Chapter 13
Evolving from Fry Fisheries to Early Life Research on Pelagic Fish Resources

Alberto García, Raúl Laíz-Carrión, Dolores Cortés, José Quintanilla, Amaya Uriarte, Teodoro Ramírez, Lidia Yebra, Jesús M. Mercado, Candela García-Gómez, Simone Sammartino, and Jesús García Lafuente

13.1 Brief Historical Background of Fry Fisheries in Northern Alboran Sea

The northern coasts of the Alboran Sea are known to have thrived from past artisanal fisheries that exploited the early life stages of fishes. This was mainly carried out by a suite of different fishing gears dating back to the eighteenth century to the end of the twentieth century (Sañez-Reguart 1791–1795 reprint 1988; Rodríguez Santamaría 1923). These fishery studies provide detailed descriptions of the fishing gears employed by fishermen exploiting the Iberian Peninsula coasts and a general account of the targeted species and their associated catches. In the Andalusian coasts of the Alboran Sea, beach seines called *boliches* were among the most common, targeting on sardines, anchovies, and a number of other fish species, as bonitos and tunas that preyed on small pelagic shoals (Fig. 13.1).

In this historical description, the Bay of Malaga is cited as most prolific in the use of this specific fishing gears exploiting nearshore fish resources of northern Alboran (Rodríguez Santamaría 1923) (Fig. 13.1). These fishing gears continued until the twentieth century and evolved reducing its size to allow the maneuvering with a smaller number of persons. Through time, this gear was modified for the fry fishing of small pelagic species. Its modifications mainly consisted in gradually diminishing the mesh of cod ends for catching postlarval stages of sardines and anchovies,

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A. García (✉) · R. Laíz-Carrión · J. Quintanilla · A. Uriarte · T. Ramírez · L. Yebra · J. M. Mercado
Instituto Español de Oceanografía, Centro Oceanográfico de Málaga, Fuengirola (Málaga), Spain
e-mail: raul.laiz@ieo.es; jose.quintanilla@ieo.es; teodoro.ramirez@ieo.es; lidia.yebra@ieo.es; jesus.mercado@ieo.es

D. Cortés · C. García-Gómez · S. Sammartino · J. G. Lafuente
Physical Oceanography Group, University of Málaga, Málaga, Spain
e-mail: ssammartino@ctima.uma.es; glafuente@ctima.uma.es

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Fig. 13.1 Engraving of a beach seine doing the encircling maneuver to catch shoaling fishes (Sañez-Reguart 1791–1795 reprint 1988; personal copy)

oftentimes capturing shoals of postlarvae and juveniles of other species, such as *Pagellus* sp., *Boops boops*, *Mullus* spp., etc. (García et al. 1981; Reina-Hervás and Serrano 1987).

The increase of the coastal populations flanking the Alboran Sea originated from the touristic boom of the mid-1960s and 1970s led to the increase of fry fishing. This fishery typified the coastal region with numerous beach seine fishing along the coast (Fig. 13.2), especially abundant in the beaches facing the Bay of Malaga (García et al. 1981). The product of the fishery was camouflaged as "*chanquete*," the local denomination for *Aphia minuta*, a transparent gobid whose adult size was similar to the fry of sardine, anchovy, and round sardinella. The abundance of sardine in the Alboran Sea led to the first scientific reports describing their distribution in the area (Oliver 1955, 1961). An actual description of the fishing methods applied in present times providing recent data from the coastal fisheries off N Alboran coastline is reported in García et al. (2012).

With the economy rising in the 1980s, the fishery expanded because its resources were guaranteed year-round. The inshore coastline of the Alboran Sea is a haven for the growth of advanced stages of sardine, anchovy, and several other commercial fish species. Thus, the iconic image of beach seine trawling was commonplace in the shores of the Bay of Malaga (Fig. 13.2). The demand for the consumption of fry became so high that another type of artisanal fishing gear, the *birorta*, also competed for these early life resources (Fig. 13.3). This kind of fishery consisted in a small type of purse seine maneuvered by two–three persons that encircled postlarval shoals, and

Fig. 13.2 Hauling in the catch of beach seine (*boliche*) for small pelagic fry (photo from A García)

Fig. 13.3 Small purse seine (*birorta*) used for fry fishing (photo from A García)

Fig. 13.4 Cod end of beach seine and its fish fry capture (photo from A García)

unlike the beach seine (*boliche*) did not trawl over the seabed (Fig. 13.2). Such was the expansion of this type of gear during the early 1980s when as many as over a hundred small boats could be counted from the beach near the Malaga port entrance (A. García, unpublished data counts).

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Upon the integration of young scientists in the late 1970s to work in the Oceanographic Center of Malaga, it was considered necessary to provide proof for banning this obsolete fishing practice. Fry fishing was so intensive and out of regulation control measures that strong management measures were urgently implemented. Catches as shown in Fig. 13.4 are exemplary of the magnitude of the impact on small pelagic resources. As a result, during the mid-1980s, the Autonomic Government of Andalucia issued a ban on fry fishing. Nonetheless, the local culinary preferences for small fish still persist, and the lack of compliance with the regulation leads to occasional confiscations of fry catches.

The extraordinary abundance of postlarval stages of small pelagics inshore, at depths less than 20 m, propitiated research focused on early life history stages (ELHS, henceforth) of small pelagic fish species, including the modification of plankton tow procedures regarding duration and plankton gear. As in the fry fishery, ichthyoplankton sampling of postlarvae was carried out at night time when larvae surface to inflate their swim bladders, a behavioral habit that initiates schooling behavior (Santos et al. 2007). To assure greater catches with larger larvae, a squared-mouth Bongo 90 (Steve Coombs, Spartel Ltd.) was designed. To reduce larval avoidance, it is geared with a black-tinted mesh (> 1 mm) (Fig. 13.5).

The open mesh employed mostly caught postlarvae which were easily sorted on board and stored in liquid nitrogen. Short tow duration (10 min) at the surface or subsurface was considered sufficient to catch postlarvae in good condition for analyzing larval growth and condition research (García et al. 2003; García et al. 2006a, b). The plankton gear developed for sampling small pelagic larvae was later used for defining the bluefin tuna spawning habitat and to carry out larval tuna research studies in the Balearic Sea, the key spawning grounds of Atlantic bluefin

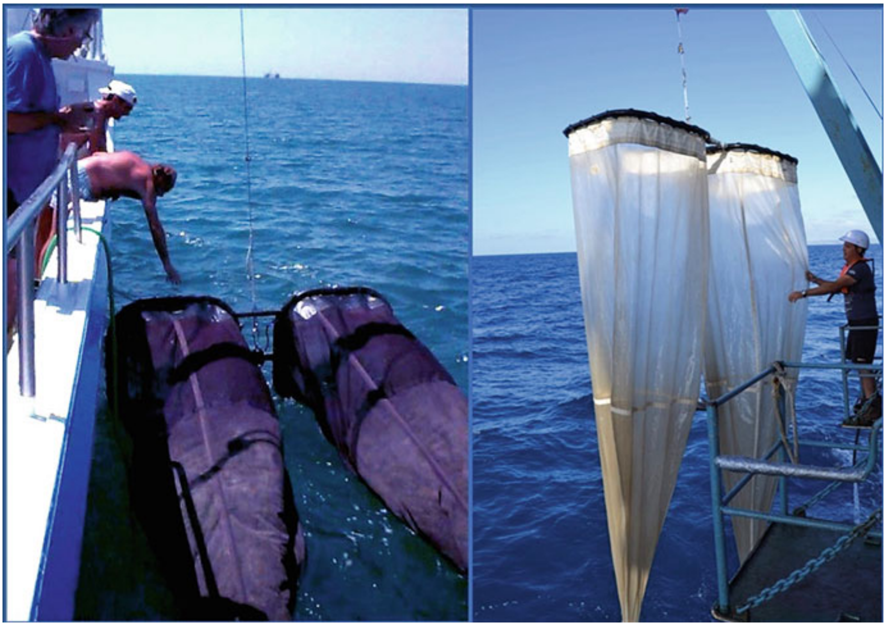

Fig. 13.5 Standard Bongo 90 net pictured in two versions: left picture, the black tint netting equipped has >1 mm mesh primarily used for nighttime hauls of small pelagic larvae; right picture, Bongo 90 equipped with 500 μm mesh (photo from A García)

tuna in the Mediterranean (García et al. 2006a, b; Alemany et al. 2010; Uriarte 2018).

