Larval stage duration, age and growth of blue lanternfish *Tarletonbeania crenularis* (Jordan and Gilbert, 1880) derived from otolith microstructure

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Abstract *Tarletonbeania crenularis* specimens were collected off Oregon in 2006 and 2009 and aged by enumeration of growth increments in otoliths (sagittae). Three microstructural zones were evident in the otoliths of juvenile and adult fish: central, middle, and external. The number of increments in the central zone are thought to be deposited during the larval phase which is restricted to the uppermost 350 m water layer. The middle zone constituted of barely visible increments, most likely represented a non-migratory behavior of transforming larvae and early juvenile stages. Well defined growth increments were found in the external zone which was presumably formed during extensive vertical migrations of juvenile and adult fish. If the enumerated increments were deposited daily, as previously validated for other myctophid species, the examined individuals indicated a shorter life span than has been formerly reported on the basis of length frequency analysis. The otolith microstructure interpretation was supported by otolith size to fish length proportions and somatic growth of larvae and postlarval fish. Otolith length to standard length relation was described by linear regression models for larvae and postlarval migratory stages with an abrupt disruption between these two groups. The number of growth increments in otoliths plotted against standard length showed a curvilinear growth for larvae and for the postlarval fish. The lack of information on the size at age of transforming larvae and non-migratory early juveniles did not allow us to estimate a complete growth model for *T. crenularis*. However, a pronounced decrease in growth between larval and postlarval migratory phases was distinguished. The uncoupling of otolith and somatic growth was interpreted as a merged effect of downward migration of larvae to the mesopelagic transformation depth, prolonged stay of transforming larvae and early juveniles at this depth without performing diel vertical migrations, and shrinkage during metamorphosis. Back-calculated hatch dates suggests a prolonged spawning season of this species without any distinct peak.

Keywords Otolith · Age · Microstructure · *Tarletonbeania*

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Introduction

The blue lanternfish (*Tarletonbeania crenularis*) (Jordan and Gilbert, 1880) is a subarctic myctophid

species that undergoes diel vertical migrations. Passing through the thermocline during their migrations (Pearcy 1964), this species belongs to the "active" group of myctophids, similar to other myctophid species like *Ceratoscopelus townsendi* or *Lampadena urophaos* (Childress and Nygaard 1973). They also belong to the "facultative" category of neustonic ichthyoplankton (Doyle 1992), as a species occasionally abundant in the neuston because of diel vertical migration.

The genus *Tarletonbeania* contains two species, and both live in the North Pacific Ocean: *T. crenularis* mostly occur in the eastern part including Gulf of Alaska and Bering Sea while *T. taylori* occur in western part from Oyashio Currents to Kamchatka (Wisner 1976; Becker 1983; Moser et al. 1984; Beamish et al. 1999; Rogachev et al. 2000; Doyle et al. 2002; Sinclair and Stabeno 2002; Brodeur and Yamamura 2005; Ivanov et al. 2005). Despite some difficulty in identifying them as separate species (Mead 1953; Wisner 1976), our samples were collected off Oregon where only *T. crenularis* occurs.

T. crenularis probably spawns all year (Doyle et al. 2002; Auth et al. 2007) with pelagic larvae hatching from eggs at <3.0 mm SL and transformation occurring at 19.3–21.7 mm SL (Bolin 1939; Moser and Ahlstrom 1970; Matarese et al. 2003). Small larvae undertake restricted diel vertical migrations between 0–200 m during the night and 10–350 m during the day (Ahlstrom 1959; Auth et al. 2007) with a tendency toward increasing length with depth (Auth et al. 2007). The largest larvae do not migrate to the surface at night (Doyle 1992: Fig. 10c, d).

Adult *T. crenularis* are one of the six most abundant planktivorous mesopelagic fishes in the North Pacific (Beamish et al. 1999), and are prominent in neuston off Oregon (Doyle 1992) as one of the three primary species from the dominant teleost family Myctophidae (Phillips et al. 2009). The vertical distribution and migrations of adult *T. crenularis* differ geographically. In the center of the species distribution area, off Oregon, adults migrate between depths 0–850 m (peak 0–50 m) at night and 200–850 m (peak 350 m) during the day (Pearcy 1977; Pearcy et al. 1977). In the southern part of their range, near the Baja California peninsula, they reside in slightly deeper depths whereas in the north off British Columbia, their vertical distributional range is narrower. In all their vertical distribution is tightly associated with the main scattering layer (Paxton 1967; Taylor 1968).

