

## **Chapter 14. PROCESSES AND PATTERNS OF INTERACTIONS IN MARINE FISH POPULATIONS: AN ECOSYSTEM PERSPECTIVE**

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1. Introduction
  2. Species interactions: from processes to patterns
  3. System-level perspectives: from patterns to processes
  4. Discussion
- Appendix: Models that are referred to in the text  
Acknowledgements  
Bibliography

### **1. Introduction**

A marine ecosystem has no apparent boundaries and lacks the clear objective or purpose that can be ascribed to other, more tractable, biological or ecological entities (e.g. cells, individuals or populations). It contains water, nutrients, detritus, and numerous kinds of organisms of different sizes and with different life history traits, ranging from bacteria, phytoplankton, zooplankton, and fish to mammals and birds. All these living and non-living components are connected in complex food webs through changing and evolving interactions, which make ecological systems extraordinarily complex (Polis, 1999). In addition, humans have been exploiting marine organisms for many centuries. Within the last half-century in

particular, fishing impacts have considerably altered natural ecosystems (ICES, 2000).

Scientists have long studied ecosystems, particularly in the terrestrial environment, resulting in numerous mathematical scale- and time-dependent models and theories. Reductionism and holism are two basic approaches that are used to understand processes and patterns (defined here as regularities in what we observe in nature (Lawton, 1999)). Reductionist approaches focus on the dynamics of a limited number of species (limited for practical and technical reasons). In general, these studies are based on single-species dynamics, but might be enriched by adding and formalizing species interactions. Holistic approaches focus on aggregated entities and processes, without necessarily considering the dynamics and interactions of individual species. These approaches are inclusive in terms of the number of species components, but are not detailed at the species level.

Because simple patterns can emerge from complex interactions and simple interactions can produce complex patterns, there is a continuing ecological debate between those who argue that all systems are different and unique, i.e. contingency and chaos reign, and others who argue that patterns are observable and reproducible, i.e. there is order and generalities occur. In the marine environment, fishing adds complication to the dynamics of the ecosystems, and has the potential to perturb existing patterns and generate new ones. In the present review we describe different attempts and several recent advances that have been made in ecology to formulate processes and patterns of interactions in fish populations, and that can help to understand marine ecosystem dynamics. Although this chapter is devoted to marine fish, some of the reviewed studies belong to fresh-water ecosystems, which are sometimes better documented than marine ecosystems. We critically review these different approaches to describe and understand the changing nature of marine ecosystems by analysing processes and patterns. Finally we advocate integrative studies that assemble all accumulated knowledge in a multidisciplinary way and that could provide an efficient framework for studying marine ecosystems.

## **2. Species interactions: from processes to patterns**

Species interactions include competition, predation, disease- and parasite- transmission, parasitism and mutualism. Fishing is a special case that involves interactions between fish and humans. In marine fish populations, these interactions usually require individuals to be found at short distances from one another. This matching in time and space of different species is related to their own migration patterns and habitat selection, which in turn depend on a number of factors. These factors include the searching for (prey) or avoidance of (predators, competitors) contact with individuals of other species. Therefore, individuals interact because of their particular biology, and their biology is a result of species interactions—a typical “chicken-and-egg” situation, which makes it difficult to interpret many observations. In the context of fishing impacts, it is also sometimes difficult to disentangle “natural” processes and patterns from those that have been caused by fishing.

The processes involved in species interactions can be simplified in models, which can then be used to identify patterns that might emerge at the community or

ecosystem level. However, we also recognise that fish species' interactions can be complex, because of the behaviour of fish, their ability to learn, the fact that they live in an environment that is largely unpredictable, and their evolutionary history. This means that emergent patterns might be the result of a number of different causal processes, and a variety of process models should be used in order to fully understand community dynamics. In this section, we describe some of the models that are used to describe species interactions (including those involving fishers), the underlying behavioural processes affecting fish, and some of the attributes of fish that might modify the patterns generated by these models. We focus on feeding interactions (predation and competition relationships) because almost all multi-species models that are applied in fisheries science refer to these types of interactions; other potential interactions (parasitism and mutualism) are implicitly considered not to be important in determining marine ecosystem dynamics.

### *2.1 Predator-prey systems*

Two-species predator-prey systems have been the subject of investigation since the 1920s, with the pioneer studies of Volterra (1926) and Lotka (1932), both of whom independently proposed the first predation model. This classical model of predation is based on some simplifying assumptions (Appendix), including that the birth and death processes respectively in the prey and predator populations are exponential. Analysis of the Lotka-Volterra model system shows that, apart from the point where both predator and prey populations are extinct, there exists another positive equilibrium point, and the dynamics of the system are such that the predator and prey populations exhibit cycles of abundance. This model system has didactic interest but has not been satisfactorily applied to real situations in the marine environment.

Since the development of the Lotka-Volterra model, numerous studies have proposed different formulations for predator-prey interactions, resulting in systems that exhibit contrasted dynamics. In a general formulation of a predator-prey system, three processes must be specified:

1. the intrinsic growth rate of the prey population in the absence of predators,
2. the functional response of the predator, which describes the factors affecting the number of prey consumed by a predator per unit of space and time, and
3. the numerical response of the predator, which describes the rate of conversion of prey into predators.

For these three processes, the choice of the mathematical functions, which contain important biological information, is crucial to the dynamics of the studied systems (Yodzis, 1994). We will examine each process in more detail below.

#### **Intrinsic growth rates of prey populations**

The Lotka-Volterra model assumes that prey populations exhibit a Malthusian (exponential) growth rate, which is not realistic. Subsequent predator-prey models assumed logistic, density-dependent growth (Verhulst, 1838), where a "carrying capacity" of the habitat is specified for the prey populations.

In fish populations, the concept of having a constant carrying capacity is seldom realistic, but population growth rates of many species are found to vary inversely

with population density because of competition for food. In upwelling ecosystems, consumption by pelagic fish is usually exceeded by plankton production (review in Bakun, 1989), and competition is not expected to be a limiting factor. Nonetheless, density-dependent growth is often observed. A possible explanation concerns the effect of schooling. Most pelagic fish species occur in dense schools of several ten thousand individuals, at least during the daytime, and usually maintain a high level of aggregation during the night. Many demersal species do the same during their early stages of development. Sometimes two or more species of pelagic fish school together, forming a "mixed-school" of individuals of similar size and body shape. Average school size generally increases in response to an increase in population size (Fréon and Misund, 1999), although recent unpublished data from the South African purse seine fishery suggest that this relationship might not be linear. Bakun (1989) proposed that any increase in mean school size in response to an increase in population density would increase local competition for food and oxygen inside the school, thereby decreasing population growth rates.

Growth rates of prey populations are not only limited by the carrying capacity of their environments, but can also be reduced when their densities decrease. The "school-trap hypothesis" (Bakun and Cury, 1999) states that a fish species that occurs in a mixed-school with a more abundant species must effectively subordinate its specific needs and preferences to the "corporate volition" of the school. This hypothesis received recent support from field observations on estuarine clupeoid fish by Maes and Ollevier (2002). School-traps could promote large amplitude, out-of-phase population oscillations of small pelagic fish species. The school-trap hypothesis implies that adaptive changes in population dynamics ("school-mix feedback"; Bakun, 2001) could occur much faster than those related to genetic evolutionary processes.

Growth rates can also be affected by predators which, apart from having a direct, consumptive effect on their prey, can also cause them to move to safer but less productive habitat. As a result, the prey will experience both reduced individual growth and decreased survival (e.g. Tonn et al., 1992). Similarly, Power (1987) gave observational and experimental evidence that large armoured catfish (Loricariidae), although severely resource-limited in the deeper part of pools in a Panamanian stream, avoided shallow, rich areas because of the greater risk of predation by birds.

### **Functional responses of predators to their prey**

There are a number of different ways of modelling the functional responses of predators to their prey (see Appendix), depending mainly on what one assumes about how predators interact with one another. When predators do not interfere with one another in their feeding activities ("*laissez-faire*", Caughley and Lawton (1976)), the functional response of the predators depends only on their prey densities, not on predator density. The Lotka-Volterra model assumes that the number of prey consumed per unit of time is a linear function that is not limited by prey numbers (Czaran, 1998). According to Holling (1959), feeding consists of two types of activity: searching for prey and handling them. He assumed (i) that the total time dedicated to feeding is the sum of search time and handling time, and (ii) that the handling time is a constant. The Holling type II response assumes that the attack rate is proportional to the number of prey in the environment (Begon et

al., 1996). The Holling type III response assumes that predators are inefficient at handling prey when prey are not abundant (Yodzis, 1994).

Some of these assumptions are nullified if the prey populations are schooling species. Encounter rates between predator and prey will remain constant with an increase in prey biomass unless there is a substantial increase in the number of schools. There is always more than enough prey in a school to satiate a predator or a group of them, and predators are not observed to follow a given school for many hours. As a result, an increase in schooling fish prey does not necessarily result in a proportional increase in prey accessibility and therefore consumption. Density-dependent mortality in prey can also result from changes in schooling behaviour of predators. Anderson (2001) showed experimentally that predatory kelp bass (*Paralabrax clathratus*) responded to an increase in their prey density (kelp perch *Brachyistius frenatus*) by a strong increase in aggregation, and an increased predation rate. This experimental result was consistent with observed patterns of density-dependent mortality of prey in field studies.

In contrast to Holling's (1959) models, another family of models assumes the existence of predator interference through trophic or reproductive competition, disease transmission, cannibalism, or density-dependent emigration (Yodzis, 1994). In this category, a common functional response is the one of Hassel and Varley (1969), which assumes that the predation rate decreases when predator abundance increases and, for a given density of prey, the greater the abundance of predators, the slower the rate of consumption by a predator. This general formulation can be applied to a large number of predator-prey systems, but their behaviour becomes unrealistic in the particular case when the predator population tends to zero, because the predation rate tends towards infinity.

This problem also occurs for ratio-dependent formulations of the predator functional response. Initially proposed by Arditi and Ginzburg (1989), ratio-dependent formulations assume that consumption rate decreases proportionally as predator abundance increases, because the same resource must be shared by a greater number of consumers. The choice between a prey-dependent versus a ratio-dependent functional response is a controversial and topical subject. Supporters of ratio-dependence endeavour to show that this formulation better accounts for the behaviour of natural ecosystems. For example, Ginzburg and Akçakaya (1992) showed marked differences between prey- and ratio-dependent models in the response of trophic food chains following an increase in primary production in the system. In the ratio-dependent model, all the trophic levels responded proportionally to the increase, whereas in the prey-dependent model, the responses differed according to the trophic level considered and the number of trophic levels in the system. According to the same authors, the first response appears to be common in the food chains of lakes.

The different models of functional responses of predators to their prey aim at representing simple, specific foraging strategies. However, some variations on the general foraging strategy can occur which produce different patterns of interactions. Foraging strategy defines species-specific behaviour that has evolved through natural selection to maximize individual fitness (Hart, 1997). Foraging tactics (or modes of foraging) are behavioural variations within the strategy that allow animals to vary their behaviour in response to local conditions or to variations in prey type. Tactics can be seen as behavioural variations used by a predator

to overcome the detection and handling problems posed by the anti-predator defences of the prey. Therefore, strategies and tactics are two levels in a hierarchy (Wootton, 1984). The interaction between predator and prey is dynamic through evolutionary time, with each actor evolving behaviour to outwit the other. According to Endler (1991), the interaction is not true coevolution, but rather an "arms race". Foraging tactics might change during the development of individuals. Ontogenetic shifts in morphology are often associated with ontogenetic niche shifts and, in some species, there is interplay between behaviour and morphology (Meyer, 1987).

Hart (1997) established that tactical variability in fish foraging behaviour exists and variations have functional significance. Some species are more flexible than others in their ability to vary their foraging tactics, mainly because of morphological constraints. Some species are highly specialized in their hunting behaviour, e.g. stationary search (sit-and-wait) and prey capture by ambush. Other species can alternate ambush and chase in open water, and solitary or cooperative chasing. Different hunting activities are related to significant differences in growth rates of the species, especially when they are forced to use the same tactic for a long time (e.g. Eklöv, 1992; Eklöv and Diehl, 1994). There are limits set by morphological structures such as the jaws, but these structures are not totally rigid, and significant behavioural flexibility can be accommodated (Galis et al., 1994; Hart, 1997). The same applies for tactics of prey capture, manipulation and handling by predators (e.g. Vinyard, 1982; Helfman, 1990). This flexibility can generate greater than expected variability in fish diet, as shown in the next sub-section. Furthermore, the level of hunger modifies feeding behaviour, which becomes less efficient and exposes the predator itself to a greater risk of predation (Miyazaki et al., 2000).

From a review of different search paths used by different species of fish, Hart (1997) suggested that, rather than a set of discrete tactics, there is a continuum between the extremes of movement speeds, with one extreme being continuous search and the other sit-and-wait search. An interesting and apparently common tactic is the saltatory search in which the forager stops and searches the entire volume of water in front of it and then moves on until a new unsearched volume is available (O'Brien et al., 1990). The saltatory search allows the encounter of several prey simultaneously and hence prey selection.

Learning aspects in fish behaviour are poorly known but are likely to play a significant role (reviews in Fréon and Misund, 1999; Brown and Laland, 2001). Learning can allow foragers to adapt to spatial and temporal variation in prey properties (Hart, 1997; Ehlinger, 1989). Hart (1997) hypothesises that fish can use a suite of foraging tactics involving searching for and handling prey to cope with the variability of prey or patch types encountered and their spatial distribution. Furthermore, the effects of learning on prey handling and predator hunger state combine additively and interactively (hungrier fish learn more efficiently than less hungry ones).

### **Numerical responses of predators**

The most widely used predator numerical response function corresponds to a "laissez-faire" situation (see Appendix), representing a balance between gains to the predator population (proportional to the quantity of prey consumed by a predator), and its losses. Interference can also be taken into account, affecting the predator consumption rate (the functional response) or the predator growth rate.

The predator numerical response function of Leslie (1948) is based on the assumption that the predator population grows logistically, with a carrying capacity that is proportional to the abundance of prey. A problem with this formulation is that the carrying capacity of the predators is zero when prey abundance is zero. Because predators incur maintenance costs, their carrying capacity should be zero at some positive threshold of prey abundance (Yodzis, 1994).

**Patterns that result from predator-prey interactions**

Different theoretical patterns can emerge from different combinations of processes affecting predator-prey interactions. For example, a predator-prey system that has density-dependent growth of the prey and a type II Holling functional response can exhibit very different dynamics, depending on the predators' handling efficiency (Figure 14.1). When handling efficiency is small, the predator goes extinct (Figure 14.1a), when it is intermediate both populations coexist in a stable equilibrium (Figure 14.1b), and when it is large the predator and prey populations exhibit cyclic oscillations (Figure 14.1c).

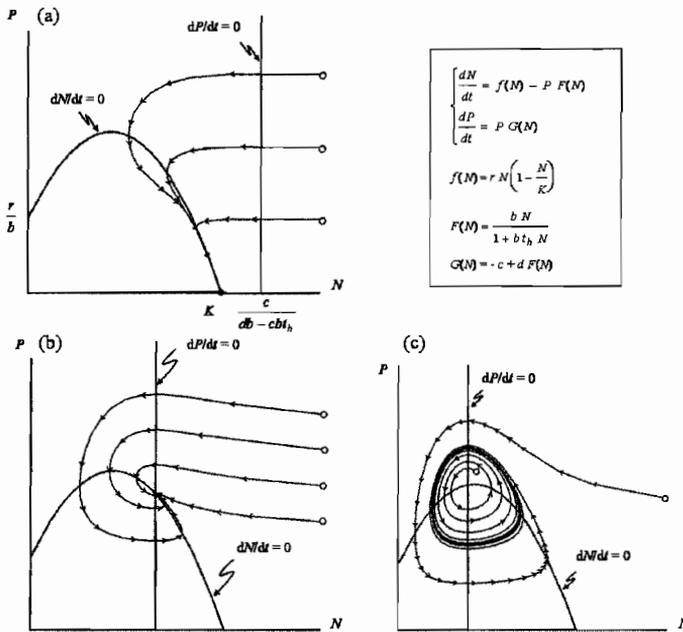


Figure 14.1 Stability properties of a predator-prey model that has density-dependent growth of the prey population (formulae presented in the upper-right panel), a type II Holling functional response and a "laissez-faire" numerical response for the predator (adapted from Czarán, 1998). The effect of the interactions on the dynamics of the system depends on the efficiency of prey handling by their predators. (a) Stable equilibrium point with predator extinction, (b) stable coexistence of both species, and (c) stable limit cycle.  $N$  = prey density;  $P$  = predators density;  $f(N)$  = intrinsic growth rate of prey with carrying capacity  $K$ ;  $F(N)$  = functional response of predators to prey;  $G(N)$  = numerical response of predators to prey;  $t_h$  = handling time (the inverse of handling efficiency);  $r$ ,  $b$ ,  $c$  and  $d$  are constants.

Michalski and Arditi (1995a; b) conducted a theoretical study of complex food webs, in which they proposed a generalisation of predator-prey models that included a Holling type II functional response and a numerical response with interference in the consumption rate. Using arbitrary values of the parameters, the authors applied the model to a theoretical system consisting of 11 species (Michalski and Arditi, 1995a). At equilibrium, only a few links persisted (Figure 14.2a). By imposing a variation of 60% in the values of parameters that describe prey selectivity and competition among predators, the effective structure of the trophic web changed radically (Figure 14.2b-f). When the system at equilibrium was disturbed (e.g. by changing the abundance of a species), the same authors (Michalski and Arditi, 1995b) showed that their multi-species model leads to systems that are rich in interspecies links when they are far from equilibrium, and poor in links when they approach it. A consequence of these results is that the structure of food webs can vary with seasonal variations in species abundance as well as variations in the parameters for competition efficiency and food preferences. The difficulty is to determine the temporal variation of these parameters in applying this kind of model to real systems.

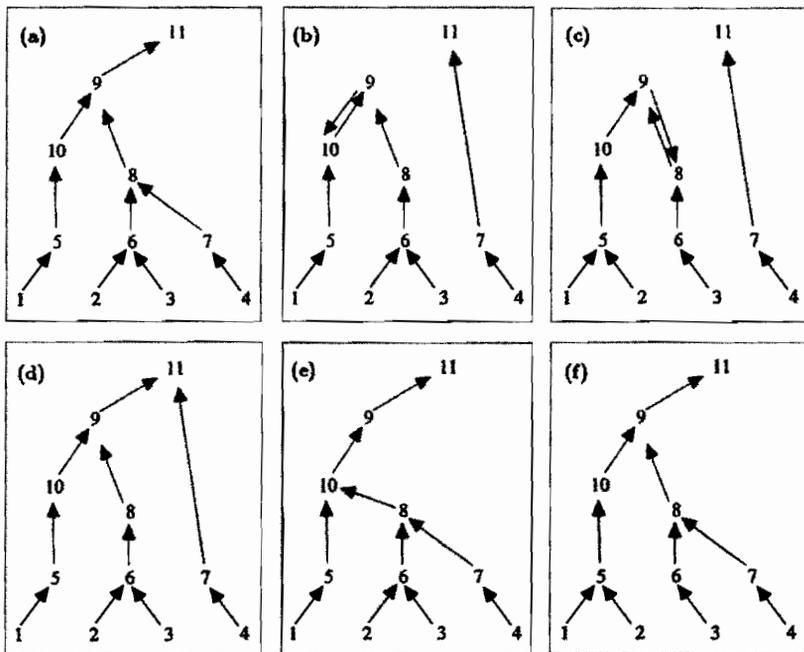


Figure 14.2 Representations of equilibrium states for a trophic web of 11 species, modelled using a system of coupled equations that assume logistic growth for the "forage" species (species 1 to 4), and Holling type II functional responses for predators, and numerical responses with interference by predators for consumption rates. The different trophic structures are obtained from different values for food preferences and competition efficiencies. The arrows indicate the presence of effective interspecies links (from Michalski and Arditi, 1995a).

