3 Habitats

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Summary

The habitats of populations of small, pelagic fish, especially anchovy and sardine, in the Benguela, California, Humboldt, and Kuroshio-Oyashio current systems, and in the NE Atlantic, are described and discussed in regard to future climate change. These stocks have been the primary concern of the Small Pelagic Fish and Climate Change (SPACC) program of International GLOBEC. Each of these regions and stocks has a unique set of climate and ocean conditions and their variability. However, they also share common characteristics. Spawning and development occurs within broad ranges of temperature (12–26 °C) and salinity (<30–36) and in regions of high plankton production, associated with either upwelling or freshwater. Often, sardine are more oceanic and anchovy more coastal, often associated with wind-driven upwelling and rivers. Sardine tend to make longer migrations between spawning and feeding regions than do anchovy. The habitat of most populations of small, pelagic fish expands when the population size is large and contracts when it is small, often into refugia. Climate change may affect populations of small, pelagic fish by causing poleward shifts in distribution due to warming, some of which have already occurred. Other potential effects are due to changes in winds, hydrology, currents, stratification, acidification, and phenology.

Introduction

Small, pelagic fish, especially anchovy and sardine, abound in many, productive regions of the world ocean. Their habitats include areas with coastal and oceanic upwelling and freshwater influence and can be characterized by both geography (properties of the coast and bottom) and hydrography (properties of the water). The effects of climate change, be it of natural or anthropogenic origin, on populations of small, pelagic fish, are mediated by their habitats. Our objectives in this chapter are to describe the habitats of the major stocks of small, pelagic fish and comment on the possible effects of climate change on these habitats and, in turn, on the populations. Finally, we present future challenges.

Small Pelagic Fish and Climate Change (SPACC) is a program of International Global Ecosystem Dynamics (GLOBEC) that uses the comparative approach (*cf.* Mayr, 1982) to assess the impact of climate variation and change on ecosystems in which small pelagic fish, particularly anchovy and sardine, play an important role. The regions on which SPACC is focused (Fig. 3.1) include, in the Pacific, the California Current (Canada, US, and Mexico), the Humboldt Current (Peru, Chile), and the Kuroshio-Oyashio Region (Japan), and, in the Atlantic, the Benguela Current (South Africa, Namibia), the Canary Current (Morocco, Western Sahara, Mauritania, and Senegal), and the European Atlantic (Portugal, Spain, and France). Other regions, including the Mediterranean and Baltic Seas, the Gulf of California, waters off Australia, Korea, Taiwan, and China, and certain open ocean regions (e.g. the western tropical Pacific), contain significant populations of small, pelagic fish but have not been a focus of SPACC. Stocks of some of these other regions are treated elsewhere in this volume, but not in this chapter.

Anchovy (*Engraulis*) and sardine (or pilchard: *Sardinops*, *Sardina,* and *Sardinella*) are the genera that have been studied most within SPACC. Other genera receiving attention have been jack, or horse, mackerel (*Trachurus*), true mackerel (*Scomber*), sprat (*Sprattus*), herring (*Clupea*), and round herring (*Etrumeus*). Interactions, or replacements,

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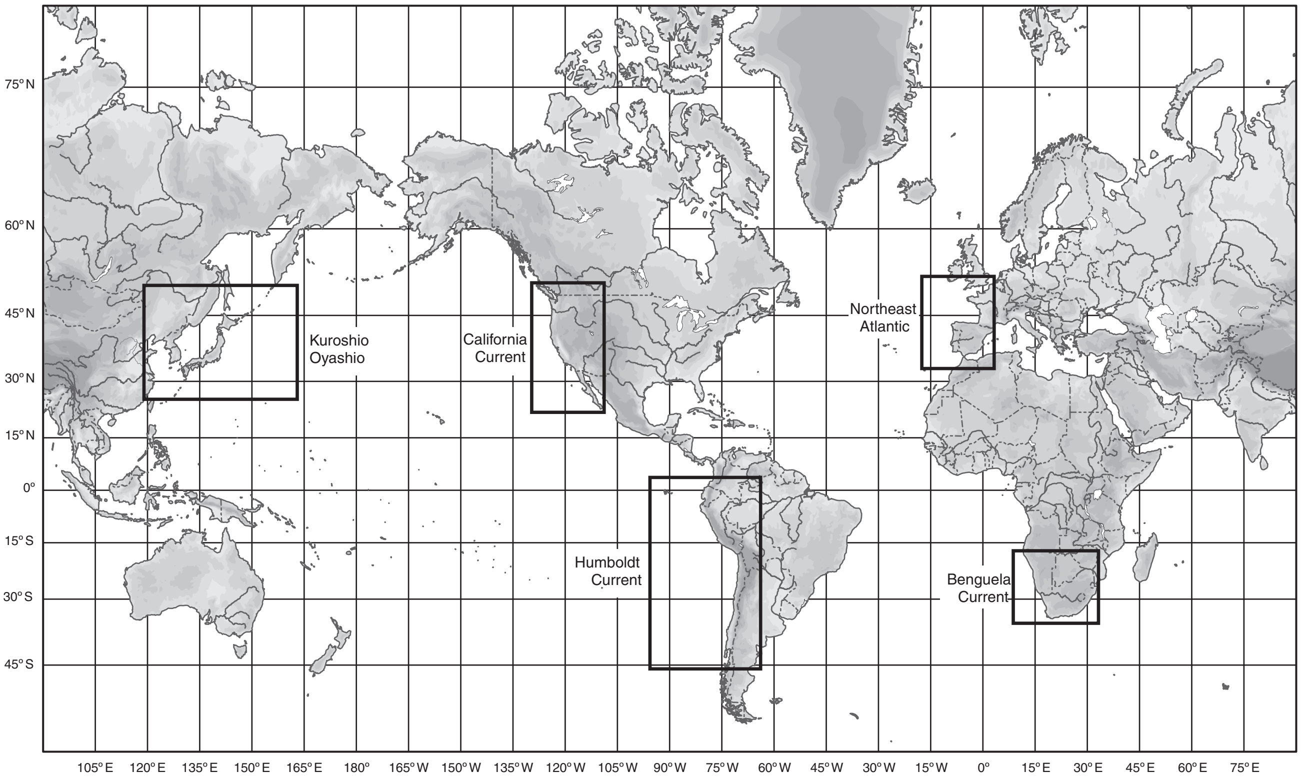


Fig. 3.1. World map showing SPACC regions treated in this chapter.

among these taxa and anchovy and sardine are of particular interest. Genetic studies of anchovy and sardine (Grant and Bowen, 1998; Lecomte *et al*., 2004) indicate six major regions of speciation of these taxa: the California Current, Humboldt Current, Kuroshio–Oyashio, Australia, Benguela Current, and the European Atlantic. These regions are, in general, synonymous with those of SPACC, with the exception of Australia. These studies show "shallow" evolutionary relationships, indicating recent expansion into current habitats. This, in turn, indicates that habitats of each taxon may share common characteristics. Further, this may allow generalities in regard to the effects of climate change on these taxa.

Anchovy and sardine often differ from one another in regard to their individual characteristics and habitats (Barange *et al*., 2005; cf. van der Lingen *et al*., 2005a). In general, anchovy feed on larger particles, have a smaller body (length, weight), and migrate less than sardine. Anchovy are also more often associated with regions of coastal upwelling or freshwater influence, while sardine occur further offshore.

SPACC is unusual among research programs in that all of the populations it studies have been and/or are exploited. In 2004, 25% of world fish landings were small, pelagic fish, including the Peruvian achoveta (*Engraulis ringens*) the world's largest single-species fishery, itself 11% of global landings (http://www.fao.org). In general, these fish inhabit regions of high productivity, often due to nutrients supplied by wind-driven upwelling but also in fresh water, and low diversity, including plankton and fish. This, combined with their planktivory, hence feeding low in the food web, results in productive, single-species populations ideal for exploitation. While these, like all, exploited populations are susceptible to, and have experienced, over-exploitation, they may be resilient, due to their fast growth and young age of reproduction and thus high productivity.

Climate change effects on fish populations will be understood only if they are distinguishable from other effects, especially fishing and density dependent processes. To this end, in this chapter we focus on the habitat of fish, as feasible, during all stages of development: egg, larva, juvenile, and adult feeding and spawning. Because our information is from diverse sources worldwide, it is not uniform. Our goal is to assess differences and similarities using this information. We are also particularly interested in comparing anchovy and sardine and the roles of geography and hydrography in their responses to climate change. Here, geography means location in Earth coordinates, e.g. latitude and longitude, and bottom depth. Hydrography refers to currents and water properties, e.g. temperature, salinity, and contained plankton. Variability in the distribution, abundance, and size of populations of pelagic fish may be better explained by hydrography than geography. Often, though not always, the size of populations of these taxa in a region vary out of phase (Schwartzlose *et al*., 1999). The cause of their variation remains unknown but may involve both the environment, hence habitat, and density-dependent processes (Lluch-Belda *et al*., 1992; Schwartzlose *et al*., 1999; Jacobson *et al*., 2001; Alheit *et al*., 2008; this volume, Chapter 12).

In this chapter, we first describe the habitats for the major, SPACC regions and stocks. We then synthesize these regional descriptions, highlighting similarities and differences. Finally, we briefly address the effects of past and future climate change on small, pelagic fish, as mediated by habitat.

Regional descriptions

California Current (CC)

The northern anchovy (*Engraulis mordax*) and Pacific sardine (*Sardinops sagax*) are the two dominant species of small, pelagic fish off the West Coast of North America. Both exhibit large, multi-decadal variations in population size, both in and out of phase, inferred from historical scientific and fisheries data (Schwartzlose *et al.*, 1999; this volume, Chapter 9) and paleo-oceanographic studies (Soutar and Isaacs, 1974; Baumgartner *et al*., 1992; this volume, Chapter 4). Data are both fisheries-dependent (e.g. landings data during periods of high and moderate population size) and fisheries independent (e.g. ichthyoplankton and adult acoustic-trawl surveys, largely independent of population size).

Physical characteristics

The west coast of North America (Fig. 3.2a), from Vancouver Island, Canada, to Baja California, Mexico, is influenced by the California Current, wind-driven upwelling, and, to a lesser extent, runoff (Hickey, 1979, 1998; Lynn and Simpson, 1987, 1990). The California Current originates off British Columbia and flows south past the US west coast to Baja California. It is of lower salinity (< ca. 33.2) than water of the oceanic N. Pacific to the west and coastal upwelling and the Davidson Current to the east. The latter is a poleward-flowing current that is strongest and extends furthest nouth, beyond Point Conception, in winter; it is subsurface in summer. In spring, NW winds induce upwelling, contributing to the geostrophically balanced California Current. Water upwelled is from the California Undercurrent and typically cool (<15 °C) and high in salinity (> 33.2). Open-ocean upwelling forced by wind-stress curl (Chelton 1982, Pickett and Schwing 2006), in addition to wind-induced, coastal upwelling, has recently received attention in regard to sardine habitat (Rykaczewski and Checkley, 2008). A near-shore, equator-ward jet can develop in spring, particularly off Washington and Oregon.

*Northern anchovy (*Engraulis mordax*)*

The range of *Engraulis mordax* extends from Vancouver Island, Canada to Baja California, Mexico (Fig. 3.2b). The northern anchovy consists of one genetic stock (Smith, 2005; Lecomte *et al*., 2004). However, it has two distinct spawning areas (Richardson, 1981), and its range expands and contracts with increases and decreases in the size of the population (MacCall, 1990; this volume, Chapter 5). Spawning generally occurs in areas with wind-driven, coastal upwelling or river runoff, with peak spawning in January–March off southern and central California (Lasker and Smith, 1977; Moser *et al*., 1993, 2001) and June–August off Oregon/Washington (Richardson 1981, Emmett *et al*., 1997). Waters with anchovy spawning are presently, in general, cold (12–16 °C), of high salinity (33.5–33.7) (Checkley *et al*., 2000), although off the northwest coast, spawning appears to be related to the Columbia River plume (Richardson, 1981; Emmett *et al*., 1997), and these areas often have abundant nutrients, resulting in abundant diatoms and copepods, including *Calanus pacificus.* During El Niño, e.g. in 1983, spawning can occur along much of the NW coast. In general, these are regions with both enhanced nutrient supply and water-column stability (cf. Lasker, 1975).

Juveniles and adult northern anchovy are abundant off California, Oregon, and Washington in spring but decline in abundance during the summer, perhaps due to predation. Consistent with variation of its northern limit, the abundance of the northern anchovy off Oregon and Washington exhibits significant interannual fluctuations, and has increased notably in recent years in Puget Sound, Washington. Regular sampling off the Columbia River since 1998 (every 2 weeks at 12 stations at night; Emmett *et al*., 2006) shows large interannual fluctuations, with peak abundance in April and May and lagging ocean productivity (Peterson and Schwing, 2003) by several years.

*Pacific sardine (*Sardinops sagax*)*

Pacific sardine is presently more abundant than the northern anchovy and, consistent with past fluctuations, has a large range, extending from Canada to Baja California (Fig. 3.2c) (Parrish *et al*., 1989). The Pacific sardine consists of three subpopulations (Gulf of California, not further considered; Baja California Sur Inshore, BCSI; and Central California Offshore, CCO; Smith 2005), although these have not been found to be genetically distinct (Smith, 2005, and references therein). During peak population size, the CCO subpopulation is the largest and adults occur from Baja California to Canada. During low population size, the range of the Pacific sardine contracts and the BCSI subpopulation dominates, with the inshore waters off Baja California perhaps being a refuge (Mais, 1974). Spawning and early development of the CCO population occurs primarily in relatively low

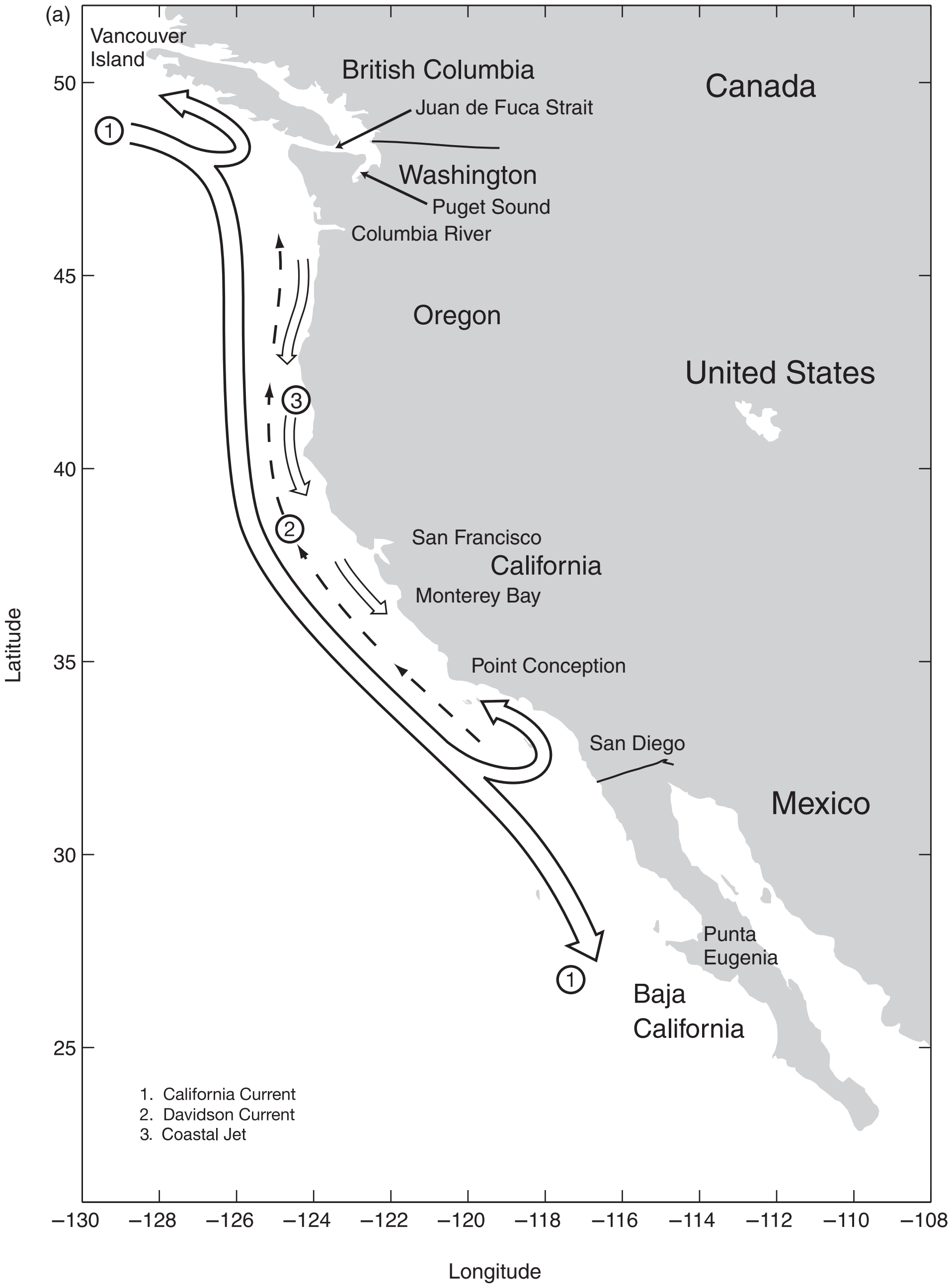


Fig. 3.2. California Current region. (a) Circulation. (b) Distribution of northern anchovy (*Engraulis mordax*). (c) Distribution of Pacific sardine (*Sardinops sagax*). Note that these distributions are the maximal ranges. As discussed in the text, these distributions become smaller at lower population size. (See also Alheit, 2008.)

