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# Epibenthie Fish Larvae in the Great Barrier Reef Lagoon near Lizard Island, Australia

Jeffrey M. Leis, Barry Goldman and Sally E. Reader

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**Abstract** Epibenthic fish larvae near Lizard Island in the Great Barrier Reef Lagoon were sampled with a plankton sled during daylight in November 1981 and January–February 1982. Abundance in the epibenthos was highly variable, and although many types of larvae were present, few were concentrated there relative to the water column. Among those taxa concentrated in the epibenthos, abundances were low and variances were high. Larvae of bregmacerotids, callionymids, clupeids, monacanthids, pinguipedids, platycephalids, pseudochromids, and especially schindleriids, leiognathids and terapontids were concentrated in the epibenthos. Few reef fish larvae were epibenthic. There was some evidence of diel and ontogenetic movements into and out of the epibenthos. Our limited sampling indicates that conventional midwater plankton sampling is adequate for most fish larvae found in the Lizard Island area, but for the larvae of the above ten families, this could produce large underestimates of abundance.

The bottom (i.e. epibenthos) of the water column is potentially important in the early life histories of many fishes, but this region is not adequately sampled by conventional plankton gear. Omission of the epibenthos in studies of fish larvae in shallow, coastal, temperate waters can result in serious underestimates of abundance of important taxa (e.g. Brewer et al., 1981; Barnett et al., 1984; Jahn and Lavenberg, 1986). Further, larvae in the epibenthos are much less subject to transport by currents than are larvae in the rest of the water column (Williams et al., 1984). This is potentially important in considerations of dispersal and recruitment. In coral reef areas, larval fishes of the epibenthos have been neglected apart from a few, largely anecdotal observations (e.g. Powles and Burgess, 1978; Leis, 1986b) and the pump study of Powles (1977).

We undertook a pilot study of the taxonomic composition and abundance of larval fishes in the epibenthos of inter-reef areas in the Lizard Island region of the Great Barrier Reef Lagoon, Australia, where we were conducting studies of fish larvae using conventional plankton nets (Leis, 1982, 1986a; Leis and Goldman, 1984, 1987). Our purpose was to determine if reef fish larvae were concentrated in the epibenthos to an extent which would have seriously biased studies based on conventional sampling. We found that some fish larvae were concentrated in the epibenthos, but that few of these were reef-dwelling taxa. We present the results of this pilot study as a basis for, and stimulus to, future work on epibenthic fish larvae in tropical areas.

## Materials and methods

Samples were taken in the Great Barrier Reef Lagoon near Lizard Island, Australia (14°40′S, 145°27′E). Sampling locations were chosen on the mid- and outer shelf (Fig. 1), and bottom type varied both among and within sampling locations from thick *Halimeda* beds to open sand. All samples were taken during daylight.

The sampler used was a non-closing plankton sled similar to that of La Bolle et al. (1985) except its mouth was 1 m wide and 0.30 m high, and it was made of aluminium. A digital flow meter was fixed in the net mouth. The bottom of the net was 65 mm above the weighted runners, so the epibenthic stratum sampled was nominally from 65 to 365 mm above the bottom, although sand in the catch indicated the bottom itself was sampled on occasion.

The sled was launched from a 7 m boat fitted with a winch, and wire equal to 3× water depth was paid out while underway. Contact of the sled with the bottom was confirmed by vibration of the wire. Typically, the sled was towed along the bottom at about 70 cm/sec (range 30–91) for 10 minutes before retrieval. The time the sled was on the bottom and the transit time through

