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Larval growth of two species of lanternfish at nearshore waters from an upwelling zone based on otolith microstructure analyses

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Summary

Larval growth and hatching days of lanternfishes *Diogenichthys laternatus* and *Myctophum nitidulum* (Myctophidae) collected in September 2012 in nearshore waters (<1 km offshore) at Mejillones Bay, northern Chile, were estimated on the basis of microstructure analyses of sagitta otoliths, to establish potential differences in early traits of both species from the productive coastal waters of the Humboldt Ecosystem. Growth increments were well defined, and no accessory primordia were observed in the analyses of the largest individuals in either species (8.61 and 9.17 mm BL, respectively). Both larval species displayed slow and similar growth rates: 0.057 ± 0.016 mm day^{-1} for *D. laternatus*, and 0.061 ± 0.005 mm day^{-1} for *M. nitidulum*. A large variability in the size-at-age in larvae of both species was detected. However, a recent otolith growth index showed all *M. nitidulum* in similar condition 5 days before capture, but with three *D. laternatus* in better condition and only one in a poorer condition than the other *D. laternatus* individuals. Growth trajectories estimated by the microincrement width of sagitta otoliths, indicated the presence of fast- and slow-growing larvae for both species. Also, the back-calculated 'birth' days suggest a large hatching pulse for *D. laternatus* near the third-quarter moon. The small sampling size of *M. nitidulum* precluded a robust conclusion on hatching patterns, although most individuals were hatched between the third quarter and the new moon. It is suggested that the slow growth rates estimated for both larval species might be caused by cold waters from upwelling events and/or allometric growth during early development of these lanternfish.

Introduction

Myctophid larvae are the most abundant and speciose group and an important part of oceanic larval fish assemblages (Sassa et al., 2002; Olivar et al., 2012). The morphology of myctophid larvae is quite diverse, with almost all typical body forms of teleost fishes represented among the larval myctophids. This diversity is related to the high variety of feeding habits among the myctophid larvae, allowing the co-existence of many different species (Conley and Hopkins, 2004; Sassa and Kawaguchi, 2005). However, few studies deal with larval growth strategies among myctophids (Linkowski, 1991, 1996; Linkowski et al., 1993; Conley and Gartner, 2009; Bystydzieńska et al., 2010).

In the Humboldt Current, the most abundant and recurrent larval species are *Diogenichthys laternatus* and *D. atlanticus* (Evseenko, 2006; Acuña and Cabrera, 2007). Larval *D. laternatus* occurs in shallower waters (0–20 m layer) during non-upwelling conditions, whereas in upwelling conditions the larvae are found below 20 m depth (Rojas et al., 2002). These larvae are opportunistic diel feeders and predate upon invertebrate eggs, nauplii, ostracods, copepods, copepodites, larval mollusks and polychaetes, juvenile Nemertea and tintinnids (Rodriguez-Graña et al., 2005).

Another important species in the Humboldt Current is *Myctophum nitidulum,* the second most important fish prey in the diet of the jumbo squid (Rosas-Luis et al., 2011). The larval period including metamorphosis is approximately 65 days, and the relationship between fish growth and otoliths changes as a function of the lunar phases (Giragosov and Ovcharov, 1992). In the Kuroshio Current, larval *M. nitidulum* occurs mainly in the 75–100 m layer (Sassa et al., 2002), and appears frequently off northern Chile but at low abundance during the austral spring season (Loeb and Rojas, 1988; Rojas et al., 2002).

The microstructure of larval *Diogenichthys laternatus* otoliths has not been examined previously. The daily character of growth increments in lanternfish otoliths (sagittae) has been observed and verified in tropical, subtropical and tropical-temperate myctophids during juvenile and adult stages (Gartner, 1991a,b; Suthers, 1996; Hayashi et al., 2001; Moku et al., 2001), as well as larval stages (Moku et al., 2005). A lunar periodicity in the deposition of the increments in *Myctophum asperum* has also been described (Hayashi et al., 2001). The 'larval zone' of the myctophid otoliths is formed during the presence of larvae in highly dynamic epipelagic layers (Greely et al., 1999) where they perform restricted diel vertical migrations (Sassa et al., 2007).

The goal of this research was to compare the early life histories of these two myctophid fish found in the coastal waters of an upwelling zone, on the basis of the sagittal otolith microstructure of the larvae.