salinity water at the inshore edge of the California Current off southern and central California and off Baja California (Parrish *et al.*, 1989; Checkley *et al.*, 2000). Spawning has been noted off Oregon and Washington (R. Emmett, unpublished data). Offshore eddies have been hypothesized to be important regions of retention and growth of sardine larvae and juveniles (Logerwell and Smith, 2001). Significant interannual variation occurs in the geographic extent of spawning, extending further offshore during La Niña and being compressed shoreward during El Niño (e.g., Lynn, 2003). Juvenile and adult Pacific sardine occur off California, Oregon, Washington, and Canada, indicating a northward migration from spawning to juvenile nursery to adult feeding areas. Significant variation in sardine production on the decadal scale is explained by variation in open-ocean upwelling forced by wind-stress curl (Rykaczewski and Checkley, 2008).

Sardine migrate annually from spawning grounds off southern California northward to the Pacific Northwest and Canada and occasionally into southeast Alaska. It is

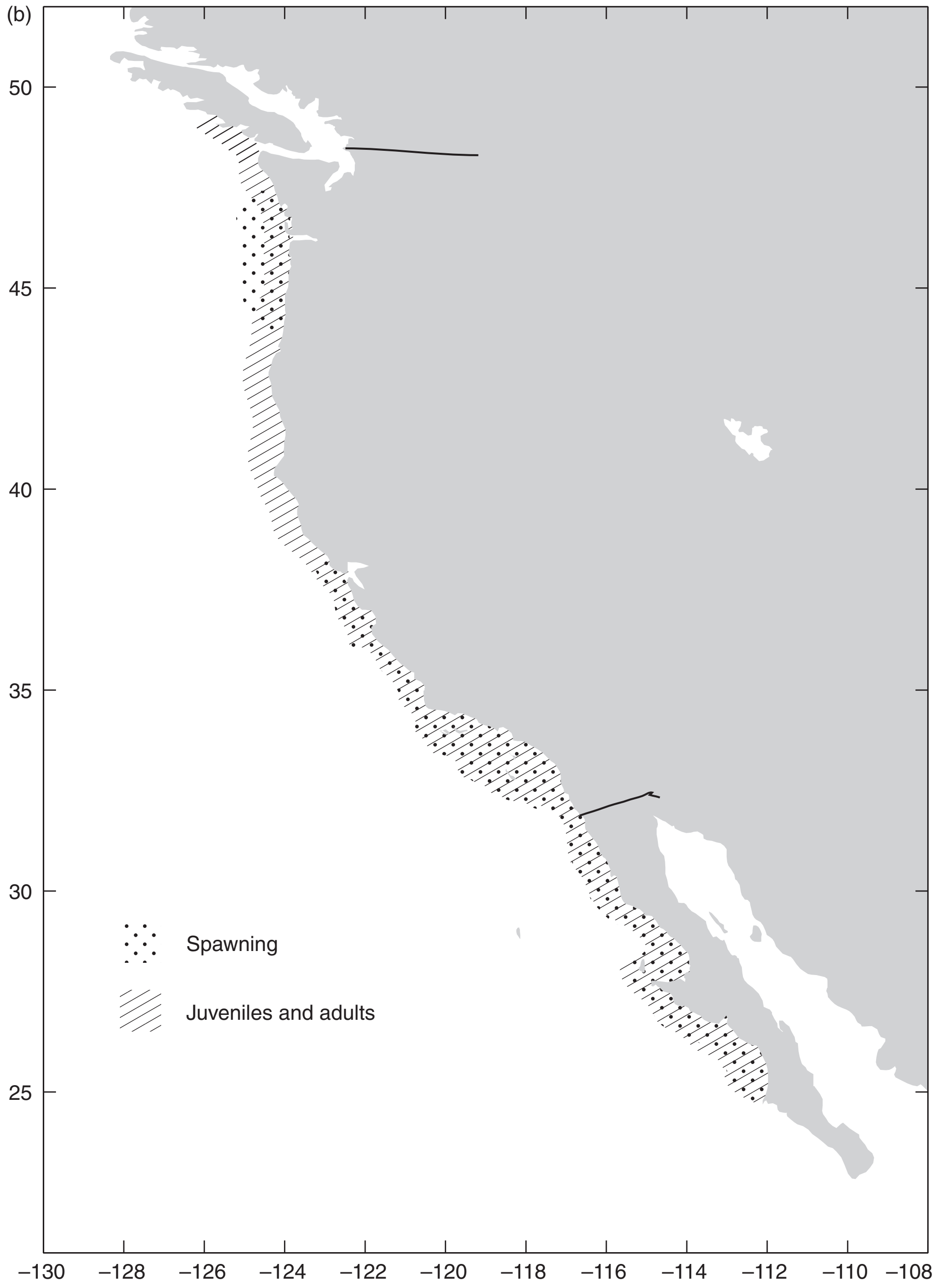


Fig. 3.2 (*cont.*)

generally believed that the northward migration is to spawn and feed, as coastal upwelling in this area results in a ready source of phytoplankton and zooplankton for sardine. Analysis of stomach contents of sardine in Canadian waters indicates an affinity for phytoplankton, primarily diatoms, but there is a definite prevalence of copepods and the eggs and later stages of euphausiids in most years (Emmett *et al.*, 2005; McFarlane *et al.*, 2005).

The mechanism underlying the annual northward movement of sardine is not well understood but the rate of migration may be limited by the rate of northward progression of the local spring and the associated 12 °C isotherm (Emmett *et al.*, 2005; D. Ware, Aquatic Ecosystem Associates, Nanaimo, B.C., Canada, unpublished data). During its annual spring and summer northward expansion, the adult sardine population appears to remain relatively offshore but once it reaches the area of the Columbia River and the mouth of Juan de Fuca Strait there is a tendency to move inshore. Sardine generally arrive off the coast of southwest Vancouver Island by late June and are

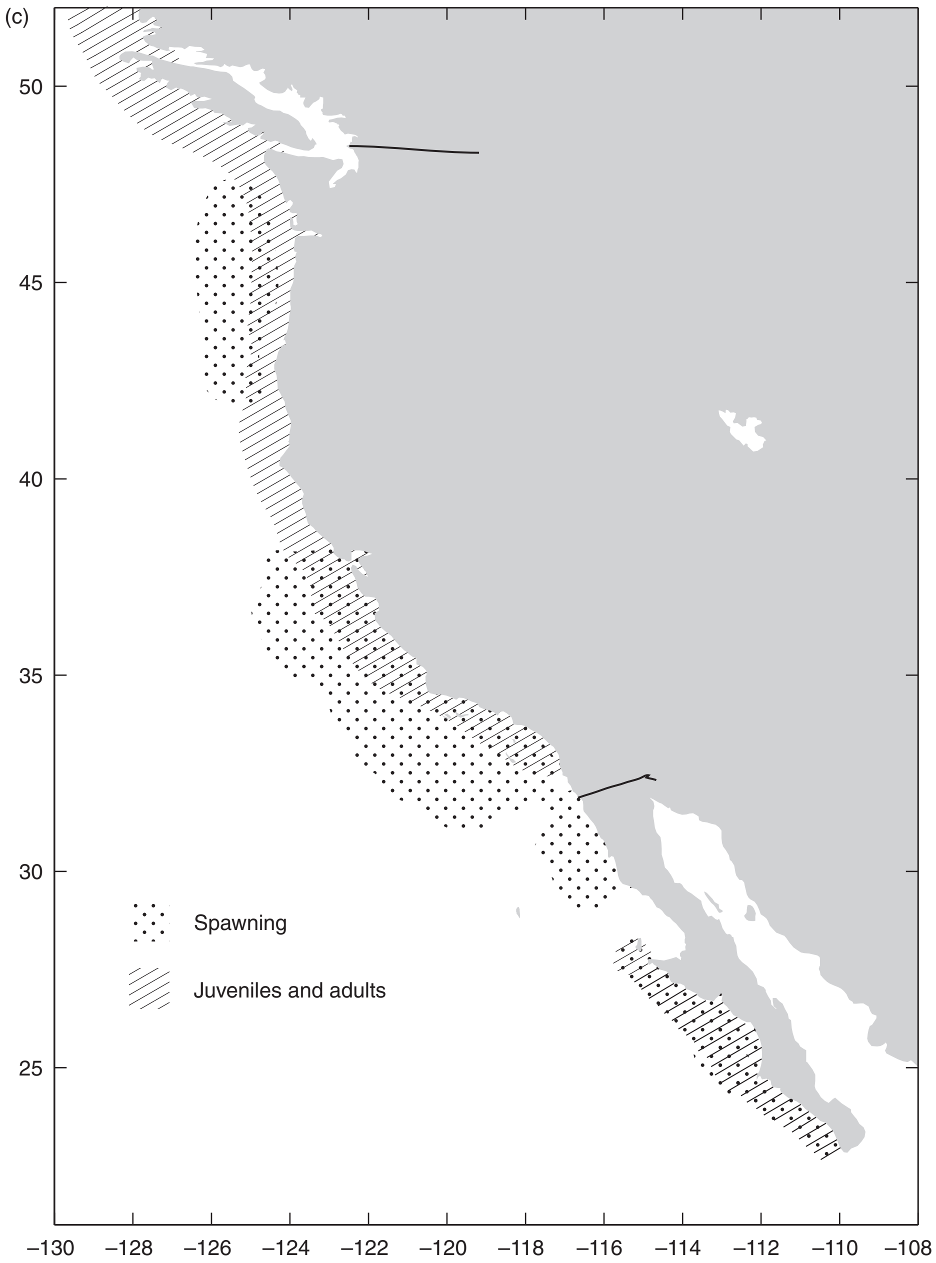


Fig. 3.2 (*cont.*)

frequently found in substantial quantities in the inlets of the west coast of Vancouver Island shortly thereafter, possibly due to the elevated sea surface temperatures and high phytoplankton concentrations. McFarlane *et al.* (2005) found that the northern limit of sardines in Canadian waters was broadly related to the sea surface temperature off the west coast of Vancouver Island and northward into Hecate Strait (53–54° N) during the months of June through August. By October, as sea temperatures begin to cool, sardine begin to move southward again, although 0-age sardine do not appear to migrate but stay in coastal waters.

Canadian waters are occasionally conducive to sardine spawning but in general are too cold. During the warm years associated with intense El Niños, such as in 1997 and 1998, limited spawning occurred off Vancouver Island but the fate of the eggs and any resulting progeny is unknown. Although the habitat for sardine becomes unfavourable in the winter and the bulk of the adult sardine population migrates southward again, both juvenile and adult sardine frequently over-winter in inlets of the west coast of British Columbia, at times (e.g. 2005) mixing with schools of Pacific herring (*Clupea pallasi*).

Generalizations

Analyses of both recent and past (1950–2000) spawning of the northern anchovy and Pacific sardine from Baja California to central California allow the following generalizations. Anchovy tends to spawn in regions of wind-driven coastal upwelling and river runoff, while sardine spawn in more oceanic water, perhaps upwelled due to wind-stress curl and Ekman pumping (Rykaczewski and Checkley, 2008). Both taxa spawn in the upper water column (Curtis *et al*., 2007 and references therein). This results in anchovy and sardine spawning in water of different characteristics and at different times. Anchovy spawn primarily January–March in 12–16 °C, high salinity (> 33.2) water, or in lower salinity water near river plumes. Sardine spawn primarily April–June in water 12–14 °C off California (Checkley *et al*., 2000; Moser *et al*., 2001) and 14–16 °C in May–July off Oregon/Washington (Emmett *et al*., 2005), during periods of large population size, and of lower salinity. Exceptions include spawning during El Niño, when coastally upwelled water is not of high salinity and anchovy spawn in lower salinity water (Checkley *et al*.,2000), and in periods of low sardine abundance, when this species spawns later in the year (summer) and in 14–21°C, high salinity water, primarily in inshore waters off Baja California. At any one time, particularly during a period of low abundance of a species, not all habitat that appears suitable is used for spawning (cf. Smith,1990; Reiss *et al*., in press). Importantly, the CC system does not exhibit a single, normal state but, rather, variability is the norm, with conditions apparently favoring anchovy, sardine, or both at any given time, as indicated in the paleo-oceanographic record (this volume, Chapter 4).

Humboldt Current (HC)

Physical characteristics

The Humboldt Current system extends along Chile, Peru, and Ecuador, including the Galapagos Islands (Fig. 3.3a). The ecosystem is characterized by intense coastal upwelling and high productivity that vary between years, particularly with ENSO,[1] and multi-decadally for the whole Pacific basin (Chavez *et al*., 2003) and for the coastal zone (Purca, 2005).

The main surface current flows northward and has two branches: the Peru Current (PC) and the Peruvian Coastal Current (PCC). Between these the Peru–Chile Undercurrent flows southward carrying equatorial waters below 100 m and extending 250 km offshore (Zuta and Guillén, 1970; Morón, 2000). In addition, the Southern Extension of the Cromwell Current (SECC) flows near the coast below 50 m to 300 m, with high oxygen content.

Four types of surface water masses exist: Cold Coastal Water CCW (14–18 ºC and 34.9–35.0), Surface Subtropical Water SSW (18–27 °C, 35.1–35.7), Surface Equatorial Water SEW (> 20 °C, 33.8–34.8), and Surface Tropical Water (> 25 °C, < 33.8) (Zuta and Guillen, 1970; Guillén, 1983). Northern upwelling is supplied by waters of the SECC between 4 and 8ºS, central upwelling by the PCC, and southern upwelling by the Sub-Antarctic Temperate Water, SATW (< 15 °C, < 34.7) (Morón, 2000).

A recent analysis of time series of salinity to 60 nm offshore and by latitude (O. Morón, personal communication) showed a preponderance of the CCW from 1960 to the start of 1970s; strong influence of SSW from the early 1970s to mid 1980s; and since, dominance of CCW. These findings have important implications for anchovy and sardine dynamics. The oxygen minimum layer is a boundary for the vertical distribution of organisms. During El Niño, the central coast shelf, normally hypoxic or anoxic, becomes oxygenated, due to the strong development of the SECC. A significant increase of macrobenthos biomass and displacement of coastal and demersal species toward the edge of the shelf have been reported (Tarazona, 1990).

