Can Models of Soft-Sediment Community Structure Be Complete Without Parasites?[1]

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Synopsis. Most of the organisms that live in marine, soft-sediment environments are hosts for parasites. Rates of infection by micro- or macroparasites can be quite high, but vary in space and time. Despite the prevalence of parasites, their potential influence on soft-sediment communities is poorly understood. None of the conceptual models of soft-sediment community structure or dynamics published to date considers the impact of parasitism. A variety of potential direct and indirect effects of parasites on host populations and communities are discussed. The greatest challenge for future research in this area is the development of experimental methods for manipulating the abundance of parasites under field conditions.

INTRODUCTION

During the past two decades, considerable progress has been made in understanding the processes that structure assemblages of invertebrates inhabiting nearshore, soft-sediment environments. Early efforts sought a general explanation for observed discontinuities in the distribution and abundance of deposit- and suspension-feeders with sediment type (*e.g.,* Rhoads and Young, 1970; Levinton, 1972). Subsequent studies revised and expanded on this simple, trophic-based categorization, placing greater emphasis on variation in mobility (sedentary tube-builder *vs.* active burrower) and negative effects of adults on settling larvae (Woodin, 1976; Brenchley, 1981, 1982).

Throughout the late 1970s and 1980s, the focus of most ecological research in soft-sediment habitats shifted from the distribution and dynamics of functional groups of species (*sensu* Woodin and Jackson, 1979) to the mechanisms and strengths of interactions among particular species. Controlled field and laboratory manipulations were embraced as the method of choice. These experimental studies investigated intra- and interspecific competition, predation, biotic disturbance and refugia, factors affecting larval settlement and recruitment, and mechanisms of successional replacement (see Wilson, 1990, for a recent review). The direct negative effects of phys-

ical stress (*e.g.,* mortality due to heavy sedimentation [Peterson, 1985]) have been less extensively investigated, but a recent experimental study by Peterson and Black (1988) demonstrated that the level of mortality caused by sedimentation may depend on the prior history of competitive stress experienced by the buried organisms.

The above studies have examined an impressive array of interactions and taxa. Many of them have demonstrated strong effects of adult-adult and adult-larval biotic interactions, both competitive and predatory. Yet one potentially important factor has been overlooked in every investigation: the fact that an appreciable proportion of the organisms examined in these studies may have been infected by parasites. All the 'major players' in soft-sediment communities: the clams, snails, worms, crabs, amphipods, and seagrasses, are hosts for micro- and macroparasites (*sensu* Anderson and May, 1979; May and Anderson, 1979; Dobson and Hudson, 1986). There is nothing unusual about this omission. Of two recent books on the ecology of soft-sediment habitats, Gray (1981) fails to mention parasites, and Reise (1985) devotes only two sentences to the subject. General textbooks in marine ecology do not treat population and community-level effects of parasites in much greater depth. Valiela (1984) refers only to the impact of disease on sea urchin-kelp interactions; Levinton (1982) devotes three paragraphs to the general topic, but cites no specific studies.

The truth of the matter is that, while there is abundant evidence that parasites negatively affect individual hosts, there are only

a few well-documented cases of parasites causing large declines in natural host populations in soft-sediment environments. One of the best examples is the wasting disease that nearly eliminated eelgrass populations from the North Atlantic during the 1930s, and continues to cause localized dieoffs of eelgrass beds (Den Hartog, 1987; Short et al., 1987; Muehlstein, 1989). For most soft-sediment communities, however, we simply do not know what impact parasites are having. With the existing data we can begin by examining three more fundamental questions:

1) What are the primary parasites of soft-sediment organisms?

2) How prevalent are parasitic infections?

3) How might parasites affect host individuals, populations, and communities?

I will address these questions in turn with the aim of identifying some of the potential impacts of parasites on assemblages of organisms living in marine soft-sediment habitats. A complete review of the literature on host-parasite interactions in these habitats is beyond the scope of this paper.

