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ABSTRACT: Structures on the otoliths of arrowtooth flounders *Atheresthes stomias* have been identified that correspond with hatching and settlement. Analysis of length frequency profiles and back-calculation of otolith dimensions suggested that arrowtooth flounders hatch at a mean standard length (SL) of 8–9 mm. They are planktonic for 145 d, and become benthic at 40–43 mm SL. Averaged over 14 years, the mean dates for hatching and settlement were April 15 and September 8, respectively. The hatch and settlement periods were protracted, with a 95% prediction interval (PI) of 37 days for each period. This wide 95% PI in hatch and settlement dates is a function of a long hatching period, not year-to-year fluctuations in hatch date.

INTRODUCTION

The arrowtooth flounder *Atheresthes stomias* is a common North Pacific flatfish that will probably experience increased commercial fishing pressure. Presently, at least one processor is making surimi from arrowtooth flounders (C. Hicks, Alaska Department of Fish and Game (ADF&G), Kodiak, personal communication). Because of its large biomass and possible expanded exploitation, there is considerable interest in describing the early life history of this species.

Otolith surface patterns in subarctic fish species display an opaque appearance during periods of fast growth; during slow growth hyaline material is deposited. In temperate and polar species, winter cessation of growth is reflected in an annulus, a band of hyaline material on the otolith (Williams and Bedford 1973; Beckman and Wilson 1995). There also may be other periods in the life history of a fish when growth slows (Geffen and Nash 1995). At hatching or shortly after, the fish switches from endogenous to exogenous energy sources as yolk material is exhausted. At settlement, a flatfish changes from primarily pelagic prey to benthic and demersal prey. These physiological transi-

tions may temporarily disrupt energy and nutrient flow, leaving an identifiable growth discontinuity on the otolith. No systematic examination of the otoliths from early life history stages of arrowtooth flounders has been previously published.

The objectives of this study were to: (1) link identifiable structures on the otoliths to major early life history stages, (2) estimate mean fish length at hatch and benthic recruitment, (3) estimate mean dates of hatch and settlement to the benthos, (4) determine the duration of planktonic existence, (5) describe growth rates of planktonic fish, and (6) discuss inter- and intra-annual variability in the timing of reproduction.

The findings of this study will provide a context within which questions about reproductive success, strength of year classes, and potential effects of fisheries and climate change might be framed.

METHODS

Fish used in these analyses included a subset equal to 2,795 planktonic arrowtooth flounders collected incidentally during National Marine Fisheries Service

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(NMFS) Gulf of Alaska surveys over 14 years between 1978 and 1992. Larvae were collected as early as February 20 and as late as July 31 using various ichthyoplankton-selecting gear types. Larvae were measured for standard length (SL) in millimeters. Date of capture, time of capture in Greenwich Mean Time (GMT), location of capture by NMFS station and latitude and longitude, gear type, mean gear depth (meters), mean bottom depth (meters), and haul duration were recorded. Detailed sampling methods are referenced in Table 1.

Juvenile arrowtooth flounders were also collected in benthic trawls from Kachemak Bay, Alaska in August 1996 ($n = 154$) for the purpose of describing a fish length–otolith length relationship. These fish were collected from 2 different vessels. The first vessel, the 20-m Alaska Department of Fish and Game (ADF&G) R/V *Pandalus*, fished a 400-mesh eastern trawl with 364-kg Nor'Eastern Astoria V trawl doors. The mesh was 3.2 cm in the cod end, 8.9 cm in the intermediate, and 10.2 cm in the body and wings. These samples were taken while sampling locations described in Bechtol and Yuen (1995), and targeted age-1 and older arrowtooth flounders. A second vessel, an 8.5-m University of Alaska skiff, deployed a 3-m plumbstaff beam trawl with a double tickler chain. The net mesh was 7 mm in the body and 4 mm in the cod end (Abookire 1997). The latter vessel sampled flatfish nursery areas nearshore.