These dynamic predator-prey models are not easily applied to real predator-prey systems, but they are important tools for exploring complexity in the behaviour of interacting populations. Different studies using such models show their sensitivity to parameter values, to initial conditions, and to the formulation of functional and numerical responses of the predators. Furthermore, they exhibit a wide variety of behaviours, from periodical dynamic to stable coexistence of two species. The results produced by these models have to be cautiously interpreted, because the same equations can lead to very different dynamics, even qualitatively. Predator-prey models have been used to explore the stability of multispecies systems, which is a topical field of investigation in ecology and fisheries science. The use of different concepts or definitions of the stability of ecological systems is at the origin of most of the controversy existing on the subject. It is therefore essential to specify that, here, the stability of mathematical systems of differential equations corresponds to the existence of a stable steady state for all variables of the system (alternatively, stability can be defined as the opposite of temporal variability, and in this case, it is measured by the coefficient of variation of the state variables of the system—Tilman, 1999). Gardner and Ashby (1970) and May (1972) are among the first to have examined the mathematical stability of complex multispecies systems. They tested whether systems that consist of a large number of interacting populations are stable, i.e. all trajectories of the variables converge towards an equilibrium. The authors showed that stability decreases when the size of the system (species richness) and its connectance increase. Using different formulations of predator-prey systems, DeAngelis (1975), Gilpin (1975) and Pimm (1979) reached similar conclusions. More recently, Michalski and Arditi (1999) showed that the risk of population explosions increases with the connectance and species richness of a system.

### **Effects of fishing in predator-prey systems**

#### *The Schaefer model and its derivatives*

The Schaefer (1954) model is a simple stock assessment model, still used in many instances, e.g. tropical and tuna fisheries (Hilborn and Walters, 1992). It is a modified logistic (Verhulst) model, and its dynamics are such that a fished population will grow rapidly when it is reduced far below carrying capacity, but the population growth rate will be zero at carrying capacity. Any removal by fishing will always maintain the population below carrying capacity, and the maximum sustainable yield (MSY) occurs when the population is at half its carrying capacity.

The Schaefer model can be extended to a multi-species case by coupling single-species Schaefer equations through species interaction terms, which are simple multiplicative terms like those found in the Lotka-Volterra model. The main results of the single-species Schaefer model can only be extended to the multi-species case under restricted circumstances. Kirkwood (1982) showed that the total MSY will correspond to exploitation at half the total pristine biomass only in the restrictive case of a multi-species assemblage where the species are independent and/or competitive and/or mutualistic, and predation interactions are close to zero.

Ströbele and Wacker (1991) considered a two-species system using the Schaefer model. They explored the theoretical consequences, in terms of catch, when differ-

ent types of interactions (predation, competition, mutualism) and different fishing scenarios are modelled. They showed that, in the case of mutualistic species, the theoretical fishing yield would be greater than the one obtained with independent species. If the species are competitive, the yield is smaller (Figure 14.3). In the case of predation interactions, if the prey are selectively fished the effect is similar to the competition case. This result would be expected, because a decrease in the biomass of prey will cause a decrease in the biomass of its predators. If predators are selectively fished, the same effect is obtained as for the mutualism case. When both predators and prey are fished, the system is more complex, and the results depend on the relative magnitudes of the parameters of predation, catchability and intraspecific competition (Appendix).

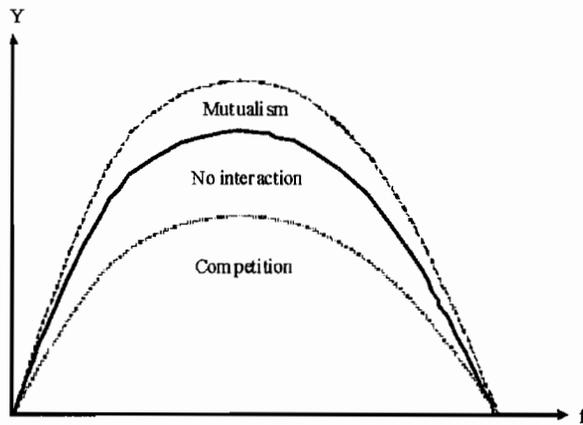


Figure 14.3 Total catch ( $Y$ ) as a function of fishing effort ( $f$ ) for a two-species system (adapted from Ströbele and Wacker, 1991).

#### *A krill-whale system under exploitation*

There are few applications of predator-prey system models in fisheries science. Among the fisheries applications is May et al.'s (1979) study on multi-species assemblages in the Antarctic. They (and thereafter Beddington and May (1980) and Flaaten (1988)) used the predator-prey model of Leslie and Gower (1960), which consists of a combination of a Lotka-Volterra-type linear functional response of predators to prey, and a Leslie numerical response of the predators. They first investigated the behaviour of a classical predator-prey (whale-krill) model under fishing.

Both populations were exploited at rates that were multipliers of the intrinsic growth rates of the respective populations. Simulations showed that when fishing mortality rates exceeded population growth rates, the whale population collapsed or the whole system collapsed. In contrast, when fishing mortality rates were inferior, there existed a unique equilibrium where the presence of whales had the trivial effect of decreasing the fishing yield and the abundance of krill. When the exploitation of whales increased, the abundance of krill increased, which caused an

increase in the growth rate of the remaining whales. Thus, when half the pristine biomass of krill was removed by predation, the maximum sustainable yield (MSY) for whales occurred when fishing effort was 19% greater than in the single-species case. The MSY for krill increased with fishing on whales, the maximum being reached when the whales went extinct.

May et al.'s (1979) analysis was made more complex by adding to the model another krill predator and competitor of the whales (seals), or by adding another intermediate trophic level between whales and krill (cephalopods). One of the conclusions of this study was that, in different multi-species configurations, the only possible generalisation is that the concept of MSY can be applied to the top trophic levels, and that their MSY occurs at effort values that are greater than those corresponding to half the pristine biomass.

Yodzis (1994) criticized the Leslie model used in May et al.'s (1979) study because the combination of a Leslie numerical response and a *laissez-faire* functional response (type II) is biologically paradoxical, and invalidates the structure of the model. Indeed, in this case, the interference between predators is strongly linked to available prey (numerical response), but the predators have no interference among themselves for consumption rates (functional response). Yodzis (1994) showed that the results obtained by May et al. (1979), and subsequently by Flaaten (1988), depend fully on the choice of the Leslie model. This is important to highlight, because Flaaten (1988) advocated intense reductions in the stock of marine mammals in order to increase fishing yields of fish of commercial interest. In addition, we showed how erratic the behaviour of the Leslie model (and also the Hassel-Varley and Arditi-Ginzburg models) becomes when prey densities are low.

## 2.2 Diet selection and food webs

Foraging behaviour can involve «decisions» (sensu Dill, 1987) such as where to feed, when to change feeding grounds, and which food items to select. Because successful feeding is obviously one of the major components of "fitness" (others being predator avoidance and successful reproduction), behavioural ecology applied to feeding behaviour has been based on the assumption that decisions made while foraging maximise the net rate of energy gain per unit time. This is the basis of optimal foraging theory, proposed by MacArthur and Pianka (1966) and Emlen (1966). It is unclear how fish manage to assess the profitability of their prey, which depends on a lot of factors related to the energetic return from the prey (prey mass, energetic content and digestibility) and handling time (which varies with a number of factors including size relative to forager, body shape, presence or absence of appendages or defensive mechanisms, swimming speed and agility, etc.). Hughes (1997) suggests that this assessment is possible because, through experience or genetic programming, foragers come to respond to a small set of key stimuli indicating the probable profitability of their prey. Empirical *in situ* studies suggest that the effects of morphological constraints, such as predator and prey sizes, on encounter rates and handling times are key factors determining predators' diets (reviews in Persson and Diehl, 1990; Mittelbach and Osenberg, 1994; Hart, 1997; Hughes, 1997).

There are a number of existing models of trophic interactions in aquatic communities or ecosystems. Attempts at modelling trophic interactions (see Appendix

for details of the models) make different assumptions or simplifications (usually acknowledged by the authors of those models) about diet compositions. We describe below four ways in which diet composition can be represented.

### **Fixed diets**

In a fixed diet, the composition of prey items making up the diet is fixed according to an average derived from stomach-content data. For example, fixed diets are used in Ecopath models (Christensen and Pauly, 1992), which represent foodwebs at a theoretical equilibrium state. However, a fixed diet is an oversimplification of fish behaviour. Feeding can change as a result of changes in foraging tactics, changes in prey abundance and predator experience. Hughes et al. (1992) indicate that performance in all phases of handling prey, from initial recognition to final ingestion, can improve as fish gain experience of specific prey. By comparing hatchery-reared naive fish to wild-caught fish, Reiriz et al. (1998) found that learning had a visible effect on the pattern of selection for three live prey types by juvenile Atlantic salmon (*Salmo salar*). Finally, feeding behaviour might be altered in several ways by the risk of predation while foraging. These alterations include timing and location of feeding, searching mode, feeding rate, prey-handling tactics, vigilance and social behaviour (Lima and Dill, 1990; Connell, 2002). As a result, risk of predation can influence diet selection, causing a forager to broaden its diet or to prefer safer but less profitable prey (Godin, 1990; Sih, 1993). It is likely that the optimal diet is a trade-off between maximising energy gain and minimising mortality (Milinski, 1993; Hughes, 1997).

### **Proportional diets**

Proportional diets result from indiscriminate feeding, so that the diets represent the availability of prey items in the environment; the diet is proportional to prey abundance and availability. Proportional feeding is a simple, attractive assumption, but unfortunately it is frequently not true. Many species of predators feed disproportionately on any acceptable prey whose relative abundance is high (Hughes and Croy, 1993). This can be interpreted by a number of untested hypotheses, of which the most common is that there is a benefit from learning and from the development of a "search image" (*sensu* Tinbergen, 1960) favouring detection and capture of prey. There are also many mechanisms that allow prey to avoid, deter or evade predators (reviews in Smith, 1997 and Godin, 1997), thereby violating the assumption of equal vulnerability or accessibility.

Predator avoidance can be achieved by habitat selection; crypsis (body shape and colour resembling the background or mimicking another object like a plant); behavioural avoidance of detection such as "freezing" behaviour or immobility, diel timing of movements, predator recognition (which is related to genetic differences and learning), predator labelling and predator inspection. Predator deterrence mechanisms can be subdivided into morphological deterrents such as body armour, size and arrangement of spines, production of strong electrical discharges; behavioural deterrents like aposematic (=warning) signals in poisonous fish, mimicry of a predator or a poisonous species, pursuit deterrence and pursuit invitation displays, alarm signalling, distress signals, mobbing of predators, shoaling and schooling (but see Connell (2000) for possible exceptions). Evading predators can be achieved by defences mitigating predator capture of prey such as fleeing, hid-

ing, deflecting the attack to certain parts of the prey's body (for instance by displaying eyespots (*ocelli*) on the tail) and shoaling, which has numerous advantages like dilution of risk, predator confusion, possibility of synchronised shoal evasive manoeuvres, transmission of information among shoal members (reviews in Pitcher and Parrish, 1993; Godin, 1997; Fréon and Misund, 1999).

In order to relax the assumption of permanent free access to prey by predators, Walters and Juanes (1993) proposed the concept of a "foraging arena", which assumes that predation takes place largely in spatial patches. The foraging arena concept is now implemented in the ECOSIM II modelling software (Walters et al., 1997), which attempts to model vulnerability distributions by treating the prey as being in one of two behavioural states: "invulnerable" and "vulnerable". Exchange between these states could represent both behavioural and physical processes. The model ignores predator handling time/satiation, following the observation that predators with full stomachs are not a common field observation. This approach represents a great improvement on previous approaches, although the assumption of absence of satiation is probably not equally applicable for different species and habitats.

### **Size-based diets**

In some instances, diets are based on size constraints and are proportional to potential prey, as is assumed for the OSMOSE model (Shin and Cury, 2001). The assumption, made in most size-structured models, that predation by piscivores is size-dependent with an increase in prey size range with the size of the forager, could be impaired if handling efficiency for smaller items decreases in large fish. Available evidence on this topic, although limited (Persson and Greenberg, 1990; Juanes, 1994), does not support such a decrease in efficiency. More worrying can be the concern that prey size at maximum profitability is expected to increase as fish grow from larvae to adult and, as a result, large fish are expected to prefer large prey (Galis, 1990). Such size preferences can be specified in most size-structured models.

### **Optimal diets**

If diets are assumed to be optimal, they are necessarily based on the most profitable prey type, thereby maximising the net energy gained per unit time. The basic prey model (BPM) of diet choice (Stephens and Krebs, 1986) assumes that foragers encounter prey types sequentially. Two major sources that violate assumptions of the BPM have been identified by Hughes (1997): hunger state and learning. Hungrier individuals are less selective than partly satiated ones (Ivlev, 1961; Kislalioglu and Gibson, 1976) and this may reflect the priority given to the restoration of a positive energy budget as quickly as possible, even at the cost of reduced foraging efficiency. An alternative explanation is that packing constraints become more critical as the stomach of the predator fills (Hart and Gill, 1992). Furthermore, profitability in BPM and related models is usually estimated without taking into account digestion time, because many foragers continue to feed while digestion is in progress. Nonetheless, because digestibility varies according to prey type, profitability calculated by taking into account physiological processes gives

opposite ranking of prey compared to ranking based only on behaviour (Kaiser et al., 1992).

### **Competition among predators**

As far as we know, none of the current tropho-dynamic models takes into account the effect of competition among predators on diet selection. They also currently ignore the influence of predators on the foraging behaviour of their prey. Competition among predators might not only affect the foraging rate on a given species, as in the functional response model of Hassel and Varley (1969), but also diet selection according to two processes: acceleration of the depletion of prey and alteration of foragers' behaviour. The acceleration of depletion will obviously reduce the encounter rates and thereby discourage selective feeding. Depletion could be anticipated by predators, having noticed the presence of competitors. As a result, predators could adopt an opportunistic strategy of 'first-come-first-served', resulting in a broadening of their diets independently of encounter rates with prey (Dill and Frazer, 1984; James and Poulin, 1998). The alteration of foragers' behaviour can result from contest competition and could cause differential changes in foraging behaviour according to their competitive rank or dominance (Milinski, 1982).

### **Patterns that result from trophic interactions**

The mechanisms controlling foraging and predation at the individual level can be complex and variable. As a result, it is easy to criticize any trophic model, because all aspects of fish behaviour cannot be taken into account. Fish behaviour is a result of interplays among adaptive evolutionary processes between predators and prey in the long-term, habitat selection and ontogenic changes in the medium-term, and flexibility in behaviour using learning and memory in the short-term. Even highly complex and sophisticated trophic models that make use of several thousand parameters (e.g. Fulton, 2001) represent gross oversimplifications of reality, because they are based on many hypotheses and assumptions, not all of which can be tested or analysed by sensitivity analyses.

More difficult than criticising is finding a constructive approach that can identify key processes that control trophic flows at the level of populations. Key parameters at the level of individuals or small groups and at high time- and space- resolutions do not always result in key parameters at the level of populations and at low spatio-temporal resolutions, because averaging effects can smooth most of the variability. According to Persson et al. (1997) "size-structured competitive and predator-prey interactions, in combination with resource-dependent individual growth, have the potential to enhance the diversity of behaviours, both with respect to individual and population processes".

In complex system modelling exercises, one has to distinguish between processes that appear as output or emerging properties of the model, and those that are incorporated as input. Typically, factors that control migration and habitat selection at large scales would be treated better as forcing factors in spatially-resolved trophodynamic models, in order to reflect the frequent mismatch in space and time between predator and prey. In contrast, factors that control micro-habitat selection would be considered best as output variables from rules or equations describing predator-prey interactions.

From theoretical considerations, Fryxell and Lundberg (1994) analysed the effect of adaptive diet selection by predators on population stability, showing that this selection enhances the stability properties of a predator-prey system only under a small range of parameter values. Otherwise, adaptive diet choice was found not to be an important stabilizing factor. In contrast, Gleeson and Wilson (1986) showed theoretically that a predator foraging on two competing prey species according to the optimal diet model (Stephens and Krebs, 1986) could prevent the weaker competitor from becoming extinct if the dominant competitor was the more profitable prey in terms of energy maximisation. However, this result does not differ substantially from predictions of models based on frequency-dependent prey selection.

Pioneer ecological studies considered that diet selection played an essential role in community stability. MacArthur (1955) argued that population densities should be more stable when they pertain to complex trophic webs, i.e. those consisting of many species and/or many interactions. Making an analogy with the diversity index of Shannon and Weaver, he quantified the stability of trophic webs by the amount of information circulating along their different trophic pathways. He found that species assemblages are stable in two cases (here, the notion of stability refers to resistance of a system to perturbation): either when the assemblage consists of a large number of species for which the diets are not diversified, or when the assemblage consists of few species which are largely polyphagous. Thus, according to MacArthur (1955), when the trophic energy can flow through many different pathways, the consequences of the disappearance of an interaction or of a species component should be less detrimental for the community than when there are few pathways. In marine ecosystems, diet selection depends largely on the appropriate size ratio between a predator and its prey (Scharf et al., 2000). This leads to complex trophic webs with most predator species having multiple prey species and most prey species having multiple predator species (Cury et al., 2003). Some modelling studies suggest that size-based diet selection can explain the relative stability (as opposed to temporal variability) of the biomass and size spectrum of fish communities compared to the dynamics of individual species (Shin and Cury, 2001; 2004).

One of the difficulties in modelling predator-prey relationships lies in the fact that most fishes are simultaneously predators and prey (Werner and Gilliam, 1984; Connell, 2002), whereas most models focus on the effects of habitat selection or other parameters in just one species. These models do not always reflect the individual's trade-off between their foraging activities and their avoidance of predation. Predators have been considered only as a source of risk to which prey respond (fixed risk assumption of constant attack rates over time or patch-specific risks of predation), whereas in nature predators respond to prey behaviour, especially by moving in search of patchy prey areas or changing their timing. Reviewing the few existing models that incorporate both prey and predator mobility in a predator-prey model based on game theory, Lima (2002) showed that those models can reveal new and unexpected classes of behavioural phenomena that occur at large spatial scales. Under some conditions, predators might appear to ignore prey distributions and distribute themselves according to the distribution of the resources of the prey. Such complex and sometimes counter-intuitive interactions in population dynamics, with "negative switching", were previously described by

Abrams (1992) and Abrams and Matsuda (1993) who incorporated in their models equations for the dynamics of the resources and flexible behaviour in more than one species.

The stability of predator-prey structure in individual-based models incorporating spatial configurations is determined by the relative mobility of predators and prey, and prey mobility in particular has strong effects on stability (McCauley et al., 1993). Other factors of stability in models are provided by aggregative behaviour in predators, high variance in prey abundance and some degree of segregation between prey species when alternative prey species are incorporated (Holt, 1984; Comins and Hassell, 1987). The influence of refuge on model stability is more variable, with some kinds of refuge providing stabilisation whereas others are destabilising (McNair, 1986).

### **Effects of fishing in trophic models**

#### *Multi-species virtual population analysis (multi-species cohort analysis)*

Single-species virtual population analysis (VPA) is currently the method that is most often used in fish stock assessments when historical data of catch by age are available (Hilborn and Walters, 1992). It allows the estimation, for a given stock, of matrices of fish numbers and fishing mortality rates by age for each past year from matrices of natural mortality rates and past catch by age and time.

One of the hypotheses on which VPA is based is that natural mortality is known and generally constant over year and age. However, natural mortality varies with fish age; in particular, young fish are more subject to predation than older and larger ones (Stokes, 1992). The basis for extending cohort analysis to a multispecies case is to better estimate natural mortality by taking into account fish diets. MSVPA was first established and applied by Andersen and Ursin (1977), Pope (1979) and Helgason and Gislason (1979) in the North Sea ecosystem. It consists of dividing the natural mortality rate of a cohort into two components: the mortality rate due to predation by other species included in the model and the residual mortality rate due to other natural causes. To estimate the predation mortality rate, the food of each age group is partitioned among the different potential prey, with the available food for a predator only a fraction of the potential food biomass. A coefficient is introduced, which lies between 0 and 1, and represents the suitability of a prey class as food for a predator class. Suitability is determined by prey size, the overlap of the predator and prey in time and space, and the probability of encounter linked to the respective behaviour of the predator and its potential prey. The coefficients represent a substantial synthesis of biological knowledge concerning the different stages of species' life cycles, their spatial distributions, their behaviour, and their feeding habits (Ursin, 1982).

Since its formation in 1984, the "Multi-species Assessment Working Group" of ICES (International Council for the Exploration of the Sea) has been charged with evaluating, each year, North Sea fish stocks using MSVPA, thereby complementing traditional analyses using VPA (Pope, 1989). MSVPA is also applied in the Baltic Sea (Sparholt, 1991). Their analyses have shown that predation mortalities are high (Pope, 1989), and taking them into account substantially modifies the biological reference points that are defined using single-species analyses (Gislason, 1999).

