Spatial and seasonal variation of the gonad index of *Diadema antillarum* (Echinodermata: Echinoidea) in the Canary Islands

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**SUMMARY:** *Diadema antillarum* Philippi occurs in high density populations in the Canary Islands, creating extensive barren areas. During one year we determined seasonal changes in the algal abundance and population densities, test diameter, gut contents and gonad index of sea urchins in two localities (Abades and Boca Cangrejo). Boca Cangrejo shows higher algal cover and species richness than Abades. The sea urchin population at Abades had a higher density and smaller urchins than Boca Cangrejo. Boca Cangrejo sea urchins showed higher specific richness in gut contents than Abades urchins. The sea urchin population at Abades did not have a clearer reproductive periodicity or higher gonad index than the Boca Cangrejo population. Temporal and spatial changes in gonad periodicity of *Diadema antillarum* are attributed, at least in part, to benthic food availability (algal cover and algal species number) and intra-specific competition.

**Keywords:** algal cover, Canary Islands, *Diadema antillarum*, gonad periodicity, gut content, locality influence.

**RESUMEN:** *Diadema antillarum* Philippi presenta unas densidades altísimas en las islas Canarias, eliminando casi por completo la cubierta vegetal de los fondos rocosos litorales. Durante un año, hemos muestreado estacionalmente los cambios en la abundancia de algas y las densidades poblacionales, diámetros de caparazón, contenidos intestinales e índice gonadal de los erizos en dos localidades (Abades y Boca Cangrejo). Boca Cangrejo presenta mayores coberturas y riqueza algal que Abades. La población de erizos en Abades es más densa y esta formada por erizos de menor tamaño que en Boca Cangrejo. La riqueza algal en los contenidos estomacales es mayor en los erizos de Boca Cangrejo que la de los de Abades. Los erizos de Boca Cangrejo presentan una clara periodicidad reproductiva e índices gonadales superiores a los erizos de Abades. Las variaciones espaciales y estacionales en la periodicidad gonadal de *Diadema antillarum* pueden ser atribuidas, al menos en parte, a la disponibilidad bentónica de alimento (recubrimiento y número de especies de algas) y a la competencia intraespecífica.

**Palabras clave:** cobertura algal, islas Canarias, *Diadema antillarum*, periodicidad gonadal, contenido intestinal, influencia de la localidad.

**INTRODUCTION**

The sea urchin *Diadema antillarum* Philippi has a tropical-subtropical amphiatlantic distribution. According to Lessios *et al.* (2001), there are two genetically separate forms, one from the western and central Atlantic (*D. antillarum*-a) and one from the eastern Atlantic (*D. antillarum*-b). The latter form is found from the Madeira Archipelago to the Gulf of Guinea, including the Selvages, Canary and Cape Verde Islands.
High densities of the sea urchin *Diadema antillarum* occur at the Canary Islands and Madeira (Alves et al., 2001; Brito et al., 2002; Tuya et al., 2004a, b). These urchins have produced extensive barren grounds on rocky substrata between 0.5 and 50 m depths (unpublished observations). The intensity of the effect of the sea urchins is inversely proportional to water movement (Alves et al., 2001). Barren grounds of *D. antillarum* are shallower in sheltered areas than in exposed areas (unpub. obs.).

Temperature and photoperiod are thought to regulate gonad development of *Diadema antillarum* (Lessios, 1981; Illiffe and Pearse, 1982; Garrido et al., 2000; Capo et al., 2001). In the Caribbean, where seasonality is less marked than in temperate regions, reproductive seasonality seems to be less pronounced in this urchin (Randall et al., 1964; Lewis, 1966; Lessios, 1981; Illife and Pearse, 1982). Distinct peaks in gonad maturation may occur in areas with major fluctuations of physical variables (Lessios, 1981). Comparisons between conspecific sea urchin populations have shown a clear increment in gonad index periodicity with increasing latitude (Pearse, 1969, 1970, 1974). However, considerable variation in this general pattern may occur under particular conditions in the same region (Lessios, 1981; Illife and Pearse 1982).

A peak in the gonad index of *Diadema antillarum* was observed by Lewis (1966) in Barbados during low temperature periods (May 1963 and April 1964). Bauer (1976) also found a maximum gonad index related to low temperature periods at the Florida Keys. Illife and Pearse (1982) suggested that high temperature periods inhibit gonad growth. Capo et al. (2001) noted that *Diadema antillarum* in the laboratory had more spawning episodes at 24°C than at 26°C. Other factors such as benthic food availability, photoperiod and population characteristics (densities) may also influence gonad growth (Lessios, 1981; Illife and Pearse, 1982).

