

Small-scale spatial and temporal variability of larval fish assemblages at an isolated oceanic island

L. C. P. Macedo-Soares^{1,*}, A. S. Freire¹, J. H. Muelbert²

¹Laboratório de Crustáceos e Plâncton, Departamento de Ecologia e Zoologia, Universidade Federal de Santa Catarina, 88040-900, Campus Universitário, Florianópolis, Santa Catarina, Brazil

²Laboratório de Ecologia do Ictioplâncton, Instituto de Oceanografia, Universidade Federal do Rio Grande, 96201-900, Campus Carreiros, Rio Grande, Rio Grande do Sul, Brazil

ABSTRACT: This study investigated the small-scale spatial distribution and temporal variability of larval fish assemblages at Saint Paul's Rocks along the Mid-Atlantic Ridge. Larvae were collected during 8 expeditions in 2003, 2004 and 2005 from surface horizontal plankton samples at different distances around the archipelago and inside a cove located between the main islets. Identification resulted in 80 taxa distributed across 29 families; 72 taxa represented individual species. Myctophidae was the most diverse family, followed by Gonostomatidae. The larvae of reef fish, such as the endemic damselfish *Stegastes sanctipauli* and the blenny *Entomacrodus vomerinus*, were most abundant. Pelagic fish larvae were also common in the samples, but at low abundances. Reef fish larvae were also the most abundant and frequent in the cove, while at distances up to 500 m and >500 m from the islets, larvae of pelagic species such as the lanternfishes *Ceratoscopelus warmingii* and *Lampadena luminosa*, and the flyingfish *Oxyporhamphus micropterus* were more representative. Cluster analysis superimposed on a non-metric multidimensional scaling indicated 4 significantly different groups (SIMPROF, $p < 0.05$) within the samples. Indicator species analysis revealed 4 fish larvae assemblages in the surface layer: a reef assemblage, a neritic assemblage, a nighttime oceanic assemblage and a daytime oceanic assemblage. Our findings illustrate the distribution of fish larvae that inhabit the surface waters around Saint Paul's Rocks and provide information about the temporal variability in larval abundance of some reef and pelagic species.

KEY WORDS: Saint Paul's Rocks · Equatorial Atlantic · Ichthyoplankton · Reef fish larvae

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INTRODUCTION

Oceanic islands and seamounts play an important role in larval fish ecology, since they provide habitats in which the larvae of both pelagic fishes and resident species can survive and grow (Koubbi et al. 1991, Dower & Perry 2001). Shallow areas above the summits of a seamount can support rich communities of pelagic and demersal fishes (Dower & Mackas 1996). Oceanic islands, for example, are a source of eggs and larvae that contribute to the formation of the larval fish assemblages in the surrounding open

waters (Boehlert & Mundy 1993). Oceanic islands and seamounts may represent hotspots of biodiversity for pelagic migratory fishes in the open ocean (Morato et al. 2010); in seamounts this hotspot hypothesis has recently been challenged and evaluated using recent species databases (Rowden et al. 2010).

The formation, maintenance and disruption of larval fish assemblages are all influenced by oceanographic features, such as interactions between local topography and circulation that affect larval retention, dispersal and recruitment (Boehlert & Mundy

*Email: luiscpms@yahoo.com.br

1993, Genin 2004). Certain biological features, such as larval behaviour, are also important. For example, directional homing can be more effective in late larval stages when larvae can swim faster than average current speeds (Leis & Carson-Ewart 2002, Genin 2004).

Spatial scale is an important parameter when analyzing the patterns of fish larvae distribution around islands (Boehlert & Mundy 1993). As such, studies using smaller spatial scales can demonstrate changes in the structure of larval fish assemblages in terms of distances from islands, which can provide a better understanding of the ways in which fish larvae are making use of the environments around these areas. Since Leis & Miller's (1976) work, a general pattern has emerged in the observations made of larval fish assemblages around islands (e.g. Leis 1982, Nonaka et al. 2000, Rodríguez et al. 2001). As a result, the spatial structure of fish larvae has been classified into at least 4 main assemblages: (1) unique to embayment areas, (2) extreme nearshore, (3) intermediate nearshore and (4) offshore (Boehlert & Mundy 1993).

Although issues related to the taxonomy of fish larvae still hamper identification all the way to the species level, several studies have been conducted to investigate the formation of larval fish assemblages in major oceanic regions. Studies have been undertaken in the Pacific Ocean (Moser & Smith 1993, Franco-Gordo et al. 2002, Hernández-Miranda et al. 2003), the Indian Ocean (Gray & Miskiewicz 2000, Muhling & Beckley 2007, Muhling et al. 2008), the Indo-Pacific region (Leis 1993), the Southern Ocean (Koubbi 1993), the Antarctic region (Loeb et al. 1993) and the Atlantic Ocean (Olivar & Shelton 1993, Richards et al. 1993, Sanvicente-Añorve et al. 1998, Nonaka et al. 2000, Mafalda et al. 2006, Moyano & Hernández-León 2011). Owing to the large dimension of oceanic islands, several studies that investigated ichthyoplankton communities (e.g. Leis & Miller 1976, Leis 1982, Boehlert et al. 1992, Rodríguez et al. 2001, Moyano & Hernández-León 2011) were unable to sample all the vast surrounding waters of these islands (e.g. Leis 1982). As a result, a very small number of studies (e.g. Boehlert et al. 1992, Castro & Landaeta 2002) have described how fish larvae communities are spatially structured around oceanic islands.

Saint Paul's Rocks is a unique geophysical scenario, with a complex hydrodynamic system, and represents a hotspot of biodiversity along the Mid-Atlantic Ridge. It is an important area owing to the concentration of pelagic fishes (Vaske et al. 2005), the diversity and endemism of reef fishes (Feitoza et

al. 2003) and the high abundance of zooplankton when compared to the oceanic area northeast of the Fernando de Noronha-Rocas Atoll chain (Larrazábal et al. 2009, Macedo-Soares et al. 2009). Recent studies in the area have focused on the ecology and biology of decapod larvae and adults (Koettker et al. 2010, Freire et al. 2011), adult fishes (e.g. Feitoza et al. 2003, Vaske et al. 2003, Ferreira et al. 2009) and the distribution and abundance of ichthyoneuston (Lessa et al. 1999). However, no studies have been published to date about fish larvae distribution or larval fish assemblages around Saint Paul's Rocks.

Formation, maintenance and disruption of the assemblages at Saint Paul's Rocks may be related to the system of currents which promotes vertical mixing between water masses (Travassos et al. 1999). The decapod larvae community, for example, exhibit 2 assemblages inhabiting the waters around Saint Paul's Rocks, one concentrated in the cove and the other inhabiting the surrounding waters (Koettker et al. 2010).

The objective of this study was to describe for the first time the small-scale spatial distribution of larval fish assemblages around Saint Paul's Rocks. The results also provide information about temporal variability of larval fish assemblages with relation to oceanographic features. Additionally, we tested the hypothesis that the composition, abundance and diversity of fish larvae vary depending on the distance from the archipelago at which they were collected.

