THE FUNCTIONING OF MARINE ECOSYSTEMS

Philippe CURY, Lynne SHANNON, and Yunne-Jai SHIN

'Not only is the science incomplete, but the [eco]system itself is a moving target, evolving because of the impact of management and the progressive expansion of the scale of human influences on the planet' C.S. Holling, 1995.

ABSTRACT

There is considerable evidence that environmental variability plays a major role in controlling abundance and distribution of marine populations and that fisheries alter ecosystem functioning and state. This overview documents emergent ecosystem-level ecological patterns and answers meaningful questions regarding the exploitation of marine resources. Do marine ecosystems function differently from terrestrial systems? Are there multiple stable marine ecosystem states? In marine ecosystems, does removal of top predators result in fundamental changes in the plankton (top-down "trophic cascades"), as observed in lakes? Alternatively, are marine ecosystems characterized by bottom-up control such that fishing predatory fish does not disturb community structure and function? Does heavy exploitation of forage species, such as anchovies and sardines, cause changes in the functioning of upwelling ecosystems? The key to answering these questions and exploring whether general principles apply lies in understanding the mechanisms responsible for these observed emergent patterns. Different types of energy flow in marine ecosystems are reviewed: bottom-up control (control by primary producers), top-down control (control by predators) and wasp-waist control (control by dominant species). Answers to the questions depend on the different energy flow mechanisms assumed to operate. No general theory can be ascribed to the functioning of marine ecosystems. However, tentative and partial generalisations are proposed, for example that bottom-up control predominates, top-down control plays a role in dampening ecosystem-level fluctuations, trophic cascades seldom occur, and wasp-waist control is most probable in upwelling systems. Regime shifts, alternation and large-scale synchronised fluctuations in fish stocks, stability of fish communities and emergent features such as size spectra are potentially important patterns when assessing states and changes in marine ecosystems. New and meaningful indicators, derived from our current understanding of marine ecosystem functioning, can be used to assess the impact of fisheries and to promote responsible fisheries in marine ecosystems.

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1. INTRODUCTION

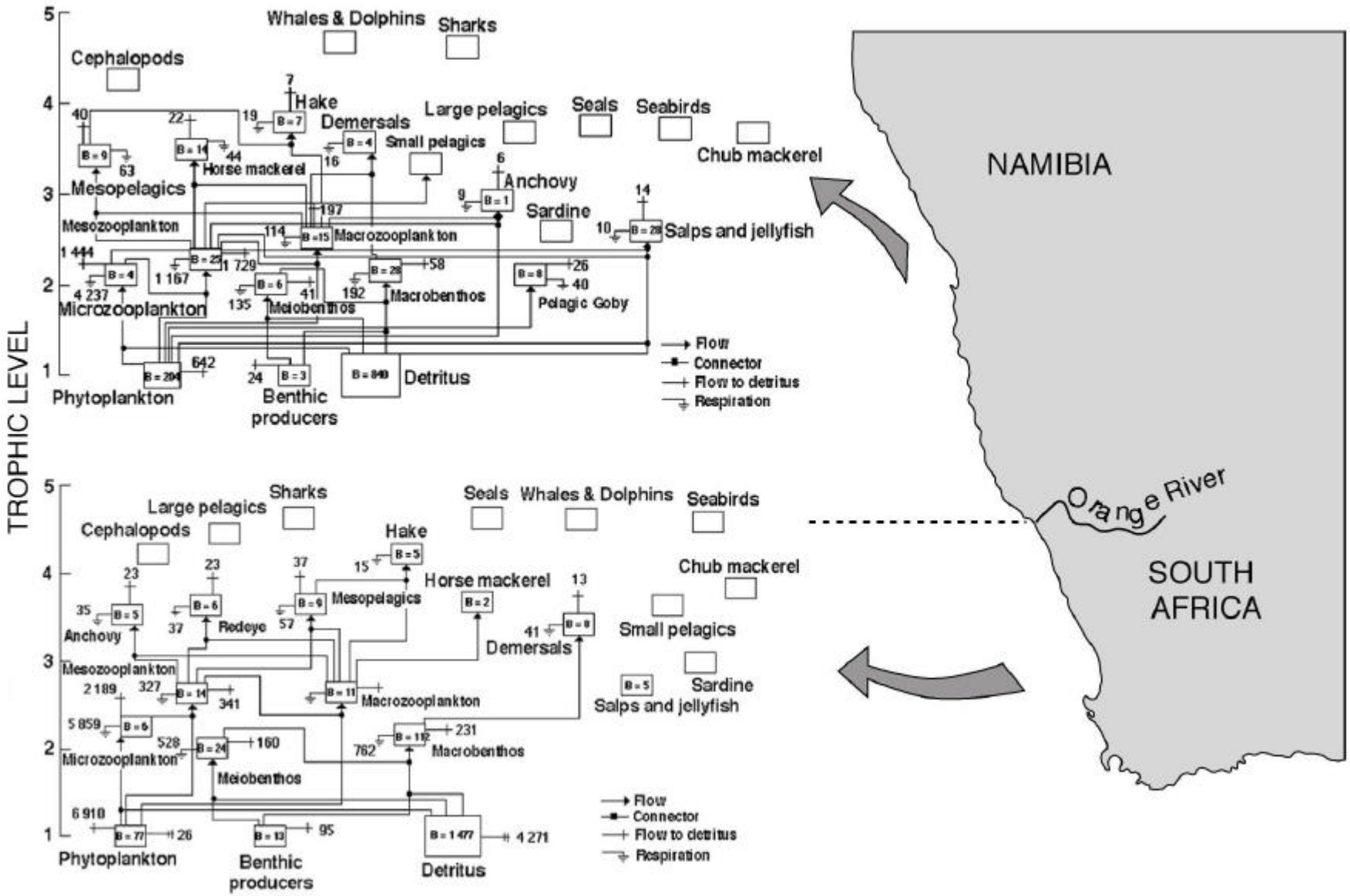
[1] Although the term "ecosystem" is quite recent (Tansley, 1935), it is now part of the mainstream of ecological science. An ecosystem is defined as "a spatially explicit unit of earth that includes all of the organisms, along with all the components of the abiotic environment within its boundaries" (Likens, 1992). This definition remains vague as ecosystems have no apparent boundaries and lack the sort of clear objective or purpose that can be ascribed to other, more tractable, biological or ecological entities (e.g. cell, individual or population). A marine ecosystem contains detritus, hundreds of kinds of organisms including bacteria, phytoplankton, zooplankton, fishes, mammals, birds, etc. All these components are connected in a complex food web by evolving interactions (Figure 1). Until recently, fisheries management has been largely based on single species approaches (Beverton, 1984). However, ecosystem management represents a paradigm shift, as well as a new attitude towards the exploitation of renewable marine resources (Christensen *et al.*, 1996). The ecosystem is now viewed as an integrative level for ecological studies, and its overall complexity is perceived as critical to its sustainability (Costanza *et al.*, 1997). Ecosystems carry out a diverse array of processes that provide both goods and services to humans. It also becomes important to understand what impacts an ecosystem can tolerate before major structural changes occur, and how reversible these changes are. In this respect, improved understanding of ecosystem dynamics is critical to predict and manage the consequences of environmental variability and human impacts, such as those induced by marine fisheries, an activity targeting specific species and size-classes.

[2] This overview aims to answer meaningful questions regarding the exploitation of marine resources, such as:

- Do marine ecosystems function differently from terrestrial systems?
- Are there multiple stable states in marine ecosystems?
- Which species are most critical, and which ecological processes are most sensitive to exploitation?
- Does the removal of top predators have a strong impact on lower trophic levels?
- Does the removal of large portions of forage fish species, such as anchovies and sardines, result in changes in the functioning of upwelling systems?

[3] The key to answering these questions and finding out whether general principles can apply, lies in understanding the mechanisms responsible for the observed emergent ecological patterns. Marine ecosystem functioning depends on its structure, diversity and integrity. Alteration or disturbance of one or several components of marine ecosystems can have strong effects on higher or lower trophic levels, depending on whether food webs are controlled by resources or by predators. In this paper we review different types of energy flow in ecosystems and how they possibly influence the dynamics of marine communities. For this purpose, we present recent theoretical ecological knowledge; we illustrate it with case studies, and explore whether simple questions, such as those posed above, can have simple answers.

Figure 1. (opposite) Food webs in the northern and southern Benguela, showing the complexity of the interactions between the different components of the ecosystems. Important differences in the functioning of the ecosystem can be noticed between two close and fairly similar upwelling systems (Adapted from Shannon and Jarre-Teichmann, 1999).


