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Two methods of sampling fish larvae over reefs: a comparison from the Gulf of California

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Abstract. I compared the sampling properties of two methods for collecting fish larvae over reefs: nighttime collecting with a light trap, and daytime collecting with a small plankton net that could be steered by a diver. Samples were collected in the Gulf of California during summer, 1989 and 1990. The 90 light-trap samples yielded 9406 larvae from 31 families, while the 75 plankton-net samples yielded 17852 larvae from 43 families plus unidentified anguilliforms. Four families were collected only in the light trap, and 16 families plus the anguilliforms were collected only with the plankton net. With one exception, the families that were collected by only one method were rare. Twenty-seven families were collected by both methods, but only 13 were collected at least five times by each. The average catch per sample differed significantly between methods for 9 of these 13 families. In each case, the plankton net yielded more larvae per sample. The distribution of larvae among families was less equitable in light-trap samples than in plankton-net collections, primarily because clupeids were so dominant in the former. However, the taxonomic composition of light-trap and plankton-net collections was broadly similar. Seven families were shared among the ten most abundant families for each method, and the relative abundances of taxa (47 families plus anguilliforms) were strongly correlated between methods. A comparison of larval size-distributions for 12 families indicated that the size structure of catches usually differed between collecting methods. In four families there was little overlap in the size classes collected, in five families the distributions overlapped broadly but had different shapes, and in three families the size distributions were similar. Although the light trap collected larger larvae on average, its catches were not limited to settlement-stage or transition larvae. Larvae of at least ten families were present over reefs in all size classes, but the combination of both sampling methods was usually required to detect this. Based on their abundance and wide size distribution over reefs, at least some larvae from these ten families may remain over reefs throughout development. However, additional data are required to determine the importance of water over reefs as a larval habitat.

Introduction

Methods are well developed for sampling larval fish populations in the open water of neritic and oceanic environments. There is a large literature dealing with the designs of various plankton nets and trawls, opening–closing mechanisms for discrete depth hauls, and environmental sensing systems. In addition, manuals proposing standard equipment and methods for large-scale surveys of fish eggs and larvae have been published (e.g. Kramer et al. 1972, Smith and Richardson 1977). However, open-water ichthyoplankton methods are poorly suited to shallow water over complex reef structures because submerged rocks and coral pose a hazard to research vessels and towed sampling gear.

A variety of alternative methods are available for sampling fish larvae around complex reef environments. Methods that have been employed include diver-steered plankton tows (Marliave 1986), diver-pushed nets (Smith et al. 1987), visual censuses (Kingsford and Choat 1989), free-fall nets (Kobayashi 1989), and night-lighting (Dennis et al. 1991, Victor 1991). Several additional sampling methods, including plankton pumps (Taggart and Legget 1984, Powlik et al. 1991), larval purse seines (Murphy and Clutter 1972, Kingsford and Choat 1985), light traps (Doherty 1987), and moored channel nets (Keener et al. 1988), may also be suitable for use in close proximity to reefs. However, there have been very few studies of fish larvae over reefs (see Leis 1991a), and none of these alternative sampling methods have been widely used in such environments. Consequently, their sampling properties and limitations are not well known, and it is difficult to select the best sampling methodology for a particular research subject (see Omori and Hamner 1982, Kingsford 1988, Leis 1991a).

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Field comparisons of methods can help to elucidate sampling properties (e.g. Murphy and Clutter 1972, Powlik et al. 1991). In this paper I report on a comparison between two methods for collecting fish larvae over reefs: nighttime collecting with a light trap, and daytime collecting with a small plankton net that can be steered by a diver. I selected these two kinds of gear because they can sample fish larvae very close to reef structures (0 to 1 m) over a range of depths and topography. Furthermore, I wanted to collect a wide range of larval size classes, and I had reason to expect that the size selectivities of the two gears would complement each other. Daytime tows with small plankton nets are likely to be biased towards small larvae (Clutter and Anraku 1968, Barkley 1972, Murphy and Clutter 1972), and light traps primarily attract large larvae (Doherty 1987, Milicich 1989, Thorrold and Milicich 1990, Thorrold 1992, Choat et al. 1993). My comparison of sampling properties is based on a series of collections taken over rocky reefs in the Gulf of California, Mexico (Brogan 1992), and it focuses on taxonomic composition, catch rates, and larval size-frequency composition.

After comparing sampling properties, I also discuss the possibility that some larvae remain over reefs throughout development, rather than dispersing offshore. It has been argued that larvae should disperse away from reefs in order to decrease predation risk, increase dispersion of siblings, or enhance larval feeding (e.g. Johannes 1978, Barlow 1981, Doherty et al. 1985). A review of the larval biology of coral reef fishes (Leis 1991 a) supported the idea that the larvae of few taxa, if any, remain over coral reefs during development. However, studies from Canada (Marliave 1986) and New Zealand (Kingsford and Choat 1989) suggest that larval development over reefs may occur more commonly in temperate regions. The Gulf of California provides an interesting case study because its warm temperate climate (Maluf 1983) and rocky reefs support a predominantly tropical reef fish fauna, similar to that found throughout the tropical eastern Pacific (Thomson and Gilligan 1983, Thomson et al. 1987).

Materials and methods

Sampling gear

My light trap was modeled after those described by Doherty (1987), but is smaller, has only two chambers rather than three, and the operation of lamps does not alternate between chambers. Advantages of my design are its low cost ($100 US in 1988), availability of components, and ease of construction. Its chief disadvantage is the absence of a timer to facilitate automatic operation (Doherty 1987). The trap consists of three main assemblies: the trap body, the waterproof core, and the protective cage (Fig. 1). The trap body was constructed of wood and coated with marine varnish. The 12 × 15 cm opening in the top of the trap was covered with a piece of clear acrylic plastic. The four sides of the upper chamber were fitted with pyramid-shaped, clear plastic funnels that tapered from 18 × 18 cm down to 1 × 10 cm vertical slots. The partition separating the upper and lower chambers was fitted with clear plastic slots that tapered from 6.5 × 15 cm down to 1 × 15 cm. The lower trap body was provided with two 2.5 cm drain holes (closed with rubber stoppers) for removal of samples. The upper part of the waterproof core (inside the trap body) was constructed from a 4.5 cm clear plastic tube, and the lower portion was made from 10 cm PVC (polyvinyl chloride) pipe. These two pieces were joined by a PVC reducer and bushing. Two 6 W fluorescent lamps were wired, attached to a clear plastic strip, and inserted in the upper core. The lamps were powered by two 6 V motorcycle batteries (6N4-2A) connected in series, and the required circuit board was taken from a battery-powered fluorescent camping lantern. Both ends of the core were sealed with removable rubber end caps and hose clamps. The projecting lower portion of the core was protected from damage by a cage (2.5 cm PVC pipe) that was attached to the bottom of the trap body.