MATERIALS AND METHODS

Study area

Saint Paul's Rocks is the smallest and the most isolated archipelago in the Brazilian Exclusive Economic Zone. It is made up of a small group of 10 islets and rocky points that rise up from the deep ocean. It is the highest and steepest point on the Saint Peter Saint Paul Massif, a large mass of connected mountains forming an independent portion of the Mid-Atlantic Ridge. This massif is 90 km long, 21 km wide and over 3000 m in height from the base, and is formed by plutonic rocks from the upper mantle and a small sedimentary covering (Sichel et al. 2008, Campos et al. 2009). Saint Paul's Rocks is located in the equatorial Atlantic Ocean (0° 55' 01" N, 29° 20' 44" W) around 1000 km from the northeastern coast of Brazil and 1800 km from the African coast (Fig. 1). The nearest oceanic islands are the Fernando de Noronha Archipelago, 650 km to the south-

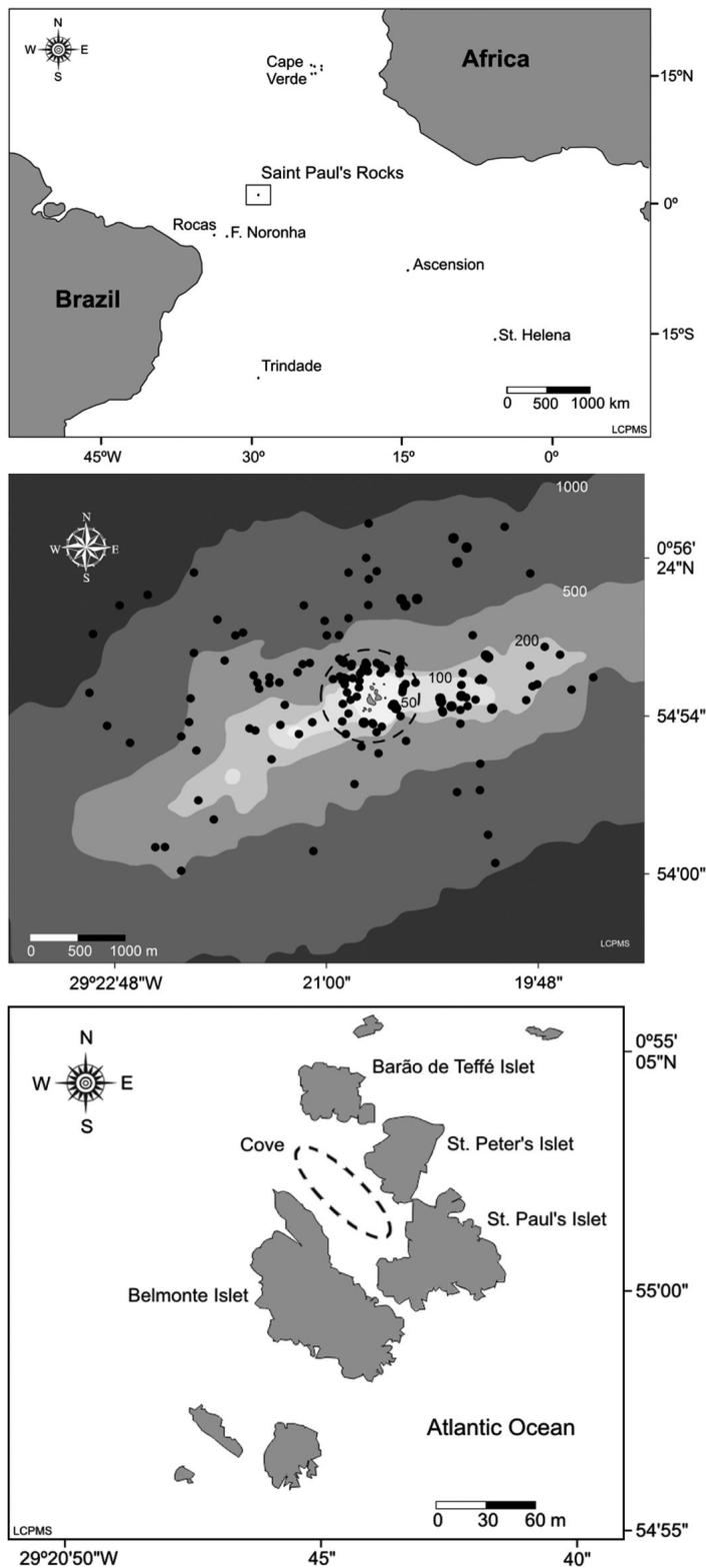


Fig. 1. Saint Paul's Rocks (top) nearshore and offshore sampling sites (middle) (black circles, depth in m) and the main islets and the cove (bottom). Dashed circle in the middle panel represents the boundary between D1 and D2 (\leq and $>$ 500 m from the islets respectively); dashed-line ellipse in the bottom panel represents sampling in the cove

west (Edwards & Lubbock 1983a). In the southeast direction, Ascension Island and St. Helena are both a long way from Saint Paul's Rocks, 1940 km and 3220 km, respectively (Edwards & Lubbock 1983b).

The 4 main islets of Saint Paul's Rocks, Barão de Teffé, Saint Peter, Saint Paul and Belmonte, form an elongate cove with depths of between 4 and 25 m (Fig. 1). In the sublittoral zone, structural complexity down to depths of 45 m is provided by zoanthids, sponges, bryozoans, tunicates, polychaetes and the algae *Caulerpa racemosa* (Forsskål) J. Agardh. Corals are only conspicuous in rocky walls and the external areas of the cove (Amaral et al. 2009).

The westward-flowing South Equatorial Current (SEC) is the main surface current in the area, and its northern branch (SECn) reaches the archipelago with speeds of 0.2 to 0.4 m s^{-1} . In the opposite direction, the Equatorial Undercurrent (EUC) flows at depths between 40 and 150 m and at speeds ranging from 0.7 m s^{-1} in its core to about 0.1 m s^{-1} at its edges (Bowen 1966, Stramma & England 1999, Araujo & Cintra 2009). The area is under the influence of the Intertropical Convergence Zone (ITCZ) between January and May, which increases precipitation during this period (the rainy season). From June, the ITCZ moves northward and rainfall in the area decreases (the dry season). The strength of the southeast trade winds in Saint Paul's Rocks is fairly constant at around 7 m s^{-1} (Soares et al. 2009).

Satellite data acquisition

Sea surface temperature (SST) and chlorophyll data were used to characterize the oceanographic conditions during the study period. Data were obtained from level 2 satellite images from moderate resolution imaging spectroradiometer (MODIS)/Aqua sensor, with 1 km spatial resolution. Daily images were acquired from the Ocean Color web site (<http://oceancolor.gsfc.nasa.gov>) for January 1, 2003 to December 31, 2005. Images were initially processed with the software SeaDAS 6.1 and gridded in 5×5 km daily matrices (25 km^2) around Saint Paul's Rocks with MATLAB R2009a.

Plankton sampling and processing

Plankton samples were collected during 8 expeditions to Saint Paul's Rocks in April, August and November 2003, March and December 2004, and January, May and July 2005. Sampling in the ocean environment was conducted around the archipelago at 2 sampling distances: up to 500 m from the islets (D1) and greater than 500 m (D2) (Fig. 1). Three samples were taken at D1 and 6 at D2 during the dusk and night (between 18:00 h and 22:14 h) and during the dawn and morning (between 06:30 h and 12:00 h). A total of 18 samples were collected at randomly selected sites. Six samples were also taken inside the cove in each month except for April 2003. The sampling path covered the whole site (Fig. 1), and sampling was paused for 10 min outside the cove between each plankton tow. A total of 186 samples were collected, 42 inside the cove and 144 in the waters around the archipelago.

Surface horizontal hauls lasting 10 min were performed with a 2 m long conical-cylindrical plankton net with 200 μm mesh size, 0.5 m mouth diameter and equipped with a flowmeter (General Oceanics). The plankton net was completely submerged and sampled the first 0.5 m of the water layer. It was towed behind the boat, which was navigated in a circular path to avoid the motor foam. Mean (\pm SD) volume of water filtered was $54.08 \pm 21.80 \text{ m}^3$. Surface water temperature, surface salinity (by refractometer) and GPS position of each sample station were recorded when the plankton community was sampled. Local depth at sampling stations ranged from 25 to 2000 m.

