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REPORT

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Nocturnal orientation to reefs by late pelagic stage coral reef fishes

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Abstract The nocturnal orientation behaviour of the late pelagic stages of two reef fish families (Apogonidae and Pomacentridae) was examined using behavioural cages deployed in the field. The behavioural cages enabled the fish to choose between swimming towards or away from the reef in response to natural cues. Overall, 55% of fish displayed a choice in the experiments, however, the proportion varied between the two families, with 67% of pomacentrids and 27% of apogonids displaying a choice. In both families, of the fish which displayed a choice, the proportion of fish swimming towards the reef was significantly greater than 50%, as random movement would predict (64% of pomacentrids and 67% of apogonids swam towards the reef). This proportion did not vary significantly among four field sites with different current regimes and geographic locations. The results suggest that the late pelagic stages of reef fish display nocturnal orientation behaviour, possibly in response to sound, which may aid in their settlement on reefs.

Key words Apogonidae · Pomacentridae · Presettlement · Larvae · Orientation · Coral reef fish

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Introduction

Orientation is central to many aspects of animal behaviour especially in the selection of habitats (Williamson 1995). The ability to orient to a wide range of stimuli has been demonstrated for many taxa: orientation to celestial features by insects (Chittka and Geiger 1995, Menzel et al. 1996) and migrating birds (Wiltschko and Wiltschko 1991; Chappell and Guilford 1995), chemosensory orientation by migrating eels (Crnjar et al. 1992) and salmonids (Dittman and Quinn 1996) and magnetic field orientation by sharks (Kalmijn 1988) and birds (Wiltschko and Wiltschko 1996). Stobutzki and Bellwood (1997) have demonstrated that the late pelagic stages of coral reef fishes have sufficient swimming abilities to modify their dispersal and return to reefs. However, this swimming will only aid in their return to reefs if the pelagic stages can locate and orient with respect to reefs. For the late pelagic stages of reef fishes the ability to detect the location of reefs will permit them to actively modify their position relative to reefs and potentially control the location, timing and pattern of their settlement.

Oriented swimming behaviour has been implicated in the return of decapod larvae to coastal settlement sites. In both crabs (Shanks 1995) and lobsters (Ennis 1986; Cobb et al. 1989) oriented swimming by the late pelagic stages has been identified as potentially a major factor contributing to recruitment patterns. In reef fishes the existence of gregarious settlement (Breitburg 1991), habitat (Sale et al. 1984) and reef region (Williams 1982) specificity and the avoidance of potential competitors at settlement (Sweatman 1985) all suggest that the late pelagic stages have complex behaviours which influence their dispersal and settlement patterns. Furthermore, observations of released late pelagic stage reef fishes by Leis et al. (1996) suggest that they display orientated swimming with respect to reefs. However, these field observations were made during daylight. As most reef fishes settle at night (Sweatman 1985; Dufour and Galzin 1993), nocturnal orientation behaviour may play a central role in the return of the pelagic stages to reefs.

This study, therefore, provides a preliminary examination of nocturnal orientation behaviour of the late pelagic stages of two reef families, the Pomacentridae and Apogonidae. A field experiment was conducted to examine orientation behaviour at night in response to natural cues from the reef. The experiment demonstrated that the late pelagic stages orient towards the reef and also provided preliminary information with regard to the potential cues employed in this orientation.

Materials and methods

Behavioural cages

Orientation with respect to the reef by late pelagic stages was examined using behavioural cages. The cages were designed for use in the field, at night and without the presence of an observer. The cages were also designed to minimise their interference with possible orientation cues.

The cages were constructed from black 2 mm gauge plastic mesh, supported by a frame of 16 mm diameter perforated plastic tubing (Fig. 1). When submerged the tubing was filled with water to ensure no air remained inside, as this might refract sound. The apparatus was transparent to sound and permitted water flow. The cages were collapsible for easy transport and when in the water they were held open by struts.

The cages consisted of three sections (Fig. 1), the main area where the fish were introduced and two opposing traps. In the main area two opposing corners funnelled down to the entrances of the traps. When the cages were deployed, one trap of the cage faced towards the reef and the other trap faced the open ocean. The main area of the cage was large (1 m corner to corner and 50 cm deep) relative to the size of the fish allowing them to move in any direction before they encountered a wall. The funnels into the traps were constructed from the tops of 1.25 l plastic soft-drink bottles, providing small entrances to the traps (15 mm diameter). The lids of the bottles were used to close off the funnels before the cages were removed from the water, preventing fish from moving between sections of the cage. All three sections had velcro openings which permitted access to the fish.

