Abstract. – We compared sampling performance of four nets and two aggregation devices for larval and pelagic juvenile coral-reef fishes. The six sampling devices were deployed simultaneously over three nights near a coral reef at Lizard Island, northern Great Barrier Reef, Australia. The resulting 83 samples captured 57,701 larval and pelagic juvenile fishes of 70 families (excluding clupeoids which were not considered in this analysis). The bongo net took the most families, and the light-trap the fewest. In all methods, a few families dominated the catch. Dominance was least in the Tucker trawl catches and greatest in light-trap catches, where pomacentrids constituted 93% of the catch. Composition of catches was similar for the four nets. Catches from the light-trap were markedly different from those taken by net; catches taken by light-seine showed similarities to those taken by both net and light-trap. For four abundant families (Apogonide, Gobiidae, Lutjanidae, Pomacentridae), the bongo net gave the overall highest density estimates, although those from purse-seine were frequently equivalent to bongo-net estimates. The Tucker trawl provided the lowest density estimates in most cases. Catches of bongo, neuston, and seine nets were similar in size structure and were dominated by small larvae; overall, however, bongo nets collected the greatest size-range of fishes. The Tucker trawl did not collect small larvae well nor did it collect significantly greater densities of large larvae and pelagic juveniles than the bongo net. Fishes collected by aggregation devices were generally larger than those taken by net, and light-traps caught very few fish <5 mm. Light-traps collected greater numbers of large pomacentrids (>6 mm) than other methods. In an extended sampling period of five nights, both aggregation devices showed obvious peaks in the density of large pelagic pomacentrids and mullids; these patterns were not detected by the nets.

Manuscript accepted 24 February 1993.
Fishery Bulletin, U.S. 91:195-209 (1993).

A comparison of towed nets, purse seine, and light-aggregation devices for sampling larvae and pelagic juveniles of coral reef fishes*

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Almost all species of marine teleost fishes have a pelagic phase in the early part of their life history (Moser et al. 1984). Size, morphology, and behavior of larval and pelagic juvenile phases vary greatly (Moser 1981), and this makes accurate sampling of these fishes problematical (Murphy & Clutter 1972, Frank 1988, Suthers & Frank 1989, Brander & Thompson 1989). The problem is exaggerated in tropical waters due to high taxonomic and developmental diversity and the presence of many demersal species with extended pelagic phases (Leis & Rennis 1983, Leis & Trnski 1989, Leis 1991b). Studies of the pelagic phase can provide important information on population biology of reef fishes. Despite its brevity, the high mortality and dispersion characteristic of this phase can have important demographic consequences for many species (Victor 1986). There is now a widespread interest in the process of recruitment in coral reef fishes (Doherty & Williams 1988, Warner & Hughes 1989), and sampling techniques which cover the full size-range of the pelagic phase are needed.

A number of different methods are available to sample this complex assemblage of early-life-history stages, including towed nets, purse-seines, and various types of aggregation devices which attract fish into collection sites or traps. These methods differ in their method of deployment and capture, and each has its own set of advantages and disadvantages. All have biases in number, identity, and sizes of pelagic fishes collected (Clutter & Anraku 1968, Clarke 1983 and 1991). For the pelagic phase of reef fishes, there have been few attempts to evaluate the relative bias of different sampling methods. Recent studies have provided information on the comparative performance

*Contribution of the Lizard Island Research Station. Authorship alphabetical.

of nets and light-traps (Gregory & Powles 1988), nets and plankton pumps (Brander & Thompson 1989), and towed nets and purse-seines (Kingsford & Choat 1985), but have dealt with the less-diverse fauna of temperate waters.

The purpose of this study was to compare several types of towed and seine nets and an automated light-trap (Doherty 1987) in terms of taxa, numbers, and sizes of larvae and pelagic juveniles of coral reef fishes captured. These methods represent the range of sampling devices currently used to collect larval and pelagic juvenile fishes. For the towed nets, we used dimensions and mesh size normally employed to sample larval and pelagic juvenile fishes. We used designs of purse-seine and light-trap which had been subject to thorough field testing (Kingsford & Choat 1985 and 1986, Kingsford et al. 1991, Doherty 1987). For each sampling device we obtained the following information: (1) Taxonomic composition of samples at the level of family; (2) patterns of density and size structure in selected taxa; and (3) temporal patterns in the density of selected taxa over short time-periods. The program also provided information on the logistic constraints associated with each sampling method.

Our findings will be useful to those designing sampling programs for larval and pelagic juvenile stages of demersal fishes in tropical and other areas, and should have some generality because the taxa sampled included a wide variety of body shapes and swimming capabilities. Among the taxa studied are families of great importance in coral reef ecosystems as adults (Apogonidae, Atherinidae, Callionymidae, Gobiidae, Labridae, Pomacentridae), and several are also important in commercial, sport, or subsistence fisheries throughout the tropics (Carangidae, Lethrinidae, Lutjanidae, Mullidae, Nemipteridae, Platycephalidae, Scaridae). All are abundant in ichthyoplankton samples in tropical coastal areas, especially in the Indo-Pacific.

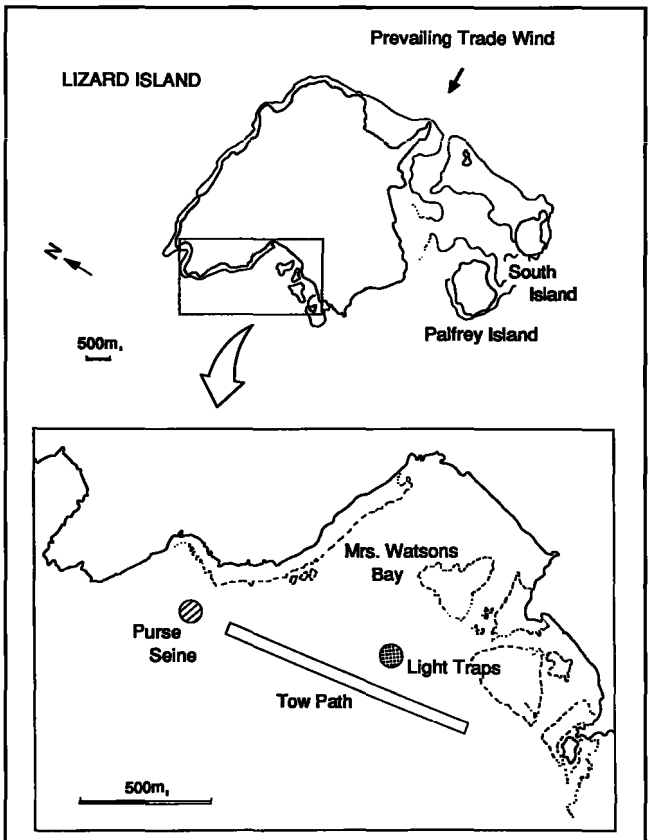

Figure 1
Lizard Island, Great Barrier Reef, Australia, showing location of study area and position of sampling sites for light-traps, towed nets, and purse-seines at Watsons Bay. Coral reefs are shown as broken lines. Lizard Island (145°26'E, 14°40'S) is located 30 km off the eastern coast of mainland Australia.

Materials and methods

Sampling and identification procedures

We sampled at 150–600 m off the fringing reefs at Watsons Bay on the NW side of Lizard Island in the lagoon of the northern Great Barrier Reef, Australia (145°26'E, 14°40'S). Water depth was 20–30 m over a sandy bottom (Fig. 1). This site was chosen for its proximity to the logistic support offered by the Lizard Island Research Station, a base for much work on the pelagic phase of coral reef fishes (Leis 1991b). Also, it offered relatively sheltered conditions from the 15–25 kn southeasterly winds present during the sampling period. This was particularly important for the continuity of sampling over a number of nights.

We sampled on the nights of 2, 3, 5, 6, and 7 December 1986, starting at a minimum of 1.25 h after sunset. Sampling never continued past 0200 h. New moon was on 2 December 1986. Nocturnal sampling reduces potential bias due to vertical distribution because ichthyoplankton show little vertical stratification at night in the study area (Leis 1986, 1991a). In addition, the nets should operate at peak efficiency at night due to lessened visual avoidance. Finally, the aggregation devices are effective only at night because they depend on self-generated light to attract fishes.

