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Temperature, selective mortality and early growth in the short-lived clupeid *Spratelloides gracilis*

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Abstract:

Six cohorts of the silver-stripe round herring *Spratelloides gracilis*, a fast-growing and short-lived tropical clupeid, were collected as juveniles and then as adults during austral summers from November to February in 1998–1999 and 1999–2000, using light traps in the Dampier Archipelago, Western Australia. Otolith analysis allowed backcalculation of size and growth rate at age to examine the relative influences of selective mortality and water temperature on early growth. Negative size-selective mortality and growth-selective mortality between the juvenile and the adult stages was found only in the cohort that was the smallest and slowest growing in the period immediately following hatching. Selective mortality preferentially removed members of this cohort that were smaller from age 0 to 15 days, and slower growing from 0 to 10 days, resulting in an elevation of size at age to, or even above, that of cohorts that had not undergone this process. Size and growth rate at 5 day age intervals in the first 20 days after hatching differed among cohorts within and between summers and were strongly and positively correlated (r^2= 0·61–0·83) with water temperature.

Keywords: environmental factors • Indo-Pacific region • life-history traits • otolith • pelagic fishes • size

INTRODUCTION

Changes in rates of survivorship during larval and juvenile stages are thought to be the principal cause of the variable nature of recruitment in stocks of marine fishes (Houde 1987; Cushing 1990; Leggett & Deblois 1994). Early mortality is in turn strongly dependent on the growth rate of individuals so that fast growing cohorts often have higher rates of survivorship and consequently contribute disproportionately to the abundance of juvenile and adult life history stages (Bailey & Houde 1989).

Environmental factors, notably temperature, have a strong controlling influence on larval and juvenile growth of temperate marine fishes (Houde, 1989; Blaxter, 1991; Heath 1992). Tropical fishes are typically subjected to water temperatures above 20°C with low seasonal variation and they generally have high growth rates (Pauly, 1998). For this reason, it has been suggested that food, rather than temperature is the major factor in determining early growth of tropical fish (Houde 1989). However, relatively few studies have attempted to verify this hypothesis, particularly for multiple cohorts (Thorrold & Williams 1989; Milton *et al.* 1993; Wang & Tzeng 1999; Meekan *et al.* 2003). This reflects the difficulty of capturing representative collections of the same cohort of fish when life history stages can occupy different habitats, each requiring specialized sampling gear (Meekan *et al.* 2006).

The relationship between growth rates and the larval environment is often confounded by the selective nature of mortality in the plankton. Bigger and/or fast-growing larvae and juveniles tend to have higher survivorship than smaller and/or slow-growing individuals (Anderson 1988; Miller *et al.* 1988; Bailey & Houde 1989). Any comparison of the growth rates of cohorts and environmental factors is thus difficult if selective mortality does not act equally on all cohorts (Nielsen & Munk 2004). In order to determine the influence of the environment on cohort growth and survivorship, the effects of size-selective mortality must be disentangled from those of environmental factors (Sinclair *et al.* 2002).

The tropical sprat, *Spratelloides gracilis* (Themminck & Schlegel 1846), provides an ideal model for examining the relative effects of environmental factors and selective mortality on growth rate of cohorts. This species is pelagic throughout its life history but resides in nearshore waters around coral reefs where light traps can collect the late stage larvae, the juveniles and the adults abundantly (Meekan *et al.* 2001) and with equal efficiency (Meekan *et al.* 2000). It grows extremely fast, and has a very short life span of less than four months (Milton *et al.* 1991). Maturity is attained from 35 mm standard length (Milton & Blaber 1991) to 45 mm fork length (Dalzell 1985) and spawning occurs throughout the year. *S. gracilis* has clear and interpretable otoliths for which daily deposition of increments has been validated (Milton *et al.* 1990). It has been demonstrated that this species can undergo size-selective mortality between larval and juvenile stages (Meekan *et al.* 2006). All these biological characteristics mean that the growth of several cohorts experiencing different environments can be analysed from samples collected over few months.

Here, we use otolith analysis to describe daily patterns in the growth of six cohorts of *S. gracilis* from hatching to adulthood. Specifically, growth trajectories of adults (~60 days old) and juveniles (~30 days old) of the same cohorts were back-calculated from otoliths and compared during the first 20 days of life in order to determine: i) the influence of larval growth traits on juvenile survivorship; ii) the extent of size/growth selective mortality between juvenile and adult stage in this species and iii) the relative influences of water temperature and size/growth-selective mortality in determining the early growth patterns of the cohort.

MATERIALS AND METHODS

Collection techniques

Light traps (Doherty 1987; see Fig. 1 in Meekan *et al.* 2001 for design) were deployed in the Dampier Archipelago, Western Australia, from November 1998 to February 1999 and from November 1999 to February 2000. Traps were set at five different stations, but only samples collected at Rosemary Island (Fig. 1A) were used in this study as these collected approximately 90% of catches of *S. gracilis*. Sampling occurred during eleven nights centred on the new moon of each month except in December 1999 when a cyclone warning reduced sampling effort to only 9 nights (Table I). At each station, two traps were moored so that their entrance slits were approximately one meter below the surface. Traps were deployed on the same moorings each month and a timer and switch system ensured that they operated for the same number of hours each night. Only five traps could be deployed or removed on the same day so that two days were required to deploy or remove the 10 traps (2 traps per station at five stations). Thus, only one trap per station was deployed on the first and last night of each monthly trip while two traps collected fish at each station for the remaining nine nights of each month. Overall, sampling effort resulted in 20 light trap catches for all but one month. Although effort was reduced to 9 nights, a larger research vessel allowed deploying and removing all traps at once so that 18 light trap catches were available in December 1999 (Table I). Every morning, fish caught by each trap were removed and immediately preserved in 70% ethanol.

Light traps collected a total of 56 997 *S. gracilis*. As this collection was very large, it was necessary to select a representative subsample of fish for otolith analysis.

This was achieved by measuring the standard lengths (SL) of up to 60 fish that were randomly selected from each daily catch (4 788 individuals in the subsample). These measurements revealed bimodal size distributions in most months, with a first peak in abundance at around 28 mm SL and a second peak at 45 mm SL (Fig. 2). Patterns of pigmentation and presence of eggs in thousands of individuals indicated that fish in the 1st and 2nd peaks were unambiguously composed of juveniles (with less pigment and no eggs) and adults (a clearly defined silvery stripe and the frequent presence of eggs) respectively. A total of 50 juveniles and 50 adults were then selected from each monthly collection in proportion to their abundance in 1mm size classes of SL within an approximately 15mm size range centred on each peak. As the size ranges sampled around each peak were broad in order to include the full range of growth rates for each cohort, subsequent age estimation revealed individuals from a wide range of hatch dates. Some individuals were removed so that our analyses only compared individuals in the cohort that had hatched within an approximately 20d window and thus were likely to have developed under similar environmental conditions. This resulted in a reduction of total sample size for analysis from 583 to 417 adult and juvenile fish of three cohorts (November, December, January) in each of two austral summers (1998/1999; 1999/2000) (Table II). Cohorts were labelled by the month during which juveniles were first sampled, so that adults of the same cohort were sampled the following month. For example, the November 1998 cohort (coded 98Nov) consisted of juveniles sampled in November and adults sampled in December.