TROPHIC LEVEL
Whales & Dolphins
Sharks
Cephalopods
Hake
Demersals
Large pelagics
Seals
Seabirds
Small pelagics
Chub mackerel
Horse mackerel
Mesopelagics
Anchovy
Sardine
Mesozooplankton
Macrozooplankton
Salps and jellyfish
Microzooplankton
Meiobenthos
Macrobenthos
Pelagic Goby
Phytoplankton
Benthic producers
Detritus
Flow
Connector
Flow to detritus
Respiration
NAMIBIA
Orange River
SOUTH AFRICA
Redeye

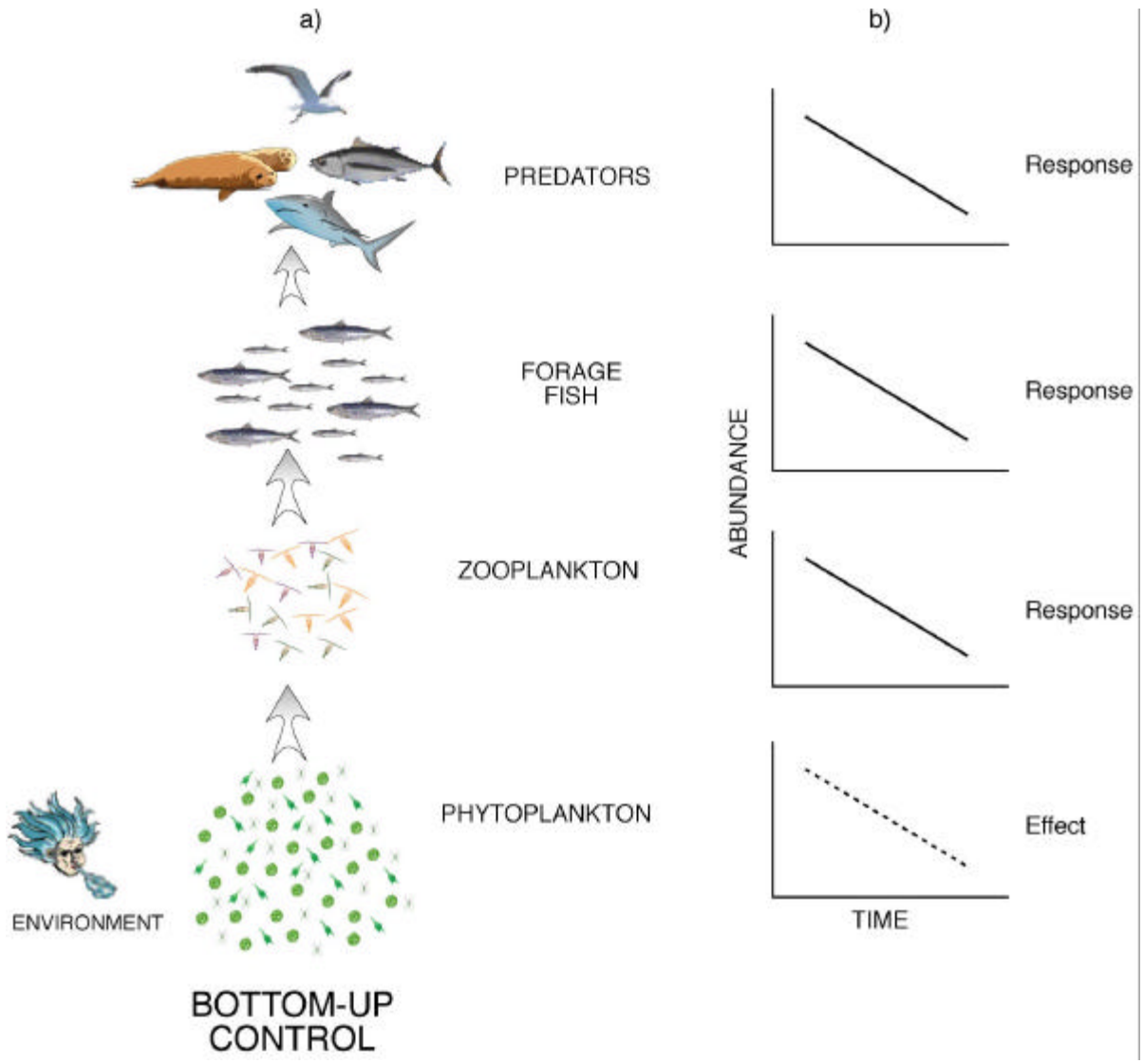


Figure 2. (a) Bottom-up control within a simplified four-level food web in a marine ecosystem. (b) The physical environment being less favourable controls the decrease in abundance of the phytoplankton, which in turn has a negative impact on the abundance of the zooplankton. The diminution of the zooplankton controls the decrease in abundance of the prey fish, which itself leads to a decrease in the abundance of the predators (the control factor is a solid line and the responses are dashed lines).

2. BOTTOM-UP CONTROL: THE VERY SMALL DRIVE THE VERY LARGE

[4] Victor Hensen is considered the father of quantitative marine ecology. In 1887, he thought of planktonic populations as rapidly revolving links in a food chain leading from the very small to the very large (Smetacek, 1999). Analogous to agronomy, where crop yields can be predicted from the control of the input, Hensen made the assumption that food supply regulates adult fish stocks, and quantitative studies of phytoplankton and zooplankton production would permit predictions of fish yields (Verity, 1998). From this deduction was born the notion that ecosystems were 'bottom-up' controlled (Figure 2(a)). In other words, the regulation of food-web components derives from either primary producers, or the input of limited nutrients (Pace *et al.*, 1999).

[5] Recently, Micheli (1999) analysed twenty natural marine systems, and found that nutrients generally enhance phytoplankton biomass. Plants dominate terrestrial ecosystems but the ocean contains less than one per cent of plant biomass (Smetacek, 1999). The realization that the ocean's animals are fed by a thin soup of minute algae, the phytoplankton, and that this resource can limit the global productivity of the ecosystems, was puzzling. Environmental forcing controls

the carrying capacity and fish biomasses in marine ecosystems, but apparently not in a simple way. It took time to realize that the marine environment is a dispersive and heterogeneous one. Species are not evenly distributed spatially and their marine populations, particularly of fishes, fluctuate widely from year to year. Since the pioneering work of Hjort in 1914, it was recognized, and is still highly influential today, that renewable processes in fish population dynamics are highly irregular, depending on recruitment strength, and that marine fish species comprise many self-sustaining populations (Sinclair, 1997). There is now considerable evidence that natural variability in ocean circulation and mixing plays a major role in generating fluctuations in marine productivity, as well as in the distribution of populations. Food availability and physical constraints – such as retention, concentration or enrichment processes that are associated with currents and turbulence – are now considered as important factors that affect larval survival, fish recruitment and ultimately stock abundance (Cury and Roy, 1989; Bakun, 1996; Chambers and Trippel, 1997). Several recurrent patterns can illustrate how the physical environment plays a structuring role in shaping abundance and distribution of marine populations in space and time.

2.1 Ecosystem responses to drastic environmental changes

[6] The structure and function of marine ecosystems respond drastically to inter-annual changes and inter-decadal climatic variations. This has been documented for the California Current, the Gulf of Alaska (McGowan *et al.*, 1998), the North Atlantic (Aebisher *et al.*, 1990) and off Chile (Hayward, 1997). Parallel long-term trends across four marine trophic levels, ranging from phytoplankton, zooplankton, herring to marine birds, have been related to environmental changes in the North Sea (Aebisher *et al.*, 1990). Even though the mechanisms behind the parallelism of trends remain unclear, the effect of the environment was identified as the driving force for structuring several components of the ecosystem. Using trophic mass-balance models, the multiple and complex changes that occurred in the Bering Sea ecosystem between the 1950s and 1980s were shown to be largely driven by environmental changes (Trites *et al.*, 1999). Inter-annual environmental fluctuations, such as El Niño events, affected the structure of the plankton community, the spatial distribution of fish and invertebrates, the recruitment success of pelagic fish and the mortality of birds and mammals in the northern Pacific (McGowan *et al.*, 1998). Large-scale perturbations have taken place during the past twenty years in the Pacific where a dramatic shift of the atmospheric forcing occurred in the mid-1970s (Hayward, 1997). Inter-decadal regime shifts, such as the one experienced in the entire North Pacific Basin and the California Current in the late 1970s to the early 1980s, appear to have altered the productivity of marine ecosystems, at various trophic levels (Polovina *et al.*, 1994). There has been a generally increased frequency of southern species moving north, a substantial lowering of secondary productivity and fish landings, a major decline in seabirds, and changes in species composition in most sectors of the ecosystems (McGowan *et al.*, 1998). However, the biological response to the inter-decadal regime shift in the Gulf of Alaska is thought to have been in the opposite direction to that of the California Current. It seems that there are large-scale biological responses in the ocean to low-frequency climatic variations. However the mechanisms by which climate exerts its influence vary as components of the ecosystem are constrained by different limiting environmental factors. Thus similar species at the same trophic level may respond quite differently to climate change (Hayward, 1997). Findings from one system cannot necessarily be extrapolated to others, and predicting the effects of global-scale environmental change on ecosystems does not appear to be a straightforward exercise.

