SUSTAINABLE EXPLOITATION OF SMALL PELAGIC FISH STOCKS CHALLENGED BY ENVIRONMENTAL AND ECOSYSTEM CHANGES: A REVIEW

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ABSTRACT

Small pelagic fish contribute up to 50% of the total landing of marine species. They are most abundant in upwelling areas and contribute to food security. Exploited stocks of these species are prone to large interannual and interdecadal variation of abundance as well as to collapse. We discuss why small pelagic fish and fisheries are so "special" with regard to their biology, ecology, and behavior. Two adjectives can sum up the characteristics of pelagic species: variability and instability. Analyses of the relationships between small pelagic fish and their physical environment at different time-scales illustrate the complexity of the interplay between exploitation and environmental impacts. How small pelagic fish species are positioned and related within the trophic web suggests that these species play a central role in the functioning and dynamics of upwelling ecosystems. Finally, we discuss the sustainable exploitation of small pelagic fisheries through appropriate management, focusing on the resilience to exploitation, a comparison of different management options and regulatory mechanisms. We recommend that statistical, socio-economical, and political merits of a proposed two-level (short- and long-term) management strategy be undertaken.

Despite constant progress in understanding the complex processes involved in the variability of pelagic stock abundance, especially at short and medium time scales, our ability to predict abundance and catches is limited, which in turn limits our capacity to properly manage the fisheries and ensure sustainable exploitation. Substantial progress can be expected from an integrated modeling approach of spatialized models coupling hydrodynamics, biogeochemical, and ecological processes.

Although there are many definitions of "small pelagic fish," this expression most commonly refers to shoaling epipelagic fish characterized by high horizontal and vertical mobility in coastal areas and which, as adults, are usually 10–30 cm in length. The upper limit is often the most debated, since some authors use the term "medium-sized pelagic fish" to designate larger fish ranging from about 20–60 cm (Bas et al., 1995). This distinction between the two size groups simultaneously allows distinctions to be made with regard to the position of the species within the food web: the conventional "small pelagic fish" includes typical forage species like sardine and anchovy preying on phytoplankton and/or micro-meso- zooplankton, while the group of "medium-sized pelagic fish" includes mostly species from intermediate trophic levels like horse-mackerel, mackerels, and coastal tunas. When adult, the latter species prey mainly on macro-zooplankton, ichthyoplankton, and small fish or mollusks. In this work, we will focus mainly on the conventional "small pelagic fish," but will also often refer to, or contrast findings with, medium-sized pelagic fish. When referring to both small and medium-sized pelagic fish, we will use the terms "pelagic fish" or "coastal pelagic fish" to separate them from the large oceanic tunas, although not all medium-sized pelagic fish remain on the continental shelf for the duration of their whole life cycle.
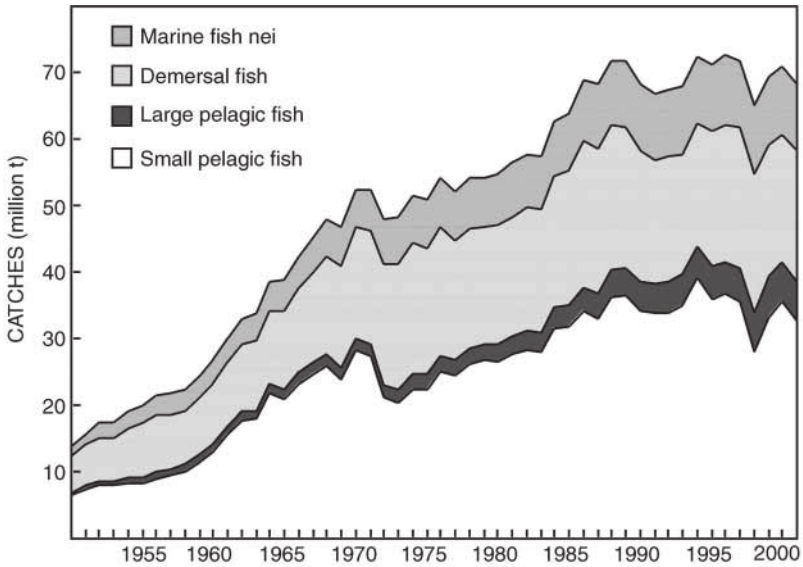
Figure 1. World pelagic and demersal marine fish catch from 1950–1999 (data source FAO, Fish-Stat, www.fao.org).

Small pelagic fish are abundant in all oceans and seas except the Antarctic, where large euphausids (a schooling species of zooplankton) constituting the krill occupy a similar trophic level. According to FAO data (FAO, 2002; Fig. 1), small pelagic fish contributed up to 39 million t or 50% of the total landing of marine species. The ratio of pelagic/demersal catches varied from 1.0–2.1 over the last 51 yrs, with a positive trend at least partly related to overexploitation of the higher trophic levels (Pauly et al., 1998). Although these official landing statistics are likely to be inaccurate for some countries (Watson and Pauly, 2001), the relative values given here provide consistent trends during the last decades.

Despite their usually low commercial value, small pelagic fish provide a substantial source of income for many developing countries due to their abundance, especially in the four major upwelling regions located on the eastern border of the Pacific and Atlantic Oceans. In these regions, a few species of small pelagic fish represent a large amount of the total fish biomass. This is typically the case for Peru (Peruvian anchoveta and sardine) and Chile (anchoveta, sardine and also horse-mackerel, a medium-sized pelagic species) in the Humboldt Current ecosystem, Mauritania and Senegal (sardine and sardinella) in the Canary Current ecosystem, Namibia and South Africa (sardine, anchovy and horse-mackerel) in the Benguela Current ecosystem and, to a lesser extent, Mexico (sardine and anchovy) in the California Current ecosystem. In this work we will often refer to these productive areas and others, such as the Kurushio-Oyashio Extension (Japanese sardine), the North Sea and the Norwegian Sea (the latter two being inhabited by several herring stocks) or the Gulf of Guinea (sardinellas). In some of these regions, coastal pelagic fish contribute substantially to food security, either directly (human consumption of fresh, smoked, or frozen fish) or indirectly (income for a component of society).

Many examples of small pelagic fishery collapses occurred during the second half of the 20th century (Figs. 2A,B) and, in most cases, these collapses were clearly associated with an abrupt decline in the corresponding fish stock biomass with delayed re-
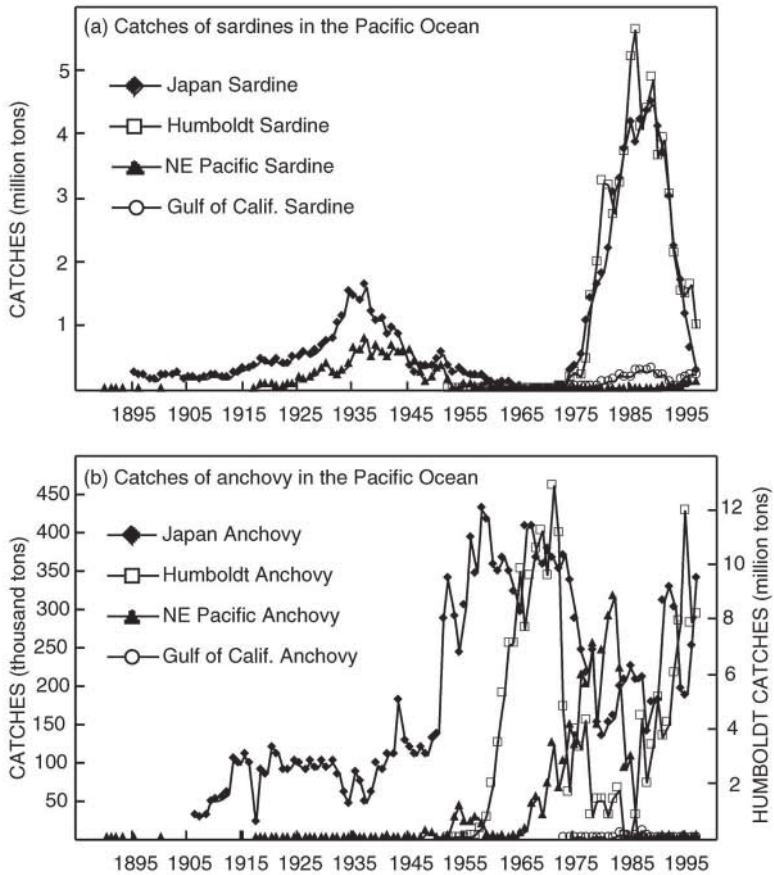
Figure 2. Catches of (A) sardine and (B) anchovy in the Pacific Ocean [source: Scientific Committee on Oceanic Researh Working Group (SCOR WP) 101].

covery, if any (Troadec et al., 1980; Beverton, 1990; Hutchings, 2000). Whether these biomass variations were mainly driven by natural variability (due to environmental changes and/or species interactions), exploitation, or both has been, and is still, debated at length (Lluch-Belda et al., 1989; 1992a; Schwartzlose et al., 1999). In this work we will try to shed more light on this issue and propose management strategies aimed at minimizing the risk of stock and fishery collapse. This introduction is followed by four sections and a final section of general conclusions and recommendations. In the first section we explain why small pelagic fish and fisheries are "unique" in terms of their biology, ecology, behavior, and commercial aspects. The second section gives details on the relationships between small pelagic fish and their physical environment at different time-scales. The third section indicates how small pelagic fish are related within the trophic web and presents some modeling approaches in this regard. Finally, the fourth section deals with the sustainable exploitation of small pelagic fisheries through appropriate management, focusing on the resilience to exploitation, different management options, and regulatory mechanisms.

Why Pelagic Fish and Fisheries Are "Unique"

Habitat

By definition, pelagic fish live in the pelagic domain, that is, they move freely in the water-column where they spend most of their time. Most of the small pelagic fish species are epipelagic, that is, they live in the uppermost layer of the ocean, usually at depths of 0–200 m, although the limit of the deeper boundary varies according to the species and region. For instance, *Sardinella aurita* Valenciennes in Cuvier and Valenciennes, 1847 off the Gulf of Guinea migrate in deeper waters (>200 m) out of the upwelling season (Longhurst and Pauly, 1987). Many medium-sized pelagic fish are found in a wider range of depths, typically from the surface to 500 m. The view that pelagic fish are remote from the sea floor is largely incorrect. Firstly, a minority of pelagic species, such as herrings and capelins, are demersal spawners, laying adhesive eggs on the bottom (Blaxter and Hunter, 1982). Secondly, many pelagic species, especially medium-sized ones, are frequently found close to the bottom during daytime and are therefore vulnerable to semi-pelagic fishing gear and even to bottom trawls. Some of these species (e.g., horse-mackerel and mackerel) feed on or near the bottom, but for others, like the gilt sardine *S. aurita,* only the sediment found in their stomachs testifies to their bottom activity and suggests that they might make use of the bacterial film (Nieland, 1982). Therefore, the reason for large "pole shaped schools" (Petitgas and Levenez, 1996) several tens of meters high and of which only the base is in contact with the bottom for prolonged periods of time remains unclear.

Morphology

Small pelagic fish are characterized by a streamlined body shape (fusiform and laterally compressed) and forked caudal fin. These characteristics make them good and fast swimmers, despite their small size. Another typical phenotypic trait of coastal pelagic fish is their discrete coloration, ranging from dark gray to silver. The flanks are usually highly reflective and the dorsal surface dark in order to render the fish inconspicuous to predators: light is reflected in such a way that it matches the background light against which the fish is viewed (Blaxter and Hunter, 1982). Pelagic fish are also capable of camouflage by adjusting the state of the melanophores on their dorsal surface.

The body of most small pelagic fish species is fragile, comprised of soft tissue and a thin skin. Physical protection is provided by small scales that cover nearly the whole body in most species, and by the mucus produced by their skin. Scales and mucus are easily lost by manipulation or contact with fishing gears, leaving the thin skin exposed to wound infection by bacteria, fungal diseases, or external parasites. Small pelagic species are extremely frail, subjected to unexpectedly large mortality occurring during the catch process: most of the small pelagic fish that come into contact with fishing gear but escape it, or make close contact with other fish during fishing, are likely to die (Misund and Beltestad, 1995). Furthermore, when excess catches occur (exceeded quota or saturation of the fishing unit by capturing too much to be handled or processed on board), or when non target-species or sizes are caught, fish are dumped, and most, if not all, die. These additional sources of mortality are usually not reported by fishers and are difficult to estimate.

Another consequence of the fragility of small pelagic fish, aggravated by their small size, is the difficulty in tagging them. Few small pelagic species survive tagging, especially when external tags are used (Blaxter and Hunter, 1982). Internal magnetic tags are better adapted but still result in high mortality, or tag extrusion (Winters, 1977), and require sophisticated means of detection (Parker, 1972; Hoff et al., 1988). As a result of these difficulties in tagging small pelagic fish, their stock structure is usually poorly known. Nonetheless, recent advances in this field have been made using genetic markers and parasite occurrence (see last section on "Sustainable Management of Small Pelagic Fisheries").

Biology

Most pelagic fish species are pelagic spawners and fertilization is external. Fertilized eggs become embryos after a few days and hatched larvae have a typical pelagic phase of a few weeks, even in the case of bottom spawners. Because most of the eggs of pelagic fish are small, the yolk sac is small and quickly absorbed. The yolk sac phase is therefore short and the larvae have to feed quickly to avoid death by starvation. This pelagic stage of eggs and larvae with little mobility is a common feature of the life history of pelagic fish, and is a stage shared with most marine species. As we will see in the next sections, this stage has enormous implications in terms of colonization by species and recruitment success (i.e., young fish entering the actual fishery).

The fecundity of pelagic fish species is high, both in absolute (Fig. 3) and relative values. Typically, a female lays 50,000 eggs during a spawning season, which in temperate areas, varies in duration from a few weeks to several months when spawning does not occur all year through, as is often the case in sub-tropical and tropical areas. There is no parental care and cannibalism of eggs and larvae is often severe (Alheit, 1987; Valdés Seinfeld et al., 1987; Valdés Seinfeld, 1991).

On average, only one or two of the many eggs spawned by each female during the spawning season have to survive to ensure the equilibrium of the population. This means that the normal fate of an egg or larvae, prior to metamorphosis from the larval stage, is death. Mortality rate decreases dramatically with age (Smith, 1985) and therefore the motto for teleost larvae is "grow, or die" (Iles, 1980). Because pe-
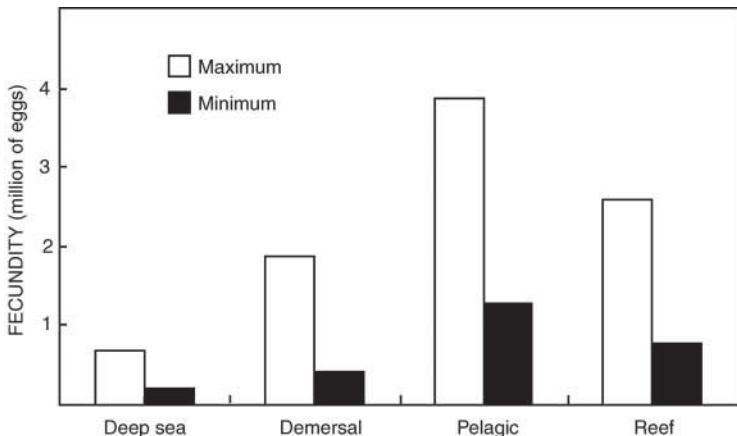
Figure 3. Absolute fecundity by category of fish [number of species = 305 (min) and 317 (max) respectively); source: FishBase, Froese and Pauly, (2000)].

lagic eggs and larvae are very vulnerable to predation and have strict requirements in terms of feeding and environmental conditions, they are faced with a continuous series of "survival windows" with low probability of success (Bakun, 1996). Genetic studies indicate that only a few individuals that spawned "at the right place and at the right time" contribute to the reproductive success. Due to the large interannual variability of environmental conditions (transport, temperature, abundance of prey, etc.) the "right place and right time" are likely to vary from year to year. This supports the idea of the evolutionary selection of an opportunistic reproductive strategy for a species, consisting of high fecundity associated with an extended spawning period over a wide area. This strategy allows a continual "testing" by these species of favorable environmental conditions and is likely to explain population outbursts observed from time to time. Nonetheless, simulation studies backed by some genetic studies suggest that an opposite strategy of natal homing may also be viable (Le Page and Cury, 1997; see also section "Pelagic Fish within the Ecosystem" for more details).

Another typical trait of pelagic fish is their short life span, although in that respect we have to distinguish between two categories. In anchovy-like species, the average life span typically ranges from 2–5 yrs, first sexual maturity occurs during the first year and only one or two cohorts significantly contribute to the fishery. In sardine-like species, the life span is 5–8 yrs and normally several cohorts above 2–3 yrs contribute to the fishery, although these numbers might be substantially reduced in stocks where exploitation decreases the average life span. Because the coefficient of variation of recruitment is inversely proportional to the longevity (Longhurst, 2002), this reduction in the number of year classes of exploited stock must be of serious concern, as much for long-lived species as well as for those that are shorter-lived.

In pelagic fish, growth rate tends to be inversely related to fish length (Kawasaki, 1983). Despite their small size, small pelagic fish grow relatively fast, with values of the coefficient k of the von Bertalanffy equation ranging from 0.2–0.8. We already mentioned (introduction) that small pelagic fish prey on phytoplankton and/or micro- and meso- zooplankton. Many of these species can switch from particulate to filter feeding (James, 1988; van der Lingen, 1994). However, pelagic fish most often prefer particular prey species of certain sizes: in the southern Benguela, anchovy *Engraulis capensis* Gilchrist, 1913 feed preferentially on large copepods (Richardson et al., 1998), whereas sardine *Sardinops sagax* (Jenyns, 1842) derive most of their energy from small calanoid copepods, anchovy eggs, crustacean eggs, and nauplii (van der Lingen, 1999, 2002). Medium-sized pelagic fish are usually particulate feeders, preying mainly on macro-zooplankton, ichthyoplankton, and small fish or mollusks.

Behavior

A major characteristic of pelagic fish is their gregarious spatial behavior. Pelagic fish are rarely observed alone and usually display 2–4 levels of aggregation during the day, suggesting a fractal structure: (1) core concentrations or nucleus of fish densely packed within a school or shoal; (2) school or shoal; (3) clusters of schools, also termed aggregations; and sometimes (4) large concentrations or sub-stocks (Fig. 4). The characteristics of these entities vary largely in time, space, and according to the species. Typical average values are given in Table 1. The spatial dynamics linking nucleus, school, cluster, concentrations, and the whole stock are still poorly understood and the few studies on the topic do not suggest a general pattern shared by different species or even by the same species within the ecosystem (Barange et al., 1999;
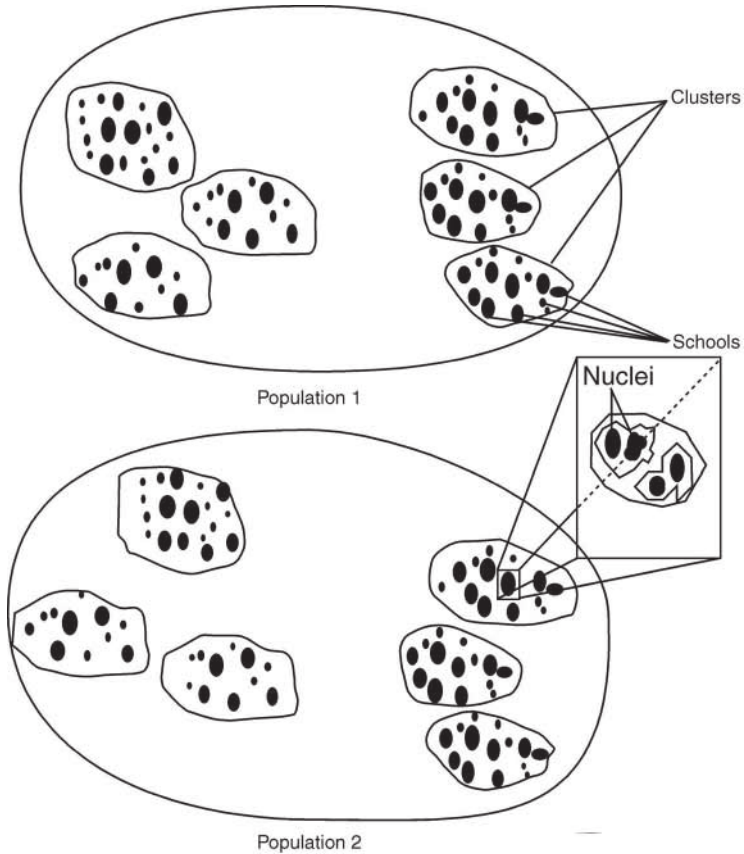
Figure 4. Simplified diagram showing the "fractal" distribution of pelagic fish species (adapted from Fréon and Misund, 1999).

Fréon and Misund, 1999; Mackinson et al., 1999; Bahri and Fréon, 2000; Petitgas et al., 2001).

Fish school biomass ranges from a few 100 kgs to 100s of t. The packing density within a school usually varies from 1–100 fish m^{-3} according to the species, fish size (density inversely correlated to fish length), presence of predators, food density, and the activity of fish at the time: feeding, escaping predators, spawning, etc. (Pitcher and Parrish, 1993; Fréon and Misund, 1999). Fish in a school are usually polarized and relatively evenly distributed, at least at the scale of a few meters. Within large schools, the different core units might behave relatively independently from one another (Fréon et al., 1993a).

The function of schooling has been long debated and nowadays it is accepted that this behavior has evolved in response to different needs and has a multi-purpose function related to: survival of predator attacks (effective evasion maneuvers, confusing effect, increased global vigilance, dilution effect, etc.), effectiveness of feeding, hydrodynamic advantages, migration, reproduction, and learning (Pitcher and Parrish, 1993; Fréon and Misund, 1999). At night, dense schools of fish often disperse in looser shoals or dense layers, although many species are still found in dense schools during the night because they detect one another by means of the low light intensity

Table 1. Typical characteristics (orders of magnitude) of the different levels of aggregation of pelagic species.

