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## Diet of the “key herbivore” *Diadema antillarum* in two contrasting habitats in the Canary Islands (Eastern-Atlantic)

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**RESUMEN:** Se analizó el contenido estomacal de 30 ejemplares del erizo *Diadema antillarum* recolectados estacionalmente durante dos años en dos ambientes diferentes (blanquiales y frentes de ramoneo) en las islas Canarias (Tenerife). Los resultados muestran la influencia del ambiente en la dieta del erizo *Diadema antillarum*. No se encontraron variaciones anuales en la dieta, sin embargo si detectamos diferencias entre las dietas de erizos de blanquial y los del frente de la zona ramoneada. *Diadema antillarum* es un ramoneador herbívoro, si bien consume invertebrados, especialmente en zonas de blanquial donde las macroalgas son escasas. En los contenidos estomacales, el grupo de las algas filamentosas se encontró en mayor proporción que los demás grupos algales o animales, independientemente del ambiente, mes o año.

**Palabras Claves:** contenido intestinal, comunidades submareales, islas Canarias, *Diadema antillarum*.

**ABSTRACT:** We analyzed the gut content of 30 sea urchins of the species *Diadema antillarum* which were collected seasonally over the course of two years from two different marine environments (barren grounds and grazing fronts) in the Canary Islands (Tenerife). Results show the influence of these two habitats on the diet of the sea urchin *Diadema antillarum*. No annual variations in diet were recorded; however we did find seasonal variations in diet in both barren and grazing front habitats. *D. antillarum* is mainly an herbivorous grazer but it also consumes invertebrates, especially in barren areas where seaweeds are scarce. Within the gut contents, filamentous algae were found in larger proportion than any other algal or animal group, independent of environment, month or year.

**Keywords:** gut content; subtidal communities; Canary Islands; *Diadema antillarum*.

## INTRODUCTION

Sea urchins are widely distributed throughout the world's oceans and often serve important roles, for example controlling macroalgal populations and organizing the structure of shallow subtidal communities (*e.g.* Lawrence 1975; Sammarco 1982; Vadas 1985; Harrold & Reed 1985). However, there is variation in feeding preferences among echinoid species and preferential feeding can have different effects on the structure of benthic communities. Although echinoids may have specific food preferences, our knowledge of what they consume is often determined by food availability. This is often the case for sea urchins that are generalist consumers (Lawrence 1975; Ogden 1976). For example, John *et al.* (1992) showed that *Diadema antillarum* Philippi, 1845 along the tropical African coast preferred filamentous and fleshy seaweeds of the different available types. In contrast Sammarco (1977; 1982) noted that high densities of *D. antillarum* in the Caribbean produced an important change in algal composition, the urchin tended to feed on crustose forms and microalgae.

Most regular echinoids are herbivorous and their diets consist mainly of seaweeds. They may be omnivorous or entirely carnivorous when animal matter is the primary food source available as is the case in overgrazed sites (Himmelman & Steele 1971; Lawrence 1975; Chapman 1981; Harrold & Reed 1985; Vadas 1985; Sebens 1986; Vadas *et al.* 1986; Witman 1987; Briscoe & Sebens 1988). In many regions, the intensive grazing and behavioural activities of echinoids create halos (Ogden *et al.* 1973; Andrew & Choat 1985; Andrew 1994), barren grounds or coralline pavements (Breen & Mann 1976; Ayling 1981).

At high densities, grazing activity of sea urchins becomes intense and food availability becomes limiting. In barren grounds, sea urchins intensify their grazing activity and become less selective in their food preference (Lawrence & Sammarco 1982). When sea urchins are in low abundance, algal beds flourish in the rocky subtidal zone. As sea urchins increase in number, they begin to aggregate along the edge of algal beds forming a destructive grazing "front" (Whartog & Mann 1981). In the Canary Islands, these "grazing fronts" advance across the algal bed and can rapidly create extensive barren grounds that are denuded of fleshy macroalgae (Aguilera *et al.* 1994; Brito *et al.* 2004; Tuya *et al.* 2004a; Tuya *et al.* 2004b).

