

Hatching patterns and larval growth of a triplefin from central Chile inferred by otolith microstructure analysis

Pamela Palacios-Fuentes · Mauricio F. Landaeta ·
Nicole Jahnsen-Guzmán · Guido Plaza ·
F. Patricio Ojeda

Received: 31 January 2014 / Accepted: 9 April 2014 / Published online: 20 April 2014
© Springer Science+Business Media Dordrecht 2014

Abstract The subtidal rocky reefs are home to a diverse range of marine animals, including small cryptic fishes, characterised by a bipartite life cycle, with benthic adults and pelagic larval stage that lasts from several days to several months. Using the otolith microstructure analysis, this study determines the hatching and larval growth patterns of the abundant triplefin *Helcogrammoides chilensis* (Pisces: Tripterygiidae). Fish larvae were collected during September–October 2010 and between July 2012 and April 2013 in nearshore waters (<500 m) of central Chile. Nearshore time series of ichthyoplankton samples showed that large abundance of this species

occurs during early austral spring and autumn seasons. Body lengths ranged from 3.11 to 16.57 mm (1–57 days old). Sagittal microincrement analyses estimate that during the main reproductive season, larval growth rates are slow, varying between 0.145 and 0.156 mm day⁻¹ at a weekly scale. Back-calculated hatch days and circular statistics indicate a major hatch pulse occurring near full moon of the lunar cycle. These results suggest that reproduction occurs coupled with the upwelling season, which reduces the probability of starvation, and hatching occurs during spring tides (full moon), which increases larval dispersion and population connectivity.

Handling Editor: Thomas Mehner

P. Palacios-Fuentes (✉) · M. F. Landaeta
Laboratorio de Ictioplancton (LABITI), Facultad de
Ciencias del Mar y de Recursos Naturales, Universidad de
Valparaíso, Avenida Borgoño 16344, Reñaca, Viña del
Mar, Chile
e-mail: pame.palacios.fuentes@gmail.com

N. Jahnsen-Guzmán
Facultad de Ecología y Recursos Naturales, Universidad
Andrés Bello, Santiago, Chile

G. Plaza
Escuela de Ciencias del Mar, Pontificia Universidad
Católica de Valparaíso, Valparaíso, Chile

F. P. Ojeda
Facultad de Ciencias Biológicas, Pontificia Universidad
Católica de Chile, Santiago, Chile

Keywords Otolith · Lunar cycle · Hatching
pattern · Tripterygiidae · *Helcogrammoides
chilensis*

Introduction

The nearshore subtidal rocky reef assemblages in temperate waters harbour a large number of small invertebrates and fish species which derive food and/or shelter from the reef substratum (Jones, 1988). Additionally, assemblages that occur sympatrically with large brown kelps, such as mussel beds and sponge gardens, as well as the kelps itself, can be considered as settlement substrate for numerous cryptic fish with pelagic larval stages lasting from several days to several months (Palma and Ojeda 2002;

Pérez-Matus et al. 2012; Plaza et al. 2013). Among them, tripterygiids, commonly known as triplefins, encompass 29 genera and 163 species (Kohn and Clements 2011) and are found in tropical, temperate and polar regions (Nelson 2006). They are characterised by the spawning of benthic eggs attached by filaments to the rocky substrate in a single layer in the subtidal zone (Ruck 1973, 1980). During this developmental period, the males guard and protect their territory and the eggs, providing them with oxygenated water while cleaning them of detritus. This parental care occurs until the hatching of 3–6-mm-long planktonic larvae with pigmented eyes, small yolk sacs and open mouths (Ruck 1973, 1980). Hatchlings have a pelagic larval duration of approximately 2–4 months (Smith and Shima 2011; Plaza et al. 2013), and after that, they settle to the fronds of several different macroalgae (McDermott and Shima 2006). The triplefin *Helcogrammoides chilensis* occurs along the coast of Chile from 20°18'S to 36°45'S in the southern Pacific, inhabiting shallow waters along exposed rocky coasts (Williams and Springer 2001; Cancino et al. 2010). Pelagic larval stages are found throughout the year in nearshore waters (Pérez 1979; Hernández-Miranda et al. 2003; Landaeta et al. 2009). However, there still are important gaps in the knowledge of the early life history of this species.

Otolith microstructure has become an important indicator of the early life traits of fishes because otoliths are indicators of not only age and growth patterns, but also hatching times, settlement, metamorphoses, migration and condition (Landaeta and Castro 2006; Gagliano and McCormick 2007; Sponaugle 2010). Also, otoliths of fish larvae may provide information on biophysical interactions such as the effects of low-salinity plumes in coastal waters (Landaeta et al. 2012), ocean acidification (Munday et al. 2011), vertical mixing and ice melting (Zenteno et al. 2014); the information obtained through the analysis of daily fish otoliths microstructure has been a critical component of fisheries management and of ecological and oceanographic processes (Sponaugle 2010).