Object	Number of fish	Total weight	Global size
Fish	1	100 g	20 cm
Nucleus	10^4	1 t	$10 \times 5 \times 3$ m
School	10^5	10 t	$20 \times 10 \times 5$ m
Cluster	10^8	10^4 t	10×10 n.mi
Sub-stock	10^{10}	10^6 t	100×100 n.mi

(moon light, bioluminescence) or their lateral line (Blaxter and Hunter, 1982; Gray and Denton, 1991; Marchal, 1993; Fréon et al., 1996; Fréon and Misund, 1999).

Several species of similar size and body shape quite often gather in a single school, although it seems that different species do not always intermingle within the same school but rather occupy different locations (Parrish, 1989; Fréon and Misund, 1999). The evolutionary advantage of such assemblages of fish species is still debated among the scientific community. Because it is now accepted that a minimum school size is necessary for fish to benefit from the many advantages of schooling and that many of these benefits increase with increasing school size (reviews in Wolf, 1985; Fréon and Misund, 1999; Krause and Ruxton, 2002), the first explanation for a mixed school is that individuals join it to gain access to the benefits of being in a larger group.

Two recent and complementary hypotheses suggest that the advantages of mixed schools may go beyond this simple share of increased benefits. The first one, called the "meeting point hypothesis," states that a less abundant species (at least at the local geographical scale) might make use of the school of a more abundant species to re-aggregate. Joining the school of another species will increase the encounter rate between isolated individuals or small schools and other schools, in order to constitute bigger schools that are more conducive to the survival of the species (Fréon and Dagorn, 2000). Therefore, this first hypothesis suggests that mixed schools represent only a provisional aggregation pattern and act as a meeting point for a given species to find more conspecifics and finally form a bigger monospecific school when some critical biomass is reached or exceeded. The second recent hypothesis is the "school-trap hypothesis," which states that a fish species driven to school together with a more abundant species must effectively subordinate its specific needs and preferences to the "corporate volition" of the school (Bakun and Cury, 1999). The school-trap hypothesis can lead to the theory that adaptive changes in the population dynamics ("school-mix feedback"; Bakun, 2001) occur much faster than those related to genetic evolutionary processes (Bakun, 2005; this issue).

The reason for the upper levels of aggregation (cluster and concentrations) is not always known and is not necessarily unique: habitat selection, reproduction, functional assemblage, etc. In many cases, these upper levels of aggregation do not concern a single species of pelagic fish, even in the cases where no mixed schools are observed and the spatial distribution of schools belonging to different species might display some structure (Massé et al., 1996).

Finally, another important behavioral trait of fish, shared at different degrees by all fish species, is their faculty to learn from previous experiences. Even after only a single occurrence, if stressful enough, a previous experience may become a "one trial learning." The consequence of this behavior to stock assessment and management has been largely underestimated. It will obviously take a long time for an evolution-

ary process governed by fishing pressure to select against schooling, a strong, complex, and effective selected behavior occurring early in the ontogeny of pelagic fish. Nonetheless, learning how to avoid or escape from fishing gears as a group might, to a large extent, counter the negative effect of schooling on the vulnerability to fishing gears (review in Fréon and Misund, 1999) and besides, there can be interplay between evolution and learning (Anderson, 1995).

Ecology

Small pelagic species often constitute the bulk of the fish biomass in marine ecosystems, especially in very productive ones like eastern boundary currents. This abundance contrasts with the low number of dominant small pelagic species. According to FAO (1997), 186 fish species are exploited by world pelagic fisheries, but 50% of total pelagic landings are represented by only seven abundant species (anchoveta, Atlantic herring, Japanese pilchard, South American pilchard, chub mackerel, capelin, and Chilean jack mackerel). As an example, the number of species of small pelagic fish inhabiting the whole South African marine domain is smaller than any other taxa or group of species (Gibbons et al., 1999), whereas pelagic species are estimated to be the most abundant group in the southern Benguela, followed by mesopelagic fish, hakes, and other demersal species (Shannon, 2001). Because these few small pelagic species occupy a mid-trophic position in the food web and seem to play an important role in the functioning of the ecosystem, the corresponding ecosystems have been termed "wasp-waist" by Rice (1995). In the section "Pelagic Fish within the Ecosystem" we will see how different species in an ecosystem interact with or depend on others by means of the conventional "bottom-up" or "top-down" versus "wasp-waist" types of control.

The reliance of commercial pelagic fish species on regions of high productivity constrains their distribution and thus characterizes the habitat with which the species are associated, that is, usually coastal areas. The main processes responsible for large-scale high productivity are upwelling, and, to a smaller extent, tidal mixing and river discharges (FAO, 1995a; Bakun, 1996). Both processes bring into the euphotic zone nutrients that initiate primary production by photosynthesis (phytoplankton), upon which the rest of the trophic web is built. These enrichment processes occur mainly on the continental shelf, but can also extend beyond it when the processes are intense and/or when the shelf is narrow, as is the case off Chile (Yáñez et al., 1996). Within the spatial distribution of a pelagic fish stock, higher fish densities are observed in areas where food concentration is greater, such as in frontal or convergence zones (see next section).

Seasonal migrations of small and medium-sized pelagic fish are often observed and, according to the accessibility of the fish, the corresponding fisheries are either seasonal or follow the fish in their migration. The migration distance can vary from a few 100 km to more than 1000 and the distance and timing may vary according to fish age (reviews in Harden Jones, 1968; McCleave et al., 1984; Dingle, 1996; Fréon and Misund, 1999). Migrations are evolutionary adaptations in response to seasonal changes in food abundance or to the need for spawning in a given area where hydrological conditions are favorable for survival. Usually these migrations occur along the coast, but some species, like the Atlanto-Scandinavian herring, undertake open sea migration (Bakken, 1983). The spatio-temporal pattern of migrations can vary on an interdecadal scale for reasons not always clearly understood, such as changes
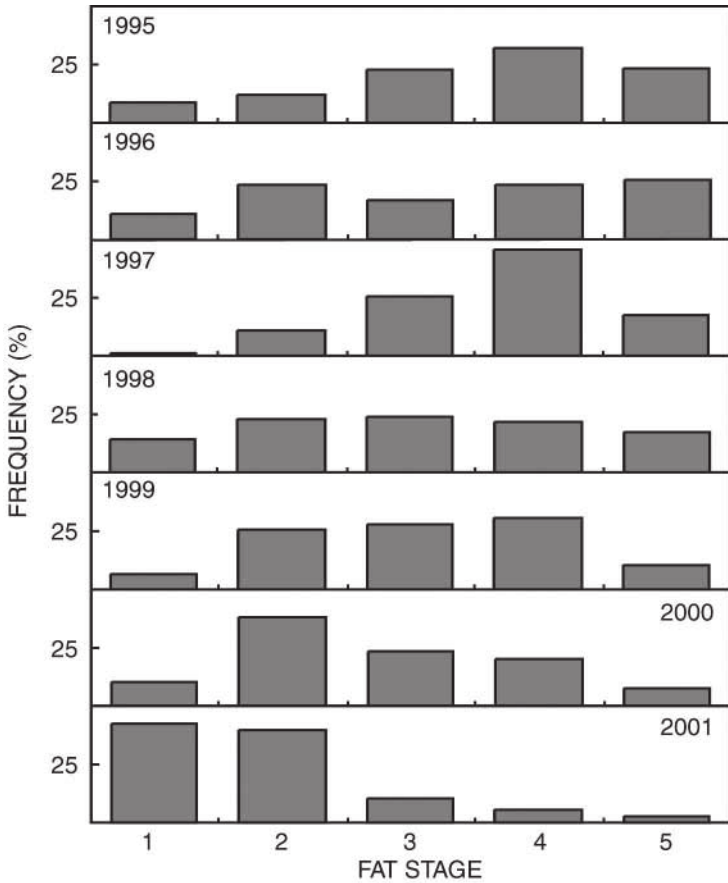
Figure 5. Change in the fat stages (amount of mesenteric fat; 1 = min; 5 = max) of the anchovy *Engraulis encrasicolus* (synonymy *E. capensis)* of South Africa (redrawn from van der Lingen and Hutchings, in press.). Note that year 2000 and 2001 were years of substantial population level, as shown in Figure 6.

in the fish stock abundance, overexploitation of some fragment of the population, or changes in environmental conditions (McCleave et al., 1984; Fréon and Misund, 1999).

The whole distribution area of a pelagic fish stock can vary from year to year, not only with changes in productivity but also with species abundance. In addition, this often involves the "chicken and egg" situation (see next section). When their abundance decreases, some small pelagic fish species, like sardine or herring, might decrease their area of distribution accordingly, resulting in a smaller than expected change in overall density within the reduced range. Furthermore, these species may continue to form schools of the same magnitude, although there will be fewer such schools. Because the ability of fishers to locate these schools remains high and is aided by technology, catches and catch rates are maintained despite reduced abundance. As a result, the catchability of the stock increases and catch rates do not decrease dramatically when the stock declines, until the reduced abundance of schools begins to impact fishing success or the stock even collapses (Fox, 1974; MacCall, 1976; Ultang, 1976; Mackinson et al., 1997; Fréon and Misund, 1999). [In the fishery

biology literature, catchability and availability are used either synonymously or a distinction is made between catchability, as describing small scale interactions between the fish and the fishing unit, and availability, meaning the large scale match between fish distribution and the fleet range. Following common practice, we will use catchability in the broad sense, which covers both spatial scales]. Consequently, there is no warning to the fishing sector that could encourage a reduction in the rate of exploitation at a time when a reduction in exploitation is most required to ensure that the fishery is sustained. For other species, like anchovy, a change in abundance has little effect on its area of distribution but rather results in a dramatic change in the overall fish density (Barange et al., 1999).

Population Dynamics and Stock Assessment

Because the vast majority of marine species have a very high fecundity, density dependent processes are expected to regulate their abundance to a certain degree. The observed large variability in condition factor, fecundity, growth, etc. reinforces this idea of regulation of the population (Fig. 5). Not surprisingly, the cornerstone of population dynamics is the stock-recruitment relationship proposed in the middle of the 20th century by the "fathers" of this discipline (Ricker, 1954; Beverton and Holt, 1957). In these theoretical relationships, recruitment first increases with increasing biomass of the parental stock (left slope of the curve) and then decreases or levels off (right side of the curve). The left slope of the curve is relatively consistent among stocks (Myers et al., 1999). Nonetheless, after half a century of intensive studies on population dynamics of pelagic fish, few examples clearly demonstrate the reality of the right part of these functions for pelagic fish (Zheng, 1996), which in most cases poorly fits the observed data, although some consistency can be observed when applying meta-analysis on a large dataset regrouping pelagic and demersal species (Myers and Barrowman, 1996). The poor fit of such relationships demonstrates the difficulty of producing precise predictions of recruitment and future catches, as well as the need for management strategies that are robust with respect to this uncertainty. These difficulties in understanding the population dynamics of pelagic fish encouraged the development of direct methods of assessment like acoustic, ichthyoplankton, or aerial surveys (reviews in Gunderson, 1993).

The two most frequently advocated reasons to explain the poor fit of the stock/recruitment relationships are the error associated with both terms of the equation (parental stock and recruitment estimates) and the dampening effects of environmental factors on this relationship (see next section). Although measurement errors in stock and recruitment are obviously important, they are insufficient to explain the lack of relationship as demonstrated in the case of the anchovy population of the southern Benguela, where these errors are fairly well quantified (Fig. 6). The influence of environmental factors is certainly a more likely candidate for this explanation; we will expand on this topic in the next section.

Exploitation

Nearly all fisheries targeting pelagic fish take advantage of the gregariousness of pelagic fish to make large catches using efficient gears (von Brandt, 1984; Fréon and Misund, 1999; Parrish, 1999; Misund et al., 2002). Purse seining is by far the most efficient way of catching surface schooling species when they concentrate in large enough schools. It is estimated that over three quarters of the total world catch is
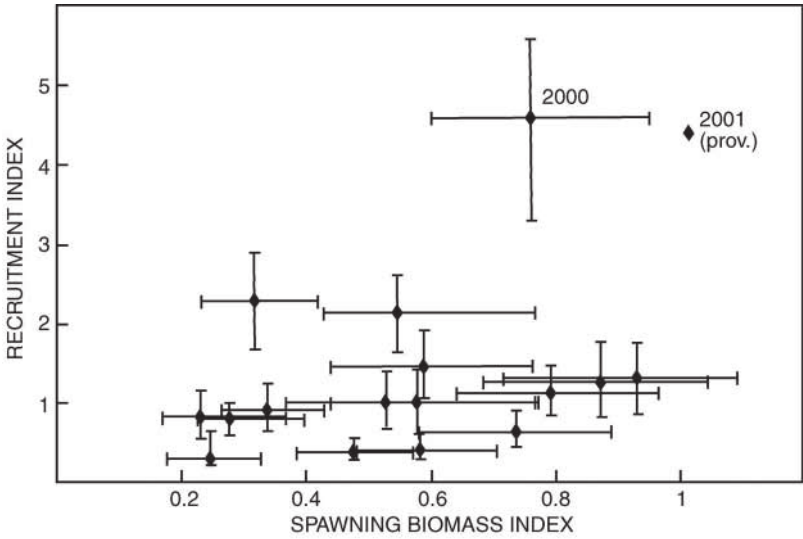
Figure 6. Stock-recruitment relationship of the anchovy *Engraulis encrasicolus* (synonymy *E. capensis)* of South Africa (Jose de Oliviera, Marine and Coastal Management (MCM), pers. comm.).

taken using purse seines. A purse seine is a large net (300 m to a few km), the top of which is kept at the surface by a line of floats while the lower part of the net sinks, due to the force of a leadline, usually up to a depth of 30–50 m, depending on the height of the purse seine. A purse seine net is set from the aft of a boat in an approximate circle around a fish school.

Typically, a purse seine can encircle schools of several tens of tons in just a few minutes, when fish schools are not of the order of several hundred tons as in some fisheries, such as the horse-mackerel fishery of Talcahuano, Chile (Hancock et al., 1995). The purse seine is closed underneath by hauling up the purse line that is located along the side of the vessel. In most industrial fisheries, fish are pumped directly from the net, and the pumping rate can be over 10 t min^{-1}. In semi-industrial fisheries, fish are loaded into the boat using large scoop nets operated by a winch, while in artisanal fisheries, all operations are manual (the portion of the net containing fish is pulled aboard). In all cases, the remaining fish are squeezed into the net and suffer from oxygen depletion and scale loss. Diving below the net has shown a typical "rain" of scales and experimental studies revealed that the survival rate of fish released after the net bursts is extremely low 120 hrs later (from 0%–5%), and this is mainly due to scale loss (Misund and Beltestad, 1995). Similar or slightly lower survival rates are expected when fish are dumped before being loaded on board. Although these low survival rates do not favor the learning processes already mentioned (behavior sub-section), it is possible that surviving fish can learn from purse seine experiences because fishers often miss targets when trying to circle fish schools: purse seine fishing success varies between 60% and 80%, depending on the species and fisheries.

Pelagic trawls —also called midwater trawls— are more efficient than purse seines when schools are too small or too deep to be reached by surface gear like a purse seine or when fish are dispersed in dense layers. A pelagic trawl is a net bag towed behind a single vessel or between two vessels operating together. The net entrance is wide (several tens of meters), made of large meshed net and parallel ropes that con-

centrate the fish into the trawl mouth. It is kept open by two or four diverging doors, a submerged float line on the upper part and heavy weights at the bottom. Nowadays, several electronic sensors monitor the depth and opening of the trawl as well as the quantity of fish entering and remaining in the net. When the codend is sufficiently full (usually after a period of 10–120 min) the net is wound up onto a powerful net drum with 5–50 t pulling capacity. No survival is expected once fish have been so heavily compressed in the net and loaded on board. In contrast, survival is not negligible for fish that escape from the midwater codend: estimates of survival rate vary from 10%–90% (review in Fréon and Misund, 1999).

Secondary fishing gears used for small and medium-sized pelagic fish are semi-pelagic trawls, bottom trawls, gill-nets (including surrounding gill-nets), beach seines, and hand lines. The latter three gears are mainly used in small-scale fisheries (Seck, 1980; Misund et al., 2002). In some countries like Senegal, Côte d'Ivoire, or Venezuela, small-scale fisheries, operating with small wooden canoes modified by the addition of an outboard engine, contribute to the vast majority of the landings, catching more than a 100,000 t of pelagic fish yr^{-1} (Fréon and Weber, 1983; Bard and Koranteng, 1995).

Because pelagic fish are highly aggregated, the time taken to catch them is short in comparison to the time spent searching for them. Modern fishing of pelagic fish is mostly dependent on detection and location of fish shoals by hydroacoustic instruments (Misund, 1997). Larger purse seiners (> 40 m) have a low frequency, low-resolution sonar (18–34 kHz) for detecting fish shoals at long range, and a high-frequency, high-resolution sonar (120–180 kHz) for more detailed mapping of shoal size and fish behavior in relation to the vessel and the net. In addition to this equipment, pelagic trawlers have sophisticated net sonde or trawl sonar that looks both upwards and downwards and facilitates the depth adjustment of the net according to fish behavior (Misund et al., 2002). Visual detection of schools or of bird species associated with them is also important in pelagic fisheries (especially for large pelagic fish) and fishers make use of visual aids such as powerful binoculars, and of bird radars.

Despite the tremendous assistance of this modern fish finding technology, the first thing a fisher looks for when leaving the harbor is not fish or birds but other fishing vessels targeting the same species. This is by far the most efficient way to locate an aggregation when enough vessels are involved in the fisheries. Cooperation versus competition among fleets is a characteristic of pelagic fisheries (Hancock et al., 1995; Gaertner et al., 1999). Figure 7 illustrates how strong the competition for fishing within an aggregation can be and how important it is to be able to access the core of the concentration for good catches. Quite often two fishing boats try to circle the same school and one can easily imagine the disputes that result from this competition. In the case of the sac-roe herring fishery of Alaska, where the fishing season is open for just a few days, if not just minutes to a few minutes or hours, strict rules of priority have been defined and the fleet is surveyed by plane (Belinay, 1994).

In most small pelagic fisheries and in a large number of medium-sized pelagic ones, more than 90% of the catch is processed into fishmeal, which is used for animal consumption. Therefore the price of fish is extremely low, in the order of a few U.S. dollars per metric ton. Because the cost of pelagic fish largely depends on the global market of fishmeal, which itself competes with the soya meal market (Durand, 1995), some crises observed in the artisanal fishery can even find their roots on the global market (Fréon and Weber, 1983). In the worst cases, pelagic fish are used as soil fer-
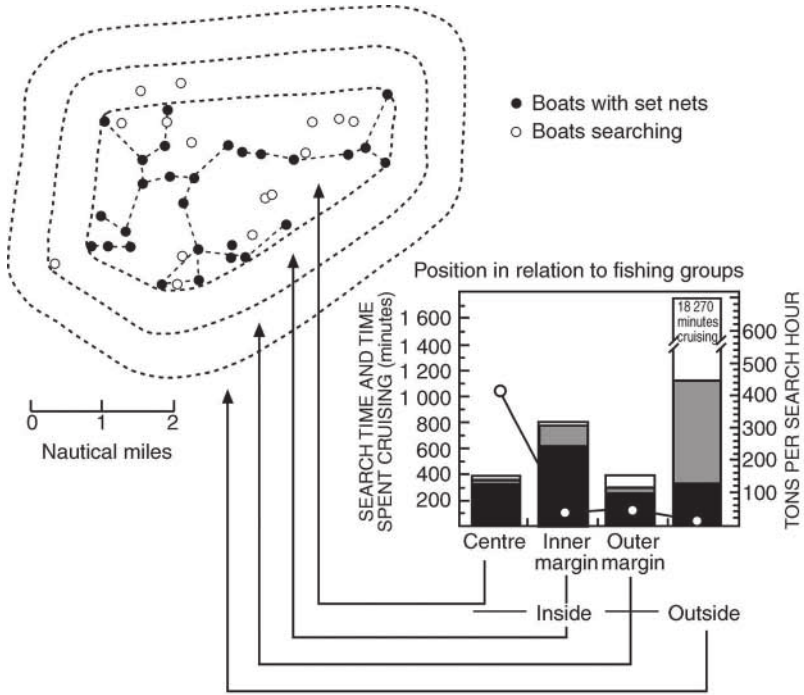
Figure 7. Distribution of purse seiners exploiting a cluster of schools in the horse mackerel (*Trachurus murphyi*) fishery of Talcahuano, Chile. Example of radar recording of boats with set net (filled circles) or not (open circles). Finely dotted lines show the nearest neighbor distance (NND) of boats with a set net (NND = 0.57 ± 0.27 nm). Modified after combination of Figures 4 and 8 from Hancock et al. (1995) and by addition of non-fishing ships (data kindly provided by the authors).

tilizer, which correspond to the lowest trophic level in the terrestrial food web. Although we understand that not all of the 40 million t of pelagic fish caught every year can be sold for human consumption, there is obviously room for a large improvement of the present situation. Many pelagic species used for fishmeal (anchovy, sardine, gilt-sardine, horse-mackerel) are suitable for human consumption as fresh, smoked, or frozen fish, providing that they are suitably handled and processed. Alternatively, more elaborate fish products such as fish pasta or surimi-like products can be made from these species (Patrick Soisson, COMAPECHE, pers. comm.). Encouraging such a move would not only enhance food security of some countries but would also generate more profit from smaller catches. Depending on retained governance options, this can result either in limiting the risk of overexploitation or encouraging it due to political and or economic pressure.

