# Spatial and temporal patterns of abundance and recruitment of ghost shrimp *Trypaea australiensis* across hierarchical scales in south-eastern Australia

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ABSTRACT: Spatial and temporal variation in abundance and recruitment of burrowing ghost shrimp *Trypaea australiensis* was examined across 3 south-eastern Australian estuaries using a hierarchical sampling design, over a 2 yr period. We tested the hypothesis that abundances of shrimp were different between plots (10s to 100s of metres apart), sites within estuaries (kilometres apart), estuaries (100s of kilometres apart) and through time. More frequent sampling at 1 site also examined temporal variation at scales of months, seasons and years. Another aim was to investigate the reliability of using counts of burrow openings to indirectly measure the relative abundance of *T. australiensis*. Significant and interactive variability was detected at the scale of plots for the mean numbers of shrimp and recruits. Components of variation, however, suggested there was patchiness in abundance at all spatial scales within estuaries, particularly between replicates separated by metres. Indeed, between-replicate variance was greater than for any of the temporal scales examined. Despite this small-scale patchiness, patterns of abundance and recruitment were generally consistent across broad geographic areas. Numbers of shrimp generally increased throughout spring and summer periods, and recruitment also occurred during these times. The patterns of variation observed in this study highlight the importance of including appropriate scales of sampling in future monitoring studies of *T. australiensis* and in experiments concerned with detecting the effects of bait harvesting on populations of shrimp. We also conclude that counting burrow openings is not a reliable predictor of the relative abundance of *T. australiensis*.

KEY WORDS:  Spatial variation · Temporal variation · Patchiness · Bait harvesting · Yabby pump · Estuaries · New South Wales

## INTRODUCTION

Burrowing ghost shrimp (Thalassinidea) inhabit mainly soft sediments throughout a range of marine environments worldwide (Dworschak 2000, Felder 2001). The importance of these taxa to ecological processes, such as the effects of their bioturbating activities on the structure of benthic communities and physical and biogeochemical properties of sediments, has been well documented (Posey 1986, Ziebis et al. 1996, Berkenbusch et al. 2000). Many studies have also (1) considered various aspects of thalassinid biology (reviewed by Felder 2001), (2) highlighted the significance of some species to commercial and recreational bait fisheries (Wynberg & Branch 1991, McPhee & Skilleter 2002a) and (3) examined the effects of bait-harvesting on populations of shrimp, associated infaunal communities and the sediment environment (Wynberg & Branch 1994, Contessa & Bird 2004, Skilleter et al. 2005). Comparatively few studies have quantitatively investigated spatial and temporal variation in abundance of ghost shrimp over hierarchical scales and

across a wide geographic range. Understanding such variation provides a logical starting point for experiments that explain patterns in ecology, and also a scientific basis for the assessment and management of anthropogenic impacts (Underwood 1992, Underwood et al. 2000).

Previous studies of other soft-sediment benthos have examined variations in abundance at a hierarchy of spatial and temporal scales (Morrisey et al. 1992a,b). These studies, like others done for biota on rocky shores (reviewed by Fraschetti et al. 2005), have demonstrated the inherent patchiness of populations and assemblages of organisms through time and space and highlighted the general inadequacies of sampling at single spatial and temporal scales. Nevertheless, most quantitative studies of thalassinid shrimp have been restricted to single sites, estuaries, or locations (e.g. Tunberg 1986, Dumbauld et al. 1996, Berkenbusch & Rowden 1998). Furthermore, many studies have often not sampled appropriately at these scales, having either too few replicates within sampling areas (e.g. Rowden & Jones 1994, Berkenbusch & Rowden 1998), or having enough replicates but only within single, relatively small areas or transects (e.g. Tamaki et al. 1997). Counts of burrow openings have also been used to indirectly estimate numbers of ghost shrimp (e.g. Wynberg & Branch 1991), which may be unreliable for some thalassinids (McPhee & Skilleter 2002b).

*Trypaea australiensis* (Dana, 1852) is a relatively abundant species of burrowing ghost shrimp, which occurs in intertidal sediments of estuaries and sheltered bays along much of the east coast of Australia. It is a popular bait item used by recreational anglers targeting a range of estuarine and inshore finfish (McPhee & Skilleter 2002a). Previous quantitative studies of *T. australiensis* are uncommon and, as for other species of ghost shrimp worldwide, have often been conducted on limited spatial and temporal scales (Coleman & Poore 1980, McPhee & Skilleter 2002b). Consequently, our knowledge of spatio-temporal variability in the abundance of *T. australiensis*, and indeed other thalassinid shrimp, is poor.

A quantitative, rapid and repeatable method of sampling *Trypaea australiensis* has been developed and described elsewhere (Rotherham & West 2003). Using this sampling methodology, the primary aim of the present study was to quantify variation in the abundance of *T. australiensis* over a hierarchy of spatial and temporal scales in south-eastern Australia. The general hypothesis tested was that the abundance of *T. australiensis* was significantly different at each of the spatial and temporal scales investigated. A second aim was to examine spatial and temporal variability in the relationship between counts of burrow openings and numbers of *T. australiensis*.

## MATERIALS AND METHODS

**Study area.** The study was done between Port Hacking and Moruya on the south-eastern coast of New South Wales (NSW), Australia (Fig. 1). The 3 estuaries sampled included Port Hacking and the Shoalhaven and Moruya Rivers. These estuaries were selected because they contained large tidal flats that support populations of *Trypaea australiensis*. Although the 3 estuaries differ in size and morphology, they all have permanently open connections to adjacent coastal waters. The ranges of water temperatures were similar across sites (12 to 30°C). Mean salinity measurements were also typical of marine-dominated estuaries (>27 ppt) across all sites.

