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Ontogenetic shift in the schooling behaviour of sardines, *Sardina pilchardus*

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Intraspecific variability in the characteristics of fish schools is often affected by the size of individuals. In this study, juvenile and adult sardine schools detected in five hydroacoustic surveys (2004–2008) in the North Aegean Sea (eastern Mediterranean) were analysed in an effort to identify differences in a suite of school descriptors (i.e. positional, energetic, morphometric) and define the size at which schooling behaviour changed from juvenile to adult. Juveniles exhibited discrete schooling characteristics and microhabitat preferences compared to adult fish. Specifically, schools of juvenile sardines were smaller, more elongated and irregular than those of adults, they backscattered less energy and were located higher in the water column. Based on the length frequency distributions of experimental pelagic trawl catches, the length at which 50% of sardines shifted behaviour from juvenile school structure to the more typical adult school form was estimated at 10.7 cm. This length almost coincides with several ontogenetic changes in biology (i.e. first maturity, allometric change in the length–weight relationship and onset of phytoplankton consumption). Several size-dependent school features observed in this study are partly attributed to the higher feeding demands of juvenile fish and the need to avoid intraspecific competition and predation.

A school is a mass of constantly moving fish (Misund 1993) with its structure being largely a result of the trade-off between the two main drivers of schooling behaviour: predation and feeding. School structure is species specific, affected by environmental conditions (biotic and abiotic) and intrinsic attributes of species or population such as physiological status, behaviour and the size of individuals (Fréon & Misund 1999). Within-species variability in school characteristics is generally considered greater than that between species (Brehmer et al. 2007). Numerous studies have managed to discriminate schools of different species (e.g. Simmonds et al. 1996; Horne 2000; Lawson et al. 2001; Fernandes 2009; Robotham et al. 2010). Correct species (or age) identification of observed schools is essential for estimating biomass by means of hydroacoustics (Horne 2000; Petitgas et al. 2003; Simmonds & MacLennan 2005). However, intraspecific variability may often be too high to allow correct assignment of schools to species (Scalabrin et al. 1996). The study of school typology is important for sampling design, for upgrading species identifications (Muino et al. 2003) along with related implications (Trenkel et al. 2011), and for understanding species biology, ecology and the factors that control schooling behaviour.

Schools consist of similar-sized individuals (Pitcher & Parrish 1993; Hoare et al. 2000) and their morphological and positional characteristics may change with fish size (Mikheyev 1995; Brehmer et al. 2000; Hoare et al. 2000; Petitgas et al. 2004). The latter could be related to size-dependent food requirements and predation risk, leading to changes in the cost/benefit balance of alternative school shapes and sizes (Hoare et al. 2000) and/or to the ontogeny of schooling behaviour. The development of schooling behaviour, which is species dependent, usually starts from the larval stage and may last for a substantial period of the juvenile stage before being fully developed (Fréon & Misund 1999).

In the European sardine, variability in school characteristics in two regions from the Spanish Atlantic coasts have been attributed to the different age structure of the populations (Muino et al. 2003). Differences in age structure were also considered responsible for the interannual differences observed in small pelagic fish schools (mainly anchovy, *Engraulis encrasicolus*, and sardine) along the Mediterranean coasts of Spain (Iglesias et al. 2003). However, differences in positional, morphometric and energetic school descriptors between juvenile and adult sardines have not been explicitly addressed.

In the present study, we examined intraspecific variability in schooling behaviour for European sardine in the North Aegean Sea in relation to fish size. We compared the school descriptors and identified those related to the school structures of juveniles and

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adults. Moreover, we analysed the length frequency distributions of experimental pelagic trawl catches to estimate the length at which 50% of the fish shifted their behaviour from the characteristic school structure of juveniles to that observed in the adult stage. We aimed at explaining the results in terms of species biology and ontogeny and the factors known to control schooling behaviour.

METHODS

Sampling Design and Acoustic Data

Acoustic data were collected on board R/V PHILIA in the North Aegean Sea (eastern Mediterranean, Greece; Fig. 1) during early summer 2004–2008. Sardine is one of the most important species for local fisheries (Machias et al. 2007) and its stock is currently considered as fully exploited (Antonakakis et al. 2011). Extended regions of the North Aegean Sea have been recently characterized as important nursery grounds of sardine (Tsagarakis et al. 2008; Giannoulaki et al. 2011). Moreover, early summer is an appropriate period to compare juveniles with adults since they are both abundant in the study area (Nikolioudakis et al. 2011).

A towed Biosonics DTX split beam echosounder operating at 38 kHz was used to detect fish schools at an approximate vessel speed of 8 knots. Echo sounding took place along predetermined parallel transects perpendicular to the coast and spaced 10 nautical miles apart, except in the case of enclosed gulfs in which transect design was random (zigzagged). During 2007 and 2008, a denser transect grid was sampled in the eastern part of the study area (see Fig. 1 for details).

