

Investigation of larval settlement pathways in the marine bryozoan, *Bugula neritina*



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ABSTRACT

Bugula neritina is a sessile marine bryozoan with a pelagic larval stage. Larvae frequently settle on boat hulls, facilitating the introduction of *B. neritina* to bays and estuaries worldwide. Adrenergic agonists, such as norepinephrine, inhibit larval settlement in a variety of marine invertebrate species, including *B. neritina*. Light also inhibits larval settlement of *B. neritina*, yet the underlying mechanisms by which light and adrenergic compounds exert their effects on larvae are largely unknown. Octopamine is considered the invertebrate analog of norepinephrine, and may be one endogenous compound involved in larval settlement pathways. In this study, we investigated the effects of norepinephrine and the adrenergic antagonist phentolamine on larval settlement, and found that norepinephrine inhibited larval attachment and increased larval swimming behavior, while phentolamine increased larval attachment and decreased larval swimming behavior. We used fluorescent labeling and immunocytochemistry to localize sensory system components, and found that larvae possess adrenergic-like receptors and octopamine-like immunoreactivity. We also exposed larvae to phentolamine in both dark and light conditions, and found that light inhibited larval attachment, but phentolamine blocked those inhibitory effects. Based on these results, we put forth a putative mechanistic explanation for the effects of both light and adrenergic compounds on *B. neritina* larval settlement behavior. This study sheds light on previously unknown pathways underlying larval settlement behavior of bryozoans, and may aid in the development of effective, non-toxic biofouling control strategies.

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1. Introduction

Found in warm-temperate and subtropical waters worldwide, *Bugula neritina* (Linnaeus 1758) is a sessile marine bryozoan with a pelagic larval stage (Ryland et al., 2011). Larvae frequently attach to boat hulls, and the species is regarded as one of the most widespread fouling bryozoans. A cosmopolitan distribution was reported for *B. neritina* as early as the 18th century, and shipping likely played a role in its introduction to bays and estuaries around the globe (Winston and Woollacott, 2008). Sequencing of the mitochondrial gene cytochrome c oxidase I suggests that *B. neritina* is actually a complex of three cryptic species (Mackie et al., 2006, Davidson and Haygood, 1999), which may have distinct native ranges (Fehlauer-Ale et al., 2014). Native and non-native boundaries for *B. neritina* therefore remain unclear, but the range of the bryozoan is expanding (Winston and Woollacott, 2008). (From this point on, *B. neritina* will be used to refer to the species complex, or *sensu lato* definition of the organism.) Increased knowledge of the

mechanisms controlling larval settlement behavior in fouling organisms like *B. neritina* will allow us to better understand factors that are responsible for their success as invasive species, and will enable us to develop improved strategies for preventing biofouling and further anthropogenic transport of non-native species to coastal ecosystems worldwide.

Many aspects of larval anatomy and behavior of *B. neritina* are well documented (e.g., Lynch, 1947, Woollacott and Zimmer, 1971). Adult colonies are comprised of branching, hermaphroditic zooids, and are typically brown to dark purple in color. Sexually reproduced embryos are brooded in modified zooids called ovicells, which release larvae that are non-feeding (aplanktotrophic, Wendt, 1996) and typically spend <24 h as plankton prior to settling (e.g., Wendt and Woollacott, 1999). There is an inverse relationship between duration of larval swimming and metamorphic success (Wendt, 1996). Larvae swim through the water column using cilia that cover most of the surface of their barrel-shaped bodies, collectively referred to as the ciliated corona (Woollacott and Zimmer, 1971). Larvae often swim in a spiraling motion, and hold sensory structures in advance as they move through the water and begin exploration of a substratum.

The sensory apical disc consists of a central sensory cap made up of neural plate cells surrounded by a ring of ciliated ray cells and a crown

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of rigid cilia (Lynch, 1947, Santagata, 2008). The neural plate cells of the sensory cap extend basally into paraxial nerve cords, which connect with the neuromuscular ring (Santagata, 2008). Nerve fibers also extend from the neuromuscular ring to the pyriform organ, which consists of three long cilia that extend from the glandular pyriform groove (Fig. 1). These cilia, collectively referred to as the vibratile plume, are held in advance as larvae swim and spin through the water, and, along with the apical disc, are thought to play a chemosensory role during both the pelagic phase and the early stages of *B. neritina* settlement (Lynch, 1947).

Prior to attachment, larvae alight on a surface and spin counter-clockwise for 5–10 min, actively feeling the substratum with the vibratile plume (Lynch, 1947). All visible ciliary activity then halts for a brief moment prior to eversion of the internal sac. This invaginated epithelium is held within the body of planktonic larvae, and functions as an adhesive organ during settlement. Once the internal sac is everted, metamorphosis is initiated and the animal is permanently attached to the substratum. The newly metamorphosed progenitor zooid, or ancestrula, gives rise to all other zooids in the colony via asexual budding (Lynch, 1947). Colonies can become reproductive and release larvae within just twelve days of metamorphosis (Wendt, 1998).