Materials and methods

Larval *Diogenichthys laternatus* and *Myctophum nitidulum* were collected during the night in September 2012 at near-shore waters (<1000 km from shore) in Mejillones Bay (23°S, 71°W), northern Chile. Fish larvae were collected with oblique hauls using a standard bongo net (60-cm diameter, 300 μm mesh size) with one TSK flowmeter (Tsurumi-Seiki Co., Ltd., Yokohama, Japan) mounted in the frame of the net. Subsequently, the nets were washed onboard and all zooplankton samples (n = 32) were fixed initially with 5% formalin buffered with sodium borate and preserved in 96% ethanol after 12 h. Some studies have shown that formalin may damage otoliths of small specimens (Brothers, 1984); however, in other species formalin-preserved individuals (Ré, 1983), as well as the sagittal otoliths of small larval myctophids, showed no signs of any dissolving.

In the laboratory all larval fish were separated, counted and identified to the lowest possible taxon using characters as defined by Olivar and Fortuño (1991) and Moser (1996). The body length (BL), which corresponded to the notochord length (from the tip of the snout to the tip of the notochord in pre-flexion larvae) or the standard length (from the tip of the snout to the base of the hypural bones in inflexion and post-flexion larvae), was measured to the nearest 0.01 mm on each larva under an Olympus SZ-61 stereomicroscope (Olympus America Inc., Tokyo, Japan) with a 5.0M pixel, Moticam 2500 video camera connected to a PC with the Moticam Image Plus 2.0 software (Motic Group Co. Ltd., Xiamen, China).

Using insect needles, the left and right sagittae otoliths were removed from 117 larval *D. laternatus* (3.11–8.61 mm SL) and 21 larval *M. nitidulum* (3.32–9.17 mm SL) (Fig. 1). The conclusions based on the small number of *M. nitidulum* larvae for otolith microstructure analysis need to be considered with some caution. The otoliths were embedded in epoxy resin on glass slides. The daily age was determined by counting the number of otolith increments from the first distinguishable increment after the primordium or 'core' (Brothers, 1984), with a Motic BA310 light microscope (Motic Group Co. Ltd.) at ×1000 magnification under oil immersion. The longest radius of each sagitta was measured three times and the average used. The perimeters and areas of the otoliths were then measured once using the Moticam Image Plus 2.0 software.

Three independent counts were performed on both left and right sagittae. The counts were performed after a prominent hatch mark (Fig. 1). We consider the first mark in the sagitta otolith as a hatch mark rather than a yolk-sac exhaustion mark, taking into account that embryo development, hatching, and yolk-sac absorption occur very quickly in these fishes (Gjøsæter and Tilseth, 1988). When the coefficient of variation (CV = standard deviation/mean × 100) of the increment counts among the three readings was <5%, the average of the three counts was calculated and utilized for the analysis. When the CV was >5%, the otolith reading was discarded. Daily periodicity of growth increments has been described for *M. nitiludum* (Giragosov and Ovcharov, 1992), but those of *D. laternatus* have not been validated. Daily increments has been observed and verified in tropical, subtropical, and subtropical-temperate myctophids (Gartner, 1991a; Suthers, 1996; Hayashi et al., 2001; Moku et al., 2001, 2005), and therefore we assume that this is the case with *D. laternatus* otoliths. Age estimates using the left and right sagittae within individuals were the same for *D. laternatus* (Wilcoxon signed-rank test, $W = 313.5$, $P = 0.19$) and *M. nitidulum* ($W = 8.5$, $P = 0.78$), thus the right sagittae were utilized for the analyses.

Microincrement widths cannot be compared directly (Hovenkamp and Witte, 1991) because if microincrements 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 both species, 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

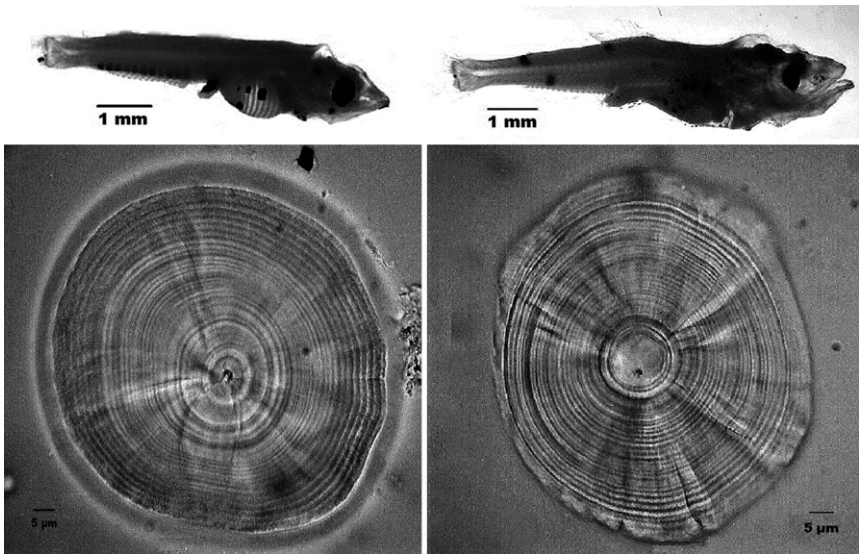

Fig. 1. Photographs of larval myctophids and their sagitta otoliths (left, *Diogenichthys laternatus*; right, *Myctophum nitidulum*).

