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**Determinants of selective mortality during the early
life history of *Spratelloides delicatulus* in the
northern Great Barrier Reef**

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**For the research degree of Master of Science
in Marine Biology
within the School of Marine and Tropical Biology
James Cook University**

ABSTRACT

Early life stages of small clupeids are characterized by high mortality rates, mainly driven by predation and starvation. This mortality is thought to be selective for traits such as size, growth and body condition. It has been demonstrated that larvae with slow growth and reduced body condition do not have sufficient energy reserves to cope with suboptimal environments and will undergo environmental stress. Environmental stress can affect larval performance, increasing their susceptibility to mortality through predation and starvation. Thus, environmental conditions underlie selective mortality of fish by hindering growth rates during the vulnerable early stages. In fish larvae, otoliths are a good tool to explore the effects of the environment on survival as a daily record of growth is imprinted within them. In addition, otolith shape asymmetry (Fluctuating Asymmetry – FA) can give an insight of environmental stress, as the latter has a direct influence on metabolic rates, which regulate otolith accretion.

In this thesis, selective mortality and the effect of the environment on larval growth, size and body condition were studied in cohorts of the tropical sprat, *Spratelloides delicatulus*, sampled during their larval and juvenile stages at Lizard Island, Great Barrier Reef, Australia. Otolith microstructure analysis allowed back-calculation of size-at-age and daily growth rates. In addition, data of three environmental factors, temperature, Chlorophyll-*a* (Chl-*a*) and wind-induced turbulence was collected, allowing the examination of relationships between growth and the environment, and FA and body condition.

The first part of this thesis explores size and growth selection and the influence of the environment on those traits. The results demonstrate that *S. delicatulus* underwent positive size-selective mortality. However, smaller individuals exhibited faster growth rates which could have had increased survival through enhanced anti-predatory response. Additionally, a

cohort of larvae that experienced warmer waters were larger and grew faster than the cohort that hatched earlier in the year, suggesting that temperature could be one of the main factors driving growth rates during early life history.

The second part of the thesis investigates the influence of environmental stress on growth and body condition, and the link of the latter with fluctuating otolith asymmetry. It was found that slow-growing larvae were more dependent on the environment than those with higher growth rates. As a result, slow growers exhibited poor body condition and higher otolith FA, which was maintained through ontogeny, suggesting that individuals with insufficient energy reserves were not able to compensate for otolith asymmetry. The findings highlight the importance of environmental conditions during early life stages of *S. delicatulus* and the link between slow growth, poor body condition and high otolith asymmetry as drivers of selective mortality.

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1 General Introduction

1.1 Selective mortality and the early life history of marine fishes

It has been recognised for almost a century that the mortality rates suffered by the larval and juvenile stages of marine fishes are a central determinant of subsequent fluctuations in the size of adult populations (Hjort 1914; Bailey and Houde 1989; Houde and Zastrow 1993; Letcher et al. 1996). While larval mortality is high (in the order of more than 99% for many species), it does not necessarily happen randomly (Meekan et al. 2006b). Although the factors driving this process are known, there is lack of understanding of the relative importance of each factor, the context in which they act and their potential interactions. In general, mortality is thought to target individuals that exhibit traits that make them more vulnerable when exposed to adverse conditions. These traits include yolk-sac size, fish size, prior growth history, body condition and behaviour (Gagliano et al. 2007a; McCormick and Meekan 2007; Takasuka et al. 2007; Fuiman et al. 2010; Holmes and McCormick 2010). Size, development and growth are inextricably linked – individuals that are in more advanced developmental stages tend to be larger, and the faster fish grow, the faster they tend to develop. Therefore, in order to examine selective mortality, particular focus has been given to the processes that control larval growth (Garcia et al. 2003; Fox et al. 2007).

The growth-mortality hypothesis (Ware 1975) is the most broadly accepted explanation of the process of selective mortality of fish larvae and juveniles. The three main phenomena thought to contribute to this are: (1) the bigger-is-better hypothesis, (Miller et al 1988) (2) the growth-selective predation hypothesis (Hare and Cowen 1997; Takasuka et al. 2004a), and (3) the stage-duration hypothesis (Anderson 1988). The first proposes that larvae that attain larger body size are less susceptible to predation than smaller members of the same

cohort (Leggett and Deblois 1994); the second suggests that slow-growing larvae are more susceptible to mortality by predation, irrespective of relative size within the cohort (Takasuka et al. 2003); while the third proposes that larvae that grow fast and are able to reduce the time they spend in the smallest larval stages where they are most vulnerable to predation minimize the likelihood of mortality by predation (Leggett and Deblois 1994).

There is a great deal of evidence for negative size-selective mortality (i.e. the loss of smaller individuals within a cohort or population) during the larval stages of marine fishes (e.g. Bergenius et al. 2002; Takasuka et al. 2003; Takasuka et al. 2004a; Grorud-Colvert and Sponaugle 2006; Meekan et al. 2006a; Shoji and Tanaka 2006). Negative selection appears to be a pervasive, strong and important phenomenon, with 77% of 40 studies included in a recent review by Perez and Munch (2010) demonstrating the selective loss of smaller, slower-growing fishes during early life history, with selection occurring at an intensity five times that witnessed in terrestrial organisms. Therefore, this thesis focuses on growth as the main driver of selective mortality, according to the growth-selective predation and stage-duration hypotheses.

1.2 Selective mortality and environmental factors

Predation of larval fishes occurs within the context of the environmental conditions within the plankton. Physical and environmental factors drive patterns of larval growth and in so doing, influence patterns of selection and survivorship. For example, cohort strength of both Atlantic cod (*Gadus morhua*) (Campana 1996) and tropical goatfishes (*Mullidae*) (McCormick and Molony 1995) were positively correlated with water temperature so that in years where warm water allowed larvae to grow faster, greater numbers survived and cohort strengths of juveniles and adults were larger. However, environmental and growth variables may not necessarily relate in a simple linear manner. For example, temperature increases

under conditions of low food density caused a decrease in somatic growth of larval King George whiting, *Sillaginodes punctata* (Barber and Jenkins 2001). Similarly, larval growth rates of cod, haddock (*Melanogrammus aeglefinus*) and capelin (*Mallotus villosus*) (and subsequent recruitment) were also found to be enhanced by high temperature only in the presence of increased food (Loeng 1989). Conversely, Anderson & Dalley (2000) assessed growth rates of larvae and juveniles of Atlantic cod and proposed that during years when temperatures were above average and food was scarce, larval and juvenile growth rate decreased. These observations can be explained by warmer temperatures enhancing metabolic rates, so that a higher ration of food is required just to maintain body functions. Energy should be allocated to somatic growth only when sufficient resources are available (Fey 2006). However, the combination of both cooler temperatures and low food can be particularly influential on survivorship. For example, selective mortality of Atlantic cod was more than threefold stronger during a year with both cooler conditions and low food availability (Meekan and Fortier 1996). Consequently, covariance between temperature and food supply can enhance or hamper growth rates during early life stages.

In addition, physical forces, such as water turbulence can have an important effect in the ability of larvae to attack and capture their food prey (Dower et al. 1997). While small-scale turbulence favours prey encounter rates (Rothschild and Osborn 1988), high water turbulence can alter larval swimming behaviour, impeding the attack and capture of prey (MacKenzie and Kiørboe 2000; Utne-Palm and Stiansen 2002). The influence of high turbulence on feeding behaviour can be stronger in younger larvae that have not yet developed all swimming structures or that exhibit a body morphology that is less efficient for swimming and foraging (Kloppmann et al. 2002; Oshima et al. 2009). However, fish can alter their feeding strategy depending on the levels of water turbulence. For example, they can be selective for bigger prey items during periods of small-scale turbulence and shift to

opportunistic feeding during periods of high wind stress (MacKenzie and Kiørboe 1995; Hillgruber and Kloppmann 2000). In addition, water turbulence may not only affect prey encounter rates, but also have a direct effect over larval survival, as more energy is required to swim in turbulent water (Oshima et al. 2009). Therefore, water turbulence, coupled with factors such as swimming ability and feeding behaviour, is an important factor to take into account when studying larval growth and mortality (Dower et al. 1997).

1.3 Fluctuating asymmetry as a means of detecting environmental stress and body condition

Our understanding of the synergistic effects of physical and biotic factors on growth and survivorship of larval fishes would be greatly increased if we were able to find a simple means of detecting periods when larvae were undergoing environmental stress. In taxa with bilateral symmetry such as fishes, both sides of a trait are expected to develop identically; however, random perturbations of the internal cellular development due to environmental stress can produce asymmetry (Møller and Swaddle 1997). This is known as “fluctuating asymmetry” (FA), and is defined as the incapacity of an organism to attain identical development on the left and right sides of a trait (Møller and Swaddle 1997). In wild populations, individuals that exhibit FA experience reduced mating success (Polak 2008), reduced fertility and fecundity (Diaz et al. 2004), higher vulnerability to parasites (Møller 1992; Folstad et al. 1996; Sahyoun et al. 2007) and altered interspecific dynamics (Thornhill 1992; Bergstrom and Reimchen 2003; Reimchen and Bergstrom 2009). Since growth, reproduction and body maintenance constitute fitness components and FA arises from the inability of an organism to allocate energy into the former processes when stressed (Møller and Swaddle 1997), FA has been extensively used to measure fitness of wild populations (Clarke 1995).

Nevertheless, a lack of consistent evidence has raised controversy around the efficacy of FA as a fitness indicator (Bjorksten et al. 2000). For example, nutritional stress of house sparrows failed to yield significant correlations with feather FA, suggesting that either developmental instability in this species does not arise from food stress or that, in this particular case, FA is not a good indicator of developmental instability (Vangestel and Lens 2011). Likewise, fluctuating asymmetry of sexual and non-sexual traits in stalk-eyed flies showed no significant correlation to male quality when subject to low food regimes (Bjorksten et al. 2000). Further research showed that temperature stress increased flies mortality due to desiccation but did not have a significant effect on trait FA (Bjorksten et al. 2001). However, the incongruent evidence supporting FA as a fitness indicator could be due to several reasons. First, it is possible that FA may only correlate with reduced fitness when individuals are subject to extreme environmental conditions (Palmer 1994; Rasmuson 2002; Grønkjær and Sand 2003) or in laboratory controlled experiments (Bjorksten et al. 2000). Second, weak correlations between fitness and FA in natural populations could be due to the fact that selective pressure has already removed asymmetric individuals from the population (Møller and Swaddle 1997). Third, the traits where FA was measured may have not been susceptible to developing asymmetry (Møller and Swaddle 1997). Yet controversy also exists here; while some argue that only traits that “directly influence fitness” could show increased FA under stressful situations (Eggert and Sakaluk 1994; Polak 2008), others hypothesize that vestigial traits show higher levels of FA than functional traits, since natural selection would remove asymmetrical traits over generations (Crespi and Vanderkist 1997). In addition, sexually related traits (in the presence of sexual dimorphism) could potentially exhibit more deviations from perfect symmetry when stressed, as they require more energy investment which individuals are not able to afford when disturbed (Møller and Swaddle 1997). Despite the controversy, FA is still used as a sign of environmental stress in certain

organisms given that departures from the default state, bilateral symmetry, can be easily measured (Palmer 2004), it constitutes an early sign of stress in populations (Clarke 1995), it requires simple and inexpensive sampling (Lens et al. 2002) and, depending on the trait, FA can be measured by non-destructive procedures (Lens et al. 2002).

As mentioned above, choice of the right trait will provide unequivocal evidence of reduced fitness through FA. Otoliths are an ideal trait to explore the relationship between fitness and FA as they play an important role in essential functions such as balance, acoustic and navigation (Lychakov and Rebane 2005; Panfili et al. 2005). Furthermore, since they record daily/annual fish growth, they allow linking environmental stress to survival during early life history (Gagliano et al. 2007b; Sponaugle 2010). For example, embryos of the tropical damselfish *Pomacentrus amboinensis* originated from clutches exposed to high cortisol levels exhibited reduced developmental stability, reflected in higher egg mortality and increased otolith asymmetry of hatchlings (Gagliano and McCormick 2009). Small recruitment pulses of lizardfish in the Caribbean have been associated with increased otolith asymmetry in settlers, probably due to environmental stress experienced during the pelagic larval phase (Lemberget and McCormick 2009). Otolith FA was also found to vary with fish condition in larvae of a common tropical damselfish, where individuals reared under continued poor feeding regimes displayed increased otolith asymmetry than those fed ad-libitum (Gagliano and McCormick 2004). This finding is especially important since bilateral differences of otoliths and emergence of FA during early stages can affect recruitment of tropical reef fish by hindering individuals from hearing the sound of suitable settlement habitats (Gagliano et al. 2008). In temperate regions, otolith FA has demonstrated to be a good indicator of condition in populations subject to long-term exposure to food stress (Grønkjær and Sand 2003) However, interannual variation of environmental conditions and its effects on larval growth and development can obscure the relationship between otolith FA,

environmental stress and mortality. For example, variation in zooplankton abundance and water stratification produced significant differences in otolith FA of Mediterranean anchovy larvae collected during two consecutive years (Somarakis et al. 1997). High otolith FA was observed during the year when larvae encountered reduced copepod abundance and lower water temperature (Somarakis et al. 1997). Thus, investigating the synergistic effects of environmental factors on developmental stability can provide clearer evidence of the relationship between FA and condition.

Even when otolith FA may be an adequate indicator of body condition in larvae, it may not necessarily be an adequate indicator of fitness. Weak positive correlations between FA and slow growth were found in adult European anchovy, *Engraulis encrasicolus* (Kristoffersen and Magoulas 2009). Otolith FA also failed to correlate significantly to salinity and heterozygosity of the estuarine clupeid *Ethmalosa fimbriata*; although high salinity was known to have a negative effect on fish condition (Panfili et al. 2005). This can be due to the fact that an organism is particularly vulnerable to environmental stressors that can cause phenotypic variation only during certain life phases (Polak and Trivers 1994; Rasmuson 2002), such as the larval and juvenile stages in fish (Lychakov et al. 2006). Based on the hypothesis that high otolith FA represents a survival disadvantage to larvae (Gagliano and McCormick 2009), it can be expected that selective mortality would remove asymmetrical individuals from the population during early life stages (Gagliano et al. 2008), so otolith FA would be higher in larvae than in adults (Kristoffersen and Magoulas 2009).

