THE EFFECTS OF BIOTURBATION BY THE BURROWING SHRIMP CALOCARIS MACANDREAE ON A SUBTIDAL MACROBENTHIC COMMUNITY: FURTHER EVIDENCE FOR THE IMPORTANCE OF FUNCTION OVER IDENTITY

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THE EFFECTS OF BIOTURBATION BY THE BURROWING SHRIMP *CALOCARIS MACANDREAE* ON A SUBTIDAL MACROBENTHIC COMMUNITY: FURTHER EVIDENCE FOR THE IMPORTANCE OF FUNCTION OVER IDENTITY

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ABSTRACT.– The effects of bioturbation by the burrowing shrimp *Calocaris macandreae* on the structure and diversity of the associated macrobenthic community were quantified in a benthic mesocosm experiment. Areas of subtidal sediment were subjected to eight months of continuous disturbance from shrimps at a density equivalent to 14 individuals m⁻², whilst other areas remained undisturbed. The density of shrimp treatments was comparable to natural field densities. Whilst no differences were observed for univariate measures of diversity, multivariate analysis demonstrated significant differences in community structure between the associated fauna within shrimp treatments and the associated fauna of control areas. These differences were solely due to changes in the abundance of the numerically dominant species. Comparisons of the current study to previous, similar studies of different bioturbating species demonstrated that functionally similar organisms are more likely to have analogous effects than are organisms which are functionally different but taxonomically similar.

INTRODUCTION

The importance of biological interactions in setting the community structure of marine, benthic assemblages has long been established. Many processes have been identified; adult-larval interactions (Woodin 1976), predation (Holland et al. 1980), competition (Hollertz et al. 1998) and bioturbation (Brenchley 1981). Of all these processes, it is perhaps the latter that has recently been the subject of most investigation (e.g. Warwick et al. 1990, Brey 1991, Widdicombe & Austen 1998). A few studies have taken the sediment processing or turnover created by the entire biota as a single environmental variable (e.g. D’Andrea et al. 1995). This approach assumes all bioturbators to have the same qualitative effects on the fauna, with effects differing only as a result of the size and frequency of disturbance (Petraitis et al. 1989). However, recent studies have demonstrated that macrofaunal bioturbators with different modes of activity do not all have the same effect on the diversity and structure of associated communities (Widdicombe & Austen 1999). This means it is vital to establish the exact role played by different bioturbating species. 
or functional types rather than extrapolate from an assumed consequence of sediment disturbance.

Thalassinidean shrimps are deep burrowing decapods that process large volumes of sediment (Rowden & Jones 1993) and constitute an important component of many benthic communities (Aller & Dodge 1974, Suchanek 1983). The realization that the bioturbatory activities of these shrimps have a potential impact on the structure of macro-infaunal communities has generated many studies on this subject. The majority of these have concluded that the response of specific infaunal groups to bioturbation is predictable. Thalassinidean shrimps were shown to reduce the number of tube-dwelling polychaetes and other sedentary organisms whilst increasing the abundance of the more mobile organisms (Brenchley 1981, Posey 1986, Posey et al. 1991). From these studies, Posey et al. (1991) predicted that an organism’s ability to survive bioturbation was influenced by its mobility such that organisms able to regain their spatial position within the sediment after being disturbed were more resistant than those that could not. However, such generalisations on the effects of shrimp disturbance on their associated benthic infauna (e.g. Rhoads & Young 1970, Brenchley 1981) are based upon studies of just two shrimp families, the Callianassidae (Posey 1986) and the Upogebiidae (Brenchley 1981, Posey et al. 1991). Given the variability in feeding strategy and burrowing behaviour between different thalassinidean shrimp species (Nickell & Atkinson 1995), the general application of such bioturbatory effects to all burrowing shrimps requires information from other shrimp families. This paper reports on a mesocosm experiment which investigates the affect of Calocaris macandreae, a member of the family Axiidae, on the associated fauna. With reference to previous investigations comparisons will be made between these three thalassinidean families and the suitability of generic hypotheses will be examined.

