Depletion of benthic invertebrates by bar-tailed godwits *Limosa lapponica* in a subtropical estuary

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ABSTRACT: This study (1) investigated functional (capture rate, foraging success) and numerical (density) responses of bar-tailed godwits *Limosa lapponica* to an experimental decrease in densities of their prey, and (2) estimated seasonal depletion of the stock of their main prey, the mictyrid crab *Mictyris longicarpus*, in a subtropical estuary. It was predicted that if intake rates of the godwits are in the vicinity of the gradient section of a functional response curve, i.e. are directly determined by prey density, they will respond rapidly to experimental reduction in the density of their prey. Bar-tailed godwits did respond rapidly, both functionally and numerically, to a decrease in the density of *M. longicarpus*, indicating that their intake rate was limited by food availability. The estimated seasonal depletion of the stocks of *Mictyris* by the godwits was 88% of the initial standing stock. Despite the virtual disappearance of *Mictyris* from sediment samples through the course of a non-breeding season, local densities of godwits did not change between October and March, implying that adequate rates of intake could be maintained throughout their residence period.

KEY WORDS: Bar-tailed godwit · *Limosa lapponica* · *Mictyris longicarpus* · Prey density manipulation · Prey depletion · Subtropics

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INTRODUCTION

Local densities and intake rates of shorebirds (Charadrii) spending the non-breeding season on intertidal flats and estuaries are determined primarily by the instantaneously available stock of benthic prey (Goss-Custard 1984, Piersma 1987). However, during a non-breeding season, intake rates can be reduced by at least 3 factors, which, when they operate over a large area, may eventually lead to the shorebirds' starvation and/or emigration from a wintering site. These factors are (1) interference competition among foraging birds (e.g. Goss-Custard et al. 1984, Triplet et al. 1999), (2) deterioration of the nutritional value of individual prey items (e.g. Zwarts & Wanink 1993, Zwarts & Ens 1999) and (3) depletion of the available prey stocks (e.g. Goss-Custard et al. 1996, Zwarts et al. 1996).

Prey depletion by wintering shorebirds has received much attention over the past 2 decades and is known

to depend on a range of factors, including initial prey and predator densities, predator residency period and prey (re)production (reviewed by Székely & Bamberger 1992, Meire et al. 1994, Zwarts & Ens 1999, van der Meer et al. 2001). Wolff & Smit (1990) and Wolff (1991) compared prey exploitation by shorebirds at 2 of the most important wintering areas along the East Atlantic Flyway, the temperate Wadden Sea (54° N) and subtropical Banc d'Arguin (19° N). The authors estimated that shorebirds annually remove 17% of the standing stock of benthos in the former and 83 to 133% in the latter. They argued that annual predictability of the food supply in the north temperate estuaries is low (e.g. Zwarts et al. 1992, Zwarts & Wanink 1993, Beukema et al. 1993, but see Beukema et al. 2001) because of frequent stochastic mortality of benthos (e.g. due to severe winters, Camphuysen et al. 1996), absence of reproduction in the winter, and irregular recruitment. Consequently, food available to shore-

birds may be plentiful in some years but scarce in others (Meire et al. 1994, Zwarts & Ens 1999). Thus, shorebird populations may be maintained via, e.g. density-dependent mortality mechanisms at such levels so as to not overexploit food stocks in poor years (e.g., Wolff 1991). In this case, on average, consumption by shorebirds should be independent from benthic production (or the initially available prey stock) (e.g. Fig. 15.5 in van der Meer et al. 2001). In other words, the 'safety margin' between shorebird consumption and benthic production (or the standing stock at the onset of a non-breeding season) has to be high. On the local scale, at least at prime feeding sites because of the initially large prey stocks, shorebird intake rates can be independent of densities of their primary prey (e.g. Goss-Custard 1977, Gill et al. 2001, Goss-Custard et al. 2001, Goss-Custard unpubl.) unless a considerable proportion of the harvestable (sensu Zwarts & Wanink 1993) fraction is removed (e.g. Goss-Custard et al. 2001) or dies off (e.g. Zwarts & Ens 1999).