All arrowtooth flounders >276 mm SL were excluded to ensure only juveniles were examined and to minimize potential bias from the sexual dimorphism in

size of mature fish (Rickey 1995; Zimmerman 1997). The juvenile fish were measured for SL (millimeters), total length (TL; millimeters) and wet weight (grams). Sagittal otoliths from 50 fish were removed and stored in a 50% glycerin solution with thymol crystals added to the solution as an antifungal agent. This process clears the otolith for surface pattern examination. The otoliths remained in the solution for approximately 6 months before examination.

Figure 1 illustrates an arrowtooth flounder otolith and identifies the focus as a very small hyaline area at its center. The kernel is a dense, opaque structure surrounding the focus. Otolith total length (OL), kernel length (KL), and focus diameter (FD) were measured using a dissecting microscope with a micrometer and reflected fiberoptic light. Otoliths were examined against a black background that made the hyaline zones appear black and the opaque zones appear white. All measurements were made laterally along the anterior–posterior plane which passed through the focus.

Otolith length was measured and compared for size differences between identifiable right and left otoliths using a one-way ANOVA. Approximately 21 d after the initial reading, OL, KL, and FD were again measured and compared using one-way ANOVA tests to determine if otolith clearing had stopped.

Sizes at hatching and benthic recruitment were estimated by examination of a SL frequency histogram of 2,795 planktonic fish. The mode of the SL distribution was assumed to estimate the mean SL at hatching, and the largest arrowtooth flounder found in the plankton was assumed to estimate the SL at recruitment to a benthic environment. It is not possible to calculate a variance using these methods or to calculate a mode using the 2 largest planktonic fish. Additional sampling of this size range would not be very fruitful due to their scarcity in the water column.

Additionally, SL and TL of benthic arrowtooth flounders were regressed against OL. The resultant equation was solved using the mean FD and mean KL to estimate mean fish size at completion of the formation of focus and kernel.

Julian dates of capture were regressed against the natural log of SL of larvae. The resulting equation was solved using natural logs of estimates of mean larval SL at hatch and benthic recruitment, allowing mean dates for these events to be predicted (Mendenhall and Sinich 1996). The difference between these dates was used to estimate planktonic duration. The difference between mean SL at hatch and benthic recruitment was divided by the mean duration of the planktonic stage to estimate larval growth rates in $\text{mm} \cdot \text{d}^{-1}$. This equation assumes linear growth, but such an assump-

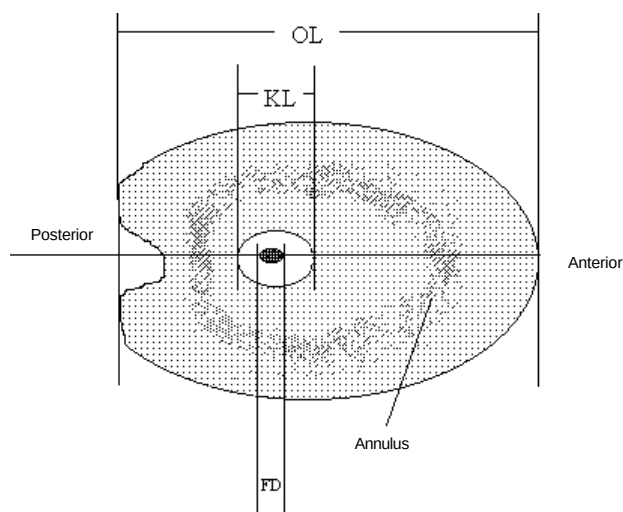


Figure 1. Diagram of an arrowtooth flounder otolith. OL = otolith length, KL = kernel length, FD = focus diameter. The horizontal line is the measurement plane.

Table 1. Cruise and reference information for arrowtooth flounder larvae collected by NMFS. WGOA = Western Gulf of Alaska, SS = Shelikof Strait.

