

# Environmental influences on the replenishment of lizardfish (family Synodontidae) in Caribbean Panama

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**Abstract** Lizardfish (family Synodontidae) are little studied despite their potentially important predatory role in epibenthic coral reef communities. The present study documented the temporal and spatial larval supply patterns of five Caribbean lizardfish species together with environmental variables (solar radiation, rainfall, water temperature, onshore-offshore winds, alongshore winds and wind-induced turbulence) to examine: (1) whether species within the same family respond differently to their developmental environment and (2) if larval supply in year-round warm waters is influenced by climatic changes. To address these questions, late-stage larvae of *Synodus foetens*, *Synodus intermedius*, *Synodus poeyi*, *Saurida suspicio* and *Saurida brasiliensis* were collected in replicate light traps in three different reef habitats (back-reef, lagoon and exposed) in the San Blas Archipelago, Panama, over 18 consecutive lunar months. Although replenishment of lizardfish occurred year-round, the temporal and spatial supply patterns were species-specific: *S. foetens*, *S. intermedius* and *S. poeyi* were most abundant during the dry season while *S. suspicio* and *S. brasiliensis* were most prevalent during the wet season. When seasons were analysed separately, water temperature explained 39 and 26% of the variance in light trap catches of

*S. foetens* and *S. intermedius*, respectively, in the dry season while wind-induced turbulence accounted for 25% of the variability in *S. suspicio* and *S. brasiliensis* catches during the wet season. These findings stress the importance of analysing larval supply in conjunction with environmental data at a high taxonomic resolution to better understand the mechanisms that drive replenishment in reef systems at low latitudes.

**Keywords** Recruitment · Supply · Larvae · Temperature · Turbulence · Coral reef

## Introduction

Tropical coral reefs are complex and diverse systems, yet the ecological role of many cryptic species and their contribution to food webs, energy flow and maintenance of reef communities have been largely ignored (e.g., Depczynski and Bellwood 2003). This knowledge is particularly important when assessing resilience and recovery processes of coral reefs (e.g., Bellwood et al. 2004). Most replenishment studies of reef-associated fish have focused on abundant and often conspicuous species, which are typically planktivores or herbivores/detritivores, while the replenishment dynamics of cryptic predatory species, such as lizardfish (family Synodontidae), have seldom been studied. Although lizardfish are a common component of tropical reef systems and may have a strong influence on the structure of epibenthic communities because of their predatory role (Sweatman 1984), information on their biology and ecology is scarce. Documenting temporal fluctuations in larval distribution and abundance patterns is an important step towards understanding more about the population dynamics and ecology of this group of benthic predators.

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Sampling in tropical waters has often been hindered by the rare and patchy distributions of early to late-stage larvae and the difficulty of identifying them beyond family level (Leis and McCormick 2002). The majority of distribution and abundance studies of pre-settlement stage reef-associated larvae have consequently been examined at the family level or above. Species within one family may respond differently to the same developmental environment (e.g., Papua New Guinea: Srinivasan and Jones 2006; Caribbean Panama: Robertson and Kaufmann 1998), but this information is likely to be masked when several species of the same family are pooled together (McCormick and Milicich 1993; Kingsford and Finn 1997). Moreover, members of the same family may exhibit very different life history strategies (Thresher et al. 1986; Robertson and Kaufmann 1998; Depczynski and Bellwood 2005) and replenishment fluctuations will affect the adult populations of these species differently. Short-lived species with rapid maturation will be affected more severely by temporal variability in replenishment than longer-lived species (Robertson and Kaufmann 1998). Detailed information about replenishment processes at a high taxonomic resolution is necessary to gain insight into the dynamics of adult populations and has important implications for management and conservation models.

Larval fish supply to tropical reefs fluctuates at all time scales examined, ranging from days to years (e.g., Robertson and Kaufmann 1998; Wilson 2001; Lozano and Zapata 2003; D'Alessandro et al. 2007). Temporal variability in spawning patterns explains some of this variability (e.g., Meekan et al. 1993; McIlwain 2002), although studies have often failed to detect a strong link between reproductive output and replenishment strength (e.g., Robertson et al. 1993; Srinivasan and Jones 2006). This decoupling of production and replenishment suggests that biological and physical processes during the planktonic phase may account for much of the variability in larval supply. While spawning and recruitment at high latitudes are strongly seasonal and often driven by environmental conditions such as temperature (Cushing 1995), equatorial waters tend to have year-round replenishment (Robertson 1992; Wilson 2001; Srinivasan and Jones 2006). Few studies have examined the effect of seasonal changes in environmental variables, such as temperature, rainfall and solar radiation, on larval supply at such low latitudes (Wilson and Meekan 2001). Although pelagic conditions at low latitudes may fluctuate less throughout the year, replenishment processes may still respond to climatic changes associated with dry and wet seasons. For example, in Caribbean Panama heavy rainfall during the wet season can potentially influence primary production and larval feeding conditions in nearshore waters because of increased nutrient-rich terrestrial runoff, while the strong

onshore winds during the dry season may influence spawning activity, fertilisation success, larval transport, feeding rates and growth (Robertson et al. 1999 and references therein). The dry season also has higher solar radiation and slightly lower temperatures that may influence larval replenishment and growth (Wilson and Meekan 2001; Bergenius et al. 2005). Examining the relationship between temporal supply patterns and environmental variables is an important starting point in understanding the processes that regulate replenishment in low latitudinal waters.

The aim of the present study was to document the temporal and spatial larval supply patterns of five species of Caribbean lizardfish in the San Blas Archipelago, Panama. Previously, Wilson (2001) examined late-stage lizardfish larvae at the family level and found them to be abundant in light traps all throughout the year in San Blas. In this study, however, lizardfish larvae were studied at a higher taxonomic resolution and in conjunction with environmental variables to answer the following questions: (1) Do closely related species respond differently to their larval environment? (2) Is larval supply influenced by environmental cues, such as temperature, at very low latitudes where seasonal changes tend to be subtle? Identifying the environmental attributes that influence the temporal patterns of larval fish abundance at the species level is the first step to building predictive models of population dynamics and will aid in the future management of coral reef systems under climatic change.

## Materials and methods

### Study species

Temporal and spatial supply patterns were examined for five late-stage larval lizardfish (family Synodontidae): *Synodus foetens*, *Synodus intermedius*, *Synodus poeyi*, *Saurida suspicio* and *Saurida brasiliensis*. Two more lizardfish species, *Synodus synodus* and *Trachinocephalus myops*, occurred in very small numbers during the sampling period. They were omitted from the temporal and spatial analyses because of their low abundances. Lizardfish belong to the order Aulopiformes and represent an abundant component of light trap catches in the Caribbean (e.g., Valles et al. 2001; Wilson 2001). They have a bipartite lifecycle with a pelagic larval stage and a bottom-dwelling adult stage that can be reef-associated. Lizardfish are known to be voracious predators of small fish and crustaceans (Sweetman 1984). Larvae were identified according to Ditty et al. (2006) and B. Victor (pers. comm.). Two lizardfish species, *S. intermedius* and *S. poeyi*, exhibit similar morphological features as pre-settlement stage larvae and great

care was taken to ensure correct identification at a high morphological resolution.

