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Research Article

Western Atlantic introduction and persistence of the marine bryozoan *Tricellaria inopinata*

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Abstract

Most species of bryozoans have short-lived larvae with limited dispersal potential, yet many of these species possess global distributions. In this study, we report the first occurrence from the western Atlantic Ocean of the widely distributed arborescent bryozoan *Tricellaria inopinata* d'Hondt and Occhipinti-Ambrogi, 1985. This species was collected in Eel Pond, Woods Hole, Massachusetts, in September 2010. At that time, *T. inopinata* colonies had already formed dense conspecific aggregations at some collection sites, despite the presence of several other arborescent bryozoans. Sites were monitored throughout 2011 to track the success of this introduction, and to assess the reproductive timing of *T. inopinata* in Eel Pond. To determine the likelihood of *T. inopinata* persisting in Eel Pond and competing with previously established bryozoans, rates of metamorphic initiation, metamorphic completion, and overall offspring survivability were compared to one of the other dominant arborescent species. Finally, we provide taxonomic details to aid in identifying these animals, consider the potential mode of transport, and discuss the potential ecological implications resulting from this introduction.

Key words: biological invasions, Bryozoa, anthropogenic dispersal, fouling, non-indigenous species

Introduction

The unintentional transport of organisms *via* shipping traffic is a well-known means of dispersal for many marine species (e.g., Allen 1953; Carlton 1985; Carlton and Geller 1993). Indeed, anthropogenic transport has a disproportionate effect in certain phyla, allowing for numerous species to achieve distributions that far exceed their inherent dispersal potential. Such is the case for the phylum Bryozoa, which is dominated by sessile species that have short-lived larvae with limited dispersal capability. For instance, *Bugula stolonifera* Ryland, 1960 releases non-feeding larvae that will usually initiate metamorphosis within four hours of release (e.g., Woollacott et al. 1989; Wendt and Woollacott 1999). Due to anthropogenic dispersal, however, this species can be found in sub-tropical and temperate waters worldwide (see Rodgers and Woollacott 2006, Ryland et al. 2011). Watts et al. (1998) examined the geographic distribution of 197 globally distributed species of bryozoans and found that

species abundance coupled with the animals' ability to foul, best explained the observed distributions. We report here on the introduction, establishment, and potential ecological implications of another widely distributed bryozoan, *Tricellaria inopinata* d'Hondt and Occhipinti-Ambrogi, 1985. Prior to our study, *T. inopinata* was not known to occur on the western side of the Atlantic Ocean. In 2010, however, colonies of this arborescent species were recovered in Eel Pond, Woods Hole, Massachusetts, where they have established a persistent population that is poised to spread to surrounding areas.

Tricellaria inopinata is a recently described species that was first found in a small portion of the Lagoon of Venice in 1982. Because of the ongoing long-term surveying effort within the lagoon stemming from 1978, it was thought to have been a recent introduction (d'Hondt and Occhipinti-Ambrogi 1985). Although the vector of transport that introduced these animals into the area was unknown, it has been hypothesized that the introduction could have occurred *via*

shipping traffic, or in association with the shellfish fishery (Occhipinti-Ambrogi 1991; 2000). By 1989, *T. inopinata* colonies could be found throughout much of the lagoon (area ≈ 550 km², and were seemingly only restricted by areas that routinely received an influx of fresh water (Occhipinti-Ambrogi 1991). *Tricellaria inopinata* spread throughout the lagoon despite the presence of numerous, previously established bryozoans and was found to overgrow several other species of arborescent bryozoans. Additionally, *T. inopinata* was epibiotic on various other organisms, including mussels, sponges, ascidians, and barnacles (Occhipinti-Ambrogi 1991), documenting a generalist larval settlement pattern. Such a pattern could provide these animals with a competitive advantage after being introduced to new areas, particularly when available substrate is a limited resource.

