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RESEARCH ARTICLE

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Experimental analysis of the contribution of swimming and drifting to the displacement of reef fish larvae

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Abstract The extent to which behaviour affects the dispersal of pelagic larvae in reef fishes has been a topic of major discussion among marine ecologists. Here, we experimentally quantified the extent to which the displacement of late-stage larvae of *Abudefduf saxatilis* is due to active movement (i.e. swimming) and drifting. We consider drifting as the component of larval displacement accounted for by the current. Drifting was quantified by comparing larval displacement to the displacement of passive particles in an extended flow chamber that gave larvae the free choice of swimming (i.e. swim with or against the current or not swim at all). We also determine whether drifting results from currents exceeding larval swimming capabilities or from the behavioural choice of larvae of not to swim against adverse currents. To do this, we compare the speeds of larval swimming in the extended flow chamber to those obtained in a smaller chamber in which larvae are behaviourally forced to swim due to space constraints and a retaining fence (most available data on larval swimming is based on this sort of chamber). Within the extended chamber, larvae tended to face the current and swim slower than it. This resulted in a net displacement increasingly determined by drifting. We also found that in the extended chamber, larvae swam at speeds between one and six times slower than the speeds they achieved in the "behaviourally modifying" smaller chamber. This suggests that the net displacement in the extended chamber was in part due to the behavioural choice of the larvae of not to swim. The importance of this "behavioural drifting" is discussed in terms of energy savings required for successful completion of the larval period and post-settlement survival. The idea that larvae may modulate their swimming behaviour raises caution for the use of published data regarding swimming capabilities of reef fish larvae when assessing the extent to which these fish actively affect their dispersal.

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Introduction

Dispersal is a key process in several aspects of the biology and conservation of marine species, such as reef fishes and other benthic organisms with pelagic larvae (Roberts 1997; Shulman 1998; Underwood and Keough 2001; Mora and Sale 2002; Planes 2002; Mora et al. 2003). However, studying dispersal in reef fishes has been challenging mainly because of technical difficulties associated with tracking small and behaviourally active propagules in vast expanses of water and the limited precision of alternative indirect approaches for tackling this process (reviewed by Leis 2002; Mora and Sale 2002).

Traditionally, there was a prevailing assumption among coral reef fish ecologists that larval dispersal was passively mediated by hydrodynamic processes (Sale 1970; Leis and Miller 1976; Roberts 1997). However, the recent recognition of behavioural and physiological capabilities of reef fish larvae has led to the belief that larvae are active in the pelagic environment and possibly capable of directing their own dispersal (reviewed in Kingsford et al. 2002; Leis 2002). Specifically, recent evidence shows that reef fish larvae are quite capable swimmers in terms of both speed and endurance (Stobutzki and Bellwood 1994; Leis and Carson-Ewart 1997; Stobutzki and Bellwood 1997; Stobutzki 1998; Bellwood and Fisher 2001) and can detect aural (Tolimieri et al. 2000; Leis et al. 2002) and olfactory (Atema et al. 2002) cues, both of which could be used for orientation. The realisation that larvae can propel themselves and possibly orient themselves in the pelagic environment has led to the idea that the larvae of reef fishes can navigate. Such an idea has profoundly affected our assessment of how reef fish pop-

ulations are regulated (the open-closed population paradigm, see Warner and Cowen 2002, and associated papers, Leis 2002; Mora and Sale 2002). The possibility of larval navigation has led to a reassessment of how hydrodynamic processes affect larval dispersal (cf. Roberts 1998; Sale and Cowen 1998; Bellwood et al. 1998), how dispersal should be mathematically modelled (Wolanski et al. 1997; Armsworth et al. 2001) and how marine reserves should be designed (Stobutzki 2000). Strong genetic differentiation found among populations has also been attributed to navigational capabilities of larvae allowing them to return to their natal reefs (Taylor and Hellberg 2003). However, the extent of navigational capabilities and their use for dispersal purposes is poorly understood, and a subject of some interest in marine ecology (e.g. Roberts 1998; Colin 2003; Warner and Palumbi 2003), which highlights the need for detailed studies about larval navigation in reef fishes.

