

Limited infaunal response to experimental trawling in previously untrawled areas

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There is considerable argument about the effects of bottom trawling on the benthos. Many studies have been done on recently trawled grounds, where community composition has already been modified, and further effects are likely to be minimal. This study tests the effect of trawling on macroinfaunal assemblages in an area where little or no trawling had occurred in the previous 15 years. A spatially replicated Before-After, Control-Impact (BACI) design was used, with adjacent trawl and control corridors. Sampling was done in the same two small sites within each corridor before and after trawling to minimise confounding due to spatial variation. Despite this rigorous design, changes consistent with an effect of trawling were not detected. At only one of the three locations was a potential effect detected. These inconsistent results could be due to different disturbance regimes at each location, influencing the vulnerability of fauna to further disturbance. Given the high levels of variability in infaunal assemblages, however, the changes could also be due to asynchronous natural variation. The combination of high spatial and temporal variability, in association with light trawling gear, means that prawn trawling in South Australia does not have consistent effects on infauna.

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Introduction

There is a consensus that dragging trawl gear across the sea floor is detrimental to marine biota and habitats (Jones, 1992; Engel and Kvitek, 1998; Hall, 1999). Watling and Norse (1998) suggested that, with the possible exception of agriculture, bottom trawling and dredging may be the most physically damaging and widespread of all human activities. Fishers have been complaining about the impact of bottom trawling since the 13th century (de Groot, 1984), blaming it for declines in commercial fish and shellfish stocks, of both target and non-target species. Trawling is believed to affect stock abundances directly by removing or killing individuals, and indirectly by affecting structures and organisms that serve as habitat and food (Sainsbury, 1988; Hall, 1999).

Despite these concerns, the intensity and extent of bottom trawling have continued to increase throughout

the world, particularly over the last few decades (Hall, 1999). In heavily fished areas of the North Sea, every square meter of the sea floor is trawled on average seven times a year (Goñi, 1998). With improvements in technology, trawlers can now operate at depths down to 1200 m (Judd, 1989), over rough ground, and near obstacles; areas that were *de facto* refuges from trawling until as recently as ten years ago (Watling and Norse, 1998). The destructive potential of the gear used has also increased. The weight of the gear dragged along the sea floor is now as much as 13 tons when empty (Watling and Norse, 1998). “Tickler” chains and chain matrices, used to improve catch rates, increase the amount of damage as much as tenfold (Bridger, 1970).

A number of studies have investigated the impact of trawling on various components of the marine ecosystem, with mixed results. Demonstrating an impact of trawling on the benthos is not an easy task for a number of reasons. The severity of the damage caused varies,

depending on the trawling regime, the trawl gear used (type, configuration and weight), the type of sediment and biota, and the natural disturbance regime (Jones, 1992; Kaiser and Spencer, 1996). In addition, the benthos is highly variable, both in time and space, which can confound sampling designs that attempt to detect effects of trawling (Lindgarth *et al.*, 2000). Quantifying the effects of trawling is also hindered by a lack of areas known to have not been recently trawled. The majority of research has been done in heavily fished areas such as the North Sea. The already-disturbed state of these areas is one explanation for why some studies have found that experimental trawls had no significant effect on the benthos (Bergman and Hup, 1992; Jennings and Kaiser, 1998; Kaiser, 1998).

The aim of this study was to investigate the effects of otter trawling for western king prawns (*Penaeus latissulcatus*) on the benthos in South Australia. Here, we concentrate on infauna. Previous studies (mostly on the effects of pollution) suggest that infaunal assemblages are good indicators of disturbance because of their sensitivity to habitat alterations, and importance to the structure and function of marine systems (Bilyard, 1987). Infauna are taxonomically and functionally diverse, and numerous other species, including those of commercial importance, depend directly or indirectly on them (Bilyard, 1987). The activities of infauna also affect important characteristics of the sediment, increasing the water and oxygen content, topographic detail, microbial activity and erosion resistance, decreasing compaction, and altering the grain size (Hall, 1994).

Trawling intensity in South Australia is relatively light. Less than 6% of the bottom has been trawled annually in recent years within Gulf St Vincent, where this study was conducted (J.E.T., unpublished results). Despite this low intensity, trawling could still have important detrimental effects for this area. The waters off southern Australia are well known for their high levels of biological diversity and endemism (Lewis *et al.*, 1998). The gulfs are unusual in that they are “inverse estuaries” where salinity (and water temperature) increase progressively towards the head of each gulf. These waters are important nursery areas for a number of commercially important fish and shellfish species, particularly in the extensive seagrass beds (Lewis *et al.*, 1998).

This study tests the hypothesis that bottom trawling affects macroinfaunal assemblages. We predicted that the structure of these assemblages (taxonomic composition and relative abundances) would diverge after trawling, from that of the same locations before trawling, and that of untrawled sites. The location and design of this experiment make it more sensitive and robust than most previous studies, as trawling in the vicinity of the study sites has been minimal for at least ten to 15 years. The ability to detect effects in a naturally

variable system was maximised by adopting a replicated, paired, control and impact experimental design, with sampling done both before and after trawling. Unlike most previous studies (particularly those using remote sampling gear), confounding of the before and after samples by spatial variability was minimised by sampling precisely the same small sites pre- and post-trawling.

Materials and methods

Site selection

Three locations, 13–16 km apart, were chosen haphazardly in upper-central Gulf St Vincent (GSV), South Australia (Figure 1). Bye (1976) describes the oceanography of GSV, and Shepherd and Sprigg (1976) give a large-scale description of the sediments and epibiota. The water depth was ~20 m at all locations. The distribution of trawling effort in GSV has been recorded in 30 nmi² blocks since the fishery began in 1968. At the time of the study (1999), the block containing location 1 was last trawled during the 1997/1998 season, but the trawling intensity had been very light since at least 1988/1989 (<1000 minutes total fishing time in ten years in the entire block). The blocks containing locations 2 and 3 had not been trawled since 1985. Lack of trawling activity was due initially to a closure after collapse of the fishery in the early 1980s (Lewis *et al.*, 1998), and subsequently to a preference for the southern gulf area. The sediment at locations 1 and 3 was medium-coarse sand and shell fragments, while at 2, it was fine silt.