For the reasons stated above, *H. chilensis* can be used as a model species, because its life traits (e.g. benthic eggs, parental care, pelagic larvae and slow growth) are similar to other cryptic species that inhabit rocky reef habitats of temperate waters. Therefore, through the use of otolith microstructure analysis, the aim of the current study was to reveal the early life

history traits of triplefin *H. chilensis* larvae from nearshore rocky reef habitat. For this purpose, daily ages, growth patterns and back-calculated hatch dates were estimated to determine the relationship between hatching patterns and the lunar cycle.

Materials and methods

Fieldwork

Fish larvae were collected from nearshore waters at two locations along the central Chilean coast (Fig. 1). Three oceanographic samplings were performed during September and October 2010 on-board the RV Ilán from Pontificia Universidad Católica de Chile. Ichthyoplankton samples were collected using a Bongo net (60-cm mouth diameter, 300- μ m mesh size), equipped with a TSK flow meter (The Tsurumi-Seiki Co., Ltd., Tsurumi-ku, Yokohama, Japan) to quantify the filtered seawater, from surface to near-bottom depths (\sim 20 m) during the dawn and night hours (1900–2300 h) at one nautical mile off of El Quisco Bay (33°24'S, 71°43'W). During the study period, dawn occurred around 2000 h and sunrise at 0730 h. Five to eight trawls at 1–2 knots were conducted during each oceanographic sampling at the same location. Filtered seawater by net ranged from 34.1 to 316.4 m³ [mean \pm one standard deviation (SD) 201.5 \pm 76.5 m³]. All of the plankton samples ($n = 38$) were initially fixed with 5 % formalin and buffered with sodium borate, and after 12 h, they were preserved in 96 % ethanol. This methodology reduces initial dehydration of larvae and has previously been demonstrated not to significantly affect otolith structure (Santos et al. 2005).

Additionally, from October 2012 to April 2013, 23 cruises were carried out <500 m off Montemar, in the northern area of Bahía Valparaíso. A total of 160 ichthyoplankton samples were collected from these surveys, using the same methodology previously described. Filtered seawater by net ranged from 18.8 to 322.2 m³ (173.7 \pm 59.5 m³).

Laboratory analysis

Fish larvae from 2010 were sorted from the plankton samples in the laboratory. Identification of larval *H. chilensis* was performed following the criteria