Effective larval navigation requires several physiological and behavioural attributes. Physiologically it requires the ability to detect and swim towards a reef while behaviourally it requires the larvae to "decide" to actively move to that reef (Mora and Sale 2002). Current knowledge suggests that larvae can detect reefs and have the swimming capabilities to reach them (see above), however, little is known about the behavioural component to navigation (but see Fisher and Bellwood 2003). The behavioural decision of reef fish larvae to swim is critically important because this is what determines the importance of the swimming ability itself (i.e. whether it is used for dispersal or not). At present, experimental trials intended to determine the swimming capabilities of reef fish larvae have been particularly important in putting an upper bound to the possible swimming performance of reef fish larvae. However, the behavioural link to this performance (or in our words the behavioural "decision" of larvae to use these capabilities) is missing because in these experiments larvae have been forced to swim (by using small chambers with retaining fences; e.g. Stobutzki and Bellwood 1994, 1997; Stobutzki 1998) and because species that refuse to swim in these chambers have often been excluded from analyses (Leis and Stobutzki 1999). Some important attempts have been made to follow larval and post-larval reef fishes in the field but the conclusions drawn from these studies are limited by the short duration of such observations (5–10 min) and by the fact that behaviours might be affected by the presence of divers (Leis and Carson-Ewart 1997; Leis and Stobutzki 1999; Hindell et al. 2003). This paper is intended to experimentally assess this behavioural component of swimming to larval displacement.

Larval displacement in the pelagic environment results from the interaction between hydrodynamics and the "navigational skills" of a larva. In the absence of active movement, hydrodynamics can contribute to displacement in the form of drifting. Drifting can be a component of larval displacement if water currents exceed the swimming capabilities of larvae and/or if larvae "decide" not to swim. This paper is intended to experimentally assess the contribution of swimming and drifting to the displacement of reef fish larvae. Here we used late-stage larvae of the Sergeant major, *Abudefduf saxatilis*, as our focal species. We first quantified the displacement of larvae in an extended flow chamber that reduced space constraints and gave larvae the behavioural freedom of movement (i.e. swim forwards, backwards, hold position or not swim at all). The contribution of swimming and drifting to this displacement was quantified by comparing the displacement observed in the larvae with that expected from passive particles. Similarities in displacement between the larvae and that expected from passive particles will indicate the existence of drifting while differences will indicate the contribution of swimming. To assess the causes of drifting, we compared the swimming speeds observed in this extended chamber with the speeds achieved in a traditional chamber, which forces larvae to swim due to space limitations and a retaining fence. We expect the latter chamber to indicate the full extent of the swimming capabilities of the larvae while the former to indicate voluntary swimming speeds. Thus, the comparison of swimming speeds between these chambers will indicate the extent to which larvae are voluntarily using their swimming capabilities, and to what extent larval displacement is influenced by the current.

There have been many studies focussing on the physiology of swimming in fishes (reviewed by Webb 1993). The energetics of swimming in temperate fishes is well understood, and how this pertains to migrations has been investigated (see Dodson 1997). However, the capabilities of temperate fishes are not necessarily the same as those of coral reef fishes (Leis and Stobutzki 1999). Besides phylogenetic differences between the two groups, most coral reef fishes have fully developed fins at a smaller size than temperate taxa (Leis and Carson-Ewart 1997). Studies of swimming, and energetics of movement in tropical reef fishes are fewer and knowledge in this field is less comprehensive (Leis and McCormick 2002).

Materials and methods

Species analysed and collection of specimens

We focus our study on the late-stage larvae of *A. saxatilis* (Pomacentridae). This species was chosen because it was the most abundant larval fish species at our study site. This species is commonly found throughout the Caribbean inhabiting shallow fore and back reefs (Humann and Deloach 2002). As larvae, *A. saxatilis* spends on average 18.2 days (±1.1 SD) in the plankton (Wellington and Victor 1989). In this study, larvae were defined following Leis and Stobutzki (1999) as any reef fish that was still in the pelagic phase of life. Larval fish were collected and tested at the Institute for Marine Studies Research Station at Calabash Caye, in Turneffe Atoll,

