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The population dynamics of *Ophidiaster ophidianus* (Echinodermata: Asteroidea) in the Azores, at the north-western periphery of its distribution

J. MICAEL[1], M.J. ALVES[2] AND A.C. COSTA[1]

[1]CIBIO-Azores, Research Center in Biodiversity and Genetic Resources, Department of Biology, University of the Azores, Ponta Delgada Campus, PT-9501-801 Ponta Delgada, São Miguel, Azores, [2]Centro de Biologia Ambiental and Museu Nacional de História Natural, Universidade de Lisboa, Rua da Escola Politécnica, 1250-102 Lisboa, Portugal

The warm water Ophidiaster ophidianus *has a protected status in the Mediterranean Sea and also occurs in the shallow subtidal of the Azorean Archipelago. From April 2007 to August 2009, the population structure and seasonal abundance of* O. ophidianus *was studied at different depths within a marine conservation area offshore from São Miguel (SAC: PTMIG0020, Natura 2000).* Ophidiaster ophidianus *showed a marked seasonal trend in abundance, with higher numbers being recorded from 5 m depth during spring and autumn, and higher numbers at 10 m depth in summer and winter. Densities ranged from 9 to 16 individuals per 100 m^2 over the sampling period. The size–frequency distribution of* O. ophidianus *was uni-modal for each sampling month. Small individuals dominated at 5 m depth, intermediate-sized individuals at 10 m and larger individuals were more frequent at 15 m. The present study establishes population parameters for* O. ophidianus *and provides the necessary information for management purposes at the north-western periphery of its range in the Azores.*

Keywords: echinoderms, population dynamics, depth distribution, migration, range distribution

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INTRODUCTION

Echinoderms typically have extremely broad geographical and bathymetric distributions, occurring from intertidal to abyssal depths in all seas (Clark A.M., 1968). Many inhabit a broad spectrum of substrata ranging from sand and mud, to the coralline biocenose, debris, rock and wood. Detailed information on patterns of abundance and the spatial distribution of asteroids are, however, scarce and dominated by descriptive information dating back to the last century (Clark H.L., 1904; Coe, 1912; Caso, 1972; Franz *et al.*, 1981; Birkeland, 1982; Gage, 1986; Dance & Savy, 1987). Quantitative studies are equally few (Scheibling, 1980; Freeman *et al.*, 2001; Guzmán & Guevara, 2002; Howell *et al.*, 2002; Verling *et al.*, 2003; Entrambasaguas *et al.*, 2008).

Asteroids play an important role in benthic ecosystem functioning at a variety of scales. Examples include the association of high population densities of *Astropecten irregularis* (Pennant, 1777) with the availability of suitable prey species such as the bivalve *Spisula subtruncata* (da Costa, 1778) and the cumacean *Diastylis rugosa* Sars, 1865 (Freeman *et al.*, 2001), and the association between *Acanthaster planci* (Linnaeus, 1758) population explosions with the destruction of hermatypic corals in the Indo-West Pacific region (Endean, 1973). The strong influence of asteroids on benthic communities may result, partly, from the wide range of trophic levels that members of this group occupy (Paine, 1966, 1969; Guillou, 1996; Ellis & Rogers, 2000; Verling *et al.*, 2003). For example, some 'keystone' asteroid species have highly specific prey preferences that either directly or indirectly control the distribution and abundance of other benthic organisms (Paine, 1969; Birkeland, 1982; Ambrose, 1993; Tuya *et al.*, 2004). For this reason, some starfish species have become the subject of management studies (Kelleher & Kenchington, 1992; Simberloff, 1998; Pratchett, 2005; Houk & Raubani, 2010). One aspect of the conservation of any vulnerable species is to establish its optimal environmental requirements by analysing the size structure and abundance of its component populations throughout its spatial distributional range (Andrewartha & Birch, 1954; Krebs, 1978; Gaston, 1994; Caughley & Gunn, 1996). There is no such information available on the Azorean population of the warm-water asteroid *Ophidiaster ophidianus* (Lamarck, 1816) (Echinodermata: Asteroidea: Ophidiasteridae). This species is distributed from the Mediterranean Sea to the Gulf of Guinea, and has been reported from the Atlantic islands of St Helena, Cape Verde, Canary Islands, Madeira and the Azores (Clark & Downey, 1992). Its geographical centre of occurrence, the region with highest abundance, used to be the Mediterranean Sea, on the coasts of Algeria, Messina and Naples (Koehler, 1924). Currently, *O. ophidianus* is strictly protected in the Mediterranean (Barcelona Convention 92/43/CEE) and is considered a vulnerable species in Spain (Catálogo Nacional de Especies Amenazadas 2007). In contrast, within