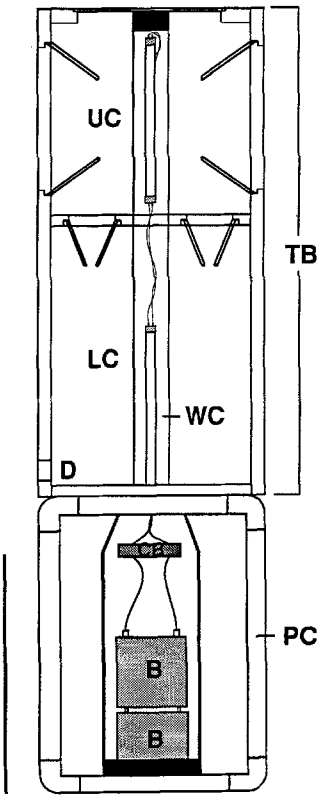


Fig. 1. Schematic diagram of light trap. B: batteries; CB: circuit board; D: drain; LC: lower chamber; PC: protective cage; TB: trap body; UC: upper chamber; WC: waterproof core. Scale bar = 30 cm

The plankton net was a 0.5 m diam, 2 m long conical design with 0.5 mm mesh and a 0.3 mm mesh cod-end bag. The net was towed with a three-point bridle at 1.0 to 1.5 m/s by a 4 m inflatable boat. Filtered volumes were estimated from a calibrated Oceanics flowmeter mounted in the mouth of the net. When working very close to the reef, two 19 × 51 cm plywood panels with handles were hinged to the upper rim of the net with carabiners. These panels made effective, adjustable diving planes which allowed a diver to ride the net assembly and control its depth so that the stratum 0 to 1 m from the reef could be sampled. Lead weights (5 to 10 kg, depending on the maximum depth of the tow path) were used to help achieve the proper depth range. The plywood panels and weights were removed from the net during the stepped oblique tows that were employed farther from the reef.

Study sites

Samples were collected at five localities in the central and southern Gulf of California (Fig. 2) during June, July, and August 1989 (125 samples), and July and August 1990 (40 samples). One to several sites were sampled at each locality. All sites (except at B) were

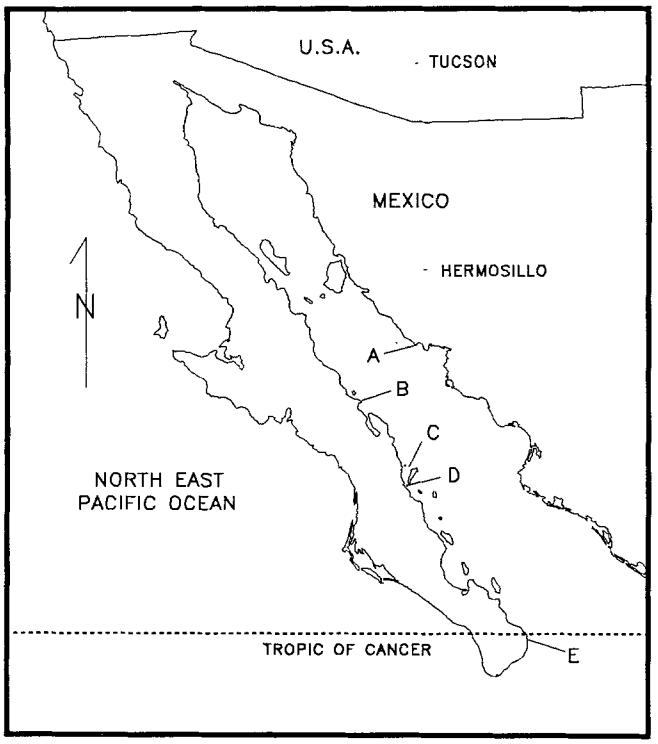


Fig. 2. Five study localities in Gulf of California, Mexico. A: Bahía San Carlos; B: Punta Santa Inez; C: Isla Coronado; D: El Juncalito; E: Punta Los Frailes. Map dimensions are 1210 km (vertical) × 1080 km (horizontal)

arrayed along steep rocky coastlines, and consisted of consolidated rock and boulder reefs that extended ~50 m offshore before encountering sand bottoms at 15 to 30 m depth. The site at B was shallower and had a more gently sloping bottom, but few collections were taken there (6 in 1989).

Sampling protocol

I collected fish larvae at nominal distances of 1, 20, and 100 m from shore at each site. These distances located sampling among boulders (1 to 5 m depth), over deeper reef (10 to 20 m depth), and over sand bottoms beyond the reef margin (20 to 30 m depth), respectively. At most, one set of light-trap samples and one set of net tows was taken in a 24 h period (a set comprises three samples taken in immediate succession, one at each distance from shore). I strived to collect complete sets on each sampling occasion, but sea conditions or equipment problems occasionally prevented this. Consequently, the number of samples taken at 1, 20, and 100 m from shore was 32, 29, and 27 for the light trap, and 26, 23, and 25 for the plankton net. In addition, two light-trap samples taken 10 m from shore and one net tow taken 50 to 100 m from shore were included in the analyses.

Light-trap sampling commenced ~1 h after sunset. The light trap was weighted (8 kg) and suspended 1 m below a tethered float from where it illuminated a volume several meters in radius. This volume encompassed depths from the surface to ~3 to 5 m. The normal fishing period was 20 min/sample, but 4 of the 90 samples were slightly longer (21 to 24 or 30 min). The order in which the distances were sampled was alternated on a haphazard basis. At the end of each fishing period, the light trap was lifted into the boat, its contents were drained through a cod-end bag (0.3 mm mesh), and the sample was immediately preserved in 5% formalin or 95% ethanol.

The same localities, sites, and distances from shore were sampled during the day with the plankton net (most samples taken between 09.00 and 12.00 hrs). Tows at a nominal distance of 1 m from shore were diver-guided (see earlier subsection "Sampling gear") so that the stratum just above reef surfaces lying at depths of 1 to 5 m was sampled. Tows at 20 and 100 m from shore were not diver-guided, but were conducted as stepped oblique tows from 5.5 m depth to the surface. Using a small hand winch and a 20 kg dead-weight depressor, the net was lowered to maximum depth, allowed to sample for 1 min, and then stepped up to the surface, sampling eight additional strata (including the surface) for 1 min each in the process. Depths of tows were estimated from the length of wire out and wire angle as measured with an inclinometer. Complete tows took ~15 min. The tendency for the net to clog varied widely, and filtered volumes ranged from 22 to 259 m^3 (108.4 ± 41.7, mean ± 1 SD). At the conclusion of each tow, the net was washed down with pumped seawater and the sample was immediately preserved in 5% formalin or 95% ethanol.

Sample processing and analysis

All fish larvae were removed from plankton samples with the aid of a stereomicroscope, and identified to family using standard references (e.g. Leis and Rennis 1983, Moser et al. 1984, Okiyama 1988, Leis and Trnski 1989). Although identification to lower taxonomic levels was possible in some families (especially among the larger specimens), all comparisons were done at the family level. After identification and enumeration, larvae were measured, and size-frequency distributions were constructed for the 12 families with at least 10 larvae collected by each method. Notochord lengths were measured prior to completion of flexion, and standard lengths were measured on postflexion larvae. Measurements were made by placing the larvae in petri dishes, passing them over a 1 mm grid, and scoring them in 0.5 mm size classes. Size classes were subsequently combined into 1 mm intervals for the purpose of presentation. Damaged larvae were not measured, and one very large collection of clupeids was subsampled. Size-frequency distributions of larvae in light-trap and plankton-net samples were compared using the Kolmogorov-Smirnov (K-S) test (Sokal and Rolf 1981). Comparisons in this paper are based on pooled data from the samples collected at 1, 20, and 100 m from shore. Differences among samples from different distances from shore will be described elsewhere.

