Short-term Temporal Fluctuation of Very-nearshore Larval Fish Assemblages at the Arrábida Marine Park (Portugal)

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ABSTRACT

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Understanding processes affecting fish recruitment and population connectivity is of major importance to the management of Marine Protected Areas. Fluctuations in recruitment of coastal fishes can be affected by processes occurring during the early life stages such as the dispersal and availability of larvae. In nearshore temperate environments, there is a lack of knowledge about the patterns of larval supply or biophysical interactions that may influence recruitment variability in these populations. With the objectives of investigating within season (Spring-Summer period) fluctuations that may affect recruitment, and of understanding patterns of larval retention close to the reefs, we used a plankton net attached to an underwater scooter to investigate weekly variation in the composition of fish larval assemblages, larval density and diversity and ontogenetic patterns of occurrence of fish larvae in the extreme nearshore environment of the Arrábida Marine Park (Portugal). The results from multivariate analysis (PERMANOVA and SIMPER) have showed a lower number of species dominating the assemblage, and significant differences in the abundance between species, when compared to previous studies. The presence of larvae in several developmental stages indicates some degree of retention. These findings are important to the management of the Marine Park.

ADDITIONAL INDEX WORDS: *Larval fish assemblages, Larval retention, Temporal variation*

INTRODUCTION

The best design and distribution of Marine Protected Areas (MPA's) requires a deep knowledge of the connectivity patterns between local populations of marine organisms, and particularly of the patterns of supply of new individuals to these populations (LEIS, 2003). Many coastal fish species that live associated to demersal habitats (like reefs) have limited dispersal in the adult phase but have pelagic early life history stages that allow for dispersal from the natal populations and for connection between different populations. Given this potential for large dispersal, marine populations are traditionally considered as open (KRITZER and SALE 2006). However, recent evidence, mainly for coral reef species (see reviews by SWEARER *et al*., 2002, and LEIS, 2006; COWEN *et al*., 2006, ALMANY *et al*., 2007, GERLACH *et al*., 2007), has shown that self-recruitment can, for some species, be higher than previously expected, as fish larvae may be retained close to the natal reefs and thus recruit locally. Some studies indicate that biophysical interactions can strongly influence the position of larvae in the water column contributing to retention close to the shore and increasing self-recruitment, showing that marine populations can vary from entirely closed to fully open (SPONAUGLE *et al.*, 2002). These interactions between complex larval behavior and physical factors depend on local conditions and on early life history traits which are highly variable among species (SPONAUGLE *et al*., 2002; LEIS, 2006). Although some evidence of retention also exists for temperate rocky reefs (review by HICKFORD and SCHIEL, 2003; BORGES *et al.*, 2007a; CARRERAS-

CARBONELL, 2007), further investigation is needed to understand differences between coastal species in their patterns of dispersal or retention.

In addition to spatial variability in larval abundance patterns, temporal fluctuations of larval availability often occur, affecting the supply of new individuals to local populations in different years. These fluctuations can be caused by several factors, and can occur at different scales, from circadian to interannual, and these should be considered when trying to understand which factors affect replenishment and population dynamics, as ecological patterns can be misunderstood if the proper scale is not considered (GRAY, 1996). Processes occurring at a scale of minutes or meters can, in fact, strongly influence larval dispersal (LARGIER 2003).

The Arrábida Marine Park is an excellent model for the study of ecological processes structuring nearshore communities. This Marine Park was designated in 1998, but has only been implemented very recently (the management plan was approved in 2005). Some studies previous to the implementation of the Marine Park have shown that there is a highly diverse larval fish assemblage (BELDADE *et al*., 2006, BORGES *et al*., 2007a,b) which reflects the high diversity of the adult assemblage (HENRIQUES *et al.*, 1999). These studies also showed that small-scale patterns in the vertical distribution of larvae could contribute to retention close to the reefs, for some species.

In spite of these studies on the composition and temporal and spatial dynamics of local larval assemblages, patterns of temporal occurrence of these larval fish assemblages and patterns of

variation for individual species at a small temporal scale have not yet been investigated. This study aims at understanding weekly fluctuations of these larval assemblages occurring at the fully protected area of the Arrábida Marine Park, very close to the adults' reefs, and at analyzing the ontogenetic developmental patterns that may be related to larval retention close to the reefs.

