Journal of Experimental Marine Biology and Ecology
293 (2003) 173–191

Journal of
EXPERIMENTAL
MARINE BIOLOGY
AND ECOLOGY

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Impact assessment of an invasive flatworm, *Convoluta convoluta*, in the Southern Gulf of Maine

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Received 26 July 2001; received in revised form 5 February 2003; accepted 27 March 2003

Abstract

Convoluta convoluta (Abildgaard 1806) is a small (2–3 mm long) acoellous turbellarian flatworm from Europe that has invaded the Gulf of Maine within the last 5 years. Although it has been reported in densities of up to 19 individuals/cm^2, its ecological impact remains unknown. In its native habitat, it consumes harpacticoid copepods and primary settling mussels <0.5-mm shell length. This study estimated the impact of *C. convoluta* on juvenile blue mussel populations (*Mytilus edulis* Linnaeus 1758) around the Isles of Shoals in the southern Gulf of Maine, USA as well as looking at their distribution in their new habitat. We surveyed worm densities at sites of differing wave exposure over three substrates (hard substrates, bladed algae, filamentous algae) to quantify patterns of worm abundance. We found worms on all substrate types with their highest abundances occurring in areas of maximal sunlight exposure and minimal physical disturbance. We showed a definite pattern of consumption of mussels in the lab and found *C. convoluta* to consume up to 35% of primary settling mussels in the field, but only under certain conditions. Per capita impact on juvenile mussels was found to vary greatly in correlation with mussel recruitment rate and water temperature, but not with the consumption of harpacticoids. Our results also suggested that per capita interaction strength was reduced by intraspecific density-dependent competition and water temperature. The overall impact of *C. convoluta* on mussel populations in the southern Gulf of Maine is therefore estimated to be minimal.

Keywords: Acoel; Biological invasions; Impact; Invasive species; *Convoluta convoluta*; Flatworm; Rocky subtidal; Gulf of Maine

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doi:10.1016/S0022-0981(03)00166-7

1. Introduction

The benthic food web in the Gulf of Maine contains relatively few species (Witman, 1985). As low diversity communities generally contain empty or poorly defended niches, they are often more susceptible to invasion (Stachowicz et al., 1999; Levine and D'Antonio, 1999; Levine, 2000). The Gulf of Maine is no exception, hosting a suite of both comparatively old and recent invaders (Ruiz et al., 2000; Berman et al., 1992). While some of these invaders, such as the introduced alga *Codium fragile* (Prince and LeBlanc, 1992), have affected ecosystem level changes (Parker et al., 1999; Prince and LeBlanc, 1992; Carlton, 1989), the impact of other invaders remains uncertain (Parker et al., 1999).

Convoluta convoluta (Abildgaard 1806) is an acoellous turbellarian from the Baltic region. The native distribution of *C. convoluta* extends from the White Sea down through the Mediterranean Sea and out to the Canary Islands where it is common on various benthic macroalgae (Karling, 1974). Its maximum adult size is typically between 2 and 3 mm, but it can reach up to 9 mm in some locations. It was first observed in North America in Halifax in 1995, and by 1999, it had reached at least the southern Gulf of Maine in densities of up to 19 per cm^2 (Rivest et al., 1999). It was present as early as 1996 at the Isles of Shoals, Maine (J. Witman, unpublished photo quadrats). In its native habitat, it forms a symbiotic relationship with diatoms from the genus *Lichmophora* (Apelt, 1969). Although it is known to feed on harpacticoid copepods, and small juvenile mollusks, including primary settling plantigrade mussels < 0.5 mm (Mamkaev and Seravin, 1963; Drobyasha and Mamkaev, 1974; Rivest et al., 1999), its impact on populations of these species has not been evaluated.

Mussels play a variety of important roles in benthic and intertidal community structure within the Gulf of Maine (Bertness, 1999; Leichter and Witman, 1997; Witman and Dayton, 2001). They are an important prey source for a variety of mobile predators within the Gulf (Ojeda and Dearborn, 1991; Leichter and Witman, 1997), forming the base of many important trophic interactions (Bertness, 1999). As filter feeders, they channel energy from pelagic organisms into the benthic food web. They function as a dominant space holder, restricting barnacles to the upper intertidal on wave-exposed shores (Menge, 1976). In the subtidal zone, mussels function as a foundation species, both providing a substrate for algal growth which is then consumed by herbivores (Witman, 1987), as well as a refuge from disturbance for a variety of infaunal organisms (Witman, 1985).

As juveniles, plantigrade blue mussels (*Mytilus edulis* Linnaeus, 1758) first undergo a phase of primary settlement and growth on filamentous algae before returning to the water column and settling in dense beds (Bayne, 1964). Massive recruitment failure due to *C. convoluta* predation on juvenile mussels could drastically alter adult mussel population densities and distributions in the Gulf of Maine. This in turn could ultimately alter the trophic and physical structure of the subtidal community.

Given that overall impact is determined by the range, abundance, and per capita impact of an invader (Parker et al., 1999), we attempted to put together a picture of how the invasion of *C. convoluta* is affecting mussel populations with the Gulf of Maine. The range of *C. convoluta* in the Western North Atlantic is currently from eastern Nova Scotia to the southern Gulf of Maine. Abundance can be determined by taking samples of worm densities on a variety of relevant substrates. Per capita interaction strength in this case is defined by number of mussels consumed per worm per day (Menge et al., 1994) during a given settlement period. As mussel settlement is highly variable, and it is possible that worm densities are heterogeneous, it was necessary to begin to examine the relationship between mussel settlement rate, worm densities, and per capita interaction strength.

Worm functional response (Holling, 1959) and the effect of competition between worms for prey resources could profoundly alter relationship between worm density, mussel settlement density, and worm–mussel per capita interaction strength. Local impact may also change with water temperature, light intensity, and/or the presence of alternate prey items. Each of these variables as well as worm population densities may vary seasonally and spatially. Worm abundance may vary as a function of depth and different substrate types, giving settling mussels a refuge.