2.2 Regime shifts and synchronized large-scale fluctuations

[7] Changes in the abundance of pelagic fish species have been recorded in many marine ecosystems, based on catch statistics (e.g. Schwartzlose *et al.*, 1999), biomass surveys (e.g. Hampton, 1992) and records of seabird guano harvests (e.g. Crawford and Jahncke, 1999). It was hotly debated whether collapses of pelagic fish stocks were caused by overfishing, which allowed competing species to dominate (Francis and Hare, 1994). However records of scale-deposition

from anaerobic sediments show that large-amplitude fluctuations for pelagic fishes (e.g. sardine or anchovy) occurred even in the absence of any fishery over a period of 2000 years (Soutar and Isaacs, 1974). Sediment records of $\delta^{15}N$ and biological indicators were used to reconstruct the abundance of Pacific salmon over the past 300 years (Finney *et al.*, 2000). Marked shifts in Sockeye salmon populations occurred over decades during this period, and some pronounced changes appear to be related to climatic change. These regime shifts can alter the nutrient cycles and may have significant impact on the productivity of the ecosystems. Since the beginning of modern fisheries, the emerging patterns of decadal-scale variation in pelagic fish populations have also exhibited a substantial degree of global synchrony, sometimes between remote areas (Schwartzlose *et al.*, 1999) (Figure 3(a)). This synchrony is most probably driven by global climatic teleconnections (Bakun, 1996; Klyashtorin, 1997). Drastic change of states in one abundant prey resource is expected to have major consequences on the functioning of the ecosystem. Small pelagic fish are forage fish in marine systems; they represent an important source of food for numerous top predators, such as large pelagic fish, demersal fish, marine birds and mammals (Anonymous, 1997). The collapse of a prey species, induced by climate or/and fisheries, is most often associated with massive mortality of mammals, birds and predatory fishes (Cury *et al.*, 2000). However, the collapse of an abundant forage fish can also have an impact on other species at the same trophic level.

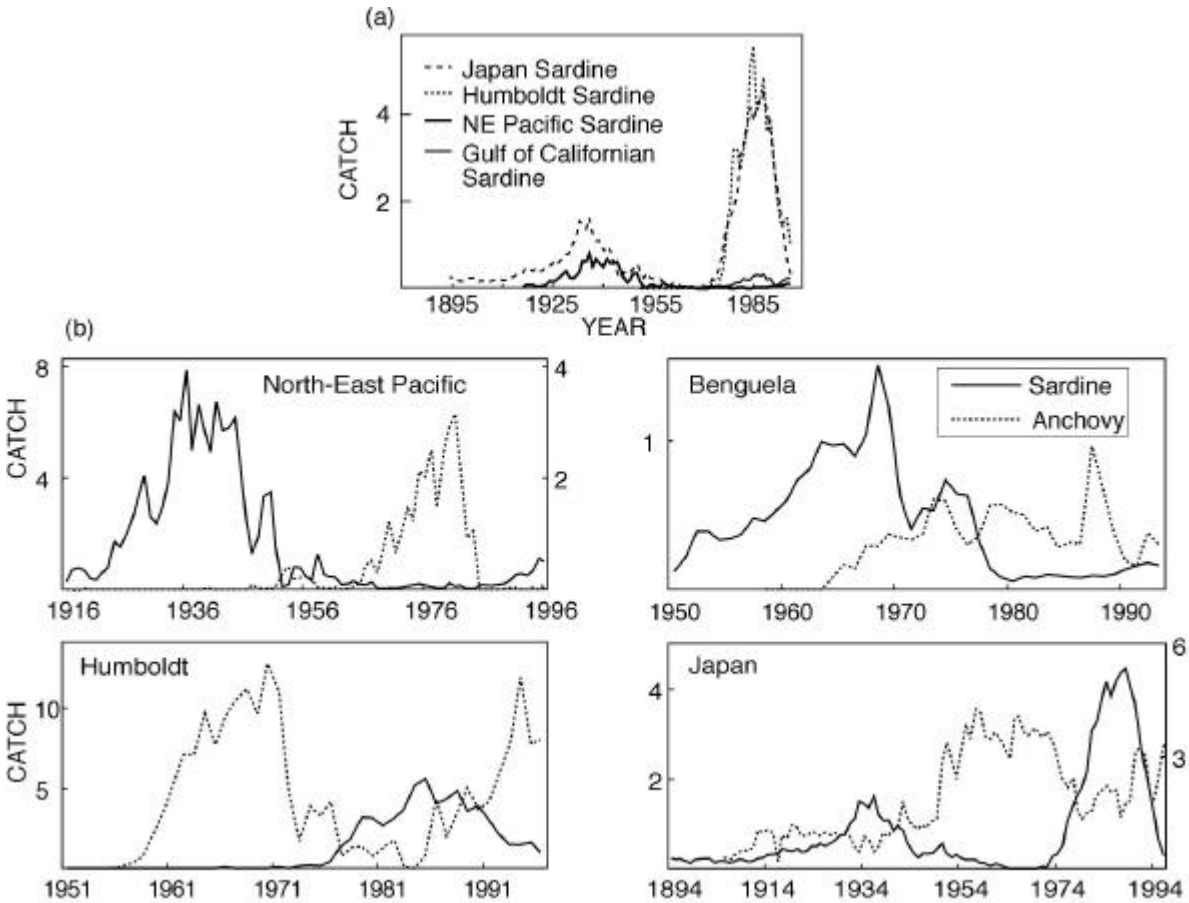


Figure 3. Global patterns of decadal abundance, as illustrated by pelagic fish catch (in million tonnes) in several ecosystems.
(a) Decadal-scale regime shifts suggest the existence of multiple stable states in pelagic fish assemblages. The synchrony of fish populations between remote ecosystems suggests strong climatic connection.
(b) The alternation between different pelagic fish suggests replacement between redundant species.
(Adapted from Schwartzlose *et al.*, 1999, and Bakun, 1998).

2.3 Alternating steady states and pelagic fish assemblages

[8] Strong environmental effects on fish populations result in large fluctuations in species composition. It also appears that alternating steady states are observed at the level of fish assemblages on decadal scales. For example, upwelling systems tend to be dominated by one species of sardine (or sardinella) and one species of anchovy, but most often only one of the two is dominant at any particular time. Alternating patterns between small pelagic fish species have been observed in most upwelling ecosystems during the past decades (Figure 3(b)). A regime shift between two species is considered to operate when, after removal of a species, biomass is restored by density compensation of the other species. This process may occur between two redundant species, i.e. belonging to the same guild or functional group (Lawton and Brown, 1993). The mechanisms that are generally invoked in direct competition are not completely satisfactory to explain species alternation (Hall, 1999) because sardine and anchovy usually do not occupy the same space (sardine are usually found farther offshore) and do not eat the same type of food (e.g. off South Africa, anchovy preferentially feed on large zooplankton whereas sardine prefer phytoplankton and small zooplankton (Van der Lingen, 1994)). These arguments led several authors to consider that competition is magnified by schooling behaviour within mixed-species schools (Bakun and Cury, 1999). Analysing changes in abundance of pelagic species in response to environmental changes, Skud (1982) concluded that the dominant species responds to environmental factors, while the subordinate species responds to the abundance of the dominant one. From an ecosystem perspective, climatic factors are thought to affect fluctuations in abundance of a species, whereas its absolute density is rather controlled by intraspecific competition (Skud, 1982; Serra *et al.*, 1998). Under bottom-up control, the physical environment drastically affects the overall productivity (i.e. the carrying capacity) of ecosystems, but, more importantly, also the dynamics of fish assemblages in a more-or-less predictable way. For pelagic ecosystems, recurrent patterns in fish abundance can be expected. These decadal-scale patterns of alternation are important for long-term management, as exploitation reduces the biomass of the dominant species, which is usually the target species, and sometimes precipitates its collapse (Beverton, 1990).

[9] Decadal-scale regime shifts suggest the existence of multiple stable states in pelagic communities, resulting in sustained or un-sustained pelagic fisheries. Within a pelagic community, alternation also suggests that harvesting a prey species will favour a competing species, provided that the latter is only lightly exploited. However, in the northern Benguela ecosystem off Namibia, commercially valuable sardine began to show signs of collapse in the 1970s. The fisheries targeted anchovy heavily, with the view that reducing anchovy would benefit its competitor, viz. sardine (Butterworth, 1983). The attempt to enhance sardine abundance failed, and both anchovy and sardine underwent major declines in the late 1970s. In comparison, off South Africa, anchovy were conservatively managed when sardine collapsed in the late 1960s, allowing anchovy to reach large biomasses and support a large fishery during the 1980s.

