

Sustained swimming abilities of the late pelagic stages of coral reef fishes

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ABSTRACT: The sustained swimming abilities of the late pelagic stages of 9 families of reef fishes were measured at 13.5 cm s^{-1} . There was a 25-fold difference in abilities among the families. Acanthurid juveniles swam on average for 194.3 h, covering the equivalent of 94.4 km. In comparison nemipterids swam for only 7.4 h, the equivalent of 3.6 km. The distances covered by other taxa ranged from 8.3 to 62.2 km. Among the families swimming ability was related to size and age but this relationship explained little of the variation present ($R^2 = 0.403$). Our results demonstrate that the pelagic stages of reef fishes are competent swimmers and capable of actively modifying their dispersal. This has direct implications on the replenishment of reef fish populations, especially with respect to mechanisms for self-seeding and maintenance of regional biogeographical patterns.

KEY WORDS: Swimming · Dispersal · Pelagic juveniles · Reef fish · Recruitment · Self-seeding

INTRODUCTION

For the past 2 decades, the primary emphasis of reef fish ecology has been to determine the factors which influence population size and structure (Doherty & Williams 1988). The bipartite life cycle of most reef fishes, with a pelagic early life stage and a benthic reef associated stage (Sale 1980), complicates our understanding of their ecology. Early studies focused on post-recruitment events until extensive temporal variation in numbers suggested other factors were also important (Sale 1980). It was initially proposed that stochastic recruitment events were the major determinants of population numbers (Doherty & Williams 1988). This led to numerous studies of recruitment patterns and the possible factors influencing these patterns (e.g. Victor 1983, 1986). By the late 1980s the general consensus was that recruitment patterns were driven by recruit availability and therefore dependent up on the events occurring during the pelagic stage (Doherty 1991).

Research then focused on the pelagic stages themselves, primarily their open water distributions (Leis 1991). Studies found that hydrological patterns alone

could not predict or explain the observed distributions (reviewed by Leis 1991). This discrepancy has been interpreted as being due to either the inadequacies of the hydrological data or the behaviour of the fish (Wolanski 1993). Whilst physical oceanographers have concentrated on the former aspect, many reef fish biologists have emphasised the role of behaviour (Kingsford & Choat 1989, Cowen et al. 1993, McCormick & Milicich 1993). Despite this widespread view that behaviour is important, empirical data on the abilities of these fishes is limited.

Our aim was to directly measure the degree of control the late pelagic stages have over their dispersal. Sustained swimming is one major way in which the pelagic stages could modify their dispersal. Previously, researchers have assumed that the swimming abilities of the pelagic stages of reef fishes were negligible (e.g. Williams et al. 1984). This assumption was based on the few studies available, which rely largely on temperate species (reviewed by Miller et al. 1988). The observed distribution patterns of the pelagic stages of reef fishes, however, provide indirect evidence that they are capable of actively altering their distribution. In this study we will provide direct empirical data on the extent to which these fish are capable of horizontal movement and the degree of interfamilial variation.

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METHODS AND MATERIALS

Swimming chamber design. A multi-lane portable swimming chamber was built to measure sustained swimming abilities in the field (modified after Stobutzki & Bellwood 1994). The chamber was constructed out of clear perspex with 6 raceways, 30 mm wide, 50 mm high and 390 mm long (Fig. 1). Water flow was generated by a 2400 W centrifugal pump. A header tank with T-piece diffuser ensured flow was evenly distributed to each raceway. At the start of each raceway the water flowed through a 40 mm long section of flow straighteners to minimise turbulence.

The system layout follows Stobutzki & Bellwood (1994). Although originally designed to measure critical swimming speeds, this apparatus is also useful for determining sustained swimming abilities. A water exchange system between the reservoir and an open aquarium system ensured a constant water temperature ($30.2 \pm 0.7^\circ\text{C}$, $\pm\text{SE}$). The area where the fish swam was partially covered by a sheet of black plastic which provided a stimulus for the fish to maintain position and reduced disturbance by movement outside the chamber.

