The functional capabilities of reef fish larvae: implications for dispersal during the pelagic phase

Thesis submitted by

Rebecca Fisher, BSc (Hons) (JCUNQ)

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James Cook University, North Queensland

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Abstract

This thesis examined the extent to which tropical reef fish larvae are capable of influencing their dispersal and settlement patterns by quantifying swimming performance and behavioural characteristics throughout their pelagic phase. The provision of food to late stage *Amphiprion melanopus* larvae increased average sustained swimming distances from 6.9 km to 12.2 km, and the maximum swimming distances from 11.8 to 28.7 km. There was also a significant relationship between sustained swimming time and experimental swimming speed, with fish at slower speeds swimming longer and covering greater total distances. Results for *Amphiprion melanopus* suggested that larvae could sustain swimming at speeds of 8.5 bls^{-1} and 50% of their U-crit. This was supported by observations on late stage larvae of nine species (from the families Apogonidae, Lethrinidae and Pomacentridae) captured in light traps off Lizard Island. These data on swimming ability were used to estimate the swimming speeds that other reef fish taxa should be able to maintain for significant lengths of time (12 – 48 hours). The results suggest that many reef fish families are able to sustainably swim 2 – 3 times faster than previously estimated. The feeding and swimming speed studies suggest that previous flume-based estimates of sustained swimming underestimate the potential abilities of reef fish larvae. Consequently, sustained swimming behaviour by reef fish larvae could have a much greater impact on modifying larval dispersal than previously thought.

The intrinsic swimming speeds and nocturnal swimming activity of five reef fish species were quantified throughout their larval phase. Video techniques were used to obtain undisturbed observations of swimming behaviour in captive bred

larvae. Larvae were found to maintain relatively high swimming speeds throughout development. Speeds were consistent among three anemonefish species (Amphiprioninae), which swam an average of 3.9 and a maximum of 8.4 body lengths per second. The results support short duration experimental and *in-situ* evidence of high sustained swimming speeds. However, the most striking aspect is that larvae routinely swim at such speeds without external stimuli. The proportion of time larvae spent swimming at night increased rapidly towards the end of the larval phase in all the species examined. In addition, the relative swimming speeds of larvae were significantly greater at night than during the day. Patterns of nocturnal activity appear to relate to the active nocturnal settlement behaviour of larvae. The pattern of swimming, and speeds achieved, suggest that an active behavioural mechanism for self-recruitment is well within the capabilities of the reef fish larvae examined.

Knowledge of the extent of differential water column use by larvae is essential to assess the extent to which they are capable of influencing their dispersal patterns using active behaviour. An experimental light trap was designed to enable the discrete depth sampling of late stage reef fish larvae in the field. This design was used to describe the vertical distribution of late stage larvae off Lizard Island on the Great Barrier Reef in Australia. The largest numbers of late-stage reef fish larvae were found in the upper layers suggesting they migrate into surface waters at night, possibly as part of the settlement process. Several reef fish families were found throughout the water column. This distribution was not attributed to species-specific depth preferences within these families. There were, however, consistent size-specific vertical distributions among families, with larger individuals near the surface

and smaller individuals in the middle of the water column, suggesting subtle differences in water column use within species. Some families appear to occur solely near the bottom, indicating family level differences in vertical distributions. The presence of highly structured vertical distributions in late stage reef fish larvae, both among and within species, provides evidence of differential water column use by settlement stage reef fish larvae. The findings of this study emphasise the potential importance of water column use in the overall dispersal and settlement strategies of reef fish larvae.

Overall, the results of this thesis show that tropical reef fish larvae are capable of exerting considerable control over their dispersal patterns during the larval phase, as well as modifying patterns of recruitment and levels of self-recruitment on reefs. It is clear that tropical reef fish larvae are not passive particles. For benthic or brooded species this applies throughout the larval phase. These abilities need to be taken into consideration when constructing oceanographic models of dispersal. If the full potential of larvae behaviour is realised, it may be that reef fish populations of some families are maintained primarily by self-recruitment. If this is true our current understanding of reef fish population dynamics will change dramatically.

Chapter 1: Introduction

Many shallow water marine taxa have locally restricted distributions as adults, with dispersal among populations and locations occurring primarily through the production of larvae that reside for some period of time in the pelagic environment. Although the extent of its role is still debated (Anderson et al. 1981, Eckert, 1987; Mapstone & Fowler, 1988; Forrester, 1990; Jones, 1990, 1991, Schmitt & Holbrook 1999), most marine ecologists agree that the distribution and abundance of many marine taxa are significantly influenced by the dispersing effect of their planktonic larvae (Roughgarden et al. 1985, Alexander & Roughgarden 1996, Doherty & Williams 1988, Underwood & Fairweather 1989, Doherty & Fowler 1994). The patterns and extent of dispersal during the larval phase have important implications for the population dynamics of marine organisms, potentially affecting the degree of genetic connectivity among populations (Doherty et al. 1995, Shulman & Berminghams 1995, Bohonak 1999), levels of self-recruitment (reviewed in Swearer et al. 2002), and adult population dynamics (Doherty and Williams 1988, Doherty & Fowler 1994, Olson 1985, Roughgarden et al. 1985). In addition, knowledge of the extent and nature of larval dispersal among reefs is an essential prerequisite for designing zoning plans and for successful fisheries management (Williams et al. 1984, Warner et al. 2000, Botsford et al. 2001, Shanks et al. 2003)

Factors potentially affecting the horizontal dispersal of fish larvae (and other marine taxa) have been summarised in a review by Leis (1991a). These include: 1) spawning behaviour of the adults, 2) hydrographic structure at a variety of scales and the interaction of this with topography, 3) duration of the pelagic period, 4) the

behaviour of the larvae and 5) larval mortality and growth and their variations in space and time. Based primarily on work from temperate regions, it has generally been considered that larval fish are poor swimmers having relatively undeveloped locomotory capabilities (see Blaxter 1986 and references therein). Early evidence of poorly developed swimming abilities of temperate species may have contributed to the belief that "horizontal swimming by larvae probably makes, at best, a minor contribution to the observed distribution" (Leis 1986). Similarly, poor swimming capabilities have been reported for invertebrate larvae (Chia et al. 1984). For many years the term "planktonic", meaning passive drifters, has been applied to the larvae of both invertebrates and fishes. When producing dispersal models, largely for conservation and fisheries purposes, it was assumed that larvae do not have any control over their distribution patterns Their dispersal away from, as well as movement back to reefs, was believed to be largely dependent upon oceanic currents (e.g. Black 1993, Jenkins & Black 1994, Roberts 1997). This idea has lead to the "open populations paradigm", that suggests that reef fish populations are maintained by a continual supply of larvae from various (usually upstream) sources (e.g. Roberts 1997).

While the traditional view has been that most marine populations have widely dispersed larvae and constitute "open" populations, this idea has been strongly challenged in recent years, with increasing evidence of high levels of self-recruitment in a wide variety of marine taxa (reviewed by Swearer et al. 2002). High levels of self-recruitment may in part be due to active larval behaviour. Selection pressure on the evolution of some form of active behaviour is likely to be quite high, given the obvious advantages such behaviour would have on improving the survival

and recruitment success of larvae. If organisms are well adapted to their environment then some degree of efficiency in their behaviour should be expected (Armsworth 2001). A larva that can actively search for, find and settle on a reef is much more likely to survive the pelagic phase if these processes are not left simply to chance and oceanic currents. In addition, a behavioural mechanism for avoiding advection from natal reefs would clearly be advantageous for larvae arising from isolated reefs and islands, where such larvae face limited settlement success downstream. However, limited dispersal may also be advantageous even in more complex reef systems if there is a significant risk of not finding a suitable downstream settlement site. Furthermore, it is axiomatic that the natal reef represents a location that contains suitable habitats for growth to adulthood and successful reproduction. Whether or not dispersal is advantageous to larvae depends on the scales of spatial and temporal variability in habitat quality (Barlow 1981). A recent review by Strathmann et al. (2002) found that the advantages of dispersal over large scales are not apparent, even for taxa that are site associated as adults. They suggest an alternative hypothesis for the evolution of pelagic larvae; that dispersal may be a bi-product of an ontogenetic migration from, and then back to, the parental habitat. Furthermore, because it is axiomatic that the natal reef represents a location that contains suitable habitats for growth to adulthood and successful reproduction, they suggest that selection may even favour larval retention or larval return rather than dispersal (Strathmann et al. 2002).

The main two mechanisms that can be employed by marine larvae to actively influence their dispersal are directed swimming behaviour and vertical migration. A recent review by Sponaugle et al. (2002) clearly identified the potential impact of

such behaviour on the degree of self-recruitment in marine populations. Furthermore, Sponaugle et al. (2002) highlight the extent to which active self-recruitment behaviour is critically dependent on the behavioural and sensory capabilities of larvae and the rate that these abilities develop during their pelagic phase.

1.1. Directed Swimming

For tropical reef fish larvae, the potential effect of active swimming behaviour has received considerable attention. Recent work has shown that settlement-stage larval reef fishes have substantial swimming abilities, exhibiting both high swimming speeds (Leis & Carson-Ewart 1997, Bellwood & Fisher 2001) as well as excellent sustained swimming capabilities (Stobutzki & Bellwood 1997). These studies indicate that prior to settlement, many species of larvae are capable of swimming against average current speeds (at least for short periods; Leis & Carson-Ewart 1997) and may potentially cover considerable distances (Stobutzki & Bellwood 1997). Given their capabilities, reef fish larvae could potentially have a considerable impact not only on their dispersal patterns, but also on their chances of successfully finding a reef on which to settle (see recent reviews by Montgomery et al. 2001, Leis & McCormick 2002).

Active horizontal swimming behaviour has been recognized as a potentially important factor that may influence the dispersal patterns and settlement success of fish larvae and has been recently incorporated into dispersal models by Wolanski et al (1997) and James et al. (2002). These models represent the first attempts to couple active swimming behaviour with oceanic data to predict dispersal and recruitment

patterns of tropical reef fish larvae. However, such attempts are limited by our current understanding of the behaviour and swimming capabilities of these larvae. All data on the sustained swimming abilities of reef fish larvae have been obtained under an experimental situation where larvae were not permitted to feed while swimming (e.g. Stobutzki & Bellwood 1997). This is an unrealistic situation, as larvae have been observed to feed whilst swimming in the field, and at speeds that are sometimes considerably greater than the experimental speeds (Lies & Carson-Ewart 1997). A second problem is that experimental studies have only investigated a single swimming speed (13.5 cms^{-1}; Stobutzki & Bellwood 1997, Stobutzki 1998, Dudley et al. 2000). Furthermore, we know from both laboratory (Stobutzki & Bellwood 1994, Fisher et al. 2000, Bellwood & Fisher 2001) and field studies (Leis & Carson-Ewart 1997) that reef fish larvae of some species are able to swim at considerably faster speeds, at least for short periods of time. The impact of food availability and swimming speed are two critical factors, that remain to be evaluated.

In addition, although we do have some knowledge of the swimming performance of larvae during development (Fisher et al. 2000), there is very little information regarding the spontaneous behaviour of reef fish larvae, particularly throughout development. Although field studies have measured the *in-situ* speeds of larvae and found them to be quite fast, this has been in a disturbed situation where divers are following larvae (Leis & Carson-Ewart 1997). These experiments have also been conducted only on settlement stage larvae and over short periods of time. If we are to adequately understand the potential impact of larval behaviour, it is essential to establish what swimming speeds larvae choose to adopt when undisturbed and how swimming behaviour changes throughout development.

Furthermore, while it is suspected that larvae may swim actively at night during settlement (Dufour & Galzin 1993, Shenker et al. 1993, Holbrook & Schmitt 1997, Kingsford 2001) this has never been confirmed in the laboratory, and the time that such nocturnal activity begins has never been examined. This information is crucial to our understanding of the full behavioural potential of these larvae.

1.2. Vertical distribution

The other important mechanism whereby larval fish may significantly influence their dispersal or enhance their settlement success is vertical migration. Fish larvae are generally capable of precise movement within the water-column by orientating towards various cues, active swimming and gas bladder modulation (Richards & Lindeman 1987). The larvae of many invertebrates are also known to be able to actively influence their vertical distribution (Forward et al. 1984, Forward & Rittschof 1994, Queiroga et al. 2002). Such behaviour can potentially lead to significantly different patterns of dispersal of larvae relative to passive particles (Heath 1992). Modelling studies have shown that if larvae can exploit the vertical structure of water currents at different depths, then the extent that they can influence their dispersal is greatly increased (Armsworth 2001). Furthermore, the energetic expenditure required to find and settle on a reef may be greatly reduced (Armsworth 2001). Numerous studies have included vertical migration behaviour in models of larval dispersal (Tremblay et al. 1994, Verdier-Bonnet et al. 1997, Jenkins et al. 1999), and it is clear that such behaviour may significantly influence dispersal patterns.

It is well known that Crustacean larvae undergo vertical migrations to ride favourable current patterns to facilitate horizontal transport (Forward et al. 1984, Forward & Rittschof 1994, Queiroga et al. 2002). Vertical migration in relation to varying currents has also been recorded in fish larvae as a mechanism to avoid advection and facilitate up-stream transport in estuarine systems (Rijnsdorp et al. 1985, Forward et al. 1996, Yamashita et al. 1996, Jager 1999, Groiche et al. 2000). Similar mechanisms have been inferred for reef fishes by several authors, such as McIlwain (1997) who suggested that it is likely that larvae were influencing the timing of their transport into the lagoon of Ningaloo reef by migrating into the surface waters of the offshore environment in the late afternoon. Vertical migrations into wind driven currents in surface waters has also been suggested as a mechanism for enhancing settlement by other authors (e.g. Thorrold et al. 1994b, Shenker et al. 1993). Simulations demonstrate that active vertical migration in tidal currents can significantly influence the seasonal variability of larvae as well as the direction and rate of larval transport (Smith & Stoner 1993, Chen et al. 1997).

Recent work on the development of the visual abilities of larval reef fishes indicate that late stage larvae may be capable of feeding at considerable depths in the water column, possibly up to 250 m in depth (Job & Bellwood 2000). The presence of well-developed swim bladders (Leis & Rennis 1983) and well-developed swimming abilities (Fisher et al. 2000, Stobutzki & Bellwood 1994, Leis & Carson-Ewart 1997) suggests that larval reef fishes should be capable of relatively rapid vertical movements and precise vertical maneuvering. Indeed, there is evidence to suggest that larval reef fish may utilize vertical movement as part of a mechanism to influence their position during settlement (Cowen et al. 2000). Despite the apparent

ability of larval reef fish to modify their vertical position and the potential importance of this behaviour on their dispersal patterns, the vertical distribution of larval fish in the field has only been briefly examined (but see Leis 1986, 1991b, Doherty & Carleton 1997, Hendriks et al. 2001). Information on vertical water column use is crucial to understanding the potential capability of tropical reef fish larvae to influence their dispersal patterns and recruitment success using active behaviour.

1.3. Sensory capabilities and larval orientation.

For active behaviour to be effective in influencing dispersal patterns, larvae need to have the capabilities to detect and respond to the presence of suitable habitat at a variety of scales. For coral reef fishes, recent findings have shown that larvae have well-developed sensory abilities and may have the potential capabilities to locate reefs and actively search for suitable settlement sites (see recent reviews by Montgomery et al. 2001, Kingsford et al. 2002, Leis & McCormick 2002). On small scales both visual (Job & Bellwood 1996, 2000) and chemosensory (Arvedlund & Nielsen 1996, Arvedlund et al. 1999, 2000) cues may be used for active habitat selection by settling larvae. On a larger scale, several *in-situ* experiments have demonstrated that late stage larvae are capable of responding to the presence of reefs at considerable distance (Leis et al. 1996, Stobutzki & Bellwood 1998, Leis & Carson-Ewart 1999). Long distance detection of reef location may be possible through the use of either auditory (McCauley & Cato 1998, Tolimieri et al. 2000) or chemical (Atema et al. 2002) cues, although the later could only be used from down

reef locations. Other navigational cues that may be available for fishes include a magnetic compass, inertial mechanisms, sun compass, polarised light and electric fields (Montgomery et al. 2001, and papers therein), all of which could provide directional cues for navigation over considerable distances.

1.4. Aims and Scope

Although the traditional view of the passive larva has largely been discarded, the degree to which larval behaviour may modify dispersal patterns or assist self-recruitment is still undetermined and remains an area of considerable debate (see Roberts 1997, 1998; Bellwood et al. 1998; Sale & Cowen 1998; Mora & Sale 2002). While it is clear that ocean currents will affect the dispersal of marine larvae, the extent to which larval behaviour may override the effect of currents has not been clearly established. The primary aim of this dissertation was to combine several approaches to examine the behavioural abilities of larvae to obtain an overall picture of the potential for these larvae to influence their dispersal patterns and recruitment success using active behaviour. The aim of the first chapter of the thesis was to determine the maximum performance of reef fish larvae by examining two critical factors, food and swimming speed that may influence their sustained swimming capabilities. Accurate information on the swimming capabilities of larvae are essential, given that they are now being incorporated directly into models of larval dispersal. The second chapter uses a new approach to quantify undisturbed, routine swimming speeds of five species of tropical reef fishes throughout their larval phase. Changes in the nocturnal activity of larvae are also described throughout

development. This chapter provides the first description of routine swimming behaviour of larvae during their entire larval phase and firmly establishes that a behaviourally mediated mechanism of self-recruitment is within the normal behavioural repertoire of these larvae. In the third chapter, a unique methodology is developed that allows discrete vertical sampling of late stage reef fish larvae in the field. The new technique is used to provide the first discrete description of the nocturnal vertical distribution of late stage larval reef fishes throughout the water column off the leeward side of Lizard Island. This chapter determines the extent of differential water column use in late stage reef fish larvae and evaluates the potential impact of vertical distribution on larval dispersal and recruitment success of reef fishes. In the final discussion information on swimming ability and vertical distribution is synthesised to describe the potential for several different reef fish families to influence their dispersal using active behaviour.

Chapter 2: Functional swimming performance of reef fish larvae: factors influencing sustained ability

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2.1 Introduction

Recent studies have demonstrated that horizontal swimming capabilities of larvae can potentially have an important impact on the overall dispersal patterns as well as the recruitment success of reef fishes (Armsworth et al. 2001). Clearly, a good understanding of the horizontal swimming capabilities is vitally important in order to properly assess the overall impact that these larvae may have on their dispersal patterns.

Current information on the swimming abilities of reef fishes comes from two quite different methodologies. The first approach as been to follow late stage larvae directly in the field (Leis & Carson-Ewart 1997, 1998). These have invariably been short duration observations (< 10 min) that have been conducted only on late stage larvae. The other approach has concentrated on obtaining estimates of maximal performance measures of swimming ability using current flumes (Stobutzki & Bellwood 1994, 1997, Fisher et al. 2000). In particular, flume experiments have been conducted to examine the sustained swimming capabilities of these larvae, that measure long term swimming performance (e.g. Stobutzki & Bellwood 1997), as

well as estimates of U-crit, or maximum swimming speed, over short time scales (Stobutzki & Bellwood 1994, Fisher et al. 2000, Bellwood & Fisher 2001).

Flume based sustained swimming experiments are carried out by placing fish in an experimental flume and swimming them at a single speed until exhaustion (see Stobutzki & Bellwood 1997). Such experiments provide a measure of the maximum long-term swimming performance of larvae and have provided valuable empirical data on the ability of larvae to influence their dispersal over extended periods of time. Long-term information of this kind is essential if we are to properly assess the impact that these larvae may have on their dispersal patterns and recruitment success. However, at present all sustained swimming experiments for tropical reef fish larvae have been conducted using unfed larvae swum at a single experimental speed (Stobutzki & Bellwood 1997, Fisher et al. 2000). No attempt has been made since these initial experiments to broaden our understanding of the sustained swimming capabilities of these larvae.

Previous studies examining sustained swimming performance using unfed larvae have demonstrated that during swimming larvae utilise almost all of their body reserves and that the energy reserves of larvae have a considerable impact on the total effective distance that these larvae will be able to swim (Stobutzki 1997a). This suggests that sustained experiments conducted on unfed larvae are largely measuring the energy reserves of these larvae, rather than their sustained capabilities. It is unrealistic to expect larval fish to undergo swimming migrations without feeding, and feeding is likely to have a considerable impact on their sustained abilities. Indeed, larvae have been observed to feed whilst swimming *in-situ* at considerable speeds (Leis & Carson-Ewart 1998).

In addition, our understanding of the sustained swimming abilities of late stage larval reef fishes has been based primarily on experiments conducted at only one current speed (13.5 cms^{-1}; Stobutzki & Bellwood 1997, Stobutzki 1997a, Dudley et al. 2000). This speed was selected because it approximated the mean current speed around reefs in the Lizard Island region (Frith et al. 1986) and was therefore considered to provide estimates of swimming ability at a speed relevant to dispersal. The speeds at which larvae have been found to swim *in-situ* are considerably higher than that used in these sustained swimming experiments (Leis & Stobutzki 1999), suggesting that some larvae may be capable of sustaining considerably greater speeds than those recorded by Stobutzki & Bellwood (1997). In addition, the few studies that have examined the critical swimming abilities (U-crit) of larvae suggest that their maximum speeds are much higher than those seen in the field (Stobutzki & Bellwood 1994, Fisher et al. 2000). For some species speeds may approach the maximum limits for sustained aquatic locomotion (Bellwood & Fisher 2001).

It is well established that frictional drag increases with the square of swimming speed (Bone 1975, Vogel 1994) and that the metabolic power required for swimming will therefore increase with the cube of swimming speed (Schmidt-Neilson 1984). This theoretical principle has been adopted by Armsworth (2001) and Armsworrth et al. (2001) to predict how energetic costs change with swimming speed in reef fish larvae. There is also good experimental evidence that the metabolic cost of swimming increases with swimming speed in adult and juvenile fishes (Beamish 1970, 1990, Graham et al. 1994). Such theoretical considerations and experimental evidence suggest that swimming time should drop off rapidly as swimming speed increases. However, we currently have no empirical data on the effect of swimming

speed on the sustained swimming performance of tropical reef fish larvae, and the extent that they conform to theoretical considerations is not known.

Current speeds around reefs are known to vary considerably (Frith et al. 1986, Kench 1998). For example, Frith et al. (1986) showed that around a single reef in the Northern Great Barrier Reef, currents range from < 5 cms^{-1} to 60 cms^{-1}. Given such variation in ambient current speeds, the abilities of larvae to enhance or resist dispersal may depend critically on their swimming abilities over a range of current speeds. Although at present we have estimates of sustained capabilities at a single speed (13.5 cms^{-1}; Stobutzki & Bellwood 1997) and estimates of maximum swimming speed such as U-crit (Stobutzki & Bellwood 1994; Fisher et al. 2000) and short-term (<10 min) *in-situ* measurements (Leis & Carson-Ewart 1997), we still do not know how sustained swimming capabilities of larvae change with swimming speed. Current speeds around reefs are often dominated by tidal movements (Frith et al. 1986, Kench 1998), and therefore fluctuate on a scale of 12 to 24 hours. In order to understand the potential of reef fish larvae to influence their dispersal, we need to examine the maximum swimming speeds that larvae are able to maintain on such a time scale.

Furthermore, the overall impact of swimming behaviour could potentially be much greater than the values reported by Stobutzki & Bellwood (1997) if larvae are capable of maintaining swimming activity for substantial lengths of time at much higher swimming speeds. Larvae would have the greatest influence on dispersal patterns and recruitment success if they swim at the fastest possible speed that they are capable of maintaining, and it is this maximum sustainable speed that needs to be determined to properly understand the potential of larval behaviour.

Information on the swimming abilities of late stage larvae is now being incorporated into models examining the effect of larval behaviour on dispersal patterns and recruitment success (Wolanski et al. 1997, Armsworth 2000, Armsworth et al. 2001, James et al. 2002). It is becoming increasingly important to obtain reliable estimates of the swimming abilities of larvae. However, existing flume-based estimates of sustained swimming on unfed larvae may dramatically underestimate the swimming abilities of larvae in the field. Furthermore, if swimming data are to be effectively incorporated into dispersal models we need to know how sustained swimming performance of larvae varies with swimming speed and how fast larvae are able to swim for significant lengths of time (i.e. 12 to 24 hours).

The aim of this study was therefore, twofold: Firstly, to assess the impact of food availability on the sustained swimming ability of reef fish larvae. Secondly, to examine the relationship between swimming speed and sustained swimming ability and to quantify the maximum sustainable swimming speeds of late stage reef fish larvae.

2.2 Materials and Methods

2.2.1 Effects of feeding

The influence of food on swimming time: Anemonefish larvae provide an excellent model for examining the functional capabilities of late stage tropical reef fishes because they are relatively easy to rear in captivity. Lab-reared larvae of *Amphiprion melanopus* were used for this experiment to ensure that all larvae within a batch were in a relatively similar physical condition at the start of the experiment.

Rearing procedures were modified after Job & Bellwood (2000). Larvae were reared in 200L glass aquaria using cultured rotifers and *Artemia* nauplii. Wild caught plankton was not used for these experiments to ensure that all larvae within and among batches received similar quality food throughout development. Larvae reared under these conditions are similar to wild caught larvae in terms of both their length and developmental rates (Job & Bellwood 2000). In addition, a direct comparison of U-crit speed and sustained swimming time for reared larvae and larvae caught in light traps at Lizard Island, suggest that swimming capabilities of reared larvae are broadly similar, or may slightly underestimate the swimming capabilities of wild caught larvae (Table 2.1). As such, data obtained using larvae reared in captivity should be considered conservative with respect to the potential swimming capabilities of these larvae in the field.

Table 2.1. A comparison of U-crit and sustained swimming time for reared and wild caught larval *Pomacentrus amboinensis* showing means and 95% confidence limits. ANOVA indicated a significant difference in the swimming speeds of reared larvae and wild caught larvae ($F_{1,25} = 10.5$, $p = 0.003$). The 95% Confidence limits suggest no significant difference in the sustained swimming capabilities of reared and wild caught larvae.

Source of larvae	U-crit (cms^{-1})[a]	Sustained swimming (hours)[b]
Reared	26.89 ± 3.61	53.86 ± 46.94
Wild caught	38.66 ± 5.04	46.34 ± 15.15

[a] For U-crit, wild caught data were obtained from Lizard Island and reported in this thesis (Table 2.2). Reared data were obtained for one batch of larvae reared at Lizard Island, as well as from published data from Fisher et al. (2000; Figure 5a, total lengths > 10.4). [b] For sustained swimming, data for wild caught larvae were obtained from Stobutzki (1998; Table 2, Figure 2). Reared data were obtained from Fisher et al. (2000, Figure 4b, developmental age 0.8 and 1).

At 7 days post hatch, larvae were transferred to a six channel experimental swimming flume. Details of the swimming flume as well as calibration methodology are given in Stobutzki (1997b) and Stobutzki & Bellwood (1997). Two fish were placed in each channel and all fish were allowed to acclimatise for several minutes before the start of the experiment. Larvae were swum at a speed of 7 cms^{-1}, a speed known to be sustainable for late stage *Amphiprion melanopus* (Fisher et al. 2000). At the start of the experiment all fish were swum for approximately 2 hours without feeding. Stressed fish showing deleterious effects of catching and handling, were removed from the experiment to avoid confounding the results. After two hours, swimming channels with fish still remaining were randomly allocated to a 'fed' or 'unfed' treatment. During feeding, the current flume in all channels was stopped for 10 minutes and newly hatched *Artemia* nauplii (Prime Artemia Incorporated Great Salt Lake brine shrimp eggs) were added to the 'fed' channels. Remaining *Artemia* were removed from the water exiting the swimming channel using a 62 μm sieve. Feeding stops were performed four times per day, at 4 hourly intervals between 8 am and 8 pm throughout the experiment. The experiment was then repeated for a further 4 replicate clutches of larvae. Experiments were terminated after a maximum of 6 days of continuous swimming, at which point any remaining larvae were sampled.

The data were analysed by calculating the mean and maximum time swum for fed and unfed fish for each clutch and compared using a paired t-test (Zar 1999). This test was selected because it permits a direct comparison of the two feeding treatments within each batch, thus avoiding confounding effects due to differences in quality or size between batches (cf. Bellwood & Fisher 2001). For graphical simplicity, however, the mean of the five clutches was plotted for both the maximum

and mean swimming duration for each treatment. At the start of each experiment, the maximum speed (U-crit, see Brett 1964) was determined for each clutch. These were compared with the experimental speed to indicate the relative level of activity during sustained swimming. A sample of larvae was also obtained and fixed in Marine Bouin's then stored in 70% ethanol. Using these samples, measurements were made of wet and dry weight, standard length and body depth. A mean was obtained for each clutch and used as the value for that clutch. Means presented in the results represent the mean and standard error between the five clutches.

Amount of food ingested: Estimates of the number of *Artemia* nauplii ingested by larvae during the 10 min feeding break were obtained from videos of larvae in the swimming channels. Of the films taken only 4 individuals were clearly visible throughout the feeding stop and were therefore used for analysis. Ingestion was signified by a feeding strike. For late stage larval anemone fishes feeding success is close to 100% (Job & Bellwood 1996), therefore counts of feeding strikes provide a good estimate of individual consumption. Counts were converted to equivalent dry weights using published data for newly hatched Great Salt Lake *Artemia* nauplii (Garcia-Ortega et al. 1998). These were expressed as a percentage of mean dry body weight of the fish swum. An estimate of the energy obtained by larvae during feeding breaks was calculated by converting the known biochemical composition of newly hatched *Artemia* nauplii (Garcia-Ortega et al. 1998) to energy values following Henken et al. (1986). These were expressed as joules per gram of fish wet weight per hour to facilitate comparison with literature values. Energy values were adjusted for

assimilation (Brett & Groves 1979) as well as metabolic and respiratory costs or "apparent heat increment" (Beamish & Tripple 1990).

Maximum feeding speed: Estimates of the maximum swimming speed larvae are able to maintain and still show feeding behaviour was obtained from late stage larval *Amphiprion melanopus* as well as late stage *Pomacentrus amboinensis*. These experiments were conducted using the same six channel experimental swimming flume, using a method modified from the U-crit technique described by Brett (1964). Between 4-8 larvae were transferred to the swimming flume and allowed to acclimatise for several minutes. The swimming flume was then started and the speed increased in two-minute intervals by 2 cms^{-1} increments. At the start of each new interval newly hatched *Artemia* sp. were added to the water reservoir of the swimming flume and carried by the current flow through the swimming channels. Larvae could be clearly seen to be feeding by their distinctive feeding strike, as observed above. The last speed that a fish was observed feeding and the maximum speeds able to be maintained by larvae were recorded.