[10] Alternation of pelagic fish species is a rule that has exceptions. What has relatively few exceptions is the observation that, when not replaced by another species, the collapse of a dominant prey due to exploitation or other natural causes, alters the abundance and distribution of predator communities (see also the “wasp-waist control” section below). The conceptual model based on food limitation and responses to increased resource availability by elevated standing stocks, is regarded as the paradigm (Hunter and Price, 1992). Bottom-up control offers a comprehensive framework for understanding how different components could react to environmental changes or to changes at the bottom of the food chain (Figure 2(b)). However, it appears that certain taxa are better than others at regulating the flux of materials through the food web, and that predation is as important as resource limitation (Verity, 1998).

3. TOP-DOWN CONTROL: THE VERY LARGE DRIVE THE VERY SMALL

[11] As species mostly interact through predation, the existence of top-down control, which means the regulation of lower food-web components by one or several upper-level predators, should be critical in the functioning of marine ecosystems (Figure 4(a)). Predation mortality is estimated to be the major source of mortality for marine exploited species. An analysis of six marine ecosystems (Benguela Current, Georges Bank, Balsfjord, East Bering Sea, North Sea, Barents Sea) suggests that predation represents between two to thirty-five times fishing mortality (Bax, 1991). This does not mean that fishing has negligible effects on species dynamics, but rather implies that it can affect the whole ecosystem, as species are tightly connected through the predation process.

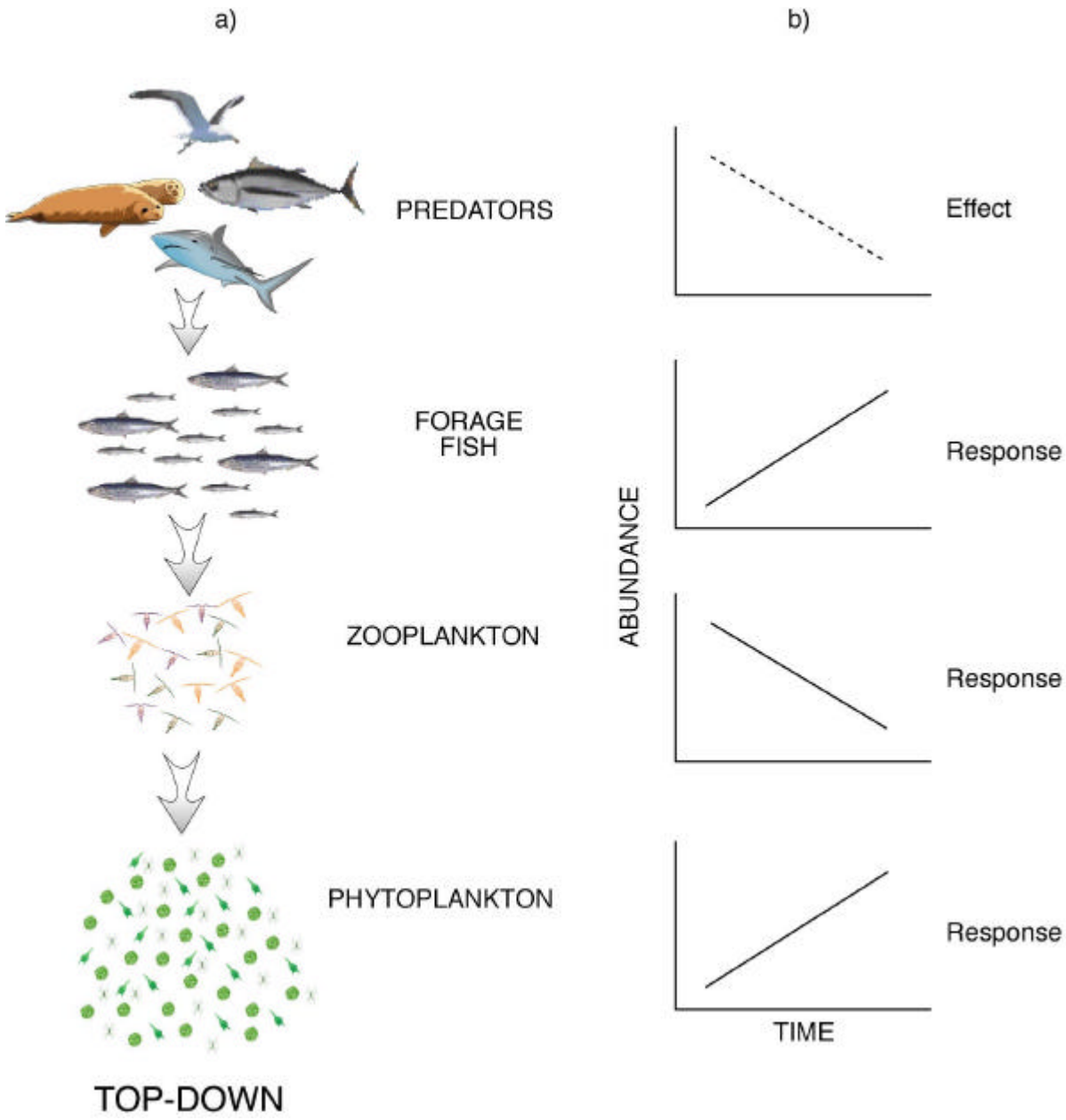


Figure 4. (a) Top-down control within a simplified four-level food web in a marine ecosystem. (b) The decreasing size of the top predator populations lead to a reduced predation on the prey that leads to an increase in the abundance of the prey fish. The increased predation of the fish prey on the zooplankton lead to a decrease in the population size. The diminution of the zooplankton abundance reduces the grazing pressure on the phytoplankton, which consequently becomes more abundant. (The control factor is in solid line and the responses are dashed lines).

3.1 When bigger fish eat smaller fish

[12] In terrestrial and aquatic ecosystems, the range of potential prey for a given species depends largely on their morphometric characteristics. It is observed for different taxonomic groups that the mean size of prey increases with the predator size. This is the case for aquatic species, for which body size is considered to be the main constraint in the predator's ability to catch a prey (Lundvall *et al.*, 1999).