WHAT PARASITES INFECT SOFT-SEDIMENT ORGANISMS?

Several excellent reviews offer a wealth of information on the parasites of soft-sediment organisms (Kinne, 1980, 1983; Rohde, 1982; Sindermann, 1990). Microparasites that infect soft-sediment organisms include viruses, bacteria, fungi, and a variety of protozoans. Macroparasites are represented by numerous taxa including acanthocephalans, cestodes, nematodes, and rhizocephalans, but digenetic trematodes are the most common metazoan parasites of soft-sediment invertebrates. The digenetic trematode life cycle is complex, typically including one definitive and two intermediate hosts. In marine environments, a bird or fish most commonly serves as definitive host for the adult fluke. Gastropods are the most common first intermediate hosts for pre-cercarial larval stages (sporocysts and rediae), but a few trematodes exploit clams or annelids as first intermediate hosts. A wide variety of organisms serve as second intermediate hosts for the encysted metacercarial stage of the digenean life cycle. These include gas-

tropods, clams, annelids, crustaceans, brachiopods, and sipunculans.

HOW PREVALENT ARE PARASITIC INFECTIONS?

Existing information is insufficient to answer this question with any degree of certainty for most natural populations of soft-sediment organisms. Information is most complete for commercially important species of oysters and crabs (Sindermann, 1990). High percentages (>50%) of oysters in certain beds can become infected by protozoans such as Haplosporidium nelsoni (Haskin and Andrews, 1988) or Perkinsus marinus (Andrews, 1988). Outbreaks of these disease organisms are often associated with particular levels of salinity and water temperature, and can cause high levels of mortality, sometimes exceeding 90% of the bed. Sporocysts of bucephalid trematodes can infect more than a third of the oysters in some localized inshore sites (see references in Table 13-10 of Lauckner, 1983). Prevalences of castrating infections by rhizocephalan barnacles in commercially harvested populations of blue crabs (Callinectes sapidus), sand crabs (Portunus pelagicus), and king crabs (Paralithodes spp. and Lithodes spp.) may exceed 50% (see references in Sindermann, 1990). Similarly, epicaridean isopods may infect and castrate >50% of the individuals in some commercially important shrimp populations (see references in Sindermann, 1990). Population outbreaks of nemertean worms that prey on the brood of some species of commercial crabs (e.g., Cancer magister, Wickham, 1986) can cause high rates of egg mortality.

Fewer estimates of parasite prevalence (% of hosts infected) and intensity (number of parasites per host) are available for the non-commercial host species that have been the primary subjects of experimental field studies (Wilson, 1990). Measurements of the prevalence of microparasite infections in populations of such species are especially limited. Rates of infection by macroparasites in particular host species have been documented in some detail due largely to the efforts of individual investigators. For example, Kuris and coworkers have estimated the prevalences of a variety of macro-

TABLE 1. *Prevalence of digenetic trematode, pre-cercarial larval infections in selected soft-sediment gastropod populations.*

