What causes recruitment variation in snapper (*Chrysophrys auratus*, Sparidae)?

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Abstract

For animals with complex life cycles, like fishes, the factors that contribute to interannual variability in recruitment are important aspects of their ecology. Long-term monitoring in Port Phillip Bay, Australia suggests that snapper, *Chrysophrys auratus* (Sparidae), experience high juvenile recruitment variation, which is closely related to variation in larval abundance. I studied four potential causes of variation in snapper recruitment: larval behaviour, diet, growth, and selective mortality.

Diel vertical migratory (DVM) behaviour of snapper larvae and their prey were investigated using depth-stratified sampling (four depths: surface, 4, 8, 11 m) over four 24 h sampling periods. Snapper larvae displayed DVM behaviour of nocturnal diffusion and diurnal aggregation at approximately 4 m depth. Snapper larvae had highest foraging success at the 4 m depth. This suggests that the observed DVM was related to feeding success, and that the 4 m depth provided optimal foraging conditions. These results have important implications for developing individual-based biophysical models of larval transport that include interaction with prey fields and larval foraging success.

I analysed stomach contents of snapper larvae from seven years of sampling (2004-2011) to determine diet composition, prey selectivity, prey quality and trophic niche breadth, and compared larval diet to prey availability (5 years of zooplankton data; 2006-2011). In higher recruitment years, larvae were characterised by either a constant or dome-shaped trophic niche breadth and an increase in prey quality with increasing larval size. Snapper larvae from lower abundance years were generalist foragers characterised by an increase in trophic niche breadth, but not prey quality, with increasing larval size. Changes in foraging strategies were concordant with changes in the prey environment, with low zooplankton densities corresponding with generalist diet (lower larval abundance) years and high zooplankton densities with specialist diet (higher larval abundance) years.

Using the same seven year larval data set, I assessed whether growth-rate dependent effects on larval survival were a driver of recruitment variation. Average daily growth rates, estimated from otolith daily rings, were positively correlated with larval abundances, with higher abundance years characterised by higher growth rates. Foraging success, measured as estimated carbon content of consumed prey, was higher in two years with fast larval growth. Furthermore, cladoceran prey densities best
explained interannual variation in larval growth, indicating a link between prey availability and larval growth.

Finally, to determine if growth-selective mortality was occurring in this population, and, if so, how important was this process in influencing recruitment dynamics, I compared larval traits of the previously aged initial larval cohorts (year-classes) to larval traits of 0-age (young-of-year) recruits. I found that selective mortality acted on larval growth in only some years. Years with high larval prey availability and higher recruitment were characterised by either weak or no selective mortality, while years with lower larval prey availability and lower recruitment experienced high selective mortality. Larval traits (otolith growth, cumulative size, pelagic larval duration, size-at-hatch) of the initial and surviving cohorts were not related to recruitment strength. However, larval traits of 0-age recruits predicted juvenile growth, which suggests a potential carry-over of larval traits to the juvenile stage.

The links between prey availability, larval growth, and larval survival suggests that prey production, acting either directly through prey availability or indirectly via selective mortality, is an important driver of recruitment dynamics of snapper.
Declaration

i. The thesis comprises only my original work towards a PhD except where indicated in the Preface,

ii. Due acknowledgement has been made in the text to all other material used,

iii. The thesis is fewer than 100,000 words in length, exclusive of tables, maps, bibliographies and appendices
Preface

Two substantially unchanged multi-authored papers are included in this thesis. Chapter 1 was previously published as Murphy, H.M., Jenkins, G.P., Hamer, P.A., Swearer, S.E. (2011) Diel vertical migration related to foraging success in snapper *Chrysophrys auratus*. *Marine Ecology-Progress Series* 433:185-194. Author contributions were GPJ, PAH, SES, HMM conceived and designed the sampling protocol; PAH and HMM collected the data, with help from technical staff; HMM did the laboratory work and analysed the data; HMM wrote the manuscript and GPJ, PAH, and SES provided editorial comments.

Chapter 2 was previously published as Murphy, H.M., Jenkins, G.P., Hamer, P.A., Swearer, S.E. (2012) Interannual variation in larval survival of snapper (*Chrysophrys auratus*, Sparidae) is linked to diet breadth and prey availability. *Canadian Journal of Fisheries and Aquatic Sciences* 69(8): 1340-1351. Author contributions were GPJ and PAH conceived and designed the sampling protocol; PAH, other research scientists, and technical staff collected the data; HMM sorted samples, did all stomach analyses, zooplankton sorting and analysed the data; HMM wrote the manuscript and GPJ, PAH, and SES provided editorial comments.

I used samples collected from two long-term monitoring programs at Fisheries Research Branch, Department of Primary Industries, Queenscliff for Chapters 2-4. I used snapper larval samples and zooplankton samples collected from ichthyoplankton surveys of Port Phillip Bay from 2004-2011, as well as 0-age recruits sampled in Port Phillip Bay from 2000-2011. 0-age recruit otolith preparation was completed by Fish Ageing Services.
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General introduction

Understanding population dynamics is an important goal of ecology. Organisms with complex life cycles, where individuals undergo ontogenetic transformation (metamorphosis), are ubiquitous in nature (Wilbur 1980). Research on larval characteristics (e.g. size, condition, growth rate) of organisms, such as insects, marine invertebrates, fishes, and amphibians, provides important information on survival processes of early life history stages and how these processes impact on the abundance of adults (McCormick & Hoey 2004, Van Allen et al. 2010, Crean et al. 2011, Hellmann et al. 2011). In marine fishes, recruitment variability, which in this study is defined as the number of new juveniles entering the population each year, is commonly attributed to variable mortality rates of the larval stage (Houde 1987, Cushing 1990, Pepin 1991). The larval stage has high cumulative mortality, as the longer larvae spend in this vulnerable stage the greater the risk of predation and starvation (Houde 1987) (Fig. 1). Even small changes in cumulative mortality rates of larvae can result in an order of magnitude difference in number of surviving juvenile recruits (Shepherd & Cushing 1980). Consequently, much research has focused on factors affecting mortality of larval life stages, such as starvation, predation, and growth (Leggett & DeBlois 1994), and their relationships with biological, physical, and behavioural processes (Bailey & Houde 1989, Fiksen et al. 2007, Leis 2007) (Fig. 1).
A species known to show high recruitment variability is snapper, *Chrysophrys auratus* (Sparidae) (Francis 1993, McGlennon et al. 2000, Fowler & Jennings 2003, Hamer & Jenkins 2004). Snapper are considered one species throughout its distribution in southern Australia and New Zealand, and snapper is closely related to *Pagrus major* (red sea bream) from Japan (Orrell et al. 2002, Gomon et al. 2008). Snapper are the basis of important recreational and commercial fisheries in New Zealand and Australia. Snapper are demersal, with juveniles and small adults generally occupying sheltered bays and inlets and adults found in shelf waters, with seasonal spawning aggregations occurring in some large, sheltered marine bays (Fowler & Jennings 2003, Gomon et al. 2008, Hamer et al. 2011). Snapper are highly fecund, serial broadcast spawners that produce batches of eggs for an extended spawning period (Scott et al. 1993). Timing of spawning varies with latitude, but typically corresponds to water temperatures between 18-22 °C, and the most intensive spawning occurs from November to February in the southern states of Australia (Jenkins 1986, Coutin et al. 2003, Fowler et al. 2003). Snapper eggs are positively buoyant, the larvae are pelagic.
for 18-28 days (Fowler & Jennings 2003), and settlement occurs at 10-12 mm SL (Battaglene & Talbot 1992). Snapper are long-lived (up to 40 years in Australian waters) and mature at 4-5 years (approximately 40 cm total length), with populations often dominated by a few year-classes due to high recruitment variation (Coutin et al. 2003).

The variability in recruitment of snapper has been investigated in New Zealand and Australia. Using otoliths to back-calculate settlement dates, research in New Zealand found interannual recruitment strength in snapper may originate in the pre-settlement phase, rather than the post-settlement phase (Francis 1994a). Similar results were found in two large Australian bays, Port Phillip and Spencer Gulf (Fowler & Jennings 2003, Hamer et al. 2010). Subsequent research in New Zealand has focused on potential factors that may affect snapper larval survival. Survival of snapper larvae was higher in a year of strong winds and high productivity, with higher larval survival correlated with an increase in prey availability, rather than predation or sea surface temperature (Zeldis et al. 2005). These results contradict earlier research by Francis (1993), which found a correlation between sea surface temperature and snapper recruitment, and possibly indicates an indirect link between temperature and recruitment success (i.e. the same climatic factors influencing water temperature may also be influencing prey availability). This PhD dissertation contributes to furthering our understanding of how abiotic (temperature, dispersal) and biotic (larval growth, behaviour, productivity) factors affect survival of larval snapper and subsequent recruitment.

Recent research has found that fish larvae display a wide-range of behaviours that can influence their dispersal and recruitment success. These behaviours include horizontal swimming speed (reviewed by Leis 2006), use of olfactory and visual cues for orientation (reviewed by Kingsford et al. 2002, Leis 2006), and diel vertical migratory (DVM) behaviour (reviewed by Sponaugle et al. 2002, Leis 2006). The most commonly studied larval behaviour is DVM (reviewed by Neilson & Perry 1990). Diel vertical migratory behaviour can influence the horizontal dispersal of fish larvae when current shear is not uniform with depth, which can result in larvae being retained in optimum areas for feeding or causing advection of larvae from nursery areas (Sponaugle et al. 2002, Leis 2006, 2007). The most common drivers of DVM behaviour are light,
prey concentrations, predator avoidance, thermoclines, tides, and changes in buoyancy in larvae (reviewed in Neilson & Perry 1990). Diel vertical migratory behaviour is taxon-specific and can change throughout ontogeny. Therefore, factors that influence vertical migrations and the effects of DVM on larval survival are likely to vary across taxa and environments (Garrido et al. 2009). In Chapter 1, I described the DVM behaviour of pre-flexion and flexion stage snapper larvae, and related their behaviour to environmental factors, prey availability, and foraging success.

Starvation and predation are considered the main factors affecting fish larval survival (e.g. Leggett & DeBlois 1994, Cushing 1995). Food-deprived fish larvae can experience high mortality either directly due to starvation or indirectly through slow growth and poor condition, which can increase their vulnerability to predation and disease by prolonging larval developmental stages (Bailey & Houde 1989). Cushing’s (1972, 1990) match-mismatch hypothesis proposed that recruitment depends on the temporal overlap of food availability and/or abundance as marine fish larvae disperse from spawning to nursery grounds, rather than a specific critical period at the transition from endogenous to exogenous feeding, as proposed by Hjort (1914). Fish larvae do not prey on the entire sampled prey field, but select for specific prey taxa and stages (Munk 1997), and prey selection can change with ontogeny as fish larvae become more proficient at capturing prey (Blaxter 1986, Pankhurst 1994, Scharf et al. 2000). Previous studies have found links between availability of specific prey types, such as the copepod naupliar stage, during the first-feeding stage and recruitment strength (Zeldis et al. 2005, Castonguay et al. 2008), and there is evidence that matching of later larval developmental stages with specific prey taxa can also have an impact on recruitment strength (Voss et al. 2006, Dickmann et al. 2007). In Chapter 2, snapper larval diet composition, prey selectivity, trophic niche breadth, prey quality, and prey availability were used to investigate the link between prey availability and interannual variation in larval abundance.

Large larval size-at-age and/or fast larval growth is often associated with high survival and recruitment, which is the basis of the growth-mortality hypothesis (e.g. Hare & Cowen 1997, Jenkins & King 2006, Meekan et al. 2006). The growth-mortality hypothesis, which incorporates feeding success and predation into one integrated framework, predicts that larvae experiencing superior feeding conditions due to
temporal and spatial overlap with preferred prey display increased larval growth, and lower mortality by starvation and predation (Anderson 1988). The growth-mortality hypothesis is comprised of three mechanisms (hypotheses): bigger-is-better, stage duration, and growth-selective. The bigger-is-better mechanism is based on the finding that larger and older larvae are less vulnerable to predation as they are more able to avoid capture and “grow out” of the size-range predators target more quickly than younger, less developed larvae (e.g. Bailey & Batty 1984, Blaxter 1986, Miller et al. 1988, Dower et al. 2009). The stage-duration mechanism is based on the observation that there is less variation of larval size at metamorphosis than age, which indicates that metamorphosis is size rather than age dependent (Chambers & Leggett 1987, Houde 1987). The growth-selective hypothesis predicts that the nutritional/physiological state of individual larvae may influence its probability of capture, independent of size or developmental stage (Takasuka et al. 2003, Takahashi & Watanabe 2004, Takasuka et al. 2004). In Chapter 3, I used snapper larval otoliths to determine if fast larval growth was found in higher larval abundance years, as predicted by the growth-mortality hypothesis. Prey availability (Cushing 1972, 1990) and temperature (Houde 1987) are considered the most important underlying processes that influence variation in fish larval growth, and I also considered both of these factors when attempting to determine what is the main driver of interannual variability in snapper larval growth.

Marine fishes undergo a high rate of mortality in early life history stages (Bailey & Houde 1989). Mortality is often not random, but selective, preferentially removing smaller and slower growing individuals within cohorts (Meekan et al. 2006). The growth-mortality hypothesis predicts that fast growth in the plankton should result in high recruitment; however, fast larval growth can be a reflection of larvae either encountering ideal prey and temperature conditions or selective-mortality by predation or starvation of slow growing individuals (Meekan & Fortier 1996, Robert et al. 2007). Selective mortality may only occur in poor years, while in good years, with optimum temperature and prey availability, there is little variation in larval traits and all larvae do well (Sogard 1997, Meekan et al. 2006). Patterns of selective mortality may also not be maintained through time (Gagliano et al. 2007b, Robert et al. 2007) or occur in all populations of a species (Searcy & Sponaugle 2001), which may explain why several studies have found the predicted link between larval growth and recruitment in marine
fishes (Meekan & Fortier 1996, Sirois & Dodson 2000, Jenkins & King 2006, Smith & Shima 2011), while other studies have not (van der Veer et al. 1994, Campana 1996, Ringuette et al. 2002). In Chapter 4, I used otolith microstructure of 0-age snapper to investigate how larval traits, such as fast growth, were related to abundance of surviving 0-age recruits and if selective mortality for fast larval growth was occurring.

In summary, I considered four potential drivers of variation in marine fish recruitment: larval behaviour, diet, growth, and selective mortality. In Chapter 1, I investigated the DVM behaviour of snapper larvae in Port Phillip Bay (PPB), Australia over four 24 h periods, with the aim to describe the DVM behaviour of snapper larvae and to determine its relationship to environmental factors, temperature, salinity, dissolved oxygen, and fluorescence, densities of important zooplankton prey, and foraging success. In Chapter 2, I used seven years of larval data and five years of zooplankton data to describe the feeding ecology of snapper larvae in PPB by considering diet composition, prey selectivity, trophic niche breadth, prey quality, and prey availability. I also investigated the hypothesis that juvenile recruitment variation is related to larval feeding ecology by comparing interannual variation in larval diet to the known interannual variation in juvenile densities. In Chapter 3, I utilised the otolith microstructure measurements from the snapper larvae analysed for Chapter 2 to determine interannual variation in daily growth rates and growth trajectories. I also tested whether interannual variation in larval growth was related to foraging success, prey availability and/or temperature. In Chapter 4, I investigated if growth-selective mortality was occurring in this population by comparing larval growth, based on otolith microstructure measurements, of the initial larval population and 0-age snapper. And if size-selective mortality was occurring, how important was it in influencing recruitment dynamics.
Chapter 1
Diel vertical migration related to foraging success in snapper
*Chrysophrys auratus*

Abstract

The vertical distributions of marine fish larvae can change markedly over time due to changes in diel vertical migration (DVM). DVM is thought to be influenced by a number of factors including light levels and prey availability. In Port Phillip Bay, Australia, the DVM of snapper (*Chrysophrys auratus*, Sparidae) larvae and their prey were investigated using depth-stratified sampling (four depths: surface, 4, 8, 11 m) over four 24 hour sampling periods. I sampled ichthyoplankton at the same location twice in two spawning seasons (austral summers of 2008/2009 and 2009/2010). Sufficient snapper larvae for analysis of DVM behaviour occurred once in each season. At both 24 hour sampling times, snapper larvae displayed the same DVM behaviour of nocturnal diffusion and diurnal aggregation at ~ 4 m depth. The water column was homogenous for temperature, salinity, dissolved oxygen, and fluorescence during the two 24 hour periods. Two out of six important zooplankton prey of snapper larvae were also aggregated at ~ 4 m depth during the day. Gut analyses indicated that larvae only fed during daylight hours and had an average digestion time of three to five hours. Snapper larvae had highest foraging success at the 4 m depth, which was supported by minimal digestion of prey at time of capture. This suggests that the observed DVM was related to feeding success, and that the 4 m depth provided optimal foraging conditions. These results have important implications for developing individual-based biophysical models of larval transport that include interaction with prey fields and larval foraging success.
Introduction

Diel vertical migration (DVM) in marine fish larvae can be a behavioural trait exhibited from the time of hatching (Leis 2004). This relatively simple, but variable, behaviour can influence the horizontal dispersal of larvae when current shear is not uniform with depth (Sponaugle et al. 2002, Leis 2006, 2007), a feature typical of both tidal and wind-driven currents. For example, as wind currents decrease exponentially with water depth (Black et al. 1993), larvae closer to the surface will often encounter stronger currents, and greater horizontal displacement, than larvae in the mid or bottom sections of the water column. Tidal currents vary on a diurnal or semi-diurnal cycle, and fish larvae can migrate vertically to use ebb or flood tides to aid in retention or dispersal (Neilson & Perry 1990). The effect of vertical migrations on dispersal has been documented in estuarine fishes (e.g. Fortier & Leggett 1983). The incorporation of larval behaviour, particularly vertical migration, into individual-based biophysical models (IBMs) of larval dispersal and recruitment in fish is becoming more common and is recognised as an important consideration if such models are to accurately predict individual dispersal histories (Fox et al. 2006, Leis 2007, Vikebo et al. 2007).

