



Early growth and recruitment in Atlantic mackerel *Scomber scombrus*: discriminating the effects of fast growth and selection for fast growth

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ABSTRACT: We tested the hypothesis that strong recruitment in Atlantic mackerel *Scomber scombrus* occurs only in years when larval growth is fast and predation pressure — as measured by selection for fast growth — is weak. Four annual cohorts of larvae (1997, 1998, 1999 & 2000) were sampled on the Magdalen Shallows, southern Gulf of St. Lawrence, and 1 yr old mackerel juveniles were sampled the year after in the mackerel fishery of the southern Gulf. The early larval growth trajectories of both larvae and juveniles were back-calculated from the analysis of the sagittal otolith. Interannual differences in growth measured in the larvae persisted in the juveniles. The growth of larvae was significantly higher in 1999, an exceptional year class, than in the 3 other weak year classes. Surviving juveniles of the strong 1999 and the weak 1997 year classes grew equally fast during the first 40 d of larval life, but selection for fast growth was mild in 1999 and severe in 1997. We conclude that fast early growth measured in 1 yr old juveniles reflected fast growth of the entire larval population in 1999, and strong selective mortality against slow-growing larvae in 1997. Early growth was slow in larvae and juveniles of the weak 1998 (mild selection) and 2000 (no selection) year classes. Consistent with the hypothesis, the combination of fast growth and weak selection for fast growth unique to the 1999 cohort resulted in exceptional recruitment.

KEY WORDS: Fish larvae · Juveniles · Growth selection · Otolith microstructure · Survival · Recruitment · Atlantic mackerel · *Scomber scombrus*

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INTRODUCTION

The early developmental stages of marine fish experience massive mortality during life in the plankton (Houde 2002). It is generally accepted that the number of fish that survive this relatively short period is a reliable predictor of year-class strength (Leggett & Deblois 1994, Platt et al. 2003). Central hypotheses on recruitment determination assume that fast-growing larvae have a higher probability of surviving (Anderson 1988, Cushing 1990) than slow-growing larvae, which are eliminated from the population by the combination of (1) higher vulnerability to predators at a given age — the 'bigger-is-better' mechanism (e.g. Miller et al. 1988), (2) longer exposure to intense predation during plankton life — the 'stage-duration' mechanism (e.g. Chambers & Leggett

1987), and/or (3) higher energy gain for predators preying on slow growers — the 'growth-selective predation' mechanism (Takasuka et al. 2003, 2004).

According to these hypotheses, strong recruitment should be associated with fast growth in the plankton. However, a major issue arising when trying to link early growth and recruitment is that fast growth in a cohort of larvae sampled at sea can either reflect fast growth of the population in general under optimal conditions of temperature and food, or the removal of slow-growing larvae by predators. When size-selective predation is mild, fast growth of the population in general will lead to high survival and good recruitment. Alternatively, intense size-selective predation will simultaneously decimate slow-growing larvae (Beyer & Laurence 1980, Takasuka et al. 2003) and increase the apparent aver-

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age growth of the survivors sampled at sea (Meekan & Fortier 1996). In this situation, low recruitment can become associated with apparent fast growth (Holtby et al. 1990). This duality in the meaning of fast growth measured at sea may explain the conflicting reports on the relationship between early growth and recruitment in marine fish. Some studies have shown a strong and positive correlation between recruitment and early growth (Campana 1996, Ottersen & Loeng 2000, Jenkins & King 2006). Others have reported an absence of correlation (van der Veer et al. 1994, Bailey et al. 1996) or indications of an inverse relationship (van der Veer et al. 1994, Ringuette et al. 2002).

The above considerations lead to the prediction that strong recruitment will occur only in years when observed larval growth is fast and selection for fast growth is weak. In the 3 other potential cases (fast growth & strong selection; slow growth & strong selection; slow growth & weak selection) recruitment is expected to be weak. The Atlantic mackerel *Scomber scombrus* is an ideal model species to test these predictions because it exhibits (1) high and variable early growth rates (D'Amours et al. 1990), (2) cannibalistic behaviour during the larval stage, which implies size-selective predation (Fortier & Villeneuve 1996), (3) clear otolith microstructure enabling the back-calculation of growth trajectories (D'Amours et al. 1990), and (4) high interannual variability in recruitment (Ringuette et al. 2002, Grégoire et al. 2004).

In this study, we assessed the relative importance of fast growth and selection for fast growth in explaining the observed larval growth of Atlantic mackerel in 4 yr of sampling in the southern Gulf of St. Lawrence. First we estimated selection for fast growth by comparing back-calculated otolith increment width at age between a reference larval population (all larvae with age ≤ 11 d at capture) and survivors to age ≥ 16 d (Meekan & Fortier 1996). Second, we confirmed that any selection for fast growth measured during the larval phase was maintained in later life by comparing the growth of larvae sampled in a given year to the back-calculated larval growth of juveniles captured 1 yr later. These comparisons included years of low recruitment (1997, 1998, 2000) and a year of exceptionally high recruitment (1999). The present study focuses on interannual differences in early growth and recruitment. The environmental control of these differences in growth will be assessed in another study.

