Advantages of using crest nets to sample presettlement larvae of reef fishes in the Caribbean Sea

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Identifying the spatial and temporal patterns of larval fish supply and settlement is a key step in understanding the connectivity of meta-populations (Sale et al., 2005). Because of the potentially dispersive nature of the pelagic larval phase of most reef fishes, tracking cohorts from hatching to settlement is extremely difficult (but see Jones et al., 1999). However, for many studies it is sufficient to sample larvae immediately before settlement. Many coral reef fish species use mangrove and seagrass beds as nursery habitats (Nagelkerken et al., 2001; Mumby et al., 2004) and larvae of these species must pass over the reef crest in order to arrive at their preferred settlement habitats. The ability to sample this new cohort of larval fishes provides opportunities for researchers to explore the intricacies of the transition from larva to juvenile (Searcy and Sponaugle, 2001). Quantifying the potential settlers also provides valuable information about the spatial and temporal supply of presettlement larvae (Victor, 1986). Therefore a number of larval sampling methods were developed, one of which is the use of crest nets (Dufour and Galzin, 1993).

Crest nets are rigid-frame tapering nets that are fixed to the substrate in shallow water immediately behind the crest of the reef (see Doherty and McIlwain, 1996 for full description). The top of the crest net is above the surface of the water and currents and wave action force larvae into the mouth of the net. Because of the turbulence of the water coming over the reef crest and the fact that the whole water column is filtered, net avoidance by larval fishes is estimated to be minimal. Channel nets (Shenker et al., 1993) and light traps (Doherty, 1987), on the other hand, remain the dominant methods for sampling settlement-stage larval fishes on western Atlantic reefs. Surface channel nets are floating nets that are free to swivel with the prevailing current. Where crest nets are positioned in the shallow back reef, channel nets are positioned in deeper channels between mangroves, further away from the reef. Crest nets have been widely used in the Pacific Ocean to quantify the larval abundance of coral reef fishes immediately before settlement (Leis et al., 1998; Dufour et al., 2002; Leis et al., 2003; McIlwain, 2003; Lecchini et al., 2004). Despite the apparent success of sampling reef fishes in the Pacific Ocean with crest nets, there are currently no reports of crest nets being employed for sampling reef fishes in the Caribbean Sea. The first objective of this study was to simultaneously deploy crest and channel nets to compare the abun-dance and species richness of larval fishes sampled. It was hypothesized that crest nets would capture more larvae by sampling the whole water column on the reef crest as opposed to channel nets that sample only surface waters.

Larval reef fish possess impressive swimming capabilities (Leis and Carson-Ewart, 1997) and have the ability to detect reefs at a distance (Myrberg and Fuiman, 2002) and can therefore influence their own dispersal. However, many other abiotic factors can still influence their growth, survival, transport, and eventual arrival at a suitable settlement habitat. The abundance of larvae present is related to lunar period in some areas (Robertson et al., 1988, Thorrold et al., 1994; Sponaugle and Cowen, 1996), but this abundance is not fully correlated with peaks in abundance in other areas (Kingsford and Finn, 1997). Larval growth rates and swimming ability vary with water temperature in some species (Green and Fisher, 2004) and winds can alter the strength and direction of supplying currents. The second objective of this study was to explore correlations between certain abiotic factors (lunar phase, water temperature, and prevailing wind) and the number of species and individuals collected by each net type.

