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Annual reproductive cycle, spatial distribution, abundance, and size structure of *Oreaster reticulatus* (Echinodermata: Asteroidea) in Bocas del Toro, Panama

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Abstract The structure, distribution, and population abundance of *Oreaster reticulatus* (Linnaeus, 1758) in 47,157 ha of shallow-water habitat in the archipelago of Bocas del Toro, Panama, were assessed from May to October 2000. The reproductive cycle of the sea star was studied in Isla Solarte, from February 2000 to February 2001. In total, 4,818 sea stars were recorded with a mean density of 149.7 ind. ha^{-1}, and a population of over 7 million was estimated for the archipelago. *O. reticulatus* was absent in ca. 50% of the evaluated areas, possibly due to high runoff and sedimentation; highest density was observed in an intermediate-runoff regime (255 ind. ha^{-1}). About 45% of the population was found in substrata dominated by seagrass (*Thalassia testudinum*) and coarse, calcareous sand, 51% occurred in habitats where coral reef patches were mixed with seagrass, and 4% exclusively on coral reefs. The average size, based on the major radius, was 9.5 cm (3–21 cm), with a population structure composed of ca. 83% juveniles and 17% adults. The average reproductive size, measured as major radius, was 15 cm, and the minimum was 7 cm. Both males and females with a maximum stage (IV) of gonad development were observed throughout the year. The gonad index showed three peaks of maximum reproductive activity, which is not comparable to studies from other localities. The reproductive cycle did not seem to be related to water temperature, which ranged from 27°C to 30°C, but may respond more closely to changes in local rainfall. This relationship was not statistically significant based on this 1-year study. These data provide a useful baseline for management of local populations in the face of an increasing harvest for the aquarium trade and as souvenirs.

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Introduction

Oreaster reticulatus is an asteroid widely distributed on both sides of the Atlantic, from North Carolina to as far south as Brazil and the Cape Verde Islands in western Africa (Scheibling 1980a; Hendler et al. 1995). Throughout the tropical Caribbean, *O. reticulatus* inhabits calm, shallow waters (Scheibling 1980a). Studies from St. Croix (Virgin Islands) and the Grenadines indicate that the species is found more abundantly on coarse, calcareous sandy bottoms that are isolated or surrounded by seagrass like *Thalassia testudinum*, *Halodule wrightii*, *Syringodium filiforme*, and calcareous macroalgae like *Halimeda incrassata* and *Penicillus capitatus* (Scheibling 1980a,b,c, 1981a). These sea stars are also found in soft sand and mud substrates that are typical of mangroves, lagoons, and some shallow reef environments (Hendler et al. 1995).

O. reticulatus is an omnivore that feeds on a great variety of epiphytic microorganisms such as filamentous algae, diatoms, and small detritus particles in St. Croix and the Grenadine Islands (Scheibling 1980d, 1981b, 1982a). The number of microorganisms it consumes generally depends on their availability and its ability to capture them (Scheibling 1981a). *O. reticulatus* seems to prefer echinoids like *Meoma ventricosa*, *Tripneustes ventricosus*, *Echinometra viridis*, holothuroid juveniles like *Holothuria mexicana*, and meiofauna such as polychaete worms, copepods, ostracods, and crab larvae (Scheibling 1981b, 1982a). It can also consume sponge tissue (Wulff 1995).

Adult *O. reticulatus* form aggregations known as "fronts" in scattered sand patches surrounded by seagrass meadows. These aggregations depend on the availability of substrata rich in benthic organisms

(Scheibling 1980a,b, 1981b, 1985). The larvae and juveniles are mostly found in seagrass such as *Thalassia testudinum* and *Syringodium filiforme*, presumably finding protection against predators (Scheibling 1980a,b, 1982b, 1985). In addition, the sea star behaves gregariously, with higher densities associated with an annual reproductive cycle (Scheibling 1980a,c). *O. reticulatus* is gonochoric (Scheibling 1981c; Hendler et al. 1995). Spawning has not been observed in situ, and it may occur at night (Scheibling 1981c; Metaxas et al. 2002). Like other echinoderms, maturity and reproductive capacity are related to its somatic growth, and sea stars reach sexual maturity at an approximate radius of 12 cm in the Virgin Islands and the Grenadines (Scheibling 1980a,b, 1981c). A key factor in the production of gametes is food availability, since nutrients are transferred and used during development and maturation of the gonads (Scheibling 1980b,c, 1981c).

Scheibling's contribution to the ecology and biology of *O. reticulatus* is comprehensive and unique, although the work has been limited geographically to few localities in the Caribbean (e.g. Virgin Islands, Grenadines, Bahamas). The present study assessed the distribution and density of *O. reticulatus* in the extensive Archipelago of Bocas del Toro (Panama), and evaluated its annual reproductive cycle in relation to total rainfall and temperature at a single site, Isla Solarte. We expected that both parameters could affect the reproduction of this organism. Distribution/density data on *O. reticulatus* were compared among depths, habitats (e.g. seagrass meadows, coral reef structures, interspersed seagrass, and coral patches), and hydrographic regimes (e.g. Bahía Almirante and Laguna de Chiriquí). One goal was to provide baseline information for resource managers, since there is increasing commercial extraction of sea stars for the aquarium trade and as souvenirs, locally and in other areas of the Caribbean (Clark 1933; Scheibling 1980a; Sloan 1985).

