Impacts of habitat features and predation on distributions of mudflat clams

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University of California, Los Angeles
Marine Biology Quarter 2000
OBEE 106 & 165
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Abstract

Though the congeners *Nutricola (=Transennella) confusa* and *Nutricola tantilla* occupy an important ecological niche on mudflats, there is little published information concerning their population dynamics. We sought to determine what causational factors influence shifts in the relative distributions of these clams. Twelve cores were taken from Westside Park in Bodega Bay Harbor, California, in areas varying in macroalgal cover by *Ulva expansa*. Presence of the macroalgae, *Ulva*, heavily affected both species, but a steeper negative response in *N. confusa* populations was noted. There was also a significant increase in the relative number of *N. confusa* disarticulated shells when *N. confusa* decreased in dominance. Juvenile *Cancer magister* (Dungeness crabs) are unique predators of these clams in that they live among the *Ulva* and leave disarticulated shells when foraging. We therefore hypothesize that selective predation by *C. magister* on *N. confusa* is responsible for the shifts in relative abundances between *Nutricola* spp. noted. We examined the transport of dead shells in the field to determine if shell material could be considered an accurate tool in surveys. Dead shell material was not transported by tidal flow or wave action, which means its presence is an accurate representation of clams that previously lived in specific areas on the mudflat. Variations in sediment grain size were also examined in order to eliminate them as a controlling factor between *Nutricola* spp. distributions. There was no difference in response observed between *N. confusa* and *N. tantilla*. Juvenile *Cancer magister* were used in a laboratory feeding experiment to determine if *N. confusa* and *N. tantilla* are treated differently as prey. Though large, juvenile *C. magister* did not exhibit any selective predation between *Nutricola* spp., small, juvenile *C. magister* selectively preyed on *N. confusa*. Therefore, selective predation by small, juvenile *C. magister* is most likely limiting the distributions of *N. confusa* relative to *N. tantilla* in areas around *Ulva*. 
**Introduction**

The brooding, congeneric bivalves *Nutricola (= Transennella) confusa* (Gray) and *Nutricola tantilla* (Gould) are common among infaunal assemblages of mudflats on the west coast (Asson-Batres 1988, Everett 1994). These small clams, ranging from 1 to 7 mm, play an important role in tidal flats by serving as the primary food source for many birds, crabs, and snails (Leavitt 1981, Asson-Batres 1986, Ruiz 1987, Everett 1989, Harline and Miller 1995, Grosholz et al. 2000). In spite of being very abundant and easily accessible, little published information exists concerning the population ecology of these species. What few observations have been made are mainly based on un-replicated sampling that gives little insight into what factors control population dynamics (Gray 1982, Leavitt 1988, Everett 1994, Harline and Miller 1995). There seems to be a general consensus throughout these studies that the relative densities of *N. confusa* and *N. tantilla* do change significantly over different areas of the flat, but the reasons for these shifts in dominance are widely speculative and unconfirmed.

Gray (1982) and Leavitt (1988) suggested that sediments of certain grain sizes might have different effects on *N. confusa* and *N. tantilla*. Gray (1982) hypothesized that *N. confusa* better tolerates larger grain sizes than *N. tantilla*. Leavitt (1988) felt that both species respond negatively to small grain sizes. The conclusions reached in both studies are mainly based on anecdotal reports and little attempt was made to quantify or replicate the observations.

In a preliminary study on the Bodega Harbor mudflat (Schinske 2000), the effect of the seasonal macroalgal mats, *Ulva expansa*, was examined on each species (see also Everett 1994). This study found that densities of both species are negatively correlated
with *Ulva* cover, but that *N. confusa* responds more negatively than *N. tantilla*. The results also suggested that the monitoring of dead shell material might serve as a good way to compare the causes of mortality over different areas of the mudflat, and thereby show if predation on *Nutricula* differed between species.