1.4 Study species and aims

The tropical sprat, *Spratelloides delicatulus*, is an ideal model to investigate the interplay of the intrinsic and environmental factors that influence survival of young fishes. This sprat is short-lived and matures 62 to 68 days after hatching (Milton and Blaber 1991).

Since it spawns throughout the year at low latitude (Milton et al. 1995), it is exposed to a broad temperature regime and is likely to exhibit variability in growth and developmental rates. They also have otoliths that can be used as a historical record of individual growth and developmental stress as increments in the otoliths are deposited daily (Milton et al. 1990b; Milton et al. 1993). Recent studies of closely related species have shown that they undergo size selective mortality during the early life history that has a major influence on cohort strength (Meekan et al. 2006a). Durieux et al (2009) showed that this process was strongly and positively correlated with water temperature so that fish grew faster and survived better in warmer water. However, this result does not preclude the possibility that water temperature co-varied with other physical and biotic factors such as food availability and turbulence.

This study examines the effects of temperature, food availability and turbulence on the growth and selective mortality of the fast-growing sprat, *S. delicatulus*. The relative effects of these factors over the majority of the species' life history are investigated, and the extent to which environmental stress is expressed in the fluctuating asymmetry of otoliths, and how this relates to patterns of selective mortality, is examined.

The thesis is divided into two chapters that are structured as separate publications. Specifically, the thesis:

- (1) explores whether selective mortality operates during early life of the tropical sprat, *S. delicatulus*, and the extent of the influence of the environment on growth.
- (2) investigates the influence of environmental stress on developmental instability and survivorship of *S. delicatulus*.

2 Selective mortality and environmental factors

2.1 Introduction

Larval mortality and recruitment variability have been a primary focus of fisheries oceanography for almost a century (Dower et al. 1997; Myers 1998). High mortality rates experienced by larvae of small pelagics can lessen recruitment strength leading to year-to-year variability in population size (Allain et al. 2007). It is widely accepted that the main drivers of mortality during early life stages are starvation and predation (Dower et al. 1997) and they are intimately related. Mortality by predation is mainly determined by larval behaviour (Masuda 2011), which could be influenced by poor individual body condition resulting from starvation (Hoey and McCormick 2004).

Larval phenotype that may lead larvae to predation and starvation include size (the bigger-is-better hypothesis - Miller et al. 1988), growth history (the growth-selective predation hypothesis - Takasuka et al. 2003) and the ability of larvae to reduce the time they spend in that vulnerable stage (the stage-duration hypothesis - Leggett and Deblois 1994). The importance of each factor is species-specific and while for some fish, larger size conveys a survival advantage due to increased swimming capabilities and foraging activity, some others are not favoured by larger size, as they become more conspicuous to predators (Holmes and McCormick 2009; Holmes and McCormick 2010).

Since changes in the main environmental factors (temperature and food abundance) can promote or hinder larval growth, environmental conditions underlie selective mortality during early life stages (Buckley et al. 2010). In a context of climate change and ocean warming, it is fundamental to investigate species-specific responses of larvae to environmental conditions. This is especially important in fish, since as poikilotherms, most

cannot regulate their internal temperature and any changes will have a direct impact on metabolic processes, energy needs and ultimately, on their survival (Munday et al. 2008; Munday et al. 2009). As larvae in tropical waters are not exposed to high seasonal and diurnal fluctuations of temperature they are expected to be more vulnerable to changing temperature regimes (Green and Fisher 2004). However, while gross predictions concerning the impact of increased temperature on survival can be made, there are few data that examine the direct impact of temperature change on growth processes of young fishes in tropical marine environments.

The tropical sprat, *Spratelloides delicatulus*, is an ideal model to investigate the interplay of the intrinsic (e.g. size and growth history) and environmental factors that influence larval survival. This species is short-lived and matures 62 to 68 days after hatching (Milton and Blaber 1991). Since it spawns throughout the year at low latitude (Milton et al. 1995), it is exposed to a broad temperature regime and is likely to exhibit variability in growth and developmental rates.

Here, I explore the size and/or growth selection of larvae and the influence of the environment on larval growth over two consecutive monthly cohorts of *S. delicatulus* sampled on the northern Great Barrier Reef (GBR), Australia. Using data sets of size and growth rate back-calculated from otolith increment widths, I examine: (1) if larger size and/or higher growth rate conveys a survival advantage; (2) the relative influence of key environmental factors (temperature, wind stress and Chl-*a*) and size-selective mortality on growth rates.

2.2 Materials and Methods

2.2.1 Sampling design

S. delicatulus were collected during peaks of recruitment in November and December of 2006 at Lizard Island, GBR, Australia (14°40'S, 145°28'E) using light traps (Meekan et al. 2001). Moored light traps are the most efficient method to catch baitfish as they do not represent a selectivity factor themselves (Meekan et al. 2001). It has been observed that larvae collected in light traps do not exhibit superior swimming, orientation or sensory capabilities (Leis & Carson-Ewart 1997, Leis & Carson-Ewart 2003). Therefore, light trap sampling provides a representative sample of the *Spratelloides* population in Lizard Island (Doherty 1987; Milton et al. 1991).

Light traps were deployed at 3 sites (approximately 400 m apart) located on the leeward side of the Island, adjacent to the Research Station and suspended from a buoy approximately 1m from the surface over 12-16 m water depths. Traps were deployed at dusk and collected at dawn. After collection, *S. delicatulus* were sorted from the light trap sample and preserved in 70% ethanol. The preservation method might have produced shrinkage of larval *S. delicatulus*, however, final length was not converted to fresh length before data was analysed. Even when differences in individual shrinkage could represent a source of variation in standard lengths among samples, we assumed that shrinkage is constant among all individuals included in analyses (Theilacker 1980, Cunningham et al. 2000).

Standard lengths (SL, mm) of all individuals in samples were measured and length-frequency graphs were then used to distinguish single cohorts of juveniles in both November and December sampling. One cohort per month was identified and fish for otolith analysis were selected from successive catches of these cohorts separated by a week, on the 11th and 17th of November and the 22nd and 28th of December. Up to 35 fish were chosen from the

peaks in the size-frequency distribution of the cohort in proportion to their abundance in 1 mm size classes centred on the peak. As the size ranges sampled around each peak were broad, subsequent age estimation (see below) revealed individuals from a wide range of hatch dates. Some were removed so that the analyses only compared individuals that had hatched within a 10 d window, and thus were likely to have developed under similar environmental conditions. The final sample size of fish collected in November was 64 individuals (11th November, n = 34; 17th November, n = 30) while the sample size of fish collected in December was 61 individuals (22nd December, n = 26; 28th December, n = 35).

2.2.2 *Otolith analysis*

Sagittal otoliths were extracted under a dissecting microscope, cleaned and mounted on a microscope slide using thermoplastic glue. Once mounted, transverse sections centred on the otolith nucleus were ground and the other end was polished using lapping film (3 to 12 μm grades depending on otolith size). Slides were examined using a compound microscope (at 200 x magnification), photographed and images analysed using Optimas 6.5 software. Number and widths of increments were measured from the nucleus to the edge of the otolith along the longest axis (Campana 1992). Since daily deposition of increments in *S. delicatulus* has been previously validated (Milton et al. 1990b; Milton et al. 1993), each increment was assigned to 1 day (d) of age

Daily records of growth from hatching to the time of capture were estimated by back-calculating size-at-age from increment widths (Campana 1992) using the Biological Intercept technique (Campana and Jones 1992). The first increment closest to the core was assumed to be deposited within the otolith at hatching (Campana & Neilson 1985; Wellington & Victor 1989), corresponding to a fish size of 4.4 mm SL (Leis and Carson-Ewart 2000).

2.2.3 Environmental factors

Daily mean water temperature was recorded by a data logger located at 6 m depth, approximately 500 m away from light traps moorings. Data was retrieved from the AIMS Sea Temperature Monitoring Program (<http://data.aims.gov.au/seatemp/do/gotoStart.do>).

The main prey item of the study species consists of calanoid copepods, accounting for approximately $\frac{3}{4}$ of dry weight of the stomach contents (Milton et al. 1990a). Since copepods are phytoplankton grazers and Chl-*a* concentration is representative of the phytoplankton standing stock (Bautista and Harris 1992), Chl-*a* concentration of surrounding waters was assumed to be a proxy measure of food availability for *S. delicatulus* (Munk 1993). Chl-*a* concentration is commonly used in growth studies of small pelagics as proxy for food availability. Surface water samples were collected every afternoon from the 10th November to 31st December on the leeward side of Lizard Island, 100-400 m from the deployment site for the light traps. This area is distant from the reef lagoon, thus no substantial tidal influence that could have confounded direct comparison of water samples exists. Each was subsampled and filtered onto two replicate glass fibre filters (Whatman GF/F) and stored at -18°C until analysis. Chl-*a* concentration ($\mu\text{g L}$) was measured fluorometrically using a Turner Designs 10AU fluorometer after grinding the filters in 90% acetone (Parsons et al. 1984). The fluorometer was calibrated against Chl-*a* extracts from log-phase diatom cultures (Chl-*a* and Chl-*c*). The extracted chlorophyll concentrations were determined spectrophotometrically using the wavelengths and equation specified by Jeffrey and Humphrey (1975).

Hourly observations of wind speed and direction from November 10th to December 31st were obtained from an automatic weather station at Willis Island (<http://www.bom.gov.au/climate/>), 1.5°SE from Lizard Island where the physical conditions

are representative of the conditions of the study site (Milicich 1994). Wind-induced turbulence ($E, W \text{ m}^{-3}$) was calculated at 1 m of the water column according to the following equation:

$$E = (5.82 \times 10^{-6}) W^3$$

where W is wind speed (m s^{-1}) (Oakley and Elliott 1982). Wind direction remained constant throughout the evaluated period, thus it was not considered in the computation of turbulence.

2.2.4 *Statistical analyses*

Back-calculation of size-at-age and growth assumes that there is strong relationship between otolith and somatic growth. Evidence for this assumption was obtained by calculating a regression between otolith radius and standard length, which was linear and highly significant, with standard length accounting for most of the variability in otolith size ($r^2 = 0.82, p < 0.001, n = 125$). Analysis of co-variance (ANCOVA) was used to determine whether the relationship between standard length of fish and otolith size was consistent within the November and December samples.

Selection on size and growth was examined by a comparison of size-at-age and growth rates between the two successive samples of each cohort, each separated by 7 d (Meekan and Fortier 1996). For this analysis, growth histories were subdivided into seven 3 d intervals as the youngest individual collected by light traps was 21 d of age. Differences in back-calculated size-at-age and growth rates between samples of each cohort through the seven intervals above mentioned were assessed using repeated-measures MANOVA (Chambers and Miller 1995). When statistical significance within cohort was found, one-factor ANOVA was used to detect the interval where the difference in size or growth between

samples occurred (Chambers and Miller 1995). A Bonferroni correction was used and the significance level for the ANOVA set at $\alpha = 0.05/7 = 0.007$ (Rice 1989).

The relative effects of the environment on larval size and growth were examined using linear mixed effects models LME (Pinheiro and Bates 2000; Zuur et al. 2009). Daily observations of size and growth from 3 d to 21 d of age were used as the dependent variable. The fixed components of the LME were the environmental variables (with 1 d lag) while the random component was each individual. Individual was treated as a random factor to account for individual variability in growth rates and size.

Initially, the models examined the effects of temperature on daily size and growth of each cohort (November and December). Since individual growth measurements were correlated, the LME was extended with a residual temporal correlation structure, ARMA (Zuur et al. 2009). Daily size measures were also highly correlated, however, since every size observation depends on the observation from the previous day, the correlation could not be removed. In addition, because individual fish size increases with time and so did temperature during the study period (Appendix 1) data needed to be detrended. Hence, daily individual size was detrended fitting the data to a generalized growth model described by Shnute (1991) where size was the dependent variable and age the predictor. Subsequently, the residuals of this model were used as the dependent variable in a linear regression between size and temperature.

Daily records of Chl-*a* and wind-induced turbulence during early life of fish collected in December were available, thus were included in another LME that explored the effects of temperature, Chl-*a* and wind-induced on size and growth. The same procedure for residual auto-correlation used above was applied. Models were developed using the R (R Development Core Team 2007) function *lme*.

2.3 Results

2.3.1 *Size-frequency distributions*

Standard lengths (SL) of the November cohort ranged from 22 to 31 mm, while SL of the December cohort ranged from 18 to 31 mm (Figure 1). Back-calculated hatch date frequency distributions showed that larvae sampled in November hatched between the 1st and 9th of October, while individuals sampled in December hatched between the 19th and 28th of November.