Corresponding author:
J. Micael
Email: jfmicael@yahoo.com

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the Azorean Archipelago, that is, at the north-western limit of its distribution, *O. ophidianus* is the most widely distributed asteroid species on the coastal bedrock (Marques, 1983). *Ophidiaster ophidianus* is easily recognized by its small disc and five arms that are moderately long and cylindrical, with rounded tips. Individuals may vary from orange-red, with or without spots of brown, to bright red. Azorean individuals are usually brightly coloured. The only comprehensive study of this species in the Azores has been upon its reproductive biology (Micael *et al.*, 2011). The present research was established as a complementary study to this one and to establish the abundance, spatial distribution and size structure of *O. ophidianus*, thereby providing the local information necessary for management purposes.

MATERIALS AND METHODS

Study area and sampling procedure

The study was conducted at Ponta da Galera—Caloura, on the southernmost point of São Miguel Island (Latitude 37°46′N; Longitude 25°29′W) (Figure 1). Ponta da Galera (37°42′N 25°30′E) is a sub-surface basaltic delta (of 176 ha) and represents a lava flow. The shallow water sea-bed is a mix of massive lava blocks and boulders (2 m maximum diameter), seated on a sand and gravel substrata, in different proportions depending, in part, on depth. Ponta da Galera is a special conservation area (SAC: PTMIG0020) under the Natura 2000 network and which comprises 7586 m of coastline, representing 3.5% of São Miguel's total.

To evaluate the abundance and distribution of *Ophidiaster ophidianus* within the study area, 18 censuses were made, between April 2007 and August 2009. Sampling was undertaken by the same divers who counted and measured *O. ophidianus* individuals within 10 quadrats, each of 9 m^2 (Micael *et al.*, 2010). The quadrats were placed randomly within 3 depth levels (0–5 m, 6–10 m and 11–15 m). This sampling method allowed for direct spatial and temporal comparisons, and has been applied successfully to echinoderms elsewhere (Benedetti-Cecchi *et al.*, 1998; Linnane *et al.*, 2003; Roberts *et al.*, 2003; Verling *et al.*, 2003) and in the Azores (Micael *et al.*, 2010).

Abundance and size-classes

At each depth level, *Ophidiaster ophidianus* individuals were counted and each one was measured *in situ* (the length between the madreporic disc (as the standard point) and the tip of the first arm (nearest arm to the madreporic disc)) to the nearest mm using a flexible ruler (Barker & Nichols, 1983; Freeman *et al.*, 2001; Verling *et al.*, 2003).

Seawater surface temperature

Seawater temperature data for the sampling period (April 2007 to August 2009) were obtained from satellites NOAA12, NOAA16, NOAA17 and NOAA18 as Advanced Very High Resolution Radiometer (AVHRR) images, and processed with Terascan software; available at http://oceano.horta.uac.pt/detra/temperatura.php.

Data analysis

Obtained data were grouped into 12 size-classes (each of 10 mm, the smallest being 6 cm, the largest 17 cm). A multivariate statistical analysis (analalyisis of variance (ANOVA)) with fixed factors, combined with an *a posteriori* Student–Newman–Keuls multiple comparison test, was applied to compare *Ophidiaster ophidianus* abundance at each sampling month (18 months), each depth (3 levels), and each size-class (12 classes). Levene's test was used to test for homogeneity of variances. Spearman's rank correlation analysis was used to assess relationships between abundance and size, between

