

Planktonic duration in fourteen species of intertidal rocky fishes from the south-eastern Pacific Ocean

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Abstract. The planktonic duration (PD) was determined in fourteen intertidal rocky fishes from the south-eastern Pacific Ocean by counting the otolith micro-increments from hatch check to a transition mark (TM). TMs were validated by comparing the PDs estimated from post-settlers with the total increment counts from otoliths of more recent (new) settlers. In 11 species (79%), the most common TM corresponded to a notable decrease in increment width after settlement. The PDs ranged from 45 days in the kyphosid *Girella laevis* to 135 days in the labrisomid *Auchenionchus variolosus*, and eight species (57%) had mean PDs of longer than three months. The mean observed size-at-settlement (SAS_M) values ranged from 17.5 ± 7.2 mm TL in *Gobiesox marmoratus* (Gobiesocidae) to 40 ± 5.5 mm TL in *Calliclinus geniguttatus* (Labrisomidae) and showed low variability within species of the same family. PDs were markedly longer in intertidal rocky fishes than in other littoral and reef fishes in tropical and temperate waters. A lengthy and variable duration of the pre-settlement phase, along with a relatively consistent size-at-competence within closely related species, are suggested as mechanisms through which these fishes may increase their probability to settle in the spatially restricted habitat of exposed rocky pools.

Additional keywords: intertidal fishes, otolith increment, settlement

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Introduction

Most demersal fishes have a pelagic larval phase that, in combination with dispersal and settlement processes, can influence their biogeographic ranges and recruitment patterns as well as the connectivity among populations (Victor 1986b; Cowen and Sponaugle 1997; Hickford and Schiel 2003; Geffen *et al.* 2011; Kingsford *et al.* 2011; Kohn and Clements 2011). The information gathered to date has demonstrated a significant variability in pelagic larval duration in these fishes, ranging from a few days to several months within and among species (Bay *et al.* 2006; Kingsford *et al.* 2011; Macpherson and Raventós 2006; Kohn and Clements 2011). Most studies have suggested that the distribution ranges of fishes are likely controlled by factors other than the duration of the planktonic phase (Victor and Wellington 2000; Macpherson and Raventós 2006; Kingsford *et al.* 2011). In other studies, a fixed larval duration has been associated with synchrony between the timing of spawning and subsequent settlement (Robertson *et al.* 1990; Meekan *et al.* 1993), whereas a variable larval duration appears to be

associated with specific environmental conditions (e.g. lunar or tidal periods) to maximise settlement at a competent size (Victor 1986b; Sponaugle & Cowen 1994; Cowen and Sponaugle 1997; McIlwain 2002; Plaza-Pastén *et al.* 2003; Hale *et al.* 2009). In contrast, a positive correlation between larval duration and growth rate has been reported in several studies (Shiao *et al.* 2002; Shima and Findlay 2002). Thus, the extent to which pelagic larval duration is either ecologically based or mediated by the pivotal influence of growth rate, which is itself associated with the concomitant effects of variations in temperature and productivity, is unclear (Victor 1986a).

Studies of the pelagic larval duration of demersal fishes have been carried out mainly in tropical areas and temperate waters in the Northern Hemisphere using settlement marks recorded in their otoliths, which are associated with the change from pelagic to benthic life (Victor 1982; Victor 1986a; Victor 1986b; Kingsford and Milicich 1987; Wellington and Victor 1989; Sponaugle and Cowen 1994; Wilson and McCormick 1997; Jenkins *et al.* 1996; Raventós and Macpherson 2001; Soeparno

