The influence of prawn trawling on sessile benthic assemblages in Gulf St. Vincent, South Australia

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Abstract: Most experimental studies on the effects of trawling on the benthos use remote sampling techniques and are conducted in recently trawled areas. Thus it is difficult to determine the effects of trawling on previously unfished areas, and the fates of individual animals cannot be followed. In this study, I follow the fates of individuals of several sessile taxa when exposed to experimental trawling in areas that have not been trawled for some 15–20 years. Although there was a significant trawling by location effect for all multivariate analyses and most individual taxa, I found that trawling had an overall negative effect on the benthos. Epifauna at trawled sites decreased in abundance by 28% within 2 weeks of trawling and by another 8% in the following 2–3 months (compared with control sites). Seasonal seagrasses were also less likely to colonise trawled sites than untrawled sites. The persistence of most taxa declined significantly in trawled areas compared with untrawled areas. In contrast to this, the recruitment rates of several taxa into visible size classes increased after trawling, presumably because of a reduction in competition.

Résumé : La plupart des études des effets du chalutage sur le benthos utilisent des techniques d'échantillonnage à distance et sont menées sur des surfaces récemment soumises au chalutage. Il est ainsi difficile de déterminer les effets du chalutage sur des surfaces où on n'a pas encore pêché par chalutage et, de plus, le sort d'animaux individuels ne peut pas être suivi. La présente étude suit le sort de plusieurs taxons sessiles exposés à un chalutage expérimental à des sites sur lesquels on n'a pas pêché par chalutage depuis environ 15–20 ans. Il y a un effet significatif du chalutage × site dans toutes les analyses multidimensionnelles et pour la plupart des taxons considérés individuellement; l'effet global du chalutage est négatif pour le benthos. L'épifaune décline en abondance de 28 % en moins de 2 semaines après le chalutage et d'un 8 % supplémentaire dans les 2–3 mois qui suivent (par comparaison aux sites témoins). Les herbes marines saisonnières sont aussi moins susceptibles de coloniser les sites soumis au chalutage que les sites où il n'y a pas eu de pêche. La persistance de la plupart des taxons diminue de façon significative aux sites de chalutage par rapport aux sites sans chalutage. En revanche, les taux de recrutement de plusieurs classes de taille visibles augmentent chez de nombreux taxons après le chalutage, sans doute à cause d'une réduction de la compétition.

[Traduit par la Rédaction]

Introduction

The consequences of bottom trawling for marine communities are coming under increasing scrutiny worldwide. As a result, an increasing number of studies have documented the effects of trawling, or lack thereof, on infaunal and epifaunal abundance and community composition, scavengers, sediment structure and turbidity, and structural characteristics of the benthos (for recent reviews, see Jennings and Kaiser (1998), Hall (1999), and Turner et al. (1999)). However, it has often proven difficult to detect an effect of trawling, especially on animal abundances, despite several reports likening the practise to forest clearcutting (e.g., Watling and Norse 1998). There are two major reasons for this. Firstly, many studies are carried out in areas that have been repeatedly trawled over a number of years, and thus the community has probably already been modified and vulnerable species removed. In many locations, unfished areas that could be used to experimentally determine the effects of trawling on virgin ground simply do not exist (e.g., Kaiser et al. 1998). Those areas that are unfished probably remain that way because they are poor fishing grounds, suggesting that there may be fundamental differences to fished areas in the benthic assemblages as well. Secondly, most studies have used remote sampling methods to determine changes in abundance (e.g., grab samples, remote video, trawl nets, and benthic sledges, but see Van Dolah et al. (1987)). Although differential global positioning systems (dGPS) now allow sites to be relocated with a high degree of precision, it is still impossible to relocate individual animals with these methods, even for sessile epifauna. In combination with the high degree of spatial variability in organism abundance in many areas of the world's oceans, this means that only relatively large changes can be detected, and determining the fate of individual animals is difficult or impossible. As an example, a large study on Australia's Great Barrier Reef has shown that a single pass of a trawl only removes about 10% of the epifauna, and effects are only detectable in catches after several passes over the same location (Poiner et al. 1998). Such intensive trawling is rare in experimental studies, although not in

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commercial practise. For instance, in one area of the North Sea, 9% of the surface area of the seabed is trawled in excess of five times a year (Rijnsdorp et al. 1998), and some locations may be trawled intensively for many years.

In this paper, I examine the effects of trawling for penaeid prawns (shrimp) on the sessile epibenthos in Gulf St. Vincent, South Australia. Gulf St. Vincent is one of two large semienclosed inverse estuaries on Australia's southern coast in which extensive prawn trawling occurs, with the other (Spencer Gulf) having broadly similar habitat types (J.E. Tanner, personal observation). Given the large number of studies examining the effects of trawling on the benthos, there were two key objectives to this study. The first was to obtain a precise measurement of the changes in assemblage structure and abundance of individual taxa by monitoring a set of permanently marked quadrats both before and after trawling. This method has rarely been applied in studies examining the effects of trawling, partly because most trawl grounds are in water depths that preclude access by scuba divers and partly because most trawling occurs over soft sediments with many of the fauna of interest being mobile (but see Van Dolah et al. (1987)). The second objective was to examine in greater detail the demographic processes of change associated with trawling. To date, most studies simply report changes in numbers of animals present and possibly their size structure. The use of permanent quadrats allows mortality and recruitment rates to be estimated also, giving the potential to estimate longer-term effects. For example, if recruitment rates are high after trawling, recovery will be rapid compared with if they are low. In this paper, I concentrate on epifauna, with the infuana discussed in Drabsch et al. (2001).

