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ORIGINAL PAPER

Orientation of Mediterranean fish larvae varies with location

Amélie Rossi[1,2] · Jean-Olivier Irisson[3] · Marc Levaray[2] · Vanina Pasqualini[1,2] · Sylvia Agostini[1,2]

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Abstract

Fish larvae at settlement represent a determining stage for maintaining coastal fish populations. This early life stage is decisive for the dispersal, recruitment, and habitat colonisation of coastal fish species. This study aims at observing the orientation behaviour of eight Mediterranean fish taxa, in four families, at settlement stage in two experimental sites along the north-east Corsican coastline (north-west Mediterranean Sea), a Sandy and a Rocky coastal site with different environmental characteristics. The objective was to detect if there were differences in directionality (i.e. the ability of individuals to maintain a fixed bearing in their environment) and orientation (i.e. the consistency among the bearing of individuals at species level) between the two coastal sites for the tested species. We also tried to identify the environmental factors that may influence directionality and orientation. The results show strong directionality for most fish larvae, with proportions of directional individuals generally exceeding 80%, either at community or species level ($4 \leq n \leq 46$ per species). Only the white seabream, *Diplodus sargus*, showed significant orientation behaviour, towards a cardinal direction, towards the sun in both experimental sites, as well as towards the coast in the Sandy site and towards the open sea in the Rocky site. The other species did not show significant orientation. This study supports the theory that orientation behaviour is dependent both on species and the environment perceived by the fish larvae. This kind of work is important for developing predictive models of marine population settlement and presents key elements for protection and management of coastal areas.

Introduction

Behavioural abilities of coastal fishes at settlement stage have long been underestimated (Leis 2006). However, recent studies have shown that fish larvae approaching settlement stage (named below "fish larvae") are able to swim and orientate during their migration from the egg hatching area to their settlement habitats (Lecchini et al. 2005; Leis 2006; Staaterman et al. 2012). They are also able to choose a preferred habitat rather than settle on the first habitat they come across (Arvedlund and Kavanagh 2009). These characteristics are important because they determine the dispersal potential and the structure of future coastal fish stocks (Almany et al. 2006; Leis 2010; Sponaugle et al. 2012).

However, the mechanisms governing orientation behaviour of fish during their pelagic life are still poorly understood, particularly because orientation abilities and behaviours seem to be differ among species, spatially and temporally (Leis et al. 2014, 2015). Several environmental variables influence larval fish orientation, such as the odours coming from reefs or lagoons (Lecchini et al. 2013; Paris et al. 2013; Morais et al. 2017) and sounds from coastal areas (Simpson et al. 2004; Tolimieri et al. 2004; Wright et al. 2008; Radford et al. 2011). However, the detection distances differ among fish larvae senses, ranging from a few metres for visual cues, several metres to kilometres for hearing, and up to a few kilometres for olfaction (Atema et al. 2002; Kingsford et al. 2002; Montgomery et al. 2006). Other variables can be used to orient, such as the position of the sun in the sky and the amount of light perceived, used

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✉ Amélie Rossi
rossiamelie@gmail.com

1 Università di Corsica Pasquale Paoli, UMR/CNRS 6134 Sciences Pour l'Environnement, 20250 Corte, France

2 Università di Corsica Pasquale Paoli, UMS/CNRS 3514 STELLA MARE, 20620 Biguglia, France

3 Sorbonne Universités, UPMC Université Paris 06, CNRS, Laboratoire d'Océanographie de Villefranche-sur Mer (LOV), 06230 Villefranche-sur-Mer, France

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to set an internal compass (Mouritsen et al. 2013; Faillettaz et al. 2015) or the geomagnetic field (O'Connor and Muheim 2017). Both suggest a potential for large-scale navigation by fish larvae.

In situ observations of larval behaviour are uncommon, particularly in temperate areas and for Mediterranean species. Most studies on fish larvae orientation and sensory abilities have been carried out on coral reefs species, in tropical environments or around small islands (e.g. Irisson and Lecchini 2008; Irisson et al. 2009; Mouritsen et al. 2013; Paris et al. 2013; Leis et al. 2014, 2015). Few studies have been carried out in temperate regions (Trnski 2002; Hindell et al. 2003; Clark et al. 2005; Leis et al. 2006), in particular in the Mediterranean Sea, and rarely along continuous coastline (but see Faillettaz et al. 2015).

In the Mediterranean Sea, coastal habitats are mostly constituted of shallow heterogeneous rocky bottoms, sandy coastlines and *Posidonia oceanica* seagrass meadows, a marine phanerogam endemic to the Mediterranean, constituting a key habitat for many bentho-coastal species. The island of Corsica (north-west Mediterranean Sea, France) typically presents a number of habitats, which can range from shallow bottoms with a long progressive slope to steep rocky slopes. The presence of *Posidonia oceanica* meadows can also be noted, generally deep-seated in sandy bottoms, as well as the presence of coastal lagoons that mix with other waters of variable physico-chemical conditions (Pasqualini et al. 1998; Garrido 2012). Furthermore, several studies demonstrated the importance of rocky habitats for Mediterranean species, particularly for Sparidae, like species of the genus *Diplodus* (García-Rubies and Macpherson 1995; Harmelin-Vivien et al. 1995; Vigliola et al. 1998; Vigliola and Harmelin-Vivien 2001; Cheminée et al. 2011). Coastal lagoons can also be considered as attractive nursery area for some coastal fish species, principally for the gilthead seabream *Sparus aurata* (Chaoui et al. 2006; Morais et al. 2017).