I could not compare the efficiencies of the light trap and plankton net in the standard way (e.g. larvae/m^3) because the volume of water from which the light trap attracts larvae is unknown and is likely to vary between species, age classes, and times (see Paragraph 1 of "Discussion"). As an alternative, I compared catch rates in terms of the mean number of larvae per sample (the four long light-trap samples were converted to a 20 min equivalent). Since a 20 min light-trap sample and a 15 min plankton tow take the same amount of time for gear deployment, sampling, and retrieval (about 30 min), this is a fair comparison of the number of larvae caught per unit of field time. Although this metric may be a poor estimator of larval abundance during any particular fishing period (because sample volumes vary), when averaged across each data set, it provides a rough comparison of relative gear performance. I compared mean catches statistically (using the Mann-Whitney U-test, Zar 1984) only in those families that were collected at least five times by each gear.

Results

The 165 samples (both gears combined) contained 27 258 larvae from 47 families plus unidentified anguilliforms (Table 1). The light trap collected fewer families than the plankton net (31 vs 43 plus anguilliforms). This was probably due, in part, to the smaller number of larvae it collected (9406 vs 17 852 in net collections). Sixteen light-trap samples contained no fish larvae, but all plankton-net samples had larvae in them. Four families (Elopidae,

Table 1. Summary of occurrences (occ.), number (*n*) of fish larvae, and percent gear total accounted for by each taxon in 90 light-trap samples and 75 plankton-net samples taken over reefs in the Gulf of California

Taxon	Light trap			Net tows			Combined catch		
	occ.	*n*	(%)	occ.	*n*	(%)	occ.	*n*	(%)
Elopiformes									
Elopidae	1	2	(0.02)	0	0	(0)	1	2	(0.01)
Anguilliformes	0	0	(0)	8	14	(0.08)	8	14	(0.05)
Clupeiformes	0	0	(0)	3	88	(0.49)	3	88	(0.32)
Clupeidae	45	4 631	(49.23)	45	3 875	(21.71)	90	8 506	(31.21)
Engraulididae	22	130	(1.39)	19	156	(0.87)	41	286	(1.05)
Gonorynchiformes									
Chanidae	1	5	(0.05)	5	17	(0.10)	6	22	(0.08)
Stomiiformes									
Photichthyidae	1	2	(0.02)	12	338	(1.89)	13	340	(1.25)
Myctophiformes									
Myctophidae	1	1	(0.01)	22	210	(1.18)	23	211	(0.77)
Synodontidae	3	3	(0.03)	3	3	(0.02)	6	6	(0.02)
Ophidiiformes									
Bythitidae	4	16	(0.17)	15	62	(0.35)	19	78	(0.29)
Ophidiidae	0	0	(0)	2	3	(0.02)	2	3	(0.01)
Gobiesociformes									
Gobiesocidae	18	39	(0.41)	34	274	(1.53)	52	313	(1.15)
Beloniformes									
Exocoetidae	1	1	(0.01)	6	9	(0.05)	7	10	(0.04)
Hemiramphidae	4	5	(0.05)	5	9	(0.05)	9	14	(0.05)
Atheriniformes									
Atherinidae	6	12	(0.13)	1	1	(0.01)	7	13	(0.05)
Beryciformes									
Holocentridae	0	0	(0)	1	1	(0.01)	1	1	(<0.01)
Syngnathiformes									
Syngnathidae	0	0	(0)	2	3	(0.02)	2	3	(0.01)
Scorpaeniformes									
Scorpaenidae	2	2	(0.02)	6	7	(0.04)	8	9	(0.03)
Perciformes									
Percoidei									
Carangidae	6	6	(0.06)	37	658	(3.69)	43	664	(2.44)
Coryphaenidae	0	0	(0)	1	2	(0.01)	1	2	(0.01)
Ephippididae	0	0	(0)	4	4	(0.02)	4	4	(0.01)
Gerreidae	37	582	(6.19)	25	452	(2.53)	62	1 034	(3.79)
Haemulidae	12	52	(0.55)	39	744	(4.17)	51	796	(2.92)
Lutjanidae	4	7	(0.08)	17	62	(0.35)	21	69	(0.25)
Mullidae	0	0	(0)	7	12	(0.07)	7	12	(0.04)
Sciaenidae	3	4	(0.04)	19	51	(0.29)	22	55	(0.20)
Serranidae	0	0	(0)	1	1	(0.01)	1	1	(<0.01)
Mugiloidei									
Mugilidae	1	1	(0.01)	17	29	(0.16)	18	30	(0.11)
Polynemidae	1	2	(0.02)	0	0	(0)	1	2	(0.01)
Sphyraenidae	0	0	(0)	12	30	(0.17)	12	30	(0.11)
Labroidei									
Labridae	3	3	(0.03)	0	0	(0)	3	3	(0.01)
Pomacentridae	21	253	(2.69)	50	743	(4.16)	71	996	(3.65)
Scaridae	1	1	(0.01)	0	0	(0)	1	1	(<0.01)
Blennioidei[a]	3	9	(0.10)	9	124	(0.69)	12	133	(0.49)
Blenniidae	8	10	(0.11)	15	81	(0.45)	23	91	(0.33)
Chaenopsidae	36	690	(7.34)	42	1 826	(10.23)	78	2 516	(9.23)
Dactyloscopidae	5	7	(0.08)	22	471	(2.64)	27	478	(1.75)
Labrisomidae	36	1 050	(11.16)	53	992	(5.56)	89	2 042	(7.49)
Tripterygiidae	46	1 267	(13.35)	50	3 122	(17.49)	96	4 389	(16.10)
Gobioidei									
Gobiidae	24	546	(5.80)	54	2 001	(11.21)	78	2 547	(9.34)
Microdesmidae	1	1	(0.01)	3	4	(0.02)	4	5	(0.02)
Scombroidei									
Istiophoridae	0	0	(0)	1	1	(0.01)	1	1	(<0.01)
Scombridae	3	3	(0.03)	29	278	(1.56)	32	281	(1.03)
Trichiuridae	0	0	(0)	1	1	(0.01)	1	1	(<0.01)
Stromateoidei									
Nomeidae	0	0	(0)	1	2	(0.01)	1	2	(0.01)

Table 1 (continued)

Taxon	Light trap			Net tows			Combined catch		
	occ.	*n*	(%)	occ.	*n*	(%)	occ.	*n*	(%)
Pleuronectiformes									
Cynoglossidae	0	0	(0)	3	6	(0.03)	3	6	(0.02)
Paralichthyidae	0	0	(0)	8	12	(0.07)	8	12	(0.04)
Soleidae	0	0	(0)	10	20	(0.11)	10	20	(0.07)
Tetraodontiformes									
Balistidae	0	0	(0)	31	467	(2.62)	31	467	(1.71)
Tetraodontidae	0	0	(0)	4	13	(0.07)	4	13	(0.05)
Unidentified	0	0	(0)	35	197	(1.10)	35	197	(0.72)
Disintegrated	5	63	(0.67)	40	367	(2.11)	45	439	(1.61)
Totals		9 406			17 852			27 258	

[a] Unidentified blennioids are small labrisomids or tripterygiids that could not be identified to family

Table 2. Mean number of larvae per sample for 13 families of fishes collected at least five times in both light trap and plankton net. Mean values based on all light-trap and plankton-net collections and compared using Mann-Whitney U-test. See Table 1 for number of occurrences and number of larvae for each family. NS: not significant at $p > 0.05$

