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Cypris settlement and dwarf male formation in the barnacle *Scalpellum scalpellum*: A model for an androdioecious reproductive system

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ABSTRACT

Cypris settlement and metamorphosis into dwarf males were studied in the androdioecious barnacle *Scalpellum scalpellum* using field collected samples from the North Sea, and experiments with laboratory reared larvae, observed with video. In the field sample, dwarf males were always situated on the rim of the mantle aperture and almost invariably confined to two areas (receptacles) located along the scutal plates near their contact to the terga. In the laboratory experiments, cyprids settling on the mantle rim always developed into males. Those settling elsewhere, whether on the external surfaces of the adults, or on their hydroid substratum, always developed into hermaphrodites. The numbers settling as males did not differ significantly from those settling as hermaphrodites, suggesting that genetic sex determination may operate in *S. scalpellum*. The N. Sea sample comprised 52 adult hermaphrodites. Of these 15 (29%) lacked males altogether, while 37 (71%) carried males with an average of 4.7 per hermaphrodite. On the hermaphrodite, a thin lamella along the mantle rim protects the settling and metamorphosing male from accidental damage or dislocation by the beating cirri. The cyprid gains additional protection by starting almost immediately after settlement to penetrate into the receptacle tissue. After 12–24 h the developing dwarf male can be almost completely buried. It appears that the cyprid does not use any preformed burrow, but actively descends into the hermaphrodite integument.

1. Introduction

Stalked and acorn barnacles (Cirripedia Thoracica) offer an interesting testing ground for theories on the evolution of reproductive strategies, since this taxon contains species with pure hermaphrodites, species with dioecy (separate sexes), and species androdioecy, a system where both hermaphrodites and a separate male sex occur together (Charnov, 1987; Crisp, 1983; Darwin, 1851; Høeg, 1995; Kelly and Sanford, 2010; Urano et al., 2009; Yamaguchi et al., 2007, 2008; Yusa et al., 2012). The diversity of reproductive strategies found in barnacles is most likely coupled to differences in population density between the species (Charnov, 1987; Urano et al., 2009; Yamaguchi et al., 2008; Yusa et al., 2012), and variation can exist even at low taxonomic levels. A further interesting aspect is that barnacle males are always minute (dwarf males) compared with their hermaphrodite or female partners (Klepal, 1987). The diversity of reproductive systems in barnacles and the fact that their adults do not move around, but are permanently attached, make them both excellent models for population level studies on sex allocation and well suited for laboratory experiments on sex determination (Charnov, 1987; Svane, 1986). Studies on the role of males in androdioecious species (Weeks et al., 2006) would be especially important, because in barnacles this strategy may well be an intermediary stage in the evolution from hermaphroditism to dioecy or the reverse. In androdioecious barnacles, hermaphrodite specimens that sit in groups can fertilize each other using their penis (Kaufmann, 1965: Fig. 1), whereas reproduction in solitary hermaphrodites must rely entirely on the presence of dwarf males (Buhl-Mortensen and Høeg, 2006; Svane, 1986). We therefore predict that the role of males in androdioecious barnacles becomes increasingly important as population density declines (Yusa et al., 2012). Unfortunately, few researchers have used population-wide samples to study barnacles with dioecious or androdioecious sexual systems (Buhl-Mortensen and Høeg, 2006; Ozaki et al., 2008; Yusa et al., 2010), while only Svane (1986) and Gomez (1975) have used laboratory experiments to investigate the role of their males. Here we use the androdioecious barnacle *Scalpellum scalpellum* as a model to study the distribution of males in a natural populations and their specific position on their hermaphrodite partners. In addition, we perform laboratory experiments to investigate the settlement of cyprids as dwarf males on hermaphrodite *S. scalpellum*.

