



Contrasting displacement of the sea cucumber *Holothuria arguinensis* between adjacent nearshore habitats



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ABSTRACT

Many sea cucumber species are subjected to exponentially increasing fisheries worldwide; management of their populations should take into account their behavior. Yet, studies relating feeding rates and displacement of sea cucumbers are, to date, scarce. The abundance, particulate organic matter (POM) consumption and displacement of the sea cucumber *Holothuria arguinensis* were compared between two adjacent, vegetated, habitats: a macroalgal dominated bed and a seagrass meadow formed by *Cymodocea nodosa*, at the island of Gran Canaria (eastern Atlantic). Abundances of *H. arguinensis* did not differ between the macroalgal bed and the seagrass meadow. No differences were found neither in POM consumption nor POM content between habitats. Movement of *H. arguinensis* occurred continuously during the day and nighttime, i.e. without resting periods. No sheltering behavior was observed. Faster and longer displacements were detected on the seagrass meadow than in the macroalgal bed, probably as a result of the different topography between habitats, independently of the daily period (day vs. night) and the moon phase. As a result, differences in locomotion of *H. arguinensis* between the two habitats are not connected with differences in POM consumption rates between habitats. These results could be useful for managing current and future fisheries of this species in the Mediterranean Sea and the Atlantic Ocean.

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1. Introduction

Despite the importance of sea cucumbers for marine ecosystems (Anderson et al., 2011; Uthicke, 2001; Wheeling et al., 2007), and the exponential increase of their fisheries worldwide (Conand, 2004; Purcell et al., 2012; Toral-Granda et al., 2008), behavioral studies relating feeding rates and displacement on these organisms are still scarce. The behavior of holothurians has been traditionally studied separately; for example, through multiple-choice selection feeding indoor experiments (Uthicke and Karez, 1999; Zamora and Jeffs, 2011), by measuring total displacements of individuals on the field (Graham and Battaglene, 2004; Shiell and Knott, 2008), or by observing punctual spawning events (Mercier et al., 2007; Morgan, 2009). Although some studies have been conducted on the movements of tropical species in the Pacific (Graham and Battaglene, 2004; Mercier et al., 2000b; Purcell and Kirby, 2006), little is known about this behavior of Atlantic species.

Deposit-feeding sea cucumbers process large volumes of benthic sediments, from which they assimilate bacterial, fungal and detrital organic matter (OM) (Kitano et al., 2003; Navarro et al., 2013a; Slater et al., 2011; Yokoyama, 2013). According to the OM availability, sea cucumbers have developed two main different feeding strategies:

i) continuous search for food (Mercier et al., 1999; Slater, 2010; Uthicke and Karez, 1999), or ii) selection of organically rich particles (Hammond, 1983; Paltzat et al., 2008; Rainer and Herndl, 1991). In this sense, Yamanouchi (1956) suggested that aspidochirote holothurians could be classified into those that feed continuously (e.g. *Holothuria mexicana*, *Holothuria atra*, *Holothuria edulis*, *Holothuria flavomaculata* and *Isostichopus badionotus*) (Hammond, 1982b), and those that shelter during periods of reduced feeding activity (e.g. *Holothuria thomasi*, *Actinopyga agassizi*, *Euapta lappa* and *Stichopus chloronotus*).

Coastal landscapes typically encompass a range of habitats with different composition and abundance of organisms (Tuya et al., 2008), that may influence the way OM is distributed (Alongi, 1997; Sauchyn et al., 2011). As sea cucumbers tend to concentrate in areas with high content of OM (Sibuet, 1984; Slater et al., 2011; Yingst, 1982), differences in spatial distribution patterns of animals are also expected (Mercier et al., 2000a).

Displacements of holothurians can also be influenced by other factors like light intensity, that can alter ecological functions of aquatic animals such as daily activity rhythm, migrations, aggregation behavior, etc. (Dong et al., 2010; Mercier et al., 2000a; Shiell and Knott, 2010). Many holothurians exhibit a marked photophobic behavior (Navarro et al., 2012, 2013a; Purcell et al., 2012), which is considered by some authors a response to predation (Dance et al., 2003; Eckert, 2007; Francour, 1997; Mercier et al., 1999). Light intensity, however, does not only vary during day and night periods, but also during nighttime

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as a result of the different moon phases throughout a lunar cycle. Some echinoderms are known to alter their behavior (e.g. spawning events) according to this lunar cycle (Coppard and Campbell, 2005; Hereu et al., 2004; Muthiga, 2005; Muthiga and Jaccarini, 2005). However whether displacements of sea cucumbers can also be affected by these lunar cycles, or not, is still unknown. Previous studies on the effects of light intensity on the behavior of tropical sea cucumbers have been reported (Mercier et al., 1999, 2000a; Purcell, 2010); however, studies concerning temperate species are still scarce.

Management of commercial sea cucumber stocks is, in part, based on estimations of population densities, which, in turn, depend on knowledge of habitat preferences (Shiell and Knott, 2008). Studying the behavior of sea cucumbers is important to: i) design of no-take zones, by sizing them accordingly to the usual and maximum displacements of target species (Purcell and Kirby, 2006); ii) establishment of diurnal or nocturnal fishing periods, by determining whether target species move continuously throughout the day and night periods or show a resting period during the day or night (Shiell and Knott, 2008); and iii) to avoid underestimations of population abundances due to sheltering, if a certain species remains sheltered during a period of the day (Graham and Battaglene, 2004; Purcell, 2010).