Near Oregon, *T. crenularis* prey mainly on euphausiids, amphipods, and salps, and the largest specimens also consume bathylagid fish (Collard 1970; Hart 1973; Tyler and Pearcy 1975; Brodeur and Yamamura 2005; Suntsov and Brodeur 2008). In turn, *T. crenularis* constitutes an important prey item for many predators in the North Pacific, including jumbo squid (Field et al. 2007; Zeidberg and Robison 2007), salmon, Sockeye salmon, albacore, Pacific hake, and sablefish (Rogachev et al. 2000; Hart 1973, Davies et al. 1988; Buckley et al. 1999; Nomura and Davis 2005), and Dall's porpoises (Ohizumi et al. 2003).

The microstructure of *T. crenularis* 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 subtropical-temperate myctophids (Gartner 1991a; Suthers 1996; Hayashi et al. 2001; Moku et al. 2001, 2005). The central part in sectioned myctophid otoliths is most often described as the "larval zone" and is formed during the occurrence of larvae in highly dynamic epipelagic layers (Ozawa and Peñaflor 1990; Gartner 1991a, b; Greely et al. 1999) where they perform restricted diel vertical migrations (Badcock and Merrett 1976; Loeb 1979a, b; Karnella 1987; Sassa et al. 2007). The published nomenclature of the "middle zone" in myctophid otoliths (Gjøsæter 1987; Young et al. 1988; Ozawa and Peñaflor 1990; Gartner 1991a, b; Giragosov and Ovcharov 1992; Linkowski et al. 1993; Suthers 1996; Linkowski 1997; Greely et al. 1999; Hayashi et al. 2001; Moku et al. 2001; Shelekhov 2004; Takagi et al. 2006) is more complex and often controversial due to different interpretations of the relation between otolith formation and migratory behavior and/or ontogenesis. The external part of otolith microstructure is enhanced by circadian rhythm and cyclic diel environment changes, particularly the temperature gradient traversed by stages that exhibit vertical migration (Gibson 1978; Torres et al. 1979; Campana and Neilson 1985), which is the case in myctophids (Gartner 1991a; Hayashi et al. 2001).

The aim of this study was to assess the basic biological features such as age, duration of early life history traits and growth that could be derived from otolith microstructure of *Tarletonbeania crenularis*,

an important component of pelagic/mesopelagic ichthyofauna assemblages in the Eastern North Pacific region.

Materials and methods

Sampling

In 2004, the Northwest Fisheries Science Center (NWFSC) Fish Ecology Division and the Cooperative Institute for Marine Resources Studies (CIMRS) initiated a Stock Assessment Improvement Program (SAIP) survey of the ecology of larval and juvenile fish off central Oregon and Washington. Larvae were sampled with a 60 cm diameter bongo net with a 332 μm mesh fished obliquely from ~100 m to the surface at night. Juvenile and adult fishes were sampled with a midwater Nordic 264 rope trawl with 3 mm stretched knotless web liner sewn into the cod end. A Nordic trawl was towed at night for ~15 min with the headrope target depth of 30 m. For more detailed collection methodology see Phillips et al. (2007 and 2009) and Auth (2009).

For the purposes of this study, 99 individuals of postlarval stages (juvenile to adult) of *T. crenularis* were obtained from two SAIP cruises using the chartered commercial fishing vessel "Piky", in 2006, one during August and the other in September. Of these, 62 specimens were examined from a single tow in the August cruise at station HH37 (44.00° N and 125.0° W), and 37 specimens were examined from two tows at stations HH37 and CR40 of the September cruise (46.16° N and 124.92° W) (Fig. 1). At sea, midwater micronekton samples were split into individual quart bags with approximately 10% freshwater added, frozen, and stored at −20°C. In the lab individual *T. crenularis* were identified using Wisner (1976), measured to the nearest mm standard length, and then preserved in 70% ethanol. In addition to the juvenile and adult material, 13 larvae were examined from Bongo cruises in June 2009, stations: HH46 (43.99° N and 125.28° W) and NH45 (44.65° N and 125.12° W), and in July 2009, stations CR40 and CR50 (46.16° N and 125.18° W) (Fig. 1). The larvae were preserved at sea in 95% ethanol and identified in the lab using Matarese et al. (1989). The standard length (SL) range of larval and juvenile to adult specimens collected for otolith
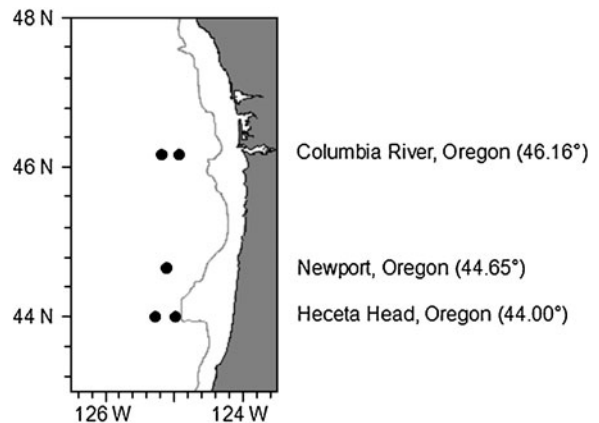
Fig. 1 Sampling localities of *Tarletonbeania crenularis* used in this study for otolith examination. The line represents the 200 m isobath