Methods

Site description

Gulf St. Vincent is a large (~7150 km^2), relatively shallow (generally <30 m) embayment on the southern coast of Australia (Shepherd and Sprigg 1976). As a result of minimal freshwater input and high summer evaporation rates, it is an inverse estuary, with salinity increasing towards the head of the gulf. Water exchange with the open ocean is restricted by Kangaroo Island, which also protects the area from high wave activity. Most of the gulf is depositional, with few areas of hard substrate, although calcrete commonly occurs less than 200 mm below the sediment surface and may provide attachment points for some sessile species. The mean grain size of sediments in the northern gulf, where this study was conducted, is ~0.25 mm, with calcium carbonate predominating (Waters 1976). The dominant fauna are adapted to living in soft sediments. Seagrasses occur extensively in shallow waters, covering an area of almost 2500 km^2 (Edyvane 1999). Most seagrass meadows occur from the intertidal zone to about 15 m deep, although some species, notably in the genus *Halophila*, extend considerably deeper. The composition of the epibenthos in this region is highly variable (J.E. Tanner, personal observation), and locating several similar sites in areas that had not been trawled for at least 10–20 years, but were considered to be trawlable, was not possible in the limited time available. The resulting variability in the composition of the epifaunal assemblage complicated interpretation of the results and reduced the power of statistical tests but provides greater ability to generalise over the gulf as a whole.

Bottom trawling for prawns began in Gulf St. Vincent in 1968. Fishing pressure rapidly escalated and reached a peak with 16 boats fishing for a total of 15 200 h in 1982. Since then, effort has declined, and in recent years the fishery has been restricted to 10 boats fishing for about 2000 h (30–40 nights) per year in total. Currently, the boats involved in this fishery are a maximum of 15.2 m long and use a triple otter trawl with a maximum total headline length of 27.43 m. The gear is relatively light, with two 200 kg otter boards to spread the nets and two 240 kg skids to separate them. The total spread of the nets when trawling is approximately 20 m.

Experimental design

To examine the effects that trawling had on the benthic fauna in Gulf St. Vincent, three locations in the northern gulf were selected for experimental trawling using a multiple before–after, control–impact (MBACI) design. These locations were in ~20 m of water, the shallowest depth at which extensive commercial trawling occurs, and in areas that have not been recently trawled. Fishing effort in the gulf has been recorded in blocks of ~30 n.mi.^{2} (nautical miles^2) since the fishery started. The block containing location 1 was trawled in 1997–1998, but total trawling time in the previous 10 years was less than 1000 min, and discussions with the fishers indicated that this occurred further out to sea than the experimental location. The blocks containing locations 2 and 3 had not been trawled since 1985. Prior to this, more extensive trawling had occurred in these fishing blocks, but the area was closed to protect suspected spawning areas and has not been used since reopening because of substantial reductions in overall effort. Thus the locations used represented typical trawling ground that had not been trawled for at least 14 years. Casual inspection of *Pinna bicolor* (a large, long-lived, erect bivalve) showed no evidence of trawl damage, further supporting the contention that these areas had not been trawled recently. Such damage was obvious 1 year after trawling, although it is not known how much longer it remains so.

At each of the three study locations, two adjacent sites (trawl and control) were established using dGPS. Each site was 0.5 n.mi. long and 200 m wide. At both sites, a series of ten 3 m × 3 m permanent quadrats were marked by steel pegs driven below the sediment surface to allow the net to pass freely over the top of them. Each of these quadrats was divided into nine 1 m × 1 m subquadrats, which were also marked out in a similar manner to facilitate comparisons between censuses. Each peg was tagged with a fluorescent streamer that projected above the sediment surface so that it could be relocated subsequent to trawling. Quadrats were randomly located (using random number tables) in an area of approximately 50 m × 20 m, about the maximum that could comfortably be covered by an encumbered diver in a single dive. These quadrats were set up and photographed in August 1999 to quantify the abundance of epifauna. A digital video camera was used to photograph every ¼ m^2, with the permanently located steel pegs ensuring precise matching between censuses. These digital photographs were then merged into a single photomosaic of each 9-m^2 quadrat, which was the sampling unit. The numerical abundances of sponges, bryozoans, ascidians, and the bivalve *Pinna bicolor* in each quadrat were determined, and the fate of individual animals was followed over time. The three former groups were not identified to a lower taxonomic level because of the large number of relatively rare species present and the poor taxonomic knowledge of marine fauna in this region. Other sessile taxa, including soft corals, sea pens, and hydroids, were extremely rare (<1% each) and were not quantified. As it was not always possible to accurately distinguish and identify animals less than 2 cm in diameter because of poor visibility on some days, animals smaller than this were not included. Thus recruitment is defined here as the entry of an organism into this size class. The percent cover of seagrass was also quantified by placing a random grid of 25 points over every ¼ m^2 photograph. Infauna were sampled from areas adjacent to two of the quadrats at each site and are discussed elsewhere (Drabsch et al. 2001).

The trawl sites were trawled over a series of three nights by a commercial prawn trawler (*Jillian Sandra*) involved in the fishery in October 1999. A series of 10 adjacent passes were made over the entire site at a speed of 3.5 knots, which was repeated for a total of 20 passes. As the sweep of the nets was approximately 20 m, this resulted in the entire site being covered twice on average. Trawling was conducted in a fashion identical to commercial trawling, with the exception that each shot was only 10 min compared with 1–2 h in commercial trawling.

One week after trawling, locations 2 and 3 were recensused to determine the effect of the trawl on the benthic assemblage. Poor weather prevented location 1 from being censused at this time, and this location was not surveyed again until January 2000, 3 months after trawling. Locations 2 and 3 were also recensused at this time to assess any delayed effects of trawling or short-term recovery.