Globally, the distribution of *T. inopinata* is disjointed, with populations reported on the Pacific Coast of North America, Japan, Australia and New Zealand, in addition to those described in the Mediterranean (see Occhipinti-Ambrogi and d'Hondt 1994 and references therein) and northern European waters (De Blauwe 2009). Specimens collected in the Pacific were originally identified as *T. occidentalis* Trask, 1857, and some confusion existed as to whether or not *T. inopinata* was synonymous with *T. occidentalis* (e.g., Gordon and Mawatari 1992). Dyrynda et al. (2000), however, re-analyzed descriptions and specimens of *T. inopinata* and *T. occidentalis*, and documented that sufficient anatomical differences existed between them to allow for their identification as separate species. Further, these authors concluded that material collected from the Pacific that was anatomically similar to *T. inopinata* from the Adriatic and Atlantic should be assigned to *T. inopinata*. Shortly after its establishment and spread in the Venice Lagoon, *T. inopinata* was found in the Atlantic in 1996 in the northwest of Spain (Fernández-Pulpeiro 2001). The species was subsequently collected in southern England in 1998 (Dyrynda et al. 2000), in various locations in the Netherlands, Belgium, and France in 2000 (De Blauwe and Faasse 2001), and has recently been reported in Wales and Ireland (Ryland et al. 2009). Prior to our report, however, *T. inopinata* had not been reported elsewhere in the Atlantic. In this study, we document the first occurrence of *T. inopinata* in the western Atlantic Ocean, and provide taxonomic details to aid in identifying this species. Additionally, we provide insight into the reproductive timing of the populations established in Eel Pond, as well as empirical data on offspring survival and timing of metamorphic initiation and completion, in comparison to a dominant Eel Pond bryozoan, *B. stolonifera*.

Methods

As part of an ongoing research program, bryozoan assemblages in Eel Pond have been continuously monitored since 2006. *Tricellaria inopinata* was not known to occur in the area, but was found at several collecting sites in 2010. These sites were followed for the remainder of 2010, and throughout 2011, to track the success of this initial introduction, and to assess the survivability and reproductive timing of *T. inopinata* in Eel Pond. To aid in this, PLEXIGLAS® settling plates (15 × 15 cm) were submerged in early April 2011 under the Woods Hole Marine Biological Laboratory pier. At the time of submergence, none of the species of erect bryozoans that survived over winter in Eel Pond were found to possess polypides. Settling plates were routinely examined for bryozoan ancestrulae using a dissecting scope. To be able to continually monitor new recruitment, the settling plates were scraped clean after examination.

Induction of larval release

To assess reproductive effort over time, as well as to procure larvae for subsequent experimentation, bryozoan colonies were routinely collected and induced to release larvae. Bryozoans collected from Eel Pond were returned to the laboratory and maintained overnight in 38-liter glass aquaria equipped with a power filter providing water flow and aeration. Unfiltered seawater (UFSW) collected from Eel Pond concurrent with animal collection was used in the aquaria, and the temperature was set to mimic ambient water temperature at the time of collection. To induce larval release, dark-adapted colonies were removed from the aquaria, transferred to 1.5-liter glass bowls containing UFSW, and exposed to fluorescent light. Many bryozoan larvae are positively phototactic on release and will aggregate on the illuminated side of the bowl, facilitating larval collection. Groups of larvae were transferred to polystyrene weighing dishes, which were then placed in the dark to induce larval settlement. After the

Figure 1. *Tricellaria inopinata* colony (**A**) and close-up of an individual branch (**B**) showing biserially arranged autozooids, large lateral avicularia, and filled ovicells. The specimen was fixed in 95% EtOH prior to imaging, causing the embryos to loose pigmentation and appear white. Scale bars = 5 mm (**A**) and 150 μm (**B**).

majority of individuals had initiated metamorphosis, the dishes were transferred into the aquaria and maintained there until completion of metamorphosis.

