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REPORT

Patterns of recruitment of coral reef fishes in a monsoonal environment

R. A. Abesamis · G. R. Russ

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Abstract The abundance of newly settled recruits of coral reef fishes was monitored at a total of 11 sites at two islands and two coastal locations in the central Philippines for a 20-month period (February 2008 to September 2009) that included two monsoon cycles. Recruitment occurred throughout the year. Most of the abundant species exhibited protracted recruitment seasons. This confirms the expectation of extended breeding of reef fishes at lower latitudes. The annual pattern of recruitment of reef fishes as a group was predictable. Annual fluctuations of sea surface temperature and wind strength largely explained the pattern. Rainfall, however, did not significantly influence the pattern of recruitment. Peaks in density and species richness of recruits occurred during the southwest monsoon and the second inter-monsoonal period of the year (July to October) when temperatures were highest and when most of the sites were sheltered from winds or when winds were weak. Conversely, lowest density and species richness were observed during the northeast monsoon (November to March) when temperatures were lowest and most sites were exposed to winds. The same pattern could also be seen in the recruitment of both damselfishes (Pomacentridae) and wrasses (Labridae), notwithstanding a tenfold difference in abundance of recruits between the two families. The pattern was fairly consistent across most sites, among most of the species that were examined, and between the 2 years that were sampled. This study is one of the few to provide insights into the influence of environmental factors on the recruitment patterns of fishes on Indo-Pacific coral reefs situated at lower latitudes.

Keywords Coral reef fish · Reproduction · Recruitment seasonality · Monsoons · Philippines

Introduction

The demographic structure and population dynamics of marine species with a pelagic larval phase and a benthic adult phase can be heavily influenced by recruitment (i.e., the addition of juveniles to a population) (Doherty and Williams 1988; Roughgarden et al. 1988; Underwood and Fairweather 1989). Recruitment is highly variable in time and space at many scales, reflecting the variability and unpredictability of processes in the pelagic environment that affect growth and survivorship of larvae (Doherty 1991; Caley et al. 1996). The degree of seasonality of the environment can influence the annual timing of recruitment. Timing of reproduction may also be adapted to match oceanographic conditions that are favourable to the survival of larvae (Johannes 1978; Cushing 1987). In coral reef fishes, seasonality of recruitment is most obvious on reefs closer to the limits of the tropics (23.5°N and S). Highly seasonal recruitment is typical of populations at higher latitude reefs, where most juveniles settle within a

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R. A. Abesamis · G. R. Russ
School of Marine and Tropical Biology and ARC Centre of
Excellence for Coral Reef Studies, James Cook University,
Townsville, QLD 4811, Australia

R. A. Abesamis (✉)
Silliman University-Angelo King Center for Research
and Environmental Management (SUAKCREM),
6200 Dumaguete City, Negros Oriental, Philippines
e-mail: rene.abesamis@jcu.edu.au

relatively short period during the warmer half of the year, forming distinct 'year-classes' (e.g., southern Great Barrier Reef, ~23.5°S, see Russell et al. 1977; Williams and Sale 1981). In contrast, recruitment on lower latitude reefs is less seasonal, and there may be no period without some settlement (e.g., Victor 1986; Robertson et al. 1993 in the Caribbean Panama, ~9.5°N). The importance of recruitment in modifying population structure and dynamics will likely differ between higher and lower latitude reefs (Srinivasan and Jones 2006). However, it is difficult to make generalisations about what environmental conditions have the strongest effects on the variability of spawning and recruitment (Doherty 1991; Robertson 1991). The relative importance of environmental factors that determine the timing and strength of spawning activity and recruitment will likely vary among geographic locations at similar latitudes and even among closely related species (Robertson 1990; Clifton 1995; Lemberget et al. 2009).

Coral reefs closer to the equator are subject to monsoonal conditions that are characterised more by annual wind and precipitation cycles than by changes in ambient sea temperature. Reef fishes in equatorial regions may time their spawning during periods when winds and currents are at their weakest, presumably to limit the advection of larvae away from natal reefs and increase the chances of settlement to suitable habitats (Johannes 1978). Fishes may also pattern spawning activity to take advantage of upwelling events caused by monsoon winds (McIlwain et al. 2006). Furthermore, even at lower latitude reefs, temperature may still play a role in mediating settlement success of reef fishes by increasing larval growth rates (Wilson and Meekan 2002). However, few studies have assessed the role of the monsoons in the dynamics of recruitment of reef fishes. Most of the studies that have related patterns in spawning, larval supply and settlement with environmental variables at lower latitudes were conducted in the Caribbean (Robertson 1990; Clifton 1995; Sponaugle and Cowen 1996, 1997; Robertson et al. 1999; Wilson 2001). Surprisingly, little is known about the patterns of spawning and recruitment of reef fishes at lower latitudes in the Indo-Pacific region and the extent to which monsoonal conditions influence these patterns. To date, the only study which related environmental data with observed patterns of recruitment of reef fishes in a low latitude location in the Indo-Pacific region is that of Srinivasan and Jones (2006) (Kimbe Bay, Papua New Guinea, ~5.5°S). The paucity of knowledge is regrettable considering Indo-Pacific coral reefs that are closer to the equator, such as those in Southeast Asia, have the most diverse fish communities (Myers 1999; Carpenter and Springer 2005), and yet are some of the most threatened reefs in the world (Burke and Selig 2002; Hoegh-Guldberg et al. 2009). Addressing this knowledge gap must begin with gathering basic information on temporal and spatial patterns of reproduction and recruitment.

The main objective of this study was to determine the temporal (annual) pattern of recruitment of common coral reef fishes in the central Philippines, where two monsoon seasons occur per year. Density and species richness of newly settled recruits were monitored for 19 separate months over a 20-month period at offshore (island) and inshore (coastal) locations separated by up to 40 km. Temporal variability of recruitment was evaluated against fluctuations in sea surface temperature, wind speed and rainfall to determine which (if any) of these environmental variables could have a strong effect on the pattern of recruitment.