CONCLUSION

Coastal pelagic fish dominate world catches but provide less economic returns than expected due to the poor commercial use that is made of fish products. Due to a number of specificities of pelagic species in terms of their habitat, morphology, biology, behavior, ecology, population dynamics, and their vulnerability to modern fishing gear, they are subject to large interannual and interdecadal fluctuations in their biomass that challenges the sustainability of their exploitation. In short, two adjectives can sum up the characteristics of pelagic species: variability and instabil-

ity. These two attributes are largely shared with a very different but also short-lived group of marine species, the cephalopods (squids and octopus). Small pelagic fish and cephalopods contrast with most demersal species. However, when over-exploited, some stocks of semi-demersal species (like pollock, haddhock, and hake) partly resemble pelagic fish stocks: they are short lived due to reduction in life expectancy, the pelagic phase is dominant (young fish), they have high relative fecundity, and they exhibit characteristic schooling behavior.

Pelagic Fish and their Physical Environment

In this section, we will detail the relationship between coastal pelagic fish and their physical environment at different time and spatial scales in an attempt to understand the various processes involved and how we can possibly use this knowledge for modeling their dynamics and forecasting their abundance.

Our perception of the respective effects of the physical environment and exploitation on marine resources has varied considerably through time. Schematically, five periods can be defined, although their boundaries are debatable: (1) *before 1900, the "mother nature period":* marine resources are considered inexhaustible, regardless of their exploitation; (2) *1900–1950, the start of heavy industrial exploitation, beginning of scientific studies and awareness of the role of environmental factors:* the oceanographic environment is thought to affect mainly larval survival and recruitment success (Hjort's (1914) "critical period"); (3) *1950–1975, the reign of conventional stock assessment and fishery management:* Ricker (1954) and Beverton and Holt (1957) invented fish population dynamics. Fishing mortality is considered to be the major force driving stock abundance; (4) *1975–1995, the doubt period:* many failures occurred in fishery management (stock collapses due to overfishing) and there is renewed interest in the role of environmental factors. Simultaneously, there is a growing concern for the role of socioeconomic factors in stock assessment; and (5) *after 1995, the era of ecosystem-based management:* following the model of terrestrial ecology management, and due to the growing role of environmentalists in the protection of the environment, fishery management tends to be imbedded in marine ecosystem management. Marine protected areas (MPAs) are implemented and fisheries tend to be controlled by access (e.g., fishing rights) or market rights (ecolabeling).

The effects of environmental factors on pelagic fish species can be schematically subdivided according to three time scales at which they impact the fishery: short term (from instantaneous effects to circadian, tidal, lunar, and seasonal scales), medium term (interannual scale), and long term (interdecadal and centurial scales). Different processes are involved in each situation.

Short-Term Influences

Because they are very mobile and good fast swimmers, pelagic fish can react immediately to changes in their physical environment. By performing either vertical or horizontal migration in order to remain in their preferred habitat or microhabitat, they avoid mortality caused by adverse conditions. Nonetheless, this is not always the case and some mass mortality of pelagic fish has been observed in upwelling ecosystems due to lack of oxygen or large-scale high concentration of hydrogen sulfide (Gammelsrød et al., 1998; Weeks et al., 2002). In the most common situation, envi-

ronmental variability will only result in fish movements, which can be associated with changes in the aggregation pattern and will consequently affect the catchability and availability of the exploited fish stocks. In this case, although the influence of environmental conditions on the fishery is fast and over a short term, it can persist for fairly long periods of time, as long as environmental conditions do not change as outlined below.

Small-scale environmental changes, like internal waves, rip or tide currents, etc., can result in rapid movement of pelagic fish (e.g., Castongay and Gilbert, 1995). Although these movements can be temporarily detrimental to fishing operations, they are of finite duration and reversible, thus they can be easily overcome by fishers.

Diurnal changes in the vertical distribution of most pelagic fish form part of a normal cycle which usually consists of migration to the upper layers at the end of the day, associated with a lower level of aggregation than during the rest of the day; before sunset, fish start to aggregate in dense schools and then migrate to deeper layers (review in Neilson and Perry, 1990). These migrations are mainly driven by distributional changes in prey and predator species and by light levels that modify the mutual detection of the species. This diurnal cycle can be largely altered by any changes responsible for a modification in the visibility of the fish, such as the turbidity of the water column, the presence of bioluminescent plankton, or changes in light intensity of the sun and moon, depending on cloudiness or moon phase. The success of fishing operations largely depends on the depth of the fish and on their level of aggregation. This is particularly true for purse seining because only surface and subsurface schools can be caught in the upper layer. In Peru for instance, most El Niño events are characterized by the intrusion of a warm surface layer over the continental shelf that can persist for several months. As a result, some species of fish like anchoveta *Engraulis ringens* Jenyns, 1842 and sardine *Sardinops sagax* (Jenyns, 1842) move into deeper and cooler water where they are considerably less accessible to surface gears and in coastal refuge areas (Pauly and Tsukayama, 1987; Bertrand et al., 2004; Ñiquen and Bouchon, 2004). This situation can last for more than 6 mo, as in the case of the persistent El Niño event of 1997/98 (Ñiquen and Diaz, 2002). Other deviations from the usual vertical distribution of pelagic fish might arise from anoxic conditions in the water column.

Although, at the weekly scale, there are many reports of catches and distributions of large pelagic fish (tuna and swordfish species) related to sea surface temperature (SST), SST fronts, and oxygen concentration (reviews in Sund et al., 1981; Brill, 1994), relationships between environmental factors and small pelagic fish species are less salient. Anchovy spawning is thought to be related to certain temperature ranges (Lasker et al., 1981; Fieldler, 1983; Richardson et al., 1998; van der Lingen et al., 2001) and in the North Sea, herring biomass distributions seem to be related to SST and salinity, with greater densities often associated with strong gradients in these parameters (Maravelias and Reid, 1995). A similar association of anchovy, sardine, and jack mackerel distributions with thermal fronts was demonstrated in northern Chile (Castillo et al., 1996). In Côte d'Ivoire, pelagic fish catches were related to a pattern of SST at particular lags of a few weeks, which was associated with enrichment in zooplankton, as fish tend to be more abundant in newly productive areas (Mendelssohn and Cury, 1987). In contrast, a number of studies failed to find a clear relationship between small pelagic fish distribution and SST. For example, the spawning distribution of the Californian anchovy was related to temperature in some studies,

but not in others (Lasker et al., 1981; Fieldler, 1983). In South Africa, Kerstan (1993) attempted to predict sardine distributions using data from nine research cruises but reported that environmental variables (including temperature) could only explain 2%–10% of the variance in the sardine density. This last result was confirmed by Agenbag et al. (2003) who incorporated satellite-derived SST and 11 yrs of data from the South African fishery into General Linear Models and General Additive Models: most of the variance was explained by temporal and spatial variables while all variables derived from SST explained only 0.5%–1.5% of the variance of the catch per set of Cape anchovy (*E. capensis*), sardine (*S. sagax*), and round herring *Etrumeus whiteheadi* Wongratana, 1983.

Although there are few scientifically proven relationships between SST and small pelagic fish distributions —possibly due to the lack of information at small enough spatial and temporal scales— near real time satellite thermal images are nonetheless quite commonly used by pelagic fishing fleets in an attempt to locate the best fishing spots (Santos, 2000).

Alongshore horizontal displacements of fish stocks are also observed in response to modifications in the environment, which can alter the regular pattern of seasonal migration. This occurs in Peru, where most El Niño events result in the displacement of the anchoveta stock from the central and northern parts of the Peruvian continental shelf to southern Peru and northern Chile (Bakun, 1996; Ñiquen and Diaz, 2002; Yáñez et al., 2002), in addition to the above-mentioned vertical movements. Similarly, in the northern Benguela, where strong and persistent incursions of the Angola-Benguela front ("Benguela Niños") displace to northern Namibia tropical species like the gilt sardine *S. aurita*, originating from Angola, and move sardine (*S. sagax*) southwards. In this case, *S. aurita* is less accessible to the Angolan fleet but *S. sagax* is more accessible to the Walvis Bay fleet off Namibia, despite adverse effects of the Benguela Niños on its overall abundance (Gammelsrød et al., 1998; Boyer and Hampton, 2001; Boyer et al., 2001). Conversely, winter intensification of the upwelling in the central part of the Benguela results in the incursion of up to 50% of the stock of *S. sagax* from Namibia into Angola. Similar displacement of *S. aurita* and *Sardinella maderensis* (Lowe, 1838) stocks are described by Binet (2001) in northern Angola and Congo, in reaction to "Guinean Niños" that involve the north equatorial counter current.

Onshore or offshore movements in response to hydrological changes are also reported for many pelagic species. Preceding the abovementioned vertical and alongshore displacement of anchoveta and sardine in Peru and Chile during El Niño events, the fish are found closer to shore and therefore they are more available to the fishery at the beginning of the event (Ñiquen and Diaz, 2002; Yáñez et al., 2002). However, this phenomenon is not observed during all El Niño events and the forcing factors responsible for such differences are still to be identified (Miguel Ñiquen, IMARPE, pers. comm.).

Pelagic fish can also modify their aggregation level under certain conditions, although this is not always fully understood but commonly attributed to environmental changes. When fish move in response to environmental changes as indicated above, changes in aggregation can be seen either as a direct consequence of the movement itself or as an indirect one related to the new conditions found in the place to which they moved (e.g., abundance of prey and/or predators). The density, biomass, and shape of the school vary in a manner that does not always follow the well-known

diurnal or seasonal patterns (Swartzman et al., 1994; Swartzman, 1997). Changes in the overall abundance of prey and their local density or patchiness are certainly major influences, but environmental forcings like the thermal structure (Gammelsrød et al., 1998), turbidity of the water, and changes in current speed and velocity also play a major role, or even interact with biotic factors as suggested by Bertrand et al. (2002).

The success of pelagic fisheries is largely dependent on these short-term influences that mainly affect the catchability and availability of fish; fishers quickly detect them and adjust their fishing patterns accordingly, especially when diurnal or lunar cycles are involved (Anthony and Forgarty, 1985; Fréon et al., 1994). In contrast, when the forcing factor(s) persist over long time periods, as is the case during El Niño events, short-term responses might last for several weeks or months and can affect the sustainability of fisheries because they can dramatically increase the availability of the resource, which can lead to its collapse in the case of an already overexploited stock. This situation is more likely to occur in circumstances where environmental changes positively influence the fish availability in the short term, and negatively affect their abundance in the medium term, as shown by surplus production models taking into account both types of effects (Fréon et al., 1993b).

Medium-Term Influences

This section focuses first on the environmental processes affecting larval survival that lead to interannual variability in fish recruitment success, then it briefly mentions other processes affecting later stages of development. The first part of this section consolidates several reviews that provide details and in depth analysis of these processes (Cushing, 1982, 1990; Wooster and Bailey, 1989; Heath, 1992; McKenzie, 2000).

For the last 50 yrs, interannual variability of fish recruitment has been a major research focus in fisheries oceanography. The "critical period" hypothesis of Hjort (1914, 1926) states that the numerical value of a year class is determined at a very early stage and that early first feeding of larvae seems to be the most vulnerable stage in the life history of fish. From observations in the North Sea, Cushing (1975) elaborated on Hjort's hypothesis and proposed that the production of fish larvae can match or mismatch the production of their food. The "match-mismatch" hypothesis highlights the importance of the timing of spawning in temperate areas where spawning must be tuned to the onset of the spring production cycle, and has since been updated (Cushing, 1990). In subtropical regions, a temporal mismatch between spawning and food might be less critical due to the extended production and spawning cycles (Cushing, 1982). Several authors reviewed or tested the applicability of the match-mismatch hypothesis and it appears that it lacks support from field data in many cases (Bainbridge et al., 1974; Sinclair and Tremblay, 1984; Sinclair 1988).

From extensive studies on feeding of anchovy larvae, Lasker (1975, 1978) showed that larvae are relatively inefficient in capturing food and that fairly high concentrations of the right type of food are necessary to keep larvae alive. Lasker's observations indicated that suitable larval feeding grounds are restricted to chlorophyll-rich subsurface layers associated with the thermocline in stratified layers and that storm-related wind mixing can destroy the vertical stratification and disperse the larvae's preys within the water column. These observations formed the basis of Lasker's stable-ocean hypothesis (Lasker, 1981). Support for Lasker's stable-ocean hypothesis is

found in Peterman and Bradford (1987). Using a time series of the anchovy mortality rate from 1954–1984, they showed that there is a negative relationship between the anchovy mortality rate and the number of calm periods per month. A modeling study by Wroblewski et al. (1989) provided further insight into Lasker's stable-ocean hypothesis. This study showed that optimal conditions for larval survival occur when a wind event strong enough to deepen the mixed layer into the nutricline is followed by a period of calm. This period between storms must be long enough for larvae to develop into a stage where short-term starvation can be endured.

Parrish et al. (1981) noted that in the California Current many species spawn in locations where, or at times when, offshore transport is minimal. Fish reproductive strategies seem to have evolved in order to avoid the adverse effect of offshore transport of eggs and larvae. Using a comparative approach between eastern boundary current ecosystems, Parrish et al. (1983) found a general pattern of avoidance of intense wind-induced turbulent mixing and of strong offshore-directed Ekman transport in the spawning habits of sardines and anchovies.

Rothschild and Osborn (1988) proposed that turbulent water motion at small scales (mm–cm) favors the encounter rates between predators and prey. This means that the apparent prey concentration perceived by planktonic predators such as fish larvae is higher in turbulent water than in calm water, if other factors (especially food concentration) remain unchanged. Direct laboratory observation of cod larvae feeding on live copepods confirmed the positive impact of small-scale turbulence on encounter rates (MacKenzie and Kiørboe, 1995). However, encounter is only one part of the feeding process and larvae must also pursue and capture their encountered prey. Experimental observations showed that pursuit success decreased with increasing turbulence (MacKenzie and Kiørboe, 2000). MacKenzie (2000) provided a comprehensive review of how turbulence affects feeding and growth of larval fish and recruitment. He provided examples of field studies demonstrating contrasting effects of turbulence on feeding, growth, and mortality rates and states that this is due to a failure to directly sample the relevant process and the covariation of many ecosystem processes as water columns become more (or less) turbulent. We still need to identify which of the many oceanographic processes that turbulence influences has/have the most impact on fish growth and survival (Mackenzie, 2000).

The Optimal Environmental Window hypothesis (Cury and Roy, 1989) is an attempt to reconcile contrasting, and often conflicting, hypotheses or results between fish recruitment and upwelling intensity. By combining the major hypotheses available in the late 1980s relating recruitment variability to the environment into a unique framework, the authors proposed that there is a dome-shaped relationship between recruitment variability and upwelling intensity. A comparative analysis between upwelling systems and species supported the existence of these non-linear relationships. The optimal environmental window can be viewed as the application of Bakun's triad (Bakun, 1996) in upwelling ecosystems to explain recruitment variability. Bakun (1996) proposed that three major classes of processes combine to yield favorable reproductive habitats for coastal pelagic fish and also many other types of fish. The three processes are: enrichment (upwelling, mixing, etc.), concentration (convergence, fronts, etc.), and processes favoring retention within (or drift toward) an appropriate habitat. Bakun (1998) illustrated how the triad might help in understanding the major spatio-temporal patterns of fish reproduction by providing a set of ocean triad configurations in upwelling regions.
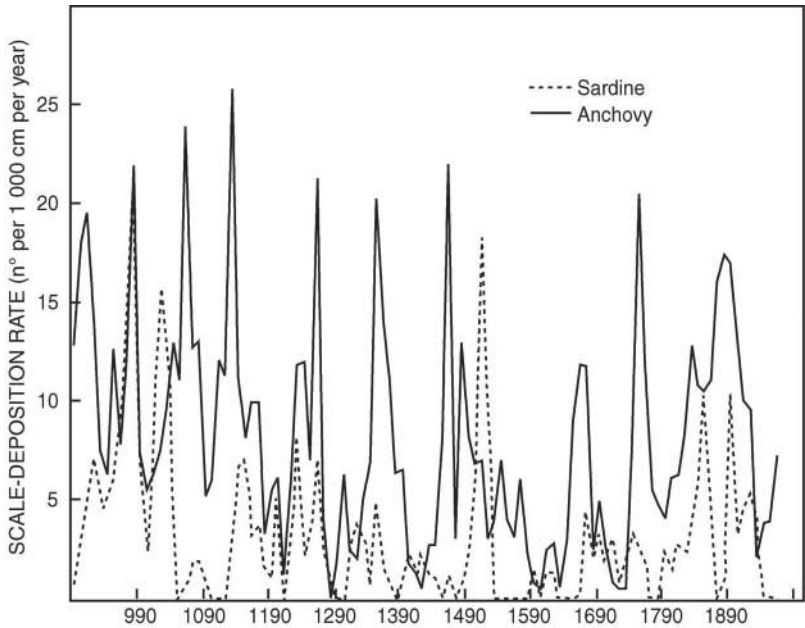
Figure 8. Reconstructed time series of pelagic fish abundance in the Santa Barbara Basin, California, from core sediment analysis (Baumgartner et al., 1992).

Environmental processes might also affect pelagic stocks at later stages of fish development, including the post-recruitment period. Peterman et al. (1988) found a lack of correlation between the abundance of recruits (> 1 yr) and the abundance of 4.5 d- and 19 d-old larvae, although this result partly contradicts a previous study by Peterman and Bradford (1987, op. cit.) on the same population. Several authors (e.g., Smith, 1985; Rothschild, 1986) argue that the environmental impact is likely to be limited after recruitment because natural mortality is much more stable and changes in growth rates can only be responsible for moderate variation in biomass lower than an order of magnitude. Nonetheless, some documented examples indicate substantial environmental effects during this post-recruitment period. Those effects can impact the mortality of fish or their growth rates, but also the sexual maturation period which can be critical for the fecundity of the fish, although effects such as these are often difficult to distinguish from purely density-dependent effects, as found by Overholtz (1989) in Atlantic mackerel. Anthony and Fogarty (1985) indicate that the growth rate of Atlantic herring *Clupea harengus harengus* Linnaeus, 1758 is related to both age-2 abundance and summer water temperature. Similar findings were made in the case of herring from the North Sea (Heath et al., 1997). Haist and Stocker (1985) found that SST of 12°–13°C was optimal for both juvenile growth and adult "surplus energy" (defined as the sum of ovary weight and increase in weight in 1 yr) of the Pacific herring *Clupea harengus pallasi* Valenciennes, 1847 in the Strait of Georgia. Similar discoveries of the role of environmental conditions on growth were made for sardine (Iles, 1973) and other pelagic fish such as sardinellas (Cury and Fontana, 1988). Temperature in the months prior to spawning was also found to influence the fecundity of pelagic fish such as the Baltic herring *Clupea harengus membras* Linnaeus, 1761 (Laine et al., 1998) and of Japanese anchovy *Engraulis japonicus* Temminck and Schlegel, 1846 (Imai and Tanaka, 1997). The processes responsible

for changes in growth rate, fecundity, or mortality according to environmental factors are not always clearly identified, but in most of the given examples they seem related to food abundance, intermingled with density-dependence.

Long-term Influences and Global Synchrony

Long-term variations in pelagic fish stock abundance (or to a lesser extent availability) are documented in many ecosystems (Glantz, 1992; Spencer and Collie, 1997; Francis et al., 1998; Schwartzlose et al., 1999). Indices of abundance on such long time periods are derived either from the analysis of core sediments (Fig. 8) or from commercial catch data (Fig. 2). These data indicate trends, long-term autocorrelations, or pseudo-periodic variations occurring at multi-decadal scale, often interpreted as the result of environmental forcing, although other processes, like interactions between species, diseases, or exploitation can also be advocated as unique or additional and intermingled forcing factors (see next section). Alheit and Hagen (1997, 2001) describe the history of the Bohuslän herring fishery in the Baltic Sea, which displays alternating periods of high catch rate and collapses that dramatically impacted the economy of this region from the medieval period up to the recent modern period. The authors associated the so-called Bohuslän periods with climatic and hydrographic conditions characterized by cold water in the North Sea —English Channel— Skagerrak, increased ice cover off Iceland and the Baltic Sea, and changes in the wind regime. Similar examples of long-term changes are reported for other pelagic stocks (e.g., Kawasaki, 1994; Klyashtorin, 1998; Hare and Mantua, 2000). In all of these instances, correlations between stock abundance and environmental variables only result from empirical studies and the processes responsible for the environmental forcing are not fully understood. Nonetheless, the apparent synchrony of variation in abundance displayed by some large pelagic stocks located in remote areas around the globe is arousing much interest and might suggest some form of common global environmental forcing.

Kawasaki (1983) was the first to notice that, during the 20th century, several of the world's largest populations of sardine *S. sagax* experienced large, long-term changes. He showed that a pattern of ocean-wide synchrony emerges when one looks very broadly at the sardine landings from three regions of the Pacific Ocean (Japan, California, and Peru-Chile) that have supported very large sardine fisheries. The collapse of the Japanese and Humboldt sardine populations in the late 1980s and early 1990s reinforced Kawasaki's point of view (Lluch-Belda et al., 1992a; Bakun, 1998; Schwartzlose et al., 1999). Moreover, two of the other largest coastal pelagic fish populations of the world, the Peruvian anchoveta and the South African sardine, appeared to rise and fall directly out of phase with the Pacific sardine (Lluch-Belda et al., 1989, 1992b; Crawford et al., 1991). Many of the very large groundfish populations of the sub-Arctic North Pacific have also been varying substantially in phase with the sardine (Bakun, 1998). Catches of several salmon species around the Pacific Rim indicate that there is some coherence in the low frequency, large amplitude variation in the corresponding populations (Beamish and Bouillon, 1993), which in turn are out of phase with the anchovy populations (Beamish et al., 1999).