METHODS

Experimental design: The experiment was carried out in the mesocosm facility of the NIVA marine research station Solbergstrand, Oslofjord, Norway. The mesocosm has been described in detail by Berge et al. (1986). Four 1 m x 1 m square boxes were filled to a depth of 30 cm with a fresh, sandy mud sediment collected from 40 m depth in Bjørhodenbukta (59° 43.8’ N 10° 32.2’ W), a sheltered bay in the inner part of Oslofjord. A Day grab was used as this enabled sampling to concentrate on the surface sediment where the majority of the small infauna resides. The 1 m x 1 m boxes were placed and maintained in a 5 m x 7 m indoor, epoxy resin coated concrete basin. A constant water depth of 100 cm was achieved by continuously pumping in water from 60 m depth from the fjord and allowing it to run to waste. The sediment was allowed to settle for two days before four areas 30 cm in diameter were partitioned off in each box. To create experimental treatment areas to which shrimps could be added, partitions were constructed of plastic mesh with an aperture of 1.5 mm, thus allowing the smaller macrofauna to pass between the putative disturbed and undisturbed areas. The presence of these mesh walls caused no apparent disruption to the water flow across the sediment. This was assessed by visual examination of areas both inside and outside the enclosures which potentially could have been in the “shadow” of the mesh, none of which showed any sediment discoloration associated with oxygen depletion or any occurrence of Beggiatoa sp. The area set aside to be disturbed represented 30% of the total surface area of each box. Positioning of the enclosures was such that control samples taken outside of the enclosed areas were as close to the partitioning walls as those taken in the disturbed areas thus ensuring any effect the mesh may have had on the sediment or infauna was consistent within treatments and controls. At the end of the experiment 5 of the shrimp treatment areas contained no evidence of shrimp activity and no shrimps were recovered when the sediment was sieved. Observations from this study, and subsequent experiments, have indicated that C. macandreae may leave treatment areas during the first few weeks of the experiment. After this time any shrimps still present will remain for the full duration of the experiment. Consequently, the impact of shrimp bioturbation in these abandoned areas over the course of the experiment was insignificant. This enabled us to compare the fauna from within partitioned areas with the fauna from control samples.

Calocaris macandreae were collected from an area of soft sediment, water depth of 90 m, just north of Solbergstrand. The shallower burrows of C. macandreae, compared to other thalassinidean species, meant it was possible to collect these shrimps using a Day grab. Approximately one animal was found in each grab equating to a field density of 10 C. macandreae per m². Each shrimp was placed in a small, plastic mesh container which was immersed in continuously flowing seawater. As they are intraspecifically aggressive, each shrimp was transported in a separate container. On 2nd September 1995, a single C. macandreae was added to each enclosure equating to a density of 14 individuals m⁻². This density represented a realistic density compared to the natural field density of 10 individuals m⁻². Temporary mesh lids were attached to the enclosures in order to prevent the shrimps from escaping before they had burrowed. These lids were removed once the animals had left the surface which was generally after less than 12 hours. Any animals which had failed to burrow after 24 hours were removed and replaced.

Sampling: Sampling took place 8 months after the start of the experiment, on 8th May 1996. The size and positions of all the burrow entrances were mapped and the average number of burrow openings per shrimp ± 95% confidence intervals was calculated. Using 6.8 cm diameter plastic cores, two samples were taken near to burrowing activity within each enclosure with a further four sets of two samples taken in the undisturbed areas outside each of the enclosures. These were sieved over a 250 µm mesh, fixed in a 10% formaldehyde solution and
then sorted under a binocular microscope. All animals were identified to the lowest possible taxonomic level. The remainder of the enclosure was coarsely sieved to collect and enumerate all surviving *C. macandreae*.

**Data analysis:** Data analysis followed methods described by Clarke (1993) and Clarke & Warwick (1994) using the PRIMER (Plymouth Routines in Multivariate Ecological Research) software package. Multivariate data analysis was by non-metric multi-dimensional scaling (MDS) using the Bray-Curtis similarity measure. Analysis was carried out on untransformed, single square root (\(\sqrt{\cdot}\)) transformed, double square root (\(\sqrt{\sqrt{\cdot}}\)) transformed and presence/absence data. As the power of the transformation increases the relative influence of the rarer species becomes greater. This enables the effects on different elements of the assemblage to be determined. Two-way crossed ANOSIM was carried out to identify differences in the community structure between areas of shrimp activity and the controls, accounting for potential box effects. Means with 95% confidence intervals were calculated for measures of number of species, number of individuals, species richness (Margalef), Shannon-Wiener diversity and Pielou's evenness. Significance levels were assigned to these results using Kruskal-Wallis one way analysis of variance. This method was preferred because, unlike ANOVA, it makes no assumptions based on variance or normality. SIMPER was used to identify the species responsible for any dissimilarity between shrimp treatments and controls. The mean abundance of these species in the shrimp treatments and in the controls was compared using Kruskal-Wallis one way analysis of variance.