We concentrated our analyses on data from 3, 5, and 6 December because we were able to take and process all planned samples from all gears only on these nights. For some gears, it was possible to examine temporal trends over the full sampling period.

Six different sampling devices were deployed each night. Three nets were towed from the 14 m catama-

ran RV *Sunbird* at 1 m/s along a fixed 1 km path. The towed nets were fitted with flowmeters and were washed with pumped seawater. Details of each collection device are as follows.

1 A neuston net of mouth dimensions 1.0×0.3 m with 0.5 mm mesh was rigged to sample water between the bows of the catamaran. Typically, the net sampled to a depth 0.1 m and filtered 187–312 m^3/tow. Four tows were taken per night.

2 A bongo net (McGowan & Brown 1966) of 0.85 m mouth diameter per side, and with 0.5 mm mesh, was towed from an "A"-frame at the stern. The RV *Sunbird* draws 1m, and the net was towed so its top was 1m below surface and on the vessel's centerline in water which had not been disturbed by the passage of its twin hulls. The volume of water filtered for each side of the net was 498–673 m^3/tow. Samples from only the port-side net were analyzed. Four tows were taken per night.

3 A Tucker trawl (Tucker 1951) with nominal mouth dimensions of 2×2 m and of 3 mm mesh was towed in the same position as the bongo net. At a towing speed of 1 m/s, a diver estimated that the bottom bar of the net trailed the top bar by ~0.5 m, so the effective mouth area was ~3.8 m^2. Between 3240 and 4570 m^3 of water were filtered per tow. Four tows were taken per night. Both the bongo net and the Tucker trawl used the same depressor.

Time constraints and the logistics of rigging and deploying each net precluded randomising the order of bongo and Tucker trawl tows, so they were taken in blocks of four, with the order alternating from one night to the next. Neuston net samples were taken during the Tucker trawl tows.

4 A plankton mesh purse-seine of 14×2 m (Kingsford & Choat 1985) of 0.28 mm mesh was used to take samples of ~32 m^3 each. This estimate was based on the ideal cylinder of water enclosed by the net at the beginning of pursing and made no allowance for herding of fishes during deployment or loss during pursing. There was no estimate of variation in the volume enclosed by the net sets. The net was deployed from a 4 m dinghy adjacent to the northern end of the tow path (Fig. 1). Wind conditions precluded effective deployment of this net at greater distances offshore. Two to four samples were taken per night.

5 Two automated light-traps (Doherty 1987) were deployed from an anchored boat adjacent to the center of the tow path and ~700 m from the purse-seine site. Traps were positioned at ~10 m apart. Entries into the trap were at 0.5–1 m below surface. The second trap began to sample 30 min after the first, and both traps sampled for hourly intervals, resulting in continuous sampling in overlapping, 1 h segments. The trap deployment was staggered to allow for clearing and processing of each trap after the 1 h fishing period. Eight to nine 1 h light-trap samples were taken per night.

6 A battery-powered fluorescent light source identical to that in the trap (Doherty 1987) was deployed from a second boat anchored at the purse-seine site. After 1 h in the water, the light was set adrift and the water around it immediately sampled by the same purse-seine used in **(4)** above. Our estimates of what was attracted to the light included only those individuals that were within ~2 m (i.e., radius of the seine at pursing) of the light at the time of seining. Four to five light-seine samples were taken per night. Purse-seine (no light, **(4)** above) and light-seine samples were interspersed during the night.

Our goal was to sample simultaneously using six methods in the same location over several nights, so as to avoid confounding comparisons of methods with temporal or spatial variation. The purse-seine, light-seine, and light-trap samples were taken throughout the nightly sampling period. At the same time, the RV *Sunbird* sampled with the towed nets. Logistic problems required two compromises in this program. Bongo tows and Tucker trawl tows (and simultaneous neuston tows) were done in sequential blocks of four each night as discussed in **(3)** above. The purse-seine and light-trap samples were taken 700 m apart because it was not possible to duplicate these devices and thus randomize their positions. The RV *Sunbird* tow track covered the area between these two.

Fishes from the towed nets, purse-seines, and light-seines were immediately fixed in 10% formalin seawater. Samples from the light-traps were maintained alive until returned to the Research Station where they were subsequently fixed in 100% ethanol or 10% formalin seawater. All fish were transferred to 70% ethanol for at least a month prior to measurement.

For light-traps and light-seines, density is expressed as number per sample. Catches from the towed net and purse-seine collections were standardized to the number of fishes/1000 m^3 on the basis of flowmeter records or purse-seine geometry.

All fishes were removed from samples and identified to family following Leis & Rennis (1983) and Leis & Trnski (1989). Standard lengths were measured to the nearest 0.1 mm using a Bioquant software package that allows for measurement of enlarged *camera lucida* images of fish and accommodates curvature of specimens. The accuracy of electronic measurement was monitored by measuring subsamples manually with calipers and eye-piece micrometers. In a few samples with very large numbers of certain taxa such as gobiids, the catch was subsampled and a minimum of 10% of the sample measured. For some analyses, fishes were divided into small (<6 mm) and large (≥6 mm) size-groups. This was done because, on the basis of results reported here, the light-

trap captures few larvae <6 mm, and we wished to compare density estimates among gears for the sizes of fishes captured by the light-trap. Damaged fish (~3% of total) were excluded from the length analysis.

The terminology of early-life-history stages of fishes is complex and ultimately arbitrary, whether based on morphological or ecological criteria (Kendall et al. 1984, Kingsford 1988, Leis 1991b). We were primarily interested in taxa of which the adults are benthic on coral reefs, but did not want to exclude semipelagic reef-associated taxa by use of an ecological term like 'presettlement', nor did we wish to exclude partially- or fully-transformed but still pelagic individuals of benthic taxa by the use of a morphological term like 'larva'. Therefore, we use the terms 'larvae' and 'pelagic juveniles' for the fishes collected during this study, or refer to them collectively as 'pelagic fishes'.

Larval, transforming, juvenile, and adult clupeoid fishes of several types (including *Spratelloides* spp., *Dussumeria* sp., *Stolephorus* sp., and probably *Herklotsichthys* sp.) were captured in large numbers, mainly by light attraction. These clupeoid fishes represented a distinct assemblage of fishes with a different age and size structure and adult habitat than the reef species of primary interest to us. These clupeoids are not considered here, but will be dealt with in a separate publication.

Reduction of data sets and analytical procedures

Sampling produced a data set comprising 70 families of fishes (exclusive of the Clupeidae and Engraulidae) collected from the sampling nights of 3, 5, and 6 December by six methods. For ease of analysis and unambiguous interpretation, it was necessary to reduce the number of families treated. We initially removed from consideration any family which did not constitute at least 1% of the catch of at least one method. The removal of taxa of this level of rarity would be unlikely to influence the outcome of the analyses (Green 1979). This excluded 51 families, leaving 19 (referred to as 'abundant families') for analysis beyond simple listing of numbers of families sampled (e.g., Table 1). Relative-abundance information obtained by all six sampling methods for the 19 abundant families was subjected to Principal Component Analysis (PCA) using the variance-covariance matrix. As a check, the same analysis was run incorporating the next 10 most-abundant families; this generated identical patterns. Reducing the data set from 29 to 19 families did not change the resulting pattern.

The PCA analysis identified patterns in the complex data set of 19 families sampled by six methods. Many of these 19 families were relatively rare and contributed little to the variation in the data set. A detailed examination of the factors contributing to these patterns required factorial analyses such as multivariate analysis-of-variance (MANOVA). These procedures are best carried out with a reduced number of variables, which allows a clearer interpretation of trends in the data. This called for a further reduction in the number of families analyzed.

To achieve this reduction, the data set of 19 families collected by nets was subjected to a PCA, which identified the taxa that contributed most substantially to the variation in the data set. This PCA identified apogonids, atherinids, gobiids, lethrinids, mullids, and pomacentrids as major contributors (95.2%) to the variation in the data set. These six taxa were used in a MANOVA. This design provided sufficient degrees of freedom for testing and interpreting the significance of method and night of sampling. The analysis was carried out on samples from nets only.

For graphic display of trends in sampling by nets, the eight most-important taxa from the PCA were depicted. These were apogonids, atherinids, gobiids, lethrinids, lutjanids, mullids, pomacentrids, and labrids. Labrids were included in this group at the expense of schindleriids, as they were an abundant reef-associated taxon of considerable interest to reef fish biologists. This substitution did not affect the cumulative variance accounted for by the eight families.