Holothuria arguinensis Koehler and Vaney, 1906 is a sea cucumber geographically distributed in the north-east Atlantic, from the Berlengas Islands (Portugal) (Rodrigues, 2012) to Morocco and Mauritania, including the Canary Islands and the transition zone to the Mediterranean Sea (the Alborán Sea). Recently, this sea cucumber has been also registered in the eastern Mediterranean coast of Spain (Gonzalez-Wangüemert and Borrero-Perez, 2012). This species is frequently found on macroalgal-dominated beds and seagrass meadows of the Canarian Archipelago, where individuals are often covered with seagrass leaves and algae as camouflage (Navarro, 2012). Recently, this species has become a target species in some sea cucumber fisheries of the Mediterranean Sea (González-Wangüemert and Borrero-Pérez, 2012) and Mauritania (pers. comm. S. Purcell).

The aim of this study was to evaluate differences in the feeding and movement patterns of *H. arguinensis* between two coastal, vegetated, habitats at Gran Canaria Island. Specifically, the following hypotheses were set out: (i) the abundance of *H. arguinensis* varies between

habitats (a macroalgal bed vs. a 'seagrass' meadow); (ii) there is no difference in POM consumption between habitats; and (iii) the movement of *H. arguinensis* (here quantified through traveled distances and speeds) varies between habitats, day vs. night periods and moon phases.

2. Material & methods

2.1. Abundance patterns

This study was carried out in Gran Canaria Island (28° N, eastern Atlantic) at the location of Playa del Cabrón (PC, 27°52'16" N; 15°23'08" W; Fig. 1). This location encompasses rocky substrates covered by brown macroalgae (mainly seaweeds of the genera *Cystoseira*, *Sargassum*, *Lobophora* and *Dictyota*) and sandy substrates covered by extensive patches of the seagrass *Cymodocea nodosa*. These habitats are at ca. 3–8 m depth. To determine differences in *H. arguinensis* abundances between these two habitats, 4 haphazardly (6 × 20 m) underwater transects were placed using a plastic metric tape on each habitat. On each transect, the total number of adult individuals of *H. arguinensis* was annotated on a slate by one observer using SCUBA. The 6-m width of transects was estimated by observers. Underwater visibility in the area remained stable during all sampling, typically ranging between 20 and 30 m. These transects were repeated at 3 different days on April 11th, 18th and 26th 2013 to determine whether abundance patterns were temporally consistent at random times. All the observations were made at the same time of the day (08:00 h); both habitats were sampled consecutively in the same dive, with a difference of 15 min approximately. The level of replication was established to optimize the cost/benefit of sampling, particularly taking into account previous observations in the study area (Navarro et al., 2012, 2013b). To test for differences in abundances of *H. arguinensis* between habitats and days, a 2-way, permutation-based, ANOVA was carried out. The analysis included the factors: (1) 'Habitat' (fixed factor with two levels: macroalgal bed vs. seagrass meadow) and (2) 'Day' (random factor with three levels). Data were square root-transformed to achieve homogeneous variances.

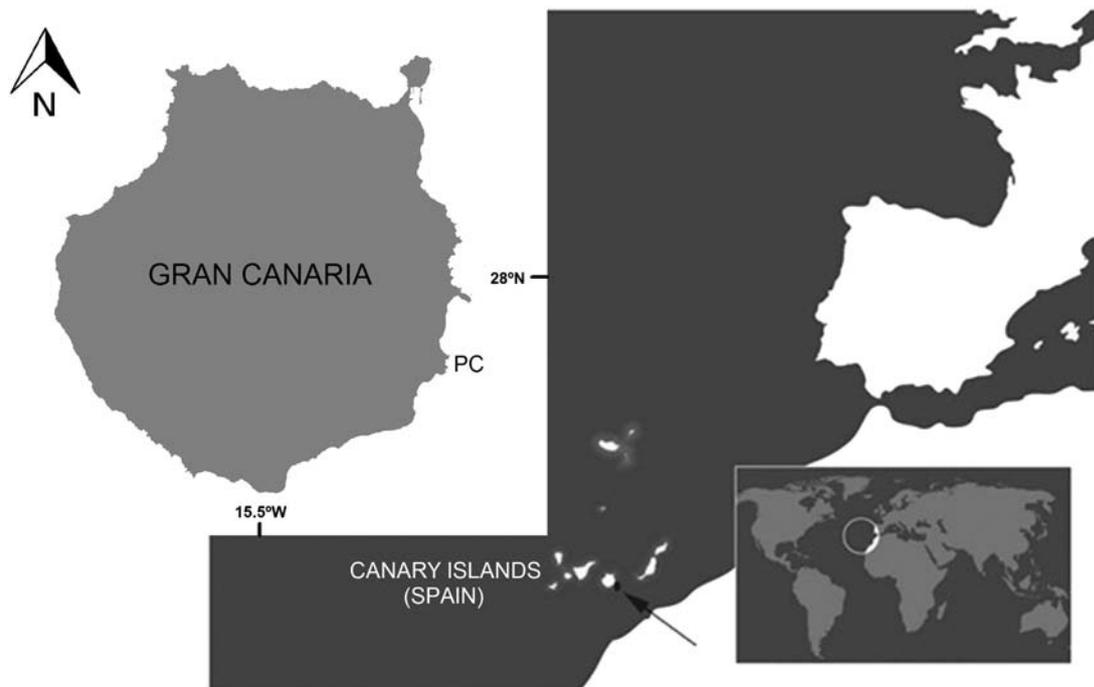


Fig. 1. Location of the study area in the eastern Atlantic (right) and the study site at Gran Canaria Island (left), PC: Playa del Cabrón.