examination was 4.6–16.5 mm and 25.5–78.0 mm respectively.

Otolith analysis

Otoliths from larvae were dissected, dried, and mounted on microscope slides with Eukitt® while those from larger fish were cleaned in a commercial solution of Clorox before mounting. Larval otoliths were transparent enough to be examined directly under a light microscope. Otoliths from juvenile and adult fish were prepared by grinding and polishing from both sides to obtain thin transparent sagittal sections. Otolith sections were examined and photographed with a light microscope (LM) Olympus BX50 at different magnifications. Increment counts were conducted at 1000× magnification under immersion oil. A few otoliths were also examined using a scanning electron microscope (SEM) Philips XL30, after etching with 1% HCl for 180 s (Linkowski 1987, 1991). Otolith growth increments were enumerated from the first distinguishable increment after the primordium or "core" (Brothers 1984). The daily increments within each otolith zone were counted three times. If counting error within any of those zones exceeded 5%, the otolith was excluded. Additionally, two otoliths were excluded due to unreadable patterns in the middle zone. Following this procedure increment numbers were successfully estimated for all larvae, 86 of 99 postlarval specimens within the central zone only, and 84 of 99 postlarval specimens within all three zones. On the basis of

validated daily growth increments in the otoliths of other myctophid species (Gartner 1991a; Moku et al. 2001), daily growth increments in *T. crenularis* otoliths were assumed. To determine the relations between the otolith length vs. fish length and the standard length vs. age, linear and curvilinear regression models were fitted to the data. Models were selected on the basis of the best fit evaluated by the correlation coefficient (r). Total number of increments was used to estimate age and the timing of hatch. Data for ANCOVA analysis were log transformed to obtain homogenous variance. Statistical analysis and graphs were plotted using Statistica 8.0.

To avoid misunderstandings by using terms of otolith microstructure related to life history traits we chose to use nomenclature based on the location of particular features in otolith sections. This nomenclature was originally introduced by Giragosov and Ovcharov (1992), and assumed the existence of three zones of growth increments within otoliths of certain myctophid species: the central, middle, and outer (external) zones.

Results

The relation between otolith size (OL) and fish standard length (SL) for *T. crenularis* was linear for larvae as well as for juveniles and adults, however a conspicuous shift of otolith growth pattern appeared between larval and postlarval fish (Fig. 2). ANCOVA analysis indicated significant differences ($p<0.001$) in both elevation ($t_{2,72}=5.427$), and slopes ($t_{2,71}=10.5$) of the regressions.

Otoliths of *T. crenularis* larvae were characterised by a typical incremental structure observed in many families of marine fishes (Fig. 3), whereas three distinctive incremental growth sequences (otolith microstructure zones) were identified in juvenile and adult specimens (Fig. 4a, b). A central zone (CZ) was composed of relatively well defined, thin growth increments deposited around a single central primordium (CP) (Fig. 3). The mean number of increments in the CZ was 103.1 with (min-max) range of 80–139. The number of increments in the examined larval otoliths varied from 8 to 68, and thus was below the minimum number observed in CZ growth sequence in postlarval otoliths. Around the CZ the presence of small, peripheral, multiple accessory primordia (AP)

as secondary growth centers were observed (Fig. 4a). The appearance of the AP reflected deposition of darker, less transparent, barely visible but countable, growth increments forming the middle zone of the sagittae (MZ) with similar width to increments in the EZ. Moreover, the MZ increments were resistant to selective etching (Fig. 4b). MZ was composed of 51 to 102 (average 72.6) increments, which were sometimes grouped into 11-16 thick, broadly spaced rings/bands (Fig. 4a). There was a significant negative Pearson correlation ($r^2=0.1618$; $p<0.001$) between the number of increments in the central and the middle zone of otoliths ($y=112.34 − 0.3853*x$) (Fig. 5). The mean total number of increments in these two zones (CZ and MZ) was 175.7, with (min-max) range of 152–207.

