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ORIGINAL PAPER

The effects of a parasitic copepod on the recent larval growth of a fish inhabiting rocky coasts

Pamela Palacios-Fuentes · Mauricio F. Landaeta · Gabriela Muñoz · Guido Plaza · F. Patricio Ojeda

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Abstract Parasites can infect larval, juvenile or adult marine fishes; however, the effects of parasites on the growth and condition of fish larvae have seldom been investigated. This study analysed the effects of a parasitic copepod on the larval growth of the Chilean triplefin *Helcogrammoides chilensis* (Tripterygiidae) based on the microstructure of the sagittal otoliths. Fish larvae were collected during the austral spring of 2010 off central Chile. Their body length ranged from 5.1 to 16.6 mm (2 to 57 days old). They were parasitised by a penellid larval copepod that was always externally attached to the ventral side of the fish's gut. The prevalence of the copepod ranged from 2.7 % to 20.8 %, with one to four parasites per fish larva. Relationships between otolith size (radius, perimeter) and larval size were equal for parasitised and unparasitised fish larvae ($P>0.05$). Larval growth was also similar for unparasitised (0.21 mm/day) and parasitised fish larvae (0.19 mm/day) ($P>0.05$). However, a comparison of same-aged larvae showed that the larvae with copepods were smaller in both length and estimated body volume than the larvae without copepods. The Recent Otolith Growth Index, indicated that larval *H. chilensis* with copepods showed a reduction in recent growth and condition compared with those without evidence of copepods ($P<0.05$). Nevertheless, a higher parasite load (two vs. one pennellids) did not decrease the condition of the larval fish. The infestation of pennellids on coastal fish larvae may therefore induce an increase in the pelagic larval duration and potentially affect the settlement rates of this intertidal fish.

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: mauricio.landaeta@uv.cl

G. Muñoz
Laboratorio de Parasitología, Facultad de Ciencias del Mar y de Recursos Naturales, Universidad de Valparaíso,
Avenida Borgoño 16344, Reñaca,
Viña del Mar, 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

Introduction

Parasite diversity in marine fish is widely known, especially for those fish that have economic importance, because a parasite may produce several types of negative effects in its host. For example, the parasite may affect the host's, somatic growth, reproduction, behaviour (Ho 2000; Pino-Marambio et al. 2007) and/or survival (Loot et al. 2004) and consequently affect the commercial value of a biological resource (Yuniar et al. 2007; Antonelli et al. 2012). The major consequences of parasitism on any host may include physiological or mechanical effects. Physiological effects include the drain of metabolic resources or a reaction of the host, locally or generally, to the invasion of tissues or secretions by the parasite, resulting in a decreased activity level (Neilson et al. 1987). In contrast, mechanical effects imply that the presence of the parasites produce pressure on the tissues or organs of the host, altering their functionality (Coustau et al. 1991).

Young fish are in early stages of immunological and general physiological development (Uribe et al. 2011).

Therefore, it is probable that they are more vulnerable to the effects of parasites than adult fish (Fogelman and Grutter 2008). For these reasons, larval and juvenile fish can be dramatically affected by parasites (e.g. Fogelman and Grutter 2008; Jones and Grutter 2008; Grutter et al. 2010a). For instance, postlarval fishes may suffer from stress caused by hydrodynamic drag at low Reynolds numbers due to the size of the parasites relative to the length of the fish. This disadvantage may affect the ability of the host to capture prey and avoid predators (Felley et al. 1987). Indeed, the prey uptake by herring larvae infected with the cestode *Scolex pleuronectis* was 50 % lower than for unparasitised fish in the North Sea (Heath and Nicoll 1991). It is therefore plausible that a reduction of prey capture, together with the direct impact of infestation, depresses the growth and survival of larvae and juvenile fish (Mladineo 2003; Jones and Grutter 2008). Specific cases have been described, particularly for fish larvae. For example, anchoveta larvae parasitised by caligid copepods were smaller at the same age than larvae without parasites (Herrera 1990), and parasitised juvenile cardinal fish were 3–9 % shorter than unparasitised fish (Fogelman and Grutter 2008). More recently, Grutter et al. (2010a) found that coral reef fish *Pomacentrus moluccensis* with internal parasites had lower larval growth than conspecific larvae without parasites, based on growth rates estimated from hatching or after settlement.

For those fish species with a bipartite life cycle (pelagic, dispersive larval stage and demersal juvenile), the infection of larvae with ecto- and/or endoparasites affecting larval growth may increase the pelagic larval duration (PLD), the time that an individual spends in the vulnerable larval stages before settlement. Then, small length-at-age and/or low individual growth rates (the latter generally based on measurements of otolith microstructure) due to parasitism can serve as a proxy for estimating individual survival probabilities (Dower et al. 2009). Growth rates and growth history in fishes can be determined by analysing the microstructure of otoliths. The increment width has been utilised as an indicator of feeding rates (Folkvord et al. 1997; Aguilera et al. 2009), effects of environmental factors (Oozeki and Watanabe 2000; Landaeta and Castro 2006; Landaeta et al. 2011) and condition (Paperno et al. 1997).