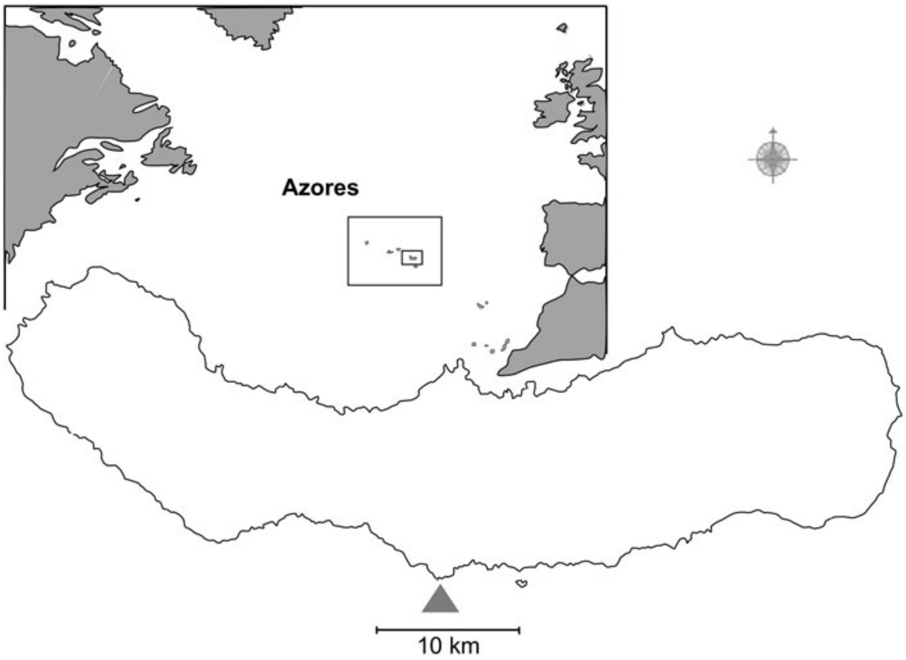

Fig. 1. Study location at Ponta da Galera—Caloura, on the southernmost tip of São Miguel Island.

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abundance and temperature, and between size and temperature. All analyses were carried out using the software package STATISTIC 7 (StatSoft, Inc. 2004).

RESULTS

Ophidiaster ophidianus showed a marked seasonal trend in abundance, ranging from a minimum of 9 individuals per 100 m^2 in October 2007 to a maximum of 16 individuals per 100 m^2 in May 2008 (Figure 2). However, monthly density values were not statistically different (ANOVA, $P = 0.855$, Table 1), revealing that the observed variation of abundances depends on the depth (ANOVA, $P < 0.001$, Table 1)—between March and June and between September and November (spring and autumn months, respectively), higher abundances of *O. ophidianus* were recorded from 5 m depth whereas between July and August and December and February (summer and winter months, respectively) higher abundances were identified from 10 m depth (Figure 3); and monthly density values present different dynamics for each size-class—the modal size of *Ophidiaster ophidianus* ranged from a minimum of 8 cm arm length in June 2007, May 2008 and June 2008, to a maximum of 14 cm in August 2007 (Figure 3). Individuals of <6 cm arm length were not found. The percentage of individuals at the modal size varied from 17.9% (September 2008) to 36.6% (April 2007). Individuals are capable of producing gametes at the smallest (arm length of 6 cm) observed size (Micael *et al.*, 2011) and, therefore, the whole population comprised mature individuals. To clarify the interpretation of population dynamics, size-classes were divided into 3 categories, that is, small individuals (arm length: 6–9 cm); intermediate (arm length: 10–13 cm); and large individuals (arm length: 14–17 cm). The majority of the population of *O. ophidianus* comprised intermediate-sized individuals at all times. In June 2007, May and June 2008, however, small individuals dominated and in August 2007, large individuals were most common (Figure 4).

There were significant differences in the individual's size–frequency distribution of *Ophidiaster ophidianus* between depths (ANOVA, $P < 0.001$) (Figure 3). Small individuals dominated at 5 m depth, intermediate individuals at 10 m and large individuals were more frequent at 15 m.

In the months with the highest recorded densities (all depths combined), small adults were the most abundant, as shown by a significant inverse correlation between the number of individuals per sampling month and modal size ($r = -0.549$, $P < 0.05$). The abundance of *O. ophidianus* (total values for each month) was significantly different among several pairs of size-class units, as shown by the *a posteriori* Student–Newman–Keuls multiple comparisons test (Table 2). Abundances were significantly higher among the 7–13 cm size-classes, as compared with the others.

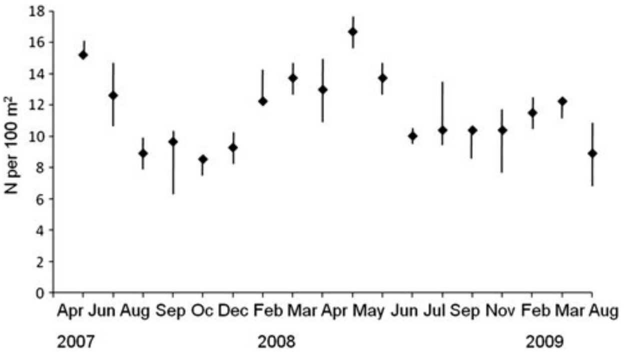

Fig. 2. Variations in the densities (numbers per 100 m^2) of *Ophidiaster ophidianus* over the course of the sampling period. Vertical lines represent the standard deviation.

