

Trophodynamic indicators for an ecosystem approach to fisheries

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Acknowledging ecological interactions, such as predation, is key to an ecosystem approach to fisheries. Trophodynamic indicators are needed to measure the strength of the interactions between the different living components, and of structural ecosystem changes resulting from exploitation. We review trophodynamic indicators derived from models, as well as from emergent patterns such as trophic cascades and regime shifts. From 46 indicators identified in the literature, six (catch or biomass ratios, primary production required to support catch, production or consumption ratios and predation mortality, trophic level of the catch, fishing-in-balance, and mixed trophic impact) were selected because of their ability to reveal ecosystem-level patterns, and because they match published criteria. This suite of indicators is applied to the northern and southern Benguela ecosystems, and their performance is evaluated to depict drastic and contrasted ecosystem changes. A few complementary indicators are suggested as needed to detect the trophodynamic impacts of fisheries and ecosystem changes. Trends in indicators are sensitive to the choice of trophic level made for certain species. Trophodynamic indicators appear to be conservative, because they respond slowly to large structural changes in an ecosystem. Application of the selected indicators to other marine ecosystems is encouraged so as to evaluate fully their usefulness to an ecosystem approach to fisheries, and to establish international comparability.

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Introduction

The Reykjavík declaration of 2001, reinforced at the World Summit on Sustainable Development in Johannesburg in 2002, requires nations to base policy governing exploitation of marine resources on an ecosystem approach. To fulfil this challenge, a strategy is needed that is based on the development of ecosystem-based indicators coupled with operational frameworks that bridge the gaps between scientific results, social needs, and a comprehensive and

effective ecosystem approach to fishing (EAF). From an ecological point of view, this means that interactions between the different components within marine ecosystems have to be acknowledged, understood, and quantified (Cury *et al.*, 2003).

The strength of ecological processes such as trophodynamic interactions, i.e. predation and competition, has been recognized as being of great importance in fish population dynamics (Bax, 1998). Trophic interactions raise two concerns for fisheries management. The first is the decline

in the food resource upon which some component of the ecosystem subsists, necessitating its departure to other localities or causing its decline (Link, 2002). The second is the indirect effect of decreasing fish biomass on ecosystem functioning (e.g. regime shifts). To be useful in tracking progress towards sustainable development, indicators need to be closely linked to clear objectives (what is to be achieved, or what definitely needs to be avoided), and translated into reference points (Garcia and Staples, 2000). This review focuses on descriptive and performance indicators as a tool for cross-system comparisons. We briefly summarize the important processes and patterns, and review trophodynamic indicators derived from models of trophic interaction, as well as from observed patterns. A selection is then proposed on the basis of the criteria of Rice and Rochet (2005). Finally, this suite of indicators is applied to the northern and southern Benguela, two well-studied ecosystems, and their performance is evaluated.

An extensive, though not exhaustive, review found more than 200 different indicators of ecosystem status (Rice, 2000). However, the challenge is not to find indicators of ecosystem status, but rather to evaluate their performance (Rice, 2003). Potential indicators are obtained mainly from model outputs or statistical analyses. Trophodynamic indicators are grouped here according to their linkage to specific objectives, i.e. indicators used to characterize single foodweb components (e.g. population, species, functional group, trophic level) and indicators used to characterize ecosystem state.

Main quantitative indicators covering aspects of trophic ecology are presented in Table A1 of the Appendix. Most indicators are simple or composite (e.g. ratios) measures of flows of some currency (mass or energy), but some are based on other metrics, e.g. position in the food chain (trophic level), number of trophic links (connectance), or probabilistic considerations (information). Most system indicators (Table A1, part b, of the Appendix) have been related to ecosystem maturity (Odum, 1969; Christensen, 1995, 2000), and they depend upon the formulation of the underlying foodweb model (e.g. aggregation or disaggregation of trophic groups, diverse assumptions about structural and functional parameters; Rice, 2003).

A selection of indicators

The trophic indicators listed (Table A1 of the Appendix) were considered with respect to the criteria developed by ICES (2001), modified by Rice and Rochet (2005). Six were subsequently selected on the basis of their perceived suitability for fisheries management purposes. Their ability to quantify effects of fishing was then evaluated in a preliminary scoring procedure on the basis of the nine criteria (Table 1). The procedure was to ask participants of the SCOR-IOC Working Group 119 task force on trophodynamic indicators to score the different individual indicators,

then to discuss the results collectively to obtain the final evaluation.

The relative change in species (or functional group) composition within the catch or surveyed community can be quantified by means of biomass ratios (preferable to catch ratios), to characterize ecosystem changes (e.g. piscivorous:zooplanktivorous fish). Such ratios are easily understood and measurable, and are often, but not exclusively, sensitive to fishing. However, finding theoretical foundations for setting reference points is problematic, and these would have to be defined empirically based on historical data.

The primary production required (PPR) to support catches (Y) in a system is expressed as a percentage of the total primary production available in the system during a given period, and may be computed as

$$PPR = \sum_{\text{paths}} \left[\frac{Y_i}{P_i} \times \prod_{\text{predator, prey}} \frac{Q_{\text{predator}}}{P_{\text{predator}} \times EE_{\text{predator}}} \times DC'_{\text{predator, prey}} \right] \quad (1)$$

(for symbols used in equations, see Appendix). PPR can be used to compare effects of fishing at different trophic levels (Pauly and Christensen, 1995), quantifying the ecological expense of fishing in an ecosystem. Considerable uncertainty (consequently with heavy assumptions) still exists about the trophic structure of the lower part of the foodweb (i.e. plankton) in modelled upwelling systems, with implications for PPR estimates. Therefore, the estimate of relative PPR is strongly dependent on a realistic estimate of actual primary production (Jarre-Teichmann and Christensen, 1998), which is often not available on an ecosystem scale.

The proportion of production by different components, and the proportion of the total consumption of each prey taken by each predator group, can be used to quantify the relative importance of prey or predators (consumers). The importance of predation and/or fishing mortality relative to total mortality in any particular group may be helpful in monitoring changes in trophic structure within or among systems. Predation mortality is often larger than fishing mortality (Bax, 1991; Jarre *et al.*, 1991), but their relative importance may change through time, or differ between systems. Effects of fishing will be most apparent in cases of tight trophic coupling, such as between forage fish subject to heavy fishing pressure and seabird predation (Crawford and Dyer, 1995).

