Bigger is better: size-selective mortality throughout the life history of a fast-growing clupeid, *Spratelloides gracilis*

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ABSTRACT: A cohort of the fast-growing sprat *Spratelloides gracilis* was sampled during late-larval, juvenile and adult life-history phases using light traps on the North West Shelf of Western Australia. Otoliths from 154 larvae, juveniles and adults that hatched during a 20 d window were analysed to produce back-calculated daily records of size-at-age and growth rate. These traits were compared among sequential samples using repeated-measures MANOVAs (multivariate analyses of variance) to determine whether selective mortality occurred in the cohort. Late-stage larvae in our catches averaged 23 ± 3 d of age and were 22 ± 2 mm standard length (SL), while juveniles averaged 47 ± 6 d of age and 36 ± 6 mm SL. We found that individuals that survived the larval stage to become juveniles underwent strong selective mortality. This selective mortality acted to preferentially remove fish that were slow-growing and/or relatively small members of the cohort. The size variation on which this selection acted was present at hatching and propagated by growth during the larval stage. Size at hatching is principally determined by egg size, implying that maternal contributions had an important influence on the outcome of selective events. We found no evidence of selective mortality operating during the transition of juvenile sprats to adulthood. Adults averaged 78 ± 6 d of age and 44 ± 5 mm SL. Log-linear analyses indicated that the cohort underwent 8.6 % mortality mm^{-1} SL and had a daily mortality rate of 3.7 % between larval and adult stages. Given an average linear growth rate of 0.96 mm d^{-1} during the larval phase, this suggests that selective mortality based on size (bigger-is-better) was approximately twice as important as mortality due to age differences (stage duration) among members of the cohort.

KEY WORDS: Larval fish · Otoliths · Size selection · Growth rate · Selective mortality · Predation · Bigger-is-better · Stage duration

INTRODUCTION

Marine fishes undergo very high rates of mortality during early life-history stages (Bailey & Houde 1989). This mortality does not happen in a random or haphazard fashion; rather, it is often selective, preferentially removing the slower growing and smaller individuals within cohorts. Selective mortality is thought to occur because fast-growing fish require less time to transit stages that are the most vulnerable to predators (the stage-duration hypothesis; Houde 1987, Cushing 1990).

Fast-growing fish also tend to be the larger members of a cohort. This size advantage reduces their vulnerability to predators relative to smaller individuals of the same age (the bigger-is-better hypothesis; Miller et al. 1988). Collectively, these theories are known as the growth–predation hypothesis (Anderson 1988).

The relative importance of the stage-duration and bigger-is-better hypotheses to the process of selective mortality has been a subject of considerable debate. As growth rate and size-at-age are invariably correlated, it has meant that disentangling the effects of these traits

in field studies has been extremely difficult (Hare & Cowen 1997). For this reason, laboratory experiments have been used to investigate the relative importance of size and age (Leggett & DeBlois 1994). However, the laboratory approach suffers from complications of the artificial constraint of animals within tanks and the focus by researchers on only a portion of the 'predation sequence' (Fuiman 1989), typically predator capture success (Fuiman & Magurran 1994). For logistical reasons, experimental studies generally only examine the interaction between a single species and size class of predator and its prey (Litvak & Leggett 1992, Pepin et al. 1992, Taylor 2003), whereas, in the field, larval fish inhabit an environment that contains numerous species of predators of a great range of sizes. The likelihood of predation for individual members of a cohort will reflect the cumulative effects of all size classes and species of predators within the pelagic environment (Bailey & Houde 1989, Paradis et al. 1996).

As the number of predators to which fish are susceptible declines with increasing size (Bailey & Houde 1989), the growth–predation hypothesis predicts that the importance of selective mortality should decline as individuals grow through larval and juvenile phases to become adults. This idea is difficult to test, as it requires representative collections of the same cohort of fish at successive life-history stages, each of which may take months or even years to complete. Furthermore, larvae, juveniles and adults can occupy very different habitats, each entailing specialised gear to attain representative samples. Consequently, no study has been able to examine the relative importance of selective mortality throughout the entire life cycle of a marine fish.