**Sampling design.** Within each estuary, 2 sandflat sites separated by 1 to 2 km were selected and included: Maianbar and Cabbage Tree Basin in Port Hacking, Shoalhaven Heads and Old Man Island in the Shoalhaven River and Garlandtown and Quondolo Island in the Moruya River. Since none of these sites was closed to
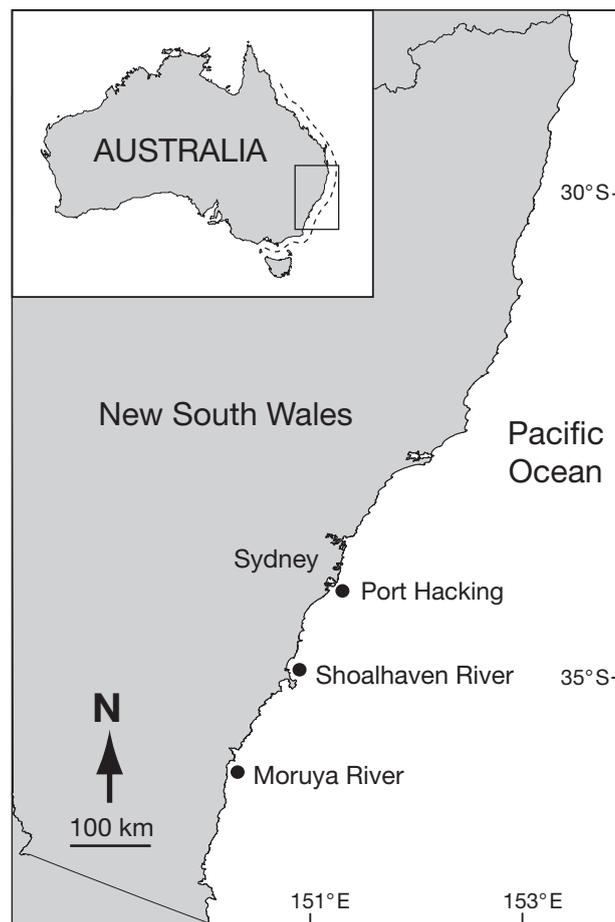


Fig. 1. Location of estuaries sampled in south-eastern Australia. Dashed line on insert shows approximate distribution of *Trypaea australiensis*

commercial and/or recreational harvesting, it was assumed that collection of *Trypaea australiensis* for bait occurred at all sites, which was confirmed during the study.

Within each site in each estuary, 3 plots of $10 \times 10$ m separated by 50 to 100 m were selected randomly. On each sampling occasion, 5 random 0.1 $m^2$ quadrats separated by at least 1 m were placed in each plot. Twelve pumps of a yabby pump (see Rotherham & West 2003, for a description of this gear) were then carried out in each quadrat.

Sampling of *Trypaea australiensis* with a yabby pump provides relative estimates of abundance in terms of catch-per-unit-effort (CPUE), rather than absolute densities. Pilot experiments demonstrated that 12 pumps of the yabby pump within the 0.1 $m^2$ quadrat provided the optimal level of effort for sampling the relative abundance of *T. australiensis* (Rotherham & West 2003). Greater effort (e.g. 16 pumps) did not catch significantly more shrimp. Potential increases in sampling efficiency throughout the study period were assumed to be negligible, given that several thousand pumps had been completed during the pilot work. All sediments sampled were coarse- to medium-grain sands, and differences between sites were unlikely to have significantly affected the efficiency of sampling.

The experimental design incorporated nested spatial scales ranging from metres (between quadrats), 10s to 100s of metres (between plots), kilometres (between sites within estuaries) and 100s of kilometres (between estuaries). Sampling was stratified at each site to include the intertidal zone where *Trypaea australiensis* occurred. Unlike rocky shores, which are multi-scalar and can undergo significant changes in elevation within a few metres, vertical zonation in tidal flats is often less obvious given their planar nature and larger size. Therefore, variation between plots in the present study represents within-site variation, and no attempt was made to examine vertical differences in the abundance of *T. australiensis*.

Sampling was done at all spatial scales over a 2 yr period (January 2001 to January 2003); approximately monthly for the first 12 mo and quarterly for the second 12 mo (April 2001 and April 2002 were not sampled). To investigate differences in abundance between seasons and years with respect to the amount of variation between months within seasons and years, the Maianbar site was sampled approximately monthly for the entire 2 yr period. Sampling of all spatial scales at each time was done over a 3 to 5 d period on outgoing tides, with sampling generally commencing 2 h before low tide when sandflats became exposed. While the same $10 \times 10$ m plots were sampled at each site on each occasion, random placement of the quadrats ensured independence of samples between times and the same quadrats were not sampled on each occasion.

Prior to pumping the quadrat, the numbers of burrow openings were counted to investigate the relationship between numbers of burrows and the relative abundance of *Trypaea australiensis*. Contents of the pump were sieved over a 1.56 mm mesh; shrimp retained were stored in snap-lock plastic bags and frozen. In the laboratory, shrimp were defrosted and data were collected, including sex (presence/absence of pleopods), total length (TL), carapace length (CL) and wet weight (g). Additional morphometric measurements were also taken and will form the basis of future publications relating to the reproductive biology and growth of *T. australiensis*.

Environmental variables were measured concurrently with sampling of ghost shrimp on most occasions. Salinity (ppt) and water temperature (°C) were measured in mid-depth water adjacent to the sampling site with a handheld MC-84 meter.

**Analyses of data.** Spatial patterns of abundance of *Trypaea australiensis* were examined over a temporal period of 2 yr using analysis of variance (ANOVA). The total number of individuals, burrows, biomass, males and females, and the number of recruits (≤5 mm CL) were determined for each quadrat at each sampling time. Data were analysed using a nested and orthogonal analysis of variance model. Spatial scales were random, nested factors that were orthogonal to time (a random factor). Time was considered a random factor as the general hypothesis tested was that abundances of *T. australiensis* changed through time. The model did not allow construction of a conventional *F*-ratio for the factors of estuary and site. Post hoc pooling of higher-order interactions that were not significant at p > 0.25, allowed a standard *F*-ratio to be used (Winer et al. 1991). When post hoc pooling of interactions could not be done, the analysis proceeded as if interaction terms were significant, in which case no test was done (Underwood 1997).

