CHAPTER 8 - Trophic dynamics of small pelagic fish

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Abstract

Literature on the trophic ecology of small pelagic fish (primarily anchovy *Engraulis* spp. and sardine *Sardinops sagax* but including the genera *Brevoortia, Clupea, Sardina, Sprattus* and *Strangomera*) and their interactions with plankton are reviewed using case studies describing research on some economically and ecologically important small pelagic fish from upwelling and temperate non-upwelling ecosystems. Information from morphological studies of the feeding apparatus, field studies on dietary composition and foraging behaviour, and laboratory studies that have provided data for the parameterization of bioenergetic and other models of these small pelagic fish are presented, where available. Two or more small pelagic fish species are described in each case study, and disparities in trophic dynamics between co-occurring anchovy and sardine are consistently seen, supporting the hypothesis that species alternations between the two could be trophically-mediated. Linkages between climate and fish are described for many of the systems, and possible impacts of climate change on some of the species are described.

Introduction

Small pelagic fish are in general microphagous planktivores, and their high abundance levels in upwelling systems in particular was attributed to their ability to feed directly on phytoplankton and hence benefit from a short and efficient food chain (Ryther, 1969; Walsh, 1981). This two-step food chain hypothesis, with small pelagic fish being regarded as essentially phytophagous and feeding on large, chain forming diatoms such as *Chaetoceros* and *Fragilaria* (Yoneda and Yoshida, 1955; Bensam, 1964; Loukashkin, 1970; King and Macleod, 1976) was initially well supported (Longhurst, 1971; Durbin, 1979; Walsh, 1981). However,
subsequent studies challenged this hypothesis and suggested that clupeoids consume both phytoplankton and zooplankton (Cushing, 1978), with significant feeding on phytoplankton considered likely where strong upwelling is a persistent feature of the environment (e.g. off Namibia and Peru), whereas feeding on phytoplankton would be less common and zooplankton would become the dominant food source of species living where upwelling is weaker and less persistent (e.g. the southern California coast; Blaxter and Hunter, 1982). A comprehensive review of the diets of commercially important clupeids concluded that few true phytophagists exist, and that most clupeids are omnivorous microphagists that derive the bulk of their energy from zooplankton (James, 1988). Additionally, most microphagous clupeoids possess two feeding modes and switch between the two when conditions dictate, generally filter-feeding on smaller food particles and particulate-feeding on larger food particles (Blaxter and Hunter, 1982). The ability to switch between these feeding modes makes these species highly opportunistic and flexible foragers which are able to maximise their energy intake through employing the feeding mode most appropriate to a particular food environment. The high abundance and success of small pelagic fish in upwelling areas in particular was attributed to this flexibility in feeding behaviour, which enables them to efficiently utilize a wide range of particle sizes and hence take advantage of their dynamic trophic environment (James, 1988).

The objective of this chapter is to provide an updated synthesis on the trophic dynamics of small pelagic fishes by using seven case studies selected to describe trophic aspects of a wide range of economically and ecologically important small pelagic fishes, primarily anchovy and sardine, from upwelling and temperate non-upwelling ecosystems (Table 8.1). Published literature describing morphological, experimental, and field studies is reviewed, and some
unpublished data, where available, is incorporated into each case study. Two or more species of small pelagic fish co-occur and often have shown alternating species dominance in the systems reviewed (see Barange et al., this volume), and whilst Blaxter and Hunter (1982) considered that different species of clupeoids existing in the same habitat would tend to show strong overlap in food habits, Schwartzlose et al. (1999) hypothesized that species alternations between anchovy and sardine might be linked to changes in habitat (such as food or temperature fields) that resulted in one species being favoured over the other. However, for the two species to show different responses to the same environmental forcing (e.g. a changed trophic environment) requires that they show some ecological differences, and trophic disparities between co-occurring species from each region are highlighted where they occur.

The case studies describe trophic aspects of small pelagic fish in each system and provide the bulk of this chapter, and consistent patterns among and between coexisting species are identified and implications of these discussed. Whether anchovy and sardine are sufficiently trophically distinct such that changed food environments could impact their population variability is assessed, climate-fish interactions for many of the systems are also detailed, and possible impacts of climate change on some of the species are described.

The Benguela Current upwelling system

A substantial amount of research has been conducted to examine the trophic dynamics of anchovy (Engraulis encrasicolus) and sardine (Sardinops sagax) in the Benguela Current system. This research has consisted of morphological studies that described and compared the structure and development of the feeding apparatus; field studies that investigated diet and assessed feeding periodicity; and laboratory studies that examined aspects of feeding behaviour
and enabled the parameterization of a variety of processes such as ingestion, respiration, 
excretion and evacuation rates. Empirical results from laboratory experiments were used to 
construct carbon and nitrogen budget models for each species which were used to quantify the 
effect of different food environments upon fish growth. Together, these studies have provided a 
wealth of information that has permitted detailed comparison of the trophic ecologies of 
anchoy and sardine from this system. Unfortunately, however, almost all of the work has been 
conducted on juveniles and adults, and knowledge concerning the trophic ecology of larvae of 
these small pelagic fishes is limited to descriptions of the diet of only three individuals (King 
and Macleod, 1976). Whereas preliminary studies on the trophic ecology of a third small 
pelagic species from the Benguela (the redeye round herring Etrumeus whiteheadi) have been 
performed (Wallace-Fincham, 1987), only results from the research on anchovy and sardine are 
described in more detail, below.

The gape diameter of juvenile anchovy appears larger than that of sardine of a similar 
size (Fig. 8.1a) and indicates that anchovy are capable of ingesting larger prey than are sardine 
(Booi, 2000). The branchial basket of both species show many similarities in structure and 
development (King and Macleod, 1976); gill arch length and gill raker length increase with 
increasing fish length for both species, and juveniles of both species and adult sardine show an 
increase in the number of gill rakers with increasing fish length although the number of gill rakers 
remains constant for anchovy of >80 mm standard length (SL) (Fig. 8.1b). Gill raker gap also 
increases with increasing fish length and for fish up to ±40 mm SL the gill raker gap is about the 
same for both species; however, the rate of increase in gill raker gap with fish length is higher in 
anchoy than in sardine such that anchovy >40 mm have a larger gill raker gap than do sardine,
and an adult anchovy has a gill raker gap about twice as large as does an adult sardine (Fig. 8.1c).

Additionally, there is a marked dissimilarity in the structure and alignment of gill raker denticles between the two species, which in sardine are elaborate spine-like projections terminating in a serrated nodule that are unidirectionally aligned along the entire gill raker length, whereas in anchovy gill raker denticles are simple, spine-like projections in structure that are randomly arranged along the gill raker axis (King and Macleod, 1976).

Early studies of the diet of anchovy and sardine in the Benguela reported that sardine stomach contents were dominated by phytoplankton (predominantly diatoms) with a mean annual ratio of 2:1 by volume of phytoplankton to zooplankton (Davies, 1957), and that anchovy displayed a “preference” for phytoplankton (Robinson, 1966). Similarly, King and Macleod (1976) considered adults of both species to be phytoplanktophagus and juveniles zooplanktophagous, the dietary switch being attributed to a decrease in porosity of the filtering mechanism with increasing fish size. Additionally, stomach contents of adults showed good correlation with the ambient plankton, leading those authors to conclude that both species were essentially non-selective feeders feeding primarily on phytoplankton. However, those studies assessed relative dietary importance using frequency-of-occurrence data and estimation of the volume of different food types, both of which are likely to overestimate the contribution made by phytoplankton (James, 1987); the volumetric method particularly so because of the low carbon : volume ratio of phytoplankton compared to zooplankton (which is even lower for nitrogen; one unit volume of copepod has almost 8 times as much nitrogen as that contained within one unit volume of phytoplankton; van der Lingen, 2002).
More recent dietary studies of sardine and anchovy in the southern Benguela ecosystem that assessed relative dietary contribution according to the carbon content of ingested prey have shown that zooplankton contributes a far greater amount to dietary carbon than does phytoplankton for both species, although phytoplankton can be an important dietary contributor in localized regions or at particular times of the year for both species (James, 1987; van der Lingen, 2002). Results obtained from measurements of the stable isotope ratios of carbon and nitrogen in plankton and anchovy, which integrate the relative contributions of isotopically distinct dietary components over a period of time as opposed to the “snapshot” provided by stomach content analysis, did not support the suggestion that adult anchovy are predominantly phytophagous (Sholto-Douglas et al., 1991). However, whereas zooplankton is the dominant food source for both species, anchovy and sardine consume different fractions of the zooplankton and appear to partition this resource on the basis of food particle size. Anchovy derive the bulk of their carbon from larger (>1.5 mm) zooplankton, typically calanoid copepods and euphausiids captured through size-selective particulate-feeding, although smaller zooplankton and phytoplankton captured via filter-feeding can make a substantial contribution to dietary carbon, for example off the west coast (Fig. 8.2a; James, 1987). In contrast, sardine derive the bulk of their dietary carbon from smaller (<1.2 mm) zooplankton, typically calanoid and cyclopoid copepods and crustacean eggs and nauplii captured through non-selective filter-feeding (Fig. 8.2b; van der Lingen, 2002).

Size-based partitioning of zooplankton also appears to apply to younger life history stages of the two species, which shoal together as juveniles in the southern Benguela ecosystem and aggregate inshore along the South African west coast during austral winter (Mar-Aug). Studies on
the diet of juveniles caught in the same midwater trawl (and hence from presumably mixed-
species shoals or at least from a similar if not the same ambient food environment) found that
whereas both species consumed similar types of food (namely crustacean eggs and nauplii, and
copepods, with very little phytoplankton being found), sardine ingested significantly smaller
copepods than did anchovy (Figure 8.2c, d; Louw et al., 1998), this difference being attributed to
the product of differences in gill raker morphology, feeding behaviour, and within-shoal position
of the two species. Similar work comparing the stomach contents of anchovy and sardine pre-
recruits (i.e. post-larvae and juveniles of 25-75 mm total length) caught in the same Methot net
haul (and hence from presumably mixed-species shoals) also indicated that sardine consumed
smaller prey than did anchovy (Booi, 2000). Pre-recruits of both species fed on phytoplankton
(principally the diatom Coscinodiscus gigas and the dinoflagellate Peridinium spp.) and
zooplankton (copepod eggs and nauplii, and cyclopoid copepods), and although phytoplankton
was numerically dominant zooplankton contributed the major proportion to the diet of both
species when converted to carbon equivalents. Overlap in dietary niche breadth indicated that pre-
recruits of both species feed in a similar trophic niche, but in eight of the ten mixed shoals
examined prey size frequency distributions differed significantly, with sardine ingesting smaller
prey than did anchovy in all but one instance (Booi, 2000). Despite the limited sampling and
hence preliminary nature of the research examining trophic differences between early life history
stages of anchovy and sardine, the results obtained to date suggest that the two species exhibit
size-based partitioning of available zooplankton prey as early as the pre-recruit stage.

In addition to partitioning the zooplankton resource on the basis of size, sardine and
anchovy also appear to employ different foraging strategies. Anchovy show a marked feeding
periodicity in the southern Benguela, with peak feeding by recruits occurring at dusk and that by spawners occurring at dawn (James, 1987). Feeding periodicity in anchovy appears to be associated with vertical migration, with high feeding activity at night coinciding with shoal dispersal in the surface waters, whereas low feeding activity during the day coincides with shoal aggregation and descent into deeper water (James, 1987). Similarly, anchovy in the northern Benguela also show highly significant day/night differences in shoal depth (Thomas and Schülein, 1988). In contrast to anchovy, sardine >25 g wet weight appear to feed continuously and show no peaks in feeding activity throughout the diel cycle, although fish <25 g do show a peak in feeding activity at or around sunset (van der Lingen, 1998a). In the southern Benguela, vertical migration by sardine appears to be highly variable, with fish being observed throughout the water column during the day (in many cases being on or near the bottom) but forming a scattering layer close to the surface at night (Coetzee, 1997). Sardine in the northern Benguela show no significant difference in shoal depth between night and day, but tend to form small, scattered schools by night and dense schools by day, whilst generally remaining in the upper 20 m of the water column (Hampton et al., 1979; Kruger and Cruikshank, 1982; Thomas and Schülein, 1988).

Laboratory experiments have shown that both anchovy and sardine filter-feed on small particles and particulate-feed on large particles (James and Findlay, 1989; van der Lingen, 1994) but have different threshold sizes at which they change from filter- to particulate-feeding (Fig. 8.3a). Filter-feeding is the principal feeding mode of sardine, with food particles of <1.2 mm maximum dimension eliciting a filter-feeding response whilst larger particles elicit particulate-feeding at low concentrations but filter-feeding at high concentrations (van der Lingen, 1994). Sardine are less efficient at retaining particles <0.4 mm but are able to entrap particles down to
0.01 mm in size, and also display size-selectivity during particulate-feeding. In contrast to sardine, particulate-feeding is the primary feeding mode for anchovy, which switch from filter- to particulate-feeding at a threshold prey size of 0.7 mm (James and Findlay, 1989). The minimum particle size that can be entrapped by anchovy during filtering is 0.20 - 0.25 mm, hence a large portion of phytoplankton is unavailable to anchovy. Anchovy are highly size-selective, selecting for the largest particle available. A comparison of predictive equations of weight standardized clearance rate as a function of particle size for both species demonstrates that sardine are more efficient at removing particles <0.6 mm in size, anchovy having distinctly higher clearance rates on particles larger than this size (Fig. 8.3a; van der Lingen, 1994). Sardine are therefore more efficient removers of small particles, whilst anchovy remove large particles more effectively. The smaller gill raker gap and more elaborate denticle structure of adult sardine compared to adult anchovy are likely to be responsible for the higher retention of small prey such as phytoplankton by sardine compared to anchovy.

Energetic costs of feeding for both sardine and anchovy were determined through laboratory experiments that measured respiration rates during each of the feeding modes (James and Probyn, 1989; van der Lingen, 1995). For both species, respiration rate increased with swimming speed for both modes, although the shape of the functional relationship was linear for sardine but log-linear for anchovy. At a given swimming speed, filter-feeding by sardine is energetically cheaper than particulate-feeding, which is in contrast to anchovy where particulate-feeding is the energetically cheapest feeding mode (Fig. 8.3b; van der Lingen, 1995). James and Probyn (1989) argued that the change in body shape and increased drag associated with flared operculae during filter-feeding was responsible for the increased metabolic costs of filter-feeding.
by anchovy. Whilst opercular flaring by sardine during filter-feeding does occur and must increase
drag and therefore energetic costs, the higher cost of particulate-feeding in this species has been
ascribed to the higher relative importance of inertial forces compared to viscous (= drag) forces
for sardine relative to anchovy (van der Lingen, 1995). Additionally, the formation of a compact
shoal during filter-feeding by sardine in particular may confer a hydrodynamic advantage and
hence reduce energy expenditure during filter-feeding. The experimental procedures used in
determining the energetic costs of feeding also allowed estimation of the respiratory quotient (RQ,
an index of the type of physiological fuel involved in metabolism) for each species; anchovy had
an RQ of 0.92 ± 0.18 (James and Probyn, 1989) whereas that for sardine was 0.96 ± 0.10.
Although this difference is not statistically significant it suggests that sardine is able to utilize
carbohydrate to a greater degree than is anchovy, and implies a more herbivorous diet of the
former compared to the latter (van der Lingen, 1995).

Experiments conducted to determine excretion and absorption efficiencies of anchovy and
sardine, and assess the effect of food type on these, showed that both species excrete the majority
of their nitrogen in the form of ammonia, both show greater absorption efficiencies for nitrogen
than for carbon, and both absorb these elements more efficiently from zooplankton than from
phytoplankton (James et al., 1989b; van der Lingen, 1998b). Where the two species differ
however, is in their retention of nitrogen; sardine excrete more than half of their ingested and
absorbed nitrogen rations (62 and 66%, respectively) whereas anchovy excrete less than half of
their ingested and absorbed nitrogen rations (42 and 48%, respectively). Hence anchovy appear to
be more efficient retainers of nitrogen than are sardine.
Carbon and nitrogen budget models that used the same basic growth equations and
examined how growth varied under different food environments (phytoplankton,
microzooplankton and mesozooplankton) as a function of foraging time and prey size and
concentration have been developed for anchovy (James et al., 1989a) and sardine (van der
Lingen, 1999). Despite the fact that budget models were not identical in terms of their input
parameters and hence cannot be directly compared, they differ notably in two respects. Firstly,
the two species regulate their swimming speed during feeding (and hence their energetic
output) according to different properties of the food environment. When feeding on
zooplankton, sardine regulate their swimming speed according to prey concentration and swim
faster at higher concentrations (van der Lingen, 1999), whilst anchovy regulate their swimming
speed according to prey size, with larger zooplankton eliciting faster swimming speeds (James
et al., 1989a). The second major difference in the budget models derived for sardine and
anchovy pertains to the effect of the food environment upon potential growth. Sardine showed
positive growth over most of the input (particle size, prey concentration and foraging time)
ranges in each of the three food type-feeding behaviour scenarios (filter-feeding on
phytoplankton, filter-feeding on microzooplankton, and particulate-feeding on
mesozooplankton; van der Lingen, 1999), with the maximum scope for growth occurring for
sardine filter-feeding on dense concentrations of microzooplankton. Anchovy, on the other
hand, only showed positive growth over a limited portion of the input range when filter-feeding
on either phytoplankton or microzooplankton, but showed positive growth over most of the
input ranges, and maximum scope for growth, when particulate-feeding on mesoplankton
(James et al., 1989a). Additionally, modelled maximum scope for growth values for anchovy
were almost three times as high as sardine maximum values.
The studies described above have been summarized in van der Lingen et al. (2006a), and provide strong evidence that anchovy and sardine in the Benguela Current upwelling system are trophically distinct, and minimize their dietary overlap by resource partitioning according to prey size, this partitioning arising from the different morphological features of the branchial apparatus and different feeding behaviours and associated metabolic attributes (e.g. relative energetic costs of the different feeding modes) characteristic of sardine and anchovy in the Benguela. Van der Lingen et al. (2006a) considered sardine to have evolved a “steady-state” trophic strategy in which they feed primarily on that fraction of the zooplankton (small calanoid and cyclopoid copepods) characterized by a relatively high degree of population stability, and show positive growth over a wide range of prey types, sizes, and concentrations. However, the sardine’s relatively slow metabolic rate and inefficient (compared to anchovy) retention of nitrogen suggests that the transfer of primary production into sardine tissue would occur at a moderate rate. In contrast, because anchovy feed primarily on zooplankton (large calanoids) that are considered to show a greater degree of population variability, they were considered to have evolved a “feast-or-famine” trophic strategy – under suitable (i.e. a food environment dominated by large zooplankton) conditions they would show rapid growth as a result of their fast metabolic rate and efficient retention of ingested nitrogen, but under unsuitable conditions their growth would be minimal or even negative. Those authors hypothesized that the trophic difference between anchovy and sardine implies that the size spectrum of the planktonic food environment will affect the feeding success of each species, with food environments dominated by small particles favouring sardine over anchovy since sardine are more efficient removers of small particles and can collect such food particles
through employing relatively cheap filter-feeding. Hence sardine should have a greater net energetic gain in small particle-dominated environments than anchovy, as was shown by the respective carbon and nitrogen budget models constructed for these species. In contrast, anchovy are inefficient removers of small particles, and filter-feeding is the energetically most expensive feeding mode for this species. Food environments comprising mainly large particles will favour anchovy over sardine, due to the anchovy's greater efficiency at removing large particles through relatively cheap particulate-feeding.

