Climate forcing, food web structure, and community dynamics in pelagic marine ecosystems

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Introduction

The study of food webs has historically focused on their internal properties and structures (e.g. diversity, number of trophic links, connectance) (Steele 1974; Pimm 1982; Cohen et al. 1990). A major advance of these investigations has been the recognition that structure and function, within a food web, are related to the dynamic properties of the system (Pimm 1982). Studies that have focused on community dynamics have done so with respect to internal forcing (e.g. competition, predation, interaction strength, and energy transfer; May 1973), and have lead to important advances in community ecology, particularly in the complex field of community stability (Hasting 1988). During the last two decades, there has been increasing recognition that external forcing—either anthropogenic (Parsons 1996; Jackson et al. 2001; Verity et al. 2002) or environmental (McGowan et al. 1998; Stenseth et al. 2002; Chavez et al. 2003)—can profoundly impact entire communities, causing a rearrangement of their internal structure (Pauly et al. 1998; Anderson and Piatt 1999; Steele and Schumacher 2000) and a deviation from their original succession (Odum 1985; Schindler 1985). This phenomenon has mostly been documented in marine ecosystems (e.g. Francis et al. 1998; Parsons and Lear 2001; Choi et al. 2004).

The susceptibility of large marine ecosystems to change makes them ideal to study the effect of external forcing on community dynamics. However, their expansive nature makes them unavailable to the investigational tools of food web dynamics, specifically *in situ* experimental perturbations (Paine 1980; Raffaelli 2000; but see Coale et al. 1996; Boyd et al. 2000). To date, studies on population fluctuations and climate forcing in marine ecosystems have been primarily descriptive in nature, and there have been few attempts to link the external forcing of climate with the internal forcing of food web interactions (e.g. Hunt et al. 2002; Hjermann et al. 2004). From theoretical (May 1973) as well as empirical studies in terrestrial ecology (Stenseth et al. 1997; Lima et al. 2002) we know that the relative strength of ecological interactions among different species can mediate the effect of external forcing. It follows that, different communities, or different stages of the same community, can have diverging responses to a similar external perturbation. In a marine context, such phenomenon was clearly perceived in the Gulf of Alaska, where a relatively small increase (about 2°C) in sea surface temperature (SST) during the mid-1970s co-occurred with a dramatic change of the species composition throughout the region (Anderson and Piatt 1999). However, in 1989 an apparent shift of the Gulf of Alaska to pre-1970s climatic conditions did not result in an analogous return of the community to the pre-1970s state (Mueter and Norcross 2000; Benson and Trites 2002). An even clearer example of uneven community responses following the rise and fall of an external perturbation is the lack of cod recovery

from the Coast of Newfoundland and Labrador in spite of the 1992 fishing moratorium (Parsons and Lear 2001).

In this chapter, we review how marine pelagic communities respond to climate forcing.

We emphasize the mediating role of food web structure (i.e. trophic interactions) between external climate forcing and species dynamics. This we do by summarizing studies from three different and well-monitored marine pelagic
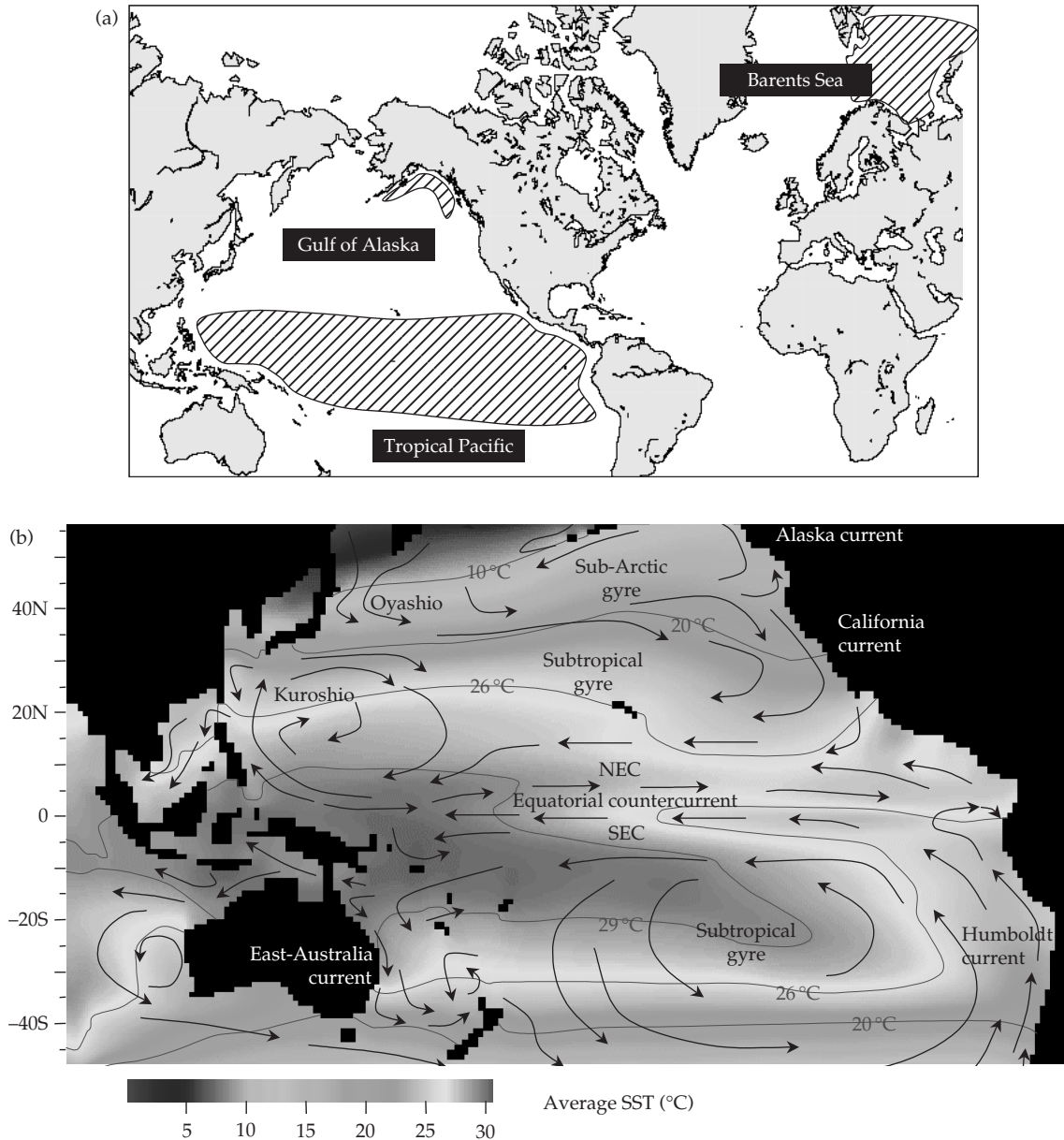
(a)

Barents Sea

Gulf of Alaska

Tropical Pacific

(b)

Alaska current

10 °C   Sub-Arctic gyre

40N

Oyashio

20 °C

California current

Subtropical gyre

26 °C

20N

Kuroshio

NEC

Equatorial countercurrent

0

SEC

–20S

29 °C

Subtropical gyre

Humboldt current

East-Australia current

26 °C

–40S

20 °C

Average SST (°C)

5   10   15   20   25   30

Figure 12.1 (a) Location of the three pelagic ecosystems reviewed in the present study. Also shown are the detailed maps of each system. (b) Tropical Pacific (TP). (NEC = North Equatorial Current, SEC = South Equatorial Current.) See plate 9. (c) Gulf of Alaska (GOA). (ACC = Alaska Coastal Current.) (d) Barents Sea (BS).
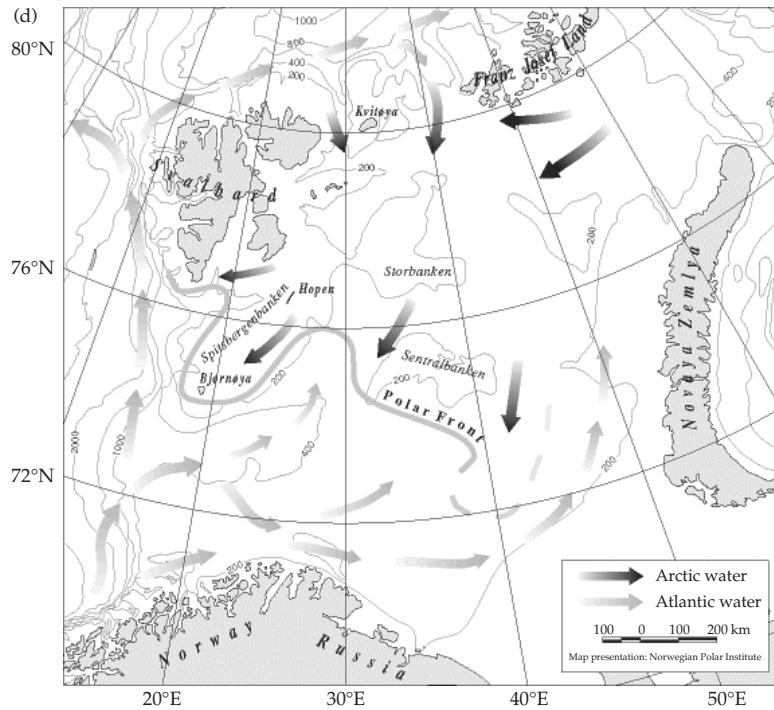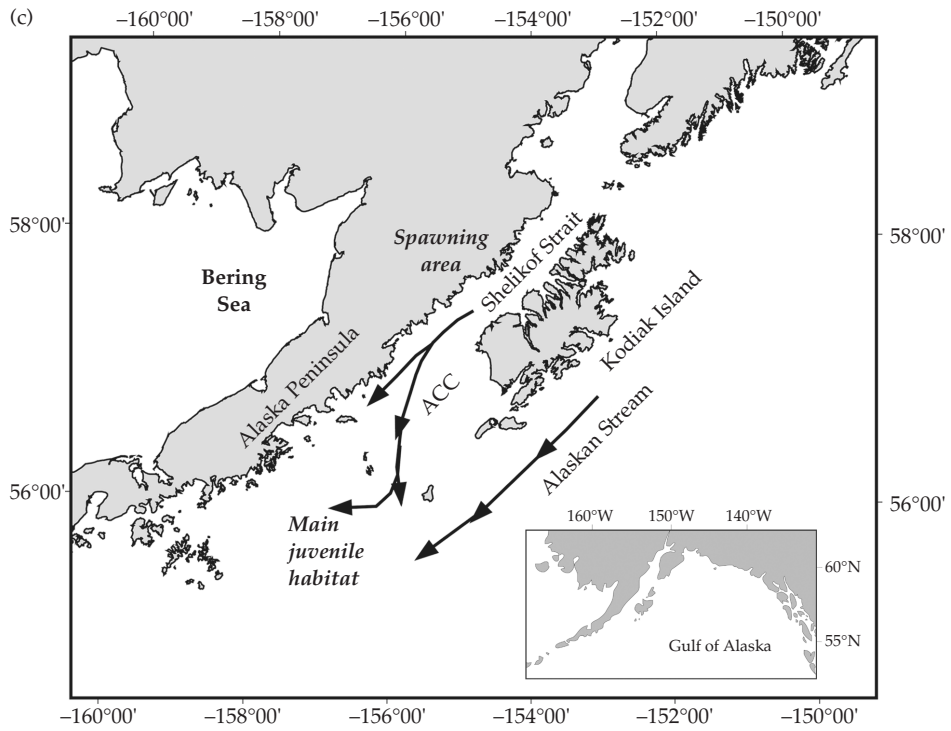
Figure 12.1 (*Continued*)

ecosystems (Figure 12.1(a)): (1) the Tropical Pacific (TP); (2) the western Gulf of Alaska (GOA), and (3) the Barents Sea (BS). These communities are strongly impacted by climate (Anderson and Piatt 1999; Hamre 2003; Lehodey et al. 1997, respectively), but have also fundamental differences in the way they respond to its forcing. In the GOA and (particularly) in the BS systems, food web interactions play a major role in determining the fate of their communities, while in the TP trophic forcing plays a minor role compared to the direct effects of climate. We suggest that such differences are to a large extent the result of dissimilar food web structures among the three pelagic ecosystems.

In this chapter we describe the physics, the climate forcing, and the food web structure of the investigated systems. We then examine their community dynamics in relation with the food web structures and climate forcing. The chapter ends with generalizations on how to link trophic structure and dynamics in large, pelagic, marine ecosystems. We emphasize climate and community processes occurring in the pelagic compartment at the temporal scales perceivable within a period less than a human generation (10–40 years). We recognize that the present review is based on information and data that were not originally meant to be used in community studies, and for this reason it is unbalanced in the level of information provided for each trophic assemblage. Typically, the information is available in greater detail for species that are commercially important. However, to our knowledge, this is the first explicit attempt to link external (climate) and internal (trophic) forcing in the study of community dynamics in large marine ecosystems (but see Hunt et al. 2002; Hjermann et al. 2004), and should be most relevant to advance the knowledge of structure and dynamics also in marine pelagic food webs.