Materials and methods

Geographic setting of the study area

This study was conducted off south-eastern Negros Is. in the Bohol Sea, central Philippines (9.06–9.43°N, 123.23–123.40°E; Fig. 1). As with the Philippines in general, this area is influenced by the reversing wind pattern of the East Asian monsoon (Wyrtki 1961). From November to early March, strong winds from the northeast (northeast monsoon) predominate, while from July to September, strong winds blow from the southwest (southwest monsoon). However, much of the study area is sheltered from the southwest monsoon due to tall mountains in south-eastern Negros (e.g., Cuernos de Negros, elevation: 1,903 m; Fig. 1). Winds during inter-monsoonal months (April to June and October) are lighter and more variable in direction. Sea surface temperature fluctuates by about 3°C annually (about 27–30°C) (NOAA Coral Reef Watch Program, http://coralreefwatch.noaa.gov/satellite/index.html) (Fig. 2a). Temperatures are lowest from January to March during the northern hemisphere winter. During this period, the northeast monsoon brings cool winds from mainland Asia. Temperatures are highest from June/July to November, during and towards the end of the southwest monsoon. The wet and dry seasons that are typical of many regions of the Philippines are not very pronounced in this area, but from November to April rainfall is usually lower compared to the rest of the year [Type III climate based on classification by the Philippine Atmospheric, Geophysical and Astronomical Services Administration (PAGASA) (http://kidlat.pagasa.dost.gov.ph/cab/cab.htm)]. The area may also be affected by several typhoons annually, but it is situated away from the main path of typhoons (up to 20 typhoons may affect the Philippines throughout the year).

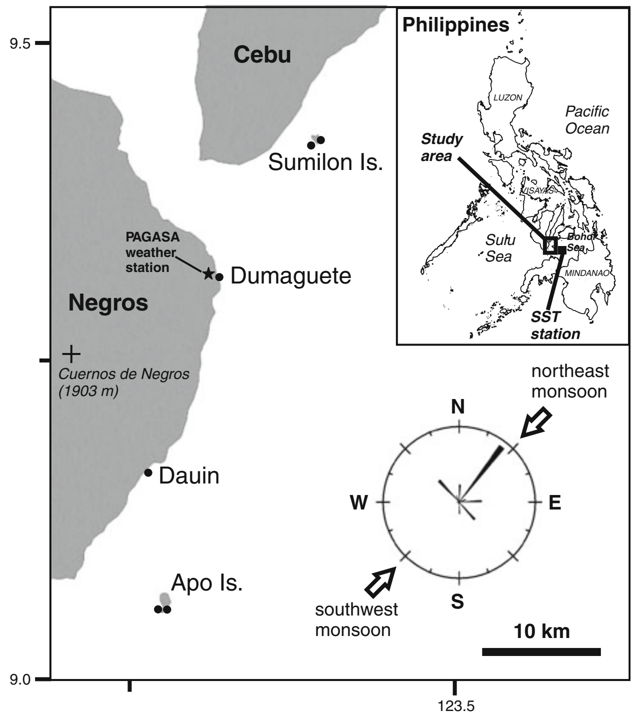


Fig. 1 Map of the study area showing the two islands (Sumilon and Apo) and two coastal locations (Dumaguete and Dauin) where recruitment of reef fishes was monitored over a 20-month period. Black dots also indicate the locations of sites on the two sides of each island that differed in their exposure to the two monsoons. The wind chart shows the frequency distribution of daily wind direction for 1 year (January to December 2008) recorded at a weather station in Dumaguete. *Inset* map shows the location of the study area in relation to the entire Philippines. The *inset* map also shows the location of the sea surface temperature (SST) virtual monitoring station (a 0.5°longitude × 0.5°latitude area) of the NOAA Coral Reef Watch Program (see "Materials and methods")

Study sites

Two small islands and two coastal locations 15–40 km apart were surveyed in order to gain insights into recruitment patterns within the ~300 km^2 study area (Fig. 1). The two islands were Sumilon (0.2 km^2) and Apo (0.7 km^2). They are about 40 km from each other and about 2 and 7 km away, respectively, from their nearest-neighbouring large island (Negros and Cebu, respectively). Coral reefs surround much of Sumilon and Apo to a depth of more than 50 m. Reefs are steeper and more developed along the southern half of the two islands. The two coastal locations were situated along the south-eastern coast of Negros in Dauin municipality and Dumaguete City. Dauin and Dumaguete are about 20 km apart. The reefs in both coastal locations are found less than 300 m from shore between depths of <1–30 m and are patchily distributed, separated by sand or seagrass.