Trophic level (TL) expresses the position of organisms within a foodweb. The mean TL of the catch may be computed for each year, from

$$\overline{TL}_k = \frac{\sum_{i=1}^m Y_{ik}}{TL_i \sum_{i=1}^m Y_{ik}} \quad (2)$$

The mean TL of fisheries landings can be used as an index of sustainability. The TL of fish usually increases during

Table 1. Selected trophodynamic indicators scored according to nine criteria (1-cc, concreteness; 2-tb, theoretical basis; 3-pa, public awareness; 4-co, cost; 5-mm, measurement; 6-ah, availability of historical data; 7-ss, sensitivity; 8-rs, responsiveness; 9-sp, specificity; see Rice and Rochet, 2005) in evaluating the capability of ecosystem indicators to measure the impact of fishing (the number of asterisks represents scores from 1 = low to 5 = high; see Appendix for the symbols used).

Indicator	1-cc	2-tb	3-pa	4-co	5-mm	6-ah	7-ss	8-rs	9-sp	Strengths or weaknesses
1. Y or B ratios	*****	**	***	Y*** B*	**	Y**** B**	Y* B****	***	**	Y-derived indicator may not reflect biological dynamics.
2. PPR for Y	**	****	*	*	*	*	**	**	****	Y-derived indicator may not reflect biological dynamics.
3. P and Q a) P/Q ratios b) Q proportion c) Predation M	**	***	*	**	**	*	**	**	*	Reflects dynamics/status of exploited and non-exploited stocks. Data requirement may be great.
4. TL of Y	***	***	***	****	***	****	***	***	****	Tracks fishing down the foodweb. TL may remain constant despite changes in Y composition and foodweb changes/collapse. May be slow to respond to large ecosystem change.
5. FiB	***	****	***	****	***	****	****	****	****	Indicates whether Y-change consistent with TL being fished. May miss foodweb collapse at low TL if high-TL Y is sustained. Depends on TL and Y in reference year: consider periods (“regimes”) separately.
6. TI	*	****	**	*	*	**	***	**	**	Takes account of direct and indirect (often unexpected) effects. Derived from static model; may not reflect dynamic effects.

ontogeny, because larvae and juvenile fish are likely to feed at lower levels than conspecific adults (Pauly *et al.*, 2001). Fisheries tend first to remove large, slow-growing predatory fish, so reducing the mean TL of the fish remaining in the system. Therefore, a decline in TL may occur within species as well as among species, eventually leading to declining trends of mean TL in the catches extracted from an ecosystem, a process now known as “fishing down marine foodwebs” (Pauly *et al.*, 1998).

The fishing-in-balance index (FiB) is computed as

$$\text{FiB} = \log \left[\frac{\left(\sum_i Y_{ik} 10^{\text{TL}_i} \right)}{\left(\sum_i Y_{i0} 10^{\text{TL}_i} \right)} \right] \quad (3)$$

where the subscript 0 refers to the year at the start of a series, which serves as an anchor (Pauly *et al.*, 2000). Because production is higher at low TL than at high TL, catches tend to increase, at least initially, if TL declines (i.e. when the fisheries start targeting species lower in the foodweb; Pauly *et al.*, 1998). This process led Pauly *et al.* (2000) to suggest the dimensionless FiB index designed, given an estimate of the transfer efficiency between TL, to

maintain a value of zero when a decrease in TL is matched by an appropriate catch increase (and conversely), and to deviate from zero otherwise. An increase in FiB indicates expansion of a fishery (geographically, or expansion beyond the initial ecosystem to stocks not previously exploited, or only lightly exploited) or that bottom-up effects have occurred, e.g. increased primary productivity (Pauly and Watson, *in press*). Conversely, a decrease indicates geographic contraction of the fisheries, or a collapse of the underlying foodweb (impairing the ecosystem functioning), leading to the “backward-bending” plots of TL vs. catch originally presented in Pauly *et al.* (1998). A decrease in FiB will also be observed if discarding takes place that is not reflected in the reported catches (Pauly and Watson, *in press*). FiB requires the assumption that transfer efficiency is constant (and known sufficiently well) across trophic levels (Pauly *et al.*, 2000). Nevertheless, FiB is believed to provide a better indicator of ecosystem change than catch or catch composition, because of its integrative nature (Garcia and Staples, 2000).

Mixed trophic impact (TI) is a measure of the relative impact of a change in the biomass of one component on other components of the ecosystem (Ulanowicz and Puccia, 1990). The analysis is based on an input–output method

used to assess direct and indirect economic interactions (Leontief, 1951). Through matrix calculations, TI quantifies the net effects of one species on every other species in a system, taking into account positive effects of a prey species on its predator (weighted relative to its proportion in the diet), negative effects of a predator on its prey (weighted according to the fraction of the production of a prey that is consumed by the predator), and the indirect effects one species may have on another through trophic interactions. Matrices are constructed of relative net impacts of each group on every other, scaled between -1 and 1 . An assumption is that the trophic structure remains constant, implying that TI should not be used in a predictive sense, but rather as a type of sensitivity analysis, to identify those groups that may have large trophic impacts on others, and so might be suitable indicators for monitoring fisheries effects across an ecosystem.

Comparing the northern and the southern Benguela

General description

The northern and southern Benguela are dynamic and comparable upwelling systems, in which the fisheries target largely similar demersal (Cape hakes, *Merluccius capensis* and *M. paradoxus*) and pelagic fish species (sardine, *Sardinops sagax*; anchovy, *Engraulis encrasicolus*; horse mackerel, *Trachurus t. capensis*). However, the two ecosystems have followed very different trajectories since the 1950s in terms of exploitation, species composition, structure, and dynamics (Figure 1). A regime shift was documented in the northern Benguela (Boyer and Hampton, 2001) as the result of overexploitation, whereas the southern Benguela exhibits variability that appears to be within natural limits (Cury and Shannon, 2004). Trophic models of the two ecosystems are available (Shannon and Jarre-Teichmann, 1999; Shannon *et al.*, 2003; Roux and Shannon, 2004), and were standardized for comparative purposes according to the methods described by Moloney and Jarre (2003). Two models were used for each system to describe the foodwebs under different productivity levels of pelagic fish (northern Benguela, 1980–1989 and 1995–1999; southern Benguela, 1980–1989 and 1990–1997), and these were used as case studies for the application and interpretation of the six selected trophic indicators, to assist in testing their usefulness.

