The behavioural response of coral reef fish following introduction to a novel aquarium environment

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ABSTRACT

Following the construction of a large-scale public aquarium, we were presented with an opportunity to investigate how wild caught Caribbean reef fish respond to their first encounter with a novel environment. Within the constraints of this opportunity, we designed a behavioural study to determine the reef fishes' response to a new habitat in relation to their locomotory mode. Nine species of fish representing three locomotory modes: carangiform, sub-carangiform and labriform/sub-carangiform were observed over a four-week period following their first introduction to the aquarium. Fish activity levels and spatial distribution were quantified in relation to time since their first encounter with the novel environment. The most important result was that, regardless of locomotory mode or ecology, all of the species extensively explored the novel environment rather than settle on the first habitat that they encountered. This is a particularly interesting result for territorial species. More specifically, however, there were significant differences between species in activity through time. Carangiform activity level was lowest in the initial phases of an encounter with the novel environment subsequently rising to a stable level. The other species had variable activity throughout the study, but all of them exhibited a phase of low activity at some stage during the study. In terms of the fishes' use of the 2.5 million litres of water, six species utilised the whole of the aquarium based on a predefined zoning scheme. Although the initial activity level was low, carangiform swimmers used at least 90% of the zones in the early phases of an encounter with the novel environment and subsequently used all of the zones. Sub-carangiform species also used 100% of the zones by the end of the study. Three of the four labriform/sub-carangiform swimmers used a maximum of 90% of the zones. There was no significant difference between species in their use of the zones. However, each individual zone was subject to differential use by the fish. Owing to the extensive scale of the aquarium, we discuss the applicability of the behavioural results obtained to the natural environment in the context of the ecology of the species of fish studied.

INTRODUCTION

The way in which a fish utilises a given habitat determines its acquisition of food, refuge or territory. More specifically, the differential ability of each species of fish to exploit a given resource is a function of their ecomorphological relationships (Motta *et al*, 1995) such as body size (Gill and Hart 1994, 1996; Aburto-Oropeza *et al.*, 2000) and locomotory ability (Webb, 1984; Webb *et al.*, 1996) in relation to the available resources. Coupled with these functional constraints is the dynamic ability to respond to resource opportunities, which vary on a spatial and temporal basis (Letourneur, 2000), which will also be influenced by the learning abilities of the fish (Croy and Hughes, 1991a). Hence, the behaviour of fish studied within a given habitat will be a consequence of a combination of these factors.

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In the natural environment, we observe fish at a particular point in their life where we assume they have experience, and therefore, some prior knowledge of the environment around them. In essence, we take a snapshot look at a particular period during their life within their chosen habitat. One potentially important concept that is difficult to quantify at present is how the fish would react to a novel environment about which they have no prior experience. We see an example of this during recruitment to a coral reef where the ability of fish larvae to discriminate between habitats is crucial for post settlement survival owing to the species-specific and individual requirements (Eckert, 1987; Doherty, 1991). The functional and learning abilities of a newly settled fish will influence the outcome of this initial period of an encounter with the novel environment. However, this is not the only time in the life cycle where a fish may encounter surroundings different to those to which it was previously exposed. Following natural (e.g. hurricane, volcanic) or anthropogenic (e.g. dynamite) perturbations, adult fish are likely to encounter a vastly changed topography and resource availability. In situations of this nature, the response of the adult fish will also be influenced by their ability to learn about the new environment and their functional capabilities. In addition, their specific resource requirements and the existence of other species competing for similar resources will shape the resettlement process.

In this context, aquariums can represent a change of habitat and resources when fish are first introduced. The modern day public aquarium aims to provide a representative display of the natural environment and the scale of some are large enough to provide an array of habitat opportunities ready for exploitation by the fish following first introduction.

The Blue Planet Aquarium, built in Ellesmere Port, Cheshire, UK was opened in July 1998. Prior to its opening to the public, an opportunity arose to investigate different Caribbean reef fish species from first introduction to the main aquarium exhibit. In order to take advantage of this opportunity, we had to work within the schedule of the aquarium staff which was determined by the arrival dates and acclimatisation of the fish. With these constraints in mind, we designed a behavioural ecology study that would increase our understanding of how the different species of reef fish responded to exposure to a novel environment in relation to their locomotory classification.

Although this is not a common occurrence, data obtained from such studies provide an opportunity to determine how fish react when introduced to an aquarium, representing a controlled environment, and provide possible correlates with data based on fish responses to new opportunities arising through such events as habitat displacement within their natural environment.

The principal aim of the study, therefore, was to investigate species-specific behavioural response to a novel environment in relation to time since a first encounter. We assumed that, in general, the rate of learning by the fish would be a major factor immediately on an encounter with the new environment (Hughes, 1997) and during the subsequent days, declining to a stable level after 5–7 days, as has previously been shown for laboratory studies on fish learning related to foraging by Croy and Hughes (1991a). We hypothesised that, during this period of learning, different species would react to a new habitat opportunity according to their functional capabilities such as locomotory mode and also their ecological determinants. This would likely have a bearing on the exploratory behaviour of the fish and would be manifest by differential use of the new environment. Hence, we predicted that spatial activity would be a function of both the rate of learning and the locomotory ability of the species.

METHODS

All observations took place between 13 June and 7 July 1998 at the Blue Planet Aquarium, Ellesmere Port, UK. The focus for the study was the main exhibit tank measuring 34 m × 26 m × 5 m (approx.) and containing 2,500,000 L of water maintained at 22°C and 32% salinity (Figure 1). The aquarium display, constructed entirely of cement, simulated a coral patch reef environment and was consistent with structures common to this type of coral reef (including massive and branching hard corals and sponges; pers. obs.). Where the bottom of the tank was not part of the coral reef structure, it was either a sand or hard substratum. Illumination from above the water provided a 12 : 12 h light : dark regime. Light levels, in units of $\mu\mathrm{E\,m^{-2}\,s^{-1}}$ were measured three times at the central point of each defined zone of the tank (Figure 1) using a submersible Macam Q102 radiometer with an SD101Q Cos sealed detector. Water movement was also measured three times at the central point of each zone with a current meter (Z210, A. Ott, Kempten).

All fish were collected by conventional techniques (net or line) along the coast of Florida, USA. Following standard transportation methods, the fish arrived at the aquarium a minimum of 13 h after capture. Following an acclimation period, which lasted approximately 1 h within a featureless, circular quarantine tank, the fish were introduced into the main tank through an access gate (Figure 1). Throughout the study period, food was haphazardly distributed by hand from the above water walkway three times a day, behavioural observations were never made during or around feeding times.

Nine species of fish were selected from the 15 species introduced, to represent a range of locomotory types (as defined by Blake, 1983) and in each case, at least two examples of a particular type were studied (Table 1). All the fish were adults in multiple species groups (Table 1) except for *Pomacanthus paru* which was represented by two advanced intermediate specimens. *Selene vomer*, *Caranx latus* and *Alectis ciliaris* were selected to represent carangiform swimmers that principally use their caudal fin as a propulsive force and confine undulations of the body to the posterior third of the body (Blake, 1983). This form of propulsion requires a high aspect ratio fin and is used by pelagic fish for sustained swimming. In a progression towards propulsion with a greater involvement of the anterior of the body, *Lutjanus griseus* and *Ocyurus chrysurus* were selected as sub-carangiform swimmers. Sub-carangiform fish are characterised by a highly flexible, low aspect ratio caudal