To break apart these factors, we measured the consumption rates of mussels and harpacticoids by worms under conditions of varying worm densities, settlement density and water temperature both in the field and in the laboratory. In order to make a conservative worst-case scenario estimation, we assumed all differences in mussel settlement in the field were due to worm consumption. Once these data were gathered, we looked at percentage of settlement failures under these varying conditions to estimate overall impact.

2. Methods

2.1. Study site

This study was conducted from June to November 2000 at the Isles of Shoals, a group of rocky islands 10 km offshore in the southern Gulf of Maine, 42°/58′ N–70°/37 W (Fig. 1). Field experiments were conducted in the shallow rocky subtidal zone at Smith's Cove on the southwest corner of Appledore Island. The habitat at 4-m depth was a sloping coralline barren that had previously been reported to contain high densities of *C. convoluta* (Rivest, personal communication). Field surveys were conducted at four sites: Smith's Cove, the northeast side of Duck Island, Broad Cove on the northeast side of Appledore Island, and on the southwest side of Star Island. Broad Cove and Duck Island sites were fully exposed to the open ocean, while both Smith's Cove and the Star Island site were relatively sheltered. Lab experiments on *C. convoluta* were conducted in flowing seawater tables at the Shoals Marine Laboratory on Appledore Island.

2.2. Distribution and abundance survey

Worm densities were surveyed in late August on three substrates where worms were commonly found: bladed brown and green algae (*Laminaria* sp., *Ulva lactuca, Agarum cribrosum*), hard substrates (crustose coralline algae and bare rock), and filamentous algae (*Polysiphonia* sp.). The first two substrates were sampled at the Broad Cove, Duck Island, Star Island, and Smith's Cove locations. Filamentous algae were sampled at Broad Cove and Smith's Cove. Sites were divided into four depth zones, 0–3, 3–6, 6–9, and 9–12 m. Ten samples were taken haphazardly within each depth zone. Photos were taken of the first two substrates using a Nikonos close-up kit. Slides were divided into 1-cm^2 areas. Seven

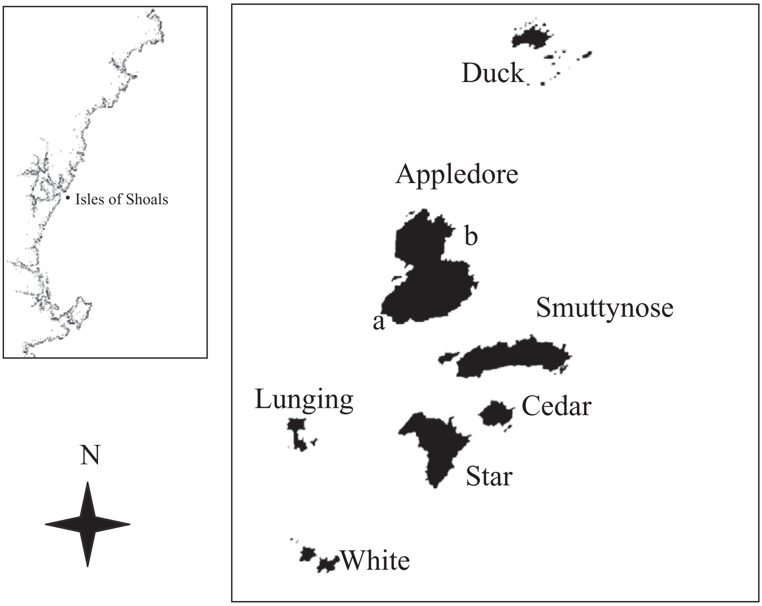

Fig. 1. Map of the Isles of Shoals. Smith's Cove is indicated by a, and Broad Cove is indicated by b. Inset is a map of the coastline with the location of the Isles marked.

areas were subsampled in each photo, and the number of worms in these areas was averaged for each photo to avoid psuedoreplication (Hurlbert, 1984).

As filamentous samples were three-dimensionally complex, photography proved inadequate for accurate measurement of worm densities. Therefore, filamentous samples were removed from the benthos and placed in individual Zip-Lock™ plastic bags. Bags were taken back to the lab, and the number of worms in each sample was counted. Algal volume was measured using volume displacement as in Hacker and Steneck (1990). Samples of *Polysiphonia* spp. were later digitally photographed and surface area of these samples was estimated using NIH imaging software. Volume of the samples was then measured using volume displacement. A linear regression was used to estimate the surface area to volume ratio of *Polysiphonia* spp. ($SA = 0.0575 * V + 0.156$, $r^2 = 0.982$, $p \leq 0.0001$), and worm densities were transformed from worms per cm^3 to worms per cm^2. Samples were analyzed using two-way ANOVA for each substrate with site and depth zone as independent variables.

2.3. Mussel collectors

Mussel collectors were used as replicate worm aggregation sites in field trials and to collect prey for lab trials. Collectors consisted of PVC plates (8 × 8 cm) attached to bolts in the Smith's Cove urchin barren. The procedure to attach the collectors to the substrate consisted of placing bolts into cracks in the substrate. Cracks were then filled with epoxy (Kop-Coat A-788 Splash Zone Compound) and plates were elevated 5 cm off the substrate by PVC spacers placed around the bolts. On the top of each plate, two 7.5 × 7.5-cm squares of 2.5-cm gauge cotton mesh were folded into 9-cm^2 squares and attached to the plate with cable ties to create a surface for mussel settlement. Plates were allowed to soak for 48 h in unfiltered flowing seawater to accumulate a biofilm before being taken to the field. Upon removal, plates were sealed in sandwich boxes underwater to minimize the loss of mussels through handling. Back at the lab, the mesh containing the newly settled mussels, harpacticoid copepods, and other organisms, was removed for use in experiments determining per capita interaction strength and functional response.