Fish were introduced into the cage via releasing containers in the bottom of the main area (Fig. 1). The fish were held in the releasing containers for 20 min before releasing them into the main area of the cage. This was achieved by the use of an O-shaped sugar-based candy. This formed a sacrificial link in a strap which held down the lid on the releasing container. When the candy fully dissolved, the lid was opened by elastic bands. The releasing containers enabled the operators to leave the area before the fish were released. This prevented the fish from responding to the presence of the operators or the boat.

Mooring system

Four cages were moored 1 m apart, in a line parallel to the reef edge. In this way, each cage was held perpendicular to the reef edge with one trap facing the reef and the other trap facing the open sea. The cages were held at a depth of 3 m at the lowest tide and at least 30 m from the reef. The cages were attached to the mooring by a rope at each corner (Fig. 1), which prevented any changes in orientation of the cages. The mooring consisted of two sets of parallel horizontal ropes to which the cages were attached (Fig. 2). The horizontal ropes were held in place by vertical ropes which were attached to concrete blocks on the substratum and held taut by sub-surface buoys. Anchors (6 kg) at each corner of the mooring prevented sideways movement. The entire mooring was submerged to avoid noise from waves breaking on surface buoys.

Experimental sites

Four experimental sites (Fig. 3) at Lizard Island, Great Barrier Reef, Australia (14° 14′S, 145° 27′E) were used over two consecutive summers, November to January, 1994–5 (sites A and C) and 1995–6 (sites B and D). Experiments were run across the new moon periods to coincide with natural settlement periods on reefs (Milicich et al. 1992). Sites were chosen to cover a range of current directions and geographic orientations. At sites A and C (Fig. 3) the reef edge was present in only one direction and so the cages were moored in a single orientation with respect to this reef edge. At site A the predominant current ran longshore, while at C it ran off the reef towards the cages. At sites B and D (Fig. 3) there were two reef edges, one parallel to the main island and one perpendicular to this. At these sites two orientations of the cages were used, one facing each reef edge. At site B the predominant current was longshore, parallel to the main island; at site D the current was perpendicular to the main island, coming from offshore. The predominant current direction was determined by observing the direction of movement of neutrally buoyant particles at the depth of the cages. This was noted each time fish were introduced to the cages and collected. The sites were used for a varying number of nights, depending on light trap catches. The number of nights at each site were as follows: A-7, B-18, C-9, D-10.

Experimental procedure

All specimens used were late stage pelagic individuals (= late-stage pelagic larvae, *sensu* Leis et al. 1996) collected in light traps following Stobutzki and Bellwood (1997). The light traps were moored over sand, off the reef edge, in approximately 12 m of water. The traps hung in the top 1 m of the water column. The traps fished all night and were emptied by 7:00 am. The fish were maintained in darkened aquaria with flowing water. Experiments were conducted at dusk the same day fish were collected. Members of the families Pomacentridae (18 species) and Apogonidae (4 species) were used as they were the most abundant taxa in the light traps.

The mean number of fish used per cage was 25 (± 0.8 SE). This varied due to unpredictable light trap catches. Fish were placed in the cages between 5 and 5.45 pm and collected between 6 and 6.30 am the next day. Preliminary observations found that fish would rarely leave the shelter of the releasing container during daylight.

Before the cages were removed from the mooring in the morning the openings of the funnels were closed to prevent fish escaping from the traps. The number and type of fish present in each section of the cage was recorded and from this the direction of movement was inferred. Disturbance bias and cage/mooring effects were minimised by alternating daily the side of the mooring approached by the boat and the position and orientation of the individual cages on the mooring.

Data analysis

The results were analysed with respect to the proportion of fish displaying a “choice” in the cages and the proportion of these fish which moved towards the reef. Fish found in the traps were assumed to have displayed a choice of direction. The questions addressed

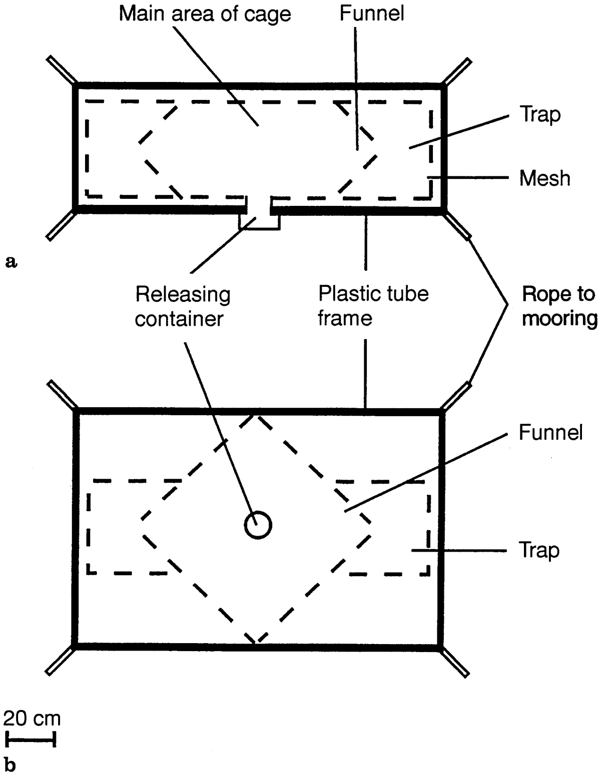

Fig. 1a,b Schematic diagram of behavioural cages **a** lateral view, **b** view from above

