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Effects of harvesting callianassid (ghost) shrimps on subtropical benthic communities

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Abstract

The effects of harvesting of callianassid shrimp (*Trypaea australiensis*) on the abundance and composition of macrobenthic assemblages in unvegetated sediments of a subtropical coastal embayment in Queensland, Australia were examined using a combination of sampling and manipulative experiments. First, the abundance and composition of the benthic infauna in an area regularly used for the collection of shrimp for bait by recreational anglers was compared with multiple reference areas. Second, a BACI design, with multiple reference areas, was used to examine the short-term effects of harvesting on the benthic assemblages from an intensive commercialised fishing competition. Third, a large-scale, controlled manipulative experiment, where shrimp were harvested from 10,000 m^2 plots at intensities commensurate with those from recreational and commercial operators, was done to determine the impacts on different components of the infaunal assemblage.

Only a few benthic taxa showed significant declines in abundance in response to the removal of ghost shrimp from the unvegetated sediments. There was evidence, however, of more subtle effects with changes in the degree of spatial variation (patchiness) of several taxa as a result of harvesting. Groups such as capitellid polychaetes, gammarid amphipods and some bivalves were significantly more patchy in their distribution in areas subjected to harvesting than reference areas, at a scale of tens of metres. This scale corresponds to the patterns of movement and activity of recreational harvesters working in these areas. In contrast, patchiness in the abundance of ghost shrimp decreased significantly under harvesting at scales of hundreds of metres, in response to harvesters focussing their efforts on areas with greater numbers of burrow entrances, leading to a more even distribution of the animals. Controlled experimental harvesting caused declines in the abundance of soldier crabs (*Mictyris longicarpus*), polychaetes and amphipods and an increase in the spatial patchiness of polychaetes. Populations of ghost shrimp were, however, resilient to harvesting over extended periods of time. In conclusion, harvesting of ghost shrimp for bait by recreational and commercial fishers causes significant but localised impacts on a limited range of benthic fauna in unvegetated sediments, including changes in the degree of spatial patchiness in their distribution.

Keywords: Human impacts; Recreational harvesting; Spatial patchiness; Subtropical benthic communities; *Trypaea australiensis*

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1. Introduction

In coastal areas around the world, the harvesting of invertebrates for use as bait by recreational fishers is a widespread phenomenon (e.g. Klawe and Dickie, 1957; Blake, 1979a,b; McLusky et al., 1983; Creaser et al., 1983; Kingsford et al., 1991; Fairweather, 1991; Wynberg and Branch, 1991; Olive, 1993; Van den Heiligenberg, 1987; Ambrose et al., 1998) that has been associated with a broad range of direct and indirect impacts on target species and other components of the ecosystem (Underwood, 1993). Any integrated assessment of the sustainability of recreational fishing should include consideration of the impacts from the collection of bait but this component is often ignored (McPhee et al., 2002).

Unvegetated intertidal sediments are often dug over to harvest a variety of invertebrates, including callianassid (ghost) shrimp, polychaetes and bivalves (Hailstone and Stephenson, 1961; Jackson and James, 1979; Brown and Wilson, 1997; Ambrose et al., 1998; Beal and Vencile, 2001), but few studies have examined systematically the impacts of this fishery in Australia (but see Rotherham and West, 2003; Contessa and Bird, 2004). Elsewhere, the removal of these organisms and the associated disturbance to the sediments (Dayton and Oliver, 1980; Peterson, 1982; Skilleter, 1996) has been shown to have marked effects on the biota in these habitats. Jackson and James (1979) showed that digging for lugworms, *Arenicola marina*, in unvegetated sediments led to increased mortality of another commercially and recreationally important species, the cockle *Cerastoderma edule*, due to smothering and exposure on the surface during low tide. Similar effects on small bivalves were noted by Peterson (1976) in relation to harvesting of callianassid shrimp, *Callianassa californiensis*, in Californian coastal lagoons. A large proportion (~53%) of infauna exposed as a result of bait collection using a yabby pump may also fall prey to foraging gulls (Wynberg and Branch, 1991; see also Peterson, 1977; Blake, 1979a,b). Many of the invertebrates that live in these unvegetated habitats are important food items for fish and crustaceans (Quinn, 1992; Shaw and Jenkins, 1992; Coull et al., 1995), but also for migratory shorebirds (Zharikov and Skilleter, 2003, 2004), suggesting the potential for indirect impacts from harvesting to be widespread.

In this paper, we provide an integrated picture of how the harvesting of callianassid shrimp (*Trypaea australiensis* Dana, 1852; known locally as yabbies) affected the abundance and composition of the benthic community of unvegetated sediments in subtropical Moreton Bay, SE Queensland. Yabbies are widely distributed, occurring on most estuarine mud- and sandflats in SE Queensland (Hailstone and Stephenson, 1961) and are harvested by recreational and commercial fishers from virtually any accessible site within the region (Skilleter, 2004). Harvesting of yabbies potentially causes changes to the sediments (e.g. granulometry, compaction: Wynberg and Branch, 1994) and this may influence the organisms that are found in these habitats because of the often close association between soft-sediment infauna and sedimentary parameters (e.g. Sanders, 1958, 1960; Gray, 1974; Rhoads, 1974). Callianassid shrimp are efficient bioturbators (Roberts et al., 1981; Suchanek, 1983) and levels of bioturbation are often important in determining the composition of the surrounding benthic communities in soft-sediments (Brenchley, 1981; Murphy, 1985; Posey, 1986). Callianassids also have an important regulatory role in many sedimentary biogeochemical processes (e.g. Koike and Mukai, 1983; Waslenchuk et al., 1983; Schlacher and Wooldridge, 1996) that directly influence the structure of meio- and macrofaunal communities (Branch and Pringle, 1987; Dobbs and Guckert, 1988; Wynberg and Branch, 1994). Finally, some callianassids, including *T. australiensis*, are active deposit-feeders (Boon et al., 1997) and the influence of deposit-feeders on surrounding community composition is well known (e.g. Rhoads and Young, 1970; Brenchley, 1981; Hunt et al., 1987). Clearly, the removal of large numbers of callianassid shrimp has the potential to cause marked changes in the benthic community through a sizeable disturbance.

First, the abundance and composition of the benthic infauna in an area subjected to persistent recreational harvesting were compared with that in two reference areas, only accessed by bait fishers occasionally. This was done to determine if the regular harvesting of yabbies was associated with a decrease in species richness and abundance of infauna as had been shown in temperate systems (e.g. Peterson, 1977; Wynberg and Branch, 1994).

Second, impacts on the benthic assemblages from bait collection for an annual commercialised fishing competition, the Straddie Classic, were examined using a Before–After/Control-Impact (BACI) study. This was done to determine whether localised, intense periods of harvesting caused impacts over and above those associated with more prolonged and regular harvesting activities. Commercialised fishing competitions are open to the general public and anglers compete to catch the heaviest fish of various species. Up to 1500 anglers may participate in these competitions which can last for a week and bait for use in the Straddie Classic is often sourced from only a few localised sites (McPhee and Skilleter, 2002a) over a relatively short period of time. Intense 'pulse' disturbances such as this have the potential to cause marked changes to benthic systems (Underwood, 1989), even when imposed on systems already exposed to chronic stresses.

Third, information collected during the first two components of this study and from creel and observational surveys of the harvesting activities of fishers (McPhee and Skilleter, 2002a) was used to design a large-scale, controlled manipulative experiment where yabbies were harvested from 1 ha (10,000 m^2) plots to examine the impacts on the benthic fauna. Previous studies examining the impacts from bait harvesting have all been done at relatively small spatial scales (e.g. McLusky et al., 1983; Wynberg and Branch, 1991, 1994; Contessa and Bird, 2004) which often does not reflect those at which harvesting by recreational and commercial operators usually occurs.

Keough et al. (1993) cautioned against the interpretation of studies on bait-harvesting based around the examination of relatively small areas and/or where the reference (control) areas were adjacent to harvested areas because of the potential for confounding with other factors causing change in the dynamics of the bait populations. In the present study, the 1-ha plots manipulated in the controlled experiment represented an area sufficient to account for the patterns of 'foraging' of bait-harvesters (McPhee and Skilleter, 2002a) and shorebirds (Zharikov and Skilleter, 2003). The reference areas for the examination of the impacts from persistent harvesting and the examination of the Straddie Classic Fishing Tournament were located >1 km from the putatively impacted location.

Throughout the study, multiple spatial scales were incorporated explicitly to test hypotheses about whether disturbance from harvesting led to increased or decreased spatial patchiness in the distribution and abundance of the benthic animals (e.g. Warwick and Clarke, 1993). Harvesters targeting yabbies and other infauna often search on the basis of visible cues, such as the density of burrow openings (personal observation). In this case, the expectation would be that harvesting would reduce spatial patchiness because the density of yabbies would decline in large-density patches, making them more similar to small-density patches. Alternatively, if the spatial distribution of burrow openings and animals is more uniform, then harvesters may cause an increase in patchiness by removing animals from some patches but not others (McPhee and Skilleter, 2002a). The focus of analyses in this study was on groups such as tellinid bivalves, amphipods, polychaetes and crabs because these taxa had been shown to be impacted by bait harvesting elsewhere (e.g. Jackson and James, 1979; Van den Heiligenberg, 1987; Brown and Wilson, 1997) and/or were important in the diets of migratory shorebirds foraging in the region (Zharikov and Skilleter, 2003, 2004).

2. Methods

2.1. Spatial scales and study sites

The different spatial scales (Fig. 1) examined in this study were selected on the basis of other work in the region demonstrating significant variation in the abundance of benthic infauna at scales ranging from metres to hundreds of metres (Zharikov and Skilleter, 2003, 2004; Skilleter unpublished data; see also Morrisey et al., 1992) and the distances over which harvesters moved when collecting bait (McPhee and Skilleter, 2002a). The primary spatial scales included in each of the components of the study were: Locations (scale of kilometres), among Sites (within Locations; scale of hundreds of metres) and Plots (within sites; scale of tens of metres).