Belize (17°16.4′N, 87°48.7′W). Late-stage larvae of *A. saxatilis* were collected from fish attracting devices (FADs) using hand nets. A FAD consists of a black plastic hose joined together to form a cylindrical frame, which is covered in a black plastic mesh (4 cm mesh size). The FADs were placed at the end of the dock of the research station and were quickly colonised by late-stage larvae of this species. We used fish of the smallest size class present in our collections, and chose individuals within a similar range of body sizes (mean ± 1SD total length = 1.58 ± 0.24 cm) to avoid individuals that delayed their settlement, or had settled some time ago, and to reduce variations in swimming performance related to development. All specimens were collected in the morning and were held in fresh seawater with an aeration stone in a 24 L black plastic bucket for at least 4 h before trials. This allowed us to test fish right after collection and reduce stress associated with captivity (Pankhurst and Sharples 1992).

Laboratory water system

Water to feed the two different chambers was provided through a unique water delivery system. Water was pumped directly from the ocean (via a 0.55 kw waterfall pump, Cal Pump model PW5000) through PVC pipe (diameter = 3.3 cm) to a head of 3.8 m. At the head, a U-joint returned water to the ocean. This allowed a constant water pressure at the base of the pipe where the chambers were joined to the system with a T-joint.

Contribution of swimming and drifting to larval displacement

The displacement of larvae was quantified in an extended swimming chamber, which reduces space constraints and gives larvae the freedom of swimming (i.e. swim forwards, backwards, hold position or not swim at all). This 280-cm-long chamber was constructed from white plastic eaves trough (see Fig. 1 for more details). Two identical sections of flow straighteners (each 10-cm long) were placed directly in front of the water inflow in order to reduce the turbulence of the flow throughout the chamber. The top of the inflow/flow-straightener section of the chamber was covered with clear plastic (further reducing the turbulence of the water entering the swimming area) and sealed with silicone adhesive. The swimming area of the chamber was left uncovered. Although we did not calculate the boundary layers of the extended chamber, we observed that fish tended to swim in the middle of the chamber, and did not seem able to take advantage of the boundary layers as they commonly drifted with the currents (see Fig. 3c). We conducted some gross profiling of water flow within the chamber using passive neutral particles and found no eddy formation along the swimming area. Different flow rates within the chamber were attained by the use of a multi-turn gate valve at the inflow and a plastic gate at the outflow of the chamber (Fig. 1). Both the valve and the gate were adjusted accordingly to attain the desired current speeds. Water speed was calculated by dividing the