MATERIALS AND METHODS

Study area. The Gulf of St. Lawrence is an inland sea connected to the Atlantic Ocean by the Cabot and Belle-Isle straits (Fig. 1a). Within the southern part of

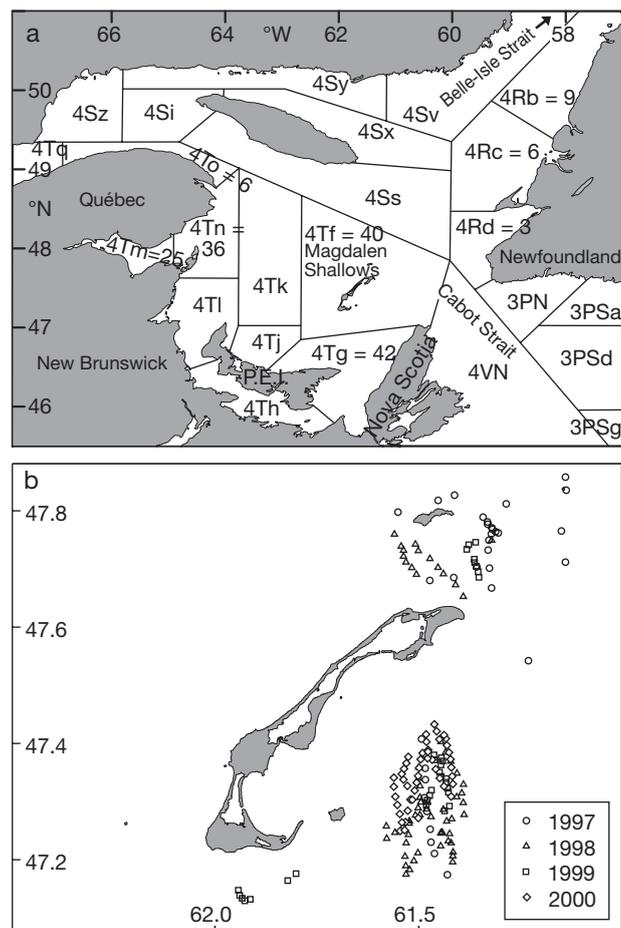


Fig. 1. (a) Gulf of St. Lawrence in eastern Canada, with number of 1 yr old juvenile Atlantic mackerel captured in each NAFO (Northwest Atlantic Fisheries Organization) fishing subdivision. (b) Magdalen Shallows, with stations where larvae were captured from 1997 to 2000

the Gulf, the Magdalen Shallows form a discrete bank covering ca. 50 000 km² with an average depth of 50 m. The Magdalen Shallows are one of the main spawning grounds for the Atlantic mackerel stock of the Gulf, and for other species such as yellowtail flounder *Limanda ferruginea*, American plaice *Hippoglossoides platessoides* and Atlantic cod *Gadus morhua*.

Recruitment data. Following Runge et al. (1999) and Ringuette et al. (2002), the proportion of Age 3 fish in the catch-at-age of the Canadian mackerel fishery was used as the recruitment index (MACREC). The catch-at-age is an estimation of the total number of fish of each age caught in the fishery in each year. See Runge et al. (1999) for a complete description and discussion of the MACREC index.

Sampling of Atlantic mackerel larvae and juveniles. Fish larvae were sampled from June to mid-August in the years 1997 to 2000. This period covered both spawning and the entire duration of the larval stage of mack-

erel in the southern Gulf. Sampling effort was concentrated in the depth range 20 to 45 m within the south-eastern and northeastern areas of the Magdalen Islands (Fig. 1b), where ichthyoplankton concentrations were highest. Surveys of 1 d duration were conducted on a 15 m boat at intervals of ca. 1 wk, depending on weather conditions. During each survey, the sampling gear was deployed 8 to 12 times from 16:00 to 24:00 h. It consisted of a rectangular frame carrying 2 nets of 750 μm mesh and 1 m² mouth aperture (Drolet et al. 1991). Mackerel larvae were sorted fresh and preserved in 95 % ethyl alcohol immediately after capture.

One year old juvenile mackerel were obtained in 1998, 1999, 2000 and 2001 from annual sampling of the mackerel fishery by the Department of Fisheries and Oceans, Canada. Fish from all year classes are randomly sampled from commercial landings throughout the Gulf of St. Lawrence (Fig. 1a). The sagittal otolith of 39 to 45 one yr old juveniles randomly sub-sampled in each year was preserved dry for early growth analysis (Table 1).

Otolith analysis. In the laboratory, the standard length of all mackerel larvae was measured to the nearest 0.1 mm. Stratified sub-samples of larvae were assembled for growth analysis by randomly selecting individuals from predetermined length classes within each year (Table 1). Sagittal otoliths were selected for growth analyses (Fig. 2). Daily deposition of increments has been validated for sagittae of Atlantic mackerel larvae (D'Amours et al. 1990). Sagittae from larvae and 1 yr old juveniles were mounted on slides using Crystalbond[®] thermoplastic cement, under a dissecting microscope. Otoliths of 1 yr old juveniles were polished on both sides using 30 μm and 3 μm metallurgical lapping films to obtain a thin layer allowing the visualisation of the hatch mark and the initial growth rings. The number of increments was counted and the distance between increments was measured at 1000 \times (larvae) and 670 \times (juveniles) using a microscope connected to an Image-Pro Plus[®] image analysing system with a digital camera. In juvenile fish, age determination was reliable up to ca. 40 d, after which daily increments were difficult to visualize in most cases. The origin and slope of the regression of log standard length on age did not differ significantly

Table 1. *Scomber scombrus*. Number of Atlantic mackerel larvae and 1 yr old juveniles collected and used for otolith analysis in each year

Year class	Number of larvae collected	Number of larval otoliths analysed	Number of juvenile otoliths analysed
1997	2371	338	40
1998	15299	366	45
1999	217	211	39
2000	1401	343	43