2.4. Worm delivery devices

To determine per capita interaction strength, it was necessary to transplant different densities of worms onto the mesh of mussel collectors. Worms could not simply be pipetted or brushed onto experimental mussel collectors in the shallow subtidal. Worms were instead placed into ‘worm delivery devices’ made from 5-cm diameter PVC pipe ends. One end of these tubes was covered with nitex glued around the pipe rim. The other end was secured by a plug screwed into the tube. Tubes were taken to the plates in a sealed Zip-Lock® bag. To add worms to a plate, the bag was opened, placed over the mesh of the plate, and squeezed until any worms that had escaped the collector were transferred to the mesh. Next, the tops of the tubes were removed. To ensure all worms were transferred to the mesh, the underside of the plug was placed on top of one tuft of mesh while the open end of the tube was placed over the second tuft. A plastic pipette was used to blow water through the Nylon netting to move the worms from inside the tube to the mesh below. The pipette was then used to gently blow worms off of the underside of the plug and on to the mesh below, while the plug itself prevented any worms from drifting away.

2.5. Field trials, mid-summer

The effect of *C. convoluta* on plantigrade densities was first measured during two periods of differing recruitment, July 6–9 and 21–23, 2000. Filamentous algae laden with worms were collected 2 days prior to the experiment. Twenty-four hours prior to the experiment, worms were separated into treatments of 100 and 200 worms per plate. Worms were placed in open worm delivery devices resting in half-filled 6-oz Nalgene jars in a flowing seawater table to prevent worm loss. Before removal to the field, devices were filled with seawater, capped, and placed in seawater filled Zip-Lock® bags. The devices and 30 numbered plates were taken to the study site where bolts had been arrayed in a 9 × 2-m area. Plates were attached to the bolt and seeded randomly with ten 0-, 100-, or 200-worm treatments ($n = 10$ replicate plates per treatment).

To allow settlers to accumulate on plates, and to let worms consume these settlers, the experiment was allowed to run for 48 h. At the end of the experiment, plates were taken to the lab, mesh was cut off and put in a 6-oz Nalgene jar half-filled with a 2% ethanol solution. Jars were sealed and gently agitated for 60 s to kill and shake off harpacticoids and plantigrades. The mesh was then rinsed into the solution to wash off the last few organisms and removed. Debris was allowed to settle out before being pipetted into a Wildco plankton counting wheel. All mussels < 0.5-mm shell length and harpacticoid copepods were counted. As trials were run during periods with differing recruitment rates, treatment and trial effects were compared for each prey item using two-way ANOVA. Mean mussel recruitment and harpacticoid immigration densities for a given trial were estimated using the number of recruits on 0-worm treatment plates. Per capita interaction strength was estimated with the following equation:

$$I = ((P_0 - P_t)/W)/D \tag{1}$$

where I is the per capita interaction strength in number of prey items consumed per worm per day, P_0 is the mean number of prey items present in the 0-worm treatment for a given trial, P_t is the number of prey items in a statistically significant treatment, W is the number of worms in the treatment, and D is the number of days the experiment ran. Per capita interaction strength was estimated for prey items whose settlement rates were significantly altered by worm presence. To estimate the importance of harpacticoids as an alternate food source, a linear regression was performed between harpacticoid and mussel interaction strengths. To determine the effects of predator and prey densities on potential per capita impact, worm–plantigrade interaction strengths were $\log(x+1)$ transformed if needed to maintain homoscedacity and compared using two-way ANOVA with trial and treatment as independent factors.

2.6. Field trials, late summer

By mid-August, worm densities were so high that clean mussel settlement plates were covered with worms after 24 h. Therefore, while worm density treatments were seeded on experimental plates according to the above protocol, in a third trial on August 7–9, worm densities were counted for analysis at the end of the trial. During the fourth trial, no worms were added, and the plates were allowed to remain in the field for 8 days from October 1 to 8. Data from both trials were analyzed using linear regressions of the number of worms versus densities of potential prey items. When significant, interaction strength was estimated using Eq. (1) with P_0 set to the number of prey items estimated to be remaining with 0 worms. If the regression was not significant, P_0 was set to the mean settlement or immigration density of a given prey item. Harpacticoid and mussel interaction strengths were compared as mentioned above using linear regression.

2.7. Lab trial, summer

C. convoluta is known to regurgitate the hard exoskeleton of animal prey items after consumption (Mamkaev and Seravin, 1963). This provided an ideal method to examine the feeding rate of *C. convoluta* in the lab. We used an array of forty 6-oz Nalgene jars filled with unfiltered seawater and partially submerged in a flowing seawater table. Jars in each row were grouped by two, one jar containing worms, the other merely seawater as a control for natural mortality of mussels. Jars with worms contained a fixed number of worms (0, 50, 100, 150, 200) with one treatment randomly placed per row. A random number of worms between 1 and 50 were also added to each jar to generate continuous distribution of worms. Worms were kept in the jars for 2 days prior to the beginning of the experiment, at which time all debris at the bottom of the jar was pipetted out and fresh water was added. Mussel collectors were kept in the field for 3 days prior to the experiment. As each collector contained two pieces of mesh, one piece was placed in a randomly assigned worm treatment jar while the second was placed into the adjacent control. Treatments and controls were randomly interspersed.

After 48 h, jars were removed, capped, and agitated gently for 60 s. Debris was allowed to settle and was then pipetted out. Mussels <0.5-mm shell length and harpacticoids, both dead and alive, were counted. Four milliliters of ethanol was then added to jars which were capped and vigorously shaken for 60 s. After suspended debris settled, it was pipetted out, and counts of harpacticoids and mussels <0.5 mm were added to counts of prey items left alive after the experiment.

Data were analyzed by linear regression between number of prey items consumed, as defined by empty exoskeletons, and the number of worms. Per capita interaction strength for consumed prey items was calculated by subtracting the number of prey items found dead in a jar minus the mean number of dead prey items in the no worm treatments and dividing by the duration of the experiment. To examine potential density-dependent effects on per capita interaction, we performed a linear regression on per capita interaction strength (number of prey items consumed divided by the number of worms times length of trial) vs. number of worms. To estimate any density-dependent effects of prey density on their own mortality, we performed a linear regression between number of prey items in control jars and number of dead prey items.