Statistical methods

To determine the effects of trawling on the sessile epifaunal assemblage present, a nonparametric multivariate analysis of variance was used (NP-MANOVA; Anderson 2001) to test for differences between treatments (control vs. trawl) and locations. NP-MANOVA uses random permutations of the original data to calculate *P* values and is somewhat analogous to the more familiar analysis of similarities (Clarke 1993), but allows for tests of interactions between factors. This procedure was chosen because of the general inability of ecological data to adequately meet the assumptions of parametric MANOVA, although NP-MANOVA does have its own restrictions. As the current version cannot handle a repeated-measures design, the change in abundance of the different epifaunal taxa had to be analysed for each census interval (August–October, October–January, and August–January) separately. This procedure also avoided problems associated with location 1 being missing from the second census. Differences between samples were quantified using Euclidean distances, as zeroes generally indicated no change rather than absence of the taxon (especially with only four taxa present). Trawling was analysed as a fixed factor, whereas location was random, and a total of 4999 permutations of the residuals under a reduced model were performed (see Anderson 2001). Significant terms were further analysed using a posteriori pairwise comparisons conducted in a similar fashion to the complete analysis. Nonmetric multidimensional scaling (MDS) was used to visualise differences in change over time between samples. The MDS was based on Euclidean distance, with untransformed data, and was performed using PC-ORD (MjM Software, Gleneden Beach, Ore.). This technique reduces a multidimensional scatter plot into a lower number of dimensions while preserving the maximum amount of variation in the data, which allows relationships between individual points to be more easily visualised.

Individual taxa (including seagrass) were analysed with conventional univariate ANOVA (analysis of variance) with the same design using SPSS (SPSS Inc., Chicago, Ill.). For seagrass, only abundance at locations 1 and 2 in the final (January) census was analysed. There was no seagrass present at the initial census, and data on abundance at location 1 was not available for the second census. Location 3 was not included in this analysis, as seagrass was never observed to occur there. Normal probability plots and Cochran's test for homogeneity of variances were used to test ANOVA assumptions and indicated that analyses could not be improved by transforming the data.

To determine the potential mechanisms by which trawling alters the structure of epifaunal assemblages, both persistence and recruitment of the four main taxa were examined. Differences in persistence were analysed using generalised linear models (GLM) with a binomial distribution and logit link function, whereas for recruitment, a Poisson distribution and log-link function were used (McCullagh and Nelder 1989). These analyses were performed with SPlus (MathSoft Inc., Cambridge, Mass.). Persistence here refers to persistence within the quadrat, and animals that did not persist may have still been alive but have been moved from the quadrat either by the trawl or by currents. Similarly, recruitment does not equate to settlement but includes existing animals that grew large enough to be censused and, more importantly, adults that moved into the quadrats. Movement of adults was common for these so-called sessile organisms and occurred because animals were either adapted to being rolled around by currents or were only attached to pieces of shell, etc., which could be moved without damage to its attached fauna.

Results

For all three time intervals, change in epifaunal composition was strongly influenced by the interaction between location and trawling (Table 1), indicating that the effects of trawling are location dependent. Changes in the control sites at locations 2 and 3 were very similar between the pre- and post-trawl censuses, indicated by the high overlap between the two groups of filled symbols in Fig. 1*a*, although location 3 was more variable. Pairwise comparisons showed that the two control sites did not differ significantly (P = 0.74). The two trawl sites differed from each other (P < 0.002), and at each location, the change at the trawl site differed from that at the control site (location 2, P < 0.002; location 3, P = 0.034). Univariate ANOVAs indicated that changes in the abundance of *Pinna* ($F_{[1,36]}$ = 22.8, P < 0.001), sponges ($F_{[1,36]}$ = 4.2, P = 0.048), and bryozoans ($F_{[1,36]}$ = 10.2, P = 0.003) were all significantly affected by the trawling by lo-

Table 1. Nonparametric multivariate analysis of variance for changes in composition of the epifaunal assemblages as the result of trawling between censuses.

Source	df	SS	*F*	*P*
Pre- to post-trawl 1				
Treatment	1	1096	1.21	0.46
Location	1	895	26.14	0.0002
Treatment × location	1	903	26.38	0.0002
Residual	36	1232		
Post-trawl 1 to post-trawl 2				
Treatment	1	1777	1.06	0.48
Location	1	1427	18.40	0.0002
Treatment × location	1	1681	21.66	0.0002
Residual	36	2794		
Pre- to post-trawl 2				
Treatment	1	1274	1.15	0.39
Location	2	2014	18.58	0.0002
Treatment × location	2	2213	20.41	0.0002
Residual	54	2927		

cation interaction. *Pinna* and sponges decreased only at the trawl site at location 2, not at the control sites or the location 3 trawl site (Figs. 2*b*, 2*c*). Bryozoans declined at all four sites, irrespective of trawling, with the decrease being greatest at location 2 trawl and least at location 2 control (Fig. 2*d*). Bryozoans at location 3 did not seem to be influenced by trawling. Ascidian abundance did not change with either trawling ($F_{[1,1]} = 1.3$, $P = 0.46$) or location ($F_{[1,1]} = 0.4$, $P = 0.63$, Fig. 2*a*).

At the multivariate level, changes between the second and third censuses were similar to changes between the first two censuses, although pairwise comparisons indicated that the two control sites differed ($P = 0.004$). Again the MDS plot shows that the location 2 trawl site differed most from the other sites (Fig. 1*b*). Univariate analyses indicated that the effect of prior trawling on *Pinna* ($F_{[1,36]} = 26.6$, $P < 0.001$), sponges ($F_{[1,36]} = 7.4$, $P = 0.01$), and bryozoans ($F_{[1,36]} = 10.2$, $P = 0.003$) depended on location. Again ascidians did not respond to either trawling ($F_{[1,1]} = 22.6$, $P = 0.13$) or location ($F_{[1,1]} = 15.7$, $P = 0.16$). Sponges decreased at all but the location 2 trawl site (Fig. 2*c*), whereas bryozoans continued to decrease at all sites (Fig. 2*d*).