The average water speed was calculated by dividing the volume of water flowing over the weir in a unit time by the total cross-sectional area of the chambers.

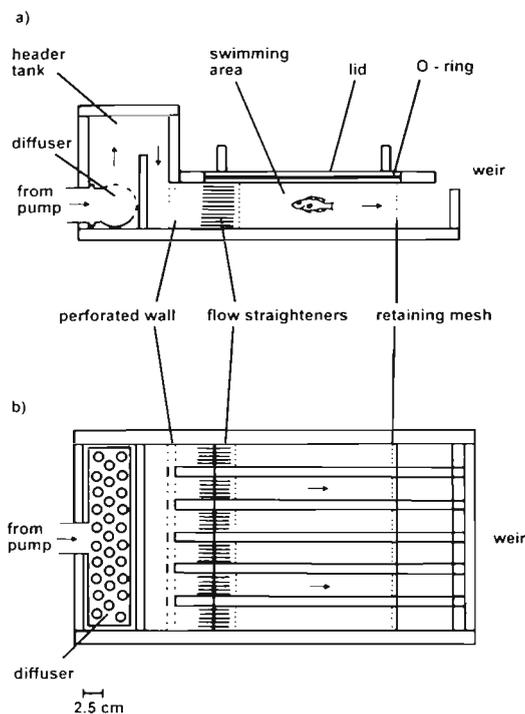


Fig. 1. Schematic section of the swimming chamber: (a) lateral view; (b) view from above

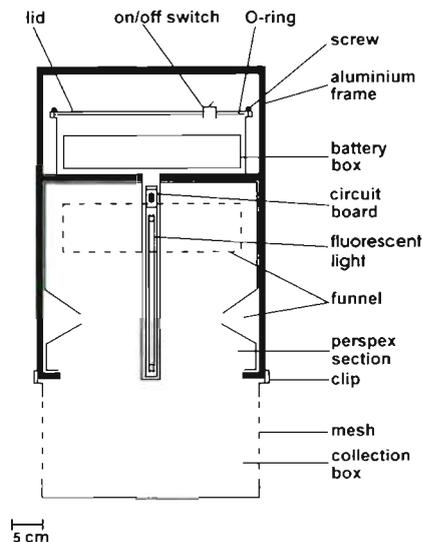


Fig. 2. Schematic diagram of the light trap

Neutrally buoyant particles were then videoed in the chambers moving past a grid. This procedure was used to check for boundary layers (which were negligible; the water velocity in the 0.5 cm closest to the wall was not significantly different to that in the center of the chamber). The video calibration also checked that the water speed was the same in all raceways and verified the initial flow calibrations.

Collection of specimens. Fish were collected and tested at the Lizard Island Research Station, in the northern section of the Great Barrier Reef, Australia ($14^\circ 14' \text{S}$, $145^\circ 27' \text{E}$). All specimens were pre-settlement and collected using light traps. The traps were modified after Doherty (1987) to be manageable from small boats and to reduce maintenance and cost. They consisted of a perspex section, where the fish entered the trap, above a removable collection box where the fish were retained (Fig. 2). The perspex section had 4 entrance funnels and the light source was a single 8 W fluorescent tube powered by 16 D-cell batteries. The perspex section was protected by an aluminium frame to which a buoy was attached. The collection box had mesh sides which permitted substantial water movement. This helped maintain the fish in good condition.

The traps were moored off the reef edge, over sand in 8 to 12 m of water. The entrance openings were in the top 1 m of the water column. The lights were switched on at 18:00 h and the traps emptied by 07:30 h. The fish were maintained in darkened aquaria with fresh, flowing sea water. All fish were swum within 16 h of capture, the majority within 6 h.

Specimens were identified to family based on Leis & Rennis (1983). To identify to species, a number of reference specimens were permitted to settle after

which identification was possible based on colour patterns.