Despite its usefulness in stock assessment, there are some limitations to MSVPA. Mortality rates are assumed to be constant, but projections of the models simulate management measures that could affect the biomass of predators and, consequently, the predation mortality of their prey. A limitation in the model structure is that the choices of species included in the analyses are essentially determined by data constraints. The species that are studied are those that are exploited, i.e. those for which catch data are available, but other species could affect the dynamics of the exploited species. In addition, estimation of the suitability coefficients requires comprehensive ecological knowledge. Since 1981, this has necessitated large annual sampling surveys in the North Sea for stomach content analyses of the main exploited species (Stokes, 1992).

#### *Ecopath and Ecosim models*

Polovina (1984) and Christensen and Pauly (1992; 1995) developed the Ecopath model to estimate trophic fluxes within an ecosystem. Knowing the magnitudes of the fluxes should allow estimates to be made of exploitable biomass and, reciprocally, the fraction of the system production that is consumed by predators and by fishing activities. In this compartmental approach, some species are aggregated into functional groups that are linked by biomass fluxes. The modelled system is assumed to be stationary, which implies that the gains in biomass equal the losses from each species group. Ecopath models of marine ecosystems provide estimates of biomass, catches, production, consumption, diets, and ecotrophic efficiency for each trophic group at equilibrium. In 1998, Ecopath was used in about sixty applications in different marine ecosystems (Pauly et al., 1998). The different studies synthesize an important amount of local knowledge. Comparisons of the models have yielded some interesting results about the state and functioning of marine exploited ecosystems, with the calculation of some useful trophic indicators like fractional trophic levels or mixed trophic impacts.

Ecopath provides a static representation of the trophic structure of an ecosystem, but does not allow one to explore the consequences of management measures or variations in trophic fluxes. Ecosim was developed by Walters et al., (1997), and is the dynamic version of Ecopath. It re-expresses the linear equilibrium equations of Ecopath as differential equations. In their modelling work, Walters et al. (1997) succeeded in establishing links between the parameters estimated by Ecopath and those included in the differential equations of Ecosim. The use of existing data without requiring additional measurements and experiments is one of the advantages of Ecopath and Ecosim models. However, this is also one of the weaknesses of Ecosim, which is evident at two different levels. First, Ecosim is not applicable over a large range of biomass values because the parameters are estimated from the Ecopath model, which is at equilibrium. Second, the link with Ecopath constrains the choice of functions for growth of the primary producers, and functional responses of the predators. These functions affect the dynamics of predator-prey models, as was shown in a previous section.

#### *Size-structured models*

With the use of partial differential equations, some authors modelled the biomass flux through ecosystems, from the smallest organisms to the largest (e.g. Silvert

and Platt, 1978). These equations generally do not consider the actual species, but only the dynamics of the biomass per size group (length or weight).

Generally, these models were not used when investigating the effects of fishing on fish communities. Recently, Benoît and Rochet (2004) proposed an improved time- and size-dependent continuous model of biomass flux, and they investigated the effects of fishing on size spectra. They found that fishing should affect the curvature and the regularity of the size spectrum. Using a MSVPA-type model that was size-structured, Gislason and Rice (1998) found a linear relationship between the slope of the size spectrum and fishing mortality. This is consistent with empirical results which suggest that the slope and the intercept of size spectra vary quasi-linearly with fishing mortality when the size spectrum is obtained by plotting the log(fish number) against log(fish length) (e.g. Rice and Gislason, 1996; Bianchi et al., 2000). Consequently, linear models can be used to understand and predict the effects of fishing at the level of communities. An individual-based model (Shin and Cury, 2004) that assumed that predation is an opportunistic and size-based process, also resulted in a linear relationship between the slopes of size spectra and fishing mortality. However, when small fish were included in the model, the simulated marine size spectrum appeared to be curved towards the small sizes of fish, suggesting that the smallest fish undergo the greatest predation mortality. The attributes of curved size spectra should provide information about the level of overexploitation in a given ecosystem.

### 3. System-Level Perspectives: from patterns to processes

#### 3.1 *Ecosystems, food webs and food chains*

Ecosystems are viewed in many ways ranging from complex and changing adaptive systems (Allen, 1988; Mullon et al., 2002) to simplified ecological components or assemblages that interact through known processes (such as predation) acting on the structure of food webs or food chains. There is also a long and continuing controversy in community ecology among those who focus on idiosyncratic aspects of natural systems and their uniqueness, and those who perceive the general principles that structure natural assemblages (Hairston and Hairston, 1997). This controversy is particularly intense when trophic levels are used to represent food web dynamics and food chains.

Food web theory remains controversial largely because of the intricate complexity resulting from numerous interactions and the resulting lack of prediction about population dynamics in natural systems (Figure 14.4). Polis and Strong (1996) believe that communities are too complex to show general patterns and that no natural groupings of organisms into trophic levels are possible; trophic levels are non-operational concepts with no useful correspondence to reality (Polis and Winemiller, 1996).

The quantitative study of food webs has only recently come into its own, stimulated by theoretical work on factors that might constrain patterns of trophic connection within food webs (Morin and Lawler, 1995). According to Hairston and Hairston (1993), food webs provide the theoretical possibility of obtaining detailed information about the flow of energy through a community and can be used to partition the influences of species that feed at more than one trophic level. However, Hairston and Hairston (1993) found some serious difficulties in the use of

food webs. Among these is the fact that quantitative assessments of the strength of most of the links is rarely practical and that competition is of necessity either ignored or assumed to exist.

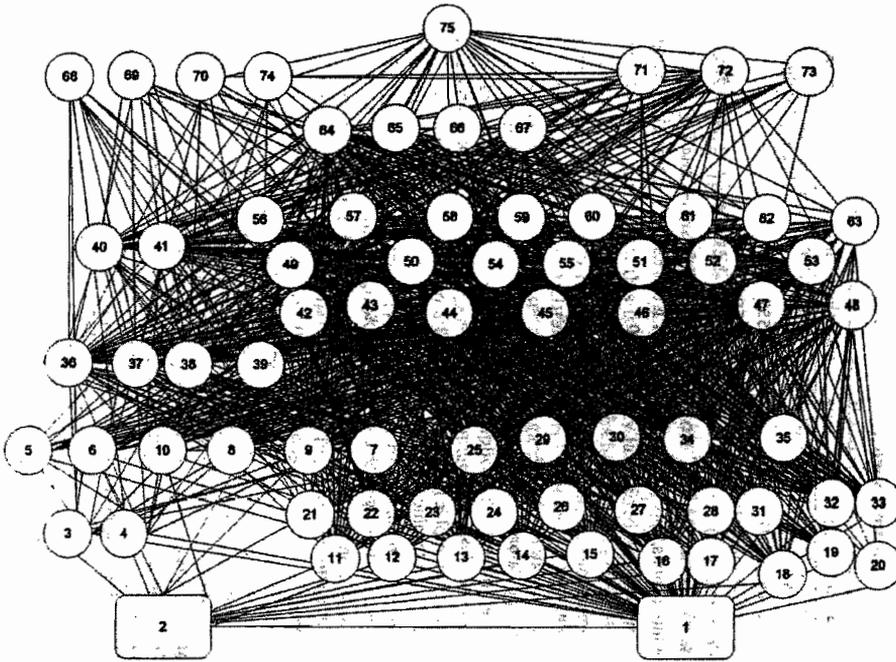


Figure 14.4 Species and links for a northwest Atlantic food web, assuming that interactions among 75 components have similar strength in time and space (from Link, 1999).

Despite the complexity of natural ecosystems, which is real, observable patterns emerge at different levels of organisation and these can be helpful for ecosystem-based management (ICES, 2000). Polis (1999) insisted that food web dynamics appear to be much more important in water than on land, because aquatic systems appear less reticulate and less diverse than terrestrial systems (Strong, 1992). In their famous paper, which has inspired many ecologists, Hairston et al. (1960) interpreted the greenness of the world using a simple holistic argument combined with a reductionist approach. They predicted cascading trophic effects across the food chain and that whether or not organisms are predator- or resource-limited depends on their position in the food chain.

In our quest to understand and generalise ecosystem functioning we need to identify causal factors, and when and where each factor assumes importance. For this purpose we critically review different theories and ways of extracting and analysing patterns in aquatic ecosystems. In the following paragraphs we present different types of patterns, and the associated processes that control them.

### 3.2 Bottom-up control or the control by primary production

#### Ecosystem responses to drastic environmental changes

Using an analogy with agriculture where crop yields can be predicted from the control of the input, Hensen (1887, in Smetacek, 1999) 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 concept that ecosystems were 'bottom-up' controlled, i.e. the regulation of food-web components is made by either primary producers or the input of limited nutrients (Pace et al., 1999) (Figure 14.5).

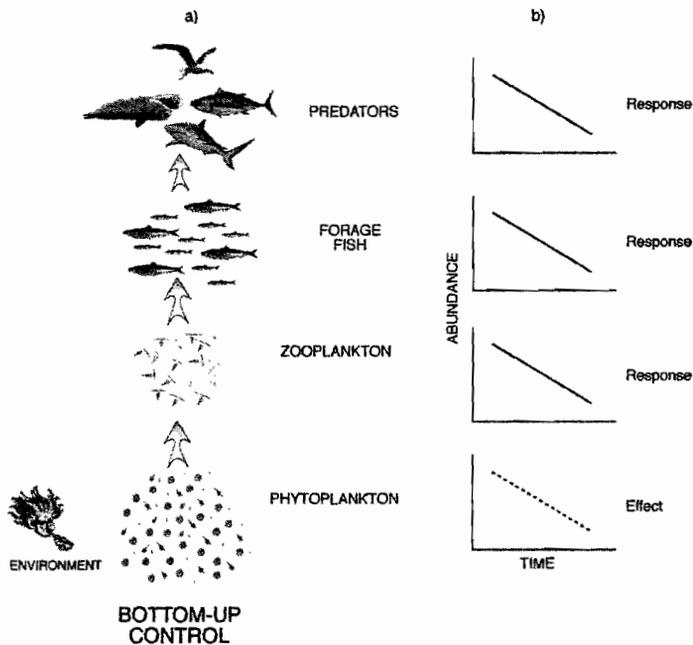


Figure 14.5 a) Bottom-up control within a simplified 4-level food chain in a marine ecosystem; b) The physical environment (sensu Cushing, 1996) being less favourable controls the decrease in abundance of the phytoplankton, which in turn has a negative impact on the abundance of the zooplankton. The decline in zooplankton abundance 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 the dashed line and the responses are the solid lines) (from Cury et al. 2003).

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 global (terrestrial and aquatic) plant biomass (Smetacek, 1999). Consequently, nutrient limitation is generally thought to be much more severe in water than on land (Polis, 1999). Large parts of the ocean are still considered to be 'blue deserts', despite the fact that this view is being challenged by modern primary production estimates. For

example in the previously-designated "oligotrophic" subtropical Pacific, primary production estimates are 170–220 gC m<sup>-2</sup> y<sup>-1</sup>, and are potentially as large as 350 gC m<sup>-2</sup> y<sup>-1</sup> if one includes dissolved organic carbon production (Karl et al., 1998). In the most productive areas, such as the upwelling areas of the four eastern boundary current regions, primary production averages 672g C.m<sup>-2</sup>.y<sup>-1</sup> (Carr, 2002).

Despite certain limitations in productivity for several systems and despite large interannual environmental variability, it appears that the effects of changes in primary productivity rarely cascade upwards to affect biomass of marine pelagic fish consumers (Micheli, 1999). This weak link between primary producers and herbivores can partly explain why parallel long-term trends are only rarely observed across several marine trophic levels, as would be expected under a theoretical bottom-up control scenario (Figure 14.5).

Records of sardine- and anchovy- scale-deposition from anaerobic sediments show that large-amplitude population fluctuations occurred even in the absence of any fishery (Baumgartner et al., 1992), and they are most probably related to environmental changes. However, this has not been formally demonstrated and other hypotheses, involving competition, can account for such patterns (Ferrière and Cazelles, 1999). The effect of the environment on population dynamics has been emphasized in recruitment studies. Food availability (Cushing, 1996) and physical processes (Bakun, 1996) exert a significant pressure on larval fish survival, which determines subsequent fish abundance (Cury and Roy, 1989). In many cases, fish recruitment in the marine environment is viewed as being controlled by bottom-up forces (e.g. Menge, 2000), implying that the availability to the fish of primary production often determines recruitment (Cushing, 1996). Recruitment of fishes that feed on different trophic levels at the adult stage is thus controlled by the environment experienced by their larvae, which usually feed on similar trophic levels at the bottom of the food chain (i.e. fish larvae mostly feed on small zooplankton).

The structure and function of marine ecosystems can respond drastically to interannual changes and interdecadal climatic variations. This has been documented for the California Current, the Gulf of Alaska (McGowan et al., 1998), the North Atlantic (Aebischer et al., 1990) and off Chile (Hayward, 1997). Parallel long-term trends across four marine trophic levels, ranging from phytoplankton, zooplankton and herring to marine birds, have been related to environmental changes in the North Sea (Aebischer et al., 1990). Hollowed et al. (2001) analysed the effect of ENSO (El Niño Southern Oscillation) and PDO (Pacific Decadal Oscillation) on northeast Pacific marine fish production and found that these climatic events, occurring on two principal time scales, play an important role in governing year-class strength of several fish stocks. The North Pacific climatic regime shifts in the mid 1970s and late 1980s (Hare and Mantua, 2000) affected the dynamics of the Korean marine ecosystem (Zhang et al., 2000). Primary production in Korean waters increased after 1988, and was followed by a significant increase in zooplankton biomass after 1991. The 1976 regime shift off Korea manifested itself as reduced biomass and production of saury, but biomass and production of sardine and filefish increased. After 1988, Korean sardine collapsed and were replaced by mackerel. Trends in abundance of zooplankton and salmon in the North Pacific also correspond to changes in the intensity of the Aleutian Low Pressure System (Polovina et al., 1994). It has been suggested that water column stability, determined by strength of the Aleutian Low Pressure System,

influences phytoplankton production, which in turn affects species at higher trophic levels.

Interannual 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). In the mid-latitudes of the western Pacific, correlations between SOI (Southern Oscillation index), SST, chlorophyll-a, zooplankton and catch of pelagic fish suggest a bottom-up effect that is more pronounced during certain months of the year, and that modifies the dynamics of the ecosystem in the South Sea of Korea (Kim and Kang, 2000). 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). Interdecadal 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; Francis et al., 1998). There has been a general 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 these ecosystems (McGowan et al., 1998). However, the biological response to the interdecadal regime shift in the Gulf of Alaska is thought to have been in the opposite direction to that of the California Current.

There are large-scale biological responses in the ocean to low-frequency climatic variations. However, the mechanisms by which the 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) according to the structure of the ecosystem. For example, in the northern Benguela ecosystem, sardines have been found to respond more quickly to environmental change than anchovy. According to McFarlane et al. (2000), one method of measuring climate change and regime shift is to observe the dynamics of species that potentially could be affected. Obvious environmentally-induced ecological changes are expected in ecosystems, although findings in 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.

Bottom-up control is the conventional trophic flow control that seems to dominate most ecosystems (Cury et al., 2003). Environmental changes are pervasive, but in most cases difficult to detect at different trophic levels. Literature documenting the relationship between abundance of pelagic fish and environmental variability is plentiful. However the role of the environment on food abundance versus the direct effect of the environment on early life stages are entangled concepts. Several strong patterns, linked to the environment, appear in the form of regime shifts and synchrony between remote fish populations.

### **Regime shifts and synchronised large scale fluctuations**

Daan (1980) was the first to review the concept of replacement of a depleted stock by other species. He used a very tight definition of replacement and concluded that the only true replacement of species occurred in the North Sea. Many analyses of alternating trends in abundance of fish stocks have since been undertaken, with

species replacement being more loosely defined, and many hypotheses being formulated to explain these "regime shifts". An early indicator of a change in species dominance is an increase in the abundance of the sub-dominant species; a decrease in the dominant species is often only observed at a later stage (Lluch-Belda et al., 1992). Catch statistics (e.g. Kawasaki, 1991), fish scale deposits in sediments (e.g. Baumgartner et al., 1992), biomass research surveys (e.g. Hampton, 1992) and records of seabird guano harvests (Crawford and Jahncke, 1999) have revealed changes in the abundance of anchovy or sardine stocks in many regions of the world. Initially, there were heated debates as to whether collapses of pelagic species were caused by overfishing, thereby allowing competing species to dominate (Francis and Hare, 1994). However, fishing was soon shown to be secondary to other causes when evidence of these fluctuations was found in scale deposits for periods prior to commercial fishing off California (Soutar and Isaacs, 1974; Baumgartner et al., 1992), Peru and Chile and off southern Africa (Shackleton, 1987). Coherent patterns of abundance in the northeastern Pacific Ocean over the past 2,200 years were observed for salmon, sardine and anchovy (Finney et al., 2002). These long-term changes across large regions demonstrate the strong role of large-scale climate forcing on lower trophic levels, which subsequently affects fish and ecosystem changes.

Off western South Africa, guano records suggest that anchovy *Engraulis encrasicolus* was the dominant pelagic fish in the 1920s (Crawford and Jahncke 1999). Horse mackerel *Trachurus trachurus capensis* was abundant in the 1940s and early 1950s, sardine *sardinops sagax* in the late 1950s and early 1960s, chub mackerel *Scomber japonicus* in the late 1960s, *E. encrasicolus* in the 1970s and 1980s and *S. sagax* in the mid 1990s (Crawford, 1999). The sequence of pelagic species succession differed off Namibia; *S. sagax* was dominant in the 1960s, *Trachurus capensis*, pelagic goby *Sufflogobius bibarbatus* and to a lesser extent, also *E. encrasicolus*, were abundant in the late 1970s and early 1980s, whereas *S. japonicus* was dominant in the late 1970s and early 1980s (Crawford et al., 1985; Crawford et al., 1987).

Despite plentiful data showing changes in abundance phases of sardine and anchovy populations in the productive regions of the world's oceans, the mechanisms responsible for initiating, sustaining and terminating sudden increases in population sizes on a decadal time-scale still remain much of a mystery (Lluch-Belda et al., 1992). It is likely that many of the factors accounting for variability in fish stocks play important roles in effecting regime shifts. The mechanisms involved must act on large spatial scales because there is coherence in stock fluctuations in these regions (Crawford et al., 1991; Schwartzlose et al., 1999). Matsuda et al. (1992) modelled environmental effects on pelagic species replacements, listing five possible mechanisms explaining pelagic species dominance in ecosystems: environmental change impacting different species directly, density-dependence in changes of the intrinsic reproductive rate, phase polymorphism of species, competition between species and fluctuations in a one-predator-two-prey-species situation.

There are five regions in the world where anchovy (*Engraulis* spp.) and sardine (*Sardinops sagax*) stocks co-exist and are intensively fished. These are the Japanese system (the western boundary of the North Pacific), the California Current system (the eastern boundary of the North Pacific), the Humboldt Current system (the eastern boundary of the South Pacific), the Canary Current system (the east-

ern boundary of the North Atlantic) and the Benguela system (the eastern boundary of the South Atlantic). It is generally accepted that sardines in all these regions except the Canary system are the same species, namely *S. sagax* (Parrish et al., 1981). The sardinellas *Sardinella aurita* and *S. eba* occur in the Canary Current system. Anchovies belong to different species of the genus *Engraulis*. In addition to co-occurring in these five regions, both anchovy and sardine (*S. sagax*) are also found off Australia. However, harvesting of these species is limited in this region, therefore data are scarce and stocks in this region have been largely omitted from comparative studies in the literature. The anchovy *E. encrasicolus* and sardine *Sardina pilchardus* co-occur in the Mediterranean Sea. However, catch per unit effort data of the two species in the fishery off the northeast coast of Spain have been less variable than those from oceanic regions where the main pelagic fisheries of the Mediterranean operate (Morales-Nin and Pertierra, 1990). The authors suggest that the environment fluctuates less in this region than in productive up-welling regions, such as off California.

#### *Linkages between regions*

Shifts in dominance of sardine and anchovy have been discussed in depth by Skud (1982) and Lluch-Belda et al. (1992) (see also Bakun, Chapter 24). Fluctuations in the size of the populations of sardine in the Japan, California and Humboldt Current regions are well matched and are influenced by global scale environmental variation (Kawasaki et al. 1991) (Figure 14.6). In contrast, the species groups of the Benguela and Canary Current systems are out of phase with these three Pacific regions (Schwartzlose et al., 1999). Recently, Alheit and Hagen (1997) showed that alternating periods dominated by herring *Clupea harengus* and sardine *Sardina pilchardus* in the eastern Skagerrak, English Channel and Bay of Biscay are governed by the same climate variations.