The change of plankton gear and sampling at night was mainly aimed to collect larger sized larval specimens, centered on postlarval stages for its longer age history. A historical time series analysis of the Californian anchovy egg and larval abundance of the CalCOFI surveys was not able to relate neither of these variables to the recruitment success of the Californian anchovy (*Engraulis mordax*) (Bradford 1992). The study concluded that recruitment success was not related to egg and larval abundance, postulating that the abundance of postlarval stages of sizes around 15 mm would have a greater repercussion on annual recruitment.

Consequently, in the first analysis between the standard Bongo 40 tows and the Bongo 90, anchovy larval size increased to an average catch of 15 mm (Fig. 13.6) larvae in favor of the Bongo 90 gear. Furthermore, the size range of larvae being collected also increased. This net was later applied in an Atlantic bluefin tuna project (TUNIBAL) aiming to sample bluefin larvae following an ICCAT recommendation promoting research of bluefin larvae. The project showed great success in collecting large numbers of Atlantic bluefin tuna larvae since its first implementation (García et al. 2003). Similar sampling techniques were also adopted in the spawning grounds of Atlantic bluefin tuna spawning in the Gulf of Mexico, where this type of gear excelled all others in a suite of other ichthyoplankton nets (Habtes et al. 2014).

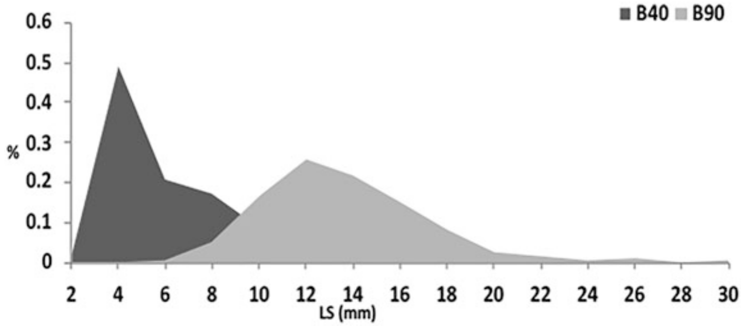

Fig. 13.6 Comparative anchovy larval catch between the B40 and B90 plankton nets

Thus, this plankton gear has become the standard type of gear for collecting small and large pelagic larvae in the field, specifically for undertaking larval growth and condition studies (Cortés 2006; García 2006) as well as ELHS trophodynamic studies based on stable isotopes analysis (Uriarte 2010; Laíz-Carrión et al. 2011). In conclusion, the sampling methods of ELHS applied in these studies stem from observing the conducts of fry fisheries.

13.2 Spawning and Nursery Scenarios of Small Pelagic

13.2.1 Coastal Hydrodynamics and Planktonic Productivity Drivers

According to the existing literature, small pelagics are particularly abundant in upwelling areas (Cole and McGlade 1988; Cury et al. 2000) where the enrichment in nutrients cascades throughout the food web, increasing planktonic production and thereby, potential larval food resources. The degree of recruitment will depend on the coupling between the timing of spawning and favorable environmental conditions for the survival of ELHS (Cury and Roy 1989; Bakun 1996; Brochier et al. 2009). The usual physical forces driving the processes that shape these conditions are winds (wind-inducing upwelling, particularly), tides, and offshore mesoscale and submesoscale (10–100 km) processes, which have a potential for conveying energy to the coastal ecosystem and make it available for mixing. All of them, referred to the northern Alboran Sea, are shortly revisited below.

From geographic and oceanographic viewpoints, the northern Alboran Sea is divided into two differentiated areas. The first one goes from Punta Europa in the eastern exit of the Strait of Gibraltar to Punta Calaburras, some 100 km to the east (Estepona area or EA, hereinafter, Fig. 13.7). The second area spreads to the east of this point and includes the productive Bay of Malaga (Malaga area, or MA). This division is motivated by the Atlantic Jet, which flows relatively close to the coast in

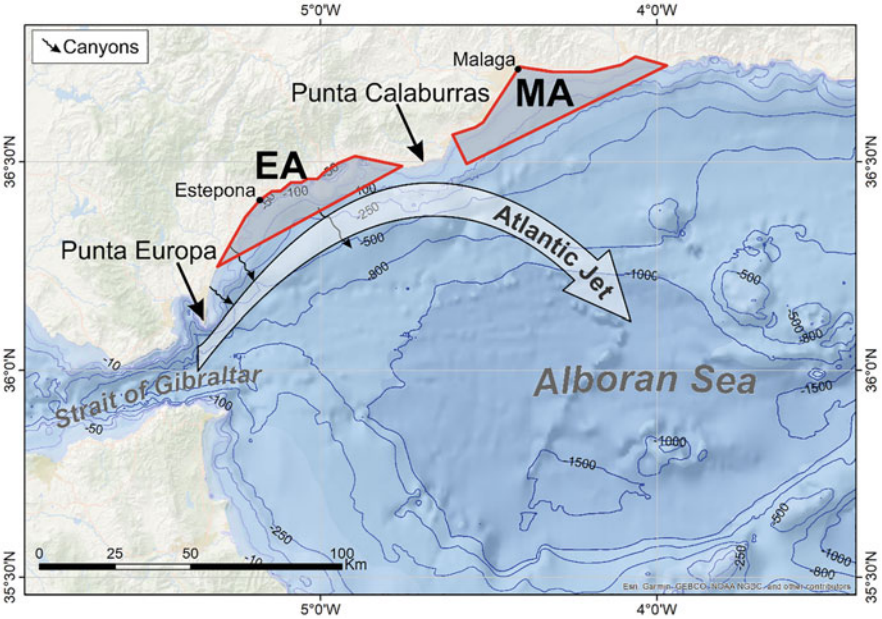

Fig. 13.7 Map of the Alboran Sea sketching the typical path of the Atlantic Jet and the two areas EA and MA mentioned in the text. Winding arrows indicate the location of submarine canyons

EA and exposes the region to its direct impact, but it detaches from the Spanish shore and starts veering to the southeast nearby Punta Calaburras, leaving the MA region partially sheltered from its influence. The jet separation from the shore as it flows past Punta Europa and Calaburras forces cyclonic circulation in both areas, which endows them with characteristics of retention zones. The retention of larvae is one of the processes that define the Bakun triad, which ultimately influences the survival of larval cohorts (Agostini and Bakun 2002; Agostini and Bakun 2002; Patti et al. 2010).

Because of the similar shoreline orientation, both areas show a similar response to wind dynamics. Westerlies induce upwelling and cool surface waters, while easterlies advect surface waters from offshore, warming the coastal environment and driving downwelling. Nine years (2003–2011) of data in the Alboran Sea (Era-Interim reanalysis, Dee et al. Dee et al. 2011) reveal the bimodality of winds, easteries, and westerlies, the former being slightly more frequent (48% versus 41%) and weaker (5.9 ms^{-1} versus 7.1 ms^{-1}) on average. In wintertime, however, westerlies are more frequent and intense (Sarhan et al. 2000). Upwelling in these regions enriches the water column and enhances primary production, which, along with their retention characteristics, meet the three conditions of the "Bakun triad" (Bakun 1996; Agostini and Bakun 2002) which define suitable environmental conditions for the spawning and nursery habitats.

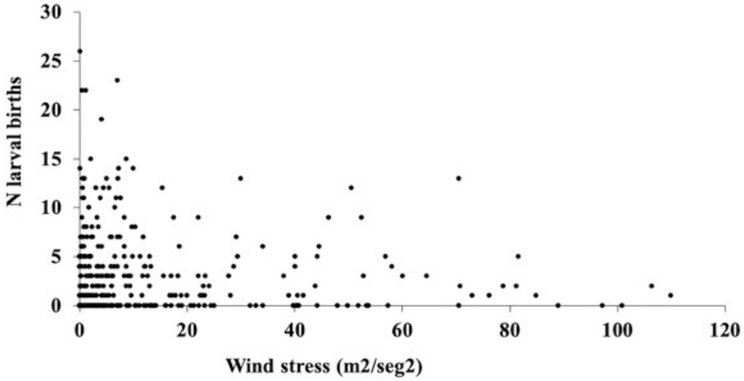

Fig. 13.8 The number of larvae born in relation to the wind stress indices observed during birthdates of all sampled sardine larvae sampled during the ECOMALAGA time series (1995, 1997–2003)

The findings from sardine larval cohorts sampled in the ECOMALAGA project (Camiñas et al. 1998) on a seasonal basis starting in 1995 and later during the period from 1997 to 2003 have shown the biological impact of wind on larval growth rates, as likewise, the effect of strong storms which may cause diminished growth rates (Maillet and Checkley 1991). The effect of coastal winds off the MA region affects sardine's spawning strategy where mature sardines prefer calm wind periods for spawning. It is in agreement with the "stable ocean" hypothesis (Lasker 1981) by which calm periods allow the formation of plankton patches, a potential food for the spawned offspring (Fig. 13.8).