Otolith analysis

Both sagittae were extracted from each of the selected fish and cleaned of adhering tissue. One sagitta was mounted over the edge of a glass slide using thermoplastic glue and then oriented internal face up, rostrum outside the glass and the core inside the edge of the glass. The protruding portion was ground off using lapping film (9, 3 and 1 µm grades). The otolith was then mounted on a new glass slide so that it sat upright on its cut edge, in the centre of the slide. The upright portion was then ground on the same series of lapping films to produce a thin transverse section that contained the core. Sections were viewed with a microscope at 1000x magnification using an immersion oil objective and photographed using a Sony XC-77CE high resolution CCD camera. The public domain ImageJ program developed at the U.S. National Institute of Health (NIH) available at http://rsb.info.nih.gov/ij/ was used to measure the distance of each daily increment to the core along the longest axis of the otolith for each fish. Daily increment deposition has been validated for *S. gracilis* by Milton *et al.* (1990) and we assumed that the first increment closest to the core of the otolith was formed at the time of hatching (Campana & Neilson 1985; Wellington & Victor 1989). Age determination error of less than a day was obtained from the repeated analysis (2 readings per otolith) of a subsample of 40 randomly selected fish (20 juveniles and 20 adults). Given the relatively precise nature of age estimates, all otoliths were analysed once by the same observer (ED).

Back-calculation of size from otoliths assumes proportionality between otolith and somatic relative growth rates (Vigliola *et al.* 2000). The assumption was verified by calculating a highly significant and strong ($r^2 = 0.88$, $P < 0.001$, $n = 583$) allometric (c = 1.193, t-test, $P < 0.001$, $n = 583$) relationship between these variables for fish ranging from 21 to 55 mm SL. Given this relationship between otolith and body size in *S. gracilis*, we followed Vigliola *et al.* (2000) and used the modified Fry back-calculation model. This model included a biological intercept, corresponding to the fish size (L_{op}) and the otolith radius (R_{op}) at hatching (age 0). It was assumed that L_{op} was 4.4 mm SL

(Leis & Carson-Ewart 2000) and for R_{op} we used the mean of the radius at age 0 day (R_o) of all individuals ($R_{op} = 9.957\mu m$; $n = 583$).

Data analyses

We compared size and growth rates at age of juveniles and adults of the same cohort in order to detect any size- and/or growth-selective mortality using repeated measures (RM) MANOVAs (Chambers & Miller 1995). Once this was done, size and growth data back-calculated from juvenile and adults were pooled where no size/growth selective mortality was detected and compared among cohorts using RM MANOVAs. Since the youngest individual analysed was collected 20 d after hatching, back-calculated standard lengths at age 0 (hatching), 5, 10, 15 and 20 d and back-calculated growth rates at 0-5, 5-10, 10-15 and 15-20 d age intervals were used, respectively, as repeated measures in these analyses; then a contrast analysis was performed at each age (for size) and age intervals (for growth rates). Growth rates for a given age interval were calculated for each individual as the increase in fish size divided by the increase in fish age over that interval for that individual (i.e. Growth = $\Delta L/\Delta t$). Following this, individual size and growth rate at 5 d age intervals were averaged for fish of the same cohorts and mean size/growth values correlated with mean monthly sea surface temperature (SST) during the month of hatching using simple linear Pearson correlation. All statistical analyses used Statistica software (Statsoft). Monthly SST data for the Dampier Archipelago was derived from satellite remote sensing for one degree latitude by one degree longitude boxes (IGOSS-NMC products).

RESULTS

Water temperature

Between October and February, SSTs increased from 25.5 to 30-31°C (Fig. 1B). Mean monthly SSTs were higher in the summer of 1998/1999 than summer of 1999/2000, with the greatest difference of 1.2°C between summers occurring in January.

Light trap catches

A total of 56 997 *S. gracilis* ranging in size from 17 to 57 mm SL were collected during the 1998/1999 and 1999/2000 austral summers with most fish collected in December in both years (Table I). Catches were higher throughout the warmer 1998/1999 summer than the cooler 1999/2000 summer, with a total of 42 899 fish collected between November 1998 and February 1999, while only 14 098 individuals were collected during the same period in the following year (Table I). Abundance of fish smaller than 37mm (*i.e.* juveniles) followed the same patterns as total catch with greater numbers per trap in 1998/1999 summer and in December of each summer (Table I).

Population growth trajectory

The growth of *S. gracilis* in the Dampier Archipelago was extremely rapid (Fig. 3). Fish from cohorts that were sampled for the first time by light traps were juveniles that had been spawned approximately one month prior to capture (Table II). When the cohort was then re-sampled a month later these fish had already become adults at a relatively small size of 40-50 mm SL. Despite large differences in size and age at capture, both juvenile and adult samples encompassed the full range of growth trajectories with fish sampled from lower to upper limits of the population growth envelope (Fig. 3).

Selective mortality

Growth trajectories of juvenile fish collected in December 1998, January, November, December 1999 and January 2000 did not differ from that of adults from the same cohorts (Table III), implying no detectable size/growth-selective mortality for these 5 cohorts. In contrast, back-calculated size-at-age and growth rates of fish collected as juveniles in November 1998 were significantly different from that obtained from fish of the same cohort collected as adults in December 1998 (Table III). Contrast analysis revealed that adults of this November 98 cohort had significantly larger size at age 0, 5, 10, and 15 d, and higher growth rate for 0-5 and 5-10 d age intervals than juveniles of the same cohort. Therefore, those fish that survived to become adults in December 1998 were bigger at hatching and grew significantly faster at younger ages than the juveniles of the same cohort collected in November 1998 (Fig. 4). This implies that size/growth-selective mortality occurred sometime during the transition of these fish between juvenile and adult stages.

Comparison of growth patterns among cohorts and summers

Adult and juvenile samples were pooled for each cohort (with the exception of the November 1998 cohort where size/growth-selective mortality occurred) and analysed using RM MANOVAs. This detected highly significant differences in both size-at-age (factor Age x pooled sample, multivariate Wilk's $\lambda = 0.544$, $F_{24,1421} = 11.282$, $P < 0.001$) and growth rate (factor Age x pooled sample, multivariate Wilk's $\lambda = 0.754$, $F_{18,1154} = 6.720$, $P < 0.001$) among cohorts (Fig. 5). For any given month, size-at-age was typically larger and growth rate faster during the warmer summer of 1998/1999 than the colder summer of 1999/2000 (Fig. 5). Smallest sizes / slowest growth rates were recorded during the month of November when water temperatures were relatively cool. Size-at-age and growth rate increased with temperatures during December and January (Fig. 5, Fig. 1B). The juveniles caught in November 98 were significantly smaller and slower-growing at all ages younger than 10d than any other cohort. From 10 to 20 d after hatching, these juveniles grew faster so that at 20 d after hatching, individuals caught in November 1999 were significantly smaller than the juveniles caught in November 1998. Strong ($r^2 = 0.61 – 0.83$), positive and significant correlations were found between water temperature and fish size at all ages, except at hatching (Fig. 6). Likewise, strong ($r^2 = 0.66 – 0.78$), positive and significant correlations were found between water temperature and fish growth rate at 0-5, 5-10, 10-15d and 0-20d but not at the 15-20d age interval (Fig. 6).