This study aims at gaining insights on the in situ orientation behaviour at settlement stage of several fish species that are commonly found along the coasts of the Mediterranean Sea. The objectives are, first, to quantify the directionality of swimming behaviour and test the effect of various environmental variables, such as luminosity, the proximity of coast, and the current and wind intensities; second, to evaluate the orientation abilities of the species tested according to various cues such as the cardinal north, the sun azimuth, and the direction of the coast, current and wind. Within the framework, the relative attractiveness of two types of coastal sites is tested (Fig. 1): a Rocky site with some *P. oceanica* meadows, which has a high potential as a nursery zone, as shown by numerous previous studies (Harmelin-Vivien et al. 1995; García-Rubies and Macpherson 1995; Cuadros et al. 2017; Cheminée et al. 2017) and a Sandy site, which can also be considered as attractive because it is located over the largest *P. oceanica* seagrass meadow located around Corsica (Pasqualini et al. 1998) and is close to the largest coastal lagoon of Corsica (Chaoui et al. 2006; Faria et al. 2006; Abecasis and Erzini 2008; Morais et al. 2017).

Materials and methods

Study area

The study was conducted in the north-west Mediterranean Sea, on the north-east coast of the island of Corsica (France, Fig. 1). This area is close to both one of the most important urban areas of Corsica (Bastia city) with a commercial port, and a marina, and to wilder areas, including large *P. oceanica* meadows. The study area includes a sampling site (42°40′58″N; 9°26′57″E), above a mix of rocks, seagrass and sand, where all fish larvae were collected for this study and two experimental sites, where fish larvae behaviour was tested with an experimental device called the DISC, as described below. The sampling area near Bastia city is interesting because it contains a variety of habitats (a rocky coast in the north, a sandy coast in the south, a *P. oceanica* seagrass meadow, and is close to a lagoon), some of which may be nursery zones for coastal fish species (Guidetti 2000; Grenouillet et al. 2002). The study area is also characterised by a low general coastal drift current from north to south (Pluquet 2006; Stépanian et al. 2010).

All fish larvae sampled were tested for behavioural observations in the two experimental sites, which are approximately 14 km apart. The first experimental site (42°43′13″N; 9°27′37″E) is located off a rocky coastline, near the Miomo marina, north of the sampling site. At this Rocky site, the device was deployed at a distance from the coast ranging between 200 and 400 m, and over depths about 20–30 m. The second experimental site (42°37′09″N; 9°29′36″E) is located off a sandy coastline, south of the sampling zone, above the largest *P. oceanica* meadow of the area. It is close to the Marana lagoon, which presents a natural connection to the sea and is classified as a Natural Reserve (Pasqualini et al. 2017). At this Sandy site, the device was deployed at a distance from the coast between 1.3 and 2 km but still above depths of about 20–25 m. Because depth was constant at the two sites, the effective distance to potential settlement habitats remained constant and the environmental cues coming from the potential habitats of settlement were, therefore, kept at equivalent distances between the two experimental sites.

Sample collection

Sample collection was carried out each month from May 2016 to July 2017 during the 4 days around the new moon

