

Jellyfish overtake fish in a heavily fished ecosystem

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Over the past half century fishing has led globally to a reduction in the mean trophic level of commercially landed species, with a significant decline from large predatory fish toward plankton-eating pelagic species and low trophic-level invertebrates [1]. An implied endpoint of this 'fishing down marine food webs' is a proliferation of previously suppressed gelatinous plankton (jellyfish) [2] thriving on the food no longer consumed by fish. We report here that, in the heavily exploited northern Benguela off Namibia, a transition towards this endpoint has occurred, and jellyfish biomass (12.2 million tonnes (MT)) now exceeds the biomass of once-abundant fish (3.6 MT). This is a profound ecosystem change, with possible consequences from carbon cycling to fish stock recovery.

The northern Benguela is a highly productive eastern-boundary ecosystem fertilised by upwelling, nutrient-rich waters. Historically the region supported large stocks of fish, including sardines (*Sardinops sagax*) and anchovies (*Engraulis encrasicolus*), but heavy fishing pressure has reduced stocks, and total landings have fallen from around 17 MT in the late 1970s to just 1 MT now (Figure 1A). Prior to this period of heavy exploitation, large jellyfish (Scyphozoa and Hydrozoa) were not prominent in the Benguela ecosystem: reports of extensive plankton sampling in the 1950s and 1960s do not mention large jellyfish, although numerous small gelatinous species (e.g. ctenophores) were observed (for example [3]).

Following early collapses of pelagic fish stocks (in the 1960s), reports of the large

