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REPORT

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Vertical distributions of late stage larval fishes in the nearshore waters of the San Blas Archipelago, Caribbean Panama

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Abstract Light traps were used to describe the vertical distribution of late larval stages of reef fishes in the San Blas Archipelago during three successive new moon periods. Traps were deployed in the lagoon and at an exposed site on the outer reef edge. At each site, two traps were anchored at the surface and two traps just above the bottom. Most families of reef fishes that were abundant in catches displayed clear patterns of depth preference. The larvae of gerrids, pomacentrids and lutjanids were predominantly captured in shallow traps, while gobiids, labrids, apogonids and blenniids were usually collected in deep traps. Studies that used lights to aggregate and collect larval fishes display marked differences in the composition of catches between the Great Barrier Reef (GBR) and the Caribbean. In order to determine whether such results were due to biases inherent in different sampling methods, or to locality-specific patterns of larval behaviour, we simultaneously deployed light traps and dip-netting around lights during three new moons in the San Blas Archipelago. We found that these sampling techniques collected differing components of the larval fish assemblage from the same water mass. However, there remains good evidence for the existence of locality-specific responses to light in older larval stages, suggesting that broad generalisations about patterns and causes of vertical distributions may be difficult to achieve.

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Introduction

Zooplankton assemblages display patterns of vertical stratification in both freshwater and marine ecosystems (Hutchinson 1967; Hanley 1988; Neilson and Perry 1990). While vertical distributions and movement patterns of ichthyoplankton have been described in temperate marine environments (Heath 1992), there have been relatively few comparable studies of this behaviour by young fishes in the waters around coral reefs (Leis 1991a, 1991b; Bolhert et al. 1992; Cowen and Castro 1994). Such information is central to an understanding of larval ecology, since vertical distributions will influence the transport and dispersal of fish larvae by currents and interactions between larvae, their food and predators (Leis 1991a, 1991b; Heath 1992; Cowen and Castro 1994; Jenkins et al. 1998, 1999).

Nearly all studies of the vertical distributions of the larvae of coral reef fishes have used net tows to describe patterns. This technique samples only very young pre- or immediately post-flexion larvae, as older larval stages are able to avoid collection due to advanced sensory and swimming abilities (Choat et al. 1993). Such young larvae provide limited information, since it is well known that larval fishes display marked changes in patterns of vertical distribution among ontogenetic stages (Fortier and Harris 1989; Heath et al. 1991; Olivar and Sabates 1997). To date, only one study has attempted to describe the vertical distributions of older larvae. Doherty and Carleton (1997) used light traps to sample young fishes in the nights just prior to their settlement around a single coral reef on the GBR. They found that most were collected in surface waters, while the larvae of only two families (the Holocentridae and Chaetodontidae) were more abundant in deeper samples. While this suggests that, similar to younger forms, older larvae also display taxon-specific patterns in vertical distribution, it is dif-

ficult to determine the generality of these results, given the limited spatial extent and duration (only six nights) of their sampling.

Here, we use light traps to describe the vertical distribution of larvae in the waters close to coral reefs in the San Blas Archipelago, Caribbean Panama. Spatial and temporal variation in these patterns was assessed by sampling in different reef habitats and by conducting the sampling program over a number of months. In addition, we report the results of a sampling technique comparison. In a previous study in the Archipelago, Victor (1986) used dip-netting around a light in shallow water to sample larval fishes. His catches of reef fishes were dominated by taxa that are rarely captured in light traps on the GBR, such as labrids and acanthurids (Victor 1991). There are two possible interpretations of these results. They may reflect locality-specific differences in behaviour of larvae, or they may result from the biases inherent in each sampling technique. If the former is the case, then the patterns of distribution described by our study should be interpreted with caution when comparisons are made between regions such as the Caribbean and the GBR. In order to distinguish between these possibilities, we concurrently sampled larval fishes using light traps and netting around lights in the Archipelago and compared the species composition and abundances of catches from both techniques.

Methods

Study site

The San Blas Archipelago (9°34′N, 78°58′W) extends along the Caribbean coast of Panama in Central America. The sites sampled in this study were at the Smithsonian Institute's field station, the lagoon and an exposed outer reef site that was subject to prevailing winds from the north-east (Fig. 1) Sampling was conducted during the dry season, which is characterised by low rainfall and strong trade winds (Robertson 1992). The dry season receives less recruitment than the wet season, although many taxa still have peak episodes of replenishment during this period (Robertson 1992; Robertson and Kaufmann 1998; Wilson 2001). Mean tidal variation in the Archipelago is 0.4 m (maximum 0.6 m) and water temperatures ranged from 27 to 29 °C during the study period.