2.2. Patterns in POM consumption between habitats

On the 25th of April 2013, a set of 30–45 sediment subsamples were collected immediately adjacent to *H. arguinensis* individuals, while another set of 30–45 sediment subsamples were collected from *H. arguinensis* feces, at both the macroalgae bed and the seagrass meadow (total of 120–180 subsamples), to determine the POM consumption in each habitat. One sediment and one feces subsample was collected from each individual. To optimize the cost/benefit of laboratory analysis, pools of 10–15 subsamples were performed, having a total of 3 sediment and 3 feces analyzed samples from the macroalgae bed and another 3 sediment and 3 feces samples from the seagrass meadow. The selection of individuals was randomly performed by divers (separated ca. 10–20 m from each other). All samples were collected using a modified bulb pipette (Rafalowski and Plante, 2013): the pipette tip was cut to have a wider suction diameter, which let the feces enter without breaking. All sediment samples were collected from the first 5 mm of sand. The Particulate Organic Matter (POM) percentage at each habitat was calculated for both sediments and feces samples through gravimetry, following Navarro et al. (2013a). Samples were oven-dried at 60 °C for 24 h. Each sample was divided into 3 subsamples of ca. 0.5 g; empty crucibles of known weight (CWempty) were used to place subsamples (n = 18) and determine their weights (CWfull). The crucibles were introduced in a furnace at 550 °C for 2 h and then weighted to obtain the ash weight (CWashes); the ash percentage (inorganic matter), the % of POM and the POM consumption were then calculated (Brenner and Binford 1988; Dar and Ahmad 2006; Wolkenhauer et al., 2010; Navarro et al., 2013a):

$$\%Ashes = \frac{CWashes - CWempty}{CWfull} \times 100.$$

$$\%POM = 100 - \%Ashes.$$

$$POM\ consumption = \%POM\ in\ sediment - \%POM\ in\ feces.$$

To test for differences in POM content between habitats a *t*-test was used. To test for differences in POM consumption between habitats, a Mann–Whitney rank sum test was used, as variances remained heterogeneous despite data transformation.

2.3. Patterns of movement

The study was carried out at the study location on April 2013. Animals were marked via a scratching technique, which has been effective to mark some holothurian species, e.g. *Holothuria whitmaei* (Shiell, 2006) and *Holothuria sanctori* (Navarro et al., 2013a). The success of the technique was locally demonstrated previously through a pilot study. Individuals, however, may display high rates of activity immediately after manipulation (6–12 h in this case), until movements are similar as those displayed by unmarked individuals.

In the field, individuals were marked in situ by SCUBA divers during daylight using a scalpel. Marked numbers were ca. 3–4 cm long, 2–3 cm wide and 1 mm deep (Navarro et al., 2013a; Shiell, 2006). At the study location, individuals (n = 6) were tagged at the two habitats, ca. 100 m apart to avoid cross-movements of animals between habitats. The total length (TL) of individuals was also measured, from mouth to anus, with a metric tape to the nearest 0.5 cm. Only one site per habitat was selected due to logistic reasons (Navarro et al., 2012, 2013b). Observations of marked animals were carried out every 12 h approximately, corresponding to two time intervals: 08:00–20:00 h (daytime) and 20:00–08:00 h (nighttime) during 3 consecutive days. The first observation started 12 h after marking. On each time interval, distances and speeds traveled by each marked individual, as well as the total distance traveled throughout the entire period, were calculated using a compass, a metric tape and a dive computer in the field, and principles of basic trigonometry afterwards (Navarro et al., 2013a; Tuya et al., 2004). For successive

observations, the position of animals was established using previously marked points in the reef and in the seagrass meadow using tagged metal stakes. Displacements between successive intervals were, however, considered to follow a straight line; usually this movement is naturally random (Graham and Battaglene, 2004; Purcell and Kirby, 2006) and does not follow a straight line; an underestimation is, therefore, assumed (Carpenter, 1984). In the case of individuals moving in the macroalgae bed habitat, divers additionally annotated whether the animals were sheltered or visible.

This experiment was repeated on 3 different lunar phases, hence including 3 days within each of the three lunar phases, to determine whether distinct moon phases could alter movement patterns of *H. arguinensis*. The first tagging was conducted at new moon (10th–12th April), the second tagging at first quarter (17th–19th April) and the third tagging at full moon (25th–27th April). The third quarter phase was omitted, as light intensity is often similar to the first quarter (McDowall, 1969).

To test for differences in speeds and overall traveled distances between daily periods, habitats, moon phases and days within moon phases, a 4-way, permutation-based, ANCOVA was used. The analysis included the factors: (1) 'Period' (fixed factor with two levels: day vs. night), (2) 'Habitat' (fixed factor with two levels: macroalgal bed vs. seagrass meadow), (3) 'Moon phase' (fixed factor with three levels: new moon, first quarter and full moon) and (4) 'Day' (random factor with three levels, nested within 'Moon phase'). The size (body length) of tagged individuals was used as a covariate. Data were square root-transformed to achieve homogeneous variances. Because speeds and traveled distances by individuals are positively correlated since the sampling periods had exactly the same duration (12 h), only results from the ANOVA performed on speeds were presented, for the sake of brevity.

