

Parasitism and soft-bottom community structure: studies in a polychaete–amphipod system

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Impacts of the trematode parasite *Zoogonus rubellus* on individuals of its host, the infaunal sandworm *Nereis virens*, were explored to assess influences that parasites might have on the structure of soft-bottom infaunal communities. Parasites were common in sandworms collected from a mudflat in Maine, with prevalence reaching 100% for large, commercial-sized sandworms and intensities of infection often exceeding 100 metacercariae per host. Parasitism was determined to be costly as sandworms exposed to parasites in the laboratory had higher mortality and foraged less on a main prey item, the amphipod *Corophium volutator*, than unexposed controls. As *Nereis* and *Corophium* are key intermediate-level members in infaunal communities, it is argued that parasitism of sandworms might directly and indirectly influence the structure of soft-bottom communities.

INTRODUCTION

Researchers have long known that parasites can reduce the fitness of hosts and impact host populations (e.g. Mouritsen et al., 1998). At the community level, however, impacts of parasitism are poorly understood and until recently ecologists have ignored the possibility that parasites might directly and indirectly influence community structure in ways similar to impacts caused by physical stresses, predation, and competition (Poulin, 1999). In soft-bottom communities, impacts of parasites seem likely due to evidence that parasites influence host behaviour, life history, distribution, and population dynamics of infauna (e.g. McCurdy et al., 2000; McCurdy, 2001). Impacts of parasitism on community structure should be strongest in systems where parasitism is common, virulence is high, or when hosts function as key species in the community (Poulin, 1999).

Impacts of parasitism on the sandworm *Nereis virens* (Annelida: Polychaeta) and populations of its main prey item, the amphipod *Corophium volutator* (Crustacea: Amphipoda) were studied. Both species inhabit intertidal mudflats and sandflats in North America, northern Europe, and Japan (Commito, 1982; Shepherd & Boates, 1999). The *Nereis*–*Corophium* system is ideal for community-level studies because both species play key roles in maintaining the physical structure of mudflats and transferring energy among trophic levels. Specifically, *C. volutator* is the primary prey item for millions of migratory birds and juvenile fish, stabilizes mudflats via burrow construction, and feeds on detritus, algae, and bacteria (reviewed by Shepherd & Boates, 1999). *Nereis virens* forages on numerous species (including *C. volutator*) and serves as a prey item for bloodworms, fish, and shorebirds (Commito, 1982; Ambrose, 1984). Research on interactions between *N. virens*, *C. volutator*, and parasites is timely in that many populations of both species have declined in recent years, which in the case of *C. volutator* has been linked to

infections by trematodes (Mouritsen et al., 1998). *Nereis virens* is also harvested as bait (Shepherd & Boates, 1999).

We investigated impacts of the trematode parasite *Zoogonus rubellus* on survival and foraging behaviour of *N. virens* sandworms. Stunkard (1938) demonstrated that mud snails (*Ilyanassa obsoleta*) shed cercariae that infect sandworms as second-intermediate hosts (final hosts of the parasite include eels and flatfish). Little is known about infections of *Z. rubellus* trematodes in natural populations of sandworms, so our first objective was to characterize infections in sandworms at a commercially-important mudflat by assessing prevalence, intensity of infection, and relating infection status to host size (age).

In addition to characterizing infections of *Z. rubellus* in sandworms from the field, we conducted experiments in the laboratory to assess impacts of parasitism on survival and foraging activity of sandworms. Even small reductions in survival could reduce recruitment significantly because sandworms are semelparous and mature slowly (Brafield & Chapman, 1967). To assess whether foraging activity of sandworms was affected by parasitism, sandworms exposed to parasites and unexposed sandworms were housed experimentally with groups of amphipod prey. By using an experiment in the laboratory, changes in amphipod populations due to predation by sandworms vs mortality or emigration caused disturbance of burrowing sandworms could be separated (a concern in previous field studies, e.g. Commito, 1982). If parasitism is costly, it was predicted that infected sandworms would forage less on amphipods and impose lower rates of disturbance-related mortality on amphipods.

