

# Pelagic larval duration, size at settlement and coastal recruitment of the intertidal blenny *Lipophrys pholis*

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*To study some early life history traits of *Lipophrys pholis*, 110 recruits (TL ≤ 30 mm) were collected in April and May 2013 during the low tide periods in four rocky beaches along the west (Cabo do Mundo, Peniche and Vale do Homem) and south (Olhos de Água) Portuguese coasts. Pelagic larval duration, size at settlement and age at coastal recruitment were back-calculated from the microstructure of otoliths. Pelagic larval duration estimated from micro-increment counts until the settlement marks ranged from 57 to 73 days and showed a latitudinal reduction trend from north to south. This variable seems to be related in 30% with the regional seawater temperatures probably through the direct effect on the somatic growth. Settlement sizes (~19 mm) did not show any regional differences suggesting that this is a more conservative character within species. The mean age at coastal recruitment varied between 69 and 93 days, but northern individuals were recruited at an older age. Back-calculated spawning, hatching and settlement dates appear to be unrelated to the lunar cycle for *L. pholis*.*

**Keywords:** Blennies, *sagittae*, micro-increments, early life history

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## INTRODUCTION

For fish ecologists recruitment, in general, is defined as the number of individuals which survive from the eggs to a certain age or stage in their life history (Carr & Sims, 2006). In the present work recruitment is defined as the completion of settlement of pelagic larvae and return of the early juveniles to the adult spawning grounds. Early life history traits, such as duration of the planktonic larval stage and size-at-settlement, are closely linked to the fish recruitment success (Chambers & Leggett, 1987; McCormick, 1994; Radtke *et al.*, 2001). These variables reflect the interaction of the individual's developmental physiology with exogenous factors (e.g. food and temperature) (McCormick, 1994). Temperature, in particular, causes variation in rates of fish development in the embryonic, larval and juvenile stages (Green & Fisher, 2004). A decrease in the rate of ontogenetic development caused by a change in temperature usually results in a longer pelagic larval duration, increasing the exposure to the high-risk pelagic larval environment (Atkinson, 1996). Moreover, through its effect on growth, temperature can influence the size of the organism at which ontogenetic transformations occur (Green & Fisher, 2004), which may determine the fish's subsequent growth schedules and survival (McCormick & Molony, 1995).

Several studies have suggested that the pelagic larval duration seem to be a flexible early life history trait in both littoral and demersal fishes (McCormick, 1999; Sponaugle *et al.*, 2006; Kendall *et al.*, 2013). However studies on the conservative or flexible pattern of the size at settlement in fish are, at present, scarce (Juncker *et al.*, 2006). The shanny *Lipophrys pholis* (L. 1758) can be easily used as a fish model to understand connectivity of marine populations, to monitor dispersal in planktonic larvae and to study recruitment processes. It is an intertidal blennioid fish usually found in NE Atlantic and Mediterranean Sea shores (Zander, 1986; Almada *et al.*, 2001). In Great Britain, *L. pholis* breeds during spring and early summer (Milton, 1983), while in Portugal it occurs in the cooler months, from October/November to May (Faria *et al.*, 1996). At higher latitudes the reproductive season tends to start later and to end sooner, when conditions become favourable for larval dispersion and juvenile growth; while in low latitudes *L. pholis* has a protracted breeding and recruitment season (Conover, 1992). The reproductive season should end when the time available is not enough for late-born juveniles to grow and reach the minimal size to survive during the winter (Conover, 1992). In Portugal, the early juveniles can grow almost without interruption during the warmer months and those which recruit in early winter are able to reach the minimum size to be sexually mature within 1 year (Faria *et al.*, 1996). During the breeding period the males establish territories in crevices and stones where spawning takes place (Qasim, 1957; Dunne, 1977;

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Almada *et al.*, 1990). The nests contain 3–8 batches of eggs from a single or multiple females deposited at different times during the course of a breeding season (Qasim, 1957). It is also known that *L. pholis* males are capable of multiple spawning episodes (Ferreira *et al.*, 2011). According to captive experiments embryonic development lasts 16 days at 17°C (Faria *et al.*, 2002). After hatching the pelagic larvae disperse to the coastal area and individuals apparently return to a particular set of rock tide pools, 2–3 months later, in early winter to settle (Faria *et al.*, 1996). Recent findings show that *L. pholis* adults can orient themselves toward their home pools, suggesting that homing abilities may begin with the onset of sexual maturation and not during a hypothetical imprinting phase during larval development, such as other marine species (Jorge *et al.*, 2012). After metamorphosis and settlement, characterized by pronounced morphological and physiological changes, early juveniles (15–16 mm) show a typical behaviour associated with a benthic mode of life (Qasim, 1957; Faria & Almada, 2001; Faria *et al.*, 2002). Recruitment of fishes <20 mm ceases 3 months after the end of the breeding season (Faria *et al.*, 1996). Information regarding the temporal occurrence in the wild of these early life history events is nonexistent, because available data have been obtained through captive experiments.

