

# TEMPORAL PATTERNS OF LARVAL SETTLEMENT OF *DIADEMA ANTILLARUM* (ECHINODERMATA: ECHINOIDEA) IN THE CANARY ISLANDS USING AN EXPERIMENTAL LARVAL COLLECTOR

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## ABSTRACT

Settlement of *Diadema antillarum* Philippi was measured at two barren ground sites, Abades and Masca (Tenerife), between April 2002 and April 2003, in order to assess the suitability of settlement collectors and to obtain settlement patterns of this keystone herbivore in the subtidal rocky bottoms of the Canary Islands. Three samplers containing small plastic balls (experimental collectors) with a very high exposed surface area ( $0.04 \text{ m}^2 \text{ ball}^{-1}$ ) were deployed monthly over 1 yr. Post-larvae and early juvenile sea urchins (newly settled urchins) were recovered from the samplers by washing individual collectors. Bimodal peaks in settlement were observed at both locations, with a primary peak in late summer/fall (Aug–Oct) and a secondary increase in late winter (Jan–Feb). Samplers collected a monthly maximum of 24–26 ( $\pm 2$ –16) newly settled urchins/sampler. The primary settlement pulse corresponded roughly to the annual pattern of reproductive periodicity (gonad index-GI) of *D. antillarum* at Boca Cangrejo (Tenerife). GI peaked during spring (Apr–May–Jun) with a secondary peak in December. The secondary increase in settlement may be due to higher larval survival during favorable planktonic conditions.

The eastern Atlantic form of the sea urchin *Diadema antillarum* Philippi appears in Madeira, Selvages Islands, Canary Islands, Cape Verde Islands, and the Guinean Gulf (Lessios et al., 2001). Large populations can dominate subtidal rocky bottoms (0.5–50 m) at Madeira, Selvages, and Canary Islands (Aguilera et al., 1994; Alves et al., 2001; Tuya et al., 2004b). In many sites in the Canary Islands, densities can exceed  $10 \text{ ind m}^{-2}$  (Casañas et al., 1998; Brito et al., 2002; Tuya et al., 2004b), thus this species has a major impact on the coastal ecosystem. The mass mortality observed in the Caribbean (Lessios et al., 1984; Lessios, 1988a) has not occurred in the Canary Islands (Aguilera et al., 1994; Tuya et al., 2004b).

Grazing by sea urchins eliminates fleshy macroalgae cover, transforming large portions of the littoral rocky reef into over-grazed urchin barrens dominated by encrusting coralline algae and some invertebrates (principally sponges and bryozoans). The main consequences of this dominance are the loss of algal cover (Alves et al., 2003; Tuya et al., 2004a,b) and probably other indirect effects on macroinvertebrates and fishes such as competition for space and resources.

Despite the ecological importance of *D. antillarum*, we know very little about the reproductive biology of the eastern Atlantic populations. Reproductive periodicity at Gran Canaria (Garrido et al., 2000) and Tenerife (Bacallado et al., 1987) show the same seasonal pattern. The highest gonad index (GI) peak occurs during spring (Apr–Jun) and a second less conspicuous peak in fall (Oct–Dec), with slight monthly differences between localities (Bacallado et al., 1987; Garrido et al., 2000). Larval settlement or recruitment in the eastern Atlantic has not been studied, in contrast to the Caribbean (Bak et al., 1984; Bak, 1985; Hunte and Younglao, 1988; Lessios,

1988b; Carpenter, 1990; Karlson and Levitan, 1990; Forcucci, 1994; Lessios, 1994). However, many of these Caribbean studies were focused on the consequences of a mass mortality event that occurred in 1982–1984. Recruits of *D. antillarum* prefer cryptic habitats (Hunte and Younglao, 1988) and clean surfaces free of seaweeds in Caribbean areas (Bak, 1985), probably an adaptive response to avoid predation (Bak, 1985).

The pelagic larval life of many invertebrates is influenced by biotic and abiotic factors such as currents, water temperature, predation, and food availability (McEdward and Miner, 2001). *Diadema antillarum* has a planktotrophic echinopluteus larva with a planktonic phase of approximately 36 d (Eckert, 1998) and characteristics that may reduce planktonic larval mortality. For instance, a large larval size and arm mobility up to 90° make them less vulnerable to planktonic predators (Eckert, 1998). These larval features may help explain the success and high densities of this echinoid in the Canary Islands.