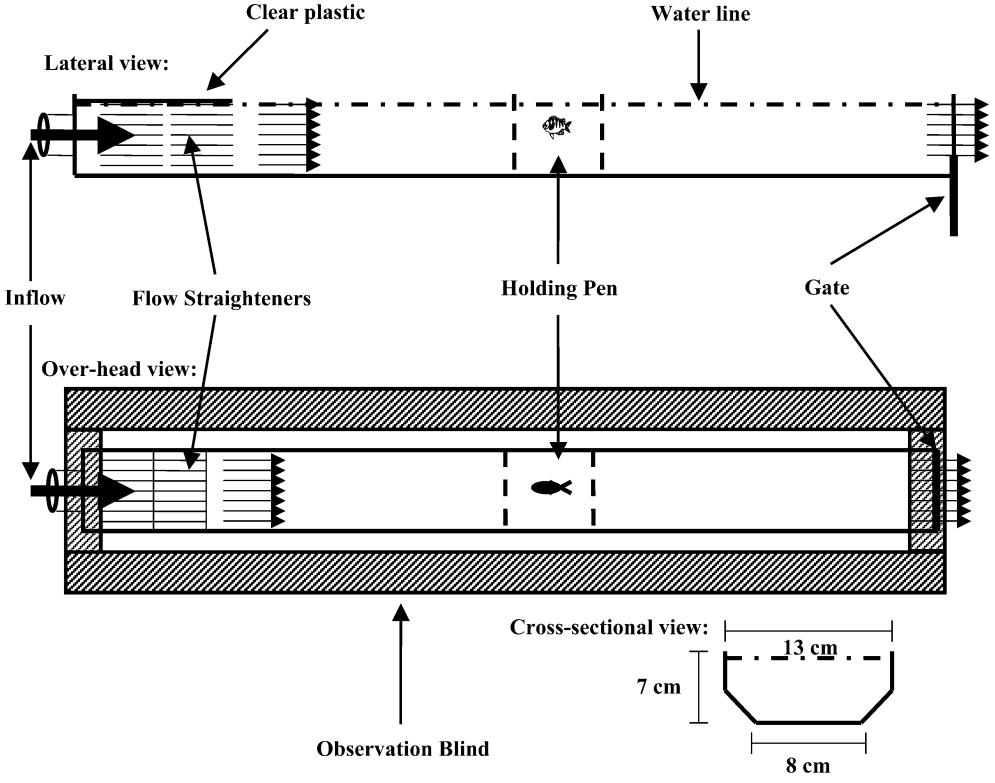


Fig. 1 Schematic representations of the lateral, over-head and cross-sectional views of the extended swimming chamber. Diagram not to scale. See text for description

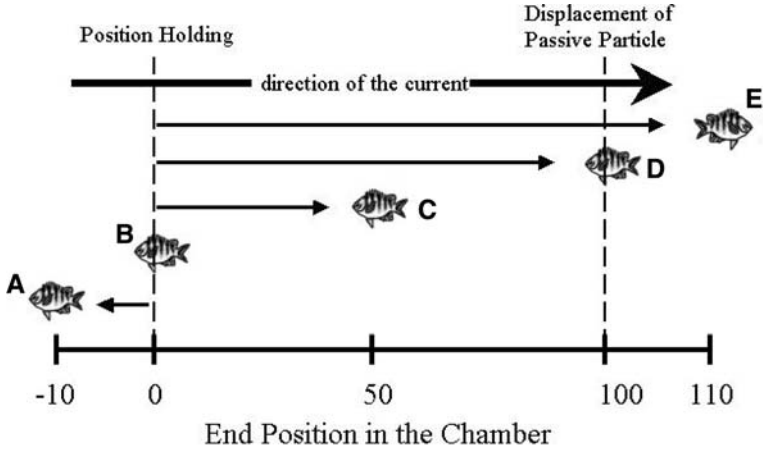
volume of water flowing over the outflow gate in a unit time by the cross-sectional area of the chamber. A 60 cm high wooden observation blind covered in black plastic sheet was placed over top of the chamber forming walls on all sides (Fig. 1) to minimise observer disturbance. The observation blind reduced external visual cues that could be used for orientation. A tape measure was placed along the outer edge of the wall to allow observers to measure larval position along the length of the chamber.

Once the chamber was set, individual larvae were introduced into a mesh holding pen located in the middle of the swimming area (Fig. 1) and allowed to acclimatise for 5 min at a current speed of 5 cm s^{-1}. Acclimatisation at 5 cm s^{-1} was used to reduce the stress of the following exercise trial and to reduce the effects of disorientation associated with a sudden exposure to a current. The speed of the water was then adjusted accordingly to one of five experimental speeds: 5, 10, 20, 30 and 40 cm s^{-1}. These speeds were chosen to simulate the range of current regimes that could be experienced by a larva in the pelagic environment. Once the acclimatisation period was over, the holding pen was removed and the start and end positions of the larva were recorded at time intervals corresponding to the amount of time it would take a passive, neutral particle to travel 100 cm at each current speed (i.e. every 20 s at 5 cm s^{-1}; 10 s at 10 cm s^{-1}; 5 s at 20 cm s^{-1}; 3.3 s at 30 cm s^{-1}; 2.5 s at 40 cm s^{-1}). A trial ended after either the larva swam to the front of the chamber (0 cm), or to the rear of the chamber (280 cm), or after seven time intervals had elapsed.

For each time interval in a trial, the difference between the start and end position of the larva in the chamber was taken as its displacement. The net displacement of that larva at that particular current speed was the average displacement for all time intervals of the trial. In comparison to the passive particle, a larval net displacement of 100 cm is equivalent to total passive drift. Negative values of net displacement indicate that swimming was forward into the current and that the larva swam faster than the water current (Fig. 2). Positive values between 0 and 100 indicate that the larva faced the current but was pushed backwards by it (Fig. 2). Positive values larger than 100 indicate that the larva swam in the same direction as the current (Fig. 2).