Materials and methods

Study site

Fieldwork was conducted at Turneffe Atoll, Belize (17°16′5″N, 87°48′57″W, Fig. 1A). Turneffe Atoll is part of the Meso-American Barrier Reef System (MBRS) that runs along southern Mexico through the waters of Belize, Guatemala, and Honduras. The MBRS is the world's second largest coral reef system after the Great Bar-
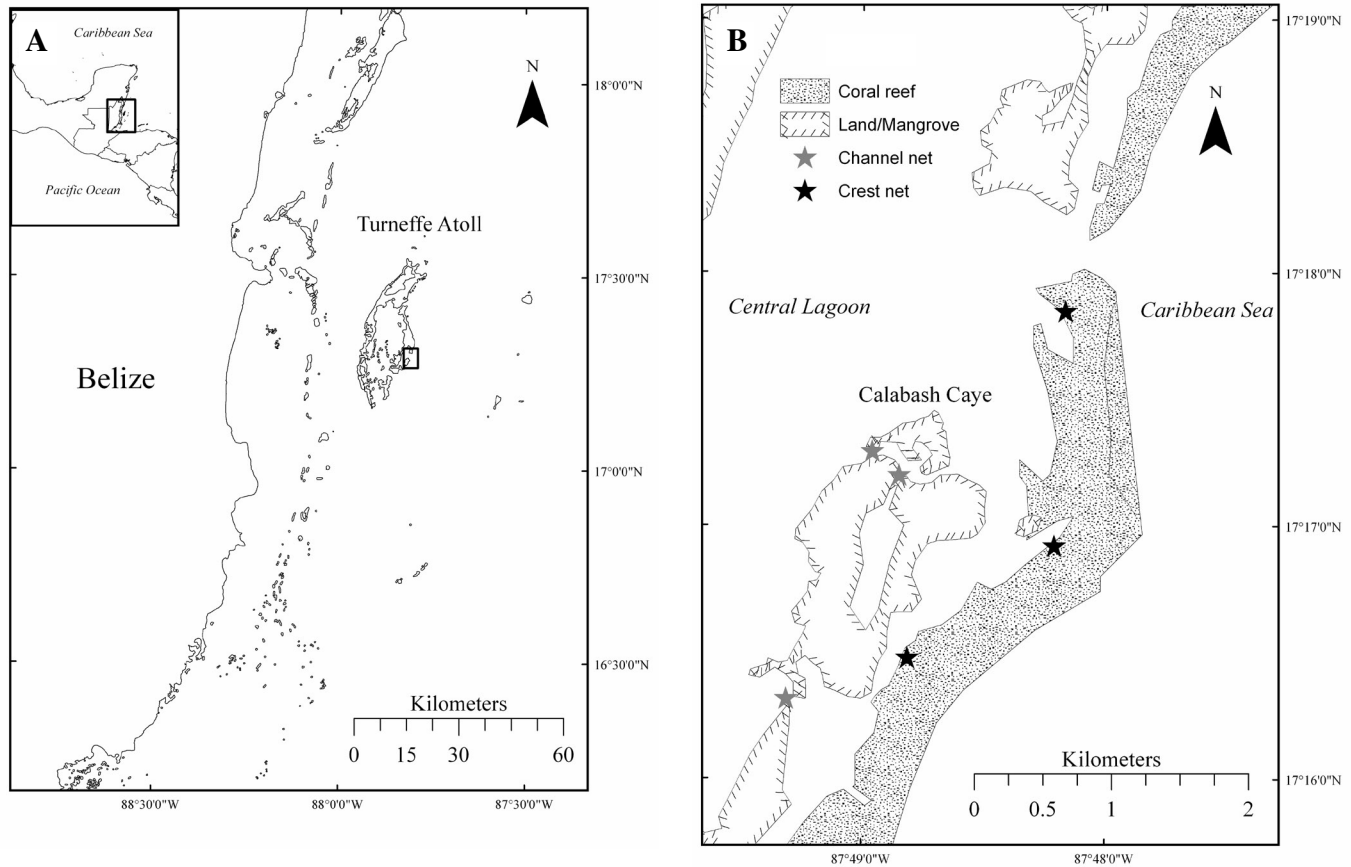
Figure 1

Maps indicating the position of Turneffe Atoll, Belize (**A**) and the positions of crest and channel nets around Calabash Caye (**B**). The inset in map A indicates the position of Belize in Central America and the rectangle around Turneffe Atoll specifies the area enlarged in map B.

rier Reef in Australia. Turneffe Atoll is a large offshore ring of islands bordered by coral reefs. It has a large central lagoon that contains many mangrove islands and channels. The atoll is located outside the coastal barrier reef, approximately 46 km west of mainland Belize (Fig. 1A).

Larval collection and identification

The definnition of "larva" will follow that of Leis (2006): the posthatching pelagic life history stage of demersal fishes (which is equivalent to the presettlement stage of Kingsford and Milicich, 1987). Larvae were sampled with crest nets and channel nets from 6 July to 26 August 2005, 24 January to 4 March 2006, and 17 May to 28 July 2006. One crest net was positioned in shallow water directly behind the reef crest in each of three sites approximately 1 km apart (Fig. 1B). The crest nets had a mean width of 5.85 m, a mesh size of 2 mm, and were situated in 65–90 cm of water at each site. One surface channel net (Shenker et al., 1993) was placed in each of three separate mangrove channels leading to the central lagoon, each net with a square mouth (2 m × 1 m) with 1.6-mm mesh. It was not our intent to optimize the per-

formance of either net. Therefore, although there were differences in net cross-sectional area, mesh sizes, and placement locations between crest and channel nets, these differences represent how each net has been typically deployed.