Table 1. Multivariate statistical analysis (analysis of variance) comparing *Ophidiaster ophidianus* abundance at each depth (three levels), each sampling month (18 months) and each size-class (12 levels) (bold numerals—statistically significant values; $P < 0.01$) (Levene's test; $P > 0.05$).

Fixed factor	df	MS	F	*P*
Month	17	1.090	0.646	0.855
Depth	2	22.872	14.253	**0.000**
Size-class	11	23.924	18.610	**0.000**
Month*depth	34	1.532	0.944	0.562
Month*size-class	187	1.828	1.726	**0.000**
Depth*size-class	22	2.608	2.234	**0.000**
Month*depth*size-class	374	23.924	29.615	**0.000**

There was a significant inverse relationship between the number of individuals collected each month and seawater temperature (Figure 5) ($r = -0.625$, $P < 0.05$) but not between the modal size-class and seawater temperature ($r = 0.329$, $P > 0.05$). In general, the number of individuals observed was highest during spring (between March and June) when the water temperature was rising, and lowest in August, just before the highest recorded seawater temperature and in October and December, when the seawater temperature was decreasing (Figure 5).

DISCUSSION

At this study site in the Azores, *Ophidiaster ophidianus* showed a marked seasonal trend in mean abundance with higher numbers recorded during spring and summer. Differences in mean abundance between sampling months, however, were not significant (ANOVA, $P = 0.855$). Densities (9–16/100 m^2) recorded herein were similar to those identified for *Linckia laevigata* (highest density 15/100 m^2) (also Ophidiasteridae) (Yamaguchi, 1977), but 10 times less than those reported for *Asterias rubens* (highest density 171/100 m^2) and *Leptasterias polaris* (highest density 210/100 m^2) (Asteriidae) (Himmelman & Dutil, 1991). The lowest abundance of *O. ophidianus* coincided with the peak of gamete release in early autumn (Micael *et al.*, 2011), suggesting that spawning individuals were not in the sampled area.

The size distribution of *Ophidiaster ophidianus* showed that the population in question predominantly comprised individuals of an intermediate size (between 10 and 13 cm arm length). The number of large individuals (arm length: 14–17 cm) was inversely related to abundance suggesting a migration of these adults to other areas. Although the majority of the *O. ophidianus* were of an intermediate size ($10 < R < 13$ cm), and were recorded from ~5 m depth, larger individuals tended to occur deeper whereas smaller ones tended to be seen in shallow depths. A similar pattern of distribution related to depth has been identified for other asteroids, for

