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Comparison of the two alternative early life-history strategies of the Antarctic fishes *Gobionotothen gibberifrons* and *Lepidonotothen larseni*

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ABSTRACT: Two major early life-history strategies of notothenioid fishes in the lower Antarctic are identified based upon the length of pelagic development: species that complete pelagic development within 1 summer season ('summer larvae') and species with extended pelagic development that continues over winter months ('winter larvae'). These 2 life-history strategies were compared using otolith techniques to reveal growth histories, hatching periods, and development rates of larval *Gobionotothen gibberifrons* (summer larvae) and *Lepidonotothen larseni* (winter larvae) from the Antarctic Peninsula (summer 1986/87) and South Georgia (summers 1987/88 and 1988/89). Back-calculated growth over the first 40 d after hatching was modeled exponentially and instantaneous growth rates (r) were calculated. Both species grew at similar rates with respect to length (r = 0.01) and with respect to weight (r = 0.02 to 0.03). The hatch period of both species was delayed off the Antarctic Peninsula (late-November to mid-December) compared to South Georgia (early to mid-November), as is the onset of the productive season at higher latitudes. Summer larvae have no growth advantage but do develop more quickly than winter larvae, offering the ability to reduce the time spent in a vulnerable life-history stage. As currently hypothesized, winter larvae may take advantage of an extended period for growth, using pelagic resources unavailable to summer larvae, or recruiting to the demersal environment when competition from summer recruits is lowest.

KEY WORDS: *Gobionotothen gibberifrons* · *Notothenia gibberifrons* · *Lepidonotothen larseni* · *Nototheniops larseni* · Larvae · Otoliths · Hatch period · Growth

INTRODUCTION

The Antarctic marine environment is cold and very productive, but highly seasonal; phytoplankton productivity is largely limited to the short summer season (El-Sayed 1985). Low phytoplankton concentration during winter, alone insufficient to support Antarctic planktotrophic larvae (Olson et al. 1987), is likely the strongest common selective pressure upon the biology of Antarctic fauna (Clarke 1988). A common set of life-history adaptations has been observed among Antarctic benthic invertebrates: large yolky eggs, low fecundities and reduced reproductive effort, brood-protection, direct development of large larvae, limited or no pelagic development, and slow growth (Thorson 1950, Arnaud 1977, White 1977, Clarke 1979, 1983, Picken 1980). These adaptations, as a group, have been generalized as 'Thorson's Rule'.

Fish are also important members of the benthic fauna and show similar adaptations except that all species have pelagic larvae (North & White 1987, Kock & Kellermann 1991). As with invertebrates, the presumed food limitation during the winter season was long believed to be the single most important factor shaping the early life-history strategies of fish. Larvae were hypothesized to begin feeding in the plankton at the time of peak prey abundance (Everson 1984) and subsequent pelagic development would likely be restricted to the summer season (Marshall 1953).

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Our understanding of the true nature of the pelagic environment, especially during winter months, is improving. Evidence now suggests that year round the pelagic environment is not as hazardous to larval development as originally thought. Pelagic development is, in fact, no less common among some groups of Antarctic benthic invertebrate larvae than elsewhere (Pearse et al. 1985, 1991, Pearse & Bosch 1986), and many larval fish have very long pelagic development stages that continue over winter (Kellermann 1986, 1989a). A closer look at the life-history patterns displayed by larval Antarctic fish will help us identify how both the environment and inter-specific interactions shape larval development strategies.

The Antarctic fish community is highly endemic and dominated by a single suborder, the Notothenioidei, which accounts for more than 95% of the individuals in most coastal areas (Kock 1992). Most Notothenioidei are demersal and restricted to the continental slopes and shelves where they have diversified to fill niches that in other ecosystems are filled by many fish taxa (Eastman 1991, 1993).

The early life-history strategies of the Notothenioidei may be grouped by the number and size of larvae produced, altricial or precocial development (see Flegler-Balon 1989), and the duration of the pelagic period. Kock & Kellermann (1991) have identified 3 strategies: (1) species that produce few, large larvae (precocial) with pelagic development independent of season, and (2) species that produce many small larvae (altricial) with pelagic development either restricted to the productive summer months or (3) extended over the winter months.

Precocial larvae hatch from large (2.5 to 5.0 mm) eggs that are produced in relatively small numbers. The larvae are large and well developed when they begin feeding, giving them the ability to take advantage of the patchy distribution of larger zooplankton and ichthyoplankton and better ability to escape predators (Kock 1985, Kellermann 1986). Precocial larvae include the Channichthyidae, Artididraconidae, the larger Nototheniidae (particularly the genera *Trematomus* and *Pagothenia*), and most Bathydraconidae (Kock & Kellermann 1991). Precocial larvae are represented by species with different hatching periods throughout the year and include all species that hatch in winter and all species from the higher Antarctic latitudes (ibid.).

Altricial larvae hatch from small (0.8 to 2.5 mm) eggs that are produced in large numbers. In favorable conditions many more altricial larvae than precocial larvae may survive to settlement. However, altricial larvae hatch and begin feeding at a small, relatively undeveloped state, making them highly vulnerable to starvation and predation. These species (mainly Nototheniidae) spawn in late winter and spring and hatch exclusively in the spring and summer seasons. Kock & Kellermann (1991) identify this as the most prevalent reproductive strategy in the lower Antarctic latitudes.

Altricial larvae include 'summer larvae', species that complete pelagic development entirely within the brief productive period of the spring and summer season, and 'winter larvae', all species that remain in the water-column over winter. Among the Nototheniidae, summer larvae include *Gobionotothen gibberifrons*, *Trematomus newnesi*, and *Lepidonotothen nudifrons*; and winter larvae include *Lepidonotothen larseni*, *Lepidonotothen kempi*, *Gobionotothen marionensis*, and *Trematomus scotti* (Kellermann 1989a, b, Kock & Kellermann 1991).

The focus of this research is a comparison of the 2 alternative altricial life-history strategies in terms of hatch period, growth, and development rate. Summer larvae are hypothesized to have evolved to take advantage of elevated prey levels during the summer, allowing for relatively rapid growth and development rates to achieve an ecologically viable size for settlement in a relatively short time. This would minimize the time spent in a hazardous pelagic environment and a vulnerable life stage when much of the regulation of year-class strength occurs (Thorson 1950, Houde 1987). Three hypotheses may explain the adaptive significance of multi-season development (i.e. winter larvae). (1) Larvae are able to take advantage of winter resources unavailable to single season developers at a time when competition is reduced (Kock & Kellermann 1991). (2) An extended pelagic phase allows a prolonged period for growth that allows larvae to settle at a larger size and more developed stage or compensates for an inability to grow to a minimum settlement size and development stage before the end of summer. (3) A prolonged pelagic phase allows new 'recruits' to enter the demersal environment at a different time of year than summer larvae when inter-specific competition in the new habitat is lowest (Kellermann & Schadwinkel 1990).