This study was done on North Stradbroke Island in Moreton Bay, Queensland (Lat. 27° S, Long. 153° E;

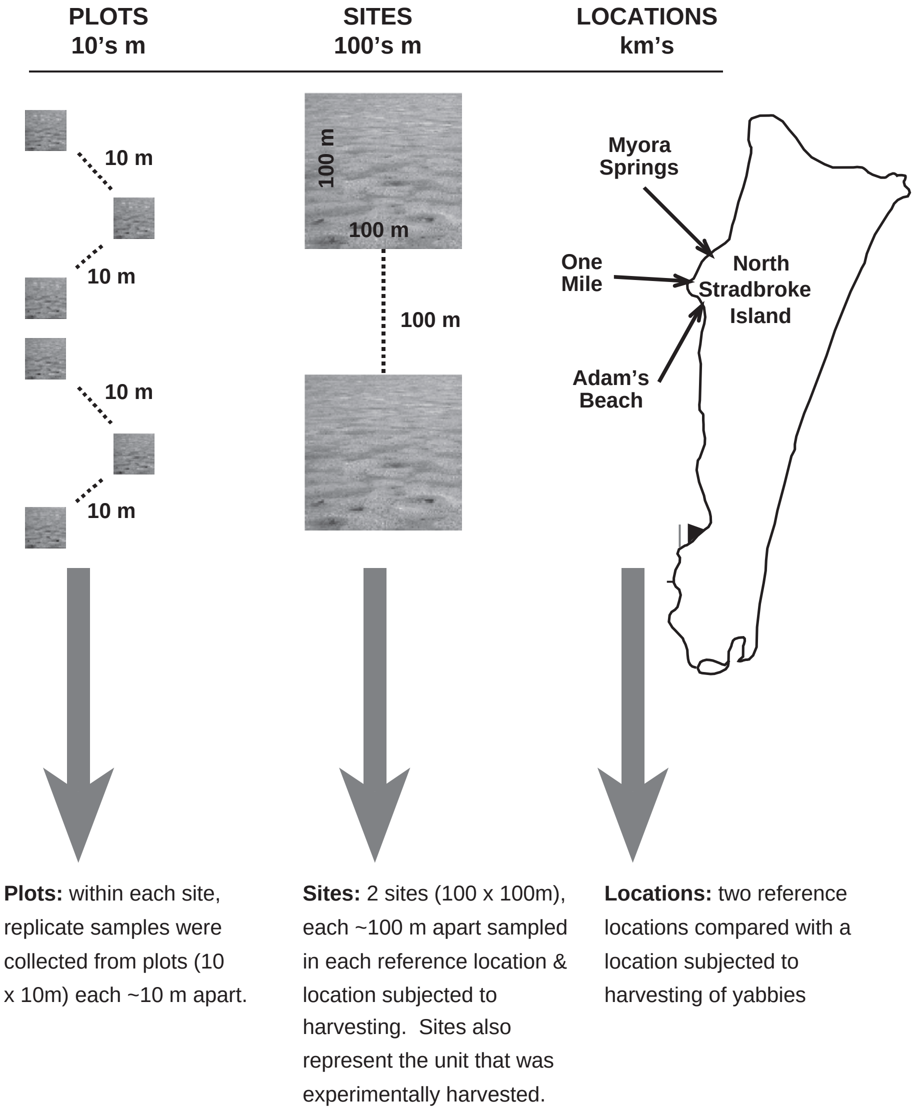


Fig. 1. Schematic showing the spatial scales incorporated into the studies on the impacts associated with the harvesting of yabbies (*Trypaea australiensis*).

Fig. 2). Moreton Bay is a large subtropical, estuarine embayment with semidiurnal tides with a range of 1.5–2.0 m (Dennison and Abal, 1999) exposing the intertidal area on average for 5.5 to 6.5 h per low tide. The substratum in the study area consists of fine sand (mean grain size 0.204 mm) with a small (2%) silt (grain size <0.063 mm) fraction, and it has a micro-relief of intermingling elevated ridges and pools (Thompson, 1992).

2.2. Impacts associated with recreational harvesting

In 1996, samples were collected to determine whether the abundance and composition of benthic infauna differed between an area regularly used for harvesting of yabbies and nearby areas where harvesting was infrequent or did not occur. One Mile (Fig. 2) was chosen as the putatively impacted area because it was adjacent to the main boat ramp

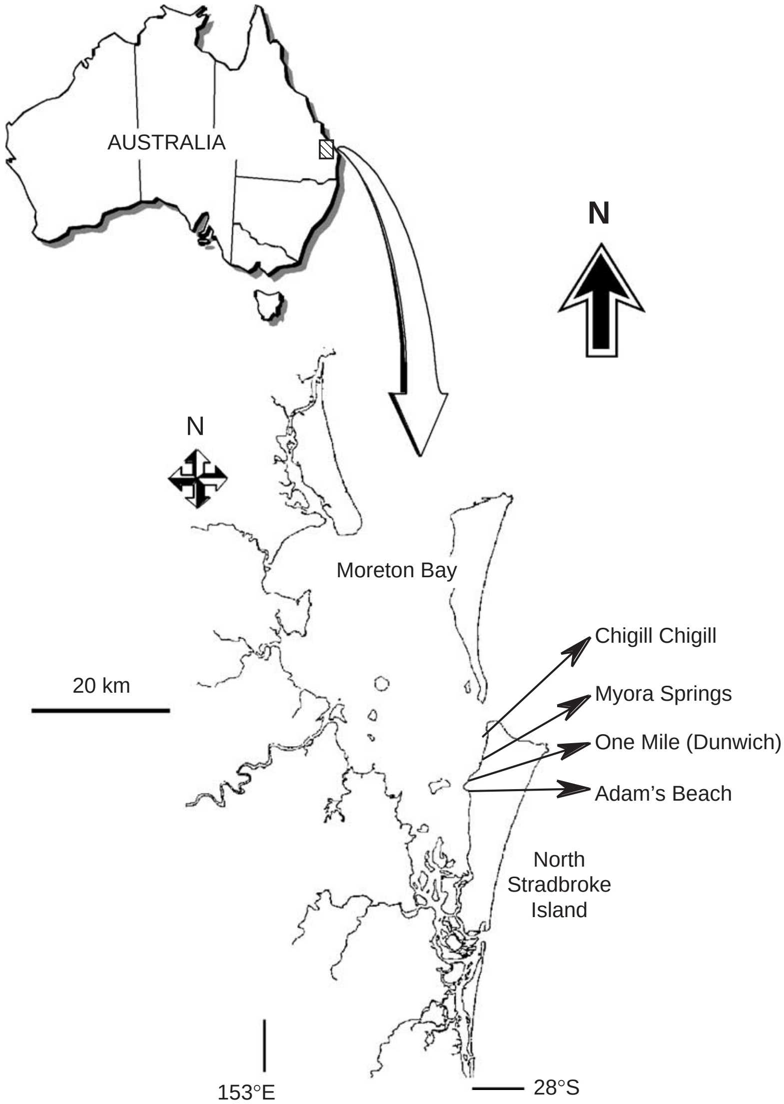


Fig. 2. Map of Australia and the Moreton Bay region of SE Queensland showing the position of the three locations in eastern Moreton Bay used to examine the effects of recreational harvesting on benthic macrofauna.

in the township of Dunwich, on North Stradbroke Island. The area is readily accessible for bait collection by fishers using the boating facilities and many visitors collected bait from this sandflat before traveling to other parts of the island for fishing. It was also the major area for the collection of yabbies used in the annual Straddie Classic Fishing Tournament (McPhee and Skilleter, 2002a). Two other locations, Adam's Beach and Myora Springs (Fig. 2) served as references areas because they contained a similar range of habitats to One Mile but little or no bait collection was done at either location (Curley, 1996; Sturkie, 1996; McPhee and Skilleter, 2002a; personal observations).

Samples were collected from the mid-intertidal, primarily an unvegetated area, in which most harvesting of yabbies occurred. Observations of the activities of recreational fishers harvesting bait at One Mile (Sturkie, 1996) indicated that few harvesters ventured far into the seagrass beds to pump for yabbies, although yabbies do occur in these habitats (personal observations).

Four replicate cores (15 cm diameter×10 cm deep) were collected from each of two plots in the sites in the seagrass and unvegetated habitats. Samples were fixed in 7% formalin/seawater containing the stain Rose Bengal. The sediments were then sieved across a 500-μm mesh sieve and the contents retained in the sieve were preserved in 70% ethanol until sorting when all animals were removed, identified to the lowest taxonomic level possible and counted.

2.3. Impacts from a commercialised fishing competition

Impacts on the benthic assemblages from bait-harvesting for the 1998 Straddie Classic Fishing Tournament were examined using a Before–After/Multiple Control-Impact experimental design (e.g. Underwood, 1992). The design incorporated the same spatial scales as in the general sampling described above, but based on preliminary analysis of the data from the first part of the study, the number of plots per site was increased from two to four to account for the small-scale (tens of metres) spatial variability in the abundance of the dominant fauna. Samples were collected approximately 1 week before the start of the Straddie Classic and, again, 1 month after completion of the competition. Within each of the three locations (One Mile, Adam's Beach and Myora Springs), two sites were selected haphazardly, but ensuring they were at least 100–150 m apart. Four replicate samples were collected from each of four Plots per Site in each Location. Plots were selected haphazardly, with the only criterion being that they were at least 2 m from the nearest patch of seagrass (primarily *Zostera capricorni*). From within each of the plots, four replicate cores (15 cm diameter×10 cm deep) were collected. Samples were then fixed, stained, sorted and identified as described previously.

2.4. Controlled experimental harvesting

A controlled field experiment was done to determine the specific effects of harvesting of yabbies on benthic macrofauna and to allow comparisons with the results obtained from the sampling programmes. The experiment was done at Chigill Chigill on the western shore of North Stradbroke Island, Moreton Bay between October 1998 and February 2000. Six 100×100 m (1 ha) sites were permanently marked with 40-cm-long wooden stakes pushed half-length into the substratum at the corners and half-distance in between. The sites were located at the same tidal height along a visually uniform stretch of the mudflat without any natural barriers (creeks, sloughs, etc.). Adjacent plots were separated by 75–100 m. Three of the sites were designated at random for experimental manipulations and the remaining three sites served as controls that were undisturbed apart from sampling to determine the abundance of the benthic fauna (see below). The sites were isolated from the nearest land-based access point (>2 km on either side of the study area) onto the mudflat and shallow, submerged banks and islands precluded easy access from the water, preventing any uncontrolled bait-harvesting within the plots.

Yabbies, *T. australiensis*, were harvested from the experimental sites using a yabby pump, a device widely employed in the region by bait collectors (Hailstone and Stephenson, 1961). The usual procedure for collecting yabbies with a yabby pump is to push the unit into the substratum and extract the sediment, which is then dumped onto the substratum to collect suitable sized animals. Typically, the pump is pushed into the substratum at the same point a number of times. The harvester then moves to a new point and begins the process again. Teams of two people, a pumper and a collector, worked through the experimental sites pumping in areas with visible yabby holes. The effort was roughly uniform among the three experimental sites and equaled ca. 4–5 pumper-hours per plot per harvesting event. All yabbies with a carapace length (CL) of 7+ mm were removed (98.2% of the total) from the sites and subsequently counted. This is the size preferred by bait harvesters (McPhee and Skilleter, 2002a). Harvesting of the sites was done on eight occasions: November 1998, January, March, May, June, July, and December 1999, and February 2000, thus simulating multiple harvesting events (McPhee and Skilleter, 2002a; Zharikov and Skilleter, 2004).