### Study area

The study was conducted in the San Blas Archipelago, which extends along the Caribbean coast of Panama (9°34' N, 78°58' W). The San Blas has two distinct seasons, a dry season from mid-December to mid-April and a wet season from mid-April to mid-December. The dry season is characterised with strong onshore (northerly) winds and slightly cooler water temperatures while the wet season has heavy rainfalls, light and variable winds and warmer temperatures. Average sea surface temperatures only fluctuate by a couple of degrees Celsius throughout the year and the annual variation in water level amounts to ~50 cm (e.g., Robertson et al. 1999; Wilson 2003). The tidal regime changes seasonally with complex patterns of diurnal and semi-diurnal tides. The waters around the San Blas Archipelago represent an oligotrophic environment with no wind-induced upwelling (D'Croz et al. 1999); however, nutrient-rich terrestrial runoff may enrich the nearshore waters during wet season (D'Croz et al. 1999). The reef system itself is penetrated with a number of channels resulting in a complex pattern of water currents (Robertson et al. 1999).

### Sampling protocol

Late-stage larvae were collected in light traps over 18 consecutive lunar months from December 1996 to June 1998 encompassing one wet season and two dry seasons. Light traps enable replicate sampling in many locations simultaneously providing a synoptic picture of supply patterns within a reef system (Doherty 1987). They can be deployed in a range of different habitats, in contrast to stationary nets (i.e., crest and channel nets) that require locations with higher current flows or wave action. Due to the small tidal range in San Blas, light traps are better suited for sampling late-stage larvae at both temporal and spatial scales (Wilson 2003). Since light traps are active sampling devices, they are selective towards photopositive larvae and may introduce sampling bias in certain environmental conditions, such as high turbidity and current speeds; the latter is likely to favour stronger swimmers. Potential sampling bias was believed to be minimised in the present study because of low turbidity levels in San Blas coupled with relatively low current flow (D'Croz and Robertson 1997). The light traps were moored just below the surface in three different reef habitats: back-reef, lagoon and exposed. Three replicate light traps were deployed at each site about 100 m apart and 50–100 m away from the reef edge. A detailed description of the

sampling design is outlined in Wilson (2001). Reef fish larvae usually arrive on the reef to settle in lunar pulses (e.g., Robertson 1992; Sponaugle and Cowen 1996a). Light traps were therefore sampled for 19 consecutive days centred on the new moon in each lunar month resulting in 342 days of total sampling. Light traps collect late-stage larvae ready to settle into their juvenile/adult habitat. Previous findings show a strong correlation between magnitude of reef fish settlement and light trap catches (e.g., Milicich et al. 1992; Sponaugle and Cowen 1996b; Valles et al. 2001). Here monthly light trap catches are used as a relative measurement of supply of late-stage larvae ready to settle.

### Environmental data collection

Rainfall ( $\text{mm d}^{-1}$ ), solar radiation ( $\text{W m}^{-2} \text{h}^{-1}$ ), wind speed ( $\text{m s}^{-1}$ ) and direction (degrees), water temperature ( $^{\circ}\text{C}$ ) and tidal range (cm) were recorded near the Smithsonian Research Station in San Blas as a part of the Smithsonian monitoring program. Most data were recorded hourly except for water temperature that was measured every 106 min and water level that was monitored every 6 s. Rainfall was calculated as total precipitation per day and tidal range was calculated as maximum difference in water level at night (during the hours of sampling; from 1800 h to 0600 h). All other variables were calculated as daily averages. Wind-induced turbulence ( $\text{W kg}^{-1}$ ) (e.g., Mackenzie and Leggett 1993; Utne-Palm and Stiansen 2002) was calculated from a boundary layer model (Oakey and Elliott 1982; Oakey 1985; Agrawal et al. 1992), based on the energy dissipation rates ( $\varepsilon$ ) and wind and depth:

$$\varepsilon = [(p_a/p_w)C_D]^{3/2} \times [W^3/(0.4z)] \times (1\text{Wm}^{-3}/0.001\text{m}^2\text{s}^{-3}) \\ = (5.82 \times 10^{-9})W^3/z,$$

where  $p_a$  = density of air ( $1.2 \text{ kg m}^{-3}$ , Loder and Greenberg 1986),  $p_w$  = density of seawater ( $1,025 \text{ kg m}^{-3}$ , Lueck 1988),  $C_D$  = coefficient of drag between the water surface and the wind (0.0015, Loder and Greenberg 1986),  $W$  = daytime wind speed ( $\text{m s}^{-1}$ ), 0.4 = von Karmann's constant (Lumley and Panofsky 1964) and  $z$  = sampling depth (1.5 m).

Wind velocity and direction were combined into two orthogonal vectors representing onshore-offshore (north-south; NS) and alongshore (east-west; EW) winds (e.g., Bergenius et al. 2005). The vectors were derived by applying cosine (NS) and sine (EW) functions to daily wind directions that had been converted into trigonometric degrees, and then multiplied with daily wind speed. Each vector contains information about wind direction as indicated by positive (north or east) and negative (south or west) signs and the magnitude of wind speed.

As environmental data were only available for 339 of the 342 sampling days, any analysis with environmental variables was examined for the duration of the 339 days.

## Data analysis

### *Seasonal and spatial comparisons*

Magnitudes of temporal supply for each species were compared between the dry and wet seasons and between the two dry seasons using Mann–Whitney *U*-tests. The magnitude of larval supply among the three reef habitats was compared for the entire data set and separately for dry and wet seasons. As the data failed to meet the assumptions for ANOVA, Kruskal–Wallis analysis for ranks was applied. If the result was significant, a Mann–Whitney *U*-test with the corresponding Bonferroni corrected  $\alpha$  of 0.02 was used for post hoc paired comparisons.

Due to one single night of high larval influx of *S. foetens*, *S. intermedius* and *S. poeyi* in lunar month 16, data analyses were run twice; once with and once without the data point. This protocol was followed because the single data point may obscure any underlying patterns representative for the remaining 341 days.