The total number of all growth increments in the examined otoliths of postlarval fish varied from 185 to 504 in all three zones combined. Thus, based on the assumption of daily increment deposition, the examined fishes (with larvae omitted) were calculated to be 6 to 17 months old. Because our sampling occurred only in the uppermost layers of the water column, metamorphosing larvae and non-migratory early juveniles specimens were not collected. Thus, a significant gap of information on the size of larvae and juveniles between 69 and 184 days old, did not allow us to estimate the growth model for *T. crenularis*. The number of increments (age in days) plotted against standard length showed a curvilinear growth for larvae (SL=1.3451+0.4055 * Age – 0.0028 * Age^2; $r=0.9335$; $p<0.001$), and for the postlarval fish (SL=−25.84+0.3167 * Age – 0.0002 * Age^2; $r=0.9586$; $p<0.001$) (Fig. 6). Back-calculated hatch dates from out limited number of specimens suggested a prolonged breeding season of this species in the Eastern North Pacific, with no distinct spawning peak (Fig. 7).
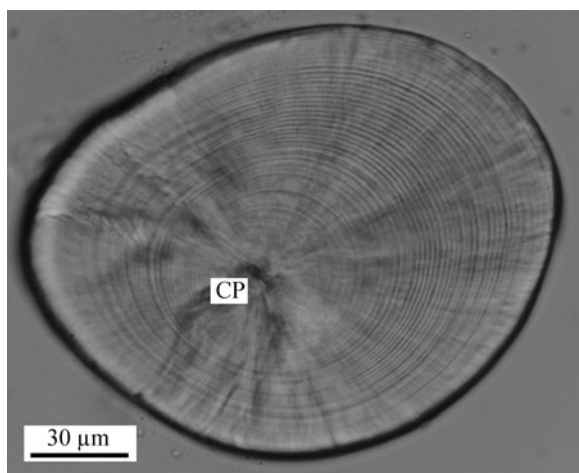
Discussion

Daily growth increments have been validated for only a few species of myctophid (Gartner 1991a; Suthers 1996; Hayashi et al. 2001; Moku et al. 2005). It is widely accepted that variables such as photoperiod, temperature, feeding, growth, and circadian rhythm have a potential to influence otolith deposition (see review by Campana and Neilson 1985). Additionally,

