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Diel patterns of abundance of presettlement reef fishes and pelagic larvae on a coral reef

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Abstract Most presettlement reef fish settled at night at One Tree Island, Great Barrier Reef. Fish were sampled day and night using channel nets located on the reef crest, and a plankton-mesh purse-seine net in the lagoon (1992–1994). Catches of fish at night were generally tens to hundreds of times greater than those taken during the day. Preflexion fish, as well as postflexion and pelagic juveniles, were taken in greater numbers at night. Preflexion forms were a combination of those that had hatched from demersal eggs and later stages that had been transported over the reef crest. Highest numbers of postflexion and pelagic juvenile forms of Apogonidae, Blenniidae, Gobiocidae, Gobiidae, Labridae, Lutjanidae, Mugilidae, Mullidae, Pomacentridae, Scaridae, Serranidae and Tripterygiidae were found at night. Observations, while SCUBA diving, and purse-seine samples in the lagoon indicated that the only resident larvae were of the genera *Spratelloides* and *Hypoatherina*; most of the fishes caught in nets, therefore, were immigrants. Patch reefs, sampled for new settlers early in the morning and late in the day, indicated that the majority of apogonids (*Apogon doederleini*, >95%) settled at night. Although greater numbers of pomacentrids were found in morning counts (e.g. *Pomacentrus wardi*), if data were converted to an hourly rate, many pomacentrids showed a similar hourly rate of settlement day and night. Depth-stratified sampling in waters near One Tree Island (to 20 m) indicated that some taxa rise to the surface at night. This behaviour, perhaps combined with avoidance of diurnal predators may explain on-reef movement of potential settlers soon after dark. Studies on settlement cues, therefore, need to focus on night-related phenomena.

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Introduction

In contrast to the benthic phases of reef fishes (Sale 1991), there are few data on the presettlement phase (Leis 1991; Victor 1991). Recently, however, information has been published on the early life history stages including the following: taxonomy (e.g. Leis and Rennis 1983; Leis and Trnski 1989); horizontal and vertical distribution patterns (Leis 1986, 1991); the influence of oceanography (Kingsford et al. 1991; Milicich 1994); condition (McCormick and Maloney 1992) and swimming abilities (Stobutzki and Bellwood 1994; Leis and Carson-Ewart 1997). Conventional ichthyoplankton nets (e.g. Leis and Goldman 1987), purse seines (Kingsford et al. 1991) and light traps (Doherty 1987; Milicich 1994) have been used to collect these data.

The arrival of potential settlers at a reef and the process of settlement is a subject of intense interest to scientists, particularly given that many assumptions on the availability of potential settlers underpin models of the population dynamics and assemblages of fishes (Doherty and Williams 1988). Attempts have been made to compare the abundance patterns of larvae with patterns of recruitment to reefs (Stephens et al. 1986), but a major problem has been selecting sampling equipment that provides accurate assessments of the abundance of presettlement fish. Light traps have revolutionised the sampling of fish that are close to settlement (Doherty 1987). Moreover, these devices have been used to describe patterns of abundance of potential settlers adjacent to reefs over most of the recruitment season of some fishes and among years (Milicich et al. 1992).

A potential limitation of light traps that are used to measure the abundance of potential settlers is that it must be assumed that all larvae approaching a reef do so at night. Although there is some evidence from patterns of settlement on reefs that this is generally the case (Robertson et al. 1988; Sweatman and St John 1990;

Booth 1992), the assumption is largely untested. A notable exception is the work of Shenker et al. (1993, Bahamas), who used tethered nets to determine that 97% of reef fish were collected on flood tides at night. From a methodological point of view, the knowledge that light traps and other methods that are only used at night can provide accurate information on abundance of potential settlers is a prerequisite for broader-scale applications of these methods to measure the replenishment of reefs.

The timing of the arrival of fish at a coral reef is interesting in terms of behaviour, the processes influencing survivorship and the complexities of finding suitable habitat in which to settle (Robertson 1991; Victor 1991). Although some potential settlers may be close to reefs (Doherty et al. 1996) and have good swimming abilities (Leis et al. 1996), approaching a reef is fraught with problems. Firstly, fish must remain close enough to the reef to be able to settle. Secondly, they face a so-called 'wall of mouths' around the perimeter of the reef during the day (Hamner et al. 1988; Kingsford and MacDiarmid 1988) and potentially at night from fish (e.g. apogonids, pempherids, holocentrids, lutjanids; Hiatt and Strasberg 1960; Gladfelter 1979; Hobson 1991) and invertebrates (e.g. corals). Once they reach the reef complex they must also avoid demersal fishes and predatory invertebrates. Settlers may initially hide in the sand, as for some labrids (Victor 1983), settle away from hard substrata and move to them at a later time (Finn and Kingsford 1996), seek out the coral matrix and the presence or absence of adults (Sweatman 1983, 1985) or settle directly on continuous reef (Williams 1983). More information, however, is required on the nature of the timing of settlement so that a better resolution of this period in the life history of fishes can be gained.

The objective of this work was to determine the diel patterns of supply of potential settlers to a coral reef. The approach was to sample day and night using different types of sampling equipment, so that conclusions could be made without major confounding problems such as net avoidance (e.g. Murphy and Clutter 1972). The specific aims were to: (1) collect fish using channel nets on the flood tide entering the One Tree Island lagoon during the day and at night; (2) sample lagoonal waters during the day and at night with a plankton-mesh purse seine that would reduce problems of avoidance that are generally encountered with more traditional ichthyoplankton nets (Kingsford and Choat 1985); (3) count numbers of recruits early and late in the day on patch reef; (4) identify fishes in aggregations of larvae that are resident in the lagoon during the day, because it is possible that some types of larvae are resident in the lagoon regardless of time of day (Leis 1994); (5) collect data on the vertical distribution patterns of presettlement fishes outside the lagoon at One Tree Island so that the results could be related to the findings from nets that were tethered on the crest of the reef.

Materials and methods

Study area

One Tree Island is unique in that it has the only ponding lagoon on the Great Barrier Reef. The lagoon is generally isolated from the surrounding ocean for a half of each tidal cycle (Ludington 1979). The level of the tide (2.0–5.5 m to breach the reef crest) and wind velocity determines the duration and water velocity of the flood-tide pulse. Only when the crest is covered, therefore, can settlers enter the lagoon. Current speeds of up to 130 cm/s were measured on the reef crest with a flowmeter.

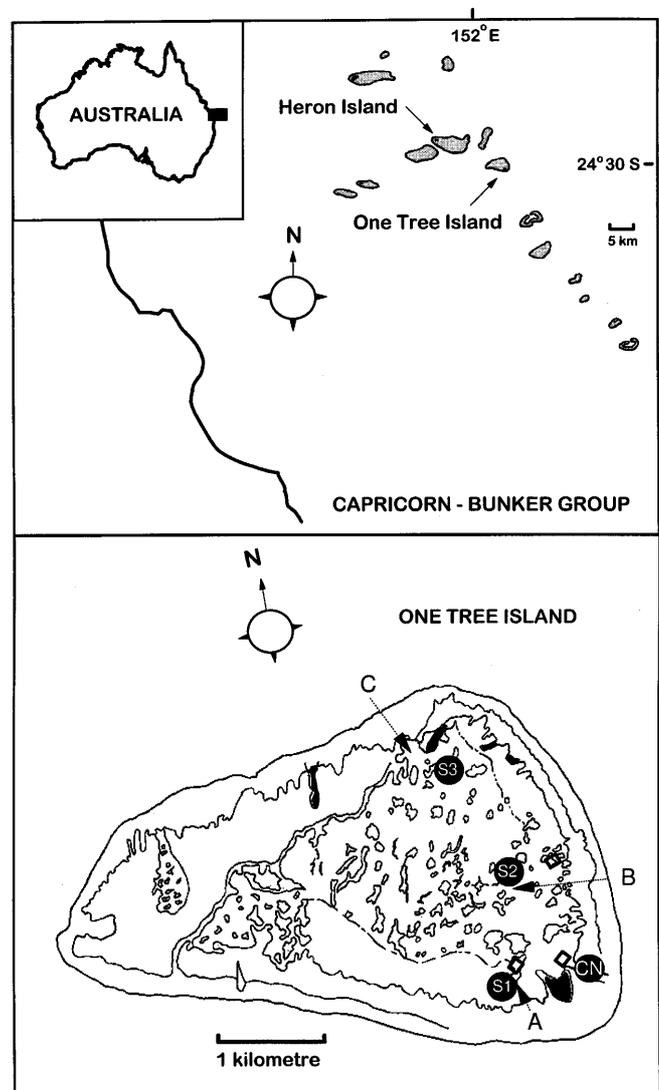


Fig. 1 Map of One Tree Island showing the shape of the ponding lagoon (land/rubble banks are in black) and the position of channel nets (CN), purse seine sampling sites (S1–S3) and sites A–C for patch reefs. Open squares indicate the areas in which searches were made for aggregations of presettlement fishes. The inset shows the location of One Tree Island in relation to the mainland and other reefs of the Capricorn Bunker Group on the southern Great Barrier Reef of Australia. True north is indicated

Channel nets

Nets tethered in channels were used to collect fish on flood tides during the day and at night on the windward side of One Tree Island. Sampling was done on multiple days at four times, 19–25 January 1992; 19–24 February 1993; 25 June–2 July 1993; 8 January–2 February 1994. With the exception of the June–July sampling, these times corresponded to the time when fish are settling into the lagoon (e.g. Williams 1983; Kingsford and Finn 1997). Reef fish larvae were captured in June–July and were therefore included in the day/night comparisons. On times 1–3, three replicate 10-min tows were taken on flood tides during the day and at night. Replicate collections were taken sequentially from a channel net, so strictly speaking they were part of a time series. In 1994, two nets were fished that were approximately 20 m apart, $n = 3$ 10-min tows. All samples were taken in a tidal channel (CN, Fig. 1). On some occasions both flood tides occurred at around dusk and dawn; this was used in summer 1993 to describe changes in catches with levels of ambient light and was done over a period of 5 days (19–24 February 1993). Current speed in the channel varied from 8 to 130 cm/s.