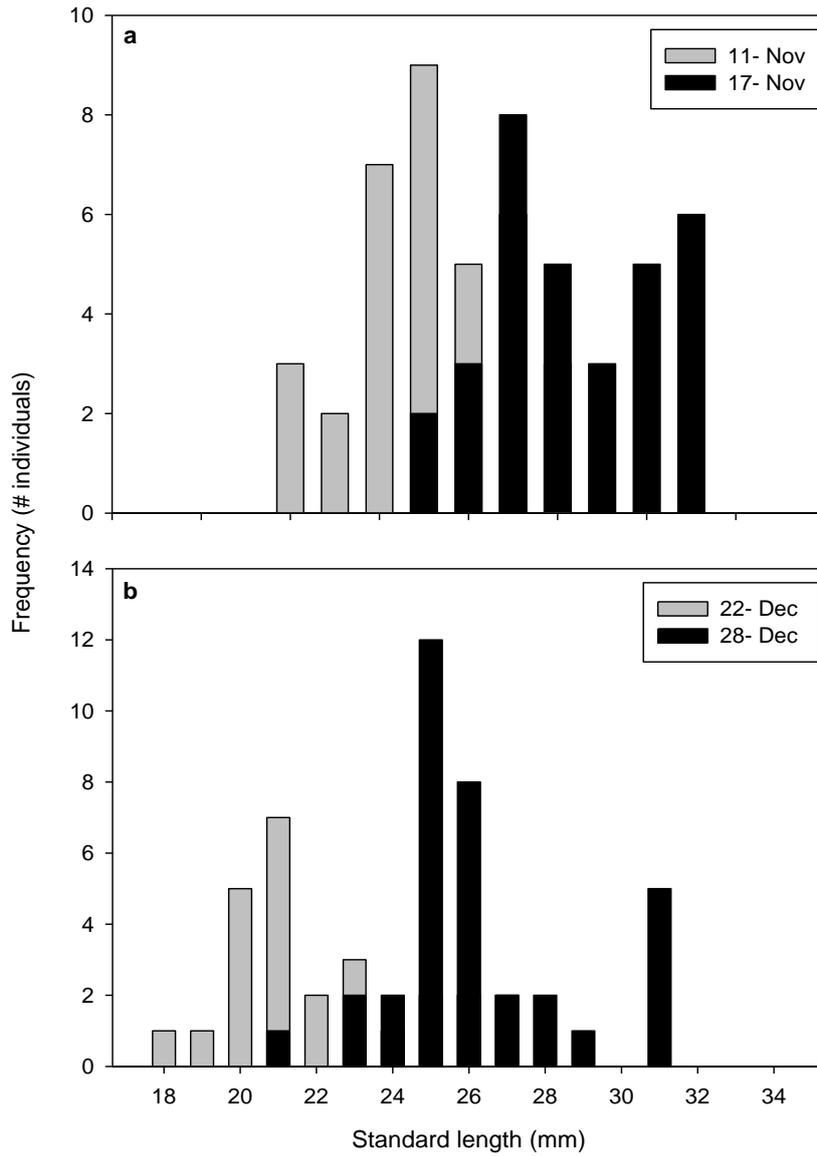


Figure 1. Size frequency distributions (Standard length – SL) of *S. delicatulus* collected by light traps at Lizard Island, GBR on the (a) 11th (grey bars; n=34) and 17th (black bars; n=30) November and (b) 22nd (grey bars; n=26) and 28th (black bars; n=35) December 2006.

2.3.2 *Size-at-age and otolith growth*

Estimated ages ranged from 33 to 47 d, with averages of 37 (± 0.47 SE) and 42 d (± 0.40 SE) of fish captured on the 11th and 17th of November, respectively. Estimated ages of fishes captured on the 22nd and 28th of December ranged from 24 to 39 d, with averages of 28 (± 0.55 SE) and 34 (± 0.54 SE) d, respectively. There was a linear relationship between fish size and otoliths size that did not differ significantly between samples of the same cohort (ANCOVA; $F = 3.768$, $df = 1$, $p = 0.057$ in November; $F = 0.001$, $df = 1$, $p = 0.979$ in December). However, intercepts were statistically different (ANCOVA; $F = 14.296$, $df = 1$, $p < 0.01$ in November; $F = 33.702$, $df = 1$, $p < 0.01$ in December).

2.3.3 *Size and growth selective mortality*

Back-calculated size-at-age of the cohorts differed between months. From 9 d after hatching, fish collected in November (samples collected on 11th and 17th November combined) were smaller-at-age than those collected during December (samples collected on 22nd and 28th December combined) (Figure 2). Similarly, the cohort collected in November grew more slowly than the December cohort at all times from hatching until 21 d of age (Fig. 3). Growth trajectories also varied between months, with the November cohort showing a pattern of rapid increase from hatching and up to 6 d old, then a plateau in growth until 21 d after hatching, except from 18 d which shows an unusual elevated instantaneous growth rate. The December cohort followed a smooth parabolic pattern, with a sharp increase in growth between hatching and 6 d of age followed by a slower rate of increase that peaked at 12 d and then slowly declined (Figure 3).

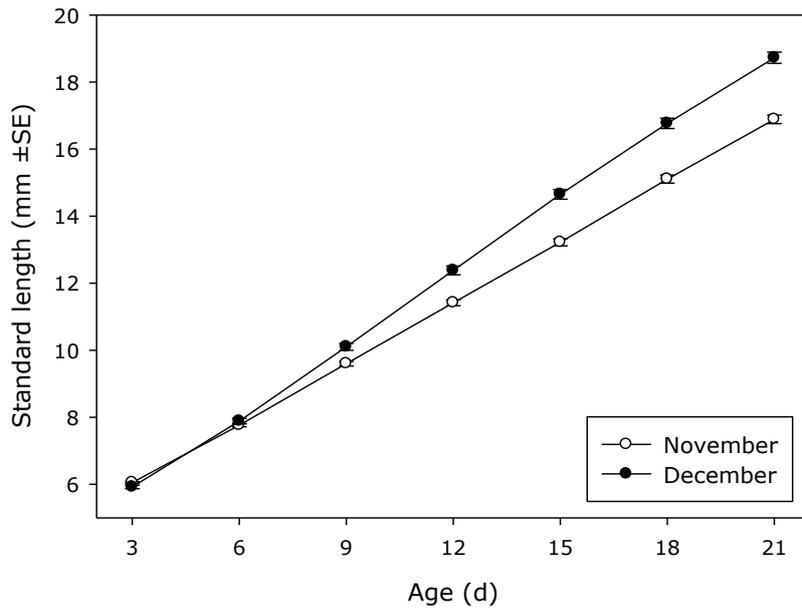


Figure 2. Mean back-calculated standard length (mm) over 3 d intervals of *S. delicatulus* collected at Lizard Island, GBR using light traps during November (open circles; n=64) and December 2006 (filled circles; n=61). Error bars represent standard errors

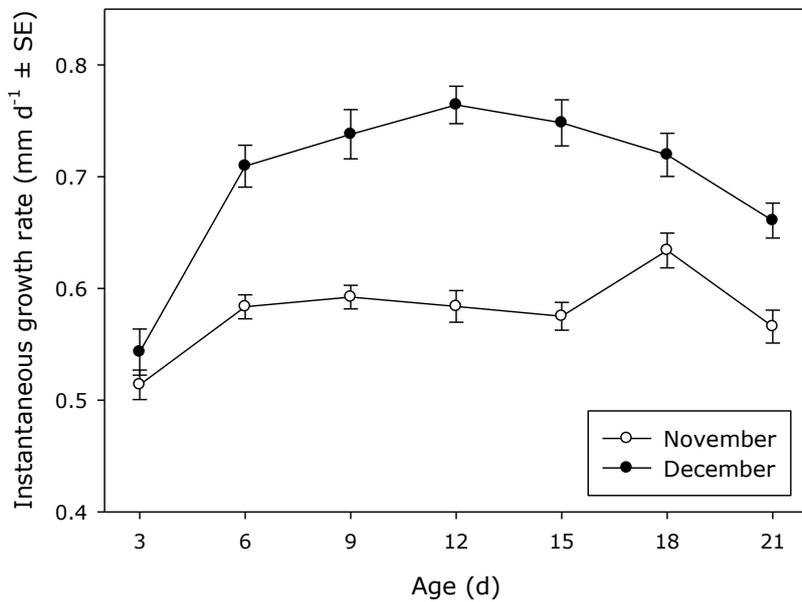


Figure 3. Mean back-calculated Instantaneous growth rate (mm d⁻¹) over 3 d intervals of *S. delicatulus* collected in Lizard Island, GBR using light traps during November (open circles; n=64) and December 2006 (filled circles; n=61). Error bars represent standard errors

Repeated-measures MANOVA revealed that the November cohort underwent size-selective mortality during the larval stage (Wilk's lambda = 0.737, $p = 0.004$). Despite significant differences in size-at-age among individuals collected on the 11th and 17th November, univariate analyses did not detect the specific interval at which those differences were occurring. Even when differences in size-at-age over the larval stage are very small and the statistical analyses did not reveal significant results at any particular interval it is possible to see that size-selection changed direction over time (Figure 4). Larger fish survived over small conspecifics at the beginning and end of the larval stage, while between 9 and 18 d after hatching, smaller fish exhibited a survival advantage (Figure 4).

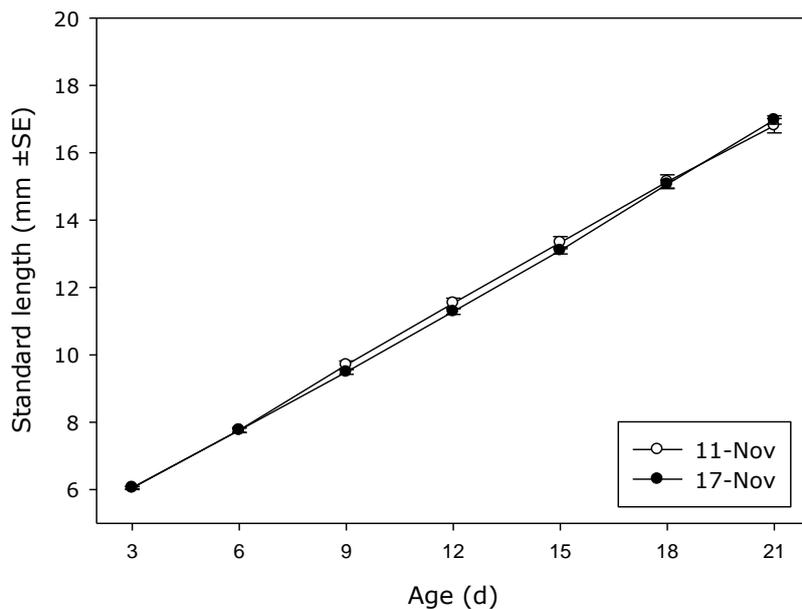


Figure 4. Mean back-calculated standard length (mm) over 3 d growth intervals of *S. delicatulus* collected by light traps at Lizard Island on the 11th (open circles; n=34) and 17th (filled circles; n=30) November, 2006. Error bars represent standard errors

In addition, growth selective mortality was detected when comparing successive samples of the same cohort (Wilk's lambda = 0.764, $p = 0.014$) and one-way ANOVA yielded significant differences in growth rate at 21d of age ($F_{1,62} = 12.464$, $p < 0.001$). Despite the lack of statistical differences at any other growth interval, individuals collected on 11th November exhibited slower growth during most of the larval stage (Figure 5).

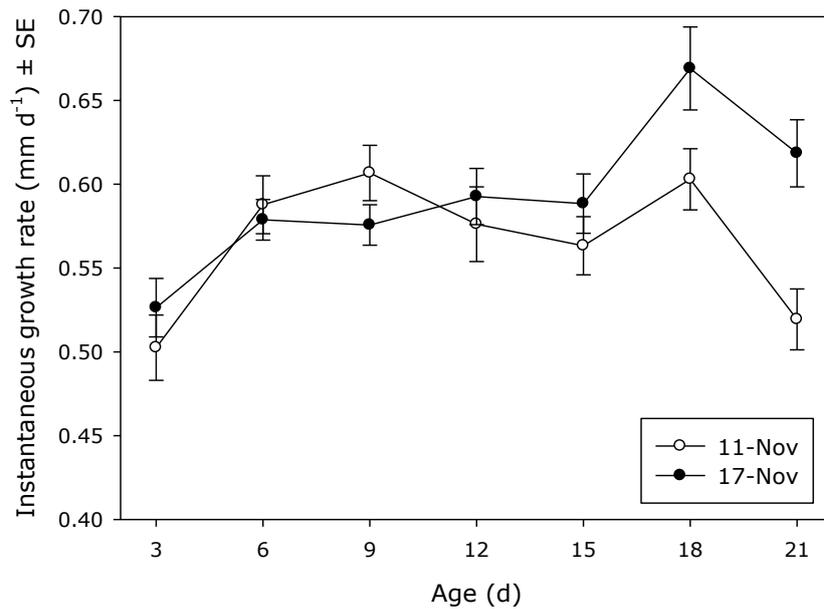


Figure 5. Mean instantaneous back-calculated growth rate (mm d^{-1}) over 3 d growth intervals of *S. delicatulus* collected by light traps at Lizard Island on the 11th (open circles; $n=34$) and 17th (filled circles; $n=30$) November, 2006. Error bars represent standard errors

For the December cohort, repeated-measures MANOVA also detected significant differences in size-at-age between successive samples (Wilk's lambda = 0.793, $p = 0.043$). In this case, positive size-selection operated until 15 d after hatching and from then on, smaller larvae were selectively removed from the population (Figure 6). In addition, significant differences in size were conspicuous at 3 d after hatching (ANOVA, $F_{1,59} = 12.81$, $p < 0.001$).

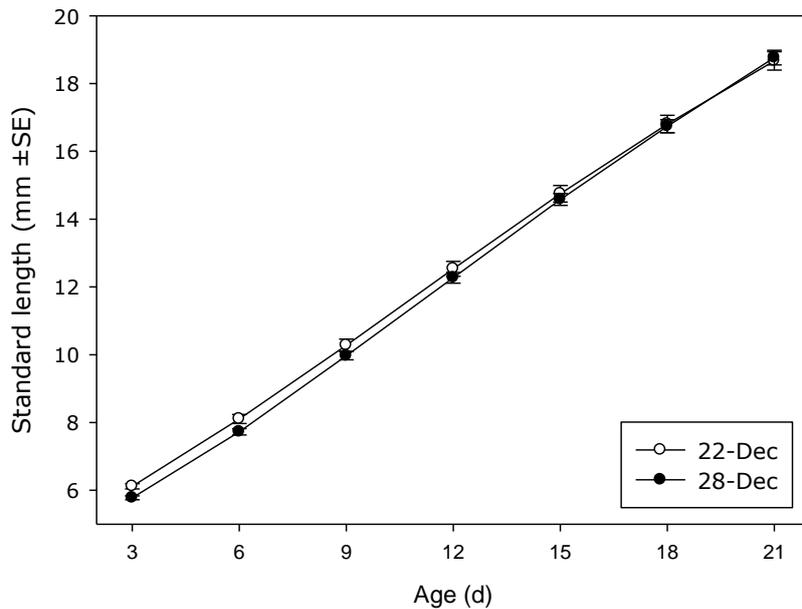


Figure 6. Mean back-calculated standard length (mm) over 3 d growth intervals of *S. delicatulus* collected by light traps at Lizard Island on the 22nd (open circles; n=26) and 28th (filled circles; n=35) December, 2006. Error bars represent standard errors

Instantaneous growth rates also differed significantly among samples (Wilk's lambda = 0.771, $p = 0.024$) of the December cohort, indicating that this cohort had also undergone growth selective mortality. Similar to the November cohort, survivors grew faster during most of the larval stage (Figure 7). No significant differences between samples were revealed at any particular growth interval.