### *Time-series analysis*

Day-to-day comparisons between environmental variables and light trap catches were examined using time-series analysis. Total larval catches and environmental variables (solar radiation, rainfall, temperature, tidal range, NS and EW vectors and wind-induced turbulence) for each sampling day were concatenated into single time-series of 339 days for each variable. Some of the environmental data contained missing values. These were replaced by taking the mean of adjacent data points (e.g., Milicich et al. 1992). When missing values occurred over several days, as was the case for the wind and tidal data, these were omitted from the final analysis in order to not introduce bias. Data sampled over successive time intervals tend to be non-independent. Stationarity is a prerequisite for time-series analysis and it was therefore important to remove any autocorrelation and cyclic patterns in the data set prior to analysis. Stationarity was examined using autocorrelation function (ACF) and partial autocorrelation function (PACF) of the raw data after it had been  $\ln(x + 1)$  transformed to stabilise the variance. Autoregressive Integrated Moving Average (ARIMA) models were then fitted to the time-series. Although ARIMA models are frequently used for forecasting purposes, they were here only used as a means of filtering to remove non-stationarity. The number of *p* (autoregressive), *d* (difference) and *q* (moving average) parameters used in the ARIMA models were

determined by examining the ACF and PACF plots for each variable. Each model was run several times with a different combination of parameters. The model residuals were then analysed in ACF and PACF plots to ensure that non-stationarity had been removed. The normal distribution and variance of the residuals were also examined in order to determine the best model fit. In addition, the test parameters Schwarz's Bayesian Criterion (SBC), the Durbin–Watson coefficient and the Box–Ljung statistic were applied to assess the suitability of the model. Once the best models were determined, the residuals from these models were used in cross-correlation functions (CCFs) for pairwise comparisons between larval supply and environmental variables. The CCF examines the day-to-day influence of a single environmental variable on larval supply at different time lags. Maximum number of lags included in the analysis was set to 6 days and negative lags were not considered meaningful and hence ignored (Kingsford and Finn 1997). Time-series analysis was applied for the entire data set and separately for the dry and wet seasons.

The synchrony of daily supply among the three reef habitats was examined by separating the total daily light trap catches of each species by habitat. Time-series of 342 days were then compared between habitats using cross-correlation functions following the same procedure as described above.

### *Univariate regression tree analysis*

Nonparametric univariate regression tree models were used as an exploratory tool to analyse the influence of environmental variables on the abundance of *S. foetens*, *S. intermedius*, *S. poeyi*, *S. suspicio* and *S. brasiliensis*. These represent a powerful tool for analysing complex ecological data because of the way they deal with count data (that can contain many zeros), non-linearity, different types of response variables (e.g., continuous, categorical) and their invariance to transformation of explanatory variables (De'ath and Fabricius 2000). From the available explanatory variables the model determines the best binary split of the response variable so that the between-group variances are maximised relative to the within-group variances. Hence each split forms increasingly homogeneous groups that are mutually exclusive and the variance explained increases with each split until 100% of the variance is accounted for. Cross-validation is a commonly used method to determine the number of splits that best describes the significant systematic variation in the data (De'ath and Fabricius 2000). The response variables (*S. foetens*, *S. intermedius*, *S. poeyi*, *S. suspicio* and *S. brasiliensis*) were fourth-root transformed to stabilise the variance. Total light trap catches for each species were pooled per 3 days to reduce the presence of zeros. The

explanatory variables consisted of rainfall, solar radiation, water temperature, tidal range, NS and EW vectors and wind-induced turbulence. Missing values were dealt with in the same manner as for the time-series analysis. A series of 50 10-fold cross-validations were run for each model to select the best size tree using the 1-SE rule (De'ath and Fabricius 2000). Analyses were run for the entire data set and separately for the dry and wet seasons.

All data analyses were ran in SPSS except regression tree analyses that were conducted in S-plus (see De'ath and Fabricius 2000).

## Results

### Composition

Seven species of lizardfish were identified in the light trap catches during the 18 lunar months of sampling. The most abundant species was *S. foetens* with 772 larvae followed by *S. intermedius*, *S. suspicio* and *S. poeyi* with 767, 747 and 721 larvae, respectively. *S. brasiliensis* was the fifth most abundant species with 195 larvae. Two lizardfish species were excluded from further analysis because of their very low numbers: 26 *Trachinocephalus myops* larvae and 14 *Synodus synodus* larvae.

### Temporal larval supply patterns

*Synodus foetens*, *S. intermedius*, *S. poeyi* and *S. suspicio* were present in all 18 lunar months of sampling, while *S. brasiliensis* occurred in all months except one (Fig. 1a–e). The magnitudes of catches, however, varied considerably between months and displayed species-specific peaks. The temporal supply patterns of all species were characterised by generally low daily abundances disrupted by a few high pulses of larval influx. Species within the same genus displayed similar temporal abundance patterns. *S. foetens*, *S. intermedius* and *S. poeyi* larvae were most prevalent from the end of wet season and through the second dry season (Fig. 1a–c). *S. foetens* and *S. poeyi* larvae were most abundant in lunar month 16 in the second dry season, while *S. intermedius* larvae were caught in highest numbers in lunar month 11 in the wet season. A high number of *S. poeyi* (262 larvae), *S. foetens* (143 larvae) and *S. intermedius* (23 larvae) were collected in the lagoon during one night of sampling in lunar month 16. This single data point contributed considerably to the total abundance of larvae caught in this month, and comprised one-third of the total number of *S. poeyi* larvae collected during the sampling period. No *S. suspicio* or *S. brasiliensis* larvae were sampled during this night. *S. foetens* larvae were least abundant in lunar month 4 and 5 in the

dry and wet season, respectively. *S. intermedius* larvae were least abundant in lunar month 10 while *S. poeyi* larvae were least abundant in lunar month 9 in the wet season. *S. suspicio* larvae were more evenly distributed throughout the sampling period (Fig. 1d). Catches were highest in lunar month 10 and lowest in lunar month 15 in the second dry season. Larvae of *S. brasiliensis* occurred in low numbers throughout the sampling period except for two higher pulses in lunar month 7 and 11 in the wet season (Fig. 1e). The high influx of *S. brasiliensis* larvae in lunar month 11 occurred over one single night and coincided with high catches of *S. foetens*, *S. intermedius* and *S. poeyi*.

