

## Climate Variability, Fish, and Fisheries

P. LEHODEY,<sup>a</sup> J. ALHEIT,<sup>b</sup> M. BARANGE,<sup>c</sup> T. BAUMGARTNER,<sup>d</sup> G. BEAUGRAND,<sup>c</sup> K. DRINKWATER,<sup>f</sup>  
J.-M. FROMENTIN,<sup>g</sup> S. R. HARE,<sup>h</sup> G. OTTERSEN,<sup>f</sup> R. I. PERRY,<sup>i</sup> C. ROY,<sup>j</sup> C. D. VAN DER LINGEN,<sup>k</sup> AND  
F. WERNER<sup>l</sup>

<sup>a</sup>CLS-MEMMS, Ramonville St. Agne, France

<sup>b</sup>Baltic Sea Research Institute, Warnemünde, Germany

<sup>c</sup>GLOBEC International Project Office, Plymouth, United Kingdom

<sup>d</sup>CICESE, Ensenada, Mexico

<sup>e</sup>Sir Alister Hardy Foundation for Ocean Science, Plymouth, United Kingdom

<sup>f</sup>Institute of Marine Research, Bergen, Norway

<sup>g</sup>IFREMER, Sète, France

<sup>h</sup>International Pacific Halibut Commission, Seattle, Washington

<sup>i</sup>Pacific Biological Station, Nanaimo, British Columbia, Canada

<sup>j</sup>Institut de Recherche pour le Développement, Plouzané, France

<sup>k</sup>Marine and Coastal Management, Cape Town, South Africa

<sup>l</sup>University of North Carolina, Chapel Hill, North Carolina

(Manuscript received 31 August 2004, in final form 21 March 2005)

### ABSTRACT

Fish population variability and fisheries activities are closely linked to weather and climate dynamics. While weather at sea directly affects fishing, environmental variability determines the distribution, migration, and abundance of fish. Fishery science grew up during the last century by integrating knowledge from oceanography, fish biology, marine ecology, and fish population dynamics, largely focused on the great Northern Hemisphere fisheries. During this period, understanding and explaining interannual fish recruitment variability became a major focus for fisheries oceanographers. Yet, the close link between climate and fisheries is best illustrated by the effect of “unexpected” events—that is, nonseasonal, and sometimes catastrophic—on fish exploitation, such as those associated with the El Niño–Southern Oscillation (ENSO). The observation that fish populations fluctuate at decadal time scales and show patterns of synchrony while being geographically separated drew attention to oceanographic processes driven by low-frequency signals, as reflected by indices tracking large-scale climate patterns such as the Pacific decadal oscillation (PDO) and the North Atlantic Oscillation (NAO). This low-frequency variability was first observed in catch fluctuations of small pelagic fish (anchovies and sardines), but similar effects soon emerged for larger fish such as salmon, various groundfish species, and some tuna species. Today, the availability of long time series of observations combined with major scientific advances in sampling and modeling the oceans’ ecosystems allows fisheries science to investigate processes generating variability in abundance, distribution, and dynamics of fish species at daily, decadal, and even centennial scales. These studies are central to the research program of Global Ocean Ecosystems Dynamics (GLOBEC). This review presents examples of relationships between climate variability and fisheries at these different time scales for species covering various marine ecosystems ranging from equatorial to subarctic regions. Some of the known mechanisms linking climate variability and exploited fish populations are described, as well as some leading hypotheses, and their implications for their management and for the modeling of their dynamics. It is concluded with recommendations for collaborative work between climatologists, oceanographers, and fisheries scientists to resolve some of the outstanding problems in the development of sustainable fisheries.

---

Corresponding author address: P. Lehodey, CLS-MEMMS, 8–10 rue Hermès, 31526 Ramonville St. Agne CEDEX, France.  
E-mail: PLehodey@cls.fr

## 1. Introduction

The field of fisheries oceanography can be said to have started in the 1870s when Spencer Fullerton Baird, a fisheries biologist and the first U.S. Fish Commissioner, recognized the importance of the environment for fluctuations in fish stocks. However, for several decades it was still widely held that the abundance of sea fish was boundless, and fluctuations in catches essentially were caused by variations in migratory patterns (Ottersen et al. 2004). Early in the last century a more systematic search for relations between physical conditions and different aspects of fish stocks was initiated in Norway by Helland-Hansen and Nansen (1909). It is now understood that marine ecosystems change on a variety of time scales, from seasonal to centennial and longer. Many of these time scales are forced by atmospheric and climate-related processes, and therefore it is well understood by marine scientists that climate variability is a strong driver of changes in fish populations and in fisheries. For example, observations in the western English Channel of sea temperature, plant nutrients such as phosphorus, the presence or absence of “cold” or “warm” water zooplankton species, and the abundance of sardine changed between 1925 and 1935 and reversed in 1965 and 1979, forcing what was called the Russell Cycle (Russell et al. 1971) and what today would be called “climate regimes” or “ecosystem states.” These terms have become more frequently used as an increasing number of similar changes are documented in the different oceans and linked to large-scale ocean climate variability, often conveniently identified by climate indices like the Southern Oscillation index (SOI), Pacific decadal oscillation (PDO), or North Atlantic Oscillation (NAO), although these indices may be too restrictive to explain climatic variance at regional levels. A very large part of the observations describing climate-related changes in the marine ecosystems come from the fisheries that are directly affected by fluctuations in the abundance of the exploited stocks. Other sources of information concerning either the lower trophic levels (phyto- and zooplankton) or the noncommercial species (seabirds and marine mammals) result mainly from scientific research programs. The literature devoted to the effects of climate variability on these components of the marine system is rapidly growing, as it is also the case for other ecosystems, that is, freshwater and terrestrial ecosystems (e.g., see Hurrell et al. 2003; Gian-Reto et al. 2002; Stenseth et al. 2004, chapters 15–16).

There is now ample evidence of the ecological impacts of recent climate change, from polar terrestrial to tropical marine environments. The responses of both

flora and fauna span an array of ecosystems and organizational hierarchies, from the species to the community levels. Despite continued uncertainty as to community and ecosystem trajectories under global change, this review exposes a coherent pattern of ecological change across systems. Although we are only at an early stage in the projected trends of global warming, ecological responses to recent climate change are already clearly visible.

While the seasonal patterns in dynamics of fish populations are well known to fisheries scientists and fishermen, and are used in fishery operations (i.e., seasonal migrations either for feeding or spawning), abrupt changes present more difficult questions: have fish moved away or has the stock collapsed? Is it due to a natural cause, or to overfishing? Will the fish come back or be replaced by another species? Or more generally, is there a stationary or nonstationary relationship between climate and ecosystems? These questions motivated the creation of the first international oceanographic organization in 1902, the International Council for the Exploration of the Sea (ICES). Despite obvious progress, these questions remain largely unanswered a century later. This paper reviews advances in our knowledge of the impacts of climate variability on fish population and their fisheries, at time scales from seasonal to multicentennial, based on studies of various species covering marine ecosystems from equatorial to subarctic regions. These studies are central to the research program of Global Ocean Ecosystems Dynamics (GLOBEC), a component of the International Geosphere–Biosphere Program (IGBP), and are also supported by the Intergovernmental Oceanographic Commission (IOC) of the United Nations Educational, Scientific and Cultural Organization (UNESCO) and the Scientific Committee for Oceanic Research (SCOR).

## 2. Seasonal variability

The atmospheric effects of seasonal variability are particularly evident in marine upwelling systems. For example, the Southern Benguela upwelling system off the west coast of South Africa is characterized by strong seasonal patterns in prevailing wind direction, which results in seasonal changes in upwelling intensity (Shannon 1985; Shillington 1998). Strong southeasterly winds that blow during austral summer (October–March) drive the upwelling process, with upwelling intensity reaching its maximum in January. During winter, cyclonic low pressure systems that pass south of the African continent and are accompanied by northwesterly winds push surface waters onshore, and upwelling is minimal. The seasonality in upwelling in the South-

ern Benguela is in contrast to that in the Northern Benguela, which is active year-round and provides a continuous flow of production to shelf waters to the north (Shannon and Nelson 1996). Like other eastern boundary upwelling systems, the Southern Benguela supports abundant populations of small pelagic fish, namely anchovy *Engraulis encrasicolus* and sardine *Sardinops sagax*. These species are the target of an established purse-seine fishery and are used to produce fish meal and oil (anchovy), and human and pet food (sardine). Catches by the fishery have averaged close to 400 000 tonnes  $\text{yr}^{-1}$  over the past 50 yr, and although the fishery initially targeted sardine, anchovy have dominated since the mid-1960s.

To produce adequate survival of the young, fish reproductive strategies are generally well tuned to the seasonal variability of their environment (Cushing 1982; Parrish et al. 1983; Bakun 1996). In the Southern Benguela, intense wind mixing and strong wind-induced offshore transport of surface waters create an unfavorable environment for fish to successfully reproduce. As a result, both anchovy and sardine populations in the Southern Benguela have developed a novel reproductive strategy that is tightly linked to the seasonal dynamics of major local environmental processes. The principal characteristic of their reproductive strategy is the spatial separation between spawning and nursery grounds (Fig. 1).

The reproductive strategies of anchovy and sardine in the Southern Benguela have been a major focus of research over the last two decades, providing almost 20 yr of high-quality seasonal quantification of the abundance and distribution of adult spawners, eggs, larvae, and recruits. Anchovy become sexually mature in their first year and concentrate in spring and early summer over the Agulhas Bank where they spawn several times during an extended reproductive season between October and March with a major peak in November and December (Hutchings et al. 1998; Fig. 1). In contrast to anchovy, sardine mature in their second year, spawn not only over the Agulhas Bank but also occasionally off the west coast (van der Lingen et al. 2001), and spawn year-round with peaks in September/October and February/March (van der Lingen and Huggett 2003).

For both species, eggs spawned over the western Agulhas Bank (WAB) are transported to the productive west coast nursery grounds via a northwesterly flowing, shelf-edge jet current associated with a strong thermal front between cold upwelled water and warm oceanic water (Bang and Andrews 1974). This coastal jet acts as a major "conveyor belt" that transports early life history stages from the WAB spawning area to the

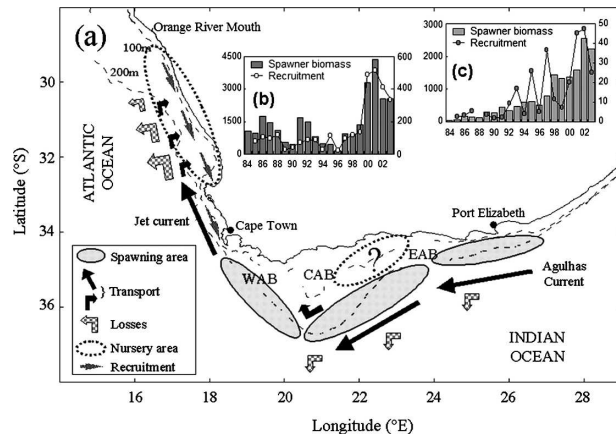


FIG. 1. (a) Map of the Southern Benguela off South Africa showing the locations of small pelagic fish spawning grounds (anchovy and sardine both spawn over the Agulhas Banks, but the sardine spawning habitat off the west coast is not shown for clarity) and nursery grounds (although the west coast is considered to be the major nursery ground, the south coast may in some years act as a significant nursery ground), and transport and loss processes that impact on eggs and larvae; and time series of spawner biomass (bars) and recruitment strength (circles and lines) of (b) anchovy and (c) sardine from hydroacoustic surveys of 1984–2003. The 100- and 200-m depth contours are shown, and WAB, CAB, and EAB are defined in the text.

nursery grounds. On reaching the west coast, eggs and larvae may be lost offshore through divergence of the jet, or in mesoscale eddies or filaments, or may remain over the shelf and move inshore through either passive transport or active swimming. Juvenile anchovy approximately 4 months old appear in catches made off the west coast from March onward, with around 70% of landings consisting of young of the year. Juveniles then migrate southward to the Agulhas Bank spawning grounds in spring (Hutchings et al. 1998; Fig. 1). Anchovy and sardine eggs spawned over the central and eastern Agulhas Bank (CAB and EAB, respectively) could follow one of three possible pathways; they could be transported shoreward onto the WAB and hence into the jet current, retained on the CAB and EAB and recruit on the south coast, or entrained by the Agulhas Current and advected into the southern Indian or Atlantic Oceans.

Transport processes between spawning and nursery grounds can act as a critical determinant of recruitment success (Shelton and Hutchings 1982), and several empirical studies have focused on transport and related processes (Shannon et al. 1996; Boyd et al. 1998; Korubel et al. 1998). For example, observations showed that above-average southeasterly winds during the spawning season were followed by poor anchovy recruitment over the period 1984–94 (Fig. 2; Boyd et al.

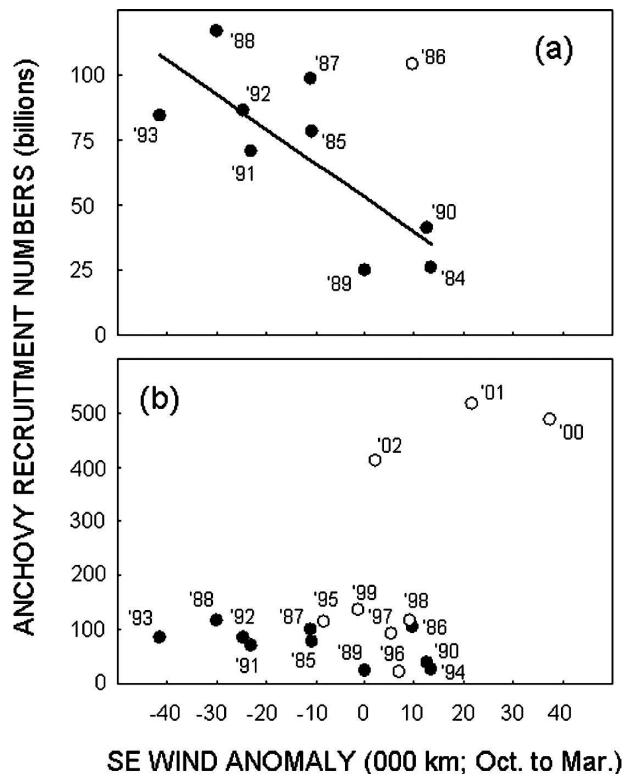


FIG. 2. Relationship between anchovy recruitment numbers and the cumulative southeast wind anomaly at Cape Point for (a) the period 1985–94 (note that the data point for 1986 was not included in generating the linear regression (see Boyd et al. 1998) and (b) the period 1984–2002 (data collected after 1994 are shown as empty circles). From van der Lingen and Huggett (2003).