Prior to all ANOVAs, data were tested for homogeneity of variances using Cochran's test and, where necessary, transformed to ln $(x + 1)$. No data remained heterogeneous after transformation. Data were not tested for violations of the assumption of normality, as ANOVA is considered robust to such violations in large, balanced designs (Underwood 1997).

Components of variation were measured for each of the spatial scales (i.e. estuaries, sites, plots and replicates) from the mean square estimates in ANOVAs done on untransformed data (Winer et al. 1991). Owing to significant spatio-temporal interactions at the scale of plots, the contributions of each spatial scale to the total measures of variation were calculated independently for each time of sampling and then averaged. When a negative estimate was obtained from the analysis, the corresponding factor was removed from

the model and the mean square estimates for the remaining factors recalculated. Providing that levels of replication are balanced (as here), this method produces the same results as using residual maximum likelihood (Fletcher & Underwood 2002).

Investigations of temporal patterns at a hierarchy of scales were not possible across all spatial scales, as populations were sampled approximately monthly for the first 12 mo and quarterly for the second year. The Maianbar site, however, was sampled approximately monthly (n = 22) for the entire 2 yr period. To ensure a balanced design, 2 of the months were randomly selected from each season, and temporal patterns of abundance (total number of individuals, burrows, biomass, males, females and recruits ≤5 mm) were then examined between months, seasons and years, using a 4-factor ANOVA. Temporal scales were random, nested factors that were orthogonal to plots (also a random factor). *F*-ratios for main effects of year and season were constructed by post hoc pooling of non-significant interaction terms at p > 0.25. Because there were significant spatio-temporal interactions in ANOVAs, components of variation for each of the temporal scales (i.e. months, seasons and years) were calculated separately for each plot.

The relationship between number of burrow openings (dependent variable) and relative abundance of *Trypaea australiensis* was investigated using linear regressions. Analysis of covariance (ANCOVA) examined whether the relationship between the number of burrows and relative abundance changed through time and between sites.

## RESULTS

### Spatial and temporal patterns of abundance

ANOVA results for selected sets of data are summarised in Table 1. Patterns of abundance of *Trypaea australiensis* were similar across most sets of data. There were no significant differences between estuaries (where post hoc pooling allowed a test of this factor), and relative abundances generally increased throughout the spring and summer months of each year (Figs. 2 to 4; figures for biomass, males and females showed similar patterns and are not shown for brevity). Although differences between sites were observed for most estuaries and variables (Figs. 2 to 4), no formal tests of this factor were possible in the ANOVA model. Significant time × plot interactions in ANOVA across all data sets indicated that differences between plots existed, but that the magnitude of variation differed between sampling times (Table 1). This pattern was clear for the first year of the study, as there were concomitant increases in variation between plots across most sites as the numbers of shrimp increased during spring and summer (Fig. 2).

The calculation of components of variance for each spatial scale confirmed the low contribution of the scale estuaries to the total variance (Table 1). Although these calculations also verified the relative importance of the scale of plots, there was more variation at the scale of sites for most analyses. The spatial scale associated with the greatest variability, however, was the

Table 1. *Trypaea australiensis*. Results of ANOVA testing for differences in mean numbers of (a) individuals, (b) burrows, (c) biomass, (d) males, (e) females and (f) recruits among sampling times (T), estuaries (E), sites (S) nested within estuaries and plots (P) nested within sites within estuaries. All factors considered random. *F*-ratios shown (significance of *F*-test: *p < 0.05; **p < 0.01; ***p < 0.001). *F*-ratios are not shown for interaction terms that were pooled (or eliminated) at p > 0.25. Variance components derived from ANOVA done separately for each time of sampling (n = 15) and then averaged are shown for each spatial scale (see 'Materials and methods'). Standard errors are in parentheses

| Source of variation | df | (a) Individuals | (b) Burrows | (c) Biomass | (d) Males | (e) Females | (f) Recruits[a] |
|---|---|---|---|---|---|---|---|
| Time | 14 | 18.29*** | 1.89 | 16.59*** | 11.00*** | 14.79*** | 5.33*** |
| Estuary | 2 | 0.78 | No test | 1.37 | 0.81 | 0.72 | No test |
| Site (Estuary) | 3 | No test | No test | No test | No test | No test | No test |
| Plot (Site, Estuary) | 12 | 16.51*** | 16.26*** | 8.30*** | 10.40*** | 12.74*** | 5.07*** |
| T × E | 28 | | 2.41** | | | | 1.47 |
| T × S (E) | 42 | | 1.83** | | | | 2.28*** |
| T × P (S, E) | 168 | 2.05*** | 2.85*** | 1.69*** | 1.46*** | 1.62*** | 1.50*** |
| Residual | 1080 | | | | | | |
| Cochran's *C* | | 0.02 | 0.03 | 0.02 | 0.03 | 0.03 | 0.02 |
| **Variance components** | | | | | | | |
| Estuary | 2 | 1.18 (0.69) | 39.74 (20.82) | 4.54 (1.66) | 0.27 (0.2) | 0.4 (0.18) | 0.15 (0.11) |
| Site | 3 | 8.04 (1.16) | 69.10 (12.59) | 10.04 (2.3) | 3.07 (0.84) | 1.94 (0.3) | 0.14 (0.05) |
| Plot | 12 | 5.87 (1.05) | 77.25 (8.35) | 9.62 (2.2) | 1.03 (1.03) | 1.9 (0.43) | 0.11 (0.04) |
| Residual | 72 | 9.27 (0.78) | 81.29 (9.09) | 33.57 (3.45) | 3.69 (0.37) | 5.10 (0.35) | 0.59 (0.14) |