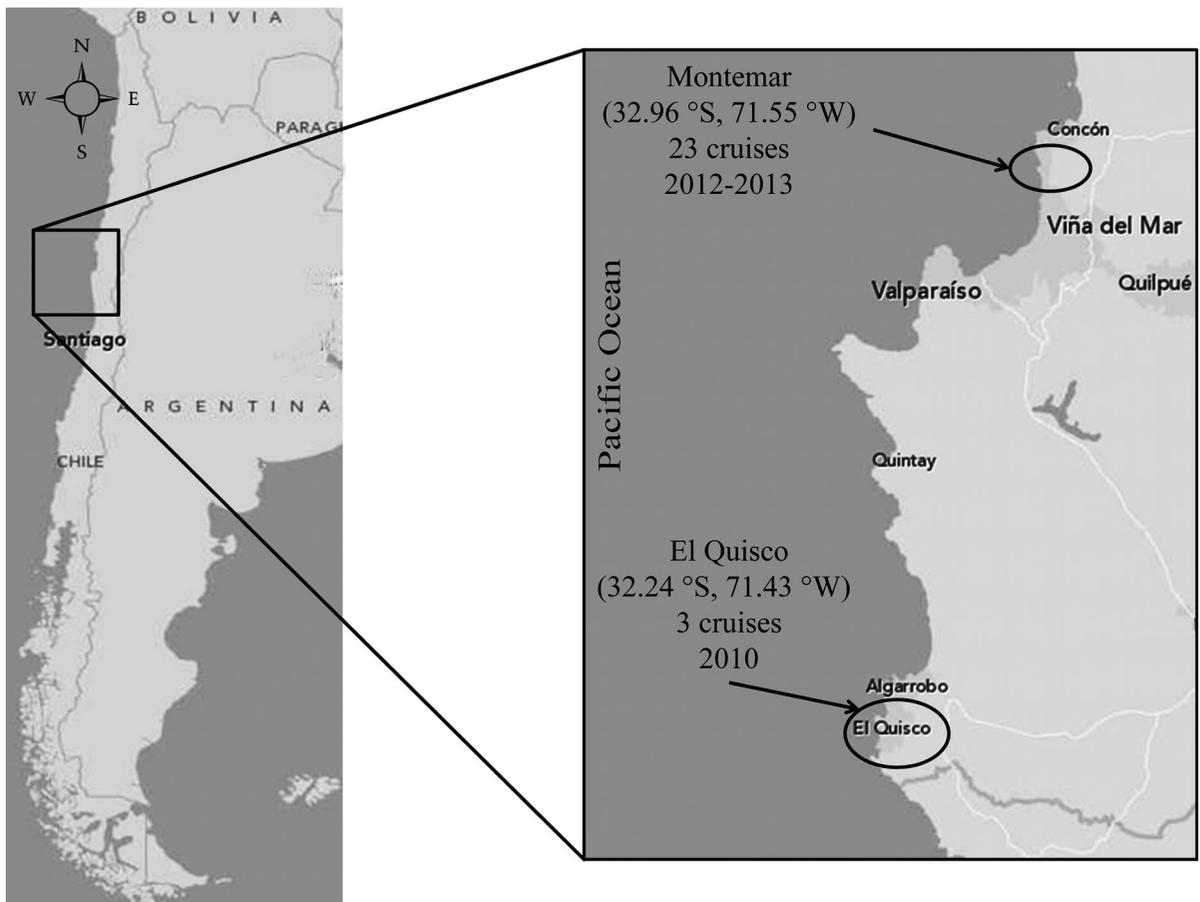


Fig. 1 Sampling locations. 2010 cruises were carried out in El Quisco bay at the South of Valparaíso, and the times series cruises were performed in Montemar, at the north of the bay

described by Ciechowski (1975) and Pérez (1979). Larval densities were expressed as individuals/1,000 m³. Developmental stages of larvae were classified into two groups: preflexion and postflexion (flexion and postflexion larvae pooled together into the latter group).

The left and right sagittae otoliths were removed using dissecting needles from 189 randomly selected larval *H. chilensis* (3.11–16.57 mm SL), collected at El Quisco Bay during 2010. Larvae were previously measured (notochord length, NL, larvae measuring 3.11–6.50 mm or standard length, SL, larvae measuring 6.50–16.57 mm) to the nearest 0.01 mm under an Olympus SZ-61 stereomicroscope (Olympus Corporation, Shinjuku-ku, Tokyo, Japan) using a Moticam 2500 (5.0 Mpixel) video camera (Motic Instrument, Inc., Richmond, BC, Canada) that was connected to a

PC containing the Moticam Image Plus 2.0 software (Motic China Grup, Co., Xiamen, China). Otoliths were embedded in epoxy resin on a glass slide. Age was determined by counting the number of daily increments from a dark prominent increment (the hatch mark, Fig. 3) to the otolith edge using a Motic BA310 light microscope (Motic Instrument, Inc., Richmond, BC, Canada) at 1,000× magnification under oil immersion. Hatch marks that formed on the first day after hatching have not been validated for *H. chilensis*. However, a similar hatch mark has been described in recently hatched larvae of triplefin *Forsterygion nigripenne* (Kohn and Clements 2011). Image analysis software (Moticam Image Plus 2.0) was used to obtain the mean values, resulting in three independent measurements, for both the longest radius of the sagitta and increment width.

Three separate readings were performed on both sagittae. In cases where the increment counts between the three readings were within 5 % of each other, modes (or averages, if all counts were different) were calculated and utilised for the analyses. If the readings varied from >5 % of each other, the otolith was discarded (13 otoliths were discarded from the total otolith analyses). Only sagittae were used for the analyses because they were the larger pair of otoliths and we found that age estimates using the left and right sagittae within individuals were the same (Wilcoxon signed-rank test, $P = 0.71$), so right sagittae were utilised for the analyses. Recently, the daily periodicities of the growth increments have been validated for juvenile stages of *H. chilensis* and *H. cunninghami* (Mansur et al. 2013) and even in other tripterygiid species (*Forsterygion capito*, *F. varium*, *Ruanoho whero*) (Kohn and Clements 2011) as well.

Data analysis

Least-square linear regression analyses were performed between microincrement counts (age) and larval lengths separately for each cruise of 2010, where the slope corresponds with the larval growth rate and the intercept to the estimated hatch size. To compare the temporal variability in the larval growth rates, slopes were compared using a one-way ANCOVA (Zar 1999).

The back-calculated hatching dates were related to the lunar cycle. For each sampling date, the days since the new moon (DNM) were counted and assigned DNM values from 0 to 29 for each date, where 0 represents the new moon. The DNM values were converted to angles ($^{\circ}$) by dividing by 29 (the length in days of the lunar cycle) and then multiplying by 360° so that the data could be analysed using circular statistics. To assess whether the hatching events showed lunar periodicity, we analysed the data using the Rao's spacing test (Batschelet 1981). This test is more powerful and robust than many other circular goodness-of-fit tests (Russell and Levitin 1995), being able to analyse bimodal and multimodal distributions, whereas other tests, such as the Rayleigh, are not (Bergin 1991). Additionally, the Rayleigh test was used to maintain comparability with other studies that used circular statistics. The null hypothesis that hatching events would be equally or randomly spaced throughout the lunar cycle was tested for the overall

data. The angular mean and 95 % confidence intervals were also calculated using the software PAST (Paleontological Statistics, Hammer et al. 2001).