et al. 2012). This method, developed by Victor (1982), allows pelagic larval duration to be determined by counting the number of primary increments from hatching to the settlement mark. Pelagic larval duration data collected using this methodology in the Southern Hemisphere are more scarce (but see Kingsford and Milicich 1987; Kingsford 1990; Jenkins and Black 1994; Hamer and Jenkins 1997; Buratti and Santos 2010; Kohn and Clements 2011). The lack of studies is particularly evident in intertidal fishes that after a pelagic life recruit to intertidal areas to use rocky pools either as a transitory habitat during their juvenile phase or as a permanent residence over their entire life. New recruits must cope with many biotic and abiotic factors due to the temporal and spatial limitations of rocky pools (Gibson 1982; Metaxas and Scheibling 1993; Pulgar *et al.* 2006). Hence, it is reasonable to hypothesise that such a dramatic change in environment would be recorded as transition marks in their otoliths, similar to those reported to characterise the settlement process from pelagic to subtidal benthic life in other reef fishes; consequently, it should be possible to determine the duration of the pre-settlement phase before intertidal fishes are recruited into rocky pools. These groups of fishes are good models with which to provide a wider framework of pelagic larval duration for comparative purposes because they encompass a variety of phylogenetically related families of fishes that are distributed worldwide. Therefore, the present study aimed to determine the durations of the pre-settlement phases of fourteen species of intertidal rocky fishes in the south-eastern Pacific Ocean using the transition marks recorded in their otoliths.

Materials and methods

Study area and sampling methods

The juvenile fish used in the present study were collected from rocky intertidal pools at three localities separated by ~10 km of sandy beaches along the central Chilean coast: Las Cruces (LC: 33°30'S; 71°37'W), El Tabo (ET: 33°31'S; 71°40'W), and Isla Negra (IN: 33°24'S; 71°43'W). The oceanography and coastal hydrography of the study areas have primarily been described based on the area between IN and LC (Hernández-Miranda *et al.* 2003; Aiken *et al.* 2007). Juveniles were captured with hand nets, aided by the use of 20% benzocaine (BZ-20), on a monthly basis from April 2010 to December 2011. The captured fish were placed in labelled plastic bags and transported to the laboratory, where they were measured to the nearest 0.1 mm in total length (TL). The collected specimens were preserved in 95% ethanol until they were examined in the laboratory. Overall, 1250 juveniles ranging from 13 to 175 mm TL and belonging to fourteen species were collected during the study period.

Otolith extraction and preparation procedures

The left and right sagittae and lapilli from all species were removed from preserved juveniles under a dissecting microscope. Sagittae were stored in polyethylene microvials, mounted in epoxy resin on slide glasses and then polished with 800- to 2000-grit lapping films and 4000-grit grinding paper until the nucleus became clearly visible. Once extracted, the left and right lapilli were immediately fixed on a small drop of transparent fingernail varnish and then smoothly polished on only one side

for ~30 s with a fine lapping film (400 grit; 3 µm). Counts of the daily increments were made across an area of distinctive primary increments from the first check surrounding the primordium along the longest (rostral) axis, including both pre- and post-settlement increments. All counts and measurements of primary micro-increments were carried out using an image analysis system composed of a light microscope, a CCD camera and measurement software (Leica Application Suite; LAS EZ ver 1.8.0) at magnifications of 400–1000×. The primary increments in both the sagittae and lapilli were distinctive in most species, but in clinids and gobids, the increments in the lapilli become very narrow. Hence, measurements from the sagittae were used throughout the present study to ensure consistency among species. The daily periodicity of primary increments has been validated in *Scartichthys viridis* (Hernández-Miranda *et al.* 2009), and recently for juveniles of the following eight intertidal fishes in central Chile (Mansur *et al.* in press): *Helcogrammoides chilensis*; *Helcogrammoides cunninghami* (Tripterygiidae); *Auchenionchus microcirrhoides*; *Auchenionchus crinitus* (Labrisomidae); *Hypsoblennius sordidus* (Blenniidae); *Gobiesox marmoratus*; *Syngnathus sanguineus* (Gobiesocidae); and *Myxodes viridis* (Clinidae). For the remaining five species, the periodicity of the formation of primary increments was assumed to be daily based on previous studies of other intertidal fishes (Kohn and Clements 2011; Soeparno *et al.* 2012). No significant differences in increment number between the left and right sagittae were found in six species for which more data were available (*A. microcirrhoides*, *Girella laevis*, *H. chilensis*, *S. viridis*, *G. marmoratus* and *S. sanguineus*; Table 1). Hence, the mean counts from three replicates, made by the same observer, taken from otolith sections with distinctive increments, irrespective of otolith type, were used for age determination; when counts differed by more than 5%, the sample was rejected. A total of 908 otolith samples satisfied our criteria and were used for further otolith analyses (Table 1).