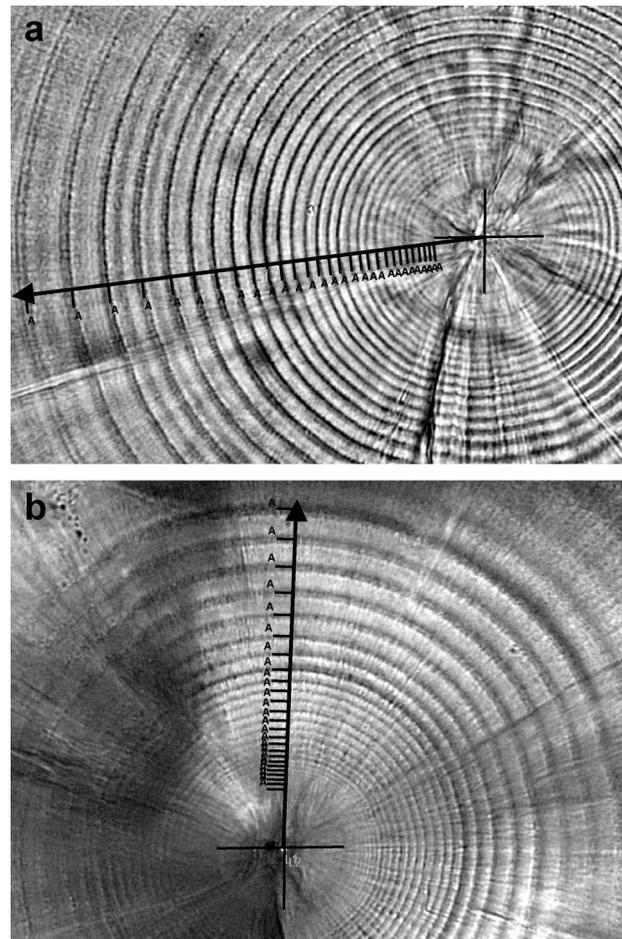


Fig. 2. *Scomber scombrus*. Atlantic mackerel sagittal otoliths at 1000 \times magnification: (a) 16.5 mm larva and (b) 1 yr old juvenile (261 mm long). Extent of central cross indicates diameter of core. A: delimitation between growth increments

between larvae sampled before or after sunset (ANCOVA, $p = 0.08$) confirming the absence of significant gear avoidance in daytime. Therefore larvae from daylight and darkness collections were used without discrimination in subsequent analyses.

Growth analysis. Interannual differences in growth during larval life were assessed by comparing early growth trajectories of larvae captured among the 4 yr. Given that daily growth data are auto-correlated because the same individuals are compared at different ages, repeated-measures MANOVA was used to test for among-group differences in growth trajectory (Chambers & Miller 1995, Meekan & Fortier 1996). Pillai's Trace, a more robust statistic than Wilk's Λ in the case of unequal sample sizes, was selected as the test statistic. Post hoc F -tests were used to determine at what age differences in increment width occurred among years (Hand & Taylor 1987). A similar analysis was performed on the initial growth trajectories (age 0

Table 2. *Scomber scombrus*. Range of age at capture used to represent growth of reference population during a given age interval, and its sample size for each year. Note that due to low sample size, the 16 to 20 d age interval was not included in repeated-measures MANOVA, but was used in comparison of otolith growth rate between larvae and 1 yr old juveniles (Fig. 8)

Growth interval (d)	Range of age (d) at capture	Sample size			
		1997	1998	1999	2000
1–5	6–10	45	74	97	122
6–10	11–15	236	88	80	130
11–15	16–20	46	132	20	75
16–20	>20	12	47	8	3

to 40 d) of 1 yr old juveniles from the same 4 year classes.

To measure selection for fast growth during larval life, the same statistical approach was used to compare the early growth of a reference larval population (age ≤ 11 d) to that of larvae surviving to age ≥ 16 d (Meekan & Fortier 1996). These age classes provided a sufficient number of larvae in each group for statistical tests. To verify that any pattern of selection for fast growth was maintained from the larval stage to the juvenile stage, the early growth trajectory of 1 yr old survivors was compared to that of the larval population born in the same year, i.e. the same cohort. In all analyses involving larvae, repeated-measures MANOVA were performed on 5 d age intervals (1–5, 6–10, 11–15, 16–20 d) to determine the age interval at which divergences in growth trajectory occurred among groups. Ideally, the growth of survivors over a given age interval should be compared to the growth of fish that were captured immediately at the end of the age interval (Meekan & Fortier 1996). For example, over the age interval 1 to 5 d, the growth of survivors should, if possible, be compared to the growth of larvae that were 6 d old at capture and, thus, have not experienced additional growth selection after 5 d of age. Unfortunately, this is usually impossible because of the limited number of larvae sampled (Meekan & Fortier 1996). In the present analysis, we used larvae aged 1 to 5 d older than the age interval studied (Table 2), providing a conservative estimate of selection for fast growth (Meekan & Fortier 1996, Sirois & Dodson 2000).

RESULTS

Recruitment strength

Three of the 4 yr considered led to weak recruitment (1997, 1998, 2000) while 1999 was an exceptionally abundant year class (Fig. 3). Almost 80% of all mackerel fished by the commercial fleet in 2002 were new

recruits from the 1999 cohort. This year class is the strongest since 1982.

Relationship between otolith and somatic growth

A strong linear relationship was found between otolith radius (OR) and standard length (SL), with both log-transformed, indicating that otolith growth is a reliable estimate of somatic growth ($SL = 0.7725 \times OR - 0.5753$, $r^2 = 0.91$, $p < 0.0001$, $n = 1258$). The slope and intercept of the linear relationship did not differ significantly among the 4 yr (ANCOVA, $p = 0.12$), and residuals were evenly distributed on either side of the regression line. We assumed the same proportionality between otolith and somatic growth for juvenile fish during their larval life. Otolith growth was used as a proxy for somatic growth because back-calculation of daily increments was not possible past the age of ~ 40 d in juvenile fish.