The geography and the physics

Tropical Pacific

The physical oceanography of the TP, roughly between 20°N and 20°S, is strongly dominated by the zonal equatorial current systems (Figure 12.1(b); see Plate 9). Under the influence of the trade winds blowing from east to west, the surface water is transported along the same direction (north and south equatorial currents: NEC and SEC). During transport, surface water is warmed up and creates a warm pool with a thick layer (about 100 m) of water above 29°C on the western side of the oceanic basin. The warm pool plays a key role in the development of El Niño events (McPhaden and Picaut 1990). In the eastern and central Pacific, this dynamic creates an equatorial divergence with an upwelling of deep and relatively cold water (the "cold tongue") and a deepening thermocline from east to west. The general east–west surface water transport is counterbalanced by the north and south equatorial countercurrents (NECC and SECC), the equatorial undercurrent (EUC) and the retroflexion currents that constitute the western boundaries (Kuroshio and east Australia currents) of the northern and southern subtropical gyres. The TP presents a weak seasonality, except in the far western region (South China Sea and archipelagic waters throughout Malaysia, Indonesia, and the Philippines) that is largely under the influence of the seasonally reversing monsoon winds. Conversely, there is strong interannual variability linked to the El Niño Southern Oscillation (ENSO).

Western Gulf of Alaska

The Gulf of Alaska (herein referred to as GOA) includes a large portion of the sub-Arctic Pacific domain, delimited to the north and east by the North American continent, and to the south and west by the 50° latitude and 176° longitude, respectively (Figure 12.1(c)). In the present chapter we focus on the shelf area west of 150° longitude—the most studied and commercially harvested region of the entire GOA. The continental shelf of the GOA is narrow (10–150 km), and frequently interrupted by submerged valleys (e.g. the "Skelikof Sea Valley" between Kodiak and the Semidi Islands) and archipelagos (e.g. Shumagin Islands). The offshore surface (<100 m) circulation of the entire GOA is dominated by the sub-Arctic gyre, a counterclockwise circulation feature of the North Pacific. A pole-ward branch of the

sub-Arctic gyre, flowing along the shelf edge, forms the Alaska current/Alaska stream. This current varies in width and speed along its course—from 300 km and 10–20 cm s^{-1} east of 150° latitude to 100 km and up to 100 cm s^{-1} in the GOA region (Reed and Schumacher 1987). The coastal surface circulation pattern of the GOA is dominated by the Alaska coastal current (ACC) flowing southwestward along the Alaska Peninsula. The ACC is formed by pressure gradients, in turn caused by freshwater discharge from the Cook Inlet area. The average speed of the ACC ranges around 10–20 cm s^{-1}, but its flow varies seasonally, with peaks in the fall during the period of highest freshwater discharge (Reed and Schumaker 1987). The ACC and its associated deep-water undercurrents, play an important biological role in the transport of eggs and larvae from spawning to nursery areas of several dominant macronekton species of the GOA (Kendall et al. 1996; Bailey and Picquelle 2002). Royer (1983) (cited in Reed and Shumacher 1987) suggested that the Norwegian coastal current is an analog of the ACC, having similar speed, seasonal variability, and biological role in the transport of cod larvae from the spawning grounds to the juvenile nursery habitats.

Barents Sea

The BS is an open arcto-boreal shelf-sea covering an area of about 1.4 million km^2 (Figure 12.1(d)). It is a shallow sea with an average depth of about 230 m (Zenkevitch 1963). Three main current systems flow into the Barents determining the main water masses: the Norwegian coastal current, the Atlantic current, and the Arctic current system (Loeng 1989). Although located from around 70°N to nearly 80°N, sea temperatures are substantially higher than in other regions at similar latitudes due to inflow of relatively warm Atlantic water masses from the southwest. The activity and properties of the inflowing Atlantic water also strongly influence the year-to-year variability in temperature south of the oceanic Polar front (Loeng 1991; Ingvaldsen et al. 2003), as does regional heat exchange with the atmosphere (Ådlandsvik and Loeng 1991; Loeng et al. 1992). The ice coverage shows pronounced interannual fluctuations. During 1973–75 the annual maximum coverage was around 680,000 km^2, while in 1969 and 1970 it was as much as 1 million km^2. This implies a change in ice coverage area of more than 30% in only four years (Sakshaug et al. 1992). In any case, due to the inflow of warm water masses from the south, the southwestern part of the BS does not freeze even during the most severe winters.

Climate forcing

Pacific inter-Decadal Oscillation

The GOA and the TP systems are influenced by climate phenomena that dominate throughout the Pacific Ocean. These are the Pacific inter-Decadal Oscillation (hereon referred to as Pacific Decadal Oscillation, PDO; Mantua and Hare 2002), and the ENSO (Stenseth et al. 2003). The PDO is defined as the leading principal component of the monthly SST over the North Pacific region (Mantua et al. 1997). During a "warm" (positive) phase of the PDO, SSTs are higher over the Canadian and Alaskan coasts and northward winds are stronger, while during a cool phase (negative) the pattern is reversed (Figure 12.2; see also, Plate 10). The typical period of the PDO is over 20–30 years, hence the name. It is believed that in the last century there have been three phase changes of the PDO, one in 1925 (cold to warm), one in 1946 (warm to cold), and another in 1976 (cold to warm; Mantua et al. 1997), with a possible recent change in 1999–2000 (warm to cold) (McFarlane et al. 2000; Mantua and Hare 2002). The pattern of variability of the PDO closely reflects that of the North Pacific (or Aleutian Low) index (Trenberth and Hurrell 1994). The relationship is such that cooler than average SSTs occur during periods of lower than average sea level pressure (SLP) over the central North Pacific, and vice versa (Stenseth et al. 2003). It bears note that a recent study by Bond et al. (2004) indicates that the climate of the North Pacific is not fully explained by the PDO index and thus it has no clear periodicity.

El Niño Southern Oscillation

Fluctuations of the TP SST are related to the occurrence of El Niño, during which the equatorial

surface waters warm considerably from the International Date Line to the west coast of South America (Figure 12.2). Linked with El Niño events is an inverse variations in SLP at Darwin (Australia) and Tahiti (South Pacific), known as the Southern Oscillation (SO). A simple index of the SO is, therefore, often defined by the normalized Tahiti minus Darwin SLP anomalies, and it has a

period, of about 4–7 years. Although changes in TP SSTs may occur without a high amplitude change of the SO, El Niño and the SO are linked so closely that the term ENSO is used to describe the atmosphere–ocean interactions over the TP. Warm ENSO events are those in which both a negative SO extreme and an El Niño occur together, while the reverse conditions are termed La Niñas
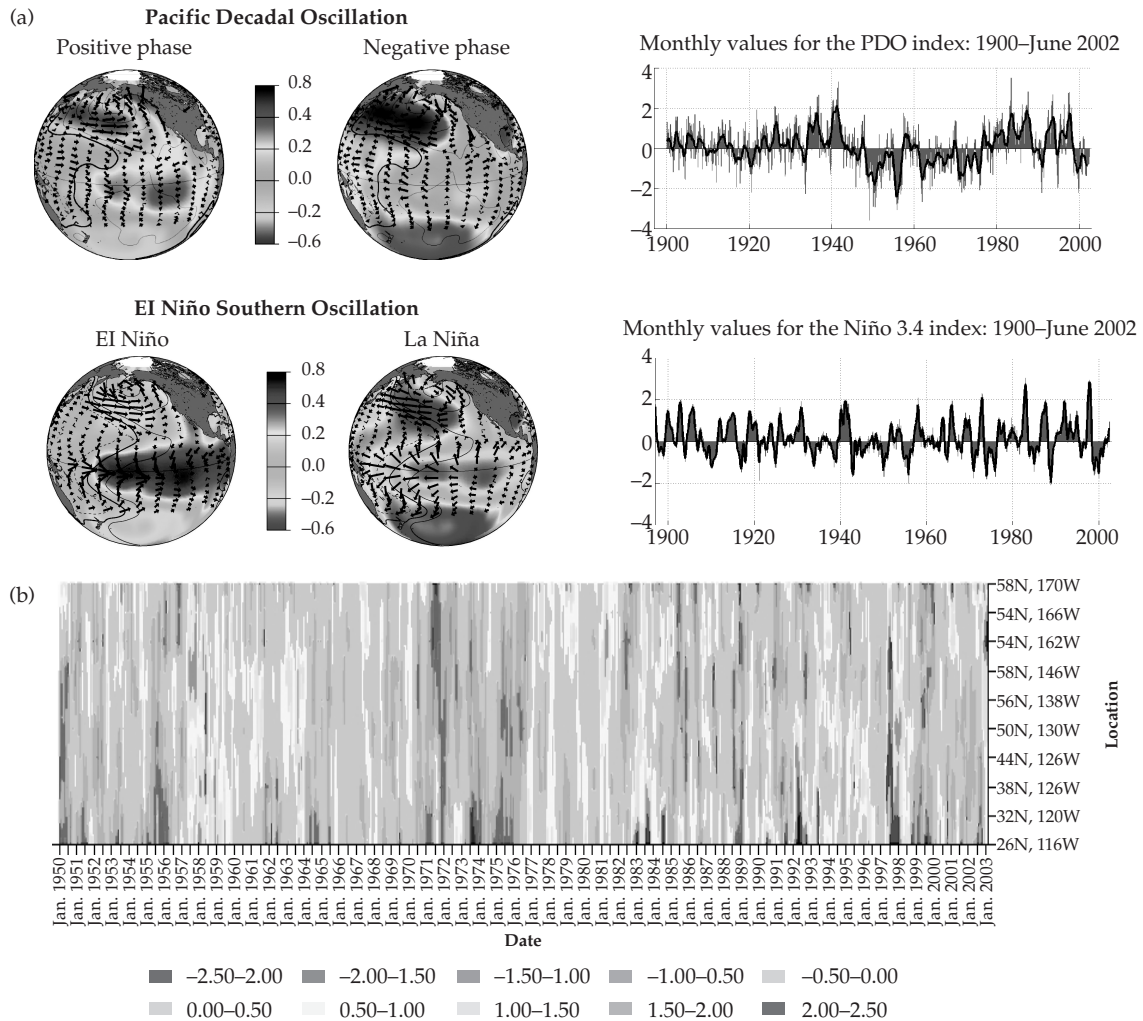

Figure 12.2(a) SST anomalies during positive and negative phases of the PDO (upper panel) and ENSO (lower panel), and time series of the climate index. During a positive PDO phase, SST anomalies are negative in the North Central Pacific (blue area) and positive in the Alaska coastal waters (red area) and the prevailing surface currents (shown by the black arrows) are stronger in the pole-ward direction. During a positive phase of the ENSO, SST anomalies are positive in the eastern Tropical Pacific and the eastward component of the surface currents is noticeably reduced. (b) Time series of temperature anomalies in different locations of the North Pacific. The graph shows area of intense warming (yellow and red areas) associated with the ENSO propagating to the North Pacific, a phenomenon termed El Niño North condition (updated from Hollowed et al. 2001). See Plate 10.

(Philander 1990; Stenseth et al. 2003). Particularly strong El Niño events during the latter half of the twentieth century occurred in 1957–58, 1972–73, 1982–83, and 1997–98.

Typically, the SST pattern of the TP is under the influence of interannual SO-like periodicity (i.e. 4–7 years), while the extra-TP pattern is under the interdecadal influence of the PDO-like periodicity (Zhang et al. 1997). However, El Niño/ La Niña events can propagate northward and affect the North Pacific as well, including the GOA system, a phenomenon known as Niño North (Figure 12.2; Hollowed et al. 2001). During the latter half of twentieth century, there have been five warming events in the GOA associated with the El Niño North: in 1957–58, 1963, 1982–83, 1993, and 1998. The duration of each event was about five months, with about a year lag between a tropical El Niño and the Niño North condition (Figure 12.2). The likelihood of an El Niño event to propagate to the North Pacific is related to the position of the Aleutian Low. Specifically, during a positive phase of the PDO, the increased flow of the Alaska current facilitates the movement of water masses from the transition to the sub-Arctic domain of the North Pacific, in turn increasing the likelihood of an El Niño North event (Hollowed et al. 2001). It has also been reported that the likelihood of El Niño (La Niña) events in the TP is higher during a positive (negative) phase of the PDO (Lehodey et al. 2003).