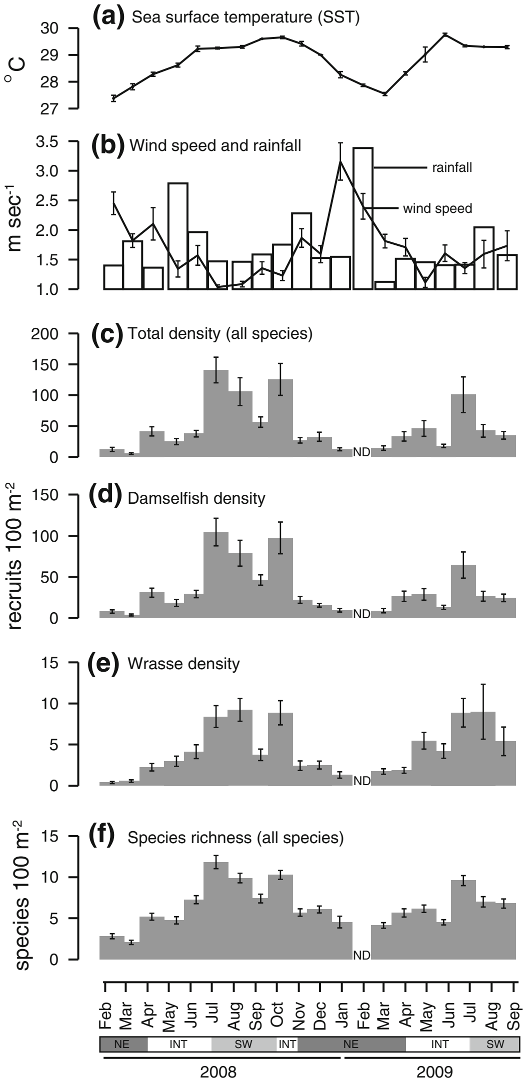


Fig. 2 Temporal patterns of sea surface temperature, wind speed and rainfall (**a**, **b**) versus temporal patterns of recruit density (total, damselfishes, wrasses) and species richness averaged for all sites (**c**–**f**). Monsoons indicated by different shades of grey along *x*-axis. *NE* northeast monsoon, *SW* southwest monsoon, *INT* inter-monsoon. Position of plotted data between calendar months reflects change in timing of lunar months relative to calendar months. *Error bars* are ±SE. *ND* no data

Visual census of recruits

Samples of monthly recruit abundance of coral reef fish were taken by an experienced observer (R.A.A.) by counting all non-cryptic recruits along 50-m-long × 2-m-wide belt transects laid parallel to the shoreline following a depth contour. The sampling strategy aimed to include as many species and reef habitat types as practically possible. Sampling took place at 11 sites that were unequally distributed among the four locations, two depths (reef slope and reef flat) and two wind exposures (northeast and southwest). North-eastern (NE) and south-western (SW) Sumilon, and south-eastern (SE) and south-western (SW) Apo were sampled. At each of these sides of the two islands, two depths (3–4 m, 10–12 m) were sampled, each with three replicate transects. Hard coral cover in the deeper sites (reef slope) of the two islands ranged from 35 to 70% except on NE Sumilon where sand, dead coral and rock dominated benthic cover. Soft corals and/or coral rubble dominated benthic cover in the shallower (reef flat) sites. All transects in SW Sumilon and SE Apo were situated inside a no-take marine reserve. In Dauin, surveys were done on patch reefs (50–120 m long × 20–80 m wide) found within a stretch of coast about 1 km long. Only two depths were sampled (3–4 m, 8–12 m), each with five replicate transects. Hard coral cover on those patch reefs ranged from 30 to 60%. Almost all transects in Dauin were situated inside two no-take marine reserves. In Dumaguete, the seaward edge of a shallow patch reef (about 200 m long × 100 m wide) was surveyed. Only one depth (3–4 m) was sampled with three replicate transects. Hard coral cover on this patch reef ranged from 30 to 35%.

Surveys of recruits were conducted for 19 separate months over a 20-month period (late February 2008 to early September 2009). The only month that was not sampled was February 2009 due to inclement weather. Unfavourable weather also prevented surveys at certain sites during some months: February 2008 (Dumaguete site); January 2009 (Sumilon and Apo sites); July 2009 (SW Sumilon at 3–4 m); August 2009 (SW Apo sites); and September 2009 (Dauin at 3–4 m). Moreover, replicate samples were incomplete in Dauin during 2 months: August 2009 (only 3 transects at 8–12 and 3–4 m) and September 2009 (only 3 transects at 8–12 m). Due to logistical constraints, random sampling among sites could not be performed but the order in which islands and coastal locations were surveyed during each month was not fixed. Within each site, transects had a random starting point wherever practical but the same general area was sampled almost every month.

Recruits of a particular month are fish that settled during, and survived to the end of, a lunar cycle. Past studies and reviews indicated that larval settlement on reefs tends to be higher around the new moon and lower around the full moon (Victor 1986; Doherty 1991; Wilson 2001). This lunar periodicity of larval settlement was confirmed in a pilot study at Dauin where the abundance of new recruits settling on 15 individually marked branching coral colonies were monitored every 2–3 days over 2 lunar cycles. Surveys of recruits were therefore performed around the full moon (2 days before to 7 days after) in order to capture the peak settlement periods within each lunar cycle. All sites were sampled within 3–4 days except when field work was delayed for 2–3 days because of inclement weather. The time interval between consecutive monthly surveys at each site was about 4–5 weeks (26–35 days; mode = 28 days or 4 weeks). Consistent timing of monthly surveys was used to help reduce variability in the data caused by mortality of early recruits (due to predation).

In order to avoid counting older fish that did not settle within the previous 4–5 weeks, only those fish that were below an arbitrary threshold size were counted. For many species, the threshold size was set at <20 mm total length (TL), e.g., damselfishes (Pomacentridae), wrasses (Labridae), parrotfishes (Scaridae), etc. For species that had larger recruits, e.g., butterflyfishes (Chaetodontidae) and surgeonfishes (Acanthuridae), threshold sizes were set at <30 and 40 mm TL, respectively. These size limits allowed for several mm of growth after settlement. Estimates of threshold sizes were guided by family-level information on sizes of late stage pre-settlement larvae and newly settled recruits available in the literature (Leis and Rennis 1983; Leis and Trnski 1989; Victor 1991; Paddack and Sponaugle 2008). Data on sizes of newly settled recruits from the pilot study that was done in Dauin supplemented the basis for these threshold sizes. Threshold size was set at <20 mm TL for species that had no information on sizes at the recruit stage. In order to maintain the accuracy of size estimates during surveys, the observer always used a ruler that was attached to the top of his recording slate as a guide.