Juvenile dungeness crabs (*Cancer magister* Dana) are unique among predators of *Nutricula* spp. in that they generally do not consume any shell material and leave one half of the shell fully intact and disarticulated (Asson-Batres 1986). *Cancer magister* settles primarily during the early summer and selects sandy areas with an over story of macroalgae above all other habitat types (Poole 1965, McMillan et al. 1995). Juveniles have been shown to use *Nutricula* spp. as a main component of their diets, and years of particularly high *C. magister* settlement can severely deplete populations of these clams (Asson-Batres 1986, Everett 1989). Their unusual feeding tactics may allow dead shell material to serve as an indirect measure of different types of mortality on the mudflat.

Dead articulated shells are left after “natural” or non-predatory deaths and disarticulated shell halves are left behind due to predation by *C. magister* (Asson-Batres 1986). Schinske (2000) found that a decrease in the relative density of *N. confusa* correlated to an increase in disarticulated *N. confusa* shells, and therefore a probable increase in predation by *C. magister* on this species. However, a wider array of samples is needed in order to confirm this trend. It is also necessary to test dead shell transport on the mudflat if the monitoring of shells is to be considered an accurate assessment of clam death in specific areas.

Since *C. magister* settle at a set annual time (Poole 1967), concentrate themselves in areas of macroalgal cover (McMillan et al. 1995), and prey heavily on *Nutricula* spp.
(Asson-Batres 1986, Everett 1989), it seems that they could easily cause a shift in relative species abundance around Ulva if one species of clam was preferred. We hypothesize ($h_{a1}$) that selective predation on the part of juvenile C. magister is responsible for the differences in response to Ulva observed between N. confusa and N. tantilla (Schinske 2000). A laboratory feeding experiment was used to determine if C. magister treat N. confusa and N. tantilla equally as prey items ($h_o$). The reliability of dead shell counts as an indicator of predation on the mudflat was also tested by measuring the amount of shell transport due to tidal flow and wave action. We further sought to determine if sediment grain size plays a role in the shifts in abundance in our samples ($h_{a2}$). Through this combination of field and laboratory work, we hoped to determine what environmental differences between habitats and predator-prey interactions cause shifts in dominance between N. confusa and N. tantilla.

**Materials and Methods**

**Field Surveys**

Our study site was located near the boat ramp of Westside Park, Bodega Bay, CA (Fig. 1), approximately 0.4 km north of the site described in Schinske (2000). By using a different site we hoped to: 1) confirm density correlations with Ulva and dead shell material at a second site, and 2) search for the small, introduced clam, Gemma gemma, and a new, undescribed species to see if their presence influences Nutricola densities around Ulva. Sediment cores were taken from 12 locations, four from each of three habitat types: Ulva absent, edge of Ulva bed, and Ulva dense. The cores had a diameter of 11.5 cm and a depth of 3 cm. Each row of cores was separated by 10 m. While in the field, the cores were run through a 1 mm sieve to extract clams. The sieve contents were
then placed in labeled bags and brought back to the lab. The number of live clams and
dead articulated and disarticulated shells were counted for each species. Linear
regressions were used to test the relationships of live clam populations with the presence
of Ulva cover and the abundance of dead shells. Analysis of variance was performed to
determine if this information differed significantly from surveys at the Schinske (2000)
site. Live clams were then retained for use later in the study.

Twenty-five live N. confusa and 25 N. tantilla of varying sizes were set aside for
allometric comparisons between species. Standard lengths and depths were measured for
each clam (Fig. 2). The wet tissue mass was then indirectly estimated by subtracting the
weight of the empty shell from the total weight of the live clam with tissue. Linear
regressions were applied to length vs. depth and length vs. tissue mass measurements for
the two species. Analysis of covariance and the test of homogeneity were used to test the
differences in the relationships between species. Log / log regressions of clam length vs.
tissue weight were also calculated for both species. This resulted in a linear curve by
which we could calculate the average tissue mass for clams of each species used in
feeding trials with Cancer magister.

Sediment grain size analysis

Sediment samples were obtained from each of the twelve coring sites near the
boat ramp. These samples were taken back to the lab and dried in a convection oven
overnight. The dried sediment was then crushed into individual grains of sediment. Each
sample was run through a 1.0 mm sieve to eliminate shells from sediment. Next, the
samples were put through a series of six sieves ranging from 0.045 to 0.5 mm. The series
of sieves were placed on an automatic rocker for ten minutes. After this process, the
sediment remaining in each sieve was weighed and recorded according to specific size classes. The total weight of each sample was calculated in order to obtain the percentage weight for each size class. The upper limit of each size class was multiplied by the percentage of material in that size class to obtain a measurement in percent mm units. The mean grain size was then calculated by adding these values and dividing by 100. The statistical test of homogeneity was conducted to see if densities of the two species responded in the same way to the differences in mean grain size.