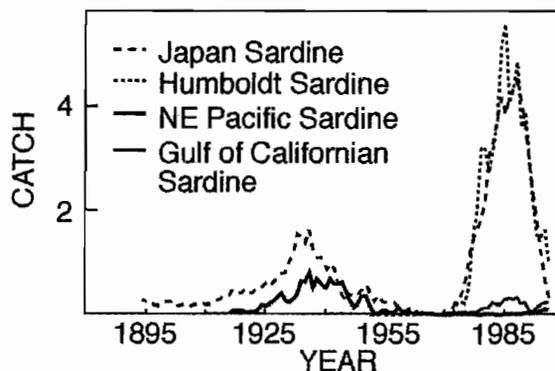


Figure 14.6 Synchronized long-term catches (t) of sardine in the North-Western Pacific by Japan, in the Humboldt off Peru and Chile combined, and in the Gulf of California from 1895–1996. (Data from Schwartzlose et al., 1999).

In the Pacific Ocean (Japan, California and Humboldt systems), fluctuations of sardine populations in the three regions are more closely linked than fluctuations

of anchovy or chub mackerel stocks (Crawford et al., 1991). It is possible that the climate influences biological aspects of sardine, which differ from those of the other two species (Crawford et al., 1991). Sardine was found to be more abundant during periods of increased global air and sea temperatures, and anchovy stocks declined during such periods (Lluch-Belda et al., 1992). However, manifestations of other events associated with changes in temperatures, rather than temperature changes themselves, may cause fluctuations in temperature and stocks to coincide (Lluch-Belda et al., 1992). Matsuda et al. (1992) put forward a cyclic model of dominance of pelagic fish species off Japan, and MacCall (1996) showed a similar sequence of pelagic fish dominance off California; a peak in abundance of planktivorous *Sardinops sagax* is followed by a peak in *Engraulis* sp., then the more predatory *Scomber japonicus* dominates and the cycle repeats itself.

There is a significant negative relationship between temperature in the northern Benguela and the Canary Current systems (Crawford et al., 1991). The abundance of sardine in these two regions is negatively related. The two systems seem to be linked largely through the influence of Benguela Niños, which result from the southward intrusion of tropical water into the northern Benguela system off Namibia, associated with cooling in the equatorial Atlantic (Shannon and Pillar, 1986). Anchovy population sizes in the northern Benguela system are related to those in the Canary system one year later, and anchovy population sizes in the southern Benguela are related to those in the Mediterranean the same year (Crawford et al., 1991).

Crawford et al. (1991) investigated the trans-oceanic linkages between the Atlantic and the Pacific through global climate. They postulated that three factors influence trends in abundance of fish species in the two oceans, namely solar radiation, sea surface temperature and ecosystem changes. Solar radiation influences sea surface temperature in the North Pacific in the same year, but influences sea surface temperature in the North Atlantic and air temperature in the Northern Hemisphere two years later. This is reflected in a two-year lag between sardine catches off Japan and England. Sardine in the California, Humboldt, Canary and Benguela current regions have been found to extend into cool waters during warm periods, and also sometimes into warm waters when cooling occurs. Japanese sardine, although always the dominant species, tend to become more abundant as the Kuroshio Current cools. Hence it is possible that warming of cool areas or vice versa can allow sardine to extend its range into new areas (Crawford et al., 1991). Climatic impacts on epipelagic prey species are likely to influence predators and competitors too.

#### *Changes in spatial distribution*

Associated with changes in the relative abundance of anchovy and sardine is spatial variation of the two species. Both species expand and contract the area across which they occur as stocks increase or decrease in size; sardine spawning distributions usually change in the alongshore direction whereas the spawning ranges of anchovy seem to expand or contract about a geographic centre. MacCall's (1990) "basin hypothesis" states that spawners are expected to contract to the most favourable habitats at low levels of abundance, when effects of density dependence are low. Modelling of anchovy and sardine in the southern Benguela region showed that anchovy and sardine spawned in areas less favourable to survival

when they were at low abundances (Shannon, 1998), suggesting that other environmental factors may have restricted suitable areas available for spawning.

### Alternating steady states and pelagic fish assemblages

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 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 over past decades (Figure 14.7). The mechanisms that are generally invoked involve the environmental effects that will favour one or the other species. Analyzing changes in abundance of pelagic species in response to environmental changes, Skud (1982) concluded that dominant species respond to environmental factors, and subordinate species respond to the abundance of the dominant ones. Thus, 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). Recently the competition between species was shown to be magnified by schooling behaviour within mixed-species schools (Bakun and Cury, 1999). Thus the 'school trap' hypothesis constitutes a potential mechanism of competition that could drive one species to ever-lower abundance, rationalizing observed patterns of alternation. These multi-year patterns of alternation are important for long-term management, as exploitation reduces the biomass of the dominant species, which is usually the target species at the time, and sometimes precipitates its collapse. Within a pelagic community, the removal of the dominant species should favour the subordinate species, provided that the latter is only lightly exploited.

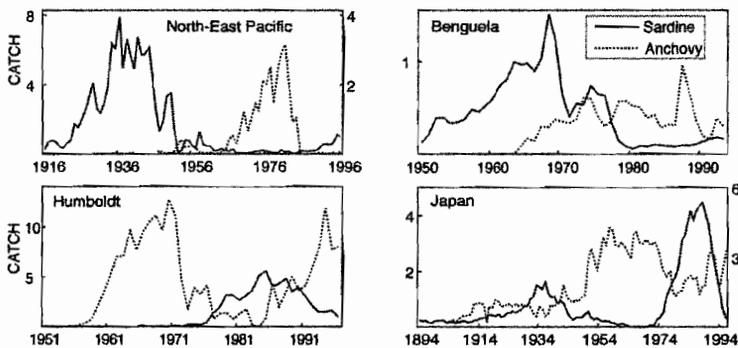


Figure 14.7 Alternation between sardine (solid line) and anchovy (dashed line) as illustrated by the changes of species abundance in catch time series for the north-east Pacific, Japan, the Humboldt and the Benguela currents (Schwartzlose et al., 1999).

3.3 Top-Down control or the control by predation

Trophic interactions between fish species play an important role in ecosystem structure. Predation mortality is believed to be the major source of mortality for marine exploited species (Bax, 1991). By analysing six marine ecosystems (Benguela Current, Georges Bank, Balsfjord, East Bering Sea, North Sea, Barents Sea), Bax (1991) estimated that predation amounted to between two and thirty-five times fishing mortality. This does not imply that effects of fishing are negligible, but rather that fishing has the potential to affect the whole ecosystem because species are tightly linked through trophic interactions. Therefore, it is thought that regulation of ecosystem components at low trophic levels by species at higher trophic levels (termed top-down control) may be critical to marine ecosystem functioning (Figure 14.8).

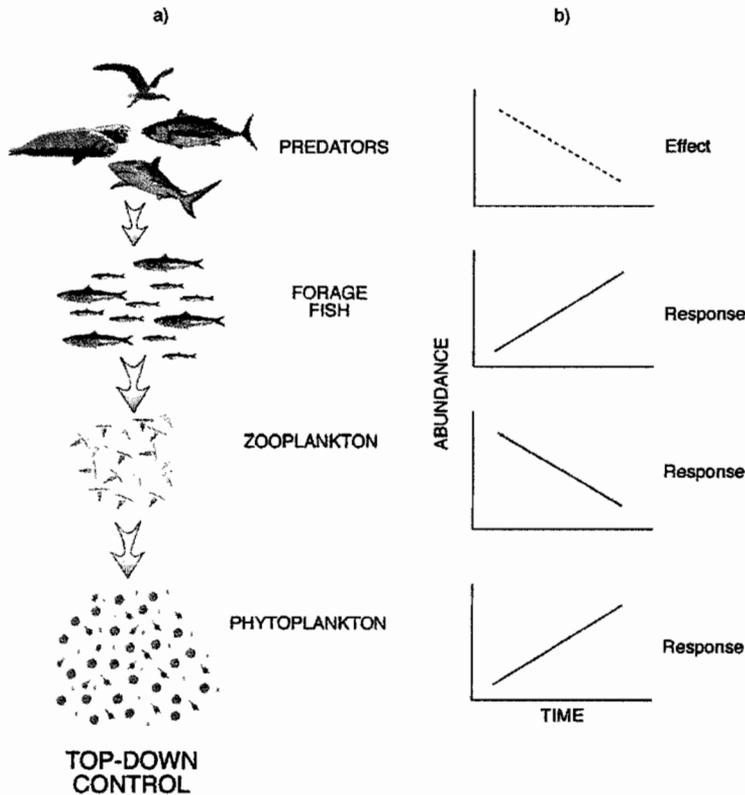


Figure 14.8 a) Top-down control within a simplified 4-level food chain in a marine ecosystem b) The decreasing size of the top predator populations leads to reduced predation on the prey, which in turn leads to an increase in abundance of the prey fish. Increased predation of fish prey on zooplankton leads to a decrease in the zooplankton population size. The smaller zooplankton abundance reduces the grazing pressure on the phytoplankton, which consequently becomes more abundant (the control factor is in dashed line and the responses are in solid lines) (from Cury et al. 2003).

### Size based predation process: an empirical approach

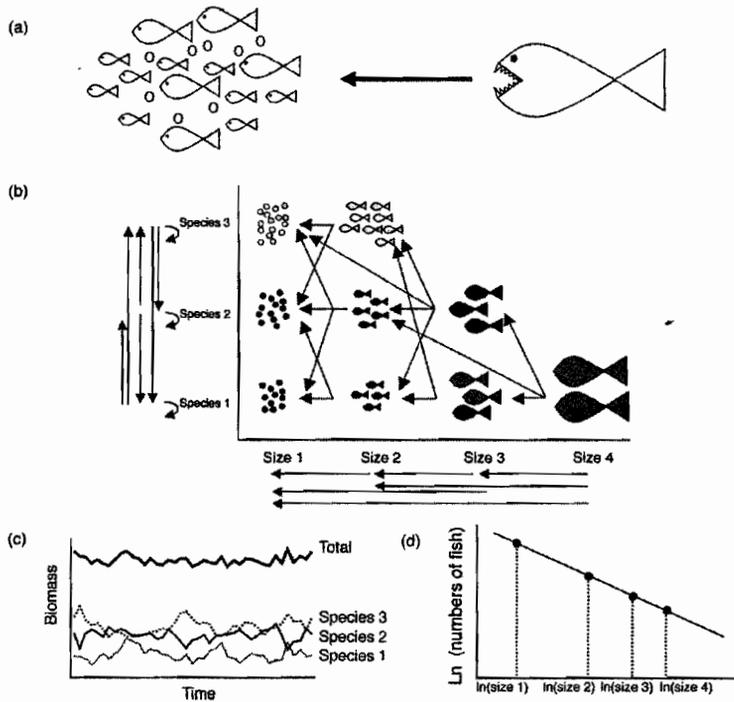


Figure 14.9 (a) Bigger fish eat smaller fish: fish prefer prey smaller than about 1/4 to 1/3 their own size as predators are constrained by the size of their jaw. (b) Who is eating whom? This simple opportunistic feeding behaviour generates complex trophic webs, wherein fish have multiple predators, 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 fish 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 (from Cury et al. 2003).

Ursin (1973) wrote that “[fish] stomach contents are a simple function of local prey availability and suitability, this latter often simply being a function of size”. This is the case in marine food webs, where feeding may be considered opportunistic and less dependent on prey taxonomy than on prey size. In aquatic species, the ability of a predator to catch its prey is mainly constrained by body size of the predator compared to that of the prey (Lundvall et al., 1999). Because water is eight hundred times denser than air, a streamlined morphology enables fish to move efficiently through this medium. Appendages for handling and capturing large prey are uncommon among fish. Therefore, size-based predation dominates

in aquatic communities (Sheldon et al., 1977). Unlike a lion in the terrestrial world, a predatory fish can only prey on items that are small enough to be swallowed whole. Therefore, because jaw size is related to fish size, it is generally accepted that the size ratio between predator and prey determines whether predation occurs (Figure 14.9a).

Strong patterns emerge from size-based predation (Fig 14.9b). Fish tend to prey on a diversity of species and have a diversity of predators. As larvae, fish feed at the base of the foodweb, but as adults, they have higher trophic levels, feeding on organisms at one or several trophic levels below their own (Rice, 1995). During ontogeny as a fish grows, it moves from one trophic level to another and the relationship between trophic level and the logarithm of the body length is linear, with a steeper slope for top predator species (Pauly et al., 2001). Teleost eggs and larvae are found at the base of the piscivorous food chain. In addition, teleost eggs are mostly of uniform size, about one millimetre in diameter (Cury and Pauly, 2000). Thus “community predation” (Sissenwine, 1984) may occur because each fish species potentially competes with every other fish species. Gulland (1982) aptly compares predation in aquatic versus terrestrial systems by stating that “fish have no direct terrestrial counterparts—a fox or lion does not start competing with mice.”

Cannibalism often occurs in aquatic systems and may cause large mortalities of pre-recruits. For example, in the Eastern Baltic cod stock (*Gadus morhua*), cannibalism may be the cause of death of between 31% and 44% of individuals in the first 2 years of life (Neuenfeldt and Köster, 2000). In contrast to the terrestrial situation, two aquatic species can be simultaneously a predator or a prey of each other, depending on their size. For example, North Sea cod preys on herring but adult herring are also able to feed on cod larvae (Stokes, 1992). This suggests that, on a species basis, there are two top-down control mechanisms acting in competition with one another, whereas on the basis of size, there is one top-down control mechanism operating (Figure 14.9b).

Dynamics of marine food webs are complex and evolving, because of the large number of potential interactions between species, size groups or age groups, and across different trophic levels. Despite these complex trophic interactions, strong patterns have emerged at the ecosystem level. These patterns were already recognized by May (1974), who stated that “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”. One commonly observed pattern in this respect is the relative stability of total fish biomass in spite of the large variations in biomasses of individual marine species (Figure 14.9c). An example is the North Sea ecosystem during the 1970s, when there were large changes in the species composition of catches (herring and mackerel catches sharply declined whereas gadoid catches increased), yet total catch was maintained at a relatively stable level (May et al., 1979). May et al. (1979) believe that year-class strength has been controlled from the top down, i.e. that herring and mackerel biomasses were reduced by fishing and that, as a result of reduced predation by these species on gadoid larvae, gadoids have become more abundant. It has been shown theoretically that stability is favoured by top-down control operating by means of multiple and weak trophic interactions between species (McCann, 2000; Shin and Cury, 2001). Weak interactors may stabi-

lize ecosystems by dampening oscillations caused by strongly interacting species (Polunin and Pinnegar, 2002). This is explained by size-based predation in the marine ecosystem; fish consume a wide variety of prey, thereby exerting stabilizing forces at the population level (Bax, 1998).

Stability extends beyond the population level to size spectra at the community level. Fish abundance and biomass decrease with fish size; depending on the underlying parameters assumed, the relationships are described by linear or dome-shaped functions (e.g. Bianchi et al., 2000). This suggests that energy transfer through marine ecosystems occurs by means of interactions that are size-based rather than species-dependent. Accordingly, bottom-up control by primary producers can affect the scale of an ecosystem's productivity, but top-down control can be the stabilizing force. By targeting the large size classes of an ecosystem, fishing may be considered analogous to apex predation. Variations in the slopes and intercepts of the size spectra of an ecosystem may reflect this top-down control. For example, Pope and Knights (1982) found that heavier exploitation in the North Sea than in the Faroe Bank ecosystem was reflected in the steeper slope of the observed size spectrum for the North Sea ecosystem.

### Keystone species and trophic cascades

The impact of a species on other species depends on its environment, its abundance and how it interacts with other species in the same ecosystem (Lawton, 1999). Because all interactions are not equally strong, it is not necessary to measure or understand each and every interaction, but rather to determine which interactions are most significant and to focus attention on these. Once this approach was adopted, the important role of certain key species in structuring ecosystems was recognized. Further, it was recognized that representing ecosystems as a network of complex interactions may be misleading (e.g., Figure 14.4).

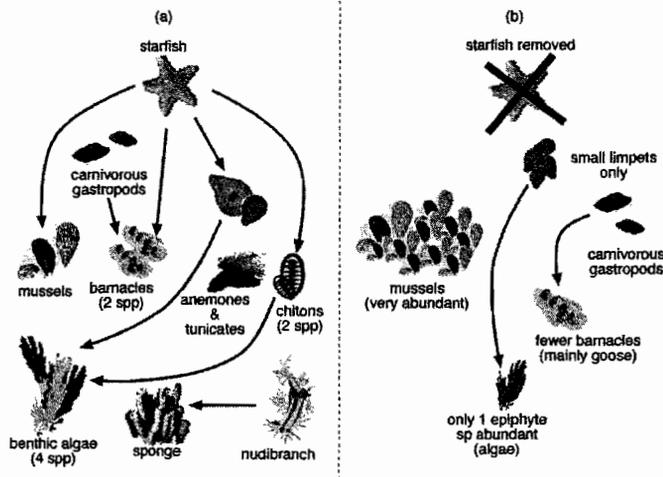


Figure 14.10 Schematic representation of the keystone role of predatory starfish *Pisaster ochraceus* in an intertidal ecosystem in Washington (based on Paine, 1966). (a) *Pisaster* sp. predation maintains a diverse community. (b) removal of *Pisaster ochraceus* allows mussels to dominate, and reduces species diversity.

*Keystone species*

A variety of definitions have been used to describe the term “keystone species”, but the most widely accepted is that a keystone is a species “whose impact on its community or ecosystem is large, and disproportionately large relative to its abundance” (Power et al., 1996). In other words, a keystone species affects community or ecosystem level processes to a larger extent than would be assumed likely if one considered only its relative abundance (Bond, 1993); by definition, keystone species are not abundant species. Keystone species interact strongly with other species through predation and competition and also by ecosystem engineering (physical modification of habitat). Although keystone species are often found high in the food chain, they are not exclusively found at the highest trophic levels (Power et al., 1996). Invasive alien species may be considered to be keystone species as their impact in a newly invaded ecosystem may be disproportionately large relative to their initial biomass. Subsequently, such a species may proliferate and become dominant in the absence of predators and diseases (Power et al., 1996). It has been suggested that in the future, conservation management would benefit most from identification and maintenance of keystone species as opposed to attempts to manage all species considered to be important or vulnerable in a given ecosystem (Power et al., 1996).

Most examples of marine keystone species are from the intertidal zone. Paine (1966) was the first to suggest that some species are keystones by showing that predatory starfish are able to prevent other species from monopolizing a limited resource. When the starfish *Pisaster ochraceus* was present in the intertidal region in Mukkaw Bay, Washington, algae, mussels, barnacles, chitons, limpets, sponges and nudibranchs coexisted (Figure 14.10a). However, removal of the starfish allowed its most important prey species, the mussel *Mytilus californianus*, to become abundant. This in turn reduced species diversity and the ecosystem was effectively converted to a mussel monoculture (Figure 14.10b). Although a species can be a keystone in one place over a given period, it is unlikely that it always remains a keystone species (Mills et al., 1993; Menge et al., 1994, Power et al., 1996, Lawton 1999). For example, Sanford (1999) concluded that the environment can have large effects on keystone interactions; during cool upwelling periods, the interaction between *Pisaster* and *Mytilus* is weakened.

An example of a marine keystone species from beyond the intertidal region is the jellyfish *Aurelia aurita*, which was shown to exert top-down control on zooplankton, thereby determining zooplankton community structure in a shallow cove in Denmark (Oleson, 1995).

Keystone species are rarely positively identified in marine ecosystems. However, in some instances they may operate in conjunction with dominant species, causing major changes in ecosystem structure and functioning to cascade down marine foodwebs.

*Trophic cascades*

Trophic cascades occur when the abundance, biomass or productivity of a population or trophic level is altered across more than one link in a food web, as a result of reciprocal predator-prey effects (Pace et al., 1999) (Figure 14.8). Strong (1992) discussed evidence that trophic cascades were mostly observed in aquatic systems containing few species, representing an exceptional case of food web mechanics,

indicating that structure can only be perceived for a subset of the whole ecosystem. Thus the trophic architecture of highly diversified terrestrial ecosystems is more likely a complex web than a trophic ladder. For several authors these assertions provoke questions about why, despite omnivory and the complex linkages of real food webs, manipulations of top predators in communities sometimes trigger chain-like trophic cascades (Power, 1992; Hairston and Hairston, 1997).