Benthic composition along each transect was estimated during the first 5 months of the survey period. The type of substrate (e.g., hard coral, soft coral, macroalgae, dead coral, rock, sand, etc.) at every 0.5 m point intercepted by the 50-m transect was recorded and expressed as a percentage of all points per transect (% cover). The purpose of the benthic surveys was to provide a baseline description of reef habitat at each site in order to detect changes in habitat caused by disturbances (e.g., coral bleaching, typhoons) that could affect recruit abundance during the study. However, additional benthic surveys were not conducted after the first 5 months of the study because the few disturbances (i.e., 3 typhoons) that affected the study area did not cause major damage to the reef habitat at each site.

Weather data and sea surface conditions

Data on sea surface temperature (SST) for the period covered by the recruitment surveys were obtained from the NOAA Coral Reef Watch Program (http://coralreefwatch.noaa.gov/satellite/index.html). The program has a ‘virtual’ SST monitoring station located in the Bohol Sea close to the study area (Fig. 1). The SST monitoring station is a 0.5° longitude × 0.5° latitude area. Data on SST are derived from nighttime measurements made by the Advanced Very High Resolution Radiometer (AVHRR) carried on NOAA's Polar-Orbiting Environmental Satellites (POES). The temporal resolution of the data was biweekly, giving 7–10 days of SST measurements for every 4–5 weeks period covered by the monthly recruitment surveys. Daily data on wind velocity and rainfall during the recruitment surveys were obtained from a weather station at Dumaguete airport operated by the PAGASA. This weather station is located almost at sea level <1 km from the coast and about 1–30 km away from the individual recruitment monitoring sites (Fig. 1). The data on wind showed that wind speed was highest in January and February during the northeast monsoon and weakest around July during the southwest monsoon (Fig. 2b). This wind pattern is due to the fact that when south-westerly winds predominate, Dumaguete is on the leeward side of Negros (see wind chart in Fig. 1). However, the pattern in wind speed also directly reflects the seasonal change in sea surface conditions within much of the study area. Wind stress (i.e., drag caused by wind moving over water) causes seasonality of wave action. Surface waters east of Negros are generally more turbulent during the northeast monsoon than the southwest monsoon (R. Abesamis, personal observations over >2 years). The sheltering effect of Negros during the southwest monsoon is most noticeable in Dumaguete but can still be felt at Dauin and Sumilon. Occasionally, however, the two latter sites can be affected by storm surge when the southwest monsoon is intensified by typhoons. Apo Island, on the other hand, is not sheltered by Negros during the southwest monsoon. Thus, surface waters around Apo can be rough during both monsoons. The data on rainfall was probably an accurate index of rain intensity for the entire study area. Peaks in rainfall during certain months were caused by the intertropical convergence zone and several typhoons and storms that affected the area, as opposed to just localised rain in the Dumaguete area (Fig. 2b). Heaviest rainfall was recorded in early February 2009, when a storm brought more than 250 mm of rain in just 1 day.

Data analyses

The temporal pattern of 'collective recruitment' (i.e., recruits of all species combined) was described by averaging monthly total recruit density and species richness across all 11 sites. Significant differences among monthly average values (19 months) were then determined using one-way ANOVA. Planned contrasts were made after each ANOVA to determine inter-annual and seasonal differences. For inter-annual comparisons, data from March to September in 2008 were contrasted with data from the same months in 2009. For comparisons between seasons, data from northeast monsoon (November to March), southwest monsoon (July to September) and inter-monsoonal months (April, May, June and October) were contrasted with each other. The overall temporal pattern of recruitment of two common families, the damselfishes and the wrasses, were compared. Special interest was given to these two families because they dominated recruit species composition and comprised 80% of cumulative recruit abundance. Monthly recruit densities of the damselfishes and wrasses were summarised and analysed following the same approach as that for total recruit density.

Potential effects of SST, wind speed (as a proxy for wind stress) and rainfall on the temporal pattern of collective recruitment were tested using multiple regression analyses. Average recruit density and species richness values were computed for each location (Sumilon, Apo, Dauin and Dumaguete) for every month surveyed, giving a sample size of $n = 73$ for each regression. Monthly values for each environmental variable were computed by averaging (for SST and wind speed) or summing (for rainfall) biweekly or daily values within each 4–5 weeks period that corresponded to each monthly recruitment survey. The potential effects of SST, wind stress and rainfall on the temporal pattern of recruitment of the damselfishes and wrasses were also tested following the same procedures.

Most variables were transformed in order to conform to the assumptions of parametric statistical procedures [log $(x + 1)$ for total recruit density, damselfish density, wind speed, rainfall; $(x)^{1/2}$ for species richness; $(x + 0.001)^{0.25}$ for wrasse density]. All statistical analyses were performed in Statistica (ver. 8).

Species-level analysis of temporal patterns of recruitment was limited to the most abundant species, i.e., species that had a cumulative abundance of ≥50 recruits recorded from all sites. Only the data from sites where each species was most abundant were used in this analysis. The duration of the recruitment period of each species was estimated by counting the number of months when recruitment was considered significant. To determine which months had significant recruitment, two arbitrary thresholds of abundance were applied. The first threshold was set at ≥1% of the adjusted total abundance in 1 year. This was adapted from Srinivasan and Jones (2006) and was used in the present study in order to directly compare results between the central Philippines and Kimbe Bay, Papua New Guinea. The second threshold was set at ≥5% of the adjusted total abundance in 1 year to provide more conservative estimates of duration of the recruitment period. To compute the adjusted total abundance of a species in 1 year, average abundance values for each month that was surveyed for 2 years (March–September) were initially computed then added to the raw abundance values of other months. The abundance value of each month was then expressed as a percentage of the adjusted total abundance in 1 year.