This paper examines, for the first time, some life history traits of *L. pholis*, such as duration of the pelagic larval stage, size at settlement and age at coastal recruitment, inferred from the otolith microstructure of early recruits. The effect of the lunar cycle on the timing of these early life history traits is also explored. This information jointly with the historical collection data from surface seawater temperatures form the basis of a discussion about the larval growth, settlement and juvenile recruitment mechanisms for this species.

## MATERIALS AND METHODS

### Biological sampling

One hundred and ten recruits (young juveniles  $\leq 30$  mm) were collected in April and May 2013 in four rocky beaches equally spaced ( $\sim 300$  km) along the Portuguese coast from north to south (Cabo do Mundo: 41°13'N 8°42'W; Peniche: 39°26'N 9°13'W; Vale do Homem: 37°22'N 8°49'W; and Olhos de Água: 37°05'N 8°11'W) (Table 1; Figure 1). Individuals were captured with hand-nets in rocky pools during the low-tide periods. For each site individuals were collected from three tide pools (replicates) spaced at about 50 m apart. Fish were kept in seawater cooled with ice, rapidly transported to the laboratory and killed with a lethal dose of 2-phenoxyethanol. All fishes were measured (total length: TL, 0.1 mm), distributed by size classes (at intervals of 1 mm) and frozen ( $-20^{\circ}\text{C}$ ) in Eppendorf tubes filled with seawater prior to further analysis.

### Otolith microstructural analysis

Sagittal otoliths were carefully extracted from the otic cavity of fishes using a binocular microscope and cleaned of

**Table 1.** Sampling location, collection date, fish length, spawning and hatching dates, size at settlement, age of recruits, pelagic larval duration, somatic growth rate, otolith growth rate and individual sea surface temperatures for *Lipophrys pholis* used in this study. Data were present as mean  $\pm$  SE.

Sampling site	Collection date	n	Total length (mm)	Spawning date	Hatching date	Size-at-settlement (mm)	Age of recruits (days)	Pelagic larval duration (days)	Somatic growth rate (mm day <sup>-1</sup> )	Otolith growth rate ( $\mu\text{m day}^{-1}$ )	Sea surface temperature (°C)
Cabo do Mundo	2 May 2013	33	16–30 (22.9 $\pm$ 0.6)	17 December 2012–18 February 2013	27 February 2013–14 April 2013	18.6 $\pm$ 0.2	93 $\pm$ 3	73 $\pm$ 1	0.219	2.25 $\pm$ 0.08	13.10 $\pm$ 0.05
Peniche	8 May 2013	38	15–30 (22.1 $\pm$ 0.7)	3 January 2012–31 March 2013	11 March 2013–7 May 2013	18.9 $\pm$ 0.2	77 $\pm$ 3	64 $\pm$ 1	0.248	2.35 $\pm$ 0.08	13.31 $\pm$ 0.05
Vale do Homem	27 April 2013	17	15–30 (25.9 $\pm$ 1.3)	1 January 2013–25 February 2013	26 February 2013–4 May 2013	19.1 $\pm$ 0.4	78 $\pm$ 4	57 $\pm$ 2	0.289	2.90 $\pm$ 0.15	14.08 $\pm$ 0.09
Olhos de Água	26 April 2013	22	16–30 (23.8 $\pm$ 0.9)	5 January 2013–19 March 2013	17 February 2013–7 May 2013	19.1 $\pm$ 0.3	69 $\pm$ 3	58 $\pm$ 3	0.313	3.03 $\pm$ 0.11	14.92 $\pm$ 0.07