In preliminary sampling at Turneffe Atoll, near zero or zero catches occurred during daylight hours, which was consistent with the findings of Shenker et al. (1993). Therefore, collections were made only at night. Both types of nets were deployed nightly and the catch was retrieved and identified each morning. All individuals of all species of larval reef fishes were counted each day. Where species could not be determined, the lowest taxonomic category that could be unambiguously determined was used. Larvae were examined live and identified (Humann and DeLoach, 2002; Richards, 2005). Over the course of the study a number of specimens of all species were preserved in 95% ethanol for later validation.

Environmental variables

Mechanical flowmeters (model 2030R6, General Oceanics, Inc., Miami, FL) were deployed with each net. These

meters are equipped with a high-resolution rotor for low-speed flow and had a minimum threshold of approximately 6 cm/sec. The mean nightly measurement of flow was used to calculate the total volume of water filtered by each net. Underwater temperature loggers (Hobo Pendant Temperature Logger, Onset Computer Corp., Bourne, MA) provided a fine-scale record of the temperature of water being sampled (temperature data were not available for 2005). Wind speed and wind direction data were obtained from an automated weather station at Belize City International airport (17°53′N, 88°30′W). These wind reports provided a reasonable record of prevailing conditions at Turneffe Atoll because of the proximity and lack of geographic obstacles between the two points. The mean nightly wind direction was given a positive value for an on-shore wind and a negative value for an off-shore wind. Finally, a variable incorporating both the nocturnal illumination and tidal periodicity of the lunar cycle was calculated (see D'Alessandro et al., 2007). The hours of nocturnal flood tides were calculated for each sampling night with tide prediction software (JTide, vers. 5.1, P. Lutus, freeware software available online) and this number was multiplied by the percentage of the moon that was visible (full moon=100%).

Statistical analyses

Species-environment ordinations (CANOCO, vers. 4.5, Microcomputer Power, Ithaca, NY) were used to establish the relative importance of individual environmental factors (sampling season, wind, water temperature, and nocturnal flood tides) in explaining the overall variance in larval abundance and species richness in the catch. The species and environmental data were found to be linear and were examined by redundancy analysis (RDA). An RDA plot shows the best fit of multivariate data in a two-dimensional ordination.

The temporal supply of fish larvae was investigated by using correlation plots and circular statistics (Rayleigh z; Zar, 1984). Cross-correlation plots were used to compare the timing of the capture of larvae in the two different environments, namely behind the reef crest where crest nets were used and the mangrove channels where channel nets were used. Once both net types were shown to collect larvae synchronously (see *Results*), the data for both nets were combined into a single time series. Auto-correlations were then plotted to examine the temporal periodicity of the catch. To achieve this, all three sampling periods were concatenated into a continuous time series to ensure that more than 2.5 continuous lunar cycles were included (the minimum necessary for auto-correlation analysis for an examination of lunar periodicity). Each day was assigned a number corresponding to its point in the lunar cycle (lunar days 1–29, 1=new moon). To ensure that the cycles were continuous, any overlapping lunar days between the sampling periods were deleted (from the middle period, spring 2006). The final time-series had 164 days, from which 14 overlapping days were deleted.
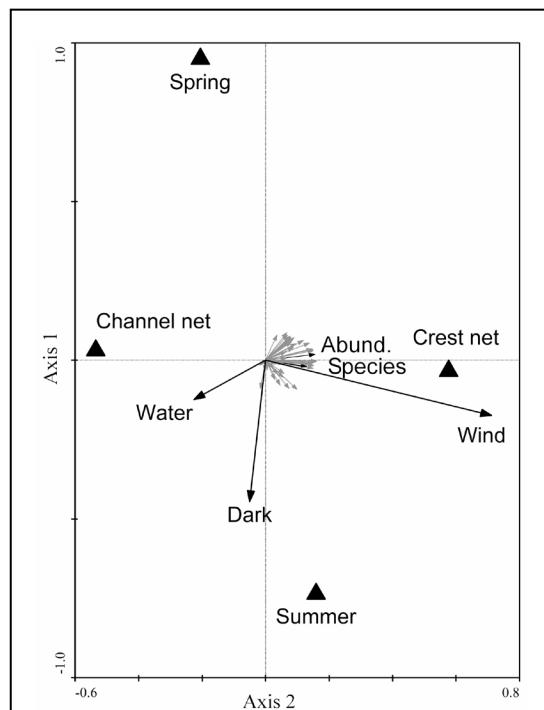

Figure 2
Redundancy analysis plot of flow-corrected data. The angle between two variables represents the correlation between them (0°=positive correlation, 90°=no correlation, 180°=negative correlation), and the length of the arrow represents the magnitude, i.e., the longer the arrow, the greater the correlation coefficient. Environmental variables are shown as labeled arrows. Water = water temperature, Dark = hours of moonless, nocturnal flood tide, and Wind = average speed (km/h) of onshore wind. Categorical variables are shown as triangles. Species are shown as unlabelled grey arrows; individual species names have been omitted. Abundance and species richness are shown as black arrows labeled as Abund. and Species, respectively.