Shell Transport

Shells of both *N. confusa* and *N. tantilla* were painted with red oil-based spray paint and allowed to dry. Fifty to 60 articulated and 60-70 disarticulated shells were placed within the sediment at each of three sites on the mudflat within a 15 cm quadrat. These sites were 0.73 m above MLLW. Each site was marked with a stake that was placed a meter away from the site to avoid flow disturbance. We returned to the site of shell deposition after one full tidal cycle. During this time, sustained wind velocities reached 20 mph with 36 mph gusts out of 80 degrees (ENE). As a result of the intense winds, the waters were unusually turbulent which represents an extreme in the wave conditions for our study environment.

In order to calculate shear velocity ($u^*$), tidal flow was measured at two of these sites, three hours into a strong ebbing tide going from a high of 1.98 m above MLLW to – 0.18 m below MLLW. Shear velocity is a measure of the fluctuations in velocity near the bed. With a large enough shear velocity, particles on the bed will be set into motion (Denny 1988).
The measurements of flow velocity were obtained by injecting fluorescein (1g/1L salt water) into the water column at specific heights (0.2 cm – 25 cm) above the bed. The flow of the fluorescein was calculated as the time it took the dye to travel 0.20 m away from the site. The profile of velocity measurements above the bed was used to calculate u* values (Denny 1988).

*Predation by Cancer magister*

A laboratory experiment was conducted to test the foraging behavior of juvenile *Cancer magister* for *N. tantilla* and *N. confusa*. The control and all three treatments were conducted in 8 black square tanks each measuring 18 cm x 18 cm x 15 cm. Due to that *C. magister* is a nocturnal feeder and are most active at night (Asson-Batres 1986), all treatments were run for 12 hours at night in the dark. The tanks contained 3 cm of sediment with 9.7 cm water depth. Water was supplied by a flow-through, filtered sea water system at the Bodega Marine Laboratory. Each tank consisted of separate flow to ensure identical conditions. The sediment used in the experiment was obtained from the same locations as the clams. It was run through a 1 mm sieve to partially remove any organisms and was frozen overnight to further exclude organics. All clams used for our control and treatments were placed at approximately the same depths in sediment, thus eliminating prey burial depth as a factor that may influence predator foraging decisions (Smith et al. 1999).

Eight crabs were obtained for our experiment by seining and hand catching in Campbell Cove, Bodega Bay, California. The same 8 crabs were used for the three treatments, with consistent 48-hour starving periods in-between treatments. Crabs ranged
from 40.5 mm to 79.5 mm (CW including 10th anterolateral spines). All crabs were sexually immature from instars VI to IX (Poole 1965).

The control accounted for any dead or crushed clams that might occur due to causes besides the crab, and tested the accuracy in our ability to recover all clams when sieving. Fifty clams of each species were set in a checkerboard arrangement (10 x 10) and replicated 4 times (Fig. 3).

The first treatment tested for the foraging behavior of *C. magister* when given a choice between the two clam species. 50 clams of each species were set up in a similar manner as the control (Fig. 3). Eight crabs were placed separately in the tanks.

Treatments two and three tested the foraging behavior of *C. magister* when given the same density of only one clam species. Treatment two contained 100 *N. confusa* and treatment three contained 100 *N. tantilla* (Fig. 3). The eight crabs were again distributed in separate tanks. After 12 hours, the crabs were removed and the sediment from each tank was sorted through a 1.0 mm sieve to recollect any remaining live clams and dead shell material.