The design of the harvesting experiment was intended to mimic the spatial scales and intensity of harvesting of yabbies by recreational and commercial harvesters operating in SE Queensland and therefore provide a realistic indication of whether such harvesting causes impacts on benthic assemblages. Several sources of information were used to ensure that the intensity of harvesting applied to the experimental plots was of the correct order of magnitude.

On average, ca. 350 yabbies (SE: ±40: range 115–834 individuals) were removed from each of the one hectare experimental plots on each harvesting episode (see Results). The pattern of our experimental harvesting was modelled on the patterns exhibited by recreational harvesters collecting bait for the 1998 Straddie Classic Fishing Tournament (McPhee and Skilleter, 2002a). The information used to determine the patterns of experimental harvesting including the number of steps taken between each point where pumping was done and the number of times each point was pumped by a recreational harvester. Recreational bait collectors harvested ca. 84 yabbies per episode (SE: ±12; range: 30–300 individuals), covering an average distance of ca. 700 m (SE:±39) in doing so. Each patch that is pumped is approximately 4 m^2 in area (McPhee and Skilleter, 2002b), so the harvest of yabbies by recreational fishers participating in the Straddie Classic equates to ca. 84 yabbies per 2,800 m^2 or ca. 300 yabbies per hectare per episode.

Second, based on the total number of harvesters collecting yabbies during the Straddie Classic (Table 1, McPhee and Skilleter, 2002a), ca. 4500 yabbies were removed from One Mile and ca. 3900 yabbies from Amity Point over 7 days. The area at One Mile and Amity available for harvesting was ca. 4 ha and 1.6 ha, respectively, equating to a total harvest from a commercialised fishing competition of between 160 (One Mile) and 350 (Amity) yabbies per hectare per episode (day). Although data are limited, these levels of harvesting recorded during the Straddie Classic were also similar to those recorded elsewhere in Moreton Bay for recreational harvesters not involved in competitions. The average harvest per episode in northern Moreton Bay was, for example, ca. 160 yabbies (SE: ±39; range 20–460 individuals; n=12 creel surveys) per episode (unpublished data). Again, these figures are close to the intensity used for the harvesting experiment.

Third, between 1997 and 2000, daily log-book returns from commercial yabby harvesters, indicated that the average harvest per day was ca. 1100 (SE: ±11) yabbies, but 42% of operators harvested less than 800 yabbies per day and 12% harvested less than 400 yabbies per day. Commercial operators use identical methods and pumps to the recreational sector. Although the area from which these animals were taken during each episode is not recorded in the log-book records, it seems a reasonable assumption that this area would be of the same order of magnitude as for recreational harvesters, simply on the basis of the logistical constraints associated with the tidal range and walking across the soft mudflats. While this indicates that commercial operators are, on average, harvesting yabbies more intensively than the levels employed in the experiment, a proportion of these

Table 1
Summaries of asymmetrical analyses of variance on the abundance of different taxa in the mudflat habitat from three different locations in eastern Moreton Bay

Variable	Harvested vs. Controls	Between Controls	F-test sites	F-test plots	>Spatial variation
Total number of individuals	ns	*	ns	ns	
Gammarids	ns	***	ns	***	Harvested
Mictyris longicarpus	ns	ns	ns	ns	
Molluscs	ns	**	ns	ns	
Gastropods	ns	***	ns	ns	
Bivalves	ns	***	ns	*	Harvested
Tellina diluta	ns	***	ns	**	Harvested
Polychaetes	ns	ns	ns	***	Harvested
Capitellids	ns	ns	ns	**	Harvested
Oligochaetes	ns	ns	ns	ns	
Polychaete families	ns	ns	ns	ns	
Gastropod species	ns	***	ns	ns	
Bivalve species	ns	***	*	*	Harvested

One Mile is exposed to recreational yabby harvesting and is shown as the 'Harvest' location. Myora Springs and Adams Beach were designated as 'Controls'. N=4 replicates from each of two plots within two sites per location. Data were transformed to $\log_e(x+1)$ where necessary to meet the assumptions of heteroscedasticity after Cochran's test. Results are shown for the asymmetrical comparison of One Mile with the average of the two Controls (Impact vs. Controls) and the measure of variation between the Control locations. ***P<0.001, **P<0.01, *P<0.05, ns=P>0.05. Results for F-test Sites and F-test Plots are based on two-tailed F-tests for significant differences in levels of variation between the Harvested and Control locations at these two spatial scales. For two-tailed tests, ns denotes not significant, P>0.10, *P<0.10, **P<0.05, ***P<0.01 (after Underwood, 1992).

operators are operating at similar levels to those we employed. Overall, these calculations suggest that the intensity of employed in the experiments was well within the range exerted by recreational and commercial harvesters operating in the region, with recreational harvesters at one end of the scale and commercial operators at the other. The experiment was designed to fall in between these two extremes, given logistical constraints prevented the experiment incorporating different harvesting intensities in the design.

2.4.1. Abundance of yabbies and soldier crabs (controlled pumping)

To determine the abundance of yabbies in each of the six sites, exhaustive, controlled pumping was done using a yabby pump (McPhee and Skilleter, 2002b). The number of pumps needed to extract all the yabbies from a single point was determined in a previous study in the same region (Skilleter, unpublished data). The pumps at a single point were considered as a set. The number of sets needed to harvest all the yabbies in a 2×2-m (4 m^2) quadrat was determined from a pilot experiment where the cumulative percentage of yabbies harvested from a quadrat was plotted against the number of sets completed. These data indicated that complete harvesting of a 4-m^2 quadrat required 18 sets of 7 pumps per point.

The density and size–structure of yabbies were estimated in each of the six sites at the beginning of the experiment in October 1998 and on five other occasions: March, July, August and December 1999 and February 2000. Estimates were obtained in each of ten 4-m^2 quadrats per plot on the first five occasions and in fifteen 4-m^2 quadrats on the final occasion. Sediment collected from each of the quadrats was passed through a 2.0-mm sieve and the retained yabbies were collected. In the laboratory, yabbies were counted and their carapace length (from the tip of the rostrum to the end of the carapace) measured with calipers to the nearest millimetre. Densities of the Indo-Pacific soldier crab, *Mictyris longicarpus* (Latrielle) were also estimated using this method. The method of sampling used here captured *T. australiensis* and *M. longicarpus* with the carapace length of ≥2 mm and ≥5 mm, respectively.

2.4.2. Abundance of infauna

The abundance of small benthic infauna in each of the six sites was determined on three occasions, October 1999, January and May 1999. On each occasion, five replicate cores were collected to a depth of 15 cm into the substratum, at three haphazardly selected plots within each site, using a 15-cm diameter PVC core. Each plot was at least 10 m apart. Samples were then fixed, stained, sorted and identified as described previously.

2.4.3. Abundance of deep-burrowing and mobile fauna

Sampling using small hand-held cores, taken to a depth of 15 cm, does not adequately estimate the abundance of those animals that are able to burrow deep into the substratum, nor those that are more patchily distributed and more mobile than the relatively sedentary small infauna. Estimates of the abundance of these taxa were obtained at the end of the experiment, using the method developed for yabbies. All the material collected using exhaustive pumping (described above) from 15, 4-m^2 quadrats per plot, was sieved across a 2-mm mesh sieve, fixed in formalin and sorted in the laboratory.

2.5. Statistical analyses

2.5.1. Impacts from recreational harvesting

Data on the total number of individuals and the number of different taxa were analysed using three-factor asymmetrical analyses of variance (Underwood, 1992; Glasby, 1997) to compare the abundance in the harvested location (One Mile) with the average of the two control locations (Myora Springs and Adam’s Beach). Two nested scales of sampling were incorporated into the design: sites within each location and plots within each site. Where possible, nested levels were pooled to increase the power of the test for specific differences among the locations (Winer et al., 1991). Additionally, two-tailed F-tests were used to compare the amounts of variation at different spatial scales to determine whether there were differences in the patchiness of the fauna in the harvested location compared with the control locations (see Underwood, 1992).

Differences in community composition in the three locations were examined using PERMANOVA, a non-parametric multivariate analysis of variance (Anderson, 2001, 2004a), based on the Bray–Curtis similarity measure on untransformed and fourth-root transformed data. The patterns of dispersion (variability) of samples within the three locations were examined using PERMDISP, a non-parametric test for multivariate dispersion (Anderson, 2004b), also based on the Bray–Curtis similarity measure on untransformed and fourth-root transformed data. At present, these programs can only analyse data for a two-factor design, so a two-stage process was used. First, variation between sites within each location was examined using a two-factor analysis (Sites and Plots within Sites). None of these analyses showed significant variation at the scale of Sites (P>0.25: but there was significant variation at the small scale of plots), so the final analysis examined variation among the three Locations with a single nested term of Plots, with four levels (pooled from the two sites). Differences in community composition were also examined graphically using non-metric multidimensional scaling (ordination) using the Bray–Curtis similarity measure on fourth-root transformed data (Clarke, 1993).

2.5.2. Impacts from the fishing competition

Data on the total number of individuals and the number of different taxa were analysed using four-factor asymmetrical analyses of variance (Beyond-BACI) to compare the pattern of change from Before to After (Period) the Straddie Classic Tournament in the harvested location (One Mile) to the average pattern of change in the reference locations (Underwood, 1992). Two nested scales of sampling were incorporated into the design: sites within each location and plots within each site. Where possible, nested levels were pooled to increase the power of the test for specific differences among the locations (Winer et al., 1991). Additionally, two-tailed F-tests were used to compare the amounts of variation at different spatial scales to determine whether there were differences in the patchiness of the fauna in the harvested location compared with the control locations (see Underwood, 1992).

Detection of asymmetrical changes in the composition of the community using multivariate analyses is problematic because of current limitations in the complexity of designs which can be handled in available software. Ideally, analysis of the multivariate dataset would make use of the same logical approach used for single variables (e.g. abundances), but this was not possible. As an alternative, several different approaches were used to examine the nature of the changes in the community composition from Before to After the fishing tournament and whether these temporal fluctuations varied between the harvested location and the reference locations.

(1) For each location, data were analysed to determine if there were small scale (between sites and among plots) variation in community composition before and after the fishing tournament. In all cases, there was significant variation among the plots within each site, but there were no significant differences between the sites. The term for sites was therefore removed from subsequent analyses, and a single nested term for Plots was analysed (with eight levels). Differences in community composition in the three locations after the Straddie Classic were examined using a two-factor PERMANOVA, comparing the three locations, with a nested factor of plots within locations.