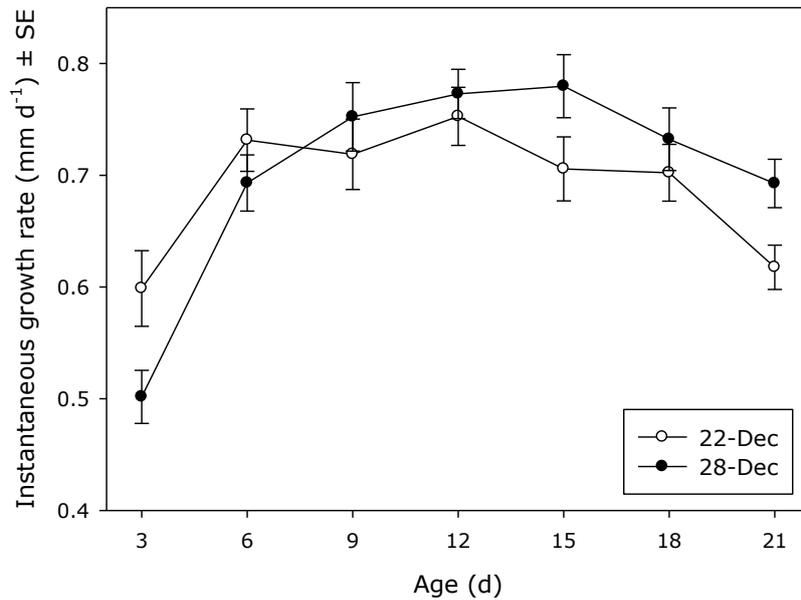


Figure 7. Mean instantaneous back-calculated growth rate (mm d^{-1}) over 3 d growth intervals of *S. delicatulus* collected by light traps at Lizard Island on the 22nd (open circles; $n=26$) and 28th (filled circles; $n=35$) December, 2006. Error bars represent standard errors

2.3.4 Selective mortality and environmental factors

LME models detected significant effects of month and temperature on growth.

Overall, temperature accounted for around 7% of the variance in growth rate (Table 1).

Table 1. Summary of results of linear mixed effects models (LME) that investigated the effect temperature and month (November, December) on growth rate of *S. delicatulus* collected by light traps at Lizard Island. SE is standard error. Only significant variables and interactions are included.

a) Growth Rate

	Estimate ± SE	t(df)	<i>p</i>
Intercept	-0.36 ± 0.11	-3.41 (1997)	<0.0001
Temperature	0.04 ± 0.004	9.43 (1997)	<0.0001

Adjusted $r^2 = 0.07$

Subsequently, turbulence and Chl-*a* data were included in the LME models for the analysis of size-at-age and growth patterns of the December cohort. Temperature, Chl-*a* and turbulence were all found to have significant effects on growth rate while only Chl-*a* and wind-induced turbulence had a significant effect on size-at-age, although in both cases, the environmental variables explained only 2% of the variance in the data set. Growth rate was positively correlated to temperature and Chl-*a* concentration, while negatively correlated to wind-induced turbulence (Table 2a). Conversely, Chl-*a* concentration and wind-induced turbulence revealed a positive and negative correlation with size-at-age respectively (Table 2b).

Table 2. Summary of results of linear mixed effects models (LME) that examined the effect of temperature, Chl-*a* concentration and wind-induced turbulence on cohort a) growth rate and b) size-at-age of *S. delicatulus* collected by light traps in December at Lizard Island. SE is standard error. Only significant variables are included.

a) Growth Rate

	Estimate \pm SE	t(df)	<i>p</i>
Intercept	-0.945 \pm 0.48	-1.96 (987)	0.0498
Temperature	0.06 \pm 0.02	3.37 (987)	0.0008
Chlorophyll- <i>a</i>	0.09 \pm 0.04	2.26 (987)	0.0239
Turbulence	-5.99 \pm 1.91	-3.13 (987)	0.0018

Adjusted $r^2 = 0.02$

b) Size-at-age

	Estimate \pm SE	t(df)	<i>p</i>
Intercept	-0.04 \pm 0.01	-2.94 (1042)	0.0034
Chlorophyll- <i>a</i>	0.17 \pm 0.04	4.46 (1042)	<0.0001
Turbulence	-4.38 \pm 1.63	-2.68 (1042)	0.0074

Adjusted $r^2 = 0.02$

2.4 Discussion

Selective mortality is seen as the mechanism underlying correlations between environmental factors and growth rates in cohorts of larval fishes. Under conditions that support fast growth, such as high temperatures and abundant food, larger fish receive a survival advantage as they are less susceptible to gape-limited predators (the bigger-is-better hypothesis - Miller et al. 1988). These conditions may also allow fish to grow swiftly through early life stages, when they are most susceptible to predation (the stage-duration hypothesis, Houde 1989). However, where selective mortality does not act equally on all cohorts, it may weaken correlations by removing slow-growers and thus raising average growth rates of

cohorts so that they resemble those of fish that inhabited more favourable conditions (Durieux et al. 2009).

In the present study, individuals from the cohort collected during November were smaller-at-age and grew slower during the larval stage than those collected during December. Those differences may have been due to more benign environmental conditions encountered by individuals born later in the year. These results are not surprising, since differences in larval growth between consecutive months have also been observed in *Sardina pilchardus* inhabiting temperate systems (Alemany et al. 2006). Also, cohorts of European anchovy larvae that hatched in warmer months experienced higher growth rate, larger size-at-age and exhibited lower mortality rates than cohorts that hatched at the beginning of winter (La Mesa et al. 2009). Therefore, even small variations in environmental conditions can induce large differences in growth and size-at-age during early life stages.

I found evidence for size-selective mortality during the larval stage. In November, from 3 d after hatching and until the mid larval stage, no significant differences in growth rates were detected; however, the direction of selective mortality changed from negative, at the beginning of the larval stage, to positive, during the mid larval stage. Conversely, at the end of the larval stage, differences in growth rate become more conspicuous and the selective pressure shifted towards smaller, slow-growing individuals. In December, positive size-selective mortality was also observed until 15 d after hatching, however, larger individuals exhibited slower growth rates. It is possible that the difference in the direction of size-selection could be driven by growth variability during the larval phase. It has been observed that slight changes in larval growth rates can produce high variation in selective mortality (Parma & Deriso 1990, Rice et al. 1993). Variability in growth rate is an especially important driver of selective mortality during the larval stage, when fish are more vulnerable to predation (Fontes et al. 2011). Nevertheless, while such inconsistencies in the direction of

selective mortality during ontogeny have been found in other tropical reef fishes (McCormick and Meekan 2007; Gagliano et al. 2008), both Meekan et al. (2006a) and Durieux et al. (2009) found that the closely-related species *S. gracilis* experienced size-selective mortality that always removed smaller, slow-growing fish from hatching until the juvenile stage. In this study, the demonstration that cohorts were undergoing selective mortality is consistent with the idea that this process underlies correlations between growth rates of *S. delicatulus* and environmental variables. However the erratic nature of its action, combined with other sources of non-selective mortality such as advection, probably account for the modest correlations between these environmental variables and growth rates of the cohorts.

When analysing the relationship between temperature, larval size and growth rate in both cohorts, I found that this environmental factor was significantly correlated only to growth rate. The link between temperature, growth rate and survivorship has been documented in closely-related species of *Spratelloides* (Meekan et al. 2006a; Durieux et al. 2009) and in other reef fishes in the tropics (Bergenius et al. 2005; Sponaugle et al. 2006; Figueira et al. 2009). However, the effect of water temperature on larval growth ranges from strong (Baumann et al. 2006b; Allain et al. 2007; Baumann et al. 2009) to moderate or weak (Searcy and Sponaugle 2001; Bergenius et al. 2005). In addition to potential changes in the action and direction of selective mortality, this variation is likely due to a number of biological and environmental factors, including the study species, year-to-year changes in the temperature regime, temporal and spatial scale of the study and covariance between environmental factors (Gonzalez-Salas and Lenfant 2007; Yasue and Takasuka 2009; Hinrichsen et al. 2010). Additionally, the present study was carried out over a relatively short duration and limited spatial scale, which allows little possibility for marked variation in temperature. Under such circumstances, small-scale patchiness in food may overwhelm any influence of temperature on growth, weakening correlations among the two variables

(Meekan et al. 2003; Bergenius et al. 2005; Sponaugle et al. 2006). Moreover, it is usually difficult to ascribe variation in growth rates solely to temperature, because covariance with other environmental factors not considered in the regression models can lead to equivocal results (Alemany et al. 2006; Hinrichsen et al. 2010). During the study period, there was a marginally significant correlation between water temperature and Chl-*a* (Spearman's $\rho = 0.43$, $p = 0.003$). Thus, even when both factors were not highly correlated, the extent of the influence of temperature on larval growth cannot be completely disentangled from the effects of Chl-*a*. Fitting size-at-age data to a growth model allowed obtaining residuals that did not increase with time (detrended) (Appendix 2), which avoided detecting a significant relationship between size and temperature due to model artifacts. Therefore, the lack of a significant correlation between temperature and larval size could suggest that this factor is more important on driving growth during early life of *S. delicatulus*. This result is not surprising, since fish growth is regulated by intrinsic (nervous, endocrinological and neurocrinological systems) as well as environmental factors (temperature, salinity, food availability) (Boeuf & Payan 2001), whereas size-at-age is more dependent on maternal contributions that affect egg size and oil globule size (Chambers & Leggett 1996).

Subsequently, when adding Chl-*a* concentration and wind-induced turbulence to the regression model, I obtained a significant correlation between these two factors and size-at-age of fish from the December cohort. Size was positively correlated with Chl-*a* concentration and negatively correlated with wind-induced turbulence. Also, I found positive correlations between growth rate and temperature and Chl-*a* concentration, whereas negative relationships were found between this trait and wind turbulence. Zooplankton abundance is recognized as the main driver of larval distribution of small clupeids in temperate systems (Olivar et al. 2010) and positive relationships between size-at-age and Chl-*a* have been observed in other clupeids. For example, size and abundance of larval European anchovy and

sardine have shown significant correlations with sea surface temperature and Chl-*a* concentration depending on the area of distribution (Giannoulaki et al. 2008; Schismenou et al. 2008; Bacha et al. 2010; Catalan et al. 2010). However, correlations found in the present study between size and growth and the environment were weak. Stronger correlations between temperature and Chl-*a* concentration and growth rates have been found for temperate sprats, demonstrating the strong dependence of growth and survival on environmental conditions (Baumann et al. 2006b; Baumann et al. 2006a; Baumann et al. 2006c).

Negative correlations between wind-induced turbulence and larval size and growth rate are consistent with the hypothesis that increased water turbulence limits larval growth, especially in small clupeids. As mentioned above, wind stress not only affects the ability of individuals to locate and consume prey, but it enhances energy demands of larvae in order to swim in turbulent water (MacKenzie and Kiørboe 2000; Oshima et al. 2009). Therefore, increased wind stress can drive larvae above their tolerance limits, reducing growth during periods of high vulnerability (Alemany et al. 2006). Such an influence of wind stress on larval and juvenile growth of *Sardina pilchardus* has previously been observed during periods of stable water temperature (MacKenzie 2000; Alemany et al. 2006).

In summary, few studies have considered changes in the intensity and direction of selective mortality in the plankton as a possible cause of variation in the strength and form of relationships between the growth rate of larval fishes and environmental factors in tropical areas. This study shows that repeated sampling of cohorts over time provides a means to examine and illustrate the effects of these processes. In combination with concurrent measurements of the environment, this can provide a unique insight into the factors determining growth of larval fish and ultimately, recruitment success.

2.4.1 *Conclusions*

Larger size-at-age does not appear to represent a survival advantage to larval *S. delicatulus*. Conversely, growth selection is the main factor driving mortality during early life stages of this species. Although it was demonstrated that environment plays an important role in determining larval growth rate, conflicting evidence about the direction of the relationships does not allow reaching conclusion about the environmental factor accounting for most of the variability in growth.

3 Interrelationships between growth, environmental factors and condition

3.1 Introduction

Environmental factors drive the population dynamics of marine pelagic fishes (Palomera et al. 2007; Leggett and Frank 2008). While favourable environments promote recruitment and lead to healthy stocks, suboptimal conditions (e.g. abnormal temperature regimes, low food availability, increased pollution, etc) reduce larval survivorship and ultimately stock abundance (Lindgren et al. 2010). Fishes can alter their behaviour and physiology to accommodate for stressful environments, but this is energetically expensive and those individuals that lack resources to undertake such changes will not be able to endure adverse conditions (Møller and Swaddle 1997) and ultimately may have stronger selective mortality (Bréda and Badeau 2008). For these reasons, knowledge of the degree to which fishes are subject to environmental stresses can provide an insight into the processes driving the variability inherent in population size and structure.

In many organisms, environmental stress is expressed through enhanced developmental instability, defined as a random variation in physiological and growth processes that hinder the normal development of an organism (Palmer 1994). Fluctuating asymmetry (FA) is one phenotypic manifestation of developmental instability (Polak 2008) and is defined as the inability of an organism to attain identical development on the left and right sides of a trait (Møller and Swaddle 1997). In general, individuals with higher FA are expected to be “less well adapted to their environment” (Polak 2008). The relationship between levels of FA and stress depends on the species, the choice of trait and the levels of stress experienced by an individual (Bjorksten et al. 2000).

Although a lack of clear evidence has contributed to a controversy about the suitability of FA as a suitable proxy for some species (Clarke 1998; Lens et al. 2002), FA within the otoliths or earbones of tropical marine fishes has been shown to be an appropriate indicator of the effects of environmental stress on individual fitness and survival (i.e. Gagliano and McCormick 2004; Gagliano et al. 2008). For example, Lemberget & McCormick (2009) found a close relationship between FA of otoliths and recruitment strength of a tropical lizardfish (*Saurida suspicio*). Developing otolith asymmetry during the late larval stage was also correlated with the ability of tropical damselfish to locate suitable settlement habitats, potentially increasing their vulnerability to predators (Gagliano et al. 2008). These studies show that at least for some fast-growing tropical fishes, FA of otoliths could provide an insight into the effects of environmental conditions on growth and survivorship.

