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Modelling effects of fishing in the Southern Benguela ecosystem

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A mass-balanced model of the Southern Benguela upwelling ecosystem was constructed using Ecopath. The effects of altered fishing on three abundant small pelagic fish, and on hake, are explored using Ecosim for three scenarios of top-down and bottom-up control: (1) bottom-up control of zooplanktivorous fish by zooplankton dampens effects of altered fishing; (2) wasp–waist control (top-down control of zooplankton by their predators and bottom-up control of predators by small pelagic fish) causes vigorous effects to propagate through the ecosystem; and (3) effects of mixed control (neither top-down nor bottom-up control) are intermediate between the former two scenarios. Heavier fishing may be sustainable under one scenario of control, whereas fisheries may crash if another type of control is assumed. The key to predicting ecosystem effects of fishing is understanding the way in which components of the ecosystem interact.

Key words: Benguela, ecosystem, effects of fishing, pelagic fish, trophic models, upwelling.

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Introduction

Models of trophic flows quantify the interactions between components of an ecosystem, and may be useful in assessing the direct and indirect effects of fishing. Ecopath, an ecosystem modelling tool which has gained much momentum (Christensen and Pauly, 1992), has been extended into Ecosim to address aspects of fishing (Walters *et al.*, 1997). This dynamic approach to modelling energy flow is showing great potential in addressing fisheries effects on ecosystems (e.g. Kitchell *et al.*, 2000). We present an attempt at using Ecopath with Ecosim to compare ecosystem effects of fishing in the Southern Benguela upwelling system under different combinations of bottom-up and top-down control.

Methods

Jarre-Teichmann *et al.* (1998) constructed a trophic flow budget for the Southern Benguela ecosystem during the 1980s using Ecopath. The model has later been refined and new data incorporated (Shannon and Jarre-Teichmann, 1999). Based on this model, we used Ecosim to investigate the impacts of changing fishing mortality. All settings in Ecosim assumed default values, with the exception of "flow control", which determines the type of control between groups. Three scenarios of flow control were explored: (a) bottom-up control of predators by their zooplankton prey (low zooplankton vulnerability to predators; i.e. donor control); (b) all interactions of mixed control type (neither bottom-up nor top-down); and (c) top-down control of zooplankton (predator control) and bottom-up control of pelagic predators by small pelagic fish, including anchovy, sardine, round herring, saury, flying fish, etc. (food limitation for predators of small pelagics). This scenario will be referred to as "wasp–waist" control (Cury *et al.*, this volume).

We also considered three scenarios to explore the impacts of altered fishing on three of the most abundant small pelagic fish groups – anchovy (*Engraulis capensis*), sardine (*Sardinops sagax*), and round herring (*Etrumeus whiteheadi*) – and on the commercially most important fish – hake (*Merluccius capensis* and *M. paradoxus*) – off South Africa: (1) a permanent fourfold increase in fishing mortality on anchovy, sardine and round herring; (2) a temporary fourfold increase (pulse) in fishing mortality on anchovy, sardine and round herring, after which fishing mortality was restored to the original level; and (3) a temporary fourfold increase (pulse) in fishing mortality on hakes, after which fishing mortality was restored to the original level. In all scenarios, the model was run for 10 years without a change in fishing, so that stability was reached prior to perturbation of the ecosystem, after which runs continued for an additional 40 years.

Results

When there is bottom-up control of predators by zooplankton, effects of altered fishing are small and dampened (Fig. 1). This is caused by intense competition between species eating zooplankton. Under wasp–waist control, however, major perturbations propagate through the systems, because competition for zooplankton food is not intense and ecosystem components respond more readily to changes in fishing pressures. Mixed control type interactions gave intermediate results.

Permanent fourfold increase in fishing mortality on anchovy, sardine, and round herring (Fig. 1a).

Anchovy and sardine stocks collapsed under all three flow control scenarios. By contrast, round herring was little affected, as fishing mortality was small at the outset. Under bottom-up control of small pelagic fish by zooplankton, the system stabilized at new biomass values: anchovy at half of its original biomass, and sardine at 40%. Populations of predators of small pelagic fish (seals, cetaceans, seabirds, and large pelagic fish) stabilized at smaller sizes. By comparison, groups such as other small pelagic fish, horse mackerel and cephalopods, competing with anchovy and sardine for zooplankton prey, stabilized at larger population sizes than were maintained before fishing increased. Under wasp–waist control, chub mackerel, horse mackerel, and other small pelagic fish were able to take advantage of reduced anchovy and sardine, competitors for zooplankton prey. Large pelagic fish were reduced to a stable level at 43% of their original biomass. Abundance decreased steadily over 50 years when there was mixed control. Anchovy and sardine catches were sustainable at about twice their original levels when bottom-up control was considered. In contrast, the fisheries collapsed under wasp–waist control. Fishing of round herring at four times the original fishing mortality (still only at F=0.12) was sustainable for the 40-year simulation period under all three control types. Nevertheless, heavier exploitation had detrimental effects on other groups feeding on round herring.

Pulse fishing on anchovy, sardine, and round herring (Fig. 1b).