All samples were preserved in 4% buffered formaldehyde-seawater solution. For samples collected in the waters around the archipelago, ichthyoplankton were sorted and each sample counted in its entirety under a stereomicroscope. In contrast, 5 samples from the cove that had large quantities of larvae were subsampled with a 10 ml scoop (Boltovskoy 1981), and at least 100 larvae in each sample were sorted. Larvae were identified to the lowest possible taxonomic level according to morphometric and meristic characteristics using the larval development stages described by Fahay (1983), Moser (1996), Olivar et al. (1999), Richards (2005), Bonecker & Castro (2006), Evseenko (2008) and Victor (2010). Additional literature was also used: for example, Moser et al. (1984), Leis & Trnski (1989), Olivar & Fortuño (1991), Olivar & Beckley (1997) and Neira et al. (1998). Taxonomic classification was according to Nelson (2006).

Data analysis

Larval abundance collected in the surface layer was standardized to individuals (ind.) 100 m^{-3} of filtered water. For all analyses, samples were classified as coming from 1 of 3 areas: inside the cove (42 samples), D1 (50 samples) or D2 (94 samples). Frequency of occurrence was calculated as the number of samples in which each taxon was caught as a proportion of the total number of samples.

A single-factor ANOVA was applied to test any temporal variability in SST and chlorophyll *a* (chl *a*) among the months of the year (Zar 1996). Whenever significant differences were detected in the ANOVA, Tukey's multiple comparison test was used. Both tests were conducted with Statistica 7.

Species richness was used in each area and throughout the study period as an indication of species diversity (Pianka 1966, Magurran 2004), which has been used in several earlier studies (e.g. Briggs 1994, May 1994, Samadi et al. 2006, Floeter et al. 2008). Species accumulation curves were constructed for each area and for each month in each area (Colwell 2005) using the expected richness function (Mao Tau estimator), which represents the observed number of species by randomizing the order of sequential accumulation. The method provides 95% CIs and allows for direct statistical comparison of richness between sample sets (Colwell et al. 2004). Furthermore, sample effort can be evaluated from the point at which species accumulation curves stabilize. When sampling effort was not sufficient to determine the total species richness of an area, the first-order jackknife estimator of species richness was used. This method reduces the bias of estimation, and it is based on the number of unique species in the sample, i.e. the number of species that occurred in only one sample (Colwell & Coddington 1994). The estimator was computed with 1000 runs and randomization without replacement.

The presence of different assemblages of fish larvae was identified by means of cluster analysis superimposed on non-metric multidimensional scaling (nMDS) using the Bray-Curtis index for similarity between samples and considering the mean abundance of those taxa whose frequency of occurrence was greater than 1%. Taxa abundances were fourth-root transformed in order to reduce the weighting of abundant species (Field et al. 1982). The similarity matrix was clustered using the group average method. When the stress value was in the range of 0.1 to 0.2, a combination of cluster and nMDS analysis was needed to verify the adequacy and mutual

consistency of both representations (Clarke & Warwick 2001). Significant differences between the groups formed by cluster analysis were tested with similarity profile analysis (SIMPROF) to a 5% significance level. All these tests were performed with the Primer-6 software package (Clarke & Warwick 2005).

Groups that were significantly different according to the SIMPROF test ($p < 0.05$) were subjected to an indicator species analysis (ISA) (Dufrene & Legendre 1997). The indicator value ranges from 0 (no indication) to 100 (perfect indication) and was determined from a combination of the species' relative abundance and its relative frequency of occurrence. The statistical significance of the indicator value was evaluated with a Monte Carlo randomization procedure (Dufrene & Legendre 1997). This test was conducted with PC-ORD 4.1 software. Finally, indicator species were used to characterize the larval assemblages for each clustered group. For species richness and larval fish assemblage analysis, only larvae identified at a specific level and taxa that represented a single species were considered.

RESULTS

Oceanographic conditions

Satellite images from Saint Paul's Rocks revealed 2 distinct oceanographic settings: a warm period with low chl *a*, and a cold period with high average chl *a* (Fig. 2). Between March and May, mean SST was significantly ($F = 291.0$, $p < 0.001$) higher (above 28°C) than between June and August (below 27°C in both 2004 and 2005). Mean chl *a* (0.095 mg m^{-3}) was significantly ($F = 69.9$, $p < 0.001$) lower in March and April than it was in June and August (0.202 mg m^{-3}). Highest chlorophyll values were recorded in July for all 3 yr analyzed.

SSTs measured *in situ* together with each sample during the 8 expeditions ranged from $28.7 \pm 0.1^\circ\text{C}$ in January 2005 to $26.4 \pm 0.1^\circ\text{C}$ in November 2003. With the exception of January 2005 and November 2003, *in situ* data varied in accordance with the 3 yr of data

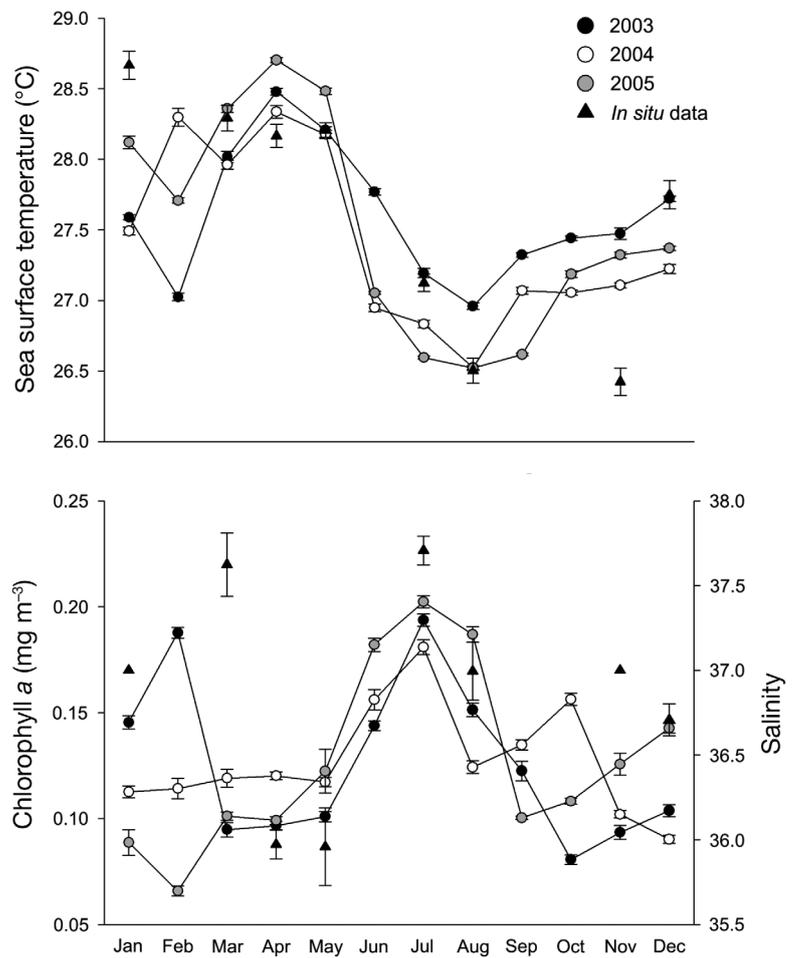


Fig. 2. Sea surface temperature (SST) and surface chl *a* (mean \pm SE) from daily MODIS/Aqua satellite images for a 25 km² area around Saint Paul's Rocks. *In situ* (mean \pm SE) SST and salinity are shown for comparison

obtained from satellite images (Fig. 2). Mean (\pm SE) salinity measurements ranged from 37.7 ± 0.1 in July 2005 to 35.9 ± 0.2 in May 2005.