### Seasonality

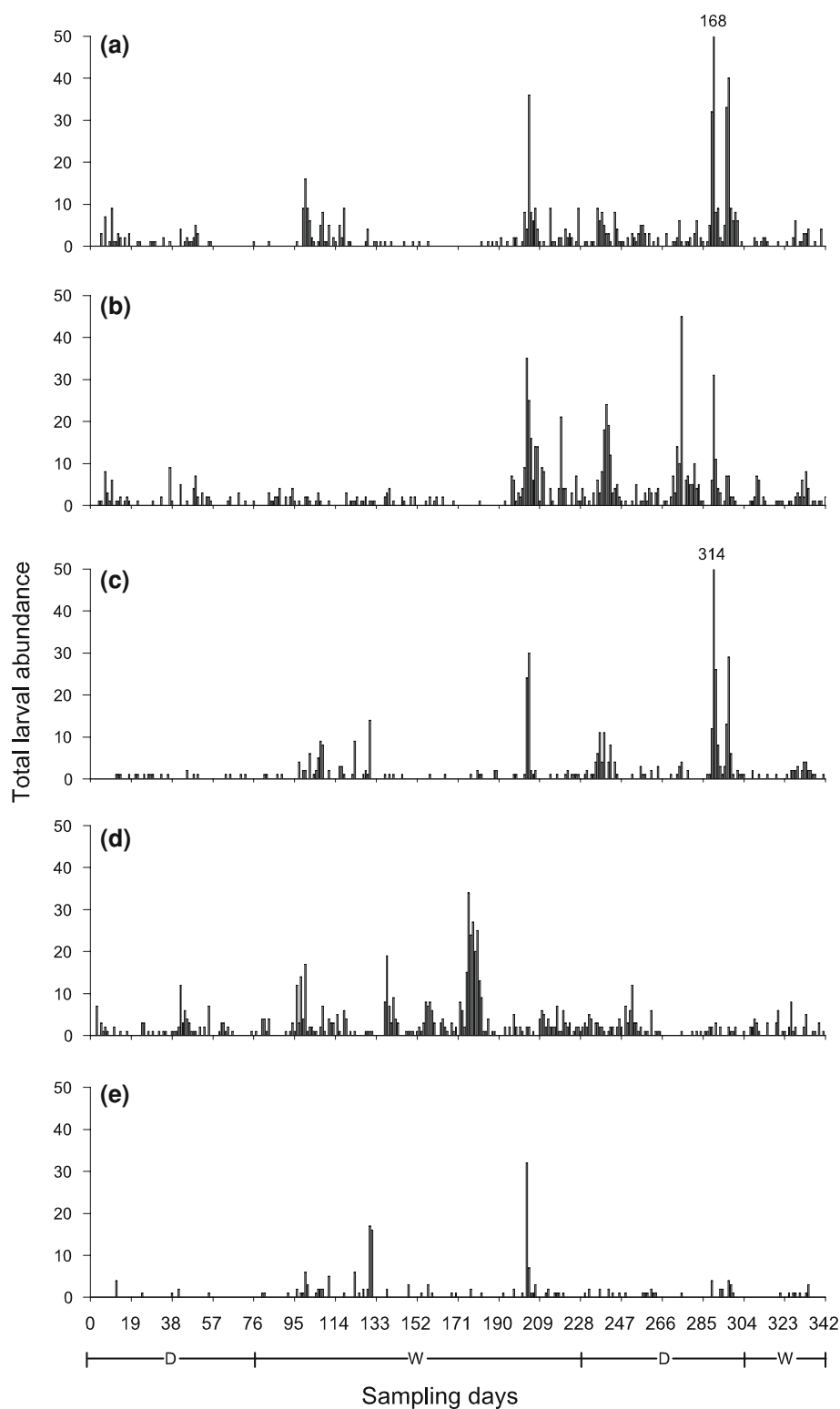
Although larvae were caught in light traps all throughout the year, four of five species exhibited seasonal abundance patterns. *S. foetens*, *S. intermedius* and *S. poeyi* were significantly more abundant during the dry season (Mann–Whitney *U*-test,  $P < 0.05$ ), while *S. suspicio* larvae were significantly more abundant during the wet season (Mann–Whitney *U*-test,  $P < 0.05$ ). All species, except *S. suspicio* were more abundant in light trap catches during the second dry season compared with the first dry season (Mann–Whitney *U*-test,  $P < 0.05$ ).

### Spatial distribution

*Synodus foetens* larvae were more abundant in the lagoon compared with the back-reef (Mann–Whitney *U*-test,  $P < 0.02$ ) but otherwise there were no differences between habitats (Fig. 2a). When the single data point of high influx in lunar month 16 was omitted from the analysis, catches were lower in the lagoon than in the back-reef (Fig. 2b, Mann–Whitney *U*-test,  $P < 0.02$ ). During the dry season larval catches were higher in the lagoon compared with the back-reef and the exposed reef (Mann–Whitney *U*-test,  $P < 0.02$ ), while there was no significant difference between the latter two reef habitats (Fig. 3a). *S. foetens* larvae occurred in lower numbers in the lagoon compared with the back-reef when the data point of high influx was excluded (Fig. 3b, Mann–Whitney *U*-test,  $P < 0.02$ ). There was no significant difference in larval supply between the three habitats in the wet season (Fig. 3a).

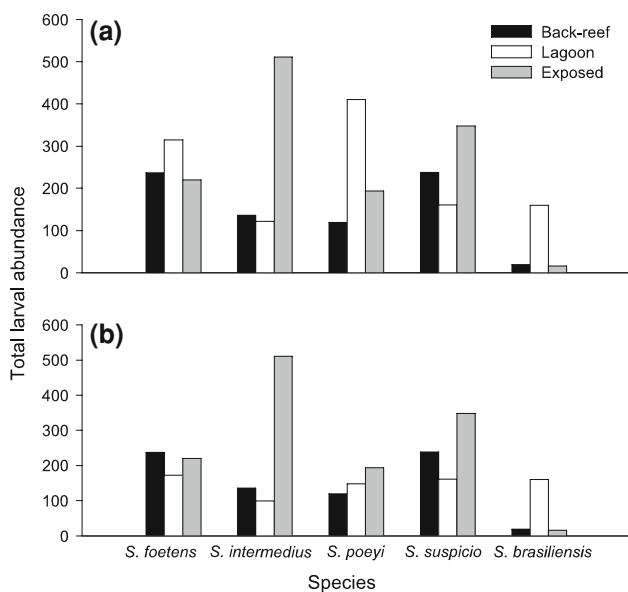
Catches of *S. intermedius* larvae were higher in the exposed habitat compared with the back-reef and the lagoon (Mann–Whitney *U*-test,  $P < 0.02$ ), while there was no significant difference between the latter two habitats (Fig. 2a). There were no changes in this abundance pattern when the single data point of high influx in lunar month 16 was omitted from the analysis (Fig. 2b). During the dry season larvae were most prevalent in the exposed habitat

**Fig. 1** Total daily light trap catches of (a) *Synodus foetens*, (b) *Synodus intermedius*, (c) *Synodus poeyi*, (d) *Saurida suspicio* and (e) *Saurida brasiliensis* that have been concatenated into a single time-series of 342 days. Larvae were sampled over 19 days centred on the new moon for 18 consecutive lunar months. The category between the tick marks on the x-axis represents one lunar month. D and W indicate dry and wet seasons, respectively



followed by the back-reef and the lagoon (Fig. 3c, Mann–Whitney  $U$ -test,  $P < 0.02$ ). This pattern remained the same when the data point of high influx was excluded from the analysis (Fig. 3d, Mann–Whitney  $U$ -test,  $P < 0.02$ ). In

the wet season larvae were caught in higher numbers in the exposed habitat compared with the lagoon and the back-reef (Fig. 3c, Mann–Whitney  $U$ -test,  $P < 0.02$ ). There was no difference in abundance between the latter two habitats.



**Fig. 2** Distribution of total light trap catches of *Synodus foetens*, *Synodus intermedius*, *Synodus poeyi*, *Saurida suspicio* and *Saurida brasiliensis* among the three reef habitats (back-reef, lagoon and exposed) for (a) the entire sampling period and (b) the entire sampling period excluding the single data point of high larval influx in the lagoon in lunar month 16

*Synodus poeyi* larvae were more abundant in the lagoon compared with the exposed habitat and the back-reef (Fig. 2a, Mann–Whitney  $U$ -test,  $P < 0.02$ ). When the data point of high influx in lunar month 16 was excluded from the analysis, however, larval abundances were highest in the exposed habitat followed by the lagoon and the back-reef (Fig. 2b, Mann–Whitney  $U$ -test,  $P < 0.02$ ). There was no significant difference between the latter two habitats. During the dry season larvae were more abundant in the lagoon compared with the other two habitats (Mann–Whitney  $U$ -test,  $P < 0.02$ ), while there was no significant difference between the back-reef and the exposed reef (Fig. 3e). When the data point of high influx was excluded, larvae were less abundant in the lagoon compared with the back-reef and the exposed habitat (Fig. 3f, Mann–Whitney  $U$ -test,  $P < 0.02$ ). There was no significant difference in larval abundance between the three habitats during the wet season (Fig. 3e).