Since the fish populations are certainly far too widely separated to interact through direct exchanges, a large scale climatic signal was first proposed as being the driving force of the observed synchronies (Lluch-Belda et al., 1989, 1992b; Bakun, 1996; Klyashtorin, 2001). The climatic regime shift of the mid-1970s is well documented in

the northern Pacific and it is a strong candidate to account for several of the changes in salmon observed during the late 1970s in that region (Polovina et al., 1994; Hare and Mantua, 2000). For the small pelagic populations, the situation is unclear. SST was first considered but SST trends have not been consistent in the various regions inhabited by populations of small pelagics: during the mid-1970 to mid-1980s, when the eastern Pacific was in a definite warm phase, the northwestern Pacific, where sardines were expanding equally dramatically, was in, if anything, a cool phase (Bakun, 1998). Klyashtorin (2001) suggested that the Atmospheric Circulation Index (ACI) is a reliable climatic index for long-term regular changes in the major commercial fish stocks because it characterizes the dominant direction ("meridional" or "zonal") of air mass transport. Zonal or meridional components of the ACI were found to correlate with the long-term fluctuations of the main commercial catches of Pacific salmon, Japanese, Californian, Peruvian, South African, and European sardine, Alaskan pollock, Chilean jack mackerel, Atlantic and Pacific herring as well as Atlantic cod (r = 0.70−0.90), because those catch series (except anchovy) also display a pronounced spectral maximum of 54−58 yrs (Klyashtorin, 2001). Spencer and Collie (1997) observed shorter periodicity (around 40 yrs) because they used time series shorter than 80 yrs.

Recently, there have been some major unexplained departures from synchrony. The first is the apparent time lag of about one decade in the California Current relative to the Japanese and Peruvian systems (see appendix in Schwartzlose et al., 1999). The California sardine population has been expanding since the early 1990s while at the same time in the South Pacific, anchovy became the dominant population and sardine declined to low levels. As a consequence, the sardine populations of the Humboldt and California systems are now in an opposite phase of abundance. Secondly, the apparent link between the Pacific and South Atlantic sardine populations (out of phase situation between the Pacific and the Benguela) also seems to have vanished. Moreover, opposite patterns are occurring within the Benguela system. In the southern Benguela, the anchovy population reached a record high level in 2000, while the sardine population has shown a positive trend for the last 15 yrs (Beckley and van der Lingen, 1999; Marine and Coastal Management, unpubl. data).

The way in which global synchrony among pelagic populations is demonstrated is debatable. Firstly, the criterion used to identify populations such as these is not consistent. In some cases, the unit used is the fairly well defined stock (e.g., sardine stocks of Japan, the southern Benguela, and the northern Benguela; Peruvian anchoveta stock), while in other circumstances many stocks are regrouped at a broad scale (e.g., North Pacific sardine stocks from Mexico to Canada; South Pacific sardine stocks from Peru and Chile). Secondly, there are, by definition, few possible low frequency patterns in commercial fishery time-series (the most commonly used) of largely auto-correlated data available for periods usually ranging from 40−100 yrs. Finally, commercial catches poorly represent the variation in abundance of stocks because of anthropogenic external factors (trends in industrialization, technological improvements, and economical health of the countries, fishery management, wars, etc.). A statistical analysis of FAO national catches over the last 49 yrs, based on k-means analysis and artificial neural network indicates that, although it is possible to identify many contrasting patterns of variability for marine fisheries, pelagic fish display all kinds of patterns and only a small proportion of the documented synchronies have been identified, even when it is claimed that they occur between national

stocks. Most of the synchrony detected by these statistical tools occurred at the regional level, rather than at the global scale (Fréon et al., 2003).

Regional synchrony might be easier to explain than global synchrony because consistent low frequency environmental change is more often observed at the basin scale than at the planetary one. How those basin-scale climatic changes translate into several local effects on the shelf is still largely unknown, although promising hypotheses have been proposed recently to explain coherent regime changes observed during the last 40 yrs in the Pacific (Francis et al., 1998; McFarlane et al., 2000; McFarlane and Beamish, 2001; MacCall, 2002). Rothschild (1995) suggested that the fishing-independent variations in abundance occurring at large multi-decadal scales are related either to multidecadal fluctuations in primary production or to changes in the trophodynamic pathways by which primary production is transformed to fish biomass.

In summary, it appears that large-scale synchronies between widespread marine fish populations occurred over more than a decade, from the mid-1970s to late 1980s. However, it is becoming more and more obvious that, for the small pelagic populations, the situation that prevailed from the mid-1970s to late 1980s is no longer holding true. Global synchrony in fisheries must be further investigated before it becomes a solid paradigm. Regional synchrony forced by climatic changes at a basin-scale might be easier to explain, although empirical observations accumulated so far suggest that the catch dynamics of the main Pacific commercial species are more closely correlated with the global climatic indices than they are with their corresponding regional indices (Klyashtorin, 2001). But, there is no satisfactory explanation for this so far.

Global synchrony forced by environmental changes is also advocated to explain multi-centennial regimes of anomalous salmon, sardine, and anchovy abundance in the North Pacific. Using the technique of core sediment analysis of isotopes in nursery lakes of Alaska (Finney et al., 2000) a 2200 yr record of sockeye salmon abundance indicates two major shifts in abundance (Finney et al., 2002). These have been attributed to major changes in the ocean-atmosphere circulation in the northeastern Pacific. When compared to similar reconstructed series of paleoceanographic records of Pacific sardine and northern anchovy over the last 1600 yrs (Baumgartner et al., 1992), Finney et al. (2002) concluded that these last two series are out of phase with the sockeye salmon series at the very low-frequency level. In contrast, at the higher multi-decadal frequency, fishery data of the 20th century suggest that sardine co-varies with salmon but is out of phase with anchovy (Beamish et al., 1999).

Alternation Between Small Pelagic Fish Species and Regime Shifts: From an Environmental Perspective

An alternation between two species is considered to operate when, following the decrease in the biomass of one species due to collapse resulting from adverse environmental effects, overfishing, or internal dynamics of this species, the total biomass is restored by density compensation of another redundant species; i.e., belonging to the same guild or functional group. Strong recurrent patterns of alternating steady states of pelagic fish species are observed on decadal scales in many ecosystems (Lluch-Belda et al., 1989). For example, upwelling systems tend to be dominated by one species of sardine (or sardinella) and one species of anchovy, but most often only one of the two dominates at any particular time (Bakun, 2005; this issue; Polovina,
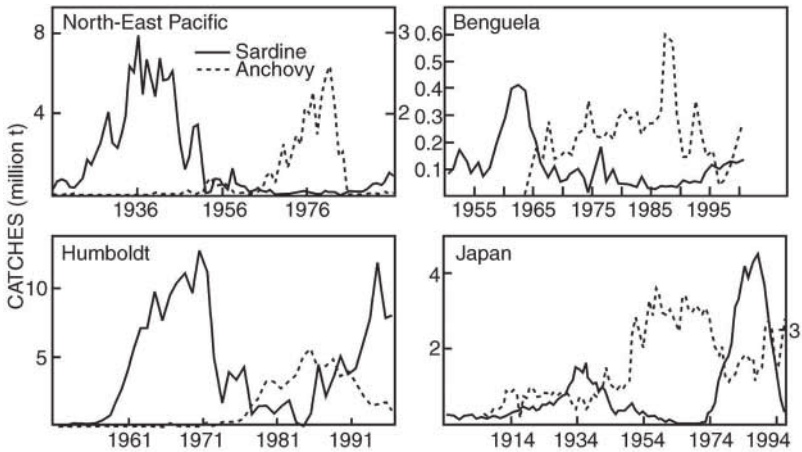
Figure 9. Catch time series of sardine and anchovy in different ecosystems illustrating the alternation between the two species (source: SCOR WG 101).

2005; this issue). However, the two species can remain abundant at the same time over several years (Figs. 8,9), and the replacement of one species by another does not systematically occur. Sardines have not been replaced by anchovy in California for the past 20 yrs. In the northern Benguela, both sardine and anchovy populations are at an historically low level (Boyer and Hampton, 2001), whereas off South Africa, anchovy and sardine have been abundant during recent years.

Many factors have been proposed to explain alternation between species. Environmental conditions are thought to be the main driving factors affecting this alternation, as climate can preferentially favor one species over the other, a point of view that we will develop in this section. It is thought that some of the major alternation of species occurred in periods during which abrupt changes in the environment have been recorded (regime shifts). Bakun and Broad (2002) listed four major shifts in the Pacific: (1) the early 1940s off the west coast of North America; (2) the late 1960s in the Humboldt system; (3) the late 1980s in the Humboldt system, off Japan and in parts of the North Pacific (also suggested in the Benguela region); and (4) the late 1990s off the west coast of North America.

Regime shifts in abundance of the Japanese sardine were considered a result of a combination of long-term environmental regimes, interannual variability in recruitment success, and density-dependent recruitment (Wada and Jacobson, 1998). Francis et al. (1998) suggested a model of environmental forcing in the northeast Pacific by which climate changes initially result in a modification of the wind stress, which affects horizontal and vertical flow, altering the mixing and the depth of the surface layer, as well as the location and characteristics of mesoscale features. These changes will then lead to a bottom-up modification, first in the primary production and in the timing of blooms, among other factors, which in turn will affect the secondary production (zooplankton) and ultimately, the trophic level of pelagic species.

Physico-chemical forcing is reflected in changes in phytoplankton communities (Mitchell-Innes and Pitcher, 1992) and the community structure of zooplankton (Verheye et al., 1998), thereby influencing food available to small pelagic fish. Kawasaki and Omori (1988) proposed that warming leads to higher SST and increases in phytoplankton populations, which allows the Japanese sardine population to in-
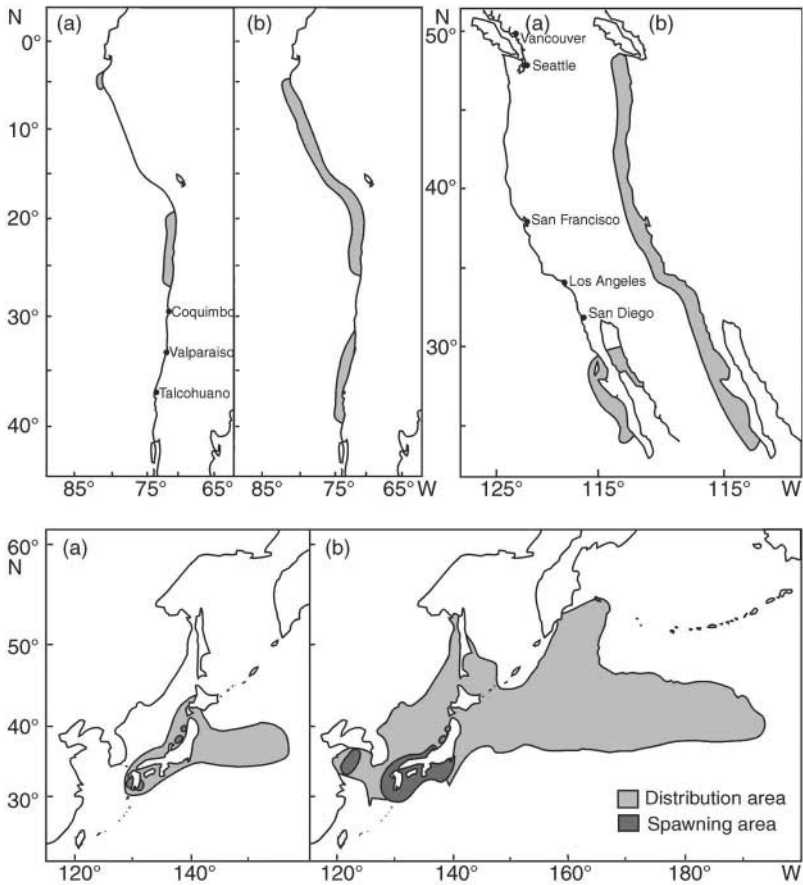
Figure 10. Change in the distribution area of three pelagic fish stocks during (a) low and (b) high abundance periods (Lluch-Belda et al., 1989).

crease. Large amplitude variations (from 60%–100%) in the abundance of phyto- or zooplankton have been reported in the North and South Pacific (review in Bakun and Broad, 2002). However, there is no evidence that increased sardine abundance is linked to increases in primary productivity in the California system (Lluch-Belda et al., 1992a). Van der Lingen (1994) and van der Lingen et al. (2001) suggested that regime shifts are associated with structural changes in the ecosystem (plankton size particles), leading to environmental conditions favoring one species over the other, for example, by means of the contraction or expansion of suitable habitat.

Analyzing changes in abundance of pelagic species in response to environmental changes, Skud (1982) concluded that the dominant species responds to environmental factors, while the subordinate species responds to the abundance of the dominant one. Thus, environmental factors can trigger changes in the abundance of one species that produce dynamic changes between two competing species. This may be the case in regions where diets of pelagic fish are similar. For example, there is intense competition for food between the Far Eastern sardine *Sardinops melanostictus* (Temminck and Schlegel, 1846) and the Japanese anchovy *E. japonicus*; both species feed on similar proportions of phyto- and zooplankton (Kawasaki and Omori, 1988). However, recent studies question the role of direct competition, as sardine and an-
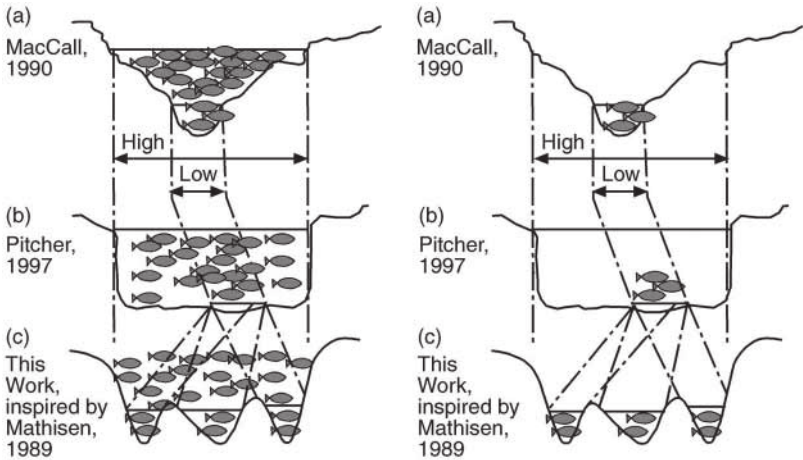
Figure 11. Three different basin theories showing the changes in habitat area according to left panel high or right panel low abundance. Profil of basins indicate relative habitat quality: deeper basin is better habitat.

chovy do not usually have the same spatial distribution (sardine are usually found farther offshore) and do not necessarily feed on the same type of food. An example is off South Africa, where anchovy preferentially feed on large zooplankton, whereas sardine prefer phytoplankton and small zooplankton (James, 1987; van der Lingen, 1994). These arguments led several authors to consider that competition should be magnified by schooling behavior within mixed-species schools (see next section).

Alternation of pelagic fish species is a rule that has exceptions and has received considerable attention. These multi-year ecological patterns of alternation are important for long-term management, as exploitation reduces the biomass of the dominant species, which is usually the target species, and sometimes precipitates its collapse (see next section).

Spatial Aspects

The above-mentioned large fluctuations in abundance are often associated with spatial changes. Both sardines and anchovies exhibit large expansions and contractions of range, which can be associated with their levels of abundance. Strong patterns of variation in spatial coverage of the sardine have been observed in Japan, as well as in the California, Canary, Humboldt, and Benguela Currents (Lluch-Belda et al., 1989; Barange et al., 1999; Schwartzlose et al., 1999). During periods of high abundance, sardine in each of these regions, and to a lesser extent, anchovy in California and in the southern Benguela, have a propensity to extend their range and sometimes also shift their geographic center (Fig. 10). This difference in the range of expansion between sardine and anchovy has been attributed to a difference in migratory ability between the two species, sardine being more migratory than anchovy and becoming increasingly so with age. Habitats for sardine in the eastern boundary currents have extended into cooler regions during warm periods (Schwartzlose et al., 1999). These observed patterns should be regarded as long-term patterns as it is sometimes difficult to track them at an interannual scale, as for example, in the case of the sardine in the southern Benguela (Barange et al., 1999). Not only migratory, but also spawning patterns, can change through time. Thus, in the mid-1960s, South African sardine

spawners appear to have contracted their spawning range to a southern cell when their abundance decreased and that of anchovy increased (Crawford, 1981).

Population theory of density-dependent habitat selection has received a lot of theoretical attention with the "basin theory" and its application to fisheries (MacCall, 1990). In this theory, the spatial dynamics of pelagic fish is viewed as a process where fish first colonize the most favorable areas, but as they become more abundant, density-dependent factors force them to move to less favorable areas (Fig. 11A). However, Pitcher (1997) argued that density-dependent habitat selection is not required to explain higher local densities, as it can only be attributed to schooling behavior, whereas, in contrast to MacCall's theory, these high densities can occur at any place within the basin (Fig. 11B). Another way to model the spatial dynamics of pelagic fish is to view it as a number of dynamic basins that are colonized by fish, but that are dynamic due to the changing environment (Fig. 11C). These patterns and associated dynamics are important for fisheries management because, in all three basin theories, the catchability of fish may increase with decreasing biomass. Overexploitation of pelagic fish and the resulting depleted biomasses may not only greatly affect their distributional range, but may also reduce their lifespan and their migrational range, thereby usually also increasing their availability to fisheries at low population levels.

The Temporal and Spatial Scales Issue

The above sub-sections show that environmental influences are complex, not fully understood, and vary according to the temporal and spatial scales at which they are studied. As pointed out by several authors (review in Hofmann and Powell, 1998), fish populations interact with their environment over a hierarchy of temporal and spatial scales in which they respond to perturbations through pathways of energy transfer at long and short time scales. Although individuals are ultimately influenced only by their local surroundings, these local variations can result from a wide range of spatio-temporal forcing factors. Short-term environmental variability at small or medium spatial scales mostly affects the catchability of the fish rather than its abundance, except for rare and intense environmental events responsible for mass mortality. Medium-term environmental effects at medium spatial scales mostly impact the yearly stages of fish and therefore affect recruitment. The effects of long-term changes in the environment on fish populations are more difficult to detect and should be subdivided into multi-decadal and multi-decennial scales.

The more debatable environmental effects are those occurring at the multi-decadal temporal scale and the large spatial scale. How these global climatic changes are reflected at the regional scale is still speculative. Coastal modeling is developing rapidly and embedded 3D hydrodynamic models should shed light on the scale transfer between oceanic features and coastal ones. The next question to answer will be which ecological processes relate these climatic changes to pelagic fish populations. In this respect, many mechanisms have been proposed, including the influence of temperature anomalies on migration patterns, related predation factors, and reproductive success, as well as the influence of zooplankton productivity on early life history and feeding conditions. Recently, a hypothesis relating to the intensity of the California current has been suggested as a potential mechanism to account for the recent sardine outburst. Under conditions of a slow, meandering California Current, retention of eggs and larvae spawned in the offshore habitat is greater than under conditions

of fast, straight flow (MacCall, 2002). Coupling or integration of hydrodynamics, biogeochemical, and ecological models should allow testing of such hypotheses.

The sustainability of resource exploitation is mainly challenged by the variability in abundance at interannual and mostly interdecadal scales. If this variability was mainly due to environmental forcing and if such forcing were predictable, management action might be more effective. The previously mentioned studies on long-term influence, although mainly empirical, do not suggest the existence of clear periodicity in the physical and biological series but rather a pseudo-periodicity of around 40–60 yrs. This pseudo-periodicity and the fact that both environmental and biological time series are very noisy, make the prediction of pelagic fish abundance difficult but still open the door to some management strategies that will be proposed in the last section of this work. In the next two sub-sections we review the attempts of modeling environmental effects and the associated difficulties.

Review of Studies Modeling Environmental Effects on Small Pelagic Fish.—The first attempts at modeling environmental effects were based on empirical relationships between an environmental variable (V) thought to influence the abundance or catchability of the stock on one hand, and the biomass (B), catch per unit of effort (CPUE), catches (C), or recruitment (R) on the other. This relationship was explored using a simple linear regression such as:

$$B, CPUE, C \text{ or } R = f(V) + \varepsilon$$

(1)

where $f(V)$ is a function of the environmental variable V and ε is the residual or error term. In most cases, $f(V)$ is a linear function or is linearized by logarithmic transformation. Examples of such attempts are numerous and many of them can be found in proceedings of symposiums on this topic (Anonymous, 1978; FAO, 1983a,b, 1984; Larrañeta and Wyatt, 1989; Kawasaki et al., 1991), but most of them have failed to predict the fate of the stocks in the long-term. The reasons for such failures are numerous: (1) lack of understanding of the ecological processes (stage of development impacted by the environment and corresponding lag to be incorporated in the regression; effect on abundance versus effect on catchability; key environmental variable; etc.); (2) hypotheses generated from data instead of using data to test hypotheses; (3) non-linear (especially non-monotonic) relationships not explored; (4) spurious correlation due to testing of too many variables during a preliminary exploratory analysis (although seldom reported) without adjusting the number of degrees of freedom (df) accordingly; (5) spurious correlation due to artificial increase of the number of df in relation to spatial and temporal autocorrelation; (6) elimination of significant outlier points without serious justification, while these points might be a clue to understanding a major forcing effect; (7) interdecadal regime-shift occurring after the period for which a given time series was used to study intra-decadal relationships; (8) measurement biases and errors on both the dependent and independent variables (e.g., trends in time series of abundance indices resulting from fishery data are usually negatively biased due to increased efficiency resulting from technological improvement and accumulated knowledge of fishers). Additional consideration of the technical issues on the use of environmental indices can be found in Barange (2001).

Principal Component Analysis (PCA) and related tools have also been used to explore functional relationships between environmental variables and fishery data. This method is still a correlation-based approach with the same limitations as the regression approach, although it allows the incorporation of several variables, with no distinction between dependent and independent variables. PCAs are useful in generating hypotheses without preliminary assumptions, and spatial effects can be incorporated.