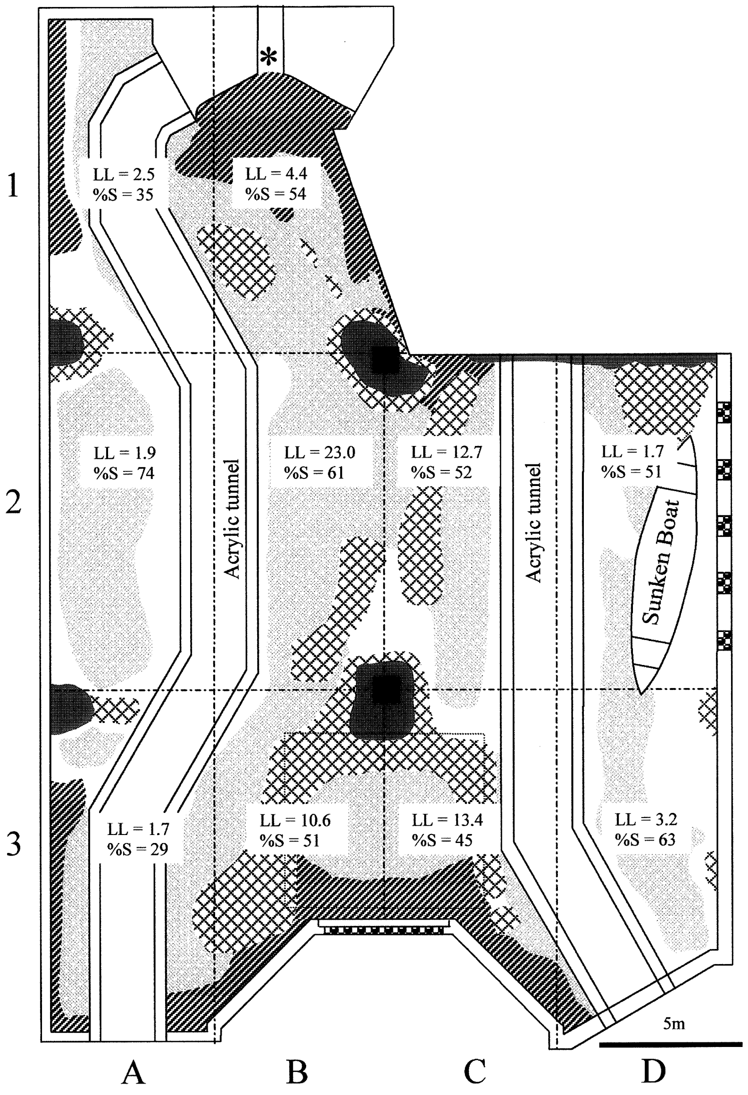

Figure 1. Plan view of the main exhibit tank, Blue Planet Aquarium incorporating the grid system (zones A1 – D3) used to divide up the tank for observational data collection. Key: LL = mean light level μE m^{-2} s^{-1}; % S = estimate of the % of zone area containing no structures, overhangs or tunnel. ▨ = Submerged overhangs surface to 0.5 m; ▩ = Submerged coral reef formations; ☐ = Sandy substratum; ☐ = Hard substratum; ▣ = Above water concrete platform; ■ = Metal Supporting structure; ▦ = viewing window; $*$ =Access Gate (All species introduced from this point); — · —· = Position of above water walkways and zone boundaries; - - - =6 m deep section, the remainder of the tank was 3.5–5 m deep.

Table 1. List of species observed and maximum number of individuals in aquarium during study. The swimming mode and the time between release and initiation of Phase I observations is given. n = number of behavioural observations

Species	Common name	Max no.	Phase I initiated	Swimming mode	*n*
Alectis ciliaris	African Pompano	26	On release	Carangiform	7
Selene vomer	Lookdowns	30	On release	Carangiform	8
Caranx latus	Horse-eye Jack	15	On release	Carangiform	5
Lutjanus griseus	Gray Snapper	13	Within 12 h	Subcarangiform	7
Pomacanthus paru	French Angel	2	Within 12 h	Labriform/Sub-carangiform	6
Ocyurus chrysurus	Yellowtail Snapper	50+	On release	Subcarangiform	8
Anisotremus virginicus	Porkfish	50+	Within 12 h	Labriform/Sub-carangiform	5
Abudefduf saxatilis	Sergeant Major	11	On release	Labriform/Sub-carangiform	7
Haemulon sciurus	Bluestriped Grunt	6	On release	Labriform/Sub-carangiform	8

fin, making them better suited to rapid acceleration than steady swimming. The remaining four species of fish were selected for their use of both the labriform and the sub-carangiform swimming types. *Haemulon sciurus, Anisotremus virginicus, Abudefduf saxatilis* and *P. paru* use their pectoral fins for propulsion when moving slowly over short distances. These labriform swimmers shift to sub-carangiform locomotion if acceleration or sustained swimming is required (Helfman *et al.*, 1997; pers. obs.).

Throughout this study, we considered the effect of time following introduction to a novel environment to be an influence on the spatial activity of the nine species of Caribbean reef teleosts. Therefore, two major aspects of the activity of each species of fish were examined in relation to time: (1) the level of locomotory activity; and (2) spatial distribution.

Visual observations were made from the above water walkways approximately 2 m from the water surface (Figure 1). All observations took place before the aquarium was open to the public, and any potential for disturbance by staff and labourers working around the aquarium was considered to be negligible as no fish were seen to react during the studies. Owing to some restrictions in accessibility to the aquarium and differences in the arrival dates and times of species, our observations were made on an opportunistic basis. The time of day when a species was observed was between 10 a.m. and 1 p.m. each study day.

For all visual observations the tank was divided into 10 zones of approximately equal size delineated by the above water walkways (Figure 1). Zones were labelled on a grid system from A1–D3 (Figure 1). Observations were made within two distinct time periods. Firstly, a series of between three and eight observations were made for each species between 13th and 24th June 1998. These were initiated either from the moment of introduction to the new environment (six species; Table 1) or within the first 12 h (three species which arrived during the night prior to their first observation; Table 1), and referred to as Day 1 in the subsequent analysis. In addition to the nine species studied, there were other species of teleost present during the observation periods (Table 2). Secondly, a single final observation was made for each of the nine species on the 6th or 7th July 1998. At this stage, there were a total of 15 different species in the tanks (Table 2) all of which had been present since 25th June 1998.

To investigate the effect of exposure to a novel environment on the relative activity levels of each species over time, a focal fish was chosen at random from a species group and sampled instantaneously at 30 s intervals for a period of 15 min. At each sample point we recorded in series the zone in which the focal fish was located. Any fish observed on a boundary between zones was recorded as being in the zone next visited. The level of locomotory activity of the fish was therefore defined within each 30 s interval according to three categories:

Type 0 = remained within a particular zone
Type 1 = moved to an adjacent zone
Type 2 = moved through one or more zones

Table 2. List of additional species present in the aquarium and the number of individuals of each species. The presence of each species in relation to the phase of the study is given

Species	Common name	Max no.	Phase present
Holocentrus ascensionis	Squirrelfish	2	I, II, III, IV
Carangoides crysos	Blue runner	50+	III, IV
Epinephelus guttatus	Red Hind	2	II, III, IV
Diodon histrix	Porcupinefish	2	I, II, III, IV
Balistes vetula	Queen Triggerfish	3	II, III, IV
Carcharias taurus	Sand Tiger Shark	4	IV

The fish had no individual identifiable markings; therefore, on each sampling occasion we chose any one individual fish from a group of the target species and followed it for the duration of the sampling period. We recorded whether the focal fish remained with the other fish in the group throughout the sample period. *H. sciurus and A. saxatilis* were treated as single fish observations, as they tended to be solitary or form very loose small aggregations. In addition, we noted any interactions of the focal fish with other fish sharing the vast aquarium. During 17% of observations, the focal fish disappeared from the view of the observer and the sampling was prematurely terminated. This was taken into account in the subsequent analysis by standardising the sample time.

Based on the principle that the rate of learning in fish decreases significantly from Day 1 reaching a constant level after around five days (Croy and Hughes, 1991a, b) we divided the recording of data into phases according to the time since introduction:

Phase I (Day 1)—the naïve period owing to no previous experience

Phase II (Day 2–4)—the period when the fish show a dramatic change in learning

Phase III (Day 5–13)—the period where the learning has reached a constant level

Phase IV (Day 18+)—the final record for a species, 10+ days after Phase III.

The data did not meet the assumptions of parametric statistics (Siegel and Castellan, 1988) and were therefore analysed using the non-parametric tests, $\chi^2$and Friedman ANOVA (with multiple comparison calculated manually with reference to Siegel and Castellan (1988)). All analyses were undertaken with the SPSS software.

