ORIGINAL ARTICLE

Distribution of decapod larvae in the surface layer of an isolated equatorial oceanic archipelago: the cases of benthic *Grapsus grapsus* (Brachyura: Grapsidae) and pelagic *Sergestes edwardsi* (Dendrobranchiata: Sergestidae)

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Abstract Two different decapod larval assemblages inhabit the marine environment of Saint Paul's Rocks, differentiating the inlet from the surrounding oceanic waters. Larvae of the crab *Grapsus grapsus* and of the holopelagic shrimp *Sergestes edwardsi* are abundant in superficial waters of the archipelago and have previously been shown to be good indicators of the inlet and adjacent oceanic waters, respectively. We investigated the horizontal, diel and temporal distribution of these species at Saint Paul's Rocks. Horizontal surface hauls were conducted from 2003 to 2005, in the inlet and at four increasing distances from the archipelago, in the morning and at night, using a 200-μm mesh net. Larvae of *G. grapsus* were identified in samples from all expeditions and abundance was found significantly higher at night in the inlet site. Only larvae in the first zoeal stage were found in samples, highlighting the importance of the area for this species reproduction. On the contrary, the distribution of larvae of *S. edwardsi* was typical of a holopelagic species, which are permanent residents of the water column and spawn in oceanic areas, indicating that the islands are of little influence to them.

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Introduction

During their pelagic period, larvae are exposed to the variation of many ecological factors that influence their chances of survival, development, dispersion and recruitment (Anger 2001). The abundance and distribution of decapod larvae in marine habitats are influenced by factors such as temperature, salinity, light, mortality rates of each stage, food availability, vertical migration, distance from spawning sites, the speed and direction of currents and the duration of their pelagic period (e.g. Sastry 1983; Anger 2001; Queiroga and Blanton 2004).

The presence of larvae of certain species in a given area indicates the presence of the corresponding adult species (Boltovskoy 1981), while the presence of the first larval stage indicates that reproduction occurs in that area (Anger 2001).

Larval dispersion occurs when: (1) the larval stages found are more developed as time from the hatching larval stage and distance from the parental population increase and (2) the first larval stage encounters a surface current from the initial parental population, where abundance diminishes progressively heading seaward. On the other hand, if all stages of development are only found present near the parental site throughout the water column, this leads to larval retention (Queiroga and Blanton 2004; Fogarty and Botsford 2006; Cowen and Sponaugle 2008). Recent work suggests that retention of larvae in the natal habitat is more frequent than suspected and, therefore, that populations may be less open (or more closed) than originally thought (Sponaugle et al. 2002; Levin 2006; Morgan

et al. 2009). Most recent articles published about dispersal emphasize retention, but tend to ignore those larvae that are not retained. If even a small fraction of these successfully recruit elsewhere, their significance for connectivity may be great (Levin 2006).

Available information indicates that larvae of virtually all decapod species perform some kind of diel vertical migration, especially nocturnal migration (Queiroga and Blanton 2004). This occurs when larvae descend to greater depths during the day, avoiding exposure to visual predators, ultraviolet rays and unwanted physical and chemical parameters, then rising to the surface mainly at night to search for food. To a certain degree, the ability to control the vertical position in the water column allows for control in the extent and direction of horizontal dispersion (Queiroga and Blanton 2004).

Islands usually cause disruption in the flows of oceanic systems, where mainly advective processes cause variations in biomass and biological production in the adjacent regions (Boehlert et al. 1992). Saint Paul's Rocks is a small group of rock points and islands that rise from abyssal depths, from about 4,000 m, up to a few meters above the surface (Edwards and Lubbock 1983a). The combination of this abrupt topography with the local currents can create complex mechanisms of vertical migration and topographic blockage of zooplankton and micronekton (Genin 2004).

Two different decapod larval assemblages inhabit the Saint Paul's Rocks, differentiating the inlet from the surrounding oceanic waters (Koettker et al. 2010). In this study, larvae of *G. grapsus* Linnaeus, 1758 and *Sergestes edwardsi* Krøyer, 1855 were treated as representatives of two different functional groups, determined by their adult habitats: benthic or pelagic, respectively. The larvae of the species *Grapsus grapus* had the highest relative abundance in the inlet waters, while larvae of *S. edwardsi* presented the highest relative abundance and frequency of occurrence in the surrounding waters of Saint Paul's Rocks (Koettker et al. 2010). The larval distribution and abundance pattern observed during the 4 months (distributed along 1 year of sampling at Saint Paul's Rocks) for *G. grapsus* was similar to the pattern observed for other benthic decapods, such as *Plagusia depressa* Fabricius, 1775, *Platypodiella spectabilis* Herbst, 1794 and other species of Grapsidae, Xanthidae and Alpheidae. The pattern exhibited by *S. edwardsi* was also observed for *Sergestes curvatus* Crosnier and Forest, 1973, *Sergestes henseni* Ortmann, 1893 and for the genera *Gennadas* Bate, 1881 and *Lucifer* Thompson, 1829 (Koettker et al. 2010).

The rocky shore crab *G. grapsus* is a semi-terrestrial and carnivorous species that mainly occurs in oceanic islands. This species is very abundant at the Brazilian oceanic islands (Saint Paul's Rocks, Rocas, Fernando de Noronha and Trindade). It also occurs at the Caribbean Islands,

along the Eastern Pacific coastline and islands (from Baja California to northern Chile) and at the Galapagos Islands (Freire et al. 2011). The first larval stage of this species is the only stage that has been described to date (Guerao et al. 2001). *G. grapsus* dominates the benthic macrofauna of the emerging area of Saint Paul's Rocks (Freire et al. 2011), where reproduction exclusively occurs and dispersion depends on the marine currents.