METHODS

Study area

Sampling was performed in two sites inside the fully protected area of the Arrábida Marine Park, over the rocky reefs where the adults of several coastal species live. Given its geographical location (Figure1), south of two capes (Cabo da Roca and Cabo Espichel) on the western Portuguese shore (*c.a.* 30 Km south of Lisbon), and the presence of high cliffs along the shore, the area is protected from the prevalent northern winds, having calm conditions all year round. These conditions allow the study of nearshore communities and sampling very close to the complex shallow rocky reefs that result from the disintegration of these cliffs.

Sampling

Samples were collected using a plankton net (0.30 m mouth diameter, 350 μm mesh size and a diameter: length ratio of 1:3) attached to an underwater Apollo AV-1 scooter at a sampling speed of about 1.5 knots. For more details on the sampling apparatus see BELDADE *et al.* (2006).

Depth and tidal phase effects were randomized and in each week samples were collected at two depth strata and at several tidal phases. For nine consecutive weeks from 03 June to 31 July 2008, a total of 98 samples were collected very close to the reefs where the adults live, at two depths: 49 samples close to the bottom (at about 50 cm from the substrate: average maximum depth = 8.55, SD = 1.28, N = 48) and 49 samples at about 1m below the surface. In each sampling day the diver would collect a bottom and a surface sample (in order to eliminate for possible depth effects) at each of the two sites. Mean volume filtered was 7.21 m^{-3} (SD = 2.38, N = 98). The average number of larvae collected per sample was 12.23 (SD = 18.98, N = 98).

Most samples were preserved in 80º ethanol (some of the initial samples were fixed in 4% formalin) buffered with sodium borate. Larvae were sorted and identified under a stereomicroscope to the species level when possible and were assigned to an ontogenetic level, according to the flexion stage, and were classified in pre-flexion, flexion or post-flexion stage larvae.

Data analysis

Two diversity indices were calculated for each sample, the Shannon diversity index (H') and the average taxonomic distinctness index (Delta*), as a measure of the taxonomic spread of species among samples (CLARKE and WARWICK, 2001). Four taxonomic levels were considered, from species to order, assuming equal step-length between each level.

We used the PERMANOVA+ for PRIMER software to perform a PERMANOVA analysis to test for differences between weeks in the assemblage structure, based on Bray-Curtis similarities between samples, after log (x+1) transformation of abundance data, considering the factor week as fixed and unrestricted permutation of raw data. Samples without larvae and larvae that could not be identified to at least the family level were excluded from the analysis. This reduced the number of samples obtained in the first week to one and thus this week was not included in the analysis. In order to detect which weeks differed, PERMANOVA Pairwise comparisons were also conducted.

The SIMPER routine was used to detect the species that most contributed to explain the similarity between samples in each week. This procedure was based on Bray-Curtis similarity between samples, after a log (x+1) transformation. A 90% cut off for low contributions was used.

RESULTS

Assemblage composition

A total of 1192 larvae were caught and identified, comprising 23 taxa, belonging to 8 families. From these, 96.7% of the larvae could be identified to the species level. Only 1.35% of the larvae could not be identified given their bad condition.

Six species contributed to more than 95% of the total catch (Figure 2). The tripterygiid *Tripterygion delaisi* was the most abundant species with an average abundance of 1.159 larvae m^{-3} (SD = 2.405, N = 95). The gobiid *Gobius xanthocephalus* was the second most abundant species with 0.354 larvae m^{-3} (SD = 0.941, N = 95), followed by *Pomatoschistus pictus* (average 0.178 larvae m^{-3}, SD = 0.469, N = 95).

Three species had individual contributions of *c.a.* 1% of the total: the gobiesocids *Lepadogaster candolii* and *Lepadogaster lepadogaster* with average abundances of, respectively, 0.028 larvae m^{-3} (SD = 0.124, N = 95) and 0.022 larvae m^{-3} (SD = 0.088, N = 95) and the atherinid *Atherina presbyter* (average abundance = 0.022 larvae m^{-3}, SD = 0.152, N = 95).