Offspring survival and timing to metamorphic initiation and completion

As a means to assess overall health of *T. inopinata* colonies in Eel Pond, as well as to determine the likelihood of this species establishing and competing with other bryozoans, experiments were conducted examining the time to metamorphic initiation, time to metamorphic completion, and overall offspring survivability, as compared to one of the other dominant arborescent bryozoans in Eel Pond, *B. stolonifera*. Gravid colonies of both species were collected on 27 July 2011 and maintained in the dark in glass aquaria. Larval release was conducted as previously described with one exception. Approximately 45 min after exposure to light, all larvae from both species were removed from the glass dishes and discarded. Larval release was allowed to occur for an additional 15 min, after which larvae were sampled and immediately utilized in the experiment. With this modification, we were able to ensure that larvae only differed in age by up to 15 min. Ten groups of larvae (*T. inopinata*: n=14-23; *B. stolonifera*: n=19-24) were

transferred to polystyrene weighing dishes and placed in the dark, as light has previously been shown to effectively prevent metamorphic initiation in bryozoans under laboratory conditions (e.g., Wendt 1996). Initiation of metamorphosis was assessed hourly for a total of four hours, after which free-swimming larvae were counted, removed, and the dishes then submerged in glass aquaria. Metamorphic completion was initially assessed at 18h after release, and then in two-hour intervals until both species had achieved a 95% completion rate. The experiment was allowed to continue for a total of 72h, at which time those individuals that had not completed metamorphosis were counted and the experiment terminated.

Results

Taxonomic description

Colonies of *Tricellaria inopinata* from Eel Pond appear whitish-grey to straw-colored and grow as erect, compact tufts (Figure 1), generally not exceeding 4 cm in height. Superficially, colonies resemble two other common Eel Pond bryozoans, *Bugula stolonifera* and *B. simplex* Hincks, 1886; due to heavier calcification in *T. inopinata*, however, the species can be distinguished by touch. Additionally, anatomical differences become readily apparent under even slight
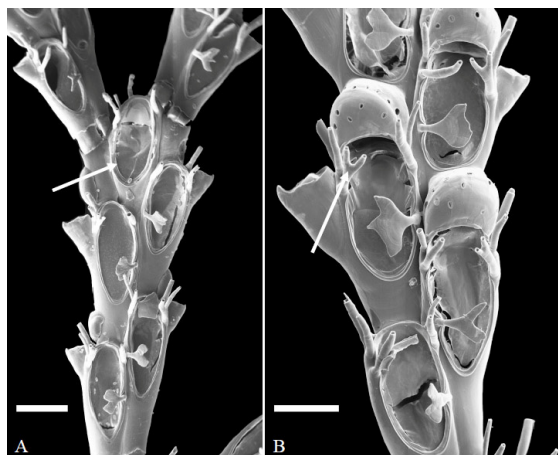
Figure 2. SEM of non-ovicellate (**A**) and ovicellate (**B**) *Tricellaria inopinata* autozooids. The scutum, a modified spine that partially covers the frontal membrane, is prominent and highly variable, ranging in shape from slender to broad and from forked to wavy. Occasionally, it is missing entirely (**A**). Autozooid spines are prominent as well, and the most basal of the 3 external spines is often forked (**B**). Scale bars = 200 μm (**A**) and 150 μm (**B**).

magnification, and the following characteristics can be used to distinguish *T. inopinata* from other erect bryozoans. In colonies of *T. inopinata*, zooids are arranged bi-serially and do not possess vibracula (Figure 2). Moveable pedunculate avicularia, similar to those described in *Bugula* spp., are not found in *T. inopinata*. Large lateral avicularia, however, are found on many, but not all, zooids. Pronounced spination about the operculum of the zooid is common in this species, with generally two internal and three external spines for each zooid. The most basal of the three external spines is often forked, but this characteristic is not constant within colonies. The scutum is prominent in this species, but the shape can vary dramatically within an individual colony from slender to broad and from forked to wavy (Figure 2). In some instances, the scutum was missing entirely from zooids immediately preceding a bifurcation (Figure 2a). Ovicells are situated distally to the maternal zooid and are multi-pored. The height and width of the ovicells was approximately equal (n = 20), a consistent characteristic within and among colonies.