2.2.2 Swimming speed

Empirical relationship between swimming speed and sustained time: The direct relationship between experimental swimming speed and sustained swimming time was examined using lab-reared late pre-settlement stage larvae of *Amphiprion melanopus*. Rearing procedures followed section 2.2.1, with the exception that larvae were also fed wild caught plankton (62-410 μm) throughout development. At 7 days

post-hatch, larvae were transferred to the same six channel experimental swimming flume used in feeding experiments. Two fish were placed in each channel and allowed to acclimate for several minutes before the start of the experiment. After initial acclimation, water flow was gradually increased over a period of 2 minutes to the required experimental speed. Five experimental speeds were used: 4, 7, 10, 13 and 16 cms^{-1}. These speeds were chosen to cover the full range of speeds that late stage *A. melanopus* larvae are capable of sustaining (Fisher et al. 2000). At each speed, three separate clutches of larvae were swum (i.e. each batch was swum at one speed only), with the exception of 13 cms^{-1}, for which only two clutches of larvae were available.

For each clutch, the maximum swimming speed of the clutch (U-crit) was estimated based on a sample of 8 – 12 individuals. Speed increments used were equivalent to 3 body lengths per second (2.1 cms^{-1}) with a time interval of 2 min, following Bellwood and Fisher (2001). A sample of larvae for morphological measurements was also obtained from each clutch at the start of each experiment (fixed in Marine Bouin's for 24 – 48 hours, then stored in 70% ethanol). Mean, minimum and maximum total lengths were recorded for each clutch from these specimens.

The maximum and mean time swum, as well as the equivalent distance traveled for each experimental swimming speed were plotted based on the means of the three replicate clutches. These means were compared statistically using ANOVA's and Tukey's tests for each variable separately. The assumptions of normality and homogeneity of variances were tested graphically using qq and predicted versus residual plots respectively. After square root transformations were

applied to the variables "average time swim" and "average distance traveled" the data were found to meet these assumptions. These transformed data were used in the analyses.

Maximum and mean swimming times were also examined in relation to the swimming speed of larvae in body lengths per second (bls^{-1}). Speed in bls^{-1} was calculated by dividing the experimental swimming speed (cms^{-1}) by total length (cm). For maximum swimming time, speed in bls^{-1} was calculated using the largest individuals in each clutch. For average swimming time the average total length from each clutch was used. In addition, swimming times were examined in relation to the swimming speed of the larvae relative to their maximum swimming speed (U-crit). Relative speed was calculated by dividing the experimental swimming speed by the U-crit (cms^{-1}) of each clutch. For maximum swimming time, relative speed was calculated using the maximum U-crit from each clutch. For average swimming time, relative speed was calculated using the average U-crit of each clutch.

A regression analysis of $\log_{10}$ time swum versus $\log_{10}$ experimental speed was used to produce a predictive model of how swimming ability is related to experimental speed for both maximum as well as average swimming time. ANOVA of regression was used to test if this relationship was significant and a Student's t-test was used to determine if there was a significant difference between the two slopes (Zar 1999). Confidence limits (95%) were used to examine if these slopes differed significantly from –3 at alpha = 0.05.

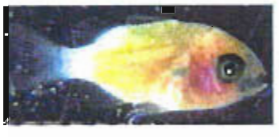
Maximum sustainable swimming speeds in a range of reef fish larvae: Experiments examining the maximum sustainable swimming speed were carried out

using a range of commonly occurring species from Lizard Island. Larvae were caught using lights traps following the design of Stobutzki & Bellwood (1997) over two Austral summers from Nov 2000 to Jan 2001 and Nov 2001 to the end of Dec in 2001. Larvae were swum either using the same swimming channel as used for *Amphiprion melanopus* larvae or a swimming flume that was almost identical but with half the number of channels (so that a higher current speed could be obtained). Nine species of larvae were swum in total over both field seasons. Five of these were from the family Pomacentridae (*Pomacentrus amboinensis*, *Pomacentrus molluccensis*, *Pomacentrus nagasakiensis*, *Chromis* sp. and *Dischistodus prosopotaenia*), three from Apogonidae (*Apogon trimaculatus* and two other unidentified species) and a single lethrinid (Table 2.2). Several U-crit trials were conducted to determine the average U-crit of each species and these samples were retained to obtain an estimate of mean length. Separate groups of larvae were swum using standard sustained swimming procedures at speeds of 5 cms^{-1} intervals. The first speed examined was that equivalent to the average U-crit of that species (this defines the zero point or the maximum speed larvae could maintain for only short lengths of time). New groups of larvae were then swum at consecutively decreasing speeds until the speed that most of the larvae (<80%) could swim for 24 hours was determined. The proportion of larvae remaining after 24 hours at each speed was recorded. At least two groups of larvae from separate light trap catches were used at each swimming speed. A value of 24 hours of continuous swimming was used to represent a "substantial" length of time for these larvae. Experiments examining the sustained swimming capabilities of *A. melanopus* found that if larvae were fed during the experiment they could maintain swimming activity significantly longer than

unfed larvae, and in some cases, indefinitely (Figure 2.1, this chapter). Sustained swimming experiments carried out over longer periods are probably measuring energy reserves of larvae, and not sustained swimming abilities.

The proportion of larvae remaining after 24 hours at each experimental swimming speed for all nine species of larvae examined at Lizard Island were plotted against the swimming speed of the larvae expressed in body lengths per second (bls^{-1}) as well as the experimental swimming speed expressed as a proportion of U-crit. Sigmoidal regressions were fitted to each family individually, as well as all three families together using Sigmaplot 4.1. Three-parameter sigmoidal regressions are appropriate given that the upper and lower values are bounded by one and zero respectively. Residuals from each regression were saved and F ratios used to determine if the relationship between the proportion of larvae remaining and relative swimming speed differed significantly among the three families for speed relative to length as well as speed relative to U-crit. In addition, relative speeds were divided into categories and the proportion of larvae remaining for each category was averaged across all species. The highest relative swimming speed at which the proportion of larvae remaining did not differ significantly from 1.0 (all larvae were able to swim for 24 hours at that relative swimming speed) was determined using 95% confidence limits calculated from these averages.

Table 2.2. Details of the study species used for maximum sustainable swimming speed experiments at Lizard Island. Values are means +/- SE.

Species	Family	U-crit (cms^{-1})	Total length (mm)
 *Pomacentrus amboinensis*	Pomacentridae	38.9 ± 2.3	14.6 ± 0.2
 *Pomacentrus molluccensis*		30.9 ± 1.9	14.6 ± 0.2
 *Pomacentrus nagasakiensis*		36.5 ± 1.9	16.1 ± 0.2
 *Chromis* Sp.		35.1 ± 1.3	10.7 ± 0.2
 *Dischistodus prosopotaenia*		29.4 ± 0.8	12.2 ± 0.2
 *Apogon trimaculatus*	Apogonidae	23.8 ± 1.0	16.5 ± 0.3
 *Unidentified A*		24.4 ± 0.6	18.2 ± 0.3
 *Unidentified* B		18.6 ± 0.6	11.8 ± 0.2
 *Lethrinus* sp.	Lethrinidae	45.3 ± 2.7	23.2 ± 0.5

Sustainable swimming speeds across a variety of reef fish families: The experiments conducted so far to examine the influence of swimming speed on sustained swimming capability of larvae, and to determine the maximum sustainable swimming speed of larvae, have required large numbers of larvae over extensive periods of time to complete. The number of larvae used for the sustainable swimming studies for the nine species examined at Lizard Island ranged from 53 to to 109 individuals for each species. Very few species, or even families, occur in such high numbers in light traps catches at Lizard Island. As an alternative, the maximum sustainable swimming speeds across several reef fish families were determined using three different methods.

Method 1: Estimating sustained ability based on length. This method assumes that other reef fish larvae are capable of sustaining a similar relative speed in terms of their length, and was calculated as bl * (relative speed), where bl is the mean total length of each family expressed in cm (from Stobutzki & Bellwood 1997) and (relative speed) is the maximum sustainable swimming speed expressed in bls^{-1}. Maximum sustainable speed in *A. melanopus* is based on the speed larvae are able to maintain on average for 24 hours and in the other species examined at Lizard Island the speed at which a large proportion of larvae (>80%) were able to maintain swimming activity for 24 hours. For both *A. melanopus* and the nine species examined at Lizard Island, this speed was around 8.5 bls^{-1} (Figures 2.4 and 2.6).

Method 2: Estimating sustained ability based on U-crit. This method assumes that other reef fish are capable of sustaining a similar relative speed in terms of their U-crit (maximum speed, Brett 1964) and was calculated as U-crit * (relative U-crit).

Average U-crit values were obtained from direct measurements from as many species as possible from each family caught in light traps at Lizard Island (Appendix). A maximum number of 10 individuals were swum of each individual species and mean U-crit estimates for each family were calculated from all individuals swum. Values for relative U-crit were determined as the maximum sustained swimming speed as a proportion U-crit for *A. melanopus* and the nine species used for sustained experiments at Lizard Island. For both *A. melanopus* and the nine other species, this speed was around 50% of the average U-crit (Figures 2.4 and 2.6).

Method 3: Estimating sustainable speeds based on sustained swimming time at 13.5 cms^{-1}. This method is based on the empirically derived relationship between log_{10} sustained swimming time and log_{10} swimming speed for *A. melanopus* and was calculated as $10^{(\log_{10}(t)-c)/(slope)}$, where (t) is sustained swimming time in hours (24) and values for (c) were calculated from published sustained swimming data at 13.5 cms^{-1} (from Stobutzki & Bellwood 1997). The slope was taken directly from the empirical relationship for *A. melanopus* based on the average of each clutch (-2.95), because this provides the most conservative estimate of swimming ability (Figure2.5).

Predicted sustainable swimming speeds from each model were compared to observed values for the nine species examined at Lizard Island (from Table 2.2). Observed values of sustainable swimming speed were taken as the speed at which greater than 80% of larvae were able to maintain swimming for 24 hours. Because larvae were swum at 5 cms^{-1} speed intervals, a range of +/- 2.5 cms^{-1} was used to represent the error associated with speed measurements. Sustainable swimming

speeds estimated using the three different methods were compared using Pearson Correlation and were also compared to *in-situ* field values (Leis & Carson-Ewart 1997) via regression analysis.

2.3 Results

2.3.1 Effects of feeding

The influence of food on swimming time: A total of 87 fish from 5 clutches were swum: 44 "fed" and 43 "unfed". The mean length of fish in each clutch at the beginning of the experiments ranged from 5.5 to 7.6 mm standard length (Table 2.3). The experimental speed (7 cm s^{-1}) as expressed in body lengths per second ranged from 9.2 to 12.8 bls^{-1}, which is equivalent to approximately half (35 to 85%) of the maximum speed (U-crit) of each clutch (Table 2.3).

Table 2.3. Summary statistics for *Amphiprion melanopus* larvae used in feeding experiments. Standard errors refer to variation among clutches (n = 5).

	Maximum	Minimum	Mean
Standard length (mm)	7.6	5.5	6.6 ± 0.5
Relative speed (Body lengths s^{-1})	12.7	9.2	10.6 ± 0.8
U-crit (cms^{-1})	19.9	8.2	16.3 ± 2.3
Experimental speed (% U-crit)	85	35	48 ± 10

(maximum and minimum values are based on batch means)

Feeding larvae during swimming experiments was found to significantly increase their average swimming duration ($t = 4.9$, $df = 4$, $P < 0.005$), with fed fish

being able to swim about twice as long as unfed fish (Figure 2.1A). Feeding increased the equivalent distances covered by larvae from around 6.9 km to 12.2 km. The effect of food on the sustained swimming ability of larvae was even greater when only the longest swimming individual from each clutch for each treatment was considered. Feeding larvae significantly increased the maximum swimming duration of fed larvae to more than double that of unfed larvae ($t = 5.3$, $df = 4$, $p < 0.005$, Figure 2.1B). This increased the equivalent distance covered before exhaustion from 11.8 km to 28.7 km.

Of the fed larvae swum, 5 were preserved and used for measurements. After six days of swimming these larvae increased their total standard length by 1.5 mm, which is equivalent to a 3.0 % increase per day. They also increased in wet weight by 10.4 mg, an increase of 10.4 % per day from their original wet weight (Table 2.4). During the six days of swimming the fed larvae had also undergone metamorphosis, developing the colour patterns of a settled juvenile (Figure 2.2). Measurements were also made for 2 batches of larvae left undisturbed in rearing tanks. These larvae were found to grow by 4.0 ± 0.2 % in length and 16.9 ± 2.0 % in wet weight per day. MANOVA (using wet weight and standard length) found no significant difference in the daily growth rates of *Amphiprion melanopus* larvae left undisturbed in rearing tanks and those from the fed swimming treatment (Pillai's trace $F = 2.44$, d.f. = 2, 7; $p = 0.79$).

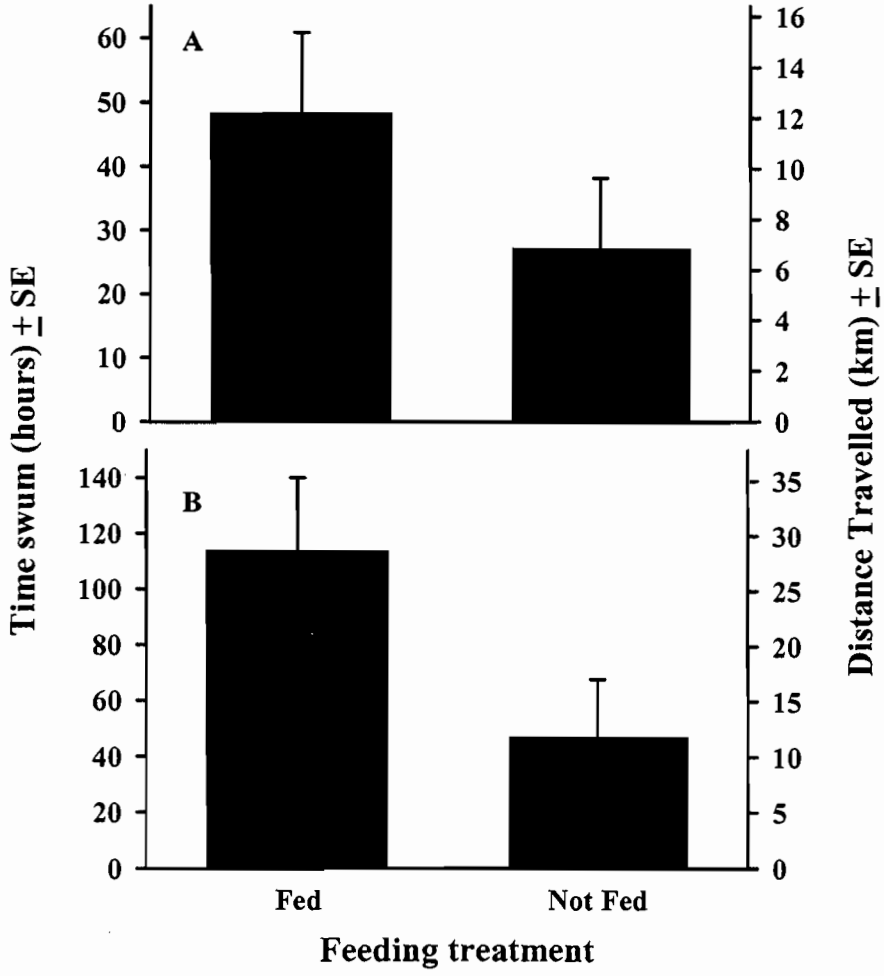


Figure 2.1. A comparison of the sustained swimming time and equivalent distance travelled between fed and unfed larval *Amphiprion melanopus* (n = 5). Mean time swum for each treatment for each clutch (A) and the maximum time swum for each treatment for each clutch (B). Standard errors are calculated from the overall mean of each treatment across all clutches.

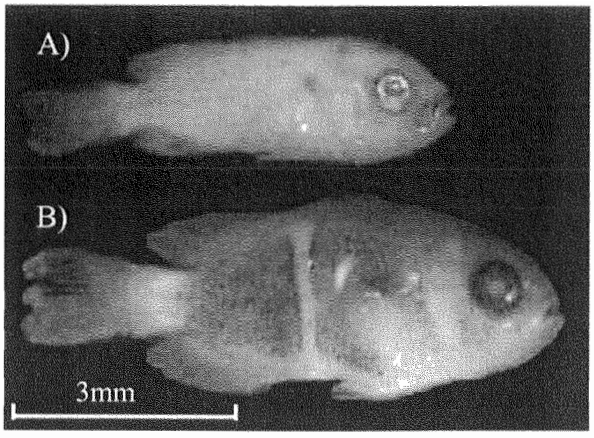


Figure 2.2. A visual comparison of fed larval *Amphiprion melanopus* at the start of the experiment (A) and at the end of the feeding experiment (B).

Table 2.4. Standard length and wet weight summary statistics for fed larval *Amphiprion melanopus* at the start of the feeding experiment and after swimming for six days. Daily growth rates are also shown for fed larvae from the swimming treatment as well as for larvae left undisturbed in rearing aquaria over a similar age period.

		Length (mm)	Weight(mg)
Fed larvae from swimming treatment	At start	7.6 ± 0.1	11.5 ± 0.2
	After swimming	9.1 ± 0.3	21.8 ± 2.4
	Growth day^{-1}	0.25	1.7
	% growth day^{-1}	3.0%	10.4%
Larval in rearing aquaria	% growth day^{-1}	4.0%	16.9%

Amount of food ingested: The number of *Artemia* nauplii ingested in a feeding stop and therefore the amount of energy obtained per day for fed larvae varied considerably. Larvae consumed a minimum of 692 and a maximum of 1344 individual *Artemia* nauplii each day over the four feeding stops (Table 2.5). This is equivalent to between 86 and 167 % of the mean dry weight of the larvae, and between approximately 2252 and 4374 Joules per g wet weight of larvae per day (Table 2.5).

Table 2.5. Quantities and energetic value of food fed to *Amphiprion melanopus* larvae during the feeding experiments. Standard error based on 4 individuals.

	Number of *Artemia* ingested (number day^{-1})	Weight of *Artemia* ingested* (% larval body weight)	Equivalent energy** ($jg^{-1}day^{-1}$)
Maximum	1344	166.9	4374
Minimum	692	85.9	2252
Mean	977 ± 151	121.3	3179

* Calculated from *Artemia* counts using values presented in Garcia-Ortega et al. (1998)

** Approximated from *Artemia* counts using values presented in Brett & Groves (1979), Henken et al (1986), Beamish & Tripple (1990) and Gargacia-Ortega et al. (1998).

Maximum feeding speed: The maximum swimming speeds that larvae are able to swim and still maintain feeding behaviour were examined using 11 individuals of *Pomacentrus amboinensis* over 2 occasions and 20 individuals of *Amphiprion melanopus* over 3 occasions (Table 2.6). Larvae of both species were observed to feed actively whilst swimming, however, for both species this was at considerably

slower speeds than their maximum sustainable speed (U-crit; Table 2.6). *Pomacentrus amboinensis* larvae were able to feed at speeds of up to 7.1±1.4 cms^{-1}, which is about 53% of their maximum (U-crit) speed (Table 2.6). *Amphiprion melanopus* larvae were still able to feed at speeds of 3.5±0.6 cms^{-1}, which is around 28% of their maximum speed (Table 2.6).

Table 2.6. The maximum speed larval *Pomacentrus amboinensis* and *Amphiprion melanopus* are able to swim and still maintain feeding behaviour.

	No. of larvae	U-crit (cms^{-1})	Max feeding speed (cms^{-1})	% U-crit speed
Pomacentrus amboinensis	11	15.1 ± 1.5	7.1 ± 1.4	53 %
Amphiprion melanopus	20	14.3 ± 1.5	3.5 ± 0.6	28 %

2.3.2 Swimming speed

Empirical relationship between swimming speed and sustained swimming time: *Amphiprion melanopus* larvae used for the sustained swimming experiments ranged in size from 7.2 to 8.6 mm total length, with average clutch U-crits ranging from 10.3 to 17.4 cms^{-1} among the 14 clutches (Table 2.7). The maximum clutch U-crits ranged from 18.6 to 25.2 cms^{-1}, which is considerably higher than the fastest experimental speeds used in the sustained swimming experiments (16 cms^{-1}) (Table 2.7).

Table 2.7. Summary statistics for *Amphiprion melanopus* larvae used in sustained swimming experiments. n = 14 clutches of 7 – 12 individuals.

	Average ± SE	Range
Standard length (mm)	8.14 ± 0.11	7.22 - 8.56
Average U-crit (cms^{-1})	14.59 ± 0.54	10.34 – 17.41
Maximum U-crit (cms^{-1})	21.45 ± 0.65	18.6 – 25.2

There was a significant difference in swimming duration between the five experimental speeds (Table 2.8), with swimming duration increasing considerably at slower speeds (Figure 2.3A). Sustained swimming time increased relatively smoothly with decreasing swimming speed, with maximum swimming times increasing to a greater extent than average swimming times (Figure 2.3A). For mean time swum, there did not appear to be any sudden increase in swimming performance, with post-hoc tests showing that the five speeds form three, gradually increasing, overlapping subsets (Table 2.8). For maximum swimming time however, the increase in swimming performance with decreasing swimming speed was more dramatic, with post-hoc tests showing no significant difference in maximum sustained swimming time between 16, 13 and 10 cms^{-1}, a significant increase in maximum swimming time at 7 cms^{-1} and a further significant increase at 4 cms^{-1} (Figure 2.3A, Table 2.8).

Along with sustained swimming time, the equivalent distance traveled by larvae was also highest at the slowest swimming speeds (Figure 2.3B). For average distance swum there was a gradual increase with decreasing speed and post hoc tests indicated only two, broadly overlapping subgroups (Table 2.8). In contrast, there again appeared to be a sudden jump in the maximum distance swum with decreasing

swimming speed between the 7 and 10 cms^{-1} speeds, although post hoc analysis did not find this jump to be statistically significant (Figure 2.3B, Table 2.8). After this rapid increase, maximum distance swum appeared to increase only slightly with the slower speed of 4 cms^{-1}, and post hoc tests indicated no significant difference in the maximum distance swum between the two slowest speeds (Table 2.8).

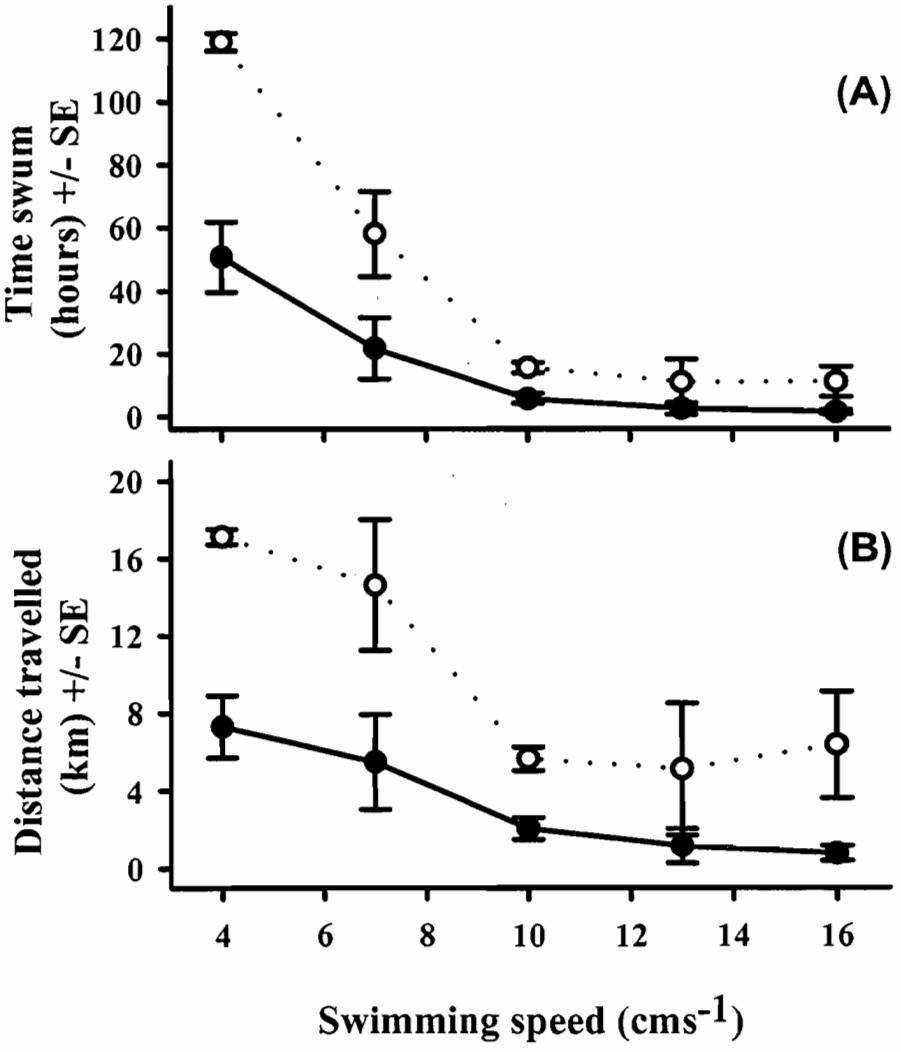


Figure 2.3. Average swimming duration versus experimental swimming speed in *Amphiprion melanopus* (n = 3 clutches, except for 13 cms^{-1}, where n = 2). (A) Time swum and (B) equivalent distance traveled. Longest swimming individual from each clutch (○) and average for each clutch (●).

Table 2.8. ANOVA results comparing average time swum, maximum time swum, average distance traveled and maximum distance traveled at the five different experimental speeds (4, 7, 10, 13 and 16 cms^{-1}) for larval *Amphiprion melanopus*.

Variable	$F_{4,9}$	P	Homogeneous subsets
Average time swum	12.691	0.001	(4-10); (10-16)
Maximum time swum	40.963	0.000	(4); (7); (10-16)
Average distance traveled	5.208	0.019	(4-7); (7-16)
Maximum distance traveled	5.789	0.014	(4-10); (7-16)

Maximum as well as average swimming time increased exponentially with decreasing experimental speed when expressed in body lengths per second (Figure 2.4A). For both maximum and average swimming time, *A. melanopus* first starts to show a high level of sustained swimming performance at swimming speeds less than 8-9 bls^{-1} (Figure 2.4A). Maximum as well as average swimming time also increased exponentially with decreasing experimental speed expressed as a proportion of the U-crit for each clutch (Figure 2.4B). For average swimming time, it appears that fish only start to show significant swimming ability at speeds slower than 50% of the average U-crit (Figure 2.4B). For maximum swimming time fish start to show some measure of sustained swimming performance at speeds around 80% of their maximum U-crit (Figure 2.4B). The difference between mean and maxim time swum is much smaller for speed expressed as a proportion of U-crit than for speed expressed as a proportion of length (Figure 2.4).

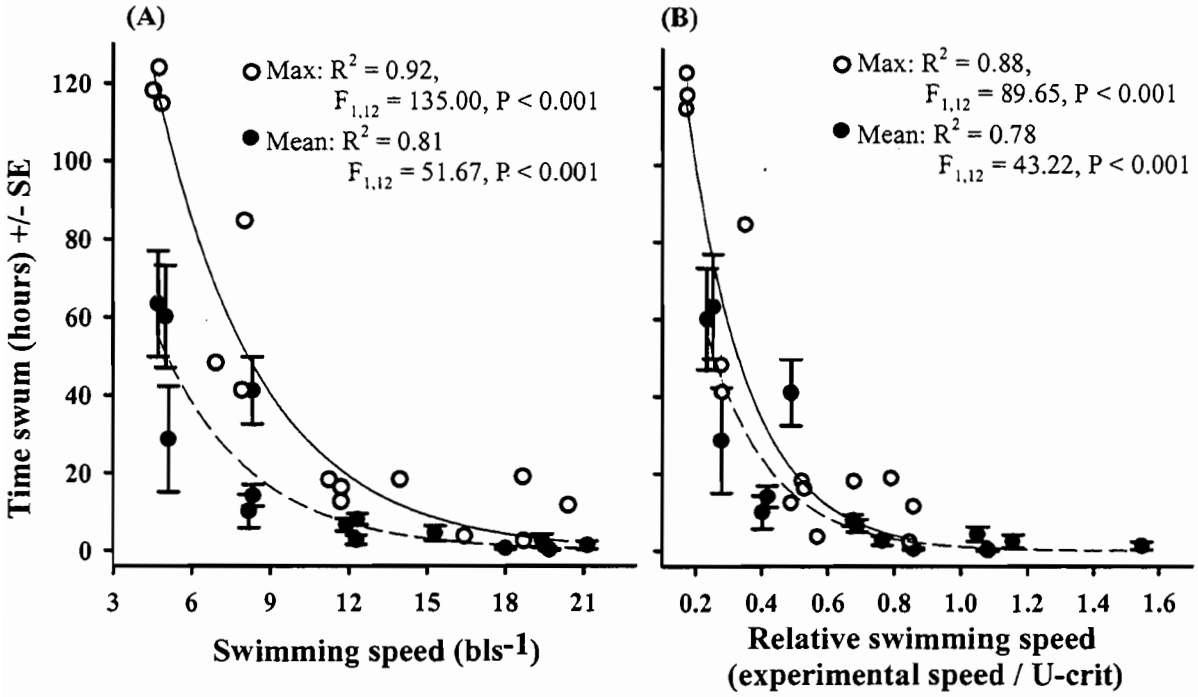


Figure 2.4. Sustained swimming time for each clutch of *A. melanopus* versus swimming speed in body lengths per second (bls^{-1}) (experimental speed / total body length) (A) and relative swimming speed (experimental speed / U-crit) (B). (○) Maximum time swum (speed based on maximum total length and maximum U-crit for each clutch); (●) Average time swum (speed based on average total length and average U-crit for each clutch). Exponential decay regression lines have been fitted to each relationship. The dashed lines show the relationship for average time swum, and the solid lines show the relationship for maximum time swum. All regressions are significant ($p < 0.0001$), however F values did vary, as did R^2 values.