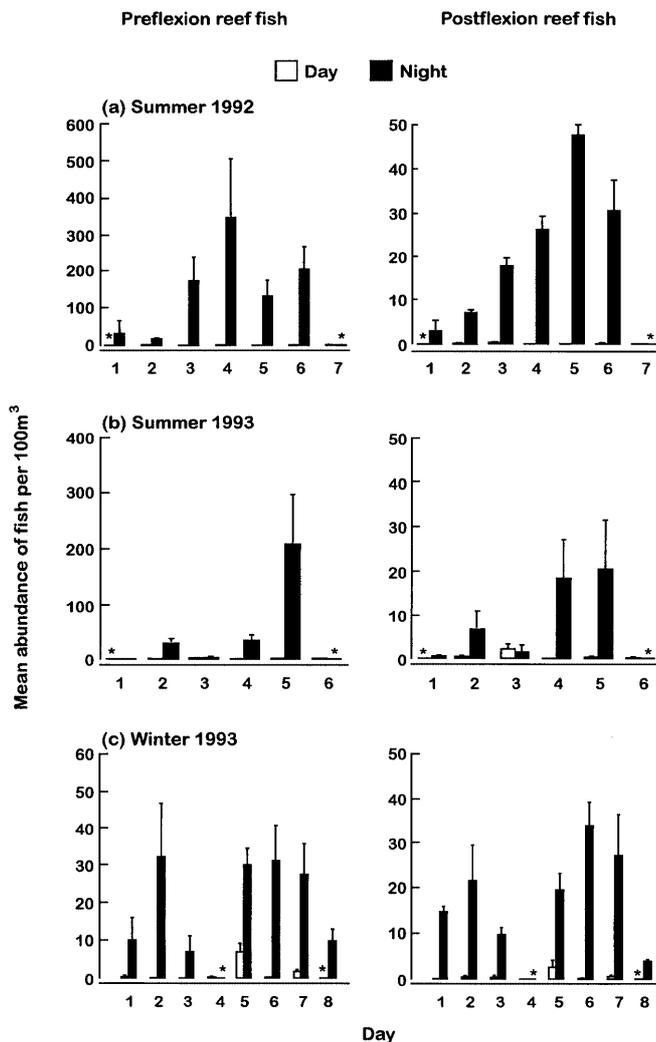


Fig. 2a–c Mean abundance of preflexion and postflexion reef fish at three times of sampling during the day and at night, 1992–1993. The days of sampling for each time are indicated. Asterisks indicate nights when sampling could only be done in twilight conditions (dawn or dusk). Variation for the three sequential hauls with the net = +SE

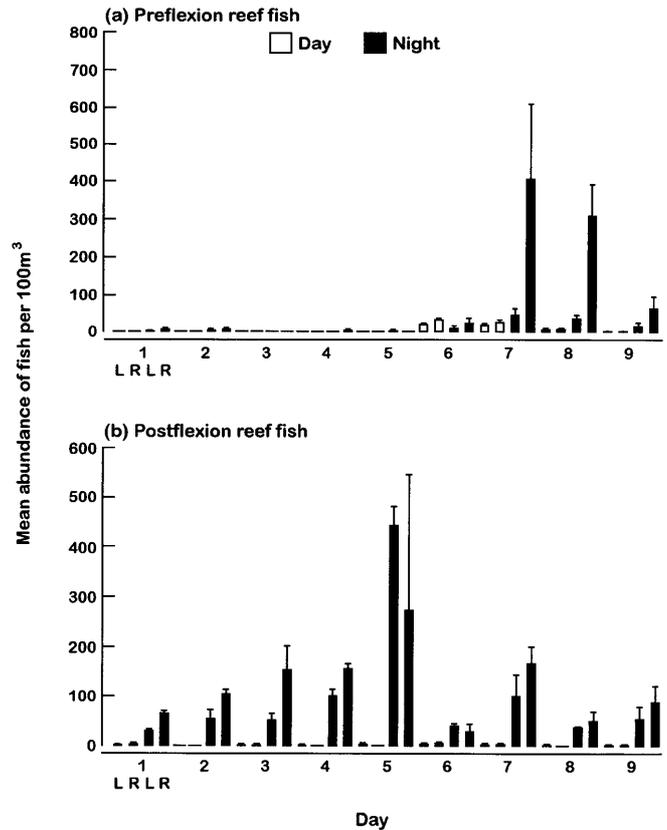


Fig. 3 Mean abundance of preflexion (a) and postflexion (b) reef fish during the day and at night in summer 1994. The days of sampling for each time are indicated. Data are given for nets on the left (L) and right hand (R) sides of a tidal channel (CN, Fig. 1). Variation for the three sequential hauls with each net = +SE

Nets were square (0.75×0.75 -m mouth) and had a 1:12 ratio of area of mouth to open sifting surface. The 0.5-mm mesh was organised as a 3-m box and 2-m pyramid (for design see Kingsford and Murdoch 1998). The bridle was tethered to stakes in such a way that it did not interfere with the entrance to the net (diagram in Kingsford and Finn 1997). A General Oceanics 2030 flowmeter was used to measure the volume of water filtered and was located ~ 0.25 m from the edge of the frame, where average flow into the net was expected. Current speeds during 10-min tows were also estimated with the flowmeter.

Purse seine

It was highly likely that low catches in nets during the day were partly due to avoidance. Plankton-mesh purse-seine nets have been used in other studies to minimise the effect of avoidance when making day/night comparisons (Murphy and Clutter 1972). A 15×3 -m (0.28-mm mesh) seine (for design, see Kingsford and Murdoch 1998) was used to sample the lagoon during the day and at night. At most sites waters were 4–5 m deep and, therefore, the seine sampled most of the water column. Because the distribution of presettlement fish is notoriously variable in space, replicate tows ($n = 3$) were taken at three sites during the day (Fig. 1). For logistical and weather-related reasons, only sites 1 and 2 were sampled at night. Care was taken not to shine lights in the vicinity of the seine while sampling took place at night, because many small fish are photopositive (Doherty 1987). Diel sampling was done at 7 times: 12, 13, 14, 28, 29, 30, 31 January 1995.

Table 1 Total number of fish captured during the day and at night for each time of sampling. The percentage of prefixion (postflexion) fish is indicated. Families are given in alphabetical order. *Sc/B/complex* Prefixion Blenniidae or Schindleriidae

