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Interannual variation in larval abundance and growth in snapper *Chrysophrys auratus* (Sparidae) is related to prey availability and temperature

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ABSTRACT: Fish have complex life cycles that contribute to interannual variability in recruitment. The growth–mortality hypothesis has received broad acceptance as a driver of recruitment variability, with cohorts comprised of fast-growing large-at-age larvae having high larval survival and subsequent juvenile recruitment. Long-term monitoring in Port Phillip Bay, Australia, suggests that snapper *Chrysophrys auratus* (Sparidae) experience high variation in juvenile recruitment, which is closely related to variation in larval abundance. Using a 6 yr data set of snapper larval abundance, we assessed whether growth rate-dependent effects on larval survival were a driver of recruitment variation. Mean daily growth rates, estimated from otolith daily rings, were positively correlated with larval abundances, with higher abundance in 3 of the 6 years characterised by both higher larval growth rates and increased 0-age survival. Daily growth trajectories diverged among higher and lower abundance years early in development. Increased availability of copepod nauplii prey and higher temperatures best explained the interannual variation in larval growth. Fast growth in years of higher larval abundance, and a link between prey production, temperature and fast larval growth, support the importance of the larval stage to recruitment dynamics of marine fish populations.

KEY WORDS: *Chrysophrys auratus* · Snapper · Larval growth · Otolith · Recruitment

INTRODUCTION

Understanding the factors driving population dynamics is a fundamental aim of ecology. This is especially challenging for organisms with complex life cycles, where individuals undergo ontogenetic transformation (metamorphosis), and often inhabit different environments (Wilbur 1980). Research on the larval characteristics (e.g. size, condition, growth rate) of these organisms, such as fishes, provides important information on the mortality processes of early life history stages and the subsequent impact on the abundance of adults (e.g. Jenkins & King 2006, Sponaugle et al. 2006, Fontes et al. 2011). For marine fishes, which are characterised by high fecundity and a pelagic larval stage with high mortality rates, even small changes in growth and mortality rates within the first weeks and months of development can result in orders of magnitude differences in juvenile abundance (Houde 1987).

Higher larval survival as a direct result of increased growth, mediated by size-dependent predation, is the basis of the growth–mortality hypothesis (Cushing 1975, Anderson 1988). The growth–mortality hypothesis is comprised of 3 distinct, but related, mechanisms (hypotheses): bigger is better, where larger-at-

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age larvae are less vulnerable to predation (e.g. Litvak & Leggett 1992, Leggett & DeBlois 1994); stage duration, where faster-growing larvae spend less time in the vulnerable larval stage (Chambers & Leggett 1987); and growth-selective mortality, where the growth rate of the individual larva may influence its probability of capture independent of size or developmental stage (Takasuka et al. 2003, 2007). The growth–mortality hypothesis and its 3 mechanisms have received broad acceptance in fisheries science, with large-at-age fish larvae and fast larval growth often associated with high survival and recruitment (e.g. Hare & Cowen 1997, Shima & Findlay 2002, Meekan et al. 2006). However, growth during the late-larval and juvenile stages (Campana 1996, Sim-Smith et al. 2012) may be more important for high recruitment success in some species, and previous studies have also found no relationship between fast growth in the early life stages and recruitment (van der Veer et al. 1994, Bailey et al. 1996, Ringuette et al. 2002, Oshima et al. 2010). As observed variability in larval growth can be driven by selective mortality, starvation, temperature and their interactions (Anderson 1988), a greater understanding of these mechanisms is crucial in linking early life history characteristics and subsequent recruitment success.

Prey availability (Cushing 1972, 1990) and temperature (Houde 1987) are considered the 2 most important underlying processes that influence variability in fish larval growth, while turbulence (Dower et al. 1998) and light availability (Buckley et al. 2006) are also thought to have an influence, albeit of lower importance. Prey availability and foraging success are considered important factors for reducing the probability of mortality by starvation and predation (Hare & Cowen 1997). However, few studies have clearly demonstrated a strong relationship between prey availability and larval growth and survival (Rilling & Houde 1999, Robert et al. 2007, Zenitani et al. 2007). This may be due to the difficulty in quantifying the prey field at an appropriate scale for larval fish, ontogenetic changes in both prey and predator behaviour, and stochastic environmental variability (Pepin 2004, Young et al. 2009). Despite these difficulties, a few recent studies have found strong links between foraging success and fast growth in marine fish larvae (Dower et al. 2009, Sponaugle et al. 2009, Robert et al. 2013), suggesting that knowledge of factors affecting larval growth can be key to understanding the link between the environment and fish production (Leggett & DeBlois 1994).

Temperature is often considered a more important influence on growth in temperate marine fish larvae than prey densities (Dower et al. 2002, Buckley et al. 2004, Munk 2007), although variability in larval growth rates has been found in the absence of temperature variability (Sponaugle et al. 2009), and the influence of temperature on larval growth may vary throughout ontogeny (Robert et al. 2009). Furthermore, correlative studies between environmental variables, such as temperature, and recruitment are common in the literature but can break down over time (reviewed in Myers 1998), which suggests there may be an indirect or spurious link between temperature and recruitment success (i.e. the same climatic factors influencing water temperature may also be influencing prey availability). Recruitment variability is most likely controlled by a combination of factors, such as a match/mismatch between larval occurrence and prey availability, temperature, predation, and larval retention in nursery areas (Houde 2008).