There are three main forms of DVM in marine larval fishes: nocturnal ascent (type I), where the larvae move up at dusk and down at dawn (Neilson & Perry 1990); nocturnal descent (type II), where the larvae move down at dusk and up at dawn (Neilson & Perry 1990); and nocturnal diffusion, where the larvae are distributed evenly throughout the water column during the night and aggregate to a specific depth during the day (e.g. Brewer & Kleppel 1986, Davis et al. 1990, Jenkins et al. 1998). Diel vertical migratory behaviour can vary taxonomically, with nocturnal ascent being the most commonly observed pattern for marine fish larvae (Neilson & Perry 1990). Vertical behaviour can also vary ontogenetically, with older larvae commonly demonstrating a more pronounced DVM pattern compared to smaller, less developed pre-flexion stages (Neilson & Perry 1990). Marine fish larvae may vertically migrate in response to a variety of factors, including to avoid predators (Yamashita et al. 1985); to optimise feeding success (Fortier & Leggett 1983, Munk et al. 1989); and to influence larval dispersal (reviewed in Leis 2006).

In marine temperate fish larvae, patterns of DVM behaviour have more often been interpreted as responses to prey-predator interactions rather than abiotic factors
(Neilson & Perry 1990, Sabates 2004). Although a relationship between prey density and larval DVM behaviour has been found for numerous taxa, for example herring (Munk et al. 1989), sandeel (Jensen et al. 2003), and mackerel (De LaFontaine & Gascon 1989), other studies have found no such relationship (e.g. Brewer & Kleppel 1986, Jenkins et al. 1998). However, the relationship between prey availability and DVM may be more complicated where it is not just the availability of prey that is important, but, rather, the ability of fish larvae to obtain high foraging success in relation to multiple environmental factors (Munk et al. 1989). Since the majority of marine fish larvae are visual predators (Blaxter 1986), foraging success may be a trade-off between optimal light levels, prey availability (Fortier & Leggett 1983, Munk et al. 1989) and/or turbulence (Dower et al. 1998). Furthermore, the patterns of DVM behaviour for the same species can change among sampling periods, years, and locations (Sclafani et al. 1993). This suggests that a combination of factors, such as light levels, turbidity, temperature, predation and foraging success, may be important in determining the extent and variety of DVM behaviour.

Snapper (*Chrysophrys auratus*, Sparidae) is an important fishery species in Australia and New Zealand and displays high recruitment variation, which strongly influences the dynamics of fishery production (Francis 1993, McGlennon et al. 2000, Fowler & Jennings 2003, Hamer & Jenkins 2004). Recent work in Port Phillip Bay (PPB), Australia has demonstrated that the recruitment dynamics of juvenile snapper are closely matched to those of the larval stage (Hamer et al. 2011). Understanding what influences snapper larval survival has become an important focus for research on this species throughout its wide distribution (e.g. Fowler & Jennings 2003, Zeldis et al. 2005).

Diel vertical migratory behaviour of some sparid species has been investigated, and nocturnal ascent is the most common DVM pattern found in this family (e.g. Tanaka 1985, Joyeux 2001, Ruso & Bayle-Sempere 2006). In this study, I measured the DVM behaviour of snapper larvae in PPB over four 24 hour periods. I compared the observed larval behaviour to the measured vertical variation in a range of environmental variables, including temperature, salinity, dissolved oxygen, and fluorescence; the densities of important zooplankton prey; and the foraging success of the larvae. I aimed
to describe the DVM behaviour of snapper larvae and to determine its relationship to environmental factors and foraging success.
Methods

Sampling of snapper larvae and zooplankton

Depth-stratified sampling of snapper larvae was undertaken twice in each of the austral summers of 2008/2009 and 2009/2010 in PPB, Australia (Fig. 2). In both years, sampling took place at the same location, which had a bottom depth of 12 m, in the eastern region of PPB (Fig. 2). This location and depth was chosen based on previous knowledge of snapper spawning and the occurrence of larval stages (Hamer et al. 2011) (Fig. 2). Sampling was initiated when snapper larvae were found in the field by a concurrent monitoring program occurring in the same area. In both years, the 24 hour sampling occurred once in mid-December and once in mid-January. Ichthyoplankton samples were collected continuously over ~ 24 hour (2200-1900 hrs) using a 500 µm mesh plankton net with a circular mouth of 80 cm in diameter. The water column was divided into four strata for ichthyoplankton and zooplankton sampling: surface (top 1 m of the water column), 4 m, 8 m, and 11 m depths. The four strata were sampled in a random order in blocks that were repeated nine times in each of the four 24 hour sampling events. For each ichthyoplankton sample, the net was deployed for 12 minutes at each specified depth stratum. A closing mechanism (choker) was used to prevent the net from sampling the water column while being deployed and retrieved. A General Oceanics flowmeter (Florida, USA; model number: 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.

Zooplankton samples were collected using an 80 µm mesh plankton net with a circular mouth of 30 cm in diameter. The zooplankton net was clipped to a pulley and allowed to run down the rope attached to the ichthyoplankton net until it hit the larger net. The zooplankton net was left to fish at the specified depth stratum for 2 minutes, and a closing mechanism (choker) was used to prevent the net sampling the water column while being deployed and retrieved. A General Oceanics flowmeter (Florida, USA; model number: 2030) was used to determine the volume of water filtered with each tow. Material from the cod-end was filtered through a 50 µm mesh sieve and immediately preserved in 4% buffered formaldehyde solution.

At the end of each block of ichthyoplankton and zooplankton tows, a Hydrolab DS4X water quality sonde was deployed to record temperature, salinity, and
fluorescence. The data were acquired at 2 m intervals between the surface and the bottom of the water column. Three times throughout the 24 hour sampling period a niskin bottle was used to sample water at each depth for laboratory determination of chlorophyll $a$ concentrations that were used to calibrate the fluorometer readings.

Figure 2 Map of Port Phillip Bay, Australia. Sampling was conducted in the same area and depth range in the eastern part of the bay (labelled by black dot).

**Foraging success**

Snapper larvae were identified based on the descriptions in Neira et al. (1998). All snapper larvae were removed from ichthyoplankton samples and stored in vials with 95% ethanol until used for diet analysis.
The standard length (SL, tip of snout to tip of notochord) and gape width (distance between left and right postero-ventral tips of the articular bones (Kiorboe et al. 1985)) of all intact snapper larvae were measured to 0.1 mm under a dissecting microscope 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 and similar amongst larvae (Theilacker 1980).

After the SL and gape width were measured, each 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. Each food item in the gut contents was identified to lowest possible taxonomic level, and its maximum width was measured. The stomach contents of all snapper larvae from each sample were analysed, except when there were more than 20 snapper larvae in a sample. When this occurred, a sub-sample of 20 snapper larvae were randomly chosen and used for stomach content analysis and the remaining larvae measured for SL.

**Zooplankton**

In the laboratory, zooplankton samples were sieved through a 40 µm mesh and transferred to freshwater to give a total volume from 200 mL to 2 L, depending on the concentration of zooplankton in the sample. One mL sub-samples were drawn out of the suspended zooplankton sample with a Hensen-Stempel pipette until at least 200 individuals were counted. Zooplankton was identified to the lowest taxonomic level possible.

**Data analysis**

Snapper larval abundances were standardised to number per 1000 m$^{-3}$ based on flowmeter determinations of the volume of water filtered per tow. The stomach contents of the snapper larvae were used to determine diet composition and to measure average foraging success of larvae by tow. I used %N, which was the number of prey items of a category as a percentage of the total number of prey items found in the stomachs of the larvae in each tow, to compare diet composition between depths.

Zooplankton abundances per m$^3$ were calculated using the formula:

$$D = \frac{N_{VS}}{N_{SV}}$$
Where \( N \) is the number of organisms; \( N_A \) is the number of 1 mL aliquots; \( V_S \) is the volume of subsample; and \( V \) is the volume of water filtered through the zooplankton net measured by the flowmeter.

The vertical distribution pattern of snapper larval densities were analysed using a three factor ANOVA with respect to date (2008/2009 and 2009/2010), depth strata (surface, 4 m, 8 m, 11 m), and day/night sampling. I used univariate tests (ANOVAs) to determine the vertical behaviour of individual taxa/groups of zooplankton. Mean larval foraging success (measured as mean number of prey per larval stomach by tow) was analysed using a three factor ANOVA (date, depth strata, and day/night sampling). I used Pearson correlations \((r)\) to determine if larval densities and zooplankton densities were related across plankton tows. The vertical pattern of environmental variables was analysed using ANOVAs. Datum from one tow was eliminated from the dataset (surface tow 29 from 2009/2010) as it was continually an outlier when the datum was transformed. I found very low numbers of both zooplankton and ichthyoplankton in this tow, which suggests that the nets failed to deploy properly. Snapper larval densities from both years were log10 \((x+1)\) transformed, zooplankton densities were fourth-root transformed, and average larval foraging success per tow was square root transformed to meet ANOVA requirements of homoscedasticity of variances (Levene’s test: \(p > 0.05\)) and normal distribution (Shapiro-Wilk test: \(p > 0.05\)).
Results

Vertical behaviour of snapper larvae

Sufficient larvae for DVM analyses were sampled in one of the two 24 hour sampling events in each year. These two dates were January 2009 (hereafter 2008/2009) and December 2009 (hereafter 2009/2010). A total of 36 ichthyoplankton samples were taken in each of the 24 hour periods, with 24 day tows and 12 night tows.

In 2008/2009, 1283 snapper larvae were sampled, ranging in size from 2.0 – 7.5 mm SL (mean (SD): 4.5 (± 0.87) mm SL), and in 2009/2010, 187 snapper larvae were sampled, ranging in size from 2.5- 6.0 mm SL (mean (SD): 3.9 (± 0.62) mm SL). Using a three factor ANOVA (year, day/night sampling, and depth strata), there was no significant difference in standard length between depth strata (ANOVA: p = 0.761) and day/night sampling (ANOVA: p = 0.148), but there was a significant difference in mean standard length between years as the larvae from 2008/2009 were 10% longer than in 2009/2010 (Komolgorov- Smirnov: $D = 0.484, p < 0.001$).

There were significant interactions between date and day/night sampling and day/night sampling and depth strata for snapper larval densities (Table 1). Higher densities of snapper larvae were sampled in 2008/2009 compared to 2009/2010, and 21% more larvae were sampled at night compared to the day in 2008/2009 (Fig. 3 a, b). For both years, snapper larvae showed higher densities at the 4 m and 8 m depths during the day (Fig. 3 a, b). There were significant differences in snapper larval densities between the surface and 4 m (post hoc Tukey: $p < 0.001$), 4 m and 11 m (post hoc Tukey: $p = 0.01$), and surface and 8 m (post hoc Tukey: $p < 0.001$) depth strata. Densities of snapper larvae were not significantly higher at any depth strata during the night in 2008/2009 but were generally highest between the surface and 8 m depths in 2009/2010, although there were no significant depth effects (Fig. 3 a, b).
Table 1  *Chrysophrys auratus*. Analysis of variance of log (x+1) transformed snapper larval densities with respect to date, day/night sampling, and depth strata over two sampling periods.

<table>
<thead>
<tr>
<th>Source</th>
<th>df</th>
<th>MS</th>
<th>F-ratio</th>
<th>p-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Day/night</td>
<td>1</td>
<td>4.312</td>
<td>13.682</td>
<td>0.001</td>
</tr>
<tr>
<td>Depth</td>
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<td>1.936</td>
<td>6.144</td>
<td>0.001</td>
</tr>
<tr>
<td>Date</td>
<td>1</td>
<td>18.472</td>
<td>58.604</td>
<td>&lt;0.001</td>
</tr>
<tr>
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<td>0.977</td>
<td>3.099</td>
<td>0.034</td>
</tr>
<tr>
<td>Day/night x date</td>
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<td>1.491</td>
<td>4.730</td>
<td>0.034</td>
</tr>
<tr>
<td>Depth x date</td>
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<td>0.180</td>
<td>0.570</td>
<td>0.637</td>
</tr>
<tr>
<td>Day/night x date x depth</td>
<td>3</td>
<td>0.029</td>
<td>0.092</td>
<td>0.964</td>
</tr>
<tr>
<td>Error</td>
<td>55</td>
<td>0.315</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

**Environmental variables**

For the two 24 hour sampling events where enough snapper larvae were sampled to analyse their DVM, there was partial cloud cover and light winds (5-10 knots onshore SSW). There was no evidence of a thermocline, as temperature varied less than a degree from surface to bottom. There was no significant difference in temperature between depths in 2008/2009 ($F_{6,56} = 2.126, p = 0.067$) (Fig. 4 a). Temperature varied significantly between depths in 2009/2010 ($F_{6,48} = 3.963, p = 0.003$), and the difference was between the surface and 4, 6, 8, 10 m depths (post hoc Tukey tests: $p < 0.05$), not between depths (Fig. 4 a). There was also no evidence of a halocline, as salinity did not vary significantly between depths in 2008/2009 ($F_{6,56} = 0.067, p = 0.999$) and 2009/2010 ($F_{6,48} = 2.518, p = 0.060$) (Fig. 4 b). Dissolved oxygen was significantly different by depth in 2008/2009 ($F_{6,56} = 5.435, p < 0.001$) and 2009/2010 ($F_{6,48} = 7.248, p < 0.001$). These differences were between the surface and 6, 8, 10, 11 m depths (post hoc Tukey tests: $p < 0.05$) in 2008/2009, and between the surface and 6, 8, 10 m depths (post hoc Tukey tests: $p < 0.05$) and between 2 m and 8 m (post hoc Tukey test: $p < 0.05$) in 2009/2010 (Fig. 4 c). Fluorescence varied between depths in 2008/2009 ($F_{6,56} = 3.970, p = 0.002$) and 2009/2010 ($F_{6,48} = 7.118, p < 0.001$), and these differences were between the surface and 8, 10, 11 m depths (post hoc Tukey test: $p < 0.05$) in 2008/2009 and between 10 m and the surface, 2, 4, 6, 8 m depths in 2009/2010 (Fig. 4 d).
**Figure 3** Log (x+1) transformed densities of *Chrysophrys auratus* larvae in day and night sampling, pooled by depth, in (a) 2008/2009 and (b) 2009/2010. Mean values ±SE are shown. Note that the scales are different in (a) and (b).
Figure 4 Depth profiles of measured environmental variables measured at every 2 m and averaged over a 24 hour period from two years (2008/2009 and 2009/2010) of sampling (a) temperature (°C), (b) salinity (‰), (c) dissolved oxygen (mg/L), and (d) fluorescence (μg/L). Mean values ±SE are shown.

Foraging success of snapper larvae

Snapper larvae had food in their stomachs from 0500 to 2100 in 2008/2009 and from 0500 to 1900 in 2009/2010 (Fig. 5 a, b), and all stomachs were empty by midnight. This allowed me to estimate the digestion time of prey to be between three and five hours, based on the block of sampling where larvae last had prey in their stomachs (at the end of the day at 2100 (2008/2009) and 1900 (2009/2010)) compared to all sampled larvae having empty stomachs in the block of sampling around midnight. For the majority of larvae, their stomach contents were not highly digested, enabling accurate identification and measurement of prey items. There were no clear feeding peaks, with larvae feeding continuously throughout the daylight period (Fig. 5 a, b).
The samples from 2009/2010 had a higher percentage of larvae with food in their stomachs than samples from 2008/2009 (Fig. 5 a, b).

**Figure 5** Average percentage of *Chrysophrys auratus* larvae feeding throughout a 24 hour period in (a) 2008/2009 and (b) 2009/2010. Mean values ±SE are shown. Sunrise was at 0600 and sunset at 2100. Larvae had empty stomachs from midnight to sunrise.

Analysis of variance of average foraging success of snapper larvae in relation to date, depth, and day/night sampling indicated a significant interaction between depth strata and day/night sampling (Table 2). Snapper larvae were only foraging during the day (Fig. 5 a, b), and snapper larvae had high foraging success at 4 m compared to the other three depths in both years (Fig. 6 a, b). At 4 m the larvae had 90% more food in their stomachs compared to the surface (post hoc Tukey: *p* < 0.001), 50% more food in their stomachs compared to 8 m (post hoc Tukey: *p* < 0.001), and 95% more food in their stomachs than at 11 m (post hoc Tukey: *p* < 0.001) (Fig. 6 a, b).
Table 2  Analysis of variance of square root transformed mean *Chrysophrys auratus* larval foraging success with respect to date, depth, and day/night sampling over two sampling periods.

<table>
<thead>
<tr>
<th>Source</th>
<th>df</th>
<th>MS</th>
<th>F-ratio</th>
<th>p-value</th>
</tr>
</thead>
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<td>1.746</td>
<td>8.969</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Depth</td>
<td>3</td>
<td>2.655</td>
<td>16.281</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Date</td>
<td>1</td>
<td>0.027</td>
<td>0.168</td>
<td>0.683</td>
</tr>
<tr>
<td>Day/night x depth</td>
<td>3</td>
<td>2.096</td>
<td>12.853</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Day/night x date</td>
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<td>0.246</td>
<td>1.507</td>
<td>0.255</td>
</tr>
<tr>
<td>Depth x date</td>
<td>3</td>
<td>0.374</td>
<td>2.293</td>
<td>0.088</td>
</tr>
<tr>
<td>Day/night x date x depth</td>
<td>3</td>
<td>0.231</td>
<td>1.414</td>
<td>0.248</td>
</tr>
<tr>
<td>Error</td>
<td>55</td>
<td>0.163</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Figure 6  Square root transformed average foraging success (measured as average number of prey per *Chrysophrys auratus* larva by tow) in daytime tows only, pooled by depth in (a) 2008/2009 and (b) 2009/2010. Mean values ±SE are shown.

The diets of snapper larvae differed between years. In 2008/2009, snapper larvae had a broad diet that included copepod nauplii, calanoid copepodites, the cladocerans *Penilia, Evadne* and *Podon*, invertebrate eggs, and bivalve veligers (Fig. 7 a). In
2008/2009, larvae sampled at the 4 m depth stratum, where average foraging success was highest, had a diet composed primarily of calanoid copepodites (40%) and copepod nauplii (33%) (Fig. 7 a). In 2009/2010, snapper larvae had less diet breadth with only three prey items dominating their diet: invertebrate eggs, copepod nauplii and calanoid copepodites (Fig. 7 b). At the 4 m depth stratum their diet was composed of 75% copepod nauplii and 21% calanoid copepodites (Fig. 7 b).