The family Tripterygiidae is composed of 29 genera and includes 163 species. The family is distributed worldwide in polar, temperate and tropical regions (Kohn and Clements 2011). In Chile, tripterygiids are represented by three species, *Helcogrammoides chilensis* (Cancino in De Buen 1960), *Helcogrammoides cunninghami* (Smitt 1898) (Pérez 1979; Pequeño 1989) and *Helcogrammoides antarcticus* (Tomo 1981) (Williams and Springer 2001; Cancino et al. 2010). Species of this family have a bipartite life cycle. Demersal eggs develop attached to the substrate (Rico et al. 2010) and hatch after 20 days into a planktonic larvae that settles within 2 to 3 months (Kohn and Clements 2011). Juvenile and adult stages are carnivorous (Berrios and Vargas 2004; Boyle and Horn 2006; Rojas and Ojeda 2010), feeding on small prey with high motility and high energetic value (e.g. amphipods, isopods and harpacticoid copepods) (Muñoz and Ojeda 1998; Berrios and Vargas 2004). The Chilean triplefin, *H. chilensis*, distributed between Iquique (20°18′ S) and Talcahuano (36°45′ S), lives in the highly exposed rocky intertidal zone (Williams and Springer 2001; Cancino et al. 2010), where its larvae are highly abundant in plankton samples throughout the year in central Chile (Pérez 1979; Hernández-Miranda et al. 2003; Landaeta et al. 2008).

In view of the high abundances of *H. chilensis* in central Chile and the previous studies of ectoparasites, including copepods, in this species (Herrera 1990), our objective is to determine the potential effects of parasitic copepods on the growth rates of *H. chilensis* larvae. Therefore, we hypothesise that copepods have a negative effect on the recent growth and condition of intertidal fish larvae. This effect can be measured by analysing the microstructure of the otolith.

Methods

Fieldwork

Three oceanographic collections were performed during September and October 2010 on board the RV Ilán, a vessel from the Pontificia Universidad Católica de Chile. Hydrographic data were obtained with vertical tows of a conductivity–temperature–depth profiler (Seabird SBE-19 CTD, Seabird Electronic, Inc.; Bellevue, Washington, USA) from the surface to near-bottom depths (~20 m) during the dawn period and at night (1,900 to 2,300 h). These tows were made 1 nautical mile off El Quisco Bay (33°24′ S, 71°43′ W). Ichthyoplankton samples were collected using a Bongo net (60 cm mouth diameter, 300 μm mesh size) equipped with two TSK flow meters (The Tsurumi-Seiki Co., Ldt.; Tsurumi-ku, Yokohama, Japan) to quantify the water filtered. Five to eight trawls at 1–2 knots were completed during each oceanographic sample in the same location. The volume of seawater filtered by the net ranged from 34.1 to 316.4 m^3/tow (mean ± one standard deviation, 201.5±76.5 m^3/tow). All plankton samples (n=38) were initially fixed with 5 % formalin buffered with sodium borate. After 12 h, they were preserved in 96 % ethanol.

Laboratory work

In the laboratory, all fish eggs and larvae were removed and counted, and larval triplefin *H. chilensis* were identified following Pérez (1979). A randomly selected group of undamaged larvae of *H. chilensis* were observed. The body length (BL) was measured to the nearest 0.01 mm from the

Table 1 Summary of results for larval abundance of triplefin *H. chilensis* (mean, standard deviation or SD, median) and ectoparasite prevalence, obtained during three cruises conducted during the austral of spring 2010 off El Quisco Bay, central Chile

Date	No. of larvae	Larval abundance (individual per 1,000 m^3) Mean ± SD	Median	Prevalence (%)
2 September 2010	86	49.81±24.10	43.83	14.24
9 September 2010	539	542.16±750.46	231.37	2.67
4 October 2010	259	88.72±88.17	77.36	20.80

tip of the upper maxilla to the tip of the notochord in preflexion larvae (notochord length) and to the base of the hypurals in flexion and postflexion larvae (standard length). Larval height (LH) was measured from the base of the pectoral fins with a Moticam 2500 of 5.0 MPx (Motic Instrument, Inc.; Richmond, BC, Canada) connected to a stereomicroscope Olympus SZ-61 (Olympus Corporation, Shinjuku-ku, Tokyo, Japan) and Motic Images Plus 2.0 software (Motic China Grup, Co.; Xiamen, China). Larval volume was estimated as BL × $(LH)^2$ (Hovenkamp and Witte 1991). No attempt was made to correct the lengths for the effects of preservation. Larval triplefin were converted to abundance (numbers, 1,000 m^{-3}) based on the filtered volume estimated by the flow meters.

External parasites were identified according to their buccal structure and appendages (Castro and Baeza 1986, 1989). The prevalence of parasites corresponds to the percentage of hosts in a sample parasitised by a certain parasite species (Bush et al. 1997).

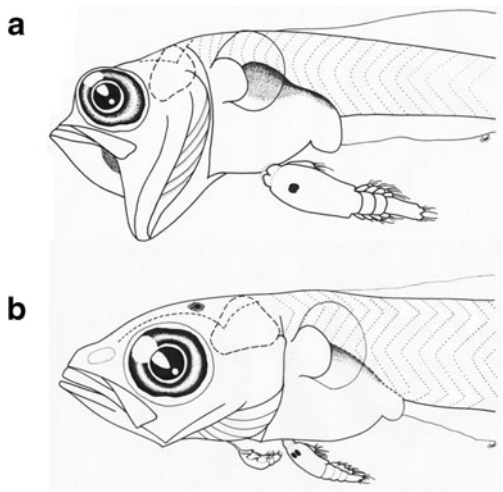

Fig. 1 Anterior portion of larvae of triplefin *H. chilensis* parasitised with Pennellidae on the ventral side of the gut. **a** Preflexion larvae of 6.3-mm BL with one ectoparasite; **b** postflexion larvae of 10.1-mm BL with two ectoparasites