Taxa	Summer 92			Summer 93			Winter 93			Summer 94				
	Day		Night	Day		Night	Day		Night	Day		Night		
	n	%	n	%	n	%	n	%	n	%	n	%		
Acanthoelminidae	-	-	-	-	-	-	-	-	3	0 (100)	-	1	0 (100)	
Acanthuridae	-	-	-	-	-	-	-	-	-	-	-	-	-	
Ammodontidae	-	-	-	-	-	-	-	-	1	0 (100)	-	-	-	
Anguilliformes	-	-	-	-	-	-	-	-	5	0 (100)	-	2	0 (100)	
Apogonidae	-	8 (92)	49	100 (0)	11	37 (63)	12	75 (25)	141	71 (29)	21	76 (24)	119	0 (100)
Atherinidae	-	18 (82)	11	17 (83)	35	11 (89)	3	0 (100)	8	0 (100)	281	0.4 (99.6)	176	5 (95)
Balistidae	-	-	-	100 (0)	4	100 (0)	-	-	-	-	-	-	-	-
Belontiidae	-	-	-	-	1	0 (100)	-	-	-	-	-	-	-	-
Blenniidae	4	50 (50)	383	0.01 (99.9)	5	0 (100)	3	66 (34)	27	59 (41)	4	0 (100)	69	0 (100)
Bothidae	5	0 (100)	22	68 (34)	16	44 (56)	23	74 (26)	37	68 (34)	9	22 (78)	39	8 (92)
Bregmaceroideae	-	-	-	-	-	-	2	100 (0)	-	-	-	-	1	0 (100)
Callionymidae	-	-	3	100 (0)	3	60 (30)	2	0 (100)	111	88 (12)	-	-	18	0 (100)
Carangidae	-	-	92	7 (93)	4	100 (0)	74	5 (95)	1	0 (100)	3	66 (34)	25	32 (68)
Chaetodontidae	-	-	1	0 (100)	-	-	1	100 (0)	-	-	-	-	1	0 (100)
Clupeidae	5	20 (80)	481	16 (84)	15	53 (47)	21	24 (76)	17	47 (53)	13	8 (92)	567	2 (98)
Cresidae	-	-	1	100 (0)	-	-	1	100 (0)	-	-	-	-	-	-
Cynoglossidae	-	-	-	-	-	-	-	-	3	34 (66)	-	-	2	0 (100)
Echeneidae	-	-	-	-	-	-	-	-	1	100 (0)	-	-	-	-
Eleotridae	3	(100)	12	0 (100)	-	-	-	-	-	-	-	-	-	-
Exocoetidae	-	-	2	0 (100)	1	1 (100)	5	80 (20)	-	-	6	0 (100)	5	0 (100)
Fistulariidae	-	-	-	-	-	-	-	-	-	-	1	0 (100)	2	0 (100)
Gerreidae	-	-	-	-	-	-	-	-	1	0 (100)	25	0 (100)	24	0 (100)
Gobiidae	1	0 (100)	3	0 (100)	1	100 (1)	4	75 (25)	1	0 (100)	1	0 (100)	23	0 (100)
Gobiidae	-	-	403	12 (88)	10	60 (30)	278	48 (52)	33	70 (30)	87	66 (34)	3724	0.3 (99.7)
Gonostomatidae	-	-	-	-	-	-	1	0 (100)	-	-	-	-	-	-
Holocentridae	-	-	-	-	-	-	3	100 (0)	-	-	-	-	-	-
Labridae	2	50 (50)	165	0.6 (99.4)	5	40 (60)	11	63 (37)	5	60 (40)	1	100 (0)	57	0 (100)
Lethrinidae	-	-	7	100 (0)	-	-	9	100 (0)	-	-	2	100 (0)	2	50 (50)
Lutjanidae	-	-	3	66 (34)	1	0 (100)	23	95 (5)	-	-	6	100 (0)	20	25 (75)
Microdesmidae	-	-	-	-	-	-	-	-	20	60 (40)	-	-	6	0 (100)
Monacanthidae	-	-	4	25 (75)	1	100 (0)	3	100 (0)	7	100 (0)	-	-	2	0 (100)
Monodactylidae	-	-	-	-	-	-	-	-	2	100 (0)	-	-	-	-
Mugilidae	-	-	1	100 (0)	-	-	-	-	-	-	3	100 (0)	6	17 (83)
Mullidae	-	-	16	44 (56)	-	-	1	0 (100)	-	-	37	11 (89)	-	-
Muraenidae	-	-	-	-	-	-	-	-	1	0 (100)	-	-	-	-
Myctophidae	-	-	-	-	-	-	-	-	1	0 (100)	-	-	1	0 (100)
Nemipteridae	-	-	4	75 (25)	-	-	16	86 (14)	11	73 (27)	-	-	10	0 (100)
Nomeidae	-	-	2	0 (100)	1	0 (100)	-	-	3	0 (100)	-	-	-	-
Opichthinae	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Ostraciidae	-	-	2	100 (0)	2	100 (0)	-	-	-	-	-	-	-	-
Pegasidae	-	-	1	0 (100)	-	-	-	-	-	-	-	-	-	-
Pemppheridae	-	-	-	-	-	-	-	-	-	-	-	-	1	0 (100)
Platycephalidae	-	-	2	100 (0)	-	-	2	0 (100)	3	100 (0)	1	0 (100)	1	0 (100)
Pleisopiidae	-	-	-	-	-	-	-	-	8	63 (37)	-	-	11	0 (100)
Pleuronectidae	-	-	-	-	-	-	2	100 (0)	-	-	-	-	1	0 (100)

Pomacentridae	1	100 (0)	1856	99.6 (0.4)	6	83 (17)	717	100 (0)	1	100 (0)	1	100 (0)	5	60 (40)	2	50 (50)	14	29 (71)
Pracanthidae	1	100 (0)	2014	100 (0)	—	—	5	100 (0)	—	—	—	—	—	—	—	—	1	0 (100)
Pseudochromidae	1	100 (0)	—	—	—	—	4	0 (100)	5	100 (0)	—	—	—	—	—	—	5	0 (100)
Scaridae	—	—	—	—	—	—	—	—	—	60 (40)	—	—	—	—	—	—	100	0 (100)
Schindleriidae	—	—	20	10 (90)	—	—	—	—	1	0 (100)	—	—	—	—	—	—	30	0 (100)
Scombridae	—	—	2	50 (50)	6	50 (50)	—	—	—	130	—	—	—	—	—	—	4	0 (100)
Scorpaenidae	2	50 (50)	19	5 (95)	5	100 (0)	9	89 (11)	1	100 (0)	—	—	—	—	—	100 (0)	21	10 (90)
Sc./Bl. complex	—	—	—	—	1	100 (0)	131	100 (0)	1	100 (0)	—	—	—	—	—	—	—	—
Serranidae	—	—	40	45 (55)	—	—	4	0 (100)	—	—	—	—	—	—	—	—	1	0 (100)
Siganidae	—	—	—	—	—	—	—	—	2	100 (0)	—	—	—	—	—	—	1	0 (100)
Soleidae	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	0 (100)
Sphyraenidae	—	—	—	—	—	—	1	100 (0)	—	—	—	—	—	—	—	—	1	0 (100)
Syngnathidae	—	—	2	0 (100)	—	—	—	—	1	0 (100)	—	—	—	—	—	—	1	0 (100)
Synodontidae	—	—	1	0 (100)	1	100 (0)	4	100 (0)	3	34 (66)	—	—	—	—	—	100 (0)	8	0 (100)
Terapomidae	—	—	1	0 (100)	—	—	—	—	2	100 (0)	—	—	—	—	—	100 (0)	—	0 (100)
Tetraodontidae	—	—	—	—	—	—	—	—	6	50 (50)	—	—	—	—	—	0 (100)	1	0 (100)
Trichuridae	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Trichonotidae	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Triglidae	1	100 (0)	2	100 (0)	—	—	1	100 (0)	—	—	—	—	—	—	—	—	5	0 (100)
Tripterygiidae	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	100 (0)
Uranoscopidae	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—

Aggregations of presettlement fishes

It is possible that some fishes spend most or all of their presettlement phase in the lagoon (Leis 1991, 1994). Aggregations of larvae were observed by SCUBA in One Tree Island Lagoon in January–February of 1994 and 1995 and, where possible, larvae were sampled by pushing or in some cases throwing a 0.28-mm mesh plankton net over them. Observations were made at three sites (~5000 m² each) on 33 days in 1994–1995. Larvae were identified from samples and in some cases (for *Spratelloides* and *Hypoathetina*) larvae could be identified by eye (based on gut and body length).

Patch reefs

Counts of newly settled fish were made early (0630–0800 hours) and late (1700–1900 hours) in the day on patch reefs to determine diel patterns of settlement. Fish were counted every day from 8 January–1 February 1994 at sites A and B (Fig. 1); $n = 6$ (1 × 1 × 1-m) reefs. In 1995, fish were counted early and late on six random days (13, 14, 15, 26 January, 7 February 1995) at sites A and C, $n = 9$ and 6 reefs, respectively. It was possible that the input of fishes was at the same rate, but the data were skewed to a category because the number of hours that separated censuses varied for times that included night (~16 h) and those that included day (~8 h). Thus, data were also expressed as number per unit time.

Vertical distributions of presettlement fish

Presettlement fish were sampled in four depth strata outside the lagoon near One Tree Island in January 1995 from the RV Lady Baston off the reef slope at the northern and northwestern edge of the reef (Fig. 1). Fishes were sampled at four depths, surface (0–1 m), upper (7 m), lower (14 m) and bottom strata (20 m). We used an opening/closing net that was lowered to target strata in the closed position on the cable from winch 1, the strain of the net was then taken on the bridle so that the net fished for 10 min, in which time it sampled about 270 m³ of water. At the end of the tow the net was retrieved on winch 2 in the closed position. A boom was used to ensure that the net fished to the side of the vessel and outside of the wake. The net had a circular mouth (0.5 m³), a cylinder of 3 m and a cone of 2 m. The mesh was 0.28 mm and had a mouth area to sifting surface ratio of 1:10. The net was towed at ~100 cm/s. It took approximately 3 h to complete a series of tows ($n = 2$), so the order of tows was randomised with respect to depth to avoid bias as a result of temporal change in the abundance of fishes in the area.