The detailed recent history is reflected in the time-series of catches shown in Figure 2a, namely a sequential exploitation and depletion of the three main stocks in the northern Benguela (sardine, anchovy, and hake). Few management measures could be implemented effectively there until Namibia's independence and proclamation of a 200-mile EEZ in 1990. Since independence, hake catches have recovered only modestly, sardine catches have remained insignificant, and horse mackerel has continued to dominate

the total biomass landed, as it has since the late 1970s, although it has declined slowly since the late 1980s. Total catches have steadily decreased from a peak of >2 million tonnes in 1968 to around 0.5 million tonnes in the late 1990s.

In the southern Benguela, a bottom-trawl fishery targeting hake had been established even before 1950, catches slowly increasing from around 50 000 to 140 000 t between 1950 and 1977, when a 200-mile Fishing Zone was proclaimed by South Africa (Payne, 1995). Since then, hake catches have risen only slightly. Horse mackerel never dominated the South African catches, though sardine constituted the bulk of the landed biomass until 1965, before being replaced by anchovy until the mid-1990s. Recently, landings of both sardine and anchovy have increased. The total catch shows fluctuations around 0.5 million tonnes, without a clear trend, from the early 1960s to the present (Figure 2a). Fisheries have been carefully managed, for example by maintaining annual pelagic fish catches well below 25% of estimated annual biomass since the early 1990s.

Catch ratios

The ratio between demersal and total catch increased in both systems during the second half of the 20th century (Figure 2b), but only moderately so in the southern Benguela (from 20% to 36% between 1950 and 2000; observed range 16–45%). In comparison, the ratio in the northern Benguela increased from approximately zero before 1960 (when catches were mostly sardine, and there was little local or foreign interest or knowledge of demersal resources) to 90% in 2000, when catches of small pelagics were insignificant, and the bulk of the landings was large horse mackerel (largely demersal, in contrast to small horse mackerel, which are caught pelagically) and hake targeted by demersal trawlers. The difference in trends results from the earlier establishment of a trawl fishery in the southern than in the northern Benguela.

Mean trophic level (TL) of catch

The trajectory of the mean TL of catches in the northern Benguela underwent three distinct phases (Figure 2c, d). From 1950 to 1964, the TL remained around the low value of 2.7 (corresponding to the TL of sardine). The TL then increased rapidly to values in excess of 3.8 between 1965 and 1972, following the rapid development of the hake fishery and the decline of the sardine stock. Finally, from 1972 to 2000, the index remained stable at an average value of 3.7 (s.d. = 0.1), without a trend over the past 29 years ($F = 0.69$, $p > 0.4$). The apparent stability is due to the continuing decline of small pelagics in the catches, and the partial replacement of hake by horse mackerel (medium TL) during a period of general decline in overall catches.

In the southern Benguela, the trajectory displays a significant dip between 1958 and 1965, when catches

