How do swimming ability and behaviour affect the dispersal of coral larvae

V. Pizarro, J.C Thomason[2]

1) Universidad Jorge Tadeo Lozano, Departamento de Biología Marina, Bogotá, Colombia
2) Newcastle University, School of Biology, Newcastle upon Tyne, United Kingdom

Abstract. Most marine larvae have a free-swimming phase before settling. This phase could be important for retention, dispersal, and connectivity. It was thought that coral larvae swimming capabilities were so poor that currents advected them. Nowadays it is accepted that coral larvae have some ability to control their position. This study describes, from laboratory observations, the swimming capabilities and changes in swimming behaviour with age of *Montastraea annularis* and *M. faveolata* larvae, and how these might promote or hinder dispersal. Three larvae from each species were observed and their position, swimming velocity, and behaviour were recorded every five minutes. GLM ANOVA was used to determine the effects of age on velocity and depth. To determine the effect of age on larvae behaviour a binomial logistic regression analysis was performed. The results show the capability of larvae to alternate swimming pattern, velocity and depth which enables them to explore suitable substrata for settlement. This capability can be used to control their position in the water column, and reduce or increase dispersal. Additionally, we found, for the first time 1) swimming velocity and depth varied with age for *M. annularis*; and, 2) the probability of settlement increased with age for both species.

Key words: swimming behaviour, larval age, larval dispersal, *Montastraea*

Introduction

Almost all marine invertebrates have free-swimming larvae (Young et al. 2002). Until recently it was widely assumed that while in the plankton, larvae were advected by currents as passive particles (e.g. Jackson 1986), and that the duration of planktonic larval stages were correlated to the dispersal distance (Strathmann 1985; Shanks et al. 2003a). Nowadays it is known that larvae can swim or change their behaviour avoiding advection (Byers, Pringle 2006). Thus, larvae can disperse further than predicted (Leis, Carson-Ewart 2003), or settle very close to their parents reducing genetic dispersal (Cowen et al. 2006). Swimming ability can also be crucial on searching for a suitable substratum on which to settle (Kingsford et al. 2002). The alteration in swimming behaviour during active searching for settlement sites is often in response to specific cues (e.g. Krug, Zimmer 2000; Baird et al. 2003; Hadfield, Koehl 2004).

Swimming capabilities vary among marine larvae. Reef fishes and decapod crustaceans are capable swimmers, overcoming in some cases local currents (Zeldis 1985; Luckenbach, Orth 1992; Leis, Carson-Ewart 2003). Coral larvae and cyphonautes larvae are examples of poor swimmers (e.g. Abelson 1997; Shanks et al. 2003b; Strathmann, Grünbaum 2006).

Even weak currents move faster than coral larvae (Brooke, Young 2005). However, both capable and poor swimmers can avoid being adversely advected by currents by modifying their behaviour and controlling their position in the water column (Fuchs et al. 2004; Brooke, Young 2005). For coral larvae this behaviour appears to be mediated by the detection of water pressure (Stake, Sammarco 2003).

Larval life histories influence swimming behaviour and later settlement processes. In many cases, larvae can extend their time in the plankton but this has increased associated costs (Pechenik 1990). For lecithotrophic larvae these costs may be depletion of energy reserves and larval senescence (Pechenik 1990). Surprisingly little is known about changes in swimming behaviour as coral larvae age, and how these changes could affect dispersal. Mundy and Babcock (1998) found that five out of six species of coral larvae responded either to light quantity or quality. Additionally, they observed that competent larvae were more positive geotactic than non-competent larvae. In 2005, Brooke and Young reported that the larvae of ahermatypic coral *Oculina varicosa*, when fully developed, swam towards the surface in a spiral fashion.

Larvae of benthic organisms spend most of their time in the water column either searching for food

and/or a suitable substratum on which to settle. Studying the swimming behaviour is important to understand population ecology processes such as settlement, recruitment, and population composition (Mumby 1999). Before we can understand how dispersal is influenced by the swimming behaviour of the invertebrate larvae, is essential to determine the swimming abilities of planktonic larvae throughout the entire larval period. Using coral larvae reared in the laboratory, the aim of this study was to document changes in larval swimming behaviour (categories, velocity and depth) with age, and how these changes could promote or hinder dispersal from parental reefs. We hypothesised that changes in swimming behaviour will occur with age and that these changes would enhance settlement. We studied coral larvae from *Montastraea annularis* and *M. faveolata*, two of the most important reef builder species in the Caribbean.