**The California Current upwelling system**

The trophic ecologies of Pacific sardine *Sardinops sagax* and northern anchovy *Engraulis mordax* are described in this case study, which encompasses research conducted on these small pelagic fish species from the Gulf of California and Baja California as well as recent studies from the northern California Current system as far north as British Columbia in Canada. Additional studies exist on the diets of other clupeoid fishes such as Pacific herring (*Clupea pallasi*) and American shad (*Alosa sapidissima*) but are described elsewhere (Brodeur et al., 1987; Miller, 2006; Miller and Brodeur, in press).

The first gill rakers of Pacific sardine have been observed on the lower limb of the first gill arch in the form of five small protusions in a larva of 13.4 mm SL (Villalobos and Rodriguez-Sanchez, 2002). Fairly long (0.5-1.2 mm) gill rakers occur up to a fish size of about 35 mm SL (Villalobos-Ortiz, 1998), this size being the same as that recorded by Matarese *et al.* (1989), based on external morphological characters, as the size at which the transformation from the larval to the juvenile stage occurs. Because of the relatively poor development of gill
rakers until the fish is about this size, larval feeding is selective. Arthur (1956) concluded that
the crustacean food of sardine larvae is procured by visual detection and active attack.
Northern anchovy larvae adopt an S-posture, approach their prey by pectoral fin sculling and
finfole undulation, then open the mouth, straighten the body and engulf the prey (Hunter,
1972), and this is almost certainly true for *Sardinops* larvae as well as for many other clupeoids
(Hunter, 1981; Blaxter and Hunter, 1982).

At 50 mm SL the gill rakers of Pacific sardine are longer (1.4-2.6 mm) and number
around 42 on the lower part of the first gill arch (Villalobos-Ortiz, 1998), the denticles are just
beginning to develop (Scofield, 1934), and the fish can perhaps filter-feed. At about 70 mm SL
the gill rakers have reached their adult proportion and filter-feeding appears likely, and at 100
mm SL, the denticles are considered to be fully developed (Scofield, 1934). The pattern of
increase in gill raker number through the ontogeny of Pacific sardine can be described using an
asymptotic equation developed by Villalobos and Rodriguez-Sanchez (2002). Detailed
information on ontogenic changes in gill raker morphology of northern anchovy are not
available, but the number of gill rakers remains constant over the size range 80-140 mm SL
(James and Chiappa-Carrara, 1990; Chiappa-Carrara and Gallardo-Cabello, 1993) and is
substantially less than sardine of the same size range. In Pacific sardine, the gap between the
gill rakers on the first gill arch increases with fish size, from about 64 µm at 35 mm SL to 250
µm at 290 mm SL (Villalobos-Ortiz, 1998), this increase also being recorded by CICIMAR
(1983). Comparative analysis of Pacific sardine sampled from commercial catches at
Magdalena Bay, Baja California Sur, has shown that the gap between the gill rakers on the first
arch is relatively wide, being 127.6–132.0 µm (CICIMAR, 1983), whereas that for sardine
sampled from the Gulf of California was 90.2–96.5 microns (Molina-Ocampo, 1993). Whereas
some of the co-occurring small pelagic fish species in these areas have similar or narrower gill
raker gaps than shown by Pacific sardine (round herring *Etrumeus teres* has a gill raker gap of
97.5–107.0 µm; thread herring *Opisthonema libertate* of 60.6–64.4 µm; and anchoveta
*Cetengraulis mysticetus* of 59.5–61.3 µm; CICIMAR, 1983; Molina-Ocampo, 1993), these
species lack the highly specialized gill raker denticles characteristic of sardine. The gill raker
gap of northern anchovy also increases with fish size, from around 360 µm at 80 mm to 590
µm for fish of 145 mm SL (Chiappa-Carrara and Gallardo-Cabello, 1993), substantially wider
than that of the other species.

The most comprehensive study of the feeding of larval sardine and anchovy is the thesis
by Arthur (1956) who reported qualitative results from the examination of prey taxa of larvae
sampled in 1951 and 1952. Both species fed only during the day, and eggs, nauplii, and
juvenile stages of copepods composed almost all the identifiable food of sardine (Fig. 8.4a).
The diet of anchovy larvae (Fig. 8.4b) was found to be very similar, except that this species is
more euryphagous than that of sardine with about 40% of their diet (by number) consisting of
noncrustacean food particles. Laboratory studies have shown that northern anchovy larvae are
able to subsist for up to 20 days on a diet of the dinoflagellate *Gymnodinium splendens*, albeit
at a depressed growth rate (Hunter 1981). Copepod nauplii become increasingly important as
anchovy larvae increase in length and compose the bulk of particulate food when all sizes of
larvae are considered. The increase of prey size with larval growth is reported for both Pacific
sardine and northern anchovy larvae (Fig. 8.4c). Arthur (1976) reported that in one of his
samples most of the larger (>10 mm) specimens of both species were “literally crammed” with
the pteropod *Limacina bulmunoides*, with up to 50 pteropods in the intestine (compared with the normal one or two food items in the gut).

Berner (1959) also reported that copepod eggs and nauplii were found to be the most important element in the diet of larvae of *Engraulis mordax* sampled in 1954, although he pointed out that the size intervals of food (minimum and maximum) ingested by anchovy larvae of various sizes was wider than previously suggested. Berner (1959) showed monthly maps of distribution of feeding and non-feeding anchovy larvae captured in 1954 between Point Conception and the southern end of the Baja California peninsula and observed that stations occupied by feeding anchovy larvae were concentrated mostly north of Bahia Magdalena, Punta Eugenia and the Southern California Bight. The first two areas have been defined as Biological Action Centers (BAC; Lluch-Belda *et al.* 2000), where productivity is enhanced by topography when seasonal upwelling conditions are diminished or lacking. In theory, both processes develop favourable mixing conditions resulting in enhanced biological production. Thus, the Southern California Bight and BACs are areas of higher biological productivity that the rest of the California Current system where stations occupied by feeding anchovy larvae suggests that they take advantage of the favourable conditions available in these areas.

Lewis (1929) found a significant similarity between the species and numbers of diatoms and dinoflagellates in the digestive tract of adult Pacific sardine and those in surface plankton hauls, although crustaceans (particularly copepods) were at times also common in stomach contents. From this, Parr (1930) concluded that zooplankton was the principal food of sardine:
“both diatoms and dinoflagellates being merely incidental”. Radovich (1952) also showed that the bulk of the food was crustaceans. Sardine dietary data are less complete from the northern California Current as sardines were absent from this region for almost 50 years during their period of low abundance (see Barange et al., this volume and Alheit et al., this volume). In earlier samples from Vancouver Island, Hart and Wailes (1932) found sardine diet to be “mainly diatoms supplemented with copepods and other animals and plants”. Sardines again became available in the northern California Current in the 1990s (Emmett et al., 2005; McFarlane et al., 2005), and copepods (both adults and copepodites) and euphausiid eggs were the dominant prey by number in this region, with all other taxa together contributing only about 20% of the diet of sardine off Oregon and Washington. In terms of wet weight, however, adult euphausiids (comprising T. spinifera and E. pacifica) contributed ~50% and copepods 30% to sardine diet (Table 8.2). The remaining prey came from a diverse range of taxa although these contributed very little numerically or gravimetrically to the total diet. There was substantial spatial variability in sardine diet in the northern California Current, with fish off Washington feeding predominantly on phytoplankton (84% by weight) whereas those from Oregon, particularly those collected off the continental shelf, fed mainly on crustaceans (Emmett et al., 2005). There was also substantial between-cruise variability in the composition and amount of food consumed; however, there were no differences in feeding intensity among different times of day. Off British Columbia, McFarlane et al. (2005) found that five prey groups (phytoplankton, euphausiids, euphusiid eggs, copepods and larvaceans) made up the majority of prey consumed, but there was substantial interannual variability in their diets.
Fewer studies have been made of the food and feeding habits of *Sardinops* in Mexican waters. However, Radovich (1952) recorded gut contents in 24 fish (80 – 184 mm SL) from four Pacific localities off central Baja California in late September and early October and concluded that sardine was omnivorous and probably a non-selective filter-feeder on principally diatoms and dinoflagellates (Fig. 8.5a, b), and that the diet should therefore closely match what is available. Ramírez-Granados (1957) also reported on sardine off the Pacific coast and confirmed a general opinion that juvenile sardine fed mainly on crustaceans, but became almost exclusively a phytoplankton feeder (on diatoms) when larger (CICIMAR, 1983). Diatoms such as *Rhizosolenia*, *Bacteriastrum*, *Thalassiothrix*, *Melosira*, *Coscinodiscus*, *Amphora* and *Navicula* dominated ingested phytoplankton (almost 70% by number of total plant species), and adult and juvenile copepods the zooplankton component (nearly 90% of total animal groups); zooplankton predominated in fish of 84 – 100 mm SL in September, and in larger fish of 168 -190 m SL in November and December. Hence in addition to feeding on diatoms sardine are also able feed on zooplankton, especially copepods and invertebrate eggs.

In the Gulf of California, a detailed study was made by López-Martínez (1991), based on stomach contents from 90 fish (95 – 184 mm SL) caught in February 1990 just north of Isla Tiburon. She showed that zooplankton (especially calanoid copepods and larval brachyurans) was important in the smaller specimens (16% by volume), but that in the large size groups the diet became increasingly phytoplanktonic, with the diatom *Coscinodiscus* and dinoflagellate *Protoperidinium* predominating (zooplankton comprising only 2% volume); in general, sardine apparently ate what was available.
On an examination of stomachs of northern anchovy collected in northern Baja California, southern, and central California, Loukashkin (1970) suggested that the northern anchovy is an omnivorous species subsisting either on phytoplankton or zooplankton, or on both at the same time, feeding indiscriminately on planktonic organisms available within the area occupied. He found that zooplankters seem to be preferred in the anchovy diet (comprising 86.5% by number), of which the most frequently and abundantly dominant prey in the diets were crustaceans (50.8%), mainly copepods (29.3%) and euphausiids (9.5%) in all stages from eggs to adults, with the remainder of the diet consisting of zooplankters (35.8%), unidentified material (2.5%), and phytoplankton (11.0%; mainly diatoms [7.2%] belonging to the genus *Chaetoceros*, *Coscinodiscus*, and *Thalassiosira*). However, despite the fact that at times phytoplankton contributed up to 100% of the stomach contents (mainly in anchovy sampled in May and June, the season of peak phytoplankton blooms) their role in anchovy diet on the whole seems negligible. Baxter (1967) suggested that anchovy are indiscriminate filter feeders, and observed them to be predatory on small fish at times, even their own kind. Loukashkin (1970) agreed that northern anchovy is primarily a filter feeder, feeding mostly during the day, but he pointed out that it may also be a particulate or selective feeder, depending on the size of the available food. Loukashkin (1970) also pointed out that the same dual tendency in feeding patterns was observed in Pacific sardine, and that other planktophagous pelagic fish occurring with anchovy schools or in the general vicinity feed on the same plankton available to the anchovy.

Working in the Southern California Bight, Koslow (1981) made direct field measurements of northern anchovy feeding by collecting plankton samples from the wake of
feeding schools and comparing zooplankton species composition and size structure with control samples taken in front of or to the side of the school. Results indicated consistent, size-selective feeding on the dominant zooplankton taxa, which ranged from chaetognaths, small copepods such as *Clausocalanus*, *Ctenocalanus* and *Paracalanus*, copepods, and larvaceans. Koslow (1981) observed a significant positive relationship between the proportion of a taxa consumed and its size, and considered northern anchovy to be an effective size selective planktivore over a 1000-fold range in prey size. Preferential feeding on the basis of prey type was only observed for the large calanoid copepod *Calanus pacificus*.

Analysis of stomach contents of northern anchovy caught off the west coast of Baja California showed that whilst diatoms, anchovy eggs, crustaceans, dinoflagellates and protozoans numerically dominated anchovy diet (Fig. 8.5c, d), zooplankton (principally anchovy eggs and crustaceans) provided the bulk of dietary carbon (Chiappa-Carrara and Gallardo-Cabello, 1993). Peak feeding occurred shortly after dawn, and whereas northern anchovy filter-feed on prey 0.05-1.5 mm and particulate-feed on larger prey, size-selective, particulate-feeding on zooplankton was considered to be the dominant feeding mode (James and Chiappa-Carrara, 1990).

The numerically dominant prey taxa for anchovy in 1981 in the northern California Current were calanoid copepods and the pteropod, *Limacina helicina*, which together accounted for around 89% of the total number of prey consumed (Table 8.2). However, during the last few years, copepods were still important by number but the euphausiid, *Thysanoessa spinifera*, was the dominant prey by wet weight (~97%), with other taxa contributing less than
1% (Miller, 2006; Miller and Brodeur, in press). There was no evidence of phytophagy in either time period but since the sample size was relatively limited, we cannot say that anchovy in this region do not subsist partially on phytoplankton, but various types of microzooplankton and mesozooplankton appear to be the dominant prey overall (see also Brodeur et al., 1987).

Like many other clupeoid fishes with rather fine and numerous gill rakers, northern anchovy and Pacific sardine are considered both filter-feeders and particulate-feeders, although the relative importance of these two feeding modes is still not clear. Laboratory studies by Leong and O’Connell (1969) showed that northern anchovy capture *Artemia* nauplii by filter-feeding, but captured the much larger *Artemia* adults individually by direct biting (particulate-feeding) when each food was presented separately, and that food biomass was accumulated more rapidly by biting than by filtering. The authors hypothesized that the anchovy could not sustain its daily food requirements by filtering alone off southern California, except in limited areas of high plankton concentration. Later, O’Connell (1972) analyzed the role of biting activity as response of the fish to mixed size assemblages of food organisms. He concluded that the ratio of biting to filtering activity in small schools varies with the relative concentration of *Artemia* adults and nauplii in the water, and suggested that the anchovy is a selective feeder and that food-organism size is a major determinant of feeding mode choice.

Anchovy and sardine showed some overlap in the prey items consumed in the northern California Current, although there were some major differences in the relative amounts of prey taken. Diet overlap (Percent Similarity Index; PSI) was only about 3% by number but was close to 25% by weight, due to the common use of *T. spinifera* by both species. Anchovy
generally showed a higher overlap (mean PSI = 32.2%) with other nekton collected in the same
sampling than did sardine (7.9%), indicating a greater potential for trophic interactions (Miller,
2006; Miller and Brodeur, in press). Stable isotope analyses revealed distinct differences in
diets of the two species with anchovies being more enriched in $^{13}$C, and more dependent on
recently-upwelled production, than sardine. Anchovy also showed consistently higher $\delta^{15}$N
values than sardine when collected during the same sampling period, indicating that they fed at
a slightly higher trophic level than sardine (Miller, 2006). Examination of the prey sizes
showed further differentiation between the feeding of these species (Fig. 8.6). Although the
northern anchovy examined were substantially smaller than the Pacific sardine (mean length =
148.6 mm vs. 237.2 mm), they actually consumed significantly larger (t-test on log-
transformed data; $p < 0.001$) prey items (mean ± se = 6.12 ± 0.29 mm) than did sardines (2.98
± 0.09 mm), despite a similar range of prey sizes taken.

**The Humboldt Current upwelling system**

This case study reviews the trophic dynamics of small pelagic fish in the Humboldt
Current system with the emphasis on anchovy *Engraulis ringens* and sardine *Sardinops sagax*,
and notes on some trophic aspects for common sardine (*Strangomera bentincki*) off Chile.

In the first published work on feeding of larval anchovy off Peru, Rojas de Mendiola
(1974) showed that feeding was mainly diurnal and that the main prey items were copepod
eggs and nauplii, centric diatoms, and dinoflagellates, with selection by size appearing to
occur. As larvae increased in size they showed an increase in the zooplankton fraction in the
total diet, and by 10 mm larvae were feeding exclusively on zooplankton. Rojas de Mendiola
and Gomez (1981), and Ware et al. (1981), conducted ex-situ experiments that showed that the prolarval stage lasted 2.75 days at 18 ºC and that feeding started 40 h after the disappearance of the yolk, when the eyes were completely pigmented and the mouth open. The minimum concentration of food necessary to initiate first feeding was about 80 particles.ml$^{-1}$ for prey of 14-20 µm, and larvae did not feed on chain-forming phytoplankton but on round diatoms and dinoflagellates. The percentage of larvae feeding and gut fullness increased with age, and ingested prey width was also proportional to larval size and averaged 1-2% of body length.

In a comparative study on feeding by larval anchovy and sardine off Peru, Muck et al. (1989) showed that these species presented significant differences in the relationships between body length and mouth width, and between body length and gut length, with anchovy having a larger mouth than a sardine of the same size (Fig. 8.7), but with a shorter gut. In addition, the relationship between the proportion of larvae with mouth and eye functionality and SL showed that first feeding in anchovy starts at around 2.7 mm and is completed at a length of ca. 4 mm, whereas sardine start to first feed at ca. 4 mm and are all feeding by 5 mm. The minimum size of anchovy with food in the gut was 3.02 mm and for sardine was 4.07 mm. Additionally, the species and size composition of prey in the guts of first feeding larvae (anchovy of 3-3.5 mm SL and sardine of 4-4.5 mm SL) were significantly different, with anchovy feeding almost exclusively on a pure phytoplankton diet (comprising 77% by number of phytoflagellates and dinoflagellates, and with a mean width of 29.6 ± 25.3 µm) and sardine feeding almost exclusively on zooplankton (copepod eggs and nauplii, with a mean width of 72.1 µm; Muck et al., 1989). For older anchovy and sardine larvae (>5.5 mm) there was a wide overlap in diet for all stages of calanoid copepods, and phytoplankton was a less important prey item.
Valenzuela et al. (1995) studied the dietary composition and prey size of sardine and anchovy larvae off central Chile (32°S-33°S) and found that the diet of both species was composed mostly of copepod eggs (frequency of occurrence > 60%) but also some phytoplankton, with the diatoms *Skeletonema* and *Chaetoceros* contributing 89% by number of ingested phytoplankton cells. Anchovy did not show a significant relationship between prey width and mouth width whereas sardine did, indicating that the latter tends to feed on larger prey items with increasing mouth width and also with increasing body length. Anchovy ingested small particles independently of body size, with around 70% of the diet composed by prey having a width <10% of mouth width. In sardine, almost 60% of the diet consisted of prey of a width 20-30% of the mouth width. According to Valenzuela et al. (1995), the presence of phytoplankton in gut contents could be explained by fish ingesting zooplankton that had fed on phytoplankton or ingesting copepod faecal pellets.