MATERIALS AND METHODS

Survey

To assess parasite loads in a natural population of *Nereis virens*, samples were collected from the intertidal mudflat at

Strawberry Creek, Great Island, Maine (43°49'N 69°58'W; see McCurdy, 2001 for a description of the site). Sandworms were collected from randomly-chosen 0.25×0.25 m patches by digging up to 50 cm deep during the day (10 July, 2001) and removing sandworms that were foraging on the surface at night (17 July, 2001).

Following their collection, sandworms were housed in filtered seawater (55- μ m mesh) at Bowdoin College's Coastal Studies Center. Sandworm size was assessed as wetmass and sandworms were housed without sediment for 24 h prior to weighing them to reduce variation in mass due to sediment ingested in the field. Each sandworm was dissected by cutting it into 1-cm segments and squashing segments between glass slides to look for metacercariae (McCurdy, 2001). For sandworms that weighed \leq 1 g the total number of metacercariae present were counted. However, for sandworms $>$ 1 g only whether or not infections were present was determined because the thickness of large sandworms and high intensities of metacercariae (often $>$ 1000) precluded accurate counts of trematodes. A logistic regression test was used to determine whether the likelihood that sandworms infected by metacercariae was related to wetmass. To assess whether intensity of infection was related to sandworm wetmass, a Spearman rank test was used because the assumptions of analysis of variance (ANOVA) were violated.

Experiments

Sandworms used in laboratory experiments were collected from the mudflat at Card Cove, Great Island, Maine (43°47'N 69°56'W) on 17 July, 2001. This site was chosen because it is located near Strawberry Creek (2.2 km distant), but preliminary collections of sandworms showed that background levels of *Zoogonus rubellus* were low at this site (likely due to low densities of intermediate-host snails; McCurdy, 2001). Only small adult sandworms were retained (first setigerous segment \geq 1 mm in width (Commito, 1982); mean \pm SE wetmass=0.22 \pm 0.03 g) because small sandworms were less likely to be infected by trematodes already (see Results). As a result, sandworms in our experiments had *very* low background levels of infection for their size (median \pm upper, lower quartiles =6 \pm 1, 11.5 metacercariae, N=12).

To infect sandworms with metacercariae of *Z. rubellus*, 100 adult *Ilyanassa obsoleta* ($>$ 14 mm; McCurdy et al., 2000) were collected from Strawberry Creek and housed in separate plastic cups at 24°C for 24 h (McCurdy, 2001). Each sandworm that was to be exposed to cercariae was then housed in a separate plastic cup with 140 ml of filtered seawater and 10 ml of seawater infested with cercariae taken from snails that had shed *Z. rubellus*. Unexposed controls were housed individually in cups with filtered seawater and given 10 ml of seawater collected from cups containing snails that did not shed cercariae.

Impacts of parasitism on survival of *N. virens* were assessed by housing 47 sandworms that had been exposed to cercariae and 46 unexposed controls in individual plastic cups containing seawater. These sandworms were then checked every 24 h to determine when each sandworm died, at which time it was dissected to measure its parasite load. Kaplan–Meier analysis was used to compare survival among sandworms exposed to cercariae