Upwelling of the Equatorial Undercurrent occurs in the Galapagos. This may serve as a refuge for small, pelagic fish of the HC during periods of low population size (M. Niquen, unpublished data).

Anchoveta (Engraulis ringens)

Anchoveta is widely distributed along the coast of South America between 04º30 S and 42º30 S (Fig. 3.3b). Off the Peruvian coast, two population units are recognized: the north-central stock, from northern limit to 15º S, and the southern stock, from 15º S to the southern limit of the Peruvian maritime domain (IMARPE, 1973; Pauly and Tsukayama, 1987; Csirke, 1996). Anchoveta is associated with the CCW and sea surface temperatures of 14–22 °C, salinities of 34.9–35.1, and occurs in the upper 70 m. Under average conditions, its concentration is high near the coast in austral spring and summer and low, extending 100 nm offshore, in autumn and winter. During warming events and El Niño, anchoveta is concentrated near the coast and migrates southward.

The northern and central areas (04º30–14º S) contain the main spawning ground. The highest egg concentration is found in the upper 30 m (Santander and de Castillo, 1973). The spawning area is related to the influence of the CCW with salinities between 34.9 and 35.0.

Three levels of carrying capacity for anchoveta have been proposed (Csirke *et al*., 1996): the highest in the 1960s until the collapse in 1972, the lowest from 1973 to 1983, and an intermediate level from 1984 to 1994, updated to 2001 by Ayón *et al*. (2004). During the 1990s, anchoveta had five years (1992–96) of high abundance similar to those of the 1960s, but since then has remained at an ‘‘intermediate’’ level.

Different factors affect spawning and recruitment. El Niño is the most striking of these, impacting the

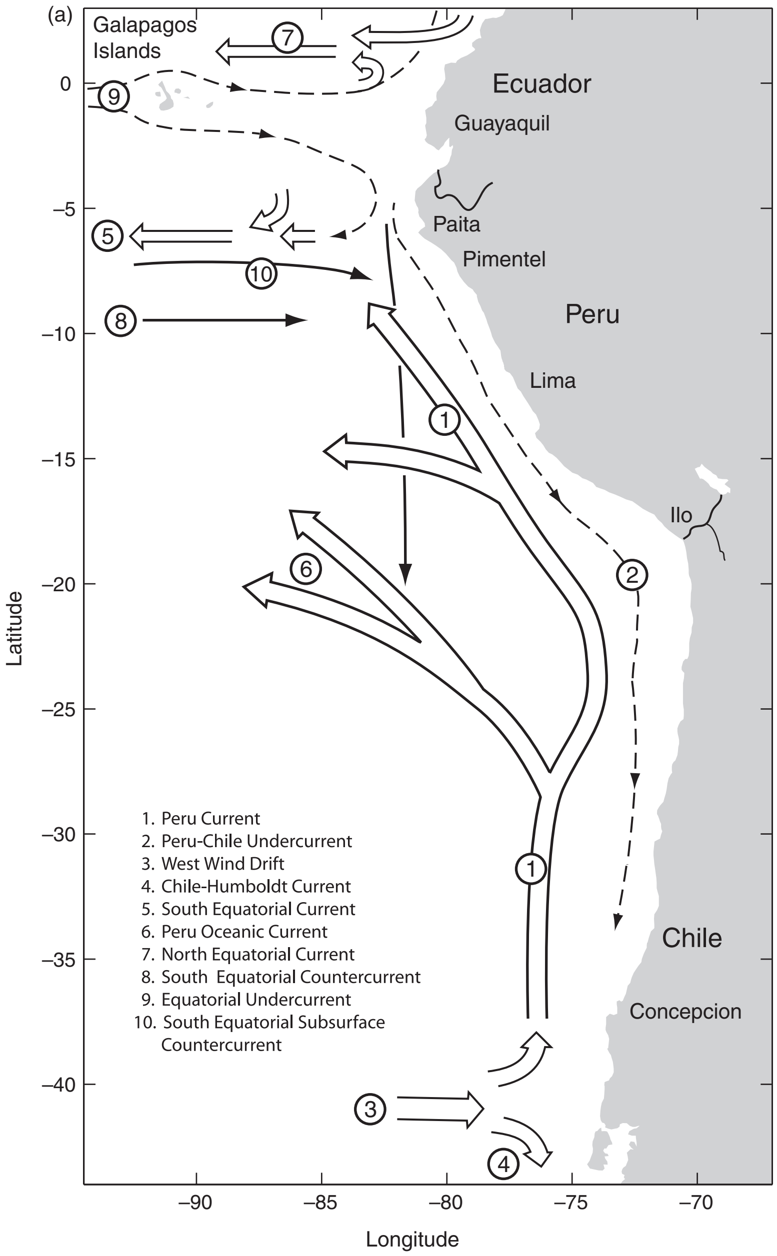
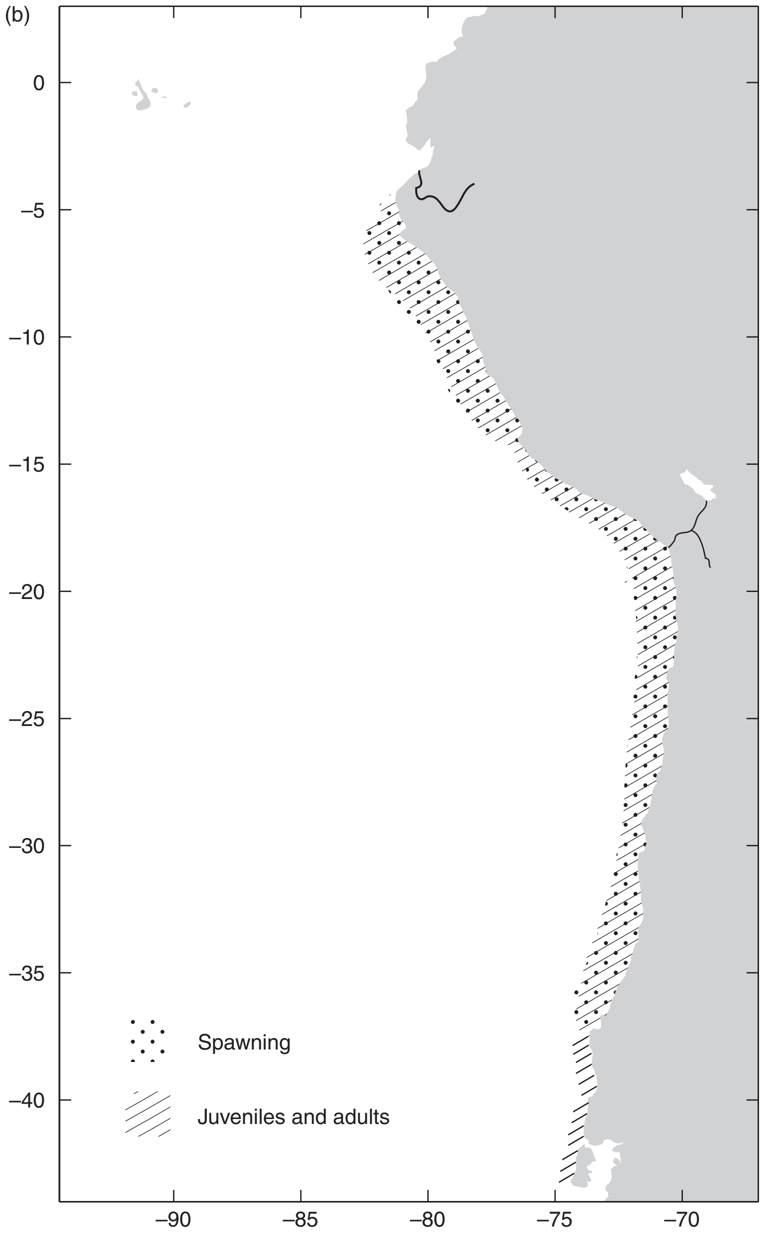


Fig. 3.3. Humboldt Current region. (a) Circulation. (b) Distribution of anchovy (*Engraulis ringens*). (c) Distribution of sardine (*Sardinops sagax*). Note that these distributions are the maximal ranges. As discussed in the text, these distributions become smaller at lower population size. (See also Alheit *et al.*, 2008).

spawning process and eventually changing the main peak from winter–spring to summer and by lowering its intensity (Santander and Zuzunaga, 1984). Long-term changes have also been observed in the extension of spawning areas with increasing abundance. However, after the 1997–98 El Niño, the areas widened and the center of the distribution shifted northward compared with the 1960s. Another factor is the effect of the fishery on spawning biomass and/or recruits.

The feeding and food environment of the anchoveta has been studied for decades. Anchovy larvae feed mainly on phytoplankton, with flagellates as the main item of the diet. As larvae grow, their preference changes to zooplankton (Muck, 1989). Studies of stomach contents of postlarval (juvenile and adult) anchoveta collected during 1953–82 show variation with latitude and distance from the coast. In the north-central region near the coast, it feeds more on phytoplankton but, further offshore, more on zooplankton. In the southern region it feeds more on zooplankton, and this also occurs at a higher temperature (Pauly *et al.,* 1989), probably because of warming associated with a change of water mass. This spatial strategy can help to explain the



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observed long-term variability of zooplankton volumes. In the 1960s, zooplankton volumes were high but diminished with decreasing anchoveta abundance. By the end of the 1980s, both started to recover, but this was more marked in anchoveta than in zooplankton (Ayón *et al*., 2004). Recent analysis suggests that, after the 1980s, anchoveta has been feeding more on zooplankton (P. Espinoza, Instituto del Mar del Perú, personal communication), which could explain why zooplankton abundance has not recovered to the levels observed in the 1960s.

Anchoveta is the prey of higher trophic level species like mackerel and jack mackerel (Muck and Sánchez,1987; Pauly *et al,*. 1987); demersal species like hake, though mainly during warm periods (Sánchez *et al*., 1985; Muck, 1989); seabirds like cormorants, boobies and pelicans (Jahncke and Goya, 1998); and sea mammals (Muck and Fuentes, 1987). When sardine was abundant it preyed on the first life stages of anchoveta. Adult anchoveta cannibalize their own eggs, especially when the population is large (Santander, 1987). Pauly and Soriano (1989) considered that during warm periods, anchoveta eggs and larvae have a higher mortality rate because of the increase of predation by zooplankton and taxa of other trophic levels, including anchoveta.

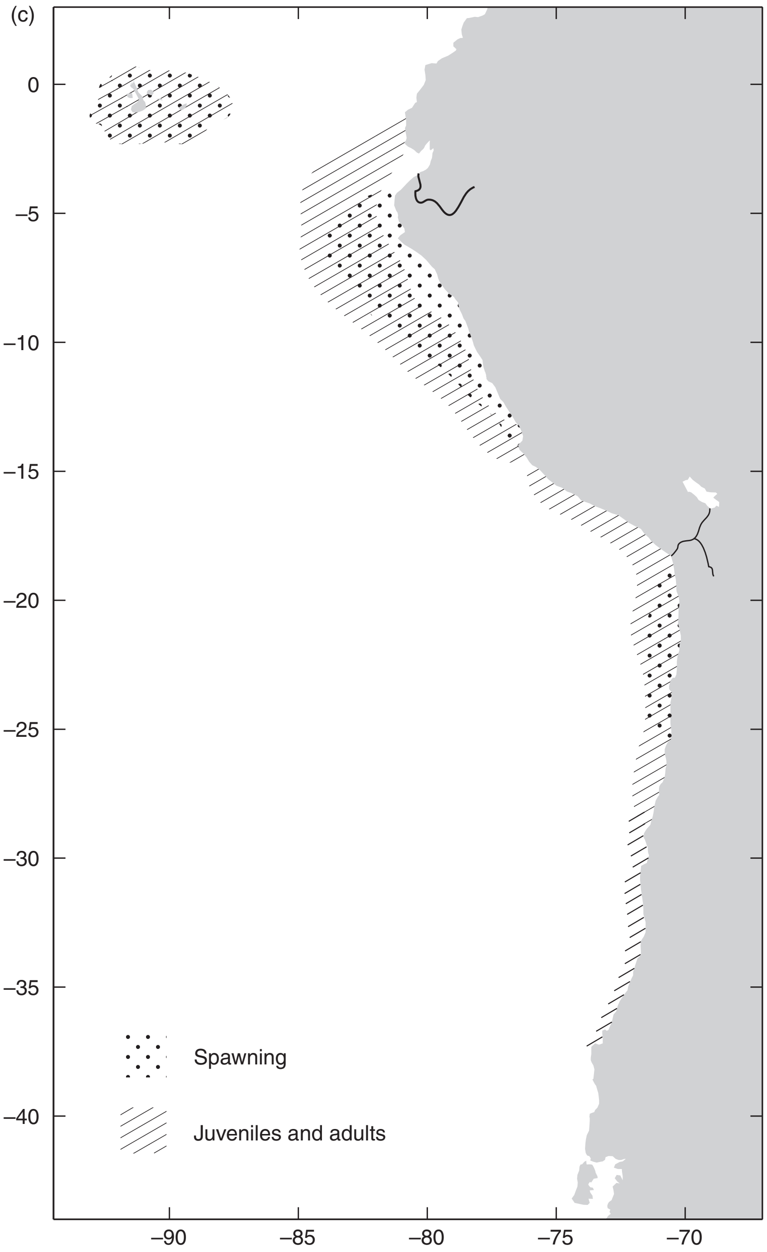

Fig. 3.3 (*cont.*)

Sardine (Sardinops sagax)

Sardine has a wide distribution in the SE Pacific, including off Peru in SSW with temperatures of 19–22 °C and salinities of 35.0–35.3 (Santander and de Castillo, 1981) (Fig. 3.3c). In general, the adult distribution is far offshore of the intense upwelling zone, although juveniles are distributed in the same areas as anchoveta. This species extends its area of distribution during warm periods and El Niño, as in 1982–83, when it occurred near the coast in high densities and in the southern region, because of the southward advection of SSW. Sardine occur as far south as 42° S off Chile (Parrish *et al*., 1989).

The increase of the sardine population started after the decline of anchoveta in the start of the 1970s. The period of high abundance coincided with the period of major influence of SSW in the first 60 nm offshore, probably favoring good recruitment. By the start of the 1990s, sardine entered into a new period of low abundance (Csirke *et al*., 1996) that coincided with less SSW near the coast.

The spawning area of sardine varies greatly with distance from the coast and with latitude. Between 1966 and 1971, spawning was poor and restricted to the northern areas. It expanded southward after the anchoveta decline. Major spawning concentrations occurred in SSW

(Santander and Flores, 1983) near the coast after migrating from the equatorial zone (Santander and Zuzunaga, 1984; Arntz and Fahrbach, 1996;). After the 1997–98 El Niño, sardine spawning diminished drastically and has been sparse and restricted to areas off Pimentel (P. Ayón, unpublished data).

*Jack mackerel (*Trachurus murphyi*) and mackerel (*Scomber japonicus*)*

Jack mackerel (*Trachurus murphyi*) and mackerel (*Scomber japonicus*, also called chub mackerel) are transboundary species widely distributed off Peru and Chile (Serra, 1983; Arcos *et al*., 2001 and references therein;). Both species are frequently caught in the same areas and associated with SSW (Tsukayama, 1982, Santander and Zuzunaga, 1984), although other authors (Santander and Flores, 1983) consider that mackerel is also associated with the SEW and jack mackerel was probably related to the SECC with high oxygen content. Before the 1990s, the major concentrations off Peru were found north of 11° S, and mainly north of 7° S, between depths of 50 and 150 m. However, after those years, their concentrations were restricted south of 14° S. Mackerel has been reported off Chile at 45° S, but with a typical southern boundary of 25° S, while jack mackerel has been observed at 52° S, with a large fishery at 35–38° S, off Talcuhuano (Serra 1983).