We also sought to explore the energy maximization theory as a concept of optimal foraging theory by observing the foraging behavior of each crab for treatments 2 and 3. Optimal foraging theory states that a predator chooses its diet in order to maximize the net energy intake per unit foraging time (Schoener 1971, Charnov 1976, Pyke et al. 1977, Elner and Hughes 1978). Every animal is either a time minimizer or an energy maximizer. A time minimizer has a fixed energy requirement and requires extra time to perform other tasks. This means that the organism’s fitness is greatest when the time spent to gain energy is minimized (Schoener 1971). An energy maximizer has a fixed
amount of time and its maximum fitness is attained when it gains more food in an allotted
time (Schoener 1971). Therefore, whichever the method, the rate of energy intake while
foraging would be maximized by calculating the energy yield per handling time (Pyke et
al. 1977). This is referred to as the prey value, by which a predator is able to rank prey
types according to the energy maximization model (Elner and Hughes 1978, Juanes and
Hartwick 1990). Thus, the handling times for each clam species by each crab were
needed in order to determine any selectivity on the part of *C. magister*.

The observations were conducted using a red floodlight covered with red filter
paper (ROSCO #26) that transmits only light of 660-700 nm in wavelength.
Invertebrates have a very low relative sensitivity for wavelengths above 600 nm (Meech
and Brown 1976). Therefore, the color red, which is around 660-760nm in wavelength,
is not highly detectable by our crabs. From these observations, each crab’s handling time
(Ht) was obtained for both clam species as well as the rejection rate (number of rejected
clams / 1 clam consumed). Ht was measured from the time the crab picked up the clam
(chelipeds moved toward maxillipeds) to the time it was completely consumed. We
judged that the clam was completely consumed when the crab removed its chelipeds
away from its maxillipeds and started walking to find more clams. The total Ht was then
calculated:

\[ \text{Total Ht} = \text{Ht for clam consumed} + (\text{Ht for clam rejected} \times \text{rejection rate}) \]

In the above equation, it must be noted that the searching time for the clams is eliminated.
The burial depth of the individual clam is regulated when they were placed in the tank,
and the density of 100 clams in a small square tank allows the crab to encounter many clams merely by taking one walking step. The handling times obtained were then used to calculate the prey value, or profitability, for each clam using the equation noted by Charnov (1976):

\[
\text{Profitability (prey value)} = \frac{\text{energy gained}}{\text{time of feeding period}} = \frac{\text{mass of clam}}{\text{total Ht}}
\]

The mass of each clam species was obtained from the log/log regressions of clam length vs. tissue mass (discussed in Results).

**Results**

**Field Surveys**

*Gemma gemma* and the unidentified species were observed only at very high tidal levels at the boat ramp site. None were found in areas near *Ulva*, so they presumably have little or no influence on the interactions focused on in this study. Patterns in the densities of *N. confusa* and *N. tantilla* did not differ significantly between the boat ramp site and the Schinske (2000) site (ANOVA p=0.47). Clam populations were negatively correlated with increasing *Ulva* presence and *N. confusa* was more strongly affected than *N. tantilla* (Fig. 4). Cores from outside of *Ulva* had virtually an equal chance of *N. confusa* or *N. tantilla* being dominant (t-test p=0.52). At both the edge of the *Ulva* and in dense *Ulva*, however, *N. tantilla* always dominated *N. confusa* within a core.

A significant correlation was found between *N. confusa* presence relative to *N. tantilla*, and the number of *N. confusa* disarticulated shells (Fig. 5 linear regression
p<0.01). As *N. confusa* became relatively less dominant in our cores, there was an increase in the proportion of *N. confusa* disarticulated shells. No such relationship was observed between *N. tantilla* and its disarticulated shell material.

Allometric comparisons between the two species proved significant (Fig. 6a ANCOVA p<0.025, test of homogeneity p<0.05). *Nutricola tantilla* is relatively deeper than *N. confusa* for all but very large clam lengths. All clam sizes used in the laboratory predation experiment fell within the area of the regression where *N. tantilla* is deeper. Relationships between length and tissue mass for the two species followed the same trends where *N. tantilla* had a relatively higher tissue mass (Fig. 6b). However, these regressions were not significantly different, most likely due to the inherent error in our balance when measuring such small masses. The log / log regression equation for clam length vs. tissue mass gave a mass of .0098 g tissue mass for *N. confusa* and .0117 g tissue mass for *N. tantilla*. These masses correspond to the clam length of 4.5 mm, which is the average length of clam used in our *C. magister* feeding trials.