Looking at the whole 5-month period, pairwise comparisons show that changes in epifauna between the control and trawl sites are different at both locations 1 and 2 ($P < 0.002$) but not at location 3 ($P = 0.44$). Changes were consistent at locations 1 and 2 control sites ($P = 0.24$) but not at the location 3 control site ($P = 0.023$). For the trawl sites, locations 1 and 3 responded similarly ($P = 0.53$), but both differed from location 2 ($P < 0.002$). The location 2 trawl site clearly differs from other sites in the MDS plot and has a much higher degree of variability (Fig. 1*c*). All five other sites (control and trawl) show some overlap. Univariate ANOVAs indicate that trawling-induced changes in the abundance of ascidians ($F_{[2,54]} = 5.7$, $P = 0.005$), *Pinna* ($F_{[2,54]} = 28.9$, $P < 0.001$), and bryozoans ($F_{[2,54]} = 5.8$, $P = 0.005$) are affected by location. Sponges are affected by trawling irrespective of location ($F_{[1,2]} = 24.5$, $P = 0.038$), decreasing slightly at trawl sites but remaining stable at control sites (Fig. 2*c*).

Fig. 1. Multidimensional scaling plots showing the effect of trawling on change in community composition at different locations over three time periods: (*a*) change between pre-trawl and first post-trawl census, (*b*) change between first and second post-trawl censuses, and (*c*) change from pre-trawl to second post-trawl census. The stress values of 0.11, 0.09, and 0.14, respectively, indicate that the two-dimensional plot provides an adequate representation of the data. Open shapes, trawled; solid shapes, control; circles, location 1; triangles, location 2; squares, location 3.

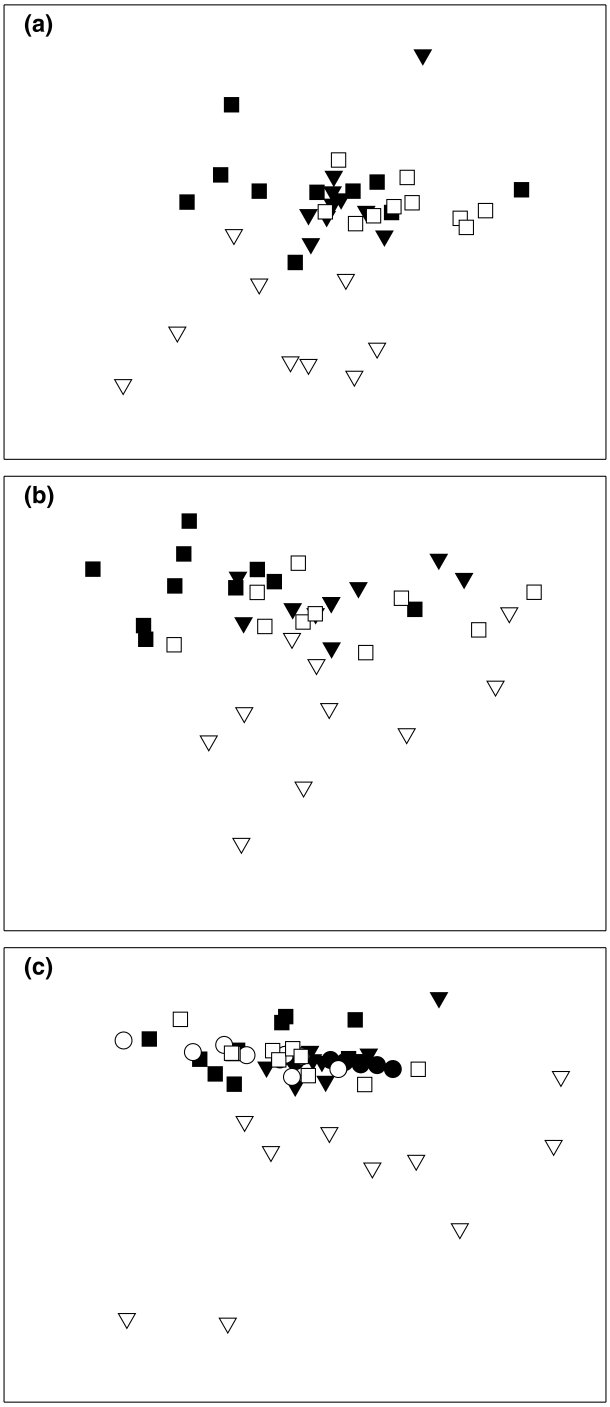
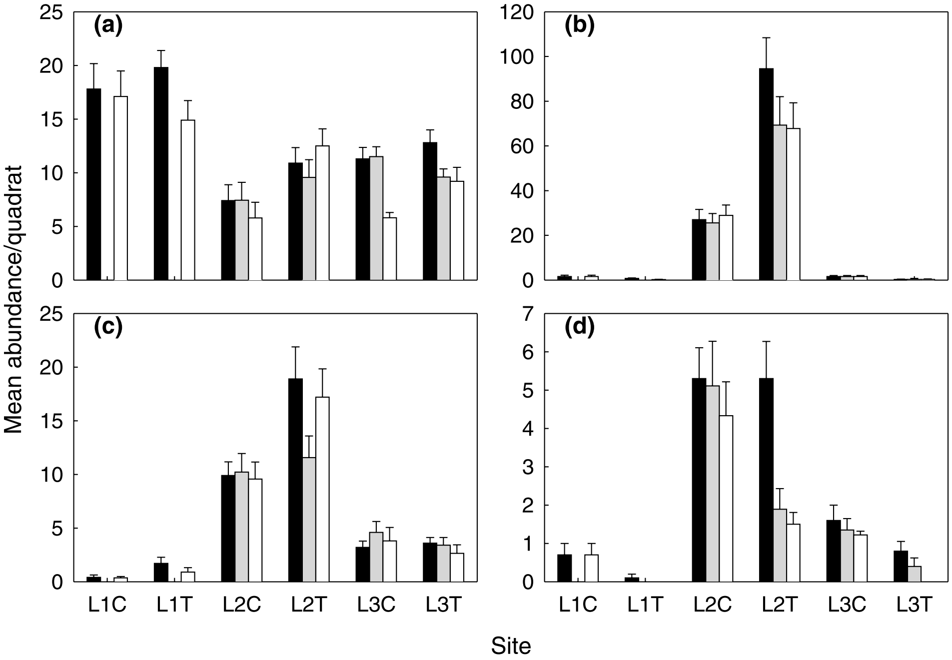


Fig. 2. Changes in mean abundances in 9-m^2 quadrats of (*a*) ascidians, (*b*) *Pinna*, (*c*) sponges, and (*d*) bryozoans over time: solid bar, census 1; shaded bar, census 2; open bar, census 3; L1C, location 1 control site; L1T, location 1 trawl site, etc. Error bars represent 1 standard error.