Llanos et al. (1996) analyzed prey size of four Clupeiform larvae (sardine, anchovy, common sardine and Pacific menhaden *Ethmidium maculatum*) collected in Concepción Bay off central Chile. Anchovy ingested the largest particles, and *E. maculatum* the smallest, respectively. The gut contents of younger larvae contained small prey such as copepod eggs, nauplii, dinoflagellates and mollusc larvae, whereas older larvae also ingested larger prey such as copepodites. Llanos et al. (1996) and Balbontin et al. (1997) found that the quantitative increment in mouth width with larval size was similar and that the size range of particles in the diet overlapped widely in all four species, indicating a similar use of food resources.
According to Rojas de Mendiola (1989), the first reports on the food and feeding habits of adult anchovy off the Peruvian coast were published by Vogt (1940) and Sears (1941). However the first dedicated study of anchovy diet was performed by Rojas (1953), who observed a clear numerical dominance of diatoms in the diet with the most important species being *Coscinodiscus centralis*, *Coscinodiscus perforatus*, *Gyrosigma* sp. and *Thalassiothrix frauenfeldii*. Rojas de Mendiola (1989) compiled a database based on the frequency of occurrence of prey in anchovy stomach contents and synthesized information from studies conducted over the period 1953-1974. Key points that emerged were that the food and feeding habits of anchovy change with length, with larvae ingesting round diatoms, postlarvae feeding on zooplankton (primarily copepod eggs and nauplii), juveniles being largely zooplanktivorous and adults being mainly phytoplanktivorous. Pauly et al. (1989) summarized the database on anchovy dietary information from Alamo (1989) and Rojas de Mendiola (1989) for the period 1953-1982, and listed a total of 259 different food items that had been identified in anchovy stomach contents. Using results based on numerical abundance Pauly et al. (1989) suggested that in the north-central part of Peru anchovy rely less on zooplankton than in southern Peru; that the mean zooplankton fraction of anchovy diet increased with distance offshore; and that more zooplankton was consumed when sea surface temperature was high.

Research conducted during the 1990’s, also based on numerical abundance, showed that chain-forming (*Skeletonema*, *Chaetoceros* and *Thalassiosira*), group-forming (*Asterionellopsis*) and solitary (*Coscinodiscus*) diatoms, dinoflagellates (*Protoperidinium*) and copepods (*Centropages*, *Corycaeus*, and *Oncaea*) were important contributors to anchovy diet, with anchovy eggs making a less important contribution (Alamo et al., 1996a, b; Alamo et al.,
Chapter 8: Trophic Dynamics

During the main El Niño period, the trophic spectrum of sardine was represented by 23 genera of diatoms (mainly *Pseudonitzchia*, *Chaetoceros*, and *Asterionella*), seven dinoflagellate genera (mainly *Protoperidinium*), one silicoflagellate genus, copepods, euphausiids, amphipods, decapod zoea and megalope larvae, molluscs, and anchovy eggs (Blaskovic *et al*., 1998; Espinoza *et al*., 1998a). The numerical proportion of phytoplankton items was higher in sardine stomach contents than seen in anchovy (Fig. 8.8). Prey common to both fish species included the copepods *Calanus*, *Clausocalanus*, and *Corycaeus*, and the diatoms *Chaetoceros*, *Coscinodiscus*, and *Rhizosolenia*.

The large majority of published work describing the diet of anchovy and sardine off Peru considered phytoplankton to be as or more important than zooplankton. The first work that questioned this paradigm was by Konchina (1991), who showed that assessing the diet with qualitative, numerical ratios or frequencies of phyto- to zooplankton produced erroneous results. When prey weight was considered, the zooplankton fraction comprised 90% of anchovy stomach content mass and 50% for sardine, leading Konchina (1991) to conclude that
sardine is situated closer to the base of the food web than anchovy. Additionally, anchovy is able to eat macroplankton including migrating mesopelagic fish 5 cm long, and this ability to seek large, heavy, and high calorie food items over the continental slope provides this species with the opportunity to reach high levels of prey biomass, far surpassing that available to sardine.

Konchina’s (1991) conclusion regarding the trophic position of anchovy is supported by a recent extensive study performed by Espinoza and Bertrand (in press) who studied more than 21,000 anchovy stomachs sampled during 23 acoustic surveys conducted over the period 1996-2003. Numerically, phytoplankton dominated anchovy diet and comprised 99.52% of prey items whilst copepods only accounted for 0.07% by number. However, this view dramatically changes when the carbon content of prey items is considered; zooplankton was by far the most important dietary component (comprising 98.0% of dietary carbon), with a strong dominance of euphausiids (67.5%) followed by copepods (26.3%) (Espinoza and Bertrand, in press). Previous studies that concluded that the diet of Peruvian anchovy was mainly based on phytoplankton, or that phytoplankton and zooplankton played a similar role, were based on qualitative descriptions of anchovy diet such as frequency of occurrence and numerical percentage, rather than carbon content. Espinoza and Bertrand (in press) also showed that stomach fullness varied with latitude, with higher values encountered off northern (<6ºS) and southern Peru (>13ºS), and that stomach fullness also increased with distance from the coast and often reached maximum values at stations more than 120 km from the coast. However, these mean patterns were not a good representation of reality at any one moment, and those authors emphasized the marked variability in stomach content fullness data between surveys,
illustrating anchovy's plasticity: "inside its range of overall viable conditions anchovy is therefore able to forage efficiently at any time, any place, and any temperature" (Espinoza and Bertrand, in press).

Estimates of ingestion rate, gastric evacuation rate, and daily ration of Peruvian anchovy have been estimated through analysis of diel dynamics in stomach contents, and are summarized in Table 8.3. Pauly et al. (1989) reported that feeding starts near noon and is continuous until near midnight, and estimated a daily ration of 0.45 g·d\(^{-1}\) (mixed phyto- and zooplankton) for anchovy with a mean live weight of 20.4 g. During the El Niño of 1997-98, estimated daily ration showed a declining trend from March 1997 until end of winter 1998 (Table 8.3), but by November-December 1999 it was similar to that computed by Pauly et al. (1989), suggesting the return to pre-El Niño values. All daily ration estimates assume anchovy to have a marked diurnal feeding cycle. Espinoza and Bertrand (in press) studied variability in stomach fullness with respect to the time of the day using generalized additive models (GAMs), and their results confirmed that the main feeding activity occurred during daylight hours, between 07h00 and 18h00 (Fig. 8.9). Whilst this general pattern was observed for most surveys, nighttime feeding was important in in some cases.

Off Chile, the first descriptive studies on the feeding of *E. ringens* were carried out by Mann (1954) and De Buen (1958). Trophic studies including analysis of the trophic spectrum and seasonal variations in the diet on common sardine (*Strangomera bentinckii*) and anchovy from the central-south area of Chile were carried out by Arrizaga and Inostroza (1979), Arrizaga (1983), and Arrizaga et al. (1993). Those authors concluded that the two species
exhibited the same feeding strategy and used the same prey resources, both species feeding
almost exclusively on a pure phytoplankton diet, particularly on diatoms of the genus
Skeletonema. Zooplankton was scarcely represented, accounting for <1 % by number and
consisting mainly of copepod remains. Nevertheless, a recent study carried out by Rebolledo
and Cubillos (2003) point out that on the basis of frequency of occurrence data, phytoplankton
and zooplankton are of comparable importance in the diet of both species. Trophic studies
conducted off Chile indicate that the diatoms Skeletonema, Chaetoceros, Nitzschia and
Coscinodiscus are the most important phytoplankton prey for both common sardine and
anchovy, and both species appear to show a preference for Skeletonema, although this may be
an artefact of the tendency of this diatom to form chains and its high level of abundance. Of the
zooplankton, copepods and other crustaceans showed the highest frequency of occurrence for
both species, followed by invertebrate eggs in the case of common sardine and cirripede larvae
in the case of anchovy (Rebolledo and Cubillos 2003). Both species exhibit a high degree of
trophic overlap for phyto- and zooplankton prey, and hence are assumed to be positioned at the
same trophic level (Arrizaga et al., 1993). Finally, using stable isotope analysis Hückstädt et al.
(2007) estimated the trophic level of anchovy to be 3.63, indicating a strong preference for
zooplankton and supporting the results obtained by Espinoza and Bertrand (in press) for
anchovy in the northern Humboldt.

Balbontín et al. (1979) carried out laboratory experiments by supplying pieces of fish
liver in order to determine the preference for prey size for E. ringens and S. bentincki, and
showed that a particle having a volume <6 mm$^3$ is preferred by anchovy, while common
sardine preferred particles <4 mm$^3$. Filter-feeding was the most usual feeding mode in common
sardine whereas anchovy tended to particulate-feed (bite) on food particles. Those authors hypothesized that the larger particles ingested by anchovy could be a comparative advantage in terms of energy intake compared to common sardine.

The Northwestern Pacific (Kuroshio Current) system

This case study reviews the trophic ecologies of Japanese sardine *Sardinops sagax melanostictus* and Japanese anchovy *Engraulis japonicus*, two dominant and alternating small pelagic fish distributed in the northwestern Pacific, including the warm Kuroshio Current system. Some studies on the diets of other small pelagic fish from this region have been reported, including Pacific round herring (*Etrumeus teres*) and Pacific herring (*Clupea pallasii*) (see Nakai *et al.*, 1955; Yokota *et al.*, 1961; Hirota *et al.*, 2003; and Tanaka *et al.*, 2006 for round herring; and Irie *et al.*, 1979 for herring), but are not described here.

Japanese sardine has been recognized as planktivorous since the early study by Kishinoue (1908), although the size and type of plankton that comprises the food of this species changes with development. Copepod eggs and nauplii are the dominant food items during the post-larval stage (<10 mm total length [TL]; Yokota *et al.*, 1961; Nakai *et al.*, 1962; Kidachi, 1968; Nakata, 1988; Nakata, 1995; Hirakawa and Goto, 1996). Yokota *et al.* (1961) reported that copepod nauplii of 150-200 µm in length are fed on by larvae of several pelagic fishes including Japanese sardine, and Nakai *et al.* (1962) revealed that the size of nauplii ingested is related to fish size; sardine <5.8 mm TL fed mainly on nauplii 60-80 µm wide whereas sardine of 11-14 mm TL fed on nauplii of 200-300 µm wide. Hirakawa and Goto (1996) identified ingested nauplii to genus, finding that nauplii of *Oithona* spp. and *Paracalanus* spp. dominated the alimentary tract of sardine larvae of
Juvenile sardine tend to feed on larger prey items such as copepodite or adult stages of copepods, other crustacean zooplankton, appendiculata, and planktonic larvae of various animals (Yamashita, 1955; Yokota et al., 1961; Nakai, 1962; Watanabe and Saito, 1998; Tanaka 2006).

Copepods are generally dominant, with calanoid (e.g. *Paracalanus, Calanus*) and poecilostomatoid (e.g. *Oncaea, Corycaeus, Oithona*, and *Microstella*) copepods frequently found in stomach contents. Phytoplankton such as diatoms are ingested by sardine from a size of approximately 40-50 mm body length, arising from the development of the gill rakers (Yamashita, 1955; Nakai, 1962), although phytoplankton is more often found in the stomachs of larger fish.

Sub-adult and adult sardine feed omnivorously on plankton, and whilst copepods are important prey items, phytoplankton such as diatoms have often been reported as “dominating” sardine stomach contents (Kishinoue, 1908; Nakai, 1938; Nakai et al., 1955; Yamashita, 1955; Li et al., 1992), sometimes by volume (Kawasaki and Kumagai, 1984) or weight (Hiramoto, 1985). Genera of diatoms frequently found in sardine stomachs include *Chaetoceros, Skeletonema, Rhizosolenia, Coscinodiscus, Thalassiosira, Thalassionema, Nitzschia*, and *Eucampia* that are captured via filter-feeding (Azuma, 1994). Differences in the specific composition of stomach contents (e.g. dominance by copepods or diatoms) depend upon locality and season (Nakai, 1962) and sardine migration patterns (Hiramoto, 1985). However, Kishinoue (1908) and Nakai (1938) both noted that fish with a high degree of stomach fullness always had zooplankton-filled
stomachs, whereas those having a low degree of fullness had stomach contents dominated by phytoplankton. In some cases, adult sardine feed on fish eggs and larvae; Kidachi (1968) noted that the eggs of Japanese anchovy are sometimes found to dominate sardine stomach contents, and Azuma (1994) reported egg cannibalism by sardine during their spawning season. Feeding usually occurs in the daytime for all sardine life history stages from larvae to adult (Yoneda and Yoshida, 1955; Nakai et al., 1962).

The feeding habits and trophic level of Japanese anchovy are generally considered to be similar to those of Japanese sardine. Anchovy post-larvae of <10 mm TL feed mainly on copepod eggs and nauplii (e.g. Nakai et al., 1962; Kuwahara and Suzuki, 1984; Hirakawa and Ogawa, 1996; Hirakawa et al., 1997), and both size and the taxonomic groups of copepods ingested (e.g. *Paracalanus* spp. and *Oithona* spp.) are similar to those fed on by sardine. Copepodite and adult stages of copepods are important in the diet of anchovy of 10-40 mm TL, among them *Paracalanus* spp. and *Oithona* spp. that were frequently found in anchovy from Pacific coastal waters (Uotani et al., 1978; Uotani, 1985; Mitani, 1988). Poecilostomatoid copepods (e.g. *Oncaea* spp. and *Corycaeus* spp. of approximately 200-400 μm in width) often dominate stomach contents of juvenile and mature anchovy of >40 mm TL (Takasuka, 2003; Tanaka, 2006; Tanaka et al., 2006). Diatoms have also been found in stomach contents of juvenile and mature anchovy (Nishikawa, 1901; Nakai et al., 1955; Yamashita, 1957; Shen, 1969; Li et al., 1992), following gill raker development and therefore the ability to filter-feed. Large organisms such as euphausiids, larvae and eggs of fish and other animals are also ingested by anchovy, and the larvae of benthic animals such as bivalves and decapods are found in anchovy stomachs from fish collected from inshore habitats compared to those
collected from offshore habitats (Tanaka, 2006). Cannibalism is sometimes found in sub-adult and mature fish (Takasuka et al., 2004). In general, however, copepods of small size are considered to be the dominant dietary component of Japanese anchovy juveniles and adults. Feeding by anchovy occurs usually in the daytime (Nakai et al., 1962; Uotani, 1985).

Whereas the feeding habits of Japanese sardine and anchovy are generally similar for all developmental stages, comparative studies suggest some notable differences. Nakai et al. (1955) reported that although sardine and anchovy juveniles and adults both feed mainly on copepods and diatoms, the frequency of occurrence of phytoplankton is higher in sardine stomach contents than in anchovy stomach contents. Li et al. (1992) compared the prosome length of copepods ingested by the two species and showed that the mode for sardine occurs at a smaller size than for anchovy (Fig. 8.10). These differences may be due to differences in gill raker structure and hence differing retention abilities, since sardine have a higher number of gill rakers, and a smaller gap between gill rakers, than do anchovy of the same size (Fig. 8.11; Nakai, 1938; Tanaka, 2006).

However, Li et al., (1992) concluded that competition for food might play an important role in anchovy and sardine dynamics because of the overlap in dietary spectrum between the two species. Recently, Tanaka (2006) compared stomach contents of the two species collected at the same time and found that in the case of juveniles, stomach contents were very similar for anchovy and sardine of a similar size. However, significant differences were observed in the diets of sub-adults of similar size, with anchovy stomach contents being mainly composed of small copepods whereas sardine stomachs were filled with thousands of euphausiid eggs. Interestingly, the width of the euphausiid eggs fed on by sardine was similar to, or even larger than, that of the copepods fed on by anchovy. This phenomenon may be explained by a differential ability to retain
euphausiid eggs (*e.g.* due to differences between anchovy and sardine of the mouth or other feeding structures such as the epibranchial gland) rather than by differences in gill raker spacing. The fact that sardine shows a feeding behaviour known as “gulping”, which is intermediate behaviour between particulate- and filter-feeding and during which fish ingest a few particles in one mouth-opening act (Azuma 1994), may possibly also be involved. In summary, substantial dietary overlap between anchovy and sardine occurs from the larval to juvenile stages, which implies potential competition between the two species at these life history stages. In the sub-adult and adult stages, however, sardine shows a higher degree of herbivory, and consumes smaller zooplankton, than does anchovy. Additionally, sardine also appear to be better able to retain what may be called “elusive” prey organisms (such as euphausiid eggs) that have a smooth membrane and are not efficiently retained by anchovy, most likely due to differences in morphology (of the gill raker but possibly also other feeding structures such as the jaw) and in feeding behaviour.

