

Seasonal variations in early life traits of *Sindoscopus australis* (Blennioidei: Dactyloscopidae): hatching patterns, larval growth and bilateral asymmetry of otoliths

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Early life traits (ELT) of the sand-burrowing cryptic marine fish Sindoscopus australis (family Dactyloscopidae) were compared between cohorts hatched during winter and spring 2013, in nearshore rocky reefs off central Chile. Pelagic larvae were similarly abundant during both periods, but larger larvae were collected during austral spring. The sagittal otolith microstructure and size analyses also indicated that size-at-hatch was larger (4.7 mm) for the winter cohort, but winter larvae experienced slower growth rates ($0.145 \text{ mm day}^{-1} \pm 0.008$). Conversely, larvae from the spring cohort hatched at smaller sizes (2.9 mm), but they grew faster ($0.182 \text{ mm day}^{-1} \pm 0.008$). Hatching periods were coupled with the lunar cycle; in winter, hatching events were related to neap tides (first and third quarter moon), increasing chances of self-recruitment. Meanwhile, during spring, hatching occurred during spring tides, particularly over the new moon, decreasing chances of larval mortality by predation. Otolith traits used to test asymmetry among cohorts showed inconsistent results. Only sagittal perimeter presented fluctuating asymmetry, showing higher variance for the winter cohort. We conclude that this burrowing species displays different reproductive tactics at a seasonal scale.

Keywords: otolith, Dactyloscopidae, sand stargazer, larval growth, nearshore

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INTRODUCTION

Marine fish species use different reproductive tactics to reduce mortality during their early life stages. Among the tactics employed, spawning may occur at mid depths at the shelf-break during upwelling events, increasing the chances of egg and larval onshore transport (e.g. hakes, Grote *et al.*, 2012; Landaeta & Castro, 2012). Small pelagic species, such as anchovies and sardines, spawn in surface waters during the austral winter, when the Coriolis effect is driven by northern winds increasing coastal retention (Castro *et al.*, 2000; Cubillos *et al.*, 2007). Subsequently, post-larvae that display diel vertical migrations also retain individuals in coastal areas (Parada *et al.*, 2008; Landaeta & Castro, 2013). Rocky intertidal and subtidal species, such as clingfish and triplefin, hatch from benthic egg masses per lunar phase (Contreras *et al.*, 2013; Palacios-Fuentes *et al.*, 2014) and their larvae are retained in nearshore waters by poorly understood oceanographic processes (Hernández-Miranda *et al.*, 2003; Landaeta *et al.*, 2015). Marine fish species inhabiting sandy bottoms utilize windward coastal areas as

nursery grounds, where breaking waves may disturb large predators and food resources are abundant (Patrick & Strydom, 2014).

Nearshore environments off central Chile are characterized by a well-mixed water column and spatial homogeneity in autumn-winter and the onset of a thermocline in spring and summer, when winds influence upwelling and sea breezes intensify (Hernández-Miranda *et al.*, 2003; Narváez *et al.*, 2004), leading to an increase in chlorophyll-*a* concentration and invertebrate settlement during spring-summer (Navarrete *et al.*, 2002; Wieters *et al.*, 2003). Environmental forcing varies at a seasonal scale in coastal marine areas (Huyer, 1983; Mittelstaedt, 1991), thus it is expected that fish eggs and larvae will be subject to variability in their early life traits (ELT), as an adaptive response to the environment. For example, hake, *Merluccius gayi* Guichenot, 1848, change their spawning location, egg size and the vertical migration pattern of their larvae between the main (spring) and secondary (early autumn) reproductive seasons (Landaeta & Castro, 2012). Among ELT, hatching patterns, growth and survival have crucial importance in determining the recruitment level of year classes in fish populations (Watanabe *et al.*, 2014) and may vary at differing temporal and spatial scales (Plaza *et al.*, 2003; Rodríguez-Valentino *et al.*, 2015). Additionally, developmental instabilities (i.e. the failure of an individual to produce a consistent phenotype

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in a given environment; Zakharov & Graham, 1992) may also occur, thereby affecting ELT of marine fishes (Somarakis *et al.*, 1997; Lemberget & McCormick, 2009).

Otoliths represent a practical tool for studying ELT in marine fishes and developmental instability through bilateral symmetry (Palmer & Strobeck, 1986). Otoliths are hard calcium carbonate structures and constitute an integral part of the hearing and equilibrium components in fishes (Gagliano *et al.*, 2008). Through diel variations in calcium and protein deposition, bipartite structures known as daily growth increments often form at the microstructural level of the otolith (Campana, 1984); therefore, otolith microstructure examination may be used to determine growth rates and survival of fish larvae (Brothers *et al.*, 1976; Bustos *et al.*, 2015). Because otoliths are paired structures, they also offer an opportunity to measure departures from perfect symmetry, especially in fish larvae, since their growth rates are faster, their capability to tolerate stress is lower, and the link between growth performance and fitness is stronger (Zenteno *et al.*, 2014; Díaz-Gil *et al.*, 2015).