Each location included an east-west orientated “control” corridor and an adjacent “impact” (trawl) corridor, ~200 m wide by 0.5 mm (937 m) long. The close proximity of the control and trawl corridors within locations minimised any pre-trawl differences in the benthic assemblages due to spatial variation. Two 2 m × 1 m sampling sites, within 10–20 m of each other, were chosen randomly near the centre of each corridor and marked out with steel pegs. Sampling therefore, was done at more than one spatial scale (sites were nested within corridors, and corridors within locations).

Experimental trawling

Trawling was done at night and under supervision by a locally chartered commercial triple otter prawn trawler (the “Jillian Sandra”) in October 1999. The combined sweep of the nets was ~20 m. The two 102 m × 213 cm otter boards weighed 200 kg each and the two skids 240 kg each (in air). The trawler made ten adjacent passes along each trawl corridor, which was then repeated to ensure complete coverage, so on average, the entire corridor was trawled twice. By-catch was

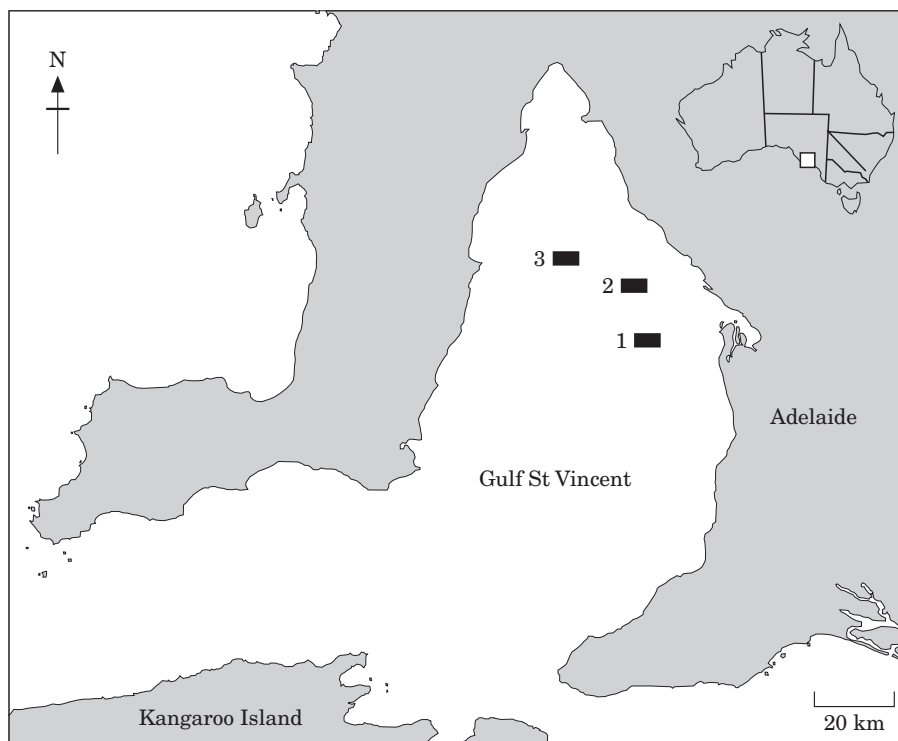


Figure 1. Map of Gulf St Vincent, South Australia, showing placement of the study locations.

discarded when the vessel was outside of the study corridors. A DGPS was used for accurate navigation (± 10 m), and the vessel's speed was 3.5 knots during trawling.

Sampling

The before-trawl sampling was done two months prior to trawling. SCUBA divers collected samples of sediment to 150 mm deep using corers made of 40 mm internal diameter PVC pipe. The relatively small size of the cores enabled more samples to be collected and processed in the time available, which improved the precision and power of the study. Small units are also more efficient when sampling aggregated organisms (as is the case for most infauna; Elliot, 1981). The samples were fixed in 10% formalin in seawater and buffered with borax immediately after collection. On the pre-trawl sampling trips, twelve replicate cores were collected from each site. Graphs of the standard error of the mean number of taxa and total abundance per core sampled for each site asymptoted before $n=10$, indicating that statistical precision for these variables was optimised with ten replicates. Therefore, ten samples were collected at each site after trawling.

The post-trawl samples were collected at locations 2 and 3 within a week of trawling. However, bad weather prevented sampling at location 1 until the next scheduled

cruise in January 2000. Tracks left by the trawler's otter boards and skids were evident within all trawl corridors. Between the otter board tracks, the footline and net had removed 28% of the epifauna (J.E.T., unpublished results) and the topographic features of the sediment such as mounds created by burrowing animals. Epifauna in all trawled quadrats showed signs of damage, indicating that the trawl had passed directly over them at least once. Trawl board marks were also evident in the vicinity of some quadrats, but were not sampled.

The samples were washed through 2-mm and 1-mm-mesh sieves, with the fauna being picked out from the retained sediment under water. Most polychaetes were identified to family, with families that were common and containing a number of distinctly different gross morphologies (Spionidae, Syllidae, Ctenodrilidae) divided further into groups based on these differences. Other phyla were identified to suborder or higher, depending on taxonomic knowledge of the group for the study area. All infauna retained on the sieves were included in the analysis.

Statistical methods

The "before-after, control-impact" (BACI) design is a factorial design in which the evidence for an impact appears as a significant Time (Before vs. After the impact) by Treatment (Control vs. Impact) interaction

(Green, 1979). In light of the potential for “background noise” to confound results, analyses were done at the phylum level as well as at the highest level of taxonomic resolution achieved (referred to subsequently as “high resolution”). Polychaetes alone were also analysed at the family level, in case the use of phyla and other high level taxa obscured any patterns. Location 1 was analysed separately because the post-trawl samples were collected well after those from the other two locations, and the data were therefore temporally confounded. The analyses from location 1 should be interpreted with caution, as the data are not properly replicated (Hurlbert, 1984). The results from location 1 were used only to back up the results from the location 2 and 3 samples (referred to subsequently as 2+3).

Multivariate procedures

The non-parametric multivariate analysis of variance program, NP-MANOVA (Anderson, 2001), was used to test for differences among the infaunal assemblages between times and treatments (types and abundances of taxa in the replicate core samples). This program has been designed to test multivariate ecological hypotheses that require a complex multi-factorial experimental design such as BACI. The current version of NP-MANOVA has a constraint on the maximum number of factors (two), and thus the analysis had to be done in two steps. We used NP-MANOVA despite this shortcoming as traditional MANOVA does not give reliable results with most ecological data sets, and no other non-parametric alternative is capable of multi-factorial MANOVA (Anderson, 2001). The hypothesis predicts an interaction between Time and Trawling (trawled sites should vary through time differently to untrawled sites). Analyses were thus done with the factors Time (before vs. after) and Trawling (trawled vs. untrawled) by pooling sites and locations, for the standard test of an interaction between Time and Treatment ($n=40$ for the 2+3 samples and $n=20$ for the location 1 samples). Analyses were also done with the factors Time and Site ($n=10$), making Time \times Site the interaction of interest, to reveal any differences within and between locations and their responses to trawling.