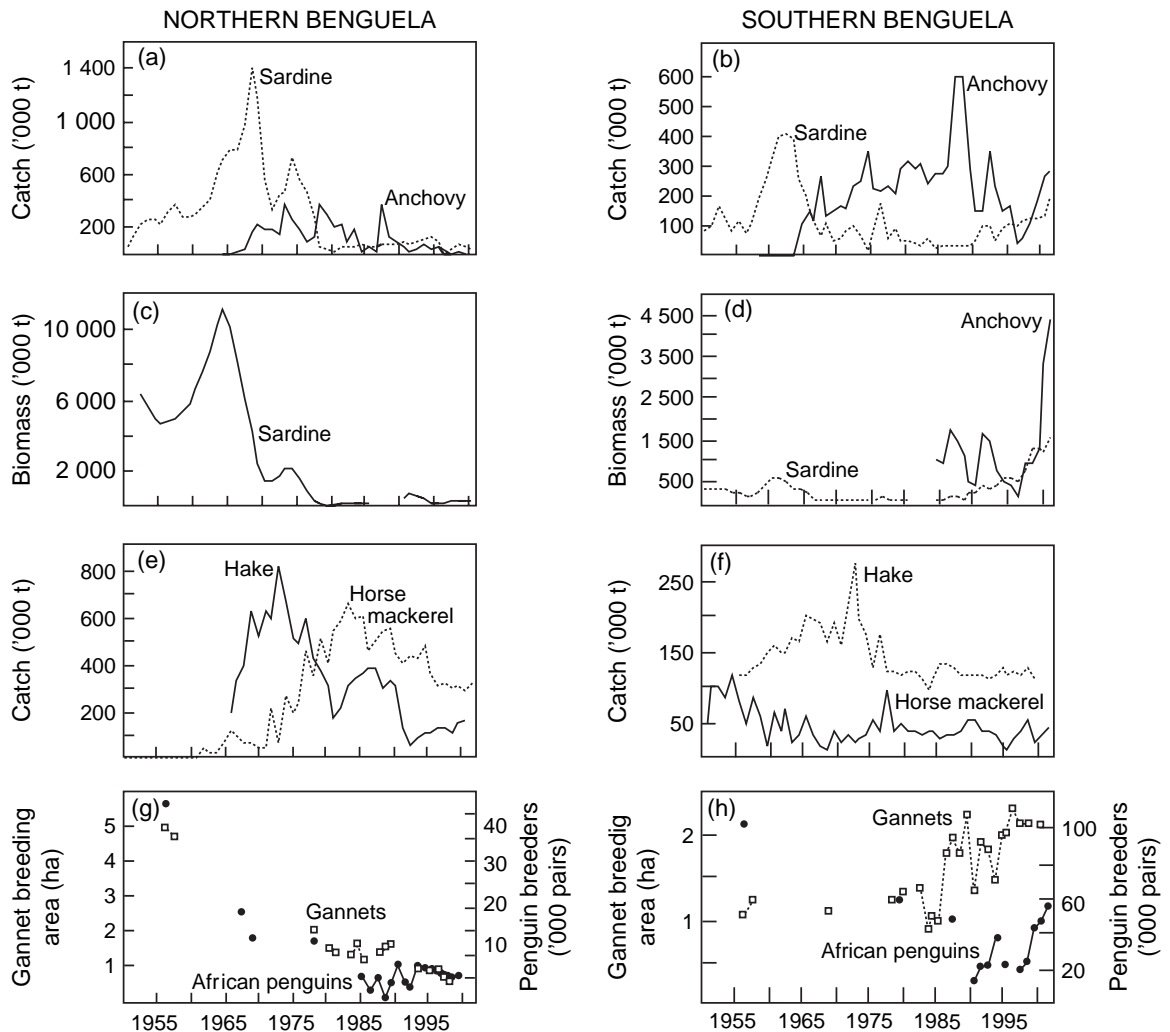


Figure 1. Historical records of key species abundance and catches in the northern and southern Benguela over the past five decades (redrawn from Cury and Shannon, 2004).

were dominated by sardine (Figure 2d). From 1966 to 1991, the TL increased slowly (average slope 0.004 per year), but significantly ($p < 0.005$), but declined slightly thereafter. The rising trend is due to the slowly increasing hake catches and the replacement of sardine (TL = 3) by anchovy (TL = 3.5) as the dominant small pelagic species. The slight decline during the 1990s cannot be interpreted as an effect of “fishing down the foodweb”, because hake catches remained remarkably stable. In fact, the decline reflects the increasing contribution of sardine following the successful recovery of that stock during the 1990s.

Fishing-in-balance (FiB) index

The trajectory of the FiB index (Figure 2e) in the northern Benguela shows a rapid increase between 1960 and 1972,

reflecting the rapid expansion of the pelagic fishery, followed by an expansion of the trawl fishery and declining pelagic catches. From 1972 to 2000, the FiB shows a slight but significant overall decline (with a slope of -0.07 per annum, $r^2 = 0.49$, $p < 0.0001$). The main factor contributing to this negative trend is the overall decline in total catches (Figure 2a), and the increasing relative contribution of horse mackerel to the catches.

Because the fishery in 1950, the reference year, was more developed in the southern than in the northern Benguela, the amplitude of FiB changes is much smaller in the southern Benguela. Nevertheless, the increasing trend apparent between the mid-1960s and 1988 seems to track the overall increasing catches of anchovy, which peaked in 1987 and 1988. The reverse trend in the 1990s reflects the increasing contribution of sardine (Figure 2a). FiB plots

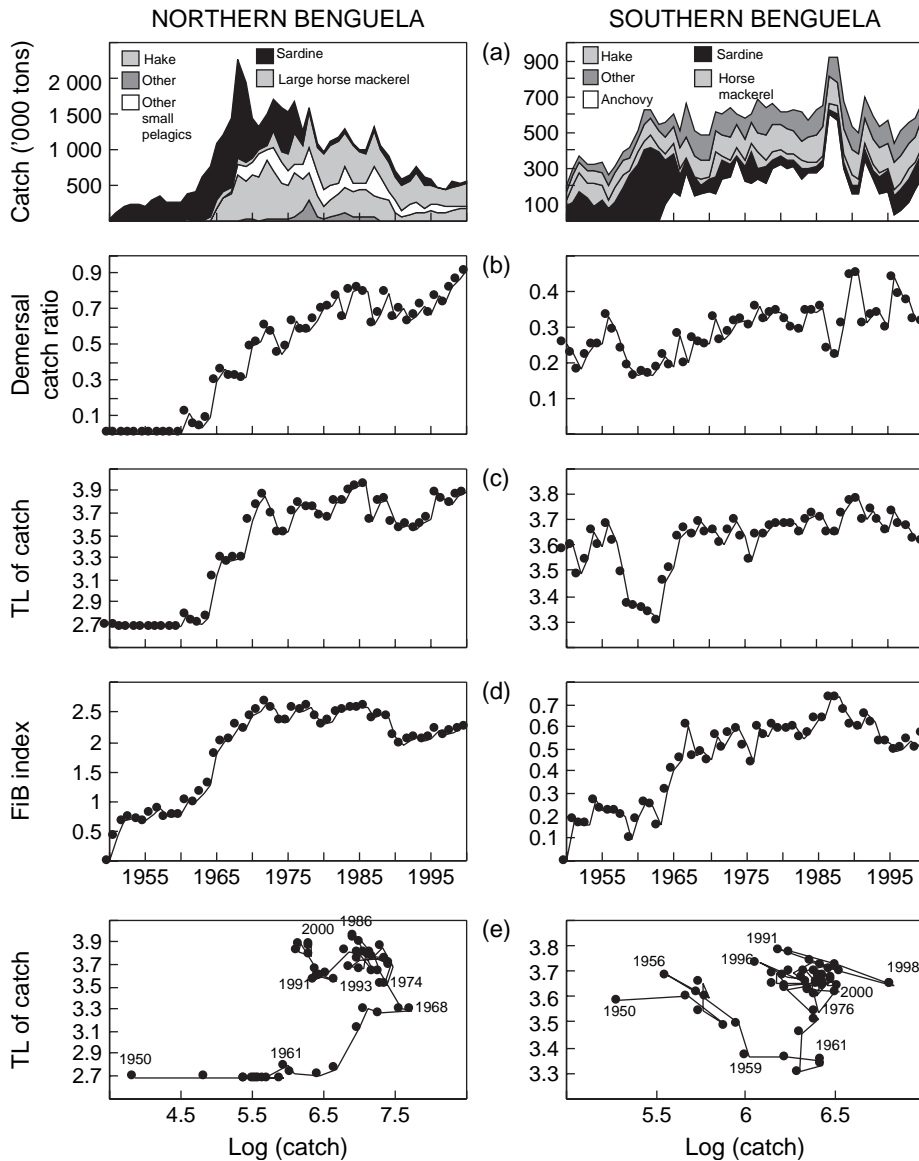


Figure 2. Annual indicators derived from catches in the northern and southern Benguela, 1950–2000: a) catch, b) ratio of demersal catch:total catch, c) mean trophic level of catch, d) fishing-in-balance index (TE = 10%), e) trophic level of catch vs. logarithm of catch (t).