### The Northeastern Atlantic and Mediterranean systems

This case study is an updated review of published and unpublished information on feeding habits and trophic ecology of sardine (*Sardina pilchardus*) and anchovy (*Engraulis encrasicolus*) in waters around the Iberian Peninsula, including the Atlantic and Mediterranean shelves. The original information was provided by studies of morphology (Andreu, 1953, 1960, 1969), abundance (ICES, 2005) and trophic ecology (see Tables 8.4 and 8.5) of the selected species. Trophic studies included either analysis of stomach contents (generally by prey abundance but also by biovolume; most recently by estimation of prey carbon content) or stable isotope composition (carbon and nitrogen isotopes in muscle).
Studies on the morphology of the feeding apparatus in the Iberian region are available mostly for sardine, although some measurements were also made on anchovy (Andreu, 1953, 1960, 1969). The larvae of both species lack the mechanism for concentrating planktonic particles and must capture individual prey. The filtering apparatus of juvenile and adult *S. pilchardus* was described in detail by Andreu (1969), with some data for *E. encrasicolus* for comparison. The main components of this apparatus are the five pairs of branchial arches, each supporting one series of gill rakers covered with denticles on the anterior side and branchiae on the posterior (the latter are only found on the first four branchial arches). The gill rakers develop along the supporting basihyal bones and those of the first arch over the sides of the tongue, thus forming an efficient filter for food particles. Gill rakers appear when sardines reach 15 mm in length and increase in number and size with growth (Fig. 8.12a). In contrast, the number of gill rakers does not vary significantly with body length in anchovy. The separation between gill rakers, as well as the number and separation between denticles, increases as a power or logarithmic function of size (Fig. 8.12b). The power coefficients are <1, as the rate of increase in both number and separation of gill rakers and denticles decreases with size. Considering the sardines sampled at Vigo (Galicia, NW Spain), the morphology of the gill rakers changes little after they reach 15-20 cm in length, suggesting that the filtering apparatus is fully developed in sardines after they reach the first year of life (ICES, 2005). The mesh formed by gill rakers and denticles is about 40 μm on average, although sardines can capture particles smaller than this size (Garrido et al., 2007). Gill rakers are also present in anchovy, but are present in lower numbers and are more widely separated than in sardine (Fig. 8.12a, b). In addition, the gill raker gap increases at a faster rate with fish size in anchovy than in sardine (Fig. 8.12b), indicating that anchovy is less suited to filter-feeding than is sardine. Other co-occurring planktivorous species such as *Trachurus*...
trachurus and Sprattus sprattus display gill raker gaps similar to those of anchovy and clearly larger than those of sardine (Andreu, 1969).

The morphological studies conducted by Andreu (1969) also detected substantial differences in the number of gill rakers and the separation between gill rakers of sardine from different regions; those from the Mediterranean Sea have fewer gill rakers that are more widely separated than sardine from Atlantic waters. This was explained as an adaptation to the higher plankton abundance in the Atlantic, which would benefit filter-feeding, while Mediterranean sardines would preferentially capture individual prey (Andreu, 1969).

The variability of prey items found in the stomachs of S. pilchardus has puzzled scientists for a long time; earlier reports indicated the presence of items as varied as mud (Lebour, 1920, 1921) or even pollen from terrestrial plants (Oliver, 1951; Oliver and Navarro, 1952), but mostly cited the numerical dominance of phytoplankton as preferred prey. The composition of diet varied largely among the first quantitative studies, ranging from reports of almost purely herbivorous to zoophagous diets (Table 8.4). As a result, S. pilchardus became considered as an opportunistic feeder, the composition of stomach contents reflecting prey availability in the water. In this way, phytoplankton cells were less abundant in the stomachs of sardines from the Mediterranean compared to those from the Atlantic (see review in Andreu, 1969).

When estimates of sardine diet composition were made taking account of prey biovolume or weight, the dominance of zooplankton became apparent. The same occurred when the carbon content of the prey was estimated (Garrido et al., in press). The dominance of zooplankton
biomass in sardine stomach contents (on average ca. 70%) is reflected by the stable isotope
collection of muscle, which represents the diet integrated over a longer period than can be
observed when analysing stomach contents. Isotopic studies suggested that most of the nitrogen-
forming structural muscle proteins in adult sardines originated from the assimilation of
zooplankton, while only a small portion of carbon could be derived from phytoplankton (Bode et
al., 2004). Copepods, generally the group dominating total zooplankton biomass such as *Acartia
clausi*, *Temora* spp. and other calanoids, or cyclopoids such as *Oithona nana* and *Oncaea* spp.
(Massuti and Oliver, 1948; Varela *et al.*, 1990; Garrido, 2002; Cunha *et al.*, 2005; Garrido *et al*.,
in press), were also dominant in sardine stomach contents. In some cases, reports focus on species
well recognizable in stomach contents such as *Euterpina acutifrons* and species of *Micosetella*,
*Corycaeus* and *Centropages*, noting that many others, particularly small individuals, are difficult
to recognize because of partial digestion (e.g. Massuti and Oliver, 1948). Other zooplankton
groups such as tintinnids or cladocerans, were also among the most abundant prey both in the
Mediterranean (Massuti and Oliver, 1948) and the Atlantic (Navarro and Navaz, 1946; Varela *et al*.,
1988, 1990; Garrido, 2002; Cunha *et al.*, 2005; Garrido *et al*., in press). Fish eggs in sardine
stomach contents have also been noted (Silva, 1954; Varela *et al.*, 1988; Garrido, 2002), and one
study has considered fish eggs as a major contributor to sardine dietary carbon off the Iberian
Peninsula, especially during the winter months (Garrido *et al.*, in press).

There are no detailed data on diel variability in sardine feeding but some information from
the Mediterranean suggests that feeding activity occurs mainly during daylight (Andreu, 1969).
Seasonal variability in sardine feeding intensity has been recently documented for fish sampled off
western and southern Portugal (Garrido et al., in press), with the relative contribution by phytoplankton (including dinoflagellates and diatoms) being highest in spring and summer. Phytoplankton appears to increasingly contribute to the food of sardine as they become larger, as shown by both stomach content (Massuti and Oliver, 1948) and isotope studies (Bode et al., 2003). Such ontogenic change in diet can be related to changes in the morphology of the feeding apparatus, which is fully developed at sizes above 15 cm in length (Andreu, 1969). Large sardine are able to take full advantage of filter-feeding because they can swim at the required speed for capturing diluted prey (Cushing, 1978). In contrast, the filtering apparatus of young individuals is insufficiently fine, hence small fish rely on the capture of individual prey via particulate-feeding. Recent experimental work has shown that filter-feeding appears to be the dominant feeding mode of adult *S. pilchardus* and that the switch to particulate-feeding occurs at a particle size of around 750 µm, that this species is able to entrap phytoplankton cells as small as 4 µm during filter-feeding, and that sardine show selective feeding, preferentially ingesting fish eggs compared to other prey types when fed cultured, mixed prey assemblages and selecting copepods and decapods over other zooplankton prey when fed wild-collected, mixed prey assemblages (Garrido et al., 2007). Whereas phytoplankton may be captured incidentally by sardines when using filter-feeding to feed on copepods, as suggested by (Cushing, 1978), the large amount of phytoplankton biomass that is occasionally found in sardine stomach contents (e.g. Cunha et al., 2005) calls for more studies. To date there is no specific information on the direct contribution of organic matter from phytoplankton to the nutrition of *S. pilchardus*, although recent estimates indicate this to be significant with average annual values of phytoplankton carbon ranging between 14.0 and 19.4% of total stomach content carbon for fish sampled off the south
and west coasts of Portugal, respectively (Garrido et al., in press). Dinoflagellates were generally
dominant over diatoms in stomach contents both in Mediterranean (Massuti and Oliver, 1948) and
Atlantic waters (Garrido et al., in press), although the presence of diatoms may increase in spring
in the latter (e.g. Varela et al., 1990; Garrido, 2002). An additional interest regarding feeding on
phytoplankton by sardines is their role as vectors of phytoplankton toxins to upper trophic levels
(Costa and Garrido, 2004).

In contrast to results found for adults, the food of sardine larvae is almost exclusively
composed of zooplankton. Among these, eggs and early developmental stages of copepods
constitute the bulk of contents, either by numerical abundance (Lebour, 1920, 1921; Conway et
al., 1994; Fernández and González-Quirós, 2006; Munuera, 2006) or by their contribution to total
ingested carbon (Munuera, 2006). The maximum size of prey consumed increases with larval size,
although larger larvae continue to feed on a high proportion of small particles. Copepod eggs up to
183 μm in diameter were consumed mostly by larvae of intermediate sizes (10-15 mm), and the
largest larvae (13 to 22 mm) fed almost exclusively on nauplii and copepodites of calanoids such
as Paracalanus, Pseudocalanus and Clausocalanus (Conway et al., 1994; Fernández and
González-Quirós, 2006; Munuera, 2006). Whilst phytoplankton remains were generally rare in
larval sardine stomach contents, larvae have been reported as feeding exclusively on
phytoplankton in some instances (Rasoanaviro et al., 1991), and phytoplankton may also
constitute unidentified residuals in stomach contents (Conway et al., 1994). Seasonal variations in
stomach contents of larvae are small, suggesting that they are largely specialised in their food
preferences, although their stable isotopes content reveals that larvae are able to track seasonal
changes in the isotopic signature of plankton (Munuera, 2006). Significant changes, however,
were found in larval stomach contents during daily cycles (Conway et al., 1994; Munuera, 2006), with maximum feeding following dawn (Fernández and González-Quirós, 2006) but also occurring in the afternoon. Diurnal feeding patterns varied according to location, particularly in coastal areas (Munuera, 2006).

There is surprisingly little information on the diet and feeding rates of *E. encrasicolus* in European waters. To our knowledge there are only three papers dealing with the diet of adults in the Mediterranean (Tudela and Palomera, 1995, 1997; Plounevez and Champalbert, 2000), one for adults in the Bay of Biscay (Plounevez and Champalbert, 1999), two on larvae in the Mediterranean (Conway et al., 1998, Tudela et al., 2002), and a PhD thesis with some information on larval anchovy diet in the Bay of Biscay (Munuera, 2006). In all cases, however, the bulk of the diet determined from stomach content analysis is composed of zooplankton. Whereas the scarcity of data precludes the extraction of general patterns for this species there are a number of observations worth mentioning.

Copepods dominate the diet composition of adult anchovy, with the genera *Centropages* (*C. typicus* and *C. chierchiae*) and *Temora* (*T. stylifera* and *T. longornis*) appearing as important food items both in the Mediterranean and the Bay of Biscay. Small cyclopoids of the genera *Oncaea, Oithona* and *Corycaeus*, and small calanoids such as *Clausocalanus, Pseudocalanus*, and *Paracalanus* also occur regularly in stomach contents of anchovy from in both areas (Plounevez and Champalbert, 1999, 2000). Two copepod species, *Candacia armata* and the harpaticoid *Microsetella rosae*, appear as an important food source in the Mediterranean but not in the Bay of Biscay. Large items such as fish larvae, euphausiids and larger copepods (*Candacia, Temora,*
Centropages) often dominate in terms of prey biovolume in adult anchovy stomach contents (Plounevez and Champalbert, 2000).

Tudela and Palomera (1997) report that although *E. encrasicolus* is mainly a diurnal feeder there is a difference between the size of prey consumed during the day and during the night, with copepods and other small prey ingested during the day and the occasional presence of decapod larvae and mysids observed in the stomach contents of fish sampled at night. Plounevez and Champalbert (1999) also observed that gut fullness in the plume of the Gironde River was about half that in offshore waters, although the concentration of zooplankton in the river plume was twice as high that in offshore waters. Both observations can perhaps be related to visual acuity (Fiksen *et al*., 2005), since anchovy are only able to detect large prey at night, and will also experience reduced visibility in the turbid waters of the Gironde river plume.

Studies on anchovy in the Mediterranean do not report cannibalism (Tudela and Palomera, 1997; Plounevez and Champalbert, 2000), whereas in the Bay of Biscay anchovy eggs were systematically observed in stomach contents of adult anchovies (Plounevez and Champalbert, 1999). It is difficult to ascertain whether this difference reflects a difference in behaviour or methodological differences (season and time between capture and spawning allowing for digestion of eggs).

A detailed study by Conway *et al* (1998) on anchovy larvae in the Adriatic Sea indicated that copepod eggs and nauplii, in particular cyclopoid nauplii, dominated the diet of smaller (< 6 mm) larvae; from this size onwards the copepod *Oithona spp.* became the dominant item in the diet.
diet, comprising 25-75% (by number) of the items in the gut. Conway et al. (1998) also reported observing the dinoflagellate *Peridinium* and pollen in the guts of larvae. The two other studies also report a diet dominated by copepod eggs, nauplii and copepodites (Tudela et al., 2002; Munuera, 2006), with larger larvae showing an increase in the size range of ingested prey in parallel with an increase in the incidence of copepodites in the diet. However, biochemical measurements such as lipid composition (Rossi et al., 2006) suggest that microzooplankton might be an important component of the diet of early anchovy larvae. Furthermore, Munuera (2006) did not find differences in the isotopic signature of sardine and anchovy larvae from the Bay of Biscay, indicating that both are at the same trophic level. Bergeron (2000) analysed digestive enzymatic activity of anchovy larvae in the Bay of Biscay, and found a clear spatial pattern in nutritional condition which increased from the middle shelf towards the shelf edge, perhaps associated with the increased planktonic productivity of the shelf edge (Albaina and Irigoien, 2004). Bergeron (2000) also observed that after a strong wind event the nutritional condition of the larvae decayed, suggesting a negative effect of strong turbulence on ingestion.

Information on the diets of anchovy and sardine indicates that both species share a common trophic resource, as the identified plankton species are roughly the same and the two species are distributed over basically the same geographic area. Thus trophic level estimates using either average dietary data (Froese and Pauly, 2006) or stable isotope content of muscle (Bode et al., 2006; Munuera, 2006) are remarkably similar for both species. Such estimates, however, are only valid for large spatial and temporal scales, where individual and instantaneous feedings are largely integrated. The ample variability of actual diets with spatial locations and the mobility of these species would likely compensate for their trophic overlap. In addition, the morphology of
the feeding apparatus of sardine is more adapted to filter-feeding than that of anchovy, thus
creating a potential mechanism to avoid food competition.

The Northwestern Atlantic system

Menhaden (the genus *Brevoortia*) species occupy a unique ecological niche in the food webs of estuarine and coastal ecosystems of North and South America. Like other small pelagic fish menhaden are a schooling species that feed on plankton; what is atypical about menhaden is the size spectra of the food items they consume — menhaden feed directly on nanoplankton. Coupled with the fact that some of the species of menhaden occur in great numbers, they take on an ecological role in the trophic structure of these ecosystems. The menhaden species of the US East Coast and Gulf of Mexico, *Brevoortia tyrannus*, *B. gunteri*, and *B. patronus*, have been the most studied species of the genus, thus most of this discussion is conditioned on data from experimental and field studies on these species.

For a relatively large animal, Atlantic menhaden are able to filter extremely small plankton particles. The small and fragile nature of their food items has made it difficult to characterize their diet, a problem compounded by the fact that Atlantic menhaden diet changes ontogenetically with changes in the morphology of their mouth parts and branchial basket used to feed. First-feeding Atlantic menhaden larvae feed on individual plankton particles such as large dinoflagellates and zooplankton (Chipman, 1959; June and Carlson, 1971), and continue to feed in this manner until they metamorphose into juveniles, at which time their branchial baskets and gill rakers adapt to filter-feeding.
As juveniles and adults, Atlantic menhaden are omnivorous, feeding on both phytoplankton and zooplankton. Chipman (1959) and June and Carlson (1971) examined the stomachs of post-metamorphic juveniles and observed a variety of phytoplankton and zooplankton prey in the diet. They also noticed that juveniles consumed smaller food items than younger larvae. Adults, like the juveniles, also feed on phytoplankton and zooplankton (Peck, 1893). These observations led Peck (1893) to suggest that Atlantic menhaden diet was simply a reflection of the composition of the plankton where the fish were feeding; this hypothesis holds true today and is further supported by field studies and laboratory experiments. Jeffries (1975) characterized the contribution of zooplankton to the diet of juvenile Atlantic menhaden and found the fish adaptable to local plankton availability. Lewis and Peters (1994) showed that Atlantic menhaden can derive nutritive value from the detrital cellulose they consume along with phytoplankton and zooplankton. These studies reinforce the idea that Atlantic menhaden diet can be qualitatively described by the composition of the plankton. Owing to difficulties in measuring menhaden stomach contents, we must rely on feeding studies to predict what portion of the plankton community menhaden consume.

Ontogenetic change in the structure of the gill rakers results in an ontogenetic change in the filtering ability of menhaden over the size spectra of juvenile to adult. Atlantic menhaden filtering efficiency has been measured with two experiments that characterized particle retention over an ecologically relevant size spectrum of plankton. The study done with large migratory adult Atlantic menhaden (≈260 mm fork length, FL) showed that older menhaden had a minimum particle threshold size of 13 μm diameter (Durbin and Durbin, 1975); however, the clearance rate data for these fish also suggests that significant retention (10% efficiency) does not occur for
particles <30 μm in diameter. Adult fish were highly efficient when filtering zooplankton. The second study was done with Atlantic menhaden of a transitional size between juvenile and adult (≈14 cm FL), and showed that the menhaden feeding apparatus changes ontogenetically since these fish were able to retain particles as small as 5-7 μm and showed significant retention efficiencies for particles of 7-9 μm (Friedland et al., 1984). However, these fish filtered some zooplankton at a lower efficiency than phytoplankton, suggesting they have maximum filtration efficiency at a size intermediate between phytoplankton and zooplankton.

The gill rakers of Atlantic menhaden form a physical sieve that retains plankton particles (Monod, 1961; Friedland, 1985). Menhaden, like other filter-feeding species (MacNeill and Brandt, 1990; Matsumoto and Kohda, 2001; Tanaka et al., 2006), show an ontogenetic shift in the physical dimensions of the apertures of the sieve formed by their gill rakers (Fig. 8.13). In Atlantic menhaden, this shift is allometric, adapting various sized menhaden to the habitats they utilize. Menhaden juveniles retain the ability to filter the smallest size fractions of plankton while they reside in estuaries. The transition to larger gill raker apertures coincides with their migration to coastal ocean habitats characterized by plankton communities with lower concentrations of phytoplankton biomass and a general shift to larger sized particles, including higher concentrations of zooplankton (Hulbert, 1963; Malone and Chervin, 1979; Muylaert and Sabbe, 1999; Sin et al., 2000; Kimmel et al., 2006). Therefore, as migratory fish they filter more water to concentrate food, which would be hydrodynamic and energetic burdens if they retained the raker spacing they had as juveniles. The allometry in gill raker apertures also affects the foraging of the size range of adult Atlantic menhaden, which find themselves competing with other clupeid fish such as American shad (Alosa sapidissima; Munroe, 2002), and Atlantic herring (Clupea...
harengus; Gibson and Ezzi, 1992). These species are able to particulate-feed in addition to filter-
feeding, and are thus less likely to make much use of phytoplankton by direct filtration. The
ontogenetic changes in Atlantic menhaden appear adapted to allow this species to filter smaller
particles than other clupeid fishes.

Resource partitioning among menhaden species has also been observed based on
functional morphology and feeding studies of fish from the Gulf of Mexico. Castillo-Rivera et
al. (1996) examined the trophic morphology of finescale menhaden (Brevoortia gunteri) and
gulf menhaden (B. patronus), and reported that B. patronus has more denticles per mm of gill
raker and significantly longer gill rakers, than does B. gunteri. Hence B. patronus has a finer-
meshed branchial apparatus, and should be able to retain smaller food items, than B. gunteri.