Figure 7 Percent composition of the prey items in the diet of Chrysophrys auratus larvae during the day pooled by depth in (a) 2008/2009 and (b) 2009/2010.

Zooplankton

Only zooplankton taxa/stages that were preyed upon by snapper larvae were considered in the zooplankton analyses. These included copepod nauplii, bivalve veligers, calanoid copepodites, and three cladoceran genera (Penilia, Podon, and Evadne). I was interested in the interaction between day/night sampling and depth for zooplankton taxa/stages and how this may relate to DVM behaviour of snapper larvae. Three factor univariate ANOVA tests indicated depth by day/night interactions for both
copepodites (\( F_{3, 55} = 3.453; \ p = 0.023 \)) and Podon (\( F_{3, 55} = 3.453; \ p = 0.001 \)). For copepodites, the interaction was driven by depth stratification of copepodites at 4 m during the day, with increased densities at 4 m compared to 11 m (post hoc Tukey: \( p = 0.027 \)) and 8 m (post hoc Tukey: \( p = 0.038 \)) (Fig. 8 a). For Podon, the interaction was driven by lower densities of Podon at 11 m compared to the surface (post hoc Tukey: \( p = 0.014 \)), 4 m (post hoc Tukey: \( p = 0.003 \)), and 8 m (post hoc Tukey: \( p = 0.005 \)) during the night, and higher densities at 8 m compared to the surface during the day (post hoc Tukey: \( p = 0.006 \)) (Fig. 8 b). Evande demonstrated a date by depth interaction (\( F_{3, 55} = 4.938; \ p = 0.004 \)) with higher densities of Evadne at 4 m compared to 11 m (post hoc Tukey: \( p = 0.001 \)) and 8 m (post hoc Tukey: \( p = 0.002 \)), and increased densities at the surface compared to 11 m (post hoc Tukey: \( p = 0.005 \)) and 8 m (post hoc Tukey: \( p = 0.008 \)) in 2009/2010 (Fig. 8 c). Correlations of transformed snapper larval densities and zooplankton taxa/ stages was significant for Penilia densities (\( r = 0.674; \ p < 0.001 \)) employing a conservative \( p \) value of 0.004 to account for multiple testing (i.e. 2 dates x 6 zooplankton taxa/ stages).
Figure 8 Fourth root transformed densities of (a) calanoid copepodites (b) Podon in day and night sampling, pooled by depth and year and (c) Evadne in day and night sampling, pooled by depth, in 2009/2010. Note scales are different in each graph. Mean values ±SE are shown.
Discussion

Snapper larvae in PPB exhibited nocturnal diffusion and aggregation at a specific depth stratum during the day. For two sampling times in different years, larvae aggregated during the day around 4 m at a site in the eastern area of PPB, which had a maximum depth of 12 m. Aggregation during the day and nocturnal diffusion has been seen in other marine fish larvae, including sandeel (Jensen et al. 2003), King George whiting (Jenkins et al. 1998), and herring (Haslob et al. 2009). However, nocturnal ascent, rather than nocturnal diffusion, is more commonly seen in other larval sparid species, including the closely related Pagrus major (e.g. Tanaka 1985, Kinoshita & Tanaka 1990). Diel vertical migratory behaviour demonstrated by estuarine sparid species is thought to influence dispersal into, or retention within, estuarine nursery habitat (e.g. Kinoshita & Tanaka 1990, Forward et al. 1998, Trnski 2001). In this study on a sparid that is not estuarine-dependent, and spawns immediately in the known settlement and nursery areas (Hamer et al. 2011), DVM behaviour of larvae would appear unlikely to be related to dispersal or retention advantages, but rather to other benefits to larval survival, such as foraging success.

Consistent aggregation at the 4 m depth stratum by snapper larvae was accompanied by higher foraging success, albeit on different prey items on each sampling date. While it is possible that the snapper larvae caught at 4 m did not feed at this depth, prey were not highly digested in the majority of samples, suggesting recent ingestion (Young & Davis 1992). While the estimate of three to five hours for gut evacuation for snapper larvae in the field has not been tested in the laboratory, this evacuation rate is similar to other temperate larval fishes (four to six hours) (Govoni et al. 1986). The lack of feeding by snapper larvae at night coupled with their diffusion throughout the water column supports a link between feeding behaviour and the observed DVM. Diffusion of the larvae at night could also be in response to relaxation or removal of a gradient, such as light, and the larvae were then passively responding to turbulence (Munk et al. 1989, Ponton & Fortier 1992) or the larvae were not able to regulate their depth in the absence of light (Leis 2004).

The consistent DVM behaviour of snapper larvae occurred despite vertical homogeneity for the majority of environmental parameters (temperature, salinity, dissolved oxygen, and fluorescence) in both the day and night sampling. The lack of
water column stratification is consistent with other studies in PPB (Black et al. 1993). Two of the six zooplankton taxa/stages were aggregated at 4 m during the day (copepodites and *Evadne* in 2009/2010), which may have influenced the vertical behaviour of snapper larvae. However, the majority of the zooplankton prey were not stratified in the water column, except for *Podon* which had type I DVM (up at dusk and down at dawn). There was a strong correlation between snapper larval densities and *Penilia* densities, although *Penilia* were not stratified in the water column. This strong correlation may be a reflection of similar processes influencing the patchiness of both snapper larvae and *Penilia* densities, and the higher densities of both at night. The measured environmental variables do not clearly explain the DVM behaviour and high foraging success of snapper larvae at 4 m. However, other unmeasured variables may have had an affect on larval DVM behaviour, such as light, turbulence, and predators.

The influence of optimal light levels for foraging success on the vertical behaviour of marine fish larvae has been found in Artic cod (Ponton & Fortier 1992), sand lance (Gilbert et al. 1992, Ponton & Fortier 1992), and herring (Munk et al. 1989). Furthermore, in previous studies where zooplankton prey and environmental variables were not stratified, fish larvae were found to aggregate near the surface to obtain optimal feeding conditions (Fortier & Leggett 1983, Munk et al. 1989, Jensen et al. 2003). Snapper larvae are visual feeders (Pankhurst et al. 1991), and previous work in aquaculture studies has found that photoperiod alone has a profound effect on development of snapper larvae with long photoperiods (up to 18 hours a day) thought to improve the performance of snapper larvae by providing more feeding opportunities (Fielder et al. 2002). While light attenuation was not measured during these two sampling periods, data on light attenuation at this sampling site in December 2010 showed high light attenuation (light attenuation coefficient 0.33 m$^{-1}$) (H. Murphy, unpublished data). Chlorophyll $a$ concentrations were higher in 2010/2011 than the previous two years (H. Murphy, unpublished data), so light attenuation may have been lower during the 24 hour sampling, with more light reaching the 4 m and 8 m strata in 2008/2009 and 2009/2010 compared to 2010/2011. Snapper larvae may have been avoiding the surface due to UV radiation (Browman 2003), and positioned themselves at a depth where there was a trade off between light and prey availability, which resulted in high foraging success and aggregation of snapper larvae at 4 m.
Turbulence may affect the feeding success and vertical behaviour of snapper larvae. The influence of increased microscale turbulence on larval feeding can be positive with increased gut fullness as the size of the prey consumed by larvae increase (Dower et al. 1998), but increased turbulence can also reduce the probability of larvae catching their pursued prey (MacKenzie & Kiorboe 2000, Werner et al. 2001). Obtaining optimal turbulence levels for predator-prey encounters and capture may play an important role in larval vertical behaviour. This question can be addressed by using hydrodynamic modelling of turbulence velocities at different depths within a survey site.

Avoidance of predators may also affect the vertical behaviour of fish larvae (Neilson & Perry 1990). The presence of piscivorous and gelatinous zooplankton predators in the vicinity of fish larval patches could be expected to have an effect on the vertical distribution of fish larvae (e.g. Brewer et al. 1984, Yamashita et al. 1985). While I did not directly measure the presence of gelatinous and piscivorous predators while sampling, future research using echosounders to measure the presence of schooling predators and using surveys to count and identify gelatinous predators would provide information on number and type of predators that larvae are encountering.

Diel vertical migratory behaviour may become more pronounced as marine fish larvae develop ontogenetically (reviewed in Neilson & Perry 1990). I found that snapper larvae aggregated around 4 m during the day irrespective of size class, from newly hatched to flexion. The majority of larvae sampled were 16 days post hatch or younger and it is thought that snapper larvae settle after three to four weeks [at approximately 10-12 mm SL (Battaglene & Talbot 1992)]. I was not able to sample pre-settlement, late-stage snapper larvae, which could be a result of net avoidance via detection of water movement from the net. Alternatively, late-stage snapper larvae may be closely associated with the bottom and therefore were missed by the nets, which fished at approximately 1 m off the bottom for the deepest stratum. In a previous study, settlement-stage snapper larvae were found to demonstrate directional swimming behaviour and were closely associated with the soft bottom of an estuary in New South Wales, Australia (Trnski 2002) and have been previously captured in PPB and Victorian estuaries using a small demersal beam trawl (Hamer & Jenkins 2004). It is possible that
DVM behaviour of late-stage (post-flexion) snapper larvae may be lacking or at least markedly different than the younger larvae.

In conclusion, snapper larvae were found to demonstrate DVM behaviour, specifically nocturnal diffusion and aggregation around the 4 m depth during the day in two rounds of 24 hour sampling. Aggregation of snapper larvae around 4 m during the day appears to be linked to foraging success, although the drivers behind higher foraging success at this depth were unclear as the majority of the measured environmental variables were not stratified in the water column. While it is unlikely that the pattern of nocturnal diffusion and daytime aggregation will change spatially and temporally, further work is required to determine how bottom depth, different climatic conditions (i.e. cloud cover, wind, air pressure), and predator abundance may affect the consistency of the aggregation depth in this species. This study provides further evidence of DVM behaviour in early to flexion-stage fish larval development, and, while in this instance the DVM behaviour may not be directly related to providing a dispersal or retention advantage, the behaviour could have an important influence on horizontal dispersal of larvae and their interactions with prey and predator fields. Irrespective of the proximal drivers of DVM, it is important to consider the nature of this behaviour when attempting to explain and model the processes that influence larval survival and subsequent juvenile recruitment (Leis 2006, 2007).
Chapter 2

Interannual variation in larval survival of snapper (Chrysophrys auratus, Sparidae) is linked to diet breadth and prey availability

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Abstract

Larval snapper, *Chrysophrys auratus* (Sparidae), sampled over seven years had different diets and feeding strategies in lower versus higher larval abundance years. I analysed stomach contents of snapper larvae from each year to determine diet composition, prey selectivity, prey quality and trophic niche breadth, and compared larval diet to sampled prey availability. Snapper larvae from higher abundance years were specialised foragers selecting for calanoid nauplii at 2-4 mm SL and calanoid copepodites and cladocerans at > 4 mm SL. These larvae were characterised by either a constant or dome-shaped trophic niche breadth and an increase in prey quality (size of consumed prey) with increasing larval size. Snapper larvae from lower abundance years were generalist foragers characterised by an increase in trophic niche breadth, but not prey quality, with increasing larval size. Changes in foraging strategies were concordant with changes in the prey environment, with low zooplankton densities corresponding with generalist diet (lower larval abundance) years and high zooplankton densities with specialist diet (higher larval abundance) years. These findings suggest that snapper larval survival and juvenile recruitment strength is linked to changes in larval diet that relate to prey abundance and composition.
Introduction

Understanding recruitment variation is a key focus of fisheries ecologists worldwide (Leggett & DeBlois 1994). Variable recruitment to fish populations is thought to be commonly determined by processes influencing the larval stage (Cushing 1990, Leggett & DeBlois 1994), with prey availability considered a major factor affecting larval survival and juvenile recruitment rates (Hjort 1914, Anderson 1988, Cushing 1990). Food-deprived fish larvae can experience high mortality either directly due to starvation or indirectly through slow growth, which can increase their vulnerability to predation and disease by prolonging larval developmental stages (Bailey & Houde 1989). Cushing’s (1972, 1990) match-mismatch hypothesis proposed that recruitment depends on the magnitude of temporal and spatial overlap in the distributions of food resources and marine fish larvae as larvae move from spawning to nursery areas. Variations of the match-mismatch hypothesis are still used as a framework for studies of recruitment variability, but results of studies linking seasonal production of prey and recruitment variation have been inconsistent (e.g. Fossheim et al. 2006, Lee et al. 2006, McClatchie et al. 2007).

Larval feeding ecology can provide information on the mechanisms underlying recruitment variation of fish populations (Cushing 1990). Fish larvae do not feed indiscriminately, but are selective based on specific prey characteristics (Govoni et al. 1986), such as size, catchability, and visibility (Munk 1997). Furthermore, as visual acuity (Blaxter 1986, Pankhurst 1994) and foraging ability (Scharf et al. 2000) improve throughout ontogeny, changes in prey selectivity, niche breadth, and foraging success can also occur. This is evident in the ontogenetic shift in diet seen in many marine fish larvae from small copepod nauplii at first feeding to copepodites and/or cladocerans later in development (e.g. Robert et al. 2008, Dower et al. 2009, Young et al. 2010). While first feeding larvae are thought to be particularly vulnerable to starvation, there is evidence that matching of intermediate larval life-stages with suitable prey stages can also be important for larval survival (Voss et al. 2006, Dickmann et al. 2007).

Marine fish larvae are commonly thought to experience a food-limited environment (e.g. Hinrichsen et al. 2003), so energy intake must be maximised. One way that fish larvae can increase their energy intake and reduce their susceptibility to starvation is to increase their niche breadth in order to ingest a wide range of prey sizes.
and types (e.g. Reiss et al. 2005). While an increase in niche breadth with larval size has been found in some fish larval feeding studies (Pepin & Penney 1997, Dower et al. 2009), a constant relationship between niche breadth and larval size has been found in others (Pearre 1986, Munk 1997, Voss et al. 2009). A constant relationship between niche breadth and larval size suggests a specialised diet where small prey items are replaced by larger items, resulting in the size ratio between the smallest and largest prey items in the diet remaining the same (Pearre 1986). High prey densities may allow fish larvae to feed on optimal prey sizes or types throughout ontogeny, allowing for a constant niche breadth (Pearre 1986, Scharf et al. 2000). The absence of a general pattern in niche breadth in larval fishes indicates a degree of flexibility in the foraging strategy of fish larvae to changing prey compositions and densities (Munk 1995).

A species known to show high recruitment variability is snapper, *Chrysophrys auratus* (Sparidae) (formerly *Pagrus auratus*) (Francis 1993, Fowler & Jennings 2003, Hamer & Jenkins 2004). Sampling of juvenile snapper has shown high recruitment variability in Australia (Fowler & Jennings 2003, Hamer & Jenkins 2004) and New Zealand (Francis 1993). Recent sampling of snapper larvae in Port Phillip Bay (PPB), Australia has shown that abundances of sampled post yolk-sac larvae closely matched the variation in 0-age snapper densities sampled three months after the larval sampling (P. Hamer unpubl. data, Hamer et al. 2010). Research in New Zealand has also found that interannual variation in juvenile snapper recruitment may originate in the pre-settlement stage rather than later life stages (Francis 1994a, Zeldis et al. 2005). Furthermore, interannual variability in snapper larval abundances was found to be related to variability in primary productivity and mesozooplankton prey populations in New Zealand’s largest snapper spawning area (Zeldis et al. 2005).

This study is based on a seven year (2004-2011) data set of snapper larval densities and a five year (2006-2011) data set of zooplankton densities in PPB, Australia. My aims were to 1) describe the feeding ecology of snapper larvae in PPB by considering diet composition, prey selectivity, trophic niche breadth, prey quality, and prey availability, and 2) investigate the hypothesis that juvenile recruitment variation is related to larval feeding ecology by comparing interannual variation in larval diet to the known interannual variation in juvenile densities.
Methods
Field

Over seven years (2004-2011), ichthyoplankton and zooplankton were sampled during daylight hours from late November to early January at six areas within PPB, Australia, namely Carrum (C), Central Bay (CB), Frankston (F), Hobsons Bay (HB), Mordialloc (M) and Point Wilson (PW), and at Port Phillip Heads (H), the entrance to PPB (Fig. 9). Snapper larvae were previously found to feed only during daylight hours (Murphy et al. 2011). Each area was sampled on at least two occasions, with one sampling time in late November/early December and one sampling time in late December/early January. Sampling across all areas was continuous between late November and early January, so the time between sampling the same area varied from two to four weeks. This sampling period was chosen to overlap with the expected peak spawning period for snapper in Victoria based on previous gonadosomatic index, daily ageing and larval abundance data (Jenkins 1986, Coutin et al. 2003, Hamer et al. 2011).

Zooplankton

Zooplankton was sampled concurrently with the ichthyoplankton from 2006 to 2011. Sampling was conducted with a 30 cm diameter, 80 µm mesh plankton net. When the ichthyoplankton net was at the bottom step (see below), the zooplankton net was clipped to a pulley and allowed to run down until it hit the larger net. Immediately upon reaching the ichthyoplankton net, the zooplankton net was slowly retrieved at a constant rate. The sample was preserved in a 4% buffered formaldehyde solution. A General Oceanics flowmeter (model 2030) was used to determine the volume of water filtered with each tow.

Ichthyoplankton

Detailed information on the sampling method can be found in Hamer et al. (2011). Briefly, on each sampling occasion, five randomly placed, stepped oblique plankton tows were used to sample the entire water column at each area. Ichthyoplankton samples were collected using a 500 µm mesh plankton net with a circular mouth of 80 cm diameter. Five depths were sampled: 0.5 m 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. Each tow consisted of a series of approximately 1.5 minute pauses at each of the 5 depths as the net was lowered.
and again as it was retrieved. Total tow duration varied depending on the water depth, with the average duration being 20 minutes. A General Oceanics flowmeter (model 2030) was used to determine the volume of water filtered each tow. Material from the cod-end was filtered through a 500 µm mesh sieve and immediately preserved in 95% ethanol.

**Figure 9** Map of Port Phillip Bay, Australia. Seven years of sampling was conducted at the following 6 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).

**Laboratory**

**Zooplankton**

In the laboratory, zooplankton samples were sieved through a 40 µm mesh and transferred to freshwater to give a total volume from 200 mL to 2 litres, depending on the concentration of zooplankton in the sample. One mL sub-samples were drawn out of the suspended zooplankton sample with a Hensen-Stempel pipette until at least 200
individuals were counted. Zooplankton was identified to the lowest taxonomic level possible.