a residual is a measure of an individual's departure from the population, it can be viewed as an indicator of condition (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. Additionally, an outlier analysis was carried out, to identify those individuals that were in the best/worst condition (deviations of the size-at-age).

The back-calculated hatching days were related to the lunar cycle. The days after the new moon were counted (DNM), and thereby assigned DNM values from 0 to 29, in

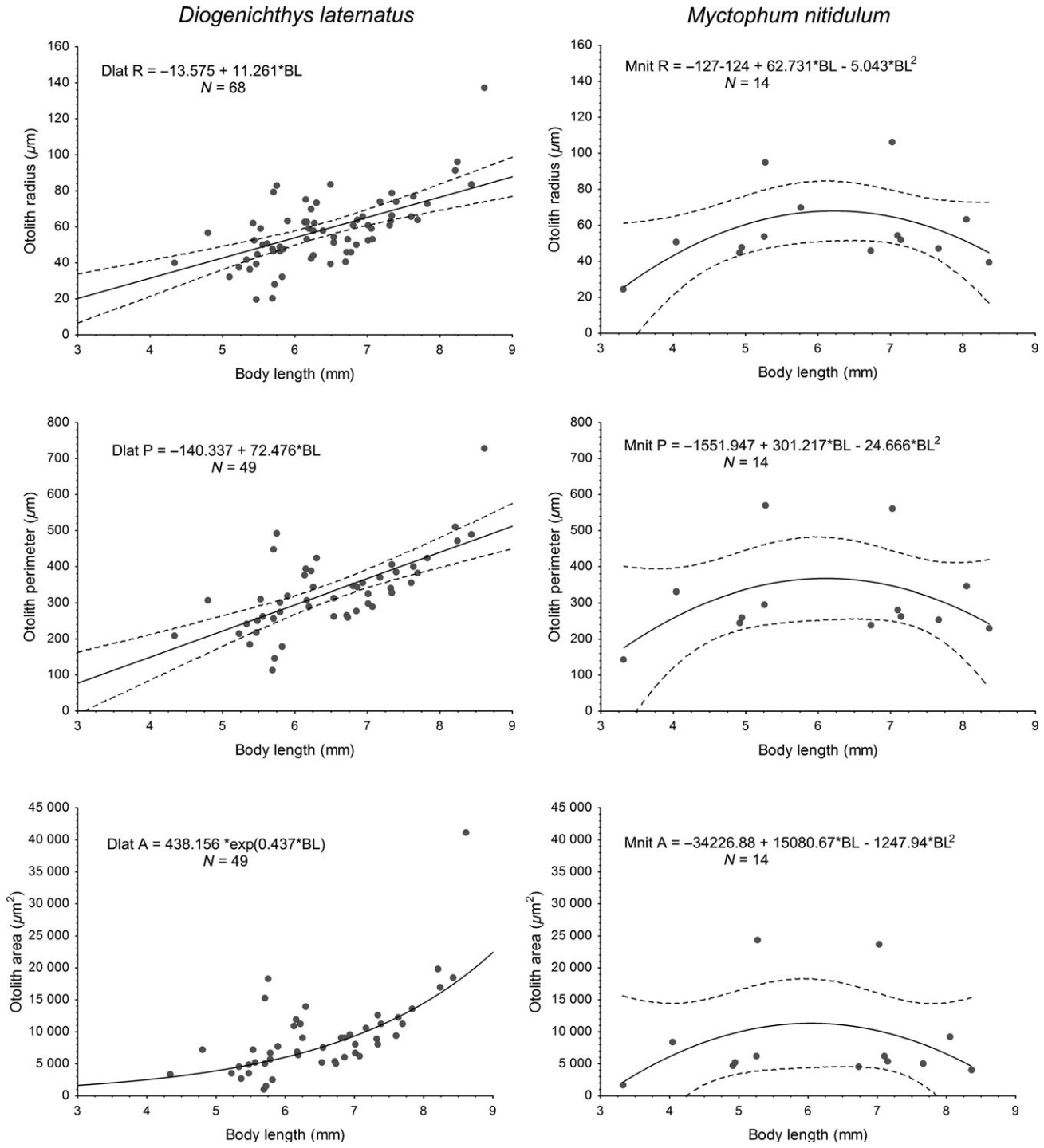

Fig. 2. Morphometric relationships of sagitta otolith size (radius, perimeter and area) and larval body sizes of two Myctophidae from northern Chile.