*Diadema antillarum* generally feeds at night and makes long excursions over reef or rocky areas and sand flats in the Caribbean (Randall *et al.* 1964; Ogden *et al.* 1973; Carpenter 1984) and in the Canary Islands (Casañas *et al.* 1998; Tuya *et al.* 2004c). This nightly movement pattern of the sea urchin is usually termed "homing" or "crevice fidelity" and refers in particular to the repeated occupation of the same refuge (Carpenter 1984). Many authors consider this behaviour to help the organism reduce or avoid predation (Nelson & Vance 1979; Carpenter 1984; Sala & Zabala 1996; James 2000; Barnes & Crook 2001; Levitan & Genovese 1989). However, the homing behaviour of echinoids may be influenced by a variety of abiotic and biotic factors (Carpenter 1984; Dance 1987; Sala & Zabala 1996; James 2000; Tuya *et al.* 2004c; Hereu 2005).

Among these abiotic factors, water turbulence is an important factor that affects *D. antillarum* abundance (Alves *et al.* 2001) and modifies sea urchins grazing activity since high energy environments may reduce urchin grazing capability (Kawamata 1998). However, these environments may also supply more food to the sea urchin populations (Rogers-Bennett *et al.* 1995).

We decided to conduct a study to find differences which may exist in species composition of *D. antillarum* diets. In order to do this *D. antillarum* gut contents were recorded at two contrasting habitats: sheltered and exposed. Our aims were to clarify three points: (1) Does habitat influence the diet of *Diadema antillarum*? (2) Is there inter-annual or inter-seasonal variation in diet within each habitat? (3) Which algal or animal groups are present in the diet of *D. antillarum* in each habitat?

## MATERIAL AND METHODS

We studied gut contents of *Diadema antillarum* at two contrasting habitats in Abades (28°08'26"N - 16°26'04"W), south-east Tenerife (Canary Islands). At this single study location we removed urchins at a depth of 4-10 m. We compared gut contents of sea urchins from a grazing front with high water turbulence to that of urchins from a more sheltered adjacent barren ground.

The grazing front consisted of a dense bed of *D. dichotoma* (Hudson) J.V. Lamouroux, *D. liturata* J. Agardh, *D. pfaffi* Schmetter, and also *Asparagopsis taxiformis* (Delile) Trevisan de Saint-León. Erect algal cover in the grazing front was up to 75 %. Generally, overhead this algal band we found an algal community dominated by *Lobophora variegata* (J.V. Lamouroux) Womersley ex E.C. Oliveira and *Stypocaulon scoparium* (Linnaeus) Kützing, and occasionally mixed with *Padina pavonica* (Linnaeus) Thivy.

Barren ground areas are dominated by encrusting coralline algae with scattered patches of filamentous algae and microalgae (mainly *Blennothrix lynbyacea* (Kützing ex Gomont) Anagnostidis & Komárek, *Lyngbya lutea* (C. Agardh) Areschoug, *Ceramium* sp. and *Pseudochlorodesmis furcellata* (Zanardini) Boergesen. Other species such as *Padina pavonica*, *Dictyota dichotoma*, *D. pfaffii* and *Lobophora variegata* are present in crevices. *L. variegata* may also be present on rocks, displaying a crustose morphology adapted to high grazing pressures.

Sea urchin density and mean body size were different at the two habitats. In the grazing front, sea urchins were sparsely distributed throughout the period of the study (mean density: < 5 urchins m<sup>-2</sup>; Hernández unpublished data). The highest sea urchin density was observed in barren grounds (mean density: 10.5 urchins m<sup>-2</sup>; Hernández unpublished data). Throughout the study period, sea urchins in the grazing front were bigger (mean test diameter: ~50 mm; Hernández unpublished data) than those in barren grounds (~35 mm Hernández unpublished data).

In each habitat, thirty individuals were collected seasonally (Spring-Summer-Autumn-Winter) during two years (2002-2003). All collections were made in the morning to minimize complications from a daily feeding rhythm (Lawrence & Sammarco 1982; Carpenter 1984). Algal species found in the analyzed guts were divided into seven functional groups according to Steneck & Dethier (1994): microalgae, filamentous, foliose, articulate, foliose corticated, macrophytes corticated and crustose for statistical analysis (Table 1). Invertebrate species were divided into two functional groups according to their motility: sessile and vagile (Table 1).