2.8. Lab trial, fall

The lab experiment was repeated on October 8–10 using 1-cm-high petri dishes to minimize potential vertical spatial escapes for harpacticoid copepods. This was done after experimental confirmation of observed worm phototaxis (Brian Rivest, unpublished data) in summer lab trials. Three rows of five samples each were set up as described previously. Mussel collectors were left in the field for 9 days, as mussel recruitment rates were low. During the trial, water temperatures were allowed to fall to 1–3 °C, as this reflects Gulf of Maine winter water temperatures. Results were analyzed using the same techniques described above.

3. Results

3.1. Distribution

Analysis of variance on bladed algal samples showed higher worm densities at Smith's Cove, the site of lowest wave exposure. Star Island was excluded from the analysis, as bladed algae at the site had been replaced by the invasive algae *C. fragile* down to 8 m. Site was the only variable which significantly affected worm densities ($F=29.50$, $df=2$, 102, $p \leq 0.0001$, Fig. 2) when Star Island was excluded. Post-Hoc Tukey–Kramer tests showed

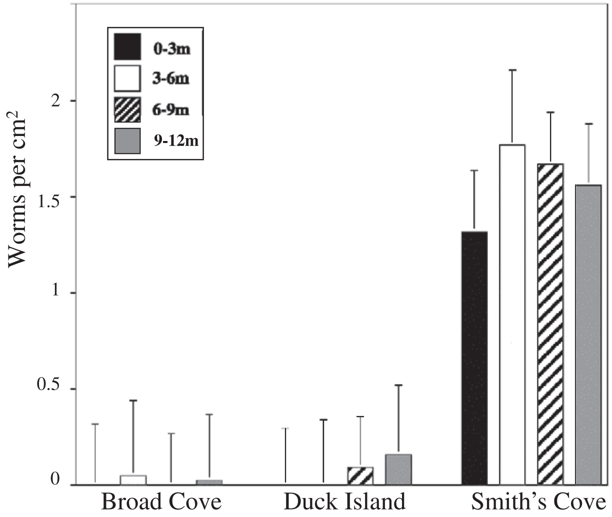

Fig. 2. Distribution of worms on bladed algae across a depth gradient at three sites. Data represent means ± 1 standard deviation.

that Smith's Cove was the only significantly different site of the three, with nonzero worm densities, while mean worm density was around 0 worms/cm^2 for wave-exposed Duck Island and Broad Cove sites.

In hard substrate samples, worm densities differed by site ($F = 11.12$, $df = 3, 135$, $p \leq 0.0001$), depth ($F = 9.408$, $df = 3, 135$, $p \leq 0.0001$), but site interacted with depth ($F = 9.667$, $df = 9, 135$, $p \leq 0.0001$, Fig. 3). A Tukey–Kramer test revealed that the only

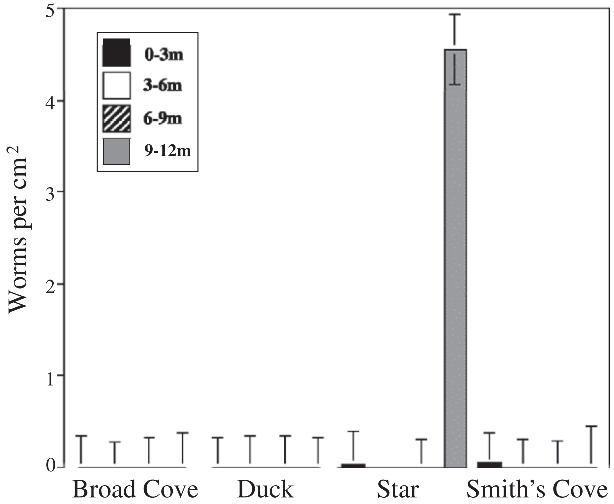

Fig. 3. Distribution of worms on hard substrates across a depth gradient at four sites. The only significant worm densities were at Smith's Cove at 9–12 m. This is also the only urchin barren included in sampling.

site with mean nonzero worm densities was the 9–12-m site at Smith's Cove, an urchin barren, which had a mean worm density of 4.5 worms/cm^2. All other sites were either in or around algal or mussel beds, and thus hard substrates were subject to scouring by algae or sediments.

Worm densities on filamentous algae were low both in extremely shallow (0–3 m) and deep (9–12 m) depth ranges but were high in intermediate depths. Densities showed both an effect of depth ($F = 9.23$, $df = 3, 63$, $p \leq 0.0001$, Fig. 4) as well as an interactive effect of site and depth ($F = 8.573$, $df = 3, 63$, $p \leq 0.001$), though there was no significant site effect ($F = 1.038$, $df = 1, 63$, $p \leq 0.312$). A Tukey–Kramer test revealed that while the 3–6 and 6–9 m were the only depths with mean nonzero worm densities, they differed in the depth of maximum worm density. At Broad Cove, it was 3–6 m, while at it was 6–9 m at Smith's Cove. At both sites, mean maximal worm densities were approximately 3 worms/cm^2.

3.2. Field trials

During mid-summer trials, some bolts and plates in the Smith's Cove barren were lost due to bolts being hidden by dense algal overgrowth or were ripped out by fishing gear. Eight samples were lost from trial one and two were lost from trial two. Variance in the recruitment and migration rates of the three prey items were found to be homogeneous (Bartlett's test: small plantigrades, $p \leq 0.253$; harpacticoids, $p \leq 0.251$) and were therefore not transformed prior to ANOVA.

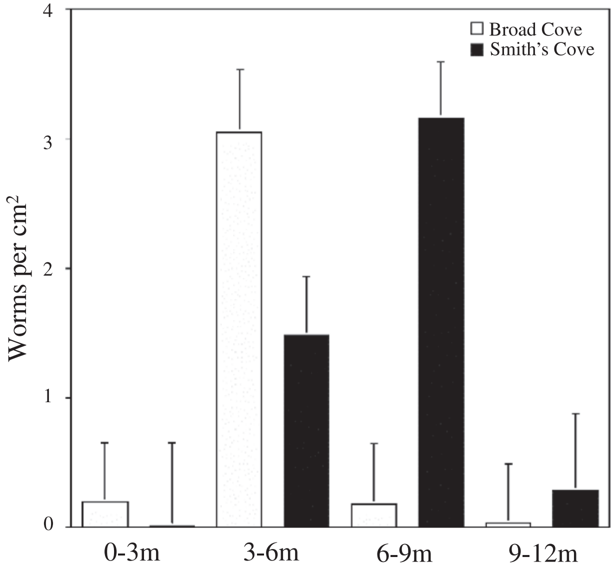

Fig. 4. Distribution of worms on filamentous algae across a depth gradient at Broad and Smith's Cove. Densities were near zero at both deep and shallow depth zones. Maximum worm densities at both sites were found to be approximately 3 worms/cm^2.