Composition and abundance of larval fish assemblages

A total of 4335 fish larvae were caught and 80 taxa were identified that belonged to 29 families (Table S1 in the supplement at www.int-res.com/articles/suppl/m444p207_supp.pdf). Seventy-two taxa were representative of individual species. However, identification was possible to the species level for only 49 of these 72 taxa, and 23 of them could only be identified to the family or genus level (e.g. Trachipteridae and *Coryphaena* sp.). The 8 remaining taxa could be members of 2 or more species (e.g. *Cyclothone* spp.).

Myctophidae had the highest species richness (29), followed by Gonostomatiidae (5), Exocoetidae (4), Labridae (3), Pomacentridae (3) and Scombridae (3) (Table S1 in the supplement).

Of the 29 species captured in the cove, 8 were exclusive to the cove. Species richness was highest in D1 with 38 species (11 of them exclusive). In D2, 52 species were identified and 18 were exclusive to that area. Thirteen species were common to all areas: *Cyclothone acclinidens*, *C. alba*, *C. pseudopallida*, *Ceratoscopelus warmingii*, *Diaphus metopoclampus*, *Lampadena luminosa*, *L. urophaos*, *Lampanyctus nobilis*, *Lepidophanes guentheri*, *Stegastes sanctipauli*, *Entomacrodus vomerinus*, *Gempylus serpens* and *Thunnus obesus* (Table S1 in the supplement). Species richness was observed to increase with sampling distance from the archipelago, concurrently with sampling effort (cove, $n = 42$; D1, $n = 50$; D2, $n = 94$). However, the overlap between the CIs for species accumulation curves for all areas indicated that this difference was not significant (Fig. 3).

The species accumulation curves demonstrated that sampling effort was not sufficient to record total species richness for any of the areas. The first-order jackknife estimator of species richness (\pm SD) returned 48 ± 6 species for the cove, 55 ± 5 species for D1, and 77 ± 8 for D2. When species richness was analyzed over time for each area (Fig. 3), there was no marked monthly variability in species richness except in May and July 2005, when species richness was greatest, mainly for D1 and D2, respectively.

Structure of larval fish assemblages

The ichthyoplankton was dominated by reef fish, which formed the 5 most abundant species and accounted for 87% of the total catch. The highest abundances measured were for the endemic damselfish *Stegastes sanctipauli* at 228.3 ± 140.8 ind. 100 m^{-3} (70.8% of the total catch) and occurred in 22.6% of all samples. The blenny *Entomacrodus vomerinus* was

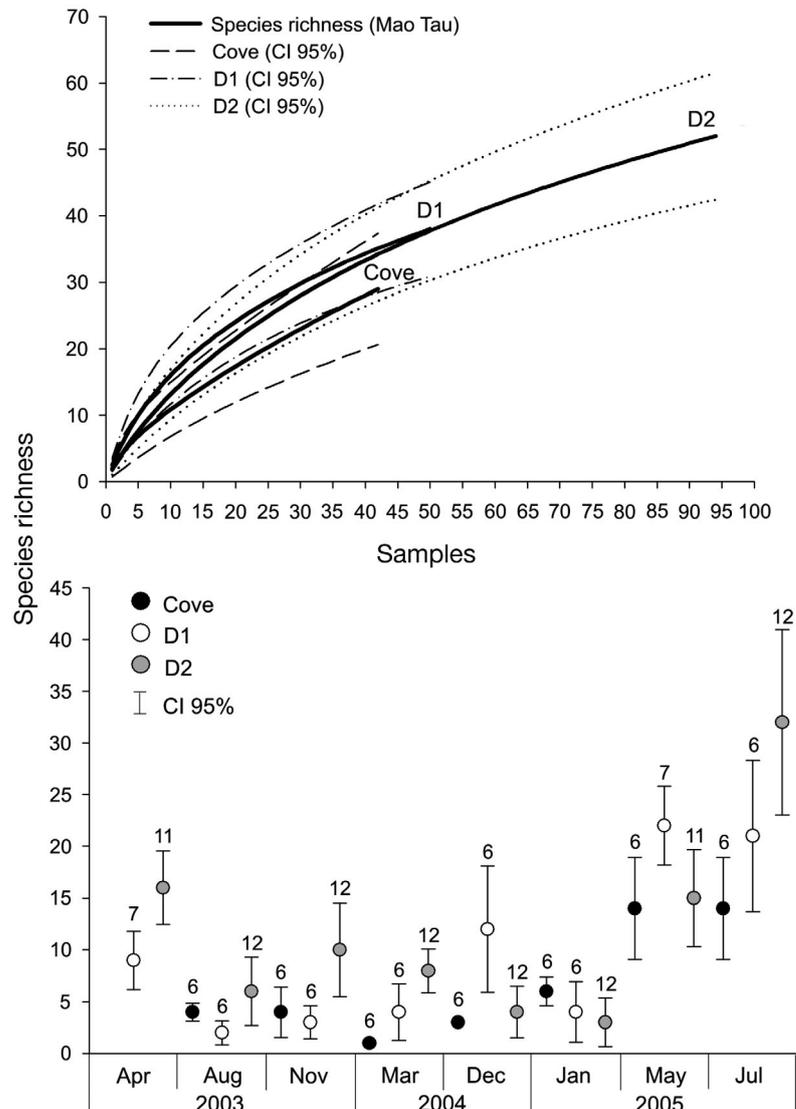


Fig. 3. Species richness accumulation curves and species richness over the sampled months in the cove, at D1 (≤ 500 m from the islets, see Fig. 1) and at D2 (> 500 m). Numbers above the 95% CI bars indicate number of samples considered for each monthly species richness calculation

second in rank, accounting for 14.8% of the total catch (47.9 ± 17.0 ind. 100 m^{-3}), with 17.7% frequency of occurrence. Larvae of pelagic fishes such as the lanternfish *Ceratoscopelus warmingii* and the flyingfish *Oxyporhamphus micropterus* had low abundances but high rates of occurrence in the samples (18.8% and 17.2%, respectively).

In the cove, the principal species as measured by both abundance (72.5%) and occurrence (40.5%) was the damselfish *Stegastes sanctipauli*, followed by the blenny *Entomacrodus vomerinus* and the scaled blenny *Malacoctenus triangulatus*. These 3

species alternated in dominance in the cove over the sampled months. *S. sanctipauli* was dominant at night in December 2004, and both at night and during the day in January 2005. *E. vomerinus* dominated samples at night in August 2003 and May and July of

2005, and during the day in May of 2005. *M. triangulatus* dominated the catches at night in November 2003 and during the day in August and November of 2003 (Fig. 4). Other species with high abundances in different months were also important in the cove.