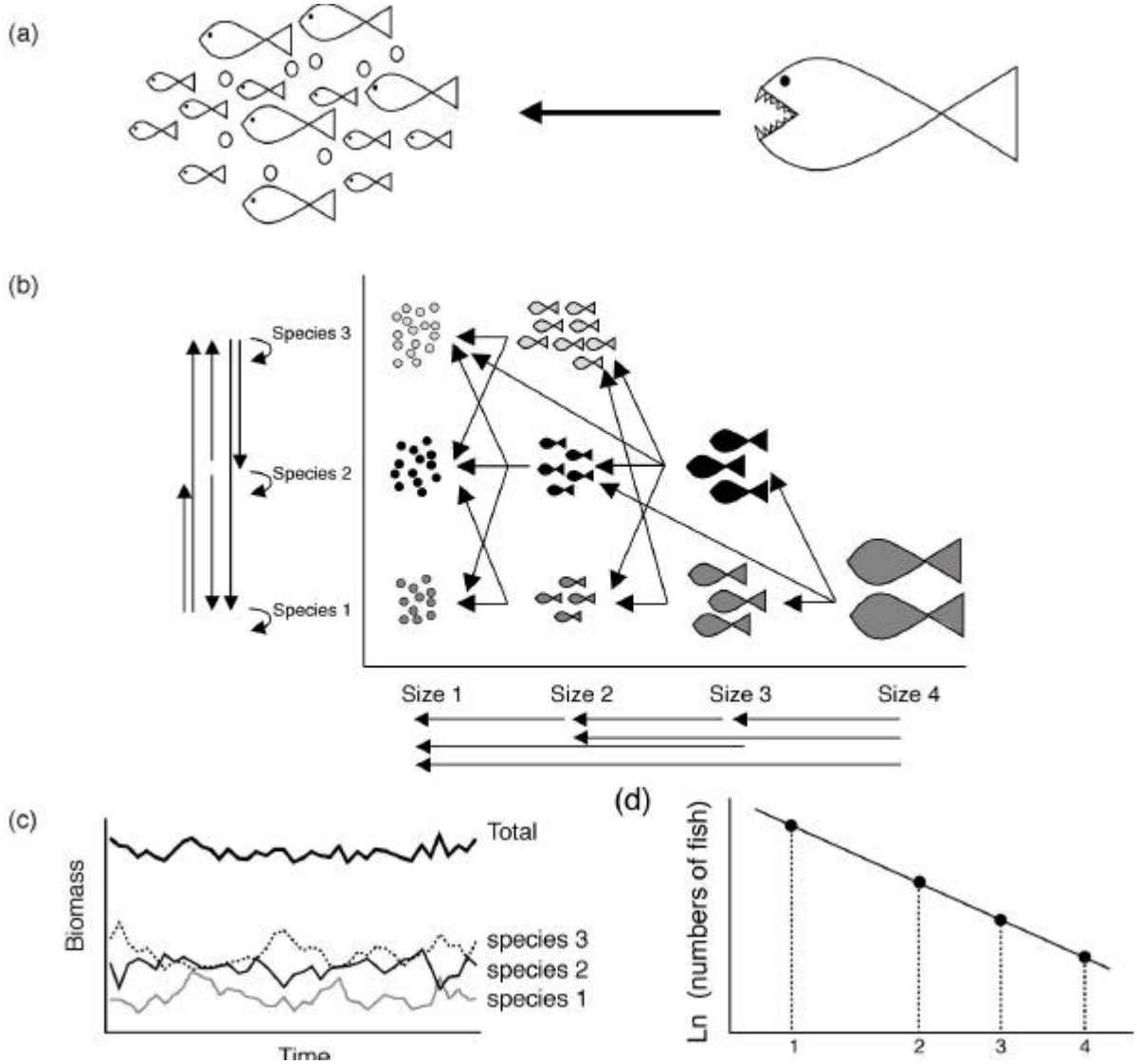


Figure 5. (a) Bigger fish eat smaller fish: fish prefer prey that are less than about 1/4 to 1/3 of their own size, as predators are constrained by the size of their jaws.
(b) Who is eating whom? This simple opportunistic feeding behaviour generates complex trophic webs, wherein fish have multiple predators, multiple prey and multiple competitors. A fish can feed on different trophic levels (omnivory), on its own progeny (cannibalism), and on early-life stages of its predators (e.g. eggs and larvae). Three species are represented on the vertical axis, and four size classes on the horizontal axis. Along the axes, the thin arrows correspond to the potential predation interactions between species and size classes. Cannibalism is represented by loops along the vertical axis. Within this framework, the arrows relating fishes correspond to a theoretical example of a trophic web.
(c) Complexity-stability: a recurrent pattern is the relative stability of the total fish biomass compared to that of individual species. Size-based predation implies multiple and weak trophic interactions between species, which have been theoretically proved to favour stability.
(d) Size-based predation provides an explanation for observed size spectra in marine ecosystems. A remarkably linear relationship is obtained when the logarithm of the numbers of fish in a size class is plotted versus the logarithm of the median size of the size class.

[13] According to Sheldon *et al.* (1977), the size-based predation process in the aquatic environment is supported by the fact that fish live in a medium that is eight hundred times denser than air, where only a streamlined morphology facilitates active and efficient movements. In this context, the development of appendages, which would help to handle and capture large-sized prey is not common among fishes. Thus, a predatory fish must have a jaw large enough to swallow its prey as a whole. A lion can catch a prey bigger than itself, but a fish generally cannot. As the size of the jaw is related to fish size, the predation process is believed to be largely determined by the size ratio between predator and prey (Figure 5(a)). As suggested by Ursin (1973) "[fish] stomach contents are a simple function of local prey availability and suitability, this latter often simply being a function of size." The feeding process in marine food webs can be considered as opportunistic and less dependent on prey taxonomy than on prey size.

[14] Strong patterns emerge from this feeding behaviour (Figure 5(b)). Firstly, fish diets comprise large prey diversity. Generally, fish larvae feed at the base of the food web and when they become adults, they occupy higher trophic levels and feed at one or several trophic levels below their own (Rice, 1995). Fish species appear to commonly have multiple predators and multiple preys. Secondly, cannibalism is also common in fish communities and can represent an important source of pre-recruit mortality (Claessen *et al.*, 2000). For instance, for the Eastern Baltic stock of cod (*Gadus morhua*), between age 0 and age 2, a year class may lose about 31% to 44% of its initial number as a result of cannibalism (Neuenfeldt and Köster, 2000). Finally, eggs and larvae are all located at the base of the piscivorous trophic levels (Jones, 1982). Particular to all species of teleosts is the rather homogeneous size of their eggs, about one millimetre in diameter (Cury and Pauly, 2000). The first consequence is that pre-recruits are subjected to what might be called "community predation" (Sissenwine, 1984), with every fish species potentially competing with every other (Figure 5(b). As stated by Gulland (1982): "fish have no direct terrestrial counterparts – a fox or lion does not start competing with mice." The second consequence is that two species can be simultaneously a predator or a prey of each other, according to their stage in their life cycle (i.e. their size). For instance, North Sea cod is known to be a predator of herring, but it is also its prey, since adult herrings feed on cod larvae (Stokes, 1992). This suggests two competing top-down control mechanisms, on a species basis, but one unidirectional top-down control on the basis of size (Figure 5(b)).

[15] Thus, considering the number of potential interactions between the different species, trophic levels or age groups, marine food webs appear to have complex and evolving dynamics. However, patterns of trophic interactions have been shown to exhibit strong emergent properties at the level of the ecosystem. As stated by May (1974), "if we concentrate on any one particular species our impression will be one of flux and hazard, but if we concentrate on total community properties [...] our impression will be of pattern and steadiness." A recurrent observation is the relative stability of the total fish biomass compared to that of individual species in marine ecosystems (Figure 5(c)). For example, in the North Sea during the 1970s, fisheries have experienced important variations in the species composition of catch, but the total catch remained relatively stable: herring and mackerel catches collapsed while those of gadoids increased (May *et al.*, 1979). May *et al.* (1979) assumed that year-class strength is regulated by top-down control; as a result of fishing, the decrease in the biomass of mackerel and herring resulted in reduced predation pressure on the larvae of gadoids, and consequently in improved recruitment. In the context of size-based predation, fish can be considered as general predators that may represent stabilizing forces on populations because they eat a variety of prey and target the most abundant species (Bax, 1998). Therefore, top-down control may operate through multiple and weak trophic interactions between species, a case which has been theoretically proved to favour stability (McCann, 2000; Shin and Cury, 2001).

[16] The relative stability of the size spectrum is also a recurrent feature at the level of the community (Figure 5(d)). Contrasting with changes in species composition, the size spectra of marine ecosystems exhibit remarkably constant shapes, decreasing functions, which are linear or

dome-shaped depending on the metrics used (e.g. Bianchi *et al.*, 2000). This observation suggests that, beyond strict species interactions, size-based interaction controls energy transfer in the marine environment. In this regard, primary production (bottom-up control) may act as a scale factor that determines global productivity of the ecosystem, but the stabilization process may be under top-down control. In this context, fishing acts as an apex predator, targeting the largest size classes. It has been shown that this top-down effect can be assessed by the variations in the slopes and intercepts of the ecosystems size spectra. In a comparison between North Sea and Faeroe Bank ecosystems, Pope and Knights (1982) showed that heavier exploitation in the North Sea led to a steeper slope of the observed size spectrum.

3.2 All species are not equal

[17] As everything is not strongly connected to everything else, there is no need to measure or understand everything, but rather to determine the significant interactions. Once this idea was accepted, it was rapidly recognized that certain key species play a more important role than others in structuring ecosystems.