*Snapper larvae*

Snapper larvae were identified based on the descriptions in Neira et al. (1998). The standard length (SL, tip of snout to tip of notochord) and gape width (distance between left and right postero-ventral tips of the articular bones (Kiorboe et al. 1985)) of all intact snapper larvae were measured to the nearest 0.1 mm under a dissecting microscope using an ocular micrometer. No adjustments to measured SL were made to account for preservation although minimal shrinkage was likely to have occurred in 95% ethanol (Theilacker 1980). 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 and used for stomach content analysis and the remaining snapper larvae were measured for SL. Each 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 (magnification: 50x). Each food item in the gut contents was identified to lowest possible taxonomic level, and its maximum width (μm) was measured. In the samples from 2008-2011, the prosome length (copepodites) (μm) or total length (nauplii and other prey) (μm) was also measured.

**Data analysis**

*Zooplankton*

Zooplankton abundances per m³ were calculated using the formula:

\[ D = (NV_S)(NAV)^{-1} \]

Where N is number of organisms; \( N_A \) is the number of 1 mL aliquots; \( V_S \) is the volume of the subsample (mL); and \( V \) is the volume of water (m³) filtered through the zooplankton net measured by the flowmeter.

Zooplankton data were \( \log_{10} (x+1) \) transformed to meet assumptions of normality (Shapiro-Wilk test: \( p > 0.05 \)) and homogeneity of variances (Levene’s test: \( p > 0.05 \)). Analysis of variance (ANOVA) was used to determine if there was variation in zooplankton densities amongst years, sampling areas, and sampling times.
**Snapper larvae**

For description of the diet of snapper larvae, snapper were grouped into 1 mm SL size classes. I calculated the %N of prey items, which is the number of individuals of each prey type as a percentage of the total number of prey items found in the stomachs of the larvae in each year. I pooled larvae for tow (replicate), sampling time and area for each year as differences in diet varied more between years than within years, with the exception of 2009/2010.

For the analysis of prey selectivity in snapper larvae, I compared mean zooplankton densities to the diet of snapper larvae from each round of sampling from 2006-2011. I only did selectivity analyses on the main preferred zooplankton prey, namely calanoid nauplii (*Paracalanus* spp. and *Acartia* spp.), calanoid copepodes (*Paracalanus* spp., *Gladioferens inermis*, *Bestiola similis*), bivalve veligers, and cladocerans (three genera: *Podon*, *Evdane*, *Penilia*), rather than all potential prey types (e.g. Jenkins 1987). Based on changes in diet composition, I grouped snapper larvae into two categories for prey selection analysis: 2.0-3.9 and 4.0-6.0 mm SL. Pearre’s C index of prey selection was used to statistically test, using $X^2$, the selectivity of prey categories in the diet (Pearre 1982). The index was calculated as

$$C = \pm \left[ \frac{(|a_d b_e - b_d a_e| - n/2)^2}{a b d e} \right]^{1/2}$$

Where $C$ is Pearre’s index for snapper larval selection of prey $a$, where $a_d$ is the abundance of prey $a$ in the diet, $b_e$ is the abundance of all other prey in the environment, $b_d$ is the abundance of all other prey in the diet, and $a_e$ is the abundance of prey $a$ in the environment. Values without subscripts are expressed as: $a = a_d + a_e$, $b = b_e + b_d$, $d = a_d + b_d$, $e = a_e + b_e$ and $n = a_d + a_e + b_d + b_e$. The sign of $C$ is based on $(a_d b_e - b_d a_e)$, and the index varies from -1 (prey avoidance) to +1 (prey selection), with 0 indicating random prey selection (Pearre 1982).

In order to investigate prey size-related trends in feeding, I used trophic niche breadth as a measurement of the range of prey sizes foraged upon by snapper larvae. Trophic niche breadth is the standard deviation of log-transformed mean prey widths (Pearre 1986). Since larval diet and prey selection varied more between years than within years, I grouped snapper larvae into 0.5 mm SL length classes, pooling for
sampling area and time, to obtain the maximum number of larval size classes that contained at least three larvae with one or more prey items in their stomachs (Pearre 1986, Pepin & Penney 1997). Weighted regressions, using total number of prey per length category, were used to determine the relationship between trophic niche breadth and larval size for each year.

Differences in prey quality in the larval diet were investigated using prey width as a direct measurement of prey quality as larger prey were generally higher in estimated carbon content based on literature values for calanoid nauplii (Hygum et al. 2000), bivalve veligers (Omori 1969, Jespersen & Olsen 1982), calanoid copepodites (Hay et al. 1991, Mauchline 1998), and cladocerans (Uye 1982). Snapper larvae in each cohort were grouped into 0.5 mm SL length classes, pooling for sampling area and time, so trends in prey width with increasing larval size could be related with changes in niche breadth and diet composition. All statistical tests were performed using SYSTAT 12 statistical package.
Results
Zooplankton abundance

While the zooplankton samples contained many taxa, including larvaceans, cyclopoid copepodes, and harpacticoids, I focused on the zooplankton taxa that were the main diet components of snapper larvae. These prey items were calanoid nauplii (*Paracalanus* spp. and *Acartia* spp.), calanoid copepodites (*Paracalanus* spp. *Gladioferens inermis*, *Bestiola similis*), cladocerans (*Podon*, *Evadne*, *Penilia*), and bivalve veligers. The samples from area H (Port Phillip Heads) were excluded from the analyses as the zooplankton densities were very low and very few larvae were sampled in this area (82 snapper larvae or 4% of total larvae collected over seven years).

A three factor ANOVA (year, sampling area, and sampling time) indicated a significant interactive effect amongst year, sampling area, and sampling time on log-transformed zooplankton densities \(F_{20, 245} = 2.338, p = 0.001\). Using post hoc Tukey’s tests, total densities of the preferred main diet components in 2006/2007 were significantly lower than 2007/2008, 2008/2009, and 2009/10 (all \(p < 0.01\)), prey densities in 2007/2008 were significantly lower than 2009/2010 (\(p = 0.02\)), and prey densities in 2010/2011 were significantly lower than 2008/2009 and 2009/2010 (Fig. 10). Differences in preferred zooplankton densities varied by up to two fold between higher and lower years. Post hoc Tukey’s tests indicated there was no significant difference in prey densities between sampling times (\(p > 0.05\)), and no significant differences amongst areas (\(p > 0.05\)). When graphs were examined, prey densities were lower at HB compared to other areas, and, in sampling time two, prey densities were higher in 2009/2010 and 2007/2008, and lower in 2006/2007 and 2008/2009 (Fig. 10).

Three factor ANOVAs (year, sampling area, sampling time) for log-transformed individual taxa/genera indicated significant interactions amongst year and sampling area for calanoid nauplii \(F_{20, 245} = 2.766, p < 0.001\) and calanoid copepodites \(F_{20, 245} = 5.103, p < 0.001\). Post hoc Tukey’s tests indicated that calanoid nauplii densities were significantly lower in 2006/2007 and 2010/2011 compared to the other four years (all \(p < 0.01\) and higher in 2009/2010 compared to 2007/2008 and 2008/2009 (all \(p < 0.05\)) (Fig. 10). Post hoc Tukey’s tests indicated there was no significant difference in calanoid nauplii densities between areas (\(p > 0.05\)), although, when graphs were examined, nauplii densities were higher at F compared to C and HB (not shown).
Densities of calanoid nauplii varied as much as five times between higher and lower larval abundance years. Post hoc Tukey’s tests indicated that calanoid copepodites had greater densities in 2008/2009, 2009/2010, 2010/2011 compared to 2006/2007 and 2007/2008 (all \( p < 0.01 \)) (Fig. 10). Calanoid copepodite densities were greater at CB compared to HB and PW areas (post hoc Tukey’s tests: all \( p < 0.05 \)) (not shown). For log-transformed cladoceran densities, there was a significant interaction amongst year, sampling area, and sampling time \( (F_{20,245} = 2.651, p < 0.001) \). Post hoc Tukey’s tests indicated that cladoceran densities were lower in 2006/2007 and 2008/2009 compared to the other three years (all \( p < 0.010 \)) and there were higher cladoceran densities in sampling time 1 \( (p < 0.001) \) (Fig. 10). Densities of cladocerans were greater at CB and F compared HB and PW areas (not shown) (post hoc Tukey’s tests: all \( p < 0.05 \)).

**Figure 10** Mean densities of total preferred prey (■), calanoid nauplii (□), calanoid copepodites (■), and cladocerans (■) in (a) sampling time one and (b) sampling time two. Mean ±SE values shown.

**Fish larval abundance, diet, and prey quality**
Over the seven years, 1969 snapper larvae were sampled. Larval abundance varied amongst the seven years of sampling with higher abundances found in four years (2004/2005, 2007/2008, 2008/2009, 2009/2010) and lower abundances found in three years (2005/2006, 2006/2007, 2010/2011) (Table 3). This pattern of interannual variation in larval abundance was closely matched by the variation in juvenile densities sampled three months after the larval sampling (P. Hamer, unpubl. data, Hamer et al. 2010, Table 3). The majority of snapper larvae were sampled in sampling time one in the eastern areas (F, C, M) of PPB (Table 3), which corresponds with the main suggested spawning area for snapper (Hamer et al. 2010). The majority of snapper larvae sampled (95%) were in the size range of 2-6 mm SL, which corresponds with 3-12 days post hatch (H. Murphy unpubl. data). Mean temperature varied between years, with highest mean temperatures in 2007/2008 (20.8 ±0.5 ºC) and 2009/2010 (20.8 ±0.6 ºC), both higher abundance years, and lowest in 2006/2007 (18.6 ±0.8 ºC) and 2008/2009 (17.8 ±0.6 ºC), a lower and higher abundance year, respectively. Undersampling of small snapper larvae may have occurred due to the mesh size of the nets, as no yolk-sac snapper larvae were sampled and 40% more larvae sized 3-4 mm SL than larvae 2-3 mm SL, which would not be an expected pattern driven by mortality. A similar result was found in New Zealand, where snapper larvae less than 3 mm SL were undersampled using an 365 μm net (Zeldis et al. 2005). Also, very few late-stage pre-settlement snapper larvae were sampled [10-12 mm SL (Battaglene & Talbot 1992)].

In addition to the main prey types found in the stomachs of the seven cohorts of snapper larvae, prey items that were not present consistently across years included invertebrate eggs, decapod zoea, harpacticoid copepodites, harpacticoid nauplii, polychaete larvae, and fish larvae. High larval abundance years were characterised by a shift from predominately copepod nauplii at 2-4 mm SL to cladocerans (2004/2005 and 2008/2009) or copepodites (2009/2010) at > 4 mm SL (Fig. 11). In 2007/2008, very few (20%) snapper larvae > 4 mm SL had prey in their stomachs, but a shift to larger prey was evident (Fig. 11 b). Snapper larvae in 2009/2010 had an unusual diet that included snapper larvae, other fish larvae, and a high number of bivalve veligers, which was not seen in other years (Fig. 11 d). However, the majority of snapper larvae in 2009/2010 were sampled at one area (PW) in sampling time one. Larval diet in lower abundance
years (2005/2006, 2006/2007, 2010/11) did not have as clear a shift in diet composition at 4 mm SL compared to higher abundance years (Fig. 12). In lower abundance years, calanoid nauplii were important prey items for smaller larvae (2-4 mm SL), and a range of prey items occurred in the diet of larvae > 4 mm SL, including cladocerans, copepodites, calanoid nauplii, and bivalve veligers (Fig. 12).

**Table 3** *Chrysophrys auratus.* Total number of snapper larvae sampled, number analysed, mean larval length, and sampling area where majority of larvae were sampled in each sampling round (sampling 1: late November/ early December; sampling 2: late December/ early January). Areas: Frankston (F), Mordialloc (M), Point Wilson (PW), and Port Phillip Heads (H). Recruitment rank of high (H) or low (L) based on density of juvenile snapper (source: P. Hamer unpubl. data, Hamer et al. 2010).

<table>
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<tr>
<th>Round</th>
<th>Total sampled</th>
<th>Total analysed</th>
<th>Mean length (mm) (±SD)</th>
<th>Area sampled</th>
<th>Densities juvenile snapper</th>
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<tr>
<td>2004/2005</td>
<td>1 521</td>
<td>368</td>
<td>4.39 (±0.96)</td>
<td>F, M H</td>
<td></td>
</tr>
<tr>
<td></td>
<td>2 63</td>
<td>58</td>
<td>4.72 (±1.65)</td>
<td>H</td>
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<tr>
<td>2005/2006</td>
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<td>31</td>
<td>3.05 (±0.61)</td>
<td>F L</td>
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<tr>
<td>2006/2007</td>
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<td>63</td>
<td>4.08 (±0.81)</td>
<td>F L</td>
<td></td>
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<tr>
<td></td>
<td>2 42</td>
<td>42</td>
<td>4.30 (±1.14)</td>
<td>F</td>
<td></td>
</tr>
<tr>
<td>2007/2008</td>
<td>1 213</td>
<td>147</td>
<td>3.46 (±0.64)</td>
<td>M, C H</td>
<td></td>
</tr>
<tr>
<td></td>
<td>2 102</td>
<td>95</td>
<td>3.03 (±0.50)</td>
<td>F</td>
<td></td>
</tr>
<tr>
<td>2008/2009</td>
<td>1 245</td>
<td>172</td>
<td>3.23 (±0.63)</td>
<td>F H</td>
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<td>2 350</td>
<td>151</td>
<td>3.36 (±0.53)</td>
<td>F</td>
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<tr>
<td>2009/2010</td>
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<td>148</td>
<td>3.93 (±0.73)</td>
<td>PW H</td>
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<td>2010/2011</td>
<td>1 30</td>
<td>30</td>
<td>3.73 (±0.31)</td>
<td>F L</td>
<td></td>
</tr>
<tr>
<td></td>
<td>2 5</td>
<td>5</td>
<td>4.81 (±1.22)</td>
<td>M</td>
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</table>
Figure 11 Percent composition of main prey items in the diet of *Chrysophrys auratus* larvae in 1 mm SL size classes in the following four higher larval abundance years, pooling across sampling areas and times: (a) 2004/2005, (b) 2007/2008, (c) 2008/2009, and (d) 2009/2010. Number of *Chrysophrys auratus* larvae used in the analysis and the proportion of snapper larvae with food in their stomachs are indicated above each size class. Calanoid nauplii (Nau), bivalve veligers (Bvel), cladocerans (Cla) and calanoid ay have been a refl
Figure 12 Percent composition of main prey items in the diet of *Chrysophrys auratus* larvae in 1 mm SL size classes in the following three lower larval abundance years, pooling across sampling areas and times: (a) 2005/2006, (b) 2006/2007, and (c) 2010/2011. Number of *Chrysophrys auratus* larvae used in the analysis and the proportion of larvae with food in their stomachs are indicated above each size class. Calanoid nauplii (Nau), bivalve veligers (Bvel), cladocerans (Cla) and calanoid copepodites (Cop).

Using Pearre’s C index for prey selection, there was a general pattern of prey selection amongst years. For snapper larvae 2.0-3.9 mm SL, there was positive selection for calanoid nauplii, negative selection for copepodites, and close to neutral selection for cladocerans and bivalve veligers (except in 2009/2010) (Table 4). Only three cohorts were considered (2006/2007, 2008/2009, and 2009/2010) when analysing prey selectivity of larvae 4.0-6.0 mm SL due to low numbers of large larvae with prey in their stomachs in samples from 2007/2008 and 2010/2011. The pattern of prey selection was mainly positive for cladocerans (significant in 2008/2009) and calanoid nauplii and negative for calanoid copepodites (significant in 2008/2009) and bivalve veligers, with exception of significant positive selection for bivalve veligers in 2009/2010 (Table 4).
Intra-annual and interannual differences in prey selection were also found. For example, there was strong positive selection for cladocerans and bivalve veligers in 2008/2009 and 2009/2010, respectively, in sampling time one only (Table 4). Two higher larval abundance years (2008/2009 and 2009/2010) also had stronger prey selection than the other years (Table 4).

In three of the four high larval abundance years, there was no relationship between trophic niche breadth and larval size (Table 5) (Fig. 13 a). In 2004/2005, the highest larval abundance year with the largest size range of sampled larvae, the relationship between trophic niche breadth and larval size was linear when larval length categories were restricted to 5.0 mm SL ($r^2 = 0.811$, $y = 0.042x - 0.011$, $p = 0.014$, $n = 6$). However, when larger larval size categories (5.5-7.5 mm SL) were included in the analysis, the relationship between trophic niche breadth and larval length was best described with a second order polynomial regression, with its maximum at 4.0 mm SL (Table 5) (Fig. 13 b). In two of the three lower larval abundance years, there was a significant linear relationship between trophic niche breadth and larval size (Table 5) (Fig. 13 c). There were insufficient snapper larvae with food in their stomachs to analyse niche breadth in 2010/2011.

When considering the main prey items in the larval stomachs, cladocerans (mean width: 161 ± 54.4 μm; estimated carbon content: 0.17 ± 0.15 μg C) and calanoid copepodites (mean width: 156 ± 77.4 μm; estimated carbon content: 0.11 ± 0.08 μg C) were the largest prey items, followed by bivalve veligers (mean width: 93 ± 25.4 μm; estimated carbon content: 0.004 ± 0.003 μg C) and calanoid nauplii (mean width: 69.1 ± 17.6 μm; estimated carbon content: 0.09 ± 0.03 μg C). In three of the four higher larval abundance years, mean prey width increased with larval length (Fig. 14 a). Mean prey width increased three to six times from smallest to largest larvae in these years. In 2007/2008, a high larval abundance year, there were few large larvae with prey in their stomachs; however, prey widths increased 30% from 2 to 4 mm SL in this year (Fig. 13 a). In the three lower abundance years, mean prey width did not increase with larval length (Fig. 14 b).
Table 4 Values of Pearre’s “C” selection index for predation by snapper larvae on four main diet components: calanoid nauplii (Nau), bivalve veligers (Bvel), cladocerans (Cla) and calanoid copepodites (Cop). * Indicates value is significantly different than 0 (p < 0.05).