Larvae of *T. inopinata* have previously been described in detail (Occhipinti-Ambrogi and d'Hondt 1994). They are barrel-shaped non-feeding coronate larvae, also referred to as buguliform. Expanded coronas extend aborally, equatorially, and orally in position, with small pallial sinuses (type AEO/ps) (see Zimmer and Woollacott 1977). Early-stage embryos can appear pink while in the ovicell, but larvae are cream-colored with orange-red eyespots. As with the larvae of many bryozoans that brood their embryos, *T. inopinata* larvae are positively phototactic on release and rapidly initiate metamorphosis once sequestered in the dark. Completion of metamorphosis results in a squat ovoid ancestrula that lacks a scutum (Figure 3). Ancestrular spines are pronounced, although spine length is highly variable. Spines generally number between 8 and 10, and can be arranged symmetrically or asymmetrically around the operculum. Characteristic of most of these newly metamorphosed individuals, are two rhizoids that often proceed down the length of the ancestrula and expand into broad to tripartite tips (Figure 3).

Observation of occurrence in Eel Pond

Tricellaria inopinata colonies were first collected from Eel Pond in September 2010 (Salinity = 34 psu, Temperature ≈ 25ºC). During a routine collection conducted in July, these animals were not observed. Rather, collection sites were dominated by two arborescent bryozoans common to the area, *B. stolonifera* and *B. turrita* Desor, 1848. Prior to the September collection, however, there was a dieback of both of these species, possibly due to decreased salinity in Eel Pond resulting from heavy rainfall in late August and early September (http://water.weather.gov/precip/). At the time of first observation, *T. inopinata* could be found attached to submerged substrates throughout Eel Pond. Indeed, because of the decrease in abundance of the two previously dominant bryozoans, *T. inopinata* had already begun to form dense aggregations at several sites. Additionally, *T. inopinata* colonies were found to be epibiotic on several different Eel Pond organisms, including fucoid algae and the solitary ascidian *Styela clava* Herdman, 1881 (Figure 4), as well as on surviving *B. stolonifera* and *B. turrita* colonies. Aggregations of *T. inopinata* persisted throughout the fall, but began to diminish in early December (34 psu, 5ºC). By January 2011 (35 psu, 4ºC), *T. inopinata* colonies had died back, leaving only a few, sporadic isolated colonies. Some of these colonies survived the near-freezing temperatures and ice formation common to Eel Pond in the

Figure 3. SEM of *Tricellaria inopinata* ancestrulae. Ancestrulae possess conspicuous spines surrounding the operculum, which generally number between 8 and 10. All ancestrulae lack a scutum, and most possess two rhizoids that aid in attachment. Scale bars = 75 µm (**A**) and 50 µm (**B**).
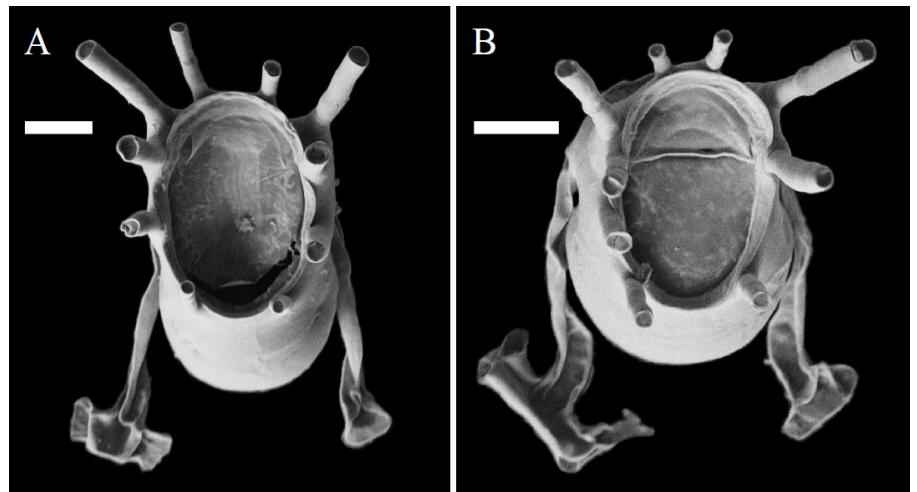

Figure 4. *Tricellaria inopinata* colonies growing on the solitary ascidian *Styela clava* (**A**) and the fucoid alga *Ascophyllum nodosum* (**B**). Scale bars = 1 cm.

winter and persisted through March 2011 (36 psu, 5ºC), but no functional autozooids were found in any collected colony through this time.