To test for directional movements of animals at each habitat, a Rayleigh's Uniformity Test (Fisher, 1993; Mardia and Jupp, 2000; Zar, 1998) and a Rao's Spacing Test (Mardia and Jupp, 2000) were performed. Both tests take as the null hypothesis that data are uniformly distributed; however, conceptual differences between both tests should be noted. In the Rayleigh's test, a longer mean vector means greater concentration of the data around the mean, and thus less likelihood of the data being uniformly distributed. The Rao's test assess if the spacing between adjacent points is roughly equal around the circle; if the actual spacing deviate from this value, then the likelihood that the data are uniformly distributed is reduced. In both cases, observations from the different moon phases were pooled to work out a clearer, overall, directional movement of animals at each habitat.

3. Results

3.1. Abundance patterns

A total of 103 *H. arguinensis* individuals were recorded (67 on the macroalgal bed and 36 on the seagrass meadow). The abundance of animals was larger on the macroalgal bed (4.6 ± 0.005 ind $100\ m^{-2}$, mean \pm SE) than on the seagrass meadow (2.5 ± 0.007 ind $100\ m^{-2}$), but differences were not statistically significant (ANOVA, 'Habitat', $F = 50.39$, $P = 0.103$; Table 1).

Table 1
ANOVA results testing the effect of 'Habitat' and 'Day' on abundances of *H. arguinensis*.

Factor	df	MS	F	P
Habitat	1	1763.8	50.39	0.103
Day	2	7.9	0.10	0.935
Habitat \times Day	2	35.0	0.44	0.674
Residual	18	80.0		

3.2. Patterns in POM consumption between habitats

The mean POM of ingested sediments by *H. arguinensis* was $1.20 \pm 0.33\%$, while the mean POM in feces was $0.81 \pm 0.21\%$. POM contents in feces were lower than in surrounding sediments at all cases; therefore, *H. arguinensis* had a positive POM consumption from sediments. Neither the POM contents in sediment and feces ($1 \pm 0.31\%$ in macroalgal bed and $1.4 \pm 0.35\%$ in seagrass meadow; t -test, $t = -0.85$, $P = 0.44$; $t = -0.73$, $P = 0.51$) nor the POM consumption ($29 \pm 12\%$ in macroalgal bed and $48 \pm 23\%$ in seagrass meadow; Mann–Whitney rank sum test, $U = 3.5$, $P = 0.70$) varied significantly between habitats.

3.3. Patterns of movement

Movements of *H. arguinensis* occurred continuously, without any resting period during the day or the nighttime. From a total of 36 marked animals, only data from 33 individuals was collected; three individuals in the macroalgal habitat were only observed at 1 or 2 times (not always on successive periods), probably as a result of longer traveled distances than expected, and so ignored in further analyses. To maintain a balanced design for statistical analyses, a minimum of $n = 5$ individuals (selected randomly when data from 6 individuals was available), was considered ($n = 5$; $N = 30$). The total traveled distance (72 h) ranged between 3.74 and 59.28 m (mean distance = 24.06 ± 12.54 m, $N = 30$); the mean traveled distance per day was 8.02 ± 4.18 m. Speeds varied between 0.05 and 0.82 m h^{-1} (mean speed = $0.33 \pm 0.17 \text{ m h}^{-1}$, $N = 30$). Faster speeds were registered on the seagrass meadow than on the macroalgal bed (Fig. 2a, b; ANCOVA: 'Habitat', $F = 11.28$, $P = 0.009$, Table 2), independently of the daily period and moon phase (Fig. 2, ANCOVA: 'Habitat × Period

Table 2

ANCOVA results testing the effect of 'Habitat', 'Period', 'Moon phase' and 'Day' over speeds of *H. arguinensis*.

Factor	df	MS	F	P
Covariate = size	1	373.5	0.59	0.519
Habitat	1	4182.8	11.28	0.009
Period	1	221.9	0.66	0.517
Moon phase	2	934.2	0.32	0.716
Day (moon phase)	6	2864.9	7.32	0.0002
Habitat × Period	1	43.4	0.30	0.776
Habitat × Moon phase	2	439.6	1.19	0.352
Period × Moon phase	2	2308.4	6.53	0.025
Habitat × Day (moon phase)	6	370.5	0.95	0.478
Period × Day (moon phase)	6	350.1	0.89	0.510
Habitat × Period × moon phase	2	460.7	3.07	0.072
Habitat × Period × Day (moon phase)	6	149.8	0.38	0.958
Residual	143	391.3		

× Moon phase', $F = 3.07$, $P = 0.072$; 'Habitat × Period', $F = 0.30$, $P = 0.776$; 'Habitat × Moon phase', $F = 1.19$, $P = 0.352$; Table 2). The body size of individuals did not affect the speed of animals (ANCOVA: 'Size', $F = 0.59$, $P = 0.519$, Table 2).