which 0 represented the new moon. The DNM values were converted to angles (°) by dividing by 29 (the length in days of the lunar cycle) and then multiplying by 360°, so that the data could be analyzed using circular statistics. To assess whether the hatching events showed lunar periodicity, the data were analyzed using the Rao's spacing test (Batschelet, 1981). We also used the Rayleigh test for a departure from randomness. The null hypothesis that the hatching events would be equally or randomly spaced throughout the lunar cycle was tested. The angular means and 95% confidence intervals were also calculated.

Results

Sagittal otolith morphometry and microstructure

Growth increments were well defined over most of the sagitta otoliths, and no accessory primordia (AP) were observed in the largest individuals analyzed of either species (*Diogenichthys laternatus*, 8.61 mm BL; *Myctophum nitidulum*, 9.17 mm BL) (Fig. 1).

For larval *D. laternatus*, sagitta radius varied from 19.43 to 137.63 μm, and increased at a linear rate of 11.26 μm for each mm that the larva grows (Fig. 2). Similarly, the perimeter of the otolith ranged between 113.50 and 729.50 μm, increasing at a linear rate of 72.47 μm mm^{-1}. The sagitta area (A) experienced an exponential growth, following the model A = 438.15 * exp(0.437*BL) (Fig. 2). Sagittal otolith basic morphometry of larval *M. nitidulum*, on the other hand, followed a polynomial growth model, in radius, perimeter and area (Fig. 2). Otolith radius varied from 24.73 to 106.16 μm in larvae of 3.32 and 7.02 mm BL, respectively. Perimeter varied from 144.7 to 569.2 μm, and the area ranged from 1651.4

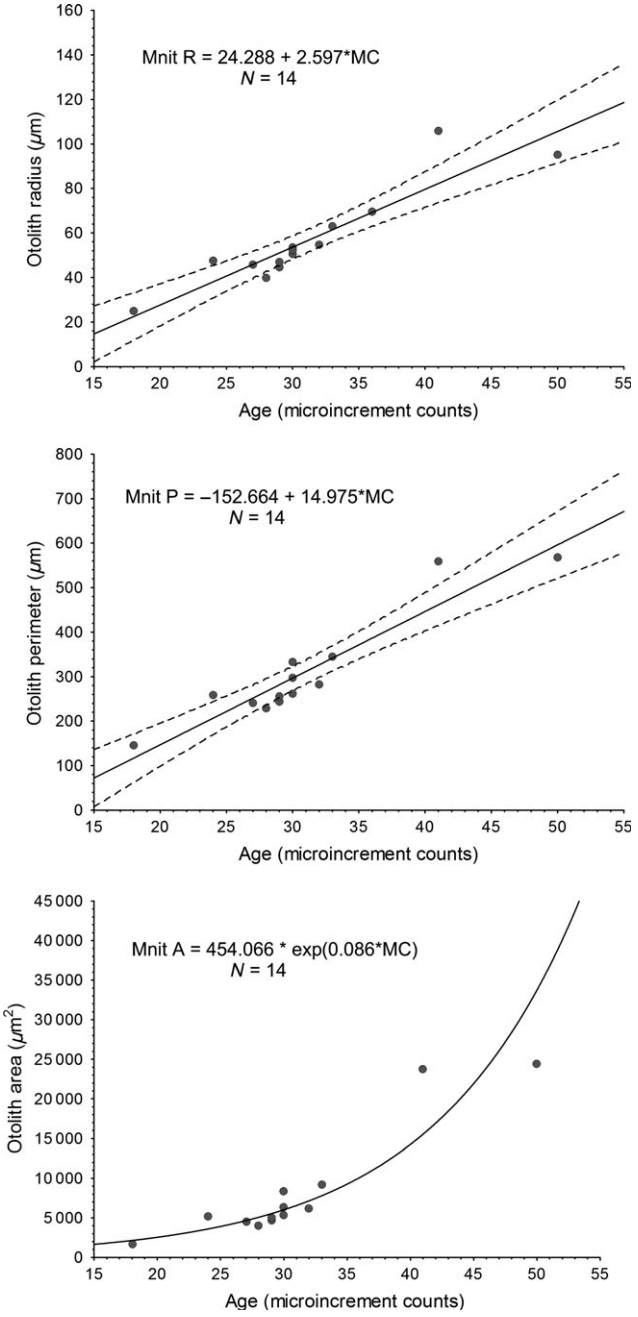

Fig. 3. Morphometric relationships of sagitta otolith size (radius, perimeter and area) of larval *Myctophum nitidulum* with estimated age (microincrement counts).