Sergestes edwardsi is an oceanic pelagic species and has been recorded at depths ranging from 5,100 m up to the surface. Because of their swimming ability and large size, adults may be considered either micronekton or macroplankton (Pakhomov and Froneman 2000); therefore, we refer to them as holopelagic herein. Its distribution is restricted to the Atlantic, ranging from Newfoundland (Canada) to Rio Grande do Norte (Brazil), in the Western Atlantic; and from Madeira Island (Portugal) to Angola, in the Eastern Atlantic (Melo 1996). At Saint Paul's Rocks, adults of this species were sampled near surface during night and at greater depths during the day (Holthuis et al. 1980).

This study aims to describe the distribution of larvae of *G. grapsus* and *S. edwardsi* in the surface waters off Saint Paul's Rocks, since they could serve as models for other benthic and pelagic decapod species, respectively. We also discuss the dispersion and retention of these species and their diel variation.

Materials and methods

Study area

Saint Paul's Rocks is one of the smallest and most isolated groups of oceanic islands in the world. It is the highest and steepest point of the Saint Peter and Saint Paul massif, linked to the Atlantic Mid-Ocean ridge, close to the Equator (0°55′N and 29°21′W). This massif is about 90 km long and 21 km wide at the 3,000 m depth contour (Sichel et al. 2008). The archipelago has an emerged area of about 16,000 m^2, extends up to 400 m and can reach a maximum height of 18 m above sea level. It is located at approximately 500 km from the nearest archipelago (Fernando de Noronha), 1,000 km from the Brazilian coast and 1,890 km from Senegal, on the African Coast (Edwards and Lubbock 1983a; Feitoza et al. 2003) (Fig. 1).

The four main islands (Belmonte, St. Paul's, St. Peter's and Barão de Teffé) are separated by narrow channels and form a horseshoe-shaped inlet with depths ranging from 4 to 25 m (Feitoza et al. 2003) (Fig. 2). There is a lighthouse and a scientific station housing Brazilian researchers on Belmonte Island, which comprises the largest emerged area of the four.

Fig. 1 Location of Saint Paul's Rocks and other oceanic islands in the Tropical Atlantic, between South America and Africa
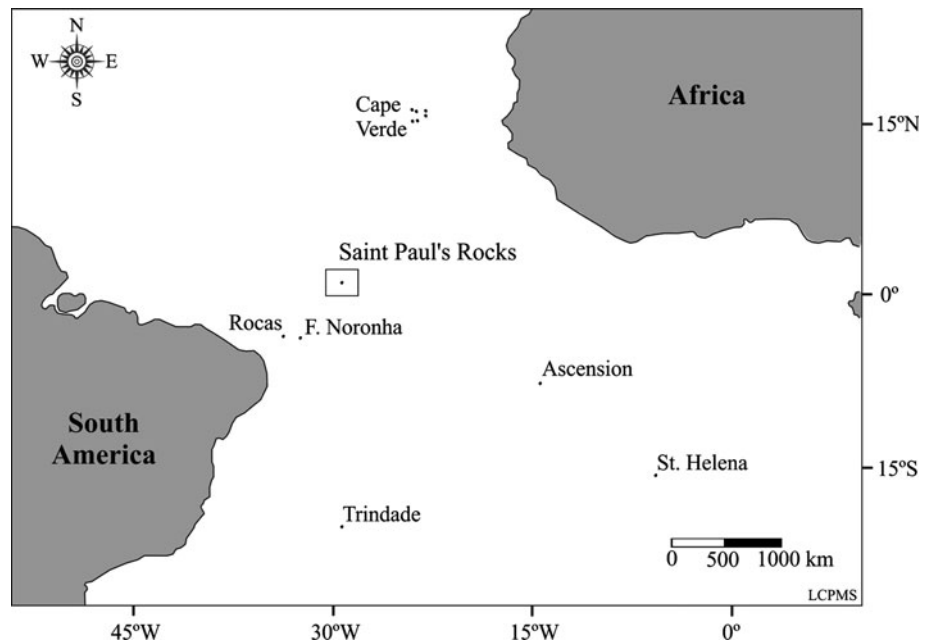
Fig. 2 Map showing the main islands of Saint Paul's Rocks (is.) and the inlet
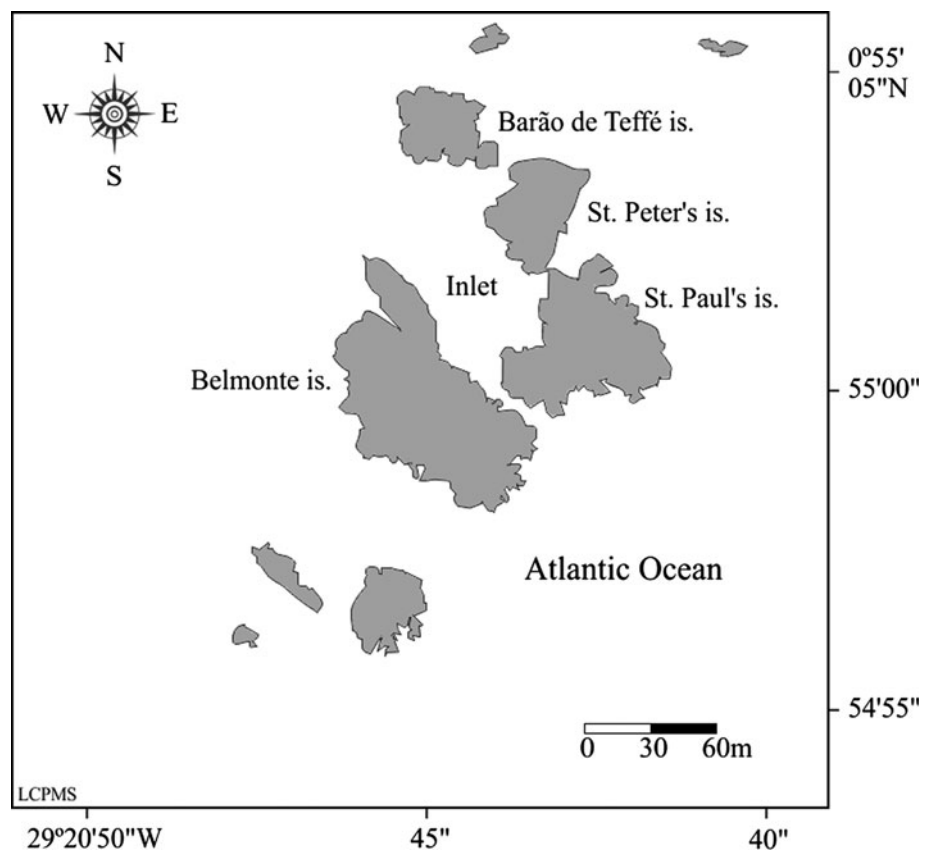
Sampling and processing