Family	Light trap	Net tows	*p*
Clupeidae	50.896	51.667	0.024
Engraulididae	1.443	2.080	0.796 [NS]
Gobiesocidae	0.418	3.653	0.002
Carangidae	0.065	8.773	<0.001
Gerreidae	6.418	6.027	0.441 [NS]
Haemulidae	0.576	9.920	<0.001
Pomacentridae	2.743	9.907	<0.001
Blenniidae	0.109	1.080	0.198 [NS]
Chaenopsidae	7.579	24.347	0.053 [NS]
Dactyloscopidae	0.078	6.280	0.006
Labrisomidae	11.482	13.227	<0.001
Tripterygiidae	13.827	41.627	0.013
Gobiidae	5.946	26.680	<0.001

Polynemidae, Labridae and Scaridae) were collected only in the light trap, and 16 families plus the anguilliforms were collected only in the plankton net (Table 1). With the exception of balistids, which were common in plankton tows (31 occurrences, 467 larvae) and absent from light-trap samples, the families that were collected by only one method were rare (1 to 30 larvae each). Twenty-seven families were collected by both methods, but only 13 were collected at least five times by each. In 9 of these 13 families, the mean catch per sample was significantly greater for the plankton net. The 4 other families I compared statistically had similar mean catches for the two methods (Table 2). Several additional families appeared to be better collected with the plankton net, but their rarity or absence in light-trap samples precluded statistical comparisons (see Table 1). Most striking in this regard were photichthyids, myctophids, scombrids, and balistids. From 210 to 467 larvae of these families were collected in the plankton net, while only 0 to 3 were collected in the light trap.

The distribution of larvae among families was less equitable in light-trap samples than in plankton-net collections. Only 8 families contributed at least 1% of the larvae in light-trap samples, and the 10 most abundant families accounted for 98% of the catch (Fig. 3A). By comparison, 15 families contributed 1% or more of the larvae in net tows, and the top 10 families accounted for only 84% of the total (Fig. 3B). Clupeids ranked highest in abundance in collections by both methods, but they were much more dominant in the light-trap samples (49 vs 22% in net tows). However, >65% of the clupeid larvae collected in the light trap were taken in a single sample. If clupeids from this sample are excluded, relative abundance of clupeids in the light-trap samples drops to 25%, and the dominance relationships of families appear more similar between methods.

Although the light-trap and plankton-net samples differed in the number of larvae collected and in several taxonomic details, the two methods provided similar information about the relative abundances of families within larval assemblages over reefs. For example, 7 families were shared among the 10 most abundant families for each method, and 10 families were shared among the 15 most abundant. Furthermore, relative abundances in light-trap and plankton-net samples were strongly correlated, either when all taxa were included ($n = 47$ families plus anguilliforms, $r^2 = 0.728$, $p < 0.0001$) or when only the 15 most abundant families were included ($r^2 = 0.712$, $p < 0.0001$). When the single extraordinarily large collection of clupeids was excluded from the light-trap data set (but all other clupeids were included), the correlation was strengthened (Fig. 4, $n = 47$ families plus anguilliforms, $r^2 = 0.841$, $p < 0.0001$).

In general, differences between larval size distributions for the two sampling methods were more pronounced than taxonomic differences. In nine families, the differences in distributions were highly significant (K-S test, $p < 0.001$), and in one family (Pomacentridae) the difference was marginally significant (K-S test, $p < 0.05$). There was no statistical difference between the size distributions of bythitids and blenniids collected by the two methods (K-S test, $p > 0.05$), but these two comparisons suffered from small sample sizes and a cautious interpretation is advised. I grouped the families according to the nature of the differences between methods.

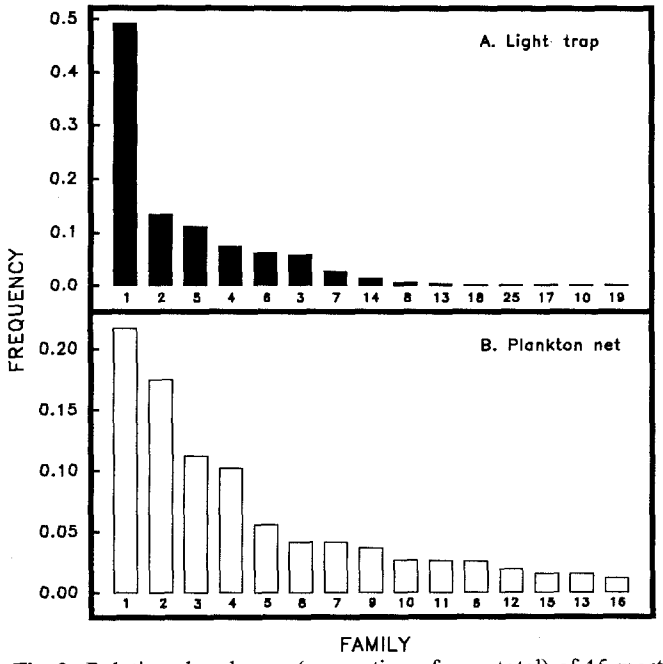


Fig. 3. Relative abundances (proportion of gear total) of 15 most abundant families in light-trap and plankton-net samples. Numeric codes are based on family ranks in combined data set. 1: Clupeidae; 2: Tripterygiidae; 3: Gobiidae; 4: Chaenopsidae; 5: Labrisomidae; 6: Gerreidae; 7: Pomacentridae; 8: Haemulidae; 9: Carangidae; 10: Dactyloscopidae; 11: Balistidae; 12: Photichthyidae; 13: Gobiesocidae; 14: Engraulididae; 15: Scombridae; 16: Myctophidae; 17: Blenniidae; 18: Bythitidae; 19: Lutjanidae; 25: Atherinidae

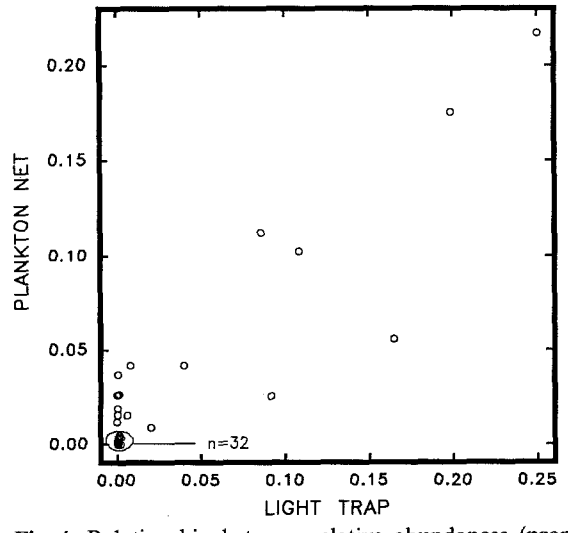


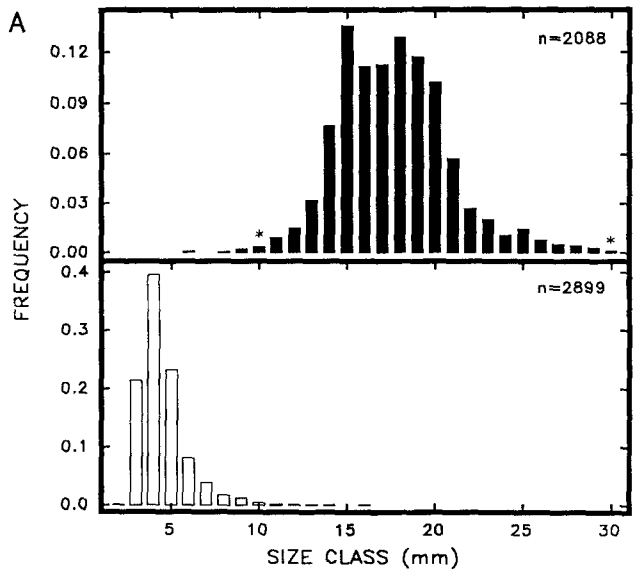
Fig. 4. Relationship between relative abundances (proportion of gear total) of 48 taxa (47 families plus anguilliforms) in 90 light-trap and 75 plankton-net samples ($r^2 = 0.841$, $p < 0.0001$). A single large sample of clupeid larvae was excluded from analysis (see Paragraph 3 of "Results")