Data derived from otoliths were used to compare the timing of the hatch, growth rates, and development rates of larvae of 2 species, *Gobionotothen gibberifrons* (summer larvae; formerly *Notothenia gibberifrons*) and *Lepidonotothen larseni* (winter larvae; formerly *Nototheniops larseni*), from 2 different regions, the Bransfield Strait region of the Antarctic Peninsula and South Georgia. The hypotheses presented here are difficult to test directly, but we can tell which hypotheses are consistent with the early life-history data collected from otoliths and which hypotheses require modification.

MATERIALS AND METHODS

Field collection of samples. Larvae for this work were made available from 3 summer cruises, 1 along the west coast of the Antarctic Peninsula and 2 in the coastal waters surrounding South Georgia.

The Research on Antarctic Coastal Ecosystem Rates program (RACER) sampled a 250 × 100 km grid of stations in the western Bransfield Strait off the Antarctic Peninsula (Huntley et al. 1991). Stations were sampled with either oblique tows in the upper 50 m using a 0.7 m diameter bongo net with 330 and 505 µm mesh (69 'fast' stations) or in 2 discrete layers (0–100 and 100–200 m) with oblique tows of paired opening and closing Nansen nets with 330 µm mesh (25 'slow' stations). RACER began in the summer of 1986/87 with a series of 4 cruises in December, January, February, and March aboard the RV 'Polar Duke'. One half (n = 63 *Gobionotothen gibberifrons*, n = 18 *Lepidonotothen larseni*) of the larvae from the January cruise (January 19-February 2, 1987) was preserved in 100% methyl alcohol and examined in this work. The size and geographic distribution of the remainder were reported by Loeb (1991); there was no substantial difference in the mean length of larvae in the 2 sub-groups.

The 2 cruises off South Georgia were both demersal fish surveys of the US Antarctic Marine Living Resources program (US AMLR). The first cruise was a joint American-Polish study aboard the Polish RV 'Professor Siedlecki' (December 18, 1987, to January 10, 1988). The samples analyzed in this study were collected from 13 stations using an experimental technique where larval fish were caught in conjunction with bottom trawl operations in coastal waters around South Georgia and at Shag Rocks. Four plankton nets (505 µm mesh and 12 mm mesh with a 505 µm liner) were placed at various positions (4, 12, 16, and 28 m) from the head rope of a commercial bottom trawl. After capture, larvae (n = 11 *Gobionotothen gibberifrons*, n = 499 *Lepidonotothen larseni*) were preserved in isopropyl alcohol.

The second cruise off South Georgia was aboard the NOAA ship 'Surveyor' (January 4 to February 2, 1989). This cruise sampled the upper 180 m in a grid of 47 stations around the island using a 0.6 m diameter bongo net with 505 µm mesh. Additional samples were collected with several 'yo-yo' tows (where the bongo was brought up and down repeatedly in the upper 30 m) and with the use of a 2 m Isaacs-Kidd midwater trawl. The larvae (n = 64 *Gobionotothen gibberifrons*, n = 278 *Lepidonotothen larseni*) were preserved in buffered isopropyl alcohol.

A sub-sample of the larvae available from each cruise was randomly selected for detailed otolith analysis. Additional samples were randomly chosen for more measurements of gross otolith dimensions, larval morphometrics, and larval development state.

Morphometrics. Measurements of standard length (from the tip of the snout to the base of the caudal fin) were taken with calipers to the nearest 0.1 mm. To measure dry weight, samples were placed in a storage desiccator and allowed to dry at room temperature for 1 wk and then weighed upon a Cahn microbalance to the nearest 0.001 mg. The samples were then returned to the desiccator and re-weighed after 6 to 24 h. This was repeated 3 times and the mean weight of each sample was used.

Development state was noted by observing readily visible changes in the morphology of external features (pelvic fins, pectoral fins, dorsal and anal fins, and flexion state). The rate of development may be described by bracketing the timing (or size range) of each development event between the youngest (or smallest) observed larva to have attained a specific development state and the oldest (or largest) larva to have not yet reached that state.

Otolith techniques. Age (the estimated ring count) and otolith growth histories (the otolith radius at each sequential ring) were obtained from sagittal otoliths excised from each larva. Otolith data were collected with light microscopy using a video-coordinate digitizing system. A randomly selected sub-sample was also examined with scanning electron microscopy (SEM). All ring counts and measurements were made along the most clearly readable axis. The number of rings within any unreadable region along the selected axis was estimated as a function of the distance from the otolith's center and the average ring width at that radius among other otoliths from the same group. Detailed otolith methodologies are described in Ruzicka & Radtke (1995).

A comparison of the estimated ring counts of individual *Lepidonotothen larseni* and *Gobionotothen gibberifrons* otoliths examined with both light microscopy and SEM (selected from each of the same sample groups considered here) has shown that SEM counts are usually greater (Ruzicka & Radtke 1995). This difference was significant among the *L. larseni* from South Georgia 1987/88 and is attributed to the lower resolving power of light microscopy (ibid.). Ages, hatch dates, and growth rates estimated from both light microscopy and SEM derived data are presented together.

RESULTS

Morphometrics

The standard lengths and dry weights of *Gobionotothen gibberifrons* and *Lepidonotothen larseni* were distributed normally; these distributions are summarized in Table 1. No correction was made for sample

Table 1. *Gobionotothen gibberifrons* and *Lepidonotothen larseni*. Mean standard lengths and weights (±1 SD) of larvae collected off South Georgia in the summers of 1987/88 and 1988/89 and within the Bransfield Strait off the Antarctic Peninsula in the summer of 1986/87. Data are distributed normally

	Standard length (mm)	Dry weight (mg)
Gobionotothen gibberifrons		
South Georgia 1987/88	12.19 ± 2.38 (n = 11)	1.42 ± 0.49 (n = 11)
South Georgia 1988/89	22.49 ± 2.01 (n = 64)	15.73 ± 4.71 (n = 54)
Peninsula 1986/87	16.64 ± 1.76 (n = 63)	3.61 ± 1.62 (n = 55)
Lepidonotothen larseni		
South Georgia 1987/88	11.88 ± 1.44 (n = 30)	0.45 ± 0.16 (n = 32)
South Georgia 1988/89	17.61 ± 3.18 (n = 49)	4.42 ± 1.96 (n = 48)
Peninsula 1986/87	16.28 ± 1.53 (n = 17)	1.17 ± 0.38 (n = 18)

shrinkage in this work. Comparison of fresh and preserved lengths of *L. larseni* (Ruzicka unpubl. data) showed that the larvae shrank very little after 3 yr of storage in 90% ethanol, only 2.3% (±1.7%, n = 22) on average. However, the degree to which the larvae shrank before preservation is unknown.