A temperate marine fish species with a long-term record of high recruitment variability is the snapper *Chrysophrys auratus* (Sparidae) (formerly *Pagrus auratus*) (Fowler & Jennings 2003, Hamer & Jenkins 2004, Zeldis et al. 2005). Recent research in Australia and New Zealand indicates that patterns of survival in the larval stage drive interannual recruitment variability in this species (Fowler & Jennings 2003, Zeldis et al. 2005, Hamer et al. 2010). In New Zealand and Australia, variation in snapper year-class strength was best explained by interannual variation in sea surface temperature (SST), with strong recruitment in years with a higher mean SST, faster larval growth, and decreased larval duration (Francis 1993, 1994, Fowler & Jennings 2003). However, the relationship between temperature and snapper recruitment was found to break down over time (Zeldis et al. 2005, Fowler et al. 2010), and, instead, a link between prey availability and snapper larval survival was found (Zeldis et al. 2005). To further explore the hypothesis that larval survival drives snapper recruitment patterns, we aimed to document whether years of high larval abundance were correlated with fast larval growth and recruitment success, and, if correlated, investigate how prey production and temperature may be driving this pattern. We used 6 years of samples from a 7 yr data set of snapper larval abundances in Port Phillip Bay (PPB), Australia, to (1) determine interannual variability in daily growth rates and growth trajectories and (2) test whether interannual variability in growth was related to variability in foraging success, prey availability and/or temperature.

MATERIALS AND METHODS

Ichthyoplankton sampling

For 7 yr (2004/2005 to 2010/2011), from late November to early January, ichthyoplankton were sampled at 7 areas within PPB (Fig. 1). This sampling period was chosen to overlap with the expected peak spawning period for snapper in PPB based on previous gonadosomatic index and larval abundance data (Jenkins 1986, Coutin et al. 2003). The pelagic larval stage of snapper is 18 to 28 d (Fowler & Jennings 2003), and settlement occurs at 10 to 12 mm standard length (SL) (Battaglene & Talbot 1992). These sampling methods have been previously described in Hamer et al. (2011). Briefly, on each sampling occasion, 5 randomly placed oblique plankton tows were conducted within each area, and each area was sampled on 2 occasions, late November/early December and late December/early January. Ichthyoplankton samples were collected using a 500 µm mesh plankton net with a circular mouth of 80 cm diameter. Each oblique tow consisted of a series of approximately 1.5 min pauses at each of the 5 depths as the net was lowered and again as it was retrieved. The 5 depths were just below the surface, ¼ of total depth below the surface, ½ of total depth below the surface, ¾ of total depth below the surface, and approximately 1 m above the bottom. Total tow duration varied depending on the depth, with a mean duration of 20 min. A flowmeter (General Oceanics model 2030) was used to determine the volume of water filtered in each tow. Material from the cod-end was filtered through a 500 µm mesh sieve and immediately preserved in 95% ethanol.

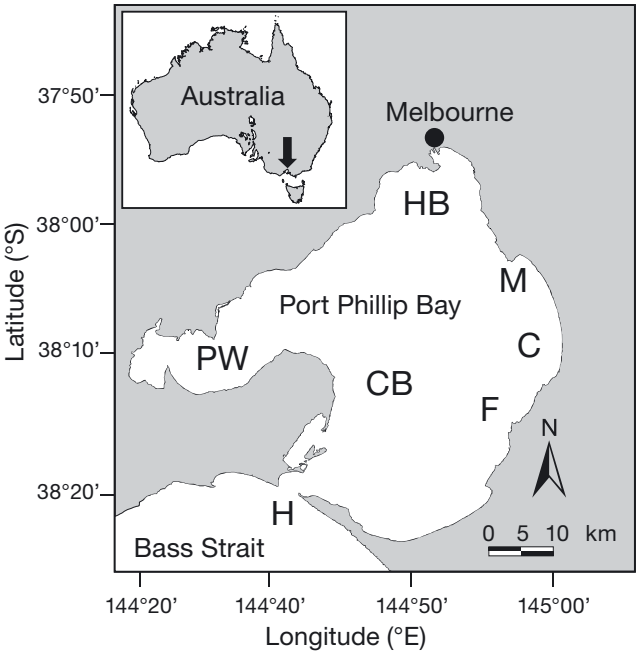

Fig. 1. Port Phillip Bay (PPB), Australia. Six years of ichthyoplankton sampling was conducted at the following 7 areas within the bay: Carrum (C), Central Bay (CB), Frankston (F), Hobsons Bay (HB), Mordialloc (M), Point Wilson (PW), and one area at the entrance of PPB, Port Phillip Heads (H)

Temperature

Daily temperature was obtained from a fixed temperature logger deployed at 3 m depth in the Hobsons Bay area by Fisheries Victoria Research Branch, Queenscliff Centre, Victoria, Australia.

Otolith preparation and analysis

Snapper larvae were identified based on the descriptions in Neira et al. (1998). The SL (tip of snout to tip of notochord) of all intact snapper larvae was measured to the nearest 0.1 mm under a dissecting microscope (Wild-Heerbrugg M5A) using an ocular micrometer. No adjustments to measured SL were made to account for preservation shrinkage, although this would be expected to be minimal in 95% ethanol (Theilacker 1980). However, all snapper larvae were sampled and preserved in the same way, so any shrinkage effects would be expected to be consistent across all years.