Fig. 2 Otolith length plotted against standard length of *Tarletonbeania crenularis* sampled off Oregon. Larvae: SL=4.1981+68.9281 * OL (r^2=0.8304; $p<0.001$), juveniles to adults: SL=−1.4609+ 37.7728 *OL (r^2=0.9397; $p<0.001$). ▲ = larvae, ● = juveniles to adults
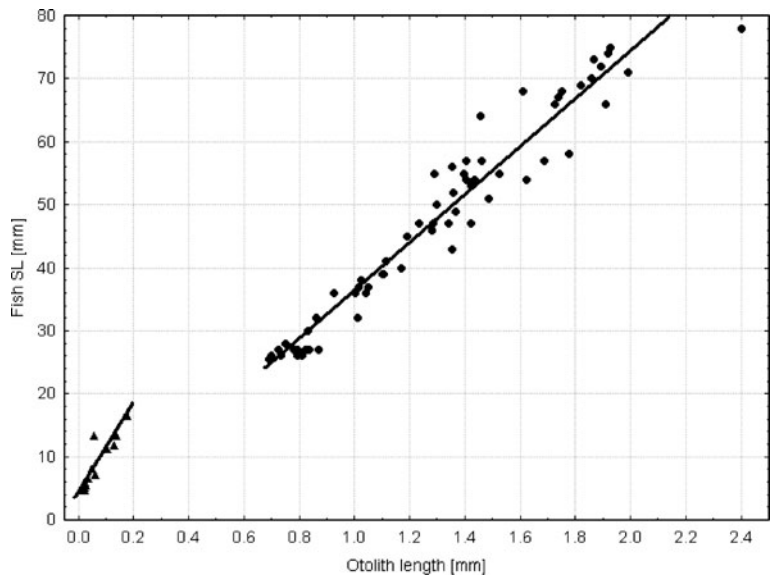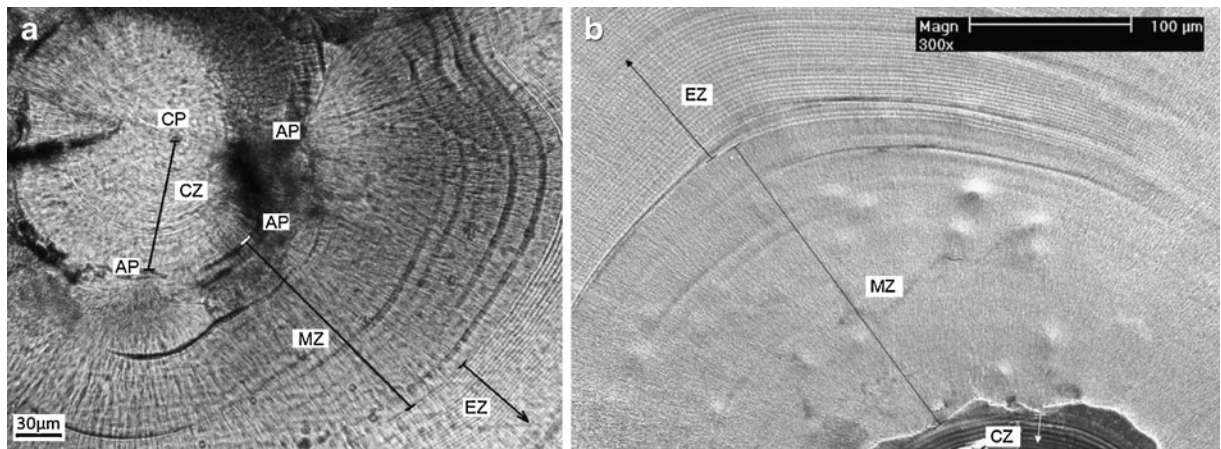
mesopelagic fish exhibit vertical distribution patterns, such as diel or lunar migrations and periods of non-migratory behavior in some developmental stages (e.g., Clarke 1973; Badcock and Merrett 1976; Karnella 1987; Linkowski 1996; Hayashi et al. 2001; Shelekhov 2004; Takagi et al. 2006; Sassa et al. 2007) that may further influence otolith microstructure (Gjøsæter 1987; Gartner 1991a; Linkowski 1991, 1996, 1997; Takagi et al. 2006). This makes the myctophid otolith a particularly useful tool to decipher duration and chronology of some life history events.

Fig. 3 Photomicrograph of sagittal plane *Tarletonbeania crenularis* larva otolith (SL=16.5 mm). CP = central primordium

Myctophid larvae occur in dynamic surface ocean layers and undertake restricted diel vertical migrations (Badcock and Merrett 1976; Loeb 1979a, b; Karnella 1987; Sassa et al. 2002, 2007). Despite some interspecific differences in the behavior of myctophid larvae (Loeb 1979a, b; Sassa et al. 2002, 2007) and the timing of deposition of the first accessory primordia (Linkowski 1991; Suthers 1996), the number of increments deposited in the central zone of the otolith is thought to indicate the duration of the larval stage, when larvae are usually resident in the uppermost 200 m water layer (Gartner 1991a, b; Sassa et al. 2004; Moku et al. 2005). This duration has been described in few of the >250 of myctophid species. Published results indicate relatively low (min-max) number of increments in the central zone, e.g. 30–50 for *Benthosema suborbitale* (Gartner 1991b), 22–52 for *Ceratoscopelus warmingii* (Linkowski 1997), 31–48 for *Diaphus kapalae* (Suthers 1996), 33–43 for *Myctophum nitidulum* (Giragosov and Ovcharov 1992), and 30–64 for *Symbolophorus californiensis* (Takagi et al. 2006). In contrast with published data for other myctophids, *T. crenularis* has two to five times more increments within this part of otolith. This phenomenon might be explained partially by the distributional range of the different species. *T. crenularis* occurs in high latitudes and cool habitat of the NE Pacific, whereas the published results refer mostly to tropical and subtropical myctophid species. However, a specific morphology of *T. crenularis* and other

Fig. 4 Sagittal sections of *Tarletonbeania crenularis* otolith (sagitta) examined under **a** light microscope (LM) and **b** scanning electron microscope (SEM). CZ = central zone, MZ = middle zone, EZ = external zone, CP = central primordium, AP = accessory primordium

Gonichthyini tribe larvae (Moser and Ahlstrom 1970; Moser et al. 1984; Matarese et al. 1989) which also have a high number of increments in CZ (Bystydzieńska and Linkowski, unpubl. data) might constitute a tribe-specific characteristic due to unknown benefits of a prolonged occurrence of their larvae in the epipelagic zone.