**RESULTS**

**Calocaris macandreae activity**

At the end of the experiment 11 of the 16 enclosed areas contained active shrimps. The remaining 5 areas displayed no evidence of previous burrowing activity and no extant shrimps were recovered. These 5 treatments have not been included in the data analysis used to identify differences in macrobenthic communities between areas disturbed by shrimps and those areas left undisturbed. In the areas where the shrimps were active they constructed burrow systems with 8.4 ± 0.9 burrow openings per shrimp.

**Multivariate measures of community structure and diversity**

Two-way nested ANOSIM indicated that there were no box effects regardless of the data transformation used. Significant differences were observed between the communities of shrimp disturbed areas and the communities from the undisturbed controls, for untransformed \(R=0.167, p=0.015\) and single square root (\(\sqrt{\cdot}\)) transformed \(R=0.137, p=0.016\) data. There were no significant differences between disturbed and undisturbed areas when using more severely transformed data. This indicates that the differences in community structure between the shrimp treatments and the controls is due to changes in the relative abundances of the numerically dominant species rather than changes in species identities among less abundant species.

**Univariate measures of community structure and diversity**

There were no significant differences between the areas which contained shrimps and the controls for number of species, number of individuals or any of the diversity measures (Table I).

**The response of individual species to shrimp disturbance**

By comparing samples from areas containing *C. macandreae* with control areas, SIMPER analysis indicated which species were responsible for the patterns observed in the MDS ordinations. The difference, or dissimilarity, between the faunas of shrimp and control areas was high (34.9%), and 80% of that dissimilarity was due to changes in the abundance of six numerically dominant species.
The species most responsible for the dissimilarity between shrimp and control areas was the capitellid polychaete *Heteromastus filiformis*. This species contributed over a third of the total dissimilarity. The cirratulid polychaete *Chaetozone setosa* contributed almost a further quarter (Table II).

Although all six species highlighted by SIMPER made a major contribution to the dissimilarity between shrimp and control areas (Table II), only three species showed a significant difference in mean abundance between shrimp occupied and control areas. *Chaetozone setosa* and *Pholoe minuta* were significantly more abundant in areas impacted by *C. macandreae* compared with the controls. In contrast, *Pseudopolydora pauchibranchiata* was most abundant in areas without shrimp disturbance. The remaining three species (*Cossura longocirrata, Heteromastus filiformis* and *Nuculoma tenuis*) showed no significant difference in abundance between shrimp-disturbed and control areas (Table II).

It is surprising that there was no significant difference between the mean number of *Heteromastus filiformis*, despite SIMPER analysis identifying this species as having contributed most to the dissimilarity between the fauna of *C. macandreae* areas and that of control areas. Further examination of the SIMPER results showed that the ratio between the mean and standard deviation in the percent contribution of *H. filiformis* to the overall dissimilarity was high (1.41), indicating *H. filiformis* was contributing a consistent amount to each pairwise comparison of dissimilarity between shrimp and non-shrimp samples. Additionally, this species was a consistent contributor to the similarity between samples from within treatment areas. In shrimp treatments, *H. filiformis* contributed 35.5% of the similarity with a ratio of 2.42, whilst in control areas it contributed 45.83% of the similarity with a ratio of 2.98. The Kruskal-Wallis test is a one-way analysis of variance by ranks that tests whether *k* independent samples could have been drawn from the same continuous population. All observed values are replaced by ranks and the sum of ranks in each treatment group is found. This test determines whether these sums of ranks are so disparate that they are likely to have come from different populations. If the number of observations is low, the influence of a small number of unusually high or low values may result in a failure to demonstrate significant differences between treatments. Multivariate techniques that compare values in a pair-wise manner generate a large number of values from a small number of observations and are, therefore, less affected by these outlying values. Consequently, multivariate techniques may detect underlying differences, between groups, that are undetectable by univariate techniques (Warwick & Clarke 1991).