Results

Abundance and larval size distribution

A total of 847 larval *H. chilensis* were collected during the three 2010 spring cruises, with abundances varying from 3.5 to 2,344.4 ind. $1,000\text{ m}^{-3}$ (mean \pm SD 202.7 ± 440.3 ind. $1,000\text{ m}^{-3}$). Larval sizes varied from 3.11 to 16.57 mm (mean \pm SD 6.45 ± 2.45 mm), and they differed significantly among the cruises from 2010 (Kruskal–Wallis test, $H = 291.84$, $P < 0.01$; Table 1); the larvae from the second cruise in El Quisco (2010) were the smallest (mean 5.41 mm) (Tukey's test, $P < 0.01$) compared to lengths obtained from the first (mean 7.25 mm) and third cruise (mean: 8.39 mm). In the nearshore time series 2012–2013, larval abundance varied from 3.4 to 546.9 ind. $1,000\text{ m}^{-3}$ (47.4 ± 85.7 ind. $1,000\text{ m}^{-3}$). Two abundance peaks were observed, the major during early austral spring (October 2012; mean \pm SE 283.36 ± 15.89) and another in April 2013 (mean \pm SE 133.96 ± 55.04) (Fig. 2).

Otolith microstructures, ages and growth of larvae

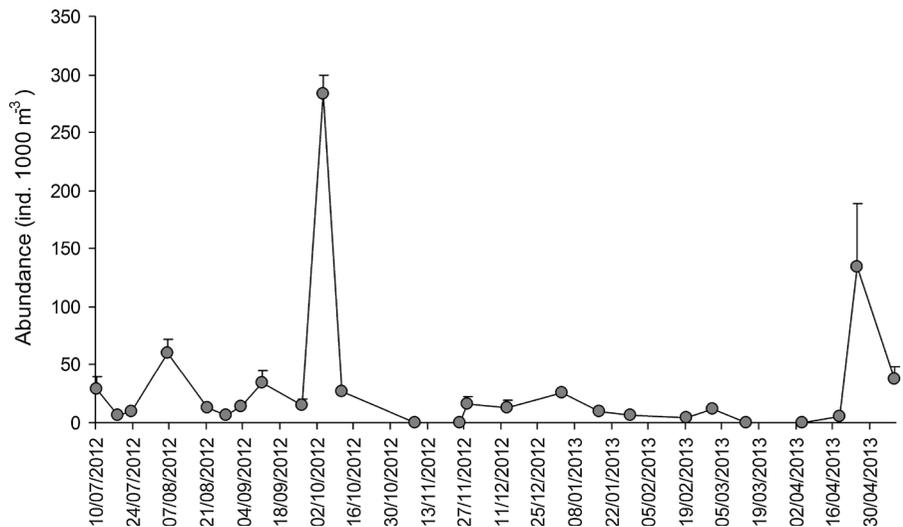
Sagitta microincrement widths (i.e. the distance between two consecutive opaque bands) ranged from 0.60 to 2.01 μm (mean \pm SD $1.28 \pm 0.24\ \mu\text{m}$). The hatch marks that were observed in the sagitta otoliths of the larval *H. chilensis* collected from September to October 2010 (Fig. 3) ranged from 10.11 to 16.90 μm ($13.94 \pm 1.31\ \mu\text{m}$). The sagitta radii ranged from 14.76 to 100.90 μm ($32.47 \pm 14.29\ \mu\text{m}$).

The microincrement counts (ages) ranged from 1 to 57 days. The linear models estimated the larval growth rates between 0.145 and 0.156 mm day^{-1} and hatch sizes from 5.39 to 6.23 mm BL. However, there were no significant differences in the growth rates (slopes) among samplings (one-way ANCOVA, homogeneity of slopes, $F = 0.36$, $P = 0.70$), so a global model was established (Linear regression, intercept: 5.684 mm, slope: $0.152\ \text{mm day}^{-1}$, $P < 0.01$) (Fig. 4). Nevertheless, the size-at-age was significantly larger for larvae captured during early October (one-way ANCOVA, $F = 10.38$, $P = 0.05$).

Table 1 Larval size (mm) and least-square linear models of larval *Helcogrammoides chilensis* growth rates for each sampling cruise and for all season (global model)

	Size range (mm)	Intercept	SE	Slope	SE	F	P	df
2 September 2010	3.64–11.42	5.435	0.332	0.145	0.016	86.48	<0.01	34
9 September 2010	3.11–15.06	5.396	0.160	0.156	0.008	347.84	<0.01	60
4 October 2010	4.20–16.57	6.230	0.206	0.147	0.010	213.79	<0.01	46
Global model	3.11–16.57	5.684	0.126	0.152	0.006	594.09	<0.01	174

The intercepts correspond to the hatch sizes (mm) and the slopes to growth rates (mm day⁻¹) estimated for the models
SE one standard error, df degrees of freedom

Fig. 2 Mean abundance of larval *Helcogrammoides chilensis* (ind. 1,000 m⁻³) in nearshore waters off central Chile from July 2012 to April 2013. Bars correspond to one SD

Hatching patterns and lunar periodicity

The raw record of *H. chilensis* hatchings at El Quisco Bay began on July 17 (day 198 of a Julian year) and finished on October 3 (day 276). The circular statistics of the back-calculated hatching days fitted in a lunar cycle (of 29 days per month) and revealed a large pulse of hatching just after full moon and a second one prior full moon (Fig. 5). In fact, the mean angle vector occurred at day 13 of the lunar cycle (90 % confidence = 11.4–14.91 days). The Rayleigh ($R = 0.451$, $P < 0.001$) and Rao's spacing tests ($U = 240.9$, $P < 0.001$) indicated that the hatching patterns of larval *H. chilensis* were not uniform over the lunar cycle.