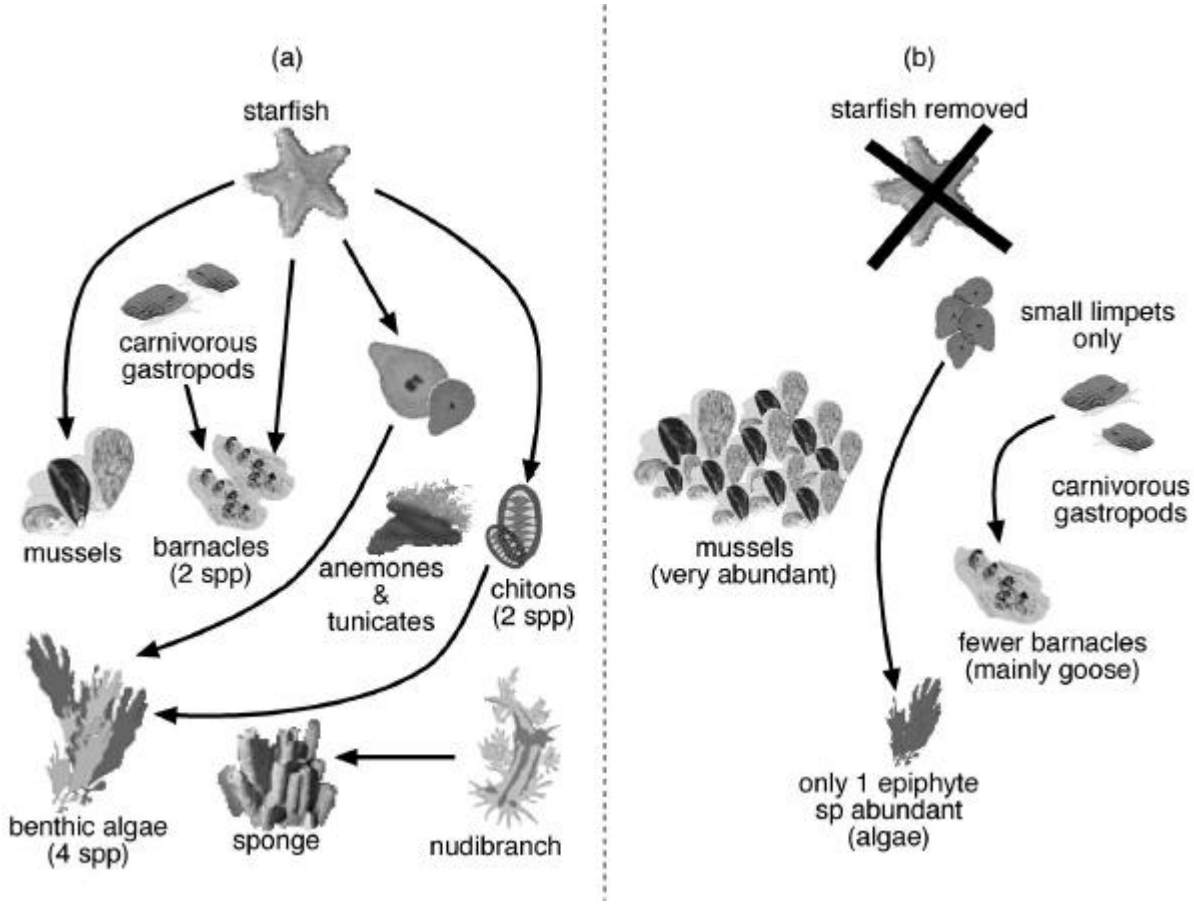


Figure 6. Schematic representation of the keystone role of predatory starfish *Pisaster* in an intertidal ecosystem in Washington (based on Paine, 1966).
(a) *Pisaster* predation maintains a diverse community.
(b) removal of *Pisaster* allows mussels to dominate, and reduces species diversity.

3.2.1 Keystone species

[18] The most widely used definition for keystone species is one "whose impact on its community or ecosystem is large, and disproportionately large relative to its abundance" (Power *et al.*, 1996), i.e. keystone species affect processes at the community or ecosystem level to a greater extent than would be expected based upon their relative abundance alone (Bond, 1993). Keystone species are likely to occur near the top of the food chain, although they are not

necessarily at the highest trophic levels (Power *et al.*, 1996) and they are by definition not abundant. They have an impact on other species by means of consumption, competition, etc., and also by physically modifying habitat characteristics (ecosystem engineering). Ecologists devoted a lot of attention to identifying keystone species in nature, as it was suggested that the future of conservation management might lie in maintaining keystone species rather than attempting to protect and manage all species subjectively considered to be important or vulnerable (Power *et al.*, 1996).

[19] Paine (1966) examined the top-down effects of predatory starfish in rocky intertidal communities, showing for the first time that some species play key roles in ecosystems by preventing single species from monopolizing a limited resource. In the presence of the starfish *Pisaster ochraceus*, the intertidal community at Mukkaw Bay, Washington, comprised a diverse assemblage of algae, mussels, barnacles, chitons, limpets, sponges and nudibranchs (Figure 6(a)). When the keystone predator, *Pisaster ochraceus*, was experimentally removed, its most important prey species, the mussel, *Mytilus californianus*, was able to proliferate, reducing species diversity and effectively reverting the ecosystem to a monoculture of mussels (Figure 6(b)). Sanford (1999) found that the strength of the *Pisaster-Mytilus* interaction is reduced during periods of cool upwelling, concluding that a change in keystone interaction strength as a result of environmental changes could have large impacts on ecosystems.

[20] There are very few examples of marine keystones that are not from the intertidal region. One example is the top-down control by the jellyfish *Aurelia aurita*, shown to determine the structure of the zooplankton community in a shallow cove in Denmark (Oleson, 1995). Species newly introduced to an ecosystem (e.g. invasive aliens) may have strong effects that are disproportionately large relative to their biomass, i.e. they may be considered to be keystones even if they are not formally components of the ecosystems. Nevertheless, these species may subsequently become dominant as they benefit from the absence of predators and diseases in their new environment (Power *et al.* 1996). Kitchell *et al.* (1999) examined the possible keystone effects of apex predators, such as sharks, tunas and billfishes, in the Central North Pacific, finding that no single species at high trophic levels could be considered as a true keystone. In their simulations using an ECOSIM model, Kitchell *et al.* (1999) found no evidence that strong predatory effects were propagated through the system, affecting species at lower trophic levels. Even removal of fisheries, shown to act in a similar way to a keystone predator, did not have effects on the first two trophic levels of the ecosystem.

[21] Although keystone species are not frequently identified in marine ecosystems, in some cases they can cause, in addition to other changes in dominant species, major changes to ecosystem structure and functioning through trophic cascades down the marine food web.

3.2.2 Trophic cascade

[22] Trophic cascades are defined as reciprocal predator-prey effects that alter the abundance, biomass or productivity of a population community or trophic level across more than one link in a food web (Pace *et al.*, 1999) (Figure 7B). True trophic cascades imply keystone species (Paine, 1980), taxa with such top-down dominance that their removal causes precipitous change in the system. They result in inverse patterns in abundance or biomass across trophic links in a food web. These trophic interactions were first described in lakes (see Carpenter and Kitchell (1993) for a review) and intertidal zones (Paine, 1980; Estes and Duggins, 1995). They were thought to be relatively unusual sort of food web mechanics and a form of biological instability (Strong, 1992) restricted to particular types of marine ecosystems (Hall, 1999). However, new examples are emerging from studies in several contrasted ecosystems, suggesting that cascade effects can be revealed in diverse marine ecosystems, even in unexpected places such as the open ocean (Pace *et al.*, 1999). Trophic cascades can have strong impacts on ecosystems and can stabilize them in alternate states.