Unlike nets, aggregation devices did not allow for adjustment of fish densities to a common volume. Moreover, aggregation devices collected a different set of fishes. An additional PCA run on light-trap and light-seine data identified atherinids, gobiids, labrids, lethrinids, mullids, and pomacentrids as taxa, which explained over 90% of the variability in the data set. The families selected showed a strong relationship to the overall abundance ranking, although two relatively rare taxa (lethrinids and mullids) were included.

Aggregation devices sample an unknown volume of water. Because catches by aggregation devices could not be standardized to number of fish per unit volume, we made separate comparisons of nets and aggregation devices. The variables used were mean number/1000 m^3 for nets, and mean number/sample for aggregation devices. A factorial analysis was designed to test for differences in sampling method (fixed) and time (random). For factorial analyses, residual analysis was performed (Snedecor & Cochran 1980) to check assumptions of normality and homogeneity of variance. Taylor's Power Law (Taylor 1961) was used to determine the appropriate transformation.

Canonical Discriminant Analysis and Tukey's Studentized Range Test (HSD) were used to display the differences detected. For MANOVA, the multivariate test statistic (Pillai's Trace) was used because it is

less likely to involve Type-I error and is more robust to heterogeneity of variance than comparable tests (Green 1979). All analyses were performed using SAS Version 6 (SAS 1987).

A more subjective procedure was used to select taxa for size-frequency measures. For meaningful comparisons, it was necessary to select taxa that were well represented in the collecting devices and that covered a reasonable size-range (>8 mm) within each method. Apogonids, gobiids, lutjanids, and pomacentrids met these criteria and also accounted for over 95% of the variation in the main data set from net sampling. Catches for nets and aggregation devices were analyzed separately. For net catches, density was expressed as mean number/ 1000 m^3 within 2 mm size-classes among the different methods and compared by one-way ANOVAs. With aggregation devices, the variable was the number of fish per sample and comparisons were made by *t*-tests.

Results

The 83 samples contained a total of 57,701 fishes of 70 families, excluding clupeoids (Table 1). Table 2 lists families which constituted at least 1% of the individuals taken by any sampling method and records their size-ranges by method. We refer to these as 'abundant families'.

Taxonomic composition and size structure of the samples

There were marked differences in taxonomic composition of the samples among methods. The bongo net collected the largest number of families overall (Table 1), including all of the abundant families and a wide size-range within most families (Table 2). The light-trap collected the fewest families overall and only

Table 1

Number of samples, total individuals, and numbers of families of fishes (clupeoids excluded) taken by six sampling methods on the nights of 3, 5, and 6 December 1986 off Lizard Island, Great Barrier Reef. Volume of water sampled by aggregation devices is unknown.

Sampling method	Number of samples	Number of fish	Volume of water sampled (m^3)	Number of families
Light-trap	26	7624	unknown	20
Seined light	14	2707	unknown	37
Purse-seine	7	812	224	25
Neuston net	12	2418	2861	31
Bongo net	12	43417	6833	63
Tucker trawl	12	723	47100	29
Total	83	57701	—	70

Table 2

Numbers and size ranges of the 19 families of fishes which made up >1% of the catch of at least one method on 3, 5, and 6 December 1986 off Lizard Island, Great Barrier Reef. Clupeoids are excluded. Size-range in mmSL, and total number of individuals within the taxon (*n*).

	Sampling method											
	Light-trap		Light-seine		Bongo net		Purse-seine		Neuston net		Tucker trawl	
Family	SL	*n*	SL	*n*	SL	*n*	SL	*n*	SL	*n*	SL	*n*
Apogonidae	5.4–9.3	4	1.6–9.8	211	1.6–15.5	10295	1.6–6.8	86	1.7–6.2	491	2.3–5.1	99
Atherinidae	6.7–19.1	20	7.6–61.7	135	6.0–25.2	14	6.8–24.7	2	16.0–56.3	110	15.2–39.3	36
Bothidae			3.2–5.3	3	1.4–7.7	76					3.0–10.0	10
Callionymidae			1.3–3.5	35	1.1–4.9	1003	1.3–2.9	11	1.6–3.9	94	1.9–4.5	6
Carangidae			1.9–57.4	19	1.8–7.6	1555	1.9–4.0	7	1.8–4.5	63	2.2–14.2	13
Ephippididae					1.7–8.7	81					5.8–7.5	14
Gobiidae	3.7–10.5	235	1.2–17.7	643	1.1–10.1	8386	1.4–8.6	487	1.4–20.3	1207	1.9–9.0	258
Labridae	5.1–8.8	48	1.5–13.1	47	1.6–6.0	876	1.7–5.9	21	2.0–5.3	27	2.2–4.1	9
Lethrinidae	8.4–16.6	45	1.9–18.0	24	1.8–4.7	380	2.6–3.3	3	1.9–4.4	17	2.6–11.3	9
Lutjanidae			2.1–5.2	76	1.8–6.6	2740	2.1–7.4	33	1.8–4.9	105	2.5–8.4	48
Microdesmidae			1.5–4.8	10	2.0–4.3	100	2.2–3.2	9	3.3–5.4	6	2.9–6.3	7
Monacanthidae	46.6	1	1.5–23.3	13	1.2–4.6	608	1.9–3.3	3	1.8–3.7	11	2.0–6.3	22
Mullidae	11.2–21.9	51	21.5–39.7	54	2.4–4.9	8	5.1–23.6	2	22.4–30.2	10		
Nemipteridae	6.4–9.3	28	1.8–12.3	42	1.5–5.6	1548	1.8–5.2	15	1.6–5.0	75	4.2–4.8	4
Pinguepididae	2.0	1	1.4–6.5	30	1.3–5.6	2838	1.4–4.6	20	1.7–5.5	109	2.3–4.8	9
Platycephalidae			2.1–3.1	6	1.6–8.3	469	2.8–5.5	6	2.4–4.2	3		
Pomacentridae	5.3–14.9	7124	1.8–25.1	1248	1.0–14.6	496	1.9–9.4	22	1.8–11.7	30	6.4–14.6	68
Scaridae			1.6–4.4	30	1.7–4.6	136	2.2–4.0	34	2.5–7.7	10		
Schindleriidae					2.0–16.2	219	3.1–8.3	8	4.1–10.7	25	4.4–17.7	79

the larger individuals of most families. Analysis of the catch by method (Tables 1,2) suggests that the apparent selectivity of the light-trap reflects size-specific rather than taxonomic biases. The absence of certain taxa from the light-trap during the sampling period may mean that few large individuals were in the sampling area. Table 3 shows that, with the exception of bothids, schindleriids and carangids, taxa not caught by the light-trap were represented by relatively small individuals in the catch by other methods. Whether large carangids were present in more than trivial numbers is unclear. A single 57.4 mm carangid was taken by the light-seine, but the next-largest carangid taken by other methods was 14.2mm. The question of selectivity by light-traps must be resolved by more comprehensive sampling.

The light-seine and Tucker trawls captured most of the abundant families in all sizes. The neuston net and purse-seine captured the same abundant taxa, with size-ranges similar to one another. The exceptions were mullids, microdesmids, gobiids, and atherinids, for which the neuston net captured larger individuals. For the mullids and microdesmids, size distributions produced by the two methods overlapped slightly.

Catches by all methods were dominated by a few abundant families of fishes. The first five most-abundant families listed in Table 2 accounted for 80% or more of the catch by all methods. The Tucker trawl was the most equitable in terms of abundance distributions, and the light-trap the least. However, the rank order of abundant families was not the same for all methods (Fig. 2). The dominant families for all towed nets and the purse-seine were gobiids and apogonids. For light-trap and light-seine the dominant families were pomacentrids, followed by gobiids. Small apogonids, although consistently abundant in net samples, were not captured by light-aggregation devices. In light-trap catches, a single family—the Pomacentridae—accounted for 93% of individuals collected.

For most collecting methods, there was a high degree of consistency among samples. Results of PCA (Fig. 3) showed that samples taken by light-trap were

Table 3

Comparison of maximum size of the 19 abundant taxa (Table 2). Maximum size captured by light-trap is compared with maximum size captured by five other methods tested on 3, 5, and 6 December 1986 off Lizard Island, Great Barrier Reef. Taxa listed in increasing order of maximum size captured by 'other methods' (maximum size captured by the next-best 'other method').

