

D.T. Wilson

Patterns of replenishment of coral-reef fishes in the nearshore waters of the San Blas Archipelago, Caribbean Panama

Received: 26 July 2000 / Accepted: 30 March 2001 / Published online: 12 July 2001
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Abstract The magnitude and synchrony of spatial and temporal patterns of larval supply to the San Blas Archipelago were measured using three replicate light traps in each of three habitats (exposed, lagoon and back-reef) over 18 consecutive lunar months from December 1996 to June 1998. Traps were sampled for 19 consecutive nights centred on the new moon in each month. A total of 125 species from 44 families of reef fishes were collected, of which the Pomacentridae, Gerridae, Synodontidae, Lutjanidae, Blenniidae, Apogonidae and Labridae were the most abundant in catches. The spatial pattern of replenishment for these families was systematic, with highest abundance recorded in the lagoon and lowest abundance in the back-reef habitat (total abundance lagoon = 18,440; back-reef = 5,243 individuals). The timing and magnitude of catches for the 12 most abundant species were often significantly correlated both among species and habitats during the sampling period. I concluded that replenishment to San Blas occurs by the continuous influx of multi-specific, meso-scale (hundreds of metres) larval patches, and that larvae within these patches appear to actively select suitable settlement habitats immediately prior to nightly settlement.

Communicated by G.F. Humphrey, Sydney

D.T. Wilson
Department of Marine Biology,
James Cook University,
Townsville, Qld. 4811, Australia

E-mail: Dave_T_Wilson@hotmail.com
Tel.: +684-633-4456
Fax: +684-633-5944

D.T. Wilson
Smithsonian Tropical Research Institute,
Naos Marine Lab, Unit 0948, APO AA 34002, USA

Present address: D.T. Wilson
Department of Marine and Wildlife Resources,
P.O. Box 3730, Pago Pago, A. Samoa 96799, USA

Introduction

Adult populations of coral-reef fishes are replenished by highly complex cyclic supply processes involving the interactions of a suite of physical and biological factors acting on the larval stage prior to its arrival in the benthic environment. The nature of this replenishment process is extremely variable both in time and space (Doherty 1991; Caley et al. 1996) and can play an important role in shaping the demographic structure of reef-fish populations (Doherty and Fowler 1994a, b; Booth and Brosnan 1995). To gain an insight into the mechanisms involved in the replenishment process, we first require basic information on the spatio-temporal patterns of replenishment. To date, work documenting these patterns has involved a variety of techniques, including surveys or collections of newly settled fish, back-calculation of settlement patterns from the otoliths of settled fish (Doherty 1991; Wilson and McCormick 1997) or collections of fish larvae just prior to their settlement in reef habitats, using channel nets (Shenker et al. 1993), crest nets (Dufour and Galzin 1993) or light traps (Sponaugle and Cowen 1996a, b; Hendriks et al. 2001).

Together, these studies have demonstrated that the replenishment process is strongly seasonal in many localities. For example, on the Great Barrier Reef (GBR), the majority of replenishment occurs during a relatively short period over the summer months from October to March each year (Milicich and Doherty 1994). In contrast, in some localities in the Caribbean, replenishment can occur year-round (McFarland et al. 1985; Robertson et al. 1988, 1993). These differences in the duration of replenishment events may result from fundamental differences in the dynamics of populations between regions (Shulman and Ogden 1987; Robertson 1988; Thresher 1991).

While the duration of replenishment events may vary among regions, within-season events are often consistent, with sporadic pulses of larvae on a background of low or negligible replenishment (Doherty 1991). For

example, Milicich (1994) used light traps to document the patterns of replenishment to reef habitats at Lizard Island on the GBR during a single 3-month summer sampling period. She found that approximately 80% of the pre-settlement fishes collected in light traps occurred during one episode that lasted for only six nights. Such peaks in abundance are often multi-specific, with replenishment events closely synchronised among different species (Milicich and Doherty 1994; Sponaugle and Cowen 1996b).

In addition to temporal variation, there is also considerable spatial variability in the replenishment process that can be of a fixed or random nature. Active avoidance of some reef habitats, such as lagoons, by pre-settlement fishes implies that they are capable of structuring their distributions in nearshore waters prior to settlement and is an example of fixed variability (Doherty et al. 1996). Examples of random variation in replenishment are shown by the monitoring of recruitment to standard units of habitat separated by tens to thousands of metres. Ten-fold or greater differences in the magnitude of replenishment at such spatial scales are commonplace and it has been suggested that this reflects the patchy nature of spatial distributions of pre-settlement fishes in the plankton (Doherty and Williams 1988; Doherty 1991).

While these studies provide an insight into the processes determining replenishment, the patterns they describe may be confounded by a number of factors, particularly where supply is determined from collections of individuals that have already become established in adult reef habitats. In these situations, mortality and migration may act to alter or obscure recruitment patterns (Robertson and Kaufmann 1998). For these reasons, sampling techniques that target larval fish immediately prior to or during the replenishment process, such as light traps, crest or channel nets, are preferred. Of these, light traps have the advantage that they can operate in numerous localities simultaneously allowing synoptic pictures of distributions to be constructed (Doherty 1987).

The implicit assumption in studies measuring larval supply is that the number of larvae arriving in nearshore waters (replenishment) accurately represents the number of fish settling into juvenile habitats (recruitment). This has previously been examined in the Caribbean for two coral-reef fishes, *Stegastes partitus* and *Acanthurus bahianus* (see Sponaugle and Cowen 1996a). These workers used light traps and biweekly visual census, coupled with settlement patterns back-calculated from otoliths, to show that patterns of replenishment and recruitment were closely linked. A similar study by Milicich et al. (1992) also identified a close link between catches in light traps and recruitment of three pomacentrid species on the GBR.

To date, most studies examining both spatial and temporal variations in replenishment have been conducted on the GBR (Milicich 1994; Doherty and Carleton 1997) and at one locality (Barbados) in the Caribbean (Sponaugle and Cowen 1996a, b). No study

has attempted to use this technique in the extensive coral-reef habitats of the western Caribbean. This region is of particular interest, since studies of newly settled fish have suggested that the replenishment process can occur throughout the year, unlike the GBR and Barbados (Robertson et al. 1988). In this study, I used light traps to examine spatial and temporal patterns in the replenishment of populations of reef fishes. By describing the distribution patterns of larvae simultaneously at various spatial and temporal scales, trends in replenishment may provide the basis for interpreting the processes acting on larvae as they approach reef habitats. Specifically, the present study aimed to describe the temporal (nightly) patterns in the magnitude of replenishment by sampling over 18 consecutive lunar months. Additionally, I aimed to describe spatial patterns of replenishment by sampling concurrently in three reef habitats.

Materials and methods

Study site

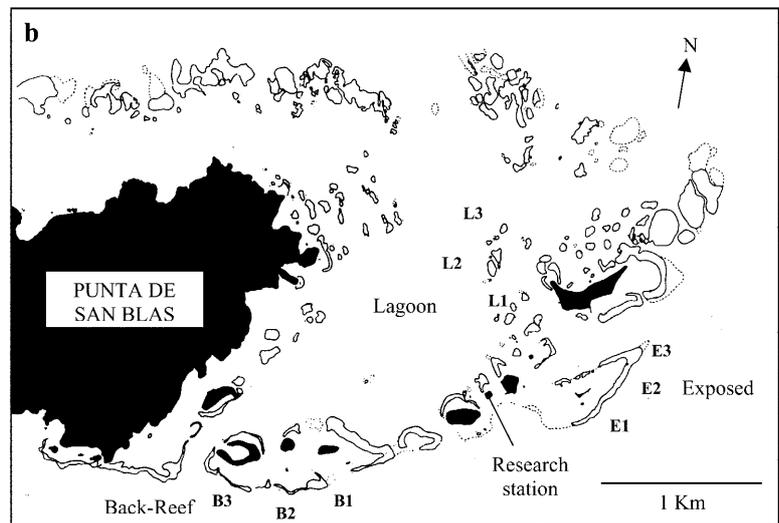
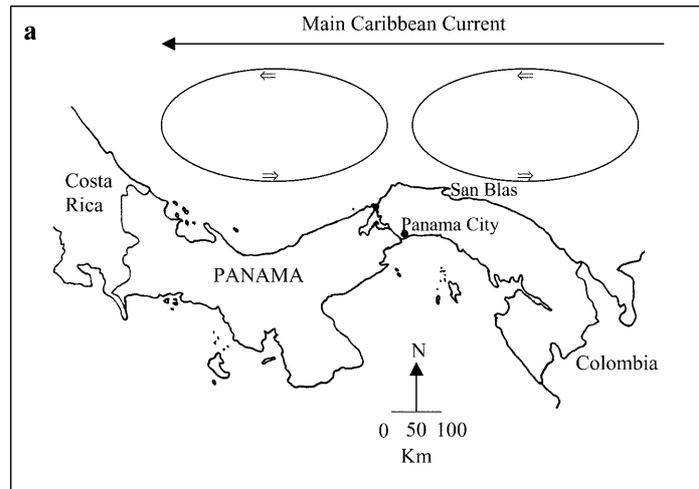
San Blas Point is a fringing reef extending up to 5 km offshore (9° 34' N, 78° 58' W). The region undergoes distinct wet (May–December) and dry (January–April) seasons (Cubit et al. 1989). The former is characterised by light and variable winds, mild currents and intense periods of rainfall, while the latter is characterised by very low rainfall and consistent 25–30 km h⁻¹ northerly winds that produce strong currents and turbid waters (D'Croz and Robertson 1997). Sea-surface temperature ranges from 26°C to 32°C during the year and salinity, between 33‰ and 35‰ (Marine Environmental Science Program, MESP 1999). The maximum tidal range in San Blas is 0.6 m (Panama Canal Commission 1998). The Main Caribbean Current (MCC) flows westward off the coast of Panama and generates two large eddies that circulate along the coast (Lessios et al. 1984; Fig. 1a). Although upwelling events do not occur on the Caribbean coast, intense periods of rainfall create substantial river discharge that are enriched with nutrients that flood nearshore reefs (D'Croz and Robertson 1997; Robertson et al. 1999). For greater oceanographic detail, including local current patterns, see Robertson et al. (1999).