*Sediment grain size analysis*

A slight difference was observed between the sediments obtained from the various core sites. The test of homogeneity showed that there was no significant difference between the abundance of *N. tantilla* and *N. confusa* relative to mean sediment size (p=0.864). In other words, these two species act similarly to shifts in sediment grain size and this factor does not seem to limit the abundance of these two congeners relative to each other.
Shell transport

Despite the intensity of the winds, we found that the painted shells had not moved from the study sites. This is a clear indicator that even the small, dead shells of our species of clams do not move around during high wave action.

To check the hypothesis that shells do not move around on the mudflat due to tidal flow, we calculated the shear velocity within the boundary layer (u*) (Fig. 7a and b). The u* values at sites 1 and 2 were about 0.4 and 0.5 cm s\(^{-1}\) respectively. The u* values required to transport 0.5 mm grains typically begin at 1.0 cm s\(^{-1}\) (Pawlik and Butman 1993). Being that the shells of *N. tantilla* and *N. confusa* range from 1 to 7 mm in standard length, the u* values at our sites are not nearly high enough to move the shells from the bed. Therefore, our surveys of dead shell material provide an accurate representation of live clam distributions and abundance in our study areas.

Predation by Cancer magister

All 100 clams were recovered alive from each of the control tanks, confirming that the cause of clam death in the treatments was due to predation by *C. magister*. This also demonstrates the accuracy of the recovery process in locating all living clams left when ending treatments.

A significant correlation was found between the total number of clams eaten and the total number of disarticulated shells found in all three treatments (R\(^2\)= 0.91) (Figure 8). This serves as further proof that disarticulated shells found in nature represent a direct ratio of clams eaten by *C. magister*.
The raw numbers of clams eaten between smaller and larger juvenile *C. magister* for all three treatments were noted to be substantially different (Figure 9a and 9b). The crabs were thus divided into two categories: “small” crabs, which ranged from 40.5 mm to 48.1 mm, and “big” crabs, which ranged from 59.4 mm to 79.5 mm. According to Poole (1965), the small crabs were all in the 6th or 7th instar, while the big crabs were all in the 8th instar. Thus, all data will be shown according to these categories.

Among individuals of big crabs, there was no significant difference in the number of clams eaten between the three treatments (Comparison of Means, Fisher’s Least Squares Test, p > 0.6) (Figure 9b). There was also no significant difference found between the number of clams eaten by big crabs and the number eaten by small crabs in treatments 2 and 3 (Fisher’s Test, p > 0.5) (Figure 9a and 9b). Small crabs did not eat a significantly different amount of clams between treatments 2 and 3 (Fisher’s Test, p > 0.8) (Figure 9a). In contrast, the difference in the number of clams eaten by small crabs in treatment 1 in compared to the numbers eaten in treatments 2 and 3 was close to significance (Fisher’s Test, p < 0.16) (Figure 9a). The number of clams eaten by small crabs in treatment 1 was compared to the number eaten by big crabs in all treatments and was also found to be close to significance (Fisher’s Test, p < 0.1) (Figure 9a and 9b). The difference in the number of clams eaten in treatment 1 between small and big crabs was significant (Fisher’s Test, p = 0.04) (Figure 9a and 9b), implying that small crabs ate less clams when given a choice between two species.

The proportion of each clam species eaten in treatment 1 was calculated based on a simplified equation derived from the analysis of preference model by Chesson (1983 and 1989):
Proportion of *N. confusa* eaten = (# of *Nc* eaten) / (# of *Nc* and *Nt* eaten).

Small crabs ate a significantly larger average proportion of *N. confusa* than *N. tantilla* (non-paired t-test, t = 3.826, df = 6, p < 0.01) (Figure 10a). Big crabs, however, did not seem to express any significant selectivity over the two clam species (non-paired t-test, t = 1.112, df = 6, p = 0.3) (Figure 11a).

In the calculations for prey values, *N. confusa* had a significantly higher profitability than *N. tantilla* for small crabs (non-paired t-test, t = 3.874, df = 5, p=0.01) (Figure 10b). The profitability of both clam species did not present any significant difference for big crabs (non-paired t-test, t = -0.632, df = 3, p < 0.6) (Figure 11b).