Early life stages of sand-dwelling fishes from eastern boundary currents have been scarcely studied until now, and include the family Dactyloscopidae, known as sand stargazers. The Chilean sand stargazer *Sindoscopus australis* (Fowler & Bean 1923) is the only dactyloscopid that inhabits cold temperate waters and is known only from coastal waters of Chile at about 23°–36°S where it is found at depths of 2 m or less (Dawson, 1977). There is no information about how many spawning seasons this stargazer has. Adults display paternal care of egg clutches, behind pectoral fins, during embryonic development. Larvae are pelagic, occur in near-shore waters, and grow at slow rates (0.09–0.21 mm day⁻¹), with significant interannual variations (Herrera *et al.*, 2007; Rodríguez-Valentino *et al.*, 2015). Nonetheless, there is no information about variability of the ELT of this species at a seasonal scale.

Therefore, the objective of this study was to compare the seasonal variation (winter vs spring spawned) in the early life traits of *Sindoscopus australis*, a sand-dwelling fish inhabiting a coastal area of central Chile, using sagittal otolith microstructure and size. It was expected that ELT would vary at seasonal scale, with faster growth rates and fewer developmental instabilities for those larvae hatched during the spring season, when seawater temperature is higher.

MATERIALS AND METHODS

Fieldwork

From mid austral autumn (8 May) to spring (17 December) 2013, 10 nearshore (<500 m offshore) night-time surveys were conducted at El Quisco Bay (EQB, 33°24'S 71°43'W), central Chile, on board an artisanal vessel (Table 1). For each sampling date, eight repetitions of oblique hauls of a Bongo net (60 cm diameter, 300 µm mesh size) with one TSK flowmeter mounted in the frame of the net were performed for 15–20 min from a depth of 20 m to surface, in a zone with maximum depth of 30 m. Seawater volumes filtered by the net ranged from 37.3 to 1453.1 m³ (mean ± 1SD: 142.8 ± 176.1 m³). Subsequently, the nets were washed on board and all zooplankton samples (N = 160) were initially fixed with 5% formalin buffered with sodium borate and preserved in 96% ethanol after 12 h. This procedure has no effect on the microstructure of the otolith (Palacios-Fuentes *et al.*, 2012, 2014; Contreras *et al.*, 2013).

Laboratory work

In the laboratory, all larval fish were separated, counted and identified into the lowest possible taxon. Identification of the sand stargazer larvae, *Sindoscopus australis*, was based on the criteria described by Herrera *et al.* (2007). Larval abundance was standardized to individuals (ind.) 1000 m⁻³ using the flowmeter counts (Table 1). The standard length (from the tip of the snout to the base of the hypural bones, SL) was measured to the nearest 0.01 mm using an Olympus SZ-61 stereomicroscope with a Moticam 2500 (5.0 M Pixel) video camera connected to a PC with the Moticam Image Plus 2.0 software. No corrections for shrinkage were carried out on the larval measurements.

The left and right sagittae otoliths were removed from 296 larvae (4.28–18.21 mm SL, N_{winter} = 180; N_{spring} = 116; Figure 1) using dissecting needles. No otoliths were broken during the process. The otoliths were embedded in epoxy resin on a glass slide. The daily age was estimated by counting the number of otolith increments with a Motic BA310 light microscope at 1000× magnification under oil immersion. The longest radius of a sagitta was measured three times and its mean was used for further analysis. The perimeters and areas of the otoliths were then measured once using the Moticam Image Plus 2.0 software.

Table 1. Summary of the sampling dates off El Quisco Bay, central Chile.

Sampling day	Season	Mean	SD	Median	Minimum	Maximum
08-05-2013	Autumn	–	–	–	–	–
20-06-2013	Autumn	–	–	–	–	–
24-07-2013	Winter	53.36	61.93	33.21	2.06	239.3
01-08-2013	Winter	23.41	22.05	15.90	7.92	95.38
29-08-2013	Winter	36.29	26.82	25.82	10.79	101.62
24-10-2013	Spring	85.90	76.33	46.36	12.66	259.28
28-11-2013	Spring	38.79	42.83	26.81	2.22	122.13
05-12-2013	Spring	62.83	32.76	48.05	20.42	145.14
12-12-2013	Spring	26.37	26.23	20.05	12.36	85.19
17-12-2013	Spring	15.82	5.62	15.97	9.72	21.61

SD, standard deviation. Abundances expressed as ind. 1000 m⁻³.