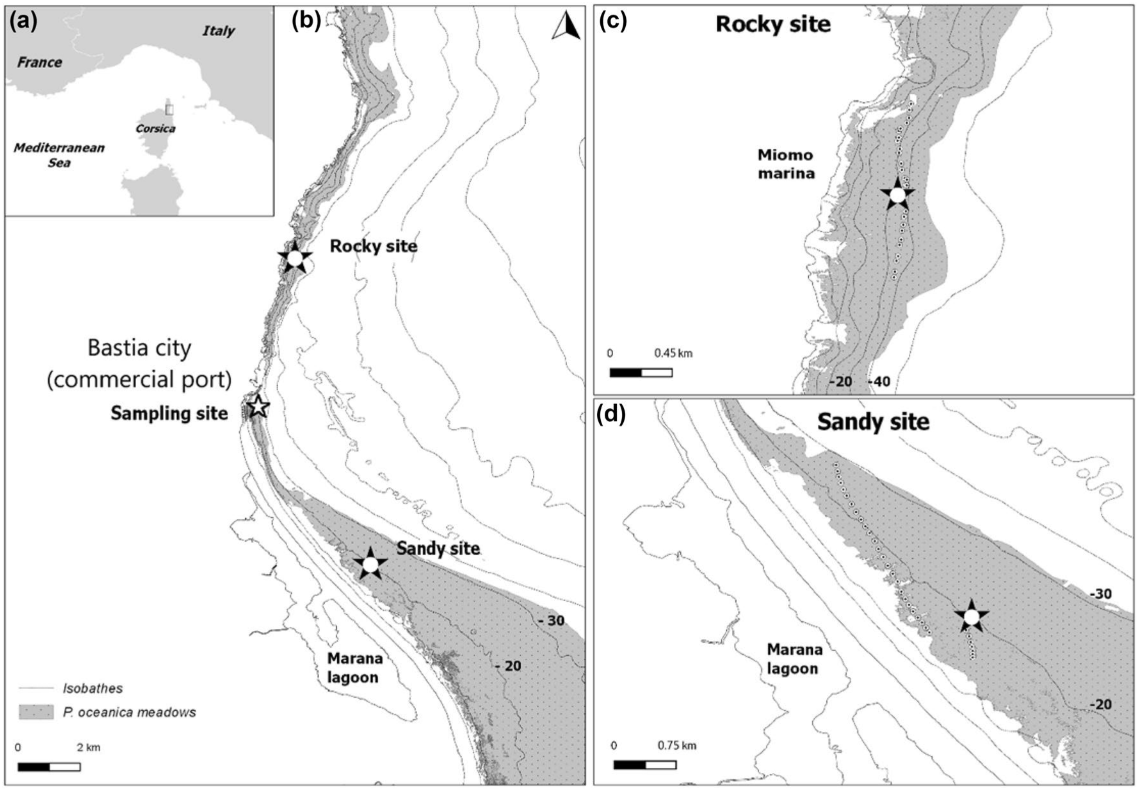

Fig. 1 Map showing **a** the location of the island of Corsica in the north-west Mediterranean Sea, **b** the study area on the north-east Corsican coastline with the detail of the location of sampling and experimental sites. The sampling site is represented by a white star and the experimental sites by black star with white circle. The other two parts of the map focus on the two experimental sites: **c** on the Rocky site ($n = 129$) and **d** on the Sandy site ($n = 139$) with the position of some DISC deployments

with an effort depending on meteorological conditions. Sampling was conducted at night, with light traps called CAREs (Lecaillon 2004). After the collection, fish larvae were stored in 10-L buckets at ambient temperature until their transfer to the laboratory. In the laboratory, fish larvae were kept in acclimation tanks with a constant seawater renewal at temperature similar to the in situ temperature of seawater to prevent thermal shock. Field experiments were carried within the 24 h of capture (in 90% of larvae) or, at most, within 36 h. The study focused on eight common coastal Mediterranean species collected during the sampling campaign. For three species, the sample size was considered large enough for full statistical exploitation ($n > 20$ in each experimental site, Table 1): the white seabream (*Diplodus sargus*), the saddled seabream (*Oblada melanura*) and the gilthead seabream (*Sparus aurata*). The other five species had a smaller sample size ($n < 20$, Table 1): the cardinal fish *Apogon imberbis*, the damselfish (*Chromis chromis*), the Mugilidae (classification done at family level because genus and species level were undetermined), the axillary seabream (*Pagellus acarne*), and the picarel (*Spicara smaris*).

Table 1 Species collected in this study over their month of capture with the number of individuals tested (n) and their proportions of directional individuals on the two experimental sites

Family	Sampling month	No of individuals tested	
Species		Sandy site	Rocky site
Large samples ($n > 20$) (proportion of directional larvae %)			
Sparidae			
Diplodus sargus	June	43 (98%)	46 (100%)
Oblada melanura	July	39 (87%)	39 (97%)
Sparus aurata	February	28 (89%)	29 (90%)
Small samples ($n < 20$)			
Apogonidae			
Apogon imberbis	September	6	6
Pomacentridae			
Chromis chromis	July	7	7
Mugilidae	September–January	15	18
Sparidae			
Pagellus acarne	November	4	4
Spicara smaris	June	15	9
Total		139 (85%)	129 (91%)

Behavioural experiments

The observations of the orientation behaviour of fish larvae were carried out using a *Drifting* In Situ *Chamber*, abbreviated hereafter as DISC (Paris et al. 2013). The DISC comprises a surface buoy that carries a GPS tracker, an acrylic frame, a circular behavioural observation chamber (21 cm diameter × 10 cm height), a GoPro Hero 3+ camera oriented towards the chamber, a custom-made electronic compass (Arduino based) to track the DISC rotation, a supplementary analogue compass, a drogue allowing the drift of the device with the ambient current, make it rotate on itself, and also to keep the DISC fixed in the water mass. The DISC was lowered and drifted with the surrounding water, allowing the fish larvae to be observed with no human perturbation. The DISC frame was made of transparent acrylic with approximately the same density as seawater and the observation chamber was made of transparent mesh on the top and the side walls, which allowed the fish larvae to perceive environmental cues such as sound, odour and light. The position of the fish larvae in the observation chamber provided information on their orientation. Indeed, the DISC's rotation forces fish larvae to compensate their trajectory if they want to maintain a fixed bearing. Before deployments, the DISC was pulled to the surface and a single fish larva was placed in the behavioural chamber. Then, the DISC was gently lowered to 5-m depth for observations. Each deployment lasted 15 min with 5 min of acclimation and 10 min of observation. Time, GPS position, and weather conditions were recorded during the deployments. Each larva was observed once at the Rocky site and once at the Sandy site.