RESULTS

Where a focal fish was a member of a group, it remained with the other shoal members for 91% of the observations throughout the observational sample period, hence the activity of any one focal fish closely matched that of the other individuals of the shoaling target species. There was a low level of interaction recorded between the fish species in the tank (33 occasions from 1560 records) with only 5 records of aggression. The few interactions observed were occasional mixing of shoals and inspection behaviour particularly when a species was first introduced to the aquarium.

Inter-specific activity

Significant differences in activity levels were observed among species (Friedman ANOVA, $\chi^2 = 18.667$, df=8, $p = 0.017$) with the carangiform fish being the most active followed by the sub-carangiform and then the labriform swimmers (Figure 2). Following Friedman ANOVA multiple comparison testing *Alectis ciliaris* was shown to have a significantly greater level of activity than *H. sciurus*, *O. chrysurus*, *P. paru*, *A. virginicus*, and *A. saxitilis* ($|R_u - R_v| \geq 15.18$ at $p = 0.05$). Whereas, *H. sciurus* had significantly lower activity levels than *A. ciliaris*, *S. vomer*, *C. latus* and *L. griseus* ($|R_u - R_v| \geq 15.18$). We therefore categorised the species into two groups based on their activity relative to the most and least active species: Group 1: active species; and Group 2: low activity species (Figure 2). Group 1 consisted of the three carangiform and one of the sub-carangiform species (*A. ciliaris*, *S. vomer*, *C. latus* and *L. griseus*). Group 2 was represented by the other species of sub-carangiform (*O. chrysurus*) and the labriform/sub-carangiform swimmers (*H. sciurus*, *P. paru*, *A. virginicus*, and *A. saxatilis*). There were no significant difference between the overall activity levels of fish classified within the same locomotory group (Friedman ANOVA multiple comparisons $|R_u - R_v| \leq 15.18$).

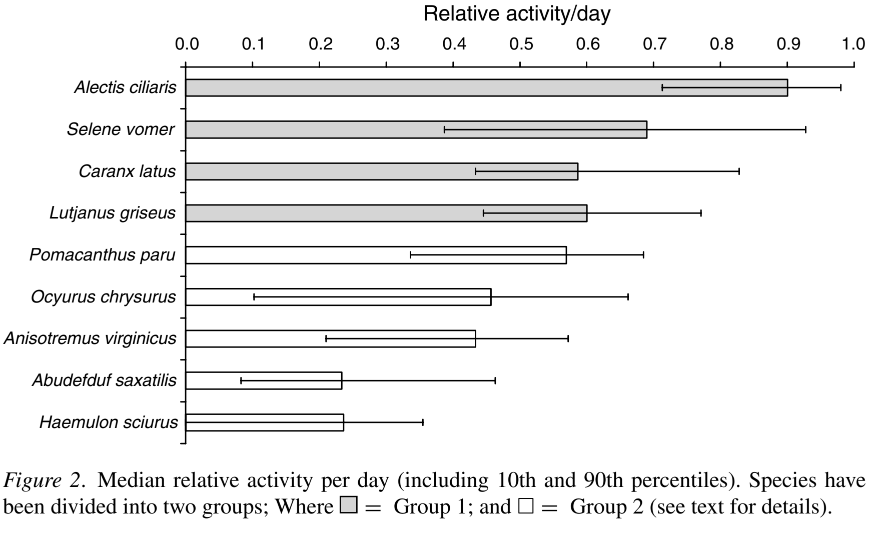

Figure 2. Median relative activity per day (including 10th and 90th percentiles). Species have been divided into two groups; Where ▨ = Group 1; and ☐ = Group 2 (see text for details).

Table 3. Statistically significant changes ($p < 0.05$) in activity within and between the different Phases based on data in Figure 4. (see text for details of Phases)

Species	Phases I and II	Phase III	From Phase III to IV
Alectis ciliaris	Increase	Stable	Stable
Selene vomer	Increase	Decrease	Stable
Caranx latus	Increase	Stable	Stable
Lutjanus griseus	Stable	Decrease+ increase	Decrease
Pomacanthus paru	Stable	Stable	Decrease
Ocyurus chrysurus	Increase	Decrease	Increase
Anisotremus virginicus	Stable	decrease	stable
Abudefduf saxatilis	Decrease	decrease	stable
Haemulon sciurus	Increase	decrease	increase

Individual species activity

When considering observations in their temporal sequence (Phase I–IV) through the study a number of significant changes in activity occurred and these were analysed in relation to the locomotory mode of the fish. Over the course of the various Phases of the study, some species exhibited stable activity levels, notably the carangiform swimmers (Table 3; Figure 3(a–c) while other species showed variable levels of activity (Table 3, Figure 3). All the species showed some degree of low activity (Type 0) during the observational period with the carangiform swimmers having the lowest activity during Phase I and all other species in the latter Phases (Figure 3). During Phases I and II, five species significantly increased their activity (*S. vomer* $\chi^2 = 24.36$, df $= 1$, $p < 0.001$; *C. latus* $\chi^2 = 15.92$, df $= 1$, $p < 0.001$; *A. ciliaris* $\chi^2 = 15.14$, df $= 1$, $p < 0.001$; *O. chrysurus* $\chi^2 = 6.36$, df $= 1$, $p = 0.01$; *H. sciurus* $\chi^2 = 8.78$, df $= 1$, $p = 0.003$; Table 2), three species did not significantly change activity level (*L. griseus* $\chi^2 = 3.45$, df $= 1$, $p > 0.06$; *A. virginicus* $\chi^2 = 1.38$, df $= 1$, $p = 0.24$; *P. paru* $\chi^2 = 0.67$, df $= 1$, $p = 0.41$; Table 3) and a single species, *A. saxitilis*, significantly reduced activity ($\chi^2 = 4.88$, df $= 1$, $p = 0.03$; Table 3).

Carangiform swimmers

When considering all the fish species studied, this category of swimmers utilised the greatest amount of Type 2 activity. Two of the three species classified as carangiform swimmers, *C. latus* and *A. ciliaris*, had a similar pattern of activity (Table 2, Figure 3a,c). During Phases I and II their activity increased reaching a constant level for the remainder of the study. (Phases III and IV, *C. latus* all $\chi^2 < 1.71$, df $=$ 1, $p > 0.18$; *A. ciliaris* all $\chi^2 < 2.47$, df $= 1$, $p > 0.12$). The other species in this category, *S. vomer,* was similar in its overall pattern to the other two species but with greater variability in activity level (Figure 3b). This species exhibited the same initial increase in activity between Phases I and II, however, during Phase II activity at first reduced ($\chi^2 = 5.68$, df $= 1$, $p = 0.02$) but then subsequently increased ($\chi^2 = 21.79$, df $= 1$, $p < 0.001$; Figure 3b). Throughout Phase III, *S.*