Host species	Habitat	Number of samples (range of n)	Site	Percent infected		Reference
				Median	Range	
Batillaria minima	mangrove sand flat	8 (61–138)		34.2	1.4–100.0	Sousa, unpubl. data
Buccinum undatum	sand bottom (20–30 m depth)	11 (27–286)		17.0	10.0–23.0	Køie, 1969
Cerithidea californica	tidal mud/sand flat	187 (16–744)	muddy	21.0	1.7–91.1	Sousa, unpubl. data
			sandy	10.2	0.0–36.4	
Cerithidea pliculosa	mangrove channel	2 (101/282)		45.1	34.8–55.4	Sousa, unpubl. data
Hydrobia stagnorum	brackish pond	PS* (16,326)		37.8	—	Vaes, 1977
Hydrobia ulvae	marsh pool	8 (252–626)		?	11.0–33.0	Rothschild, 1941
Ilyanassa obsoleta	tidal mud flat	12 (353–1,153)		4.5	2.0–8.5	Miller and Northrup, 1926
Ilyanassa obsoleta	tidal mud flat	14 (144–586)	high	59.8	41.5–81.8	Gambino, 1959
			low	7.8	3.5–43.0	
Ilyanassa obsoleta (>1 cm only)	tidal mud flat	34 (300 each)	high	14.0	5.0–27.0	Sindermann, 1960
			low	2.0	0.0–5.0	
Ilyanassa obsoleta	tidal mud flat	56 (10–59)	zone a	10.0	0.0–60.0	Curtis and Hurd, 1983
			zone b	93.0	0.0–100.0	
Nassarius reticulatus	mud bottom	8 (200 each)	shallow	46.7	36.1–49.4	Tallmark and Norrgren, 1976
			deeper	≈2.0	—	
Olivella biplicata	sandy beach	1 (224)		36.2	—	Onuf, 1972
Pirenella conica (>6 mm only)	lagoonal sand/mud	41 (15–211)		33.0	0.0–83.0	Taraschewski and Paperna, 1981

* Only value for pooled sample reported by author.

TABLE 2. *Prevalence of digenetic trematode, pre-cercarial larval infections in selected soft-sediment bivalve populations.*

Host species	Habitat	Number of samples (range of n)		Site	Percent infected		Reference
					Median	Range	
Abra tenuis	mud flat	2	(72/500)		2.0	0.03–4.0	Campbell, 1985
Cerastoderma edule	estuarine mud/sand	28	(82–655)	muddy sandy	0.9 1.2	0.0–4.2 0.3–4.1	Sannia and James, 1978
Cerastoderma glaucum	brackish pond	PS*	(115)		1.7	—	Vaes, 1977
Gemma gemma	tidal sand flat	1	(824)		0.4	—	Stunkard and Uzmann, 1958
Hiatella arctica	tidal sand flat	2	(13/136)		9.9	0.4–15.4	Stunkard and Uzmann, 1958
Macoma inconspicua	tidal sand flat	PS	(1,138)		1.1	—	Ching, 1965
Mya arenaria	tidal sand flat	PS	(>1,000)		<0.3	—	Stunkard and Uzmann, 1958
Transennella tantilla (adults only)	tidal sand flat	1	(200)		39.5	—	Kabat, 1986

* Only value for pooled sample reported by author.

parasites in populations of the shore crab, *Hemigrapsus oregonensis,* at several sites along the Pacific coast of the U.S. The crab is sometimes collected for bait by fishermen, but is of little commercial value. Rates of infection and castration by epicaridean isopods range from 20–91% (Kuris *et al.,* 1980). Parasitic nematodes infect 13–64% of the crabs (Poinar and Kuris, 1975), and occasional outbreaks of nemertean worms prey heavily on brooded egg masses (Shields and Kuris, 1983).

Larval digenetic trematodes are not only the most common, but also the most comprehensively studied parasites of non-commercial soft-sediment invertebrates. Consequently, I will restrict my discussion to this group of parasites for the remainder of this section. Even published data on rates of larval trematode infection must be interpreted with caution. Traditionally, most marine parasitologists have devoted their efforts to the elucidation of parasite life cycles, and have only rarely investigated population or community-level effects of parasites. As a result, investigations of trematode life cycles typically have been based on small, non-random samples, and published descriptions of such cycles either contain no estimates of overall infection rate or what amount to subjective estimates

without supporting data. In some studies, sizeable samples of hosts have been examined, but usually little or no effort is made to collect random samples, or sampling procedures are simply not described. There is no way of knowing if such samples are representative of the size/age structure of the host population; most haphazardly collected samples will be biased towards larger individuals. This sampling procedure also makes it impossible to assess levels of small-scale, spatial variation in infection rates because the sample is often collected over a broad area or, alternatively, from one spot. Further, a single sample provides no information on temporal variation in parasitism rates. An additional problem arises when infection rates by trematodes are determined by cercarial shedding rather than by dissection. The shedding method can greatly underestimate true levels of infection because immature infections that are not releasing cercariae go undetected (Curtis and Hubbard, 1990).