Treatment of data

In formal analyses of day/night comparisons with channel nets, only the total catches over three hauls for each of the paired nets on each night in 1994 were used. In this analysis a 2-factor analysis of variance (ANOVA) was used, where the factor diel (treatments day and night, $a = 2$) was treated as a fixed factor and day (treatments 9 days, $b = 9$) as a random factor. A similar analysis was used for seines, but this was treated as a 3-factor ANOVA where an additional factor 'site' was treated as random (factors and treatments: Diel, $a = 2$, Day, $b = 4$, Site, $c = 2$). In analyses of total reef fish in the vertical distribution study, diel (treatments day/night, $a = 2$) and depth ($b = 4$) were treated as fixed factors and day ($c = 2$) as random. In all cases data were tested for homogeneity using Cochran's test. If the test result was significant, then the data were transformed using the $\ln(x + 1)$ transformation and again tested using Cochran's test. If data were still heteroscedastic then the ANOVA was done anyway, because ANOVA is robust to violations of assumptions of normal distribution of data. If the Cochran's test was significant, then a more conservative value of P was used ($P = 0.01$; according to Underwood 1997).

Terminology

Presettlement fishes that included pelagic juvenile fishes were classified according to the identifications in Leis and Rennis (1983), Moser et al. (1984), Okiyama (1988) and Leis and Trnski (1989). The term presettlement fish or phase (*sensu* Kingsford and Milicich 1987) refers to all the developmental stages from hatching to settlement on the reef. In some cases fishes do not settle because they have a pelagic life style as adults (e.g. *Spratelloides*, *Hypoatherina*). In these cases metamorphosis into a juvenile represents the end of this presettlement phase. The focus of this study was on fish that actually settle and it is only these fishes that have been classified as reef fish in this study. The term 'potential settler' has been used to refer to fishes that are of a size/developmental phase that suggests they are capable of settling and are close to suitable habitats in which they could settle. All fishes were classified according to developmental form using the terms 'preflexion', 'postflexion' and 'pelagic juvenile' (terminology of Leis and Rennis 1983) so that very small fish could be distinguished from larger individuals that were approaching settlement. Measurement of fish size refers to standard length (=notochord length in very small fishes). Fishes from channel nets (January to February 1994 only), seines and vertically stratified tows were measured.

Results

Channel nets

Most presettlement reef fish were captured at night, at the four times of sampling, and this pattern was most conspicuous for postflexion fishes (Figs. 2, 3; Table 1). Mean catches at night were up to 370× those of the day for preflexion fish and 450× for postflexion fish. There was a significant diel × day interaction in ANOVA for preflexion and postflexion fish for summer 1994 data (Table 2). Although abundance at night was higher than during the day, in this comparison, the magnitude of differences between catches in the day and at night varied greatly by day. Differences in the magnitude of effect between day and night were partly the result of large differences in catches among days.

All abundant taxa had abundance maxima at night (Table 1). The families of reef fish that ranked in the top ten in abundance (Apogonidae, Blenniidae, Gobiidae, Labridae, Mugiloididae, Mullidae, Pomacentridae, Scaridae, Serranidae and Tripterygiidae) were all most

Table 2 Analysis of variance for abundance of preflexion and postflexion fishes collected in channel nets, day and night (factor Diel) on eight days in summer 1994, $n = 2$ nets. Diel was treated as a fixed factor and Day as a random factor. Data were tested for normality using Cochran's test, variances = 18, $df = 1$, preflexion fish $C = 0.324$ *n.s.*; postflexion fish $C = 0.231$ *n.s.*; all data were transformed $\text{Ln}(x + 1)$

Source of variation	df	Preflexion fish		Postflexion fish	
		MS	F	MS	F
Diel	1	18.295	31.08*	163.33	683.6***
Day	8	21.187	21.187***	0.786	3.29*
Diel × Day	8	1.756	2.983*	1.053	4.41**
Residual	18				

* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$; *n.s.* not significant

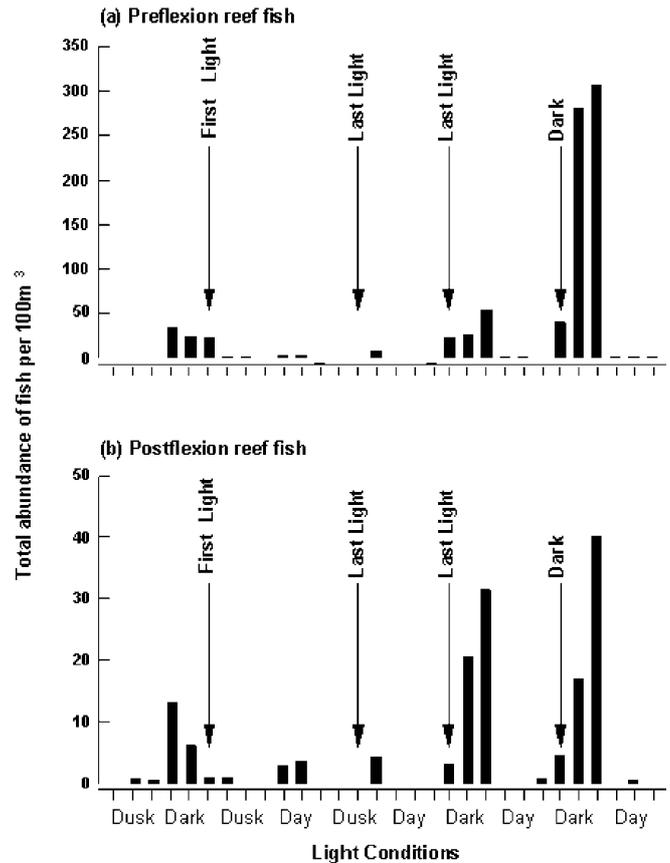


Fig. 4 Total numbers of preflexion (a) and postflexion (b) reef fish in sequences of tows near first light or last light at dawn and dusk over 5 days in February 1993 (*day* = low light, *dusk* = very gloomy, *dark* = no trace of sunlight). Timing of input was according to a sequence of three tows. Catches dropped off quickly at first light, dawn, and increased quickly after last light, dusk; $n =$ three 10-min tows for each replicate light condition

abundant in tows at night. Variation in number of preflexion reef fish was partly the result of hatchings after dark (especially Pomacentridae) and the advection of later-stage larvae over the reef crest (especially Gobiidae, Pomacentridae, Pseudochromidae). Postflexion reef fishes that were most abundant at night were the Apogonidae, Blenniidae, Gobiidae, Labridae, Lutjanidae, Mugiloididae, Mullidae, Pomacentridae, Scaridae, Serranidae and Tripterygiidae (Table 1). Most of the postflexion fishes had developed fins and some had the colouration of newly settled fishes (e.g. apogonids *Apogon doederleini* and *Cheilodipterus quinquelineatus*). Members of some families were caught day and night, including preflexion forms of Apogonidae, Gobiidae, Monacanthidae, Nemipteridae, Scorpaenidae and Synodontidae.

Greatest catches of some pelagic and non-reef-associated taxa were also taken at night and included the anguilliforms (leptocephali), Callionymidae, Clupeidae, Schindleriidae and Triglidae (Table 1). Some, however, showed little difference between day and night (e.g. Bothidae and Carangidae). Catches of carangids were generally greatest in the presence of gelatinous

zooplankton, including ctenophores and medusae (especially *Aurelia*), with which these fish commonly associate (Kingsford 1993).

There was a clear relationship between increases in the abundance of reef fishes and the onset of darkness (Fig. 4). In series of tows that bridged the period between last or first light and total darkness, highest numbers were always found in darkness. This suggested that the input of fishes increased quickly during darkness and/or dropped off at first light. If this is an indication of proximity of the fishes to the reef crest, then we assume they must be very close. Alternatively, this could simply be an indication of rapid changes in net avoidance with changes in light levels.

Although there was great diel variation in abundance, a broad size range of reef fishes was caught in nets by day and night (Fig. 5). Nets captured fishes that ranged in size from 2 to 50 mm standard length. Most of the fishes that were greater than 20 mm SL were: Syngnathidae, Blenniidae, Gobiidae and Mullidae. The size range of some taxa, for which there were adequate numbers, *Spratelloides* (Clupeidae), *Hypoatherina* (Atherinidae), did not change greatly between day and night (Table 3). This suggested that, for some species, avoidance was unlikely to explain variation in diel patterns of abundance. For some taxa there were differences in mean size, with greatest sizes usually found at night. The sizes and developmental forms of many of the reef fishes corresponded well to the literature on the sizes and form at which fishes settle, especially for the Gobiidae, Apogonidae, Labridae, Scaridae and some of the Pomacentridae (Kingsford and Finn 1997).

Seines

Greatest numbers of reef fish were caught at night in seines and this pattern was consistent on all nights and at all sites (Fig. 6). Catches at night were 2–40 times those of day-time collections. Although catches at night were always greater than those during the day, the magnitude of differences varied with day (resulting in a two-way diel \times day interaction for preflexion fish) and site and this resulted in a significant 3-way interaction in ANOVA between diel, day and site for postflexion fish (Table 4). Most taxa were only found in waters of the lagoon at night. It was assumed, therefore, that these fish had entered the lagoon over the reef crest at night, as was concluded for channel nets. A wide size range of presettlement reef fish were caught in seines, from numerous newly hatched larvae (especially pomacentrids) to postflexion apogonids, mullids and large syngnathids and almost all of these were caught at night (Fig. 7, Table 5).

