Effects of the macroalgae, *Ulva*, on the relative distributions of two mud flat bivalve congeneres and their dead shell material

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Abstract

The green macroalgae, *Ulva expansa*, covers much of the lower tidal mud flat during summer months in Northern California. This bloom often results in the smothering of filter feeders and bivalves, including *Transennella confusa* and *T. tantilla*. I surveyed areas on the mud flat with varying amounts of *Ulva* for the presence of dead and living *Transennella*. No living representatives of either species were recovered from areas with dense *Ulva* cover. *T. confusa* dominated areas completely free of *Ulva*, whereas *T. tantilla* existed in greater numbers under sparse cover. This suggests that *T. confusa* and *T. tantilla* actually occupy slightly different habitats. Physiological tolerances to different conditions or selective predation may mediate this partitioning of habitat. Articulated shell remains represent a constant proportion of live *T. tantilla*. Very few dead, articulated *T. confusa* shells were recovered. This probably had to do with the primary causes of mortality in areas where *T. confusa* live. This study shows many significant and almost significant trends relating to the distributions of live and dead *Transennella* shells. It appears that the causes of these interesting correlations could easily be tracked down in fully replicated and controlled studies.
Introduction

Tidal mud flats support a wide array of infaunal and epifaunal invertebrates. The interactions between infaunal species is generally limited to indirect competition stemming from the destruction of burrows through bioturbation (Ronan 1981). Recent studies, however, have shown that seasonal interactions with macroalgae may have a more direct effect on infauna (Everett 1994 & 1991).

Transitional areas in habitats can serve as sources of valuable information concerning the organisms whose distributions are limited by the transition. Biological and physical factors that negatively affect an organism are often concentrated in transitional zones of their habitat. This can result in interesting gradients leading from the prime habitat, through the transition, and into markedly less fit habitat (Krebs 1994). One such transition zone may be present at the borders of seasonal algal mats on mud flats.

The green macroalgae, *Ulva expansa*, blankets mud flats during summer months (Everett 1991). The duration of its presence most likely depends on nutrient availability due to local upwelling (Soulsby et al. 1985, Bach & Josselyn 1979, Perkins & Abbott 1972). Everett (1991) found that seasonal *Ulva* blooms had dramatic effects on mud flat infaunal community structure. The lophophorate, *Phoronopsis viridis*, and the bivalve, *Macoma nasuta*, both suffered in areas of algae cover. Other studies have also shown the ability of algal cover to smother or inhibit settlement of bivalves (Perkins & Abbott 1972).
Lower grain sized sediment tends to be both more nutrient enriched and less oxygenated than sediment of larger grain size (Krebs 1994). In a student report, grain size analysis led the researchers to hypothesize that the small mudflat clams of the genus *Transennella* prefer sediments above .175mm in size (Leavitt 1981). Lower energy environments are prone to both smaller sediment grain size and *Ulva* accumulation on mud flats. The presence of *Ulva* generally results in an even lower energy environment below the mat, and can therefore lead to a build-up of even smaller sediments (Frostick & McCave 1979). Through this process, correlations between *Ulva* cover and grain size amplify the effect of low energy sediment sorting. This may be one mechanism by which *Ulva* decreases the fitness of an area for some bivalves.

The small clams, *Transennella confusa* and *Transennella tantilla*, live in the top few centimeters of sediment in tidal mud flats (Harline & Miller 1995). They are mainly deposit feeders at the sediment-water interface, but may also participate in some suspension feeding (Everett 1994, Maurer 1967). Yearly variation in their densities on the flats can range from hundreds to none per 10cm core (Everett 1994, Grosholz 2000). Understanding issues concerning *Transennella* is of particular importance considering the recent introduction of the predatory green crab (*Carcinus maenas*) to mud flats (Grosholz 2000). Very little published information exists concerning the ecology and distributions of *T. confusa* and *T. tantilla* despite their ease of accessibility and high abundance.

Harline and Miller (1995) looked for variation in the distributions of these clams over differing tidal heights. *T. confusa* dominated most areas until lower tidal levels were reached. At that point *T. tantilla* attained slightly higher densities. The surveys, however, were conducted at the relatively large interval of one sample per 20 meters.
Whereas tidal height changes extremely slowly over distance on the flat, other environmental factors such as transition to *Ulva* cover or shift in sediment size, can change much more quickly. For this reason, it is suspect to assume that the changes in distributions as seen here are due to tidal height and not more subtle, localized changes in habitat structure.