	Maximum size (mm) captured by	
Taxon	Light-trap	Other methods
Callionymidae	not caught	4.9(4.5)
Microdesmidae	not caught	6.3(5.4)
Pinguepididae	2.0	6.5(5.6)
Scaridae	not caught	7.7(4.6)
Platycephalidae	not caught	8.3(5.5)
Lutjanidae	not caught	8.4(7.4)
Ephippididae	not caught	8.7(7.5)
Bothidae	not caught	10.0(7.7)
Nemipteridae	9.3	12.3(5.6)
Labridae	8.8	13.1(6.0)
Apogonidae	9.3	15.5(9.8)
Schindleriidae	not caught	17.7(16.2)
Lethrinidae	16.6	18.0(11.3)
Gobiidae	10.5	20.3(17.7)
Monacanthidae	46.6	23.3(6.3)
Pomacentridae	14.9	25.1(14.6)
Mullidae	21.9	39.7(30.2)
Carangidae	not caught	57.4(14.2)
Atherinidae	19.1	61.7(56.3)

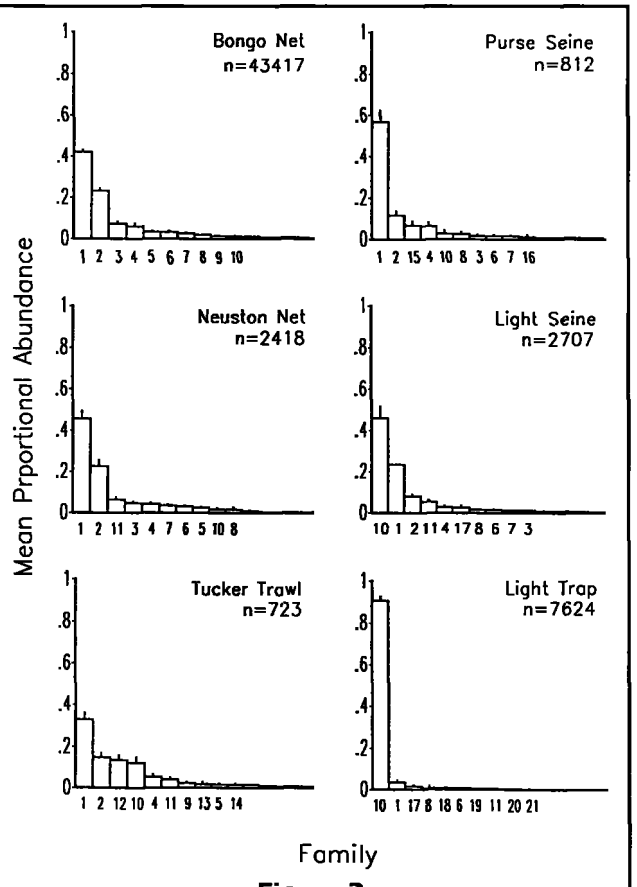

Figure 2

Mean proportional abundance (±1 SE, vertical axis, shown only upward) and ranked taxonomic categories of fishes (clupeoids excluded) collected by six sampling methods off Lizard Island, Great Barrier Reef on 3, 5, and 6 December 1986. Other sample data are given in Table 1. Key to taxa: **1** Gobiidae, **2** Apogonidae, **3** Pinguepididae, **4** Lutjanidae, **5** Carangidae, **6** Nemipteridae, **7** Callionymidae, **8** Labridae, **9** Monocanthidae, **10** Pomacentridae, **11** Atherinidae, **12** Schindleriidae, **13** Ephippididae, **14** Bothidae, **15** Scaridae, **16** Microdesmidae, **17** Mullidae, **18** Lethrinidae, **19** Synodontidae, **20** Scombridae, **21** Blenniidae.

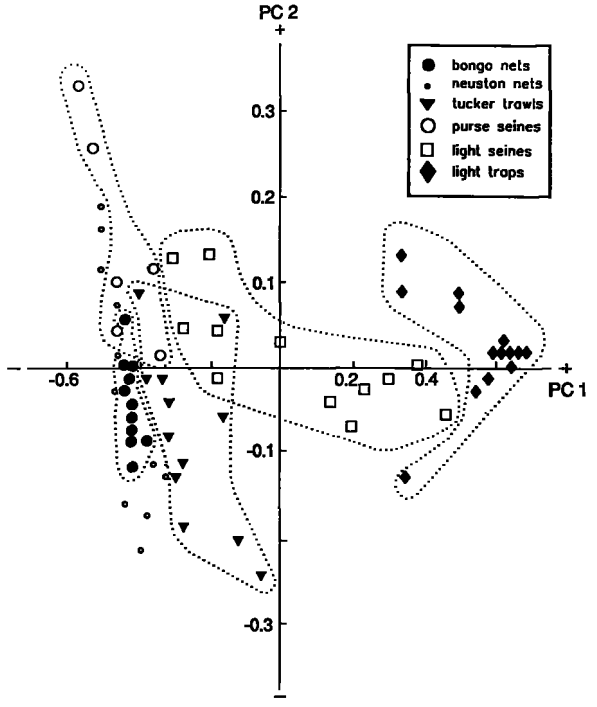

Figure 3

Results of Principal Components Analysis on proportional abundances of 19 families of fishes collected by six sampling methods on 3, 5, and 6 December 1986 off Lizard Island, Great Barrier Reef. Principal Components 1 and 2 are plotted. Differences between number of replicate samples and number of symbols for each method are due to overlap of some symbols.

distinct from net samples, and that samples taken by light-seine were intermediate between net and light-trap samples. Tucker trawl samples were almost completely distinct from bongo, neuston, and seine net samples. Bongo net samples formed a more discrete group than did the neuston and seine net samples.

The data sets for size analysis were heterogenous. Therefore, we attempted only to test for differences in density among methods within selected size-classes using single-factor ANOVA (df 3,39; $p<0.05$). The power of these tests to detect differences among methods was low. For apogonids, gobiids, lutjanids, and pomacentrids, there were sufficient numbers for statistical comparisons across the first three size-classes (i.e., <6 mm, Fig. 4). For all four families, density estimates provided by the bongo net were as high as, and in many cases higher than, those provided by the other nets. The Tucker trawl provided the lowest density estimates.

For the larger sizes (>6 mm), low or zero catches in some size-classes precluded statistical tests in most cases. We compared the Tucker trawl, which is designed to capture such large stages with the bongo net. The few tests that were possible show that in no instance did the Tucker trawl provide higher density estimates than the Bongo net (Fig. 4).

Two taxa, pomacentrids and gobiids, were sufficiently abundant to allow for comparisons of density by 2 mm size-classes between the aggregation devices. For pomacentrids we tested the 7–15 mm size-classes. Light-traps caught significantly higher numbers of pomacentrids in the 7, 9, and 11 mm size-classes than the light-seines (Fig. 4B). The two aggregation devices provided similar estimates of numbers for the 13 and 15 mm size-classes (Fig. 4B). The difference in overall density for pomacentrids sampled by light-traps and light-seines is due to the greater number of pomacentrids in the 7, 9, and 11 mm size-classes in the light-trap catches. Pomacentrid larvae >14 mm were collected by the light-seine on one night only.

Although we did not statistically test the gobiid data, the light-seine appeared to collect greater numbers of smaller (<4 mm), and the light-trap greater numbers of larger (>8 mm), individuals (Fig. 4B). The light-seine collected few gobiids >6 mm and the light-trap almost no gobiids <6 mm. Sizes of apogonid and lutjanid fishes sampled by the light-seine were similar to those of the purse-seine (Fig. 4C). No lutjanids and only four apogonids were collected by the light-traps.

Results of pooled samples from three nights for eight taxa (Materials and methods) by the different nets (Fig. 5) reflect both entry of fish into nets and subsequent extrusion. Most of the fishes taken by all nets were small (Table 2, Fig. 4). Bongo nets consistently provided the highest estimates of density of small fishes, especially gobiids, apogonids, lutjanids, labrids, and lethrinids. This reflects both the low-avoidance and high-retention properties of this fine-mesh net. The purse-seine filtered only small volumes of water, but provided high estimates of density, especially for gobiids, apogonids, and lutjanids (Fig. 4). Extrusion is probably minimal, due to the passive mode of filtering and the very fine mesh of this seine. Neuston nets provided low estimates of density for all families except two that concentrate in the surface layer—atherinids and mullids (Leis 1991a). Density estimates from the Tucker trawl were low for all families, most probably due to the loss of smaller larvae through its large mesh. Both atherinids and mullids, which attained large size (Table 2), were also poorly represented in Tucker trawl catches, possibly because the Tucker trawl did not sample the neustonic habitat of these taxa.