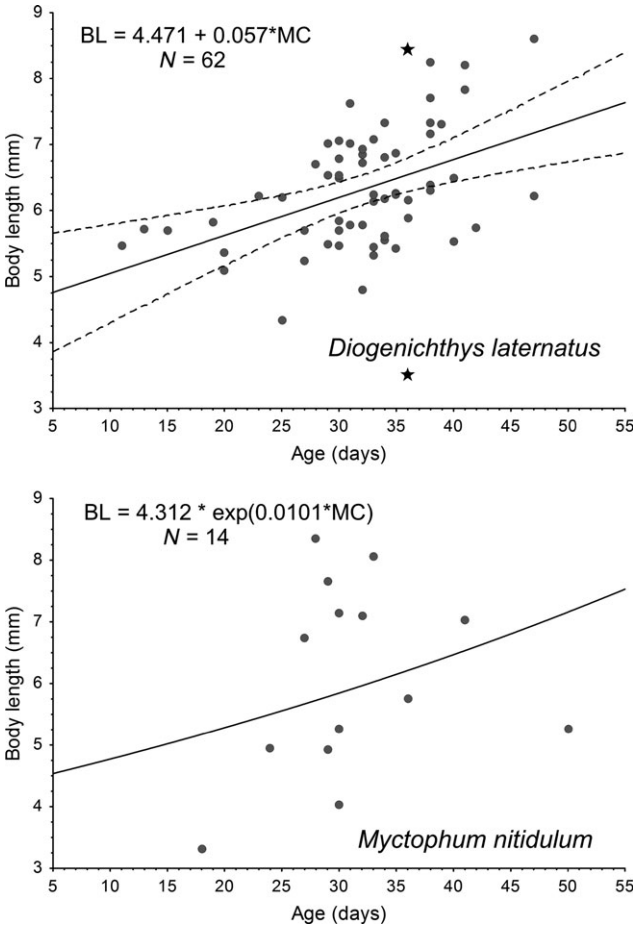

Fig. 4. Estimated growth models for both larval Myctophidae species from northern Chile. Solid line = the model; dashed line = 95% confidence intervals.

to 24,400.0 μm^2. The non-linearity of these relationships suggests that body length is an inadequate proxy of growth during the larval development of this species. Therefore, for *M. nitidulum* larvae, the otolith morphometrics were related to estimate age (i.e. microincrement counts). Both radius and perimeter showed a significant relationship ($P < 0.01$) with age (Fig. 3), growing at a rate of 2.59 and 14.97 $\mu m\ day^{-1}$, respectively. Similarly, the otolith area showed an exponential growth with age, A = 454.06 * exp(0.086*age) (Fig. 3).

Larval growth rates

The linear regression model adjusted for microincrement counts (age) and body length (BL) of larval *Diogenichthys laternatus* (Fig. 4), reveal a significant relationship, BL = 4.716 + 0.057(age), $R^2 = 0.175$, $F_{(1,60)} = 12.81$, P = 0.0006. Therefore, the model estimated a hatch size of 4.716 mm (±standard error, 0.527) and a linear growth rate of 0.057 (±0.016) mm day^{-1}. Only two individuals showed atypical sizes-at-age in larval *D. laternatus* (outliers marked as stars, Fig. 4).

As well as the body length-otolith size relations, the relationship between larval *Myctophum nitidulum* size and age (otolith microincrement counts) did not follow a linear trend, and was better explained by a log model, BL = 4.312 * exp (0.101*age). Estimations of *M. nitidulum* larval growth based on the log model were around 0.061 ± 0.005 mm day^{-1}.

ROGI and outlier analyses

The recent otolith growth index (ROGI) was estimated for both species (Fig. 5). The outlier analysis of ROGI data from larval *D. laternatus* showed the presence of four outliers, i.e. larvae with ROGI values larger/smaller than expected, only 6.5%. On the other hand, the outlier analysis of ROGI data from *M. nitidulum* indicated that data contained no outliers, i.e. all residuals were within ±2 standard deviations. In biological terms, all larvae of this species were in similar condition within the 5 days prior to capture. Particularly for larval *M. nitidulum*, linear relationships were detected among otolith features (size, width, counts), which allowed the ROGI analysis; on the other hand, the otolith features and the larval length showed non-linear relationships.