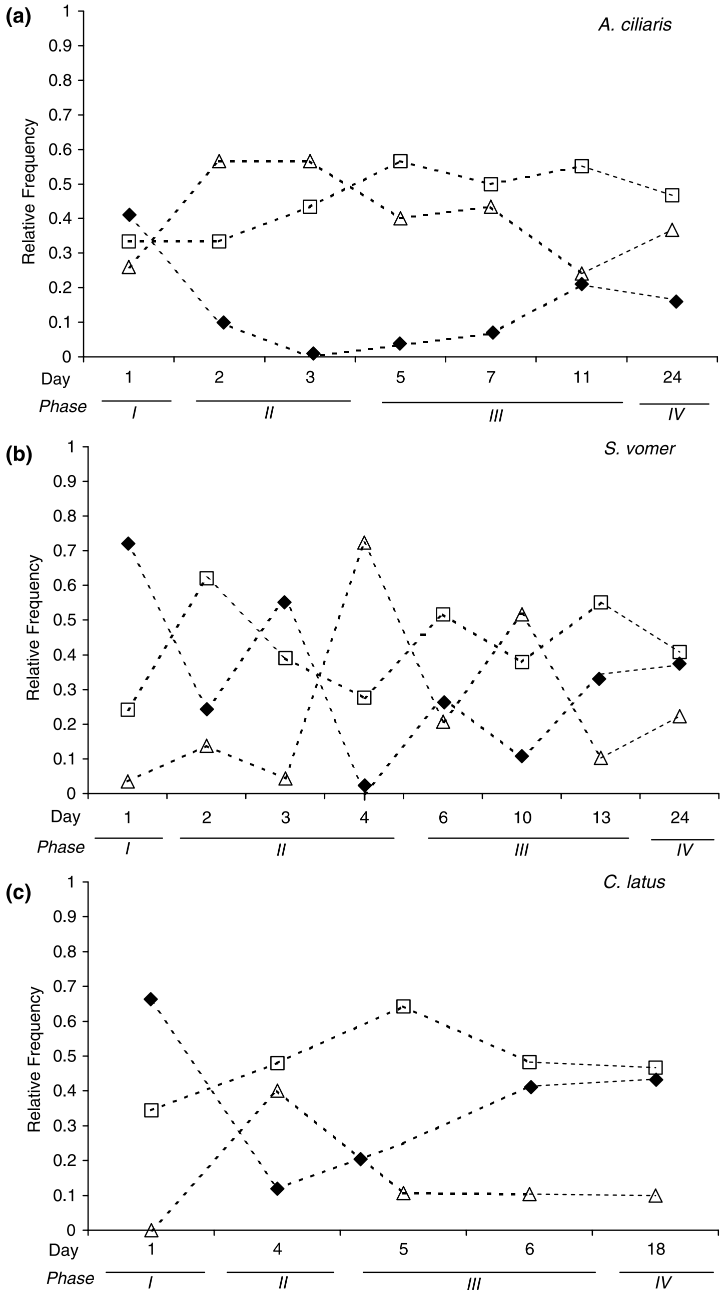

Figure 3. The relative frequency of Activity, Parts (a), (b), and (c).

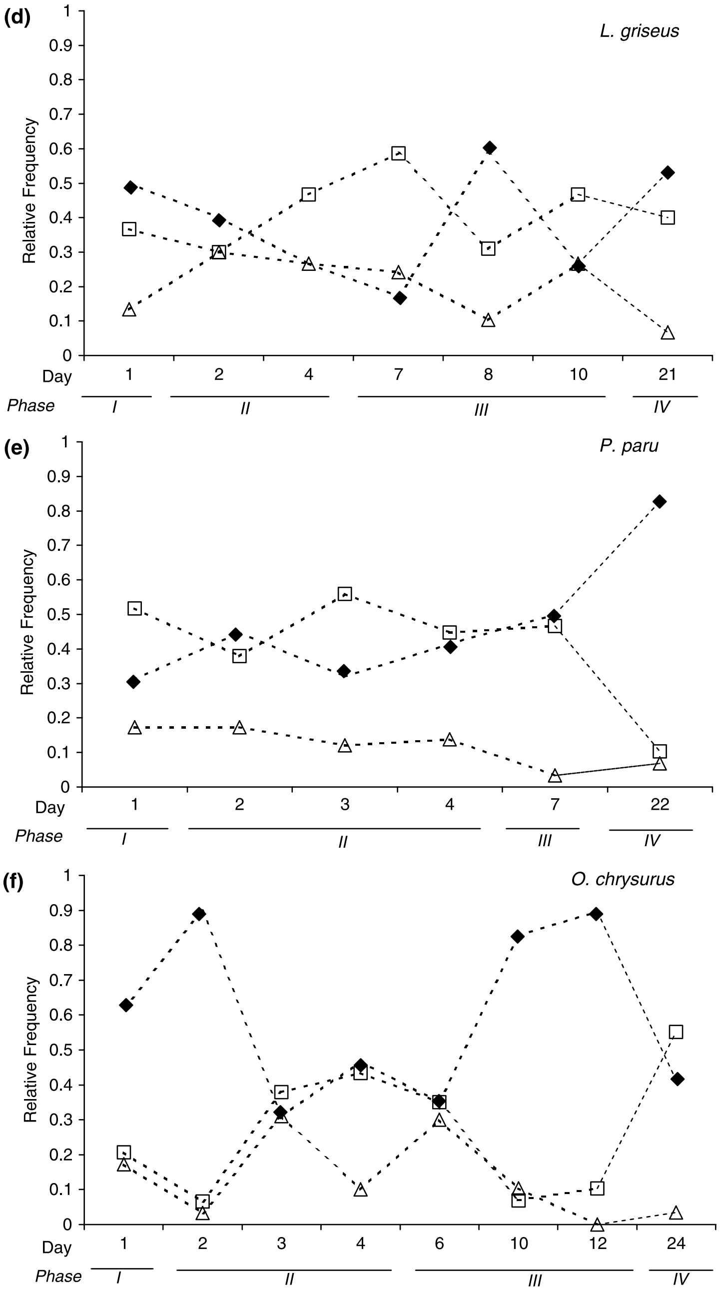

Figure 3. The relative frequency of Activity, Parts (d), (e), and (f).

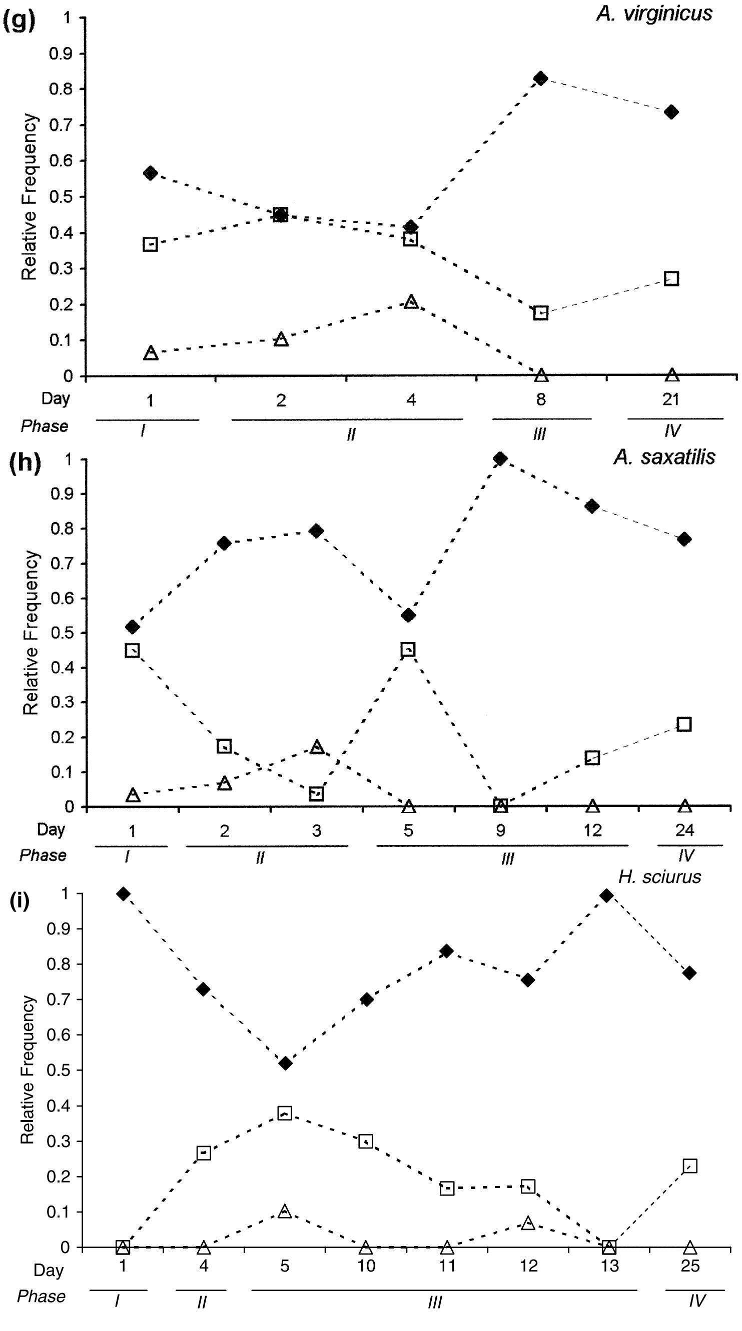

Figure 3. The relative frequency of Activity Type 0 (♦), 1 (□) and 2 (△) used by each species through time, where (a) = *Alectis ciliaris*, (b) = *Selene vomer*, (c) = *Caranx latus*, (d) = *Lutjanus griseus*, (e) = *Pomacanthus paru*, (f) = *Ocyurus chrysurus*, (g) = *Anisotremus virginicus*, (h) = *Abudefduf saxatilis* and (i) = *Haemulon sciurus*. Points are joined for ease of interpretation of activity levels both within and between Phases. The Phase of observation is indicated by the horizontal line below each day (see text for details).

vomer gradually reduced its activity (all $\chi^2 > 4.86$, df $= 1$, $p < 0.03$; Figure 3b), however, no significant change was found between the level of activity at the end of Phase III and the beginning of Phase IV ($\chi^2 = 0.04$, df $= 1$, $p = 0.84$).