Mechanical theory based on drag suggests that metabolic power required for swimming should increase with the cube of swimming speed (Schmidt-Neilson 1984). If metabolic cost is directly related to the sustainable swimming time of larvae, then time swum should also decrease with the cube of swimming speed. Consequently, a graph of log time swum, versus log swimming speed should yield a

linear relationship, with a theoretical slope of exactly –3. There was a significant linear relationship between $\log_{10}$ sustained swimming time and $\log_{10}$ swimming speed for both maximum and average abilities for each clutch (Figure 2.5). The relationship between swimming time and speed followed the basic equation $\log_{10}$ (time) = -2.95 $\log_{10}$ (speed) + 3.39 for average swimming time, and $\log_{10}$ (time) = -2.12 $\log_{10}$ (speed) + 3.58 for maximum swimming time. No significant difference was found between the slopes for the relationship of declining swimming time with

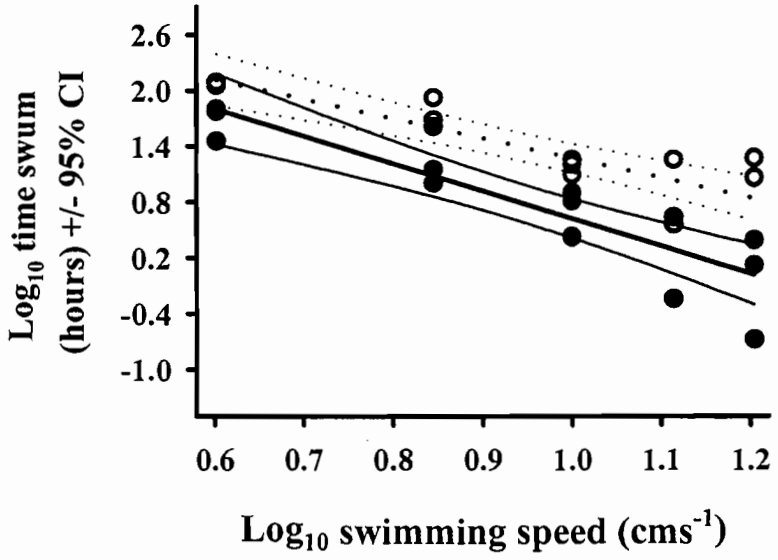


Figure 2.5. Sustained swimming time (hours) versus experimental swimming speed (cms^{-1}). Data have been Log_{10} transformed. Least squares regression lines have been fitted separately to the longest swimming individual from each clutch (○) ($y = -2.12x + 3.39$; $R^2 = 0.77$; $F_{1,12} = 40.24$; $P < 0.001$) and the average time swum for each clutch (●) ($y = -2.95x + 3.58$; $R^2 = 0.78$; $F_{1,12} = 42.44$; $P < 0.001$). 95% Confidence limits are shown for each regression.

increasing swimming speed for average sustained swimming time and maximum sustained swimming time, ($t = 1.83$, $df = 24$, $P > 0.05$). Confidence limits (95%) indicated that while the slope of the relationship for average time swum was not significantly different to the theoretically predicted slope of –3 (i.e. 95% CI of slope = -3.96 to -1.96 overlap -3), the slope for maximum time swum was significantly less (i.e. 95% CI of slope = -2.86 to -1.39 are less than -3).

Maximum sustainable swimming speeds in a range of reef fish larvae: Maximum sustainable swimming speeds were examined in nine species of reef fish larvae, five from the family Pomacentridae, three from the Apogonidae and a single species from the Lethrinidae. The relationship between the proportion of larvae remaining and relative swimming speed differed significantly among the three families for speed expressed relative to length, but not for speed expressed relative to U-crit (Figure 2.6).. The Pomacentridae appeared to be able to sustain swimming speeds considerably higher relative to their length than the Apogonidae (Figure 2.6A). *Amphiprion melanopus* larvae were capable of maintaining speeds around 8.5 bls^{-1} (Figure 2.4A), which lies somewhere between the Pomacentrids and Apogonids examined at Lizard Island. The nine species examined appeared to be able sustain a much more consistent swimming speed relative to their average U-crit than their speed relative to length (Figure 2.6B). When averaged across all nine species, it appears that larvae could maintain swimming for 24 hours at speeds around 7-10 bls^{-1} (midpoint 8.5 bls^{-1}) and around 45-55% of their U-crit (midpoint 50% U-crit) (Figure 2.7). This is also consistent with data obtained for the *Amphiprion melanopus* larvae reared in aquaria, which also showed significant sustained swimming abilities at a speed of around 50% of their U-crit (Figure 2.4B).

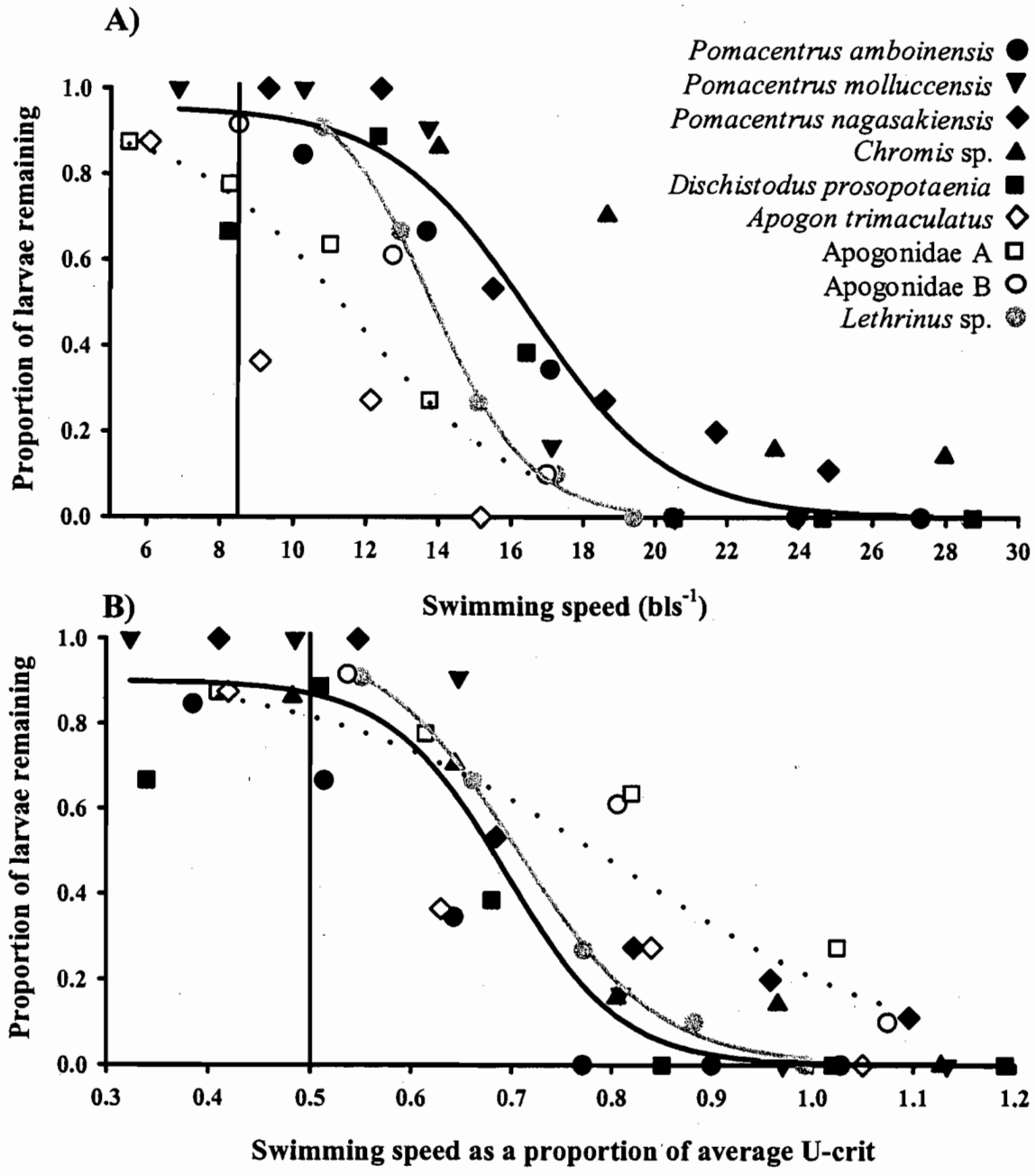


Figure 2.6. Proportion of larvae able to sustain swimming activity for 24 hours at different swimming speeds expressed in bls^{-1} (A) and as a proportion of the average U-crit for each species (B). Data are for nine species of reef fish larvae captured in light traps near Lizard Island. Black markers represent species from the family Pomacentridae (five species), unfilled markers the Apogonidae (three species) and grey markers a single species from the Lethrinidae. Vertical lines indicate the speed *Amphiprion melanopus* larvae could sustain for 24 hours relative to their length (A) and their average U-crit (B). Fitted three-parameter sigmoidal regressions are shown for each family. F ratios using residuals from fitted regressions indicate that the relationship between the proportion of larvae remaining and relative swimming speed is significantly different among the three families for speed expressed relative to length ($F_{36,42} = 1.82$, $P = 0.035$), but not for speed expressed relative to U-crit ($F_{36,42} = 1.244$, $P = 0.253$).

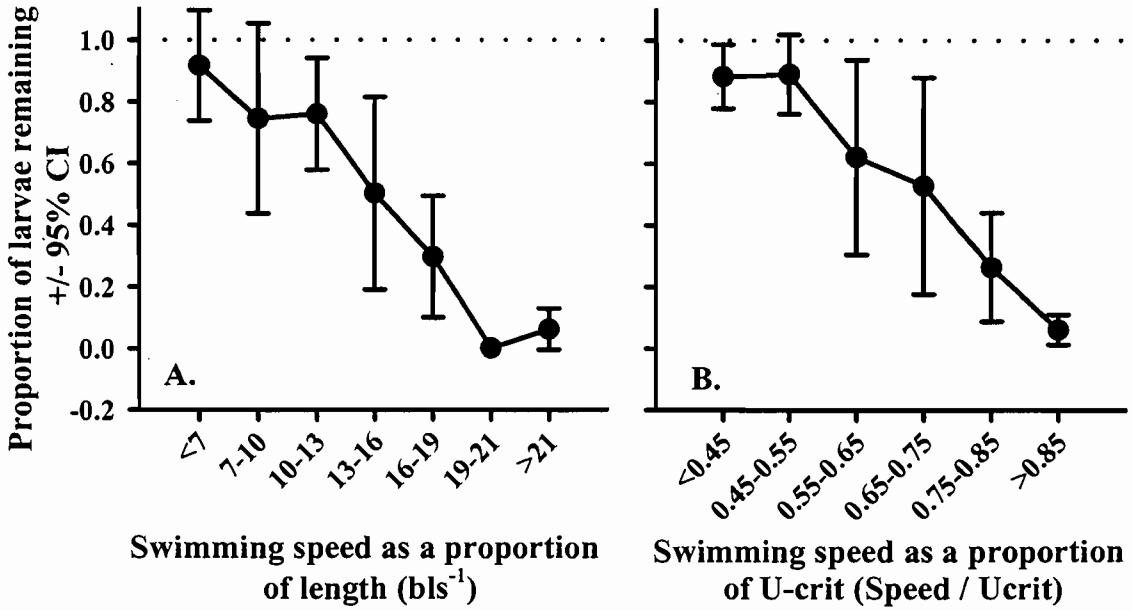


Figure 2.7. Proportion of larvae remaining after 24 hours +/- 95% Confidence Limits versus swimming speed expressed relative to length (body lengths per second) (A) and relative to U-crit (B). The dotted line indicates that all larvae were remaining after 24 hours at that relative speed. Data for all species has been pooled and the proportion remaining after 24 hours averaged for each relative speed category. The 95% Confidence limits indicate the highest relative speed at which the proportion of larvae remaining after 24 hours is not significantly different from 1.

Sustainable swimming speeds across a range of reef fish families:

The maximum sustainable swimming speeds predicted using the three different methods and actual sustainable speeds for the nine species measured at Lizard Island were compared (Table 2.9). Method 1 was the worst predictor of sustainable swimming speed; consistently underestimating observed values for most species. Both methods 2 and 3 were equally good at predicting observed sustainable speeds

(Table 2.9). A comparison of the values attained using the three different methods of predicting sustainable swimming speed shows that all three methods give remarkably similar results for a wide range of reef fish taxa (Table 2.10). Significant relationships were found among sustained swimming speeds estimated using all three methods (Table 2.10).

Table 2.9. A comparison of the maximum sustainable swimming speeds predicted using the three different methods and actual sustainable speeds measured at Lizard Island, for the nine species for which data are available. The column " >80% remaining" represents the speed at which 80% or greater of larvae were able to maintain swimming for 24 hours. Because larvae were swum at 5 cms^{-1} speed intervals, the range represents the error associated with speed measurements. A "↓" indicates that the method underestimates observed speeds for that species, whereas "↑" indicate that the method overestimates observed speeds. Bolded values lie within the observed range.

Family	method 1[a]	method 2[a]	method 3[b]	>80% remaining
Pomacentrus amboinensis	**12.4**	19.5 ↑	**16.9**	12.5-17.5
Pomacentrus molluccensis	12.4 ↓	15.5 ↓	16.8 ↓	17.5-22.5
Pomacentrus nagasakiensis	13.7 ↓	**19.2**	**19.8**	17.5-22.5
Chromis sp.	9.1 ↓	**17.5**	**14.8**	12.5-17.5
Dischistodus prosopotaneia	10.4 ↓	**14.7**	11.5 ↓	12.5-17.5
Apogon trimaculatus	14.0 ↑	**11.9**		7.5-12.5
Unidentified A	15.5 ↓	**12.2**	**12.2**	7.5-12.5
Unidentified B	**11.2**	**9.3**		7.5-12.5
Lethrinus sp.	19.7 ↓	**22.7**	**23.0**	22.5-27.5

[a]Values for Methods 1 and 2 were obtained from Table 2.2. [b]values for method 2 were obtained from Stobutzki (1998) for the five Pomacentridae, and from Stobutzki & Bellwood (1997) for the families Apogonidae and Lethrinidae. Both the Apogonidae and Lethrinidae are based on family means because species level data were not available.

There were clear differences in the maximum swimming abilities of settlement stage reef fish larvae from different families. The fastest swimming family was the Acanthuridae, which can potentially sustain speeds of between 25 and 30 cms^{-1} (Table 2.10). Other fast swimming families included the Lethrinidae and Lutjanidae, which should be able to sustain swimming at speeds of between 19 and 26 cms^{-1} (Table 2.10). Many of the other reef fish families can swim at considerably fast speeds, with sustainable speeds varying from 10 to 23 cms^{-1} (Table 2.10). In total, the late pelagic stage larvae of 4 out of the 9 families of reef fishes examined should be able to sustain swimming at speeds greater than 13.5 cms^{-1}, based on estimates from all methods, suggesting they should be able to maintain speeds equal to or greater than average current speeds around Lizard Island (Frith et al. 1986). If the highest estimate for each family from the three methods is used, then all the families examined should be able to sustain swimming at speeds greater than 13.5 cms^{-1} (Table 2.10). The largest differences among the three methods were observed in the families Pomacanthidae and Chaetodontidae, both of which had much higher estimates for method 3, suggesting these families can sustain swimming longer than expected based on both their length and their average U-crit.

Table 2.10. Estimated sustainable swimming speeds for larvae in nine reef fish families. The highest values predicted by each method (8.5 bls-1, 50% U-crit and 24 hours) are highlighted in bold. In-situ measurements of swimming speed (Leis & Carson-Ewart 1997) are also included for comparison (Field).

	Estimated sustained swimming speed (cms^{-1}) based on:			
Family	Method 1 [a] ($8.5\ bls^{-1}$)	Method 2 [b] (50% of U-crit)	Method 3 [c] (24 hours)	Field [d]
Apogonidae	**14**	10	13	6
Nemipteridae	13	**16**	10	11
Pomacentridae	13	**18**	17	18
Pomacanthidae	12	10	**19**	22
Monocanthidae	17	13	**19**	-
Chaetodontidae	14	17	**23**	17
Lethrinidae	20	19	**23**	19
Lutjanidae	23	**26**	23	25
Acanthuridae	25	**30**	27	34

[a] Total lengths from Stobutzki & Bellwood (1997). [b] Average U-crit for each family measured from larvae caught in light traps from Lizard Island (Appendix) [c] Log_{10} (time) = -2.95 log_{10} (speed) + c (c was calculated from mean times swum at 13.5 cms^{-1} from Stobutzki & Bellwood [1997]). [d] Family means from Leis & Carson-Ewart (1997).

Table 2.11. Correlation matrix between the three different methods of estimating maximum sustainable swimming speed. * indicates a significant correlation coefficient ($\alpha = 0.05$).

Method 1	r = 1		
Method 2	r = 0.85*	r = 1	
Method 3	r = 0.73*	r = 0.68*	r = 1
	Method 1	Method 2	Method 3

The estimates of maximum sustainable swimming speeds were also consistent with field estimates of average short term swimming speeds (Leis & Carson-Ewart 1997; Table 2.10; Figure 2.8). Of the three methods, method 1 (based on total length) was the only method that did not show a significant relationship with field data (Figure 2.8). Confidence intervals suggested that the slopes for both methods 2 and 3 were not significantly different than 1, indicating that *in-situ* short term field speeds are strongly correlated with estimated sustainable swimming speeds of larvae.

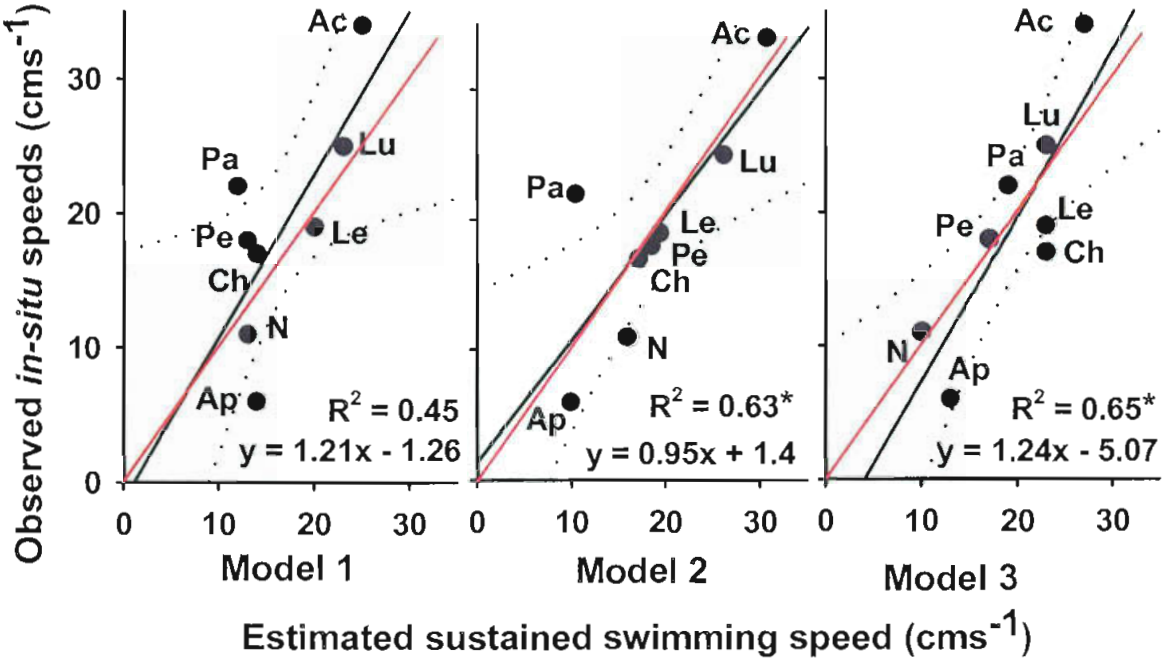


Figure 2.8. The relationship between estimated sustainable swimming speed (cms^{-1}), as estimated by the three different methods, and the observed short term swimming speed, *in-situ* (Leis & Carson-Ewart 1997). * indicates a significant R^2 ($\alpha = 0.05$). Solid lines represent fitted regressions, dotted lines represent 95% Confidence Limits and the red line a relationship of 1:1 (field values are the same as estimated values). Ap = Apogonidae, Ac = Acanthuridae, Ch = Chaetodontidae, Le = Lethrinidae, Lu = Lutjanidae, M = Monocanthidae and N = Neminteridae. Pa = Pomacanthidae and Pe = Pomacentridae.

2.4 Discussion

2.4.1 Effects of feeding

Fed larvae remaining at the end of the experiments showed no evidence of malnutrition, had undergone metamorphosis and even after several days of swimming were not exhausted. This is in stark contrast to unfed larvae, which were unable to maintain their position at the end of the experiment. The apparently healthy nature of fed larvae after swimming for several days is supported by the fact that these larvae grew by about 62 % in body weight and 18 % in standard length during the swimming bout (corresponding to 10.5% and 3.0 % growth per day respectively). These growth rates are comparable to those observed for larvae remaining in rearing tanks (16.9 % in body weight and 4.0 % in standard length per day). The values are also comparable to other values reported in the literature for larvae and juveniles of various taxa (c.f. Kiorboe et al. 1987, Naas et al. 1992, Watanabe & Saito 1998). During swimming trials on unfed larvae, lipids, carbohydrates and proteins were all used extensively during swimming bouts (Stobutzki 1997a). The magnitude of the increase in swimming performance due to feeding shown in this study, as well as the healthy condition of larvae even after swimming for several days indicates that previous sustained swimming trials without feeding may simply be measuring the energy reserves of larvae. Stobutzki (1997a) found a good correlation between swimming duration and initial energy reserves of larvae. It seems that other than food, there may be little restriction on swimming endurance of at least some species of reef fishes. This finding is particularly striking considering that in the present study larvae were swum at around half of their maximum speed.

By-products of swimming activity in fishes include creatine and lactate (Franklin et al. 1996). Fish must deal with these effectively in order to sustain swimming for long durations. Franklin et al. (1996) found that larval fish appear to be able to clear lactate an order of magnitude faster than rates reported for adult fish, which may explain the apparently indefinite swimming capabilities of some larvae. Furthermore, the fact that larval fishes may have a greater ability to remove the by-products of sustained swimming than adults suggests that the remarkable endurance swimming observed in larval reef fishes may be an adaptive response to the unique demands of the pelagic environment.

The results of Stobutzki & Bellwood (1997) show that some late stage larval fishes are able to swim considerable distances even without food. The greatest decrease in energy stores was seen in the heaviest species, which also swam for the longest duration (Stobutzki 1997a). For these species feeding during swimming events may not be as important, and these species may be able to find and settle on reefs without needing to feed during the settlement phase. For the smaller bodied species, as in the *Amphiprion melanopus* larvae used in this study, energy reserves are less, and food is more likely to be a limiting factor for swimming endurance. It seems therefore, that current estimates of swimming capabilities are likely to be most inaccurate for the smaller bodied species. Given food, the swimming performance of smaller bodied larvae may be considerably greater than is currently recognised. However, even for the larger bodied species, feeding during swimming migrations may significantly increase the condition of larvae at settlement, which is likely to considerably improve chances of survival once they reach a reef and settle (Kerrigan 1996, McCormick 1998, Booth & Hixon 1999). Laboratory studies have indicated

that feeding history can have marked effects on the condition of the liver, gut epithelium, muscle fibres, larval duration and size at metamorphosis (Green & McCormick 1999). Therefore, even for larger bodied species, feeding during swimming is likely to be important.

The importance of food in influencing the sustained swimming capabilities of marine larvae, and the condition of larvae at settlement (and subsequent growth and survival) is quite obviously limited only to those larvae capable of actively feeding during their time in the pelagic environment. For non-feeding larvae, such as those of many invertebrates, the costs of swimming are likely to be considerably greater. Recent studies have found profound demographic effects of protracted swimming on post-settlement growth and survival of larval invertebrates (Marshall et al. 2003).

The amount of food fed to larvae during the experiment was between 86 and 167 % of the fish's dry body weight each day. Larvae were able to obtain this food during a total of only 40 minutes of feeding time throughout the day, with larvae ingesting between 20.5 and 41.7 % of their body weight in a single feeding stop (based on dry weight estimates). These values are comparable to values obtained for other larval fishes (cf. Watanabe & Saito 1998). The amount of *Artemia* ingested provides the larvae with approximately 2252 – 4374 joules per gram fish wet weight per day ($jg^{-1}day^{-1}$). This estimate may be compared to the estimated energetic cost of swimming from Stobutzki (1997a). She found that settlement stage reef fishes used between 154 $jg^{-1}day^{-1}$ (for a lethrinid swimming at 7.1 BLs^{-1}) and 1090 $jg^{-1}day^{-1}$ (for *Pomacentrus amboinensis* swimming at 9.9 BLs^{-1}), which is less than half the amount available to the larvae during the experiment (taking into account an 80% assimilation efficiency and 32% heat loss; Brett & Groves 1979, Beamish & Tripple

1990). It seems therefore, that larvae were supplied with more than enough energy to maintain swimming; at least at the experimental speed larvae were swum.

Larvae were able to feed even while swimming at speeds of between 28 and 50% of the their U-crit, or maximum swimming speeds. This is consistent with observations in the field that larvae could feed whilst swimming at considerable speeds (Leis & Carson-Ewart 1998). Such results indicate that larvae would not necessarily need to stop swimming activity in order to feed successfully and that they may feed even whilst undergoing active swimming migrations, such as when trying to reach a reef immediately prior to settlement.

Existing estimates of sustained swimming duration and distances based on larvae that were not fed during swimming experiments, may be unrealistic. Larvae are probably able to swim considerably greater distances than currently suggested. Models that examine the efficiency of different behavioural strategies on larval dispersal need to consider the effect that feeding may have on the conclusions drawn from such models. Even at high relative swimming speeds, only limited exposure to food appears to provide larvae with more than sufficient energy for swimming migrations and still allow larvae enough resources for growth. Sustained swimming may not be particularly detrimental to larvae and long-term maintenance of position seems possible, especially if larvae utilise boundary layers.

2.4.2 Swimming speed

Current estimates of the sustained swimming abilities of reef fish larvae are based on swimming experiments conducted at a single current speed (Stobutzki &

Bellwood 1997, Dudley et al. 2000). In the present study sustained swimming abilities in late stage *Amphiprion melanopus* larvae, as well as nine other species, were found to be highly dependent upon swimming speed, suggesting that studies based only on a single speed may misrepresent sustained capabilities of reef fish larvae at faster and / or slower speeds. For *A. melanopus,* significant sustained swimming abilities do not occur until below speeds of around 7 cms^{-1}, which is approximately half the speed used in the experiments of Stobutzki & Bellwood (1997). Although swimming time increased exponentially with decreasing speed, the equivalent distance traveled by larvae did not, because at slower speeds larvae have to swim longer to cover a similar distance. The speed at which reef fish larvae are likely to have the most influence in retarding dispersal or enhancing settlement success, will be the fastest speed they can maintain for substantial lengths of time. At faster speeds they cannot maintain swimming and overall distances covered drop off rapidly (Figure 2.3). At slower speeds larvae must swim longer to cover similar overall distances and so swimming behaviour becomes less effective (Figure 2.3). For late stage *A. melanopus* larvae this speed is around 7 cms^{-1}, and is equivalent to 8-9 bls^{-1}, or around 50% of their average U-crit. At this speed larvae could swim continuously for around 24 hours. In addition, feeding experiments on similar aged *A. melanopus* larvae were also conducted at this swimming speed. The results of these experiments suggested that *A. melanopus* could potentially maintain swimming activity indefinitely at this speed (Figure 2.2). Data on the nine other reef fish species examined from light trap catches at Lizard Island supported these results, with larvae from three families all able to sustain swimming at speeds similar to 50% of their U-crit. For the nine species that were examined, the relationship between the proportion

of larvae remaining after 24 hours and relative swimming speed was found to be significantly different for speed expressed relative to body length, but not for speed relative to U-crit. This is probably because fish swimming at a similar speed in body lengths per second are not necessarily swimming at a similar level of relative activity (Drucker 1996). This is also reflected in the fact that the difference between maximum and minimum time swum for *A. melanopus* was considerably smaller if speed is expressed relative to U-crit rather than to length (see Figure 2.4). This suggests that a proportion of U-crit will be a more robust way of estimating sustainable swimming speeds across different families than will body length.

The cost of swimming in fishes should be a direct reflection of the power required and the drag that must be overcome. Mechanical theory suggests that the costs should be proportional to speed cubed (Schmidt-Neilson 1984; Vogel 1994). If time swum is a direct result of metabolic cost, then the slope of the relationship should be exactly –3, on a log-log scale. For *A. melanopus* the slope is –2.95 for mean swimming time and -2.12 for maximum swimming time, and is statistically only significantly less than –3 for maximum swimming time. This slightly reduced slope may be due to increased costs associated with swimming in lower Reynolds numbers (Re) (Ware 1978, Schmidt-Neilson 1984). Re values change over the speed range examined from 300 at 4 cms^{-1} to over 1200 at 16 cms^{-1}, and at the slowest speeds are very close to the transition zone between forces arising from inertial as opposed to viscous effects as a fish moves through water ($Re < 200$, Webb & Weihs 1986). Differences may also arise because time swum may not be related to energetic cost in the same way at different speeds. At slow speeds, fish utilize an aerobic muscle system fueled mainly by lipids, whereas at faster speeds fish use an anaerobic

muscle system fueled by glycogen stored in the muscle fiber (Bone 1975). This dual nature of the musculature systems makes it difficult to theoretically determine the dependence of energetic expenditure on swimming speed and how this may relate to time swum (cf. Bone 1975). Despite the slightly reduced slope, the relationship between swimming time and speed compares well with theoretical expectations, suggesting that swimming ability in larvae may be strongly influenced by physical constraints, and that this relationship may have a broad application in reef fish taxa.

Estimates of the maximum sustainable swimming speed in a range of reef fish taxa based on length, U-crit and the predictive model produced remarkably consistent results (Table 2.10 & 2.11). However, there were some differences. For example, estimates based on U-crit and length produced lower estimates than predicted by the model based on their sustained abilities at 13.5 cms^{-1} for both the Chaetodontidae and the Pomacanthidae (Table 2.10). This suggests that these families may show greater sustained swimming abilities than might be expected based on their maximum swimming speeds or their length. Despite these exceptions, the similarities between the three methods are remarkably consistent given that they are based on different assumptions and utilize entirely different biological information.

What is even more striking is that *in-situ* field estimates of swimming speeds of larvae also coincide well with the predicted values (Figure 2.8). The *in-situ* estimates of swimming ability obtained by Leis & Carson-Ewart (1997) are valuable in that larvae are able to "select" their swimming speed. The average *in-situ* speeds for each family are very similar to the predicted values and suggest that short-term field observations are a good estimate of sustained abilities. This also supports

previous findings that swimming flume experiments produce comparable estimates of swimming capability to *in-situ* measures (Leis & Stobutzki 1999). The remarkable consistency between the three different methods of predicting maximum sustainable swimming speeds of larvae, and the independent support from field observations, suggests that there may be underlying physical factors driving swimming abilities in reef fish larvae. This may allow the swimming capabilities of different taxa of reef fish to be predicted with some accuracy and supports suggestions that it may be possible to predict swimming abilities using morphological features such as relative propulsive area (Fisher et al. 2000) and length (Bellwood & Fisher 2001). Such morphological parameters, as well as theoretical principles may prove to be highly useful for predicting swimming performance of reef fish larvae, and will avoid the necessity of time consuming swimming experiments.

Central to these issues are the abilities of younger stage reef fish larvae. However, it is difficult to know how the results of this study may be applied to younger larvae. The only study that has swum fish throughout development at similar speeds in bls^{-1} found that there was an increase in sustained swimming performance during ontogeny (Fisher et al. 2000). Given that the different species developed their U-crit abilities at different rates with size (Fisher et al. 2000), standardizing swimming speed relative to U-crit may explain some of the changes that occurred throughout development. If their sustained swimming data are examined in terms of experimental speed relative to the U-crit abilities of each species throughout development (Figure 2.9), it seems clear that the sustained swimming abilities of larvae did not improve until their U-crit abilities had reached double the experimental swimming speed (i.e. relative speed < 0.5). This is consistent with the

results found in the present study for settlement stage *A. melanopus*, and suggests that younger larvae are likely to show a significant level of sustained capabilities but only at slower speeds (< 0.5 of U-crit).