All snapper larvae from the samples were analysed, except when there were more than 20 snapper larvae in a sample. When this occurred, a sub-sample of 20 larvae was randomly chosen for otolith removal and gut analysis. A larva was placed in a drop of water on a glass slide and the otoliths were illuminated with cross-polarizing filters under a dissecting microscope (50× magnification) (Wild-Heerbrugg M5A). The otoliths were removed from the head of the larva, cleared of any adhering tissue, and left to air dry on a glass slide. A drop of immersion oil was added once the otoliths were dry.

We aimed to age and measure the growth rates of approximately 10 larvae from each of the 7 areas from each sampling time. However, in some years very few larvae were sampled at specific areas and sampling times, which prevented us from ageing 70 larvae from each sampling time. Larvae were chosen randomly from each size class (e.g. 2–3, 3–4, 4–5 mm SL) to ensure all sizes were represented. Daily increment peri-

odicity in snapper larval and juvenile sagittal otoliths has been previously validated (Francis et al. 1992, Fowler & Jennings 2003). Otolith radii and increment width were measured along the rostral axis under 1000× magnification using an oil immersion, compound microscope (Olympus BX-51) with an attached video camera. ImagePro Plus version 6.3 was used to count and measure the increments. If the percentage of standard deviation around the mean increment width from the 2 otolith measurements was greater than 10% and/or the increment counts were not the same, the otolith was aged and/or measured a third time. Using these criteria, 9 otoliths were rejected after a third reading. Furthermore, the diet and age data from 2008/2009 were not included in this study due to sample preservation issues, which affected otolith readability and measurement accuracy.

The ages of snapper larvae were calculated by adding 2 d to the number of increments counted. Previous studies found that the first increment forms at 1 and 3 d post hatch (dph), approximately when the larva starts feeding, and we used 2 d as a mean (Francis et al. 1992, Kingsford & Atkinson 1994, Fowler & Jennings 2003).

Diet and temperature

After the otoliths were removed, the larva was transferred to a drop of glycerol and the gastrointestinal tract was dissected out for dietary analysis using electrolytically sharpened tungsten needles under a dissecting microscope (Wild-Heerbrugg M5A). Each food item in the gut contents was identified to lowest possible taxonomic level.

We were interested in how prey availability and temperature affected interannual variability in recent growth of snapper larvae. Zooplankton were sampled concurrently with each ichthyoplankton tow from 2006 onwards using an 80 µm mesh net, so sampled snapper larvae were matched with sampled prey in both sampling times for 4 years of data (for more details see Murphy et al. 2012). The mean temperature experienced by each larva during its lifetime, based on temperature readings from Hobsons Bay, was averaged for each sampling time and year.

Data analysis

The mean daily growth rate was calculated for each year using linear regressions of larval size-at-age. Mean daily larval growth rates were used to determine if larval growth was related to larval abundances and/or 0-age recruit abundances.

Univariate repeated measures analysis of variance (ANOVA) was used to examine variability in mean otolith increment group widths (MIGW) among years. We pooled increment widths over 3 d as the majority of the sampled larvae were 9 d or younger. For this analysis only, we pooled for sampling time and area to include all 6 years in the analysis due to low sample sizes at specific areas and times in some years. In 2005/2006, snapper larvae were only sampled in the early sampling period at the Frankston area, and in 2010/2011, only one snapper larva sampled at one area (Carrum) in the late sampling period was old enough for repeated measures ANOVA. To examine the significant difference in MIGW among years, we considered each MIGW separately using ANOVAs followed by post hoc Tukey's tests.

Growth and its variance can increase with age; therefore, larval growth was detrended from age by calculating an index of growth performance that allowed for interannual comparisons of recent larval growth among different ages and with concurrently sampled zooplankton (Dower et al. 2002, Baumann et al. 2003, Robert et al. 2009). We used the formula:

$$DG_{ij} = (G_{ij} - G_j)\,\mathrm{SD}_j^{-1} \quad (1)$$

where DG_{ij} is the detrended growth of individual i at age j, G is otolith growth (increment width), and SD_j is the standard deviation of growth at age j (Robert et al. 2009). The last 3 d of full growth before capture were considered, excluding the last increment as it may not have fully formed (Dower et al. 2002, Robert et al. 2009), which meant that only larvae of 5 dph or older could be used. An ANOVA was used to compare the index of recent detrended growth, pooled by tow, among years.

Foraging success was measured as the biomass of ingested prey expressed as carbon. The main prey types in the snapper larval diet were calanoid nauplii (*Paracalanus* sp. and *Acartia* sp.), calanoid copepodites (*Paracalanus* sp. *Gladioferens inermis*, *Bestiola similis*), cladocerans (3 genera: *Podon*, *Evadne*, *Penilia*), and bivalve veligers (Murphy et al. 2012). The carbon content of prey categories were estimated using literature values for calanoid nauplii (Hygum et al. 2000), bivalve veligers (Omori 1969, Jespersen & Olsen 1982), calanoid copepodites (Hay et al. 1991, Mauchline 1998), cladocerans (Uye 1982), and fish larvae (Hislop & Bell 1987, Legendre & Michaud 1998). As the gut capacity of fish larvae increases with body size, the residuals of the linear regression of carbon content of ingested prey on

snapper larval length was calculated as a length-independent index of foraging success. An ANOVA was used to determine if foraging success, pooled by tow, varied among years. Linear regressions were used to determine if mean foraging success of larvae 5 to 14 dph was related to the index of recent detrended growth, and if foraging success of all larvae was related to temperature.