Left and right sagittal and lapilli otoliths were dissected from a subsample of randomly selected infected and non-infected larvae (n=99, from 5.13 to 16.57 mm in length) as described by Landaeta and Castro (2006). The otoliths were embedded in epoxy resin on a glass slide and observed under transmitted light with a Motic BA310 compound microscope (Motic Instrument, Inc.; Richmond, BC, Canada) at ×1,000 magnification under oil immersion. The longest radius of the otoliths was measured three times. The average of these three values was used for the analyses. The perimeter and area of the otoliths were measured once with Motic Image Plus 2.0 software. The fish age (days) was estimated by counting the number of increments, starting from a conspicuous dark mark near the primordium (hatch check). Three independent readings were made on each sagitta. Because the lapilli were difficult to read, their readings were discarded. The mode of the three readings was selected. If all counts were different, the mean value was estimated. Because the counts of the left and right sagittal otoliths were the same (Wilcoxon paired test, P=0.86), the counts of the left sagittal otolith were used for the analysis. The daily formation of the increments has recently been validated for *H. chilensis* (Lidia Mansur, Pontificia Universidad Católica de Chile, personal communication).

Data analysis

Least-squares linear regression analyses were performed between otolith measurements (radius, perimeter) and larval length for both unparasitised (UPL) and parasitised (PL) larvae. The larval size and otolith area were related by exponential models. The relationships between otolith shape and body size from UPL and PL larvae were compared with a multiple slope test (Zar 1999). Estimates of larval growth were obtained using least-square linear regression models as a first approach. The growth analyses were performed separately for both groups of *H. chilensis* larvae. The slope for each group was used as the population growth rate of that group. The slopes were then compared with a multiple slope test (Zar 1999). Because the growth rates did not differ significantly between groups (multiple slope test, $|t|$=0.35; P>0.05), a residual analysis was performed after a unique linear fit was adjusted for all larvae.

Increment widths cannot be compared directly (Hovenkamp and Witte 1991) because if microincrements that were formed at different radii are compared, the increment of the largest radius, on average, will be wider. To estimate a recent otolith growth index (ROGI) for the UPL and PL larvae, the residuals of the relationship between the sum of the widths of the most recent five increments and the radius of the otolith were calculated. The rationale for residual analysis is that because a residual is a measure of an individual's departure from the population, it can be viewed as an indicator of condition