were whether the response was consistent across the sites and whether the proportion moving towards the reef was greater than expected due to random movement. If the fish were swimming randomly 50% of the fish which displayed a choice would be expected to be found in the trap facing the reef.

Proportions were used as the number of fish in each cage varied. The data were transformed [arcsine (square root (x)] (Zar 1984) prior to analysis. For both families a nested ANOVA (Zar 1984) was used to compare the proportion of fish which made a choice among sites and among days nested within sites. Nested ANOVAs of the same design were then used to determine whether the proportion of fish moving towards the reef varied among sites or days nested within sites. The mean proportion of fish moving towards the reef and the 95% confidence interval (CI) were back-calculated from the transformed data for each family and compared to 50% as expected from random movement. This was also repeated for each site separately

The previous analysis assumes that all fish in the cage made an independent decision, which is not necessarily the case. Because an average of 25 fish were placed in each cage, schooling or gregarious behaviour may have influenced the results. The results were, therefore, also analysed in terms of each cage as a single data point. Each cage was classified as whether the majority of fish moved towards or away from the reef. Regardless of schooling or gregarious behaviour, if the movement was random the number of cages in which the majority moved towards the reef would be expected to be equal to the number of cages in which the majority moved away. For each family a Chi-squared test (with Yates Correction as there was only 1 degree of freedom, Zar 1984) was used to determine whether significantly more cages had the majority of fish move towards the reef than away.

The fact that most cages contained individuals from both families may have permitted behavioural interactions between the families which could have influenced the proportion of fish displaying a choice or moving towards the reef. This was examined by comparing those cages in the main experiment (at sites B and D) which contained pomacentrids only ($n = 50$) with those containing both families ($n = 97$). Two-way nested ANOVAs were used to determine whether the proportion of pomacentrids displaying a choice or moving towards the reef was dependent on whether apogonids were present or not, whether there was an effect of site, if there was any interaction among these two factors and whether there was any influence of day nested within both factors. The effect of the pomacentrids on the behaviour of the apogonids could not be investigated as only two cages were deployed with apogonids alone. Prior to all ANOVAs the residuals were checked graphically to verify the assumptions of normality and homoscedasticity (Zar 1984).

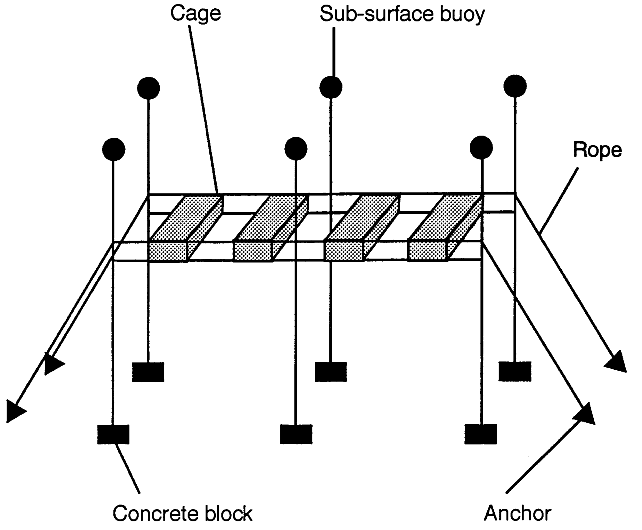

Fig. 2 Schematic diagram of mooring system for behavioural cages. Mooring is not shown to scale

Results

In total the responses of 2939 fish were examined (897 apogonids and 2042 pomacentrids), of which 1601 (55%) made a choice. Among the sites, there was no difference in the proportion of fish displaying a choice for either family (Tables 1, 2). The average proportion of fish making a choice did differ between the two families. On average only 26.9% (+ 2.13 SE) of apogonids chose a direction, compared to 66.6% (+ 1.71 SE) for pomacentrids. The pomacentrids showed significant variation among days within sites in the proportion making a choice (Table 2).