A keystone species is usually involved when a true trophic cascade takes place (Paine, 1980), because removal of a species with strong top-down effects causes major perturbations to propagate through a food web, resulting in inverse patterns of abundance or biomass across trophic links. Trophic cascades in lakes (see Carpenter and Kitchell, 1993 for a review) and intertidal zones (Paine, 1980; Estes and Duggins, 1995) were the first to be documented. Initially, it was thought that trophic cascades involved fairly abnormal food web mechanisms and that they were a manifestation of biological instability (Strong, 1992) restricted to certain kinds of marine ecosystems (Hall, 1999). More recently, occurrences of trophic cascades have been reported from a variety of ecosystems, including the open ocean (Pace et al., 1999).

Ecosystems can be strongly impacted by trophic cascades, being stabilized in alternate states through these types of trophic interactions. Predation can result in cascading effects by limiting grazer abundance, thereby enhancing biomass of producers (Posey et al., 1995). The suite of interactions between sea otters, urchins and kelp in Alaska (Estes and Duggins, 1995) is a good example of how the appearance and properties of an ecosystem can be affected by trophic cascades (Pace et al., 1999). Sea otters are considered to be keystone species in the Alaskan ecosystem and, when abundant, their predation pressure on urchins reduces urchin grazing on kelp, stabilizing the kelp forest system. When sea otter abundance is low, urchins proliferate, heavily grazing the kelp and reducing its productivity. Another example of a trophic cascade has been described in the sub-Arctic North Pacific, where pink salmon (*Oncorhynchus gorbuscha*) feed on macrozooplankton and phytoplankton, thereby controlling the biomass of these plankton groups in summer. Shiimoto et al. (1997) found inverse relationships between biomass of the planktivorous pink salmon and biomass of zooplankton, and between zooplankton and phytoplankton biomass. A third example involves trophic cascades in marine pelagic ecosystems in which changes in the abundance of consumers can have cascading effects down the food chain, sometimes all the way down to phytoplankton (Micheli, 1999). However, weak plant-herbivore interactions make true trophic cascades difficult to detect in these systems; zooplanktivores negatively affect mesozooplankton biomass, but mesozooplankton seldom affects phytoplankton (Micheli, 1999). Polunin and Pinnegar (2002) suggest that omnivory, which is common in marine systems, may mask trophic cascades.

Coastal fisheries and their management appear to be having profound effects on ecosystems by altering trophic cascades (Pace et al., 1999). The reduction in abundance of pinnipeds in western Alaska may be related to overfishing of their prey, as well as to climatic change (Estes et al., 1998). This could have forced killer whales (*Orcinus orca*), which prefer to prey on marine mammals, to consume more sea otters, with severe consequences for urchins and kelp. In addition to the potential direct effects of fishing on fish species, there is also competition between fish-

eries and top predators for valuable prey resources. For example, off South Africa the Cape fur seal preys on many commercially exploited fish species. A suggested solution to reduce this competition with fisheries has been to curb seal population growth by culling. However, there is controversy about the success of such a proposal; seal culling has not been shown likely to cause cascades through the ecosystem, nor to have any beneficial effects on stock sizes of fish species consumed by these seals (Yodzis, 2001). In fact, direct competition between marine mammals and fisheries generally seems to be limited (Trites et al., 1997). Despite this, there may be indirect competition for primary production to sustain both marine mammal stocks and fisheries catches. This may result in what has been termed "food-web competition", particularly as fisheries continue to expand at a fast rate (Trites et al., 1997).

We have seen that there are difficulties in identifying keystone species, particularly because certain species may only be keystones for certain states of an ecosystem or over certain periods. Similarly, we have seen that trophic cascades are transitory and dynamic. Their effects are not necessarily felt all the way to the lower trophic levels of an ecosystem (Pace et al., 1999). Decades of intense fishing may destroy cascades that previously occurred; it is possible that reduction in populations of top predators as a result of fishing may allow prey populations to increase and in that way enhance their effects in the marine community (Steneck, 1998). Managing fisheries such as these solely on the basis of the keystone characteristics of a species and whether trophic cascades occur would be impractical, unless there is strong evidence to support these mechanisms (Hall, 1999). Despite these complications, a top-down approach can be helpful in understanding many of the ecological patterns observed, and in estimating the possible consequences, at an ecosystem level, of removing top predators.

To improve fisheries and an ecosystem approach to management, Mills et al. (1993) propose that scientists focus their attention on determining the strength of interactions between species, rather than attempting to identify which species are keystones in each ecosystem, as has often been the focus in the past. The former makes more sense given that exploited species are not usually keystones and therefore changes in their abundance often have little impact on their prey or competitors (Jennings and Kaiser, 1998). For example, removal of substantial proportions of abundant forage fish may have large impacts on their prey, competitors and predators, in a similar manner to removal of a keystone species (Shannon and Cury, 2004).

### **Top-down effects of fishing and 'fishing down the marine food web'**

Elton (1927) first noted that food chains are short and their length is variable among natural systems within a rather low range. Although five- to six-link food chains are possible, energy transfer between trophic levels is inefficient, and most communities fall in the range of one- to four-link food chains (Morin and Lawler, 1995; Menge, 2000). Mean chain length is shorter in terrestrial than aquatic ecosystems (Hairston and Hairston, 1993). Thus, Pimm (1991) reports that the number of trophic levels in terrestrial systems is typically three whereas aquatic pelagic systems are typically characterized by four trophic levels. Shelf and coastal systems have longer food chains than do upwelling and oceanic ones (Christensen and

Pauly, 1993). However, there are exceptions. For example, in models of the southern Benguela upwelling system, which spans both upwelling and shelf areas, the maximum trophic level was found to be 5.2 compared to 4.7 in the northern Benguela (Shannon, 2001). Thus adding or removing one trophic level can strongly affect the control operating at a particular trophic level in an ecosystem.

By altering productivity levels in a food-web in a northern California river, Wootton and Power (1993) observed alternating control by trophic level, and between food chains of three and four links. Menge and Olson (1990) predicted that, rather than alternating, predation increases in importance and competition decreases in importance from high to low trophic levels, and that, in addition, food chain length decreases with increases in environmental stress. Fretwell (1987) hypothesized that food chains varied in length as a consequence of variable environmental gradients of nutrients and productivity, emphasizing the role of productivity gradients as the prime determinant of food-chain dynamics in terrestrial systems. Exploring food-chain length in lakes, Post et al. (2000) found that ecosystem size, and not resource availability, determines food-chain length in natural ecosystems.

Food chain length is a topic that has received a lot of attention in terrestrial ecology but consensus has not been reached regarding its role in ecosystem functioning. The debate now shifts to a search for when and where a suite of interacting constraints operates to determine variation in food-chain length (Post, 2002). Because of the intricate nature of predation in the marine environment and the difficulty in assigning a trophic level to a particular fish species or group of fish species, the literature on the length of marine food-chain is scarce. However examination of the global fisheries suggested that the mean trophic level of the catch has been decreasing as a result of 'fishing down marine food webs' (Pauly et al., 1998; 2000). By removing top predators first, i.e. shortening food chain length, predatory pressure was released on small forage fish that constituted the food of top predators. This could potentially lead to a subsequent increase in small forage fish biomass, and hence of harvests. When analysing global fish catches, it appears that pelagic fish species reached a plateau in the mid-1980s, i.e. ten years after the stabilization of the demersal fish catch, suggesting a possible increase in forage fish species during the heavy exploitation of their predators in the 1970s and 1980s (Cury et al., 2000).

As noted by Caddy and Garibaldi (2000), such a decline in trophic level could in some cases be a 'bottom-up' effect due to an increase in nutrients in naturally nutrient-limited marine production systems, even if all levels of the food web are being exploited at a constant rate. In fact, an increase in forage fish abundance, in turn, might even lead to subsequent increases in fish predator biomass and harvest. Analysing the FAO database, Caddy and Garibaldi (2000) found contrasting results suggesting that some ecosystems are controlled by a change in marine productivity, i.e. they are bottom-up controlled, whereas others seem to be controlled by the abundance of the predators, i.e. a top-down control. Since the decline of piscivores in the Northwest Atlantic in the early 1970s, increased biomass of benthivores has been observed. In the North Sea the 'outburst' of gadoids, which was favoured by increasing zooplankton (*Calanus*) and pelagic fish abundance, was followed by a decline in the biomass of planktivores (herring and mackerel), related to high gadoid abundance (the so called 'gadoid dome'). Intensive fishing

competed with sea bird breeding colonies for sand eels. In the Mediterranean Sea, the supply of nutrients from land run-off has been proposed as a major factor affecting zooplanktivores and resulting in peak landings of piscivores (e.g. swordfish and hake). Sharp increases in planktivores in the Eastern Central Atlantic and in the Southeast Pacific do not appear to be primarily related to depletion of predators and in the North Atlantic, removing top predators may be the likely cause of the increase in landings of shelf planktivores. By contrast, in the Mediterranean, the increase in planktivores seems to be a bottom-up response to increased marine productivity. These analyses are based on data that were not collected specifically to study ecosystems, and therefore that basically do not have the resolution to do so. Overall they suggest contrasting patterns, as opposed to gradual and continuous changes. Caddy and Garibaldi (2000) propose that 'punctuated equilibria' or 'regime shifts', involving actual changes in ecosystems, are important phenomena that reflect ecological changes but also changing exploitation strategies. In addition, different strong and changing patterns seem to exist. Caddy and Garibaldi (2000) concluded from their analysis that the release of predatory pressure on zooplanktivores, leading to expanded biomasses, is ambiguous at the high scale of aggregation of the FAO database.

In the Black Sea, several authors attributed the numerous ecological changes that have occurred during the last decades to anthropogenic eutrophication (Zaitsev and Mamaev, 1997). Using both a statistical and a mass-balance dynamic modelling approach, Daskalov (2002) explored the relative contribution of bottom-up versus top-down control. Time series of piscivorous and planktivorous fish, zooplankton, phytoplankton and phosphate content in surface waters of the Black Sea were considered between the 1950s and the 1990s. Alternating trends across these consecutive trophic levels were found. The author attributed this cascading effect to the overexploitation of large predators, such as dolphins, mackerel, bonito and bluefish. As the fish predators were depleted, the planktivorous fish biomass increased considerably in the early 1970s, and consumption of the zooplankton increased. Jellyfish biomass also increased considerably during the 1980s, affecting zooplankton abundance. The subsequent increase in phytoplankton biomass apparently resulted in the depletion of nutrients in the surface layer since 1975. Comparing different scenarios using Ecosim, Daskalov (2002) concluded that top-down control was the more likely determinant of the structure of the Black Sea ecosystem, given that both overfishing and anthropogenic eutrophication are responsible for these observed changes.

Ecosystem changes in the Northwest Atlantic have been drastic during the last three decades. The cod biomass decreased from 2.5 to 0.05 million tons due to overexploitation (Bundy, 2001). A trophic cascade operated in the 1990s, during which time capelin abundance, released from strong predation pressure from finfish, increased; zooplankton decreased in abundance, whereas primary producers increased in abundance. Meanwhile the abundance of harp seal increased from 1.9 to 5.0 million animals, which, it is believed, might prevent cod from recovery (Bundy, 2001).

The effect of removing top-predators by overexploitation and the resulting top-down effect or "fishing down the food web" is sometimes well illustrated, like in the Black-Sea or in the Northwest Atlantic. However, fishing out a top predator can also cause complex changes in community dynamics. Such an effect of the

overexploitation of large apex fish species was recently illustrated. Ecologists have long speculated how predatory fish species are able to achieve large body size, given that their juveniles must grow through a predation-competition phase involving the very species that will be their prey later in life. According to Walters and Kitchell (2001), large, dominant fish species that are the basis of many fisheries may be naturally successful due partly to "cultivation" effects, where adults crop down forage species that are potential competitors/predators of their own juveniles. This "predator-prey role reversal" (Barkai and McQuaid, 1988), or cultivation effect, is apparently common in freshwater communities, and may also explain low recruitment success due to depensatory effects of some major marine stocks following severe declines (such as Newfoundland cod). Implications for fisheries are twofold: by depressing the abundance of large fish predators, fisheries release the top-down control on small fish, and in doing so they increase the risk of depensatory effects due to competition/predation by small fish, preventing the rebuilding of stocks of large fish species (Figure 14.9b). In the Central Baltic clupeid predation on cod eggs (Koster and Schnack, 1994) has resulted in the system being either cod-dominated or clupeid-dominated.

Shortening the food chain by removing top predators can consequently result in a lack of resilience, which is observed for populations of most large fish species (Hutchings, 2000; 2001). However top-down control mechanisms are sometimes dampened by redundant species and complex interactions that are unfortunately rarely documented. For example, Link and Garrison (2002) noticed a shift in the abundance and size composition of fish predators during the last four decades in the Georges Bank fish community. These changes were attributed to fishing pressure. A remarkable shift from cod to spiny dogfish was observed but there were no apparent changes in total fish consumption by the six major predators, despite changes in predator size, structure and abundance. There was a shift in the dominant piscivore in the Georges Bank ecosystem, revealing that exploitation and competition between cod and spiny dogfish were certainly high and that no cascading effects were found in this particular ecosystem. A cross-ecosystem comparison suggests that trophic cascades are stronger in the aquatic environment than in the terrestrial one, despite high variability among systems (Shurin et al., 2002).

### 3.4 *Wasp-waist control or the control by dominant species*

Recently the role of dominant pelagic fish has been emphasized as they might exert a major control on energy flows, and this has been termed wasp-waist control (Figure 14.11). In upwelling systems few pelagic fish species occupy the intermediate trophic level, feeding mostly on phytoplankton and/or zooplankton. These species can exhibit large biomasses, which vary radically in size according to environmentally driven recruitment strength. These characteristics are thought to inflict constraints on lower and higher trophic levels. Hairston and Hairston (1993) mentioned that planktivorous fish could reduce herbivorous zooplankton, which would lead to an increase in phytoplankton density. This idea was further developed using data on lakes (e.g. Carpenter and Kitchell, 1993) and the topic received considerable attention from both terrestrial (Schoener, 1989) and aquatic ecologists (Persson et al., 1991). Consumption efficiencies of herbivores on primary

producers are much higher in freshwater pelagic communities (32%) than in terrestrial communities (3%) (Hairston and Hairston, 1993). By comparison, the topic only recently received attention in the context of marine ecosystems. Pauly and Christensen (1995) estimated that for the period 1988–1991, 8% of global aquatic primary production was required to support the sum of the mean reported world fish catches (94.3 million tons) and discards (27 million tons). This value is higher if one considers upwelling systems alone; Pauly and Christensen (1995) calculated that a mean of 25.1% (confidence interval 17.8–47.9%) of primary production in upwelling systems was required to sustain catches and discards, suggesting strong links between trophic levels. Micheli (1999) found that interannual fluctuations in mesozooplankton biomass were negatively correlated with those of zooplanktivorous fish, indicating that fish predation can potentially control mesozooplankton biomass. By means of meta-analysis, 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). In the Central Baltic Sea, Kornilovs et al. (2001) also showed an influence of sprat biomass on the production of cladocerans in summer.

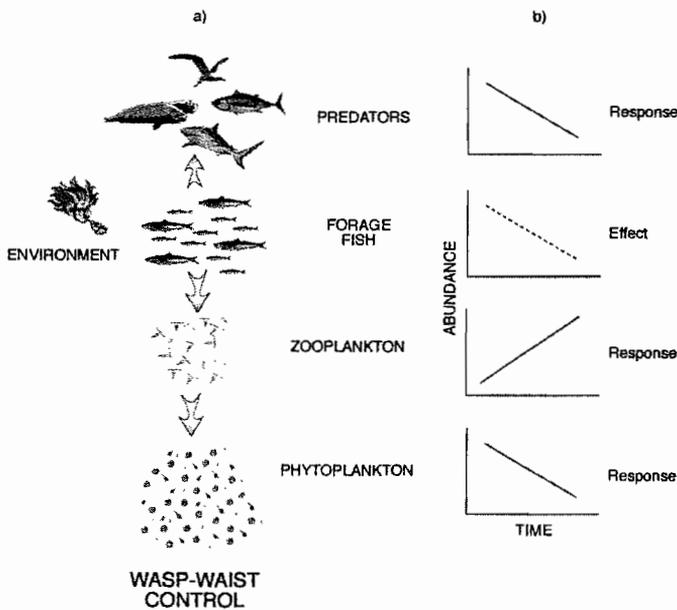


Figure 14.11 a) Wasp-waist control within a simplified 4-level food chain in a marine ecosystem b) The abundance of the prey fish (small pelagic fishes), which is dependent on the environment, controls both the abundance of predators and primary producers. A decrease in abundance of prey fish negatively affects abundance of the predators. The same decrease in abundance of prey fish reduces predation on zooplankton, which becomes more abundant. A larger zooplankton population increases grazing pressure and diminishes phytoplankton abundance (the control factor is a dashed line and the responses are a solid line). The environment (sensu Sinclair, 1988) is considered to have a direct physical effect on pelagic fish recruitment, but no effect on the whole food-chain (from Cury et al. 2003).

Conversely, bottom-up control of fish predators by small pelagic fish has been noticed, as several (but not all) predatory fishes suffer when their prey stocks collapse in the Benguela, the Guinea, and the Humboldt currents (Cury et al., 2000). When pelagic fish stocks recover, the depleted predators may recover quickly, or with delays of a few years to several decades, highlighting the complex response of the ecosystem to change. Despite great plasticity in life-history characteristics, many bird populations are unable to counter the effects of longer-term fluctuations in prey resources (Crawford, 1999). An example is birds off Namibia in the 1970s; horse mackerel and pelagic goby replaced sardine in the diets of seabirds after the sardine stock collapse. These fish were unavailable to penguins and gannets at colonies situated south of Lüderitz as they were either distributed too far north or they occurred too deep in the water column. The result was massive declines in seabird populations in this region (Crawford et al., 1985). A comparative analysis of trends in seabird abundance in Peru and southern Africa emphasizes the dependence of seabirds on anchovy and sardine for reproductive success and growth (Crawford and Jahncke, 1999).

These few examples illustrate a wasp-waist control, under which abundant small pelagic fish constitute mid-trophic-level populations that exert both bottom-up control on top predators and, more surprisingly, top-down control on zooplankton. These effects can eventually cascade down to phytoplankton in freshwater ecosystems, but this is rarely the case in the marine environment. Reproduction of marine animals is mediated by spatially and temporally varying oceanographic processes, affecting most of their life cycles. Marine animals with a pelagic larval stage are likely to offer ample opportunities for differential reproductive success. Under wasp-waist control, the environment plays a direct role (*sensu* Sinclair, 1988 and Bakun, 1996) in determining the strength of pelagic fish recruitment, i.e. it has an effect on any particular trophic level of the food chain (Figure 14.11).

### 3.5 *Mixed and/or changing controls*

Scientists who agree that trophic interactions are important debate whether primary control is by resources or predators. The issue of the relative contributions of top-down versus bottom-up control is not new; it has been debated extensively in terrestrial ecology but consensus has not yet been reached (Power, 1992; Matson and Hunter, 1992). There is general agreement that top-down and bottom-up forces act on populations and communities simultaneously, and that understanding their relative contributions is an important step for future ecosystem approaches to management (Cury et al., 2003). Hunter and Price (1992) offer a compelling argument for the primacy of bottom-up forces in food webs: "... the removal of higher trophic levels leaves lower levels intact (although perhaps greatly modified), whereas the removal of primary producers leaves no system at all". But one must recognize that this assertion leaves almost unanswered the challenging question of what are the factors that can change consumer efficiency. The discussion is no longer about which type of control occurs, but rather about what controls the strength and relative importance of the various forces under varying conditions (Matson and Hunter, 1992).

Link and Brodziak (2002) have compiled a comprehensive report on a suite of metrics that are available for analysing changes and functioning of the Northeast

U.S. continental shelf ecosystem over the last forty years. They categorized these metrics into abiotic and biotic. Abiotic metrics include physical metrics such as the North Atlantic Oscillation, a measure of the air pressure difference between two sites, and temperature anomalies. A possible shift is suggested from a cool to a warm temperature phase. Chemical metrics were not readily available as they require synoptic coverage. Link and Brodziak (2002) propose that key chemical indicators be identified from the array of important nutrients, metals, and toxins that can be monitored. Biotic metrics were plentiful, and from these the authors concluded that the observed changes in the Northeast U.S. continental shelf ecosystem are attributable to top-down forcing (fishing is the dominant top-down effect), as well as strong bottom-up environmental forcing of the zooplankton community. The environment is listed as a second key forcing factor which can determine recovery. There has been a shift in relative biomasses of demersal and pelagic fish communities: demersal fish abundance has decreased whereas pelagic fish have increased. Although species composition has changed over time, the standing biomass of the whole ecosystem and its main sub-components (e.g. phytoplankton, zooplankton, different feeding guilds) have remained relatively constant. Available biotic metrics included a) biomass trends (e.g. zooplankton, separate species), b) species diversity indices (species dominance measures, species evenness etc.), c) food web indices (linkage, density, number of species eating or being eaten by a given species), total consumption, diet compositions, ratio of consumption of a fish species and the landings of that species) and d) system-level indices (energy, exergy, free energy, information content, system-level consumption, flux rates, resilience, stability, persistence, resistance). The third category of metrics considered is human metrics. Human metrics are those derived from effort, landings and profits, and include landings, trawl revenues, fishing effort, CPUE, fishing activity and landed values. Link and Brodziak (2002) write "changes in fishing practices and fishing communities, such as diversification to target non-groundfish resources, have probably contributed to sustaining the fishing fleet while target species abundances have declined and regulations have increased".