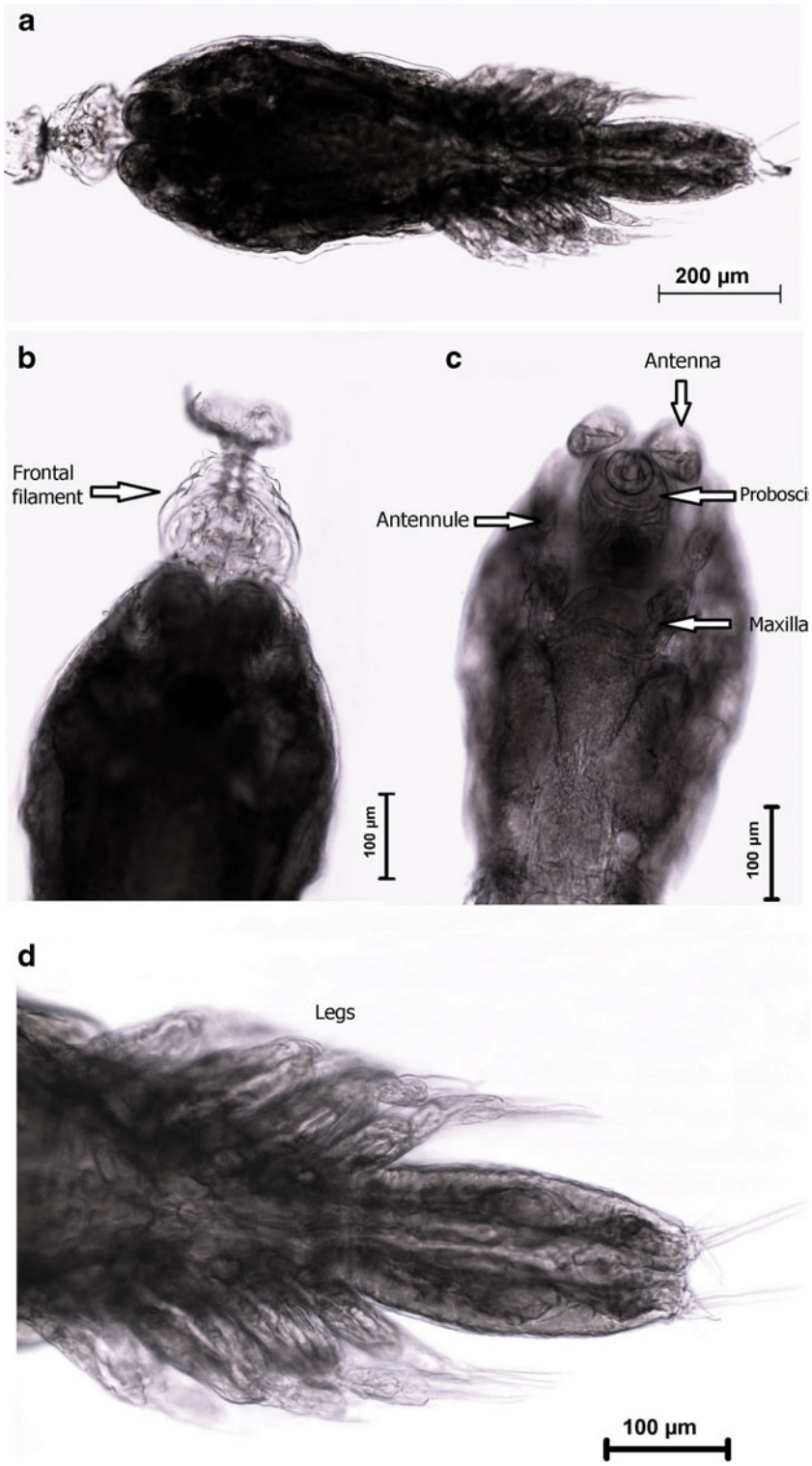

Fig. 2 **a** Chalimus copepod of family Pennellidae, **b** frontal filament for attachment, **c** detail of antennae and antennules and the proboscis, **d** abdominal appendages

(Aguilera et al. 2009). According to this relationship, the residuals of the regression will be positive if the increment width is greater than expected. This outcome indicates that the amount of otolith growth has been greater than average. If the increment width is smaller than expected, the residuals will be negative. This outcome means that the amount of otolith growth has been less than average. Finally, the ROGIs of UPL and PL larvae were compared with a Mann–Whitney *U* test. This test was also used to compare the ROGIs of larvae with one and two ectoparasitic copepods.

Because certain authors have questioned the use of the residual analysis (García-Berthou 2001), we proposed an

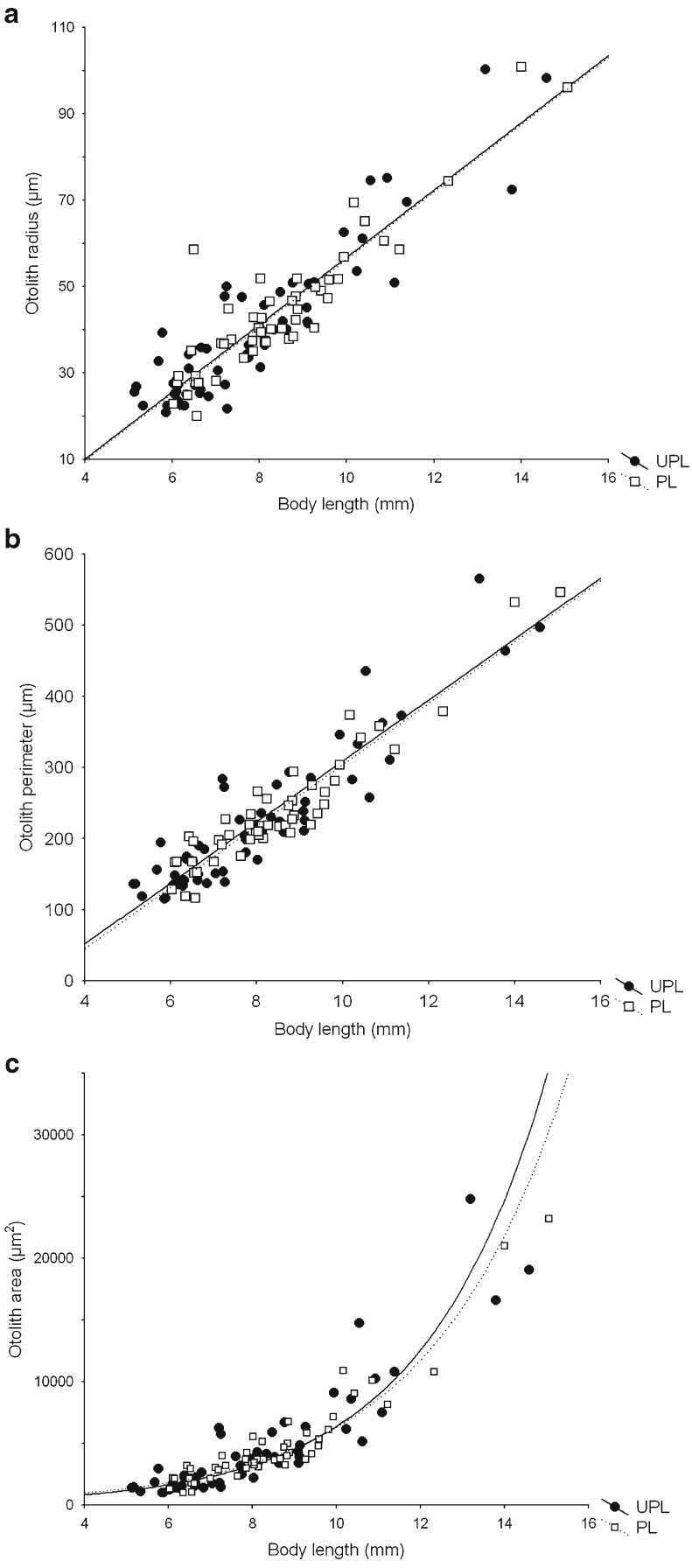

Fig. 3 Relationships between otolith shape and larval size for unparasitised (*UPL*) and parasitised (*PL*) larvae. **a** Linear fit between sagittal radius and body length, **b** linear fit between sagittal perimeter and body length, **c** exponential model of relationship between otolith area and larval length

alternative analysis to compare the larval condition between PL and UPL. In this analysis, both variables (the sum of the five outermost increment widths, excluding the last one, and the largest radius of the sagittal otolith) were log transformed so that the variances would be independent of the mean. Regression analyses were then performed for PL and independently for UPL. Finally, both linear regressions were compared with a multiple slope test.