It has not been decisively resolved whether or not ecologically significant depletion of benthic prey by shorebirds over their residence period occurs at warm-climate non-breeding sites (e.g. Schneider 1985, Kalejta 1993, Mercier & McNeil 1994). By contrast to the north temperate region, warm-climate wintering sites have more stable abiotic conditions, benthic (re)production occurs during periods of intensive shorebird predation (Alongi 1990, Kalejta & Hockey 1991), and they also support higher shorebird densities (Summers 1977, Zwarts et al. 1990, Hockey et al. 1992, Kalejta 1993). Currently, these sites are hypothesised to allow for a higher level of exploitation of benthic stocks by the shorebirds, and consequently have relatively low-standing benthic biomass densities (Wolff & Smit 1990, Wolff 1991, but see van der Meer et al. 2001). If the purported low ratio between the benthic stocks and shorebird consumption indeed exists in a warm-climate wintering area, a converse local-scale foraging situation should be true. The intake rate achieved by an individual forager should be in the vicinity of the functional response gradient, i.e. it should be directly limited by the prey density throughout a non-breeding season.

Three lines of evidence can be used to test the hypothesis of the lower ratio between the benthic stock and shorebird predation pressure in warm climates as compared to the cold-climate wintering areas. (1) Initial benthic stocks and their depletion (exploitation level) over a non-breeding season can be compared. However, in the absence of data on long-term annual fluctuations in the benthic food supply, shorebird consumption (Kalejta & Hockey 1991, Dittmann & Vargas 2001) and the proportion of the standing stock that can actually be harvested by the birds in tropics/subtrop-

ics, such comparisons may be unreliable at present (Piersma et al. 1993a). (2) Functional response curves can be measured directly (e.g. Gill et al. 2001) to determine whether the rate of intake is indeed limited by the density of prey, as would be expected in a predator-prey system with a quick turn-over of matter and energy. However, such responses are often difficult to measure in the field, and our ability to predict the shape of a functional response curve from the generally available field data (e.g. prey type and size, handling time, forager density) is currently limited (Ens et al. 1994, Goss-Custard unpubl.). (3) The third line of evidence can come from experiments manipulating prey densities in the field (e.g. Cummings et al. 1997). This approach uses a converse logic as compared to (2). Specifically, if the rate of intake is in the vicinity of the gradient of a functional response curve, then depleting food densities in the field should negatively affect intake rates or lead to emigration of predators from the impacted areas. This is the approach taken in this study, although data pertinent to points (1) and (2) have also been collected and are presented.

In this study numerical (density) and functional (capture rate and feeding success) responses of bar-tailed godwits *Limosa lapponica* to changes in prey densities were studied in a manipulative field experiment conducted at a spatial scale roughly corresponding to the local scale of movements of the birds (e.g. Cummings et al. 1997, Chamberlain & Fuller 1999). Sediment disturbance due to manual removal of the callianassid shrimp *Trypaea australiensis* (Skilleter 2002) resulted in a decrease in densities of several other benthic organisms that constitute the bulk of diet of the godwit. It was predicted that if the intake rate is limited by the density of prey available to the birds, a reduction in prey density will cause rapid numeric (emigration out of the impacted plots) and functional (decrease in capture rate and/or foraging success) responses by the birds.

MATERIALS AND METHODS

Study area. The study was carried out on the western shore of North Stradbroke Island, Moreton Bay, Queensland, Australia (27° 25′ S, 153° 25′ E) between October 1998 and November 1999 (Fig. 1). Moreton Bay is a large estuarine system with semidiurnal tides exposing the intertidal area on average for 5.5 to 6.5 h per low tide. Moreton Bay supports up to 80 000 wintering shorebirds, including more than 20 000 bar-tailed godwits (Thompson 1990a). The study area is known to support godwit densities considerably higher than elsewhere in the Bay (Thompson 1990b), and thus can be considered a 'preferred site'. This minimised

Fig. 1. Map of Australia with Moreton Bay, showing North Stradbroke Island and the study area

the chance of obtaining a significant relationship between foraging rates and prey densities by virtue of sampling at a site with already poor feeding conditions (e.g. Goss-Custard et al. 1984). The intertidal flats on the western (estuarine) side of the island are characterised by 3 broad zones: a mangrove fringe along the upper shore (primarily *Avicennia marina*), an essentially unvegetated mid-intertidal zone, and extensive seagrass (*Zostera capricornii*, *Halophila ovalis*, and *Syringodium isoetifolium*) beds along the lower intertidal zone.