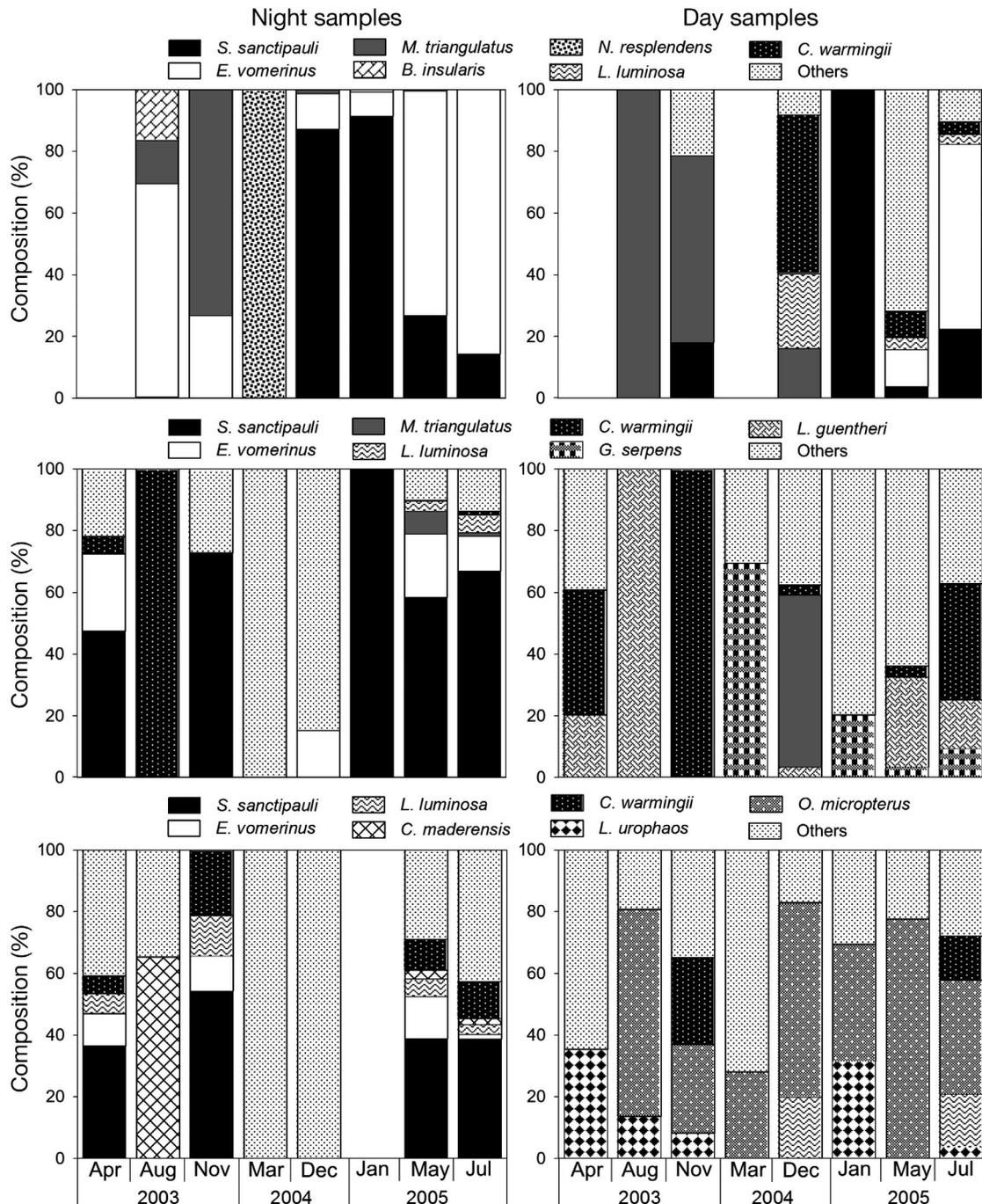


Fig. 4. Monthly variation of the composition of fish larvae assemblages (night and day samples) in the cove (top), at D1 (middle) and at D2 (bottom, see Fig. 3) in April, August and November of 2003, March and December of 2004 and January, May and July of 2005. Number of samples at the cove and D1: 3 in each period, except at D1 in April (n = 4 in day) and in May (n = 4 at night). At D2, 6 samples were considered in each period, except in April (n = 5 in day samples) and in May (n = 5 at night). See Table S1 in the supplement at www.int-res.com/articles/suppl/m444p207_supp.pdf for full species names

The wrasse *Bodianus insularis* was conspicuous at night in August 2003 and the larvae of the pelagic lanternfishes *Ceratoscopelus warmingii* and *Lampadena luminosa* were abundant in January 2005 during the day.

The damselfish *Stegastes sanctipauli* was also the most abundant species at D1 (37.4%), mainly in night samples, in April and November of 2003 and January, May and April of 2005 (Fig. 4). Larvae of pelagic species became important to the assemblage structure during the daytime when they presented a higher proportion in the total composition, in particular the lanternfish *Ceratoscopelus warmingii* in April and November 2003 and July 2005, *Lepidophanes guentheri*, another lanternfish, in August 2003 and May and July 2005, and the snake mackerel *Gempylus serpens* in March 2004 and January 2005. Furthermore, the scaled blenny *Malacoctenus triangu-latus*, which shared dominance in the cove, was also

found in D1 samples. In D2, the lanternfishes *C. warmingii* and *Lampadena luminosa* contributed to the composition of the nighttime community in several months, despite their low abundance (Fig. 4). Moreover, *S. sanctipauli* remained the most abundant species in April and November 2003 and May and July of 2005. Larvae of pelagic fishes dominated the daytime samples, in which the flyingfish *Oxyporhamphus micropterus* and the lanternfish *L. urophaos* alternated in dominance throughout the study period.

Mean larval abundances of the main reef fish species decreased between the cove and D2 (Fig. 5). *Stegastes sanctipauli* larvae occurred during almost all of the studied period, and the highest abundances occurred in December 2004 and January 2005 at the cove and in May and July of 2005 at both D1 and D2. For the blenny *Entomacrodus vomerinus* high abundances were recorded in December 2004, in all sam-