The DISC device was used for the first time in the Mediterranean Sea by Faillettaz et al. (2015), but it was developed and tested in 2008, then used in various tropical environments (Irisson et al. 2009; Paris et al. 2013; Leis et al. 2014). It was also compared with another method for tracking larval fish orientation behaviour in situ (following of larvae by Scuba divers) and the results were very similar (Leis et al. 2014). Thus, the DISC device allows in situ observations of fish larvae orientation behaviour, even in temperate environment and during cold seasons, with no human perturbations.

Data processing

The collected DISC data were processed after each deployment day with the open-source software package *discr* (https://github.com/jiho/discr, modified from Irisson et al. 2009). The position of the larvae was recorded on the images at 10-second intervals via a graphical interface (ImageJ). The recorded positions correspond to the *raw data* relative to the top of the images, which are thereafter corrected according to the DISC's rotation, to make them relative to the north, and correspond to the *rotated data*. These rotated positions form the basis for the directionality and orientation analyses. *Directionality* is assessed at individual level and is significant when rotated positions are aggregated in a unimodal pattern, which means that the larva kept a bearing. *Orientation* is assessed from directional individuals, by testing if their mean directions point the same way, meaning that they all kept the same bearing (Faillettaz et al. 2015). The *precisions* of directionality and orientation are the inverse of their variance. High precision means high concentration of positions (for directionality) or mean directions (for orientation).

The influence of several environmental factors on the precision of directionality was studied: the distance to the coast, the wind and current strengths, the sun position and cloud cover. Distance from the coast was measured from the closest shore point to the midpoint of the deployment. The current strength was determined from the horizontal displacement of the DISC. Wind and cloud cover information were obtained from meteorological data (Météo-France®) gathered from the Sisco marine station located 6-km north from the Rocky site and from the international airport of Bastia Poretta located 8-km south from the Sandy site. Finally, the solar index, including the time of the day and the sun position, was calculated according to the formula of Faillettaz et al. (2015), as follows: solar index = $(t_{deployment} - t_{sunrise})/(t_{sunset} - t_{sunrise})$; with $t_{deployment}$, the mean time of the deployment, and $t_{sunrise}$ and t_{sunset} are the sunrise and sunset times on the day of the deployment. This solar index ranges from 0 at sunrise to 1 at sunset, and combines the effect of the zenith (angle from the vertical) and azimuth (bearing) of the sun.

The orientation bearings were compared to the bearing of various environmental cues; the closest point on coast, the current (determined from the DISC's horizontal drift), the wind and the solar azimuth (computed from coordinates and time of the day).

Statistical analysis

For all deployments, the angle between each position (at 10-s intervals), the centre of the observation chamber and the north (i.e. is bearing) was computed. The Rayleigh test was used to evaluate the concentration of bearings (i.e. the directionality) of each fish larva in the observation chamber. The Rayleigh test computes a statistic, the r value, which quantifies this concentration, i.e. the precision of directionality. These angular statistics were done in R version 3.3.3.

To test directionality precision differences among species, non-parametric tests were used: the Kruskal–Wallis H test and Mann–Whitney pairwise tests. To test the influence of environmental cues on directionality precision, r was logit transformed and a linear regression with each environmental variable was computed and tested by permutation with the software PAST version 3.20.

To test for orientation, the mean bearings of directional fish larvae were used in another Rayleigh test, per species. The *r* statistic of the second test is a measure of the species' orientation precision. When a bimodal distribution of individual bearings was suspected, Rao's test was used instead.

To assess the influence of various environmental cues (direction of coast, current, wind, and sun azimuth) on the orientation bearings, the difference between the mean bearing of the fish larva and the mean bearing of the cue during each deployment was computed, for directional larvae only. These new bearings, relative to each cue, were tested with another Rayleigh test. If the test was significant and that the mean relative bearing was around 0/360°, it meant that the larvae oriented towards the cue. Conversely, if the angles were around 180°, the larvae oriented away from the cue. Graphical results were produced with the software NCSS 12.

All species were considered for the evaluation of directionality and environmental cues influence on directionality precision. For orientation examination, only species with large sample sizes ($n \geq 20$) were analysed because a significant Rayleigh test can be interpreted as a unimodal concentration, towards a preferred orientation, only when the sample size is reasonably large (Batschelet 1981).

Results

A total of 164 fish larvae were tested, belonging to four families and eight taxa among which seven were identifiable to species. The fish larvae of each taxon tested at the two experimental sites, Sandy and Rocky, and are summarised in Table 1.

Directionality of individuals

The majority of fish larvae tested were directional in a cardinal reference (Rayleigh test on individuals, uniform distribution, $P < 0.05$). The delay between capture and experimentation did not influence directionality precision in either species (Mann–Whitney, $P_{all} > 0.05$). Once the results of all fish larvae pooled, 85% swam directionally in the Sandy site and 91% in the Rocky site. More precisely, the three species with large samples (*D. sargus*, *O. melanura*, *S. aurata*) had proportions of directional individuals greater than 80% on both experimental sites (Table 1).

