



Different settlement strategies explain intertidal zonation of barnacles in the Eastern Mediterranean



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ABSTRACT

The Mediterranean mid-littoral zone is inhabited by two sympatric chthamalid barnacles: *Chthamalus stellatus* and *Euraphia depressa*. *C. stellatus* extends from the high midtidal zone, above the algal belt, to the supra-littoral fringe, *E. depressa* is restricted to the uppermost intertidal levels in wave-beaten places and to cryptic habitats lower on the shore within the belt of *C. stellatus*. Previous studies have suggested that the reason for the fragmented distribution pattern of *E. depressa* is competitive displacement by the sympatric *C. stellatus*, following random settlement. This hypothesis is in agreement with the common model of zonation suggested by Connell that lower distribution limits are determined by biotic factors (competition and predation), while upper limits are set by physical factors. It is hard to test the validity of this model for this barnacle pair since the early ontogenetic stages of the species are morphologically indistinguishable, hindering our ability to understand distribution processes. Using 16S mtDNA as a genetic marker in a multiplex PCR system, cyprids and spats were individually identified. Settlement and recruitment rates were assessed using settlement plates, and the effect of post-settlement processes was tested with transplantation of settlers between zones. Results showed different strategies in each species: settlement of *E. depressa* was habitat-specific, while settlement of *C. stellatus* was random. Shifting individuals of *C. stellatus* to the high and cryptic zones resulted in high mortality; however, exposing juveniles of *E. depressa* that settled in artificially cryptic low shore habitat to *C. stellatus* presence had no effect on their survival. These findings do not agree with the formerly suggested hypothesis that zonation is mainly determined by post-settlement factors, and that the interspecies boundary is determined by interspecific competition, implying that competition model cannot be adapted to Mediterranean intertidal zonation and that other models, dominated by physical enforcement and pre-settlement recruitment-limiting factors, may prevail in this ecosystem.

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1. Introduction

Barnacles are dominant organisms on most rocky shores, forming distinct belts on hard intertidal substrata. In many regions two or more barnacle species occupy different vertical levels (Stephenson and Stephenson, 1949). In the Eastern Mediterranean, the two chthamalids *Chthamalus stellatus* and *Euraphia depressa* are the most common barnacles in the intertidal zone (Lavie et al., 1993; Lipkin and Safriel, 1971; O'Riordan et al., 2010).

The intertidal barnacle *C. stellatus* is widespread, with a Mediterranean distribution extending to the Atlantic, from the west coast of Africa and into northern Europe. Its vertical distribution extends from the high midtidal zone, above the algal belt, to the supra-littoral fringe (Dando et al., 1979; Southward, 1964). The other chthamalid,

E. depressa, is distributed in the Mediterranean and the Black seas (Klepal and Barnes, 1975). This species has a more restricted and fragmented vertical distribution and is found either at the uppermost intertidal levels in wave-beaten places, or in cryptic habitats lower on the shore (Crisp et al., 1981). Its distribution usually extends above *C. stellatus* in the splash zone, with small aggregations in crevices within the supra-littoral fringe. Cryptic (hypobiotic) populations of *E. depressa* are found under stones and in cavities within the belt of *C. stellatus*, and occasionally below it, in the subtidal zone (Achituv and Safriel, 1980; Klepal, 1971, and Lavie et al., 1993). The morphology of the shell plates, displaying distinguishable lineaments, is traditionally used as criteria for identification of these species (Southward, 1964).

Achituv and Safriel (1980) described an extreme hypobiotic populations of *E. depressa* in Mikhmoret (central Israeli coast) and in the Suez Canal, where it occupies bottom-facing surfaces of stones in the shallow subtidal, and morphologically differs from the exposed populations. Consequentially, they suggested that the reason for the fragmented distribution pattern of *E. depressa* is competitive displacement by *C. stellatus*. Klepal and Barnes (1975) compared the interaction between

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E. depressa and *C. stellatus* to that of *Semibalanus balanoides* and *C. stellatus* on northern shores. They stressed that, similar to the case of northern sympatric *Chthamalus* and *Semibalanus* studied by Connell (1961), competition for the most suitable settlement sites favors *C. stellatus* over *E. depressa*, since it has faster growth rate, with greater metabolic activity and lower critical temperature. Shemesh et al. (2009) reported a population of *E. depressa* in Jerba, Tunisia, where it occupies the lower barnacle zone, immersed in water, in the absence of *C. stellatus* (personal observation, Achituv), and suggested this as an evidence for the action of interspecific competition between the two barnacles, conforming to the zonation model advanced by Connell (1961, 1972). According to this model, following random larval settlement, biotic selective factors (competition or predation) determine the lower limit of each species, while the upper limit is set by physical selective factors. These mechanisms were later tested and confirmed in both aquatic and terrestrial ecosystems (Chapman, 1973; Heller, 1971; Iwasaki, 1995; Lubchenco, 1980; Menge and Sutherland, 1976; Noda, 2009; Wethey, 1983). Other prospective models place the emphasis on pre-settlement recruitment-limiting factors (Denley and Underwood, 1979; Grosberg, 1982; Roughgarden et al., 1994; Underwood and Fairweather, 1989), or on physical factors as major determinants of inter-species boundaries (McLachlan, 1996; Miyamoto et al., 1999).