In sea urchins, gametogenesis and intragonad reserves of nutrients in nutritive phagocytes (NP) are linked. Nutritive phagocytes are renewed during pregametogenesis and used in gametogenesis. In both sexes, the gonad grows based on the increase in nutrient reserves in the NP (Walker et al., 2001). The nutrient status of the sea urchin has been shown to influence gonad production in both field (Meidel and Scheibling, 1998) and laboratory studies (Garrido and Barber 2001).

Negative growth in *D. antillarum* is density-dependent thus allowing increased survivorship and reproductive output under resource constraints. This ability can be important for maximizing the energy available for reproduction (Levitan, 1989).

Only two studies on the reproductive periodicity of the eastern Atlantic populations of *D. antillarum* have been conducted (Bacallado et al., 1987; Garrido et al., 2000). Both studies were carried out in the Canary Islands and showed a gonad index peak during the end of spring that was related to an increase in temperature.

In the Canary Islands the temperature reaches a distinct maximum in late summer and a minimum in winter in shallow waters. In winter, the upward movement of nutrients maximizes phytoplankton production (Braun et al., 1980). Whether benthic algal production is seasonal in the Canary Islands is often debated, but it seems that there is one clear peak of algal cover and algal richness during spring (M.C. Gil-Rodríguez and J. Afonso Carrillo, unpublished observations). This seasonal algal availability suggests a possible spatial and seasonal connection between sea urchin gonad production and benthic food availability in the Canary Islands.

In this study, we examine the spatial and seasonal variation of the gonad indices of the sea urchin *Diadema antillarum* at two contrasting sites off the southeast coast of Tenerife, that differ in sea urchin density and food availability. The study of these parameters could clarify the role of food availability (algal cover and number of species) in determining gonad periodicity.

**MATERIAL AND METHODS**

**Study sites**

Two study sites were established at 4-6 m on the south-eastern coast of Tenerife Island, Abades (28°08′26″N, 16°26′04″W) and Boca Cangrejo (28°24′22″ N, 16°18′52″W) (Fig. 1). Current and wind regimes and the seasonal fluctuations of other oceanographic parameters are similar in both localities (J.G. Braun personal communication; Brito et al., 2002). Nevertheless, Abades has high densities of small individuals of *D. antillarum* and low macro-algal cover, usually called “urchin barren grounds”, and Boca Cangrejo has low densities of large individuals and high macro-algal cover.
Therefore, there are two well defined situations: Abades with high densities and low food availability and Boca Cangrejo with low densities and high food availability (see results).

Characterization of the sea urchin populations

Density and individual test diameter were determined using the same method as Harmelin et al. (1980), Turón et al. (1995) and Casañas et al. (1998). Densities were estimated by counting all individuals in 10 × 2 m linear transects. Ten replicate transects placed at random were made at each sampling date. For the statistical analysis, four “life form” groups were considered: Filamentous and fleshy algae (FF) with 35 identified species; Large corticated calcified algae (LC) with 4

Algal cover measurement and species richness

Quadrats (0.25 × 0.25 m) were used for visual sampling of algal cover (Dawes, 1998). Sampling was done every season (March, June, September and December, 2002) at Boca Cangrejo and Abades. The percentage of algal cover of dominant species in each quadrat was noted; species that filled less than 1% of the quadrat were considered as 1% of the cover. Twenty replicates placed at random were made at each sampling date. For the statistical analysis, four “life form” groups were considered: Filamentous and fleshy algae (FF) with 35 identified species; Large corticated calcified algae (LC) with 4

Table 1. – List of algal species included in the different life-form groups: Filamentous and fleshy (FF); Large corticated/calcified algae (LC); Articulated algae (AR); Crust algae (CR).