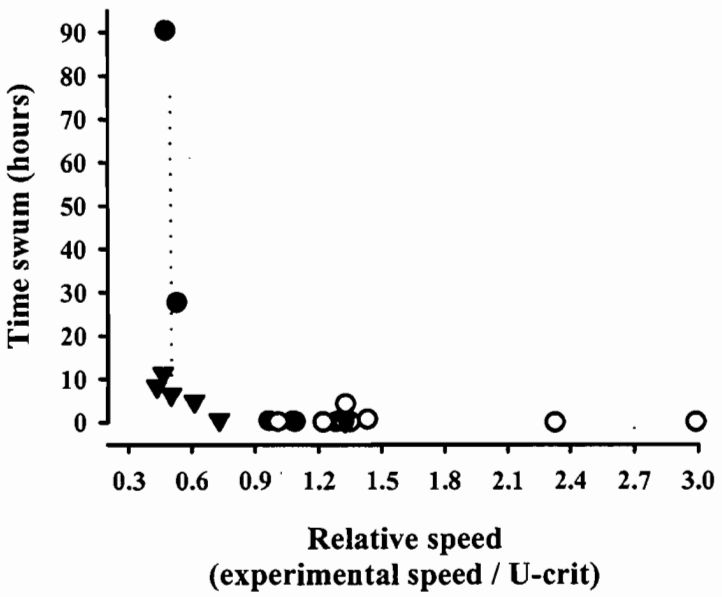


Figure 2.9. Sustained swimming time (hours) versus relative swimming speed (experimental swimming speed (cms^{-1}) / U-crit) for *Sphaeramia nematoptera* (○), *Pomacentrus amboinensis* (●) and *Amphiprion melanopus* (▼ throughout development. Dotted line indicates where experimental speed equal 50% of U-crit. Data obtained from Fisher et al. (2000).

If estimates of sustainable swimming speeds are accurate, then some of the faster swimming larvae, such as the Chaetodontidae and Acanthuridae that have been reported to swim in the field at speeds of up to 39 and 65 cms^{-1} respectively (Leis & Carson-Ewart 1997) could potentially maintain sustained swimming activity at speeds as high as 23 - 30 cms^{-1} for over 12 hours. These speeds are 2 – 3 times greater than the experimental swimming speed that has been used for the majority of sustained swimming experiments on reef fish larvae (13.5 cms^{-1}, Stobutzki & Bellwood 1997), and rival current speeds around many reefs (Hamner and Hauri 1981, Andrews 1983, Wolanski and Pickard 1983, Pitts 1984, Thorrold et al. 1984, Frith et al. 1986, Cowen and Castro 1994). This would mean that larvae could maintain their position for extended times, even against relatively fast currents and that, during the settlement process, they could swim distances reported in Stobutzki & Bellwood (1997) in less than half the time.

The implications for slower swimming species, however, are even more profound. The results suggest that many of the poorer swimming taxa (e.g. Apogonidae, Amphiprioninae) should be able to cover considerable distances if allowed to swim at slow speeds. Given access to food and the potential for larvae to feed sustainably deep in the water column (Job & Bellwood 2000), where water currents are theoretically weakest (Armsworth 2000), even these slow swimming species may be able to prevent advection from reefs for considerable lengths of time. For larvae that are highly developed at hatching, such as those of the Amphiprioninae (Job & Bellwood 2000; Fisher et al. 2001) the probability of self-seeding of populations is high, and this is supported by high levels of genetic

differentiation in these fishes (Bell et al. 1982). For slower developing taxa, such as the Pomacentrinae and Apogonidae (Fisher et al. 2000), it seems likely there may be a period of early dispersal where the ambient currents may exceed swimming abilities. However, for a large part of their pelagic phase, these larvae have the potential to maintain their positions relatively near to reefs for indefinite lengths of time.

2.4.3 Conclusions

The results of this chapter clearly show that the potential of tropical reef fish larvae to influence their position, using active horizontal swimming behaviour, is considerably greater than previously recorded. This chapter has examined the functional swimming abilities of larvae, focusing on late stage individuals, and demonstrates conclusively that these larvae can sustain swimming activity at fast speeds that may exceed average current speeds around reefs. Additionally, it appears that larvae may be able to sustain such swimming activity indefinitely if given access to food. These results leave no doubt about the potential for late stage individuals to have an impact on their choice of settlement locations on a relatively large scale. In addition, the results also suggest that even young larvae may show considerable sustained swimming abilities, especially at slower speeds. Given access to deep water, and the ability to select slow speeds, active avoidance of advection is becoming an increasingly plausible mechanism for high levels of local retention in reef fish larvae.

Chapter 3: Swimming behaviour and nocturnal activity of reef fish larvae

Submitted for publication to Marine Ecology Progress Series

3.1 Introduction

Much of the work on swimming abilities of reef fish larvae has concentrated on maximal performance measures such as U-crit (maximum sustainable swimming speed) and sustained swimming trials, both of which were measured in current flumes (e.g. Stobutzki & Bellwood 1997; Fisher et al. 2000). These studies examined the maximum performance capabilities of larvae, and provide an upper limit to the potential impact of active swimming on larval dispersal. This work has been explored more fully in the previous chapter, which shows that many reef fish larvae have excellent swimming capabilities. However, maximal performance measures of swimming ability provide no information about the swimming activity that larvae actually adopt in nature. Animals may use predominantly slow speed locomotion when undisturbed with maximal speeds only being used for rare activities such as escaping predators (Irschick 2000). Although we know that reef fish larvae can maintain fast speeds for considerable lengths of time, and perhaps indefinitely given access to food (Chapter 2), the question remains, at what speed do larvae choose to swim in an undisturbed situation? This question is critical if we are to fully

understand the extent to which larval behaviour may influence larval dispersal patterns or provide mechanisms for active self-recruitment.

As already mentioned in the introduction to the previous chapter, an alternative approach to these maximal performance measures has been to follow late stage larvae directly in the field. Initially used for tracking the settlement behaviour of ascidian larvae (Olson 1985), this method has recently been adapted for documenting the swimming behaviour of late pelagic stage reef fish larvae (e.g. Leis & Carson Ewart 1997) as well as newly recruited temperate fish species (Hindell et al. 2003). This method has the advantage that larvae are able to "choose" their swimming speed, although the extent to which the observer changes the "normal" behavioural patterns and chosen swimming speeds of the larvae is unknown. Furthermore, all *in-situ* observations to-date have been restricted to late stage pelagic larvae that are generally considered to be competent to settle on the reef. Given that larval behaviour is likely to change considerably at settlement, these studies may be of limited value in evaluating the behaviour of younger larvae. It is during this prolonged larval stage that active swimming is likely to have the greatest impact on their dispersal. Information on the unforced swimming behaviour of larvae at hatching and throughout their larval phase is crucial to our understanding of the impact that larval behaviour may have on their dispersal, particularly when considering behavioural mechanisms for active self-recruitment. The present study therefore, used captive-reared larvae and video techniques to provide the first quantitative account of the intrinsic swimming speeds of reef fish larvae throughout the larval phase.

Central to the question of active behaviour and control of dispersal is the issue of nocturnal as opposed to diurnal behaviour. To date, all work on the swimming capabilities of larvae, as well as swimming behaviour, has been conducted during the day or under conditions of constant light (e.g. Leis & Carson-Ewart 1997, Stobutzki & Bellwood 1997). Settlement by many reef fish larvae occurs at night (Dufour & Galzin 1993, Shenker et al. 1993, Holbrook & Schmitt 1997, Kingsford 2001). It therefore appears that reef fish larvae do actively swim at night, at least in the later part of their larval phase. However, it is not known when this active nocturnal swimming behaviour in larval reef fishes first occurs, and if the intrinsic swimming speeds of larvae differ between the day and night.

One of the most effective ways for studying the swimming speed and activity of larvae is by filming undisturbed larvae in rearing aquaria. This technique has been used for temperate (Hunter 1972, Hunter & Kimbrell 1980), and subtropical species (Fuiman et al. 1999) and may be readily applied to the larvae of tropical reef fishes. The advantage of this method is that the activity levels, behavioural patterns and preferred swimming speeds of larvae can be quantified throughout the entire larval period, with little or no disturbance to the larvae. In addition, the use of infrared filming techniques means that the behaviour of larvae can be examined during the day and night. By filming larvae in undisturbed conditions in rearing aquaria, this study represents the first to examine intrinsic swimming speeds and nocturnal swimming activity in reef fish larvae throughout their larval phase. This permits a direct evaluation of the potential for these larvae to actively facilitate self-recruitment via spontaneous swimming and intrinsic behavioural activity.

3.2 Materials and Methods

3.2.1 Larval rearing

Larval rearing was conducted using a closed saltwater aquarium system in the James Cook University Research Aquarium. Adult brood stock were kept in >1000 L aquaria and were fed a diet of chopped pilchards, prawns and the sergestid *Ascetes* twice per day. For the demersal spawning species (*Amphiprion melanopus, Amphiprion percula*, *Premnas biaculeatus*, *Pomacentrus amboinensis*), eggs were laid on artificial substrata and were transported to rearing tanks prior to hatching. Eggs from the mouth brooding species (*Sphaeramia nematoptera*) were obtained directly from brooding adults. Larvae were reared in a light and temperature controlled room in 104 L aquaria covered externally by black opaque plastic (Figure 3.1). Water temperature in the rearing tanks was maintained at 27.5-29^{o}C using two 100 Watt submersible aquarium heaters. Larvae were fed >52 μm filtered, wild-caught plankton, supplemented occasionally by rotifers and *Artemia*, at prey densities between 3-6 individuals per ml. A 13:11 day/night photoperiod was used for all larval rearing. The alga *Nannochloropsis* sp. was used to green the water during the day, and the tanks were flushed slowly with fresh seawater at night. This provides a gradual light gradient, allowing the larvae to "choose" their preferred light intensity by adjusting their depth. Each rearing tank was illuminated during the day using four 36 Watt "daylight" fluorescent tubes. These globes provide a light spectrum that is relatively similar to that of natural daylight. A single 8 Watt

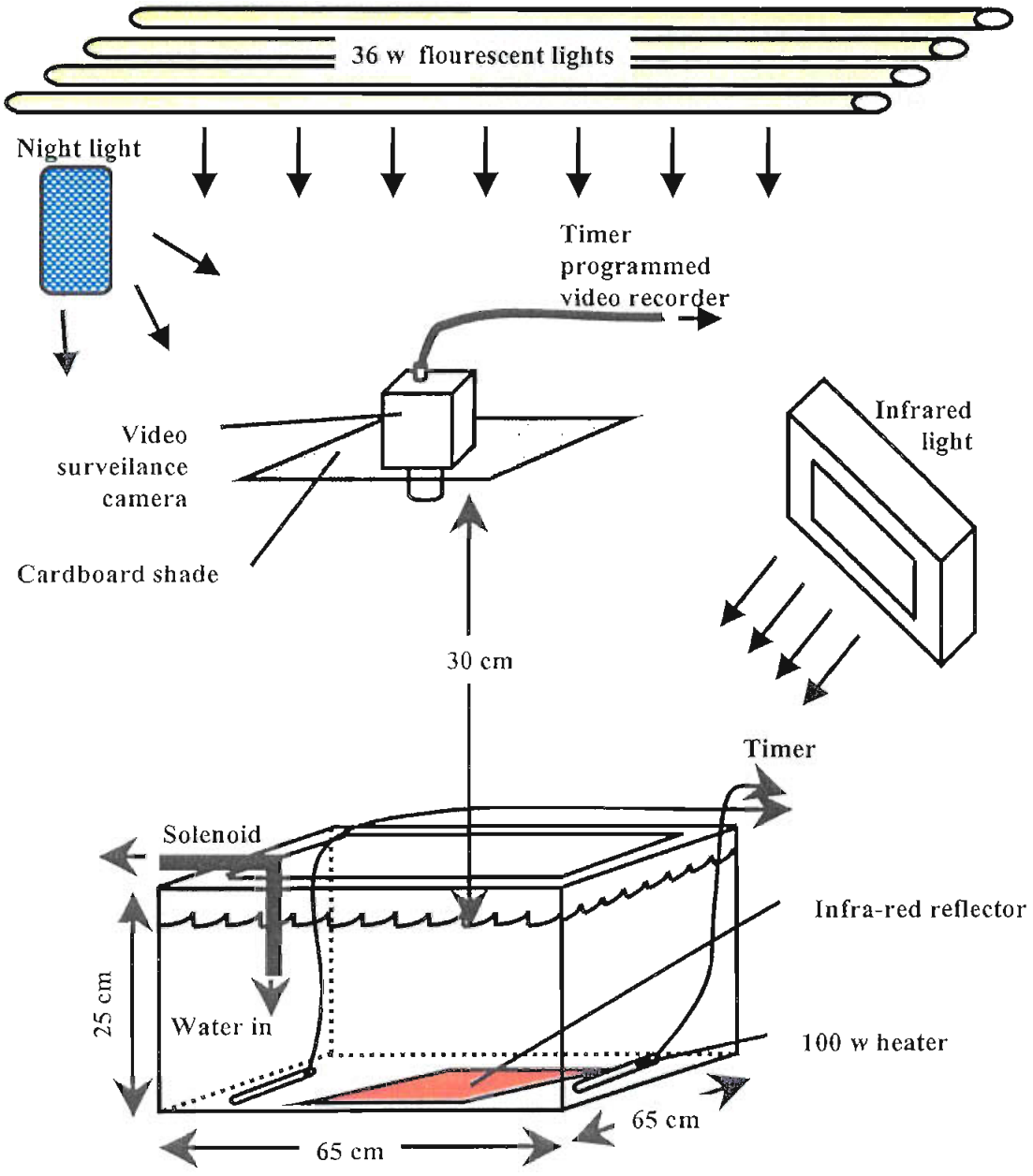
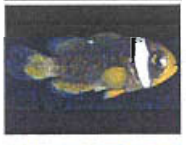


Figure 3.1. Experimental set-up used for examining undisturbed swimming and nocturnal behaviour of larvae throughout development

fluorescent "daylight" globe was used to illuminate both tanks at night. This was covered in several layers of neutral density filter material so that the light output at the tank surface was equivalent to that of half moon light intensity at night. The size and growth rates of larvae reared using this protocol closely resemble those of larvae in the field (Job & Bellwood 2000). Three clutches were raised of each of three anemonefish species (Amphiprioninae; Pomacentridae): *Amphiprion melanopus*, *A. percula* and *Premnas biaculeatus*. In addition, a single clutch of *Pomacentrus amboinensis* (Pomacentrinae; Pomacentridae) and *Sphaeramia nematoptera* (Apogonidae) were raised. Details of the study species used can be found in Table 3.1. All five of these species were filmed throughout their larval phase at regular intervals.

Table 3.1. Details of the study species used for swimming behaviour and nocturnal activity experiments.

Species		Subfamily	Family	larval duration	Egg duration
	*Amphiprion melanopus*	Amphiprioninae	Pomacentridae	8-9 days	7-8 days
	*Amphiprion percula*	Amphiprioninae		8-9 days	7-8 days
	*Premnas biaculatues*	Amphiprioninae		8-9 days	7-8 days
	*Pomacentrus amboinensis*	Pomacentrinae		20-21 days	3-4 days
	*Sphaeramia nematoptera*	N/A	Apogonidae	24-26 days	6-7 days

3.2.2 Filming, video analysis and data extraction

Larvae were filmed using an infrared-sensitive, black and white camera. This was centrally mounted 30 cm above the surface of the rearing tank (Figure 3.1). The field of view ranged from 11.4 to 65.3 cm^2 at the surface, which is equivalent to a minimum of 0.3% and a maximum of 1.8% of the surface area of the rearing tank. Both the filming area and the surface area of the tank represent quite large areas relative to the size of the fish throughout their development. The largest larvae account for only 0.24 % of the filming area and 0.004 % of the surface area of the rearing tank. Given these dimensions it is unlikely that larval swimming behaviour would be influenced by edge effects of the rearing tank. Larvae were never observed to associate with the walls of the tank until after settlement.

For filming at night, the rearing tank was illuminated using a 14 Watt infrared light (output range > 800 nm). Adult fishes are insensitive to wavelengths greater than 750 nm (Levine & MacNichol 1982, McFarland 1991). Reef fish larvae also appear to be insensitive to infrared light throughout development (Job & Shand 2001). Larvae were filmed twice during the day (1-3 hours after "lights-on" and 1-3 hours before "lights-off") and twice during the night (1-2 hours after "lights-off" and 1-2 hours before "lights-on"), with each filming period lasting 10 to 15 minutes. The two day and night time slots will be referred to as "early" and "late" and are nested within day and night. The camera was linked to a VHS VCR programmed to record during the selected filming times. Ten minutes prior to filming, a timer was used to turn off the aeration and heaters in the larval rearing tanks during the filming period both during the day and at night. At night a solenoid was used to turn off the water

flow during filming (water flow was turned off during the day at all times due to the use of green water culture techniques). As the whole filming process was automated no human activity was necessary and filming could be conducted under completely undisturbed conditions. A curtain of black cloth surrounding the entire rearing area ensured minimal disturbance at other times.

Recorded VHS video was captured using a Windows operated Studio MP10 capture box and subsequently converted to mpeg format digital video files. Every filming slot (4 per day) was saved as a separate video file. These were transferred to a Linux system where a minimum of 10 individual fish were tracked using the digital tracking program "Vedda" (by R. Beare, CSIRO Mathematical and Information Sciences, Sydney, Australia). This program records the position, area, shape and orientation of the fish every frame ($1/25^{th}$ of a second). The position of larvae is given as a series of x,y co-ordinates expressed in pixels across the field of view. These x,y co-ordinates were converted to instantaneous distance in pixels which was calculated using Pythagoras' theorem and averaged over two frames to smooth tracking inconsistency caused by image noise. The maximum and mean instantaneous speed measurements for each individual fish from each video file were obtained; speeds were also converted to body lengths per second (bls^{-1}). In addition, the instantaneous speed measurements for each frame were allocated to a swimming speed category (<1, 1-4, 4-10, 10-20 and > 20 bls^{-1}) and used to calculate the percentage of time that each individual fish spent swimming at different speeds during the time that it was observed. For night video files the number of frames (time) larvae spent either in "active" or "inactive" swimming behaviour was manually recorded (all daytime fish showed "active" behaviour). These data are

expressed as the percentage of the time that the observed larvae spent in active behaviour at night. These data extraction procedures resulted in 3 data sets: 1) the mean and maximum swimming speed of each tracked larva, 2) the time spent by each tracked larvae in each speed category and 3) the time spent in active behaviour at night.

3.2.3 Data analysis

Paired t-tests were used to compare all variables between the two filming times (early and late), both day and night for all filming days. A sequential bonferroni correction was applied to account for multiple tests (Rice 1988). No significant difference between early and late was found for any variable either during the day or night and thereafter all analyses were performed on the pooled observations from both time slots. Daytime swimming data and the percentage of time larvae spend active at night at each age were available from at least three separate clutches for each age for the three anemonefish species, but only a single clutch was available for *Pomacentrus amboinensis* and *Sphaeramia nematoptera*. These last two species were not included in statistical analyses, but were included in graphical comparisons. All analyses were performed using the means of three clutches at each age.

A two-way MANOVA with species and age as fixed factors was used to compare the mean and maximum daytime swimming speeds of larvae, and time spent active at night, for the three anemonefish species throughout development. Statistical analyses were performed using SPSS, and model assumptions were

examined using residual plots. The percentage of time larvae spent active at night was square-root transformed to meet the assumptions of the analysis.

As no significant effect was found due to age in either the mean or maximum relative swimming speed (bls^{-1}) of the three anemonefish larvae throughout development, the unforced swimming speeds of these three species were compared to the two other species (*Pomacentrus amboinensis* and *Sphaeramia nematoptera*) by averaging across all ages. The percentage of time all five species spent in active behaviour at night was compared throughout development based on developmental age following Fisher et al. (2000). Developmental age (= [egg duration + experimental age] / [egg duration + larval duration]) was used to ensure that the five species were compared at comparable developmental stages.

The proportion of time larvae spent swimming in each speed category was explored graphically using stacked bar graphs and compared among species. Bar stacks represented the average at each age. For anemonefish larvae these averages were based on the means of the three clutches, whereas those for the other two species were based on means of individual fishes. Only ages of *Pomacentrus amboinensis* and *Sphaeramia nematoptera* that were comparable to the developmental ages represented by the anemonefish were included when comparing among the five different species.

The mean and maximum swimming speed of *Amphiprion melanopus*, *Amphiprion percula*, *Premnas biaculeatus*, *Pomacentrus amboinensis* and *Sphaeramia nematoptera* in body lengths per second ($bl\ s^{-1}$) were converted to swimming speeds in $cm\ s^{-1}$ using average total length data for each species at each age from Fisher et al. (2000) and unpublished data for *Amphiprion percula* and

Premnas biaculeatus. Changes in mean and maximum undisturbed swimming speeds were then examined throughout ontogeny for these five species, using scatter plots, regression and analysis of variance of regression. Mean and maximum swimming speeds expressed in cm s^{-1} were then compared with U-crit estimates of swimming speed for each of the species for which U-crit data are available in Fisher et al. (2000), using linear regression. ANOVA was used to test the significance of this relationship and 95% confidence limits used to determine if the slope of this relationship was significantly different from 0.5 (this represents 50% of U-crit, which is the estimated swimming speed that larvae should be able to maintain for significant lengths of time; Chapter 2, Figure 2.6).

As larvae only show swimming behaviour near settlement, quantitative night time swimming speed data were obtained for the last two experimental ages, 7 and 9 days after hatching (data were obtained from two clutches of *Amphiprion melanopus* and one clutch of *Premnas biaculeatus*). Because these species settle at around 8-9 days after hatching, these days are around settlement for these species. The mean and maximum swimming speeds during the day and night were compared between these two ages based on the means of the three clutches using a two-way factorial MANOVA with age and day/night as fixed factors. This analysis was performed using SPSS, and model assumptions were tested using residual plots.

3.3 Results

3.3.1 Undisturbed swimming speeds in body lengths per second (bls^{-1})

The average and maximum relative swimming speeds (bls^{-1}) of the anemonefish larvae were both relatively consistent among the three species examined, as well as throughout development (Figure 3.2). The MANOVA revealed no significant difference in either the mean or maximum relative swimming speeds (expressed in body lengths per second, bl s^{-1}) among species or across ages, although a significant effect of age was found for the percentage of time larvae spent actively swimming at night (Table 3.2). Anemonefish larvae swam at a mean speed of 3.9 bl s^{-1} throughout development (Figure 3.2A) and their maximum swimming speeds averaged 8.4 bl s^{-1} (Figure 3.2B).

Table 3.2. Two-way MANOVA of mean and maximum daytime swimming speed and time larvae spend active at night. Species and age were entered as fixed factors and the analysis is based on clutch means at each age (n = 3). Only anemonefish species are included. Between subject effects are only shown for significant multivariate tests.

Multivariate tests (pillai's trace)	F	df	p
Species	1.94	6, 52	0.092
Age	3.39	12, 81	< 0.001
Species x Age	1.63	24, 81	0.054
Between subject effects (Age)			
Mean speed	0.87	8, 27	0.493
Maximum speed	1.93	8, 27	0.134
Time spent active at night (%)	21.95	8, 27	< 0.001

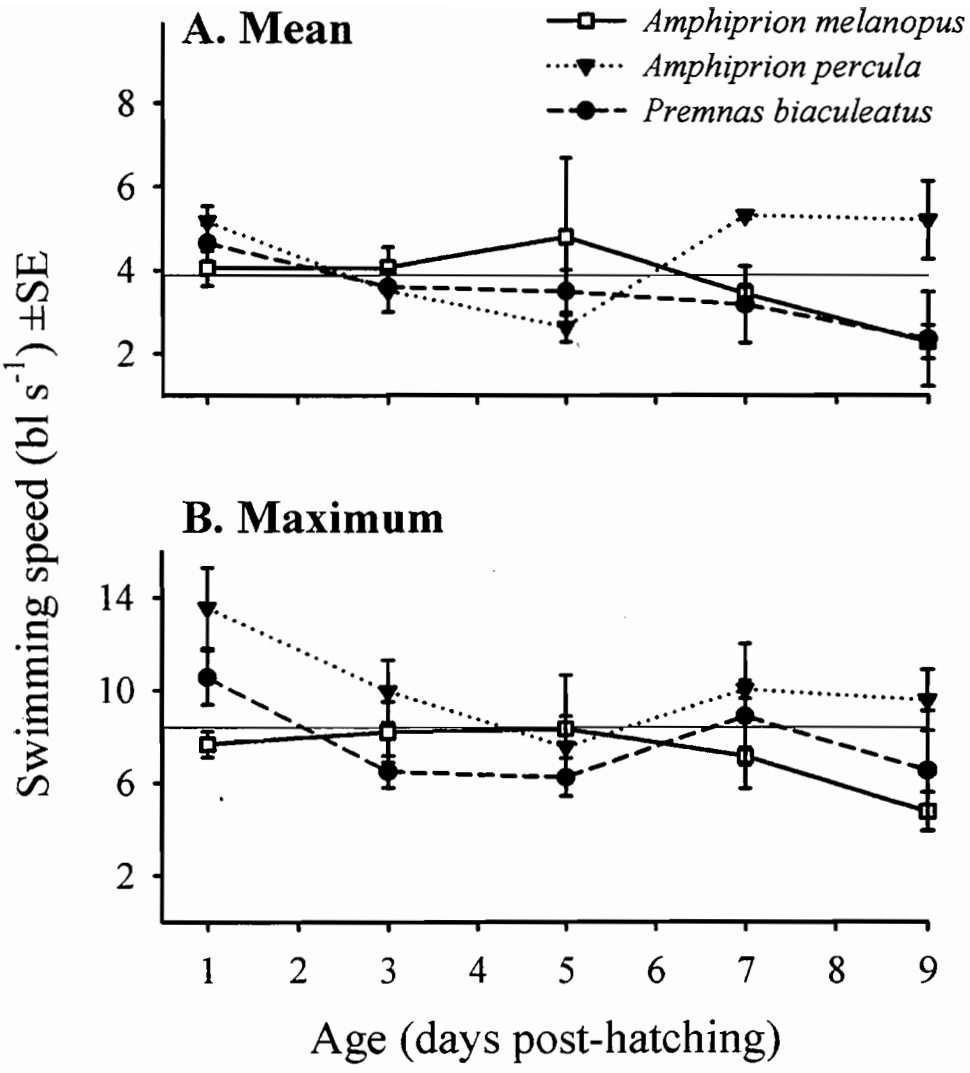


Figure 3.2. Mean (A) and maximum (B) passive daytime swimming speeds for the three anemonefish species (*Amphiprion melanopus, Amphiprion percula* and *Premnas biaculeatus*) vs age. Means and standard errors are based on the average of three clutches at each age (n = 3). Reference lines indicate the mean swimming speed across all three species and all ages.

A comparison of the mean and maximum swimming speeds of all five species (averaged across age) suggests that there are differences in the unforced swimming speeds of larvae at higher taxonomic levels. The intrinsic swimming speeds of *Sphaeramia nematoptera* larvae were slower than all the pomacentrid species examined (Figure 3.3). Of these, *Pomacentrus amboinensis* larvae swam at the highest speeds (Figure 3.3).

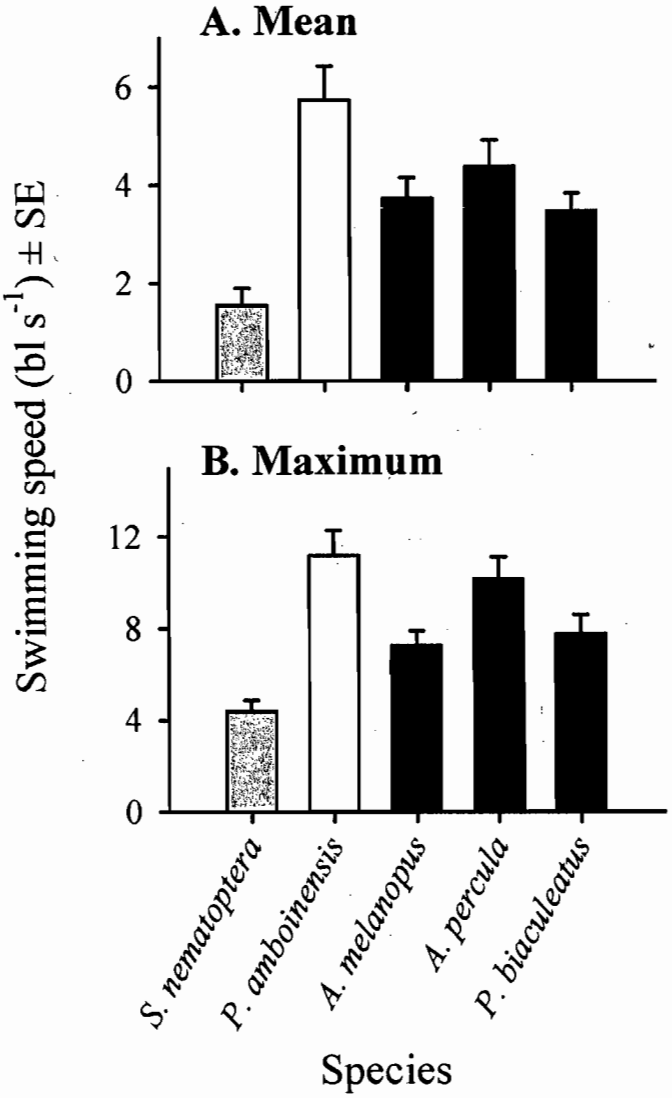


Figure 3.3. Mean (A) and maximum (B) passive daytime swimming speeds for all five study species averaged across age (n = 5, except for *S. nematoptera*, for which n = 4). Anemonefish – solid bars; Apogonidae – grey bar; Damselfish – open bar.

The time larvae spent swimming at different speeds was relatively consistent among the three anemonefish species throughout development (Figure 3.4). In general, anemonefish larvae spent most of their time swimming at speeds between 1 and 10 bls^{-1}, and spent less time swimming at either higher of lower speeds (Figure 3.4). The distribution of time larvae spent swimming at each speed appeared to be uni-modal, at the scale examined, suggesting that larvae were not utilizing a burst and glide form of swimming behaviour. The anemonefish spent approximately $1/3^{rd}$ of their time swimming at speeds between 4 and 10 bls^{-1} (Figure 3.4). A uni-modal distribution of time larvae spent swimming at different speeds was also found in *Pomacentrus amboinensis* larvae as well as *Sphaeramia nematoptera* larvae (Figure 3.4). There were, however, subtle differences in the amount of time larvae of these two species spent swimming at different speeds. *Pomacentrus amboinensis* larvae spent a considerably greater amount of time swimming at speeds in excess of 10 bls^{-1} whereas *S. nematoptera* larvae spent most of their time swimming at speeds less than 4 bls^{-1} (Figure 3.4).