Between April 2003 and July 2005, eight expeditions were conducted at Saint Paul's Rocks during which 186 samples were collected in April, August and November 2003; March and November/December 2004; January, May and July 2005. During each expedition, 18 plankton samples were collected at four distances from Belmonte Island, with an equal number of replicates sampled at dawn/during the morning (between 6.30 a.m. and midday) and at dusk/

during the night (between 6.00 p.m. and 10.14 p.m.). In addition, six plankton samples were taken in the inlet (three at dawn/morning and three at dusk/night), with the exception of April 2003. Those samples collected around the archipelago (outside the inlet) were considered as 'open ocean'. Although they correspond to the same expedition, November and December 2004 were separated for some analyses because the open ocean samples were collected in late November, whereas the inlet samples were collected in early December.

The open ocean samples were collected at four different distances from Belmonte Island: D1 (<500 m); D2 (between 501 and 1,200 m); D3 (between 1,201 and 2,000 m) and D4 (>2,001 m) (Fig. 3).

Horizontal surface plankton tows lasting 10 min were performed with a conical-cylindrical net with a 50-cm-diameter mouth and 200-μm mesh, coupled to a General Oceanics flowmeter. At each sampling station, measurements were taken of the surface temperature (thermometer) and salinity (refractometer) and the latitude and longitude coordinates (GPS) were recorded. All samples were preserved in 4 % buffered seawater-formaldehyde solution. Some samples were sub-sampled with a Folsom splitter (McEwan et al. 1954) in fractions that varied from 1/2 to 1/32.

Larvae of *G. grapsus* and *S. edwardsi* were identified according to Guerao et al. (2001) and Gurney and Lebour (1940), respectively. Identification was conducted under stereoscopic and optical microscopes.

Data analysis

Data on larvae of *G. grapsus* were analysed separately for the inlet and the open ocean by performing an analysis of variance (ANOVA), due to the large difference between the abundance figures for each habitat. Data on larvae of *S. edwardsi* in the two habitats were analysed together in the ANOVA since they fell within the same range of abundance. Only two distances from Saint Paul's Rocks were considered in the ANOVA for both species: D1 (<500 m) and ≥D3 (>1,201 m) because these distances had the same number of replicates for all months and day/night periods. Data for all distances were only used for the one-way ANOVA of *G. grapus* abundances collected at night.

Three-way ANOVA was done to test the effect of distance, month and day period on the abundance of larvae of *S. edwardsi* in both the inlet and the open ocean. A two-way ANOVA was done to test the effects of the month and day period on the abundance of larvae of *G. grapsus* in the inlet and also to test the effect of month and distance on abundance in the open ocean. One-way ANOVA was done to investigate the effect of distance on the abundance of larvae of *G. grapsus* in samples collected at night in both the inlet and the open ocean. Biological data were log-transformed ($x + 1$). The Shapiro–Wilks and Bartlett tests were applied a priori and the Tukey's test a posteriori (Zar 1996; Underwood 2006). These tests were conducted using STATISTICA 7 software.