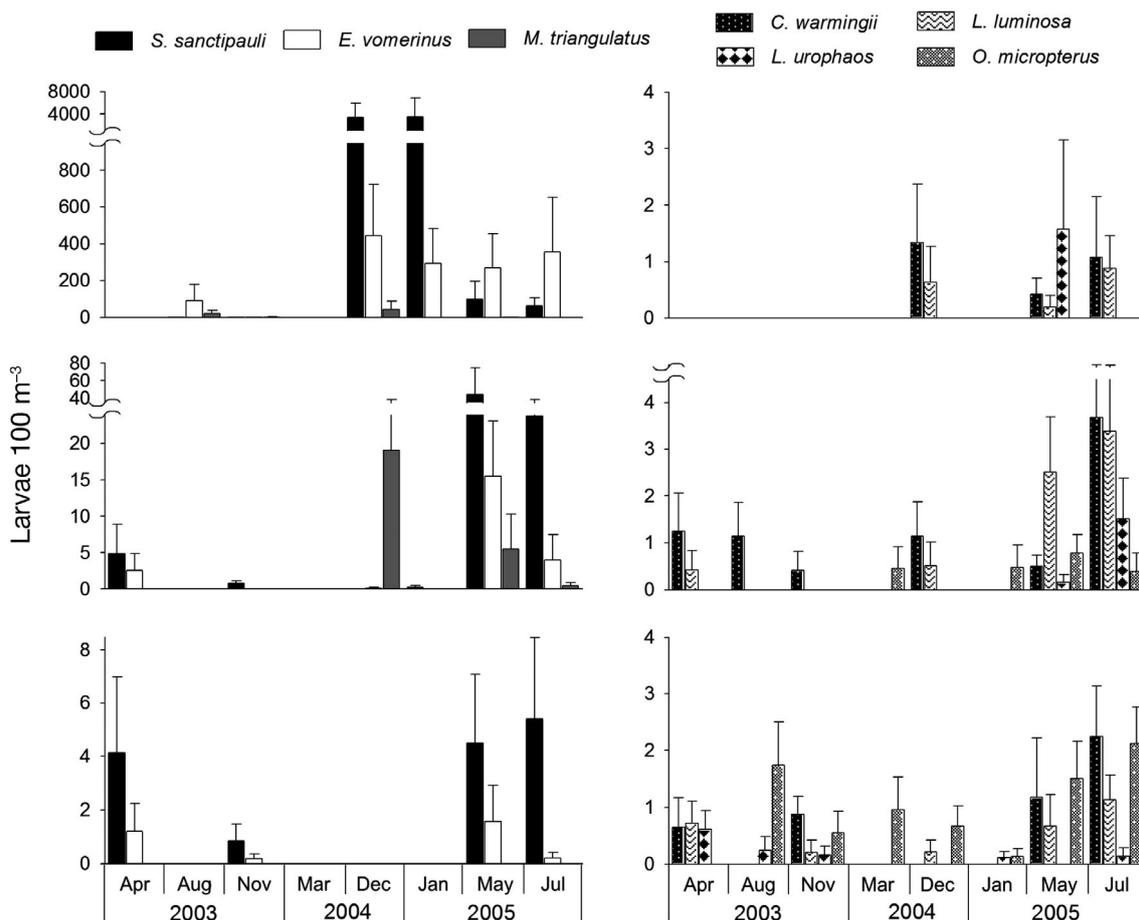


Fig. 5. Mean (\pm SE) abundances of the main species of reef and pelagic fish larvae in the cove (top), D1 (middle) and D2 (bottom, see Fig. 3) in April, August and November 2003, March and December 2004 and January, May and July 2005. Number of samples at the cove and D1: 6 in each month, except at D1 in April and May ($n = 7$). At D2, 12 samples were considered in each month, except in April and May ($n = 11$). See Table S1 in the supplement at www.int-res.com/articles/suppl/m444p207_supp.pdf for full species names

pled months in 2005 at the cove and in May and July 2005 at D1. Scaled blenny *Malacoctenus triangulatus* larvae reached maximum abundance in December 2004.

Larvae of pelagic fishes occurred throughout the period of analysis, mainly at D1 and beyond D1 (at D2). At the cove they were only recorded during the last 4 sampled months (Fig. 5). Mean abundances were similar across the 3 sites, in contrast to what was observed for reef species. However, larvae of some pelagic fishes displayed the highest abundances at a particular site: *Lampadena urophaos* was recorded at the cove in May 2005, *Ceratoscopelus warmingii* was abundant at D1 in July 2005, *L. luminosa* was observed in D1 during May 2005 and beyond D1 in July 2005 and *Oxyporhamphus micropterus* was dominant beyond D1. Despite greater abundance in the cove, *L. urophaos* occurred more frequently in samples collected beyond 500 m than elsewhere. In this same region, *O. micropterus* was not captured in April 2003. Scombrid larvae occurred only in March 2004 and May 2005, predominantly in D1 and D2.

The cluster results superimposed on the nMDS analysis revealed 4 groups distinguished at the 16% of similarity level (Fig. 6). The 4 groups were significantly different statistically according to the SIMPROF test. Group A was only made up of D2 daytime samples, and Group B was similar, containing mainly D2 daytime samples and a small number of D1 day samples. In Group C, most of the samples that clustered together were collected in D1 during both the day and the night, and those from D2 were collected at night. Group D mainly contained samples from the cove.

According to ISA, 4 different larval fish assemblages were identified: a daytime oceanic assemblage characterized by a bristlemouth *Cyclothone pallida*, a lanternfish *Lampadena urophaos*, and the flyingfish *Oxyporhamphus micropterus*, all of which

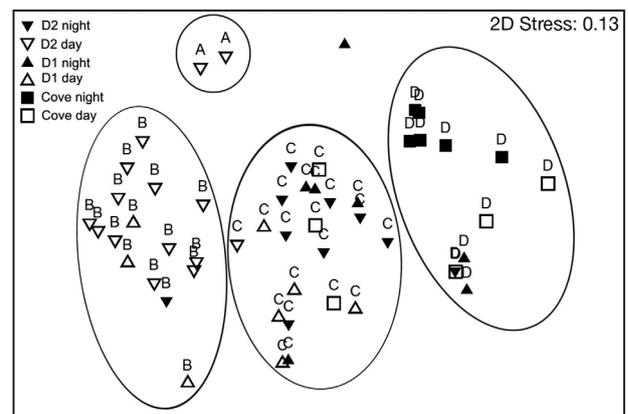


Fig. 6. Non-metric multidimensional scaling (nMDS) representation of fish larvae assemblages from Saint Paul's Rocks. Groups identified by cluster analysis (similarity level 16%) are superimposed on the graph. The nMDS analysis is based on group-average linking of Bray-Curtis similarity calculated from fourth-root-transformed abundance data for 41 species

are indicator species for Groups A and B (Table 1); a nighttime oceanic assemblage in Group C characterized by the lanternfishes, *Ceratoscopelus warmingii* and *Lampadena luminosa*, which also characterized the neritic assemblage; and the reef assemblage that was formed by Group D, in which the indicator species were the damselfish *Stegastes sanctipauli* and the scaled blenny *Malacoctenus triangulatus*, both of which are species associated with reefs.

DISCUSSION

Structure of fish larvae assemblages

At Saint Paul's Rocks larval fish assemblages showed 2 different settings: assemblages influenced only by a spatial distribution of dominant species and assemblages characterized by dominant species with

Table 1. Results of indicator species analysis indicating larval fish assemblages at Saint Paul's Rocks from 2003 to 2005. Only species with significant results ($p < 0.05$) according to the Monte Carlo test are shown

Indicator species	Indicator value (%)	Monte Carlo p-value	Clustered groups	Larval fish assemblages
<i>Cyclothone pallida</i>	45	0.028	A	Daytime oceanic assemblage
<i>Lampadena urophaos</i>	72	0.004	A	
<i>Oxyporhamphus micropterus</i>	72	0.001	B	Nighttime oceanic and neritic assemblages
<i>Ceratoscopelus warmingii</i>	86	0.001	C	
<i>Lampadena luminosa</i>	67	0.001	C	
<i>Stegastes sanctipauli</i>	60	0.032	D	Reef assemblage
<i>Malacoctenus triangulatus</i>	38	0.041	D	

both spatial and day/night influences. In the first assemblages setting, reef assemblage was characterized by the damselfish *Stegastes sanctipauli*, a high abundance of larvae of reef spawners and a low species richness. A neritic larval assemblage was characterized by the lanternfishes *Ceratoscopelus warmingii* and *Lampadena luminosa*, as well as the high abundance and occurrence of larvae of pelagic spawners. In the second assemblages setting, *C. warmingii*, *L. luminosa* and pelagic spawners larvae also characterized the nighttime oceanic assemblage. Finally, larvae of the flyingfish *Oxyporhamphus micropterus* and high richness characterized daytime oceanic assemblage.

These larval fish assemblages followed the pattern that was first described by Leis & Miller (1976) and then later confirmed in more recent studies (e.g. Boehlert et al. 1992, Nonaka et al. 2000). At Johnston Atoll in the tropical Pacific Ocean, ichthyoplankton surveys resulted in 9 larval assemblages (Boehlert et al. 1992). Three of those assemblages followed the same pattern of fish larvae spatial distribution recorded at Saint Paul's Rocks. The first assemblages were composed of island taxa, the second assemblage of oceanic mid-water taxa like the lanternfishes (Myctophidae) and the fourth assemblage of oceanic taxa from the upper stratum of the water layer, such as the flyingfishes (Exocoetidae) recorded in Saint Paul's Rocks daytime oceanic assemblage. The other assemblages were characterized by rare taxa or taxa with restricted occurrence. In the Abrolhos Bank, 4 major assemblages were identified (Nonaka et al. 2000) in relation to a spatial distribution. Three of these assemblages were similar to those recorded in Saint Paul's Rocks in the present study. The Abrolhos Bank assemblage consisted mainly of fish larvae associated with coral reefs, the transitional assemblage consisted of larvae of mesopelagic fishes, such as Myctophidae, and the oceanic assemblage consisted mainly of larvae of Myctophidae and the bristlemouths (Gonostomatidae) (Nonaka et al. 2000).