DISCUSSION

S. gracilis is a very fast growing and short lived clupeid fish. At our study site in the Dampier Archipelago, Western Australia, *S. gracilis* grew at the upper margin of its known range in growth rate, with mean instantaneous rate at 20 d after hatching attaining 0.91 mm.d^{-1}, so that individuals of 45 mm SL (*i.e.* adult size) were only around 60 d of age. The oldest fish collected in our study attained an age of only 99 d. These growth rates compare with a low for the species of 0.37 mm.d^{-1} recorded in the Solomon Islands and a high of 1.19 mm.d^{-1} at 30 d after hatching at Lizard Island, Great Barrier Reef, Australia (Milton *et al.* 1991).

Size and growth-selective mortality was detected between the juvenile and adult stages only in the cohort of fish collected as juveniles in November and adults in December 1998 (Fig. 4). Selective mortality preferentially removed fish that were smaller / slower-growing in the period immediately following hatching, so that size-at-age of the adult cohort was close to or the same as that of cohorts captured as juveniles in December and January of that summer (Fig. 5). This cohort was smallest at hatching and grew slowest during early life history (the juveniles captured in November 1998, Fig. 4 and 5), consistent with the predictions of the growth-mortality hypothesis (Anderson 1988; Miller *et al.* 1988; Houde 1989). Similarly, field studies of other temperate and tropical species have also found selective mortality to act on slower growing cohorts (*e.g.* Meekan & Fortier 1996; Takasuka *et al.* 2003; Raventos & Macpherson 2005; Vigliola *et al.* 2007).

Selective mortality was not detected in the cohort of fish first collected in November 1999, despite this cohort growing slowly and having a relatively small size at age at 20d after hatching (Fig. 5). This implies that growth rates and size at age during the earliest part of the life history are more important as determinants of the occurrence of selective mortality than at older ages, a finding again consistent with the growth-mortality hypothesis. Selective mortality resulted in the adults collected in December 1998 having average sizes at hatching that were larger than those of any other cohort (Fig. 5). Prior to the action of selection, the population of juveniles from which these survivors originated had the smallest size at hatching of any cohort. There was also an increase in variability in mean hatching size, probably reflecting the relatively small sample size of adults. 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. Changes in the trait of size at hatching show the importance of parental contributions to the outcome of selective events operating on later stages, consistent with the findings of studies on this (Meekan *et al.* 2006) and other species (Marteinsdottir & Steinarsson 1998; Vigliola & Meekan 2002; Berkeley et al 2004; Vigliola *et al.* 2007).

We found size/growth-selective mortality occurring between the juvenile and adult life history stages in only one of six cohorts of *S. gracilis*.. These findings suggest that survivorship during the juvenile stage in this species is mostly independent of growth and size-selective mortality. However, this does not mean that both mechanisms are not occurring during the larval stage of this species. Meekan *et al.* (2006) detected size-selective mortality during the transition of *S. gracilis* from larvae to juveniles at Ningaloo reef, 600 km south of the Dampier Archipelago. Here, we were unable to sample larvae, as the smallest fish that recruited to our sampling gear (light traps) were already juveniles. As the importance of size-selective processes will decline as fish grow, due to the reduction in the number of predators to which they are susceptible (Bailey & Houde 1989), selective mortality is likely to have occurred earlier in the life history. Our study shows that growth and size selective mortality on earlier stages would have had relatively little influence on the strong correlation between size/growth at age of *S. gracilis* and water temperature from 0-20d after hatching. Indeed, the effect of this selective mortality would be to raise average growth rates for the cohort, in turn decreasing the strength of correlations between water temperature and growth rate by reducing the variation in growth present in the data set. This assumes that selective mortality acts in a consistent direction in all cohorts, by always removing the smallest, slowest-growing individuals, as generally appears to be the case under natural selection (*e.g.* Hovenkamp 1992; Sogard 1997; Hare & Cowen 1997; Shima & Findlay 2002; Raventos & Macpherson 2005; Vigliola & Meekan 2002; Folkvord 2005).

Size/growth at age from 0-20d after hatching of *S. gracilis* were very strongly correlated with temperature (r^2 values ranging from 0.61 - 0.83, Fig. 6). Relationships of this strength are unusual; relatively few studies have found that water temperatures could explain more than 30% of the variance in larval growth (McCormick & Molony 1995; Meekan *et al.* 2003), and most have recorded weaker correlations (Searcy & Sponaugle 2000; Wilson & Meekan 2001, 2002; Bergenius *et al.* 2005). One obvious reason that these correlations were relatively robust might be that most cohorts underwent little size/growth-selective mortality. We have shown that this process would be likely to weaken any correlation between environmental factors and growth rates, and this may have confounded earlier studies (Sinclair *et al.* 2002). However, we do not know to what degree our correlations reflected the relative contributions of temperature and food to growth, as we did not measure food availability for *S. gracilis*. In the tropics, it has been argued that due to relatively fast growth rates and thus high rates of food intake required by fish in larval stages, food supply should be the primary determinant of growth rate variability (Houde 1989). In our study the strength of the correlations between size/growth at age during the first 20d after hatching and temperature imply that even in this very fast growing species, growth rates are unlikely to be solely determined by food availability. This idea is supported by field evidence that shows that temperature rather than food might be an important determinant of growth rates of the larvae of tropical reef fishes (Meekan *et al.* 2003). Interestingly, water temperature was not correlated with size at hatching of *S. gracilis*. This suggests that the effect of parental identity and provisioning on size at hatching over-rides that of the physical environment in which the eggs develop (Marteinsdottir & Steinarsson 1998; McCormick 2003).

During the warmer 1998-99 summer we collected almost 3 times the number of *S. gracilis* than in the cooler summer of 1999-2000. As growth was positively correlated with sea surface temperature, growth rates of *S. gracilis* were also higher on any given month of 1998/99 than 1999/2000. Our data were too limited to infer whether faster growth during the warmer summer was merely coincidental, or reflected a causal phenomenon. However, a positive correlation between growth rates and abundance on an inter-annual basis is consistent with both temperate and tropical studies of growth rate during the early life history of marine fishes (*e.g.* Meekan & Fortier 1996; Campana 1996; Meekan *et al.* 2003; Jenkins & King 2006). At monthly intervals the correlation between growth rate and catches broke down, so that catches increased in both summers from November to December with warming surface waters, but declined in the warmest months of January and February (Table I). This contrasts with a number of studies that have found strong relationships between monthly growth rates and cohort size (Bergenius *et al.* 2002; Shima & Findlay 2002; Wilson & Meekan 2002). There are a number of possible explanations for this lack of correlation. Unlike other studies, we examined the abundance of the study species in both juvenile and adult stages and it is possible that factors other than growth also influence abundance of adults, such as advection and non-selective predation.