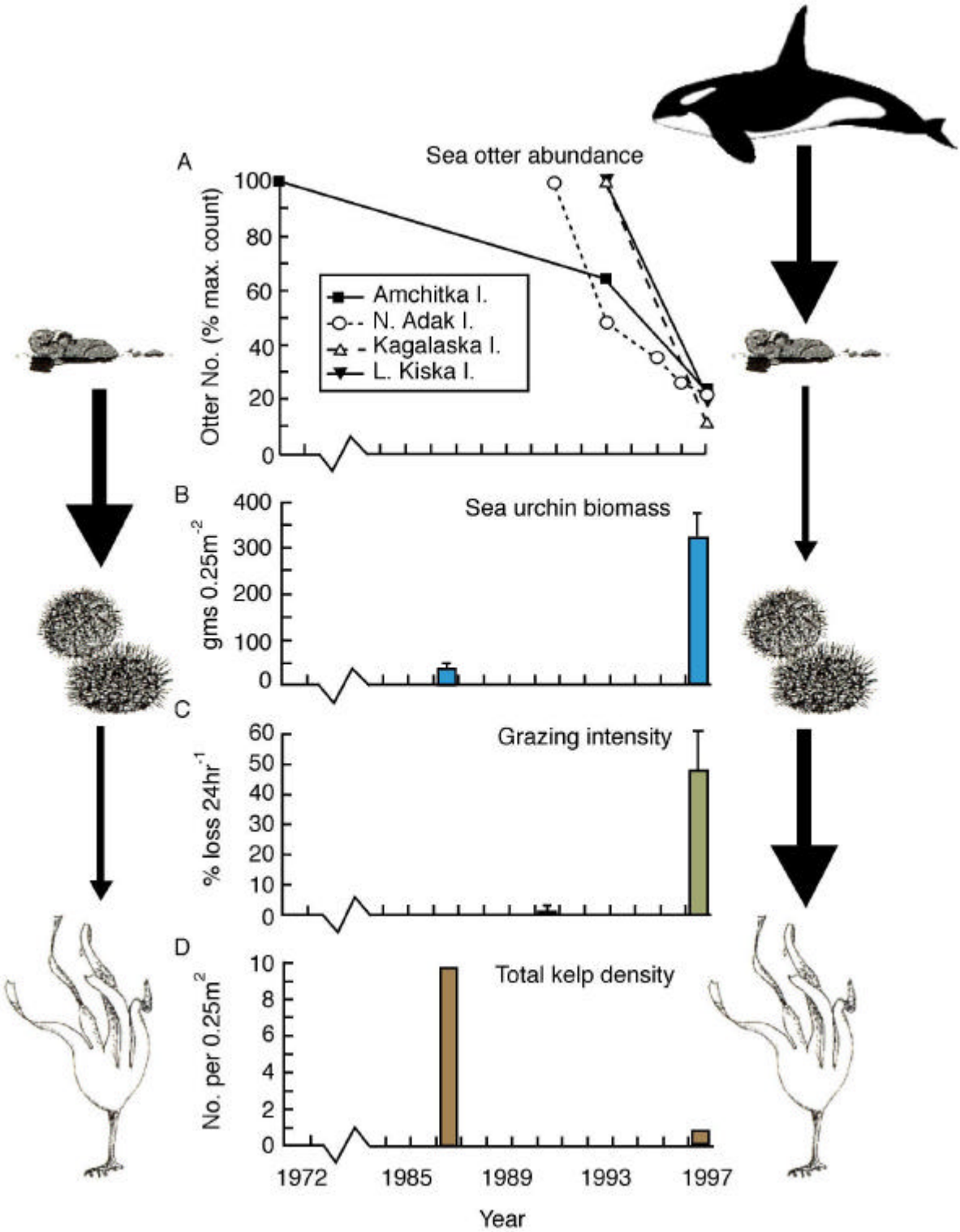


Figure 7. Trophic cascades illustrated in the Aleutian archipelago, western Alaska.
On the left is shown how the ecosystem was organized when the sea otters are abundant: they predate heavily on the sea urchin biomass, which remains low, the resulting weak grazing intensity allows a high density of kelps.
On the right, the addition of killer whales as an apex predator limits the sea otter abundance, then the sea urchin biomass can develop and the resulting grazing intensity constrains the kelp density to low levels.
Heavy arrows represent strong trophic interactions; light arrows represent weak interactions.
(redrawn from Estes *et al*., 1998).

[23] An example is the otter-urchin-kelp interaction in Alaska (Estes and Duggins, 1995). When otters, considered to be keystone species, are abundant, they stabilize a system of abundant kelp forest by reducing urchin grazing (Figure 7 left). When present in low abundance, sea otters shift the system to urchin dominance, with substantial reductions in kelp coverage and productivity (Figure 7 right). As stated by Pace *et al.* (1999) this illustrates how trophic cascades can induce dramatic shifts in both the appearance and properties of ecosystems. Another example is the possibility that the feeding effect from the pink salmon (*Oncorhynchus gorbuscha*) controls summer macrozoo- and phytoplankton biomass in the sub-Arctic North Pacific. By exploring relationships between species at different trophic levels, the biomass of the planktivorous pink salmon was found to be inversely related to zooplankton biomass, which in turn is inversely related to phytoplankton biomass (Shiomoto *et al.*, 1997). In pelagic marine ecosystems, alterations of consumer abundance can cascade down food webs to affect phytoplankton biomass, but this effect is hardly ever detected (Micheli, 1999). Zooplanktivores tend to decrease mesozooplankton abundance, but the mesozooplankton commonly has no effect on the phytoplankton, making the loose coupling between herbivores and plants pervasive (Micheli, 1999). Humans are interacting with top predators. In western Alaska, killer whales (*Orincus orca*) may have recently begun to prey on sea otters, driving a population decline with drastic effects on urchins and kelps (Figure 7 right). It is possible that the behaviour of killer whales toward sea otters has recently changed due to the collapse of their preferred food, the marine mammals. Further, the cause of the decrease in pinniped abundance might be related to overfishing and climate change (Estes *et al.*, 1998). As stressed by Pace *et al.* (1999), this provides a good example of one of many cases in which it appears that fisheries and fish management are altering trophic cascades, with profound consequences for food webs in coastal ecosystems. Humans also compete with top predators for valuable marine resources. South African fur seals feed on several commercially important fish species. The problem is apparently an easy one to solve. If top predators compete with fisheries, then fisheries should also compete with predators by culling the expanding seal population. In fact, and as illustrated by Yodzis (2001) the expecting results of doing so are controversial as no obvious cascading effects or probable increase of fish resource are to be expected from such culling. This might be the case for most mammal populations for which direct competition with fisheries appears to be limited (Trites *et al.*, 1997). Even though direct competition between fisheries and marine mammals for prey appears to be rather limited, indirect competition might occur for primary production, which sustains both fisheries and marine mammals. The rapid expansion of fisheries may thus lead to so-called ‘food-web competition’ (Trites *et al.*, 1997).

[24] Trophic cascades are transitory dynamic interactions and hence exhibit variations in their strength and duration. Not all cascades propagate to lower trophic levels or have significant impacts on ecosystem processes, as numerous compensatory mechanisms dampen or eliminate them (Pace *et al.*, 1999). Fishing usually greatly reduces the abundance of top predators, and it stands to reason that the abundance of prey populations and their effects on marine communities will increase after release from predator control (Steneck, 1998) (Figure 7B). Many trophic cascades that formerly arose might have disappeared after decades of intense fishing (Steneck, 1998). In this instance, defining proper baselines for both fisheries and conservation objectives will be laborious. Few species are keystone species, and sometimes a keystone species is only revealed for certain configurations of the ecosystem. It would be unreasonable to manage fisheries by solely arguing that a particular species is a keystone species and that cascade actually occurs, unless strong evidence supports such mechanisms (Hall, 1999). Despite those difficulties, adopting a top-down approach can help to understand several observed ecological patterns and to get a glimpse of the possible consequences at an ecosystem level when removing top predators.

[25] Although much attention has been devoted to determining which species are keystones in various marine ecosystems, it may be more useful for management purposes to focus on the strength of interactions between species, as proposed by Mills *et al.* (1993). Support for this

approach lies in the fact that exploited species are rarely keystones and thus changing their abundances may have small or inconsistent effects on their prey or competitors (Jennings and Kaiser, 1998). At the same time, removing large proportions of forage species may have similarly large impacts on their prey, competitors and predators to those species with typical "keystone" attributes (Shannon and Cury, in prep.). The effect of removing large portions of pelagic fish species, such as anchovies and sardines, in the functioning of upwelling systems is explored in the next section.

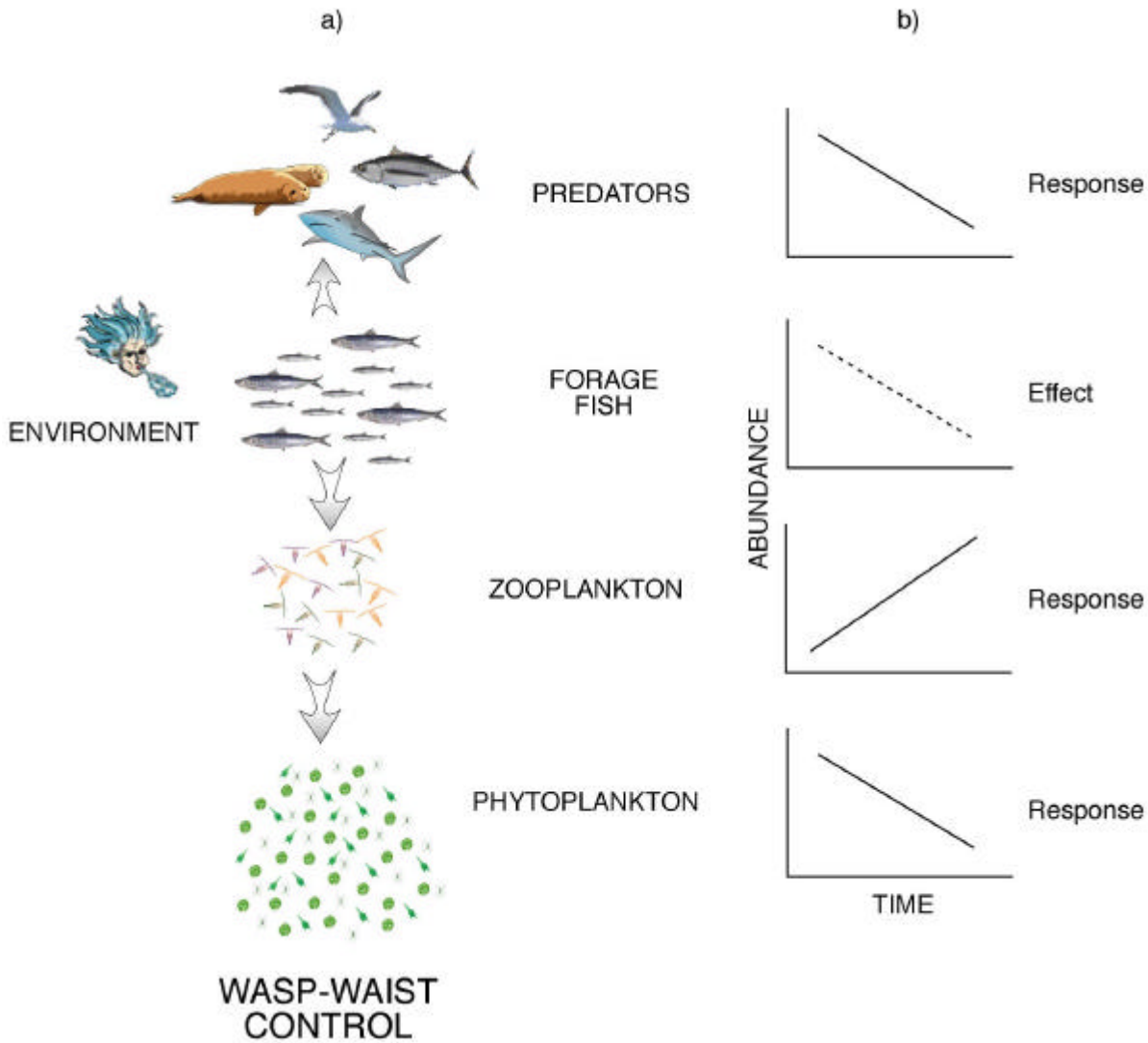


Figure 8. (a) Wasp-waist control within a simplified four-level food web in a marine ecosystem.

