

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 algae 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: VARIACIÓN ESPACIAL Y TEMPORAL DEL ÍNDICE GONADAL DE *DIADEMA ANTILLARUM* (ECHINODERMATA: ECHINOIDEA) EN LAS ISLAS CANARIAS. – *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 genet-

ically 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; Illiffe 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; Illiffe 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. Illiffe 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; Illiffe 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.

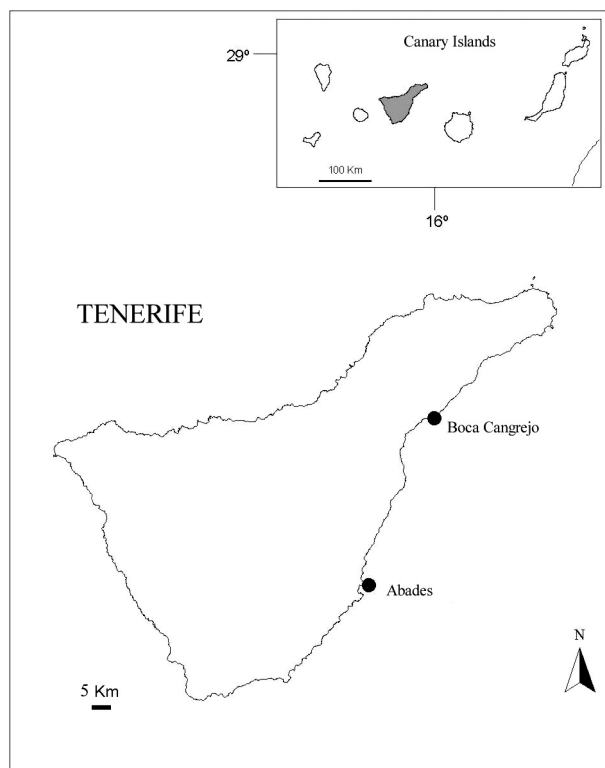


FIG. 1. – The Abades and Boca Cangrejo locations where algal cover was measured and sea urchins were collected.

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 locality every season during 2002 (March, June, September and December). Thirty individuals were collected at each date to measure test diameter (TD) to the nearest 0.1 mm. The total number of individuals to be measured was obtained for each locality following Kingsford (1998) sampling effort indications.

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).

Algal “life form” groups	Algal species
Filamentous and fleshy (FF)	<i>Acrochaetium</i> sp. <i>Blennothrix lyngbyacea</i> (Kützing ex Gomont) Anagnostioliis and Komàrek <i>Bryopsis</i> sp. <i>Calothrix crustacea</i> Schousboe et Thuret ex Bornet et Flahault <i>Ceramium</i> sp. <i>Chaetomorpha</i> sp. <i>Cladophora liebetruthii</i> Grunow <i>Cladophora</i> sp. <i>Cladophoropsis membranacea</i> (Hofman Bang ex C. Aardh) Børgensen <i>Colpomenia sinuosa</i> (Mertens ex Roth) Derbis and Solier <i>Dictyota dichotoma</i> (Hudson) J.V. Lamoroux <i>Dictyota pfaffii</i> Schmetter <i>Diplothamnion jolyi</i> Hoek <i>Hydroclathrus clathratus</i> (C. Agardh) M.A. Home <i>Hinckia intermedia</i> (Rosenvinge) P.C. Silva <i>Laurencia intricata</i> J.V. Lamoroux <i>Laurencia</i> sp. <i>Lyngbya confervoides</i> C. Agardh <i>Lyngbya</i> sp. <i>Oscillatoria lutea</i> C. Agardh <i>Oscillatoria</i> sp. <i>Pseudochlorodesmis furcellata</i> (Zanardini) Børgensen <i>Rizoclonium tortuosum</i> (Dillwyn) Kützing <i>Schizothrix</i> sp. <i>Sphacelaria fusca</i> (Hudson) S.F. Gray <i>Sphacelaria tribuloides</i> Meneghini <i>Stypocaulon scoparium</i> (Linnaeus) Kützing <i>Stylonema alsidii</i> (Zanardini) K.M. Drew <i>Taonia atomaria</i> (Woodward) J. Agardh <i>Ulothrix flacca</i> (Dillwyn) Thuret <i>Urospora laeta</i> (Thuret ex Bornet) Børgensen <i>Ulva</i> sp. <i>Wrangelia argus</i> (Montagne) Montagne
Large corticated/calcified algae (LC)	<i>Asparagopsis taxiformis</i> (Delile) Trevisan de Saint-Léon <i>Dasycladus vermicularis</i> (Scopoli) Krasser <i>Lobophora variegata</i> (Lamoroux) Wamersley ex Oliveira <i>Padina pavonica</i> (Linnaeus) Thivy
Articulate (AR)	<i>Amphiroa</i> sp. <i>Jania adhaerens</i> J.V. Lamoroux <i>Jania</i> spp.
Crust (CR)	Unidentified corallinales Unidentified Phaeophyceae