In summary, despite the presence of selective mortality, larval growth rates of cohorts of *S. gracilis* were strongly correlated with water temperature. The effect of selective mortality between juvenile and adult stage was to raise the mean size at age during early growth to, or even above those of other faster growing cohorts that had not undergone this process. On an inter-annual basis, faster growth might have a positive influence on fish abundance, although this correlation broke down within a summer for unknown reasons. Our study shows that it is possible to disentangle the relative influences of environmental factors and selective mortality on the early growth of cohorts of marine fishes.

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Table I. Date of sampling and light trap catches of *Spratelloides gracilis* at Rosemary Island in the Dampier Archipelago (Western Australia). Juvenile catch corresponds to the catch of individuals smaller than 37 mm. Catches are given as number of fish (Nb fish) and mean number of fish per trap (Nb fish/trap).

Summer	Month	Trap in - out	Nb nights	Nb traps	Total catch		Juvenile catch	
					Nb fish	Nb fish/trap	Nb fish	Nb fish/trap
1998/99	Nov-98	14 – 25 Nov 1998	11	20	10 568	528	9 598	480
	Dec-98	15 – 26 Dec 1998	11	20	24 110	1206	18 081	904
	Jan-99	13 – 24 Jan 1999	11	20	2 176	109	1 190	60
	Feb-99	11 – 22 Feb 1999	11	20	6 045	302	3 655	183
1999/00	Nov-99	3 – 14 Nov 1999	11	20	1 701	85	1 231	62
	Dec-99	4 – 13 Dec 1999	9*	18	10 086	560	8 226	457
	Jan-00	4 – 15 Jan 2000	11	20	919	46	134	7
	Fev-00	31 Jan–11 Feb 2000	11	20	1 392	70	566	28

* field work was shortened due to cyclone warning but a larger research vessel allowed deployment of 2 traps during the first and last night of sampling, while only one trap could be deployed on the first and last night of other months.

Table II. Hatch date window, mean age, and number (*n*) of *Spratelloides gracilis* of 6 cohorts collected by light traps in summers 1998/1999 (coded 98Nov, 98Dec, and 99Jan) and 1999/2000 (coded 99Nov, 99Dec, 00Jan) at the juvenile and adult stages in the Dampier Archipelago (Western Australia) and used in back-calculation analyses.

Summer	Cohort	Hatch date window	Stage	Mean age ± sd (d)	Size at capture ± sd (mm)	*n*
1998/99	98Nov	9 – 28 Oct 1998	Juvenile	33 ± 5	27.4 ± 2.8	46
			Adult	60 ± 7	43.9 ± 1.9	24
	98Dec	11 Nov – 5 Dec 1998	Juvenile	27 ± 4	26.5 ± 2.5	50
			Adult	63 ± 7	46.5 ± 3.4	22
	99Jan	6 – 29 Dec 1998	Juvenile	32 ± 6	26.8 ± 3.8	35
			Adult	63 ± 6	43.8± 3.3	36
1999/2000	99Nov	24 Sept – 20 Oct 1999	Juvenile	37 ± 6	28.1 ± 3.2	42
			Adult	58 ± 7	45.3 ± 2.6	30
	99Dec	6 – 17 Nov 1999	Juvenile	30 ± 3	27.5 ± 3.1	22
			Adult	56 ± 3	44.8 ± 2.9	23
	00Jan	24 Nov – 12 Dec 1999	Juvenile	37 ± 5	29.8 ± 4.0	49
			Adult	65 ± 6	45.3 ± 2.9	38

Table III. Summary of results of RM MANOVAs that compared back-calculated standard lengths at 0, 5, 10, 15 and 20 d age (coded SL) and back-calculated growth rates at 0-5, 5-10, 10-15 and 15-20 d age intervals (coded G) between juvenile and adult stages for 6 cohorts of *Spratelloides gracilis* collected in 1998/1999 (coded 98Nov, 98Dec, and 99Jan) and 1999/2000 (coded 99Nov, 99Dec, 00Jan). One RM MANOVA was performed for each cohort and multivariate test for repeated measures reported below for factor Age x Stage. df: degrees of freedom; F: value of F statistic; *P*: associated probability to Wilk's multivariate test.

Summer	Cohort code	Variable code	df	Wilk's λ	F	*P*
1998/99	98Nov	SL	4, 65	0.637	9.26	< *0.001*
		G	3, 66	0.803	5.39	< *0.002*
	98Dec	SL	4, 67	0.953	0.83	0.512
		G	3, 68	0.972	0.65	0.586
	99Jan	SL	4, 66	0.889	2.06	0.096
		G	3, 67	0.926	1.79	0.157
1999/2000	99Nov	SL	4, 67	0.917	1.52	0.206
		G	3, 68	0.950	1.18	0.320
	99Dec	SL	4, 40	0.842	1.88	0.133
		G	3, 41	0.842	2.56	0.067
	00Jan	SL	4, 82	0.940	1.31	0.272
		G	3, 83	0.950	1.44	0.235

FIGURE LEGENDS

Fig. 1. A. Map of Dampier Archipelago, Western Australia, with location of sampling sites where light traps were deployed (filled star shows site where most *Spratelloides gracilis* were collected). B. Mean monthly sea surface temperature (SST) of the area during the sampling periods (summers 1998/1999 and 1999/2000) were obtained from satellite remote sensing data.

Fig. 2. Monthly size frequency distributions of *Spratelloides gracilis* collected by light traps in summers 1998/1999 and 1999/2000 in the Dampier Archipelago, Western Australia. The dotted line indicates the limit in size between juvenile (fish smaller than 37 mm) and adult (fish larger than 37 mm). Cohorts were labelled by the month during which juveniles were first sampled, so that adults of the same cohort were sampled the following month. For example, the November 1998 cohort (coded 98Nov) consisted of juveniles sampled in November and adults sampled in December 1998.

Fig. 3. Back-calculated size-at-age data (dots) of *Spratelloides gracilis* collected by light traps in summers 1998/1999 and 1999/2000 in the Dampier Archipelago, Western Australia. Juvenile (circle) and adult (square) size-at-capture data are shown. n = 18 988 size-at-age records from 417 fish.

Fig. 4. Mean size-at-age (A) and mean growth rate (B) from hatching to 20d back-calculated from otoliths of juvenile (filled circles, n = 46) and adult (open circles, n = 24) *Spratelloides gracilis* captured by light traps in the Dampier Archipelago, Western Australia, in November and December 1998. Error bars represents ± standard errors.

Fig. 5. Mean size at age 0, 5, 10, 15, 20 d (A) and mean growth rate at 0-5, 5-10, 10-15, 15-20 and 0-20d age intervals (B) of cohorts of *Spratelloides gracilis* captured by light traps in summers 1998/1999 and 1999/2000 in the Dampier Archipelago, Western Australia. Samples of juveniles and adults from the same cohort collected in successive months were pooled except for November 1998 where size-selective mortality was detected. Size-at-age and growth rate of these 7 pooled samples of fish are respectively compared by RM MANOVA (factor Age x pooled sample) followed by contrasts analysis. Different letters indicate significant differences at 5% with smaller letters being for smaller values. Error bars represents ± 95% confidence intervals.