The central zone of *T. crenularis* otoliths is bordered by multiple accessory primordia (AP) as secondary growth centers, that initiate the formation of the middle zone (MZ). Similar otolith micro-structures have been reported in two other representatives of the tribe Gonichthyini (Linkowski 1991), and several species belonging to other tribes (Gartner 1991a; Linkowski 1991; Linkowski et al. 1993; Suthers 1996). The increments in the middle zone of some *T. crenularis* otoliths were combined into thick bands similar to "postlarval zone bands (PZB)" (Gartner 1991a) in the tropical species *Benthosema suborbitale* (Gartner 1991a) and *Myctophum nitidulum* (Giragosov and Ovcharov 1992), and *Electrona antarctica* from the Southern Ocean (Greely et al. 1999). Other published results indicate lower (min-max) number of increments in the middle zone of several myctophid species, e.g. 13–43 for *Benthosema suborbitale* (Gartner 1991b), 69–89, 24–54, and 20–65 for *Ceratoscopelus warmingii* (Tsarin 1994; Linkowski 1997; Takagi et al. 2006, respectively), 10–12 for

Fig. 5 Relation between number of increments in the middle zone and number of increments in the central zone of *Tarletonbeania crenularis* otoliths: $y = 112.34 - 0.3853*x$; confidence interval 0.95 ($r^2 = 0.1618$; $p < 0.001$)
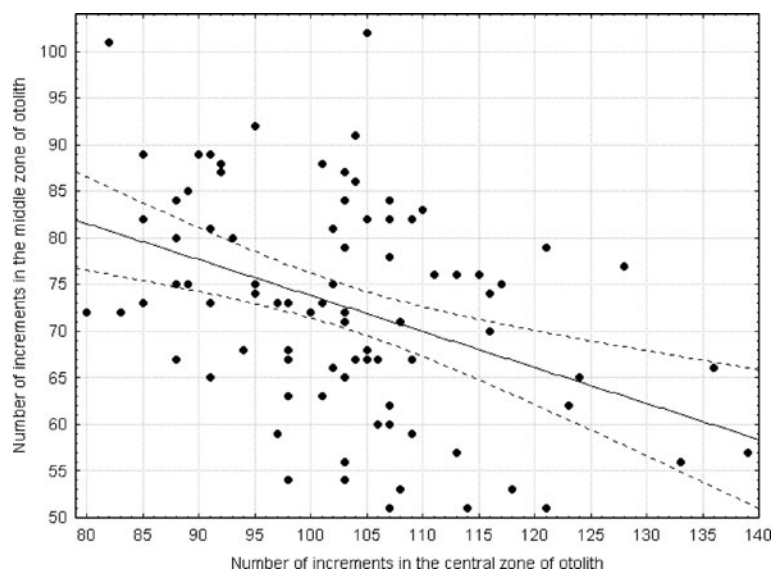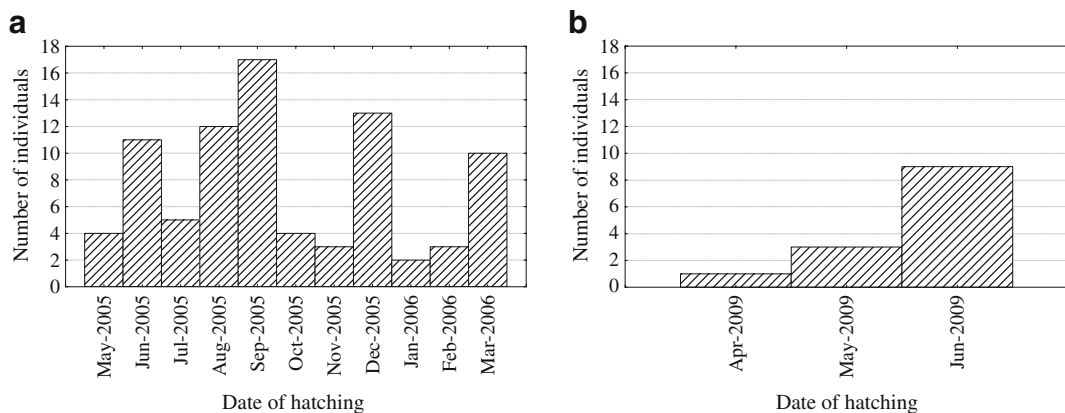
Fig. 6 Growth of *Tarletonbeania crenularis* off Oregon, determined from microstructure of otoliths. Larvae SL=1.3451+0.4055 * Age − 0.0028 * Age^2 (r=0.9335; p<0.001), juveniles to adults SL=−25.84+0.3167 * Age − 0.0002 * Age^2 (r=0.9586; p<0.001). ▲ = larvae, ● = juveniles to adults
