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Selective byssus attachment behavior of mytilid mussels from hard- and soft-bottom coastal systems

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ABSTRACT

In both sedimentary and rocky coastal habitats, epibenthic mytilid mussels use byssal threads for attachment to the substratum and to form beds with high densities of individuals. Number and attachment strength of byssal threads can be adjusted according to external factors such as hydrodynamic forces or predators, but it is unknown whether mytilid mussels distinguish between substrata of different quality for byssus attachment in different habitat types. In field studies, we examined the attachment strength of the mussel *Perumytilus purpuratus* growing on Pacific hard- and soft-bottom shores in Chile and of the blue mussel *Mytilus edulis* from an Atlantic rocky shore in France and a sedimentary shore in the North Sea (Germany), respectively. In additional laboratory experiments, we studied mussel substratum selectivity of both bivalve species from soft and hard bottoms by offering living versus dead, barnacle-fouled vs. unfouled, and firmly attached vs. loose conspecifics. In the field, attachment strength of *P. purpuratus* on hard bottoms was substantially higher than on soft bottoms even though mussels produced more byssus in the latter habitat. In contrast, blue mussels *M. edulis* showed only a slightly reduced attachment strength on soft compared to hard bottoms. In the soft-bottom habitat, fouled individuals from the edge of a blue mussel bed were especially strongly attached. In the byssus attachment behavior experiments, *P. purpuratus* from both habitats showed a significant preference for living conspecifics and those from soft bottoms preferred firmly attached conspecifics. Blue mussels had no preference for particular conspecifics except those from soft-bottom habitats, which preferred fouled over clean mussels. In general, in the choice experiments hard-bottom *M. edulis* produced more byssus. Our results confirmed that mytilid mussels may show active substratum choice for byssus attachment, which depends on mussel species and habitat type. The results suggest that mussels are adapted to a particular habitat type, with *P. purpuratus* showing lower adaptation to soft-bottom areas while *M. edulis* shows successful strategies for both environments.

1. Introduction

One major determinant for population dynamics and the survival potential of marine species in both rocky and soft-bottom coastal habitats is their ability to resist biotic and abiotic stressors such as predation and dislodgment by waves (e.g. Reise, 1985; Denny and Gaylord, 2010). Especially, strong hydrodynamic forces can pose a challenge for benthic invertebrate species, which might need to adjust their body size, morphology and also their behavior to persist (e.g. Helmuth et al., 2006). Thus, coastal organisms have evolved a suite of strategies to cope with environmental conditions and habitat quality (e.g. substratum types) to ensure survival and persistence (e.g. Wethey, 2002; Harley, 2008). Knowledge of strategies used by benthic individuals to resist stressful conditions is thus essential to understand the ability of species to occur within a habitat and to expand their geographic ranges. Additionally, natural removal of sessile and semi-sessile habitat-forming organisms (e.g. bivalves, corals, sponges, or kelps) by hydrodynamic forces has a controlling influence on community structure in intertidal habitats (Levin and Paine, 1974; Paine and Levin, 1981). Consequently, how different ecosystem engineers can cope with predominant environmental conditions is also crucial for the occurrence and dynamics of their associated organisms.

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Ecosystem-engineering organisms including byssus thread producing mussels colonize coastal systems characterized by stressful conditions (such as strong hydrodynamic forces), because they have different adaptive attachment strategies allowing persistence and recovery (Levin and Paine, 1974; Carrington et al., 2009; and see Carrington et al., 2015 for review). Increasing hydrodynamics enhance the risk of dislodgment (Witman and Suchanek, 1984), which decreases with mussel attachment strength (e.g. Carrington, 2002a; Carrington et al., 2008). It is known that mussels can adapt their attachment strength by means of increased byssus production (Denny and Gaylord, 2010; Carrington et al., 2015), which depends on mussel size, with small-sized individuals typically producing more byssus threads than large-sized conspecifics (e.g. Babarro and Carrington, 2013). While mussels might also adjust the thickness of byssus in response to hydrodynamic variability (Carrington et al., 2015), they mostly enhance or decrease the number of byssus threads (Carrington et al., 2008; Babarro and Carrington, 2013).

The ability to attach byssal threads to the substratum and to form dense aggregations has permitted mussels to colonize both hard- and soft-bottom habitats, where they can attach to each other because little suitable attachment substratum is available (see for example Young, 1983a; Berkman et al., 1998; Buschbaum, 2000). Specifically, reciprocal byssus attachment between conspecifics results in dense aggregations of individuals (Okamura, 1986a; Alvarado and Castilla, 1996) in which the position of an individual seems to be important for dislodgement risk since individuals in the center may be better protected from drag forces than bivalves at the edge of a mussel bed (Witman and Suchanek, 1984; Okamura, 1986b; Bell and Gosline, 1997; wa Kangeri et al., 2014). Thus, predictable conspecific signals can be critical for survival and individual persistence through firm attachment in different habitats. Specifically, shells of recently dead mussels, for example, are common in mussel beds (Buschbaum, 2001; Gutiérrez et al., 2003), yet they do not offer the same hold as shells of living conspecifics. Similarly, neighboring conspecifics that are firmly fastened to the substratum can be important for attachment strength of an individual. Furthermore, epibenthic molluscs are frequently overgrown by epibionts, which may influence their performance at various levels, e.g. by increasing hydrodynamic forces for an overgrown individual (e.g. see Laudien and Wahl, 1999; Buschbaum and Saier, 2001; Buschbaum et al., 2016). Therefore, mussels seeking byssus attachment sites may prefer clean conspecifics.