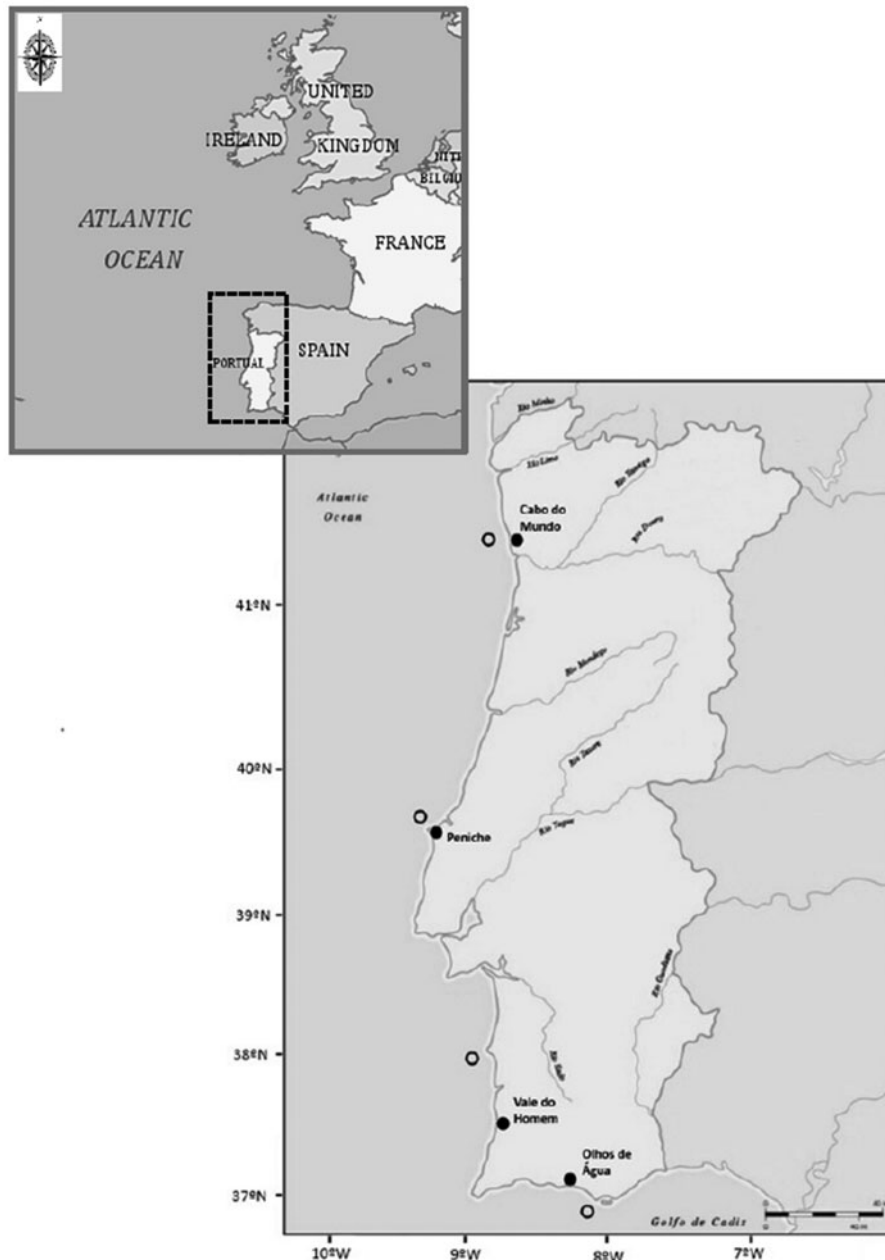


Fig. 1. *Lipophrys pholis* sampling regions (black dots) and SST buoy positions (open dots) along the Portuguese coast.

adherent tissues with ultrapure water (Milli-Q-Water). Left otoliths were mounted on microscope glass slides with the sulcus acusticus down using a drop of epoxy resin (Buehler, EpoThin). The otoliths were manually ground in the sagittal plane with silicon carbide paper (Hermes, 2500) and polished with alumina paste (Struers, AP Paste) to expose the core. Whole otoliths were photographed in a light microscope (Olympus, CX41) coupled to a USB digital camera (Olympus, SC30) at 200 $\times$  and 400 $\times$  magnifications. Images were acquired using a computer program (Olympus, AnalySIS getIT). If needed, successive series of microphotographs from each otolith were made to obtain a complete image of the otolith radius. The quality of the digital images was improved using a free software program (Paint.NET v3.5.10). The diameter and radius of otoliths were measured ( $\mu\text{m}$ ) in their longest axis using a free software program

(Olympus, MeasureIT). To back-calculate the spawning time, 16 days were added to the counted micro-increments, which corresponds to the number of days before hatching (i.e. embryonic period) (Faria *et al.*, 2002). It was also assumed that the first micro-increment represents the hatching check as observed in other related species (Raventós & Macpherson, 2001). The micro-increments in sagittae are deposited on a daily basis in early juveniles of this species (Carvalho *et al.*, 2014). Pelagic larval duration was estimated by counting the daily rings from the hatch check until the settlement marks (McCormick, 1994). Settlement marks in the otoliths were visually identified using the optical density transitions and the abrupt change in increment width(s) (McCormick, 1994). The formation of the settlement marks was recently validated for this species and occur at the transition from the pelagic to the benthic environment in new

settled fish (Carvalho *et al.*, 2015). The number of micro-increments was blind counted by three independent readers and average values were used. Otoliths in which the coefficient of variation was higher than 10% were rejected. The averages of every 10 successive increment widths from the hatch check to the otolith edge were used for otolith growth-increment analysis.