Results

A total of 53,579 larval reef fishes were caught that represented 33 families and 59 identified species (Table 1). On an average night, a crest net trapped 166.3 larvae (standard deviation [SD]=407.4) and 8.5 species (SD=5.8), whereas a channel net trapped 4.1 larvae (SD=12.2) and 0.9 species (SD=1.5). See Table 1 for list of families and species sampled by both net types.

Ordinations

There was a strong distinction between the species assemblages caught in the two net types (Fig. 2). Only data for 2006 sampling periods are presented in Figure 2, as no water temperatures were available for 2005

Table 1

Total number of fish larvae sampled with crest and channel nets at Turneffe Atoll, Belize, during the three sampling periods (summer 2005, spring 2006, and summer 2006). Barred lutjanids refers to *Lutjanus apodus*, *L. analis*, *L. cyanopterus*, *L. griseus*, and *L. jocu*. Striped *Stegastes* refers to *Stegastes diencaeus*, *S. leucostictus*, and *S. variabilis*.

Family	Genus	Species	Summer 2005 Crest net	Summer 2005 Channel net	Spring 2006 Crest net	Spring 2006 Channel net	Summer 2006 Crest net	Summer 2006 Channel net	Total
Acanthuridae	*Acanthurus*	*bahianus*	1	0	0	0	8	0	9
	Acanthurus	*chirurgus*	5	0	0	0	1	0	6
	Acanthurus	*coeruleus*	10	0	2	0	8	0	20
Achiridae	*Achirus*	sp.	0	0	0	0	3	0	3
Antennariidae	*Histrio*	*histrio*	5	1	0	0	2	0	8
		All others	7	0	1	0	8	0	16
Apogonidae	*Apogon*	*maculatus*	302	26	53	6	464	10	861
	Apogon	*quadrisquamatus*	207	1	15	0	63	0	286
	Astrapogon	*puncticulatus*	114	5	261	0	212	1	593
Aulostomidae	*Aulostomus*	*maculatus*	0	0	2	0	1	0	3
Labrisomidae	*Starksia*	spp.	534	0	20	0	270	0	824
Bothidae	*Bothus*	spp.	43	18	8	4	28	5	106
Callionymidae	*Paradiplogrammus*	*bairdi*	123	0	25	0	924	1	1073
Carangidae		All species	20	2	9	1	13	0	45
Chaetodontidae	*Chaetodon*	*capistratus*	25	1	0	0	7	0	33
	Chaetodon	*ocellatus*	5	0	0	0	0	0	5
Cynoglossidae	*Symphurus*	spp.	129	0	29	0	6	0	164
Diodontidae	*Chilomycterus*	*antennatus*	5	0	0	0	0	0	5
Elopomorpha		All species	471	221	627	251	1759	173	3502
Gerreidae	*Eucinostomus*	spp.	13,450	296	1557	21	10,592	17	25,933
Gobiesocidae	*Arcos*	*rubiginosus*	0	0	0	0	3	0	3
Gobiidae	*Bathygobius*	*curacao*	1	0	0	0	177	0	178
	Ctenogobius	*saepepallens*	0	0	97	1	13	0	111
	Gnatholepis	*thompsoni*	2043	0	882	0	2623	12	5560
	Priolepis	spp.	23	0	5	0	226	0	254
	Unknown	spp.	3503	1	329	0	1108	0	4941
Labridae	*Halichoeres*	spp.	296	0	23	2	184	0	505
	Thalassoma	*bifasciatum*	21	0	3	0	31	0	55
	Xyrichtys	spp.	83	0	232	1	30	1	347
Lutjanidae	Barred lutjanids	All	150	12	8	1	18	2	191
	Lutjanus	*synagris*	0	1	4	0	1	0	6
	Lutjanus	*mahogoni*	4	0	0	0	0	0	4
	Ocyurus	*chrysurus*	2	0	6	0	0	0	8
Microdesmidae		All species	39	1	52	7	63	4	166
Monacanthidae	*Cantherines*	sp.	1	0	4	0	1	0	6
	Monacanthus	*ciliatus*	184	2	0	0	23	4	213
	Monacanthus	*tuckeri*	113	8	22	1	105	9	258
Ogcocephalidae	*Ogcocephalus*	*nasutus*	3	0	0	0	6	0	9
	Halieutichthys	*aculeatus*	4	0	0	0	2	0	6
Ophidiidae		All species	5	0	5	0	21	0	31
Ostraciidae	*Lactophrys*	spp.	77	1	32	0	3	0	113
Paralichthyidae	*Syacium*	spp.	0	0	11	0	4	8	23
Pomacanthidae	*Pomacanthus*	spp.	2	0	3	0	2	0	7
Pomacentridae	*Abudefduf*	*saxatilis*	13	0	6	0	3	2	24
	Microspathadon	*chrysurus*	0	0	0	0	1	0	1