Fig. 3 Locations of the 186 samples collected in the inlet and the open ocean over a total of eight expeditions. *Circles* indicate distances from Belmonte Island (*dashed white*: 500 m, *dashed black*: 1,200 m and *solid black*: 2,000 m). *D1*: <500 m, *D2*: 501–1,200 m, *D3*: 1,201–2,000 m, *D4*: >2,001 m
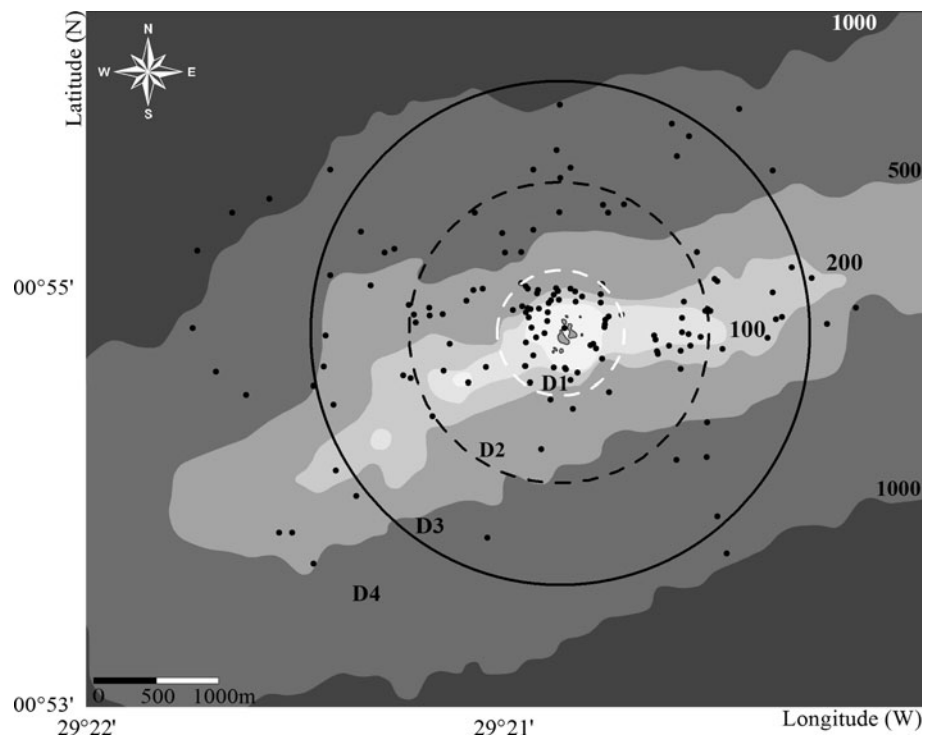
Golden Software's Surfer 8 was used to construct distribution maps showing the larval abundance of *G. grapsus* and *S. edwardsi* by plotting the abundance at each sampling station.

Results

The mean water temperature varied from 26.4 °C in November to 28.7 °C in January. August, November and July presented the lowest mean temperatures (<27.5 °C) for both periods of the months in which samples were collected, while all other months had mean temperatures higher than 27.5 °C. Salinity varied from 36.0 in April and May to 37.7 in July.
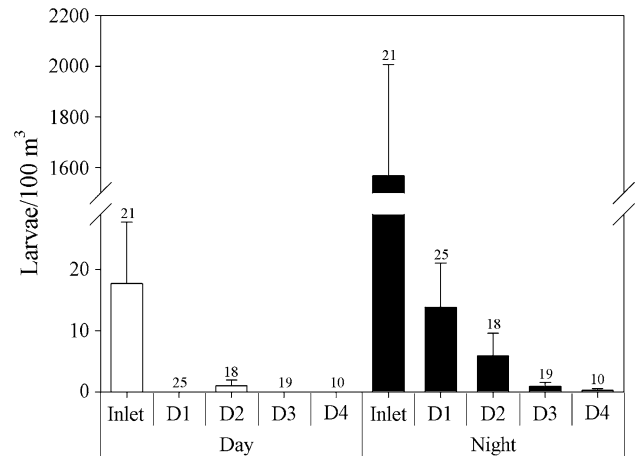
Grapsus grapsus

Out of a total of 186 samples collected in the surface waters off Saint Paul's Rocks over eight expeditions (144 from the open ocean and 42 from the inlet), the larvae of *G. grapsus* were captured in 47 samples, 27 from the inlet and 20 from the open ocean. Thirty-nine of these 47 samples were collected at night, while just 8 were day samples. Larvae of *G. grapsus* occurred in all samples from the inlet collected at night, with abundance values ranging from 24 to 8,018 larvae/100 m^3. All larvae of this species collected in samples from this study were in the first larval stage.

Larvae of *G. grapsus* occurred in only 14 % of open ocean samples, ranging from 2 to 175 larvae/100 m^3. Larvae of *G. grapsus* were not found during the day in any of the months at D1 or at ≥D3. During the day, these larvae only occurred in two samples, both collected at D2, one in January and the other in May, with abundance of 1 and 17 larvae/100 m^3, respectively.

The mean larval abundance in the inlet at night (1,569 ± 438 larvae/100 m^3) was much higher than under other conditions. At night, we observed a trend where the mean larval abundance decreased as sampling distance from Saint Paul's Rocks increased. Mean abundance in daytime inlet samples was 18 ± 10 larvae/100 m^3, which is comparable with the abundance observed at D1 at night (14 ± 7 larvae/100 m^3) (Fig. 4).

When we tested the spatial variation of the abundance of larvae of *G. grapsus* collected at night during all months, the results showed that abundance was significantly higher in the inlet than in samples collected at all open ocean distances (degrees of freedom = 4; F = 82.7; p = 0.00; error degrees of freedom = 88) (Fig. 4).

When the open ocean samples were analysed separately, *G. grapsus* larval abundance was significantly higher in

Fig. 4 Abundance (mean + se) of larvae of *G. grapsus* collected in the inlet and at all distances (*D1*: <500 m, *D2*: 501–1,200 m, *D3*: 1,201–2,000 m, *D4*: >2,001 m) during the day and at night in all sampling months. Figures above *error bars* indicate the number of samples included in the analysis

Table 1 Two-way ANOVA to test the effects of temporal (F1), spatial (F2 for the open ocean) and diel (F2 for the inlet) factors and their interaction on the abundance of larvae of *G. grapsus* sampled at night in both the open ocean and inlet, showing F values

| Degrees of freedom	Temporal 7	Spatial/ diel 1	F1 × F2 7	Error degrees of freedom
G. grapsus—open ocean (only night)	3.1[*]	9.9[**]	1.5[ns]	32
G. grapsus—inlet	2.8[*]	163.8[**]	1.3[ns]	28

For spatial variation, we assessed D1 and ≥D3. D2 was not considered since the number of replicates was not equivalent to the remaining distances, and D4 was included in the category ≥D3

[*] p < 0.05, [**] p < 0.01, *ns* nonsignificant

May compared with November 2003 and January. With regard to distance, D1 had significantly higher larval abundance than D3 (Table 1 and Fig. 5).