We were interested in how prey availability and temperature affected larval growth. Because of the limited age range of the snapper larvae sampled, we focused on the most common prey type in the diet, which were calanoid nauplii. We used 3 variables (temperature, calanoid nauplii, and an interaction term between calanoid nauplii and temperature) in single and multiple linear regressions to determine the best fit model that explained the interannual variation in the index of recent detrended growth for larvae 5 to 14 dph in 4 years of sampling (2006/2007, 2007/2008, 2009/2010, and 2010/2011), pooled by tow. 2004/2005 and 2005/2006 were not used in this analysis as there was no data on zooplankton availability for these years.

Assumptions of ANOVA were examined using box and normal probability plots, and MIGW, temperature, prey biomass (carbon content), and prey densities were log(x+1) transformed to satisfy the assumptions of homogeneity of variances. SYSTAT 12 was used for all statistical analyses.

Table 1. *Chrysophrys auratus*. Number of larvae sampled in each round of sampling and used in stomach and ageing analyses, and the area(s) where the majority of larvae were sampled. *C. auratus* larval abundances from 2004 to 2008 are published in Hamer et al. (2011). Round 1 was late November/early December and Round 2 was late December/early January. C: Carrum; F: Frankston; H: Port Phillip Heads; M: Mordialloc; PW: Point Wilson

Year	Round	No. larvae sampled	No. larval stomachs analysed	No. otoliths analysed	Area(s) with most snapper larvae	Larval abundances (× 1000 m^{-3})
2004/2005	1	521	368	40	F, M	34.0
	2	63	58	29	H	
2005/2006	1	31	31	30	F	1.0
	2	0	0	0		
2006/2007	1	63	63	31	F	4.4
	2	42	42	12	F	
2007/2008	1	213	147	42	M, C	15.0
	2	102	95	29	F	
2009/2010	1	258	148	44	PW	12.7
	2	46	43	20	F	
2010/2011	1	30	30	22	F	2.0
	2	5	5	4	M	
Total		1374	1030	303		

RESULTS

The ages of 303 snapper larvae from 6 years were measured (Table 1). There were 3 higher (H) larval abundance years (H2004/2005, H2007/2008, H2009/2010) and 3 lower (L) abundance years (L2005/2006, L2006/2007, L2010/2011) (Table 1). The majority of snapper larvae (72%) were sampled in the eastern areas of PPB (Carrum, Frankston, Mordialloc), which corresponds with the main suggested spawning areas for snapper, with the exception of H2009/2010, where the majority of larvae were sampled at Point Wilson (Hamer et al. 2011) (Table 1). The majority of snapper larvae were 3 to 12 dph (247 or 82%), which corresponds with the size range 2 to 6 mm SL (Fig. 2). The oldest larva was 21 dph sampled in L2010/2011(Fig. 2).

Larval growth

In this study, there was a positive linear relationship between snapper larval size and otolith radius (r^2 = 0.832, p < 0.001, n = 303). Mean daily growth rates (slopes of the length–age regression) varied between years: H2004/2005 and H2009/2010 had the highest daily growth rates of 0.30 mm d^{-1}, followed by H2007/2008 with 0.28 mm d^{-1}, L2006/2007 with 0.26 mm d^{-1}, and L2005/2006 and L2010/2011 with 0.25 mm d^{-1} (Fig. 2). There was a significant linear regression between larval abundance and larval mean daily growth rates (y = 0.046x + 0.232, r^2 = 0.863, p = 0.007, n = 6) (Fig. 3a), and a linear regression between larval abundance and 0-age recruit densities (y = 0.320x + 1.589, r^2 = 0.966, p < 0.001, n = 6) (Fig. 3b).

Univariate repeated measures ANOVA found a significant difference in individual MIGW (Increments 1–3, 4–6, 7–9) among years (Table 2). ANOVAs showed significant differences in MIGW among years in all increment groups (Table 3, Fig. 4a). Average increment widths in H2009/2010 were larger than the other 5 years (Fig. 4).

There was a significant difference in the index of recent detrended growth among years (ANOVA: $F_{5,99}$ = 9.557, p < 0.001). Post hoc Tukey's tests indicated that the