Flexible views of the varying roles of top-down and bottom-up forces need further examination to reach any possible generalization (Power, 1992). As discussed previously, in fisheries ecology there has been a long tradition of relating climate and fisheries (Cushing, 1982), assuming that recruitment strength is limited by food availability. With overexploitation, the importance to ecosystem functioning of removing large apex predators has also been emphasized. In rocky intertidal habitats the role of predation has been noted for a long time by marine ecologists. These studies, among others, have been developed by scientists who were interested in evaluating the impact of a particular type of control in ecosystems. For marine ecosystems, the context and complexity of the discussion is expanding, with new case studies being presented and new ways emerging of considering the relative importance of top-down versus bottom-up control. In the following section we discuss ecological factors that can affect controls, the evidence of mixed and changing controls for fish communities, and how better spatial and temporal resolutions can help to understand the contributions of the different controls.

### **How ecosystem structure affects trophic controls**

A particular structure or configuration of an ecosystem can reveal the type of trophic control operating. This can be observed, for example, in contrasted environmental contexts. Most studies in marine rocky intertidal habitats have demonstrated the existence of strong top-down control by consumers. Menge (2000) reviews twenty examples of top-down control in different intertidal habitats documented during the 1980s, many of them involving mussel and barnacle interactions. In those examples, strong top-down effects of predators were capable of controlling prey communities on temperate and tropical rocky coasts. However, in many comparative studies, key physical environmental gradients can mitigate the impact of top-down forces, such as hydrodynamic forces and thermal/desiccation stress. Assuming that recruitment of a species at the basal level of food webs is a bottom-up effect when it increases the abundance of prey organisms, Menge (2000) documented five case studies in South Africa, New England, Oregon and New Zealand where both top-down and bottom-up controls were acting simultaneously on rocky intertidal community structure (no fish species were involved). Menge (2000) concluded that bottom-up effects are in fact tightly linked to top-down processes and can be important determinants of community structure in rocky intertidal habitats, although present knowledge is limited and the field needs to be expanded.

Changing control in fish communities has been documented in several other cases. In the northern Baltic the increase in herring abundance in the late 1980s appeared to be the result of weakened top-down regulation as a result of a sharp decline of its main predator, the cod. Meanwhile the herring was affected by the availability of suitable-sized plankters, which was environmentally controlled, i.e. by salinity. A possible top-down effect of cod on herring and a bottom-up process mediated via changes in mesozooplankton species composition seem both to have contributed to the dynamics of the herring in the Baltic (Flinkman et al., 1998). A second example of changing control is the overexploitation of the sparid and serranid fish communities off North-West Africa in the 1960s releasing predation pressure on octopuses, which in turn became abundant successively in Morocco and Mauritania at the beginning of the 1960s, and in Senegal in the mid-1980s (Gulland and Garcia, 1984). Weakened top-down trophic control led to strong relationships between upwelling intensity and octopus recruitment in the three upwelling systems (Faure et al., 2000).

Just as trophic cascades discussed previously are transient and dynamic, it appears that bottom-up and/or top-down control may operate according to the structure of the ecosystem. In some instances described, both top-down and bottom-up control appear to be acting together on the same species (e.g. both control types have been reported to affect the northern Baltic herring), whereas in other instances, one type of control has replaced another when the "dominant" control mechanism regulating a species group has diminished (e.g. overfishing has disturbed the usual top-down control of octopus by sparid fish, so that environmental factors became more important regulators of octopus). Trophic controls can be changed by the structure of the ecosystem, but also by spatial or seasonal constraints.

### **Spatial and temporal dependence of trophic controls**

The interactions that occur within an ecosystem produce structure and determine the way the system functions; the temporal and spatial scales of the processes occurring in marine ecosystems are inextricably linked (Murphy, 1995). The marine environment is a dispersive and heterogeneous one and 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 (Sinclair, 1988). Food availability but also 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). Fish populations have geographical closure of their life cycles and climatic factors can affect the spatial context of marine populations in many ways by modifying the dynamics of the spawning or feeding areas, consequently changing recruitment success or migration patterns (Sinclair, 1988). Fish have large-scale ontogenetic habitat shifts in marine ecosystems and predation is one of several ecological constraints that shape their distribution. Since interactions can be spatially patchy (highly localized), most processes are scale-dependent. For example the population dynamics of predators and prey within a specific region can be uncoupled (Murphy, 1995) and rather than addressing the whole ecosystem, we can instead concentrate on a particular region at a particular time period.

Seasonal or year-to-year environmental fluctuations as well as spatial heterogeneities have consequences for ecosystem dynamics. A preliminary approach would be to visualize the distribution of different biomasses per trophic level for different species (or group of species having the same food requirements) as potential patterns of interactions within an ecosystem. This representation can provide a baseline for exploring local trophic control between two or more different species (Drapeau et al., 2004). For example, on an island where marine seabirds breed, the foraging range and distribution of seabird prey (e.g. anchovy) in time and space can provide valuable indicators of potential interactions.

Time lags are obviously more difficult to appreciate. In the "match-mismatch" hypothesis, Cushing (1969) developed the idea that the production of fish larvae matches or mismatches the production of their food, resulting in successful or unsuccessful recruitment. Consequently the control of the abundance of fish recruits depends on the abundance but also the availability of their prey, the zooplankton. In this particular case the temporal variability of the physical environment may or may not be translated into effects at higher trophic levels in the food chain. Several recent papers tentatively explore the relationship between recruitment and dynamics of the food chain in order to explain fluctuations in fish stocks. The importance of seasonality on ecosystem dynamics was illustrated in British Columbia by exploring the links between time series from oceanographic data, zooplankton data and seabird breeding data (Bertram et al., 2001). When spring is early and warm, the duration of the overlap of seabird breeding and copepod availability in surface waters is reduced, creating a mismatch of prey and predator populations. Cooney *et al.* (2001) identify a critical time-space linkage between the juvenile stages of pink salmon and herring in shallow-water nursery areas and seasonally-varying oceanic states, the availability of appropriate zooplankton forage, and the kinds and numbers of predators. These ecosystem-level

mechanisms influenced the mortality of the fish, which were shown to be habitat-dependent and to exhibit strong food-type preferences.

Using different dynamic models of interactions in a spatially structured ecosystem, Murphy (1995) explored predator-prey linkages in Southern Ocean food webs. Krill is strongly influenced by large-scale abiotic factors, i.e. over the ocean basin scale. The introduction of spatial structuring changes the relative prey availability for the different predator groups and increases the complexity of the responses. This analysis reveals that there are probable shifts between the influence of food concentration and through-flow systems within and between seasons. It also reveals that analysing interactions only in the temporal dimension may result in misleading inferences being made about key processes. This reinforces the need for considering both spatial and temporal dimensions in an ecosystem approach.

A satellite-based estimate of potential primary production in the four eastern boundary currents (i.e., California, Humboldt, Canary, and Benguela Currents) produced values 4–150 times larger than the ones derived from the observed current fish catch, using an idealized food chain of 2.6 links and an average trophic efficiency of 10% (Carr, 2002). This discrepancy between potential and observed productivity was attributed in the Benguela to the temporal mismatch between feeding and high primary production (Shannon and Field, 1985). For the different eastern boundary currents the explanation apparently lies in the different trophic structures and spatial accessibility of the food in the ecosystems. Carr (2002) estimated that the yield for each upwelling system was an upper bound that would be decreased to 10–20% by environmental accessibility. Thus, despite large primary production found in upwelling systems, food availability affected by spatial and temporal constraints could lead to the unexpected result that small pelagic fish populations are likely to be food-limited (Micheli, 1999; Cury et al., 2000).

Hunter and Price (1992) offered a synthetic framework regarding the controversy around top-down versus bottom-up control and suggested that instead of asking “Do resources or predators regulate this particular population?” ecologists should rather ask “what factors modulate resource limitation and predation in this system, determining when and where predators or resources will dominate in regulating populations?” The relatively few studies on trophic controls in different parts of the ocean, compared to lakes or terrestrial ecosystems, do not allow generalizations to be made. However, a number of recent studies on trophic interactions should help to understand the respective role of top-down versus bottom-up controls in marine ecosystems. The examples presented above are recent, tentative ways of seeking mechanistic rather than correlative understandings of complex natural systems. They are surely the first examples of a long, future list that will recognize the importance of interactions in time and space as one of the key elements in understanding dynamical trophic controls in marine ecosystems.

#### 4. Discussion

Fish interact strongly, mainly through trophic interactions. Predation is pervasive and plays an important role in shaping marine communities. However everything is not strongly connected to everything else, and not all production is suitable for the next trophic level. Spatial and temporal constraints, particularly those associated with habitat selection, partly determine the strength of the interactions. Com-

ponents of the ecosystems are linked in a variable and changing manner, suggesting that there is no need to measure or understand everything, but rather to determine the significant interactions, i.e., when, where and how they can potentially structure the dynamics of the ecosystems. In the speciose marine environment, predation interactions among fish appear to be common, analogous to freshwater systems (Pace et al., 1999), rocky intertidal habitats (Menge, 2000), or benthic marine ecosystems (Pinnegar et al., 2000) where trophic cascades have been described. Patterns of interactions that involve fish in coastal or open marine systems, most of which were presented above, are summarized in Tables 14.1 to 14.4. All the described patterns concern interactions between only a few selected species that comprise the ecosystem, and that are usually of economic interest for fisheries. Despite the quality of the data and of the evidence, which varies greatly between case studies, controls can be found to be bottom-up as well as top-down in marine open systems, with a tendency of recent studies to favour an interplay between the two types of control, as in the case of the wasp-waist control. Alterations of resource availability and consumers often result in general patterns of community change, but not always. The species composition of an ecosystem may change, although the structure, in terms of the composition of the different trophic levels, may remain the same. It also appears difficult to draw generalities from case studies that sometimes contradict previous studies. For example, and surprisingly, top-down processes do not always control the upper trophic levels, as predicted in most theoretical studies, and lower trophic levels appear to be bottom-up controlled in most cases, but not all.

Ecosystems can be resilient to exploitation and do not always exhibit drastic changes in their composition or structure, a situation exemplified by the North Sea (the proportion of large fish has diminished, average fish sizes have decreased . . .). In these cases, species redundancy at intermediate trophic levels (planktivorous fish) or at high trophic levels (large fish predators) plays an important role in delaying any drastic changes in the functioning of ecosystems. However, in many cases, regime shifts and alternative steady-states can substantially modify the structure and dynamics of marine systems. The effect of predator removal offers a compelling example of induced changes at lower trophic levels. The shift from a cod-dominated towards a pelagic-dominated ecosystem in the Atlantic is a documented example that has received many theoretical interpretations.

For a given species within the ecosystem, the nature of the control can change through time according to the configuration of the ecosystem. The dynamics of the octopus populations off West Africa are illustrative of a top-down control released following the overexploitation of predatory fishes, and which later became controlled by bottom-up forces (i.e., the strength of the upwelling). Overexploitation of top predators and 'fishing down the food web' may not only lead to an increase in the biomass of planktivorous fish, but also to cascading effects throughout the different trophic levels, as has been observed in the Black Sea.

Fish recruitment is mainly considered to be bottom-up controlled, but in many cases the formal link between recruitment strength and the dynamics of primary production is not sufficiently documented, casting doubt on the way the environment is controlling recruitment, i.e., directly through dynamic environmental structures (*sensu* Sinclair) or indirectly through the food chain (*sensu* Cushing).

Recruitment studies should focus on linking the environment to trophic interactions in the context of marine food-webs.

Process-oriented models often predict a rich variety of dynamic behaviours that depend on the complexities of the interactions involved. At the other end of the spectrum, pattern-oriented studies predict that only a portion of the habitat or a particular assemblage within the ecosystem can exhibit a strong dynamic structure. Both approaches reveal the transient nature of ecosystems. Ecologists have been analysing ecological interactions in two different and most often exclusive ways using reductionist or holistic approaches respectively; but as stated by Elton (1927), a combination of the two methods would be the best procedure. However seventy-five years after this ecological wish formulated by Elton, it is still more a direction for future research on ecosystem dynamics than actual research objectives.

No general theory can be ascribed to the functioning of marine ecosystems, which results in poor predictive power for fisheries management. Past observational experiences can provide guesses or conjectures of the potential dynamics of the system. Recently, tentative and partial generalizations have been proposed (Cury et al., 2003). For example, trophic cascades are mostly found in lakes or in hard substrata marine ecosystems and mainly for less complex food webs, whereas wasp-waist control is most probable in upwelling systems. This constrains the field of possibilities and introduces opportunities for stimulating comparisons and generalizations.

Stating that "ecological patterns and the laws, rules and mechanisms that underpin them are contingent on the organisms involved, and their environment," Lawton (1999) recognized that this contingency is manageable at a relatively simple level of ecological organisation or for large sets of species, over large spatial scales, or over long time periods, but that it becomes overwhelming for intermediate scales, such as at the level of the community. Currently, neither the empirical database, nor insight gained from interaction models, appear sufficient to permit a synthesis relating cause and effect at the community level (Lawton, 1989).

Patterns of interaction do exist and should be regarded as the focal entry point to ecosystem approaches to management. Nevertheless, ecological understanding and models of ecosystem functioning are provisional and subject to change (Christensen et al., 1996). As stressed by Hairston and Hairston (1997), any attempt to understand broad ecological patterns will be challenged by the complexity of nature.

This scepticism reflects concerns about the realism of basic models used to analyse the properties of food webs. Even though it is possible to identify interaction processes that are involved and several patterns that emerge, only very few generalisations across systems have been made and predictions are mostly out of reach when considering the dynamics of ecological systems. Moreover, and as recently stated by Mace (2001), in terms of making realistic predictions about the future, ecosystem models have not yet proven themselves as management tools. Hall (1999) stated that we must admit our ignorance of the true importance of the effects of fisheries acting through species interactions in marine systems. However, since then many studies have provided new syntheses and field examples showing that fishing effects on ecosystems are paramount and can help fisheries management (Jackson et al., 2001; Walters and Kitchell, 2001; Daskalov, 2002). Several

years to decades will be necessary for marine ecologists to refine concepts and to find the appropriate data, which are mostly lacking at present, to strengthen their hypotheses on the functioning of marine ecosystems.

Ecosystems ecology is an emerging discipline that still needs to find its way by formalizing principles, and by building theories for the marine environment. Exploring complexity of ecosystems by linking processes and patterns together is a necessary step to integrate our fragmented and disciplinary knowledge on ecosystems into a framework. This integration could provide the "ecoscope" to study marine ecosystems (a term proposed by Ulanowicz, 1993), i.e. a powerful multidisciplinary tool that will explore the complexity of their dynamics. It is challenging, as it requires that we:

- Develop macroecological studies of the oceans to characterize patterns of ecosystem components, based on large amounts of data (Parsons, 2003).
- develop process- and pattern-oriented studies coupled through integrated field, experimental and modelling studies;
- provide a broad view of ecosystem studies where collection of data at different scales is explicitly prescribed in sampling design of field studies and where top-down versus bottom-up control are simultaneously assessed;
- provide accepted, clear and testable definitions of the terms that are used for characterizing ecological processes;
- develop new observation systems by recognizing that ecological and biological data that are collected for single-species fisheries management are necessary but insufficient for understanding ecosystem dynamics. Detailed predictions require detailed knowledge and an understanding of interaction processes;
- promote comparative and retrospective studies among marine ecosystems to evaluate regime shifts and types of controls, and develop models to evaluate ecological changes within ecosystems and assess anthropogenic changes;
- evaluate states and changes in marine ecosystems by defining new ecosystem-based indicators for fisheries management, assess the usefulness of these indicators for management purposes and apply them to various fisheries.

Ecosystems ecology should become a multidisciplinary field of research of the marine environment and a central focus for fisheries management. This represents a new framework that would challenge the difficulties of understanding the dynamics of complex systems at appropriate scales by enabling repeatable patterns to be tracked by indicators, and by incorporating existing scientific knowledge on processes into models and ultimately into fisheries management.

**TABLE 14.1**  
**Documented bottom-up control that involves fish species in marine ecosystems.**

<b>Location</b>	<b>System</b>	<b>Species interactions involved</b>	<b>Reference</b>	<b>Comments</b>
Mediterranean Sea	Coastal and open systems	Nutrients (land runoff)-planktivores (sardine-anchovy-sprat)-piscivorous (horse mackerel, whiting)-large piscivorous (swordfish, hake)	Caddy and Garibaldi (2000)	FAO data base
Mediterranean Sea	Northern coastal systems	Land run-off-zooplanktivores-piscivorous fish (hake, swordfish)	Skud (1983)	
Western Gulf of Alaska	Coastal system	Shrimp and capelin- harbor seal and sea lion	Hansen (1997)	
North Sea	Coastal system	Sandeels-sea birds	Furness and Tasker (1997)	
North Atlantic Georges Bank	Coastal system	Environment (NAO)-zooplankton-cod and Haddock	Hofmann and Powell (1998)	Indirect environmental effect sensu Cushing. Large scale environmental effects
North Atlantic Georges Bank	Gulf stream rings	Environment (ring dynamics)-fish recruitment (cod, haddock,...)	Hofmann and Powell (1998)	Direct environmental effect sensu Sinclair.: Small scale environmental effects
Guinea and Humboldt currents	Upwelling systems	Pelagic fish (anchovy and sardina)-piscivorous fish ( <i>Scomber</i> and <i>Sarda</i> )	Cury et al. (2000)	Dampening effects for most predator species
Northern and southern Benguela	Upwelling system	Pelagic fish (sardine and anchovy)-marine sea birds (penguins)	Crawford et al. (2001)	
North-western Mediterranean Sea	Coastal systems	Environment (global: NAO and local: river runoff and wind mixing)-recruitment of 13 commercial fish and invertebrate species	Lloret et al. (2000)	Indirect environmental effect sensu Cushing proposed but not demonstrated
North Atlantic	Coastal system	Environment (westerly weather)-phytoplankton-zooplankton-herring-marine birds	Aebisher et al. (1990)	Observed parallel long-term trends across four marine trophic levels

North-east Pacific	Alaskan coastal systems	Environment (decadal scale change, regime shift)-zooplankton-salmon	Francis and Hare (1994)	
Northeast Pacific	California and Alaska	Environment (decadal scale change, low frequency variation)-zooplankton-benthic and pelagic communities	McGowan et al. (1998)	Complex responses of the different components of the ecosystems Change in spatial distribution of many species due to environmental changes
Northeast Pacific	Coastal systems including Gulf of Alaska and Bering Sea	Environment (ENSO-PDO)-recruitment of groundfish and pelagic fishes	Hollowed et al. (2001) McFarlane et al. (2000)	Indirect environmental effect sensu Cushing proposed Large scale environmental effects
Central North Pacific	North-western Hawaiian Islands	Environment (regime shift mid-1970s)-phytoplankton-reef fishes & spiny lobsters- marine birds and monk seals	Polovina et al. (1994)	
Central Baltic Sea	Pelagic Ecosystem	Cod-pelagic fish (Sprat)	Mollman and Koster (1999)	No top down control of pelagic fish on mesozooplankton
Pacific Ocean	Pelagic ecosystems: California, Kuroshio-Oyashio, Peru currents, Central North Pacific and Subartic Pacific	Environment (regime shift in the mid-1970s) – macrozooplankton – higher trophic levels	Hayward (1997)	Complex response of high trophic levels to environmental changes
Northern Pacific	Coastal systems	Large scale climatic change (ocean atmosphere linkage)-benthic taxa-sardine-anchovy versus Alaskan salmon	Finney et al. (2002) Baumgartner et al. (1992)	Paleoecological reconstruction over 2,200 years Anchovy and sardine vary out of phase with salmon over low frequency
Pacific Ocean	Coastal systems	El Niño disturbance (ENSO)-primary production-benthic production-pelagic fish- marine birds and pinnipeds	Glynn (1988)	Complex responses due to confounding effect of numerous interactions acting upon local conditions

*continued next page*

TABLE 14.2  
Documented top-down control that involves fish species in marine ecosystems.