Materials and methods

Study area

Bocas del Toro Province is located in the west of the Republic of Panama, between 8°30′ and 9°40′N and 82°56′ and 81°8′W. It has an area of 8,917 km^2, with an archipelago of ca. 3,500 km^2, formed by seven large, forested islands and hundreds of mangrove cays (Rodríguez et al. 1993; Guzmán and Guevara 1998). The continental shelf to the north of the province is narrow. The near-shore zone has maximum depths of 20–50 m and is composed of two large lagoons, Bahía Almirante and the Chiriquí Lagoon (Fig. 1). The mainland and the islands receive rainfall throughout the year, with somewhat drier periods in March and September/October, and two periods of higher rainfall in July and December (Guzmán and Guevara 1998). The bottom topography, climate, geology, and reef distribution of the archipelago have been described previously (Rodríguez et al. 1993; Greb et al. 1996; Guzmán and Guevara 1998, 1999). In this study, we divided the archipelago into three hydrographic units, mostly based on runoff regime (sensu Guzmán and Guevara 1998): high-runoff in the Laguna de Chiriquí (high number of large rivers), intermediate-runoff in northwest Bahía Almirante, and low-runoff in southeast Bahía Almirante (Fig. 1).

Population density, distribution, and size structure

To evaluate the distribution and abundance of the populations of *Oreaster reticulatus* (Linnaeus, 1758) in the archipelago, sampling sites were located using a map with a scale of 1:50,000. The entire insular and continental subtidal coastal area was delineated to a depth of 10 m, and divided into continuous and shore-parallel grids of ca. 2 km^2 (240 grids for the whole archipelago). Subsequently, 120 grids were randomly chosen as sampling sites, representing the diversity of existing habitats in the shallow subtidal coastal zone of the archipelago. All surveys were done between May and September 2000.

Based on a maximum work depth of 10 m, two sampling depths corresponding to 1–5 m and 5–10 m were established at each site. Three replicate belt-transects of 100 m×6 m were done at each depth, totaling a survey area of 1,800 m^2 (0.18 ha) by depth and 3,600 m^2 (0.36 ha) by site. Two divers swam a 6 m long PVC pipe simultaneously along the transect, with each diver evaluating a band 3 m wide. A compass was used to maintain a fixed course along the route and depth gradient. It was not possible to census both depths at every site, due to limited depth or the proximity to the mouth of rivers. Habitat/substratum was recorded during the assessment and classified into three types: seagrass meadows, coral reef structures, and heterogeneous, with corals and seagrass interspersed.

The census consisted of counting individuals of *O. reticulatus*, both adult and juvenile (=2 cm), present in the designated area within each transect (100 m×6 m), and measuring their size in situ using a ruler with 0.1 cm accuracy. Early juveniles were generally dark green, sometimes with thin bands of light green or rusty orange (sensu Scheibling 1980a). The major radius was obtained by measuring from the centrodorsal plate of the disk to the distal end of the largest arm, and the minor radius was measured from the centrodorsal plate to the margin of the disk in the inter-radius between arms (Ummels 1963; Berovides-Alvarez and Ortiz-Touzet 1981).

Data on the distribution and abundance of *O. reticulatus* was mapped using the geographical information system (GIS). Digital classification of the study area was based on a combination of digital images from three sources: topographic maps with a scale of 1:50,000, color aerial photographs with a scale of 1:25,000, and LANSAT TM-5 satellite images. Satellite images were processed using the program ERDAS Professional Imagine V8.4. The programs used for the integration of the information and to produce the maps of distribution and density were MIPS V3.1 (Map and Image Processing System) and ArcView V3.0 in PC platform.

