SPATIO-TEMPORAL SETTLEMENT PATTERNS OF THE NON-NATIVE TITAN ACORN BARNACLE, *MEGABALANUS COCCOPOMA*, IN NORTHEASTERN FLORIDA

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ABSTRACT

Individuals of the non-native titan acorn barnacle, *Megabalanus coccopoma*, have been documented at several locations in the southeastern United States in the past eight years, but little work has been done on the basic biology of *M. coccopoma* in U.S. waters, nor has anyone documented active settlement in local areas. We collected recently-settled *M. coccopoma* spat at sites within the main channel and some of the adjacent feeder creeks of the Intracoastal Waterway of northeastern Florida to compare spat abundance over time, between channel and creek environments, and among sites. Spat were present almost exclusively between April and July with most settlement occurring relatively close to either St. Augustine Inlet or Matanzas Inlet. No spat were observed at any of the feeder creek collection sites; the lower salinity there may be intolerable to *M. coccopoma* larvae.

KEY WORDS: introduced species, larval settlement, *Megabalanus coccopoma*

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INTRODUCTION

The dramatic increase in oceanic shipping and travel by humans in the last century has lead to substantial increases in the introduction of non-native aquatic invertebrates worldwide (Pimentel et al., 2005). While often innocuous, introduced species can cause significant economic and environmental damage and are second only to habitat destruction in causing local extinctions (Pimentel et al., 2000). Once introduced, non-native aquatic invertebrates can often spread rapidly due to high fecundities and life history stages capable of long-range dispersal, e.g., zebra mussels.

The sub-tropical waters of the southeastern United States are a hot spot for introductions of non-native marine invertebrates from tropical and sub-tropical climes (Carlton and Ruckelshaus, 1997). Within the last few decades alone, introductions of the green mussel, *Perna viridis*, the charru mussel, *Mytilus edulis*, and the titan acorn barnacle, *Megabalanus coccopoma* (Darwin, 1854), have been reported in Florida and other parts of the southeastern United States.

*Megabalanus coccopoma* is native to tropical Pacific waters from Mexico to Peru and made its first appearance in the United States as a result of a natural range expansion during an El Niño event in 1982-1983 (Newman and McConnaughey, 1987). *Megabalanus coccopoma* has also been introduced into the Atlantic, being found in various parts of Brazil in the 1970s (Lacombe and Monteiro, 1974; Lacombe, 1977; Lacombe and Rangel, 1978). Young (1994) suggested that *M. coccopoma* likely first colonized the Brazilian seashore in the 1930s or 1940s. The titan acorn barnacle has since been found off the coast of Belgium (Kerckof, 2002) and on the Gulf and Atlantic coasts of the United States (Perreauld, 2004; Alan Power, personal communication, 2006). Titan acorn barnacles were first reported in the United States from Louisiana in 2001 (Perreauld, 2004), and the first reported sighting on the Atlantic coast of the United States was in 2006 near Brunswick, Georgia (Alan Power, personal communication). Since then they have also been reported (mostly in state Department of Natural Resources documents) in South Carolina and Florida, but little formal work has been done to document their current distribution or biology. Researchers at the Guana Tolomato Matanzas National Estuarine Research Reserve (GTM NERR) conducted a survey of introduced species within the Intracoastal Waterway (ICW) near St. Augustine and Matanzas Inlets in 2007 (Rick Gleeson, personal communication). Specimens of adult *M. coccopoma* were found on hard structures as far north as Caps Dock (CD) and as far south as the Whitney Laboratory (WL) (Fig. 1). Adult *M. coccopoma* have also been found on offshore buoys along the coast of Florida as far south as Flagler Beach (Maia McGuire, personal communication).

The present study focuses on describing the spatial and temporal patterns of settlement of *M. coccopoma* in the Intracoastal Waterway (ICW) near St. Augustine, Florida, where *M. coccopoma* was first documented in Florida. Perreauld (2004) reported only adult specimens in Louisiana with no apparent second-generation offspring; this suggests that the introduced specimens did not successfully reproduce. Here we present data showing significant settlement of *M. coccopoma* spat in certain parts of the ICW of northeastern Florida.

MATERIALS AND METHODS

*Megabalanus coccopoma* spat were collected at 13 locations in the ICW and several of its feeder creeks in northeastern Florida (Fig. 1). Collection sites were located both north and south of the St. Augustine Inlet and Matanzas Inlet. Sites were divided into two environmental categories, viz., channel and creek sites. Channel sites included collectors attached to...
RESULTS

Settlement showed a clear annual pattern with settlement beginning sparsely in March, peaking in early summer, and then dwindling through August (Fig. 2, Table 1). Spat were most abundant from May through July in 2008, with a similar large settlement in July, 2007. Acorn barnacle spat were essentially absent from September, 2007, through February, 2008, although a few individuals were observed on the collection plates in October and November, 2007. Tukey’s post-hoc means comparison test revealed four groupings of abundance ranging from nearly absent in the fall, winter, and early spring months, to the largest individual settlement period in May, 2008 (see DOI: 10.1651/09-3148.1 — on-line Supplemental Table 1). Settlement abundances in July, 2007, and June and July, 2008, were intermediate.