The presence/absence taxa data matrix between frequency and taxa was transformed to a frequency taxa and functional group data matrix for statistical analysis.

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<b>Algal functional groups</b>
<b>Microalgae</b>
<i>Blennorhix lyngbyaceae</i> (Kützing ex Gomont) Anagnostidis et Komárek
<i>Calothrix crustacea</i> Schousboe et Thuret ex Bornet et Flahault
Diatom (unidentified)
<i>Lyngbya confervoides</i> C. Agardh ex Gomont
<i>Lyngbya lutea</i> (C. Agardh) Areschoug
<i>Lyngbya</i> sp.
<i>Oscillatoria</i> sp.
<i>Schizothrix</i> sp.
<b>Filamentous</b>
<i>Acrochaetium</i> sp.
<i>Ceramium</i> sp.
<i>Chaetomorpha</i> sp.
<i>Cladophora</i> sp.
<i>Cladophoropsis membranacea</i> (Hofman Bang ex C. Agardh) Boergesen
<i>Diplohamnion jolyi</i> Hoek
<i>Hinckia intermedia</i> (Rosenvinge) P.C. Silva
<i>Myrionema strangulans</i> Greville
<i>Polysiphonia</i> sp.
<i>Pseudoclorodesmis furcellata</i> (Zanardini) Boergesen
<i>Rhizoclonium tortuosum</i> (Dillwyn) Kützing
<i>Siphonocladales</i> sp.
<i>Sphacelaria fusca</i> (Hudson) S.F. Gray
<i>Sphacelaria</i> sp.
<i>Sphacelaria tribuloides</i> Meneghini
<i>Ulothrix flacca</i> (Dillwyn) Thuret
<i>Urospora laeta</i> (Thuret ex Bornet) Boergesen
<b>Foliose</b>
<i>Ulva</i> sp.
<b>Corticated foliose</b>
<i>Dictyota dichotoma</i> (Hudson) J.V. Lamoroux
<i>Dictyota</i> sp.
<i>Lobophora variegata</i> (J.V. Lamoroux) Womersley ex E.C. Oliveira
<b>Corticated macrophytes</b>
<i>Codium intertextum</i> F.S. Collins and Hervey
<i>Codium</i> sp.
<i>Stypoculum scoparium</i> (Linnaeus) Kützing
<b>Articulated calcareous</b>
<i>Amphiroa</i> sp.
Articulated calcareous (unidentified)
<i>Corallina elongata</i> J. Ellis and Solander
<i>Jania adhaerens</i> J.V. Lamouroux
<i>Jania rubens</i> (Linnaeus) J.V. Lamouroux
<b>Crust</b>
Crust coralline (unidentified)

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<b>Invertebrate functional groups</b>
<b>Sessile</b>
Bivalve mollusk
Bryozoa
Hydroid
Sponge
<b>Vagile</b>
Copepod
Gastrop mollusk
Nematode

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**Table 1.** List of algal and invertebrate taxa identified in guts of *Diadema antillarum* and grouped into seven algal functional groups and two invertebrate functional groups.

Similarity in the frequency of taxa and functional groups observed in guts of *D. antillarum* was analyzed by calculating Bray-Curtis similarity coefficients (Clarke & Green 1988). For graphical representation, a two dimensional non-metric multidimensional scaling (nMDS) using ordination was carried out (Clarke 1993; Clarke & Warwick 2001). Analysis was performed on a frequency taxa and functional group matrix.