(2) The patterns of dispersion (variability) of samples within the three locations after the fishing tournament were examined using PERMDISP, based on the Bray–Curtis similarity measure on fourth-root transformed data. Again, variation between sites within each location was examined using a two-factor analysis (Sites and Plots within Sites). None of these analyses showed significant variation at the scale of Sites (but there was significant variation at the small scale of plots), so the final analysis examined variation among the three Locations with a single nested term of Plots, with 8 levels (pooled from the two sites). Differences in community composition were also examined graphically using non-metric multidimensional scaling (ordination) using the Bray–Curtis similarity measure on fourth-root transformed data.

2.5.3. Controlled experimental harvesting

Data on the abundance of yabbies, based on controlled pumping, were analysed with a three factor, hierarchical mixed model ANOVA, with factors Time (fixed; a=6 levels), Treatment (fixed; b=2 levels), Site (random, nested in Treatment; c=3 levels) with n=10 quadrats sampled per site on each occasion. On the final date, where 15 quadrats were sampled, a random subset of these data was chosen for the analysis to maintain a balanced design. For this, and all subsequent analyses, post-hoc pooling of mean square estimates was used to increase the power for specific terms in the ANOVAs following the principles detailed in Winer et al. (1991). Comparisons of the size-frequency distributions of yabbies in the control and harvested plots were done with two-sample Kolmogorov–Smirnov tests, on the pooled data from the animals harvested from the three plots per treatment on each of the eight harvesting events.

Data on the abundance of infauna were analysed with four factor, hierarchical mixed model ANOVAs, with factors Time (fixed; a=3 levels), Treatment (fixed; b=2 levels), Sites (random, nested in Treatment; c=3 levels) and Plot (random, nested in Time×Plot(Treatment); d=3 levels) with n=4 cores sampled per site on each occasion. Additionally, two-tailed F-tests were used to compare the amounts of variation at different spatial scales (1 ha Sites within each treatment and Plots within each Site) to determine whether there were differences in the patchiness of the fauna under harvesting compared with the control sites.

Data on the composition of the benthic assemblage in the control and harvest sites were analysed separately on each of the three occasions (October 1998, January and May 1999) using two-factor, non-parametric multivariate analyses of variance (PERMANOVA) on untransformed and fourth-root transformed data. The factors were Treatment (fixed) and Plots (nested within treatment, random). The patterns of dispersion of samples within the two treatments were examined with PERMDISP. Again, data were analysed separately for each of the sampling periods. A two stage process was used because of the current limitations in the complexity of the designs that can be analysed. First, variation among Treatments and Sites within each Treatment was examined using a two-factor analysis. None of these analyses showed significant variation at the scale of Sites, so the final analysis examined variation between the two Treatments with a nested term of Plots, with nine levels (three plots from each of three sites per treatment).

3. Results

3.1. Impacts associated with recreational harvesting

3.1.1. Effects on abundance and diversity

Despite the sustained and regular harvesting of yabbies from the mudflats around One Mile, there was no indication that this was associated with significant differences in the abundance or diversity of macrofaunal animals in the sediments there compared with similar habitats in places rarely used for bait-harvesting. There was considerable variation in the abundance of animals between the two reference locations. Eight of the 13 variables analysed showed significant differences in abundance between the two reference locations (Table 1; Figs. 3 and 4). The magnitude of the differences between the two reference locations often exceeded those between the reference locations and the harvested location (One Mile) (e.g. gastropods, *Tellina diluta*, capitellids: Fig. 3). In some cases, there was a trend towards more animals in the harvested location than either of the control locations (e.g. numbers of individuals, gammarids, polychaetes and oligochaetes: Fig. 3), but these differences were not significant (Table 1). As an example, the total number of individuals at One Mile (harvested location) was 21–45% greater than at either of the two reference locations, but these varied by 30%. The significant variation in the abundance of animals between the controls would reduce the power to detect any significant impact, given the variance associated with the reference locations forms the denominator for the appropriate F-test (Underwood and Chapman, 2003).

The numbers of species of bivalves (Fig. 4A) and gastropods (Fig. 4B) and the number of families of polychaetes (Fig. 4C) at One Mile (harvested) were intermediate between the levels observed at the two reference locations and no significant difference in these measures of richness were detected between the harvested location and the average of the reference locations (Table 1). The number of species of bivalves and gastropods varied significantly between the two reference locations.

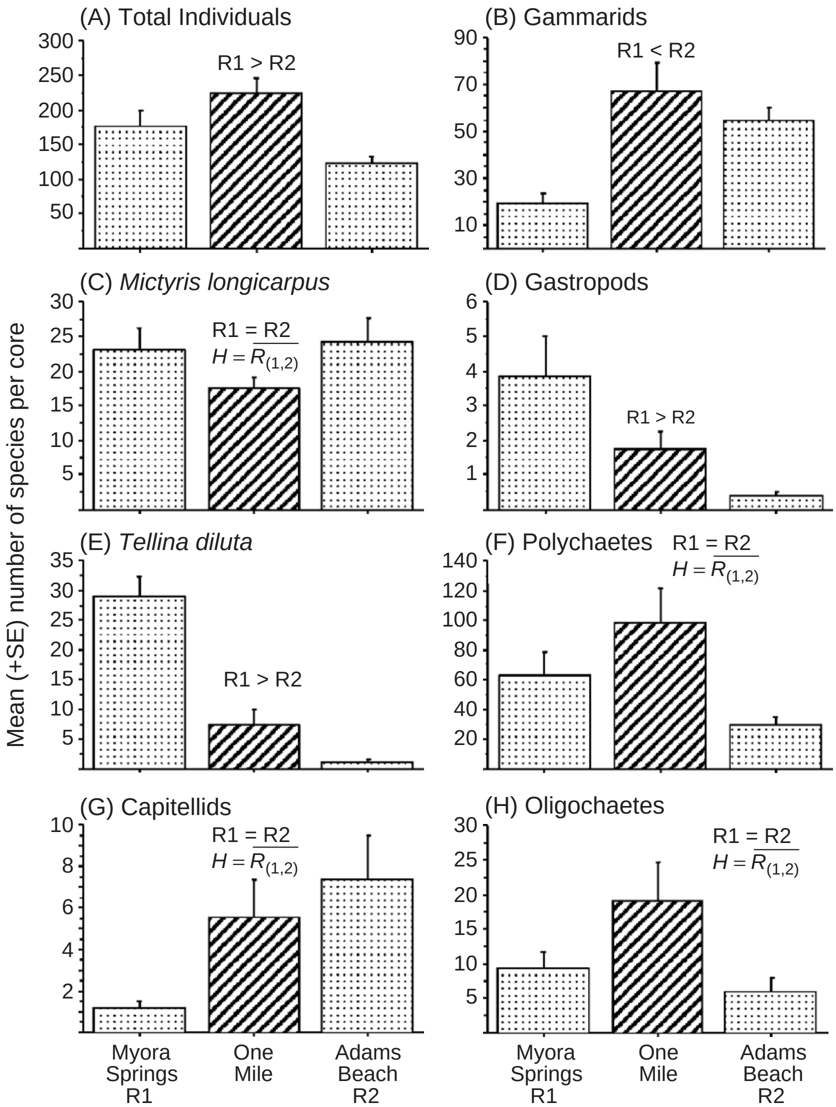


Fig. 3. Mean (+SE) number of animals in different taxa per 225 cm^2 core from the mudflat at three locations in eastern Moreton Bay. One Mile is exposed to recreational yabby harvesting (H), Mora Springs and Adams Beach are reference locations (R1 and R2). (A) Number of individuals, (B) gammarid amphipods, (C) *Mictyris longicarpus*, (D) gastropods, (E) *Tellina diluta*, (F) polychaetes, (G) capitellid polychaetes and (H) oligochaetes. N=16 cores for each location (four replicates from each of two plots in two sites per location). $\bar{R}_{(1,2)}$=average of two reference locations.

For six different groups (gammarids, bivalves, *T. diluta*, polychaetes, capitellids and numbers of bivalve species), there was significantly more variation evident among the plots (tens of metres) in the harvested location compared with the reference locations (Table 1). That is, the abundance of these groups was significantly more variable (patchy) at this small scale in the harvested location than elsewhere. In one case, the number of bivalve species, there was also a significant difference in the spatial variation at the scale of sites (100 m apart), again with the harvested location being more patchy than the reference locations.

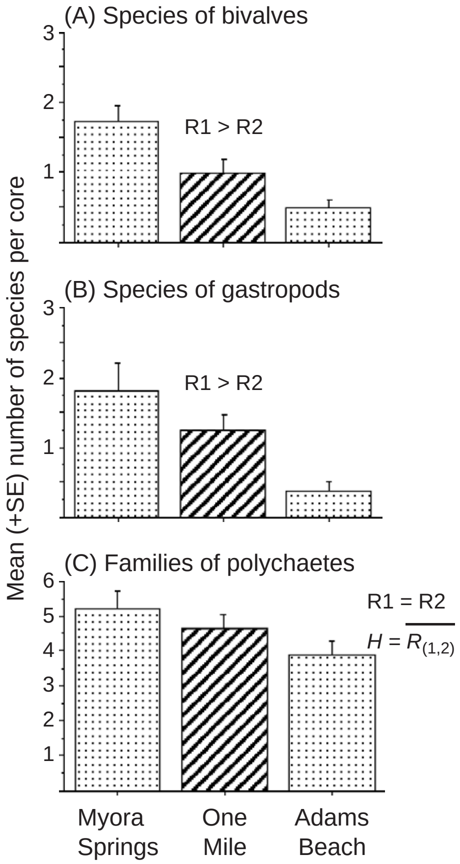


Fig. 4. Mean (+SE) number of taxa per 225-cm^2 core from the mudflat at three locations. One Mile is exposed to recreational yabby harvesting (H), Mora Springs and Adams Beach are reference locations (R1 and R2). (A) Number of species of bivalves, (B) number of species of gastropods and (C) number of families of polychaetes. Other details as in Fig. 3.

3.1.2. Effects on community composition

The composition of the benthic community varied significantly among each of the three locations (PERMANOVA, P<0.001, Fig. 5A) but there was no indication that the harvested location (One Mile=OM) was any more distinct than the two reference locations (Adam's Beach=AB; Myora Spring=MS) were from each other (AB vs. OM, P<0.035, MS vs. OM, P<0.03, AB vs. MS, P<0.01). There was also significant variation at the smaller spatial scales within each of these locations (PERMANOVA, P<0.001).

There were no differences in the patterns of dispersion among the three locations at any of the spatial scales examined: among samples within locations, among samples within plots, nor among the plots within a location. Generally speaking, this indicates that the variability within and among plots in each of the three locations was similar, with no indication that community composition was more patchy in the harvested location than in the reference locations, despite the findings for individual taxa described above.