The presence of yolk could not be detected in any larvae studied in this work. Flexion occurred early in *Gobionotothen gibberifrons* and was observed in all larvae including the youngest (22 d) and smallest (8.4 mm). Flexion in *Lepidonotothen larseni* occurred between 43 and 52 d (11.4 to 18.1 mm), the youngest post-flexion and the oldest pre-flexion larvae, respectively. All observed *G. gibberifrons* had visible rays forming in the dorsal, anal, and pectoral fins. Rays first became apparent in these fins slightly later in *L. larseni*, between 25 and 47 d old (10.2 to 16.4 mm). All fins had become well formed in the oldest *G. gibberifrons* observed, 54 to 79 d old (18.6 to 27.0 mm). In contrast, pelvic fin buds had only just appeared in the oldest and largest *L. larseni*, 68 to 78 d old (16.7 to 23.2 mm). These ages are estimated from ring counts on otoliths examined under light microscopy.

Hatch dates

Assuming that otolith ring counts accurately reflect age in days, the approximate hatch date may be determined by subtracting the estimated age from the capture-date of each larva (Figs. 1 & 2, Table 2). The otolith data show that during any particular year, hatching of both species occurs over a period of about

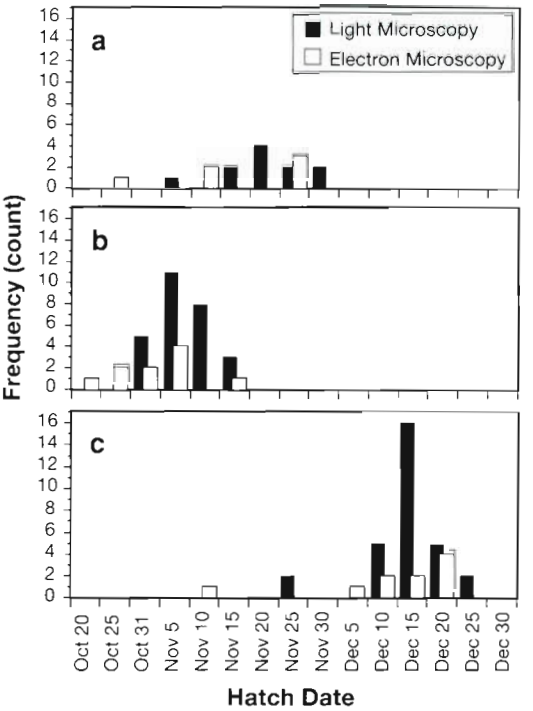

Fig. 1. *Gobionotothen gibberifrons*. Hatch date distributions. (a) South Georgia 1987/88; (b) South Georgia 1988/89; (c) Antarctic Peninsula 1986/87

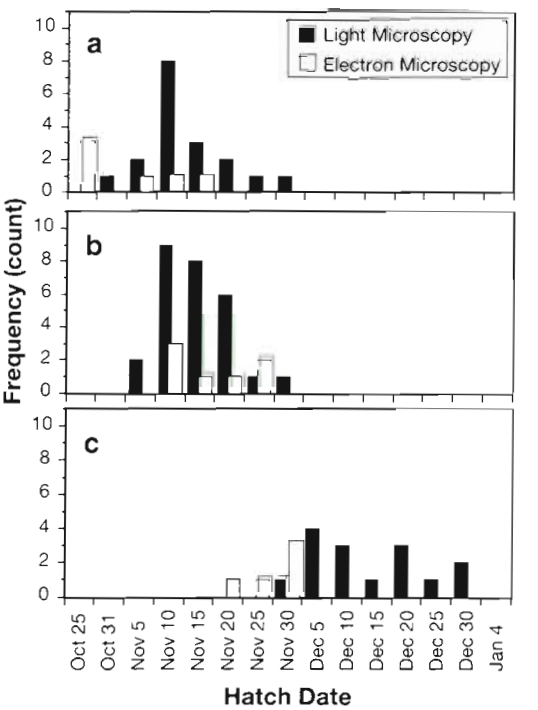

Fig. 2. *Lepidonotothen larseni*. Hatch date distributions. (a) South Georgia 1987/88; (b) South Georgia 1988/89; (c) Antarctic Peninsula 1986/87

Table 2. *Gobionotothen gibberifrons* and *Lepidonotothen larseni*. Mean age and hatch dates (±1 SD) of larvae from South Georgia (1987/88 and 1988/89) and the Bransfield Strait off the Antarctic Peninsula (1986/87) as estimated from otoliths examined under light microscopy and SEM

	Age (d)		Hatch date	
	Light microscopy	SEM	Light microscopy	SEM
Gobionotothen gibberifrons				
South Georgia 1987/88	33 ± 8 (n = 11)	40 ± 12 (n = 6)	22 Nov 1987 ± 8 (n = 11)	17 Nov 1987 ± 13 (n = 6)
South Georgia 1988/89	71 ± 4 (n = 27)	78 ± 8 (n = 10)	8 Nov 1988 ± 5 (n = 27)	3 Nov 1988 ± 7 (n = 10)
Peninsula 1986/87	38 ± 6 (n = 30)	41 ± 12 (n = 10)	16 Dec 1986 ± 7 (n = 30)	13 Dec 1986 ± 13 (n = 10)
Lepidonotothen larseni				
South Georgia 1987/88	44 ± 10 (n = 18)	58 ± 12 (n = 6)	15 Nov 1987 ± 7 (n = 18)	5 Nov 1987 ± 9 (n = 6)
South Georgia 1988/89	69 ± 7 (n = 27)	68 ± 6 (n = 7)	16 Nov 1988 ± 6 (n = 27)	18 Nov 1988 ± 6 (n = 7)
Peninsula 1986/87	39 ± 11 (n = 15)	57 ± 5 (n = 5)	15 Dec 1986 ± 10 (n = 15)	27 Nov 1986 ± 5 (n = 5)

1 mo. The variability of *Lepidonotothen larseni* hatch dates was only slightly greater than that of *Gobionotothen gibberifrons*, suggesting that there is just 1 peak hatch period for both species.

Growth

If a significant correlation exists between somatic growth and otolith growth, then detailed knowledge of an otolith's growth history (integral to the otolith's structure) offers detailed knowledge of the growth history of the individual fish from which it came. This method is commonly used to back-calculate fish sizes and track larval growth through time (e.g. Wilson & Larkin 1982, Penney & Evans 1985, Nishimura & Yamada 1988, Thorrold & Williams 1989, Jenkins & Davis 1990, May & Jenkins 1992).

The relationships between otolith size (longest diameter) and fish size at the time of capture are shown in Figs. 3 (standard length) & 4 [ln(dry weight)]. The linear least-squares regression method was used to describe the relations (Table 3). Since the purpose was to predict one variable (larval size) from the value of another (otolith diameter), a Model I rather than Model II regression was applied (Sokal & Rohlf 1981).