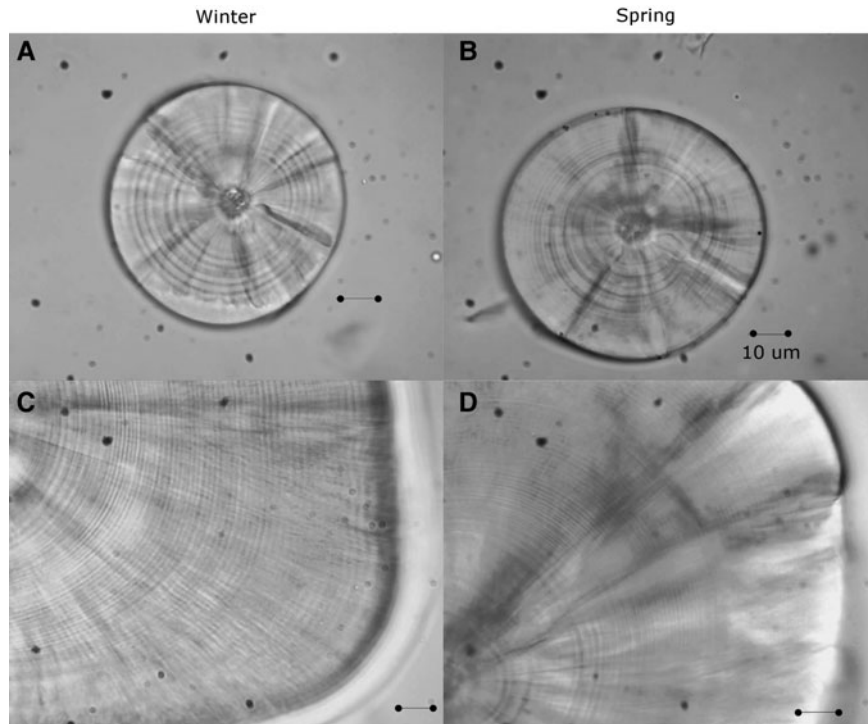


Fig. 1. Sagittal otoliths of larvae of sand stargazer *Sindoscopus australis*. (A) Larvae of 4.53 mm SL and 9 microincrements; (B) larvae of 4.28 mm SL and 10 microincrements; (C) larvae of 15.89 mm SL and 51 microincrements; (D) larvae of 18.21 mm SL and 68 microincrements. All bars correspond to 10 μm .

Three independent counts were performed on the right and left sagittae. The counts were performed after a prominent hatch mark. When the coefficient of variation ($\text{CV} = \text{standard deviation}/\text{mean} \times 100$) of the increment counts among the 3 readings was $< 10\%$, the mode of the three counts was calculated and utilized for the analysis. When CV was $> 10\%$, the otolith reading was discarded ($N_{\text{winter}} = 4$; $N_{\text{spring}} = 1$). Once selection of the values was done, a comparison of readings was carried out using a Wilcoxon matched pairs test, testing the hypothesis that the reading of the left sagitta and right sagitta did not differ. The daily periodicity of the growth increments for *Sindoscopus australis* or other Dactyloscopidae has not been validated; however, several species of the suborder Blennioidei have been validated for daily periodicity in coastal waters of central Chile and elsewhere (Hernández-Miranda *et al.*, 2009; Kohn & Clements, 2011; Mansur *et al.*, 2013).

Data analysis

Significant variations in the standardized larval abundance among sampling days and between winter (July–August 2013) and spring (October–December 2013) were compared utilizing a Kruskal–Wallis H test, because data were not normally distributed (Shapiro–Wilk test, $W = 0.72$, $P < 0.001$), followed by post-hoc analyses for pairwise comparisons of periods.

Simple linear regressions by least-squares ($\text{SL} = a + bA$) between the micro-increment counts (age, A) and larval lengths (SL) were adjusted, separately for winter and spring dates. In this case, the slope corresponded to the population growth rate, and the intercept corresponded to the estimated hatch size. To compare the population growth rate between seasons, slopes were compared with one-way ANCOVA (Zar, 2010). Also, a Gompertz growth model was fitted, with $w = W_{\text{inf}} e^{-ke^{-gt}}$, where W_{inf} = asymptotic size = $w_0 e^k$, $k = a$ adimensional parameter, w_0 = size at hatch, and

g = instantaneous growth rate at $t = t_0$. Linear and Gompertz models were compared using the Akaike Information Criterion (AIC).

The hatching days were back-calculated and related to the lunar cycle. To compare distribution patterns, hatch day frequencies for each season were converted to Julian days and then converted to angles ($^\circ$) by dividing by 365 and then multiplying by 360° , so data could be analysed using circular statistics. Similarly, for each sampling date, the days since new moon (DNM) were counted, and thereby assigned DNM values from 0 to 29 for each date, in which 0 represented the new moon. DNM values were converted to angles ($^\circ$) by dividing by 29 (the length, in days, of the lunar cycle) and then multiplying by 360° . To assess whether the hatching events showed lunar periodicity, the data were analysed using the Rao's spacing test (Batschelet, 1981); the null hypothesis that the hatching events would be equally or randomly spaced throughout the lunar cycle was tested for each data set.