<table>
<thead>
<tr>
<th>Algal “life form” groups</th>
<th>Algal species</th>
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<tbody>
<tr>
<td>Filamentous and fleshy (FF)</td>
<td>Acrochaetium sp.</td>
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<td></td>
<td>Blennothrix longicea (Kützing ex Gomont)</td>
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<td></td>
<td>Anagnostolis and Komárek</td>
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<td>Bryopsis sp.</td>
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<td></td>
<td>Calotrichus crustaceae Schousboe et Thuret ex Bornet et Flahault</td>
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<td></td>
<td>Ceramium sp.</td>
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<td></td>
<td>Chaetomorpha sp.</td>
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<td>Cladophora liebetruthii Grunow</td>
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<td>Cladophora sp.</td>
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<td></td>
<td>Cladophoropsis membranacea (Hofman Bang ex C. Aardh) Børgensen</td>
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<td></td>
<td>Colpomenia sinuosa (Mertes ex Roth) Derbis and Solier</td>
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<td></td>
<td>Dictyota dichotoma (Hudson) J.V. Lamoroux</td>
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<td></td>
<td>Dictyota pflfigii Schnetter</td>
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<td></td>
<td>Diplothamnion jolyi Hoek</td>
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<td></td>
<td>Hydroclathrus clathratus (C. Agardh) M.A. Home</td>
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<td></td>
<td>Hincksia intermedia (Rosenvinge) P.C. Silva</td>
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<td></td>
<td>Laurencia intricata J.V. Lamoroux</td>
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<td>Laurencia sp.</td>
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<td></td>
<td>Lyngbya confervoide C. Agardh</td>
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<td>Lyngbya sp.</td>
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<td></td>
<td>Oscillatoria lutea C. Agardh</td>
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<td>Oscillatoria sp.</td>
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<td>Pseudochlorodesmis furcellata (Zanardini) Børgensen</td>
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<td></td>
<td>Rizoclonium tortuosum (Dillwyn) Kützing</td>
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<td>Schizocladia sp.</td>
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<td>Spachelaria fusca (Hudson) S.F. Gray</td>
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<td>Spachelaria tribuloides Meneghini</td>
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<td></td>
<td>Styphocaulon scoparium (Linnaeus) Kützing</td>
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<td></td>
<td>Stylocoma alsides (Zanardini) K.M. Drew</td>
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<td></td>
<td>Taonia atomaria (Woodward) J. Agardh</td>
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<td></td>
<td>Ullothrix flacca (Dillwyn)Thuret</td>
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<td>Urospora laeta (Thuret ex Bornet) Børgensen</td>
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<td>Ulva sp.</td>
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<td></td>
<td>Wrangelia argus (Montagne) Montagne</td>
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<td>Large corticated/calcified algae (LC)</td>
<td>Asparagopsis taxiformis (Delile) Trevisan de Saint-Léon</td>
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<td></td>
<td>Dasycladus vermicularis (Scopoli) Krasser</td>
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<td></td>
<td>Lobophora variegata (Linnaeus) Wamersley ex Oliveira</td>
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<td></td>
<td>Padina pavonica (Linnaeus) Thivy</td>
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<td>Articulate (AR)</td>
<td>Amphiroa sp.</td>
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<td>Jania adhaerens J.V. Lamoroux</td>
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<td>Jania spp.</td>
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<td>Crust (CR)</td>
<td>Unidentified corallinules</td>
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<td>Unidentified Phaeophyceae</td>
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</table>
identified species; Articulated algae (AR) with 3 identified species; and Encrusting algae (CR) with 2 identified species (Table 1). These algal groups facilitate the ecological interpretation of the algae community’s influence on the gonad periodicity of *Diadema antillarum*. Algal species were identified using the Afonso and Sanson (1999) identification key and the field guide by Haroun et al. (2003). The mean number of species observed in each season was termed benthic algal species richness.

We used algal cover and benthic algal species richness (number of species) as an indirect method for measuring the spatial and seasonal changes in food availability.

**Analysis of gut contents**

In both localities we seasonally (March, June, September and December 2002) obtained guts from thirty sea urchins (the same urchins used for obtaining gonad material) and preserved them in 70% alcohol for posterior algae identification. To avoid daily rhythm variation in feeding (Lawrence and Sammarco, 1982; Carpenter, 1984) all collections were made in the morning. We counted the number of species of algae present in the gut of each individual and calculated the average number of species for each season. For the statistical analysis, the algal species were grouped according to their life form as in Table 1.

**Analysis of gonad index**

Thirty individuals were collected monthly (February 2002 to January 2003) at the same phase of the moon to avoid complications from a lunar spawning cycle (Pearse, 1975; Lessios, 1981; Illife and Pearse, 1982), in both localities. The horizontal diameter and oral-aboral axis of the tests were measured. The sea urchins were dissected and the total volume of the gonad was measured to the nearest 0.1 ml by displacement in sea water. To obtain the dry body weight, the test and lantern were dried for 24 hours at 110°C and weighed to the nearest 0.01 g (Garrido et al., 2000).

Gonad index (GI) was calculated following the method of Lessios (1981): GI = (ml gonad volume/g dry body weight) × 100.