[a]ln (*x* + 1) transformed
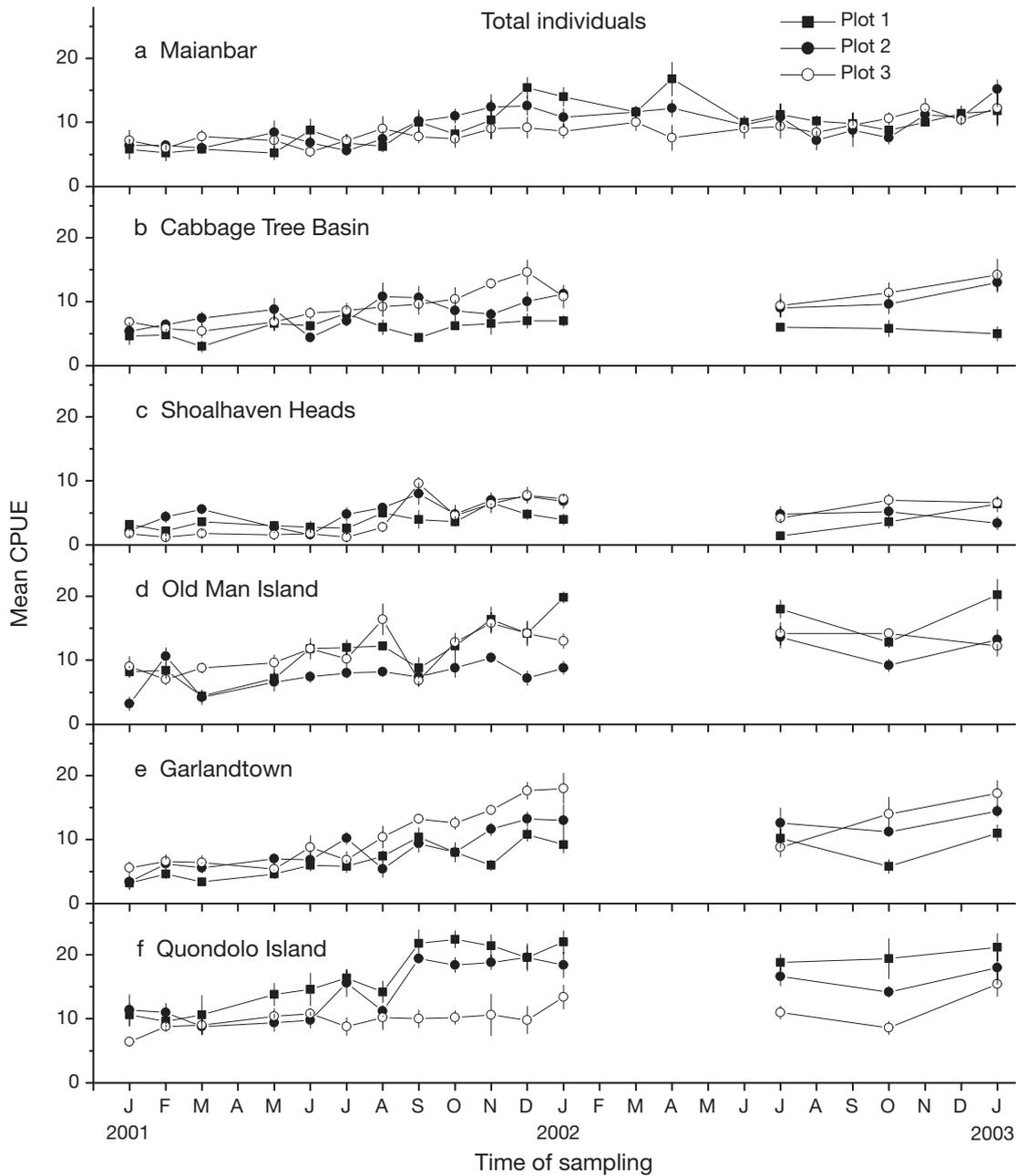
Fig. 2. *Trypaea australiensis.* Mean (±SE) number of individuals (CPUE: catch-per-unit-effort) from 5 replicate quadrats, from each of 3 replicate plots for each of 2 sites within (a,b) Port Hacking, (c,d) Shoalhaven River and (e,f) Moruya River between January 2001 and January 2003

residual (between replicates within plots). This result suggests there was also considerable patchiness of *Trypaea australiensis* at the smallest spatial scale (i.e. metres).

Because the Maianbar site was sampled approximately monthly for the entire 2 yr period, it was possible to compare patterns of abundance of *Trypaea australiensis* at a hierarchy of time scales, which included months, seasons and years. There were temporal–spa-