3.2. Impacts from a commercialised fishing competition

3.2.1. Effects on abundance and patchiness

Two taxa, polychaetes (Fig. 6A) and bivalves (Fig. 6B), showed patterns of temporal change in abundance from Before to After the Straddie Classic Fishing tournament that were different in the harvested location (One Mile) than in the reference locations (Table 2). The number of polychaetes showed a marked increase at One Mile, in contrast to the slight decrease in abundance evident in the two reference locations (Fig. 6A). The abundance of bivalves increased at a significantly greater rate in

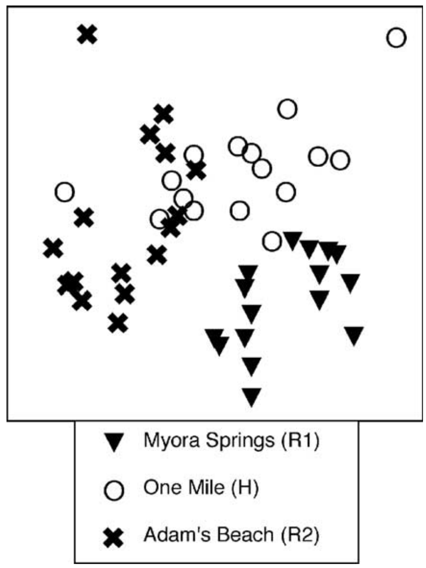


Fig. 5. nMDS ordination on fourth root transformed data for the abundance of macrofauna in the mudflat habitat from three different locations (One Mile=harvested; Myora Springs and Adam's Beach=reference locations). Stress=0.18. Data are for four replicates from each of two plots per site in each location.

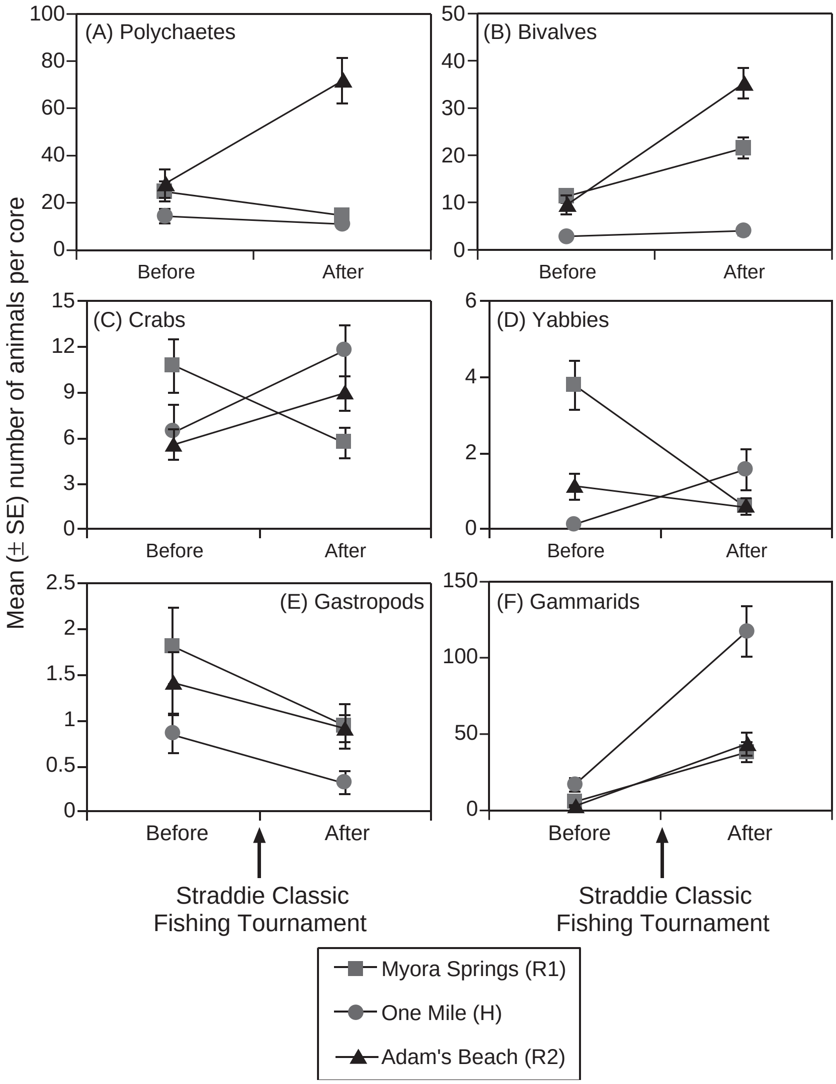


Fig. 6. Mean (±SE) number of (A) polychaetes, (B) bivalves, (C) crabs, (D) yabbies, (E) gastropods and (F) gammarid amphipods from the mudflats at three locations in eastern Moreton Bay before and after the Straddie Classic Fishing Tournament. One Mile is exposed to recreational harvesting of ghost shrimp, Myora Springs and Adam's Beach are reference locations. N=32 cores from each location (four replicates from each of four plots in two sites per location).

the harvested location than in either of the reference locations (Fig. 6B).

For the other taxa, the changes in abundance from Before to After the fishing tournament varied considerably between the harvested location and the reference locations, but also between the two reference locations. There was also considerable variation at small spatial scales (between sites and among plots). The test for a significant interaction between Period (Before vs. After) and Harvest vs. Between Controls was dominated by the considerable variation that existed in the temporal trajectories in the reference locations. For example, the total number of crabs (primarily *M. longicarpus*—Fig. 6C) and yabbies (Fig. 6D showed a marked increase in one of the reference locations but a decrease in the other. In other cases, such as the number of gammarid amphipods (Fig. 6F), the abundance increased in all

Table 2
Summaries of asymmetrical analyses of variance on the abundance of different taxa in the mudflat habitat from three different locations (one harvested=One Mile, 2 reference locations=Adam's Beach and Myora Springs) in eastern Moreton Bay

Variable	Period×Harvested vs. Controls	Period×Between Controls	F-test sites	>Spatial variation	F-test plots	>Spatial variation
Total number of individuals	ns	ns	***	Harvest[a]	ns	–
Gammarids	ns	ns	*	Harvest[b]	*	Harvest[b]
Crabs	ns	ns	ns	–	ns	–
Yabbies	ns	***	**	Harvest[a]	*	Harvest[c]
Gastropods	ns	ns	ns	–	ns	–
Bivalves	***	ns	ns	–	ns	–
Polychaetes	*	ns	**	Harvest[a]	**	Harvest[b]

N=4 replicates from each of two plots within two sites per location. Data were transformed to $\log_e(x+1)$ where necessary to meet the assumptions of homoscedasticity after Cochran's test. Results are shown for the asymmetrical comparison of the interactions between the temporal change (Before to After=Period) and the comparison of Harvested vs. Controls or Between Controls. Other details as in Table 1.
[a] Significant patchiness exists in either the Harvested location or Control locations averaged across both times.
[b] Significant patchiness exists in either the Harvested location or Control locations AFTER the Straddie Classic.
[c] Significant patchiness exists in either the Harvested location or Control locations BEFORE the Straddie Classic.

three locations, but the pattern in the harvested location was similar to one reference location but not the other. Despite the obvious differences in the temporal patterns between the two reference locations, the spatial–temporal interaction (Period x Between Controls) was rarely significant (Table 2), reflecting the significant variation present at the smaller spatial scales.

There was strong evidence for greater patchiness in the abundance of animals, at the scales of Sites and Plots, in the harvested location compared with the reference locations (Table 2). If a pattern of greater patchiness in the harvest location was related to the fishing tournament, the expectation was that there would be a significant result for comparisons of variation among samples collected After the fishing tournament, but not Before or vice versa (if harvesting reduced spatial patchiness). This pattern was observed for three taxa, the number of gammarids at the scales of Sites and Plots and the number of polychaetes and yabbies at the scale of Plots. The number of yabbies was significantly more patchy at the scale of Plots Before the Straddie Classic but this pattern was not detected After, suggesting that intense harvesting led to a decrease in patchiness, as teams focussed on areas with large numbers of holes present.

3.2.2. Effects on community composition

The composition of the benthic community varied significantly among the three locations Before and After the Straddie Classic Fishing tournament (PERMANOVA, Locations—P<0.002). Analysis of the data collected After the tournament indicated that the difference between the two reference locations (Myora and Adam's Beach: average dissimilarity=37.6%) was as great as the difference between the harvested location (One Mile) and either of the reference locations (average dissimilarity: Myora vs. One Mile=33.4%; Adam's Beach vs. One Mile=38.2%). There was also significant small-scale variability in community composition among the Plots within each location (PERMANOVA: P<0.0002). Stress values for the MDS ordinations were relatively large (>0.20) so the plots are not presented as they provide little in the way of additional interpretation (Clarke, 1993).

The patterns of dispersion of individual samples were similar among the three locations Before the Straddie Classic (PERMDISP, P>0.10), as were the levels of heterogeneity of replicates within the plots in the different locations (P>0.09). The dispersion of the individual plots was also similar in the three locations (i.e. the magnitude of the differences among the plots were similar in each location) before the start of the fishing tournament (PERMDISP, P>0.06). After the Straddie Classic though, there were significant differences in the dispersion of the replicate samples among the three locations (P<0.002), with the samples from One Mile (harvested location) being significantly less dispersed than the samples from either of the reference locations, which were not different from each other (average dispersion—One Mile=0.82, Myora=1.03, Adam's Beach=1.15). The dispersion of the replicate samples within the plots was similar in all three locations (*P*>0.87) and there was no significant difference in the dispersion of the plots among the three locations (*P*>0.41).

3.3. Experimental impacts

3.3.1. Abundance of yabbies (controlled pumping)

A total of 8338 yabbies was removed from the three harvested sites over the course of 15 months (October 1998–December 1999). Despite the large number of yabbies that were removed, there was no significant impact on the abundance of yabbies in the harvested compared with the control sites (Table 3). On most dates, there was a trend towards more yabbies to be present in the control sites (Fig. 7A), but this was masked by significant variation among the three sites within each treatment. When the abundance of large (>7 mm CL) yabbies (i.e. the size range removed during harvesting—see below) was analysed separately there was still no indication of a significant decline in the abundance of yabbies as a result of the harvesting (Table 3), although the magnitude of the difference between the control and harvested sites was larger on most dates than when all sizes were considered, with more yabbies being present in the control sites (Fig. 7B).