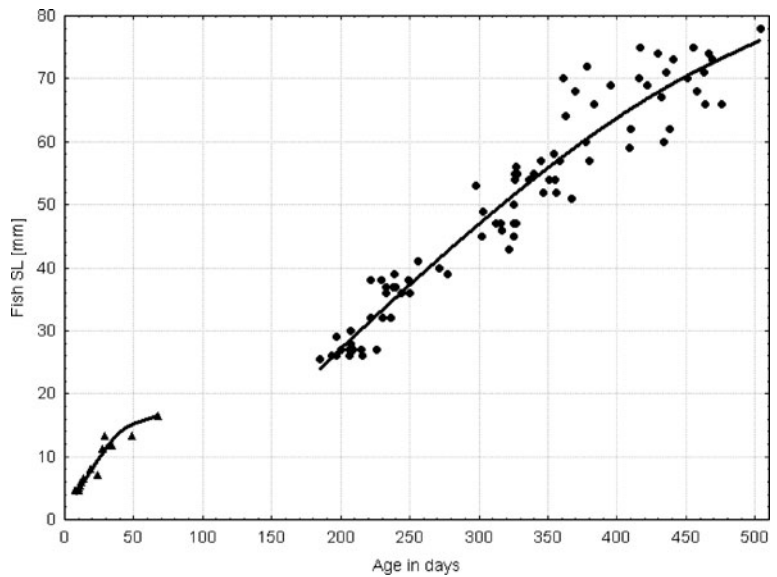
Diaphus kapalae (Suthers 1996), 38–60 for *Electrona antarctica* (Greely et al. 1999), 5–9 for *Lampanyctodes hectoris* (Young et al. 1988), 15–40 for *Lepidophanes guentheri* (Gartner 1991b), 20–35 for *Myctophum nitidulum* (Giragosov and Ovcharov 1992), and 23–61 for *Symbolophorus californiensis* (Takagi et al. 2006). In contrast to the published data for other myctophids, except for *C. warmingii* (Tsarin 1994), we observed the middle zone of the *T. crenularis* otoliths had more numerous increments. The interpretation of the MZ origin is more complicated than the CZ. Gjøsæter (1987), who first described the microstructure of the central part of myctophid otoliths, was convinced that the primary cause of the change of otolith structure and the appearance of so called "perinuclear

zone" was due to metamorphosis. Gartner (1991a) coupled an effect of metamorphosis with an abrupt environmental change and did not agree that duration of the metamorphosis could be reflected by a deposition of a whole "post-larval zone" (MZ) of the otolith. The appearance of AP does not constitute evidence of metamorphosis itself because they appear either as pre- (Linkowski 1991; Suthers 1996) or post-transformational structures (Brothers 1984; Campana 1984), and thus may only indicate a habitat shift. For example, such secondary primordia are evident in the pelagic juvenile starry flounder (*Platichthys stellatus*) when they shift from a pelagic to demersal habitat (Campana 1984) as well as in many other species due to various transitional events during