North Atlantic Oscillation

The BS is influenced by North Atlantic basin scale climate variability, in particular that represented by the North Atlantic Oscillation (NAO) (Figure 12.3; see also Plate 11). The NAO refers to a north–south alternation in atmospheric mass between the subtropical and subpolar North Atlantic. It involves out-of-phase behavior between the climatological low-pressure center near Iceland and the high-pressure center near the Azores, and a common index is defined as the difference in winter SLP between these two locations (Hurrell et al. 2003). A high (or positive) NAO index is characterized by an intense Icelandic Low and a strong Azores High. Variability
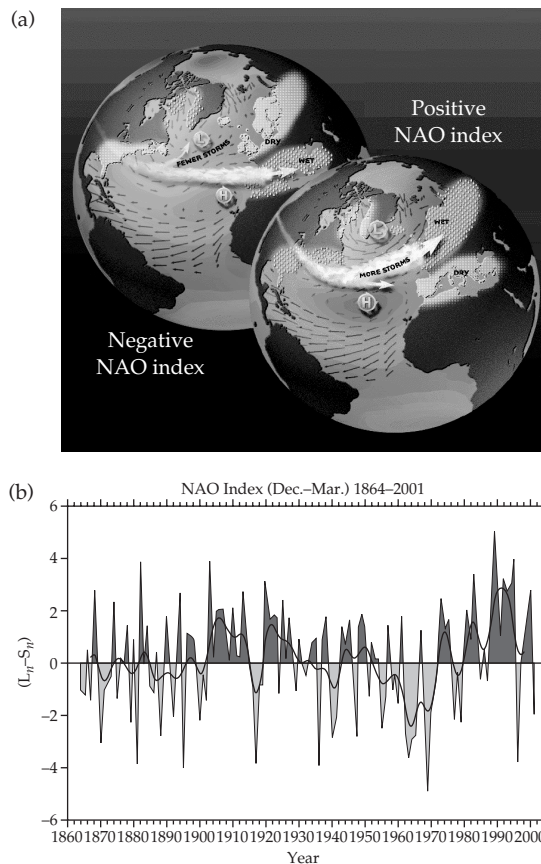
Figure 12.3 The NAO. (a) During positive (high) phases of the NAO index the prevailing westerly winds are strengthened and moves northwards causing increased precipitation and temperatures over northern Europe and southeastern United State and dry anomalies in the Mediterranean region (red and blue indicate warm and cold anomalies, respectively, and yellow indicates dry conditions). Roughly opposite conditions occur during the negative (low) index phase (graphs courtesy of Dr Martin Visbeck, www.ldeo.columbia.edu/~visbeck). (b) Temporal evolution of the NAO over the last 140 winters (index at www.cgd.ucar.edu/~jhurrell/nao.html). High and low index winters are shown in red and blue, respectively (Hoerling et al. 2001). See Plate 11.

in the direction and magnitude of the westerlies is responsible for interannual and decadal fluctuations in wintertime temperatures and the balance of precipitation and evaporation over land on both sides of the Atlantic Ocean (Rogers 1984; Hurrell 1995). The NAO has a broadband spectrum with no significant dominant periodicities (unlike ENSO). More than 75% of the variance of

the NAO occurs at shorter than decadal time-scales (D. B. Stephenson, web page at www.met.rdg.ac.uk/cag/NAO/index.html). A weak peak in the power spectrum can, however, be detected at around 8–10 years (Pozo-Vazquez et al. 2000; Hurrell et al. 2003). Over recent decades the NAO winter index has exhibited an upward trend, corresponding to a greater pressure gradient between the subpolar and subtropical North Atlantic. This trend has been associated with over half the winter surface warming in Eurasia over the past 30 years (Gillett et al. 2003).

A positive NAO index will result in at least three (connected) oceanic responses in the BS, reinforcing each other and causing both higher volume flux and higher temperature of the inflowing water (Ingvaldsen et al. 2003). The first response is connected to the direct effect of the increasingly anomalous southerly winds during high NAO. Second, the increase in winter storms penetrating the BS during positive NAO will give higher Atlantic inflow to the BS. The third aspect is connected to the branching of the Norwegian Atlantic Current (NAC) before entering the BS. Blindheim et al. (2000) found that a high NAO index corresponds to a narrowing of the NAC towards the Norwegian coast. This narrowing will result in a reduced heat loss (Furevik 2001), and possibly in a larger portion of the NAC going into the BS, although this has not been documented (Ingvaldsen et al. 2003). It should be noted that the correlation between the NAO and inflow to and temperature in the BS varies strongly with time, being most pronounced in the early half of the twentieth century and over the most recent decades (Dickson et al. 2000; Ottersen and Stenseth 2001).

Food web structure

To facilitate the comparison of the three food webs, we have grouped the pelagic species of each system in five trophic aggregations: *primary producers, zooplankton, micronekton, macronekton, and apex predators*. This grouping is primarily associated with trophic role, rather than trophic level. M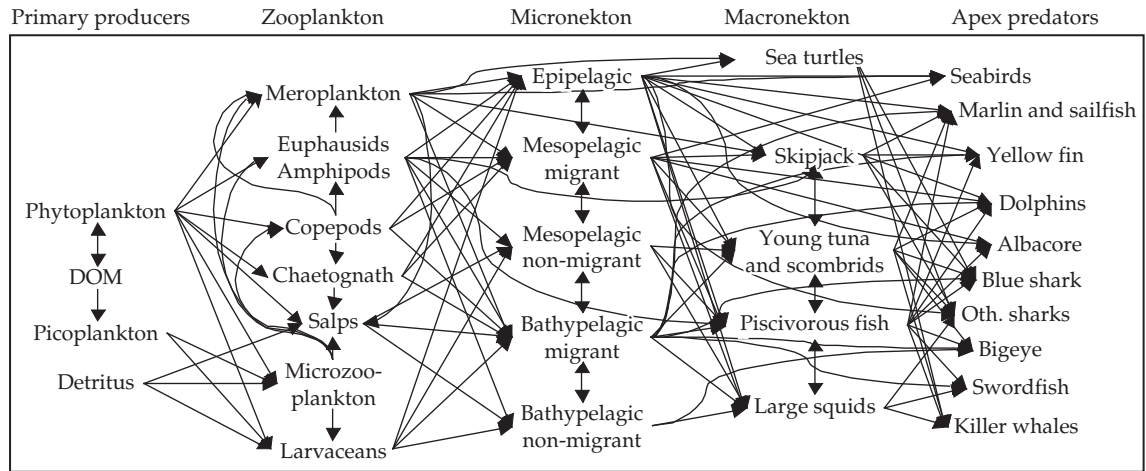acronekton includes all large (>20 cm) pelagic species that are important consumers of other pelagic resources (e.g. micronekton), but are preyed upon, for the most part, by apex predators. Micronekton consist of small animals (2–20 cm) that can effectively swim. Typically, macronekton, and to a smaller extent, micronekton and apex predators, include commercial fish species (tunas, cod, pollock, herring, and anchovies) and squids. In the following, we summarize available information on food web structure, covering for the most part trophic interactions, and, where relevant (e.g. TP), also differences in spatial distribution among the organisms of the various trophic assemblages.
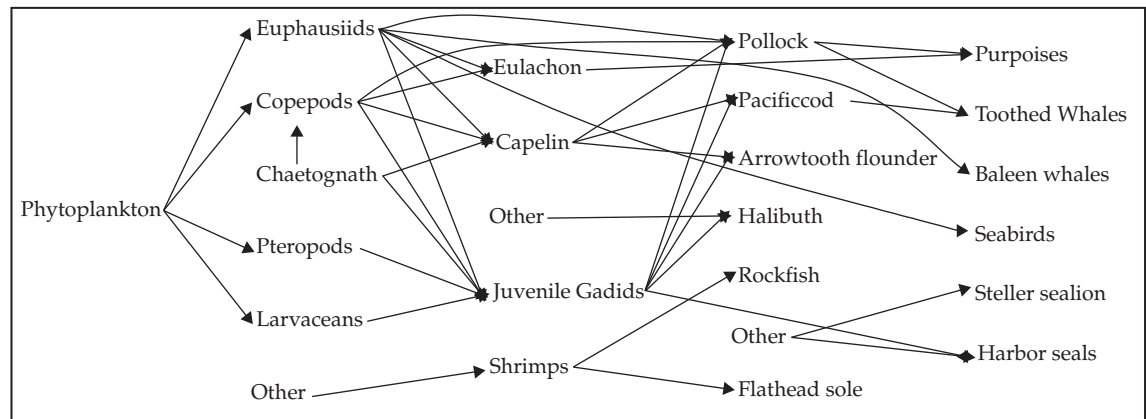
Tropical Pacific

The TP system has the most diverse species assemblage and most complex food web structure among the three pelagic ecosystems included in this chapter (Figure 12.4). Part of the complexity of the TP food web is due to the existence of various spatial compartments within the large pelagic ecosystem. The existence of these compartments may ultimately control the relationships with (and accessibility to) top predators, and affect the community dynamics as well (Krause et al. 2003). In the vertical gradient, the community can be divided into epipelagic (0–200 m), mesopelagic (200–500 m), and bathypelagic groups (<500 m), the last two groups being subdivided into migrant and non-migrant species. All these groups include organisms of the main taxa: fish, crustacean, and cephalopods. Of course, this is a simplified view of the system as it is difficult to establish clear vertical boundaries, which are influenced by local environmental conditions, as well as by the life stage of species.

In addition to vertical zonation, there is a pronounced east–west gradient of species composition and food web structure in the TP. Typically, there is a general decrease in biomass from the intense upwelling region in the eastern Pacific toward the western warm pool (Vinogradov 1981). While primary productivity in both the western warm pool and the subtropical gyres is generally low, the equatorial upwelling zone is favorable to relatively high primary production and creates a large zonal

Tropical Pacific

Primary producers   Zooplankton   Micronekton   Macronekton   Apex predators

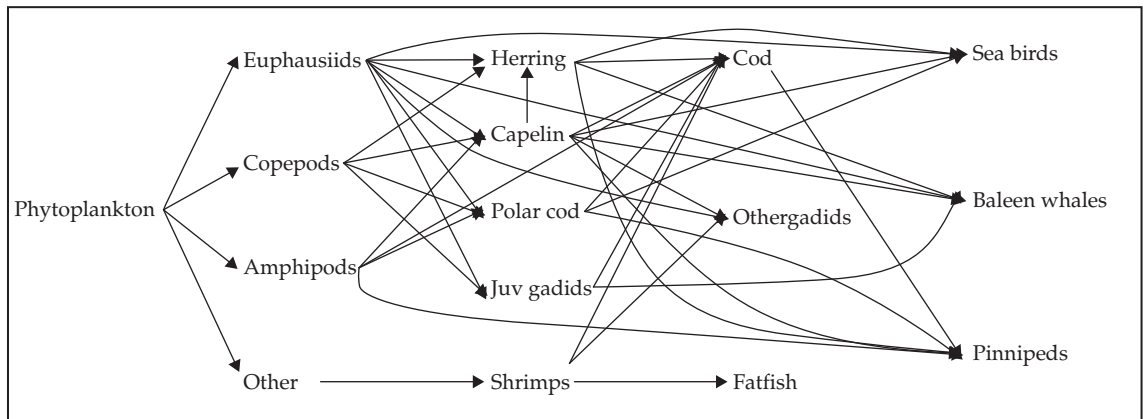**Gulf of Alaska**

Barents Sea

Figure 12.4 Simplified representation of the food web for each studied system. Arrows point from the prey to the predator DOM: Dissolved Organic Matter

band, in the cold tongue area, of rich mesotrophic waters. However, primary productivity rates in this area could be even higher as all nutrients are not used by the phytoplankton. This "high-nutrient, low-chlorophyll" (HNLC) situation is due for a large part to iron limitation (Coale et al. 1996; Behrenfeld and Kolber 1999). Another important difference between the east and west TP appear in the composition of plankton (both phyto and zooplankton). In regions where upwelling is intense (especially the eastern Pacific during La Niña periods), diatoms dominate new and export production, while in equatorial and oligotrophic oceanic regions (warm pool, subtropical gyres) a few pico- and nanoplankton groups (autotrophic bacteria of the microbial loop) dominate the phytoplankton community (Bidigare and Ondrusek 1996; Landry and Kirchman 2002).

Based on size, the zooplankton assemblage can be subdivided into micro- (20–200 μm), meso- (0.2–2.0 mm), and macrozooplankton (2–20 mm). Flagellates and ciliates dominate the microzooplankton group; however, nauplii of copepods are abundant in the eastern equatorial region, in relation with more intense upwelling. Pico- and nanoplankton are consumed by microzooplankton, which remove most of the daily accumulation of biomass (Landry et al. 1995; Figure 12.4). Copepods dominate the mesozooplankton group, as well as the entire zooplankton assemblage of the TP (Le Borgne and Rodier 1997; Roman et al. 2002). Gueredrat (1971) found that 13 species of copepods represented 80% of all copepod species in the equatorial Pacific. However, meso- and macrozooplankton include a very large diversity of other organisms, such as amphipods, euphausiids, chaetognaths, and larval stages (meroplankton) of many of species of molluscs, cnidaria, crustaceans, and fish. Another group that has a key role in the functioning of the pelagic food web but has been poorly studied is what we can name "gelatinous filter feeders." In particular, this group includes appendicularians (a.k.a., larvaceans) and salps. Salps and larvaceans filter feed mainly on phytoplankton and detritus. Though by definition, the zooplankton described above is drifting in the currents, many species undertake diel vertical migrations, mainly stimulated by the light intensity.