Analysis of the dietary components of these two species showed a significant difference in
their diets, with zooplankton (tintinids, ostracods and calanoids) predominating in B. gunteri
stomachs whereas phytoplankton comprised the majority of stomach contents of B. patronus
(Fig. 8.14). In addition, B. patronus has longer epibranchial organs (responsible for the
concentration of food particles by microphagous fish, with development of this organ
appearing to be related to the degree of microphyag; Blaxter and Hunter, 1982) and a
significantly longer intestine, than does B. gunteri, providing further support for the hypothesis
that the former exhibits a higher degree of phytophagy than the latter.

The relationship between menhaden and plankton is also distributional in nature. Of the
suite of physical and biological parameters that control menhaden migration and local movement,
the distribution of food resources appears to be of primary importance. The distribution of Atlantic
menhaden juveniles is correlated with gradients of plankton biomass reflecting gradient search
behaviour of the fish (Friedland et al., 1989; Friedland et al., 1996). Though not as clearly
defined, the meso-scale distribution of adult gulf menhaden in the Gulf of Mexico also appears to
be conditioned by similar mechanisms (Kemmerer et al., 1974; Kemmerer, 1980).

The Baltic Sea system

The clupeids herring (Clupea harengus L.) and sprat (Sprattus sprattus L.) are the
commercially important small pelagic fish species in the Central Baltic Sea, and the main
planktivores in the area (Möllmann et al., 2004). Herring spawn benthic eggs in coastal areas and
use the deep basins of the area as feeding grounds. There are both autumn- and spring spawners
with the latter presently dominating for unknown reasons (Parmanne et al., 1994). Beside the
abundant Main Basin Herring (stocks assessed in ICES Sub-division 25-29+32, excluding the
Gulf of Riga; ICES 2006), a number of coastal and gulf stocks exist in the Baltic Sea (Aro, 1989).
Even more uncertainty exists about the structure of the sprat stock(s). Sprat are generally spring-
spawners and show the opposite behaviour to herring, i.e. they spawn in the deep basins and have
their main feeding areas in shallower waters (Aro, 1989). The biomass of the main basin herring
stock declined continuously during the recent three decades, while the sprat stock increased to
unusually high levels since the 1990s (see Barange et al., this volume). In this case study we
describe the trophic ecology of the two species and summarize the processes which potentially led
to these opposite trends in stock size.

Numerous studies on the feeding ecology of herring and sprat have been performed in
different areas of the Baltic Sea (e.g. Popiel, 1951; van Khan et al., 1972; Zalachowski et al.,
Chapter 8: Trophic Dynamics

Möllmann et al. (2004) reviewed interannual variability and differences in the diets of both herring and sprat based on long-term data. Both species preyed mainly upon calanoid copepods, with *Pseudocalanus acuspes* (formerly called *P. elongatus*; Renz and Hirche, 2006) dominating the diet of herring whereas sprat generally preferred *Temora longicornis*. The highest feeding activity of both fish species occurred in spring and summer, the main reproductive periods of calanoid copepods (Hansen et al., 2006; Renz and Hirche, 2006). The most important food item for both predators in spring was *P. acuspes*, whereas in summer sprat switched to *T. longicornis* and to a lesser degree to *Acartia* spp. Since the late 1970s the total stomach fullness has decreased and the fraction of empty stomachs increased in both species, and this has occurred in parallel with a decrease in the amount of *P. acuspes* in the diets of both herring and sprat. The decrease in *P. acuspes* in the diet of both fish species can be related to the long-term decrease in this major Baltic mesozooplankton species during the 1980s and 1990s, caused by a climate-driven reduction in salinity (Möllmann et al., 2000, 2003b). In contrast, the populations of *T. longicornis* and *Acartia* spp. have increased, profiting from warming since the late 1980s (Möllmann et al. 2000, 2003b).

Generally, the main differences in the feeding ecology of herring compared to sprat are the inclusion of larger food items, *e.g.* macrozooplankton and 0-group fish in larger herring specimens (Hardy, 1924; Last, 1989), and the ability to switch between filter-feeding and particulate-feeding modes (Gibson and Ezzi, 1992). In the Baltic Sea, mysids (larger than copepods) provide an...
additional food for herring in winter and autumn. Generally, older copepodite stages and adult
copepods dominate the diets of herring and sprat (Fig. 8.15), indicating particulate-feeding by
both fish species (Möllmann et al., 2004). Baltic herring are occasionally found feeding on
younger copepodite stages, indicating a low availability of older stages and forcing the fish to
filter-feed on smaller prey (Möllmann et al., 2004). Both planktivores are known to selectively
feed on certain prey species and stages. Flinkman et al. (1992) showed that herring select
reproducing female copepods, because of their larger body size and better visibility due to their
attached egg sacs. Casini et al. (2004) compared autumn and winter herring and sprat diets with
in-situ prey availability and found a preference for T. longicornis and P. acuspes but avoidance of
Acartia spp. Recent investigations within the GLOBEC-GERMANY project (http://www.globec-
germany.de) support this preference for spring-summer, and also indicate that both fish show a
strong selection for C4-5 and adult female copepods (Bernreuther unpublished data).

Considerable dietary overlap between both species is typical, being highest among large
sprat and small herring (Möllmann et al., 2004). Consequently, competition may play an
additional role in determining the diets of both species, and in the Baltic appears to be most
pronounced in spring when herring return from their coastal spawning areas into the deep basins,
where sprat are reproducing (Möllmann et al., 2003a). Both fish species feed at this time of the
year on reproducing P. acuspes stages which dwell in the halocline of the deep basins (Hansen et
al. 2006; Renz and Hirche, 2006). Later in summer sprat move into their coastal feeding areas
(Aro, 1989; Parmanne et al., 1994), which reduces competition (Möllmann et al., 2004).
Strong inter- and intraspecific competition is usually manifested in pronounced changes in fish growth and condition. These have been observed for herring and sprat in the Baltic, with individual weight and condition of herring decreasing since the 1980s (e.g. Cardinale and Arrhenius, 2000; Möllmann et al., 2003a; Möllmann et al., 2005), and of sprat later in the early 1990s (Cardinale et al., 2002; Möllmann et al., 2005). Recent studies indicate the importance of the composition of the zooplankton community for fish growth and condition; Rönkkönen et al. (2004) showed growth rates of herring in the northern Baltic to be explicitly dependent on the abundance of *P. acuspes*. The condition of herring in the Central Baltic Sea was shown to depend on the population size of this copepod (Möllmann et al., 2003a; Möllmann et al., 2005). Food availability, especially *P. acuspes* population size, has been further hypothesized to be crucial for the growth of sprat as well (Cardinale et al., 2002; Möllmann et al., 2004). However, while the decreasing availability of *P. acuspes* and the resulting competition between herring and sprat may affect both fish species, sprat growth and condition during the 1990s in particular seemed to be mainly determined by intra-specific competition within the unusually large sprat stock (Möllmann et al., 2005; Casini et al., 2006).

Providing evidence of food limitation requires sound estimates of individual food intake, and two approaches have been applied for deriving consumption estimates for Baltic clupeids; (i) gastric evacuation modelling (Köster and Schnack, 1994; Temming, 1996), and bioenergetic modelling (Rudstam, 1989; Arrhenius and Hansson, 1993). Using the latter approach, Arrhenius and Hansson (1999) demonstrated young-of-the-year herring to be food-limited. Estimates of individual daily ingestion rates using the gastric evacuation model approach indicate that juvenile sprat (1-2 g body weight) have evacuation rates that are 1.5 times higher than those of similar
sized herring, which indicates that small sprat realise higher consumption rates even if their stomach content mass and dietary composition are very similar to those of herring. Recent investigations indicate that sprat stomach contents, at least in the deep Baltic basins, are too low to support the observed annual growth, supporting the hypothesis of food-limitation in these regions (Temming, unpublished data).

The difference in individual weight trajectories over time leads to the question of whether one of the species is able to out-compete the other when co-occurring in an identical environment. Monthly data on mean stomach contents of sprat and herring of the same length-class do not show significant differences (Bernreuther, unpublished data), a result confirmed by a similar study performed off the Scottish West coast (De Silva, 1973).

In summary, Baltic herring and sprat are ecologically quite distinct from each other, with herring growing larger, having shallow spawning areas and spawning earlier in the year, and being able to filter feed but also consuming larger prey items at larger fish sizes. Sprat spawn deeper and later, and do not appear to be able to filter-feed. Despite these differences, when observed together in the deep central basins of the Baltic Sea the diet of herring and sprat is remarkably similar, consisting almost exclusively of three dominant copepod species. Filter-feeding does not play a role in these regions as generally only older and larger copepodite stages occur in the diet. When stomach contents are compared between individual herring and sprat of the same size no consistent difference is observable. However, differences in gastric evacuation indicate that equal stomach contents translate into higher consumption rates of sprat compared to herring, pointing to a possible competitive advantage for sprat. Another advantage might emerge from the potential of
sprat to exploit the most preferred (and energy rich) copepod species earlier in the season, with the
consequence of a severe depletion of this resource prior to the arrival of herring in the basin.
These two effects might serve as an explanation for the earlier decline (in the 1980s) in herring
weight at age when compared to a similar decline in sprat (in the 1990s).

Discussion

The detailed descriptions on aspects of the trophic dynamics of small pelagic species
provided in the case studies above may be synthesized into generalizations that appear to be
broadly applicable between different systems.

Firstly, small pelagic fish are omnivorous and most species described above derive the
bulk of their nutrition from zooplankton (Table 8.6), as suggested by James (1988). Previous
studies indicating that phytoplankton was the dominant dietary component were erroneous and
were biased by the methodology used which assessed prey importance on the basis of numerical
occurrence or frequency of occurrence instead of biovolume or contribution by mass or carbon
content. Larvae and juveniles of most small pelagic species feed predominantly on zooplankton,
although the almost exclusive feeding on phytoplankton reported for first-feeding Humboldt
anchovy larvae makes this species the exception to this generalisation. Although zooplankton is
generally the dominant dietary component of small pelagic fish, phytoplankton increases in
dietary importance (to differing degrees for different species) as fish grow, arising from the
ontogenic development of the branchial basket which allows the retention of small particles.
Secondly, in all but one of the case studies described above, co-occurring species pairs show size-based partitioning of the zooplankton resource, particularly at the adult stage. For the anchovy/sardine species pair, sardine generally feed on smaller zooplankton (often cyclopoid, poecilostomatoid and small calanoid copepods) than do anchovy (larger calanoid copepods and euphausiids), and phytoplankton is generally more important for sardine than for anchovy. Hence sardine consistently feed at a lower trophic level than do anchovy. These results are clear from analyses of stomach contents of anchovy and sardine conducted in the southern Benguela Current system, the northern California Current system, the northern Humboldt Current system, and the northwestern Pacific. Stable isotope analyses of both species in the northern California Current system showed anchovy to have higher isotopic values for both $^{13}$C and $\delta^{15}$N than sardine, which adds support to this generalization. However, whereas mean isotopic values for anchovy were also slightly higher than those for sardine from the Iberian system the results were not statistically significant, indicating that, on average, both species occupied equivalent trophic positions. Clear resource partitioning by prey size also occurs between finescale menhaden and Gulf menhaden in the Gulf of Mexico, but is not obvious for herring and sprat in the Baltic Sea, indicating that competition between members of this species pair is higher than in the other systems and possibly arising from the fact that the Baltic system is a relatively oligotrophic system compared to the other case studies described. Size-based partitioning of zooplankton prey may also occur for early life history stages since anchovy larvae tend to have a larger mouth width (gape), and to ingest slightly larger prey, than do sardine larvae of similar size in some systems. However these differences are small and not obvious in all case studies, and there is generally substantial overlap in the type and size of prey ingested by larvae of co-occurring species. Pre-
recruit and recruit anchovy and sardine in the southern Benguela Current system do appear to show resource partitioning by prey size.

Differences in diet are considered to arise primarily from differences in morphology of the feeding apparatus, with one of the species pair having a finer branchial basket with more gill rakers and a smaller gill raker gap than the other species (Table 8.6). Gulf menhaden have a finer branchial basket than do finescale menhaden, and sardine have a finer branchial basket than do anchovy in the Benguela Current system, the California Current system, the northwestern Pacific, and the northeastern Atlantic; unfortunately, morphological studies on the branchial basket of Humboldt Current species have not been conducted to date. The ability to retain very small particles by sardine has been demonstrated by experimental studies, with southern Benguela sardine able to retain particles of 13-17 µm and Iberian sardine particles as small as 4 µm; southern Benguela anchovy can only retain particles >200 µm.

Resource partitioning is also likely to arise from different trophic behaviours (Table 8.6). Anchovy and sardine are capable of both filter-feeding and particulate-feeding, and whilst feeding mode choice will depend on factors such as prey size and concentration and ambient light levels, sardine appear to be primarily filter-feeders and are generally considered as being non-selective in most systems although they have been observed to exhibit prey size selectivity or prey type selectivity in laboratory studies, particularly when particulate feeding. Additionally, sardine, particularly adults, generally do not show feeding periodicity and have been reported as feeding throughout the diel cycle in the Benguela Current, Humboldt Current and northeastern Atlantic systems. These characteristics are in marked contrast to anchovy which are strongly size selective,
appear to feed primarily by particulate feeding, and show strong feeding periodicity, primarily feeding during daylight, in most systems.

Anchovy and sardine are therefore trophically distinct, and this trophic distinction appears in some but not all other pairs of small pelagic fish species. The differences between anchovy and sardine described in the case studies above may be at least partly responsible for the alternations or regime shifts observed between these species as suggested by Schwartzlose et al. (1999). For the southern Benguela Current system, van der Lingen et al. (2006a) suggested how different physical scenarios can lead to food environments being dominated by either small or large particles that might favour one species over the other (Fig. 8.16). Phytoplankton biomass and size structure in that system are closely related to physico-chemical conditions, being dominated by large, chain-forming diatoms under intermittent mixing conditions (such as occur during upwelling) but dominated by small, nanoflagellates during stable, warm conditions (Mitchell-Innes and Pitcher, 1992). In turn, zooplankton community structure is affected by phytoplankton community and size structure, with large copepods such as Calanoides and Calanus exhibiting higher rates of ingestion of large phytoplankton cells compared with small cells (Peterson, 1989), and displaying enhanced growth rates under diatom-dominated conditions compared to flagellate-dominated conditions (Walker and Peterson, 1991). In contrast, small copepod species such as Oithona appear to be favoured when small cells predominate (H.M. Verheye, Marine and Coastal Management, unpublished data). Based on this, van der Lingen et al. (2006a) suggested that different physical scenarios can lead to food environments being dominated by either small or large particles, which would tend to favour sardine or anchovy, respectively.
Support for the hypothesis that changes in zooplankton community size structure can drive alternations between sardine and anchovy in the southern Benguela was provided by Shannon et al. (2004), who examined the effect of changing the relative availability of phytoplankton and zooplankton (comprising meso- and macrozooplankton) to anchovy and sardine in trophic models that simulated alternations between the two species. Shannon et al. (2004) concluded that modelled shifts between an anchovy-dominated system and a sardine-dominated system were “...likely to have been caused by changes in the availability of mesozooplankton to anchovy and sardine.”, and that those changes occurred in opposite directions for the two species and were assumed to be mediated through changes in environmental conditions.

Recent observations of simultaneously high abundance levels of both anchovy and sardine in the southern Benguela (van der Lingen et al., 2006b) appear contrary to the hypothesis that trophic differences between these two species might be partly responsible for alternating periods of species dominance. However, during species alternations the subdominant genus may initiate a recovery while the other is still abundant (Schwartzlose et al. 1999), which may have been the case in the southern Benguela. Additionally, zooplankton abundance in that system during austral autumn/winter increased 100-fold between the 1950s and the mid-1990s (Verheye et al., 1998), apparently due to intensified upwelling and increased primary and secondary productivity (Verhey, 2000). This substantially increased production by the lower trophic levels may also account for the high combined biomass of anchovy and sardine in the southern Benguela.

Regime shifts between anchovy and sardine in the northern Humboldt Current system off Peru have been linked to differences in their trophic position and a restructuring of the
ecosystem, with changes in trophic relationships occurring during warm and cool phases (Alheit and Ñiquen 2004; Alheit et al., this volume). Schwartzlose et al. (1999) proposed that food and temperature may drive shifts in abundance between sardine and anchovy, and indeed during warm conditions (El Niño – El Viejo; see Chavez et al., 2003) smaller species of phytoplankton and zooplankton occur, favouring sardines (Ulloa et al. 2001; Chavez et al. 2002; Fiedler 2002; Alheit and Ñiquen 2004). Furthermore, sardine recruitment is probably enhanced by warm conditions (Schwartzlose et al., 1999; McFarlane et al., 2002). On the other hand, during cold conditions (La Niña – La Vieja; see Chavez et al., 2003) larger plankton species that should favour anchovy are present and abundant, and anchovy is also adapted to cooler water than sardine in the northern Humboldt system. An El Niño event should thus favour sardine more than anchovy. However at the end of the 1997–98 El Niño, the anchovy population was high while the sardine population was depleted. Consequently, considering only temperature and plankton composition is insufficient to explain anchovy and sardine alternations, and Bertrand et al. (2004) used an integrated approach to propose a hypothesis related simply to the range of habitat available to explain species alternations. Indeed, as these species do not share the same ecological niche in terms of water masses, tolerance to abiotic factors, migrating and feeding capacities, climatic oscillations at different temporal scales (El Viejo-La Vieja, El Niño-La Niña) lead to oscillations of the range of their respective habitat (habitat sensu lato), and then to alternation of anchovy and sardine populations. In addition, Bertrand et al’s (2004) hypothesis explains a paradox in sardine dynamics which arises from the observation that sardines are abundant during the same periods in the eastern and western Pacific, i.e. during ‘warm’ periods in the eastern Pacific that correspond to ‘cold’ periods in the western Pacific (Chavez et al., 2003), even if the Kuroshio Current is much warmer than the
Humboldt Current (see Alheit et al., this volume for further discussion on temperature and sardine in the Kuroshio Current). Off Peru, production is associated with coastal upwelling, which is stronger during cold conditions. When strong, coastal upwelling allows extension of the habitat (mainly cold coastal waters) favourable to anchovy, and anchovy attain higher absolute biomass levels than do sardine which take advantage of the periods when weakening of the equatorial trade winds disrupts upwelling. On the contrary, off Japan, high production is related to offshore upwelling present along the frontal zone of the Kuroshio (Kimura et al., 1997, 2000a), and in this system the dominant small pelagic fish is sardine, which is strongly associated with the Kuroshio Current. The frontal zone provides better feeding conditions for first-feeding sardine larvae than does coastal waters (Kimura et al., 2000b), and during ‘eastern’ El Niño-El Viejo conditions, the Kuroshio Current is strongest which leads to higher productivity in the frontal zone, with benefits to sardine recruitment (Sugimoto et al., 2001). Thus, the western Pacific sardine would profit from the increase in frontal productivity related to ‘eastern’ El Niño-El Viejo periods that also favour sardine in the eastern Pacific.