1998). This inverse relationship was ascribed to increased wind resulting in offshore displacement of the jet current, which increased advective loss and hence reduced the transport of larvae to the nursery grounds. More recently, a study using a hydrodynamic model coupled to a particle tracking model (Penven et al. 2001; Mullon et al. 2003) showed that simulated transport of eggs and larvae had a pronounced seasonal signal and was highly dependent on the location of spawning (Huggett et al. 2003); successful simulated transport to nursery grounds was maximum when particles were released on the WAB from November to January. The good match between modeled and observed spawning patterns highlights the major role played by the seasonal dynamics of passive transport of early life history stages in shaping the reproductive strategies of anchovy and sardines in the Southern Benguela system (Hutchings et al. 2002).

However, the very high anchovy recruitment observed since 2000 (Fig. 1) and a lack of consistency in the pattern of seasonal climatic variability preceding those high recruitment events suggest that the relation-

ship between seasonal wind patterns and recruitment strength is more complex than previously thought (Roy et al. 2001). Studies on the reproductive ecology of anchovy showed a significant eastward shift of the anchovy spawning grounds after 1995 (van der Lingen et al. 2002). This would mean that eggs spawned on the CAB and EAB could well have a totally different early life history compared to their counterparts spawned over the WAB, and that their contribution to recruitment could be variable from one year to another and/or controlled by processes other than successful transport between spawning and nursery grounds. This would inevitably lead to the failure of correlations such as that presented in Fig. 2. These recent events in the Southern Benguela are a good illustration of the complex nature of biological systems and of their ability to evolve with their changing environment. Nonstationarity seems to be the rule (Bakun 2002), and this will prevent simple linear empirical models from being used as predictive tools for fisheries management.

### 3. Interannual variability

The most obvious driver of interannual variability is that characterized as the El Niño–Southern Oscillation (ENSO). Historically, the term “El Niño” was used to describe only the coastal warming of the near-equatorial Pacific Ocean off Peru. Climate scientists have arbitrarily chosen definitions for what is and what is not an “ENSO event” (Trenberth 1997), and today, they call warm phases of ENSO El Niño and cool phases “La Niña.” In this article, we will follow this convention, using El Niño as shorthand for the warm phase of the large-scale ENSO, which may or may not be associated with the coastal El Niño off Peru. Hence, ENSO is an irregular oscillation of 3–7 yr involving a warm (El Niño) and cold (La Niña) state that evolves under the influence of the dynamic interaction between atmosphere and ocean (Philander 1990). Although ENSO effects are felt globally, the major signal occurs in the equatorial Pacific with an intensity that can vary considerably from one event to another. The warm waters in the surface layer of the western equatorial Pacific (the warm pool) have a temperature above 28°C year-round, inducing an atmospheric convection connected to the colder eastern Pacific Ocean through the atmospheric zonal Walker circulation. During El Niño events, the warm pool extends far to the east in the central Pacific and reaches the coast of Peru during the most powerful events. Conversely, during La Niña the warm pool is confined to the extreme west of the equatorial Pacific. These east–west displacements of the warm pool are accompanied by changes in the Walker

circulation that are reflected by the SOI, calculated from the difference in sea level pressure between Tahiti and Darwin. A strong negative index indicates an El Niño while a positive index reveals a La Niña event.

Contiguous to the warm pool, the equatorial upwelling in the central and eastern Pacific is generated by the trade winds that result in a vertical circulation bringing relatively cold and nutrient-enriched deep water toward the surface. This equatorial divergence occurs within a mean westward zonal flow, the South Equatorial Current (SEC). The biological consequence of the equatorial upwelling is a large zonal band with high primary production frequently called the cold tongue that prolongs the highly productive coastal upwelling system along Peru and Chile. However, the primary productivity in the tropical Pacific is strongly affected by ENSO variability. During the development of El Niño events, the cold tongue retreats east of the international date line accompanying the warm waters extension into the central Pacific and the displacement of the atmospheric convective zone. The decreasing intensity in equatorial upwelling and primary production in the equatorial upwelling system is associated with this displacement. During the same period, stronger wind stresses occur in the western Pacific and increase primary production in this region (Lehodey 2001).

#### a. Anchovies and sardines in Peru and Chile

The effects of El Niño events on the anchovies (*Engraulis ringens*) and sardines (*Sardinops sagax*) along the coasts of Peru and Chile have long been observed. An El Niño event has three major impacts in the coastal upwelling system off Peru: (i) it increases coastal temperatures by up to 8°C; (ii) it reduces plankton production by lowering the thermocline, which inhibits upwelling of nutrients; and (iii) by changing trophodynamic relationships, it creates a more tropical predator and prey environment. Sardines seem to do well or even thrive under these conditions, and El Niño events usually do not harm the sardine stocks in the Humboldt Current. In contrast, anchovies suffer severely, particularly under strong events.

The first reaction of these small pelagic species is to move away from the warm water. Sardines of the Peruvian northern and central stock move very far south and sometimes mix with the southern Peruvian–northern Chilean stock (Mendez 1987). Anchovies move in three directions. Some move south, but anchovies are not able to carry out as long a migration as the much larger sardines. Other anchovies move deeper down to 80 or 100 m, but these regions have lower food content. Anchovies also try to escape by moving very close to the coast where cold water pockets may remain

for some time (Muck and Sanchez 1987; Yanez et al. 2001). However, this increases their vulnerability to fisheries. Valdivia (1978) reports that during the 1972 El Niño, anchovies were so highly concentrated on the coast that 170 000 tonnes were caught on one single day (roughly 4% of the total annual catch in this year).

Warming of the coastal waters is accompanied by a marked decrease in zooplankton biomass. A comparison between neutral (1981) and El Niño conditions (1983) indicates that the decrease was mainly due to copepods, which were reduced to about one-sixth of their normal abundance (Carrasco and Santander 1987). During the 1997/98 El Niño event there was a shift in the size spectrum of crustacean zooplankton toward small-sized copepods (González et al. 2000). Abundances of small cyclopoid copepods (*Oncaea spp.* and *Oithona spp.*) increased by a factor of 3 to 10 between January 1997 and January 1998. It has been proposed that the decrease of zooplankton volumes and biomass off Peru and northern Chile observed between 1968 and 1974 was due to a similar shift in size distribution of copepods creating a feeding environment more favorable for sardines than anchovies (Alheit and Niquen 2004).

In addition to higher vulnerability to fisheries and change in feeding conditions associated with the development of an El Niño event, two important anchovy predators, horse mackerel (*Trachurus murphyi*) and mackerel (*Scomber japonicus*), migrate deeper into the anchovy area (Muck and Sanchez 1987), increasing predation pressure on anchovy eggs, juveniles, and adults (Alheit and Niquen 2004). The biomass of mackerel and horse mackerel in the anchovy habitat more than doubled and, at the peak of the 1972 and 1976 El Niño events, it increased even 3.5-fold. The timing and the dependence of these migrations on coastal SST have been demonstrated by ichthyoplankton surveys, fishery catch data, and the temperature preferences of both species (Muck and Sanchez 1987). At the same time, sardines will move closer to the coast (Yanez et al. 2001) and, consequently, predation pressure on anchovy eggs and, maybe, larvae will increase (Alheit and Niquen 2004).

During the well-documented last 40 yr, the Humboldt Current system was affected by three very strong El Niño events. Biomass and catches of anchovy were reduced by the 1972/73 El Niño, but recovered thereafter before continuing their declining trend that started two years earlier (Fig. 3). In 1982/83, another very strong El Niño event affected the anchovy population, which was already at an extremely low population level. Surprisingly, one year later, the anchovy started a very successful recovery, which continues to

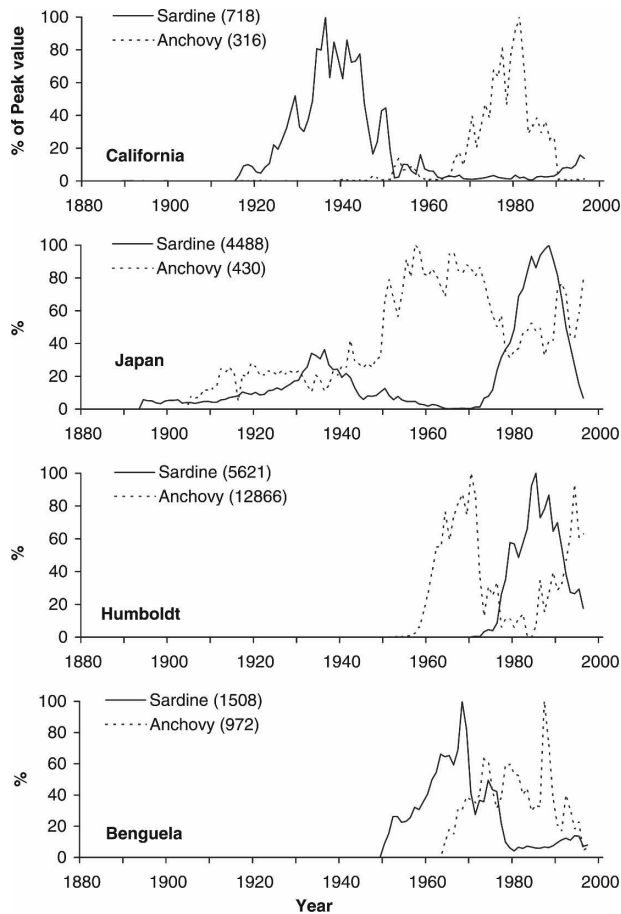


FIG. 3. Observed catch of anchovy and sardine relative to the maximum peak value of their series (value in thousand of tonnes between brackets) during the last century in the Pacific (California, Japan–Kuroshio, and Peru–Humboldt systems) and Atlantic (Benguela system) Oceans. Redrawn from Schwartzlose et al. (1999).

the present. In 1997/98, a strong El Niño event again struck the anchovy stock at the peak of its abundance. Catches recovered very quickly and reached pre-1998 levels. Therefore, independently of the timing of ENSO, the anchovy recovered after each event. Although anchovy and sardine populations are strongly affected by interannual ENSO variability and by extremely high fishing mortality like in the late 1960s and early 1970s, their long-term dynamics appear to be controlled by decadal-scale climate variability leading to alternating anchovy- and sardine-favorable periods (see section 5b below).

#### b. Tropical tuna species

Population dynamics of tuna in the tropical Pacific Ocean are strongly influenced by ENSO. Large-scale movements of tuna in the western central equatorial

Pacific have been correlated with the position of an oceanic convergence zone where the warm pool meets colder, resource-rich waters extending from the eastern Pacific (the cold tongue). This convergence zone shifts from east to west (in some cases 4000 km in 6 months) and back again in response to ENSO cycles (Lehodey et al. 1997). A basin-scale spatial population model (Fig. 4) has been developed to investigate the mechanisms that link climate and environmental changes and the dynamics of these tuna populations (Lehodey 2001). This model successfully reproduced the responses of the population dynamics of skipjack tuna to changes in their physical and biological habitat (Lehodey et al. 2003).

In addition to the impacts on their movements and migrations, ENSO-related variability also affects the recruitment and total abundance of these tuna populations. Results from statistical population dynamics modeling point to a clear link between tuna recruitment and climatic fluctuations (Fig. 5). The results also indicate that not all tuna respond in the same way to ENSO cycles. Recruitment of tropical tunas (such as skipjack and yellowfin) increased following El Niño events. Subtropical tunas (i.e., south Pacific albacore) show the opposite pattern, with low recruitment after El Niño events and high recruitment after La Niña events (Lehodey et al. 2003). Model simulations reproduced skipjack and yellowfin recruitment increases in both the central and western Pacific during El Niño events, a result of four mechanisms: the extension of warm water farther east (ideal spawning habitat is found in warm, 26°–30°C water), enhanced food for tuna larvae (due to higher primary production in the west), lower predation of tuna larvae, and retention of the larvae in these favorable areas as a result of ocean currents. The situation is reversed during La Niña events, when westward movement of cold waters reduces spawning success in the central Pacific; then the bulk of recruitment is centered in the warm waters of the western Pacific.

When all the favorable conditions occur together, then high peaks of recruitment are observed. This was the case, for example, in the final phase of the powerful 1997/98 El Niño event. In the second half of 1998, the skipjack purse-seine catch was concentrated in a small area in the equatorial central Pacific, and contained a high number of juvenile skipjack between 4 and 8 months in age. Satellite imagery indicated that this same area was the site of a major bloom in phytoplankton some 4 to 8 months before. The catch in 1998 was an all-time record; ironically it led to a drop of 60% in the price of skipjack, which were so abundant they could not all be processed by the canneries.