Fig. 6. Correlation between mean seawater temperature during month of hatching and mean size at age 0, 5, 10, 15, 20 d (A) and mean growth rate at 0-5, 5-10, 10-15, 15-20 and 0-20d age intervals (B), respectively, of cohorts of *Spratelloides gracilis* captured by light traps in summers 1998/1999 and 1999/2000 in the Dampier Archipelago, Western Australia. Samples of juveniles and adults from the same cohort collected in successive months were pooled except for November 1998 where size-selective mortality was detected. Regression lines are shown only to aid visual interpretation of trends.

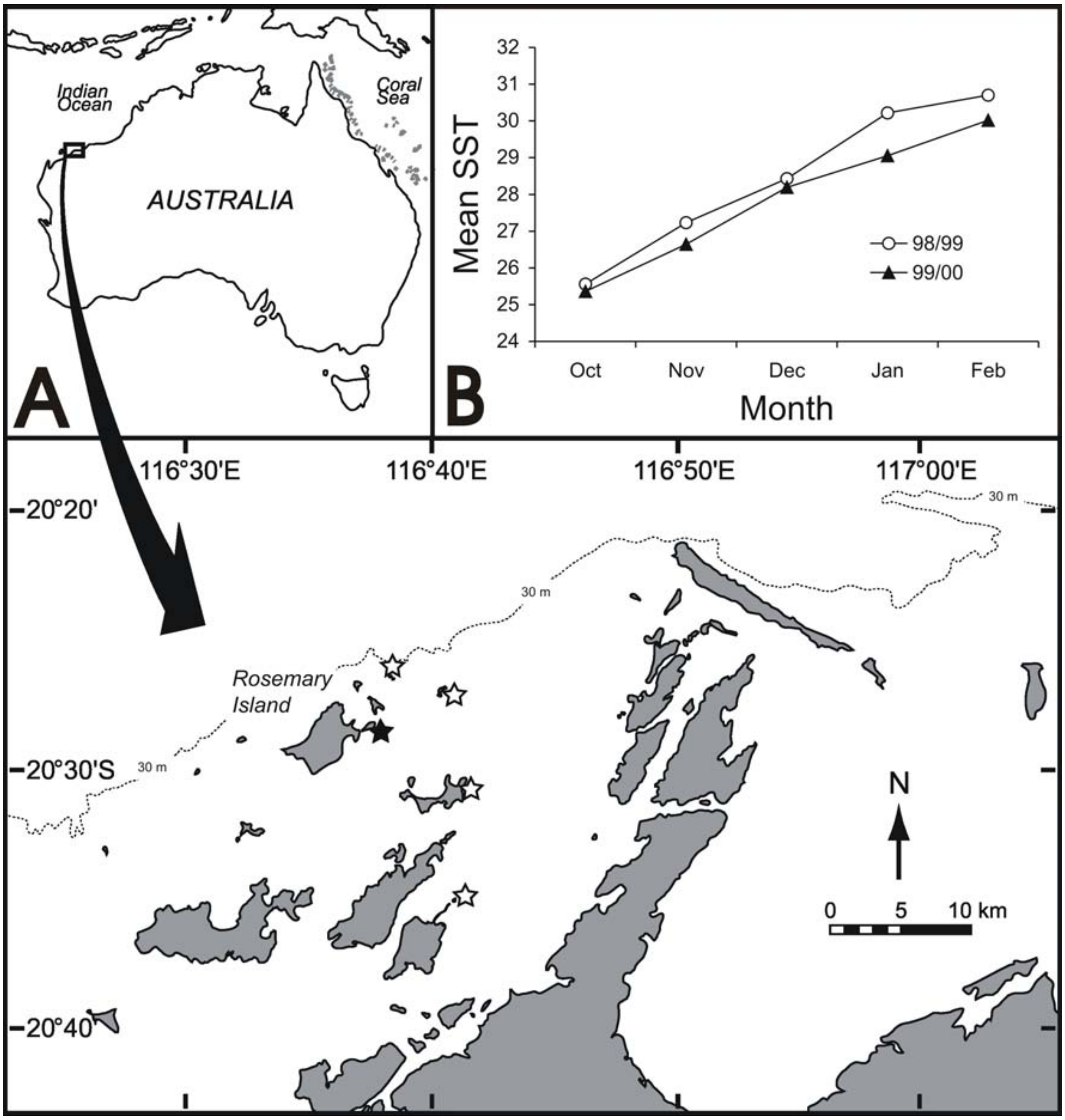

Indian Ocean
Coral Sea
AUSTRALIA
A
B
Mean SST
32
31
30
29
28
27
26
25
24
Oct
Nov
Dec
Jan
Feb
Month
98/99
99/00
116°30'E
116°40'E
116°50'E
117°00'E
20°20'
20°30'S
20°40'
30 m
Rosemary Island
N
0
5
10 km

Fig. 1.