Planktonic duration (PD) was defined as the number of days between the first well-defined increment near the primordium to a transition mark recorded in the sagittal otoliths of each species. The term 'planktonic duration' was used instead of 'pelagic larval duration PLD' because the juveniles of these species settle into intertidal pools as already transformed juveniles. In addition, it is unclear whether these fishes are exclusively pelagic during their entire pre-settlement phase or whether they have a temporal subtidal permanence before settling in intertidal pools. To determine whether the transition zone was linked to the settlement of juveniles into intertidal pools, the otolith microstructure features of recently settled fish were characterised to identify the presence and/or absence of settlement marks. Because fish that have recently settled into intertidal pools are expected to be already transformed juveniles, they were identified using a quantitative approach rather than the description of their morphological characteristics. The juveniles collected were considered recently settled fish if they were shorter than the observed overall minimum mean size-at-settlement (MSAS_M). The SAS_M for each species was determined using a historical database of monthly fish size surveys taken from 1997 to 2012, using catch-and-release procedures described by Hernández-Miranda and Ojeda (2006) as part of a protocol to

Table 1. Overall statistics (mean, range and variation coefficient, VC) of total length, planktonic duration (PD) and observed size-at-settlement (mSAS) of fourteen species of intertidal fishes collected in Central Chile from April 2010 to December 2011

Sc: species code; n: number of otoliths analysed; Years: the number of monitoring years from which mSAS was obtained; M = mean; Tm: transition mark type; AP: accessory primordia; Yr: year; Tn: total number of fish collected and released across years as part of the monthly monitoring procedures; SpS: spawning strategy. Tk: denotes Tukey's post-hoc tests after rejecting the null hypothesis of the absence of significant differences in mean PD among species. Different letters denote significant differences at $\alpha = 0.05$

Family/species	Total length (mm) of all fish collected in rock pools			Planktonic duration (days) based on transition marks				Planktonic duration (days) based on total age of new settlers				Transition marks in otoliths		Observed size-at-settlement (mm) based on an historical database				SpS		
	M	Range	Vc	M	Range	VC	n	Tk	M	Range	VC	n	Tm	Ot	M	Range	Vc		Yr	Tn
Labrisomidae																				
<i>Auchenionchus crinitus</i>	50.5	25–117	52	73.0	56–92	19	13		75.3	65–83	12	3	I	S	26.5	26–28	5.3	2	31	Benthic
<i>Auchenionchus microcirrhitis</i>	46.4	22–165	73	71.5	57–89	21	80	a	73.5	52–89	20	7	I	S	28.2	21–45	19	16	4,311	Benthic
<i>Auchenionchus variolosus</i>	86.1	40–120	34	110.6	82–138	26	6		112.2	1			I	S	39.5	30–49	21	4	229	Benthic
<i>Calliclinus geniguttatus</i>	48.7	34–87	41	107.5	83–135	21	7		110.6	92–120	10	4	II	S	40.0	30–49	14	3	222	Benthic
Bovichtidae																				
<i>Bovichthys chilensis</i>	61.8	49–121	20	88.0	60–95	13	56						I	S	34.5	20–48	26	15	3,199	Pelagic
Kyphosidae																				
<i>Girella laevisfrons</i>	82.3	27–141	40	68.6	55–77	15	70	b					AP	S	24.2	15–32	26	13	8,095	Pelagic
<i>Graus nigra</i>	98.9	60–151	26	65.4	58–76	13	26	b					AP	S	25.8	15–39	28	13	5,257	Pelagic
Tripterygiidae																				
<i>Helcogrammoides chilensis</i>	35.0	25–73	25	95.2	78–115	25	190	a	96.3	80–113	11	10	I	S	25.5	25–3	13	16	15,858	Benthic
<i>Helcogrammoides cunninghami</i>	35.0	29–50	17	75.3	59–95	15	27	c					I	L	25.4	2–3	12	16	4,194	Benthic
Blenniidae																				
<i>Hypsoblennius sordidus</i>	45.3	28–86	31	88.0	76–100	19	70	e	92.5	83–108	10	6	I	S	28.4	22–35	15	16	3,346	Benthic
<i>Scartichthys viridis</i>	83.5	42–175	33	97.8	72–124	22	222	a					I	S	30.2	12–45	28	16	39,456	Benthic
Clinidae																				
<i>Myxodes viridis</i>	69.3	29–112	43	95.0	69–118	24	13		98.2	92–105	6	4	I	S	29.5	27–32	7.8	4	28	Benthic
Gobiesocidae																				
<i>Gobioxos marmoratus</i>	43.7	13–102	44	72.5	61–98	29	105	c	74.5	65–88	10	8	I	S	17.5	12–40	41	16	2,728	Benthic
<i>Sicyases sanguineus</i>	43.7	13–102	44	76.6	59–100	31	115	c	78.2	66–99	12	12	I	S	22.0	11–35	32	11	743	Benthic