Year	Cruise	Dates	General Location	n	Reference
1978	4DI78	4/1 to 4/17	WGOA	37	Dunn and Rugen (1989)
1979	1MF79	2/20 to 3/7	WGOA	47	Dunn and Rugen (1989)
	5TI79	5/19	WGOA	1	"
1981	1SH81	3/6 to 3/27	WGOA	30	Dunn and Rugen (1989)
	2SH81	4/19 to 4/22	WGOA	12	"
	3SH81	5/22 to 5/25	SS	6	"
	4MF81	5/20 to 5/21	SS	2	"
1982	1DA82	4/4 to 4/19	WGOA	18	Dunn and Rugen (1989)
	2DA82	5/22 to 5/31	WGOA	4	"
1984	1SH84	4/7 to 5/4	WGOA	155	Dunn and Rugen (1989)
1985	1DI85	3/13 to 3/25	WGOA	17	Dunn and Rugen (1989)
	1PO85	3/29 to 4/20	WGOA	57	"
	2MF85	5/4	SS	1	"
	2PO85	5/16 to 6/8	WGOA	258	"
1986	1GI86	3/30 to 4/20	WGOA	593	Dunn and Rugen (1989)
	2MF86	5/4	SS	1	"
1987	3MF87	5/21	SS	1	Dunn and Rugen (1989)
	4MF87	6/18 to 6/20	WGOA	5	"
1988	1MF88	4/1 to 4/12	SS	318	Dunn and Rugen (1989)
	2MF88	4/24 to 5/1	SS	8	"
	4MF88	5/20 to 6/6	WGOA	47	"
1989	1MF89	4/7 to 4/10	SS	3	Savage (1990)
	2MF89	4/27 to 5/4	SS	12	"
	3MF89	5/9 to 5/22	SS	33	"
	4MF89	5/29 to 6/5	SS	107	"
1990	1MF90	4/8 to 4/10	SS	5	DeWitt and Clark (1992)
	2MF90	5/7 to 5/14	SS	24	"
	4MF90	5/28 to 6/4	SS	48	"
1991	1MF91	4/8 to 4/10	SS	14	DeWitt and Clark (1993)
	2MF91	4/17 to 4/27	SS	122	"
	3MF91	5/4 to 5/10	SS	44	"
	4MF91	5/18 to 5/25	SS	131	"
	5MF91	7/23 to 7/31	WGOA	283	"
1992	3MF92	5/3 to 5/13	SS/WGOA	139	Schleiger et al. (1995)
	4MF92	5/18 to 5/28	SS/WGOA	200	"

tion is probably unrealistic for the entire 145-d planktonic period. A second growth estimation, the instantaneous growth rate (G), was calculated using the equation

$$G = (\log_e Y_2 - \log_e Y_1) / (t_2 - t_1)$$

where Y_2 and Y_1 are SL estimates at hatching and settlement, and t_2 and t_1 are the predicted mean Julian dates of hatch and settlement. Then G was multiplied by 100 and expressed as a percentage to estimate the specific growth rate of planktonic flounders (Busacker et al. 1990).

The associated variances around the estimates of the planktonic period provided a measure of the mean variability in hatch and settlement timing in the population for all years' data combined. Interannual variation in early life history parameters was examined by comparing mean larval SL during April 8–10 (early in the season) among the years 1984, 1986, 1988, and 1991 with a one-way analysis of variance (ANOVA). These years were selected because sufficient numbers of larvae were collected for the analysis.

In addition, a multiple linear regression model was fitted to the ichthyoplankton data in the form of

$$Y = B_0 + B_1x_1 + B_2x_2 + B_3x_3 + \dots B_{26}x_{26}$$

(complete model)

$$Y = B_0 + B_1x_1$$

(reduced model)

where

Y = standard length of larva,
 x_1 = Julian day of capture,
 $x_2 - x_{13}$ = indicator variables coded for year, and
 $x_{14} - x_{26}$ = interaction variables between year and Julian day.

The complete and reduced regression models were compared using a nested F -test (Mendenhall and Sinich 1996) to determine if the year of capture explained significantly more of the variability in SL than Julian day of capture alone.