Sub-carangiform swimmers

The two species classified as sub-carangiform swimmers did not have a similar response although they used a moderately high level of Type 2 activity. *O. chrysurus* increased its activity during Phases I and II ($\chi^2 = 21.47$, df $= 1$, $p < 0.001$; Table 3), whereas *L. griseus* had stable levels of activity over this same period ($\chi^2 < 1.2$, df $= 1$, $p > 0.27$; Table 2). During Phase III both species varied considerably in their activity level (Figure 3d, f). The activity of *L. griseus* firstly decreased and then subsequently increased (both changes $\chi^2 > 6.15$, df $= 1$, $p < 0.02$; Figure 3d), whereas *O. chyurus* decreased its activity ($\chi^2 = 11.61$, df $= 1$, $p < 0.001$; Figure 3f) after which it remained at a low level ($\chi^2 = 0.58$, df $= 1$, $p = 0.45$). For both species Phase IV activity was significantly different from the final observation of Phase III ($\chi^2 > 4.44$, df $= 1$, $p < 0.04$).

Labriform/sub-carangiform

These fish used Type 0 and 1 activities demonstrating that their movements were over shorter distances than the other categories of swimmers. A stable level of activity was seen in *P. paru* throughout the first three Phases of the study ($\chi^2 < 1.17$, df $= 1$, $p > 0.27$; Table 2; Figure 3e), only in Phase IV was its activity significantly reduced ($\chi^2 = 7.06$, df $= 1$, $p = 0.007$; Figure 3e). Similarly, *A. virginicus* activity was stable during Phases I and II ($\chi^2 < 0.83$, df $= 1$, $p > 0.36$; Figure 3g), which included utilising Type 2 activity, but there was a subsequent reduction in activity, particularly Type 2, during Phase III ($\chi^2 = 10.55$, df $= 1$, $p = 0.001$; Figure 3g) which continued for the remainder of the study ($\chi^2 = 0.76$, df $= 1$, $p = 0.38$; Figure 3g).

H. sciurus and *A. saxatilis* were highly variable in their levels of activity throughout the four Phases of the study. *H. sciurus* was the only species with 100% Type 0 activity (no movement between zones) during Phase I (Figure 3i), however, it did significantly increase its activity by the end of Phase II ($\chi^2 = 8.78$, df $= 1$, $p = 0.003$; Figure 3i). The activity of *H. sciurus* did not change significantly during Phase III until day 13 ($\chi^2 = 8.22$, df $= 1$, $p = 0.004$) when, once again, activity was 100% Type 0 (Figure 3i). During Phase IV, activity was at a relatively low level, however, it was not significantly different from three out of the five observations in Phase III ($\chi^2 < 0.36$, df $= 1$, $p > 0.54$). *A. saxatilis* was the only species that displayed reduced activity during Phases I and II ($\chi^2 = 4.88$, df $= 1$, $p = 0.03$; Table 2; Figure 3h). In Phase III, this species utilised a moderate level of Type 1 activity followed by a highly significant reduction to 100% Type 0 activity ($\chi^2 = 15.98$, df $= 1$, $p < 0.001$). Activity had

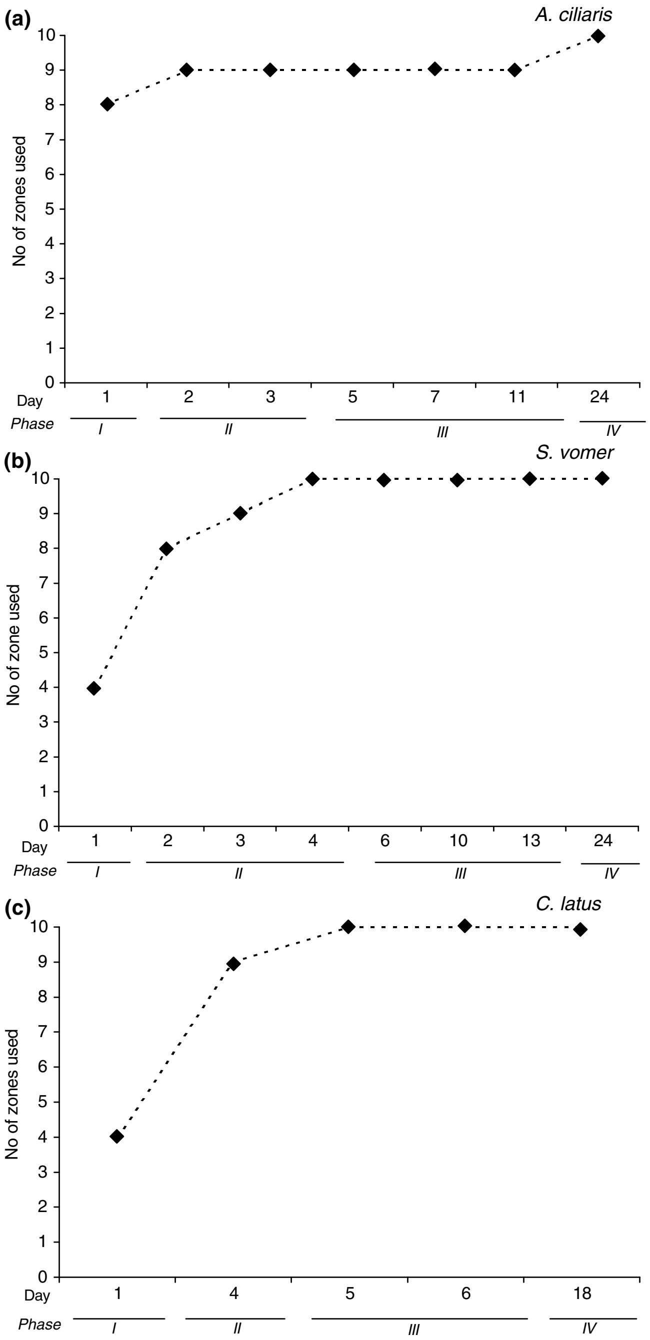

Figure 4. Cumulative number of zones, Parts (a), (b), and (c).