**Discussion**

The elimination of sediment grain size as a cause for the differences in distribution and abundance of the two *Nutricola* species, leaves the factor of predation by crabs as a logical explanation of these observations. Waves and tidal currents do not transport dead shell material, so surveys finding shifts in the numbers of disarticulated shells can be considered accurate. Therefore, field surveys and experiments still point towards selective predation by *C. magister* as the controlling factor in the relative distributions of *Nutricola* spp. around *Ulva*.

In the lab, small crabs had a more difficult time eating the clams than big crabs when given a choice between two species (Figure 9a and 9b). This may be due to
different foraging tactics employed by juvenile *C. magister* in eating the two different clam species. The different foraging tactics may be a result of a possible difference in physiology between *N. confusa* and *N. tantilla* that imposes difficulty in consuming one of the species. The consumption by small crabs was not limited by their body size, for they ate about the same number of clams as big crabs when their food supply consisted of only one species (Figure 9a). Small crabs significantly favored *N. confusa* over *N. tantilla*, which follows from the significant difference in the profitability of the two clams (Figure 10a and 10b). While obtaining the handling times, we observed that all crabs manipulated their prey in their maxillipeds before consuming or rejecting them. While handling *N. tantilla*, the small crabs twirled the clam around in their maxillipeds for several minutes, but then often ended up rejecting the clam without cracking the shell. Frequent rejections greatly increased the handling times for *N. tantilla*, thus negatively influencing the amount of energy intake during a foraging period. Though *N. tantilla* is relatively deeper than *N. confusa* (Figure 6a and 6b), and therefore should have a relatively higher tissue mass, the larger handling time for small crabs does not allow maximization of this energy. Boulding (1984) noted that crabs usually preferred the smaller, more easily opened clams due to the fact that the shell-breaking time had a strong influence on prey selection. The big crabs, on the other hand, did not display any difficulty in handling either of the two species (Figure 11a and 11b), and therefore did not demonstrate selective predation for either *Nutricola* species.

Asson-Batres (1986) noted that juvenile *C. magister* always try to open all small bivalves that they encounter. With unlimited prey availability, crabs choose to consume the optimal prey; however, suboptimal prey is chosen even when optimal prey is present
(Elner and Hughes 1978). This is because crabs reject the suboptimal prey (in our case *N. tantilla*) when they first encounter it, but then consume it after a sequence of encounters. Elner and Hughes (1978) stated that crabs are not visual hunters. They are not able to see overall prey availability, but instead encounter prey one by one with their walking legs as they crawl over the sediment. The recognition time of the optimal prey influences their diet indirectly and especially within an extremely short range (Elner and Hughes 1978), like in our experimental set up. They also possess a very short-term memory (Elner and Hughes 1978). If better prey is not found after rejection of the suboptimal prey, then they accept the suboptimal prey. This may be the reason that small juvenile *C. magister* were able to consume a larger number of *N. tantilla* when they made up the entire food supply in treatment 3. This also proves that total rejection cannot be assumed for *N. tantilla* by the small crabs because it depends on local abundances. The crabs’ rapid readjustment to availability of different quality prey (Elner and Hughes 1978) may be a representation of their interactions with the heterogeneous distribution of prey in nature.

Though our study began with the notion that all juvenile *C. magister* displayed the same foraging behaviors, it is sensible that the smaller crabs would behave differently from the bigger crabs. Feeding preferences are expected to change with alterations in foraging efficiency, which naturally leads to feeding specialization and switching (Partridge and Green 1984). Smaller animals tend to have different nutritional requirements than bigger animals due to their different growth rate. Their smaller size also affects their feeding abilities, as shown by the small crabs’ inability to consume *N. tantilla* in comparison to the big crabs.
Smaller crabs are poor competitors in their natural habitat (Partridge and Green 1984). Time is a definitive constraint in cases where predators are themselves heavily preyed upon (Boulding 1984). When juvenile *C. magister* settle in summer months, they have a limited time for heavy foraging before other predators, such as wintering birds, arrive later in the season. For energy maximization, it is necessary for small crabs to consume a prey with higher profitability, such as *N. confusa*, which requires less time to handle.