### Sea surface temperatures

Sea surface temperature varies on multiple temporal and spatial scales along the Portuguese coast (Lemos & Sansó, 2006). The mean daily sea surface temperature experienced by each fish during the pelagic larval duration was retrospectively estimated taking into account the date estimated from otolith microstructure (i.e. period of time from the hatching check until the settlement marks) overlapped with the available historical data of the sea surface temperature from the Portuguese coast. The sea surface temperature data were obtained from floating Datawell coastal buoys of the Instituto Hidrográfico da Marinha Portuguesa located nearest the *L. pholis* sampling points and anchored near the 100 m bathymetry (Leixões CSA92/D: WGS 84 - 41°19'N 8°59'W, depth: 83 m; Nazaré CSA88/1D: WGS 84 - 39°33'N 9°12'W, depth: 88 m; Sines CSA83/1D: WGS 84 - 37°55'N 8°55.73'W, depth: 97 m; and Faro CSA82/D: WGS 84 - 36°54'N 7°53'W, depth: 93 m) (Table 1; Figure 1). It was also assumed that *L. pholis* larvae may be locally retained within the coastal environment since rocky intertidal fish larvae appear to be able to avoid off-shore dispersal (Marliave, 1986).

### Data analysis

All data were normally distributed (Shapiro–Wilk's test) with equal variance (Levene's test) after log<sub>10</sub> transformation. One-way analysis of variance (ANOVA) was used to explore the mean differences in pelagic larval duration, size at settlement and age of the recruits between locations (factor), followed by a Tukey post hoc test, if needed. Linear regression analyses were used to examine the relationships between pelagic larval duration and sea surface temperature, and between otolith measurements (otolith diameter and radius) and total length (TL) of recruits. The somatic growth rates obtained from the slopes of the linear regressions between TL and age of the recruits for each site were used to retrospectively estimate the individual size at settlement. One-way analysis of co-variance (ANCOVA) was used to compare the regional somatic growth rates. The age of the recruits was used to back calculate the spawning, hatching and settlement dates (identified through the settlement marks) for each fish. The distribution of these activities over the lunar cycle was also estimated for each individual. The duration of lunar cycle was considered 29.53 days, the new moon was set as the first day of the lunar calendar and each lunar phase was encompassed by the day of each quarter phase  $\pm 3$  days (Sponaugle & Pinkard, 2004). Rayleigh circular statistics were used to test for the occurrence of nonrandom distribution of these activities through the moon cycle (Batschelet, 1981). All analyses were performed according to standard statistical procedures (Zar, 1996). A level of significance ( $\alpha$ ) of 0.05 was used. Data were presented as mean values  $\pm$  standard error (SE).

## RESULTS

Micro-increments were clearly visible between the hatching check and the otolith edge. Two different otolith increment width profiles were observed along the radius of sagittae. A regular increase of the increment width was observed from the hatch check to the following 35 to 55 days (3.0–3.5  $\mu\text{m}$ ) for all individuals/sites. Afterwards there was a decrease of the increment width that reached the initial value (1.5  $\mu\text{m}$ ) at the otolith edge (110 to 120/130 days) for the northern individuals. For the southern individuals after this initial decrease until the 65 days, there was a steady increase in the increment width through the otolith radius with a final drop in the otolith edge. The visual analysis of the plot showed an abrupt increase of the width of increments that took place in the zone where the settlement occurred (40 to 55 days post-hatching) (Figure 2).

The settlement marks appeared to be of two different types (Figure 3). A sharp decrease in increment width across the settlement mark completed within a few increments was categorized type Ia and a multi-increment transition mark was categorized type Ib. These two settlement marks were observed in 62% and 38% of the individuals, respectively.

There were significant differences in the pelagic larval duration of *L. pholis* between sampling regions (ANOVA:  $F_{3,106} = 61.999$ ,  $P < 0.05$ ), except for the two southern locations (Tukey test,  $P > 0.05$ ). There was however a general shortening of the pelagic larval duration from north to south (Cabo do Mundo:  $73 \pm 1$  days; Peniche:  $64 \pm 1$  days; Vale do Homem:  $57 \pm 2$  days; Olhos de Água:  $58 \pm 3$  days) (Table 1). The overall PLD was  $64.4 \pm 0.8$  days (coefficient of variation of 12.4%). The variation of the pelagic larval duration could be explained in 30% by the sea surface temperature (Figure 4).