While the main skipjack and yellowfin spawning

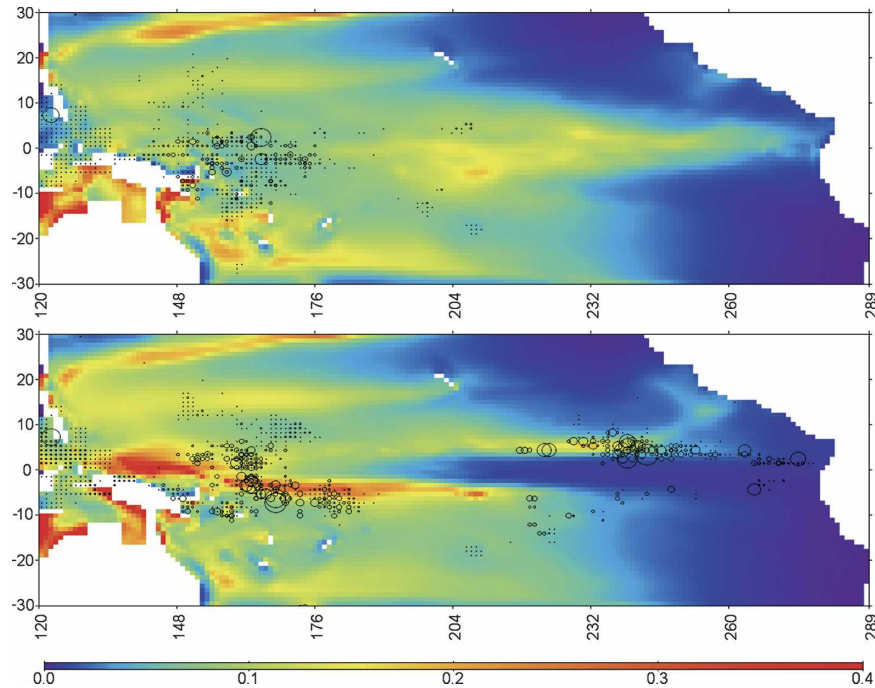


FIG. 4. Predicted distribution of skipjack tuna during (top) El Niño (Dec 1997) and (bottom) La Niña (Dec 1998) phases in the Pacific Ocean and observed catch rates of all fisheries (proportional to the circles).

grounds in the western central Pacific are associated with the warm pool, those of albacore roughly extend through the central Pacific on each side of the equatorial  $5^{\circ}\text{N}$ – $5^{\circ}\text{S}$  band and consequently are under the influence of the productivity of the equatorial upwelling. Primary productivity is out of phase between the western (warm pool) and central (equatorial upwelling) Pacific, which is directly linked to the ENSO cycle (Lehodey 2001); the same mechanisms that explain fluctuations in skipjack and yellowfin tuna recruitment in the western Pacific cause opposite fluctuations of albacore in the central Pacific (Fig. 5). The extension of the warm waters in the central Pacific during El Niño events that extends the skipjack spawning grounds may also conversely reduce those of the albacore.

#### 4. Interdecadal variability

##### a. The Pacific decadal oscillation

In the winter of 1976/77 an abrupt shift occurred in the climate of the North Pacific. The change was first documented in sea level pressure (Trenberth 1990) and eventually found in sea surface temperatures, air temperatures, and precipitation, among other physical variables (Graham 1994; Trenberth and Hurrell 1994; Miller et al. 1994). This change came to be termed a

“regime shift” (Miller et al. 1994; Hare and Francis 1995) and brought focus to interdecadal climate variability in the North Pacific. Other broad-scale regime shifts were identified in the mid-1920s, late 1940s, and potentially in the late 1990s. This pattern of decade-long climate regimes punctuated by abrupt climate regime shifts was named the Pacific (inter) decadal oscillation (Mantua et al. 1997). One PDO reconstruction based on tree rings identified 11 reversals between 1662 and the present (Gedalof and Smith 2001).

During the “positive” phase of the PDO, the Aleutian low pressure system deepens and shifts southward, winter storminess in the North Pacific intensifies, SSTs are anomalously warm along the coast of North America and cool in the central Pacific, upwelling is enhanced and mixed layer depth shoals within the Alaska gyre, and geostrophic transport increases into the Alaska Current from the Westwind Drift. During the “negative” phase of the PDO, conditions are generally the opposite of those in the positive mode. The PDO index is the leading principal component from an unrotated EOF analysis of observed monthly SST anomalies (after removal of a global long-term warming trend) north of  $20^{\circ}\text{N}$ . The monthly PDO index is often averaged within seasons and/or years to create an annual index that is used in examining climate–biological linkages.

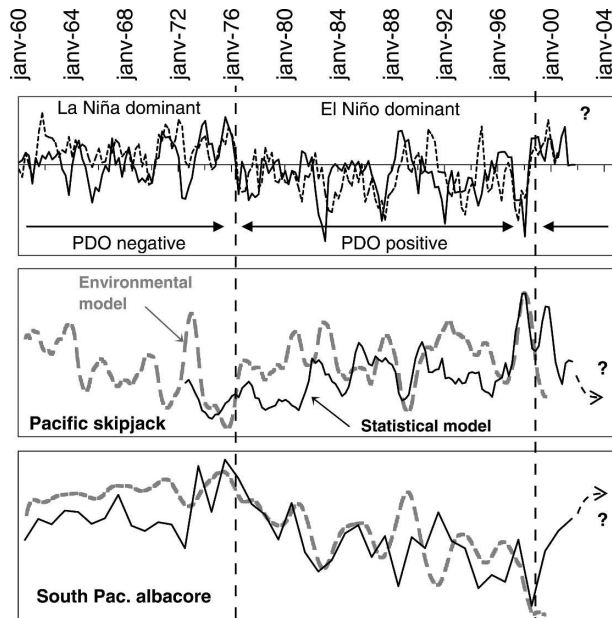


FIG. 5. Tuna recruitment (relative indices) in the Pacific. (a) Fluctuation of the SOI (thick curve) and PDO (dotted line) climate indices, (b) Predicted recruitment time series for skipjack, and (c) South Pacific albacore tuna from a statistical population dynamics model MULTIFAN-CL (Hampton and Fournier 2001) and from a spatial environmental model (Lehodey et al. 2003).

### 1) NORTH PACIFIC SALMON

Decadal- (and longer) scale fluctuations of Pacific salmon populations occur in the northeast (NE) Pacific Ocean and have been shown to be coherent with changes in the climate of the North Pacific (Beamish and Bouillon 1993) as indexed by the PDO and various indices tracking the character of the Aleutian low pressure system. Salmon are iconic species for the people of the North Pacific. Large runs of salmon returning to rivers and migrating deep inland each year were (and remain even today) important events that sustained coastal societies for centuries. There are five main species of Pacific salmon: sockeye (*Oncorhynchus nerka*), pink (*Oncorhynchus gorbuscha*), chum (*Oncorhynchus keta*), coho (*Oncorhynchus kisutch*), and chinook (*Oncorhynchus tshawytscha*), and each have somewhat different life histories. All, however, are anadromous fish, that is, they lay their eggs, hatch, and spend some portion of their very early life in freshwater, then migrate to marine environments where they feed and grow, ultimately returning to their natal stream to spawn and die. Life spans of Pacific salmon are typically from 2 to 5 yr depending on the species. The major Pacific salmon-producing countries are the United States, Japan, Russia, and Canada.

In the northeast Pacific, changes in atmospheric patterns associated with the PDO (SST) pattern tend to

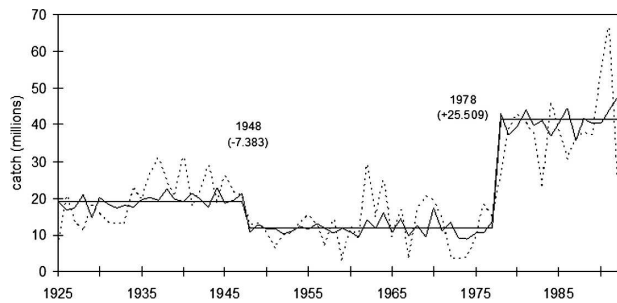


FIG. 6. Productivity periods ("regimes") in the North Pacific for pink salmon from central Alaska, determined using a two-step intervention model. Landings are shown by the dashed line, the thick solid line is the fitted values, and the straight line indicates the estimated means of the regimes. Redrawn from Hare and Francis (1995).

have their largest impacts on coastal and continental shelf environments, which are the crucial environments for coho and chinook salmon during all of their marine phase, and for sockeye, pink, and chum salmon when they migrate through these regions from spring to fall as juveniles. Since the 1920s three productivity periods of pink salmon from central Alaska have been identified, with shifts in the late 1940s and late 1970s (Hare and Francis 1995; Fig. 6); it is widely believed that another important shift for salmon in the NE Pacific occurred in 1999. During the positive phase of the PDO since 1977, two inverse production regimes for Pacific salmon became apparent in the NE Pacific, such that when salmon stocks in Alaska and northern British Columbia were doing well, stocks in southern British Columbia and the states of Washington, Oregon, and California did poorly (Hare et al. 1999). However, this dichotomy appeared to break down after 1999, when the California Current system cooled but Alaska continued to warm, producing conditions more favorable to salmon in both regions (Bond et al. 2003; Peterson and Schwing 2003).

Ocean productivity and feeding conditions for salmon in their overwintering regions of the oceanic North Pacific are crucial to establishing the final weight of individual salmon and whether they will have sufficient energy to migrate upriver to spawn. For similar reasons, feeding conditions in the open Pacific impact the total biomass of salmon populations. Changes in productivity were observed during the positive phase of the PDO that persisted from the late 1970s to (possibly) the late 1990s. Increased winds caused the ocean pycnocline to shoal (Bakun 1996), reducing the upper mixed layer depth and generating higher light levels and higher productivity of the food web, as observed for plankton biomass in the Gulf of Alaska in the 1980s (Brodeur and Ware 1992).



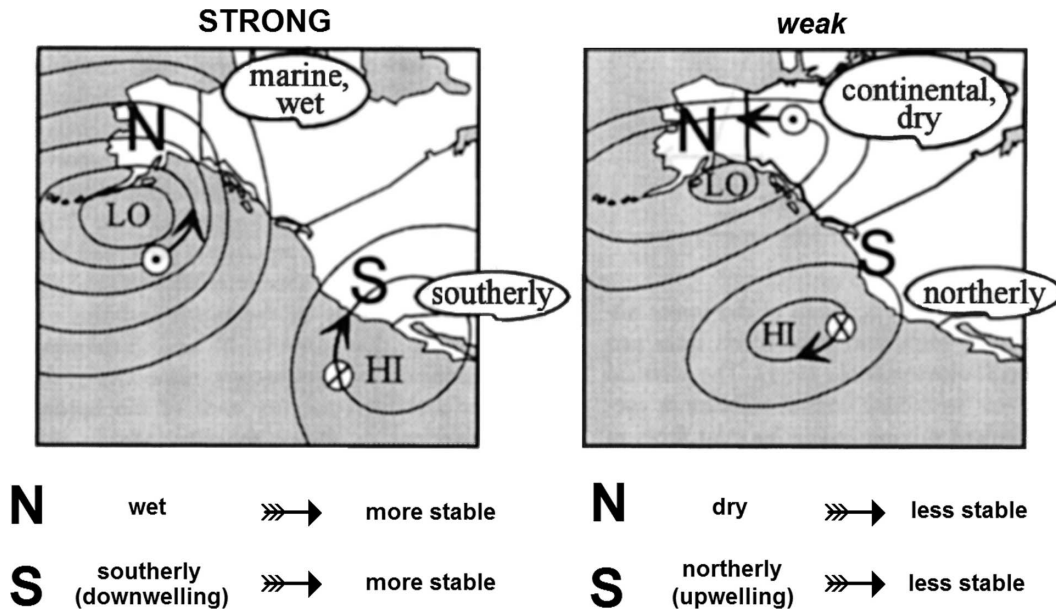


FIG. 7. Positions of Aleutian low and California high pressure systems during positive PDO conditions (strong Aleutian low) and negative PDO conditions (weak Aleutian low). The relative climate impacts to continental shelf regions of the NE Pacific are also indicated. Circle with dot inside represents flow out of the page (upwelling); circle with cross inside represents flow into the page (i.e., downwelling). From Gargett (1997).

Gargett (1997) hypothesized the existence of an optimal stability window to explain the observed relationship between variability in the PDO pattern and the inverse production pattern for Pacific salmon (Fig. 7). She proposed that during the positive phase of the PDO, the Aleutian low pressure system is deeper and centered more westward, with the associated California high pressure system centered more eastward over the North American continent. The result of this configuration is more precipitation in the northeastern North Pacific leading to greater vertical stability of the water column, resulting in greater biological productivity and more food for the salmon (this region has an excess of nutrients, but a lack of vertical stability). In contrast, in the continental United States, which is dominated by the California high pressure system, coastal winds during this PDO phase are predominately from the south, which favors downwelling and weakens the supply of nutrients, thereby decreasing general biological productivity with less food for salmon. When the PDO is negative, the Aleutian low pressure system is weaker, and its center tends to move eastward whereas the California high pressure system moves westward. This results in drier conditions and more vertical mixing off Alaska leading to reduced food productivity, but stronger upwelling-favorable winds and greater biological productivity off California.

However, biological and interspecific interactions can modulate this simple mechanism. Despite appar-

ently more favorable feeding conditions in the central Gulf of Alaska in the 1980s, the mean sizes of individual salmon returning to their natal rivers to spawn has been declining since the late 1970s (Pyper and Peterman 1999). It appears that the positive effect of increased food supply on the growth of salmon in the Gulf of Alaska was offset by increased abundances of salmon, resulting in greater competition and smaller individual body sizes (Pyper and Peterman 1999; Ruggerone et al. 2003).

## 2) NORTH PACIFIC GROUND FISH

The groundfish fisheries of Alaska and the Pacific west coast are the largest and most valuable of all U.S. fisheries, accounting for about 50% of total fish landings. The fisheries were not fully developed until the 1970s, about the time at which they became actively managed. Catches are closely monitored and catch quotas are set based upon assessments of population status. Groundfish populations in the Bering Sea and Gulf of Alaska are routinely surveyed, and annual estimates of population status, recruitment, and growth are generated and published. Population surveys are also conducted on crab and shrimp.