Of the fish which displayed a choice, the proportion of fish moving towards the reef did not vary among sites for either family (Table 3, Fig. 3). This suggests that both families displayed a consistent response to the presence of the reef across all sites. Overall the proportion of fish moving towards the reef in both families (Table 4) was significantly greater than 50%, which random movement within the cages would predict. If the sites are examined individually, the proportion of fish in each family moving towards the reef ranges from 55. 5 to 95.2%. The variances, however, are

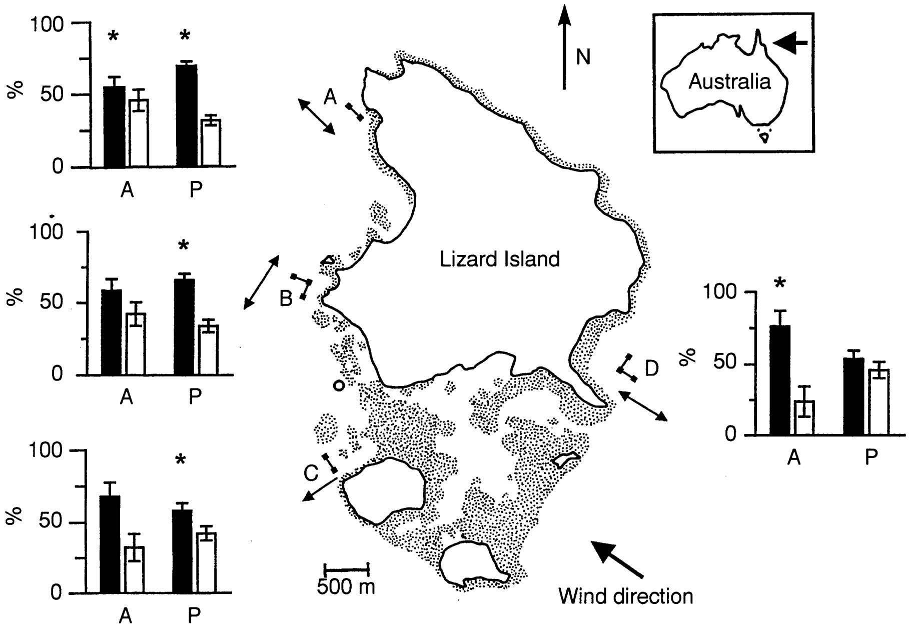

Fig. 3 The mooring sites of the behavioural cages at Lizard Island, Great Barrier Reef, Australia and the average percentage (± SE) of fish swimming towards (solid bars) or away (open bars) from the reef at each site; *A* - Apogonidae, *P* - Pomacentridae. * denotes where movement by a family at an individual site was significantly different from 50%. The arrows indicate the predominant current direction at each site. The moorings are not to scale

Table 1 Mean percentage of fish displaying a choice, in each family at the four sites

Site	Pomacentridae		Apogonidae	
	Mean	SE	Mean	SE
A	67.66	3.93	34.01	5.80
B	67.12	3.49	28.94	4.95
C	69.29	4.28	59.80	7.90
D	66.64	4.9	19.2	5.52

Table 2 Results of ANOVAs investigating the influence of site and days nested within sites, on the proportion of fish displaying a choice, in each family. Probabilities are displayed in parenthesis

Source of variation		Pomacentridae	Apogonidae
Site	F	1.01 (0.398)	0.87 (0.468)
	df	3, 38	3, 30
Day (site)	F	2.26 (< 0.0001)	1.03 (0.440)
	df	38, 164	30, 112

Table 3 Results of ANOVAs investigating the influence of site and days nested within sites, on the proportion of fish moving towards the reef, in each family. Probabilities are displayed in parenthesis

Source of variation		Pomacentridae	Apogonidae
Site	F	0.40 (0.754)	0.28 (0.838)
	df	3, 37	3, 29
Day (site)	F	1.42 (0.074)	1.20 (0.269)
	df	37, 159	29, 59

Table 4 Pooled mean percentage of fish moving towards the reef in each family, with 95% confidence limits. * denotes a significant difference from 50%

Family	Mean %	95% CI	*n*
Pomacentridae	64.3	*58.5–69.8	200
Apogonidae	67.1	*53.6–79.4	92

Individual site values (95% CI of mean): Pomacentridae A (*51.3–67.3), B (*64.3–75.2), C (*54.2–77.1), D (48.1–66.5), Apogonidae A (*50.6–92.3), B (39.1–84.4), C (30.0–84.1), D (*77.0–99.7)

large. The pomacentrids displayed significant movement towards the reef at sites A, B & C and the apogonids at sites B and D (Table 4, Fig. 3). Those sites with no significant response showed the same trend as seen overall (i.e. net movement towards the reef), as indicated by the ANOVA but a significant difference was not detected due to the large variances around the means (Table 4, Fig. 3). Overall, there were no sites at which either family displayed a net movement away from the reef, while all sites recorded a significant movement towards the reef for at least one family (Table 4, Fig. 3).