Furthermore, the wind regime influences sardine larval population growth rates of different seasonal and annual sardine cohorts sampled in 1995 and during the period 1997–2003 as described in Fig. 13.9 (García 2006).

Westerlies in the nursery grounds of MA and EA affect all the northern Alboran Sea coast, promoting the fertilization of the surface layers and phytoplankton blooms (Sánchez-Garrido et al. 2014). These intense events of wind-induced upwelling are frequent, and they are followed by relatively calm periods that allow for a partial stratification of the water column (Mercado et al. 2007). This sequence of events may result beneficial, favoring the growth of larvae inhabiting nursery waters (García 2006).

Tides follow winds in importance as a physical mechanism influencing the environmental conditions in the northern Alboran Sea (Sánchez-Garrido et al. 2015). Inside the Mediterranean Sea, tides are almost inexistent except for a few places. One of them is nearby the Strait of Gibraltar and, of course, the strait itself (García Lafuente et al. 2000). Even though tidal vertical oscillations are very reduced (amplitude less than few tens of cm), the associated tidal currents can become important; the closer to the strait, the greater the current, so that tidal dynamics is enhanced in EA with regard to MA. Actually, García Lafuente et al. (1999) reported tidal currents up to 50 cm/s in the submarine canyons located in EA (Fig. 13.7),

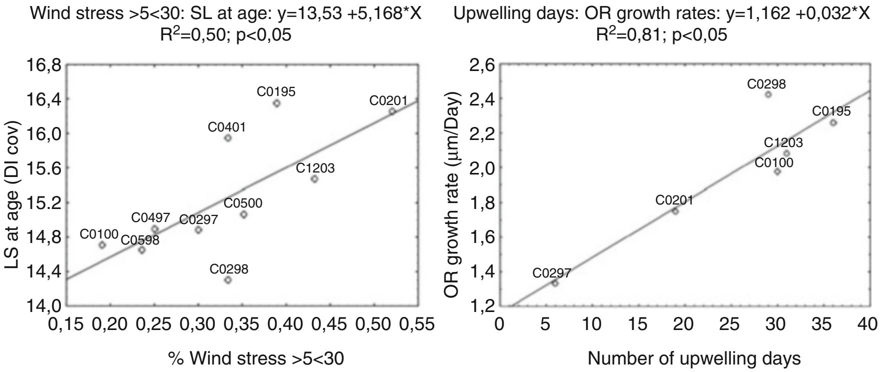

Fig. 13.9 Lineal relationship of SL at age with wind stress (ranging from >5 to < 30 and otolith radius (OR) growth rates with the percentage of wind stress and upwelling days undergone by sardine's larval life duration (C stands for cohort, then month/year) collected under the ECOMALAGA time series

whereas numerical simulations indicate values of only a few cm/s in MA. The available kinetic energy of tidal origin is therefore much greater in EA than in MA.

Significant differences between both regions also arise from the response to offshore mesoscale processes. In EA, the proximity of the jet to the shore (Fig. 13.7) causes a close dependence of the region dynamics on the fluctuations in the position of the Atlantic Jet, which are linked to the hydrodynamics of the water exchange through the Strait. Sarhan et al. (2000) showed that the north-to-south variation of the main path of the jet drives upwelling in a comparable way to the classical wind-induced upwelling, although the latter is more productive biologically due to the characteristics of the upwelled water. This mechanism is much weaker in the MA region and is concomitant with the wind regime to a large extent.

Considering the physical processes that act on both areas altogether, the EA region presents more vigorous dynamics driven by tides and by the transfer of energy from offshore mesoscale processes linked to the proximity of the Atlantic Jet. Wind-induced dynamics is similar in both regions, so that differences among them arise from the intensity of the two other mechanisms, which are noticeably more vigorous in EA. It means more available energy for mixing here and, hence, more potential for primary production, which is a positive feedback. But there is also a negative aspect related to the stability of EA as a retention area, because the accumulation of energy may eventually lead to instabilities. Sánchez-Garrido et al. (2013) showed that EA is a region prone to the release of submesoscale eddies that wander across the Alboran Sea carrying biological products with them. Even though it is essentially driven by the same mechanisms, the MA region has weaker dynamics because the energy input from offshore and the tidal energy are secondary processes, and the main driving and fertilizing mechanism here is the wind-driven upwelling. Neither instabilities like those reported in EA are observed in MA, so that the stability of this region as a retention area is considerably greater, which has obvious biological advantages for the reproduction strategy of small pelagic species and other coastal dwelling species.

13.3 Phytoplankton and Zooplankton Variability of the Alboran Sea Coast

The coastal hydrodynamics in the Alboran Sea which affects the formation of advection and upwelling processes that propitiate phytoplankton production and enriches plankton communities has been highlighted widely. In fact, the northwestern Alboran Sea represents the most productive area in the Western Mediterranean Sea in terms of chlorophyll-a (Chl-a), primary production and phytoplankton abundance (Rodríguez et al. 1998; García-Gorriz and Carr 2001; Ruíz et al. 2001, 2013; Bosc et al. 2004; Mercado et al. 2008, 2012, 2014; Patti et al. 2010; Navarro et al. 2011). Consequent with the Alboran Sea's high phytoplankton production, zooplankton biomass and production estimates of the Alboran Sea (García and Camiñas 1985; Sampaio et al. 2005; Yebra et al. 2017) have ranked among highest in the western Mediterranean (Champalbert 1996; Siokou-Frangou et al. 2010). A quarterly monitoring project carried out in MA since 1992, ECOMALAGA, describes the temperature/salinity time series (Fig. 13.10), as well as the mesozooplankton abundance and chlorophyll concentration (Fig. 13.11). The data were obtained from quarterly samplings performed principally in January–February (winter), March–April (spring) July–August (summer), and October–November (autumn). These data indicate that the annual maximum in temperature and minimum in salinity is normally obtained in summer-autumn. However, the occurrence of annual cycles departing significantly from these typical cycles is frequent (for instance, see the periods 1994–1995 and the years 1999 and 2003; Mercado et al. 2007, 2012).

The TS time series depicts strong seasonal differences in which temperature between winter and spring/summer periods differs by 6°C. Likewise, the salinity profiles provide a picture of upwelling events observed, such as that of 1993, 1999, and 2012. Such hydrographic seasonal variability shows its influence in the mesozooplankton and chlorophyll *a* variability (Fig. 13.11). The upwelling events that occurred during 1993 and 1999 showed peaks of mesozooplankton abundance and chlorophyll *a* values, while that of 2012 was mainly reflected by the peaks of chlorophyll *a* concentration. Nevertheless, the gap observed in 2013 was covered by another monthly sampling project of MA (REMALA) that also showed strong upwelling events in the winter of 2013 and summer of 2014 (see Fig. 13.10).

These data show the complex time variability patterns that feature the plankton community in the Alboran Sea. Thus, conspicuous peaks in the abundance of mesozooplankton are often registered (years 1993, 1998–1999), which are normally attributable to copepods, but it does not apply in every case. It is also notable that peaks of zooplankton often were not related to periods of elevated phytoplankton biomass (Fig. 13.11).