Empirical Multiple Regression Analysis and General or Generalized Linear Models (GLMs: Draper and Smith, 1966) allow the incorporation of several independent variables into the model, including non-environmental ones like the fishing effort and the fishing unit characteristics. The general expression of these models is:

$$B, CPUE, C \text{ or } R = f(V1, V2, \dots) + \varepsilon$$

(2)

(same notation as equation (1), $V1$, $V2$, etc. being independent variables). The contribution of each term is adjusted for other variables in the model. The strength of these models is their capacity to reflect more complexity than simple regressions. The resulting difficulty is the corresponding decrease in the number of df that can lead to spurious correlations. GLMs allow the incorporation of categorical variables (also called class variables) in addition to continuous variables, which require as many df as the number of classes, minus one. Although this is demanding in terms of degrees of freedom, it allows for combining the strength of the multiple regression and the multiple analysis of variance (MANOVA). Categorical variables such as year, month, moon phase, period of the day, area, vessel, and fishing gear characteristics can be incorporated in order to derive less biased abundance indices, especially when the sampling design is not fully balanced, as is always the case when fishery data are used. Furthermore, continuous environmental variables such as temperature, turbulence, or upwelling indices can be categorized in order to explore non-linear effects, including non-monotonic ones.

General additive models (GAMs: McCullag and Nelder, 1989; Hastie and Tibshirani, 1990) are extensions of the GLMs. They allow the exploration of the nonlinear relationship that may exist in a data set without the need to transform or categorize continuous variables (e.g., Cury et al., 1995). The general form of such models is:

$$S(B, CPUE, C \text{ or } R) = T1(B) + T2(V) + \dots + \varepsilon$$

(3)

where the functions $S()$ and $T()$ are unknown and must be non-parametrically estimated from the data. The ε are independent, identically distributed, zero mean random variables, usually assumed to be Gaussian but not restricted to that assumption. GAMs accommodate non-linearities by replacing linear terms with a choice of smoothers applied over a user-given span. The optimal fit is obtained by iteration and the results are displayed in a graphical form where smoothed functions show the relationships between a response variable and a predictor with no a priori assumptions of the shape of these functions (Fig. 12). The shape of the transformed values is expected to reflect known ecological processes. This method is less mathematically rigorous than GLM, but still displays approximated significance levels. GAMs are not recommended for data sets that are too small (roughly, n < 30) because the
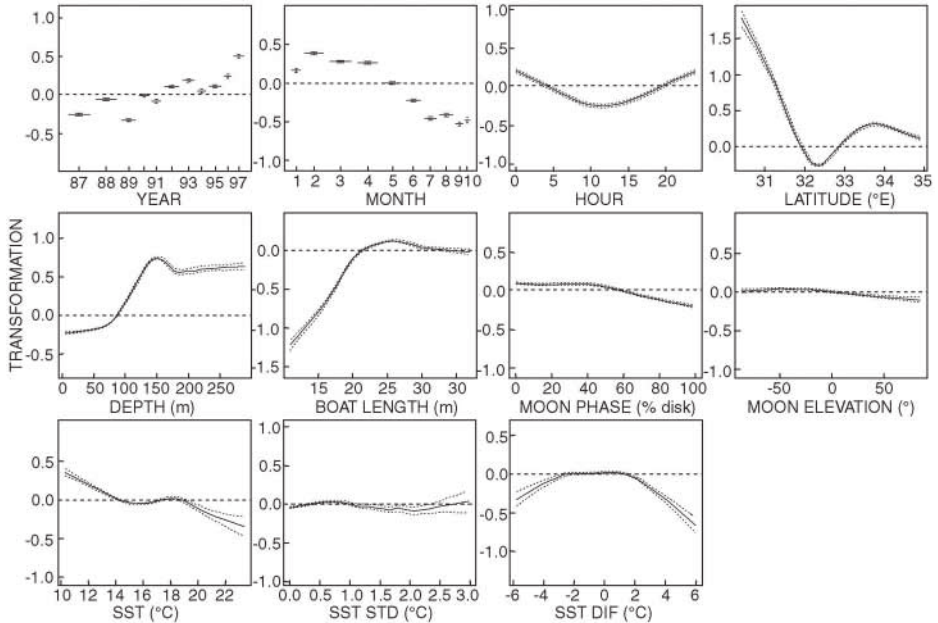
Figure 12. Tracking nonlinear effects using general additive models (GAM): the example of the influence of spatial, temporal, environmental and fishery factors on the catch per set of round herring (*Etrumeus whiteheadi*) in the South African fishery (after Agenbag et al., 2003).

smoothing functions require a minimum span to be efficient and therefore the confidence intervals are increased at each extremity of the time series. A recommended approach is to start exploring the shape of the relationships in the model using GAM and then to reproduce them by simplified functions in the GLM (e.g., Agenbag et al., 2003).

A less empirical modeling approach consists of the incorporation of an environmental variable into conventional models used in stock assessment. Three major kinds of models were modified: (1) Stock-recruitment relationship:

$$R = f(S, V)$$
(4)

where R is the recruitment expressed as number of fish entering the fishery or their total biomass, S the spawning stock biomass, V an environmental variable, and $f()$ the modified stock-recruitment function, usually derived from conventional functions proposed by Ricker (1954) or Beverton and Holt (1957). Parrish and MacCall (1978) or Stocker et al. (1985) provide examples of such modifications; (2) Separable Virtual Population Analysis (VPA). In this modified VPA, the fishing mortality is allowed to vary according to changes in catchability:

$$F_{(a,y)} = s(a) f(y)$$
(5)

where $F_{(a,y)}$ is the fishing mortality for age a during year y, and $s(a)$ an empirical age-specific function often related to catchability (Doubleday, 1976; Pope, 1977), while $f(y)$ is a year-specific factor (Megrey, 1989). These functions can incorporate an en-

vironmental factor influencing catchability; (3) surplus production models can be expressed as:

$$CPUE = q(V)B \propto (V) - q(V)^2 E/h + \varepsilon$$

(6)

where $q(V)$ and $B\propto(V)$ are functions reflecting changes in the catchability coefficient and the carrying capacity respectively according to an environmental variable V. The CLIMPROD software, distributed by FAO, allows the selection and fit of the most appropriate model through a user-friendly interface linked to an expert-system (Fréon et al., 1991; 1993b).

Artificial intelligence approaches, such as expert systems, neural networks, or fuzzy logic, can be used to model environmental effects. One can distinguish between a top-down approach and a bottom-up one. In the top-down approach, the modeler decides on the kind of relationships and/or processes that should be incorporated in the model and the artificial intelligence is then only used to fit the model. This approach was used by Korrûbel et al. (1998) and Painting and Korrûbel (1998) to predict the South African anchovy recruitment from seven environmental and biological variables acting over a given threshold. The above-mentioned CLIMPROD software also falls into this category as far as the selection of a modified surplus-production model is concerned. In the bottom-up approach, the modeler incorporates a non-limited set of environmental variables thought to influence the stock or the fishery, and allows the model to find weighting factors for all of them through an iterative approach. This is typically the case for unsupervised neural networks, which in a sense, are related to empirical multiple regressions and PCAs. This approach was used by Aoki and Komatsu (1997) to test Japanese sardine recruitment against eleven variables (five hydrographic, three biological, and three climatic ones).

Individual-based models (IBMs) and similar object-oriented models can be considered as process-orientated tools to investigate the effect of environmental and biological variables on fish population dynamics. IBMs can describe interactions between the environment and individuals having different behavior and life history traits within a population, as they permit the spatial representation and integration of environmental, ecological, and biological data (DeAngelis and Gross, 1992; Tyler and Rose, 1994; Letcher et al., 1996; Grimm, 1999; Werner et al., 2001; Mullon et al., 2003). These models have been mainly used to investigate the mechanisms underlying recruitment variability at different (usually small) temporal and spatial scales. They can be coupled to hydrodynamics models to allow testing of the effects of passive transport on spawning patterns or survival of early life stages of fish (Mullon et al., 2002, 2003; Huggett et al., 2003; Parada et al., 2003).

Steps and Associated Difficulties in Modeling Environmental Effects

Most attempts at using models to predict the effects of the environment on fisheries failed after some years of use, thus fishery management is seldom based on such models (Myers, 1998; Barange, 2001). The reasons for such failures are numerous, not always fully understood in terms of processes, and are not necessarily the same in every case. In the following paragraphs we try to indicate the successive steps to follow for modeling environmental effects and discuss the associated difficulties.

The first step when trying to model environmental effects on a fishery is to identify the type of influence of environmental factors: on abundance, catchability, or both. This distinction is not always obvious and the key aspect to consider is the time lag between the occurrence of the environmental change and the response of the fishery; typically, environmental influences on abundance lag by several months or years while environmental effects on the catchability is either instantaneous or lag by a few days or weeks. Nonetheless, in the case of short-lived species or species exploited only during their first year of life, the distinction between these two types of effects can be difficult due to autocorrelation in time series. Furthermore, in some instances environmental effects can influence both the abundance and the catchability of the stock.

If the environmental influence is on abundance, the second modeling step is identifying the critical stage of development at which this influence occurs. Nonetheless, this task is hampered by the existence of correlations between the abundance of the different stages of development of the fish (Rothschild, 1986). Any of the above-mentioned empirical approaches can be used, but a more appropriate solution is expected from process-oriented and spatialized studies like IBM.

The next step will be defining the appropriate spatial and temporal window in which the process occurs. Depending on the critical stage of development influenced by the environment, one would focus on the spawning grounds during the spawning period (effect of the environment on the parental stock or on the very early stages), on the nursery grounds after the spawning season (effect of larval stage or pre-recruits) or on the whole area of distribution all year round (effect on recruits and adults). Making use of cross-correlations at fine temporal scales (typically 1 mo) between an environmental factor and abundance at several stages, combined with spatial analysis when relevant, can be helpful in this identification.

Choosing the key environmental variable is a crucial step because the frequent co-linearity observed in these variables may lead to a spurious correlation. The corresponding model will fail when the correlation between these variables weakens. A typical example is the correlation between two indices related to two different processes: on the one hand upwelling indices, proportional to a directional component of the square of the wind velocity and reflecting enrichment and transport processes, on the other hand the turbulence index, proportional to the cube of the absolute magnitude of the wind speed (regardless of its direction) and used as a proxy for food availability. Any strong anomaly in the wind direction will weaken this correlation. Another typical example is the correlation between SST and upwelling indices: these two variables are usually highly correlated in upwelling areas, except when other processes operating on large scales influence temperature.

Fully understanding the ecological processes involved in the effects of environmental variables is a crucial final step, although strongly linked to and intermingled with the two previous ones. The order in which these three steps should be taken depends on the status of our understanding. Different physical (e.g., advection of larvae) or biological (e.g., mortality, growth) processes can potentially occur at the same location or time and can involve the same environmental variable but nonetheless should be modeled differently with different linear or non-linear equations. The problem is even more complex when, as suggested by many conflicting results, no single process and/or no single environmental variable is responsible for large variations in recruitment. Our experience in the Benguela region suggests that the

large variability in anchovy recruitment can be mainly due to anomalies in transport success between the spawning and nursery grounds in some years, but to anomalies in ichthyoplankton retention and food enrichment in the nursery area in others (Hutchings et al., 1998; Roy et al., 2001; Roy et al., 2002; Mullon et al., 2003).

Using meta-analysis on several fish stocks, Myers (1998) found that correlations for populations at the limit of a species' geographic range have often remained statistically significant when revisited. This means that in the northern hemisphere, populations close to the northern limit of the species range show positive correlations while those at the southern limit show negative correlations. It is mainly in these situations that environmental influences might be successfully modeled. Our final recommendations to improve research on this topic, partly inspired by Myers' (1998) work, can be summarized as follows: (1) do not start modeling before understanding the ecology of the species and the ecosystem; (2) keep in mind that process-oriented approaches are more demanding than empirical ones, although less risky; (3) recognize that many patterns may simply be artifacts, but do not ignore non-linear relationships, especially non-monotonic ones; (4) carry out modeling on the relevant processes at the appropriate spatial and temporal scales; (5) consider that the influence of the environment is not necessarily limited to early life history; (6) test general hypotheses on many populations at once and look for consistency of results across similar ecosystems (comparative approach); (7) separate exploratory from confirmatory analysis; (8) use data splitting (Cox, 1975) to validate the models; (9) correct for the loss of df caused by autocorrelations in space and time (make use of pre-whitening or re-estimation of the number of df; de-seasonalize time series if time resolution is lower than 1 yr); (10) do not systematically test all possible time and space combinations of a given variable and do not make use of all available environmental variables; a rule of thumb should be to remove as many additional df as previous modeling attempts; (11) take into account the effects of changes in exploitation patterns; (12) use all available indices of abundance (CPUE, catch per set, biomass estimates from surveys or population dynamics models, etc.) because they all have their meaning and value; 13) accept the idea that a model is not valid forever due to changes in the ecosystem dynamics and in the fishery; and 14) do not try to extrapolate model results beyond the extent of the spatial and temporal scales examined.

Conclusion

The short-term influence of the environment is largely dominated by its effects on the behavior, distribution, and hence catchability of the fish. In contrast, medium- and long-term effects are mainly reflected in the mortality and growth of young fish, which translate into interannual or interdecadal changes in abundance. Despite constant progress in understanding the complex processes involved in the variability of pelagic stock abundance, especially at short and medium time scales, our ability to model and predict pelagic fish abundance is limited. Substantial progress can be expected from an integrated modeling approach of spatialized models coupling hydrodynamics and biogeochemical processes and ecological processes at the individual species level, but also at the level of the whole ecosystem as expressed in the next section.

Pelagic Fish Within the Ecosystem

Pelagic fish, like most other fish components of marine ecosystems, are heavily fished and global catches continue to increase (Fig. 1). As noted by Cury et al. (2000), it is doubtful that the global pelagic fish catch will continue to increase at an annual rate of 4.3%, as has been the case worldwide since the 1950s, without any ecosystem disruptions at different trophic levels. The modern desire to understand ecosystem dynamics and particularly the ecosystem effects of fishing (ICES, 2000) faces serious limitations, as we lack points of reference in most cases. The structure of pristine marine ecosystems is not known and most of the time, pristine ecosystems are inaccessible or out of reach. However, data from early fisheries in the northwest Atlantic suggest that abundance of demersal stocks was an order of magnitude greater than at present (Steele and Schumacher, 2000). Relative to the current ecosystem structure, these authors suggest that alternative patterns have occurred in the past, involving a very slow growth rate of the demersal fish, small pelagic stocks, negligible invertebrate predators and efficient transfer of primary production to fish. These speculations demonstrate the need for a better understanding of the functioning of marine ecosystems. In this section we will review current hypotheses and patterns in ecosystems that are linked to pelagic fish stock dynamics.

Bottom-up, Top-down, and Wasp-waist Controls in Upwelling Ecosystems

Pivotal Role of Pelagic Fish in Upwelling Systems.—In upwelling systems, pelagic fish species occupy a crucial intermediate trophic level as they mostly feed on phytoplankton and/or zooplankton. They also develop large biomasses, which vary radically in size according to recruitment strength, and which are dominated by one, or at most, several schooling species in a given ecosystem which undergo large interannual fluctuations in biomass as shown in the Benguela ecosystem (Fig. 9). Pelagic fish in upwelling systems serve as forage fish (Anonymous, 1997), and consequently play an important role in the functioning of marine ecosystems. As in the case of any other species in the ecosystem, the role of small pelagic fishes mostly depends on trophic flow control. In other words, who is controlling whom in a marine ecosystem? For many years, ecologists have been debating the importance of bottom-up (the control by food) versus top-down (the control by predation) control in terrestrial and freshwater ecology (Matson and Hunter, 1992), and the discussion is no longer about which occurs, but rather about what controls the relative importance and strength of the various forces that are acting between the components of the ecosystem. The literature on trophic flow control in the marine environment is limited and in particular, the role of pelagic fish is not often documented. In what follows, we explore the role of pelagic fish in upwelling systems using three different perspectives; i.e., considering three different types of trophic flow controls and illustrating each by means of case studies.

Bottom-up Control and Pelagic Fish.—In 1887, Victor Hensen viewed planktonic populations as rapidly revolving links in a food chain, leading from the very small to the very large (Hensen, 1887; Smetaceck, 1999). Using an analogy with agriculture where crop yields can be predicted from the control of the input, Hensen made the assumption that food supply regulates adult fish stocks, and quantitative studies of phytoplankton and zooplankton production would permit predictions of fish yields (Verity, 1998). From this deduction was born the notion that ecosystems were "bot-
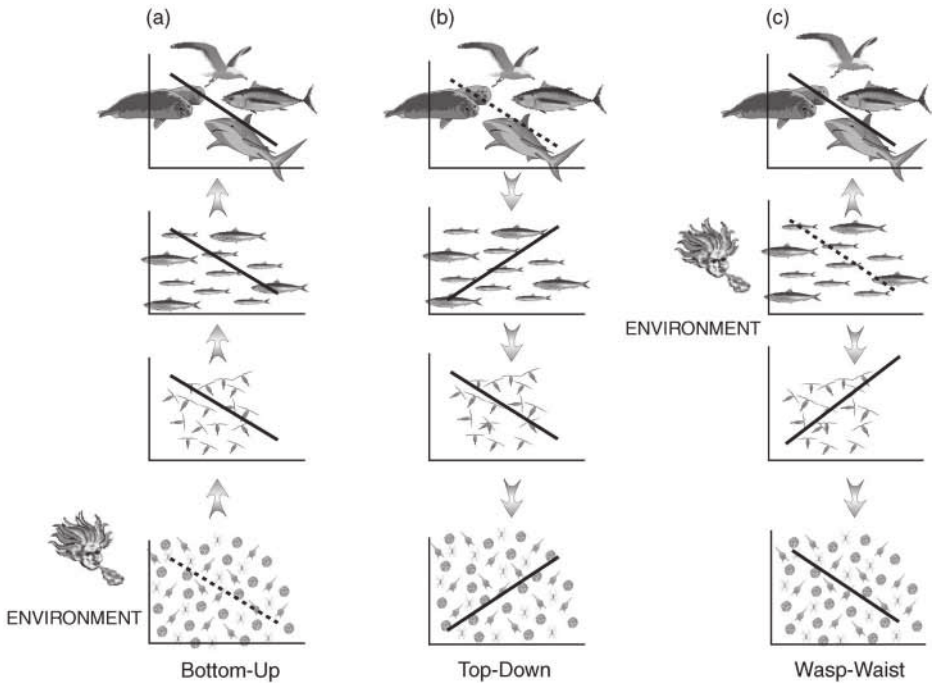
Figure 13. Different types of trophic controls within a simplified four-level food web in a marine ecosystem and the role of pelagic fish. The control factor is represented by a dotted line and the responses by solid lines (after Cury et al., 2002). *Bottom-up control:* The physical environment, being less favorable, 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. *Top-down control:* The decreasing size of populations of the top predator 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. *Wasp-waist control:* The abundance of the prey fishes (small pelagic fishes), which are dependent on the environment, controls both the abundance of predators and primary producers. The environment is considered here to have a direct physical effect on pelagic fish recruitment (sensu Sinclair, 1988), but no effect on primary productivity and the food chain.

tom-up" controlled (Fig. 13A). In other words, the regulation of food-web components is thought to be by means of either primary producers or the input of limited nutrients (Pace et al., 1999). Accordingly, parallel long-term trends across marine trophic levels could be predicted. According to this theory, fish recruitment in the marine environment can be viewed as being typically controlled by bottom-up forces (e.g., Menge, 2000). This implies that fluctuations in primary production would determine the strength of the recruitment (Cushing, 1996).

This bottom-up control has been the main hypothesis used to explain fluctuations in recruitment of pelagic fish. Currently, there is considerable evidence that natural variability in ocean circulation and mixing plays a major role in generating fluctuations in fish recruitment as illustrated in the previous section. Physical factors can act directly on egg or larval mortality (not necessarily through the intermediary of the primary production) and even in a situation where more food is produced, this will not necessarily mean better larval survival.

Identifying bottom-up control in a marine ecosystem means observing changes at several trophic levels. The impact of environmental variability on different trophic levels within a particular ecosystem is seldom documented, except in certain cases, where major environmental changes seemed to have affected ecosystems. The structure and function of marine ecosystems sometimes 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 (Aebisher 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 (Aebisher et al., 1990). Hollowed et al. (2001) analyzed 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.

These dynamics are assumed to be driven by oceanic changes. Environmental changes are pervasive and, in most cases, difficult to detect. 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 North Pacific (McGowan et al., 1998). Large-scale perturbations have taken place during the past 20 yrs 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–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.

It seems that 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 McFarlane et al. (2000), one method of measuring climate change and regime shift is to observe the dynamics of species that could be affected. Obvious environmentally-induced ecological changes are expected in ecosystems and bottom-up control is the most conventional type of trophic flow control that seems to dominate most ecosystems (Cury et al., 2002). However, findings in one system cannot necessarily be extrapo-

lated to others, and predicting the effects of global-scale environmental change on ecosystems does not appear to be a straightforward exercise.

Top-down Control and Pelagic Fish.—Because species mostly interact through predation, the existence of top-down control, which means the regulation of lower food-web components by one or several upper-level predators, should also be critical in the functioning of marine ecosystems (Fig. 13B). Piscivory is the largest source of fish mortality in most marine ecosystems, and usually it represents a larger amount than fisheries' catches (Bax, 1998; Overholtz et al., 1999). Christensen (1996) estimated that finfish consume three times the total global catches of finfish. An analysis of six marine ecosystems (Benguela Current, Georges Bank, Balsfjord, East Bering Sea, North Sea, Barents Sea) reveals that predation is 2–35 times higher than fishing mortality (Bax, 1991). This does not mean that fishing has negligible effects on species dynamics but rather implies that it can affect the whole ecosystem as species are tightly connected through predation. Pauly et al. (2000a) demonstrated that fisheries have been fishing down aquatic food webs by removing substantial amounts of piscivorous fish, which occupy high trophic levels, and subsequently shifting fishing effort to species at lower trophic levels. As fisheries removed substantial amounts of small pelagic fish during recent decades, one must carefully consider the implications for other components of the ecosystem.