Swimming methodology. The fish were placed in the raceways and allowed to acclimatise at 2 cm s^{-1} for 10 min. The speed was then increased slowly to 13.5 cm s^{-1} . This speed was selected as it approximates the mean current speeds around reefs in the region (Frith et al. 1986). The fish were then left until fatigued, as indicated by the fish lying against the rear mesh unable to maintain position in the flow. Once the fish had fatigued, they were removed and the total length (TL) recorded. One or two fish were placed in each raceway. The fish were of different taxa and did not visibly interfere or school with each other. The fatigue times of paired and single fish were compared using a 2-way ANOVA, with factors species and pairing. The data were transformed $[\log(x + 1)]$ to reduce heteroscedasticity.

While swimming, the fish were observed regularly. The mean time between observations was $87 \pm 6.9 \text{ min}$ ($\pm \text{SE}$) (maximum time was 4 h). The time to fatigue was taken as the last time the fish was seen swimming. Fish were not fed before or during the swimming trials.

Data analysis. The time to fatigue for each individual was converted to an equivalent distance travelled, i.e. at 13.5 cm s^{-1} the fish would swim the equivalent of 0.49 km h^{-1} . A stepwise multiple regression was used to examine the relationship between total length (TL), pelagic larval duration (PLD) and swimming ability among families. The correlation between TL and PLD was also determined.

PLDs were obtained from the literature (Brothers et al. 1983, Brothers & Thresher 1985, Thresher et al. 1989, Wellington & Victor 1989) and D. Wilson (unpubl. data; pomacentrids and *Chaetodon plebius*) and G. Wilson (unpubl. data; *Lethrinus atkinsoni*). Where PLDs for each species were not available, the mean value for the family was used. Ages of the acanthurid juveniles were based on direct otolith ring counts of the study specimens (following Lou & Molt-schaniwskyj 1992, Choat & Axe 1996).

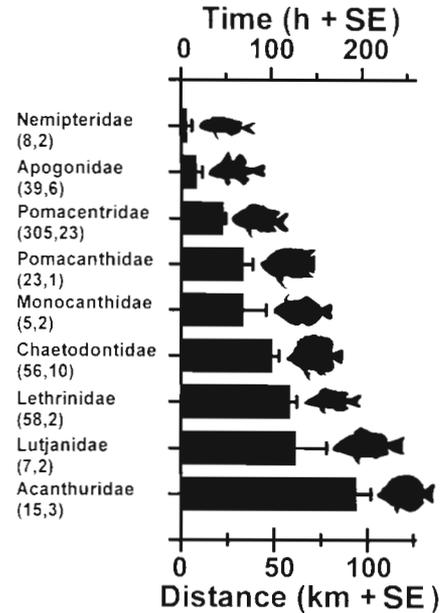


Fig. 3. Average time to fatigue for each family and equivalent distance travelled. Numbers of individuals and species tested are shown in parentheses

RESULTS

Analysis showed that there was no effect of the number of fish in a chamber on the fatigue time ($F_{1,64} = 0.179$, $p = 0.6779$). This was constant across the species, i.e. there was no interaction between species and the presence of another fish ($F_{12,64} = 1.538$, $p = 0.1340$).

Estimates of sustained swimming abilities revealed large differences among the 9 families (Fig. 3). Acanthurids displayed the greatest overall swimming ability with an average duration of $194.3 \pm 15.5 \text{ h}$ ($\pm \text{SE}$) travelling the equivalent of $94.4 \pm 7.5 \text{ km}$ ($\pm \text{SE}$). The maximum distance swum was by a 28.8 mm lutjanid, which covered the equivalent of 140.2 km in just under 14 d (Table 1). At the other end of the scale were the nemipterids, swimming on average only $7.4 \pm 4.8 \text{ h}$ ($\pm \text{SE}$), covering the equivalent of $3.6 \pm 2.5 \text{ km}$ ($\pm \text{SE}$). This is