The symmetry of sagitta otoliths was analysed following Palmer & Strobeck (1986), using radius, perimeter and area as morphological traits. To avoid the effect of the trait size on the asymmetry, index $R - L/[(R + L)/2]$ was calculated for each otolith trait. Subsequently, skewness and kurtosis, and the variance (F test) were compared among winter and spring cohorts, and tests for normality were applied as done previously (Shapiro–Wilk test). $P < 0.05$ was considered significant.

RESULTS

Larval abundance and size distribution during winter and spring 2013

During 2013, larval abundance of *Sindoscopus australis* varied from 2.06 to 259.28 ind. 1000 m^{-3} (mean \pm SD and median,

respectively: 46.01 ± 50.58 ind. 1000 m^{-3} , 25.57 ind. 1000 m^{-3}). Larvae were totally absent in the plankton samples during May and June 2013, and then appeared and increased their abundance to reach the maximum value during October, thereafter diminishing until December (Table 1). There were significant differences in larval abundance among samplings (Kruskal–Wallis test, $H = 20.36$, $P = 0.004$), with greater larval abundance in late October than in early August (Table 1). However, larval abundances for winter and spring cohorts were similar (Mann–Whitney U test, $U = 748$, $P = 0.245$).

Size distribution of larvae from austral winter and spring were not normally distributed (winter: $W = 0.86$; $P < 0.001$; spring: $W = 0.955$; $P < 0.001$); larvae collected during winter (range: 4.35–15.89 mm SL) were significantly smaller than those collected in spring (range: 4.28–18.21) (Mann–Whitney test, $U = 6761$; $P < 0.001$) (Figure 2).

Larval growth and size-at-age variations

For larvae collected during winter, otolith readings differed between right and left sagittae (Wilcoxon paired test, $W = 1072.5$, $P = 0.02$); therefore, only right sagittae were used for further growth analysis.

The parameters of the linear and Gompertz models are given in Table 2. During austral winter, based on simple linear models, the estimated growth rate for larval

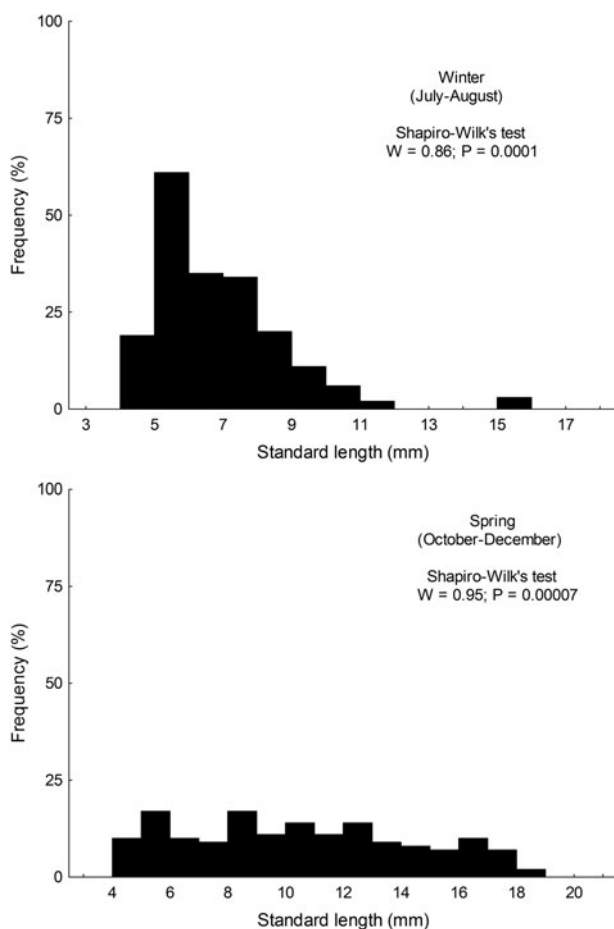


Fig. 2. Standard length distribution of larval *Sindoscopus australis* collected during austral winter and spring 2013.

Sindoscopus australis was $0.145\text{ mm day}^{-1} \pm 0.008$, while for spring it increased significantly to $0.182\text{ mm day}^{-1} \pm 0.008$ (homogeneity of slopes test, $F = 14.96$; $P < 0.001$; Figure 3). Both linear and Gompertz models estimated hatch sizes that differed between winter (linear = 4.13 mm; Gompertz = 4.73 mm) and spring (linear = 2.99 mm; Gompertz = 2.92 mm). Nonetheless, size-at-age of larvae compared using linear models was similar for both cohorts (winter = 9.09 mm SL; spring = 9.03 mm SL) (one-way ANCOVA, $F = 0.15$; $P = 0.69$).