Directionality precision (*r* values from the Rayleigh test) was first compared among experimental sites and then species (Fig. 2). Precision was not different between the Sandy and Rocky sites, when all species were pooled (Mann–Whitney, $P_{all} > 0.05$). Within each site, however, species displayed different precisions (Sandy; Kruskal–Wallis, $H = 40.66$, $P < 0.001$; Rocky: $H = 33.56$, $P < 0.001$). In the Sandy site, Mugilidae had lower *r* values than *C. chromis*, *D. sargus*, *O. melanura* and *S. aurata* (Mann–Whitney pairwise, $P_{all} < 0.05$). *D. sargus* had higher directionality precision than *S. smaris* (Mann–Whitney pairwise, $P < 0.05$). In the Rocky site, *D. sargus* and *O. melanura* were more directional than the Mugilidae (Mann–Whitney pairwise, $P < 0.05$). The directionality precisions were significantly different among species within the Sparidae family on the Rocky site (Kruskal–Wallis, $H = 17.64$, $P = 0.001$) and on the Sandy site (Kruskal–Wallis, $H = 14.62$, $P = 0.005$). Warm-season species (*C. chromis*, *D. sargus*, *O. melanura*, *S. smaris*) had significantly higher directionality precision than

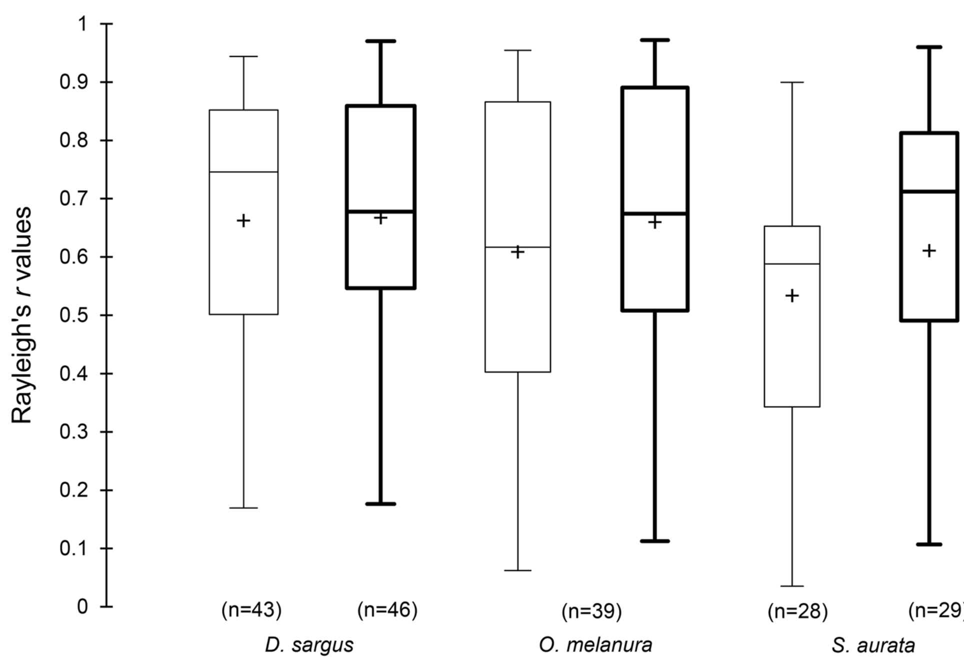

Fig. 2 Standard boxplots of *r* values directionality precision (Rayleigh test) for species with large sample sizes. The boxplots with thin lines represent the values in the Sandy site and the boxplots with bold lines those in the Rocky site. The average *r* values are delayed as the crosses in the boxes

cold-season species (*A. imberbis*, Mugilidae, *P. acarne*, *S. aurata;* Mann–Whitney, $P<0.0001$).

Environmental variables measured in the two experimental sites did not significantly influence directionality precision, in all species or in the pooled families of Sparidae and Mugilidae (Linear regression tested by permutations, $P_{all}>0.05$).

Orientation by species

Among the three abundant species tested for orientation, only *D. sargus* showed a significant cardinal orientation in the two experimental sites, to the south-west in the Sandy site and to the east in the Rocky site (Table 2). *D. sargus* also showed significant orientation relative to both the sun and coast directions in the two experimental sites.

In the Sandy site, *D. sargus* significantly oriented towards the sun and the coast (respectively: $r=0.47$, $P=0.001$; $r=0.45$, $P=0.002$; Table 2). In the Rocky site, *D. sargus* oriented towards the sun but away from the coast (respectively: $r=0.43$, $P=0.003$; $r=0.38$, $P=0.011$; Table 2; Fig. 3).

Orientation relative to the current and the wind direction was significant for *D. sargus* only in the Sandy site. The current was mostly heading south and the wind heading north in June when *D. sargus* was present. In both experimental sites, the orientation precision was higher for the orientation relative to the sun azimuth, a bit lower for the orientation relative to the coast or for cardinal orientation. The lowest *r* values were found for the orientations relative to the current and the wind.

Oblada melanura and *S. aurata* displayed no significant orientation, neither cardinally nor towards any environmental cue tested (Table 2). Finally, no bimodal pattern was observed for *O. melanura* and *S. aurata*, either in the Sandy or Rocky sites.