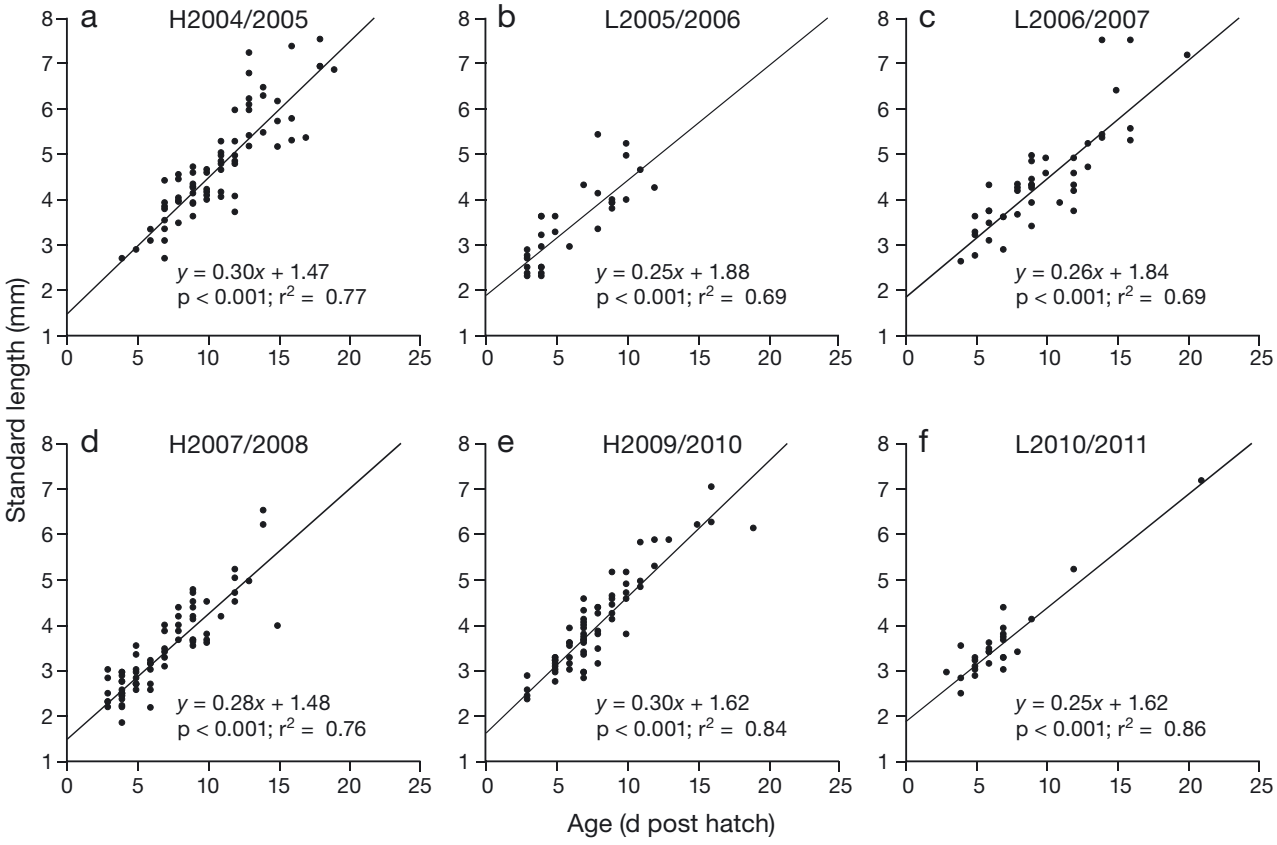

Fig. 2. *Chrysophrys auratus*. (a–f) Linear regressions of larval length at age for 6 year classes of snapper. Higher (H) and lower (L) recruitment years are indicated

index of recent detrended growth in H2004/2005 and H2009/2010 was significantly higher than in L2005/2006, L2006/2007, H2007/2008, and L2010/2011 (all $p < 0.001$) (Fig. 5).

Effects of temperature and prey on larval growth

There was a significant difference in foraging success (estimated carbon content of prey biomass) among years (ANOVA: $F_{5,110} = 2.670$, $p = 0.026$), and post hoc Tukey's tests indicated that foraging success was higher in H2004/2005 and H2009/2010 compared with L2006/2007 ($p < 0.003$). However, mean foraging success by tow was not related to the index of recent detrended growth. The relationship between foraging success and temperature, pooled by year, was marginally non-significant ($y = 38.379x + 20.489$, $r^2 = 0.634$, $p = 0.058$, $n = 6$) (Fig 5b).

Linear and multiple regression analyses indicated that interannual variability in the index of recent detrended growth was best explained by positive relationships with 2 independent variables: calanoid nauplii and temperature (Growth = 1.255Nauplii + 5.979Temperature – 8.940) (Table 4, Fig. 6). However, the relationship between recent detrended growth and temperature was marginally non-significant (Table 4). Temperature and calanoid nauplii densities were moderately correlated ($r = 0.436$).

DISCUSSION

Mean larval daily growth rates inferred from otolith microstructure were correlated with larval abundances, with snapper larvae from higher abundance years characterised by faster growth. Furthermore, larval abundance was strongly related to 0-age recruit densities. This suggests that interannual variability in larval growth influences survival rates of snapper larvae and recruitment strength, which supports the 'bigger is better' hypothesis. Similar to our study, previous studies have found that fast-growing members of a cohort are more likely to survive and contribute to recruitment (Meekan & Fortier 1996, Bergenius et al. 2002, Jenkins & King 2006, Robert et al. 2007, Fontes et al. 2011). But the crucial life stage for growth and survival in marine fish varies between