The main spawning area of jack mackerel off Peru is the frontal zone of 14–18° S (Santander and Flores, 1983), where upwelling CCW and SSW meet 100–150 nm offshore, with surface temperatures higher that 18°C and oxygen content higher than 5 ml l^{-1}. In this area, larvae are displaced offshore by the Ekman transport. Spawning has also been observed in other places of the Peruvian coast but with low concentrations of eggs. Jack mackerel occurs off Chile between the Peru border and 25° S and off Talcuhuano (Serra, 1983). Spawning occurs January–May. Jack mackerel is known to migrate to spawn extensively in oceanic waters off Chile, as far west as New Zealand, and return to the coastal nursery and adult feeding areas, where the fishery occurs (Arcos *et al*., 2001).

Mackerel spawn between August and March with a peak in the austral summer and, under average conditions, off the north-central region of Peru. During El Niño, spawning increases and higher concentrations of eggs and larvae occur (Santander and Flores, 1982), probably associated with SSW. Mackerel spawn off Chile primarily near the border with Peru and, less so, off Talcahuano (Serra, 1983).

Benguela Current (BC)

Physical characteristics

The waters off southern Africa are dominated by the southward-flowing Agulhas Current on the east and south coasts, the northward flowing Benguela Current on the west coast, and coastal upwelling, particularly on the west coast (Fig. 3.4a). The Agulhas turns eastward at the southern tip of Africa, forming the Agulhas Retroflection and Agulhas Return Current. The Benguela Current extends from the SW tip of Africa (34° S) to the Angola–Benguela front, near 16° S. The Benguela Current has a well-defined mean flow confined mostly near the continent, and a more variable, transient flow on its western side. The latter is dominated by large eddies, while the former includes the Benguela Jet off Cape Town. Upwelling is notable in isolated locations off the south and west coasts, particularly adjacent to Cape Town, south of the Orange River, between Luderitz and Walvis Bay, and the north coast of Namibia. Persistent, intense upwelling of Luderitz, and its associated cold temperatures and offshore transport, preclude spawning by small, pelagic fish and thus forms a natural, biogeographic boundary.

*Anchovy (*Engraulis encrasicolus*) and sardine (Sardinops sagax)*

Small pelagic fish have been relatively well studied in the southern Benguela off South Africa. The anchovy (*Engraulis encrasicolus*) and sardine (*Sardinops sagax*) habitat in southern Africa extends from Baia dos Tigres in southern Angola (14° S, 10° E), down the west coast to Cape Town, across the Agulhas Bank, and to the Natal Bight just north of Durban, a distance of approximately 5000 km, with a notable gap in the central Benguela region in the vicinity of the Luderitz upwelling cell (Fig. 3.4b). Boundaries at the northern and eastern margins occur when temperatures rise above 22–24 °C, at the Angola–Benguela Frontal region and on the east coast, in both cases where the continental shelf narrows and warm water approaches close inshore.

The fish habitat is restricted to the continental shelf and only extends a short distance beyond it in a few locations with strong advection, such as the southern tip of the Agulhas Bank. There are no known extensions into the warm, oligotrophic ocean interior. The strong Agulhas Current on the east coast, the jet current on the west coast, and low phytoplankton concentrations offshore on both coasts largely limit the habitat to the continental shelf. Few epipelagic fish occur in the vicinity of the powerful upwelling cell at Luderitz, where cold water, high turbulence, and offshore transport prevail.

Elsewhere, the cool water coincides with enriched phytoplankton concentrations (from DeMarcq *et al*., 2007). This extends far offshore near the Angola–Benguela front, associated with strong offshore displacement. The width of the zone of enriched plankton decreases at Luderitz (27° S), then widens on the South African west coast as far as 33° S before narrowing again. While surface concentrations of chl *a* decline on the Agulhas Bank, there are extensions offshore

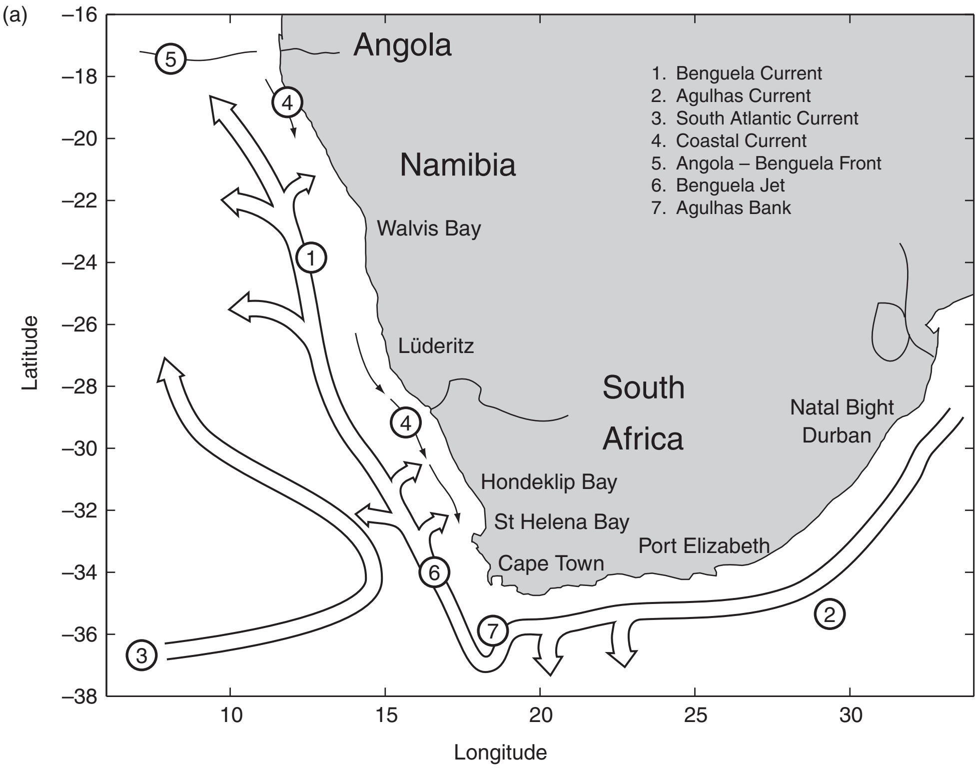

Fig. 3.4. Benguela Current region. (a) Distribution of anchovy (*Engraulis encrasicolus*). (c) Distribution of sardine (*Sardinops sagax*).

associated with a subsurface ridge at 22° E and at 26° E, where the Agulhas Current diverges from the coastline. A narrow belt of cool, phytoplankton-rich water extends up the east coast in winter, with a spawning microhabitat, consisting of a wider shelf and upwelling in the Natal Bight (Lutjeharms *et al*., 2000) in the extreme east. The east coast is the location of the famous "Sardine Run," which occurs in June–July each year and comprises about 3%–13% of the total biomass in the southern Benguela region.

Mesozooplankton concentrations are moderate to high throughout the Benguela upwelling system and peak on the west coast near St Helena Bay (33° S) and just downstream (NW) from the Luderitz upwelling cell at 23–25° S (Hutchings *et al*., 1991) with declining levels in warmer water of the boundary zones. Pelagic fish therefore migrate against food gradients to spawn in locations upstream of the main nursery grounds. These costly migrations may account for the poor fish yield relative to primary productivity in the Benguela relative to the Humboldt Current system (Hutchings, 1992; Ware 1992).

Anchovy eggs are found in spring and early summer predominantly over the Agulhas Bank between Cape Point and Port Elizabeth (Fig. 3.4b), although they are reported from the east coast as far north as Durban and also off the west coast during years of anomalously warm water (van der Lingen and Huggett, 2003). An eastward shift in anchovy egg (and spawner) distributions from being predominantly to the west of Cape Agulhas to predominantly to the east occurred in 1996 and has persisted since (van der Lingen *et al*., 2002). Sardine eggs occur around the South African coast from Hondeklip Bay (32° S) to Durban, principally during summer off the west and/or south coasts but also in winter off the east coast during the annual migration known as the sardine run (Connell, 2001) (Fig. 3.4c). Both the west and the south coasts have been the dominant site of summer spawning by sardine during different periods, with a recent shift from the west coast over the period 1994–2000 to the south coast (to the east of Cape Agulhas) from 2001 onwards (van der Lingen *et al*,. 2005b). Winter spawning off the central Agulhas Bank may be linked to a phytoplankton surface maximum in the austral autumn (March to June) (Demarcq *et al*., 2007).

Spawning habitat for both species has been characterized in terms of a variety of environmental variables, both physical (e.g. SST, salinity, water depth, mixed layer depth and current speed) and biological (*e.g*., phytoplankton and zooplankton biomass and production) using co-inertia analysis, single parameter quotient (SPQ) analysis, and temperature-salinity plots (Twatwa *et al*., 2005, van der Lingen, 2005). These studies indicate that anchovy egg habitat is characterized by a narrower range for many environmental variables than is sardine egg habitat, and that anchovy eggs are found in waters of 17–21 °C and sardine at 15–21 °C, with other variables being roughly similar for both species.

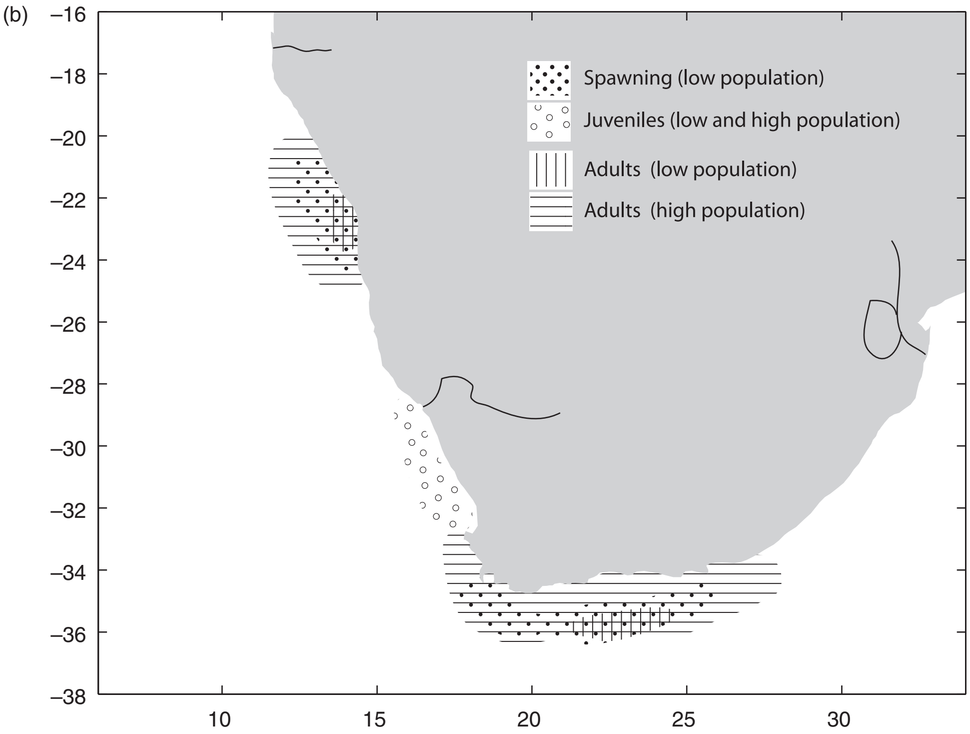

Fig. 3.4 (*cont.*)

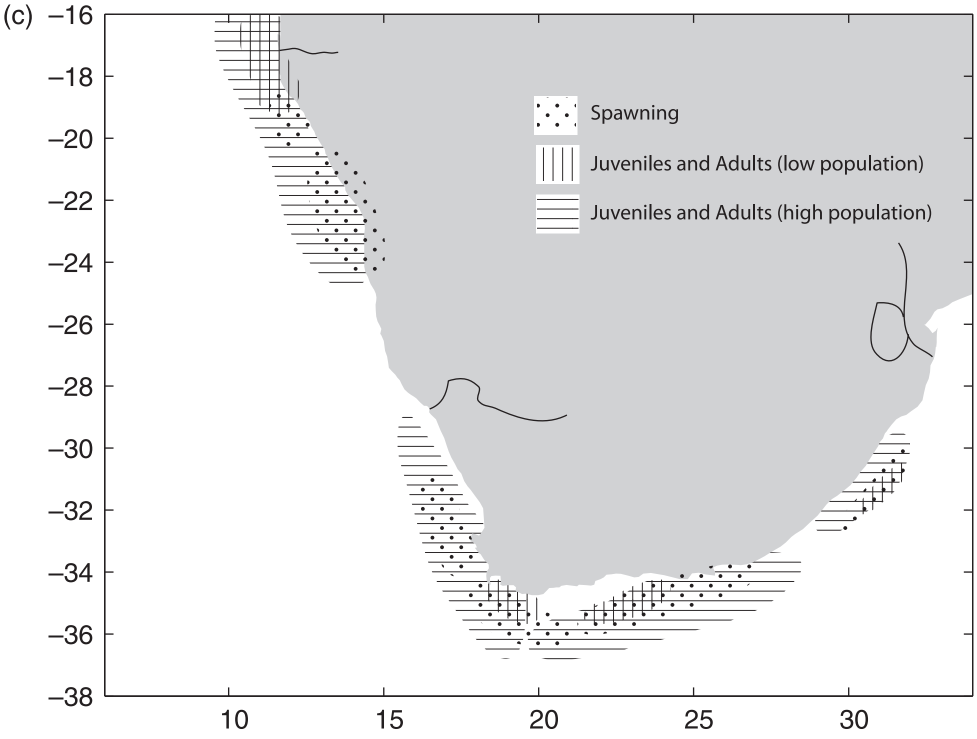

Fig. 3.4 (*cont.*)

Anchovy spawning was significantly related to temperature, salinity, phytoplankton and zooplankton biomass, but not to current speed, wind speed, mixed-layer depth, and zooplankton production. Sardine spawning was significantly related to water depth and zooplankton biomass, but not to other variables. The recent shift eastwards in spawning habitat of sardine was accompanied by an upward shift in spawning temperature to for 22–24 °C in November (summer). Minimum surface temperature thresholds for spawning of 13–14 °C characterize the west coast between 22° S and 33° S, which, combined with strong offshore advection of buoyant eggs, preclude this area as a spawning habitat. However, the broad shelf on the west coast of South Africa is a suitable nursery area for juveniles of both species, indicating tolerance to both warm and cool waters at different life stages.

Eggs and resultant larvae of both species spawned on the South African coast are transported to the west coast nursery area by a shelf-edge jet current (van der Lingen and Huggett, 2003). Anchovy larva size increases progressively both alongshore (equatorward) and cross-shelf, indicating transport at the shelf edge and shoreward movement of larvae as they grow. The shoreward movement of pre-recruits to the nearshore habitat against the predominant offshore Ekman drift is currently subject to analysis and modeling exercises (C. Parada, University of Washington, Seatttle, Washington, USA, unpublished data), as both active and passive transport are required to move young fish shorewards in sufficient numbers to account for observed recruitment. Active directed swimming by a 20 mm larva at one body length s^{-1} for 12 hours day^{-1} would require 105 days to swim the 180 km from offshore of the continental shelf to the nearshore region (van der Lingen *et al*., 2006). A decline in upwelling–favorable wind stress in the austral autumn (March–May) may facilitate this movement, and vertical migration of larvae to below the Ekman layer would minimize offshore transport during strong southerly winds in summer months. Single-parameter quotient analysis for pre-recruits and early juveniles of 20–40 mm SL (van der Lingen, unpublished data) indicates that sardine are found in warmer waters than are anchovy, offshore on the west coast and on the Agulhas Bank.

The juvenile habitat was most recently described by Barange *et al.* (1999). Recruits of both species are found primarily off the west and southwest coasts, although some south coast recruitment of sardine has been observed, but generally much less than that observed off the west coast (J.C. Coetzee, Marine and Coastal Management, Cape Town, South Africa, personal communication). Juveniles migrate, against a food gradient, to the south coast, where they metamorphose and, at the end of their first (anchovy) or second (sardine) year, spawn. Low oxygen occurs in a bottom mixed layer close inshore along the entire west coast, reaching a maximum from February to May each year, but it does not appear to geographically restrict the habitat of pelagic fish, as they occupy the well-oxygenated and productive upper mixed layer and the pycnocline.