Ascidian abundance declines at all sites, except location 2 trawl where it increases (Fig. 2*a*). *Pinna* show no change at control sites but decrease at the trawl site at location 2 (Fig. 2*b*). Bryozoans decrease at all sites except for the control site at location 1 (Fig. 2*d*).

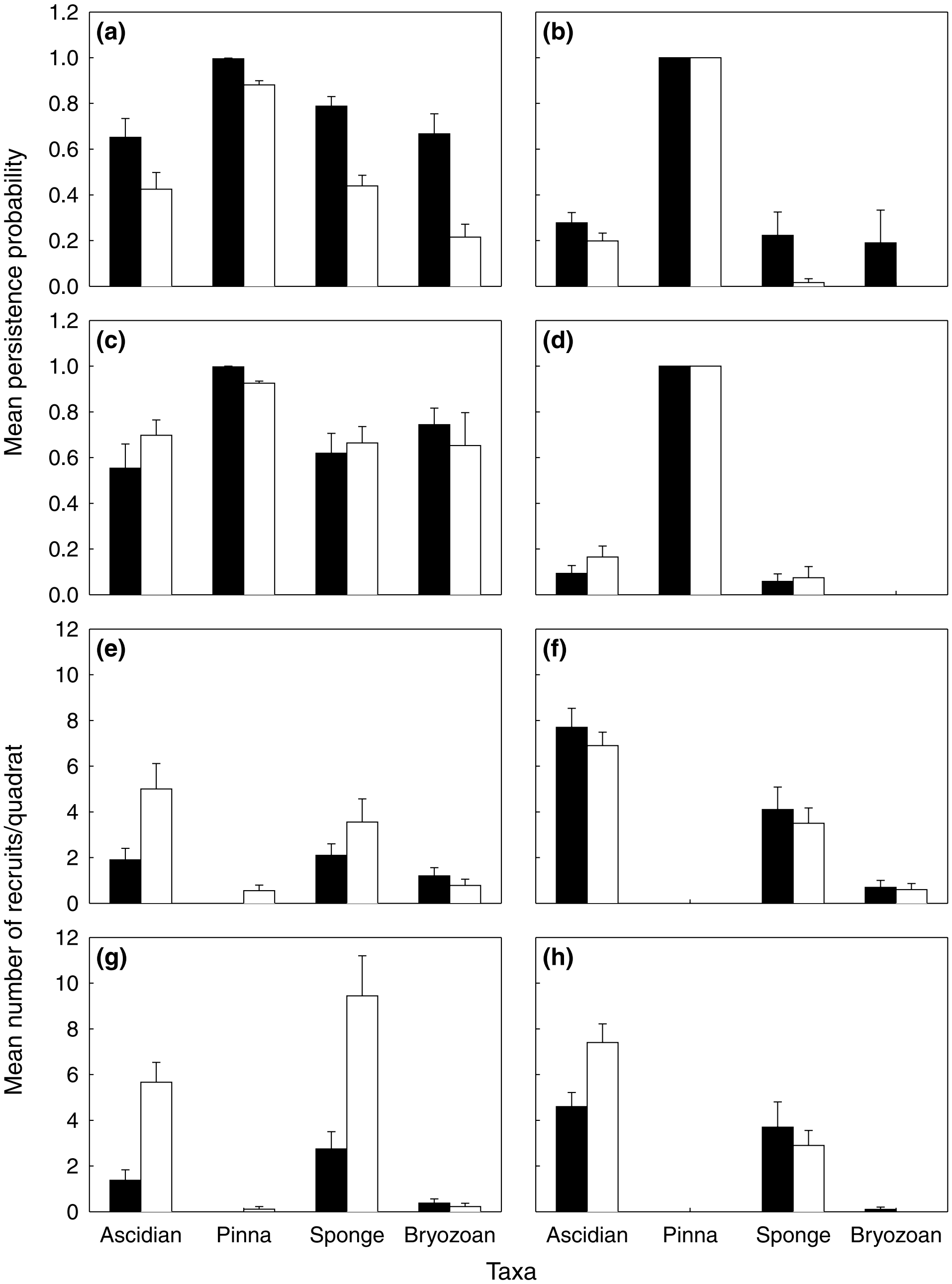
Over all three locations and both treatments, there were 10 instances of individual taxa declining by more than 25% over the entire 5-month study period (see Fig. 2). Nine of these declines occurred at trawl sites, with only one being at a control site (ascidians at location 3). This is a significant bias towards decline at trawl sites (binomial test, $P = 0.011$), indicating that trawling does have an overall negative (although variable) impact on the abundances of sessile epifaunal species. During the first 2 months (with only two locations), there were only five declines, all being at trawl sites ($P = 0.031$), so the negative effect of trawling is not always immediately obvious. There were only three instances of taxa increasing in abundance by greater than 25%, sponges at location 3 control site over the first period and ascidians and sponges at location 2 trawl over the second period. No taxon increased by 25% at any site over the entire 5 months.