Larval growth trajectories

Increment width for the duration of the larval period was 1.67 ± 0.67 μm (mean ± standard deviation) for *D. laternatus* and 1.37 ± 0.56 μm for larval *M. nitidulum*. Otolith growth trajectories showed linear trends but high variability among individuals as well as between species (Fig. 6). For larval *D. laternatus*, growth trajectories varied from 0.034 to 0.064 $\mu m\ day^{-1}$; for larval *M. nitidulum*, the range was from 0.027 to 0.041 $\mu m\ day^{-1}$ (Fig. 6).

Back-calculated hatch days, lunar cycle and circular statistics

For the study period, the estimates of the hatch days for *D. laternatus* varied from Julian day 208 (26 July) to day 244 (31 August) and from Julian day 205 (23 July) to day 237 (24 August) for *M. nitidulum*. A unimodal hatching pulse was detected by the back-calculated hatch date of both species, and in the case of *D. laternatus* the pulse occurred near the third-quarter moon (angular mean: day 20.4, 95% confidence: days 18.4–22.3) (Fig. 7). Directional tests showed that estimated hatching days of *D. laternatus* were non-uniform around the lunar cycle (Rayleigh test, $R = 0.476$, $P < 0.01$; Rao's $U = 227.4$, $P < 0.01$). The angular mean of back-calculated hatch days for *M. nitidulum* was at day 24.6 of the lunar cycle, showing a large variance (between days 21.3 and 28.7). The limited sampling number precluded a more robust analysis, indicated by contrasting results of the directionality analyses ($R = 0.475$, P = 0.039; Rao's $U = 144.5$, P = 0.230).

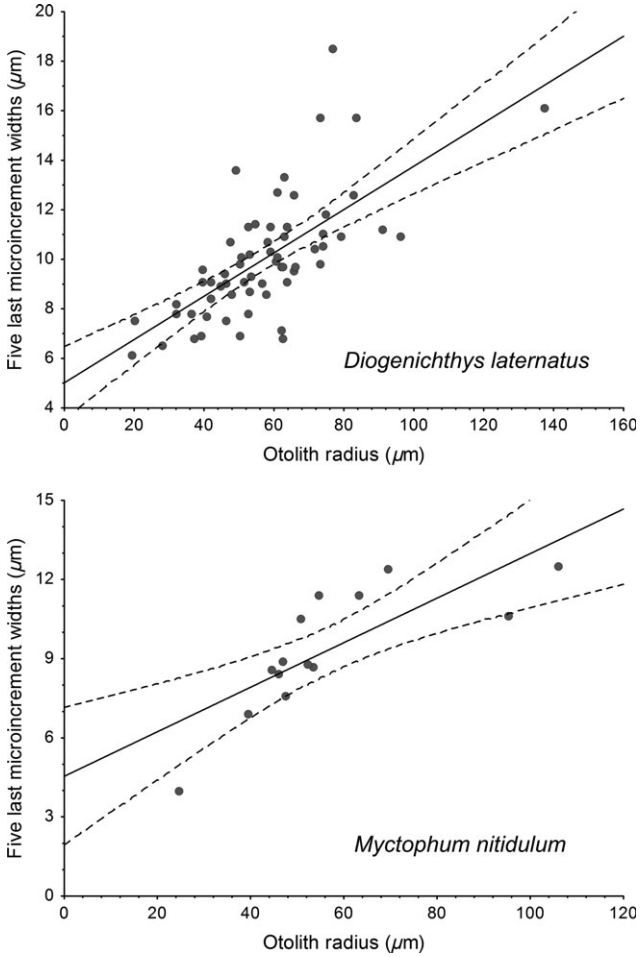

Fig. 5. Linear relationships between sagittal radius and length of five outermost microincrements of larval *Diogenichthys laternatus* and *Myctophum nitidulum*.

Discussion

The intrusion of larval lanternfishes into nearshore areas from upwelling zones is not unusual along the Humboldt Current. In northern Chile, larvae of *Diogenichthys laternatus*, *Lampanyctus parvicauda* and *Triphoturus oculeus* (Loeb and Rojas, 1988; Rojas et al., 2002; Rodriguez-Graña and