The overall otolith radius and diameter ranged from 138 to 323  $\mu\text{m}$  and from 263 to 588  $\mu\text{m}$ , respectively. A positive significant correlation was found between the otolith measurements and the fish length (otolith radius:  $Y = 9.56X + 19.38$ ,  $R^2 = 0.82$ ,  $N = 110$ ,  $P < 0.05$ ; otolith diameter:  $Y = 17.99X + 39.90$ ,  $R^2 = 0.86$ ,  $N = 110$ ,  $P < 0.05$ ). A significant positive relationship was also found between fish length and age of the recruits for all the sampling sites (Cabo do Mundo:  $Y = 0.22X + 2.60$ ,  $R^2 = 0.83$ ,  $N = 33$ ,  $P < 0.05$ ; Peniche:  $Y = 0.25X + 2.87$ ,  $R^2 = 0.88$ ,  $N = 38$ ,  $P < 0.05$ ; Vale do Homem:  $Y = 0.29X + 2.37$ ,  $R^2 = 0.88$ ,  $N = 17$ ,  $P < 0.05$ ; and Olhos de Água:  $Y = 0.31X + 2.16$ ,  $R^2 = 0.85$ ,  $N = 22$ ,  $P < 0.05$ ) (Figure 5). The size at settlement was estimated for each individual, but did not present any significant regional differences (ANOVA:  $F_{3,103} = 2.595$ ,  $P = 0.057$ ) (Table 1). The average size at settlement was  $18.9 \pm 0.1$  mm (coefficient of variation was 5.9%). All fishes settled between 18 and 20 mm long.

The age determination of the recruits from *L. pholis* captured at Cabo do Mundo, Peniche, Vale do Homem and Olhos de Água ranged from 57 to 119 days, 50 to 109 days, 45 to 100 days and 49 to 95 days, respectively. There were significant differences in the age of the recruits of *L. pholis* between sampling regions (ANOVA:  $F_{3,106} = 12.769$ ,  $P < 0.05$ ), with the north location recording the older individuals (Tukey - test,  $P < 0.05$ ) (Table 1). Significant differences exist between regional somatic growth rates (ANCOVA:  $F_{3,105} = 3.35$ ,  $P = 0.02$ ), except for the two southern regions (ANCOVA:  $F_{1,36} = 0.36$ ,  $P = 0.55$ ) (Table 1).



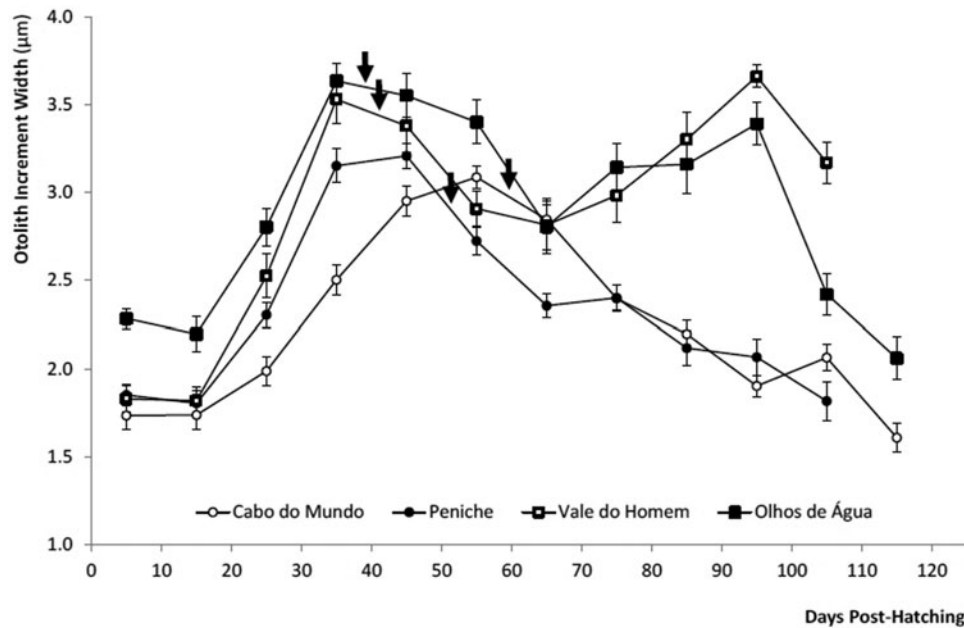


Fig. 2. Profile of the micro-increments width (mean values  $\pm$  standard errors) from the hatch check to the otolith edge. The individuals captured were grouped according to the sampling regions. The settlement mark formation was also identified (black arrows).

The observed frequency dates for the spawning, hatching and settlement of *L. pholis* (Table 1) showed that these biological events occurred during all phases of the lunar cycle, and none of these activities was related with a particular phase of the moon (Rayleigh Tests:  $P > 0.05$ ).