Under bottom-up control, all components recovered fully within 10 years after fishing had returned to the original level. Recovery of anchovy and sardine is fast, their predators (large pelagic fish, seabirds, and mammals) and competitors (e.g. cephalopods) took longer to

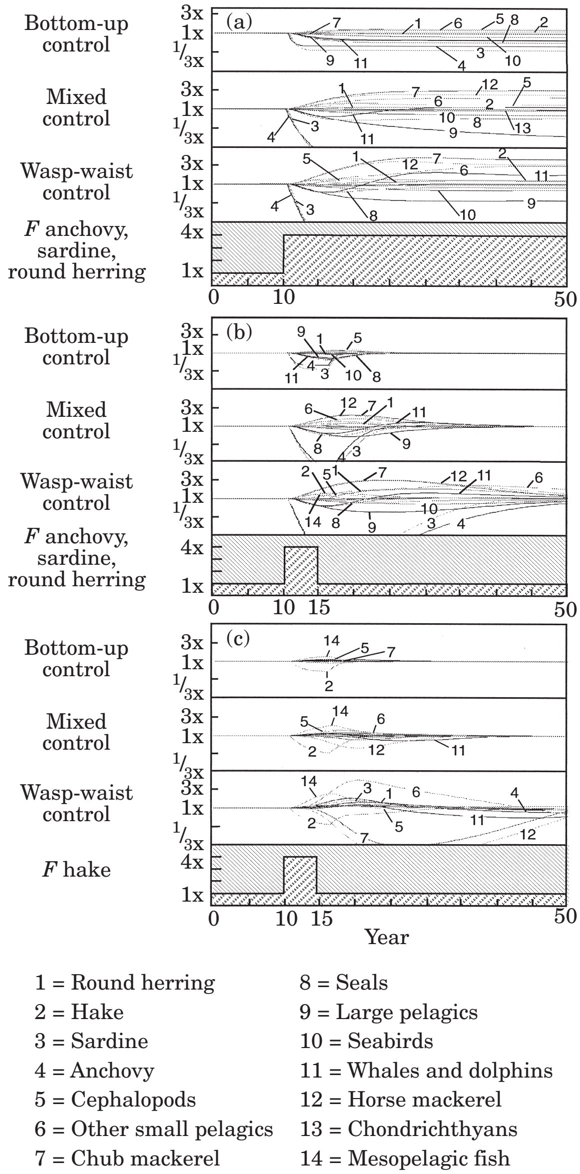

Figure 1. Ecosim simulation of effects on biomass of (a) a permanent fourfold increase in fishing mortality (F; lower panel for each scenario) of small pelagics (anchovy, sardine, and round herring) from year 10 onward, and of a temporary fourfold increase in F of (b) small pelagics and (c) hake from years 10 to 15, after which F was restored to the original level, based on three alternative types of flow control: bottom-up, mixed, and wasp–waist control. Biomass is plotted relative to original biomass (1 × line). Species (groups) indicated by numerals (1: round herring; 2: hake; 3: sardine; 4: anchovy; 5: cephalopods; 6: other small pelagic fish; 7: chub mackerel; 8: seals; 9: large pelagic fish; 10: seabirds; 11: cetaceans; 12: horse mackerel; 13: chondrichthyans; 14: mesopelagic fish).

recover. Mixed and wasp–waist control required longer recovery times and responses were more pronounced. All components recovered fully within 15 years under mixed control, whereas many groups had not fully recovered by the end of the simulation period under wasp-waisted control. Anchovy biomass only reached 86% of its original size by the end of the simulation period.

Pulse fishing on hake (Fig. 1c)

Heavy fishing reduced the biomass of hake, thereby favouring some of its prey species, such as mesopelagic fish and cephalopods. Horse mackerel were negatively affected by the increased biomass of mesopelagic fish which compete for zooplankton food. All groups recovered within 10 years after fishing had returned to the original level under bottom control, and within about 20 years under mixed control. Mesopelagic fish responded almost immediately to a change in fishing mortality in hake, whereas groups such as chub mackerel, saury, and other small pelagic fish had a delayed (3–4 years) response. Wasp–waist control perturbed the system greatly, many groups not having returned to their original level even after 35 years.

Discussion

Ecosim modelling indicates that heavier fishing on small pelagic fish favoured competing species through enhanced availability of zooplankton prey. The increase in abundance of these competitors delayed the recovery of the target species once fishing returned to the original level. Predators of small pelagics declined and were slow to recover. Higher fishing mortality on predators allowed mesopelagic fish to become more abundant, thereby negatively impacting other species through increased competition for zooplankton prey. Effects of changes in fishing mortality were dampened when there was bottom-up control by zooplankton, whereas top-down control of zooplankton caused vigorous responses of components, and recovery was slower. These results are similar to those obtained by Mackinson *et al.* (1997), who used Ecosim to compare the trophic impacts of harvesting in three upwelling ecosystems. They showed that heavy exploitation of small pelagics led to an increase in biomass of their prey and competitors, and a corresponding decline in biomass of predators. When top-down control was applied to the Peruvian system, components fluctuated wildly and underwent larger changes in biomass than under bottom-up control.

Our model suggests that ecosystem effects of fishing are determined to a large extent by the way in which interactions between components within a system are linked. Results were very different under different combinations of top-down and bottom-up control between selected groups at different trophic levels. Understanding the way an ecosystem functions in terms of internal control between components appears to be a key to predicting ecosystem effects of fishing.

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