Fish, crustaceans (large euphausiids), and cephalopods dominate the micronekton group, with typical sizes in the range of 2–20 cm. These organisms, together with the gelatinous filter feeders, are the main forage species of the top and apex predators (Figure 12.4). Many species of zooplankton and micronekton perform diel vertical migrations between layers of the water column that are over 1,000 m apart. One important benefit of this evolutionary adaptation is likely a decrease of the predation pressure in the upper layer during daytime (e.g. Sekino and Yamamura 1999). The main epipelagic planktivorous fish families are Engraulidae (anchovies), Clupeidae (herrings, sardines), Exocœtidae (flyingfish), and small Carangidae (scads), but an important component also is represented by all juvenile stages of large-size species (Bramidae, Coryphaenidae, Thunnidae). The oceanic anchovy (*Enchrasicholinus punctifer*) is a key species in the epipelagic food web of the warm pool as it grows very quickly (mature after 3–5 months) and can become very abundant after episodic blooms of phytoplankton. Meso- and bathypelagic species include euphausiids, deep shrimps of the Sergestidae, Peneidae, Caridae, and numerous fish families, Myctophidae, Melamphaidae, Chauliodidae, Percichthyidae, and Stomiatidae. The micronekton consume a large spectrum of prey species among which the dominant groups are copepods, euphausiids, amphipods, and fish. More detailed analyses (Legand et al. 1972; Grandperrin 1975) showed that prey composition can differ substantially between micronekton species, especially in relation to predator–prey size relationships: smallest micronekton prey mainly upon copepods, medium size micronekton consumes more euphausiids, and large micronekton are mostly piscivorous.

Tuna dominate the macronekton in the TP food web, although this group also includes large-size cephalopods, and sea turtles. Skipjack tuna (*Katsuwonus pelamis*) is the most abundant and productive species of the TP and constitute the fourth largest fisheries in the world (FAO 2002; ~1.9 million tons per year). Juveniles of other tropical tuna, particularly yellowfin tuna (*Thunnus albacares*) and bigeye tuna (*Thunnus obesus*) are frequently found together with skipjack in the

surface layer, especially around drifting logs that aggregate many epipelagic species. With these well-known species, there are many other scombrids (*Auxis* sp., *Euthynnus* spp., *Sarda* spp., *Scomberomorus* spp., *Scomber* spp.), and a large variety of piscivorous fish (Gempylidae, Carangidae, Coryphaenidae, Trichiuridae, Alepisauridae), and juveniles of apex predators (sharks, marlins, swordfish, and sailfish). The largest biomass of the most productive species, skipjack and yellowfin tuna, is in the warm waters of the Western and Central Pacific Ocean (WCPO), but warm currents of the Kuroshio and east Australia extend their distribution to 40°N and 40°S (roughly delineated by the 20°C surface isotherm). Most macronekton species are typically predators of the epipelagic micronekton but many of them take advantage of the vertical migration of meso- and bathypelagic species that are more particularly vulnerable in the upper layer during sunset and sunrise periods.

Apex predators of the TP food web include adult large tuna (yellowfin *T. albacares*, bigeye *Thunnus obesus* albacore *Thunnus alalunga*), broadbill swordfish (*Xiphias gladus*), Indo-Pacific blue marlin (*Makaira mazara*), black marlin (*Makaira indica*), striped marlin (*Tetrapturus audax*), shortbill spearfish (*Tetrapturus angustirostris*), Indo-Pacific sailfish (*Istiophorus platypterus*), pelagic sharks, seabirds, and marine mammals. The diets of apex predator species reflect both the faunal assemblage of the component of the ecosystem that they explore (i.e. epi, meso, bathypelagic) and their aptitude to capture prey at different periods of the day (i.e. daytime, nightime, twilight hours). All large tuna species have highly opportunistic feeding behavior resulting in a very large spectrum of prey from a few millimeters (e.g. euphausiids and amphipods) to several centimeters (shrimps, squids and fish, including their own juveniles) in size. However, it seems that differences in vertical behavior can be also identified through detailed analyses of the prey compositions: bigeye tuna accessing deeper micro- and macronekton species. Swordfish can also inhabit deep layers for longer periods than most apex predators. This difference in vertical distributions is reflected in the diets, swordfish consuming a larger proportion of squids

(e.g. Ommastrephidae, Onychoteuthidae) than the other billfishes. Blue sharks consume cephalopods as a primary component of their diet and various locally abundant pelagic species (Strasburg 1958, Tricas 1979). Whitetip and silky sharks are omnivorous. They feed primarily on a variety of fish including small scombrids, cephalopods, and to a lesser extent, crustaceans. The whitetip sharks consume also a large amount of turtles (Compagno 1984) and occasionally stingrays and sea birds. Thresher, hammerhead, and mako sharks feed on various piscivorous fish including scombrids and alepisaurids, and cephalopods.

Marine mammals encountered in the TP system permanent baleen whales, toothed whales, and dolphins. However, most of baleen whales are not permanent in the tropical pelagic food web as they only migrate to tropical regions for breeding, while they feed in polar waters during the summer. The diets of toothed whales (killer whale, sperm whale, and short-finned pilot whale) are mainly based on squids (the sperm whale often taking prey at considerable depths), and fish. Killer whales are also known to prey on large fish such as tuna and dolphinfish and sometime small cetaceans or turtles. All the dolphins consume mesopelagic fish and squid. Spotted and common dolphins are known also to prey upon epipelagic fish like flying fish, mackerel, and schooling fish (e.g. sardines).

Tropical seabirds feed near or above (flyingfish, flying squids) the water surface, on a large variety of macroplankton and micronekton (mainly fish and squids), including vertically migrating species likely caught during sunset and sunrise periods. They have developed a remarkably efficient foraging strategy associated with the presence of subsurface predators (mostly tuna) that drive prey to the surface to prevent them from escaping to deep waters. Therefore, as stated by Ballance and Pitman (1999), ''subsurface predators would support the majority of tropical seabirds and would indirectly determine distribution and abundance patterns, and provide the basis for a complex community with intricate interactions and a predictable structure. This degree of dependence has not been found in non-tropical seabirds.'' An example of such potential interaction is that a decrease in tuna abundance would not have

a positive effect on seabirds despite an expected increase of forage biomass, but instead would have a negative effect as this forage becomes less accessible.

Western Gulf of Alaska

The trophic web of the GOA includes several generalist (e.g. Pacific cod) and opportunistic (e.g. sablefish) feeders (Figure 12.4). In addition, different species exhibit a high diet overlap, such as juvenile pollock, and capelin, or the four dominant macroneckton species (arrowtooth flouder, Pacific halibut, cod, and pollock; Yang and Nelson 2000). As with other systems included in our review, diet patterns can change during the species ontogeny. In general, zooplanktivory decreases in importance with size, while piscivory increases. Also, within zooplanktivorous species/stages, euphausiids replace copepods as the dominant prey of larger fish. In the GOA, as well as in the BS systems, the structure of the food web is also influenced by climate forcing, as shown by noticeable diet changes of many macronekton and apex predators over opposite climate and biological phases.

In contrast to tropical regions, primary production in Arctic and sub-Arctic marine ecosystems varies seasonally with most annual production confined to a relatively short spring bloom. This seasonal pattern is mainly the result of water stratification and increased solar irradiance in the upper water column during the spring. In the GOA system, primary productivity varies considerably also with locations. Parsons (1987) recognized four distinguished ecological regions: (1) the estuary and intertidal domain, 150 g C m^{-2} per year; (2) the fjord domain, 200 g C m^{-2} per year, (3) the shelf domain, 300 g C m^{-2} per year, (4) the open ocean domain, 50 g C m^{-2} per year. These values, particularly for the shelf area, are considerably higher than those observed in the BS and similar to those observed in the east TP. A number of forcing mechanisms can explain the high productivity in the GOA system, including a seasonal weak upwelling (from May to September, Stabeno et al. 2004), strong tidal currents with resulting high tidal mixing, high nutrient discharge from fresh water run off, and the presence of a strong pycnocline generated by salinity gradients (Sambrotto and Lorenzen 1987).

Euphausiids, copepods, cnidarians, and chaetognaths constitute the bulk of the zooplankton assemblage of the GOA food web. Given the paucity of feeding habits data at very low trophic levels, we assume that the zooplankton species feed mainly on phytoplankton (Figure 12.4). This is a common generalization in marine ecology (e.g. Mann 1993), which, nonetheless, underscores the complex trophic interactions within the phytoplankton and zooplankton assemblage (e.g. microbial loop). However, microbial loop organisms are particularly important in oligotrophic environments, such as the west TP system, and supposedly play a minor role in more productive marine ecosystems, such as the GOA, the BS systems, and the cold tongue area of the TP system.

The most abundant and common micronekton species in the GOA food web are capelin (*Mallotus villosus* Müller), eulachon (*Thalicthys pacificus*), sandlance (*Ammodytes hexapterus*), juvenile gadids (including Pacific cod and walleye pollock), Pacific sandfish (*Trichodon trichodon*), and pandalid shrimps (*Pandalus* spp.). Pacific herring (*Clupea harengus pallasi*) are also important, but their presence is mainly limited to coastal waters and to the northern and eastern part of the GOA. The range of energy density of these micronekton species is very broad (Anthony et al. 2000), as it is also the nutritional transfer to their predators. Eulachon have the highest energy density (7.5 kJ g^{-1} of wet weight), followed by sand lance and herring (6 kJ g^{-1} of wet weight), capelin (5.3 kJ g^{-1} of wet weight), Pacific sandfish (5 kJ g^{-1} of wet weight), and by juvenile cod and pollock (4 kJ g^{-1} of wet weight). Juvenile pollock feed predominantly on copepods (5–20%) and euphausiids (69–81%), the latter becoming more dominant in fish larger than 50–70 mm in standard length (Merati and Brodeur 1996; Brodeur 1998). Other common, but less dominant prey include fish larvae, larvaceans, pteropods, crab larvae, and hyperid amphipods. Capelin diet is similar to that of juvenile pollock, feeding mostly on copepods (5–8%) and euphausiids (72–90%) (Sturdevant 1999). Food habits of other micronekton species are poorly known in this area; however, it is reasonable to assume that

most of their diet is also based on zooplankton species.

The GOA shelf supports a rich assemblage of macronekton, which is the target of a large industrial fishery. The majority are demersal species (bottom oriented), such as arrowtooth flounder (*Atherestes stomias*), halibut (*Hippoglossus stenolepis*), walleye pollock (*Theragra chalcogramma*), Pacific cod (*Gadus macrocephalus*), and a variety of rockfishes (*Sebastes* spp.). Walleye pollock currently constitute the second largest fisheries in the world (FAO 2002, second only to the Peruvian anchoveta); however, the bulk of the landings comes from the Bering Sea. In the GOA, arrowtooth flounder (*A. stomias*) presently dominate the macronekton assemblage, with a spawning biomass estimated at over 1 million metric tones.

The macronekton species of the GOA food web can be grouped in piscivorous (arrowtooth flounder, halibut), zooplanktivorous (pollock, atka mackerel, some rockfish), shrimp-feeders (some rockfish, flathead sole), and generalist (sablefish and cod) (Yang and Nelson 2000). Within these subcategories there have been noticeable diet changes over time. For example, in recent years (1996) adult walleye pollock diet was based primarily on euphausiids (41–58%). Other important prey include copepods (18%), juvenile pollock (10%), and shrimps (2%). However, in 1990 shrimps where more dominant in pollock diet (30%) while cannibalism was almost absent (1%) (Yang and Nelson 2000). Adult Pacific cod has also undergone similar diet changes. Recently they feed on benthic shrimps (20–24%), pollock (23%), crabs (tanner crab *Chionoecetes bairdi*, pagurids, 20–24%), and eelpouts (Zoarcidae). In contrast, during the early 1980s they fed primarily on capelin, pandalid shrimps, and juvenile pollock (Yang 2004). Arrowtooth flounder feed predominantly on fish (52–80%), among which pollock is the most common (16–53%), followed by capelin (4–23%) and herring (1–6%). Shrimps are also well represented in the diet of arrowtooth flounders (8–22%), however their importance, together with that of capelin, has also decreased in recent years, while that of pollock has increased (Yang and Nelson 2000). Pacific halibut feed mainly on fish, particularly pollock (31–38%). Other common prey

include crabs (26–44%, tanner crab and pagurids) and cephalopods (octopus 3–5%). Flathead sole feed almost exclusively on shrimps (39%) and brittle stars (25%). Atka mackerel is zooplanktivorous (64% copepods, 4% euphausiids), but also feed on large jelly fish (Scyphozoa 19%). Sablefish can equally feed on a variety of prey, including pollock (11–27%), shrimps (5–11%), jellyfish (9–14%), and fishery offal (5–27%). The rockfish of the GOA food web can be grouped among those that feed mainly on shrimps (rougheye, short-spine), euphausiids (Pacific ocean perch, northern, dusky), and squids (shortraker).