Although much of the evidence on the importance of the growth–predation hypothesis has been derived from temperate environments, an increasing number of studies demonstrate that these processes also operate in tropical systems (Searcy & Sponaugle 2001, Bergenius et al. 2002, Vigliola & Meekan 2002, Wilson & Meekan 2002, Meekan et al. 2003, Hoey & McCormick 2004). The apparent ubiquity of size-selective mortality in fish populations allows predictions of the hypothesis to be tested on tropical fish that are relatively fast growing compared to temperate equivalents. In some of these tropical species, life cycles are completed in only a few months, rather than the years or even decades that are required in temperate environments.

The sprat *Spratelloides gracilis* is a good example of a fast-growing tropical fish. It is an ideal candidate for tests of the predictions of the growth–predation hypothesis, as representative samples of the same cohort can be captured at different stages of a life history that only lasts a maximum of 4 mo (Milton et al.

1991). Here, we use otolith analysis to back-calculate age, size and growth rates of individuals from a cohort of *S. gracilis* captured as late larvae, juveniles and adults in the nearshore waters of the NW Cape in tropical Western Australia. Growth and size were compared between surviving fish and the entire cohort from which they originated using repeated-measures MANOVAs (multivariate analyses of variance), in order to determine the relative importance of size-selective mortality throughout the life history of this species. We estimated mortality rates of the cohort based on both size and age, and used these to calculate the relative importance of stage-duration and bigger-is-better processes to the selective survivorship of this species.

MATERIALS AND METHODS

Study species. *Spratelloides gracilis* is broadly distributed across the Indo-Pacific region and is an important trophic link in coral reef ecosystems (Milton et al. 1991). *S. gracilis* grows extremely fast, completing its life history in a few months. Maturity is attained at 50 to 60% of maximum size, and the oldest individual of this species ever recorded attained an age of only 4 mo (Milton et al. 1991). *S. gracilis* is pelagic throughout its life history, but is reef associated, residing in nearshore waters around coral reefs, where it is a very abundant component of light trap (Doherty 1987) catches throughout its life history (Meekan et al. 2001). Mesocosm experiments have shown that these different stages are collected with equal efficiency by light traps (Meekan et al. 2000).

Light-trap collections. Sampling was conducted on 5 cruises, each of 10 d duration, centred on successive new moons in the austral summer months (October to February) of 1997/1998. Light traps were deployed at Stations A to H along a cross-shelf transect on the NW Shelf of Western Australia and moored at stations near South Muiron Island (Meekan et al. 2003, in press; see Fig. 1 in Meekan et al. 2006). The light-trap program has been described in detail by Wilson et al. (2003a,b) and Meekan et al. (2003, 2006).