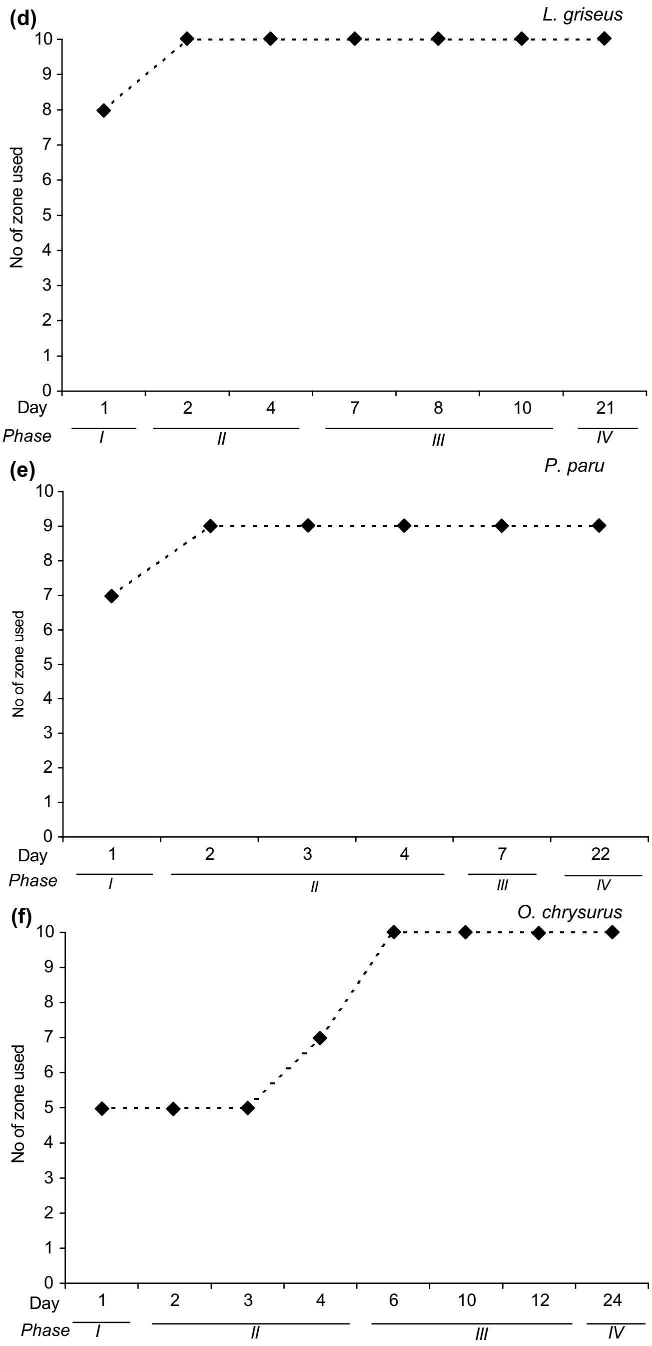

Figure 4. Cumulative number of zones, Parts (d), (e), and (f).

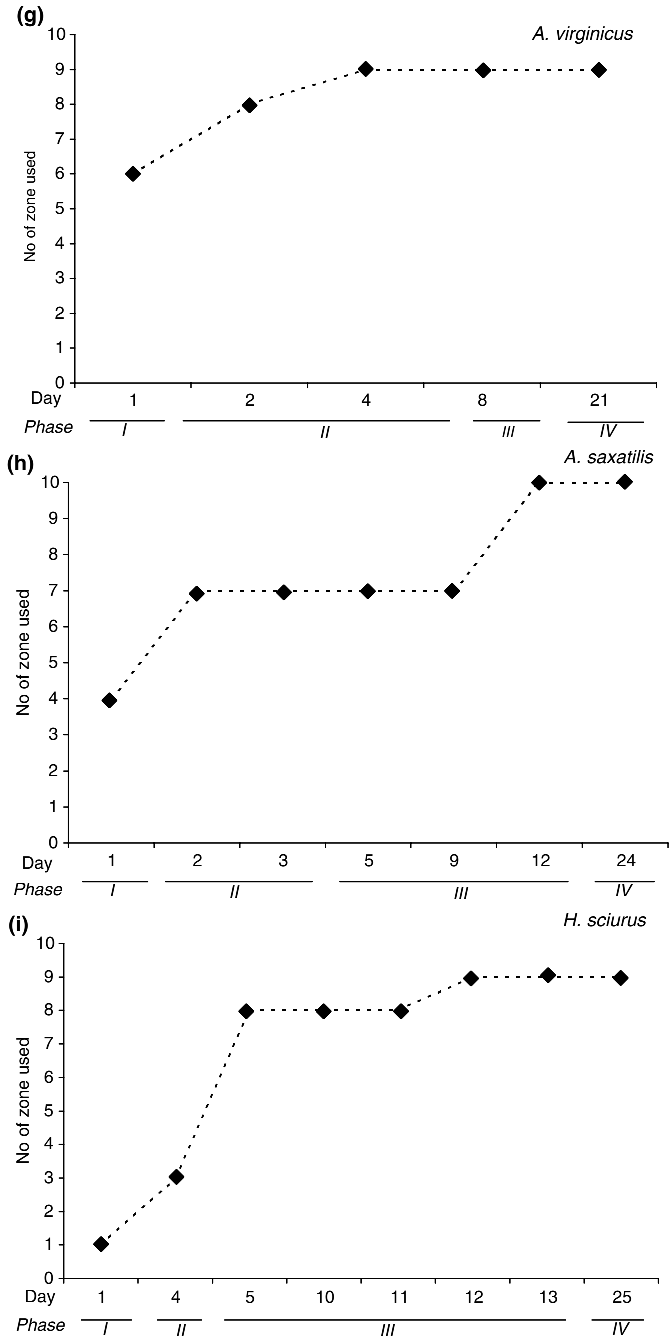

Figure 4. Cumulative number of zones used by the fish during the study period, where (a) = *Alectis ciliaris*, (b) = *Selene vomer*, (c) = *Caranx latus*, (d) = *Lutjanus griseus*, (e) = *Pomacanthus paru*, (f) = *Ocyurus chrysurus*, (g) = *Anisotremus virginicus*, (h) = *Abudefduf saxatilis* and (i) = *Haemulon sciurus*.

Table 4. Percentage frequency of zone use for the nine species observed. Mean (±S.D.) percentage zone use is shown for comparison between zones.

	Zone									
Species	A1	A2	A3	B1	B2	B3	C2	C3	D2	D3
Alectis ciliaris	7.5	13.2	13.2	13.2	13.2	11.3	11.3	9.4	5.7	1.9
Selene vomer	6.1	8.2	8.2	14.3	14.3	10.2	12.2	12.2	8.2	6.1
Caranx latus	8.3	8.3	11.1	11.1	11.1	11.1	11.1	13.9	8.3	5.6
Lutjanus griseus	6.7	8.9	13.3	6.7	11.1	13.3	11.1	11.1	6.7	11.1
Pomacanthus paru	7.5	12.5	15.0	12.5	12.5	10.0	15.0	7.5	0.0	7.5
Ocyurus chrysurus	5.7	5.7	17.1	17.1	20.0	11.4	8.6	2.9	5.7	5.7
Anisotremus virginicus	3.8	7.7	15.4	11.5	15.4	19.2	11.5	11.5	0.0	3.8
Abudefduf saxatilis	6.5	3.2	12.9	12.9	19.4	16.1	12.9	9.7	3.2	3.2
Haemulon sciurus	3.6	10.7	14.3	10.7	10.7	21.4	14.3	10.7	3.6	0.0
Mean % use	6.2	8.7	13.4	12.2	14.2	13.8	12.0	9.9	4.6	5.0
S.D.	1.6	3.1	2.6	2.8	3.5	4.2	1.9	3.2	3.1	3.3

increased moderately at the end of Phase III ($\chi^2 = 4.29$, df $= 1$, $p = 0.04$; Figure 3h) and this level was maintained into Phase IV ($\chi^2 = 0.88$, df $= 1$, $p = 0.35$; Figure 3h).

Spatial distribution

Six of the nine species of fish were observed to use all the zones over the study period (Figure 4). The three species that did not were *H. sciurus* (which was not observed in zone D3; Table 4), *A. virginicus* and *P. paru* (both of which were not observed in zone D2; Table 4). Overall, the most frequently visited zone was B2 (the centre of the tank) and the least visited zones were D2 and D3 (Table 4). The number of zones used during Phase I (day of release) varied considerably between species and locomotory mode (Figure 4).

Carangiform swimmers

All Carangiform swimmers were observed in 100% of the zones over the study period and had used at least 90% of them by the end of Phase II (Figure 4(a–c)).