Discussion

Off central Chile, our results suggest that reproduction of *H. chilensis* occurs throughout the year, with a main pulse

during early austral spring season. Otolith microincrement analysis indicates growth rates around 0.15 mm day⁻¹ during the first 2 months of the larval pelagic phase of the species and back-calculated hatch days suggest a main pulse around full moon, a period characterised by spring tides.

The peak abundances of larval *H. chilensis* occurred during September 2010 and October 2012 (austral early spring season). This period is characterised by the increase in southerly winds, which induce upwelling events of cold waters in the area (Hernández-Miranda et al. 2003; Narváez et al. 2004). In these upwelling zones, subtidal and intertidal fishes are larger and in better condition (i.e. higher RNA/DNA ratios) compared with those of non-upwelling zones (Pulgar et al. 2013). Therefore, the temporal match of hatching events and the upwelling season may have a positive impact on the survival of early life stages of *H. chilensis*.

Larval growth rates of *H. chilensis* estimated using the linear models were 0.15 mm day⁻¹, similar to

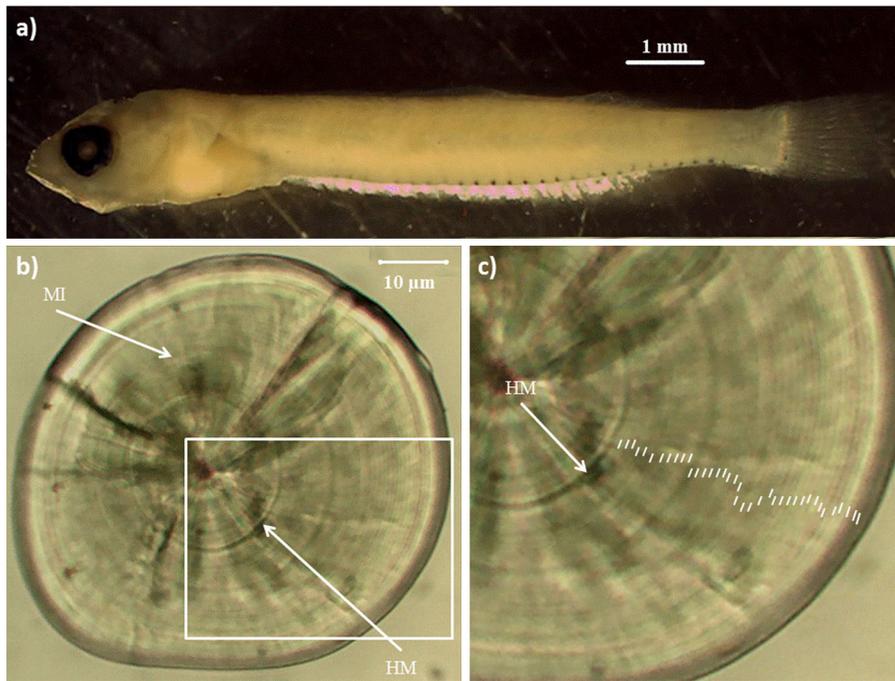


Fig. 3 *Helcogrammoides chilensis* a) larvae, b) sagitta otolith microstructure, where *HM* hatch mark, *MI* microincrements, and c) Sagitta otolith close up which shows the HM and each MI

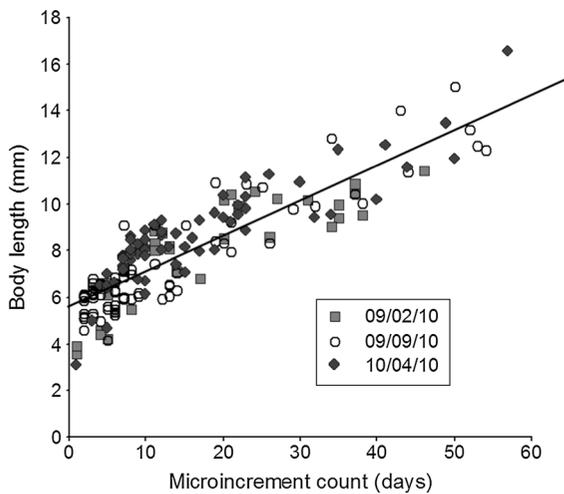


Fig. 4 Larval growth of *Helcogrammoides chilensis* in three different sampling dates. The *continuous line* corresponds to the larval growth rate of the global model including the larvae from the three cruises

those of other demersal species from Chilean waters with pelagic larvae, such as the mote sculpin *Normanichthys crockeri* (0.15–0.20 mm day⁻¹)