The Bray-Curtis similarity measure was used in NP-MANOVA, because it is not affected by joint absences, and is one of the most reliable measures of “ecological distance” (Clarke, 1993). The data were fourth-root transformed to prevent abundant taxa from influencing the Bray-Curtis similarity measure excessively (Clarke, 1993). Time and Trawling were treated as fixed factors, but Site was treated as random. Significance levels for all tests were calculated by conducting 4999 permutations of residuals under a reduced model (Anderson and Legendre, 1999). If the interaction

between the two factors was significant, the source of the difference was found by using pair-wise *a posteriori* comparisons.

Non-metric multidimensional scaling (nMDS) ordinations provided a visual indication of the similarity of assemblages at each site, before and after trawling, based on the mean abundance per core for each taxon at each site ($n=10$). Similarity is indicated by the distance between the positions assigned to the sites in the two-dimensional plots. The Bray-Curtis similarity measure was used to calculate the distances, after fourth-root transformation. Stress values associated with these plots indicate the magnitude of distortion between the original ordination and the two-dimensional graphs. The values obtained (≤ 0.13 , Figure 1) indicate they are adequate for interpretation (Clarke, 1993), and three-dimensional plots did not greatly improve their interpretability. The PRIMER program (Plymouth Routines in Multivariate Ecological Research; Clarke, 1993) was used for these ordinations. Ordinations were done for the 2+3 and location 1 data separately, and at both high and low (phylum) levels of taxonomic resolution.

Univariate procedures

The number of taxa and of individual animals per core are widely used indicators of disturbance, and are examined here. A diversity index was not used as they lack sensitivity (Warwick and Clarke, 1991) and different indices can give conflicting results (Hurlbert, 1971). The three most common phyla and high-resolution taxa were also analysed separately. Standard multi-factorial ANOVA was used to test for a significant Time \times Trawling interaction in the number of taxa and total abundance at each site. The interaction between Time, Location and Trawling was also of interest for the 2+3 data, as it tests for differences in the effect of trawling between the two locations. When a significant interaction was found, Student-Newman-Keuls (SNK) tests were used to locate the source of the difference. The 2+3 data had four factors; Time (fixed and orthogonal), Trawling (fixed and orthogonal), Location (random and orthogonal), and Site (random and nested within both Trawling and Location). For the location 1 data, there were three factors, with the same structure as the 2+3 data, but without Location. Cochran's Test was used to test for homogeneity of variance. Heterogeneous data were transformed using $\log_e(x+1)$. If transformation did not remove heteroscedasticity, the raw data were analysed. The traditional alpha value of 0.05 was used to define significance in all analyses including the heterogeneous data, as ANOVA is robust to all but serious heterogeneity, and a more conservative alpha value increases the chance of Type II errors, which are more detrimental in impact studies (Underwood, 1993). Post-hoc pooling of the Time \times Location \times Trawling

Table 1. Multivariate ANOVAs for effects of trawling, at high taxonomic resolution and at the phylum level, for locations 2 and 3, and separately for location 1.

| Source | d.f. | SS | F | p | SS | F | p |
|--------------------------|------|---------|------|-----------------------|---------|------|--------|
| (a) 2+3, high resolution | | | | (b) 2+3, phylum level | | | |
| Time | 1 | 6 686 | 1.54 | 0.16 | 3 120 | 1.72 | 0.23 |
| Site | 7 | 153 426 | 8.74 | 0.0002 | 45 565 | 7.60 | 0.0002 |
| Time \times Site | 7 | 30 351 | 1.73 | 0.0028 | 12 692 | 2.12 | 0.0074 |
| Residual | 144 | 361 082 | | | 123 263 | | |
| (c) 1, high resolution | | | | (d) 1, phylum level | | | |
| Time | 1 | 6 197 | 1.77 | 0.11 | 648 | 1.46 | 0.32 |
| Site | 3 | 10 132 | 1.18 | 0.24 | 837 | 0.28 | 0.94 |
| Time \times Site | 3 | 10 529 | 1.23 | 0.19 | 1 334 | 0.44 | 0.87 |
| Residual | 72 | 206 156 | | | 72 564 | | |

interaction (for 2+3) and Time \times Site interaction (for Location 1) with the Residual was done when $p > 0.25$ (Winer *et al.*, 1991) to improve the power of the test of the interaction (Time \times Trawling) indicative of impacts.

Results

Multivariate analyses

We sampled a total of 1719 individuals, belonging to 67 high-resolution taxa and nine phyla (Appendix). Polychaetes accounted for 62% of individuals, crustaceans 20%, and nemertean 10%. No consistent and unambiguous effects that could be ascribed to trawling were detected. Although there were significant Time \times Site interactions at both taxonomic resolutions (Table 1a and b), pairwise tests did not reveal variation consistent with the predicted effects of trawling. For example, at high taxonomic resolution, temporal changes at location 2 were consistent with an effect of trawling, as only the trawled sites changed. At location 3, however, the opposite occurred, with only the control sites changing. When sites and locations were pooled within Trawling, the Time \times Trawling interaction was not significant ($p = 0.80$), which again indicates no overall effect of trawling. Analyses on polychaetes alone at the family level gave similar results, and are not reported further.

The nMDS plots also do not indicate strong consistent effects of trawling (Figure 2). If trawling had large effects, trawled and untrawled sites would show a greater separation after trawling (solid symbols) than before (open symbols). Instead, the plots reveal large spatial and temporal variation that does not match this pattern.

No effect of trawling was detected at location 1, as the Time \times Site interaction was not significant for either phylum or high-resolution analyses (Table 1c and d). The first level effects of time and site were also not significant, indicating that little spatial or temporal variation occurred at this location. Repeating the

analysis with sites pooled into treatments (i.e. testing the Time \times Trawling interaction) did not make any difference to the results.