One climate descriptor for the northwestern Pacific that has been related to population dynamics of Japanese sardine is the Aleutian Low Pressure (ALP) (Yasuda et al. 1999; Yatsu and Kaeriyama 2005). Yasuda et al. (1999) hypothesized that an amplified ALP intensifies westerly winds during winter and early spring, which results in the low spring SST east of Japan including the Kuroshio extension and Kuroshio-Oyashio mixed water region where sardine migrate and feed. The intensified wind and low SST imply a higher biological productivity owing to the nutrient supply due to wintertime deepening of the surface mixed layer (see Alheit et al., this volume), and this higher productivity might sustain the recruitment of the sardine in the fragile
metamorphosic stage. In fact, significant positive correlations were found between the natural
mortality coefficient during the period from the postlarval stage to age 1 and winter-spring SST in
the Kuroshio extension and its southern recirculation area (Noto and Yasuda 1999). In this
context, however, it remains to be discussed why anchovy population level has been low and/or
decreasing during periods of high sardine population levels, and vice versa, even under the same
level of plankton biomass. Species alternations between Japanese anchovy and sardine in the
northwestern Pacific may be a consequence of the difference in preferred prey size between
sardine and anchovy in the sub-adult and adult stages. For example, it is possible that fluctuations
in zooplankton biomass caused by changing climate regimes differ for small and large sized
zooplankton, possibly even in opposite phases, which would result in food environments better
suited to sardine and anchovy, respectively, as described above. This may cause differences in
prey availability for the two species during the same regime, and may finally influence population
dynamics through biological aspects such as egg production. There are some data that show inter-
annual and inter-decadal changes in plankton biomass (Odate 1994; Nakata and Hidaka 2003),
and Nakata and Hidaka (2003) in particular showed inter-annual fluctuation in large (prosome
length >1 mm) and small (<1 mm) copepods separately, although the two patterns were
apparently not consistent with patterns in fluctuations of anchovy and sardine. This suggests that
plankton dynamics should be further studied in order to account for their stock dynamics.

Alternatively, it may be that physical environmental factors directly impact on the survival
of early life stages. For example, Takasuka et al. (2007) revealed a difference in optimal
temperature for growth between anchovy and sardine larvae, and hypothesized that temperature
shifts caused by climate regimes may account for the difference in survival through growth, and
therefore the observed species alternations. If so, feeding might accessorily accelerate species
alternation, since competition between early life stages arising from their dietary overlap could
mean that the species with higher survival rates would consume the bulk of available food. For
either the trophic or optimal temperature hypothesis, however, there has not yet been clear
biological evidence and further work on these are required. Furthermore, it should be considered
that species alternations in the western Pacific have occurred not only in the Kuroshio system, but
also in waters to the west of Japan (the Tsushima Current system; see Alheit et al., this volume).

Coexisting populations of sardine and anchovy in areas around the Iberian Peninsula and
in the Mediterranean (e.g. Andreu, 1969) have shown multidecadal oscillations in population size
in both Atlantic (Anadón, 1950) and Mediterranean fisheries (Muzinic, 1958), with periods of 25-
35 years in which one species clearly dominated. Although early studies did not find clear
relationships between the alternating periods of sardine and anchovy in Galicia (Anadón, 1950),
longer time-series of fishery data integrated over the NW Iberian Atlantic coastline (ICES, 2005,
2007) have identified multidecadal periods of relative dominance of sardine and anchovy (Fig.
8.17). Quasi-decadal scales are characteristic of climatic, oceanographic and fish abundance
indices, as found in other upwelling regions (e.g. Chavez et al., 2003; Alheit et al., this volume).
In the Iberian case, however, sardine and anchovy showed synchrony in positive and negative
phases up to 1978, as their populations increased and decreased simultaneously. This pattern was
broken and moved to asynchrony thereafter, with sardine and anchovy showing opposite phases.
Direct effects of climate on plankton and sardine populations have been shown in subzones of the
study area: for instance, north wind intensity in winter and early spring is related with poor sardine
recruitment and landings off Portugal and Galicia, likely by increasing larval dispersion (Guisande
61
et al., 2004; ICES, 2007), whilst moderate upwelling enhanced anchovy recruitment in the eastern
Bay of Biscay (Borja et al., 1998; ICES, 2007). Indirect effects of climate and oceanographic
conditions may operate through changes in productivity and structure of plankton communities
(Chavez et al., 2003, van der Lingen et al., 2006a) while the availability of appropriate prey would
favour the dominance of one or another species of planktivorous fish (Fig. 8.16). Adult sardines
are better suited to filter-feeding on small copepods than anchovies, but the latter are efficient
predators of large copepods (van der Lingen et al., 2006a). In this way, sardine dominated
landings in the Iberian Atlantic when small copepods (e.g. Acartia) were abundant, while periods
of anchovy dominance were related to relatively high abundances of large copepods (e.g.
Calanus, Fig. 8.17). Variations in the intensity and periodicity of upwelling, caused by climatic
factors, were identified as the drivers for changes in the size-structure and composition of
plankton (van der Lingen et al., 2006a, Fig. 8.16) although the association between upwelling
intensity and a particular fish species seems to vary among geographic locations (Chavez et al.,
2003, Bertrand et al., 2004). This suggests that other effects not directly related to differences in
food preference, such as Bakun’s loophole hypothesis (Bakun and Broad, 2003) or intraguild
predation (Valdes Szeinfeld, 1991) might have to be considered to explain observed species shifts.

Intraguild predation (IGP) seems to be a common interaction between small pelagic fishes
(Table 8.7), as is the case in most systems (Arim and Marquet, 2004). Intraguild predation is
defined as competitors that eat each other (Polis et al., 1989), in this case adults that compete for
food and at the same time predate on the early stages (eggs and larva) of the competitor. In that
sense, cannibalism, also widespread in small pelagics (Table 8.7), can be considered as an extreme
case of intraguild predation, where adults of the same species compete for food and at the same
time eat their own offspring. Cannibalism makes sense from the evolutionary point of view of the
gene or individual, as it increases the reproductive condition of the adult whilst at the same time
reducing the number of competitors for the offspring. It would be a problem if the adult was to eat
more of its own offspring than that of the other adults, but this is unlikely in the frame of a school
spawning in a mixed environment.

Although recognised, little attention is usually paid to the role of IGP. This effect can be
divided in three components: i) the individual, ii) population dynamics of the species and iii)
consequences for the ecosystem. At the individual level there is little information about the role of
IGP in the energetic budget of small pelagic fishes and IGP is often considered to play a minor
role. However, this may not necessarily be the case; in a detailed seasonal study, Garrido (2002)
found cannibalism to play an important role in the diet of Atlantic-Iberian sardine. At the
population dynamics level, predation on the early stages may play quite an important role in
recruitment (Valdes-Szeinfeld and Cochrane, 1992). For example, cannibalism accounted for 22%
of anchovy egg mortality off Peru (Alheit, 1987); up to 56% of anchovy egg mortality could be
due to predation by sardine off South Africa (Valdes Szeinfeld, 1991), and Baltic sprat at times
consume >60% of their own egg production (Köster and Möllmann, 2000). Finally, IGP has
important consequences on the ecosystem structure because predation between competitors
releases pressure on their common prey and may increase the dominance of one species over the
other when food is abundant (Mylius et al., 2001). This final property could influence the
observed cycles of alternating dominance shown by small pelagic fish and described above, as
well as amplify climatic signals (Hsieh et al., 2005).
In addition to its hypothesized effect in impacting on population variability and species alternations, the trophic difference between anchovy and sardine is also likely to have habitat implications. Both anchovy and sardine are adapted to the coastal upwelling domain, but anchovy are likely to be favoured in such an environment because the blooms of large phytoplankton (diatoms) there promote the development of communities of large zooplankton, as described above. However, because of their ability to efficiently feed on small prey, sardine should be better-adapted to survive in the small particle-dominated oceanic environment than anchovy, and this, together with their better-developed swimming capabilities arising from their larger body size, may enable sardine to exploit the oceanic domain during certain periods as hypothesized by MacCall (this volume).

Herring and sprat in the Baltic Sea have similar diets and are not markedly trophically distinct, yet they show opposite trends in stock size, emphasizing the fact that mechanisms other than trophodynamics impact on species alternations. Baltic sprat reproductive success has been shown to be sensitive to climate-driven temperature conditions; MacKenzie and Köster (2004) found a positive correlation between sprat recruitment and the NAO index, as well as average water column temperature in May, and Alheit et al. (2005) also reported an association between the NAO index and sprat biomass. In an exploratory analysis relating recruitment to monthly depth-specific temperatures, Baumann et al. (2006) observed significant temperature-recruitment correlations between March and July in mid-water depths, confirming the results of MacKenzie and Köster (2004). However, in July to August, correlations shifted to surface waters, with August temperatures in surface waters explaining most of the variability in sprat recruitment (Baumann et al., 2006). These results indicate the importance of direct and indirect effects of temperature on
Baltic sprat recruitment. After spawning in spring, sprat eggs occur at depths where the water temperature is affected by winter cooling, and egg and larval development is influenced by extremely low water temperatures. Consequently, weak year classes of Baltic sprat have been associated with severe winters when temperatures of <4°C were observed in the intermediate water layer (Köster et al., 2003; Nissling, 2004). This direct effect of low temperature on eggs and larvae may explain the observed correlations in spring (MacKenzie and Köster, 2004; Baumann et al., 2006).

The stronger correlations of surface temperature and recruitment in summer (Baumann et al., 2006), may be due to food availability and match-mismatch with the food production (Voss et al., 2006). Sprat larvae prey mainly on the copepod *Acartia* spp. (Voss et al., 2003), and higher water temperatures during the 1990s have resulted in a drastic increase in the standing stock of this copepod (Möllmann et al., 2003b). Voss et al. (2006) computed an index of larval mortality which suggests a higher survival of summer over spring-born sprat larvae, with pronounced differences in survival for older larvae. Independent indices of larval growth (from analyses of the RNA:DNA ratio) support this survival pattern and could be linked to the temporal variability in prey abundance. Growth was faster but less variable in spring- than in summer-born larvae, indicating a strong selection for fast growth in April-May but a less selective environment in June-July (Voss et al., 2006). The advantage for summer-born larvae may be due to the demographic status of the *Acartia* spp. population; while nauplii are abundant and only very low concentrations of larger copepodites can be found in spring, the situation is reversed in summer. These results suggest that the increased availability of *Acartia* spp. during the critical late-larvae stage has contributed to the high reproductive success and eventually to the unusually high sprat stock.
during the 1990s. The state of knowledge on herring recruitment in the Baltic is generally lower
than for sprat, but the observation that the decreasing growth and condition of herring observed
since the 1980s occurred in parallel with a negative trend in recruitment suggests an effect of
condition and growth on recruitment. The Gulf populations (e.g. Gulf of Riga) of herring seemed
to have profited from the warmer regime, especially through enhanced copepod production
assuring larval survival (G. Kornilovs, pers. comm.). The populations of coastal copepods (e.g.
_Acartia_ spp.) have increased in the recent warmer period (Möllmann _et al._, 2000). Unfortunately,
almost nothing is known about the larval ecology of the open-sea herring stocks, but the fact that
warmer temperatures and enhanced food production did not positively influence recruitment of
the Baltic main basin herring stocks points to the importance of the link between growth and
condition.

Our present understanding of the effects of variability in climate on herring and sprat
populations in the Baltic Sea is summarized in Figure 8.18. Climate variability affects salinity and
oxygen (S/O_2_) through runoff and inflows of North Sea water, and temperature (T) through direct
air-sea interaction. Changes in S/O_2_ influence _P. acuspes_ availability for small pelagic species and
hence their growth and condition. Increased inter- and intra-specific competition with the enlarged
sprat stock further contributed to herring and sprat growth changes. The large sprat stock during
the 1990s is to a large degree a result of high reproductive success, caused by the direct effect of
temperature on egg and larval survival, and the indirect effect of _Acartia_ spp. availability.

Because menhaden distributions in the northwestern Atlantic are correlated with plankton
distributions there is reasonable evidence to predict where menhaden will distribute and what
components of the plankton community they will consume, thus we are equipped to consider what
the impact of future changes to climate and ecosystem condition may have on menhaden, and vice
versa. Climate change impacts and anthropogenic effects on estuaries may be inexorably
intertwined since many aspects of climate change could affect the nutrient dynamics of estuaries.
The thermal requirement of an organism will be challenged by the anticipated increases in global
temperature, but in addition, climate change will produce changes in precipitation, solar radiation,
humidity, wind, and potential evaporation over a drainage system that will affect the physical and
biological suitability of menhaden habitats (Hulme 2005). Estuarine habitat for menhaden is
already in a fragile state because of chronic nutrient loading and hypoxic conditions (Hagy et al.,
2004). Eutrophication is creating hypoxic conditions that are lethal to menhaden populations, in
particular juvenile populations, which are estuarine dependant and more sensitive to oxygen levels
than adults (Shimps et al., 2005). Climate change is likely to affect each estuarine system
differently due to difference in the physical nature of each estuary and the amount of development
and nutrient loading associated with the watershed.

Plankton feeding organisms provide a service to the function of estuaries and coastal
ecosystems by removing particles from the water column and facilitating nutrient cycling
(Breitburg, 2002; Jung and Houde, 2003; 2005). Menhaden populations are capable of filtering
significant quantities of water (Oviatt et al., 1972), which results in the removal of phytoplankton
and zooplankton from the water column, and detrital material which menhaden have been shown
to digest at low levels (Lewis and Peters, 1994). Menhaden may accelerate the deposition of
nutrients to the benthos via the formation of their fecal pellets thus affecting the distribution of
oxygen consuming material in the water column and benthos (Lane et al., 1994). Cyanobacteria
appear viable after gut passage through menhaden (Friedland et al., 2005), which may contribute
to the development of summer bloom patterns in estuaries (Davis et al., 1997). The diminishment
of menhaden populations caused by eutrophication and climate change effects will alter these
filtering functions provided by menhaden, thus contributing to the instability of estuarine and
coastal ecosystems.

Predicted effects of climate change on upwelling systems have been described by Fréon et al. (this volume), and changes in productivity are one area of focus of that chapter. Given the
trophic difference between sardine and anchovy, and between members of some other small
pelagic species pairs, a change in productivity that results in a change in zooplankton
composition, particularly zooplankton size composition, seems likely to have an impact on the
population variability of and species alternations between these species. Altered wind stress
that would enhance coastal upwelling (Bakun, 1990, 1992; Shannon et al., 1996) and result in a
trophic environment dominated by large particles would tend to favour anchovy over sardine,
whereas a reduction in coastal upwelling could act to favour sardine. Conversely, increases in
sea surface temperature (e.g. Roux, 2003) or an increased frequency and intensity of the
advection of warm tropical water into upwelling systems (e.g. Siegfried et al., 1990) that result
in a trophic environment dominated by small particles may also tend to favour sardine over
anchovy. Whilst trophic differentiation represents one possible mechanism that may impact on
population variability and species alternations of small pelagic fish it should not be considered
alone, and the effects of other mechanisms on population variability, including those
mentioned above, should be considered.
Chapter 8: Trophic Dynamics

Conclusions

General conclusions regarding the trophic dynamics of small pelagic fish species, in particular the so-called SPACC species (i.e. anchovy and sardine), are listed below:

1. Anchovy (*Engraulis* spp.) and sardine (*Sardinops sagax* and *Sardina pilchardus*) are omnivorous but derive the bulk of their dietary carbon from zooplankton, and previous descriptions of exclusive or near-total phytophagy by these species are erroneous and were based on inappropriate methodology;

2. The two species show ontogenetic changes in diet: larvae and juveniles are typically almost exclusively zooplanktivorous (an exception being anchovy larvae in the northern Humboldt Current system), and the relative dietary importance of phytoplankton increases with fish size due to elaboration of the branchial basket;

3. Size-based partitioning of the zooplankton resource between anchovy and sardine is typically observed, with sardine feeding on smaller zooplankton than do anchovy;

4. This trophic partitioning arises from different trophic morphologies, with anchovy having a coarser branchial basket and sardine a finer branchial basket, and different feeding behaviours, anchovy being predominantly size-selective particulate feeders and typically showing feeding periodicity whereas sardine appear to be predominantly filter feeders and typically do not show feeding periodicity;

5. Phytoplankton tends to be more important in the diet of sardine than anchovy, and this, together with the trophic partitioning referred to above, means that sardine feed at a lower trophic level than do anchovy;
6. Because of this trophic partitioning, changes in the size and/or species composition of the zooplankton community may be implicated in species alternations between anchovy and sardine, and periods of anchovy or sardine dominance have coincided with periods of changed zooplankton community structure in some of the case studies described above; and

7. From a trophic perspective, climate change appears more likely to have an indirect (i.e. impacting on the food) rather than a direct impact on anchovy and sardine (see Box 8.1).

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Box 8.1 Trophically-mediated impacts of climate change on anchovy and sardine

An hypothesized outcome of climate change is alterations in physical forcing that are likely to affect the productivity of marine ecosystems and the composition of their lower trophic levels, particularly the phytoplankton (see Fréon et al., this volume, and references therein). If such changes in phytoplankton composition result in changes in the zooplankton community, in particular zooplankton size structure, then this could favour anchovy over sardine or vice versa, depending on how zooplankton size has changed.

For example, altered wind stress that results in an increase in the frequency and/or intensity of coastal upwelling could result in a food environment dominated by large particles (i.e. diatoms and larger zooplankton) as suggested in Figure 8.16, which would provide a more favourable trophic environment for anchovy than for sardine. This enhanced food environment could have a positive impact on reproductive output (e.g. through an increase in the quantity and/or quality of eggs produced during the spawning season) and hence on population size. However, increased upwelling will also result in increased Ekman transport of surface layers that, should it occur over the reproductive season, would increase the dispersal of eggs and larvae to unfavourable offshore habitat. Hence whereas increased upwelling would have a positive impact on anchovy adults this would be balanced by the negative impact on early life history stages, of both anchovy and sardine. Additionally, increased upwelling would also reduce water temperatures, which could result in different larval survival of the two species under the optimal growth hypothesis. Similarly, the increased stratification of surface waters predicted to arise from global warming will decrease the vertical supply of nutrients to the euphotic zone. Because small dinoflagellates will be less negatively impacted by this reduction in nutrients than the larger diatoms, this could also act to change phytoplankton composition, with subsequent impacts on zooplankton community structure. Such a scenario would provide a more favourable trophic environment for sardine than for anchovy, but the likely overall reduction in productivity could negatively impact both species.