Otolith analysis. Up to 50 *Spratelloides gracilis* were haphazardly selected and measured for standard length (SL) from each light-trap sample. The frequency distributions of SL were then adjusted for the total number of fish collected in each trap and compiled by cruise. A strong cohort of sprats was evident in the size–frequency distributions as late-stage larvae in December, juveniles in January and adults in February. To include both fast-growing and slow-growing members of the cohort in the analysis, a broad range of sizes was defined as the cohort and up to 100 fish were
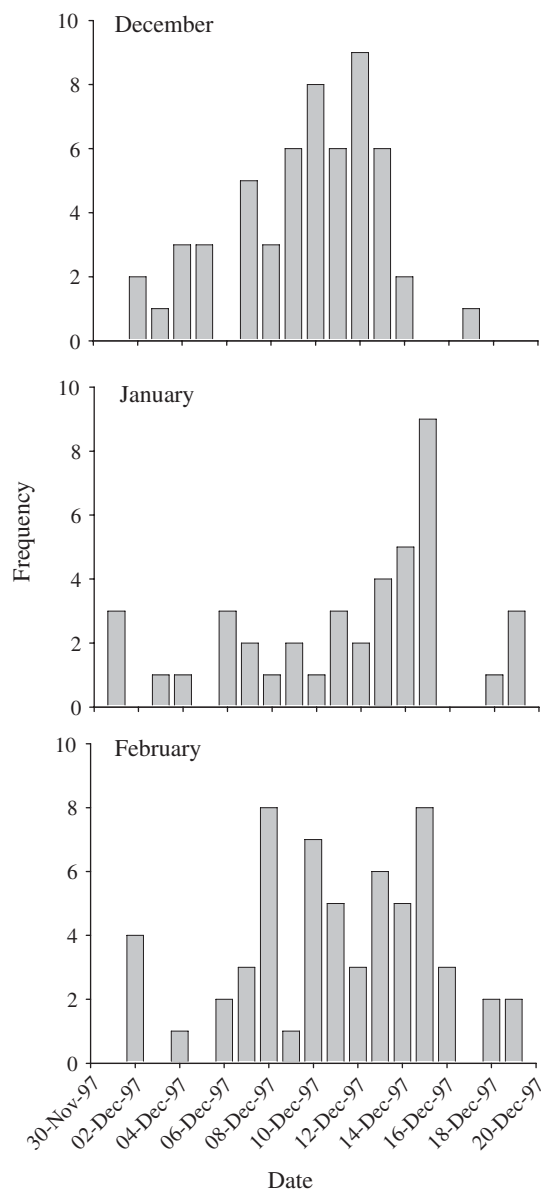
Fig. 1. *Spratelloides gracilis*. Frequency distributions of hatch date of sprat collected by light traps during cruises at NW Cape, Western Australia, in December 1997 and January and February 1998

The glue was then heated, and the otolith was re-orientated so that it sat upright on the cut edge in the centre of the slide. The upright portion of the otolith was then ground on lapping film to produce a thin transverse section that contained the nucleus. Sections were viewed under immersion oil with a compound microscope using transmitted light at 1000× magnification. An image analysis system (OPTIMAS) was used to measure the width of each increment from the nucleus along the longest axis of the otolith. Daily deposition of increments has been validated for *S. gracilis* by Milton et al. (1991), and we assumed that the first increment closest to the nucleus of the otolith was formed at the time of hatching (Campana & Neilson 1985, Wellington & Victor 1989).

As the dates of sample collections were known, ages derived from this analysis could be used to calculate the hatch dates of all individuals. This information was then used to restrict the analysis of size and growth rates to only those individuals that hatched within a 20 d window. This was done to ensure that our analyses compared individuals from the cohort that had developed in similar environmental conditions and resulted in a reduction of our sample size to a total of 154 fish (Fig. 1).

Data analysis. Otolith radii and increment widths provided daily growth records of *Spratelloides gracilis* from hatching to adulthood. Back-calculation of size from otoliths assumes that there is proportionality between otolith and somatic growth. The assumption was verified by calculating a regression relationship between otolith radius and standard length. This analysis was highly significant, and there was a linear relationship between these variables ($r^2 = 0.87$, $p < 0.001$, $n = 250$). As the correlation between otolith and body size of *S. gracilis* was strong, we were able to back-calculate the size-at-age of each fish for every day between hatching and capture using the biological intercept technique (Campana 1990). As newly hatched larvae were not collected during our study, we used the size-at-hatching of 4.4 mm SL reported by Leis & Carson-Ewart (2000) for *S. gracilis* in the back-calculation formula. Repeated-measures MANOVAs were used to compare the estimates of size and the growth trajectory of the cohort back-calculated from the otoliths of fish from each of the different cruises (Chambers & Miller 1995).

Repeated-measures MANOVAs were used to compare the size-at-age and growth rates of representative samples of the cohort collected as late-stage larvae in December, juveniles in January and adults in February. As the youngest individual collected in December was 18 d of age, we compared the growth and size at 6 d intervals from hatching until 18 d among the 3 samples of the cohort.

sampled in proportion to their abundance in 1 mm SL size classes within the size range for each cruise. These size ranges included fish from 16 to 31, 25 to 51 and 31 to 60 mm SL collected in December, January and February, respectively.