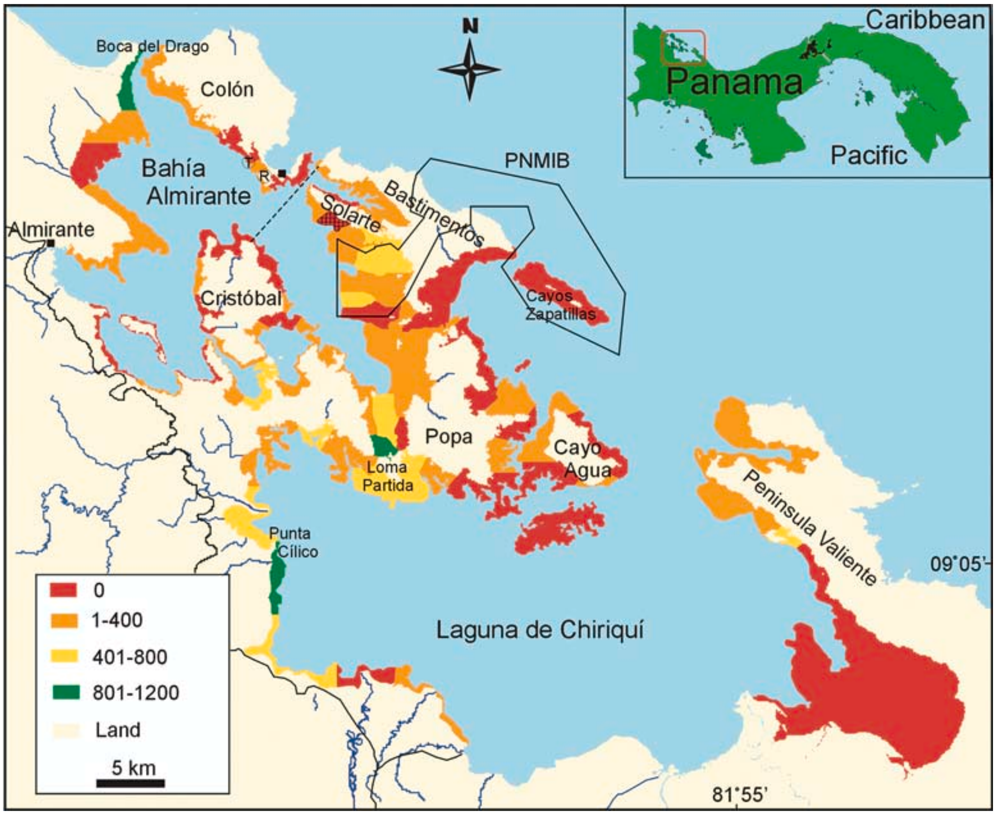
Annual reproductive cycle and minimum reproductive size

To determine the reproductive cycle of *O. reticulatus*, we collected ten adult individuals (9–21 cm major radius) every month during the full moon for 13 months (February 2000–February 2001), except during the first month, during which 15 individuals were dissected. Not all individuals were reproductive at the time of collection. The collection site was located south of Isla Solarte (Fig. 1). Sea stars were drained, and weight and size were measured following the protocol of Berovides-Alvarez and Ortiz-Touzet (1981). Gonads were removed from the body cavity of all five arms, weighed (to a precision of 0.1 g), and classified according to their sex and stage of development (presence/absence), particularly stages III and IV (sensu Scheibling 1981c; Sewell and Chia 1994). The testes were cream-colored and the ovaries were intense orange at sexual maturity. The gonad index (GI) was calculated according to Scheibling (1981c): (gonad wet weight)/(drained body wet weight)×100.

During the 13-month study period, changes in mean sea surface temperature were recorded at a depth of 3 m, using thermographs located at Isla Colón (Fig. 1). Monthly rainfall data were obtained from a meteorological station at Isla Colón (Fig. 1).

We used histological techniques to confirm the presence or absence of growth (III) and mature (IV) reproductive stages of development on all previously sexed individuals (sensu Sewell and

Fig. 1 *Oreaster reticulatus*. Map of the Republic of Panama (*upper right insert*) showing the location of the archipelago of Bocas del Toro and the density distribution (ind. ha^{-1}) of the sea star, to a maximum depth of 10 m, from Boca del Drago to the northern point of Peninsula Valiente. Coastline areas without any color were not surveyed. *Solid line polygon* indicates the marine protected area of the Parque Nacional Marino Isla Bastimento (*PNMIB*). *Black grid area* indicates the collecting site for the reproductive study, southern Solarte Island. *Dashed line* indicates the northwest–southeast regime border in Bahía Almirante. Symbols (*T*) and (*R*) at southern Isla Colón indicate temperature and rainfall stations, respectively



Chia 1994). The gonads were fixed in Bouin's solution for 24 h, washed in 50% alcohol, and preserved in 70% ethanol. They were dehydrated in different grades of alcohol, washed in xylol, and embedded in paraffin. Tissue blocks were serially sectioned at 8 μm, and the sections were stained with hematoxylin and eosin, following standard histological procedures (Humason 1972).

In order to determine the minimum reproductive size of *O. reticulatus*, another 59 small (< 12 cm, based on Scheibling 1981c) individuals of the population were haphazardly collected from the same study site in January–February 2001. They were drained for 10 min, measured as above, and partially dissected to verify the presence or absence of gonads (gonads were not extracted or weighed). The size and weight of the 135 individuals measured during the monthly evaluations of the reproductive cycle were included in this analysis.