Back-calculated hatch days and lunar cycle

Back-calculated hatch days during austral winter were mostly during neap tides, at first or third quarter moon (Figure 4). Moreover, during austral spring most of the hatch period occurred during spring tides, particularly at new moon (Figure 4). Circular statistics indicated that hatching did not follow a uniform distribution throughout the lunar cycle, either for winter (Rao's $U = 268.8$, $P < 0.0001$) or for spring ($U = 262.8$, $P < 0.0001$).

Otolith bilateral symmetry

Sagittal radius showed a leptokurtic distribution during winter and spring season, while the other traits were platykurtic (Table 3, Figure 5). Only the symmetry of perimeter of sagitta otoliths showed normal distribution for winter and spring seasons (winter, Shapiro–Wilk's test, $P = 0.576$; spring, $P = 0.382$) and no skewness during winter (Table 3). Because skewness of the traits was positive or zero and negative for winter-spawned and spring-spawned larvae, respectively (Table 3), a genetic basis for directional asymmetry is doubtful, and skewness was caused by exceptional, asymmetric otoliths. When comparing perimeter asymmetry between seasons, winter-spawned individuals showed more variance (0.001) than those from spring-spawned larvae (variance = 0.0006) (F -test, $F = 1.505$, $P = 0.038$); therefore, larvae from winter experienced more fluctuating asymmetry than those from spring.

DISCUSSION

Several differences arose in the early life traits of the sea star-gazer, *Sindoscopus australis*, hatched during the austral winter and spring seasons off central Chile. Larval size and growth rates were higher during spring than in winter, but size-at-hatch was smaller for the spring cohort. Hatching pattern also changed from occurring during first and third quarter (i.e. neap tides) during winter to happening during

Table 2. Parameters of the linear and Gompertz growth models for larval *Sindoscopus australis*.

Season	Linear	Gompertz
Winter	$a = 4.13$, $b = 0.145$, AIC = 128.36	$W_{\text{inf}} = 1169.2$, $k = 5.509$, $g = 0.0035$, AIC = 121.68
Spring	$a = 2.99$, $b = 0.182$, AIC = 248.29	$W_{\text{inf}} = 22.9$, $k = 2.059$, $g = 0.0024$, AIC = 242.43

AIC, Akaike Information Criterion.