**Data analysis**

Seasonal and spatial variations in density, test diameter, algal cover, species richness in gut content and gonad index were analyzed using a two-way ANOVA. We performed an ANOVA for each life-form group. The two orthogonal factors, locality (L) and season (S), were used as fixed factors.

Cochran’s test was used to evaluate homoscedasticity. Data that did not meet this requirement were log transformed (log (x + 1)). We lowered the significance level to 0.01 for transformed data that still had a heterogeneous variance (Underwood, 1981 and 1997).

The SPSS-11/5 statistical packet was used for descriptive statistics. The GMAV-5 programme (Underwood et al., 2002) was used for two-way ANOVA with Underwood’s (1977; 1981) specifications.

**RESULTS**

**Sea urchin populations**

The sea urchin populations were different in the two localities and the interaction locality x season had a significant effect, but no seasonal effect was detected (Table 2). Populations at Abades had a higher density (annual mean: 9.44 ind./m² ± standard deviation: 0.43) than those at Boca Cangrejo (annual mean: 3.62 ind./m² ± 1.52) (Fig. 2).

Test size showed differences between localities and the interaction locality x season had a significant effect (Table 2). The sea urchins from Abades were smaller (TD annual mean: 36.88 mm ± 11.05) than those from Boca Cangrejo (TD annual mean: 63.83 mm ± 11.98) (Fig. 2).

**Algal cover and species richness**

Locality and the interaction locality x season had a significant effect on algal cover (Table 3). Boca
Cangrejo had higher algal cover than Abades in all seasons (Fig. 3). The annual mean was 41.05% / 0.0625 m<sup>2</sup> in Abades and 80.92% / 0.0625 m<sup>2</sup> in Boca Cangrejo (Fig. 3). Maximum algal cover in Abades was found in spring (62%) and autumn (55%). Maximum algal cover in Boca Cangrejo occurred in summer (95%) (Fig. 3).

The interaction locality x season had a significant effect on species richness. Figure 3 shows a species richness peak during spring in Abades but not in Boca Cangrejo. This locality showed higher species richness than Abades throughout the entire year (Fig. 3).

These results indicate two clearly differentiated situations: Abades, with high densities of small individuals of *D. antillarum*, low algal cover and algal species richness, usually called “urchin barren grounds”; and Boca Cangrejo with low densities of large individuals, high macro-algal cover and higher species richness (Fig. 3).

Spatial and seasonal variation of algal life-form groups

Filamentous and fleshy (FF) algae increased during spring (31% of total cover) in Abades but were present during all seasons without conspicuous peaks (between 5 and 18% of total cover) in Boca Cangrejo (Fig. 4).

Like FF, LC had maximum cover during spring in Abades (10% of total cover). In Boca Cangrejo, maximum cover was in summer (20% of total cover), followed by spring (10% of total cover) (Fig. 4).

Cover of AR in Boca Cangrejo was consistently higher than in Abades (Fig. 4). Abades did not have conspicuous cover in any season (Fig 4). In Boca Cangrejo this algal group (AR) was present in all seasons, varying from 3% cover in winter to 20% cover in summer (Fig. 4).

Finally, crustose algae (CR) had the highest cover (18-45%; Fig. 4).
Spatial and seasonal variations of *Diadema antillarum* gut contents

In Boca Cangrejo, even though other algal groups had greater cover on rocky bottoms (Fig. 4), filamentous and fleshy (FF) group was more abundant in the digestive tracts of *Diadema antillarum* (Fig. 4). The same algal group was the most abundant in the guts of *D. antillarum* at Abades in all seasons with a clear peak in spring (Fig. 4).

The number of algal species in the digestive tracts of *D. antillarum* differed with locality (Table 4, note that the significant level was lowered to \(p<0.01\)). The gut contents of the sea urchins of Boca Cangrejo had a higher number of algal species (mean of 4.17 species) than those of Abades (mean of 1.53 species) (Fig. 4).

FF was significantly affected by the main factors locality and season (Table 4). Boca Cangrejo had a higher number of FF species (Fig. 4) than Abades. In Abades, a small peak in FF richness occurred in spring, in Boca Cangrejo the peak was in autumn. In Abades, this peak coincided with the increase in species richness but in Boca Cangrejo the species richness was always high (Fig. 4).

LC was significantly affected by the locality and the interaction locality x season. This shows a seasonal variation in gut richness that depends on the location’s characteristics (Table 4). In Abades during the same season, a peak in LC species richness coincided with a high number of species of LC being found in the gut contents (Fig. 4).

AR showed differences in the interaction locality x season (Table 4). Some species of AR appeared in the guts during spring, summer and autumn. In Boca Cangrejo, this group of algae always appeared in the guts.