Field sampling

The study was conducted in the nearshore coral-reef environment in the San Blas Archipelago over 18 consecutive lunar months from 31 December 1996 to 4 June 1998 (Fig. 1). Originally, a sampling period of 2 years was planned in order to compare seasonal patterns in replenishment between years; however, owing to the unexpected closure of the Smithsonian's research facilities in San Blas, the sampling period was reduced to only 18 months.

The light-trap design used throughout the study is described elsewhere (see Stobutzki and Bellwood 1997). Briefly, the trap consisted of a single Plexiglass chamber with a tube running through its centre. The chamber was open to the exterior by four horizontal slits (7 cm high by 25 cm wide), through which photo-positive organisms entered the trap. The slits were tapered to a height of 1.5 cm inside the trap to inhibit escapement. An 8 W DL (Day-Light) fluorescent tube was used as a light source. The light was encased within a central tube of clear Plexiglass, while the power pack was housed in a high-tensile (70 m WR) plastic case above the light. The Plexiglass chamber was protected by an aluminium frame, to which a surface buoy was tied. When the trap was removed from the water after fishing, catches accumulated in a detachable plastic collection box at the trap base. Mesh sides per-

Fig. 1a, b Location of sampling sites on the Caribbean coast of Panama, San Blas Archipelago. **a** Panama, major current patterns (arrows indicate flow directions) and **b** Punta de San Blas, showing the three sampling habitats for the spatial and temporal sampling of replenishment. *E1–E3* Exposed traps, *L1–L3* lagoon traps and *B1–B3* back-reef traps



mitted water movement through the collection box to maintain the catches in good condition.

Three replicate light traps were deployed in each of three nearshore habitats: exposed (exposed to onshore winds throughout much of the sampling period), lagoon and back-reef (Fig. 1b). Each of the areas sampled using light traps was chosen as representative of the entire habitat (exposed, lagoon or back-reef), given a number of selection criteria. These included the area of the habitat suitable for the deployment of traps, local currents and accessibility during all weather conditions. Traps within a habitat were moored about 100 m apart in order to avoid any overlap in the sampling fields between traps, and at a distance of 50–100 m from the reef margin. Traps were anchored on the reef slope in water depths of 20 m in the exposed and back-reef habitats and 12 m in the lagoon. Entrance slits were 1–1.5 m below the surface. Traps were deployed prior to dusk each day and retrieved the following morning at dawn, being lit for 12–13 h. After the catches had been cleared, the traps were rinsed and left to dry, before being randomly re-deployed to fixed moorings in the evening.

Long-term monitoring of recruitment to the reefs of San Blas by Robertson (1992) over 28 lunar months, indicated that 90–95% of reef-fish recruitment took place within a 19-consecutive-night period centred on the new moon (see Fig. 1 in Robertson 1992). Consequently, light traps were sampled for a period of 19 consecutive nights centred on the new moon in each lunar month. In order to confirm that this pattern accurately reflected replenishment of reef habitats, light traps were sampled every night during two complete lunar cycles from 13 March 1998 to 11 May 1998.

Catches were removed from the traps each morning, sorted in the laboratory and preserved in 75% ethanol. Most fishes could be identified to species level or type, although some very small taxa were grown out in aquaria to confirm identifications.

Statistical analysis

Spatial and temporal patterns of replenishment to San Blas Point

Prior to analysis, the raw data sets from the three traps in each habitat (exposed, lagoon, back-reef) were averaged and each 19-consecutive-night sampling period concatenated to produce a single time series of mean values for analysis (342 nights). Individual traps failed to operate on 18 nights of sampling. On these occasions, catch records from the remaining traps in the same habitat were used to calculate average nightly catches. Multivariate cluster analysis was used to examine general relationships of spatial (habitat) and temporal (season) patterns in catches of pre-settlement fishes. Prior to analysis, data were transformed to $\log_{10}(x + 1)$ values to improve multivariate normality and stabilise the variance. To reduce the presence of zeros in the data set, only species where more than 50 individuals were collected were used in the analysis. This gave a data set of 47 species for analysis. Collections were pooled, so that each sample consisted of the average monthly catch for each species within a particular habitat. A Bray-Curtis dissimilarity matrix was then generated from the data set and used as the basis for a flexible unweighted (UPGMA) clustering strategy

(Bray and Curtis 1957). The main clusters produced by the analysis were plotted as a dendrogram, determined using the test provided by Sandland and Young (1979). To confirm these results, analysis of the data sets was repeated using an ordination technique, non-metric multidimensional scaling (MDS). Clusters identified by the dendrogram were mapped onto the plot produced by the MDS to compare the results of both forms of analysis. Lunar months associated with the transition between wet and dry seasons were assigned to either season on the basis of the weather conditions during the first half of the lunar month. For example, if this period was associated with heavy rainfall, the lunar month was assigned as a "wet" season month. In order to more closely examine seasonal patterns, samples were also split among habitats (exposed, lagoon and back-reef) and classification and ordination analysis repeated on each separately.

Larval patch size (all taxa combined)

Individual light-trap catches from each habitat were compared using time-series analysis. Since trapping was conducted in periods of 19 consecutive nights centred on the new moon in each of 18 consecutive lunar months, samples were concatenated to provide a single time series of 342 nights. As only two replicate traps were deployed in the first four lunar months, these were excluded from the analysis, providing a time series of 266 nights. Each data point (night) was the individual catch record of a single light trap operating on that night (species pooled). The presence of autocorrelation in these time series was examined using autocorrelation function (ACF) plots (Chatfield 1997). Data sets were transformed to $\ln(x+1)$ values in order to stabilise the variance. Auto Regressive Integrated Moving Average (ARIMA) models were then fitted to the data. Serial dependency was removed from the series by differencing (subtracting each data point from the next) depending upon the seasonality found within the data, to ensure that they were stationary. The autocorrelation coefficients of most time series decayed exponentially suggesting the data required first-order differencing (Chatfield 1997). The number of autoregressive (AR) and moving average (MA) parameters were determined by inspecting the autocorrelogram. A model was then fitted to the series and its reliability confirmed by examining the autocorrelogram to ensure that serial dependency had been removed. In addition, the residuals from the model were plotted to examine normality. The residuals computed from the ARIMA model were then used in the subsequent cross-correlation analysis. Temporal coherence of nightly replenishment among the replicate light traps within each habitat and among habitats were calculated using cross-correlation functions (CCFs). The CCFs were used to estimate how well the timing of replenishment was synchronised among traps, generated by computing Pearson correlation coefficients between two time series as one series was progressively shifted night by night across the other series (see Milicich et al. 1992). All time-series analyses were conducted using the STATISTICA programme.

Species-specific variations in replenishment

A scree plot of Cramer values (Belbin 1988) was used to identify the 12 species that contributed most variance to the data matrix, and thus to the separation of sample groups in the cluster analysis.

Larval-patch composition

Individual species data sets collected in each lunar month of sampling were concatenated giving a time series of 342 nights of sampling. Each data point (night) was the average of all traps operating on that night. Correlations in the timing and magnitude of replenishment among species were calculated using cross-correlation functions (CCF; described above). For this analysis, low-frequency signals in the data sets were removed using ARIMA models

(Chatfield 1997; Pyper and Peterman 1998) and residuals cross-correlated to produce a table of correlations at a lag of 0 nights.

Variations in larval abundance between seasons and among habitats

The species identified using Cramer values (Belbin 1988), nearly all of which were also the most abundant in catches, were further analysed individually using univariate techniques. Levene's test (Zar 1996) indicated that these did not conform to the assumptions of normality required by parametric analysis. Consequently, the mean numbers of pre-settlement reef fishes collected nightly in light traps operating in each habitat, and between seasons, were analysed using non-parametric Kruskal-Wallis tests and Tukey-type multiple comparisons where appropriate (Zar 1996).

Nightly time series for each of the 12 species (342 nights) were split into habitat components (exposed, lagoon and back-reef) and analysed using cross-correlation functions (CCF) as described above. Each data point (night) was the average of the three traps operating in a habitat. Residuals from the ARIMA model were cross-correlated to produce a table of correlations at lags ranging from -1 to 1 night. These same data sets were then split into individual light-trap catches (nine light-trap time series). To examine individual species' larval-patch size, all light-trap time series were cross-correlated with each other using CCFs.

Results

Lunar patterns of replenishment

A total of 5,181 pre-settlement reef fishes were collected by light traps during the two lunar cycles of sampling. Of these, 4,701 fish or 91% of the total catch were collected within a 19-consecutive-night period centred on the new moon in each cycle (Fig. 2).