The specific contributions of swimming (active movement) and drifting to the net displacement were quantified independently for each larva. We considered active movement as the amount of net displacement not due to the movement induced by the current (Fig. 2). This was calculated as:

$$\text{Active movement} = |\text{Net displacement of the larva} - \text{Displacement of the passive particle}|$$



	A	B	C	D	E
Displacement	-10	0	50	100	110
Active Movement	110	100	50	0	10
Passive Movement	0	0	50	100	100
Swimming Speed	110 / t	100 / t	50 / t	0 / t	10 / t

Fig. 2 Possible behavioural responses of fish larvae in the swimming chamber and the respective values corresponding to each of the four variables measured in this study. The end position of each larva was recorded after a time interval equal to the time required for a passive particle to travel 100 cm at that current speed. As a case example, larva "A" ended 10 cm ahead of the starting position. Its displacement was −10 (negative sign indicates that it swum forwards and faster than current). The active swimming value of this larva was the 100 cm it swam to overcome the current plus the 10 cm it displaced forwards thus totaling 110. Although water current reduced the absolute displacement of the larva from its starting position, in this case, it did not contribute directly to the displacement. Therefore, drifting (or the contribution of water current to displacement) was zero. Swimming speed for this larva was calculated by dividing the distance it traveled actively by the length of the time trial. Similar examples are given for when larvae ended behind the releasing point (larvae B to E)

Drift was considered as the contribution of water current to the net displacement of the larva (Fig. 2) and was quantified as:

Drift = Displacement of the passive particle
– Active movement.

Drift was quantified only in larvae with positive values of net displacement (i.e. that ended downstream of the releasing point; Fig. 2). Any larva with negative net displacement (i.e. that ended upstream of the releasing point) did not experience any drift. In these cases, drift values were recorded as zero. In any case where the net displacement of the larva exceeded 100 cm, a value of 100 cm of drift was assigned since in those cases drifting would have contributed maximally to larval displacement. In almost all cases, larval displacement in this chamber was less than 100 cm (see Fig. 3a) therefore, values of drifting commonly varied between zero (i.e. swimming speed was stronger than or equal to the current speed) and 100 cm (not swimming at all). We used one-way ANOVAs to test for variations in net displacement, active movement and drifting among current speeds.

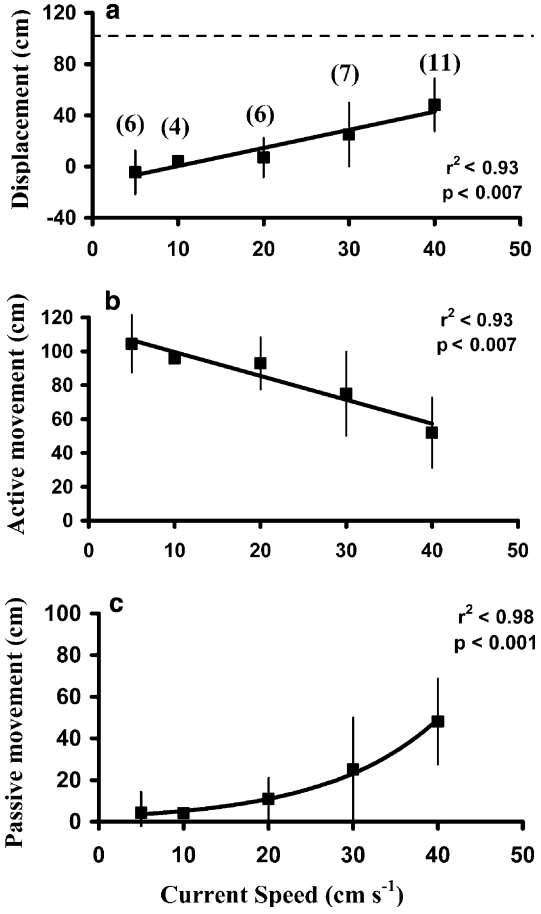


Fig. 3 Variations in larval displacement at different current speeds (**a**) and how that displacement is accounted for by active swimming (**b**) and drifting (**c**). In the plot (**a**), the dashed line represents the displacement of a passive particle for the duration of one time interval. Numbers in brackets indicate sample size. All values expressed as mean (±1SD). Trend lines were fit to mean values