The hypothesis that top-down removal of predators is affecting production at lower trophic levels has been tested in most exploited ecosystems (Caddy and Garibaldi, 2000). This appears to have been the case in the North Atlantic, amongst other areas, where fishing down marine food webs may have been a likely cause of the increase in landings of shelf planktivores. Using the FAO catch time series, Caddy and Garibaldi (2000) also show that in the case of the eastern central Atlantic and in the southeast Pacific, it took a long time to observe a sharp increase in planktivores. They attributed this delay to varying strength of upwelling (i.e., bottom-up control), a change in harvest technology or a possible lag between the release of predation and the response at an ecosystem level. These results, obtained with data that were not collected for the purpose of studying ecosystem dynamics, provide some contrasting patterns of interaction in several ecosystems. However, the authors suggest that the actual changes in ecosystems more closely follow patterns of "punctuated equilibrium" rather than just continuous change in the relative abundance of the various species (Caddy and Garibaldi, 2000).

During the last four decades there has been a drastic shift, both in abundance and size composition, in the piscivorous community on Georges Bank, which was attributed to fishing pressure (Link and Garrison, 2002). The total amount of fish consumed did not decline, as expected, as the size of fish in these populations declined and the total consumption of predators on Georges Bank was relatively constant. However, one of the principal effects of intensive fishing was a major shift in the allocation of biomass in the ecosystem. Intense fishing intensity would result in a shift of the energy flow in marine ecosystems. In the Yellow Sea, Jin and Tang (1996) analyzed the fish community during different decades and concluded that the depletion of most demersal fish and large size pelagic fish resulted in an increase of small planktivorous fish. In the Black Sea, the sharp decrease of top marine predators, together with increased impact of eutrophication, led to increases in planktophageous species (Daskalov and Prodanov, 1998). In the central Baltic Sea, after the decrease in stock size of the cod as the top predator, the ecosystem moved from a cod-domi-

nated system in the 1980s to a clupeid (sprat)-dominated system in the 1990s, which appears to have a strong impact on the abundance of zooplankton (Kornilovs et al., 2001).

Analyzing the structural changes in an exploited fish community in the northern North Sea, Jennings et al. (1999) showed that there are differential effects of fishing on species with different life history parameters, illustrated by a shift towards small species with fast life histories as fishing effort increased. This supports the fact that fishing has had greater effects on slower growing, larger species with late maturity. Pelagic fish appear to be more resistant to exploitation; all species are not equal with respect to their life history traits.

More pelagic fish may be expected when large top predators are heavily exploited. This pattern is observed in many ecosystems, but with varying intensities and delays. Control by predators (top-down control) plays an obvious role in dampening ecosystem-level fluctuations, but mostly it appears that pelagic fish populations will react differently according to the structure of the ecosystem, sometimes with important delays.

Wasp-waist Control.—More recently, the role of pelagic fish has been emphasized in upwelling systems, where they might exert a major control on energy flows, both upwards to their predators and downwards to their zooplankton prey. This has been termed "wasp-waist control" (Fig. 13C). In 20 open marine ecosystems, Micheli (1999) found that interannual fluctuations in mesozooplankton biomass were negatively correlated with those of pelagic fish, indicating that fish predation can control mesozooplankton biomass. Similar top-down control of zooplankton by sardine, sardinellas, herring, or anchovy was also detected in the northern Baltic (Arrhenius, 1997) as well as off South Africa, Ghana, Japan, and the Black Sea (Cury et al., 2000). In the central Baltic Sea, Kornilovs et al. (2001) also detected an influence of sprat biomass on the production of cladocerans in summer. Conversely, bottom-up control of fish predators by small pelagic fish has been found in the Benguela and the Guinea Currents, as predatory fish appear to suffer from the collapse of their prey (Cury et al., 2000). Once food becomes abundant again, the recovery of the depleted fish predator biomass may be immediate, or delayed by short or long periods, highlighting the complex response of the ecosystem to change. Despite great plasticity in life-history characteristics, many seabird populations cannot dampen the effects of longer-term fluctuations in prey resources (Crawford, 1999). This was the case off Namibia in the 1970s, when sardine in the diets of birds was replaced mainly by horse mackerel and pelagic goby. Because these fish were either distributed too far north, or occurred too deep in the water column, they were unavailable to penguin and gannet colonies situated south of Lüderitz, causing massive decreases in seabird populations in this region (Crawford et al., 1985).

In the Benguela system, guano harvests were related to trends in the abundance of breeding seabirds, which in turn reflected the abundance of forage fish (Crawford and Shelton, 1978). Shifts in the dominance of anchovy and sardine off southern Africa strongly influence the distribution and abundance of the African Penguins (Crawford, 1998). The collapses of penguin colonies along the west coast of southern Africa, and an overall 25% decline in the African Penguin population coincided with a decrease in sardine during the 1980s (Crawford, 1998). When the sardine stock began to increase in size in the 1990s, west coast colonies stabilized and new colonies were formed near Cape Town. However, a major decrease in the number of penguins

at Dyer Island on the south coast, associated with reduced availability of small pelagic fish in this vicinity, accounted for a further reduction of 19% in the overall African Penguin population (Crawford, 1998). Another direct impact of fishing on the ecosystem is caused by the practice of discarding fish or offal at sea. Predators with flexible foraging strategies take advantage of discarded fish. This can allow scavenger seabirds and marine mammals to become more abundant, and outcompete others with less flexible modes of feeding (David, 1987; Ryan and Moloney, 1988; Berruti et al., 1993; Furness, 1999).

These examples illustrate wasp-waist control, where abundant small pelagic fish constitute mid-trophic-level populations that exert both top-down control on zooplankton and bottom-up control on top predators (Fig. 13). It is important to stress that under wasp-waist control, the environment plays a direct role [sensu Sinclair (1988) and Bakun (1996)] in determining the strength of the recruitment (i.e., it does not act directly through the primary production sensu Cushing, 1996).

Three different types of energy flow in ecosystems can thus be considered, resulting in different and contrasting views on how pelagic fish populations interact with the other components of the ecosystem. These considerations can be explored by studying ecosystem dynamics using trophic models.

Trophic Models and Their Difficulties

Before the late 1970s, provision of scientific advice for the management of fisheries was largely restricted to information obtained from assessments of single exploited fish stocks. Gradually, direct and indirect effects of both harvesting and predation gained recognition. Starfield et al. (1988) and Crawford et al. (1989) viewed multispecies models as a means of testing the effectiveness of more specific models, as opposed to striving to understand the ecosystem or evaluate harvesting strategies. However, multispecies models of today are also useful in achieving the latter two objectives (Whipple et al., 2000). "Holistic" models as opposed to coupled single-species models soon began to attract attention. According to the holistic modeling approach, an ecosystem is considered to be a functional whole with distinct "emergent" properties that are absent at lower organizational levels such as the community or population level (Mann et al., 1989). Holistic models include those of Beverton and Holt (1957), the North Sea fisheries model of Anderson and Ursin (1977), and spatial and temporally explicit DYNUMES models (Laevastu, 1990) such as DYNUMES III, the Bering Sea ecosystem model of Laevastu and Larkins (1981). Many of these kinds of ecosystem models are biomass-based, largely because fisheries are measured in terms of total catches. However, ecosystem models using other units of flow have also proved useful; e.g., carbon budget models (Bergh et al., 1985) and models of nutrient cycling (Moloney, 1992). During the 1980s, the ICES Multispecies Working Group was established to seek ways of incorporating interactions between species in fish stock assessments (Pope, 1991). Arising from the work of Andersen and Ursin (1977), and based on contributions by Helgason and Gislason (1979), Pope (1979), and Sparre (1980), Multispecies Virtual Population Analysis (MSVPA) was developed to take into account mortality caused by both fishing and predation. MSVPA is a data-intensive approach (Sparre, 1991); detailed age-specific catch data and extensive diet data are required inputs. Uncertainty around MSVPA model results is high given the large number of parameters involved (Whipple et al., 2000). Further,

suitability coefficients must be estimated to define the importance of each prey species age class for each predatory species age class.

Heavy parameterization requirements have largely limited the use of holistic models, and restricted MSVPA to the fish groups within an ecosystem. IBMs, which model populations by summing individuals, have been incorporated into multispecies models (Rose et al., 1999) and are possibly more holistic than MSVPA models. However, heavy data requirements are again often problematic, and computer time and memory demands restrict the extent to which whole ecosystems can be realistically modeled.

Ecopath with Ecosim is a dynamic simulation tool in which changes in biomasses and consumption of all groups within an ecosystem can be simultaneously modeled (Pauly et al., 2000b). This is a major advantage above MSVPA type models because trophic interactions for all trophic levels are well represented, including those at lower trophic levels, often lumped into a category such as "other food" in MSVPA models (Walters et al., 1997). Ecopath with Ecosim can be applied to a wider range of ecosystems than the MSVPA type models because data requirements are fewer and sufficient data are usually readily available (Whipple et al., 2000). It provides a standardized modeling approach to analyze food webs, facilitating meaningful comparisons to be made between ecosystems. Spatial dynamics of ecosystems are considered using Ecospace, an extension of Ecopath with Ecosim (Walters et al., 2000). Biomass per species is allocated dynamically across the defined spatial grid and fishing effort is spatially defined. Horizontal movement is modeled between cells, depending on the allocation of preferred habitat and predation risk per species group. Ecospace is a relatively new approach incorporating biotic and physical habitat constraints and seasonal migration, amongst other factors, to produce a useful tool for fisheries policy exploration (Pauly et al., 2000b; Walters et al., 2000).

Larkin (1996) notes that in order to achieve successful ecosystem management, it is necessary to (1) distinguish between environmental and fishing effects, (2) understand the dynamics underlying interactions between species, and (3) consider the ways in which fisheries will respond to changes in stocks. Using Ecopath with Ecosim, it is possible to partly address the latter two actions. Other trophic models address the first one (e.g., Collie and DeLong, 1999). Ecopath with Ecosim builds on the mass-balance approach and makes it possible to explore the effects of altered fishing mortality of selected groups on the whole ecosystem. In this way, resistance and resilience of the ecosystem towards different fisheries management options can be explored. In discussing the strengths of Ecosim, Whipple et al. (2000) mention its usefulness in focusing monitoring effort on variables that are likely to be sensitive to changes over time. Jennings and Kaiser (1998) believe that, if refined, Ecopath with Ecosim should prove to be a valuable tool with which to model spatial structure and complexity, and assess ecosystem effects of fishing, thereby assisting development of ecosystem management advice.

Alternation Between Small Pelagic Fish Species and Regime Shifts: From the Ecosystem Dynamics Perspective

While the alternation between small pelagic fish species was interpreted from the environmental effect point of view in the sub-section "Alternation between small pelagic fish species and regime shifts: from an environmental perspective," here we develop the point of view of the dynamics of the ecosystem (internal dynamics or an-

thropogenic effects), although both points of view are not completely independent, nor exclusive.

Interaction Dynamics Within the Ecosystem.—The temporal dynamics of small pelagic fishes involve intermittent rarity; that is, the alternation of variable periods of time where extremely low abundance is followed by very high abundance. Reconstructing time series of past fish abundances over several hundred years can provide a clear demonstration of the instability of pelagic fish populations, even without any fishery (e.g., Baumgartner et al., 1992; fig. 8). Thus an analogy with the catastrophe theory (Zeeman, 1978) has been used several times to illustrate observed alternative stable states (Peterman et al., 1979; Cury, 1988).

Vandermeer (1993) investigated the dynamics of a community composed of two predators and two prey, and showed that if the predators demonstrate asymmetric preferences for their prey, then the community can no longer be sustained and one prey goes extinct. Among the many theoretical models that have been developed, one should be mentioned because it constitutes a generalization of a two species competition model applied to the Pacific sardine data. Assuming two interacting populations affected both by intra- and interspecific competition, Ferrière and Cazelles (1999) demonstrated that the distribution of time spent in phases of rarity involves strong regularity. Specifically, intermittent rarity of this dynamic system, composed of interacting species, is governed by a well-defined power law. The authors showed that the scaling exponent ($-3/2$) could represent a universal feature of intermittent rarity: it does not depend on the demographic parameters of species; it is insensitive to environmental stochasticity. It also implies that the dynamics of rarity have no characteristic time scale and can only be supported by the prediction of a $-3/2$ power law which might underlie intermittent rarity in marine fish community dynamics. In other words, although the dynamics in population outbursts look qualitatively very different, rarity phases possess the same statistical property. In practice this generalization offers a general form of prediction, in which one can calculate the frequency of occurrence of rarity phases of any duration.

The school trap hypothesis (Bakun and Cury, 1999) appears to offer a mechanism for Skud's (1982) observation (previously introduced in the section on Biology) that a dominant species responds to environmental factors, while a subordinate species responds to the abundance of the dominant one. To recap, it postulates that a fish species driven to school together with a more abundant species must effectively subordinate its specific needs and preferences to the "corporate volition" of the school. Thus the dominant species would largely control the "corporate volition" of the schools. On the other hand, since the needs of the subordinate species are not optimized, its variability may be controlled more by the adverse effects of the "school trap" than by the environmental variation itself. This school behavior involving mixed species, driven by the needs of individuals, may inflict costs at the population level and could account for the apparent inverse correlation between the population variations of assemblages of pelagic species (see Bakun, 2005; this issue).

Modeling by Shannon et al. (2004) suggests that size structure of the mesozooplankton community is a possible driving force behind the shifts in dominance of small pelagic fish in the southern Benguela ecosystem. Van der Lingen (1994, 1999) and James (1987) have shown that anchovy feed by biting large mesozooplankton and macrozooplankton, whereas sardine filter-feed small mesozooplankton. In the southern Benguela ecosystem, changes in the zooplankton community structure

(Verheye et al., 1998) suggest long-term, continuous environmental change. Such regime shifts, driven by long-term change in the plankton community, can occur only if there is a major differentiation between the dominant pelagic species. Off Peru, larvae of anchoveta *E. ringens* and sardine *S. sagax* have different diets; anchoveta larvae feed on phytoplankton whereas sardine larvae feed on zooplankton (Muck et al., 1989). By comparison, diets are similar in older anchoveta and sardine (Muck et al., 1989).

Anthropogenic Effects.—Fishing may trigger interdecadal changes in pelagic fish abundance or alter the changes from their natural course. Modeling by Silvert and Crawford (1988) supports this; they found that replacement of one pelagic fish species by another could be attributed to a combination of fishing and competition between predatory fish species for forage fish. Management options for the Peruvian system considered the potential for anchoveta to recover following a collapse, if fishing and predation pressures are light (Muck, 1989). This would require heavy fishing on important predators of anchoveta (Muck, 1989), namely horse mackerel and mackerel (Muck and Sanchez, 1987), with no guarantees for a successful outcome for anchoveta. Similarly, Cisneros-Mata et al. (1996) modeled fluctuations of sardine in the Gulf of California, concluding that fishing has large effects on a modeled sardine stock undergoing long-term environmental forcing, and that recovery is slow (20–40 yrs) after modeled fishing is stopped. However, the model showed that the sardine stock in the Gulf of California shows resilience; it is able to recover after a near collapse.

Within a pelagic community, the removal of the dominant species should favor the subordinate species, provided that the latter is only lightly exploited. This line of thinking led to the targeting of anchovy when the commercially valuable sardine collapsed off Namibia in the 1970s; it was thought that reducing anchovy would be beneficial to sardine, its competitor (Butterworth, 1983). However, sediment core analysis (Shackleton, 1987, 1988) suggests that the two species did not compete. This attempt at reversing the collapse in sardine failed, and both anchovy and sardine severely declined in the late 1970s. In contrast, when sardine off South Africa collapsed in the late 1960s, anchovy were conservatively managed, which enabled anchovy to attain large biomasses, resulting in a successful anchovy fishery during the 1980s. Using an age-structured model to investigate the alternation between anchovy and sardine populations in the southern Benguela system, Korrûbel (1992) found that harvesting was important in determining the dominance of stocks.

Fishing can affect both exploited and unexploited species that compete with exploited species for food, as for example, in hake and horse mackerel (Crawford et al., 1987). Adult horse mackerel *Trachurus trachurus capensis* Castelnau (1861), and juvenile hake *Merluccius* spp. have similar diets and feeding grounds, so that a decrease in one of these species can improve feeding conditions for the other (Krzeptowski, 1982). The interactions between the two species are further complicated because hake feed on horse mackerel (Konchina, 1986). Another example from the Benguela system is that of chub mackerel *Scomber japonicus* Houttuyn, 1782 and anchovy. The diets of both species comprise substantial proportions of macrozooplankton (Baird, 1978; Armstrong et al., 1991), so that increased fishing on anchovy reduces competition between anchovy and chub mackerel, perhaps enabling chub mackerel to become more abundant (Shannon et al., 2000). Off Peru, the biomass of anchoveta and hake are inversely correlated (Espino and Wosnitza-Mendo, 1989),

probably because of predation (Muck, 1989). Heavy fishing on anchoveta affects the dominance of other species (Muck, 1989).

Other anthropogenic effects, such as contamination, modification of the quantity and quality of river discharges (more nutrients and contaminants, less natural debris) and the building of offshore structures (e.g., oil platforms), are less likely to directly affect small pelagic species because their habitat is usually extended and widely open to the ocean. Notable exceptions are those of closed or semi-closed areas like the Baltic Sea, where contamination and eutrophication play a major role in the ecosystem in general and on the small pelagic species in particular (e.g., Hansson and Rudstam, 1990).

Conclusion

Three different theoretical ways of considering energy flow through ecosystems have been presented. Top-down, bottom-up, or wasp-waist control produces different models of ecosystem dynamics, and consequently different possible ecosystem responses to fisheries activity and management, and different possible mechanisms to explain alternation between pelagic fish species (Cury et al., 2002). Obviously, the difficulty lies in our ability to determine the controlling factors within an ecosystem. Climate (bottom-up) as well as fishers (top-down) alter the functioning of marine ecosystems. However, an ecosystem is not driven entirely by only one type of control, but by a subtle and changing combination of control types that might depend on the ecosystem's state, diversity, and integrity.

In conclusion, it is now generally believed that regime shifts and alternation between small pelagic fish species are primarily environmentally driven and that fisheries hasten or intensify these collapses of pelagic fish stocks (Collie and Spencer, 1993; Jennings and Kaiser, 1998; Fréon, 1999). Alternation of species purely due to the internal dynamics of the ecosystem, without any external (environmental or anthropogenic) influence, cannot be excluded but is difficult to prove because few data are available for long time periods without major modifications of these external factors. The type of control (bottom-up, top-down, or wasp-waist) may also influence the chronology of the events. Furthermore, environmental, anthropogenic, and ecosystem effects are often intermingled.

Sustainable Management of Small Pelagic Fisheries

Following the "reign of conventional stock assessment and fishery management," there was a growing awareness of the necessity to view fisheries as part of the ecosystem and to appreciate not only population dynamics considerations, but also biological, social, economic, and political objectives (e.g., Rothschild, 1973). More recently, ecological and ecosystem aspects have been added to this list. In this section we will first deal with the issue of stock structure and its implications for resilience to exploitation, then we will review the different management options, and afterwards, the different regulatory mechanisms. Finally we present a tentative two-level management strategy as an attempt to address the challenge of conciliating all the issues related to small pelagic fish developed in this section.

STOCK STRUCTURE AND RESILIENCE TO EXPLOITATION

Fishery management is based on stock assessment, which leads to the central question of the identification of stock units and of their structure. Traditionally, the identification of stock units was based on the distribution of the species (trying to identify gaps of low or nil abundance between regions) and knowledge of their reproductive migration (location of spawning, nursery, and foraging grounds). Later on, electrophoretic genetic studies were used, giving contrasting results. More recently, powerful techniques like differentiation of mitochondrial DNA and geochemical signature in otoliths indicate that stock structure may be more complex than initially thought. In some pelagic species, occurrence of parasites can give an indication of stock structure, as shown by Lester et al. (2001).

The loss of small pelagic fish species diversity has not been, and is not currently, an issue in biological conservation as almost no pelagic fish species are endangered (Beverton, 1990). It seems that populations reduced to the order of one-thousandth of their peak sizes for extended time periods (e.g., more than 20 yrs in the case of the Californian sardine), can form a nucleus for subsequent recovery when conditions become favorable again (Beverton, 1990). In this sense, reduction of intraspecific diversity does not represent the same kind of threat as does species extinction. However, theoretical arguments as well as new findings contradict any simplified views of, and possible impacts on, fisheries. The threats to intraspecific genetic diversity need particular attention in large and highly fluctuating populations. Ryman et al. (1995) emphasized that the long-term genetic effects with regard to allelic diversity of reduced population sizes are more dramatic for large populations than they are for small ones. Considering the evolutionary scale, low levels of gene diversity in *Sardinops* and mutation-drift disequilibria are consistent with a strong reduction in population size of an ancestral *Sardinops* population before the late Pleistocene dispersal to the corners of the Indian-Pacific Oceans (Grant and Leslie, 1996; Grant and Bowen, 1998). Recently observed population collapses are also likely to have a serious negative impact on the evolutionary potential of the species, as a lot of rare alleles, which may be of importance for future adaptation, will be lost (Ryman et al., 1995). However, the immediate biological implications of excessive losses of alleles for fisheries management are not clear and would most likely go undetected in a typical genetic study. In bottom spawners like herring, managing within-species diversity seems feasible on the basis of spatial management units (Smedbol and Stephenson, 2001).