The results were then examined in a more conservative manner, in terms of the number of cages in which the majority of fish moved towards the reef compared to the number of cages in which most fish moved away. The results for both families suggest that there were significantly more cages in which the majority of fish moved towards the reef than away (Table 5). This suggests that if schooling occurred the schools also responded to the presence of the reef.

The influence of the presence of apogonids on the behaviour of the pomacentrids appeared to be negligible. The presence of apogonids in the cages did not

Table 5 Number of cages in which the majority of fish moved towards or away from the reef for both families. The Chi-squared results test if the proportions within each family were different. Probabilities are displayed in parenthesis

	Pomacentridae	Apogonidae
Number of cages towards the reef	130	53
Number of cages away from the reef	58	28
χ_1^2	26.81 (< 0.0001)	7.11 (< 0.005)

Table 6 Results of ANOVAs testing for the influence of the presence of apogonids, experimental sites, any interaction and days on (A) the proportion of pomacentrids displaying a choice in the cages and (B) the proportion moving towards the reef. Probabilities are shown in parenthesis

Source of variation		Proportion displaying a choice	Proportion moving towards the reef
Presence of apogonids	F	0.001 (0.945)	0.18 (0.675)
	df	1, 30	1, 29
Site	F	0.08 (0.774)	0.25 (0.626)
	df	1, 30	1, 29
Interaction	F	0.16 (0.688)	0.62 (0.438)
	df	1, 30	1, 29
Day (Site * apogonids)	F	2.11 (0.003)	1.90 (< 0.0001)
	df	30, 113	29, 104

significantly alter the proportion of pomacentrids displaying a choice or moving towards the reef at any site (Table 6). There was, however, significant variation among days nested within sites, in the proportion of pomacentrids moving towards the reef for these sites (A, D).

Discussion

Orientation behaviour is central to the location and selection of habitats by animals (Williamson 1995). If the pelagic stages of reef fish are to actively control their dispersal and return to reefs, orientation with respect to reefs is essential. From the results of this preliminary study it appears that the late pelagic stages are capable of responding to reefs in relatively close proximity and may actively move towards reefs at night. The combination of this orientation behaviour with the previously demonstrated swimming abilities (Stobutzki and Bellwood 1994, 1997) suggests that the late pelagic stages could actively control their dispersal especially during the settlement phase when they return to reefs.

It is unclear why only 55% of the fish tested displayed a choice (i.e. moved into a trap). Given the time available, one may expect all of the fish to have moved out of the main cage area. However, the cages may have limited the ability of fish to demonstrate a choice. There may have been insufficient space within the cages for the fish to make a choice before coming into contact with the walls or the trap entrances may have been too small to permit rapid entry. The results could also be due to variation among individuals. Some individuals may have been less competent to settle. Such variation is an inherent feature of behavioural studies (Raimondi and Keough 1990). However, despite these factors, there was a consistently greater movement of fish towards the reef, irrespective of the geographic location of the cages (Tables 2, 3, Fig. 3). This response was apparent from both the analysis of the proportion of fish moving and the number of cages in which the majority of fish moved towards the reef (Tables 4 and 5).

While the proportion moving towards the reef was consistent for both families (Table 3), the proportion of fish which made a choice varied greatly between the two families (26.9% for apogonids, 66.6% for pomacentrids) (Table 2). This could be due to developmental or behavioural differences between the families. The two families may be at different levels of development when collected by the light traps. A proportion of the apogonids, for example, may not have reached the settlement stage. The families may also respond differently to the presence of the cages or there may be differences in their natural nocturnal behaviour. Apogonids might be expected to have better night vision (McFarland 1991) and so may be more disturbed by the presence of the cage. Many morphological and developmental characteristics vary among the pelagic stages of reef fish families (Leis 1991). Swimming abilities have been shown to be highly variable in the late pelagic stage (Stobutzki and Bellwood 1994, 1997) and it is likely that behaviour will show comparable variation among taxa.

As more than one fish was placed in each trap there is the potential for intra- and inter-family interactions. Schooling behaviour is believed to be important during settlement of some species (Breitburg 1991), while some pre-settlement mullids (McCormick and Milicich 1994) have been seen schooling in the pelagic environment. The present study does not permit the evaluation of the presence or absence of schooling behaviour in the cages. However, if schooling occurred the schools also appeared to display preferential movement towards the reef (Table 5). The responses of the two families may also have been influenced by interactions between the families. However, for the pomacentrids at least there did not appear to be any influence of the presence of apogonids on either the proportion of fish displaying a choice or the proportion moving towards the reef (Table 6). There was, however, a significant difference among days, nested within sites, in the proportion of pomacentrids making a choice (Table 1) and, at sites A and D, in the proportion moving towards the reef

(Table 6). It is not possible to resolve the factors responsible for the variation at this level although differences in daily species composition, current intensities or prevailing weather conditions are likely to be contributing factors. Further experiments examining these factors would be valuable.