Reproductive timing of Tricellaria inopinata in Eel Pond

Collection sites within Eel Pond were monitored weekly beginning in March 2011 for initial colony re-growth. No sign of re-growth was observed until late May (35 psu, 14ºC). Colonies that overwintered were found to possess newly budded autozooids at the tips of the colonies, although no functional autozooids were found in the interior of the colony. Additionally during this time period, numerous small colonies were observed, potentially having arisen from over-wintering rhizoids. Functional autozooids were found throughout these smaller colonies. None of the autozooids on any collected colony possessed a filled ovicell, nor were any ancestrulae found on submerged settling plates. By early June (35 psu, 17ºC), colonies were found to possess brooded embryos, which appeared pink in the multi-pored ovicells. None of the collected colonies were found to release larvae after exposure to light. Within one week, however, collected colonies were found to release larvae, and numerous *T. inopinata* ancestrulae and juveniles were found growing on the submerged plates (33 psu, 20ºC). By late June (33 psu, 21ºC), collected colonies possessed numerous brooded embryos within the colony, and exposure to light resulted in the release of thousands of larvae from collected colonies. High rates of larval release were found throughout the summer and fall (31-35 psu, ≤ 25ºC), but began to decrease in mid-December (35 psu, 8ºC). Reduced larval output was observed in collected colonies until early January (35 psu, 6ºC), when approximately 35 colonies released only 8 larvae. None of these larvae initiated metamorphosis, and no brooded embryos were found in any colony examined after release.

Offspring survival and timing to metamorphic initiation and completion

Both species tested experienced high rates of metamorphic initiation and completion over the duration of the experiment (Figure 5). For *B. stolonifera*, 213 out of 216 (98.6%) of the larvae sampled initiated metamorphosis, and 210 (98.6 %) of those that initiated completed metamorphosis. For *T. inopinata*, 174 out of 185

(94.1%) larvae initiated metamorphosis, of which 169 (97.1%) completed metamorphosis. Timing for metamorphic initiation and completion were similar for the two species as well. For *B. stolonifera*, 90% of sampled individuals initiated metamorphosis within 1h, while 90% completed metamorphosis within 30h after release (Figure 5). For *T. inopinata*, 90% of sampled individuals initiated metamorphosis within 2h, and 90% had completed metamorphosis within 32h.