monitor growth in the intertidal pools in the study area. These data were used to calculate SAS_M as follows:

$$SAS_M = \frac{1}{n} \sum_{i=1}^n a_i$$

where 'a' corresponds to the size of the shortest fish collected in each year and 'n' is the number of years from which data are available.

To validate the transition mark, the increment number (i.e. total age) of recently settled fish was related to the duration of the pre-settlement phase of older fish, calculated based on the transition marks in the otoliths. The relationship was built across species and not using individual fish; i.e., each plot corresponded to a mean value of the relationship between mean observed PD (derived from recently new settlers; see Fig. 2 in 'results') and mean PD determined using otolith settlement marks. A significant linear regression of the form $Y = a + bX$ with slope ($b = 1$) was used to indicate that otolith-based determinations of the pre-settlement phase using transition marks are reliable. The PDs of the fourteen species were compared using a one-way ANOVA along with a post-hoc Tukey's test after confirming the assumptions of normality and homogeneity of variance.

Results and discussion

Transition mark types in otoliths

A characteristic feature of the sagittal otoliths of fishes collected in intertidal pools, irrespective of species and families, is the existence of a marked shift from opaque to hyaline deposition when otoliths are viewed under induced light using a stereomicroscope (Fig. 1a, a_1). This macro-structural feature was either absent or present very close to the edges of the otoliths in recently settled fish of the nine species for which recently settled juveniles were available (Table 1). At the micro-structural level, the shift from opaque to hyaline deposition coincided with the presence of transition marks (TM; Fig. 2b). The most common TM was either a prominent concentric check or a very wide perturbation followed by a marked decrease in increment width (Fig. 1b, c_1 , d). This transition mark type occurred in 11 (79%) of the 14 species, irrespective of fish size. Type III transition marks were restricted to blenniids and tripterygiids (27%) and were characterised by a gradual decrease in increment width. For the kyphosids *G. laevisfrons* and *G. nigra*, the shift from opaque to hyaline deposition was more irregular due to the occurrence of new growth centres (accessory primordia; AP; Fig. 1e) from which wider primary increments were initiated. Because no recently settled fish of this species were available for analysis, the position of the innermost AP was used to determine the duration of the pre-settlement phase.

Planktonic duration

The relationship between the mean total age of recently settled fish (independent variable) and the mean duration of the pre-settlement phase (dependent variable) across species was significantly linear ($Y = a + bX$; $a = 1.03 \pm 0.059$; $b = -7.26 \pm 5.84$; $r^2 = 0.97$; $n = 9$ species; $F_{(1,7)} = 1525.17$; $P < 0.001$; Fig. 2), showing an equivalence between estimations of the