Results

A total of 40,913 new recruits of 120 species of reef fish from 16 families were recorded during the surveys. Species composition was dominated by the damselfishes (43 species) and wrasses (35 species). Damselfishes comprised 73% of total recruit abundance, wrasses just 7%. The five most abundant species were four damselfish species (*Pomacentrus moluccensis*, *Chromis ternatensis*, *Chromis viridis* and *Chromis retrofasciata*) and one species of anthias (*Pseudanthias tuka,* Serranidae, subfamily Anthiinae). Together, the recruits of these five species accounted for 54% of the total number of recruits recorded.

New recruits were observed during all months sampled, but a distinct temporal pattern was present. Peaks in total recruit density were recorded during the southwest monsoon and the second inter-monsoonal period of the year, in June–July, July–August and September–October 2008 and June–July 2009 (Fig. 2c). Total density during peak months averaged between 100 and 140 recruits 100 m^{-2}. During other months, density was typically less than 30–50% of peak levels. Lowest levels of recruit density were observed during the northeast monsoon, in February and March 2008 and December–January and March–April 2009, averaging between 5 and 15 recruits 100 m^{-2} (Fig. 2c). This temporal pattern was also evident in the density of recruits of damselfishes and wrasses, notwithstanding a tenfold difference in abundance of recruits between the two families (Fig. 2d–e). However, recruit density of wrasses also peaked in July–August 2009. The temporal pattern in species richness mirrored the temporal patterns in density (Fig. 2f). On average, 10–12 species per 100 m^{-2} were recruiting during months of highest recruit densities. In contrast, only 2–7 species per 100 m^{-2} on average were recruiting during other months.

Significant differences in monthly levels of recruit densities (total, damselfish and wrasse) and species richness were detected among the 19 months that were sampled (Table 1). Total recruit density was significantly greater (by 64%) in 2008 than in 2009 (March to September). Similarly, damselfish recruit density was significantly higher (by 47%) in 2008 than in 2009. However, no significant inter-annual variation was detected for species richness of recruits and density of wrasse recruits. Significant variation in recruit densities and species richness was detected between all seasons that were compared (Table 1). Average recruit densities and species richness were always lowest during the northeast monsoon (November to March), highest during the southwest monsoon (July to September) and were at intermediate levels during the inter-monsoonal months (Table 1).

Peaks in recruit densities and species richness were recorded during or around the southwest monsoon, when SST values were highest and wind speed values lowest (Fig. 2a–f). Conversely, lowest densities and species richness occurred during the northeast monsoon, when SST values were lowest and wind speed values highest. Regression models indicated significant effects of SST and wind speed on monthly average recruit densities and species richness (Table 2). SST always had a positive effect,

Table 1 Summary of 1-way ANOVAs and subsequent planned contrasts to determine significant differences in average recruit densities and species richness among 19 months, between 2 years (2008 vs. 2009) and between seasons

	ANOVA	Planned contrasts							
	(Months, *df* = 18)	2008	2009	NE	SW	NE	INT	SW	INT
a. Total density (all species)		60.0 ± 5.5	40.8 ± 5.2	18.0 ± 2.0	83.4 ± 8.1	18.0 ± 2.0	46.7 ± 4.9	83.4 ± 8.1	46.7 ± 4.9
	F = 23.4	9.9		186.2		40.6		63.5	
	P = <0.001	0.002		<0.001		<0.001		<0.001	
b. Damselfish density		44.5 ± 4.1	27.1 ± 3.1	11.5 ± 1.2	60.1 ± 5.5	11.5 ± 1.2	34.8 ± 3.7	60.1 ± 5.5	34.8 ± 3.7
	F = 21.4	18.8		166.0		36.1		56.8	
	P = < 0.001	<0.001		<0.001		<0.001		<0.001	
c. Wrasse density		4.5 ± 0.4	5.0 ± 0.6	1.5 ± 0.2	7.4 ± 0.7	1.5 ± 0.2	4.3 ± 0.4	7.4 ± 0.7	4.3 ± 0.4
	F = 11.9	1.8		119.8		34.0		31.8	
	P = <0.001	0.18		<0.001		<0.001		<0.001	
d. Species richness (all species)		6.9 ± 0.3	6.2 ± 0.2	4.2 ± 0.2	8.9 ± 0.3	4.2 ± 0.2	6.3 ± 0.2	8.9 ± 0.3	6.3 ± 0.2
	F = 27.4	1.3		220.4		31.7		100.7	
	P = < 0.001	0.25		<0.001		<0.001		<0.001	

Variables tested were the density and species richness of the recruits of all species combined and the densities of the recruits of damselfishes and wrasses. Average density (individuals 100 m^{-2} ± SE) and species richness (species 100 m^{-2} ± SE) values are indicated for years and seasons that were compared. *NE* northeast monsoon (November to March), *SW* southwest monsoon (July to September), *INT* inter-monsoonal months (April, May, June and October)

Table 2 Summary of regression models to assess the potential effects of environmental variables on temporal patterns of recruitment

	Model			SST			Wind speed			Rainfall		
	R^2_{adj}	F	P	R_p	t	P	R_p	t	P	R_p	t	P
a. Total density (all species)	0.45	20.71	<0.001	0.35	3.10	0.003	−0.41	−3.71	<0.001	−0.12	−1.03	0.30
b. Damselfish density	0.43	19.30	<0.001	0.33	2.90	0.005	−0.40	−3.64	0.001	−0.08	−0.67	0.50
c. Wrasse density	0.36	14.56	<0.001	0.37	3.34	0.001	−0.27	−2.36	0.02	−0.14	−1.15	0.25
d. Species richness (all species)	0.52	27.02	<0.001	0.42	3.84	<0.001	−0.43	−3.96	<0.001	−0.17	−1.44	0.16

Dependent variables were the monthly density and species richness of the recruits of all species combined and the monthly densities of recruits of the two families that dominated recruit species composition and overall abundance (damselfishes and wrasses). Monthly density and species richness values were averaged for each location (Sumilon, Apo, Dauin and Dumaguete), resulting in $n = 73$ for each regression. Independent variables were monthly average sea surface temperature (SST), average wind speed (as the proxy for wind stress) and total rainfall. R^2_{adj} = adjusted R^2 value of the regression model, R_p = partial correlation coefficient of independent variable

and wind speed always had a negative effect, on recruitment. The models, however, did not suggest any significant effect of rainfall on recruit densities or species richness (Table 2; Fig. 2b–f).