The range of otolith and somatic sizes from each South Georgian cruise was narrow. Combining data from the 2 cruises provided a more precise description of the relation between otolith and somatic size, which was derived from data covering nearly the complete size range in which growth histories are calculated. The validity of pooling data from these 2 cruises rests on the assumption that the same relationship exists between otolith size and larval size for larvae of the same species caught during different years (but within the same region).

Analysis of covariance (Snedecor & Cochran 1980) was used to compare the separate regression models generated from both cruises off South Georgia (Table 4). The 2 years' regression models of standard length against otolith diameter for South Georgian *Lepidonotothen larseni* did not differ significantly. The 2 models for South Georgian *Gobionotothen gibberifrons* differed significantly at $\alpha = 0.05$, but the pooled model was still considered more accurate in view of the very weak correlation between the otolith diameters and standard lengths of the 1988/89 samples. The model generated from the pooled South Georgian *G. gibberifrons* data did not differ significantly from the model generated from the unpooled 1987/88 samples (equal slopes, $p = 0.1275$; equal intercepts, $p = 0.9270$)

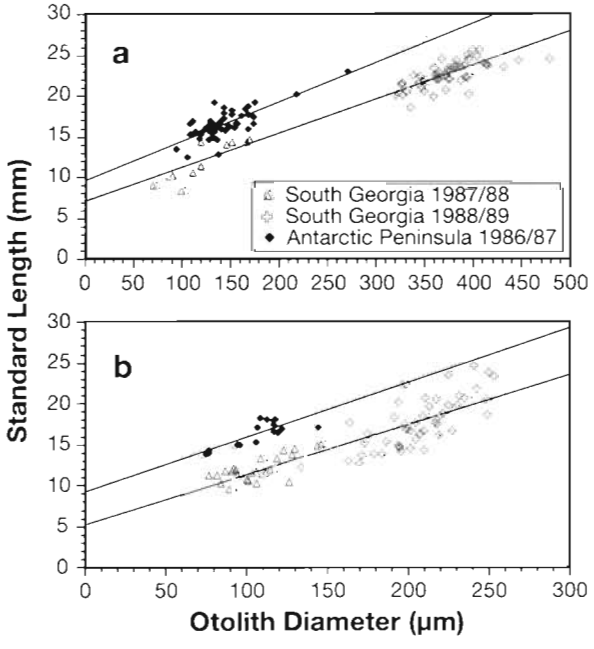

Fig. 3. *Gobionotothen gibberifrons* and *Lepidonotothen larseni*. Relationships between the otolith diameters (OD) and standard lengths (SL) of larvae collected off the Antarctic Peninsula in the summer of 1987/88 and off South Georgia in the summers of 1987/88 and 1988/89. Data from the 2 South Georgia cruises were pooled. (a) *G. gibberifrons*: Antarctic Peninsula ($SL = 9.5520 + OD \times 0.0480$, $R^2 = 0.598$) and South Georgia ($SL = 6.8868 + OD \times 0.0418$, $R^2 = 0.897$). (b) *L. larseni*: Antarctic Peninsula ($SL = 9.0787 + OD \times 0.0668$, $R^2 = 0.628$) and South Georgia ($SL = 5.0777 + OD \times 0.0611$, $R^2 = 0.748$)

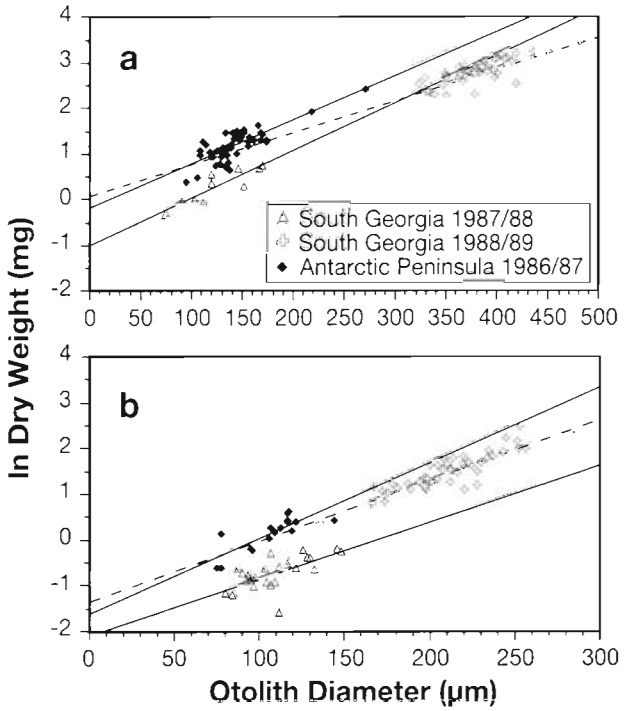

Fig. 4. *Gobionotothen gibberifrons* and *Lepidonotothen larseni*. Relationships between the otolith diameters (OD) and ln(dry weight) (lnW) of larvae collected off the Antarctic Peninsula in the summer of 1986/87 and off South Georgia in the summers of 1987/88 and 1988/89. (a) *G. gibberifrons*: Antarctic Peninsula ($lnW = -0.2224 + OD \times 0.0096$, $R^2 = 0.649$), South Georgia 1987/88 ($lnW = -1.0555 + OD \times 0.0104$, $R^2 = 0.778$), and South Georgia 1988/89 (dashed line, $lnW = 0.1135 + OD \times 0.0068$, $R^2 = 0.639$). (b) *L. larseni*: Antarctic Peninsula ($lnW = -1.6803 + OD \times 0.0167$, $R^2 = 0.659$), South Georgia 1987/88 ($lnW = -2.5285 + OD \times 0.0156$, $R^2 = 0.404$), and South Georgia 1988/89 (dashed line, $lnW = -1.3659 + OD \times 0.0132$, $R^2 = 0.793$)

nor from the unpooled 1988/89 samples (equal slopes, $p = 0.0953$; equal intercepts, $p = 0.8234$). Therefore, the pooled data were used to back-calculate larval lengths for both species. The regressions of ln(dry weight) against otolith diameter were clearly significantly different for both species, and larval weights were back-calculated using models generated from unpooled data.