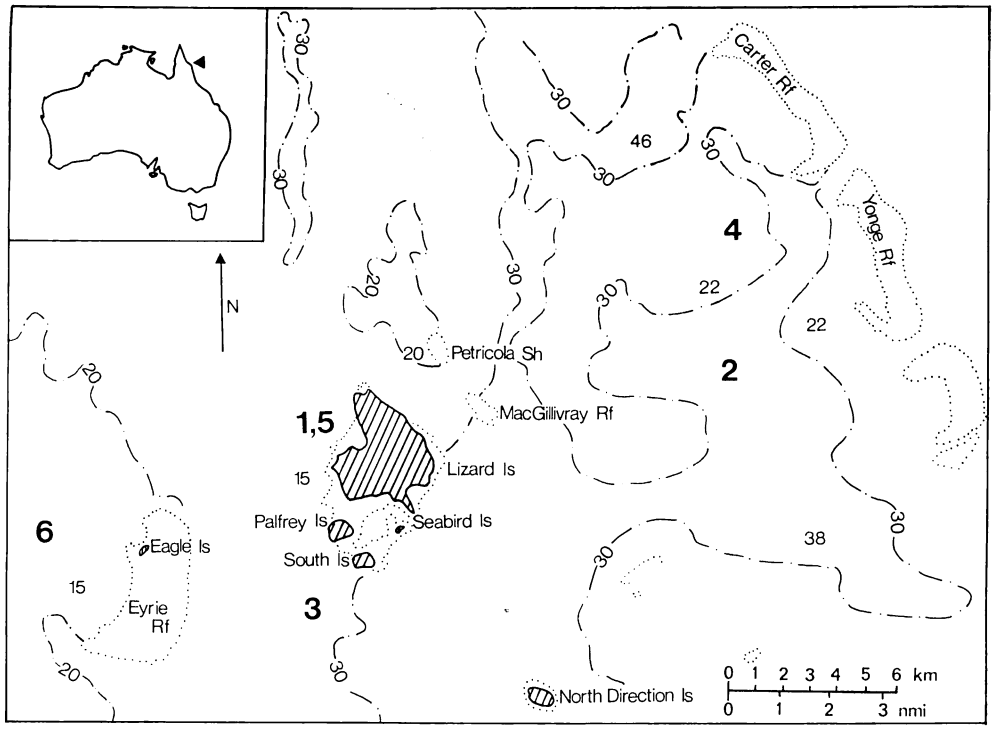


Fig. 1. The Lizard Island region of the Great Barrier Reef Lagoon showing sampling locations 1–6 as detailed in Table 1. Depths are in metres. Dotted lines portray reefs.

the water column were recorded. Area of bottom sampled per tow ranged from 177 to 473 $m^2$. The net was washed with pumped seawater. Samples usually contained sand, algae and benthic macroinvertebrates. Large invertebrates and algae were carefully washed in a sieve and discarded. The contents of the sieve were added to the rest of the sample and preserved in 5–10% seawater formalin.

The whole sample was sorted in the laboratory with the aid of a dissecting microscope at 8–10×, and all fish larvae removed. The larvae were identified, primarily after Leis and Rennis (1983) and Leis and Trnski (in press). Larvae were generally in poor condition, and identification beyond family level was not attempted. Larvae were divided into preflexion and postflexion stages to examine ontogenetic patterns (Leis, 1986a). No attempt was made to distinguish postflexion *Schindleria* larvae from juveniles or the paedomorphic adults, all of which co-occurred in the samples.

Because the net was open, it sampled the water column as well as the epibenthos. We corrected for water column contamination by first obtaining estimates of the water volume sampled during travel to and from the bottom ($V_C$) by retrieving the sled as soon as it hit the bottom. By subtraction from normal sled tow volumes, this also allowed us to estimate the epibenthic volume sampled ($V_T - V_C = V_B$, where V is volume in 100 s of $m^3$, T is total, B is bottom and C is contamination). We next obtained an estimate of the concentration of larvae (W, in no. per 100 $m^3$) in the supra-epibenthic water column from the sled contamination samples or from conventional oblique samples taken nearby and within a few days of the sled samples (see Leis and Goldman, 1987, for sampling details). Contamination (C) was defined as $C = WV_C$. The larvae captured on the bottom were thus $E = T - C$, where T is total larvae in the sample. Negative values of E were considered to be zero. E was converted to abundance in the epibenthos ($A_E$, in number per 100 $m^2$ where $A_E = E/D$ and $D = V_B/0.3$ m, because the net mouth was 0.3 m high and 1 m wide). Because replicate samples were taken in both the epibenthos and water

column, it was possible to calculate 95% confidence intervals for $A_E$. The correction for contamination introduced additional variance, but this was unavoidable with an open net.