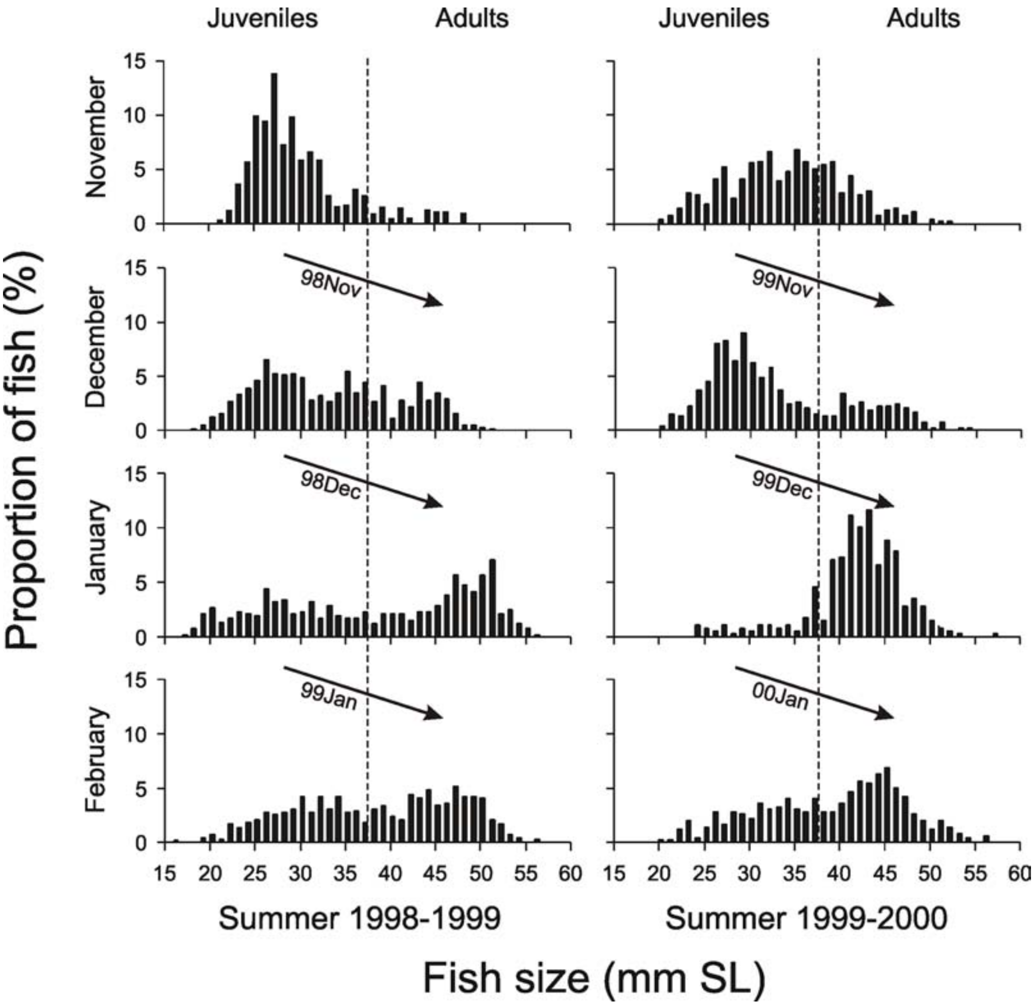
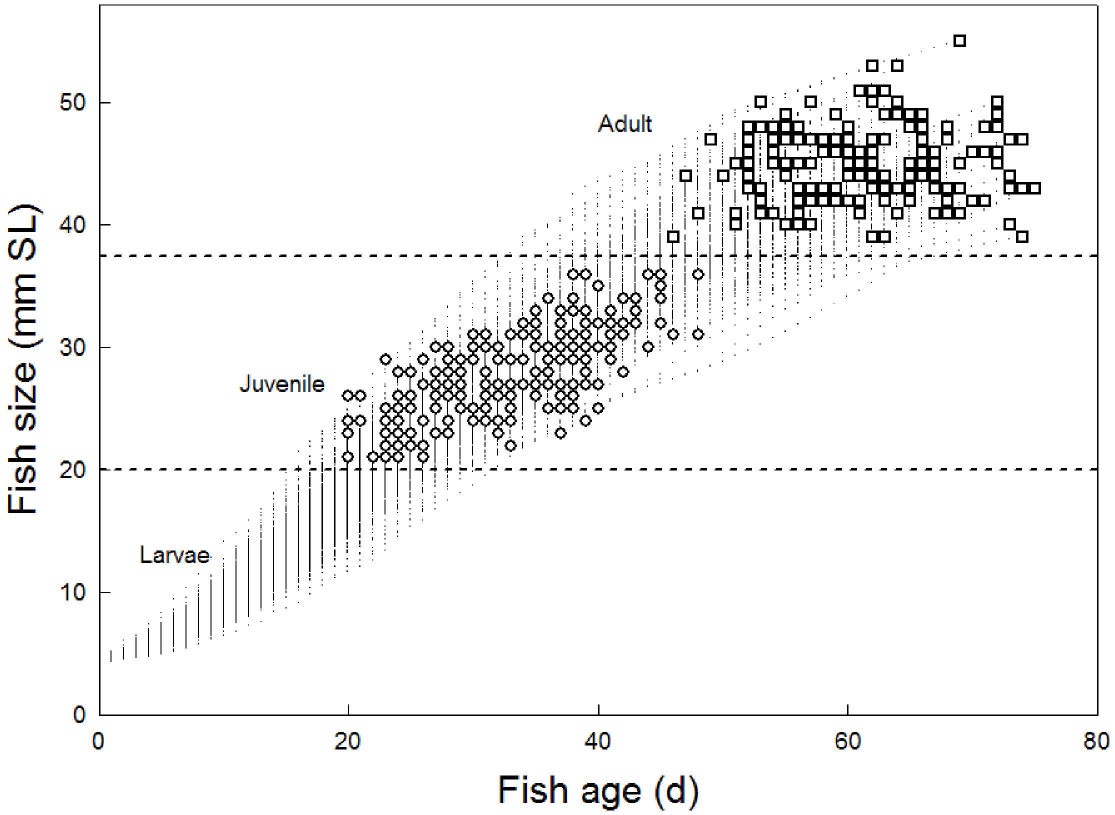

Juveniles
Adults
Juveniles
Adults
November
December
January
February
Proportion of fish (%)
98Nov
99Nov
98Dec
99Dec
99Jan
00Jan
0
5
10
15
15
20
25
30
35
40
45
50
55
60
Summer 1998-1999
Summer 1999-2000
Fish size (mm SL)

Fig. 2.