In parallel to acoustic sampling, experimental fishing with a pelagic trawl was carried out at sites with high fish densities (Simmonds & MacLennan 2005). During hauling, echo sounding was also carried out and vessel speed approximated 4 knots. Experimental fishing was required to estimate species composition and length frequency distribution of the observed schools and complied with ethical specificities for experimental fishing of the EU and National research projects mentioned in the acknowledgements. The majority of small pelagic fish caught were brought onto the deck dead. Onboard work included identification of fish to the species level and recording of the total biomass per species. The catch (dead or alive) was returned to the sea immediately after the recordings with the exception of a representative sample of at least 100 individuals per species which was used to estimate length frequencies to the nearest mm. This subsample was immediately frozen after being measured and was transferred to the laboratory (for further analysis in another study).

Echograms were processed with the Myriax Echoview software setting −70 dB as threshold for the analysis. We processed echoes located between 5 m below the surface and 0.5 m above the seabed. School detection was performed using the relevant algorithm of the Myriax Echoview software. During scrutiny of echograms each school detected was assigned to a specific species based on (1) the catch composition of trawl hauls and (2) the shape and size characteristics of the school, taking into account previously gained experience (Simmonds & MacLennan 2005; Tsagarakis et al. 2012). In addition, sardine schools were classified as juveniles and adults according to the length composition of the catch. Age group classification was based on the length at first maturity of the species. This length had been estimated at 118 mm in the Central Aegean Sea in the early 2000s (Ganias et al. 2003) but a more recent investigation in the North Aegean Sea (at the same area and period as the current study) reported that all fish >100 mm were mature (Nikolioudakis et al. 2011). Hence, we considered fish >100 mm as adult fish.

Following the processing of echograms, a series of school descriptors were exported or estimated for each school detected. These descriptors (see Table 1 for details) expressed positional (depth, altitude, closest neighbour), energetic (mean volume backscattering strength, MVBS) and morphometric characteristics related to size (height, length, area, perimeter) and shape (elongation, rectangularity, circularity, fractal dimension). Morphometric descriptors were corrected according to Diner's (2001) algorithm.

Data Analysis

To minimize the error related to false assignment of schools to species or stages (juveniles or adults), we analysed schools detected in areas with high relative abundance of each sardine group (Fig. 1).

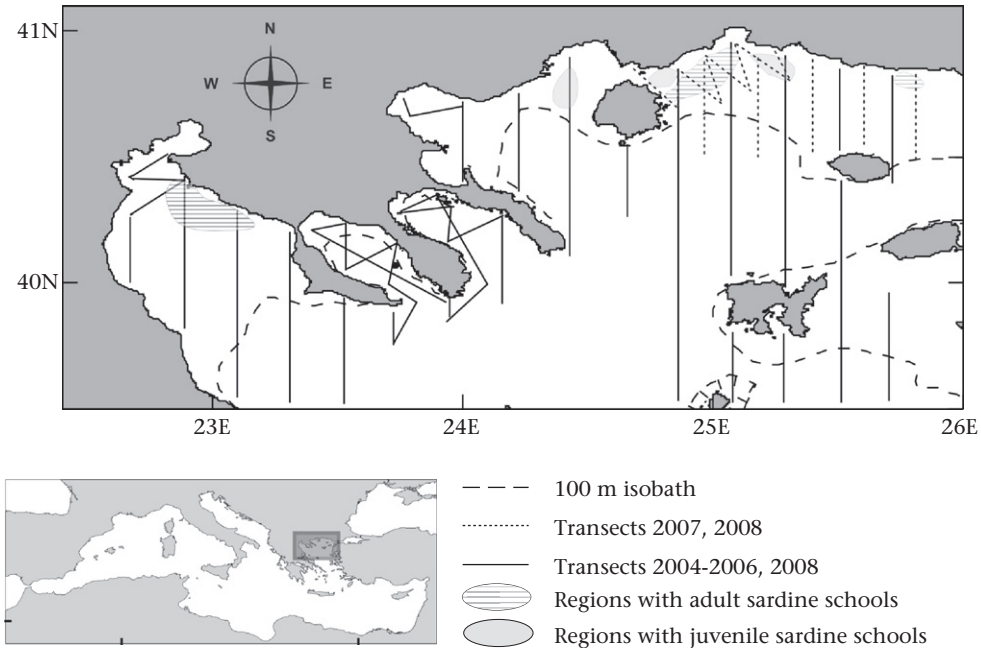

Figure 1. North Aegean Sea: study area. Transect design, 100 m isobath and regions with high juvenile or adult sardine abundance are indicated.