Aggregations of presettlement fishes in the lagoon

Spratelloides ($n = 11$ aggregations) and *Hypoatherina* ($n = 4$ aggregations) were the only species that were

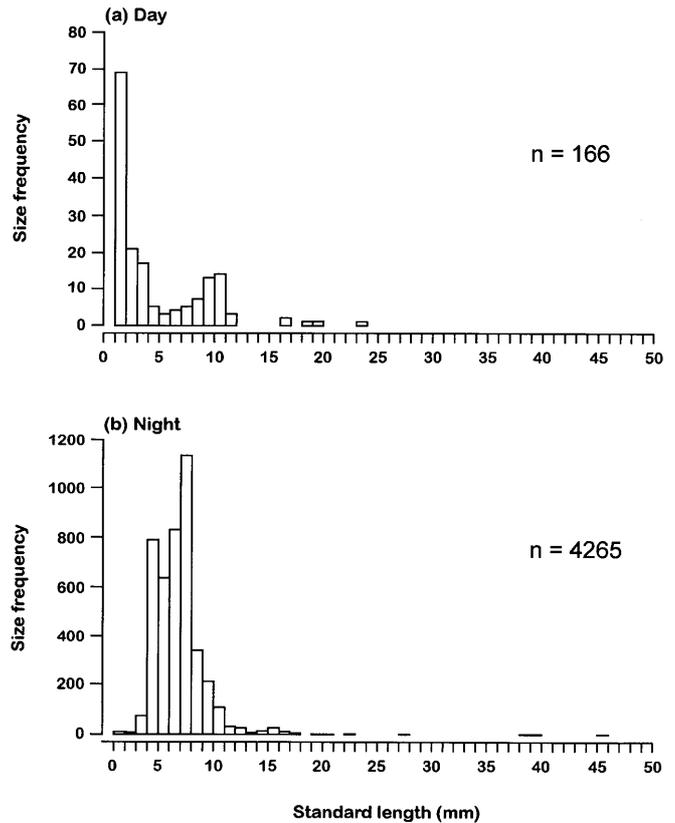


Fig. 5 Size frequency of reef fish day (a) and night (b) (pooled data for all days) in channel nets summer 1994

observed in large aggregations in the lagoon (200–5000 individuals per aggregation) during sampling at three sites on 33 days. Spot sampling of fishes in aggregations showed that preflexion and postflexion fish were present, corroborating the conclusions of Schmitt (1986) and Leis (1993) that at least some of these fishes undergo their early life history in lagoons.

Patch reefs

There was great variation in the numbers of newly settled pomacentrids and apogonids that were collected from patch reefs early and late in the day (Table 6). Ninety-eight percent of apogonids were collected in the morning, indicating that they had settled overnight. Seventy-eight percent of pomacentrids were found in the morning counts. The numbers of some newly settled pomacentrids were very low, but many species showed few differences between counts in the morning and afternoon. In contrast, some taxa (e.g. *Pomacentrus wardi*) showed strong evidence for settlement at night. When data were expressed as an hourly rate, apogonids still showed a peak in input during the night. In contrast, for most pomacentrids there was little difference in settlement rates between night and day.

Table 3 Sizes of fish (SL in mm) collected in channel nets in January to February 1994. Mean size, size range, standard deviation (SD) and sample sizes (*n*) are given

Taxa	Day				Night			
	Range	Mean	SD	<i>n</i>	Range	Mean	SD	<i>n</i>
Acanthoclinidae	–	–	–	–	10.0	10.0	–	1
Acanthuridae	2.0	2.0	–	1	–	–	–	–
Anguilliformes	–	–	–	–	12.5–13.5	13.0	0.7	2
Apogonidae	1.5–24.0	4.5	5.3	21	4.5–13.0	8.8	1.6	119
Atherinidae	3.0–36.0	17.8	3.7	281	4.0–51.0	27.3	9.9	176
Blenniidae	10.5–12.0	11.4	0.8	4	5.0–28.0	13.2	3.7	69
Bothidae	5.5–19.0	11.9	4.5	9	5.0–23.0	10.7	4.0	39
Bregmacerotidae	–	–	–	–	10.5	10.5	–	1
Callionymidae	–	–	–	–	3.0–5.0	3.9	0.6	18
Carangidae	3.0–7.0	4.5	2.2	3	4.0–13.0	5.6	2.1	25
Chaetodontidae	–	–	–	–	17.0	17.0	–	1
Clupeidae	5.5–38.0	18.9	10.7	13	2.5–38.0	15.7	7.3	567
Cynoglossidae	–	–	–	–	6.0–6.5	6.3	0.4	2
Excoetidae	2.5–24.0	6.8	8.5	6	3.5–30.0	11.0	11.3	5
Fistularidae	8.5	8.5	–	1	8.0	8.0	–	1
Gerreidae	8.0–12.0	10.1	0.9	25	7.0–11.0	9.2	1.2	24
Gobiesocidae	5.0	5.0	–	1	3.0–6.0	5.0	0.5	23
Gobiidae	1.5–19.5	3.8	3.8	87	2.0–18.0	7.0	1.8	3724
Labridae	3.5	3.5	–	1	5.0–10.0	7.1	1.6	57
Lethrinidae	2.0	2.0	0.0	2	4.0–5.5	4.8	1.1	2
Lutjanidae	2.0–4.0	2.8	0.8	6	4.0–12.0	6.2	2.2	20
Microdesmidae	–	–	–	–	9.0–28.0	17.5	8.8	6
Monacanthidae	–	–	–	–	6.5–8.5	7.5	1.4	2
Mugiloididae	2.0–3.5	2.5	0.9	3	3.0–8.0	5.2	1.6	6
Mullidae	–	–	–	–	4.0–6.0	5.1	0.5	37
Myctophidae	–	–	–	–	9.0	9.0	–	1
Nemipteridae	–	–	–	–	5.0–10.0	6.3	1.5	10
Pempheridae	–	–	–	–	4.5	4.5	–	1
Platycephalidae	8.0	8.0	–	1	8.0	8.0	–	1
Plesiopidae	–	–	–	–	9.0–17.5	11.3	2.2	11
Pleuronectidae	–	–	–	–	6.0	6.0	–	1
Pomacentridae	3.5–8.5	6.0	3.5	2	3.0–11.0	6.5	2.9	14
Priacanthidae	–	–	–	–	5.5	5.5	–	1
Pseudochromidae	–	–	–	–	9.0–12.5	10.9	1.4	5
Scaridae	–	–	–	–	6.0–11.0	7.7	0.7	100
Schindleriidae	–	–	–	–	9.0–20.0	16.1	3.0	30
Scombridae	3.0	3.0	–	1	7.0–11.0	8.5	1.8	4
Scorpaenidae	–	–	–	–	5.0–10.0	7.0	1.2	21
Serranidae	–	–	–	–	5.0	5.0	–	1
Siganidae	–	–	–	–	20.0	20.0	–	1
Soleidae	–	–	–	–	4.5	4.5	–	1
Sphyraenidae	–	–	–	–	20.0	20.0	–	1
Sygnathidae	4.5	4.5	–	1	8.0–46.0	22.3	16.4	8
Synodontidae	3.0–4.5	3.9	0.4	9	–	–	–	–
Teraponidae	8.0–8.5	8.3	0.4	2	9.0	9.0	–	1
Trichonotidae	–	–	–	–	10.0–25.0	14.7	6.3	5
Triglidae	2.0–2.5	2.2	0.3	3	5.0	5.0	–	1

Vertical distribution

Vertical distribution suggested that postflexion reef fish migrate to surface waters at night (Fig. 8, Table 7). Differences in patterns of vertical distribution were found between day and night. Few fishes were found in surface waters during the day, but a mean of 10 or more fishes per 100 m³ were found at night and this pattern was consistent on both nights of sampling. An interaction between diel and day was found in ANOVA that was indicative of patterns of distribution that changed day and night (Table 8). Greatest mean abundance of reef fish was found at 20 m on day 1, but this pattern was not found on day 2. Ninety percent of the reef fishes caught in depth-stratified tows were postflexion fishes.

Discussion

The greatest input of presettlement fishes to the lagoon at One Tree Island was on flood tide at night. Based on data from nets tethered in channels, about ninety percent of all the late-stage fishes caught arrived at night. Shenker et al. (1993) used 1 × 2-m channel nets and also found that the input of fishes to reefs was greatest at night (97%). Dufour and Galzin (1993) studied the input of fishes to reefs at Moorea, French Polynesia and also found great differences in catches between day and night.