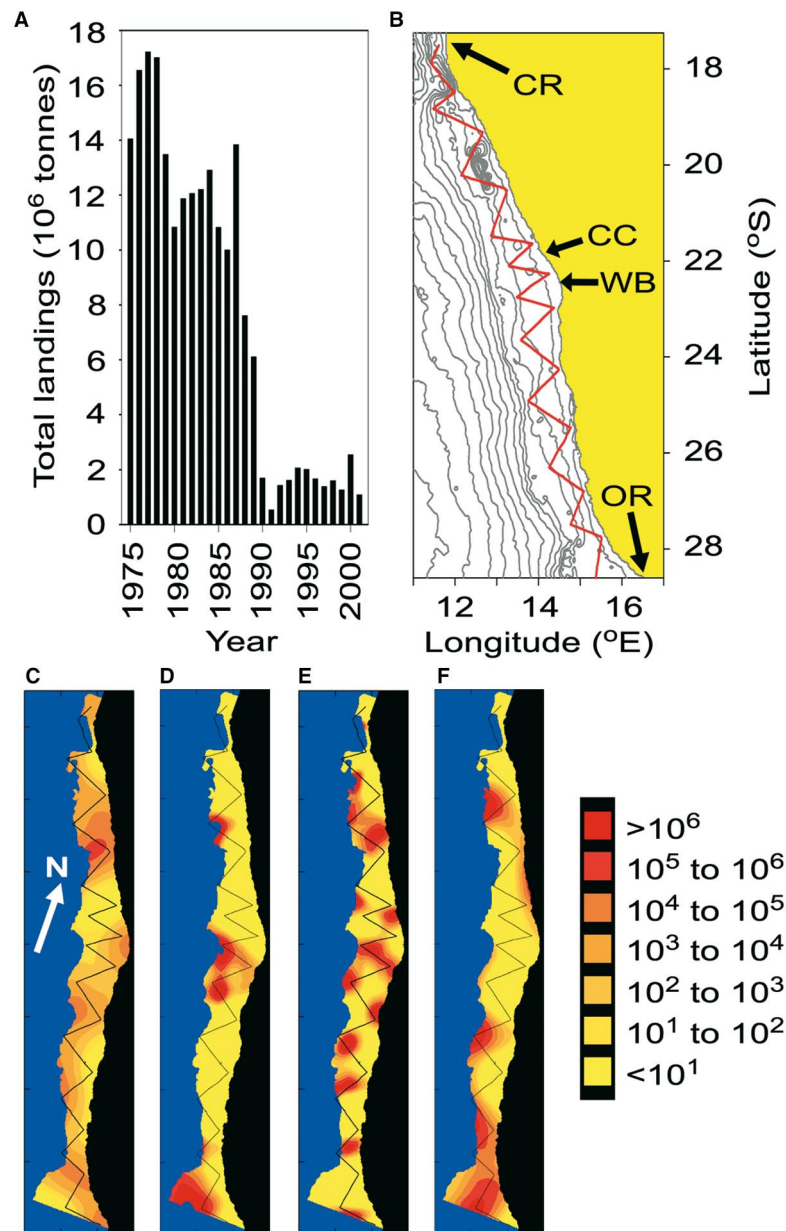


Figure 1. Fish and jellyfish in the Namibian Benguela. (A) Time series of total fish landings from the northern Benguela (from FISHSTAT+ www.fao.org/fi/statist/FISOFT/FISH-PLUS.asp. Data are Capture Production in the South East Atlantic Major Area 47, Western Coastal Subarea, Divisions 1.3 Cunene, 1.4 Cape Cross, and 1.5 Orange River, covering 15°S to 30°S and from the coast to 10°E). FISHSTAT+ data extend from 1975 only, so do not cover the large sardine crash in the 1960s [11]. (B) Bathymetric map (grey contour lines at 100, 200, 300, 500, 700, and 1000 to 4500 in 500 m increments) and the cruise track (solid red line) followed southward from the Angola–Namibia border to the Namibia–South Africa border. CR, Cunene River; WB, Walvis Bay; CC, Cape Cross; and OR, Orange River. (C–F) maps of distribution of jellyfish and fish from 17°15'S 11°28'E to 28°45'S 15°50'E: (C) *Chrysaora hysoscella*; (D) *Aequorea forskalea*; (E) Cape horse mackerel/Cape hake; and (F) clupeids (sardine, anchovy and round herring combined). Colour scale is density, tonnes per nautical mile².

and conspicuous jellyfish *Chrysaora hysoscella* (mean umbrella diameter ~27 cm [4]) and *Aequorea forskalea* (mean umbrella diameter ~13 cm [4])

became increasingly common [5]. Since the 1990s, reports of these jellyfish have been ever-increasing, particularly because of the nuisance they now

cause to fishing (bursting trawl nets, spoiling catches), power generation (blocking power station coolant intakes) and diamond mining (blocking alluvial sediment suction). Despite their present prevalence (the term 'jellyfish explosion' has been used [6]), the ascendance of jellyfish has not been quantified, and ecosystem studies have had largely to ignore jellyfish because of a lack of quantitative data on biomass and distribution [6].

We have conducted a series of research cruises to study *C. hysoscella* and *A. forskalea* (previously *A. aequorea*) in the northern Benguela (for example [4,7]). The most recent, in August 2003, was a survey to map distribution and estimate biomass. We used multi-frequency scientific echosounders and trawl nets to sample jellyfish and fish (see Supplemental data available on-line with this issue) along the entire Namibian shelf — between the Angolan and South African borders and the 25 m and 350 m depth contours, an area of 33,710 square nautical miles (Figures 1B–F). We estimate that the biomass of jellyfish was 12.2 million tonnes (99% by mass *A. forskalea*, mean jellyfish density 361 T n.mi⁻², standard error 22 T n.mi⁻²), and that the total biomass of fish was 3.6 MT (Cape horse mackerel 1.1 MT, mean 33 T n.mi⁻², SE 1.5 T n.mi⁻²; Cape hake 1.7 MT, mean 50 T n.mi⁻², SE 2.3 T n.mi⁻²; clupeids 0.8 MT, mean 23 T n.mi⁻², SE 1.0 T n.mi⁻²). Our fish biomass estimates are consistent with independent fish stock assessments conducted by others for fishery-management purposes (see Supplemental data) and our maps of jellyfish distribution are consistent with recent qualitative surveys [7].

Jellyfish biomass has increased substantially in several locations worldwide, perhaps as a consequence of fishing [8]. Ecosystem shifts from dominance by fish to dominance by jellyfish may be irreversible as jellyfish are predatory upon fish eggs and larvae, and strong competitors for fish food [9,10]: jellyfish may thus impede the recovery of fish stocks even after a cessation

of fishing. Jellyfish proliferation may also be climatically driven [8], either directly or in response to the impact of environmental perturbations on abundance and distribution of fish: an El Niño event in the Benguela in 1963 contributed to the sharp decline in sardine biomass [11], and may have presaged the early establishment of jellyfish. In the north Atlantic there is a significant link between climate, as encapsulated by the North Atlantic Oscillation index, and jellyfish abundance. During the last boreal winter (2005/06) the North Atlantic Oscillation was in a pronounced negative phase (see <http://www.cgd.ucar.edu/cas/jhurrell/indices.data.html#naopcdjfm>) and, if previous patterns persist [12], this could result in outbreaks of jellyfish in coastal waters on both sides of the ocean this summer (2006). Such outbreaks have consequences for fisheries [9] and are trophic dead-ends (jellyfish have few predators) with consequences for carbon cycling. Jellyfish play potentially major controlling roles in marine ecosystems and, in this era of apparent jellyfish ascendancy, marine ecosystem managers and modellers cannot afford to ignore them.

Supplemental data

Supplemental data, including details of the acoustic sampling and analysis methods, are available at <http://www.current-biology.com/cgi/content/full/16/13/R492/DC1/>

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