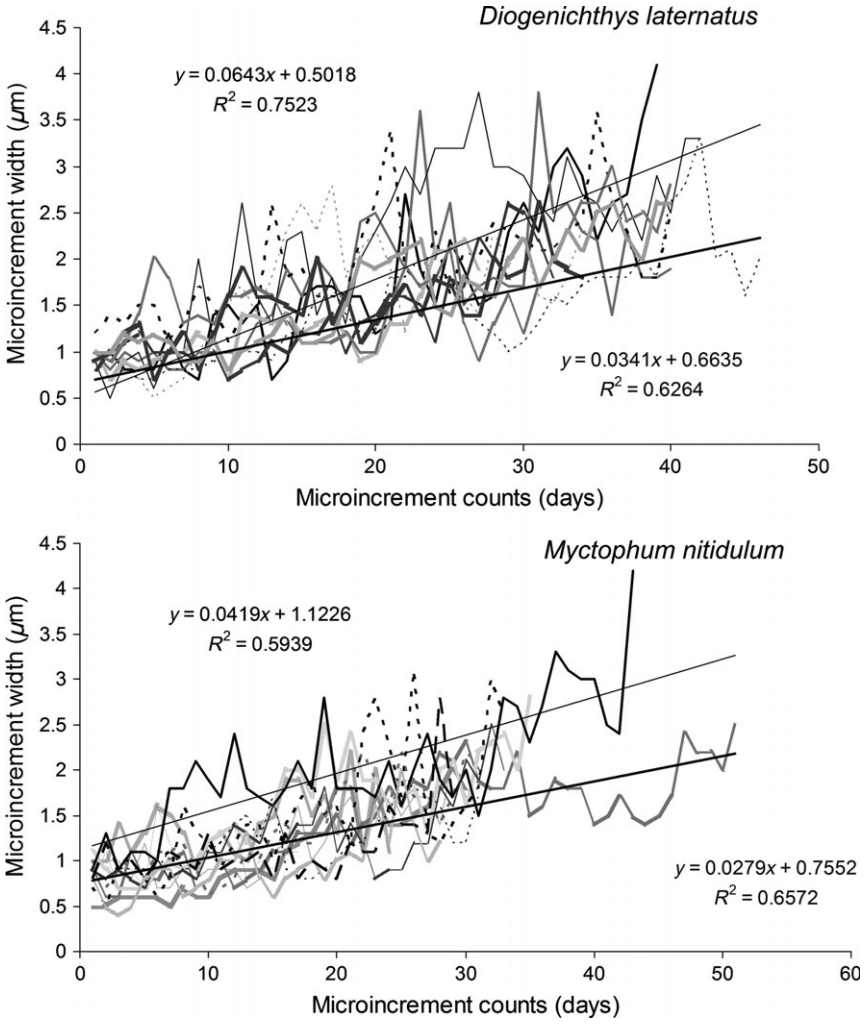

Fig. 6. Temporal variation of daily increment widths (μm) during larval development of myctophid (*Diogenichthys laternatus* and *Myctophum nitidulum*). Linear models show growth trajectories of fastest and slowest individuals per each species.

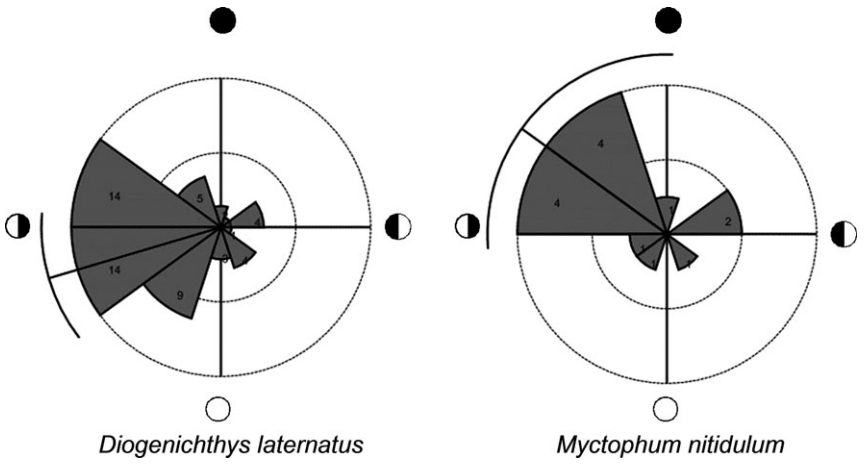

Fig. 7. Lunar cycle hatching patterns of Myctophidae, Mejillones Bay, northern Chile. Line = angular mean; bar = 95% confidence interval.

Castro, 2003; Rodriguez-Graña et al., 2005) is frequently collected, while central Chile is dominated by larvae of *Hygophum bruuni* and *Lampanyctus iselinoides* (Hernández-Miranda et al., 2003; Landaeta et al., 2008, 2009).