The predicted standard lengths and weights are displayed as growth profiles (Figs. 5 & 6 respectively). Growth of individual larvae was modeled exponentially:

$$l_{age} = l_0 e^{r(age)}$$
$$w_{age} = w_0 e^{r(age)}$$

where *age* is the number of days from hatching, l_{age} is the standard length at a given age, l_0 is the standard length at hatching, w_{age} is the dry weight at a given age, w_0 is the dry weight at hatching, and r is the instantaneous growth rate (Table 5). The data were fit linearly using a Model II (geometric mean) regression (Ricker 1973) after back-calculated larval sizes had

Table 3. *Gobionotothen gibberifrons* and *Lepidonotothen larseni*. Functional relations between otolith diameter and standard length and between otolith diameter and ln(dry weight) (±95% confidence intervals) of larvae collected off South Georgia (1987/88 and 1988/89) and in the Bransfield Strait off the Antarctic Peninsula (1986/87) determined by linear least-squares regression

	Standard length = $a + b$(Otolith diameter)					ln(Dry weight) = $a + b$(Otolith diameter)				
	a	b	R^2	p	n	a	b	R^2	p	n
Gobionotothen gibberifrons										
South Georgia 1987/88	3.9013 ± 4.0021	0.0645 ± 0.0309	0.743	0.0010	10	−1.0555 ± 0.5871	0.0104 ± 0.0045	0.778	0.0005	10
South Georgia 1988/89	11.1664 ± 4.8363	0.0306 ± 0.0127	0.332	<0.0001	49	0.1135 ± 0.5960	0.0068 ± 0.0016	0.639	<0.0001	46
South Georgia pooled	6.8868 ± 1.3141	0.0418 ± 0.0038	0.897	<0.0001	59	–	–	–	–	–
Peninsula 1986/87	9.5520 ± 1.6772	0.0480 ± 0.0114	0.598	<0.0001	50	−0.2224 ± 0.3037	0.0096 ± 0.0021	0.649	<0.0001	49
Lepidonotothen larseni										
South Georgia 1987/88	5.5510 ± 2.7971	0.0594 ± 0.0252	0.533	<0.0001	23	−2.5285 ± 0.9272	0.0156 ± 0.0084	0.404	0.0008	24
South Georgia 1988/89	0.8878 ± 4.8987	0.0803 ± 0.0231	0.522	<0.0001	47	−1.3659 ± 0.4301	0.0132 ± 0.0020	0.793	<0.0001	47
South Georgia pooled	5.0777 ± 1.5907	0.0611 ± 0.0086	0.748	<0.0001	70	–	–	–	–	–
Peninsula 1986/87	9.0787 ± 3.2008	0.0668 ± 0.0295	0.628	0.0002	16	−1.6803 ± 0.7480	0.0167 ± 0.0069	0.659	0.0001	16

Table 4. *Gobionotothen gibberifrons* and *Lepidonotothen larseni*. Results of analysis of covariance to compare the regressions of otolith size against fish size (standard length and dry weight) from samples collected off South Georgia in the summer of 1987/88 with the regressions from samples collected off South Georgia in the summer of 1988/89. Underlined probabilities are considered significant at $\alpha = 0.05$

	Standard length	Dry weight
Gobionotothen gibberifrons		
Equality of slopes	$F_{[1,55]} = 4.744$ $p = \underline{0.0337}$	$F_{[1,52]} = 3.387$ $p = 0.0714$
Equality of adjusted means	$F_{[1,56]} = 1.041$ $p = 0.3120$	$F_{[1,53]} = 8.285$ $p = \underline{0.0058}$
Lepidonotothen larseni		
Equality of slopes	$F_{[1,66]} = 0.809$ $p = 0.3717$	$F_{[1,67]} = 0.574$ $p = 0.4513$
Equality of adjusted means	$F_{[1,67]} = 3.706$ $p = 0.0585$	$F_{[1,68]} = 36.081$ $p < \underline{0.0001}$

been natural-log transformed. For each group of larvae, the mean correlation coefficient was >0.95, for both length and weight models. The individual growth rates within each group were normally distributed.

With respect to both length and weight, the growth rates over the first 40 d calculated using light microscopy data were significantly greater than rates calculated using SEM data among the *Lepidonotothen larseni* from South Georgia 1987/88 and the Antarctic Peninsula 1986/87 (*t*-test, $p < 0.05$, $\alpha = 0.05$). This is consistent with the observation that very narrow rings (<0.5 µm) may be unobserved with light microscopy (Ruzicka & Radtke 1995).

Testing the back-calculation method

The model used to reconstruct growth histories may be tested by comparing predicted past size distribu-

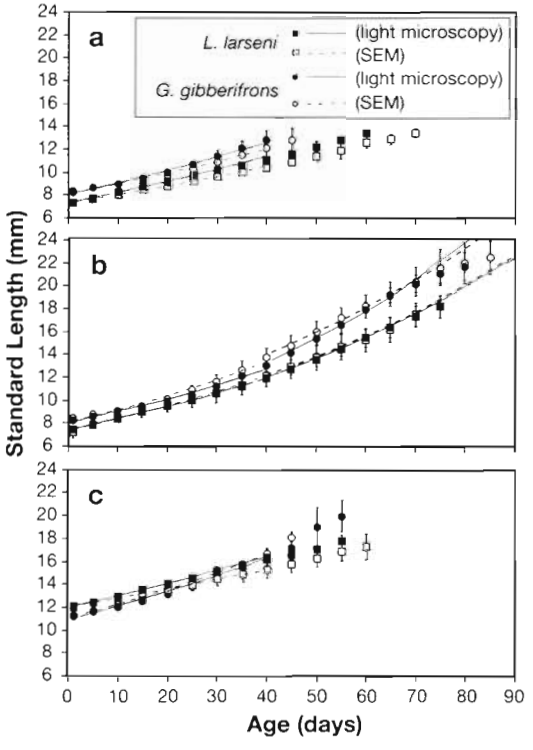

Fig. 5. *Gobionotothen gibberifrons* and *Lepidonotothen larseni*. Reconstructed growth histories of *G. gibberifrons* and *L. larseni*, with respect to length. Lengths of individual larvae were back-calculated from otolith data derived from light microscopy and SEM. The mean lengths (±1 SD) are plotted here in 5 d intervals. Growth of individual larvae over the first 40 d was modeled exponentially; the mean growth models (Table 5) are overlain upon the back-calculated lengths. (a) South Georgia 1987/88; (b) South Georgia 1988/89 (also showing the growth model after 40 d), (c) Antarctic Peninsula 1986/87

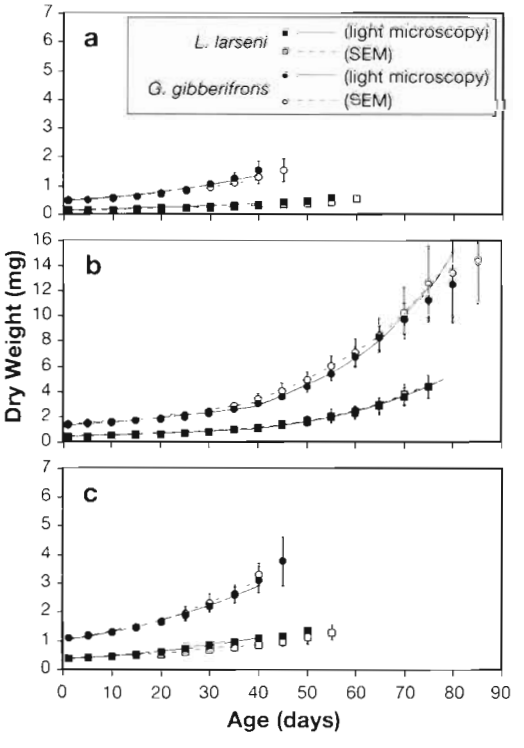

Fig. 6. *Gobionotothen gibberifrons* and *Lepidonotothen larseni*. Reconstructed growth histories of *G. gibberifrons* and *L. larseni*, with respect to dry weight. Weights of individual larvae were back-calculated from otolith data derived from light microscopy and SEM. The mean weights (±1 SD) are plotted here in 5 d intervals. Growth of individual larvae over the first 40 d was modeled exponentially; the mean growth models (Table 5) are overlain upon the back-calculated weights. (a) South Georgia 1987/88; (b) South Georgia 1988/89 (also showing the growth model after 40 d); (c) Antarctic Peninsula 1986/87