Discussion

Directionality of individual larvae

This first study conducted on fish larvae orientation behaviour over two coastal sites in the Mediterranean Sea, supports that the species tested have directional abilities that are consistent with the literature (Paris et al. 2013; Faillettaz et al. 2015). The majority of studies on fish larvae orientation have been conducted in tropical environments and mainly with the Pomacentridae family (Leis et al. 2014), however, in the Mediterranean Sea, the only species of this family is *C. chromis*. This species was somewhat directional; its mean *r* values were greater than 0.5 at the two experimental sites. This result was similar to Faillettaz et al.'s (2015) samples (mean $r=0.5$) and also to the congeneric species *Chromis atripectoralis* studied by Leis et al. (2014) in Australia (mean $r=0.67$). Apogonidae have also been well studied, especially in tropical environments and *A. imberbis* directionality was similar to other Apogonidae species,

Table 2 Orientation of species with large sample sizes relative to environmental cues

Cues	Species					
	D. sargus		*O. melanura*		*S. aurata*	
	Sandy site	Rocky site	Sandy site	Rocky site	Sandy site	Rocky site
Cardinal bearing	$m=236°$	$m=93°$	$m=213°$	$m=97°$	$m=80°$	$m=106°$
	$r=0.45$	$r=0.34$	$r=0.26$	$r=0.18$	$r=0.17$	$r=0.30$
	$P=0.002$	**$P=0.031$**	$P=0.252$	$P=0.489$	$P=0.501$	$P=0.095$
Sun	$m=18°$	$m=301°$	$m=90°$	$m=306°$	$m=261°$	$m=315°$
	$r=0.47$	$r=0.43$	$r=0.37$	$r=0.29$	$r=0.19$	$r=0.33$
	$P=0.001$	**$P=0.003$**	$P=0.066$	$P=0.143$	$P=0.397$	$P=0.059$
Coast	$m=18°$	$m=167°$	$m=358°$	$m=171°$	$m=214°$	$m=192°$
	$r=0.45$	$r=0.38$	$r=0.26$	$r=0.34$	$r=0.18$	$r=0.23$
	$P=0.002$	**$P=0.011$**	$P=0.256$	$P=0.067$	$P=0.456$	$P=0.259$
Current	$m=79°$	$m=4°$	$m=25°$	$m=97°$	$m=154°$	$m=240°$
	$r=0.37$	$r=0.11$	$r=0.17$	$r=0.25$	$r=0.26$	$r=0.12$
	$P=0.017$	$P=0.721$	$P=0.578$	$P=0.228$	$P=0.187$	$P=0.681$
Wind	$m=214°$	$m=81°$	$m=94°$	$m=319°$	$m=354°$	$m=30°$
	$r=0.39$	$r=0.15$	$r=0.37$	$r=0.19$	$r=0.23$	$r=0.18$
	$P=0.011$	$P=0.528$	$P=0.064$	$P=0.438$	$P=0.261$	$P=0.420$

For each species, *m* is the mean angle (°) relative to the cue direction (0° = towards the cue, 180° = away from it); *r* is the result of Rayleigh test for orientation relative to the cues ranging from 0 (no orientation) to 1 (maximum precision); *P* is the *p* value of the Rayleigh test (bold = $P<0.05$)

