Patterns of variability in early-life traits of fishes depend on spatial scale of analysis

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1. INTRODUCTION

The life cycle of most coastal fish species is made up of a vagrant planktonic phase (corresponding to the stages of eggs and larvae) and a relatively sedentary phase (i.e. post-settlers to adults [1]). The spawning precedes the planktonic phase and its onset is related to environmental features [2]. The transition stage termed ‘settlement’ coincides temporally with the metamorphosis from the larva to the benthic juvenile and divides the life cycle into the two above-mentioned phases [3]. The pelagic larval duration (PLD expressed as ‘number of days’) corresponds to the period between hatching and settlement. PLD is regulated by both genetic [4] and environmental factors [5].

To understand where larvae produced in a given place (e.g. in a marine reserve) are exported to, it can be crucial to collateral information relating to egg-release dates, PLD in open waters and direction and strength of currents within the temporal window corresponding to the larval stage. Data about PLD and spawning dates are thus important for estimating or modelling larval dispersal (e.g. by mean of Lagrangian simulations), thus providing strategically useful information on connectivity and relevant management goals (e.g. the creation of networks of marine reserves).

2. MATERIAL AND METHODS

The model species of this study (D. sargus sargus) is an ecologically and economically relevant species in Mediterranean sublittoral rocky reefs [12,13]. Adults are relatively sedentary and demersal [13], and produce pelagic eggs that hatch and release larvae after 3 days [14]. After metamorphosis, post-larvae settle into very shallow (0.5–1 m depth) coastal habitats [13].

Early post-larvae (settlers) were collected in June 2009, along approximately 200 km of the Apulian Adriatic coast, across the north-south axis (approx. 1°, from 41.2°N to 40.2°N). Seven sectors of the coast were used as sample locations. Each location was roughly 8 km in length and locations were separated by 15–30 km. Within each location, two sites (represented by embayments with shallow rocky habitats alternated with sand patches) were randomly selected. A handnet was used to collect 10 specimens per site (n = 140). Specimens were stored in 95 per cent ethanol within several minutes of capture. All specimens were collected across locations within 8 days in order to prevent or reduce any relevant temporal bias.

The specimens sampled were measured (standard length, ±0.1 mm) before removing the otoliths. In fishes, spawning date and PLD can be assessed through the analysis of daily rings (or growth increments) on otoliths [3]. Otoliths develop around a primary nucleus, which forms during the embryonic development, and grow by apposition of daily rings. PLD can therefore be accurately assessed by counting the number of daily rings between the primordium and the settlement mark (i.e. the first major transitional point; for details about otolith microstructure see [15]). Spawning date can be identified by back-calculations from the post-settlement age.

One sagittal otolith was removed from each specimen and processed following a standard procedure [15]. The daily rings were read using a high-powered microscope. For each specimen, the hatching date was back-calculated by subtracting the number of growth increments from the spawning date. The spawning date was then calculated by subtracting 3 days (corresponding to the time between spawning and larval release in D. sargus sargus) [14] from the estimated hatching date.

To test for potential spatial variability in PLD and spawning dates, two analysis of covariance (ANCOVA) were run, where ‘location’ (Lo) was treated as a random factor with seven levels, ‘site’ (Si) was used as a random factor nested within Lo, with two levels, and the fish ‘standard length’ (SL) as the covariate. Ten
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3. RESULTS

Fish size ranges between 0.9 and 1.4 cm SL (1.11 ± 0.01 cm, mean ± s.e.).

PLD values ranged on the whole from 13 to 19 days. The average PLD value per site varied from 14.4 ± 0.4 (mean ± s.e.) to 17.6 ± 0.16 (mean ± s.e.; figure 1). Coefficients of variation were quite low and ranged from 0.03 to 0.11. On the whole, back-calculated spawning dates ranged from 4 to 24 May 2009. No significant effect of the covariate ‘fish size’ was detected on PLD or spawning dates. PLD and dates of spawning significantly varied over the scale of sites, whereas no significant differences were detected among locations (table 1).

4. DISCUSSION

The present study provides the evidence that spawning date and PLD are spatially variable at a scale of kilometres. It is not easy to interpret this outcome on the basis of the available literature, where spatial variability has been investigated exclusively at small (tens of kilometres [2,8]) or large scales (hundreds–thousands of kilometres [1,7]), without any spatial hierarchy in the adopted sampling designs. From this perspective, the present study provides for the first time to our knowledge, a multiple-scale assessment of spatial variability in spawning dates and PLD. On a relatively small spatial scale (kilometres), the observed differences in spawning dates and PLD could be attributed to small-scale variability in environmental and oceanographic features and processes (e.g. small areas of retention, coastal gyres) and/or in the food availability and growth conditions, which are known to influence PLD and the onset of spawning [2,3,5]. Strictly, with respect to the variability in PLD, this point is particularly important for species facing, at the larval stage, the strong environmental variability typical of coastal waters (e.g. for species with coastal larvae like D. sargus sargus), where freshwater inputs, sewage discharges, etc. may locally represent more or less suitable conditions for settlement.

Table 1. ANCOVA on PLD and spawning dates. (Standard length (SL) was set as covariate. n.s., not significant; Res, residuals; MS, mean squares. See text for factor labels. ***p < 0.001.)

<table>
<thead>
<tr>
<th></th>
<th>PLD</th>
<th>spawning dates</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>MS</td>
<td>pseudo-F</td>
</tr>
<tr>
<td>source</td>
<td>d.f.</td>
<td></td>
</tr>
<tr>
<td>SL</td>
<td>1</td>
<td>21.94 n.s.</td>
</tr>
<tr>
<td>Lo</td>
<td>6</td>
<td>7.75 n.s.</td>
</tr>
<tr>
<td>Si(Lo)</td>
<td>6</td>
<td>9.34 ***</td>
</tr>
<tr>
<td>Res</td>
<td>125</td>
<td>1.02 n.s.</td>
</tr>
<tr>
<td>total</td>
<td>139</td>
<td></td>
</tr>
</tbody>
</table>

Estimates of PLD and spawning dates are being used in a variety of applications [16,17], including the estimate or modelling of population connectivity of fishes [9]. The significant small-scale spatial variability detected in the present study for PLD and spawning dates suggests that modelling dispersal and connectivity without taking into account variability at multiple scales may fail to generalize patterns of dispersal/connectivity (traditionally based on single-value estimates without any proper spatial assessment). Defining variability in spawning date and PLD at multiple scales (both temporal and spatial), therefore, can be pivotal to proper delineate connectivity patterns at larval stages and provide effective clues for management (i.e. design of marine reserve networks, [11]).

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