Table 5. *Gobionotothen gibberifrons* and *Lepidonotothen larseni*. Mean instantaneous growth rates (r) (±1 SD) of *G. gibberifrons* and *L. larseni* during the first 40 d after hatching. Growth was modeled exponentially with respect to length, $l_{age} = l_0 e^{r(age)}$, and weight, $w_{age} = w_0 e^{r(age)}$, (see 'Results: Growth') from otolith data collected with light microscopy and SEM. In every case, the mean correlation coefficient (R^2) was >0.95

	Light microscopy					SEM				
	r (length)	l_0	r (weight)	w_0	n	r (length)	l_0	r (weight)	w_0	n
Gobionotothen gibberifrons										
South Georgia 1987/88	0.0110 ± 0.0016	8.08	0.0275 ± 0.0049	0.45	11	0.0096 ± 0.0019	8.12	0.0235 ± 0.0050	0.46	6
South Georgia 1988/89	0.0115 ± 0.0010	7.97	0.0195 ± 0.0020	1.28	27	0.0126 ± 0.0020	8.01	0.0221 ± 0.0041	1.28	10
	0.0146 ± 0.0013[a]		0.0401 ± 0.0037[a]			0.0126 ± 0.0018[a]		0.0368 ± 0.0055[a]		
Peninsula 1986/87	0.0099 ± 0.0010	10.89	0.0265 ± 0.0032	1.01	30	0.0102 ± 0.0013	10.99	0.0275 ± 0.0037	1.03	10
Lepidonotothen larseni										
South Georgia 1987/88	0.0108 ± 0.0014	7.35	0.0250 ± 0.0030	0.14	18	0.0089 ± 0.0017	7.30	0.0201 ± 0.0036	0.14	6
South Georgia 1988/89	0.0119 ± 0.0007	7.40	0.0244 ± 0.0018	0.41	27	0.0122 ± 0.0016	7.38	0.0253 ± 0.0044	0.40	7
	0.0126 ± 0.0014[a]		0.0402 ± 0.0057[a]			0.0125 ± 0.0014[a]		0.0395 ± 0.0051[a]		
Peninsula 1986/87	0.0079 ± 0.0005	11.95	0.0272 ± 0.0015	0.37	15	0.0059 ± 0.0004	12.03	0.0203 ± 0.0022	0.38	5

[a]Growth rate of larvae after the first 40 d

tions with the findings of studies that have sampled from the same cohorts earlier in the season. This is possible with the 1986/87 Antarctic Peninsula cohorts where the RACER program sampled larvae during a series of 4 cruises (December through March). The standard length distributions of both species during each month were reported by Loeb (1991).

Table 6 shows the standard length distribution of each species in December as predicted from the otoliths of larvae caught in January and the actual size distribution of the larvae in December. A Wilcoxon's rank sum test (Hollander & Wolfe 1973) was employed to compare the predicted standard lengths (counting rings inwards from the outer edge to December 24, the midpoint of RACER sampling) to the actual standard lengths. In the case of *Gobionotothen gibberifrons*, the difference was not statistically significant whether using light microscopy or SEM derived data. The predicted lengths of *Lepidonotothen larseni* in December were significantly less than the larvae actually encountered when using light microscopy derived data. The error in the model when using light microscopy is likely to be the result of the lower resolving power of the light microscope and unseen rings. There was no significant difference when SEM data were used.

Inter-specific differences in growth

Do summer larvae grow faster than winter larvae? In most cases, the mean *Gobionotothen gibberifrons* instantaneous growth rates were greater than *Lepidonotothen larseni* growth rates (Table 5). A *t*-test (Moore & McCabe 1989) was used to make a cohort-by-cohort comparison of the instantaneous growth rates of the 2 species (Table 7). Only *G. gibberifrons* from South Georgia 1988/89 (older than 40 d, as analyzed under light microscopy) and from the Antarctic Peninsula 1986/87 grew significantly faster with respect to length. With respect to weight, only *G. gibberifrons* from the Antarctic Peninsula 1986/87 (as analyzed under SEM) grew significantly faster than the winter larvae.

Growth in the literature

Otolith derived growth rates are similar to rates measured by following cohorts through time (Table 8). The literature provides some evidence that *Gobionotothen gibberifrons* grow slightly faster than *Lepidonotothen larseni* (with respect to length). However, the literature provides no examples where the growth rates of both species were measured together during the same year and in the same region. Growth of *G. gibberifrons* shows great inter-annual variability at South Georgia.

Table 6. *Gobionotothen gibberifrons* and *Lepidonotothen larseni*. Predicted and actual standard length distributions (±1 SD) of larvae in the Bransfield Strait, December 1986, compared with a Wilcoxon's rank sum test (H_0: predicted size = actual size; H_1: predicted size ≠ actual size). Underlined probabilities are considered significant at $\alpha = 0.05$

	Length (mm)	Wilcoxon's rank sum test Difference[a] (95% CI)	Detection limit[b]	W	p	n
Gobionotothen gibberifrons						
Actual size (Loeb 1991)	11.9 ± 1.0					4
Predicted size (light microscopy)	12.0 ± 0.8	0.1 (−1.4, 1.3)	1.3	497.0	0.8447	29
Predicted size (SEM)	12.4 ± 1.9	0.2 (−1.4, 2.1)	1.7	77.5	0.7766	10
Lepidonotothen larseni						
Actual size (Loeb 1991)	13.9 ± 0.3					7
Predicted size (light microscopy)	13.3 ± 0.7	−0.7 (−1.3, 0.0)	0.7	95.5	0.0420	12
Predicted size (SEM)	14.1 ± 0.5	0.2 (−0.6, 0.9)	0.8	40.5	0.2192	5

[a]Point estimate of predicted size − actual size
[b]Maximum difference of predicted length from actual length not considered significant (based upon the 95% confidence interval of the difference)

DISCUSSION

The use of otoliths in this study to accurately measure the age and back-calculate the hatch dates of individual larvae rests upon the assumptions that ring deposition is daily and begins at hatch. In teleost fish, daily rings are common in the otoliths of adults and larvae (Jones 1986, Campana 1989). Daily rings have been experimentally validated in 3 Antarctic species (White 1991): *Trematomus newnesi* (Radtke et al. 1989), *Lepidonotothen nudifrons* (Hourigan & Radtke 1989, Radtke & Hourigan 1990), and *Harpagifer antarcticus* (White 1991, citing unpubl. data). There is also indirect evidence of daily ring deposition in *Lepidonotothen larseni* (Radtke & Targett 1984). The assumption that ring deposition commonly begins at hatch in the Notothenioidei is supported by the observation that the core edge represents a hatch check in *L. nudifrons* (Hourigan & Radtke 1989).