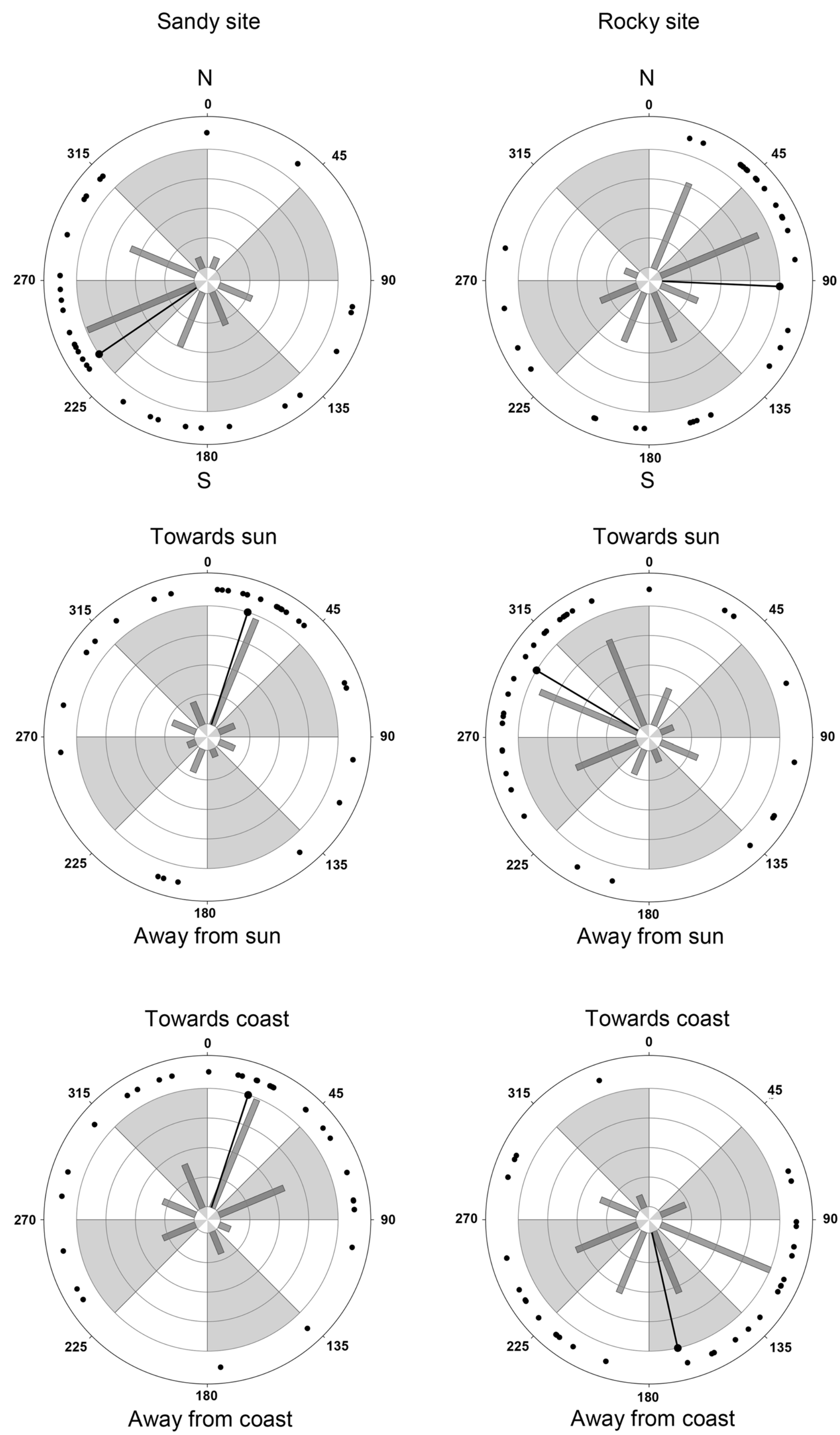

Fig. 3 Orientation of *D. sargus* on the Sandy (left) and the Rocky (right) sites, from top to bottom: in cardinal bearing, relative to the sun azimuth and relative to the coast direction. Each dot represents the average direction of one individual. The grey bars correspond to the proportions of individuals in the 45° sections, the longer the stick is, the higher the proportion of individuals in the section. The mean bearings relative to the cues across individuals are represented by the black line

such as those studied by Paris et al. (2013). Mugilidae larvae could not be successfully identified down to species level. At family level, they were generally less directional than other species tested. This may be the result of this taxon representing multiple species, each with different orientation behaviours.

For the most diverse and numerically abundant family in this study, the Sparidae, the directionality precision values varied among species. No values exist in the literature for *P. acarne*; here, its *r* values ranged from 0.15 to 0.44. These values were derived from a small number of individuals (four at each site) and this species should be further investigated to build on these initial results. *S. smaris* presented results similar to Faillettaz et al. (2015) with a mean directionality close to 0.4 at both sites.

For the three Sparidae species with large sample size at each site ($n > 20$), the directionality precision values were not significantly different among species. For *O. melanura*, directionality precision was higher in this study (mean r of 0.61 in the Sandy site, 0.65 in the Rocky site) than in Faillettaz et al.'s (2015) study where the mean was close to 0.3. In this study, *D. sargus* can be compared to its counterpart of the same genus, *Diplodus annularis*, in the work of Faillettaz et al. (2015). Here again, directionality is clearly higher in this study with mean *r* values of 0.66 and 0.68 at the Sandy and Rocky sites and a median *r* value of 0.74 when combining both sites, while *D. annularis* had mean and median *r* values close to 0.3 (Faillettaz et al. (2015). In the study of Leis et al. (2006) carried on two temperate Sparidae species (*Acanthopagrus australis* and *Pagrus auratus*), average directionality precisions ranged between 0.38 and 0.73.

The three abundant Sparidae species were morphologically similar with slim and transparent bodies. Their pelagic larval durations were relatively long, ranging from 20 to 50 days (Macpherson and Raventós 2006; Faria et al. 2011). The Mugilidae were more pigmented and robust than the Sparidae.

Apogon imberbis and *C. chromis* were the most pigmented with a relatively short pelagic larval duration relative to other species, of around 20 days (Macpherson and Raventós 2006).

Regarding seasonality, results seem to indicate that warm season species have higher precision. This may be due to higher overall behavioural abilities of species developing in this season (which has been shown for swimming speeds by Leis et al. 2013).

Orientation of species: comparing Sandy and Rocky coastal sites

Orientation by species can only be analysed for the three species with large sizes ($n > 20$): *D. sargus*, *O. melanura* and *S. aurata*. Only *D. sargus* showed significant orientation, both in the Sandy or Rocky sites, cardinally as well as relative to the coast and the sun directions. The results showed that *D. sargus* oriented to the South-west on the Sandy site and to the North-east on the Rocky site, towards the sun direction in both experimental sites and towards the coast in the Sandy site but away from it on the Rocky site.