Interannual differences in early larval growth

Interannual differences were found in the growth trajectory of larvae up to the age of 15 d (Fig. 4, repeated-measures MANOVA: $p < 0.001$). Growth in the age interval 3 to 10 d was significantly higher in the strong year class of 1999 than in any other year (Table 3). During this age interval, differences in growth between 1999 and the other years tended to increase and reached 30% by the age of 10 d. Differences in growth among the 1997, 1998 and 1999 cohorts attenuated over the 11 to 15 d age interval but growth remained slower in 2000 (Fig. 4).

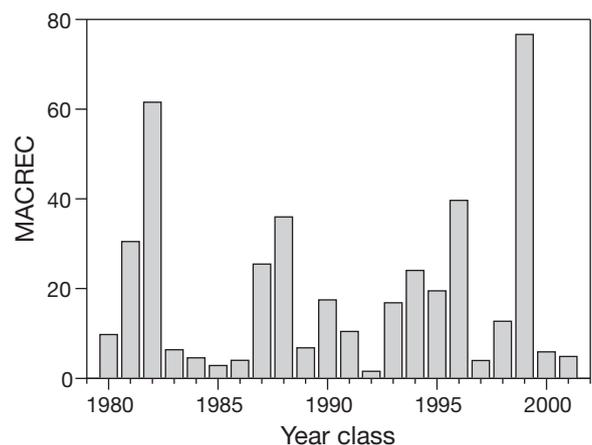


Fig. 3. *Scomber scombrus*. Recruitment index for mackerel for year classes 1980 to 2001 (MACREC). Index is percentage of age 3 fish (recruits) in overall commercial landings for eastern Canada and represents recruitment 3 yr later of fish hatched in a given year. Fig. 3 modified from Grégoire et al. (2004)

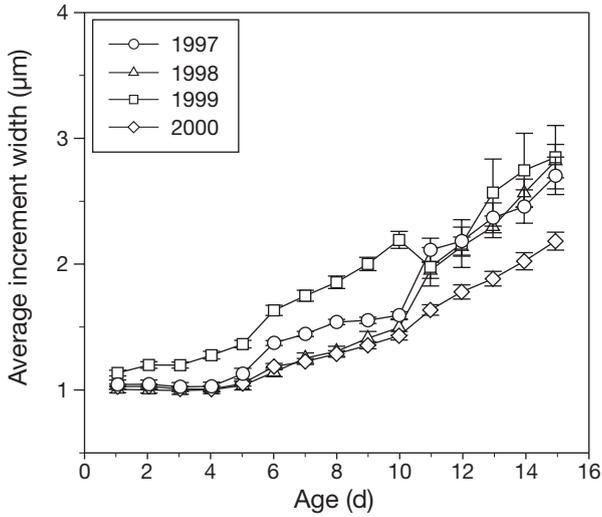


Fig. 4. *Scomber scombrus*. Average increment width at age as measured on sagittal otoliths of larvae sampled in 1997, 1998, 1999, and 2000. Mean values \pm SE are shown. Only data contributing to repeated-measures MANOVA analyses in each 5 d age interval were included (Table 2)

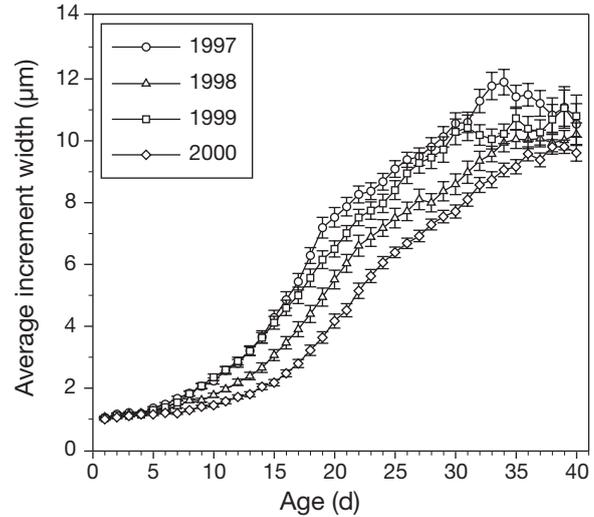


Fig. 5. *Scomber scombrus*. Average increment width at age over the 0 to 40 d interval as measured on sagittal otoliths of 1 yr old juveniles from 1997, 1998, 1999, and 2000 cohorts. Mean values \pm SE are shown

In 1 yr old juveniles, mean otolith growth during the larval stage increased in a sigmoid pattern with age, reaching a plateau around the age of 35 d (Fig. 5). The early larval growth of juvenile survivors differed significantly between years (repeated-measures MANOVA: $p < 0.0001$). The 1997 and 1999 cohorts were characterized by fast growth, while growth was intermediate and weak for the 1998 and 2000 year classes respectively. Growth during the strong 1999 year class did not differ from growth in 1997, but was

significantly higher than in 1998 and 2000 (post-hoc F -tests: $p < 0.05$). Differences in growth among the similar 1997/1999 and the other yr appeared as early as age 5 d (2000) and 6 d (1998) (Table 4). Divergence among growth trajectories intensified with age up to 15 d, after which it stabilized. By 15 d of age, growth in 1997 and 1999 was about 33 and 100% higher than in 1998 and 2000, respectively. Interannual differences in growth persisted throughout most of larval life, before attenuating past the age of 30 d.