<table>
<thead>
<tr>
<th>Sampling round</th>
<th>Size class (mm)</th>
<th>Prey type</th>
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<td></td>
<td></td>
<td>Nau</td>
<td>Bvel</td>
<td>Cla</td>
<td>Cop</td>
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<td>2006/2007 1</td>
<td>2.0-3.9</td>
<td>0.002</td>
<td>-0.058</td>
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<td>4.0-6.0</td>
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<td>2.0-3.9</td>
<td>0.024</td>
<td>0.006</td>
<td>0.025</td>
<td>-0.136</td>
<td></td>
</tr>
<tr>
<td></td>
<td>4.0-6.0</td>
<td>-0.053</td>
<td>-0.002</td>
<td>0.014</td>
<td>-0.082</td>
<td></td>
</tr>
<tr>
<td>2007/2008 1</td>
<td>2.0-3.9</td>
<td>0.014</td>
<td>-0.093</td>
<td>-0.021</td>
<td>-0.003</td>
<td></td>
</tr>
<tr>
<td>2</td>
<td>2.0-3.9</td>
<td>0.029</td>
<td>-0.073</td>
<td>0.001</td>
<td>-0.059</td>
<td></td>
</tr>
<tr>
<td>2008/2009 1</td>
<td>2.0-3.9</td>
<td>0.013</td>
<td>-0.018</td>
<td>0.002</td>
<td>-0.152*</td>
<td></td>
</tr>
<tr>
<td></td>
<td>4.0-6.0</td>
<td>-0.064</td>
<td>-0.012</td>
<td>0.316*</td>
<td>-0.176*</td>
<td></td>
</tr>
<tr>
<td>2</td>
<td>2.0-3.9</td>
<td>0.207*</td>
<td>-0.062</td>
<td>0.057</td>
<td>-0.156*</td>
<td></td>
</tr>
<tr>
<td></td>
<td>4.0-6.0</td>
<td>0.100</td>
<td>-0.067</td>
<td>0.017</td>
<td>-0.167*</td>
<td></td>
</tr>
<tr>
<td>2009/2010 1</td>
<td>2.0-3.9</td>
<td>0.013</td>
<td>0.121</td>
<td>-0.029</td>
<td>-0.159*</td>
<td></td>
</tr>
<tr>
<td></td>
<td>4.0-6.0</td>
<td>-0.019</td>
<td>0.303*</td>
<td>0.029</td>
<td>-0.158*</td>
<td></td>
</tr>
<tr>
<td>2</td>
<td>2.0-3.9</td>
<td>0.100</td>
<td>-0.020</td>
<td>-0.022</td>
<td>-0.080</td>
<td></td>
</tr>
<tr>
<td></td>
<td>4.0-6.0</td>
<td>0.066</td>
<td>-0.031</td>
<td>-0.022</td>
<td>-0.070</td>
<td></td>
</tr>
<tr>
<td>2010/2011 1</td>
<td>2.0-3.9</td>
<td>0.188*</td>
<td>-0.040</td>
<td>-0.036</td>
<td>-0.057</td>
<td></td>
</tr>
</tbody>
</table>
Table 5 Interannual relationships between niche breadth $S$ to *Chrysophrys auratus* larval length $L$ (mm), with $r^2$ values and the number of 0.5 mm length categories ($n$) used in the analyses. Larval abundances are categorised as higher (H) or lower (L).

<table>
<thead>
<tr>
<th>Year</th>
<th>Larval abundance</th>
<th>Model</th>
<th>$n$ (categories of SL)</th>
<th>$r^2$</th>
<th>$p$</th>
</tr>
</thead>
<tbody>
<tr>
<td>2004/2005</td>
<td>H</td>
<td>$S = -0.0171 (L)^2 + 0.1746 (L) - 0.2527$</td>
<td>10 (2.5-7.5)</td>
<td>0.821</td>
<td>0.001</td>
</tr>
<tr>
<td>2005/2006</td>
<td>L</td>
<td>$S = 0.0844 (L) - 0.1181$</td>
<td>7 (2.0-5.0)</td>
<td>0.900</td>
<td>0.001</td>
</tr>
<tr>
<td>2006/2007</td>
<td>L</td>
<td>$S = 0.068 (L) - 0.057$</td>
<td>6 (2.0-5.0)</td>
<td>0.775</td>
<td>0.021</td>
</tr>
<tr>
<td>2007/2008</td>
<td>H</td>
<td>$S = 0.059 (L) - 0.042$</td>
<td>5 (2.0-4.0)</td>
<td>0.455</td>
<td>0.211</td>
</tr>
<tr>
<td>2008/2009</td>
<td>H</td>
<td>$S = 0.012 (L) + 0.059$</td>
<td>7 (2.0-5.0)</td>
<td>0.211</td>
<td>0.360</td>
</tr>
<tr>
<td>2009/2010</td>
<td>H</td>
<td>$S = 0.020 (L) + 0.009$</td>
<td>6 (2.5-5.0)</td>
<td>0.201</td>
<td>0.373</td>
</tr>
</tbody>
</table>
Figure 13 Trophic niche breadth (standard deviation of the log prey width) regressed against 0.5 mm *Chrysophrys auratus* larval size categories, pooling for sampling area and time, for: (a) three higher larval abundance years (2007/2008, 2008/2009, 2009/2010), which showed no relationship between trophic niche breadth and larval length, (b) 2004/2005, a higher larval abundance year in which there was a polynomial relationship between trophic niche breadth and larval length and (c) two lower larval abundance years (2005/2006 and 2006/2007).
Figure 14 Trend of mean prey width by 0.5 mm *Chrysophrys auratus* larval size categories, pooling for sampling area and time, for: (a) four higher larval abundance years (2004/2005, 2007/2008, 2008/2009, 2009/2010) and (b) three lower abundance years (2005/2006, 2006/2007, 2010/2011). Mean ±SE values shown.
Discussion

Snapper larvae from higher abundance years were specialist foragers while larvae from lower abundance years were generalist foragers. While there was evidence of a mismatch between larval abundances in 2007/2008 and 2009/2010 (higher in sampling time one) and zooplankton densities (higher in sampling time two), both of these years were higher larval abundance years, which suggests that differences in foraging strategy appears to be more related to variability in interannual, rather than intra-annual, prey fields. Preferred zooplankton prey densities were up to two times greater, and calanoid nauplii densities as much as five times greater, in years of higher larval abundance compared to lower abundance years. The importance of an interannual match in larval abundance and prey availability was also been found in New Zealand, where, in a three year study, higher snapper larval abundance occurred in a year characterised by naupliar densities up to four times higher than two lower abundance years (Zeldis et al. 2005).

While the smallest and largest size classes of snapper larvae were undersampled, high numbers of first-feeding and flexion larvae were sampled, which provides insight into their diet and foraging strategies and encompasses a key developmental and feeding transition. The diet of snapper larvae 2-4 mm SL in both higher and lower abundance years was dominated by copepod nauplii. In higher abundance years, snapper larvae > 4 mm SL had a diet dominated by cladocerans or calanoid copepodites. In lower abundance years, the diet of larvae > 4 mm SL was not dominated by any one prey type. While the majority of marine fish larvae switch from copepod nauplii in the early life-history stages to calanoid copepodites in later life-history stages (e.g. Pepin & Penney 1997, Voss et al. 2003), the switch from copepod nauplii to cladocerans has also been found in several species (e.g. Dickmann et al. 2007, Robert et al. 2008). Cladocerans, particularly *Podon* and *Evadne*, have large, distinctive black eyes that contrast with the environment and red pigmentation on their bodies, which may make them easier to detect than calanoid copepodites (Zaret 1980, Wong et al. 2008). Furthermore, capture success of cladocerans by fish larvae is usually higher than capture success of copepods, probably due to copepods being more evasive and faster swimmers than cladocerans (Drenner et al. 1978, Mills et al. 1984).
Calanoid nauplii are an important prey item for first-feeding snapper larvae, and the interannual pattern of larval abundance is closely matched to calanoid nauplii densities. A mismatch between calanoid nauplii production and larval developmental stages in 2006/2007 may have increased the risk of larval starvation and prompted a generalist feeding strategy (Cushing 1972, 1990). Furthermore, the match of specific prey types and recruitment success may not be limited to the first-feeding stage, but also when larvae switch from feeding on calanoid nauplii to larger prey items such as copepodites and cladocerans (Voss et al. 2006, Robert et al. 2008, Laurel et al. 2011). The majority of preferred prey of snapper larvae had higher densities in the higher recruitment years, which was also seen in the high recruitment year of the New Zealand study by Zeldis et al. (2005). However, while calanoid copepodite and cladoceran densities were low in 2006/2007, they had average densities in 2010/2011. Low survival of snapper larvae in 2010/2011 may indicate that the shift from calanoid nauplii to larger prey types is less important than a match in prey type for first-feeding larvae. In support of this finding, larval year class strength was determined shortly after first feeding in New Zealand snapper larvae (Zeldis et al. 2005).

Snapper larvae actively selected for prey and did not randomly forage on all available prey types in their environment. This was especially evident in the strong negative selection against cyclopoid copepods, which never occurred in the larval diet in any of the years, even though cyclopoid copepods were present in all zooplankton samples. This may have been due to the differences in swimming behaviour of cyclopoids and calanoids (Buskey et al. 1993), with the less active cyclopoids not as vulnerable to predator detection (Williams & Brown 1991). In both larval size classes, calanoid copepodites were consumed in disproportionately small numbers compared to their densities in the environment. Negative selection for calanoid copepodites has been found in other studies where cladocerans have been the main prey for intermediate-sized marine fish larvae (e.g. Robert et al. 2008).

Prey selectivity varied between sampling times, especially in two of the higher abundance years (2008/2009 and 2009/2010). This variation in prey selection may have been a reflection of the variable prey densities between sampling times in these years (higher in sampling time one in 2008/2009 and higher in sampling time two in 2009/2010). Furthermore, piscivory by snapper larvae was found only in 2009/2010 at
sampling time one at PW area, which was also the only sampling time snapper larvae were selecting positively for bivalve veligers. The high prevalence of bivalve veligers in the larval diet in combination with lower prey densities indicate a potential mismatch between preferred zooplankton prey and larval distribution, which may have promoted piscivory at the PW area, as cannibalism is more common during periods of starvation or hunger (Folkvord 1991). While there were differences in prey selectivity between sampling times, the overall pattern of prey selection was consistent amongst years, with selection for calanoid nauplii and cladocerans and against calanoid copepodites. Prey selection was also weaker in lower larval abundance years. Prey selectivity has been found to decrease with decreasing prey concentrations, which has been interpreted as a fish larval foraging strategy to increase prey consumption (Munk 1995).

There were three types of relationships between trophic niche breadth and larval size in snapper, which demonstrates the flexibility in foraging strategies in this species. In the first type, niche breadth did not increase with larval size in three of the four higher abundance years. This constant relationship between niche breadth and larval size indicates selective foraging by fish larvae, with the replacement of calanoid nauplii with cladocerans or copepodites at ~ 4 mm SL, resulting in the relative size ratio of the smallest and largest prey items in the diet staying the same as the larvae shifted to larger prey in higher abundance years. A constant relationship between niche breadth and larval size has been seen in other species (e.g. Munk 1997, Voss et al. 2009). In these three higher abundance years, prey quality in the diet, measured as prey width, increased with larval size, which was a reflection of specialisation on more profitable prey items, such as cladocerans and calanoid copepodites.

In the second type of relationship, seen only in the highest abundance year 2004/2005, snapper larvae had a polynominal relationship between niche breadth and larval size, with its maximum around 4 mm SL. The largest size range of snapper larvae was sampled in 2004/2005, and trophic niche breadth was narrow early and late in development, where larvae specialised on copepod nauplii and cladocerans, respectively. This pattern of trophic niche breadth was also found in Atlantic bluefin tuna Thunnus thynnus, with transitions between specialised and generalised diets throughout development (Catalan et al. 2011). Prey quality increased with larval size in this year, even when a generalist foraging strategy was evident early in development.
Zooplankton densities were not sampled in this year, but this pattern of niche breadth indicates the flexibility of larvae to react to potentially varying prey environments. Furthermore, the high abundances of 0-age snapper from this year (P. Hamer unpubl. data, Hamer et al. 2010) indicates this foraging strategy of generalised and specialised diets throughout ontogeny resulted in high larval survival.

In the third type of relationship, for two of the lower abundance years, 2005/2006 and 2006/2007, trophic niche breadth increased with larval size. In these years snapper larvae were employing a generalist feeding strategy by including both small and large prey sizes in their diet with increasing larval size, rather than switching exclusively to larger prey around 4 mm SL. This resulted in an increasing size ratio between the smallest and largest prey items in the diet throughout ontogeny. In spite of this, prey selectivity was still evident and non-preferred prey items, such as cyclopoid copepodites, were not included in the diet.

Furthermore, prey quality did not increase with larval size in the three lower abundance years (2005/2006, 2006/2007, and 2010/2011), which suggests generalist foraging strategies in 2005/2006 and 2006/2007 did not allow larvae to maximise their energy intake, unlike larvae in 2004/2005 (Munk 1995, Dickmann et al. 2007). A six year study of radiated shanny Ulvaria subbifurcata larval diet and prey availability found that an increase in trophic niche breadth with larval size did not necessarily correspond with an increase in the prey consumption rate (energy intake) (Young et al. 2010). The ability of fish larvae to adapt their foraging strategies to variable prey environments may provide a survival advantage by allowing fish larvae to feed at low prey densities (Munk 1995). The size range of larvae sampled in these lower abundance years was 2-6 mm SL, and the pattern of trophic niche breadth may change with larval size, as seen in 2004/2005. However, the low abundances of 0-age snapper sampled in 2005/2006, 2006/2007, and 2010/2011 (P. Hamer unpubl. data, Hamer et al. 2010) suggests there were limited survival advantages from a generalist larval foraging strategy that did not result in an increase in prey quality in the diet.

The relationship between zooplankton densities, larval diet, feeding strategy and larval survival suggests that understanding the biophysical process influencing prey availability and composition is an important factor to being able to predict recruitment fluctuations in this species. Correlative studies between environmental variables, such
as temperature and salinity, and fish recruitment are common in the literature, but often breakdown over time (Myers 1998). Recruitment in snapper has been positively correlated with water temperature in the juvenile stage in New Zealand (Francis 1993); however, the relationship with water temperature is less straightforward in this study as cooler temperatures were found in both higher and lower larval abundance years. Similarly, sea surface temperature remained fairly constant throughout the three year study period in New Zealand, but variation in snapper larval abundances occurred (Zeldis et al. 2005). While temperature is known to be an important influence on larval growth rates (Anderson 1988, Houde 1989), food densities, photoperiod, and temperature can all be correlated with larval growth, and it is important to tease apart these relationships (Buckley & Durbin 2006). Ongoing studies of mechanisms driving recruitment variation in snapper will involve determining growth rates of snapper larvae from otolith microstructure to further investigate the inter-relationships between temperature, prey availability and larval survival.

There have been fewer correlative studies linking prey availability and recruitment (Runge et al. 1999, Beaugrand et al. 2003, Castonguay et al. 2008). In New Zealand, a three year study suggested that increased survival of the larval fish guild, including snapper, was related to physically-driven higher production of phytoplankton and mesozooplankton (Zeldis et al. 2005). Current research investigating the link between nutrients, phytoplankton, and zooplankton productivity may indicate that similar relationships are occurring in PPB. The strength of the link between prey availability, larval foraging, and larval abundance in this study suggests that larval survival and 0-age snapper recruitment could be predicted by development of biophysical models (Megrey et al. 2007, Rose et al. 2008, Hinckley et al. 2009).

In conclusion, snapper larvae in this long-term study showed flexibility in feeding strategies, which maximised their feeding potential; however, broadening of trophic niche breadth without increasing prey quality in the diet in low density prey fields did not result in high survival in this species, as measured by larval abundances. This may have been due to a mismatch between prey availability, especially calanoid nauplii, and the occurrence of larvae in lower abundance years. Patterns of larval abundance were matched by observed variation in 0-age snapper densities, which emphasises the importance of understanding how factors such as prey availability and
larval foraging affect larval survival, as this appears to be the main driver of recruitment variation in this species.
Chapter 3
Zooplankton prey availability and consumption rates drive interannual variation in larval abundance and growth in a temperate marine fish
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 large-at-age and/or fast growing 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 juvenile recruitment variation, which is closely related to variation in larval abundance. Using a six year data set of snapper larval abundance, I assessed whether growth-rate dependent effects on larval survival were a driver of recruitment variation. Larval abundances were higher in three of the six years. Average daily growth rates, estimated from otolith daily rings, were positively related to larval abundances, with higher abundance years characterised by higher growth rates. Daily growth trajectories diverged amongst higher and lower abundance years early in development. Cladoceran prey densities best explained interannual variation in growth, indicating a direct link between prey availability and larval growth. Foraging success, measured as carbon content of ingested prey, was also higher in the two years with the fastest larval growth. Temperature was found to be less important to larval growth than prey availability. Fast growth in higher larval abundance years indicates the importance of prey production to recruitment dynamics of marine fish populations.
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 larval characteristics (e.g. size, condition, growth rate) of these organisms, such as fishes, provides important information on 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/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 (Anderson 1988). The growth-mortality hypothesis is comprised of three distinct, but related, mechanisms (hypotheses): bigger-is-better (e.g. Litvak & Leggett 1992, Leggett & DeBlois 1994), where larger-at-age larvae are less vulnerable to predation; stage-duration (Chambers & Leggett 1987), where faster growing larvae spend less time in the vulnerable larval stage; and growth-selective, where the growth rate of the individual larva may influence its probability of capture independent of size or developmental stage (Takasuka et al. 2003, Takahashi & Watanabe 2004, Takasuka et al. 2004). The growth-mortality hypothesis and its three mechanisms have received broad acceptance in fisheries science, with large-at-age fish larvae and/or fast larval growth often associated with high survival and recruitment (e.g. Hare & Cowen 1997, Jenkins & King 2006, Meekan et al. 2006). However, some studies have found that growth the juvenile stage (Campana 1996) is more important for high recruitment success, while others have found no relationship between fast growth in the early life history stages and recruitment (van der Veer et al. 1994, Bailey et al. 1996, Ringuette et al. 2002). Because observed variation 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 (e.g. Cushing 1972, 1990) and temperature (Houde 1987) are considered the most important underlying processes that influence variation in fish larval growth, with turbulence (Dower et al. 1998) and light availability (Buckley et al. 2006) 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 (Buckley & Durbin 2006, Robert et al. 2009). 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, Robert et al. 2009, Sponaugle et al. 2009), suggesting that knowledge of factors affecting larval growth can be key to understanding the link between the abiotic and biotic 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). However, variation in larval growth rates has been found in the absence of temperature variation (Sponaugle et al. 2009). Furthermore, food densities, photoperiod, and temperature can all be correlated with larval growth, and it is important to tease apart these relationships (Buckley & Durbin 2006, Robert et al. 2007). Long-term data sets and modelling can be useful in investigating the effects of these confounding variables on larval growth rates and survival (Buckley & Durbin 2006).