The geographic characterization of adult distribution in the southern Benguela was most recently performed also by Barange *et al.* (1999). Anchovy are found over the Agulhas Bank off the south coast whereas adult sardine have been found off both the south and west coasts during different periods. There has been a noticeable eastward shift in distributions of anchovy and particularly sardine over the past decade (van der Lingen *et al*., 2005b, Fairweather *et al*., 2006).

Much less is documented on the life history stages of pelagic fish off Namibia. There have, until recently, been few studies of the early life history stages of pelagic fish in the northern region (e.g. Stenevik *et al*., 2001). Despite the massive decline in biomass of both species compared to historical population sizes (Griffiths *et al*., 2004), both sardine and anchovy still spawn in localized areas in similar habitats, although within a much smaller range and with much lower densities than previously observed. Spawning of both species occurs in summer and autumn towards the Angola–Benguela frontal area at 15–20° S at 19–21 °C, and older sardine further southwards on the central Namibian shelf at 20–23° S and during austral spring in cooler upwelled water of 14–17 °C. Juveniles of both species occur close inshore in the central–northern Namibian shelf (18–22° S). Low dissolved oxygen concentration influences the distributions of anchovy and sardine eggs and larvae, and may impact their recruitment success (Ekau and Verheye, 2005). A combination of a decaying algal blooms and accumulated oxygen debt can result in hydrogen sulfide eruptions which result in mass mortalities, although pelagic fish are less affected than rock lobster or inshore species such as mullet (Bakun and Weeks, 2004). The collapse of the Namibian sardine population, together with the eastward shift of southern Benguela sardine to the Agulhas Bank, has meant that there is a dearth of sardine in the entire cool-water upwelling regime of the Benguela system from Cape Point to Cape Frio, despite high phytoplankton and zooplankton levels and productivity.

Population changes are dramatic in the Benguela system, with contrasting trends in the northern and southern populations (this volume, Chapter 9). In the southern Benguela, peak annual catches of sardine (400 000 tonne) occurred in 1961–2, with a VPA[2]-estimated biomass of 2 million tonne (Butterworth, 1983). As sardine declined, emphasis shifted to anchovy and catch levels were maintained at 300–400 000 tonnes for the next 30 years, but dominated by anchovy. Sardine recovered in the period 1984–2003, peaking at approximately 4 million tonnes biomass. Anchovy fluctuated through the 1990s, but good recruitment in 2000 and 2001 led to record high population levels of both species. In the northern Benguela, sardine dominated the catches, peaking at 1.3 million tonnes, from a VPA-estimated population biomass of 6–7 million tonnes (Butterworth, 1983). A steep decline saw a shift to target anchovy and juvenile horse mackerel and a midwater fishery for horse mackerel developed. Fishing effort was directed to anchovy, perceived to be a direct competitor of sardine, but after a few years anchovy biomass and catches decreased to low levels and horse mackerel became the dominant planktivore in the northern Benguela. Sardine started improving in the early 1990s, but a combination of a huge low oxygen event in 1994, a Benguela Niño in 1995, and sustained warming in the northern Benguela has continued to suppress sardine biomass in the northern Benguela, in stark contrast to the southern Benguela (Boyer and Hampton, 2001, Boyer *et al*., 2001). There was some speculation that sardine moved into the southern Benguela following poor environmental conditions in the north, but no fish were detected at intermediate localities during the past decade. Ironically, some fish were caught in southern Angola in Namibian purse seines in 1994 and 1995, indicating a portion of the stock was still present in the northern portion of the Angola–Benguela frontal region, despite the warm water. Most of the fish were shifted southwards several degrees of latitude, making them more available to the purse-seine fleet based at Walvis Bay (Boyer *et al*., 2001). Speculation about the role of large carnivorous jellyfish in predation of fish eggs and larvae continue, but no historical time series of jellyfish abundance exists. Alternatively, predation by horse mackerel on sardine eggs and larvae and enhanced mortality of adult sardine from other predators, such as seals, may be keeping sardine repressed, when it is limited in its range, in addition to the warm water effects of diminished plankton on the nursery grounds. Fishing pressure has been severely limited in Namibia, yet despite these low levels of effort, fishing mortality may still be a significant part of the total mortality of sardine, which has still not recovered.

Northeast Atlantic (NA)

Physical characteristics

The Northeast Atlantic (European Atlantic and Canary Current) is a more complex oceanographic region than other major eastern boundary systems, mainly due to the greater irregularity of the European and northwest African coastline and bathymetry (Fig. 3.5a). The largely meridional orientation of the coast is interrupted by significant zonal stretches in the Bay of Biscay and the Gulf of Cadiz. Also, the Straits of Gibraltar form a salient topographic feature where dense Mediterranean water enters from a shallow sill (ca. 300 m) in the Gulf of Cadiz and rapidly sinks to below 1000 m with a profound impact to slope dynamics and regional circulation. The dominant offshore sources of water in the NA are two eastward flowing basin-scale currents, both transporting North Atlantic Central Water (NACW, 8–18 °C, 35.2–36.7): the North Atlantic Current (NAC) at the north of Iberia (48–53° N), with a branch flowing into the Bay of Biscay, and the Azores Current (AC) at the south of Iberia (34–35° N), with its northerly edge affecting coastal circulation off western Iberia and its southerly component feeding the Canary Current. Some exchange between the two (NAS and AC) is enabled by the broad, slow, generally southward-flowing Portugal Current. Cape Blanc (21° N), on northwest Africa, has NACW to the north and South Atlantic Central Water (8–18 °C, 34.7–36.3) to the south (Sverdrup *et al*., 1960). These features are major contributors to a complex and variable circulation system onto which are superimposed multi-scale seasonal variations in atmospheric forcing, heating, and input of buoyancy through river discharges (e.g. Hernandez-Leon *et al*., 2007 and references therein; Relvas *et al*., 2007).

Given that sardine and anchovy in the NA are almost exclusively constrained within the continental shelf (with the bulk of both species in the Iberian Peninsula being found at the inner shelf and only juvenile anchovy in the Bay of Biscay having a clearly oceanic phase), shelf area and coastal circulation are important physical characteristics of their habitat. Shelf width is generally narrow off the Iberian Peninsula but becomes progressively wider at the French coast. Off western Iberia, the Iberian Poleward Current (IPC), subsurface and density driven, is a dominant feature of mesoscale circulation outside the summer upwelling season, flowing northwards along the shelf edge with warmer, less saline and oligotrophic water (Peliz *et al*., 2005). Outside the season of upwelling, the IPC has been shown to interact with the Ekman layer, enriched by river runoff off northern Portugal, creating a barrier to offshore advection of eggs and larvae (Santos *et al*., 2004). During the upwelling season (April–September), the surface signature of the IPC is lost but there are recent indications that it may persist as a subsurface poleward current (Relvas *et al*., 2007). Off northern Spain, the shelf is narrow and circulation controlled by local features, such as small river plumes, local wind-induced upwelling, and capes, bays, and deep canyons. The main hydrographic feature on the shelf is the variable extension of the IPC off northern Spain, creating fronts parallel to the coast, reducing cross-shelf fluxes, and fronts perpendicular to the coast as the IPC advances eastwards off the north Iberian coast (González-Quirós *et al*., 2004; Llope *et al*., 2006). Off France, the shelf hydrography is predominantly under the influence of river runoff from the Loire and Gironde but also from the Adour, which flows in front of the Cap Breton Canyon, an important area for anchovy and sardine

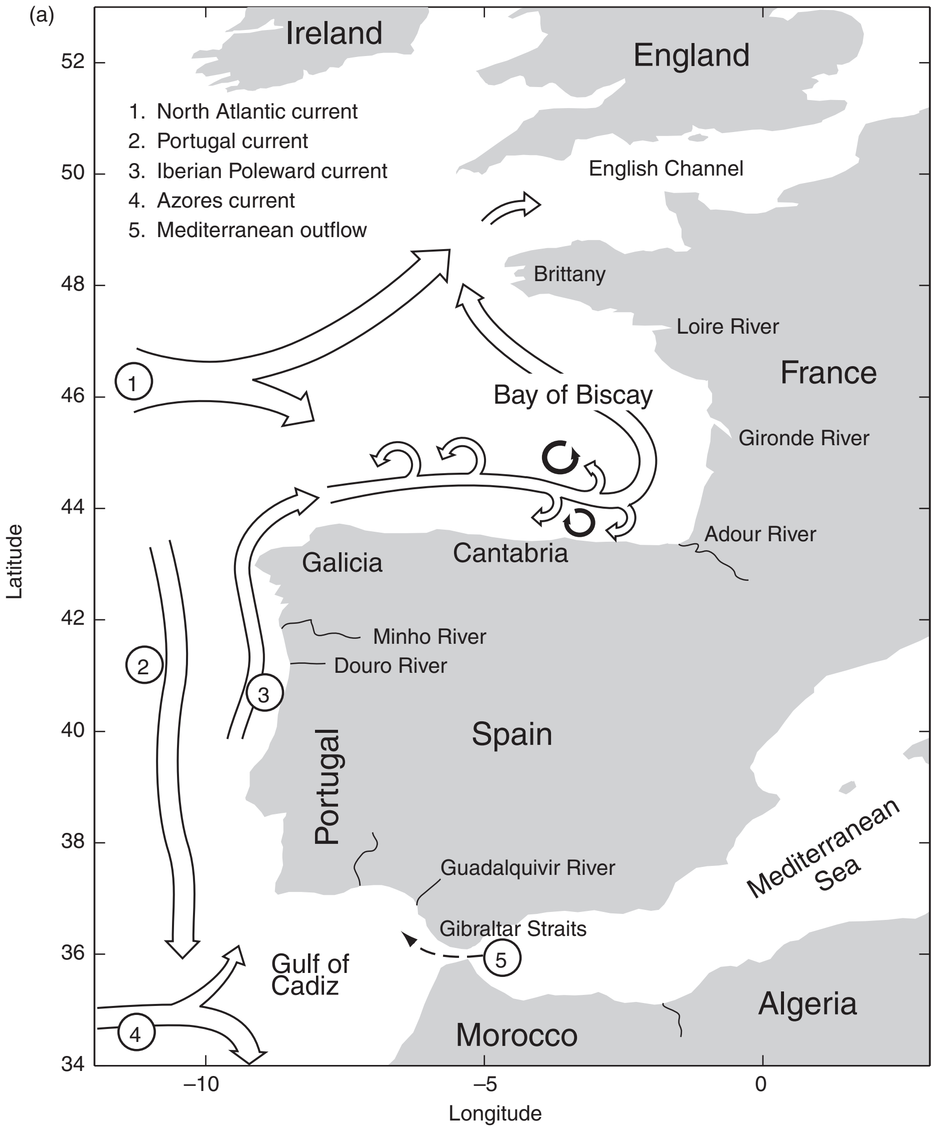

Fig. 3.5. Northeast Atlantic region. (a) Circulation. (b) Distribution of anchovy (*Engraulis encrasicolus*). (c) Distribution of sardine (*Sardina pilchardus*). Note that these distributions are the maximal ranges. As discussed in the text, these distributions become smaller at lower population size.

spawning. Wind-driven upwelling partially controls primary production and offshore transport along the coast north of the Adour river in spring. The IPC, which flows in winter along the northern coast of Spain, turns counterclockwise in the south-western part of the Bay of Biscay and flows northward (Pingree and Le Cann, 1990). At the shelf break, large amplitude internal waves can result in the vertical pumping of sub-pycnocline water, which can reach the surface. These colder and productive waters can be directly observed via satellite, for they generate frontal structures at the surface (Bardey *et al*., 1999). Off the shelf, hydrography is characterized by intense mesoscale activity, with cyclonic and anticyclonic eddies (Pingree and Le Cann, 1992; van Aken, 2002). This ensemble of oceanic features results in a mosaic of potential habitats for anchovy and sardine in the Bay of Biscay (Koutsikopoulos and Le Cann, 1996).

Bay of Biscay anchovy (Engraulis encrasicolus)

The main spawning areas of the Bay of Biscay anchovy are the Gironde and Adour river plumes, the smaller but abundant Cantabrian river plumes, shelf edge fronts, and oceanic eddies (Fig. 3.5b) (Motos *et al*., 1996, 2004; ICES 2004; Sagarminaga *et al*., 2004; Bellier *et al*., 2007; Ibaibarriaga *et al*., 2007). All these are recurrent features where the potential for high biological production exists (Valencia *et al*., 2004). Spawning starts at low rates in the southeast corner of the Bay of Biscay and extends to most of the southeast Bay of Biscay, with two consistent centers: the coastal region in front of the Gironde estuary and the shelf,

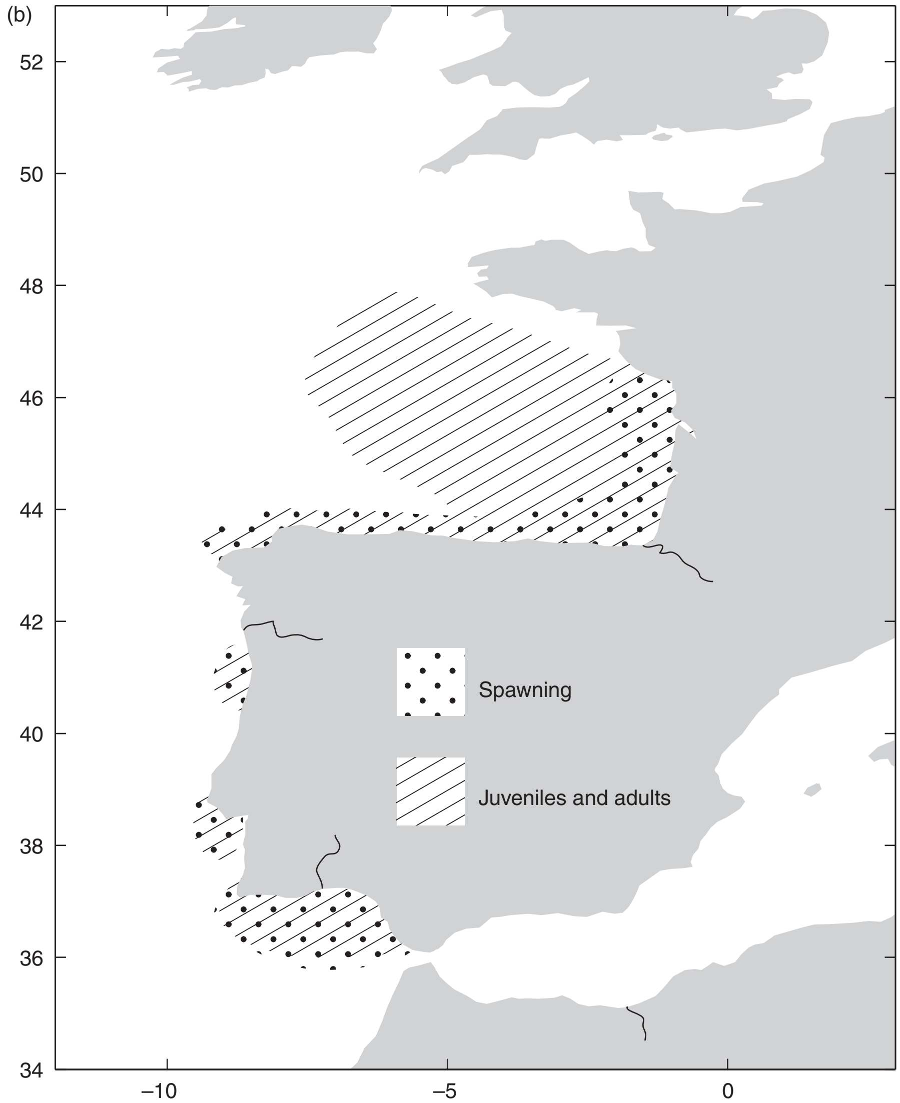

Fig. 3.5 (*cont.*)

shelf break and oceanic regions in the southernmost Bay. In June, the coastal and oceanic spawning regions appear well separated. During the summer, spawning is scattered all along the shelf and close to the shelf break in northern areas. Moreover, some authors have suggested that coastal and oceanic regions are used by different components of the anchovy population. One-year old anchovy spawn in coastal areas, whereas two- or more year old individuals are in oceanic areas close to or beyond the shelf (Massé, 1996; Motos *et al*., 1996; Uriarte *et al*., 1996; Vaz and Petitgas, 2002). Macroscopic maturity studies conducted by Lucio and Uriarte (1990) showed that smallest anchovy reach maturity slightly later than bigger individuals, consistent with younger fish spawning in coastal areas and slightly later than older fish at the shelf break and oceanic areas.