The objective of this study was to quantify the seasonal reproduction and settlement patterns of this keystone herbivore in rocky subtidal ecosystems in the Canary Islands using a new artificial collector. We were particularly interested in determining how gonad periodicity affects patterns of settlement.

## MATERIAL AND METHODS

**GONAD INDEX STUDY.**—Thirty individuals were collected monthly from February 2002 to January 2003 at Boca Cangrejo (28°24'22" N 16°18'52" W) in Tenerife (Fig. 1) during the same phase of the moon to minimize complications from a lunar spawning cycle (Pearse, 1975; Lessios, 1981; Illife and Pearse, 1982). Sea urchins were dissected and total volume of the gonad was measured to the nearest 0.1 ml by displacement in seawater. The test, gut, and lantern were dried for 24 hrs at 110 °C and weighed to the nearest 0.01 g (Garrido et al., 2000). GI was calculated following the method of Lessios (1981):  $GI = (\text{ml gonad volume})/(\text{g dry body weight})^{-1} \times 100$ . During each collection, sea surface temperature (SST, °C) was measured with a hand-held thermometer at 1 m depth at the collection site.

**SETTLEMENT STUDY.**—We define settlement as the appearance of postlarvae and early juveniles (newly settled urchins; Fig. 2) on experimental samplers over a 1 mo interval (Keesing et al., 1993; Gosselin and Jangoux, 1998; Tomas et al., 2004).

Settlement was recorded at two barren grounds of Tenerife Island: Abades (28°08'26" N 16°26'04" W) and Masca (28°17'37" N 16°52'06" W; Fig. 1) with different oceanographic conditions, but a similar *D. antillarum* population structure (Abades: mean density ( $\pm$  SD) ( $n = 10$ ,  $10 \times 2$  m transects):  $8.03 \pm 1.76$  urchins  $\text{m}^{-2}$ ; mean test diameter ( $n = 50$ ):  $28.14 \pm 3.58$  mm – Masca: density ( $n = 10$ ):  $8.26 \pm 1.54$  urchins  $\text{m}^{-2}$ ; mean test diameter ( $n = 50$ ):  $35.06 \pm 4.06$  mm). Settlement was recorded monthly from April 2002 to April 2003, but 3 mo were not sampled due to inclement weather (April and February 2002 at Masca and December 2002 at Abades).

The experimental sampler (Fig. 3A) used to measure monthly settlement was a modification of the echinoderm settlement intensity technique described by Keesing et al. (1993). One hundred molded 3.9 cm diameter plastic balls or “experimental collectors” originally used as fish-tank filters (biofilters) (Fig. 3B), were placed into a  $50 \times 50$  cm net bag closed with a thin rope (Fig. 3A). The smooth, dark interior of the collector has a very high surface area ( $0.04 \text{ m}^2 \text{ ball}^{-1}$ ), favorable for larval settlement and subsequent metamorphosis (Hunte and Younglao, 1988). Samplers were placed at 5–6 m depth and anchored to the rocky bottom by a 1.5 m long plastic rope. An air-filled plastic bottle attached to the opposite side was used to maintain vertical position and height off the bottom. We deployed three replicate samplers at each experimental site and recovered them each month. Before samplers were brought to the surface,