For aggregation devices, we compared densities of the important families identified by PCA, excepting apogonids and lutjanids which were rare or absent from light-traps. Light-traps collect mainly large individuals, so the samples were subdivided by size

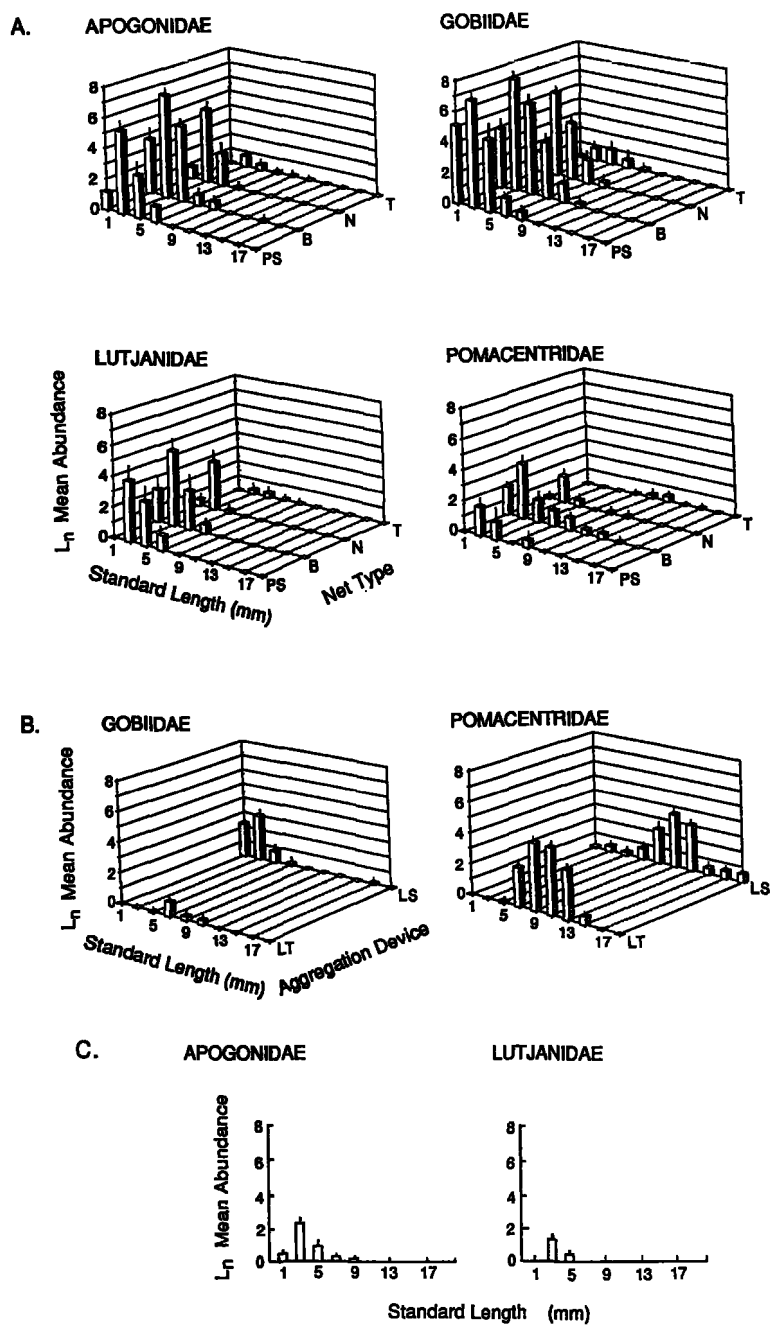

Figure 4

Analysis of size structure in selected families of fishes collected by six sampling methods on 3, 5, and 6 December 1986 off Lizard Island, Great Barrier Reef. **(A)** L_n mean density/1000 m^3 (±SE) of four taxa in each of ten 2 mm size-classes collected by purse seine (PS), bongo net (B), neuston net (N), and Tucker trawl (T). **(B)** L_n mean density per sample (±SE) of gobiids and pomacentrids collected by light-trap (LT) and light-seine (LS). Size-classes as in (A). **(C)** L_n mean density per sample (±SE) of apogonids and lutjanids collected by light-seine. Size-classes as in (A).

(Table 4). Only three significant ($p<0.05$) differences were detected by *t*-tests. The light-trap caught greater numbers of large pomacentrids, the light-seine greater numbers of large atherinids and small gobiids.

Among-night variation

Larval and pelagic juvenile fishes may vary in density at a particular location over short time-periods ranging from hours to days. We examined the among-night variation in two contexts. First, we used factorial analysis to examine the variation attributable to method of sampling and sampling period (nights) in the net collections. Second, we examined the ability of nets and aggregation devices to detect trends in density of large individuals of some families over a longer time-period (five nights).

A multivariate factorial analysis of variance was used to examine trends in mean density in six families: apogonids, atherinids, gobiids, lethrinids, mullids, and pomacentrids. Although both factors were significant (Table 5), the significant interaction between methods and nights (Pillai's Trace $F=1.65$; df 36, 186; $p<0.01$) indicates that differences among methods were not consistent over nights.

Canonical Discriminant Analysis was used to display the relationship between methods and night of sampling. Canonical variates 1 and 2 explained 93% of the variation in the data set (Table 6). Figure 6 illustrates the main conclusions from this analysis. Tucker trawls, and neuston and bongo nets each sampled a distinct fish fauna with little among-night variation. Purse-seine samples overlapped with those of the bongo nets on two nights and were the most variable, both within and among nights, probably reflecting the influence of few samples of small volume. Tucker trawl samples were characterized by consistently low numbers of the