Significant variation between months was also detected in the inlet, where larval abundance was significantly lower in November than in July. The histogram shows that fewer larvae of *G. grapsus* were collected in November than the other months and that May presented the highest mean larval abundance in the inlet. With regard to diel variation, larval abundance was significantly higher at night (Table 1 and Fig. 6).

The distribution map of larvae of *G. grapsus* illustrates the higher concentrations of larvae in the inlet and at D1, with few larvae at the most distant stations. The larvae sampled at D2 were collected to the east and west of Saint Paul's Rocks (Fig. 7).
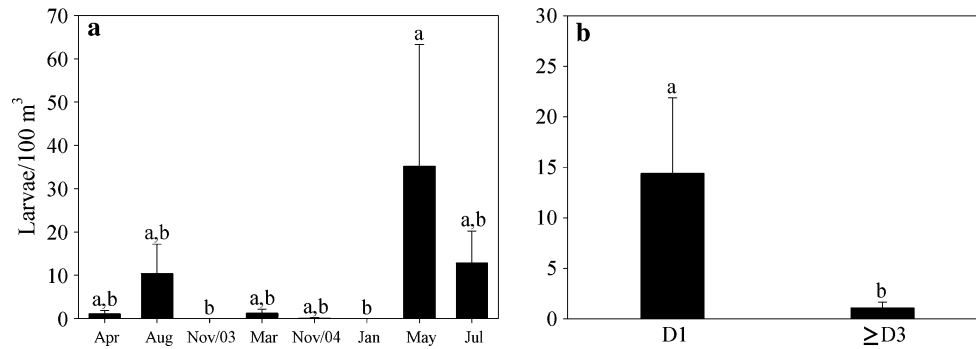
Fig. 5 Abundance (mean + se) of larvae of *G. grapsus* collected in the open ocean (*D1*: <500 m, ≥*D3*: >1,201 m) at night, illustrating ANOVA and Tukey's test results shown in Table 1 (*different letters* represent significantly different means): **a** temporal variation with pooled data from day and night samples collected in both distances and **b** spatial variation with pooled data from day and night samples collected in all months

Fig. 6 Abundance (mean + se) of larvae of *G. grapsus* collected in the inlet, illustrating ANOVA and Tukey's test results (*different letters* represent significantly different means): **a** temporal variation with pooled data from day and night samples and **b** diel variation with pooled data from all months
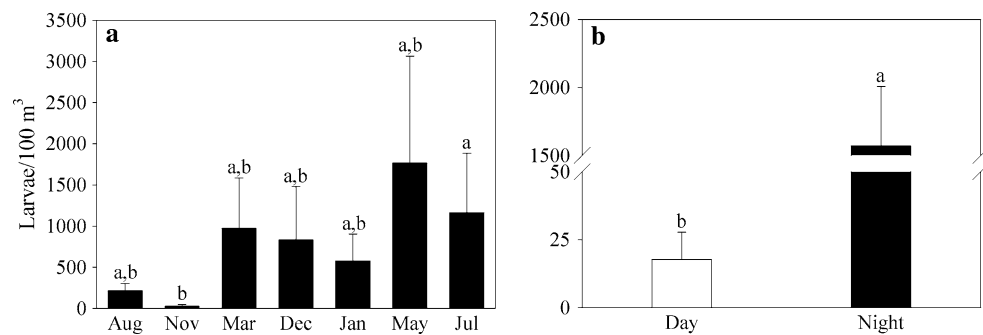
Sergestes edwardsi

Larvae of *S. edwardsi* were present in 61 samples, 9 from the inlet and 52 from the open ocean. Forty-one of these were night samples and 20 were day samples. Larvae of *S. edwardsi* occurred in 33 % of open ocean samples and 21 % of inlet samples. Larval abundance ranged from zero to 35 larvae/100 m³ in the open ocean and from zero to 8 larvae/100 m³ in the inlet. Larvae of this species were identified in all mysis stages (I, II and III). Furthermore, protozoeae II and III of the genus *Sergestes*, and protozoeae I and decapodits of Sergestidae were also identified. Some of these were probably larvae of *S. edwardsi*.

When all months were analysed together, larvae of *S. edwardsi* had highest mean abundance in D1 at night. The magnitude of larval abundance in the inlet, in the open ocean and in the day periods was the same. Larvae of this species showed a trend of being found farthest from the archipelago during the day and closest at night (Fig. 8).

When the differences between months were analysed, the ANOVA results for this species indicated significant interaction between temporal, spatial and diel factors, with the highest mean abundance found at night at distance ≥D3 (Table 2 and Fig. 9).

The highest abundance of larvae of *S. edwardsi* was found in samples taken at approximately 1,200 m west of

Saint Paul's Rocks. In most samples in which larvae of this species occurred, abundance was lower than 10 larvae/100 m³. Larvae were sampled at all distances from the open ocean and in the inlet (Fig. 10).

Discussion

The temperature and salinity values reported in this study and those recorded by Koettker et al. (2010) 1 year earlier are similar to those that have been found previously in the area from in situ and remote sensing observations (Pérez et al. 2005; Macedo-Soares et al. 2012). These values are compatible with the characterization of Tropical Surface Water, described as the dominant water mass in the surface layer of the area, which presents temperature and salinity of about 27.0 °C and 36.0, respectively (Stramma and Schott 1999; Medeiros et al. 2009).