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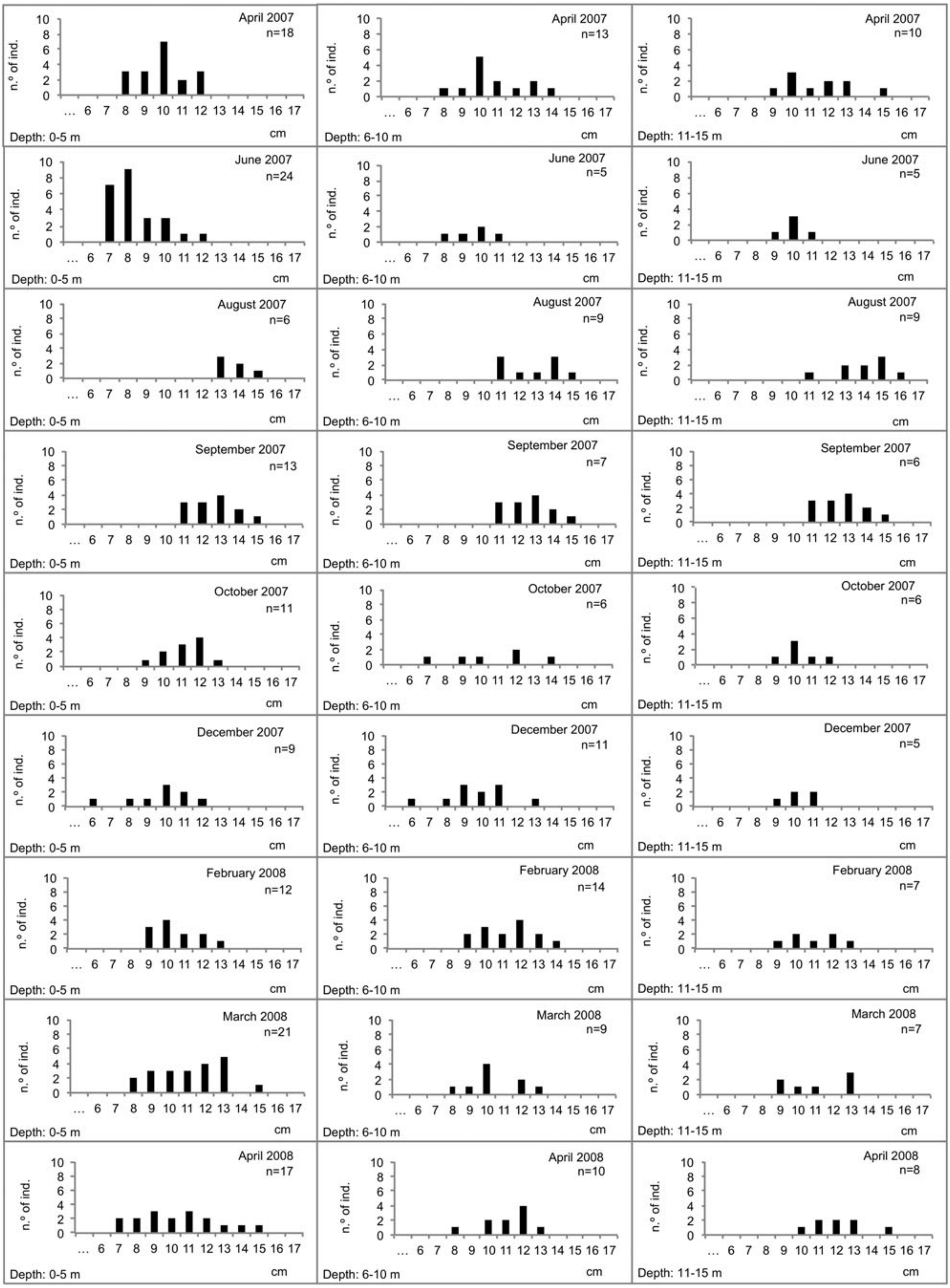

Fig. 3. Numbers of individuals of *Ophidiaster ophidianus* collected at each depth at Ponta da Galera from April 2007 to August 2009.

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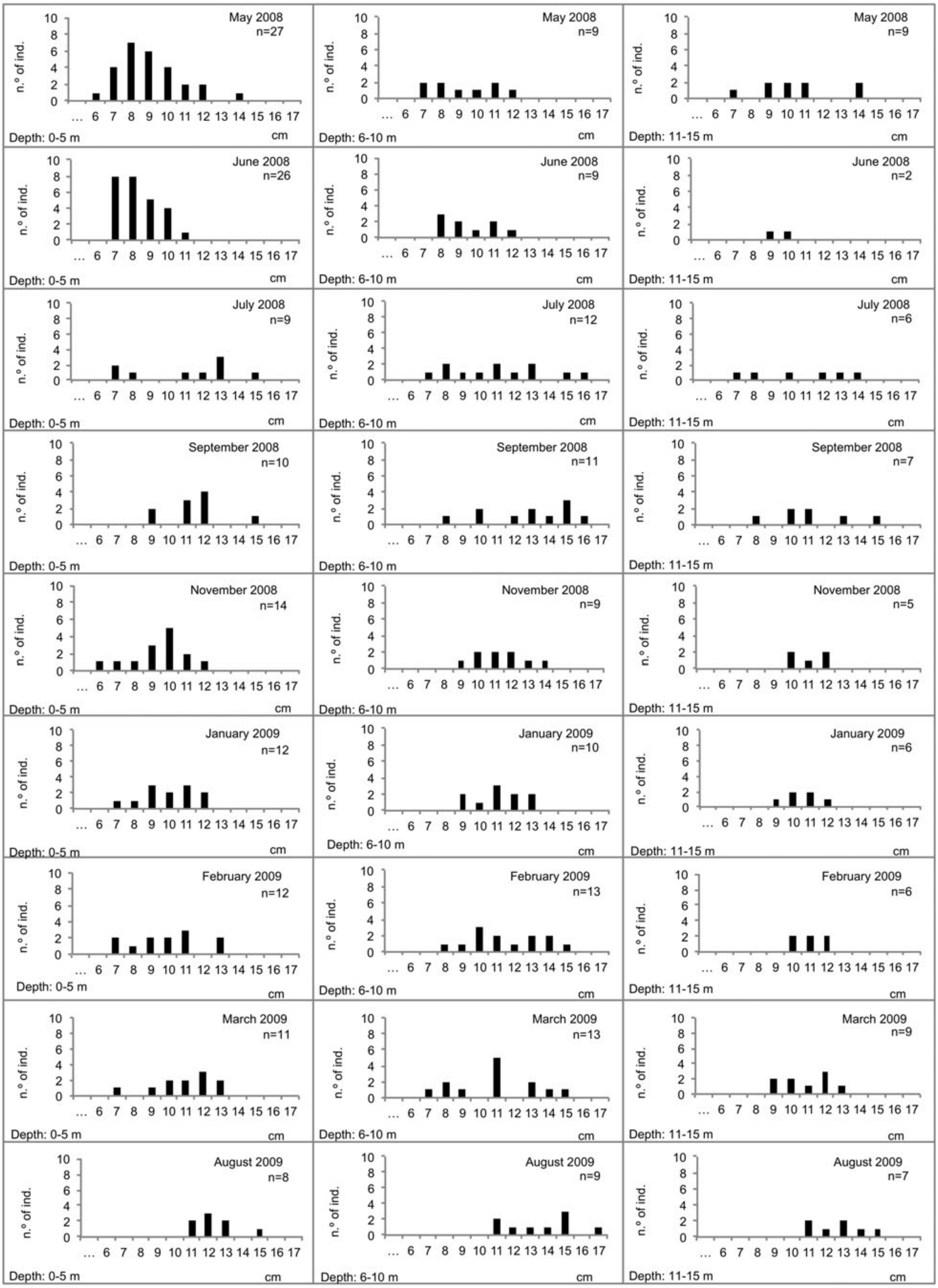