were also examined assuming a higher transfer efficiency (TE) than 10% (even as large as 20%; i.e. including the 12% used in Shannon *et al.*, 2003), as well as a variable TE in that of the demersal fish assemblage, according to the models used. However, in the northern Benguela, catch ratios of planktivorous:piscivorous fish and small pelagics + small hake:large pelagics + large hake, increased as a result of the observed increase over the two decades in catches of horse mackerel relative to piscivorous hake. The small increase (4%) in the consumption of small pelagic fish (excluding small hake) by predators, relative to their consumption of demersal fish, in the southern Benguela reflects an increase in biomass of mesopelagic fish off South Africa between the 1980s and 1990s. Overall, the ratios

Ratios of catch, biomass, production, and consumption

For both ecosystems, ratios of production, consumption, biomass, and catches of the various groupings of small pelagic fish relative to demersal fish were lower in the

1990s than in the 1980s (Table 2), indicating a decline in the relative biomass of planktivorous fish and/or an increase in the models used. However, in the northern Benguela, catch ratios of planktivorous:piscivorous fish and small pelagics + small hake:large pelagics + large hake, increased as a result of the observed increase over the two decades in catches of horse mackerel relative to piscivorous hake. The small increase (4%) in the consumption of small pelagic fish (excluding small hake) by predators, relative to their consumption of demersal fish, in the southern Benguela reflects an increase in biomass of mesopelagic fish off South Africa between the 1980s and 1990s. Overall, the ratios

Table 2. Trophodynamic indicators derived from standardized trophic models of the northern and southern Benguela ecosystems for different periods (pel – pelagics, i.e. clupeids [i.e. sardine, round herring, *Etrumeus whiteheadi*], anchovy, pelagic goby, other small pelagic fish, small horse mackerel, mesopelagic fish, chub mackerel; dem – demersals, i.e. all hake, benthic-feeding and pelagic-feeding demersal fish, large horse mackerel; smf – small pelagic fish and small hake, i.e. clupeids, anchovy, pelagic goby, other small pelagic fish, small hake, but excluding mesopelagic fish; laf – large hake and large pelagics, i.e. large hake, snoek, *Thyrstites atun*, tuna, linefish; pla – planktivorous fish, i.e. clupeids, anchovy, pelagic goby, other small pelagic fish, horse mackerel, mesopelagic fish, small hake; pis – piscivorous fish, i.e. large hake, snoek, tuna, linefish, pelagic-feeding and benthic-feeding (includes some detritivores) demersal fish, chub mackerel; pfp – pelagic fish predators, i.e.: seabirds, seals, cetaceans, large pelagic fish, large hake, chub mackerel).

Indicator	Namibia			South Africa		
	1980–1989	1995–1999	% Change	1980–1989	1990–1997	% Change
TL of Y	3.7	3.7	0	3.7	3.8	2
Total Y (t km ⁻² y ⁻¹)	6.0	2.8	-53	3.0	2.5	-18
Total fish B (t km ⁻²)	66	58	-13	32	36	12
B of pfp (t km ⁻²)	6.7	5.7	-16	3.9	4.9	24
PPR to sustain fishery (t km ⁻² y ⁻¹)	983	465	-53	451	455	1
% PPR	17	7	-55	3.8	3.9	2
PPR/Y	165	165	0	148	182	23
P – pel/dem	3.2	3.1	-4	1.9	1.8	-7
Q – pel/dem	4.1	3.9	-5	3.3	3.0	-7
Q – pel/dem by predators	4.4	4.1	-5	1.9	2.0	4
B – pel/dem	2.4	2.4	0	1.6	1.5	-6
P – smf/laf	8.5	8.0	-6	15	10	-30
P – pla/pis	6.8	6.4	-5	4.8	4.4	-9
Y – smf/laf	0.77	0.84	10	3.7	2.0	-44
Y – pel/dem	0.35	0.29	-20	2.3	1.7	-26
Y – pla/pis	2.0	2.3	12	3.2	1.8	-42

indicate a shift towards greater importance of demersal fish in the Benguela over the time periods modelled.

Primary production required (PPR) to sustain catches

In the northern Benguela, the PPR to sustain catches decreased by more than 50% in accordance with the reduction in catches, as indicated by the similar PPR:catch ratios in the two periods. By comparison, the PPR in the southern Benguela was similar in both periods, though catches were smaller in the later period. This meant a 23% increase in the ratio of PPR to catch, indicating that catches were more ecologically expensive in the later period, in accord with the estimated increased TL of the catch.

Mixed trophic impact (TI)

For the two northern Benguela models, the group displaying the largest differences in TI between periods is large horse mackerel (Figure 3a). Horse mackerel sustain a major commercial fishery off Namibia and, because they migrate vertically through the water column, horse mackerel trophically integrate to a certain extent the pelagic and demersal systems. More abundant in the 1980s, horse mackerel had, at that time, larger effects on their

competitors and predators. TI also provides an indication of changes in the trophic importance of other groups in the ecosystem. For example, chub mackerel (*Scomber japonicus*), anchovy, and sardine stocks had all undergone severe declines by the second period, leading to a reversal from negative (competition for common prey being the dominant factor) to positive TI in the second period (large horse mackerel also feed to some extent on the other three species which, at low abundance, no longer strongly compete with horse mackerel for prey).

In the southern Benguela, sardine abundance increased in the 1990s, reflected in the larger net negative TI on its competitors (e.g. anchovy, other small pelagic fish, horse mackerel), and larger positive TI on its predators (e.g. seabirds, cetaceans, large pelagic fish; Figure 3b).