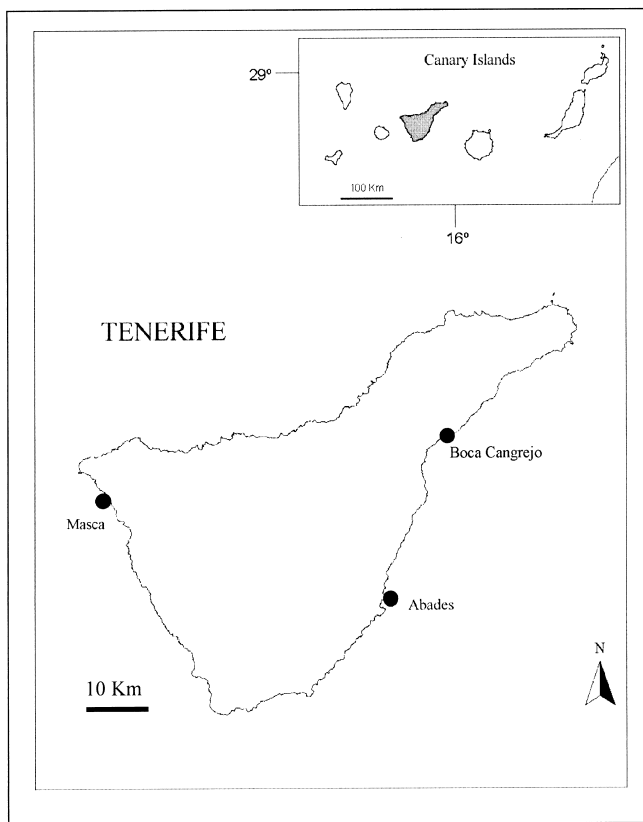


Figure 1. Location of Tenerife, Canary Islands showing Abades and Masca where samplers were placed and Boca Cangrejo where sea urchins were collected for gonad analysis.

a plastic bag was placed around the sampler in order to reduce loss of early settlers. Samplers were transported to the laboratory to count recent metamorphosed urchins.

The following washing technique was used to remove all organisms from the samplers (Keesing et al., 1993): Once in the laboratory, each sampler was placed in a separate container with 5 l of seawater and 0.125 g of benzocain (anesthetic) in 10 ml of alcohol for 2 hrs to dislodge attached material (Keesing et al., 1995; Nash et al., 1995). All experimental collectors of each container were then washed individually and examined to ensure that all newly settled urchins were recovered. If necessary, remaining individuals were removed with forceps. The experimental collectors were reused, after 1 d in a tank with 5% hydrochloric acid to eliminate sessile animals (such as bryozoans, hydrozoans, serpulids, and sponges).

After the collectors were washed, each container with the washed sample had a variable volume of water to which we added a sufficient amount of formaldehyde (up to 5%) to fix all organisms. After 48 hrs the wash was strained through a 200  $\mu\text{m}$  mesh filter to retain *D. antillarum* post-larvae with a test diameter of  $515 \pm 17 \mu\text{m}$  (Eckert, 1998). The biological material retained in the mesh was stored in 70% alcohol in 100 ml plastic bottles. All material retained was inspected under a stereomicroscope (20 $\times$ ) and all echinoids separated for identification using Eckert (1998) and Hernández et al. 2005) (Fig. 2).

**DATA ANALYSIS.**—An orthogonal two-way ANOVA was used to analyze settlement variation between sites and months, with site and months as random factors. Homocedasticity was obtained after transforming the data using  $\log(x + 1)$ . The SPSS-11/5 statistical packet was

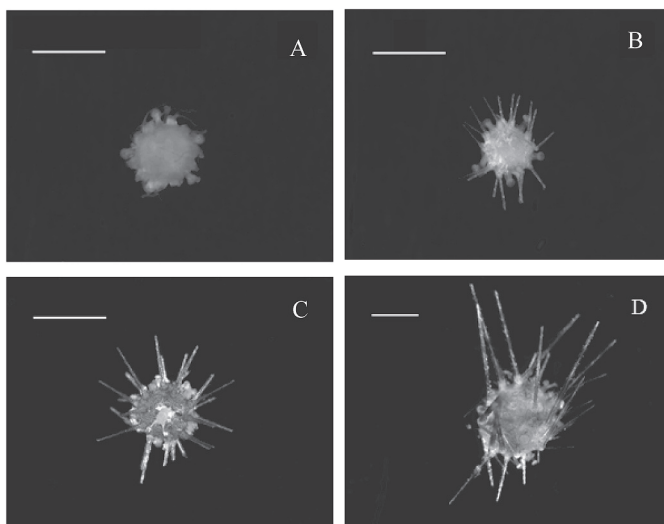


Figure 2. Different stages of newly settled *Diadema antillarum* recovered from experimental settlement collectors, from (A) postlarvae, to (B, C, D) early juveniles; scale bar = 1 mm.

used for descriptive analysis and GMAV-5 program (Underwood et al., 2002) was used for two-way ANOVA with Underwood's (1977; 1981) specifications.