When individual demographic rates for the four main taxa were examined, the trend was for persistence to decrease at trawl sites relative to control sites in the first (trawling) period, with few differences in the second period. Conversely, recruitment was often higher at trawl sites over all periods, especially at location 2 (Figs. 3, 4). For period 1 (trawling), trawling decreased the persistence of all taxa (GLM: ascidians $F_{[1,35]} = 6.3$, $P = 0.017$; *Pinna* $F_{[1,28]} = 112.4$, $P < 0.001$; sponges $F_{[1,37]} = 14.6$, $P = 0.0005$; bryozoans $F_{[1,29]} = 12.2$, $P = 0.0017$) consistently at both locations (Figs. 3*a*, 3*b*; test for interaction between treatment and location $P > 0.3$ for all taxa).

During period 2, the only taxon to display an effect of trawling on persistence was *Pinna*, which continued to experience increased mortality at trawl sites (GLM: $F_{[1,26]} = 93.5$, $P < 0.001$; Figs. 3*c*, 3*d*), with all other taxa having the same persistence probability at both trawl and control sites (ascidians $F_{[1,35]} = 2.8$, $P = 0.11$; sponges $F_{[1,34]} = 0.6$, $P = 0.43$; bryozoans $F_{[1,23]} = 0.01$, $P = 0.92$). Over the entire 5 months, *Pinna* ($F_{[1,40]} = 78.6$, $P = 0.001$) and sponges ($F_{[1,47]} = 4.1$, $P = 0.05$) had lower persistence in trawl than control sites, whereas ascidians had marginally lower persistence ($F_{[1,57]} = 3.7$, $P = 0.06$). Bryozoans displayed an interaction between location and treatment ($F_{[2,30]} = 9.8$, $P = 0.005$), with trawling decreasing persistence at locations 1 and 2 but not at location 3 where no bryozoans survived in either treatment (Fig. 4*e*).

Recruitment rates in period 1 (trawling) were greater at trawled than untrawled sites for *Pinna* only (GLM: $F_{[1,38]} = 36.4$, $P < 0.001$; sponges $F_{[1,38]} = 0.23$, $P = 0.64$; bryozoans $F_{[1,38]} = 0.8$, $P = 0.37$; Figs. 4*e*, 4*f*). The effect of trawling on the recruitment of ascidians varied with location ($F_{[1,36]} = 9.6$, $P = 0.0038$), with a substantial increase at location 2 and a small decrease at location 3. During the second period, recruitment of *Pinna* also increased in trawled relative to control sites ($F_{[1,38]} = 6.9$, $P = 0.012$), whereas again there was no effect for bryozoans ($F_{[1,38]} = 1.6$, $P = 0.21$; Figs. 3*g*, 3*h*). For ascidians and sponges, there was an interaction between treatment and location (ascidians $F_{[1,36]} = 8.3$, $P = 0.007$; sponges $F_{[1,36]} = 9.7$, $P = 0.004$), although prior trawling increased recruitment at both locations for ascidians, but only at location 2 for sponges, with a slight decrease at location 3. Over the full 5 months, recruitment of bryozoans was not affected by trawling ($F_{[1,58]} = 1.2$, $P = 0.28$), whereas that of *Pinna* increased ($F_{[1,58]} = 61.2$, $P <$

Fig. 3. Effect of trawling on mean persistence of major taxa present in Gulf St. Vincent during period 1 (*a*) location 2 and (*b*) location 3, and period 2 (*c*) location 2 and (*d*) location 3, as well as recruitment (*e*–*h*) for these same periods and locations: solid bars, control sites; open bars, trawled sites. Period 1 is when trawling occurred; period 2 is between the two post-trawl censuses. Error bars represent 1 standard error.



0.001; Figs. 4*b*, 4*d*, 4*f*). Ascidians and sponges showed more complex behaviour, with results dependant on location (ascidians $F_{[2,54]} = 6.1$, $P = 0.004$; sponges $F_{[2,54]} = 7.0$, $P = 0.002$). Trawling decreased ascidian recruitment slightly at location 1 but increased it at locations 2 and 3 (Figs. 4*b*, 4*d*, 4*f*). Sponges increased recruitment rates at locations 1 and 2 in response to trawling but decreased at location 3 (Figs. 4*b*, 4*d*, 4*f*).

There was a marginally significant effect of trawling on cover of the seagrass *Halophila ovalis* in January 2000 (two-way ANOVA: $F_{[1,1]} = 145.5$, $P = 0.053$). Both trawl sites had substantially less seagrass than the control sites (Fig. 5), although cover at the control sites was highly variable, with some quadrats having no seagrass and others up to 18%.

Discussion

While the effects of trawling in this study were generally mediated by some unmeasured characteristics of the locations used, overall there was a decline in the abundance of sessile epifauna at trawl sites compared with untrawled control sites. Of the four dominant taxa present (at six sites), there were nine instances of a decline by more than 25% at the trawl sites compared with only one such decline at the

Fig 4. Effect of trawling on mean persistence and recruitment of major taxa present in Gulf St. Vincent over the entire 5-month study period at (*a, b*) location 1, (*c, d*) Location 2, and (*e, f*) Location 3. Solid bars, control sites; open bars, trawled sites. Errors bars represent 1 standard error.