pre-settlement phase made by ageing recently settled fish (Fig. 1e) and using the otolith transition marks (t-test; $t_{cal} = 0.40 < t_{\alpha(0.05)} = 3.59$; d.f. 7). The length of the pre-settlement phase calculated based on otolith transition marks was highly variable across species, ranging from 55 days in *G. laevisfrons* to 135 days in *Auchenionchus variolosus* (VC 19–31%; Table 1). The highest and lowest mean values were restricted to labrisomids (102.6 ± 14.2 days) and kyphosids (67.0 ± 2.3 days), respectively. A one-way ANOVA carried out in 10 species (with sufficiently large sampling sizes) showed significant differences in the mean duration of the pre-settlement phase, although members of the same family tended to exhibit similar mean values (Tukey *t*-test, Table 1). SAS_M ranged from 17.5 mm TL in *Gobiesox marmoratus* to 40 mm TL in *Calliclinus geniguttatus*. There was no clear pattern in SAS_M across families, although species with larger mean SAS_M values (independent variable) tended to have longer mean pre-settlement phases (dependent variable) ($Y = a + bX$; $a = 32.21 \pm 12.49$; $b = 1.89 \pm 0.43$; $r^2 = 0.61$; $n = 14$ species; $F_{(1,12)} = 18.38$; $P < 0.001$; Fig. 3).

Settlement mark types

A distinctive finding that emerged from the current study is that the presence of a very distinctive transition mark in both the macro and micro-structure of otoliths is linked to fish settlement in intertidal pools, irrespective of otolith type or species. A sharp decrease in increment width after a transition mark in otoliths was the most common TM pattern found across species. This pattern was similar to the Type I (a & b) settlement marks described by Wilson and McCormick (1999) in tropical reef fishes and also similar to findings from other studies that aimed to determine planktonic larval duration in intertidal and tidal habitats in temperate waters (Raventós and Macpherson 2001; Wilson and McCormick 1999; Ahrenholz and Morris 2010; Beldade *et al.* 2007; Kohn and Clements 2011). The reduction in increment width after fish settle in intertidal rocky pools is expected because these ontogenetic movements involve a drastic change in lifestyle, during which fish must cope with changing environmental conditions and the limited, enclosed nature of intertidal pools (Gibson 1982; Jordaan *et al.* 2011). Moreover, the transition mark coincided with a change from opaque to hyaline deposition irrespective of otolith type and species. Because this feature can be easily measured using a stereomicroscope, size-at-settlement can be back-calculated without polishing the otoliths. This finding could be very useful for further studies related to the characterisation of size-at-settlement in these species on larger spatial and temporal scales. For the kyphosids *G. laevisfrons* and *G. nigra*, the opaque-hyaline transition was somewhat more variable due to the occurrence of accessory primordia, and this feature was used to determine the duration of the PD. Similar phenomena have been reported in other demersal fishes, in which similar structures were observed (Toole *et al.* 1993; Modin *et al.* 1996; Gunnarsson *et al.* 2010).

Planktonic duration size and size-at-settlement

In the present study, the PD was highly variable across species, ranging from 50 to 135 days, with overall mean values close to