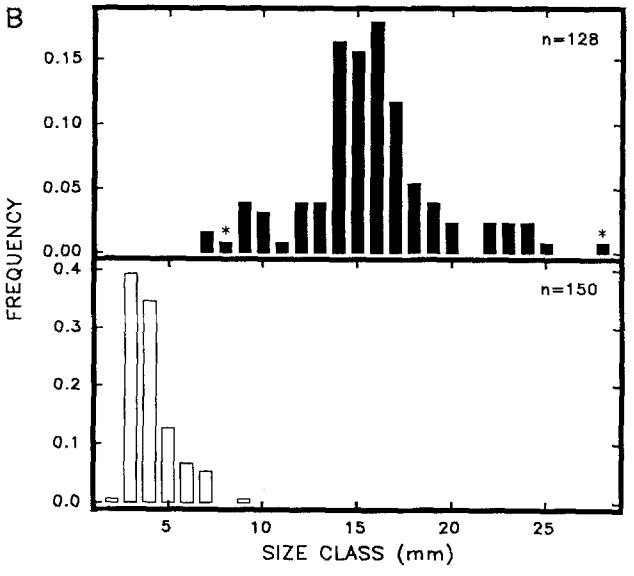
In four families, the modes for the two gears were widely separated, and there was little overlap of size distributions. The light-trap samples were dominated by large larvae and the plankton net predominantly caught small larvae. Nearly all clupeid larvae (Fig. 5A) from the light trap were >10 mm, while nearly all larvae from plankton tows were <10 mm. The pattern for engraulidids (Fig. 5B) was similar to that of clupeids. Two groups of large gerreid larvae with modes at 10 and 14 mm (Fig. 5C) were taken by the light trap, but most gerreids in the net samples were <6 mm. Relatively few (49) haemulid larvae were taken by the light trap, most were 9 to 10 mm (Fig. 5D). Haemulid larvae <5 mm dominated plankton-net collections, but a few large larvae were taken (11 to 12 mm). The sizes at which the light trap collected more larvae than the plankton net (corrected for the difference in number of samples for each gear) were: clupeids, 10 to 30 mm; engraulidids, 8 to 28 mm; gerreids, 7 to 19 mm; haemulids, 9 to 10 mm.

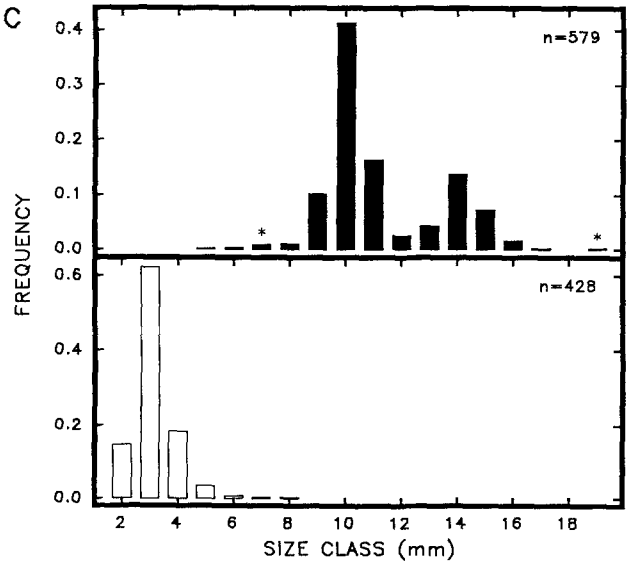
In five other families, the size classes collected by the two methods broadly overlapped, but the distributions had different shapes. In gobiesocids (Fig. 5E) and tripterygiids (Fig. 5F), the modal size classes from the light trap were near the largest sizes collected, while the modal classes in plankton-net collections were near the smallest sizes. The size distribution of labrisomids from net tows was unimodal, with a pronounced peak at 4 mm, but the light-trap distribution was relatively flat between 3 and 9 mm (Fig. 5G); one very large labrisomid larva (21 mm) was taken in the light trap. Chaenopsid larvae from the light trap (Fig. 5H) had peaks at 4 and 8 mm, and a tail extending up to 15 mm; the distribution for the plankton net had a single peak at 4 mm, and few larvae >8 mm were collected. However, the largest chaenopsid collected (18 mm) was taken in a net sample. The size distributions for bythitid larvae (Fig. 5I) differed by the presence of 5 mm larvae in the net collections (probably due to shrinkage), and a greater proportion of 8 mm larvae in the light trap. However, few bythitids were collected, and the differences were not significant (K-S test, $p > 0.05$). The sizes at which the light trap was more effective than the plankton net were: gobiesocids, 7 to 8 mm; tripterygiids, 7 to 13 mm; labrisomids, 6 to 21 mm; chaenopsids, 8 to 15 mm; bythitids, inconclusive.

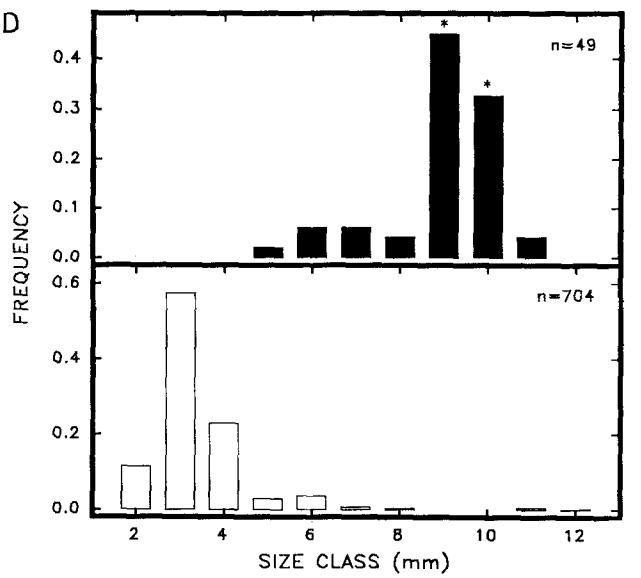
For gobiids, pomacentrids, and blenniids, the size distributions for the two methods appeared more similar than they did for the previous families. Goby larvae collected by both methods had a mode at 3 mm, followed by a rapid decrease in abundance of larger larvae (Fig. 5J). However, the greater proportion of larvae in the upper tail of the light-trap distribution resulted in a statistically significant difference between methods (K-S test, $p < 0.001$). Nearly all pomacentrid larvae from both methods were in the 2 and 3 mm size classes, but a few settlement-stage *Stegastes rectifraenum* (10 to 12 mm) and a single settlement-stage *Chromis atrilobata* (19 mm)