continued

Table 1 (continued)

Family	Genus	Species	Summer 2005 Crest net	Summer 2005 Channel net	Spring 2006 Crest net	Spring 2006 Channel net	Summer 2006 Crest net	Summer 2006 Channel net	Total
Pomacentridae	*Stegastes*	*adustus*	3	0	0	0	1	0	4
(continued)	*Stegastes*	*partitus*	2	1	0	0	23	1	27
	Striped *Stegastes*	All	171	2	0	1	258	12	439
Scaridae	*Sparisoma*	spp.	329	3	359	3	838	0	1532
Scorpaenidae	*Scorpaena*	spp.	44	2	202	1	64	2	315
Serranidae	*Diplectrum*	spp.	45	5	0	0	5	0	55
	Pseudogramma	*gregoryi*	95	0	38	0	117	0	250
	Rypticus	sp.	2	0	0	0	5	0	7
	Hypoplectrus	spp.	0	0	0	0	7	0	7
Sphyraenidae	*Sphyraena*	*barracuda*	125	13	6	0	39	6	189
Syngnathidae	*Cosmocampus*	spp.	341	1	111	0	95	0	548
Tetraodontidae	*Sphoeroides*	spp.	0	0	7	3	16	0	26
	Canthigaster	spp.	435	0	24	7	26	0	492