All experimental manipulations and observations of godwits were done in the middle (unvegetated) sandy zone of the intertidal. 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 microrelief of intermingling elevated ridges and pools (Thompson 1992). The possible effect of manipulations on sediment grain size was not investigated because the size of the prey normally consumed by the godwits was considerable larger than the sediment grain size (cf. Quammen 1982). Therefore, no confounding effect on godwit foraging efficiency was anticipated.

Experimental manipulations and assessment of the densities of benthos. Mechanical perturbation of soft sediments inevitably leads to significant amounts of disturbance with effects on the associated infauna (e.g. Skilleter 1996). At larger scales, artificial removal of benthic invertebrates (e.g. for bait) has been shown to significantly reduce the abundance of non-target macrofauna (e.g. Wynberg & Branch 1994, Ambrose et al. 1998). This study used the expected effects of sediment disturbance associated with harvesting of the burrow-dwelling callianassid shrimp *Trypaea aus-*

traliensis (McPhee & Skilleter 2002) on non-target macrofauna (crabs, polychaetes and bivalves) to examine the responses of bar-tailed godwits, which rely on these smaller invertebrates as prey.

Six 100 × 100 m (1 ha) study plots were permanently marked with 40 cm long wooden stakes. The plots were located at the same tidal height along a visually uniform stretch of the mudflat without natural barriers. Adjacent plots were separated by 75 to 100 m. Three of the plots were designated at random for experimental manipulations involving direct removal of *Trypaea australiensis* using a hand-operated suction pump, and the remaining 3 plots served as undisturbed controls, apart from sampling of benthic fauna. *Trypaea* removals were carried out in November 1998, January, March, May, June, July, September and December 1999. The procedure for harvesting *Trypaea* with a pump (a 0.70 m length, 0.05 m diameter tube, with a handle and a plunger) pushes the unit into the substratum with visible *Trypaea* holes and extracts the sediment, which is then dumped onto the substratum to collect organisms. The pump is pushed into the substratum at the same point several times, after which the harvester begins the process again at a new point. Teams of 2 people (a pumper and a collector) gradually worked through each experimental plot, walking from one side to the other and pumping in areas with visible *Trypaea* holes. This ensured that the entire surface of an experimental plot was subjected to the effects of pumping, as the plots were laid out in typical *Trypaea* habitat (Hailstone & Stephenson 1961). The sampling effort was uniform among the 3 experimental plots and equalled ca. 4 h per plot per harvesting event. All captured *Trypaea* with carapace lengths (CL) of ≥7 mm were removed from the plots.

Core samples were collected using hand-held cores just before the start of *Trypaea* removal, in October 1998, and then on 3 more occasions in January, May and November 1999 (Periods 1 to 4) to determine the abundance of benthic macrofauna in the plots. On each occasion, 5 replicate cores were collected from each of 2 different depths, 5 and 15 cm, into the substratum, at 3 randomly selected sites within a plot, using a 15 cm diameter PVC core. Collecting sites were at least 10 m apart.

All cores were preserved in 4% Rose Bengal-stained formaldehyde solution, sieved across a 1.0 mm mesh sieve and the retained organisms identified to various taxonomic levels. The following taxa, given in the

order of their importance in the godwit diet as determined from faecal analysis (Zharikov & Skilleter 2002) and visual observations, were analysed in this study: mictyrid crab *Mictyris longicarpus*, macrophthalmid crabs (*Macrophthalmus crassipes*, *M. punctulatus*, *Macrophthalmus* sp. and *Enigmaplax* sp., combined), polychaetes (Capitellidae, Cirratulidae, Maldanidae, Nephytidae, Nereididae, Opheliidae, Orbiniidae, Spionidae, and Syllidae families, combined), and bivalves (unidentified tellinids and mactrids).

Shorebird observations. Godwits were normally present in the study area from early October until mid-April (Thompson 1992, author's pers. obs.). Godwit observations were conducted over 1 complete low tide period per plot per month, starting in 1998 with the post-breeding arrivals of these shorebirds in October, and ending in late March 1999, shortly before their northward departure. Additional density and foraging activity data were collected in the subsequent season, in early November 1999. Due to logistical constraints, it was not always possible to conduct shorebird observations immediately after *Trypaea*-removal (disturbance) sessions when the strongest impact of the experimental manipulations on the benthos and its predators would have been expected. As we were interested in the immediate responses of the shorebirds to the manipulations of their prey densities, only the data collected within 2 to 3 wk after a disturbance event were included in formal statistical analyses. This provided for 3 sets of density data and behavioural observations for the godwits: November 1998, and February and March 1999 (Periods 1 to 3). However, the entire shorebird data-set is presented to show the overall trends in density and foraging behaviour.