Vertical distribution

Previous work in the Archipelago has demonstrated that 95% of the monthly recruitment of reef fishes occurs in the 19 consecutive nights centred on the new moon (Wilson 2001). For this reason, light traps were used to sample the vertical distributions of reef fish larvae for 19 consecutive nights centred on the new moon in each of three consecutive lunar cycles, from 21 October to 8 November 1997, from 20 November to 8 December 1997 and from 20 December 1997 to 7 January 1998. Traps were deployed in the lagoon and at an exposed windward site (Fig. 1). At each site, two traps were moored 1.5 m below the surface and two were moored 1.5 m above the bottom. Each trap was separated from its nearest neighbour by approximately 100 m. Water depth in the lagoon was 12 m and 20 m at the exposed site. The light trap design was similar to that of Stobutzki and Bellwood (1997). Briefly, the trap consisted of a single perspex chamber with a tube running through its centre attached to a waterproof (water resistant to 70 m) electrical housing. The chamber opened to the exterior by horizontal slits (1.5 cm high by 25 cm wide), through which photopositive organisms could enter the trap. The slits were tapered to discourage escapement. An 8-W fluorescent tube was used as a light source. The perspex chamber was protected by an aluminium frame, to which a buoy was tied. When the trap was removed from the water after fishing, catches accumulated in a detachable plastic filter (500 μm mesh) box on the trap base. Traps were deployed at dusk each night and retrieved the following day at dawn. Catches were preserved in 75% ethanol. In the laboratory, fishes were sorted from invertebrates, counted and wherever possible identified to species.

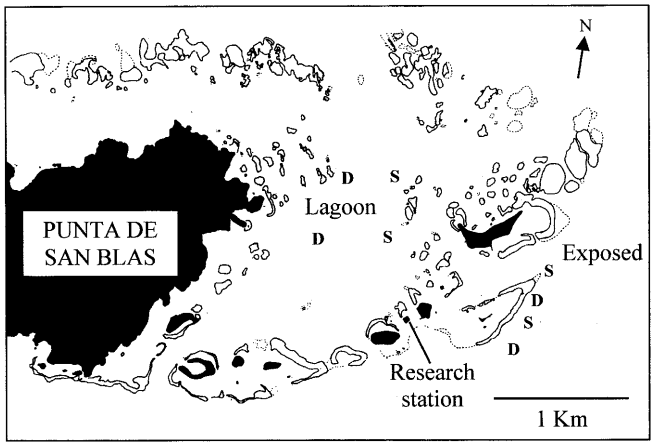

Fig. 1 Sites where vertical distribution patterns of reef fish larvae were sampled using light traps in the San Blas Archipelago, Caribbean Panama. *S* Surface traps; *D* deep traps. (Modified from Robertson et al. 1999)

Light trap and netting comparison

Netting and light trap sampling were conducted at or near the time of the new moon from 21 October to 8 November 1997, from 24 November to 4 December 1997 and from 24 December 1997 to 1 January 1998. The duration of sampling in the second and third of these cycles was restricted to only 11 and 9 nights respectively due to inclement weather conditions. On each night, sampling commenced after dark between 1900 and 2000 h. A kerosene lamp and a fluorescent light were used in the dip-net sampling. These lights were hung over the water from the end of docks at the Smithsonian field station. Each type of light was separated from the other by approximately 100 m. Below the light an aquarium dip-net (mouth dimensions 20×12 cm with 500 μm mesh) was drawn through surface waters, then periodically emptied into a container. The different lights were sampled sequentially for 15 min periods, each for a total of 30 min per night.

Immediately prior to the start of netting, a light trap was deployed on a mooring adjacent to the station, approximately 100 m from the lights at the ends of the docks. After 1 h the trap was retrieved and the catch preserved in alcohol. Most fishes could be immediately identified to species or type, although it was occasionally necessary to grow out very small larvae in an aquarium before they could be identified.

Data analysis

Data sets from the vertical distribution study were analysed using an agglomerative, hierarchical clustering technique to discern associations among samples. Dissimilarity was calculated with the Bray-Curtis coefficient (Bray and Curtis 1957) and incremental

sums of squares strategy used to cluster samples into groups. The test provided by Sandland and Young (1979) was used to determine the significance of divisions in dendrograms. In order to confirm the results of clustering techniques, data sets were re-analysed using an ordination technique, multidimensional scaling (MDS) (Field et al. 1982). Prior to analyses, raw data were standardised using a $\log_{10}(x+1)$ transformation to improve multivariate normality. To reduce the number of zero values, data sets were pooled among nights of sampling within each new moon period and species where fewer than ten individuals were collected were then excluded. This gave a data set of 42 species for the analysis.

Monthly collections for the nine most abundant families of reef fishes were analysed using the non-parametric Kruskal-Wallis test to determine whether catches differed between deep and shallow traps, as the data sets failed to meet the assumptions of parametric tests (Levene's test; Zar 1996). Data sets from the netting and light trap comparison could not be analysed using multivariate techniques due to the sporadic occurrence of diagnostic taxa in catches. The data sets could not be stratified by time in order to avoid this problem due to relatively low catch rates. Consequently, samples were pooled and the composition of catches by each technique compared visually.