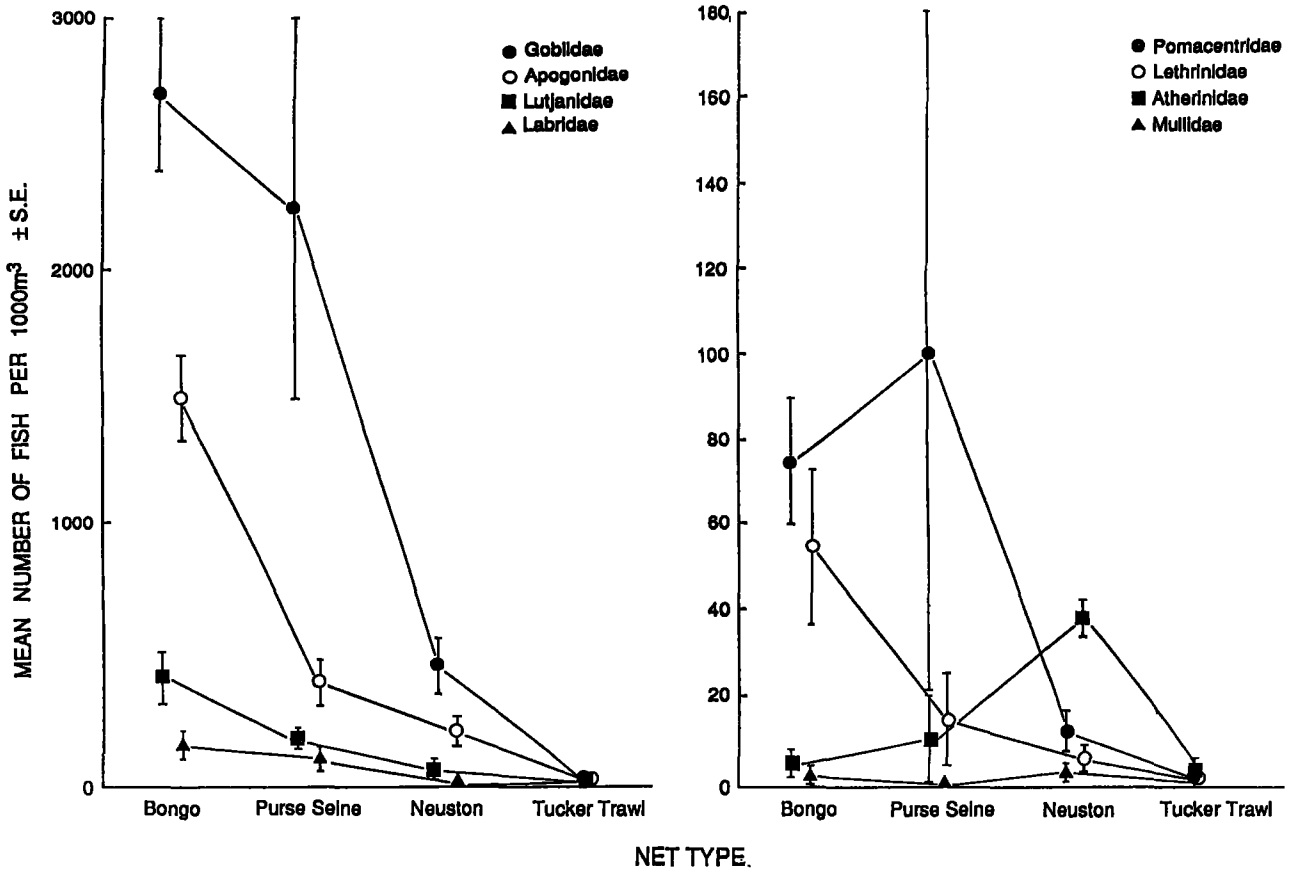

Figure 5

Mean densities of eight selected families (see Materials and methods) collected by four different net types on the nights of 3, 5, and 6 December 1986 off Lizard Island, Great Barrier Reef.

Table 4

Density of six taxa of larval and juvenile fishes collected by aggregation devices on 3, 5, and 6 December 1986 off Lizard Island, Great Barrier Reef. Data are mean densities (with 1SE) of fish per sample pooled over three sampling nights. Fish are divided into two size-classes: <6 mmSL (Small) and >6 mmSL (Large). * $0.05>p>0.01$; NS $p>0.05$.

Family	Size	Light-seine	Light-trap	p
Atherinidae	S	0.29± 0.22	0	
	L	9.36± 1.98	0.65± 0.25	*
Gobiidae	S	45.50±10.13	0.12± 0.08	*
	L	0.43± 0.23	8.92± 3.98	ns
Labridae	S	1.57± 0.62	0.04± 0.04	ns
	L	0.21± 0.11	1.54± 0.64	ns
Lethrinidae	S	0.43± 0.23	0	
	L	1.29± 0.34	1.38± 0.77	ns
Mullidae	S	0	0	
	L	3.86± 1.61	1.65± 0.68	ns
Pomacentridae	S	1.36± 0.52	0.27± 0.16	ns
	L	87.79 ±13.10	273.38±32.63	*

Table 5

Multivariate analysis of variance of density data for apogonids, atherinids, gobiids, lethrinids, mullids, and pomacentrids (see Materials and methods) from off Lizard Island, Great Barrier Reef. Factors include sampling methods (purse-seine, bongo net, neuston net, Tucker trawl) and nights (3, 5, and 6 December 1986). Data are ln(x+1) transformed. Test statistic used is Pillai's trace. Significance levels: **$0.01>p>0.001$; ***$p<0.001$.

Source	F	Numerator df	Denominator df	p
Method	11.53	18	9	***
Night	4.05	12	54	***
Method×Night	1.65	36	186	**

dominant families; neuston, by higher numbers of atherinids, a neustonic group. The significant interaction is attributable largely to the purse-seine result.

Table 6

Standardized canonical coefficients from the Canonical Discriminant Analysis of density of fishes over each method by night combination, from samples taken off Lizard Island, Great Barrier Reef on 3, 5, and 6 December 1986. Data were ln(x+1) transformed.

Family	CAN 1	CAN 2
Apogonidae	5.031*	0.675
Atherinidae	-1.129	1.961*
Gobiidae	1.463	0.585
Lethrinidae	-1.005	-1.279
Mullidae	0.177	0.595
Pomacentridae	0.184	-0.736
Canonical variate	Proportion	Cumulative
1	0.793	0.793
2	0.134	0.927

* Consistently high values in total, between and within canonical structure. These variables contribute significantly to the discriminatory power of the canonical variate.

Data from all five nights provided more information on patterns of temporal change for some taxa (Fig. 7). We focused on the comparative ability of the different methods to detect changes over time in numbers of the larger (>6 mm) individuals of some families because we wished to know the best methods for identifying temporal pulses of large larvae and pelagic juveniles of reef fishes. Large pomacentrids and mullids serve as appropriate examples. Although absolute numbers of fishes taken by nets and aggregation devices could not be directly compared, temporal changes in patterns of density could be evaluated among these methods. Comparisons were made using all methods, although bongo net data were available for the nights of 3, 5, and 6 December only.

Data from the two aggregation devices indicated that large pomacentrids increased in density from the 2nd to a peak on the 5th, and decreased over the 6th and 7th (Fig. 7). This pattern was not present in the data from nets, each of which provided a different temporal pattern of density.

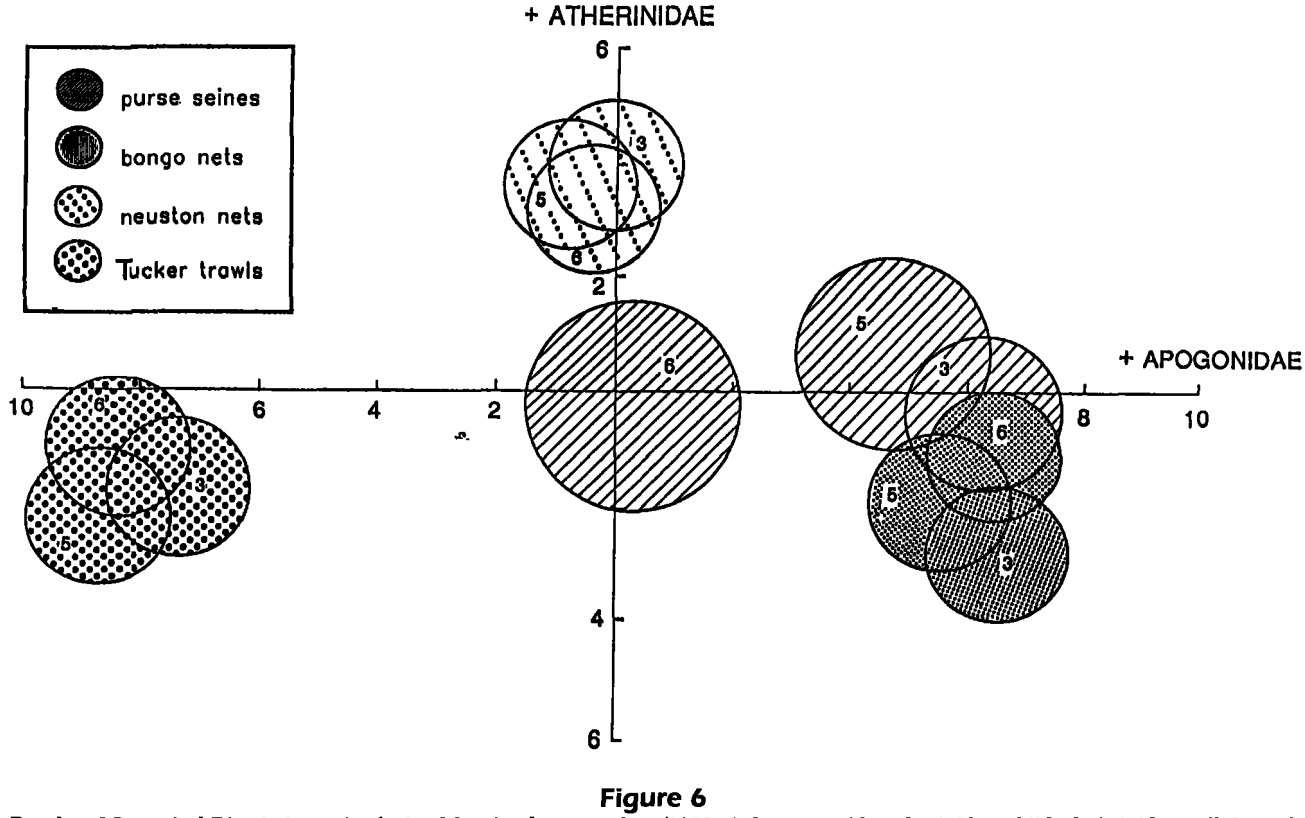

Figure 6

Results of Canonical Discriminant Analysis of density data (numbers/1000m³) for apogonids, atherinids, gobiids, lethrinids, mullids, and pomacentrids taken by four net types on the nights of 3, 5, and 6 December 1986 off Lizard Island, Great Barrier Reef. Factors analyzed were net type and night of sampling. Canonical variates 1 and 2 are displayed. Numbers superimposed on circles refer to the day of sample.