While many aspects of larval anatomy and behavior of *B. neritina* are well documented, the underlying pathways that control larval settlement remain largely unknown. Antifouling research into natural substances that deter marine invertebrate settlement can provide insight into these pathways. Adrenergic compounds, such as norepinephrine (NE), reduce larval settlement in *B. neritina* (Shimizu et al., 2000) and a variety of other marine invertebrates; including the bivalve *Crassostrea virginica*, and the crustacean *Balanus amphitrite* (Gohad et al., 2010). That these compounds exert similar effects on species from an array of phyla suggests that there may be a conserved mechanism of reception across invertebrate taxa. While many studies have

looked at the effects of adrenergic compounds on marine invertebrate settlement, Gohad et al. offer some of the first insight into the underlying mechanisms of this inhibition. The effects of adrenergic compounds on larval settlement are typically tested in solution, but NE also deters barnacle cyprid (*Balanus amphitrite*) settlement when covalently conjugated to a polymer surface (Gohad et al., 2010). A further study revealed the presence of adrenergic-like receptors in sensory setae on cyprid antennules (Gohad et al., 2012). These findings suggest that NE may be detected in cyprid larvae by adrenergic-like receptors located in sensory structures.

It is possible that *B. neritina* larvae, like *B. amphitrite* cyprid larvae, possess adrenergic-like receptors within sensory structures that bind exogenous NE, thereby triggering a pathway of settlement inhibition. It is also possible that NE acts by permeating larval tissue and binding endogenous receptors involved in controlling settlement pathways. These two explanations need not be mutually exclusive, as NE could conceivably act as a sensory stimulus, and also mimic the action of an endogenous neuroactive compound.

While it is unknown whether marine invertebrates possess receptors specific for NE, a multitude of invertebrate species possess receptors for a similar compound, octopamine (Roeder, 1999). Octopamine is considered the invertebrate analog of NE and the two compounds only differ structurally by the addition of one hydroxyl group to the benzene ring in NE (Fig. 2). Octopamine regulates a variety of physiological and behavioral processes ranging from locomotion to photosensitivity in phylogenetically diverse invertebrates (Roeder, 1999). Octopamine receptors are known targets for adrenergic antagonists in insects (Evans, 1981) and have been proposed as binding sites for adrenergic compounds in marine invertebrates (e.g. Wendt et al., 2013). It is therefore possible that NE exerts its inhibitory effects on marine invertebrate larvae by permeating cells and acting on octopamine receptors, which are likely part of an endogenous pathway controlling

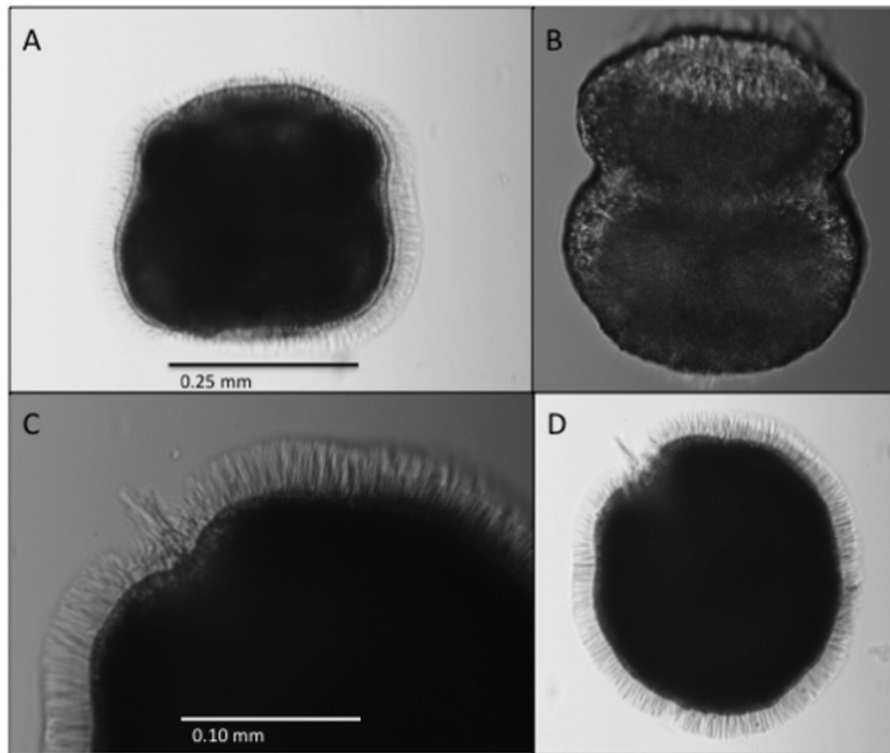


Fig. 1. A) A lateral view of a *Bugula neritina* larva shows the ciliated corona (CC), which functions as the larval locomotory organ, and the sensory apical disc (AD), which is kept foremost during larval swimming and surface exploration. B) Larvae fixed with 4% paraformaldehyde can become distorted and drop cilia. The neuromuscular ring (NR) underlies the constricted region of the larval body. Two pigmented eyespots, or ocelli (though not visible in this black and white image), lie just above the neuromuscular ring on the posterolateral side of the larval body (opposite the apical disc and pyriform groove). C) An apical view of a larva shows the ciliated corona and the sensory vibratile plume (VP). D) The vibratile plume extends from the pyriform groove, while the cells of the ciliated corona occur across most of the entire surface of the larval body.

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