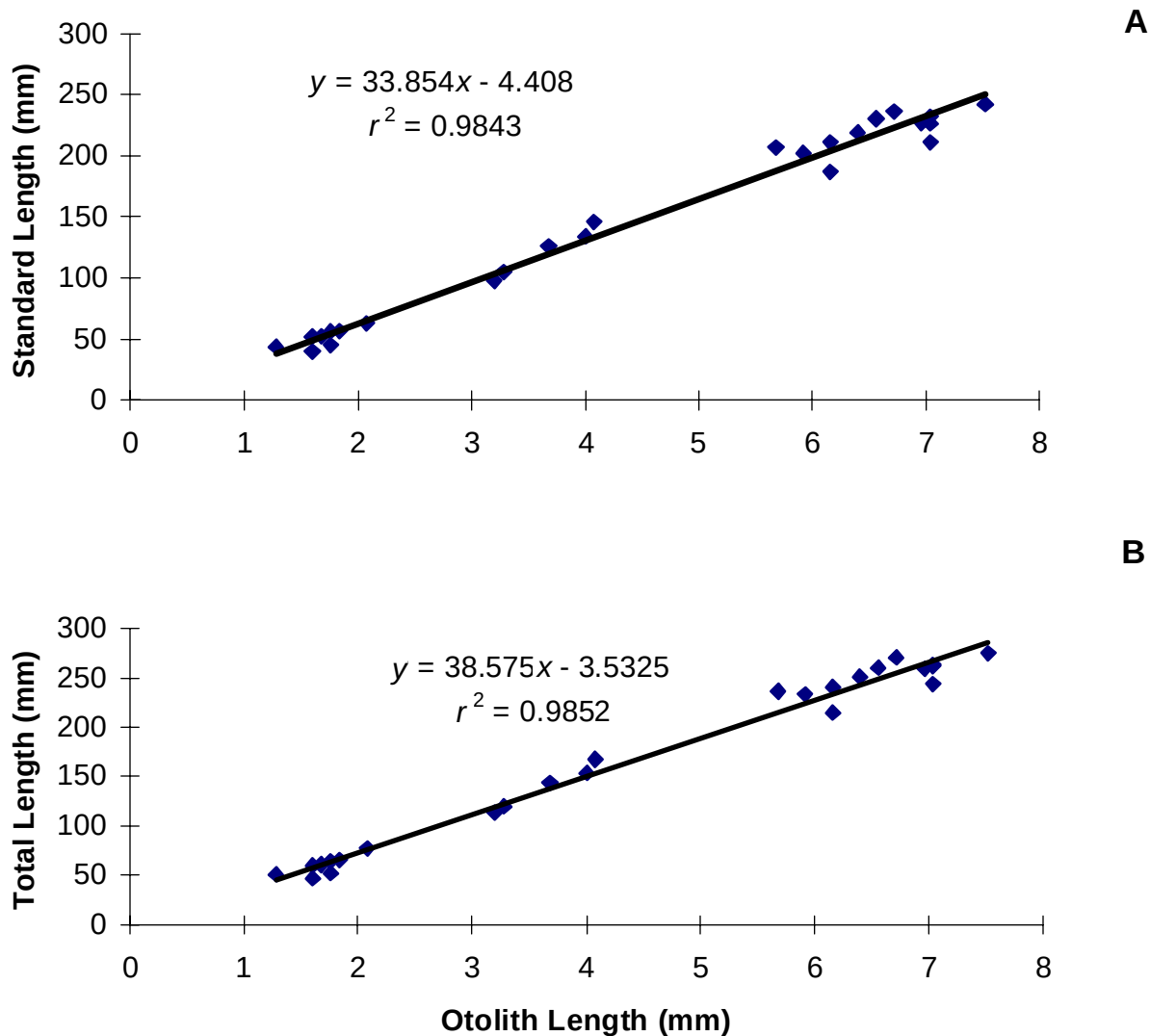


Figure 2. Relationship between otolith length and standard body length (A) and total body length (B) of juvenile (benthic) arrowtooth flounders.

RESULTS

Otolith Analysis from Benthic Fish

There was no significant change in OL ($F = <0.000001$, $P > 0.99$, $df = 49$), FD ($F = 1.09$, $P = 0.30$, $df = 49$), or KL ($F = 0.79$, $P = 0.377$, $df = 49$), of benthic fish after an additional 3 weeks of treatment in glycerin and thymol solution. The OL was similar for right and left otoliths ($F = 0.00087$, $P = 0.97$, $df = 21$).

A simple linear regression model best fit the relationship between benthic fish TL or SL, and OL (Figure 2). The TL model was solved using the mean FD we calculated (0.312 mm; $SD = 0.0447$) and mean KL (1.251 mm; $SD = 0.246$), which estimated mean length at completion of formation of these structures at 8.8 mm (± 0.9 , 95% PI; Mendenhall and Sinich 1996) and 44.7 mm (± 0.9 , 95% PI), respectively.