Univariate Analyses

Only three univariate variables exhibited changes indicative of an impact of trawling. Changes to total abundance for 2+3 mirrored the multivariate patterns discussed above. The Time \times Treatment \times Location interaction was significant (Table 2a), with total abundance decreasing at the trawled sites of Location 2 and the control sites of 3 (Figure 3a, SNK tests).

The number of taxa per core was also greater at location 2 than 3, but interactions indicative of an effect of trawling were not significant (Table 2b). Individual taxa exhibited asynchronous variation in abundance over time and space (Figure 3c–h), but the Time \times Treatment interactions indicative of trawling impacts were never significant (Table 2c–h). The polychaete Ctenodrilidae type 1 and crustacean Tanaidacea changed in a manner consistent with an effect of trawling at one location only (they were very rare at the other location), as indicated by significant Time \times Location \times Treatment interactions (Table 3f and g, SNK tests). Ctenodrilidae 1 were common but decreased over time at location 2, particularly at the trawl sites (Figure 3f). Tanaidacea were common but decreased at location 3, decreasing slightly more at the trawl sites (Figure 3h). For location 1, the Time \times Treatment interaction was not significant for any of the univariate variables ($p > 0.17$ in all cases). Post-hoc pooling of the Time \times Location \times Treatment (for 2+3) or Time \times Site (for Location 1) with the residual enabled a more powerful test, but did not change the significance of any results.

In summary, there was considerable variation in abundances of taxa among locations (separated by 13–16 km) which at the scale of sites (tens of meters) was substantially reduced or not detectable (Table 2).

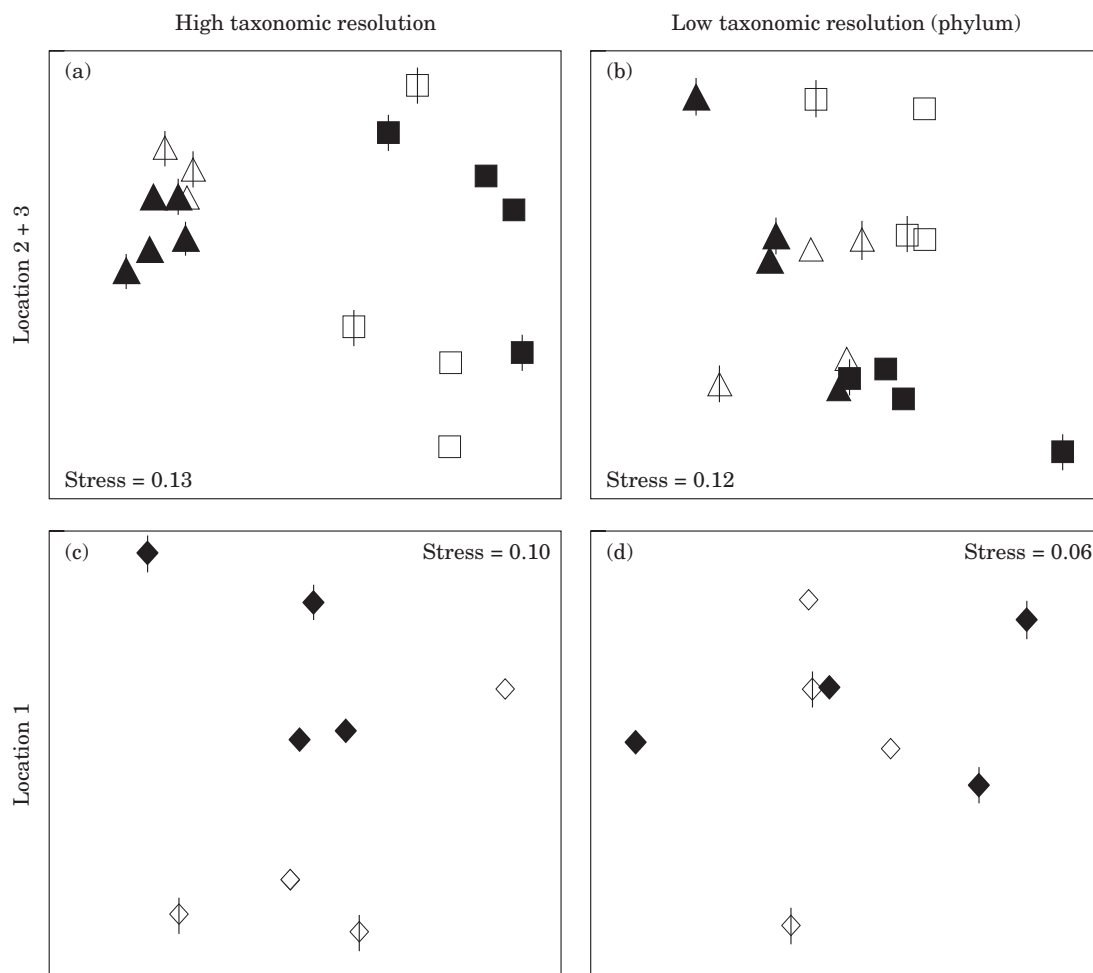


Figure 2. Non-metric multi-dimensional scaling (nMDS) ordinations, showing differences in the infaunal assemblages at the sites within locations 2 and 3, and location 1, before (open) and after (solid) trawling. Symbols with vertical lines refer to trawl sites. ▲ = Location 2, ■ = Location 3, ◆ = Location 1. $n=10$.

This larger scale variation appeared, in general, to swamp any variation that could have been attributable to trawling.

Discussion

The results do not support the hypothesis that trawling causes changes to infaunal assemblage structure as a general phenomenon. While the patterns of change at one location (2) and in two taxa supported the hypothesis, patterns at the other two locations and in other taxa did not. One possible reason for this is that different locations and taxa show differing susceptibilities to trawling, as has been found in other studies (e.g. Collie *et al.*, 1997; Engel and Kvitek, 1998; Kaiser, 1998; Kaiser and Spencer, 1996). Alternatively, the different patterns observed may be due to asynchronous, but natural, spatial and temporal variation. Thus, the

changes at location 2 cannot be rigorously ascribed to trawling, as substantial changes also occurred at control sites, and so may have occurred by chance. Several other studies have failed to detect effects of trawling on infauna (e.g. Gibbs *et al.*, 1980; Hall *et al.*, 1993; Simbora *et al.*, 1998), although none of these used a strictly controlled experimental trawling regime.