Physical changes associated with the PDO have been associated with dramatic and long-term change in the biota of the North Pacific, including groundfish (Hare and Mantua 2000). The scope of community changes that accompanied the 1976–77 regime shift were per-

haps best captured by a small-mesh shrimp trawl survey conducted annually in the Gulf of Alaska between 1953 and 1997 (Anderson and Piatt 1999). Beginning in the late 1970s, the composition of the trawl catches shifted from primarily forage species such as shrimp and capelin to higher trophic level species, primarily gadids (cod and pollock) and flatfish (sole, flounder, and halibut). This change phased in over several years, and the new composition persisted until the late 1990s. The increase in relative biomass of groundfish derived from increased productivity for many groundfish species in the period after 1977. Beamish (1993) showed that exceptional year classes were produced between 1976 and 1978 for many commercial species of groundfish along the entire coast of North America, a synchrony he attributed to ocean climate. Many of the shrimp and crab populations in the Gulf of Alaska have yet to recover and have not supported a commercial fishery since the late 1970s. Similar results were found in a retrospective analysis of Bering Sea bottom trawl surveys (Connors et al. 2002). At three index sites in the Bering Sea, groundfish abundance increased 100%–200% between 1960–80 and 1980–2000. Flatfish species, pollock, cod, and noncrab benthic invertebrates showed the greatest increase.

A number of studies have focused on northeast Pacific flatfish–environmental relationships and the decadal-scale nature of recruitment variability. Pacific halibut (*Hippoglossus stenolepis*) has been managed under international convention for 80 yr with catch and biological sampling and data collection dating back to 1935. Clark and Hare (2002) showed that recruitment of Pacific halibut is driven by environmental conditions rather than by spawning stock size. High and low recruitment regimes match the annual PDO index, with high recruitment occurring during positive PDO phases and low recruitment occurring during negative PDO phases (Fig. 8). Several species of flatfish, including flathead sole (*Hippoglossoides elassodon*), northern rock sole (*Lepidostetta polyxystra*), and arrowtooth flounder (*Atheresthes stomias*) had increased incidences of above-average recruitment events in the decade after 1977 (Wilderbuer et al. 2002). Conversely, Greenland turbot (*Reinhardtius hippoglossoides*) recruitment abruptly declined beginning in 1977 and has shown no signs of returning to pre-1977 levels.

While the ecosystem response to the climate shift of 1976/77 is unequivocal, there is evidence that many species fluctuate on other time scales, most notably to El Niño events. Pacific cod (*Gadus macrocephalus*), wall-eye pollock (*Theragra chalcogramma*), and Pacific hake (*Merluccius productus*) all produce more strong year classes when El Niño events are transmitted to Alaskan

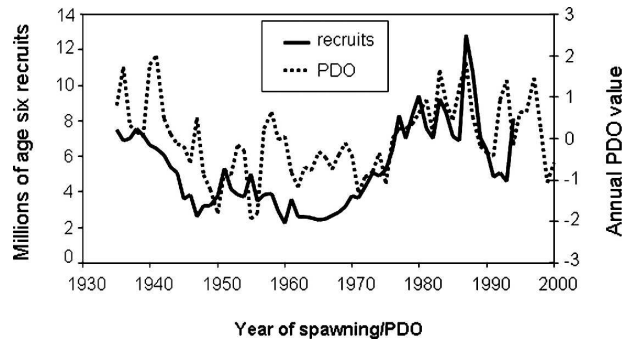


FIG. 8. Comparison of the annual PDO index and recruitment of Pacific halibut at age 6. Recruits are indexed to the year in which they were spawned and the numbers for that year class are first estimated at age 6.

waters (Hollowed et al. 2001). Along the west coast of the United States, rockfish populations have declined almost uniformly and continuously over the past 30 yr. Much of this decline is due to overfishing that resulted from an overestimate of the productivity of West Coast rockfish stocks (Ralston 2002). However, it has also been noted that the last great recruitment event for most West Coast rockfish was in the mid-1970s when ocean waters were cooler and more biologically productive (Love et al. 2002).

In the North Pacific, there is evidence for climatically forced bottom-up and top-down processes playing important roles in ecosystem changes. Fish population variability derives from both types of processes. Top-down processes include predation by other marine animals and fishing activities; bottom-up processes include oceanic productivity and the survival of very young fish. As with salmon, much of the synchrony in groundfish recruitment and long-term trends is believed to derive from bottom-up processes driven by the PDO. The enhanced biological productivity in Alaskan waters during the positive phase of the PDO results in an overall increase in groundfish though the response is not uniform across species. In addition to the doubling of zooplankton biomass in the Alaska Gyre following the 1976/77 regime shift, there was a marked change in the developmental timing of the dominant zooplankton species *Neocalanus plumchrus* (Mackas et al. 1998). Between the 1970s and 1990s the peak period of maximum biomass shifted from mid-July to early June. The effect of such a change in zooplankton availability may be to favor species with an earlier spawning period over those with a life cycle that produces offspring during the summertime. Temperature and advection also have been found to play an important role in survival of several groundfish species including pollock (Quinn and Niebauer 1995), herring (Zebdie and Collie 1995),

and several species of flatfish (Wilderbuer et al. 2002).

The bottom-up forcing of groundfish stocks, when integrated over a decade or longer, in turn leads to top-down impacts on some species. Indicative of reaching a carrying capacity, growth rates in flatfish, including halibut (Clark et al. 1999) and rock sole (Walters and Wilderbuer 2000) respond to the size of the populations. In the 1990s, during a period of sustained high population abundance, halibut of a given age weighed as little as 30% as similar-aged halibut 30 yr earlier. The disappearance of shrimp and forage fish following the 1976/77 regime shift was shown to lag the increase in groundfish, suggesting that predation was the operative mechanism (Mueter and Norcross 2000).

#### b. The North Atlantic Oscillation

The opposite atmospheric conditions between the eastern and western sides of the northern North Atlantic, the so-called “see-saw” effect between Greenland and northwestern Europe, have been known for centuries (see van Loon and Rogers 1978; Rogers 1984). This is an effect of what is now known as the NAO. The NAO is described by a number of climate indices, typically derived either from the simple difference in surface pressure anomalies between stations on Iceland and either the Azores, Lisbon, or Gibraltar, or by principal component analysis of sea level pressure fields. All the indices are highly correlated, especially on seasonal and longer time scales (Hurrell et al. 2003; Jones et al. 2003). During positive, high-index, phases of the NAO, the westerly winds are strengthened and moved northward, causing increased precipitation and temperatures over northern Europe and the southeastern United States, and drier and cooler conditions in the Labrador Sea and Mediterranean regions. Roughly opposite conditions occur during the negative-index phase. During the twentieth century the NAO underwent substantial decadal variation. In the early 1900s, the index was high but declined distinctly around 1950 to a minimum in the 1960s, which was its most extreme and persistent negative phase. From 1970 onward, there were large quasi-decadal fluctuations plus a gradual increase in the NAO index, which resulted in its most extreme and persistent positive phase during the late 1980s and early 1990s (Parsons and Lear 2001; Hurrell et al. 2003). These conditions were reflected in the air and sea temperatures and ice conditions throughout the North Atlantic.

A high NAO index generally means stronger southwest winds over the Barents Sea region, carrying relatively warm moist air. This leads to warmer sea surface temperatures, which are also enhanced by the increased Atlantic inflow into the Barents Sea during high NAO

years. Sea ice tends to be pushed farther northward. Over the Labrador Sea, in these same years, the northwest winds carry cold Arctic air masses farther south, causing winter air temperatures to decrease. This, in turn, results in earlier and more ice formation and the stronger northwest winds push the ice farther south, leading to more extensive ice coverage (Colbourne 1994; Drinkwater 1996; Deser et al. 2000). The cold, windy conditions in winter also result in high air–sea heat exchanges leading to extensive cooling of the waters over the shelf and in the Labrador Sea (Cayan 1992) and to deep convection (Dickson et al. 1996). In years of low NAO, the opposite tends to occur. The NAO tends to account for approximately 50% of the variance in most of the local physical variables (winter air temperatures, sea ice extent, annual mean subsurface ocean temperatures, etc.) in the Labrador (Drinkwater and Mountain 1997) and the Barents (Ottersen and Stenseth 2001) Seas.

Based on one of the world’s most studied species, the North Atlantic cod (*Gadus morhua*), we demonstrate below how these NAO-related variations have produced fluctuations in three of the main stocks of this species (North Sea, Barents Sea, and Newfoundland–Labrador stocks). Atlantic cod is one of the major North Atlantic fish resources, and fisheries records date back 500 yr or more (Kurlansky 1997).

#### 1) THE NORTH SEA COD STOCK

The decade of strong gadoid recruitment in the North Sea during the 1960s, the so-called “gadoid outburst” (Cushing 1984), coincided with the period when the NAO displayed the most persistent negative phase in the instrumental record. The transports of the North Atlantic Current, the Slope Current through the Faeroe Shetland Channel, and inflows into the North Sea were all at long-term lows, as were the southwesterly winds over the North Sea, which affected both transport and mixing processes (Parsons and Lear 2001). Furthermore, both the inflowing water masses and sea surface temperatures within the North Sea were cool, in response to NAO forcing. In the 1990s, when recruitment to the North Sea gadoid stocks was generally poor, the NAO was in a persistent and strong positive phase and the regional environmental conditions had flipped to their opposite extreme states (Parsons and Lear 2001). By means of principal component and canonical correlation analyses, Sirabella et al. (2001) confirmed this picture of a positive NAO phase with high sea temperature being unfavorable for North Sea cod recruitment. This relationship, which also is seen for Irish Sea cod, is suggested to result from a limitation in energy resources necessary to achieve higher metabolic rates

during warm years (Planque and Fox 1998). These results fit into the pattern suggested by Ottersen (1996) and Planque and Fredou (1999) of cod recruitment being positively related to temperature for cold-water stocks and negative for stocks occupying relatively warm waters.

A recent study suggests that long-term changes in plankton also influence the variability in cod recruitment. Using a zooplankton index derived from principal component analysis, Beaugrand et al. (2003) showed that an index based upon the quality and quantity of plankton prey explained 48% of the variability in the North Sea cod recruitment. Periods of high recruitment (e.g., the gadoid outburst) coincided with a temporal match between larval cod occurrence and its main prey *Calanus finmarchicus*, higher copepod biomass and euphausiid abundance, and prey of suitable size. On the other hand, the periods of low recruitment (after the mid-1980s) corresponded to the opposite conditions in the plankton environment (Fig. 9). The change in the quality and quantity of plankton prey was related negatively to fluctuations in sea surface temperature. Increasing sea temperature may have had a double negative impact on larval cod survival in the North Sea. Temperature increases metabolic rate and therefore increases the energy demand while at the same time it decreases the quality and the quantity of prey available for larvae (the energy supply). Temperature rise may have therefore resulted in an energy imbalance for larval cod, which caused increased larval mortality (the hypotheses of size-specific survival or growth-dependent mortality; Gallego and Heath 1997; P  pin 1993).

## 2) THE BARENTS SEA COD STOCK

The southern Barents Sea is highly productive, and the Arcto-Norwegian (or Northeast Arctic) cod stock of the region is the world's largest. As opposed to the relatively warm North Sea region, good recruitment of cod in the arcto-boreal Barents Sea is dependent on higher-than-average temperatures (S  tersdal and Loeng 1987; Ottersen and Stenseth 2001; Sirabella et al. 2001). The main reasons for this link may be (i) higher primary production due to a larger ice-free area, (ii) a larger influx of zooplankton carried by the increased inflow of Atlantic water masses from the southwest, and (iii) higher temperatures promoting higher biological activity at all trophic levels (Sakshaug 1997; Drinkwater et al. 2003). Warm conditions in the Barents Sea are related to a positive NAO phase, and links between the NAO and cod recruitment in this region have been demonstrated (Ottersen and Stenseth 2001).

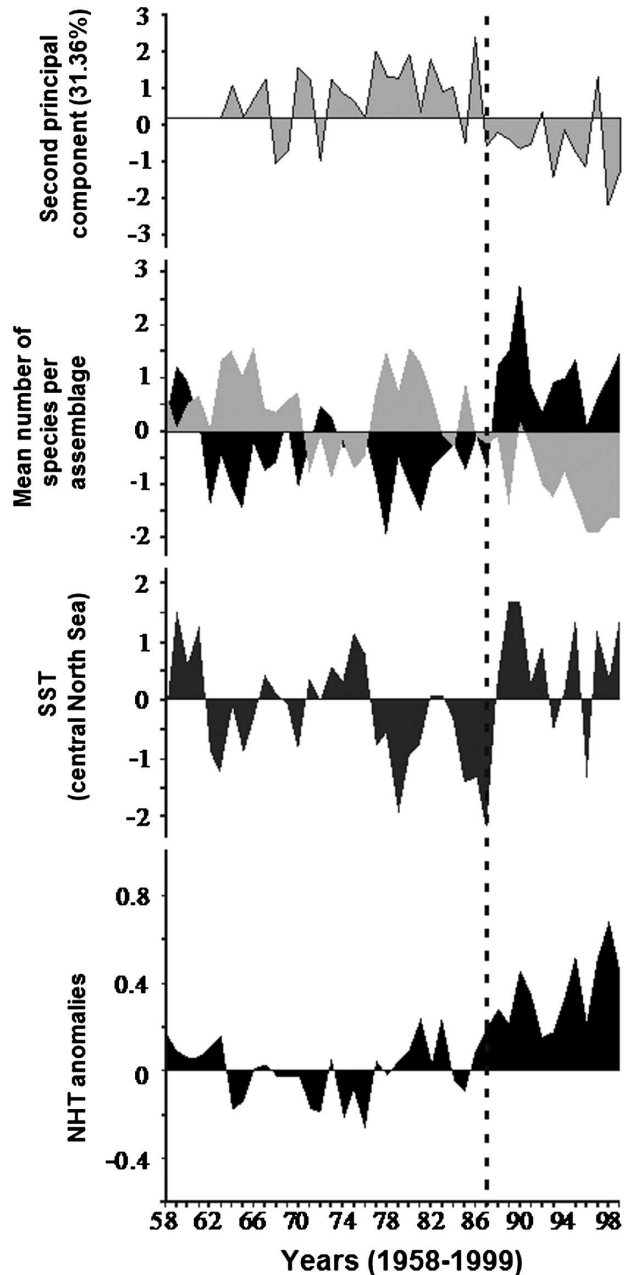


FIG. 9. Long-term (1958–99) changes in (a) fish recruitment (mainly gadid species, haddock, and cod) as revealed by the second principal component of recruitment series; (b) calanoid copepod species composition (temperate species in black, subarctic species in gray); (c) sea surface temperature anomalies; and (d) Northern Hemisphere temperature anomalies. [Modified from Beaugrand (2004).]