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 meas-

ured. 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, gut 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): $GI = (\text{ml gonad volume} / \text{dry body weight}) \times 100$.

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

TABLE 2. – Two-way ANOVA on the effects of locality and season on density and test diameter of *Diadema antillarum*.

Source	df	MS	F	p
Density				
Locality	1	677.45	102.84	0.000
Season	3	6.6756	0.34	0.797
Locality x Season	3	19.363	2.94	0.039
Residual	72			
Test diameter				
Locality	1	43578.15	1017.51	0.000
Season	3	413.3056	0.81	0.565
Locality x Season	3	507.661	11.85	0.000
Residual	232	42.8282		

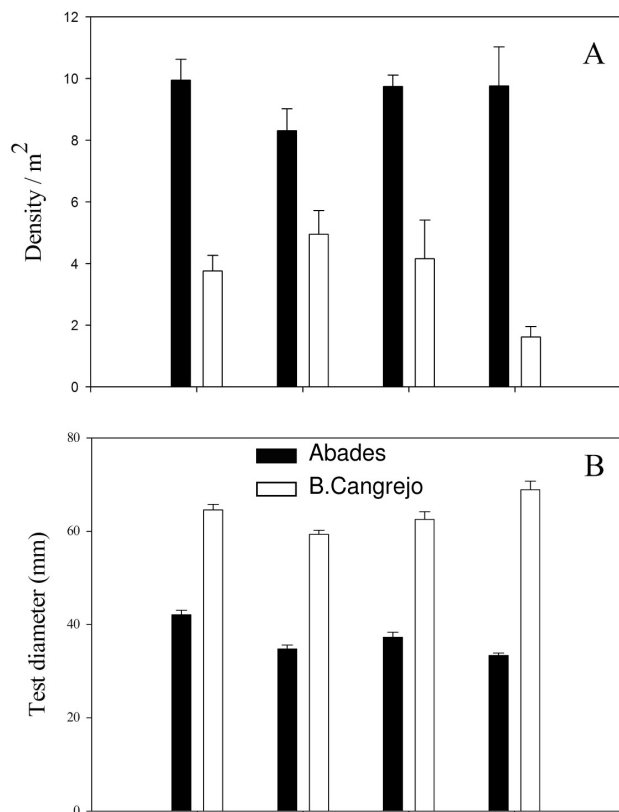


FIG. 2. – A: Mean (+ SE) of sea urchin densities by m², estimated using 10 x 2 meter linear transects and ten seasonal replicates; B: Mean (+ SE) of horizontal sea urchin test diameter (mm) for both habitats (n = 30).

TABLE 3. – Two-way ANOVA on the effects of locality and season on total algal cover and algal species richness.

Source	df	MS	F	p
Total algal cover				
Locality	1	67774.06	18.98	0.022
Season	3	5283.94	1.48	0.377
Locality x Season	3	3569.89	2.90	0.037
Residual	152	1232.13		
Algal sp richness				
Locality	1	209.31	5.27	0.105
Season	3	26.91	0.68	0.621
Locality x Season	3	39.69	21.40	0.000
Residual	152	1.85		

Cangrejo had higher algal cover than Abades in all seasons (Fig. 3). The annual mean was 41.05% / 0.0625 m² in Abades and 80.92% / 0.0625 m² 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).