The spawning season of the Bay of Biscay anchovy population begins in mid March, triggered by the warming of surface waters, and extends to August with a peak in May and June, when the maximum rate of warming and the onset of stratification occur (Motos *et al*., 1996).

Irigoien *et al*. (2005) characterized the environmental and hydrographic conditions of the realized spawning habitat of anchovy using single quotient analysis and bi-variate plots. The main variables used for those analyses were sea surface temperature (SST) and sea surface salinity (SSS). Anchovy eggs are present in warm waters (15–19 °C) with low salinity (<35). Instead of considering the absolute values of SST and SSS, the anomalies of SST and SSS indicate a preference for a combination of both variables with respect to the average situation: either warmer waters with lower salinities or colder water with higher salinities. These two situations may represent the two main spawning sites: the Gironde river plume in the north and the shelf break and oceanic regions in the south, respectively. Ibaibarriaga

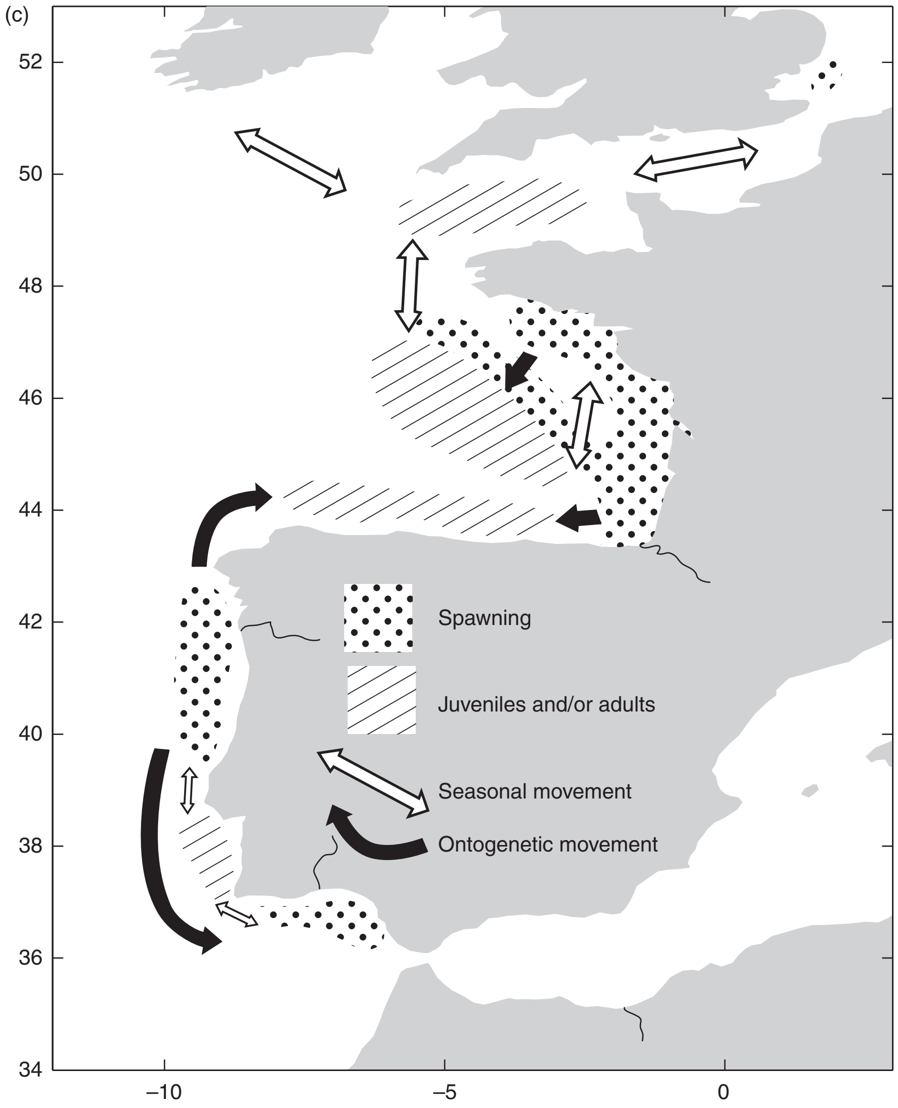

Fig. 3.5 (*cont.*)

et al. (2005) use generalized additive models (GAMs), including a bivariate smoothing of SST and SSS, to model the realized egg production in space. Planque *et al.* (2007) go a step further and uses GAMs on presence/absence of CUFES (Continuous Underway Fish Egg Sampler, Checkley *et al.*, 1997) egg abundance to predict the anchovy potential spawning habitat as a function of environmental variables derived from hydrological model simulations. The best predictor was bottom temperature, followed by surface temperature and mixed-layer depth. Surface and bottom salinity were not significant. Even if potential habitat can be characterized in terms of environmental and hydrographic variables, its relationship to realized and successful habitats will depend on additional factors, such as the population abundance, and the age structure and the environmental and hydrographic conditions after spawning. For instance, it is well known that the anchovy spatial distribution changes depending on the overall level of the population. In years with high adult abundances, eggs cover most of the sampling area, going well beyond the habitat predicted from hydrological conditions, whereas in years with low adult abundance eggs are found in discrete aggregations restricted to the more favorable sites. Uriarte *et al.* (1996) and Somarakis *et al.* (2004) show a linear relationship between the positive area and the total spawning biomass for anchovy. Similar relationships have been observed for anchovy and sardine in the CC (Reiss *et al.*, in press).

After spawning, anchovy larvae first appear in April and are generally present until August. In June, young larvae are found in the middle French shelf, whereas older larvae are found in the southeastern area, on the Cantabrian shelf, and in oceanic waters. This age gradient could be due to advection, due to NE winds, preferential areas, or their combination (Etxebeste, E., AZTI, San Sebastian, Spain, pers. commun.).

Larvae metamorphoze into juveniles at approximately 30–40 days of age and these can be found from July to November. Until 1998, information on the distribution of juvenile anchovy was obtained only from the fishermen that use them as live bait for tuna fishing in summer and early autumn. However, since the pilot surveys conducted in 1998 and 1999 (Uriarte *et al*., 2001), regular autumn surveys targeting anchovy juveniles have taken place (ICES, 2005). Early juveniles are found mainly offshore, beyond the Cantabrian and French shelves, whereas older juveniles are found on the shelf and near the Gironde. The lack of a significant difference in larva growth between areas (Etxebeste, L., pers. commun.) is consistent with the hypothesis of Uriarte *et al.* (2001) that larvae are advected off the shelf and juveniles return to coastal zones to overwinter. Data from the commercial fishery (Uriarte *et al*.,1996 and references therein) support the idea that in October and November juveniles can be found all along the Cantabrian and French coasts. In addition, the hydrological conditions of the Bay of Biscay in autumn are characterized by downwelling, high turbulence and vertical mixing which, when combined with the eastern drift, may facilitate homing during migration of the juveniles. The juveniles moving towards the coast for the winter would comprise the new recruits to the population that would spawn the next spring.

Anchovy occur elsewhere than the Bay of Biscay in the NA. There are populations in the Gulf of Cádiz. Along the Spanish Cantabrian coast, to Galicia and Portugal, are areas where anchovy appear irregularly. In recent years, an increase of anchovy, together with other species with more southern affinities, like sardine and red mullet (*Mullus surmeletus*), has been detected in survey trawling in the North Sea (Beare *et al*., 2004a,b). Anchovy has been present in the North Sea up to the East coast of Scotland and the Baltic in the past (Calderwood 1892; Cunningham 1890, 1895, 1896), with spawning and supporting fisheries on the Dutch coast (Cunningham, 1896). The recently detected increase (Beare *et al*.,2004a,b) is associated with the regional increase in sea temperatures hypothesized to be associated with climate change.

*European Atlantic sardine (*Sardina pilchardus*)*

Sardine is widely and continuously distributed along the eastern Atlantic shelf from Mauritania to the English Channel (Parrish *et al*.,1989), with occasional occurrences along Senegal in the south (Fréon *et al*., 1979) and off the coast of Scotland in the north (Beare *et al*., 2004a) (Fig. 3.5c). Sardine is also found in all oceanic eastern Atlantic islands, including the Azores, Madeira and the Canary Islands, as well as within most of the Mediterranean coastal habitat, with the exception of the southwest corner. Within this broad distribution, recent results from the European Union project SARDYN (SARdine DYNamics and stock structure in the northeast Atlantic, http://ipimar-iniap.ipimar.pt/sardyn) show the existence of five genetically distinct units: the first three are related to isolated islands (Azores and Madeira) and the Mediterranean Sea, while the entire sardine distribution area along the Atlantic coast can only be separated in two genetically distinct units (Kasapidis *et al*., 2004), with the limit somewhere around the Bay of Agadir, Morocco (30.3° N, 9.6° W). Within European waters, where more data on sardine population dynamics and habitat occupation are available, the species is mainly found around the Iberian Peninsula and the Armorican (NW France) shelf and up to Brittany and the western English Channel.

The population dynamics and habitat of the NA sardine are complex. A gradient in some genetic and biological characteristics along this wide area (Laurent *et al*., 2006; Silva *et al*., 2006; Stratoudakis *et al*., 2007) suggests a limited degree of mixing between distant units, although specific oceanographic features that could act as barriers to sardine gene flow or specific permanent oceanographic regimes that could lead to different coastal habitats have not been identified (Peliz *et al*., 2005; Santos *et al*., 2005; Mason *et al*., 2006). Oceanographic conditions along the NA coast form a mosaic of small and mesoscale heterogeneous habitats, but with similar large-scale properties, and create a wide distribution of suitable habitats for sardine in terms of temperature (Coombs *et al*., 2006), food availability (Smyth *et al*., 2005), and potential spawning grounds(Stratoudakis *et al*., 2004; Bernal *et al*., 2007; Planque *et al*., 2007).

Sardine distribution along the NA coast is nearly continuous from the Strait of Gibraltar to the English Channel (Fig. 3.5c). However, life history characteristics (such as longevity, maximum age, length at maturity, growth, duration of spawning and recruitment strength) differ between regions. The spatial distribution of young and old individuals is different, with old fish being observed more offshore over the continental shelf and young fish more inshore. Spatial fidelity of young fish to recruitment hotspots has been observed off northern Portugal and in the Gulf of Cadiz at depths <30 m during the summer months, while, for adult populations, pronounced local variations have been reported. In both cases, the physical and/or biological conditions which could promote recruitment hotspots or variability in the adult population distribution are still unclear (ICES, 2006). Spawning habitats also show some permanent features, with spawning confined to the shelf and to temperatures of 12–17 °C, but with variation along the time series that is not clearly related to environmental variables or to the stock size (Bernal *et al*., 2007). Bathymetric constraints and some unknown environmental variables allow the separation of the spawning habitat into four geographic nuclei, located in south Iberia, west Iberia, the Cantabrian coast, and the Armorican shelf (Bernal *et al*., 2007; Planque *et al*.,2007). Recruitment areas, i.e. areas dominated by juveniles, are located near the main spawning areas, but further restricted to inshore grounds in the Armorican shelf, and west and south Iberia. Increased retention in those areas (Santos *et al*., 2004) has been generally suggested as the main reason for the spatial persistence of these recruitment spots. Adult habitat spreads beyond the offshore edge of these recruitment areas or else to more oceanic areas (near the shelf edge in the Armorican shelf), as suggested by the adult distribution found in acoustic surveys.

The general picture of sardine habitat along the European Atlantic coast is of some spatial persistence in the distribution of distinct life stages that seem to be associated with some known (temperature, retention areas, bathymetry) and unknown physical properties of the ocean. Nevertheless, this average picture can be perturbed, sometimes greatly, by variations of the mean distribution patterns of the adult population, which may be caused by oceanographic or other environmental forcing. The interannual variability in spatial patterns, associated with spatial gradients in life history characteristics, makes it difficult to establish the limits of the potential habitat for the entire sardine population. In addition, recent observations off the northwest North Sea suggest that the habitat of European sardine may be expanding northward as a result of increasing sea temperatures (Beare *et al*., 2004 a, b). If this hypothesis is confirmed, it is expected that the spatial extent of sardine habitat in European waters will expand to northern waters, as already seen for a number of species (Perry *et al*., 2005).

The Canary Current ecosystem (not shown) can be divided into two areas that overlap at the Cape Barbas (22° 30 N) – Cape Blanc (20° 20 N) transition region. The temperate *Sardina pilchardis* is confined to the NACW and extends from off Iberia to the Cape Juby-Cape Barbas (29° 20 N–22° 30 N) region. The more tropical *Sardinella* sp. is present south of Cape Blanc to Senegal (14° N). The intermediate area between Cape Barbas and Cape Blanc is a transition zone in which either species exists depending on the prevailing hydrological conditions (S. Kifani, Institut National de Recherche Halieutique, Morocco, pers. commun., Hernandez-Leon *et al*., 2007).

Kuroshio-Oyashio (KO)

Physical characteristics

The near-surface currents of the region of spawning of anchovy and sardine are dominated by the Kuroshio from the south, Oyashio from the north, their convergence (KO Transition Zone) off Honshu, and the Kuroshio Extension to the east (Fig. 3.6a) (Ichikawa and Beardley, 2002; Yasuda, 2003). A fraction of the Kuroshio also flows, as the Tsushima (Warm) Current, into the Japan/East Sea. These northward-flowing currents are warm and of high salinity, while the southward-flowing currents (e.g. Oyashio) are cold and of lower salinity. Fronts, meanders, and eddies are characteristic of this region. There is significant interannual to interdecadal variation in these features, particularly the path of the Kuroshio and the trajectory of the Kuroshio Extension. These have important implications for the dynamics of anchovy and sardine (Nakata *et al*., 2000; Yasuda, 2003).

*Japanese anchovy (*Engraulis japonicus*)*

Three stocks of Japanese anchovy are thought to exist, based on fishing and migration patterns: the Pacific stock, Tsushima Current stock, and the Seto Inland Sea stock (Fig. 3.6b) (Fisheries Agency and Fisheries Research Agency of Japan, 2005). Distributions of the two offshore stocks depend on their size. The Seto Inland Sea stock is confined to that sea. The Pacific stock is distributed along the Pacific coast of Japan, with an eastern boundary of ca. 155° E during low abundance and beyond 180° E during high abundance. The western and southern boundaries are 29° N 129° E in years of small population size. The northern limit of its migration area corresponds to the northern coast of Honshu during low abundance and north Kuril Island (47° N 150° E) during high abundance.

Spawning grounds of the Pacific stock are located in coastal areas from 32° N 131° E to 38° N 142° E during low abundance (Mori *et al*., 1988; Kikuchi and Watanabe, 1990; Ishida and Kikuchi, 1992; Zenitani *et al*.,1995; Kubota *et al*., 1999). During high abundance, spawning is observed not only in the inshore areas off the Pacific coast but also in the offshore areas beyond the Kuroshio axis, from 29° N 130° E to 43° N 155° E, and the spawning grounds of this stock connect to those of the Tsushima Current stock. Spawning of the Seto Inland Sea stock is throughout that sea, and the offspring of the Pacific stock also migrates into this area.