Although some studies of fish larvae distribution, or even assemblages, included sampling during the day and at night (e.g. Leis & Miller 1976, Rodríguez et al. 2000), only a few considered these 2 time periods when analyzing their results (e.g. Leis 1986, Dower & Perry 2001, Diekmann et al. 2006). In the present study, the field design provided the same sampling effort at day and night, which allowed the composition of larval assemblages to be analyzed in relation to day and night periods. Thus, results showed that in relation to the oceanic assemblage

there is a day/night effect on an assemblage's composition in relation to dominant species.

At Cobb Seamount, total abundance of fish larvae and of the lanternfish *Stenobrachius leucopsarus* larvae was significantly higher at night than during the day (Dower & Perry 2001). At Great Meteor Seamount, *Cyclothone* spp. was representative of the upper layer assemblage and had a higher concentration of larvae, mainly in the upper 150 m of the water column during both day and night periods. In contrast, *Hygophum* sp. larvae were more associated with the intermediate water layer and had a higher concentration between 50 and 100 m depth at night (Diekmann et al. 2006). According to Diekmann et al. (2006), since many species did not show vertical migratory behaviour, these changes in species composition at 150 m would be possible by active vertical circulation in the water column above the seamount summit. In the present study, the horizontal subsurface sampled did not allow any inference to be made about vertical migration behaviour at Saint Paul's Rocks, because fish larvae were caught only in the upper 50 cm below the surface. However, the shift in the oceanic assemblage between day and night periods may be indicative of changes in the vertical distribution of fish larvae at least near the bottom layer of the water column. This shift was not observed in neritic and cove assemblages that occurred at lower depths.

For pelagic fish larvae, similarities in composition have been recorded between oceanic areas (Richards et al. 1993, Sanvicente-Añorve et al. 1998, Ekau et al. 1999, Hernández-Miranda et al. 2003, Muhling et al. 2008), at seamounts (Dower & Perry 2001, Diekmann et al. 2006, Sobrinho-Gonçalves & Cardigos 2006) and at the nearshore and around oceanic islands (Leis & Miller 1976, Leis 1986, Boehlert et al. 1992, Nonaka et al. 2000, Rodríguez et al. 2000, 2001, Castro & Landaeta 2002, Moyano et al. 2009, Moyano & Hernández-León 2011), because most of the larvae of pelagic species recorded have a circumglobal or circumtropical distribution.

In relation to reef fish larvae, the relatively low species richness near the islets may be due to the absence of corals in shallow habitats, which may provide less structural complexity in the cove than at other coral reefs where live coral cover contributes to habitat complexity (Wilson et al. 2007). Diversity is high near coral reefs because structural complexity provides several different habitats that support fish larvae (Leis 1993). At Saint Paul's Rocks, corals are only conspicuous on rocky walls and in other areas outside the cove (Amaral et al. 2009). The low rich-

ness of adult reef fish could also contribute to this low diversity, since Saint Paul's Rocks has been considered an impoverished zone of the Brazilian Province (Floeter & Gasparini 2000). The low richness of reef fishes in small oceanic islands is due in part to their limited shallow habitats (Robertson 2001), which in Saint Paul's Rocks is about 0.2 km². Sampling may have also contributed to the relatively low species richness since sampling effort was lowest at the cove, and horizontal plankton sampling may have contributed to an underestimation of the abundance of larvae from some demersal fish species (Choat et al. 1993). The result of the first-order jackknife estimator for the cove, in the same way as that for D1, was consistent with previous estimates of the adult reef fish richness (67 species) in the area (Feitoza et al. 2003, Vaske et al. 2005, Ferreira et al. 2009).

Life history strategies may be responsible for differences in diversity among areas. The larvae of some reef fish that release pelagic eggs were absent from nearshore samples collected from waters around the Hawaiian Islands (Leis & Miller 1976). In line with this, the larvae of some species that are important in the adult reef fish community of Saint Paul's Rocks, such as those in the families Muraenidae, Pomacanthidae, Holocentridae and Kyphosidae (Ferreira et al. 2009), were absent from samples collected in the cove, which suggests that there was a degree of decoupling of the reef fish adult and larval communities. On the other hand, larvae from non-pelagic eggs are overwhelmingly dominant in the cove samples, reducing evenness and diversity in the community.

Furthermore, in offshore areas, diversity may be increased by mesopelagic and bathypelagic species, which are distributed in the water column according to the abundance of their potential prey (Moser & Smith 1993) and depth of the thermocline (Longhurst 1985). Myctophidae and Gonostomatidae, for example, are the most speciose families with high abundance and frequency in oceanic samples (e.g. Sanvicente-Añorve et al. 1998, Rodríguez et al. 2001). Myctophidae includes mesopelagic and bathypelagic fishes and their spatial distribution is influenced by water masses so that their vertical distribution is concentrated above 200 m depth where the larvae can feed on small zooplankton (Koubbi et al. 1991, Sassa & Kawaguchi 2004). Similarly, Gonostomatidae are bathypelagic fish that have a circumglobal distribution (Briggs 1960, Fahay 1983) and usually have high species richness in oceanic samples (Rodríguez et al. 2000, 2001, Castro & Landaeta 2002, Moyano et al. 2009, Moyano & Hernández-León 2011).

The dominance of reef fish larvae in the community was related to the high abundance of adults in the area, as has already been recorded at seamounts and other islands (Dower & Perry 2001, Castro & Landaeta 2002). The endemic damselfish *Stegastes sanctipauli*, listed as vulnerable by the International Union for Conservation of Nature and Natural Resources (IUCN) (Roberts 1996), was the second most abundant reef fish at Saint Paul's Rocks, while *Entomacrodus vomerinus* exhibited high abundances in tide pools at the islets (Ferreira et al. 2009, Mendes 2009). Although larvae of some abundant reef fishes including Acanthuridae, Chaetodontidae, Labridae and Scaridae occur at greater distances from the shore (Boehlert & Mundy 1993), the results of the present study demonstrated that *S. sanctipauli* larvae were predominantly found inside the cove, although they were also present in neritic and oceanic samples. This difference is probably related to life history strategies contributing to self-recruitment, since pomacentrids like *S. sanctipauli* release non-pelagic eggs, which helps to keep larvae in the parental habitat after hatching. On the other hand, Acanthuridae, Chaetodontidae, Labridae and Scaridae spawn pelagic eggs, a strategy that encourages greater dispersal of the recently hatched larvae (Leis & Miller 1976, Boehlert & Mundy 1993).

Therefore, the larval reef fish assemblage at Saint Paul's Rocks corresponded to the embayment assemblage described by Leis & Miller (1976), and was formed mainly by reef-associated species with non-pelagic eggs, such as those of Pomacentridae, Blenniidae and Labrisomidae, plus species that have pelagic eggs, like Labridae and Scaridae (Leis & Miller 1976, Nonaka et al. 2000). Some oceanic species with pelagic eggs were also present (Myctophidae, Exocoetidae and Scombridae), although they were numerically less important to the composition of the assemblage.

The neritic assemblage was dominated by mesopelagic species belonging to Myctophidae, such as the lanternfishes, *Ceratoscopelus warmingii* and *Lampadena luminosa*. In the western north Pacific Ocean, *C. warmingii* was the most abundant fish larvae in the Myctophidae assemblage (Sassa et al. 2004), and in nearshore waters around Oahu Island, Hawaii, the concentration of *C. warmingii* increased at distances of 0.5 to 3.0 km from the coast (Leis 1982). Species like *L. urophaos*, which was more representative of the oceanic samples from Saint Paul's Rocks, have been associated with the neritic assemblage in other studies (Boehlert & Mundy 1993). In the present study, *L. luminosa* replaced *L. urophaos* in the neritic assemblage.