Discussion

Taxonomic verification

As documented in previous descriptions of *Tricellaria inopinata* (e.g., d'Hondt and Occhipinti-Ambrogi 1985; Dyrynda et al. 2000; De Blauwe and Faasse 2001), colonies collected in Eel Pond displayed a high degree of anatomical variation (see Figures 2 and 3). For instance, spine count, pattern, and size were found to vary across ancestrulae. In adults, the presence of a bifid spine was inconsistent from zooid to zooid, as was the presence of lateral avicularia. Perhaps the most striking example, however, occurred in the shape and size of the scutum, which displayed large amounts of variation even within a colony. Indeed, it was this type of anatomical variation that initially led to confusion as to the proper identification of these animals, relative to previous species' descriptions of other *Tricellaria* congeners. In their description of the bryozoans of New Zealand, Gordon and Mawatari (1992) remarked that it was puzzling that *T. inopinata* was erected as a new species, as the description given by d'Hondt and Occhipinti-Ambrogi (1985) was within the range of variation for *T. occidentalis*. As previously mentioned, however, Dyrynda et al. (2000) re-analyzed descriptions and specimens of *T. inopinata* and *T. occidentalis*, and concluded that the scutum was one of the distinguishing features for these species, and described the scuta in *T. occidentalis* as "invariably slender or only slightly spatulate." Further, according to d'Hondt and Occhipinti-Ambrogi (1985) and De Blauwe and Faasse (2001), only two other *Tricellaria* species possess multi-pored ovicells: *T. occidentalis* and *T. prasescuta* Osburn, 1950. In *T. occidentalis*, the ovicell is reported to be 1.5-2.0 times wider than it is high, in *T. prasescuta* the ovicell is reported to be 1.5-2.0 times higher than it is
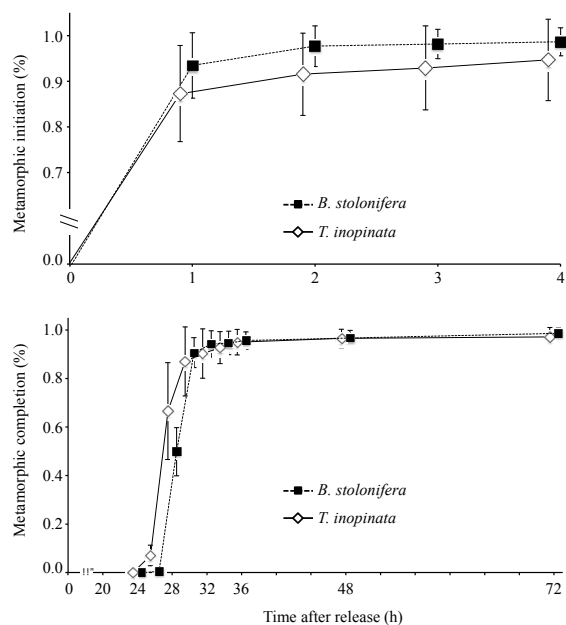
Figure 5. Percentage of individuals initiating and completing metamorphosis over time for *Bugula stolonifera* and *Tricellaria inopinata* offspring. Similar rates of overall survival, metamorphic initiation and metamorphic completion were observed between the two species throughout the duration of the experiment. Bars = 1 S.E.

wide, while in *T. inopinata* the ovicell height and width are roughly equal. Hence, colonies collected in Eel Pond are characteristic of *T. inopinata*.

Vector of transport

As with the invasion by *T. inopinata* into the Mediterranean, it remains unclear how these animals were transported across the Atlantic Ocean and introduced to the Woods Hole, MA region. Occhipinti-Ambrogi (1991, 2000) suggested shipping traffic and the shellfish fishery as likely vectors that introduced *T. inopinata* to the Mediterranean. Due to a lack of an appropriate aquaculture fishery in the Woods Hole region, it is unlikely that *T. inopinata* could have been introduced in such a manner. Therefore, shipping traffic appears to be the most likely vector. As previously stated, shipping has been implicated in the dispersal of many marine organisms. For instance, Schwaninger (1999) provided convincing genetic evidence that the invading population of the

bryozoan *Membranipora membranacea* Linnaeus, 1767 in the Gulf of Maine stemmed from populations in northern Europe. For the introduction of *T. inopinata*, there are no major shipping lanes that include the Woods Hole region, but there are vessels that routinely conduct trans-Atlantic voyages that could potentially connect Woods Hole to northern Europe or the Mediterranean. The Woods Hole Oceanographic Institution possesses several ships capable of trans-Atlantic voyages. For example, in 2008 the Research Vessel (R/V) *Knorr* travelled from Woods Hole to northern Europe and back in late summer and fall (http://strs.unols.org/Public/diu_schedule_view.aspx?ship_id=10037&year=2008). More recently, the R/V *Knorr* travelled to Aveiro, Portugal, in July 2010, and returned to Woods Hole on August 1, 2010 (http://strs.unols.org/Public/diu_schedule_view.aspx?ship_id=10037&year=2010). Interestingly, *T. inopinata* was reported in a nearby, heavily used port in Ria de Aveiro (Marchini et al. 2007). While it seems unlikely that an erect bryozoan colony attached to a ship's hull could survive the trans-Atlantic voyage, it is worth noting that many arborescent bryozoans undergo an annual cycle of colony die-back and re-growth. During this cycle, the arborescent portion of the colony will die off, most likely due to deterioration in environmental conditions. When conditions improve, however, colonies will grow back, presumably stemming from the root-like projections that remained attached to the substrate. Numakunai (1967) found that *B. neritina* Linnaeus, 1758 rhizoids collected during winter budded zooids after approximately 10 days of incubation at 20ºC. Hence, if even a portion of the rhizoids survived the trans-Atlantic trip, it remains possible that at the completion of the voyage, a new zooid could form that would eventually develop into a reproductively mature colony.