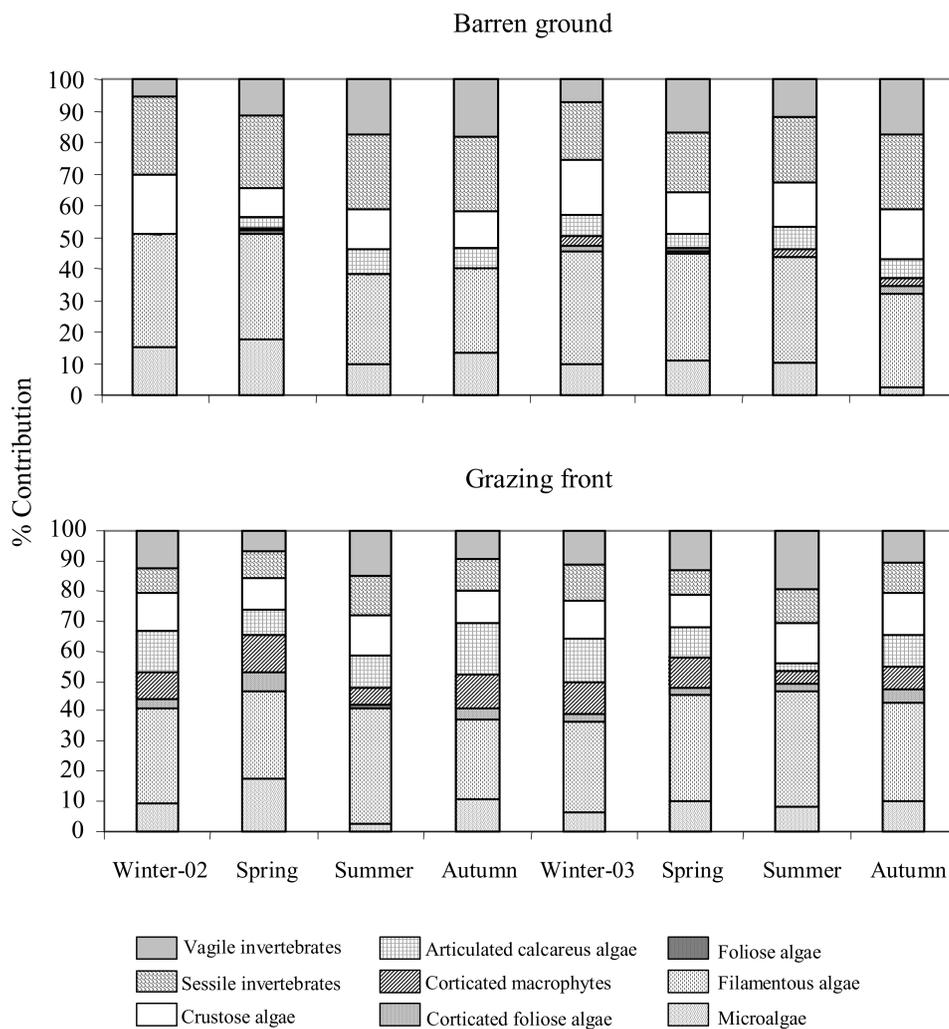
One-way analysis of similarity (ANOSIM) was performed to test differences between habitats. A two way nested analysis of similarity in gut content composition (taxa and functional group) was carried out between year and season for each habitat (Clarke & Green 1988).

The SIMPER protocol was used to examine taxa and functional groups that contributed to create the patterns shown by MDS analysis (Clarke 1993; Clarke & Warwick 2001).

## RESULTS

A total of 45 taxa were found in the gut contents of *Diadema antillarum*: 8 microalgae, 17 filamentous algae, 1 foliose alga, 3 corticated foliose algae, 3 corticated macrophytes, 5 articulated calcareous algae, 1 crustose alga, 4 sessile invertebrates and 3 vagile invertebrates (Table 1).

In both barren ground and grazing front, algae comprised a higher proportion of the gut contents of *D. antillarum* compared with invertebrates (Figure 1). However, the percentage of invertebrate groups was higher in urchins from the barren habitat than in urchins from the grazing front. Filamentous and microalgae functional groups were the most important groups in the guts of *D. antillarum* from the barren habitat although the sessile invertebrates were present. In the grazing front, filamentous and then articulated and corticated macrophytes were the most important groups.