Results

Vertical distribution

Nearshore light traps collected a total of 48,671 fish from 36 families during the three lunar cycles of the study. Samples were dominated by three families of clupeoids, which accounted for 87% of all catches. A total of 6,103 reef fishes were caught and these were equally distributed between deep and shallow traps (1.12 ± 0.018 per h, t-test, $t = 0.37$, $p = 0.75$). Apogonids, gerrids, pomacentrids, synodontids, labrids, gobiids, blenniids, lutjanids and acanthurids accounted for 92% of the total catch of reef fishes (Table 1).

The classification analysis split the samples into four major clusters (Fig. 2a). Both locality and depth effects were evident in the data. The first split of the dendrogram separated all catches made by deep traps at the exposed site from the remaining samples. The next split separated most catches made by shallow traps at the exposed site from most lagoon catches. Generally, light traps deployed in the lagoon collected a lower richness and abundance of larvae than those at the exposed site (Fig. 2b). All deep catches from the lagoon were then split from the remaining shallow traps. The species composition of each of the groups identified by the dendrogram is shown in Fig. 2b.

The groups identified by the cluster analysis matched those in the MDS analysis (Fig. 2c). As in the dendrogram, there was a major division in the data between samples at the exposed and lagoon sites. Shallow catches were separated from deep catches in both exposed and lagoon sites. Of the nine most abundant families of reef fishes collected by the traps, seven displayed clear patterns of depth preference (Table 1). Both apogonid and blenniid larvae were predominantly captured in deep traps, as were the larvae of gobiids and labrids (Kruskal-Wallis $H = 3.857$, $p = < 0.05$). In contrast, the larvae of gerrids, pomacentrids and lutjanids were predominantly captured in shallow traps (Kruskal-Wallis $H = 3.857$, $p = < 0.05$; Table 1). Abundances of acanthurids and synodontids did not differ significantly between shallow and deep traps (Kruskal-Wallis $H = 0.429$, $p = 0.513$ and $H = 1.190$, $p = 0.275$ respectively).

Patterns in the depth distribution of fishes collected in the shallow traps tended to be consistent among all species within a family. However, this was not the case for families that were predominantly captured in deep traps, with some species displaying a trend in abundance opposite to that of the remainder of the family. For example, *Astrapogon puncticulatus*, an apogonid, was most abundant in catches in shallow traps, while the family as a whole tended to be more abundant in deep traps (Table 1). Similarly, the labrid *Thalassoma bifasciatum* was more abundant in catches in shallow traps, while most other members of this family were more abundant in catches in deep traps (Table 1).

Light trap and netting comparison

Netting and light traps collected similar total numbers of reef fish per h of sampling (14.29 ± 0.73, one-way ANOVA, $F = 0.034$, $p = 0.95$). Catches by netting around both kerosene and fluorescent lights peaked in the first few nights of sampling and then declined. In contrast, catches in the light trap peaked just before the new moon (Fig. 3). Catch compositions of the different sampling methods are summarised in Table 2. Netting using the kerosene lamp caught 23 species from 16 families, while netting using the fluorescent light yielded 39 species from 23 families. A total of 42 species from 21 families were collected by the light trap. Catches using the kerosene lamp and fluorescent light were dominated by gerrids, labrisomids, labrids and monacanthids, while light trap catches were dominated by gobiids, haemulids, blenniids and labrids.

Discussion

Virtually all the abundant taxa collected in this study demonstrated vertical stratification of distribution patterns in nearshore waters. There were both similarities and differences between the patterns we identified in San Blas and those recorded for the same families of reef fishes on the GBR by Doherty and Carleton (1997) (Table 1). As in San Blas, these workers found that pomacentrids were an abundant component of catches on the GBR, and were predominantly collected by traps deployed at the surface. In contrast, Doherty and Carleton (1997) collected most apogonids and blenniids in surface traps, while these taxa were most abundant in deep samples in our study.

