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Tidal rates of settlement of the intertidal barnacles *Chthamalus stellatus* and *Chthamalus montagui* in western Europe: the influence of the night/day cycle

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Abstract

Chthamalus montagui and *Chthamalus stellatus* are abundant barnacles in western Europe. Tidal settlement of *Chthamalus* in SW Ireland and SW Portugal was studied in relation to a night and day factor and at different temporal (dates) and spatial (shores and sites) scales. Based on the identifiable cyprids and metamorphs, *Chthamalus* settlement in SW Ireland was comprised mainly of *C. stellatus* but was composed of *C. montagui* only in SW Portugal.

In SW Ireland and SW Portugal, settlement rates of *Chthamalus* (mean number of settlers per 25 $cm^2 \pm$S.E.) were higher after one day tidal cycle (597±158.7 in SW Ireland, 144±23.6 in SW Portugal) than one night tidal cycle (55±12.1 in SW Ireland, 13±2.2 in SW Portugal), but significant differences were only detected in SW Portugal. Different models were proposed for explaining this pattern related to night and day variability of the physical processes responsible for transporting cyprids to shore (1), and/or of pre-settlement behaviour (2) and/or of settlement behaviour of cyprids (3).

Spatial patterns of tidal settlement of both species or at both locations seem similar with small scale variability (between sites, 5 to 30 m apart) in settlement of *Chthamalus* being the only spatial scale at which variability was detected in both locations.

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The composition of *Chthamalus* cohorts settling during one tidal cycle differed considerably between locations/species: settlers of *C. stellatus* were mainly cyprids; settlers of *C. montagui* during the day (when most settlement occurred) were essentially metamorphs.

Keywords: Barnacles; *Chthamalus*; Night/day; Settlement; Tidal cycle; Western Europe

1. Introduction

Settlement and recruitment of intertidal barnacles have been studied extensively around the world. Settlement has been defined as the instantaneous time when an individual first takes up permanent residence on the substratum, while recruitment combines settlement with any early mortality that has occurred on the substratum up to the time of the first census (Keough and Downes, 1982; Connell, 1985).

For a barnacle, it is very difficult to measure settlement according to the above definition. Ideally, each larva should be mapped as it attaches (Connell, 1985). Connell (1985) considered daily census as sufficient to give a good estimate of settlement. In recent years, several studies using censuses of new attachments of intertidal barnacles made every 1 to a few days (e.g. Hawkins and Hartnoll, 1982; Bertness et al., 1992, 1996; Pineda, 1994; Jeffery and Underwood, 2000; Jenkins et al., 2000; Jeffery, 2002) were considered to be measuring settlement. Over longer temporal scales of measurement, as weeks to months, recruitment is the term used more often (e.g. Raimondi, 1990; Menge, 1991; Jenkins et al., 2000; Hancock and Petraitis, 2001).

In semidiurnal tidal locations, common along the Atlantic coast of Europe, there are two high and two low waters each lunar day, and the heights of successive high and low waters are approximately the same (Thurman, 1993). Since tides are always getting higher or lower at any location, due to the spring-neap tide sequence, successive high and low tides can never be exactly the same at a single location (Thurman, 1993). Thus, for a mid-intertidal barnacle, there will be two possible periods for settlement during a lunar day corresponding to both high tides. Despite the fact that this tidal regime is common throughout the world, while there are numerous studies on daily settlement variability of intertidal barnacles, much less information is available on settlement in one tidal cycle (hereafter called tidal settlement) (but see Wethey, 1984; Raimondi, 1990; Cruz, 1999).

One obvious difference between two consecutive high tides is the amount of light, being maximal when one high tide fully occurs during the night and the next high tide during the day.

Light is considered to be an important physical cue to which barnacle larvae can respond (Crisp and Ritz, 1973). A few observations made in the field at different times and with different species suggest that light plays an important role in determining settlement of cyprids. The number of settling cyprids of *Balanus eburneus* (McDougall, 1943 in De Wolf, 1973), *B. improvisus* (Weiss, 1947 in De Wolf, 1973) and *Chthamalus anisopoma* (Raimondi, 1990) was higher during the day than during the night. Recently, the same pattern was observed with *Chthamalus* species in a preliminary study done in the SW coast of Portugal (Cruz, 1999). In contrast, De Wolf (1973) also cited a few barnacle studies where this pattern was not evident. Wethey (1984), when observing variability in tidal settlement of *Semibalanus balanoides*, did not suggest any influence of the night/day cycle. However, observations made during these studies were at restricted locations and over a short duration.

Chthamalus stellatus (Poli) and *Chthamalus montagui* Southward are very abundant intertidal barnacles in western Europe, overlapping extensively in geographic range (Crisp et al., 1981). Knowledge of recruitment of these species in Europe has increased in recent years (e.g. Cruz, 1999; O'Riordan et al., 1999, 2001, 2004; Power et al., 1999; Range and Paula, 2001; Delany et al., 2003) as part of Pan-European studies under the umbrella of the EUROROCK project (MAST programme contract MAS3-CT95-0012). These showed that the recruitment of