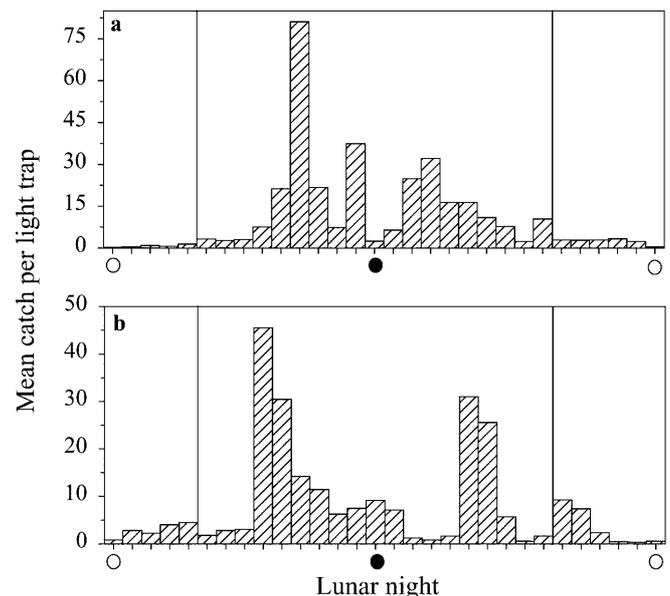


Fig. 2a, b Mean light-trap catches over two complete lunar cycles. **a** 13 March 1998 to 11 April 1998 ($n=2,035$) and **b** 12 April 1998 to 11 May 1998 ($n=3,146$), inclusive. Vertical lines represent 19-night cut-off period centred on the new moon. ● New moon, ○ full moon

Spatial and temporal patterns of replenishment to San Blas Point

Light traps collected a total of 233,864 pre-settlement fish during 32,700 h of sampling over a period of 18 months. Reef-associated clupeids, engraulids and atherinids (83.51% of total numbers) dominated catches. As reef fishes were the primary targets of my sampling,

these clupeoids were excluded from the analysis. Of the remaining catches, 38,559 were reef fishes that were composed of a total of 125 species from 44 families (Table 1). Pomacentrids, gerrids, synodontids, lutjanids, blenniids, apogonids and labrids accounted for 88.13% of the total catch of reef fishes (Table 1).

Cluster analysis revealed seven distinct groups in the catches (Fig. 3a); however, the compositions of these

Table 1 Catch composition of light traps during 18 consecutive lunar months of sampling in three habitats (exposed, lagoon and back-reef) in the San Blas Archipelago, Caribbean Panama. Values are given at family level where only one species/type was recorded

Taxon	Total catch	Percentage catch	Exposed	Lagoon	Back-reef
Acanthuridae	348	0.903	69	220	59
<i>Acanthurus bahianus</i>	20	0.052	10	5	5
<i>Acanthurus chirurgus</i>	291	0.755	57	183	51
<i>Acanthurus coeruleus</i>	37	0.096	2	32	3
Apogonidae	2,386	6.188	1,801	139	446
<i>Apogon binotatus</i>	53	0.137	44	1	8
<i>Apogon maculatus</i>	34	0.088	31	2	1
<i>Apogon planifrons</i>	13	0.034	3	7	3
Apogonid type 1	183	0.475	61	43	79
<i>Astrapogon puncticulatus</i>	1,364	3.537	1,266	15	83
<i>Phaeoptyx pigmentaria</i>	739	1.917	396	71	272
Aulostomidae	24	0.062	6	13	5
<i>Aulostomus maculatus</i>	—	—	—	—	—
Balistidae	4	0.010	0	1	3
<i>Balistes capriscus</i>	1	0.003	0	0	1
<i>Balistes vetula</i>	3	0.008	0	1	2
Batrachoididae	1	0.003	0	0	1
<i>Opsanus tau</i>	—	—	—	—	—
Blenniidae	2,410	6.250	1,494	699	217
Blenniid type 1	42	0.109	27	7	8
Blenniid type 2	924	2.396	772	61	91
Blenniid type 3	2	0.005	0	0	2
Blenniid type 4	2	0.005	1	1	0
<i>Hypoleurochilus bermudensis</i>	6	0.016	6	0	0
<i>Hypsoblennius exstochilus</i>	4	0.010	2	1	1
<i>Ophioblennius atlanticus</i>	1,414	3.667	675	625	114
<i>Parablennius marmoreus</i>	15	0.039	10	4	1
<i>Scartella cristata</i>	1	0.003	1	0	0
Bothidae	84	0.218	10	57	17
<i>Bothus lunatus</i>	41	0.106	8	26	7
<i>Bothus ocellatus</i>	23	0.060	1	18	4
<i>Bothus</i> spp.	5	0.013	0	4	1
<i>Syacium micrurum</i>	15	0.039	1	9	5
Bregmacerotidae	76	0.197	33	17	26
<i>Bregmaceros atlanticus</i>	—	—	—	—	—
Carangidae	284	0.737	75	169	40
<i>Alectis ciliaris</i>	2	0.005	0	0	2
<i>Chloroscombrus chrysurus</i>	279	0.724	74	167	38
<i>Selar crumenophthalmus</i>	2	0.005	1	1	0
<i>Selene vomer</i>	1	0.003	0	1	0
Chaetodontidae	91	0.236	8	81	2
<i>Chaetodon capistratus</i>	86	0.223	7	78	1
<i>Chaetodon ocellatus</i>	5	0.013	1	3	1
Chaenopsidae	1	0.003	0	1	0
<i>Hemiemblemaria simulus</i>	—	—	—	—	—
Congridae	27	0.070	4	22	1
Congridae spp. (leptocephalus)	—	—	—	—	—
Dactylopteridae	3	0.008	0	3	0
<i>Dactylopterus volitans</i>	—	—	—	—	—
Diodontidae	104	0.270	11	3	90
<i>Chilomycterus</i> spp.	100	0.259	11	0	89
<i>Diodon histrix</i>	4	0.010	0	3	1
Elopidae	621	1.611	21	498	102
<i>Megalops atlanticus</i>	—	—	—	—	—
(leptocephalus)	—	—	—	—	—
Gerridae	5,682	14.736	1,885	3,099	698

Table 1 (Contd.)

Taxon	Total catch	Percentage catch	Exposed	Lagoon	Back-reef
<i>Eucinostomus melanopterus</i>					
Gobiesocidae	65	0.169	18	6	41
<i>Acyrtops beryllina</i>	41	0.106	8	4	29
<i>Gobiesox punctulatus</i>	24	0.062	10	2	12
Gobiidae	576	1.494	192	77	307
<i>Coryphopterus dicrus</i>	91	0.236	31	3	57
<i>Coryphopterus personatus</i>	242	0.628	98	5	139
<i>Gnatholepis thompsoni</i>	100	0.259	28	29	43
Gobiid type 1	33	0.086	15	3	15
Gobiid type 2	11	0.029	1	0	10
Gobiid type 3	98	0.254	18	37	43
<i>Gobiosoma illecebrosus</i>	1	0.003	1	0	0
Haemulidae	584	1.515	240	52	292
<i>Anisotremus virginicus</i>	1	0.003	0	0	1
Haemulidae spp.	583	1.512	240	52	291
Holocentridae	74	0.192	31	35	8
<i>Holocentrus rufus</i>	1	0.003	0	1	0
<i>Holocentrus vexillarius</i>	6	0.016	0	4	2
<i>Sargocentron coruscus</i>	67	0.174	31	30	6
Labridae	1,775	4.603	1,261	102	412
<i>Bodianus rufus</i>	5	0.013	5	0	0
<i>Halichoeres bivittatus</i>	129	0.335	82	14	33
<i>Halichoeres pictus</i>	5	0.013	2	1	2
<i>Halichoeres poeyi</i>	29	0.075	17	5	7
Labrid type 1	10	0.026	1	0	9
Labrid type 2	208	0.539	83	15	110
Labrid type 3	25	0.065	16	2	7
Labrid type 4	3	0.008	0	2	1
<i>Thalassoma bifasciatum</i>	1,361	3.530	1,055	63	243
Labrisomidae	312	0.809	203	89	20
<i>Labrisomus nigricinctus</i>	1	0.003	0	1	0
<i>Labrisomus nuchipinnis</i>	63	0.163	33	25	5
<i>Malacoctenus macropus</i>	111	0.288	64	43	4
<i>Malacoctenus</i> spp.	91	0.236	81	4	6
<i>Malacoctenus triangulatus</i>	46	0.119	25	16	5
Lutjanidae	2,551	6.616	1,503	631	417
<i>Lutjanus apodus</i>	463	1.201	119	274	70
<i>Lutjanus chrysurus</i>	270	0.700	176	18	76
<i>Lutjanus cyanopterus/joci</i>	128	0.332	66	44	18
<i>Lutjanus griseus</i>	19	0.049	11	1	7
<i>Lutjanus mahogani</i>	1,541	3.996	1,070	241	230
<i>Lutjanus</i> sp.1	128	0.332	60	53	15
<i>Lutjanus</i> sp.2	2	0.005	1	0	1
Monacanthidae	287	0.744	88	70	129
<i>Aluterus scriptus</i>	2	0.005	1	1	0
<i>Monacanthus setifer</i>	283	0.734	86	69	128
<i>Monacanthus tuckeri</i>	2	0.005	1	0	1
Mugilidae	3	0.008	1	2	0
<i>Mugil cephalus</i>	–	–	–	–	–
Mullidae	46	0.119	9	13	24
<i>Pseudopeneus maculatus</i>	–	–	–	–	–
Muraenidae	3	0.008	1	2	0
Muraenidae spp. (leptocephalus)	–	–	–	–	–
Polynemidae	152	0.394	9	134	9
<i>Polydactylus virginicus</i>	–	–	–	–	–
Pomacanthidae	38	0.099	6	21	11
<i>Holacanthus ciliaris</i>	2	0.005	0	2	0
<i>Pomacanthus arcuatus</i>	34	0.088	5	19	10
<i>Pomacanthus paru</i>	1	0.003	0	0	1
<i>Pomacanthus</i> spp.	1	0.003	1	0	0
Pomacentridae	15,653	40.595	4,421	10,480	752
<i>Abudefduf saxatilis</i>	18	0.047	2	12	4
<i>Abudefduf taurus</i>	1	0.003	0	1	0
<i>Chromis cyanea</i>	2	0.005	0	2	0
<i>Chromis insolata</i>	10	0.026	1	9	0
<i>Chromis multilineata</i>	24	0.062	22	0	2
<i>Microspathodon chrysurus</i>	133	0.345	96	33	4

Table 1 (Contd.)