Location	System	Species interactions involved	Reference	Comments
Northwest Atlantic (area 21)	Coastal system	Piscivores (notably cod)- benthivores (invertebrates such as blue crab, lobster, prawns...)	Caddy and Garibaldi (2000)	FAO database
Northeast Atlantic	Coastal system	Fish predators (gadoids)-pelagic fish (herring, saithe, whiting, capelin)	Caddy and Garibaldi (2000)	FAO database; (possible reverse trophic flow or cultivation effect between pelagic fishes and cod)
Central Baltic Sea	Pelagic ecosystem	Cod-pelagic fish (sprat and herring)- zooplankton	Kornilovs et al. (2001)	Top -down effect between sprat and Cladocera is strong in autumn. Food competition between sprat and herring
Yellow Sea	Pelagic system	Demersal fish species and large pelagic fish-small pelagic fish	Jin and Tang (1996)	
South Africa, Ghana, Japan, and Black Sea	Coastal system	Pelagic fish-Zooplankton	Cury et al. (2000)	Meta-analysis
Sub-Arctic North Pacific	Open ocean	Pink salmon- macrozooplankton- phytoplankton	Shiomoto et al. (1997)	Seasonal control in summer
Black Sea	Coastal pelagic domain	Fishers-pelagic predators- Planktivorous fish- zooplankton-- phytoplankton- Phosphates	Daskalov (2002)	Strong top-down control coupled with weak bottom-up effect (eutrophication)
Northern Baltic Sea	Northern Baltic proper (ICES areas 28-29)	0-group herring-zooplankton	Arrhenius (1996; 1997)	
Baltic Sea	Coastal system	Fishery- cod- planktivorous fish (clupeids); Planktivorous fish-cod recruitment (clupeid-dominated system)	Rudstam et al. (1994)	Existence of two competing top-down control processes (cultivation effect)

World Ocean	Coastal and open systems	Phytoplankton-higher trophic levels	Ryther (1969)	Comparative study between observed and predicted fish yields from estimates of photosynthetic organic production rates
North Sea	Thames Estuary (nursery areas)	North Atlantic Oscillation (NAO)- Juvenile fish (flatfish, clupeids, eel, invertebrates)	Attrill and Power (2002)	Climatic variability affects the structure of the fish assemblage, recruitment and life history traits
South Sea of Korea	Coastal system	SOI-SST-Chl-a-zooplankton-pelagic fish (anchovy, sardine, mackerel)	Kim and Kang (2000)	Exploratory analysis using correlations during certain months
Barents Sea, Norwegian Sea	Coastal systems	Salinity-zooplankton-herring/capelin-cod-seals/seabirds	Blindheim and Skjoldal. (1993)	

TABLE 14.3  
 Documented Mixed or Wasp-waist Controls that involves fish species in marine ecosystems.

Location	System	Species interactions involved	Reference	Comments
Eastern Boundary Currents	Upwelling systems	Environment (upwelling intensity)- primary production (bottom-up control) Small pelagic fish-primary production (deducted top-down control)	Carr (2002)	Compare primary production and fish production from estimated yield and the observed fish catch
Experimental and natural systems	Diverse	Planktivorous fish- mesozooplankton (top-down control) Nutrients (N availability)- phytoplankton (bottom-up control)	Micheli (1999)	Comparative empirical analysis of 47 marine mesocosm experiments and from 20 natural marine systems
Northern Baltic	Coastal ecosystem	Cod- herring (top-down control) Salinity-mesozooplankton-herring (bottom-up control)	Flinkman et al. (1998)	
North Sea	Coastal system	Zooplankton – Herring- Gadoid (bottom-up control) Gadoid- pelagic fish (Herring/Atlantic mackerel) (top-down control)	Cushing (1982) Caddy and Garibaldi (2000)	
Eastern Boudary Currents	Pelagic systems	Pelagic fish (sardine, anchovy)- pelagic predators (sarda, mackerel)- marine sea birds (bottom-up control) Pelagic fish (sardine, anchovy)- zooplankton (top-down control)	Cury et al. (2000)	Comparative empirical analysis
Northern Baltic Archipelago Sea	Archipelago	Environment (NAO) -small zooplankton (bottom-up control) Herring-large zooplankton (top-down control)	Dippner et al. (2001)	

North-east Pacific	Alaska and California currents	Environment (decadal scale change, regime shift)-phytoplankton-zooplankton (bottom-up) Forage fishes-birds and mammals (bottom-up) Predatory fishes-forage fishes (top-down)	Francis et al. (1998)	Complex response at higher trophic levels
North Atlantic Georges Bank	Northeast U.S. continental shelf ecosystem	Environmental forcing-zooplankton community Groundfish-squid and American lobsters Atlantic mackerel and herring – predators and fishing	Link and Brodziak (2002)	Predatory release on zooplankton not apparent when planktivores severely reduced by fishing implies primarily environmental control of zooplankton. Large decline in groundfish abundance under intense fishing benefited groundfish prey. Low predator abundance and fishing pressure benefited pelagic fish. Fishing is the dominant forcing factor.
Bohai Sea (Yellow Sea)	China Continental shelf ecosystem	Primary production/phytoplankton-zooplankton-fish productivity	Tang et al. (2003)	Top-down, bottom-up and wasp-waist controls act during different periods

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**TABLE 14.4**  
**Documented spatial and temporal changing controls that involve fish species in marine ecosystems.**

<b>Location</b>	<b>System</b>	<b>Species interactions involved</b>	<b>Reference</b>	<b>Comments</b>
All ecosystems	All systems	Zooplankton-fish recruitment (bottom-up control)	Cushing (1990)	Match-mismatch hypothesis between food and larvae
British Columbia	Coastal ecosystem	Temperature-zooplankton-(sand lance)-marine seabirds (bottom-up control)	Bertram et al. (2001)	Match-mismatch between prey and predators
Alaska Prince William Sound	Shallow-water nursery areas	Environment-zooplankton- juvenile herring and juvenile pink salmon (Bottom-up control) Marine bird and predator fish (Pollock and adult herring) -juvenile pink salmon (role of alternative prey) (top-down control)	Cooney et al. (2001)	Time and spatial dependent trophic control: Seasonal availability of prey to predators
Southern Ocean South Georgia area	Open systems	(Abiotic factors)-krill-(fish)-whales-seals-penguins (mixed controls)	Murphy (1995)	Large spatial scale effect of abiotic factors Small spatial scale for biotic interactions Ecosystem models considering spatial structure
Eastern Central Atlantic	Upwelling ecosystem	Fishers-groundfish (sparids, serranids)-Octopus (Top-down control) Environment (upwelling strength)-Octopus (bottom-up control)	Faure et al. (2000) Caverivière and Demarcq (2001) Gulland and Garcia (1984) Caddy and Garibaldi (2000)	Changing control through time and ecosystem structure

### Appendix: Models that are referred to in the text

#### *Lotka-Volterra model*

With  $N$  and  $P$  designating the respective abundance of prey and predator, the so-called Lotka-Volterra model consists of the following system of two differential equations:

$$\begin{aligned} \frac{dN}{dt} &= N(r - aP) \\ \frac{dP}{dt} &= P(acN - d) \end{aligned} \quad r, a, c, d > 0,$$

where  $r$  is the intrinsic growth rate of the prey in the absence of the predator,  $a$  is the attack rate of the predator (or the number of prey consumed by a predator per unit of time),  $c$  is the conversion efficiency of the prey consumed into numbers of predators, and  $d$  is the mortality rate of the predators in the absence of prey.

This classical model is based on some simplifying assumptions (Czaran, 1998): the environment is homogeneous, the population is represented by a state variable that is not structured according to age or size, the predator eats only one type of prey, the birth and death processes respectively in the prey and predator populations are exponential, and the functional response of the predator (term  $aN$ ) is a linear function that is not limited by prey numbers (Figure 14.A1a).

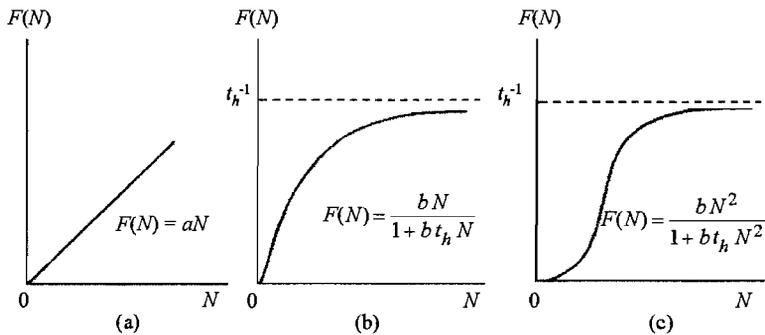


Figure 14.A1 Examples of functional responses of predators in the “laissez-faire” situation (Caughley and Lawton, 1976): no interference between predators. (a) Lotka-Volterra type, (b) type II Holling, (c) type III Holling (adapted from Murray, 1989).

Analysis of the model system shows that, apart from the point ( $N=0, P=0$ ), there exists another positive equilibrium point, and the dynamics of the system are such that the predator and prey populations exhibit cycles of abundance.

*General predator-prey models*

Since the development of the Lotka-Volterra model, numerous studies have proposed different formulations for population growth rates and interactions. Consider the general formulation of a predator-prey system:

$$\begin{aligned} \frac{dN}{dt} &= f(N) - P F(N,P) \\ \frac{dP}{dt} &= P G(N,P) \end{aligned}$$

Where  $N$  and  $P$  represent respectively the densities of prey and predator.

In such a generalized system, three functions must be specified:

- $f(N)$  : the intrinsic growth rate of the prey population in the absence of predators,
- $F(N,P)$  : the functional response of the predator, *i.e.* the number of prey consumed by a predator per unit of space and time,
- $G(N,P)$  : the numerical response of the predator, describing the production of predators, *i.e.* the rate of conversion of a prey into predators.

The Lotka-Volterra model assumes that the prey population exhibits a Malthusian growth rate, which is not realistic. Subsequent predator-prey models instead assumed logistic, density-dependent growth (Verhulst, 1838):

$$f(N) = rN \left( 1 - \frac{N}{K} \right)$$

where  $K > 0$  represents the carrying capacity of the habitat with respect to the prey (note that the Schaefer model is based on this logistic function).

There are a number of different ways of modelling predator functional responses (Table 14.A1), depending on what one assumes about how predators interact with one another. The situation called *laissez-faire* by Caughley and Lawton (1976) corresponds to predators that do not interfere with each other in their feeding activities. In such a system, neither the functional response nor the numerical response of the predators depends on their density, they depend only on prey density. The functional responses proposed by Holling (1959) belong to this category.

According to Holling (1959), feeding is composed of two types of activity: searching and handling prey. He assumed (i) that the total time dedicated to feeding is the sum of search time and handling time, and (ii) that the handling time  $t_h$  is a constant.

If the attack rate or the number of prey consumed by a predator per unit of search time is  $a$ , and the prey search time is  $t_s$ , then

$$F = \frac{\text{Numbers of prey consumed by a predator}}{\text{total time of feeding}} = \frac{at_s}{t_s + at_s t_h}$$

TABLE 14.A1:

Different formulations of functional responses of predators. Functional response is a function of the attack rate  $a$  on prey by predators:  $F = a/(a+t_h)$ . The constant  $t_h$  corresponds to prey handling time.  $b$ ,  $Q$ ,  $P_0$  are positive parameters.  $N$  and  $P$  are the prey density and the predator density respectively.

Hypothesis	Predation rate	Functional response	References
No interaction between predators (laissez-faire)	$a = bN$	$F = \frac{bN}{1+bt_hN}$	Type II, Holling (1959)
	$a = bN^2$	$F = \frac{bN^2}{1+bt_hN^2}$	Type III, Holling (1959)
Interference between predators	$a = \frac{QN^n}{P^m}$	$F = \frac{t_h^{-1}N^n}{(Qt_h)^{-1}P^m + N^n}$	Hassel and Varley (1969)
	$a = Q \left( \frac{N}{P_0 + P} \right)$	$F = \frac{t_h^{-1}N}{(Qt_h)^{-1}(P_0 + P) + N}$	De Angelis et al. (1975)
	$a = Q \left( \frac{N}{N + P} \right)$	$F = \frac{Q(1+t_h)^{-1}N}{(1+t_h)^{-1}P + N}$	Getz (1984)
Interference and ratio-dependence	$a = Q \left( \frac{N}{P} \right)$	$F = \frac{QN}{P + Qt_hN}$	Arditi and Ginzburg (1989)

and the functional response of the predator can be expressed as follows (Yodzis, 1994; Begon, et al., 1996):

$$F = \frac{a}{1 + a t_h}$$

The simplest hypothesis for the attack rate corresponds to a type II Holling response, with the attack rate proportional to the number of prey in the environment (Begon et al., 1996; Figure 14.A1b). The type III Holling response assumes that predators are inefficient at handling prey when preys are not abundant (Yodzis, 1994; Figure 14.A1c).

In contrast to Holling's (1959) models, another family of models assumes the existence of predator interference through trophic or reproductive competition, disease transmission, cannibalism, or density-dependent emigration (Yodzis, 1994). In this category, a common functional response is the one of Hassel and Varley (1969), which assumes that the attack rate decreases when predator abundance increases and, for a given density of prey  $N$ , the larger the abundance of predators, the slower the rate of consumption by a predator (Table 14.A1). This general formulation can be applied to a large number of predator-prey systems, but their behaviour becomes unrealistic in the particular case when  $P \rightarrow 0$ , when the attack rate  $a$  tends towards  $\infty$ . This problem also occurs for the ratio-dependent formulation of the functional response (Table 14.A1). Initially proposed by Arditi and Ginzburg (1989), this formulation assumes that the consumption rate decreases

proportionally with predator abundance, because the same resource must be shared by a greater number of consumers.

The most widely used predator numerical response function corresponds to a "laissez-faire" situation (Table 14.A2). It represents a balance between gains to the predator population (term  $dF(N)$ , proportional to the quantity of prey consumed by a predator, and its losses (term  $-c$ ). An interference effect can also be taken into account, affecting the predator consumption rate (the functional response) or the predator growth rate (Table 14.A2).

Structurally different, the predator numerical response function of Leslie (1948) is based on the assumption that the predator population grows logistically, with a carrying capacity  $hN$  that is proportional to the abundance of prey. A problem with this formulation is that the carrying capacity of the predators is zero when prey abundance is zero. Because predators incur maintenance costs, their carrying capacity should be zero at some positive threshold of prey abundance (Yodzis, 1994). The model of Hassel and Varley (1969) has this same problem—the predators are very resistant to a lack of food.

TABLE 14.A2:

Different formulations of the numerical response  $G$  of predators  $P$  to prey  $N$  (Yodzis, 1994). Parameters  $c, d, e, g, h$  and  $S$  are positive.

Hypothesis	Numerical response
<i>laissez-faire</i>	$G = -c + dF(N)$
Interference between predators affecting consumption rate	$G = -c + dF(N,P)$
Interference between predators affecting growth rate	$G = -c + dF(N) - eP^S$
Numerical response of Leslie (1948)	$G = g(1 - \frac{P}{hN})$

*May et al's (1979) krill-whale fishery model*

May et al. (1979) used the predator-prey model of Leslie and Gower (1960), which consists of a combination of a Lotka-Volterra-type linear functional response of predators to prey, and a Leslie numerical response of the predators (see also Tables 14.A1 and 14.A2). If  $N_1$  is the abundance of the krill population (prey) and  $N_2$  the abundance of the whale population (predator), the system dynamics are described by:

$$\frac{dN_1}{dt} = r N_1 (1 - \frac{N_1}{K}) - a N_1 N_2$$

$$\frac{dN_2}{dt} = g N_2 (1 - \frac{N_2}{hN_1})$$

The krill population is exploited at a rate  $r_f F_f$ , such that  $F_f$  represents a fishing effort multiplier equal to 1 when fishing mortality rate is equivalent to the intrinsic growth rate of the prey population  $r_f$ . Then, the corresponding fishing yield is  $Y_f =$

$r_1 F_1 N_r$ . By applying the same arguments to the predator population and transforming the equations, the following system is obtained:

$$\begin{aligned}\frac{dX_1}{dt} &= r_1 X_1 (1 - F_1 - X_1 - v X_2) \\ \frac{dX_2}{dt} &= r_2 X_2 (1 - F_2 - \frac{X_2}{X_1})\end{aligned}$$

where  $X_1 = N_r/K$ ,  $X_2 = N_2/(h N_1)$  and  $v = a h K / r_r$ .

If  $F_2 > 1$ , the whale population collapses and if  $F_1 > 1$ , the whole system collapses. If  $F_1$  and  $F_2$  are less than 1, there exists a unique equilibrium where the presence of whales has the trivial effect of decreasing the fishing yield and the abundance of krill. The production and the abundance of the whale population decrease linearly with fishing effort on krill. When the exploitation of whales increases, the abundance of krill increases, which causes an increase in the growth rate of the remaining whales. Thus, for  $v=1$  (predation of half the pristine biomass of krill), MSY occurs when  $F_2=0.59$ , whereas in the single-species case ( $v=0$ ) the corresponding fishing effort equals 0.5. For the krill population, MSY is obtained at  $F_1=0.5$ . The MSY for krill increases with  $F_2$ , the maximum being reached when  $F_2=1$ , which corresponds to extinction of the whales.

#### Complex food-web models

Michalski and Arditi (1995a; b) proposed a generalisation of predator-prey models that included a Holling type II functional response and a numerical response with interference in the consumption rate (Tables 14.A1 and 14.A2):

$$\frac{dX_i}{dt} = f_i(X) + \frac{A_i \sum_{k \in R(i)} e_{ki} X_k^{r(i)}}{X_i + \sum_{k \in R(i)} B_{ki} X_k^{r(i)}} X_i - \sum_{j \in C(i)} \frac{A_j \sum_{k \in R(j)} e_{kj} X_k^{r(j)}}{X_j + \sum_{k \in R(j)} B_{kj} X_k^{r(j)}} - \mu_i X_i$$

where  $A_p$ ,  $B_{kp}$ ,  $e_{kp}$ ,  $\mu_i$  are constant positive parameters,  $R(i)$  is the set of possible resources for species  $i$ ,  $C(i)$  is the set of consumers of species  $i$  and  $f_i(X)$  is the growth rate of species  $X_i$  in the absence of predators. For the species that are not at the base of the trophic web,  $f_i(X)$  is null.

Two auxiliary variables are used:

$$\begin{aligned}X_i^{r(i)} &= \frac{\beta_{ij} X_j^{c(i)}}{\sum_{k \in C(i)} \beta_{ik} X_k^{c(i)}} X_i \\ X_j^{c(i)} &= \frac{h_{ij} X_i^{r(i)}}{\sum_{k \in R(j)} h_{kj} X_k^{r(i)}} X_j\end{aligned}$$

where  $h_{ij}$  is the relative preference of consumer  $X_j$  for the resource  $X_i$  (among other prey species) and  $\beta_{ij}$  is the efficiency of the relative competition of consumer  $X_j$  (among other consumers) for the resource  $X_i$ .

Using arbitrary values of the parameters, the authors applied the model to a theoretical system consisting of 11 species (Michalski and Arditi, 1995a). At equilibrium, only a few links persisted. By imposing a variation of 60% in the values of  $h_{ij}$  and  $\beta_{ij}$ , the effective structure of the trophic web changed radically. By disturbing the system at equilibrium (for instance by changing the abundance of a species), the same authors (Michalski and Arditi, 1995b) show that their multi-species model leads to systems that are rich in interspecies links when they are far from equilibrium and poor in links when they approach it. A consequence of these results is that the structure of food webs can vary with seasonal variations in species abundance as well as variations in the parameters for competition efficiency and food preferences.

*Schaefer model*

The Schaefer (1954) model is a simple stock assessment model derived from the logistic model, still used in many instances, e.g. tropical and tuna fisheries (Hilborn and Walters, 1992):

$$\frac{1}{B} \frac{dB}{dt} = k - aB - F$$

where  $B$  is the biomass of a given species,  $F$  its rate of fishing mortality, and  $a$  and  $k$  are two positive constants. If  $F=0$ ,  $B_v = k/a$  is the pristine biomass of the species at equilibrium. When the species is exploited, the equilibrium biomass is  $B_e = (k - F)/a$ .