Given the high levels of natural variability inherent in marine assemblages (particularly infauna), it is important that studies on the effects of trawling are rigorously designed to avoid confounding. Inferences about trawling have been made by comparing existing trawled areas with areas believed to be untrawled or lightly trawled (e.g. Gibbs *et al.*, 1980; Collie *et al.*, 1997; Engel and Kvitek, 1998; Simbora *et al.*, 1998; Frid *et al.*, 1999), but these comparisons are spatially confounded as locations may vary naturally. Indeed, unless trawling has been excluded from an arbitrarily designated area by

Table 2. ANOVAs for effect of trawling on selected univariate variables (locations 2 and 3).

| Source | d.f. | MS | F | p | MS | F | p | MS | F | p |
|---------------------------------|------|--------|--------|--------|--------|--------|--------|--------|--------|------|
| (a) Abundance | | | | | | | | | | |
| Time | 1 | 138.76 | 23.10 | 0.13 | 1.23 | 0.77 | 0.54 | 1.37 | 0.0041 | 0.09 |
| Location | 1 | 387.51 | 188.45 | 0.0002 | 78.40 | 12.13 | 0.03 | 38.81 | 0.0029 | 0.01 |
| Trawling | 1 | 0.01 | 1.00 | 0.50 | 0.10 | 0.16 | 0.76 | 0.03 | 0.34 | 0.39 |
| Site (Lo × Tr) | 4 | 2.06 | 0.19 | 0.94 | 6.46 | 2.46 | 0.05 | 0.92 | 0.01 | 0.97 |
| Ti × Lo | 1 | 6.01 | 2.10 | 0.22 | 1.60 | 0.87 | 0.39 | 0.00 | 0.99 | 0.60 |
| Ti × Tr | 1 | 0.06 | 0.00 | 0.97 | 3.60 | 1.96 | 0.22 | 0.04 | 0.89 | 0.83 |
| Ti × Si (Lo × Tr) | 4 | 2.86 | 0.27 | 0.90 | 2.29 | 0.87 | 0.48 | 0.22 | 0.51 | 0.29 |
| Lo × Tr | 1 | 0.01 | 0.00 | 0.96 | 0.63 | 0.10 | 0.77 | 0.11 | 0.75 | 0.67 |
| Ti × Lo × Tr | 1 | 31.51 | 11.03 | 0.03 | 0.03 | 0.01 | 0.91 | 1.40 | 0.06 | 0.79 |
| Residual | 144 | 10.72 | | | 2.63 | | | 0.26 | | |
| (b) Number of taxa ^P | | | | | | | | | | |
| Time | 1 | 0.01 | 0.05 | 0.86 | 42.03 | 1.11 | 0.48 | 14.40 | 0.50 | 0.50 |
| Location | 1 | 3.88 | 16.55 | 0.02 | 280.90 | 478.13 | 0.0000 | 112.23 | 0.0031 | 0.01 |
| Trawling | 1 | 0.01 | 1.46 | 0.44 | 1.23 | 1.96 | 0.39 | 0.90 | 0.50 | 0.26 |
| Site (Lo × Tr) | 4 | 0.23 | 1.05 | 0.38 | 0.59 | 0.22 | 0.93 | 2.76 | 0.04 | 0.19 |
| Ti × Lo | 1 | 0.15 | 0.31 | 0.60 | 38.03 | 78.00 | 0.0009 | 14.40 | 0.0001 | 0.92 |
| Ti × Tr | 1 | 0.06 | 0.12 | 0.74 | 8.10 | 1.27 | 0.46 | 0.02 | 0.50 | 0.77 |
| Ti × Si (Lo × Tr) | 4 | 0.46 | 2.07 | 0.09 | 0.49 | 0.18 | 0.95 | 0.01 | 1.00 | 0.30 |
| Lo × Tr | 1 | 0.00 | 0.02 | 0.90 | 0.63 | 1.06 | 0.36 | 0.90 | 0.60 | 0.81 |
| Ti × Lo × Tr | 1 | 0.52 | 1.10 | 0.34 | 6.40 | 13.13 | 0.02 | 0.23 | 0.01 | 0.62 |
| Residual | 144 | 0.22 | | | 2.69 | | | 1.0931 | | |
| (c) Nemertea ^P | | | | | | | | | | |
| Time | 1 | 0.01 | 0.05 | 0.86 | 42.03 | 1.11 | 0.48 | 14.40 | 0.50 | 0.50 |
| Location | 1 | 3.88 | 16.55 | 0.02 | 280.90 | 478.13 | 0.0000 | 112.23 | 0.0031 | 0.01 |
| Trawling | 1 | 0.01 | 1.46 | 0.44 | 1.23 | 1.96 | 0.39 | 0.90 | 0.50 | 0.26 |
| Site (Lo × Tr) | 4 | 0.23 | 1.05 | 0.38 | 0.59 | 0.22 | 0.93 | 2.76 | 0.04 | 0.19 |
| Ti × Lo | 1 | 0.15 | 0.31 | 0.60 | 38.03 | 78.00 | 0.0009 | 14.40 | 0.0001 | 0.92 |
| Ti × Tr | 1 | 0.06 | 0.12 | 0.74 | 8.10 | 1.27 | 0.46 | 0.02 | 0.50 | 0.77 |
| Ti × Si (Lo × Tr) | 4 | 0.46 | 2.07 | 0.09 | 0.49 | 0.18 | 0.95 | 0.01 | 1.00 | 0.30 |
| Lo × Tr | 1 | 0.00 | 0.02 | 0.90 | 0.63 | 1.06 | 0.36 | 0.90 | 0.60 | 0.81 |
| Ti × Lo × Tr | 1 | 0.52 | 1.10 | 0.34 | 6.40 | 13.13 | 0.02 | 0.23 | 0.01 | 0.62 |
| Residual | 144 | 0.22 | | | 2.69 | | | 1.0931 | | |
| (d) Arthropoda ^P | | | | | | | | | | |
| Time | 1 | 0.01 | 0.05 | 0.86 | 42.03 | 1.11 | 0.48 | 14.40 | 0.50 | 0.50 |
| Location | 1 | 3.88 | 16.55 | 0.02 | 280.90 | 478.13 | 0.0000 | 112.23 | 0.0031 | 0.01 |
| Trawling | 1 | 0.01 | 1.46 | 0.44 | 1.23 | 1.96 | 0.39 | 0.90 | 0.50 | 0.26 |
| Site (Lo × Tr) | 4 | 0.23 | 1.05 | 0.38 | 0.59 | 0.22 | 0.93 | 2.76 | 0.04 | 0.19 |