Samples used for W estimates were obtained within two days of the epibenthic samples, and were taken in the same location as the epibenthic samples on three occasions, but 11 to 22 km away for sessions 3, 5 and 6.

## Results and discussion

Larvae of 43 families occurred in the epibenthos at least once. 54 types (i.e. taxon x stage categories) of larvae were found in the epibenthos. Most types occurred infrequently: 35 occurred in one sampling session (a session is one day of sampling at a location), 8 in two sessions, 8 in three sessions, 2 in four sessions, 0 in five sessions and only 1 occurred in all six sessions.

A ratio (R) of the abundance of larvae in the epibenthos to larvae in the water column was obtained by comparing mean abundance in the epibenthos from all 6 sessions, $\bar{A}_E$, to mean abundance in the water column (from the contamination estimate samples), $\bar{A}_W$. For most samples the water column (about 30 m) is about 100 times the depth of the epibenthic layer (30 cm), so a ratio of $R=\bar{A}_E/\bar{A}_W$ less than 0.01 implies no concentration in the epibenthos. Or, stated differently, water column concentrations extend to the bottom or decrease as it is approached. On the other hand, values of $R\geq 1.0$, indicate more larvae were present in the 30 cm-high epibenthic layer than in the remainder of the 30 m-high water column. In determining whether taxa are epibenthic or not, it is vital to compare abundances and concentrations in the epibenthos to those in the water column. For example, of the 10 types of larvae most abundant in the epibenthos, old and young gobiids ranked third and fourth, respectively. However, gobiid R values were $<0.002$ indicating that average concentrations in the epibenthos were less than 20% of these in the water column, and that the epibenthos was probably not an important habitat for larval gobiids.

Forty-one of the 54 larval types collected in the epibenthos had $R<0.01$, and are not considered truly epibenthic. The remaining 13 types of larvae with $R\geq 0.01$ are listed in Table 1 along with their abundances during each sampling session. For most of these epibenthic families only one stage had $R>0.01$, implying an onto-

Table 1. Fish larvae concentrated in the epibenthos. Also included are sampling data: see Fig. 1 for locations of sampling sessions. R is ratio of overall mean abundance in epibenthos to that in the water column. pre, preflexion; post, postflexion; *, all larvae (bregmacerotids do not undergo notochord flexion); **, did not occur in water column.

| | | Sampling session | | | | | | |
|---|---|---|---|---|---|---|---|---|
| | | 1 | 2 | 3 | 4 | 5 | 6 | |
| Area of shelf sampled | | mid | outer | mid | outer | mid | mid | |
| Date | | 23 XI 81 | 26 XI 81 | 24 I 82 | 31 I 82 | 8 II 82 | 8 II 82 | |
| Depth (m) | | 22–28 | 28–32 | 30 | 25–26 | 14–21 | 16 | |
| Number of replicates | | 3 | 4 | 2 | 3 | 2 | 2 | |
| Family | Stage | Larvae per 100 $m^2$ ± 95% confidence interval | | | | | | R |
| Bregmacerotidae | * | 0 | 0 | 0 | 0 | 0.8±5.7 | 0.2±2.8 | 0.04 |
| Callionymidae | pre | 0 | 0 | 3.1±9.4 | 0 | 0.4±1.5 | 1.6±6.8 | 0.02 |
| Clupeidae | pre | 0 | 0 | 88.8±33.3 | 0 | 33.2±86.5 | 4.2±17.0 | 0.17 |
| Clupeidae | post | 0.1±0.5 | 0 | 5.0±20.5 | 0 | 1.5±4.5 | 0 | 0.30 |
| Leiognathidae | pre | 0 | 0 | 0.8±4.0 | 0 | 0.1±1.5 | 0 | 0.67 |
| Leiognathidae | post | 0 | 0 | 0.3±3.2 | 0 | 0.7±9.0 | 0.1±1.4 | ** |
| Monacanthidae | pre | 2.9±5.4 | 0 | 0 | 0.5±2.1 | 0 | 0.3±1.5 | 0.03 |
| Pinguipedidae | post | 0.1±0.5 | 0 | 1.6±12.5 | 0 | 0 | 0 | 0.30 |
| Platycephalidae | pre | 0 | 0.1±0.2 | 1.2±0.9 | 0 | 0.4±1.5 | 0.1±1.4 | 0.01 |
| Pseudochromidae | pre | 0.4±1.5 | 0 | 0 | 0 | 0.2±3.4 | 0 | 0.06 |
| Schindleriidae | pre | 0.1±0.5 | 0 | 0 | 0 | 1.2±12.0 | 0 | 0.06 |
| Schindleriidae | post | 2.3±2.7 | 0.4±0.5 | 15.0±34.0 | 3.5±4.8 | 1.9+3.1 | 0.1±1.4 | 1.27 |
| Terapontidae | pre | 0 | 0 | 10.4±132.4 | 0 | 0 | 0 | ** |