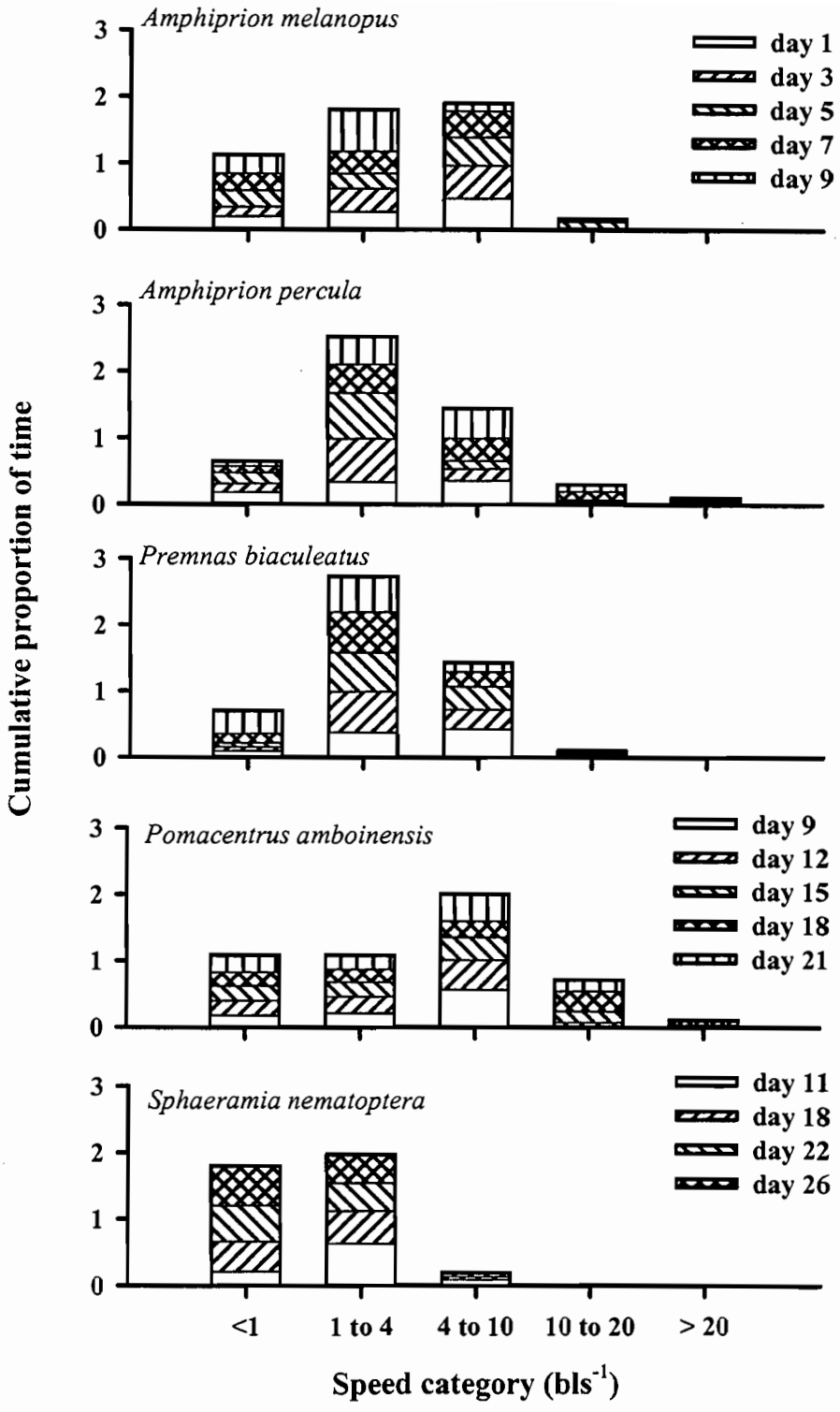


Figure 3.4: Proportion of time larvae spent swimming at different speeds for all five species (*Amphiprion melanopus, Amphiprion percula* and *Premnas biaculeatus, Pomacentrus amboinensis* and *Sphaeramia nematoptera*). Stacks show cumulative proportion for each age. Means and standard errors for the anemonefish larvae are based on the average of three clutches at each age (n = 3) and for *P. amboinensis* and *S. nematoptera* on the average of individual fish (n = 9 to 54).

3.3.2 Undisturbed swimming speeds in centimetres per second (cms^{-1})

Average swimming speeds in cm s^{-1} for all three species were comparable at hatching, ranging from 1.0 to 1.7 cm s^{-1} (Table 3.3). However, both average and maximum swimming speeds in cm s^{-1} varied considerably among the three species at settlement (Table 3.3). *P. amboinensis* were the fastest larvae at settlement (average 7.6 cm s^{-1}, maximum 14.9 cm s^{-1}), while *A. melanopus* larvae were considerably slower (average 2.9 cm s^{-1}, maximum 6.6 cm s^{-1}). This difference was largely due to the smaller size at settlement of anemonefish larvae compared to *P. amboinensis*. Their speed in body lengths per second (bl s^{-1}) is similar (Figure 3.3). Despite being a similar size at settlement to *P. amboinensis* larvae, *S. nematoptera* swam at much slower speeds compared to either of the pomacentrid species, with an average speed of only 1.1 cm s^{-1} and a maximum of 3.7 cm s^{-1} at settlement (Table 3.3).

Table 3.3. Size (total length in mm) and average and maximum daytime swimming speed (cm s^{-1}) 1-2 days after hatching and at settlement for *Pomacentrus amboinensis, Amphiprion melanopus* and *Sphaeramia nematoptera.* Size data from Fisher et al. (2000).

	Hatching			Settlement		
Species	TL	x	max	TL	x	max
Pomacentrus amboinensis	2.6	1.5	2.9	13.3	7.6	14.9
Amphiprion melanopus	4.5	1.7	3.8	7.9	2.9	6.6
Sphaeramia nematoptera	3.5	1.0	2.7	11.5	1.1	3.7

The developmental rate of swimming speed in cms^{-1} differed among the three groups of taxa examined (Figure 3.5). Swimming speed in cms^{-1} increased significantly for *Pomacentrus amboinensis* throughout development, which showed a strong increase in average as well as maximum swimming speed with age (Figure 3.5, Table 3.4). Swimming speed in cms^{-1} also increased significantly throughout development for the Amphiprionine larvae, although only for maximum swimming speed (Figure 3.5, Table 3.4). Average swimming speed in cms^{-1} did not increase significantly during ontogeny for these larvae (Figure 3.5, Table 3.4). Neither average nor maximum swimming speed increased at all for the *Sphaeramia nematoptera* larvae, which swam at consistently slow speeds throughout development (Figure 3.5, Table 3.4).

Table 3.4. Regression statistics for average and maximum undisturbed swimming speed in cms^{-1} versus age for *Pomacentrus amboinensis,* the Amphiprioninae (*Amphiprion melanopus, Amphiprion percula* and *Premnas biaculeatus*) and *Sphaeramia nematoptera.* Bold values indicate a significant R^2 at alpha = 0.05.

Average speed		R^2	F	P
Pomacentrus amboinensis	y = 0.38x – 0.21	**0.87**	$F_{1,5} = 25.65$	0.007
Amphiprioninae	y = 0.14x +1.59	0.24	$F_{1,14} = 4.04$	0.07
Sphaeramia nematoptera	y = -0.0085x + 1.41	0.06	$F_{1,4} = 0.181$	0.70
Maximum speed				
Pomacentrus amboinensis	y = 0.89x – 1.36	**0.90**	$F_{1,5} = 42.05$	0.003
Amphiprioninae	y = 0.28 + 3.57	**0.32**	$F_{1,14} = 6.21$	0.027
Sphaeramia nematoptera	y = 0.05 x + 2.90	0.36	$F_{1,4} = 1.70$	0.28

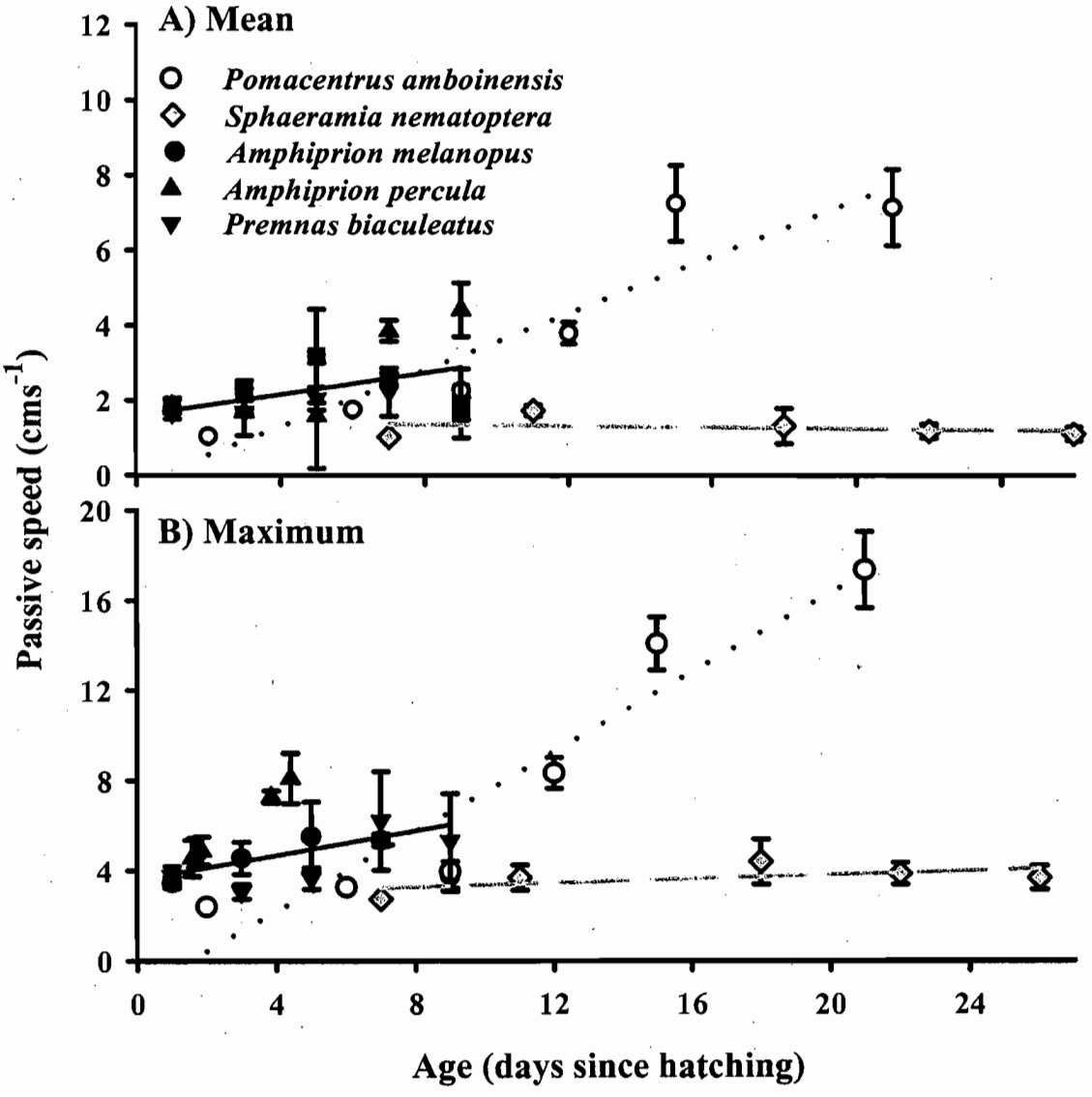


Figure 3.5. Scatter plot between mean (A) and maximum (B) unforced daytime swimming speed in cms^{-1} and age for *Amphiprion melanopus*, *Amphiprion percula*, *Premnas biaculeatus*, *Pomacentrus amboinensis* and *Sphaeramia nematoptera*. Unforced swimming speeds have been converted to cm s^{-1} based on total length data presented in Fisher et al (2000) and unpublished length data for *Amphiprion percula* and *Premnas biaculeatus*. Solid line indicates the fitted regression for the Amphiprioninae, dotted line the fitted regression for *Pomacentrus amboinensis* and the grey dashed line the fitted regression for *Sphaeramia nematoptera*. Regression statistics are summarized in Table 3.4.

There was a significant relationship between U-crit and both mean ($F_{1,15}$ = 22.67, $P < 0.001$, $r^2 = 0.62$) and maximum ($F_{1,15} = 26.45$, $P < 0.001$, $r^2 = 0.65$) unforced swimming speed (Figure 3.6). The slope of this relationship was significantly less than 0.5 for average swimming speed. On average, larvae swam at 19% of their U-crit speed (Figure 3.6). The maximum swimming speed of larvae, however, was not significantly different from 50% U-crit (as indicated by 95% confidence limits, Figure 3.6), suggesting that maximum unforced swimming speeds of larvae increase in proportion to 50% of their U-crit during development. It is clear that this relationship holds well for young larvae of all species, which fall completely within the 95% confidence limits, but as the larvae get older the variation between species increases considerably (Figure 3.6). When F-ratios were used to determine if there was a significant difference between a regression fitted to all species together (as shown on Fig. 3.6) and regressions fitted individually to each species, both average and maximum unforced swimming speed differed significantly ($F_{10,14} = 5.26$, $P = 0.006$ and $F_{10,14} = 9.11$, $P = 0.0006$ respectively) suggesting that the relationship between unforced speed and U-crit is not similar among all species. However, if only younger stage larvae were included (the last two ages before settlement excluded for each species), then there was no significant difference ($F_{4,8} = 4.02$, $P = 0.10$, $F_{4,8} = 3.44$, $P = 0.12$ respectively), suggesting that these differences were largely due to increasing variation among the species nearing settlement. Older stage *Pomacentrus amboinensis* larvae appear to swim at slightly greater speeds relative to their U-crit and older stage *Amphiprion melanopus* and *Sphaeramia nematoptera* larvae swim at slower speeds relative to U-crit (Figure 3.6).

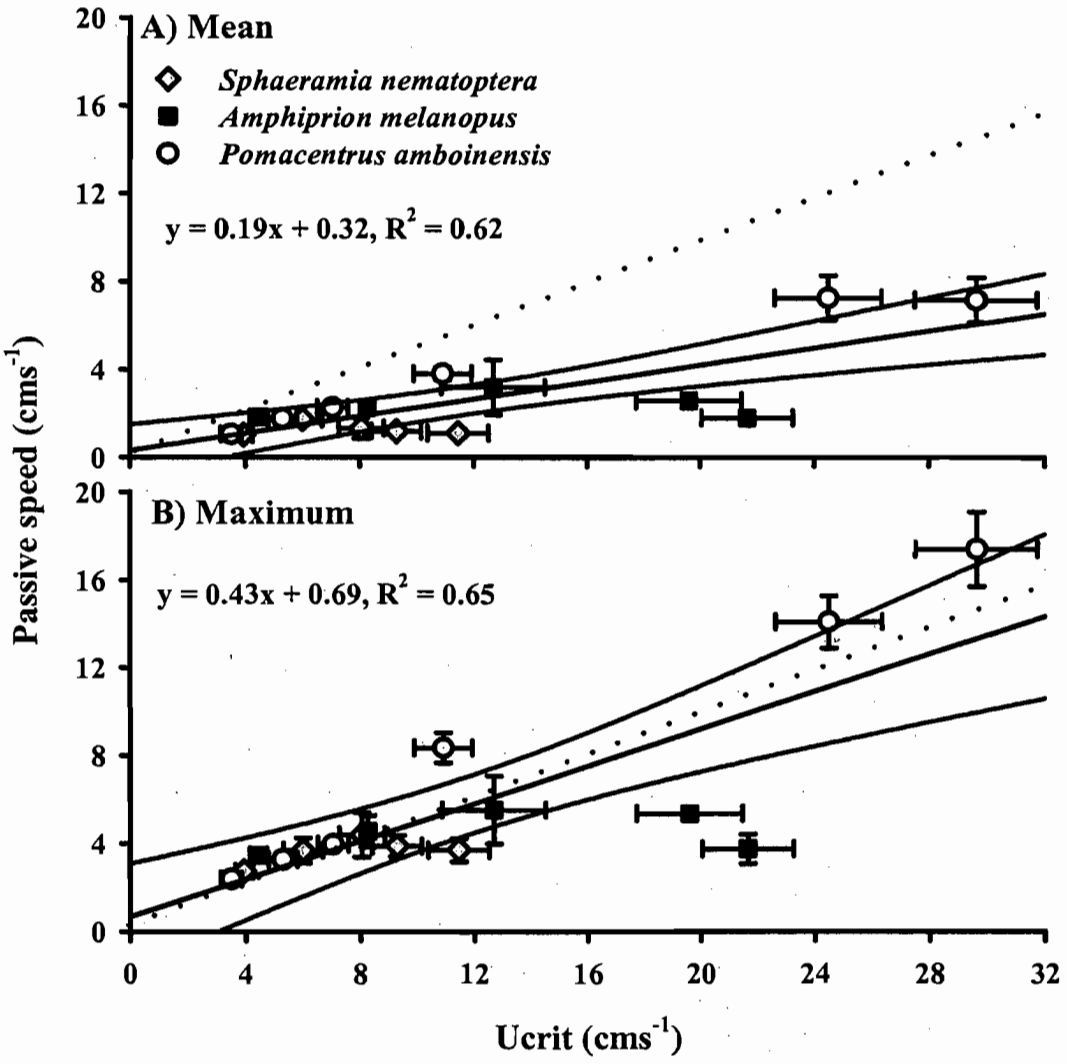


Figure 3.6. Linear regression between mean (A) and maximum (B) unforced daytime swimming speed of *Amphiprion melanopus*, *Pomacentrus amboinensis* and *Sphaeramia nematoptera* and U-crit. Unforced swimming speeds have been converted to cm s^{-1} based on total length data presented in Fisher et al (2000). The dotted line indicates an unforced swimming speed that is 50% of U-crit, the solid black line indicates fitted regression +/- 95% confidence limits based on all three species. The equations is the fitted regression across all species, including r^2 values. U-crit values were obtained from Fisher et al. (2000).

3.3.3 Nocturnal activity of reef fish larvae

The percentage of time anemonefish larvae spent actively swimming at night significantly increased throughout development but was consistent among species (Figure 3.7). The MANOVA indicated a significant effect of age, but no significant difference among the three species (Table 3.2). Post-hoc tests show a significant increase in the time larvae spend active at night between 3 and 5 days after hatching, and then another significant increase between 5 and 7 days after hatching (Figure 3.7A). Anemonefish larvae begin to spend greater than 50% of their time active at night from around 7 days after hatching, which is one or two days before settlement in these species. This developmental pattern of nocturnal activity is consistent with the single clutch of *P. amboinensis* larvae, which also showed significant levels of nocturnal activity just before settlement (Figure 3.7B). Nocturnal activity data are only available for three ages for *Sphaeramia nematoptera*, but again this is consistent, with early stage larvae showing little activity at night and activity increasing only for older larvae (Figure 3.7B).

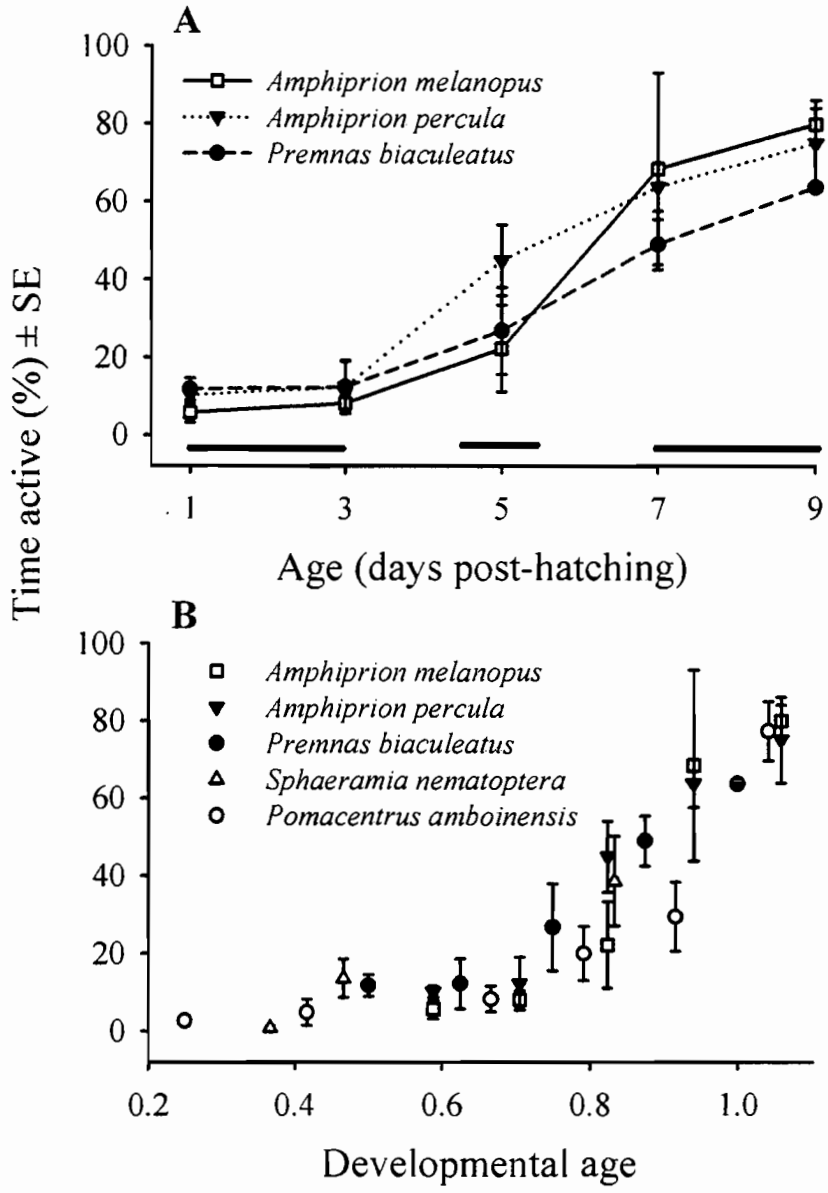


Figure 3.7. The percentage of time larvae spent in "active" behaviour at night. (A) Average at each age (expressed in days since hatching) for three species of anemonefish (*Amphiprion melanopus*, *Amphiprion percula* and *Premnas biaculeatus*). The thick lines along the x-axis indicate significant subgroups revealed by post hoc analysis of the MANOVA results for time spent active (Table 3.2). (B) Average at each age (expressed as developmental age) for all five species (the three anemonefish species, *Pomacentrus amboinensis* and *Sphaeramia nematoptera*). Mean and standard errors are based on the average of three clutches at each age for the anemonefish larvae (n=3) and on individual fish for *P. amboinensis* and *S. nematoptera* (n = 9 to 38).

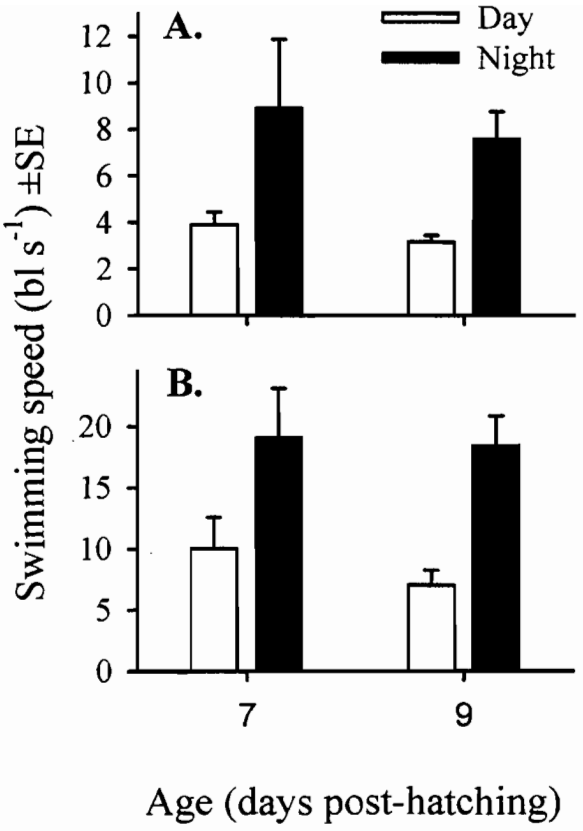


Figure 3.8. Mean (A) and maximum (B) swimming speed during day and night, 7 days after hatching and 9 days after hatching. Data are for three clutches of anemonefish larvae (1 clutch of *Premnas biaculeatus* and 2 clutched of *Amphiprion melanopus*.

Table 3.5. Two-way MANOVA of mean and maximum swimming speed of larvae during day and night for three clutches of anemonefish larvae. Time of day (day or night) and age (7 and 9 days since hatching) were entered as fixed factors and the analysis is based on clutch means at each age (n = 3). Between subject effects are only shown for significant multivariate tests.

Multivariate tests (pillai's trace)	F	df	p
Time of day (day or night)	8.48	2, 7	0.013
Age (7 or 9 days since hatching)	0.37	2, 7	0.703
Time of day x Age	0.53	2, 7	0.608
Between subject effects (Time of day)			
Mean speed	16.31	1, 8	0.004
Maximum speed	18.67	1, 8	0.003

3.4 Discussion

One of the central aims in marine biology is to understand the relationship between larval behaviour, oceanographic processes, and subsequent dispersal patterns and recruitment success. In reef systems this question has galvanized into a debate over the extent to which marine populations are open or closed. For reef fishes it is well established that some populations are partially maintained by self-recruitment (Jones et al. 1999; Swearer et al. 1999). Furthermore, Chapter 2 has clearly demonstrated that many reef fish have exceptional swimming capabilities as larvae. However, the link between larval behaviour and self-recruitment is tenuous because larval behaviour and swimming ability are invariably documented in

disturbed conditions and through maximum performance measures. The undisturbed swimming speeds and behaviour exhibited by larvae over extended periods of time was previously unknown. This Chapter, for the first time, puts behaviour and swimming ability into an ecological and oceanographic context by describing spontaneous patterns of diurnal and nocturnal swimming throughout development in several reef fish taxa. The findings of this chapter firmly place active self-recruitment within the range of potential outcomes resulting from the spontaneous sustained swimming and behavioural repertoires exhibited by these taxa. Behaviourally mediated self-recruitment may not be exceptional but a central feature of larval behavioural repertoires.

3.4.1 Diurnal unforced swimming speeds

Although it is known that reef fish larvae can swim at high speeds in flumes, this study has shown that the larvae of tropical reef fishes routinely swim at high relative speeds throughout their larval phase even in undisturbed conditions. The average swimming speeds of pomacentrid species ranged from 3.7 to 5.7 bl s^{-1}, with maximum swimming speeds up to 11.2 bl s^{-1}. The results strongly support work based on maximal performance measures of swimming ability (Chapter 2, Stobutzki & Bellwood 1997, Fisher et al. 2000) and *in situ* field observations (Leis et al. 1996, Leis & Carson-Ewart 1997), that indicate that these fishes are highly active, mobile organisms with considerable potential to control their position in the open ocean. The fact that the maximum passive speeds attained by larvae fall very close to 50% of their average U-crit values provides strong support for the hypotheses that larvae

should be able to maintain such speeds for extended periods of time (Chapter 2). The average undisturbed speeds of these larvae were also quite high, with larvae maintaining speeds of about 20% U-crit. The method used here to examine spontaneous swimming behaviour, rather than maximum performance, shows clearly that these larvae do swim at high speeds on a regular basis, and that they do this throughout development.

The average swimming speeds measured are in the range for routine-swimming speeds reported for subtropical red drum larvae (*Sciaenops ocellatus*) nearing settlement (3.3 bl s^{-1}) but are much higher than values reported for younger larvae of this same species (0.5 bl s^{-1}; Fuiman et al. 1999). The results are also considerably greater than those reported in previous studies on temperate larvae, that recorded speeds of about 1 bl s^{-1} for larvae moving freely in tanks (Blaxter 1986). The fact that high swimming speeds are maintained throughout the larval phase of the reef fishes examined is remarkable given that the relative viscosity of the environment (i.e. the Reynolds number, Re) should change considerably during larval development (Webb & Weihs 1986). At hatching, anemonefish larvae are swimming in a Re regime of around 76 and they remain in this relatively "viscous" regime (Re < 200) for nearly their entire larval phase. The consistent swimming speeds of larvae throughout development suggest that Re values of this magnitude have little impact on the swimming behaviour of these larvae.

Maximum swimming speeds of all species were 2 to 3 times faster than their average swimming speeds (up to 11.2 bls^{-1} in *Pomacentrus amboinensis*). Although these speeds are quite fast, they do not appear to represent unsustainable burst swimming speeds for two reasons: firstly, the maximum daytime swimming speeds

of late stage anemonefish larvae are similar to their average nocturnal swimming speed that appears to be sustained throughout the night (up to 11 hours). Secondly, the maximum swimming speeds were, on average, much less than the U-crit for all the species examined. A U-crit provides a measurement of the maximum sustainable speeds of larvae (Brett 1964) and is considerably slower than burst speeds.

The slower preferred swimming speeds of *Sphaeramia nematoptera* larvae are consistent with the limited swimming capabilities exhibited by apogonids both at settlement (Leis & Carson-Ewart 1997, Stobutzki & Bellwood 1997) and during development (Fisher et al. 2000), suggesting that this is a general characteristic of this family. Such differences among taxa in the preferred swimming speeds of larvae suggest that different energetic strategies may be adopted whilst in the pelagic environment. A similar pattern has been observed in some temperate species (Hunter 1981). Slower swimming speeds imply a lower food encounter rate as well as decreased metabolic requirements (Hunter 1981). Larvae in rearing tanks display markedly different feeding strategies; with pomacentrid larvae adopting an active search behaviour to acquire food while apogonid larvae adopting a "sit and wait" predatory strategy (Fisher, pers. obs., Job, pers. comm.). Similar differences have also been observed between cod and herring larvae (MacKenzie & Kiorboe 1995). This may explain the slower preferred cruising speeds of apogonid larvae and, potentially, the overall poorer swimming capabilities of this group.

Differences in trophic strategies among taxa have important implications for the potential link between oceanographic processes and larval biology and how these together may influence dispersal patterns and post recruitment success. Oceanographic processes can have a marked impact on primary production (e.g. up

welling events), that in turn can influence food availability and potentially the subsequent survival of larvae (Cowen 2002). If larvae show differences in their trophic biology then they may be affected in substantially different ways by fluctuations in food availability on both spatial and temporal scales. Although the differences among taxa in swimming speeds may have a trophic basis, these differences still have consequences for the behavioural mechanisms available to larvae for active self-recruitment. For example, the deeper depth distributions (Leis 1991b) as well as the superior visual capabilities of apogonid larvae (Job & Bellwood 2000) suggest that this group may spend a significant amount of time lower in the water column. As such, it is likely that they are exposed to relatively slower current speeds, and swimming abilities may be of reduced importance. In comparison, pomacentrid larvae occur in shallower environments where water currents are likely to be greater and, as such, their swimming abilities are likely to be of greater importance in facilitating behaviourally mediated self-recruitment.