Thus, some conspecifics could offer a better hold than others (e.g. live > dead, clean > fouled, firmly attached > loose), and the question arises whether mussels seeking attachment sites are able to distinguish between individuals and substrata of different quality. Recent studies conducted in soft-bottom habitats showed that *M. edulis* attach byssus threads primarily to large shell fragments rather than on living conspecifics, depending on levels of hydrodynamic disturbance (wa Kangeri et al., 2014). Similarly, sheltered mussels seem to invest less in byssus threads than edge-positioned (or wave-exposed) individuals (e.g. Cheung et al., 2009; wa Kangeri et al., 2016). Indeed, these findings indicate that blue mussels are capable of distinguishing between different substratum types (e.g. Khalaman and Lezin, 2015) and also suggest high plasticity in adhesion strategies of individuals within the mussel matrix. However, it is not known whether byssus placement on conspecifics is selective in mytilid mussels and how habitat predictability for attachment substratum (hard versus soft bottoms) could influence selectivity.

Based on these considerations, we examined the following specific questions, which guide the present study: (i) Is mussel attachment strength influenced interactively by size, epibiont load and mussel position within the bed matrix? (ii) Do mussels selectively attach byssus to particular conspecifics? (iii) Can habitat (substratum) predictability for attachment influence selectivity? Consequently, the main goal of our study was to examine attachment strength, and selective byssal attachment to conspecifics in two mytilid species, namely the purple mussel *Perumytilus purpuratus* and the blue mussel *Mytilus edulis*. Both species occur in both hard- and soft-bottom habitats and we studied interspecific and habitat-specific differences in attachment strength and selective byssus attachment. In field surveys, we investigated whether attachment strength or dislodgement risk of mussels is related to shell size, position of individuals within the mussel matrix, presence of barnacle epibionts, and habitat type. We specifically examined interactive effects as position (edge versus center) and epibiont presence (clean versus barnacle-fouled) could influence the expected linear relationship between size and attachment strength of individual mussels.

In controlled laboratory experiments we examined whether mussels are selective with respect to conspecifics for byssus attachment, and whether individual choice varies with habitat type (i.e. soft versus hard bottom). Thus the general hypothesis was that mytilid mussels, when offered a choice, show selectivity by attaching their byssus threads to shells of better suited conspecifics as an adaptive strategy to enhance survival. We tested whether mussels attach byssus preferentially to living instead of dead conspecifics, clean instead of fouled individuals, firmly attached instead of lose mussels.

2. Material and methods

2.1. Study sites and study species

The purple mussel *Perumytilus purpuratus* is dominant at mid to high rocky intertidal levels from Peru to southern Chile (Prado and Castilla, 2006), with marked connectivity patterns across the SE Pacific coast (Guiñez et al., 2016). The blue mussel *Mytilus edulis* is common on soft bottoms along the northern Atlantic, and N and S Pacific coasts (Molen et al., 2012).

Purple mussels were examined at two different locations in Chile (Totoralillo and Puerto Montt, Fig. 1a and b), and blue mussels were studied at two different sites in NW Europe (Concarneau, France; Sylt, Germany, see Fig. 1c and d). At all sites mussels occur in dense patches of many aggregated individuals (see Fig. 2).

Purple mussels *P. purpuratus* from hard-bottom habitats were collected at Playa Totoralillo, approximately 10 km south of Coquimbo (30°04′S, 71°22′W), where mussels occur in dense patches (Thiel and Ullrich, 2002). Purple mussels from soft-bottom habitats were studied on tidal flats near Pelluco to the south-east of Puerto Montt (41°29′S, 72°52′W, Fig. 1b), where purple mussels form scattered beds together with *M. edulis* (Buschbaum et al., 2009). Blue mussels from hard-bottom habitats were studied in Concarneau (France) (47°52′N, 03°53′E, Fig. 1c). Blue mussels from soft-bottom habitats were studied on tidal flats near the island of Sylt (55°02′N, 08°06′E) in the northern Wadden Sea (eastern North Sea) (see Fig. 1d), where they form extensive beds (Reise, 1985, Kochmann et al., 2008, Buschbaum et al., 2009; for more detailed descriptions of the study sites, see Supplementary Material S1).

2.2. Attachment strength of mussels in the field

At the four study sites, we measured the attachment strength of randomly selected individual mussels (i.e. no specific choice was made during the investigations) using a spring balance. We fastened a laboratory clamp to a mussel, and using a plastic hook we pulled perpendicularly to the substratum with the spring balance until the mussel was detached from the substratum. Occasionally some of the randomly selected mussels were deeply immersed in the bed matrix and the clamp could not be firmly attached; in those cases, a small hole (i.e. about 1 mm wide) was made in the accessible section of the mussel shell through which a hook was inserted, which had no observable effect on the mussel response. Measurements where entire mussel clumps of several individuals were detached from the mussel bed were not considered, as herein we were interested in the attachment strength of individual mussels; these cases were rare and limited to mussels from soft-bottom habitats.