**DISCUSSION**

The abundance of several macrofaunal species and, consequently, the structure of the associated communities were significantly different in areas with *Calocaris macandreae* compared with areas without these shrimps. The multiple-opening burrows constructed by *C. macandreae* during the experiment were comparable to those described by Nash *et al.* (1984), suggesting the activity of the shrimps within the mesocosm is representative of their activity in the field. The presence of *C. macandreae* had no effect on univariate measures of diversity.

The presence of *C. macandreae* affected the abundance of several macrofauna species, particularly the tube-building, spionid polychaete

<table>
<thead>
<tr>
<th>Species</th>
<th>Shrimp</th>
<th>Control</th>
<th>p-value</th>
<th>% contribution to dissimilarity</th>
<th>Cumulative dissimilarity</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Heteromastus filiformis</em></td>
<td>20.5 ± 4.9</td>
<td>25.5 ± 4.26</td>
<td>0.130</td>
<td>33.69</td>
<td>33.69</td>
</tr>
<tr>
<td><em>Chaetozone setosa</em></td>
<td>22.1 ± 3.9</td>
<td>16.5 ± 2.4</td>
<td>0.029</td>
<td>23.94</td>
<td>57.63</td>
</tr>
<tr>
<td><em>Pseudopolydora pauchibranchiata</em></td>
<td>3.9 ± 1.2</td>
<td>6.1 ± 1.1</td>
<td>0.008</td>
<td>9.68</td>
<td>67.31</td>
</tr>
<tr>
<td><em>Cossura longocirrata</em></td>
<td>4.5 ± 1.2</td>
<td>3.8 ± 0.8</td>
<td>0.545</td>
<td>6.76</td>
<td>74.07</td>
</tr>
<tr>
<td><em>Nuculoma tenuis</em></td>
<td>0.8 ± 0.5</td>
<td>1.3 ± 0.4</td>
<td>0.088</td>
<td>3.13</td>
<td>77.20</td>
</tr>
<tr>
<td><em>Pholoe minuta</em></td>
<td>1.0 ± 0.6</td>
<td>0.4 ± 0.4</td>
<td>0.033</td>
<td>2.95</td>
<td>80.15</td>
</tr>
</tbody>
</table>
Pseudopolydora pauchibranchiata, which was least abundant in areas containing C. macandreae. In many benthic communities, spionids are the most abundant tube-building organisms and, consequently, the impact of shrimp disturbance on these species has been well documented. A reduction in spionid polychaete numbers, in areas where burrowing shrimps were present, was shown by Brenchley (1981) and Posey (1986). These authors demonstrated that the burrowing activity of a callianassid shrimp reduced the abundance of several species of spionid polychaete, whilst Posey et al. (1991) observed a reduction in the numbers of Pseudopolydora kempi in areas containing Upogebia pugettensis. The results of the current study with C. macandreae are in agreement with these studies and support the "Mobility Mode Hypothesis" (Brenchley 1981) which predicted a reduction in the abundance of tube-dwelling polychaetes and other sedentary organisms, together with an increase in the abundance of more mobile organisms, in areas influenced by the activity of mobile deposit feeders. The mechanism underlying the reduction in tube-building species in the presence of bioturbation is unknown. Increased sedimentation due to shrimp activity may smother the feeding apparatus of sedentary organisms and, unable to regain a position at the sediment surface, these animals may starve. Alternatively, constant smothering and increased sediment instability around shrimp burrows may inhibit the settlement of the larvae of tube builders as suggested by Rhoads & Young (1970) and Woodin (1976). It is feasible that both these mechanisms are operating and that burrowing shrimps may affect the survival of adult and juvenile tube builders.

Whilst the response of macrofaunal communities to the disturbance caused by all burrowing shrimps may be similar, the intensity of this response has been shown to vary when comparing the impact of different shrimp species. Bird (1982) compared directly the effects of two thalassinid shrimp species, Upogebia pugettensis and Neotrypaea (as Callianassa) californiensis, and found significantly fewer spionid species within areas occupied by N. californiensis compared with beds of U. pugettensis. Whilst both are burrowing shrimps, these two species represent very different functional types. This work suggests a fundamental difference in the response of tube-building polychaetes to the activities of a deposit-feeding shrimp, N. californiensis, compared with the suspension-feeder, U. pugettensis. Widdicombe & Austen (1998) showed that the intensity at which the sediment is disturbed has a large effect on the diversity and community structure of the associated fauna. It is possible that the different responses observed in the tube-building organisms for these two shrimp species may be a consequence of different bioturbation intensities. The results from the current study indicate that C. macandreae had a similar qualitative effect on the macrofauna to that reported for both N. californiensis and U. pugettensis. Due to similarities in burrow morphology and feeding behaviour, it may also be expected that the intensities at which C. macandreae and N. californiensis create disturbance would be similar. However, before this similarity can be confirmed, studies comparing directly the effects of these burrowing shrimp species must be conducted.