Taxon	Total catch	Percentage catch	Exposed	Lagoon	Back-reef
<i>Stegastes diencaeus</i>	162	0.420	53	105	4
<i>Stegastes dorsopunicans</i>	2,419	6.274	1,079	1,236	104
<i>Stegastes leucostictus</i>	164	0.425	29	126	9
<i>Stegastes partitus</i>	4,651	12.062	1,695	2,822	134
<i>Stegastes planifrons</i>	7,569	19.630	1,322	5,825	422
<i>Stegastes variabilis</i>	500	1.297	122	309	69
Priacanthidae	11	0.029	0	10	1
<i>Priacanthus cruentatus</i>	–	–	–	–	–
Scaridae	25	0.065	23	1	1
Scarid type 1	9	0.023	7	1	1
Scarid type 2	1	0.003	1	0	0
<i>Scarus iserti</i>	15	0.039	15	0	0
Scombridae	209	0.542	78	60	71
<i>Scomberomorus regalis</i>	–	–	–	–	–
Scorpaenidae	35	0.091	13	16	6
<i>Scorpaena plumeri</i>	–	–	–	–	–
Serranidae	176	0.456	21	137	18
<i>Epinephelus cruentatus</i>	137	0.355	2	135	0
Serranid type 1	4	0.010	2	0	2
Serranid type 2	6	0.016	3	0	3
Serranid type 3	24	0.062	11	1	12
Serranid type 4	2	0.005	2	0	0
Serranid type 5	1	0.003	0	1	0
<i>Serranus tigrinus</i>	2	0.005	1	0	1
Sphyraenidae	198	0.513	52	102	44
<i>Sphyraena barracuda</i>	83	0.215	11	53	19
<i>Sphyraena picudilla</i>	115	0.298	41	49	25
Syngnathidae	6	0.016	1	3	2
<i>Cosmocampus elucens</i>	5	0.013	1	3	1
<i>Hippocampus reidi</i>	1	0.003	0	0	1
Synodontidae	3,526	9.144	1,232	1,344	950
Synodontidae spp.	–	–	–	–	–
Tetraodontidae	9	0.023	1	4	4
<i>Canthigaster rostrata</i>	1	0.003	0	1	0
<i>Sphoeroides spengleri</i>	1	0.003	0	1	0
<i>Sphoeroides testudineus</i>	7	0.018	1	2	4
Tripterygiidae	1	0.003	0	1	0
<i>Enneanectes</i> spp.	–	–	–	–	–
Uranoscopidae	1	0.003	1	0	0
<i>Astroscopus guttatus</i>	–	–	–	–	–
Unidentified	97	0.252	54	26	17
Unidentified damaged	91	0.236	53	24	14
Unidentified type 1	6	0.016	1	2	3
Totals	38,559	100	14,876	18,440	5,243

were complex. The first splits of the dendrogram separated some wet-season catches in the lagoon and exposed habitats (Fig. 3a, b – group 7), and a group of dry-season catches in the lagoon and back-reef habitats (Fig. 3a, b – group 1) from the remainder of the samples. Catches in the former group were abundant and diverse, and accounted for almost 38% of total numbers of reef fishes. *Stegastes dorsopunicans*, *S. partitus* and *S. planifrons* dominated samples in this group. In contrast, the latter group was characterised by low and depauperate catches. There were few clear divisions in the remainder of the dendrogram that could easily be accounted for by the factors of season or habitat. The non-intuitive association of samples within the clusters appeared to be largely due to the sporadic appearance of diagnostic taxa. For example, several large peaks in catches of an unidentified blenny occurred during the months of February and March in 1998 in exposed and back-reef habitats. These samples formed a distinct cluster in the

dendrogram (Fig. 3a – group 4). Similarly, a combination of high numbers of *Astrapogon puncticulatus*, *Ophioblennius atlanticus* and *S. planifrons* in some wet-season samples also clustered together (group 6). The lack of patterns attributable to habitat or seasonal effects was confirmed when the groups identified by the cluster analysis were transposed onto the plot of the MDS analysis (Fig. 3c). Although there was a gradual separation of samples from the dry to wet seasons in the plot, this trend was weak.

To clearly identify any seasonal patterns, the data sets were separated by habitat and reanalysed individually. When this was done, seasonal patterns were most obvious in catches in the lagoon (Fig. 4). Five groups of samples were produced by the cluster analysis, the first two of which contained only dry-season samples and the third consisted of a combination of both wet and dry samples. The remaining two groups contained almost entirely wet-season samples (Fig. 4a, b). Dry-

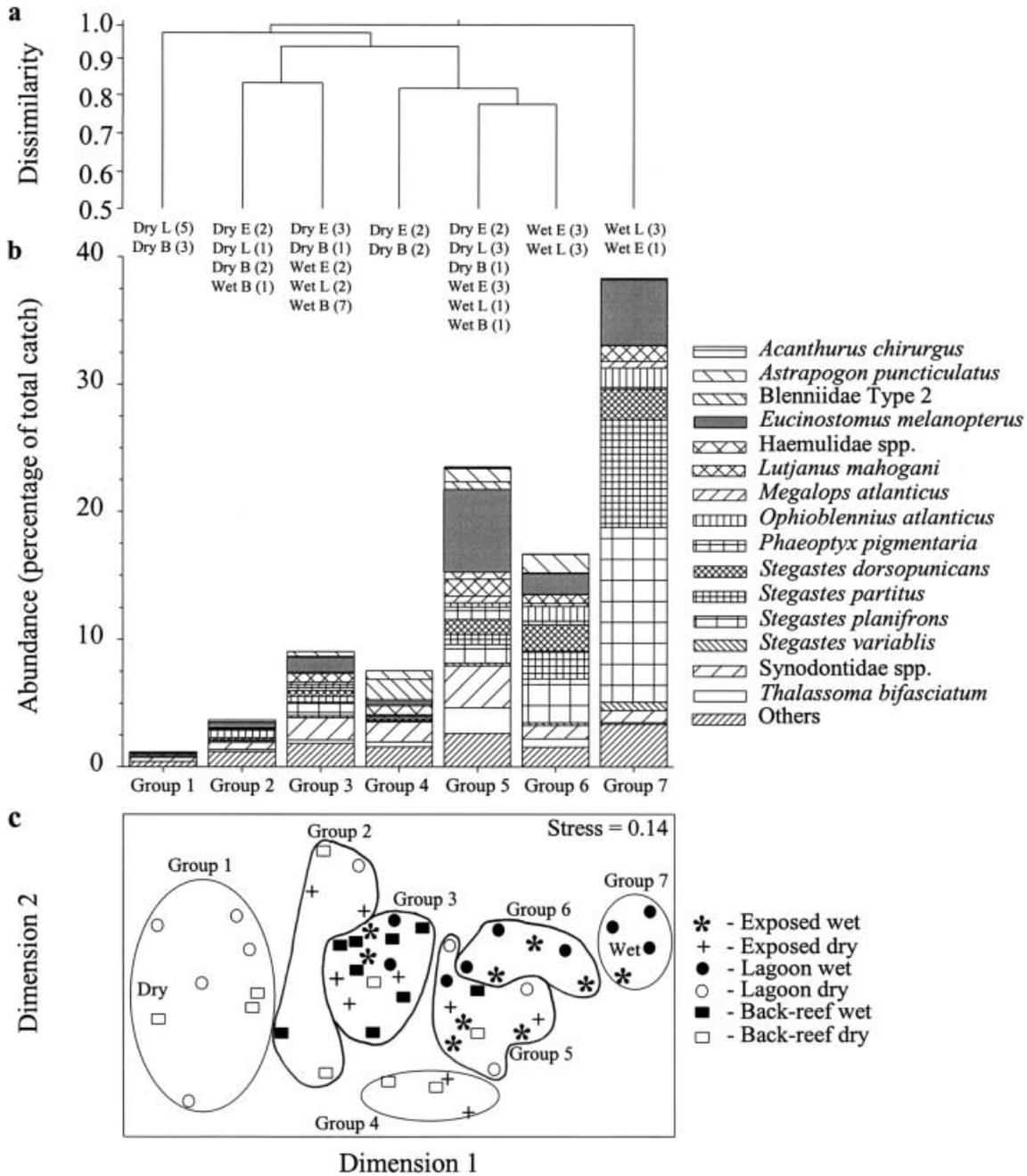


Fig. 3a–c Summary of classification and multidimensional scaling analysis on the entire data matrix. **a** Classification (UPGMA) analysis. The cluster compositions are shown as the number of wet- or dry-season samples (months) from each habitat. **b** Histogram showing the species composition for each grouping from the classification analysis, and **c** scatter plot summarising results of the multidimensional scaling analysis. Groups identified by the classification analysis are superimposed on the scatter plot

season samples composed less than 5% of the total lagoon catch and were dominated by the surgeonfish, *Acanthurus chirurgus*, and the lizardfish, *Synodontidae* spp., whereas the wet-season samples contained high abundances of *S. planifrons*, *S. partitus*, *S. dorsopunicans* and *Eucinostomus melanopterus*. Strong seasonal

differences in catches were readily identifiable in the MDS plot (Fig. 4c).