Ottersen and Stenseth (2001) suggest a mechanistic link where the NAO was considered to affect regional sea temperatures and food availability. Higher NAO index values were associated with warmer temperatures through both increased atmospheric heat transfer to the ocean and an increased Atlantic inflow. The latter

transports more *Calanus finmarchicus* into the Barents Sea and hence more food for juvenile cod. It should be noted that the link between climate, whether represented by sea temperature in the Barents Sea, inflow, or the NAO, and recruitment to Arcto-Norwegian cod has become stronger with time.

Changes in climate patterns associated with the NAO also affect predator–prey interactions in the Barents Sea. An increase in the basic metabolic rate of cod, associated with higher temperature during years of high NAO index values results in an increase in the consumption of capelin (*Mallotus villosus*) of approximately  $50\text{--}100 \times 10^3$  tonnes  $^{\circ}\text{C}^{-1}$ , which represents about 10% of the estimated total amount eaten by cod (Bogstad and Gjøvsæter 1994). Such episodes of high predation appear to be responsible for the collapse of the capelin stock with subsequent large impacts on the Barent Sea community assemblage and food web structures (Cianelli et al. 2006).

### 3) THE NEWFOUNDLAND–LABRADOR COD STOCK

Good cod recruitment off Newfoundland and Labrador tends to occur during warm years (low NAO years), but the relationship is weak (Taggart et al. 1994). During the high NAO years of the late 1980s and early 1990s when cold conditions prevailed in the Newfoundland–Labrador region, cod may have tended to move southward (Rose 2000) along with many other commercial and noncommercial species (Gomes et al. 1995). Drinkwater (2002) showed that the NAO accounted for over 50% of the variability in growth increment between 3- and 5-yr olds from the Northern Cod stock off Newfoundland. This is important because 50%–75% of the decline in biomass of the northern cod stock during the collapse was attributed to changes in growth (Sinclair 1996). The links of the NAO with recruitment and growth were suggested by Mann and Drinkwater (1994) to be through the food web. Support for this comes from modeling studies of Tittensor et al. (2003) that show large changes in abundance of *Calanus finmarchicus*, the food for larval cod, with small changes in temperature (20% for  $0.5^{\circ}\text{C}$ ; 40%–60% for  $1^{\circ}\text{C}$ ). This coupled with the fact that growth trajectories appear to be established early in life (Krohn and Kerr 1997) and mortality increases for slow growing fish perhaps explains the links between the NAO, temperature, and cod recruitment and growth for northern cod.

For all cod stocks, in addition to its impact on recruitment, the environment has an important effect on growth. Mean bottom temperatures account for 90% of the observed (10-fold) difference in growth rates between different Atlantic cod (*Gadus morhua*) stocks in the North Atlantic (Brander 1994, 1995) with warmer

temperatures leading to faster growth rates. Temperature not only accounts for differences in growth rates between cod stocks but also year-to-year changes in growth rates within a stock (Brander 2001) and hence the surplus production of the cod stocks (Dutil and Brander 2003).

## 5. Multidecadal to centennial variability

### a. Herring and sardines in the North Atlantic

One of the first observations on natural long-term variations of fish stocks was obtained from the North Atlantic. It has been known for more than 1000 yr that, periodically, large amounts of herring migrated to overwinter in the Bohuslän coast in Sweden. These periods of abundance lasted 20–50 yr and were interrupted by time spans of 50–70 yr. Nine of these Bohuslän periods are known (Cushing 1982; Alheit and Hagen 1997) as they correspond to important fishery activities; for example, catch exceeded 216 000 tonnes in the 1895/96 season and reached 270 000 tonnes during a fishing season in the eighteenth century. Several other European herring and sardine fisheries fluctuated either in phase with the Bohuslän periods (e.g., herring off southwestern England, in the eastern English Channel, and in the Bay of Biscay) or in alternation with them (e.g., the Norwegian spring-spawning herring and the sardines off southwestern England and in the English Channel; Binet 1988; Southward et al. 1988; Alheit and Hagen 1997). The fluctuations of these fisheries could be the result of real fluctuations of biomass or of decadal changes in migration routes moving the fish to areas not accessible to the limited range of the fishing methods employed in earlier historic times. Likely, fluctuations in biomass and migration routes are concomitant phenomena (Alheit and Hagen 1997).

Herring and sardines differ in their adaptation to temperature (Southward et al. 1988). The distributions of both species overlap in the English Channel. The herring is an Arcto-boreal species and the English Channel is usually the southern limit of its distribution. In contrast, the Channel usually represents the northern limit of the distribution of the sardine. A strong correlation between temperature and occurrence and abundance of both species has been recorded for the last 400 yr along the south coast of Devon and Cornwall, United Kingdom (Southward et al. 1988). The herring fishery was favored during cold periods and extended farther west, whereas the sardine fishery was then restricted to western Cornwall. During the extremely cold period called the “Little Ice Age,” in the second half of the seventeenth century, sardines were very scarce while herring were abundant. The sardine

fishery was more prevalent in warm periods. While herring abundance decreased in the south during these warm periods, it increased at their extreme northern range, as illustrated by records in fisheries of the Norwegian spring herring. These fluctuations have been associated with changes in the Icelandic ice cover (Bevertson and Lee 1965).

The Bohuslän periods coincided with cold climatic periods as indicated by the winter mildness/severity index reconstructed by Lamb (1972). As much of the decadal variability in regional air temperatures over many parts of the North Atlantic is associated with the North Atlantic Oscillation (cf. above), it is quite logical to observe that intense exploitation of fish stocks that are advantaged by cold regimes, that is, in phase with the Bohuslän periods, occurred during negative phases of the NAO. During these phases, there were cold temperatures at mid- and higher latitudes of the eastern North Atlantic, negative SST anomalies, increased ice cover off Iceland and in the northern Baltic Sea, reduced westerly winds, minimum frequency of southwesterly winds over England, and cold water in the North Sea, English Channel, and the Skagerrak (Bohuslän region). The second group of fish stocks (sardines and Norwegian spring spawning herring) thrives in opposite conditions during the positive phases of the NAO.

However, almost 100 yr after the last Bohuslän period, it remains to be explained why we have not observed any more recent Bohuslän herring periods, despite the negative period of the NAO in the 1960s. This could be due to prolonged recruitment overfishing (Corten 1990; Corten and van de Kamp 1992), nonstationarity of climate–ecosystem relationships, changes at the regional scale not accounted by the large-scale NAO climate index, or (and) finally the warming trend of the last century.

#### *b. Sardines and anchovies of the coastal upwelling systems*

Other historical, but fishery-independent records provide more evidence of dramatic multidecadal fluctuations of fish populations even in the absence of fishing. This information is contained in rare, well-preserved natural archives of marine sediments from which the rates of deposition of fish scales of small schooling planktivorous species like sardines and anchovies provide a proxy for abundance of these stocks (Soutar and Isaac 1974), in the absence of any industrial fishing. These natural high-resolution paleorecords provide valuable insight into the nature of large-scale variability of oceanic ecosystems. Depositional sites that provide such detailed histories are rare because of

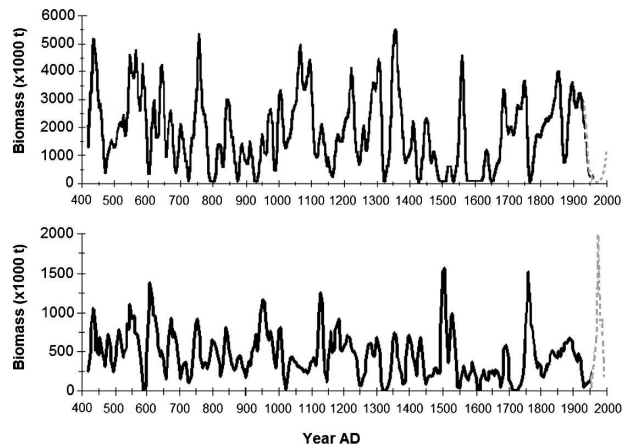


FIG. 10. (top) Sardine and (bottom) anchovy: Abundance indices based on fish scale deposition rates in sediment cores in the Santa Barbara basin (the gray dotted line is the recent period deduced from catch and fishery-independent data). [Updated from Baumgartner et al. (1996) in T. Baumgartner (2006, unpublished manuscript).]

the requisite suite of conditions to enhance the preservation of biological remains and to minimize bioturbation. The principal condition necessary is the depletion of oxygen in the overlying bottom water, which given the suitable combination of factors, provides a natural calendar of deposition with annual (or near annual) resolution for the past several thousand years (Baumgartner et al. 1996). The principal regions containing high-resolution natural records are associated with mid-water oxygen minima in the eastern boundary current systems of the North and South Pacific and the South Atlantic, as well as from silled glacial fjords (with restricted circulation) located on the poleward edges of the eastern boundary systems.

One of the most detailed records of fish scale deposition from the eastern boundary current systems, spanning 1600 yr, is from the sediments of the Santa Barbara Basin in the southern region of the California Current. Figure 10 shows reconstructed biomass time series of the Pacific sardine (*Sardinops sagax*) and northern anchovy (*Engraulis mordax*) resolved into 5-yr samples and compared with the modern series of biomass estimates. Spectral analysis of these series has shown that the reconstructed sardine biomass has significantly greater variability at the multicentennial scale of 500–600 yr than does the anchovy series. The periods of high sardine biomass appear to coincide with major periods of warming in the Northern Hemisphere climate such as the Medieval Warm Period (A.D. 950–1350), while the major periods of cooling are associated with lowered sardine biomass, in particular the period of the Little Ice Age (A.D. 1400–1800). The predominant time scale of expansion and contraction of the sardine popu-

lation is on the order of 50 to 60 yr and approximately 30 yr for the anchovies, although there is important variability for the anchovy at around 60 yr, and for both at around 25 yr.

Kawasaki (1983) compared these decadal fluctuations for the well-documented recent period (1900–83) in the three large Pacific sardine stocks (Japan, Humboldt Current, and California Current) and showed their more or less synchronous population swings (Fig. 3) with high biomass values during the 1930s and 1940s (except Peru, as no fishery was yet developed), low biomass during the late 1950s and 1960s, and increasing catches from the early 1970s to 1980 when the time series ended. Since this first analysis, additional data confirmed that sardine abundances off Japan and in the Humboldt Current peaked during the second half of the 1980s and dramatically decreased since (Fig. 3). Reconstructed time series of abundance from sediment records suggested that the Humboldt sardine also had a period of rather high biomass values during the 1930s and early 1940s just as sardine populations off Japan and California (Schwartzlose et al. 1999). The Californian sardine, however, did not show a cycle of abundance in the 1980s as in Japan and Humboldt populations. Schwartzlose et al. (1999) assume that heavy overfishing prevented this population from expanding during this period. Interestingly, in the Atlantic Ocean, examination of sardine catch fluctuations in the Benguela Current since the beginning of their industrial exploitation shows one regime of high abundance peaking in the 1960s, when sardine catches were very low in the Pacific (Fig. 3).

There is no evidence of synchronicity between the different anchovy populations, except in the simultaneous collapse of the populations in Japan and the Humboldt Current in the late 1960s/early 1970s (Fig. 3). But periods of high abundance of anchovy stocks appear out of phase of those of sardines in the last century (Lluch-Belda et al. 1992; Schwartzlose et al. 1999), although both species can be abundant during relatively long transitional periods (1975–90 in Japan; 1968–76 and 2000–2004 in Benguela), overlapping increasing and decreasing phases of both species.

In summary, the limited number of observed cycles (one or two for the sardines) and the lack of consistency in some time series do not permit firm conclusions over whether these small pelagic fish populations fluctuate in synchrony on a global scale. The most convincing observation for a basin-scale synchrony remains the fluctuation of sardine stocks off Japan and in the Humboldt Current. Even if these cycles are not necessarily synchronous, the alternating pattern between anchovy and sardine regimes seems to be more common, at least

in the last century. These stocks would fluctuate following their own dynamics, eventually interacting through food competition and predation, under the influence of the decadal variability of each semihemispheric oceanic basin, that are interconnected through different possible mechanisms (e.g., see a review in Miller and Schneider 2000).

For example, in the Humboldt Current, decreases in primary production are associated with the warm water phase. Because of the different optimal habitat temperatures of anchovy and sardine for both feeding (11°–20°C and 15°–24°C, respectively) and spawning (12°–18° and 16°–22°C, respectively; Schwartzlose et al. 1999), a warm anomaly would increase (decrease) feeding and spawning potential habitat of sardine (anchovy), while the associated decrease in primary production (and consequently zooplankton) would advantage sardines that can feed on both small zooplankton and phytoplankton and be a disadvantage to anchovies that feed mainly on zooplankton. In addition, predation on all life stages of anchovies in their reduced habitat is enhanced during these phases (Alheit and Niquen 2004). Opposite changes in cold water phases would increase (decrease) feeding and spawning potential habitats of anchovies (sardines); associated increased zooplankton abundance would benefit anchovies that can take advantage of their faster turnover and earlier maturity than sardines, thereby thriving and dominating the system. They would also increase the predation on sardine eggs. Interestingly, the sardine regime in the 1980s off Japan was also in phase with a period of lower primary and secondary production (Sugimoto et al. 2001) in the northwest Pacific.