A model temperate marine fish species with a long-term record of high recruitment variability is 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 variation in this species (Fowler & Jennings 2003, Zeldis et al. 2005, Hamer et al. 2010). To explore this hypothesis more comprehensively, I aimed to determine if years of high larval abundance were correlated with fast larval growth, and, if true, identify the proximate mechanisms.
driving this pattern. I utilised samples from a six year data set of snapper larval abundances in Port Phillip Bay (PPB), Australia to 1) determine interannual variation in daily growth rates and growth trajectories and 2) test whether interannual variation in growth was related to variation in foraging success, prey availability and/or temperature.
Methods
Field

Ichthyoplankton sampling

For seven years (2004/2005 to 2010/2011), from late November to early January, ichthyoplankton was sampled at six areas within Port Phillip Bay (PPB), Australia (Fig. 15). 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). These sampling methods have been previously described in Hamer et al. (2011). Briefly, on each sampling occasion, five randomly placed plankton tows were conducted within each area, and each area was sampled on two 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 tow consisted of a series of approximately 1.5 minute pauses at each of the five depths as the net was lowered and again as it was retrieved. The five 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 one meter above the bottom. Total tow duration varied depending on the depth, with the average duration being 20 minutes. A General Oceanics flowmeter (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.

Laboratory

Otolith preparation and analysis

Snapper larvae were identified based on the descriptions in Neira et al. (1998). The standard length (SL, tip of snout to tip of notochord) of all intact snapper larvae was measured to the nearest 0.1 mm under the dissecting microscope 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). All snapper larvae were sampled and preserved in the same way so any shrinkage effects would be expected to be consistent across all years.
Figure 15 Map of Port Phillip Bay, Australia. Six years of ichthyoplankton sampling was conducted at the following six 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).

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 (magnification 50x). The otoliths were removed from the head of the larva using electrolytically-sharpened tungsten needles and were cleared of any adhering tissue. Once the otoliths were removed, they were left to air-dry on the glass slide. A drop of immersion oil was added later to the dried otoliths.

I aimed to age and measure the growth rates of approximately 10 larvae from each of the seven areas from each sampling time, depending on availability of sampled larvae. Larvae were chosen randomly from each size class (e.g. 2-3 mm SL, 3-4 mm...
SL) to ensure all sizes were represented. Sagittal otoliths were preferred over lapilli as they produced the best increment clarity. Daily increment periodicity in snapper larval and juvenile otoliths has been previously validated (Francis et al. 1992, Fowler & Jennings 2003). One sagittal otolith was randomly chosen to age and measure growth rates from each larva. Otolith radii and increment width were measured along the rostral axis under a magnification of 1000x using an oil-immersion, compound microscope with an attached video camera. The attached video camera allowed me to count and measure the increments on a computer screen using ImagePro Plus ver. 6.3. Otoliths were examined blindly with respect to SL and sampling area. Each otolith was aged and measured twice, and the data were exported to Microsoft Excel. If the percentage of standard deviation around the mean increment width from the two 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. If the third reading did not resolve the difference in increment widths and/or age, the otolith was rejected. Using these criteria, nine 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 two days to the number of increments counted as previous field and laboratory studies found that the first increment forms between one and three days post hatch (dph), approximately when the larva starts feeding (Francis et al. 1992, Kingsford & Atkinson 1994, Fowler & Jennings 2003). Adding two days was a mean of the three previous studies.

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. Each food item in the gut contents was identified to lowest possible taxonomic level, and its maximum width (μm) was measured. In the samples from 2009-2011, the prosome length (copepodites) or total length (nauplii and other prey) was also measured. Daily temperature was obtained from a fixed temperature logger at the HB area deployed at three meter depth by Fisheries Victoria Research Branch, Queenscliff Centre.
I was interested in how prey availability and temperature affected interannual variability in recent growth of snapper larvae. Zooplankton was sampled, using an 80 μm net, concurrently with each ichthyoplankton tow from 2006 onwards, so sampled snapper larvae were matched with sampled prey in both sampling times for four years of data (Murphy et al. 2012, Chapter 2). The mean temperature experienced by each larva during its lifetime was averaged for each sampling time and year.

Data analysis

Average daily growth rate was calculated for each year, pooling for area and sampling time, using linear regressions of larval size-at-age. A linear regression was used to determine if larval abundances were related to average daily larval growth rates.

Univariate repeated measure analysis of variance (ANOVA) was used to examine variation in mean otolith increment group widths (MIGW) (increments 1-3, 4-6, 7-9) amongst years. I pooled increment widths over three days as the majority of the sampled larvae were 10 days or younger. I pooled for sampling time and area in order to include all six years in the analysis. In 2005/2006, snapper larvae were only sampled in the early sampling time at F area, and in 2010/2011, only one snapper larva sampled in the late sampling time was old enough for repeated measures ANOVA. To examine the significant difference in MIGW amongst years, ANOVAs were used 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 between different ages (Dower et al. 2002, Baumann et al. 2003, Robert et al. 2009). I used the formula:

$$DG_{ij} = \frac{(G_{ij} - G_j)}{SD_j}$$

where $DG_{ij}$ is the detrended growth of individual $i$ at age $j$, $G$ is otolith growth (increment width), and $SD$ is the standard deviation of growth at age $j$ (Robert et al. 2009). The last three days of full growth before capture were considered, excluding the last increment as it may not be fully formed (Dower et al. 2002, Robert et al. 2009), which meant that only larvae of five dph or older could be used. An ANOVA was used to compare recent growth, pooled by tow, amongst years.
Foraging success was measured as the biomass of ingested prey expressed as carbon. 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). When only the width of a prey item was measured (cohorts from 2004-2007), regressions between known widths and lengths for each prey item from 2009-2011 were used to estimate a length for the unmeasured prey item and determine its carbon content (Young et al. 2010). Since 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 compare foraging success amongst years. Linear regressions were used to determine if foraging success was related to recent three day growth and/or temperature.

Five independent variables (mean temperature, copepod nauplii densities, cladocerans densities, and interaction terms between mean temperature and mean cladoceran and copepod nauplii densities) were used in single and multiple linear regressions to determine the best fit model that explained the interannual variability in recent growth for larvae 5-14 dph in four years of sampling (2006/2007, 2007/2008, 2008/2009, and 2009/2010).
2009/2010, 2010/2011) and two sampling times (early and late). 2004/2005 and 2005/2006 were not used in this analysis as there was no data on zooplankton availability for these two years. Copepodite densities were highly correlated with the three other variables, so were removed from the analysis; the other variables were not highly correlated ($r < 0.350$).

Assumptions of ANOVA were examined using box and normal probability plots, and MIGW, temperature, prey biomass (carbon content), larval length, and prey densities were log ($x+1$) transformed. SYSTAT 12 was used for all statistical analyses.
Results

The growth rates and ages of 301 snapper larvae from six years were measured (Table 6). There were three higher larval abundance years (H2004/2005, H2007/2008, H2009/2010) and three lower abundance years (L2005/2006, L2006/2007, L2010/2011) (Table 6). The majority of snapper larvae (72%) were sampled in the eastern areas of PPB (C, F, M) in all years, which corresponds with the main suggested spawning areas for snapper (Hamer et al. 2011) (Table 6). The majority of snapper larvae were 3-12 dph (247 or 82%), which corresponds with the size range 2-6 mm SL (Fig. 16). The oldest larva was 21 dph sampled in L2010/2011 (Fig. 16).

Table 7 Univariate repeated measures ANOVA comparing pattern of mean increment group widths (MIGW) (increments 1-3, 4-6, 7-9) in larval Chrysophrys auratus otoliths among years. G-G Greenhouse-Geiser statistic, H-F Huynh-Feldt statistic.

<table>
<thead>
<tr>
<th>Source</th>
<th>df</th>
<th>MS</th>
<th>F</th>
<th>p</th>
<th>G-G</th>
<th>H-F</th>
</tr>
</thead>
<tbody>
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<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Year</td>
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<td>0.099</td>
<td>6.534</td>
<td>0.000</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Error</td>
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<td>0.015</td>
<td></td>
<td></td>
<td></td>
<td></td>
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<td></td>
<td></td>
<td></td>
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<td></td>
</tr>
<tr>
<td>MIGW</td>
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<td>60.415</td>
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<td>0.000</td>
<td>0.000</td>
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<tr>
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<td>1.970</td>
<td>0.042</td>
<td>0.076</td>
<td>0.069</td>
</tr>
<tr>
<td>Error</td>
<td>128</td>
<td>0.004</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Larval growth

In this study, there was a positive linear relationship between snapper larval size and otolith radius ($r^2 = 0.832$, $p < 0.001$, $n = 301$), which supported the use of otolith daily increment formation as a proxy for somatic growth. Average daily growth rates varied between years: H2004/2005 and H2009/2010 had the highest daily growth rates of 0.30 mm day$^{-1}$, followed by H2007/2008 with 0.28 mm day$^{-1}$, L2006/2007 with 0.26 mm day$^{-1}$, and L2005/2006 and L2010/2011 with 0.25 mm day$^{-1}$ (Fig. 16). Slopes of the regression lines were significantly different from each other (ANCOVA: $F_{1, 295} = 5.318; p = 0.022$) and post hoc Tukey’s tests indicated that the regression slopes in H2004/2005 and H2009/2010 were significantly steeper than L2006/2007 ($p < 0.05$). There was a positive linear regression between log-transformed larval abundance and
larval average daily growth rates \( (v = 0.046x + 0.232, r^2 = 0.863, p = 0.007, n = 6) \) (Fig. 17).

Figure 16 Linear regressions of larval length at age for six year classes of *Chrysophrys auratus*.

Univariate repeated measures ANOVA found a significant difference among years between and within subjects for MIGW (increments 1-3, 4-6, 7-9) (Table 7). ANOVAs showed significant differences in MIGW among years in all increment groups (Table 8; Fig. 18). Average increment widths in H2009/2010 were larger than H2004/2005, L2006/2007, and L2010/2011 (Fig. 18). MIGW also varied within years, as growth rates of snapper larvae were not uniform within years, with fast and slow growing larvae present (Fig. 18).

There was a significant difference in recent growth among years (ANOVA: \( F_{5, 99} = 9.557; p < 0.001 \)). Post hoc Tukey’s tests indicated that recent growth in H2004/2005 and H2009/2010 was significantly higher than L2005/2006, L2006/2007, H2007/2008, L2010/2011 (all \( p < 0.001 \)).
**Figure 17** Linear regression of log-transformed *Chrysophrys auratus* larval abundances and average daily growth rates ($n = 6$). Sampling years are labelled with H (higher larval abundance) and L (lower larval abundance).

**Effects of temperature and prey on larval growth**

There was a significant difference in foraging success (estimated carbon content of prey biomass) among years ($F_{5, 110} = 2.670; p = 0.026$), and post hoc Tukey’s tests indicated that foraging success was higher in H2004/2005 and H2009/2010 compared to L2006/2007 ($p < 0.003$). However, foraging success was not related to recent detrended otolith growth ($r = 0.530, p = 0.280, n = 6$) (Fig. 19). The relationship between foraging success and temperature was marginally non-significant ($r = 0.796, p = 0.058, n = 6$) (Fig. 20).

Regression analyses indicated that interannual variation in recent detrended growth was best explained by a second order polynomial relationship with cladoceran densities ($r^2 = 0.579, y = -11.866x^2 + 0.947x + 0.523, p = 0.023, n = 8$) (Fig. 21a). Mean temperature had a linear relationship with recent growth, although this relationship was
marginally non significant ($r^2 = 0.447, y = 12.472x-16.411, p = 0.070, n = 8, AIC (corrected) = 20.301$) (Fig. 21b).

Figure 18  Relationship between mean increment group widths (MIGW) (increments 1-3, 4-6, 7-9) and mean increment group width for *Chrysophrys auratus* larvae collected from 2004/2005, 2006/2007, 2007/2008 and 2009/2010. Mean ±SE values shown.
Figure 19 Relationship between foraging success and detrended recent growth amongst years for *Chrysophrys auratus* larvae, pooled for sampling time and sampling area.

Table 8 Univariate analysis of variance of mean increment group widths (MIGW) (increments 1-3, 4-6, 7-9) for six years (2004/2005-2007/2008, 2009/2010-2010/2011) of *Chrysophrys auratus* otoliths. Post hoc Tukey’s were used to test significant differences in MIGW among years.

<table>
<thead>
<tr>
<th>MIGW</th>
<th>F</th>
<th>df</th>
<th>p</th>
<th>Post hoc Tukey</th>
</tr>
</thead>
</table>
Figure 20 Mean annual foraging success (residuals of prey carbon content by larval length) and mean temperature experienced by *Chrysophrys auratus* larvae collected from six years. Mean ±SE of foraging success values shown.
Figure 21 Best fit model between detrended recent growth of *Chrysophrys auratus* larvae and (a) cladoceran density ($n=8$), and (b) mean temperature ($n=8$) sampled in 2006/2007 (0607), 2007/2008 (0708), 2009/2010 (0910), and 2010/2011 (1011). S1 is early sampling time and S2 is late sampling time.
Discussion

Average larval daily growth rates inferred from otolith microstructure were strongly related to larval abundances, with snapper larvae from higher abundance years characterised by fast growth. This suggests that interannual variation in larval growth influences survival rates of snapper larvae. Numerous studies have found that fast growing members of a cohort are more likely to survive and contribute to recruitment (Meekan & Fortier 1996, Hare & Cowen 1997, Searcy & Sponaugle 2000), and previous studies have demonstrated relationships between larval abundance and larval growth (Campana 1996, Jenkins & King 2006). The crucial life stage for growth and survival in marine fish varies between studies. While the larval stage has often been considered most critical (Bergenius et al. 2002, Jenkins & King 2006), studies have found fast growth later in development (late larval, juvenile stages) (Bailey et al. 1996, Campana 1996, Meekan & Fortier 1996) to be most important for influencing juvenile recruitment rates. This study indicates a significant relationship between growth in the early larval stages and larval abundance, which has been suggested to be an important cause of variation in subsequent juvenile recruitment rates of snapper in PPB (Hamer et al. 2010).

Interannual variation in growth trajectories was evident from the first increment group, which corresponded with the first feeding stage (four to six dph) (Pankhurst et al. 1991), with larvae from higher abundance years having a faster growth trajectory compared to lower abundance years. This result supports a previous study in New Zealand, which found snapper larval cohort strength was set by approximately eight dph (Zeldis et al. 2005). Other studies have also found that the critical stage of determining differences in growth trajectories occurs early in larval development (Jenkins & King 2006, Sponaugle et al. 2009), which further supports the importance of early larval growth on survival rates.

The main factors that affect larval growth rates are considered to be temperature and prey availability (Anderson 1988). Interannual variation in recent growth was most related to prey (cladoceran) densities. Larval growth increased with cladoceran density until six L⁻¹, with snapper larvae from H2009/2010 experiencing high growth at this prey density. While the diet of larvae in H2009/2010 contained Paracalanus spp. copepodites, rather than cladocera prey (Murphy et al. 2012, Chapter 2), calanoid
copepodites were found to be highly correlated with cladoceran densities in this study. Snapper larvae from two years that encountered the highest densities of cladoceran prey (H2007/2008 in early sampling and L2006/2007 in late sampling) had lower growth rates compared to years where snapper larvae encountered moderate levels of cladoceran densities. Snapper larvae sampled early in H2007/2008 were young, and their diet was mainly composed of calanoid nauplii rather than the larger cladocerans, so the availability of cladocerans would not be important for larval growth as these larvae were not able to target cladocerans due to their ontogeny (Murphy et al. 2012, Chapter 2). In L2006/2007, a lower larval abundance year with fewer larvae sampled in the late sampling time compared to the early sampling time, a temporal mismatch between prey availability and larvae may have negatively affected larval growth and survival. The literature is roughly divided between studies finding a relationship between fish larval growth rates and prey availability and finding no relationship between the two (Buckley & Durbin 2006). These inconsistent results could be a result of the scale of prey sampling, the need for spatial and temporal sampling, and/or identifying preferred prey rather than considering the whole prey field (Buckley & Durbin 2006, Young et al. 2009). I have been able to link recent larval growth to prey availability, although the relationship between these two variables appears to be complex and could vary depending on larval ontogeny.

Metabolic requirements 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 does 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). I sampled few larvae in L2005/2006 and L2010/2011, but the larvae that I 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). Selective mortality may have been occurring early in ontogeny in lower recruitment years, with only the most
efficient foragers surviving. I will investigate this hypothesis further in Chapter 4, using otolith microstructure from 0-age snapper.

Recent studies have found a relationship between high foraging success and fast larval growth (Dower et al. 2009, Robert et al. 2009, Sponaugle et al. 2009). Recent snapper larval growth was higher in the three higher abundance years, which was also found larval using daily growth rates and MIGW growth trajectories. Recent growth was highest in the two years with highest foraging success (H2004/2005 and H2009/2010), and lowest in the year with the lowest foraging success (L2006/2007). However, L2005/2006 and L2010/2011 were outliers, with similar, but more variable, foraging success compared to H2007/2008, but with lower recent growth. The low larval abundance and subsequent recruitment in these two years suggest that not just prey availability, but a combination of factors such as dispersal, predation, and/or temperature, may be driving larval growth and survival in these low abundance years.