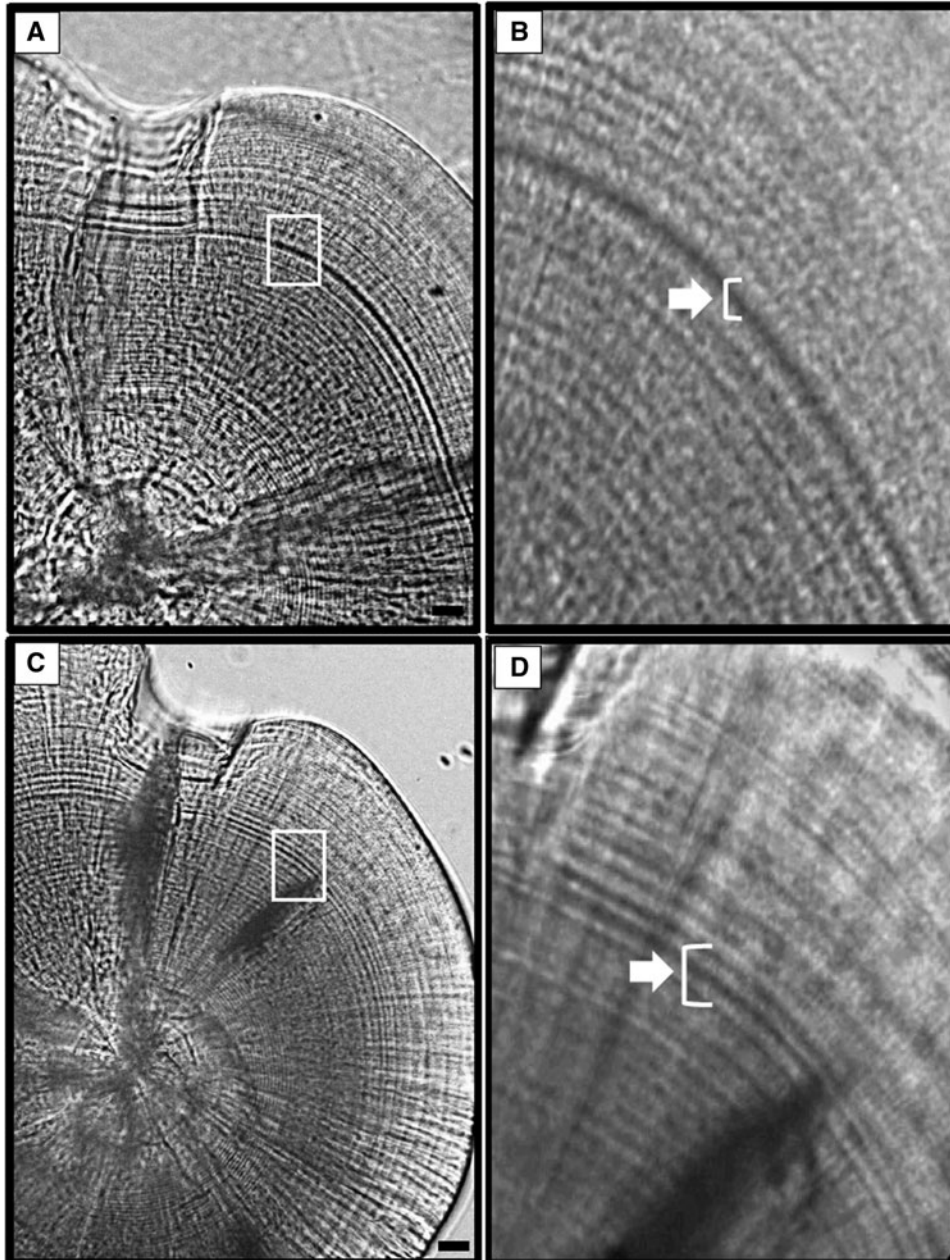
## DISCUSSION

As expected, both otolith morphometric measures showed a good relationship with fish length (TL) (Searcy & Sponaugle, 2001). Furthermore, two settlement mark types were identified, *Ia* and *Ib*, both characterized by a sharp decrease in the increment width and completed within a few micro-increments (Wilson & McCormick, 1999). These settlement marks have already been identified among individuals belonging to Gobiidae, Gobiesocidae and Blenniidae families (Beldade *et al.*, 2007), and occur in the peripheral region of the otoliths of *L. pholis* early settlers (Carvalho *et al.*, 2015). The present results indicate that the most common settlement mark for *L. pholis* was type *Ia* with 62% of frequency. Settlement mark types are known to vary among species, even within the same genus (Wilson & McCormick, 1999). In some cases (e.g. *Gobius xanthocephalus* or *Gobius paganelus*), such as in the present study, two subtypes of settlement marks could even be present within the same species (Beldade *et al.*, 2007). Mark type *Ia* also seems to be the most common settlement mark in more than 40 tropical species (Sponaugle & Cowen, 1994), and appears also to occur in 68% of Mediterranean littoral fishes, including individuals belonging to *Lipophrys* genera, i.e. *L. adriaticus*, *L. caneuae* and *L. trigloides* (Raventós & Macpherson, 2001). The structure of the settlement marks is species-specific, but dramatic reductions in increment width at settlement (i.e. individuals with type *I* settlement-marks) are related to fish in which the timing of settlement differs slightly among individuals due to the influence of the environmental history on the

developing larvae (Wilson & McCormick, 1999). It is plausible that these settlement marks reflect *L. pholis* individuals that settled successfully (type *Ia*) or individuals that settled in an unsuitable (or occupied) habitat and then moved before settling again (type *Ib*).