### c. Oceanic fishes

Most of the examples provided above refer to small pelagic fish species (anchovies, sardines, and herrings) associated with coastal regions or continental slopes. This is because small pelagic fish generally have short life spans and their abundances are thus strongly driven by the annual recruitment of young fish, a process well understood to be modulated by ocean climate. However, there are also evidences that long-term climate variability has affected larger and long-living fishes. A study using the stable  $^{15}\text{N}$  isotope provides a reconstruction of sockeye salmon abundances over the past 2200 yr from sediments of lakes in Alaska that are spawning sites of this species (Finney et al. 2002). This reconstructed time series suggests large natural shifts in sockeye salmon abundance with a long period of increasing abundances from about A.D. 100–1200, followed by a fluctuating period to the late 1900s and then a sharp decline (Fig. 11) due to a heavy commercial

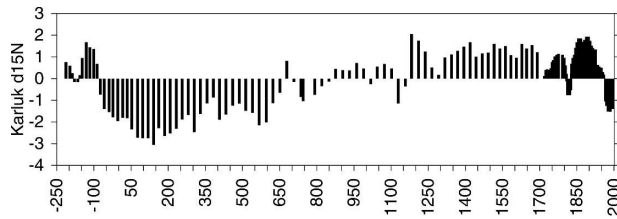


FIG. 11. Abundance index of Pacific salmon for the North Pacific Ocean, reconstructed from  $\delta^{15}\text{N}$  (‰) from Karluk Lake, Alaska. The dramatic decrease in Alaskan salmon abundance at  $\sim 100$  B.C. is contemporaneous with warming of marine waters in the Santa Barbara basin, while increased abundance after  $\sim$ A.D. 1200 corresponds to a period of glacial advances in southern Alaska and the Canadian Rockies. Redrawn from Finney et al. (2002).

harvest that significantly reduced the number of spawning sockeye salmon in the lake.

Multidecadal regimes are also observed in tuna populations (Fig. 5) and would result from the dominance of either El Niño or La Niña events during periods correlated with the PDO phases (at least for the recent period 1950–2000) that create accumulation over time of positive or negative annual recruitments in the populations. Hence, the high frequency ENSO-related recruitment signal is converted into low-frequency decadal fluctuations of the population biomass. While it is possible to discriminate two different regimes in tuna recruitment statistical estimates prior and after the mid-1970s (Fig. 5), it is too soon to assert that a new decadal regime is affecting tuna stocks in the Pacific Ocean since 1998. On the other hand, the regime shift associated with the PDO in the mid-1940s took place just before the development of the industrial tuna fisheries in the 1950s, and there is consequently insufficient information to know if a shift occurred in tuna stocks with reversed trends to those observed in the mid-1970s (i.e., we would expect an increase in albacore and a decrease in yellowfin and skipjack stocks). Nevertheless, a few indications exist. Despite a very limited fishing effort in the early 1950s, the catch rates of yellowfin in longline fisheries declined rapidly. This trend has been used by Myers and Worm (2003) in a controversial study (Walters 2003) suggesting that “industrialized fisheries typically reduced community biomass by 80% during the first years of exploitation.” Concerning albacore, catch rates continuously increased during all the 1950s and started decreasing in the 1960s, mainly because of changes in species targeting.

Another example is the bluefin tuna that provides evidence of dramatic fluctuations in the Mediterranean and eastern Atlantic, from ancestral records of catches from traps (Ravier and Fromentin 2001). The authors examined 54 time series up to four centuries old, along

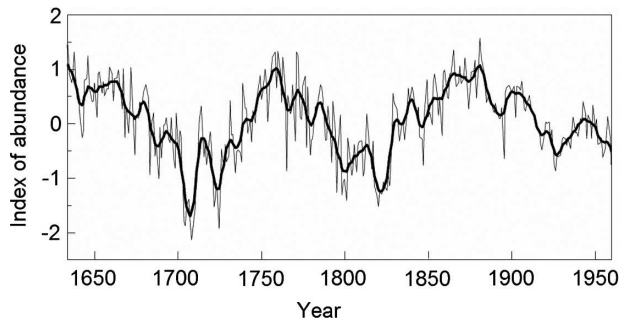


FIG. 12. Relative abundance of bluefin tuna from the eastern Atlantic and Mediterranean. The index was developed from historical records of catches in bluefin traps. From Ravier and Fromentin (2001).

the western Mediterranean and the Atlantic coasts of Portugal, Spain, and Morocco. Overall, they observed conspicuous 100-yr-long periodic fluctuations as well as 20-yr-long cycles (Fig. 12), which likely reflect true variations in abundance because of the specificities of the traps (passive gears that were not modified for centuries) and the synchrony of these fluctuations between distant locations (over more than 2000 km). The authors first hypothesized that these variations could be driven by annual fluctuations in fish recruitment, amplified by resonant effects, but a more recent study (Ravier and Fromentin 2004) indicated that fluctuations in trap catches are strongly and negatively related to changes in temperature and could result also from changes in spawning migrations attributable to modifications in the oceanographic conditions.

## 6. Conclusions

Until now, correlations have been useful to demonstrate that climate-related variability of fish populations is the rule rather than the exception. Recognizing the worldwide existence of such variability is already an important step rarely considered in fish stock management. However, despite the appealing possibility of climate-related mid- and long-term (decades) forecasts, predictions based on simple empirical correlations are not satisfactory, as many have failed the test of time (Myers 1998), which is perhaps not surprising given the complex dynamics and the multiple interactions highlighted above. Therefore, marine and fisheries scientists need to identify not only empirical correlations between large-scale climate indices and fish abundance indices, but also the mechanisms that link climate variability to the biological changes in the oceanic ecosystems and fish populations.

On their side, physical oceanographers and climatologists need to disentangle the effects of numerous



mechanisms that can result in climate variability. This is a challenge since, in addition to external forcing (e.g., variability in solar irradiance), there are potential complex interactions between internal mechanisms.

To give a synthetic view, for example, it is obvious that changes in atmospheric conditions create changes in surface wind stress, air–sea heat exchange, evaporation and precipitation, and sea ice cover in subarctic regions. Heat flux anomalies affect SST, and changes in wind stress affect wind-driven circulation. Conversely, surface water temperature anomalies associated with wind stress anomalies affect atmospheric circulation patterns (as for the ENSO-type ocean–atmosphere interaction in the equatorial region). Residuals of monthly to interannual high-frequency SST anomalies result in low-frequency signals (red noise) “memorized” in the upper and deep ocean. In the equatorial region, temperature anomalies in the upper layer are tied to wind-driven currents that flow away from the equator and eventually sink and flow back along surfaces of constant water density at depths of 100 to 400 m (McPhaden and Zhang 2002). After a decadal-scale period related to the size and configuration of the basin, the returning flows meet and rise to the surface near the equator, bringing with them cooler and nutrient-rich water. In the midlatitudes, these deep temperature anomalies can reemerge year after year during winter mixing providing a feedback to the atmosphere (Alexander et al. 1999). Eventually, part of this variability is transferred to another oceanic basin through the atmosphere. For example, the atmospheric teleconnection between the Atlantic and the Pacific is responsible for ENSO-related fluctuations of the trade winds in the North Atlantic (Klein et al. 1999; Signorini et al. 1999) with a lag of a few months. During El Niño events in the Pacific, the reduction in the Atlantic NE trade wind speeds induces a warming in the northern part of the tropical Atlantic, west of 40°W (Enfield and Mayer 1997). Similarly, the intensity of the wind-induced coastal upwelling on the eastern side of the Atlantic basin is drastically reduced, and positive temperature anomalies are recorded along the shelf off West Africa (Roy and Reason 2001). Such atmospheric teleconnections between oceanic basins and the related oceanic responses provide a mechanism whereby widely separated fish populations are exposed to coherent environmental forcing. This provides the scientific basis to account for the existence of a coherent pattern of variability between widely separated fish populations (cf. section 5b).

When discovering the complex ocean–atmosphere interactions as summarized above, marine biologists likely would despair of finding any explanation for cli-

mate-related variability of marine ecosystems and fish populations—probably just as physicists who are reading this article and discovering biological uncertainties would find themselves quite happy not to be doing biology. However, despite complexity, recent advances in modeling, computational technology, and mathematical and statistical techniques make possible realistic planetary-scale simulations of ocean physics and lower-trophic (phytoplankton) level biology (de Young et al. 2004). Therefore, it is now possible to test hypotheses and mechanisms linking climate physical forcing and biological processes by embedding biological mechanisms in numerical models that *already* integrate the complex ocean–atmosphere dynamical interactions. The first studies that have used dynamical coupling between biology and ocean physics have shown encouraging results, for example, to identify mechanisms that control grounds and seasons of spawning or spatial dynamics and movements of fish. More importantly, these studies demonstrate that when coupled to the ocean dynamics, simple biological mechanisms that were proposed a long time ago but were rarely verified until now through correlative or analytical models provide more complex but realistic results.

We can expect that in the next few years, a large diversity of models coupling biological and physical dynamics will help in answering the outstanding questions that have emerged from the present review and are summarized below.

- Fish stocks fluctuate at a myriad of time scales, due to a combination of climate variability (mainly temperature, currents, and primary and secondary productions), their own population dynamics, and the interactions (especially competition) with other species. Can we discriminate climate from biological dynamics?
- Despite the fact that climate indices might account for only a small fraction of a region’s climatic variance, in many cases there are surprisingly good relationships between climate and fish abundance indices. Can marine ecosystem sensitivity to climate influences associated with nonlinearity lead to amplification of climatic signals (Taylor et al. 2002)?
- These (population and climate) dynamics and differences in environmental affinities of species (or substocks of species) create decadal time-scale cycles of abundance dominated by one or a few species (substocks). Can we reproduce (model) these decadal-scale fluctuations by combining climate-related variability with simple ecological principles, for example, feeding and spawning habitat affinities, prey–predator interactions, and recruitment mechanisms?

- Geographically distant species/stocks can fluctuate either in phase or out of phase, likely forced by large-scale climate conditions. Are the processes responsible for this phenomenon similar in different regions?
- In some cases, the expected recovery of species (substocks) associated with its supposed adapted climate regime does not occur (sardine in California Current in the 1970s) or occurs more slowly than anticipated (herring in Barents Sea, cod in the Labrador–Newfoundland region, etc). Is this due to a completely depleted stock, replacement by a better-adapted species, a fundamental change in the entire ecosystem, or an indication that the anthropogenic warming is already affecting some species or stock already? Is there a time scale below which climate–ecosystem relationships can be considered stationary with shifts between two or a few states, and above which nonstationarity is dominating the system?

Collaborative studies on these questions are urgently needed to improving management of fisheries in an ecosystem context largely controlled by climate dynamics. They also offer a unique worldwide framework to test hypotheses and to identify key mechanisms in the complex atmosphere–ocean interactions that drive climate variability.