An additional factor that could exacerbate the effect of the potentially different bioturbation intensities associated with C. macandreae, N. californiensis and U. pugettensis is that of the quality of expelled sediment. Both C. macandreae and N. californiensis are deposit feeders and, therefore, extract organic material from the sediment before it is expelled from the burrow. Upogebia pugettensis expels sediment as a consequence of burrow excavation and maintenance and, therefore, this sediment will contain more organic matter than sediment expelled by C. macandreae or N. californiensis. Consequently, the reduced impact of U. pugettensis on spionid abundances, compared with C. macandreae and N. californiensis, may be related to the amount of food in the expelled sediment, in addition to the intensity of disturbance. Indirect evidence for differences in the organic content of sediment expelled by different burrowing shrimp species may be provided by examining the abundance of capitellid polychaetes. Bird (1982) suggested that N. californiensis reduced the abundance of capitellids, whilst Posey et al. (1991) showed densities of the capitellid Heteromastus filiformis were increased by U. pugettensis. Considering many species of capitellid have been shown to prosper in organically rich sediments (Pearson & Rosenberg 1978), the studies of Bird (1982) and Posey et al. (1991) may support the contention that sediment expelled by N. californiensis is organically impoverished compared with sediment expelled by U. pugettensis. The current study examined the effects of C. macandreae on its associated infauna and showed lower abundances of H. filiformis in areas occupied by C. macandreae than in control areas. The similarity in response of H. filiformis to the presence of both C. macandreae (this study) and N. californiensis (Posey et al., 1991) provides evidence that the similar burrowing and feeding behaviour of these two shrimp species affects the associated fauna in the same way. Whilst the effect on the macrofauna of the deposit-feeding species C. macandreae and N. californiensis may be considered the same, the effect of the suspension feeder U. pugettensis may be different. The response of the fauna to bioturbation could, therefore, be dependent on both the intensity of disturbance and the manner in which the disturbance is created.
Results from the current study, when compared to those of previous studies have highlighted differences in community response resulting from the presence of different species of bioturbating shrimps. Further differences are observed when other important bioturbating taxa are examined. Widdicombe & Austen (1998) reported that the abundance of *Pseudopolydora pauchibranchiata* was higher in areas with a moderate density (28 individuals m$^{-2}$) of *Brissopsis lyrifera*, a bioturbating urchin, than in areas without any urchins. This contrasts with the response of *P. pauchibranchiata* to *C. macandreae*. The differences in faunal response to these functionally different species were not limited to *P. pauchibranchiata*. Compared to areas with no bioturbation the abundance of the bivalve *Nuculoma tenuis* increased in low density *B. lyrifera* areas and decreased in areas with *C. macandreae*. As a deposit feeder that moves through the surface sediment, *N. tenuis* may have been more affected by sediment instability, or organic depletion associated with *C. macandreae* through the surface sediment, than by being pushed aside by *B. lyrifera*. In contrast to *N. tenuis* and *P. pauchibranchiata*, the mean abundance of the polychaete *Pholoe minuta* was higher in the presence of *C. macandreae* and lower in the presence of *B. lyrifera* compared with the controls. Two polychaete species, *Chaetozone setosa* and *Cossura longocirrata*, had higher abundances in both low density *B. lyrifera* and *C. macandreae* treatments compared with the controls. The relative success of these two polychaete species in areas subjected to sediment deposition by *C. macandreae* agrees with results from a recent study of sediment deposition due to glacial run off (Kendall et al. 2003), indicating that *C. setosa* and *C. longocirrata* are resilient to smothering.

By comparing the results from different experiments it is evident that different organisms have different structuring effects on associated communities. This suggests that functionally similar organisms are more likely to have analogous effects than are organisms which are functionally different but taxonomically similar.

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