Results

The abundance of larval *H. chilensis* at El Quisco Bay ranged from 3.55 to 2,344.44 individuals per 1,000 m^3 during the austral spring 2010 (mean ± standard deviation, 202.78±440.38 individuals per 1,000 m^3; median, 81.01 individuals per 1,000 m^3). There were significant differences in larval abundance among cruises (Kruskal–Wallis test, H=15.11, P<0.001; Table 1), with the largest abundance found in the second sample (median = 231.37 individuals per 1,000 m^3). The prevalence of ectoparasites ranged from 2.7 % to 20.8 %, with the lowest prevalence detected during the second sample (Table 1). The number of ectoparasites found for larval *H. chilensis* ranged from one to four. The parasite was always attached to the ventral side of the gut irrespective of the size of the larvae (Fig. 1a, b).

The ectoparasites were found to belong to the chalimus stages (I to IV, having a frontal filament; Fig. 2a, b) of the family Pennellidae, which are characterised by a proboscis (buccal cone; Fig. 2c). The first two pairs of legs are biramous, whereas the third and fourth are uniramous (Fig. 2d).

The otolith size estimators showed significant relationships with body size (Fig. 3; Table 2), indicating that the somatic growth of the UPL and PL larvae is reflected by the growth of the sagittal otoliths. There were no significant differences in the relationship between otolith radius and body length for the UPL and PL groups (multiple slope test, $|t|$=1.93; P>0.05) or between otolith perimeter and body length ($|t|$=2.04; P>0.05). However, the otolith area of the UPL grew more rapidly as a function of body length than the otolith area of the PL ($|t|$=1.735; P<0.001).

The age estimates based on the readings of the sagittal otoliths ranged from 2 to 57 days. For this period, the linear regression models estimated larval growth rates of 0.19 mm/day for PL and 0.21 mm/day for UPL (Table 3). However, there were no significant differences between the slopes of the linear models (i.e. the population larval growth rates) (multiple slope test, $|t|$=0.35; P<0.05) (Fig. 4a). A linear model for both groups of data was adjusted (total in Table 3), and the residual analyses indicate that the residuals of the PL were generally negative (−0.096±0.426). These results show that larval *H. chilensis* with ectoparasites were shorter than predicted by the model. This trend was evident from the comparisons of the relationships between the estimated larval volume (BL × $(LH)^2$) and age (Fig. 4b) in the UPL and PL groups. Although the slopes of the models were similar (i.e. the growth rates are the same), the intercept for the PL was smaller than the intercept for the UPL (Table 3). This result indicates that at the same age, the PL were smaller in volume than the UPL.

There was a significant relationship between the outermost five microincrements and the sagitta radius (n=71, r^2=0.75; P<0.01) for all analysed larvae. The estimated ROGI values were significantly lower for the PL than for the UPL (Mann–Whitney U test, U=308; P<0.01). This result shows that a reduction in the condition of the PL larvae occurred at least 5 days before capture. Accordingly, the linear regressions of the logarithm of the outermost five microincrements and the logarithm of the radius were compared between the UPL (Fig. 5a) and the PL (Fig. 5b) and showed a significant reduction in the condition of the PL group (multiple slope test, $|t|$=3.83; P<0.05). Finally, the ROGI values were similar for larval *H. chilensis* infested with one and two copepods (Mann–Whitney U test, U=164; P=0.976). This result indicated that a greater parasite load did not induce a heavier impact on the recent growth and condition of the larvae (Fig. 6).

Table 2 Linear regression analysis of otolith size (radius, perimeter and area of the sagitta) as a function of BL for UPL and PL larvae of *H. chilensis*

	Intercept	SE	Slope	SE	F	*P*
Radius UPL vs BL	−21.02	3.9	7.78	0.48	268.32	<0.01
Radius PL vs BL	−21.43	4.34	7.78	0.49	248.68	<0.01
Perimeter UPL vs BL	−119.64	20.41	42.89	2.47	301.69	<0.01
Perimeter PL vs BL	−127.35	19.2	43.15	2.2	383.52	<0.01
Log area UPL vs BL	0.92	0.16	2.91	0.18	273.03	<0.01
Log area PL vs BL	0.95	0.17	2.87	0.18	249.91	<0.01

Intercept, slope, corresponding standard errors (SE), F and *P* values are shown

Table 3 Linear regression analysis of larval size (BL and LV) as a function of age (MC) for UPL, PL and total larvae of *H. chilensis*

	Intercept	SE	Slope	SE	F	*P*
BL vs MC (UPL)	5.91	0.12	0.21	0.08	648.09	<0.01
BL vs MC (PL)	5.98	0.1	0.19	0.05	987.99	<0.01
BL vs MC (total)	5.93	0.08	0.20	0.05	1,415.7	<0.01
Log LV vs Log MC (UPL)	0.34	0.03	0.83	0.04	545.23	<0.01
Log LV vs Log MC (PL)	0.28	0.04	0.80	0.04	433.44	<0.01