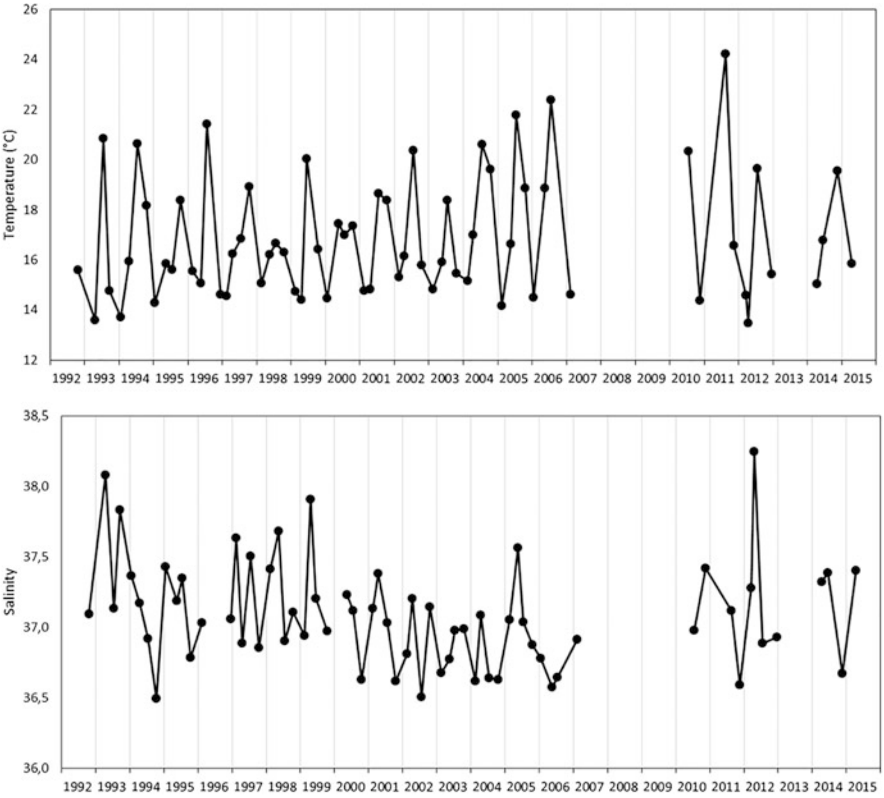

Fig. 13.10 Time series of temperature and salinity in the 20 m upper layer of a station located in the shelf of MA

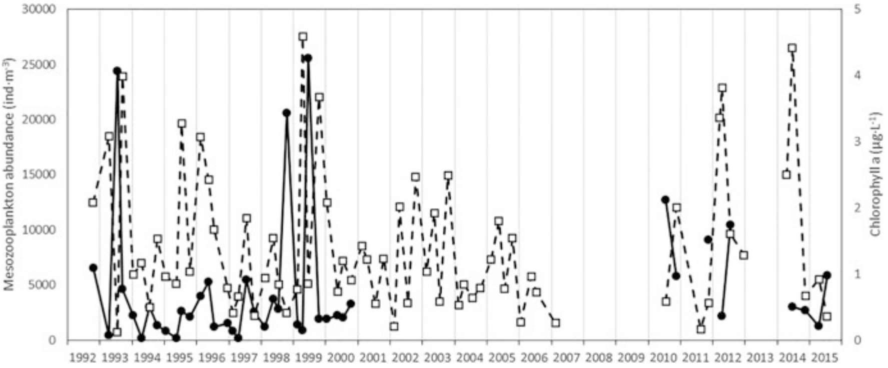

Fig. 13.11 Time series of mesozooplankton abundance (closed circles, continuous line) and concentration of chlorophyll a (open squares, dashed line) obtained in a coastal station in MA (https://www.st.nmfs.noaa.gov/copepod/time-series/es-50301/) from quarterly samplings carried out in 1992–2001 and 2010–2015 (data of chlorophyll for 2002–2007 are also shown)

This high productivity is primarily linked to the enrichment of the euphotic layer with inorganic nutrients (mainly nitrate), which supports communities of phytoplankton usually dominated by diatoms (Rodríguez et al. 1998; Arin et al. 2002; Reul et al. 2005; Mercado et al. 2005, 2007, 2011). However, the analysis of the interannual variability in the taxonomic composition reveals complex patterns (Balle 1963; Margalef 1969; Delgado 1990; Rubín et al. 1999; Mercado et al. 2005). Thus, the early works of Rodríguez et al. (1982) and Delgado (1990) reported a community dominated by small flagellates and diatoms which can be considered typical of upwelling areas. However, Mercado et al. (2005) described two well-differenced communities: one was dominated by small flagellates and diatoms (diatom-dominated community), while the other community was characterized by the dominance of coccolithophorids and dinoflagellates (non-siliceous algal-dominated communities). The analysis of time series for the period 1992–2002 revealed that both communities were temporally segregated, with diatom-dominated community prevailing from 1994 to 1997 and non-siliceous algal-dominated communities doing it from 2000 to 2002. The diatom-dominated community was mainly composed of chain-forming pennate diatoms belonging to the genus *Pseudo-nitzschia* and the centric diatoms *Thalassiosira*, *Rhizosolénia*, *Leptocylindrus*, and *Skeletonema*. The dinoflagellates belonging to the species *Scrippsiella trochoidea*, *Protoperidinium depressum*, and *Prorocentrum minimum* also appeared frequently. The second community was characterized by the coccolithophorids *Calcidiscus* and *Gephyrocapsa* and the dinoflagellates *Prorocentrum compressum*, *Ceratium extensum*, and *Ceratium furca* which were dominant during 2000–2002 (in special *Gephyrocapsa* sp.).

Irrespective of these interannual patterns, the abundance of diatoms is usually greater in spring, coinciding with greater nutrient availability. In contrast, the abundance of dinoflagellates does not follow a clear seasonal pattern. The analysis of the zooplankton abundance data also reveals a seasonal cycle characterized by maxima in summer (1964 ind m^{-3}) and minima in spring (467 ind m^{-3}, Sampaio et al. 2005). Copepods are the predominant group throughout the year, doubling their abundance in summer. However, at this time, cladocerans represent up to 40% of the relative abundance. Gelatinous plankton in general represents less than 5% of the community (Rodríguez et al. 1982; Sampaio et al. 2005). Interestingly, this seasonal cycle in zooplankton contrasts with the seasonal variations obtained for other locations in the western Mediterranean Sea, where lower biomasses of zooplankton are usually found in summer whereas higher values are obtained from April to June (Sabates et al. 1989; Fernandez de Puelles 1990; Champalbert 1996).

The joint analysis of the phytoplankton and zooplankton data series for the Alboran Sea carried out by Mercado et al. (2008) revealed that zooplankton exerts a strong top-down control on phytoplankton at the seasonal scale. However, the aforementioned interannual changes in phytoplankton composition reflected in changes in the zooplankton composition as the abundance of copepods and brachiopods decreased in 1992–1999 (possibly due to the interannual shifts in the phytoplankton communities). Furthermore, strong spring blooms of phytoplankton are normally followed by noticeable peaks of zooplankton in summer. In fact, zooplankton biomass and abundance in the NW Alboran coastal area were found to be highly correlated to chlorophyll *a* in summer (Yebra et al. 2017), indicating that taxonomic composition and abundance of the phytoplankton are the driving forces which in turn strongly influence the fate of zooplankton production (Poulet et al. 1995; Laabir et al. 1995). This planktonic production variability would in turn shape the ichthyoplankton recruitment success in the region since both abundance and quality of the potential prey for larvae vary significantly, which is probably reflected in the growth status of small pelagic larvae as is commented below.

13.4 Seasonal Characterization of the Alboran Sea Ichthyoplankton

The relative contribution of small pelagic larval catches by the fry fishery depicts the reproductive seasonality of sardine and anchovy larvae (García et al. 1981; García and Rubín 1985; García et al. 1987). The seasonal cycle extends from autumn to late spring, in which sardine larvae comprise the major fraction of catches, while in spring anchovy larvae overlap with sardine attaining its peak during the summer months. During autumn/winter, both species also overlap (Rodríguez 1990; Mafalda et al. 2008) (Fig. 13.12).