Regarding the directional movement of individuals (Fig. 3), the Rayleigh's Uniformity Test did not detect a raw movement towards a certain direction neither in the seagrass meadow nor in the macroalgal bed (Rayleigh's Uniformity Test: $Z = 0.813$, $P = 0.443$ and $Z = 0.272$, $P = 0.762$, respectively; Table 3; Fig. 4); the animals typically meandered around and often crossed their own tracks within the 3-day period. However, the Rao's Spacing Test detected a non-uniform distribution of data and, therefore, a significant directional movement towards directions 91.875° in the seagrass meadow and 80.602° in the macroalgal bed (Rao's Spacing Test: $U = 224$, $P < 0.01$ and $U = 242.8$, $P < 0.01$, respectively; Table 3; Fig. 4).

4. Discussion

The abundances of *H. arguinensis* on the macroalgal bed ($4.6 \text{ ind } 100 \text{ m}^{-2}$) coincide with previous values (2009) for the same habitat at the study region (Navarro et al., 2013b; Navarro, 2012, ca. $4 \text{ ind } 100 \text{ m}^{-2}$). This fact highlights that the abundance of adults, although may slightly vary seasonally (Navarro et al., 2013b), remains stable year-round; this is not surprising as sea cucumbers in the Canary Islands are not subjected to any specific fishery that may temporally alter natural abundances. No significant differences in abundance were found between the *C. nodosa* seagrass meadow and the macroalgal bed, despite some apparent differences (2.5 vs. $4.6 \text{ ind } 100 \text{ m}^{-2}$, respectively) were detected. Yet, a greater replication may have shown a significant difference between the two habitats.

No significant differences were detected neither in POM content nor POM consumption by *H. arguinensis* between the two habitats, despite the apparent higher contents and consumption on the seagrass meadow compared to the macroalgal bed. Insufficient replication of sediment samples may be responsible for the lack of differences between habitats. However, a similar study carried out in the same study area showed that, although POM contents vary significantly between habitats ('urchin-grazed barren' vs. macroalgal beds), these contents did not change significantly over time, with 6.27% and 4.23%, respectively, in September and 4.57% and 3.77%, respectively, in February (Navarro et al., 2013a).

It is important to note that in the present study, the % of POM in feces was always lower than in the surrounding sediment. This fact has been also observed for other sea cucumber species, such as *I. badionotus*, *H. mexicana*, *Holothuria arenicola*, *Holothuria grisea*, *Actinopyga agassizi* and *Euapta lappa* (Hammond, 1982b; Sloan and Von Bodungen, 1980), and can indicate a non-selective feeding strategy of the species. This strategy contrasts with that of the most abundant sea cucumber species

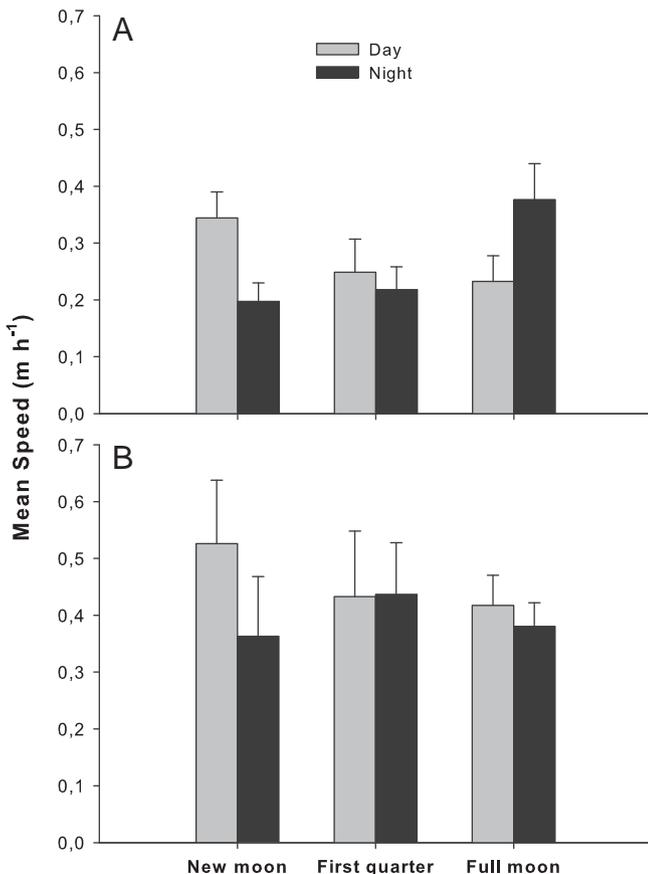


Fig. 2. Mean speeds of *Holothuria arguinensis* at (A) the macroalgal bed and (B) the seagrass meadow per moon phase and period. Error bars are + SE of means.