Fig. 3. Continued

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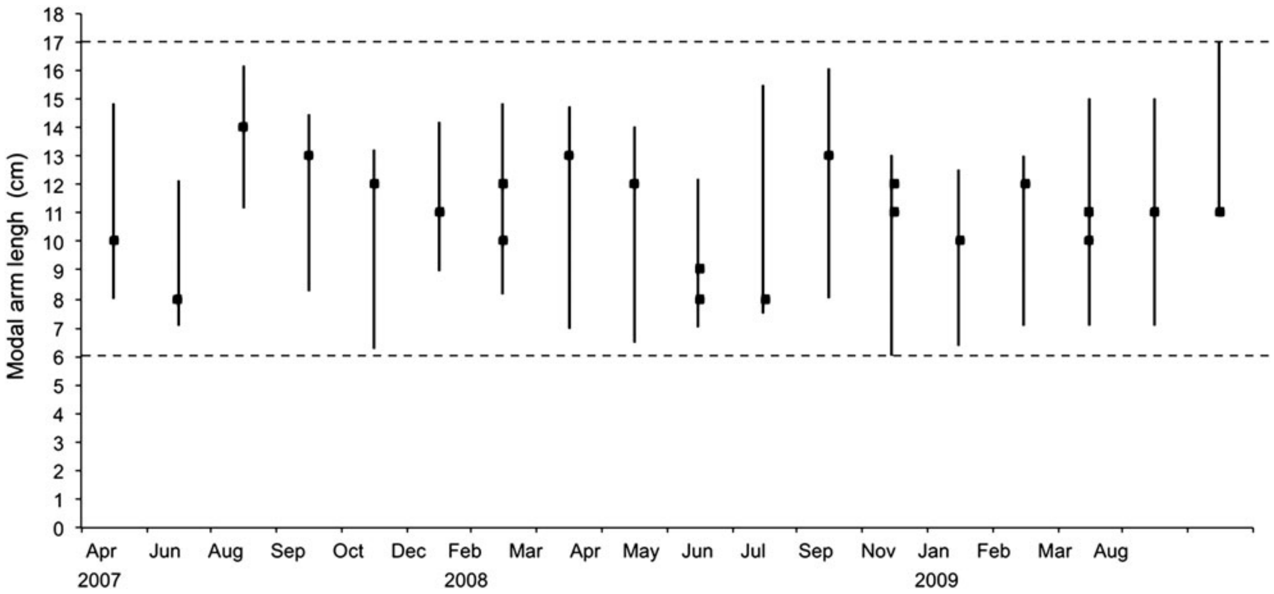

Fig. 4. Seasonal modal size-class ranges of *Ophidiaster ophidianus* from April 2007 to August 2009. Vertical lines represent the size-range.