Most pelagic fish populations are regarded as homogeneous and resilient. However, several recent studies suggest that marine fishes are subdivided into weakly differentiated populations. It is unclear which kind of genetic population structures this reflects exactly, but these studies sometimes reveal complicated spatio-temporal structure in species. Genetic heterogeneity between supposedly panmictic stocks has been noticed for the northern anchovy in California, suggesting that the central stock is a mosaic of elementary populations, sensu Lebedev (1969) (Hedgecock et al., 1989; Hedgecock, 1991, 1994). In contrast, the same authors found little genetic variation in Pacific sardines (*S. sagax*) from five widely separated localities, despite an observed north-south gradient in size-at-age, interpreted as environmentally determined. This reported difference in genetic population structure between the two species is likely due to their differences in size and morphology, and to subsequent differences in their migratory capacities. Mathisen (1989) hypothesized that the an-
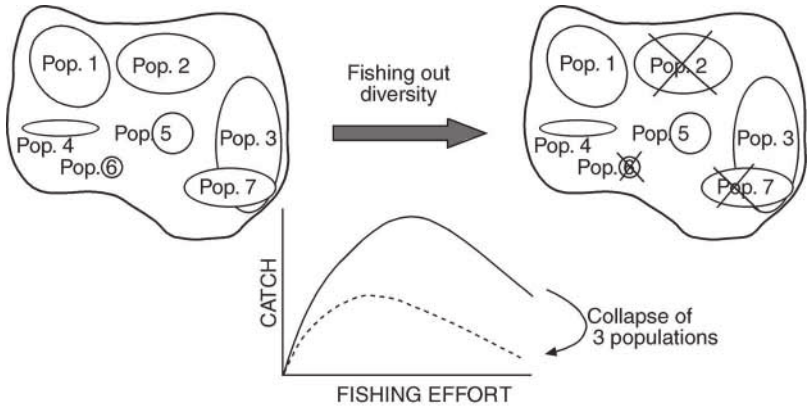
Figure 14. The erosion of intraspecific diversity may affect the productivity of the fisheries, as the disappearance of populations under an intense exploitation (from 7–4 populations) can have a detrimental effect on long-term marine fish catch. The associated decreasing productivity is illustrated by the catch-effort diagram where two catch levels are possible for a given fishing effort according to the two stocks composition (for the higher level the stock is composed of seven populations and for the lower level of four remaining populations). Redrawn from Cury and Anneville (1997).

chovy stock off Peru consists of a large number of local subpopulations adapted, to the different upwelling plumes and to spawning during a specific period of the year. Tudela et al. (1999) found genetic homogeneity for the European anchovy *Engraulis encrasicolus* (Linnaeus, 1758) in the northwestern Mediterranean despite the presence of three apparently well defined spawning grounds in this area. Other studies on the same species, but considering the whole Mediterranean and the adjacent seas, show a unidirectional gene flow from the Black Sea to the Aegean Sea, possibly through passive drift of larvae in the Bosphorus straits (Bembo et al., 1996; Magoulas and Zouros, 1999). More recently, Borsa (2002) found evidence for two genetically distinct anchovy populations in the entire Mediterranean Sea: an open-sea or oceanic population and an inshore population, while broadscale geographical variation is weak for each of these two habitat-specific forms. These last results illustrate how important the sampling scheme and scale are in relation to the genetic questions posed.

Tagging experiments and geochemical signatures in otoliths provide growing evidence of natal homing and fidelity to spawning grounds —also called "repeated homing" or "sexual homing"— of herring and demersal species (Corten, 1993; McQuinn, 1997; Robichaud and Rose, 2001; Thorrold et al., 2001) that may vary according to the geographic scale of the study (Hay et al., 2001). Limited references to small pelagic fish might simply reflect the difficulty of tagging such fragile fish, rather than the absence of such behavior. Discrete populations other than herring have been mostly hypothesized rather than demonstrated (Le Page and Cury, 1996). Sinclair (1988) and Sinclair and Iles (1989) formalized it as the "member/vagrant" hypothesis, based on the retention and isolation of larval stages through the interaction between hydrodynamic processes and natal homing (see also Page et al., 1999). McQuinn (1997) advocated the metapopulation concept for Atlantic herring to unify the divergent views of fully discrete populations (Sinclair, 1988) on one hand and dynamic population balance implying quasi-panmictic stocks on the other hand (Smith and Jamieson, 1986).

Table 2. Advantages and disadvantages of the different management strategies.

Method	Advantages	Disadvantages
Steady state	Easy to implement. Availability of reference points.	Not adapted to highly variable resources. Ignores ecosystem effects. Imposes conservative options to limit risks.
Adaptive	Flexibility in time. Decreases risks of collapses by taking major uncertainties into account. Makes use of good fishing opportunities.	Requires good annual stock assessment and fast data processing. Permanent uncertainty for fishing industry (investment, employment). Fishing allowance might not fit fleet capacity (if resource abundance too variable in time).
Predictive	Anticipation of future events (investment, employment). Makes use of good fishing opportunities.	Ecological processes not well enough understood to allow reliable predictions. Risk of over/under exploitation if poor abundance forecast. Environmental prediction required if short delay between environmental forcing and change in abundance.
Management procedure	Combines above methods. Dampens interannual variability in catches.	As above but minimized.
Ecosystem-based	Global approach. Can resolve conflicting objectives. Can reconcile fisheries management and conservation issues. Explores different options.	Difficulties of trade-off between conflicting objectives. Few tools, lack of experience and of scientifically accepted marine ecosystem indicators.

Reduction of intraspecific diversity of marine populations could potentially affect long-term sustainability of the fisheries (Sinclair et al., 1985; Cury and Anneville, 1998; Fréon and Misund, 1999). At a stock level, the extinction of one or a few constitutive sub-populations might pass unnoticed if the others had greater productivity, and some could become extinct before any signs of stock overfishing are apparent. The erosion by fisheries of intraspecific diversity could lead to a long-term decline in the productivity of marine pelagic resources with no reversibility (Fig. 14). For example, if one excludes the Peruvian anchoveta, the world catch of pelagic fish has been decreasing since 1984. Beverton (1990) noted "the possibility that the collapsed population may never be able to fully regain its former status in the ecosystem": of the nine stocks for which collapse has been documented, only one has fully regained its original size. Even though pelagic fish stocks appear more resilient than demersal fish stocks, a lack of resilience has also been observed for most pelagic fish stocks (Hutchings, 2000).

Fish population genetics is still in its infancy and in a pioneering phase, but we see an increasing integration of population genetics (Anonymous, 2001) and a growing importance for pelagic fisheries management.

Review of Management Options

Different management options were proposed to attain sustainable exploitation of marine fish (Gulland, 1974; Walters, 1986; Hilborn and Walters, 1992; Kruse et al., 1993; Pikitch et al., 1997; Anonymous, 1999) and they can be broadly subdivided into five categories that we will review in the context of pelagic fisheries: steady state management; adaptive management; predictive management; implementation of a management procedure; and more recently, attempts at ecosystem-based management (Table 2). All management options, including the oldest ones, have benefited from the concept of the precautionary principle applied to fisheries in recent years (Garcia, 1994; FAO, 1995b; Garcia, 2005; this issue) and have been revisited to account for risk factors. The following review analyses the relevance of the existing management options for small pelagic fishes.

Steady State Management.—Steady-state management techniques were first proposed in the second half of the last century. They are based on the concept of a pseudo-equilibrium of the stock that theoretically rapidly adjusts its biomass and production according to the level of exploitation. The influence of environmental and ecosystem factors is ignored (treated as residual variations). The key reference points (Caddy and Mahon, 1995) used by managers applying these techniques are unique for a given stock and vary only according to present knowledge, not to the present status of the stock. These reference points are derived either from surplus production models (maximum sustainable yield, maximum sustainable effort) or from age-structured models (e.g., F_{max} or $F_{0.1}$ derived from the yield per recruit models). The advantages of the steady state management approach lies in its ease of implementation and in the availability of those clear and scientifically-based reference points that were trusted up until recently. The weakness of the approach is that it is not adapted to highly variable resources like pelagic fish, which do not fulfill the steady-state assumption of conventional fisheries models (Spencer and Collie, 1997), especially when constant catch strategy is adopted. The large uncertainty in pelagic fish recruitment associated with environmental and ecosystem aspects impose extremely conservative constraints on the manager who wishes to limit the risks of overexploitation and collapse of the stock. Such a hard line position is difficult to maintain on a long-term basis due to pressure from the fishing and political sectors.

Adaptive Management.—Adaptive management techniques are opposite to steady-state ones in the sense that the manager adjusts (on a medium- to short-term basis) the level of exploitation of the stock according to its present status. The stock status is estimated through regular monitoring based on surveys (mostly acoustic or aerial surveys for pelagic fish) and/or analysis of commercial catches (CPUE, length frequency, oil-content, etc.), usually on a yearly basis but sometimes more frequently, in particular when the stock is endangered (e.g., Smith et al., 1993). The advantages of this approach are its flexibility, the decrease of the risks of collapse due to constant monitoring, and fast recommendation of conservative actions (when accepted), combined with the possibility of making use of good fishing opportunities when environmental and ecosystem conditions are favorable to the stock. The inconvenience of this approach is its dependence on regular (at least every year in the case of short lived species) and reliable stock assessments followed by fast data processing. Furthermore, from the fishing industry point of view, adaptive management can be perceived as generating permanent uncertainty, making any investment plan and employment difficult. In the worst case, the fishing sector will delay the whole pro-

cess by questioning the value of the assessment and requesting more surveys when the recommendation is to close the fishery (Boyer et al., 2001). At the other extreme, when the resource abruptly becomes unusually abundant, the fleet capacity may be inadequate to harvest the catch levels possible.

Predictive Management.—Predictive management should limit the previous inconvenience, providing that predictions of fish abundance on which it is based are reliable. It is based on projections of the strength of cohorts according to the influence of biotic and abiotic processes (Ultang, 1996). By giving an earlier warning to the fishing sector on the future status of the stock, economic and employment action can be taken to reduce or increase the capture and processing of the fish in a timely manner. As indicated in the section "Pelagic fish and their physical environment," there are still many uncertainties associated with prediction of pelagic fish stock abundance from models and once the strengths of given exploited cohorts are properly estimated, they are usually too old and no longer abundant enough to sustain appreciable exploitation. Therefore, very few, if any, pelagic fisheries are fully managed using the predictive approach because poor abundance forecasts would dramatically increase the risks of over- or under-exploitation of the resource. Furthermore, medium-term environmental prediction might be required if the delay between environmental forcing and change in abundance is too short to allow predictive management. At present, such a requirement is not realistic except possibly in a few instances where there is a substantial time lag in the teleconnections, allowing forecasting of large scale environmental forcing over a few months (Roy and Reason, 2001; Schneider and Miller, 2001).

Management Procedures.—Management procedures (MPs) were developed to minimize the limitations of the above three approaches. A set of clearly defined rules, which are derived on a regular basis from the stock and the fishery data into regulatory mechanisms like total allowable catch (TAC) or maximum fishing effort, is agreed upon by all parties concerned *before* implementation (Kirkwood, 1992; Butterworth et al., 1997; Cochrane et al., 1998; De Oliveira et al., 1998; Cooke, 1999). The robustness of the rules to possible errors in data and assumed population model structure and implementation are tested by simulation in order to provide a basis to evaluate acceptable tradeoffs between expected catches and risks to the resource. The rules must specify in detail which kinds of data will be used and how the regulatory mechanism will be calculated from these data, usually on a yearly basis. MPs for pelagic fisheries are typically defined for a period of 3–5 yrs and should not be modified during this interval except under exceptional circumstances. After this period, MPs can be revised if necessary, according to previous experience and additional knowledge accumulated in the interim (see Butterworth and Rademeyer, 2005; this issue, for further details on this approach). The advantages of MPs lie in a clear, transparent, and more time-efficient process of management, avoiding repeated annual time-consuming reevaluation of data and methods of limited real value. Some rules can address the issue of too much uncertainty for the commercial fishery by fixing certain thresholds of minimum allowance and/or thresholds of variation in the allowance from year to year. The simulation tests and the medium-term life span of the rules allow for a proper appraisal of the risks.

The example of the South African pelagic fishery illustrates how MPs can be applied in a complex situation and evolve through time according to new needs (Butterworth and Bergh, 1993). This purse-seine fishery is based on a short-lived multi-species
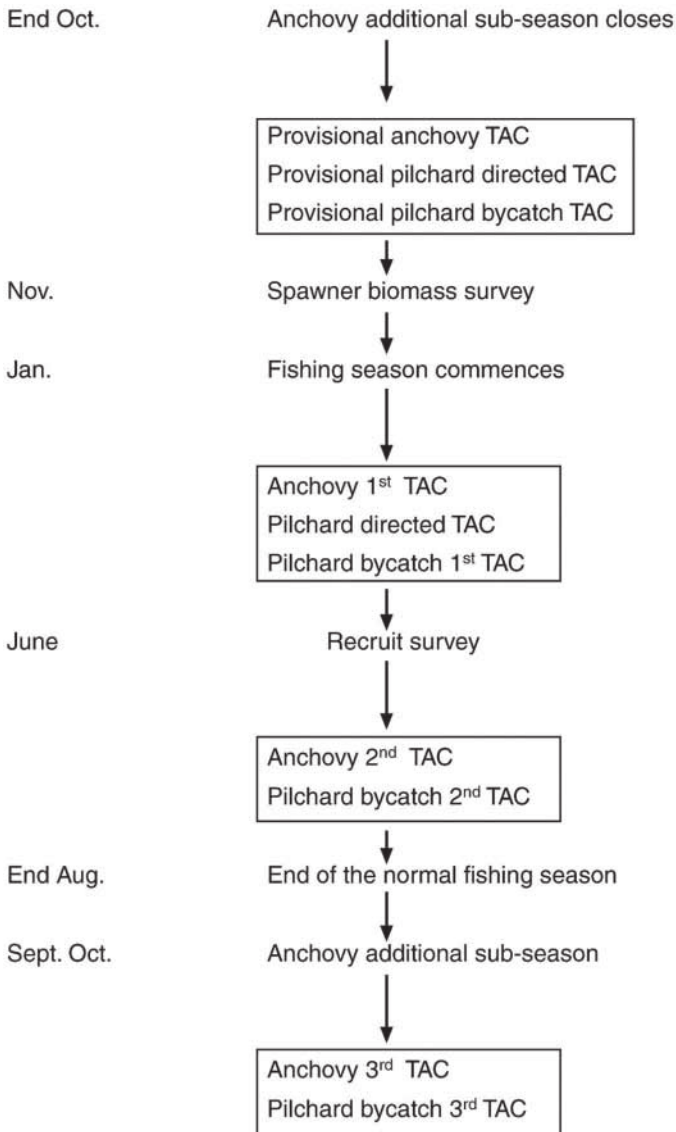
Figure 15. Present management procedure (OMP-O2) used for the anchovy and sardine fishery in South Africa (Geromont et al., 1999; J. de Oliveira, Marine and Coastal Management, and D. Butterworth, University of Cape Town, pers. comm.).

resource mainly comprised of sardine (*S. sagax*, also known locally as pilchard) and anchovy (*E. capensis*, homonym to *Engraulis encrasicolus* (Linnaeus, 1758)), the two species amounting for 60%–90% of the landings. Sardine is mainly used for canning while anchovy and other species are reduced to fishmeal and oil. A further complication in the management of this fishery arises from the high occurrence of mixed schools of young sardine and anchovy during the first part of the year.

In 1971, a global TAC for all pelagic commercial species was introduced, and until 1983 the basis for management resembled a *constant catch strategy*. From 1983, species-specific TACs were implemented for anchovy and sardine following criticisms related to the perceived level of abundance and exploitation of the different species.

Over the period 1983–1987, anchovy TACs were modified substantially in line with survey output as a result of increasing confidence in the combined egg production and acoustic survey conducted on the spawning stock in November (Shelton et al., 1993). From the experience gained and knowledge accumulated on anchovy ecology, the management procedure over the 1987–1990 period was based on a *constant escapement* (50% of the average spawning biomass level in the absence of exploitation). The decision flow began with the computation of the total catches after the end of the fishing season in September–October and the specification of an initial TAC based on an estimated escapement under different TACs, assuming that the recruitment is log-normally distributed around a median value R_{med}. Then, a revised TAC was issued in February–March, mainly based on the November spawning biomass survey. A final TAC was decided in June from the results of the May recruitment survey, which allows a direct estimate of the recruitment R_n of that year. This procedure was overridden by decision makers in 1990 when fishing closures were suggested following 2 yrs of poor recruitment. From 1991–1998 another procedure, based on *constant proportion strategy,* was applied (TACs were set at 20% of the estimated escapement that would have occurred at the end of the year had there been no fishing). This strategy was selected on the basis of simulations over a 20-yr projection of the resource dynamics and proposed different scenarios according to the level of risk for specifying future TACs. In so doing, the risk levels could be chosen by decision makers (Butterworth and Bergh, 1993). This new procedure was extended in 1994 to incorporate both anchovy and sardine management by defining two sardine TACs: directed (pure adult sardine catches used for canning) and bycatch (mainly for young sardine mixed with anchovy), which obviously depends on the anchovy TAC. Therefore, the higher the anchovy TAC, the greater the juvenile bycatch TAC, and consequently, the lower the directed sardine TAC. This trade-off in the fishery is translated by the MP into several exploitation options that are simulated, each with the same level of risks to the resources. A new operational management procedure 99 (OMP-99) was defined in 1999 for 3 yrs, with different parameters compared to the previous one, plus the addition of constraints suggested by the industrial sector, such as minimum TAC levels and maximum drops in TAC from year to year (Geromont et al., 1999). The major change incorporated in the present MP (OMP-02), is that it allows individual fishing companies flexibility in choosing their own desired pilchard: anchovy ratios (on average) for their catches instead of having these externally and globally imposed. Other modifications are the inclusion of an additional sub-season in September–October for "clean" anchovy catches (Fig. 15), taking account of bycatch drop-off through the normal season; and other constraints on TACs' absolute values and extent of change from year to year (D. Butterworth, University of Cape Town and J. De Oliveira, MCM, pers. comm.).

Ecosystem-Based Management.—Ecosystem-based management is not yet a reality but this concept is gaining popularity as indicated by recent symposia on this topic (Anonymous, 1999; Hall, 1999; ICES, 2000; Sinclair and Valdimarsson, 2003). Following a transition period based on the extension from single species management approaches to a series of surplus production or virtual population analysis (VPA) models for several species, this approach intends to reconcile stakes related to exploitation with those related to ecosystem conservation, based on the precautionary approach and the search for emergent properties of multispecies assemblages.

Alteration or disturbance of one or several components of marine ecosystems by anthropogenic, biotic, or environmental factors can have strong effects on higher or lower trophic levels. It has recently been shown that local extinction associated with overfishing precedes all other pervasive human disturbances in marine ecosystems. Paleoecological, archaeological, and historical data also show that time lags of decades to centuries occurred between the onset of overfishing and subsequent changes in ecological communities (Jackson et al., 2001). According to these authors, ecological diversity and redundancy within trophic levels are probably the most important reasons for the delay between the onset of fishing and the subsequent threshold response. These authors reviewed three types of ecosystems; i.e., coral reefs, kelp forests, and estuaries, but found none exhibiting pelagic fish as an important component (but note that upwelling ecosystems might provide a different picture). As many pelagic fish stocks exhibit "boom and bust" dynamics, redundancy between pelagic species should be regarded as particularly important for the functioning and management of the ecosystem.

Using trophic models of the southern Benguela ecosystem for two decades, indicators quantifying redundancy and species interactions have been proposed (Shannon and Cury, 2004). This ecosystem seems to have functioned in a similar way during the 1980s, when anchovy was the dominant small pelagic fish species, and the 1990s when sardine abundance increased (Shannon, 2001; Shannon et al., 2003). This was evident in similar estimates of transfer efficiencies of biomass from one trophic level to the next, similar biomass estimates per trophic level, and similarities in many other ecosystem attributes examined using trophic models for each of the two decades. Therefore, redundancy between sardine and anchovy could have been a major contributing factor maintaining stability in the functioning of the ecosystem over these two decades in the southern Benguela. Species interactions and redundancy between pelagic fish are certainly important questions that need further exploration for fisheries management.

Ecosystem management is still in its infancy and a better understanding of the functioning of ecosystems is required, especially in terms of factors which control their dynamics and the derivation of trustable and accepted ecosystem indicators. Indicators of ecosystem functioning are likely to prove useful in communicating scientific results for marine fisheries management purposes. Nonetheless, some authors argue that individual species might be more sensitive indicators of stress than the system and that there is little value in trying to manage marine ecosystems as a whole (Schindler, 1985; Bax et al., 1999). Other authors suggest that most ecosystem models, because they do not take into account environmental effects, cannot predict major changes in community structures like those observed in the Bering Sea (Trites et al., 1999). The final aim of ecosystem management is to ensure the co-viability of exploitation systems and of natural ecosystems on which the exploitation is based. More ambitious objectives, like rebuilding ecosystems towards the species mix and levels of abundance of the system before substantial fisheries began (Pitcher and Pauly, 1998), which supposes reversibility, appear less realistic. Presently, applied ecosystem management is limited to some intention to apply multispecies management in some fisheries and to the delimitations of MPAs as multi-target regulatory mechanisms in contrast to other conventional regulatory mechanisms that we will review in the next sub-section. Nevertheless, this new approach opened broad perspectives for more effective management (e.g., Beamish and McFarlane,

Table 3. Advantages and disadvantages of the different regulatory mechanisms.

Mechanism	Advantages	Disadvantages
Fish size control	Allows protection of some developmental stages (e.g., pre-recruits or old fish).	Not always easy to implement without avoiding fish dumping (poor gear selectivity). Genetic manipulation
Quota (TAC)	Relatively easy to implement and enforce. Full control of total mortality. Flexibility in time.	Variable TACs might not fit fleet capacity. Problem of mixed-species schools (encourages dumping).
Control of overall fleet capacity	Easy to enforce. Limits risks of ecosystem over-exploitation. Reduces costs and limits socio-economical problems.	Not species specific. Risk of overexploitation if increase in catchability and vice versa. Risk of overcapacity due to increasing efficiency (technology, learning, etc).
Control of standardized effort	Might be species-specific in some cases. Limits fish dumping.	Difficult to calibrate effort by several fleets. Uncontrolled changes in F if changes in q. Difficult to implement and enforce. No reduction of overhead costs. Might create socio-economical difficulties.
Time/area closure (seasonal or ad hoc base)	Allows protection of some developmental stages. Easier to enforce. Limits fish dumping.	Not protective enough if not on an ad hoc base. Difficult to decide on the optimal season. No reduction of overhead costs.
MPA and marine reserve	As above. Protect the ecosystem.	Not protective enough for pelagic species. Optimal size, number and location of MPAs?