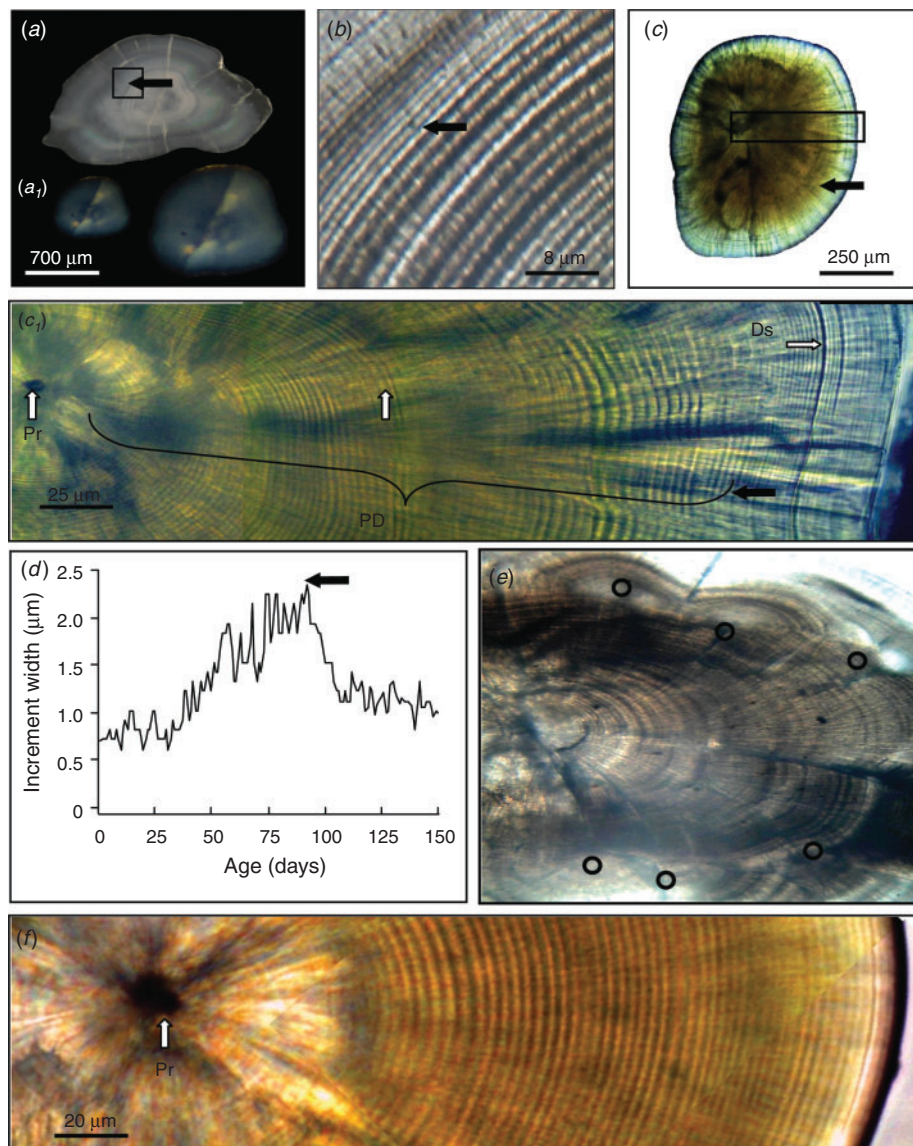


Fig. 1. Transition zones (transition mark (TM): filled arrows) in the otoliths of intertidal fishes collected in rocky pools in Central Chile. Illustration of the presence (a) and absence (a₁: left: normal scale; right: 100% magnification) of TMs (Type) in sagittae from a 95.8 and 22.3 mm TL *Auchenionchus microcirrhys*, respectively, viewed under a stereomicroscope. A magnification of microstructural feature of TM (b), microstructure view (c, c₁) and increment width profile (d) of TMs in a lapillus from a 39.5 mm TL *Helcogrammoides cunninghami*. Enclosed circles denote accessory primordia in a juvenile *Graus nigra* (e). Absence of TM in a recently settled juvenile *Sicyases sanguineus* (f: 18.5 mm TL). Pr: primordium; PD: planktonic duration; Ds: discontinuities.

three months. The observed high variability in PD is consistent with previous works on coastal fishes from tropical and temperate waters, which have also reported high variability in the duration of the pelagic phase using similar methodologies. However, the PDs obtained in the present study sometimes extended far beyond the upper limit of the pelagic larval duration (PLD), which were previously reported as between 5–70 days for reef fishes in tropical waters (Victor 1986a; Wellington and Victor 1989). In a later study, Raventós and Macpherson

(2001) reported PLDs for 42 species of Mediterranean littoral fishes, showing a high variability within species and families, and ranges from 9 to 77 days, while blenniids and tripterygiids had mean PLDs < 20 days. Similarly short PLDs (< 30 days) have also been reported in other triplefin fishes (Longenecker and Langston 2005; Riginos and Victor 2001).