tial interactions between years and plots, seasons and plots, or both, across most data sets (Table 2). Therefore, temporal patterns of variance were not the same at each plot. A lack of consistent patterns of temporal variance in ANOVA was also supported by the estimated components of variance. The only general trends were that, for most analyses: (1) variation at the scale of months was lower than for seasons and years and (2) the residual variance (which is a spatial compo-
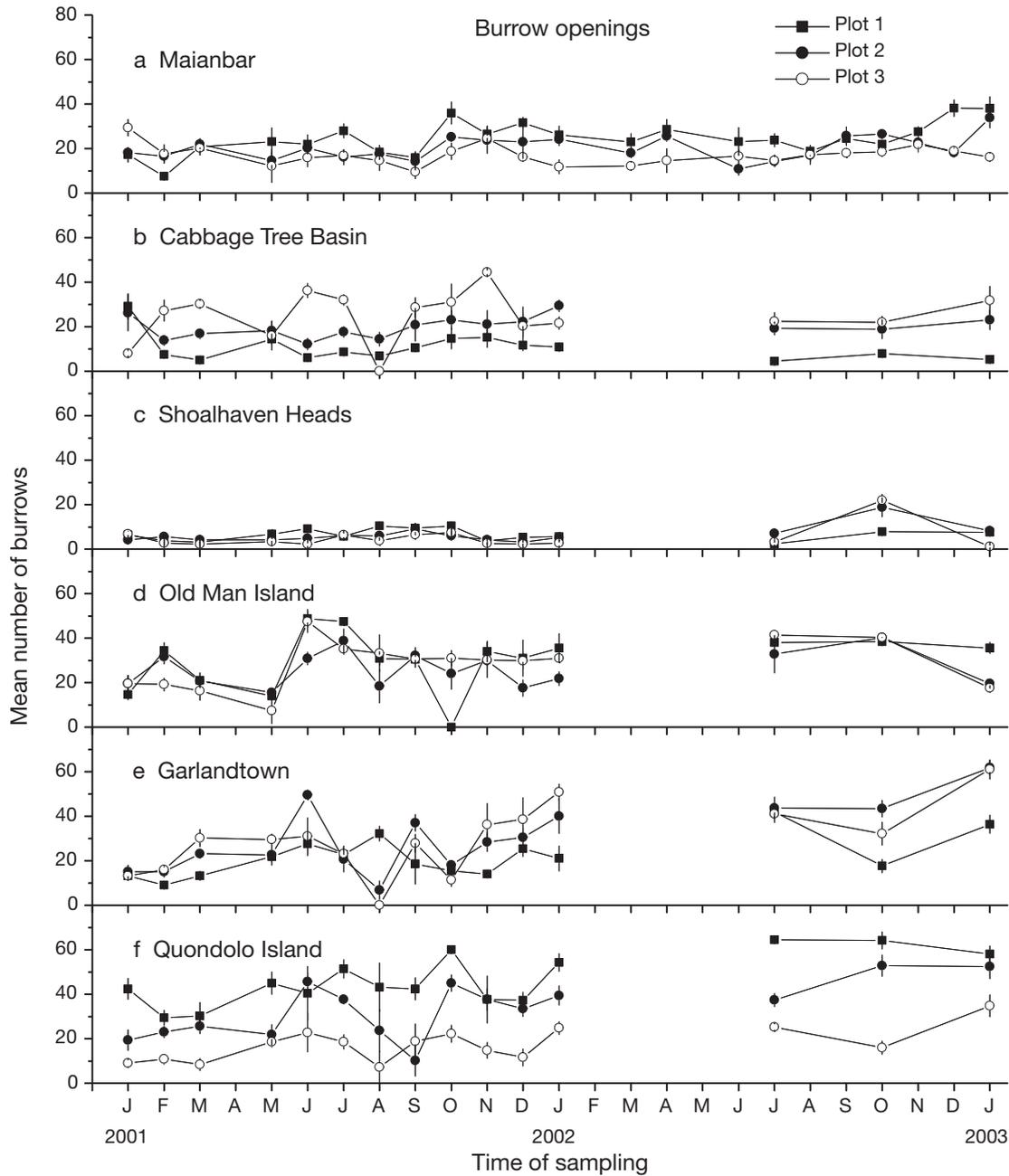
Fig. 3. *Trypaea australiensis*. Mean (±SE) number of burrows from 5 replicate quadrats, from each of 3 replicate plots for each of 2 sites within (a,b) Port Hacking, (c,d) Shoalhaven River and (e,f) Moruya River between January 2001 and January 2003

nent) was greater than any of the temporal scales investigated. The latter result supports the analyses of spatial patterns, which showed that most variation occurred between replicates at the scale of metres.

Despite the results of ANOVA and estimated components of variation suggesting that recruitment of *Trypaea australiensis* was patchy at the smallest spatial scales (i.e. between plots, sites and replicates) and