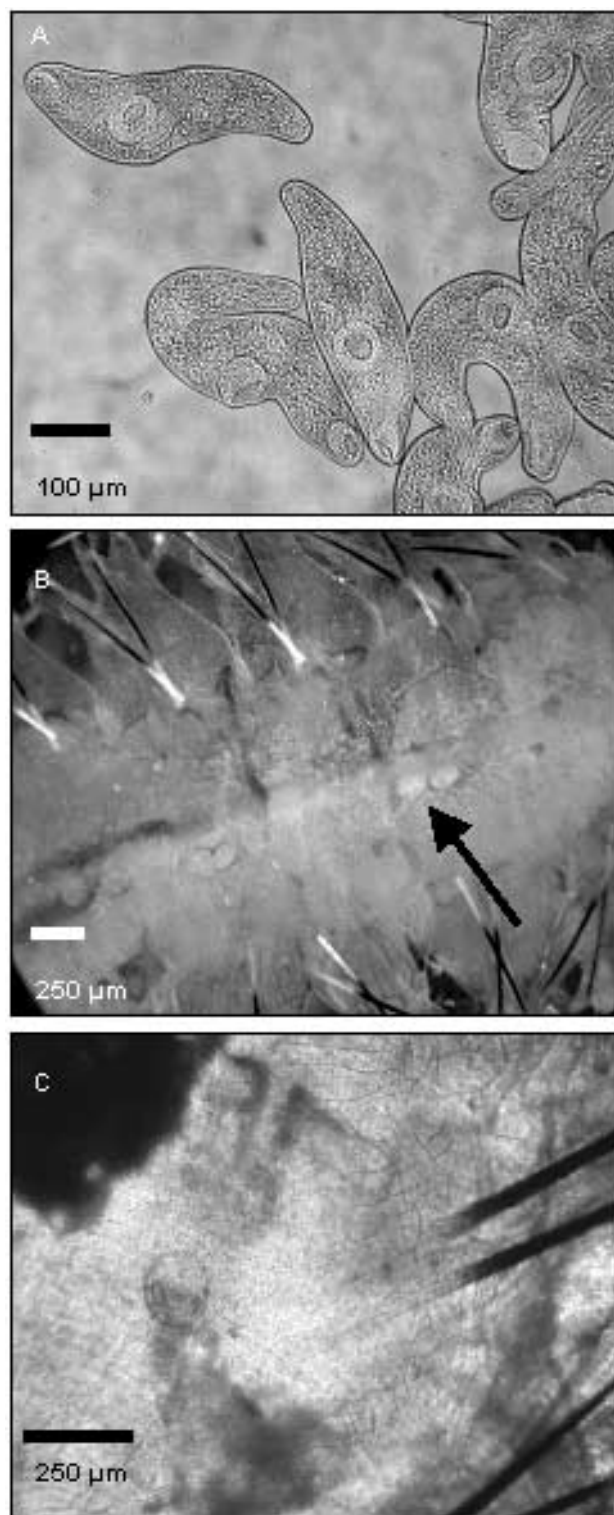


Figure 1. Micrographs of the trematode *Zoogonus rubellus* showing: (A) cercariae just released by the mud snail *Ilyanassa obsoleta*; (B) six metacercariae infecting a sandworm (*Nereis virens*) at 24 h post-infection (one indicated by the arrow); and (C) a metacercaria at 48 h post-infection infecting a parapodium of a sandworm.

vs unexposed controls and Cox's hazard regression was used to assess survival in relation to sandworm wetmass and intensity of infection (McCurdy, 2001).

To determine impacts of parasitism on foraging and disturbance-related mortality imposed by sandworms on

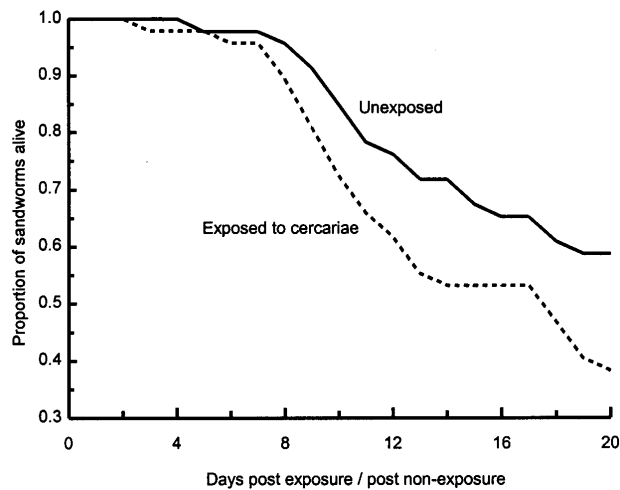


Figure 2. Cumulative survival curves for *Nereis virens* that were exposed to cercariae of the trematode *Zoögonus rubellus* in the laboratory vs unexposed controls.