Finally, all data sets were analyzed using parametric statistics. Pearson's product moment correlation analysis was used to test for the relationship between biometric variables (weight, size), and between the GI and environmental variables (temperature, rainfall). A one-way ANOVA, combined with a posteriori Student–Newman–Keuls multiple comparison test, was used to assess monthly variation in GI by sex, and differences between hydrographic regimes. Paired *t*-test and *t*-test were used to compare densities between depths, habitats, and average GI between sexes. We transformed the data when assumptions of variance (normality and homoscedasticity) were not fulfilled (Sokal and Rohlf 1995).

Results

Abundance and distribution of the populations

In total, we observed and measured 4,818 *Oreaster reticulatus* at 120 study sites, 3,521 and 1,297 in shallow and deep transects, respectively. There were no significant differences between shallow and deep sites (paired *t*-test: $t = -0.664$, $P = 0.510$, $df = 47$; sites with only one depth and sites with no individuals at both depths were not included) for total individuals (± SE: 38.9 ± 9.1 and 27.0 ± 3.6, respectively) or for density (216.4 ± 50.1 ind. ha^{-1} and 150.11 ± 19.9 ind. ha^{-1}, respectively). The average density was 149.75 ± 21.1 ind. ha^{-1}. As a result, we estimated a stock for the archipelago of ca. 7,061,896 individuals, based on 47,158 ha of coastal zone with waters < 10 m deep (see Fig. 1).

O. reticulatus was not observed in 47.9% of the archipelago, ca. 35.8% of the 120 study sites (Fig. 1, red area). Three sites with high densities (800–1,200 ind. ha^{-1}) were located to the west of Boca del Drago, to the north of Isla Loma Partida, and to the south of Punta Cílico on the western shore of the Laguna de Chiriquí. These sites represented 2.2% of the total shallow coastal habitats (Fig. 1). Intermediate to high densities (400–800 ind. ha^{-1}) were observed in nine areas in the central-southern region of the archipelago, covering 11.8% of the total area. Two of these areas are notable because of size and location, one of 1,886 ha around Isla Loma Partida, and the other of 1,331 ha within the limit of the protected area of the Parque Nacional Marino Isla Bastimento (PNMIB). Low densities (< 400 ind. ha^{-1}) were widely distributed throughout the archipelago, representing 38.1% of the total area, in particular to the west of Isla Popa and the Peninsula Valiente (Fig. 1).

In 92% of all survey sites, the dominant habitat was seagrass or seagrass interspersed with other habitats, and 8% were coral reefs. Of all sites where *O. reticulatus* was recorded (77 sites), 45% were seagrass meadows, ca. 4% were exclusively coral reefs, and ca. 51% were a mixture of both. In spite of the varied and mixed substratum within each study site, and in general for the whole archipelago, the highest densities of *O. reticulatus* were observed at sites dominated by seagrass (308.3 ± 50.9 ind. ha^{-1}), followed by 183.6 ± 30.3 ind. ha^{-1} in interspersed habitats. Densities were significantly different between interspersed and seagrass habitats ($t = 2.01$, $P = 0.048$, $df = 72$). In addition, it was observed that 31% of juveniles (based on individuals with major radius < 12 cm; Scheibling 1981c) were found in 84.6% of sites with fine sand densely covered by *Thalassia testudinum* and *Syringodium filiforme*, while in 69.2% of sites with interspersed habitats. The lowest density was observed in coral reef habitats, with 5.6 ind. ha^{-1}.

Densities were significantly different among hydrographic regimes ($F_{(2,94)} = 8.102$, $P < 0.001$); low versus high runoff regimes were similar (SNK; $P = 0.340$) and significantly different from the intermediate regime ($P < 0.004$). The highest density, 255.5 ± 44.2 ind. ha^{-1}, was observed in southeast Bahía Almirante under a low runoff regime, followed by 218.2 ± 43.2 ind. ha^{-1} and 80.9 ± 38.3 ind. ha^{-1} in Laguna de Chiriquí (high runoff) and northwest Bahía Almirante (intermediate runoff), respectively.

Population structure

The average length of the major radius for 4,818 individuals was 9.47 ± 0.03 cm (range 3–21 cm) and that of the minor radius was 5.20 ± 0.02 (1.5–14 cm). A significant relationship was observed between the major and minor radii ($r = 0.89$, $P < 0.001$, $n = 4{,}818$), consequently for the rest of the analyses we used the major radius as the measurement of size (Fig. 2A). The population structure of *O. reticulatus* presented a unimodal normal distribution, composed of 83.3% juveniles and 16.7% adults (based on maturity at a major radius length of 12 cm; Scheibling 1981c). About 7% (338 individuals) of the population was exclusively within the 12 cm size class (Fig. 2B). A small but significant inverse relationship was observed between the number of sea stars per site and individuals' average size within a site ($r = -0.39$, $P < 0.001$, $n = 77$).