Table 2. An *a posteriori* Student–Newman–Keuls multiple comparisons test contrasting the abundance of *Ophidiaster ophidianus* in each size-class (bold numerals—statistically significant values; *, $P < 0.05$; **, $P < 0.01$).

		6	7	8	9	10	11	12	13	14	15	16
Size-class	6											
	7	**0.0423***										
	8	**0.0002****	0.1069									
	9	**0.0000****	**0.0158***	0.3633								
	10	**0.0000****	**0.0000****	**0.0007****	**0.0335***							
	11	**0.0000****	**0.0000****	**0.0034****	0.0701	0.6106						
	12	**0.0000****	**0.0018****	0.1462	0.4450	0.1244	0.1491					
	13	**0.0000****	**0.0460***	0.4450	0.5525	**0.0083****	**0.0263***	0.3633				
	14	0.0747	0.6727	0.0661	**0.0019****	**0.0000****	**0.0000****	**0.0001****	**0.0111***			
	15	0.1244	0.4972	0.0570	**0.0025****	**0.0000****	**0.0000****	**0.0002****	**0.0121***	0.8652		
	16	0.9324	0.0517	**0.0002****	**0.0000****	**0.0000****	**0.0000****	**0.0000****	**0.0000****	0.1483	0.1745	
	17	0.9649	**0.0452***	**0.0002****	**0.0000****	**0.0000****	**0.0000****	**0.0000****	**0.0000****	0.1745	0.1772	0.8652

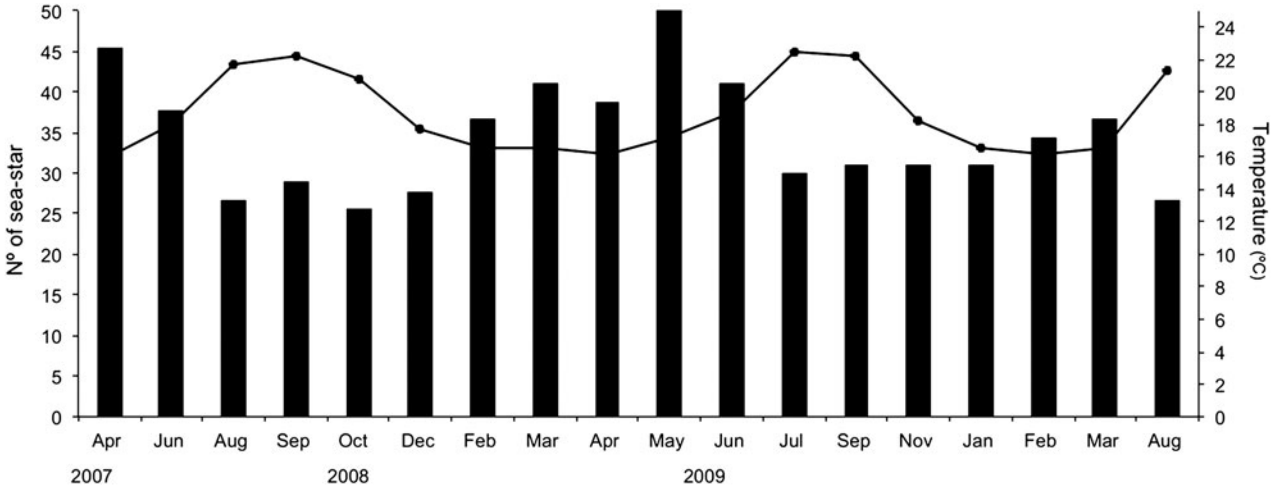

Fig. 5. Seasonal density of *Ophidiaster ophidianus* and seawater temperature at Ponta da Galera between April 2007 and August 2009.

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example, *Marthasterias glacialis* (Linnaeus, 1758) (Verling *et al.*, 2003) and *Asterias rubens* Linnaeus, 1758 (Himmelman & Dutil, 1991). Both studies showed evidences that there is a positive correlation between prey size and asteroid size distribution. In the Mediterranean Sea, *Ophidiaster ophidianus* occurs on the coralline biocenose and has an opportunistic feeding strategy (Tortonese, 1965). At the study site (Ponta da Galera) in the Azores, inhabited rocks were mainly covered by the brown alga *Dictyota* spp., the red alga *Asparagopsis taxiformis* (Delile) and erect coralline algae belonging to *Corallina* and *Amphiroa* (Frade *et al.*, 2004). Even for opportunistic asteroids, prey preferences may vary markedly. Prey selection changes with size in many asteroids (Sloan, 1980) and since most prey species are strongly localized in terms of distribution, changes in dietary preferences with age could be a major factor leading to the partitioning of different-sized individuals in relation to depth (Himmelman & Dutil, 1991). Further studies are necessary to understand how predators and potential prey species affect the densities and the structural distribution of *O. ophidianus*.