To understand the dynamics and structure of barnacle populations and communities, it is necessary to study their recruitment patterns to that habitat, by simultaneous studies of adults and juveniles (Jeffery, 2003). In many cases, it is impossible to visually distinguish between the early developmental stages of co-occurring species, since the differentiating morphological features have not yet been established (Levin, 1990; Wang et al., 2006). In the present context, cyprids and spats of *C. stellatus* and *E. depressa*, cannot yet be morphologically distinguished, hampering our ability to understand the processes controlling the distribution patterns of these species where they co-occur (Dando and Southward, 1980; Power et al., 1999).

The goal of this study was to quantify the spatial distribution of the two barnacle species in the Levant and explain their distribution with mensurative and manipulative experiments. Specifically we tested the following null hypotheses: (a) settlement is random at all zones; (b) the upper limit of *C. stellatus* and its absence from the cryptic areas are determined by post-settlement mortality due to physiological intolerance to the surrounding physical conditions; and (c) the interspecies boundary, i.e. the lower limit of the exposed *E. depressa* form, results from competitive displacement by *C. stellatus*.

2. Methods

2.1. Study site

The study site, Habonim, is a rocky shore located on the Eastern Mediterranean Israeli coast (32°37'48.20"N 34°55'9.61"E). Observations, monitoring and experiments were performed at the mid-littoral and the supra-littoral fringe shore levels. Mean and maximum spring tide amplitudes in the region are 0.25 m and 0.45 m respectively.

2.2. Zonation surveys

To quantify the zonation patterns, ten belt transects (Anderson and Pospahala, 1970) were randomly placed during Oct–Nov 2011 at different locations perpendicular to the shoreline, starting at the mean low water mark (MLW) and ending 20 cm above the upper *E. depressa* distribution limit. Each belt transect was subdivided into contiguous stratified 10 × 10 cm quadrats (Dethier et al., 1993). Precise vertical profiles of the M transects were created using a laser level (Spectra Precision Laser LL100) and a laser rod receiver (Agatec SmartRod). In each quadrat, presence or absence of cracks and crevices was recorded as a binary parameter. Live individuals of *C. stellatus* and *E. depressa*

were enumerated. Coverage percentage of macroalgae and mussels, which may compete with the barnacles for space for settlement and growth, was recorded. Large grazers (typically *Phorcus turbinatus* and *Patella caerulea*), which may positively or negatively affect barnacle abundance (O'Riordan et al., 2010), were counted.

2.3. Niche breadth and overlap estimation

The spatial niche breadths (i.e., distribution zones or belts) of *C. stellatus* and *E. depressa* were calculated per each transect using the Levin's index (Krebs, 1999; Levins, 1968), given as:

$$B_A = (B-1)/(n-1)$$

where B_A is the standardized Levin's index by the total number of quadrats per transect (n), and:

$$B = \frac{1}{\sum p_i^2}$$

where p_i is the proportion of individuals recorded in distance class i . The niche breadth measurement (B_A) maximizes when an equal number of individuals of the species is associated with each distance class. It ranges from 0 (occupancy of a single distance class) to 1 (equal occupancy of all distance classes). To quantify the spatial niche overlap between *C. stellatus* and *E. depressa*, the Morisita index (Krebs, 1999; Mueller and Altenberg, 1985) was calculated using:

$$C = \frac{2 \sum p_{ij} p_{ik}}{\sum p_{ij} \left(\frac{n_{ij}-1}{n_j-1} \right) + \sum p_{ik} \left(\frac{n_{ik}-1}{n_k-1} \right)}$$

where p_{ij} is the proportion of individuals of species j recorded in distance class i , p_{ik} is the proportion of individuals of species k recorded in distance class i , n_{ij} is the number of individuals of species j that occupies distance class i , n_j is the total number of individuals of species j per transect, n_{ik} is the number of individuals of species k that occupies distance class i , and n_k is the total number of individuals of species k per transect. This index represents the correlation between the species distributions, so that values close to 1 indicate large overlap – equal to similar densities of both species through the profile, while values close to zero would indicate limited overlap, possibly caused by niche partitioning or competitive exclusion (Mueller and Altenberg, 1985).

2.4. Evaluation of recruitment rates

Recruitment rates at different sampling intervals reflect the extent of the selective forces on the new settlers' survival, from newly attached metamorphs to successfully recruited individuals. To identify and estimate the action of these selective forces we sampled recruitment at different time intervals, from 48 h to one month interval. Five replicates of 10 × 10 cm standard settlement plates were attached to rock surfaces using stainless steel bolts. The plates were made of PVC with both sides coated with 3 M SafetyWalk (Cat #7741) (Farrell et al., 1991; Roughgarden et al., 1994). The plates were positioned sloping downwards towards the sea, with the front of the plates, facing seaward, simulating the rock surfaces. The back of the plates, facing the rock, simulated the cryptic environment. The plates were placed at five distances/heights from MLW, evenly spaced, 30 cm apart, and replaced with fresh or cleaned plates (see below) at fixed time intervals. During Aug 2009–Sep 2011 the plates were deployed (and collected) each month. During Aug–Oct 2009 and again during Jun–Sep 2010 the plates were deployed each week. During 2–17 Sep 2010 an additional set of five replicated settlement plates were deployed at high shore and low shore, every two days. In order to reuse the plates, after counting and sub-sampling for molecular analysis (see below), plates

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