Predation mortality

For all selected fish groups in the two systems, predation mortality relative to the sum of predation and fishing mortality increased between the two periods (Figure 4a). However, the indicator measures different things in the two systems. In the southern Benguela, predation mortality reflects support of a 24% larger biomass of pelagic fish predators (Table 2) in the 1990s than in the 1980s, whereas in the northern Benguela, the indicator is a measure of the

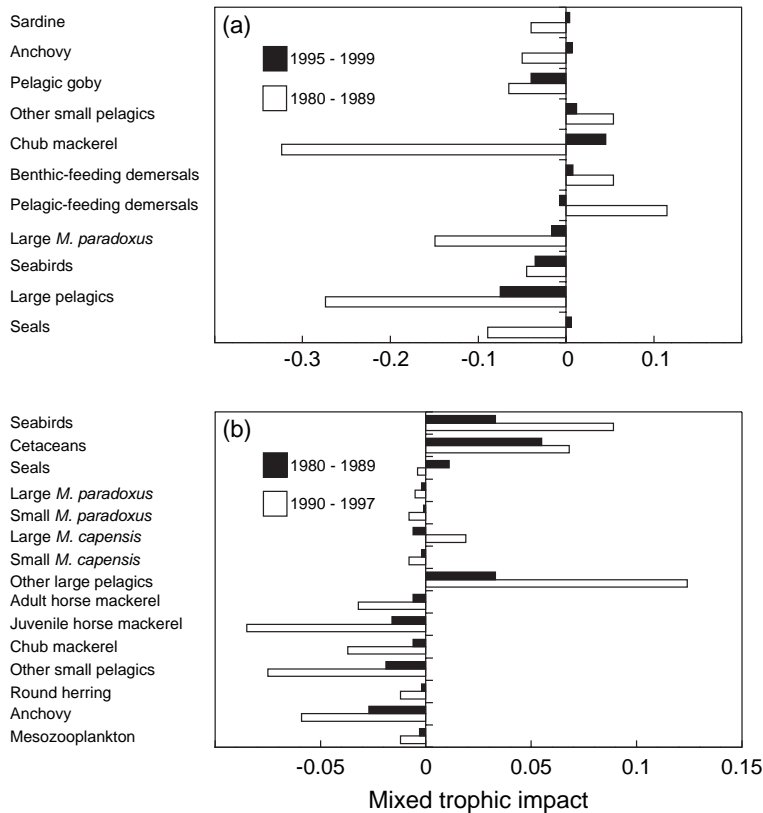


Figure 3. Mixed trophic impact (TI) on selected groups during two periods by a) large horse mackerel in the northern Benguela, b) sardine in the southern Benguela (bars indicate relative net negative and positive impacts, scaled between -1 and +1).

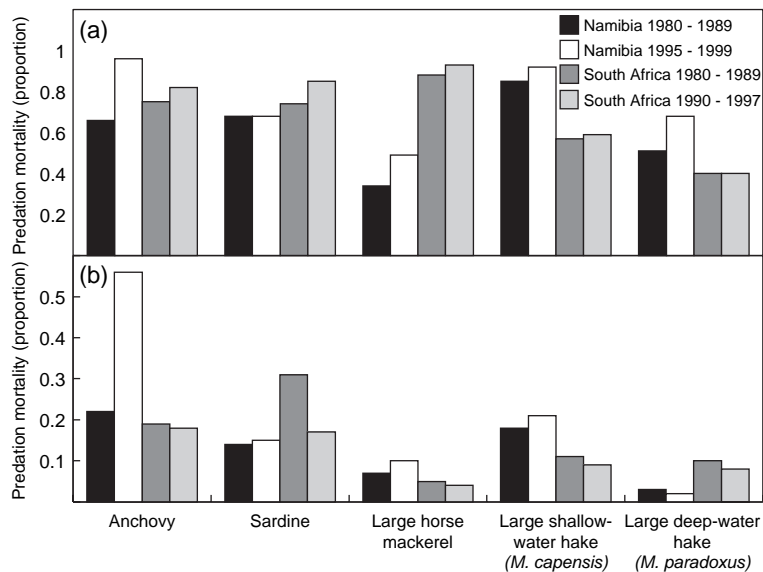


Figure 4. Annual predation mortality rates expressed as (a) a proportion of total mortality on selected fish groups, (b) a proportion of total mortality attributable to seals and seabirds.

increased pressure on the fish groups. Predator biomass off Namibia declined between the two periods (Table 2).

In the northern Benguela, anchovy predation mortality (relative to total predation and fishing) attributable to seals and seabirds more than doubled in the later period as a consequence of a large reduction in stock size and the collapse of the anchovy fishery (Figure 4b). The decrease in predation pressure exerted on sardine by seals and seabirds off South Africa during the 1990s reflects the recovery of sardine (Figure 4b).

Differences within the region

Many differences between trophic indicators for the two subsystems appear to be related to the southern Benguela model not only constituting a typical upwelling region (west coast), but also a shallow bank with diverse demersal fish assemblages (Japp *et al.*, 1994). Moreover, large parts of the northern Benguela shelf are subjected to recurrent low oxygen conditions, which might be limiting for some demersal species. The catch of pelagic fish compared with the catch in the demersal fishery (trawls and longline) is 1.5 times larger in the northern Benguela than in the southern Benguela. Similarly, ratios of consumption by and of pelagics vs. demersals are larger in the north. Conversely, catches of pelagic fish relative to demersal fish, and of small pelagic fish vs. large hake and large pelagic fish, are an order of magnitude smaller off Namibia than off South Africa. The smaller discrepancy between catch ratios of planktivorous:piscivorous fish arises from the large catch of large (planktivorous) horse mackerel in trawls. The importance of horse mackerel in the north also accounts for inflated catch ratios of planktivores:piscivores in the north, relative to those in the south (cf. pelagic:demersal ratios).