In contrast to the lagoon, the classification analysis revealed a moderately weak seasonal pattern in the data sets collected from the exposed and back-reef habitats. These are not shown here, for brevity. In the exposed habitat, this pattern was due largely to the increased level of replenishment recorded between the first and second dry seasons sampled. The lowest catches were recorded in the dry season of 1997, with dry-season samples from 1998 receiving increased replenishment. These were dominated by peak replenishment episodes for all pomacentrids. High numbers of Blenniid type 2 and *Astrapogon puncticulatus* were collected in February

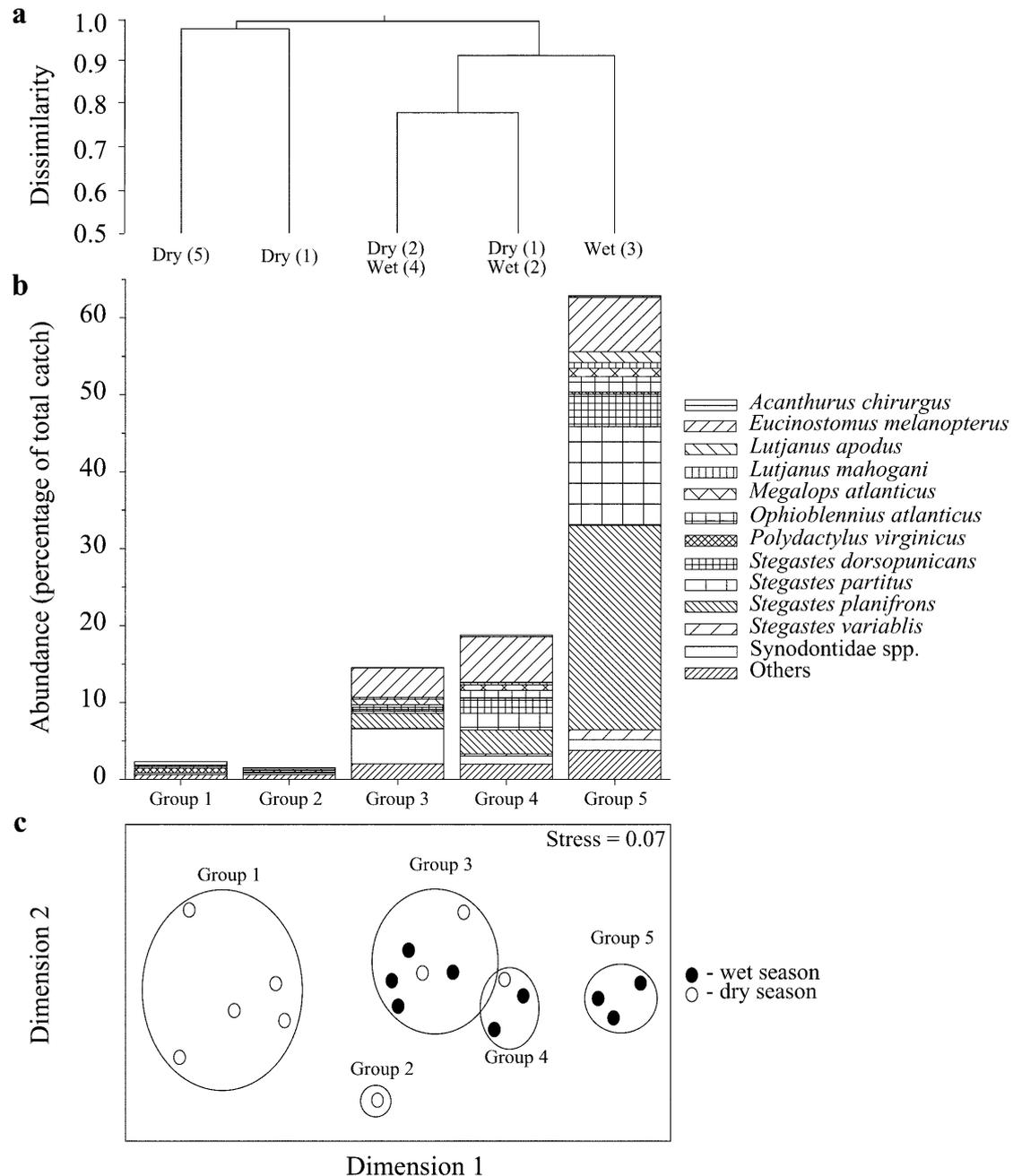


Fig. 4a-c Summary of classification and multidimensional scaling analysis on catches from the lagoon habitat; **a**, **b** and **c** are as for Fig. 3

and March 1998 and March to May 1998, respectively, with a minor peak in October–November 1998 for *A. punctulatus*. These two species were almost entirely collected in the exposed habitat (Table 1).

In the back-reef habitat, the classification and ordination analyses both produced similar results to those for the exposed habitat for the comparison between catches made during the wet and dry seasons, although this result should be treated with caution since this may be an artefact of relatively low catches in the back-reef habitat. Sporadic replenishment episodes of *E. melan-*

opterus, Synodontidae spp., Haemulidae spp., *Phaeoptyx pigmentaria* and *Thalassoma bifasciatum* were overlaid on a background of limited replenishment.

Larval-patch size (all taxa combined)

The cross-correlation analysis of nightly catches in light traps (all taxa combined) operating within each of three nearshore habitats, detected significant correlations (at a lag of 0) among all traps operating within a habitat (Table 2). Traps within the exposed habitat showed the highest levels of coherence in catches, with correlations ranging from $r=0.48$ to 0.56 (Table 2). Within-habitat correlations were consistently stronger than correlations

Table 2 Correlation coefficients (r) from the comparison of nightly catches in light traps (all taxa combined) operating in each of three nearshore habitats (*E* exposed, *L* lagoon, *BR* back reef; numbers

represent trap number; see Fig. 1b). Total length of time series 266 nights. Correlation coefficients at a lag of 0 days. n.s. non-significant result at $2 \times SE$. Within-habitat correlations in bold

Light trap	E 1	E 2	E 3	L 1	L 2	L 3	BR 1	BR 2
E 1	–	–	–	–	–	–	–	–
E 2	0.56	–	–	–	–	–	–	–
E 3	0.48	0.48	–	–	–	–	–	–
L 1	0.19	0.23	0.19	–	–	–	–	–
L 2	0.10 n.s.	0.21	0.16	0.37	–	–	–	–
L 3	0.08 n.s.	0.08 n.s.	0.14	0.35	0.23	–	–	–
BR 1	0.22	0.18	0.16	0.17	0.17	0.08 n.s.	–	–
BR 2	0.24	0.22	0.20	0.12 n.s.	0.09 n.s.	0.03 n.s.	0.46	–
BR 3	0.22	0.18	0.25	0.06 n.s.	0.15	0.09 n.s.	0.28	0.43

between traps from different habitats ($r=0.23$ to 0.56 and 0.03 to 0.25 , respectively; Table 2).

occurrence of these two taxa in catches during a few isolated events.

Species-specific variations in replenishment

Cramer values from the classification analysis were used to identify species contributing most to the groupings in the dendrograms. In order of decreasing importance these were: *S. planifrons*, *E. melanopterus*, *S. dorsopunicans*, *Lutjanus mahogani*, *S. partitus*, *L. apodus*, *O. atlanticus*, Synodontidae spp., *S. variabilis*, *Megalops atlanticus*, *P. pigmentaria* and *T. bifasciatum*. These species were also the most abundant in catches, except for *Astrapogon puncticulatus* and Blenniid type 2, which were not analysed owing to low Cramer values and the

Larval-patch composition

Time-series analysis of nightly replenishment demonstrated that, at the largest spatial scale (San Blas Point), the magnitude and timing of catches were significantly correlated at a lag of 0 among most of the 12 species, with a number of notable exceptions (Table 3). Catches of *T. bifasciatum* were poorly correlated with most other species examined except for *S. dorsopunicans* ($r=0.18$) and Synodontidae spp. ($r=0.19$). *S. planifrons* (the most abundant species in catches, $n=7,569$) failed to correlate with three other species (*E. melanopterus*, *M. atlanticus*

Table 3 Correlation coefficients (r) from the comparison of total nightly abundance among the 12 most abundant species. Total length of time series 342 nights. Correlation coefficients at a lag of 0 nights. n Number of larvae captured in light traps. n.s. Non-significant result at $2 \times SE$

Species	n	E.mel	L.apo	L.mah	M.atl	O.atl	P.pig	S.dor	S.part	S.plan	S.var	Syn
<i>Eucinostomus melanopterus</i> (E.mel)	5,682	–	–	–	–	–	–	–	–	–	–	–
<i>Lutjanus apodus</i> (L.apo)	463	0.17	–	–	–	–	–	–	–	–	–	–
<i>Lutjanus mahogani</i> (L.mah)	1,541	0.28	0.37	–	–	–	–	–	–	–	–	–
<i>Megalops atlanticus</i> (M.atl)	621	0.30	0.03n.s.	0.21	–	–	–	–	–	–	–	–
<i>Ophioblennius atlanticus</i> (O.atl)	1,414	0.14	0.35	0.30	0.12	–	–	–	–	–	–	–
<i>Phaeoptyx pigmentaria</i> (P.pig)	739	0.15	0.22	0.16	0.17	0.02n.s.	–	–	–	–	–	–
<i>Stegastes dorsopunicans</i> (S.dor)	2,419	0.22	0.28	0.37	0.26	0.33	0.20	–	–	–	–	–
<i>Stegastes partitus</i> (S.part)	4,651	0.16	0.46	0.43	0.24	0.49	0.04n.s.	0.53	–	–	–	–
<i>Stegastes planifrons</i> (S.plan)	7,569	0.06n.s.	0.32	0.30	0.10n.s.	0.25	0.02n.s.	0.41	0.50	–	–	–
<i>Stegastes variabilis</i> (S.var)	500	0.10n.s.	0.38	0.28	0.14	0.22	0.31	0.35	0.27	0.31	–	–
Synodontidae spp. (Syn)	3,526	0.19	0.14	0.21	0.15	0.20	0.10n.s.	0.19	0.24	0.23	0.16	–
<i>Thalassoma bifasciatum</i> (T.bif)	1,361	0.10n.s.	0.01n.s.	0.01n.s.	0.04n.s.	0.01n.s.	0.10n.s.	0.18	0.07n.s.	0.07n.s.	0.05n.s.	0.19

and *P. pigmentaria*) (Table 3). The strongest correlations occurred among catches of the four species of pomacentrid ($r=0.27$ to 0.53 ; Table 3). Time series of catches for the eight most abundant species in each of the three habitats are shown in Figs. 5, 6, 7, and 8 (only eight species are shown for brevity). Nightly time series of abundance of pre-settlement reef fishes for individual light traps indicated that, although catches varied widely among nights, there were consistent patterns in catches among traps operating in each habitat (Figs. 5, 6, 7, and 8). All species were characterised by large, sporadic peaks in abundance against a background of low, often continuous supply. With the exception of *L. apodus*, some individuals of all species were captured in nearly all months of sampling.