| Ti × Lo | 1 | 0.15 | 0.31 | 0.60 | 38.03 | 78.00 | 0.0009 | 14.40 | 0.0001 | 0.92 |
| Ti × Tr | 1 | 0.06 | 0.12 | 0.74 | 8.10 | 1.27 | 0.46 | 0.02 | 0.50 | 0.77 |
| Ti × Si (Lo × Tr) | 4 | 0.46 | 2.07 | 0.09 | 0.49 | 0.18 | 0.95 | 0.01 | 1.00 | 0.30 |
| Lo × Tr | 1 | 0.00 | 0.02 | 0.90 | 0.63 | 1.06 | 0.36 | 0.90 | 0.60 | 0.81 |
| Ti × Lo × Tr | 1 | 0.52 | 1.10 | 0.34 | 6.40 | 13.13 | 0.02 | 0.23 | 0.01 | 0.62 |
| Residual | 144 | 0.22 | | | 2.69 | | | 1.0931 | | |
| (e) Annelida | | | | | | | | | | |
| Time | 1 | 0.01 | 0.05 | 0.86 | 42.03 | 1.11 | 0.48 | 14.40 | 0.50 | 0.50 |
| Location | 1 | 3.88 | 16.55 | 0.02 | 280.90 | 478.13 | 0.0000 | 112.23 | 0.0031 | 0.01 |
| Trawling | 1 | 0.01 | 1.46 | 0.44 | 1.23 | 1.96 | 0.39 | 0.90 | 0.50 | 0.26 |
| Site (Lo × Tr) | 4 | 0.23 | 1.05 | 0.38 | 0.59 | 0.22 | 0.93 | 2.76 | 0.04 | 0.19 |
| Ti × Lo | 1 | 0.15 | 0.31 | 0.60 | 38.03 | 78.00 | 0.0009 | 14.40 | 0.0001 | 0.92 |
| Ti × Tr | 1 | 0.06 | 0.12 | 0.74 | 8.10 | 1.27 | 0.46 | 0.02 | 0.50 | 0.77 |
| Ti × Si (Lo × Tr) | 4 | 0.46 | 2.07 | 0.09 | 0.49 | 0.18 | 0.95 | 0.01 | 1.00 | 0.30 |
| Lo × Tr | 1 | 0.00 | 0.02 | 0.90 | 0.63 | 1.06 | 0.36 | 0.90 | 0.60 | 0.81 |
| Ti × Lo × Tr | 1 | 0.52 | 1.10 | 0.34 | 6.40 | 13.13 | 0.02 | 0.23 | 0.01 | 0.62 |
| Residual | 144 | 0.22 | | | 2.69 | | | 1.0931 | | |
| (f) Ctenodrilidae sp 1 | | | | | | | | | | |
| Time | 1 | 0.01 | 0.05 | 0.86 | 42.03 | 1.11 | 0.48 | 14.40 | 0.50 | 0.50 |
| Location | 1 | 3.88 | 16.55 | 0.02 | 280.90 | 478.13 | 0.0000 | 112.23 | 0.0031 | 0.01 |
| Trawling | 1 | 0.01 | 1.46 | 0.44 | 1.23 | 1.96 | 0.39 | 0.90 | 0.50 | 0.26 |
| Site (Lo × Tr) | 4 | 0.23 | 1.05 | 0.38 | 0.59 | 0.22 | 0.93 | 2.76 | 0.04 | 0.19 |
| Ti × Lo | 1 | 0.15 | 0.31 | 0.60 | 38.03 | 78.00 | 0.0009 | 14.40 | 0.0001 | 0.92 |
| Ti × Tr | 1 | 0.06 | 0.12 | 0.74 | 8.10 | 1.27 | 0.46 | 0.02 | 0.50 | 0.77 |
| Ti × Si (Lo × Tr) | 4 | 0.46 | 2.07 | 0.09 | 0.49 | 0.18 | 0.95 | 0.01 | 1.00 | 0.30 |
| Lo × Tr | 1 | 0.00 | 0.02 | 0.90 | 0.63 | 1.06 | 0.36 | 0.90 | 0.60 | 0.81 |
| Ti × Lo × Tr | 1 | 0.52 | 1.10 | 0.34 | 6.40 | 13.13 | 0.02 | 0.23 | 0.01 | 0.62 |
| Residual | 144 | 0.22 | | | 2.69 | | | 1.0931 | | |
| (g) Tanaidacea | | | | | | | | | | |
| Time | 1 | 0.01 | 0.05 | 0.86 | 42.03 | 1.11 | 0.48 | 14.40 | 0.50 | 0.50 |
| Location | 1 | 3.88 | 16.55 | 0.02 | 280.90 | 478.13 | 0.0000 | 112.23 | 0.0031 | 0.01 |
| Trawling | 1 | 0.01 | 1.46 | 0.44 | 1.23 | 1.96 | 0.39 | 0.90 | 0.50 | 0.26 |
| Site (Lo × Tr) | 4 | 0.23 | 1.05 | 0.38 | 0.59 | 0.22 | 0.93 | 2.76 | 0.04 | 0.19 |
| Ti × Lo | 1 | 0.15 | 0.31 | 0.60 | 38.03 | 78.00 | 0.0009 | 14.40 | 0.0001 | 0.92 |
| Ti × Tr | 1 | 0.06 | 0.12 | 0.74 | 8.10 | 1.27 | 0.46 | 0.02 | 0.50 | 0.77 |
| Ti × Si (Lo × Tr) | 4 | 0.46 | 2.07 | 0.09 | 0.49 | 0.18 | 0.95 | 0.01 | 1.00 | 0.30 |
| Lo × Tr | 1 | 0.00 | 0.02 | 0.90 | 0.63 | 1.06 | 0.36 | 0.90 | 0.60 | 0.81 |
| Ti × Lo × Tr | 1 | 0.52 | 1.10 | 0.34 | 6.40 | 13.13 | 0.02 | 0.23 | 0.01 | 0.62 |
| Residual | 144 | 0.22 | | | 2.69 | | | 1.0931 | | |
| (h) Magelonidae ^P | | | | | | | | | | |
| Time | 1 | 0.01 | 0.05 | 0.86 | 42.03 | 1.11 | 0.48 | 14.40 | 0.50 | 0.50 |
| Location | 1 | 3.88 | 16.55 | 0.02 | 280.90 | 478.13 | 0.0000 | 112.23 | 0.0031 | 0.01 |
| Trawling | 1 | 0.01 | 1.46 | 0.44 | 1.23 | 1.96 | 0.39 | 0.90 | 0.50 | 0.26 |
| Site (Lo × Tr) | 4 | 0.23 | 1.05 | 0.38 | 0.59 | 0.22 | 0.93 | 2.76 | 0.04 | 0.19 |
| Ti × Lo | 1 | 0.15 | 0.31 | 0.60 | 38.03 | 78.00 | 0.0009 | 14.40 | 0.0001 | 0.92 |
| Ti × Tr | 1 | 0.06 | 0.12 | 0.74 | 8.10 | 1.27 | 0.46 | 0.02 | 0.50 | 0.77 |
| Ti × Si (Lo × Tr) | 4 | 0.46 | 2.07 | 0.09 | 0.49 | 0.18 | 0.95 | 0.01 | 1.00 | 0.30 |
| Lo × Tr | 1 | 0.00 | 0.02 | 0.90 | 0.63 | 1.06 | 0.36 | 0.90 | 0.60 | 0.81 |
| Ti × Lo × Tr | 1 | 0.52 | 1.10 | 0.34 | 6.40 | 13.13 | 0.02 | 0.23 | 0.01 | 0.62 |
| Residual | 144 | 0.22 | | | 2.69 | | | 1.0931 | | |