Bar-tailed godwits were observed from the mangrove edge through a 20 to 40× spotting scope at distances of 50 to 150 m. Observations were conducted during daylight hours, on days with published low water heights of 0.42 to 0.88 m, during periods without rain, apart from an occasional shower, and moderate breeze. The particular plot watched on any day was picked at random. As the density of birds in the plots could be affected by the total intertidal area available for foraging, a comparison was made of published low-water heights between the days of experimental and control plot observations included in the formal analyses. The mean (±SD) heights were not significantly different: experimental = 0.64 ± 0.12 m, control = 0.63 ± 0.10 m ($F_{1,16}$ = 0.04, p = 0.85). Observations always started when half of the plot became exposed, and terminated when half of the plot was flooded by the rising tide. One to 5 min observations (n = 12 per plot per day) on randomly selected, actively foraging birds were used. For each focal bird, the numbers of probes and prey captured were dictated onto a cassette recor-

der to derive capture rates and foraging success. Since capture rate was used as a proxy for the rate of intake, it was important to know that sizes of individual prey did not differ between the treatments. This was the case, e.g., for *Trypaea* (G. A. Skilleter unpubl.). No data were available for the other benthos. Godwit density data were obtained on the same days as the focal observations by counting birds present in the plot every 20 min.

Statistical analyses. The abundances of *Mictyris*, and of the 3 other benthic taxa which were considered to be prey of bar-tailed godwits, estimated from the cores taken from 5 and 15 cm depth into the substratum, were analysed using a 4-factor mixed model ANOVA, with factors Period (fixed, a = 4 levels), Treatment (fixed, b = 2 levels), Plot (random, nested in Treatment, c = 3 levels), Site (random, nested within Period × Plot(Treatment), d = 3 levels) with n = 5 cores sampled per site at each depth on each occasion. Although analysed separately, the data from the 2 depths may not be independent because the 15 cm cores also include the top 5 cm of sediment, and consequently estimates of the abundance of benthos to this depth. The 2 estimates of abundance are presented here, however, because some crabs do burrow below 5 cm into the substratum and bar-tailed godwits are able to probe beyond this depth when foraging. Godwit data were analysed with 3-factor, hierarchical mixed model ANOVAs, with factors Period (fixed; a = 3 levels), Treatment (fixed; b = 2 levels), Plot (random, nested in Treatment; c = 3 levels).

Seasonal removal of prey (*Mictyris* per m² per season) by the godwits was calculated as a product of mean seasonal capture rates (assuming that 38% of all prey captured were *Mictyris*; Zharikov & Skilleter 2002), the proportion of time spent foraging, godwit density, and the duration of a season and duration of a low tide period (assuming equal capture rates by day and night; e.g. Scheiffarth et al. 2002). Also, mean in-plot prey densities were plotted against mean in-plot capture rates to assess the shape of the relationship between these 2 variables.

The analysed variables were: numbers of select invertebrate taxa (see 'Experimental manipulations') per 5 or 15 cm deep core (surface area of 0.07 m²), overall capture rates of prey per min of time spent actively foraging, foraging success (proportion of successful probes) and density in birds per ha. All count, capture rate and density data were $\log_e(x + 1)$-transformed to conform to the ANOVA assumptions. Foraging success data did not need to be transformed. When appropriate, post-hoc pooling of mean square estimates was used to increase the power for specific terms in the ANOVAs following Winer et al. (1991). The Statistica© software package was used for all analyses.

RESULTS

Benthic prey responses to the experimental disturbance

Abundance of crabs

The benthic cores tended to contain small *Mictyris* with CL <10 mm (author's unpubl.) as larger individuals (max. CL = 22 mm) were foraging on the surface at that time. At both depths, the *in situ* density of *Mictyris* showed a significant temporal decrease from October 1998 to January 1999 and then an increase from May 1999 to November 1999 (Period, $F_{3,12}$-values > 10.71, p-values < 0.001, Fig. 2). There were initially significantly more *Mictyris* in the experimental plots than the control plots, but by January 1999, the abundances dropped markedly and were similar in both treatments. After that time, the temporal trends in the 2 treatments diverged, with more crabs occurring in the control plots than the harvested plots. This was highly significant for the 5 cm cores (Period × Treatment interaction, $F_{3,12}$ = 4.96, p = 0.004), but not significant for the 15 cm cores, even after post-hoc pooling ($F_{3,60}$ = 1.69, p = 0.18). However, the temporal trends in the data for both depths were similar, suggesting that overall there was a significant impact from harvesting