Reproductive maturity and annual reproductive cycle

In total, 194 individuals were dissected and analyzed to evaluate the reproduction of *O. reticulatus* in Bocas del Toro. Not all individuals showed reproductive activity or gonads. A significant relationship was found between the major and minor radii of this group of individuals ($r = 0.98$, $P < 0.001$, $n = 194$; combining monthly and minimum size collections), similar to that for the whole population. Likewise, the relationship between body wet weight and the major radius was statistically significant ($r = 0.981$, $P < 0.001$, $n = 194$). Nevertheless, the correlation between gonad weight and the major radius, although significant, was quite low ($r = 0.36$, $P < 0.001$, $n = 114$; only individuals with gonads from the monthly collections were included). A mean size of 13.6 ± 0.3 cm (range 4.5–20.7 cm) and weight of 511.3 ± 24.4 g (26–1,299 g) were recorded for the whole population (reproductive and non-reproductive).

The average reproductive size was 15.1 ± 0.3 cm, with a minimum size for the whole population of 7.5 and 7.9 cm for females and males, respectively. These values are 4 cm less than the 12 cm average reported from other localities (see Scheibling 1981c). However, these minimum sizes only represented 2.7% of the population. About 87.2% of the immature or non-reproductive individuals had major radii < 12 cm (Fig. 3A), as did 25.8% of the mature or reproductive individuals (Fig. 3C). Most of the mature individuals (74.2%) were > 12 cm (Fig. 3C). Due to year-round reproductive activity and the asynchronous gonad development observed here (see below), we considered the sample of small sea stars, made for measuring minimum size in January and February 2001, to be a reliable measure of minimum reproductive size.

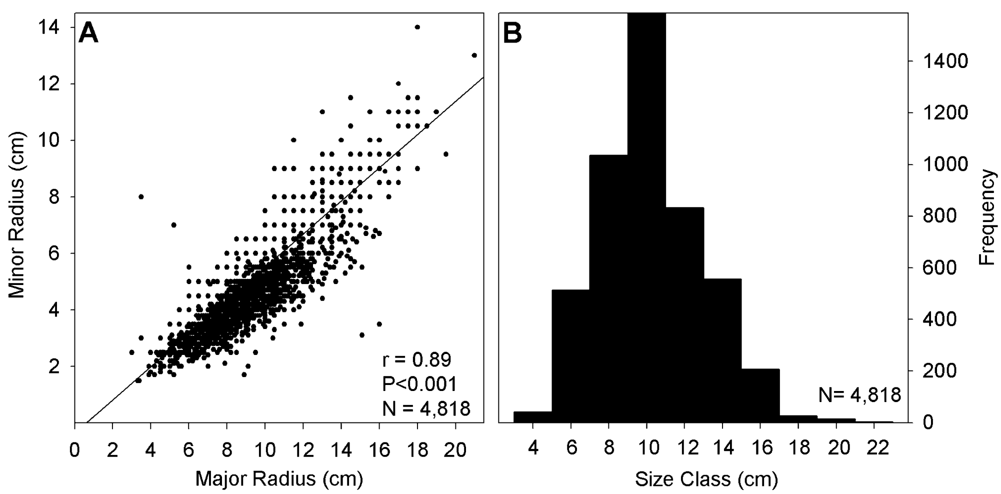


Fig. 2A, B *Oreaster reticulatus*. Relationship between the major and minor radius (**A**) and size-frequency distribution (**B**), based on major radius measured in 4,818 individuals, Bocas del Toro, Panama