Preliminary data has led researchers to theorize that *T. tantilla*, may be physiologically different from *T. confusa* such that it can better tolerate certain stresses (T. Grosholz unpublished data). This means that while both *T. confusa* and *T. tantilla* should decline in numbers as habitat fitness decreases, *T. tantilla* may decrease at a slower rate and remain at higher numbers than *T. confusa* in areas of intermediate fitness. The results of Harline and Miller could be explained by this phenomenon if the change from *T. confusa* dominance to *T. tantilla* dominance correlated to a change from higher to slightly lower habitat fitness.

Since the presence of *Ulva* on the flats is variable and results in decreased fitness for *Transennella* (Everett 1994), the seasonal mats provide an excellent medium for testing the relative responses of *T. confusa* and *T. tantilla* to stress. I set out to compare the distributions of these two species in areas varying in *Ulva* cover, and later sediment type. I thereby hoped to learn the relative tolerances of these two species to less than ideal conditions.

Studies on bivalve shell taphonomy have shown that, especially in low energy environments, dead shells are rarely transported very far after the death of the clam (Best & Kidwell 2000, Parsons-Hubbard et al. 1999, Frey et al. 1988, Beckvar 1988). Physical processes also seem to have little affect on shell articulation after death (Best & Kidwell
Therefore, if disarticulated shell remains are found, it can be assumed that predation caused shell separation and not postmortem physical processes (Best & Kidwell 2000). Predators of *Transennella* on the mud flats leave only crushed shell material (T. Grosholz unpublished data), so the presence of articulated *Transennella* shells can be attributed to death by means other than predation. I monitored the distributions of articulated and disarticulated *Transennella* shell remains in order to gain insights into causes of mortality at the different levels censused.

**Methods**

The experiment was conducted in the Bodega Marine Reserve in Bodega Harbor, CA. The tidal flat in this area forms a point that extends out from the salt marsh and is bordered by a small channel on one side, and a larger, dredged channel on the other. Dense *Ulva* lines the flat along the area where it meets the small channel. Using a ten centimeter core to four centimeters deep, two transect surveys were performed along this mat of *Ulva* near the salt marsh. In each transect, three cores were taken so that one came from underneath dense *Ulva* (100% cover), one came from the edge of the mat where the *Ulva* was sparse (approx. 50% cover), and one came from an area with no *Ulva* (Fig. 1). The cores were then run through a 1mm sieve in the field and the contents bagged for later review.

In the lab, the sieved core samples were examined for *Transennella* shells. First, articulated shells were separated from disarticulated shells and sorted by species so they could be counted. Next, 20 articulated shells of each species were randomly selected and
examined for living tissue. If there were less than 20 articulated shells for a species, all shells were examined. The percent of living clams in these sub-samples was used to estimate the number of living and dead clams represented by the articulated shells. Disarticulated shell halves were also counted by species.

At the edge of the *Ulva* bed furthest from the salt marsh, the sediment outside the algal mat seemed particularly muddy, or similar to the sediment often found below *Ulva*. It was speculated that this area had either previously been subject to *Ulva* cover, or was prone to lower energy sediment sorting due to its slightly lower tidal position. Since very small sediment grain size is also suspected to negatively affect *Transennella*, four more cores were taken in this area. Two cores came from the edge of the *Ulva*, and two came from well outside the *Ulva* (Fig. 1).

These cores were sieved in the field and *Transennella* shells were quantified in the lab as above. Once lab analysis of the shells was completed, the samples were placed in vials with 70% ethanol for storage. Chi square tests and ANOVA were used to assess the significance of differences in samples.

**Results**

As expected the transects showed a negative affect of *Ulva* on both species of *Transennella* (Fig. 2). Clam densities decreased significantly from areas absent of *Ulva* to areas with a sparse mat (Chi Square p<.025). No living clams of either species were found under dense *Ulva*.

Transects 1 and 2 revealed a shift in species dominance between areas absent of an algal mat and areas sparsely covered in algae (Fig. 3). Though both species were
negatively affected by *Ulva* presence, *T. tantilla* suffered significantly less mortality than *T. confusa* in areas of intermediate cover (Chi Square p<.025*, p<.001**). *T. tantilla* dominated all four samples taken from transects 3 and 4 (Fig. 4).

Throughout all samples in which *T. tantilla* dominated *T. confusa*, clam densities of each species represented a constant proportion of one another (Fig. 5). Densities of the two species were significantly positively correlated (ANOVA p<.05).