Table 1. Maximum and minimum swimming duration for each family, and the equivalent distance travelled

Family	Maximum duration (h)	Equivalent distance travelled (km)	Minimum duration (h)	Equivalent distance travelled (km)
Lutjanidae	288.5	140.2	25.9	12.6
Pomacanthidae	253.1	123	25.3	12.3
Acanthuridae	246.1	119.6	15.6	7.6
Chaetodontidae	243.1	118.1	6.3	3.1
Monacanthidae	238.7	116	16.5	8
Pomacentridae	231.7	112.6	0	0
Lethrinidae	228.3	110.9	0.33	0.16
Apogonidae	174.3	84.7	0	0
Nemipteridae	35.8	17.4	0	0

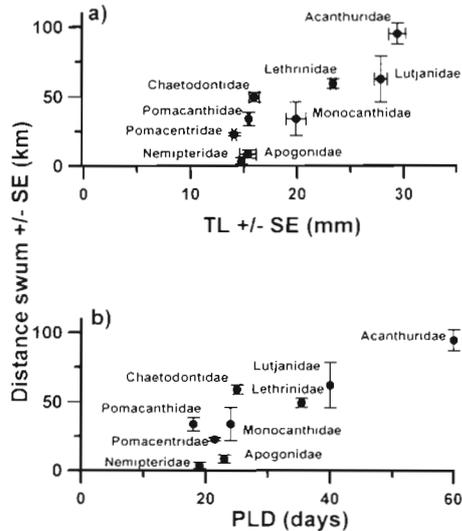


Fig. 4. Relationship between distance swum and (a) size (total length, TL) and (b) age (pelagic larval duration, PLD) among the families

still a substantial distance considering the average total length of nemipterids is only 14.8 ± 0.21 mm (\pm SE). The remaining families swam on average between 17 and 128 h and all displayed a wide range between their maximum and minimum distances (Table 1).

Swimming ability showed a significant relationship ($F_{2,352} = 120.321$, $p < 0.0001$) with both TL and PLD

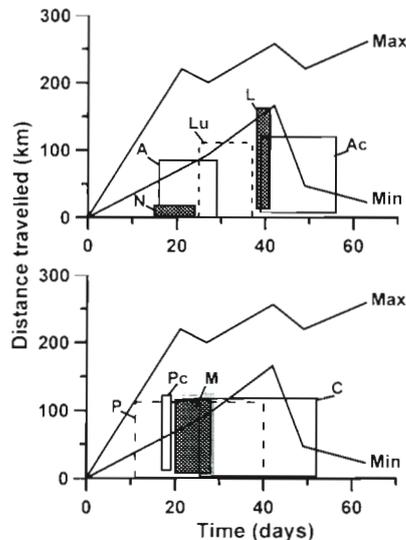


Fig. 5. Range of distances swum in each family against their PLD range, compared to the maximum (Max) and minimum (Min) distances moved by passive particles away from Lizard Island (Frith et al. 1986). Families are Ac: Acanthuridae; L: Lethrinidae; Lu: Lutjanidae; A: Apogonidae; N: Nemipteridae; P: Pomacentridae; Pc: Pomacanthidae; M: Monocanthidae; C: Chaetodontidae

(Fig. 4), given by the multiple regression equation: Distance swum = $0.464 (\pm 0.130, \text{SE}) \times \text{PLD} + 3.287 (\pm 0.248, \text{SE}) \times \text{TL} - 35.326 (\pm 4.538, \text{SE})$.

This relationship, however, explains less than half of the variation in distance swum among families, $R^2 = 0.403$. Age and size had a significant correlation but again the relationship was relatively weak ($r = 0.305$, $p < 0.0001$).

If the range of sustained swimming abilities and the PLDs of the study families are considered in relation to the distances moved by passive particles away from Lizard Island over time, a striking pattern emerges (Fig. 5). The data clearly show the high degree of variability within and among these families. In most families a section of their box lies above the minimum distance travelled by passive dispersal. This suggests that some individuals of these families would be capable of returning to their natal reef, after an extended period of passive dispersal, in a single swimming bout. Active return to reefs may therefore be possible.