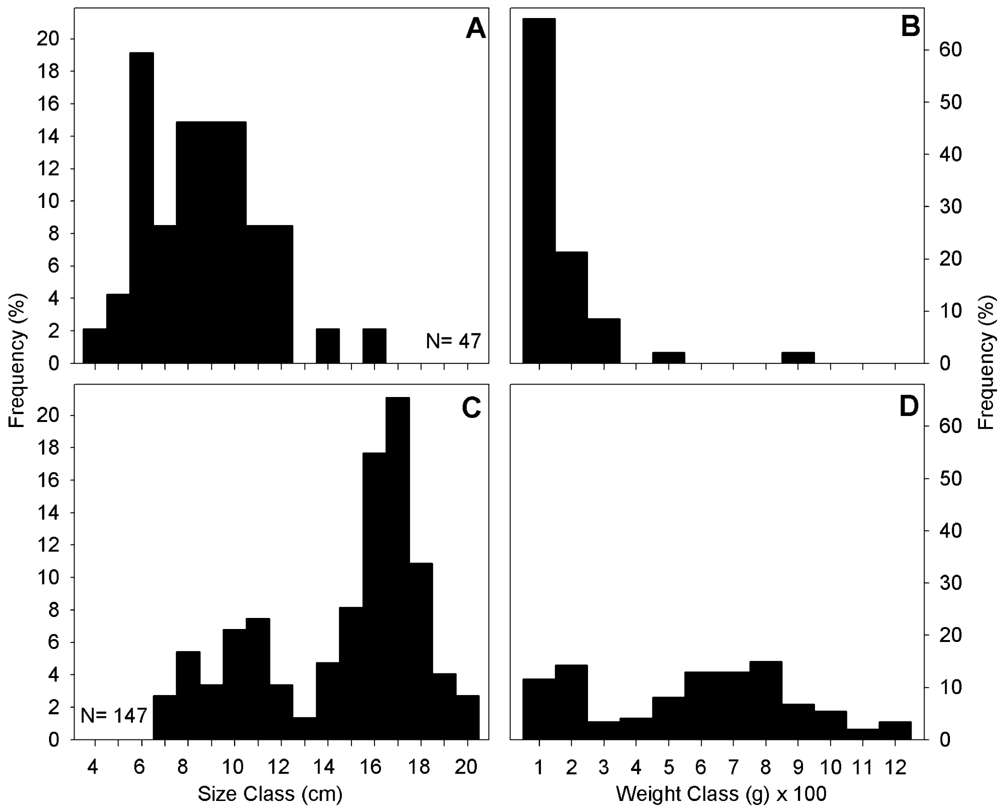


Fig. 3A–D *Oreaster reticulatus*. Size- and weight-frequency distributions for non-reproductive (**A**, **B**) and reproductive (**C**, **D**) individuals, Bocas del Toro, Panama. Only individuals dissected for the reproductive study ($n = 147$) were analyzed

The body wet weight in the studied population varied between 80 and 1,299 g for reproductive individuals, with an average of 617.3 ± 25.9 g, while immature individuals had an average of 179.7 ± 22.1 g (26–900 g). The weight frequency of non-reproductive sea stars was < 200 g in 66% of the individuals (Fig. 3B), whereas in the reproductive ones an apparently bimodal but fairly homogenous weight distribution was observed, with 58.5% of the individuals having a weight > 600 g (Fig. 3D).

We dissected and sexed 116 individuals without ambiguity ($n = 135$ from monthly collections): 53 females (46%) and 63 (54%) males. Different stages of reproductive development were identified histologically; however, 19 individuals in stage I could not be sexed. Gonad development was asynchronous within single individuals (different stages were observed in the same arm); all reproductive individuals showed gonads with different stages in any particular month. Gonads in the stages of recovery and growth (II and III) and maturity (IV) were observed histologically for both sexes, and were more easily identifiable.

Males and females with gonads in stages III and IV were observed almost every month. Between 15% and 65% of the females were in stage III of development depending on the time of the year, > 40% during May, August, October, and December, and < 40% between February and March, in June, and in November. About 20% of the males were in stage III in all months, except for April and January 2001 (Fig. 4A). A similar pattern was observed for stage IV, the maximum development, which showed two peaks with ca. 60% of females in June and February 2001, and one peak in November for males (Fig. 4B). This suggests year-round activity, or an apparent lack of synchrony in the local reproductive cycle of this species, since in many cases the maximum frequency peaks for individuals did not coincide for females and males.

The average gonad index (regardless of sex) ranged from 1.2 to 4.9, and revealed a pattern with three peaks of maximum reproductive activity, these being July and November 2000, and January 2001 (Fig. 4C). The monthly GI average varied significantly among months ($F_{(12,102)} = 3.590$, $P < 0.001$). The three peaks were not statistically different, and two main differences were observed between February 2001 versus the months of January, August, October, September, and December, and between the months of August and January with respect to July (based on SNK test). GI averages were 2.9 ± 0.9 and 2.0 ± 0.5 for females and males, respectively, and were not statistically different ($t = 1.737$, $P = 0.095$, $df = 24$). Monthly GI average was generally lower in males than in females (Fig. 4D); males were in agreement with females in three peaks out of four; nevertheless, a clear and significant relationship between the two sexes was not observed ($r = 0.352$, $P > 0.05$, $df = 13$). Three peaks of female's activity (July, November, and February 2001) coincided with the overall GI (Fig. 4C).

The average sea surface temperature and precipitation during the 13 months of the study were 28.3°C and 291.3 cm, respectively. The highest water temperatures were recorded during September and October 2000, with values of 29.8°C and 29.5°C, respectively, whereas the