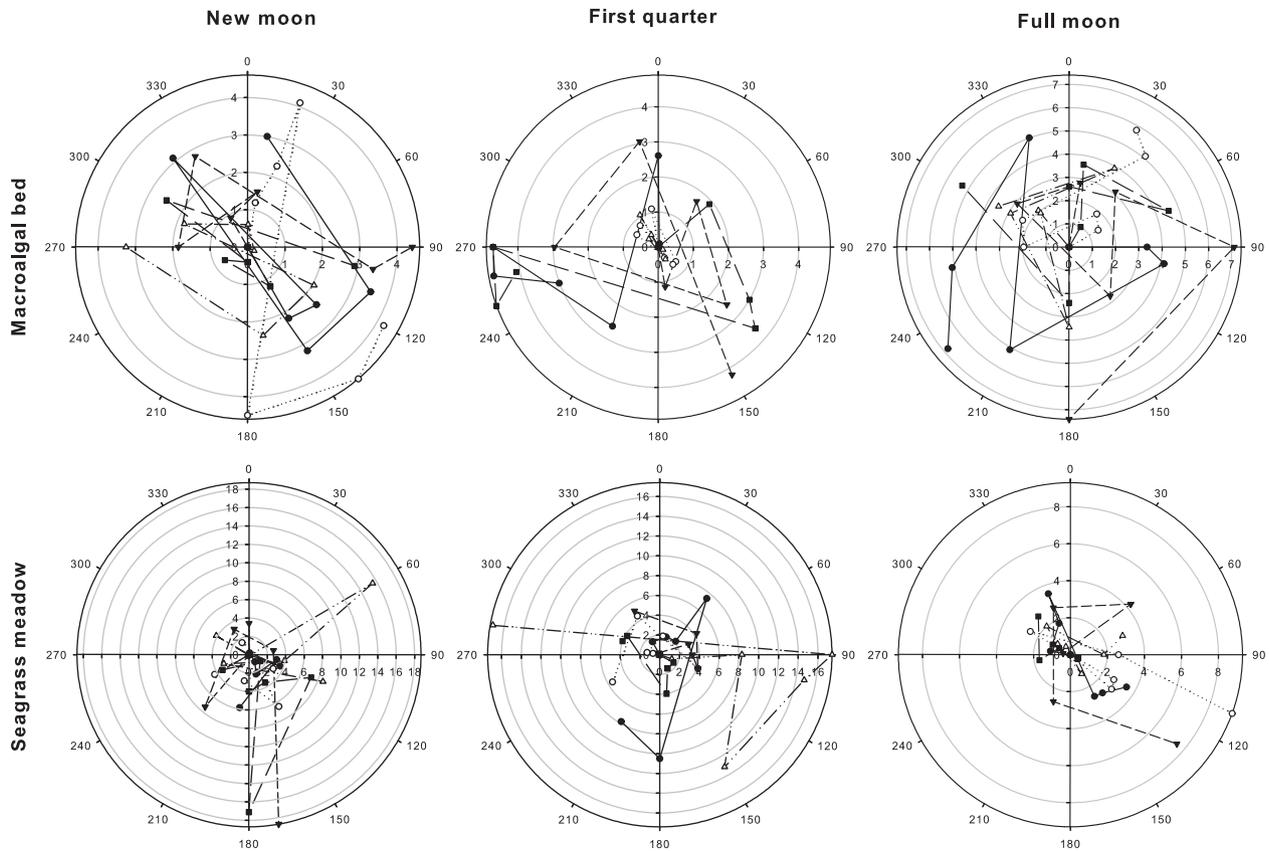


Fig. 3. Movement of tagged *H. arguinensis* at the 2 habitats (macroalgal bed and seagrass meadow) during new moon, first quarter and full moon. Distances are represented in meters and angles in degrees.

in the Canary Islands, *H. sanctori*, which recently has been categorized as a selective feeder on organic-rich sediments species. Egested feces from *H. sanctori* showed higher OM content than surrounding sediments (Navarro et al., 2013a). These two species can be found together on rock/sand mosaics in the Canary Islands, and usually share the same habitat patches for feeding purposes (Navarro, 2012). The movement of *H. arguinensis* is continuous throughout the day and nighttime, while *H. sanctori* only moves and feeds at night (Navarro, 2012). This outcome seems to suggest a connection between the feeding and movement of these two sea cucumber species. On the one hand, *H. arguinensis*, a non-selective feeder, consumes continuously sediments during 24 hour activity periods. On the other hand, *H. sanctori*, a selective feeder, exclusively moves and feeds out of their refuges during the nighttime (Navarro et al., 2013a). Moreover, numerous rests of echinoderm spines and shells were found on the digestive tract and feces of *H. arguinensis* (pers. obs), which are usually formed by large sediment particles (Pérez-Ruzafa, 1984). In contrast, egested sediment by *H. sanctori* has always smaller particle size than *H. arguinensis* and lacks rests of other organisms (Pérez-Ruzafa, 1984). According to

Mercier et al. (1999), a close relationship between feces grain size and food selectivity may exist, as fine-grained sediments usually contain more bacteria due to a greater surface/volume ratio (Levinton, 1972). This connection was observed in the present study, since mean POM contents in *H. arguinensis* feces (ca. 0.80%) were, by far, lower than in *H. sanctori* (ca. 7.72%, Navarro et al., 2013a; Navarro, 2012). However, an alternative explanation to these differences in POM contents in feces, compared to surrounding sediments, is the enrichment of sediments during the gut passage. *H. sanctori*, feeds and depletes POM at night, but during its diurnal resting time, the sediments in its guts stagnate, which could enhance bacterial proliferation, as what occurs with *Holothuria scabra* juveniles (Mercier et al., 1999). On the other hand, *H. arguinensis* depletes the POM from the sediment initially and ejects it immediately, as it feeds continuously throughout the day; consequently, the sediment does not remain for a long time stagnating in the gut and the POM content in feces is not higher than surrounding sediments. However, further specific feeding experiments should be conducted for both species to determine which is the assimilation or enrichment of ingested sediments in each section of the gut and what is the total time that sediment remains in the guts, to determine whether these differences among species are caused by the selection of organically rich particles or by the action of bacteria in the gut of the animals.