through time (Table 2), some broad-scale trends in the mean numbers of new recruits were still evident. First, peaks in recruitment generally occurred during spring and summer across all sites and estuaries. Second, there appeared to be a latitudinal gradient in the timing of recruitment, with recruitment occurring earlier in southern estuaries compared to estuaries further north.
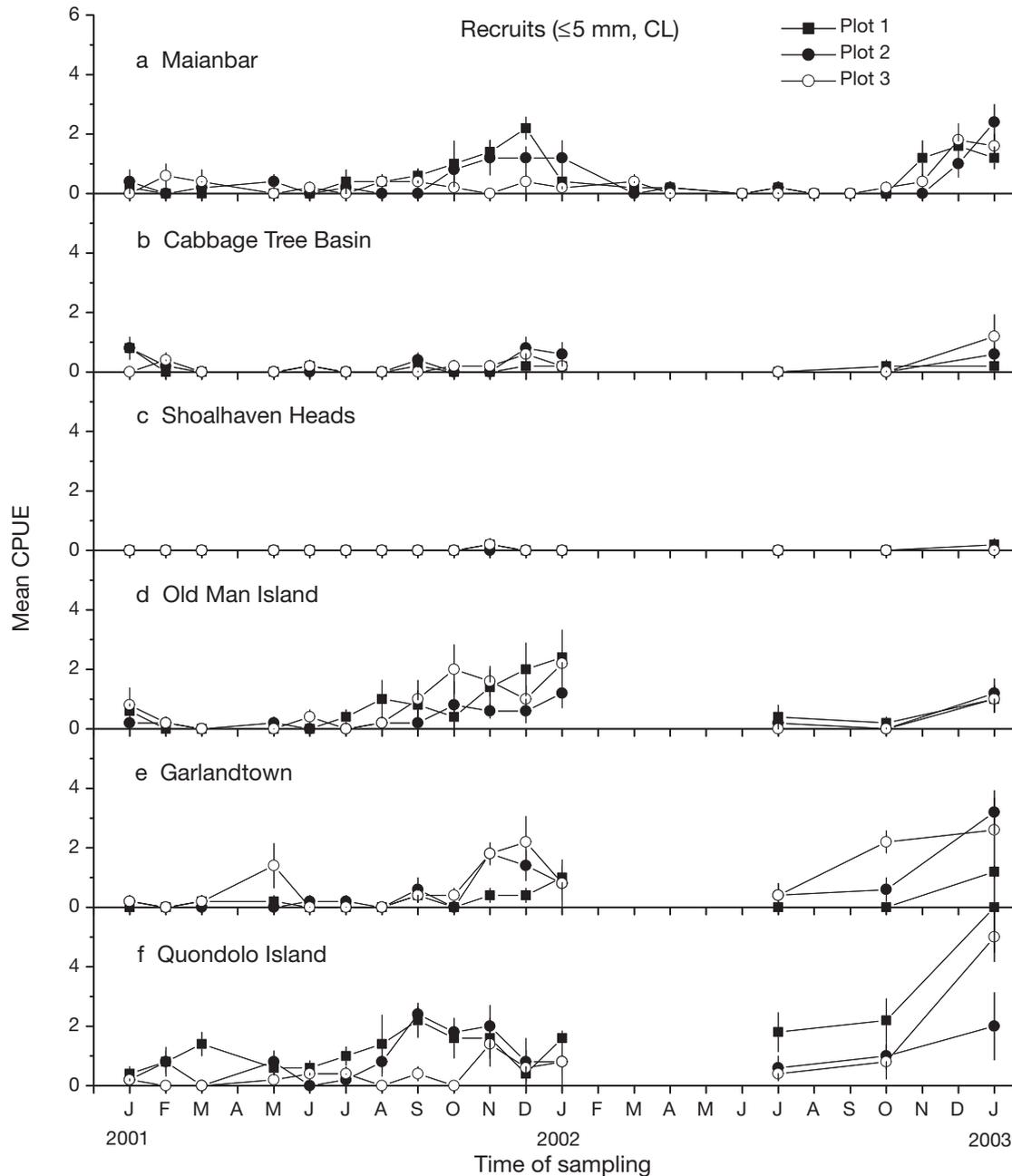
Fig. 4. *Trypaea australiensis*. Mean (±SE) number of recruits (≤5 mm CL; CPUE: catch-per-unit-effort) from 5 replicate quadrats, from each of 3 replicate plots for each of 2 sites within (a,b) Port Hacking, (c,d) Shoalhaven River and (e,f) Moruya River between January 2001 and January 2003

### Relationship between burrow openings and numbers of shrimp

The number of burrow openings was not a reliable predictor of relative abundance of *Trypaea australiensis*. Although ANCOVA revealed a significant relationship between numbers of burrows and catch rates of shrimp, a significant time × site interaction meant that the rela-

tionship was dependent on the particular time and site in question (Table 3). Further investigation of regressions between numbers of burrow openings and relative numbers of *T. australiensis* for each site and sampling occasion revealed mostly positive values for slopes of the regression lines, although values were generally small (Table 4). Similarly, $r^2$ values were small, indicating that the proportion of the variation in abundance of *T. aus-*

Table 2. *Trypaea australiensis*. Results of ANOVA testing for differences in mean numbers of (a) individuals, (b) burrows, (c) biomass, (d) males, (e) females and (f) recruits between years (Y) and among seasons (S) nested within years, months (M) nested within seasons and plots (P) at Maianbar. All factors considered random. *F*-ratios shown (significance of *F*-test: $*p < 0.05$; $**p < 0.01$; $***p < 0.001$). *F*-ratios are not shown for interaction terms that were pooled (or eliminated) at $p > 0.25$. Variance components derived from ANOVA done separately for each plot (n = 3) and then averaged are shown for each temporal scale (see 'Materials and methods'). Standard errors are in parentheses

| Source | df | (a) Individuals | (b) Burrows | (c) Biomass | (d) Males[a] | (e) Females | (f) Recruits[a] |
|---|---|---|---|---|---|---|---|
| Year | 1 | No test | 0.02 | No test | No test | No test | 0.03 |
| Season (Year) | 6 | No test | No test | No test | 3.88* | No test | No test |
| Month (Season, Year) | 8 | 1.14 | 2.11 | 7.37*** | 1.17 | 2.00 | 0.89 |
| Plot | 2 | 0.29 | 4.23* | 0.41 | 0.15 | 0.36 | 1.48 |
| P × Y | 2 | 3.95* | | 2.19 | 7.60** | 2.93 | |
| P × S (Y) | 12 | 2.96* | | 4.08** | | 2.52* | |
| P × M (S, Y) | 16 | 0.65 | 0.84 | 0.35 | | 0.52 | 1.45 |
| Residual | 192 | | | | | | |
| Cochran's *C* | | 0.09 | 0.09 | 0.09 | 0.06 | 0.06 | 0.1 |
| **Variance components** | | | | | | | |
| Year | 1 | 5.57 (3.91) | 1.76 (1.76) | 6.89 (6.25) | 4.18 (2.93) | 2.01 (1.16) | 0 |
| Season (Year) | 6 | 2.69 (1.34) | 12.62 (5.7) | 9.06 (4.79) | 0.41 (0.24) | 0.88 (0.44) | 0.12 (0.06) |
| Month (Season, Year) | 8 | 0 | 3.33 (1.83) | 1.76 (1.4) | 0.26 (0.26) | 0 | 0.04 (0.04) |
| Residual | 64 | 10.10 (0.91) | 66.88 (5.44) | 43.08 (6.1) | 3.18 (1.36) | 5.61 (0.26) | 0.34 (0.06) |