In the Azores, recruitment of *Ophidiaster ophidianus* may occur throughout the year as small individuals ($6 < R < 9$ cm) were seen every month, except August and September 2007 and August 2008. Peaks in the abundance of small individuals occurred in June 2007 and May and June 2008. In several asteroid species, episodes of recruitment are regulated by the proximity of the adult population to adjacent nursery areas (Birkeland *et al.*, 1971; Barker, 1979; Day & Osman, 1981; Jost & Rein, 1985). Such areas may have marked effects on asteroid size–frequency distributions by providing alternative habitats conducive to juvenile growth. As a consequence, juveniles often enter the adult population at a gradual rate after they have attained a relatively large body size (Rumrill, 1989). Although local aggregations of *O. ophidianus* were not observed, migration to deeper habitats may be a strategy to increase fertilization success. It may also be that mature individuals were near nursery areas not identified in this study. However, these lowest values of mature individuals coincided with non-recruitment seasons since, in the Azores, *O. ophidianus* starts to release gametes after the maximum annual temperature in September and ends just before the minimum winter temperature is reached (Micael *et al.*, 2011), that is, the months when abundances were lowest. The changes in abundance of the different size-classes could be related to natural mortality, growth of recruits and medium size individuals or the absence of young individuals.

The distributional focus of *Ophidiaster ophidianus* has been documented as the Mediterranean Sea (Koehler, 1924), where the species is now strictly protected. The Azores Archipelago thus has a peripheral geographical position in relation to the overall distribution of this species. Nevertheless, *O. ophidianus* is relatively common and individuals were abundant at Ponta da Galera (São Miguel). *Ophidiaster ophidianus* densities recorded from São Miguel were similar to those found at other sites in the archipelago, for example, Faial (Monte da Guia) at 38°31′N 28°37′W, São Jorge (Cais das Manadas) at 38°37′N 28°05′W and Flores (Porto de Santa Cruz das Flores) at 39°04′N 31°07′W (authors, personal observations).

Population densities tend to be higher at the geographical centre of a population's range than at the periphery (Rapoport, 1982). At the latter, individuals are considered more vulnerable to threats affecting population sustainability whereas those in the centre of a species' range are the last to be impacted (Brown, 1995; Sinclair *et al.*, 2007). Nevertheless, analysis of range contractions in a wide variety of animals and plants suggest that populations often collapse in the centre first, leaving isolated fragments at the periphery (Lomolino & Channell, 1995; Channell & Lomolino, 2000). Peripheral habitats may thus constitute refugia for endangered species (Sinclair *et al.*, 2007). The Azores is possibly a refuge for *O. ophidianus* where this species is not currently threatened.

Although it is premature to foresee a commercial exploitation of *Ophidiaster ophidianus* in the Azores, some illegal harvesting of other asteroid species has been reported. For example, in Panama, dried starfish are sold mostly as souvenirs to tourists and for the aquarium trade, for example Isle Grande, Portobelo and San Blas (Guzmán & Guevara, 2002). Scheibling (1980) indicated that humans are the agents most responsible for mortality of several asteroid species, having collected them for centuries. The lack of restrictions, governing the harvesting of asteroids, encourages short-term demand and the exploitation of new populations once traditional sources are diminished. In the Azores, the natural replenishment of *O. ophidianus* adult stocks appears low since there was no significant difference in the abundance of individuals over the course of the year. In the Azores, therefore, if commercial exploitation of *O. ophidianus* was allowed, over-fishing would occur quickly.

The present study provides a basis for understanding the population dynamics of *Ophidiaster ophidianus* including abundance and depth distribution with a predominance of smaller individuals in shallow waters and larger ones at deeper depths. Management strategies need more extensive data sets, however, including settlement and recruitment rates, and an understanding of trophic relationships at different sizes and, thus, ages. The data presented here, however, identifies a more vulnerable population during the months when smaller individuals are recruiting and reproduction is still taking place.

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Correspondence should be addressed to:
J. Micael
CIBIO-Azores, Research Center in Biodiversity and Genetic Resources
Department of Biology, University of the Azores, Ponta Delgada Campus
PT-9501-801 Ponta Delgada, São Miguel, Azores
email: jfmicael@yahoo.com

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