Variation in the size of nocturnal peaks that were found on different days was not surprising, given that all

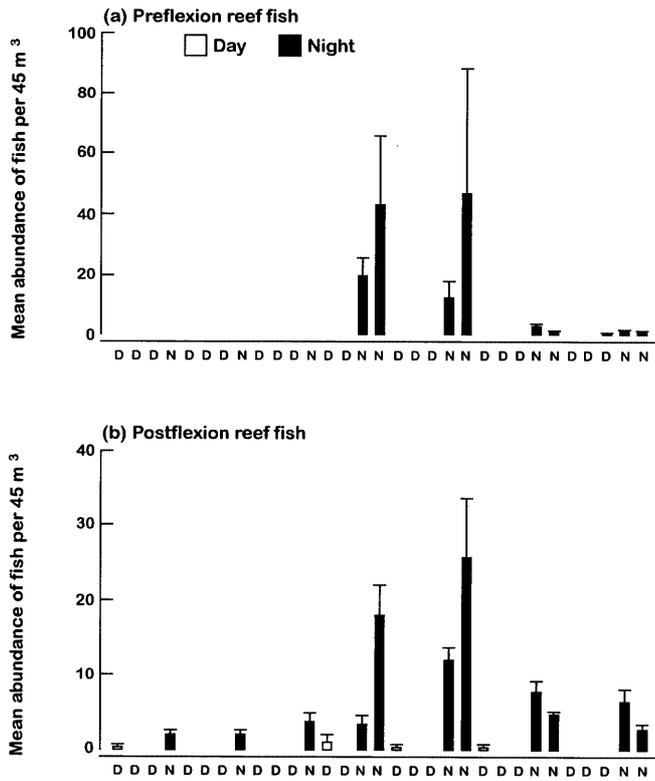


Fig. 6a, b Mean abundance of fishes (+SE) in seines ($n = 3$) during the day and at night on multiple days of sampling, January to February 1994. Sampling was done at three sites during the day (D on x-axis), but at night (N on x-axis) only one or two sites were sampled

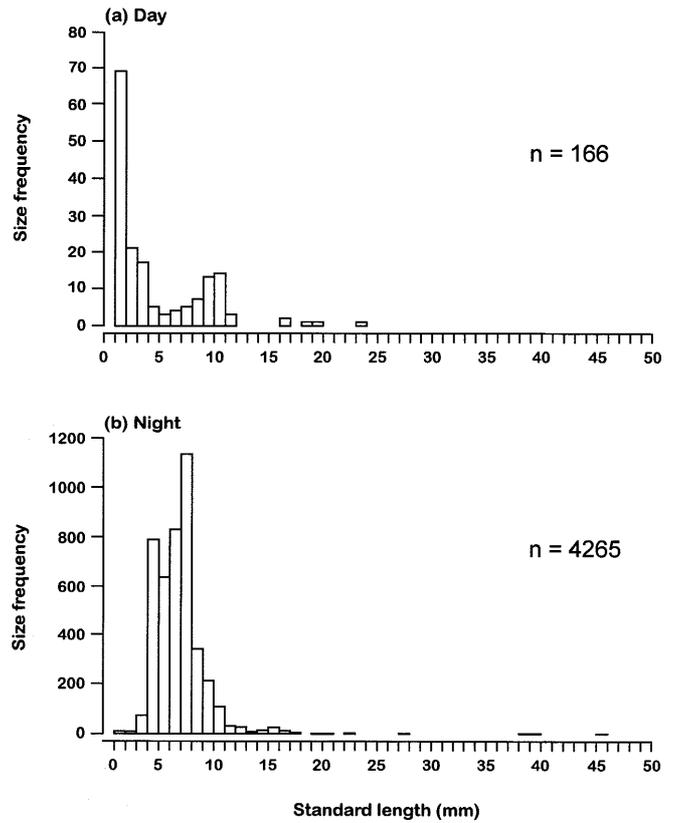


Fig. 7a, b Size of fishes in seines; data are pooled for all days of sampling and sites in January to February 1994

Table 4 Analyses of variance for abundance of preflexion and postflexion reef fishes collected in seines, day and night (factor Diel), at two sites (factor Site) on 4 days (factor day) in summer 1994, $n = 3$ seines. Diel was treated as a fixed factor and Site and Day as random factors. Data were tested for normality using a Cochran's test, variances = 8, $df = 1$, preflexion fish $C = 0.296$ *n.s.*; postflexion fish $C = 0.267$ *n.s.*; all data were transformed $\ln(x + 1)$. There was no test for the factor Diel, but results for this factor could be interpreted from the significant interactions

Source of variation	df	Preflexion fish		Postflexion fish	
		MS	F	MS	F
Diel	1	37.477	no test	48.88	no test
Site	1	0.005	0.015 <i>n.s.</i>	0.008	0.016 <i>n.s.</i>
Day	3	5.359	16.916*	1.026	1.907 <i>n.s.</i>
Diel × Site	1	0.005	0.015 <i>n.s.</i>	0.795	0.761 <i>n.s.</i>
Diel × Day	3	5.359	16.916*	0.779	0.745 <i>n.s.</i>
Site × Day	3	0.317	0.748 <i>n.s.</i>	0.538	4.028**
Diel × Site × Day	3	0.317	0.748 <i>n.s.</i>	1.046	7.825***
Residual	32	0.423		0.134	

* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$; *n.s.* not significant

descriptions of input of potential settlers to reefs have shown great variation in time (Milicich 1994; Dufour et al. 1996) and variation in recruitment (Williams 1983; Milicich et al. 1992). Some of this variation may relate to the phase of the moon (Robertson 1992) and physical phenomena such as winds (e.g. Thorrold et al. 1994a, b),

but the justification for sampling at multiple times was to get an adequate description of diel patterns of abundance. Longer time-series of fish collections that address factors influencing temporal variation in abundance are presented elsewhere (Kingsford and Finn 1997). It is also worth noting that significant numbers of presettlement reef fish larvae (especially scarids) were found in winter, well outside the predicted season of settlement (e.g. Williams 1983).

Information on the vertical distribution of presettlement fishes outside the lagoon suggested that they avoid surface waters during the day. At night many fish rose to the surface, which could facilitate transport to, or be a reflection of, active swimming to the reef crest. Vertical migrations are common in fishes such as flounder (Smith et al. 1977) and engraulids (Hunter and Sanchez 1976), but few data are available for reef fishes. Leis (1986) studied vertical distribution at 0, 3 and 6-m depths at Lizard Island and concluded that most types of larvae preferred waters greater than 3 m deep during the day and moved upwards at night. This pattern was not general for all larvae; some larvae preferred waters of less than 3-m depth or mid depths both day and night. In the present study, many larvae were still found subsurface during the night (at 7, 14, 20 m). It is possible that many larvae disperse more throughout the entire water column at night than during the day, as found for some

Table 5 Sizes (SL in mm) of fishes collected in purse seine samples from One Tree Island lagoon (Times and Sites pooled). % = preflexion (postflexion fish and pelagic juveniles), SD standard deviation. Note: data are from 60 seines during the day and 33 at night

Taxa	Day					Night				
	Range	Mean	SD	<i>n</i>	%	Range	Mean	SD	<i>n</i>	%
Anguilliformes	–	–	–	–	–	56.0–80.0	68.0	17.0	2	0 (100)
Apogonidae	8.0	8.0	–	1	0 (100)	2.5–34.0	8.7	7.9	31	16 (84)
Atherinidae	9.9–35.0	23.1	5.2	129	0 (100)	13.0–54.0	31.8	6.4	319	0 (100)
Blenniidae	–	–	–	–	–	2.3–12.0	3.9	3.3	8	88 (12)
Bothidae	10.0–17.0	13.1	2.1	10	0 (100)	5.2–15.0	9.4	3.3	10	10 (90)
Carangidae	8.0–10.5	9.2	1.3	3	0 (100)	3.0–3.9	4.6	2.0	7	71 (29)
Clupeidae	13.0–26.0	17.3	19.0	155	0 (100)	6.0–49.0	26.8	7.8	1547	0 (100)
Eleotridae	10.0	10.0	–	1	0 (100)	–	–	–	–	–
Excoetidae	–	–	–	–	–	15.0	15.0	–	1	0 (100)
Gerreidae	–	–	–	–	–	10.0–12.0	11.2	0.6	19	0 (100)
Gobiidae	3.5–9.0	6.3	3.9	2	50 (50)	2.2–18.0	6.4	3.0	213	16 (84)
Hemiramphidae	–	–	–	–	–	65.0–70.0	67.5	3.5	2	0 (100)
Labridae	10.0	10.0	–	1	0 (100)	6.0–14.0	9.1	3.0	5	0 (100)
Lethrinidae	–	–	–	–	–	3.5–5.0	4.2	0.8	3	34 (66)
Lutjanidae	–	–	–	–	–	2.7–11.0	5.8	2.3	10	60 (40)
Mugiloididae	–	–	–	–	–	4.0–6.0	4.7	1.2	3	34 (66)
Mullidae	15.9	15.9	–	1	0 (100)	16.1–18.6	17.6	1.3	3	0 (100)
Myctophidae	–	–	–	–	–	5.0	5.0	–	1	0 (100)
Nemipteridae	–	–	–	–	–	4.0–4.5	4.3	0.4	2	50 (50)
Pleuronectidae	8.5	8.2	–	1	0 (100)	–	–	–	–	–
Pomacentridae	–	–	–	–	–	2.3–6.0	2.7	0.4	246	99.6 (0.4)
Pseudochromidae	–	–	–	–	–	2.3–9.0	2.8	0.7	87	92 (8)
Scaridae	–	–	–	–	–	9.0	9.0	–	1	0 (100)
Schindleriidae	18.2	18.2	–	1	0 (100)	8.0–20.0	13.2	3.6	18	0 (100)
Scombriidae	–	–	–	–	–	4.0–5.5	5.0	0.9	3	0 (100)
Scorpaenidae	8.0	8.0	–	1	0 (100)	2.5	2.5	–	1	100 (0)
Siganidae	–	–	–	–	–	22.0	22.0	–	1	0 (100)
Sygnathidae	–	–	–	–	–	4.0–43.0	13.6	13.9	7	29 (71)
Trichonotidae	–	–	–	–	–	12.0	12.0	–	1	0 (100)
Tripterygiidae	–	–	–	–	–	7.0–16.0	11.5	6.4	2	0 (100)
Unidentified	6.0–10.5	8.3	3.2	2	0 (100)	9.0–18.0	12.3	4.9	3	0 (100)
Hatchlings	–	–	–	–	–	<3.0	–	–	3103	100 (0)