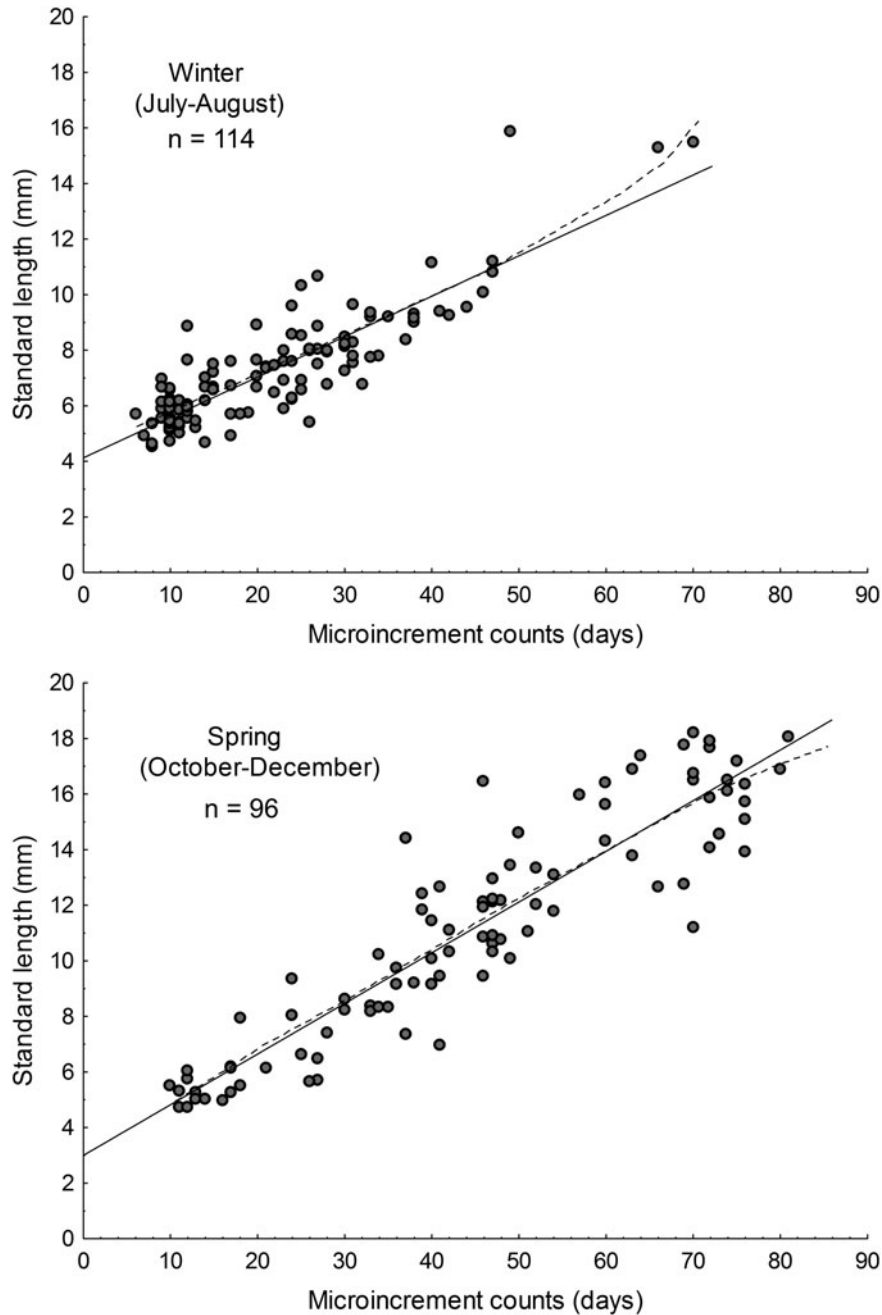


Fig. 3. Larval growth rates of *Sindoscopus australis* estimated by sagittal microstructure analysis, during (A) winter and (B) spring. Linear regression models showed in solid lines and Gompertz models showed in dotted lines.

the new moon (spring tides). Finally, only the perimeter of the sagittal otolith showed fluctuating asymmetry, with winter exhibiting more variance than did spring.

Temporal variation of the early life traits may be because of the main environmental mesoscale process occurring along Chile: upwelling events. During austral winter, north winds dominate the area, producing an Ekman layer moving onshore, and retaining early life stages of marine fishes, such as anchovies and sardines (Castro *et al.*, 2000; Cubillos *et al.*, 2007). Food availability, i.e. phytoplankton and microzooplankton are less abundant then, but it enables adequate feeding for shorefish larvae (Llanos *et al.*, 1996; Llanos-Rivera *et al.*, 2004). Seawater temperature is also

lower during winter time off central Chile (12.7°C in July off El Quisco, Narváez *et al.*, 2004), but increases rapidly during spring and summer (14.5°C in November, Hernández-Miranda *et al.*, 2003; Narváez *et al.*, 2004). Recently, Tapia *et al.* (2015) recorded the sea temperature at El Quisco as $13.02 \pm 1.22^{\circ}\text{C}$ (mean \pm SD), varying between 10.93 (July) and 18.12°C (February).

A seasonal increase in sea temperature may trigger an increase in the growth rate experienced by fish larvae, and also increases swimming capabilities and larval duration (Amara *et al.*, 1994; Johannessen *et al.*, 2000; Green & Fisher, 2004). However, there are species-specific responses to seasonal habitat temperature variations; while round