3.4.2 Nocturnal behaviour

While there were clear differences among taxa in terms of preferred swimming speeds of larvae, all five species showed similar patterns of nocturnal swimming activity during development. In all species, the highest levels of nocturnal activity were recorded shortly before settlement. Low levels of nocturnal activity by reef fish larvae early in their pelagic phase are probably associated with an energy saving strategy during the hours of darkness when larvae are unable to feed (cf. Job & Bellwood 2000). The close similarities among such ecologically different species

suggest that nocturnal activity levels may be broadly comparable in a wide range of reef fish taxa, regardless of adult or larval biology. For example, apogonids are nocturnal as adults whereas pomacentrids are diurnal, while larval apogonids have a lower light threshold for feeding than pomacentrids of similar developmental age (Job & Bellwood 2000). These differences suggest that nocturnal inactivity is not associated with inadequate visual capabilities of larvae, but is an intrinsic behavioural characteristic of the early larval phase. However, development of nocturnal activity needs to be examined across a broad range of taxa to determine if this is in fact a general pattern for reef fishes.

The late development of nocturnal activity has important implications for the possible behavioural mechanisms larvae could adopt to influence their dispersal during their early larval phase. Clearly, younger larvae do not actively swim at night, precluding the use of active horizontal swimming as a means of influencing their position in the open ocean at night. However, many reef fish larvae are known to have functional swim bladders (Leis and Carson-Ewart 2000) so they should be able to actively control their vertical distribution at night, even without active swimming behaviour. Late stage larvae show differential use of the vertical water column at night (Chapter 4) and this may also be true for younger larvae. Although some studies have found that the distribution of larvae is relatively unstructured at night (Leis 1991), others indicate that even very young larval fishes undergo active nocturnal vertical migration (Forward et al. 1996), suggesting that such behaviour may exist for some reef fish larvae. Active vertical migration by young reef fish larvae could have a considerable impact on dispersal patterns, given that current speed as well as direction can change considerably with depth (Cowen et al. 2000).

It seems likely that older stage reef fish larvae are active a night; this is when many species actively settle onto reefs (Dufour & Galzin 1993, Shenker et al. 1993 Holbrook & Schmitt 1997, Kingsford 2001). The results of this chapter clearly confirm these findings, with larvae exhibiting highly active behaviour at night nearing settlement. However, the results of my study also suggest that this active nighttime behaviour only begins in the last few days before settlement. Furthermore, the faster swimming speeds of larvae at night compared to during the day nearing settlement suggest that the onset of active nocturnal behaviour is linked to the active settlement behaviour of these larvae. It seems clear that larval behaviour changes considerably in the few days prior to settlement, providing additional evidence that settlement is an active, behaviourally mediated process.

3.4.3 Measuring undisturbed swimming speed

This study provides the first estimate of the undisturbed swimming speeds of reef fish larvae throughout development. When compared to existing flume based estimated of swimming speed, it is clear that in undisturbed conditions larvae maintain swimming at relatively slower speeds. The maximum and average swimming speeds of undisturbed larvae were approximately 50% and 19% respectively, compared to flume-based estimates of swimming speed. *In-situ* measurements of swimming speed are only available for settlement stage larvae of one of the species examined in this study, *Pomacentrus amboinensis* (Leis & Carson-Ewart 1997). Their study estimated an average *in-situ* swimming speed for this species of 11.8 cms^{-1} by following larvae around on scuba. This is mid range

between the mean (7.6 cms^{-1}) and maximum (14.9 cms^{-1}) undisturbed speeds that I have found for settlement stage larvae of this species.

It is difficult to establish to what extent the size of the rearing tank, as well as the artificial conditions of rearing, affected the swimming speeds of these larvae relative to the undisturbed swimming speeds these larvae would exhibit in the field. The presence of an enclosed environment would be most likely to effect older larvae, because the relative size of the tank would be much smaller for these larvae. It is possible that larger larvae may decrease their swimming activity and swimming speeds in response to their "enclosed" environment. This may explain why, for two of the three species examined, undisturbed swimming speed decreased relative to the average U-crit of these species towards the end of the larval phase (Figure 3.6). If this is the case, then my study may have underestimated the undisturbed swimming speeds of late stage larvae. In addition, swimming speeds of all larvae throughout development may have been higher if larvae had been exposed to more turbulent conditions, as larvae are known to increase their feeding activity in the presence of turbulence (MacKenzie & Kiorboe 1995). Furthermore, a direct comparison of U-crit between reared and wild caught larvae suggests that reared larvae may exhibit relatively poorer swimming capabilities compared to larvae from the field (Table 2.1). This suggests that the undisturbed swimming speeds reported here are probably conservative, compared to what may be expected to occur naturally in the field.

3.4.4 Implications of larval behaviour

The speeds maintained during routine swimming by reef fish larvae throughout development have important implications for the potential impact that their behaviour may have on dispersal patterns. Reef fish larvae are known to show positive rheotaxis throughout development (indeed this underpins all swimming measurements using flumes; see Fisher et al. 2000). If these larvae were to behave similarly in the field, or show other directed swimming behaviour (e.g. towards their natal reef) then even at the average spontaneous swimming speeds observed in this study, they have the potential to markedly reduce the extent of advection from their natal reef. Furthermore, current speeds decrease rapidly near the substratum. If larvae combine directed swimming behaviour with active vertical migration, avoiding faster current flows by dropping lower in the water column (see Armsworth 2001), they could potentially avoid advection from their natal reefs completely. Such a simple mechanism could largely account for recent suggestions of high levels of self-recruitment of some tropical reef fish species (e.g. Jones et al. 1999; Swearer et al. 1999; see also Cowen et al. 2000).

The results of this study strongly suggest that such a mechanism of self-recruitment is well within the capabilities of some reef fish larvae. Subsurface currents (after removal of tidal effects) within the Great Barrier Reef (GBR) lagoon in summer range from 5.6 to 15.6 cm s^{-1} in the northern section near Lizard Island (Andrews 1983, Frith et al. 1986). Because of boundary layer effects, net speeds may be much slower near the substratum. For example, in the Florida Keys, Pitts (1994) recorded speeds between 2.3 and 6.1 cm s^{-1} measured 4 m above the substratum

compared to 0.4 to 2.3 cm s^{-1} 2 m above the substratum. In comparison, the average spontaneous swimming speeds of *Amphiprion melanopus* larvae ranged from 1.7 to 2.9 cm s^{-1} from hatching to settlement (3.8 to 6.6 cm s^{-1} maximum) while larval *Pomacentrus amboinensis* swam between 1.5 and 7.6 cm s^{-1} (2.9 to 14.9 cm s^{-1} maximum). Even at hatching, these speeds could limit the impact of advecting currents while at settlement larvae could exceed prevailing current speeds.

Based on daytime swimming speeds throughout development and night time speeds near settlement, conservative estimates indicate that *A. melanopus* and *P. amboinensis* larvae could swim the equivalent of 13.1 to 30.4 km over the length of its larval phase. These calculations assume that larvae only swim actively during the day until they are 80% of the way through their pelagic phase (see Figure 3.7). In addition, they are based on average undisturbed swimming speeds, which are conservative relative to the theoretical maximum sustainable swimming speeds of these larvae (see Figure 3.6). Based on maximum speeds (which represent about 30% of the swimming time) the values would be 50.0 to 103.5 km. In comparison, based on mid-water current speeds and directions, Frith et al. (1986) estimated that larvae would be transported between 4 and 47 km $week^{-1}$ during the summer spawning season at Lizard Island. These values clearly show that the swimming speeds required for active self-recruitment by larvae are well within the range observed for spontaneously swimming larvae.

Positive rheotactic behaviour, or directed swimming, as a mechanism for avoiding advection from natal reefs would clearly be advantageous for larvae arising from isolated reefs and islands, where such larvae face limited settlement success downstream. Such a mechanism may also be advantageous even in more complex

reef systems if there is a significant risk of not finding a suitable downstream settlement site. It is axiomatic that the natal reef represents a location that contains suitable habitats for growth to adulthood and successful reproduction. Unfortunately, there are no data on either rheotactic or homing behaviour of pelagic stage reef fish larvae in the field. However, it is interesting to note that if orientation behaviour were initiated soon after hatching, from the outset larvae would have the full array of sensory cues available to them for orientation (see Montgomery et al. 2001). Fish larvae have well-developed chemosensory capabilities and there is a suite of potential chemical cues available on the leeward side of reefs (Atema et al. 2002; Kingsford et al. 2002). Furthermore, there is also a considerable amount of noise generated in the vicinity of reefs (McCauley & Cato 2000), that may provide larvae with a multidirectional navigational cue (Stobutzki & Bellwood 1998, Tolimieri et al. 2000). If larvae are able to remain within the sensory zone of their natal reef, mechanisms for open ocean navigation may be unnecessary for maintaining directed swimming behaviour. However, it is important to note that the species examined in this chapter are all from demersally spawned larvae. The smaller size at hatching of pelagically spawning species make it unlikely they would be able to influence their dispersal patterns until considerably later in the larval phase.

3.4.4 Conclusions

This study represents the first description of the undisturbed swimming speeds and nocturnal swimming activity of tropical reef fish larvae throughout development. The results demonstrate that larvae maintain relatively high swimming speeds

throughout their larval phase, although differences in swimming speeds among taxa indicate that larvae may adopt different energetic strategies whilst in the pelagic environment. However, consistent patterns of nocturnal swimming behaviour suggest that some behavioural characteristics may be similar across a range of reef fish taxa and point to active nocturnal settlement behaviour in some species. It is clear that larval reef fishes are innately highly active, mobile organisms with considerable potential to control their position in the open ocean. Furthermore, they have all the behavioural and functional attributes required for an active mechanism of self-recruitment on coral reefs. For many reef fish species, behaviour that enhances self-recruitment may be a central part of their normal behavioural repertoire.

Chapter 4: Vertical distribution of late stage reef fish larvae

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4.1 Introduction

Because the direction and speed of currents can vary considerably with depth (Cowen & Castro 1994, Bowman et al. 1994), the vertical distributions of larvae and the extent to which they migrate vertically have considerable implications for dispersal. Vertical migration has also been identified as a key factor affecting the energetic expenditure required to find and settle on a reef (Armsworth 2001, Armsworth et al. 2001), highlighting the importance of vertical migration not only during the pelagic phase, but also during the settlement process.

Hydrodynamic models, based largely on surface currents, have been used to predict the dispersal patterns of marine larvae (e.g. Roberts 1997). Such models assume that larvae occur near the surface and have limited control over their vertical movements. This assumption may be unreasonable for many marine larvae. In particular, the larvae of many tropical reef fishes have well-developed swim bladders (Leis & Carson-Ewart 2000) and advanced swimming abilities (Stobutzki & Bellwood 1997, Leis & Carson-Ewart 1997, Fisher et al. 2000) suggesting they should be capable of fairly rapid vertical movements and precise vertical maneuvering. In addition, reef fish larvae have well-developed visual abilities, and should be capable of feeding at considerable depths (Job & Bellwood 2000). Given

their considerable abilities, the potential for active vertical migration in these fishes is high, and it seems likely that differential water column usage may exist for at least some of these taxa. Indeed there is recent evidence to suggest that larval reef fish may utilize vertical movement to take advantage of vertically stratified current regimes to influence their position during settlement (Cowen et al. 2000).

Several studies have examined the vertical distribution of larval fishes in coastal (e.g. Boehlert et al. 1985, Gray 1998, Sakuma et al. 1999), island (e.g. Leis 1986, Boehlert et al. 1992) and coral reef environments (e.g. Leis 1991b, Limouzy-Paris 1997). In general these studies have found taxon-specific patterns of vertical distribution that appear to vary spatially, diurnally and with ontogeny (Leis 1986, Brodeur & Rugen 1994, Gray 1998). In particular, larvae commonly have vertically stratified depth distributions during the day, but not at night (Leis 1986), although this appears to vary depending on species (Sakuma et al. 1999). In addition, the vertical distribution of some larvae may be influenced by varied current regimes at different depths (Cowen & Castro 1994). While these studies provide valuable insights, most are based on net tow samples that leave an incomplete understanding of the dynamics of vertical distribution in reef fish larvae. Towed nets efficiently target early larval stages, however, these may be difficult to identify beyond the family level. Family-level resolution may mask species-specific depth preferences of larvae. In addition, towed nets tend to under sample late stage larvae (Choat et al. 1993), that are most likely to be actively returning to reefs and for which active vertical migration is likely to be very important. If larvae show differential use of the vertical water column structure this should be most evident for older stage larvae.

Several methods have been used to examine the vertical distribution of late stage larval fishes on coral reefs. Leis & Carson-Ewart (1999, 2001) and Leis et al. (1996), have examined the vertical distribution of late stage larva offshore from coral reefs. However, these studies have been conducted only during the day, and on a very small number of species. In addition, because of the method that has been used the maximum depth range of these larvae is unknown (larvae are followed on SCUBA by divers with a restricted diving range). Thorrold et al. (1994a, 1994b), used nets moored in tidal channels to examine the vertical distribution of late stage larvae, and found significant differences among taxa between surface and subsurface nets. However, these studies are limited because the sampling method is reliant on current flow. This makes it impossible to determine if larvae move onshore during offshore current flow, and whether or not such larvae are using the vertical structure of the water column to assist with onshore transport.

Two studies have attempted to describe the nocturnal vertical distribution of late stage larval reef fishes using surface and near bottom light-traps as their sampling tool (Doherty & Carleton 1997, Hendriks et al. 2001). Light-traps are a nocturnal collection tool known to target settlement stage larvae that are capable of avoiding conventional towed nets (Thorrold 1992, Choat et al. 1993). Although light traps cannot be used to accurately quantify larval densities, they can provide good estimates of relative abundance (Meekan et al. 2000). Because most reef fish larvae settle during the night (Dufour & Galzin 1993, Shenker et al. 1993, Kingsford 2001) light traps sample larvae at a time when they are actively settling and may provide information on the behavioural mechanisms larvae adopt during this event. Both Doherty & Carleton (1997) and Hendriks et al. (2001) found that late stage larvae

have highly structured vertical distributions at night, contrary to the results reported by nocturnal net samples of younger stage larvae (Leis 1991b). These light trap studies also demonstrated that while many taxa appear to be most abundant near the surface, there are clear distribution differences among taxa, with some species being collected in higher numbers in deeper traps.

The main problem with previous studies examining the vertical distribution of late stage larvae using light traps, is that their sampling is confounded by the fact that conventional light traps (see Doherty 1987, Stobutzki & Bellwood 1997) sample a range of depth strata simultaneously because they illuminate in all directions. In relatively clear water, such traps may sample nearly the entire water column, limiting the utility of depth comparisons. Even if such traps are placed simultaneously at different depths, an accurate description of the vertical distribution of larvae will only occur under the assumption that larvae swim towards the brightest (closest) trap. Considering that there is evidence that larval fish may change their photo-tactic response as the orientation of the light source is altered (above or below) (Olla & Davies 1990), this assumption may not be reasonable.

Aside from potential problems due to differing larval behaviour, the broad vertical sampling of conventional traps also precludes their use in finer scale examinations of vertical distribution patterns. Reef fish larvae are known to show taxon specific differences within the water column as well as between surface and bottom waters (Leis 1986, 1991b). Given that hydrodynamic regimes are also likely to differ on such a scale, it is important to examine the vertical distribution of larvae throughout the water column, rather than just at the surface and near the bottom. While many taxa appear to be caught in highest abundances in surface traps (e.g.

Doherty & Carleton 1997) whether or not these larvae are distributed near the surface or actually occur in mid-water remains to be determined. In order to answer such questions a method of sampling is required that is able to sample a relatively narrow, discrete depth stratum, so that the sampling units can be placed at multiple levels throughout the water column.

The aims of this study were therefore, two fold: Firstly, to develop a light trap able to sample discrete depths in the water column with a sufficiently narrow sampling band to allow fine-scale patterns of vertical distributions to be examined. Secondly, to use this new sampling tool to describe the vertical distribution of late stage reef fish larvae off the leeward side of Lizard Island, on the Great Barrier Reef, Australia. This study represents the first attempt to utilise a stratum-specific light traps to examine the vertical distributions of late stage larvae. Precise data on these distributions will determine the extent of differential water column use among and within taxa and provide insights into the ability of reef fish larvae to influence their dispersal and recruitment success through vertical migration.

4.2 Materials and Methods

4.2.1 Light trap design

The light traps were designed to distribute light predominantly in a horizontal direction. This enabled each light trap to sample a distinctly different depth distribution. The traps were cylindrical, 52 cm high and 50 cm maximum diameter (Figure 4.1). Light was directed horizontally using a series of nine opaque baffles, each 2 cm apart. The baffles were made of 3 mm grey perspex cut into flat rings of

50 cm external diameter and 14 cm internal diameter. Four stainless steel supporting rods were used to fix the baffles in place. The bottom half of the trap was constructed from 5 mm thick pvc pipe of 30 cm internal diameter. This was attached to the bottom baffle and sealed at the base to form a collecting basket. The collecting basket had two drainage slits cut near the base on either side, that were covered with 1 mm plastic mesh. The basket could be removed from the entire top half of the trap so that the catch could be easily retrieved and emptied into a bucket. Fish were discouraged from leaving the trap by a plastic funnel fitted onto the bottom baffle and four clear perspex directors fitted between each of the baffles.

A light source (consisting of a 30 cm tall, 8 watt fluorescent "cool white" lamp) was placed into a clear perspex tube inserted centrally through the series of baffles. The clear tube was fixed to a watertight battery box attached to the base of the collecting basket. A rechargeable sealed lead-acid 12 V, 7 Ah battery was used to power the light source. When fully charged it supplied enough power to illuminate the light source for up to 48 hours.

Stability of the traps (and therefore effective stratum specificity) was ensured by placing 2.7 kg of lead weight (2 x 3 pound dive weights) in the base of each trap. In addition, the use of the four-point suspension harness (Figure 4.1A) also minimised tilting of the traps during deployment. Only very minimal tilting was observed for surface traps, and none at all for traps placed at depth.

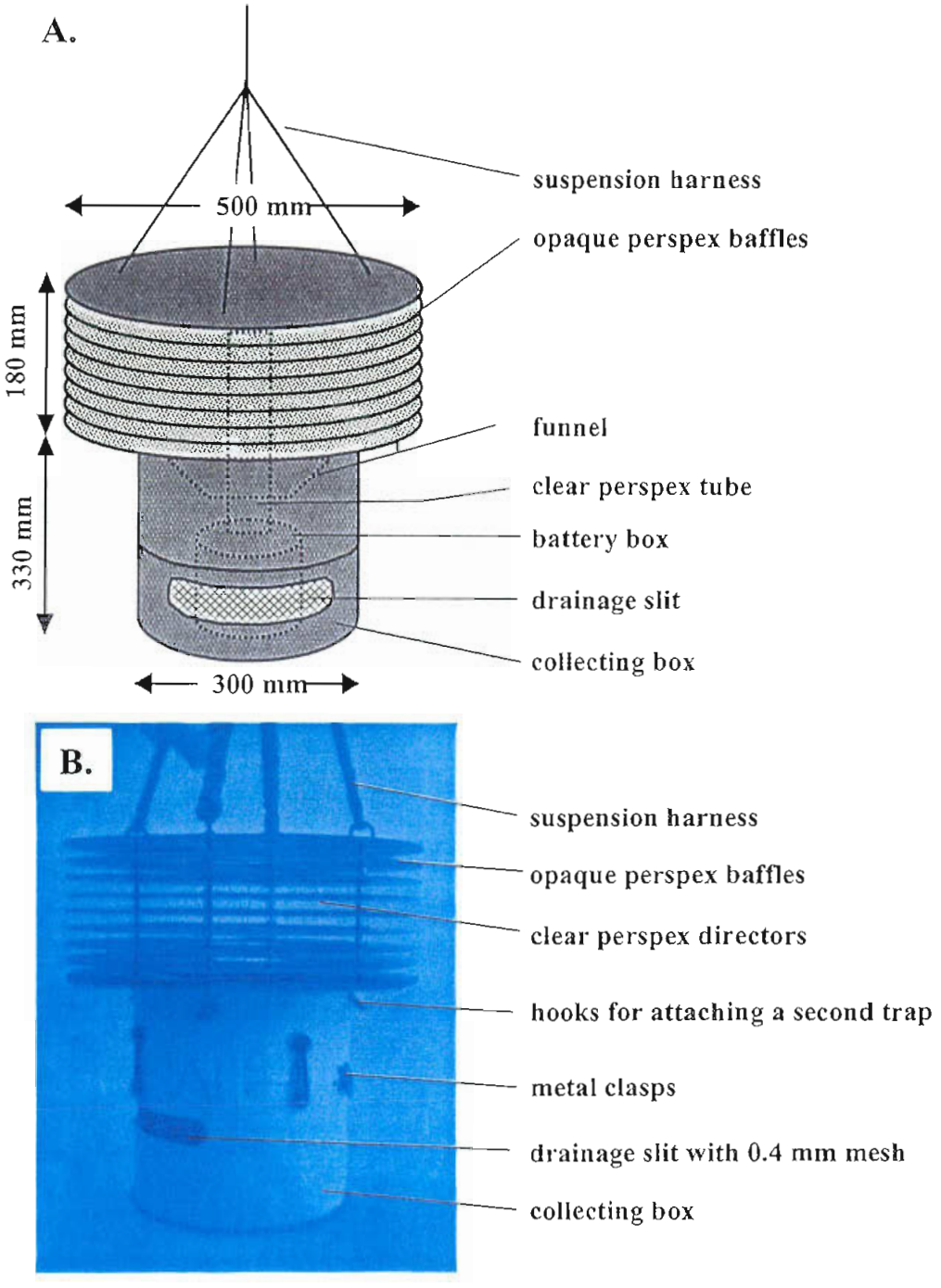

Figure 4.1. Details of the experimental light trap. (A) Schematic diagram and (B) photograph *in situ*.

4.2.2 Stratum specificity

The light distribution of the traps was measured in a 100,000 L seawater aquarium (~34 ppt) using a Li-Cor radiation sensor. This sensor detects all incident radiation from 400 – 700 nm, which is a range comparable to the visual capabilities of late stage reef fish larvae (Job 1999). Light intensity was measured along two transects placed 0.8 m and 1.6 m away from the trap and situated perpendicular to the direct line of radiation emitted from the trap light source. Light measurements were made every 10 cm along each transect from the centre of the baffles until the light levels decreased below the detection level of the light sensor (~ 10^{-3} $\mu Em^{-2}s^{-1}$). The angle of radiation was calculated by fitting a line from the edge of the outermost baffles to the outer point of the 0.8 m transect at which light levels first decreased below the detection level of the light sensor. This was compared to a theoretical angle of spread calculated from the distance between the baffles (2 cm) and the baffle width (18 cm).

Estimated light intensity at different distances from the light trap was calculated using theoretical values following the basic relationship for light attenuation in the ocean (Jerlov, 1976):

$$E_Z = \sum E_0(0,\lambda)\, e^{-2.7\, Kd(\lambda)\, Z}$$

Where E_Z is the light intensity at any given distance (Z), $E_0(0,\lambda)$ is the light intensity directly next to the light trap (Z = 0) for wavelength λ, and $Kd(\lambda)$ is the diffuse attenuation coefficient for wavelength λ. The factor 2.7 is an empirically derived correction factor for Kd (Duntley 1962), that allows for the lower attenuation from

diffuse light sources vs that which occurs for a point source or directed light beam (Dera 1992). The value for E_0 was measured directly next to the trap using the Li-Cor sensor and this was divided into its spectral components to give $E_0(0,\lambda)$ using a relative spectral output graph for the light trap, determined using a spectrophotometer. Values of Kd were taken from Jerlov's (1976) type II water classification, that approximates the water type around Lizard Island (Lythgoe et al. 1994). Mean light intensity over the illuminated area at different distances from the light trap was determined by multiplying the calculated light intensity after attenuation at each distance (E_z) by the ratio of the illumination area of the light trap at distance $z = 0$, to the area of illumination in the water column at distance z (calculated from the previously determined angle of radiation).

4.2.3 Catch efficiency

A pilot study was conducted to determine the effectiveness of the traps at catching larvae. Data for the pilot study were obtained from trapping over a total of 12 nights around the new moons in November and December 2000. The traps were deployed and samples obtained and sorted as described in section 4.2.4. The catch per unit effort of the traps were compared to data for conventional light traps (cf. Doherty 1987; Sponaugle & Cowen 1996, Stobutzki & Bellwood 1997). Data were obtained from published catch data from studies undertaken at various locations on the Great Barrier Reef, as well as from other tropical reef systems around the world. The methods employed and sampling duration of the studies varied widely, so statistical tests were not performed. However, the data for the total number of

individuals presented in each paper were converted to values of catch per sampling hour, enabling more direct comparisons. Data for the total number of families and species were not adjusted for sampling effort as species and family richness quickly asymptote. All sampling in these studies was conducted over the peak recruitment months for each sampling location.

4.2.4 Vertical distribution study at Lizard Island

Data collection: Stratified sampling using the stratum specific experimental light traps (Figure 4.1) was conducted over two recruitment seasons. The traps were hung individually on separate moorings and deployed in groups of three (top, middle and bottom) in approximately 18 meters of water, 1.5 km off the SW (leeward) side of Lizard Island (14°40'S, 145°28'E), on the Great Barrier Reef, Australia (Figure 4.2). The depths of the three traps were 2, 9 and 16 m from the surface for the top, middle and bottom traps respectively.

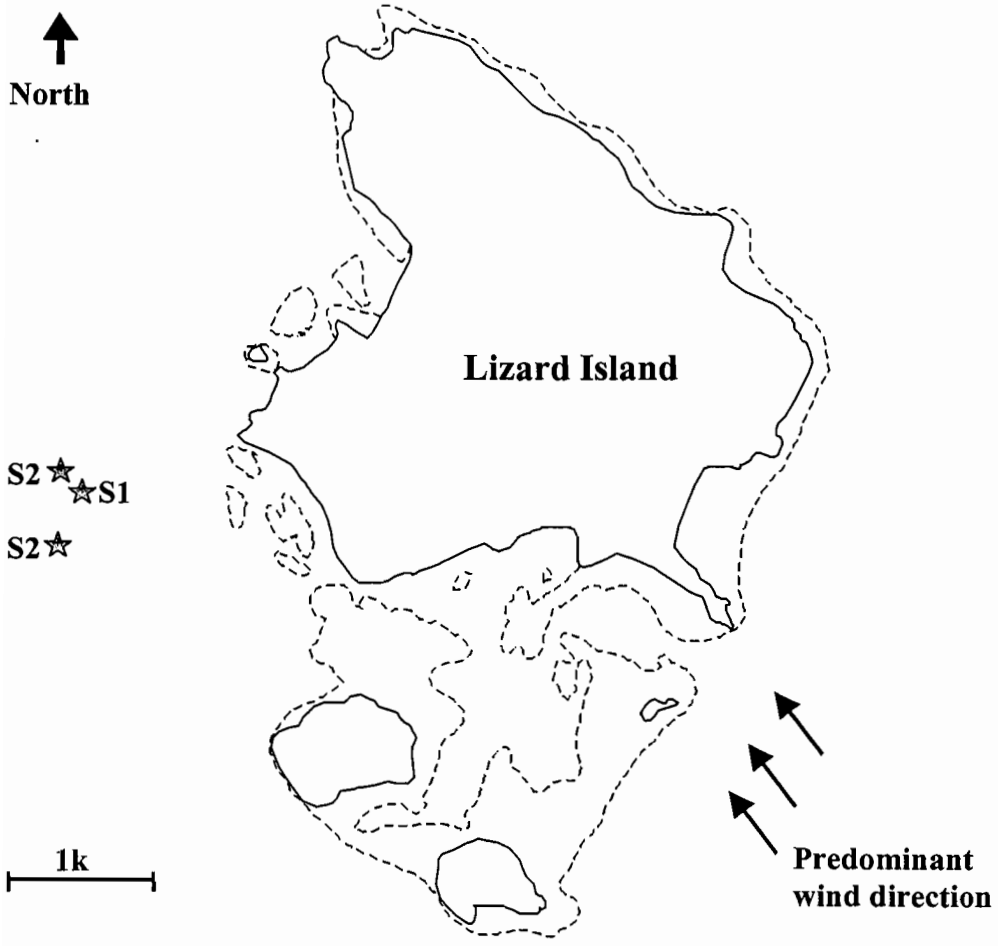

Figure 4.2. Location of light trap sampling sites at Lizard Island. S1 indicate the approximate location of the site used in the first sampling season (20 Nov 2000 to 26 Nov 2000 and 18 Dec 2000 to 4 Jan 2001) and S2 indicates the two sampling sites used in the second (11 Nov 2001 to 26 Dec 2001). Given the close proximity of the two sampling sites in season two, they were not considered independent replicates and data was pooled for both traps at each depth.

The traps were deployed over two Austral summers, with sampling occurring over 23 days during two periods in the first season (20 Nov 2000 to 26 Nov 2000 and 18 Dec 2000 to 4 Jan 2001), and continuously for 45 days during the second season (11 Nov 2001 to 26 Dec 2001). These periods covered both new moon and full moon phases. During the first season a single set of 3 traps was deployed, whereas in the second season two sets were deployed, situated approximately 400m apart. The catch was held in seawater in individually labelled buckets and returned to the research station. Here, samples were fixed in seawater buffered formalin for 24 hours and then stored in 70% alcohol prior to sorting. Samples were sorted under a dissecting microscope and all individuals were identified to lowest possible taxonomic level and counted. Individuals that could not be identified to a known species were identified as species 1, species 2 etc.

Data handling and analysis: The average numbers of larvae at each depth were compared using a two-way ANOVA with depth as a fixed factor and sampling day as a random factor. Depth was tested against the interaction (depth x sampling day). Only families for which at least one individual occurred at any depth on more than 10 nights were analysed. In addition, only nights that at least one individual of a particular family was present were included because nights when none were present provide no information regarding the depth distribution of that family. Families were analysed separately because different families were present on different nights. A Sequential Bonferroni correction was used to account for multiple tests (Rice 1988). The assumptions of ANOVA were examined by residual analysis and the data were

log transformed in order to meet the assumption of heterogeneity of variance. Data for the two trap sets in the second season were pooled before analysis because they could not be considered independent replicates. Chao quantitative estimators were used to compare species richness and were calculated using the computer program Species Diversity and Richness (Henderson & Seaby 1997). This estimator is based on abundance and was developed by Chao (1984) and is calculated as: $S = S(obs) + H/2b$, where H is the square of the number of species represented in the samples by a single individual (a), b is the number of species only represented by two individuals and S(obs) the observed species number. Chao considered this a lower bound estimator, but it can perform well when most species are infrequent (Henderson & Seaby 1997). Estimates were based on 1000 iterations at each depth, and only total (all samples) species richness values are presented.

Species-specific differences in vertical distribution were examined using bubble plots for families having more than one readily identifiable species and that occurred at more than one depth in the water column. Only species that occurred on more than five nights were included to avoid over-interpretation of the depth preference of rare species that may be absent from a depth simply due to chance.

Partial correlation coefficients were used to examine the relationship between the percentage of larvae caught near the bottom on each night and the total number of larvae caught, nightly wind speed and direction, tidal amplitude, rainfall and available moonlight. Wind speed and direction data (recorded at the Cooktown weather station; 15°30' S, 145°15' E) were obtained from the Australian Bureau of Meteorology. Tidal amplitude was calculated from the 2000 and 2001 Australian National Tide Tables. Rainfall data were obtained directly from the Lizard Island

research station. Total available moonlight was calculated by first allocating a light rating for the moon phase of each night (1 = full moon, 2 = 1st and 3rd quarter and 3 = new moon) and then summing this with a light rating allocated according to the total time the moon was above the horizon during each sampling night (1= > 9 hours, 2 = 9-6 hours, 3 = 6-3 hours and 4 = <3 hours). Astronomical data used in these estimates were obtained from Geoscience Australia, National Mapping Division. Partial correlations were calculated using all the families together, as well as separately for apogonids and pomacentrids since only these two families occurred near the bottom on enough occasions for such a comparison to be reasonable.