Material and Methods
Gamete bundles of both *M. annularis* and *M. faveolata* were collected during spawning nights in 2004 and 2005 at San Andres Island (Western Caribbean, Colombia). After spawning, gamete bundles were transported to the laboratory where fertilisation was performed. Cross fertilisation was designed to avoid both self-fertilisation and fertilisation between different species. Self-fertilisation was avoided by separating eggs and sperm after gamete bundles were collected. Egg/sperm were separated using a 60 μm plankton mesh. The eggs were rinsed several times with fresh filtered and 90 °C heated seawater. Fertilisation between different species was avoided by keeping gamete bundles, eggs and sperm from each species in labelled vials. Coral larvae were reared following Pizarro et al. (2006).

When larvae were fully developed (Young et al. 2002) observations on swimming behaviour were performed. Larvae were placed into a cylinder (1 m high x 20 cm diameter) of transparent acrylic (3 mm thick) filled with sterilised seawater (Pizarro et al. 2006). A metric ruler was fitted to the exterior of the cylinder. Three larvae were observed daily, each for one hour, and vertical position (depth), swimming velocity (cm s^{-1}), and the type of swimming behaviour they were performing. These data were recorded every five minutes. Swimming categories were named after the movement the larvae performed (table 1).

To determine the effects of the age of the larvae on the swimming velocity and swimming depth, a separate repeated measures GLM ANOVA was conducted for each response variable. Because the response data were not normally distributed and not transformable a value of α = 0.001 was taken as the

level of significance (Underwood 1997). In both cases the data were not spherical, therefore Greenhouse-Geiser adjusted F values were used. For both analyses the within subject factor was age and the response was either velocity or depth.

To examine the effect of age on the behaviour of the larvae a binomial logistic regression analysis was used to predict the probability of settlement behaviour as a function of larval age. All upward swimming categories were associated with transport behaviour, while all downward swimming categories were associated with settlement behaviour. For the remaining swimming categories transport behaviour and settlement behaviour were determined by a combination of the observed swimming category of the larvae and the depth at which the swimming category was taking place. For example, horizontal swimming in the first 10 cm of the water column was recorded as transport behaviour, whereas, if it occurred any deeper it was recorded as settlement behaviour.

Results
Twelve different swimming categories were identified for *Montastraea faveolata* larvae, and eleven of the twelve were observed for *M. annularis* larvae (Table 1). The frequency varied within categories and between species (Table 1). While for *M. annularis* the most frequent category was swimming down (28.6 %), for *M. faveolata* it was snake swimming (38.91 %).

Table 1. Name and frequency (percentage of the total number of observations) for swimming and settlement behaviour (percentage for each swimming category) of the swimming categories identified for *Montastraea annularis* (*Mann*; n = 1287) and *M. faveolata* (*Mfav*; n = 897) larvae.

Swimming category	Swimming (%)		Settlement (%)	
	Mann	*Mfav*	*Mann*	*Mfav*
Circles	0.00	2.12	0.00	36.84
Up	23.62	9.92	0.00	0.00
Spiral – up	0.31	2.23	0.00	0.00
Spiral	10.18	0.78	1.54	28.57
Horizontal	1.17	1.00	40.00	55.57
Snake	10.26	38.91[a]	0.77	0.00
Spiral – up & down	0.23	0.33	53.33	33.33
Still	22.22	11.04	3.31	25.25
Up and down	0.39	5.24	60.00	62.16
Spiral – down	0.78	3.57	100.00	100.00
Down	28.59[a]	12.26	100.00	100.00
Exploring	2.25	12.60	100.00	100.00

[a] denotes the most frequent swimming category for each species

The frequency of each swimming category did not vary with the larvae age (Fig. 1). However the most commonly observed categories appeared to have a periodicity in both species (e. g. see first panel in Fig. 1 – swimming up category). Nevertheless, the snake swimming category for *M. annularis* was the only one

that seemed to change considerably with the age of the larvae (Fig. 1). For this particular category, the frequency increased with the age of the larvae until day 9, after which it was rarely observed.
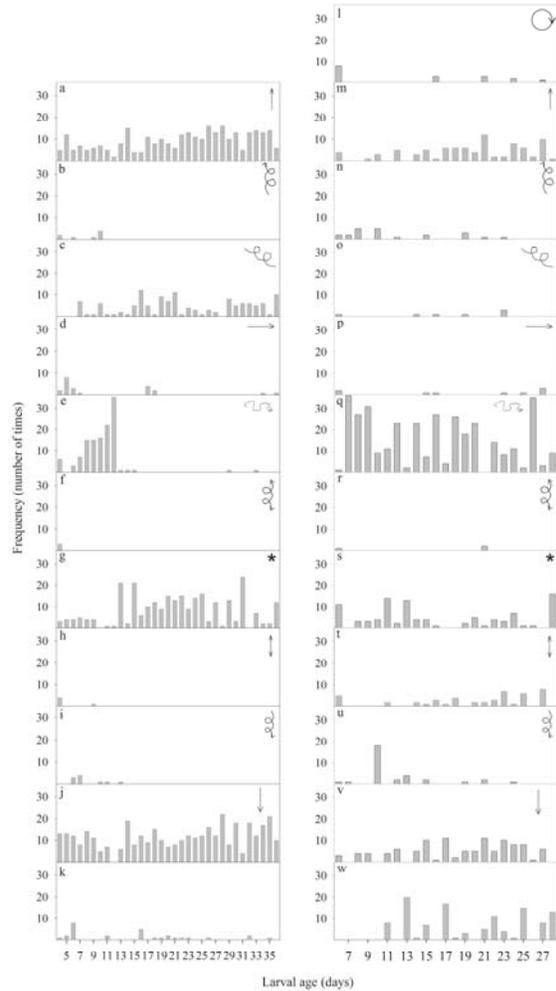

