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Seasonal comparison of the diets of juvenile European anchovy *Engraulis encrasicolus* and sardine *Sardina pilchardus* in the Gulf of Lions

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ABSTRACT

Anchovy and sardine in the Mediterranean are known to share the same habitat and, consequently, to interact with one another. These two sympatric pelagic species are planktivorous and consume a wide range of planktonic prey items during all their developmental stages, potentially overlapping their ecological niches, although the feeding interactions between these species have been poorly investigated. Here we compare the dietary habits of the juvenile phases of anchovy and sardine during different seasons in the northwestern Mediterranean Sea, through analysis of their stomach contents and of their feeding-related anatomical characteristics. In this study we show that juveniles of anchovy and sardine do not compete for food, and we describe significant dietary differences between anchovy and sardine due to their different alimentary tract morphology.

Contents

1. Introduction

Most of the fish species in the ocean are likely to share the same habitat at least during part of their life and, consequently, to interact with other species (Polunin and Pinnegar, 2008). Understanding the biological mechanisms, such as trophic relationships, by which species interact with one another, is the basis of many ecological studies, from dietary research to the elaboration of food web models.

Small pelagic fishes are likely to share many traits in relation to their morphology (e.g. structure of gill rakers), behavior (e.g., ability to filter-feed), and trophic and population dynamics (van der Lingen et al., 2009). Moreover, these species constitute the bulk of the fish biomass in many areas of the oceans and are in a mid-trophic position in the food web. Therefore their ecological role in the ecosystem is crucial, as being plankton-feeders they may have an important effect on lower trophic levels and, at the same time, potentially affect the dynamics of

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their main predators (predatory fish and marine birds), thereby exerting a wasp-waist control (Bakun, 1996; Cury et al., 2000).

Survival of juvenile fish greatly depends on their ability to capture and digest sufficient quantities of appropriate prey. Regarding the "match–mismatch" hypothesis (Cushing, 1990), a temporal and/or spatial decoupling between fish peak production and their prey is one of the main sources of recruitment variability, so changes in planktonic phenology, like a delay or an earlier plankton peak, may result in a reduction in the number of fish that recruit into an existing population (Beaugrand et al., 2003). Zooplankton seems to be the main source of food for small pelagic fish during all stages (Blaxter and Hunter, 1982; Borme et al., 2009, 2013; Costalago et al., 2012; Durbin, 1979; Morote et al., 2010; Tudela and Palomera, 1997; van der Lingen et al., 2009). In the Mediterranean Sea, European anchovy *Engraulis encrasicolus* and European sardine *Sardina pilchardus* are the most exploited species, and both have been broadly studied because their abundance and position in the food web make them particularly important for the ecosystem (Coll et al., 2009; Palomera et al., 2007). These two sympatric pelagic species are planktivorous and consume a wide range of planktonic prey items during all their developmental stages (Borme et al., 2009, 2013; Costalago et al., 2012; Morote et al., 2010; Plounevez and Champalbert, 2000; Tudela and Palomera, 1997), potentially overlapping their ecological niches, although the feeding interactions between the two species have been poorly investigated.

It is known that inter-specific variations in the feeding habits of marine fishes are consistent with inter-specific differences in the functional morphology of their feeding organs (Castillo-Rivera et al., 1996; Tanaka et al., 2006), and these differences persist across various stages of development (Turingan et al., 2005). However, prevailing knowledge related to the feeding ecology of anchovy in the northwestern Mediterranean is mainly on adults (Plounevez and Champalbert, 2000; Tudela and Palomera, 1997), and little attention has been paid to feeding behavior or morphology during the juvenile stage.

The feeding ecology of adult sardines inhabiting the Mediterranean was first evaluated by Lee (1961). Other sardine diet studies followed, including Rasoanarivo et al. (1991) in the Gulf of Lions, Morote et al. (2010) in the Catalan Sea, and Borme et al. (2013) in the Adriatic Sea, but the first two studies focused on larvae smaller than 15 mm standard length (SL) and the latter on late larvae (27 mm to a maximum of 45 mm SL). In addition, there have been two studies which considered sardine diets from late-larva through adult stages in the Gulf of Lions (Costalago et al., 2012; Costalago and Palomera, in press) and from juveniles to adults in the Aegean Sea (Nikolioudakis et al., 2012). The study conducted by Costalago et al. (2012) also evaluated stable isotope signatures in relation to diet. The current study contributes to this existing knowledge with a more comprehensive approach to the foraging ecology of small pelagic fish by comparatively studying the stomach contents, food selectivity and the feeding-related anatomical characteristics, such as gill rakers and pyloric caeca, of juvenile stages of *E. encrasicolus* and *S. pilchardus* in the Gulf of Lions.