The Alboran Sea constitutes a natural passage where the exchange of Atlantic and Mediterranean water masses occurs and endows the region with an exceptional

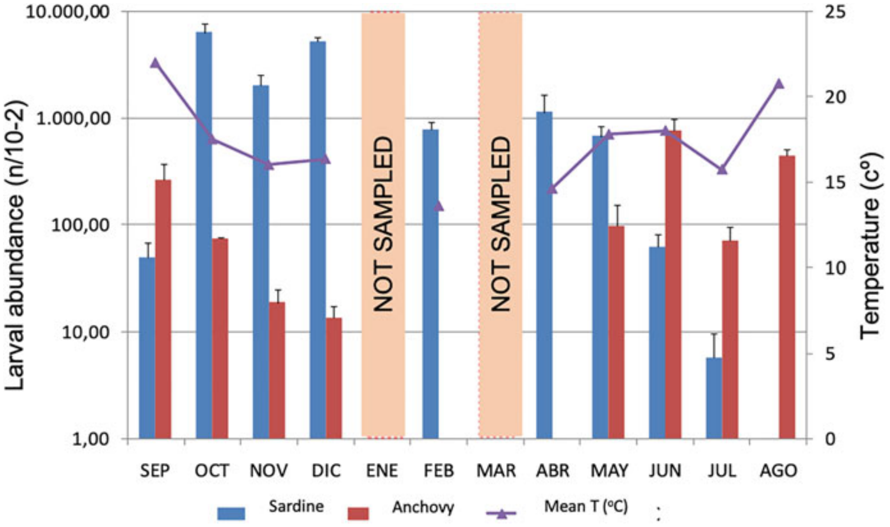

Fig. 13.12 Relative abundance of sardine and anchovy larvae in MA (N / 10 m^2), together with the average temperature at 10 m during September 2013 to August 2014 under the REMALA project (Baro et al. 2014). Note that the abundance scale is logarithmic

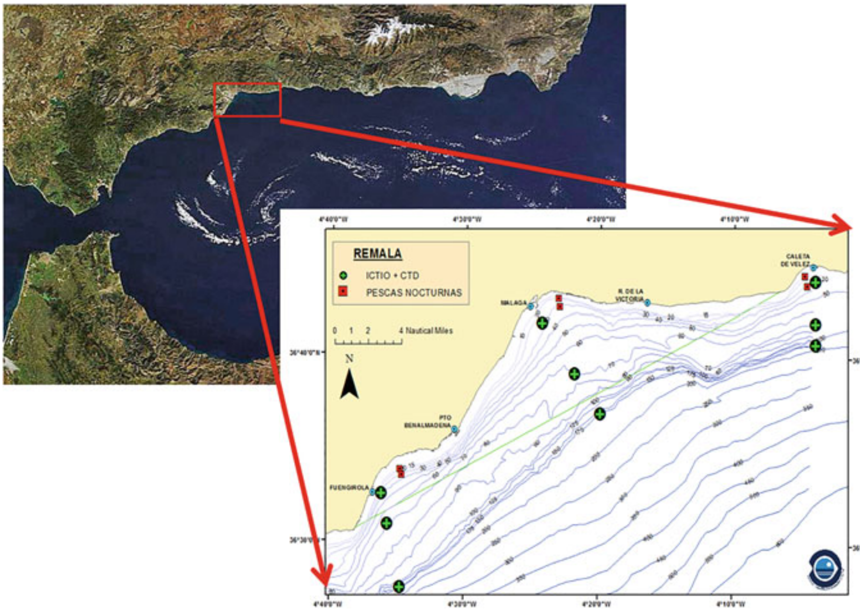

Fig. 13.13 Satellite mapping indicating study area and the ichthyoplankton and physical oceanography sampling stations in the study area during daytime (green cross) and nighttime (red square) from September 2013 to August 2014

species diversity clearly manifested in the specific composition of ichthyoplankton. An ichthyoplankton seasonal study throughout an annual cycle carried out in MA reveals the high species diversity (Marina et al. 2015; García et al. 2015). A grand total of 87 taxonomic groups were identified, in which 82 were to the species level. It is interesting to note that species of the meso- and bathypelagic domains were predominant in spite of the nine sampling stations located at shallow coastal and shelf waters (Fig. 13.13); specially noticeable is the fact that12 species representing 47.9% of the total account of larvae present during the annual cycle belonged to the Myctophidae family. Their nearshore abundance indicated an upwelling origin (Marina et al. 2015; García et al. 2015). The high species diversity is greater than that reported by Rodríguez (1990) and Mafalda et al. (2008).

The next dominant group was represented by the Clupeidae family accounting 14.38% of the total larvae collected. *Sardina pilchardus* larvae are found almost throughout the whole year (Fig. 13.14). Sardine starts spawning in September and develops its peak season during winter when temperature is lower and upwelling is more frequent and intense. Nevertheless, their larvae may still be found until late spring and early summer (Fig. 13.14).

With respect to anchovy (*Engraulis encrasicolus*), it shows the preference for warmer temperatures compared to sardine (García and Palomera 1996; Palomera et al. 2007). The Alboran Sea anchovy starts spawning in May and develops its full spawning capacity during summer and continues during autumn (Fig. 13.14).

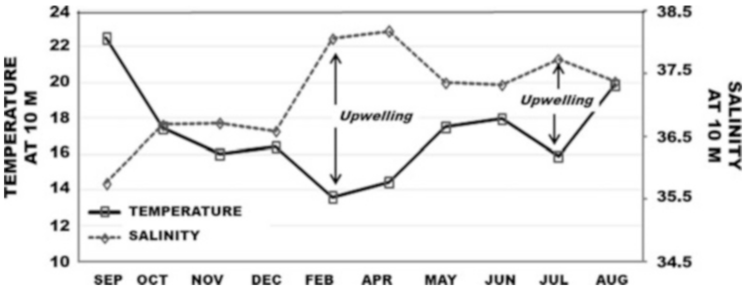

Fig. 13.14 Average monthly temperature and salinity throughout the anchovy and sardine sampling period carried out during the REMALA project (September 2013–August 2014)

Although much less abundant than the aforementioned groups, commercially important species were represented by hake (*Merluccius merluccius*), blue whiting (*Micromesistius poutassou*), axillary seabream (*Pagellus acarne*), spotted seabream (*Pagellus bogaraveo*), black seabream (*Spondyliosoma cantharus*), two horse mackerel species (*Trachurus trachurus* and *T. mediterraneus*), chub mackerel (*Scomber japonicus*), and the two Mediterranean species of mullets (*Mullus surmuletus* and *M. barbatus*).

The monthly mean temperature and salinity data collected during the surveys deviated from the annual average temperature and salinity historical series (Fig. 13.10) consequent with the observed upwelling events during winter and summer. Such events explain the high species diversity and the timing of spawning of sardine and anchovy (Fig. 13.14). During the initiation of the annual cycle, from September to December, we observed that the waters were predominantly of Atlantic origin defined by their characteristic salinity signatures. The interphase salinity between Atlantic and Mediterranean water masses is 37.5. From February to April, salinities were within the range of Mediterranean waters, explained by upwelling processes evidenced by the lower-temperature regime observed in the MA during the sampled period. From May to August, during the anchovy spawning season, salinities drop to interphase values between Atlantic and Mediterranean waters, and the temperatures rise.

It is important to remark thermic preference for warmer waters of anchovy (Palomera et al. 2007) as shown by the decrease in the abundance of anchovy larvae during July, consequential with the temperature drop resulting from the summer upwelling event (Fig. 13.12).

13.5 Ecophysiology of ELHS of Small Pelagics

13.5.1 Scientific Scope of Early Life History Research

Recruitment of small pelagic species such as sardine and anchovy is characterized by strong interannual fluctuations (Giráldez and Abad 1991) that are attributed to the survival success during the early life stages. Several factors affect fish larval mortality rates during the ELHS, although the most important ones are mortality caused by enhanced predation and/or starvation (Hewitt et al. 1985; McGurk 1986; Bailey and Houde 1989).

The survival of ELHS is therefore crucial for stock recruitment where small changes in growth rates can have important repercussions on larval mortality (Houde 1987, 2008). Mortality rates during early life are influenced by starvation and predation, generally in that sequence because starvation leads to poorer nutritional status of larvae making them more vulnerable to predation (Bailey and Houde 1989; Folkvord and Hunter 1986). Also, slower growth rates turn fish larvae extend temporally the ontogenic development at particular sensitive stages, thereby increasing predation pressure (Buckley 1984; Folkvord and Hunter 1986).

Therefore, somatic larval growth rates are critical in determining the time that larvae spend in the size classes more susceptible to be preyed upon. The research conducted on growth and condition studies at ELHS of small pelagics has shown that growth rates are influenced mainly by the surrounding temperature regime and the amount and quality of trophic resources (Ramírez et al. 2001; García et al. 2003; Mercado et al. 2007), although maternal effects can have a consequential influence on growth variability (García et al. 2003; Uriarte et al. 2016).

Temperature is a key factor controlling fish growth. Temperature affects metabolic rates of ELHS by increasing or decreasing the catabolism and anabolism of proteins and therefore the accretion of muscular tissue and the development organs during the development of ELHS. Several studies have reported enhanced larval growth at higher temperatures both in the field- and in laboratory-reared larvae (Blaxter 1991; Folkvord et al. 2004). On the other hand, nutritional condition indices are also affected by temperature. Thus, the existing studies on this subject (e.g., Goolish et al. 1984; Ferguson and Danzmann 1990) have shown that larval fish RNA/DNA tends to decrease with increasing seawater temperature. According to Goolish et al. (1984), the underlying reason for a decline in RNA/DNA in fish inhabiting increased seawater temperature would be due to the existence of a metabolic mechanism that compensates for lower RNA activity at lower temperatures, producing an increase in RNA concentration.