From a trophic perspective the predicted impacts of climate change on anchovy and sardine will be indirect, since such impacts appear more likely to affect the prey of these fish than the fish themselves. These indirect effects may act in concert with, or in opposition to, the direct impacts of climate change on the fish, such as changes in distribution arising from altered habitat or changes in survival through growth. These interactions between direct and indirect impacts of climate change on anchovy and sardine substantially reduce our ability to make predictions regarding the response of small pelagic fish to climate change.
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Table 8.1: System type, region, and species used in case studies in which the trophic dynamics of small pelagic fishes are described.

<table>
<thead>
<tr>
<th>System Type</th>
<th>Region</th>
<th>Species (and common name)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Upwelling</td>
<td>Benguela Current system (SE Atlantic)</td>
<td><em>Engraulis encrasicolus</em> (Cape anchovy)</td>
</tr>
<tr>
<td></td>
<td></td>
<td><em>Sardinops sagax</em> (sardine)</td>
</tr>
<tr>
<td></td>
<td>California Current system (NE Pacific)</td>
<td><em>Engraulis mordax</em> (Northern anchovy)</td>
</tr>
<tr>
<td></td>
<td></td>
<td><em>Sardinops sagax</em> (Pacific sardine)</td>
</tr>
<tr>
<td></td>
<td>Humboldt Current system (SE Pacific)</td>
<td><em>Engraulis ringens</em> (anchovy)</td>
</tr>
<tr>
<td></td>
<td></td>
<td><em>Sardinops sagax</em> (sardine)</td>
</tr>
<tr>
<td></td>
<td></td>
<td><em>Strangomera bentincki</em> (common sardine)</td>
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<tr>
<td>Temperate non-</td>
<td>Kuroshio Current system (NW Pacific)</td>
<td><em>Engraulis japonicus</em> (anchovy)</td>
</tr>
<tr>
<td>upwelling</td>
<td></td>
<td><em>Sardinops melanosticus</em> (sardine)</td>
</tr>
<tr>
<td></td>
<td>Iberian Peninsula, Bay of Biscay, and</td>
<td><em>Engraulis encrasicolus</em> (anchovy)</td>
</tr>
<tr>
<td></td>
<td>Mediterranean Sea (NE Atlantic)</td>
<td><em>Sardina pilchardus</em> (Atlantic Iberian sardine)</td>
</tr>
<tr>
<td></td>
<td>US East Coast and Gulf of Mexico (W Atlantic)</td>
<td><em>Brevoortia gunteri</em> (Finescale menhaden)</td>
</tr>
<tr>
<td></td>
<td></td>
<td><em>Brevoortia patronus</em> (Gulf menhaden)</td>
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<tr>
<td></td>
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<td><em>Brevoortia tyrannus</em> (Atlantic menhaden)</td>
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<td></td>
<td>Baltic Sea</td>
<td><em>Sprattus sprattus</em> (sprat)</td>
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<tr>
<td></td>
<td></td>
<td><em>Clupea harengus</em> (herring)</td>
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Table 8.2: Summary of Pacific sardine (n=151) diets collected from the northern California Current system during the June and August 2000 and 2002 GLOBEC surveys, and summary of northern anchovy diets collected from the northern California Current system during the August 1981 Oregon State University survey (n=18) and the June and August 2000 and 2002 GLOBEC surveys (n=45).

<table>
<thead>
<tr>
<th></th>
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<th></th>
</tr>
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<tbody>
<tr>
<td></td>
<td>%N</td>
<td>%W</td>
<td>%N</td>
</tr>
<tr>
<td>Phytoplankton</td>
<td>19.62</td>
<td>-</td>
<td></td>
</tr>
<tr>
<td>Mollusca</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Pteropoda</td>
<td>&lt;0.01</td>
<td>0.1</td>
<td>35.52</td>
</tr>
<tr>
<td><em>Limacina helicina</em></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Cephalopoda</td>
<td></td>
<td></td>
<td>0.09</td>
</tr>
<tr>
<td>Chaetognatha</td>
<td>&lt;0.01</td>
<td>&lt;0.01</td>
<td></td>
</tr>
<tr>
<td>Arthropoda</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Crustacea</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Copepoda (eggs)</td>
<td>6.16</td>
<td>0.3</td>
<td>53.84</td>
</tr>
<tr>
<td>(nauplii)</td>
<td>5.51</td>
<td>0.3</td>
<td></td>
</tr>
<tr>
<td>(copepodite-adult)</td>
<td>66.91</td>
<td>30.40</td>
<td></td>
</tr>
<tr>
<td>Cirripedia (nauplii-cyprid)</td>
<td>0.04</td>
<td>&lt;0.01</td>
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</tr>
<tr>
<td>(cyprid)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Cladocera</td>
<td>&lt;0.01</td>
<td>&lt;0.01</td>
<td></td>
</tr>
<tr>
<td>Decapoda (larvae)</td>
<td>&lt;0.01</td>
<td>0.01</td>
<td></td>
</tr>
<tr>
<td><em>Cancer magister</em> (megalopae)</td>
<td></td>
<td></td>
<td>5.96</td>
</tr>
<tr>
<td>Caridea (zoa)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Amphipoda</td>
<td>0.02</td>
<td>0.06</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Themisto pacifica</td>
<td>Euphausiidae (eggs)</td>
<td>Euphausia pacifica</td>
</tr>
<tr>
<td>---------------------</td>
<td>-------------------</td>
<td>---------------------</td>
<td>-------------------</td>
</tr>
<tr>
<td></td>
<td></td>
<td>11.61</td>
<td>0.16</td>
</tr>
<tr>
<td></td>
<td></td>
<td>1.54</td>
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<td></td>
<td>0.34</td>
<td>19.59</td>
</tr>
<tr>
<td></td>
<td></td>
<td>&lt;0.01</td>
<td>23.98</td>
</tr>
<tr>
<td></td>
<td></td>
<td>&lt;0.01</td>
<td>&lt;0.01</td>
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</tr>
<tr>
<td></td>
<td></td>
<td>4.63</td>
<td>5.21</td>
</tr>
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Table 8.3: Estimates of ingestion rate, gastric evacuation rate, and daily ration of Peruvian anchovy and sardine.

<table>
<thead>
<tr>
<th>Season</th>
<th>Year</th>
<th>Ingestion rate (g·h⁻¹)</th>
<th>Evacuation rate (h⁻¹)</th>
<th>Daily ration (g·d⁻¹)</th>
<th>Feeding period</th>
<th>Source</th>
</tr>
</thead>
<tbody>
<tr>
<td>Anchovy</td>
<td>Pooled data</td>
<td>0.034</td>
<td>0.1518</td>
<td>0.4480</td>
<td>11:55-23:45</td>
<td>Pauly et al. (1989)</td>
</tr>
<tr>
<td></td>
<td>1996-2003</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>07:00-18:00</td>
<td>Espinoza and Bertrand (in press)</td>
</tr>
<tr>
<td></td>
<td>Summer</td>
<td>0.0479</td>
<td>0.0902</td>
<td>0.4391</td>
<td>10:09-19:20</td>
<td>Alamo et al. (1997b)</td>
</tr>
<tr>
<td></td>
<td>Winter-spring</td>
<td>0.0453</td>
<td>0.0811</td>
<td>0.4428</td>
<td>09:23-19:00</td>
<td>Alamo and Espinoza (1998)</td>
</tr>
<tr>
<td></td>
<td>Fall</td>
<td>0.0157</td>
<td>0.1646</td>
<td>0.2657</td>
<td>09:58-02:48</td>
<td>Espinoza et al. (1998a)</td>
</tr>
<tr>
<td></td>
<td>End of winter</td>
<td>0.0192</td>
<td>0.1332</td>
<td>0.3252</td>
<td>11:00-04:00</td>
<td>Espinoza et al. (1998b)</td>
</tr>
<tr>
<td></td>
<td>Spring-summer</td>
<td>-</td>
<td>-</td>
<td>0.445</td>
<td>09:00-18:50</td>
<td>Espinoza et al. (2000)</td>
</tr>
<tr>
<td>Sardine</td>
<td>Fall</td>
<td>0.1165</td>
<td>0.2345</td>
<td>0.3243</td>
<td>12:00-24:00</td>
<td>Espinoza et al. (1998a)</td>
</tr>
</tbody>
</table>
Table 8.4: Summary of studies on the quantitative composition of *S. pilchardus* diet in Iberian waters indicating average percent composition of prey items. Su: summer; Au: autumn; Wi: winter; Sp: spring; n1: number of individuals analysed; Anal.: analysis method; Gn: gut contents by number of prey; Gw: gut contents by biovolume or weight of prey; SIC: estimations from stable C isotopes in muscle; SIN: estimations from stable N isotopes in muscle; CC: gut contents by C content of prey; phy.: phytoplankton; zoo.: zooplankton; x: mean; se: standard error; n2: number of estimations averaged.

<table>
<thead>
<tr>
<th>Year</th>
<th>Season</th>
<th>Zone</th>
<th>Stage (size; cm)</th>
<th>n1</th>
<th>Anal.</th>
<th>% phy. x (se)</th>
<th>% zoo. x (se)</th>
<th>% other x (se)</th>
<th>n2</th>
<th>Source</th>
</tr>
</thead>
<tbody>
<tr>
<td>1944</td>
<td>Su</td>
<td>Mar Cantábrico</td>
<td>Adults (13.0-17.5)</td>
<td>6</td>
<td>Gn</td>
<td>75.0 (11.2)</td>
<td>10.0 (2.6)</td>
<td>-</td>
<td>6</td>
<td>Navarro and Navaz (1946)</td>
</tr>
<tr>
<td>1946</td>
<td>Sp-Su</td>
<td>Mediterranean</td>
<td>Juveniles? (3.7-9.9)</td>
<td>90</td>
<td>Gn</td>
<td>15.1 (3.6)</td>
<td>82.2 (3.5)</td>
<td>2.7 (1.3)</td>
<td>11</td>
<td>Massuti and Oliver (1948)</td>
</tr>
<tr>
<td>1946</td>
<td>All</td>
<td>Mediterranean</td>
<td>Adults (10.0-12.5)</td>
<td>125</td>
<td>Gn</td>
<td>31.8 (3.7)</td>
<td>65.5 (3.6)</td>
<td>2.7 (1.1)</td>
<td>27</td>
<td>Massuti and Oliver (1948)</td>
</tr>
<tr>
<td>1948-49</td>
<td>Sp-Su</td>
<td>Galicia</td>
<td>Adults</td>
<td>9</td>
<td>Gn</td>
<td>36.6 (11.3)</td>
<td>57.9 (11.8)</td>
<td>5.6 (3.5)</td>
<td>9</td>
<td>Oliver (1951)</td>
</tr>
<tr>
<td>1950</td>
<td>Sp</td>
<td>Galicia</td>
<td>Adults</td>
<td>?</td>
<td>Gn</td>
<td>28.0 (18.2)</td>
<td>58.7 (14.3)</td>
<td>13.3 (13.3)</td>
<td>3</td>
<td>Oliver and Navarro (1952)</td>
</tr>
<tr>
<td>1952</td>
<td>All</td>
<td>Portugal W</td>
<td>Adults</td>
<td>300</td>
<td>Gn</td>
<td>66.2 (25.7)</td>
<td>33.8 (25.7)</td>
<td>-</td>
<td>15</td>
<td>Silva (1954)</td>
</tr>
<tr>
<td>1987</td>
<td>Wi-Sp</td>
<td>Galicia and Mar Cantábrico</td>
<td>Adults (&gt;20.0)</td>
<td>70</td>
<td>Gn</td>
<td>35.0 (13.7)</td>
<td>55.0 (13.7)</td>
<td>-</td>
<td>7</td>
<td>Varela et al. (1988)</td>
</tr>
<tr>
<td>1987</td>
<td>Wi-Sp</td>
<td>Galicia and Mar Cantábrico</td>
<td>Adults (&gt;20.0)</td>
<td>150</td>
<td>Gw</td>
<td>42.2 (16.1)</td>
<td>57.0 (16.2)</td>
<td>0.8 (0.3)</td>
<td>9</td>
<td>Varela et al. (1990)</td>
</tr>
<tr>
<td>2001-02</td>
<td>Su, Sp</td>
<td>Portugal W and S</td>
<td>Adults (20.0)</td>
<td>110</td>
<td>Gn</td>
<td>66.5 (7.3)</td>
<td>29.0 (6.4)</td>
<td>4.5 (1.4)</td>
<td>6</td>
<td>Garrido (2002)</td>
</tr>
<tr>
<td>2001-02</td>
<td>Su, Sp</td>
<td>Portugal W and S</td>
<td>Adults (20.0)</td>
<td>110</td>
<td>Gn</td>
<td>11.3 (1.9)</td>
<td>77.3 (7.8)</td>
<td>11.5 (7.5)</td>
<td>6</td>
<td>Garrido (2002)</td>
</tr>
<tr>
<td>2002-03</td>
<td>Wi-Sp, Au</td>
<td>Portugal W and S</td>
<td>Adults</td>
<td>30</td>
<td>Gw</td>
<td>5.4 (4.5)</td>
<td>94.6 (2.2)</td>
<td>0.7 (0.2)</td>
<td>4</td>
<td>Cunha et al. (2005)</td>
</tr>
<tr>
<td>1998-01</td>
<td>Sp</td>
<td>Galicia and Mar Cantábrico</td>
<td>Adults (11.0-17.9)</td>
<td>108</td>
<td>SIC</td>
<td>3.7 (1.5)</td>
<td>96.3 (1.5)</td>
<td>-</td>
<td>3</td>
<td>Bode et al. (2004)</td>
</tr>
<tr>
<td>1998-01</td>
<td>Sp</td>
<td>Galicia and Mar Cantábrico</td>
<td>Adults (11.0-17.9)</td>
<td>108</td>
<td>SIN</td>
<td>0.0 (0.0)</td>
<td>100.0 (0.0)</td>
<td>-</td>
<td>3</td>
<td>Bode et al. (2004)</td>
</tr>
<tr>
<td>1998-01</td>
<td>Sp</td>
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<td>Adults (18.0-23.0)</td>
<td>142</td>
<td>SIC</td>
<td>13.0 (3.1)</td>
<td>87.0 (3.1)</td>
<td>-</td>
<td>3</td>
<td>Bode et al. (2004)</td>
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<tr>
<td>1998-01</td>
<td>Sp</td>
<td>Galicia and Mar Cantábrico</td>
<td>Adults (18.0-23.0)</td>
<td>142</td>
<td>SIN</td>
<td>2.7 (1.2)</td>
<td>97.3 (1.2)</td>
<td>-</td>
<td>3</td>
<td>Bode et al. (2004)</td>
</tr>
<tr>
<td>2003-04</td>
<td>All</td>
<td>Portugal W and S</td>
<td>Adults (18.0)</td>
<td>491</td>
<td>Gn</td>
<td>80.3 (17.0)</td>
<td>16.9 (14.7)</td>
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<td>55</td>
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</tr>
<tr>
<td>2003-04</td>
<td>All</td>
<td>Portugal W and S</td>
<td>Adults (18.0)</td>
<td>491</td>
<td>Gw</td>
<td>17.2 (21.0)</td>
<td>55.2 (29.8)</td>
<td>27.5 (31.9)</td>
<td>55</td>
<td>Garrido et al. (in press)</td>
</tr>
<tr>
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<td>All</td>
<td>Portugal W and S</td>
<td>Adults (18.0)</td>
<td>491</td>
<td>CC</td>
<td>17.6 (20.2)</td>
<td>59.7 (28.4)</td>
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<td>55</td>
<td>Garrido et al. (in press)</td>
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<td>1991-92</td>
<td>Sp</td>
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<td>Larvae (0.4-2.4)</td>
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<td>Gn</td>
<td>0.1 (0.1)</td>
<td>87.5 (1.8)</td>
<td>12.4 (1.8)</td>
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<td>Conway et al. (1994)</td>
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<tr>
<td>2003-04</td>
<td>All</td>
<td>Mar Cantábrico</td>
<td>Larvae (0.3-2.2)</td>
<td>97</td>
<td>Gn</td>
<td>-</td>
<td>94.8 (4.1)</td>
<td>5.2 (1.4)</td>
<td>7</td>
<td>Munuera (2006)</td>
</tr>
<tr>
<td>2000</td>
<td>Sp</td>
<td>Mar Cantábrico</td>
<td>Larvae (0.4-2.2)</td>
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<td>Gn</td>
<td>-</td>
<td>93.3 (3.8)</td>
<td>6.6 (3.8)</td>
<td>3</td>
<td>Fernández and González-Quirós (2006)</td>
</tr>
</tbody>
</table>

Mean

<table>
<thead>
<tr>
<th>Stage</th>
<th>Analysis</th>
<th>% phy.</th>
<th>% zoo.</th>
<th>% other</th>
</tr>
</thead>
<tbody>
<tr>
<td>Adults</td>
<td>Gn</td>
<td>48.3</td>
<td>45.4</td>
<td>5.3</td>
</tr>
<tr>
<td>Adults</td>
<td>Gw</td>
<td>18.7</td>
<td>68.8</td>
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</tr>
<tr>
<td>Adults</td>
<td>SIC/SIN</td>
<td>4.8</td>
<td>95.2</td>
<td>-</td>
</tr>
<tr>
<td>Larvae</td>
<td>Gn</td>
<td>0.1</td>
<td>91.9</td>
<td>8.14</td>
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</table>
Table 8.5: Summary of studies on the quantitative composition of *E. encrasicolus* diet in European waters indicating average percent composition of prey items. Su: summer; Sp: spring; n: number of individuals analysed; Anal.: analysis method; PI: gut contents by preponderance index (biovolume); Gn: gut contents by number of prey; phy.: phytoplankton; copep.: copepods; cladoc.: cladocerans; other crust.: other crustaceans.