Ichthyoplankton Analysis

Lengths of planktonic arrowtooth flounders ranged from 3.4 to 40 mm SL. Examination of a length frequency histogram of 2,795 larvae (Figure 3) estimated hatch length at 8.5 mm SL, the midpoint of the most common length class. At length classes greater than 8–9 mm SL, frequency of occurrence in the plankton steadily declined. The largest planktonic arrowtooth flounders captured were 40 mm SL ($n = 2$).

The mean Julian dates for hatching and settlement were 106 (April 15; 95% PI ± 37) and 251 (September 8; 95% PI ± 37), respectively, based on the regression of mean SL and capture date. Mean planktonic stage duration was 145 d. Using these dates, the linear daily

growth increment in the plankton was $0.22 \text{ mm} \cdot \text{d}^{-1}$. The instantaneous growth rate was 0.0107 and the specific growth rate was 1.07% (Figure 4).

Using year of capture added significantly more information to the model than Julian day of capture alone to predict SL of planktonic arrowtooth flounders ($F = 31.73$, $P < 0.05$, $df = 2,793$). However, interannual variation in SL was small compared to intra-annual variation in SL during the period of April 8–10 for the years 1984, 1986, 1988, and 1991 (one-way ANOVA, $F = 1.97$, $P = 0.12$).

DISCUSSION

Hatch and Settlement Length

Two separate lines of evidence indicate a hatch length of 8 or 9 mm SL. First, in the ichthyoplankton size frequency profile, 8 and 9 mm SL larvae were the most abundant groups. Because the mesh size in most larval tows was generally $<1 \text{ mm}$, larvae 4–12 mm SL probably were fully recruited to the net. However, more sampling effort early in the season may have biased the results. Also, spatial differences, both vertical and geographic, were not considered for this project. Nonetheless, the most abundant length class captured from the plankton was newly hatched larvae that had been subjected to the least mortality. Second, the calculated mean SL when otolith focus formation is complete was 8.8 mm based on the TL-OL of benthic fish. The focus may be the prehatch otolith, because otolith ring formation begins at hatching or first feeding in several species (Hagen 1986). The beginning of ring forma-

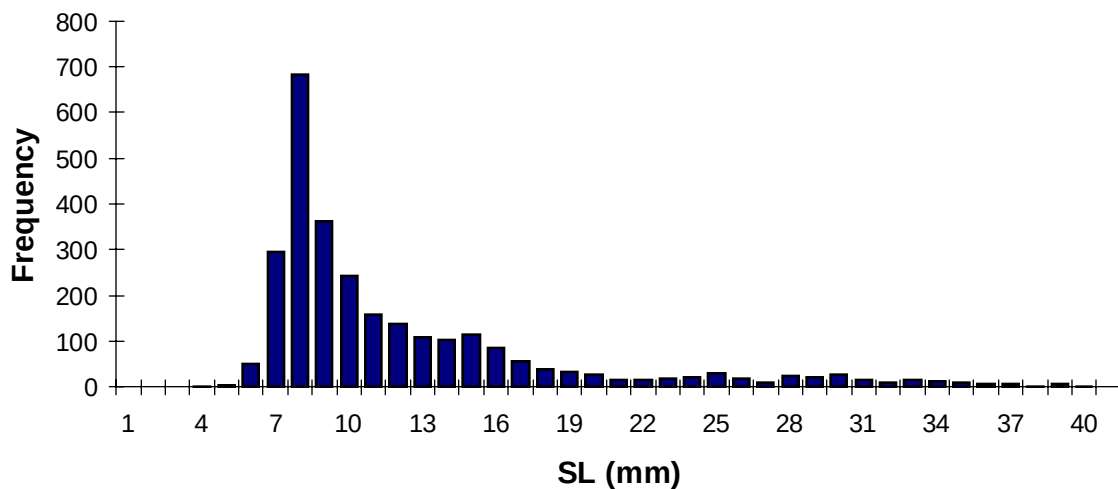


Figure 3. Standard length frequency of planktonic arrowtooth flounders, $n = 2,795$.

tion would differentiate the relatively clear focus from the more opaque surrounding material.