The presence of larvae of *G. grapsus* in all samples and the high abundance figures found at night in the inlet, demonstrate a predominance of nocturnal spawning. Preference of spawning during the night has been documented for several benthic species and is related to the lower predation rates, favouring the survival of newly hatched larvae (e.g. Christy 1982; Yamaguchi 2001). Ovigerous females of *G. grapsus* were caught during all seasons at

Fig. 7 Abundance distribution of larvae of *G. grapsus* (larvae/100 m³) in the 186 samples collected in the inlet and in the open ocean. *Circles* indicate distances from Belmonte Island (*dashed white*: 500 m, *dashed black*: 1,200 m and *solid black*: 2,000 m). *D1*: <500 m, *D2*: 501–1,200 m, *D3*: 1,201–2,000 m, *D4*: >2,001 m
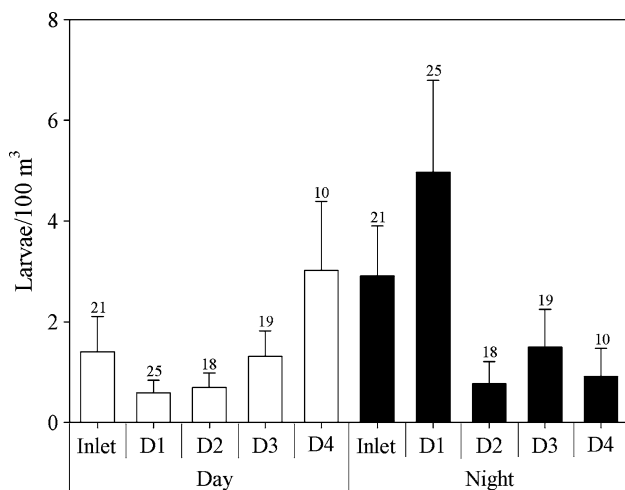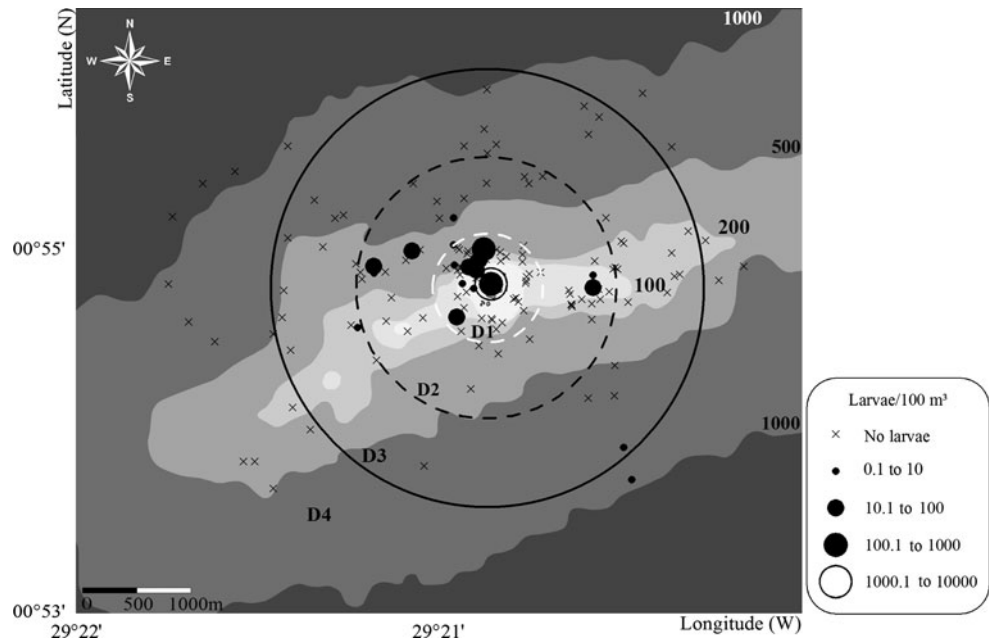
Fig. 8 Abundance (mean + se) of larvae of *S. edwardsi* collected in the inlet and at all distances (*D1*: <500 m, D2: 501–1,200 m, *D3*: 1,201–2,000 m, *D4*: >2,001 m) during the day and at night in all sampling months. *Figures* above *error bars* indicate the number of samples included in the analysis
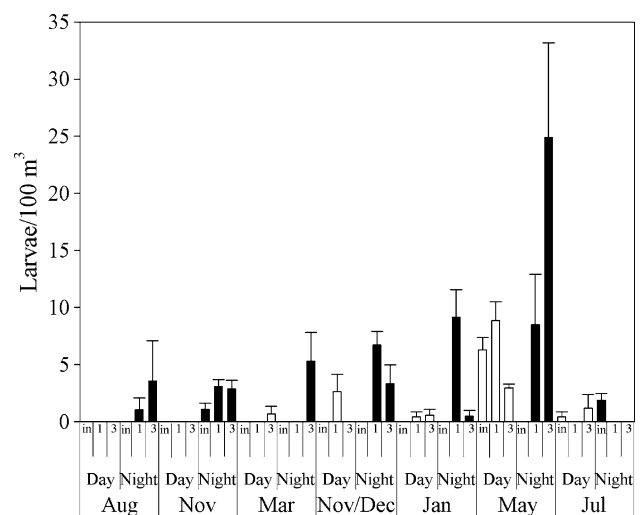
Fig. 9 Abundance (mean + se) of larvae of *S. edwardsi* collected in the inlet (in) and in the open ocean (1: *D1*: <500 m, 3: ≥*D3*: >1,201 m), illustrating ANOVA results

Saint Paul's Rocks (Freire et al. 2011), corroborating the results found for larvae and indicating that this species' reproduction must be continuous at Saint Paul's Rocks.