Discussion

The dynamics of the northern and southern Benguela ecosystems documented across different trophic levels show contrasting trajectories in various components during the past two decades. Therefore, the available information should be useful in testing the performance of trophodynamic indicators. Most of the indicators discussed (total catches, ratio demersal to total catches, ratio piscivorous to total catches) display interpretable trends in the northern Benguela (see also Willemse and Pauly, 2004), compared with their relative stability in the southern Benguela. This appears to be a reflection of the better “health” of the fisheries in south, and may be partly because management measures were implemented effectively in the south since the implementation of the 200-mile Fishing Zone in 1977 (more than 13 years earlier than off Namibia). However, the relative stability over the past 30 years of the mean TL of the catch in the south hardly reflects the important changes in the system (fluctuations of the anchovy stock and

catches), suggesting that this indicator specifically is a conservative one that responds slowly to large structural change. The absence of a trend in the northern Benguela during the same period (when the system was subjected to sequential depletion of its most important stocks) highlights the bias that results from the use of an indicator based on catches if an ecosystem has shifted productivity towards non-exploited species (such as, in this case, pelagic goby, *Sufflogobius bibarbatus*, or jellyfish). This being said, in February 2004, the Conference of the Parties to the Convention on Biological Diversity (CBD) identified mean TL of the catch (which they term the Marine Trophic Index, MTI) as one of eight indicators to be tested immediately for their ability to measure progress towards achieving a significant reduction in the current rate of biodiversity loss by 2010 (CBD, 2004). To emphasize changes in the relative abundance of higher TL fish, and to reduce bottom-up effects of productivity changes (reflected in the large fluctuations of small pelagic fish stocks and catches), Pauly and Watson (in press) recently proposed that low TL catches be excluded from global computations of MTI. This would allow top-down effects of fishing to be identified. However, for the reasons just discussed, it is also important to consider changes at the lower TLs (bottom-up effects) when attempting to track changes (via top-down or bottom-up forces) in an upwelling ecosystem such as the Benguela.

The relative stability of the mean TL of the catch, despite the known changes, emphasizes the potential danger of interpreting a single indicator without analysing the causes of the observed trajectory, or understanding the dynamics of the fisheries. The FiB index (in combination with plots of the TL of catches against catches) seems to capture not only the historical development of the fisheries in both systems, but also the differences in the state of the fisheries over time between the two areas, more accurately than any other single index derived from catch statistics. One drawback of the FiB index is that it is heavily dependent on the catches and their trophic level in the reference year. The absolute value only has a clear interpretation relative to that reference year, but if the reference year is changed, the values also change. This accounts for the difference in the range of values obtained for the two systems (Figure 2d). However, the trends in a FiB series are conserved irrespective of the base year selected. Examining the FiB separately for sub-periods characterizing different fishing and/or ecosystem “regimes” is recommended if interannual changes are to be captured in greater detail.

Quantifying changes in an ecosystem is not straightforward, and no single trophodynamic indicator can track the complexity of the observed changes in fisheries and ecosystems. Although they appear useful for understanding ecosystem and fisheries dynamics, such indicators tend to be conservative, because they respond quite slowly to structural change. Moreover, trends are sensitive to calculated TL values, emphasizing a need to improve data collection to better understand fish feeding behaviour. One

could wonder whether it might have been more informative to consider abundance and species composition from research surveys, rather than to compute the indicators used here. The use of trophodynamic indicators should not restrain scientists from using single-species metrics, but the trophodynamic indicators should be valued for improving evaluation of the dynamics of the whole ecosystem, by measuring the net effects of the underlying interactions between species groups. In that sense, they are useful in considering probable future trajectories of different ecosystem components. In the case of the southern Benguela, the indicators investigated tell us that the fisheries did not affect the structure and functioning of the ecosystem to a great extent, whereas the indicators for the northern Benguela provide a rather “optimistic” assessment in so far as they did not adequately depict the perceived “ecosystem collapse” (Bakun and Weeks, 2004).

Trophodynamic indicators have not been developed to capture bottom-up forces specifically. We propose that an environmental version of the FiB would be useful in quantifying how environmental effects propagate up through the foodweb. Such an Environment-in-Balance index (EiB) could constitute an analogue that would calculate how, for example, an increase in the planktonic production would propagate up the food chain.

Trophodynamic indicators are still descriptive, and reference points have not yet been identified, although historic time-series, even if data quality is not ideal, confirm massive changes in marine ecosystems. This highlights the need for long-term retrospective analyses to interpret trends and values correctly, and to avoid shifting baselines. Any change in the temporal dynamics or trajectory of an indicator must be interpreted in the light of other, complementary indicators, as well as general ecological knowledge.

One way to apply ecosystem indicators in fisheries management would be to focus on how they can be implemented in minimizing the adverse effects of fishing, rather than to focus on the precision of particular reference points or indicator values (Garcia and Staples, 2000). This may be a challenge beyond the scope of natural science alone. As a first step, the opportunity should be seized to apply the selected indicators to a broad selection of large marine ecosystems (LMEs), to evaluate fully their usefulness for an ecosystem approach to management, and to establish international compatibility of indicators for intersystem comparison. This may be a long-term task, but any step forward should facilitate the evaluation of the overall effectiveness of indicators used in the context of local ecosystems under local institutional management arrangements.

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Appendix. Notation

j...p	index for predator	GE	gross efficiency
i...n	index for prey	TE	transfer efficiency
k	index for year	A	assimilation (assimilated consumption)
B	biomass	R	respiration
P	production	T	throughput
PB	population growth rate (in equilibrium PB = Z; Allen, 1971)	F	fishing mortality
Y	catch	M2	predation mortality
Q	consumption	M0	other mortality
GS	proportion of food not assimilated	Z	total mortality
QB	consumption rate (ration) in time	TL	mean trophic level
DC _{ji}	percentage diet composition, DC _{ji} = weight i/ ∑ weight i;	P	production
Det	flow to detritus	PP	primary production
EE	ecotrophic (consumption) efficiency	Asc	ascendancy
		C	development capacity
		I	information
		H	statistical entropy
		Φ	overhead

Table A1. Trophic indicators used to characterize a) single foodweb components, b) changes in the functioning or structure of the whole ecosystem and their ability to capture different types of trophic controls (Bu, bottom-up; Td, top-down; Mx, Mixed).