Causes of drifting

Larval displacement due to the effect of the current (i.e. drifting) can result from the water flow exceeding the swimming capabilities of the larvae and/or if larvae decide not to swim despite being capable of doing so. To assess these possibilities, we compared the swimming speeds observed in the extended chamber (speeds voluntarily selected) with the set of speeds achievable for this species when forced to swim. Larval speeds in the extended chamber were calculated by dividing the amount of active movement in a trial by the length of that trial (Fig. 2). Here we quantified achievable swimming speeds as U_{crit} using a smaller chamber similar to that originally designed by Stobutzki and Bellwood (1994).

The single lane flow chamber has a swimming area with internal dimensions of 18.5 cm in length and 5.0 cm for both width and height. The fish are restricted to the swimming area by the use of metal retaining fences on the inflow and outflow ends. Water flow into the chamber was regulated with a multi-turn gate valve and water velocity was controlled with a second multi-turn gate valve exiting the chamber. The second gate valve was calibrated, based on the number of turns, to provide different current speeds within the chamber. Current speeds were calculated by dividing the volume of water that passed through the chamber in a unit time by the cross-sectional area of the swimming area. The maximum water velocity achieved by this system was 60 cm.s^{-1}. In the smaller chamber used to measure U_{crit}, the size of the boundary layer was calculated to be 4 mm in size along all sides at a current speed of 32 cm s^{-1}. This value was less than 10% of the total volume of the swimming area and was very small compared to the size of the fish used.

Individual fish were introduced into the chamber at a current speed of 2 cm s^{-1} and allowed to acclimate for 10 min. Current speed was then increased incrementally by three body lengths per second (where body length is the total length of the individual), at intervals of 2 min, until the larva could no longer maintain position in front of the metal retaining fence. U_{crit} swimming speed was calculated following Brett (1964) where:

$$U_{\text{crit}} = U + \frac{t}{t_i \times U_i}.$$

U is the penultimate speed, U_i is the velocity increment, t is the time swum in the final velocity increment and t_i is the time interval for each increment.

Results

All the behavioural responses measured in the extended chamber showed strong trends with current speed (Fig-

s. 3a, b, c and 4) and showed significant differences among current speeds (Displacement: $F = 9.79$, $P < 0.00004$; active swimming $F = 9.79$, $P < 0.00004$; passive movement: $F = 9.13$, $P < 0.00007$; swimming speed: $F = 9.72$, $P < 0.00004$; $n = 34$ larvae for all tests). Overall, larval displacement was positive and increased with current speeds (Fig. 3a), meaning that fish ended downstream of their starting position. Only at a current speed of 5 cm s^{-1} did larvae tend to overcome the current, and finish upstream of their starting position. The contribution of active movement to net displacement tended to decrease with increasing current speed (Fig. 3b) while the contribution of drifting increased exponentially with current speed (Fig. 3c). During the behavioural trials, larvae were observed swimming in the centre of the chamber. General swimming direction was more variable at the slowest current speed (5 cm s^{-1}) but in general larvae faced the current, did not exhibit erratic swimming bursts at any current speed, and most drifted backwards with the current particularly as current speeds increased (Fig. 3c).

Within the extended chamber, there was a fourfold variation in larval speeds among currents. Larval swimming speed tended to increase proportionally at each successive current speed until ~20 cm s^{-1} at which point swimming speeds tended to remain constant despite any further increases in current speed (Fig. 4). In the extended chamber, the minimum and maximum mean swimming speeds were 5.22 cm s^{-1} and 22.5 cm s^{-1} respectively, while fish in the smaller chamber achieved faster swimming speeds (mean U_{crit} = 31.8 cm s^{-1}, SD = ±11.0 cm s^{-1}, $n = 7$, maximum = 59.5 cm s^{-1}) (Fig. 4). No individual larva in the extended chamber achieved a swimming speed greater than the mean U_{crit} value for this species.