The remaining species with low contributions (less than 0.15% of the total) were the blennids *Parablennius pilicornis* (mean abundance = 0.014 larvae m^{-3}, SD = 0.080, N = 95) and *Coryphoblennius galerita* (mean abundance = 0.012 larvae m^{-3}, SD = 0.076, N = 95) and the sparid *Boops boops* (mean abundance = 0.010 larvae m^{-3}, SD = 0.049, N = 95). Some labrids
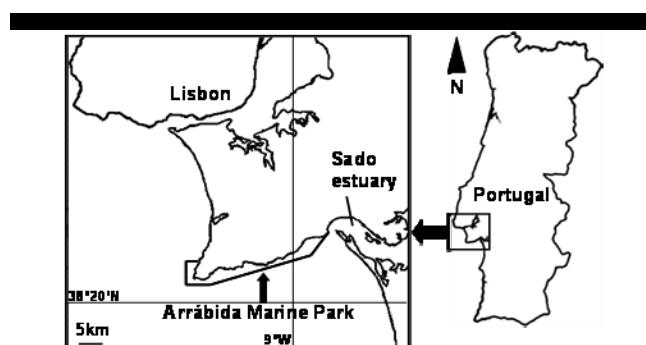

Figure 1. Study area location. Adapted from BORGES *et al.*, 2007a

Figure 2. Species composition of the assemblage. Only species contributing to at least 1% of the total are individually represented. The remaining species are grouped in the category "other".
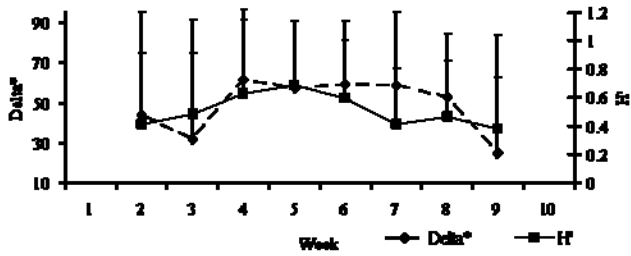
Figure 3. Weekly fluctuation, from 03 June to 31 July 08, of the two diversity indices calculated (Delta* = average taxonomic index; H' = Shannon diversity index).

(*Symphodus* spp. and *S. cinereus*) were present, but with extremely low values of abundance (ca 0.0013 larvae m^{-3} each, less than 0.001% of the total). *Trachurus trachurus* (Carangidae) and *Apletodon dentatus* (Gobiesocidae) had even lower values.

Larval Diversity

When considering the whole sampling period, average H' diversity was 0.52 (SD = 0.46, N = 74) and average Delta* was 52.27 (SD = 35.77, N = 74). Both indices also exhibited temporal fluctuations (Figure 3), and both were higher between weeks 4 and 6 (end of June/early July), with maximum values reaching 61.63 (Delta*, week 4) and 0.63 (H', week 5). From week 2 to week 3, interestingly, although a decrease in Delta* was noticed, H' diversity increased, indicating that there was an increase of species or individuals of closely related taxa. On the other hand, although Delta* was maintained, H' decreased from week 6 to 7 indicating a decrease in H' without loss of taxonomic diversity.

Structure and Abundance

The PERMANOVA results showed significant fluctuations in assemblage structure along the 9 weeks investigated: Pseudo-F (7, 73) = 1.69, P(perm) = 0.013, 999 unique permutations. Pair-wise comparisons revealed differences in assemblage structure between week 2 and weeks 3 (t = 2.12; P(perm) = 0.024; 126 perms), 7 (t = 1.97; P(perm) = 0.011; 895 perms) and 8 (t = 1.79; P(perm) = 0.012; 822 perms). Although with a weaker signal, weeks 5 and 7 also evidenced some difference in structure (t = 1.51; P(perm) = 0.055; 997 perms).