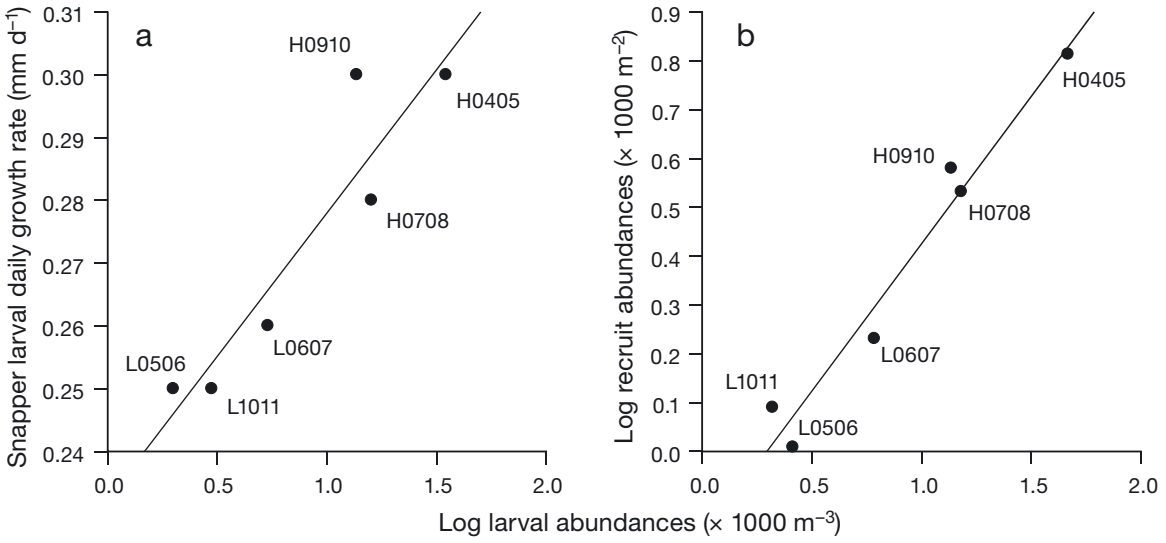

Fig. 3. *Chrysophrys auratus*. Linear regressions between (a) snapper larval mean daily growth rate and larval abundances and (b) snapper larval abundances and 0-age recruit abundances. Higher (H) recruitment years are 2004/2005 (H04 05), 2007/2008 (H0708), 2009/2010 (H0910), and lower (L) recruitment years are 2005/2006 (L05 06), 2006/2007 (L0607), and 2010/2011 (L1011)

studies. While the larval stage has often been considered most critical (Islam et al. 2010, Smith & Shima 2011), studies have found fast growth later in development (late larval, juvenile stages) (Bailey et al. 1996, Nash & Dickey-Collas 2005) to be most important for influencing juvenile recruitment rates. Our study indicates a strong relationship between growth in the larval stage, larval abundance, and recruitment of 0-age snapper.

Table 2. Univariate repeated measures ANOVA comparing pattern of mean increment group widths (MIGW) (Increments 1–3, 4–6, 7–9) (dependent variable) in larval *Chrysophrys auratus* otoliths among years (independent variable). G-G: Greenhouse-Geiser statistic; H-F: Huynh-Feldt statistic

Source	df	MS	*F*	p	G-G	H-F
Between subjects						
Year	5	0.099	6.534	0.000		
Error	64	0.015				
Within subjects						
MIGW	2	0.246	60.415	0.000	0.000	0.000
MIGW × Year	10	0.008	1.970	0.042	0.048	0.049
Error	128	0.004				

Table 3. Univariate analysis of variance of mean increment group widths (MIGW) (Increments 1–3, 4–6, 7–9) for 6 years (3 higher [H] recruitment years H2004/2005, H2007/2008, H2009/2010, and 3 lower [L] recruitment years L2005/2006, L2006/2007, L2010/2011) of *Chrysophrys auratus* otoliths. Post hoc Tukey's tests were used to test significant differences in MIGW among years

MIGW	*F*	df	p	Post hoc Tukey's test
1–3	6.260	5, 69	<0.001	H2009/2010 > H2004/2005, L2005/2006, L2006/2007, H2007/2008, L2010/2011
4–6	7.577	5, 69	<0.001	H2009/2010 > H2004/2005, L2005/2006, L2006/2007, H2007/2008, L2010/2011
7–9	3.573	5, 69	0.006	H2009/2010 > L2006/2007

Factors other than larval growth, such as spawning biomass and egg densities, may also have an impact on snapper larval abundance. Snapper spawning biomass in PPB, based on commercial catch rates, remained stable among the 6 sampling years, with the exception of an increase in commercial catch in 2009/2010 (Kemp et al. 2012, P. Hamer unpubl. data). However, snapper larval abundances and recruitment strength, based on sampling of 0-age snapper, varied over the same time period, which suggests that adult snapper biomass may not have influenced recruitment strength in these years. While stock biomass is easier to determine than total egg production, stock biomass may not always be an acceptable proxy for reproductive output (reviewed in Leggett & Frank 2008). In a previous study, snapper egg densities were found to be similar among 3 years of sampling in New Zealand even though recruitment strength varied (Zeldis et al. 2005). Rather, snapper larval densities were related to recruitment strength, with an estimated 98% of larvae dying between hatch and 8 dph (Zeldis et al. 2005). While maternal provisioning and egg densities may play an