Some recent studies have also reported relatively short PLDs for species of tropical gobiids (15.25 ± 2.5 days; Bay *et al.* 2006) and a temperate pomacentrid (15–17 days, Kingsford

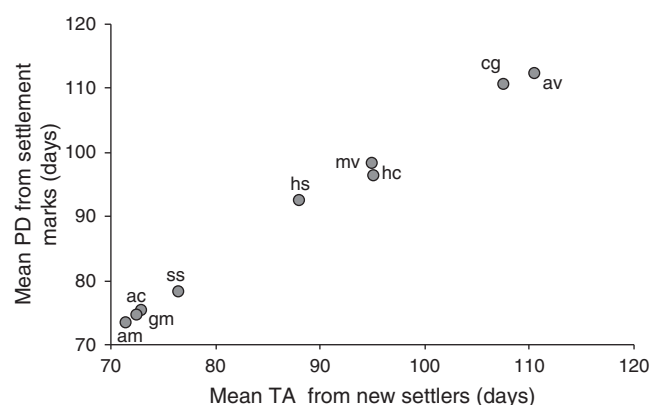


Fig. 2. Scatterplots of the relationship between the mean total age (TA) of new settlers and mean planktonic duration (PD) determined using the transition marks in sagittal otoliths of intertidal fishes collected in rocky pools in Central Chile. Letters close to the plots denote the code associated to the scientific name included in Table 1.

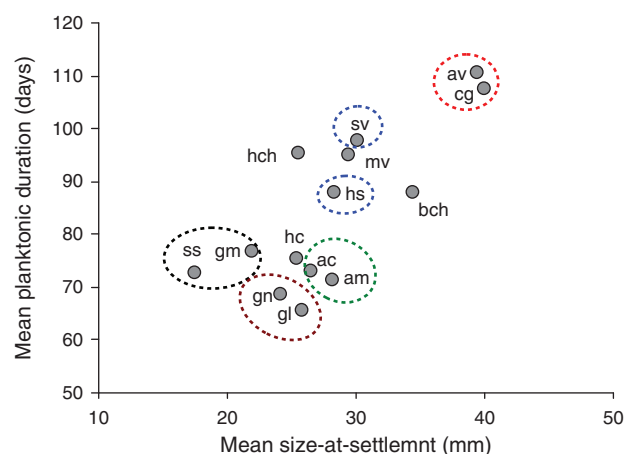


Fig. 3. Scatterplots of the relationship between the mean size-at-settlement and mean planktonic duration, determined using the transition marks in sagittal otoliths of intertidal fishes collected in rocky pools in Central Chile. Letters close to the plots denote the code associated to the scientific name included in Table 1. Plots enclosed by dashed lines denote closely related species.

et al. 2011). Additionally, Beldade *et al.* (2007) reported PLDs ranging from 11 to 39 days for 10 species of cryptobenthic fishes (Gobiidae, Gobiocidae and Blenniidae). A more recent study of 35 species of tropical fishes in Japanese waters also reported relatively short PLDs, ranging from 13 to 36 days (Soeparno *et al.* 2012). Although the PD *per se* can vary within individual and species, there is sufficient evidence that the PDs of the intertidal rocky fishes in the current study are longer than those of their counterparts in tropical and warmer temperate waters. A comparison of our results with data from the Southern Hemisphere demonstrates that our recorded PDs are similar to those from a previous study on triplefin fishes from cold temperate waters in New Zealand, where PDs of more than two months were reported for the juveniles of some species collected in

intertidal pools (Kohn and Clements 2011). Further evidence supporting the long planktonic durations found in the present study may be found in two recent studies on early life history traits determined using otolith microstructure analysis for the planktonic larvae of two clingfishes (*G. marmoratus*, *Sicyases sanguineus*; Contreras *et al.* 2013) and the triplefin *Helcogrammoides chilensis* (Palacios-Fuentes *et al.* 2012) in the same geographic location off the coast of central Chile. The oldest and largest larvae aged for both clingfish and the triplefin fish were ~one month at ~7 mm TL and ~57 days at ~16 mm TL, respectively. These size values are markedly shorter than the mean sizes-at-settlement observed in the current study (18–20 mm TL), suggesting that these species can indeed remain in pelagic or subtidal waters for longer periods before settling into intertidal rocky pools as early juveniles.