DISCUSSION

Our results demonstrate that late pelagic stage reef fish are capable swimmers. This ability could have a major effect on their dispersal patterns. The estimates provided here are conservative as the methods used probably underestimate maximum abilities. The fish were swum at a single speed, which was not necessarily their optimal speed (Weihs 1973). In addition, all had swum an unknown distance prior to capture in the light trap, and had no access to food for up to 27 h prior to, or during, the swimming trial. We recorded the minimum duration of swimming in the chamber; actual times may have been up to 4 h (1.96 km) longer. Our values are for a single sustained bout of swimming. Given food, rest and an ability to modify their position in the water column, individuals may be able to cover much greater distances in the wild. Despite these limitations, the swimming abilities recorded are much greater than expected.

There is a widespread belief that the pelagic stages are capable of actively modifying their dispersal, a suggestion which arises primarily from observations of their open water distribution patterns (e.g. Kingsford & Choat 1989, McCormick & Milicich 1993). Previously, researchers estimating swimming abilities have had to rely on the sparse data available from the larvae of temperate species (Blaxter 1986). This has resulted in the assumption that the pelagic stages' swimming capabilities are negligible (e.g. Williams et al. 1984). Studies of temperate larvae suggest that sustained swimming abilities should on average be about 1 TL s^{-1} (Miller et al. 1988). Our testing speed was 13.5 cm s^{-1} ,

which is approximately 3 to 4 TL s^{-1} for acanthurids and lutjanids and more than 10 TL s^{-1} for the smaller taxa. It is clear that the use of studies on temperate larvae to estimate the abilities of the pelagic stages of reef fishes would be misleading.

The difference between the results obtained here and previous studies is probably a result of both the environment and the nature of the pelagic stages of reef fishes. Studies of comparably sized fishes are relatively few and focus on temperate species, primarily larval clupeoids and pleuronectiforms (Blaxter 1986). These are taxonomically very different from reef fishes, which are primarily perciforms (Choat & Bellwood 1991). In addition, few of the specimens examined in the present study were larvae; most were juveniles. The few larval forms which were tested were highly specialised, e.g. tholichthys stage chaetodontids. All specimens were well developed with respect to their fins and sensory abilities and were competent to settle on the reef. The marked difference in the abilities of some reef fishes and previously studied groups therefore probably reflects differences in taxonomy, morphology and development. This highlights the need to directly assess the abilities of reef fishes.

Our results are consistent with the theory that size is a major determinant of swimming ability (Wardle 1977). Larger fish swam for longer periods (Fig. 4). This is most likely a reflection of the fact that the speed is relatively slower, being 3 to 4 TL s^{-1} for acanthurid juveniles compared to 10 TL s^{-1} for the smaller taxa. A slower relative speed requires less effort for the fish (Wardle 1977). A larger size also reflects greater metabolic reserves and a relatively lower metabolic rate. Although correlated with size, age also had a significant contribution to swimming ability as older fish are more likely to be better developed with respect to their musculature and locomotory structures. Together, however, the relationship with size and age accounted for relatively little (40.3%) of the variation in swimming ability. The remaining differences in abilities among the families may be a result of the differences in morphology and developmental stage. While all taxa were competent to settle, the extent of morphological development at settlement varied widely (Leis 1991). This variation in swimming abilities is important, as it is likely to influence the relative importance of active control versus passive mechanisms. It also highlights the need to directly assess the abilities of individual taxa, as broad generalisations will be of limited utility.