Crab larvae are a major food resource for planktivorous fish (e.g. Morgan 1990; Morgan and Christy 1997; Hovel and Morgan 1997), since their larvae have few short spines and small bodies making them most vulnerable to and preferred by fish, while spines can difficult ingestion by fish (Morgan and Christy 1997). Larvae of *G. grapsus* are relatively small compared with other crab larvae and have no lateral spines. These morphological characteristics

and the high abundance observed in the inlet suggest that larvae of *G. grapsus* are an important food resource for planktivorous fish that inhabit the area, contributing to the pelagic marine food chain and acting as a keystone species in this ecosystem. The contribution of crab larvae for the pelagic food chain has already been recorded in the mangrove/platform relationship (Schwamborn et al. 1999) and in very high concentrations (100–100,000 larvae/100 m³) of newly hatched larvae of *Pachygrapsus transversus* Gibbes, 1850 at a tropical rocky shore (Flores et al. 2007).

Table 2 Three-way ANOVA to test the effects of temporal (F1), spatial (F2) and diel (F3) factors and their interactions on *S. edwardsi* larval abundance sampled in the inlet and in the open ocean, showing F values

Degrees of freedom	Temporal 6	Spatial 2	Diel 1	F1 × F2 12	F1 × F3 6	F2 × F3 2	F1 × F2 × F3 12
S. edwardsi	22.7[**]	17.6[**]	30.4[**]	6.1[**]	3.4[**]	10.9[**]	5.2[**]

Error degrees of freedom = 84

[**] $p < 0.01$

Fig. 10 Abundance distribution of larvae of *S. edwardsi* (larvae/100 m³) in the 186 samples collected in the inlet and in the open ocean. *Circles* indicate distances from Belmonte Island (*dashed white*: 500 m, *dashed black*: 1,200 m and *solid black*: 2,000 m). *D1*: <500 m, *D2*: 501–1,200 m, *D3*: 1,201–2,000 m, *D4*: >2,001 m
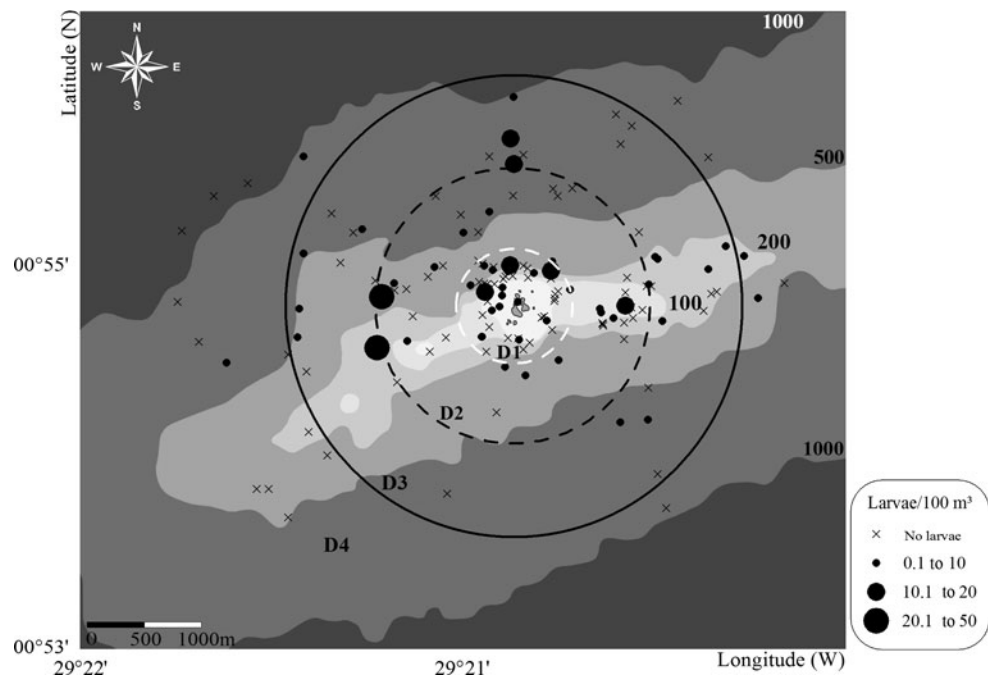
An adult population of *G. grapsus* has existed on the emerged rocks of Saint Paul's Rocks since Charles Darwin's first reports on the area until the present day (e.g. Holthuis et al. 1980; Freire et al. 2011). Although we did not conduct vertical or oblique hauls in order to sample deeper layers, the gradual decrease in abundance of larvae of *G. grapsus* as the distance from the archipelago increased and because only the first larval stage were sampled lead one to believe that the parent population of these larvae is the Saint Paul's Rocks population. In fact, oblique tows sampling the 200 m water column at the Canary Islands recorded much lower values of Grapsidae larvae than those at Saint Paul's Rock's (Landeira et al. 2010). In that study, larvae of the benthic *Calcinus tubularis* Linnaeus, 1767 and *Scyllarides latus* Latreille, 1802 were sampled in the third zoeal stage, but taking into account long distances to other upstream archipelagos and low densities of larvae. Here, the authors proposed that the most probable origin of the larvae was the Canary Islands themselves. Off the California coast, most of the early larval stages (92 %) of 45 crustacean species were also most abundant close to the adult habitat, up to 6 km from the shore (Morgan et al. 2009).