amphipods, 12 sandworms exposed to cercariae and 12 unexposed sandworms were housed in the laboratory (as described above). At 24 h post exposure/non-exposure, each sandworm was then housed in a separate container lined with mud and filled with seawater (described in McCurdy (2001)). After allowing 24 h for sandworms to burrow, 30 similar-sized adult (5.5–6.5 mm) *Corophium volutator* were added to each container (amphipods were collected at Strawberry Creek by sieving; cf. Shepherd & Boates, 1999). Six containers were included where amphipods were housed without sandworms to account for sources of amphipod mortality, such as cannibalism. Each container was then covered with a 0.5-mm mesh screen to contain amphipods and containers were placed into a running seawater table (flow=0.11 s⁻¹; filtration=55 µm). After five days, numbers of amphipods that were consumed or died from other causes were recorded. Kruskal–Wallis tests were used to compare numbers of consumed and dead amphipods among treatments because assumptions of ANOVA were violated. Dunn's method (McCurdy et al., 2000) was used to compare group medians.

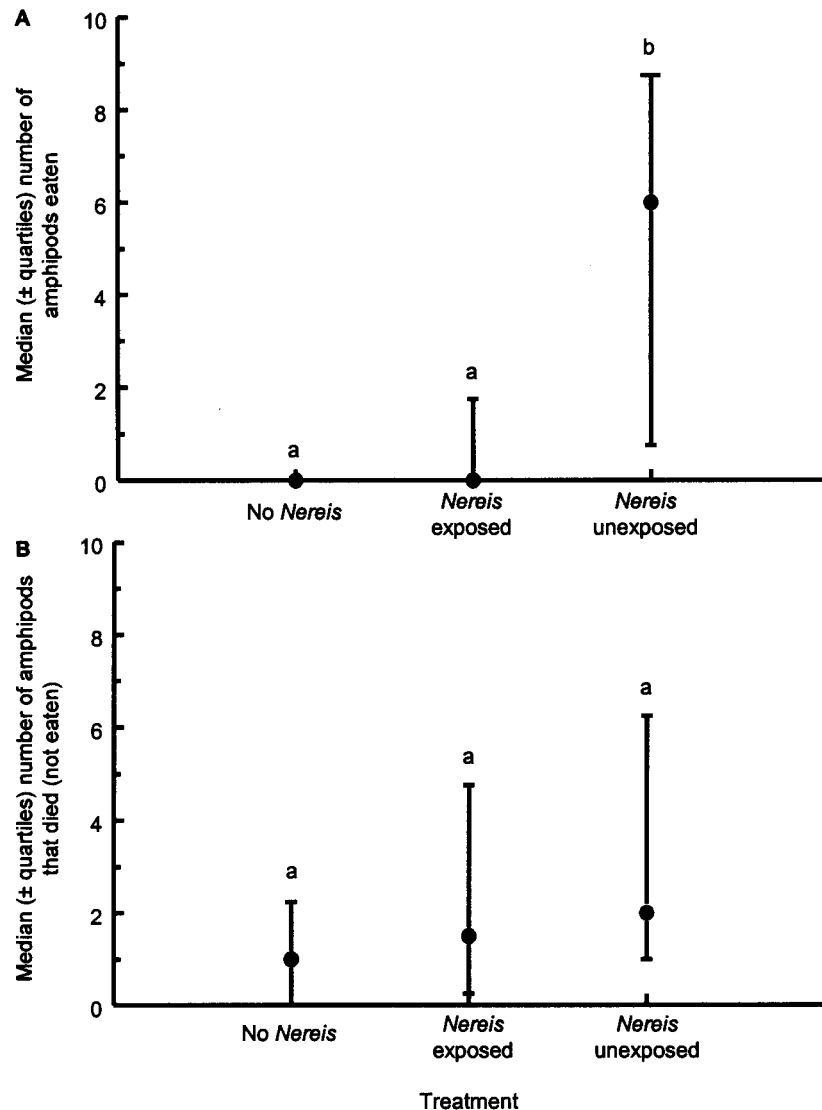


Figure 3. Median numbers of the intertidal amphipod *Corophium volutator* that (A) were eaten or (B) found dead from other causes after being housed alone (N=6), with a sandworm (*Nereis virens*) that had been experimentally exposed to cercariae of *Zoögonus rubellus* (N=12), or with an unexposed sandworm (N=12). Medians are based on replicate groups of 30 amphipods. Medians with the same letter are not significantly different from each other.

RESULTS

Survey

From our collections of *Nereis virens* at the Strawberry Creek mudflat, infections by *Zoogonus rubellus* were observed to be common in sandworms (overall prevalence=50.6%, N=81; prevalence in buried sandworms=41.1%, N=17; prevalence in sandworms on the surface=66.7%; N=64; Figure 1). Considering sandworm size, individuals of greater wetmass were more likely to be infected by metacercariae (logistic $\chi^2=7.35$, N=81, $P<0.01$). In fact, all sandworms with a mass ≥ 1.0 g (N=19) were infected by *Z. rubellus* (>500 metacercariae/sandworm). In cases where metacercariae were counted (sandworm wetmass <1.0 g), intensities of infection were also high (mean \pm SE=115.5 \pm 38.7 cercariae). Of these sandworms, those with greater wetmasses harboured higher intensities of metacercariae than those with lower wetmasses (Spearman's Rho=0.57, N=22, $P<0.01$).

Experiments