Table 3. *Scomber scombrus*. Between-year comparison of average sagittal increment width at age for larvae sampled from 1997 to 2000. Age intervals (d) during which significant differences in growth were detected (F -tests, $p < 0.05$) are given in parentheses

	Year class		
	1998	1999	2000
1997	1997 > 1998 (6–8)	1999 > 1997 (3–10)	1997 > 2000 (2–15)
1998	–	1999 > 1998 (2–10)	1998 > 2000 (11–15)
1999	–	–	1999 > 2000 (2–15)

Table 4. *Scomber scombrus*. Between-year comparison of average sagittal increment width at age for 1 yr old juveniles from the 1997 to 2000 cohorts. Age (d) beyond which differences in growth were significant (F -tests, $p < 0.05$) given in parentheses. Differences were non significant after 26 d in the 1998 vs. 2000 comparison. ns: non-significant

	Year class		
	1998	1999	2000
1997	1997 > 1998 (6)	ns	1997 > 2000 (5)
1998	–	1999 > 1998 (6)	1998 > 2000 (6–26)
1999	–	–	1999 > 2000 (5)

Selection for fast growth in early larval life: contrasting the early and late larval stages

When comparing the growth of the oldest larvae (≥ 16 d survivors) to that of a reference population (≤ 11 d), significant selection (repeated-measures MANOVA: $p < 0.0001$; F -test: $p < 0.05$) for fast-growing individuals was observed starting from the age of 7 d in 1997 (Fig. 6). Although otolith increment width was systematically larger in survivors, no statistically significant differences in growth between the population and the survivors were detected during the first 9 d of life for the weak year classes of 1998 and 2000 (Fig. 6). In 1999, the survivors and the reference population grew equally fast and no significant selection for fast growth was detected.

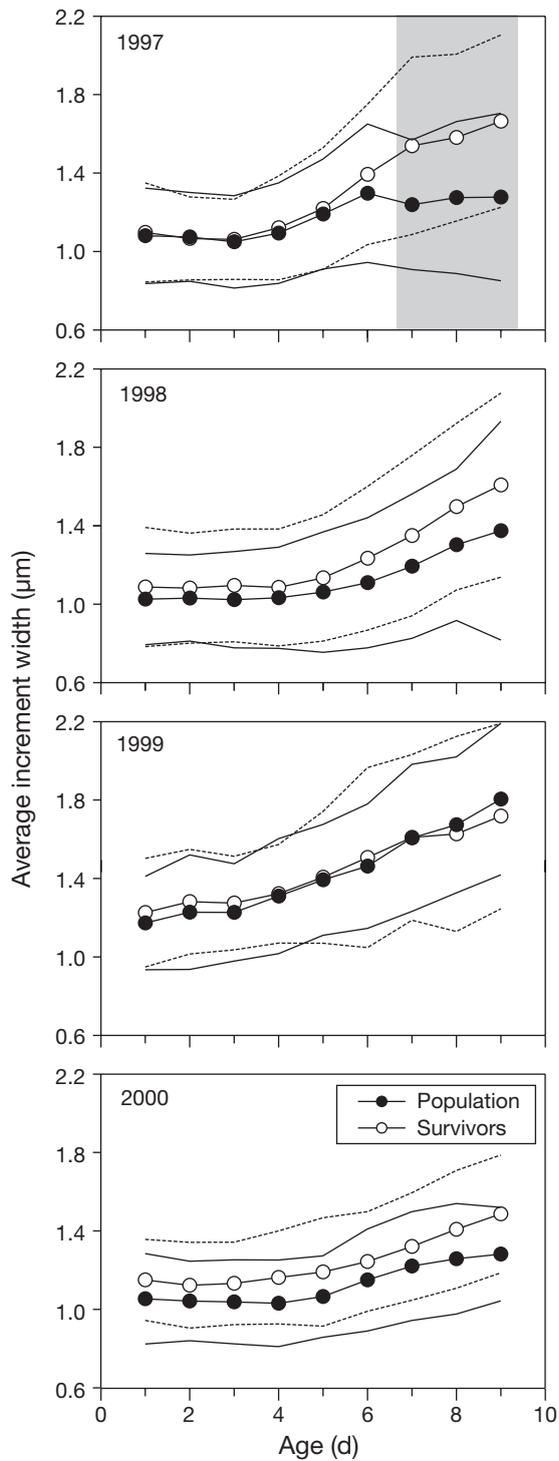


Fig. 6. *Scomber scombrus*. Comparison of average increment width at age between reference population (larvae ≤ 11 d old at capture) and survivors (larvae ≥ 16 d at capture) for 1997 to 2000. Shaded area represents age intervals for which mean increment width of survivors differed significantly from that of the larval population. Number of survivors was 32, 179, 28, and 78 in years 1997 to 2000, respectively. Standard deviation envelope represented by full lines for reference population and dotted lines for survivors