Settlement abundance was also significantly related to environment. No Megabalanus coccopoma spat were ever found at any of the creek sites (Fig. 3). Three of the four channel sites had significantly more settlement than the adjacent creek sites (CC vs. 51: t = −3.23, df = 51, P = 0.002; OC vs. 1: t = −3.72, df = 55, P < 0.001; MC vs. 46: t = −3.88, df = 47, P < 0.001; PC vs. WL: t = −1.69, df = 55, P = 0.096).

Since spat were absent at all creek sites, these data were removed from the analysis of spatial variation in settlement, and the average number of spat per plate was compared only among channel sites. Furthermore, only settlement occurring between March and August, 2008, was included in the analyses in order to properly account for the

Fig. 2. Temporal variation in mean settlement (± se) of Megabalanus coccopoma spat per collection plate. Data from all collection sites were pooled.

Collected tiles were allowed to dry for at least one month in a covered location, and then one side of each plate was analyzed under a stereo microscope for the presence of M. coccopoma spat. Since M. coccopoma are typically the only pink barnacles in the region, they were easily identifiable. Adult specimens in the area and spat that were large enough were identified using morphological parameters as outlined by Pilsbry (1916) and Young (1994) in order to ensure that no other species were present in the area that could be confused with M. coccopoma. Spat of the latter were enumerated and the density of settlement was compared among sites and collection dates using ANOVA. Comparisons of settlement density between adjacent creek and channel sites were analyzed by t-tests assuming unequal variance (Sokal and Rohlf, 1981).

channel markers 25, 51, 55, 1, 46, and 77, as well as the Conch House Marina (CH), a sign post at Fort Matanzas (FM), and a dock at the Whitney Laboratory (WL). All channel sites were within the main channel of the ICW and generally experienced much greater monthly average salinities than did the creek sites (see DOI: 10.1651/09-3148.1 — Supplemental Fig. 1). Creek sites included Casacola Creek (CC), Oyster Creek (OC), Moses Creek (MC), and Pellicer Creek (PC). Each creek site was paired with a channel site at approximately the same latitude and distance from the nearest inlet to standardize potential effects of distance from source populations. Long-term data sondes maintained by the GTM NERR are also located at 25, 1, 77, and PC, and their data allowed an analysis of environmental parameters including temperature, salinity, dissolved oxygen, and nutrient levels. Spat collectors were deployed at all sites in June, 2007, except for FM and 55, which were added in February, 2008, due to consistent loss of collectors at previously determined sites in the area.

Spat collectors consisted of four 12 cm × 12 cm quarry tiles attached to a PVC frame using plastic cable ties. These frames were then placed in the field using one of three methods. Some were fixed to 243.8-cm-long PVC pipes that were then attached to channel markers or other pole structures using hose clamps (25, 51, 55, 1, 46, 77, FM, PC). Others were suspended on a short piece of nylon rope underneath a dock (CH, WL, OC). In locations where hard structures were not present, the collectors were suspended under an anchored buoy (CC, MC). Each collector was placed such that the tiles would be approximately 1 m deep at low tide, although those suspended beneath a buoy at CC and MC were approximately 1 m below the surface at all times. Spat collectors were deployed in June, 2007, and revisited on a monthly basis until September, 2008. Each month the quarry tiles were removed and replaced with new tiles.
addition of the FM and 55 sites in 2008. While this procedure excluded all of the settlement that occurred in 2007, it kept the comparisons consistent over the time period during which collections occurred at all 13 sites. Spat abundance varied significantly among channel sites. The greatest settlement was observed at sites 51 and FM while the lowest settlement was observed at CH and WL (Fig. 4). A Tukey’s post-hoc test revealed three homogeneous subsets of settlement abundance, each showing a large amount of overlap with other subsets (see DOI: 10.1651/09-3148.1 — on-line Supplemental Table 2). The subset with the least settlement had a mean spat per plate <12. The mid- and high settlement groups ranged from mean spat per plate of approximately 3-18, and 6-20, respectively.

**DISCUSSION**

Settlement of the titan acorn barnacle, *M. coccopoma*, was observed in two successive years during the same time period. In both 2007 and 2008, settlement occurred in the late spring and early summer months, while spat were virtually absent during the intervening months of September through February. These data suggest that local populations of *M. coccopoma* are likely capable of reproduction and tend to spawn in the spring and summer. An alternative explanation, which cannot be discounted by the data presented, is that new larvae were introduced via ballast water repeatedly during the summer months of 2007 and 2008. The latter explanation seems less likely since it would require multiple introductions to the waters of northeastern Florida over several consecutive months in both 2007 and 2008, but no documented introductions prior to 2006.

Previous work in Brazil showed high temporal variation in larval abundance of *M. coccopoma* and other barnacle species that typically peaked in the months of September through November, but some settlement occurred in nearly every month (Severino and Resgalla Jr., 2005). While we observed sparse settlement at some sites in October and November, 2007, it appears that local populations of *M. coccopoma* in Florida have a single strong reproductive period. This may be due to greater fluctuations in water temperature in northern Florida than in Brazil.