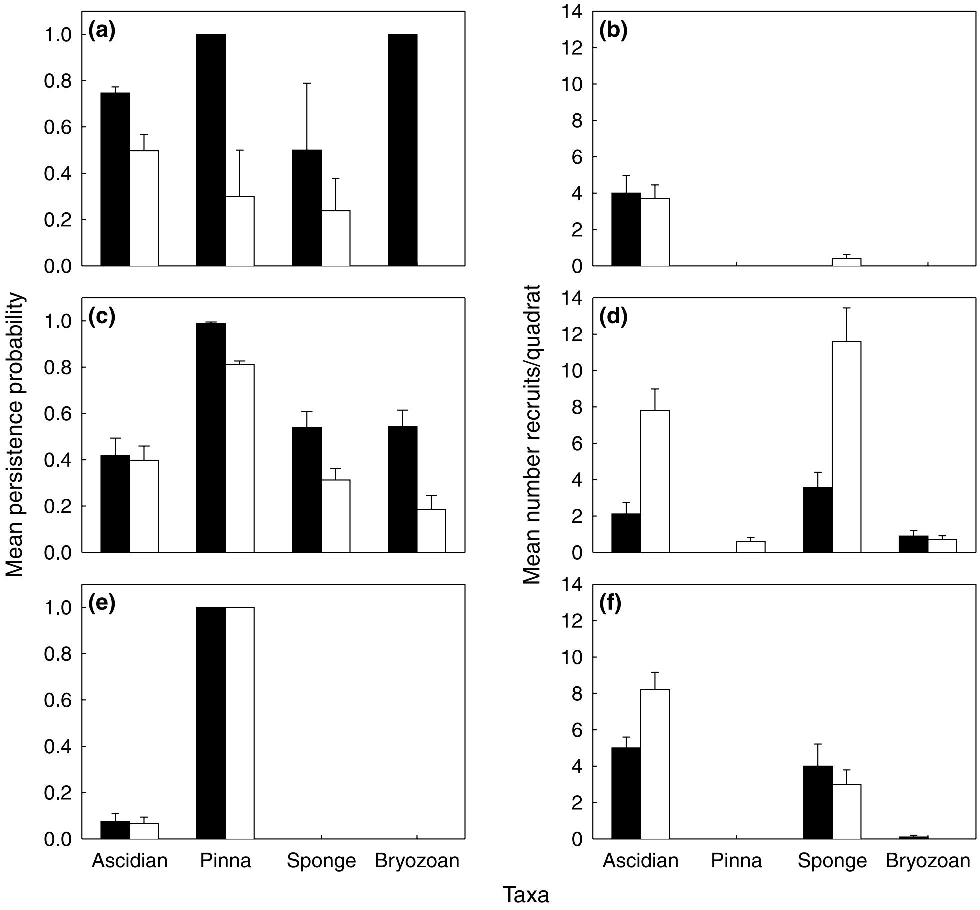
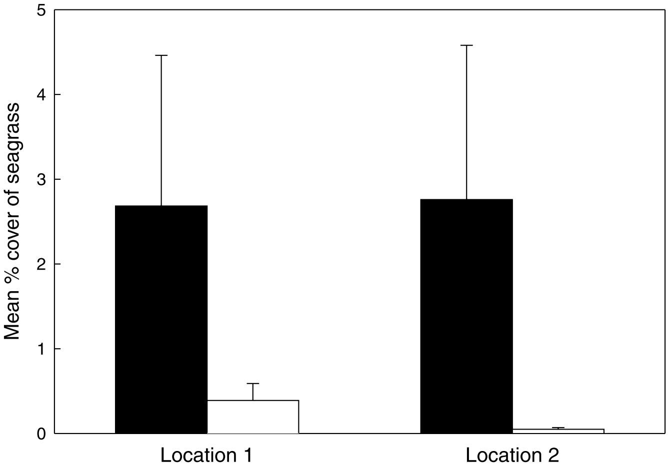


Fig. 5. Response of the seagrass *Halophila ovalis* to trawling (abundance in January 2000). Solid bars indicate control sites, open bars indicate trawled sites. Error bars represent 1 standard error.



control sites. The only taxa that did not decline at all trawl sites were ascidians and sponges at location 2 and *Pinna* at location 3. The use of permanently marked quadrats in this study means that these changes in abundance are real and not related to small-scale spatial changes in abundance that have been misinterpreted as temporal changes. This also makes the tests presented here more powerful than would otherwise be the case.

The main negative effect of trawling was on the persistence of animals present at the start of the study (prior to any trawling), with recruitment rates of some taxa actually increasing at trawled sites relative to control sites, presumably because of an increase in free space. The persistence of all taxa decreased between the pre- and post-trawl census at trawl sites relative to control sites, with this decrease being especially noticeable for sponges and bryozoans. Even at the control sites, however, persistence could be low for some taxa, especially at location 3. During the second census interval, persistence did not differ between trawl and control sites, except for *Pinna*, which showed decreased persistence at trawl sites. It is possible that *Pinna* killed by trawling remained in place long enough to be counted in the first post-trawl census but then disappeared before the second post-trawl census. Alternatively, surviving animals may have taken some time (more than the 1-week interval between trawling and censusing) to succumb to their injuries. The other taxa did not appear to experience any delayed mortality from trawling.

Though abundance and persistence clearly decreased as a result of trawling, there were several instances of large increases in recruitment rates. Although it is not known if these recruits were derived from settlement events before or after trawling, the effect on the assemblage's response to trawling is likely to be similar. Taxa that recruit extensively either via settlement or growth of pre-existing juveniles too small to be detected in the pre-trawl census are likely to recover their abundances from trawling relatively quickly. It could still take many decades for populations of these taxa to recover their former size structure, however, as the most vulnerable individuals to trawling are likely to be the large ones that may be many decades old.

Both persistence and recruitment within the study area are likely to vary with spatial scale in this study. Although both processes are likely to be naturally patchy, the imposition of a trawling disturbance is likely to exacerbate this, through patchy distribution of effort and patchy susceptibility of the assemblage to disturbance and the fact that some of the animals that fail to persist in the quadrats are likely to have been relocated but remain alive. Such relocated individuals are likely to be clumped, either in areas where they could escape under the foot rope of the trawl, such as depressions in the substrate, or where they are discarded over the side of the trawler during the on-board sorting process. Bycatch in this study was discarded outside the study site, thus at the larger spatial scale, persistence may be higher than recorded here and recruitment may be lower. This applies especially to location 3 and to a lesser extent to location 1 where the fauna appeared to be most adapted to movement.