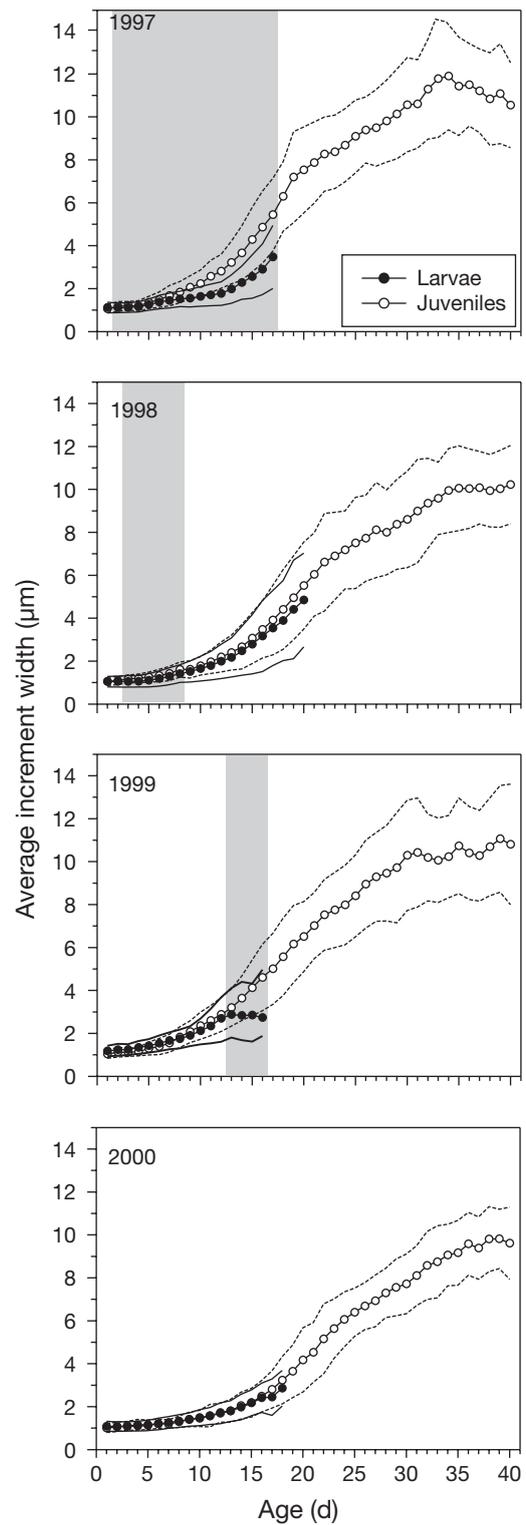


Fig. 7. *Scomber scombrus*. Comparison of average increment width at age between larval population (all larvae) and 1 yr old juveniles for 1997 to 2000. Shaded areas represent age intervals for which mean increment width of juveniles differed significantly from that of larvae. Standard deviation envelope represented by full lines for larval population and dotted lines for juveniles

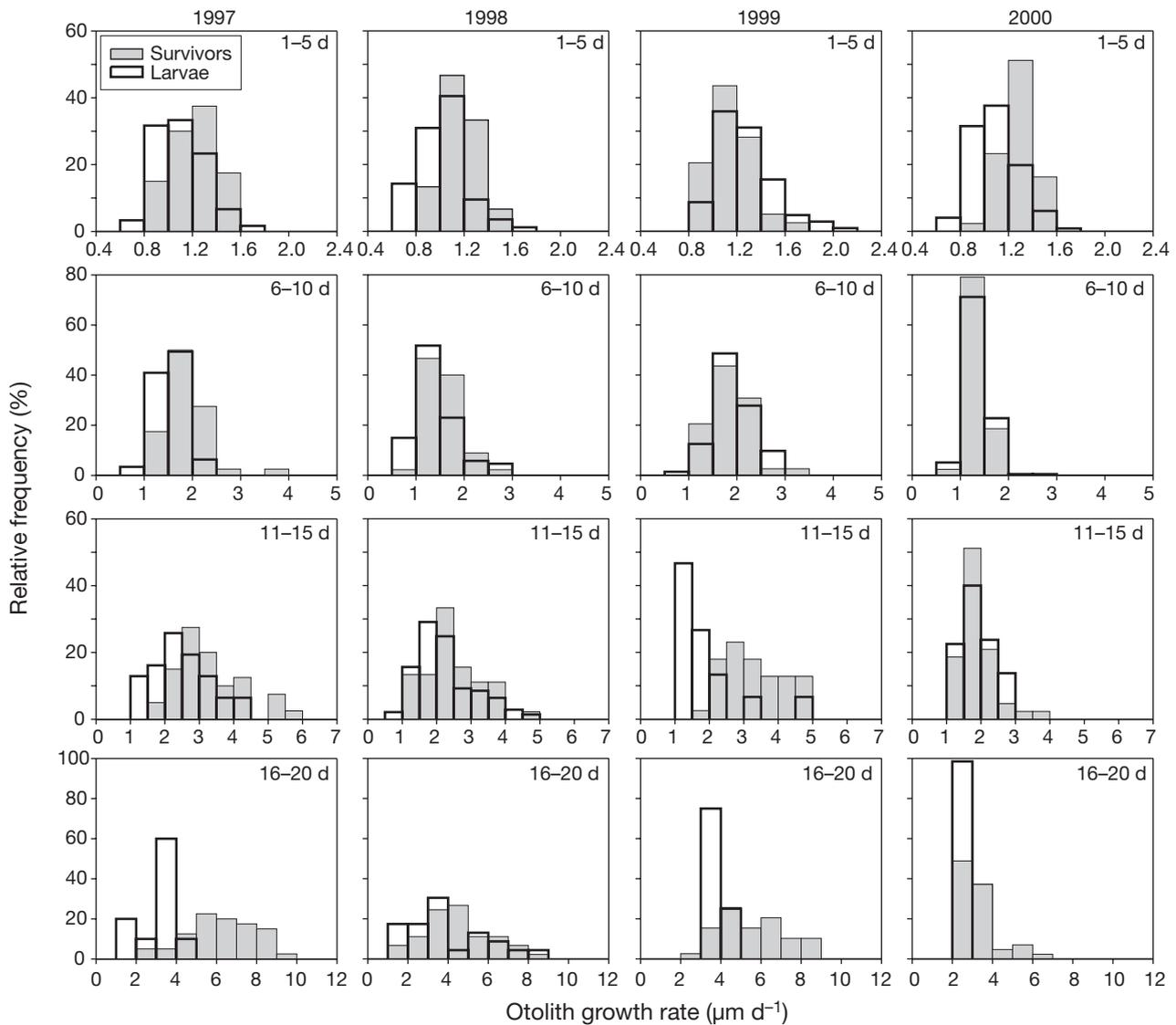


Fig. 8. *Scomber scombrus*. Frequency distributions of otolith growth rate for larvae (open bars) and juveniles (filled bars) for different 5 d age classes (1–5, 6–10, 11–15 and 16–20 d) for 1997 to 2000