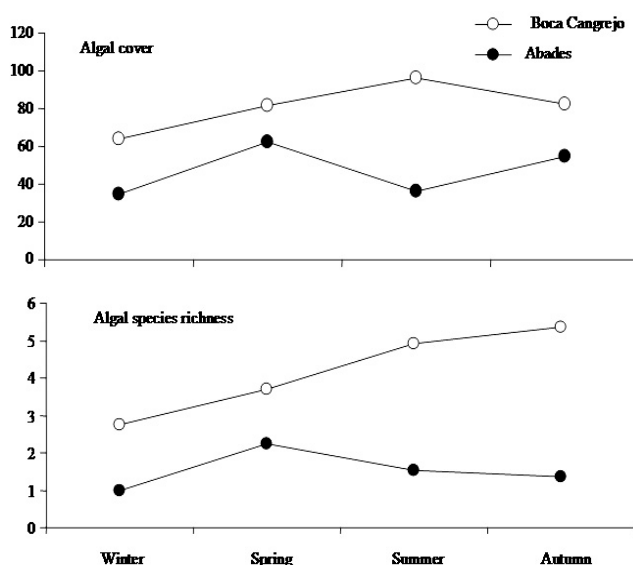


FIG. 3. – Mean of algal cover / 0.0625 m² and algal richness (n° algal species) for each locality.