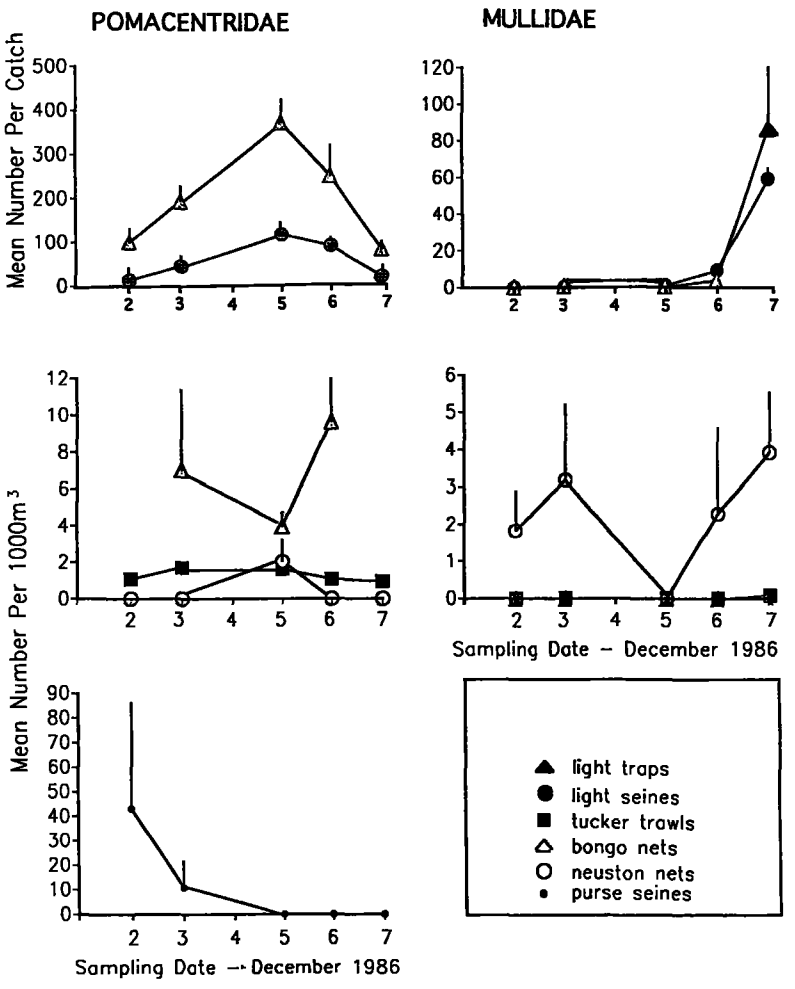

Figure 7

Changes in mean density (±SE) of large (>6 mm) pelagic pomacentrids and mullids sampled by six methods over six nights, 2–7 December 1986 off Lizard Island, Great Barrier Reef. Density estimates for the aggregation devices are not adjusted for volume sampled. Some methods did not collect large pomacentrids or mullids.

The aggregation devices indicated that large mullids were rare or absent until the 5th, and increased greatly in density on the 7th (Fig. 7). This trend was not present in data from the nets. Only the neuston net caught large mullids, but in low and variable numbers.

Discussion

The taxonomic composition obtained when sampling for larval and pelagic fishes is highly method-dependent. The bongo net captured the largest number of families, many of which were rare in the samples. Among abundant taxa, the four nets provided similar estimates of taxonomic composition. The light-trap, however, was more selective, and its catch differed in composition from that of the nets. Taxonomic composition of the light-seine samples was intermediate between the trap and nets, an expected result given its mode of operation.

Our results suggest that capture by the light-trap is dependent on fish size: larger pelagic stages are more likely to be attracted to the light and to swim into the trap than are small stages. However, trap performance may also be time-dependent. For example, apogonids, carangids, lutjanids, and scarids, which were rare or absent in light-trap catches during this study, have been captured during extended light-trap sampling around Lizard Island (M. Milicich, Griffith Univ., Nathan, Queensland, pers. commun.). The absence from light-traps at particular times may simply indicate that large or well-developed individuals of some families were not present at that time.

However, our study provides evidence that pelagic stages of some families may not be photopositive or enter traps, thus indicating some selectivity by the aggregation devices. Schindleriids were present in the net samples to adult size, yet were not captured with either of the light-aggregation methods. The net samples may have included the largest pelagic individuals of callionymids, and perhaps platycephalids and bothids, because they leave the pelagic environment (i.e., settle) at a relatively small size (see Table 3). These families were not present in the light-trap catches.

The size-distribution and density estimates of pelagic fishes captured also differ among nets. The bongo net, neuston net, and purse-seine captured predominantly smaller fishes. For abundant families, density estimates by the bongo net and purse-seine were generally similar, neuston net estimates were somewhat lower, and the Tucker trawl provided still lower estimates. The bongo net provided the highest abundance estimates for most sizes of most families. The Tucker trawl

undersampled smaller individuals, but was no better than the bongo net at capturing larger larvae and pelagic juveniles. This is consistent with the results of Kendall et al. (1987) and Clarke (1991), who compared bongo nets and larger trawls. The light-seine captured a wide size-range of fishes because it combined the sampling characteristics of both a purse-seine and an aggregation device.

Mesh size is an important determinant of catch composition because extrusion varies with mesh size. For a given mesh size, extrusion is a function of body shape and pressure across the net mesh (Clarke 1983 and 1991, Gartner et al. 1989). Body shape is species-specific, which emphasizes the importance of taxon-specific factors in methodological studies. Our results cover a comprehensive range of body shapes, from slender (gobiids) to deep bodied (apogonids and pomacentrids) to moderately deep with elongate fin spines (lutjanids), and should have general application. Purse-seines appear to herd planktonic organisms, while towed nets actively filter, often under considerable pressure; thus extrusion will vary between these two gear types regardless of mesh size. As our primary interest was in comparing a series of sampling devices in their normal working configuration, we did not attempt to test the effects of different mesh sizes within gear types.

Although vertical stratification is minimal at night in the study area (Leis 1986, 1991a), vertical distribution of the fishes could have affected apparent performance of the samplers because each method sampled somewhat differently in the vertical plane. Towed nets were deployed at fixed depths. Experience elsewhere has suggested that light-traps draw their catch from a relatively narrow depth stratum, the upper 5 m (P.J. Doherty, unpubl.). However, only in the neuston net can we confidently attribute greater catches (especially of atherinids) to vertical stratification. For this study, we assumed that vertical distribution of the fishes did not affect our evaluation of the other methods.

Horizontal or temporal variations in density may also have confounded comparisons. A position effect was possible because the aggregation devices were operated at fixed positions about 700 m apart (Fig.1). A temporal effect is possible because the bongo net and Tucker trawl tows were run in blocks and not randomized during each night's sampling, although the order of blocks was alternated among nights.

Absolute sampling efficiency of the nets was not measured. Our estimates of sampling performance were relative, because we did not obtain unbiased estimates of the true densities of small pelagic fishes. We did not attempt to use the methods of Somerton & Kobayashi (1989) to correct our net catches because we felt some of the assumptions required, especially those relating to patch size and consistency through time, were not appropriate in the case of our study. The smaller bongo net seemed to have equal or greater sampling efficiency than the larger Tucker trawl at night for large pomacentrids.

A comprehensive comparison of the six sampling methods would require two things. First, we would need to standardize all results as number of organisms per unit volume of water sampled. Second, we would require an estimate of the sampling precision of each device. For towed nets, both could be obtained because flowmeters provided estimates of the volume filtered for each tow. In the case of the purse-seine, it was not possible to obtain reliable estimates of the volume of water filtered during each deployment of the net. Minor variations in the deployment procedure can modify the dimensions of the volume enclosed by the net. At present, we have no reliable way of estimating this; therefore, for the purse-seine we have a general estimate of water filtered based on idealized dimensions of the deployed net.