Survival of sandworms exposed to cercariae of *Z. rubellus* was observed to be lower than that of unexposed sandworms over 20 d in the laboratory ($\chi^2_{[1]}=3.8$, $P=0.05$; Figure 2). Of the sandworms exposed to cercariae, intensity of infection did not relate to survival ($\chi^2_{[1]}=0.1$, n.s.). Sandworm wetmass was also unrelated to survival ($\chi^2_{[1]}=2.1$, n.s.).

The number of *Corophium volutator* eaten in the foraging experiment differed among sandworms that were exposed to cercariae, unexposed sandworms, and the treatment where sandworms were absent (Kruskal–Wallis $\chi^2_{[2]}=20.3$, $P<0.001$; Figure 3). Specifically, fewer amphipods were eaten in containers where sandworms were exposed to cercariae than in containers with unexposed sandworms ($Q=3.54$, $P<0.002$) or containers where sandworms were absent ($Q=3.96$, $P<0.001$). There was no difference in the number of amphipods eaten in containers where sandworms were present, but exposed to parasites vs where sandworms were absent ($Q=1.08$, n.s.). The number of amphipods that died due to factors other than predation did not differ among treatments with sandworms exposed to parasites, unexposed sandworms, or lacking sandworms (Kruskal–Wallis $\chi^2_{[2]}=20.3$, $P<0.001$). Of the sandworms exposed to parasites, intensity of infection did not relate to either the number of amphipods eaten or those that died from other causes (model $R^2=0.03$, N=12, n.s.).

DISCUSSION

Survey

Trematode parasites were found to be common within a natural population of the sandworm *Nereis virens*, with prevalence among commercial-sized worms (>20 cm long) at 100% and intensities of infection often exceeding hundreds of metacercariae per sandworm. Such high prevalence of trematodes is typically uncommon among infauna that serve as second-intermediate hosts of trematodes (e.g. McCurdy et al., 2000; McCurdy, 2001), although periodic bouts of high prevalence have been observed in certain populations of amphipods (Mouritsen

et al., 1998). The observation of increasingly high prevalence of trematodes among larger sandworms may be explained as an accumulation of infections with sandworm age (e.g. McCurdy et al., 2000) or the possibility that larger sandworms simply represent larger targets for cercariae (McCurdy, 2001). Additional observations across larger spatial and temporal scales are required to discern general patterns of infection because prevalence of trematodes that infect infaunal invertebrates often fluctuates over space and time (Mouritsen et al., 1998; McCurdy et al., 2000).