Intercept, slope, corresponding standard errors (SE), F and *P* values are shown

LV larval volume, *MC* microincrement counts

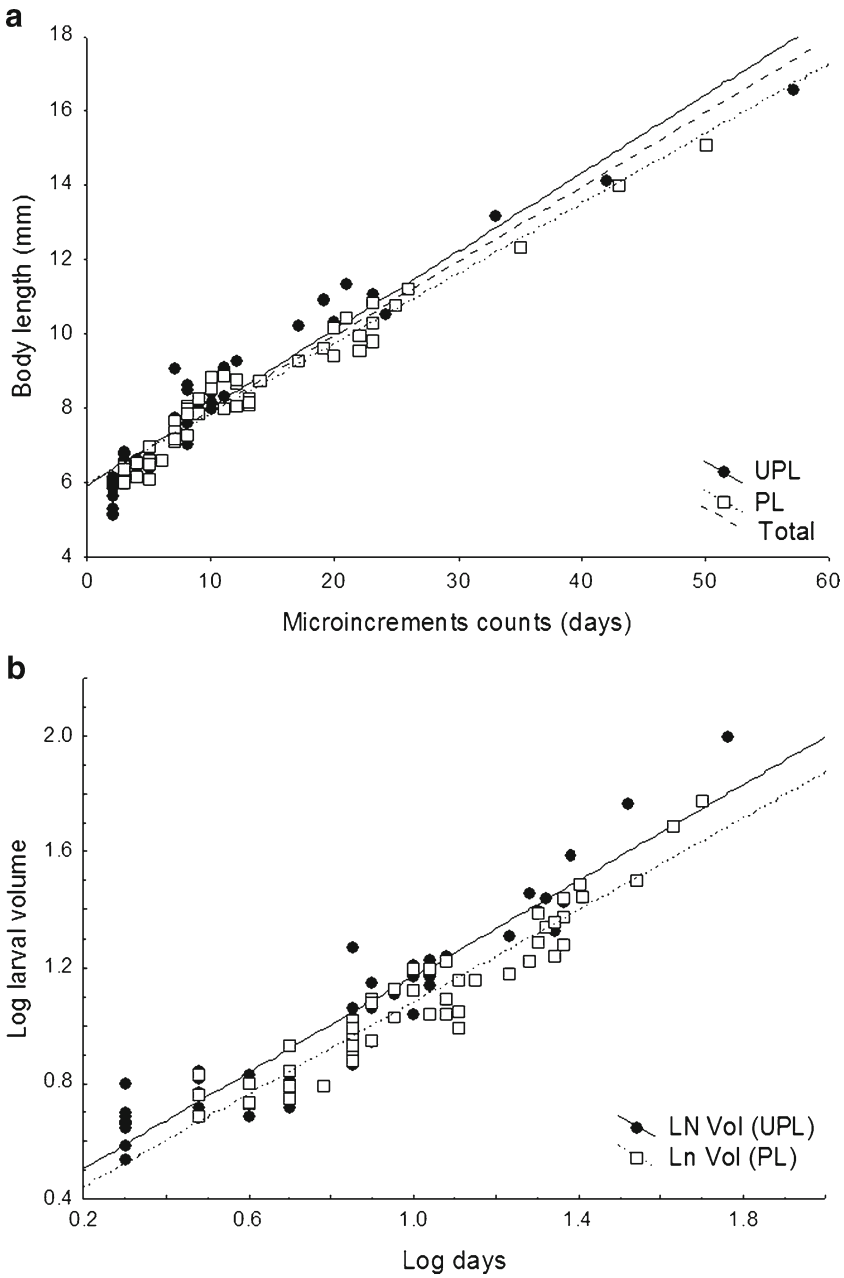

Fig. 4 Larval growth of *H. chilensis* with caligid ectoparasites (*PL*, *white squares*) and without ectoparasites (*UPL*, *black circles*) in terms of **a** body length (millimetres) and **b** total volume (cubic millimetre)

Discussion

Based on otolith microstructure, our study reveals the negative effect of parasitism by chalimus pennellids on the recent growth and condition of larval triplefin *H. chilensis* in the coastal waters of central Chile during the austral spring season.

The prevalence of ectoparasites found in this study was higher than that found for other fish larvae, even considering that local conditions, such as temperature can influence rates of infestation (Antonelli et al. 2012). For example, ectoparasite prevalence ranged between 0.9 % and 4.7 % for larval anchoveta *Engraulis ringens* (Herrera 1990), and ectoparasite prevalence was 3.6 % for larval anchovy *Anchoa* sp. on Chilean waters. In larval *P. moluccensis*, ectoparasite prevalence was 4 %, and only digenea were observed (Grutter et al. 2010a). A partial explanation for this difference may be that demersal eggs might be more susceptible to predation than planktonic eggs because planktonic eggs are not associated with parental behaviour and have more superficial larvae by the time they hatch (Grutter et al. 2008). Note, nevertheless, that parasitism by Pennellidae in adult *H. chilensis* has not yet been observed (Muñoz and Delorme 2011). This apparent absence could indicate that these larvae are only intermediate and/or alternative hosts in the life cycle of pennellids. Or this could mean that there is variability in the preference for a specific host; this situation is observed in *Argulus coregoni*, in which the parasite turns specificity when reaching a given length (Mikheev et al. 2004).