#### REFERENCES

- Alexander, M. A., C. Deser, and M. S. Timlin, 1999: The reemergence of SST anomalies in the North Pacific Ocean. *J. Climate*, **12**, 2419–2433.
- Alheit, J., and E. Hagen, 1997: Long-term climate forcing of European herring and sardine populations. *Fish. Oceanogr.*, **6**, 130–139.
- , and M. Niquen, 2004: Regime shifts in the Humboldt Current ecosystem. *Progress in Oceanography*, Vol. 60, Pergamon, 201–222.
- Anderson, P. J., and J. F. Piatt, 1999: Community reorganization in the Gulf of Alaska following ocean climate regime shift. *Mar. Ecol. Prog. Ser.*, **189**, 117–123.
- Bakun, A., 1996: *Patterns in the Ocean: Ocean Processes and Marine Population Dynamics*. California Sea Grant College System, 323 pp.
- , 2002: An empirical test for the existence of a generation-time-dependent mechanism for the rapid adaptive response of fish populations to variations in ocean climate, predation or fishery exploitation. Report of a GLOBEC-SPACC/IDYLE/ENVIFISH Workshop on Spatial Approaches to the Dynamics of Coastal Pelagic Resources and their Environment in Upwelling Areas, C. D. van der Lingen et al., Eds., GLOBEC Rep. 16, 2–4.
- Bang, N. D., and W. R. H. Andrews, 1974: Direct current measurements of a shelf-edge frontal jet in the southern Benguela system. *J. Mar. Res.*, **32**, 405–417.
- Baumgartner, T., A. Soutar, and W. Riedel, 1996: Natural time scales of variability in coastal pelagic fish populations of the California Current over the past 1500 years: Response to global climate change and biological interaction. California Sea Grant Rep. for 1992–1995, California Sea Grant College, La Jolla, CA, 31–37.
- Beamish, R. J., 1993: Climate and exceptional fish production off the west coast of North America. *Can. J. Fish. Aquat. Sci.*, **50**, 2270–2291.
- , and D. R. Bouillon, 1993: Pacific salmon production trends in relation to climate. *Can. J. Fish. Aquat. Sci.*, **50**, 1002–1016.
- Beaugrand, G., 2004: The North Sea regime shift: Evidence, causes, mechanisms and consequences. *Progress in Oceanography*, Vol. 60, Pergamon, 245–262.
- , K. Brander, J. A. Lindley, S. Souissi, and P. C. Reid, 2003: Plankton effect on cod recruitment in the North Sea. *Nature*, **426**, 661–664.
- Beverton, R. J. H., and A. J. Lee, 1965: Hydrodynamic fluctuations in the North Atlantic Ocean and some biological consequences. *The Biological Significance of Climatic Changes in Britain*, C. G. Johnson and L. P. Smith, Eds., Academic Press, 79–107.
- Binet, D., 1988: French sardine and herring fisheries: A tentative description of their fluctuations since the eighteenth century. *Long Term Changes in Marine Fish Populations: Proceedings of International Symposium*, T. Wyatt and M. G. Larraneta, Eds., 345–364.
- Bogstad, B., and H. Gjøsæter, 1994: A method for estimating the consumption of capelin by cod in the Barents Sea. *ICES J. Mar. Sci.*, **51**, 273–280.
- Bond, N. A., J. E. Overland, M. Spillane, and P. Stabeno, 2003: Recent shifts in the state of the North Pacific. *Geophys. Res. Lett.*, **30**, 2183, doi:10.1029/2003GL018597.
- Boyd, A. J., L. J. Shannon, F. H. Schülein, and J. Taunton-Clark, 1998: Food, transport and anchovy recruitment in the southern Benguela upwelling system off South Africa. *Global versus Local Changes in Upwelling Systems*, M. H. Durand et al., Eds., ORSTOM Editions, 195–210.
- Brander, K. M., 1994: Patterns of distribution, spawning, and growth in North Atlantic cod: The utility of inter-regional comparisons. *ICES Mar. Sci. Symp.*, **198**, 406–413.
- , 1995: The effects of temperature on growth of Atlantic cod (*Gadus morhua* L.). *ICES J. Mar. Sci.*, **52**, 1–10.
- , 2001: Effect of environmental variability on growth and recruitment in cod (*Gadus morhua*) using a comparative approach. *Oceanol. Acta*, **23**, 485–496.
- Brodeur, R. D., and D. M. Ware, 1992: Long-term variability in zooplankton biomass in the subarctic Pacific Ocean. *Fish. Oceanogr.*, **1**, 32–38.
- Carrasco, S., and H. Santander, 1987: The El Niño event and its influence on the zooplankton off Peru. *J. Geophys. Res.*, **92** (C13), 14 405–14 410.
- Cayan, D. R., 1992: Latent and sensible heat flux anomalies over the northern oceans: The connection to monthly atmospheric circulation. *J. Climate*, **5**, 354–369.
- Cianelli, L., D. O. Hjermmann, P. Lehodey, G. Ottersen, J. T. Duffy-Anderson, and N. C. Stenseth, 2006: Climate forcing, food web structure and community dynamics in pelagic marine ecosystems. *Aquatic Food Webs: An Ecosystem Approach*, A. Belgrano et al., Eds., Oxford University Press, 143–169.
- Clark, W. G., and S. R. Hare, 2002: Effects of climate and stock size on recruitment and growth of Pacific halibut. *N. Amer. J. Fish. Manage.*, **22**, 852–862.
- , —, A. M. Parma, P. J. Sullivan, and R. J. Trumble, 1999:

- Decadal changes in growth and recruitment of Pacific halibut (*Hippoglossus stenolepis*). *Can. J. Fish. Aquat. Sci.*, **56**, 173–183.
- Colbourne, E., S. Narayanan, and S. Prinsenberg, 1994: Climatic changes and environmental conditions in the Northwest Atlantic, 1970–1993. *ICES Mar. Sci. Symp.*, **198**, 311–322.
- Connors, M. W., A. B. Hollowed, and E. Brown, 2002: Retrospective analysis of Bering Sea bottom trawl surveys: Regime shift and ecosystem reorganization. *Progress in Oceanography*, Vol. 55, Pergamon, 209–222.
- Corten, A., 1990: Long-term trends in pelagic fish stocks of the North Sea and adjacent waters and their possible connection to hydrographic changes. *Neth. J. Sea Res.*, **25**, 227–235.
- , and G. van de Kamp, 1992: Natural changes in pelagic fish stocks of the North Sea in the 1980s. *ICES Mar. Sci. Symp.*, **195**, 402–417.
- Cushing, D. H., 1982: *Climate and Fisheries*. Academic Press, 364 pp.
- , 1984: The gadoid outburst in the North Sea. *J. Cons. Int. Explor. Mer*, **41**, 159–166.
- Deser, C., J. E. Walsh, and M. S. Timlin, 2000: Arctic Sea ice variability in the context of recent wintertime atmospheric circulation trends. *J. Climate*, **13**, 617–633.
- de Young, B., M. Heath, F. Werner, F. Chai, B. Megrey, and P. Monfray, 2004: Challenges of modeling ocean basin ecosystems. *Science*, **304**, 1463–1466.
- Dickson, R., J. Lazier, J. Meincke, P. Rhines, and J. Swift, 1996: Long-term coordinated changes in the convective activity of the North Atlantic. *Progress in Oceanography*, Vol. 38, Pergamon, 241–295.
- Drinkwater, K. F., 1996: Atmospheric and oceanographic variability in the Northwest Atlantic during the 1980s and early 1990s. *J. Northwest Atl. Fish. Sci.*, **18**, 77–97.
- , 2002: A review of the role of climate variability in the decline of northern cod. *Amer. Fish. Soc. Symp.*, **32**, 113–130.
- , and D. B. Mountain, 1997: Climate and oceanography. *Northwest Atlantic Groundfish: Perspectives on a Fishery Collapse*, J. G. Boreman et al., Eds., American Fisheries Society, 3–25.
- , and Coauthors, 2003: The response of marine ecosystems to climate variability associated with the North Atlantic Oscillation. *The North Atlantic Oscillation: Climatic Significance and Environmental Impact*, *Geophys. Monogr.*, Vol. 134, Amer. Geophys. Union, 211–234.
- Dutil, J.-D., and K. Brander, 2003: Comparing productivity of North Atlantic cod (*Gadus morhua*) stocks and limits to growth production. *Fish. Oceanogr.*, **12**, 502–512.
- Enfield, D. B., and D. A. Mayer, 1997: Tropical Atlantic sea surface temperature variability and its relation to El Niño–Southern Oscillation. *J. Geophys. Res.*, **102**, 929–945.
- Finney, B. P., I. Gregory-Eaves, M. S. V. Douglas, and J. P. Smol, 2002: Fisheries productivity in the northeastern Pacific Ocean over the past 2,200 years. *Nature*, **416**, 729–733.
- Gallego, A., and M. Heath, 1997: The effect of growth-dependent mortality, external environment and internal dynamics on larval fish otolith growth: an individual-based modelling approach. *J. Fish Biol.*, **51** (Suppl. A), 121–134.
- Gargett, A. E., 1997: The optimal stability ‘window’: A mechanism underlying decadal fluctuations in North Pacific salmon stocks? *Fish. Oceanogr.*, **6**, 109–117.
- Gedalof, Z., and D. J. Smith, 2001: Interdecadal climate variability and regime-scale shifts in Pacific North America. *Geophys. Res. Lett.*, **28**, 1515–1518.
- Gian-Reto, W., and Coauthors, 2002: Ecological responses to recent climate change. *Nature*, **416**, 389–395.
- Gomes, M. C., R. L. Haedrich, and M. G. Villagarcia, 1995: Spatial and temporal changes in the groundfish assemblages on the north-east Newfoundland/Labrador Shelf, north-west Atlantic, 1978–91. *Fish. Oceanogr.*, **4**, 85–101.
- González, H. E., M. Sobarzo, D. Figueroa, and E.-M. Nöthig, 2000: Composition, biomass and potential grazing impact of the crustacean and pelagic tunicates in the northern Humboldt Current area off Chile: Differences between El Niño and non-El Niño years. *Mar. Ecol. Prog. Ser.*, **195**, 201–220.
- Graham, N. E., 1994: Decadal-scale climate variability in the tropical and North Pacific during the 1970s and 1980s: Observations and model results. *Climate Dyn.*, **10**, 135–162.
- Hampton, J., and D. A. Fournier, 2001: A spatially disaggregated, length-based, age-structured population model of yellowfin tuna (*Thunnus albacares*) in the western and central Pacific Ocean. *Mar. Freshwater Res.*, **52**, 937–963.
- Hare, S. R., and R. C. Francis, 1995: Climate change and salmon production in the northeast Pacific Ocean. *Climate Change and Northern Fish Populations*, R. J. Beamish, Ed., Canadian Special Publication of Fisheries and Aquatic Sciences, Vol. 121, National Research Council of Canada, 357–372.
- , and N. J. Mantua, 2000: Empirical evidence for North Pacific regime shifts in 1977 and 1989. *Progress in Oceanography*, Vol. 47, Pergamon, 103–146.
- , N. J. Mantua, and R. C. Francis, 1999: Inverse production regimes: Alaska and West Coast Pacific salmon. *Fisheries*, **24**, 6–15.
- Helland-Hansen, B., and F. Nansen, 1909: The Norwegian Sea. *Fisk Dir. Skr. Ser. Hav. Unders.*, **2**, 1–360.
- Hollowed, A. B., S. R. Hare, and W. S. Wooster, 2001: Pacific-basin climate variability and patterns of Northeast Pacific marine fish production. *Progress in Oceanography*, Vol. 49, Pergamon, 257–282.
- Huggett, J. A., P. Fréon, C. Mullon, and P. Penven, 2003: Modelling the transport success of anchovy *Engraulis encrasicolus* eggs and larvae in the southern Benguela: The effects of spatio-temporal spawning patterns. *Mar. Ecol. Prog. Ser.*, **250**, 247–262.
- Hurrell, J. W., Y. Kushnir, G. Ottersen, and M. Visbeck, 2003: *The North Atlantic Oscillation: Climatic Significance and Environmental Impact*. *Geophys. Monogr.*, Vol. 134, Amer. Geophys. Union, 279 and viii pp.
- Hutchings, L., and Coauthors, 1998: Multiple factors affecting South African anchovy recruitment in the spawning, transport and nursery areas. *S. Afr. J. Mar. Sci.*, **19**, 211–225.
- , L. E. Beckley, M. H. Griffiths, M. J. Roberts, S. Sundby, and C. D. van der Lingen, 2002: Spawning on the edge: Spawning grounds and nursery areas around the southern African coastline. *Mar. Freshwater Res.*, **53**, 307–318.
- Jones, P. D., T. J. Osborn, and K. R. Briffa, 2003: Pressure-based measures of the North Atlantic Oscillation (NAO): A comparison and assessment of changes in the strength of the NAO and its influence on surface climate parameters. *The North Atlantic Oscillation: Climatic Significance and Environmental Impact*, *Geophys. Monogr.*, Vol. 134, Amer. Geophys. Union, 51–62.
- Kawasaki, T., 1983: Why do some pelagic fishes have wide fluctuations in their numbers? Biological basis of fluctuation from the viewpoint of evolutionary ecology. *FAO Fish. Rep.*, **291**, 1065–1080.
- Klein, S. A., B. J. Soden, and N. C. Lau, 1999: Remote sea surface