In spite of the problems described above, a brief look at some selected examples of data on trematode infections in gastropod, bivalve, and polychaete populations is instructive (Tables 1–4). In these cases, infection rates were determined by dissection. The prevalence of pre-cercarial larval

TABLE 3. *Prevalence of digenetic trematode, metacercarial larval infections in selected soft-sediment bivalve populations.*

Host species	Habitat	Number of samples (range of n)	Percent infected		Reference
			Median	Range	
Abra tenuis	mud flat	2 (72/500)	73.0	46.0–100.0	Campbell, 1985
Cerastoderma edule	mud flat	PS* (?)	100.0	—	Bowers and James, 1967
Cerastoderma edule	mud flat	PS (3,600)	100.0	—	Lauckner, 1971
Gemma gemma	tidal sand flat	?	≈10.0	—	Stunkard and Uzmann, 1958
Hiatella arctica	tidal sand flat	?	≈20.0	—	Stunkard and Uzmann, 1958
Macoma inconspicua	tidal sand flat	PS (1,138)	72.0	—	Ching, 1965
Mya arenaria	tidal sand flat	4 (?)	?	43.0–100.0	Uzmann, 1951
Mya arenaria	tidal sand flat	?	≈25.0	—	Stunkard and Uzmann, 1958

* Only value for pooled sample reported by author.

infections in soft-sediment gastropod populations can be quite high (Table 1). Within a host species, rates of infection may vary considerably in space and time. As noted earlier, gastropods can also serve as second intermediate hosts, but I could not find any studies that quantified the levels of metacercarial infection (either prevalence or intensity) in a soft-sediment species. Available data suggest that soft-sediment bivalve populations are less infected by pre-cercarial trematode larvae than are gastropod populations, but there are exceptions to this pattern, *e.g.*, *Transennella tantilla* (Table 2). On the other hand, bivalve populations are often heavily infected by metacercariae (Table 3). Lauckner (1980, 1983) summarizes many additional estimates of the prevalence of trematode infections in gastropod and bivalve populations.

Reports of trematode infections in polychaetes are rare. Whether this is because such infections are truly uncommon, or because they have not been looked for, is unclear. Two studies report high frequencies of metacercarial infection in polychaetes, and a third found a low percentage infection by pre-cercarial larval stages (Table 4). Although the data are obviously scant, the pattern of trematode infection in polychaete populations appears more similar to that of bivalve than gastropod populations, *i.e.*, high frequencies of metacercarial infection and relatively infrequent infections by pre-cercarial stages.

The metacercariae of microphallid trematodes are common parasites of soft-sediment crustaceans including amphipods, crabs, and shrimp, but there are relatively few quantitative estimates of their prevalence in natural host populations (see examples in Overstreet, 1983; Sparks, 1985; Lauckner, 1987; Sindermann, 1990).

POTENTIAL EFFECTS OF
PARASITES ON HOST INDIVIDUALS,
POPULATIONS AND COMMUNITIES

Parasites can have a variety of direct effects on their hosts; they can alter host physiology, reproduction, growth, and behavior. Tissue damage or disruptions of physiological processes by parasites may be sufficient to kill the host. Microparasite infections appear to cause rapid, direct mortality more often than do infections by macroparasites such as trematodes. Molluscs fully infected by larval trematodes can survive for long periods of time in nature, up to several years in some cases (*e.g.*, the salt marsh snail, *Cerithidea californica*, Sousa and Gleason, 1989; Sousa, unpubl. data). However, infections by either micro- or macroparasites can cause high rates of host mortality when acting in concert with environmental stress (Lauckner, 1980, 1983; Sousa and Gleason, 1989).