Figure 1. Frequency of each swimming category as a function of the age of the larvae for *Montrastraea annularis* (a-k) and *M. faveolata* (l-w). Pictograms identify behavioural category and are arranged in the same order as in Table 1.

Recorded swimming velocities (cm s^{-1}) for *M. annularis* were 0.01-1.4 and, 0.01-1.6 for *M. faveolata*. For *M. annularis* larvae swimming velocity and depth varied with age (repeated measures GLM SS$_{vel}$ = 2.35; df$_{vel}$ = 10.74; F$_{vel}$ = 6.44; P$_{vel}$ < 0.001; SS$_{depth}$ = 158892.15; df$_{depth}$ = 9.63; F$_{depth}$ = 7.82; P$_{depth}$ < 0.001). The larvae started to explore the water column from the first day they were fully developed. A plot of mean depth vs. day indicated that there was a periodicity in the variation of depth. Simple time series analysis using moving averages of between 2 – 4 d suggested that this periodicity was ~ 3 d (Fig. 2 a-c).

Swimming velocities of *M. faveolata* larvae did not change with age (repeated measures GLM SS = 7.30; df = 1.178; F = 2.00; P = 0.162), however depth of the larvae behaviour did change with age (repeated measures GLM SS = 488857.45; df = 5.126; F = 26.32; P < 0.001). 1 d to 5 d old larvae remained mostly at the surface and larvae between 6 d and 23 d old moved from the surface to deeper in the water column. A periodicity in the variation of the depth of ~ 3 d (Fig. 2 d-e) was also found for this species when applying a simple time series analysis.
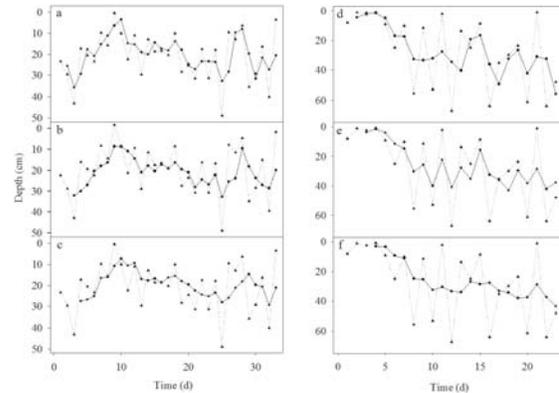

Figure 2. Mean depth of *Montastraea annularis* (a-c) and *M. faveolata* (d-f) larvae as a function of time (dotted line; *M. annularis* n= 33 and *M. faveolata* n= 23), and results of the moving averages for time series analysis (continuous line) for two (a, d), three (b, e) and four (c, f) days. Periodicity was determined by peak coincidence rather than amplitude

The probability of occurrence of settlement behaviour when compared to transport behaviour was 1.01 and 1.09 times higher with each day's increase in age for *M. annularis* and *M. faveolata* respectively (*M. annularis*: P$_{settlement\ behaviour}$ = $1/(1 + e^{-(-0.26 + 0.11\ Age)})$, Odds ratio = 1.02, P < 0.001, Log-likelihood = G = 11.38, DF = 1, P < 0.001; *M. faveolata:* P$_{settlement\ behaviour}$ = $1/(1 + e^{-(-1.31 + 0.15\ Age)})$, Odds ratio = 1.09, P < 0.001, Log-likelihood = G = 62.83, DF = 1, P < 0.001).

Discussion
This study shows for the first time that coral larvae have a range of different swimming behaviours and that 1) swimming velocity and depth of the larvae of *M. annularis* varied with age; and, 2) the probability of settlement-linked behaviour increased with age for both *M. annularis* and *M. faveolata*. The role of different swimming behaviours in pre-settlement processes of corals has only been studied somewhat superficially (e.g. Carlon, Olson 1993; Raimondi, Morse 2000). Furthermore, swimming behaviour and the relationship to transport and settlement have not been previously recognised (e.g. Morse et al. 1988;

Gross et al. 1992; Abelson 1997; Krug, Zimmer 2000; Raimondi, Morse 2000; Miller, Mundy 2003). It is common knowledge that most coral larvae are active swimmers (see Harrison, Wallace 1990). This study has clearly shown the capability of larvae to vary swimming pattern, velocity and depth which then enables them to explore suitable substrata for settlement. This capability is also likely to contribute to dispersal away from natal reefs by controlling their position in the water column (see Harrison, Wallace 1990), and may determine adult distributions on reefs (Raimondi, Morse 2000).