This subsampling provided a total of approximately 250 *Spratelloides gracilis* for otolith analysis. Sagittae were dissected from each fish and cleaned of adhering tissue. One of the pair of sagittae was mounted over the edge of a glass slide using thermoplastic glue, and the protruding portion was ground off on lapping film.

Mortality rates. As the differing life-history stages of *Spratelloides gracilis* are collected with equal efficiency by light traps (Meekan et al. 2000), size-based mortality rates were calculated by applying a smoothing function (3 d running mean) to size–frequency distributions. Peaks in the abundance of the cohort from each of the monthly samples were then used in log-linear regression analysis to calculate a mortality rate per millimetre standard length. As a large sample of individuals was aged in the otolith analysis, these ages were used in an age–length key (Stevenson & Campana 1992) to predict the ages of the remaining fish within the cohort. In the key, age categories were pooled into 5 d intervals, in order to increase sample sizes. The use of the key allowed standard lengths to be transformed to ages and the size–frequency distributions to be replotted as age–frequency distributions for each monthly sample of the cohort. As above, smoothing and log-linear regression analysis were then used to calculate a daily mortality rate for the cohort.

RESULTS

Size–frequency distributions

A total of 12 057 *Spratelloides gracilis* were collected during the December, January and February cruises. Nearly all of these fish (95%) were collected by traps either deployed near the reef at South Muiron Island or in deep water at only 2 stations (C and D) at the mouth of Exmouth Gulf (see Fig. 1 in Meekan et al. 2006). The progression of a cohort could be followed through the size–frequency distributions as late-stage larvae in December (mean size 22 ± 1.7 mm SL), juveniles in January (mean size 36 ± 6 mm SL) and adults in February (mean size 44 ± 5 mm SL, Fig. 2). Catches of the cohort declined exponentially, so that 1000s of late-stage larvae were collected by light traps in December, 100s of juveniles in January, but only 10s of adults in February.

Growth rate and size-at-age

A Von Bertalanffy growth function described age and size of the cohort hatched within a 20 d window ($r^2 = 0.871$; Fig. 3). These gave an average adult size (L_{inf}) of 53.937 mm SL and a K of 0.0226. At first capture in December, fish within the cohort averaged 23 ± 3 d of age and grew at 0.96 mm d^{-1} from 0 to 23 d after hatching. In January, fish averaged 47 ± 6 d of age and grew at 0.76 mm d^{-1} from 23 to 47 d after hatching, while in February, the average age of fish in the cohort
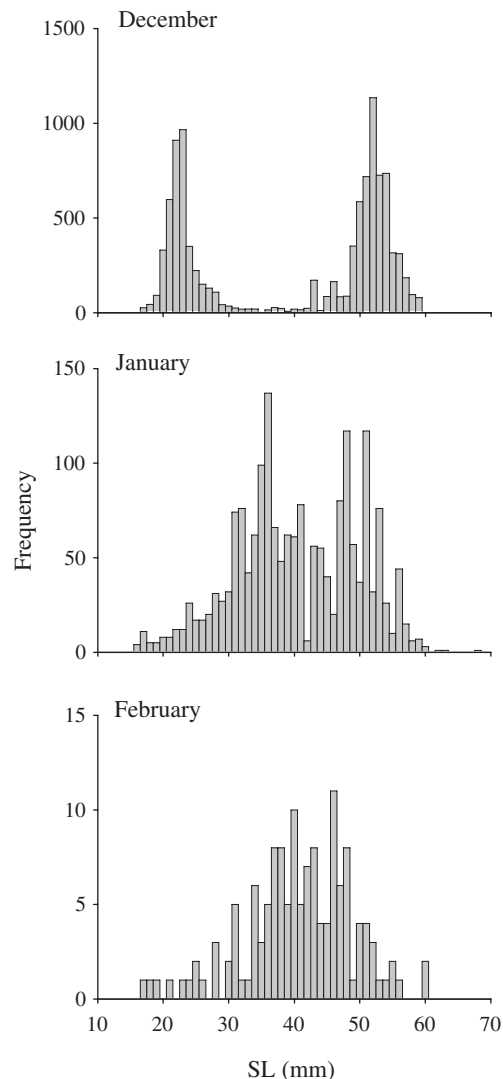

Fig. 2. *Spratelloides gracilis*. Size–frequency distributions of sprat collected by light traps during cruises at NW Cape, Western Australia, in December 1997 and January and February 1998

was 78 ± 6 d and these individuals grew at 0.57 mm d^{-1} from 47 to 78 d after hatching.