Two of the key ecological questions in marine biology are how far pelagic larvae disperse and how they locate suitable settlement sites. Swimming will directly influence both of these factors. Active swimming may contribute to the observed dispersal patterns and explain why they vary among taxa (Leis 1991). Swim-

ming against currents could prevent advection from reefs, reducing dispersal. Alternatively, swimming with currents could actively contribute to greater dispersal. Models of dispersal must consider behaviour and active swimming by the pelagic stages. Realistic models will only be possible if more direct measures of the abilities of the pelagic stages are incorporated.

For reef fishes, settlement sites include isolated reefs in the middle of oceans and specific regions in complex systems such as the Great Barrier Reef (Williams et al. 1986, Thresher 1991). Previously all mechanisms invoked to explain self-seeding of isolated reefs have utilised hydrological processes, e.g. gyres and eddies, although attempts to demonstrate their biological role have been unsuccessful (Williams & English 1992, Cowen et al. 1993). Active swimming, however, would permit individuals of some taxa to return to their natal reef in a single swimming episode (Fig. 5). Self-seeding of reefs may not require specific hydrological patterns but may be actively controlled by the pelagic young.

Active control of dispersal also has implications for complex reef systems such as the Great Barrier Reef, Australia, which display strong regional biogeographic patterns (Williams 1982). These patterns are determined by recruitment and are not explainable by passive drift (Williams et al. 1986). Active swimming provides a mechanism for active habitat selection which would help explain these patterns. The cross-shelf regions are 20 to 40 km apart and from Fig. 6 it is clear that most taxa would be capable of swimming this

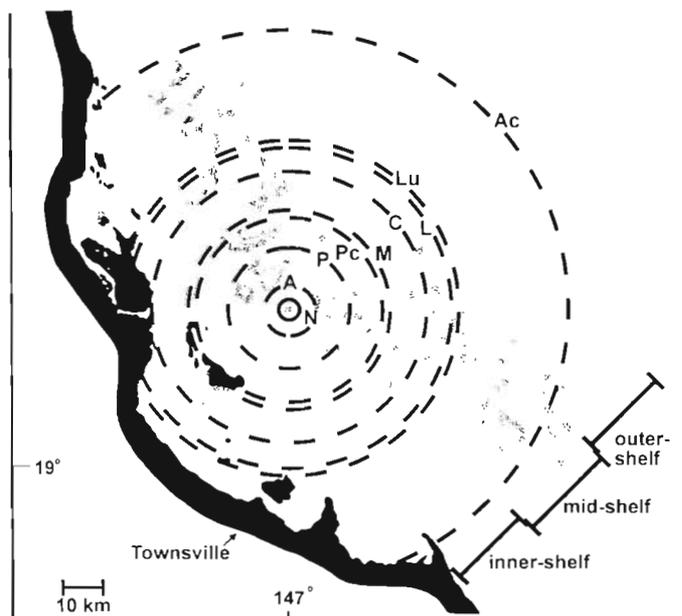


Fig. 6. Average distance swum for each family centred around a mid-shelf reef on the Great Barrier Reef (Australia). Families are labelled as in Fig. 5

distance to return to their original reef region. Alternatively, late pelagic stage fish may maintain position against currents, preventing advection and thus maintaining regional patterns.

Events which occur during the pelagic stage play a crucial role in determining the demography of reef fish communities. Previously this stage has been regarded as something of a black box out of which recruits appear. Although this study concentrates solely on the late pelagic stages (the stage at which they settle on reefs), it is the first study of its kind on reef fishes and clearly demonstrates the extent of their swimming abilities. Nevertheless several important aspects remain to be addressed. These include the changes in swimming abilities during ontogeny, the extent of variation within families, the metabolic cost of sustained swimming and the extent to which these laboratory-based abilities are realised in the field. In addition, this swimming will only be advantageous for active control of dispersal if the fish can orient with respect to reefs. An evaluation of the orientation abilities of the pelagic stages must remain a priority in future studies. While preliminary, the present study has highlighted the need to understand the degree to which pelagic stages of coral reef fishes can actively control their dispersal. It appears that active control by the pelagic stages may be a major determinant of dispersal patterns.

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