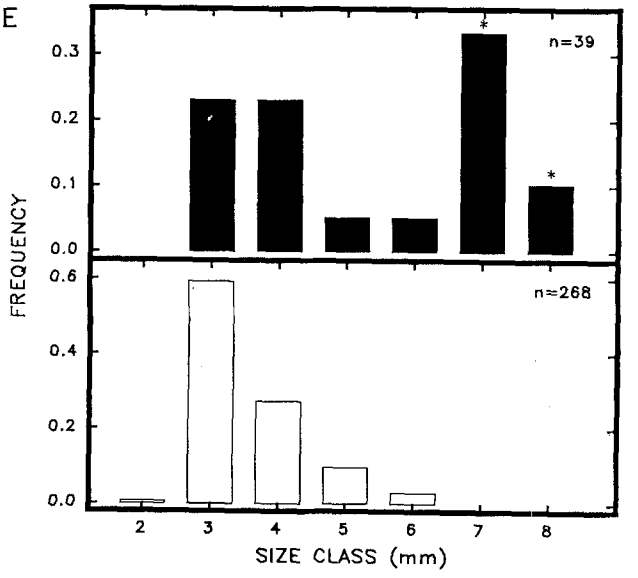
Fig. 5. Size distributions of fish larvae in light-trap samples (black histograms) and in plankton-net samples (white histograms). Size axes are scaled to include range from hatching (or birth) to settlement (or transition) (see "Materials and methods – Sample processing and analysis" for definition of sizes). Asterisks in upper panels bracket size classes for which light trap collected more larvae than plankton net (corrected for difference in number of samples taken by each gear). (A) Clupeidae, (B) Engraulididae, (C) Gerreidae, (D) Haemulidae, (E) Gobiesocidae, (F) Tripterygiidae, (G) Labrisomidae, (H) Chaenopsidae, (I) Bythitidae, (J) Gobiidae, (K) Pomacentridae, (L) Blenniidae

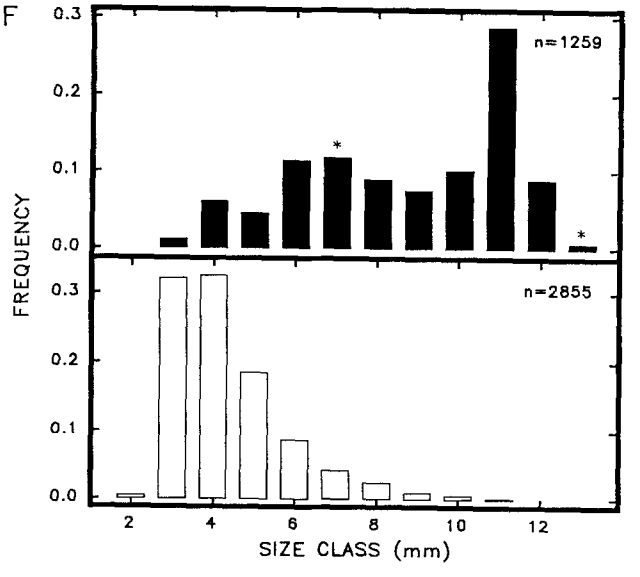












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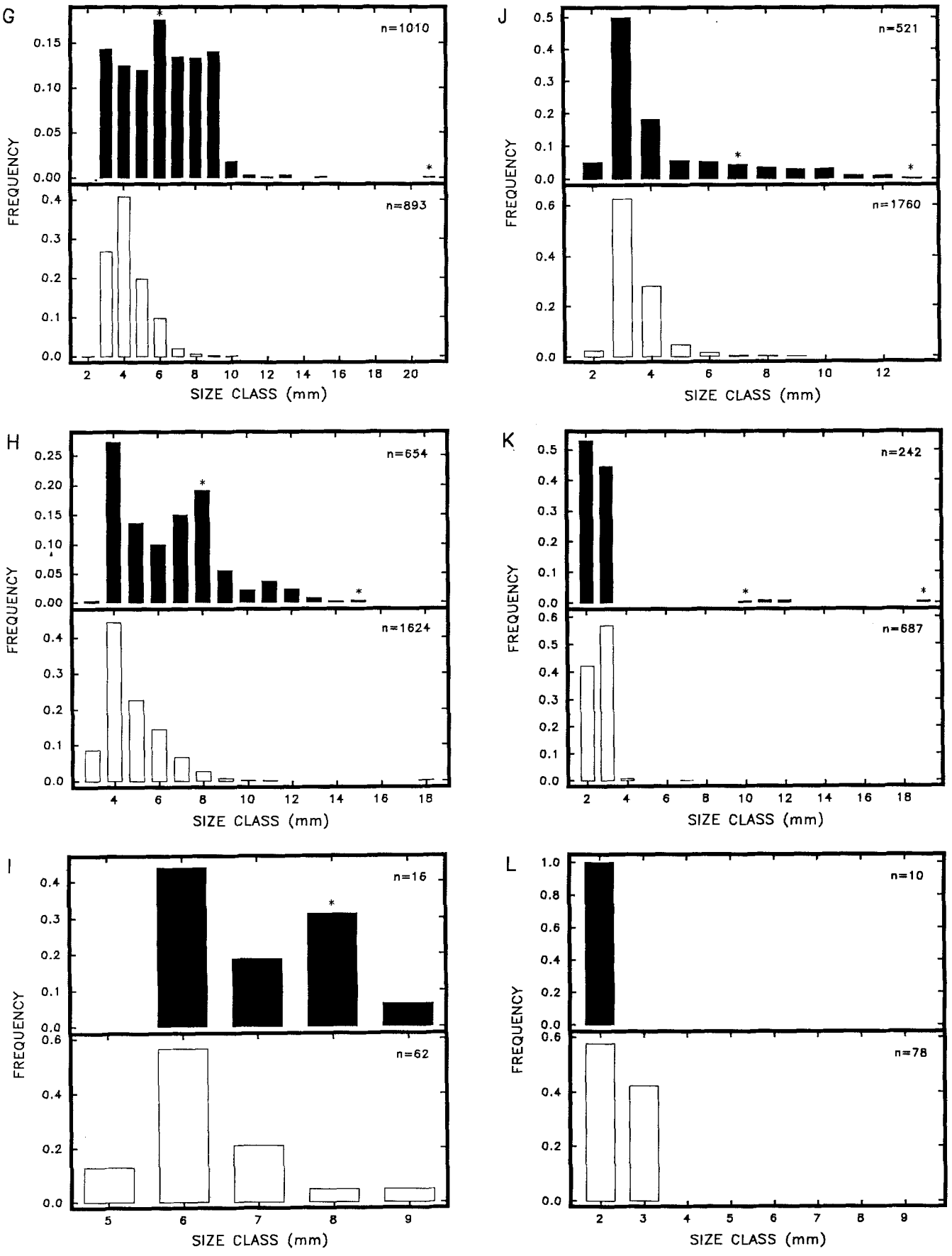

Fig. 5 (continued)

were captured in the light trap (Fig. 5K). The difference between methods was marginally significant (K-S test, $0.03 < p < 0.04$). All blenniid larvae were recently hatched; a single size class was represented in light-trap samples (2 mm) and two size classes were represented in the net collections (2 and 3 mm, Fig. 5L). The two distributions were not statistically different (K-S test, $p > 0.05$), but small sample size in the light trap ($n = 10$) weakened the test. The sizes at which the light trap was more effective than the plankton net were: gobiids, 7 to 13 mm; pomacentrids, 10 to 19 mm; blenniids, the plankton net collected more larvae in both size classes.