1999). Instead of trying to optimize the exploitation of several stocks, a new trend in ecosystem management consists of trying to avoid several thresholds or limit reference points (sensu Mace, 1994; Caddy and Mahon, 1995) for different exploited or non-exploited natural resources (Mace, 2001).

This short review (for more details see Gulland, 1974; Walters, 1986; Hilborn and Walters, 1992; Kruse et al., 1993; Pikitch et al., 1997; Anonymous, 1999) of the available management options for small pelagic fisheries suggests that none of these are fully adapted to both the short- and long-term variability in abundance of most small pelagic fish stocks, although the MPs seem more adapted than the others. The relevance of MPs is not easy to estimate, although management strategy evaluation is becoming increasingly used when evaluating the effectiveness of the MPs, particularly in Australia (Smith, 1993, 1994; Smith et al., 1999). In the next sub-section we review the different regulatory mechanisms before proposing a two-level management strategy for small pelagic fisheries.

Regulatory Mechanisms

Regulatory mechanisms that can be used in fishery management can be broadly subdivided into six categories: fish size control; quota —also called TAC; control of overall fleet capacity; control of standardized effort, time/area closure (seasonal or ad hoc basis); area closure; and finally, the related MPAs. We review all six categories in the context of pelagic fisheries (Table 3).

Fish Size Control.—Fish size control is a common regulatory mechanism used in many pelagic and other fisheries. It has at least one of the following two objectives: directly avoiding "growth-overfishing" and indirectly limiting "recruitment-over-fishing." Growth-overfishing occurs when catching fish that are too small and too young long before the cohort biomass reaches its maximum (a balance between individual growth and natural mortality). Recruitment-overfishing comes from a depletion of the parental stock that limits recruitment (left side of the stock-recruitment curve) and it can be partly controlled by a size limit which can decrease the fishing mortality of young fish before they reach their first sexual maturity. In small pelagic fish, particularly those with a short lifespan, size-at-recruitment is close to the critical size corresponding to growth-overfishing because natural mortality is high. This means that there is generally no major benefit in terms of growth-overfishing to control the fish size because the benefits from growth are outweighed by the losses due to mortality. In contrast, fish size control can be an efficient way to indirectly limit recruitment-overfishing because the size-at-first maturity is often larger than the size-at-recruitment (e.g., Fréon, 1994). Fish size control can be a very safe and conservative measure for small pelagic species when the stock is overexploited to the extent to which few cohorts are left and the reproductive success largely depends on the first reproduction. The major drawback of this regulatory mechanism is that it is not always easy to implement without avoiding fish dumping because of the poor selectivity of some pelagic fishing gears like the purse-seine. Another potential problem, although difficult to quantify, is the risk of genetic selection associated with fish size control. Fast maturing fish, that will reach their first maturity before reaching the size limit, might be selected by this regulatory mechanism (Policansky, 1993).

Quotas.—Quotas are relatively easy to implement and enforce, especially when landing sites are limited, as is often the case in industrial pelagic fisheries in contrast to small-scale fisheries. TACs provide full control of the total mortality and flexibility in modification of this control through time. Quotas are usually predefined on a yearly basis, but in some instances they can be adjusted within the fishing season when fish density or abundance is monitored more than once a year, as in the above example of the South African anchovy fishery. The shortcoming of variable TACs is that they offer little opportunity for reducing the costs of the fishery (Gulland, 1974) and might not always fit the fleet capacity. This situation occurred in South Africa in 2001, after two consecutive years of record recruitment of anchovy. An extra quota of 150,000 t was given to the fishery after the May 2001 recruit survey, in addition to the initial TAC totaling 451,000 t (including an additional sub-season quota of 80,000 t). Nonetheless, this extra allowance was poorly used: only 287,000 t (64% of the TACs) were caught in 2001, although this was well above the average catch of 112,000 t (range 41,000–180,000 t) during the period 1995–1999. Another problem of quotas is related to multi-species fisheries with different TACs per species that might not be reached simultaneously. When the fishers cannot identify the school species prior to the catch (a situation not as common as one may imagine) or when

mixed-species schools are abundant, fishers will dump the catches of schools dominated by the species for which the quota is attained. The loss of fish from the stocks resulting from dumping or unexpected mortality after gear contact ("Pelagic fish and their physical environment" section) cannot be quantified because they are usually not recorded and are ignored when determining whether the TAC has been caught and fishing must cease. This omission from the records impacts on the quality of subsequent stock assessments by indirect methods that are undertaken, as the missing data introduce additional uncertainty into the calculations.

Control of the Overall Fleet Capacity.—The control of the overall fleet capacity can be achieved by deciding on a total number of active fishing units, or by broad categorization of fishing units defined according to their fishing gear or boat type. This control is easy to enforce and cost-effective because it does not require monitoring of the landing or fishing activity. It limits to a certain extent the risk of ecosystem overexploitation by a global control of the total fishing power. Finally, the overall fleet capacity control limits socio-economical problems by enabling more stable employment to the people operating the fishing units. The drawbacks of this approach are that it is not species specific and can therefore favor the overexploitation of the more marketable or catchable species. Simulations suggest that constant fishing effort is more efficient than constant catch in stabilization of a fishery only if mortality is proportional to effort and if the price of the fish depends on the catch volume (Hannesson, 1999), but both conditions are usually not met in small pelagic fisheries. Finally, if the fleet capacity is not properly and frequently assessed, this type of control might favor the fleet overcapacity due to steadily increasing efficiency resulting from technological improvement, availability of environmental data and, in the case of young fisheries, the fishers learning from past experience.

Control of Standardized Effort.—The control of standardized effort is the answer to the previous limitations because statistical techniques like GLM or GAMs (see "Pelagic fish and their physical environment" section) can be used to correct for changes in efficiency. This standardization might be species-specific when the efficiency of fishing units changes according to the species. To a certain extent, an appropriate control of the standardized effort can decrease fish dumping in comparison to overall fleet capacity control. Nonetheless, this standardization might be difficult to apply when different gears (typically purse seine and pelagic trawl) or types of boats are used in the fishery. The intercalibration of those fleets or "metiers" is not easy, especially if they do not operate in the same segment of the stock (operating in different areas or seasons or targeting fish of different age). Moreover, if some changes in the coefficient of catchability (q) occur, they can result in uncontrolled changes in the fishing mortality (F). An additional problem arises from the difficulty in implementing and enforcing standardized effort because the theoretical unit must be translated into some figure for the existing fishing fleets. Finally, the type of control does not provide a reduction of overhead costs for the fishing sector and it might create socio-economic difficulties if all segments of the fishery are not equally treated in the control of the effort, which is a difficult exercise.

Time or Area Closure.—Time or area closure, or a combination of both, can be used on a seasonal or ad hoc basis to control fisheries. The aim is to protect some specific habitat from destruction by trawled gears, to reduce potential impacts of localized depletion of prey, or to prevent the catch of key development stages, like the early stages, when those stages are found in a specific area or at a specific season

(Gulland, 1974). This type of regulation is relatively easy to enforce, particularly for time closure. It might limit fish dumping when implemented during the period of pre-recruitment, especially if non-selective gears are used. Nonetheless, except for the protection of spawning grounds of bottom-spawners like herring and some sprat species, area closures are not adapted to the regulation of small pelagic fish because they occupy a wide pelagic habitat and their spawning season is often extended. Furthermore, protecting only the spawners will not prevent recruitment overfishing.

Marine Protected Areas.—MPAs and marine reserves differ from area closures in that they are implemented for long time periods in a given location and usually all types of fishing activities are prohibited, although the definitions and regulations are not consistent from one country to the other. MPAs serve many purposes but the main objective is long-term protection of a number of species and their habitat simultaneously (Clark, 1996; Attwood et al., 1997; Roberts, 1997; Botsford, 2005; this issue). More than a simple regulatory mechanism, MPAs and marine reserves represent a new trend toward a habitat-based ecosystem approach (Bax et al., 1999). There is a large body of literature on the optimal size, number, and location of MPAs and results are often conflicting according to the ecosystem, the rate of exploitation outside the reserve, and the objectives (Lauck et al., 1998; Côté et al., 2001). It is commonly admitted that MPAs are effective in enhancing species richness but migratory species, like small pelagic fish, will gain little protection from MPAs (Roberts, 1997).

Towards a Two-Level Management Strategy

We propose here that a two-level (short- and long-term) management strategy should be investigated for exploited small pelagic species, based on the different characteristics of this group of fish that were compiled in this study. The rationale for this proposed strategy arises from the following considerations. First, recruitment over-fishing is of major concern compared to growth over-fishing in small pelagic fish. Second, most target reference points related to steady-state assumptions are not applicable to small pelagic fish because these species display natural variations in abundance that are too large, especially in the long-term. Third, short-term prediction of pelagic stock abundance in relation to environmental changes is currently not accurate enough to allow forecasting and integration in management procedures. Fourth, interdecadal variations are not well understood, but there is growing evidence of their existence and increasing reports on their long-term autocorrelation and pseudo-periodicity around a 40–60-yr cycle for many species ("Pelagic fish and their physical environment" section), although other species may have a shorter cycle (Spencer and Collie, 1997). Fifth, pelagic fish are abundant in many ecosystems, located at a central place in the food web, and they play a major role (forage fish, predation on early stages of other species) in most of these ecosystems, therefore there is a need for ecosystem-based management of this group of species.

The first level of the management strategy that we propose would address the short-term issue. It could simply be an adaptive management approach incorporating new ecosystem-based threshold or limit reference points (LRP) as much as possible. It could be based on a simple modification of the existing MP, based, for instance, on a TAC that will vary annually according to current estimation of fish stock biomass from direct (e.g., acoustic survey; preferred for short lived pelagic fish) and/or indirect (e.g., VPA; preferred for medium and long lives species) stock assessment
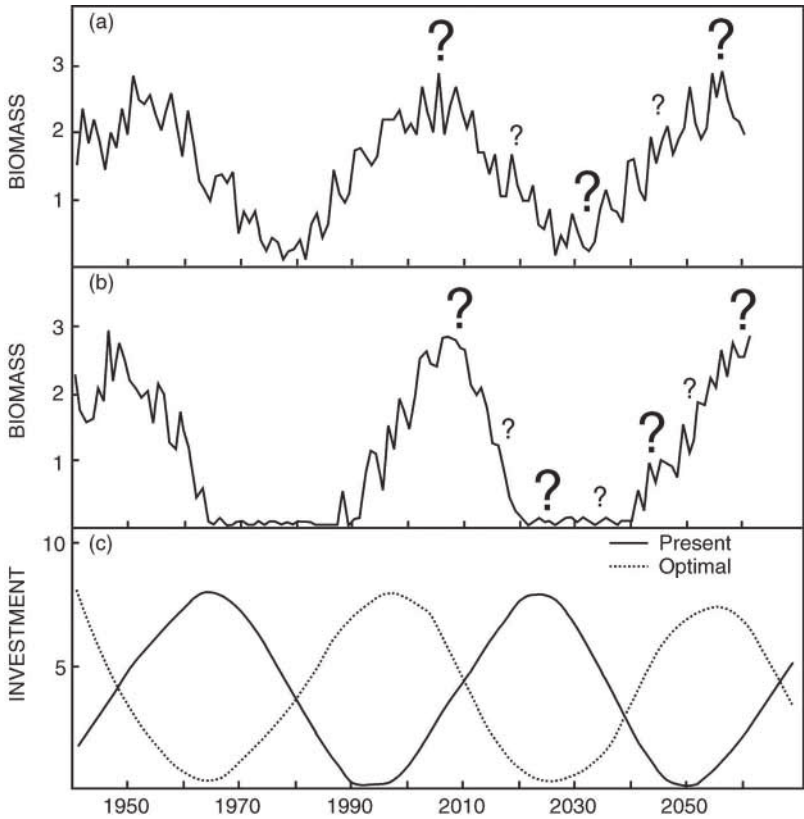
Figure 16. Schemes of typical variation in the abundance, effort and investement in pelagic fisheries: (A) pseudo-cyclic variation; (B) long periods of collapse; (C) investment strategies related to pseudo-cyclic variation. The size of question marks reflects the uncertainty about the trend in abundance over the next 10-yr period.

methods. The accuracy of these techniques is crucial for an efficient and low risk adaptive strategy and they should benefit from recent technological advances such as hydroacoustics, light detection and ranging systems (LIDAR), ichthyoplankton sampling via continuous underwater fish egg sampler (CUFES), aerial observation, etc. An example of this short-term strategy is provided by the South African OMP described in the previous section, but ideally this OMP should be complemented by incorporating LRPs as red areas (Caddy and Mahon, 1995) or "stock traffic lights" (Caddy, 2000). For instance, a minimum biomass of small pelagic fish could be left for the predators within their foraging range, especially for endangered species like some birds or mammals in certain ecosystems. Spatially resolved information on species habitat on a seasonal time scale should be processed through geographical information systems (GIS) or similar tools in order to derive such LRPs or to implement fishery closure when necessary. Complementary regulatory mechanisms, such as a minimum fish size to limit recruitment over-fishing or MPAs to protect the habitat of a variety of species and to increase biodiversity, should also be used where appropriate.

The second level of the strategy should address the problem of interdecadal variations in the abundance of pelagic fish that induce counterproductive investments in

the fishing sector (Fig. 16). Pelagic fish fishing units and related infrastructure are expensive, take at least a year to be ordered and built, and have an operational life of several tens of years —still much shorter than the duration of the pseudo-cycle of pelagic fish stock abundance. Therefore the most common scenario of overcapitalization is the following one. Fishing companies invest after a relatively long period of profit, that is, during the growing phase of fish population on the interdecadal scale. As a result, newly bought fishing units and infrastructure are operational when the targeted pelagic stock is close to its maximum production, if not when this production has already started to decline. When the fish stock reaches its minimum level or collapses due to overexploitation, the recently bought fishing units are not yet paid off and the strong competition between too many units limit or eliminate more profit (FAO, 1984). MPs and TACs are not appropriate to address this issue of counterproductive investment. Within the context of a precautionary approach, we suggest an indepth study of options for long-term fleet capacity control based on long-term autocorrelation and pseudo-periodicity of pelagic fish stock abundance (Fig. 16). The aim of this control would be to anticipate overcapitalization by encouraging investment when the stock abundance starts to take off, limiting investment when the abundance is thought to be close to its peak and forbidding investment when there are signs of a plateau being approached. The size of the question marks on Figure 16A (pseudo-cyclic long-term variation) and Figure 16B (long periods of collapse) tentatively indicates the level of uncertainty on a theoretical stock but should be refined from proper statistical analysis of several series of historical and paleontological records.

Whether or not the difference between the two patterns of long-term variability represented in Figures 16A and 16B is due only to exploitation is still debatable, although most authors suggest that exploitation is likely to extend the period for which a stock remains in a state of collapse (e.g., Collie and Spencer, 1993; Jennings and Kaiser, 1998; Fréon, 1999). This extension might occur by (1) decreasing the period of abundance due to early collapses in the descending phase of abundance when adverse environmental conditions (El Niño-like events) are amplified by exploitation, and/or (2) preventing the recovery of the population when good environmental conditions are hampered by abnormally high fishing mortality. If the assumption that exploitation is the major factor explaining differences between the two patterns of long-term variability is true, then the short-term strategy may also have an impact upon duration of stock collapses. If not, the short-term strategy would be only useful to limit unexpected short-term variability in the biomass and to prevent the collapse of the stock during a period of expected high-medium abundance under natural conditions. But there is no doubt that the short-term strategy will not change the natural course of long-term pseudo-cycles that existed even before substantial exploitation, meaning that both levels of action are necessary and that they are complementary.

Several options should be carefully considered to control fishing effort on a long-term basis, taking into account the entire social, economical, and political implications. Typically, a first set of options would be regulation, at the state level, of the number of fishing vessels constructed or imported into the country or into the region in the case of transboundary stocks. A second set of options would be to make use of a versatile national fleet or of distant-water foreign fleets. This may provide a more flexible and less risky strategy in terms of overexploitation and overcapitalization, but could result in more uncertainty because the availability of these fleets is

difficult to predict. The first risk to be carefully evaluated on the basis of the long-term strategy is the difficulty of assessing the right number of units: too high a value will not solve the problem while too low a value will not allow optimal exploitation because the fleet capacity will be saturated in case of a short-term abrupt increase in abundance. The second risk is a mismatch between the timing of the regulatory decision and the temporal variation in the stock abundance, comparable to the one occurring in the stock-option market. Too late a decision to invest or too early an incentive to sell fishing units will limit profit or worse, generate losses, while too early a decision to invest and too late an incentive to sell will increase the risk of population extinction. The efficiency of the strategy will largely depend on the accuracy of the estimation of the pseudo-cycle length. Further studies are needed to decide whether this estimation should be based on relatively short abundance or catch time series (except when paleontological records are available) or on longer climate cycles, thought to be functionally related to abundance, as suggested by Klyashtorin (2001). In any case, using the precautionary principle, the decision should be made in favor of the protection of the resource rather than the search for maximum profit or primarily on the basis of political and social considerations.

CONCLUSION.—Despite recent progress on the identification of stock units and of their structure provided by the use of modern genetic tools, many stocks of pelagic species are not clearly defined and how their structure affects their resilience to exploitation is still poorly known. Further detailed genetic and tagging studies are required to facilitate the choice of management options and regulatory mechanisms based on fine stock structure.

The review of presently used management options and regulatory mechanisms indicates that none is ideal for small pelagic fish but that some are more appropriate than the others and that these can be combined. Adaptive management and the related management procedures are definitely more suitable than steady state management and, at least at present and for most pelagic stocks, predictive management. Ecosystem management is certainly the way to go but is still in its infancy. The specific two-level management strategy that we propose to take into account short- and long-term stock variability should be further explored by specific investigations on its statistical, socio-economical, and political merits.

Conclusion and Recommendations

Small pelagic fish share many specific traits in relation to their habitat, morphology, biology, behavior (particularly their gregariousness), ecology, population dynamics (characterized by high variability at different temporal and spatial scales), and finally, their particular type of exploitation by massive capture gears. Despite their high fecundity, small pelagic fish are vulnerable to exploitation and numerous stocks have collapsed due to overexploitation. As underlined by Sadovy (2001), there is little empirical or theoretical basis to support the assumption that highly fecund species are any less at risk than those of low fecundity. Myers et al. (1999) indicate that maximum annual reproductive rate is relatively constant, regardless of the species.

The majority of small pelagic exploited stocks are threatened by exploitation, often out of phase with strong and not always well-understood variations in abundance, in relation to environmental variability (short- and long-term) and/or the internal dynamics of the ecosystem. Environmental changes can affect fisheries either at the

level of catchability or at the level of resource abundance. The lack of understanding of most of the processes still limits short-term forecasts of abundance. Process-oriented studies (modeling approach interacting with orientated data collection and experiments, etc.) and emphasis on combined analysis of different sources of spatialized environmental, ecological, and fishery data are required to improve our knowledge. A better use of GIS, as well as coupling 3D hydrodynamics models to productivity models (NPDZ) and to IBM models, provide promising ways of achieving this goal by explicitly representing and modeling spatial structure and complexity in marine ecosystems. Marine GIS are challenged by highly dynamic processes that occur in three dimensions, but present a huge potential for understanding the functioning of ecosystems, enhancing the communication between stakeholders, and helping in the ecosystem approach to fisheries management.

Interdecadal variations in abundance, characterized by a pseudo-periodicity of around 40–60 yrs, are observed in many large stocks. Growing evidence suggests the existence of regime shifts, despite the need for more investigation through the comparative approach. The global synchrony of these shifts and cycles is nonetheless questionable.

Another area that requires more research effort is the stock structure and its implication for the sustainability of exploitation. Genetic studies and tagging experiments (when possible) should improve our understanding of stock units and the functioning of fish populations.

Pelagic fish represent an important component of most ecosystems, particularly in upwelling regions where few species dominate in terms of abundance. The central position of small pelagic fish in the trophic web (forage fish) and their potential role as predators of young stages of other species make it necessary to understand the type of control that prevails (top-down, bottom-up, or wasp-waist) in order to efficiently manage ecosystems such as these. A large emphasis has been placed on the type of trophodynamics control in marine ecosystems, but, as underlined by Bax et al. (1999), whether trophodynamics itself is the appropriate focus has not been definitively debated.

In addition to environmental effects, fisheries are subjected to a combination of biological, economical, and political influences (May et al., 1979; Caddy, 1999). This is well illustrated in the California system. Off California, anchovy and sardine compete for zooplankton prey. There have been researchers who recommended heavy fishing on anchovy to allow sardine, of greater commercial value, to increase. This was unacceptable to sports fishers, who realized the importance of anchovy as prey for sports fish (May et al., 1979). Fishery management should move from the conventional approach aimed at optimizing the exploitation of all individual species and rather try to keep the trajectories of the exploited ecosystems within boundaries acceptable to all stakeholders (fishers, managers, scientists, environmentalists, public). Within the context of multiple stakeholders with divergent interests, multiple and conflicting objectives and high levels of uncertainty about the dynamics of the resources, this can be achieved by the combined use of many limit reference points rather than a sum of individual target ones (often conflicting), and by adaptive management. In the case of marine ecosystems in which exploited small pelagic species play a key role, we recommend specific statistical and socio-economical studies on the feasibility of a two-level management strategy that would combine adaptive

management (short-term) and fleet capacity control (long-term) and would take into account ecosystem considerations.

Despite many unknowns in scientific aspects related to small pelagic fish, this challenging field of research remains innovative and has generated several original hypotheses in recent years. Because experimental studies on the vast pelagic domain occupied by small pelagic fish are difficult, the comparative approach should be favored. We will certainly improve our understanding of the dynamics of exploited pelagic stocks by trying to identify common patterns among ecosystems and interpreting them in the light of the characteristics shared by these stocks, ecosystems, and types of exploitation.

Acknowledgments

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