(b) The abundance of the prey fish (small pelagic fishes), which depends on the environment, controls both the abundance of the predators and of the primary production. A decrease in the prey fish abundance affects the abundance of the predators negatively. The same decrease in abundance of the prey fish reduces the predation on zooplankton, which increases in abundance. A more abundant zooplankton population increases grazing pressure and leads to a diminishing phytoplankton abundance (the control factor is solid line and the responses are dashed lines).

4. WASP-WAIST CONTROL: SMALL PELAGIC FISHES DRIVE BOTH THE VERY LARGE AND THE VERY SMALL

4.1 Dominant species in upwelling systems

[26] Many marine ecosystems share one striking aspect in the structure of their biological communities: they typically contain a large number of species at the lower trophic levels. They also contain a substantial number of predatory fish, seabirds or marine mammals that feed at the upper and near-apex trophic levels. However, in many of the productive ecosystems of the world, and particularly in upwelling ecosystems (Canary, Benguela, California and Humboldt currents), there is an intermediate trophic level, occupied by a limited number of species of small, plankton-feeding pelagic fish, comprising massive populations that are intensively exploited and vary radically in abundance (Cury *et al.*, 2000). Small pelagic fish seem to exert a major control on energy flows in upwelling ecosystems, and this has been called wasp-waist control (Figure 8(a)). In twenty open marine ecosystems, Micheli (1999) found that interannual fluctuations in mesozooplankton biomass were negatively correlated with those of zooplankton fish, indicating that fish predation controls mesozooplankton biomass. Similar top-down control of zooplankton by sardine, sardinellas, herring or anchovy was also detected off South Africa, Ghana, Japan, in the Black Sea (Cury *et al.*, 2000), as well as in the northern Baltic (Arrhenius, 1997). Conversely, bottom-up control of fish predators by small pelagic fish has been noticed as predatory fishes suffer from the collapse of their prey in the Benguela, the Guinea, and the Humboldt currents (Cury *et al.*, 2000). Once food becomes abundant again, the recovery of the depleted predator biomass may be immediate, or delayed by short or long periods, highlighting the complex response of the ecosystem to change.

[27] Many top predators are buffered against large fluctuations in their food supply by, for example in the case of seabirds, high annual survivorship, protracted longevity, delayed sexual maturity, and a relatively low reproductive rate (Hunt *et al.*, 1996). Successful cases of prey switching have been recorded among several seabirds off California and South Africa (Crawford, 1999). However, this plasticity in life-history characteristics is sometimes insufficient to dampen the effects of longer-term fluctuations in prey resources (Crawford, 1999). This was the case off Namibia in the 1970s, when sardine in the diets of birds was mainly replaced by horse mackerel and pelagic goby. Because these fish were either distributed too far to the north, or occurred too deep in the water column, they were unavailable to penguin and gannet colonies situated south of Lüderitz, causing massive decreases in seabird populations (Crawford *et al.*, 1985).

These examples illustrate wasp-waist control, where small pelagic fish constitute mid-trophic-level populations that exert both top-down control on mesozooplankton and bottom-up control on top predators (Figure 8B). The collapse of a dominant prey can generate drastic changes at higher, but most surprisingly at lower, trophic levels. As fisheries have removed substantial amounts of small pelagic fish during the last decades, one must carefully consider the implications for the other component species. Again, it appears useful to state that numerous compensatory mechanisms tend to dampen or eliminate expected straightforward consequences, as predators can switch to another type of prey or can migrate to other feeding grounds. In spite of this, as noted by Cury *et al.* (2000), it is doubtful that the global pelagic fish catch will continue to increase at an annual rate of 4.3%, as is the case worldwide since the 1950s, without any ecosystem disruptions at different trophic levels.

5. DISCUSSION – FROM 'COMMON SENSE' AND 'PET CONCEPT' TOWARD AN ECOLOGICAL FRAMEWORK FOR DEALING WITH RESPONSIBLE FISHERIES IN MARINE ECOSYSTEMS?

[28] The success of fisheries management in the future will depend on research directed at the mechanisms underlying ecosystem dynamics and fisheries interactions (Murawski, 1991). 'Ecosystem management' presumes a reasonable understanding of the interactions among and between species complexes, as well as with their environment (Larkin, 1996). Nevertheless, the ability of marine ecology to contribute multispecies and ecosystem information useful to fisheries management has remained very limited (Botsford *et al.*, 1997; Hall, 1999). There are several reasons for this. One is the lack of detailed knowledge of most of the dynamic interactions that underlie multispecies modelling efforts (Rose *et al.*, 1996). Another is the intrinsic complexity of ecological systems that are driven by interactions at multiple levels and scales.

[29] Three different theoretical ways of considering energy flows through ecosystems have been presented. Considering top-down, bottom-up or wasp-waist control produces different ecosystem dynamics, and consequently different possible ecosystem responses to fisheries activity and management (Figures 2B, 4B & 8B). Obviously, the difficulty lies in the ability to determine the controlling factors within an ecosystem. Climate (bottom-up) as well as fishers (top-down) alter the functioning of marine ecosystems. However, an ecosystem is not driven entirely by only one type of control or another, but by a subtle and changing combination of them that might depend on its state, diversity and integrity. We have presented several case studies to illustrate the functioning of marine ecosystems, but clearly we have used the only few that are currently documented. Notably, alteration of the carrying capacity, species replacement or the existence of keystone species and trophic cascade are notoriously difficult to demonstrate. No general theory can be ascribed to the functioning of marine ecosystems, except in the light of the evolutionary theory, which results in poor predictive power for fisheries management. Recently, tentative and partial generalizations have been proposed, for example, that trophic cascades are mostly found in lakes, or in marine hard substrata ecosystems and mainly for less complex food webs, whereas wasp-waist control is most probable in upwelling systems. This restrains the field of possibilities and introduces opportunities for stimulating comparisons and generalizations. As mentioned earlier, the definition of 'ecosystem' is fairly new and the interest of the vast majority of marine ecologists is even more recent. Terrestrial ecology has a long tradition of studying ecosystems and has its own 'pet' concepts. Several 'nomad' concepts, such as keystone species or trophic cascades, can be applied in terrestrial as well as in aquatic studies. However, due to strong differences that exist between these ecosystem types (Chase, 2000; Cury and Pauly, 2000), more attention should be given to promote the development of new concepts on the functioning of marine ecosystems that will integrate such specificities (Franck and Leggett, 1994; Cury, 1994; Bakun, 2001). Nevertheless, ecological understanding and models of ecosystem functioning are provisional and subject to change (Christensen *et al.*, 1996), and common sense is not sufficient when studying complex dynamic systems. For the time being, we must admit ignorance of the true importance of the effects of fisheries acting through species interactions in marine systems (Hall, 1999). Several decades might be necessary for marine ecologists to refine concepts and to find the appropriate data to strengthen their theories on the functioning of marine ecosystems.

[30] These difficulties do not mean that an ecosystem approach to fisheries management should be abandoned or that we should just wait for more additional results on the functioning of ecosystems. Major steps are urgently needed, which will define an ecological framework for dealing with responsible fisheries in marine ecosystems. Ecological questions have to be addressed on the right scale, which often means an uncomfortably large scale (May, 1999). Comparative studies between marine ecosystems, a powerful method in ecology, should be promoted widely to bring new generalizations. Moreover, another objective should be to evaluate states and changes in marine ecosystems by defining new ecosystem indicators, to assess the

usefulness of these indicators for management purposes and to apply them to various ecosystems. This is a complex issue that needs to integrate our simplistic and disparate views of nature (Cury and Cayré, 2001). A framework for defining sustainable reference systems and indicators is actually being promoted (Garcia and Staples, 2000) and new meaningful indicators can be used to assess the impact of fisheries on ecosystems (Pauly *et al.*, 2000; Christensen, 2000). These contributions constitute major steps towards a new framework for fisheries management that incorporates our recent and incomplete, but consequential, theoretical background on the functioning of marine ecosystems.

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