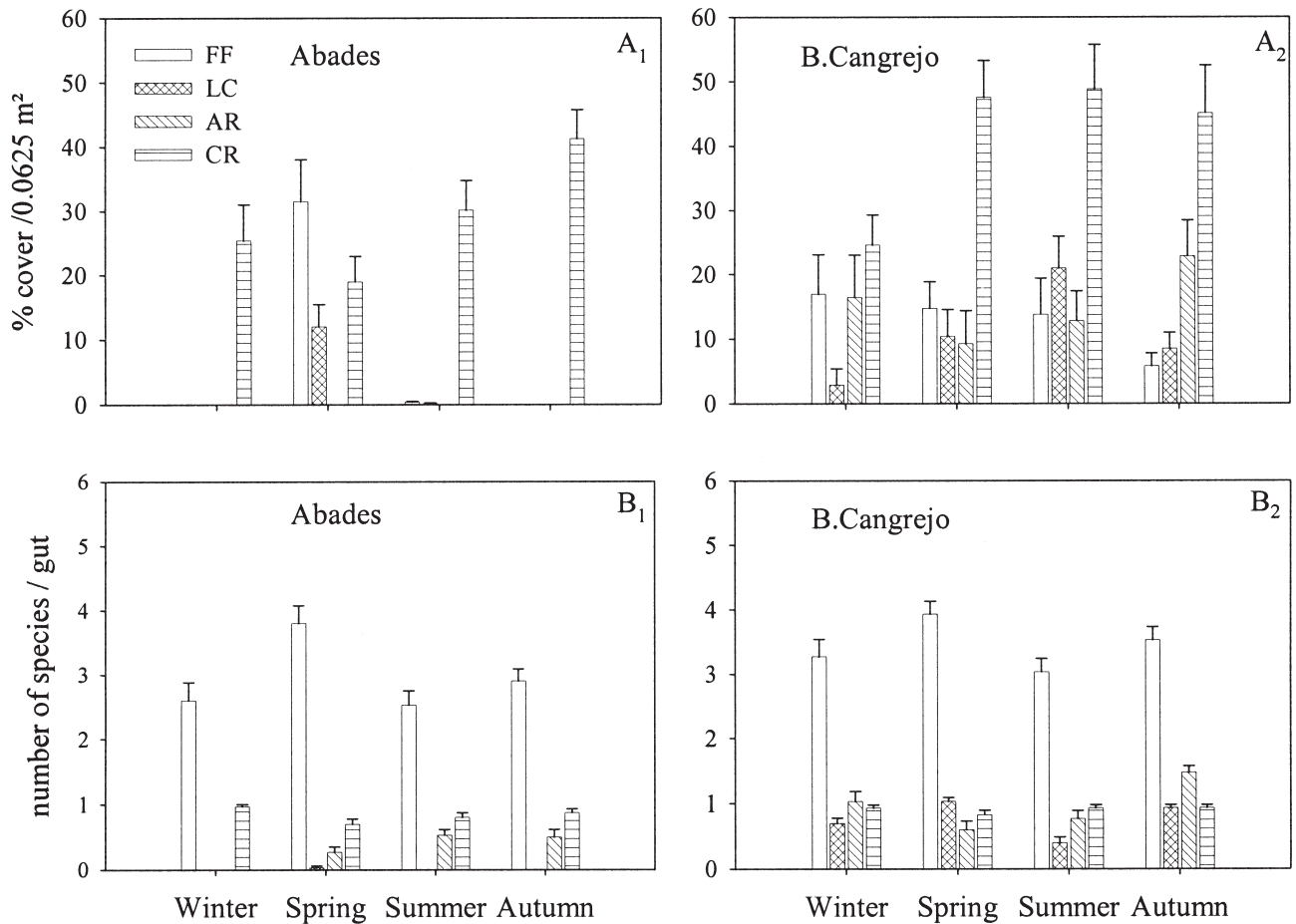


FIG. 4. – A₁- A₂. Mean (+ SE) of algal cover / 0.0625 m² (20 replicates) of the different life-form groups in both localities; B₁-B₂. Mean (+ SE) algal species number in gut contents (30 replicates) in both localities.

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.

TABLE 4. – Two-way ANOVA on the effects of locality and season on total algal richness and for the algal groups in the gut contents (log-transformed). Locality: Abades and Boca Cangrejo. [^a heterogeneity variance in spite of transformation of data, the significant level was lowered to $p < 0.01$].

Source	df	MS	F	p
Algal sp richnessa				
Locality	1	226.20	36.01	0.009
Season	3	18.94	3.01	0.194
Locality x Season	3	6.28	3.02	0.030
Residual	232	2.08		
FF				
Locality	1	13.54	13.33	0.035
Season	3	14.24	14.02	0.029
Locality x Season	3	1.01	0.60	0.613
Residual	232	1.68		
LC				
Locality	1	34.50	31.25	0.011
Season	3	1.28	1.16	0.453
Locality x Season	3	1.10	13.27	0.000
Residual	232	0.08		
AR				
Locality	1	24.70	9.49	0.054
Season	3	3.51	1.35	0.406
Locality x Season	3	2.60	7.21	0.000
Residual	232	0.36		
CR				
Locality	1	0.267	3.43	0.161
Season	3	0.361	4.64	0.120
Locality x Season	3	0.078	0.73	0.534
Residual	232	0.106		

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

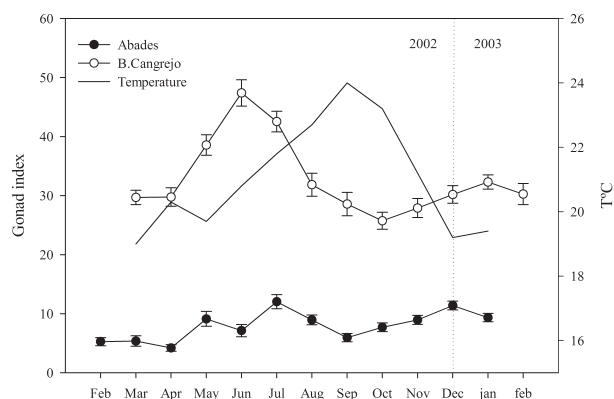


FIG. 5. – Annual variation in the monthly mean (\pm SE) values of the gonad index (30 replicates) from February 2002 to January 2003 in both localities and seawater surface temperature.

TABLE 5. – Two-way ANOVA on the effects of locality and season on gonad index of *Diadema antillarum*.

Source	df	MS	F	p
Gonad index				
Locality	1	42139.50	31.43	0.011
Season	3	1297.53	0.97	0.511
Locality x Season	3	1340.77	23.14	0.000
Residual	232	57.94		

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 higher gonad indices than those at Abades.