The orientation response demonstrated here contrasts with the results of Leis et al. (1996) who documented an orientated movement away from the reef by late pelagic stages that they released and followed in open water. Their work, however, was conducted during daylight. The present study, in comparison, focused on nocturnal orientation behaviour, as the majority of reef fishes settle at night (Sweatman 1985; Dufour and Galzin 1993). An ability to orient towards the reef at night may aid in the active return of young fish to reefs and their search for settlement sites. The difference between the orientation responses recorded here and those documented by Leis et al. (1996) may reflect a change in orientation behaviour with time of day. At night, directed movement towards reefs may be important for settlement, while during the day the pelagic stages may orient away from reefs, maintaining their position in the open ocean.

Studies of open water distribution patterns of the pelagic stages of reef fishes suggest that their behaviour is complex and sophisticated. The observed distribution patterns indicate that some active control must be occurring (Leis and Miller 1976; Leis and Goldman 1984; Leis 1986; Kingsford and Choat 1989; Kobayashi 1989). The possibility of both diurnal (Leis et al. 1996) and nocturnal (present study) orientation with respect to reefs, combined with the sustained swimming abilities of pre-settlement fish (Stobutzki and Bellwood 1994, 1997) suggests that active orientation behaviour may provide a possible mechanism for the active control of dispersal and settlement by coral reef fishes.

The present study also provides a preliminary indication of the relative importance of different cues used in the detection of reefs by the late pelagic stages. Reefs provide a wide range of potential stimuli, but their relative importance in the orientation behaviour of the pelagic stages is unknown. Rheotactic, olfactory, magnetic, visual and auditory cues may all be used. However, they differ markedly in the nature of the signal they provide.

Rheotaxis, possibly in association with olfactory stimuli, could aid in the location of reefs by the pelagic stages. Reef fish have been shown to respond to both of these cues. The response of the pelagic stages to currents in swimming chambers (Stobutzki and Bellwood 1994, 1997) demonstrates positive rheotaxis under experimental conditions. Olfactory cues appear to be important for the location of specific settlement sites by anemone fishes (Elliott et al. 1995; Arvedlund and Neilsen 1996) and other pomacentrids (Sweatman 1985), but their role in the location of reefs is unknown. In the present experiment olfaction was unlikely to have provided the dominant cue. If olfaction was employed, one would expect to see a weaker response at sites with a longshore current. This was not evident (Fig. 3). However, given the limited observations on currents and the significant variation among days (Tables 1 and 6), further detailed analyses are clearly needed.

In contrast to the above cues, magnetic, visual or auditory cues would have provided a constant directional stimulus at all experimental sites. Although magnetic senses have yet to be investigated in the pelagic stages of reef fishes, Lizard Island is unlikely to present a magnetic anomaly, as it is a continental island consisting primarily of granite (Leis et al. 1996). The late pelagic stages tested here undoubtedly respond to visual cues, as they were attracted to the light traps and their eyes at this stage are relatively well developed (Shand 1994; Job and Bellwood 1996). However, the use of visual cues to locate the reefs in this experiment remains doubtful. The experiments were conducted at night, over new moon periods, so that illumination was at its lowest levels. In addition, the cages held the fish away from the reef at a distance which was outside the known visual range of reef fishes during daylight (Douglas and Hawryshyn 1990; McFarland 1991). Given the current knowledge of the visual systems of the pelagic stages it appears unlikely that visual cues could have produced the observed orientation behaviour.

The consistent nocturnal response of the fish at all sites suggests that sound was the primary cue used for orientation towards the reef. As with visual cues, auditory stimuli would also provide a consistent cue to the location of the reef at all sites. However, unlike light, sound is transmitted through water with little attenuation (Rogers and Cox 1988). Sound can be propagated over vast distances and is highly directional (Popper and Coombs 1980; Rogers and Cox 1988). Reefs are noisy environments, with biological noise produced by invertebrates (McCauley 1994) and fish (Myrberg et al. 1986; Lobel 1992). The noise levels are greatest at night when snapping shrimp are most active and nocturnal fish produce choruses (McCauley 1995). These choruses can raise ambient sea noise for tens of kilometres around reefs (McCauley 1995). It is interesting to note that sound production on and around reefs peaks at night, over summer new moon periods (McCauley 1995) coinciding with the time of peak settlement of fishes on reefs (Milicich et al. 1992).