The SIMPER analysis revealed that a reduced number of species contributed to explain the similarity between samples in each week (Table 1). *T. delaisi* was the species that most explained this similarity in all weeks except in week 3. *G. xanthocephalus* largely explained similarities in this week, and was also a frequent component of the structure of the assemblage in the other weeks (except weeks 2 and 9). *P.pictus* was relevant to explain results in weeks 5, 8 and 9. *Lepadogaster candolii*,
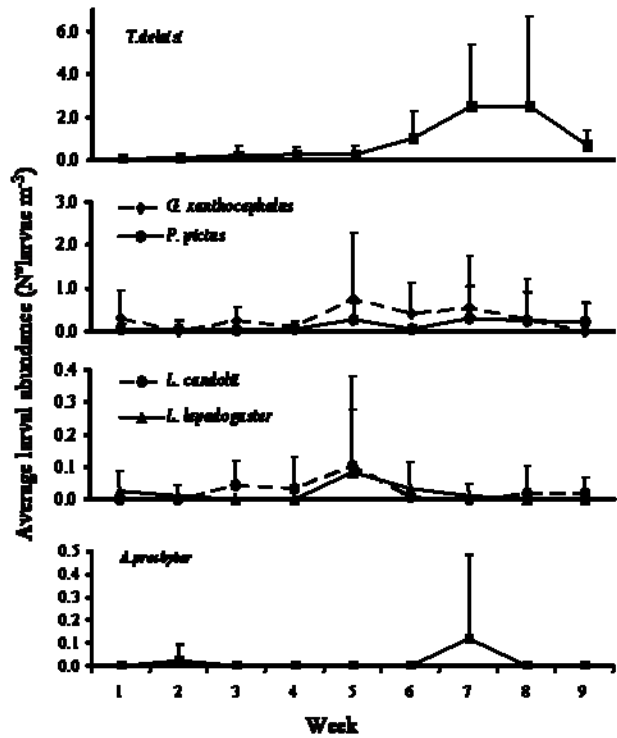

Figure 4. Weekly patterns of average larval abundance, from 03 June to 31 July 2008, for the six most abundant species. Error bars represent standard deviations.

although less abundant, was also an important contributor to assemblage structure during week 3. From Table 2 it is clear that it was the presence or absence of these most abundant species and/ or differences in their abundance that best explained the differences in the structure of the assemblages between weeks. For instance, the absence of *G. xanthocephalus* in week 2 explains part of the differences with the other weeks (Table 2, Figure 4). Also, the fact that *T. delaisi* had in week 2 lower abundance than in weeks 7 and 8 (Table 2, Figure 4), was important to explain differences in the assemblage's temporal structure. The two *Lepadogaster* species were significant to explain the difference in assemblage's structure between weeks 5 and 7 (Table 2), since in week 5 there was a peak of these two species (Figure 4).

Figure 4 shows that the larval abundance for these species is not constant throughout the reproductive season, with distinct peaks in larval abundance between weeks for the same species, and also different abundance patterns between species. In general, larval abundance was very low during June (weeks 1 to 5). *Tripterygion delaisi* showed a clear peak in middle July, during
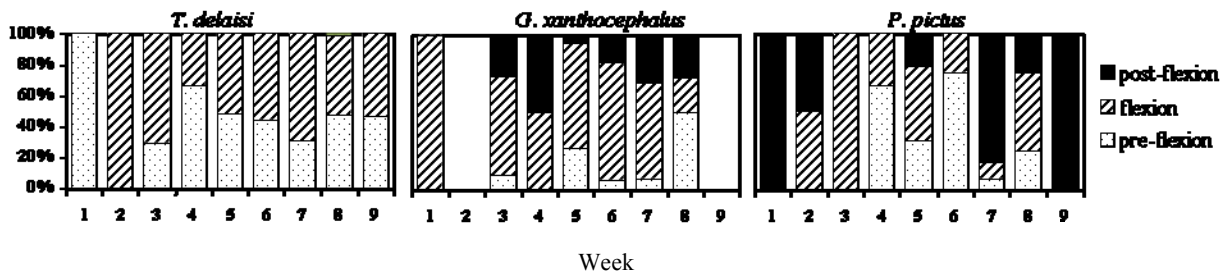

Figure 5. Temporal variation, from 03 Jun to 31 July 2008, of the proportion of larvae in the different developmental stages.

Table 1: SIMPER analysis revealing the species that most contributed to explain similarities between sample composition. Average similarity values (Av. Simil), percentage contribution (Contrib %) of the most representative species to the average similarity within each group, and cumulative percentages (Cum %) are shown. (Cut-off value for low contributions = 90%).