3.3.2. Size structure of yabby populations

Only animals that were considered to be of a size suitable for use as bait were removed from the

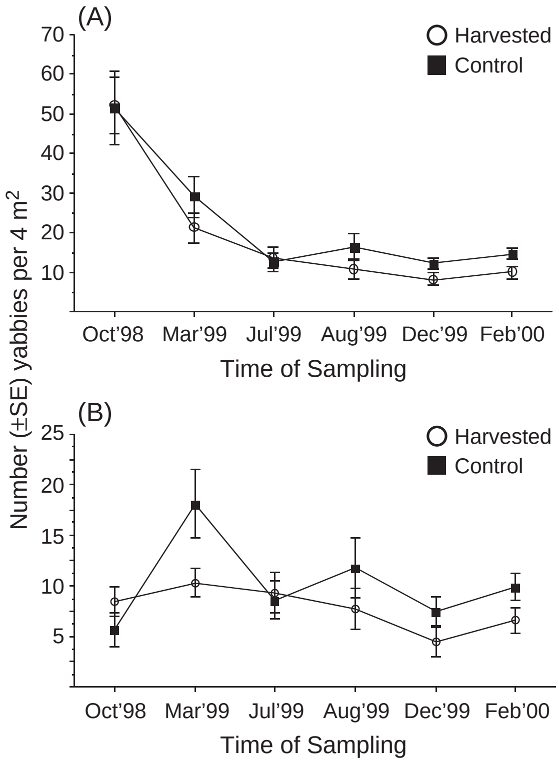


Fig. 7. Mean (±SE) density of yabbies, *Trypaea australiensis*, in 1-ha control or harvested sites sampled on six occasions after the start of experimental bait harvesting. *N*=30 pooled from 10 replicate 4-m^2 quadrats from three sites per treatment on each occasion. (A) Total number of all yabbies, (B) number of large (>7 mm CL) yabbies.

harvested sites on each occasion. The target size for removal was animals larger than approximately 7-mm carapace length although some animals that were smaller than this were occasionally retained. At the start of the experiment, in October/November 1998, the population was mostly comprised of small animals in the control and harvested sites (Fig. 8A and B), so some of these smaller animals were retained during the initial experimental harvesting (Fig. 8C). At the other times of experimental harvesting, the proportion of smaller animals that were retained was much less than in November because there were fewer smaller animals in the population being harvested.

Before the first harvesting event, the mean size of yabbies in the harvest sites was larger than in the control sites and the size-frequency distributions of yabbies in the two treatments were significantly different from each other ($\bar{X}_{\mathrm{Control}}$=4.5 mm,

Table 3
Summaries of analyses of variance on the abundance of (A) all yabbies and (B) large yabbies (>7 mm carapace length) in 4-m^2 quadrats from 1-ha harvested and control plots sampled on six occasions between October 1998 and February 2000

Source variation	*df*	All yabbies		Large yabbies	
		F	P<	*F*	P<
Time	5	16.85	0.001	5.13	0.003
Treatment	1	3.72	0.126	1.04	0.367
Time*Treatment	5	0.85	0.534	2.14	0.102
Plot (Treatment)	4	1.44	0.222	1.07	0.372
Time*Plot (Treatment)	20	1.58	0.056	0.96	0.506
Residual	324				

N=10 replicate quadrats from each of three plots per treatment on each occasion. Data were transformed to $\log_e(x+1)$ where necessary to meet the assumptions of homoscedasticity after Cochran's test.

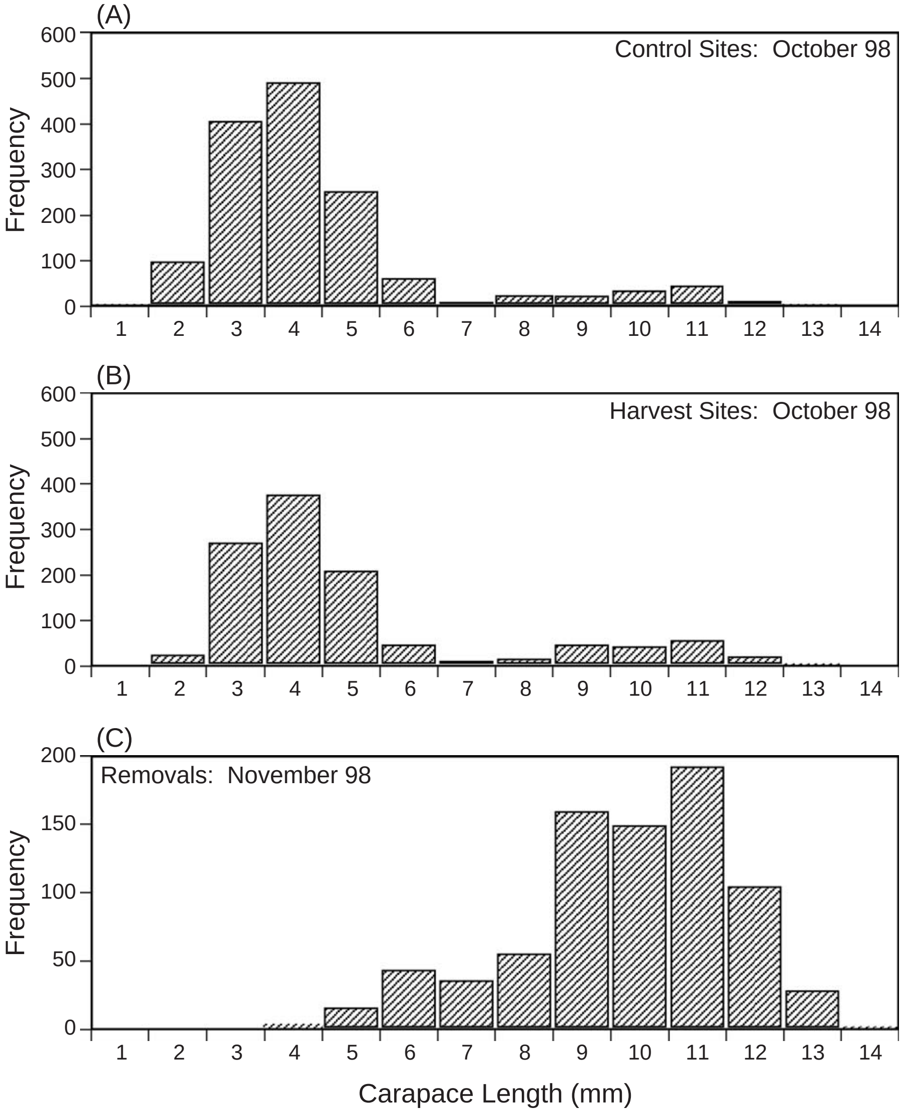
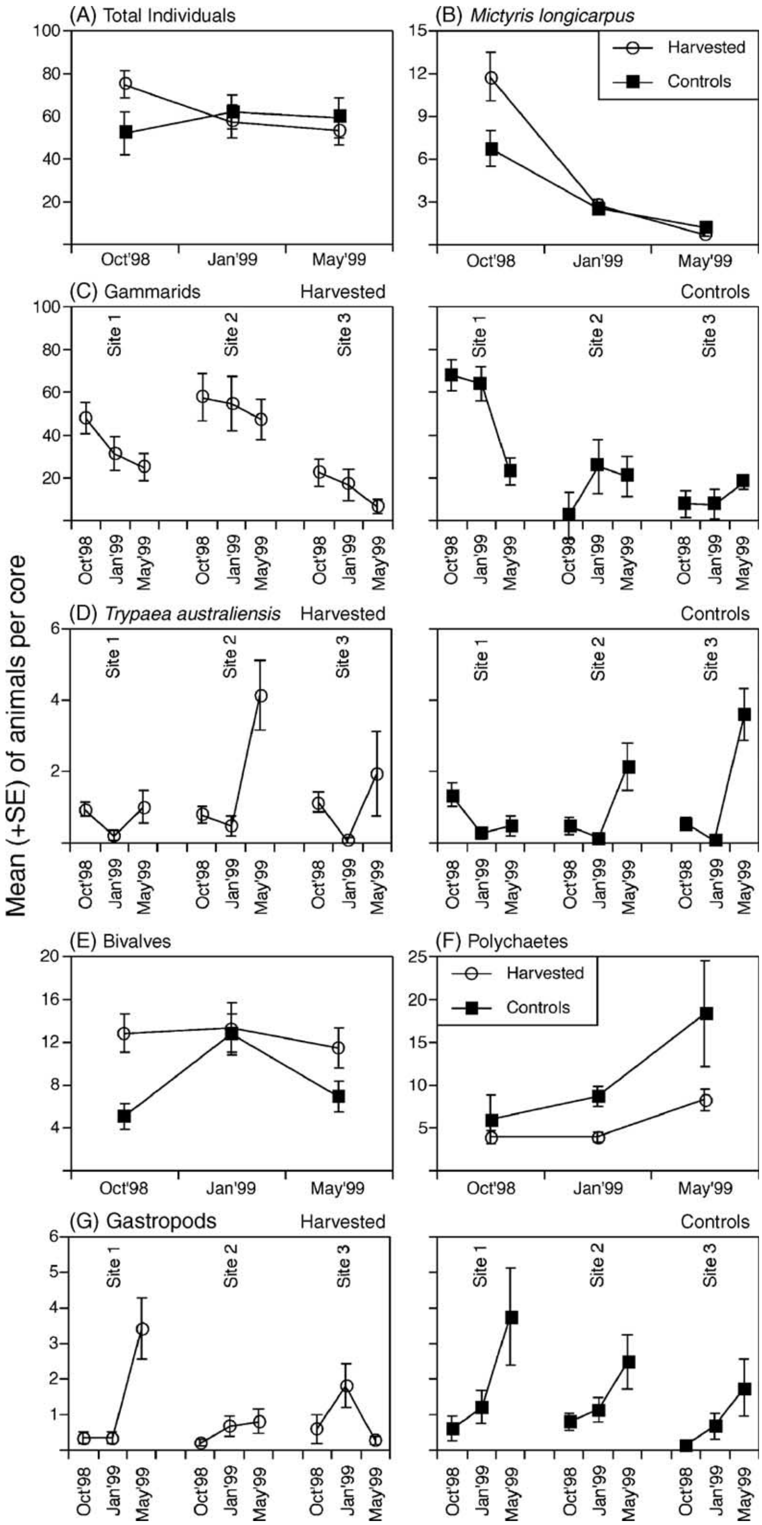


Fig. 8. Size frequency distributions of yabbies in (A) Control sites and (B) Harvest sites in October 1998 (stock assessment data) and (C) the size frequency distribution of yabbies removed from the Harvest sites in November 1998. Only animals considered to be of a size suitable for use as bait were removed from the sites (smaller animals were left on the surface of the mud).

$\bar{X}_{\mathrm{Harvest}}$=5.1 mm; $P<0.001$, Kolmogorov–Smirnov (K–S) 2 sample test). By March 1999, however, the mean size of yabbies in the control sites was greater than in the harvest sites ($\bar{X}_{\mathrm{Control}}$=8.1 mm, $\bar{X}_{\mathrm{Harvest}}$=7.9 mm; $P<0.001$, K–S 2 sample test), after the removal of 1,888 large animals during the first two harvesting events (November 98 and January 99). Between July and December 1999, there were no significant differ-

Fig. 9. Mean (+SE) number of animals in 1 hectare Control or Harvested sites sampled on three occasions after the start of experimental bait harvesting. (A) number of individuals; (B) *Mictyris longicarpus*; (C) gammarid amphipods; (D) juvenile *Trypaea australiensis*; (E) bivalves; (F) polychaetes; (G) gastropods. N=15 cores for each location (five replicates from each of three plots in each site on each occasion).