However, those years with very slow growth (1977 and 1985) are years when data are restricted to older, larger larvae. Growth rates from the single year available from the Peninsula fall at the lower end of the South Georgian range. Growth rates of peninsular *L. larseni* show little inter-annual variation and are all less than the growth rates around South Georgia. Higher growth rates off South Georgia may be indicative of a more favorable environment for growth.

The use of otoliths to reconstruct growth histories is not without disadvantages. The relation between otolith growth and somatic growth for an entire population is biased if the otolith size of individuals is strongly influenced by their differing rates of somatic growth, decoupling otolith size from somatic size; each individual would then have a unique relation between otolith size and somatic size. Since ring deposition continues even when somatic growth

Table 7. *Gobionotothen gibberifrons* and *Lepidonotothen larseni*. A comparison of the instantaneous growth rates (r) of summer larvae (*G. gibberifrons*) and winter larvae (*L. larseni*) during the first 40 d after hatching using the t-test (H_0: $r_{summer} = r_{winter}$; H_1: $r_{summer} > r_{winter}$). Instantaneous growth rates with respect to standard length and dry weight were calculated from otolith data collected with light microscopy and SEM. Underlined probabilities are considered significant at $\alpha = 0.05$

	Standard length (mm) Difference[a]	t	p	df	Dry weight (mg) Difference[a]	t	p	df
Light Microscopy								
South Georgia 1987/88	0.0002 ± 0.0012	0.34	0.3680	19	0.0025 ± 0.0035	1.53	0.0746	14
1988/89	−0.0004 ± 0.0005	−1.70	0.9523	47	−0.0049 ± 0.0010	−9.46	1.000	51
1988/89[b]	0.0020 ± 0.0007	5.44	<0.0001	51	−0.0001 ± 0.0026	−0.08	0.5303	44
Peninsula 1986/87	0.0020 ± 0.0005	8.94	<0.0001	42	−0.0007 ± 0.0014	−1.00	0.8382	42
Electron Microscopy								
South Georgia 1987/88	0.0007 ± 0.0024	0.67	0.2591	9	0.0034 ± 0.0057	1.35	0.1047	9
1988/89	0.0004 ± 0.0019	0.46	0.3273	14	−0.0032 ± 0.0046	−1.52	0.9225	12
1988/89[b]	0.0001 ± 0.0017	0.13	0.4497	14	−0.0027 ± 0.0056	−1.04	0.8413	13
Peninsula 1986/87	0.0043 ± 0.0010	9.59	<0.0001	11	0.0072 ± 0.0033	4.71	0.0003	12

[a]*G. gibberifrons* growth rate − *L. larseni* growth rate (± 95% confidence interval)
[b]Comparison of growth rates after the first 40 d between samples from South Georgia 1988/89

Table 8. *Gobionotothen gibberifrons* and *Lepidonotothen larseni*. Summary of all available instantaneous growth rates (r) of larval *G. gibberifrons* and *L. larseni* from South Georgia and the Antarctic Peninsula: from this work, reported in the literature, or estimated from size distribution data reported in the literature

Antarctic Peninsula			South Georgia		
Date	r	Source	Date	r	Source
Gobionotothen gibberifrons					
Dec–Mar '87	0.008	Loeb (1991)[a]	Jan–Mar '77	0.003	North (1990)[a]
Dec–Jan '87	0.010	This work	Dec–Mar '80	0.012	North (1990)[a]
			Dec–Jan '81	0.014	North (1990)[a]
			Jan–Mar '85	0.004	North (1990)[a]
			Dec–Jan '86	0.015	North (1990)[a]
			Nov–Jan '88	0.010	This work[b]
			Nov–Jan '89	0.014	This work
Lepidonotothen larseni					
Dec–Mar '87	0.004	Loeb (1991)[a]	Nov–Jan '88	0.009	This work[b]
Dec–Jan '87	0.006	This work[b]	Nov–Jan '89	0.012	This work
Nov–Mar '78	0.006	Kellermann (1986)			
Nov–Jan '84	0.005	Reconstructed[c]			
Nov–Feb '85	0.007	Reconstructed[d]			

[a]Growth originally modeled linearly, exponential model fit using formula: $r = [\ln(\text{length}_{\text{time2}}) - \ln(\text{length}_{\text{time1}})]/(\text{time2} - \text{time1})$

[b]Electron microscopy derived value, used when different from light microscopy value

[c]Data from Kellermann (1986, 1989a), Kellermann & Kock (1988), Sinque et al. (1988)

[d]Data from Kellermann (1986, 1989a), Kellermann & Kock (1988), Sinque et al. (1990)

ceases, slowly growing individuals will have larger otoliths, for their body size, than the population mean (Thomas 1983, Secor et al. 1989). This bias can cause an overestimation of somatic growth in a population having a wide range of growth rates (Campana 1990).

In this study, the same relationship between otolith growth and somatic growth was assumed to exist for all individuals of each population. The otolith/larval size relationships were used to accurately reconstruct the growth histories of the 1986/87 Antarctic Peninsula cohorts for both *Gobionotothen gibberifrons* and *Lepidonotothen larseni*. Besides providing indirect confirmation of daily ring formation, this field test also validates the regression used to predict larval size from otolith size. Nevertheless, the available data allow only rough approximations of the true relationships. The relationships have been derived from the combined data of different cohorts, they were developed for only a narrow range of larval sizes, and the variation among individuals is unknown.

Differences between light microscopy and SEM can be attributed to the resolution limits of light microscopy. However, while SEM has the potential for greater resolving power, this method is more costly and time consuming than light microscopy, and rings may still become obscured during the involved sample preparation (Ruzicka & Radtke 1995).

The otolith data show that both species have similar hatching patterns; the hatch dates of both species have unimodal distributions over only about 1 mo and both species hatch concurrently in each region. The otolith data also reveal that both species hatch later off the Antarctic Peninsula than off South Georgia. This has been previously observed for *Gobionotothen gibberifrons* (Kellermann 1989b) and is hypothesized to be a result of the earlier onset of the productive season at South Georgia (Kock & Kellermann 1991).