[a]ln (*x* + 1) transformed

Table 3. *Trypaea australiensis*. Summary of 2-factor ANCOVA for the relationship between the number of burrow openings (covariate) and number of individuals (dependent variable), between sites (S; Maianbar, Cabbage Tree Basin, Shoalhaven Heads, Old Man Island, Garlandtown, Quondolo Island) and sampling times (T; n = 15, from January 2001 to January 2003). $***p < 0.001$

| Source | df | MS | *F*-ratio |
|---|---|---|---|
| Covariate (Burrows) | 1 | 4015.035 | 297.26*** |
| Time | 11 | 271.086 | 20.07*** |
| Site | 5 | 653.998 | 48.42*** |
| T × S | 55 | 24.542 | 1.82*** |
| Residual | 1277 | 13.506 | |
| Total | 1350 | | |

*traliensis* explained by the number of burrows was generally low. Furthermore, these values differed between sampling times and between sites. Significant positive relationships were also more common during spring and summer months and for the Maianbar, Cabbage Tree Basin and Quondolo Island sites.

## DISCUSSION

This study has provided quantitative baseline data on patterns of abundance and recruitment of *Trypaea australiensis* in south-eastern Australia, over a range of spatial and temporal scales for which there was no existing information. Together, these data: (1) provide a context in which manipulative experiments can be used to test hypotheses explaining observed patterns and (2) identify relevant scales of variability for future monitoring studies, or experiments attempting to examine the effects of bait-harvesting activities on populations of shrimp.

Although there were significant interactions between plots and sampling times for most variables analysed, components of variation indicated that abundances of *Trypaea australiensis* were patchy at a number of spatial scales within estuaries (i.e. sites, plots and replicates). Most variation was, however, at the smallest spatial scale of replicates separated by metres. Similar small-scale spatial variability is a common pattern for organisms in marine environments (reviewed by Fraschetti et al. 2005) and highlights the need to include hierarchical spatial scales (i.e. replicates, plots and sites) in any future sampling of *T. australiensis*.

Spatial variation at the scale of metres (between replicates) was also much larger than the variance at any of the temporal scales (i.e. between months, seasons and years) examined at the Maianbar site. Further, patterns of temporal variance were inconsistent between plots. Similar findings have also been reported for intertidal microgastropods (Olabarria & Chapman 2002). Previous studies of other benthic organisms, however, have demonstrated that small-scale temporal variation (i.e. from days to months) is often larger than variation from season to season or year to year (Morrisey et al. 1992b, Underwood & Chapman 1998). Although the present study suggests

Table 4. *Trypaea australiensis*. Summary of regressions for the relationship between the number of burrow openings and number of individuals at Maianbar (MB), Cabbage Tree Basin (CTB), Shoalhaven Heads (SHH), Old Man Island (OMI), Garlandtown (GT) and Quondolo Island (QI) on each sampling occasion between January 2001 and January 2003. β: values for slope of the regression line; $r^2$: proportion of the total variance in abundance of *T. australiensis* explained by the number of burrow openings; *$p < 0.05$; **$p < 0.01$; ***$p < 0.001$

| | —— MB —— | | —— CTB —— | | —— SHH —— | | —— OMI —— | | —— GT —— | | —— QI —— | |
| | β | $r^2$ | β | $r^2$ | β | $r^2$ | β | $r^2$ | β | $r^2$ | β | $r^2$ |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Jan 2001 | 0.11 | 0.12 | 0.00 | 0.00 | 0.10 | 0.17 | 0.06 | 0.01 | −0.11 | 0.05 | 0.05 | 0.04 |
| Feb | 0.08 | 0.11 | 0.00 | 0.00 | 0.22 | 0.07 | 0.09 | 0.10 | 0.25 | 0.31* | 0.09 | 0.19 |
| Mar | 0.06 | 0.05 | 0.06 | 0.07 | 0.26 | 0.07 | −0.09 | 0.06 | 0.17 | 0.52** | 0.25 | 0.31* |
| May | 0.07 | 0.09 | 0.08 | 0.06 | 0.18 | 0.12 | −0.01 | 0.001 | 0.05 | 0.05 | 0.07 | 0.10 |
| Jun | 0.22 | 0.39* | 0.09 | 0.34* | 0.18 | 0.18 | 0.17 | 0.38* | 0.05 | 0.00 | 0.08 | 0.18 |
| Jul | 0.06 | 0.04 | 0.03 | 0.02 | 0.09 | 0.01 | 0.02 | 0.002 | −0.13 | 0.14 | 0.25 | 0.62*** |
| Aug | 0.10 | 0.06 | 0.23 | 0.18 | 0.18 | 0.17 | 0.12 | 0.16 | −0.04 | 0.03 | 0.01 | 0.008 |
| Sep | 0.36 | 0.74* | 0.23 | 0.56** | 0.07 | 0.01 | −0.05 | 0.01 | −0.03 | 0.02 | 0.08 | 0.07 |
| Oct | 0.06 | 0.04 | 0.03 | 0.01 | −0.20 | 0.06 | 0.02 | 0.008 | −0.34 | 0.25 | 0.27 | 0.66*** |
| Nov | 0.17 | 0.10 | 0.69 | 0.7*** | 0.23 | 0.04 | 0.02 | 0.002 | 0.12 | 0.22 | 0.21 | 0.36* |
| Dec | 0.25 | 0.50* | 0.13 | 0.21 | −0.46 | 0.15 | 0.14 | 0.16 | 0.15 | 0.34* | 0.28 | 0.38* |
| Jan 2002 | 0.19 | 0.29* | 0.19 | 0.33* | 0.17 | 0.06 | 0.21 | 0.19 | 0.16 | 0.26 | 0.29 | 0.63*** |
| Jul | −0.05 | 0.008 | 0.18 | 0.36* | 0.03 | 0.002 | −0.05 | 0.02 | −0.14 | 0.08 | 0.15 | 0.40* |
| Oct | −0.14 | 0.1 | 0.23 | 0.29* | 0.09 | 0.10 | 0.00 | 0.00 | 0.06 | 0.03 | 0.18 | 0.45*** |
| Jan 2003 | 0.05 | 0.02 | 0.28 | 0.56** | −0.26 | 0.18 | 0.37 | 0.40** | 0.14 | 0.28 | 0.10 | 0.07 |

that long-term temporal patterns become evident at scales of seasons and years, shorter-term variation may also occur at temporal scales not investigated here, such as days or weeks.