genetic movement into or out of the epibenthos (Table 1). For example, pinguipedid (=mugiloidid) larvae appear to move into the epibenthos as they become older while callionymid larvae move out. The much larger R value for postflexion than for preflexion schindleriids implies that they concentrate in the epibenthos as they become older. In contrast, the values for young and old clupeid larvae are similar enough that no such concentration can be implied.

Abundances of epibenthic larvae were generally low, varied considerably among locations and dates, and were highly variable even at a particular location and date (Table 1). High variability in the epibenthos should be expected. Larval fish abundances in the water column in this area are normally variable (unpublished data), and if one speculates that epibenthic larval fish composition and abundance are related to bottom type, the patchy nature of the bottom in the Lizard Island area would add to the variability. Much of the temporal variation is in accord with seasonal patterns established from conventional plankton sampling (Leis and Goldman, 1987 and unpublished). More types of larvae were found in the epibenthos at mid-shelf locations (1, 3, 5 and 6) than at outer shelf locations (2 and 4), and five families were never found at outer shelf locations. In fact, only older schindleriids were found in any numbers in outer shelf samples. Because our sampling was so limited, we cannot usefully speculate on the reasons for these apparent spatial differences.

Of the 13 types of larvae concentrated in the epibenthos, we could not unequivocally conclude that any were of reef fish species. Eight types are from families that do not live on reefs as adults. In the other five families (Callionymidae, Monacanthidae, Pinguipedidae (=Mugiloididae), Platycephalidae and Pseudochromidae), a high proportion of the species do not live on reefs as adults, but rather on soft inter-reef bottoms. Without identification of the larvae to species (presently impossible), we cannot determine whether the larvae were of reef fishes. However, even if they were, it is clear that larvae of few reef-fish families were epibenthic. In contrast, larvae of a large number of reef fish families were abundant in the water column during the day (Leis and Goldman, 1987).

Daylight conventional plankton samples will grossly underestimate abundance of the few types of larvae which were highly concentrated in the epibenthos (Table 1). For these taxa the epibenthos must be taken into account. At night, some of these larvae may be less concentrated in the epibenthos, and therefore, less undersampled by conventional plankton tows, but further study is needed to clarify this point. However, there is no evidence that the epibenthos need be considered for the majority of larvae common in the Lizard Island area, particularly the larvae of reef fishes.

Larvae of clupeid fishes have been observed in the epibenthos of tropical areas previously (Powles, 1977; Leis, 1986b). Our present work indicates that during the day, most clupeid larvae were epibenthic. At night, conventional plankton sampling has shown that at least some of these larvae move upward (Leis, 1986a and unpublished data), although we have no estimate of the proportion which do so. The clupeid larvae in our epibenthic samples were not *Spratelloides* spp., but may have been *Herklotsichthys* spp.

The paedomorphic schindleriids are extremely abundant at night in reef waters (Gosline and Brock, 1960; Watson and Leis, 1974), but their whereabouts during the day previously were unknown. We have now established that they occupy the epibenthos during the day and at least some of them move upward into the water column at night (Leis, 1986 and unpublished).