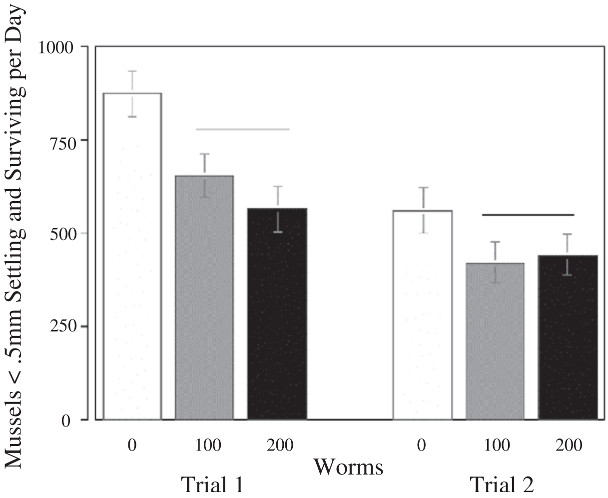

Fig. 5. Number of plantigrades <0.5 mm settling and surviving per day during trials one and two. Bars indicate lack of significant difference by ANOVA.

There was a significant negative effect of worm density ($F = 8.3117$, $df = 2$, $p \leq 0.0009$), and trial ($F = 23.657$, $df = 1$, $p \leq 0.0001$) on the densities of small plantigrades, but no interactive effect ($F = 1.448$, $df = 2$, $p \leq 0.246$, Fig. 5). The average settlement density and standard deviation of plantigrades was 36.5 ± 5.8 (S.E.) mussels/cm^2/day during trial one and 23.2 ± 5.8 mussels/cm^2/day during trial two.

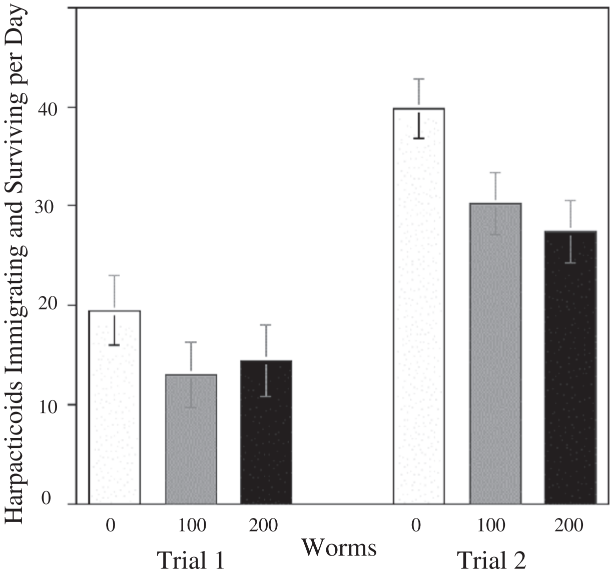

Fig. 6. Number of harpacticoids immigrating and surviving during trials one and two. Bars indicate lack of significant difference by ANOVA.

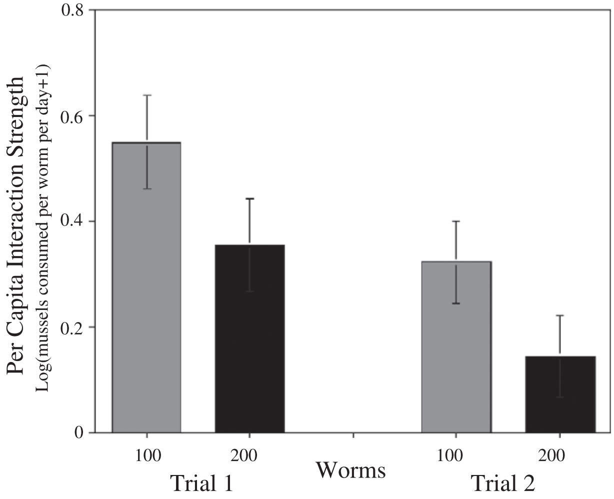

Fig. 7. Interaction strength as defined by number of mussels consumed per worm per day during trials one and two. Data are log($x + 1$) transformed. Note the decrease of interaction strength both at higher worm densities and during trial two. Settlement during trial two was significantly lower than trial one.

Harpacticoid migration rate differed during the two trials as well ($F = 39.208$, $df = 1$, $p \leq 0.0001$) with a mean of 19.5 harpacticoids/day during trial one and 39.6 harpacticoids/day during trial two. While there was an effect of worm density ($F = 4.3784$, $df = 2$,

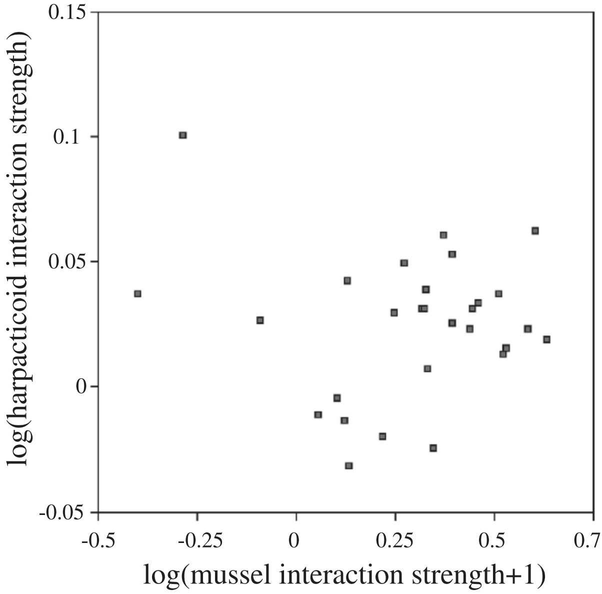

Fig. 8. Worm–mussel interaction strength vs. worm–harpacticoid interaction strength. Data is log($x + 1$) transformed. The regression is not significant ($p \leq 0.78$).