Selection for fast growth in early larval life: contrasting larvae and juveniles

When comparing the growth achieved during the larval stage by 1 yr old juveniles to the growth of the larval population (all larvae), significant selection for fast-growing individuals (repeated-measures MANOVA: $p < 0.001$) was detected in 1997, 1998 and 1999 (Fig. 7). In 1997, strong selection for fast growth (i.e. large divergence between the growth trajectories of larvae and surviving juveniles) started immediately after hatching (age 2 d) and was maintained until at least 17 d of age—the age until which larvae were in sufficient statistical abundance in that year—with the divergence between survivors and the population

increasing monotonically. Mild but significant selection for fast growth occurred in the week after hatching (age 3 to 8 d) in 1998. No significant selection for fast growth was detected until the age of 13 d in 1999. There was no indication of selection in 2000, as the early growth of juveniles—the lowest of the 4 yr—did not differ from that of the larval population.

Growth-selective survival can also be examined by comparing the growth rate frequency distribution of survivors to that of the larval population at different age intervals (Fig. 8). In all years, a general tendency for a shift in the growth rate of survivors towards higher values than those of the larval population can be observed in the 16 to 20 d age interval, corresponding to the late larval stage. In 1997 and 1998, this ten-

dency was observed in all age intervals from the beginning of the larval stage, indicating growth-selective pressure early in life. In contrast, selection for fast-growing individuals during larval life was mild and started late in 1999 (11 to 15 d age interval) and was undetected in 2000.

DISCUSSION

Sampling methods and the measure of selection for fast growth

A central assumption when estimating growth selection by comparing larvae and survivors is that the older fish actually originated from the larval population (Meekan & Fortier 1996, Hare & Cowen 1997). The stacking of otolith growth increments from the age of about 40 d onward in 1 yr old juvenile mackerel prevented the determination of a precise hatch date. Therefore, we could not verify that the larvae and juveniles born in a given year were hatched over the same period. However, the Atlantic mackerel of the southern Gulf of St. Lawrence completes spawning within a relatively brief time interval of ca. 4 wk (Grégoire 2000, D. Robert unpubl.), ensuring that larvae and juveniles hatched in a given year belonged to the same cohort and thus experienced comparable environmental conditions during early growth.

Atlantic mackerel spawn in different regions of the southern Gulf. In the present study, we assumed that the growth of larvae sampled in the vicinity of the Magdalen Shallows in a given year was representative of larval growth throughout the spawning grounds of the southern Gulf where the juveniles may have hatched. The validity of this assumption is supported first by the general similarity in the pattern of interannual variability in the early growth (0 to 15 d) of larvae (1999 > 1997 > 1998 ~ 2000) and juveniles (1999 ~ 1997 > 1998 > 2000). A second result supporting this assumption is the remarkable similarity in the selection for fast growth measured over the first weeks of life — by comparing early and late larval stages — and over the first year of life — by comparing larvae and 1 yr old juveniles. In both cases, strong selection for fast growth occurred early in 1997, while none was detected in 1999 or 2000 (Figs. 6 & 7). In 1998, selection for fast growth was statistically non significant between young larvae (≤ 11 d old) and survivors (≥ 16 d old) and barely detected when comparing larvae and juveniles. Based on these similarities in early growth dynamics between larvae sampled on the Magdalen Shallows and juveniles collected throughout the Gulf of St. Lawrence, we conclude that fish hatched in a given year belonged to the same population.

As reported in other studies (Meekan & Fortier 1996, Hare & Cowen 1997, Tanaka et al. 2006), some juveniles in 1997 displayed larval growth rates that were higher than any measured in the larval population of reference (Fig. 8). Hare & Cowen (1997) explain this paradox by the fact that, when intense selection for fast growth occurs, a very large number of larvae would have to be analysed to detect the fast-growing survivors in the reference population. The exceptional early growth of juveniles relative to larvae in 1997 nevertheless raises the possibility that the fishing gear (mostly hand lines) selected the largest, fastest-growing 1 yr old juveniles. However, as pointed out by Meekan & Fortier (1996), if the sampling gear was selective, selection for fast-growing individuals would be observed systematically in every year. As no selection was detected in 1999 and 2000, the strong selection measured in 1997 cannot be linked to gear selectivity.

Early selection for fast growth and year-class strength

Several field studies have confirmed the expected positive link between growth and survivorship in marine fish larvae (Meekan & Fortier 1996, Hare & Cowen 1997, Sirois & Dodson 2000, Takasuka et al. 2003), including scombrid larvae (Shoji & Tanaka 2006, Tanaka et al. 2006). However, the relationship between early growth and year-class strength has remained equivocal as investigations reported contradictory results (van der Veer et al. 1994, Bailey et al. 1996, Campana 1996, Ringuette et al. 2002). In this study, fast larval growth in surviving juveniles was associated with both strong (1999) and weak (1997) recruitment. This apparent inconsistency is resolved when interannual differences in selection for fast growth during the larval stage are taken into account. The larvae of the 1999 record year class grew fast in the absence of growth-selective mortality. Fast growth in that year reflected favourable conditions for growth and relaxed selective mortality (e.g. by predation or cannibalism), a combination that led to the survival of the average individual and outstanding recruitment. In contrast, the fast larval growth recorded in surviving larvae and juveniles in 1997 reflected a strong growth-selective mortality that culled the average individual and resulted in the lowest recruitment among the 4 yr studied. The 1998 cohort achieved relatively poor growth and experienced some growth-selective pressure early after hatch, a combination that resulted in weak recruitment. The 2000 cohort was spared any detectable selection for fast growth but achieved the lowest growth in all 4 yr, which resulted in weak recruitment.