(when 2005 data were analyzed separately, a very similar plot was obtained). Most species were captured in greater abundance with crest nets and rarely, if ever, caught in the channel nets. For example, the families Acanthuridae, Ogcocephalidae, and Pomacanthidae were only caught in crest nets and there were no species or families that were exclusively caught in channel nets. The summer and spring sampling periods were extremely different (Fig. 2). However, when the three sampling periods were plotted separately, very similar ordinations with respect to environmental factors were obtained. The difference between summer and spring in the combined ordination of Figure 2 could be due to the lower numbers of larvae captured in spring 2006; however, there were notable absences of families in that sampling period, e.g., no Chaetodontidae or Ogcocephalidae and only a single representative of Pomacentridae.
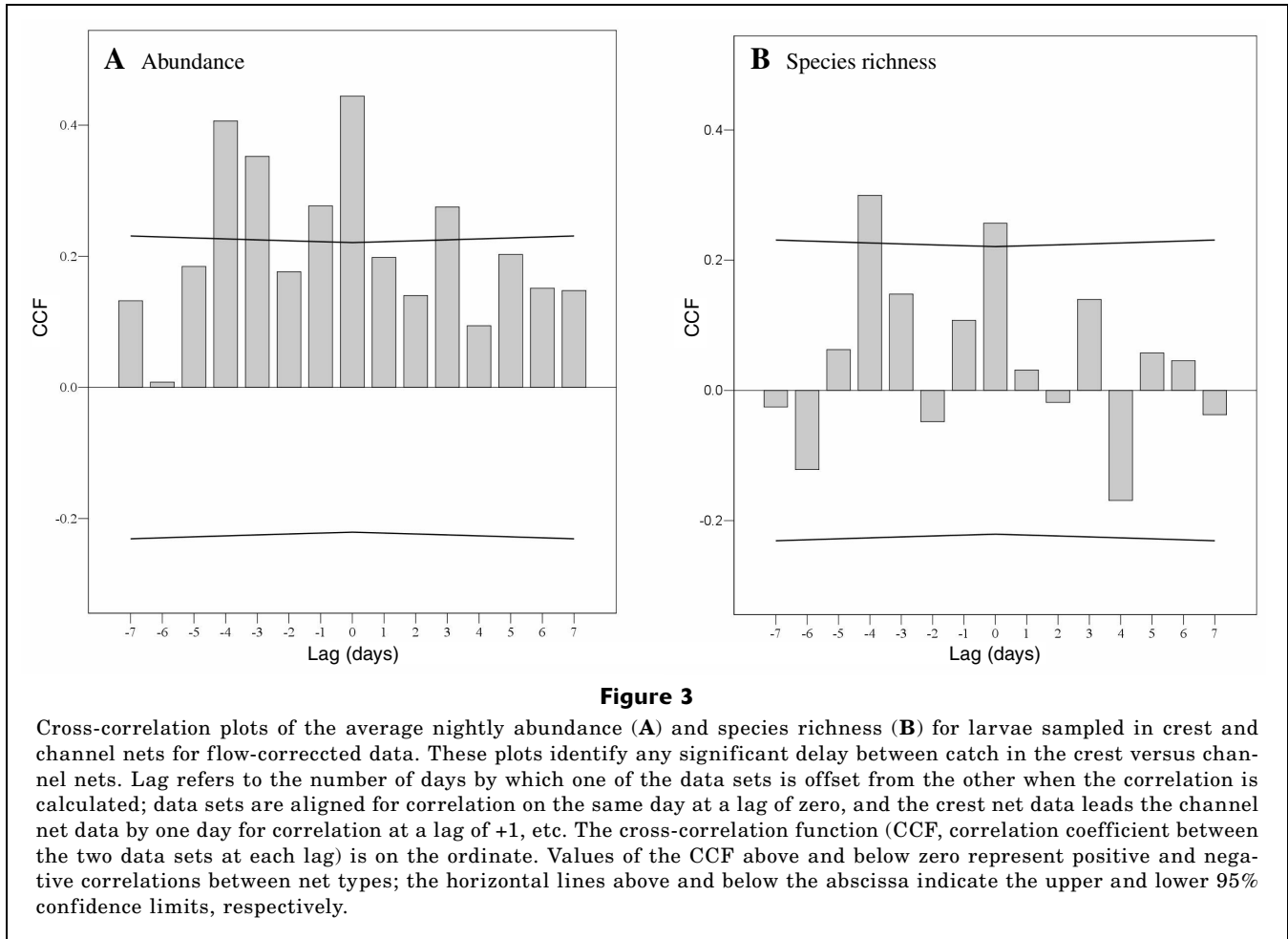
Of the environmental variables (Fig. 2), the onshore wind was positively correlated with abundance and species richness of larval reef fishes sampled in crest nets. The combined factor (nocturnal illumination and tidal periodicity) was important but did not align strongly with the other explanatory or species variables. Higher water temperatures at the net sites corresponded with fewer larvae caught because water temperature was negatively correlated with the presence of the vast majority of species.

Time series analyses

Peaks and lows in the supply of fish larvae appeared on the same nights in reef crest nets and channel nets in the mangroves (Fig. 3). The cross-correlation plots between net types revealed that catches (both in terms of abundance and species richness) were significantly correlated at a lag of zero (data sets were aligned for correlation on the same day at a lag of zero, one data set leads the other by one day for correlation at a lag of +1, etc.). For abundance, the greatest correlation between net types was at a lag of zero days (Fig. 3A). A lesser correlation at a lag of plus three days indicates that some groups of larvae took three days to pass from the reef crest to the mangrove channels. The other significant correlations at lags of –4, –3, and –1 days are more difficult to explain. There seems to be no biological reason that cohorts of reef fish larvae should arrive in the mangrove channels up to four days before they arrive at the reef crest. This finding may be a result of pooling abundances of all species and could possibly be resolved with further analysis by splitting abundances into families or species (where possible). Species richness was also correlated at a lag of zero days; however, the other significant correlation, at a lag of –4 days, was greater than that at day zero (Fig. 3B). As with abundance, there seems to be no biological explanation for this correlation and more detailed analysis may prove advantageous.