Apex predators of the GOA include seabirds, pinnipeds, and cetaceans. Among seabirds the most common are murres (a.k.a. common guillemot) (*Uria aalge*), black-legged kittiwakes *Rissa tridactyla*, a variety of cormorants (double-crested, red-faced, and pelagic), horn and tufted puffins, storm-petrels, murrelets, shearwaters, as well as three species of albatross (laysan, black-footed, and short-tailed). Pinnipedia include Steller sea lions (SSLs, *Eumetopias jubatus*) and harbor seals (*Phoca vitulina*). Cetacea include killer whales (*Orcinus orca*), Dall's porpoise (*Phocoenoides dalli*), harbor porpoise (*Phocoena phocoena*), humpback whale (*Megaptera novaeangliae*), minke whale (*Balenoptera acutorostrata*), and sperm whale (*Physester macrocephalus*) (Angliss and Lodge 2002). Humpback, minke, and sperm whales are transient species, and are present in Alaska waters only during the feeding migration in summer. Apex predators have also undergone drastic diet changes during the last 30 years. For example, a new study (Sinclair and Zeppelin 2003) indicates that in recent times SSL fed on walleye pollock and Atka mackerel, followed by Pacific salmon and Pacific cod. Other common prey items included arrowtooth flounder, Pacific herring, and sand lance. In contrast, prior to the 1970s, walleye pollock and arrowtooth flounder were absent in SSL diet, while capelin was a dominant prey. The food habits of cetaceans are poorly known, but they can reasonably be grouped in piscivorous (porpoises, killer whales, and sperm whales, feeding mainly on micronekton species) and zooplanktivorous (minke and humpback whales). Seabird diets are comprised of squid, euphausiids, capelin, sand

lance, and pollock. Piatt and Anderson (1996) demonstrated a change in seabird diets since the last major reversal of the PDO, from one that primarily comprised capelin in the late 1970s to another that contained little to no capelin in the late 1980s.

Barents Sea

The high latitude BS ecosystem is characterized by a relatively simple food web with few dominant species: for example, diatom → krill → capelin → cod, or diatom → copepod nauplii → herring larvae → puffin (Figure 12.4). However, a more detailed inspection of the diet matrix reveals some level of complexity, mostly related with shift in diet preferences among individuals of the same species but different age. The primary production in the Barents Sea is, as an areal average for several years, about 110 gCm^{-2} per year. Phytoplankton blooms that deplete the winter nutrients give rise locally to a ''new'' productivity of on average 40–50 gCm^{-2} per year, 90 gCm^{-2} per year in the southern Atlantic part, and <40 gCm^{-2} per year north of the oceanic polar front. In the northern part of the BS system, the primary production in the marginal ice zone (polar front) is important for the local food web, although the southern part is more productive (Sakshaug 1997).

The zooplankton community is dominated by arcto-boreal species. The biomass changes inter-annually from about 50–600 $mg\,m^{-3}$, with a long-term mean of about 200 $mg\,m^{-3}$ (Nesterova 1990). Copepods of the genus *Calanus*, particularly *Calanus finmarchicus*, play a uniquely important role (Dalpadado et al. 2002). The biomass is the highest for any zooplankton species, and the mean abundance has been measured to about 50,000, 15,000, and 3,000 thousand individuals per m^2 in Atlantic, Polar Front, and Arctic waters, respectively (Melle and Skjoldal 1998). In the Arctic region of the BS, *Calanus glacialis* replaces *C. finmarchicus* for abundance and dominance (Melle and Skjoldal 1998; Dalpadado et al. 2002). The *Calanus* species are predominantly herbivorous, feeding especially on diatoms (Mauchline 1998). Krill (euphausiids) is another important group of crustaceans in the southern parts of the BS.

Thysanoessa inermis and *Thysanoessa longicaudata* are the dominant species in the western and central BS, while *Thysanoessa raschii* is more common in the shallow eastern waters. Three hyperiid amphipod species are also common; *Themisto abyssorum* and *Themisto libellula* in the western and central BS, and *Themisto compressa* in the Atlantic waters of the southwestern BS. Close to the Polar Front very high abundance of the largest of the *Themisto* species, *T. libellula*, have been recorded (Dalpadado et al. 2002).

The dominant micronekton species of the BS food web are capelin, herring (*C. harengus*), and polar cod (*Boreogadus saida*). The BS stock of capelin is the largest in the world, with a biomass that in some years reaches 6–8 million metric tones. It is also the most abundant pelagic fish of the BS. Capelin plays a key role as an intermediary of energy conversion from zooplankton production to higher trophic levels, annually producing more biomass than the weight of the standing stock. It is the only fish stock capable of utilizing the zooplankton production in the central and northern areas including the marginal ice zone. *C. finmarchicus* is the main prey of juvenile capelin, but the importance of copepods decreases with increasing capelin length. Two species of krill, *T. inermis* and *T. raschii*, and the amphipods *T. abyssorum*, *T. compressa*, and *T. libellula* dominate the diet of adult capelin (Panasenko 1984; Gjøsæter et al. 2002). The krill and amphipod distribution areas overlap with the feeding grounds of capelin, especially in the winter to early summer. A number of investigations demonstrate that capelin can exert a strong top-down control on zooplankton biomass (Dalpadado and Skjoldal 1996; Dalpadado et al. 2001, 2002; Gjøsæter et al. 2002). Polar cod has a similar food spectrum as capelin, and it has been suggested that there is considerable food competition between these species when they overlap (Ushakov and Prozorkevich 2002). When abundant, young herring are also important zooplankton consumers of the BS food web. Stomach samples show that calanoid copepods and appendicularians makes up 87% of the herring diet by weight (Huse and Toresen 1996). Although data on capelin larvae and 0-group (half-year-old fish) abundance suggests that the predation of herring

on capelin larvae may be a strong or dominant effect on capelin dynamics (Hamre 1994; Fossum 1996; Gjøsæter and Bogstad 1998), capelin larvae are only found in 3–6% of herring stomachs (Huse and Toresen 2000). However, the latter authors comment that fish larvae are digested fast, and that predation on capelin larvae may occur in short, intensive "feeding frenzies," which may have been missed by the sampling.

The dominant macronekton species of the BS are Atlantic cod (*Gadus morhua*), saithe (*Pollachius virens*), haddock (*Melanogrammus aeglefinus*), Greenland halibut (*Reinhardtius hippoglossoides*), long rough dab (*Hippoglossoides platessoides*), and deepwater redfish (*Sebastes mentella*). The stock of Arcto-Norwegian (or northeast Arctic) cod is currently the world's largest cod stock. As macronekton predators, cod is dominating the ecosystem. They are opportunistic generalists, the spectrum of prey categories found in their diet being very broad. Mehl (1991) provided a list of 140 categories, however, a relatively small number of species or categories contributed more than 1% by weight to the food. These are amphipods, deep sea shrimp (*Pandalus borealis*), herring, capelin, polar cod, haddock, redfishes, and juvenile cod (cannibalism). The trophic interaction between cod and capelin is particularly strong in the BS and, as shown later, occupies a central role in regulating community dynamics. However, cod diet varies considerably during the life cycle, the proportion of fish in the diet increasing with age. The diet of haddock is somewhat similar to that of cod, but they eat less fish and more benthic organisms.

Approximately, 13–16 million seabirds of more than 20 species breed along the coasts of the BS. The most plentiful fish-eaters among Alcidae are Atlantic puffin (*Fratercula arctica*; 2 million breeding pairs) and guillemots, such as Brünnich's guillemot (*Uria lomvia*) and common guillemot (*Uria aalge*), 1.8 million and 130,000 breeding pairs, respectively. Brünnich's guillemot is the most important consumer of fish, of which polar cod (up to 95–100% on Novaya Zemlya) and capelin (up to 70–80% on Spitsbergen) are dominant in the diets. Daily food consumption by a Brünnich's guillemot is 250–300 g, and as much

as 1,300 metric tons per day for the entire population. It is suggested that this estimate represents 63% of the total amount of food consumed by seabirds in the BS (Mehlum and Gabrielsen 1995). Consumption of fish by seabirds is between 10% and 50% of the yearly catch of fish in the fisheries.

In addition to seabirds, there are about 20 species of cetaceans, and seven species of pinnipeds in the apex predator assemblage of the BS. The majority of the cetaceans are present in the BS on a seasonal basis only. Among these, the most common are minke whale (*B. acutorostrata*), white whale (*Delphinapterus leucas*), white-beaked dolphin, and harbor porpoise (*P. phocoena*). Annual food consumption of minke whale has been estimated at approximately 1.8 tons, including about 140,000 tons of capelin, 600,000 tons of herring, 250,000 tons of cod, and 600,000 tons of krill (euphausiids) (Bogstad et al. 2000). Among pinnipeds, the most common is the harp seal (*Phoca groenlandica*) whose abundance in the White Sea (a large inlet to the BS on the northwestern coast of Russia) is 2.2 million. Other pinnipeds are present in lower numbers. These include, ringed seal (*Phoca hispida*), harbor seal (*P. vitulina*), gray seal (*Halichoerus grypus*), and walrus (*Odobenus rosmarus*). Yearly food consumption by harp seal in the BS is estimated at a maximum of 3.5 million tons, including 800,000 tons of capelin, 200,000–300,000 tons of herring, 100,000–200,000 tons of cod, about 500,000 tons of krill, 300,000 tons of amphipods, and up to 600,000 to 800,000 tons of polar cod and other fishes (Bogstad et al. 2000; Nilssen et al. 2000). In spite of the high capelin consumption of harp seals, cod remains the primary consumer of capelin in the BS, with an estimated annual removal (mean 1984–2000) of more than 1.2 million tons (Dolgov 2002).

Community dynamics

In this section we summarize the community changes of the reviewed systems in relation to recent climate forcing. It is possible that some of the community changes that we describe are the result of human harvest, or a synergism between human and environmental factors. At the current

state of knowledge it is impossible to quantify the relative contribution of climate and fishing. However, as illustrated below, the synchrony of the biological changes among different components of the food web, and the large ecological scale of these changes point to the fact that climate must have occupied a central role.

Tropical Pacific

Primary production may change drastically during an El Niño event. As the trade winds relax and the warm pool extends to the central Pacific, the upwelling intensity decreases and the cold tongue retreats eastward or can vanish in the case of particularly strong events. The eastward move-ment of warm water is accompanied by the displacement of the atmospheric convection zone allowing stronger wind stresses in the western region to increase the mixing and upwelling in the surface layer and then to enhance the primary production. Therefore, primary production fluc-tuates with ENSO in an out-of-phase pattern between the western warm pool and the central-eastern cold-tongue regions.

These changes in large-scale oceanic conditions strongly influence the habitat of tuna. Within the resource-poor warm waters of the western Pacific most of the tuna species are able to thrive, partly because of the high productivity of the adjacent oceanic convergence zone, where warm western Pacific water meets the colder, resource rich waters of the cold tongue. The position of the convergence zone shifts along the east–west gradient and back again in response to ENSO cycles (in some cases 4,000 km in 6 months), and has direct effect on the tuna habitat extension. In addition to the impacts on the displacement of the fish, ENSO appears to also affect the survival of larvae and subsequent recruitment of tuna. The most recent estimates from statistical population models used for tuna stock assessment (MULTIFAN-CL, Hampton and Fournier 2001) pointed to a clear link between tuna recruitment and ENSO-related fluctuations. The results also indicated that not all tuna responded in the same way to climatic cycles. Tropical species (such as skipjack and yellowfin) increased during El Niño events. In contrast, subtropical species
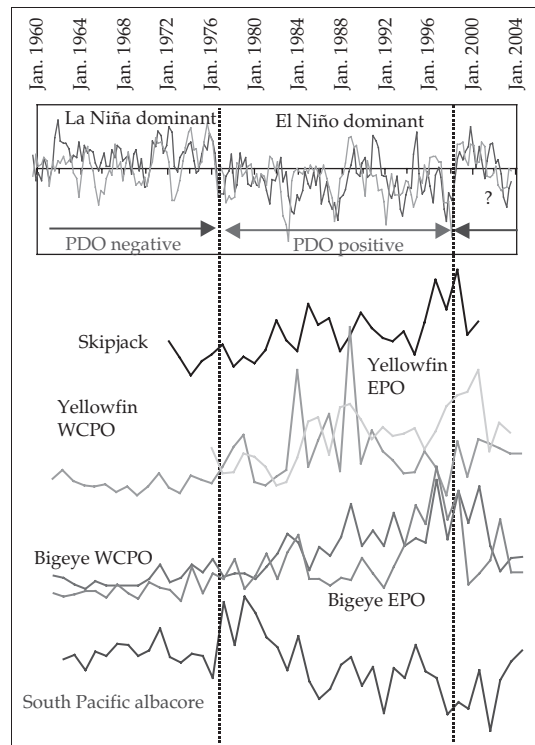

Figure 12.5 PDO, ENSO, and recruitment time series of the main tuna species in the Tropical Pacific (updated from Lehodey et al. 2003). WCPO = Western and Central Pacific Ocean, EPO = Eastern Pacific Ocean. The *y* axis of the climate indices graph has been rotated. Note that during a positive PDO phase (before 1976), El Niño events become more frequent and tropical tunas recruitment (skipjack, yellowfin, and bigeye) is favored. Conversely, during a negative PDO phase La Niña events are more frequent and the recruitment of subtropical tuna (albacore) is favored. See text for more explanations regarding effect of climate on tuna recruitment.

(i.e. albacore) showed the opposite pattern, with low recruitment following El Niño events and high recruitment following La Niña events (Figure 12.5).