Spawning takes place from February to October, and juveniles are transported by the Kuroshio and Kuroshio Extension Currents beyond 170° E longitude in spring. Feeding grounds are typically located in the Oyashio and Kuroshio–Oyashio Transition regions, from 42° N 144° E to 45° N 155° E, in summer and autumn, although the northern limit of migration areas is 41° N 142° E during low abundance. Major fishing grounds of the purse-seine fishery are located along the Pacific coast of northern Japan. Adult fish migrate southward to their spawning grounds in late autumn; however, young of the year tend to stay at the middle of their spawning migration path (35–37° N 141–143° E).

Distribution area of the Tsushima Current stock is limited to the coastal areas from 30° N 129° E to 41° N 140° E during low abundance (Fisheries Agency and Fisheries Research Agency of Japan, 2005). However, the same

(a)

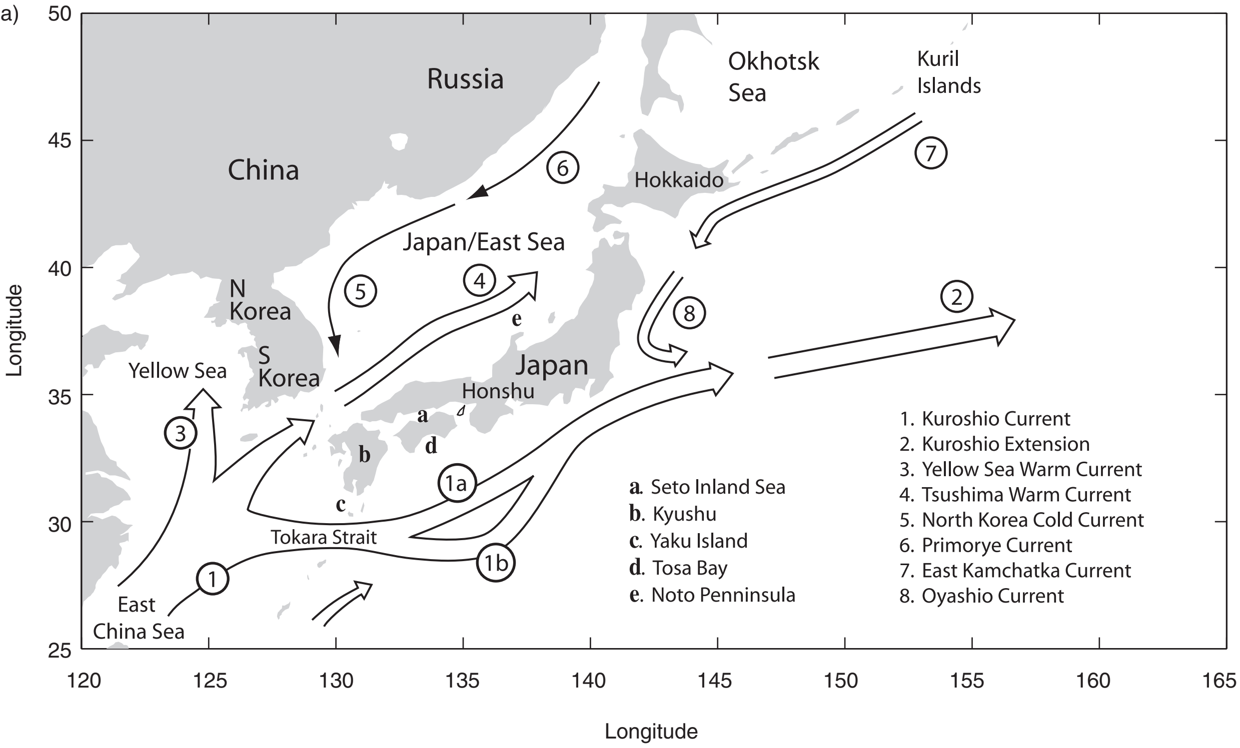

Fig. 3.6. Kuroshio–Oyashio region. (a) Circulation. 1a and 1b refer to straight and meandering patterns, respectively, of Kuroshio flow, with implications for anchovy and sardine dynamics (Nakata *et al.,* 2000; Yasuda, 2003). (b) Distribution of anchovy (*Engraulis japonicus*). (c) Distribution of sardine (*Sardinops melanostictus*).

(b)

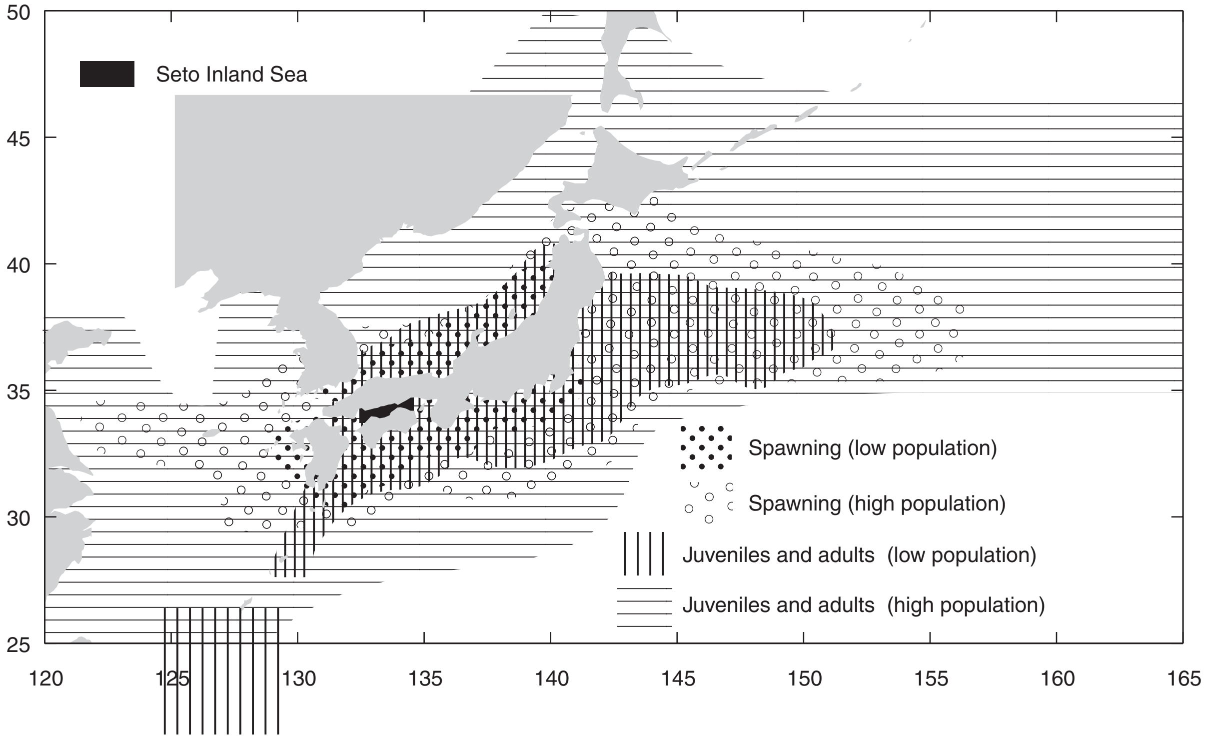

Fig. 3.6 (*cont.*)

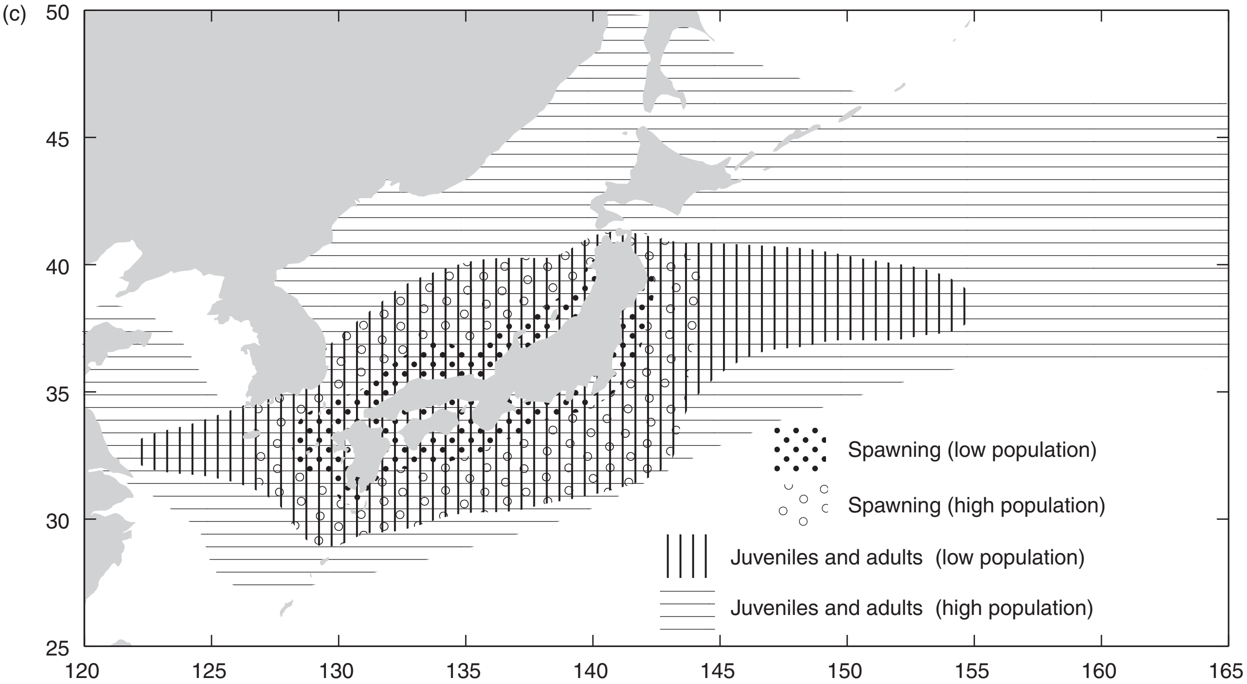

Fig. 3.6 (*cont.*)

stock is distributed from 25° N 120° E to 50° N 150° E, including the East China Sea, the Japan/East Sea and the Okhotsk Sea, except the eastern part of Yellow Sea, during high abundance.

Spawning grounds of the Tsushima Current stock are located in the coastal areas from 30° N 130° E to 41° N 140° E during low abundance (Zenitani *et al*., 1995; Kubota *et al*.,.1999). Spawning activities of the Tsushima Current stock are observed not only in the coastal areas of Japan/East Sea but also in the offshore areas of Japan/East Sea and the East China Sea (26° N 125° E to 41° N 140° E), and major spawning grounds are formed in the western area of the Japan/East Sea and the eastern area of East China Sea (30° N to 36° N and from 128° E 133° E, respectively). Spawning takes place mainly from February to June, although details are still unknown because survey cruises did not cover the whole spawning areas and spawning seasons. Migration behaviors of adult fish have not been reported in detail (Fisheries Agency and Fisheries Research Agency of Japan, 2005).

*Japanese sardine (*Sardinops melanostictus*)*

Two stocks of Japanese sardine are thought to be distributed around Japan (Fig. 3.6c) (Fisheries Agency and Fisheries Research Agency of Japan, 2005): the Pacific stock and Tsushima Current stock, based on distribution and migration patterns, although mitochondrial DNA analysis indicate no difference between these two stocks (Okazaki *et al*., 1996). Distributions of these two stocks depend on their population size. The Pacific stock is distributed off the Pacific coast of Japan and its eastern boundary extends to ca. 155° E longitude during low abundance. The northern limit of its migration is the northern coast of Honshu during low abundance; however, the same stock migrates to the coast of north Kuril Island (46° N 150° E) and the eastern boundary extends beyond 180° E during high abundance. The southern and western boundaries are 29° N and 129° 30 E, the former coinciding with that of the spawning grounds in the years of small population size.

Spawning grounds of the Pacific stock are located in the coastal areas from 31° N 131° E to 41° N 142° E and mainly around the coast of the Tosa Bay from 32° N 132° E to 33° N 135° E during low abundance (Mori *et al*., 1988; Kikuchi and Watanabe, 1990; Ishida and Kikuchi, 1992; Zenitani *et al*., 1995; Kubota *et al*., 1999). During high abundance, spawning is observed not only in the coastal areas but also offshore and beyond the Kuroshio axis, from 29° N 130° E to 41° N 144° E. Major spawning grounds are also around Yaku Island and the spawning grounds of both stocks merge in these areas during high abundance.

Spawning takes place from October to May, and juveniles are transported by and move in (migrate to) the Kuroshio and Kuroshio Extension currents to beyond

170° E longitude in spring. Feeding grounds are typically located in the Oyashio and Kuroshio–Oyashio Transition regions, from 42° N 144° E to 45° N 155° E, in summer and autumn, although the migration area is limited to north of 41° N 142° E during low abundance. Major fishing grounds of the purse seine fishery are located along the Pacific coast of northern Japan. Adult fish migrate southward to their spawning grounds in late autumn and winter; however, young of the year tend to stay at the middle of their spawning migration path, ca. 35–37° N 141–143° E.

Distribution of the Tsushima Current stock is limited to the coastal areas from 30° N 129° 30 E to 41° N 140° E during low abundance (Hiyama, 1998). However, it extends from 28° N 120° E to 50° N 150° E, including the East China Sea, the Japan/East Sea and the Okhotsk Sea, except the eastern part of Yellow Sea, during high abundance.

Spawning of the Tsushima Current stock occurs in coastal areas from 33° N 128° E to 41° N 140° E and primarily around the coast of the Noto Peninsula (35° 30 N 134° E to 38° N 140° E) during low abundance (Zenitani *et al*., 1995; Goto, 1998; Kubota *et al*., 1999; Matsuoka and Konishi, 2001). During high abundance, spawning of the Tsushima Current stock occurs not only in the coastal areas but also in the offshore areas of the Japan Sea and the East China Sea, from 29° N 131° E to 41° N 140° E, and major spawning occurs around the Yaku Island, connecting with the spawning ground of the Pacific stock (Matsuoka and Konishi, 2001). Spawning takes place mainly from March to May, and juveniles move in the Tsushima Current northward in spring. Adult fish migrate northward along the coast of Japan from 37° N to 40° N in March, from 37° N to 42° N in April, and from 39° N to 43° N in May (Hiyama, 1998).

Synthesis

Anchovy and sardine populations worldwide appear to have been established relatively recently (ca. 10^4–10^6y) (Grant and Bowen, 1998). Speciation of anchovy and sardine, conversely, occurred far earlier (ca. 10^7y) (Grant and Bowen, 1998). One predicts, therefore, significant differences between these two groups and substantial consistency within the groups in regard to inherited traits. Populations of anchovy to share are expected to share characteristics among regions, and similarly for sardine, and the two groups are expected to differ within regions. Are the habitats of these fish consistent with these expectations? If so, what are the similarities within species and between regions, and differences between species across regions? Can this information be used to predict the effects of climate change on populations of these fish, their fisheries, and their role in the ecosystem? We address these issues below.

Geography vs. hydrography

Anchovy tends to be more coastal and sardine more oceanic. The gill rakers and feeding behavior of anchovy are adapted for consuming larger zooplankton than consumed by sardine (this volume, Chapter 7). Coastal environments are nourished by wind-driven, coastal upwelling (e.g. CC, HC, BC) or fresh water influence (NA, KO) and tend to be dynamic (e.g. intermittent mixing and stratification). Oceanic environments are nourished by open-ocean upwelling, e.g. Ekman pumping, associated with wind-stress curl or divergence at fronts, and tend to be less intense (e.g. lower vertical velocities) but over broader areas (Rykaczewksi and Checkley, 2008). Plankton size may be larger in dynamic, coastal environments, with anchovy, than in more quiescent oceanic environments with sardine (Rykaczewksi and Checkley, 2008). Unfortunately, few measurements of both physics and biology exist with which to test these ideas. However, the data in this chapter, particularly for the Pacific, are largely consistent with them.