## RESULTS

Mean gonad content peaked between April and June at Boca Cangrejo (Fig. 4), remaining at a minimum through the fall months before increasing slightly in December. A comparison of settlement data between the two populations (Masca and Abades) showed significant temporal variability between sites (site  $\times$  month:  $F = 7.90$ ;  $P < 0.001$ ), even though the overall pattern of variation between sites was quite similar. Bimodal peaks in settlement were observed at both locations, with the largest peak in summer-early fall (Jul–Oct) and a smaller increase in winter (Jan–Feb) (Fig. 5). The significant interaction term is likely due to the different values recorded in October and gaps in the data due to weather problems (see methods).

The test diameter of the newly settled *D. antillarum* was  $0.75 \pm 0.17$  mm ( $n = 150$ ) at Masca and  $0.84 \pm 0.18$  mm ( $n = 255$ ) at Abades.

## DISCUSSION

**SEASONAL VARIATION IN GI.**—Our results indicating a primary peak in *D. antillarum* GI in May (April–June) and a secondary peak in December are similar to that 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). Garrido et al. (2000) reported a peak GI in April at Sardina del Norte and in May at Puerto Rico (May). Slight monthly differences may occur inter-annually and/or among islands due to variation in environmental or biotic (urchin densities or food availability) conditions. For example, Garrido et al. (2000) noted a rapid increase in water temperature as a causal factor for gonad production in Gran Canaria, but also

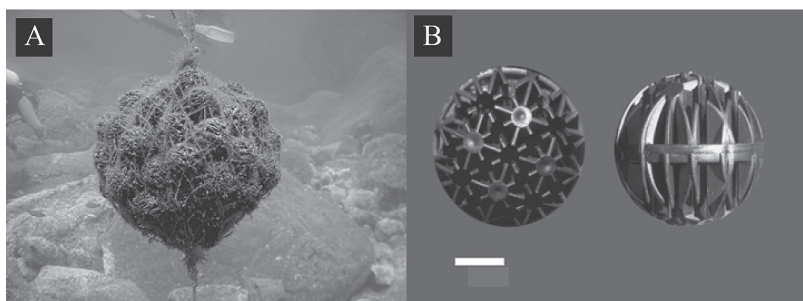


Figure 3. A) Settlement sampler unit in the study area. B) Detail of experimental collector (scale bar = 1 cm).

concluded that other parameters, such as photoperiod, phytoplankton blooms, and food availability might influence the gonad cycle. In Boca Cangrejo, the increase in GI began during the season with relatively low water temperature ( $\sim 20^{\circ}\text{C}$ ).

The existence of clear seasonality in the GI for *D. antillarum* in the Canary Islands differs from Caribbean populations of *D. antillarum*. Seasonality is less conspicuous in some areas such as Fort Randolph, Panama, or nearly non-existent for Maria Chiquita, Panama (Lessios, 1981), Virgin Islands (Randall et al., 1964), Barbados (Lewis, 1966), and Bermuda (Illife and Pearse, 1982). Only Bauer (1976) found strong seasonality in the northern Caribbean/western Atlantic area (Florida Keys-Indian Key). Thus, there may be a latitudinal trend whereby seasonality of reproduction is more distinct in higher latitude populations. Reproductive strategies are typically timed to the most favorable times of the year. Thus, gonad maturation peaks may be inconspicuous and extend for several months in areas where annual variations of environmental parameters are minimal (i.e., tropics). In the Canary Islands, primary production in oligotrophic waters, peaks in February–March (Braun, 1980), coinciding with minimum water temperatures. This minimum water temperature also leads to a subsequent growth of many benthic algal species in spring (Gil-Rodríguez, University of La Laguna, pers. comm.). *Diadema antillarum* likely responds to

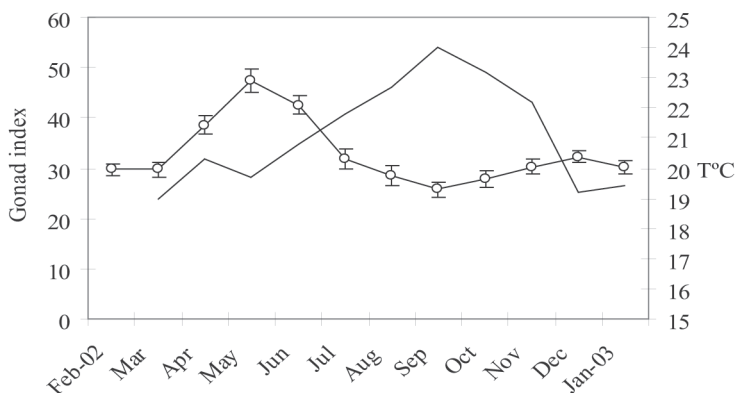


Figure 4. Annual variation in the monthly mean ( $\pm$  SD) gonad index ( $n = 30$ ) and water temperature (solid line) from February 2002 to January 2003 in Boca Cangrejo (Tenerife).