- temperature variations during ENSO: Evidence for a tropical atmospheric bridge. *J. Climate*, **12**, 917–932.
- Korubel, J. L., S. F. Bloomer, K. L. Cochran, L. Hutchings, and J. G. Field, 1998: Forecasting in South African pelagic fisheries management: the use of expert ad decision support systems. *S. Afr. J. Mar. Sci.*, **19**, 415–423.
- Krohn, M., and S. Kerr, 1997: Declining weight-at-age in northern cod and the potential importance of the early-years and size-selective fishing mortality. *Northwest Atl. Fish. Org. Sci. Council Stud.*, **29**, 43–50.
- Kurlansky, M., 1997: *Cod: A Biography of the Fish that Changed the World*. Jonathan Cape, 294 pp.
- Lamb, H. H., 1972: *Fundamentals and Climate Now*. Vol. 1, *Climate: Past, Present and Future*, Methuen, 613 pp.
- Lehodey, P., 2001: The pelagic ecosystem of the tropical Pacific Ocean: Dynamic spatial modelling and biological consequences of ENSO. *Progress in Oceanography*, Vol. 49, Pergamon, 439–468.
- , M. Bertignac, J. Hampton, T. Lewis, and J. Picaut, 1997: El Niño Southern Oscillation and tuna in the western Pacific. *Nature*, **389**, 715–718.
- , F. Chai, and J. Hampton, 2003: Modelling climate-related variability of tuna populations from a coupled ocean-biogeochemical-populations dynamics model. *Fish. Oceanogr.*, **12**, 483–494.
- Lluch-Belda, D., R. A. Schwartzlose, R. Serra, R. Parrish, T. Kawasaki, D. Hedgecock, and R. J. M. Crawford, 1992: Sardine and anchovy regime fluctuations of abundance in four regions of the world oceans: A workshop report. *Fish. Oceanogr.*, **1**, 339–347.
- Love, M. S., M. Yoklavich, and L. Thorsteinson, 2002: *The Rockfishes of the Northeast Pacific*. University of California Press, 404 pp.
- Mackas, D. L., R. Goldblatt, and A. G. Lewis, 1998: Interdecadal variation in developmental timing of *Neocalanus plumchrus* populations at Ocean Station P in the subarctic North Pacific. *Can. J. Fish. Aquat. Sci.*, **55**, 1878–1893.
- Mann, K. H., and K. F. Drinkwater, 1994: Environmental influences on fish and shellfish production in the Northwest Atlantic. *Environ. Rev.*, **2**, 16–32.
- Mantua, N. J., S. R. Hare, Y. Zhang, J. M. Wallace, and R. C. Francis, 1997: A Pacific inter-decadal climate oscillation with impacts on salmon production. *Bull. Amer. Meteor. Soc.*, **78**, 1069–1079.
- McPhaden, M. J., and D. Zhang, 2002: Slowdown of the meridional overturning circulation in the upper Pacific Ocean. *Nature*, **415**, 603–608.
- Mendez, R., 1987: Cambios bióticos y efectos sobre los recursos pesqueros y pesquerías en Chile. *Rev. Com. Permanente Pacífico Sur*, **16**, 7–96.
- Miller, A. J., and N. Schneider, 2000: Interdecadal climate regime dynamics in the North Pacific Ocean: theories, observations and ecosystem impacts. *Progress in Oceanography*, Vol. 47, Pergamon, 355–379.
- , D. R. Cayan, T. P. Barnett, N. E. Graham, and J. M. Oberhuber, 1994: The 1976–77 climate shift of the Pacific Ocean. *Oceanography*, **7**, 21–26.
- Muck, P., and G. Sanchez, 1987: The importance of mackerel and horse mackerel predation for the Peruvian anchoveta stock (a population and feeding model). *The Peruvian Anchoveta and Its Upwelling Ecosystem: Three Decades of Change*, D. Pauly and I. Tsukayama, Eds., ICLARM Studies and Reviews, Vol. 15, ICLARM, 276–293.
- Mueter, F. J., and B. L. Norcross, 2000: Changes in species composition of the demersal fish community in nearshore waters of Kodiak Island, Alaska. *Can. J. Fish. Aquat. Sci.*, **2000**, 1169–1180.
- Mullon, C., Fréon, C., Parada, P., van der Lingen, C. D., and J. A. Huggett, 2003: From particles to individuals: Modelling the early stages of anchovy (*Engraulis capensis/encrasicolus*) in the southern Benguela. *Fish. Oceanogr.*, **12**, 396–406.
- Myers, R. A., 1998: When do environment-recruit correlations work? *Rev. Fish. Biol. Fish.*, **8**, 285–305.
- , and B. Worm, 2003: Rapid worldwide depletion of predatory fish community. *Nature*, **423**, 280–283.
- Ottersen, G., 1996: Environmental impact on variability in recruitment, larval growth and distribution of Arcto-Norwegian cod. Ph.D. thesis, University of Bergen, 136 pp.
- , and N. C. Stenseth, 2001: Atlantic climate governs oceanographic and ecological variability in the Barents Sea. *Limnol. Oceanogr.*, **46**, 1774–1780.
- , J. Alheit, K. Drinkwater, K. Friedland, E. Hagen, and N. C. Stenseth, 2004: The response of fish to ocean climate variability. *Marine Ecosystems and Climate Variation: The North Atlantic*, N. C. Stenseth et al., Eds., Oxford University Press, 252 and xiv pp.
- Parrish, R. H., A. Bakun, D. M. Husby, and C. S. Nelson, 1983: Comparative climatology of selected environmental processes in relation to Eastern boundary current pelagic fish reproduction. *FAO Fish. Rep.*, **2**, 731–777.
- Parsons, L. S., and W. H. Lear, 2001: Climate variability and marine ecosystem impacts: A North Atlantic perspective. *Progress in Oceanography*, Vol. 49, Pergamon, 167–188.
- Penven, P., C. Roy, G. Brundrit, A. Colin de Verdière, P. Fréon, A. Jonhson, J. R. E. Lutjeharms, and F. A. Shillington, 2001: A regional hydrodynamic model of upwelling in the Southern Benguela. *S. Afr. J. Sci.*, **97**, 472–475.
- Pépin, P., 1993: An appraisal of the size-dependent mortality hypothesis for larval fish: Comparison of a multispecies study with an empirical review. *Can. J. Fish. Aquat. Sci.*, **50**, 2166–2174.
- Peterson, W. T., and F. B. Schwing, 2003: A new climate regime in northeast Pacific ecosystems. *Geophys. Res. Lett.*, **30**, 1896, doi:10.1029/2003GL017528.
- Philander, S. G. H., 1990: *El Niño, La Niña, and the Southern Oscillation*. Academic Press, 293 pp.
- Planque, B., and C. J. Fox, 1998: Interannual variability in temperature and the recruitment of Irish Sea cod. *Mar. Ecol. Prog. Ser.*, **172**, 101–105.
- , and T. Fredou, 1999: Temperature and the recruitment of Atlantic cod (*Gadus morhua*). *Can. J. Fish. Aquat. Sci.*, **56**, 2069–2077.
- Pyper, B. J., and R. M. Peterman, 1999: Relationship among adult body length, abundance, and ocean temperature for British Columbia and Alaska sockeye salmon (*Oncorhynchus nerka*), 1967–1997. *Can. J. Fish. Aquat. Sci.*, **56**, 1716–1720.
- Quinn, T. J., and H. J. Niebauer, 1995: Relation of eastern Bering Sea walleye pollock (*Theragra chalcogramma*) recruitment to environmental and oceanographic variables. *Climate Change and Northern Fish Populations*, R. J. Beamish, Ed., Canadian Special Publication of Fisheries and Aquatic Sciences, Vol. 121, National Research Council of Canada, 497–507.
- Ralston, S., 2002: West Coast groundfish harvest policy. *N. Amer. J. Fish. Manage.*, **22**, 249–250.
- Ravier, C., and J.-M. Fromentin, 2001: Long-term fluctuations in

- the eastern Atlantic and Mediterranean bluefin tuna population. *ICES J. Mar. Sci.*, **58**, 1299–1317.
- , and —, 2004: Are the long-term fluctuations in Atlantic bluefin tuna (*Thunnus thynnus*) population related to environmental changes? *Fish. Oceanogr.*, **13**, 145–160.
- Rogers, J. C., 1984: The association between the North Atlantic Oscillation and the Southern Oscillation in the Northern Hemisphere. *Mon. Wea. Rev.*, **112**, 1999–2015.
- Rose, G. A., B. deYoung, D. W. Kulka, S. Goddard, and G. L. Fletcher, 2000: Distribution shifts and overfishing the northern cod (*Gadus morhua*): A view from the ocean. *Can. J. Fish. Aquat. Sci.*, **57**, 644–663.
- Roy, C., and C. Reason, 2001: ENSO related modulation of coastal upwelling in the eastern Atlantic. *Progress in Oceanography*, Vol. 49, Pergamon, 245–255.
- , S. Weeks, M. Rouault, G. Nelson, R. Barlow, and C. D. van der Lingen, 2001: Extreme oceanographic events recorded in the Southern Benguela during the 1999–2000 summer season. *S. Afr. J. Sci.*, **97**, 465–471.
- Ruggerone, G. T., M. Zimmerman, K. W. Myers, J. L. Nielsen, and D. E. Rogers, 2003: Competition between Asian pink salmon (*Oncorhynchus gorbuscha*) and Alaskan sockeye salmon (*O. nerka*) in the North Pacific Ocean. *Fish. Oceanogr.*, **12**, 209–219.
- Russell, F. S., A. J. Southward, G. T. Boalch, and E. I. Butler, 1971: Changes in biological conditions in the English Channel off Plymouth during the last half century. *Nature*, **234**, 468–470.
- Sætersdal, G., and H. Loeng, 1987: Ecological adaptation of reproduction in Northeast Arctic Cod. *Fish. Res.*, **5**, 253–270.
- Sakshaug, E., 1997: Biomass and productivity distributions and their variability in the Barents Sea. *ICES J. Mar. Sci.*, **54**, 341–350.
- Schwartzlose, R. A., and Coauthors, 1999: Worldwide large-scale fluctuations of sardine and anchovy populations. *S. Afr. J. Mar. Sci.*, **21**, 289–347.
- Shannon, L. J., G. Nelson, R. J. M. Crawford, and A. J. Boyd, 1996: Possible impacts of environmental change on pelagic fish recruitment: Modelling anchovy transport by advective processes in the southern Benguela. *Global Change Biol.*, **2**, 407–420.
- Shannon, L. V., 1985: The Benguela ecosystem Part I. Evolution of the Benguela, physical features and processes. *Oceanogr. Mar. Biol. Annu. Rev.*, **23**, 105–182.
- , and G. Nelson, 1996: The Benguela: Large scale features and processes and system variability. *The South Atlantic Past and Present Circulation*, G. Wefer et al., Eds., Springer-Verlag, 163–210.
- Shelton, P. A., and L. Hutchings, 1982: Transport of anchovy, *Engraulis capensis* Gilchrist, eggs and early larvae by a frontal jet current. *J. Cons. Int. Mer.*, **40**, 185–198.
- Shillington, F. A., 1998: The Benguela upwelling system off southwestern Africa. *The Sea: The Global Coastal Ocean*, A. R. Robinson and K. H. Brink, Eds., Regional Studies and Syntheses, Vol. 11, Wiley, 583–604.
- Signorini, S. R., R. G. Murtugudde, C. R. McClain, J. R. Christian, J. Picaut, and A. J. Busalacchi, 1999: Biological and physical signatures in the tropical and subtropical Atlantic. *J. Geophys. Res.*, **104**, 18 367–18 382.
- Sinclair, A., 1996: Recent declines in cod stocks in the northwest Atlantic. *Northwest Atl. Fish. Org. Sci. Council Stud.*, **24**, 41–52.
- Sirabella, P., A. Giuliani, A. Colosimo, and J. Dippner, 2001: Breaking down the climate effects on cod recruitment by principal component analysis and canonical correlation. *Mar. Ecol. Prog. Ser.*, **216**, 213–222.
- Soutar, A., and J. D. Isaac, 1974: Abundance of pelagic fish during the 19th and 20th centuries as recorded in anaerobic sediments off California. *Fish. Bull. U.S. Fish Wildlife Ser.*, **72**, 257–275.
- Southward, A. J., G. T. Boalch, and L. Maddock, 1988: Fluctuations in the herring and pilchard fisheries of Devon and Cornwall linked to change in climate since the 16th century. *J. Mar. Biol. Assoc.*, **68**, 423–445.
- Stenseth, N. C., G. Ottersen, J. Hurrell, and A. Belgrano, Eds., 2004: *Ecological Effects of Climate Variations in the North Atlantic*. Oxford University Press, 252 pp.
- Sugimoto, T., S. Kimura, and K. Tadokoro, 2001: Impacts of El Niño events and climate regime shift on living resources in the western North Pacific. *Progress in Oceanography*, Vol. 49, Pergamon, 113–127.
- Taggart, C. T., and Coauthors, 1994: Overview of cod stocks, biology, and environment in the Northwest Atlantic region of Newfoundland, with emphasis on northern cod. *ICES Mar. Sci. Symp.*, **198**, 140–157.
- Taylor, A. H., J. I. Allen, and P. A. Clark, 2002: Extraction of a weak climatic signal by an ecosystem. *Nature*, **416**, 629–632.
- Tittensor, D. P., B. de Young, and C. L. Tang, 2003: Modelling the distribution, sustainability and diapause emergence timing of the copepod *Calanus finmarchicus* in the Labrador Sea. *Fish. Oceanogr.*, **12**, 299–316.
- Trenberth, K. E., 1990: Recent observed interdecadal climate changes in the northern hemisphere. *Bull. Amer. Meteor. Soc.*, **71**, 988–993.
- , 1997: The definition of El Niño. *Bull. Amer. Meteor. Soc.*, **78**, 2771–2777.
- , and J. W. Hurrell, 1994: Decadal atmosphere–ocean variations in the Pacific. *Climate Dyn.*, **9**, 303–319.
- Valdivia, J., 1978: The anchoveta and El Niño. *Rapp. P.-V. Réun. Cons. Int. Explor. Mer.*, **173**, 196–202.
- van der Lingen, C. D., and J. A. Huggett, 2003: The role of ichthyoplankton surveys in recruitment research and management of South African anchovy and sardine. *The Big Fish Bang: Proceedings of the 26th Annual Larval Fish Conference*, H. I. Browman and A. B. Skiftesvik, Eds., Bergen, Norway, Institute of Marine Research, 303–341.
- , L. Hutchings, D. Merkle, J. J. van der Westhuizen, and J. Nelson, 2001: Comparative spawning habitats of anchovy (*Engraulis capensis*) and sardine (*Sardinops sagax*) in the Southern Benguela upwelling ecosystem. *Spatial Processes and Management of Marine Populations*, G. H. Kruse et al., Eds., University of Alaska Sea Grant, 185–209.
- , J. C. Coetzee, and L. Hutchings, 2002: Temporal shifts in the spatial distribution of anchovy spawners and their eggs in the southern Benguela: Implications for recruitment. Report of a GLOBEC-SPACC/IDYLE/ENVIFISH Workshop on Spatial Approaches to the Dynamics of Coastal Pelagic Resources and Their Environment in Upwelling Areas, C. D. van der Lingen et al., Eds., GLOBEC Rep. 16, 46–48.
- van Loon, H., and J. C. Rogers, 1978: The seesaw in winter temperatures between Greenland and northern Europe. Part I: General description. *Mon. Wea. Rev.*, **106**, 296–310.
- Walters, C., 2003: Folly and fantasy in the analysis of spatial catch rate data. *Can. J. Fish. Aquat. Sci.*, **60**, 1433–1436.
- Walters, G. E., and T. K. Wilderbuer, 2000: Decreasing length at

- age in a rapidly expanding population of northern rock sole in the eastern Bering Sea and its effect on management advice. *J. Sea Res.*, **44**, 17–26.
- Wilderbuer, T. K., A. B. Hollowed, W. J. Ingraham Jr., P. D. Spencer, M. E. Connors, N. A. Bond, and G. E. Walters, 2002: Flatfish recruitment response to decadal climatic variability and ocean conditions in the eastern Bering Sea. *Progress in Oceanography*, Vol. 55, Pergamon, 235–247.
- Yanez, E., M. A. Barbieri, C. Silva, K. Nieto, and F. Espíndola, 2001: Climate variability and pelagic fisheries in northern Chile. *Progress in Oceanography*, Vol. 49, Pergamon, 581–596.
- Zebdi, A., and J. S. Collie, 1995: Effects of climate on herring (*Clupea pallasii*) population dynamics in the Northeast Pacific Ocean. *Climate Change and Northern Fish Populations*, R. J. Beamish, Ed., Canadian Special Publication of Fisheries and Aquatic Sciences, Vol. 121, National Research Council of Canada, 277–290.