Despite the considerable and interactive small-scale patchiness, patterns of abundance and recruitment of *Trypaea australiensis* were generally consistent across broader geographic scales (between estuaries separated by 100s of kilometres). Similar patterns are relatively uncommon in the marine ecological literature (reviewed by Fraschetti et al. 2005). Nevertheless, the observed patterns suggest that results from appropriately designed and replicated small-scale studies (e.g. within an estuary) of *T. australiensis* may be scaled up to larger areas (Thrush et al. 1997, Fraschetti et al. 2005). There are, however, potential dangers in generalising over large spatial scales, as results may be specific to the particular area or period of time studied (Fraschetti et al. 2005). Therefore, further research is necessary to determine whether observed patterns for *T. australiensis* are consistent over regional scales (i.e. locations separated by 1000s of kilometres) and longer time periods (i.e. several years).

Although we observed increases in numbers of *Trypaea australiensis* through spring and summer periods, previous studies in Moreton Bay (Queensland) have shown that abundances of this species are relatively constant through time (McPhee & Skilleter 2002b, Skilleter et al. 2005). Stable population densities with recruitment pulses are also common for quantitative studies of thalassinids elsewhere (Tamaki et al. 1997, Berkenbusch & Rowden 1998). Nevertheless, in gen-

eral agreement with findings of the present study, Dumbauld et al. (1996) reported increasing abundances of the closely related *Neotrypaea californiensis* over a 4 yr period in Willapa Bay (Washington, USA). Some authors have suggested that a lack of temporal patterns or 'neighbourhood stability' in populations of ghost shrimp is the result of juveniles quickly replacing older or dead individuals through migration and settlement from plankton (Tunberg 1986, McPhee & Skilleter 2002b). Alternatively, this stability may reflect the restricted spatial and temporal scales used in previous investigations, which has been highlighted above (see 'Introduction').

There are numerous biotic and abiotic factors that influence spatial and temporal patterns of abundance of marine benthos (Barry & Dayton 1991, Thrush 1991). Although mensurative studies (such as the present one) cannot provide evidence of factors causing observed patterns of abundance, potential explanatory hypotheses may be identified and then tested. In our study, the settlement of new recruits partly explains observed increases in numbers of shrimp during spring and summer periods. Increases in biomass were, however, larger than would be expected for recruits alone. Apparent increases in numbers of shrimp at Shoalhaven Heads were also evident, even though only 2 recruits were sampled at this site. Furthermore, as numbers of *Trypaea australiensis* increased during the spring and summer months of the first year, there were also concomitant increases in variability between plots across most sites. These patterns suggest that increases in numbers of *T. australiensis* may also be

explained by increased aggregation, perhaps in response to biotic processes (e.g. competition, reproduction, availability of food), abiotic factors (e.g. salinity, temperature, day length), or both.

Increases in numbers of *Trypaea australiensis* coincided with increases in salinity and temperature during spring and summer months. Nevertheless, burrows of ghost shrimp can provide a buffer between highly variable conditions found within estuaries (Stanzel & Finelli 2004). Therefore, future studies testing hypotheses about observed patterns should consider measuring physio-chemical properties within the burrows of shrimp and at finer spatial and temporal scales than done here.

We counted burrow openings within quadrats prior to sampling and found that relationships between burrow openings and the relative abundances of shrimp, whilst significant on some occasions, also varied significantly (and inconsistently) through time and space. Similar findings were reported for *Trypaea australiensis* at a single location in Moreton Bay, Queensland (McPhee & Skilleter 2002b). Together, these results cast doubt on the reliability of using burrow counts to provide accurate assessments of population densities of *T. australiensis*. Indeed, relationships between burrow openings and numbers of individuals should be validated for any study relying on counts of burrows to indirectly estimate abundances of ghost shrimp (see also McPhee & Skilleter 2002b).

As discussed above, the present study provides important background information for future monitoring studies of *Trypaea australiensis*, as well as manipulative experiments concerned with the effects of bait-harvesting activities by humans. The variability observed at small spatial scales, which also interacted with different temporal scales, has implications for detecting patterns of abundance and environmental impacts (Morrisey et al. 1992a,b, Olabarria & Chapman 2002). Without sufficient or optimal replication at the appropriate scales, the power of sampling programs to identify real patterns or impacts is likely to be low (Underwood & Chapman 2003). Even in apparently well-designed before-after-control-impact (BACI) studies, a lack of prior knowledge on relevant scales of variation can lead to ambiguous or non-significant results. For example, in a BACI-type harvesting experiment in Moreton Bay, Skilleter et al. (2005) found that small-scale spatial variability masked a trend for more individuals of *T. australiensis* to be caught at control sites.

Although the benefits of using hierarchical sampling designs have been recognised for some time now (e.g. Morrisey et al. 1992a,b), the present research further highlights the value of using these types of mensurative experiments as a precursor to designing more robust and reliable sampling programs. Despite the logistical problems of sampling large numbers of replicates in soft-sediments, the challenge now is to apply these designs across a wider range of thalassinid ghost shrimp in order to better understand the processes that affect these taxa.

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