These results are very interesting, firstly because they are concordant with Faillettaz et al.'s (2015) results and others' works (Leis and Carson-Ewart 2003; Berenshtein et al. 2014; Leis et al. 2014) which demonstrate that the sun is used by fish larvae for their orientation during the settlement period. Indeed, *D. sargus* was always oriented towards the sun regardless of the experimental site but also regardless of the time of day (deployments were carried out throughout the day, at different solar azimuths). Secondly, since there was a difference between the two experimental sites, the orientation may also have been influenced by the kind of coast on which the experiment took place. Because the precisions values are similar for cardinal, sun-relative, and coast-relative orientation, it is impossible to assess which cue was the most important. In particular, we cannot conclude as to whether it was the nature of the coast itself that elicited the different orientations in the two sites or whether it was the general geographic orientation of the coastline relative to the sun's direction that induced this result as a consequence of sunward orientation. Nevertheless, several hypotheses could explain the different orientation behaviour depending on the nature of the coast. For example, *D. sargus* may have been repulsed by the Rocky site because it was noisier due to the nature of the environment (rocky bed-ground, associated benthic fauna) and to the higher proximity to the coast compared to the Sandy site (Ceraulo et al. 2018). Higher sound levels may be associated with the presence of predators at day-time. Indeed, several studies have demonstrated that fish larvae can be repulsed by day-sound and attracted by night-sound from the coast (Leis et al. 2002; Tolimieri et al. 2004). In contrast, the Sandy site had a different, less diverse, fauna and was more distant from coast; so the ambient sound was certainly less important. Moreover, the Sandy site is close to a lagoon, the water plume coming from the lagoon with nutrient sources could be attractive (Paris et al. 2013; Morais et al. 2017).

Oblada melanura and *S. aurata* displayed no significant orientation in both experimental sites, although more than 80% of fish larvae were directional. *O. melanura* did not display an orientation in the Faillettaz et al. (2015) study either.

For the three Sparidae species, preferential settlement sites found in the literature are coastal reefs; the three Sparidae species tend to favour small bedrock (Cheminée et al. 2011; Calò 2016) but *S. aurata* sometimes may also choose lagoon areas as an alternative nursery (Chaoui et al. 2006; Abecasis and Erzini 2008; Isnard et al. 2015). As such, we might have assumed that these three species would present similar significant orientation and not just *D. sargus*.

Further studies need to be carried out on new species, to explain more effectively these differences in orientation behaviours between different coastal sites by identifying more precisely the influence of various environmental variables on fish larvae orientation, especially the incidence of the sun and the differences relative to the nature of the coast. Other tests would also be interesting for complementary results such as laboratory tests for odour cues (Díaz-Gil et al. 2017; Morais et al. 2017) and in situ experiments with increased sampling effort, but also in diversified conditions: with deployment times or at various distances from the coast. Other environmental cues such as magnetism or olfactory cues are difficult to evaluate in situ, but tests in diverse water masses can be carried out (Paris et al. 2013).

Auditory cues have already been tested in tropical environments and found to have an influence on fish larvae orientation, both in situ and in a controlled environment (Leis et al. 2002; Leis and Lockett 2005; Slabbekoorn and Bouton 2008; Stanley et al. 2012); this still has to be developed in a temperate Mediterranean environment. The personality of individual fish larvae should not be neglected either. In fact, several studies have shown different individual strategies for behavioural responses to changes in the environment (Mathot et al. 2012). However, larger samples and complementary experiments can compensate for these individual differences and allow to test hypotheses.

Conclusion

At the individual level, the results of this work show large proportions of directional fish larvae for all species tested. At the species level, only one species presented significant orientation. Indeed, *D. sargus* showed significant orientation cardinally, towards the sun, as well as towards the coast in the Sandy site and away from the coast in the Rocky site. This study, conducted from summer 2016 to summer 2017, offers some of the first results on orientation behaviour for several Mediterranean species in cold and warm season: it is the first study in the Corsican region and for some Mediterranean species. Some results corroborate the findings of several other studies, such as the fact that sun-based cues are used for the orientation of fish larvae. This study, in particular the orientation results, can constitute a decision support in management terms for coastal areas. Indeed, settlement patterns potentially conditioned by orientation behaviour of fish larvae represent a key point for the protection of marine coastal populations. As an example, sandy shores are generally less subject to protection efforts, while they seem attractive to one dominant species in the Corsican region. These statements have high implications for the management of Mediterranean fish species.

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Compliance with ethical standards

Conflict of interest This study was co-financed by the UMR/CNRS 6134 "Sciences Pour l'Environnement" and the UMS/CNRS 3514 STELLA MARE of the Università di Corsica Pasquale Paoli through European funding, French state, and Corsican region. The authors declare that they have no conflict of interest.

Ethical approval Collection samples were conducted with a fishing authorization delivered by the Interregional Directorate of the Mediterranean Sea with the n°355 for the UMS/CNRS 3514 STELLA MARE, Università di Corsica Pasquale Paoli. The protocol experiment on the Corsican coastline was approved by the French Ministry of Higher Education and Research ("Autorisation de Projet utilisant des Animaux à des Fins Scientifiques"), authorization n°9643. Experiments were made with efforts to minimise stress of individual samples, which is crucial both ethically and for the validity of behaviour observations.

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