<table>
<thead>
<tr>
<th>Year</th>
<th>Season</th>
<th>Zone</th>
<th>Stage (size; cm)</th>
<th>n</th>
<th>Anal.</th>
<th>% phy.</th>
<th>% copep</th>
<th>% cladoc</th>
<th>% other crust.</th>
<th>% fish eggs + larvae</th>
<th>% other</th>
<th>Source</th>
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<tbody>
<tr>
<td>1995-96</td>
<td>Su</td>
<td>Mediterranean, Gulf of Lions</td>
<td>Adults (10.2-15.0)</td>
<td>857</td>
<td>PI</td>
<td>85.0</td>
<td>2.0</td>
<td>8.9</td>
<td>1.9</td>
<td>3.3</td>
<td>Plounevez and Champalbert (2000)</td>
<td></td>
</tr>
<tr>
<td>1997</td>
<td>Sp</td>
<td>Bay of Biscay, Gironde plume</td>
<td>Adults (14.0)</td>
<td>195</td>
<td>PI</td>
<td>96.3</td>
<td>0.0</td>
<td>3.4</td>
<td>0.0</td>
<td>0.1</td>
<td>Plounevez and Champalbert (1999)</td>
<td></td>
</tr>
<tr>
<td>1997</td>
<td>Sp</td>
<td>Bay of Biscay, shelf-break</td>
<td>Adults (12.5)</td>
<td>198</td>
<td>PI</td>
<td>99.5</td>
<td>-</td>
<td>0.5</td>
<td>-</td>
<td>-</td>
<td>Plounevez and Champalbert (1999)</td>
<td></td>
</tr>
<tr>
<td>1991</td>
<td>Sp</td>
<td>Portugal W</td>
<td>Larvae (0.3-7.0)</td>
<td>545</td>
<td>Gn</td>
<td>2.1</td>
<td>8.4</td>
<td>-</td>
<td>87.5*</td>
<td>-</td>
<td>4.3</td>
<td>Ferreira and Ré (1993)</td>
</tr>
<tr>
<td>1996</td>
<td>Sp-Su</td>
<td>Adriatic Sea</td>
<td>Larvae (0.2-1.9)</td>
<td>889</td>
<td>Gn</td>
<td>0.0</td>
<td>95.0</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>5.0</td>
<td>Conway <em>et al</em> (1998)</td>
</tr>
<tr>
<td>1992</td>
<td>Su</td>
<td>Mediterranean NW</td>
<td>Larvae (0.3-1.6)</td>
<td>936</td>
<td>Gn</td>
<td>3.7</td>
<td>79.5</td>
<td>1.4</td>
<td>0.4</td>
<td>-</td>
<td>14.1</td>
<td>Tudela <em>et al.</em> (2002)</td>
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<td>2004</td>
<td>Su</td>
<td>SE Bay of Biscay</td>
<td>Larvae (0.3-1.3)</td>
<td>66</td>
<td>Gn</td>
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<td>94.0</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>6.0</td>
<td>Munuera (2006)</td>
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<tr>
<td>Mean</td>
<td></td>
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<td>Adults</td>
<td></td>
<td></td>
<td>0.0</td>
<td>93.6</td>
<td>2.0</td>
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<td>1.0</td>
<td>1.7</td>
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<tr>
<td></td>
<td></td>
<td></td>
<td>Larvae</td>
<td></td>
<td></td>
<td>1.5</td>
<td>69.2</td>
<td>0.4</td>
<td>22.0</td>
<td>-</td>
<td>29.4</td>
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</table>
Table 8.6: Comparative summary of aspects of the trophic dynamics of small pelagic fish species pairs described in the case studies.

<table>
<thead>
<tr>
<th>System</th>
<th>Species 1</th>
<th>Species 2</th>
</tr>
</thead>
<tbody>
<tr>
<td>Bengal Current</td>
<td>Anchovy (<em>Engraulis encrasicolus</em>) - coarse branchial basket; particulate-feeding dominant and energetically cheapest feeding mode; efficient remover of large (&gt;0.6 mm) particles; respiratory quotient (= 0.92); assimilation of N most efficient from zooplankton; excretes &lt;50% of ingested nitrogen; regulates swimming speed according to prey size; phytoplankton generally unimportant in juvenile and adult diet and majority of adult dietary carbon from larger (&gt;1.0 mm) zooplankton (calanoid copepods and euphausiids); strong size selectivity; exhibit feeding periodicity with peak feeding at dawn and dusk.</td>
<td>Sardine (<em>Sardinops sagax</em>) - fine branchial basket; filter-feeding dominant and energetically cheapest feeding mode; efficient remover of small (&lt;0.6 mm) particles; respiratory quotient (= 0.96); assimilation of N most efficient from zooplankton; excretes &gt;50% of ingested nitrogen; regulates swimming speed according to prey concentration; phytoplankton generally unimportant in juvenile diet but occasionally important in adult diet and majority of adult dietary carbon from small (&lt;1.2 mm) zooplankton (calanoid and cyclopoid copepods); weak size selectivity; feed throughout diel cycle.</td>
</tr>
<tr>
<td>California Current</td>
<td>Anchovy (<em>Engraulis mordax</em>) - coarse branchial basket; larvae feed on zooplankton (copepod eggs, nauplii and copepodites); phytoplankton generally unimportant in adult diet and majority of adult dietary carbon from zooplankton (copepods, anchovy eggs, euphausiids, pteropods); strong size selectivity over a 1000-fold range in prey size; exhibit feeding periodicity with peak feeding at dawn.</td>
<td>Sardine (<em>Sardinops sagax</em>) - fine branchial basket; larvae feed on zooplankton (copepod eggs, nauplii and copepodites); phytoplankton occasionally important in adult diet but majority of adult dietary carbon from zooplankton (crustaceans, euphausiids), although substantial spatial and temporal variability in sardine diet; feed throughout diel cycle.</td>
</tr>
<tr>
<td>Humboldt Current</td>
<td>Anchovy (<em>Engraulis ringens</em>) – particulate-feeding dominant feeding mode; larvae feed on phytoplankton (centric diatoms) and zooplankton; phytoplankton occasionally important in adult diet but majority of adult dietary carbon from zooplankton (copepods and euphausiids); latitudinal differences in adult diet (phytoplankton vs zooplankton) related to differences in trophic morphology; generally feed during daytime with some night-time feeding.</td>
<td>Sardine (<em>Sardinops sagax</em>) – larvae feed on zooplankton (copepod eggs and nauplii) and some phytoplankton (diatoms); phytoplankton and zooplankton (small copepods and tunicates) make equivalent contributions to adult dietary mass.</td>
</tr>
<tr>
<td></td>
<td>Common sardine (<em>Strangomera bentincki</em>) – filter-feeding dominant feeding mode; larvae feed on zooplankton (copepod eggs and nauplii)</td>
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</tbody>
</table>
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<table>
<thead>
<tr>
<th>Region</th>
<th>Anchovy (<em>Engraulis japonicus</em>)</th>
<th>Sardine (<em>Sardinops melanosticus</em>)</th>
<th>Anchovy (<em>Engraulis encrasicolus</em>)</th>
<th>Sardine (<em>Sardina pilchardus</em>)</th>
<th>Fine-scale menhaden (<em>Brevoortia gunteri</em>)</th>
<th>Atlantic menhaden (<em>Brevoortia tyrannus</em>)</th>
<th>Gulf menhaden (<em>Brevoortia patronus</em>)</th>
<th>Baltic Sea</th>
</tr>
</thead>
<tbody>
<tr>
<td>Northwestern Pacific</td>
<td>Coarse branchial basket; larvae feed on zooplankton (copepod eggs and nauplii); phytoplankton occasionally important in adult diet but small copepods dominate zooplankton dietary component; larvae of benthic animals (bivalves, decapods) consumed when fish inshore; feed during daytime.</td>
<td>Fine branchial basket; larvae feed on zooplankton (copepod eggs and nauplii); phytoplankton frequently important in adult diet but small copepods dominate zooplankton dietary component; seasonal and spatial differences in sub-adult and adult diet (phytoplankton vs zooplankton); feed during daytime.</td>
<td>Coarse branchial basket; larvae feed on zooplankton (copepod eggs and nauplii); phytoplankton unimportant in adult diet and zooplankton (large copepods, euphausiids and fish larvae) dominate prey biovolume; generally feed during daytime with some night-time feeding; diel variability in dominant dietary components.</td>
<td>Fine branchial basket but substantial spatial variability in number and spacing of gill rakers; filter-feeding dominant feeding mode; larvae feed on zooplankton (copepod eggs, nauplii and copepodites); phytoplankton occasionally important in adult diet but majority of adult dietary carbon from zooplankton (crustacean eggs, copepods, decapod zoa, and fish eggs); feed during daytime.</td>
<td>Coarser branchial basket; zooplankton (tintinids, ostracods and calanoid copepods) dominate adult diet.</td>
<td>Fine branchial basket and able to filter extremely small plankton particles; larvae feed on large phytoplankton and zooplankton whilst juveniles and adults are omnivorous; ontogenic changes in branchial basket linked to movement from estuarine (juvenile) to coastal (adult) habitats.</td>
<td>Finer branchial basket; phytoplankton (diatoms) dominates adult diet.</td>
<td>Sprat (<em>Sprattus sprattus</em>) – appear unable to filter-feed; diet dominated by calanoid copepods; exhibit selective feeding;</td>
</tr>
</tbody>
</table>
Table 8.7: Incidence of cannibalism (Can) and/or intraguild predation (IGP) shown by small pelagic fish from some of the case studies described above. Note that the authors are not aware of any publications describing cannibalism or intraguild predation for *Brevoortia gunteri*, *B. patronus*, *B tyrannus*, or *Strangomera bentincki*.

<table>
<thead>
<tr>
<th></th>
<th>Benguela</th>
<th>California</th>
<th>Humboldt</th>
<th>NW Pacific</th>
<th>NE Atl. / Med.</th>
<th>NW Atlantic</th>
<th>Baltic</th>
<th>References</th>
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<td><em>Engraulis encrasicolus</em></td>
<td>Yes</td>
<td>Yes</td>
<td></td>
<td></td>
<td>Yes</td>
<td>Yes</td>
<td></td>
<td>Plounevez and Champalbert (1999, 2000); Valdes <em>et al.</em> (1987)</td>
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<td><em>Engraulis mordax</em></td>
<td>Yes</td>
<td>Yes</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
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<td><em>Engraulis ringens</em></td>
<td></td>
<td></td>
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<td>Yes</td>
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<td></td>
<td>Alamo and Espinoza (1998); Alheit (1987); Santander <em>et al.</em> (1983)</td>
</tr>
<tr>
<td><em>Engraulis japonicus</em></td>
<td>Yes</td>
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<td></td>
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<td></td>
<td></td>
<td></td>
<td>Takasuka <em>et al.</em> (2004)</td>
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<tr>
<td><em>Sardinops sagax</em></td>
<td>Yes</td>
<td></td>
<td></td>
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<td></td>
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<td><em>Sardinops sagax</em></td>
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<td><em>melanosticus</em></td>
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<td>Yes</td>
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<td></td>
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<tr>
<td><em>Sardina pilchardus</em></td>
<td></td>
<td></td>
<td></td>
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<td>Yes</td>
<td>Yes</td>
<td></td>
<td>Garrido (2002); Garrido <em>et al.</em> (in press)</td>
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<tr>
<td><em>Sprattus sprattus</em></td>
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<td>Yes</td>
<td></td>
<td>Köster and Möllmann (2000)</td>
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<td><em>Clupea harengus</em></td>
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<td></td>
<td>Yes</td>
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<td>Patokina and Feldman (1998)</td>
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</table>
FIGURE LEGENDS

**Figure 8.1:** Morphometrics of some of the feeding apparatus of anchovy and sardine from the Benguela Current system, showing relationships between (a) gape size and total length for juvenile anchovy and sardine from the southern Benguela (redrawn from Booi, 2000); and (b) the total number of gill rakers and fish length and (c) gill raker gap and fish length, for anchovy and sardine from the northern Benguela (redrawn from King and Macleod, 1976).

**Figure 8.2:** Dietary composition of anchovy and sardine in the southern Benguela Current system, showing (a) the contribution to dietary carbon by prey size class for adult anchovy of 100-109 mm standard length on the South African west and south coasts (redrawn from James, 1987); (b) the contribution to dietary carbon by prey size class for adult sardine sampled off the South African southwest and south coasts in 1993 and 1994 (redrawn from van der Lingen, 2002); and (c, d) frequency distributions of copepod prosome length in stomach contents of juvenile anchovy and sardine from presumed mixed shoals sampled off the South African west coast (each plot represents a separate shoal; redrawn from Louw et al., 1998).

**Figure 8.3:** Results from laboratory experiments conducted on southern Benguela anchovy and sardine, showing relationships between (a) weight-standardized clearance rate (g−1.min−1) and prey size (mm) for each species (arrows labeled A and S indicate the approximate prey size at which the transition from filter-feeding to particulate-feeding occurs for anchovy and sardine, respectively; redrawn from van der Lingen, 1994); and (b) respiration rate (mg O2.g wet weight−1.h−1) and swimming speed (cm.s−1) for each species engaged in filter-feeding (“filtering”) and particulate-feeding (“biting”; redrawn from van der Lingen, 1995).

**Figure 8.4:** Changes in dietary composition (percentage number) with fish size for (a) Pacific sardine and (b) northern anchovy larvae from the California Current system (drawn using data in Arthur, 1976; note that the length classes used by that author were based on size distributions in samples and not on any definite changes in larvae with respect to age); and (c) increase in average prey width (µm) with size for sardine and anchovy larvae (drawn using data in Arthur, 1976).

**Figure 8.5:** Dietary composition (percentage number) of Pacific sardine off (a) southern California and (b) central Baja California (drawn using data in Radovich, 1952); and of northern anchovy from (c) northern Baja California to central California (drawn using data in Loukashkin, 1970) and (d) northern Baja California (drawn using data in Chiappa-Carrara and Gallardo-Cabello, 1993).

**Figure 8.6:** Relationships between predator length and prey length for northern anchovy (open circles) and Pacific sardine (closed circles) from the northern California Current system. The dashed line indicates the overall mean and the solid lines indicate the mean for each species. From T. Miller and R. Brodeur (unpublished data).

**Figure 8.7:** Relationships between mouth width and larval length (upper lines), and prey width and larval length (lower lines show the maximum and minimum prey widths) for anchovy and sardine larvae from the Humboldt Current system. Redrawn from Muck et al. (1989).

**Figure 8.8:** Dietary composition (percentage number) of (a) anchovy (n = 86) and (b) sardine (n = 56) collected off Peru during 1998 (drawn using data in Blaskovic et al. 1998); small copepods comprise *Acartia, Calocalanus, Clausocalanus, Clymnestra, Corycaeus, Euterpina, Oithona, Oncaea, Paracalanus, Harpactacoida*, copepodites and copepod remains; medium copepods comprise *Centropages, Lucicutia, Macrosetella, Mecynocera* and *Microsetella*; and large
copepods comprise *Calanus, Candacia, Euaetideus, Eucalanus, Euchaeta, Euchirella, Pontellina* and *Rhincalanus*.

**Figure 8.9:** Scatter plot (grey dots) and cubic spline smoother fit (black solid lines) of GAM models based on anchovy stomach fullness according to time of day for the complete set of 21,203 stomach contents collected off Peru over the period 1996-2003. The black dotted lines show the 95% confidence limits of GAM models. The right y-axis is a relative scale, and shows the spline smoother that was fitted to the data, so that a y-value of zero is the mean effect of the variable on the response. From Espinoza and Bertrand (in press).

**Figure 8.10:** Frequency distributions of copepod prosome length in stomachs of Japanese anchovy and sardine from the northwestern Pacific (redrawn from Li. et al., 1992).

**Figure 8.11:** Morphometrics of some of the feeding apparatus of anchovy and sardine from the northwestern Pacific, showing relationships between (a) the total number of gill rakers and fish length and (b) gill raker gap and fish body length (redrawn from Tanaka, 2006).

**Figure 8.12:** Morphometrics of some of the feeding apparatus of anchovy and sardine from Vigo, NW Spain, in the northeastern Atlantic, showing relationships between (a) mean number of gill rakers and fish length for both species, (b) gill raker separation and fish length for both species, (c) denticle length and and fish length for sardine only, and (d) denticle separation and fish length for sardine only. Redrawn using data in Andreu (1953, 1960, 1969): measurements were taken from post-larval and adult individuals and regressed against size (total length in 0.5 cm size classes), and standard errors were computed using individual measurements from 4 to >50 individuals per size class.

**Figure 8.13:** Relationship between gill raker gap and fish length for Atlantic menhaden (redrawn from Friedland et al., 2006).

**Figure 8.14:** Percentage frequency (a) and percentage number (b) of food items in the diets of the menhaden *Brevoortia gunteri* and *B. patronus* (drawn using data in Castillo-Rivera et al., 1996).

**Figure 8.15:** Percentage frequency (a) and percentage relative wet mass to the total stomach content wet mass (b), of the major prey items of Baltic Sea herring and sprat summarised from samples collected over the period 1977-1999 (drawn using data in Möllmann et al., 2004).

**Figure 8.16:** Conceptual schematic of how physical forcing may lead to environments that favour either anchovy or sardine in the southern Benguela Current system (from van der Lingen et al., 2006a).

**Figure 8.17:** Comparison of anomalies of climatic (CLI1), oceanographic (OCE1), plankton (ACI) and sardine dominance indices (RIS) in the northeastern Iberian Atlantic. CLI1 and OCE1 were extracted from Principal Component Analysis of climate indices (ftp://ftp.cpc.ncep.noaa.gov) and oceanographic variables of the northern Atlantic, respectively. Climatic variability was mainly related to latitudinal anomalies in north winds (positive values) but also in the influence of subtropical winds (negative values). Oceanographic variability was reflected by periods of relative stability and high temperature of the upper water column (positive values) alternating with others of high turbulence and low temperature (negative values). ACI indicated the relative dominance of small (*e.g.* *Acartia*, positive values) or large copepods (*e.g.* *Calanus*, negative values) and was computed from data from the Continuous Plankton Recorder survey (http://www.sahfos.org). RIS expressed the relative dominance of sardine (positive values).
or anchovies (negative values) in commercial landings (data from ICES, 2005). Further details on the data sources and analysis can be found in ICES (2007).

**Figure 8.18**: Schematic representing the effects of variability in climate on Baltic herring (left side) and sprat (right side) growth (black arrows), and sprat recruitment (grey arrows), copepod to the left is *Pseudocalanus acuspes* and to the right *Acartia* spp.; T – temperature, S – salinity, O2 – oxygen. The black arrow between sprat and herring indicates competition.
Figure 8.1
Figure 8.2
Figure 8.3
Figure 8.4
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Figure 8.5

Figure 8.6
Figure 8.7

Figure 8.8
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Figure 8.9

Figure 8.10
Figure 8.11
Figure 8.12
Figure 8.13
Figure 8.14
Figure 8.15
Figure 8.16
Figure 8.17
Figure 8.18