The long PDs of intertidal fishes reported here could be linked to the oceanographic conditions associated to the Humboldt Current System (HCS). In the HCS, Ekman transport is an intrinsic driving force for the dispersal of eggs and larval fishes at speeds of $\sim 0.2 \text{ m s}^{-1}$ in central Chile (Strub *et al.* 1998; Cowen *et al.* 2000). Under the influence of such a mechanism, it is reasonable to expect that larvae and/or early juveniles require a long time to reach intertidal areas, even with active swimming. Furthermore, the water column of nearshore zone off central Chile, where most of these fish species inhabit during their early development (Hernández-Miranda *et al.* 2003; Landaeta *et al.* 2009; Palacios-Fuentes *et al.* 2012; Contreras *et al.* 2013), is characterised by the presence of cold waters during the upwelling season (from August to March) and large diurnal fluctuation in temperature (12–16°C) (Kaplan *et al.* 2003). Because of the cold waters, long pelagic durations are expected to occur, as it has been described for the blenny *S. viridis* (92–106 days, Hernández-Miranda *et al.* 2009) and triplefin *H. chilensis* (>60 days, Palacios-Fuentes *et al.* 2012). Most of these species have a wide latitudinal distribution along the Chilean coast (Ojeda *et al.* 2000) and it is expected that at the edge of their natural distribution (around 44°S), PD will be the largest.

The planktonic duration of any larva will be a product of the conditions encountered by the larvae in the plankton, such as food and temperature (McCormick and Molony 1992; Meekan *et al.* 2003; Bay *et al.* 2006), and temperature alone is considered a good predictor of PD (Sponaugle 2010). In this scenario, the early life stages of these species are subjected to the effects of both dispersal and low temperatures associated with the cold-water HCS, which would be consistent with the long PDs observed in the present study. However, most of the intertidal fishes analysed are benthic or demersal spawners (Herrera 1984; Table 1) with a marked inshore distribution of their larval stages <500 m from shore (Hernández-Miranda *et al.* 2003), which would favour settlement at relatively short PDs and small size-at-settlement. Additionally, the circulation patterns at 33°S in nearshore waters in Central Chile may increase coastal retention by density fronts caused by upwelling events (Hernández-Miranda *et al.* 2003), river plumes and/or coastal geometry (Palma *et al.* 2006). Given these factors, the mechanisms underlying the long PD observed in the present study remain unclear.

An extended planktonic period would also suggests that the young-of-the-year (YOY) of these species delayed settlement,

perhaps to increase the chance of finding suitable conditions (e.g. onshore tidal flow) within rocky pools, as has been suggested for other reef fishes (Victor 1986a, Victor 1986b, Sponaugle and Cowen 1994, Jenkins and May 1994; McCormick 1999). For example, Cowen (1991) proposed that a long competence period would occur when settlement sites are very restricted, as is the case of rocky pools in the exposed Chilean coast. A similar scenario was proposed by Jenkins and May (1994) to explain the PDs between 100 and 150 days for the King George whiting *Sillaginoides punctata*, which settles in very restricted seagrass sites in a coastal area in southern Australia. A restricted settlement site would not only impose limitations on finding a suitable onshore circulation event, but also trigger intra- and site-specific competence after settlement in species that must share a temporally and spatially limited habitat. In addition, after settlement, the YOY of these species must cope with drastic changes in salinity and temperature on a daily basis due to the tidal cycle. Hence, it is reasonable to hypothesise that long and flexible PDs, which may be a result of the pivotal influence of hydrographical conditions associated with the HCS, combined with a strategy of reaching a specific size at competency, would enhance the probabilities of successfully arriving and adapting to the conditions of rocky pools. In the current study, the mean sizes of recently settled fish showed little variation within species of the same family, arguing in favour of a specific size for competence to settle in closely related species. This finding is consistent with previous studies in other demersal fishes, where size at competency was reported when long PDs were observed (Jenkins and May 1994; Plaza-Pastén et al. 2003).

As a corollary, the present study showed evidence of long but variable PDs along with relatively low variation in size-at-settlement in fourteen species of intertidal fishes in the south-eastern Pacific Ocean. It is unclear whether the existence of a lengthy PD is a generalised process across intertidal fishes associated with settlement in rocky pools and/or similar restricted habitats. This question deserves further research, which will ultimately reveal the ecological mechanisms that intertidal fishes have developed to successfully colonise new habitats and extend their geographic distribution ranges.

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