In contrast to the geographic differences between the habitats of these two taxa, there is no apparent general pattern in regard to hydrographic characteristics, including temperature and salinity (Table 3.1). Thus, in some cases (HC, KO, NA), anchovy tend to spawn in less saline water than do sardine. Conversely, in the CC, anchovy tend to spawn in more saline and warmer water than do sardine. Spawning seasons of anchovy and sardine are slightly (e.g. Bay of Biscay, CC, and Tsushima Current) or completely (e.g. Gulf of Cadiz and Kuroshio Current) out of phase. Anchovy and sardine in the BC appear to not differ from one another in this regard. However, these patterns are consistent with the relative source of nutrients for each of the stocks in question. Thus, for the KO and NA, anchovy spawns in waters with nutrients associated with freshwater (e.g. Oyashio (Fig. 3.6a) and Adour, Gironde and Guadalquivir Rivers (Fig. 3.5a), while sardine spawning occurs further offshore throughout the shelf in more saline water. Conversely, anchovy of the CC and HC inhabit waters enriched by upwelling. For the CC, this water is of higher salinity than at the surface, while the reverse is so for the HC. In addition, some anchovy in the CC spawn near river plumes (Fig. 3.2b), low in salinity and rich in nutrients. Thus, in each case, the hydrographic characteristics of the habitats of these fish are consistent with the water masses containing their source nutrients. Exceptions to these generalizations occur, e.g. under extraordinary conditions such as during an intense El Niño. Thus, in the CC, water upwelled during a strong El Niño off California is of lower salinity than during other years, and salinity of the spawning habitats of anchovy and sardine can be quite similar during an El Niño (Checkley *et al*., 2000).

Table 3.1. *Temperature and salinity of habitats for systems with populations of small, pelagic fish considered in this chapter*

System	Anchovy Temperature (°C)	Salinity	Sardine Temperature (°C)	Salinity	Comments
California Current (CC)	12–25	>33.2	12–24	<33.2	Spawning; lower salinity for anchovy in Columbia River plume
Humboldt Current (HC)	14–22	34.9–35.1	<19–22	35.0–35.3	Spawning
Benguela Current (BC)	12–24	34.8–36.0	12–24	34.8–36.0	Juvenile and adult distribution
Northeast Atlantic (NA)	15–19 (18)	<30–35.5 (30.1)	12–17 (13)	<30.0–>36.0 (35.3)	Spawning (range and mode)
Kuroshio–Oyashio (KO)	21	32.4	18	34.4	Spawning, Pacific (weighted mean)
	17	34.0	15	33.9	Spawning, Tsushima Current (weighted mean)
	22	31.6	n.a.	n.a.	Spawning, Seto Inland Sea (mean weighted by egg abundance)

These data are approximate, as significant variation occurs for each stock in regard to location, date, and developmental stage (n.a.: not available). References for these data are in the sections for the respective systems.

Transport and migration

All stocks, to a degree, inhabit different areas during different life stages. This results from the passive transport of eggs and larvae and the active movement (migration) of juveniles and adults. Sardine are larger and live longer, on average, than anchovy and, in some regions (CC, HC, BC, NA), migrate greater distances. For example, Pacific sardine that spawn off central and southern California are believed to migrate to feed, and perhaps spawn, as far north as off Vancouver Island, British Columbia, whereas the northern anchovy does not appear to make such a migration. Similarly, anchovy in the Bay of Biscay reside in a mosaic of locations influenced by runoff and local upwelling, while sardine spawn in similar waters but migrate longer distances, both coastally and offshore, to feed. However, both anchovy and sardine in the BC and KO undergo both significant transport downstream, as plankton, and migration upstream, as juveniles and adults. Such migrations also have implications for interpretation of the paleo-oceanographic record of fish scale deposition and inference therefrom about population size (this volume, Chapter 4).

Expansion, contraction, and refugia

Stocks of small, pelagic fish expand their geographic distribution when more abundant and contract when less abundant. Because their populations typically vary in abundance on the scale of decades (this volume, Chapter 9), their geographic distribution also varies. MacCall (1990; this volume, Chapter 12) proposed the basin hypothesis to explain this phenomenon. A related issue is habitat use. Planque *et al.* (2007) classified spawning habitat (SH) as potential SH, where conditions are suitable for fish to spawn, realized SH, where spawning occurs, and successful SH, where spawning results in successful recruitment. Recent work has demonstrated that potential SH may be much greater than realized or successful SH for stocks at low population size (Planque *et al.*, 2007; Reiss *et al.*, in press).

Refugia at small population size may exist for most stocks. However, data are sparse due to the lack and/or difficulty of both fishing and scientific surveys of stocks at low abundance. Anchovy in the CC contract into coastal upwelling areas, estuaries, and the southern California Bight. Sardine in the CC appear to contract into the inshore waters off Baja California, Mexico. Anchoveta off Peru are believed to move close to shore in isolated pockets of upwelling during low abundance. Sardine of the HC may contract to waters around the Galapagos Islands (M. Niquen, personal communication). The Japanese anchovy and sardine spawning grounds contract to waters around Honshu and Kyushu during low abundance, and expand offshore during high abundance. Hence, a general feature appears to be expansion during high abundance and contraction at low abundance to predictable locations which may be refugia.

Mortality

A process that has not been quantified spatially is mortality of all stages due to predation, starvation, or both.

Species fitness depends on the balance of birth and death. Species evolve to maximize the difference between these two processes. Thus, both food and predators must be considered as habitat characteristics. Unfortunately, little is known of natural predators and mortality for any stage of development. Exceptions are estimates of the mortality of eggs and early larvae made when applying the Daily Egg Production Method (Stratoudakis *et al*., 2006; this volume, Chapter 15, and references therein). One might hypothesize that the oceanic habitat of sardine may have lower concentrations of both food and predators and, conversely, anchovy may inhabit waters with both more food and predators. Conversely, greater predation offshore is invoked in the school-mix feedback hypothesis (this volume, Chapter 13). Cannibalism can be a significant source of mortality for anchovy in the CC (Hunter and Kimbrell, 1980), HC (Santander, 1987), and other regions (van der Lingen *et al*., 2008 and references therein).

Future climate change

At the time of writing, we know the Earth's climate is changing due to both natural and anthropogenic causes (http://www.ipcc.ch). We are beginning to achieve skill in predicting the effects of present and future climate change on ocean physics, including its state (e.g. temperature, salinity, and stratification) and dynamics (e.g. currents, upwelling, and fluxes). Collectively, these physical changes will alter the habitat of small, pelagic fish in decades and centuries to come. Freon *et al*. (2008) discusses these issues and their implications. The past behavior of systems with small, pelagic fish is the subject of several chapters in this book. However, knowledge of the past behavior of these systems may not be sufficient to predict their behavior under future climate change. Rather, an understanding of their dynamics is needed. Below, we present topics that merit consideration for the study of habitat under future climate change.

Box 3.1. Habitats of small pelagic fish under future climate change

The habitat of small, pelagic fish is a three-dimensional environment comprised of water and dissolved and particulate and living and dead matter. In contrast to demersal and benthic fish, which relate to geography, e.g. the sea bottom, pelagic fish relate to hydrography, perhaps especially temperature, salinity, and planktonic food. A key challenge to scientists is to understand these relations to be able to predict the response of populations of small, pelagic fish to future climate change.

Future climate change, associated with human-caused enhancement of CO_2 concentration and global mean temperature, may affect the environment of small, pelagic fish, and thus their populations, in several ways. Average warming of 1.1–6.4 °C is predicted globally by 2100 (IPCC, 2007), but change will vary regionally, and thus have different effects in the different SPACC regions. Latitudinal shifts in plankton (Beaugrand *et al*., 2002) and anchovy and sardine (Beare *et al*., 2004 a,b) are already apparent in the northeast Atlantic. Temporal variation may occur abruptly, as in the past (Alley *et al*., 2003; IPCC, 2007), and become more episodic (IPCC, 2007). The timing, or phenology, of ecological events, including, for example, the spring bloom, may affect fish feeding, survival, and recruitment. Interactions of changed phonologies, may lead to mismatches food supply and demand, sensu Cushing (1974). The hydrological cycle is predicted to change, with potential effects on the habitats of some species and stocks, e.g. anchovy that spawn in regions affected by freshwater. Effects on small pelagic fish of changing ocean chemistry, including enhanced concentration of CO_2 and acidification, are largely unknown but of potential significance. Simultaneous monitoring of populations of small, pelagic fish and their habitats is needed, including continued and new observing programs and the development of new technologies to this end. Perhaps the greatest challenge is to achieve a predictive understanding of the cumulative effects of future climate change of the habitats, and thus stocks, of small, pelagic fish. This is particularly difficult given the unprecedented nature of that change.

Ocean temperature

Globally, the Earth's surface is predicted to warm 1.1–6.4 °C this century (http://www.ipcc.ch). Temperature, as a habitat variable, may induce shifts in population distributions and rates (e.g. feeding, respiration, growth, birth, and death). Warming will vary regionally and is, in general, predicted to be greater at high latitudes. This may result in more rapid poleward shifts of the high-latitude (cool) than low-latitude (warm) range limits. Continued high-resolution mapping of the distribution and abundance of fish, at all stages of development, and environmental variables is needed to resolve such shifts. To this end, equipping vessels of opportunity, e.g. fishing vessels, with devices to measure and log environmental data and survey vessels with continuous egg samplers and acoustics is desirable. An increased contrast of land and sea temperatures may lead to greater upwelling, with consequences, albethey uncertain, for small pelagic fish (Bakun, 1990; Bakun and Weeks, 2004).

Winds

Currents, upwelling, and turbulence are key habitat characteristics likely to be affected by changes in wind speed and direction. Currents affect transport from spawning to nursery areas. Coastal, wind-driven upwelling is particularly important for anchovy. Both winds themselves and their effectiveness in causing upwelling are related to geography, including coastal headlands and mountains. Offshore winds, and their curl and associated Ekman pumping (oceanic upwelling), are of particular importance to some populations of sardine. Turbulence affects the encounter rate and capture success of fish larvae, which, in turn, affects feeding and mortality. Expanded measurement of wind by sea-(anemometers) and space-borne instruments is desirable.

Ocean stratification

Increased stratification, due to enhanced heat content of the upper layer of the ocean, will result in a more intense thermocline. This, in turn, will reduce vertical nutrient flux due to both diffusion and mixing at the thermocline and wind-driven upwelling. Changed winds may also affect retention and dispersal of planktonic eggs and larvae. Expanded measurement of hydrography from ships and autonomous devices (e.g. buoys, floats, and gliders) is desirable, particularly in conjuction with measurements of fish distribution and abundance of all stages.

Hydrology

A primary result of global climate change will be altered hydrology (IPCC 2007). Anchovy habitat includes river plumes (CC, NA). Anchovy and sardine off Japan inhabit currents influenced by freshwater (i.e. Oyashio). The pattern of precipitation may have important effects on the habitat of anchovy, particularly off Peru (e.g. El Niño), the NA (e.g. Ardour and Gironde Rivers), and the CC (e.g. Columbia River). Expanded monitoring of coastal ocean hydrography is needed.

Phenology

The temporal occurrences of related processes, especially the production of planktonic food and the spawning, hence first feeding, of fish is likely to be affected by climate change. Such effects are best known on land (Visser and Both 2005). The timing of the biomass peak of *Neocalanus* in the *N. Pacific* is known to vary naturally on the scale of decades (Mackas *et al*., 1998). The existence and consequence of such changes in phenology on the habitat of small, pelagic fish is largely unknown but of potential significance. However, many fish stocks considered here have protracted (months) spawning seasons and, thus, may be less susceptible to phenological changes than are stocks, generally at higher latitude, that require a closer (weeks) match of food production and spawning (Edwards and Richardson, 2004). In fact, recent data for some stocks of anchovy and sardine (CC, KO) are consistent with variation of survival being more important in the juvenile than the larval stage (M. Takahashi, Scripps Institution of Oceanography, La Jolla, California, USA, personal communication). Continuous sampling from towed (e.g. the Continuous Plankton Recorder, CPR, Reid *et al*., 2003) and autonomous (see above) devices is needed to resolve important changes in phenology.

Events

The frequency and magnitude of both single and repeating events must be considered. While predictions of change, e.g. of temperature, are gradual, past change has at times been abrupt and episodic (Alley *et al*., 2003). The consequences of this to marine populations, including small, pelagic fish, is unknown. Storms and longer-term events, e.g. El Niño, may change in frequency and intensity, also with unknown consequence to small, pelagic fish. Continued and new time series of observations of both the environment and fish are needed. Examples are the CPR survey (Reid *et al*., 2003) and the California Cooperative Fisheries Investigations (Bograd *et al*., 2003).

Acidification

The habitat of small, pelagic fish includes the ambient seawater. Carbon dioxide produced by human activities is acidifying the ocean (Orr *et al*., 2005). The solubility of biogenic minerals, particularly aragonite, will increase, particularly at high latitudes. This has known consequences for organisms with external shells, e.g. pteropods. The effects on internal structures, including otoliths of fish, is unknown. Experimental and observational studies of the effects of acidification on fish are warranted.

These effects, combined with those from other causes, particularly fishing, will have cumulative effects on populations of small, pelagic fish in ways as yet unknown. A challenge is to gain sufficient understanding of these processes and relationships to enable prediction with acceptable confidence.

A related question is how refugia may be affected by climate change. Will geographic regions which have in the past served as refugia change, e.g. due to winds and hydrography, to no longer be acceptable as refugia? Similarly, are there "hot spots," or loci of enhanced activity (e.g. spawning, feeding), that may change with climate change and, if so, how will this affect the dynamics of the populations? The recently observed eastward movement of both anchovy and particularly sardine stocks in the southern BC may be an example of this. Finally, we note (e.g. Table 3.1) that anchovy and sardine occur in a broad range of temperatures and salinities. Are these taxa able to adapt to new conditions and, if so, what are the mechanisms, rates, and limits, particularly in regard to regional changes? Genetic analyses of populations of anchovy and sardine indicate shallow population structure and low genetic diversity, implying susceptibility of these populations to change (Grant and Bowen, 1998).

Two general, overarching questions exist in regard to the anticipated rise in global and ocean temperatures in the twenty-first century. First, will the net effect of climate change on a population of small, pelagic fish be a latitudinal shift in distribution (e.g. Beare *et al*., 2004; Perry *et al*., 2005), a change in overall abundance, or both? We need mechanistic models in which we have appropriate confidence. Second, what will the effects of climate change be on the ecosystem containing populations of small, pelagic fish? Such ecosystems have been named wasp-waist (.,this volume, Chapters 8 and 13), implying strong interaction of small pelagic fish with both lower and higher trophic levels. How climate change will affect such systems is unknown.

Conclusions

Work of SPACC has shown consistent differences between taxa in habitat characteristics but similarities within each major taxon, particularly *Engraulis* spp. and *Sardinops sagax*. While variation occurs between regions (CC, HC, BC, NA, and KO), generalities exist. Anchovy tends to be coastal, derive nutrients from water influenced by coastal upwelling or freshwater, consume larger food and migrate less, while sardine tends to be more oceanic, derive nutrients from oceanic processes, eat smaller food, and migrate more, with exceptions. The occupied habitat of small, pelagic fish expands and contracts with increasing and decreasing population size, and refugia may exist for most populations.

Key questions are how the distribution, abundance, and production of small, pelagic fish will be affected by future climate change, due to natural and anthropogenic causes. Greater skill has been achieved in forecasting physical aspects of climate change. The challenge will be to achieve similar success in predicting biological characteristics, including those of small, pelagic fish.

Critical actions will be to adequately observe essential features of the habitat and the populations themselves, to develop predictive models, and to test the skill of forecasts from those models. The results of these actions can then be used to inform those who manage populations of small, pelagic fish and make policy affecting those fish, the ecosystems, and climate.

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NOTES

1 El Niño-Southern Oscillation.
2 Virtual Population Analysis.

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