Higher availability of algal cover and a greater variety of algal species provide more food and more preferred species (FF) for *Diadema antillarum* in Boca Cangrejo than in Abades. John *et al.* (1992) showed that *Diadema antillarum* of the tropical African coast preferred filamentous and fleshy algae (or FF in our groups). Sammarco (1977; 1982) noted that high densities of *D. antillarum* in the Caribbean result in a change in algal composition, favouring crustose algae and cyanobacteria assemblages that may be less palatable. Vadas (1977) showed that *Strongylocentrotus droebachiensis* (Muller) and *S. franciscanus* (A. Agassiz) exhibit strong algal preferences. Algae with opportunistic strategies (r-selection) (FF in our algal group) were greatly preferred by these urchins. Moreover, the greater variety of species FF, LC and AR seems to favour gonad development and seasonality in the individuals of Boca Cangrejo. This result is supported by the higher algal specific richness found in the gut contents of the sea urchins of Boca Cangrejo during all seasons.

Tuya *et al.* (2001) demonstrated that at Gran Canaria *Diadema antillarum* in the laboratory preferred algae such as *Dictyota* (included in our list as FF), which supports the interpretation of the gut contents found here. Other algae such as *Lobophora* (included in our list as LC), *Padina* (included in our list as LC) and *Cystoseira* (LC) were the least preferred. This demonstrates that *Diadema antillarum* has food preferences and selects algae such as FF, which could be due to the greater palatability of these algae. Spatial variability in the reproduction of *Diadema antillarum* seems to be attributed, at least in part, to different nutritive regimes between localities. The availability of its preferred algal group

(FF) seems to play an important role. Sea urchins eat a range of algal species, but which species are more nutritive? Future isotopic studies may clarify this aspect.

The existence of a clear seasonality in the GI for *Diadema antillarum* in the Canary Islands does not agree with data from several authors who have studied Caribbean populations of *D. antillarum*-b. Seasonality is less conspicuous in tropical areas such as 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

urchin gut contents and to higher gonad indices. Moreover, the seasonal changes in algal cover and gut content richness are due mainly to the most preferred algae (FF) that may be related to gonad periodicity of the Canary Islands populations of *Diadema antillarum*.

ACKNOWLEDGEMENTS

We are grateful to H.A. Lessios who provided useful comments on the first draft. Special thanks to the anonymous referees and the editor of *Scientia Marina* that improved the original manuscript. Thanks to S. Clemente, E. Cubero and D. Girard for their help in the field and in the laboratory. B. Rodríguez Martín and N. Aguilar provided valuable comments on an earlier draft. C. Wildpret, A. Molina and J. Manning for the translation work. Finally, we are grateful to the Consejería de Medio Ambiente del Gobierno de Canarias for supporting this research.