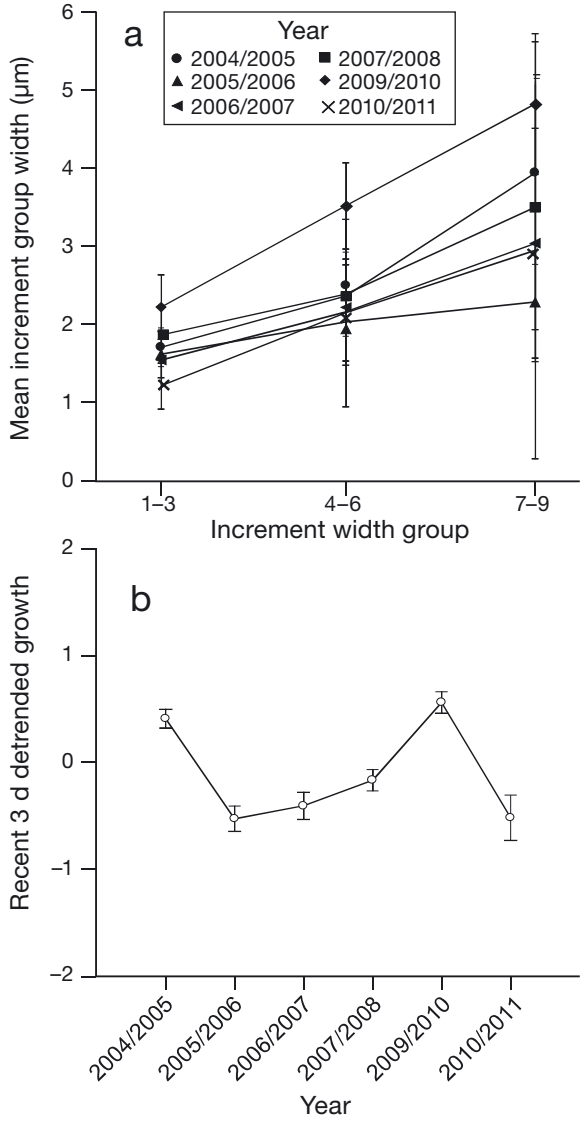

Fig. 4. *Chrysophrys auratus*. Relationship between (a) mean increment group widths (MIGW) (Increments 1–3, 4–6, 7–9) and mean increment group width for larvae collected from 3 higher (H) recruitment years H2004/2005, H2007/2008, H2009/2010, and 3 lower (L) recruitment years L2005/2006, L2006/2007, L2010/2011, and (b) indexed recent detrended growth. Mean ±SE values shown

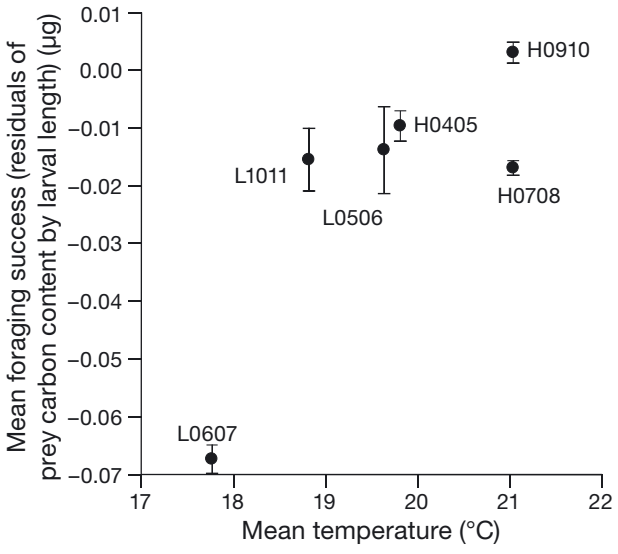

Fig. 5. *Chrysophrys auratus*. Relationship between mean foraging success per tow (residuals of prey carbon content by larval length) of larvae collected from 6 years (3 higher [H] recruitment years 2004/2005 [H0405], 2007/2008 [H0708], 2009/2010 [H0910], and 3 lower [L] recruitment years 2005/2006 [L0506], 2006/2007 [L0607], 2010/2011 [L1011]) and mean temperature. Mean ±SE values shown

important, yet currently undetermined, role in snapper recruitment variability, the strong relationship between larval abundance and 0-age snapper recruits suggests that recruitment strength is determined during the larval stage.

Interannual variability in the index of detrended recent growth was most related to preferred prey (calanoid nauplii) densities and temperature. *Paracalanus* sp. and *Acartia* sp. nauplii are important diet components for first-feeding (2 to 4 mm SL) snapper larvae, and it has previously been suggested that low densities of calanoid nauplii in L2006/2007 and L2010/2011 may have been a factor in the lower larval abundances and recruitment in these years (Murphy et al. 2012). The positive linear relationship between recent larval growth and calanoid nauplii densities, rather than a saturation asymptote (e.g. Robert et al. 2009), suggests that larval growth may be limited by low densities of *Paracalanus* sp. and *Acartia* sp. nauplii. Our findings indicate that a match/mismatch between first-feeding larvae and their preferred prey can impact snapper larval growth, survival, and recruitment. The link between prey availability and recent growth for snapper larvae suggests that individually based modelling could be a useful approach for predicting how environmental changes due to climate change are likely to influence preferred prey and snapper larval growth and survival (reviewed in Köster et al. 2003, Houde 2008)

Temperature is generally considered an important influence on larval growth, and a link between temperature and larval growth has previously been demonstrated (e.g. Meekan et al. 2003, Jenkins & King 2006, Sponaugle et al. 2006). Our findings indicate that snapper larvae from years that experienced higher mean temperatures and higher densities of preferred food had faster larval growth and increased larval survival than snapper larvae from cooler years, although the relationship between

Table 4. The best fit linear and multiple regressions between index of detrended growth and calanoid nauplii densities (N) of *Chrysophrys auratus*, temperature (T) and an interaction term between calanoid nauplii densities and temperature (INT). AIC: Akaike's information criterion