Catches of *S. suspicio* larvae were lower in the lagoon compared with the back-reef and the exposed reef (Fig. 2a, Mann–Whitney  $U$ -test,  $P < 0.02$ ). There was no significant difference between the latter two habitats. During the dry season larvae occurred in lower numbers in the lagoon (Mann–Whitney  $U$ -test,  $P < 0.02$ ), while there was no difference in larval supply between the exposed habitat and the back-reef (Fig. 3g). In the wet season larvae were more abundant in the exposed habitat compared with the back-reef

and the lagoon (Mann–Whitney  $U$ -test,  $P < 0.02$ ), while there was no difference between the latter two habitats (Fig. 3g).

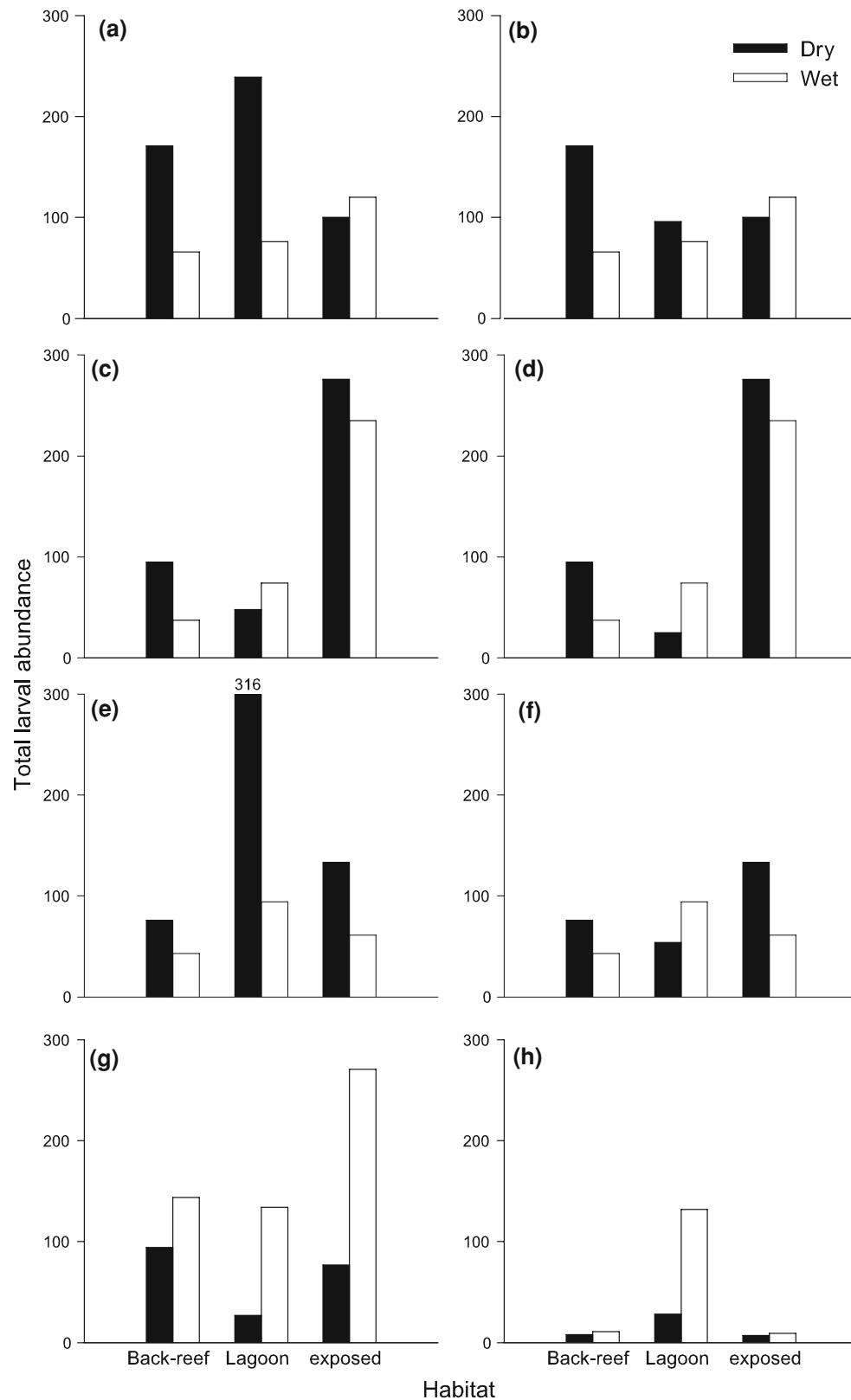
*Saurida brasiliensis* larvae were more prevalent in the lagoon compared with the back-reef and the exposed reef (Fig. 2a, Mann–Whitney  $U$ -test,  $P < 0.02$ ). There was no difference in larval abundance between the latter two reef sites. During the dry season there were no significant differences between the three habitats (Fig. 3h). In the wet season catches were higher in the lagoon compared with the back-reef and the exposed reef (Mann–Whitney  $U$ -test,  $P < 0.02$ ), while there was no difference in catches between these latter two reefs (Fig. 3h).

#### Daily supply patterns among reef habitats

The synchrony in daily catches between the three reef habitats was in general weak and variable for most species with an exception of *S. poeyi* catches that were slightly more synchronised (Table 1a–c). When the time-series were separated by seasons, however, there was a stronger cross-correlation in the dry season compared with the wet season. The synchrony between day-to-day supply in the dry season was strongest between the exposed habitat and the lagoon at no time lag (Table 1b, *S. foetens*:  $r = 0.42$ ; *S. poeyi*:  $r = 0.40$ ; *S. suspicio*:  $r = 0.25$ ; *S. brasiliensis*:  $r = 0.37$ ). Because of the low abundances of *S. brasiliensis* larvae in the back-reef and exposed habitat, however, the results for this species have to be treated cautiously. There was a higher synchrony in the daily catches of *S. poeyi* during both dry and wet seasons compared with the other species.

#### Environmental conditions

The months of the wet season were characterised with higher rainfall and sea surface temperatures, reduced solar radiation and weaker and more variable winds. The dry season exhibited stronger onshore (northerly) and along-shore (easterly) winds that resulted in higher levels of wind-induced turbulence (Fig. 4a–g). The tidal level ranged from 6.6 to 42.2 cm during the sampling period and was shorter and more diurnal in nature during the dry season compared with the wet season (Table 2). Temperatures ranged from 27.2 to 30.0°C during the course of the study (Table 2). Mean, maximum and minimum temperatures were nearly one degree lower in the first dry season compared with the second dry season, while onshore and alongshore winds were stronger and the alongshore winds were predominately easterly. The second dry season was characterised by lighter and more varied alongshore winds and higher levels of precipitation.