REFERENCES

- Afonso, J. and M. Sansón. – 1999. *Algas, hongos y fanerógamas marinas de las Islas Canarias (clave analítica)*. Servicio de Publicaciones de la Universidad de La Laguna. 254 pp.
- Alves, F.M. A., L.M. Chicharro, E. Serrao and A.D. Abreu. – 2001. Algal cover and sea urchin spatial distribution at Madeira Island (NE Atlantic). *Sci. Mar.*, 65: 383-392.
- Bacallado, J.J., A. Brito, T. Cruz, M. Carrillo and J. Barquín. 1987. – *Proyecto Bentos II. Anexo: Estudio de la biología del erizo de lima (Diadema antillarum)*. Informes para la Consejería de Agricultura y Pesca del Gobierno de Canarias. (Unpubl.). 58 pp.
- Bauer, J.C. – 1976. Growth, aggregation and maturation in the echinoid *Diadema antillarum*. *Bull. Mar. Sci.*, 26: 273-277.
- Braun, J.G. – 1980. Estudios de producción en aguas de las Islas Canarias. I. Hidrografía, nutrientes y producción primaria. *Bol. Inst. Esp. Oceanogr.*, 5(285): 147-154.
- Brito, A., M.C. Gil-Rodríguez, J.C. Hernández, J.M. Falcón, G. González, N. García, A. Cruz, G. Herrera and A. Sancho. – 2002. *Estudio de la biología y ecología del erizo Diadema antillarum y de las comunidades de sucesión en diferentes zonas de blanquial del Archipiélago Canario*. Informe para la Viceconsejería de Medio Ambiente, Gobierno de Canarias. (Unpubl.).
- Capo, T., A. Boyd, J. Bauer, D. Cole, M.W. Miller and A.M. Szmant. – 2001. Spontaneous spawning of *Diadema antillarum* under photo-thermal control: an essential step for year-round laboratory culture. *Marine Ornamental 2001: Collection, Culture & Conservation*. Lake Buena Vista, Florida. U.S.A.
- Carpenter, R.C. – 1984. Predator and population density control of homing behavior in the Caribbean echinoid *Diadema antillarum*. *Mar. Biol.*, 82: 101-108.
- Casañas, A., H.H. Larsen and R. Haroun. – 1998. Developmental stages of blanquial to herbivory by the sea urchin *Diadema antillarum* Philippi (Echinoidea: Diademata) in the Canary Islands. *Bol. Mus. Mun. Funchal.*, 5: 139-146.
- Dawes, C.J. – 1998. *Marine Botany* (2nd ed.). J. Wiley & Sons, Inc. New York. 480 pp.
- Garrido, C.L. and B.J. Barber. – 2001. Effects of temperature and food availability and spine damage in the sea urchin *Strongylocentrotus purpuratus* (Stimpson). *J. Exp. Mar. Biol. Ecol.*, 145: 205-220.
- Garrido, M.J., R. Haroun and H.A. Lessios. – 2000. Annual reproductive periodicity of the sea urchin *Diadema antillarum* Philippi in the Canary Island. *Bull. Mar. Sci.*, 67: 989-996.
- Harmelin, J.G., C. Bouchon, C. Duval and J.S. Hong. – 1980. Les échinodermes des substrats durs de l'île de Port-Cros, Parc National (Méditerranée Nord-Occidentale). Eléments pour un inventaire quantitatif. *Trav. Scient. Parc Nat. Port-Cros*, 6: 25-38.
- Haroun, R., M.C. Gil-Rodríguez and W. Wildpret de la Torre. – 2003. *Plantas marinas de las Islas Canarias*. Canseco Eds S.L. España.
- Illife, T.M. and J.S. Pearse. – 1982. Annual and lunar reproductive rhythms of the sea urchin, *Diadema antillarum* (Philippi) in Bermudas. *Int. J. Inv. Repr.*, 5: 139-148.
- John, D.M., J.H. Price and G.W. Lawson. – 1992. Tropical east Atlantic and islands: plant-animal interaction on shore food of biotic reefs. In: D. M. Jonh, S. J. Hawkins and J. H. Price (eds.), *Plant Animal Interactions in the Marine Benthos*, pp. 87-100. Clarendon Press, Oxford. UK.
- Lamare, M.D., P.E. Brewin, M.F. Barker and S.R. Wings. – 2002. Reproduction of the sea urchin *Evechinus chloroticus* (Echinodermata: Echinoidea) in a New Zealand fiord. *N. Z. J. Mar. Freshw. Res.*, 36: 716-732.
- Lawrence J.M. and P.W. Sammarco. – 1982. Effect of feeding: Echinoidea. In: M. Jangoux and J. M. Lawrence, (eds.) pp. 499-519, *Echinoderm Nutrition*. A. A. Balkema, Rotterdam.
- Lessios, H.A. – 1981. Reproductive periodicity of the echinoid *Diadema* and *Echinometra* on two coast of Panamá. *J. Exp. Mar. Biol. Ecol.*, 80: 47-61.
- Lessios, H.A., B.D. Kessing and J.S. Pearse. – 2001. Population structure and speciation in tropical seas: global phylogeography of the sea urchin *Diadema*. *Evolution*, 55: 955-975.
- Levitan, Don. R. – 1988. Density-dependent size regulation and negative growth in the sea urchin *Diadema antillarum* Philippi. *Oecologia*, 76: 627-629.
- Levitan, Don. R. – 1989. Density-dependent size regulation in *Diadema antillarum*: effects on fecundity and survivorship. *Ecology*, 70: 1414-1424.
- Levitan, Don. R. – 1991. Skeletal changes in the test and jaws of the sea urchin *Diadema antillarum* in response to food limitation. *Mar. Biol.*, 111: 431-435.
- Lewis, J.B. – 1966. Growth and breeding in the tropical echinoid *Diadema antillarum* Philippi. *Bull. Mar. Sci.*, 16: 151-158.
- Meidel, S.K. and R. E. Scheibling. – 1998. Annual reproductive cycle of the green sea urchin, *Strongylocentrotus droebachiensis*, in differing habitats in Nova Scotia, Canada. *Mar. Biol.*, 131: 461-478.
- Pearse, J.S. – 1969. Reproductive periodicities of Indo-Pacific invertebrates in the Gulf of Suez. II. The echinoids *Echinometra mathaei* (De Blainville). *Bull. Mar. Sci.*, 19: 580-613.
- Pearse, J.S. – 1970. Reproductive periodicities of Indo-Pacific invertebrates in the Gulf of Suez. III. The echinoid *Diadema setosum* (Leske). *Bull. Mar. Sci.*, 1: 697-720.
- Pearse, J.S. – 1974. Reproductive patterns of tropical reef animals: three species of sea urchin. *Proc. 2nd Int. Symp. Coral Reefs*, 1: 235-240.
- Pearse, J.S. – 1975. Lunar reproductive rhythms in sea urchins. A review. *J. Interdiscipl. Cycle Res.*, 6: 47-52.
- Kingsford, M.J. – 1998. Analytical aspects of sampling design. In: M. Kingsford and C. Battershill (eds.), *Studying Temperate Marine Environment. A handbook for ecologist*. pp. 49-83. Canterbury University Press, New Zealand.
- Randall, J.E., R.E. Schroeder and W. A. Starck. – 1964. Notes on the biology of the echinoid *Diadema antillarum*. *Caribb. J. Sci.*, 4: 421-433.
- Sammarco, P.W. – 1977. Regulation of competition and disturbance in a reef community by *Diadema antillarum*. *IV Simp. Int. Ecología Tropical*. Panamá.
- Sammarco, P.W. – 1982. Echinoid grazing as a structuring force in coral communities: whole reef manipulations. *J. Exp. Mar. Biol. Ecol.*, 61: 31-55.
- Turón, X., G. Giribert, S. López and C. Palacín. – 1995. Growth and population structure of *Paracentrotus lividus* (Echinodermata: Echinoidea) in two contrasting habitat. *Mar. Ecol. Prog. Ser.*, 122: 193-204.
- Tuya, F., J.A. Martín, G.M. Reuss and A. Luque. – 2001. Food pref-