Consistent with the conclusions of Meekan & Fortier (1996), our results emphasize how the link between recruitment and early growth or size-at-age of juveniles can be obscured by the selection of fast growing individuals. Previous studies linking early growth and recruitment generally overlooked this potential confounding effect of selection for fast growth (e.g. Campana 1996, Ottersen & Loeng 2000, Ringuette et al. 2002, Jenkins & King 2006). Nevertheless, a strong positive correlation was reported between early growth and indices of recruitment in Atlantic cod *Gadus morhua* ($r^2 = 0.80$, Campana 1996) and King George whiting *Sillaginodes punctata* ($r^2 = 0.95$, Jenkins & King 2006), suggesting that selection for fast growth played a minor role in blurring the relationship. This can be attributed to a null or constant growth-selective pressure over the few years sampled in these studies (5 & 6 yr respectively), which would not generate variability in recruitment (Rice et al. 1997). In contrast, Ottersen & Loeng (2000) reported weaker correlations ($r^2 = 0.54$ to 0.65) over longer time series (9 to 15 yr) between juvenile growth rates (based on length increments between 2 surveys) and recruitment in haddock *Melanogrammus aeglefinus*, Atlantic cod, and herring *Clupea harengus* in the Barents Sea. These authors stressed the importance of finding a closer connection between 0-group length and recruitment to enhance predictive power. We argue here that taking into account both early growth and selection for fast growth could increase substantially the predictive power of statistical models of recruitment variability.

The ontogenetic timing of selection for fast growth

Fast growth during the larval stage may be selected for later in life (Sogard 1997). At high latitudes for example, the first winter of life has been described as a major bottleneck where only those fish that achieved a minimum size as larvae and early juveniles in summer and fall survive (Conover & Present 1990, Conover & Schultz 1997, Fortier et al. 2006). Also, for migratory species, achieving fast growth during larval life may be a pre-requisite to survive the first migration as a juvenile. For example, the northernmost population of Atlantic silverside *Menidia menidia* suffers size-selective mortality directed against small individuals during its first winter migration offshore (Munch et al. 2003). In the present study, significant selection for fast growth was detected from age 7 d onward in 1997 when comparing early and late larval stages. However, the comparison of the larval population to 1 yr old juveniles indicated that significant selection for fast growth actually occurred over the entire larval stage moni-

tored in 1997 (age 2 to 17 d) and likely continued beyond (Fig. 7). Similarly, the larvae-juvenile comparison revealed periods of mild selection for fast growth early (1998) or late (1999) in larval life, which remained undetected when contrasting the early and late larval stages. These results suggest that selection for fast growth continues during juvenile life and that it is auto-correlated, with fish that were fast growers as larvae being further selected for during the first year of life. This additional selection for fish that grew fast during larval life likely occurs during the 400 km migration of juvenile mackerel leaving the southern Gulf of St. Lawrence to over-winter on the Scotian Shelf (Kulka 1977). As for other species at the northern limit of their range and high-latitude resident species (Conover & Present 1990, Conover & Schultz 1997, Munch et al. 2003, Fortier et al. 2006), surviving the energetically demanding fall migration and the first over-wintering may depend on fast early growth for the Atlantic mackerel population of the Gulf of St. Lawrence.

Within the framework of current hypotheses linking early growth and recruitment in fish (Anderson 1988, Cushing 1990, Leggett & Deblois 1994, Houde 2002), the selection of fast-growing larvae is interpreted as a symptom of intense predation that culls slow-growing larvae from the population (Beyer & Laurence 1980, Meekan & Fortier 1996, Takasuka et al. 2003). Our results generally support the hypothesis that the earlier the decimation of slow-growers by predation starts during ontogeny, the stronger its impact on the final abundance of survivors. Strong (1997) or mild (1998) selection for fast growth starting early in life (Day 2 in 1997 and Day 3 in 1998) both resulted in low recruitment despite relatively good growth at the population level at least in 1997. Mild selection starting late (Day 13) in 1999 suggests that the explosive recruitment in that year resulted from the shielding of the small larvae from predation or cannibalism. In 2000, the interesting combination of slow growth and no selection for fast growth is opened to interpretation. Either growth conditions were so poor that no fish grew fast enough to be selected for and emerge as survivors in the late larval stage or as juveniles. In this case, the recruitment of a few slow-growing juveniles to the stock could be attributed to the avoidance of predation by sheer statistical luck. Alternatively, adverse growth conditions may have coincided with a total absence of predation, with starvation decimating the larvae rather than predators. The early growth trajectory of juveniles observed in 2000 would then represent the physiological barrier of Beyer & Laurence (1980) for Atlantic mackerel. For both interpretations, the low recruitment observed in 2000 was expected.

CONCLUSIONS

The interaction between early growth and selection for fast growth appears to be an important regulator of Atlantic mackerel recruitment. Based on our results, the monitoring of both early growth and the ontogenetic timing and intensity of selection for fast growth over longer time series (e.g. decades) would help clarify how year classes form in the stock of Atlantic mackerel of the southern Gulf of St. Lawrence. This approach could lead to improved prediction of year-class strength in this and other species.

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