Size selection

Repeated-measures MANOVA demonstrated that the cohort underwent strong selective mortality between the larval and juvenile phases. Those fish that survived to become juveniles and adults were larger than the overall larval population from which they were sourced, both at hatching and throughout the first 18 d of larval life (Fig. 4, repeated-measures MANOVA, factor Cruise [December, January, Febru-
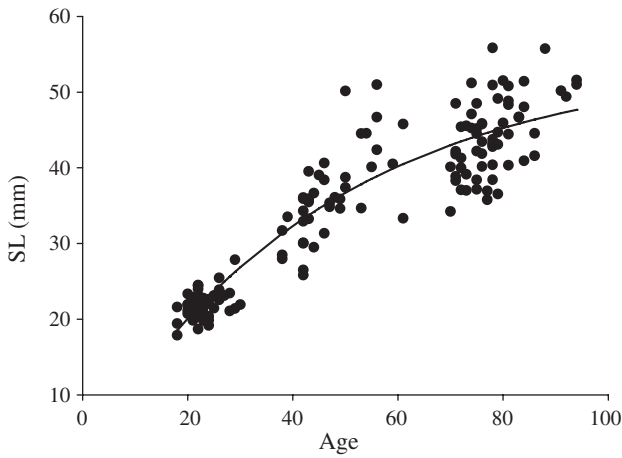
Fig. 3. *Spratelloides gracilis.* Von Bertalanffy growth function (solid line) fitted to data sets of age (d) and size (mm SL) of sprat collected by light traps during cruises at NW Cape, Western Australia, in December 1997 and January and February 1998. Parameters for the growth function: $L_{inf} = 53.94$, $K = 0.0226$, $t_0 = -0.4337$, $r^2 = 0.871$

ary] × Time [0 to 18 d] significant, Wilk's Lambda = 0.79, $F_{6,298} = 6.1$, p < 0.0001). These juvenile and adult fish also grew faster than the overall larval population in the periods from hatching to 6 d of age and from 6 to 12 d after hatching (Fig. 5, repeated-measures MANOVAs, factor Cruise [December, January, February] × Time [0 to 18 d] significant, Wilk's Lambda = 0.88, $F_{4,300} = 4.7$, p < 0.001). There was also a similar

(but non-significant) trend for faster growth rates of juvenile and adult fish than larvae in the period from 12 to 18 d after hatching. Fish that survived to become juveniles and adults did not differ in size-at-age or growth rates from hatching to 18 d larval life (Figs. 4 & 5).

Growth rates and size of fish were correlated in the first few days after hatching (Table 1). Fish that were bigger at hatching grew significantly faster from 0 to 6 d after hatching, although there were no significant correlations between size-at-hatching and growth rates from 6 to 12 and 12 to 18 d after hatching. Similarly, fish that were large at 6 d grew faster from 6 to 12 d, but size at 6 d after hatching was not correlated with growth rate from 12 to 18 d after hatching. Fish that were large at 12 d after hatching did not grow significantly faster from 12 to 18 d of age.