It seems likely that the natural disturbance regimes experienced by the different locations played a substantial role in determining the heterogeneous response observed. Location 2, which had the most abundant epifauna, appeared to be a highly stable environment with a deep layer of fine sediment. Location 1 had coarser sediment and less abundant epifauna and appeared to experience an intermediate disturbance regime, whereas location 3 had very low epifaunal abundance and experienced very strong currents. None of the epifauna appeared to be securely anchored to the bottom at the latter two locations but were instead attached to pieces of shell and simply resting on the sediment surface. At both of these locations, trawling had minimal effect except on bryozoans, which are relatively brittle and probably not adapted to movement. This movement explains the low persistence rates and high recruitment rates at location 3. Epifauna at location 2 were mostly attached to *Pinna*, which are capable of anchoring themselves in the sediment. At this location, animals that did not persist were removed from their substrate and are likely to have died. There also did not appear to be any translocation of adults into the quadrats, reinforcing the speculation that animals here are not adapted to disturbance and likely exhibited a high rate of mortality as a result of trawling rather than simply being moved to another area. Previous work has suggested that less stable habitats are less affected by trawling (e.g., Auster 1998; Jennings and Kaiser 1998; Kaiser et al. 1998) and recover more quickly (Collie et al. 2000). Even in areas with no noticeable disturbance gradient, however, location differences in response to trawling have been found in a single experiment (Lindegarth et al. 2000).

The level of damage reported here can probably be taken as the minimum effect that commercial trawling has on the benthos in areas of similar character that have not been trawled for some time. There are five main reasons for this. Firstly, the intensity of trawling was relatively low compared with what often occurs on the fishing grounds, where the same track is often repeatedly trawled (e.g., Rijnsdorp et al. 1998), increasing damage (e.g., Poiner et al. 1998). Secondly, not only is a given track likely to be trawled several times in close succession, but it may be trawled repeatedly over longer time scales. Such long-term effects, and also indirect effects that may take some time to develop, are probably best examined by a rigorous comparison of trawl grounds (preferably newly opened) to nearby untrawled areas (e.g., Thrush et al. 1998; Frid et al. 1999). Thirdly, the trawl shots were of extremely short duration (10 min), and thus the cod-end of the net contained little catch. Commercial shots in this fishery generally last for 1–2 h, with several tonnes of catch accumulating in the cod-end, which is dragged along the bottom, increasing the intensity of damage. Fourthly, the trawl doors did not appear to pass through any of the quadrats in this study; therefore, damage was caused by the foot rope, sweeps, and net itself, which are all lighter and more likely to skip over the bottom causing less damage. The doors are the most damaging component of the gear (e.g., Gibbs et al. 1980; Brylinsky et al. 1994; Auster et al. 1996) but affect only a small proportion of the substrate. Clear furrows about 0.5 m wide in which all epifauna had been "bulldozed" by the boards were observed at all three trawl sites outside of the quadrats. Finally, it is assumed that the study locations have completely recovered from any previous trawling, but this may not be the case, even though some 15 years have passed. Thus we may be dealing with the shifting baseline syndrome (Pauly 1995; Carlton 1998). Because of the very imprecise nature of existing logbook data on where trawling has occurred and the relatively low levels of effort in this fishery, it is also possible that none of the areas has ever been trawled. This is a problem for many studies of trawling, and highlights the need for accurate spatial data to be collected from day 1 of any new fishery.

I am confident that none of the locations has been trawled in the last 15 years. Although the fishing block containing location 1 has been trawled recently, the fishers clearly indicated that this effort occurred further offshore. Given the small size of the fleet and the way that the boats fish side-by-side rather than individually, this assessment is likely to be reliable. Fishing has not occurred within 10 n.mi. of locations 2 and 3 since 1985. Again, the co-operative nature of the fleet and the proximity of the fishery to a large city (Adelaide, population >1 million) mean that it is very unlikely that any unreported trawling has occurred in these areas since.

If this experiment were repeated in the current trawl grounds, it is unlikely that any effect would be detected. This is because most trawl damage occurs when an area is first trawled (Jones 1992; Jennings and Kaiser 1998), as vulnerable fauna are removed and only species capable of resisting trawl disturbance remain (e.g., Poiner et al. 1998). It is also possible that none of the current trawl grounds was ever similar to the study locations, although the fact that fishing stopped as the result of legislation reduces the probability of this. Since this study began, active commercial trawling has resumed in the vicinity of location 2. Thus, at the very least, this study gives an indication of the likely damage to epifaunal assemblages occurring in this area. Compared with many other fisheries, the trawl grounds occupy only a small portion of the available habitat in the gulf. Since a 2-year closure ended in 1993, the total area swept by the nets has ranged between 200 and 450 $\mathrm{km}^2 \cdot \mathrm{year}^{-1}$. Given that effort in this fishery is patchy, like other fisheries (e.g., Kaiser et al. 1996; Rijnsdorp et al. 1998), and that some areas are swept more than once, the total area disturbed each year may be substantially less. The total area of the gulf is about 7150 km^2, so less than 6% of the gulf is likely to be trawled in any one year.

Epifaunal species are likely to provide habitat structure for other more mobile species (e.g., Sainsbury 1988; Turner et al. 1999). Thus their loss has greater consequences than might otherwise be the case. This is especially true given the largely sedimentary nature of Gulf St. Vincent with little hard substrate, which means that most structure is biotic in nature. Although no effect on commercially important crustaceans was detected in this relatively small-scale manipulation, effects on fish were not tested because of the highly variable nature of their catches. At the larger scale of the fishery, there may, however, be consequences for the benthos that were not detected here.

Given that a substantial proportion of animals were removed, even under the light trawling regime used, and the potentially long time for large individuals to reappear in a disturbed population, it is suggested that the environmental effects of trawling would be best mitigated by concentrating activity in a small area, rather than trawling much larger areas with a longer return time. Such a policy may be more feasible in this fishery than most, as only a small proportion of the gulf (<6%) is trawled in any one year anyway. Spatial restriction of fishing activity will lead to substantial damage in the small area fished, as evidenced by the mortality rates seen here. Allowing larger areas to be fished with a longer return time will result in less damage to an area but potentially the complete loss of all larger sessile organisms, as these may take decades to recover.

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