**Summary**

Both *Nutricola* spp. respond to shifts in sediment grain size similarly, so this physical factor is not limiting *N. confusa* distributions relative to *N. tantilla* in our samples (reject $h_{a2}$). Feeding trials with *C. magister* show that small juveniles do not treat *N. confusa* and *N. tantilla* equally as prey items (reject $h_o$). *Nutricola confusa* is easier to handle and therefore a more profitable prey item than *N. tantilla* (Fig. 10b). This causes small crabs to forage optimally by eating a significantly higher proportion of *N. confusa* than *N. tantilla* when given a choice (Fig. 10a). Due to the foraging tactics of *C. magister* (Asson-Batres 1986) and the lack of shell transport on the mudflat, disarticulated shell material serves as an accurate measure of predation pressure over different areas in the field. Since relative levels of *N. confusa* disarticulated shells increase in areas where *N. confusa* is less dominant (Fig. 5) (particularly areas associated with *Ulva* Fig. 4), and since *C. magister* preferentially select areas with a macroalgal cover for settlement (McMillan et al. 1995), selective predation by small *C. magister* is
most likely at the root of shifts in relative abundance between \textit{N. confusa} and \textit{N. tantilla} in areas near \textit{Ulva} cover.

**Acknowledgements**

We would like to thank Ted Grosholz and Rico Tinsman for their advice concerning the mudflat environment. We extend much appreciation to Dr. Richard Zimmer and Dr. Cheryl Ann Zimmer for advice on the predation experimentation and flow. We thank Karl M. and Will Borgeson for the crabs, and Vic Chow for the sieves and the rocker. Many thanks to the hard working seiners who gave us many crabs and to Kelly Wong for transect information and stakes. Thank you to Dr. Malcom Gordon, Jeff Riffell, and Dean Lauritzen for their support and consultation. Lastly, we would like to thank the Bodega Marine Laboratory and the entire Marine Biology Quarter for making this experimentation possible.

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Core Sampling

- Two Sites
  - Dorm (D)
  - Boat Ramp (B)
- Density information blocked together
  - ANOVA $p > .05$
Nutricola spp. Negatively Correlated to Ulva Cover

![Graph showing the relationship between Ulva cover and the number of clams per core for Nutricola spp. with statistical significance marked as p<.001](image)

- **Ulva Absent**
- **Edge of Ulva**
- **Ulva Dense**

Core Location

# Clams Per Core

- N. confusa
- N. tantilla

- Statistical significance: p<.001
Nc dominance = Dis-articulated Nc Shells

![Graph showing the relationship between % N. confusa in Core and Live/Total. The graph includes two sites: Dorm Site and Boat Ramp Site. The correlation is significant (p<.01).]
Shell Size and Shape

*N. tantilla* is Relatively Deeper than *N. confusa*

![Graph showing the comparison between *N. tantilla* and *N. confusa* in terms of clam length and depth. The graph includes a scatter plot with lines indicating ANCOVA p<.05.]
Shell Transport by Tides

Strong Ebbing Tide

\( u_1 = 0.4 \text{ cm/s} \)

\( u_2 = 0.5 \text{ cm/s} \)
Predation by *Cancer magister*

12 hours, in dark

**Control:** Clams (50 Nt, 50 Nc)  
No crabs  
n=4

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**TT 1:** Clams (50 Nt, 50 Nc)  
1 crab  
n=8

**TT 2 & 3:** Clams (100 Nt or Nc)  
1 Crab  
n=8
Small crabs consumed less clams when given a choice.

**SMALL crabs**

- 50 Nc and 50 Nt: 10 clams
- 100 Nc: 60 clams
- 100 Nt: 60 clams

**BIG crabs**

- 50 Nc and 50 Nt: 60 clams
- 100 Nc: 60 clams
- 100 Nt: 60 clams
SMALL crabs

Proportion Eaten
p<0.009

Profitability of clams
p<0.01

Nc
Nt

Proportion Eaten

Profitability

(s/5 g)

Nc
Nt
BIG crabs

Proportion Eaten
p<0.309

Profitability of clams
p<0.572