Post-hoc pooling of the interaction term Ti × Lo × Tr with the residual (when $p > 0.25$; indicated by ^P) enabled a more powerful test of the main interaction of interest, Ti × Tr (Winer *et al.*, 1991). Results of Cochran's tests and transformations: (a), (b)=homogeneous ($p > 0.05$) and untransformed; (c), (d), (e)=homogeneous after $\log_e(x+1)$ transformation; (f), (g), (h)=heterogeneous and untransformable.

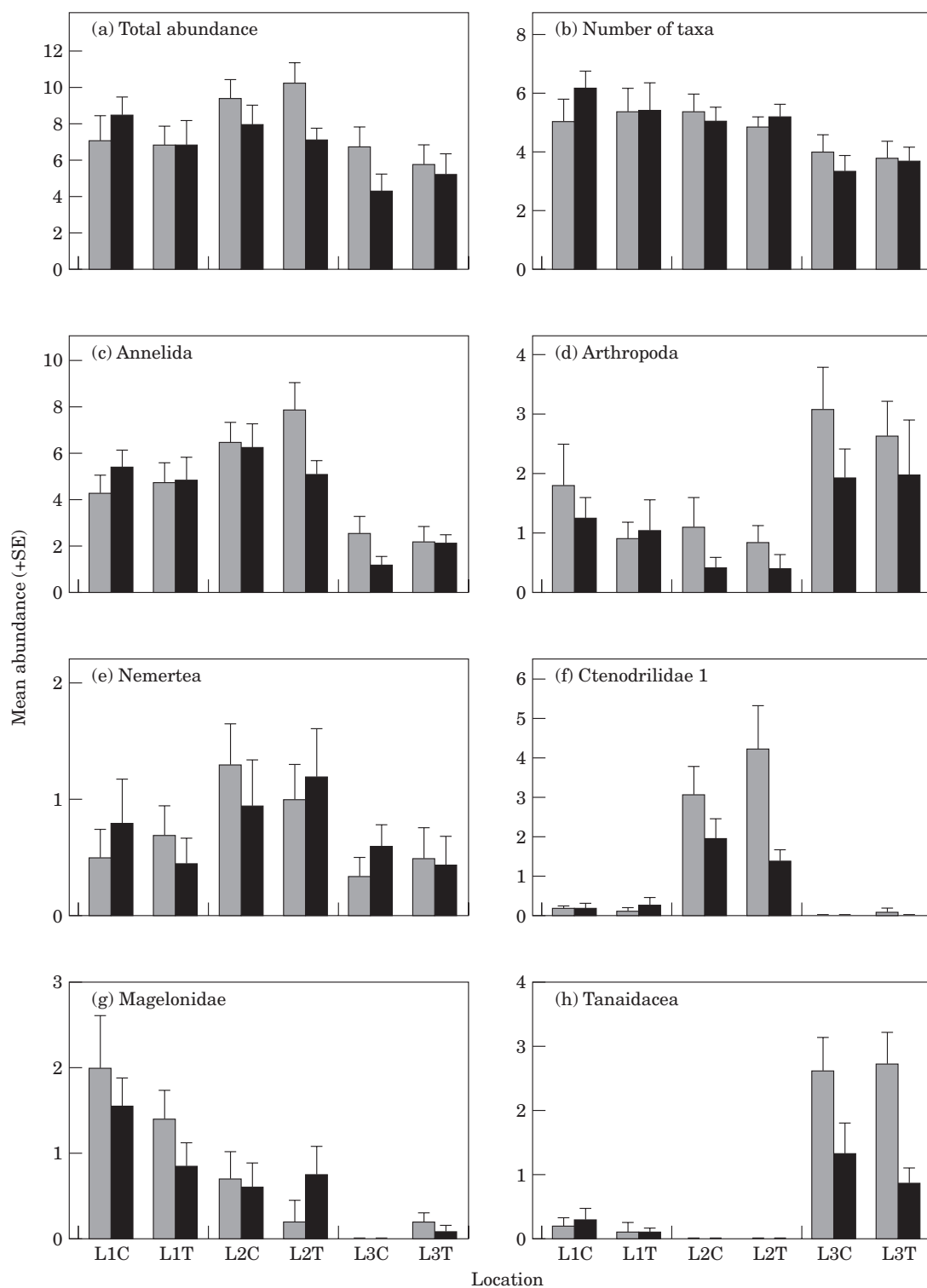


Figure 3. Changes in abundance over time (before vs. after trawling), for total abundance, number of taxa, and the three most abundant phyla and high-resolution taxa. The two sites within each corridor have been combined to simplify interpretation of the graphs. Stippled bars represent before trawling, black represents after trawling. $n=20$. L1C=location 1 control, L1T=Location 1 trawl, etc.

legislation, there is good reason to believe that trawled and untrawled areas will differ substantially. Trawling effort data, which is used to define the trawling regime, may also be unreliable as it has to be inferred from fishing logs or visual clues such as density of trawl tracks (Engel and Kvitek, 1998), and illegal trawling still occurs in "closed" areas (Poiner *et al.*, 1998). Studies that sample before and after trawling but do not include control sites (e.g. Bergman and Hup, 1992), are temporally confounded. Assemblages change naturally over time, in response to factors such as recruitment events and natural disturbances. Lindegarth *et al.* (2000) compared different combinations of single control and trawl sites of a Multiple Before-After, Control-Impact experiment and found that some pairs showed changes indicative of an impact from trawling, but others did not. Even studies that are temporally replicated with multiple sampling times both before and after trawling (Before-After, Control-Impact Paired Series BACIPS, e.g. Tuck *et al.*, 1998), but not replicated in space, are spatially confounded (Hurlbert, 1984; Thrush *et al.*, 1994). Thrush *et al.* (1994) found that spatial variation in infauna was greater and had more influence on results than temporal variation. They concluded that spatial variability confounds temporal patterns in time series data, such as that of BACIPS experiments.