The nature and intensity of sound also appear to vary widely across reef zones (McCauley 1995). Snapping shrimp noise also varies in relation to substrate type (McCauley 1994). Sound therefore, may not only provide a cue for the pelagic stages of reef fish to detect the reef but it may also allow them to distinguish between reef types and habitats within a reef. While there are no published studies on the hearing abilities of the pelagic stages of reef fishes (reviewed by Blaxter 1986; Leis 1991) directional hearing has been demonstrated in some adult reef fish (Popper et al. 1973;

Myrberg et al. 1986) and in other fish taxa (Schuijf and Budwala 1980; Rogers et al. 1988). Given the observed orientation response of the fish and the properties of sound in water, the primary cue used by the fish in this experiment appears to be auditory. However, it is likely that the pelagic stages respond to a range of other cues that vary with ontogeny and distance from the reef.

Although preliminary, this study has provided the first direct evidence of nocturnal orientation to reefs by the late pelagic stages of reef fishes, and suggests that the fish may be responding to auditory cues. The observed swimming and orientation abilities of late pelagic stage fish suggest that these fish are capable of directional swimming. They may therefore be able to actively modify both their dispersal patterns and their subsequent return to reefs.

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References

Arvedlund M, Nielsen LE (1996) Do the anemonefish Amphiprion ocellaris (Pisces: Pomacentridae) imprint themselves to their host sea anemone Heteractis magnifica (Anthozoa: Actinidae)? Ethology 102 : 1–15

Blaxter JHS (1986) Development of sense organs and behaviour of teleost larvae with special reference to feeding and predator avoidance. Trans Am Fish Soc 115 : 98–114

Breitburg DL (1991) Settlement patterns and presettlement behaviour of the naked goby, *Gobiosoma bosci*, a temperate oyster reef fish. Mar Biol 109 : 213–221

Chappell J, Guilford T (1995) Homing pigeons primarily use the sun compass rather than fixed directional visual cues in an open-field arena food-searching task. Proc R Soc London (B) 260 : 59–63

Chittka L, Geiger K (1995) Honeybee long-distance orientation in a controlled environment. Ethology 99 : 117–126

Cobb JS, Wang D, Campbell DB, Rooney P (1989) Speed and direction of swimming by postlarvae of the American lobster. Trans Am Fish Soc 118 : 82–86

Crnjar R, Scalera G, Bigiani A, Tomassini Barbarossa I, Magherini PC, Pietra P (1992) Olfactory sensitivity to amino acids in the juvenile stages of the European eel *Anguilla anguilla* (L.). J Fish Biol 40 : 567–576

Dittman AH, Quinn TP (1996) Homing in pacific salmon : mechanisms and ecological basis. J Exp Biol 199 : 83–91

Douglas RH, Hawryshyn CW (1990) Behavioural studies of fish vision : an analysis of visual capabilities. In: Douglas RH, Djamgoz M (eds) The visual system of fish. Chapman and Hall, London, pp 373–418

Dufour V, Galzin R (1993) Colonisation patterns of reef fish larvae to the lagoon at Moorea Island, French Polynesia. Mar Ecol Prog Ser 102 : 143–152

Elliott JK, Elliot JM, Mariscal RN (1995) Host selection, location, and association behaviours of anemonefishes in field settlement experiments. Mar Biol 122 : 377–389

Ennis GP (1986) Swimming ability of larval American lobsters, *Homarus americanus*, in flowing water. Can J Fish Aqua Sci 43 : 2177–2183

Job SD, Bellwood DR (1996) Visual acuity and feeding in larval *Premnas biaculeatus*. J Fish Biol 48 : 952–963

Kalmijn ADJ (1988) Detection of weak electric fields. In: Atema J, Fay RR, Popper AN, Tavolga WN (eds) Sensory biology of aquatic animals, Springer-Verlag, New York Berlin Heidelberg, pp 151–188

Kingsford MJ, Choat JH (1989) Horizontal distribution patterns of presettlement reef fish: are they influenced by the proximity of reefs? Mar Biol 101 : 285–297

Kobayashi DR (1989) Fine-scale distribution of larval fishes: patterns and processes adjacent to coral reefs in Kaneoke Bay, Hawaii. Mar Biol 100 : 285–293

Leis JM (1986) Vertical and horizontal distribution of fish larvae near coral reefs at Lizard Island, Great Barrier Reef. Mar Biol 90 : 505–516

Leis JM (1991) The pelagic stage of reef fishes: the larval biology of coral reef fishes. In: Sale PF (ed) The ecology of fishes on coral reefs. Academic Press, San Diego, pp 183–230