$p \leq 0.018$) on harpacticoid immigration and survival, there was no interaction between trial and worm density ($F = 0.613$, $df = 2$, $p \leq 0.546$, Fig. 6).

Interaction strength between small mussels and worms data $\log(x+1)$ transformed varied by trial ($F = 7.07$, $df = 1$, $p \leq 0.013$) and worm treatment ($F = 5.095$, $df = 1$, $p \leq 0.032$), but lacked an interaction effect between the two factors ($F = 0.010$, $df = 1$, $p \leq 0.923$ Fig. 7). Mussel recruitment was lower during the period of lower interaction strength. Interaction strength of worms on harpacticoids $\log(x+1)$ transformed was not affected by any of the worm treatments, trial, any interaction effect, nor was it related to worm–mussel interaction strength ($p \leq 0.78$, Fig. 8).

Regression analyses indicated that worm density had no effect on the number of small plantigrades ($p \leq 0.476$,) or harpacticoids settling and surviving ($p \leq 0.645$) in the August field trial. Both plantigrade settlement and copepod immigration densities were lower for this trial (3.9 ± 2.3 mussels/cm^2/day and 0.7 ± 0.4 harpacticoids/cm^2/day) than in either of

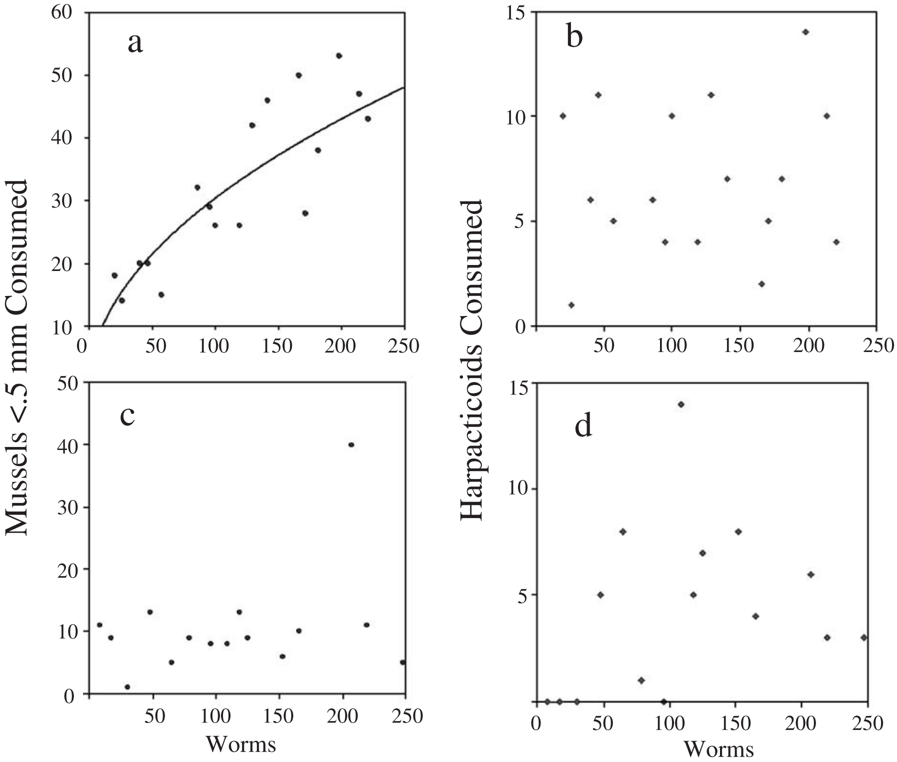

Fig. 9. Number of dead prey items vs. number of worms in experimental jars. In the summer (a and b) with water temperatures from 13 to 15 °C, note that the relationship between number of worms and dead mussels (a) plateaus at higher worm densities ($p \leq 0.0001$, $r^2 = 0.761$, $y = 0.2994x^{\cdot 0.503}$). There is no significant relationship between number of dead harpacticoids vs. number worms in experimental jars lab trial one (b). During the fall trials (c and d), water temperatures were from 3 to 5 °C. There was no significant relationship between either worms and dead mussels (c) and worms and dead harpacticoids (d).

the previous mid-summer trials. Similarly, during the October trials with mussel settlement densities of 0.7 ± 0.2 mussels/cm^2/day and 0.3 ± 0.1 harpacticoids/cm^2/day, worm density was shown to have no effect on the number of small plantigrades ($p \leq 0.48$) or harpacticoids ($p \leq 0.5$).

3.3. Lab trials

During the summer lab trial, worm density was positively related to the number of consumed plantigrades, though this curve leveled off at higher worm densities ($p \leq 0.0001$, r^2=.761, $y = 0.2994x^{0.503}$, Fig. 9a). There was no relationship between worm density and dead harpacticoids ($p \leq 0.65$, Fig. 9b). We feel that this is due to worm positive phototaxis giving harpacticoids a behavioral escape at the bottom of the jar and may have introduced experimental error. We removed this artefact in the second lab experiment, and consider this initial harpacticoid data as inconclusive, most noticeably as it does not match patterns seen in the field. The number of worms was negatively related to per capita interaction strength ($p \leq 0.016$, $r^2 = 0.314$, $y = 0.185 - 0.005x$, Fig. 10). The total number of plantigrades in a jar was unrelated to both the number of dead plantigrades ($p \leq 0.32$) and per capita interaction strength ($p \leq 0.793$). Worm density had no significant effect on number of consumed plantigrades ($p \leq 0.237$, Fig. 9c) or harpacticoids ($p \leq 0.313$, Fig. 9d) during the October trial.