591

592 Fig. 3.

593

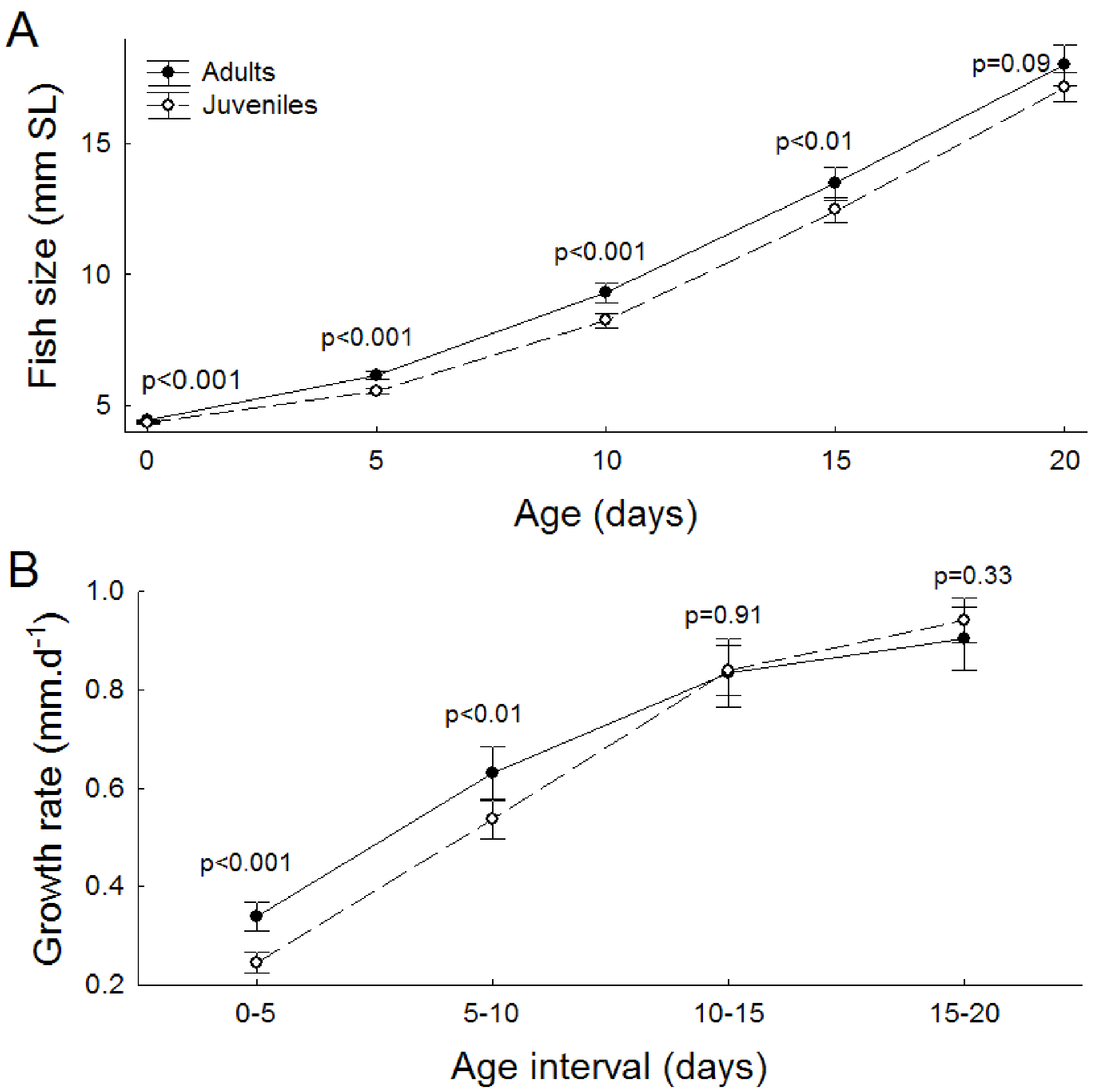

A
Adults
Juveniles
Fish size (mm SL)
15
10
5
p<0.001
p<0.001
p<0.001
p<0.01
p=0.09
0
5
10
15
20
Age (days)
B
Growth rate (mm.d-1)
1.0
0.8
0.6
0.4
0.2
p<0.001
p<0.01
p=0.91
p=0.33
0-5
5-10
10-15
15-20
Age interval (days)

Fig. 4.

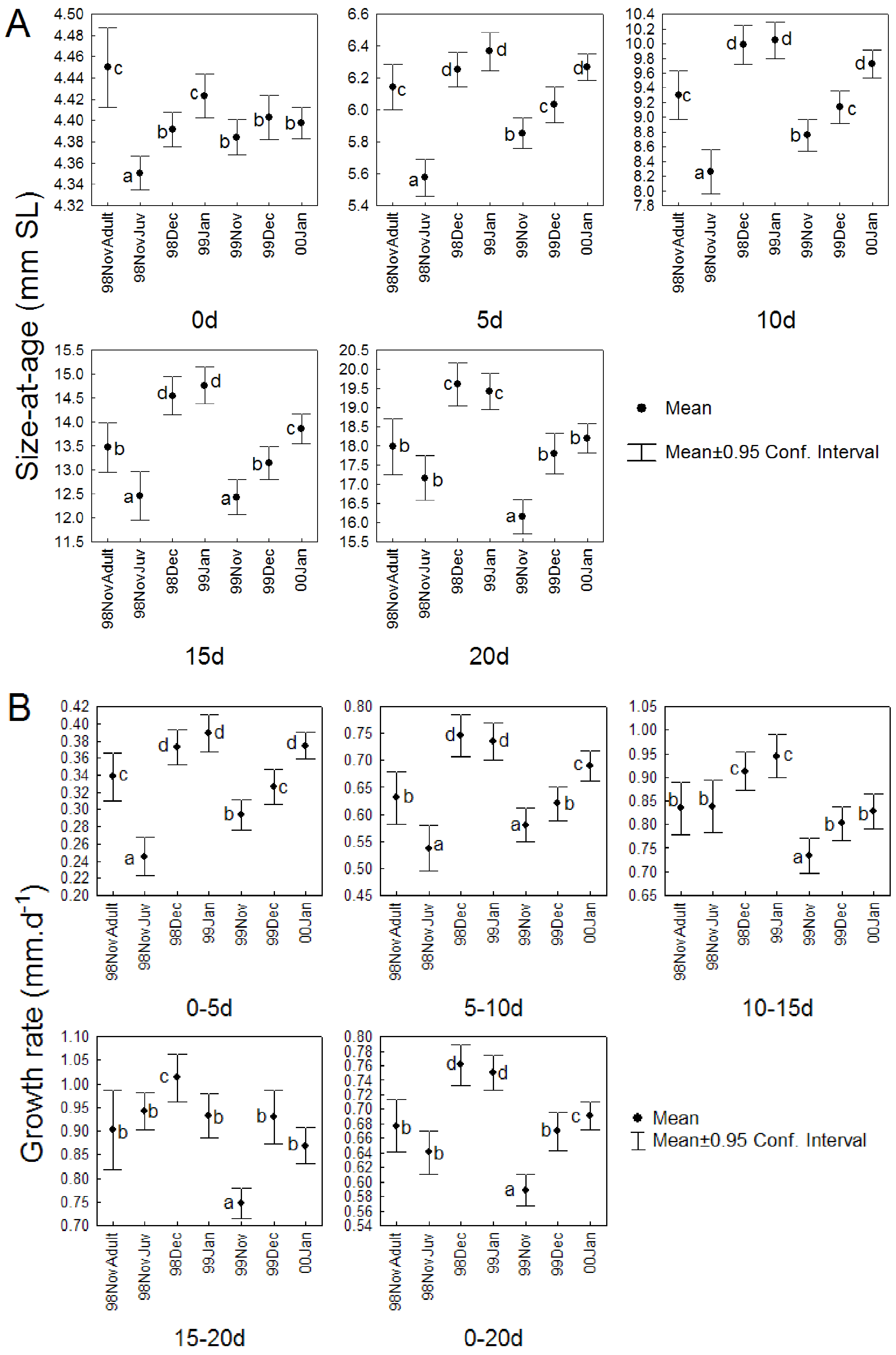

A
Size-at-age (mm SL)
4.50
4.48
4.46
4.44
4.42
4.40
4.38
4.36
4.34
4.32
c
a
b
c
b
b
b
0d
6.6
6.4
6.2
6.0
5.8
5.6
5.4
c
a
d
d
b
c
d
5d
10.4
10.2
10.0
9.8
9.6
9.4
9.2
9.0
8.8
8.6
8.4
8.2
8.0
7.8
c
a
d
d
b
c
d
10d
15.5
15.0
14.5
14.0
13.5
13.0
12.5
12.0
11.5
b
a
d
d
a
b
c
15d
20.5
20.0
19.5
19.0
18.5
18.0
17.5
17.0
16.5
16.0
15.5
b
b
c
c
a
b
b
20d
98NovAdult
98NovJuv
98Dec
99Jan
99Nov
99Dec
00Jan
Mean
Mean±0.95 Conf. Interval
B
Growth rate (mm.d-1)
0.42
0.40
0.38
0.36
0.34
0.32
0.30
0.28
0.26
0.24
0.22
0.20
c
a
d
d
b
c
d
0-5d
0.80
0.75
0.70
0.65
0.60
0.55
0.50
0.45
b
a
d
d
a
b
c
5-10d
1.05
1.00
0.95
0.90
0.85
0.80
0.75
0.70
0.65
b
b
c
c
a
b
b
10-15d
1.10
1.05
1.00
0.95
0.90
0.85
0.80
0.75
0.70
b
b
c
b
a
b
b
15-20d
0.80
0.78
0.76
0.74
0.72
0.70
0.68
0.66
0.64
0.62
0.60
0.58
0.56
0.54
b
b
d
d
a
b
c
0-20d
98NovAdult
98NovJuv
98Dec
99Jan
99Nov
99Dec
00Jan
Mean
Mean±0.95 Conf. Interval

Fig. 5.