Discussion and conclusions

Light traps and plankton nets operate on very different principles. Plankton nets actively strain larvae from the water, and net characteristics such as mouth diameter, bridle configuration, towing speed, and mesh size will interact with larval escape responses and illumination to determine the taxonomic composition and size structure of the catch (Clutter and Anraku 1968, Vannucci 1968, Lenarz 1972, Smith and Richardson 1977, Colton et al. 1980, Brander and Thompson 1989, Morse 1989, Suthers and Frank 1989, Clarke 1991). In contrast, light traps depend on the ability of larvae to see a light, and their ability and willingness to swim to and enter an illuminated enclosure. Physical factors such as water clarity and current speed, as well as development of larval visual systems, behavioral responses to light, and swimming abilities could potentially affect this process (Doherty 1987, Milicich et al. 1992, Thorrold 1992). Even under optimal conditions, some taxa or age classes may not be attracted to light traps at all. Given these differences in operating principles, there is no reason to expect light traps and plankton nets to always provide similar samples of larval fish assemblages.

However, in my study, the kinds of larvae collected by the two methods broadly overlapped (most differences were among rare taxa), and the relative abundances of families were strongly correlated. This similarity was not expected, and is surprising because net tows were taken during the day and light-trap sampling was conducted at night. Many fish larvae undertake diel vertical migrations (e.g. Leis 1991 a, b), and I expected day and night larval assemblages (and thus my plankton-net and light-trap samples) to be very different as a result. Although it was beyond the scope of this investigation to partition the variation between light-trap and plankton-net catches into a "gear" component and a "diel" component, it is likely that time of day did contribute to the differences observed. If this were so, then the sampling properties of the light trap and plankton net may be even more similar than indicated by the comparison of my samples.

The only other comparison of light-trap and plankton-net collections from a marine system indicates that the two methods do not always provide similar results. Choat et al. (1993) collected fish larvae in deep water away from the reef near Lizard Island, northern Great Barrier Reef, using a variety of gear. A comparison of relative abundances (not counting clupeoids, which were excluded from their results) between their light-trap and bongo-net samples is most relevant. Pomacentrids dominated their light-trap samples (93% of the larvae), and only one other family (Gobiidae) contributed >1% of the larvae. In contrast, pomacentrids ranked only tenth in abundance in bongo tows (1.1% of larvae), and 10 other families contributed ≥1% of the larvae. Of the 15 most abundant families in their bongo tows, 7 were absent from light-trap samples, and 3 were collected only rarely. Only 4 families were shared among the 10 most abundant families for each gear. (However, catches of the two gears may have appeared more similar if clupeoid larvae had been included.) The disparity between results from the Gulf of California and the Great Barrier Reef indicates that some site-specific factor(s) such as water conditions, the identity of larvae, or their behavioral responses to light traps and/or nets are important determinants of the differences between samples taken by these two gear types.

Direct observations and dipnetting around my light trap suggested that behavioral responses to light traps may vary, even among the subset of larvae that are attracted to lights, and this variation affects light-trap catches. For example, large larvae and pelagic juveniles of several Gulf of California taxa (scorpaenids, carangids, coryphaenids, lutjanids, mugilids, polynemids, pomacentrids, scombrids, balistids, and unidentified eel leptocephali) were frequently seen around the light trap, but rarely entered it. Large larvae of these taxa were only trapped, if at all, on nights when abundances around the light trap appeared to be especially high. Other large larvae (e.g. clupeids, gerreids, tripterygiids, and labrisomids) showed little reluctance to enter the light trap, and they were captured in large numbers.

Differences between light-trap catches from Australia and the Gulf of California suggest that larval photobehavior may also vary among settlement-stage larvae from a single family. Settlement-stage pomacentrids were extremely common in light-trap samples from the Great Barrier Reef (Doherty 1987, Milicich 1989, Thorrold and Milicich 1990, Milicich et al. 1992, Thorrold 1992, Choat et al. 1993, Meekan et al. 1993), and they appeared to be attracted to the light from huge volumes of water (Choat et al. 1993). In contrast, I rarely caught settlement-stage pomacentrids (a total of six), even though direct observations indicated they were sometimes abundant around the light-trap. The pomacentrids around my light trap were *Stegastes* spp., whereas pomacentrids collected in Australia were mostly *Pomacentrus* spp., *Chromis* spp., *Neopomacentrus* spp., and *Dischistodus* spp.

It is difficult to compare the composition of light-trap catches among regions because so few regions have been studied. Except for my studies in the Gulf of California, all the light-trap studies of which I am aware have been conducted on the Great Barrier Reef, most near Lizard Island (Doherty 1987, Milicich 1989, Thorrold and Milicich 1990, Milicich et al. 1992, Choat et al. 1993, Meekan et al. 1993). The comparisons that can be made between these studies and mine are limited, because complete lists of families and relative abundances were not always provided. In the Australian studies, 18 to 38 families were

collected compared with 31 families in the Gulf of California; 15 families were collected in light traps from both regions, but many of these made only minor contributions in one or both regions. Larvae of some families appeared to be common in collections from both regions (e.g. Clupeidae, Pomacentridae, Gobiidae), but several families that made significant contributions in one region were absent from the fauna of the other. Examples include lethrinids, nemipterids, and siganids from Australia, and chaenopsids and labrisomids from the Gulf of California. Unfortunately, no light-trap studies from the Caribbean (which has much faunal similarity with the Gulf of California) have been published. However, night-light collections taken over Caribbean reefs were dominated ($\sim$70 to 90% of the catch) by clupeid, gobiid, and blennioid larvae (Smith et al. 1987, Dennis et al. 1991, Victor 1991). These same groups contributed 89% of the larvae collected in my light trap, suggesting that light-trap samples taken over Caribbean reefs will be dominated by some of the same families as collections from over Gulf of California reefs.

One goal of comparing two gear types is to discover which is better for collecting particular taxa. For some gear, it is a simple matter to calculate sampled volumes and relative efficiencies, and these attributes can be used to choose among available gear. Unfortunately, light traps and plankton nets can not be compared directly because the volume of water a light-trap samples for any particular taxon is unknown. As an alternative, I compared the mean number of larvae per sample in light-trap and plankton-net collections, using 13 taxa frequently collected by both methods (see "Materials and methods – Sample processing and analysis"). This comparison revealed that the plankton net collected more larvae per sample in 9 of the 13 families (Table 2). In two of these cases (Clupeidae and Labrisomidae), the differences between methods were very small and probably have little biological significance, despite statistical significance. The mean catch did not differ statistically between methods in the other four families I compared. However, in the case of blenniids, power was low and a Type II error may have been committed. Inspection of the data (Table 1) suggests that several other taxa were also better collected by the plankton net, but statistical comparisons were precluded by small sample sizes in one or both gears. Atherinids may have been better collected in the light trap, but sample sizes were very small. If the size structure of catches was similar between gears, the mean catch comparisons could serve as a guide for choosing between the light trap and plankton net. However, the size structure of most families differed greatly between methods and, consequently, larval size distributions may be a more informative guide to gear performance.