OM distribution on the habitat also affects the activity of sea cucumbers. For example, the movement of juvenile *H. scabra* was higher on bare surfaces, or substrates deprived of OM, relative to substrates with high OM (Mercier et al., 1999). As a result, if the OM is unequally distributed, the capacity of locomotion is altered (Mercier et al., 1999). In the present study, although differences of traveled distances and speeds between habitats were detected (higher activity rates were found on the seagrass meadow than on the macroalgal bed), no statistically significant differences were found in POM consumption by *H. arguinensis*. Seagrasses continually produce new leaves, roots and rhizomes; the

Table 3
Results of the circular statistical analyses testing for directional movements of tagged individuals at each habitat.

Variable	Seagrass meadow	Macroalgal bed
Number of observations	90	90
Mean vector (μ)	91.875°	80.602°
Length of mean vector (r)	0.095	0.055
Concentration	0.191	0.11
Circular variance	0.905	0.945
Circular standard deviation	124.302°	138.016°
Rayleigh test (Z)	0.813 ($P = 0.443$)	0.272 ($P = 0.762$)
Rao's spacing test (U)	224 ($P < 0.01$)	242.8 ($P < 0.01$)

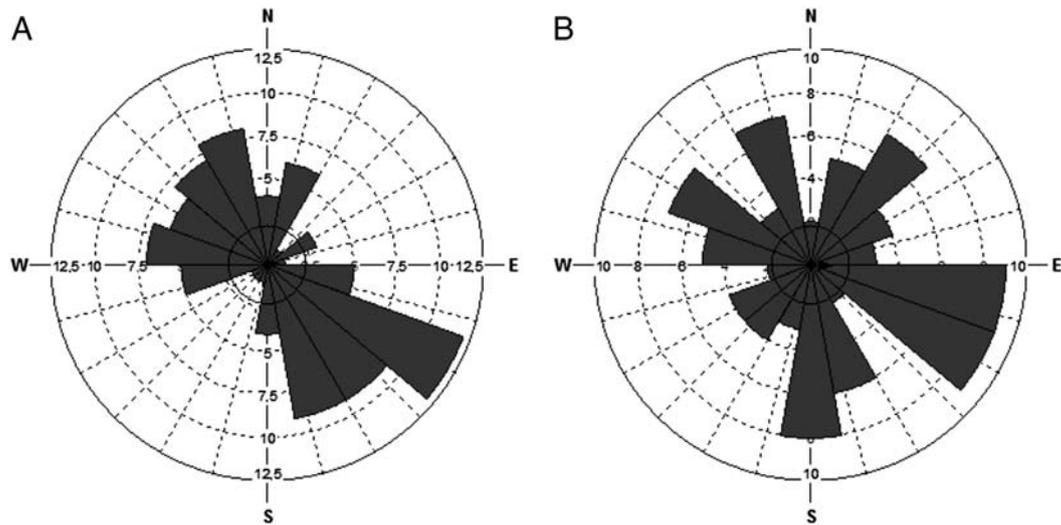


Fig. 4. Rose diagram representing the histogram of selected directions by *H. arguinensis* in both (A) the seagrass meadow and (B) the macroalgal bed. The axes represent the main cardinal compass points (North, East, South and West). The black circle represents the critical value of the Rayleigh test, in our case 0.05, and the black arrow within it, the direction and value of the *r* vector.

old portions of plants are shed off and enter the detrital food web (Bjork et al., 2008). This seagrass detritus is a significant source of organic matter that fuels many animal and microbial food webs in the sea (Hemminga and Duarte, 2000). The *C. nodosa* seagrass meadow at the study location is formed by fragmented seagrass patches interspersed with sand (García-Sanz et al., 2012); this may induce a heterogeneous distribution of OM. Hence, it is plausible that *H. arguinensis* may travel long distances to find a suitable rich sediment patch to feed on. Slater et al. (2011) states that *Australostichopus mollis* tends to rapidly move through low organic content sediment until areas with enough available food for deposit feeding are found. In the present study, *H. arguinensis* may be traveling rapidly through sandy patches and slowing down, or even stopping, when a suitable seagrass patch is found; specific studies with shorter observation periods are required in order to confirm this hypothesis.