**Fig. 3** The distribution of total larval catches of (a) *Synodus foetens*, (b) *S. foetens* excluding the single data point of high larval influx in lunar month 16, (c) *Synodus intermedius*, (d) *S. intermedius* excluding the data point of high influx, (e) *Synodus poeyi*, (f) *S. poeyi*

excluding the data point of high influx, (g) *Saurida suspicio* and (h) *Saurida brasiliensis* among the three reef habitats (back-reef, lagoon, exposed) for dry and wet seasons



**Table 1** Significant cross-correlations (significant at 2 SE) for pairwise comparisons between day-to-day larval supply of *Synodus foetens*, *Synodus intermedius*, *Synodus poeyi*, *Saurida suspicio* and*Saurida brasiliensis* among the three reef habitats (back-reef, lagoon and exposed) for (a) the entire data set, (b) dry season and (c) wet season

Habitat	<i>S. foetens</i>	<i>S. intermedius</i>	<i>S. poeyi</i>	<i>S. suspicio</i>	<i>S. brasiliensis</i>
(a) All months					
Exposed versus lagoon	0.25 (0)	ns	0.29 (0)	0.23 (0)	ns
Exposed versus back-reef	ns	0.18 (0)	0.31 (0) 0.25 (1)	0.21 (0)	ns
Lagoon versus Back-reef	0.12 (0)	0.17 (0)	0.35 (1)	ns	ns
(b) Dry season					
Exposed versus lagoon	0.42 (0)	ns	0.40 (0)	0.25 (0)	0.37 (0)
Exposed versus back-reef	ns	0.33 (0)	0.32 (0) 0.27 (1)	0.24 (2)	ns
Lagoon versus Back-reef	0.15 (1)	0.21 (1)	0.36 (1)	ns	ns
(c) Wet season					
Exposed versus lagoon	0.18 (0)	ns	ns	0.20 (0)	ns
Exposed versus back-reef	0.19 (0)	ns	0.27 (0) 0.18 (1)	0.28 (0)	ns
Lagoon versus Back-reef	0.18 (0) 0.17 (1)	0.19 (1)	0.31 (1)	0.18 (2)	0.20 (1)

The parentheses show number of lags at which the correlation is significant. Non-significant correlations are indicated by ns

### Dynamics between daily supply patterns and environmental variables

Day-to-day comparisons between larval supply and environmental variables using pairwise cross-correlations revealed a few very weak correlations with no meaningful pattern. No generalisation of the daily dynamics between larval supply and environmental variables was therefore possible.

### Regression tree analysis

Regression tree analysis for the entire sampling period showed that wind and temperature accounted for most of the variation in the temporal supply patterns (Table 3a). Temperature explained 24% of the variability in the supply pattern of *S. foetens*, with the highest number of larvae caught at temperatures between 28 and 29°C. Only very few larvae were caught at temperatures below 28°C. Alongshore winds explained 17% of larval supply for *S. brasiliensis*. Most *S. brasiliensis* larvae were caught in light traps when alongshore winds were predominately westerly. Onshore-offshore winds accounted for 13% of the variance in *S. suspicio* catches. Highest abundance of larvae occurred when the onshore-offshore winds were below 2.1 m s<sup>-1</sup>. Larval supply of *S. intermedius* and *S. poeyi* was not explained by any environmental variables in the regression tree analysis.

When dry and wet seasons were analysed separately, environmental variables explained a higher proportion of the variability in larval supply. In the dry season, temperature accounted for 39 and 26% of the variance in *S. foetens* and *S. intermedius* catches, respectively (Table 3b). Light trap catches of both *S. foetens* and

*S. intermedius* were highest in magnitude when the water temperature exceeded 28°C. No variables accounted for the variance in the catches of *S. poeyi*, *S. suspicio* and *S. brasiliensis* during the dry season.

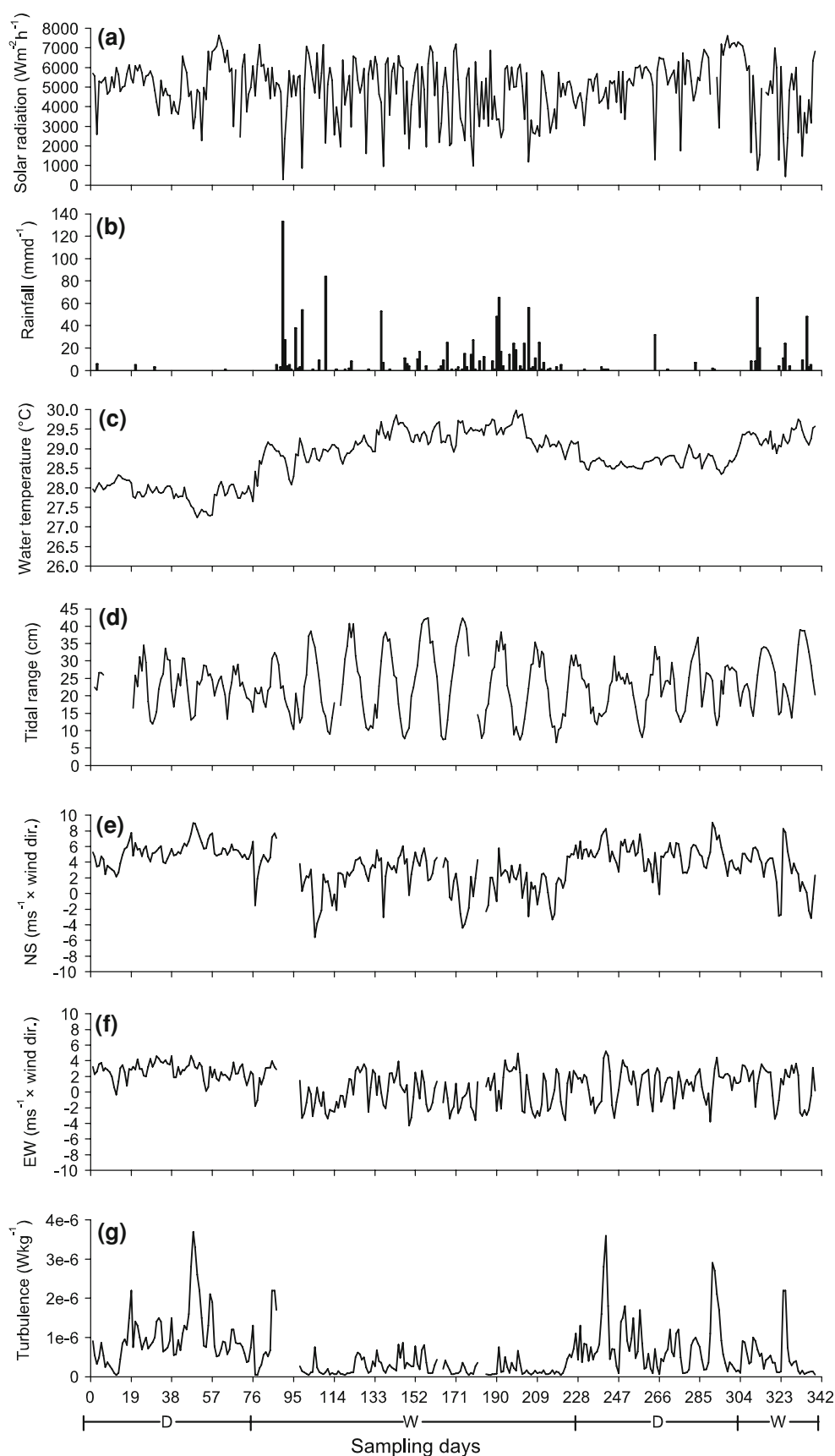
During the wet season wind-induced turbulence equally explained 25% of the variability in light trap catches of *S. suspicio* and *S. brasiliensis*, while no variables accounted for the variance in the catches of *S. foetens*, *S. intermedius* and *S. poeyi* (Table 3c). Both *S. suspicio* and *S. brasiliensis* were most abundant at turbulence levels less than  $3.0 \times 10^{-7}$  and  $3.8 \times 10^{-7}$  W kg<sup>-1</sup>, respectively. Only a low number of *S. suspicio* larvae and very few *S. brasiliensis* larvae were caught in light traps when turbulence levels exceeded this value.