Spratelloides delicatulus is one of the most common clupeids inhabiting the northern Great Barrier Reef (Milton et al. 1991). As a short-lived species (maximum age of <4 months), it experiences high daily growth rates, especially during early life stages (Milton et al. 1991). In this and co-generic species, environmental conditions, particularly water temperature, drive daily fluctuations of growth that ultimately result in selective mortality that tends to remove slower-growing, smaller individuals (Meekan et al. 2006a; Durieux et al. 2009). Furthermore, this species has clear and interpretable otoliths. These traits make it an ideal candidate for a study of the effects of fluctuating environments on otolith FA and ultimately on growth and survivorship. We hypothesized that *S. delicatulus* with slower growth rates and lower body condition would have less capacity to counteract the effects of the environment and would therefore exhibit higher otolith FA. Our aims were to determine: 1) whether individuals of consecutive samples of *S. delicatulus* underwent selective mortality; 2) the influence of the environment on growth; 3) the extent of otolith FA and its ontogenetic variation; and 4) the relationship between body condition and FA.

3.2 Materials and methods

3.2.1 Sampling design

S. delicatulus were collected using light traps moored in shallow (10 m) water near the reef edge at Lizard Island, Great Barrier Reef (14°40'S, 145°28'E). Adults, juveniles and larvae of this species are pelagic but are reef-associated, remaining in nearshore waters. As a result, all life history stages can be collected with equal efficiency by light traps (Meekan et al. 2000). Larvae and juveniles were selected from daily catches for ten days centred on the time of the new moon in December 2006.

Size-frequency histograms were used to identify two cohorts from samples collected on the 17th of December (sample 1). These cohorts were sampled again six and twelve days later, on 23rd (sample 2) and 29th of December (sample 3), respectively. Each cohort was composed of fish born within a 9 d window. In cohort 1, the first sample was composed of early and mid-stage juveniles (n = 25); the second sample consisted of mid-stage juveniles (n = 21); while the third sample composed of only late-stage juveniles (n = 15). In cohort 2, sample 1 was composed of mid- and late- stage larvae (up to 15 d old) (n = 15), while sample 2 was composed of early- and mid-stage juveniles (n = 25), and sample 3 mid-stage juveniles (n = 19).

Individual body weight was measured and livers were removed and weighed to calculate hepato-somatic index (HSI). HSI is the proportion of liver weight to total body weight and it is an estimate of the amount of energy stored in the liver (Adams and McLean 1985). These variables were used as a proxy for body condition (Kao et al. 1997). Water temperatures during the study period were provided by the Australian Institute of Marine Science Sea Temperature Monitoring Program (<http://data.aims.gov.au/seatemp/do/gotoStart.do>). Data on Chlorophyll-*a* (Chl-*a*) was

calculated by fluorometrical methods (Parsons et al. 1984) from water samples taken daily at the study site (see *Section 2.2.3* above). Wind-induced turbulence was calculated from hourly observations of wind speed and direction recorded at Willis Island weather station (<http://www.bom.gov.au/climate/>) using the equation given by Oakley & Elliot (1982) (see *Section 2.2.3* above).

3.2.2 *Otolith analysis*

Pairs of sagittal otoliths were extracted under a dissecting microscope, cleaned of adhering tissue and photographed with a camera mounted on a dissecting microscope. Otolith shape was measured using the image analysis software Optimas 6.5 through seven morphometrics: area, length, width, circularity, rectangularity, perimeter and shape. In order to calculate the latter, a Fast Fourier analysis was carried out. In this analysis the contour of each left and right otolith was traced through 128 points. This yielded 128 Cartesian coordinates, which were later transformed into Fourier descriptors as described in Castonguay et al. (1991). For subsequent analyses, only the 21 first Fourier descriptors were considered, as they contain most of the information to describe otolith shape (Bird et al. 1986). In this analysis, each descriptor represents the sum of total shape information contained in all previous descriptors. Hence, the lower descriptors (from 1 to 6) represent the overall shape of the otolith while the each descriptor adds finer detail to the shape (in this case, from 7 to 21) (Bird et al. 1986). The initial descriptor was denoted as zero and all the rest were divided by descriptor 1 in order to normalize all images (Gagliano and McCormick 2004).

Subsequently, the left otolith of each individual was sectioned and photographed. Otolith microstructure analysis allowed back-calculation of daily size-at-age and growth from

successive measures of increment width using the Biological Intercept technique (Campana 1992).

3.2.3 *Analysis of asymmetry*

Outlier measurements and otolith size-dependency can confound FA estimates (Palmer and Strobeck 2003). Signed R – L values of each cohort were tested for outliers by the Grubbs Test of Outliers (two-tailed) (Palmer and Strobeck 2003). A Bonferroni correction was applied and the significance level was set at $\alpha = 0.05/2 = 0.025$ (Rice 1989). Statistically significant outliers were removed from further FA analyses. Also, $|R - L|$ values were tested for otolith-size dependence through a Spearman Rank Order Correlation between otolith asymmetry, $|R - L|$, and otolith size, $(R+L)/2$ as described in Palmer & Strobeck (2003).

In order to associate variability between left and right sides to FA, three assumptions must be met: signed differences should exhibit a normal distribution with a mean equal to zero; kurtosis must be less than zero; and variations in the measurement of R - L should not be due to measurement error (ME) (Palmer and Strobeck 2003). The first assumption was tested using a one-sample t-test (Palmer and Strobeck 2003). Kurtosis was calculated as in Palmer & Strobeck (2003), also a visual inspection of the distributions was performed in order to check if they showed directional asymmetry or anti-symmetry. Finally, to assess ME, five otolith pairs were chosen randomly and their contour was traced three times (Lemberget and McCormick 2009). A two-way nested ANOVA was performed assigning “Side” as fixed factor and “Individual” as random factor (Palmer 1994). The mean squares (MS) of the “error” term represents the random variation in otolith shape due to ME (Palmer 1994).

3.2.4 *Statistical analyses*

Selection was examined by a comparison of size-at-age between successive samples of each cohort, each separated by 7 d (Meekan and Fortier 1996). For this analysis, records of size-at-age were subdivided into seven 3 d intervals. Differences in back-calculated size among and within cohorts at each of the 3 d intervals were assessed using repeated-measures MANOVA (Chambers and Miller 1995). When statistical significance within cohorts was found, one-factor ANOVA was used to detect the growth interval when the difference occurred (Chambers and Miller 1995) and Tukey's post-hoc tests were used to identify which samples were significantly different. A Bonferroni correction was used and the significance level for the ANOVA set at $\alpha = 0.05/7 = 0.007$.

The intensity of size selection (SI) for each cohort over each of the 3 d intervals was quantified by calculating the difference between mean size-at-age of sample 3 (after selection) and sample 1 (before selection) and dividing it by the standard deviation of sample 1 (before selection) (Vigliola et al. 2007). As sample 1 in cohort 2 contained individuals of up to 15 d of age, SI was calculated from 3 d to 15 d after hatching.

Linear mixed-effects with random intercept models (LME) were used to investigate the effects of the environment on individual daily growth in each cohort from 1 to 21 d of age. Temperature, turbulence and chlorophyll-*a* (Chl-*a*) concentration were included as explanatory fixed variables, while each individual fish was treated as a random explanatory variable. Since individual growth measurements were correlated, the LME were extended with a residual temporal correlation structure, ARMA (Zuur et al. 2009).

One-factor ANOVA was used to determine significant differences in FA of otolith area, width, circularity, rectangularity, perimeter and Fourier shape among and within

cohorts. The significance level for the within cohorts ANOVA was $\alpha = 0.05/3 = 0.017$. Data was transformed when necessary to conform to assumptions of the analysis.

The relationship between FA and body condition in both cohorts was examined using linear mixed effects with random intercept models (Zuur et al. 2009). The explanatory fixed variables included in the model were a subset of the available variables: individual standard length, body weight, hepato-somatic index (Kao et al. 1997) and otolith radius at the time of capture; again, individual fish was treated as a random explanatory variable. Otolith FA was included in the model as the. Since the present chapter uses several morphometrics to explore *S. delicatulus* otolith FA, Principal Components Analysis (PCA) was used to identify the minimum number of morphometrics, or variables, that retained most of the information contained in the original data (Kruskal 1978). Only the variables that composed the first principal component were entered in the LME.

3.3 Results

3.3.1 Growth and size-selection

Larvae from cohort 1 experienced slower growth rates than larvae from cohort 2 during most of the larval stage. Only at 15 d and 21 d after hatching did individuals from the first cohort exhibit slightly faster growth than their conspecifics (Figure 8).

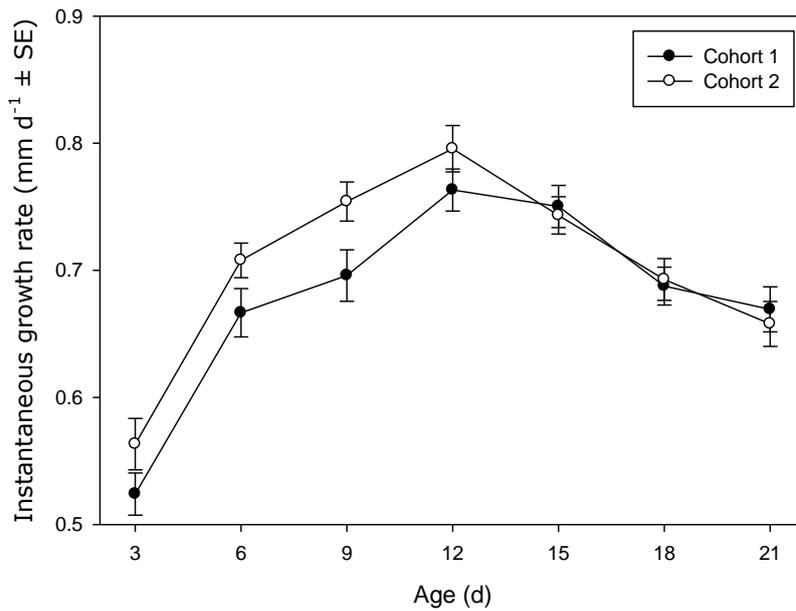


Figure 8. Mean back-calculated instantaneous growth rate (mm d⁻¹) over 3 d intervals of *S. delicatulus* collected during December, 2006 in Lizard Island for cohort 1 (n = 68) (black circles) and cohort 2 (n = 67) (white circles). Error bars represent standard errors

Size-at-age of *Spratelloides delicatulus* from cohort 2 was significantly larger than in cohort 1 (Wilk's lambda = 0.849, $p = 0.023$). Differences in size-at-age between cohorts were greatest at 15 d of age and decreased slightly until individuals were 21 d old. At 12, 15 d and 18 d of age fish from cohort 2 were significantly larger than fish from cohort 1 (Figure 9, Table 3).

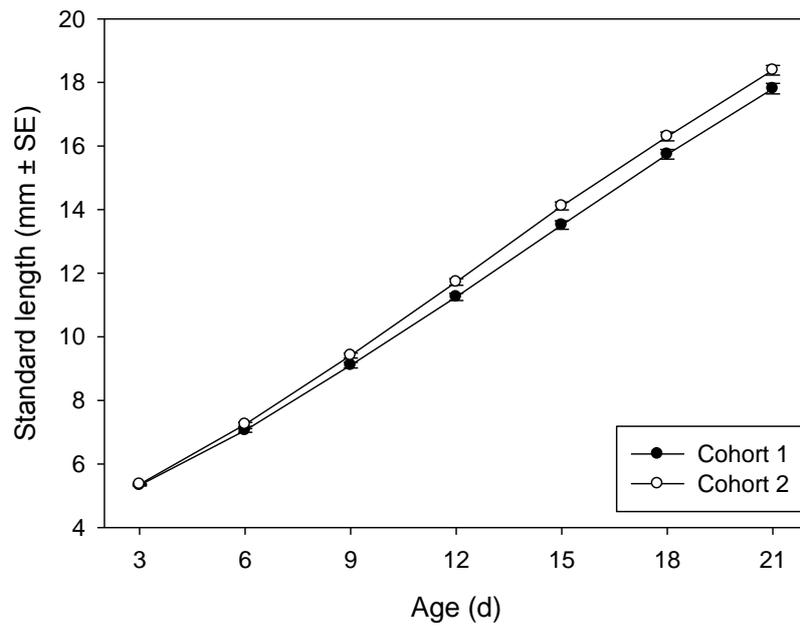


Figure 9. Back-calculated size-at-age (mm) averaged over 3 d intervals of *S. delicatulus* collected during December, 2006 in Lizard Island for cohort 1 (n = 68) (black circles) and cohort 2 (n = 67) (white circles). Error bars represent standard errors

Table 3. Comparison of back-calculated size-at-age (mm) between two cohorts for each of three age points of *S. delicatulus* collected by light traps in December at Lizard Island, GBR

Age (d)	Source	df	MS	F	<i>p</i>
3	Cohort	1	0.000	1.0	0.328
	Error	133	0.000		
6	Cohort	1	0.004	5.1	0.026
	Error	133	0.001		
9	Cohort	1	0.086	6.8	0.010
	Error	133	0.013		
12	Cohort	1	7.431	9.6	0.002*
	Error	133	0.772		
15	Cohort	1	0.223	11.2	0.001*
	Error	133	0.020		
18	Cohort	1	0.008	8.1	0.005*
	Error	133	0.001		
21	Cohort	1	0.007	7.0	0.009
	Error	133	0.001		

* significant difference at the $p < 0.007$ level

Within-cohort analysis revealed significant differences in size-at-age among the three samples of cohort 1 (Wilk's lambda = 0.805, $p = 0.034$); however, one-way ANOVAs did not detect significant differences in size-at-age at any time interval (Figure 10a). Cohort 2 also exhibited significant differences among the three samples (Wilk's lambda = 0.998, $p < 0.001$) but one-way ANOVAs failed to detect any differences in size-at-age at any time interval (Figure 10b).