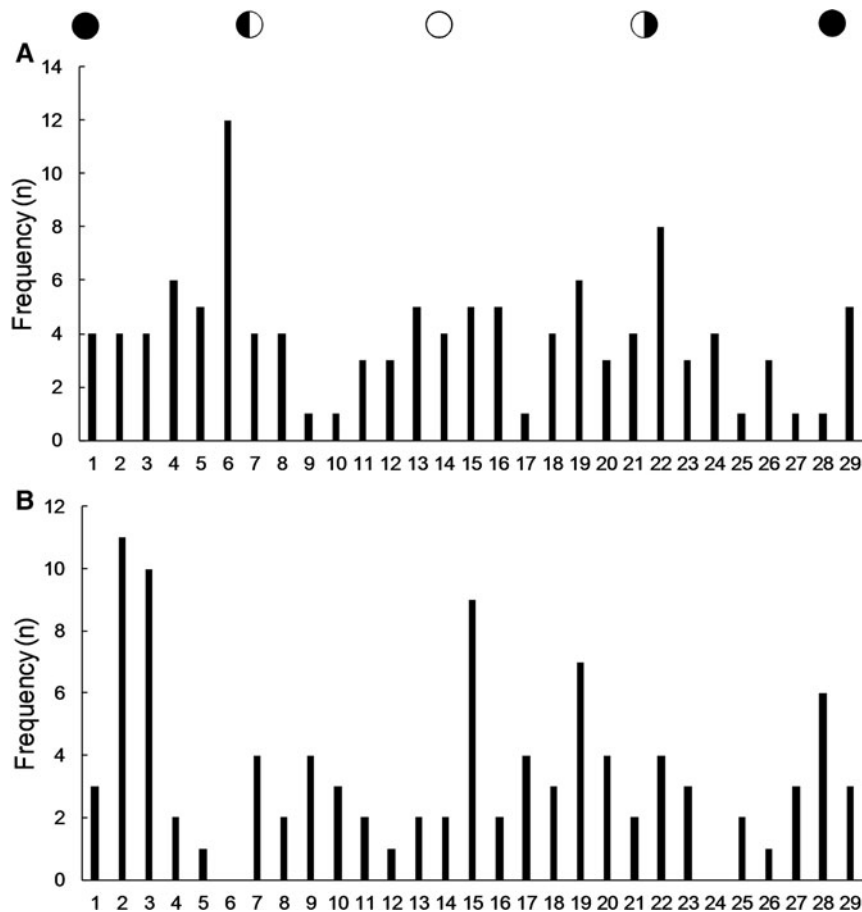


Fig. 4. Back calculated lunar hatching patterns of *Sindoscopus australis* off central Chile during (A) winter and (B) spring.

herring *Etrumeus teres* have a positive correlation between growth rate and habitat temperature, growth rate of sardines, *Sardinops melanostictus*, in the same area is independent of the seawater temperature (Watanabe *et al.*, 2014). Furthermore, seasonal variations in larval growth history may be independent of temperature, as in the coral reef fish, *Thalassoma bifasciatum* (Searcy & Sponaugle, 2000). In this study, *Sindoscopus australis* displayed variations in its growth rate between winter-hatched and spring-hatched larvae, but the environmental reasons for this remain unknown.

Variations in the size-at-hatch and size-at-age estimated by growth models indicate that seasonal variations within populations may be caused by a parental effect on the egg size-offspring fitness function (Einum & Fleming, 2002). Intrapopulation variation in egg size is larger in fish with demersal eggs and larvae, such as the sand stargazer, than in those with pelagic eggs and/or larvae; selection for variable egg sizes within populations should exist if maternal (or parental) phenotype can influence offspring environment, as is likely the case in species with demersal eggs and larvae (Einum & Fleming, 2002), and probably in adult *S. australis*.

Many marine organisms may synchronize the release of gametes or larvae with respect to photoperiod, tides, tidal amplitude or lunar cycles (Morgan & Christy, 1994). The synchrony of larval production with lunar cycle is an adaptation to maximize settlement of planktonic juveniles (Robertson *et al.*, 1990). Nonetheless, *Sindoscopus australis* varied from

having a hatching period synchronized to neap tides in winter to hatching events near new moon during spring. Hatching during neap tides during winter may increase larval retention in coastal areas, because of weaker tidal currents (Contreras *et al.*, 2013). Reproductive synchrony at new moon during spring might be beneficial because hatched larvae encounter favourable tides for transport away from rocky reef-based predators (Foster, 1987). The timing of larval release seems to be plastic at several timescales (Plaza *et al.*, 2003; Rodríguez-Valentino *et al.*, 2015; this study) and evolved because of predation on the adults, so eggs and larvae abundances not only vary between phases of each cycle, but also differ among cycles depending upon species-specific life history traits (Morgan & Christy, 1994).

Only the perimeter of the sagittae otoliths of *Sindoscopus australis* showed fluctuating asymmetry; other trait measurements departed from normality. Sagittal perimeter showed larger variance during winter compared with spring. However, inconsistencies in the response of the asymmetry among otolith traits (radius, perimeter, area) does not imply a higher developmental instability, or lower fitness, during the winter season (Díaz-Gil *et al.*, 2015). A non-normal distribution of right minus left measurements of otolith traits could be caused by the presence of some outliers (i.e. otoliths with two primordia). Also, the eyes of Dactylopscopidae shift from lateral to dorsolateral position (Watson, 2009), probably causing changes in the shape of the sagitta otoliths located in the otic capsules. During transformation, otoliths of several