Much less can be said about the other types of epibenthic larvae. The concentrations of both callionymid and monacanthid larvae increased with depth in the water column during the day (Leis, 1986a), and it is possible that their relatively small concentrations in the epibenthos (Table 1) merely reflected increased concentration with depth in the water column rather than a preference for epibenthic habitat. In any case, larvae of these two families may also migrate upward at night (Leis, 1986a). Leis (1986a) found no difference in concentration among depths for pinguipedid and platycephalid larvae, and we know of no information on vertical distribution in the water column, or of night-time abundances, of leiognathid, pseudochromid or terapontid larvae.

We found strong indications of ontogenetic as well as diel movement into and out of the epibenthos. These movements differ among species,

and further study is clearly necessary. The proportion of the larval phase spent in the epibenthic boundary layer and how this is temporally partitioned must be considered in any realistic model of the movement of these larvae with currents (Williams et al., 1984).

The foregoing discussion must be viewed with caution due to limitations of our study. We collected few samples (16) in only a few locations and times, and patchiness in the epibenthos was high. We used a small sled net and it was towed relatively slowly. This means that avoidance may have been high, and we could have underestimated abundances or missed larger larvae altogether. A sled net may be less efficient than some other methods of epibenthic sampling (Carleton and Hamner, 1987), but should be comparable in efficiency to the plankton net used for our midwater sampling. We sampled only during daylight, and some larvae might enter the epibenthos only at night. Our method of estimating contamination could have given misleading results if abundances of larvae differed greatly at a location from day-to-day or between locations more than a few km apart. Our contamination samples were never more than 2 days removed from the sled samples, but in three cases were more than 10 km from them. Finally, we have made the implicit assumptions that larvae are everywhere equivalent and that all members of a family act alike. It is conceivable that larvae in one place (e.g. epibenthos) have higher survival rates or are more likely to be retained in a given area and thus are more important to the local population than are larvae in another place (e.g. water column). We have no way of evaluating this possibility at present. Clearly, all members of a family do not act alike whether as adults or larvae, but far more detailed studies on taxonomy and ecology will be required to determine the significance of this for the epibenthos.

The results and conclusions of this study must be considered preliminary for the above reasons. However, they suggest that the epibenthos in the Great Barrier Reef Lagoon near Lizard Island is not as important a habitat for larval fishes as it is near the California coast (Barnett et al., 1984) where the epibenthos harbours the majority of the most abundant larvae. Among the many differences between the California study and our Lizard Island study is depth. The epibenthos inshore of the 10 m contour was most important in California, and we did not sample bottom less than 15 m deep. Further speculation is premature.

Concentration of fish larvae in the epibenthos is probably the result of behavioural regulation of vertical distribution by the larvae. The reasons for epibenthic concentration of fish larvae are unclear, and we can do no more than cite Leis' (1986b) list of possible advantages and disadvantages of this behaviour.

We hope this preliminary study will stimulate further work on epibenthic fish larvae of coral reef areas. Future studies should use closing nets, and areas in the immediate vicinity of reefs should also be investigated.

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(JML and SER: Division of Vertebrate Zoology, The Australian Museum, P. O. Box A285, Syndey South, NSW, 2000, Australia; BG: Lizard Island Research Station, PMB37, Cairns, Qld. 4871, Australia; BG, present address: c/o JML)

## オーストラリア大堡礁湖における底表性仔魚

**Jeffrey M. Leis • Barry Goldman • Sally E. Reader**

オーストラリア大堡礁湖 Lizard 島周辺の底表性仔魚を 1981 年 11 月と 1982 年 1, 2 月の昼間にプランクトン用ソリネットで採集した．その量は大きく変異し，底表部には水中に出現した多様な仔魚のうち少数だけが集中して観察されたばかりでなく，量的にも少なかった．サイウオ，ネズッポ，ニシン，カワハギ，Pinguipedidae，コチおよびメギスの各科，特にシラスウオ，ヒイラギおよびシマイサキの各科の仔魚は底表部に集中した．また仔魚が底表部から日周的あるいは個体発生的に移動することを示唆する証拠も見出された．通常のプランクトン採集は Lizard 島域の大部分の仔魚に対しては適切であるが，上記 10 科の仔魚に関しては生物量がかなり過少評価となることが，本研究の不十分な採集からも指摘される．