Alternatively, food availability (i.e., suitable prey density) and larval success in capturing their prey affect directly to the intake rates of proteins, carbohydrates, lipids, and other nutrients by fish larvae. Laboratory and mesocosm experiments have shown that food availability directly affects somatic larval growth, with well-fed larvae growing at faster rates than larvae under poor food availability. Food availability not only affects growth, but it also affects the biochemical composition of larval tissue. A poor nutritional condition, or even starvation caused by competition for food resources or by low prey density, not only has a direct effect on protein synthesis and tissue accretion rates, but it also turns larvae more sensitive to predators as their swimming capacity is reduced, thus prone to predators (Purcell 1985; Purcell and Grover 1990).

The findings reported by earlier research studies on larval growth (based on otolith microstructure) and nutritional condition (mainly based on RNA/DNA) clearly demonstrated the joint use of otolith microstructure and biochemical analysis as new tools for assessing the effect of the processes affecting larval survival and better understand the underlying causes of interannual fluctuations in the recruitment success of small pelagic species (Buckley 1984; Campana and Neilson 1985; Moksness and Wespestad 1989; Clemmessen 1994). Some of these studies and others demonstrated that enhanced growth at early life stages shows significant relationships with larval survival rates for many fish species around the world (Hovenkamp 1992; Takasuka et al. 2003; García et al. 2003; Meekan et al. 2006).

The implementation of these research tools was applied in the field, beginning with the NW Mediterranean anchovy which represents the greatest resource of this species in the Spanish Mediterranean (García et al. 1998). The experience gathered in these ELHS research proved in later years that the early life stages of sardines and anchovies confirm the growth-mortality hypothesis (Anderson 1988) by which growth is intricately related to larval mortality (Houde 1987, 2008).

In small pelagic larvae, enhanced growth is attained with higher RNA/DNA influenced by the amount of trophic resources between regions in western Mediterranean coasts (García et al. 1998, 2003; Quintanilla et al. 2015).

Thus, differences in somatic growth, otolith growth, and larval nutritional condition of anchovy larvae, from different spawning areas of the NW Mediterranean, suggested important effect of seawater temperature on larval condition as estimated from RNA/DNA. Those effects were confirmed by Ramírez et al. (2004) who studied the effect of temperature and microzooplankton biomass on biochemical nutrition indices of anchovy larvae in the NW Mediterranean Sea where temperature and microzooplankton accounted for >70% of the variability in RNA, DNA, and protein. However, the ratios of RNA/DNA and protein/DNA were only related to temperature. On average, both ratios in anchovy larvae decreased with temperature, probably reflecting the effect of temperature on larval metabolism, supporting the findings of previous studies conducted with other species (e.g., Goolish et al. 1984; Ferguson and Danzmann 1990).

Accurate estimates of growth rates and nutritional condition of larvae were needed to understand and predict fluctuations in recruitment. The ECOMALAGA quarterly sampling program supported the small pelagic larval sampling which is a methodological framework in establishing precision and accuracy under an EU-funded project (PARS, FAIR961371) grouping teams from different EU countries.

The research conducted involved different interlaboratory test studies, including samples of Alboran Sea sardine larvae, to analyze the precision and accuracy of otolith readings and the use of the RNA/DNA as tools for determining larval growth and nutritional condition. Among the main outcomes of the project was the publication of a practical manual of the tools used for recruitment studies of small pelagic fish species (Belchier et al. 2004) where different protocols regarding otolith microstructure analysis and nutritional condition were tested through intercalibration procedures and applied accordingly.

García et al. (2006a, b) observed differentiated larval growth patterns between the sardine stocks of the NW Mediterranean and the northern Alboran Sea. Larval daily growth rate, otolith growth rate, as well as RNA, DNA, and protein content at a given age were comparatively higher in larvae collected in the NW Mediterranean coast (Ebro Delta). From the somatic point of view, the NW Mediterranean sardine grew faster in body size in comparison to the Alboran Sea larvae which tended to distribute body mass increase by means of increasing body weight, suggesting in the latter that growth tends to build up body reserves possibly due to their dependence on intermittent pulses of productivity caused by wind-induced upwelling.

The NW Mediterranean sardine is exposed to differentiated environmental drivers prompting productivity, principally the Ebro river outflow that induces hydrographic frontal structures and the upwelling resulting from the Northern Current flow along the Catalonian coastline (Palomera et al. 2007). Therefore, these differences in growth rates and biochemical indices were attributed to a higher microzooplankton abundance in the NW Mediterranean, particularly in areas close to the Ebro Delta. According to previous studies, the higher abundance of microzooplankton in the closest areas to the Ebro Delta could also explain to some extent the differences in nutritional condition and growth rates found in anchovy larvae from different spawning sites located in the NW Mediterranean (García et al. 1998), although in the south of the Ebro river outlet, microzooplankton biomass has been reported to be much lower (García et al. 2006a, b). A previous study of Palomera and Lleonart (1989) larval mortality revealed differences between the northern and southern spawning sites in agreement with the former study of García et al. (1998) whereby greater growth rates were observed in the northern spawning site, within the surroundings of the highly productive Gulf of Lions.

It is interesting to also highlight the existence of differences in the biochemical composition of sardine larvae between different areas of the Alboran Sea. García et al. (2006a, b) reported that sardine larvae from the Almeria Bay presented higher carbohydrate content than sardine collected in the Malaga Bay. These differences in carbohydrate content could not be explained by differences in microzooplankton abundance or composition. Quite to the contrary, microzooplankton from the Almeria Bay presented higher protein content which was not reflected in different larval protein content. Based on these results, García et al. (2006a, b) suggested that larvae in the Almeria Bay could feed on other preys with higher carbohydrate content. It has been reported that sardine larvae feed actively on copepods eggs, nauplii, and copepodites, these accounting for 78–89% of the gut content (Conway et al. 1994; Yebra et al. 2019). However, there are also studies reporting passive feeding of clupeid fish larvae, including sardine, on phytoplankton (Lasker 1978; Walsh et al. 1980; Rasoanarivo et al. 1991).

Carbohydrate content of phytoplankton ranges from 14.1 to 55.8%, while protein content seems to be more stable ranging from 50.7 to 34.1%, (Ríos et al. 1998). In the case of zooplankton, the main constituents are proteins followed by lipids and carbohydrates (Jo et al. 2018; Jagadeesan et al. 2010). The inclusion of phytoplankton in the diet of sardine larvae from the Almeria Bay would explain their high carbohydrate content (García et al. 2006a, b; Mercado et al. 2007). From such findings, we can be likewise infer that the quality of feeding resources may be as important as the abundance of trophic resources.

The effect of quality feeding resources versus quantity was demonstrated in the larvae of the Mediterranean bluefin tuna in which three annual larval cohorts from 2003 to 2005 were analyzed from both the growth and condition standpoint. The greatest larval growth of bluefin tuna larvae was attained in 2003, under extreme temperature changes and extremely low production caused by the historical Mediterranean heat wave (García et al. 2013).

13.5.2 Larval Growth and Larval Condition Research Studies

Ramírez et al. (2001) revealed that the growth strategy of the ELHS of the winter-spawned sardine larvae in the northwestern Alboran Sea is characterized by a decrease of length increment growth rates with increasing larval ages, while growth in somatic mass gain tends to increase with age. This sardine larval growth strategy was corroborated by other studies conducted with northern Alboran Sea sardine larvae (Ramírez et al. 2004). However, studies conducted with sardine larvae in post-flexion stages (García et al. 2006a, b; size range from about 16 to 28 mm) found that size at age followed a linear pattern rather than a power pattern and thereby, the resulting growth rates for those size classes are constant (around 0.32 mm/day). The results of all these studies indicate that there is an inflection in sardine somatic growth rates, both in length and weight, which could be due to ontogenic changes of larvae during its development and by the changes in larval food items. Thus, Conway et al. (1994) based on the analysis of the gut content reported an increase in copepodites in the diet of sardine larvae larger than 15 mm collected in the north Iberian continental shelf.