Articulated *T. tantilla* shells were quite common in the samples, but very few articulated *T. confusa* shells were found (Fig. 6 & 7). Disarticulated shells made up 91% of dead *T. confusa* shells recovered, but only 54% of dead *T. tantilla*. Dead, articulated *T. tantilla* shells represented a function of live *T. tantilla* present (Fig. 8, ANOVA p<.05). No such relationship existed between live and dead *T. confusa* (Fig. 9).

**Discussion**

This study confirmed the negative effect of *Ulva* on both species of *Transennella* as seen by Everett (1994) (Fig. 2). That *T. tantilla* responds less dramatically to increase in *Ulva* cover (Fig. 3) raises many questions about the ecological roles of these two species. Interspecific competition is probably not involved in this case since the flats have previously supported much higher densities of both species than seen in this study (Everett 1994). Grosholz (unpublished data) suggests that this difference in response corresponds to the physiological capabilities of *T. tantilla* to handle conditions unacceptable to *T. confusa*. Such an explanation is congruent with the data collected in this experiment, but proving this hypothesis requires much more information.

Comprehensive physiological data on both species may help to explain the potential
resistance of *T. tantilla* to what otherwise seems to be poor conditions. Previous studies have suggested that densities of predatory crabs and snails are affected by the *Ulva* (Harline & Miller 1995, Everett 1994), and the effects of algal mats on bird predation remains unknown. Without testing the influence of predation over different areas, it can not be ruled out that it plays an important role in shaping the distributions of *Transennella*.

Dead shell material looked at in this study implies that predation holds a high level of importance in areas absent of *Ulva* (Fig. 6&7). Almost no articulated shells of *T. confusa* were found. Such shells would not be expected to travel far postmortem. Therefore, the dominance of disarticulated shells suggests that living *T. confusa* residing outside *Ulva* are subject to high levels of predation. The relatively high number of dead articulated *T. tantilla* shells implies that this species is more prone to smothering as a means of mortality. This seems logical since the highest numbers of *T. tantilla* were found in areas of patchy *Ulva* and/or very small sediment size.

Perhaps *T. tantilla* are selected for over *T. confusa* by certain predators. If these predators preferred to forage in areas absent of *Ulva*, then *T. tantilla* may actually gain some amount of refuge in areas with a sparse algal mat. The opposite could also be true if selective predation was operating on *T. confusa* in areas of sparse *Ulva*. Harline and Miller (1995) found no preference between species in predation by the moon snail (*Polinices lewisi*), but birds and crabs could be good candidates for this theory. Any number of simple experiments would serve to narrow down the possibilities involving variation in predation.
It is curious that only disarticulated *T. confusa* shells were recovered from areas of dense *Ulva* (Fig. 6). What happened to the live clams represented by those dead shells? If they were killed off by the invasion of *Ulva* their shells should have remained articulated. This leaves 2 possibilities. *Transennella confusa* may have lived in these areas at one time, but suffered from increased predation associated with the *Ulva* bloom. This would require predation to be both selective over *T. tantilla* and extremely intense, so that the *Ulva* did not have time to smother any clams. Considering the dramatic effect that *Ulva* is known to have over *Transennella* (Everett 1994), it seems unlikely that predators would be able to increase at such a rate that they beat out the smothering effect of the algal mat.

This leaves the possibility of shell transport. The impact of shell transport by physical processes has frequently been denounced as relatively unimportant in marine environments (Best & Kidwell 2000, Parsons-Hubbard et al. 1999, Frey et al. 1988, Beckvar 1988). I suspect that the case may be slightly different for tiny, disarticulated *Transennella* shells. Wave forces caused by the frequent winter storms of Northern California could combine with tidal fluctuation to influence the distribution of disarticulated or fragmented *Transennella* shells. When the tide lowers to areas containing shell pieces, storm waves can actually break over the surrounding sediment. The resulting physical disturbance should be more than enough to dislocate loose, disarticulated *Transennella* shells. This phenomenon may partially account for the distributions of disarticulated shells for both *T. confusa* and *T. tantilla* observed in this study. Marking and tracking *Transennella* shells, especially around periods of stormy conditions, could show that the Bodega Harbor mud flat exemplifies one of the first
places on record where physical processes dramatically influence shell distributions of dead clams.