Ecological implications

Shortly after its initial description in the Venice Lagoon, *T. inopinata* was documented to undergo a rapid range expansion, colonizing most of the lagoon and spreading to various localities in the northeastern Atlantic (e.g., Occhipinti-Ambrogi 1991; De Blauwe and Faasse 2001). Further, this species not only spread rapidly, but also appears to have had a negative effect on previously established bryozoan populations. For instance, *T. inopinata*

in Venice Lagoon was initially observed to co-exist with several bryozoan species that possessed similar growth forms (Occhipinti-Ambrogi 1991). Shortly thereafter, however, the previously established bryozoan populations decreased in abundance, such that *T. inopinata* became the dominant species at these collection sites (see Occhipinti-Ambrogi 2000). A similar phenomenon could be occurring in Eel Pond. Prior to 2010, the dominant bryozoans in Eel Pond for the majority of the reproductive season were *Bugula stolonifera* and *B. turrita*. Indeed, *B. stolonifera* was commonly found forming dense aggregations on much of the available substrate, essentially carpeting floating docks and pier pilings where it occurred. After the observed introduction of *T. inopinata* in 2010, all three species were found to become abundant late in the reproductive season. Throughout 2011, however, *B. stolonifera* never reached the abundance that had been observed in previous years, and by mid-season was completely absent from several collecting sites, which were dominated by *T. inopinata*. *Bugula turrita* was also found in reduced abundance, although its decline was not as drastic. It is unclear why this decrease in abundance occurred, but it could be a consequence of reproductive timing and competitive advantage by *T. inopinata*.

Although the timing to metamorphic initiation and completion and overall survival between *B. stolonifera* and *T. inopinata* were similar (Figure 5), there were differences in onset of reproduction in the two species. In 2011, the onset of reproduction in *T. inopinata* occurred in early June, and by mid-June, numerous ancestrulae and young colonies were found on the submerged settling plates. In contrast, the onset of reproduction in *B. stolonifera* did not occur until late June. This difference in timing could have provided *T. inopinata* sufficient time to recruit to available substrate and begin growing, preventing *B. stolonifera* from forming dense aggregations where it had done so pre-viously. Alternatively, the ability of *T. inopinata* to overgrow local species, as has been previously documented, could be the overriding factor. Throughout the summer in Eel Pond, numerous *T. inopinata* ancestrulae and young colonies were found attached to *B. stolonifera* and *B. turrita* colonies. Conversely, very few *T. inopinata* colonies were observed with non-conspecific individuals attached. Conspecific larval settlement, whereby larvae attach and metamorphose on adults of the same species, can

be common in some bryozoans (e.g., Johnson and Woollacott 2010). The ability of *T. inopinata* larvae to foul and grow on other bryozoan species, coupled with the inability of other species to settle on *T. inopinata* adults, could provide a competitive advantage that allows this species to outcompete previously established arborescent bryozoans, even after a recent introduction. It remains unknown what effect this type of settlement has on growth and reproductive output of the previously established bryozoans. What appears clear, however, is that within a year of its first observance in Eel Pond, *T. inopinata* has established itself as the dominant bryozoan despite the presence of several previously established arborescent species, and appears poised to spread to surrounding areas. The species' rapid range expansion and increase in the northeastern Atlantic since its introduction to European and British shores in the 1990s, particularly its recent success in southern England (Arenas et al. 2006), highlights the need for periodic monitoring of nearby coastal areas.

Acknowledgements

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