Repeated-measures MANOVA compared the size-at-age and growth rates of juvenile and adult fish collected in January and February at 6 d intervals from hatching to 36 d of age. This upper limit corresponded to the age of the youngest juvenile fish collected in light traps during January. No significant differences were detected in size or growth rates of adult and juvenile fish during this period (repeated-measures MANOVAs, factor Cruise [January, February] × Time [0 to 36 d] non-significant, Wilk's Lambda = 0.93, $F_{6,95} = 1.1$, p = 0.35 for analysis of size, Wilk's Lambda = 0.94, $F_{5,96} = 1.3$, p = 0.26 for analysis of growth rate), implying that mortality was not size selective during the transition from juvenile to adult phases.
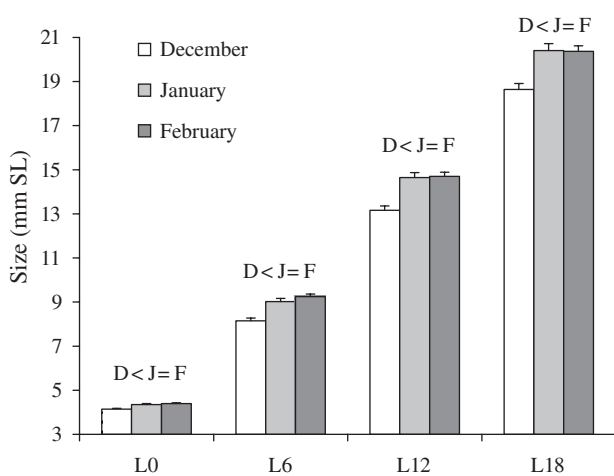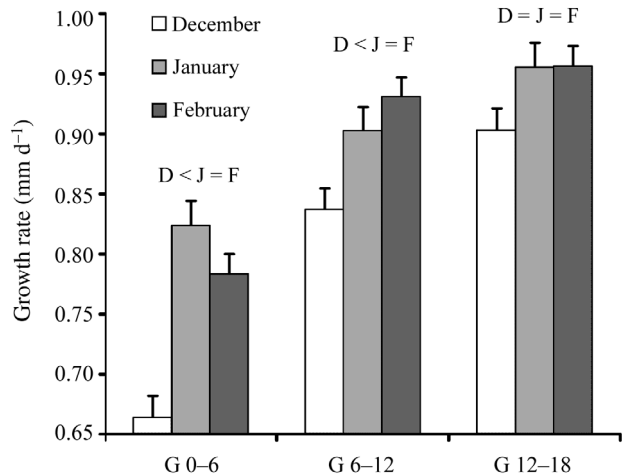

Fig. 4. *Spratelloides gracilis.* Mean size (SL, ±SD) of sprat at hatching (L0), 6 (L6), 12 (L12) and 18 d (L18) after hatching. Fish were collected by light traps as late-stage larvae in December 1997, juveniles in January 1998 and adults in February 1998. Letters above bars (D: December; J: January; F: February) show results of contrast analyses from repeated-measures MANOVA at α = 0.05

Fig. 5. *Spratelloides gracilis.* Mean growth rates (mm d^{-1}, ±SD) of sprat from hatching to 6 (G0–6), 6 to 12 (G6–12) and 12 to 18 d (G12–18) after hatching. Fish were collected by light traps as late-stage larvae in December 1997, juveniles in January 1998 and adults in February 1998. Letters above bars (D: December; J: January; F: February) show results of contrast analyses from repeated-measures MANOVA at α = 0.05

Table 1. *Spratelloides gracilis*. Summary of Spearman correlation analyses of size (SL) versus growth rate (mm d^{-1}), back-calculated from the otoliths of sprat collected as late larvae, juveniles and adults by light traps on the NW Cape, Western Australia. The analyses compared size at hatching (0), 6, 12 and 18 d and growth from 0 to 6, 6 to 12 and 12 to 18 d in the 3 samples of the cohort; N = 154 for all analyses. Bold values are significant at p < 0.05. *t* = *t*-test statistic

	Spearman	*t*	p
Size 0 vs. Growth 0–6 d	0.199	2.503	**0.013**
Size 0 vs. Growth 6–12 d	0.092	1.143	0.255
Size 0 vs. Growth 12–18 d	0.036	0.445	0.657
Size 6 vs. Growth 6–12 d	0.278	3.575	**0.0004**
Size 6 vs. Growth 12–18 d	0.088	1.089	0.278
Size 12 vs. Growth 12–18 d	0.104	1.284	0.201

Mortality rates

Log-linear regression analyses showed that *Spratelloides gracilis* underwent 8.6% mortality mm^{-1} SL (Fig. 6). In contrast, the daily mortality rate (3.7%) was little over half that of the mortality rate based on size (Fig. 6).