Variations in larval abundance between seasons and among habitats

The gerrid, *E. melanopterus*, was collected in significantly greater numbers in the wet season than in the dry season, as determined by non-parametric analysis (Table 4). Comparison of catches among habitats showed that traps operating in the lagoon collected greater numbers of this species than the back-reef habitat (Table 4). Catches in the exposed habitat could not be differentiated from the lagoon and back-reef habitats by the multiple-comparison tests. However, Table 1 indicates that catches in this habitat were less than those of the lagoon habitat but greater than those of the back-reef habitat. There were weak but significant correlations among catches of *E. melanopterus* in all three habitats determined using time-series analysis (Table 5). Comparison of time series showed that this was a result of several peaks in catches recorded in a

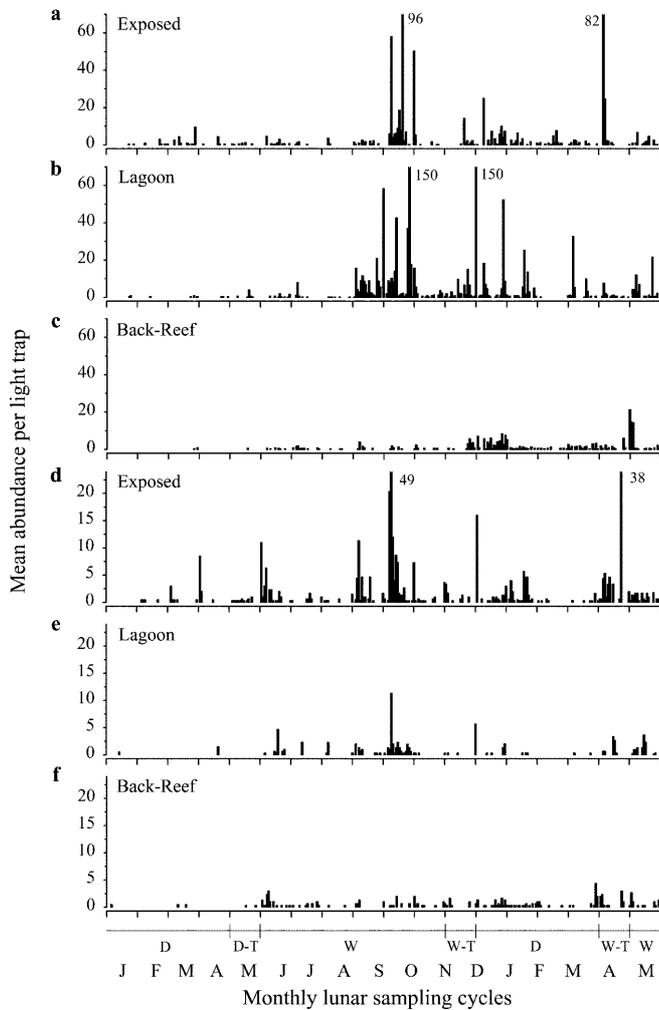


Fig. 5a-f Nightly time series of mean larval abundance collected by light traps in each of three sampling habitats (exposed, lagoon and back-reef). **a-c** *Eucinostomus melanopterus*, and **d-f** *Lutjanus mahogani*. Position of calendar months in relation to the concatenated lunar sampling cycles of 19 consecutive nights for each month (segments on horizontal axis) are shown. *D* Dry season, *W* wet season and *T* transitional months. Time series from 31 December 1996 to 3 June 1998 (342 nights)

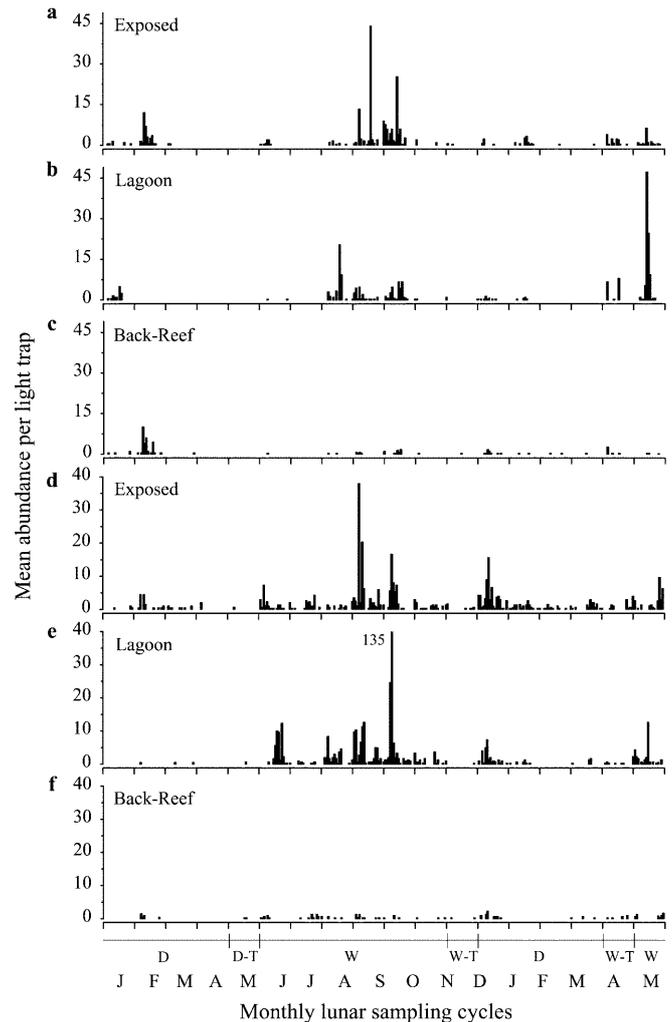


Fig. 6a-f Nightly time series of mean larval abundance collected by light traps in each of three sampling habitats for **a-c** *Ophioblennius atlanticus* and **d-f** *Stegastes dorsopunicans* shown as for Fig. 5

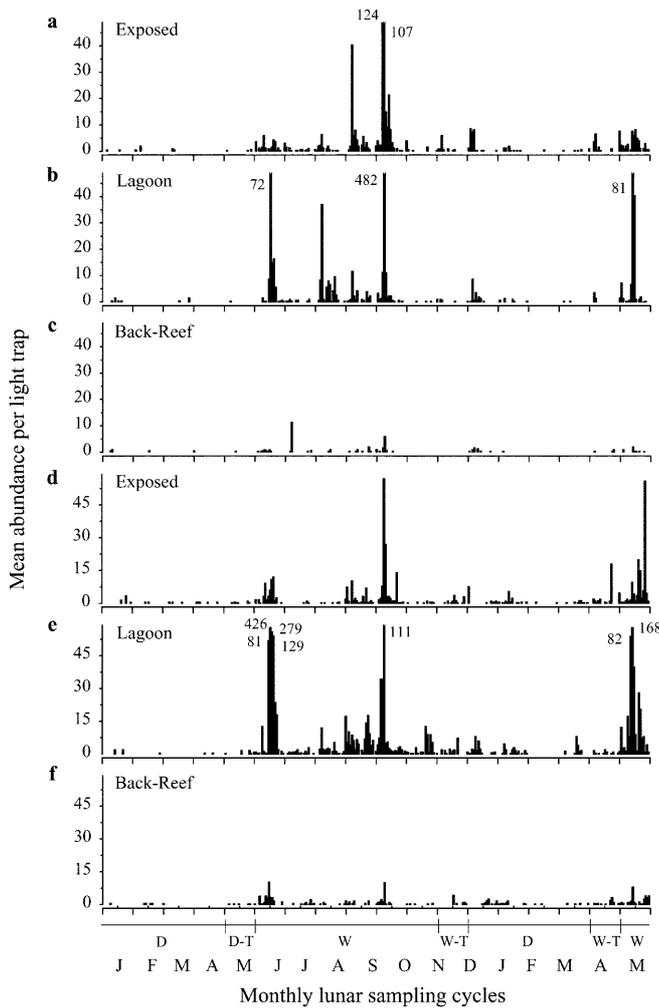


Fig. 7a–f Nightly time series of mean larval abundance collected by light traps in each of three sampling habitats for **a–c** *Stegastes partitus* and **d–f** *S. planifrons* shown as for Fig. 5

single habitat (Fig. 5a–c). For example, there was a broad peak in abundance during September and October of 1997 in exposed and lagoon habitats that was not evident in the catches in the back-reef habitat (Fig. 5a–c). Additionally, a peak in catches during April 1998 was only recorded in the exposed habitat. Times-series analysis of individual light-trap catches found that the strongest correlations were among light traps operating within a habitat, with the highest in the exposed habitat ($r=0.31$ – 0.36 ; Table 6). Correlations among traps from different habitats were often weak or non-significant (Table 6).