The sizes of larvae at each depth were compared graphically for each family using residual lengths calculated within each species. Residuals were calculated by subtracting the mean size of each species (weighted across depth) from each individual size measurement. Negative values indicate that the fish are smaller than average, and positive values indicate that the fish are larger than average. For families that occurred at all three depths, only species that were present at all depths were included in the analysis. Likewise, for families that occurred at only two depths, only species occurring at both of these depths were included. Confidence limits (95%) were used to indicate if individuals within each family were larger or smaller than average at each depth.

4.3 Results

4.3.1 Stratum specificity

The traps were found to emit light in a narrow beam that became more diffuse and rapidly decreased in intensity a relatively short distance from the light source (Figure 4.3). The maximum angle of radiation calculated from the light measurements was approximately 7.5°. This is only slightly larger than the theoretically calculated angle of 6.3°. Given a 7 m difference in depth between each trap, calculations suggest that at 7.5° the light emitted from adjacent traps would not overlap until 25 m from the light traps.

The light output immediately adjacent to the experimental light traps in seawater was 0.307 $\mu Em^{-2}s^{-1}$. Light intensity decreased rapidly with distance from the light trap due to both attenuation as well as increasing area of illumination (Figure 4.4). At around 7.4 m light intensity had dropped below levels required for feeding by late stage larval apogonids, which represent the most light sensitive recorded reef fish larvae (Job & Bellwood, 2000). By 9.6 m away from the trap the light intensity had dropped below levels equivalent to half moon light intensities at 10 m depth, and by 18.1 m light intensity had dropped below levels likely to occur during the new moon phase at 10 m depth. Light intensity values were estimated from information reported in McFarland (1986), Ryer & Olla (1998) and Job (1999). Thus at 25 m, when the light overlaps, the intensity is considerably less than ambient levels. Additionally, the width of the light beam at this distance is 4.8 m, and represents the maximum size of the sampling strata.

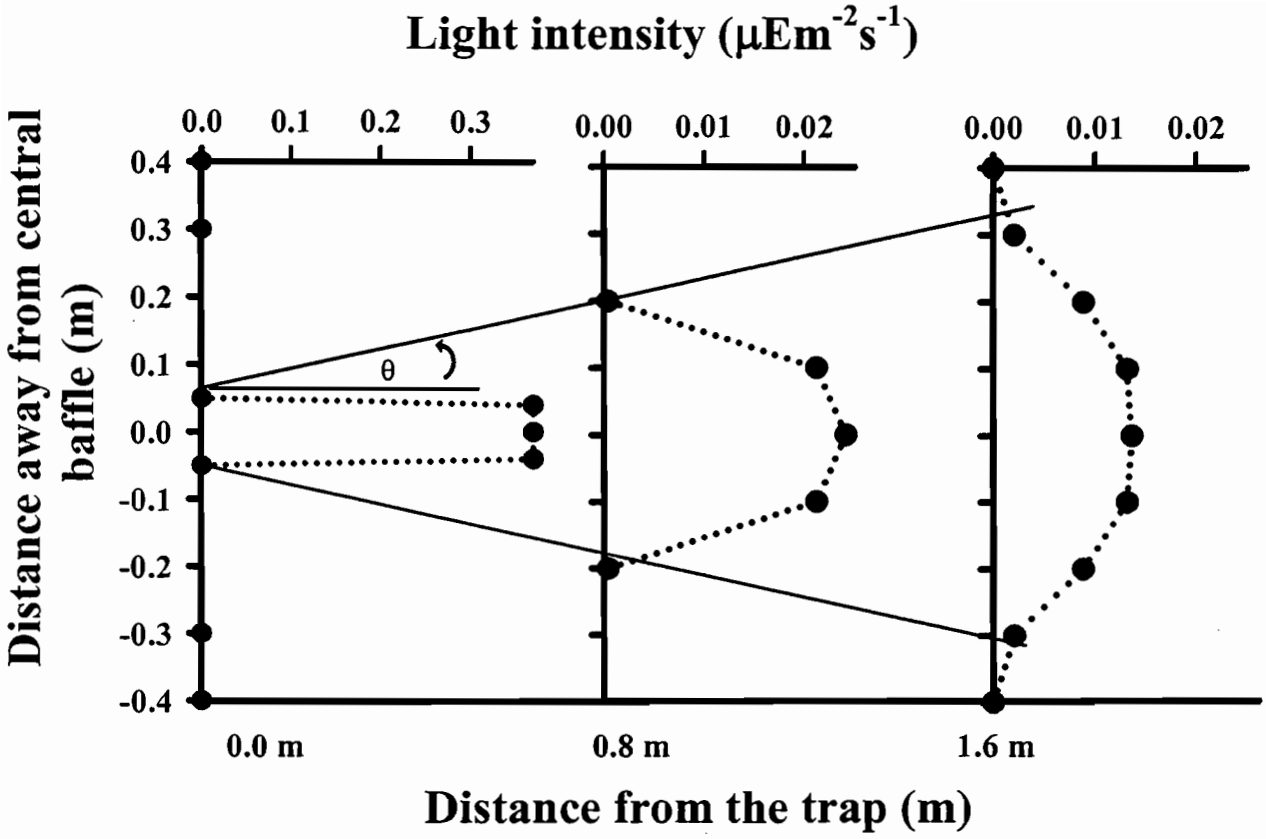

Figure 4.3. The distribution and intensity of light at 0.0 m, 0.8 m and 1.6 m away from the trap. The vertical axis represents the distance above or below the middle baffle (vertical plane). The upper horizontal axis represents the light intensity measured at each 0.1 m point along this vertical plane. The lower horizontal axis represents the distance from the trap that the measurements were taken (horizontal plane). The solid lines indicate the approximate angle of radiation (θ) where light intensity falls below detectable levels 0.8 m from the trap (θ = 7.5°).

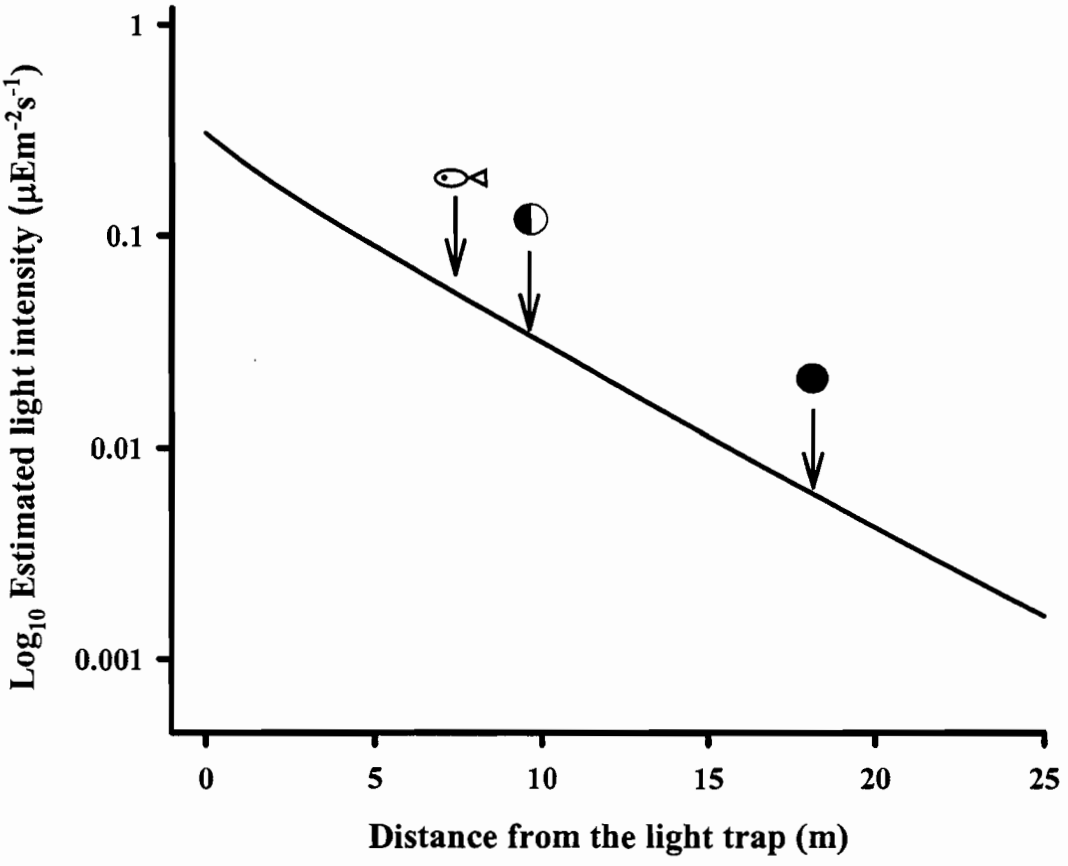

Figure 4.4. Estimated changes in mean light intensity over the illuminated area (400-700 nm) with distance from the light trap in Jerlov (1976) type II oceanic waters. The fish symbol represents the minimum light intensity required for feeding in late stage larval apogonids, the most light-sensitive recorded reef fish larvae (Job & Bellwood 2000), the half filled circle indicates the light intensity equivalent to 1st and 3rd quarter moon phases at 10 m depth, and the filled circle indicates the light intensity approximately equivalent to the new moon at 10 m depth (McFarland 1986, Ryer & Olla 1998, Job 1999).

4.3.2 Catch efficiency

When the total number of individuals, species and families caught in the pilot study were adjusted for sampling effort and compared to other studies in similar areas, it appears that the catch efficiency of the experimental traps is comparable to conventional traps (Table 4.1). There was a high degree of variation in the total number of individuals, species and families caught between studies, even when only those studies using conventional light traps are considered (Table 4.1). Total individual catches for published studies adjusted for sampling effort ranged from 0.1 individuals per hour in Barbados (Sponaguale & Cowen 1996) to 190.6 individuals per hour of the leeward side of Lizard Island (Choat et al. 1993). The experimental traps had a catch efficiency of 1.6 individuals per hour, and are on the lower range compared to other published values (Table 4.1). This is not surprising given that the traps are sampling a volume of water compared to conventional traps. The experimental traps caught a total of 35 species and 11 families over the sampling period, and is also mid range when compared to conventional traps (Table 4.1).

Table 4.1. A comparison of the catch efficiency of traps from the present study and data for conventional light traps taken from published sources. Pelagic species, or species that were clearly not larvae have been excluded.

Location	Sampling hours	Individuals / hour	Total species	Total families
Present study	132	1.6	35	11
Lizard Island (leeward), GBR[1]	40	190.6	-	20
Lizard Island (leeward), GBR[2]	75	1.5	21	8
Lizard Island (windward), GBR[3]	75	19.0	38	14
Grub reef, GBR[4]	138	4.9	46	18
San Blas Archipelago, Panama[5]	5016	1.0	83	36
Barbados, West Indes[6]	3960	0.6	64	68
Barbados, West Indes[7]	6930	0.1	23	23
Central GBR (offshore)[8]	613	10.4	-	29
Central GBR (offshore)[9]	419	8.0	-	32
San Blas Archipelago, Panama[10]	3078	0.9	108	32

[1]Choat et al. 1993, [2]Doherty 1987 (data from leeward side of Lizard Island), [3]Doherty 1987 (data from windward side of Lizard Island), [4]Doherty & Carleton 1997, [5]Hendriks et al. 2001, [6]Sponaugle & Cowen 1996 (data from 1991), [7]Sponaugle & Cowen 1996 (data from 1992), [8]Thorrold 1992, [9]Thorrold & Williams 1996, [10]Wilson 2001

4.3.3 Vertical distribution of reef fish larvae at Lizard Island

A total of 3085 individuals, comprising at least 79 species from 20 families were collected over the two sampling seasons. Most larvae were caught in large multi-species pulses that occurred around new moon, although small numbers of larvae from various families were caught throughout both sampling seasons. The

three most common families were Apogonidae, Pomacentridae and Lethrinidae, which constituted over 96 % of the entire catch (Table 4.2). Other families that occurred in reasonable numbers include the Mullidae, Blenniidae, Siganidae and Monacanthidae (Table 4.2). Most reef fish larvae occurred in the upper water column, with 79.8% of the total catch in the top traps. However, substantial numbers of larvae occurred in the middle water column, with middle traps accounting for 15.3% of the catch. Only 4.9% of larvae were caught in bottom traps. Chao-quantitative estimates of total species richness indicated that species diversity was highest in the top traps (108.7 ± 22.0), with middle and bottom traps having approximately half the number of species (54.3 ± 7.0 and 51.1 ± 12.2 respectively).

All of the most abundant families showed greatest numbers near the surface (Table 4.2). Several of these (Apogonidae, Mullidae, Blenniidae, Siganidae and Monocanthidae) showed relatively high percentages in the middle traps (17 to 37%; Table 4.2). None of the most abundant families showed high numbers near the bottom. However the Apogonidae, Pomacentridae, Lethrinidae and Monacanthidae were present at all depths (Table 4.2). All Gobiidae and Acanthuridae, as well as the single lutjanid, platycephalid and scorpaenid were caught in bottom traps. All pseudochromids, nempiterids, as well as the single chaetodontid, balistid and tetraodontid were collected in top traps (Table 4.2).

Table 4.2. Pooled catch composition (%) of fishes from bottom, middle and top trap samples off Lizard Island. Families are listed in order of decreasing abundance. Pelagic species, or species that were clearly not larvae have been excluded. The depth that each family is most abundant is highlighted in bold.

	Percentage caught at each depth			Total number of individuals
Family	Top	Middle	Bottom	
Apogonidae	**70.1**	22.1	7.8	1465
Pomacentridae	**89.4**	8.7	1.9	1265
Lethrinidae	**91.3**	7.5	1.2	253
Mullidae	**82.4**	17.6	0	34
Blenniidae	**76.9**	23.1	0	26
Siganidae	**81.8**	18.2	0	11
Monacanthidae	**50**	37.5	12.5	8
Pseudochromidae	**100**	0	0	5
Gobiidae	0	0	**100**	4
Syngnathidae	**33.3**	**33.3**	**33.3**	3
Acanthuridae	0	0	**100**	2
Nemipteridae	**100**	0	0	2
Balistidae	**100**	0	0	1
Chaetodontidae	**100**	0	0	1
Lutjanidae	0	0	**100**	1
Malacanthidae	0	**100**	0	1
Platycephalidae	0	0	**100**	1
Scorpaenidae	0	0	**100**	1
Tetraodontidae	**100**	0	0	1
Total	79.8	15.3	4.9	3085

When the catch at each depth was averaged over the sampling period, the Apogonidae showed a relatively even distribution throughout the water column, with no significant difference in the average number caught at each depth (Figure 4.5). The Lethrinidae and Pomacentridae had significantly higher abundance near the surface, but no significant difference in average abundance between the middle of the water column and the bottom (Figure 4.5). When the number of days each family was present at each depth was expressed as a proportion of the total number of days each family was caught, it was clear that while the Apogonidae showed a higher total number of individuals near the surface, they were found most frequently near the bottom (Table 4.3). For the other families occurring throughout the water column, larvae were found more commonly near the surface, except the Monacanthidae which appeared more commonly in middle traps (Table 4.3).

Table 4.3. The number of days each family was present at each depth as a percentage of the number of days each family was caught at any depth. Only families occurring on at least four nights and at all depths are included.

	Depth			
Family	Bottom	Middle	Top	Number of nights
Apogonidae	**85.7**	42.9	61.9	22
Lethrinidae	15.4	30.8	**92.3**	13
Monacanthidae	25.0	**50.0**	25.0	4
Pomacentridae	25.0	33.3	**91.7**	37

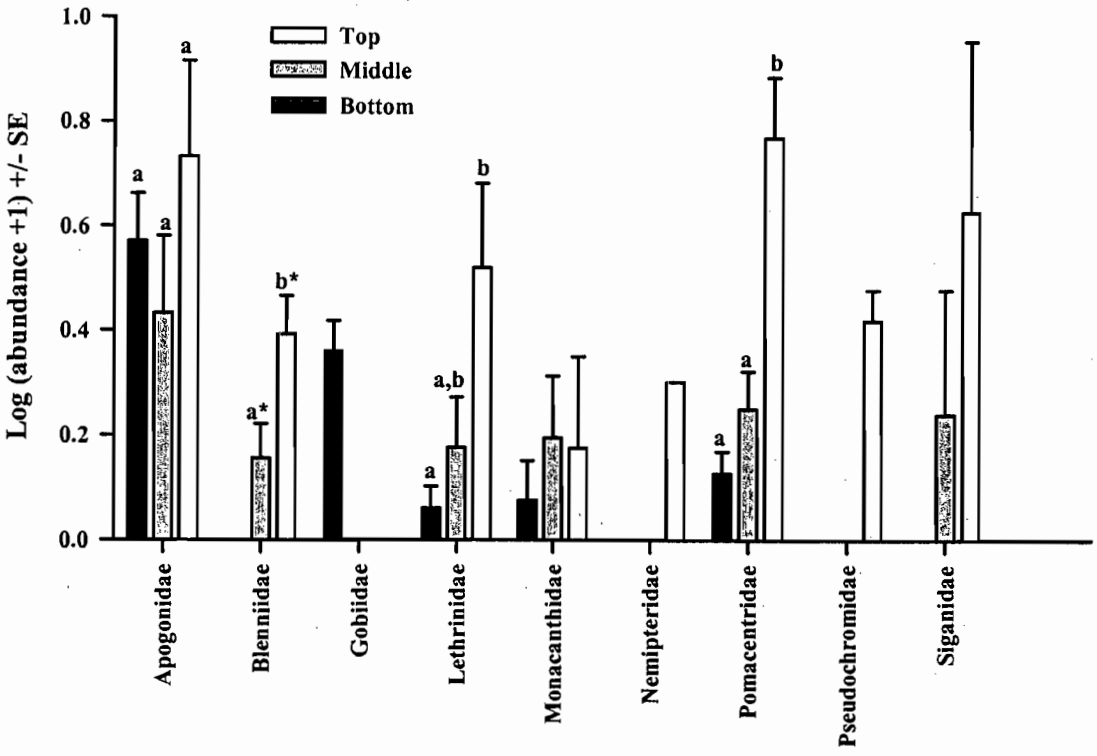

Figure 4.5. Mean nightly abundance of individuals caught in the top, middle and bottom traps for nine reef fish families. Only families occurring on more than one sampling night are included. Means are based only on days on which at least one individual was caught at any depth. ANOVAs were performed for all families occurring on more than 10 separate days. Significant differences were found in the depth distributions of the Pomacentridae ($F_{2,70}$ = 34.57, $P < 0.001$), Lethrinidae ($F_{2,24}$ = 11.14, $P < 0.001$) and Blenniidae ($F_{1,9}$ = 6.5, P = 0.03*), but not Apogonidae ($F_{2,40}$ = 2.91, P= 0.07). Letters above each bar represent significant subgroups. An * indicates subgroup is only significant before bonferroni correction.

Of the families occurring at more than one depth, only the Apogonidae and Pomacentridae had more than one species occurring on more than five nights, so a closer examination of species-specific depth preferences was conducted only for these two families. Seven of the pomacentrid and three of the apogonid species did not occur in the bottom traps at all. Only one pomacentrid group (*Chromis* spp.) occurred solely in surface traps (Figure 4.6). No taxa of either family occurred solely in the middle of the water column or solely near the bottom (Figure 4.6).

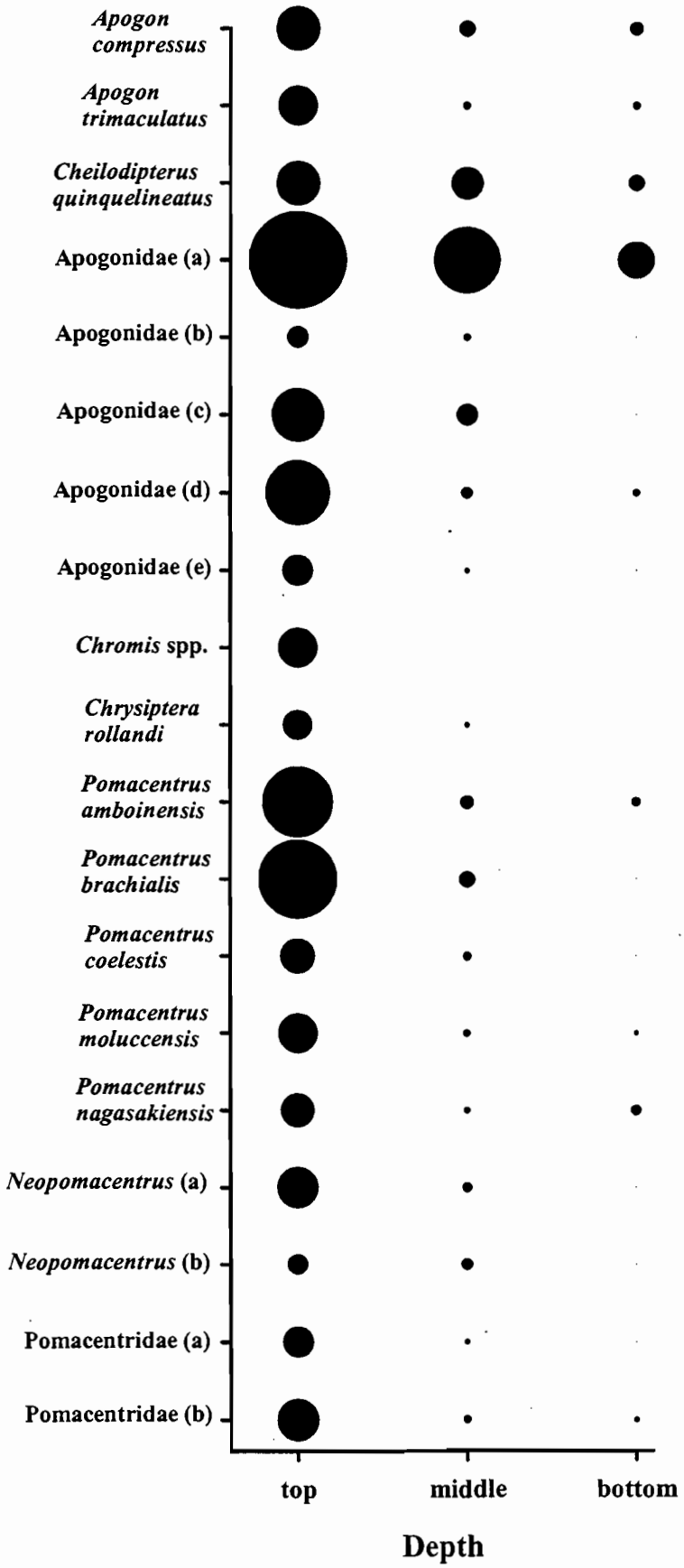

Figure 4.6. Species-specific depth distribution pattern for the 19 most common pomacentrid and apogonid species caught at Lizard Island. The area of each bubble indicates the average abundance of each species at each depth.

Partial correlation coefficients indicated a significant positive relationship between the percentage of apogonids occurring near the bottom and tidal amplitude (Table 4.4), suggesting that larger numbers of apogonids occur near the bottom when tidal movements are greater. However, this correlation was not significant after bonferroni correction. No significant correlations were found among the percentage of apogonids occurring near the bottom and any other variable, nor for any of the variables and the percentage of Pomacentridae occurring near the bottom (Table 4.4).

Table 4.4. Significance levels and partial correlation coefficients for multiple regressions between total catch, wind speed and direction, tidal amplitude, rainfall and light and the percentage of apogonid and pomacentrid larvae occurring in bottom traps. Significant values are highlighted in bold. No values are significant after bonferroni correction.

	Apogonidae		Pomacentridae	
Variables included	p	Partial Correlation	p	Partial Correlation
Total catch	0.52	-0.17	0.83	-0.04
Wind speed	0.27	0.29	0.49	-0.13
Wind direction	0.39	0.23	0.91	-0.02
Tidal amplitude	**0.04**	**0.53**	0.24	0.22
Rainfall	0.19	-0.35	0.87	-0.03
Light	0.06	-0.48	0.84	-0.04

There were clear depth related differences in the size of larvae within each species and these patterns were relatively consistent among families (Figure 4.7). Of the five families with species occurring at more than one depth, four had larger than average individuals near the surface and three of these were significantly larger (as indicated by 95% confidence limits; Figure 4.7). Lethrinid larvae were slightly smaller than average near the surface, but were still larger than those occurring in the middle of the water column (Figure 4.7). The smallest individuals for all but one family were found in the middle of the water column and this was significantly so for the Mullidae, Lethrinidae and Apogonidae (Figure 4.7). The Pomacentridae was the exception, with the smallest individuals near the bottom (Figure 4.7). Only three lethrinid larvae were caught near the bottom, all clearly larger than average (Figure 4.7). Apogonid larvae caught near the bottom were of average size (Figure 4.7).

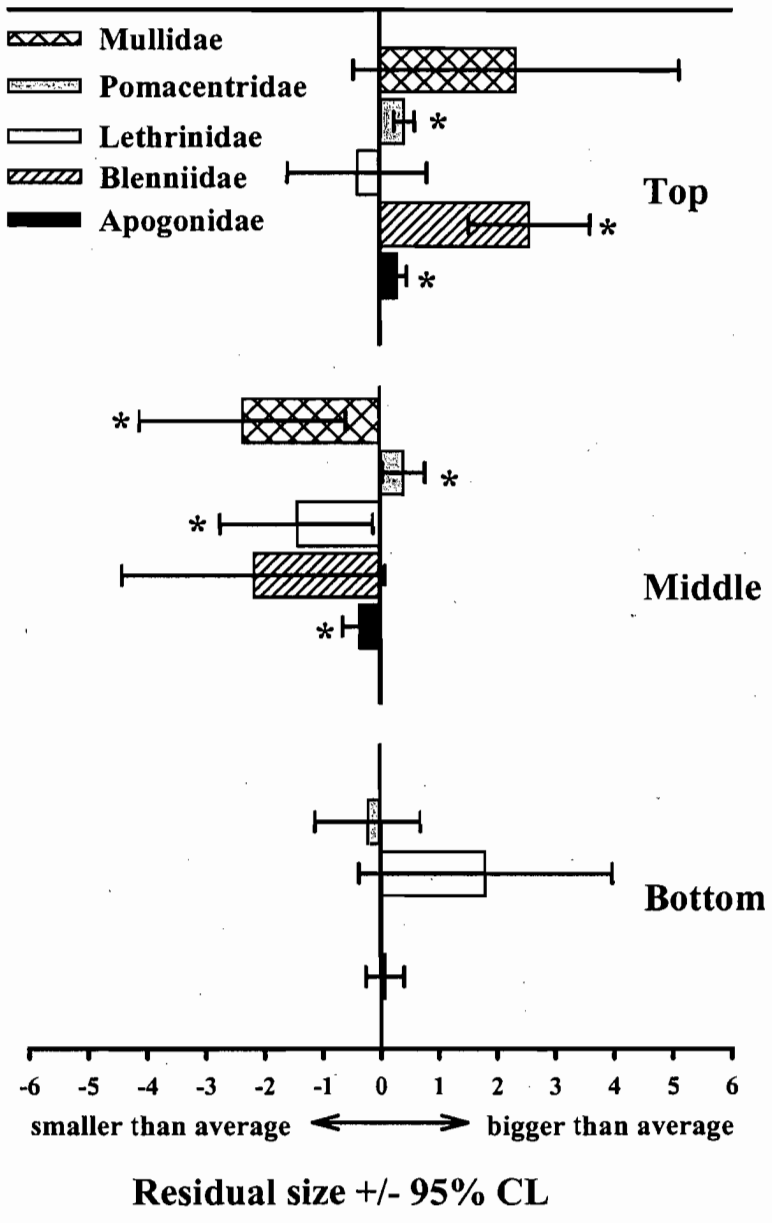

Figure 4.7. The mean residual size of larvae caught at each depth for the five most abundant reef fish families, with 95% confidence limits. Residuals were calculated at the species level but have been averaged across families. Positive values indicate that larvae are bigger than average size at that depth and negative values indicate that larvae are smaller than average. An * indicates that the larvae are significantly bigger or smaller than average (i.e. confidence limits do not overlap 0).

4.4 Discussion

4.4.1 Performance of the stratified sampling light traps

Light intensity dropped off rapidly with distance from the experimental traps. By 18.1 m away from the traps, the light intensity was roughly equivalent to that of new moon at 10 m depth, indicating that at this distance ambient light intensity was comparable to that emitted from the trap. According to the estimated angle of radiation, if placed 7 m apart (as in this study), light emitted from adjacent traps would not overlap until a horizontal distance of 25 m. This suggests that a distance of 7 m between traps is conservative and it is clear that depth strata are being sampled discretely. Indeed, if new moon light intensities are considered to be a threshold level for light trap detection, the traps could theoretically be placed as close as 4.8 m apart and still retain the ability to sample discrete depth strata. This estimate is conservative; given that the calculations for the reduction in light intensity with distance from the traps are based on the assumption that light is evenly distributed throughout the light beam as it expands (at an angle of 7.5°) away from the trap. As the light intensity decreases away from the center of the beam, the actual light intensity at the edge of the light beam is probably much lower. The ability to sample specific depth strata at this scale permits detailed vertical sampling designs and will enable us to accurately quantify the vertical distribution of late stage larvae around reefs throughout the water column.

A maximum fishing distance of around 17 m for the experimental traps is considerably less than the 95 m reported for conventional light traps (Milicich 1993).

This large difference in estimates probably occurs for two reasons. Firstly, initial light intensities (E_0) reported by Milicich (1993) are much higher (30 $\mu Em^{-2}s^{-1}$) than in this study (0.31 $\mu Em^{-2}s^{-1}$). The lower initial light intensity of the experimental traps in this study is probably caused by absorption of light by the baffles and would substantially reduce the effective fishing distance of the experimental traps. The second reason is that the calculations used by Milicich (1993) to estimate the fishing distance of conventional light traps did not take into account the expanding area of the wave front (i.e. using a point versus a uniform light source in the calculations). This would substantially reduce the effective fishing distance of her traps.

The pilot study caught an average of 1.6 individuals per hour and a total of 11 families over the sampling period, and appears to be on the lower end of the range reported in other studies in the same area. Larval catches using light traps on the leeward side of Lizard Island (where this study was undertaken) vary considerably and range from 1.5 individuals per hour (Doherty 1987) to 190 individuals per hour (Choat et al. 1993). The total number of families caught ranged from 8 to 20 for these two studies respectively. Although catches may be lower than conventional traps, the experimental traps were clearly capable of successfully catching larvae. It appears that despite the rapid attenuation of light and a design that reduces the volume of water sampled, the experimental traps are a viable collection method with adequate numbers for replication among depths or sites.