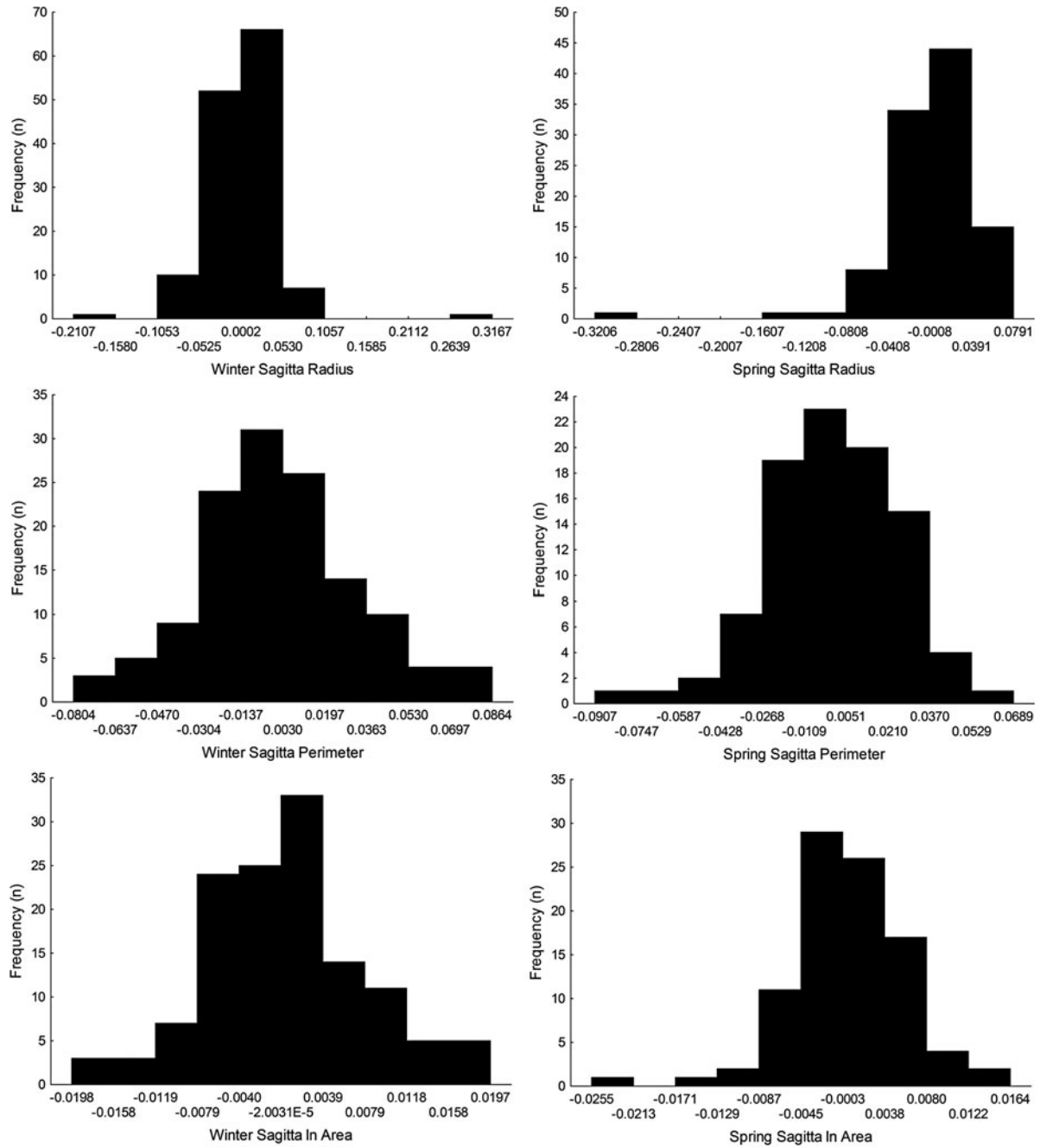


Fig. 5. Left-right symmetry of different otolith traits (radius, perimeter and area) for winter-spawned and spring-spawned cohorts of *Sindoscopus australis*.

Table 3. Otolith symmetry traits by seasonal cohort.

Otolith symmetry	N	Mean	Skewness	SE	Kurtosis	SE	Shapiro-Wilk	P
Winter-Radius	137	0.001295	1.454	0.207	18.097	0.411	0.786	7.45×10^{-13}
Winter-Perimeter	130	0.001011	0.172	0.212	0.264	0.422	0.991	0.576
Winter-In Area	130	0.000294	0.170	0.212	0.403	0.422	0.987	0.268
Spring-Radius	104	-0.000804	-3.166	0.237	20.345	0.469	0.763	1.16×10^{-11}
Spring-Perimeter	93	0.000117	-0.344	0.250	1.070	0.495	0.985	0.382
Spring-In Area	93	0.000144	-0.575	0.250	2.871	0.495	0.961	0.007

SE, standard error.

marine fish species develop accessory growth centres (AGC) (Jearld *et al.*, 1993; Brown *et al.*, 2001), which may increase the asymmetry between otoliths. Moreover, the evidence for directional asymmetry in radius and area is weak, because skewness direction varied between seasons, suggesting a lack of genetic basis for this variability (Graham *et al.*, 1993).

Therefore, the Chilean sand stargazer displays differences in its ELT in response to individual hatching times. Larger larvae are initially hatched during winter at neap tides, and experienced slower growth rates and greater developmental instabilities; while during spring, hatching occurred during spring tides, especially around new moon, producing small larvae with faster growth rates. These trade-offs may be adaptations to increased chances of survival and settlement in sandy bottoms during periods of contrasting environmental conditions in nearshore waters.

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