The majority of individuals of *L. apodus* arrived in only two months of sampling during the wet season (Table 4) in exposed and lagoon habitats (Table 1). Low catches throughout the remaining sampling period prevented the identification of any habitat differences (Table 4). While catches were correlated among habitats (Table 5), this was largely due to limited catches in all but two lunar months and should therefore be treated with caution. Correlations among individual light traps

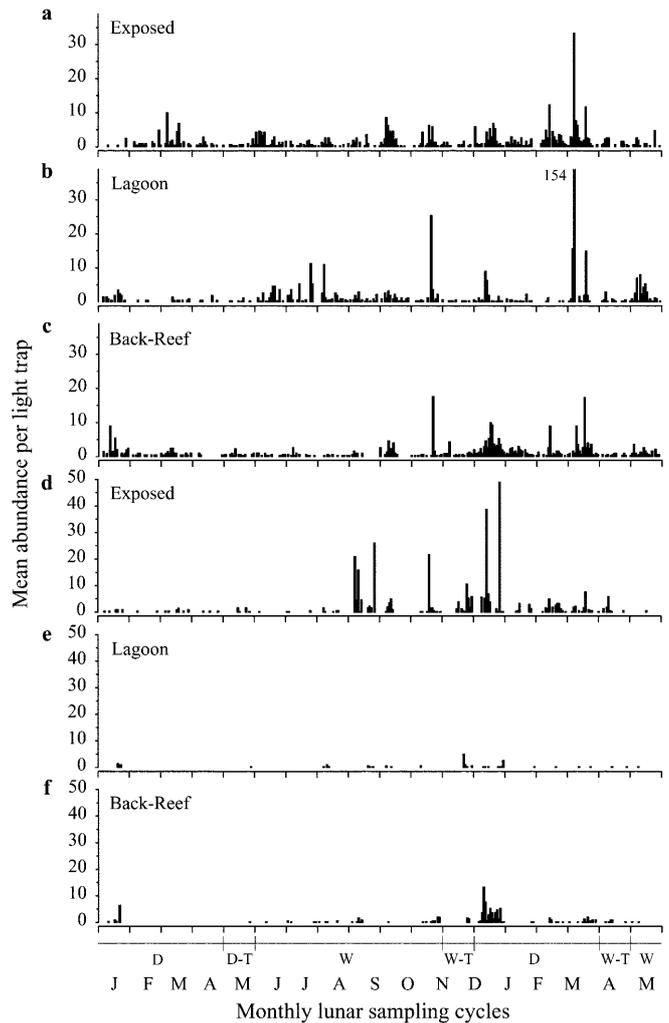


Fig. 8a–f Nightly time series of mean larval abundance collected by light traps in each of three sampling habitats for **a–c** Synodontidae spp. and **d–f** *Thalassoma bifasciatum* shown as for Fig. 5

over the study period revealed a similar pattern to *E. melanopterus*, with strongest correlations among traps operating within each of the exposed and lagoon habitats (Table 6).

Catches of *L. mahogani* were recorded in greater numbers in the wet season (Table 4), although small numbers of this species were collected year-round in all habitats (Fig. 5d–f). Light traps operating in the exposed habitat during wet and dry seasons collected more larvae than in either the lagoon or the back-reef (Table 4). Catches in the exposed habitat were significantly correlated with those in the lagoon and back-reef habitats (Table 5), although catches in the lagoon were not correlated with back-reef catches (Table 5). Correlations among individual light traps were strongest in the exposed habitat ($r=0.36$ – 0.43 ; Table 6).

M. atlanticus were captured in greater numbers in the lagoon habitat during the wet season (Table 4). Lagoon catches were significantly correlated with catches in the back-reef, but not the exposed habitat (Table 5), due

Table 4 Temporal and spatial comparison of larval abundance collected in light traps. Kruskal-Wallis (*H*) statistics shown for each of 12 species identified by Cramer values as contributing most to the classification analysis (also the most abundant). Tukey-type

multiple comparison *q* statistics are shown for habitat comparisons found to be significant. *E* Exposed, *L* lagoon, *BR* back-reef. All *q* statistics are significant at $P < 0.01$ unless indicated by n.s. (non-significant)

Species	Seasonal comparison			Habitat comparison					
	<i>H</i>	<i>P</i>	Difference	<i>H</i>	<i>P</i>	E vs L <i>q</i>	E vs BR <i>q</i>	L vs BR <i>q</i>	Site differences
<i>Eucinostomus melanopterus</i>	7.584	0.006	Wet > Dry	13.313	0.001	2.4190	2.1905	4.6095	L > BR
<i>Lutjanus apodus</i>	88.363	<0.001	Wet > Dry	0.114	0.944	n.s.	n.s.	n.s.	n.s.
<i>Lutjanus mahogani</i>	43.135	<0.001	Wet > Dry	55.680	<0.001	8.4477	5.6480	2.7997	E > L, BR
<i>Megalops atlanticus</i>	17.162	<0.001	Wet > Dry	149.898	<0.001	10.7310	2.4389	8.3001	L > E, BR
<i>Ophioblennius atlanticus</i>	20.426	<0.001	Wet > Dry	20.048	<0.001	1.9490	4.4348	2.4857	E > BR
<i>Phaeoptyx pigmentaria</i>	1.760	0.185	Wet = Dry	61.541	<0.001	7.2469	4.5914	2.6555	E > L, BR
<i>Stegastes dorsopunicans</i>	69.622	<0.001	Wet > Dry	92.747	<0.001	4.1957	11.3316	7.1358	E > L > BR
<i>Stegastes partitus</i>	138.730	<0.001	Wet > Dry	61.690	<0.001	2.6574	8.5425	5.8851	E, L > BR
<i>Stegastes planifrons</i>	167.014	<0.001	Wet > Dry	40.868	<0.001	4.1533	3.9380	8.0913	L > E > BR
<i>Stegastes variabilis</i>	6.538	0.011	Wet > Dry	5.118	0.077	n.s.	n.s.	n.s.	n.s.
Synodontidae spp.	0.077	0.781	Wet = Dry	21.605	<0.001	6.2034	1.8908	4.3112	E, BR > L
<i>Thalassoma bifasciatum</i>	1.145	0.285	Wet = Dry	57.760	<0.001	7.5153	3.894	3.6210	E > BR > L

largely to the limited number of individuals caught in the exposed habitat (Table 1). Individual light-trap catches were most strongly correlated in the lagoon habitat ($r = 0.28$ to 0.39 ; Table 6), with strong correlations also found for catches among the back-reef traps ($r = 0.25$ – 0.30). There were no significant correlations with traps operating in the exposed habitat (Table 6).

Most *O. atlanticus* were captured in the exposed habitat during the wet-season months from August to October in 1997 (Fig. 6a–c, Table 4). Other peaks in catches occurred during February 1997 in exposed and back-reef habitats and during May 1998 in the lagoon (Fig. 6a–c). Catches in the lagoon were similar to those in the exposed habitat (Table 1) but were not distinguished from the back-reef habitat by multiple comparisons (Table 4). These peaks resulted in the significant correlations identified among habitats (Table 5), although these results should be treated with caution, owing to the few sporadic appearances of this species in light traps. This was reflected in correlations among individual light traps, with highest correlations among traps operating in the same habitat, except for traps B1 and E1 ($r = 0.40$; Table 6).

In contrast, *P. pigmentaria* were collected equally in both wet and dry seasons over the duration of the study (Table 4). Most individuals of this species were collected in the exposed habitat (Tables 1, 4). Correlations among habitats were weak or non-significant (Table 5), due to the sporadic appearance of this species in catches. This pattern was also found among individual light trap catches operating in each habitat, with traps within the exposed habitat most strongly correlated ($r = 0.18$ to 0.38 ; Table 6).

The pomacentrids, *S. dorsopunicans*, *S. partitus*, *S. planifrons* and *S. variabilis* displayed similar patterns

of catches. Peak catches of these species were recorded in the lagoon and exposed habitats during the wet season with the exception of *S. variabilis*, which was collected in similar numbers in all three sampling habitats (Table 4). Catches of *S. dorsopunicans*, *S. partitus* and *S. planifrons* were correlated among all three habitats (Table 5) and displayed large peaks in abundance over brief periods of only a few nights of sampling (Figs. 6d–f, 7a–f). Catches of *S. variabilis* were only correlated between the exposed and lagoon habitats (Table 5). Correlations among individual light traps operating within each habitat were found to be the strongest, although there were a number of strong correlations among traps from different habitats (Table 6).

Synodontidae spp. were collected equally in wet and dry seasons during the study (Fig. 8a–c, Table 4). Additionally, catches separated by habitat were considerably larger in the exposed and back-reef habitats than in the lagoon (Table 4). Consistent catches of this species were punctuated by single nights of high abundances (Fig. 8a–c). Catches were correlated among all three habitats due to the consistent replenishment of settlement-stage larvae (Fig. 8a–c, Table 5). Light traps operating within each habitat were strongly correlated, with weaker correlations found among traps from different habitats (Table 6).

Individuals of *T. bifasciatum* were collected equally in both the wet and dry seasons (Fig. 8d–f, Table 4). Catches were greatest in the exposed habitat and lowest in the lagoon habitat (Table 4). Comparison of time series of catches from each habitat found significant correlations between the exposed and back-reef habitats (Table 5). Catches of this species were highly sporadic, with peaks in abundance between September 1997 and April 1998 (Fig. 8d–f). Light traps operating within each

Table 5 Correlation coefficients (r) from the comparison of average nightly catches among exposed, lagoon and back-reef habitats. Total length of time series 342 nights. Values are calculated when replenishment is lagged (LAG) by -1, 0 and +1 nights. *Exp* Exposed; *Lag* lagoon; *BR* back-reef

Taxa	Habitat combinations	LAG		
		-1	0	+1
All taxa combined	Exp×Lag	0.09	0.22*	0.13*
	Exp×BR	0.14*	0.30*	0.06
	Lag×BR	0.13*	0.19*	-0.01
<i>Eucinostomus melanopterus</i>	Exp×Lag	0.07	0.15*	0.04
	Exp×BR	0.10	0.17*	-0.02
	Lag×BR	0.15*	0.03	0.05
<i>Lutjanus apodus</i>	Exp×Lag	-0.09	0.30*	0.17*
	Exp×BR	-0.15	0.23*	0.18*
	Lag×BR	-0.06	0.33*	0.25*
<i>Lutjanus mahogani</i>	Exp×Lag	0.19*	0.20*	0.13
	Exp×BR	0.05	0.28*	0.03
	Lag×BR	-0.02	0.02	0.05
<i>Megalops atlanticus</i>	Exp×Lag	-0.04	0.04	-0.02
	Exp×BR	-0.01	0.01	-0.01
	Lag×BR	0.39*	0.32*	0.12*
<i>Ophioblennius atlanticus</i>	Exp×Lag	0.12	0.28*	0.02
	Exp×BR	0.10	0.37*	0.18*
	Lag×BR	0.04	0.18*	0.04
<i>Phaeoptyx pigmentaria</i>	Exp×Lag	-0.01	-0.01	-0.06
	Exp×BR	0.09	0.12*	-0.03
	Lag×BR	-0.03	0.01	0.01
<i>Stegastes dorsopunicans</i>	Exp×Lag	0.11	0.27*	0.13
	Exp×BR	0.14*	0.30*	-0.01
	Lag×BR	0.18*	0.09	-0.08
<i>Stegastes partitus</i>	Exp×Lag	0.16*	0.44*	0.14*
	Exp×BR	0.24*	0.18*	-0.09
	Lag×BR	0.30*	0.27*	-0.03
<i>Stegastes planifrons</i>	Exp×Lag	0.06	0.17*	0.23*
	Exp×BR	0.07	0.33*	0.26*
	Lag×BR	0.08	0.30*	0.07
<i>Stegastes variabilis</i>	Exp×Lag	0.06	0.24*	-0.06
	Exp×BR	-0.06	0.06	0.10
	Lag×BR	-0.02	-0.01	0.08
Synodontidae spp.	Exp×Lag	0.10	0.29*	0.24*
	Exp×BR	0.18*	0.21*	0.12
	Lag×BR	0.22*	0.10	0.10
<i>Thalassoma bifasciatum</i>	Exp×Lag	0.02	0.05	0.08
	Exp×BR	0.07	0.26*	0.03
	Lag×BR	0.04	0.01	0.01

* Significant at 2×SE

habitat were strongly correlated, with a number of significant correlations also recorded among traps from the exposed and back-reef habitats (Table 6).