Another potential source of host mortality attributable indirectly to parasites involves modifications in host behavior induced by infection. Such behavioral modifications may make the infected host more vulnerable to predators (Holmes and Bethel,

TABLE 4. *Prevalence of digenetic trematode, pre-cercarial (PCL) and metacercarial (MCL) larval infections in selected soft-sediment polychaete populations.*

Host species	Habitat	Parasite taxon (stage)	Number of samples (range of n)	Percent infected		Reference
				Median	Range	
Eupomatus dianthus	mud flat	PCL	1 (1,500)	0.8	—	Rankin, 1946
Nereis diversicolor	brackish pond	MCL	PS* (7,571)	>45.6	—	Vaes, 1977
Scoloplos fragilis	tidal mud flat	MCL	3 (30 each)	100.0	40.0–100.0	Brown and Prezant, 1986

* Only value for pooled sample reported by author.

1972). Depending on the life cycle of the parasite, this predation may or may not result in parasite transmission. One often cited example of parasite-induced modification of host behavior is surface crawling by the clam, *Macoma balthica,* when infected by sporocysts and metacercariae of the digenetic trematode, *Parvatrema affinis* (Swennen, 1969; Hulscher, 1973; Swennen and Ching, 1974). The clam usually lives completely burrowed in the sediment, but infected individuals move to the sediment surface during low tides where they produce conspicuous crawling tracks. Interestingly, Hulscher (1973) found that oystercatchers, important predators on the clam and the definitive hosts for *P. affinis,* sometimes reject infected clams. Hence, it is unclear whether this behavioral modification results in increased transmission of the parasite. Lauckner (1983, pp. 749–750) discusses other examples of trematodes causing surfacing and track-digging by clams. Similarly, heavy metacercaria infections of *Himasthla elongata* in the foot of the clam, *Cerastoderma edule,* greatly reduces the clam's ability to burrow (Lauckner, 1983, p. 704). Whether such modifications result in increased predation is unknown, but in studies of other clam species, individuals living closer to the sediment surface have been shown to be more vulnerable to snail (Peterson, 1982) and crab predators (Blundon and Kennedy, 1982). In any case, animals at the surface will be more vulnerable to environmental extremes.

As mentioned earlier, we have very little idea how much of the mortality suffered by soft-sediment organisms can be attributed to parasitism as compared to abiotic stresses, predation, and competition. Observed mass mortalities of certain species with no obvious cause are often ascribed by default to some unknown disease organism. Such statements should obviously be viewed with some skepticism. Lauckner (1984, 1987) has attempted to estimate the lethal impact of trematode infections on North Sea tidal flat populations of the periwinkle, *Littorina littorea,* from changes in host size-distributions over time, but the validity of such indirect analyses rests on numerous untested assumptions about rates of host recruitment and growth, as well as other sources of mortality.

While it is often difficult to state with any certainty the degree of mortality caused by parasites, the negative effect of parasitism on host reproduction is relatively unambiguous. Most infections by micro- and macroparasites cause marked reductions in the reproductive output of invertebrate hosts, often resulting in complete and permanent castration (Lauckner, 1980, 1983; Overstreet, 1983; Sousa, 1983; Sindermann, 1990). For example, Kabat (1986) estimated about a 30% loss of reproduction to parasitic castration in a population of the clam, *Transennella tantilla.* While negative adult-larval interactions may greatly reduce recruitment of some soft-sediment invertebrates (Woodin, 1976; Peterson, 1979), castration of adults by parasites prevents larvae from being produced in the first place. Generally, rates of parasitism and, therefore, castration increase with host size/age so the reproductive output of the most fecund portion of the host population (Peterson, 1983) is most negatively affected by parasites. While castrated individuals no longer contribute directly to population growth, they continue to consume resources

that might otherwise be used by uninfected individuals and, thereby, may affect population and community dynamics.