Otolith growth also provides important information to understand the variability in recruitment. Thus, for the northern Alboran Sea sardine, Ramírez et al. (2001) reported that otolith larval growth was faster for older age groups in comparison with younger larvae. These differences could be attributed to growth-dependent mortality during the earlier stages of sardine larval development (Ramírez et al. 2001). Likewise, growth-dependent mortality could explain the observed increase in nutritional condition with larval length (Ramírez et al. 2001), since well-fed larvae would also have more survival rates than poor feed or starved larvae.

The studies conducted in the Alboran Sea have also allowed further insights on how larval growth, otolith growth, and nutritional condition are related. Under ideal conditions, a close relationship between larval somatic growth and nutritional condition is expected. Thus, previous studies with other species related recent somatic fish larval growth with RNA/DNA (Buckley 1984; Hovenkamp and Whitte 1991; Westerman and Holt 1994). However, the studies conducted with field-caught sardine larvae suggest that RNA/DNA is not a good indicator of somatic growth in length or age. Thus, Ramírez et al. (2001) found that the RNA/DNA and protein/DNA ratios were weakly related to somatic larval growth in mass as well as to recent otolith growth. On the other hand, previous studies have used the width of the last three-six otolith daily microincrements as a proxy of recent larval growth in some species, showing strong correlations with RNA/DNA ratios in other fish species (Clemmessen and Doan 1996). However, the studies conducted in the North Alboran Sea with sardine larvae show that the RNA/DNA ratios in larvae is generally highly variable. This may be due to a more rapid response of RNA to exogenous factors, such as temperature (Goolish et al. 1984), while changes related with somatic and otolith growth rates have a slower response to external factors (Ramírez et al. 2004).

On the other hand, the studies conducted with sardine larvae collected in the northwestern Alboran Sea revealed that RNA, DNA, protein, and carbohydrate content of larvae is highly dependent on larval age, length, and weight (Ramírez et al. 2001; Ramírez et al. 2004; Cortés 2006). Although both length and weight at a given age are indicators of somatic growth, according to the research on sardine larvae in the Alboran Sea, weight accounts for a higher percent of variability in biochemical parameters than larval length (García et al. 2005). This higher dependence on weight can be explained by the fact that these biochemical parameters are intrinsically related to cell metabolism and tissue accretion.

Although larval growth is highly influenced by the surrounding hydrobiological conditions predominating in their nursery sites, the influence of maternal qualities cannot be overlooked (Høie et al. 1999; Green and McCormick 2005; Uriarte et al. 2016). Recent results have shown that pre-flexion larvae of bluefin reared under controlled laboratory conditions showed maternal transmission of the stable isotopes of carbon and nitrogen (Uriarte et al. 2016) enabling future prospects of analyzing the trophodynamics of spawning females.

13.5.3 *Seasonal and Interannual Variability of Larval Growth and Condition Research*

The temporal variability of larval growth and condition (RNA/DNA) research of larval stages of sardines and anchovies was enabled by the ECOMALAGA sampling time series. The temporal and seasonal variability of larval sardine (García 2006; Cortés 2006) and an interannual comparison of anchovy larvae (García et al. 2003) allowed investigating the environmental and climatic drivers that influence ELHS development.

ANCOVA using daily increments (DI) as covariant showed highest sizes at age (SL) and dry weight (DW) at age between comparably equal larval size classes of sardine larval cohorts, which is consequential to having greater daily growth rates. Maximum growth corresponded to maximum DNA and RNA content during the winters of 1995 and 2001 (Fig. 13.15). During spring, the sardine larval cohorts of 1998 and 2001 showed highest growth rates.

Motivated by the faster is better hypothesis whereby faster-growing individuals are prone to have higher survival rates (Houde 1987; Anderson 1988; Meekan et al.

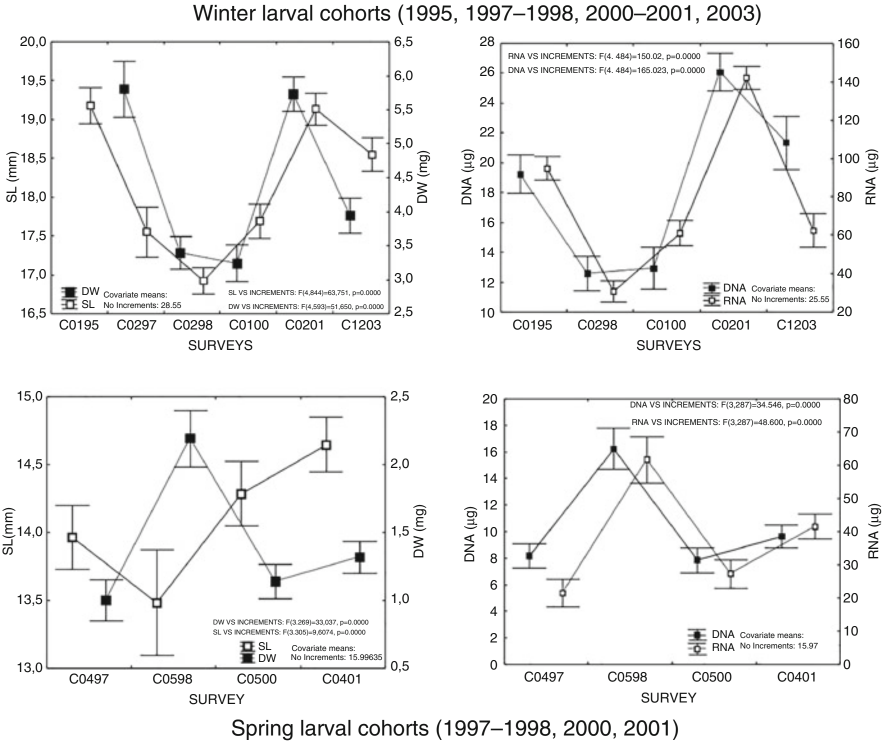

Fig. 13.15 ANCOVA analysis using estimated age (DI) with somatic variables of size and dry weight (SL and DW) (left column) and nucleic acid content with age (RNA, DNA) (right column) (ECOMALAGA time series)

2006), a field-based experiment was set to verify the consequences of enhanced larval growth in the survival of the Alboran Sea sardine and anchovy.

A field test experiment verified this hypothesis on mortality of sardine larvae. A surviving cohort of sardine larvae from its original population was analyzed by backtracking growth curves and compared with the original cohort sampled 2 weeks earlier in the same nursery site (García et al. 2007). Sardine juveniles sampled and aged on a monthly basis followed postlarval growing cohorts to their juvenile stages also indicated that surviving juveniles showed enhanced growth rates (Alemany et al. 2006).

In conclusion, larval survival of both species is clearly linked to faster growth rates and better nutritional conditions. Nevertheless, the Alboran Sea sardine can show two differentiated growth strategies, favoring growth in length or alternatively in somatic mass (García 2006). The highest larval growth occurred during the winters of 1995 and 2001. Since the Alboran Sea sardine is a protracted spawner (early autumn, September to late spring, May), significantly different seasonal growth patterns occur from winter- to spring-spawned larvae. In general, greater

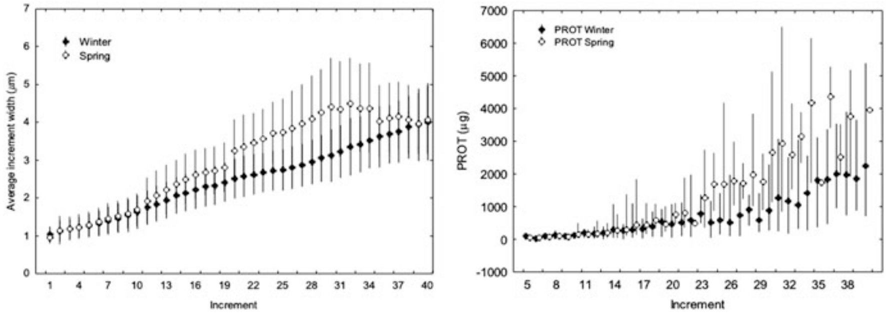

Fig. 13.16 Average increment widths observed by microstructure analysis of larval sardine otoliths (left) and protein content with estimated increments. (García 2006; Cortés 2006) (ECOMALAGA time series)

growth occurs during spring when temperatures increase (Ramírez et al. 2004; Mercado et al. 2007).

The overall larval sardine population collected from the ECOMALAGA surveys show differentiated growth patterns as shown by the accretion of daily increments considered a good proxy of growth. It corresponds to a greater protein buildup of somatic mass (Fig. 13.16). In year-by-year cases, this general picture can vary greatly because winter corresponds to greater nutrient resources, thereby enhancing growth in body mass under a low-temperature regime. On the other hand, spring shows greater hydroclimatic and nutrient variability which undoubtedly affects growth variability.