If  $F$  is expressed as the product of  $q$ , the catchability of the species, and  $f$ , the fishing effort, the fishing yield  $Y_e$  at equilibrium is:

$$Y_e = FB_e \Leftrightarrow Y_e = \frac{q}{a}(kf - qf^2)$$

$Y_e$  is a parabolic function of  $f$  and the maximum sustainable yield (MSY) corresponds to  $B_{MSY} = \frac{1}{2}B_v$ .

**Multispecies Schaefer model**

The extension of the Schaefer model to the multispecies case consists of coupling single-species Schaefer equations by including species interaction terms. For  $m$  interacting species (Pope, 1976; Kirkwood, 1982) the model system consists of  $m$  equations of the form:

$$\frac{1}{B_i} \frac{dB_i}{dt} = k_i - \sum_{j=1}^m a_{ij} B_j - q_i f \quad \text{with } i = 1 \dots m$$

If an equilibrium exists at  $B_{1e}, B_{2e} \dots B_{me}$  ( $B_{ie} \geq 0$ ), then:

$$k_i - \sum_{j=1}^m a_{ij} B_{je} - q_i f = 0 \quad i = 1 \dots m$$

This set of equations can be written in the following matrix form:

$$K - A B_e - Q f = 0$$

where  $K$ ,  $B_e$ , and  $Q$  are  $(m,1)$  matrices and  $A$  is an  $(m,m)$  matrix.

At equilibrium, the total yield of the system  $Y_e$  is given by:

$$Y_e = f Q^t B_e = f Q^t A^{-1} K - f^2 Q^t A^{-1} Q$$

#### *Virtual population analysis (VPA)*

Matrices of fish numbers  $N$  and fishing mortality rates  $F$  by age  $a$  for each past year  $t$  are estimated from matrices of natural mortality rates  $M$  and past catch  $C$  by age and time. The dynamics of the age-structured population are described by:

$$\frac{dN_{a,t}}{dt} = -Z_{a,t} N_{a,t}$$

where  $Z_{a,t} = F_{a,t} + M_{a,t}$  is the total mortality rate.

This leads to the following set of difference equations, where  $M_{a,t}$  and  $F_{a,t}$  are assumed constant over the time interval considered (usually one year):

$$N_{a+1,t+1} = N_{a,t} e^{-(F_{a,t} + M_{a,t})}$$

$$C_{a,t} = \frac{N_{a,t} F_{a,t}}{M_{a,t} + F_{a,t}} (1 - e^{-(F_{a,t} + M_{a,t})})$$

The history of the cohort is reconstituted by initializing the system with a recruitment value or the fishing mortality in the terminal age class.

#### **Multi-species virtual population analysis MSVPA (multi-species cohort analysis)**

One of the hypotheses on which VPA is based is that  $M$  is known and generally constant over year and age. However,  $M$  varies with fish age; in particular, young fish are more subject to predation than older and larger ones (Stokes, 1992). The basis for extending cohort analysis to a multispecies case is to better estimate  $M$  by taking into account predation relationships among species. MSVPA was first es-

tablished and applied by Andersen and Ursin (1977), Pope (1979) and Helgason and Gislason (1979) in the North Sea ecosystem. It consists of dividing the natural mortality rate  $M_{i,a}$  of the cohort of age  $a$  of species  $i$  into two components:  $P_{i,a}$  the mortality rate due to predation by the other species included in the model and  $D_{i,a}$  the residual mortality rate due to other natural causes. To estimate the predation mortality rate, the food of each age group is partitioned among the different potential prey. If  $\phi^{ia}$  is the biomass of class  $jb$  (species  $j$ , age class  $b$ ) available for class  $ia$ , the biomass of class  $jb$  consumed over a year by  $ia$  can be expressed as follows:

$$\frac{\phi_{jb}^{ia}}{\phi^{ia}} R_{ia} N_{ia}$$

where  $N_{ia}$  is the abundance of  $ia$  and  $R_{ia}$  its rate of consumption.  $R_{ia}$  is supposed to depend linearly on a power function of the mean individual weight of class  $ia$ . The total biomass of fish of class  $jb$  consumed during a year is then:

$$\sum_{i=1}^s \sum_{a=0}^{A_i} \frac{\phi_{jb}^{ia}}{\phi^{ia}} R_{ia} N_{ia}$$

where  $s$  is the number of species considered in the model, and  $A_i$  is the maximum age reached by species  $i$ . Hence the annual predation mortality rate of class  $jb$  becomes:

$$P_{jb} = \frac{1}{B_{jb}} \sum_{i=1}^s \sum_{a=0}^{A_i} \frac{\phi_{jb}^{ia}}{\phi^{ia}} R_{ia} N_{ia}$$

where  $B_{jb}$  represents the total biomass of class  $jb$ . The available food for a predator  $\phi_{ia}$  is only a fraction of the potential food biomass. A coefficient  $G_{jb}^{ia}$  is introduced, which lies between 0 and 1 and represents the suitability of class  $jb$  as prey for class  $ia$ :

$$\phi_{jb}^{ia} = G_{jb}^{ia} B_{jb}$$

$G_{jb}^{ia}$  is the product of three coefficients that have values between 0 and 1: the size suitability of the prey, the overlap of the classes in time and space and the probability of encounter linked to the respective behaviour of the predator and its potential prey. The coefficients  $G$  represent a substantial synthesis of biological knowledge concerning the different stages of species' life cycles, their spatial distributions, their behaviour, and their feeding habits (Ursin, 1982).

*Ecopath model*

Polovina (1984) and Christensen and Pauly (1992, 1995) developed the Ecopath model to estimate trophic fluxes within an ecosystem. The modelled system is assumed to be stationary, which implies that the gains in biomass equal the losses for each species group. Two mass conservation equations form the basis of Ecopath calculations:

Biomass consumption of group  $i$  is described by:

$$\text{Consumption } (i) = \text{Production } (i) + \text{Non-assimilated food } (i) + \text{Respiration } (i)$$

For each group  $i$ , biomass production is modelled as:

$$\begin{aligned} \text{Production } (i) = & \text{Losses by predation on } (i) + \text{Catches of } (i) \\ & + \text{Export of } (i) \text{ to adjacent systems} + \text{Losses by mortality of } (i). \end{aligned}$$

The terms of this equation can be expressed as follows:

$$\text{Production } (i) = B_i (P/B)_i$$

$$\text{Losses by predation on } (i) = \sum_j (B_j (Q/B)_j DC_{j,i})$$

$$\text{Catches of } (i) = Y_i$$

$$\text{Export of } (i) = EX_i$$

$$\text{Losses by mortality of } (i) = (1-EE_i) B_i (P/B)_i$$

where:

$B_i$  is the biomass of  $i$

$(P/B)_i$  is the production of  $i$  per unit of biomass

$(Q/B)_j$  is the consumption of  $i$  per unit of biomass

$j$  designates a predator group of group  $i$

$DC_{j,i}$  is the mean fraction of  $i$  in the diet of  $j$ , in biomass terms

$EE_i$  is the ecotrophic efficiency of  $i$  (or the fraction of the total production consumed by predation or exported from the system)

$(1-EE_i)$  then represents the fraction of the production of  $i$  that goes to detritus.

The linear equation that describes the biomass flux for each species group  $i$  is:

$$B_i (P/B)_i EE_i - \sum_{j=1}^n (B_j (Q/B)_j DC_{j,i}) - Y_i - EX_i = 0 \quad (1)$$

The resulting ecosystem model consists of  $n$  groups of species and is represented by a system of  $n$  linear equations, which allows the estimation of at least one unknown parameter per species group. Under conditions of stationarity and for a closed system (no immigration or emigration), the ratio  $(P/B)_i$  equals the mortality rate  $Z_i$ , which is often a more accessible parameter (Pauly and Moreau, 1997).

Ecopath models represent the trophic structure of an ecosystem at equilibrium, as shown in Figure A2, which results from application of Ecopath to the southern Benguela ecosystem (Jarre-Teichmann et al., 1998).

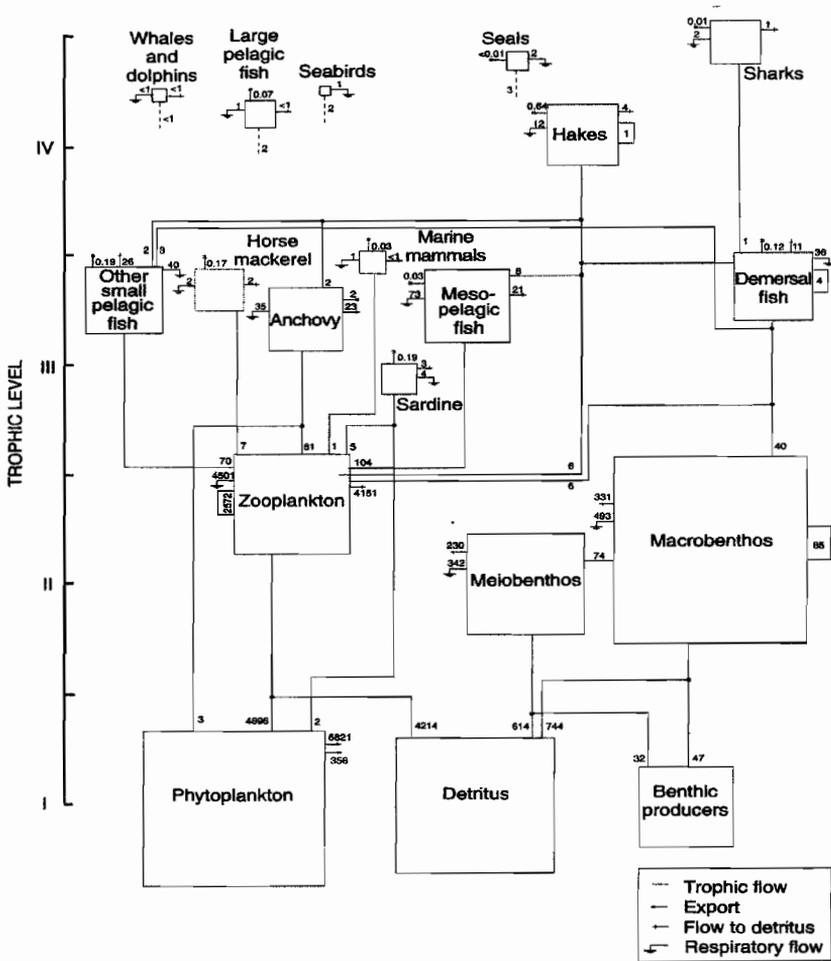


Figure 14.A2 Diagram of trophic fluxes from an Ecopath model of the southern Benguela ecosystem, 1980–1989. The surface areas of the boxes are proportional to the logarithm of their biomass. Compartments are arranged along the vertical axis in terms of their trophic levels. Fluxes are expressed in tons of wet matter per km<sup>2</sup> and per year. Trophic fluxes smaller than 0.1% of the total consumption in the system are not represented. Output fluxes are located on the upper side of the compartments and input fluxes on the lower side (from Jarre-Teichmann et al., 1998)

Trophic levels calculated in Ecopath are fractional. Detritus and primary producers (phytoplankton and benthic producers) have, by definition, a trophic level equal to 1. For all other groups, the trophic level  $TL_i$  is a function of their prey and the proportions of these in their diets. For a group  $i$ :

$$TL_i = 1 + \sum_{j=1}^n DC_{i,j} TL_j$$

where  $DC_{ij}$  is the proportion of prey  $j$  in the diet of  $i$ ,  $n$  is the number of groups in the system.

Other indices, calculated in the Ecopath software, characterize the trophic organisation of the ecosystem. Aggregation of fractional trophic levels into discrete trophic levels (*sensu* Lindeman, 1942) allows representation of the system as a trophic pyramid, and trophic efficiencies represent the proportion of material transferred from one discrete trophic level to the next.

Another index quantifies the mixed trophic impacts, i.e. the direct and indirect interactions between trophic groups. Inspired by Ulanowicz and Puccia (1990), the method successively calculates reciprocal impacts of a predator and its prey. A positive impact ( $k_{ij}$ ) that a prey  $j$  exerts on its predator  $i$  is expressed as the proportion contributed by the prey to the diet of the predator:

$$k_{ij} = DC_{ij}$$

A negative impact ( $l_{ij}$ ) that a predator  $i$  exerts on its prey  $j$  is expressed as the fraction that the predator  $i$  contributes to the total predation on the prey:

$$l_{ij} = \frac{B_i(Q/B)_i DC_{i,j}}{\sum_{k=1}^n B_k(Q/B)_k DC_{k,j}}$$

The net impact ( $q_{ij}$ ) of prey  $j$  on predator  $i$  is then defined as the difference between the positive and the negative impacts:

$$q_{ij} = k_{ij} - l_{ij}$$

#### *Ecosim model*

Ecosim was developed by Walters et al. (1997), and is the dynamic version of Ecopath. It re-expresses the linear equilibrium equations of Ecopath as differential equations. The same basic equation is used, but export of biomass out of the system is assumed null:

Production ( $i$ ) = Catches on ( $i$ ) + Losses by mortality of ( $i$ ) + Losses by predation on ( $i$ )

By including fishing and natural mortality rates (respectively  $F_i$  and  $M_o$ ), equation (1) becomes:

$$0 = B_i(P/B)_i - F_i B_i - M_o B_i - \sum_{j=1}^n Q_{ij} \quad (2)$$

where  $B_i$  is the biomass of  $i$ ,  $B_i(P/B)_i$  is the production in biomass of  $i$ , and  $Q_{ij}$  is the biomass of  $i$  consumed by  $j$ .

Equation (2) is transformed into a differential equation:

$$\frac{dB_i(t)}{dt} = f(B_i(t)) - F_i(t)B_i(t) - M_0B_i(t) - \sum_{j=1}^n c_{ij}(B_i(t), B_j(t)) \tag{3}$$

where two new terms are introduced:  $f(B_i(t))$ , which is a function representing biomass production in the absence of predation and  $c_{ij}(B_i(t), B_j(t))$ , which predicts the biomass of prey  $i$  consumed by predator group  $j$  at time  $t$ .

If  $i$  is not a primary producer,  $f(B_i(t))$  is assumed to be proportional to the quantity of ingested food:

$$f(B_i(t)) = g_i \sum_{j=1}^n c_{ji}(B_i(t), B_j(t)) \tag{4}$$

where  $g_i$  represents the efficiency of conversion of the ingested food. The multiplicative parameter  $g_i$  is assumed to account for the losses by respiration and non-assimilation that were introduced in the equilibrium equation (1) of Ecopath.

If  $i$  is a primary producer, biomass production is calculated using the following saturation function:

$$f(B_i(t)) = \frac{r_i B_i(t)}{1 + h_i B_i(t)}$$

where  $r_i/h_i$  is the maximum primary production of  $i$  when  $B_i$  is high, and by analogy with Ecopath,  $r_i$  is a maximum  $(P/B)_i = Z_i$  (or  $f(B_i)/B_i$ ) when  $B_i$  approaches 0. Parameter  $h_i$  can also be approximated using values of Ecopath parameters by considering that the system is close to equilibrium. Thus, if  $f(B_i) \approx B_i(P/B)_i$  then  $h_i \approx [r_i/(P/B)_i - 1]/B_i$ .

For the interaction functions  $c_{ij}(B_i(t), B_j(t))$ , Walters *et al.* (1997) use the expression proposed by Lotka and Volterra, namely:

$$c_{ij}(B_i(t), B_j(t)) = a_{ij} B_i(t) B_j(t)$$

Parameter  $a_{ij}$  is estimated from Ecopath, assuming that the system is close to equilibrium:

$$a_{ij} \approx \frac{B_j(Q/B)_j DC_{j,i}}{B_i B_j}$$

This expression is modified to account for the possible existence of prey biomass that is not accessible to the predator. If each prey group  $i$  has an unavailable portion  $V_{ij}$  of  $B_i$  for each predator  $j$ , the dynamic of the available biomass is described by the following equation:

$$\frac{dV_{ij}(t)}{dt} = \underbrace{v_{ij}(B_i(t) - V_{ij}(t))}_{\text{Input from the unavailable compartment}} - \underbrace{v_{ij}V_{ij}(t)}_{\text{Loss to unavailable compartment}} - \underbrace{a_{ij}V_{ij}(t)B_j(t)}_{\text{Loss by predation}}$$

where  $v_i$  is the rate of biomass exchange between the accessible and inaccessible parts of  $i$  to predator  $j$ .

Assuming that the exchange dynamic between  $V$  and  $B$  operates at a small scale compared to changes between  $B_i$  and  $B_j$ , the following expression is obtained by making the previous derivative equal zero:

$$V_{ij}(t) = \frac{v_{ij}B_i(t)}{2v_{ij} + a_{ij}B_j(t)}$$

and

$$c_{ij}(B_i(t), B_j(t)) = \frac{a_{ij}v_{ij}B_i(t)B_j(t)}{2v_{ij} + a_{ij}B_j(t)}$$

When predator biomass  $B_j$  is small,  $V_{ij} \rightarrow B_i/2$  and  $c_{ij}(B_i, B_j) \rightarrow (a_{ij}/2)B_iB_j$ , i.e. towards the initial expression of Lotka-Volterra. When  $B_j$  is large ( $a_{ij}B_j \gg 2v_{ij}$ ) and  $c_{ij}(B_i, B_j) \rightarrow v_{ij}B_i$ . Parameter  $v_{ij}$  represents the maximum mortality rate exerted by  $j$  on  $i$ , and can be estimated by Ecopath.

In their modelling work, Walters et al. (1997) succeeded in establishing links between the parameters estimated by Ecopath and those included in the differential equations of Ecosim. The use of existing data without requiring additional measurements and experiments is one of the advantages of Ecopath and Ecosim models. However, this is also one of the weaknesses of Ecosim, which is evident at two different levels. First, equation (3) is not applicable over a large range of biomass since the parameters are estimated from the Ecopath model, which at equilibrium. Second, the fixed link with Ecopath is likely to have constrained the choice of functions for growth of the primary producers, and functional responses of the predators. To understand in which category of models Ecosim belongs, an analogy with the predator-prey models described above is instructive. This comparison is necessary because the choice of functional responses is crucial and strongly determines the output dynamics. In the case of an ecosystem without exploitation, the main equation of Ecosim, which describes the biomass dynamics of group  $i$ , is:

$$\frac{dB_i(t)}{dt} = f(B_i(t)) - M_0B_i(t) - \sum_{j=1}^n B_j(t) \frac{a_{ij}v_{ij}B_i(t)}{2v_{ij} + a_{ij}B_j(t)} \quad (5)$$

Comparison with the general formulation of a predator-prey system (which was presented in a previous section of the Appendix) shows that the predator func-

tional response  $F$  used in Ecosim corresponds to the last term of equation (5), which is of the form:

$$F(B_i(t), B_j(t)) = \frac{aB_i(t)}{b + cB_j(t)} \tag{12}$$

where  $a, b, c$  are three positive constants,  $B_i$  the biomass of the prey and  $B_j$  the biomass of the predator.

This formulation does not correspond to any of the functional responses that are commonly used in general ecology (see Table A1). It takes into account interference between predators ( $B_j$  in denominator) and the existence of unavailable biomass, this last point being justified by the authors. What is maybe less justified is the choice of a Lotka-Volterra type response (when predator biomass  $B_j$  is low, the functional response tends towards the Lotka-Volterra expression), which is currently considered to be unrealistic (Murray, 1989). Other kinds of functional response expressions (e.g. "laissez-faire", ratio-dependent or interference between predators) might give different results from Ecosim.

Still by analogy, the term  $f(B_j(t)) - M_0B_j(t)$  of equation (5) corresponds, in the case where  $j$  is a predator, to the product of a predator group  $j$ 's biomass and its numerical response, and in the case of primary producers, the term corresponds to their intrinsic growth rate.

According to equation (4), the numerical response of predator  $j$  corresponds to  $(g_jF(B_p, B_j) - M_0)$ , which takes into account interference between predators in determining the growth rate. For primary producers, the function describing the population growth rate in the absence of predators corresponds to the following expression:

$$\frac{r_i B_i}{1 + h_i B_i} - M_0 B_i = \frac{(r_i - M_0) B_i - M_0 h_i B_i^2}{1 + h_i B_i}$$

Growth rate in biomass is definitely considered to be density -dependent because, for a given group  $i$ , it reaches a maximum for  $B_i^* = (r_i - M_0) / M_0 h_i$ , and decreases beyond  $B_i^*$ . But the choice and the behaviour induced by such a saturation function should be discussed in relation to the Verhulst logistic growth function, which is the most common formulation.

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