Sub-carangiform swimmers

Both sub-carangiform swimmers used 100% of the zones over the study period. *L. griseus* used 80% of the zones in Phase I and had used 100% of them by Phase II (Figure 4d). *O. chyurus*, however, only used 50% of the zones in Phase I and 70% by the end of Phase II. *O. chyurus* used the remaining zones during Phase III (Figure 4f).

Labriform/sub-carangiform

Three of the four labriform/sub-carangiform swimmers, *H. sciurus, A.virginicus* and *P. paru*, used a maximum of 90% of the zones over the study period (Figure 4e, g, i). *H. sciurus* and *A. saxatilis* showed a low level of zone use in Phase I, using one and four zones respectively (Figures 4h, i). By the end of Phase II, *A. virginicus*, *A. saxatilis* and *P. paru* had all used at least 70% of the zones, however, *H. sciurus* had only used 30% .

Physical attributes of the aquarium

The light level of each zone varied (Figure 1), but there was no water movement detected for any of the zones (0 revolutions of the current meter per 15 s measurements for all zones). Zones A2, B2 and D3 were characterised by a high percentage of space free from structures and obstacles (Figure 1) whilst zones A1 and A3 had the lowest amount of open water space (Figure 1). There was no significant specific use of one or more zones by a particular species (Friedman ANOVA $\chi^2 = 0.97$, df $= 8$, $p = 0.998$).

Each of the defined zones were, however, subject to differential use by the fish resulting in zones A1, D2 and D3 being utilised significantly less by all the fish than all the other zones (Friedman ANOVA $\chi^2 = 51.23$, df $= 10$, $p < 0.001$; Multiple comparisons ($|R_u - R_v| \geq 25.18$ at $p = 0.05$). Hence, the zones adjacent to the most centrally located zone (B2) had the highest frequency of use by all the fish (Table 3). As well as being closer to the centre of the aquarium, these zones had the highest light levels and possessed an average amount of structural features (Figure 1).

DISCUSSION

Through the application of behavioural ecology techniques to the modern aquarium environment, we have been able to effectively elucidate some of the ways in which different species of coral reef fish respond in terms of their activity and distribution to an encounter with a novel environment. The study also demonstrates that ecologically relevant data can be obtained from aquariums, thus providing an additional avenue of investigation to address the current dearth of information that exists owing to practical and logistical limitations of studying specific aspects of the fish directly on the reef.

The study was devised with two main aims: determination of how the exploration of a novel environment by reef fish varied between species with differing locomotory abilities and ecological requirements; and how these fish responded through time since their initial encounter with the environment. An implicit assumption was that the behavioural response was mediated to some degree by the rate of learning of each species. In the present study, we had to assume that this was standard for all fish species studied owing to the paucity of information and poor understanding of learning abilities of specific species (Croy and Hughes, 1991a). We suggest that this is a topic which requires much greater attention in order that further studies do not oversimplify the analysis. Nevertheless, we can assume that learning will increase the efficiency of resource use by a species (Croy and Hughes, 1991a; Hughes, 1997), which was one of the main assumptions that we applied to the present study.

Interspecific activity

We divided the nine species observed into two distinct groups based on their level of activity. The more active fish, which naturally occupy the open water around a reef (Humann, 1994) utilised the available space faster and showed less variability in activity than the less active fish, represented by the more classically defined reef associated species (Humann, 1994). However, an important and consistent result was that all species, regardless of their activity level, extensively explored the novel environmental rather than settling on the first suitable area that they encountered. From this result, we would therefore expect that on its initial encounter, any fish would first extensively explore the habitat available, with the length of time spent exploring varying according to locomotory mode. For this prediction to hold, it is also crucial for us to take into account the ecological requirements of the species and their influence on exploration.

Territorial fish, such as members of the Pomacentridae, have particular site associated requirements in terms of food and refuge and will therefore be limited to habitats that are not already occupied and that satisfy their resource requirements. Some other species, which appear less reef associated, depend on visually distinct physical features of the reef, for example, during twilight migration (Helfman and Schultz, 1984). Even species, such as the carangiforms, which appear to have the least dependence on the reef will have boundaries to their utilisation of the water column owing, in part, to their crepuscular movements towards the reef to prey upon reef species that are settling down for the night (Hobson, 1972, 1991; Helfman, 1993). In addition, the extent of movement of the fish will have an upper limit as a result of swimming capability in relation to the size of suitable habitat and resource requirements. Hence, phenotypic constraints are likely to be important influences on the behavioural response of a fish to a novel environment in addition to any predatory or competitive influences that may exist.

In our study we observed how these phenotypic constraints act, but in addition, there was a dynamic component through time. Following the initial phases, either a decrease or a more stable phase of activity was entered suggesting the fish had gained sufficient knowledge of the aquarium environment. The reef associated species took longer to enter this phase which may be a result of the length of time that it takes them to assess and learn about the heterogeneous environment typified by a reef or a result of differential learning ability of these species.

Carangiform swimmers

All carangiforms initially increased their activity, eventually reaching a plateau of relatively high activity during Phase III. This result is particularly interesting when considering the context of the study. The fish were recorded from first introduction to the novel environment (a singular occurrence), and a random individual of each species was selected on each sampling day. There was a high probability that the focal fish remained with its conspecifics in a group, hence the activity and distribution recorded was similar within a species group. In addition, an interspecific comparison of the carangiform species demonstrated that they exhibited a similar behavioural response and levels of activity.

Even though two of the carangiform swimmers (*S. vomer* and *C. latus*) had some of the lowest levels of zone use on Day 1, this category of fish used at least 90% of the zones by the end of Phase II (<4 days) demonstrating that these swimmers explored the majority of the tank soon after introduction. This increase in zone use during the initial stages was linked with an increase in both Type I and II activity.

The sustained high level of activity recorded would be expected if we consider the ecology of open water swimmers which have evolved sustained swimming allowing them to cover large volumes of water as part of their daily activity pattern. The aquarium carangiform fish therefore responded in a manner that we predicted from our knowledge of the species ecology.

Sub-carangiform

Within the study period no stable level of activity could be determined in this category of fish. In addition, there was no common response, which is likely to have been a consequence of the highly variable behavioural activity recorded for these fish. *L. griseus* and *O. chrysurus* incorporate a wide range of habitat types within their known distribution (Humann, 1994), hence this diversity of habitat association is likely to cause variation in response to newly available habitat. Also, these fish tend to have alternating periods of high and low activity (Hobson, 1991; Helfman, 1993; pers. obs.) therefore, a more specific study design may be needed to determine the subtleties in activity of this category of fish.

Labriform/sub-carangiform

There was a species-specific response, which generally corresponded with our predictions, based on the ecology of these species.

Following an initial period of active exploration, *H. sciurus* and *A. saxatilis* both lowered their levels of exploratory activity in the later phases. These fish represent species closely associated and dependent on the reef (Humann, 1994).

A. virginicus, a roaming reef species, was stable in its level of activity over the initial period with a decrease in activity towards the latter stages. This species used most of the aquarium zones within Phases I and II, then lowered its movement between zones. Again this suggests the fish were reducing their level of activity once they had learnt about the novel environment.

From the outset, *P. paru* had a high but stable level of activity, which only reduced towards the end of the study. Field observations of *P. paru* have found that they form close pairings and defend large territories that often overlap with conspecifics resulting in agonistic confrontations (Moyer *et al.*, 1983). This would suggest that the pair of advanced intermediate *P. paru* used in this study might have maintained a high level of activity as a response to defining and patrolling a territory within the novel environment, although very few aggressive interactions were recorded.

A. saxatilis was the only species studied other than *P. paru*, that forms distinct territories, however, they differ on the spatial scale of respective territory size. *A. saxatilis* forms a small feeding territory and is one of the least aggressive of the pomacentrids (DeLoach, 1999). It may, therefore, be expected that *A. saxatilis* would take less time and require less activity to set up and maintain a territory in a new environment without prior residents, which may explain the early drop in activity seen in this species. However, the important result is that this species, although territorial, explored the majority of the aquarium when it first encountered this novel environment.