(A) Total Individuals
(B) *Mictyris longicarpus*
Harvested
Controls
Oct'98
Jan'99
May'99
(C) Gammarids
Harvested
Controls
Site 1
Site 2
Site 3
(D) *Trypaea australiensis*
Mean (+SE) of animals per core
(E) Bivalves
(F) Polychaetes
(G) Gastropods

ences in the size structure of the yabby populations in the control and harvested sites but in February 2000, the mean size of yabbies was again larger in the harvested sites than the controls ($\bar{X}_{\mathrm{Control}}$=8.7 mm, $\bar{X}_{\mathrm{Harvest}}$=9.1 mm; P<0.03, K–S 2 sample test).

3.3.3. Total abundance of individuals

At the start of the experiment (October 1998), there was significantly more benthic animals present in the harvested than control sites (Fig. 9A), despite all sites being allocated to a treatment at random. The number of animals in the two treatments had converged by January 1999 and remained similar for the duration of the experiment. Despite the marked change in the relative numbers of animals in the two treatments, there was no significant difference between the harvested and control sites (Table 4). There was considerable small-scale variation at the scale of the three replicate sites and among the three plots within each site, suggesting that the power to detect a significant interaction or main effect of treatment may have been relatively poor.

Table 4
Summaries of analyses of variance on the total number of individuals and the abundance of individual taxa in 15-cm deep×15-cm diameter cores processed across a 0.5-mm sieve from each of three sites in 1-ha harvested and control plots sampled on three occasions between October 1998 and May 1999

Variable	Period	Treatment	P×T	Site (Treat)	P×Site (Treat)	Plots (P×S(T))
Total number of individuals	ns	ns	ns	***	ns	***
Mictyris longicarpus	***	ns	*[a]	ns	ns	ns
Gammarids	ns	ns	ns	***	*	***
Yabbies (juveniles)	*	ns	ns	ns	*	***
Bivalves	*	ns	ns[b]	***	ns	***
Gastropods	*	ns	ns	ns	*	**
Polychaetes	**	ns	*[c]	ns	ns	*

N=5 replicate cores from each of three plots per site per treatment on each occasion. Data were transformed to $\log_e(x+1)$ where necessary to meet the assumptions of homoscedasticity after Cochran's test. ***P<0.001, **P<0.01, *P<0.05, ns=P>0.05.

[a] Period×Treatment tested over pooled Residual+Plots(P×S(T))+P×(T).

[b] Not significant, but P<0.10.

[c] Period×Treatment tested over pooled Plots(P×S(T))+P×S(T).

3.3.4. Abundance of solider crabs

The abundance of *M. longicarpus* was also initially greater in the harvested than the control sites (Fig. 9B), but had converged by January 1999. There was a significant effect of harvesting on the abundance of soldier crabs (Table 4) seen as an initial decline in abundance between October 1998 and January 1999 that was much greater in the harvested sites than in the controls.

3.3.5. Abundance of gammarid amphipods

The abundance of gammarid amphipods did not change through time in the same way in each of the three sites in the harvested and/or control treatments (Table 4: P×Site(Treat) interaction). In each of the three harvested sites, there was an overall decrease in abundance of gammarids during the course of the experiment (Fig. 9C—Harvested), whereas there was an increase in abundance in two of the control plots but a decrease in one (Fig. 9C—Controls). This is suggestive of a potential impact on the abundance of gammarid amphipods although caution needs to be exercised. The latter plot (Site 1-Controls) started with a significantly greater density of gammarids than the other control sites, then declined in abundance to similar levels to the three harvested sites, so the change in abundance that was observed could be related to a factor other than harvesting.

3.3.6. Abundance of juvenile yabbies (T. australiensis)

There was no indication of any impact of the harvesting on the abundance of the juvenile yabbies, consistent with the results from the sampling using controlled pumping. The abundance of juvenile yabbies varied through time in different ways in the three sites from the harvested and/or control treatments (Table 4: P×Site(Treat) interaction). The overall pattern was similar in all cases though, only the relative magnitude of the change between each time varied (Fig. 9D).

3.3.7. Abundance of bivalves

The abundance of bivalves varied significantly among the sites within each of the treatments and also among the plots within each site (Table 4), reducing the power to detect a significant treatment effect. There was some suggestion of a Period×Treatment interaction (Table 4, P<0.10), seen as marked fluctuations in the abundance of bivalves in the control sites but not in the harvested sites (Fig. 9E). After the first period of harvesting (in November 1998), the abundance of bivalves increased in the control sites but not in the harvested plots. The number of bivalves subsequently declined in the control plots but not in the harvested plots, so it was difficult to interpret these patterns in relation to any simple effects from harvesting.

3.3.8. Abundance of polychaetes

There were clear indications of an impact of harvesting on the abundance of polychaete worms (Fig. 9F), with a significant interaction (Table 4) highlighting the suppression of the numbers of worms in the harvested sites. There was no significant variability among the sites within the treatments, but there was significant small scale variability at the scale of the plots within the sites.

3.3.9. Abundance of gastropods

The abundance of snails varied through time in different ways in the three sites from the harvested and/or control treatments (Table 4: P×Site(Treat) interaction). The overall pattern of change was similar in all cases with a general increase in numbers through time

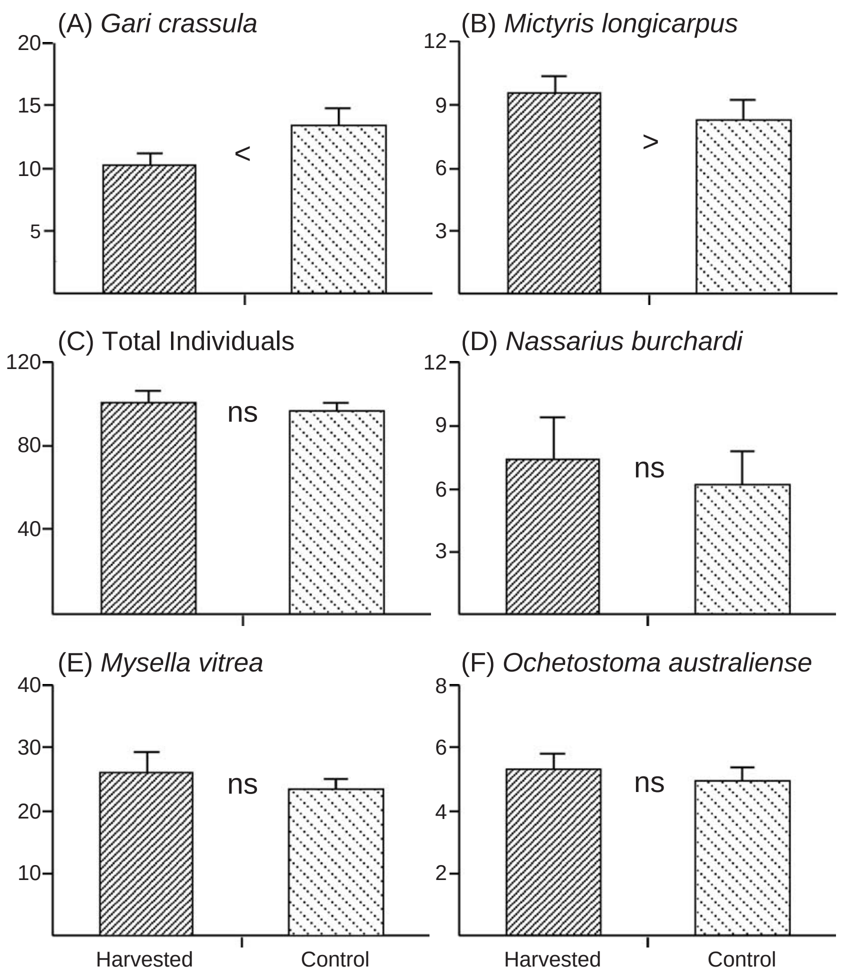


Fig. 10. Mean (+SE) number of animals sampled from 1 ha control or harvested sites sampled at the end of the experiment in February 2000. (A) *Gari crassula*, (B) *Mictyris longicarpus*, (C) total number of all individuals, (D) *Nassarius burchardi*, (E) *Mysella vitrea* and (F) *Ochetostoma australiense*. <> Signifies treatments significantly different—$P<0.05$; ns signifies treatments not significantly different—$P>0.05$ after ANOVA.

except in a single harvested site that showed an initial increase followed by a decline in abundance (Fig. 9G).

3.3.10. Spatial patchiness

The only taxon that showed a significant effect of experimental harvesting on spatial patchiness was the polychaetes. The abundance of polychaetes was significantly more patchy at the scale of 1 hectare Sites and Plots (within Sites) under harvesting compared with the control treatment.

3.3.11. Composition of the benthic assemblage

There was no indication that the harvesting affected the composition of the infaunal assemblage on any of the three occasions (PERMANOVA: October 1998—P>0.19; January 1999—P>0.83; May 1999—P>0.82). In all cases, there was significant variation in the composition of the infaunal assemblage at the smaller scale of Plots within each of the treatments. Similarly, there was no indication that harvesting affected the spatial dispersion (patchiness) of the samples, at the scale of Plots within the Treatments, or Sites within the Plots.

3.3.12. Abundance of deep-burrowing and mobile fauna

A total of 8930 individuals was collected from the samples taken at the end of the experiment using the controlled pumping method in 4-m^2 plots, including yabbies and soldier crabs. Most of these individuals were species that only occurred infrequently in the smaller, 15-cm diameter cores, collected to 15-cm depth. Two species of bivalves, *Mysella vitrea* and *Gari crassula*, comprised ca. 36% of these individuals, while two species of gastropods, *Nassarius burchardi* and an unidentified juvenile, comprised another ca. 27% of individuals. The largest animals, yabbies, soldier crabs and the echiuran, *Ochetostoma australiense*, comprised another 27% of the total individuals. No other taxon was sufficiently abundant to analyse individually.

The abundance of *G. crassula* (Fig. 10A) was significantly greater and *M. longicarpus* (Fig. 10B) was significantly smaller in the control than the harvested sites at end of the experiment in February 2000, although the magnitude of these differences was quite small. None of the other abundant taxa showed any significant effect of the 15 months of harvesting and, in most cases, the final abundance was very similar in both treatments (Fig. 10C–F). There was no significant effect of harvesting on the composition of the deep-dwelling benthic assemblage (PERMANOVA, P>0.17), but there was significant small scale variation among the three sites in each of the control and harvested treatments plots in the harvested and control treatments (PEMANOVA, P<0.002).