(a) Single foodweb components

Indicator – estimator/source

Application and comments: control (references)

Abundance – numerical, density, B, Y, cpue, ocean colour/surveys, models

Parallel or inverse trends across predator–prey and TL: Bu-Td-Mx, effect of fishery (Pauly *et al.*, 1989; Aebischer *et al.*, 1990; Caddy and Garibaldi, 2000; Cury *et al.*, 2000; Carr, 2002; Daskalov, 2002, 2003)

Production – PP and secondary production, recruitment/survey experiments, models

Trends, recruitment–environment relationships, cultivation/depensation effect: Bu (Vinogradov *et al.*, 1976; Cury and Roy, 1989; Cushing, 1996; Walters and Kitchell, 2001; Carr, 2002)

Proportion of prey in predator's diet – diet matrix, selectivity, suitability (MSVPA)/stomach content analysis

Selectivity, trophic overlap, prey-switching: mostly Bu (Christensen and Pauly, 1993; ICES, 2002; Jennings *et al.*, 2002)

Consumption – food intake/stomach content analysis, gastric evacuation experiments

State and trends: Td (Overholtz *et al.*, 1991; Bax, 1998; Christensen and Pauly, 1993)

Respiration – experiments, models

Used in efficiencies and system indices; accounting for system's heterotrophy: Td (Christensen and Pauly, 1993; Christensen, 1995; Cole *et al.*, 2000)

Throughput – sum of all flows in and out of a group or system/models

Index of system size in terms of flow: mostly Bu (Ulanowicz, 1986; Christensen and Pauly, 1993; Christensen *et al.*, 2000)

Flow to detritus – models

High values may indicate perturbed system: Td-Bu (Vinogradov *et al.*, 1976; Christensen and Pauly, 1993; Grishin, 2001)

Mortality coefficients – natural, predation and fishing mortality/assessment models, tagging experiments

Trends, matrix: Td (Sparholt, 1990; Pope and Macer, 1996; ICES, 2002)

Ecological efficiencies – ratios of flow parameters/models

Td-Bu (Kozlovsky, 1968)

Ecotrophic efficiency – dominance of removals (consumption, fishing) over production/models

Controls tend to "compete" to dominate each trophic group; if removals dominate then group is Td controlled and *vice versa*: Td-Bu (Ivlev, 1945; Kozlovsky, 1968; Christensen and Pauly, 1993)

Transfer efficiency – product of EE and GE/models

Depends on changes in trophic control through EE and changes in food quality and feeding efficiency (behaviour) through GE: Td-Bu (Kozlovsky, 1968; Pauly and Christensen, 1995; Van Rooij *et al.*, 1998)

Catch ratios – predators:prey or demersal fish:pelagic fish/surveys, landings

Approximation of B ratios, but affected by fishing practices and effort: Td-Bu (Caddy and Garibaldi, 2000; De Leiva Moreno *et al.*, 2000).

Trophic level – by group or fractional/measurements, models

Overfishing of piscivores results in decreasing TL of Y; compensatory increase in forage may reduce TL: mainly Td (Lindeman, 1942; Pauly *et al.*, 1998)

Mixed trophic impact – Relative impact of change in B of one group on others/models

Used to simultaneously assess both direct effects of predation and indirect effects of competition, without discriminating between the two: Td-Bu (Ulanowicz and Puccia, 1990)

(b) *Whole ecosystem*

Indicator – estimator/source

Application and comments: control (references)

System indicators corresponding to component indicators listed in A1 and their ratios – Total B,

P, R, net system P, flow to detritus, T, mean TE, PP:R ratio, PP:B ratio, R:B (Shrodinger) ratio, B:P ratio (~ average organism size), Q:P ratio, B:PP + R ratio (B supported)

Indicate ecosystem maturity, complexity, stability, resilience, or changes attributable to perturbation: Td/Bu (Odum, 1969; Christensen and Pauly, 1993; Christensen, 1994, 1995; Vasconcellos *et al.*, 1997; Christensen and Pauly, 1998)

Mean trophic level (of system or of fisheries) – weighted by B or Y of groups/models

Tracks fishing down the foodweb: Td-Bu (Pauly *et al.*, 1998, 2000)

Fisheries' gross efficiency – ratio of Y:PP/models

Higher in systems fished lower in the foodweb: Td-Bu (Christensen and Pauly, 1993; Christensen *et al.*, 2000)

Utilization of PP – nutrient conservation, EE of primary producers/models

Higher in mature systems: Td-Bu (Christensen and Pauly, 1998; Grishin, 2001)

Connectance index – percentage of realized links relative to possible links/models

Index of structure: linear vs. web-like linkages in the foodweb: Td-Bu (Christensen, 1995; Christensen and Pauly, 1998)

System omnivory index – reflects trophic specialization: distribution of feeding interactions among TL

Higher (specialization decreases) in immature and perturbed systems: Td-Bu (Christensen, 1995; Vasconcellos *et al.*, 1997; Christensen and Pauly, 1998)

Finn's cycling index – nutrient throughput cycled-to-total throughput ratio/models

Index of ecosystem maturity, stability, resilience: Td-Bu (Christensen, 1995; Christensen and Pauly, 1998)

Path length – average number of groups that the flow passes through/models

Similar to Finn's cycling index: Td-Bu (Christensen, 1995; Christensen and Pauly, 1998)

Mutual information – probability of flow among system components; quantifies degree of articulation in network/models

Measure of organization, higher in mature and complex systems: Td-Bu (Odum, 1969; Christensen, 1995; Christensen *et al.*, 2000)

Ascendancy – product of throughput times information; accounts for both size and organization/models

Measure of ecosystem efficiency; higher in mature and complex systems: Td-Bu (Ulanowicz, 1986; Vasconcellos *et al.*, 1997; Christensen *et al.*, 2000)

Primary production required (PPR) – energy to support consumption or catches/models

PPR is an index of the ecosystem efficiency similar to H. T. Odum's notion of "emergy": Td-Bu (Pauly and Christensen, 1995; Christensen *et al.*, 2000; Carr, 2002)

Fishing in balance (FiB) – assesses whether fisheries are ecologically balanced/models

Td-Bu (Pauly *et al.*, 2000)

Dynamic stability – persistence = time required for biomass change > 10%; resistance = 1/relative B change; resilience = resistance/recovery time (to initial state)/models

Comparisons indicate inverse relationships between stability and maturity: Td-Bu (Vasconcellos *et al.*, 1997; Perez-Espana and Arreguin-Sanchez, 1999).