CR did not show any significant variations between locality, season or interaction.
Spatial and seasonal variation of gonad index

Seasonal changes in the gonad index (GI) differed significantly with locality (Table 5). Monthly mean Gonad Indices in Boca Cangrejo were higher than in Abades (Fig. 5). For example, the maximum value of GI in the former was 47.38 and 12.04 in the latter.

The GI increased from April to June in Boca Cangrejo but no clear peak was detected in Abades (Fig. 5). After the maximum peak in spring, the mean GI decreased slowly to a minimum in late summer / early autumn in Boca Cangrejo (Fig. 5).

DISCUSSION

Levitan (1988; 1989) indicates that D. antillarum is able to change its body size in response to changes in food availability. The reduction in body size is related to energy conservation, since a smaller animal invests less energy in growth, which maximizes survivorship of individuals in areas with low food availability (Levitan, 1989). Thus, there may be a relative allocation of resources to gonad growth. Our results show that sea urchins in Abades are present in high densities and have small tests, which is indicative of low food availability. In contrast, sea urchins in Boca Cangrejo are present in lower densities and have larger tests than those at Abades, which is associated with greater food availability.

The monthly values of GI are different in the two localities (Abades-Boca Cangrejo) and only seasonal variation is clearly distinguished in Boca Cangrejo. In spite of the seasonal changes in the GI, it is probable that the sea urchins of Boca Cangrejo have a higher annual gamete output compared with urchins at Abades. In a high algal cover situation, such as at Boca Cangrejo, each sea urchin may make a larger contribution per capita to the larval pool. Lamare et al. (2002) noted that in favourable nutritive conditions the sea urchin Evechinus chloroticus (Val.) had a higher annual gamete output than urchins in areas with less conspicuous macrophytes. However, reproductive effort in Diadema antillarum is density-dependent (Levitan, 1989; 1991), thus at high population densities, increased fertilization success can compensate the decreased gamete production. Thus there is decreased production per individual, but there are more individuals. Therefore, production may be similar in both Abades and Boca Cangrejo.
A seasonal cycle in the gonad index of *Diadema antillarum* similar to that found here was reported by Bacallado et al. (1987) in Tenerife (Las Caletillas), and Garrido et al. (2000) for two localities in Gran Canaria (Puerto Rico and Sardina del Norte). However, there are timing differences between the GI peaks in their results and ours. Garrido et al. (2000) reported a gonad index peak in Sardina del Norte that was 1-2 months before (April) the peak in our data from Boca Cangrejo. This suggests inter-annual and inter-insular variations. Individuals at Abades have a gonad cycle without clear peaks, while those of Boca Cangrejo have a clear peak in spring. Sea urchin populations of Boca Cangrejo have a clearer periodicity and have a clear peak in spring. Sea urchin populations in other areas (Fort Randolph (Panama), or nearly non-existent in Maria Chiquita (Panama) (Lessios, 1981), Virgin Islands (Randall et al., 1964), Barbados (Lewis, 1966) and Bermuda (Illife and Pearse, 1982). Only Bauer (Bauer, 1976) found strong seasonality in the northern Caribbean area (Florida). In oceanographic terms, Florida is more comparable to Tenerife than any other locality in the Caribbean. However, *Diadema mexicanum* (Agassiz) of the American tropical Pacific (Culebra Island and Wraba) has strong seasonality in the GI. It has been suggested that these differences are due to differences in environmental factors in each area (Lessios, 1981). Our results supported the hypothesis that the seasonal GI variation may be linked to food availability.

Diverse reproductive strategies might take advantage of the most favourable times of the year. In this sense, gonad maturation peaks are inconspicuous and extend for several months in areas where annual variations of the environmental parameters are nearly non-existent (tropics). The waters of the Canary Islands show a peak in planktonic primary production in February-March (end of winter) (Braun, 1980), simultaneously with minimum water temperature and with important effects on the trophic network. The peaks in algal cover and species richness (food availability) that we observed during spring are related to this nutrient concentration in the water column. This peak in algal cover is more dramatic in Abades than Boca Cangrejo, because when there are few urchins the standing crop is limited by space and increasing productivity cannot increase algae standing crop (Lessios, personal communication). In the Canary Islands, a spring peak in food availability may be related to the clearly defined GI peaks of *D. antillarum* that occur during spring in Canary Islands waters (Bacallado et al., 1987; Garrido et al., 2000 and this paper) (by gonad nutrient storage).

The increase in algal cover and species richness is linked to higher species richness found in the sea
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