The strong association of settlement with channel sites and the absence of *M. coccopoma* spat at creek sites suggests that either the hydrography at the creek/channel junctures is such that *M. coccopoma* larvae are incapable of entering the feeder creeks, or that the creek environment is inhospitable to them and they either cannot survive or

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**Table 1.** One-way ANOVA results comparing the mean number of *Megabalanus coccopoma* spat per collection plate across 14 monthly collections. Spat from all sites were pooled.

<table>
<thead>
<tr>
<th>Source</th>
<th>Type III SS</th>
<th>d.f.</th>
<th>MS</th>
<th>F</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>Month</td>
<td>20805.91</td>
<td>13</td>
<td>1600.5</td>
<td>9.5</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Intercept</td>
<td>7891.3</td>
<td>1</td>
<td>7891.2</td>
<td>46.8</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Error</td>
<td>73461.7</td>
<td>436</td>
<td>168.5</td>
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<td></td>
</tr>
</tbody>
</table>

**Table 2.** One-way ANOVA results of a comparison of the mean number of *Megabalanus coccopoma* spat per collection plate among nine locations in the main channel of the Intracoastal Waterway in northeastern Florida. Collections were pooled over time from March, 2008, through August, 2008.

<table>
<thead>
<tr>
<th>Source</th>
<th>Type III SS</th>
<th>d.f.</th>
<th>MS</th>
<th>F</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>Site</td>
<td>10489.6</td>
<td>8</td>
<td>1311.2</td>
<td>4.6</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Intercept</td>
<td>11272.0</td>
<td>1</td>
<td>11272.0</td>
<td>39.5</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Error</td>
<td>57403.0</td>
<td>201</td>
<td>285.6</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Fig. 3. Pairwise comparisons of mean (± se) *Megabalanus coccopoma* spat settlement at feeder creek (left) and main channel (right) collection sites of approximately the same latitude. Spat were pooled over time.
cannot effectively settle in these locations. While the present study did not attempt to determine local current patterns associated with the feeder creeks, several of our collection sites corresponded to locations of permanent data sondes deployed by the GTM NERR. These data sondes show that the PC creek site has a much lower salinity than do any of the three channel sites. Temperature, on the other hand, is nearly identical among the sites. Therefore, it seems likely that low salinity may be an impediment to successful establishment of *M. coccopoma* populations in some areas. Very low settlement was observed at 25, the channel site at which salinity fluctuated the most; however, salinity was typically fairly high there during the time of year when settlement was observed. It is thus difficult to say whether the lack of settlement at 25 was due to low salinity or other factors.

The spatial pattern of settlement within the ICW is highly variable, with some sites receiving no appreciable settlement and others displaying consistently heavy settlement. Variability such as this is often observed in marine invertebrates with pelagic larvae, because conditions for settlement and the distances from source populations can vary widely among locations (Wethey, 1984; Raimondi, 1990; Bertness et al., 1992; Rodriguez et al., 1993; Bertness et al., 1996; Thiebaut et al., 1998; Johnson and Wernham, 1999; Etherington and Eggleson, 2000; Gilg and Hilbish, 2003, 2007). An interesting pattern emerging from the data in the present study is that settlement abundance tended to be greatest at sites nearest the inlets. The sites with the most *M. coccopoma* spat included 51 and FM. Site 51 is approximately 10.6 km north of the St. Augustine Inlet while FM is approximately 3 km north of the Matanzas Inlet. The sites furthest from either of these inlets, 25 (27.8 km) and 46 (20.32 km), had some of the lowest observed settlement. Most of the adult specimens found in the survey conducted by GTM NERR researchers tended to be near either St. Augustine Inlet or Fort Matanzas Inlet as well. The pattern is not without exceptions, however, since both CH and WL are within 10 km of an inlet but received almost no *M. coccopoma* spat over the course of the current study. The relative absence of settlement at CH and WL may be due to either local hydrodynamics that keep larvae away from these locations, or to poor environmental conditions. Since adult specimens have been found at WL (Rick Gleeson, personal communication) and we have personally observed some *M. coccopoma* at CH, it would seem that environmental conditions are not always unfavorable for survival of *M. coccopoma*. Unfortunately, consistent environmental data is not available for these two sites over the time period of the present study.

The settlement of *M. coccopoma* spat in both 2007 and 2008 suggests that local populations are reproductive and that *M. coccopoma* is becoming well-established along the Atlantic coast of the southeastern United States. The lack of settlement in feeder creeks suggest that *M. coccopoma* may have little tolerance for low salinity, and this will limit the areas it can successfully invade. Future studies should concentrate on testing the environmental tolerances of *M. coccopoma* to gain a better understanding of the habitats into which it is likely to spread.

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**Fig. 4. Spatial variation in mean settlement (± se) of *Megabalanus coccopoma* spat per collection plate at main channel collection sites. Data shown only include samples from March, 2008, through August, 2008, which were pooled over time at each location.**


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