Volumes sampled by aggregation devices cannot be estimated at this time, but preliminary calculations (below) suggest they may be large. The bongo net as operated in this study will sample ~4000 m^3/h, the Tucker trawl ~14,000 m^3/h, and we estimate the light-aggregation techniques could sample tens of thousands of m3/h. Therefore, light-aggregation techniques may be the best way to capture sufficient numbers of rarer, larger stages for useful analyses. Aggregation methods may offer considerable advantages in studies of settlement-stage reef fishes, but one must accommodate the characteristic taxonomic selectivity and unknown sample volume.

Two alternatives may explain the apparent disparity in numbers of larger pomacentrids estimated by the bongo net (average 6.9/1000 m^3; Tucker trawl catches averaged 1.49/1000 m^3) and the light-trap (average 273/h): (1) The bongo net undersamples these larger pelagic stages relative to the light-trap, or (2) the light-trap samples larger volumes of water. Assuming the two methods sample large pomacentrids with equal efficiency, the light-traps sample volumes on the order of 40,000m^3/h. This requires the trap to capture, with efficiency equal to that of the net, photopositive stages within a 7–50 m radius (to 5 m depth) of the trap, depending on the current speed (average in the area is 15 cm/s; Leis 1986) and geometry of the light field. It is not possible to choose between alternatives without a better measure of the effective volume swept by traps. Work in progress will help resolve this question.

Short-term temporal variation in the density of particular families was more obvious in the results of some methods than others. For the smaller size-classes, neuston, bongo, and Tucker nets gave consistent results

over short time-periods (Fig. 6). Catches from the purse-seine were more variable within a sampling period and showed greater variability among nights of sampling than did the towed nets. This reflects the localized sampling area and small sample volume of the purse-seine. For larger mullids and pomacentrids, similar trends in density over five nights were identified by the aggregation devices. These trends were not apparent in the data from the towed nets. Thus, the aggregation devices seem particularly suited to studies of short-term temporal variation in the larger (>6 mm) size-classes. The rapid and independent changes in density of the larger individuals of these two families suggest that larger pelagic stages are not present in the water at all times at a location. The alternative, that there are short-term taxon-specific changes in catchability due to changes in behavior of the fishes, seems less likely, but cannot be dismissed without further study.

A number of other studies have compared sampling methods for planktonic and pelagic assemblages. Purse-seines were found to be superior to towed nets for sampling larval anchovies (Murphy & Clutter 1972). Larger, faster, more-transparent nets may minimize net avoidance (Clutter & Anraku 1968). However, Smith & Richardson (1977) suggest that increased net size and towing speed may intensify the disturbance in front of the net and increase net avoidance. All towed nets in these cited studies employed towing bridles, which are a source of water disturbance and, thus, net avoidance by fishes. Towing bridles were not used in the present study, which may be why our conclusions differ from those of Clutter & Anraku (1968) and Murphy & Clutter (1972).

We agree, however, with Clarke (1991) who made detailed comparisons of the effectiveness of two types of bongo nets and a midwater trawl in capturing reef-fish larvae. He suggested that the bongo nets (0.7 m diameter with 0.183 mm mesh, and 1.25 m diameter with 2.5 mm mesh) sampled larvae as well or better than a 3 m Issacs-Kidd trawl (6 mm mesh). Clarke concluded that when densities of larvae were high, 0.7 m and 1.25 m bongo nets were the most effective methods for sampling small and large larvae, respectively. Although larger nets are assumed to capture more and larger fishes due to lessened avoidance (Clarke 1983 and 1991, Methot 1988), this was not true in our study nor is it always true in other pelagic groups (Barnes & Tranter 1965, Sands 1978, Pillar 1984).

One other significant study compared catches from a light-trap with those from a towed net. Gregory & Powles (1988) investigated a relatively simple planktonic assemblage of freshwater fishes. Based on a comparison of taxonomic composition and size of fishes, they concluded that both sampling methods should be used to avoid selectivity biases. An interesting conclusion that differs from our results was that the light-trap provided a better representation of size-classes, including smaller individuals, than did the towed net. This emphasizes the taxon-specific and, perhaps, habitat-specific nature of gear-performance measures.

We agree with Omori & Hamner (1982) that the sampling device and program selected must be question-driven (Kingsford 1988). In order to assist in the choice of appropriate methods, we summarize the performance and sampling properties of the six methods employed in this study (Table 7). Surveys of larval fishes are best accomplished with a bongo net. This will cover a significant portion of the size-range in many important taxa, including larger individuals, at least at night. No extra benefits were apparent from using the larger Tucker trawl. A major advantage of bongo nets is the relative ease with which they may be deployed and retrieved. As expected, neuston nets focused on neustonic fishes.

Surprisingly, the purse-seine provided results comparable to the bongo net despite the small volumes sampled. Among-sample variances were predictably

Table 7

Sampling characteristics of six methods used to collect planktonic and pelagic fishes at the Lizard Island study site, Great Barrier Reef.

Performance criterion	Bongo net	Neuston net	Tucker trawl	Purse seine	Light-trap	Light-seine
Size selectivity	Wide size-range; modal values at lower size.	Samples larger individuals of some taxa; modal values at lower size.	Samples larger sizes; no more effective than bongo net at night.	Primarily small individuals.	Primarily large individuals.	Wide size-range.
Taxonomic selectivity	Least-selective.	Neustonic taxa only.	Slender taxa and small individuals extruded.	Captures only shallow living taxa; undersamples rare taxa.	Selective; dependent on taxon behavior.	Combines light selectivity with characteristics of purse-seine.

higher than those of towed nets. Sampling of local-scale surface features requires the degree of spatial precision and replication provided by small purse-seines (Kingsford & Choat 1985 and 1986, Kingsford et al. 1991), but purse-seines cannot sample deeper than the upper few meters of the water column, and are difficult to operate in any but the best conditions. Localized replicated sampling may also be obtained by free-fall plankton nets (Kobayashi 1989) which, however, obscure vertical patterns and also have a small volume sampled.

Investigation of the patch size of pelagic organisms requires the ability to sample simultaneously over several spatial scales. Large-scale deployment of arrays of automated light-traps will increase replication and allow investigation of phenomena at several spatial scales without risk of temporal confounding, provided the traps can be retrieved over the same time-period. Also, both light-traps and purse-seining with aggregation devices may detect temporal pulses in the density of larger larvae and pelagic juveniles with greater reliability and precision than towed nets.

In addition to the sampling properties of the different devices, there are a number of more pragmatic considerations. Sorting and identification of samples may be a major bottleneck. This will be influenced by the size of the sample, the amount of organic material included, and condition of the fishes themselves. In this context, large samples taken by finer-mesh nets may be particularly difficult to process. Smaller or more selective samples are more readily processed, and those from purse-seines and light-traps yield living fishes suitable for rearing and experimentation. Further, the smaller the larva the more difficult it is to identify; thus, methods like the light-trap, which samples larger fishes, simplify identification.

It is clear that studies of the biology of small pelagic fishes require the use of both nets and aggregation devices either separately or in combination, depending on the type of question posed. No single method can provide a comprehensive picture of the larval and pelagic juvenile fish fauna, and few programs could cover the expense and logistic effort of the simultaneous deployment of a variety of methods. The picture one obtains of the larval and pelagic juvenile fish fauna is highly method-dependent. Which picture or combination of pictures is suitable for answering a given question varies with the question, the taxon, and the size-range of the fishes.

Acknowledgments

This project was supported by funds from the URG Griffith University to PJD, the Australian Marine Sciences and Technology funding panel to JHC and JML, and internal funds from the Australian Museum (JML) and James Cook University (JHC). Field facilities were provided by the Lizard Island Research Station and the Australian Museum. We wish to thank M. and M. Jumelet (RV Sunbird) and M. Milicich, M. Meekan, M. McCormick, N. Preston, and M. Doherty for assistance with the sampling program; D. Furlani, R. Birdsey, S. Reader, and S. Thompson for assistance in the lab; and M. Kingsford and M. Milicich for discussion of the program and critical reading of the manuscript. The manuscript benefited from the comments of anonymous reviewers.

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