At the sardine nursery site of Malaga, wind stress showed significant linear relationships with somatic growth variables of sardine larvae monitored from 1995 to 2003 (García et al. 2006a, b) (Fig. 13.9). Alemany et al. (2006) indicated that larval survival and larval and juvenile growth rates showed a positive correlation with westerlies that induce upwelling events (Sarhan et al. 2000), in the coastal shelf and calm sea weather conditions in the inshore nursery grounds.

In general, the spring larval cohorts showed faster somatic growth rates, both in length and weight, than those born during the winter season (García et al. 2005; García 2006) due to more favorable environmental conditions with higher temperatures and higher planktonic biomass coupled to spring blooms (García et al. 2005; Ramírez et al. 2005; Mercado et al. 2007). Faster somatic growth observed in the spring-spawned sardine larvae is coupled with faster otolith growth in comparison with larvae winter-spawned larvae. Consequently, spring-spawned sardine larvae have larger otoliths with wider daily increment widths than winter-spawned sardine larvae (García et al. 2005; García 2006).

In general, spring-spawned sardine larvae presented better nutritional conditions than winter-spawned larvae showing significantly higher RNA, DNA, protein, and carbohydrate content at age (García et al. 2005; Cortés 2006; Mercado et al. 2007). However, no significant differences were observed with respect to RNA/DNA between both seasonal periods suggesting the resilience of this species to changing seasonal conditions. In this case, differences in sea temperature act as a physiological driver that modulates the estimated RNA/DNA ratios. A decoupling between larval growth and biochemical indices can be observed consequent of a delayed response of larval growth to sudden changes in environmental conditions (Ramírez et al. 2004).

The variability of seasonal growth patterns in small pelagic larvae, is modulated by the temperature and feeding resources which may undergo abrupt changes. Strong changes of trophic resources for larvae can originate from changes in the phytoplankton composition as observed by Mercado et al. (2007), where a phytoplankton diatom-based community shifted towards a coccolithophorid type of community in 2001. Highest larval growth of anchovy and sardine cohorts corresponded to this year-class (García 2006; García et al. 2003). Moreover, changes in phytoplankton community may have contributed to having higher carbohydrate content in sardine larvae sampled in winter 2000 and 2001 (García et al. 2005; Cortés 2006; García 2006; Mercado et al. 2007).

With respect to the Alboran Sea anchovy, its peak spawning occurs during summer (July–August) (Rodríguez 1990). An unexpected high anchovy recruitment occurred during 2001 (Abad and Giráldez 1990). Growth data on anchovy of the 2000 and 2001 year-class were compared which yielded a field-based study on the influence of growth on annual recruitment (García et al. 2003). The 2001 anchovy larval cohort showed a 20% increase in daily growth rates in comparison to the previous year (García et al. 2003). The birth date distribution of both cohorts showed that during 2001 these were born at an earlier period (late spring) which possibly coupled with the spring bloom because zooplankton biomass was unexpectedly high in 2001 in comparison to the previous year. Furthermore, Mercado et al. (2005, 2007) revealed important interannual changes in the predominance of the different phytoplankton groups in the Alboran Sea) shifting from a diatom-based community to a coccolithophorid- and dinoflagellate-based phytoplankton grouping.

Nevertheless, it is reasonable to think that a single event like the strong 2001 anchovy recruitment must have been triggered by changes or driving forces of biological and hydro-physical nature that occurred in the Alboran Sea. Ruíz et al. (2013) observed a relationship between the variability of the path and intensity of Atlantic Jet with the anchovy recruitment. A high kinetic energy of the current favors the production in northern Alboran, but negatively impacting anchovy recruitment, possibly inducing a greater degree of larval advection and dispersion. The year 2001 constituted an outlier of the time series of data from 1988 to 2010. The climatic and hydrographic forces of the Atlantic current are also responsible for maintaining the temporal persistence of the anchovy and sardine nursery grounds (Macías et al. 2011).

13.6 New Approaches Towards ELHS Trophodynamics

The joint analysis of growth at ELHS together with other analytical tools has led way to the development of new digital imaging tools for growth otolith microstructure analysis (Nava et al. 2018). This digital imaging tool is open to otolith experts and is continuously being updated with new applications, as otolith asymmetry. It has been shown that larval trophodynamics are strongly relevant for enhancing daily growth (Pepin et al. 2015). Studies of the trophic transfer of C and N from phytoplankton to zooplankton and ichthyoplankton by determining the isotopic composition (^{13}C and ^{15}N) of different size fractions revealed that sardine and anchovy larvae modify their diet depending on the quality or the type of food available, namely, the phytoplankton and/or zooplankton groups present (Uriarte 2010; Laíz-Carrión et al. 2011; Quintanilla et al. 2015; Quintanilla 2016). Further findings show that the stable isotope of nitrogen (δ^{15}N) showed a linear relationship between faster- and slower-growing individuals with the average values of δ^{15}N by daily age class. This link was further corroborated on the species *Auxis rochei* from the Balearic Sea. Two cohorts of this species originating from two hydrographically different water masses showed differentiated growth patterns in which enhanced growth was linked to greater δ^{15}N values (Laíz-Carrión et al. 2013).

With respect to anchovy, a comparison between the NW Mediterranean anchovy and Alboran Sea anchovy stable isotope analysis linking larval growth study showed that the NW Mediterranean anchovy population showed specialized prey selectivity associated with a low productive ecosystem in contrast to the Alboran Sea population, which showed a more generalist feeding behavior associated with an ecosystem of higher food resources. The differences between ecosystems were shown by the significant differences in the δ^{13}C values indicating differences in the carbon sources of each larval habitat (Uriarte 2010). Higher growth rates recorded greater δ^{15}N values, thereby a higher trophic position which indicates a greater feeding specialization in larvae originating in less productive regions (Uriarte 2010; Quintanilla et al. 2015). From the population viewpoint, differences in the amino acid composition of anchovy egg and larvae further corroborated stock differentiation (Riveiro et al. 2003).

A similar study comparison was carried out in the Alboran Sea sardine which has nursery grounds in widely distinct environmental characteristics, the bays of Almeria and Malaga, being the former distinguished by its lower productivity consequent with the less influence of the Atlantic current (Quintanilla et al. 2020). While δ^{15}N values were conditioned by the seasonal plankton community structure particular to each nursery area, trophic levels are influenced by larval trophodynamics. In this case, higher somatic and otolith biometric growth was related to higher trophic levels due to the higher enrichment of larvae from their potential feeding resources.

Recently, these trophic relationships have been further investigated through the molecular characterization of the diet of *Sardina pilchardus* larvae in the Bay of Malaga. The development and application of new molecular tools have allowed detecting the presence of certain groups of phytoplankton and zooplankton in the gut of ichthyoplanktonic larvae. For example, specific primers and a multiplex PCR assay have been designed to target copepod species and phytoplankton groups identified as potential preys (Hernández de Rojas et al. unpubl.), allowing us to determine their contribution, at least qualitatively, to the diet of *S. pilchardus* larvae in the nursery area (Yebra et al. 2019). Also, recent developments in high-throughput sequencing techniques have allowed the metabarcoding of the entire

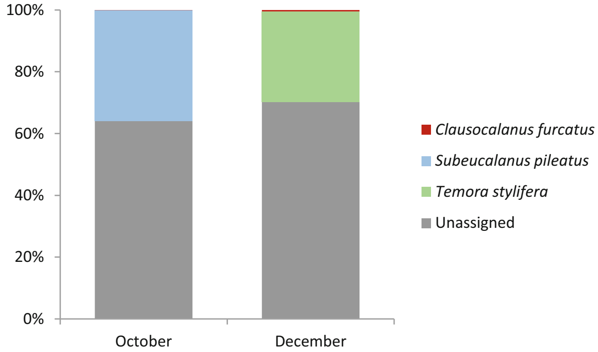

Fig. 13.17 Variability in the relative abundance of prey (OTUs detected by metabarcoding of mtCOI gene) in guts of *Sardina pilchardus* larvae collected in Bay of Malaga during autumn 2013. A shift in the main prey species (calanoid copepods) was observed through the spawning season

prey field in the gut of these larvae and its variability through the spawning season (Fig. 13.17), using the mtCOI gene as a marker. Preliminary results indicate that larval sardines have opportunistic feeding habits, rather than species-specific selectivity (Yebra et al. 2018).

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