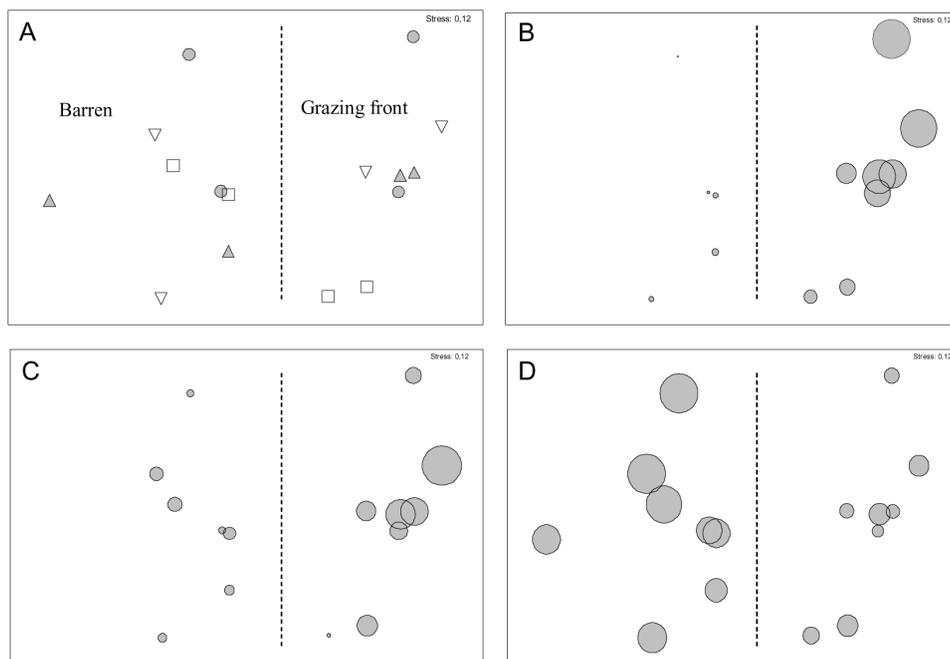
**Figure 1.** Percent of contribution of different functional groups to gut contents in barren ground and grazing front during the study period (mean  $\pm$  SE;  $n = 30$ ).

Similar results were observed for both the taxa and functional group matrices. The barren ground and grazing front samples formed two separate clusters. However, years and seasons did not show any clear pattern along the ordination space also before detected (Figure 2).

The ANOSIM procedure conducted both for taxa and functional group datasets detected significant differences between habitats (Table 2). However, no differences were detected between years within the same habitat. However, inter-seasonal variations within each habitat were found to be significant (Table 2).

Factor	Algal taxa data matrix			Functional groups data matrix		
	N° of permutations	Global R	Significance (%)	N° of permutations	Global R	Significance (%)
Habitat	999	0.267	0.1	999	0.205	0.1
<b>Barren ground</b>						
Year	35	0.021	48.6	35	-0.052	62.9
Season (year)	999	0.176	0.1	999	0.101	0.1
<b>Grazing front</b>						
Year	35	-0.042	62.9	35	-0.01	48.6
Season (year)	999	0.168	0.1	999	0.144	0.1

**Table 2.** Results of one way ANOSIM test examining differences between habitats and results of two ways nested ANOSIM test examining differences between years and seasons within years for each habitat.



**Figure 2.** Non Multidimensional scaling (nMDS) ordination of each sample taken in barren ground and in gazing front bases on functional group gut contents data and bubbles that represent the percentage contributions to difference of the most important functional groups. A: samples ordination; B: bubble c.mac; C: bubble art; D: bubble sessile.

The SIMPER procedures showed that the algae *Stypocaulon scoparium* and *Jania adhaerens* represented the most important taxa separating both habitats. Corticated macrophytes, articulated calcareous algae, sessile invertebrates and microalgae were the most important functional groups that separated the studied habitats (Table 3; Figure 2). In barren areas, sponges, *Sphacelaria* sp., *Lyngbya lutea* and hydroids were the main taxa which differed between seasons. Vagile invertebrates, filamentous algae, microalgae and sessile invertebrates were the main groups which differed between the seasons. In

Taxa	Barren-Grazing %	Functional groups data matrix	Barren-Grazing %
Gastrop mollusk	5.30	Articulate algae	18.14
Hydroid	13.93	Corticated macrophytes	23.89
<i>Jania adhaerens</i>	6.96	Microalgae	10.99
<i>Oscillatoria</i> sp	5.18	Sessile invertebrates	16.81
<i>Rhizoclonium tortuosum</i>	5.28		
<i>Sphacelaria</i> sp	4.70		
Sponge	6.16		
<i>Stypocaulon scoparium</i>	12.90		

**Table 3.** Results of SIMPER test on percentage contributions of taxa and functional groups to determine significant differences (up to 60 %) between habitats.

grazing front, *Stypocaulon scoparium*, *Jania adhaerens* and *Lyngbya lutea* were the principal taxa which differed between seasons. Articulate calcareous algae, corticated macrophytes and microalgae were the principal functional groups which differed between seasons (Table 4).