Week	Av. Simil	Species	Contrib %	Cum. %
2	49.42	*T. delaisi*	100	100
3	28.81	*G. xanthocephalus*	85.13	85.13
		L. candollii	7.86	92.99
4	38.86	*T. delaisi*	78.40	78.40
		G. xanthocephalus	17.50	95.90
5	25.78	*T. delaisi*	38.42	38.42
		G. xanthocephalus	36.71	75.13
		P. pictus	22.53	97.66
6	33.57	*T. delaisi*	75.66	75.66
		G. xanthocephalus	21.74	97.40
7	30.11	*T. delaisi*	72.47	72.47
		G. xanthocephalus	22.78	95.25
8	29.66	*T. delaisi*	70.26	70.26
		P. pictus	16.05	86.31
		G. xanthocephalus	13.69	100.00
9	24	*T. delaisi*	85.32	85.32
		P. pictus	14.68	100.00

Table 2: Average dissimilarities between groups (Av. Dissimil.) from the SIMPER analysis, average abundance (Av. Abund.), the percentage of contribution (Contrib %) of individual species that most explain differences in assemblage structure, and cumulative percentage (Cum%), cut-off value = 90%. Only the comparisons that revealed significant differences are shown.

Av. Dissimil	Species	Av. Abund.		Contrib %	Cum. %
86.06		Week 2	Week 3		
	G. xanthocephalus	0.00	0.29	38.39	38.39
	T. delaisi	0.21	0.18	30.98	69.37
	P. pictus	0.11	0.03	12.81	82.18
	L. candollii	0.00	0.06	7.43	89.61
	A. presbyter	0.04	0.00	4.69	94.30
81.41		Week 2	Week 7		
	T. delaisi	0.21	0.92	48.86	48.86
	G. xanthocephalus	0.00	0.29	22.6	71.45
	P. pictus	0.11	0.18	13.89	85.34
	A. presbyter	0.04	0.08	5.81	91.15
76.55		Week 2	Week 8		
	T. delaisi	0.21	1.01	53.09	53.09
	P. pictus	0.11	0.22	19.82	72.91
	G. xanthocephalus	0.00	0.20	16.01	88.92
	A. presbyter	0.04	0.00	4.11	93.03
77.17		Week 5	Week 7		
	T. delaisi	0.23	0.92	43.69	43.69
	G. xanthocephalus	0.38	0.29	23.15	66.85
	P. pictus	0.22	0.18	15.35	82.19
	L. lepadogaster	0.07	0.01	3.47	85.66
	A. presbyter	0.00	0.08	2.86	88.53
	L. candollii	0.08	0.00	2.55	91.08

weeks 7-8 (Figure 4). The gobiids *G. xanthocephalus* and *P.pictus* also showed temporal fluctuation on larval abundance (Figure 4), with higher values in week 5 (end of June-early July) and week 7 for both species. On the other hand, *Atherina presbyter* only occurred in weeks 2 and 7, with higher values in the latter (Figure 4).

Ontogeny

Figure 5 shows the weekly variation in the proportion of larvae of each developmental stage, for the three most abundant species. *Tripterygion delaisi* larvae were all in the pre-flexion and flexion stages with no clear pattern of bigger larvae in later weeks. However, from weeks 4 to 7, there was an increase in more developed larvae when compared to the preflexion ones. Nevertheless, no post-larval stages of this species were found in the samples. For the gobies, the same pattern applies with an increase in the proportion of more developed larvae in the weeks with greater abundance of these species (weeks 5 and 7).

DISCUSSION

This study has investigated for the first time short-term fluctuations in the structure, diversity and abundance patterns of fish larval assemblages at the Arrábida Marine Park.

Larval supply varied with time and distinct temporal patterns were found for the different species. The larvae of the most abundant species were present close to the reefs in several developmental stages, suggesting that larval development is occurring in the nearshore, indicating some degree of retention.