Western Gulf of Alaska

After the mid-1970s regime shift, the GOA has witnessed a dramatic alteration in species com-position, essentially shifting from a community dominated by small forage fishes (other than juvenile gadids) and shrimps, to another domin-ated by large piscivorous fishes, including gadids and flatfish (Anderson and Piatt 1999; Mueter and Norcross 2000). In addition, several species of

seabirds and pinnipeds had impressive declines in abundance. An analysis of the GOA community dynamics, for each trophic assemblage identified in the previous sections, follows.

Evidence for decadal-scale variation in primary production, associated with the mode of variability of the PDO, is equivocal. Brodeur et al. (1999) found only weak evidence for long-term changes in phytoplankton production in the northeast Pacific Ocean, though Polovina et al. (1995) suggest that production has increased due to a shallowing of the mixed layer after the 1976–77 PDO reversal. A shoaling mixed layer depth exposes phytoplankton to higher solar irradiance, which in sub-Arctic domains tends to be a limiting factor in early spring and late fall. There is more conclusive evidence for long-term variations in zooplankton abundance in the North Pacific Ocean. Brodeur and Ware (1992) and Brodeur et al. (1999) have demonstrated that zooplankton standing stocks were higher in the 1980s (after the 1976–77 phase change in the PDO), relative to the 1950s and 1960s. Mackas et al. (2001) determined that inter-annual biomass and composition anomalies for zooplankton collected off Vancouver Island, Canada, show striking interdecadal variations (1985–99) that correspond to major climate indices.

During the last 20–30 years, many micronekton species of the GOA community have undergone a sharp decline in abundance, to almost extinction levels (Anderson and Piatt 1999; Anderson 2000). On average, shrimp and capelin biomass decreased after the mid-1980s, while eulachon and sandfish are currently reaching historical high levels (Figure 12.6). The biomass trend of juvenile gadids (cod and pollock) is inferred by the recruitment estimates (Figure 12.7), based on fish stock assessment models (SAFE 2003). While cod recruitment has remained fairly constant, pollock recruitment had a series of strong year-classes in the mid-1970s, followed by a continuous decline up to the 1999 year-class. However, the actual strength of the 1999 year-class will only be available in coming years, as more data accumulates on the abundance of this cohort.

In the macronekton guild, the most remarkable change in biomass has been that of arrowtooth flounder, with a sharp increase in both biomass and recruitment since the early 1970s (Figure 12.7). Arrowtooth flounder now surpass, in total biomass, the once dominant gadid species, such as walleye pollock or Pacific cod. Halibut has also undergone a similar increase in biomass during the available time series. The biomass of adult
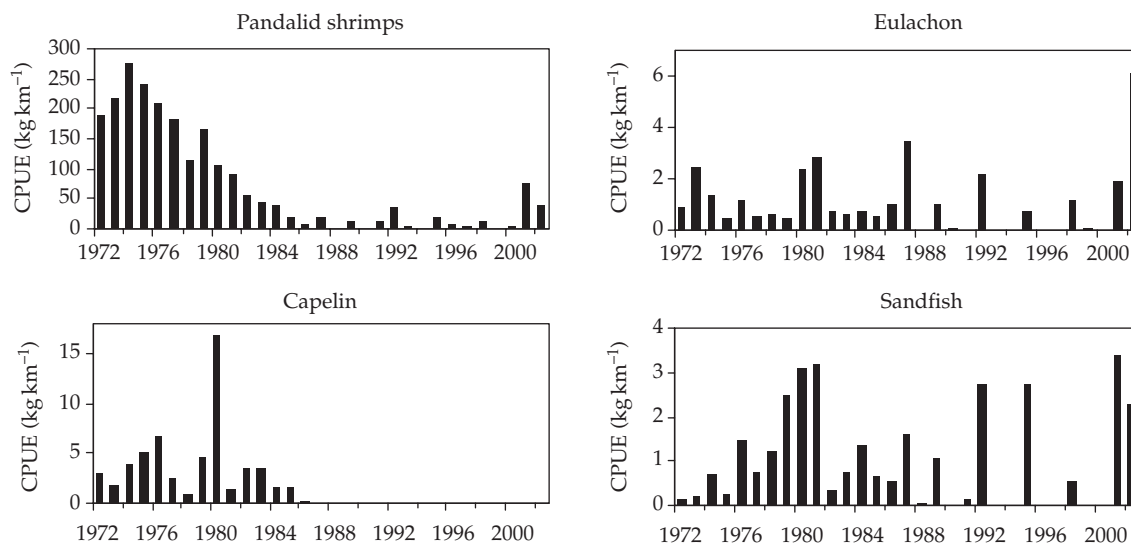

Figure 12.6 Abundance trend of non-gadid micronekton species of the GOA food web. Time series were obtained from survey data and are expressed as catch per unit effort (CPUE $kg\,km^{-1}$) (Anderson and Piatt 1999; Anderson 2000).
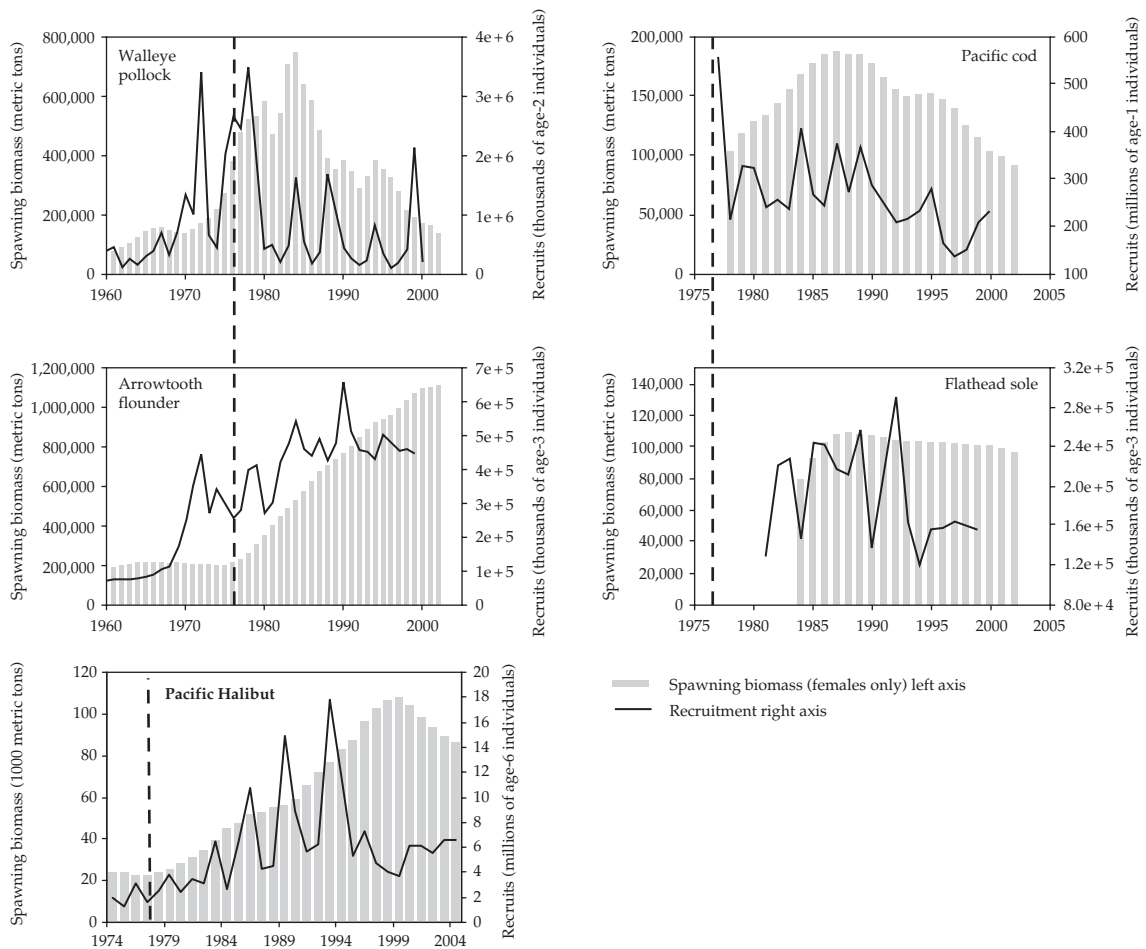
Figure 12.7 Biomass time series for the dominant macronekton species of the GOA food web (SAFE 2003). Pacific halibut time series refers to the legal area 3A, which include most of the north GOA system (halibut data courtesy of Steve Hare, International Pacific Halibut Commission, Seattle WA, USA). The vertical dashed line indicates the 1976 regime shift.

walleye pollock peaked in the early 1980s but has since then declined (Figure 12.7), as a result of several successive poor year classes. Currently, adult pollock (age 3 +) biomass is similar to that of the adult Pacific cod, whose biomass has generally increased since the 1960s, and is recently in slight decline.

Among apex predators, the best-documented and studied case of species decline has been that of the SSLs (Figure 12.8). In 1990, the National Marine Fisheries Service declared SSL a "threatened" species throughout the entire GOA region. Later on, in 1997, the western stock (west of 144° longitude) was declared "endangered" due to

continuous decline, while the eastern stock stabilized at low levels and continued to be treated as "threatened". Harbor seals (*P. vitulina*) have also declined in the GOA, compared to counts done in 1970s and 1980s. The exact extent of their decline is unavailable. However, in some regions, particularly near Kodiak Island, it was estimated to be 89% from the 1970s to the 1980s (Angliss and Lodge 2002). Declines in seabird populations have been observed in the GOA, though it should be noted that trends are highly species- and site-specific. For example, black-legged kittiwakes are declining precipitously on Middleton Island (offshore from Prince William Sound), but
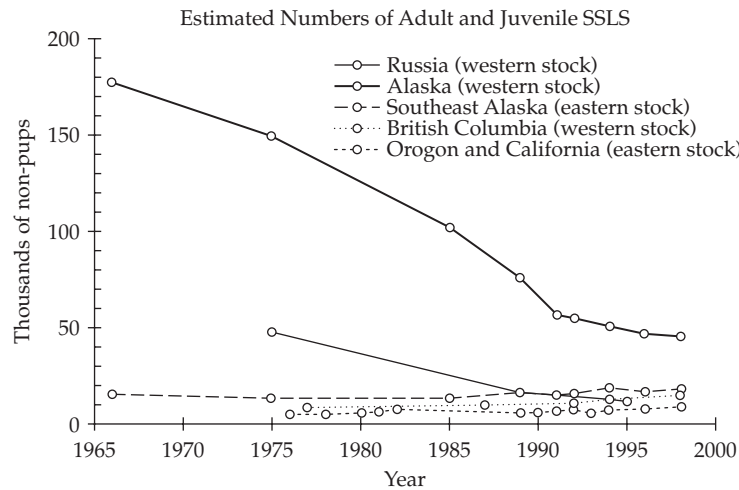
Estimated Numbers of Adult and Juvenile SSLS

Figure 12.8 SSL population trends for various locations of the North Pacific.

populations are increasing in nearby Prince William Sound, in the central GOA. Likewise, common murres are steadily increasing on Gull Island, but are rapidly declining on nearby Duck Island (both located in the vicinity of Cook Inlet). Cormorants on the other hand, appear to be declining throughout the GOA (Dragoo et al. 2000).

Barents Sea

The bulk of primary production in the BS occurs in two types of areas: close to the ice edge and in the open sea. The spring bloom along the ice edge can occur as early as mid-April when the melt water forms a stable, nutrient-rich top layer. As nutrients are exhausted, but new areas of nutrient-rich water is uncovered by the receding ice, the bloom follows the ice edge in the spring and summer. In cold years, the increased area of ice leads to an earlier and more intense ice edge bloom (Rey et al. 1987; Olsen et al. 2002). Olsen et al. (2002) found that this leads to a tendency for a higher annual primary production in cold years. However, most of it is ungrazed, due to mismatches with primary copepods consumers, for example, capelin and cod.

The zooplankton shows large interannual variations in abundance, species composition, and timing of the development of each species. The capelin can have a significant impact on zooplankton abundance, being able to graze down the locally available zooplankton in a few days (Hassel et al. 1991). Capelin biomass has been fairly stable through the 1970s and early 1980s, but since then has had two major collapses, one in 1985–90 and another in 1994–98 (Figure 12.9). The Norwegian spring-spawning herring has undergone large fluctuations in abundance throughout the twentieth century (Toresen and Østvedt 2000; Figure 12.9). At the turn of the century the spawning stock biomass was around 2 million tons, increasing to more than 15 million tons in 1945. From 1950, the biomass decreased steadily while the landings increased. In the late 1960s, the stock collapsed to a very low level (<0.1 million tons), mainly because of over-exploitation (Dragesund et al. 1980). Strong regulation of the fishery allowed the stock to recover very slowly during the 1970s, and more rapidly after 1983 (due to the strong 1983 year-class). Finally, the stock started to increase again around 1990, reaching about 10 million tons in 1997.

The cod stock declined from 3–4 million tons in the 1950s to less than 1 million tons in the late 1980s (Figure 12.10). Fishing changed the structure of the spawning stock greatly during the same period, by decreasing both the age at maturity (Jørgensen 1990; Law 2000) and the mean age (G. Ottersen, personal communication) of the spawning stock from 10 to around 7 years.