Ropke (1993) and Olivar and Sabates (1997) suggest that for temperate fishes, the vertical distributions of

Table 1 Composition of catches from shallow (*S*) and deep (*D*) traps pooled among months, shown as a percentage of total catch. Results from light trap study of depth distributions of larvae of coral reef fishes on the GBR by Doherty and Carleton (1997) are also shown. *n* Total numbers; *T* percentage of total catch for each family

Taxa	Current study					Doherty and Carleton (1997)		
	n	T	S	D	*n*	T	S	D
Acanthuridae	110	1.80	0.55	1.25				
Acanthurus bahianus			0.06	0.18				
Acanthurus chirurgus			0.46	1.02				
Acanthurus coeruleus			0.03	0.05				
Apogonidae	1,093	17.91	4.83	13.08	87	12.83	10.32	2.51
Apogon maculatus			0.20	0.49				
Apogon planifrons			0.36	0.02				
Apogon sp. 1			0.13	3.36				
Apogon sp. 2			0.57	3.51				
Astrapogon puncticulatus			3.24	0.21				
Phaeoptyx pigmentaria			0.33	5.49				
Aulostomidae	1	0.02	0.02					
Aulostomus maculatus			0.02					
Balistidae					1	0.15		0.15
Blenniidae	447	7.32	1.16	6.16	45	6.64	5.75	0.89
Blenniid type 1			0.13	3.26				
Blenniid type 2				0.20				
Blenniid type 3				0.85				
Blenniid type 4			0.31					
Blenniid type 5			0.24	1.62				
Ophioblennius atlanticus			0.46	0.02				
Parablennius marmoreus			0.02	0.21				
Bothidae	12	0.20	0.17	0.03				
Bothus lunatus			0.05					
Bothus ocellatus			0.08	0.03				
Syacium micrurum			0.02					
Paralichthys albigutta			0.02					
Bregmacerotidae	81	1.33	0.21	1.12	1	0.15		0.15
Bregmaceros atlanticus			0.21	1.12				
Carangidae	30	0.49	0.41	0.08	9	1.33	1.33	
Chloroscombrus chrysurus			0.41	0.05				
Selene vomer				0.03				
Chaetodontidae	12	0.20	0.03	0.17	5	0.74	0.15	0.59
Chaetodon capistratus			0.03	0.15				
Chaetodon ocellatus				0.02				
Chaenopsidae	16	0.26	0.02	0.24				
Hemiemblemaria simulus			0.02	0.24				
Congridae	8	0.13		0.13				
Congridae spp.				0.13				
Dactylopteridae	1	0.02	0.02					
Dactylopterus volitans			0.02					
Elopidae	71	1.16	0.60	0.56				
Megalops atlanticus			0.60	0.56				
Gerridae	1,022	16.74	16.42	0.32				
Eucinostomus melanopterus			16.42	0.32				
Gobiesocidae	1	0.02	0.02					
Gobiesox punctulatus			0.02					
Gobiidae	685	11.22	0.35	10.87				
Coryphopterus dicrus				1.32				
Coryphopterus glaucofraenum				0.02				
Coryphopterus personatus			0.02	8.68				
Gnatholepis thompsoni			0.33	0.69				
Gobiosoma saucrum				0.16				
Grammistidae					1	0.15	0.15	
Haemulidae	52	0.85	0.80	0.05				
Haemulidae spp.			0.80	0.05				
Holocentridae	7	0.11		0.11	30	4.43	2.95	1.48
Holocentrus vexillarius				0.11				
Labridae	686	11.24	3.77	7.47				
Halichoeres bivittatus			0.03	0.13				
Halichoeres garnoti			0.03	0.02				
Halichoeres maculipinna				0.02				
Halichoeres poeyi			0.02					

Table 1 (Continued)

Taxa	Current study				Doherty and Carleton (1997)			
	n	T	S	D	*n*	T	S	D
Labrid type 1			0.47	5.26				
Labrid type 2			0.02	1.29				
Labrid type 3				0.10				
Labrid type 4				0.03				
Thalassoma bifasciatum			3.20	0.62				
Labrisomidae	12	0.20	0.10	0.10				
Labrisomus nuchipinnis			0.07	0.08				
Malacoctenus triangulatus			0.03	0.02				
Lutjanidae	234	3.83	3.43	0.40				
Lutjanus sp. 1			0.36	0.02				
Lutjanus sp. 2			0.16					
Lutjanus sp. 3			0.02					
Lutjanus sp. 4			0.02					
Lutjanus chrysurus			0.50	0.10				
Lutjanus mahogani			2.37	0.28				
Monacanthidae	26	0.43	0.23	0.20	144	21.24	14.27	6.97
Monacanthus setifer			0.23	0.20				
Mullidae	5	0.08	0.05	0.03	71	10.47	10.47	
Pseudupeneus maculatus			0.05	0.03				
Nomeidae					24	3.54	3.54	
Polynemidae	8	0.13	0.10	0.03				
Polydactylus virginicus			0.10	0.03				
Pomacanthidae	1	0.02	0.02					
Pomacanthus arcuatus			0.02					
Pomacentridae	753	12.34	11.68	0.66	234	34.51	33.04	1.47
Abudefduf saxatilis			0.03					
Microspathodon chrysurus			0.12					
Stegastes diencaeus			0.13					
Stegastes dorsopunicans			4.23	0.23				
Stegastes leucostictus			0.11					
Stegastes partitus			2.67	0.10				
Stegastes planifrons			4.31	0.23				
Stegastes variabilis			0.08	0.10				
Priacanthidae	2	0.03		0.03				
Priacanthus cruentatus				0.03				
Scombridae	19	0.31	0.16	0.15	13	1.92	1.31	0.61
Scomberomorus regalis			0.16	0.15				
Scorpaenidae	1	0.02	0.02		2	0.30	0.30	
Scorpaena plumeri			0.02					
Serranidae	6	0.10	0.05	0.05	2	0.30	0.30	
Epinephelus cruentatus			0.02					
Serranid type 1				0.03				
Serranid type 2			0.03					
Serranid type 3				0.02				
Sphyraenidae	1	0.02	0.02					
Sphyraena barracuda			0.02					
Synodontidae	688	11.27	4.18	7.09	1	0.15		0.15
Synodontidae spp.			4.18	7.09				
Sygnathidae					5	0.74	0.44	0.30
Tetraodontidae	1	0.02	0.02		2	0.30	0.30	
Sphoeroides spengleri			0.02					
Tetraponidae					1	0.15	0.15	
Trichiuridae	11	0.18		0.18				
Trichiurus lepturus				0.18				