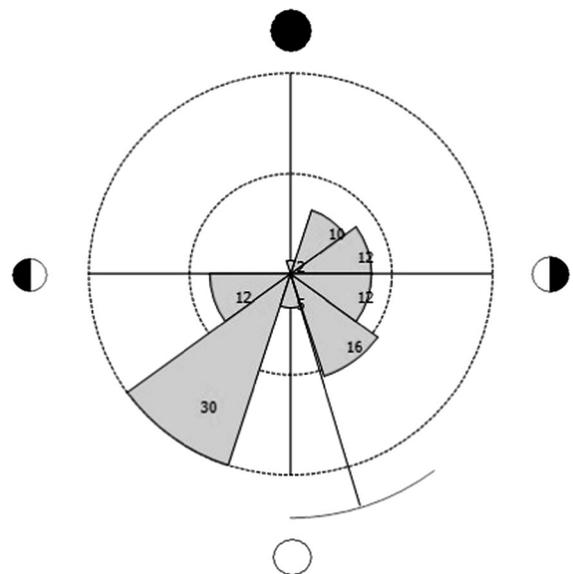


Fig. 5 Distribution of hatching abundances over the lunar cycle of *H. chilensis* during 2010. *Filled circles* represent new moons and *open circles* full moons. The *perpendicular line* corresponds to the angular mean and the *curved line* to the 95 % confidence interval. The *numbers on the figure* correspond to the proportional fish larval abundance

(Landaeta et al., 2010), rockfish *Sebastes oculatus* (0.15 mm day⁻¹) (Landaeta and Castro, 2006) and lightfish *Maurolicus parvipinnis* (0.136 mm day⁻¹) (Landaeta et al. 2012). These characteristics differ completely from those of species with life cycles that are exclusively pelagic and exhibit faster growth, such as the engraulids and clupeids, including *Engraulis ringens* (0.47 mm day⁻¹) (Hernández and Castro 2000), *Sardinops sagax* (0.40–0.66 mm day⁻¹) (Castillo et al. 1985) and the Falkland sprat *Sprattus fuegensis* (0.448 mm day⁻¹) (Landaeta et al. 2012).

The synchronising of reproduction, including hatching patterns, to a lunar cycle (29 days) (Grant et al. 2009), has been observed in several species, including sponges, corals, mollusks, polychaetes, crabs, echinoids (Sponaugle and Pinkard 2004), fishes (Mizushima et al. 2000), amphibians, birds and mammals (Grant et al. 2009). Periodicity in moon-related cues appears to be related to changes in the intensity of moonlight, time of moonrise, solar cycle and movement pattern of the moon across the night sky (Leatherland et al. 1992). All of these changes provide a set of environmental cues that assure advection, foraging and reproduction in favourable environmental conditions (deBruyn and Meeuwig 2001; Takemura et al. 2010). In addition, it is likely that fishes respond to gravitational (tidal) and geophysical forces that occur as a result of the changing position of the earth relative to the moon and sun (Takemura et al. 2010).

It has been suggested that the synchrony of larval release with a lunar cycle during full moon is related to the improved defence of broods in colonial nesting species, such as *H. chilensis*, with consequent reductions in mortality rates and decreased costs of parental care for offspring (Robertson et al. 1990). In the current study, *H. chilensis* showed a lunar pattern with a hatch peak in the full moon phase. This situation may favour larval dispersion and population connectivity given the larger tidal currents that characterise the full moon phase (Robertson et al. 1990; Christy 2003; Takemura et al. 2010; Grant et al. 2009). On the other hand, high luminosity makes the recently hatched larvae more evident to the predators (Robertson et al. 1990).

There is a lack of information regarding the reproductive biology and early life history of *H. chilensis*; therefore, it is important to continue studies and analysis of the larval stage to fully understand the dynamics of the population and estimate the larval

supply that is settling and eventually recruiting to the adult population, through studies of otolith microchemistry and fluctuating asymmetry to determine the condition of presettlement larvae.

Acknowledgments The authors want to thank to Jorge Contreras, María José Ochoa-Muñoz, Franco Salas-Berrios and Dr. Randy Finke for their field work on-board RV Ilan, and Dr. Lidia Mansur for her comments and support. Two anonymous reviewers improve with their comments a previous version of the ms. This research was supported by Comisión Nacional de Ciencia y Tecnología [FONDECYT Grant Number 1100424 to FPO, GP and MFL].