Spatial activity

By zoning the aquarium we were able to determine the extent of spatial activity of each species. In general, the use of available space was determined by the mode of swimming which was a function of time since exposure to the novel environment.

The labriform swimmers were the most likely not to use all the zones but we would not expect them to avoid an area because of physical structure, as they are highly manoeuvrable swimmers (Webb *et al.*, 1996).

Carangiform swimmers together with the sub-carangiform, *L. griseus*, and the labriform/sub-carangiform *A. virginicus* and *P. paru* showed relatively high levels of zone use during the initial phases of the study. All of these species, although classically defined as distinct in terms of swimming mode, represent the more active or roaming species that inhabit the reef environment. Conversely, the less active species *A. saxatilis*, and *H. sciurus* took longer to utilise the available space. *O. chrysurus* was the only species where we expected greater activity levels predicted from their natural movement around the reef.

There was a significant preference for some of the zones of the aquarium by all the fish species. No movement of the water was recorded hence we can discount this factor. We recorded the available light as diurnal reef fish, such as representatives from the genera studied, are known to alter activity during twilight periods of the day when light levels reduce dramatically and the fish become more vulnerable to predation (Hobson, 1991; Helfman, 1993). The zones with the highest use by the fish had the greatest light levels recorded. It is worth noting, however, that the carangiform swimmers were not of a large enough size to represent a predatory threat to the other species, hence reducing the importance of direct predatory threat as a factor determining spatial use by the fish.

General discussion

The generic behavioural response to an encounter with a novel environment by the different fish species was similar: they extensively explored their new surroundings. However, species response varied according to length of time since initial encounter. There was greater variability in activity of the more reef associated fish whereas the carangiform species, which are the least reef associated, showed the lowest variability in response to encounter with novel environment.

It has therefore been shown that introduction of fish to a novel environment results in a distinct behavioural response which is a function of swimming mode and availability of habitat. In previous studies, observations of swimming behaviour of fish within 7 h of release have been attributed to exploration of the novel environment (Kleerekoper *et al.*, 1974; Mikheev and Andreev, 1993). Kleerekoper *et al.* (1974) identified both a spatial organised pattern of movement and a temporal response controlled by the novelty of the environment. The present study was designed to observe behavioural changes over a greater temporal scale. However, if the initial activity on Day 1 had been solely associated with exploratory behaviour, then we would expect subsequent days to show a decrease in activity levels as the novelty of the environment decreased. Only one species, *A. saxatilis*, decreased its activity whereas the remaining species observed increased activity over the first two Phases. This suggests that for these species, the initial Phase was associated with an additional factor, possibly related to the length of the recovery period required following the long trans-Atlantic transportation time.

A major factor when considering the ability of a fish to learn about new surroundings is the size of the tank. Obviously the smaller the tank the quicker fish are likely to learn about the surroundings, hence a decrease in activity would be expected. We therefore assume that in our study there was a recovery stage followed by an exploratory phase which was over a long period owing to the vast size of the tank, and then stabilisation of activity in most of the species. Whether this type of response matches that occurring in the natural environment remains to be determined.

Many species of captive fish have been shown to exhibit complex social and individual behaviours that are the same as those observed *in situ* on the reef (Lorenz *et al.*, 1998). In their study Lorenz *et al.* (1998) further suggested that the range of fish behaviours seen *in situ* determines those that will be recorded in captivity, hence we will encounter behaviours in aquariums that occur at sometime in the natural environment. The Lorenz *et al.* (1998) study was, however, within an aquarium with dimensions that would be considered small in comparison to the Blue Planet Aquarium. Furthermore, the aquarium tank used in the present study had a topographical complexity similar to that of a natural coral reef. Of course, a coral reef will be different particularly in terms of fish density, diversity, resource availability and predator presence. However, large scale aquarium studies represent a useful study resource as their scale and setting is more comparable to the real situation than small-scale laboratory studies. By increasing the number of different aquariums involved in studies of this nature, we can compare situations both between aquariums and the natural environment. Therefore, it is with greater confidence that we can relate the behavioural response we have seen with what may happen in the natural environment.

Relation to the natural environment

Although this study is based on one aquarium, we can still provide some informed discussion relating to the natural setting. Our study investigated the response of fish to a novel environment, which is a scenario that is likely to occur to some extent in nature following a tropical storm event. Storms in coral reef areas occur frequently enough to be considered as characteristic of tropical latitudes where they can impact catastrophically upon the substrata and sessile biota (Stoddart, 1971). Within coral reef fish communities, severe environmental instabilities and perturbations, such as hurricanes and cyclones, have a significant influence on succession (Connell, 1978), recruitment and habitat partitioning (Sale, 1977). For the reef dwelling fish (such as the Pomacentridae), disturbances of this kind affect the type of habitat and living space available (Lassig, 1983) and thus create a need for re-colonisation. Alternatively, perturbations may be less severe but have asymmetric impact on the different life stages within the fish communities through high juvenile mortality, redistribution of sub-adults and short term spatial displacement of adults (Lassig, 1983).

Dramatic changes in habitat can have a cascading effect on resource availability which is fundamental for reef species. Tricas (1989) found that butterflyfish (Chaetodontidae) alter the size of their territory according to food availability which can itself vary in spatial occurrence and is subject to perturbation from a variety of sources. For less reef associated species (such as the Carangidae), changes in the reef structure are not likely to cause a direct effect on the fish as their immediate environment will not change dramatically but they would still need to adapt to indirect effects such as changes in the availability of food or increased turbidity (Lassig, 1983). In our study, we purposely avoided data collection during the feeding periods in order to examine the importance of spatial activity in the fish. We would assume that if we provided food at particular points in the aquarium, and at specific times, then the fish spatial activity would reflect this. If we assume that the aquarium fish obtained enough food, our results provide evidence that there are still species-specific differences in movement and distribution out with the feeding periods.

It is also important to consider the temporal variability in response by the fish as it may be a major factor when considering how a particular species will adapt to new resource opportunities. For example, when presented with novel prey, fish have the ability to modify their behaviour with respect to improving the efficiency of feeding (Wainwright, 1986). The degree of modification of the behavioural response will depend largely on the extent to which the fish concerned can adapt to the current conditions (Dill, 1983). In addition, behaviour is a dynamic process which is altered through experience (Croy and Hughes, 1991a and b) and motivation to acquire resources (Gill and Hart, 1999).

Comparing an aquarium of this size with the natural environment is reasonable when we consider that factors affecting recruitment of fish on small patch reefs are more important than on large reefs (Lowe-McConnell, 1987). Settlement and availability of habitat will play major roles in the resultant density and species make up of fish assemblages. Studies of the colonisation of artificial reefs gives us some indication of the mechanisms by which juveniles recruit to novel environments (Sale and Dybdahl, 1975). Yet there are very few opportunities for observation of post recruitment behaviour. Consequently large-scale aquarium studies are of potential value for ethological and ecological research, as previously suggested by Lorenz *et al.* (1998). Based on the fundamental behavioural techniques applied in this study it would be feasible to investigate, in an aquarium setting, the sequential response of larval fish during the settlement process. There is also potential application to ontogenetic studies that experimentally investigate the responses and identify the cues that different fish life stages utilise when encountering a novel environment. There may be ontogenetic changes in the ability of fish to respond to a new habitat particularly as experience gained through learning is likely to be influential. For example, juvenile fish are known to be less efficient feeders than older conspecifics until they have learnt about prey specific properties and escape strategies, these can only develop through experience of encounters with prey (Blaxter, 1985).

CONCLUSIONS

As field studies of fish response to new environments are limited, a consequence of the unpredictable occurrence and opportunistic nature of this type of data collection, aquarium studies provide a base from which we can address some important questions and hypotheses about the relationship between reef fish and their dynamic environment but, importantly, with an element of control. Hence, such studies can provide us with important indicators of how reef fish are likely to respond to dramatic changes in their physical environment and provide species-specific data such as variability in response to environmental changes. The next challenge is to continue to expand studies of this nature and combine them with new field techniques and technology which can determine the level of correspondence in the data obtained from the semi-natural setting of the aquarium.

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