The assemblage was composed almost exclusively of coastal species with demersal spawning. The number of taxa obtained was lower when compared to the results of previous years (BORGES *et al.*, 2007a). In particular, the dominant species in those years included not just gobies like *P. pictus* and *G. xanthocephalus*, but also a larger abundance of labrids (*Symphodus*). In 2008 (present study) *Symphodus* species were almost absent. Although the sampling effort was not the same and the scale of analysis was different, the abundance values were considerably lower for some species in the present year. *Tripterygion delaisi*, in turn, showed the highest values of abundance when compared to 2001, 2002 and 2003 (BORGES *et al.*, 2007a). In the present study, the abundance was about three times higher than that found in 2003

(which in turn had more larvae of this species than in the previous years). The scooter method was only used close to the bottom on those studies, whereas at the surface, sampling was performed with plankton trawls pulled by a boat, but there were clear vertical differences in the structure of the assemblages (BORGES *et al.*, 2007a). The differences in capture efficiency between methods could account for differences for this species (but not others).

However, BELDADE *et al.* (2006) reported that *T. delaisi* was more abundant close to the bottom in shallower areas (0-4 m) than in depths between 4 and 12 m. Moreover, even in that shallow stratum, these larvae were ten times less abundant than in 2008, which indicates high interannual fluctuations in this species occurrences. *G. xanthocephalus* showed average values of abundance higher than in 2002 but *c.a.* 3.5 times lower than in 2001 and 2.8 times lower than in 2003. *Pomatoschistus pictus* was considerably less abundant in the present study than in other years, showing greater differences (9.4 times lower) with the year 2003.

Diversity values were also lower in 2008 than in any of the previous years, even when considering that the present study included not just bottom samples but also subsurface samples, where diversity has been found to be higher (BORGES *et al.*, 2007a).

The different developmental stages present in these sites suggest that larvae of these species are able to grow locally. In the case of *T. delaisi*, no post-flexion stage larvae could be found. This may reflect capacity for avoiding the nets by these more developed larvae or they may already have switched to exploring the benthic habitat thus being no longer in the planktonic environment. Although more associated to the surface, no larvae of *T. delaisi* were found with increasing distance from shore by BORGES *et al.* (2007b), suggesting a distribution restricted to the shore.

The occurrence of clear genetic structure between populations in the Western Mediterranean (CARRERAS-CARBONELL *et al.*, 2007), indicates low dispersion for this species, consistent with both the high occurrence of late-stage larvae near reefs and a low planktonic larval duration, when compared to other temperate species (RAVENTOS and MCPHERSON, 2001).

For the gobies *G. xanthocephalus* and *P. pictus*, all developmental categories could be found nearshore, consistent with the results described in previous studies (BELDADE *et al.*, 2006; BORGES *et al.*, 2007a). Considering only the weeks where these species were most abundant, and assuming that the same cohort was being sampled, the results of an increase in the proportion of post-flexion stage larvae, may indicate local growth for these species. These results and others (review by HICKFORD and SCHIEL, 2003) suggest that retention of reef fish larvae in temperate waters may also occur.

Temporal variability of larval occurrence may be influenced by several factors. Temporal and spatial fluctuations on adults' spawning patterns may occur, influencing the time and location of larval release and the potential for dispersal (SPONAUGLE *et al.*, 2002). The differences found between species probably reflect within season differences in the spawning activity of the adults. The short term variability of adult reproductive activity can influence in turn, the potential for dispersal and survival of fish larvae, in relation to various environmental and biological factors. During April 2008 there were abnormally persistent bad weather conditions in the area with strong southern winds and high wave action. These conditions might have had an impact over the adult populations affecting their normal reproductive activity. The low abundance of fish larvae during the first four weeks of sampling in June, when higher values were expected during the normal peak of the spawning season, indicates that a delay in the spawning season of some species might have occurred. On the other hand, within season variability can also be explained by factors affecting the pelagic environment that can act to decouple the observed patters in late stage larval supply from those that could be expected from adult-related variability.

These results emphasize a strong need for regular interannual monitoring of the local assemblages and in relation with factors that might influence their occurrence and distribution, to better understand the biophysical correlates that might be acting at the study area.

Our results clearly showed that larval supply is not constant and that there is high within season variation in larval supply. This must be considered when trying to understand replenishment patterns and studies should focus on the relationship between these fluctuations and recruitment variability. Ontogenetic development and behavioural swimming capabilities studies are needed in order to best understand the resulting patterns and differences between species. Future studies should also aim at quantifying self-recruitment for those species with evidence of retention, to best evaluate the efficiency of the protective measures in the Arrábida Marine Park.

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