larvae of species in the same genus tend to be similar worldwide. While the contrasting patterns found in San Blas and on the GBR imply that this may not be true for tropical reef fishes, this result must be interpreted with caution, as the distributions reported by Doherty and Carleton (1997) were derived from very small sample sizes. For example, only 45 blenniids of four different species and 87 apogonids of six species were collected by these workers in over 80 deployments of traps. Our results are likely to be more robust, since they are based on total catches of reef fishes that were almost an order of magnitude greater than those of Doherty and Carleton (1997). However, some species in San Blas did display opposite trends in depth distribution to others in the same family, most notably the wrasse *Thalassoma bifasciatum* and the apogonid *Astrapogon puncticulatus*.

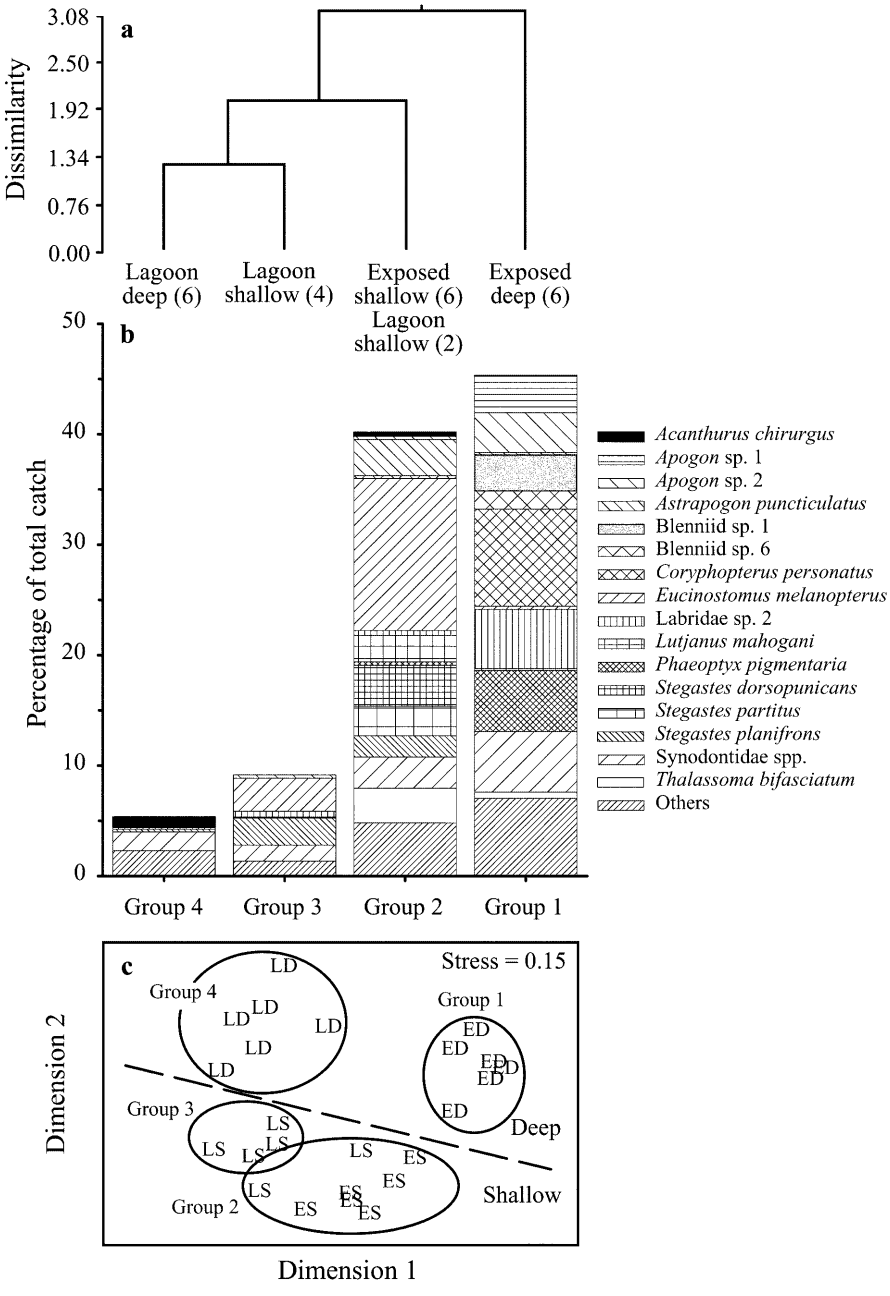

Fig. 2 Summary of Bray-Curtis classification and multi-dimensional scaling (MDS) analyses of vertical distribution data sets. **a** Dendrogram produced by UPGMA classification analysis. Numbers of sites within each group are shown in *parentheses*. **b** Histogram showing the species composition of each group. **c** Scatter plot from MDS analysis. Groupings produced by the classification analysis are superimposed on the plot. *E* Exposed sites; *L* lagoon sites; *D* deep traps; *S* shallow traps

Both were relatively abundant in catches and were predominantly collected in surface traps, while the remaining species in the same families tended to be most abundant in deep traps. The reasons for these contrasting patterns are unknown; they did not reflect the targeting of different ontogenetic stages by the light trap technique as larvae of all species were usually collected at a similar stage of development (Wilson 2001).