The severity of the disturbance caused by trawling (and the ability to detect impacts on trawling) is influenced by the natural disturbance regime (Jennings and Kaiser, 1998). The infauna in stable sediments may be less tolerant to trawling because they are not adapted to high levels of disturbance (Kaiser and Spencer, 1996). The physical severity of the trawling disturbance will also vary with sediment type, as the gear penetrates deeper into soft muds than coarse or hard-packed sands (Hall, 1999). In areas with a naturally high disturbance regime, movement of the sediment can cause a dilution of the effects of disturbance (Hall, 1999). Kaiser and Spencer (1996) found lower numbers of species and individuals in trawled areas than in untrawled areas with stable sediments, but no significant difference in areas with coarse, mobile sediments. They found that the mobile sediments had an impoverished and highly variable infaunal community, and suggested that these factors may have prevented the detection of differences between trawled and untrawled areas. In our study, location 2 had very fine sediments compared to coarse sediments at locations 1 and 3, and this may account for the apparent effect of trawling at this location only. Lack of replication within this sediment type, however, means that this interpretation is tentative.

Most studies that fail to detect effects of trawling have been criticised on the grounds that they have been conducted in areas that have been trawled previously, or that they fail to adequately account for natural variation

in organism abundance. In this study, however, we examine areas that have not been trawled for a relatively long period (15–20 years), and have carefully controlled for spatial variation. The lack of an effect is thus more likely to be due to the light trawl gear and low level of trawling used in this experiment, which is characteristic of the fishing grounds in this lightly trawled area. Poiner *et al.* (1998) in the Great Barrier Reef region found that a single pass with an otter trawl did not significantly affect the epifauna, and severe damage was only detected after repeated trawling of the same ground. Consistent with this finding, Tuck *et al.* (1998) found that repeated trawling in a Scottish sea loch caused clear long-term changes to topography and infaunal community structure. Damage would have been worse in areas subjected to the passage of the otter boards (e.g. Caddy, 1973; Brylinsky *et al.*, 1994; Gilkinson *et al.*, 1997), although these tracks only cover a small proportion of the area affected by the trawl, and were not sampled in this study.

The amount of natural temporal and spatial variability in biological assemblages can exceed changes induced by anthropogenic disturbances. We suggest that, in South Australia, prawn trawling as its current level does not cause consistently significant changes to infaunal assemblages, due to a combination of high natural variability and relatively low-impact trawling gear, particularly in areas with high levels of natural disturbance. It is likely that the degree of adaptation to disturbance and the physical environment also affect the extent of disturbance caused by trawling. This result contrasts to that found for epifauna, which experienced an average 28% decline in abundance from the experimental trawling, and which slowly declined further in subsequent months (J.E.T., unpublished results).

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Appendix

Identification and total abundances of taxa found over all sites and times sampled (from 240 cores).

| Phylum | High-resolution | Total | Phylum | High-resolution | Total |
|----------|--------------------|-------|---------------|------------------|-------|
| Annelida | Ampharetidae | 29 | Annelida | Spionidae sp 4 | 5 |
| | Arabellidae | 12 | | Syllidae sp 1 | 47 |
| | Caobangidae | 1 | | Syllidae sp 2 | 17 |
| | Capitellida | 60 | Arthropoda | Syllidae sp 3 | 14 |
| | Cirratulidae | 13 | | Terebellida | 41 |
| | Ctenodrilidae sp 1 | 229 | | Anthuridea | 3 |
| | Ctenodrilidae sp 2 | 4 | | Brachyura | 4 |
| | Dorvilleidae | 7 | | Caprellidea | 3 |
| | Eunicidae | 2 | | Caridea | 2 |
| | Flabelligeridae | 72 | | Copepoda | 31 |
| | Glyceridae | 4 | | Crustacea larvae | 1 |
| | Magelonidae | 164 | | Cumacea | 4 |
| | Nephtyidae | 103 | | Gammaridea | 130 |
| | Nereidae | 1 | | Isopoda | 9 |
| | Opheliidae | 5 | | Leptostraca | 3 |
| | Oweniidae | 15 | | Mysidacea | 2 |
| | Paraonidae | 9 | | Ostracoda | 6 |
| | Parergodrilidae | 2 | | Pycnogonida | 1 |
| | Phyllodocidae | 19 | | Tanaidacea | 150 |
| | Pilargidae | 2 | Chordata | Ascidiacea | 13 |
| | Poecilochaetidae | 8 | Cnidaria | Actinaria | 1 |
| | Polychaeta sp 1 | 1 | Echinodermata | Echinoidea | 15 |
| | Polychaeta sp 2 | 7 | | Holothuroidea | 34 |
| | Polychaeta sp 3 | 1 | | Ophiuroidea | 13 |
| | Polychaeta sp 4 | 2 | Echiura | Echiura | 3 |
| | Polychaeta sp 5 | 1 | Mollusca | Bivalvia | 34 |
| | Polychaeta sp 7 | 4 | | Gastropoda | 2 |
| | Polychaeta sp 8 | 3 | | Opisthobranchia | 4 |
| | Polynoidae | 4 | Nemertea | Polyplacophora | 1 |
| | Sabellidae | 37 | | Nemertea sp 1 | 137 |
| | Sigalionidae | 11 | | Nemertea sp 2 | 29 |
| | Spionidae sp 1 | 92 | Sipuncula | Nemertea sp 3 | 10 |
| | Spionidae sp 2 | 10 | | Sipuncula | 13 |
| | Spionidae sp 3 | 3 | | | |