In 10 of the 12 families I measured, I collected the complete range of larval sizes from hatching (or birth) to settlement (or transition for pelagic taxa) for at least some component species (see Brogan 1992). In 9 of these cases, the plankton net collected more larvae than the light trap in the small size classes, and the reverse was true for large larvae. The size at which light-trap catches began to exceed plankton-net catches varied from 6 to 10 mm, depending on family (see Fig. 5). For most families, I was able to collect all larval sizes during my study only because I used both sampling methods and their size biases complemented each other. Labrisomids and bythitids were exceptions. All size classes of labrisomids were collected by the light trap (2 mm larvae in net tows were the result of shrinkage), and all size classes of bythitids were collected by the plankton net.

Most size classes of pomacentrid and blenniid larvae were not collected in this study. In these families, the catches from both methods were dominated by recently hatched larvae (Fig. 5K, L). The plankton net caught many more pomacentrids than the light trap, but the light trap occasionally caught settlement-stage larvae that were never collected in the plankton net. Thus, both collection methods were useful. In the case of blenniids, the plankton net caught more larvae from a broader size range than the light trap, so the plankton net alone would have been adequate. However, light traps may be useful for collecting large blenniid larvae at other times or places (Milicich 1989, Thorrold 1992).

The differences between larval size distributions for the two collecting methods may have been due to gear-specific size biases, different distributions of sampling effort among microhabitats, and/or diel variations in larval assemblages. Gear-specific size biases were probably very important. Previous studies have demonstrated that daytime tows with small, bridled plankton nets suffer from avoidance, particularly by larger, faster-swimming larvae (Ahlstrom 1954, Clutter and Anraku 1968, Barkley 1972, Murphy and Clutter 1972, Smith and Richardson 1977, Suthers and Frank 1989, Leis 1991a), and light traps tend to selectively attract large larvae (Choat et al. 1993). In my study, size distributions from plankton tows typically had modes at 3 to 4 mm, and rapid, usually monotonic, declines in the number of larger larvae. This, in combination with the greater abundance of large larvae in light-trap samples, suggests that the previously documented size biases also affected my samples. Additionally, the two sampling methods may have differentially sampled larval microhabitats, as defined by distance from shore, depth, and influence of the epibenthos. Although the proportions of samples taken at each distance from shore were not exactly equal for the two sampling methods, they were very similar (see "Materials and methods – Sampling protocol"). The water depths sampled were also similar. Plankton tows sampled the upper 5.5 m of the water column, and at 1 m from shore the tows were limited to the epibenthic layer (reef surfaces lying at 1 to 5 m depth). It is more difficult to determine the depth from which the light trap drew larvae, but observations suggested that the "illuminated volume" extended from the surface to at least 3 m, and probably down to 5 m depth. At 1 m from shore, the light trap was positioned immediately above the bottom or lateral to large boulders (depending on depth and topography), so that the reef surface was illuminated. Thus, the microhabitats I sampled were as closely matched as possible. Still, differences in distribution of sampling effort could have affected my larval catches if the size of larvae varied among microhabitats. Diel patterns of hatching,

settlement, mortality, and movement could also have contributed to the difference between methods if the balance of these processes increased the number of large larvae over reefs at night and increased the number of small larvae over reefs during the day. The net effect of these processes on larval size distributions over reefs is presently unknown.

The size-distribution patterns for pomacentrids and blenniids were very different from those of the other ten families. In both these families (Fig. 5K, 5L), recently hatched larvae dominated catches, and few or no intermediate-sized or large larvae were captured by either gear. The virtual absence of larvae >2 to 3 mm in the light trap might be explained by the loss of photopositive behavior within a day or two of hatching. I have observed this pattern in larvae of several other taxa during rearing experiments (unpublished observations). The almost complete absence of larvae >3 mm in plankton tows is more difficult to explain. Larvae may have reached a size threshold at which they suddenly became very effective at avoiding the net, or perhaps young larvae were rapidly swept (or swam) away from the reef.

Until recently, it was widely accepted that the reproductive behavior of reef fishes had evolved to ensure that eggs and larvae were rapidly swept away from the reef environment (see Thresher 1984, Colin and Clavijo 1988, Shapiro et al. 1988, Robertson 1991). Offshore dispersal was assumed to be adaptive because it decreased predation by reef-based planktivores, increased dispersion of siblings (risk averaging), or enhanced larval feeding (e.g. Johannes 1978, Barlow 1981, Doherty et al. 1985). However, actual data on larval distributions and the role of these processes on them are limited (see Leis 1991 a). Evidence from coral reef areas suggests that larvae disperse at varying, often taxon-specific, distances away from reefs, but that few taxa, if any, remain over reefs throughout their development (reviewed in Leis 1991 a). However, some fish larvae do associate with reefs for varying lengths of time prior to settlement (e.g. Breitburg 1989, 1991, Kobayashi 1989, Kaufman et al. 1992), and in some families (Cottidae, Stichaeidae, Pholididae, Gobiesocidae, and Tripterygiidae) larvae may remain over temperate rocky reefs throughout development (Marliave 1986, Kingsford and Choat 1989). I found that larvae of many tropical members of the families Clupeidae, Engraulididae, Gerreidae, Haemulidae, Gobiesocidae, Tripterygiidae, Labrisomidae, Chaenopsidae, Bythitidae, and Gobiidae were abundant over Gulf of California reefs, and that all larval size classes were represented. This result contrasts with studies from coral reefs (Leis 1991 a), and suggests that at least some larvae from these families may remain in the water over reefs throughout development. However, it is not clear what proportion of larval populations remain over reefs as opposed to dispersing offshore. Larvae of clupeids, engraulidids, gerreids, and haemulids are common offshore in the Gulf (Moser et al. 1974), but the other families are rare or absent offshore. Thus, some taxa may have broad larval distributions that include reefs, whereas other taxa may be restricted to water over or near reefs. Additional data are required to make this distinction (Brogan in preparation). In any case, the assumption that the water over reefs is generally a poor larval habitat should be evaluated.

In summary, both the light-trap and the diver-steered plankton net were effective for collecting fish larvae over Gulf of California reefs. The taxonomic composition of samples taken by these two gear types was broadly similar, much more similar than in a previous comparison from the Great Barrier Reef. The average catch per sample was greater with the plankton net in several families, but the size structure of catches differed between the two gears, and larval size may be one of the most important considerations when choosing between types of gear. For most fish families, the plankton net was most effective for collecting small larvae, and the light trap was most effective for collecting large larvae. However, light-trap catches were not as dominated by settlement-stage larvae as in the published Australian studies. The collections obtained by light traps may vary strongly between regions and/or fish faunas, so extrapolations from one region or season to another are not advised. Light traps will probably gain more popularity as a sampling tool, especially as other kinds of questions about their sampling performance are addressed (e.g. Thorrold 1992). However, for many kinds of studies, light traps will best be used as an adjunct to traditional sampling methods rather than as a replacement. In my study, the combination of two sampling methods provided a more complete view of larval assemblages over reefs than either method would have provided in isolation. The gear-specific nature of results highlights the need for further development of sampling methods suitable for the complex environments around reefs.

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