Leis (1991b) found marked stratification of the vertical distribution of young (mostly pre- or immediately post-flexion) larval stages around coral reefs of the GBR during the day, although at night larvae were equally spread throughout all depths in the water column. Our study shows that such ubiquitous distributions at night are not maintained as larvae develop. Rather, older stages appear to actively control their vertical distribution in the same way as younger larvae during the day. Leis (1991b) suggested that the broad distribution of young larvae at night might result from a cessation of swimming for energy conservation and a loss of orientation. The increasing sophistication of the sensory and locomotory systems of larvae during ontogeny (Leis and Carson-Ewart 1997, 1999; Job and Bellwood 2000) may allow them to select and maintain their position in the water column at night. Studies of vertical distributions have generally found that older larvae occupy deeper waters than young larvae (e.g. Bolhert et al. 1992), although Leis (1991a, 1991b) suggested that this is not necessarily the case in all tropical regions. Leis' (1991a, 1991b) suggestion is supported by the results of our

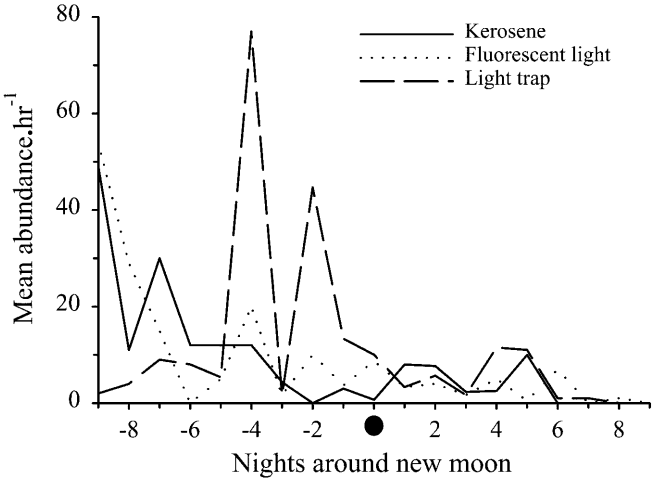

Fig. 3 Mean numbers of fish per h collected each night by the three sampling techniques. ● New moon

Table 2 Percentage composition of catches from netting and light trap sampling. Results are shown for different light sources used in the netting program. Figures are based on totals of 263 and 291 pre-settlement fish collected around kerosene and fluorescent lamps respectively and 564 fish collected in light traps

Family	Kerosene	Fluorescent	Light trap
Acanthuridae			0.71
Apogonidae	1.90	1.72	6.91
Blenniidae	0.76	2.75	8.87
Bothidae	0.38		0.18
Bregmacerotidae	0.38	0.35	0.71
Carangidae			0.18
Chaetodontidae	0.38	0.35	
Chaenopsidae		0.35	0.18
Congridae/Muraenidae	1.90		0.35
Dactylopteridae		0.35	
Diodontidae	0.76		
Elopidae	3.42	2.41	2.84
Gerridae	30.42	37.80	3.19
Gobiesocidae		1.03	
Gobiidae	3.80	2.75	38.11
Haemulidae	3.80	3.09	11.52
Hemiramphidae		0.34	
Labridae	8.75	12.03	8.33
Labrisomidae	26.62	21.65	6.74
Monacanthidae	10.27	4.12	4.79
Ostraciidae			0.18
Pomacentridae	0.76	1.03	0.18
Scombridae		0.34	0.18
Scorpionadae		0.34	0.18
Serranidae		0.34	0.53
Sphyraenidae		0.34	
Sygnathidae		4.12	
Synodontidae	5.70	2.06	5.14
Tetraodontidae		0.34	