The daily mean traveled distance of *H. arguinensis* was 8 m, which is slightly lower than *H. sanctori*, which traveled 11 m, but in exclusively 10–12 h of nocturnal activity (Navarro et al., 2013a; Navarro, 2012). Daily distances traveled by *H. arguinensis* are larger than those registered for other holothurians, e.g. *H. scabra* (1.3 m, Purcell and Kirby, 2006), *Actinopyga mauritiana* (3.02 m, Graham and Battaglione, 2004) and *Parastichopus californicus* (3.93 m, Da Silva et al., 1986). Speeds displayed by *H. arguinensis* varied between 0.05 and 0.82 m h⁻¹ (mean speed = 0.33 ± 0.17 m h⁻¹), slightly larger than those observed for *A. mauritiana* (0.04 and 0.21 m h⁻¹, Graham and Battaglione, 2004), *H. mexicana* (0.08 to 0.40 m h⁻¹), *Isostichopus badiotus* (0.04 to 0.4 m h⁻¹, Hammond, 1982a) and *H. whitmaei* (0.03 to 0.09 m h⁻¹, Shiell and Knott, 2010). It is important to take into account that both traveled distances and speeds may be somewhat higher in the present study compared to natural conditions; animals can develop an ‘escape’ behavior, with high levels of activity due to the manipulation and marking of animals. This behavior has been observed for other sea cucumber species, e.g. *Holothuria atra* (Yamanouchi, 1939), *Thelenota ananas* and *H. whitmaei* (Conand, 1991). In this study, and since an in situ marking technique was used, the error derived from allocations, where animals may display abnormal behavior caused by transportation to study sites, was reduced. Animals were exclusively affected by in situ manipulation and marking, which, in this case, was not as invasive as using anchor tags (Shiell, 2006), but might have, to some extent, influenced the normal activity of animals. As the first observations of animals were carried 12 h after marking, the recorded activity is probably higher than normal due to the effects of marking (Navarro, 2012).

Although the results from the present study showed that displacements of *H. arguinensis* were not significantly affected by its body size, there was approximately a 50% chance that the size could influence movements, as reported for other species like *H. scabra*, were larger individuals that moved significantly faster than medium and small animals (Mercier et al., 1999). Further experiments should focus on studying if this species performs size-related displacements or not and what implications would it have for management of the species.

No clear directional movements of animals towards a certain direction were detected, although there was a “tendency” to travel to the East at both habitats (80°–90°). This direction coincides with the deeper areas of the study location, that could suggest a raw migration of animals from shallow to deeper water on certain occasions, as reported for other sea cucumber species, e.g. *Stichopus variegatus*, *H. whitmaei* or *Holothuria fuscogilva* (Byrne et al., 2004; Conand, 1993; Reichenbach, 1999; Shiell, 2004). Further research should focus on these temporal and spatial movements of *H. arguinensis* to confirm this.

Throughout this study, no sheltering behavior of *H. arguinensis* individuals on macroalgal habitat was detected, as observed for other species of the study area, e.g. *H. sanctori* (Navarro et al., 2013a). This was despite observers often spent more time looking for individuals in the macroalgal bed than in the seagrass meadow, probably due to the higher level of bottom complexity of the former. The only three individuals that were only recorded one or two times during sampling in the macroalgal habitat and that were not used for later statistical analysis moved further than expected and, therefore, their displacements were not recorded. A more conscientious search by divers would have probably resulted in finding some of the greater-displacing individuals, which would have increased the estimates of displacement. The estimates of displacement are, therefore, slightly underestimated.

Although light intensity notoriously influences the movement of sea cucumbers in the study region, for example *H. sanctori* and *E. lappa* (Navarro, 2012), *H. arguinensis* moved continuously throughout the day and nighttime, which is common for some sea cucumber species, e.g. *H. whitmaei* (Shiell, 2006), *A. mauritiana*, *Actinopyga parvimensis* or *Stichopus naso* (Purcell et al., 2012). As previously indicated, Yamanouchi (1956) and Hammond (1982a) suggested a classification of aspidochirote holothurians into those that shelter during periods of reduced feeding activity, generally at daylight hours, and those that remain visible while feeding continuously. Rodgers and Bingham (1996), Mercier et al. (1999), Wheeling et al. (2007) and Navarro et al. (2013a) and Navarro (2012) found that the sea cucumbers *H. scabra*, *Cucumaria lubrica*, *H. edulis* and *H. sanctori*, respectively,

belonged to the former. In this study, it was found that *H. arguinensis* belongs to the latter group. No significant differences were detected in movement patterns of *H. arguinensis* between moon phases, contrary to other marine species, e.g. the horseshoe crab, *Limulus polyphemus*, where different rates of activity were detected between moon phases (Rudloe, 1985). As a result, movement patterns of *H. arguinensis* seem to be independent of changes in light intensity at small (daily) and medium (weekly) time scales. Ocean currents and tides may concurrently vary between moon phases (Cartwright, 1998); therefore, changes in movement patterns of sea cucumbers between lunar phases may be more affected by these alterations in water movement than by light differences per se. Future studies comparing the displacement of sea cucumbers between lunar phases should take into account these factors along with light intensity.

A factor that may affect the different locomotion of holothurians within and between habitats is bottom rugosity or topography (Navarro et al., 2013a). The macroalgal bed has a greater level of complexity and rugosity, including abundant holes, crevices, and cracks in the reef, which could make *H. arguinensis*'s movements 'slower' than in a seagrass meadow, where animals do not have to face any physical barrier for their daily movements. Navarro et al. (2013a) described the same behavior for *H. sanctori*; animals showed slower speeds in habitats with higher bottom rugosities than in habitats with lower bottom rugosity. Therefore, bottom rugosity seems to be an important factor influencing the locomotion of sea cucumbers.

These results have shown several important implications for management of current and future fisheries of *H. arguinensis*, in particular: i) mean and maximum displacements of individuals, necessary for the sizing of no-take zones or protected areas (Purcell and Kirby, 2006); ii) continuous displacement of individuals during day and night periods, without a resting period during the night, necessary for establishing a diurnal or nocturnal fishery; and iii) non sheltering behavior of individuals during day and night periods, which would help population density estimates (Graham and Battaglene, 2004; Purcell, 2010).

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