Grain size analysis was not included in this study due to time constraints. Though *Ulva* still showed a negative effect on both species in transects 3 and 4, *T. tantilla* dominated samples outside the algal mat as well as at the edge (Fig. 4). Since the most notable difference between these samples and the equivalent ones in transects 1 and 2 is sediment size, it seems quite likely that grain size does impact *Transennella*. The larger numbers of *T. tantilla* in these smaller grain areas leads me to hypothesize that *T. confusa* is less tolerant to decreasing sediment size. Since macroalgal mats often correlate to the deposition of smaller grained sediments (Frostick & McCave 1979) this could explain the absence of *T. confusa* from areas of sparse *Ulva*.

In order to more clearly assess whether or not habitat partitioning between the two species was present throughout all samples, I rated each core by the presence of features most known to affect *Transennella*. Each core received a number between 1 and 10 so that increasing number correlated firstly to increasing *Ulva* cover, and secondarily, to decreasing sediment grain size observed. Previous studies would predict, therefore, that increasing number represents less preferable conditions for *Transennella* (Everett 1994, Leavitt 1981). The densities of each species were then plotted over this habitat range (Fig. 10). The resulting curves show clear habitat partitioning. *Transennella confusa* densities quickly drop off as habitat rating increases. *Transennella tantilla* densities actually rise at first before dropping off much later. The curve representing *T. confusa* proved significant to p<.025 (ANOVA). The curve for *T. tantilla* was not significant (p<.2 ANOVA), but a greater sample size would likely increase the correlation. This
represents some of the first clear evidence pointing towards distinct ecological
differences between these two outwardly similar species. Though the variables focused
on in this experiment, \textit{Ulva} cover and sediment size, seem to play important roles in
couraging this habitat partitioning, the exact mechanisms of their influence and the
impact of predation and other factors remains unknown.

There seems to be a wealth of information concerning subtle, but important
ecological differences between \textit{T. confusa} and \textit{T. tantilla} that has yet to be exposed in
published literature. Mortality on the mud flat including predation and smothering is
such that the comparison of dead shell material serves as an accurate representation of the
primary forces affecting \textit{Transennella} over different areas. By looking more closely at
the distribution of dead shell material and isolating variables including sediment grain
size, predation, and physiological differences, the causes of the habitat partitioning
evident in this study could quickly be tracked down.

**Acknowledgments**

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MBQ students, and the BML staff for their support over the course of the quarter.
References


Figure 1  The study site showing the Ulva bed and the locations of the 10 cores taken in 4 transects. There was only subtle change in tidal height over the sample area with transects 3 and 4 slightly lower than 1 and 2. The sediment outside the Ulva in transects 3 and 4 was noticeably smaller grained than that outside the Ulva in transects 1 and 2.

![Transect and Core Locations](image)

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<th>Clam Abundance in Absent, Sparse, or Dense Ulva</th>
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Tc Ulva Absent  ▢  Tc Ulva Sparse  □  Tc Ulva Dense
Tt Ulva Absent  □  Tt Ulva Sparse  ▢  Tt Ulva Dense

Figure 2  Abundance of each species in absent, sparse, and dense Ulva. No living clams were found in dense Ulva. The negative effect on both species in sparse Ulva was significant. (Chi Square df=1, p<.025)
**Figure 3** *T. confusa* dominated areas absent of *Ulva*, whereas *T. tantilla* dominated areas of sparse *Ulva*. (Chi Square df=1, p<.025*, p<.001**)

**Figure 4** *T. tantilla* dominated *T. confusa* in all samples from transects 3 and 4. The similarity of samples from areas without *Ulva* to those from areas of sparse *Ulva* cover in transects 1 and 2 implies either previous *Ulva* cover in this area, or a negative affect due to small grain size.
Figure 5 Areas dominated by *T. tantilla* showed a significant positive relationship between the abundances of the two species (ANOVA p<.05). Not enough data points were collected to formulate a correlation between species abundances in areas of *T. confusa* abundance.
Figures 6 & 7  Full data showing live, dead articulated, and dead disarticulated clams. Ninety-one percent of dead *T. confusa* shells were disarticulated. Only 51% of dead *T. tantilla* were disarticulated.

Figures 8 & 9  Dead articulated *T. tantilla* shells reflected densities of live *T. tantilla* (ANOVA p<.05). No significant relationships existed between live and dead *T. confusa*, probably due to the low number of articulated shells found. This suggests that *T. confusa* is more subject to predation as a means of mortality and *T. tantilla* is more subject to smothering.
Figure 10  Clam abundances with increasing Ulva cover and decreasing sediment size are plotted. Tc curve is significant to $p<.025$ (ANOVA). There seems to be an element of small-scale habitat partitioning between species. Selective predation by an important predator and/or physiological differences may be responsible for this trend.