Epipelagic (e.g. *Oxyporhamphus micropterus*), mesopelagic (e.g. *Lampadena urophaos*) and bathypelagic (e.g. *Cyclothone pallida*) species were indicative of the oceanic assemblage at Saint Paul's Rocks, which corresponds to the oceanic assemblage described by Leis & Miller (1976). In this assemblage, pelagic species belonging to the Myctophidae, Gonostomatidae, Paralepididae, Phosichthyidae and Exocoetidae are overwhelmingly dominant (Leis & Miller 1976, Sanvicente-Añorve et al. 1998, Ekau et al. 1999, Nonaka et al. 2000, Diekmann et al. 2006). However, reef fish larvae are also abundant, as was the case with *Stegastes sanctipauli* and *Entomacrodus vomerinus* at Saint Paul's Rocks, since the oceanic assemblage is not exclusively composed of larvae of oceanic species (Boehlert & Mundy 1993). This is not surprising for Saint Paul's Rocks, since abrupt changes in bottom topography shortens horizontal distances between the neritic and oceanic environments.

Larval fish assemblages are strongly influenced by habitat type. Changes in habitat can cause changes in larval fish assemblages within very short distances (Leis 1993). At Saint Paul's Rocks, the abrupt change between the reef and pelagic regions results in the suppression of the nearshore assemblage formed by species from the families Gobiidae, Clupeidae, Engraulidae and Sciaenidae (Boehlert & Mundy 1993). Thus, the high abundance of reef fish larvae means that the neritic assemblage described in the present study exhibited a composition that was more similar to a transitional assemblage, as described by Nonaka et al. (2000). The distances sampled may also have contributed to differences in larval assemblages composition. In Oahu, for example, the oceanic assemblage was identified in samples collected 5 km from the island shore (Leis & Miller 1976). In the present study, samples were collected up to almost 3 km from Saint Paul's Rocks. Some reef fish larvae have been collected at points hundreds of kilometres away from the nearest adult habitat (Victor 1987), and this may have been responsible for the zero or low abundance of some taxa, such as Chaetodontidae and Labridae.

Temporal variability in larval fish assemblages

The temporal variability in fish larvae species richness at Saint Paul's Rocks demonstrated an increase in the number of fish species in months with significantly high levels of chl *a*, i.e. between June and August, with the exception of August 2003. The

period with high chl *a* concentration is mainly influenced by local circulation (Pérez et al. 2005) and by the displacement of the ITCZ to the north, which reduces cloud cover over the area (Soares et al. 2009). An increase in food supply in relation to the surrounding areas (Rodríguez et al. 1999), combined with the large quantities of zooplankton around Saint Paul's Rocks (Macedo-Soares et al. 2009), suggests some synchrony exists with the occurrence of fish larvae. Therefore, partial overlap between ichthyoplankton and plankton distribution is to be expected (Freitas & Muelbert 2004). Myctophidae larvae, for example, feed mainly on copepod nauplii and copepodites (Sabatés & Saiz 2000, Sassa & Kawaguchi 2004), and since copepods produce eggs in the water column in response to the vertical distribution of chl *a* concentrations (Nakata et al. 1994), mesopelagic larvae, like Myctophidae, migrate in the water column to feed at different depths up to the surface.

Larval fish assemblages showed a temporal variability in some dominant species that affects their structures. Reef fish larvae like the damselfish *Stegastes sanctipauli* switch dominance with other reef fish species, such as the blenny *Entomacrodus vomerinus* and larvae of pelagic species, in nighttime samples. In contrast, species like *Oxyporhamphus micropterus* and *Lampadena urophaos*, which are dominant in oceanic surrounding waters, occurred during most of the time studied. Seasonal differences in larval fish assemblages were also found at Gran Canaria Island (Moyano & Hernández-León 2011), where some abundant taxa dominated the annual assemblage. Moyano & Hernández-León (2011) inferred that the spawning period and variations in temperature accounted for the identification of 2 seasonal larval fish assemblages. At Saint Paul's Rocks, temporal assemblages were not identified, but clear temporal variations were seen among dominant species in each spatial assemblage.

Despite the lack of information on the reproductive period of some species of the reef fish at Saint Paul's Rocks, the temporal distribution of *Stegastes sanctipauli* larvae suggests that December and January, which are months with higher SSTs, are probably months with greater spawning activity, in which larval abundance peaks. *S. sanctipauli* larvae were also present in May and July, which are periods with high chl *a* concentrations, although mean larval abundance was lower than that during the other 2 peak months. Along the Brazilian coast, the spawning period of *S. variabilis* is from October to January, while 2 peaks of partial spawning have been recorded for *S. fuscus*: one during January and one in September

to October (Bessa et al. 2007, Souza et al. 2007). For *S. nigricans*, the spawning season was from June to September (Karino & Nakazono 1993). Even in an equatorial region, temperature may be a controlling factor for *S. sanctipauli* reproduction.

The waters around oceanic islands are occupied not only by reef-associated species, but also by some oceanic species (Boehlert & Mundy 1993). Flying-fishes, for example, congregate around islands during their breeding season when adults spawn near rocky substrates (Hunte et al. 1995). At Saint Paul's Rocks, flyingfishes such as *Cypselurus cyanopterus* spawn in the first quarter of the year when yellowfin tuna *Thunnus albacares* catches are high (Lessa et al. 1999, Hazin et al. 2009). *C. cyanopterus* is the main food resource for *T. albacares* in the area (Vaske et al. 2003). In the present study, larvae of *C. cyanopterus* were only caught in March, which is in accordance with the species' spawning period in the area (Lessa et al. 1999). On the other hand, another flying-fish, *Oxyporhamphus micropterus*, seems to reproduce throughout the year, since its larvae occurred in almost every month in which sampling took place.

In the same way, Scombridae mainly spawn near tropical islands (Boehlert & Mundy 1994) where primary productivity may be higher than in the open ocean and the environment is more suitable for early larvae (Boehlert & Mundy 1993). Although most of the adult specimens of *Thunnus albacares* examined in previous studies were sexually immature (Hazin et al. 2009), early larval stages were recorded mostly in March and May in nearshore and oceanic samples. For *T. obesus* and *Katsuwonus pelamis*, larvae were captured in the same period. This means that scombrid species use Saint Paul's Rocks for feeding and that part of their populations also reproduce there.

Regardless of its equatorial location, our results showed temporal shifts between dominant species in the larval fish assemblages at Saint Paul's Rocks. For reef species, peaks in abundance were probably related to the reproductive period and to larval retention. On the other hand, the presence of adults of the pelagic species in the area resulted in spawning activity of these species in the surrounding waters.

Summary and conclusions

The present study provided for the first time a detailed description about ichthyoplankton distribution and larval fish assemblages around Saint Paul's Rocks, a remote oceanic island in the Atlantic Ocean. In summary, our findings showed that fish larvae

composition, abundance and richness change with distance from Saint Paul's Rocks and characterize 3 different assemblages: reef, neritic and oceanic, with day/night influences in oceanic assemblage. Temporal shifts among dominant species were also recorded and may be related to a temporal variability in SST and chl *a* concentration. Further studies should be carried out by means of a different sampling strategy to evaluate diversity, mainly inside the cove, with emphasis on benthic reef fish species with non-pelagic eggs. Similarly, vertical sampling and sampling at distances more than 3 km from Saint Paul's Rocks could verify whether some of the reef fish species that have pelagic eggs and were absent in this study, such as those of the families Chaetodontidae, Holocentridae, Muraenidae and Serranidae, inhabit the oceanic region. This study represents baseline information to be applied to further research in the oceanic islands of the South Atlantic Ocean.

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