Based on the otolith microstructure analysis of larval *Diogenichthys laternatus*, a lunar periodicity occurs in the hatching events, showing slow growth rates during the first 2 months of life and where there is large variability in the

growth trajectories among individuals, but with a similar recent condition among them. Because of the low size number of analyzed otoliths from *Myctophum nitidulum*, the conclusions for this species must be considered with caution.

The vertical migration behavior of lanternfishes changes throughout the lunar cycle, reflected in periods of fast and slow growth in the otoliths (Linkowski, 1996). Particularly for *Myctophum asperum* and *M. nitidulum*, mean increment widths during 5 days at the time of the full moon were narrower than those around the new moon, suggesting that reduced increment growth is a result of slower growth caused by staying in deeper and colder habitat during the full moon period (Giragosov and Ovcharov, 1992; Hayashi et al., 2001). However, in the Gulf of Mexico, the upper limits of the diel vertical migration of most myctophid species are reported to be unaffected by the lunar phase (Gartner et al., 1987). In the cold waters of the Humboldt Current, *D. laternatus* showed hatching events associated with a third-quarter moon; this periodicity may be related then to lunar cycles in the vertical distribution of spawners (Cornejo and Koppelmann, 2006).

Slow growth rates have also been estimated in juvenile *Diaphus kapalae* (0.04 mm day^{-1}) from a coral reef (Suthers, 1996), and adult *Electrona antarctica* (0.061 mm day^{-1}) (Greely et al., 1999). On the other hand, larval myctophids from the eastern Gulf of Mexico display faster growth rates, varying from 0.1 mm day^{-1} for *Notolychnus valdiviae* to 0.4 mm day^{-1} for *Ceratoscopelus townsendi* (Conley and Gartner, 2009). Takagi et al. (2006) estimated similar rapid growth rates for larval *C. warmingii* (0.346 mm day^{-1}) collected in the Kuroshio-Oyashio transition zone. This variability in the larval growth pattern of myctophid may arise from differences in the water temperature (~12°C in Mejillones Bay, Rojas et al., 2002; >20°C in the Gulf of Mexico, Conley and Gartner, 2009).

The shape of larval *M. nitidulum* is characterized by a robust body whereby the body depth at the base of the pectoral fin represents 15% of BL in small larvae, and 65% of BL at 11.7 mm (Olivar and Fortuño, 1991), with a broad massive head and gut that grow during the flexion stage (Moser and Alhstrom, 1970). This change in the allometry of growth may explain the lack of a strong relationship among otolith size, age and BL, at least during the larval stage. Nonetheless, we must caution this conclusion, taking into account the low sampling size (n = 21) of the data.

Sagittal otoliths of myctophids are usually composed of a central zone (CZ), a middle zone (MZ), and external zone (EZ) (Bystydzieńska et al., 2010). Linkowski (1991) found that the formation of numerous accessory primordium (AP) occurs concurrently with transformation of the larva, leading to a dissociation of fish growth from otolith growth. No APs were observed in otoliths of either species. Therefore, larval duration for *D. laternatus* and *M. nitidulum* is at least 50 days. These results are larger than the estimations of larval duration of *M. nitidulum* from the tropical Atlantic (33–43 days, Giragosov and Ovcharov, 1992), but in accordance with estimations of the larval duration of *Electrona antartica* (30–47 days, Greely et al., 1999), *Symbolophorus californiensis* (30–64 days, Takagi et al., 2006), and *Tarletonbeania crenularis* (80–139 days, Bystydzieńska et al., 2010).

Increment widths of sagittal otoliths of larval *D. laternatus* (1.67 ± 0.67 μm) and *M. nitidulum* (1.37 ± 0.56 μm) were narrower, but more conservative than those of other myctophid species, such as *S. californiensis* (6.56 ± 9.18 μm) and *C. warmingii* (6.17 ± 5.45 μm) (Takagi et al., 2006). These results are in agreement with the estimated slow growth rates, probably related to colder seawater temperature. The low variability of sagittal increment growth observed in these two larval lanternfish species may be caused by the high plasticity of their feeding behaviour (Rodriguez-Graña et al., 2005) in order to reduce starvation in an area with low phytoplankton concentrations (Rojas et al., 2002). Although otolith growth is considered to respond conservatively to starvation, the width of the recent growth increments in larvae can respond within days of dietary change (Suthers, 1996). Therefore, a wide trophic niche, as described for larval *D. laternatus* from northern Chile, may explain the low number of individuals with 'abnormal' conditions estimated by ROGI. It seems that both species have large phenotypic plasticity in their larval growth in order to survive in an area with high advective currents and large spatio-temporal oceanographic conditions.

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