Table 6 Patterns of settlement on patch reefs in One Tree Island Lagoon: the results from 23 days in 1994 and 6 in 1995. Pomacentridae: *Chromis nitida* (*C.n*), *Dischistodus perspicillatus* (*D.p*), *Pomacentrus coelestics* (*P.c*), *Pomacentrus amboinensis* (*P.a*), *Pomacentrus nagasakiensis* (*P.n*). Apogonidae: *Apogon doederleini* (*A.d*). Calculations are also given for the percentages of fish that settle within a 12-h period at day and night

Group	<i>C.n</i>	<i>D.p</i>	<i>P.a</i>	<i>P.c</i>	<i>P.n</i>	<i>P.w</i>	Sum Pomacentridae	<i>A.d</i>
1994								
<i>n</i>	4	2	7	2	7	10	32	205
Day%	50	50	60	50	40		31	1
Night%	50	50	40	50	60	100	69	99
1995								
<i>n</i>	1	0	12	0	5	0	18	nd
Day%			14		0		15	nd
Night%	100		86		100		85	nd
Number per 12 hours								
<i>n</i>	5	2	19	2	12	10	60	205
Day%	40	50	31	50	25	0	22	1
Night%	60	50	69	50	75	100	78	99
Number per 12 hours								
Day%	58	66	48	66	40	0	35.6	2
Night%	42	33	52	33	60	100	64.4	98

reef fish and other taxa in temperate waters (Gray and Kingsford, in press).

There is a compelling argument that differences in density of fish larvae caught in plankton nets during the day and at night simply relate to avoidance (Murphy

and Clutter 1972). There were two independent sets of evidence (i.e. other than channel nets) that this was unlikely to be the case for differences in abundance found between day and night. Firstly, conspicuous nocturnal peaks in abundance were found using a

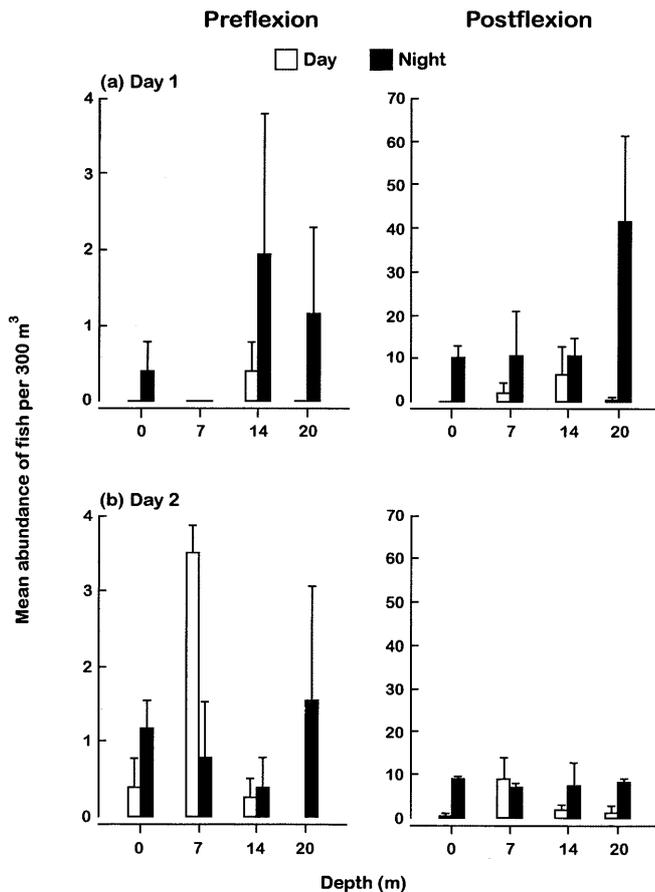


Fig. 8a, b Total reef fishes collected in depth stratified horizontal tows to 20 m. Data are presented for preflexion and postflexion fishes; $n = 2$, +SE

15 × 3-m purse seine and this pattern was consistent regardless of site. Secondly, the only larval forms (i.e. preflexion and postflexion fishes) that were observed inside the lagoon were atherinids and clupeids. An obvious criticism of the latter is that less conspicuous larvae cannot be seen. This, however, is unlikely for fishes greater than 5 mm in length, since other taxa of this size have been observed and taxonomically ground-truthed with nets in other studies, including gobiids (Breitberg et al. 1995), tripterygiids and gobioides (Kingsford and Choat 1989).

Series of hauls indicated a rapid increase in the number of presettlement reef fish immediately after dark on the flood tide. Doherty and McIlwain (1996) also found great numbers of presettlement reef fish on flood tides at night. In their study, sequential tows were done over one-hour periods and it was concluded that much greater numbers were collected in the first hour. The sampling design of Doherty and McIlwain (1996), therefore, was more appropriate to address the duration and intensity of input to reefs during a flood tide. Current speeds would have decreased greatly during the flood tide at One Tree Island. Current speed is greatest in tidal channels of the ponding lagoon as the tide rises,

but once the reef crest is broached by the tide, current speeds decrease rapidly. Although Doherty and McIlwain (1996) acknowledge that variation in current speed could confound the interpretation of patterns of input, estimates of current regime were only obtained from tide tables and were not actual measurements of current using flowmeters in nets. Given that current speed over crests can vary greatly with wind speed as well as tidal variation, input within a tidal cycle requires further scrutiny.

Although presettlement reef fishes were not found in One Tree Island lagoon, larval forms of *Spratelloides* and *Hypoatherina* were. This concurs with other studies that have concluded that these species are generally solely found, or are most abundant, in lagoons (Schmitt 1986; Kingsford et al. 1991) and probably spend their entire life in lagoons. The lack of other taxa in One Tree Island lagoon is probably an artefact of the relatively small size of the lagoon compared to other reef systems. For example, in much larger lagoons ranging from semi-enclosed (Leis 1994) to fully enclosed lagoons (Leis 1998), it has been concluded that a much greater number of taxa (number of families: 14–15) may normally complete their life cycles in lagoons.

The conclusion that the majority of reef fish settle at night has been reached by other investigators who have studied the settlement of fish early and late in the day (Table 9). In all of the studies reviewed it was concluded that 80% or more of fish settled at night. In the present study most *Apogon doederleini* settled at night, but in the case of pomacentrids, a significant proportion of fish appeared to settle during the day. No studies recalculated these percentages based on the number of hours that fish had to settle. When the data in the present study were corrected to number of fish arriving at the reef per unit time (day and night) the differences between day and night for most pomacentrids were non-existent. This, however, was not the case for *A. doederleini*, which still showed a very clear diel pattern. It is likely that the measurement of diel patterns of settlement on reefs is partly confounded by postsettlement patterns of movement that take place on a scale of hours after initial settlement. This movement may include movement among patch reefs (Frederick 1997) or re-entry to the plankton after an initial settlement (Robertson and Foster 1982). Infra-red video and tagging may answer this question (Finn and Kingsford 1996; Schmitt and Holbrook 1996).

Although consumption of presettlement fishes that approach reefs during the day has received some attention (Hamner et al. 1988; Kingsford and MacDiarmid 1988), predation at night has received little attention. It is clear that fish are an abundant type of plankton that can provide food for a wide range of nocturnal consumers from corals to adult fishes. It is likely that consumption by sessile invertebrates will be limited to very small yolk-sac larvae, such as the abundant pomacentrid larvae that were found in the lagoon at night and are known to hatch at night at certain stages of the tide (e.g.