There was a good degree of spatial coherence in the general pattern of monthly collective recruitment (Fig. 3). The peaks in recruit density during the southwest monsoon and the second inter-monsoonal period and the troughs during the northeast monsoon were detected across most sites (Fig. 3a). However, the peak in recruitment in June–July 2009 was obvious at only a few sites, and there were peaks during March–April in 2008 and 2009 that were recorded only in some sites.

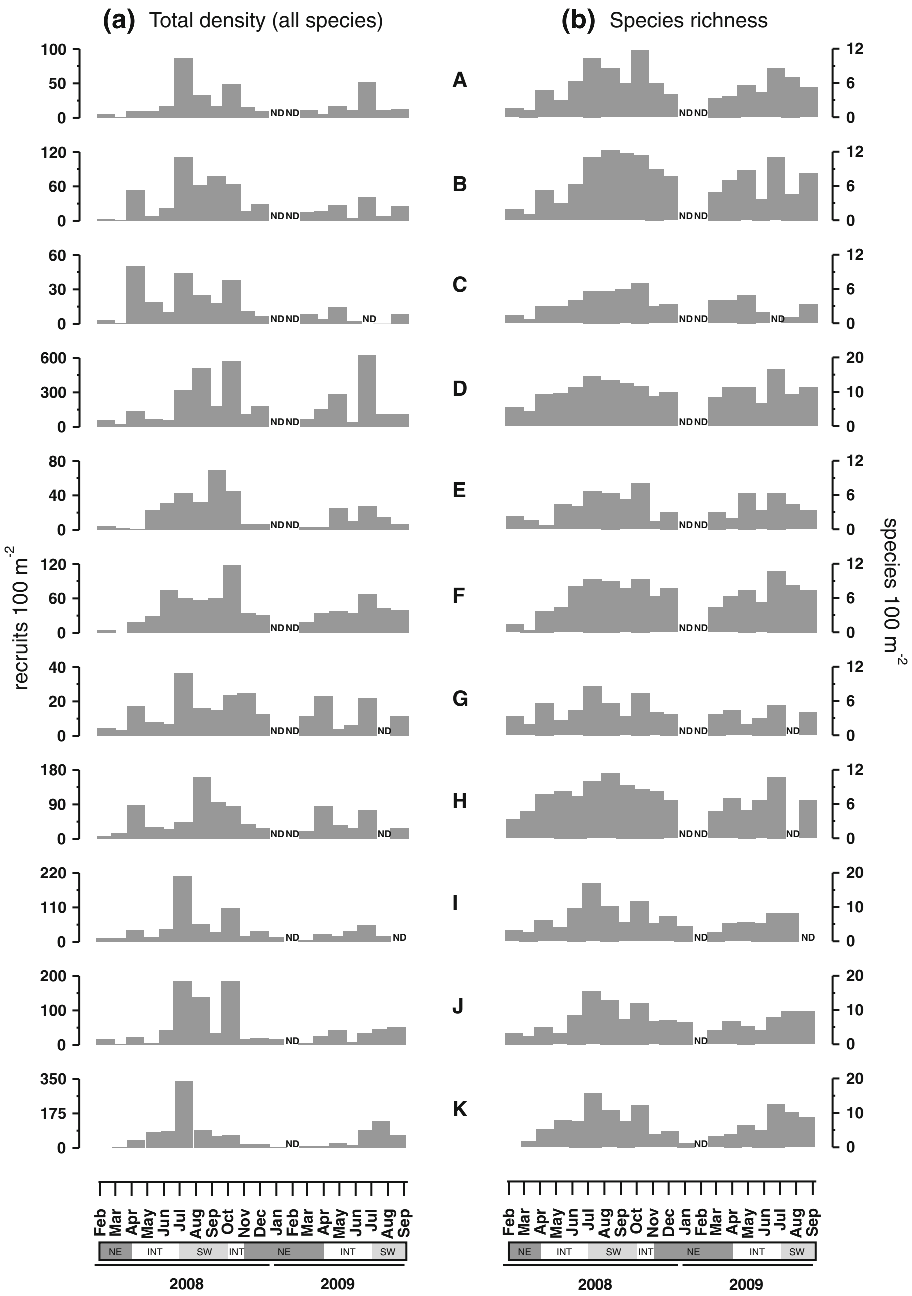
A total of 37 species, representing 7 families, had a cumulative abundance of ≥50 recruits recorded from all sites during the study (Appendix—see Electronic Supplemental Material). The species composition of this subset of species was still dominated by the damselfishes (23 species), followed by the wrasses (6 species). Most of these 37 species had protracted annual recruitment periods. Depending on the threshold value that was used, the majority of species (23–24 species in 5–6 families) had 5–7 or 9–11 months of significant recruitment (Fig. 4a, b). The shortest recruitment periods were found only in a few species of damselfish (e.g., *Chromis amboinensis*, *Dascyllus trimaculatus*, *Neopomacentrus anabatoides*, *N. azysron*, *Pomacentrus smithii*) and the cardinalfishes (Apogonidae) (Fig. 4a, b). There was considerable variation in the timing of peaks among species but most peaks occurred during the southwest monsoon and inter-monsoonal months, mainly in July and October (Fig. 5). Most of the major peaks that contributed substantially to the cumulative annual abundance of each species were also recorded in July or October. Within the damselfishes, the timing of major peaks of *Neoglyphidodon*, *Neopomacentrus* and most *Pomacentrus* spp. differed from that of *Chromis*, *Chrysiptera* and *Dascyllus* spp. in that the major recruitment peaks in the former group occurred earlier than in the latter group. At the family level, the timing of recruitment peaks of the damselfishes, wrasses, parrotfishes, anthiases and cardinalfishes were more similar to each other compared to the butterflyfishes and surgeonfishes (Appendix—See Electronic Supplemental Material). Recruitment peaks of the two latter families, which were represented by one species each (*Chaetodon baronessa* and *Ctenochaetus binotatus*, respectively), only occurred in the earlier or later part of the year, almost all during the northeast monsoon (Fig. 5).