Discussion

Experimental studies have been critical in advancing our understanding of ecological processes that would otherwise be impossible to assess under complex natural conditions. However, in extrapolating experimental data to natural conditions, it is also important to be aware of potential biases. In our study, we are conscious of two possible limitations that could have affected our results. We observed that almost all larvae faced the oncoming current and that their swimming speed mimicked slower current speeds. This indicates larval awareness of the hydrodynamic environment that they are in. This was very likely achieved through the use of visual, tactile or mechanosensory references within the chamber that inform larvae of their displacement by the water flow. Such references are likely absent in the open water (unless larvae have capabilities permitting long-distance detection of reefs; note that the longest distance larvae have been shown able to orient towards reefs is 1 km; Leis et al. 2002). The fact that larvae drifted in our chamber despite the presence of such visual references suggests that our estimates of drifting are conservative and that drifting may be more extensive in natural conditions where visual and/or other orientation cues are likely to be absent. The second limitation to address is the possibility of non-laminar water flow in our chamber. Turbulence is an important limitation influencing the results of all experimental studies on swimming ability and behaviour. Although this bias is difficult to control, we attempted to reduce the turbulence of the flow by adding two sections of flow straighteners. In spite of this potential bias, we observed some larvae, when trials were over, holding position at the outflow gate of the chamber. This suggests that larvae were capable of swimming faster than the current despite any effect of turbulence and the fact that they did not do so in experimental trials suggests that they voluntarily drifted during those trials.

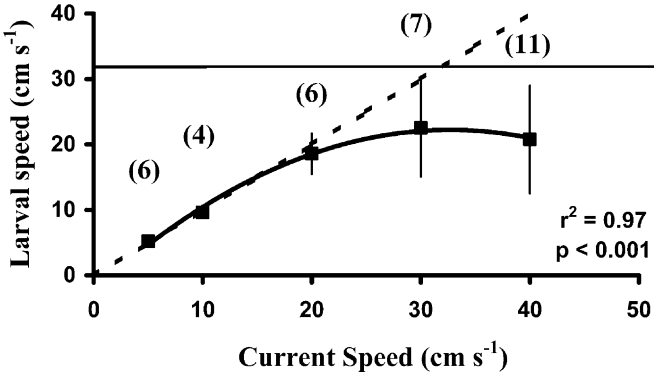


Fig. 4 The relationship between current speed and voluntary swimming speed. The solid horizontal line represents the mean U_{crit} for *Abudefduf saxatilis*, and the dashed line represents the one to one ratio. All values expressed as mean (±1SD). The trend line was fit to mean values. Sample sizes in brackets

The relative contribution of drifting and swimming to the net displacement of larvae in the plankton has been a topic of debate in the recent reef fish literature (cf. Roberts 1998 vs Sale and Cowen 1998; Bellwood et al. 1998 and Taylor and Hellberg 2003 vs Colin 2003) but it certainly remains as one of the current challenges to reef fish ecologists. Our experimental approach showed that net downstream displacement of late-stage larvae of *A. saxatilis* tended to increase as the current speed in the chamber increased (Fig. 3a). Since active movement tended to decrease with current speed (Fig. 3b) and larval swimming speeds stayed relatively constant beyond moderate currents (Fig. 4), the increase in net displacement with current speeds was better explained by drifting (Fig. 3c). However, drifting itself can be caused by (1) current speeds exceeding the capabilities of the larvae and/or (2) the larva exercising behavioural control over its swimming speed. Here, we found that in the extended chamber, larvae swum at speeds between one and six times slower than those they achieved in the smaller swimming chamber. This suggests that when the behavioural choice is given to larvae they do not use the entire potential of their swimming capabilities. This result certainly raises caution for the use of published

swimming capabilities of reef fish larvae to model the patterns of larval dispersal. Interestingly enough, drifting increased rapidly with incremental increases in current speed (Fig. 3c). This is very likely due to the combination of behavioural drifting, observed at almost all speeds, and the effect of high-speed currents exceeding larval capabilities (Fig. 4). Although it is difficult to determine whether behavioural choices in the laboratory will reflect those made in the field, the decision to drift rather than resist the current is a feasible option particularly in terms of energy saving.