Discussion

Light traps collected representatives of 44 families of reef fishes from the San Blas Archipelago, western Caribbean. Although the taxonomic diversity of fish assemblages in the Caribbean is only one quarter of that of the Indo-Pacific (Lieske and Myers 1996), my study compares favorably with other long-term studies using light traps on the GBR, such as those of Milicich (1992) and Thorrold (1992), in which 24 and 38 families were collected, respectively. These two studies from the GBR were conducted over three summer replenishment seasons. Reasons for such disproportionate catches are uncertain; however, the duration of the replenishment seasons in each locality, coupled with the continuity of sampling in each region, may play an

important role. In San Blas, replenishment is known to occur throughout the year (Robertson 1992), and my sampling programme was designed to document this process. In contrast, on the GBR, the replenishment season lasts for only a few months. Thus, trapping studies operating on the GBR have a relatively short period in which to sample the available diversity of replenishing larvae. Long-term sampling in the Caribbean will result in the collection of a greater diversity of taxa, purely as a result of the duration of replenishment episodes.

In the three geographic regions where light traps have been used to sample pre-settlement fishes (GBR: Milicich and Doherty 1994; Thorrold and Williams 1996; Gulf of California: Brogan 1994; Caribbean: Sponaugle and Cowen 1996a, b, 1997; Hendriks et al. 2001), pomacentrids and blenniids have been an important and abundant component of catches. It has been suggested that this may be due to a strong photopositive response by fishes of these families (Choat et al. 1993). Furthermore, the pelagic stages of pomacentrids and blenniids

are known to reside in surface waters during their planktonic larval stage (Leis 1991; Doherty and Carlton 1997) where light traps are usually deployed. Pomacentrids and blenniids also make up a large portion of the adult reef-fish assemblage both in the Caribbean and on the GBR (Williams and Sale 1981; Robertson et al. 1993) and are likely to be reflected in any study measuring larval abundance.

Gobiids have previously been collected in high numbers in light traps on the GBR, but are only caught in relatively low numbers in the Caribbean at Barbados (Sponaugle and Cowen 1996b) and in the San Blas Archipelago (Table 1). However, studies using different sampling techniques, such as dip-netting in very shallow water (Dennis et al. 1991; Victor 1991), have collected gobiids in high numbers in the Caribbean. Hendriks et al. (2001) collected a large number of gobiids in a single light trap operating in very shallow water (1–2 m) at the same location as Victor's (1991) dip-netting study, and also by traps operating in deep water (20 m). This deep-water preference, coupled with the abundance of gobiid larvae in shallow (<1 m) settlement habitats, suggests that the lack of gobiids collected in the current study is probably due to the behaviour of pre-settlement fish rather than the sampling technique. For example, gobiid larvae reside in predominantly deeper water as they approach the reef (Hendriks et al. 2001), then move up the substratum into suitable settlement habitats, thereby avoiding capture in surface traps set over deep water.

Another notable difference between light-trap catches in San Blas and on the GBR was the abundance of lutjanids and labrids. In San Blas, lutjanids made up 6.61% of the total catch while labrids comprised 4.58%, with *Lutjanus mahogani* and *Thalassoma bifasciatum* making up approximately half and three-quarters of the total catch of these families, respectively. On the GBR, lutjanids and labrids are rarely caught in light traps, although they make up a significant portion of adult assemblages of reef fishes (Williams and Sale 1981). Such patterns may be due to regional differences in the response of larvae to light that render these taxa less susceptible to capture on the GBR. Alternatively, it is possible that these families inhabit different depth strata on the GBR, and thus are not collected by surface traps. Sponaugle and Cowen (1996b) also failed to detect significant numbers of lutjanid and labrid larvae in Barbados; however, this may have been due either to a recruitment failure or to their restricted sampling period from March to May, since recruitment of most species at this locality appears to peak between the months of May to November (Tupper and Hunte 1994).

One other family that was captured in relatively high numbers in light traps in San Blas, but has only been occasionally recorded in catches on the GBR, was the gerrid, *Eucinostomus melanopterus*. This species comprised 9.22% of the total larval catch collected by light traps in San Blas. The abundance of this species may be explained by the proximity of extensive mangrove habitats close to the sampling sites in San Blas. These areas

are known to act as a nursery for this species prior to its migration into adult habitats of sand and seagrass within the reef lagoon (D. R. Robertson, personal communication). On the GBR, most trapping studies have been carried out in localities remote from coastal areas, so have not sampled appropriate habitats for the capture of fish of this family.

Continuous monitoring of replenishment for two lunar phases revealed that a high percentage (91%) of larvae captured during this period were collected within 19 consecutive nights centred on the new moon (Fig. 2). This pattern of lunar replenishment is similar to those described by Robertson (1992), who obtained settlement patterns from daily collections on small isolated patch reefs over 28 consecutive lunar months of sampling. For many of these species, lunar patterns probably result from comparable cycles in the production of larvae at this locality (Robertson et al. 1988, 1990). This pattern is suggested to have evolved in larvae with deterministic larval durations to maximise the abundance of similarly aged larvae arriving in benthic habitats during lunar periods that are favourable for survival (the settlement-linkage hypothesis, reviewed in Robertson et al. 1990). Thus, synchronous spawning and subsequent replenishment episodes will maximise the changes of at least some individuals from each lunar cohort surviving the transition from pelagic larvae to benthic juveniles (Robertson et al. 1990).

Sampling using light traps for 18 months supported the observation that replenishment generally occurs throughout the year in San Blas (Figs. 5, 6, 7, 8). Robertson et al. (1993) monitored the abundances of six species of newly settled damselfishes at monthly intervals for 7–10 years on small isolated patch reefs in San Blas. In their study, recruitment occurred in nearly all months of sampling, although species-specific peaks in recruitment were identified. In a similar study conducted over 11 years, Robertson et al. (1999) determined that recruitment of the wrasse, *T. bifasciatum*, was continuous. This pattern appears to be driven by seasonally extended or year-round spawning and may be unique to warm equatorial waters. In intermediate and higher tropical latitudes, spawning and recruitment are invariably seasonal, owing largely to fluctuating seawater temperatures.

Despite continuous replenishment of the reefs of San Blas in the present study, catches of most species peaked in certain months of the year (Figs. 5, 6, 7, 8; D. Wilson, unpublished data). Large, sporadic peaks in catches occurred at daily intervals that were superimposed on annual and seasonal patterns of replenishment of these species (Figs. 5, 6, 7, 8). Robertson et al. (1993) monitored the monthly spawning and recruitment levels of six species of Caribbean damselfish in San Blas for 1–3 years and found that intermensual variation in recruitment strength far exceeded the corresponding variation in spawning output. They suggested that the magnitude of recruitment was largely determined in the plankton. Similarly, in an earlier study, Robertson

sensory stimuli, including visual, auditory and chemical cues. Which of these is the most important is unknown, although the precise cue, or combination of cues, is likely to differ among species. Kingsford et al. (1991) suggested that some pre-settlement fishes may use chemical cues in order to avoid lagoon habitats on the GBR. Fishes in San Blas may also use such cues; however, in the present study, they may be used to enhance rather than reduce settlement in these habitats.

In conclusion, spatial and temporal patterns of replenishment were systematic at the habitat level for individual taxa, with many taxa preferentially replenishing particular habitats. Meso-scale (hundreds of metres) patches of larvae were multi-specific in composition in nearshore waters, with peak abundance occurring during the wet-season months for many species. By directly measuring the supply of immediate pre-settlement reef fishes in nearshore waters, the processes that influence replenishment events, such as transport mechanisms and environmental fluctuations of wind, rainfall and temperature, can be determined. Environmentally induced replenishment events are currently poorly studied; however, they are crucial to an understanding of coral-reef fish replenishment.

Acknowledgments I would like to thank M. Meekan, M. McCormick, S. Sponaugle and I. Suthers for comments on drafts of the manuscript. Logistic support was provided by the Department of Marine Biology (JCU), Australian Institute of Marine Science and the Smithsonian Tropical Research Institute, Panama. R. Robertson and P. Doherty provided helpful advice and project support. Field assistance was provided by M. Wilson, I. Hendriks, E. Vytöpil, E. Pena, M. Griffin, U. Anlauf, M. MacKenzie and the STRI, MESP team. Statistical advice was provided by J. Carleton and J. McIlwain. This research was funded by an Australian Post-graduate Research Award, Doctoral Merit Research Scheme (JCU), Merit Research Awards (JCU), STRI fellowship, STRI Research Opportunity Funds and a grant from the National Geographic Society of America (NGS no. 5395-94). I thank the Kuna General Congress and the government of the Republic of Panama for permitting fieldwork in the San Blas region.

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