Experiments

Parasitism was found to reduce survival of sandworms exposed to cercariae in the laboratory. Although preliminary, the fact that such a decrease in survival was observable after one exposure to parasites and after only 20 d suggests that parasitism is costly for sandworms. Direct costs to survival might be especially harmful to sandworm recruitment given the high prevalence and intensities of trematodes in nature (discussed above) and because sandworms are semelparous and require more than a year to reach maturity (Brafield & Chapman, 1967).

Parasitism was also associated with reduced foraging by sandworms on amphipods. In fact, foraging activity of infected sandworms did not differ from zero (i.e. treatment where sandworms were absent). It is doubtful that infected sandworms in nature stop foraging entirely on amphipods since they appear to survive long enough to acquire high parasite loads. Although such changes in behaviour could have been due in part to differences in food availability or handling stresses in the laboratory, the strength of the relationship observed suggests that parasitism does have the potential to impact on foraging by sandworms. Importantly, mortality of *Corophium volutator* was associated with predation by sandworms and not disturbance-effects as amphipods were more likely to be eaten when housed with uninfected sandworms. This result clarifies uncertainty in previous studies over the cause of decreased abundance of *C. volutator* associated with the presence of sandworms (e.g. Commito, 1982; Ambrose, 1984).

Despite evidence in infaunal systems of adaptive parasite-mediated changes in behaviour (e.g. McCurdy et al., 2000) and adaptive host responses to parasitism (McCurdy, 2001), decreased foraging activity among infected sandworms may be explained best as a side-effect of infection. This is because reduced foraging of sandworms would not appear to benefit parasites in terms of increased transmission rates to final-host fish (fish feed at or near the surface of mudflats, where sandworms usually forage; reviewed in McCurdy et al., 2000). Reduced foraging activity would also not appear to benefit hosts as it might leave less energy available to mitigate impacts of parasitism and for host reproduction.

Parasitism and community structure

In addition to impacts of parasitism at the individual and population levels, decreased survival and foraging activity of sandworms associated with parasitism could influence the structure of soft-bottom infaunal communities. Such consequences are expected because

sandworms are major predators on numerous infaunal species and they alter the physical structure of mudflats through their activities (e.g. experimental additions of *N. virens* are associated with reduced abundances of sedentary polychaetes, but increased abundance of copepods; Ambrose, 1984). Researchers have recently observed evidence of such direct impacts of parasitism on hosts following epizootics of trematodes in snails and amphipods (Mouritsen et al., 1998).

There is increasing evidence that parasites can also influence community structure indirectly by altering the outcome of competitive and predator–prey interactions between non-host species (reviewed by Poulin, 1999). Parasitism of sandworms might result in such impacts due to reduced foraging activity on *C. volutator*, which is a key intermediate-level species in soft-bottom communities (Ambrose, 1984). For example, reduced mortality of adult amphipods due to lower predation pressure from sandworms could, in turn, increase competitive pressure on other infauna, including intraspecific competition with juvenile amphipods (Wilson, 1989). In fact, numerous studies have shown that even subtle impacts on *C. volutator* populations have discernible impacts on populations of shorebird and fish predators, as well as on the physical structure of mudflats (e.g. Mouritsen et al., 1998). Abundances of *N. virens* may also influence populations of top-level infaunal predators common to our study sites, such as the bloodworm *Glycera dibranchiata* (Ambrose, 1984; Shepherd & Boates, 1999). Clearly, the role of parasitism in soft-bottom community structure is complex and requires further investigation, particularly in relation to recent impacts, such as baitworm harvesting (Shepherd & Boates, 1999). Studies that combine aspects of parasitism in conjunction with competition and predator–prey relationships should enhance efforts to conserve host and non-host species of ecological and economical importance.

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