### Discussion

This study is a first step towards understanding the population dynamics of lizardfish in the Caribbean. It demonstrates the diverse supply patterns for lizardfish in the San Blas Archipelago and emphasises the need to analyse temporal and spatial patterns at the taxonomic resolution of the species. The result stresses the complex relationship between environmental factors and larval replenishment and reinforces the importance of water temperature and wind-induced turbulence as key environmental agents influencing larval dynamics at this low latitude location.

Although larval lizardfish were present in light traps throughout the sampling period, all study species exhibited some seasonality and species-specific peaks. *S. suspicio* and *S. brasiliensis* occurred in highest numbers during the wet season while *S. foetens*, *S. intermedius* and *S. poeyi*

**Fig. 4** Daily measurements of (a) solar radiation (b) rainfall (c) water temperature (d) tidal range (e) onshore-offshore wind vector (NS) (f) alongshore wind vector (EW) and (g) wind-induced turbulence concatenated into time-series of 339 days corresponding to the days of sampling during the present study. All measurements are daily averages except rainfall that was calculated as total daily precipitation. The positive values on the y-axis for the NS and EW wind vector graphs correspond to north and east, while the negative values correspond to south and west, respectively. The category between the tick marks on the x-axis represents one lunar month. D and W indicate dry and wet seasons, respectively. The discontinuous lines on some of the graphs (tidal range, wind and turbulence) represent missing values



**Table 2** The mean ( $\pm$ SD), maximum and minimum values of solar radiation, rainfall, water temperature, tidal range, wind speed and wind-induced turbulence for each of the two dry seasons (dry1 and dry 2) and the wet season

Variable	Season	Mean $\pm$ SD	Max	Min
Solar radiation ( $\text{Wm}^{-2} \text{h}^{-1}$ )	Dry 1	5209.45 $\pm$ 1151.11	7635.00	2256.00
	Dry 2	5473.42 $\pm$ 1234.84	7629.00	1301.00
	Wet	4595.55 $\pm$ 1649.08	7199.00	283.00
Rainfall ( $\text{mm day}^{-1}$ )	Dry 1	0.20 $\pm$ 0.95	6.00	0.00
	Dry 2	0.66 $\pm$ 3.73	32.00	0.00
	Wet	6.27 $\pm$ 16.14	133.00	0.00
Temperature ( $^{\circ}\text{C}$ )	Dry 1	27.87 $\pm$ 0.26	28.33	27.24
	Dry 2	28.67 $\pm$ 0.15	29.14	28.35
	Wet	29.21 $\pm$ 0.34	29.97	28.05
Tidal range (cm)	Dry 1	23.05 $\pm$ 5.49	34.50	11.90
	Dry 2	22.08 $\pm$ 6.49	36.80	8.10
	Wet	23.78 $\pm$ 9.74	42.40	6.60
Wind speed ( $\text{ms}^{-1}$ )	Dry 1	6.08 $\pm$ 1.39	9.83	2.17
	Dry 2	5.42 $\pm$ 1.66	9.75	2.55
	Wet	3.94 $\pm$ 1.34	8.33	2.08
Turbulence ( $\text{Wkg}^{-1}$ )	Dry 1	$0.01 \times 10^{-6} \pm 6.83 \times 10^{-7}$	$3.69 \times 10^{-6}$	$3.95 \times 10^{-8}$
	Dry 2	$7.96 \times 10^{-7} \pm 7.17 \times 10^{-7}$	$3.60 \times 10^{-6}$	$6.48 \times 10^{-8}$
	Wet	$3.28 \times 10^{-7} \pm 3.91 \times 10^{-7}$	$2.25 \times 10^{-6}$	$3.51 \times 10^{-8}$

were most abundant during dry season. These species were not only most prevalent at different times of the year but also when the environmental conditions were markedly different. Similar findings have been documented for other fish families in San Blas (Robertson and Kaufmann 1998; Wilson 2001) and recently also in the equatorial waters of the West Pacific (Papua New Guinea: Srinivasan and Jones 2006) suggesting diverse replenishment strategies among closely related species at low latitudes. The present findings clearly illustrate the need to analyse supply patterns at the species level and have important implications for the input data used in predictive models to aid the management of coral reefs.

Spawning in higher latitudinal waters is believed to occur during time periods when conditions for larval growth and survival are optimal (e.g., Cushing 1995). These conditions may be extended for larger parts of the year near the equator, where annual fluctuation in water temperature is usually low, prompting the question of whether environmental influences still play an important role in replenishment processes at very low latitudes. When dry and wet seasons were analysed separately in the present study, temperature accounted for 38.7 and 25.7% of the temporal variability in *S. foetens* and *S. intermedius*, respectively, during the dry season. Larvae were most abundant when the temperature was above 28°C. The first dry season had minimum, maximum and mean water temperatures of nearly one degree lower than the second dry season. A temperature change of one degree could potentially influence production cycles and survivorships of eggs and larvae in a system with such small annual temperature fluctuation. Larvae residing in year-round warm

waters may exhibit a narrower window of tolerance to temperature changes compared with their conspecifics at higher latitudes (Stevens 1996). For example, a common garden experiment showed that early post-settlement clownfish (*Amphiprion*) larvae from higher latitudes on the Great Barrier Reef displayed greater plasticity in growth rates compared with larvae from lower latitudes (Buechler 2005). Temperature has been identified as an important contributor to larval growth in tropical waters (e.g., McCormick and Molony 1995; Wilson and Meekan 2002; Meekan et al. 2003; Bergenius et al. 2005; Sponaugle et al. 2006), and it is a widely held view that small changes in growth rate and larval durations can have large consequences for larval survivorships (e.g., Houde 1987). Indeed, two studies have identified a link between larval growth and magnitude of replenishment in San Blas (*Acanthurus chirurgus*: Bergenius et al. 2002; *Stegastes partitus*: Wilson and Meekan 2002). These findings suggest that temperature may have an important influence on replenishment even in waters where the annual temperature range is very small. It highlights the importance of analysing larval supply in conjunction with environmental variables.