Fig. 7 Estimated date of hatching of *Tarletonbeania crenularis* back-calculated from growth increments in otoliths. Individuals collected off Oregon on **a** August 9th and September 25th and 27th, 2006, and **b** June 15th and July 19th, 2009

early life (Modin et al. 1996; Neuman et al. 2001; Correia et al. 2006; Sponaugle 2009). An abrupt habitat shift is observed in some myctophid larvae species just before metamorphosis, when they initiate a downward migration to the depths within the mesopelagic zone (Gartner 1991a; Sassa et al. 2007). The non-migratory behavior of transforming larvae (Sassa et al. 2007) as well as early juveniles of several myctophid species has been documented (Clarke 1973; Badcock and Merrett 1976; Nafpaktitis et al. 1977; Karnella 1987), including *T. crenularis* (Doyle 1992). Thus, our interpretation of the middle zone is the same as the Gartner's (1991a) as amended by Linkowski (1997). We suggest that the MZ in *T. crenularis* otoliths consists of increments deposited during the downward migration of larvae to the transformation depth of several hundred meters, as well as the early juvenile period, when fish remain at the same depths where transformation occurred. We did not observe any consistent division within the microstructure of MZ that could be interpreted as a transformation check.

The material examined for the purposes of this study did not include otoliths bordered only by MZ increments. In addition, oblique sampling did not allow us to determine the depths where individuals were caught. Therefore, our interpretation must still be verified. However, the observed abrupt shift between otolith growth and somatic growth in larval and postlarval *T. crenularis* indirectly supports such an interpretation. A similar disruption was reported in several myctophid species, e.g., *Benthosema glaciale* and *Loweina rara* (Linkowski 1991), and *Ceratoscopelus warmingii* (Takagi et al. 2006). The vast difference of otolith size between the largest larvae and the smallest postlarval fish examined also supports our interpretation of somatic growth suppression during non-migratory behavior of transforming larvae and early juvenile *T. crenularis*. Since Templeman and Squires (1956) indicated that a slower growing fish tends to have larger otoliths than faster growing conspecifics at the same somatic size, this phenomenon became widely accepted and confirmed by many authors (e.g., Reznick et al. 1989; Secor and Dean 1989; Moksness et al. 1995; Takasuka et al. 2008). Cold-water habitat with low prey availability at depths where transformation occurs (Sassa et al. 2007) and/or shrinkage of the larvae due to the transformation in some species (Moser and

Ahlstrom 1970; Sassa et al. 2007) may cause a slower somatic growth rate effect during all non-migrant stages. The duration of this phase in *T. crenularis*, lasting 72.6 days on average, seems to be very long comparing to the remaining parts of the life cycle and further studies of such unique life strategy are required.

A negative correlation between the number of increments in the central and middle zones in *T. crenularis* otoliths suggests a functional relation between these two periods of early life history. A shorter presence of larvae in epipelagic layers may be compensated for with a longer non-migratory behavior of metamorphosing larvae and early juveniles.

Otoliths of postlarval fish (juveniles, subadults, and adults) examined in this study had well defined, clear increments in the external zone (EZ). These increments were presumably deposited during regular diel migrations of juveniles, subadult, and adult individuals. According to the published literature, *T. crenularis* attains maximum standard lengths of 84.0 mm TL (Wisner 1976; Becker 1983; Phillips, unpubl. data). The maximum size of examined individuals in this study was 78.0 mm SL, justifying our assumption that we included the oldest age groups. The only published information on *T. crenularis* age is that by Willis and Pearcy (1980). Based on fish length-frequency analysis and vertical distribution, Willis and Pearcy (1980) suggested the existence of three age groups (I, II and III years old individuals) responsible for the observed length frequency modes: 25–30 mm, 40–50 mm, and 55–70 mm SL, respectively. Based on otolith increment analysis, in contrast, the oldest individuals in our samples were estimated to be 17 months old. Thus, the annual production of this important species within the Northeastern Pacific ecosystem could be much higher than expected. The growth of *T. crenularis* derived from daily increments counts in otoliths of postlarval fish was slightly curvilinear, and shows a similar growth pattern to that of most myctophid species studied so far, e.g. *D. dumerilii*, and *Lepidophanes guentheri* (Gartner 1991b), and *C. warmingii* (Takagi et al. 2006), except for a long lived Antarctic species *Electrona antarctica* (Greely et al. 1999) and *Diaphus theta* (Shelekhov 2004). The shape of *T. crenularis* growth curve closely resembles that published by Takagi et al. (2006) for a slightly larger and faster growing species from NW Pacific, *Symbolophorus californiensis*.

T. crenularis spawns year-round but larvae are most abundant in January-March off the U.S. west coast (Doyle et al. 2002; Auth et al. 2007). Although our findings are based on a restricted sampling location off Oregon and a low number of specimens, our back-calculated dates of hatch for *T. crenularis* also suggested a prolonged breeding season of this species, without a distinct peak.

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