group was maintained at the 2003 level, and the model projected forward to the year 2061. This simulation served as the baseline ("status quo"). For depletion simulations, after the 2004–2010 "burn-in" period, F of a single forage fish model group was altered (from 2011 onwards), whereas F s of other model groups remained at the 2003 "status quo" levels for the 50-yr simulation period.

We estimated a measure of relative "virgin biomass" for each forage-fish species by setting F of the group in question to zero for the duration of the 50-yr projection period. The biomass recorded at the end of this simulation (2061) was taken as "virgin biomass" level for the forage-fish group in question.

We considered model simulations in which F s were increased for one forage-fish group at a time, to explore the possible ecosystem impacts of depleting forage fish in the southern Benguela. Four fishing levels were considered (Smith et al. 2011), causing the biomass of the target fish group to fall to a specified fraction of its virgin biomass at the end of the projection period (2061). The results presented here are for levels of biomass reduced to 40% of virgin biomass (B_{40}) as they provide sufficient encapsulation of the results for our purposes.