Term(s)	AIC (corrected)	ΔAIC	Weighted AIC	R^2	p-values
N, T	135.877	0	0.337	0.349	N(+): p < 0.001 T (+): p = 0.072
N, INT	136.163	0.286	0.292	0.352	N(+): p < 0.001 INT (–): p = 0.081
N, T, INT	136.884	1.007	0.204	0.365	N(+): p < 0.001 INT (–): p = 0.219 T(+): p = 0.265
N	137.313	1.436	0.165	0.315	N(+): p < 0.001
T	150.602	14.725	0.0002	0.165	T (+): p = 0.001
INT, T	151.574	15.697	0.0001	0.181	INT (+): p = 0.268 T (+): p < 0.001
INT	162.527	26.65	5.52×10^{-7}	0.002	INT (+): p = 0.698

larval growth and temperature is marginally non-significant. The linear relationship between larval growth and temperature suggests that snapper larvae are not experiencing their optimum temperature for growth, and this is confirmed by aquaculture rearing studies where the optimal temperature for snapper larval growth is 24°C (Fielder et al. 2005), which is higher than the mean temperatures experienced by snapper larvae in PPB. In New Zealand, prey availability, rather than temperature, was found to be more important for snapper larval survival, with higher larval survival found in a year with increased wind-driven vertical mixing, which resulted in increased primary and secondary production (Zeldis et al. 2005). Furthermore, previous studies have found the effect of temperature and prey availability on larval growth can change throughout development, with temperature becoming more important as larval foraging capabilities improve with ontogeny (Robert et al. 2009). In this study, very few older snapper larvae were sampled to evaluate how temperature and prey availability may affect late larval pre-settlement growth.

Metabolic requirements for fish larvae would be higher with increased temperature (Buckley et al. 2004), and the relationship between temperature and foraging success was marginally non-significant, with generally higher temperatures in higher foraging years. The method of stomach analysis did not provide data on the rate of ingestion and egestion of prey, which could have been higher in larvae experiencing higher mean temperatures (Robert et al. 2009). In cooler years, which were predominately lower larval abundance years, foraging success was low (L2006/2007) or highly variable (L2005/2006 and L2010/2011). We sampled few larvae in L2005/2006 and L2010/2011, but the larvae we did sample had a wide variety of sizes and numbers of prey in their diet, which was perhaps a reflection of a generalist foraging strategy found in some lower snapper larval abundance years (Murphy et al. 2012). However, lower recruitment outcomes in these years indicate that a generalist foraging strategy did not result in higher larval and 0-age survival.

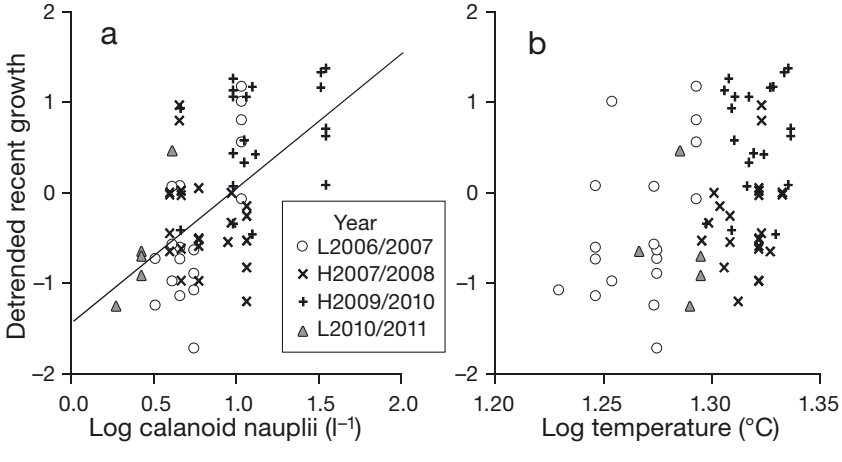

Fig. 6. *Chrysophrys auratus*. Best fit multiple regression model between index of detrended recent growth of larvae and (a) copepod nauplii and (b) temperature for 4 years of sampling (2 higher [H] recruitment years H2007/2008, H2009/2010, and 2 lower [L] recruitment years L2006/2007, L2010/2011)

Preferred prey availability and temperature explained 35% of the interannual variability in snapper larval recent growth, which suggests that additional unmeasured factors may also be important for recruitment. Growth or size-selective predation of snapper larvae, where faster-growing larger larvae experience higher survival in the plankton, may impact snapper recruitment strength. The strong relationships we found among snapper larval growth, abundance, and recruitment could be a reflection of snapper larvae either experiencing fast growth under optimal conditions of food and temperature or the re-

moval of slow-growing individuals from the population in some years (Robert et al. 2007). Faster snapper larval growth has been linked to shorter snapper larval duration and faster 0-age growth in New Zealand and South Australia, which suggests that selection for fast larval growth occurs in snapper populations (Fowler & Jennings 2003, Sim-Smith et al. 2012). We will investigate the importance of size-selective mortality for snapper recruitment using otoliths from the 0-age survivors.

In conclusion, high larval abundance years were characterised by fast larval growth and increased 0-age survival in this temperate marine fish. Interestingly, snapper larval growth, using all 3 measurement techniques (mean daily growth, growth rate, and an index of detrended recent growth), was higher in the 3 higher abundance years compared with the lower abundance years. The close correspondence of these otolith measurement techniques suggests that patterns in larval growth are set early and perpetuated throughout development. Densities of preferred prey (calanoid nauplii) and temperature were the main factors influencing snapper larval growth rates, but it is likely that other unmeasured factors may also be important for snapper larval survival and recruitment, such as predation and maternal effects. The importance of larval characteristics, such as fast growth, on larval abundance, and potentially juvenile survival and recruitment to populations of snapper, provides further evidence for the importance of early life history research for understanding population dynamics of organisms with complex life cycles.

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