At least four (spiral, snake, still and circles) of the 12 swimming categories described in this study could be considered as contributors to the dispersal of larvae in coastal waters (Porch 1998). This suggests that the remaining categories of *Montastraea* spp. larvae (spiral up, spiral down, spiral up and down, down, and up and down) could be important for retention of larvae within natal reefs (Codling et al. 2004). In contrast, if larvae enter oceanic waters, then active swimming could play a role in maintaining depth to ensure maximum dispersal. Such modification of swimming behaviour has been associated with the capacity to control a vertical position in the water column, rather than as a dispersal factor (Raimondi, Morse 2000; Bassim, Sammarco 2003; Krug, Zimmer 2004). In this regard, the observations on the frequency of the swimming categories as a function of time for each species suggest that 1) *M. annularis* larvae would control their vertical position most of the time; and, 2) *M. faveolata* would be affected the most by superficial currents. To determine whether the swimming categories of both *M. annularis* and *M. faveolata* larvae are important in maintaining position in the water column near their natal reefs or in the ocean waters to be dispersed, it is necessary to develop local hydrodynamic models (Mumby 1999). These models would predict if embryos and pre-competent larvae are retained within the natal reefs or carried away from them. However, if larval development and swimming patterns in natural environments are similar to those observed in this study, it is feasible that both self-recruitment and dispersal occur (Sammarco 1996).

The changes in depth with age for both *Montastraea annularis* and *M. faveolata* could be an indication of an increased necessity to search for a suitable substratum on which to settle. These findings are similar to those described by Vermeij et al. (2006) for *M. faveolata*. In their study larval behaviour changed from phototactic to geotactic with age, however, they assessed the vertical movement of the larvae only in standard Petri dishes ($\varnothing$ 9 cm) with approximately 1.5 cm depth. For some other invertebrates, larval distribution in the water column

varies according to the larval development stage (Thiébaut et al. 1998; Krug, Zimmer 2004). Krug (2004) observed that swimming speed in trochophore larvae increased as they developed. Of interest is the periodicity in depth observed for both *Montastraea* species, suggesting a vertical migration in the water column. As a non-feeding larvae (Vermeij et al. 2006), this migration would not be related with/to the daily vertical feeding migration observed in plankton (Pearre 2003). Vermeij et al. (2006) also observed a vertical migration in *M. faveolata* larvae. The migration seemed to be a daily light/life cycle with higher movement at night. Nevertheless, their results have to be carefully analysed due to the use of shallow Petri dishes. Indeed, Marta-Almeida et al. (2006) demonstrated that larvae that do not show diel vertical migrations were affected by currents and upwelling leading to offshore transport. We propose that in *Montastraea* spp. vertical migration is a strategy to enhance both detection of suitable substrata for settlement and also increases the dispersal away from unsuitable substrata (Krug, Zimmer 2004; Ríos-Jara 2005; Marta-Almeida et al. 2006).

In lecithotrophic or non-feeding larvae, energy reserves decrease with larval age (Wendt 1996). For lecithotrophic gregarious organisms a desperate larva hypothesis was proposed in the 50s (Knight-Jones (1951, 1953) and Wilson (1953) reviewed in (Toonen, Pawlik 2001)). This hypothesis states that larvae become less discriminatory in their settlement choice when energetic resources decrease and occurs mostly in gregarious organisms, such as bryozoans and ascidians (e.g. Wendt 1996; Marshall, Keough 2003), and in some non-gregarious gastropods (e.g. Botello, Krug 2006). In all these cases larval metamorphosis decreased with time, and even when larvae could respond to cues and initiate metamorphosis older larvae were unable to complete (e.g. Wendt 1996; Toonen, Pawlik 2001; Marshall, Keough 2003; Botello, Krug 2006). This decrease in energy may influence coral larvae velocity and swimming patterns ultimately affecting population dynamics. The observed changes in swimming velocity and swimming patterns with larvae age in this study suggest that the 'desperate larvae' hypothesis could be applicable to both *M. annularis* and *M. faveolata* species. The results suggest that larvae differing in ontogeny can display different behaviours that could affect potential dispersal. Further studies on larval swimming behaviour would help to elucidate the role of these activities on larval retention and dispersal, as well as the importance for population dynamics.

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