One potential problem with the sampling method described here, is that catches may be influenced by differences in current speed with depth because traps placed in areas of higher current velocity would sample proportionately larger areas. In addition, differences in relative turbidity of water could also potentially influence

catch rates of traps at different depths. These problems relate not only to the experimental light traps developed here, but any lights traps used for sampling reef fish larvae, and could potentially operate on both vertical and horizontal scales. I would recommend that any future studies using light traps to sample late stage larval reef fish also incorporate measurements of both current velocity as well as turbidity at all sampling locations and depths so that these problems can be properly accounted for. In addition, it is also important to point out that utilising a sampling tool dependant on photopositive behaviour by larvae may introduce potential bias because light traps are taxon specific and some families of fishes, such as the Labridae and Scaridae, are not sampled using this method. Interestingly, it appears that larval behaviour may vary with geographic location, given that both of these families are caught in high abundances in light traps in the Caribbean (see Hendriks et al. 2001). In addition, bias may be introduced if photopositive larvae show a greater affinity with surface waters, which could explain why catches in surface waters are higher. However, such a bias seems unlikely, given that most larvae are caught during times of new moon (when attraction to surface waters would be the least). In addition, the study by Hendricks et al. (2001) caught equal numbers of larvae in both deep and shallow light traps, suggesting that photopositive larvae are not necessarily attracted to surface waters.

4.4.2 Vertical distribution of late stage larvae at Lizard Island

This study clearly shows that late stage reef fish larvae exhibit distinctive vertical distribution patterns, among families, species and individuals. The

overwhelming majority of late-stage larvae occurred near the surface in large multi-species pulses, supporting earlier suggestions that greater numbers of individuals and species of settlement stage reef fish occur in surface waters at night (Doherty & Carleton 1997). The depth resolution obtained using stratum-specific light traps demonstrates these larvae occur in greatest abundances near the surface, rather than lower in the water column. In addition, larvae of the more abundant families were larger near the surface and smaller in the middle of the water column. The larger size of larvae near the surface indicates they are nearer to settlement, suggesting that larvae of some species may migrate into surface waters as an active mechanism during settlement. This has also been observed for settlement stage coral reef fishes near One Tree Island on the Great Barrier Reef (Kingsford 2001). Differences among depths may, in part, be due to size selective or taxon specific mortality at different depths. However, given the advanced swimming capabilities of these late stage larvae (Chapters 2 & 3), along with well developed swim bladders (Leis & Carson-Ewart 2000), they clearly have the ability to rapidly alter their vertical distribution. This suggests that differences in vertical distribution are probably a result of active depth selection by these larvae. At present it is not understood why reef fish larvae migrate into surface waters near settlement. Possible explanations may include potential transport advantages such as onshore water movements at the surface (e.g. Shenker et al. 1993, McIlwain 1997), navigational advantages such as the presence of chemical cues in surface waters (see Atema et al. 2002), or potentially as a mechanism to avoid predation that can be high if larvae settle directly onto the seaward side of a reef (Leis & Carson-Ewart 1998, 2002).

Although most families were more abundant near the surface, many of the widely distributed taxa also had significant numbers lower in the water column. Furthermore, if current speeds are in fact lower near the bottom, then traps placed at depth may be fishing a smaller area, and subsequently may under represent the abundance of larvae. If this is true, then the proportion of larvae occurring lower in the water column may in fact be substantially higher than reported here. In particular, both the Pomacentridae and Apogonidae (the two most abundant families) were represented throughout the water column, which is consistent with other studies (Doherty & Carleton 1997, Hendriks et al. 2001). The broad depth distribution of these taxa appears to be unrelated to species-specific depth preferences within each family. Although there were consistent differences in the size of larvae with depth, with larger larvae occurring near the surface and smaller larvae in the middle of the water column, suggesting that differences in water column usage exist within rather than among species. The larger size of larvae near the surface suggests they are more likely to be competent to settle, and supports the idea that these larvae may migrate into surface waters immediately prior to settlement. The results also suggest that smaller larvae not yet competent to settle may utilize the middle of the water column to maintain their position prior to settlement. Ontogenetic differences in water column use by late stage larvae between the upper and mid water layers highlights the importance of sampling discretely throughout the water column to properly assess the behavioural mechanisms employed by settling larvae.

Some families were caught only in bottom traps, highlighting that there may be taxon-specific differences in water column use by larvae. Although catches were very low in my study, patterns were consistent with other studies on vertical

distribution, suggesting the results may be representative of these families. Such families included the Gobiidae, Acanthuridae and Platycephalidae, all of which have also been found at depth in other studies (e.g. Hendricks et al. 2001, Leis 1991b, Gray 1998). Of particular interest are the Acanthuridae, which have been observed swimming in groups along the bottom during settlement, although this behaviour was observed during the day (Sancho et al. 1997). These results suggest that surface colonization by settling larvae does not occur in all families of reef fishes. Why some groups settle via surface waters, whereas others do not, remains an intriguing question. Among fishes, post-flexion or late-stage larvae of several temperate and tropical families have been found in or near the benthic boundary layer (reviewed by Sponaugle et al. 2002). Bottom association has been shown to significantly reduce dispersal distance in marine larvae and may lead to higher levels of local-retention (Shanks et al. 2003).

Of the families occurring in high abundance, only the Apogonidae occurred regularly near the bottom. This supports previous studies that found at least some species of apogonids to be more abundant at depth (Doherty & Carleton 1997, Hendriks et al. 2001). Because some apogonids are known to settle in off-reef sand and rubble habitats (Fin & Kingsford 1996), it is possible that those caught near the bottom were settled individuals. However, if this were so they would be expected to be larger than other members of their species, which was not the case in this study. The three lethrinids caught in bottom traps, however, were considerably larger than average, indicating they may have been settled juveniles. Although Apogonids were caught more regularly at depth, the overall number was much higher near the surface (table 4.2), where they also had a much larger mean size (Figure 4.7). This provides

support for the fact that the Apogonidae, along with many of the other taxa examined, appear to form multi-specific schools prior to subsequent settlement onto reefs via surface layers.

The percentage of apogonids near the bottom was weakly positively correlated with tidal amplitude. Tidal movements dominate currents in the Lizard Island region (Frith et al. 1986), and when tidal amplitude was large, the number of apogonids occurring near the bottom was also greater. Given the poor swimming abilities of this group (Stobutzki & Bellwood 1997, Leis and Carson-Ewart 1997, Fisher et al. 2000), it seems probable that they use the boundary layer near the sea bottom to avoid advection from the reef. Vertical migration in relation to tidal currents has been recorded in crustacean (Forward & Rittschof 1994) and fish larvae (Rijnsdorp et al. 1985, Forward et al. 1996, Grioche et al. 2000) as a mechanism to avoid advection and facilitate up-stream transport in estuarine systems. Fine-scale sampling during the night in relation to tidal movements would be required to determine the extent to which reef fish taxa use such a mechanism.

It is important to note that my study on vertical distribution has been done only at night. Several studies have shown diurnal changes in the vertical distributions of various taxa in the ichthyoplankton (e.g. Lough & Potter 1993, Brodeur & Rugen 1994). Consequently, it is likely that the daytime vertical distributions of larvae may be very different to those described here. Both Leis (1986) and Kingsford (2001) found that the upper portion of the water column seems to be avoided by most fish larvae during the day, although both of these studies included younger stage larvae. Leis et al. (1996) examined the daytime depth preferences of late-stage larvae by following them in the field. The mean depth distributions were 6.5 and 7.7 m for the

Apogonidae and Pomacentridae respectively, suggesting that a mid water distribution may be preferred by larvae of these families during the day. Daytime depth distributions may also be considerably deeper in the open ocean (Leis & Carson-Ewart 2001).

4.4.3 Conclusions

Overall, this study has shown that light traps, if modified substantially, can be successfully used to describe the vertical distribution of late stage larval reef fishes around reefs. These stratum-specific traps will greatly enhance our ability to examine the vertical distribution of late stage larval reef fishes in the field. The higher resolution sampling method used in this study clearly demonstrated a strong pattern in the vertical distribution of late stage larval reef fishes. The prevalence of high numbers in the shallow strata was consistent among several families and within species. There were also consistent differences in the sizes of larvae with depth. The results suggest that differential water column use is a widespread feature of late pelagic stage larval reef fishes and the findings emphasise the importance of water column use in the overall dispersal and settlement strategies of larvae.

Chapter 5: Final Discussion

The main goal of this thesis was to examine the behavioural capabilities of tropical reef fish larvae, to establish the potential for different families to behaviourally influence their dispersal and settlement patterns. Overall, the results indicate that larvae have the ability to exert a considerable influence on their dispersal patterns and possess features that reflect fine control of their settlement behaviour.

Given the sophisticated behavioural abilities of late stage reef fish larvae, there is little doubt they have the potential to influence their dispersal and settlement patterns at a range of spatial scales. Studies examining the sustained swimming capabilities of larvae (Chapter 2) clearly demonstrate that swimming speed has a profound effect on swimming abilities in these larvae. The results suggest that many late stage larvae can sustainably swim at speeds 2 - 3 times the average current speeds around reefs. These speeds are also 2 - 3 times faster than the speed used for all previous sustained swimming experiments (13.5 cms^{-1}). The implications of these results are considerable, and suggest that many larvae would be able to use active swimming behaviour to alter their location on a broad scale even in the presence of quite fast current flows or in much shorter periods of time than previously recorded (cf. Stobutzki & Bellwood 1997). Furthermore, given access to food it appears that larvae can sustain swimming activity at these speeds indefinitely and that swimming does not necessarily incur costs related to larval condition (cf. Stobutzki 1997, Armsworth et al. 2001). These findings present a new range of possibilities for the

potential importance of larval behaviour in influencing dispersal, settlement patterns and recruitment success of reef fishes.

Another significant finding has been the discovery of considerable behavioural changes in larvae coincident with settlement. The nocturnal activity of larvae nearing settlement increases considerably in terms of both the percentage time spent in active behaviour as well as their relative swimming speeds compared to during the day (Chapter 3). There also appears to be a shift in nocturnal vertical water column use, with larvae moving into surface waters immediately prior to settlement (Chapter 4). These studies provide strong evidence that settlement onto reefs by many tropical reef fishes is an active process under the full influence of larval behaviour. Active site selection at settlement is clearly within the capability of many larvae, and may account for small-scale spatial patterns in the settlement of reef fishes (e.g. Williams & Sale 1981) as well as larger scale patterns of recruitment (e.g. Fowler et al. 1992, Williams et al. 1984).

Central to our understanding of reef fish populations is the debate over whether marine systems are "open", receiving larval input from a number of surrounding areas and providing larvae to seed downstream reefs, or "closed" and maintained primarily by self-recruitment. The long-term survival of self-sustaining populations is clearly demonstrated by the presence of high percentages of endemic species on isolated islands and atolls (Robertson 2001). However, several studies have also recently demonstrated high levels of self-recruitment for some coral reef fish populations in less isolated situations (e.g. Jones et al. 1999, Swearer et al. 2000). In addition, a recent review by Swearer et al. (2002) suggests that self-recruitment may be a widespread phenomenon in marine populations in general. It is still unclear,

however, to what extent larval behaviour contributes to these patterns and how behaviour may interact with oceanographic processes (see Cowen 2002 for a review of oceanographic features potentially important in larval dispersal and retention).

Although it is well established that larvae have the ability to modify their position during that last few days before settlement (Stobutzki and Bellwood 1997, Cowen 2002, Sponaugle et al. 2002), to assess the potential for larval fishes to influence levels of self-recruitment using active behaviour it is necessary to examine the swimming abilities of larvae throughout their larval phase. Are the swimming capabilities of younger larvae sufficient to avoid or significantly retard their advection? This thesis provided the first description of undisturbed swimming behaviour of larvae throughout ontogeny in any tropical reef fish taxa (Chapter 3). The results clearly demonstrated that benthic spawned or brooded larvae hatch with relatively well develop swimming capabilities and that they maintain high swimming speeds throughout ontogeny. The relatively consistent undisturbed swimming speed of pomacentrid larvae during ontogeny has important implications for dispersal models incorporating larval swimming behaviour. To date all models have assumed larvae would only swim actively in the last portion of the larval phase (Wolanski et al. 1997, Porch 1998, Armsworth et al. 2001, James et al. 2002). This is certainly not true for all reef fish species and at slower speeds even young larvae should be able to maintain some swimming behaviour indefinitely. It is clear that at least two species (*Pomacentrus amboinensis* and *Amphiprion melanopus*) exhibit substantial ability to avoid advection from an early age and that this ability is well within the normal, undisturbed behavioural abilities of these larvae. In both cases, this ability provides a mechanism for active self-recruitment in these larvae.

Data on the development of swimming capabilities is restricted to a few demersal spawning reef fish taxa. This is largely because of the difficulty associated with rearing the much more delicate larvae of pelagically spawning species. Many pelagically spawned larvae are much smaller and less well developed at hatching and to have a longer pelagic larval phase (Thresher 1991). Consequently, the development of swimming capabilities may be considerably slower for such taxa, and the potential impact of behaviour may be reduced compared to demersally spawned larvae. However, given the much greater swimming abilities of many of the other reef fish families at settlement (Chapter 2; Table 2.10) it is highly likely that at least some of these families also posses the capabilities to use active behaviour as a mechanism to facilitate self-recruitment. In Figure 5.1, I have interpolated developmental rates of swimming abilities based on the length of their larval phase, and their swimming capabilities exhibited at settlement (from chapter 2) in a wide range of reef fish families, including both demersal and pelagic spawning taxa. This interpolation assumed that larvae will only swim actively during the day until 80% of the larval period is complete (Figure 3.7) and that larvae could potentially sustain swimming at speeds of 50% of their average U-crit (Figure 2.6). Swimming capability is assumed to develop linearly[1] during ontogeny (Fisher et al. 2000) and at the same rate for all species after normalization (speed at age (x) is adjusted for

[1] Although Fisher et al. (2000) claim that U-crit develops exponentially during ontogeny, an F-test comparing the fit of a linear model to that of an exponential model for their data and additional unpublished data for three extra species found no significant difference ($F_{33,33} = 1.59$, $P = 0.09$). This suggests that a linear model adequately describes the relationship between swimming ability and age.

speed of each species at settlement)[2]. Based on the potential distance larvae would theoretically be able to swim if a homing behaviour were initiated soon after

hatching, it appears that the larvae of several reef fish families have the ability to overcome currents in a system like the Great Barrier Reef (Fig 5.1). As such, these taxa theoretically have the capability to self-recruit using active behaviour. The highest potential appears to be in the Acanthuridae and Siganidae, but the Chaetodontidae, Lethrinidae, Lutjanidae, and Pomacentridae may also be able to facilitate self-recruit using behaviour (Figure 5.1). Importantly, these families include both demersal as well as pelagic spawners. It appears that while larvae from pelagic eggs may be transported farther from shore (Leis & Miller 1976, Leis 1993) the greater swimming capabilities of these families near settlement indicates they have compensatory ability that provide them with a high potential to modify dispersal patterns or behaviourally facilitate self-recruitment.

[2] An F test found no significant difference among taxa in the development of normalized U-crit throughout ontogeny for data from Fisher et al. (2000) and unpublished data for three additional species ($F_{37,33} = 0.95$, $P = 0.56$).

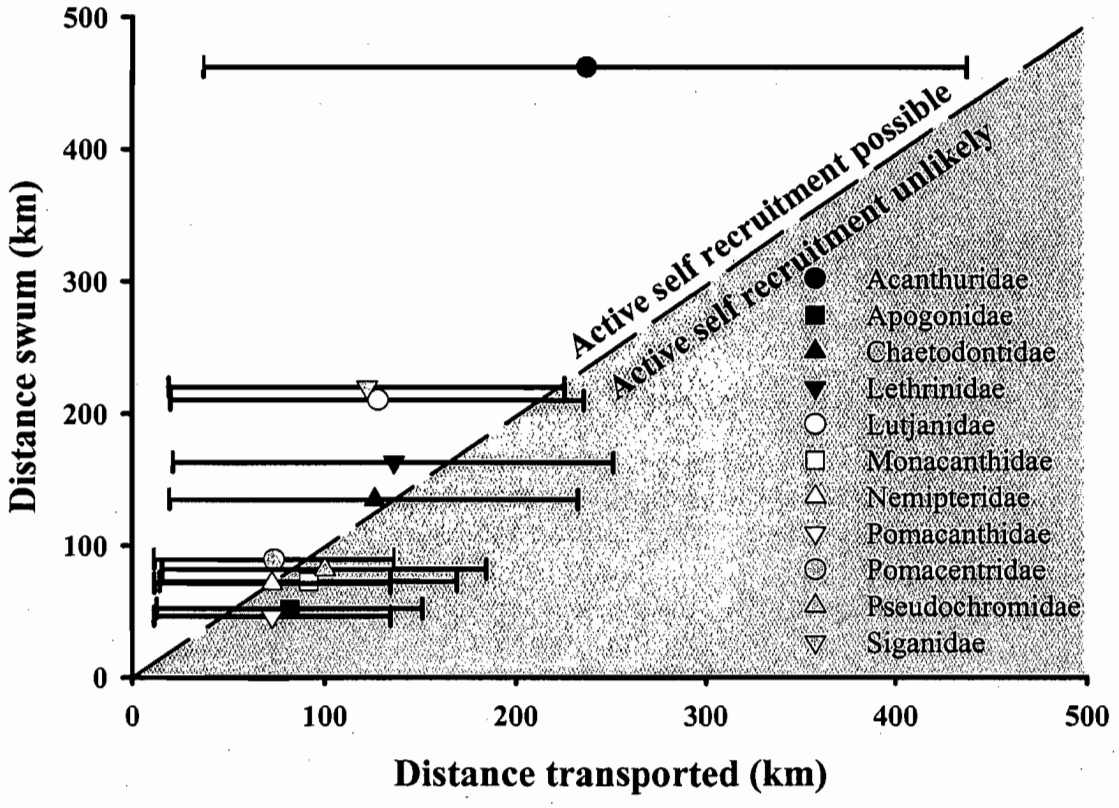

Figure 5.1. Predicted distance swum versus distance transported throughout the larval phase for 10 families of reef fishes. Distance swum is based on a 50% U-crit swimming speed (Chapter 2, Table 2.10) integrated throughout ontogeny. It is assumed that swimming develops linearly from hatching to settlement (cf. Fisher et al. 2000) and that larvae only show active swimming behaviour during the day until near settlement (Chapter 3, Figure 3.7). Distance transported is based on the mid point value of 25.5 km week^{-1} and error bars represent the range 4 to 47 km week^{-1} from Frith et al. (1986). The fitted line indicates when predicted distance swum by larvae is equal to the likely distance transported.

The potential impact of larval behaviour for all of the reef fish families would be much greater if they were to use vertical migration to avoid faster current flows at different depths (Armsworth 2001). This thesis has demonstrated differential use of the water column among families and that some families may regulate their depth distribution during settlement (Chapter 4). It also appears that some families may alter their distribution in relation to different oceanographic conditions, such as an increase in tidal currents (e.g. Apogonidae) suggesting fairly sophisticated water column use by larvae nearing settlement (Chapter 4). A similar pattern of sophisticated water column use by late stage larvae has been reported from *in-situ* observations, which show that depth selection by larvae varies among lagoonal and oceanic habitats (Leis & Carson-Ewart 2001). Vertical migration in relation to tidal currents has been recorded in crustacean (Forward & Rittschof 1994) and fish larvae (Rijnsdorp et al. 1985, Forward et al. 1996, Groiche et al. 2000) as a mechanism to avoid advection and facilitate up-stream transport in estuarine systems. There is no reason why such behaviour is not also available to the larvae of coral reef fishes, and may substantially influence horizontal dispersal patterns. Furthermore, active vertical migration may provide a mechanism for retarding advection throughout ontogeny, and this would substantially enhance the potential impact of swimming behaviour in active self-retention of these larvae.

The high potential for behaviourally mediated self-recruitment across a range of reef fish families, raises the question of whether such behaviour actually occurs. In a recent review, Strathmann et al. (2002) suggest that there are no apparent advantages of long distance dispersal by larvae and that selection may even favour

larval retention over dispersal. Armsworth et al. (2001) found that a return-based strategy by larval pomacentrids and acanthurids would be unsuccessful if energetic costs associated with active behaviour were included in their model. Their assumptions of the energetic costs associated with active swimming, however, may be unreasonable given that larvae can feed while swimming (Chapter 2) and that they maintain high swimming speeds throughout ontogeny (Chapter 3). If energetic costs are not included in their models (or are alleviated by feeding), then situations exist where a return-based strategy could be successful, particularly if the probability of finding a suitable downstream settlement site is low. A return-based strategy is likely to be even more advantageous in these models if larvae are capable of reducing rates of advection from an early age.

The use of behaviour to actively facilitate recruitment onto natal reefs requires that larvae have the sensory capabilities to navigate in the open ocean and to detect reefs from considerable distances. Whether or not larvae have the sensory capabilities to achieve this is currently unknown. The sensory capabilities of larvae have been recently reviewed in Montgomery et al. (2001), Kingsford et al. (2002) as well as Leis & McCormick (2002). Fish larvae have well-developed chemosensory capabilities and there is a suite of potential chemical cues available on the leeward side of reefs that could be used for navigation from downstream locations (Atema et al. 2002). Furthermore, there is also a considerable amount of noise generated in the vicinity of reefs (McCauley & Cato 2000), which may provide larvae with a multidirectional navigational cue from considerable distances (Stobutzi & Bellwood 1998, Tolimieri et al. 2000). Consequently, if larvae are able to remain within the sensory zone of their natal reef, mechanisms for open ocean navigation may be

unnecessary for maintaining directed swimming behaviour. If larvae are unable to remain within the sensory zone of their reef (which is likely for some species, especially pelagic spawners), then several other mechanisms that could be used include magnetic compass, inertial, sun compass, polarised light and electric fields (Montgomery et al. 2001, and papers therein), all of which could provide directional dues for navigation over considerable distances, although none have been demonstrated for the larvae of coral reef fishes. More information on the sensory capabilities of larvae, and their response to a range of navigational cues is urgently needed to determine if fish larvae have the necessary sensory capabilities to use active behaviour to influence their dispersal patterns during development in the pelagic environment.

Much of the work in this thesis has been done using larvae that were captured in light traps. It is important to note that light traps are selective sampling tools that sample a limited range of reef fish taxa. Several important families are notably excluded from light trap catches, including members of the families Scaridae and Labridae, which make up an important part of the reef fish community (Bellwood 1996). Other families, while not completely excluded, are often very rare, such as the Serranidae. Clearly, more work needs to be done on some of these rarely caught taxa, to determine how widespread the impact of larval behaviour may be for reef fishes as a group.

The dispersal patterns of marine larvae will be a result of the interaction between behaviour and the prevailing oceanographic processes. Although a detailed analysis of oceanographic processes is beyond the scope of this thesis, it is clear that these will vary considerably on large and small spatial scales, as well as temporal

scales (reviewed in Cowen 2002). The behavioural capabilities of larvae also vary considerably among taxa. These variations will lead to taxonomic, spatial as well as temporal variation in the relative importance of active behaviour and oceanography in shaping the dispersal patterns of reef fish larvae. There is no doubt that detailed oceanographic models will provide valuable insights into the likely dispersal trajectories of larvae (e.g. James et al. 2002). However, given the well developed swimming capabilities of many taxa (Chapters 2 & 3) as well as differential water column use by larvae nearing settlement (Chapter 4) it is clear that both horizontal swimming as well as vertical migration behaviour need to be incorporated into hydrodynamic dispersal models. This thesis has provided data that enables us to accurately parameterise the behavioural abilities of different taxa and will prove a valuable tool for modellers wishing to describe the dispersal patterns of larval reef fishes.

This dissertation identified the potential impact that larval behaviour may have on the recruitment success, dispersal patterns, and potential levels of self-seeding in several families of tropical reef fishes. It is clear that the capabilities of different families vary considerably, as do the behavioural mechanisms (active swimming vs vertical migration) most likely to be used. Despite this variation there is no doubt that larval behaviour can be important in influencing the dispersal patterns of tropical reef fish larvae, although the extent to which this potential is realised is, as yet, unknown. It is quite clear that, as a minimum, larval behaviour will significantly influence settlement patterns and recruitment success in many reef fish taxa. However, behaviour of larvae also has the potential to substantially influence dispersal patterns throughout the pelagic phase. For the first time this thesis has established that larval

behaviour can in fact provide a mechanism for active self-recruitment for many reef fish families. If the full potential of this behaviour is realised, our current understanding of processes influencing connectivity of marine populations will change dramatically.

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Appendix:

Swimming speeds (U-crit) of late stage larvae captured in light traps off Lizard Island, GBR Australia

Late stage larval reef fishes were collected from the leeward side of Lizard Island, Great Barrier Reef, Australia (14o14'S, 145o27'E) over two Austral summer sampling seasons (Nov 2000 to 4 Jan 2001 and 11 Nov 2001 to 26 Dec 2001). Traps were fished over night and were emptied daily every morning. Larvae were retained in opaque buckets until returned to the Lizard Island Research Station where they were placed in the shade with continuously fresh flowing seawater. Larvae from as many species as possible were used for swimming experiments, however, a maximum number of 10 individuals were swum of each individual species. Larvae were readily identifiable to families, and where possible they were also identified to species. Individuals that could not be identified to a known species were identifiable as species 1, species 2 etc. and the allocated species number was recorded.

All larvae were swum at the Lizard Island Research Station within 12 hours of capture, using several different swimming flumes (that had different maximum flow capacities to allow for different sized fishes) that were all similar in design to Stobutzki & Bellwood (1997). Swimming experiments conducted followed the critical swimming speed (U-crit) method developed by Brett (1964). U-crit gives an indication of the maximum sustainable swimming speed of a fish and involves increasing the flow rate against which the fish is swimming in gradual increments. In the present study larvae were subjected to incremental increases in flow rates equivalent to approximately 3 body lengths (BL) every two minutes until they could

no longer maintain position for the full two minutes. The equation used to calculate the critical swimming speed (U-crit) of larvae followed Brett (1964): U-crit = U + (t / ti * Ui), where U is the penultimate speed, Ui is the velocity increment (3 Body Lengths), t is the time swum in the final velocity increment and ti is the set time interval for each velocity increment (2 minutes).

There were clear differences in the maximum swimming abilities of settlement stage reef fish larvae from different families. The fastest swimming family was the Acanthuridae, which could swim on average 61.4 ± 2.6 cms^{-1} (Figure A.1). Other fast swimming families included the Siganidae and Lutjanidae, both of which were able to swim on average at speeds of greater than 50 cms^{-1}. Many of the other reef fish families can swim at considerably fast speeds, with average speeds varying from 30 to 50 cms^{-1}. This includes the Lethrinidae, Pomacentridae, Chaetodontidae and the Nemipteridae (Figure A.1). The remaining families could only sustain speeds of less than 30cms^{-1}, and are therefore considered relatively poor swimming species. This group includes the Monacanthide, Pseudochromidae., Pomacanthidae and Apogonidae (Figure A.1).

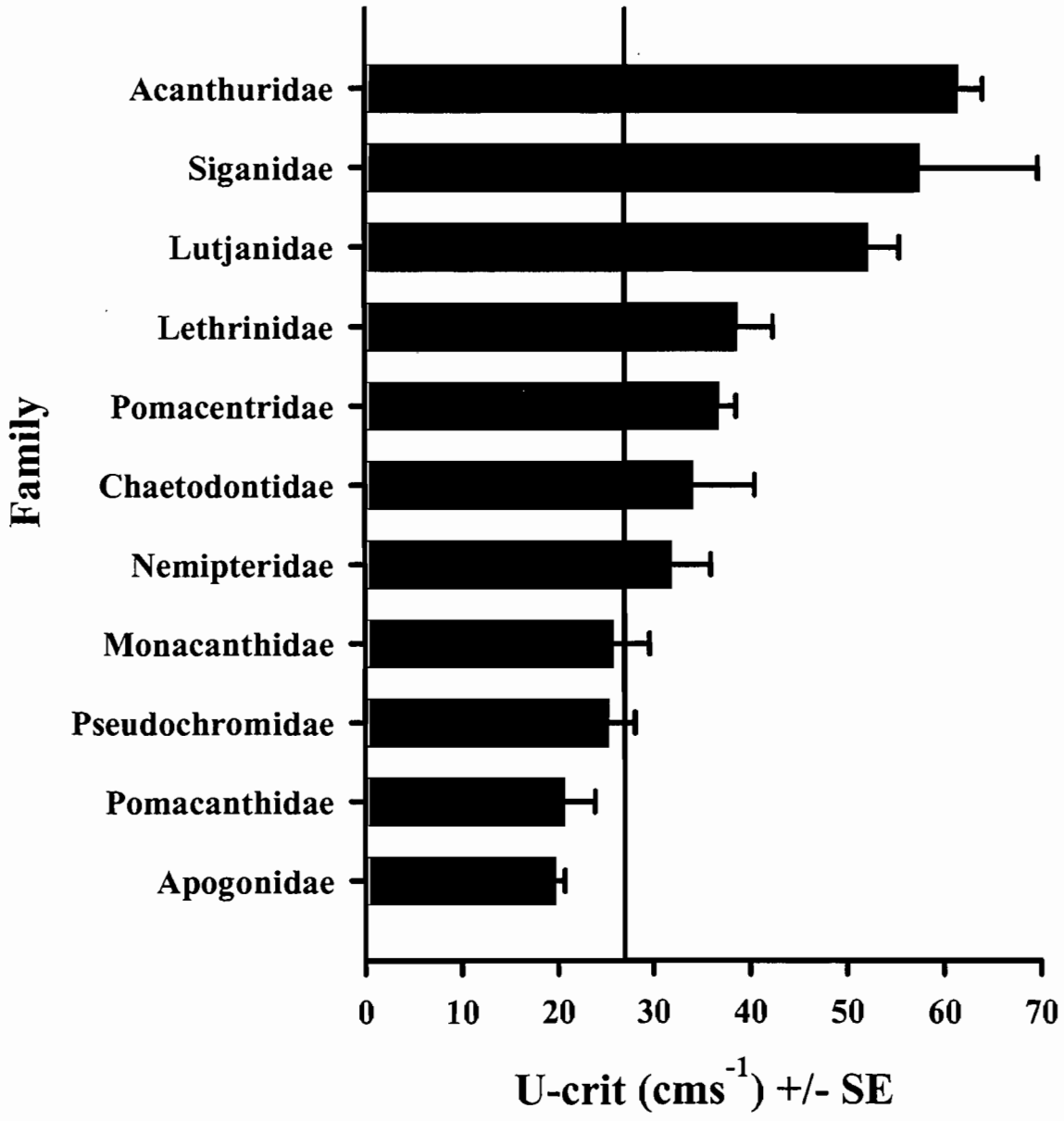

Figure A.1: Average swimming speed (U-crit) in 11 families of reef fish captured in light traps off Lizard Island, Great Barrier Reef Australia. The solid line marks a speed of 27 cms^{-1} (this is the Average U-crit that larvae would need to be able to swim sustain ably at the average current speeds around Lizard Island (13.5 cms^{-1}).