Although so far only the first larval stage of *G. grapsus* is known, the complete larval development of other Grapsidae species has been described (e.g. Cuesta and Rodríguez 2000; Cuesta et al. 2011) where the duration of their zoeal phase varies from about 30–60 days. Furthermore, the newly hatched larvae remain in the zoeal I stage for about 4 days before moulting to their next larval stage. This being said, it is unlikely that these larvae of *G. grapsus* spawned anywhere else, since Saint Paul's Rocks is over 500 km from the nearest archipelago (Fernando de Noronha). Many benthic marine populations have only a portion of their recruitment 'subsidized' from external sources (Pascual and Caswell 1991). In addition, the more isolated a site, the more likely it is that the present population is maintained entirely by self-recruitment (Sponaugle et al. 2002). Marine populations around oceanic islands with no clear source of recruitment could be washed away if mechanisms to retain and maintain the larvae near their natal populations are absent (Landeira et al. 2009).

If we assume that a larva behaves in the same way as an inert particle and that the speed at which the equatorial branch of the South Equatorial Current (SEC) reaches Saint Paul's Rocks (5.6 km/h) (Edwards and Lubbock 1983b) is constant, we could conclude that it is possible for a larva in zoeal stage I to reach Fernando de Noronha after 4 days. However, the small percentage (0.04 %) of larvae of *G. grapsus* found 2 km away from Saint Paul's Rocks (D4) indicates that there is no connectivity between the population of this archipelago and other oceanic islands of the Equatorial Atlantic. In an efficient connection, for example, between coast/platform/coast, larval dispersal can reach distances up to 15 km, as found along the northeast coast of Brazil (Schwamborn et al. 1999).

Marine populations range from entirely closed (self-sustaining populations, such as endemic island species where 100 % of recruitment is due to the settlement of offspring produced by that population) to fully open populations, recruiting only a relatively small proportion of their own offspring and receiving a high number of recruits from other populations (Sponaugle et al. 2002). It has become increasingly apparent that larvae are more likely to recruit closer to natal populations and in higher abundances than generally realized (Morgan et al. 2009; Morgan and Fisher 2010). Islands normally have coastal retention zones that allow for maintenance of the larvae near their natal sites, a result of the interaction between the main current flow and topographic relief (capes, banks, headlands and embayments) (Landeira et al. 2009). In Saint Paul's Rocks, the inlet must act as a site not only for retention, but must also be a location where the larvae of benthic species can maximize growth and survival.

Although late larvae were not found in samples, the geographical isolation of the area and the low levels of larval abundance found at the points farthest from the archipelago indicate that some type of physical process may be maintaining the larvae of *G. grapsus* in the Saint Paul's Rocks region, while another type of biological process causes late larvae to inhabit the deepest layers of the water column. Late larvae tend to keep to deeper waters, while initial larvae are most abundant in surface waters (Queiroga and Blanton 2004). Eddies serve as retention-favourable areas for a variety of larvae in regions near islands (Sponaugle et al. 2002; Queiroga and Blanton 2004), increasing plankton production by pumping nutrients in the euphotic zone (Arístegui et al. 1994), thereby providing a suitable environment for larval survival. However, little is known about this type of phenomenon in the Saint Paul's Rocks area.

Larvae of *S. edwardsi* were more frequent in the open ocean samples. Larvae and adults of Sergestidae are fully adapted to areas of the open ocean (Omori 1974). The abundance figures for *S. edwardsi* at Saint Paul's Rocks were similar to figures that have been reported for other dominant species of Sergestidae from other oceanic regions (e.g. Calazans 1994; Landeira et al. 2009; Mujica et al. 2011). Dendrobranchiata larvae, mainly represented by Sergestidae, were dominant around Saint Paul's Rocks at different stages of development (Koettker et al. 2010). Larvae of the genus *Sergestes* occurred in oceanic stations around Easter Island (Mujica 2006). This is probably related to the distribution of adults in pelagic oceanic waters, where they spawn (Landeira et al. 2009).

The relatively homogeneous distribution across the different sampling stations suggests that larvae of *S. edwardsi* can benefit from the proximity of the archipelago, but since they are independent of any substrate, they did not exhibit a strong association with the archipelago. Larvae distribution of Sergestidae was also found homogeneous around Easter Island (Mujica 2006).

The larvae of benthic species also exhibited the opposite tendency of pelagic species around the Canary Islands, in that the larvae of benthic species decreased in abundance in offshore directions, while those of pelagic species increased. While the distribution of *Gennadas* spp., *Sergestes cornutus* Krøyer, 1855 and *S. atlanticus* H. Milne Edwards, 1830 was a clear example of the pelagic pattern, other species were strongly associated with the area close to the island [e.g. *Galathea intermedia* Liljeborg, 1851, *Pagurus* spp., *Munida* spp. and *Alpheus macrocheles* Hailstone, 1835] (Landeira et al. 2009).

It is likely that the populations of other local benthic decapods (*Plagusia depressa*, *Platypodiella spectabilis* and other Grapsidae, Xanthidae and Alpheidae) follow the same pattern as *G. grapsus*, while pelagic decapods (*Sergestes curvatus*, *Sergestes henseni* and the genera *Gennadas* and *Lucifer*) are distributed in a similar manner to that of *S. edwardsi*.

In summary, the two species analysed, once adults inhabit different biological compartments, resulting in the maintenance of different ecological adaptations. Species with high parental investment, such as *G. grapsus*, have increased survival of eggs, larvae and even juveniles, which favours self-recruitment, promoting retention near the parental population. On the other hand, species whose fertilized eggs are spawned, like Sergestidae shrimps, have relatively smaller eggs and larvae with less ability to remain close to the source population (Sponaugle et al. 2002). The results of this study suggest that there is a possible retention mechanism acting on the larvae of meroplanktonic species at Saint Paul's Rocks, while larvae from holopelagic species are widely distributed through the oceanic area around the archipelago. Although later larvae of *G. grapsus* were not recorded in the 200 m water layer off the Canary Islands (Landeira et al. 2010), vertical hauls combined with descriptions of currents should elucidate the retention process.

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