Leis JM, Miller JM (1976) Offshore distributional patterns of Hawaiian fish larvae. Mar Biol 36 : 359–367

Leis JM, Goldman B (1984) A preliminary distributional study of fish larvae near a ribbon coral reef in the Great Barrier Reef. Coral Reefs 2 : 197–203

Leis JM, Sweatman HPA, Reader SE, (1996) What the pelagic stages of coral reef fishes are doing out in blue water: daytime field observations of larval behavioural capabilities. Mar Freshwater Res 47 : 401–411

Lobel PS (1992) Sound produced by spawning fishes. Environ Biol Fish 33 : 359–358

McCauley RD (1994) Distribution and levels of snapping shrimp noise in northern Australia. Report for the Defence Science and Technology Organisation. 28pp

McCauley RD (1995) Aspects of marine biological sound in Northern Australia, III: reef associated fish choruses. Report for the Defence Science and Technology Organisation. 37pp

McCormick MI, Milicich MJ (1994) Late pelagic stage goatfish abundance and behaviour. J Exp Mar Biol Ecol 174 : 15–42

McFarland WN (1991) The visual world of coral reef fishes. In: Sale PF (ed) The ecology of fishes on coral reefs, Academic Press, San Diego, pp 16–38

Menzel R, Geiger K, Chittka L, Joerges J, Kunzie J, Muller U (1996) The knowledge base of bee navigation. J Exp Biol 199 : 141–146

Milicich MJ, Meekan MG, Doherty PJ (1992) Larval supply: a good predictor of recruitment of three species of reef fish (Pomacentridae). Mar Ecol Prog Ser 86 : 153–166

Myrberg AA, Mohler M, Catala JD (1986) Sound production by males of a coral reef fish (*Pomacentrus partitus*): its significance to females. Anim Behav 34 : 913–923

Popper AN, Salmon M, Parvulescu A (1973) Sound localisation by the Hawaiian squirrelfishes, *Myripristis berndti* and *M. argyromus*. Anim Behav 21 : 86–97

Popper AN, Coombs S (1980) Auditory mechanisms in teleost fishes. Am Sci 68 : 429–440

Raimondi PT, Keough MJ (1990) Behavioural variability in marine larvae. Aust J Ecol 15 : 427–437

Rogers PH, Cox M (1988) Underwater sound as a biological stimulus. In: Atema J, Fay RR, Popper AN, Tavolga WN (eds), Sensory biology of aquatic animals, Springer-Verlag, New York Berlin Heidelberg, pp 131–150

Rogers PH, Popper AN, Hastings MC, Saide WM (1988) Processing of acoustic signals in the auditory system of bony fish. J Acou Soc Am 83 : 338–349

Sale PF, Douglas WA, Doherty PJ (1984) Choice of microhabitats by coral reef fishes at settlement. Coral Reefs 3 : 91–94

Schuijf A, Buwalda RJA (1980) Underwater localisation – a major problem in fish acoustics. In: Popper AN, Fay RR (eds) Comparative studies of hearing in vertebrates. Springer-Verlag, New York Berlin Heidelberg, pp 43–77

Shand J (1994) Changes in retinal structure during development and settlement of the goatfish *Upeneus tragula*. Brain, Behav Evol 43 : 51–60

Shanks AL (1995) Orientated swimming by megalopae of several eastern North Pacific crab species and its potential role in their onshore migration. J Exp Mar Biol Ecol 186 : 1–16

Stobutzki IC, Bellwood DR (1994) An analysis of the sustained swimming abilities of pre- and post-settlement coral reef fishes. J Exp Mar Biol Ecol 175 : 275–280

Stobutzki IC, Bellwood DR (1997) Sustained swimming abilities of the late pelagic stages of coral reef fishes. Mar Ecol Prog Ser 149 : 35–41

Sweatman HPA (1985) The timing of settlement by larval *Dascyllus aruanus*: some consequences for larval selection. Proc 5th Inter Coral Reef Symp, pp 367–371

Williams DMcB (1982) Patterns in the distribution of fish communities across the central Great Barrier Reef. Coral Reefs 1 : 35–43

Williamson R (1995) Orientation and migration in the sea, introduction. J Mar Biol Assoc UK. 75 : 1–2

Wiltshko W, Wiltshko R (1991) Magnetic orientation and celestial cues in migratory orientation. In: Berthold P (ed) Orientation in Birds. Birkhauser Basel pp 16–37

Wiltshko W, Wiltshko R (1996) Magnetic orientation in birds. J Exp Biol 199 : 29–38

Zar JH (1984) Biostatistical analysis. Prentice-Hall International, London