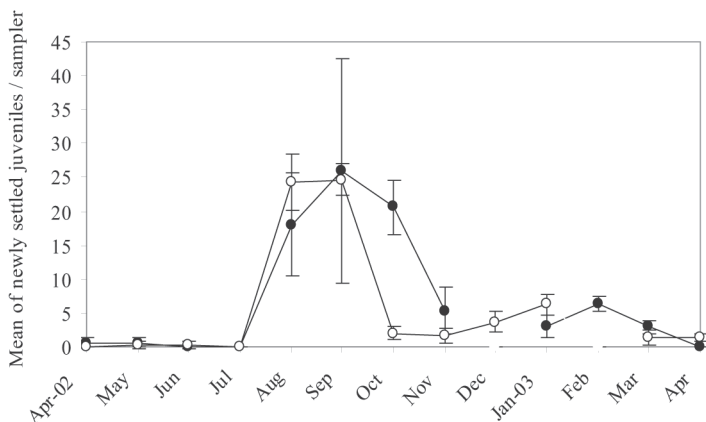


Figure 5. Monthly mean ( $\pm$  SD) number per sampler of newly settled *Diadema antillarum* at Masca (open circles) and Abades (solid circles) from April 2002 to April 2003.

this favorable nutrient period with increased gonad growth in the spring. For some urchin species in the genus *Strongylocentrotus*, nutrient concentrations have been shown to influence gonad production in both field (Meidel and Scheibling, 1998) and laboratory studies (Garrido and Barber, 2001).

**TEMPORAL PATTERN OF LARVAL SETTLEMENT.**—Settlement of *D. antillarum* was bimodal at both sites in the Canary Islands, with a primary peak in August–October (Abades) and August–September (Masca). This peak may be related to spawning as the GI peaked in April–June and spawning is presumed to occur as GI decreases. Although larvae have a planktonic period of only approximately 36 d (Eckert, 1998), this can vary depending on suitable substratum, hydrodynamics, water temperature, salinity, predation, and starvation factors (Strathmann, 1978; Palmer and Strathmann, 1981; Strathmann et al., 1992; Boidron-Metairon, 1995; Balch and Scheibling, 2001; McEdward and Miner, 2001). A second less conspicuous peak occurred in January and February, which was not related to a sharp decrease in GI, suggesting that factors other than local spawning intensity affect settlement of *D. antillarum*.

Clearly, many events occur between the time of decreasing GI and settlement. Fertilization in marine invertebrates depends to a great extent on population densities, which can vary greatly. For example, *D. antillarum* has a 50% fertilization success for 20 males  $m^{-2}$  and 10% for 5 males  $m^{-2}$  (Levitan, 1995). In addition, *D. antillarum* has a planktotrophic larva, thus variation in exogenous resources may affect time to metamorphosis (McEdward, 1984; Fenaux et al., 1985). Although larvae of many echinoderms feed on particles no larger than 50  $\mu m$  (Rassoulzadegan and Fenaux, 1979); i.e., pico- (< 2  $\mu m$ ) and nanoplankton (2–20  $\mu m$ ), cultivation of *D. antillarum* suggests that larvae feed on phytoplankton (Eckert, 1998). In the oligotrophic waters of the Canary Islands picoplankton represents as much as 94% of the phytoplankton biomass and 50%–90% of the primary production (Braun et al., 1985; Montero, 1993; Basterretxea, 1994). The secondary peak of *D. antillarum* settlement in January–February coincided with the maximum peak of planktonic productivity (Braun, 1980). Therefore, it is possible that the availability of planktonic food increases larval growth and survival as reported for other sea urchin larvae (Thorson, 1950; Chia, 1974; Olson and Olson, 1989; Boidron-Métairon, 1995), and compensates somewhat



for greatly reduced spawning. Thus, while the most substantial settlement peak is related to spawning patterns, the secondary settlement peak may be due to enhanced larval survival.

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