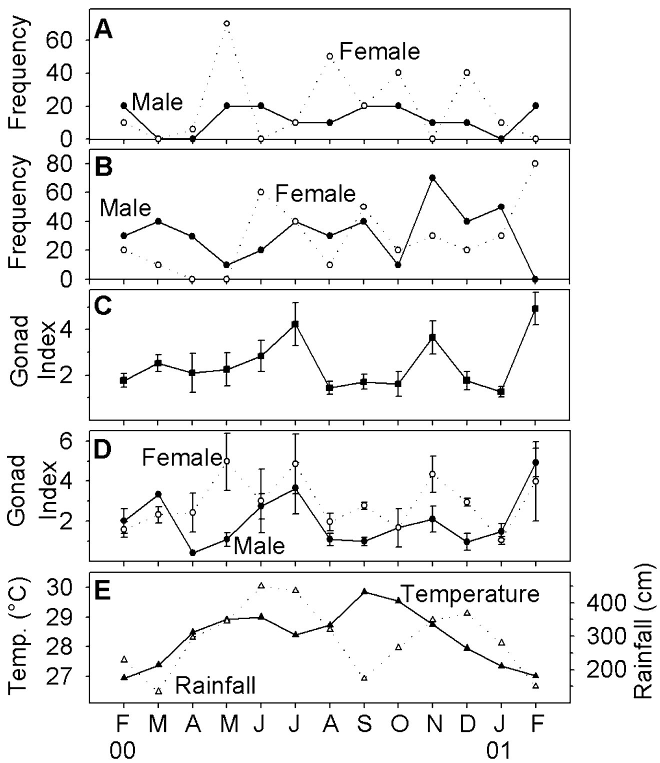


Fig. 4A–E *Oreaster reticulatus*. Monthly reproductive changes compared to environmental variables in Bocas del Toro, Panama, from February 2000 to February 2001. Percentage of male and female individuals with gonads in stage III (**A**) and stage IV (**B**), overall gonad index (**C**), gonad index by sex (**D**), and monthly means for water temperature and rainfall (**E**). *Vertical bars* represent standard error. Rainfall and sea temperature stations were located at Isla Colón (see Fig. 1)

lowest temperatures occurred between January and March (Fig. 4E). Rainfall showed a bimodal pattern during the 13-month period, with two peaks of precipitation (>300 cm) around June–July and November–December, and two lower ones in February–March and September (Fig. 4E). The total GI (Fig. 4C) was not significantly correlated with sea surface temperature ($r = -0.214$, $P > 0.05$, $df = 13$) or precipitation ($r = 0.074$, $P > 0.05$, $df = 13$). In spite of the visual coincidence between the highest GI in February 2001 and the periods of lowest temperature and precipitation, the opposite was observed for the two peaks in July and November (Figs. 4C, E). Conversely, lower reproductive activity corresponded to maximum temperature in September. Since a long-term record of water temperature does not exist for the area, it is not possible to conclude that these seasonal changes are typical for the archipelago.

Discussion

Population structure, distribution, and abundance

Oreaster reticulatus was not observed in ca. 50% of the area encompassed in this study (47,158 ha), principally in the coastal zone to the south and southeast of the Laguna de Chiriquí, where high sedimentation and runoff from major rivers may not allow the development of appropriate habitats (sensu Goldsborough and Kemp 1988). Generally, sea stars were found in higher density in seagrass habitats (*Thalassia testudinum*) and mixed substratum with semi-coarse to fine calcareous sands, less affected by runoff. Although seagrass density was not measured, more aggregations of higher density sea stars were observed in low leaf-size and density seagrass meadows. This seems to be a predictable distribution pattern, since the sea star would have less mobility in very dense seagrass beds, which would make its feeding difficult (sensu Scheibling 1980a,b, 1981c). It was frequently observed that aggregations of reproductive individuals had a greater tendency to occur in dispersed sand patches and not in beds of dense *T. testudinum*, similar to Scheibling's observations (1980a). Most juveniles were observed exclusively in very dense meadows of *T. testudinum* and *Syringodium filiforme*, where there is greater protection from predators (Scheibling 1980a).

Sea star populations were found mainly around the islands of the archipelago with better water circulation and apparently away from areas affected by high runoff, with an average density of 149.8 ind. ha^{-1}, and as high as 1,294 ind. ha^{-1}. The densities arbitrarily defined as "low" in the present study (<400 ind. ha^{-1}) included 38% of the total area, with an average of 119.9 ind. ha^{-1} (range 2–400; based on 60 sites). The overall average is somewhat lower than the 217 ind. ha^{-1} (113–350; 5 sites) reported for the Grenadine Islands (Scheibling 1980a,b), and considerably lower than the 904 ind. ha^{-1} (350–1,413; 3 sites) from St. Croix, Virgin Islands (Scheibling 1980b). Even if we use an average of 234 ± 29.2 ind. ha^{-1}, based solely on sites with sea star presence (77 sites), our density is much less than values for the populations of St. Croix.

The size distribution showed that the population of *O. reticulatus* is predominantly composed of juveniles (ca. 83%), of which 4.7% represent individuals in an early stage of development (<6 cm) and 78.5% represent sub-adults (between 6 and 12 cm radius) (according to Scheibling 1980a). This distribution is dissimilar to the findings from other localities in the Caribbean, where most of the populations (>70%) are made up of reproductive adults, with a size of ca. 20 cm, suggesting that recruitment is low and sporadic (Scheibling 1980a,b). When comparing all our sites, we found a tenuous inverse relationship between population density and size of individuals; nevertheless, this does not seem to indicate that the population growth and its structure are limited by intraspecific competition for food, as has been suggested for other areas (Scheibling 1980a,b). In Bocas del Toro, recruitment may occur year-round over the whole area, and not in specific nursery habitats, because seagrasses are widely distributed in the archipelago. Furthermore, low population density may not affect fertilization success (Metaxas et al. 2002).