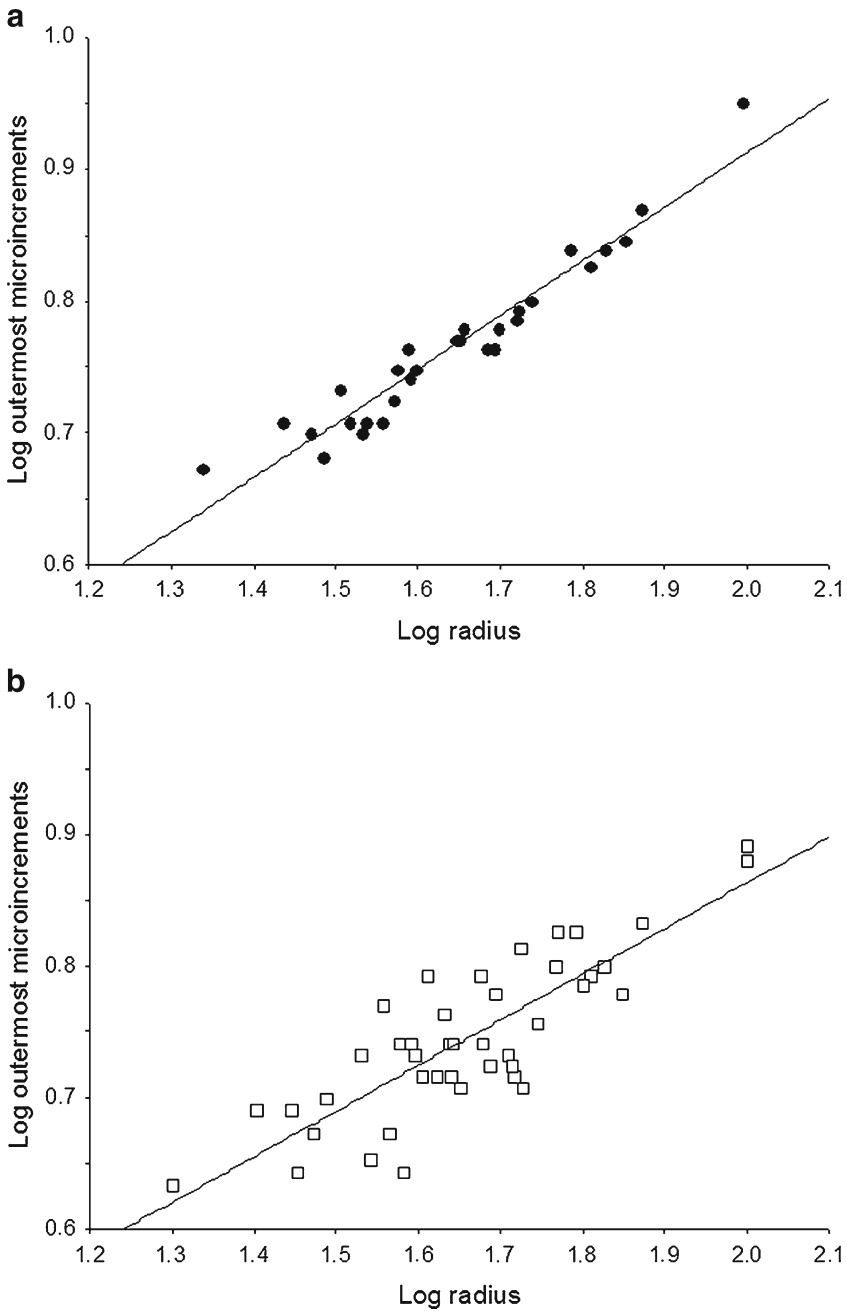

Fig. 5 Linear relationship between log-transformed data of sagittal radius and length of outermost 5 microincrements for **a** unparasitised larvae (UPL, *black circles*) and **b** parasitised larvae (PL, *white squares*)

The PL larvae showed a lower ROGI. This finding implies that they are also in poorer condition (Grutter et al. 2010b). The differences in condition between the PL and the UPL may indicate a rapid response of individual larvae to parasitism. This response takes the form of a decrease in the instantaneous growth rates of the larvae (i.e., the growth rates during the past 5 days). This response is more rapid than that described for newly settled cardinal fish larvae, which exhibited reduced growth within 10–15 days (Fogelman and Grutter 2008).

H. chilensis did not show more than four parasites in the ventral region. This finding is consistent with the explanation offered, who suggest that the intensity of parasitism shown by a potential host will result from the amount of available surface area furnished by the host, which means that the smaller the host is, it may be less parasitized (Antonelli et al. 2012). It may also be influenced by biological factors, such as the distribution of the hosts during the critical infective stage (Loot et al. 2004). In this sense, a study on *Scartichthys viridis* (Blenniidae) revealed that prevalence, abundance and richness of parasites infracommunities increased significantly with the monthly increased total length (Muñoz and Randhawa 2011).

Nevertheless, our data failed to demonstrate a significant difference in larval condition between larvae infested with