The estimate of the larval duration from otolith microstructure of *L. pholis* revealed a latitudinal pattern, i.e. a general shortening of the pelagic larval duration from north to south regions. It is well known that variation in pelagic larval duration may result from various environmental factors such as temperature, food availability and local current patterns (Jones, 1986; Lobel & Robinson, 1986; McCormick & Molony, 1995). In the present study the shorter pelagic larval duration occurred in the regions with warmer seawater temperatures (Vale do Homem and Olhos de Água); in contrast, the longest pelagic larval duration occurred in Cabo do Mundo, the region with the coldest seawater. Furthermore, 30% of the variation in pelagic larval duration was explained by individual mean temperatures experienced by larvae calculated from local sea surface temperature. These results corroborate that temperature is a dominant influence on pelagic larval duration, which decreases exponentially with increasing temperatures across species and populations of marine fish (McCormick & Molony, 1995; Benoit *et al.*, 2000; Green & Fisher, 2004). Results obtained for other tropical reef fish also reported that seawater temperature changes accounted for about 30% of the variation in larval growth (McCormick & Molony, 1995; Meekan *et al.*, 2003; Sponaugle *et al.*, 2006). Moreover, the effect of water temperature on larval growth leads to important environmental effects on the recruitment success (Sponaugle, 2010).

Daily growth for a fish can be indirectly obtained by examining the width between successive increments in otoliths. The comparison of increment widths during a particular stage of life among individuals could provide a relative measure of somatic growth (Green *et al.*, 2009). Otolith increment widths recorded in *L. pholis* are consistent with the values



**Fig. 3.** Light microscope images of two otoliths of *Lipophrys pholis* individuals collected in Cabo do Mundo (A: TL = 21 mm; age = 84 days; C: TL = 23 mm; age = 100 days) showing in a zoomed selected area (white boxes) the type Ia (B) and Ib (D) settlement marks (white arrows). 200 $\times$  magnification. Scale bar = 10  $\mu$ m.

reported for other related fish families (Wilson & McCormick, 1999). Moreover, micro-increment widths measured in *L. pholis* otoliths showed a regional variation and sites with higher sea surface temperatures had higher otolith growth rates, which is particularly evident in the peripheral rings. The effect of environmental factors in the daily growth pattern of otoliths during the fish's early life stages have been extensively studied using time-series data analysis (Maillet & Checkley, 1991; May & Jenkins, 1992; Searcy & Sponaugle, 2001), and it is generally accepted that there is a positive relationship between otolith growth rate and temperature (Campana & Neilson, 1985). Observations, both in the field and in the laboratory, have shown that micro-increment width may change in response to temperature

and diet, although the period of micro-increment deposition remained daily (Morales-Nin, 2000). Recently a field study showed that for fish larvae (*Sprattus sprattus*), otolith width increments could be closely related with *in situ* water daily temperatures (Baumann *et al.*, 2006). These results are, as expected, coincident with the somatic growth rate which was positively related with temperature, and northern fish presented a slow somatic growth compared with the most southern individuals.

The size at settlement of *L. pholis* appears to be, however, a conservative characteristic in this species. No significant differences were observed in the size at settlement for the sampling areas. Fish settled when around 19 mm long. These results are in agreement with regular field observations of

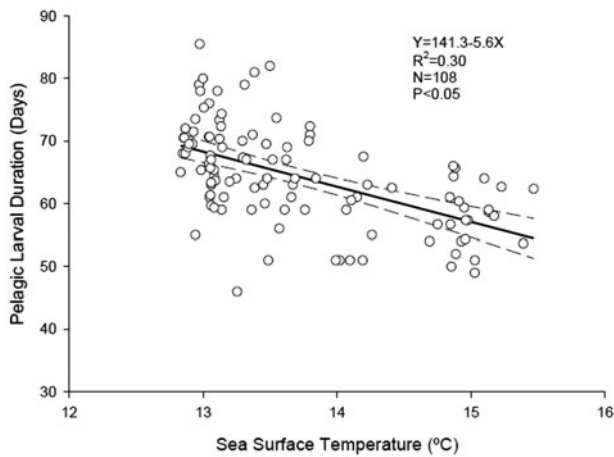


Fig. 4. Relationship between the pelagic larval duration and the average surface seawater temperature experienced by each individual over the period between hatch and settlement. The dotted lines represent the 95% interval for the linear regression.