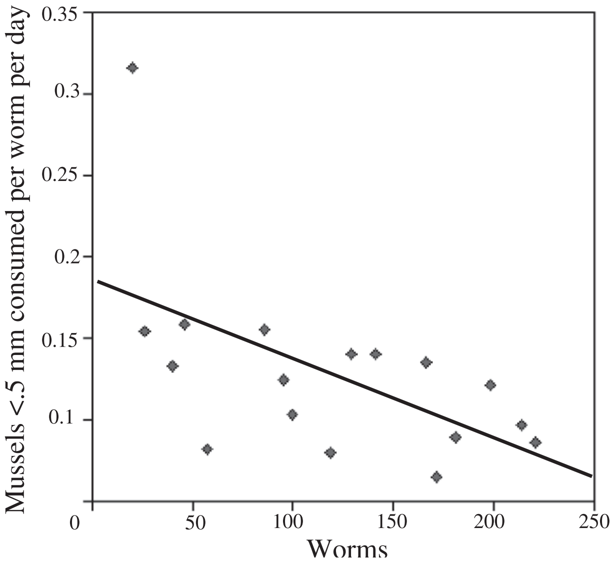

Fig. 10. Interaction strength as defined by number of mussels consumed per worm per day during lab trial one. The correlation is negative.

4. Discussion

4.1. Worm distribution

Worm distributions on filamentous algae seemed to strike a balance between access to light and inability to persist in physically disturbed environments. In the shallows (i.e. 0–3 m) on filamentous algae, it is likely that worms were easily dislodged by disturbance by wave action from any algae on which they settled. *C. convoluta* may be uncommon in the 9–12-m range due to their positive phototaxis (Rivest et al., in preparation). Maximum mean worm densities in both Broad Cove and Smith's Cove was 3 worms/cm^2, somewhere in the 3–9-m range. While there was a significant difference between sites with respect to the depth at which maximum average worm densities occurred, more sites of differing exposure need to be sampled in order to determine what abiotic conditions determine where maximum worm densities occur.

Worm distribution on bladed algae appeared to depend mostly on wave exposure. Worm densities on bladed algae did not vary with depth within sites. There was a significant difference in worm abundance, however, between wave-exposed and protected sites. The lower densities at exposed sites may be due to physical disturbance. Bladed algae are subject to much more algal movement than filamentous algae (Byrnes, personal observations) in high wave energy environments. This action may dislodge worms, lowering their densities in wave-exposed sites.

Worm densities were also low on the majority of hard substrates. The single exception to this was 9–12 m in Broad Cove, an urchin barren. All other sites had either at least moderate algal cover or were littered with shell hash from recently consumed adult mussel beds (Byrnes, personal observation). Physical disturbance at these sites, in this case the scouring of rock by algal fronds or sand moved by wave energy, may be acting to dislodge these small mobile soft-bodied flatworms. The ability of *C. convoluta* to aggregate may be improved in urchin barrens where substrate movement is minimal. Barrens may also be a preferred habitat by *C. convoluta* as there is no algae obscuring light, and thus providing worms with maximum sunlight exposure.

The abundance of *C. convoluta* undoubtedly varies over time. While this study did not take temporal variation of worm density into account, we observed a temporal difference in the colonization rates of worms in field trials. Plates were not subjected to heavy colonization in June, but plates in late August and September were quickly colonized by high densities of worms. Preliminary field collection of worms during May and June yielded few worms larger than 1 mm (Byrnes, personal observation), although these collections were after a series of several spring storms. This contrasted sharply with both our observations later in the summer as well as observations by Rivest et al. (1999), which were taken in 1996–1998 at the Isles of Shoals during August and early fall. Worm populations were found to be robust on urchin barrens outside of the Damariscotta River in Maine during February and March 2002 (Byrnes, personal observation). This pattern supports the evidence from summer distributions that physical disturbance, along with light, is responsible for regulating worm densities year-round.

4.2. Factors affecting worm impact

While presence of harpacticoid copepods as alternate prey items did not alter worm impact on mussels during the summer, intraspecific competition, functional response, and water temperature all seem to limit worm impact on settling mussels.

Two lines of evidence point to worms competing intraspecifically for prey items. The gradual tapering of the predation curve during lab trial one (Fig. 9) coupled with the negative correlation between worm density and interaction strength during this trial (Fig. 10) suggests that worm populations may be subject to intraspecific competition for food. This inverse relationship between worm density and per capita interaction strength is seen in the field at both high and medium mussel settlement rates (Fig. 7). An increase in the number of worms causes a decrease in worm–mussel interaction strength in both the lab and the field, indicating that competitive processes are occurring. We can discount the argument of worms merely spatially displacing settling mussels, as this would have resulted in markedly different mussel settlement and survival differences between 100 and 200 worm treatments.

Intraspecific competition may have important implications for changes in worm population densities over time. Rivest et al. (1999) reported densities of up to 19 worms/cm^2 on an urchin barren. This density was not found in any of our surveys, even as a maximum value. If this maximal density reflected mean worm densities during the 1999 field season, then worm populations appear to have declined markedly. A mean density of approximately 3 worms/cm^2 on filamentous algae is far from ecologically insignificant, but is so different from the 1999 densities as to suggest some processes, such as density-dependent competition, disturbance, or disease, have caused a decline in overall worm densities. A wide variety of marine invertebrate populations are similarly regulated by strong density-dependent competition (Hughes and Griffiths, 1988; Menge, 1976; Connell, 1961). Given the abundance of small mussels (authors, personal observation), indicating a large 1999 cohort of juveniles, food limitation during the previous summer would not have been a factor.

No interaction strengths were found to be greater than five mussels consumed per worm per day in the field. Mean interaction strength peaked at 2.2 mussels consumed per worm per day during field trial one in the 100-worm treatment with an outlier of 4.67 mussels consumed per worm per day. Looking at the percentage of settlement failure (Fig. 11), we see that mean worm impact then peaks at $35 \pm 7\%$ mortality in the trial one 200-worm treatment. While Mamkaev and Seravin (1963) noted that a large individual *C. convoluta* could consume up to 10 harpacticoids, it would seem that *C. convoluta* in the Gulf of Maine are consuming no more than five mussels per worm per day at most, and usually less. While competition may raise the settlement rate at which worms can achieve this maximum interaction strength, satiation at high mussel settlement rates would limit worm impact through prey swamping (Murdoch and Oaten, 1975).