Discussion

This study is one of the few to describe patterns of recruitment (settlement) of coral reef fishes in a location within the Indo-Pacific region, where reversing monsoon winds strongly influence environmental conditions. Previous studies have suggested that the monsoons play a role in determining the annual pattern of recruitment of fishes, particularly in the Philippines (Pauly and Navaluna 1983; McManus et al. 1992; Arceo 2004; Cabaitan et al. 2008). However, the present study is the first in the Philippines that related observed patterns of recruitment of fishes directly to environmental data.

New recruits were observed throughout the year, and the majority of species that were examined exhibited protracted recruitment seasons. These results confirm the expectation of extended annual breeding of reef fishes at lower latitudes (Robertson 1990; Doherty 1991; Srinivasan and Jones 2006). Of greater significance, the annual pattern of collective recruitment was predictable. Annual variability in SST and wind strength can largely account for the pattern. There was a good degree of similarity in the pattern of recruitment among sites considering the distance separating them (up to 40 km), differences in exposure to prevailing monsoon winds, habitat and depth, and large differences (up to 20-fold) in maximum average recruit densities between some sites. This indicates that the effects of SST and wind were working at a broad spatial scale,

Fig. 3 Temporal patterns of **a** total recruit density and **b** species richness averaged across all sites. *A* northeast Sumilon, 3–4 m; *B* northeast Sumilon, 10–12 m; *C* southwest Sumilon, 3–4 m; *D* southwest Sumilon, 10–12 m; *E* south-eastern Apo, 3–4 m; *F* south-eastern Apo, 10–12 m; *G* southwest Apo, 3–4 m; *H* southwest Apo, 10–12 m; *I* Dauin, 3–4 m; *J* Dauin, 8–12 m; *K* Dumaguete, 3–4 m. Monsoons indicated by *different shades* of *grey* along *x*-axis. *NE* northeast monsoon, *SW* southwest monsoon, *INT* inter-monsoon, *ND* no data



most likely during the pelagic larval phase. Rainfall, on the other hand, did not have a significant effect on the patterns of recruitment.

Results strongly suggested that the best 'window' for survival and settlement of larvae of the most common reef fish species (mostly damselfishes and wrasses) is during a 4–6 month period within the year when water temperatures are warmest and when winds are weakest locally, i.e., during the southwest monsoon and inter-monsoonal periods. Small increases in water temperature can enhance growth rates of larval reef fishes (McCormick and Molony 1995; Wilson and Meekan 2002; Meekan et al. 2003; Bergenius et al. 2005; Sponaugle et al. 2006). Faster growth, in turn, can result in higher survivorship because fewer predators would be capable of preying on larger larvae, and the time spent in the pelagic environment is shortened (Houde 1987; Anderson 1988). For instance, Wilson and Meekan (2002) showed that in San Blas in the Caribbean Panama, where water temperature varies by only about 3°C, temperature is positively correlated with larval growth and magnitude of settlement of the damselfish *Stegastes partitus* (also see Bergenius et al. 2002). On the other hand, wind can result in two physical processes that have potential consequences for the pelagic larval phase.

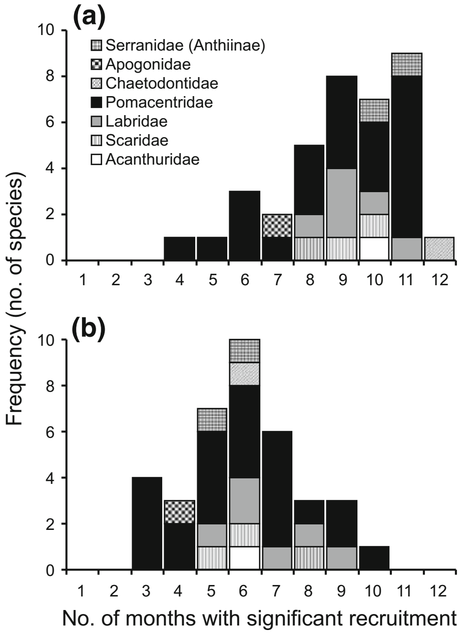


Fig. 4 Durations of the recruitment period (months) of the 37 most abundant species (grouped into 7 families in this figure) estimated using two thresholds of recruit abundance per month: ≥1% (**a**) and ≥5% (**b**) of adjusted total abundance in 1 year (see "Materials and methods")

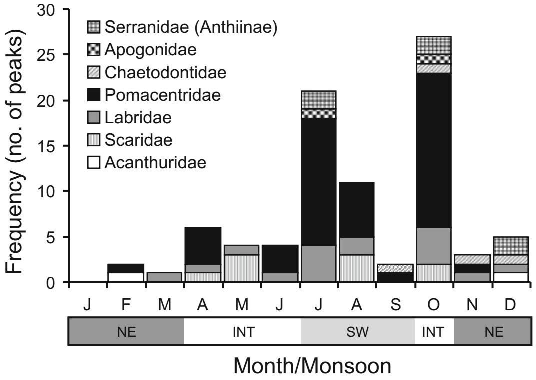


Fig. 5 Summary of the timing of recruitment peaks of the 37 most abundant species (grouped into 7 families in this figure). Note that a single species may have more than one peak in recruitment within a year (also refer to Appendix—see Electronic Supplementary Material). Monsoons indicated by *different shades* of *grey* along *x*-axis. *NE* northeast monsoon, *SW* southwest monsoon, *INT* inter-monsoon