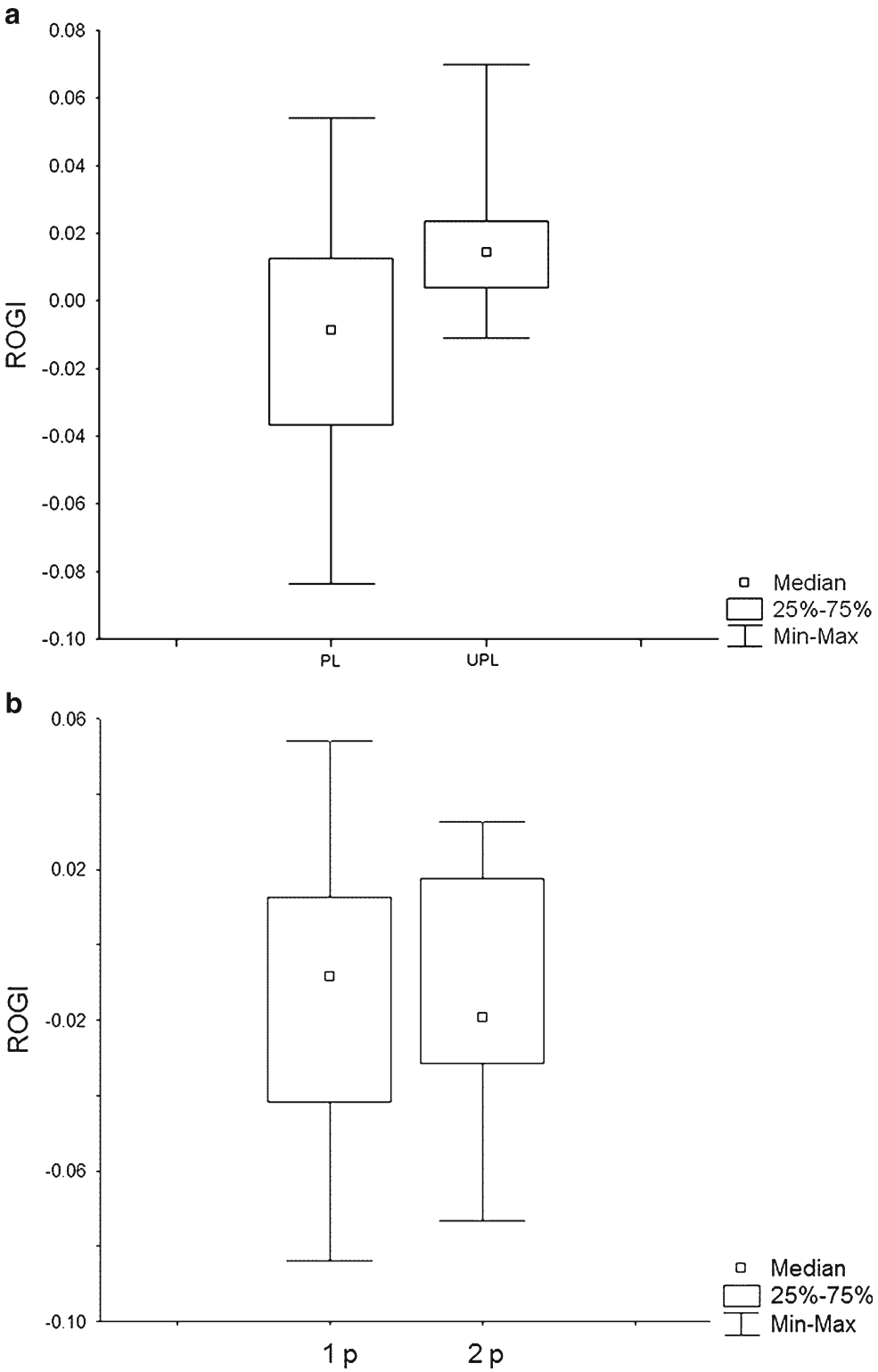

Fig. 6 *Box-and-whisker plots* of ROGI values for **a** unparasitised (UPL) and parasitised (PL) larvae of *H. chilensis* and **b** parasitised larvae with one (**a**) or two copepods (**b**). Median, quartiles, minimum and maximum values of ROGI are shown

one or two parasites. Similarly, Grutter et al. (2008) found that mortality rates did not vary significantly for different fishes exposed to one or three ectoparasites.

The larval stages of fishes are at great risk of parasitism. If they are parasitised, one of the consequences of such parasitism is the probability that direct mortality will be induced by the parasites (Fogelman and Grutter 2008; Fogelman et al. 2009; Grutter et al. 2008, 2010b). Although not all ectoparasites may directly produce lethal effects on fish larvae (Herrera 1990), other sub-lethal effects or stresses may be produced in the hosts (Felley et al. 1987), or even a pathological effects (Loot et al. 2004). For

example, Rigby and Dufour (1996) propose an increased susceptibility to predation or a reduction in competitive fitness. These sub-lethal effects were reflected in a reduction of the individual size of the PL. Although the PL and the UPL grew at the same rate (i.e. similar slopes), the PL were 1.88 % shorter than the UPL. Similarly, newly settled larval *Apogon trimaculatus* infested with mancae of cymothoids grew at the same rate (similar slope) but were 9 % shorter than uninfested individuals (Fogelman and Grutter 2008). Analogous results were found for adult *Cheilodipterus quinquelineatus* infested with *Anilocra apogonae*. The infested fish were shorter and weighed less than unparasitised fish at the same age, but the growth rates of the two groups were the same (Fogelman et al. 2009).

The effects of attached ectoparasites on larvae include an increase in hydrodynamic drag. This increase affects the swimming ability of the larvae. Because it is harder for the larvae to swim, they have more difficulty escaping predators (Herrera 1990). Reductions in swimming ability in the fish species *Acanthochromis polyacanthus* and *Neopomacentrus azysron* caused by the attached parasite *Gnathia* sp. are described by Grutter et al. (2008). The behaviour of the fish was altered. They had difficulty swimming or balancing, and they even became stationary at the bottom in certain cases. Moreover, attached ectoparasites may increase the visibility of larvae to predators (Herrera 1990).

All the effects cited above produce greater energetic costs for the larvae and retard their growth. These effects on larval energetics and growth will indirectly affect the settlement of the larvae and increase their PLD (Grutter et al. 2010b). During the additional time the larvae must spend in the plankton, they are susceptible to predation and have difficulty foraging. These factors jeopardise their survival. In conclusion, pennellids can indirectly affect the survival rates of individual *H. chilensis* larvae.

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