One can speculate about any number of additional indirect effects of parasitism on soft-sediment community structure and dynamics. Differential parasitism of particular species may alter their competitive interactions with others if survival or reproduction of the infected species is reduced (*e.g.*, Park, 1948). Parasitism might alter host movement and spatial distribution (*e.g.*, Curtis, 1987, 1990) or feeding rate (*e.g.*, Meuleman, 1972). Either of these effects could alter interactions between the host species and others in the community. For example, the mud snail, *Ilyanassa obsoleta*, reduces the abundance of postlarval and juvenile infaunal invertebrates and surface-dwelling tubiculous polychaetes, gastropods, and harpacticoid copepods (Hunt *et al.*, 1987). It can also reduce microalgal biomass and productivity (Pace *et al.*, 1979; Connor *et al.*, 1982). At the same time, *I. obsoleta* populations are often heavily infected by larval trematodes (Table 1), and at least some of these parasites are known to alter the snail's movements (Curtis, 1987, 1990) and may affect other aspects of the snail's behavior, including feeding. Therefore, larval trematode infections could be mediating biotic interactions between *I. obsoleta* and other species. However, none of the above studies of the impact of the snail on benthic assemblages investigated this possible influence of parasites, nor did any report the prevalence of parasites in the studied snail population.

When a host species constitutes an important component of a habitat's structure, reduction in its abundance by parasites may cause a variety of indirect effects on other species. For example, seagrass beds may serve as important refugia from predators for many infaunal species (*e.g.*, Peterson, 1982; Peterson *et al.*, 1984, and references therein). In addition, invertebrate larvae or suspended food may be trapped in the beds by the baffling action of the seagrass blades (Peterson, 1986). Whatever the mechanism generating higher abundances of infauna in seagrass beds, the loss of seagrasses to wasting disease (Den Hartog, 1987; Short *et al.*,

1987; Muehlstein, 1989) should have a large influence on infaunal communities. This expectation is supported by Stauffer's (1937) and Rasmussen's (1977) descriptive accounts of the dramatic changes in habitat features and fauna that followed the destruction of eelgrass beds in the northeastern United States and Denmark, respectively, during the 1930s. I know of no modern quantitative studies of changes in community structure resulting from recent seagrass dieoffs.

CONCLUSIONS

The primary purpose of this essay is to drive home the point that ecologists working in soft-sediment habitats should, at the very least, screen their study organisms for the presence of parasites. It is quite conceivable that parasites could be influencing the intra- and interspecific interactions of these species, as well as their responses to physical stresses. An honest answer to the question which titles this essay is: we simply do not know. With few exceptions, available data are insufficient to tell whether parasites exert an additive negative effect on populations of soft-sediment organisms (Holmes, 1982). In other words, we do not know if the elimination of parasites would alter host population dynamics or community structure.

Bearing this in mind, one of the greatest challenges for future research on soft-sediment, host-parasite interactions is to develop methods of manipulating parasite abundance, as we do the abundances of predators or competitors. Manipulating characteristics of host populations such as density or size-structure is relatively straightforward, but the infective stages of most parasites are microscopic and cannot be easily excluded or added. For digenetic trematodes, one solution might be to manipulate the abundance of the previous host in the life cycle. For example, if snails are the host of interest, one could attract or repel fishes or birds, which are definitive hosts, to or from certain areas, thus altering the local abundance of infective eggs and miracidia. If the second intermediate host is the one of interest, one could manipulate snail abundance, and thereby the local concentration of cercariae.

Such experiments will not be easy, and arti-
factual influences will have to be carefully
controlled for. Obviously, future progress
towards an understanding of the role of par-
asites in soft-sediment communities rests
on creative experimental solutions to the
basic problem of manipulating parasite
abundance.

Finally, study of the structure and
dynamics of parasite populations and com-
munities themselves represents an exciting
avenue of future research (Esch *et al.*, 1990).
Parasites are as much a part of soft-sedi-
ment communities as their free-living hosts.

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