References

- Batschelet E (1981) Circular statistics in biology. Academic Press, New York
- Bergin TM (1991) A comparison of goodness-of-fit tests for analysis of nest orientation in western kingbirds (*Tyrannus verticalis*). Condor 93:164–171
- Cancino C, Fariás K, Lampas S, González B, Cuevas V (2010) Descripción de los complejos estructurales óseos en *Helcogrammoides chilensis* (Blennioidei: Tripterygiidae) de la zona central de Chile. Rev Biol Mar Oceanogr 45:671–682. doi:10.4067/S0718-19572010000400011
- Castillo G, Aguilera E, Herrera G, Bernal PA, Butler JL, Chong J, González H, Oyarzún C, Veloso C (1985) Larval Growth rates of the pacific sardine *Sardinops sagax* off central Chile, determined by daily ring counts in otoliths. Biol Pesq 14:3–10
- Christy JH (2003) Reproductive timing and larval dispersal of intertidal crabs: the predator avoidance hypothesis. Rev Chil Hist Nat 76:177–185. doi:10.4067/50716-078X2003000200005
- Ciechowski JD (1975) Características y distribución de post-larvas del acorazado, *Agonopsis chiloensis* (Jenyns, 1842) Jordan y Evermann, 1898 y de *Tripterygion cunninghami* Smitt, 1898 en aguas del Atlántico frente a la Argentina (Pisces). Physis A 84:309–317
- deBruyn AMH, Meeuwig JJ (2001) Detecting lunar cycles in marine ecology: periodic regression versus categorical ANOVA. Mar Ecol Prog Ser 214:307–310. doi:10.3354/meps214307
- Gagliano M, McCormick MI (2007) Compensating in the wild: is flexible growth the key to early juvenile survival? Oikos 116:111–120. doi:10.1111/j.2006.0030-1299.15418.x
- Grant RA, Chadwick EA, Halliday T (2009) The lunar cycle: a cue for amphibian reproductive phenology? Anim Behav 78:349–357. doi:10.1016/j.anbehav.2009.05.007
- Hammer Ø, Harper DAT, Ryan PD (2001) PAST: paleontological statistics software package for education and data analysis. Palaeontol Electron 4:1–9
- Hernández EH, Castro LR (2000) Larval growth of the anchoveta *Engraulis ringens* during the winter spawning season off central Chile. Fish Bull 98:704–710
- Hernández-Miranda E, Palma AT, Ojeda FP (2003) Larval fish assemblages in nearshore coastal waters off central Chile:

- temporal and spatial patterns. *Estuar Coast Shelf Sci* 56:1075–1092. doi:[10.1016/S0272-7714\(02\)00308-6](https://doi.org/10.1016/S0272-7714(02)00308-6)
- Jones GP (1988) Ecology of rocky reef fish of north-eastern New Zealand: a review. *N Z J Mar Freshw Res* 22:445–462. doi:[10.1080/00288330.1988.9516315](https://doi.org/10.1080/00288330.1988.9516315)
- Kohn YY, Clements KD (2011) Pelagic larval duration and population connectivity in New Zealand triplefin fishes (Tripterygiidae). *Environ Biol Fish* 91:275–286. doi:[10.1007/s10641-011-9777-3](https://doi.org/10.1007/s10641-011-9777-3)
- Landaeta MF, Castro LR (2006) Larval distribution and growth of the rockfish, *Sebastes capensis* (Sebastidae, Pisces), in the fjords of southern Chile. *ICES J Mar Sci* 63:714–724. doi:[10.1016/j.icesjms.2006.01.002](https://doi.org/10.1016/j.icesjms.2006.01.002)
- Landaeta MF, Schreiber K, Bustos CA, Letelier J, Balbontín F (2009) Temporal fluctuations of nearshore ichthyoplankton off Valparaíso, central Chile, during the ENSO cycle 1997–2000. *Rev Biol Mar Oceanogr* 44:571–582. doi:[10.4067/s0718-19572009000300005](https://doi.org/10.4067/s0718-19572009000300005)
- Landaeta MF, Inostroza PA, Ramírez A, Soto-Mendoza S, Castro LR (2010) Distribution patterns, larval growth and hatch dates of early stages of the mote sculpin *Normanichthys crockeri* (Scorpaeniformes, Normanichthyidae) in the upwelling ecosystem off central Chile. *Rev Biol Mar Oceanogr* 45:575–588. doi:[10.4067/s0718-19572010000400006](https://doi.org/10.4067/s0718-19572010000400006)
- Landaeta MF, López G, Suárez-Donoso N, Bustos CA, Balbontín F (2012) Larval fish distribution, growth and feeding in Patagonian fjords: potential effects of freshwater discharge. *Environ Biol Fish* 93:73–87. doi:[10.1007/s10641-011-9891-2](https://doi.org/10.1007/s10641-011-9891-2)
- Leatherland JF, Farbridge KJ, Boujard T (1992) Lunar and semi-lunar rhythms in fishes. In: Ali MA (ed) Rhythms in fishes. Plenum Press, New York, pp 83–107
- Mansur L, Catalán D, Plaza G, Landaeta MF, Ojeda FP (2013) Validations of the daily periodicity of increment deposition of eight species of intertidal rocky fishes in the South-eastern Pacific Ocean. *Rev Biol Mar Oceanogr* 48:629–633
- McDermontt CJ, Shima JS (2006) Ontogenetic shift in microhabitat preference of a temperate reef fish *Forsterygion lapillum*: implications for population limitation. *Mar Ecol Prog Ser* 320:259–266. doi:[10.3354/meps320259](https://doi.org/10.3354/meps320259)
- Mizushima N, Nakashima Y, Kuwamura T (2000) Semilunar spawning cycle of the humbug damselfish *Dascyllus aruanus*. *J Ethol* 18:105–108. doi:[10.1007/s101640070008](https://doi.org/10.1007/s101640070008)
- Munday PL, Hernaman V, Dixon DL, Thorrold SR (2011) Effect of ocean acidification on otolith development in larvae of a tropical marine fish. *Biogeosciences* 8:1631–1641. doi:[10.5194/bg-8-1631-2011](https://doi.org/10.5194/bg-8-1631-2011)
- Narváez DA, Poulin E, Leiva G, Hernández E, Castilla JC, Navarrete SA (2004) Seasonal and spatial variation of nearshore hydrographic conditions in central Chile. *Cont Shelf Res* 24:279–292. doi:[10.1016/j.csr.2003.09.008](https://doi.org/10.1016/j.csr.2003.09.008)
- Nelson JS (2006) *Fishes of the world*. Wiley, New Jersey
- Palma A, Ojeda FP (2002) Abundance, distribution, and feeding patterns of temperate reef fish in subtidal environment of the Chilean coast: the importance of understory algal turf. *Rev Chil Hist Nat* 75:189–200. doi:[10.4067/s0716-670X2002000100018](https://doi.org/10.4067/s0716-670X2002000100018)
- Pérez R (1979) Desarrollo postembrionario de Tripterygion chilensis Cancino 1955, en la Bahía de Valparaíso (Tripterygiidae: Perciformes). *Rev Biol Mar* 16:319–329
- Pérez-Matus A, Pledger S, Díaz FJ, Ferry LA, Vásquez JA (2012) Plasticity in feeding selectivity and trophic structure of kelp forest associated fishes from northern Chile. *Rev Chil Hist Nat* 85:29–48. doi:[10.4067/s0716-078X2012000100003](https://doi.org/10.4067/s0716-078X2012000100003)
- Plaza G, Landaeta MF, Espinoza CV, Ojeda FP (2013) Daily growth patterns of six species of young-of-the-year of Chilean intertidal fishes. *J Mar Biol Ass UK* 93:389–395. doi:[10.1017/s0025315412000859](https://doi.org/10.1017/s0025315412000859)
- Pulgar J, Poblete E, Alvarez M, Morales JP, Aranda B, Aldana M, Pulgar VM (2013) Can upwelling signals be detected in intertidal fishes of different trophic levels? *J Fish Biol* 83:1407–1415. doi:[10.1111/jfb.12220](https://doi.org/10.1111/jfb.12220)
- Robertson DR, Petersen CW, Brawn JD (1990) Lunar reproductive cycles of benthic-brooding reef fish: reflections of larval biology or adult biology? *Ecol Monogr* 60:311–329. doi:[10.2307/193060](https://doi.org/10.2307/193060)
- Ruck JG (1973) Development of *Tripterygion capito* and *T. robustum* (Pisces: Tripterygiidae). *Zool Publ Vic Univ Wellingt* 63:1–10
- Ruck JG (1980) Early development of *Forsterygion varium*, *Gilloblennius decemdigitatus*, and *G. tripennis* (Pisces: Tripterygiidae). *N Z J Mar Freshw Res* 14:313–326. doi:[10.1080/00288330.1980.9515874](https://doi.org/10.1080/00288330.1980.9515874)
- Russell GS, Levitin DJ (1995) An expanded table of probability values for Rao's spacing test. *Commun Statist Simula* 24:879–888. doi:[10.1080/03610919508813281](https://doi.org/10.1080/03610919508813281)
- Santos JN, Silva MA, Vasconcellos RM, Araújo FG (2005) Efeito do tempo de conservacao dos espécimes sobre a qualidade dos microincrementos em otolitos *sagittae* de *Anchoa tricolor* (Agassiz) (Clupeiformes, Engraulidae). *Rev Bras Zool* 22:949–952
- Smith AC, Shima JS (2011) Variations in the effect of larval history on juvenile performance of a temperate reef fish. *Austral Ecol* 36:830–838. doi:[10.1111/j.1442-9993.2010.02223.x](https://doi.org/10.1111/j.1442-9993.2010.02223.x)
- Sponaugle S (2010) Otolith microstructure reveals ecological and oceanographic processes important to ecosystem-based management. *Environ Biol Fishes* 89:221–238. doi:[10.1007/s10641-010-9676-z](https://doi.org/10.1007/s10641-010-9676-z)
- Sponaugle S, Pinkard D (2004) Lunar cyclic population replenishment of a coral reef fish: shifting patterns following oceanic events. *Mar Ecol Prog Ser* 267:267–280. doi:[10.3354/meps267267](https://doi.org/10.3354/meps267267)
- Takemura A, Rahman MS, Park YJ (2010) External and internal controls of lunar-related reproductive rhythms in fishes. *J Fish Biol* 76:7–26. doi:[10.1111/j.1095-8649.2009.02481.x](https://doi.org/10.1111/j.1095-8649.2009.02481.x)
- Williams JT, Springer VG (2001) Review of the South American Antarctic triplefin fish genus *Helcogrammoides* (Perciformes: Tripterygiidae). *Rev Biol Trop* 49(Suppl. 1):117–123
- Zar JH (1999) *Biostatistical analysis*. Prentice Hall, New Jersey
- Zenteno JI, Bustos CA, Landaeta MF (2014) Larval growth, condition and fluctuating asymmetry in the otoliths of a mesopelagic fish in an area influenced by a large Patagonian glacier. *Mar Biol Res* 10:504–514. doi:[10.1080/17451000.2013.831176](https://doi.org/10.1080/17451000.2013.831176)