DISCUSSION

The fast growth of *Spratelloides gracilis* allowed us to examine the importance of size and growth-selective mortality throughout the life history of this species. We found evidence of strong selective mortality during the transition of fish from late-stage larvae to the juvenile phase of their life history. In temperate environments, selective mortality is known to occur during the larval and juvenile life-history stages of some clupeids, although no study has examined the fate of individuals beyond the juvenile phase. Selective mortality has been documented in the larvae of Japanese anchovy *Engraulis japonicus* (Takasuka et al. 2003, 2004a,b) and between the larval and juvenile stages in the European anchovy *Engraulis encrasicolus* (Allain et al. 2003). Consistent with the predictions of the growth–predation hypothesis, the incidence of size-selective mortality in *S. gracilis* declined with age and we failed to detect any selective mortality on the transition of juveniles to adulthood.

Although selective mortality did not occur during the transition of sprats from juveniles to adults, we found that adults had an important influence on the outcome of selective mortality during early life history. Our analysis showed that differences in size-at-hatching among individuals in the cohort were propagated by growth during early larval life and provided the traits on which selection acted later in the life history. Size-
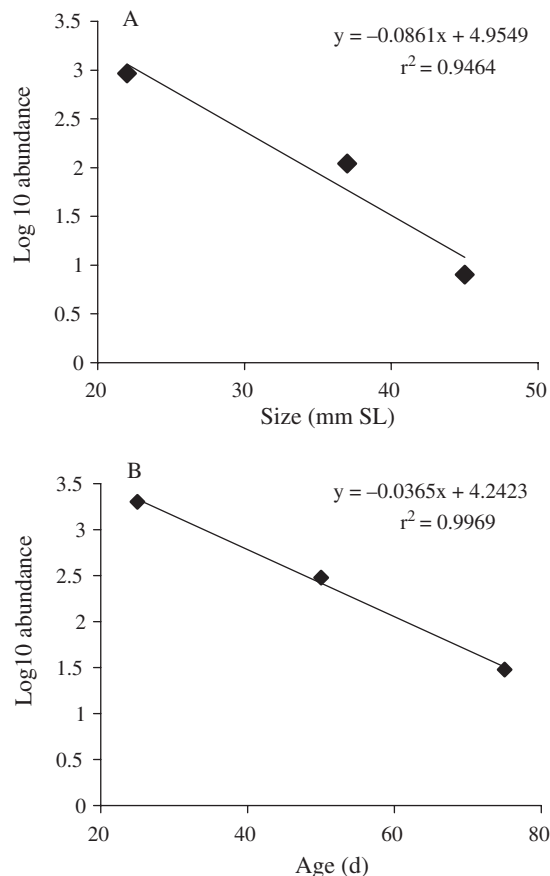

Fig. 6. *Spratelloides gracilis*. Log-linear regressions of (A) size and (B) age frequency from the 3 successive samples of the cohort of sprat collected by light traps during cruises at NW Cape, Western Australia (see 'Materials and methods' for analysis details). Equations for lines and r^2 values are shown

at-hatching is primarily influenced by egg size (Chambers 1997), which, in turn, is determined by maternal size, condition and identity (Chambers et al. 1989, McCormick 1999). Thus, adults were likely to have influenced the outcome of selective events through maternal contributions to larval size. Similar evidence for parental contributions to survivorship has been documented for a tropical reef fish by Vigliola & Meekan (2002), while, in clupeids, Riveiro et al. (2004) found that adult European sardines *Sardina pilchardus* were capable of enhancing the survival of hatching larvae by altering the biochemical composition of eggs during the spawning season. However, the latter study did not investigate whether variations in parental investment in eggs influenced mortality within cohorts.