In addition, worm predation on mussels was lower during periods of decreased settlement. For example, there was no significant alteration of mussel settlement and survival due to *C. convoluta* in the trials that occurred at the lowest settlement rates (field trials three and four). Both trials had settlement rates of less than 4 mussels/cm^2/day. This contrasts with the field trials one and two, each of which had settlement rates greater than 22 mussels/cm^2/day

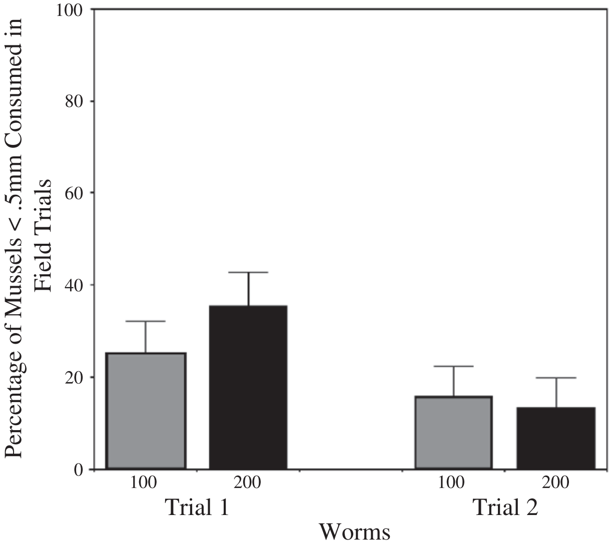

Fig. 11. Percentage of mussels consumed during field trials one and two. Highest mean settlement failure is 35% mussels consumed during trial one in the 200-worm treatment.

and significant alteration of mussel settlement and survival by worms. Field trial 3 occurred in late August while the water was still above 12 °C, discounting a temperature argument. We can therefore conclude that at low settlement rates, worm consumption of mussels is minimal, but increases dramatically above a certain threshold. Likewise, there is little significant interaction with harpacticoids when they are in low abundances.

Our data are consistent with a switch to either a third prey source (e.g. ostracods or gastropod larvae), or an increasing in reliance on worm endosymbionts. While many workers have taken the view that flatworm endosymbionts do not play a major role in worm ecological interactions (Douglas, 1992), this view is contested (McCoy and Balzer, 2001), and further light/dark experimentation with *C. convoluta* would be elucidative.

The cold-water lab trial demonstrated that at lower water temperatures, worms consumed fewer mussels. While worms were still exposed to direct sunlight, photoperiod and ambient light levels were most likely lower in October than July and August. The possibility of increased utilization of light by worm endosymbionts can therefore be discounted. While there were no treatments with more than 150 mussels in lab trial two, treatments with < 100 mussels in trial one still experienced significant predation. Fewer prey items provided can therefore be ruled out as an alternative explanation to the lack of significant predation in the second lab trial. Water temperature was allowed to drop to 2–3 °C during trial two, while flowing seawater around experimental chambers kept water temperature between 12 and 15 °C during lab trial one. This decrease in water temperature likely altered the metabolic rate of worms or triggered some other seasonal cue, either of which caused a decrease or complete cessation of feeding on mussels and harpacticoids.

Overall, competition will tend to raise the settlement rate at which satiation occurs. Impact will be minimal at low settlement densities, however, and water temperature may be positively correlated with satiation point, leading to a window of minimal impact during the winter and early spring.

4.3. Worm impact

Our field experiments showed an appreciable impact on juvenile mussel settlement at intermediate settlement densities. The impact can be as high as 35% settlement failure. The ultimate question we are asking, however, is how does this translate to changes in populations of adult mussel beds?

Studies have shown that mussels are subject to strong density-dependent mortality in the 0–1-year-old age class (McGrorty and Goss-Custardd, 1993), immediately after secondary settlement. Mussels in beds with fewer individuals tend to have higher growth rates (Petraitis, 1995). Observed worm impact peaked at only 35% settlement failure, but only when both the density of mussel settlement and abundances of worms were high. More commonly, low mortality of settling mussels due to *C. convoluta* should facilitate later survival and growth of secondary settling mussels. Coupling this with the fact that *C. convoluta* impact is both highly seasonal and is minimal on primary settling mussels at 0–3 m and below 9 m, it seems likely that adult mussel populations will be minimally effected by *C. convoluta* within the southern Gulf of Maine. This conclusion is supported by the presence of dense 1-year-old mussel beds observed around the Isles of Shoals in the summer of 2000, despite high worm densities in 1999. Whether impact will remain low if the worm invades southern warmer waters or if the Gulf itself experiences a warming event remains unknown.

5. Summary

During the summer of 2000, *C. convoluta* occurred in densities of up to 3 worms/cm^2 on filamentous algae at moderate depths, as well as densities of 5 worms/cm^2 on urchin barrens. Densities on other algae were apparently dependent on wave exposure. Worm–mussel interaction strength could be categorized by a type III functional response. This leads to a maximum impact at moderate settlement densities, but minimal impact at both low and high settlement densities. Maximum impact was estimated at 35% juvenile mussels consumed, but is typically lower. This could result in later reduction of density-dependent mortality in secondary settling mussels. This fact coupled with the high degree of seasonality of worm impact leads to the conclusion that *C. convoluta* is having a minimal impact on adult mussel populations around the Isles of Shoals in the Gulf of Maine.

Acknowledgements

This work would not have been possible without a grant from National Science Foundation for the Research Experience for Undergraduates program at the Shoals Marine Laboratory, the Brown University Undergraduate Teaching and Research Assistantship, the St. Anthony Educational Foundation, and the Andrew Mellon Foundation. Thanks also to Myra Shulman, Christopher Siddon, Douglas McNaught, Erika Brown, and Julie Ellis for the advice and help in the field. Thanks to Laura Hudson for her critical review of the manuscript. **[AU]**

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