the smallest fish found in tide pools which are on average 17.4 mm and behave like benthic juveniles (Faria *et al.*, 2002). Furthermore, it suggests that fish need to reach a minimum size to begin the settlement process. This could easily explain why southern fish settled earlier than northern individuals. If settlement is triggered by a minimum size, fish with lower growth rates should reach this minimum size later. In general the variation in size is less than variation in age at metamorphosis for marine fish and the required size may ameliorate competitive effects and reduce the risk of predation in the period immediately following metamorphosis and settlement (Chambers & Leggett, 1987). This agrees with the 'competent size' hypothesis which defends the idea that a flexible pelagic larval duration is needed to maximize competent size, because environmental conditions may change within a season and among years (Pastén *et al.*, 2003). As *L. pholis* individuals need to reach a certain size to settle it can be hypothesized that in northern and colder waters the pelagic larval duration should be long and the settlement success therefore limited compared with further south. It means that the survival to the larval stage driven

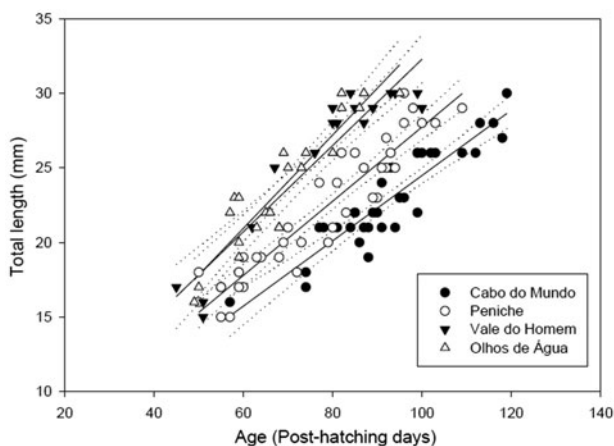


Fig. 5. Linear relationships between length and age at capture for the recruits for each sampling region. The dotted lines represent the 95% intervals for the linear regressions.

by water temperature could be an explanatory factor of the overall geographic distribution of the species.

It is known that various life history events for fish species that inhabit temperate and higher latitudes are often synchronized with periodic changes according to the moon-related cycles (Takemura *et al.*, 2010). In this study, the examination of spawning, hatching and settlement dates of *L. pholis* surviving individuals suggests that these biological events were apparently acyclic and continuous over the lunar cycle. Similar results were described for the spawning of *Ophioblennius steindachneri* (Robertson *et al.*, 1990) and *Thalassoma bifasciatum* (Sponaugle & Pinkard, 2004; Sponaugle *et al.*, 2006). Furthermore for *Sebastes inermis* the parturition dates were uniform within years over the lunar cycles in almost all settlement groups (Pastén *et al.*, 2003). These results are consistent with previous reproductive studies for *L. pholis* which showed that it is an asynchronous spawner, with eggs being produced in several batches during the breeding season (Ferreira *et al.*, 2012). It is possible that the asynchronous production of multiple batches function as a bet hedging strategy, allowing the eggs to be distributed among several males, thus reducing the risks of complete loss of progeny because of inadequate mate choice, environmental constraints and failure in larval recruitment, among other equally valid causes (Morrongiello *et al.*, 2012). Regarding hatching and settlement events, both were also randomly distributed over the lunar cycle. Settlement patterns scattered throughout the lunar cycle have not been documented for any other species. For the gobiidae *Coryphopterus glaucofraenum* for instance, settlement appears to occur in several large pulses associated with various lunar phases (Sponaugle & Cowen, 1994). A plausible explanation can be supported by the fact that flexible pelagic larval duration in *L. pholis* may enable larvae to synchronize settlement to optimal environmental conditions (Sponaugle & Cowen, 1994).

In summary, this study found significant regional biological differences in pelagic larval duration and somatic growth rate of *L. pholis* showing a latitudinal pattern along a moderate (1.8°C) sea surface temperature gradient. A consistent size at settlement was found in all sampled sites which emphasizes the fact that fish need to reach a minimum size to begin to settle. Longer planktonic periods in northern waters than in southern waters suggest that slow-growing juveniles remain in the plankton until they reach appropriate size, perhaps in response to environmental conditions, namely due to sea water temperature exposure. However, given the small dataset and a few uncertainties of some methodological aspects of the present approach, these results should be interpreted with caution. More information about the movement patterns, population structure and habitat connectivity in *L. pholis* is needed in order to improve the scientific knowledge about this species.

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