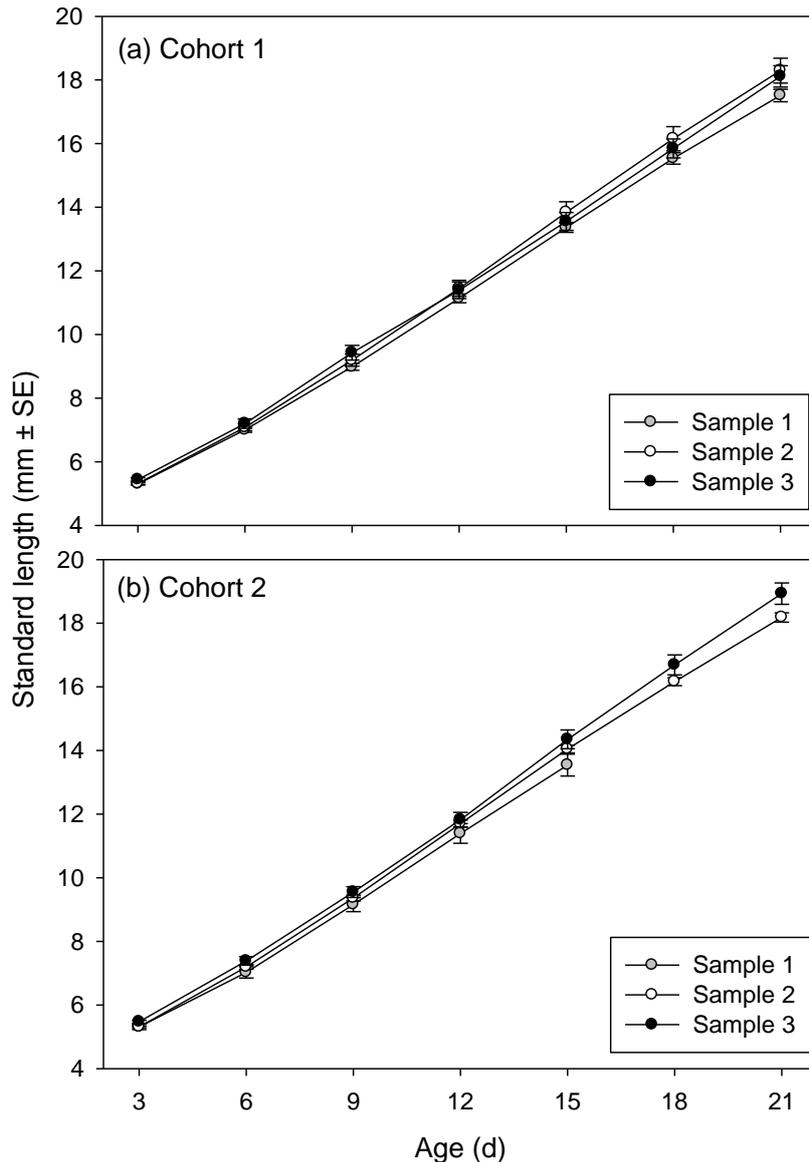


Figure 10. Back-calculated size-at-age for 3 samples averaged over 3 d intervals of (a) cohort 1 and (b) cohort 2 of *S. delicatulus* collected during December, 2006 in Lizard Island, GBR. Error bars represent standard errors

Larvae from the fast-growing cohort underwent slightly stronger selective mortality (mean $SI_{\text{Cohort 2}} = 0.52$) than individuals from the slow-growing cohort (mean $SI_{\text{Cohort 1}} = 0.45$). Although size-selection was stronger in the fast-growing cohort, it exhibited a more stable pattern throughout the period analysed, whereas selection in the slow-growing cohort fluctuated markedly (Figure 11).

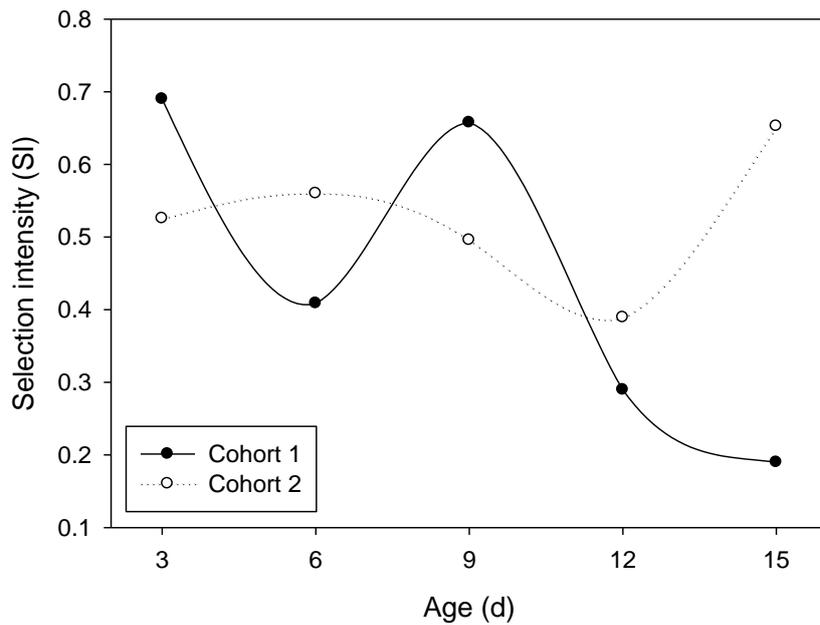


Figure 11. Size selection intensity (SI) over 3 d intervals of cohort 1 and cohort 2 of *S. delicatulus* collected during December, 2006 in Lizard Island, GBR

3.3.2 Environmental influences on growth

Growth of *S. delicatulus* in cohort 1 was influenced by all of the environmental factors measured. Wind-induced turbulence displayed a highly significant negative relationship with larval growth, while water temperature and Chl-*a* were positively correlated, although these factors accounted for only 10% of the variance in growth (Table 4a). In cohort 2, temperature was the only environmental factor that showed a significant, positive correlation with larval growth, explaining 21% of the variance in growth (Table 4b).

Table 4. Linear mixed effects models that examined the effects of temperature, Chl-*a* and turbulence on growth of (a) cohort 1 and (b) cohort 2 of *S. delicatulus* collected by light traps in December at Lizard Island, GBR. SE is standard error. Only significant variables are included

(a) Cohort 1

	Estimate ± SE	t(df)	<i>p</i>
Intercept	-0.67 ± 0.42	-1.58 (1337)	0.115
Temperature	0.05 ± 0.02	3.15 (1337)	0.002
Turbulence	-7.71 ± 1.65	-4.66 (1337)	<0.0001
Chlorophyll- <i>a</i>	0.08 ± 0.03	2.46 (1337)	0.014

Adjusted $r^2 = 0.10$

(b) Cohort 2

	Estimate ± SE	t(df)	<i>p</i>
Intercept	-5.20 ± 0.44	-11.86 (1403)	<0.0001
Temperature	0.22 ± 0.02	13.39 (1403)	<0.0001

Adjusted $r^2 = 0.21$

3.3.3 *Otolith asymmetry*

Otolith area, length, circularity and descriptors 2, 4, 8 - 10, 11 and 13 - 20 displayed size-dependence; this was corrected by dividing trait asymmetry over trait size, $|R - L| / (R + L) / 2$ (Palmer and Strobeck 2003).

A one-sample t-test showed significant departures from zero in otolith rectangularity and distributions of descriptors 5, 7, 11, 14, 16 and 17. These attributes were thus excluded from further analyses. All kurtosis values were smaller than zero and visual inspection of the remaining attributes showed that they were normally distributed. Finally, significant differences in the interaction variance (Side*Individual) indicated that ME did not affect the values of FA (Palmer and Strobeck 2003).

FA values of all five morphometrics and Fourier descriptors were higher in otoliths from individuals of the first than the second cohort. ANOVA detected significant differences in circularity ($F_{1,118} = 12.457, p = 0.001$), perimeter ($F_{1,118} = 10.987, p = 0.001$) and descriptor 3 ($F_{1,118} = 10.463, p = 0.002$) FA among cohorts (Figure 12).

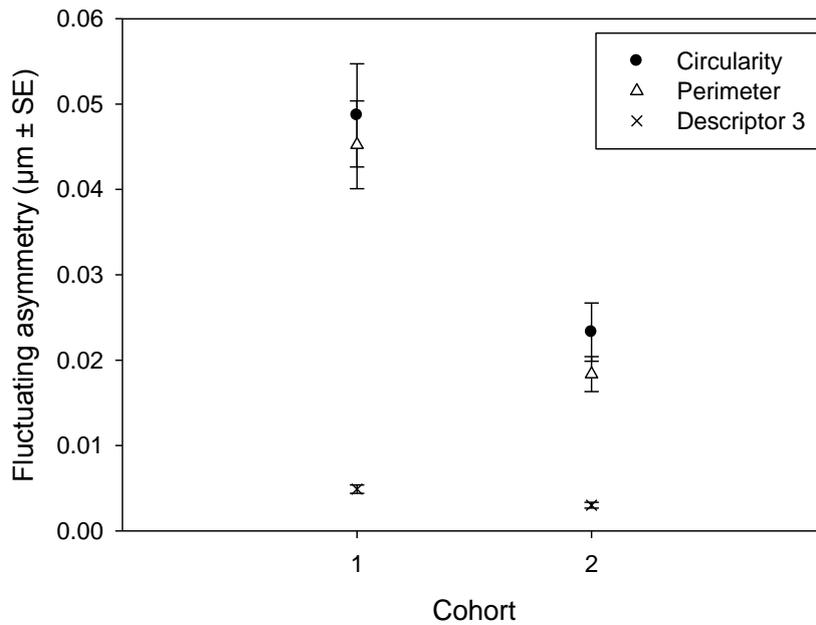


Figure 12. Mean FA (μm) of otolith circularity (black circles), perimeter (white triangles) and Fourier shape (crosses) from cohort 1 ($n = 61$) and cohort 2 ($n = 59$) of *S. delicatulus* collected during December, 2006 in Lizard Island, GBR. Error bars represent standard errors. Only significantly different morphometric variables are included

There were significant differences in FA of descriptor 6 ($F_{2,58} = 4.649, p = 0.013$) among samples of cohort 1 (Figure 13). Tukey's tests distinguished significant differences in FA of descriptor 6 between samples 1 and 3 ($p = 0.011$).

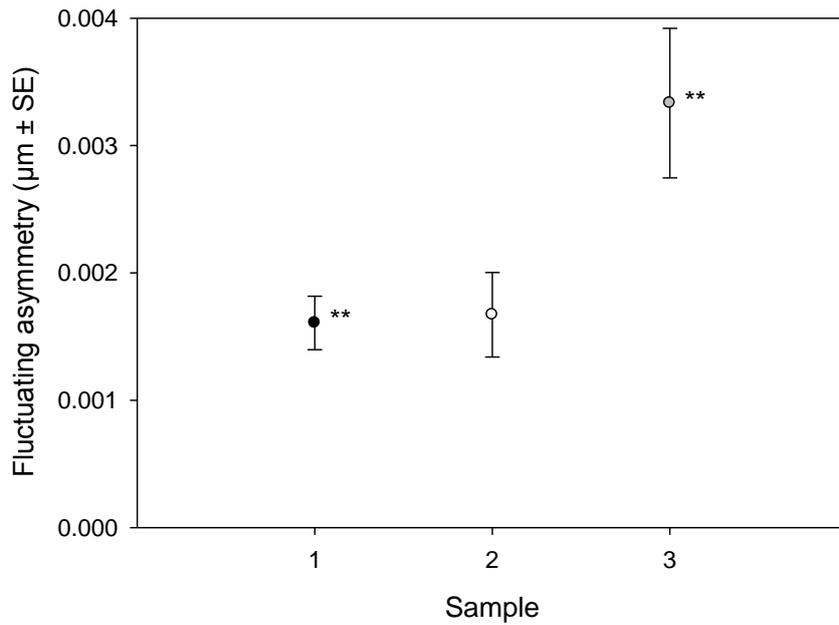


Figure 13. Mean FA (µm) of descriptor 6 from samples on 17th December (n = 25) (black circles), 23rd December (n = 21) (white circles) and 29th December (n = 15) (grey circles) of cohort 1 of *S. delicatulus* collected during December, 2006 in Lizard Island, GBR. Error bars represent standard errors. **significant difference at $\alpha = 0.017$

In cohort 2, significant differences were found for otolith circularity ($F_{2,56} = 7.021$, $p = 0.002$), descriptors 2 ($F_{2,56} = 5.913$, $p = 0.005$), 3 ($F_{2,56} = 4.844$, $p = 0.011$) and 8 ($F_{2,56} = 6.798$, $p = 0.002$) among successive samples (Figure 14). Tukey's tests revealed that FA of otolith circularity differed between samples 1 and 2 ($p = 0.002$), while FA of descriptor 2 from sample 1 differed from samples 2 and 3 ($p = 0.005$ and $p = 0.011$ respectively); descriptor 3 differed between samples 1 and 2 ($p = 0.013$); and descriptor 8, differed between sample 1 and samples 2 and 3 ($p = 0.002$ and $p = 0.014$ respectively).