We found a few arrowtooth flounder larvae as small as 3.8 mm SL (Figure 3). If SL at hatching is normally distributed around a mean of 8.8 mm SL, larvae prob-

ably hatch as small as 4 mm SL and as large as 12 mm SL. However, the smallest larvae may have been inviable embryos with the outer coat dissolved. Assuming the focus is complete at hatching, we estimated a similar SL range at hatch of 7.88–9.72 mm from the upper

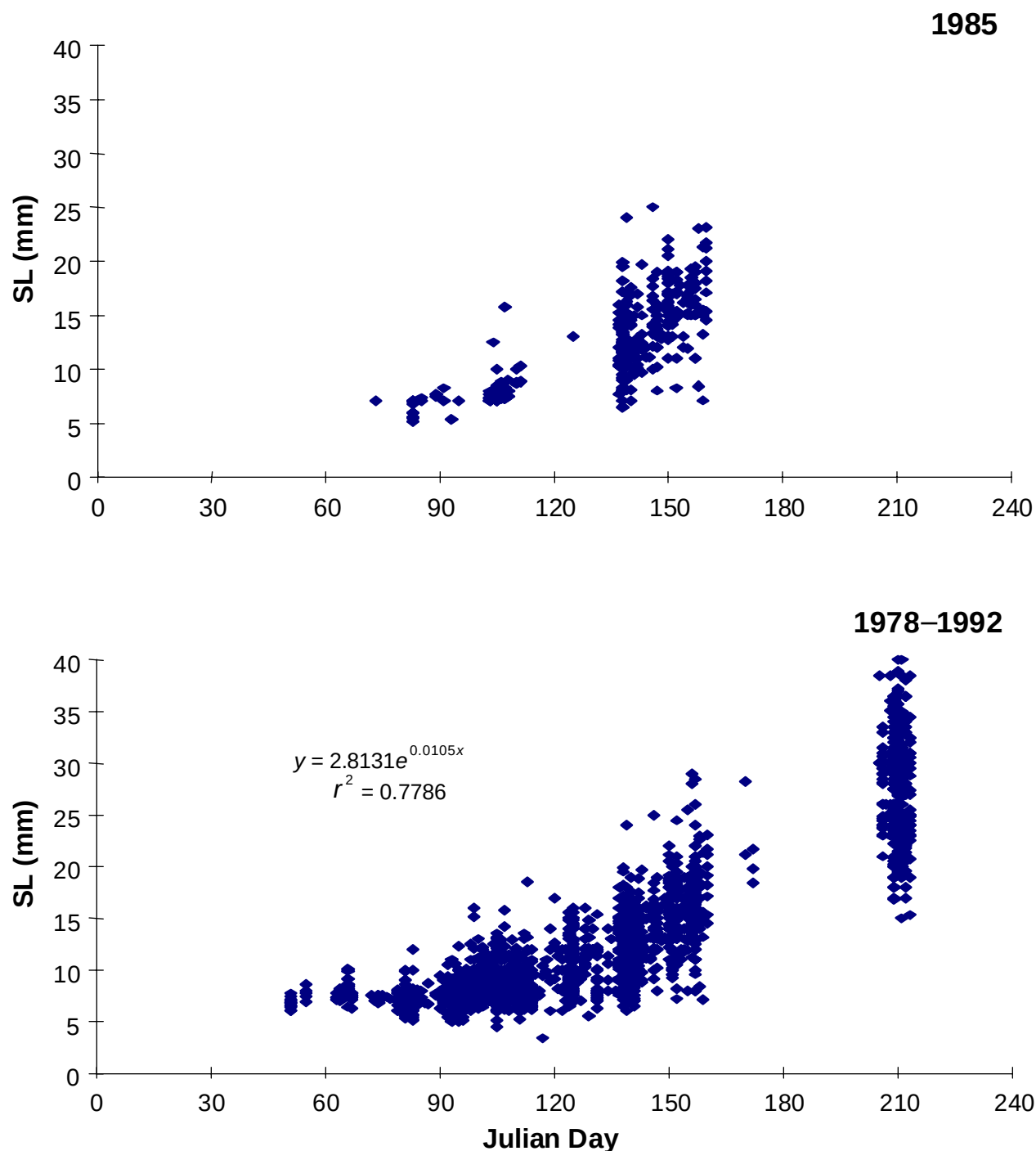


Figure 4. Standard length of planktonic arrowtooth flounders at Julian date of capture for 1985 (upper panel) compared with 1978–1992 (lower panel).

and lower 95% prediction-interval bounds around the mean FD.