The auto-correlation plot for abundance (Fig. 4A) illustrates that there was no periodicity in the flow-corrected data and that the catch on any one night was not correlated with that on the preceding or following nights. However, the plot for species richness (Fig. 4B) shows a lunar periodicity in the numbers of species caught. The significant negative correlation at a lag of 16 days (at just over half the lunar cycle) shows that greater numbers of species caught in new-moon periods
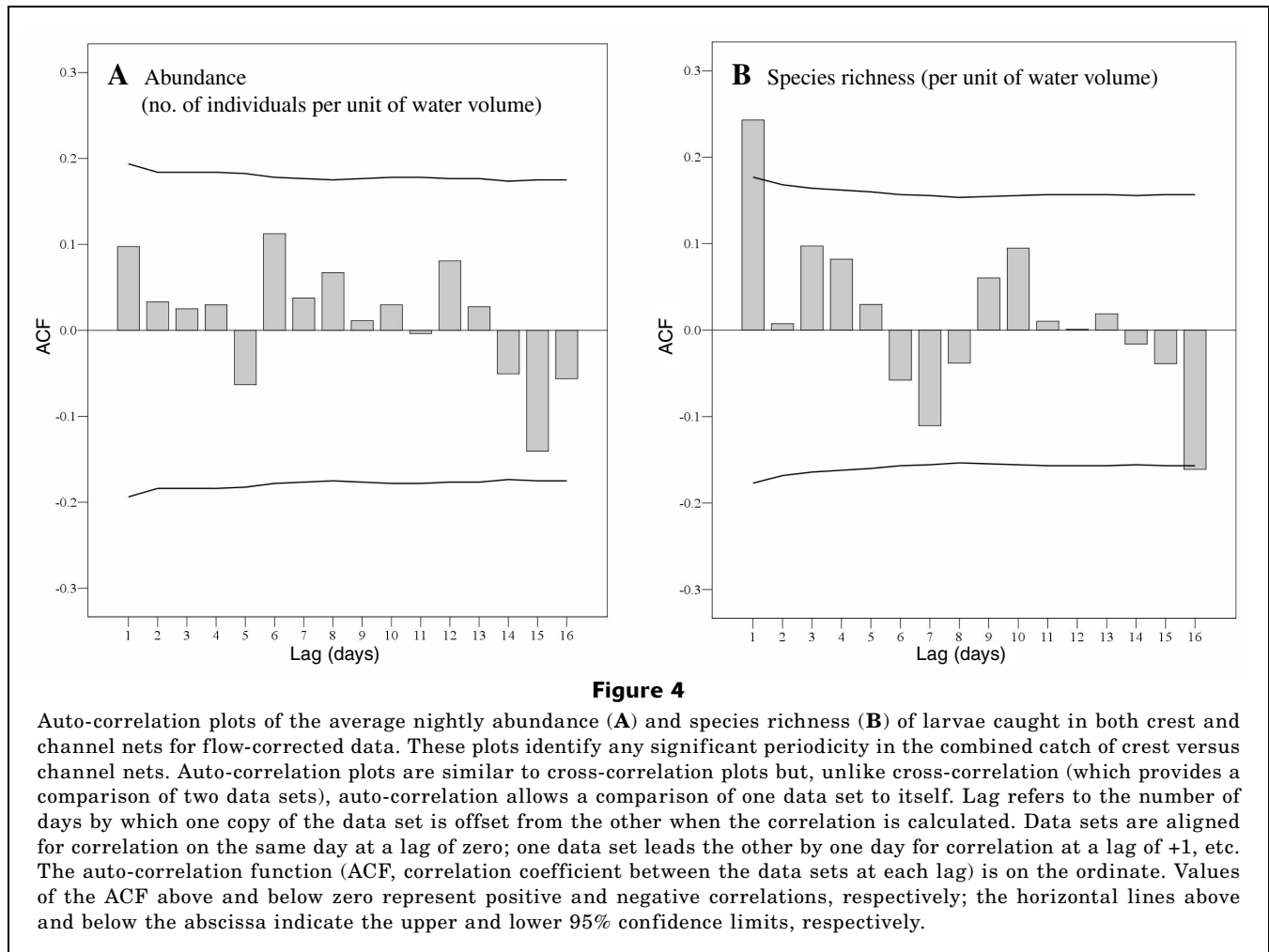
Figure 3

Cross-correlation plots of the average nightly abundance (**A**) and species richness (**B**) for larvae sampled in crest and channel nets for flow-correccted data. These plots identify any significant delay between catch in the crest versus channel nets. Lag refers to the number of days by which one of the data sets is offset from the other when the correlation is calculated; data sets are aligned for correlation on the same day at a lag of zero, and the crest net data leads the channel net data by one day for correlation at a lag of +1, etc. The cross-correlation function (CCF, correlation coefficient between the two data sets at each lag) is on the ordinate. Values of the CCF above and below zero represent positive and negative correlations between net types; the horizontal lines above and below the abscissa indicate the upper and lower 95% confidence limits, respectively.

corresponded to fewer numbers of species caught in full-moon periods.