Reproductive behavior

In general, the observed frequency distributions and the existence of a population dominated by juveniles suggest frequent recruitment within the archipelago. The average size (15.0 cm) of reproductive individuals in this population is 3 cm larger than elsewhere, where the mature reproductive size is approximately 12.0 cm radius (Scheibling 1981c). Smaller individuals with reproductive gonads (~7 cm) were found, but they made up $<3\%$ of the population. Exogenous factors may partly affect the maturity of individuals, but differences among localities in the Caribbean are difficult to explain with existing information.

Extrinsic factors such as temperature and photoperiodicity influence the seasonal and reproductive cycle of many echinoderms, including *O. reticulatus* (Scheibling 1981c). In the present study, well-developed male and female gonads were observed almost throughout the year. In the Grenadine Islands and St. Croix, *O. reticulatus* displays a conspicuous annual reproductive cycle related to temperature changes and clearly defined seasonal periods, with the highest peak of reproduction in summer and reproductive activity fairly limited during winter (Scheibling 1981c). Nevertheless, it is important to note that although the annual temperature range in both regions is quite similar (27–29°C), the period with higher temperatures (>28°C) lasts for 9 months in Panama, while in the other localities the period is almost half that. The extended period of high temperature in Bocas del Toro may permit asynchronous, year-round reproduction. Visually, the GI was highest during periods of maximum precipitation, although this relationship was not statistically significant. This may suggest that the maturity of the gonads and spawning may respond to chemical clues in the water (e.g. nutrients, salinity). However, the archipelago Bocas del Toro cannot be considered as typical of the region, since it is one of the rainiest areas of Panama and seasonal changes are not well defined (Guzmán and Guevara 1998). It would be advisable to make comparative reproductive studies at other localities in Panama, where nutrients, temperature, etc. can be evaluated simultaneously.

In this study and others (Scheibling 1981c) a greater GI was observed in females than in males, which suggests greater reproductive effort. Nevertheless, the marked differences in the GI value from site to site are notable; >15 in some areas of St. Croix during peaks of activity (Scheibling 1981c), compared to values <5 in Panama. This might reflect the multiple reproductive peaks observed in Panama, during which most population samples maintained maximum stages of maturity the whole year, suggesting several spawning events. This difference in GIs could also be associated with the size of individuals in the respective analyses; generally, at the other localities, individuals of 13–20 cm were collected, whereas in Panama the range was larger, so that more smaller reproductive individuals were included in the averages. In the Bahamas, similar to Panama, wide ranges of GI and reproductive stages have been observed in a small number of individuals, also suggesting more than one yearly spawning event (Metaxas et al. 2002).

Management recommendations

Previous studies have focused mostly on the biology of *O. reticulatus* rather than its management. This study provides baseline data on the abundance, distribution, and reproduction of *O. reticulatus* in the archipelago of Bocas del Toro, but we agree that management strategies need more extensive data sets, including settlement and recruitment rates, and estimates of inter-annual variability in the various biological and environmental parameters. Although it is premature to foresee a commercial exploitation of *O. reticulatus*, some illegal harvesting has started in Panama, and sea stars are sold as souvenirs to tourists and for the aquarium trade at some localities (e.g. Isla Grande, Portobelo, San Blas). Certain countries in the Caribbean, for example Mexico, Jamaica, Trinidad, Venezuela, and others, allow the extraction of this species without apparent restrictions, which could increase short-term demand and commerce in other areas once the populations in these countries diminish. Scheibling (1980a) indicated that humans are the agents most responsible for mortality in *O. reticulatus*, having collected them for centuries.

Only 2.8% of the shallow habitats in the Bocas del Toro archipelago are within the protected area of the PNMIB, south of Isla Bastimentos. This area, dominated by scattered and extensive seagrass meadows and small coral reef patches, harbors an average density of 615 *O. reticulatus* ha^{-1}, which is significantly greater than the average for the whole archipelago (149.7 ind. ha^{-1}), and the population is dominated by juveniles (mean major radius = 8.8 cm). Current studies are considering the possibility of modifying the limits of the protected areas to include more developed and diverse coral reef and seagrass habitats (sensu Guzmán and Guevara 1999).

Finally, it is known that the productivity, distribution, and density of seagrass habitats are in some way related to and limited by turbidity and nutrients in the environment (Pulich and White 1991; Onuf 1994). Destruction of these habitats will result from any increase in runoff and sedimentation in the coastal zone. Since 1997, coastal environments in Bocas del Toro have changed, as infrastructure such as roads, marinas, and hotels has developed (Guzmán and Guevara 1998). This has already started to affect the coral reefs (Guzmán and Guevara 2001), and could potentially modify the function of the remaining coastal ecosystems where important populations of *O. reticulatus* occur.

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