The stomach contents of fishes provide direct information about trophic interactions in the pelagic environment (Tanaka et al., 2006), and comparative analysis of the feeding related structures (i.e. gill rakers and pyloric caeca) is useful to estimate the potential for dietary overlap (Castillo-Rivera et al., 1996). The mechanisms that fishes employ for feeding are diverse, and can be altered during the ontogenetic development or depending on environmental conditions and presence and abundance of different assemblages of prey.

The spawning seasons for anchovy and sardine in the western Mediterranean are different (spring–summer for anchovy and autumn–winter for sardine Palomera et al., 2007), yet both species reach reproductive age within approximately one year (Blaxter and Hunter, 1982). Therefore, it is possible that juveniles of the two species co-occur during similar periods of the year. When this happens, competition for food could be expected between juveniles.

The present contribution provides insights on the trophic ecology of juveniles of two of the most economically and ecologically important pelagic fish species in the Mediterranean, and presents relevant information that may be useful for quantifying foraging success during periods of environmental changes. Our results may be useful for predicting how juvenile anchovy and sardine populations will respond during different production periods, and may provide an early indication of population regime shifts, which are thought to be trophodynamically mediated (van der Lingen et al., 2006).

2. Materials and methods

2.1. Sample collection

Fish and plankton samplings were conducted aboard the N.O. *L'Europe* in the Gulf of Lions (northwestern Mediterranean) (Fig. 1) during oceanographic cruises carried out in 3 different seasons: autumn (8–21 December 2007), summer (29 July–09 August 2007), and winter (11–27 January 2009).

Anchovy and sardine juveniles were captured near the plankton stations with a pelagic trawling net equipped with a small-mesh cod-end (mesh length 5 mm, ISO 1107) and towed at an average speed of 1.85 m/s over the shortest possible period (approximately 30 min) to try to avoid cod-end feeding and stressing of the fish. The samples were immediately frozen (−20 °C) after sorting on board.

Food availability was explored by sampling zooplankton by vertical tows performed with two different nets: a Working Party 2 (WP2) standard net (mesh size 200 μm; mouth opening diameter 58 cm) and a CalCOFI Vertical Egg Tow (CalVET) net (mesh size 53 μm; mouth opening diameter 25 cm). Due to the frequent malfunctioning of flowmeters, the filtered water volumes ($V = AxL$, m^3) were calculated by taking into account the area of the net mouth (A, m^2) and the length of the released wire (L, m). The final thickness of the sampled layer (ΔD, m) and the depth limits of the layer ($\Delta L = Li - Lf$, m) were computed considering the wire angle α ($\Delta D = \Delta L \cos \alpha$) (Sameoto et al., 2000). Immediately after the retrieval of the nets, plankton samples were sieved in succession through 200 μm and 50 μm mesh size for the CalVET net sample, and 3000 μm and 200 μm mesh size for the WP2 net samples. We then obtained two different size fractions: a 50–200 μm fraction, named hereafter "microplankton", from the CalVET net; and a 200–3000 μm fraction named hereafter "mesozooplankton", from the WP2 net. All plankton samples were split with a Motoda plankton splitter (Motoda, 1959). One-half of each sample was fixed and preserved in a seawater-buffered formaldehyde solution (4% final concentration) for later determination of species composition and abundance, whereas the other half was filtered through pre-dried, pre-weighed glass microfiber filters (Whatman® grade GF/C, 25 mm Ø for microplankton and 47 mm Ø for mesozooplankton) for biomass estimation. The filters were stored onboard at −20 °C.

Oceanographic parameters were also measured during the same cruises. Temperature (°C) and salinity of the water column from sea surface to the bottom (until a maximal depth of 100 m, every 1 m) were measured by a Seabird 19 CTD at each station (16 sampling stations in summer, 15 in autumn and 13 in winter, Fig. 1). We considered "surface" as the averaged data from 0 to 5 m depth, and "average" as the averaged data from 0 to 50 m depth.

2.2. Laboratory procedures

In the laboratory, qualitative and quantitative analyses of plankton were performed. Individuals were identified to the lowest taxonomic level possible under the stereo-microscope (Wild M12, at 100× magnification). The mesozooplankton samples were analyzed in aliquots representing about 10% of the sample and repeated until at least 400 copepods had been enumerated; additional subsamples were also taken for any other abundant organism (i.e. for cladocerans during summer, up to 400 individuals were counted per subsample). Microplankton samples were subsampled differently: 1 to 2% of the original volume