study, where similar numbers of older reef fish larvae were collected in deep and shallow traps, and by the work of Doherty and Carleton (1997) who found that shallow traps were far more productive than those deployed in deep water. However, the selective nature of the sampling technique may confound these results, since our findings and those of Doherty and Carleton (1997) are based only on the subset of larvae that are photopositive and willing to enter a trap. Such species may not necessarily be representative of the entire larval assemblage.

A variety of hypotheses have been proposed to explain patterns of vertical distribution in ichthyoplankton (reviewed by Heath 1992). These include both behavioural (e.g. feeding and predation: Fortier and Harris 1989) and physical factors (e.g. currents: Bolhert et al. 1992; Cowen and Castro 1994; light intensity: Blaxter 1988; Leis 1991a). Job and Bellwood (2000) recently examined the development of visual sensitivity in the larvae of coral reef fishes and found that apogonids were an order-of-magnitude more sensitive to light than pomacentrids, allowing them to feed at lower light intensities. They suggested that such differences in visual abilities account for the tendency of larval apogonids to occur in deeper water than pomacentrids (e.g. Leis 1991b; Bolhert et al. 1992).

We found that, similar to young larvae, the older larvae of apogonids were usually collected by deep traps, while pomacentrids were collected at the surface. However, these distributions are difficult to reconcile with light intensity and feeding, since we deployed traps in only 20 m or less of water. Job and Bellwood (2000) found little apparent difference in the feeding ability of the older larvae of these families at such depths, even in eutrophic coastal waters. Thus, it seems that for fish nearing the end of the pelagic stage, light levels are probably only one of a number of factors determining vertical distributions.

The extent to which we can generalise about the processes underlying vertical patterns will depend on the amount of interspecific variation that occurs in the behaviour of larval reef fishes. Our concurrent sampling of light traps and netting around lights suggested that at least some of the variation in catch composition among studies may result from the biases inherent in sampling methods (see also Choat et al. 1993), rather than differences in the response of larvae to light. Despite this result, it is obvious that larval fishes do exhibit locality-specific behaviours. Comparison of our results with those of multi-season light trap studies on the GBR (Milicich 1992; P. Doherty, unpublished data) and in Barbados (Sponaugle and Cowen 1996) shows that in all localities, pomacentrids and blenniids were relatively abundant in catches. In contrast, acanthurids, labrids and lutjanids were only collected regularly in the Caribbean, while scarids, which were abundant in Barbados, are a very rare component of light trap catches on the GBR (P. Doherty, personal communication). These patterns in catch composition do not reflect temporal differences in sampling among studies, as each deployed traps during summer recruitment seasons over a number of years. Furthermore, the results of an 18-month light trap study in San Blas (Wilson 2001) confirm that our results were typical of longer-term patterns. It is also unlikely that these differences could be attributed to the biases of the varying trap designs used by each study. Meekan et al.

(2001) compared the traps used in the present study and a larger design that has been used extensively on the GBR. They found that although there were small differences in abundance of catches, the species and size range of fishes collected by the two designs were virtually identical. Consequently, such variability in catch composition implies that the larvae of some families respond differently to light and/or are more susceptible to the sampling technique among localities. These variations in larval behaviour are intriguing and, given the proposed importance of light as a structuring factor (Blaxter 1988; Leis 1991b; Job and Bellwood 2000), suggest that broad generalisations about the vertical distributions of older larvae may be difficult to realise.

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References

Blaxter JHS (1988) Sensory performance, behaviour, and ecology of fish. In: Atema J, Fay RR, Popper AN, Tavolga WN (eds) Sensory biology of aquatic animals. Springer, Berlin Heidelberg New York, pp 203–232

Bolhert GW, Watson W, Sun LC (1992) Horizontal and vertical distributions of larval fishes around an isolated oceanic island in the tropical Pacific. Deep-Sea Res 39:439–466

Bray JR, Curtis JT (1957) An ordination of the upland forest communities of southern Wisconsin. Ecol Monogr 27:325–349

Choat JH, Doherty PJ, Kerrigan BA, Leis JM (1993) A comparison of towed nets, purse seine, and light-aggregation devices for sampling larvae and pelagic juveniles of coral reef fishes. Fish Bull 91:195–209

Cowen RK, Castro L (1994) Relation of coral reef fish larval distributions to island scale circulation around Barbados, West Indies. Bull Mar Sci 54(1):228–244