- erences of the sea urchin *Diadema antillarum* in Gran Canaria (Canary Islands, central-east Atlantic Ocean). *J. Mar. Biol. Ass. U.K.*, 81: 845-849.
- Tuya, F., A. Boyra, P. Sánchez-Jerez, C. Barbera and R.J. Haround. – 2004a. Can one species determine the structure of the benthic community on a temperate rocky reef? The case of the long-spined sea-urchin *Diadema antillarum* (Echinodermata: Echinoidea) in the eastern Atlantic. *Hydrobiologia*, 519: 211-214.
- Tuya, F., A. Boyra, P. Sánchez-Jerez, C. Barbera and R.J. Haround. – 2004b. Relationships between rocky-reef fish assemblages, the sea urchin *Diadema antillarum* and macroalgae throughout the Canarian Archipelago. *Mar. Ecol. Prog. Ser.*, 278: 157-169.
- Underwood, A.J. – 1997. *Experiments in Ecology: Their Logical Design and Interpretation Using Analysis of Variance*. Cambridge University Press, Cambridge.
- Underwood, A.J. – 1981. Techniques of analysis of variance in experimental marine biology and ecology. *Oceanogr. Mar. Biol. Ann. Rev.*, 19: 513-605.
- Underwood, A.J., M.G. Chapman and S.A. Richards. – 2002. *GMAV-5 for Windows. An analysis of variance programme*. Centre for Research on Ecological Impacts of Coastal Cities. Marine Ecology Laboratories, University of Sydney. Australia.
- Vadas, R.L. – 1977. Preferential feeding: an optimisation strategy in sea urchins. *Ecological Monographs*, 47: 337-371.
- Walker, C.W., T. Unuma, N. A. McGinn, L.M. Harrington and M.P. Lesser. – 2001. Reproduction of sea urchins. In: J.M. Lawrence (ed.), *Edible Sea Urchins: Biology and Ecology*, pp. 5-26. Elsevier, Amsterdam, The Netherlands.

Received April 6, 2005. Accepted April 26, 2006.

Scient. ed.: J. Garrabou.

Published online November 15, 2006.