4. Discussion

The general approach used here to examine the effects of bait harvesting is an improvement over previous studies. A combination of approaches was used, including general sampling of areas regularly exposed to harvesting compared with suitable reference areas, a Before–After/Control-Impact study based around a competitive fishing tournament and a controlled, manipulative experiment. Each of these components incorporated estimates of abundance at several spatial scales (Morrisey et al., 1992) allowing us to examine whether harvesting affected not only the abundance of individual taxa, but also the degree of spatial variation (patchiness) in their distribution (Underwood, 1992).

Previous studies on the impacts of bait-harvesting in soft-sediments done elsewhere (e.g. Blake, 1979a,b; Jackson and James, 1979; McLusky et al., 1983; Wynberg and Branch, 1991, 1994; Brown and Wilson, 1997) have shown widespread effects on the abundance and diversity of a broad range of taxa. This is in marked contrast to the results here where only a few taxa showed a significant decline in abundance. Importantly though, there was evidence of more subtle effects from harvesting with changes detected in the degree of spatial variation (patchiness) of several taxa.

Three lines of evidence together suggest that the disturbance associated with the recreational harvest of yabbies causes significant, but localised, impacts on benthic assemblages in subtropical Moreton Bay. First, the distribution of some taxa at One Mile was significantly more patchy than at nearby references areas. Capitellid polychaetes, total numbers of all polychaetes, gammarid amphipods, total numbers of all bivalves and the tellinid, *T. diluta*, were all relatively abundant at each of the three locations, but were significantly more patchy in their distribution on the mudflat at One Mile than the other areas. Recreational bait harvesting, specifically for yabbies, is common at One Mile because of its proximity to the boat ramp, used as a primary launching site for fishing expeditions from the island (McPhee and Skilleter, 2002a), but is relatively uncommon at the reference areas.

Second, the abundance of gammarid amphipods and polychaetes was also more variable (patchy) as a result of the short-term, intense harvesting associated with the Straddie Classic Fishing Tournament. Both these taxa showed increased patchiness in the harvested locations at the scale of sites (hundreds of metres) and plots (tens of metres) after the completion of the Classic. Additionally, at the scale of Sites (hundreds of metres) the patchiness in the abundance of yabbies decreased significantly from before to after the fishing tournament, suggesting that intense harvesting produced a more even distribution of these animals across the mudflat. The latter result is perhaps not surprising, given that experienced harvesters, such as those participating in the Straddie Classic (McPhee and Skilleter, 2002a), move to patches on the mudflat where there are apparently greater densities of animals, based on the number of holes visible on the surface (see also Beal and Vencile, 2001). Removal of the yabbies through such harvesting would lead to a more even distribution of the animals.

Third, the controlled, experimental harvesting of yabbies caused significant declines in the abundance of soldier crabs (*M. longicarpus*) and polychaete worms and a significant increase in the patchiness of the polychaetes, at scales commensurate with the activities of recreational and commercial operators (see below). In addition, there was clear evidence of a decline in the abundance of gammarid amphipods in each of the three harvested plots, although this was not detected as being significant because of a simultaneous decline in the abundance of the amphipods on one of the three control plots. In combination, these outcomes indicate that bait-harvesting of yabbies has the potential to cause significant impacts, but only on a limited range of taxa in intertidal sediments.

Capitellid polychaetes are often considered to be opportunist species, able to colonise rapidly areas that have been disturbed. Such species are thought to be adapted for life in a rapidly changing and temporally unpredictable habitat. They are widely recognised for their occurrence in disturbed sediments. Studies of benthic succession following environmental disturbances, including an oil spill (Grassle and Grassle, 1974), dredging for a boating channel (Reish, 1961), organic enrichment and pollution (Pearson and Rosenberg, 1978) and dredge spoil disposal (Oliver et al., 1977), have shown capitellids to be amongst the first arrivals into an area following the disturbance. Similarly, gammarid amphipods have been reported as early colonisers of disturbed sediments (Oliver et al., 1977), primarily via immigration from surrounding patches (e.g. Saila et al., 1972; Wildish and Thomas, 1985). While capitellid polychaetes are mostly characterised as burrowing, deposit-feeders (Fauchald and Jumars, 1979), it is less easy to generalise about a large taxonomic grouping such as the gammarids. Dittmann (1996) found that the experimental exclusion of *T. australiensis* (*Callianassa australiensis* in that study) from patches of sediment led to a reduction in the abundance of amphipods within those areas because of the loss of the burrows. She contended that the burrows provided a “promotive effect” (sensu Reise, 1983). The small tellinid bivalve, *T. diluta*, was also more patchily distributed in the sediments at One Mile than elsewhere. *T. diluta* is primarily a deposit-feeder that responds to a range of other impacts, including dredging (Skilleter, unpublished data). The change in patchiness in the distribution and abundance of these taxa is presumably a response to the patchy nature of the harvesting of yabbies from the sediments.

The significant impacts on the abundance of amphipods, polychaetes and soldier crabs observed in the large-scale experiment were not consistent with the lack of such effects on these groups observed from the sampling done in the area regularly used by recreational harvesters (i.e. One Mile) but were consistent with previous studies elsewhere (Brown and Wilson, 1997). The area used for the experimental study (Chigill Chigill) was selected because of its remote location and general inaccessibility from the nearest access points. This area is rarely, if at all, visited by recreational harvesters and, due to zoning regulations in the Moreton Bay Marine Park, is not used by commercial operators. From the perspective of the harvesting of yabbies, this site could be considered relatively pristine and undisturbed. In contrast, the area around One Mile has experienced sustained bait-harvesting for decades. Studies done elsewhere (e.g. Jackson and James, 1979; McLusky et al., 1983; Wynberg and Branch, 1991, 1994) have also been primarily focussed in areas subjected to extensive and sustained bait-harvesting. In effect, the manipulative experiment at Chigill Chigill formed a 'pulse' stress on previously undisturbed populations whereas the sustained harvesting at One Mile represents a 'press' perturbation (Underwood, 1989). Potentially, the differences in the type of disturbance to which the benthic assemblages were exposed may account for why these groups of animals responded differently to the effects of prolonged versus short-term harvesting. Press and pulse stresses are likely to cause different types of responses in populations and assemblages, over different time periods (Bender et al., 1984), but more focussed work is required to understand better the way in which press and pulse disturbances specifically affect natural populations.

Bait-harvesting is an activity that involves considerable disturbance to the sediments (e.g. Reise, 1983; Wynberg and Branch, 1994, 1997), in addition to the removal of the target species. Sediments are turned over and animals, including under-sized or undetected yabbies, are left exposed on the surface (Jackson and James, 1979; Ambrose et al., 1998; Beal and Vencile, 2001), where they often fall prey to gulls (Ambrose, 1986; Wynberg and Branch, 1991) and scavengers such as crabs and worms (Beal and Vencile, 2001; personal observation). The patches that are disturbed are typically about 4 m^2 in area: the animals in that patch are removed, before the harvester moves to another patch (McPhee and Skilleter, 2002a; Skilleter unpublished data). Interspersed with these disturbed patches are areas of sediment that are left untouched, forming a complex mosaic (Johnson, 1970), similar in appearance to an area subjected to intense ray predation (e.g. Van Blaricom, 1982; Thrush et al., 1991; personal observation) during a high tide. Impacts from ray predation on the abundance of bivalves, polychaetes and amphipods have been reported in these studies, although specific effects on spatial patchiness have not been examined in detail (but see Thrush et al., 1991 who report increased heterogeneity for the bivalve *Tellina liliana* in New Zealand). Warwick and Clarke (1993) suggested that increased spatial variability among samples may be a general symptom of the effects of environmental disturbances, based on their analyses on a range of taxa and systems, including sedimentary meio- and macrofauna , corals and fish (but see Chapman et al., 1995 for a counter-example). The increased patchiness of various sedimentary infauna, at several spatial scales, as a result of bait-harvesting is consistent with the Warwick and Clarke (1993) hypothesis, even if the result here was restricted to a few specific taxa.

Rather than an environmental disturbance, harvesting of bait could also be viewed as predation (by humans) (e.g. Castilla and Durán, 1985; Castilla, 1999) and predation has been shown to increase or decrease the patchiness of prey populations (Schneider, 1992). Which of these alternative models (i.e. disturbance versus predation) is most appropriate to understand the implications of bait-harvesting depends on whether the primary effect arises from the physical aspect of harvesting or the removal of the prey. This study was not designed to distinguish between these two (see below), but such a distinction would be of interest from an ecological perspective.

An important component of impacts associated with harvesting of intertidal animals arises from the disturbance to the habitat during the collection of animals (Underwood, 1993). In the case of the harvesting of animals from rocky shores, considerable damage to the habitat may arise depending on the methods used for locating and extracting the targeted animals. Use of crowbars, sledge-hammers and other implements may aid in exposing the animals, although this may not always be a necessary component of the harvesting routine and would likely depend on the species being harvested (e.g. cryptic versus exposed). In sedimentary environments, trampling and digging are two side-effects from harvesting that may cause significant impacts on the fauna, even as much as that caused by removal of the animals themselves (Peterson, 1977; Wynberg and Branch, 1997; Contessa and Bird, 2004).

No attempt was made to partition the effects of physical disturbance from the removal of the prey in the experiment examining the effects of harvesting of yabbies. The disturbance to the substratum from use of a yabby pump or other extractive device is an inherent element of the bait collection process: yabbies are rarely if ever found on the surface of the substratum naturally, so harvesting requires digging and turn-over of the sediments. This disturbance occurs irrespective of whether the pumping is successful or not (i.e. whether yabbies are caught from each patch of sediment). The design of the experiment focussed on duplicating the patterns of pumping employed by recreational and commercial operators, rather than removal of a specific number of animals per se. Similar levels of pumping were done on each occasion, although very different numbers of yabbies were removed, thus the results reflect the total effects of harvesting. As highlighted by Wynberg and Branch (1997), knowledge of the number of animals removed from an area alone does not provide a thorough understanding of the impacts from harvesting. The approach taken here avoided this problem, by duplicating the harvesting intensity from recreational and commercial efforts, not their success at capturing the animals.

In summary, harvesting of yabbies for bait by recreational and commercial fishers was shown to cause significant but localised impacts on a limited range of benthic fauna on subtropical, intertidal mudflats in SE Queensland. Harvesting was related to increased patchiness in the distribution and abundance of several taxa and reduced abundance for several other groups. The changes in the availability of benthic organisms have the potential to influence the foraging activities and behaviour of higher trophic levels, such as migratory shorebirds (e.g. Zharikov and Skilleter, 2003).

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