First, wind stress can generate waves and turbulent mixing of surface waters which may be detrimental to survival. Some field studies have indicated that mortality rates in fish larvae are highest during windy conditions, probably because turbulence disrupts concentrated patches of food that are critical to the survival of first-feeding larvae (Peterman and Bradford 1987; Bailey and Macklin 1994). At very small spatial scales, mild turbulent mixing could increase the encounter rates between larval fish and their prey (MacKenzie and Kiorboe 1995; Utne-Palm and Stiansen 2002; Utne-Palm 2004). However, this may increase feeding success and result in faster growth rates in larval fish (Gallego et al. 1996), thus potentially enhancing settlement.

Secondly, prevailing winds can influence dispersal of larvae over larger spatial scales (10's to 100's of kilometres) (Sponaugle and Cowen 1996). There is some suggestion that the effect of the monsoon winds on surface current patterns in the Bohol Sea can partly explain the observed annual pattern of recruitment. In the Bohol Sea, there is a dominant westward flow produced by water entering from the Pacific Ocean and exiting to the Sulu Sea through the Negros-Mindanao strait (Wyrtki 1961). In the study area, this dominant current is manifested as a strong south-westward flow. Data from a sea surface circulation model [1/32° global Navy Layered Ocean Model (NLOM), see Shriver et al. 2007] indicate that this current is enhanced by the northeast monsoon, increasing the potential for flushing of eggs and early-stage larvae out of the study area (Fig. 1). During the southwest monsoon and inter-monsoonal periods, the current weakens, potentially enhancing retention of larvae. If a good proportion of the recruits that settle on reefs that were studied are produced in the same general locality (as opposed to more distant reefs), then monsoon-induced seasonal variation in the strength of local currents will have a significant influence on the annual pattern of recruitment. In such a case, the potential effect of wind on local settlement is negative only when it enhances the dispersal of larvae away from nearby source reefs.

A comparison of the findings of the present study with similar studies from two other locations close to the equator indicates that among environmental variables, wind has the most consistent effect on settlement patterns of reef fishes, particularly in damselfishes and wrasses. For instance, the annual patterns of recruitment of damselfishes and wrasses that were described here are similar to the recruitment patterns of several damselfish species and one species of wrasse (*Thalassoma bifasciatum*) in San Blas, Caribbean Panama (~9.5°N) (Robertson 1990; Robertson et al. 1999). Recruitment of these fishes in San Blas is lower during the dry season (December to April) when northerly tradewinds produce heavy wave action. Species-specific peaks in recruitment occur throughout the wet season (May to November) when winds are lighter. Other studies at San Blas have recorded similar seasonality of larval supply of damselfish and *T. bifasciatum* (Victor 1986; Wilson 2001). Likewise, wind appears to strongly influence the patterns of reef fish recruitment on lower latitude reefs in the southern hemisphere. In Kimbe Bay, Papua New Guinea (~5.5°S), recruitment of many species of wrasses (but not damselfishes) is lower between July and

August, when monsoon winds are strongest (Srinivasan and Jones 2006).

Some general effects of wind, water temperature and rainfall emerge from the few studies of reef fish recruitment carried out at low latitude sites to date. The annual trend in wind strength in relation to temperature is somewhat similar between the Philippine and Caribbean sites studied (Lemberget et al. 2009; this study). It is likely that in other lower latitude sites with similar environmental conditions, wind and temperature interact to influence recruitment patterns of many species. However, further insights about temperature are precluded by the absence of an evaluation of its effect on fish recruitment patterns at other locations such as Kimbe Bay (the annual water temperature range there is <2°C) (Srinivasan and Jones 2006). Studies to date suggest that rainfall is influential only in areas that have an extremely pronounced wet season. For example, in Kimbe Bay, strong rainfall may persist for many weeks and reach more than 600 mm month^{-1} during the wet season (Srinivasan and Jones 2006). Heavy rainfall at that site seemed to negatively affect the recruitment of damselfishes (Srinivasan and Jones 2006). In contrast, rainfall at the Philippine and Caribbean sites is considerably less during the wet season than in Kimbe Bay and had little effect on the recruitment of damselfishes and wrasses (Robertson 1990; Robertson et al. 1999; this study).

It is tempting to extrapolate the seemingly predictable effects of water temperature, wind and rainfall to the recruitment patterns of reef fishes in all equatorial regions. However, such predictable effects for all equatorial regions are unlikely. Recruitment patterns of one butterflyfish and one surgeonfish in this study were opposite to the dominant pattern, i.e., settlement in these species was more favourable during the cooler and windier months. Other studies conducted at lower latitude reefs, including those that investigated the effects of environmental variables on larval development and settlement success in detail, highlight species-specific responses and contrasting patterns even among closely related species (Sponaugle and Cowen 1994, 1997; Robertson and Kaufmann 1998; Bergenius et al. 2005; Lemberget et al. 2009).

This study is an initial step in understanding the dynamics of recruitment of fishes on Indo-Pacific coral reefs situated in monsoonal environments. Similar studies in other equatorial locations that differ in the character of the monsoons and the degree of exposure to monsoonal conditions are warranted. More attention should also be given to resolving the patterns of spawning in the same locations to test hypotheses about the degree of coupling between timing of reproduction and larval survival. A reliable understanding of the role of the monsoons, temperature and rainfall in shaping the seasonality of spawning, and recruitment may prove useful in determining year-to-year recruitment strength, something that remains difficult to predict for fish populations in lower latitude reefs because of extended annual breeding periods.

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