Lower temperatures coupled with stronger onshore (northerly) and more persistent alongshore (easterly) winds in the first dry season may have been a contributing factor to the smaller larval catches during this period. Strong onshore winds may influence larval replenishment in a number of ways from spawning activity and fertilisation success to larval transport and feeding (e.g., Robertson et al. 1999 and references therein). It is believed that favourable levels of wind-induced turbulence enhance

**Table 3** Output from the univariate regression tree analysis for (a) entire data set, (b) dry season and (c) wet season

Species	%var	CVE	SE	1st split	2nd split
(a) All months					
<i>S. foetens</i>	24.2	0.96	0.15	$T < 28.0$ (10.9)	$T > 29.0$ (13.3)
<i>S. intermedius</i>	–				
<i>S. poeyi</i>	–				
<i>S. suspicio</i>	12.9	1.00	0.16	NS > 2.1	
<i>S. brasiliensis</i>	16.8	1.02	0.12	EW > 0.3	
(b) Dry season					
<i>S. foetens</i>	38.7	0.70	0.18	$T < 28.0$	
<i>S. intermedius</i>	25.7	1.03	0.19	$T < 28.0$	
<i>S. poeyi</i>	–				
<i>S. suspicio</i>	–				
<i>S. brasiliensis</i>	–				
(c) Wet season					
<i>S. foetens</i>	–				
<i>S. intermedius</i>	–				
<i>S. poeyi</i>	–				
<i>S. suspicio</i>	24.6	0.94	0.20	Turb > $3.0 \times 10^{-7}$	
<i>S. brasiliensis</i>	24.8	0.93	0.15	Turb > $3.8 \times 10^{-7}$	

Given are the percent variance (%var) explained by the analysis, CVeror (CVE), standard error (SE) and the number of significant binary splits. Response variables were *Synodus foetens*, *Synodus intermedius*, *Synodus poeyi*, *Saurida suspicio* and *Saurida brasiliensis* and explanatory variables were solar radiation, rainfall, water temperature (T), tidal range, onshore-offshore (NS) and alongshore (EW) wind vectors and wind-induced turbulence (Turb). The value of each binary split is provided along with '<' and '>' signs to indicate whether the lowest larval abundance was less than or greater than the value of each split. The parentheses show the variance explained by each split, while '–' indicates that no tree was formed

larval feeding conditions because of increased encounter rates between larvae and their prey (e.g., Utne-Palm and Stiansen 2002; Utne-Palm 2004). Optimal levels of turbulence may translate into increased growth and survivorship of larvae (e.g., Gallego et al. 1996). In the present study wind-induced turbulence explained 25% of the variability in the temporal supply of *S. suspicio* and *S. brasiliensis* during the wet season. These results have to be treated with caution as they are only based on a mathematical estimate of wind-induced turbulence. Studies that have examined turbulence and larval feeding in both laboratory and field conditions have often obtained contradicting results (Dower et al. 1997; MacKenzie 2000). Optimal levels of turbulence are likely to depend on a number of parameters including turbidity, light, behaviour and the larva's vertical position in the water column (Dower et al. 1997; Utne-Palm and Stiansen 2002; Utne-Palm 2004). Nevertheless, the present findings suggest that climatic influences, such as temperature and wind regime, account for some of the

variability in lizardfish replenishment. Further research is required to test this hypothesis and to understand how environmental factors translate into larval performance, survival and replenishment success.

Some of the observed patterns of temporal replenishment may be due to the way environmental conditions interact with the sampling efficiency of light traps (e.g., Leis and McCormick 2002). Lindquist and Shaw (2005) observed that lizardfish, along with most reef-associated species, were rarely caught in light traps when current speeds exceeded  $40 \text{ cm s}^{-1}$  in the north-central Gulf of Mexico. Fortunately for the present study, the tidal flow in San Blas is very low (e.g., Wilson 2003) and current velocities reach a maximum of approximately half that found to be problematic by Lindquist and Shaw (2005). Furthermore, cross-correlation analyses showed no relationship between daily catches of larvae and wind stress. In the light of this, it seems reasonable to assume that the present results were not confounded by current-driven sampling bias.

When larval supply and environmental variables were examined on a day-to-day basis rather than pooled per lunar month, cross-correlations between daily supply and environmental variables revealed only very weak relationships at various time lags. Similar weak relationships have been reported between environmental variables and daily replenishment patterns in several species in San Blas (Robertson et al. 1999; Wilson and Meekan 2001). Given the complex and changeable nature of water flow within this reef system, local currents and topography may influence the day-to-day supply patterns in less predictable ways compared with the stronger relationships found between wind, currents and larval supply in other Caribbean locations (e.g., Thorrold et al. 1994). This hydrodynamic complexity may partly explain the single high pulses of larval abundance during the sampling period. Such seemingly stochastic events may play an important role in replenishing benthic communities (Victor 1983; Shenker et al. 1993) and underscore the need for further research to examine if these episodic pulses contribute disproportionately to the demography of juveniles and adults.

Late-stage reef fish larvae have well developed sensory and locomotory abilities and may use chemical, sound and olfactory cues to navigate towards suitable settlement habitats (e.g., Leis and McCormick 2002). A growing body of literature suggests that larval behaviour plays an active role in settlement patterns (e.g., Montgomery et al. 2001; Leis 2006). Robertson et al. (1999) proposed that the weak winds during the wet season in San Blas enabled larvae to more actively determine their settlement destination compared with the dry season when currents were stronger. No general spatial patterns emerged from the present study, as larval

distributions among the back-reef, lagoon and exposed reef were species-specific. There was, however, a stronger synchrony in daily catches between the exposed and the lagoon habitat during the dry season, but only *S. foetens* and *S. poeyi* larvae were significantly more abundant in the protected habitat of the lagoon during this season. The data highlights the need to differentiate between physical and behavioural processes at a fine spatial and taxonomic resolution to understand the underlying mechanisms that determine distribution patterns of late-stage larvae.

The present study provides a snapshot of temporal abundance and distribution patterns of larval lizardfish in the San Blas Archipelago. As short time-series may mask important and consistent trends that are only detectable during long-term monitoring, observations over several years are required before the extent of replenishment variability and seasonality can be fully established (Robertson and Kaufmann 1998). Moreover, understanding the demographic effects of replenishment variability requires detailed information about life history parameters, which can vary considerably among closely related species. For example, Thresher et al. (1986) documented diverse life history strategies among four species of lizardfish within the genus *Saurida* on the Northwest shelf of Australia. The species differed considerably in adult size, time of maturation and longevity, with one species reaching sexual maturity only 60 days after settlement. Fluctuating levels of larval supply in short-lived species with rapid generation times can have important effects on the adult population (Victor 1983; Robertson and Kaufmann 1998). In worst-case scenarios, such species could potentially face extinction if larval supply fails for subsequent months (Robertson and Kaufmann 1998). It highlights the urgent need for more information on the life history of lizardfish. Only by further research into their biology and ecology will the potential effects of temporal and spatial replenishment variability on the adult population be known.

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