Off the Antarctic Peninsula, the smallest *Gobionotothen gibberifrons* larvae yet recorded (7.4 to 9.2 mm) were caught in late November which has suggested that hatching there occurs in November (Kellermann 1989b). The smallest *Lepidonotothen larseni* (7 mm) were caught between late October to early December suggesting that they hatch from late September to early November (Kellermann 1986). Whether using light microscopy or SEM, the otolith derived estimates of the hatching period of both species off the Antarctic Peninsula are significantly later than Kellermann's estimates (t-test, $p < 0.01$ in each case when otolith estimates are compared to November 15). However, otolith derived estimates do agree with Efremenko's (1979, 1983) observations that off South Georgia the smallest *G. gibberifrons* (8.5 mm) are found from September through November and that the smallest *L. larseni* (8.5 mm) are found from September through mid-December.

Summer larvae are hypothesized to take advantage of elevated prey levels during the summer to grow and develop rapidly and settle before the onset of winter, minimizing the time spent in a vulnerable life stage. A relatively narrow and seasonally tuned hatching period, such as found here for *Gobionotothen gibberifrons*, is a mechanism that would, year after year, allow larvae to begin feeding when prey are at their peak abundance (Everson 1984).

The winter larvae studied here (*Lepidonotothen larseni*) showed much the same hatching pattern as the summer larvae. This is more precise timing than was expected; the postulated benefits of winter life and absence of the time limits imposed upon summer larvae do not appear to weaken selectivity for precise hatch timing. Precise hatch timing may hold similar advantages for both strategies (increased exposure to

the food resource) with little added cost. Alternatively, precise hatch timing may be the result of competitive pressure. North & White (1987) and Kellermann (1989a) have noted that a succession of different species hatch at different sizes and times. They hypothesized that temporal and size partitioning of larval resources may represent adaptations that have the effect of reducing inter-specific competition for the food resource.

The data presented here and in the literature support the hypothesis that summer larvae generally grow faster than winter larvae. The differences in growth rates can account for fairly large differences in size by the end of summer. For example, a larva that hatches at 10 mm at the beginning of December and grows at $r = 0.010$ (as measured in this study for peninsular *Gobionotothen gibberifrons*) will reach 34 mm by early April. The same fish growing at $r = 0.006$ (as measured for peninsular *Lepidonotothen larseni*) will only reach 21 mm by early April. Not until June will peninsular *L. larseni* grow larger than 30 mm (Kellermann 1989b).

Development proceeds more rapidly in *Gobionotothen gibberifrons*. Within just 1 mo of hatching, the larvae observed here have become post-flexion and have a full complement of developing fins. By the end of summer (April), *G. gibberifrons* have reached the juvenile stage and are ready to settle (Kellermann 1989a). In contrast, pelvic fin buds have only just appeared in the oldest *Lepidonotothen larseni* observed in this study, 68 to 78 d old. *L. larseni* are found in the pre-juvenile 'transforming larva' stage as late as June (Kellermann 1989b).

Pelagic *Gobionotothen gibberifrons* have been caught into late March off both the Peninsula and South Georgia, reaching 22 to 26 and 35 to 38 mm, respectively (Efremenko 1983, Kellermann 1989a). Settlement is probably completed by April (Kellermann 1989a). Using the hatch size, hatch date, and growth rate parameters measured in this study, *G. gibberifrons* larvae settling in the first half of April off the Peninsula will be 33 to 38 mm; off South Georgia, settling larvae will be 31 to 36 mm and 56 to 58 mm (in April 1988 and 1989, respectively).

Pelagic *Lepidonotothen larseni* juveniles continue to grow over winter and settle at a larger size than *Gobionotothen gibberifrons*. Off the Antarctic Peninsula, Kellermann (1989a) reports that pelagic *L. larseni* grow to greater than 50 mm by their second summer (February/early March). Growth over winter must slow considerably from the summer. Growing at summer rates, *L. larseni* would grow to over 90 mm by the end of October (using the hatch size, hatch date, and growth rate parameters measured in this study). Instead, Kellermann (1989a) reports that peninsular *L. larseni* reach only 37 to 40 mm by late October/early November. Winter conditions are apparently more favorable for growth in waters around South Georgia; Efremenko (1979) has reported pelagic juvenile *L. larseni* 54 to 59 mm long in August. The month and size at which *L. larseni* juveniles finally take up a demersal existence are unknown.

A larger size at settlement is at least in part the result of the ability of winter larvae to continue feeding in the water column during the winter months. During summer, *Gobionotothen gibberifrons* and *Lepidonotothen larseni* larvae are both concentrated within the upper 30 m (Wörner & James 1981, North 1988) and have similar diets, preying upon copepods, calanoid copepod eggs, and euphausiid eggs and furcilia (Balbontín et al. 1986, Kellermann 1990, North & Ward 1990). *L. larseni* remain truly pelagic over winter and do not settle to the benthic environment to re-enter the pelagic environment during their second summer. In winter, they are found throughout the water column (0 to 250 m) but are most abundant in the upper 70 m (North 1988). While the winter diet of *L. larseni* has not been studied, North & Ward (1989, 1990) have found the winter diets of other larval Nototheniidae to be dominated by adult copepods. They also found that, like *L. larseni*, the major prey species was concentrated within the upper 70 m. Thus, the overwintering copepod stages are an available food source to which winter larvae have access and summer larvae do not.

The benefit that faster growth and development offer summer larvae is immediate; the time spent in the larval stage is minimized and exposure to the hazards of larval life is reduced. Small changes in growth and development stage duration are a major regulating mechanism of recruitment into the adult population (Houde 1987). The benefits of the winter development strategy may not be realized until after settlement. Reduced predation pressure and a competitive advantage over smaller, newly settling summer juveniles (both possible with settlement at a large size) and the ability to escape competitive pressure (settlement when competition is reduced; Kellermann & Schadwinkel 1990) may be achieved with an extended pelagic period.

Testing these hypotheses will require knowing the mortality rates suffered by larvae before settlement and by juveniles after settlement. During the pelagic larval period, survivorship should be greater for summer larvae. After settlement, juvenile survivorship should be greater for species with winter larvae. Unfortunately, there are few examples of repeated ichthyoplankton surveys within the same year which would allow estimations of larval mortality rates. Kellermann & Kock (1988) took advantage of such an opportunity to document an exponential decline of *Lepidonotothen larseni* abundance over the summer

months of 1977/78. Also needed is an indication of whether summer and winter juveniles are competitors in the demersal environment and whether growth of winter larvae in the plankton exceeds the growth of newly settled summer juveniles over the winter months. Do winter juveniles truly have a size advantage at the time of settlement? Little of the ecology of newly settled juvenile fish has yet been studied in the Antarctic, and criteria for predicting juvenile success are not known.

Another test of these hypotheses will be to see how well the results of this study can be applied to the Notothenioidei in general. Are the hatch period, growth, and development traits of *Gobionotothen gibberifrons* and *Lepidonotothen larseni* common to all species with summer and winter larvae, respectively? Indeed, can all species be classified into one of the 3 described strategies: precocial larvae, altricial summer larvae, and altricial winter larvae? At present, the early life-histories of most Notothenioidei remain entirely unknown.

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