## DISCUSSION AND CONCLUSION

The diet of *Diadema antillarum* sea urchins is mainly herbivorous although an important proportion consists of small invertebrates in both the western Atlantic (Randall *et al.* 1964; Sammarco 1977; 1982) and in the Canary Islands in the eastern Atlantic (Herrera-López *et al.* 2003). In our study, the most frequently occurring algal group found in gut contents was filamentous algae regardless of the habitat, year or season. Vadas (1977) recorded a preference for filamentous algae in *Strongylocentrotus* in laboratory tests and justified this preference as an optimisation strategy in order to improve adsorption, thereby increasing body size and reproductive potential. Our results suggest that this fact may also apply to *Diadema antillarum*, since filamentous algae comprised the largest proportion of gut content, independent of environment, month or year of study.

*Diadema antillarum* changes its diet depending on habitat. The proportion of seaweeds to invertebrates varies between habitats. In barren areas, the gut content showed a larger proportion of small invertebrates compared with in grazing fronts, which is directly related to food availability (Lawrence, 1975; Ogden, 1976). In barren areas, gut content of *D. antillarum* consisted of a higher proportion of invertebrates than in grazing areas where algal availability is higher than in barren areas. Similarly, the diet of sea urchins from barren areas has a larger proportion of sessile compared with vagile invertebrates. Motile invertebrates are associated with algal beds and, as expected, the diet of sea urchins from the grazing front contained more vagile invertebrates.

Our results suggest that the most consumed functional groups in grazing front were corticated macrophytes and articulated algae. The greater consumption of these groups is directly related to the greater hydrodynamic regime experienced by algal communities located only on the upper bounds of the reef. The supply of drift algae may be greater due to increased wave action which dislodges and transports plants (Rogers-Bennett *et al.* 1995) so that in this habitat sea urchins, protected in their cryptic refuges, behave as “sit and wait grazers” (Chapman & Underwood, 1992), taking advantage of “out rooted”

	1-2 %	1-3 %	2-3 %	1-4 %	2-4 %	3-4 %
<b>Barren-taxa</b>						
<i>Blennothrix lyngbyaceae</i>	5.22		7.88		9.47	5.36
<i>Ceramium</i> sp.					5.12	5.85
Copepod				5.73	6.36	6.04
Articulated calcareus	3.91	9.54	8.87			5.09
Crustose	5.74					
Gastrop mollusk	11.30	8.04	5.38	8.42		
Hydroid		6.65	5.38	7.64	7.04	7.80
Nematod		6.47	5.89	5.28		
<i>Lyngbya lutea</i>		6.11	6.46	7.37	10.84	12.22
<i>Oscillatoria</i> sp.	9.10					
<i>Polysiphonia</i>				5.31	7.35	8.67
<i>Rhizoclonium tortuosum</i>	5.33		6.64			
<i>Sphacelaria</i> sp.	9.23	9.48	5.94	7.63	5.88	7.12
Sponge	11.75	15.49	12.81	14.80	9.66	5.11
<b>Barren-functional groups</b>						
Articulate algae		18.85	14.95			
Filamentous algae	16.85		20.93		25.23	
Microalgae	16.51		21.61	18.87	29.72	29.82
Sessile invertebrates		17.36	17.07	15.51	13.44	16.24
Vagile invertebrates	27.83	36.18		35.72		20.93
<b>Grazing-taxa</b>						
Articulated calcareus	8.39	7.20	5.74		6.51	7.22
<i>Blennothrix lyngbyaceae</i>	6.16		6.74	4.06	5.33	5.60
<i>Ceramium</i> sp.	4.10					
Copepod						5.05
Crust coralline	5.35				4.52	
<i>Dictyota dichotoma</i>	6.73			5.14	5.74	
<i>Dictyota</i> sp.				3.83		
Gastrop mollusk	7.69		5.56	4.32	6.63	4.59
Hydroid	4.20	5.67		6.32		
<i>Jania adhaerens</i>		9.97	5.76	9.24	7.61	12.49
Nematode		6.22		3.82		5.42
<i>Lyngbya lutea</i>	6.65	6.16	9.42	4.79	7.59	5.11
<i>Rhizoclonium tortuosum</i>		7.99	7.55			6.72
<i>Sphacelaria</i> sp.	8.21		5.64	5.96	6.20	
Sponge		7.55	6.57	7.10	6.51	
<i>Stypocaulon scoparium</i>	4.66	10.44	10.25	7.46	6.83	8.58
<b>Grazing-functional groups</b>						
Articulate algae	23.66	28.84		28.85	25.03	25.28
Corticated macrophytes		18.59	15.32	17.40	13.48	
Filamentous algae		15.42	14.22			16.31
Microalgae	22.20		20.73	16.53	18.48	15.82
Sessile invertebrates	10.97					
Vagile invertebrates	11.53		18.19		10.21	17.11