After this crisis in the cod fishery in the late 1980s, the population has picked up; while the spawning stock was only 118,000 tons in 1987, it is now 505,000 tons. The other gadoid stocks of haddock

Figure 12.9 Time series of (a) capelin and (b) herring biomass in the BS.

and saithe have decreased by around 50% since the 1960s and 1970s; the portion of large piscivorous individuals has probably decreased even more. The biomass of the long-lived deep-water redfish decreased from around 1 million tons in the 1970s to 0.14 tons in 1986, and is still very small. The same can be said for Greenland halibut and probably long rough dab.

Abundance trends of BS pinnipeds are largely unknown, though an upward trend has been noted for the abundance of harp seal, walrus, and common seal; ringed seal in the western part of the BS may be declining. Among seabirds, the common guillemot has declined dramatically since the 1960s. Already in 1984, before the first collapse of the capelin stock, its abundance had declined by 75% (compared to 1964) because of drowning in fishing gears and perhaps also the collapse in the herring stock around 1970. In 1984–85, the capelin stock collapsed, and in 1986 the large 1983 year-class of herring emigrated from the BS. As a consequence, the largest colonies of common guillemot were further reduced by 85–90% in 1986–88.
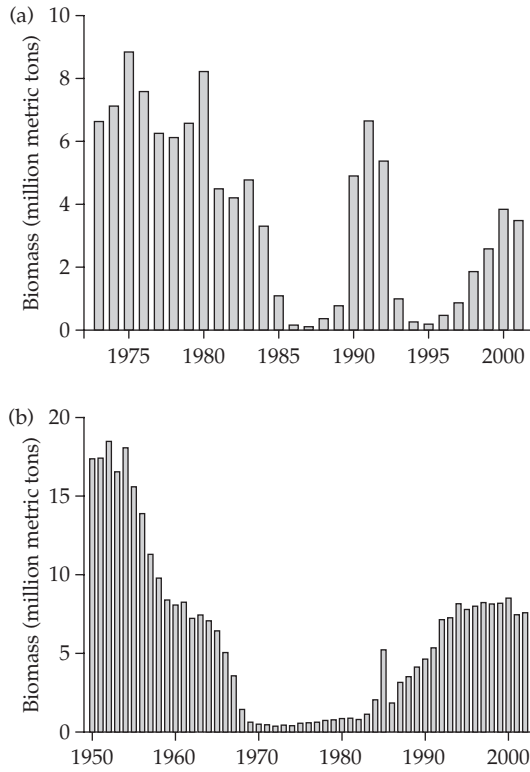
Linking climate forcing, food web structure and community dynamics

In the TP, ENSO events are a central forcing variable of the tropical tunas population dynamics (Lehodey et al. 1997, 2003; Lehodey 2001). The links between climate, habitat, and tuna recruitment have been investigated in detail with a
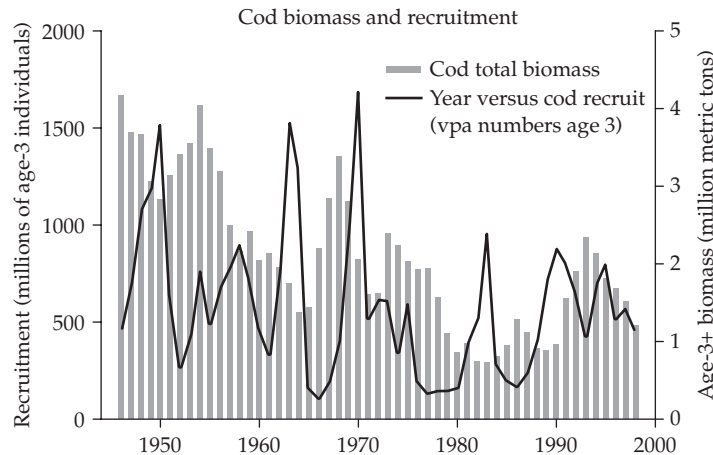

Figure 12.10 Cod biomass (age 3 and older) and recruitment (age 3) in the BS.

spatial population dynamic model (SEPODYM) that describes the population responses of tuna to changes in both feeding and spawning habitats (Lehodey et al. 2003). Results suggest that skipjack and yellowfin recruitment increases in both the central and western Pacific during El Niño events, as the 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 recruitment in the central 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 four and eight months of age. Satellite imagery indicated that this same area was the site of a major bloom in phytoplankton some 4–8 months before (Murtugudde et al. 1999). 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 grounds in the western and central TP are associated with the warm pool, those of albacore roughly extend through the central Pacific on each side of the equatorial 5°N–5°S band. The out-of-phase primary productivity between western (warm pool) and central (equatorial upwelling) Pacific led the model to predict similar out-of-phase recruitment fluctuations between species associated to one or the other areas of the TP. In addition, the extension of the warm waters in the central Pacific during El Niño events that extends the skipjack spawning grounds may conversely reduce those of the albacore (Figure 12.11). In summary, it appears that
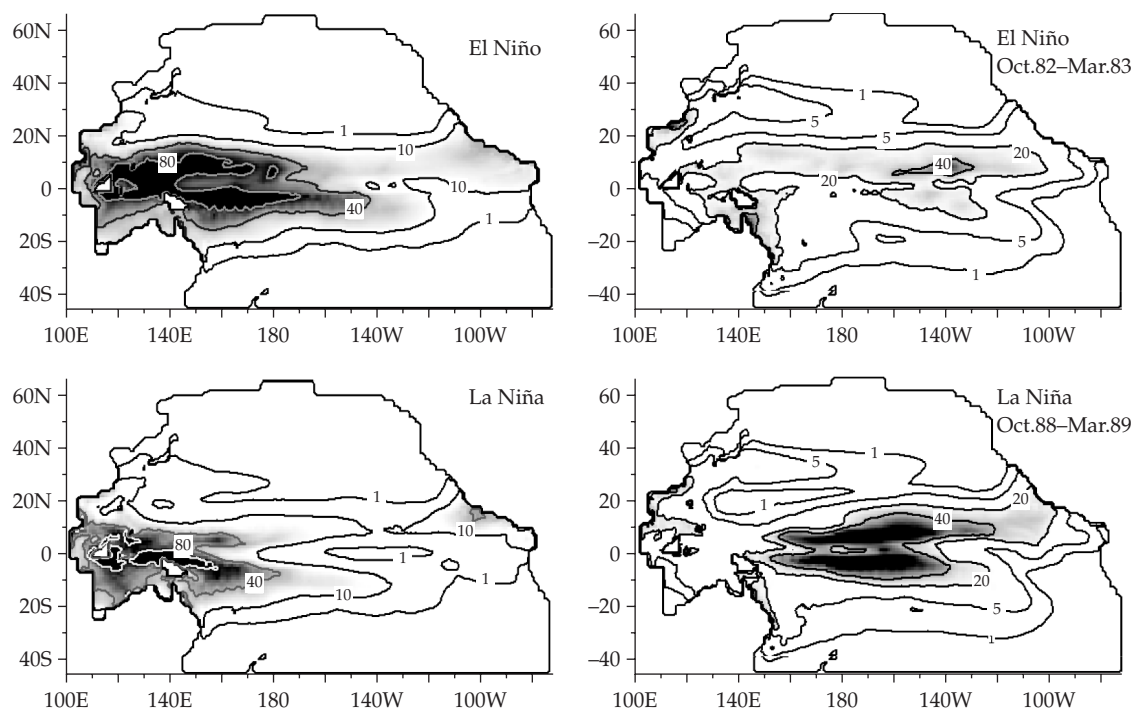

Figure 12.11 Predicted spatial distribution of the larvae and juveniles of skipjack (left) and albacore (right) tuna in the TP during ENSO phases.

tuna recruitment and population fluctuations in the TP would be controlled through physical, bottom-up and "middle-down" (larvae predation by epipelagic micronekton) rather than top-down mechanisms, the intermediate "middle" component including the juvenile and young tuna.

The species dynamics of the GOA community appear to be strongly influenced by both climate forcing and species interactions within the food web. For example, the gradual increase of macronekton during the mid-1980s resulted from a series of strong year-classes that followed the mid-1970s shift of the PDO index. High pollock recruitment may have been the result of a series of favorable conditions, including higher water temperature and lower spring wind stress (Bailey and Macklin 1994) during the larval stages, as well as limited predation and density-dependent mortality during the juvenile stage (Ciannelli et al. 2004). Immediately after the 1976 PDO regime shift, both of these conditions were common in the GOA area. Similarly, flatfish increase in recruitment was, in part, the result of a favorable larval advection from the deep offshore spawning to shallow inshore juvenile nursery grounds, conditions that appear commonly, particularly during strong El Niño events (Bailey and Picquelle 2002). Intervention analysis applied to many of the available GOA recruitment time series indicates that large flatfish recruitment (i.e. halibut and arrowtooth flounder) has significantly increased after the 1976 PDO shift, while pollock and cod recruitment has significantly increased during El Niño North years (Hollowed et al. 2001). As mentioned above, the frequency of El Niño North events in the GOA region can increase during positive PDO phases, thereby rendering more difficult the distinction between the effect of PDO or ENSO forcing in the North Pacific community dynamics.

The initial increase of macronekton biomass after the late 1970s may have triggered a series of food web interactions that directly and indirectly affected other species of the GOA community. For example, with regard to pollock, the post 1985 biomass decline was the result of mostly poor recruitment from the mid-1980s to the late 1990s. During this time frame, pollock had some

occasional strong year-classes (e.g. 1984, 1988, and 1994), but never at the level of those observed before the 1980s. Bailey (2000) has shown that during the years of the decline, pollock recruitment shifted from being controlled at the larval stage (1970s and initial part of the 1980s) to being controlled at the juvenile stage (late 1980s and 1990s). This change in recruitment control was due to the gradual buildup of piscivorous macronekton and consequent increase of juvenile pollock predation mortality. Ciannelli et al. (2004) have shown that macronekton predators, besides having a direct effect on juvenile pollock survival (via predation), can also indirectly affect their dynamics by amplifying the density-dependent mortality.

Micronekton species of the GOA community, such as capelin and pandalid shrimps, might have suffered high predation mortality after the predators buildup, with consequent decline in abundance. To date, apart from the case of juvenile pollock described above, there is no direct evidence that predation was the primary cause of the decline of forage species in the GOA community. However, studies from other sub-Arctic ecosystems of the North Atlantic, point to the fact that macronekton species set off strong top-down control on their prey (Berenboim et al. 2000; Worm and Myers 2003; Hjermann et al., 2004; but see also Orensanz et al. 1998). Also, in the GOA community a top-down control of macronekton on micronekton is consistent with the changes of the groundfish diet observed in the last 20 years (Yang and Nelson 2000; Yang 2004). In addition to top-down forcing, during the years following the PDO regime shift (i.e. late 1970s and 1980s), capelin may also have been negatively influenced by strong competition with juvenile pollock. As indicated above, these two species have an almost complete diet and habitat overlap. In the GOA, capelin are at the southernmost range of their worldwide distribution, while, pollock are at the center of their range and will be more likely to out-compete capelin during warm climate phases.

Changes of the micronekton assemblage of the GOA food web had severe repercussions on apex predators, such as seabirds and pinnipeds. Springer (1993) hypothesized that food-related

stresses have contributed to observed population declines of the seabirds. Among pinnipeds, the SSL decline in the western GOA is to these days one of the most interesting case studies in conservation biology (National Research Council 2003). Several hypotheses have been advanced to explain the decline and absence of recovery, including direct and indirect fishing effects (Alaska Sea Grant 1993), climate change (Benson and Trites 2002), nutritional stress (Trites and Donnelly 2003), parasites and disease agents (Burek et al. 2003), and, recently, top-down forcing (Springer et al. 2003). The majority of these hypotheses acknowledge the importance of direct and indirect food web interactions. For example, Springer et al. (2003) suggested that an increase of killer whale predation was responsible for the Steller's decline. According to this concept, killer whales turned to SSLs after the baleen whales of the GOA disappeared due to an ongoing legacy of the post Second World War whale hunt. In addition, one might speculate that baleen whale never fully recovered after the postwar decline due to a lack of sustainable and highly nutritious fish prey. Top-down foraging by killer whales has played a major role also on the decline of sea otter (*Enhydra lutris*) from western Alaska, with rather dramatic effects on the sea urchins (increase) and kelp (decrease) populations (Estes et al. 1998). In contrast to top-down forcing, the nutritional stress hypothesis (a.k.a., ''junk-food'' hypothesis) suggests that the SSL decline was due to a shift in their diet toward prey with lower energy and nutritional value (e.g. pollock, cod) as a consequence of the reduced availability of the high-energy forage species (Trites and Donnelly 2003).