Table 7 Size (SL in mm) of fishes collected in depth-stratified tows; range (mean) *n*. *Total* Percentage of preflexion and (postflexion, including pelagic juveniles) forms

Depth (m)	Day				Night				Total	
	0	7	14	20	0	7	14	20	%	%
Taxa										
Anguilliformes	—	—	45.0 (45.0) 1	—	—	—	14.0 (14.0) 1	—	—	0 (100)
Aponogonidae	—	4.5–9.5 (6.4) 16	5.0–7.0 (6.0) 2	8.5 (8.5) 1	5.0–10.5 (7.7) 4	5.5 (5.5) 1	5.0 (5.0) 1	5.0–7.0 (5.7) 6	6	16 (84)
Atherinidae	—	—	—	—	11.5 (11.5) 1	—	—	—	—	0 (100)
Balistidae	—	4.0 (4.0) 1	—	—	—	—	—	—	—	100 (0)
Blenniidae	—	5.0–6.5 (6.0) 3	—	—	—	—	—	8.5 (8.5) 1	—	0 (100)
Bothidae	—	18.0 (18.0) 1	12.2 (12.2) 1	9.0 (9.0) 1	—	—	10.0–12.0 (11.0) 2	7.5–8.0 (7.7) 3	—	0 (100)
Carangidae	6.0 (6.0) 2	4.9–10.5 (7.9) 9	—	5.0 (5.0) 2	4.9–6.0 (5.5) 2	4.0–5.5 (4.6) 4	—	4.0–5.0 (4.5) 3	—	50 (50)
Callionymidae	—	—	—	—	5.0 (5.0) 1	—	—	—	—	0 (100)
Chaetodontidae	—	9.0 (9.0) 1	9.0 (9.0) 1	6.5 (6.5) 1	9.5–19.5 (16.5) 13	6.0–18.0 (14.3) 8	5.0 (5.0) 1	7.5–18.0 (12.1) 26	—	100 (0)
Clupeidae	—	4.0 (4.0) 1	—	—	—	5.0 (5.0) 2	8.5–20.0 (12.2) 10	—	—	0 (100)
Dactylopteridae	—	5.5–11.0 (7.9) 14	4.5–10.0 (6.6) 16	7.9 (7.9) 1	5.0–12.0 (7.1) 36	5.0–20.0 (7.5) 42	3.5–11.0 (7.5) 37	5.0–17.0 (7.7) 102	—	0 (100)
Gerreidae	—	—	—	5.0 (5.0) 1	—	—	—	4.5 (4.5) 1	—	0 (100)
Gobiidae	—	7.2 (7.2) 1	—	—	—	—	—	13.0 (13.0) 1	—	0 (100)
Gobiesocidae	—	7.0–8.0 (7.5) 2	4.5–6.0 (5.3) 2	5.0–9.2 (7.1) 2	7.2–10.9 (8.6) 3	5.1 (5.1) 1	6.5–12.2 (8.3) 4	5.0–7.5 (6.0) 3	—	5 (95)
Hemiramphidae	—	—	—	—	—	—	—	5.0 (5.0) 2	—	100 (0)
Holocentridae	—	—	—	—	—	—	—	5.0 (5.0) 1	—	60 (40)
Labridae	4.0–5.8 (4.9) 2	5.0–6.0 (5.5) 2	5.0–9.2 (7.1) 2	—	—	6.5–17.0 (13.1) 9	5.0–9.0 (7.0) 2	5.0–5.5 (5.3) 2	—	11 (89)
Lethrinidae	—	—	—	—	—	—	—	5.0 (5.0) 1	—	100 (0)
Lutjanidae	—	5.0–6.0 (5.5) 2	5.0 (5.0) 1	—	—	—	—	5.0 (5.0) 1	—	60 (40)
Microdesmidae	—	4.9–5.0 (5.0) 2	9.2 (9.2) 1	—	—	—	—	4.0–4.5 (4.3) 2	—	29 (71)
Monacanthidae	—	—	—	—	—	—	—	5.5 (5.5) 1	—	0 (100)
Mugiloididae	—	3.9–5.0 (4.6) 4	—	—	4.2–5.5 (5.0) 8	4.5–5.0 (4.8) 3	4.0–5.0 (4.5) 4	5.0–5.5 (5.3) 2	—	48 (52)
Mullidae	—	4.0 (4.0) 1	—	—	—	—	—	4.9–5.1 (5.0) 3	—	0 (100)
Nemipteridae	—	—	—	—	9.0 (9.0) 1	—	—	—	—	50 (50)
Pomacentridae	—	—	—	—	7.0 (7.0) 1	—	—	—	—	0 (100)
Pseudochromidae	—	—	—	9.0 (9.0) 1	5.0 (5.0) 1	—	5.0–6.0 (5.5) 2	—	—	25 (75)
Platycephalidae	—	—	—	—	8.0 (8.0) 2	8.0 (8.0) 1	8.0 (8.0) 1	5.5–8.0 (7.0) 7	—	0 (100)
Scariidae	—	—	—	—	7.0 (7.0) 1	—	—	—	—	0 (100)
Scombridae	—	—	5.0 (5.0) 1	—	10.0–19.0 (13.6) 8	10.0–19.0 (13.5) 18	8.5–18.0 (13.6) 17	7.0–19.0 (13.3) 64	—	0 (100)
Scorpaenidae	—	—	—	—	—	—	—	53.0 (53.0) 1	—	0 (100)
Schmidleriidae	—	—	—	15.0 (15.0) 1	—	—	—	—	—	50 (50)
Syngnathidae	—	—	—	—	17.0 (17.0) 1	—	11.0 (11.0) 1	—	—	38 (62)
Synodontidae	—	—	—	—	—	—	—	—	—	100 (0)
Teraponidae	—	5.5 (5.5) 1	5.0–6.0 (5.7) 3	—	—	—	—	5.0–7.5 (5.9) 4	—	—
Unidentified	—	5.0 (5.0) 2	3.0 (3.0) 1	—	4.5 (4.5) 1	—	4.0 (4.0) 1	—	—	—

Table 8 Analysis of variance for abundance of total presettlement reef fish collected in vertically stratified tows in waters near One Tree Island. Diel (treatments day/night), depth (treatments tows at surface, 7, 14, 20 m), Day (days = 2), $n = 2$ tows. Diel and Depth were treated as a fixed factors and Day as random. Data were tested for normality using Cochran's test, variances = 18, $df = 1$, $C = 0.351$ n.s.

Source of variation	<i>df</i>	MS	<i>F</i>	<i>P</i>
Diel	1	17.67	10.9	n.s.
Depth	3	0.34	0.28	n.s.
Day	1	0.157	0.2	n.s.
Diel × Depth	3	2.41	13.09	0.001
Diel × Day	1	1.62	2.02	n.s.
Depth × Day	3	1.23	1.51	n.s.
Diel × Depth × Day	3	0.184	0.23	n.s.
Residual	17	0.8	0.8	

Table 9 Percentage data on day/night comparisons from other studies

Group	Day	Night	<i>n</i>	Source
18 species	7.5	91.5	204	Robertson et al. 1988
<i>Pomacentrus</i> spp.	12	88	66	Sweatman and St John 1990
<i>P. amboinensis</i>	12.5	87.5	380	Sweatman and St John 1990
<i>Dascyllus albisella</i>	20	80	148	Booth 1991

Pomacentrus wardi, Doherty 1983). Likely predators of larger presettlement fish (including those that are ready to settle) and larvae of pelagic fishes are: apogonids, holocentrids, lutjanids, belonids and squid (Hiatt and Strasburg 1960; Connell 1998).

Most of the methods used in the present study to determine diel patterns of abundance of presettlement fishes indicated that these fishes were most abundant over the reef crest and in the lagoon at night and that potential settlers choose to settle at this time. Furthermore, there was little evidence that presettlement fish, other than atherinids and sprats, were resident in the lagoon during the day. There appeared to be a rapid response to low levels of light in that presettlement fish are close enough to the reef to cross the reef crest soon after dark, if the tide is flooding at this time. The fact that input occurs at low levels of light suggests that fish are advected over the reef in strong tidal currents, as a result of near-surface distributions. Conversely, they may position themselves close to the reef and/or very quickly respond to cues from the reef that may include sound and smell. It has often been argued that there is a high risk of predation for presettlement fish that remain near reefs during the day. It is plausible, therefore, that fish settle at night to minimise the risk of predation. Alternatively, presettlement fish may approach the reef at all times of the day, but predators remove them before they get to the reef crest, and therefore it appears that they only settle at night. Although there is no way that the data obtained in the present study can differentiate between these alternatives, the latter argument appears least likely, based on present knowledge. Presettlement

reef fish generally have excellent powers of mobility (Stobutzki and Bellwood 1997) and in situ observations have demonstrated that they have excellent visual senses and respond to stimuli, such as the presence of piscivores, that divers are unaware of (J. Leis, personal communication). In conclusion, studies on cues and behaviour of fish near the time of settlement need to focus on night time, and sampling for variation in abundance of hatchlings and potential settlers over reefs is best done at night.

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