Temperature is generally considered an important influence on larval growth, and a link between increased temperatures and faster larval growth has been previously demonstrated (e.g. Meekan et al. 2003, Jenkins & King 2006, Sponaugle et al. 2006). In New Zealand, a variation in prey densities and snapper larval abundances occurred even though the sea surface temperature remained constant throughout the three year study period (Zeldis et al. 2005). In this study, mean temperature was generally lower in years with low larval growth; however, in two years with similarly high mean temperatures, larval growth rates in H2007/2008 were lower than growth rates in H2009/2010. While I found no interaction between temperature and prey availability on larval growth, other unmeasured factors or a combination of factors, such as microscale turbulence (Dower et al. 1998) and predation, may play a role in larval growth. Furthermore, previous studies have found the effect of temperature and prey availability on larval growth can change throughout development (Robert et al. 2009, Sponaugle et al. 2009). In this study, not enough older larvae were sampled to evaluate how temperature and prey availability may affect late larval pre-settlement growth.

In conclusion, fast larval growth was strongly correlated with higher larval abundance in this temperate marine fish, which was also reflected in the recruitment strength of 0-age snapper. Temperature and prey availability are considered the main factors influencing larval growth rates (Heath 1992), and both of these factors appear to
play a role in driving the interannual variability in snapper larval growth, while predation (selective-mortality) may also be important in larval growth and recruitment strength. 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.
Chapter 4
The quick and the dead: low food-resource availability results in greater growth-selective mortality in a temperate marine fish
Abstract

For animals with complex life cycles, factors that contribute to interannual variability in larval survival and recruitment are important aspects of their population ecology. In fishes, the growth-mortality hypothesis has received broad acceptance as a driver of recruitment variability, with size-selective mortality resulting in the removal of slow growing, small individuals from the population. Long-term monitoring in Port Phillip Bay, Australia suggests that juvenile snapper, *Chrysophrys auratus* (Sparidae), experience high recruitment variation, with lower recruitment occurring in years where larvae have slower growth and are encountering lower prey availability. This suggests that both the risk of starvation and predation are likely to be greater in lower recruitment years, leading to greater size-selective mortality. To test this, a five year data set of daily growth histories, based on otolith microstructure, of the initial larval cohort and the surviving 0-age (young-of-year) snapper was compiled. Selective mortality acted on larval growth, with higher recruitment years characterised by either weak or no selective mortality, while some medium and lower recruitment years experienced high selective mortality. Larval otolith traits (growth rate, cumulative size, pelagic larval duration, size-at-hatch) of the initial larval cohort and surviving 0-age snapper were not related to recruitment strength. However, larval traits of 0-age snapper predicted juvenile growth, which suggests a potential carry-over of larval traits to the juvenile stage. The variable occurrence of size-selective mortality and the carry-over of larval traits to the juvenile stage emphasises the importance of the early life-history stage to the population dynamics of a species with a complex life cycle.
Introduction

Numerous organisms have complex life cycles, where individuals undergo ontogenetic transformation (metamorphosis) (Wilbur 1980). Metamorphosis is not a ‘new beginning’ (reviewed in Pechenik 2006), and the physiological experiences and resulting phenotypes from the larval stage can ‘carry-over’ into subsequent life stages (Marshall et al. 2003, Hoey & McCormick 2004). Larval size, growth, and condition have been found to influence growth and development of subsequent life stages in insects, marine invertebrates, fishes, and amphibians (McCormick & Hoey 2004, Van Allen et al. 2010, Crean et al. 2011, Hellmann et al. 2011). For marine fishes, which are characterised by high fecundity and a pelagic larval stage with high mortality rates, variation in growth and performance in the larval stage can facilitate selective mortality on these phenotypic traits for both the larval and subsequent ontogenetic stages (Sogard 1997, Searcy & Sponaugle 2001, Vigliola & Meekan 2002, Gagliano et al. 2007b).

Higher fish larval survival as a direct result of increased growth, mediated by size-dependent predation, is the basis of the growth-mortality hypothesis (Anderson 1988). Growth rate may influence survival in a number of ways: bigger-is-better, where larger, faster-growing larvae are less vulnerable to predation (Shepherd & Cushing 1980, Miller et al. 1988, Leggett & DeBlois 1994); stage-duration, where larvae that grow and develop faster make an early transition to the juvenile stage that is less vulnerable to predation (Chambers & Leggett 1987, Houde 1987); and growth-selective, where the growth rate of the individual larvae may influence its probability of capture independent of size or developmental stage (Takasuka et al. 2003, Takahashi & Watanabe 2004, Takasuka et al. 2004). These three mechanisms are distinct in terms of the basis of selective mortality, but are related as larval growth, size, and developmental stage are correlated (Hare & Cowen 1997).

Marine fishes experience high mortality in early life (Bailey & Houde 1989). Mortality is often selective, preferentially removing smaller and slower growing individuals within cohorts (Meekan et al. 2006), although some studies have found larger and faster growing larvae to be more vulnerable to predation than smaller, slow growing individuals (Litvak & Leggett 1992, Biro et al. 2004, Sponaugle et al. 2011). The growth-mortality hypothesis predicts that fast growth in the plankton should result in higher survival probability of individuals and higher recruitment of young fish to
populations. Fast larval growth detected in a larval cohort can, however, be a reflection of either most larvae encountering ideal prey and temperature conditions or selective mortality by predation and/or starvation removing slow growing individuals (Meekan & Fortier 1996, Robert et al. 2007). Therefore, demonstrating selective mortality by comparing growth parameters among larval cohorts can be problematic. Comparisons within cohorts of larval growth parameters with those of survivors to later life stages can more clearly demonstrate the importance of selective mortality (Meekan et al. 2006, Robert et al. 2007). Selective mortality is more likely to occur in poor years because in good years, with optimum temperature and prey availability, variability in larval traits is low and all larvae do well (Sogard 1997, Meekan et al. 2006). While recent research has emphasised the importance of larval traits and selective processes on the survival of individuals post-settlement (Robert et al. 2007, Grorud-Colvert & Sponaugle 2010, Islam et al. 2010), the importance of selective mortality may vary through time (Gagliano et al. 2007b) and among populations of a species (Searcy & Sponaugle 2001). Long-term datasets provide insights into if and why selective mortality varies interannually and how this variability can affect recruitment dynamics (Robert et al. 2007, Rankin & Sponaugle 2011).

A temperate marine fish species with high recruitment variability is snapper, Chrysophrys auratus (Sparidae) (formerly Pagrus auratus) (Fowler & Jennings 2003, Hamer & Jenkins 2004, Zeldis et al. 2005). Snapper can live up to 40 years, reach sexual maturity at four to five years, and are highly fecund multiple batch spawners with a pelagic larval duration estimated to be 18-28 days and settlement at 10-12 mm SL (Battaglene & Talbot 1992, Scott et al. 1993, Francis 1994a, Coutin et al. 2003, Fowler & Jennings 2003). Recent research in Australia and New Zealand indicates that patterns of survival in the larval stage drive interannual variation in recruitment of young-of-year (0-age) in this species (Fowler & Jennings 2003, Zeldis et al. 2005, Hamer et al. 2010). Furthermore, in Port Phillip Bay (PPB), south-eastern Australia, recent studies indicate that in lower recruitment years snapper larvae experienced lower prey availability, poor foraging success, and slow growth, which is consistent with the hypothesis that these cohorts experience higher predation and starvation rates (Murphy et al. 2012, Chapter 3).
To explore whether the growth-mortality hypothesis was a driver of recruitment variability in snapper, I first determined if selective mortality was occurring in this population, and, if so, how important was this process in influencing recruitment dynamics. To investigate the occurrence of growth-selective mortality, I examined daily growth histories based on otolith microstructure of five cohorts (year-classes) for both the larval stages and surviving 0-age snapper recruits. I hypothesised that lower recruitment would be related to the occurrence of selective mortality during the larval stage. In higher recruitment years, I predicted selective mortality would be minimal or non-detectable as most larvae had fast growth. To evaluate how important selective mortality was in influencing recruitment dynamics, I related larval traits of the five initial cohorts along with those measured from otoliths of 0-age snapper recruits from seven other cohorts to post-settlement growth (carry-over of larval traits to the juvenile stage) and interannual variation in recruitment.
Methods

Sampling of 0-age snapper

Six areas within Port Phillip Bay (PPB), Australia, namely Carrum (C), Central Bay (CB), Frankston (F), Hobsons Bay (HB), Mordialloc (M) and Point Wilson (PW), were sampled for 0-age snapper from late March to early April over 12 years (2000-2011) (Fig. 22). The timing of sampling was chosen to overlap with the expected end of the larval settlement period (Jenkins 1986). For more details on sampling of 0-age snapper, refer to Hamer and Jenkins (2004). Briefly, a plumb-staff beam trawl (2.8 m mouth width) was used in this study, which was based on similar trawls designed for sampling small benthic fish and red sea bream (*Pagrus major*) in Japan (Azeta et al. 1980, Gunderson & Ellis 1986). An advantage of the plumb-staff beam trawl is a constant mouth width irrespective of sampling conditions or habitats (Gunderson & Ellis 1986). A tickler chain was used to scare the fish off the bottom into the net. Sampling was done at night as catches were previously found to be higher at night compared to day sampling (Hamer et al. 1998). Each sampling event consisted of five non-overlapping trawls of 7-10 min bottom time within each site. The latitude and longitude were taken at the beginning and end of each tow with a differential global positioning system (DGPS). Tow length ranged from approximately 350-500 m of bottom contact. All 0-age snapper were sorted from the net immediately after net retrieval and frozen for later measurement and otolith removal. The number of 0-age snapper caught in each tow was standardised to number 1000 m$^{-2}$.

Otolith preparation and analysis of 0-age snapper

In the laboratory, the 0-age snapper were thawed and measured for TL and SL to the nearest mm and weighed to the nearest 0.1 g. The sagittal otoliths were dissected out of the fish. Sagittal otoliths are preferred over lapilli for ageing in snapper because they are easier to prepare and have a clearer microstructure that allowed for more reliable increment counts (Francis 1994b, Fowler & Jennings 2003). Once removed, the sagittal otoliths were cleaned of adhering tissue, air dried for at least 24 hours, and stored in plastic vials until mounting.
Figure 22 Map of Port Phillip Bay, Australia. Twelve years of sampling was conducted at the following six 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).

The sagittal otoliths were mounted on glass slides using Crystalbond™, ground transversely using wetted 800-1200 grit abrasive paper and polished with nine and three μm imperial lapping film by hand until close to the core, followed by final polishing with aluminium oxide powder slurry on a felt pad. The thickness of the sectioned otolith was approximately 50 μm. I aimed to analyse 50 otoliths from each year. Each sectioned sagitta was examined using a compound microscope at magnification 200-400x with an attached video camera to allow counts and measures of the increments on a computer screen using ImagePro Plus ver. 6.3. Immersion oil was used to enhance optical clarity and resolution. Pre-settlement increments were counted and increment widths were measured from the primordium to the settlement mark (i.e. Fowler & Jennings 2003). The first 20 increments after the settlement mark were also measured (post-settlement increments). After the 20 post-settlement increments were measured, the remaining
increments were counted to the proximal margin along the dark band referred to as the sagittal-subcupular meshwork fibre zone (Francis 1994b).

Otoliths were examined blindly with respect to TL and collection area. Each sagitta was examined twice on two different occasions, and the data were exported to Microsoft Excel. For the pre-settlement section, if the standard deviation was greater than 10% of the mean increment width from the two otolith measurements and/or the increment counts were not the same, then the section was aged and/or measured a third time. If this third reading/measurement did not resolve the difference in increment widths and/or age, the otolith was rejected. For the first 20 post-settlement increments, if the standard deviation was greater than 10% of the mean from the two otolith measurements, then the section was measured a third time. For the remainder of the post-settlement increments, if the increment counts differed by more than 5%, the otolith was examined a third time. If this third reading did not result in correspondence between two of the readings, then the otolith was rejected. Otherwise, the mean of the counts was accepted as the best estimate. Under these criteria, four otoliths were rejected.

To determine if selective mortality was a driver of population dynamics for snapper, mean increment widths of the pre-settlement stage of 0-age snapper were compared to those measured from the initial larval cohorts. Larval increment widths were previously measured for some of the cohorts considered in this study (2005-2008, 2010-2011) (Chapter 3). However, larval increment widths were measured in the sagittal plane, while pre-settlement increment widths of 0-age snapper were measured on the transverse plane. I obtained data for pre-settlement increment widths for two cohorts (2005, 2010) of 0-age snapper that were measured on both the transverse and sagittal planes (A. Newman, unpublished Honours thesis; F. Warren-Myers, unpublished MSc thesis). I only considered the first nine increments of the pre-settlement increments of the 0-age recruits, as the sagittal grind in the sister otolith was only clear for approximately the first nine increments (H. Murphy, pers. obs.) Using paired t-tests for each of the nine increment widths measured in both the sagittal and transverse planes in sister otoliths (2005: \( n = 8 \); 2010: \( n = 24 \)), I found no significant differences in mean width for any increment in either year (2005: \( p > 0.060 \); 2010: \( p > 0.200 \)). While the small sample size in 2005 reduced the power of the t-tests, the strong
non significant results of the 2010 t-tests supported the use of the widths of the first nine increments in the transverse plane of the 0-age snapper to compare to the widths of the first nine increments of the initial larval cohorts.

**Data analysis**

The date of hatch of 0-age recruits was calculated by subtracting the total number of increments (pre- and post-settlement), plus two days to account for the delay in first increment formation, from the capture date (Chapter 3). The core (pre-settlement increments) was missed in approximately one-third of the otoliths in each year, so a mean pre-settlement duration for otoliths where the core was either partially or completely missed was used to calculate hatch dates of some 0-age recruits. Hatch dates of recruits were compared with those of the initial larval cohorts to ensure that hatch dates of the surviving recruits and larvae overlapped.

To avoid errors and assumptions of back-calculating somatic growth from otolith microstructure (Hare & Cowen 1995), comparisons of size and growth of otolith measurements were used (Campana 1996, Searcy & Sponaugle 2001, Smith & Shima 2011). To investigate if selective mortality was acting in this population, I compared the mean log-transformed mean increment width for the first 9 days amongst years and life stages (juvenile and larval). Since I found a difference in mean increment width amongst years, I compared log-transformed mean increment group widths (MIGW: days 1-3, 4-6, 7-9) for the five cohorts sampled for both larvae and 0-age recruits using repeated measures ANOVA. Mean increment widths and ages of snapper larvae from six years of sampling (2005-2008, 2010-2011) were previously determined (Chapter 3). I pooled larvae for area and sampling time due to small sample sizes of larvae in 2006 and 2011 (Chapter 3).

Early otolith growth, as a proxy for somatic growth, was estimated for both the 0-age recruits and the initial larval cohorts as the average increment width (μm day⁻¹) across the first 10 days (d) of otolith growth (e.g. Smith & Shima 2011). Larval size was estimated by averaging cumulative otolith growth (μm) at 10 d in both the 0-age recruits and the initial larval cohorts (e.g. Smith & Shima 2011). Variation in otolith size-at-hatch was indicated by comparing distances from the core to the first increment (e.g. Shima & Swearer 2009). Post-settlement growth was estimated as the average otolith increment width (μm day⁻¹) of the first 20 daily increments after the settlement mark.
This method was used instead of a regression of length-at-age, as the 0-age recruits were of different ages and lengths amongst years (Table 9). Coefficients of variation (CV) of mean otolith increment widths of the initial larval population and surviving 0-age recruits were also calculated.

Table 9 Density of *Chrysophrys auratus* 0-age recruits sampled, number of otoliths aged, and mean age and total length (TL) of aged recruits.

<table>
<thead>
<tr>
<th>Year</th>
<th>0-age densities (x 1000 m(^{-2}))</th>
<th>Number otoliths aged</th>
<th>Mean age (d) (±SD)</th>
<th>TL (mm) (±SD)</th>
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<td>12</td>
<td>98(±28)</td>
<td>74(±22)</td>
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</table>
To test if larval traits of the initial and surviving cohorts were predictors of recruitment strength, I first determined if the measured larval traits (otolith size-at-hatch, mean growth across the first 10 d, cumulative size at 10 d, pelagic larval duration (PLD)) were correlated. A principle component analysis (PCA) was used to obtain a composite measurement of larval traits for both the initial and surviving cohorts. A regression between log-transformed recruitment strength and larval traits (the first principle component score, PC1, from a PCA) was used to determine the relationship between recruitment strength and larval traits in both the initial and surviving cohorts.

To test if there was a carry-over of larval traits to the juvenile stage and how selective mortality may have affected this relationship, I used a regression between log-transformed mean post-settlement growth and larval traits (the first principle component score, PC1, from a PCA).

Mean otolith growth, cumulative size at 10 d, post-settlement growth and 0-age recruit densities were log-transformed to meet assumptions of normality and homogeneity of variance. SYSTAT 12 was used for all statistical analyses.
Results
Selective mortality

The hatch dates in five out of the six cohorts of larvae overlapped with hatch dates of 0-age recruits, which justified comparing growth rates of the initial larval stages with the surviving 0-age snapper in these five cohorts (Fig. 23). The exception was the lowest recruitment year in 2006; only five 0-age snapper and 30 larvae were sampled, and the 0-age recruits hatched in November while the larvae hatched in early December (Fig. 23). I found a marginally non-significant difference in mean growth rate in the first 9 increments amongst years (2 factor ANOVA: $F_{4,106} = 2.387; p = 0.056$), with 2007 having a lower growth rate than 2010 (post hoc Tukey: $p = 0.050$). There was also a difference in mean growth rates between the larval and juvenile stages (2 factor ANOVA: $F_{1,106} = 12.463; p = 0.001$), with the juvenile stage having higher growth than the larval stage (post hoc Tukey: $p < 0.001$). There was no significant interaction between the two factors. In order to investigate this pattern further, I looked at each year separately. I found evidence of selective mortality in two of the five years. Univariate repeated measures ANOVAs found a significant difference in MIGW (days: 1-3, 4-6, 7-9) between the initial larval and surviving 0-age recruits in 2007 and 2008 (Table 10). In 2007, MIGW of 0-age recruits were significantly higher compared to the initial larval cohort for MIGW 1-3 ($F_{1,21} = 10.053; p = 0.005$) and MIGW 4-6 ($F_{1,21} = 4.637; p = 0.043$) (Fig. 24). In 2008, MIGW of 0-age recruits were significantly higher compared to the initial larval cohort for MIGW 1-3 ($F_{1,16} = 7.448; p = 0.015$), MIGW 4-6 ($F_{1,16} = 6.203; p = 0.024$), and MIGW 7-9 ($F_{1,16} = 5.354; p = 0.034$) (Fig. 24). In 2011, 0-age recruits had higher MIGW than the initial larval cohort, although this pattern was non significant (Table 10; Fig. 24). In 2005 and 2010, there was minimal difference in MIGW between 0-age recruits and the initial larval cohorts (Table 10; Fig. 24).