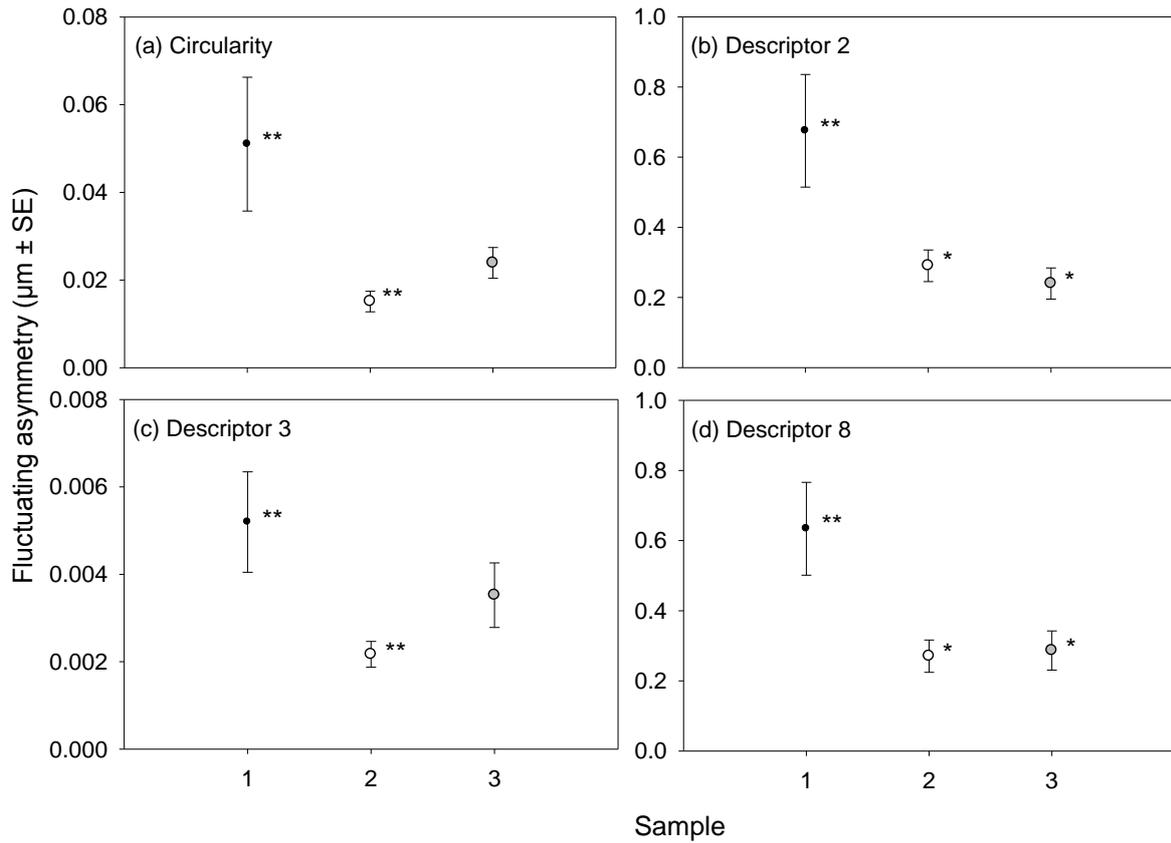


Figure 14. Mean FA (µm) of (a) circularity, (b) descriptor 2, (c) descriptor 3 and (d) descriptor 8 from samples on 17th December (n = 15) (black circles), 23rd December (n = 25) (white circles) and 29th December (n = 19) (grey circles) of cohort 2 of *S. delicatulus* collected during December, 2006 in Lizard Island, GBR. Error bars represent standard errors. **significant difference at $\alpha = 0.017$

3.3.4 FA and body condition

Fluctuating asymmetry in otolith circularity was the only explanatory variable contained in the first principal component for both cohorts, retaining 99% of the information contained in the original data and for this reason was included in the LME against body condition. Linear mixed-effects model revealed a strong ($\text{AdjR}^2 = 0.98$) negative correlation between FA in otolith circularity of cohort 1 and HSI (Table 5). For cohort 2 there were no significant correlations between FA and any measure of body condition.

Table 5. Linear mixed effects models that examined the effects of body condition on otolith circularity FA of cohort 1 of *S. delicatulus* collected by light traps in December at Lizard Island, GBR. SE is standard error. Only significant variables are included

	Estimate \pm SE	t(df)	<i>p</i>
Intercept	1.60 \pm 0.32	5.01 (62)	<0.0001
HSI	-0.55 \pm 0.23	-2.36 (62)	0.021

Adjusted $r^2 = 0.98$

3.4 Discussion

Size-selective mortality exhibited a very fluctuating pattern in the slow-growing cohort during the first 15 d after hatching. Slow growth is often seen as the cause of size-selection during the larval stage of tropical clupeids (Meekan et al. 2006a, Durieux et al. 2009). Since growth is the result of metabolic processes, individuals that can attain faster growth during the larval period are assumed to have better body condition (Hoey & McCormick 2004). Fast growers can also undergo the vulnerable larval stage faster than their slow-growing conspecifics. Thus, large variations in the selection intensity of the slow-growing cohort could be due to extended larval period, which gives a window for stronger selection due to increased predation pressure (Takasuka et al. 2003). It is also possible that slow-growers are removed from the population during days of high environmental stress, when they cannot cope with the energy demands required to overcome events such as food scarcity or varying temperature regimes (Buckley et al. 2006; Plaza and Ishida 2008). Thus, the combination of abiotic and biotic environmental factors could have made slow-growing larvae more prone to mortality as they spend more time in this vulnerable stage (Leggett and Deblois 1994).

Growth of *S. delicatulus* from cohort 1 was negatively correlated with wind-induced turbulence and positively correlated with temperature and Chl-*a* concentration. It is generally accepted that high turbulence can reduce prey encounter rates and larval growth, leading to mortality by starvation (Mackenzie and Leggett 1991). This factor can also induce mortality in small larvae due to the higher energetic cost of swimming in turbulent water (Oshima et al. 2009). Hence, wind-induced turbulence could have hindered the swimming ability of small, slow-growing larvae from cohort 1 and restricted their foraging activity. As a result, these individuals experienced lower body condition than larvae from the faster-growing cohort. The high correlation between HSI and otolith FA in larvae from cohort 1 could indicate that poor body condition led to higher levels of otolith FA in this cohort. Some authors have pointed out that otolith FA is more likely to be correlated to body condition after it has been altered by a long period of nutritional stress (Grønkjær and Sand 2003). Studies performed during an extended period of time have clearly shown the effects of nutritional stress on otolith FA. For example, Kristofersen & Magoulas (2009) observed that otolith FA of European anchovy inhabiting oligotrophic waters was negatively correlated to size-at-age and that larvae exhibited slower growth rates than individuals located in a more productive area. Somarakis et al. (1997) compared otolith FA of European anchovy larvae collected during two consecutive years. During the year of higher zooplankton abundance, larvae exhibited larger size-at-age, faster growth and lower levels of otolith FA. The authors related these interannual differences in otolith asymmetry to nutritional stress. Thus, low feeding regimes could have caused higher otolith FA in slow-growing *S. delicatulus*, which were more likely to be food limited than fast-growing conspecifics.

Otolith asymmetry in cohort 1 only revealed significant differences among samples in otolith descriptor 6, suggesting that slow-growing individuals were not able to compensate for otolith FA. While small asymmetries in otoliths are unlikely to create a disadvantage, the

functional cost of being asymmetric rises exponentially with trait size (Møller and Swaddle 1997). In fish, it is known that otolith asymmetry can impair acoustic performance, navigation and location of suitable habitats, among other behaviours (Lychakov and Rebane 2005; Gagliano et al. 2008). Conversely to cohort 1, levels of FA of the fast-growing cohort (cohort 2) were highest during the early and mid larval stage (sample 1), and tended to decline through time. This implies that these fish had the resources to compensate for asymmetry at least early during their development (Polak 2008). This ability may be critical to survival as studies in other species have shown that the costs of asymmetry are greater as the trait increases in size (Swaddle and Witter 1997).

Correlations between growth and the environment showed that the slow-growing cohort was influenced by all environmental factors considered in the model. Yet, it is impossible to point to the moment at which environmental stress initiated otolith asymmetry in *S. delicatulus*. The “compensatory growth” hypothesis can help to elucidate this problem. It states that initial asymmetries may be randomly determined, and as growth processes continue, we may expect asymmetries to decrease since compensational growth between the two sides will act to restore trait symmetry (Swaddle and Witter 1997). Under this hypothesis, asymmetry can oscillate through time and signals recent perturbations (Kellner and Alford 2003). However, initial otolith asymmetry in fish may not be random but dependent on maternal effects. It has been demonstrated that maternal stress can influence developmental stability of offspring (Gagliano and McCormick 2009). Nevertheless, if the compensatory growth hypothesis operates over *S. delicatulus*, increased otolith FA in larvae could have been the result of recent environmental stress. This response to asymmetry through ontogeny has been observed in birds. A study of domestic chickens showed that after short term perturbations individuals can increase growth of the smaller side of a trait and decrease growth of the larger side (Kellner and Alford 2003). Therefore, only *S. delicatulus*

in good body condition would have been able to allocate energy to compensate for differences between left and right otoliths, resulting in lower otolith FA at later ontogenetic stages.

In summary, the highly fluctuating size selection experienced by individuals of cohort 1 is consistent with the prediction that slow growth over extended periods drives stronger size-selective mortality. These slow-growing individuals may have been more susceptible to changing environmental conditions and exhibited lower body condition. A lack of energy reserves may have hampered their ability to compensate for asymmetric otoliths, and their otolith FA was subsequently accentuated with ontogeny. Our results suggest that low nutritional state, possibly caused by reduced feeding regimes, appeared to be the main factor driving development of otolith asymmetry and selective mortality of young *S. delicatulus*.

3.4.1 Conclusions

S. delicatulus underwent size-selective mortality during the larval stage. Smaller individuals also exhibited slow growth during the larval stage and were more vulnerable to environmental variability. In addition, small, slow-growing individuals exhibited lower body condition and higher levels of otolith FA than faster-growing conspecifics. Nutritional stress and reduced body condition may have hampered the ability of individuals to compensate otolith asymmetry through ontogeny.

4 General Discussion

In this thesis I studied the nature of selective mortality based on two traits (size and growth) during early life stages of *S. delicatulus* in the northern Great Barrier Reef. I also explored the extent of the influence of three main environmental factors, temperature, food abundance and wind-induced water turbulence on larval growth and size. Subsequently, I investigated the effects of environmental stress on body condition in order to elucidate the link between larval condition and survival. I found strong evidence that larval *S. delicatulus* underwent selective mortality, revealed by differences in growth and size among larvae from successive samples of the same cohort. However, selection removed larger individuals from the population in some cohorts and smaller individuals in others. Despite this temporal inconsistency, survivors exhibited (on average) faster growth rates during the larval stage, suggesting that overall, growth underlies the selective pressure in *S. delicatulus* larvae. More interestingly, slower-growing larvae exhibited lower body condition and were more susceptible to environmental stress than faster growing fish. This increased environmental stress was expressed through enhanced developmental instability, as evidenced by otolith FA.

Size-selective mortality exhibited an inconsistent trend during the larval stage of *S. delicatulus*. While in some cohorts larger individuals were removed from the population throughout the larval stage, in other cohorts selection removed smaller individuals at the beginning of the larval stage and then shifted towards larger individuals during the mid-larval stage. These conflicting results reflect the dynamic nature of selective mortality, which can change strength and direction through ontogeny (Gagliano et al. 2007b; Johnson and Hixon 2010). Our results contrast with those of a closely-related species, *Spratelloides gracilis*, for which the bigger-is-better mechanism governs patterns of selective mortality during early life stages (Meekan et al. 2006a; Durieux et al. 2009). This is not surprising, since patterns of

selective mortality are highly variable even within the same locality, as they depend on both biotic (e.g. individual behaviour and predator-prey interactions) and abiotic factors (e.g. temperature, water turbulence, etc) (Biro et al. 2006; Gagliano et al. 2007b; Johnson and Hixon 2010). It is possible that predator-prey interactions account for the inconsistency of our results. Recent studies suggest that in some cases, selective mortality depends on the predator community, rather than on the prey attributes (Holmes and McCormick 2010). Hence, while some species will show preference for smaller larvae, others will prey on larger individuals (Takasuka et al. 2004b; Holmes and McCormick 2009).

In contrast, growth-selective mortality operated in all cohorts of *S. delicatulus* during the larval stage. Slow growth has been attributed to reduced body condition, which can directly affect larval swimming ability and anti-predatory responses (Booth and Beretta 2004) thus, larvae with poor body condition can be selectively removed by predators in preference to larvae in better condition (Sogard 1997). However, as mentioned above, the species-specific nature of predator-prey interactions needs to be considered. For example, it has been demonstrated that small predators were selective for slow-growing Japanese anchovy larvae (*Engraulis japonicus*), whereas larger predators seemed to prey on larvae with both slow and fast growth indiscriminately (Takasuka et al. 2003; Takasuka et al. 2007). Thus, the idea that larvae in better body condition successfully escape from predatory attacks may only apply when individuals encounter small predators that cannot afford the extended energy demand required to catch fast-swimming prey. In the present study, no measure of body condition was considered for individuals in Chapter 2, thus it is not possible to conclude that smaller individuals survived due to better body condition; however, there is no doubt that fast growth promoted larval survival of *S. delicatulus*.

Consistent results were found when examining the effect of the environment on *S. delicatulus* growth and size during early life. While temperature and Chl-*a* revealed a positive

relationship with growth, turbulence was negatively correlated to this trait. It is widely accepted that growth of small pelagics is intimately related to environmental factors and generally periods of increased water productivity match those of fast larval growth (Alemany et al. 2006). Larval clupeids in the Mediterranean show a preference for surface layers of the water column with higher zooplankton abundance, as this favours growth and survival (Olivar et al. 2010). Thus, most studies of clupeids in temperate systems report positive effects of primary productivity on larval growth (Garcia et al. 1998; Catalan et al. 2006; Baumann et al. 2007; Schismenou et al. 2008; Olivar et al. 2010). Similar results describing the positive influence of water temperature on the early growth have been observed for *S. gracilis* in Western Australia (Durieux et al. 2009). Contrarily, increased wind stress could affect larval growth by driving larvae above their tolerance limits of water turbulence (Alemany et al. 2006).

Overall, the three environmental factors (temperature, wind stress and Chl-*a*) included in the model influenced slow-growing more than fast-growing larvae. Additionally, these slow-growing fish also exhibited lower body condition. A similar link between reduced growth, body condition and vulnerability to environmental factors was found in European sardine, *Sardina pilchardus*, larvae (Catalan et al. 2006) where indices of body condition based on muscle and cartilage degradation showed that 80% of pre-flexion larvae that were slow-growing were undergoing nutritional stress. Moreover, body condition of these larvae was also highly correlated to environmental factors (Catalan et al. 2006) as was the case in my study.