Our analysis of mortality rates based on size and age suggest that size was the key variable on which selective mortality acted during the early life history of *Spratelloides gracilis*. Log-linear analysis of size–frequency distributions from December, January and

February cruises found that mortality removed 8.6% of the cohort per millimetre standard length. Conversion of the size–frequency data set to age using a length–age key allowed estimation of the mortality rate based on age. Log-linear analysis of the age–frequency distributions showed that the cohort underwent mortality of 3.7% d^{-1}. Between the larval and juvenile phases, when size selection occurred, the growth rate of the cohort was roughly linear and averaged approximately 0.9 mm d^{-1}. While estimates of mortality rates are based on only 3 samples of the cohort, and for this reason should be treated with caution, our study suggests that differences in size that accrued on a daily basis would have had approximately twice the influence on mortality rates as those of age. Near the end of the larval stage (approximately 18 d after hatching), fish that survived to become juveniles and adults were on average 1.75 mm larger than the mean size of the larval population (Fig. 4). For these individuals, this size advantage was equivalent to slightly <2 d growth.

Other studies have discounted the possibility of the bigger-is-better hypothesis as a basis for selective mortality of clupeid larvae. Allain et al. (2003) examined selective mortality in larval anchovy *Engraulis encrasicolus* and attributed their results to stage duration and 'growth rate' processes. Their exclusion of size-based selection was largely due to a lack of evidence for this phenomenon in laboratory studies. As mentioned previously, these are equivocal in support for the bigger-is-better hypothesis (Leggett & DeBlois 1994), as such studies fail to replicate the complexity of natural predator assemblages and introduce artificial constraints that are likely to influence the behaviour of predators and their prey. In contrast, Takasuka et al. (2004a) found evidence for both the bigger-is-better and stage-duration hypotheses in a study of Japanese anchovy *Engraulis japonicus*. Cannibalism by juveniles focused on larvae that were smaller and slower growing, although predation by skipjack tunas *Katsuwonus pelamis* was non-selective in terms of larval size and growth.

The relative importance of the bigger-is-better and stage-duration processes will be strongly influenced by growth rate of the cohort. In species such as sprats, high daily growth rates will increase the importance of size-based selection relative to differences in age, while in slow-growing species small differences in size will take many days or even weeks to accumulate. For example, Meekan & Fortier (1996) found that in cod larvae *Gadus morhua* that grew at approximately 0.23 mm d^{-1}, individuals that survived to become juveniles of 20 mm SL were on average 12 to 13 d younger than the overall population from which they were sourced. Transition to juveniles occurred at around 80 d after hatching, when the average size difference

that accumulated between survivors and the remainder of the population of larval cod was 2.8 mm. Unlike cod larvae that become epibenthic at the end of larval life, young sprats do not undergo a transition between pelagic and benthic habitats at the start of the juvenile stage. If 36 mm SL (the mean size of the cohort in January) is chosen as an arbitrary size to define the start of the juvenile phase, then surviving fish would have attained this size only 4 d earlier, on average, than the rest of the larval population. Fish of this size averaged 42 d of age. At this time survivors were already almost 4 mm larger than the larval population, a size difference that was 1.5 times greater than that shown by larval cod at the start of the juvenile phase and achieved in only half the time.

High larval growth rates may also benefit the process of size-selective mortality, by rapidly increasing the range of size within a cohort so that there is more raw material on which selection can act. This size variation will also be present at younger ages for fast-growing species, so that the onset of selection can occur earlier. At present there is little field evidence to support these ideas; however, it is notable that size selection has been invoked to explain selective mortality in fast-growing temperate species such as the calamary squid *Sepioteuthis australis* (Steer et al. 2003).

The presence of size-selective mortality in cohorts of sprats suggests that studies seeking to compare growth rates among populations or between years should be treated with caution. Size- and/or growth-selective mortality may influence estimates of growth rates, confounding correlations between growth and environmental variables such as water temperature or food availability. Disentangling the relative influences of selective mortality and environmental factors on the recruitment success of sprats is the subject of future publications.

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