Energy resources allocated to swimming will have major impacts on metabolic resource bases, net energy gain from foraging, and reserves required for migrations (Webb 1993). In reef fish, energy reserves are necessary for successful settlement (McCormick 1998) and post-recruitment survival (Bergenius et al. 2002). We also know that sustained swimming has significant effects on lipid and carbohydrate concentrations in the body (Stobutzki 1997), and that reef fish get exhausted faster as current speeds increase (up to 50 times faster with only a fourfold increase in water current; Fisher and Bellwood 2002). Therefore, there are demonstrated benefits of conserving energy during the pelagic stage, which might be achieved by drifting. Although, this balance between energy and swimming can be further complicated by the availability of food (Fisher and Bellwood 2001) our estimates of drifting are reliable because we tested larvae soon after their collection. This reduced the likelihood of starvation effects on our results.

Gross cost of transport (GCOT) is the measure of the overall impact that swimming speed has on energy costs. Gross cost of transport is defined as the energy required to move a unit mass through a unit distance (Webb 1993). The GCOT—swimming speed relationship is U-shaped (Webb 1993), the result is that optimal swimming performance (i.e. the most energy efficient swimming speed) will fall somewhere below a fish's maximum swimming velocity. For instance, Bernatchez and Dodson (1987) showed that the energetic cost of migration increased as fish deviated from their optimal displacement rate. In *A. saxatilis*, we observe that the maximum swimming speed in the extended chamber is ~70% of its mean U_{crit}, and ~40% of the maximum U_{crit} value. The U-shaped relationship between GCOT and swimming speed implies that as current speed increases, it becomes no longer economical to attempt to overcome that current. This further supports the idea that, under natural conditions, larval fish may choose to swim well below the swimming capabilities previously reported for reef fishes.

Although we describe drifting only for the late-stage larvae of a single coral-reef fish species, we expect this behaviour to vary both among taxa and ontogenetically within species. Indeed, drifting has been previously observed in pelagic larvae. Bishai (1960), observed larvae maintaining position in the current at slow current speeds, however, at higher speeds, the larvae drifted backwards while still swimming against the current. Similarly, Hindell et al. (2003) doing in-situ observations on pelagic post-larval fishes of temperate species found the movement patterns of these fishes were related to the speed and direction of currents in ocean waters greater than 7 m depth. Based on variations in the cost of swimming among species of different body size one also could expect inter-specific variations in the degrees of drifting. Among species, the optimum swimming speed tends to decrease with increasing size of the species (Webb 1993), due to increased energetic cost of swimming with increasing body size. This suggests that under similar current regimes, larger species might be expected to drift to a greater degree than smaller species. Within species, swimming abilities tend to be poor early in ontogeny and increase exponentially with age (Fisher and Bellwood 2000). Furthermore, newly hatched larvae experience low to intermediate Reynolds numbers (Bellwood and Fisher 2001) which are characterised by viscous forces, creating drag (McHenry et al. 2003). This will increase the amount of energy required for active movement in young larvae and probably will affect their "decision" to swim. Since swimming abilities tend to be poor early in ontogeny it is likely that the late-stage larvae that we used give a conservative estimate of the degree to which fish choose to drift, and that early larval stages are more likely to choose this option.

Here, we have shown the importance of drifting on the net displacement of larvae in experimental conditions. In natural conditions, drift can reduce energy expenses, which can increase the probability of successful completion of the larval period and survival after settlement. Furthermore, this study suggests that published data on swimming capabilities of reef fish larvae cannot be easily used to assess the extent to which these fish actively affect their dispersal. Finally, it is important to consider that the strong swimming abilities with which reef fish larvae are equipped may have evolved for purposes other than dispersal, such as improving prey capture or predator avoidance and/or for the location of suitable habitat at settlement by late-stage larvae. Further behavioural studies are required if we are to fully understand how larvae behave in open water and how this affects their dispersal.

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