The transition in the otolith between the focus and the surrounding marks may represent the first feeding event and not hatching. The duration of endogenous nutrition after hatching is not known in arrowtooth flounders. In Atlantic halibut *Hippoglossus hippoglossus*, this period lasts approximately 28 to 35 d at 5°C (Blaxter et al. 1983), and Hagen (1986) reported the yolk-sac period is comparable in Pacific halibut. It is unlikely this is the case with arrowtooth flounders. Although the egg diameters of Pacific halibut and arrowtooth flounders are similar, at a given length arrowtooth larvae are more developed. At 9.5 to 10 mm SL, arrowtooth flounders have a well-developed head and yolk material is absent. In contrast, Pacific halibut have a less developed head and still depend on yolk material for nutrition (Matarese et al. 1989). This may explain the difference between Hagen's (1986) estimated otolith diameter at hatch of 0.023 mm for Pacific halibut and ours of 0.312 mm for arrowtooth flounders, because a small head probably houses a small otolith.

Arrowtooth flounders probably settle to the benthos at 40 to 45 mm SL in the Gulf of Alaska. Only 2 planktonic 40-mm SL fish were captured. This is not unexpected because settlement-length flounders are rare in the plankton.

Estimated fish length at kernel completion ranged from 44 to 46 mm. This kernel is most likely associated with planktonic growth. In studies of nursery areas in the Gulf of Alaska, the smallest arrowtooth flounders captured in benthic tows in August were 38–43 mm SL, and the minimum size captured increased in later months (A. Abookire, USGS Biological Resource Division, Anchorage, personal communication).

Growth Rates

The calculated larval growth rate of $0.22 \text{ mm} \cdot \text{d}^{-1}$ for arrowtooth flounders is slower than the larval growth

rate of $0.29\text{--}0.30 \text{ mm} \cdot \text{d}^{-1}$ for the flathead sole *Hippoglossoides elassodon*, an ecologically-similar pleuronectid (Haldorson et al. 1989). Arrowtooth flounder larvae grow faster than Pacific halibut ($0.13\text{--}0.17 \text{ mm} \cdot \text{d}^{-1}$; Hagen 1986; Liu et al. 1993). Our growth rate estimate is probably low because fish $\geq 40 \text{ mm SL}$ have settled to the benthos. Inclusion of fish that settle earlier would increase our estimate of the mean growth rate and decrease our estimate of mean duration of the planktonic stage (Figure 4). More complete sampling of larvae in the 20–40 mm SL range would improve these estimates.

Variability in Reproductive Timing

Arrowtooth flounders have a protracted hatch period. They are known to spawn December through March in the Bering Sea (Pertzeva-Ostroumova 1961), and September through March off coastal Washington State (Rickey 1995). Spawning-condition females have been observed in August in the Gulf of Alaska (Hirschberger and Smith 1983). Data on egg incubation duration at various temperatures would allow calculation of spawning seasons from our hatch date estimates. Presently, this incubation information is not available.

Hatch-length larvae (6–12 mm SL) were present in the water column in 1985 (Figure 4; upper panel) over approximately the same time period as the 1978–1992 combined data (Figure 4; lower panel). This suggests a long hatch period (at least in 1985), because within-year variability in SL at date (protracted hatch period) was larger than between-year variability in SL at date (year-to-year differences in mean hatch date). For the entire sample, multiple regression analysis determined that the year of capture accounted for significantly more variation in SL than day of capture alone. However, with the large sample size, this procedure is extremely powerful and capable of detecting small additions of information. Although mean hatch date may vary annually, most variation of SL at date for the combined sample can be attributed to an elongated hatch period.

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