Coefficients of variation of mean larval growth rates were higher in the initial larval cohorts compared to the 0-age recruits in the three medium and lower recruitment years (Table 11). In 2005 and 2010 (higher and medium recruitment years, respectively), there was minimal difference in CVs between the initial larval cohorts and 0-age recruits (Table 11).

Larval traits of the initial cohort as predictor of recruitment
Size-at-hatch, mean growth across the first 10 d, and cumulative size at 10 d were all moderately to strongly correlated (growth vs size: $r = 0.928$; size-at-hatch vs size: $r = 0.466$; and size-at-hatch vs growth: $r = 0.200$). Using these three traits in a PCA, PC1 explained 70% of the variation in the dataset, and all three traits were positively loaded onto the PC1 (larval growth: 0.910, cumulative size: 0.989, and size-at-hatch: 0.555). These loadings gave a good composite measure of “larval traits” (e.g. individuals with high PC1 scores grew quickly, were large-at-age and large-at-hatch compared to individuals with low PC1 scores). There was no relationship between larval traits and recruitment strength ($r^2 = 0.387$, $y = 0.084x - 0.194$, $p = 0.287$, $n = 5$) (Fig. 25).

**Figure 23** Hatch dates of aged 0-age recruits (in black) and larval snapper (in grey) in six years (2005-2008, 2010-2011).
Larval traits of the surviving cohort as predictor of recruitment

I aged 508 0-age snapper recruits collected over 12 years at six areas within PPB (Table 9). Recruitment varied up to 12 fold between higher and lower recruitment years (Table 9).

Larval growth rate across the first 10 d, cumulative size at 10 d, and PLD were all highly correlated (growth vs size: $r = 0.982$; growth vs PLD: $r = -0.737$; size vs PLD: $r = -0.736$), while size-at-hatch was not as highly correlated (size-at-hatch vs PLD: $r = 0.005$; growth vs size-at-hatch: $r = 0.056$; size-at-hatch vs size: $r = 0.200$). However, size-at-hatch was still included in the PCA due to its weak but positive correlation with size. Using these four larval traits in a PCA, PC1 explained 66% of the overall variance in the dataset, and larval growth and size loaded positively onto the PC1, while PLD loaded negatively (growth: 0.968; size: 0.975; PLD: -0.864). Size-at-hatch had a low PC1 loading (0.148). PC2 explained 25% of the overall variance, where size-at-hatch loaded on positively (0.986), while the other three variables had low PC2 loading (PLD: 0.174; growth: -0.069; size: 0.073). PC1 loadings gave a good composite measure of “larval traits” (e.g. individuals with high PC1 scores had fast growth, were large-at-age, and had shorter PLDs compared to individuals with low PC1 scores) (Fig. 25). There was no relationship between larval traits and recruitment strength ($r^2 = 0.023, y = 0.034x - 0.035, p = 0.938, n = 12$) or size-at-hatch (PC2) and recruitment strength ($r^2 = 0.000, y = -0.037x + 0.129, p = 0.573, n = 12$).

Carry-over of larval traits

There was a significant positive relationship between larval traits of 0-age recruits and post-settlement growth ($r^2 = 0.369, y = 0.294x - 3.600, p = 0.036, n = 12$) (Fig. 26). There was no relationship between larval traits of the initial cohorts and post-settlement growth ($r^2 = 0.027, y = 0.010x - 0.056, p = 0.946, n = 5$) nor size-at-hatch (PC2) of 0-age recruits and post-settlement growth ($r^2 = 0.053, y = 0.107x - 1.429, p = 0.472, n = 12$).
Table 10  Univariate repeated measures ANOVA comparing mean otolith increment group widths (MIGW) (days: 1-3, 4-6, 7-9) between the initial pelagic larvae (L) and the surviving benthic juveniles (J) of 5 annual cohorts of snapper *Chrysophrys auratus*. *G-G* Greenhouse-Geiser statistic, *H-F* Huynh-Feldt statistic.

<table>
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<tr>
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Table 10 cont’d Univariate repeated measures ANOVA comparing mean otolith increment group widths (MIGW) (days: 1-3, 4-6, 7-9) between the initial pelagic larvae (L) and the surviving benthic juveniles (J) of 5 annual cohorts of snapper *Chrysophrys auratus*. G-G Greenhouse-Geiser statistic, H-F Huynh-Feldt statistic.

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**Figure 24** Comparison of mean increment group widths (MIGW) between the *Chrysophrys auratus* larval cohorts and 0-age recruit survivors for 2005, 2007, 2008, 2010, 2011. (*) Indicates significant differences between MIGW (p < 0.05).

**Table 11** Coefficient of variation (CV) of mean otolith increment widths of the pelagic *Chrysophrys auratus* larval stage and surviving benthic 0-age recruits.

<table>
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<tr>
<th>Year</th>
<th>CV of larval cohorts</th>
<th>CV of 0-age recruits</th>
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<td>2005</td>
<td>20.4%</td>
<td>21.0%</td>
</tr>
<tr>
<td>2007</td>
<td>34.6%</td>
<td>18%</td>
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<tr>
<td>2008</td>
<td>29%</td>
<td>15%</td>
</tr>
<tr>
<td>2010</td>
<td>17.7%</td>
<td>21%</td>
</tr>
<tr>
<td>2011</td>
<td>57.1%</td>
<td>19.3%</td>
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Figure 25 (a) Larval traits of the initial *Chrysophrys auratus* larval cohorts were not related to recruitment. Larval traits reflect a composite of mean larval growth rate across the first 10 d, cumulative size at 10 d, and size-at-hatch. (b) Larval traits of 0-age recruits were not related to recruitment. Larval traits reflect a composite of mean larval growth rate across the first 10 d, cumulative size at 10 d, and pelagic larval duration. Note that the scale of larval traits and 0-age recruit densities differ between panels. Years are labelled as 00 (2000), 01 (2001), 02 (2002), 03 (2003), 04 (2004), 05 (2005), 06 (2006), 07 (2007), 08 (2008), 09 (2009), 10 (2010), 11 (2011).
Larval traits of 0-age recruits were positively related to post-settlement growth. Larval traits reflect a composite of mean larval growth rate across the first 10 d, cumulative size at 10 d, and pelagic larval duration. Mean post-settlement growth was averaged over the first 20 d post-settlement.

Figure 26 Chrysophrys auratus larval traits of 0-age recruits were positively related to post-settlement growth. Larval traits reflect a composite of mean larval growth rate across the first 10 d, cumulative size at 10 d, and pelagic larval duration. Mean post-settlement growth was averaged over the first 20 d post-settlement.
Discussion
Selective mortality

Over five annual cohorts of snapper larvae and 0-age recruits, growth-selective mortality was only detected in two medium and lower recruitment strength cohorts, and not in two of the medium and higher recruitment cohorts. The cohorts where selective mortality was detected were previously characterised as years with slower larval growth (Chapter 3). Slow growing larvae may have had a higher risk of mortality by starvation and/or predation due to delayed development or greater risk-taking in search of food (Litvak & Leggett 1992, Munk 1995, Paradis et al. 1996). These two cohorts also had higher variation in larval growth rates, estimated from otolith increment widths, in the initial larval cohorts compared to the survivors. Strong selective mortality in these medium and lower recruitment years would have resulted in surviving individuals representing only a small subset of the initial population. In the other medium and higher recruitment years, where larvae had fast growth (Chapter 3), there appeared to be little selective mortality. There was low variation in larval growth traits between the initial larval cohorts and survivors in 2005 and 2010, which supports previous findings where higher recruitment years were characterised by low variability in larval traits, as the majority of larvae were doing well (Sogard 1997, Meekan et al. 2006).

While there have been numerous studies on the spatial and seasonal variability in selective mortality (e.g. Searcy & Sponaugle 2001, Gagliano et al. 2007b, Johnson & Hixon 2010, Smith & Shima 2011), there are fewer long-term studies on interannual variation in growth-selective mortality (e.g. Robert et al. 2007, Rankin & Sponaugle 2011). Similar to this study, Robert et al. (2007, 2009) found lower recruitment years of Atlantic mackerel *Scomber scombrus* had higher selective mortality, which was related to lower productivity, lower larval foraging, and slow larval growth. In a six year study, Rankin & Sponaule (2011) found that selective mortality varied seasonally for *Stegastes partitus*, rather than interannually. The authors attributed this pattern to temperature differences between seasons, and no relationship was found between larval growth and recruitment (Rankin & Sponaugle 2011). My findings, in combination with these previous studies, demonstrate how the importance of selective mortality can vary over time and may be more commonly detected in years (cohorts) of relatively low recruitment.
Selective mortality occurred early in ontogeny, which was consistent with other studies (e.g. Meekan et al. 2006). However, selective mortality can be important throughout the larval period (Hare & Cowen 1997), around metamorphosis (Searcy & Sponaugle 2001), and can occur at different developmental periods in different years (Robert et al. 2007). The sampling methods used were biased against yolk-sac and late-stage pre-settlement larvae, so I was not able to determine if selective mortality affected these stages or if selective mortality occurred throughout larval development. However, the occurrence of growth-selective mortality in the first few days post hatch indicates that mortality processes operating very early in the life history are likely to be the most important drivers of recruitment variation in snapper in PPB.

Temperature is known to have a direct influence on growth-related traits in poikilotherms. Several studies have investigated how temperature can influence selective mortality, with selective mortality varying seasonally and only occurring during cooler months (Gagliano et al. 2007a, Durieux et al. 2009, Grorud-Colvert & Sponaugle 2010, Rankin & Sponaugle 2011). It is difficult to disentangle temperature from other factors that vary seasonally, such as variation in abundance of predators and prey availability (Buckley & Durbin 2006). In a previous study, foraging success and temperature may both have an effect on larval snapper growth and survival with generally lower larval growth found in cooler years and higher foraging success found in higher larval growth years, although there was high variability in foraging success in two of the three lower recruitment years (2005/2006, 2010/11) (Chapter 3). My research to date supports a hypothesis that food availability is a key limiting factor on snapper recruitment success, with selective mortality being significant in low food years. For example, selective mortality was evident in 2008, where larvae experienced high mean temperatures but lower food availability compared to another medium recruitment year (2010) (Chapter 3). Current research involving biophysical modelling of nutrients, phytoplankton, and zooplankton productivity with snapper larval survival and recruitment dynamics may provide more information on the link between environmental/bottom-up processes and snapper recruitment dynamics.

**Larval traits as predictor of recruitment**

While there was no relationship between larval traits of the initial cohorts and recruitment strength, there were higher values for larval traits in 2005 and 2010, which
were previously characterised as years with minimal selective mortality and fast larval growth. Lower values for larval traits were evident in years with slower larval growth and selective mortality (2007, 2008, 2011). While several studies have found a link between larval traits, such as fast growth, and recruitment in marine fishes (Meekan & Fortier 1996, Sirotis & Dodson 2000, Jenkins & King 2006, Fontes et al. 2011, Smith & Shima 2011), other studies have not (van der Veer et al. 1994, Campana 1996, Ringuette et al. 2002). In our study, the lack of a relationship between larval traits, especially of 0-age recruits, and recruitment strength may have been due to selective mortality acting early in larval development, with larger and faster growing larvae preferentially surviving in some medium and lower recruitment years. And, since snapper larvae from higher recruitment years had fast growth, larval growth histories of recruits from higher and lower recruitment years were similar even though recruitment varied. Numerous studies have used larval traits of survivors (i.e. competent larvae, settlers, juveniles) rather than the early larval stages to relate to recruitment dynamics (e.g. Raventos & Macpherson 2005, Rankin & Sponaugle 2011, Smith & Shima 2011). Such an approach may underestimate the importance of growth-related selective mortality during early larval development as a driver of recruitment dynamics.

**Carry-over of larval traits**

Larval traits of survivors carried-over into the juvenile stage to influence post-settlement growth. So, large-at-age larvae with fast growth and short PLDs had faster post-settlement growth compared to larvae that were small-at-age with slower growth and longer PLDs. Previous studies have found that it’s not only the number of individuals that survive to the juvenile stage, but the quality of these individuals, indicating a strong link between the larval and juvenile stages in some fish taxa (Searcy & Sponaugle 2001, McCormick & Hoey 2004, Grorud-Colvert & Sponaugle 2010). The importance of larval traits to post-settlement growth in snapper provides further evidence that early life history experiences can have long-term fitness consequences.

Size-at-hatch was not related to other larval traits of survivors (fast growth, size-at-age, PLD) or post-settlement growth. A critical determinant of larval size-at-hatch is the size of the egg from which the larva hatched (Chambers et al. 1989), and egg size is primarily influenced by maternal condition, size and age (Chambers & Leggett 1996). Size-at-hatch has been related to post-settlement growth and survival in previous studies.
(Vigliola & Meekan 2002, Gagliano et al. 2007b, Durieux et al. 2009), while other studies have found no relationship between egg diameter or larval length at hatching and recruitment (Pepin & Myers 1991, Pepin 1991, Campana 1996). The influence of size-at-hatch on larval survival may decrease throughout ontogeny as predation, prey availability, and foraging ability of larvae become more important (Kamler 2005). This may be the case for snapper due to the apparent importance of productivity in mortality processes.

Conclusions

In conclusion, recruitment in snapper was determined by processes operating very early in the life history. Selective mortality was only evident in two medium and lower recruitment years, where larvae were previously found to have encountered lower prey availability and had slower growth (Murphy et al. 2012, Chapter 3). Selective mortality was not important in two other medium and higher recruitment years, where the majority of larvae were doing well, which may have been a result of higher prey availability and faster larval growth (Murphy et al. 2012, Chapter 3). While there was no relationship between larval traits and recruitment strength, which may have been a reflection of the variable strength and occurrence of selective mortality, there was evidence of a carry-over of growth advantages immediately post-settlement. Because of the potential variability in importance of growth-selective mortality as a process influencing larval abundance, studies based only on an analysis of survivors may fail to adequately assess the influence of variation in larval traits to recruitment and the dynamics of marine populations.
General discussion and conclusions

Recruitment variation in snapper has previously been found to originate in the pre-settlement stage (Francis 1994a, Fowler & Jennings 2003, Zeldis et al. 2005, Hamer et al. 2010). The main factors that could impact on snapper larval survival are starvation, predation, and dispersal (Houde 1987). Snapper recruitment was previously found to be determined at approximately eight days post hatch in New Zealand, with a match between the occurrence of larvae and high productivity, including copepod nauplii, more important than temperature for larval survival (Zeldis et al. 2005). In my research, an interannual relationship between high calanoid nauplii and higher abundance of early stage snapper larvae was found, further supporting the importance of food and larval survival in the first week of development to recruitment strength (Chapter 2). Furthermore, I found a polynomial relationship between cladoceran prey densities and larval growth, which suggests there was an additional link between densities of larger prey taxa and larval survival (Chapter 3). Years with higher larval abundances were characterised by faster growing larvae, which supports the paradigm that fast growing, larger larvae have a survival advantage (Chapters 3). High larval abundance years were also strong recruitment years, which supported previous findings that recruitment variation of snapper originated in the pre-settlement stage (Chapter 3, 4). However, larval traits of the initial cohorts, including larval growth, were not related to recruitment strength, even though snapper larvae that were large-at-age, large-at-hatch, and had fast growth were generally found in higher recruitment years (Chapter 4). While I did not measure predation directly, I found only weak growth-selective mortality in two medium and higher recruitment years that were previously characterised as high productivity years (Chapter 4), which supports the hypothesis by Zeldis et al. (2005) that high productivity years would be expected to also have high predation risk, but high prey availability may have resulted in increased snapper larval competence and a reduced risk of predation. Dispersal into or retention in nursery areas can also affect larval survival, and I found that snapper larvae used active DVM, which appeared related to maximising feeding success, but would also be expected to have an impact on horizontal dispersal, potentially influencing larval interactions with prey and predator fields (Chapter 1). The next step, using the links I found between prey
availability, larval growth, selective mortality and DVM, is the development of an individually-based biophysical model (IBM) of snapper recruitment.

In New Zealand, a three year study using hydrodynamic modelling, in conjunction with ichthyoplankton and zooplankton sampling, suggested that increased survival of the larval fish guild, including snapper, was related to physically-driven higher production of phytoplankton and mesozooplankton (Zeldis et al. 2005). In Australia, preliminary biophysical modeling of snapper larval dispersal found that snapper larvae were highly retained in the eastern area of Port Phillip Bay (Jenkins & Hatton 2007), which corresponds with the area of known spawning aggregations of snapper and high abundances of sampled larvae (Hamer et al. 2011). However, this model considered snapper larvae as passive particles rather than displaying DVM, which may alter the retention of snapper larvae in this generally productive area of Port Phillip Bay (Chapter 2). My findings of the importance of matching prey availability to the occurrence and developmental stage of snapper larvae suggests there may be a bottom-up control on snapper recruitment, and linking an IBM with a nutrient, phytoplankton, and zooplankton productivity (NPZ) model may provide a more accurate prediction of snapper recruitment (Megrey et al. 2007, Rose et al. 2008, Hinckley et al. 2009). Further research using a biophysical-NPZ model would also investigate how warming waters and changing freshwater inflows into PPB may affect zooplankton life history stages, particularly of Paracalanus spp and cladocerans, and how this would impact on snapper larval survival and recruitment strength.

In conclusion, the results of my research build upon previous knowledge of the importance of the pre-settlement stage to snapper recruitment (Francis 1994a, Fowler & Jennings 2003, Zeldis et al. 2005), and provided further evidence that recruitment strength in snapper is determined by factors that affect larval growth rates in the plankton. The match of interannual zooplankton prey densities with larval developmental stages drives diet strategy, larval growth, and interannual survival of snapper larvae. Fast growth was an important larval characteristic for survival, and this larval trait was the basis for selective mortality in some medium and lower recruitment years. Access to the long-term dataset (five years zooplankton data, seven years larval data, and 12 years 0-age data) allowed me to link processes occurring in the plankton with survival of snapper. Inclusion of DVM behaviour, prey availability, larval growth
and mortality into an IBM model coupled with a NPZ model will further our understanding of processes that influence early-life history survival and recruitment (Leis 2006, 2007).
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