**Table 4.** Results of SIMPER test on percentage contributions of taxa and functional groups to determine significant differences (up to 60 %) among seasons of gut contents in both habitats: barren ground and grazing front. 1: Winter; 2: Spring; 3: Summer; 4: Autumn.

seaweeds. In contrast in the barren habitat, sea urchins graze out of their refuges (Tuya *et al.* 2004 c) and feed on sessile invertebrates, microalgae and the common filamentous algae of barren areas (Jonh *et al.* 1992).

Sea urchin diet does not vary over years but there is a clear seasonal variation that could be the result of the seasonal growth of seaweeds, surge action and its effect on algal availability. Seasonal growth of seaweeds in barren areas seems to have an important effect on *Diadema antillarum* diet. In addition to greater algal growth, grazing areas also have a larger proportion of out rooted seaweeds that are available due to the highly

hydrodynamic nature of these areas. Our results indicate that this phenomenon could also play an important role in the diet of *Diadema antillarum*.

In barren areas, changes in functional groups observed through gut content analysis, namely, filamentous algae, microalgae and sessile invertebrates were dependent on seasonal variations in *Diadema antillarum* diet. The main taxa found to vary seasonally in diet were invertebrates, sponges, hydroids and two filamentous algae (*Sphacelaria sp.* and *Lyngbya lutea*), both of them with a clear seasonal growth.

On the other hand, seasonal changes of *Diadema antillarum* diet in grazing habitats were mainly seen in other functional groups e.g. articulate calcareous algae, corticated macrophytes and microalgae. In this environment, *Stypocaulon scoparium* was the most important algal species to change seasonally in *D. antillarum* diet. In grazing areas, variations of *Jania adhaerens* and *Lyngbya lutea* constituted the main changes in *D. antillarum* diet. These algal species have seasonal growth which may explain why they fluctuate in *D. antillarum* diet.

This is the first study of diet in *Diadema antillarum* in barren and grazing front habitats of the Canary Islands. An interesting further study would be to examine the isotopic composition of calcareous structures of sea urchins from both habitats in order to determine their elemental composition (animal vs. vegetal). Moreover an exhaustive study of seasonal variation in species and algal beds using scrapings methods would be beneficial. A study of this type could help us to identify seasonal species and their growth periods, and perhaps aim an understanding of how algal blooms affect the diet of *Diadema antillarum*.

Gut contents of the sea urchin *Diadema antillarum* were analysed in two contrasting habitats: sheltered-barren ground and exposed-grazing front. Results show a high influence of habitat on diet of the sea urchin *D. antillarum*. In both habitats, algae comprised a higher proportion of the gut contents of *D. antillarum* than invertebrates. Overall filamentous algae constituted the largest proportion of gut contents, independent of environment, season or year. In the barren ground, filamentous and microalgae were the most important groups in the guts of *D. antillarum*, although sessile invertebrates were also important. In the grazing front, filamentous and then articulated and corticated macrophytes were the most important groups. Greater consumption of these groups is directly related to the greater hydrodynamic regime experienced by algal communities located only on the upper bounds of the reef.

There were no annual variations on diet but we have found seasonal variations in barren and grazing fronts. In barren areas, changes in functional groups, namely, filamentous algae, microalgae and sessile invertebrates were linked to seasonal variation in *D. antillarum* diet. Seasonal changes in the diet of *D. antillarum* in grazing areas resulted in the observation of different functional groups in the gut contents e.g. articulate calcareous algae, corticated macrophytes and microalgae.

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