Doherty PJ, Carleton JH (1997) The distribution and abundance of pelagic juvenile fish near Grub Reef, Central Great Barrier Reef. Proc 8th Int Coral Reef Symp 2:1155–1160

Field JG, Clarke KR, Warwick RM (1982) A practical strategy for analysing multispecies distribution patterns. Mar Ecol Prog Ser 8:37–52

Fortier L, Harris RP (1989) Optimal foraging and density dependent competition in marine fish larvae. Mar Ecol Prog Ser 51:19–33

Hanley JF (1988) Diel patterns of zooplankton behaviour. Bull Mar Sci 43:583–603

Heath MR (1992) Field investigations of the early life stages of marine fish. Adv Mar Biol 28:1–174

Heath MR, Brander K, Munk P, Rankine P (1991) Vertical distributions of autumn spawned larval herring (*Clupea harengus* L.) in the North Sea. Cont Shelf Res 11:1425–1452

Hutchinson GE (1967) A treatise on limnology. Wiley, New York

Jenkins GP, Welsford DC, Keough MJ, Hamer PA (1998) Diurnal and tidal vertical migration of pre-settlement King George whiting *Sillaginodes punctata* in relation to feeding and vertical distribution of prey in a temperate bay. Mar Ecol Prog Ser 170:239–248

Jenkins GP, Black KP, Keough MJ (1999) The role of passive transport and the influence of vertical migration on the pre-settlement distribution of a temperate demersal fish: numerical model predictions compared with field sampling. Mar Ecol Prog Ser 184:259–271

Job SD, Bellwood DR (2000) Light sensitivity in larval fishes: implications for vertical zonation in the pelagic zone. Limnol Oceanogr 45(2):362–371

Leis JM (1991a) The pelagic stage of reef fishes: the larval biology of coral reef fishes. In: Sale PJ (ed) The ecology of fishes on coral reefs. Academic Press, San Diego, pp 183–227

Leis JM (1991b) Vertical distribution of fish larvae in the Great Barrier Reef lagoon, Australia. Mar Biol 109:157–166

Leis JM, Carson-Ewart BM (1997) In situ swimming speeds of the late pelagic larvae of some Indo-Pacific coral-reef fishes. Mar Ecol Prog Ser 159:165–174

Leis JM, Carson-Ewart BM (1999) In situ swimming and settlement behaviour of larvae of an Indo-Pacific coral-reef fish, the coral trout *Plectropomus leopardus* (Pisces: Serranidae). Mar Biol 134:51–64

Meekan MG, Wilson SG, Halford A, Retzel A (2001) A comparison of catches of fishes and invertebrates by two light trap designs in tropical NW Australia. Mar Biol (in press)

Milicich MJ (1992) Light traps: a novel technique for monitoring larval supply and replenishment of coral reef fish populations. PhD Thesis, Griffith University, Brisbane

Neilson JD, Perry RI (1990) Diel vertical migrations of marine fishes: an obligate or facultative process? Adv Mar Biol 26:115–168

Olivar MP, Sabates A (1997) Vertical distribution of fish larvae in the north-west Mediterranean Sea in spring. Mar Biol 129:289–300

Robertson DR (1992) Patterns of lunar settlement and early recruitment in Caribbean reef fishes in Panama. Mar Biol 114:527–537

Robertson DR, Kaufmann KW (1998) Assessing early recruitment dynamics and its demographic consequences among tropical reef fishes: accommodating variation in recruitment seasonality and longevity. Aust J Ecol 23:226–233

Robertson DR, Swearer SE, Kaufmann K, Brothers EB (1999) Settlement vs environmental dynamics in a pelagic-spawning reef fish at Caribbean Panama. Ecol Monogr 69(2):195–218

Ropke A (1993) Do larvae of meso-pelagic fishes in the Arabian Sea adjust their vertical distribution to physical and biological gradients? Mar Ecol Prog Ser 101:223–235

Sandland RL, Young PC (1979) Probabilistic tests and stopping rules associated with hierarchical classification techniques. Aust J Ecol 4:399–406

Sponaugle S, Cowen RK (1996) Nearshore patterns of coral reef fish larval supply to Barbados, West Indies. Mar Ecol Prog Ser 133:13–28

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

Victor BC (1986) Larval settlement and juvenile mortality in a recruitment-limited coral reef fish population. Eco Monogr 56(2):145–160

Victor BC (1991) Settlement strategies and biogeography of reef fishes. In: Sale PF (ed) The ecology of fishes on coral reefs. Academic Press, San Diego, pp 231–279

Wilson DT (2001) Patterns of replenishment of coral reef fishes in the nearshore waters of the San Blas Archipelago, Caribbean Panama. Mar Biol (in press)

Zar JH (1996) Biostatistical analysis. Prentice-Hall, Englewood Cliffs