Discussion

Crest nets caught greater numbers of individuals and species per deployment than channel nets and would therefore be an advantageous sampling tool to use in studies attempting to maximize the chance of catching greater numbers of a certain species. However, the difference between net types was not solely due to the design of the net. The two net types were deployed at two different habitats. All larvae passing over the top of a small width of the reef crest were sampled as the reef slope forced them into a constrained water column. In contrast, in the mangrove channels, only the top meter of the water column was sampled and larvae were free to pass underneath the floating channel net. A comparison of the suites of larvae caught in each habitat would provide information about their settlement preferences. Such a comparison could not be made in the present study because the difference in the amount of the water column sampled was not controlled. However, Shenker et

al. (1993) reported poor catches in subsurface deployed channel nets, and this finding indicates that most larvae that are still in the water column as they pass through the mangrove channels behind the reef crest remain near the surface of the water.

Lunar periodicity of arriving settlers has been well documented in some reef fish species; greatest recruitment usually occurs at the darkest phase of the moon (Victor, 1986; Thorrold et al., 1994; D'Alessandro et al., 2007). Rayleigh z tests on non-flow-corrected data showed that significantly more larvae were caught at the new moon in the present study. When the catch was standardized by volume of water filtered however, all lunar periods had similar numbers of individuals per unit of water volume and no periodicity existed. This finding indicates that water flow was greater during the dark moon periods (new and last quarter) than during bright moon periods (first quarter and full), and the greater water flow removed the correlation between the quantity of larvae caught and the lunar period. It appears there was approximately the same number of larval fish per unit of water volume throughout the lunar cycle; the increased flow around the new moon simply carried more of them into the nets. Alterna-

Figure 4

Auto-correlation plots of the average nightly abundance (**A**) and species richness (**B**) of larvae caught in both crest and channel nets for flow-corrected data. These plots identify any significant periodicity in the combined catch of crest versus channel nets. Auto-correlation plots are similar to cross-correlation plots but, unlike cross-correlation (which provides a comparison of two data sets), auto-correlation allows a comparison of one data set to itself. Lag refers to the number of days by which one copy of the data set is offset from the other when the correlation is calculated. Data sets are aligned for correlation on the same day at a lag of zero; one data set leads the other by one day for correlation at a lag of +1, etc. The auto-correlation function (ACF, correlation coefficient between the data sets at each lag) is on the ordinate. Values of the ACF above and below zero represent positive and negative correlations, respectively; the horizontal lines above and below the abscissa indicate the upper and lower 95% confidence limits, respectively.

tively, the larvae used this increased flow to facilitate their movement to the reef and the darker conditions to improve predator avoidance. Given that larval fish near the time of settlement possess impressive swimming and sensory abilities, the effect of flow could simply be viewed as an interesting variable that masks true larval abundance in the water column.

As reported previously (Shenker et al., 1993; Thorrold et al., 1994; Kingsford and Finn, 1997), rather than deploying a net continuously, deploying a net around the new moon with an onshore wind would optimize collection efforts. The measurements of wind speed and direction at the international airport on mainland Belize were positively correlated with abundance and species richness of fish larvae at Turneffe Atoll. Because water temperature was found to be negatively correlated with the capture of almost all species, it is possible that the emptying of warm water from the lagoon negatively affects the arrival of larvae. All of these factors (lunar period, water temperature, and prevailing wind) may be further considered when trying to optimize the collection of fish larvae in stationary nets.

In assessing the effort required to install, maintain, and deploy the codend of each type of net, we found that channel nets were far easier to work with. Because of the position of crest nets, they are subject to high wave energy and strong currents. Therefore more effort is required to anchor the frame to the substrate and more time is needed to repair the unavoidable wear and tear. Channel nets, on the other hand, are quick to retrieve in the case of a storm and require very little ongoing maintenance.

Researchers need to be aware of the additional effort required to set and maintain crest nets in comparison to other types of nets. The importance of flow has also been highlighted, and great care should be taken to evaluate this variable when making comparisons of larval catch among times and locations. Environmental factors which alter this rate of flow seem to have the greatest influence on the catch of both stationary net types. Given the results of this study, there are no obvious obstacles to the use of crest nets in other parts of the Caribbean Sea where appropriate sites exist, i.e., shallow reef crest with mainly unidirectional water flow. Given the greater water flow through the

environment in which they are deployed, they are likely to collect more larvae and hence better meet the needs of researchers working on settlement-stage reef fishes.

Acknowledgments

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