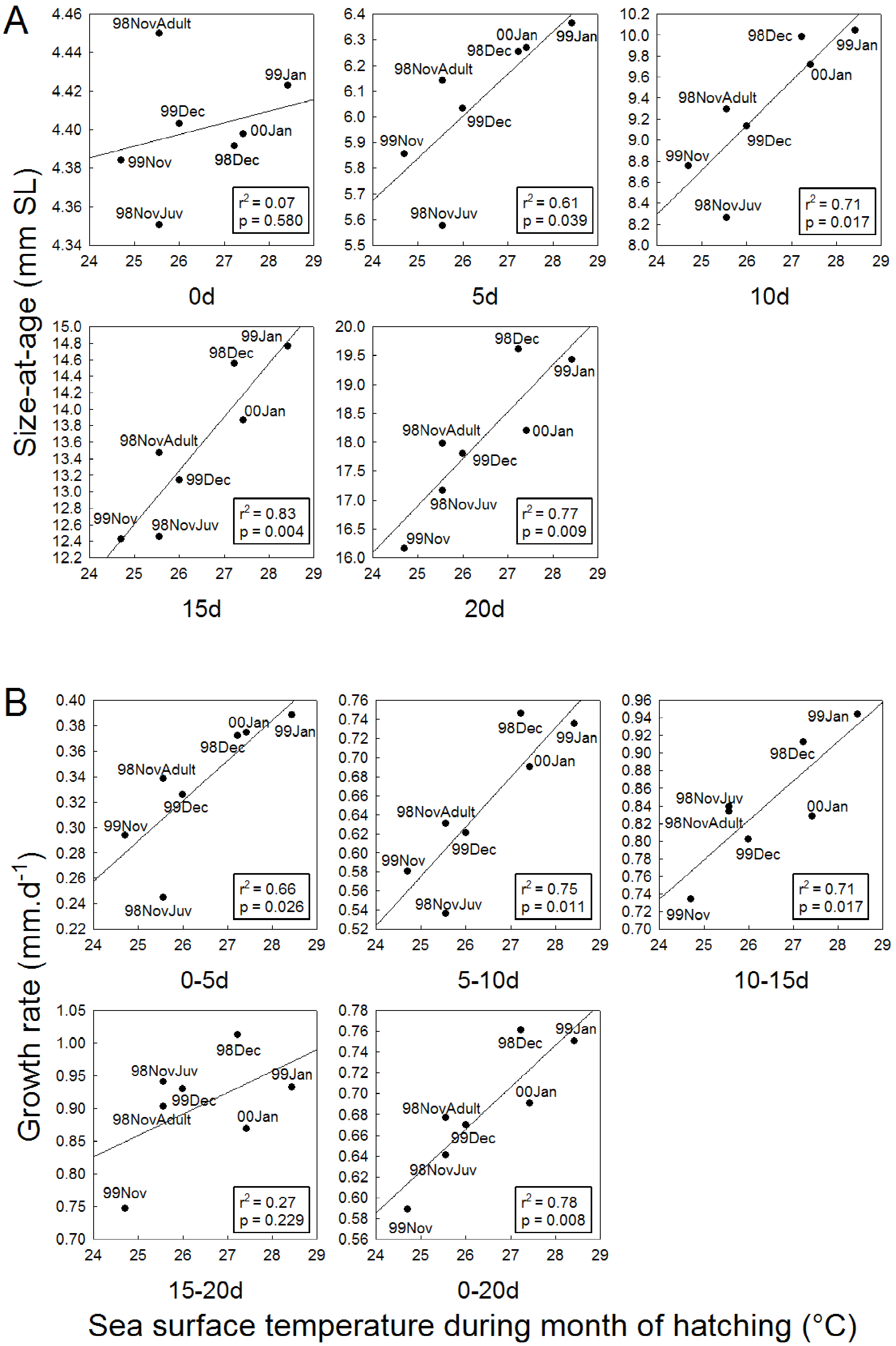

A
Size-at-age (mm SL)
0d
98NovAdult
99Jan
99Dec
00Jan
98Dec
99Nov
98NovJuv
r² = 0.07
p = 0.580
4.46
4.44
4.42
4.40
4.38
4.36
4.34
5d
00Jan
99Jan
98Dec
98NovAdult
99Dec
99Nov
98NovJuv
r² = 0.61
p = 0.039
6.4
6.3
6.2
6.1
6.0
5.9
5.8
5.7
5.6
5.5
10d
98Dec
99Jan
00Jan
98NovAdult
99Dec
99Nov
98NovJuv
r² = 0.71
p = 0.017
10.2
10.0
9.8
9.6
9.4
9.2
9.0
8.8
8.6
8.4
8.2
8.0
15d
99Jan
98Dec
00Jan
98NovAdult
99Dec
99Nov
98NovJuv
r² = 0.83
p = 0.004
15.0
14.8
14.6
14.4
14.2
14.0
13.8
13.6
13.4
13.2
13.0
12.8
12.6
12.4
12.2
20d
98Dec
99Jan
98NovAdult
00Jan
99Dec
98NovJuv
99Nov
r² = 0.77
p = 0.009
20.0
19.5
19.0
18.5
18.0
17.5
17.0
16.5
16.0
24
25
26
27
28
29
B
Growth rate (mm.d⁻¹)
0-5d
00Jan
99Jan
98Dec
98NovAdult
99Dec
99Nov
98NovJuv
r² = 0.66
p = 0.026
0.40
0.38
0.36
0.34
0.32
0.30
0.28
0.26
0.24
0.22
5-10d
98Dec
99Jan
00Jan
98NovAdult
99Dec
99Nov
98NovJuv
r² = 0.75
p = 0.011
0.76
0.74
0.72
0.70
0.68
0.66
0.64
0.62
0.60
0.58
0.56
0.54
0.52
10-15d
99Jan
98Dec
98NovJuv
98NovAdult
00Jan
99Dec
99Nov
r² = 0.71
p = 0.017
0.96
0.94
0.92
0.90
0.88
0.86
0.84
0.82
0.80
0.78
0.76
0.74
0.72
0.70
15-20d
98Dec
98NovJuv
99Jan
99Dec
98NovAdult
00Jan
99Nov
r² = 0.27
p = 0.229
1.05
1.00
0.95
0.90
0.85
0.80
0.75
0.70
0-20d
99Jan
98Dec
00Jan
98NovAdult
99Dec
98NovJuv
99Nov
r² = 0.78
p = 0.008
0.78
0.76
0.74
0.72
0.70
0.68
0.66
0.64
0.62
0.60
0.58
0.56
Sea surface temperature during month of hatching (°C)

Fig. 6.