Probably, to a greater extent than in the GOA food web, the pelagic community of the BS is dominated by a few very abundant species, resulting in strong interspecific interactions (Hamre 1994). Specifically, the relationship between cod, capelin, and young herring have been viewed as particularly important for the ecosystem functioning (Hamre 1994, 2000; Hjermann et al. in press). The recruitment of herring and cod is strongly associated with the temperature of the BS; specifically, in cold years, recruitment is always low, while in warm years, it may be low or high

(Ellertsen et al. 1989; Ottersen and Loeng 2000) (Figure 12.12). The increased westerly winds over the North Atlantic that are associated with a high (positive) NAO phase, has, at least for the most recent decades, affected BS water temperature by increasing (1) the volume flux of relative warm water from the southwest; (2) cloud cover; and (3) air temperature. Increased BS water temperature influences growth and survival of cod larvae both directly through increasing the development rate and indirectly through regulating *C. finmarchicus* production. Variation in availability of *C. finmarchicus* nauplii is an important factor for formation of strong cod year-classes. In fact, the match–mismatch hypothesis of Cushing (1982, 1990) states that the growth and survival of cod larvae depends on both the timing and magnitude of *C.finmarchicus* production. In addition, an increase of inflow from the zooplankton-rich Norwegian Sea further increases availability of food for the cod larvae (Ottersen and Stenseth 2001). High food availability for larval and juvenile fish results in higher growth rates and greater survival through the vulnerable stages when year-class strength is determined (Ottersen and Loeng 2000).

Cod and herring can potentially eat a large amount of capelin (herring eats larvae, cod eats larger stages). Therefore, capelin can be expected to experience high predation after a warm year with favorable conditions for cod and herring recruitment. This was confirmed by Hjermann et al. (2004), who found that capelin cohorts that are spawned two years after a warm year tend to be weak. It appears that the predation-mediated effect of climate has been the main mechanism of the two collapses of the capelin stock in the last two decades (1984–86 and 1992–94); a third collapse appears to be occurring at the time of writing. These collapses (stock reduction of >97%) had a huge impact on the BS community assemblage and food web structures. The most apparent impact was a drastic reduction in population of some seabird species (such as the common guillemot *U. aalge*; Krasnov and Barrett 1995; Anker-Nilssen et al. 1997) and mass migration of a huge number of harp seal toward the Norwegian coast; incidentally about 100,000 seals subsequently
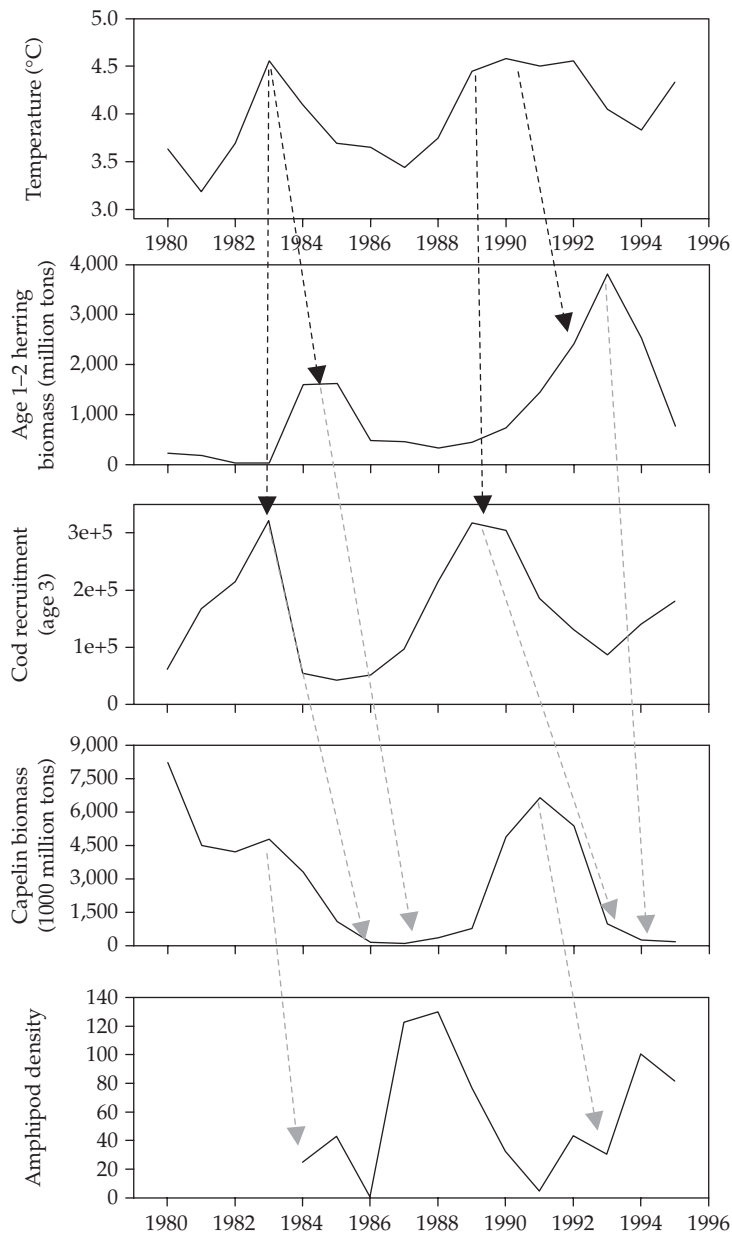
Figure 12.12 From top to bottom, time series of water temperature, herring (age 1–2) biomass, cod recruitment (age 3), capelin and amphipod (*P. libellula* and *P. abyssorum*) biomass in the BS. Arrows indicate climate (in black) and trophic (in gray) forcing on species dynamics. Water temperature in the BS (correlated with NAO index) has a positive effect on cod and herring recruitment. Herring (mostly age 1–2) and cod (mostly age 3–6) feed on capelin larvae, and adult, respectively, and consequently have a negative effect on capelin biomass. In turn, capelin feed on northern zooplankton, of which *P. libellula* and *P. abyssorum* are dominant components.

drowned in fish nets (Haug and Nilssen 1995). Also, observations of increased zooplankton biomass during capelin collapses (Figure 12.12) are indicative of the capelin impact at lower trophic levels. In the "collapse" years, herring replaced capelin as the main zooplankton feeder. By feeding also on capelin larvae, a low biomass of juvenile herring is able to block the rebuilding of the capelin stock, with the ultimate effect of replacing a large capelin biomass with a small herring biomass.

Based on these observations we conclude that the BS pelagic ecosystem appears, to some extent, to be a "wasp-waist" ecosystem, a term originally coined for upwelling regions such as the Benguela ecosystem (Cury et al. 2000). In such ecosystems,
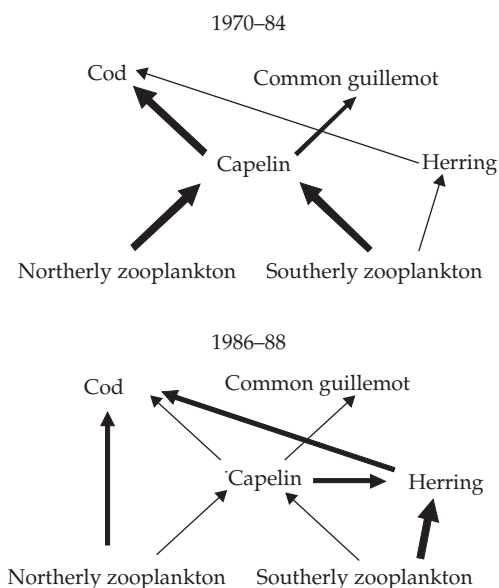
1970–84

1986–88

Figure 12.13 Conceptual model of changes in BS trophic links during years of high capelin abundance (1970–84) and capelin collapse (1986–88, "collapse" years). During "collapse" years cod diet switches from one based primarily on capelin, to another based on zooplankton and herring. Capelin decline, also has negative effects on seabird populations, such as the common guillemot. Herring replace capelin as a central forage species, and can exercise a large predation impact on capelin larvae (further delaying their recovery) and zooplankton, particularly from the Atlantic waters (southerly zooplankton). Because herring are not distributed as far north as capelin, most of the northerly zooplankton remains ungrazed during "collapse" years. Also, because herring live in the BS only for a limited period of their life cycle (see text), a large portion of the BS originated biomass is exported out of the system.

the crucial intermediate level of pelagic fish is dominated by a few species (capelin, juvenile cod, and herring in the BS), exerting top-down control on zooplankton and bottom-up control of predators (Figure 12.13).

Conclusions

The relation between structure and complexity of a food web and its stability has been a much debated issue within the field of ecology, starting with Mac Arthur (1955) and Elton (1958) who claimed that complexity begets stability—a view conveyed to many ecology students (see, for example, Odum

1963). May (1973) showed, through mathematical modeling, that the "complexity begets stability" idea might not necessarily be valid, although Maynard Smith (1974) cautioned about drawing too firm conclusions on the basis of pure theoretical analyses. It bears note that the set of empirical observations gathered in this review are not sufficient to address in full details of the issue of resilience in marine pelagic systems. In addition, the anthropogenic forcing (i.e. fishing), active in all three systems, may have synergic effect with climate, complicating the issue of community resilience even further. However, we feel that addressing the issue of community stability is particularly appropriate within the context of this book, and may offer the unique opportunity to test the traditional theoretical knowledge of complexity and stability in systems (i.e. marine pelagic) where such theories have, to date, been unexplored. By focusing on three ecological systems of different complexities and dynamics we can ask to what extent they exhibit different degrees of resilience.

A summary of selected metrics for the three inspected systems is presented in Table 12.1. Of the three, TP is the one where the ocean variability, associated with climate forcing, is most extreme. Community changes in the TP ecosystem occur likely with climate fluctuations, but high species diversity, high degree of omnivory, high connectivity, and weak species interactions contribute likely to its resilience and stability through time. In the GOA system, within the period in which community dynamics was monitored, we have witnessed only a single shift of the dominant climate forcing: a raise of the PDO index in the 1976, a brief return to pre-1976 after 1989, and what appears to be a more stable return of the PDO in recent years. Also, in recent years, it appears that the North Pacific climate is shifting toward a new mode of variability (Bond et al. 2004). The community has clearly changed after the 1976 climate change, but after a transitory shift in 1989, there was no sign of a return to the pre-1976 community state: piscivorous macro-nekton kept on rising (e.g. arrowtooth flounder), while forage species (e.g. shrimps and capelin), and apex predators (SSL and seabirds) kept on

Table 12.1 Descriptive metrics of the three pelagic ecosystems included in this review

Metrics	TP	Western GOA	BS
Extension (millions km^2)	80.0	0.38	1.4
Primary production (gC m^2 per year)	50–300	50–300	110
Dominant period of climate forcing (year)	4–10 (ENSO)	20–30 (PDO) 4–10 (Niño North)	Interannual with a weak period of about 8 years
Nodal micronekton	Epipelagic macronekton	Juvenile gadids	Capelin
Nodal macronekton	Small-size scombrids	Large flatfish	Cod
Nodal apex	Large-size scombrids, blue shark, toothed whales	Sea birds and pinnipeds	Sea birds and baleen whales
Nodal trophic links	Small-size scombrids—epipelagic micronekton	Large flatfish-micronekton	Cod-capelin-herring
	Large-size scombrids—epi and mesopelagic micronekton		
Climate trace in food web	Bottom-up and middle-down	Bottom-up and top-down	Middle-out
Ranked complexity (including diversity, number of links and connectance)	High	Average	Low
Ranked resilience	High	Low	Average

decreasing. In recent years, immediately following the alleged 1999 change of PDO regime (warm to cold), pandalid shrimps, eulachon, and sandfish appear to be recovering, but there is no sign of change in other forage (e.g. capelin) or apex predator (e.g. arrowtooth flounder) dynamics. Thus, the evidence gathered so far indicates that the 1976 climate regime shift has led the GOA community toward a new equilibrium state. However, given the top-down control of apex predators on forage species and the relatively long life cycle of large macronekton, we may have to wait few more years to fully understand whether the GOA community can ever return to a pre-1976 state.

To a larger degree than the GOA, and certainly than other sub-Arctic systems (e.g. northwest Atlantic), the dynamics of dominant BS species has a tendency to recover after collapsing. This seems to be a system dominated by three species: cod, capelin, and herring. Changes of capelin and herring abundance (via top-down and bottom-up forcing), have led the entire community to profound phase-shifts in the food web structure. During the last 30 years we have witnessed two of these transitions, one in 1985–89 and another in 1994–99, with a possible third transition occurring at the time of writing (Hjermann et al. 2004). Thus the BS community appears to be con-

tinuously shifting among two states, albeit whose magnitude may vary, mainly depending on the abundance of the main forage species of the systems.

Our survey does suggest that the more complex system (TP) is more stable (or resilient)—thus supporting the "complexity begets stability" concept. However, much work is needed before we can reach firm and general conclusions for large marine ecosystems. Such work should cover both the empirical and the analytical facets of community dynamics studies. Within the empirical framework, to overcome the objective difficulty of manipulating marine pelagic ecosystems, climate forcing should be seen as a natural "large-scale perturbation experiment" (Carpenter 1990). Within the analytical framework, we stress the importance of statistical models with structure inferred from the observed patterns of population variability (e.g. Hjermann et al., 2004). We also stress the importance of model simulations in relation to different levels of internal structures (i.e. food web) and external forcing (e.g. Watters et al. 2003). Our hope is that what we have done here might serve as a spark leading to the development of more comprehensive analysis of food web and community dynamics in large marine pelagic ecosystems.

Acknowledgements