Slow growth rates and the associated poor body condition might have hindered individuals from buffering environmental variation experienced during the first days after hatching, which was consequently expressed as increased developmental instability. I demonstrated that higher fluctuating asymmetry in *S. delicatulus* otoliths was strongly

correlated to body condition in the slow-growing cohort. In earlier studies, attempts to link body condition and developmental instability has provided conflicting results among species and life stages (Gagliano and McCormick 2004; Panfili et al. 2005; Fey and Hare 2008; Kristoffersen and Magoulas 2009). It could be argued that if larvae aim to minimize the time spent in the most vulnerable (i.e. smallest) phases, they would allocate all their energy to somatic growth, instead of storing it. Therefore, relationships between body condition and fluctuating asymmetry would be unlikely to have any biological importance. Earlier work shows that clupeids do not store lipids until they finish developing all swimming structures and can display enhanced anti-predatory responses (Díaz et al. 2009). For larvae of the *Spratelloides* genus, all bony and swimming structures are completely developed at around 20 d of age (Leis and Carson-Ewart 2000). In my study, the age range of individuals included in the regression between body condition and otolith fluctuating asymmetry was from 15 to 44 d old, meaning that most of the individuals were able to allocate energy reserves to storage.

The results of this study clearly show that slow-growing fishes are more vulnerable to varying environmental conditions. However, I could not identify the environmental factors responsible for the differences in growth rates in Chapter 3. Cohorts were sampled during the same month, thus, even when individuals differed in hatch dates, they encountered similar temperature, wind stress and Chl-*a* concentration through the first 21 days after hatching. This implies that there must be other environmental factors responsible for differences in growth rates among cohorts. Factors such as nitrates, depth and salinity have been reported to account for 50% of the variance abundance of eggs and larvae of European sardine and anchovy in the Mediterranean Sea, as river runoff alters seawater salinity and transports nutrients, influencing larval distribution (Zarrad et al. 2008; Catalan et al. 2010). In tropical systems, salinity, rain and solar radiation have been found to account for the variability in

growth rates and pelagic larval duration of several reef fishes (Wilson and Meekan 2001,2002; Bergenius et al. 2005).

The differences in growth rates observed between cohorts sampled in the same month can also be due to maternal effects. Mothers in good condition are able to allocate more energy to their eggs, promoting survival during the embryonic phase, an advantage that can be carried-over to subsequent life stages (Vigliola and Meekan 2002; Gagliano and McCormick 2007; McCormick and Gagliano 2009). Conversely, maternal stress can be translated into reduced developmental stability of offspring (Gagliano and McCormick 2009). For example, high levels of pectoral and pelvic fin asymmetry in offspring of farmed Atlantic salmon, *Salmo salar*, were observed when mothers were exposed to high concentrations of cortisol and eggs were incubated at higher than normal temperature (Eriksen et al. 2008). Since otolith asymmetry can start developing during the embryonic phase (Lychakov et al. 2006), environmental stress experienced by mothers may also generate otolith asymmetry in the progeny (Gagliano and McCormick 2009; McCormick and Gagliano 2009). Embryos of the tropical damselfish *Pomacentrus amboinensis* originated from clutches exposed to high cortisol levels (simulating maternal stress) exhibited increased otolith asymmetry and higher metabolic rates (Gagliano and McCormick 2009). High concentrations of cortisol at the end of the embryonic phase were not detrimental to hatchlings, as this hormone stimulates a more efficient conversion of yolk-reserves into somatic growth during endogenous feeding (Gagliano and McCormick 2009). However, the effect of stress-related hormones on developmental stability does represent a disadvantage through increased otolith asymmetry (Gagliano et al. 2008; Gagliano and McCormick 2009). As mentioned above, otolith asymmetry alters swimming behaviour (Helling et al. 2003), which can reduce foraging success and directly influence growth.

4.1 Conclusions

Cohort analysis showed that selective mortality removed slow-growing *S. delicatulus* larvae from the population, despite them being larger-at-age. At the same time, slow growth made individuals more vulnerable to varying environmental conditions, namely temperature, food availability and wind-induced turbulence, causing reduced body condition. The combined effects of slow growth and low body condition could have hindered individuals from buffering environmental noise during the larval stage. This gave rise to increased otolith asymmetry, which was carried over subsequent ontogenetic stages. In conclusion, these results highlight the importance of fast growth during early life stages and the role of the environment on shaping selective mortality of *S. delicatulus*.

4.2 Future directions

Field studies may provide strong evidence of the processes driving larval growth and mortality at a certain period of time. However, when linking the influence of the environment to larval growth and size, results can be obscured by factors that were not included in the models. Moreover, it is difficult to extrapolate results obtained from field studies and draw generalizations about the main factors underlying larval growth, as interannual variation of environmental conditions and covariance between two or more factors can affect the outcome. Therefore, laboratory experiments are needed to isolate and disentangle the effects of the environment on growth and selective mortality. Unfortunately, *S. delicatulus* experiences extremely high mortality under confinement and laboratory rearing may represent a source of stress itself. Thus, new methods that do not involve maintaining the species in captivity should be considered.

Recently, fish biologists have used a technique derived from *dendrochronology* (tree ring studies) to characterize how the influence of the environment varies among individuals

in a population (LeBreton and Beamish 2000; Black 2009). This technique is called *cross-dating* and it is based on the observation that variability in environmental signals are recorded in growth records and act effectively as natural markers in time series of otolith growth (Black et al. 2005). Cross-dating correlates time series of otolith growth (in this case daily increments widths) among individuals and then relates the resulting master biochronology to environmental factors controlling growth during early life stages (Black et al. 2005). Since correlations tend to be stronger when the environment is a very limiting factor (Fritts 1976), the cross-dating technique allows researchers to identify periods of environmental stress and to then ascribe them to variability in environmental factors.

Better knowledge of developmental instability and the efficacy of otolith FA as a signal of environmental stress are also required. Since evidence shows that otolith asymmetry is conspicuous only under extreme nutritional stress (Parsons 1990; GrønkJær and Sand 2003), better measures of body condition are needed. RNA/DNA ratios have been increasingly used as a reliable indicator of condition in a wide range of taxa (Olivar et al. 2009), however, these are indicative of short-term starvation (Clemmensen 1987) and, if developmental instability manifests only under severe environmental stress, the RNA/DNA ratios would probably fail to detect significant correlations between otolith FA and body condition. Long-term indices of condition, such as qualitative measure of muscles degradation, could be more efficient to detect severely-starved larvae (Catalan et al. 2006).

Further research on the repercussion of asymmetric otoliths on early life stages of tropical pelagic fishes is also needed. Studies of the effects of otolith asymmetry on demersal fishes with a pelagic larval stage have suggested that asymmetrical otoliths hamper the ability of individuals to locate suitable settlement habitats by interfering with their acoustic perception (Gagliano et al. 2008). However, *S. delicatulus* spends its entire life span in the pelagic realm and while it is expected that swimming ability of individuals with asymmetrical

otoliths is limited, the direct consequences of this need to be explored. It is possible that swimming behaviour and thus, activities such as foraging, predator avoidance and schooling are negatively affected by otolith asymmetry (Popper and Lu 2000; Helling et al. 2003; Lychakov and Rebane 2005). Laboratory experiments may help to determine the primary skills affected by otolith asymmetry, however, logistics, especially the ability to hold these pelagic fishes within adequate space, could represent a major challenge.

Finally, an area that needs further study is the variation of FA with ontogeny, as there is uncertainty about the ability of fish to adjust otolith symmetry through life. While some studies suggest that larvae are able to reduce the asymmetry of otoliths when in benign environments (Kellner and Alford 2003; Gagliano and McCormick 2004), others argue that asymmetries developed during early life stages cannot be reversed later in life (see Swaddle & Witter 1997). In the present study, larvae exhibited greater otolith FA than juveniles and adults. However, the nature of the experimental design did not allow me to draw conclusions on whether the reduced asymmetry I observed in subsequent stages was due to the ability of individuals to reduce asymmetry or due to the mortality of larvae with asymmetrical otoliths.

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6 Appendices

Appendix 1

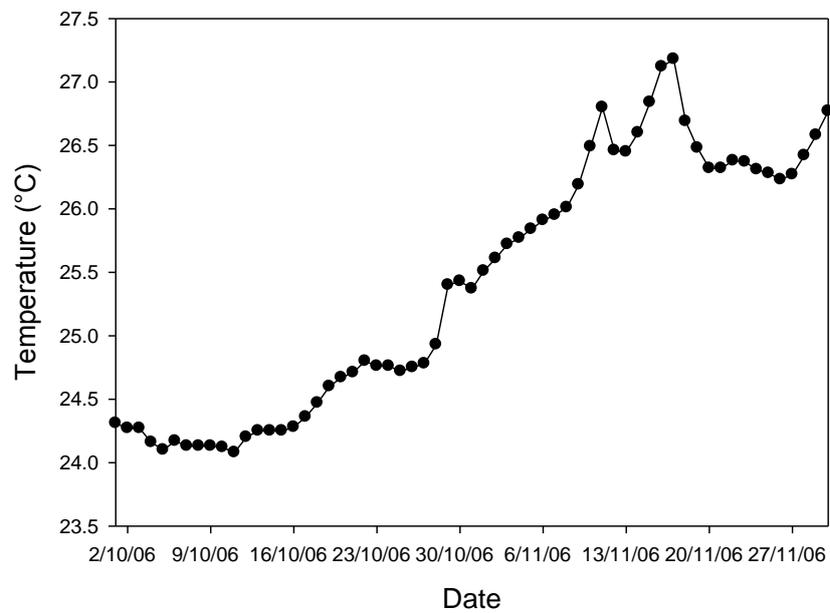


Figure A1. Water temperature experienced by larval *S. delicatulus* collected in Lizard Island, GBR during November and December, 2006.

Appendix 2

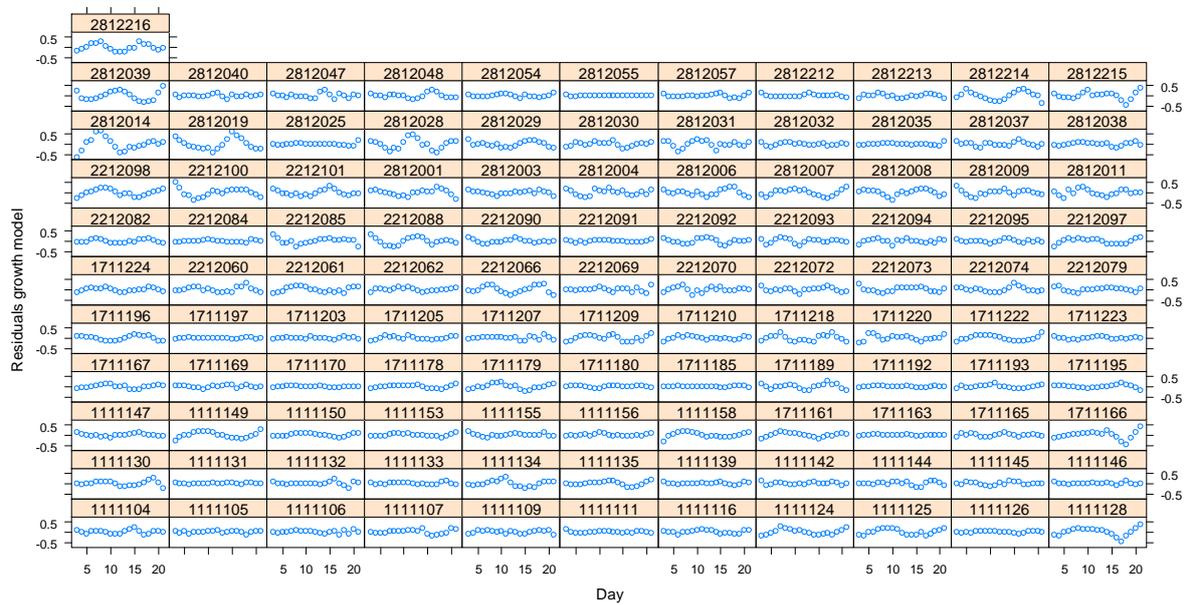


Figure A2a. Size-at-age between 3 d to 21 d after hatching of *S. delicatulus* collected in Lizard Island, GBR during November and December, 2006.

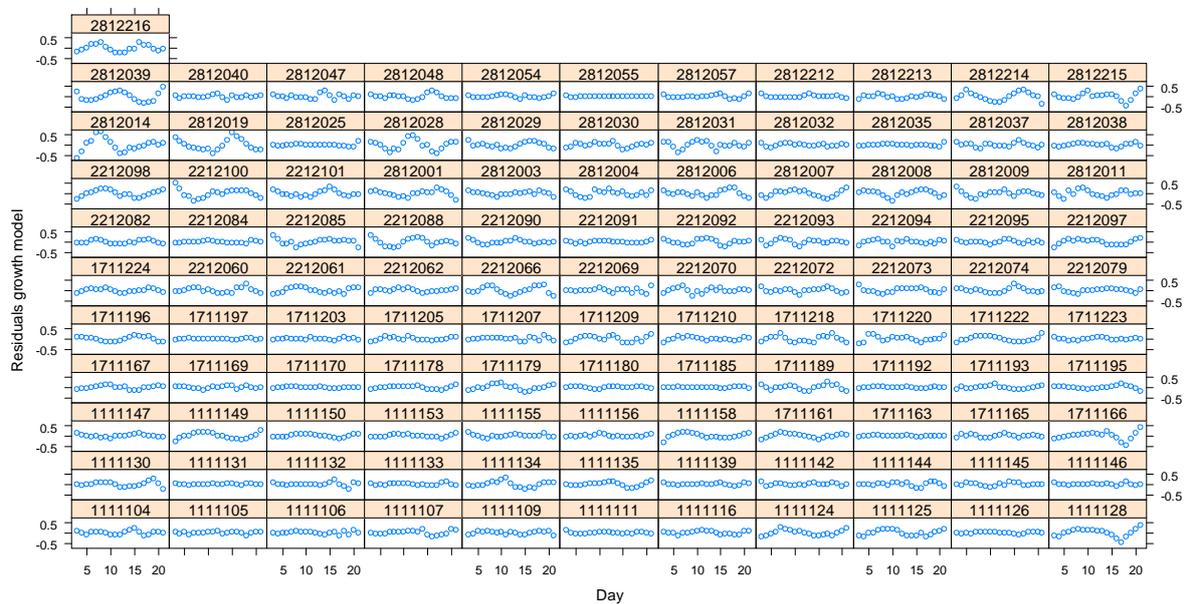


Figure A2b. Detrended size-at-age between 3 d to 21 d after hatching of *S. delicatulus* collected in Lizard Island, GBR during November and December, 2006.