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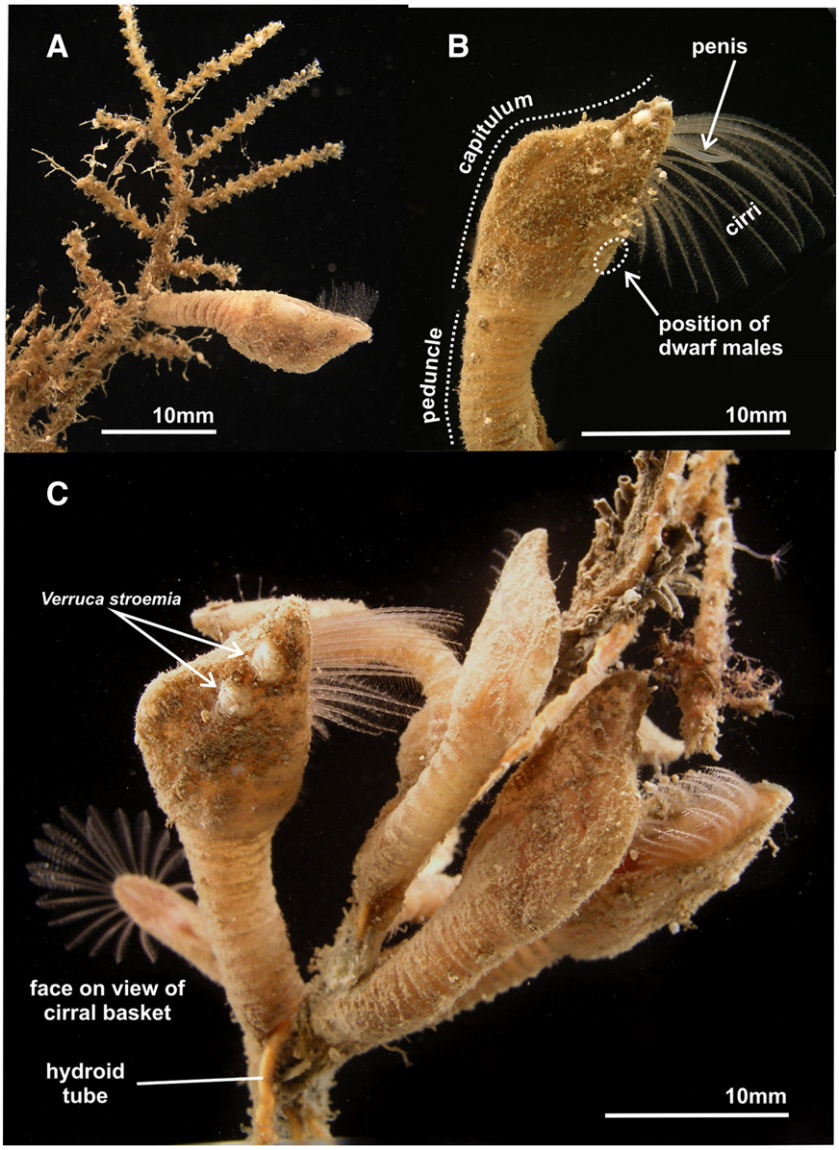

Fig. 1. Solitary and gregarious specimens of the pedunculated barnacle *Scalpellum scalpellum*. A. Solitary, adult hermaphrodite with partially extended cirri, peduncle attached to the hydroid *Nemertesia antennina*. B. Adult hermaphrodite, illustrating morphological features; the receptacle area for dwarf male settlement is indicated. C. Seven adult hermaphrodites on the hydroid *Tubularia indivisa* (one partially obscured); note how the tightly clustered specimens are attached base to base.

2. Materials and methods

In this study, specimens of *S. scalpellum* originated from two sources: from a field sample from the North Sea and from laboratory experiments using specimens collected along the west coast of Sweden.

2.1. North Sea field sample

The North Sea sample (hereafter called "field sample") derives from the Swedish Museum of Natural History (Naturhistoriska Riksmuseet, NRM) (number Cirripedia NRM-980). They were collected at Fiskebanken, N.W. of Bergen, Norway, the North Sea (no accurate position on label) at 275 m, by Tobias Anderson on the fishing vessel "Victoria" of Käringön, 1876 (no date). They were determined to species by C.A. Nilsson-Cantell. The *S. scalpellum* hermaphrodites were attached to large sea urchins *Cidaris cidaris*. A sea urchin spine could carry either several hermaphrodites or only a single one (Table 1; Supplementary material Fig. 1). All specimens from the NRM-980 sample were used here, except for a single group of four adult and four juvenile hermaphrodites that accidentally dried out during the study (these eight specimens were unusual in being attached to a hydroid that

Table 1
Dwarf males in field sample of *Scalpellum scalpellum* on spines of the echinoid *Cidaris cidaris* from the North Sea. Hermaphrodites were considered gregarious when more than one was attached to a spine. Three gregarious specimens with a capitulum length below 7 mm were classified as juveniles and are not included in the table; #Excluding the 15 hermaphrodites lacking males the mean number is 4.7 (±3.0 S.D.) males per hermaphrodite.

	Adult hermaphrodites			Males		
	Total	Without males	With males	Total	Per hermaphrodite	
					Mean (±SD)	Range
Solitary	26 (100%)	5 (19%)	21 (81%)	91	3.5 (±3.1)	0–13
Gregarious	26 (100%)	10 (38%)	16 (62%)	82	3.2 (±3.7)	0–12
All	52 (100%)	15 (28.8%)	37 (71.2%)	173	3.3# (±3.4)	0–13