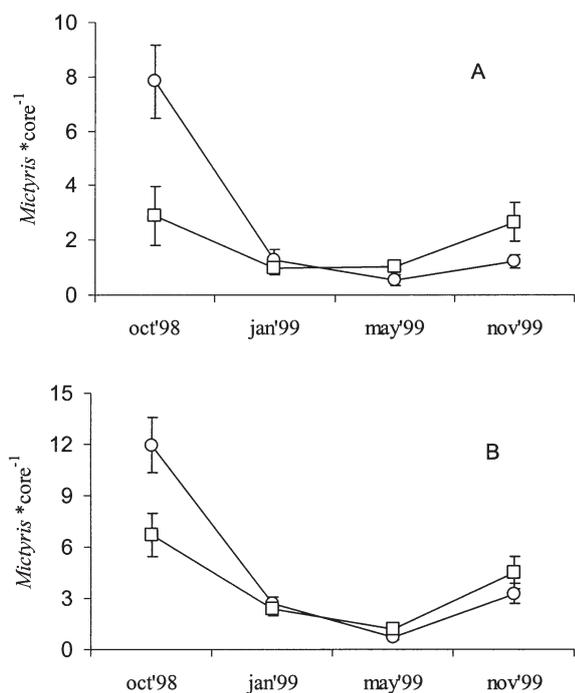on the abundance of *Mictyris*. The decrease in *Mictyris* abundance associated with the experimental manipulations was 35% in the upper 5 cm of the sediment and 17% in the upper 15 cm of the sediment.

The other group of crabs that were relatively abundant in the cores was the macrophthalmids. At least 4 species (see 'Materials and methods') occurred in the area, but these species could not be identified individually from the examination of godwit faecal samples (Zharikov & Skilleter 2002), so data were combined for analysis. There was a significant treatment effect detected for the 5 cm deep cores ($F_{1,52}$ = 6.42, p = 0.02), with significantly more of the macrophthalmids occurring in the control plots than the harvested plots (Fig. 3A). A similar trend was evident for the data from the 15 cm cores, but there was substantially more small-scale variation (Sites, $F_{48,288}$ = 1.44, p = 0.04) for these deeper cores, and the treatment effect was not significant (Fig. 3B). Importantly, and by chance, the abundance of macrophthalmids was greater in the control plots than experimental plots before the beginning of *Trypaea* removal, so the difference cannot be attributed to harvesting. No significant seasonal trend was apparent in the density of macrophthalmids (p-values > 0.17).

Abundance of polychaetes and bivalves

The abundance of polychaetes showed a significant seasonal increase in the 5 cm cores (Period, $F_{3,12}$ = 19.54, p = 0.002). No significant temporal trend was detected in the 15 cm cores (Period, $F_{3,12}$ = 3.05, p = 0.07) (Fig. 3C,D).

For the 5 cm cores, the abundance of polychaetes was initially similar in each treatment, but diverged once experimental manipulations began, with marginally significantly more polychaetes present in the control plots (Treatment, $F_{1,52}$ = 3.63, p = 0.062). The Period × Treatment interaction was significant (p = 0.002) after 3 replicate cores with extremely high numbers of polychaetes at 1 site in a control plot, which occurred in a small patch of seagrass, were replaced with the average of all other cores (Underwood 1997) collected from control plots in May 1999. The interaction suggested that the experimental manipulations had significantly depressed the abundance of polychaetes in the harvested plots. In 5 cm cores, the decrease in the abundance of polychaetes associated with the experimental impact was 46%.

For the 15 cm cores, there was a significant treatment effect, with more polychaetes occurring in the control plots throughout the experiment ($F_{1,52}$ = 5.99, p = 0.02), but, as for the macrophthalmid crabs, there was no response to *Trypaea* removal.

Fig. 2. Mean (±SE) abundances of *Mictyris longicarpus* in control (square) and experimental (circle) plots estimated per 5 cm deep (A) and 15 cm deep (B) benthic cores. First *Trypaea* removal took place between the October and November 1998 sampling sessions
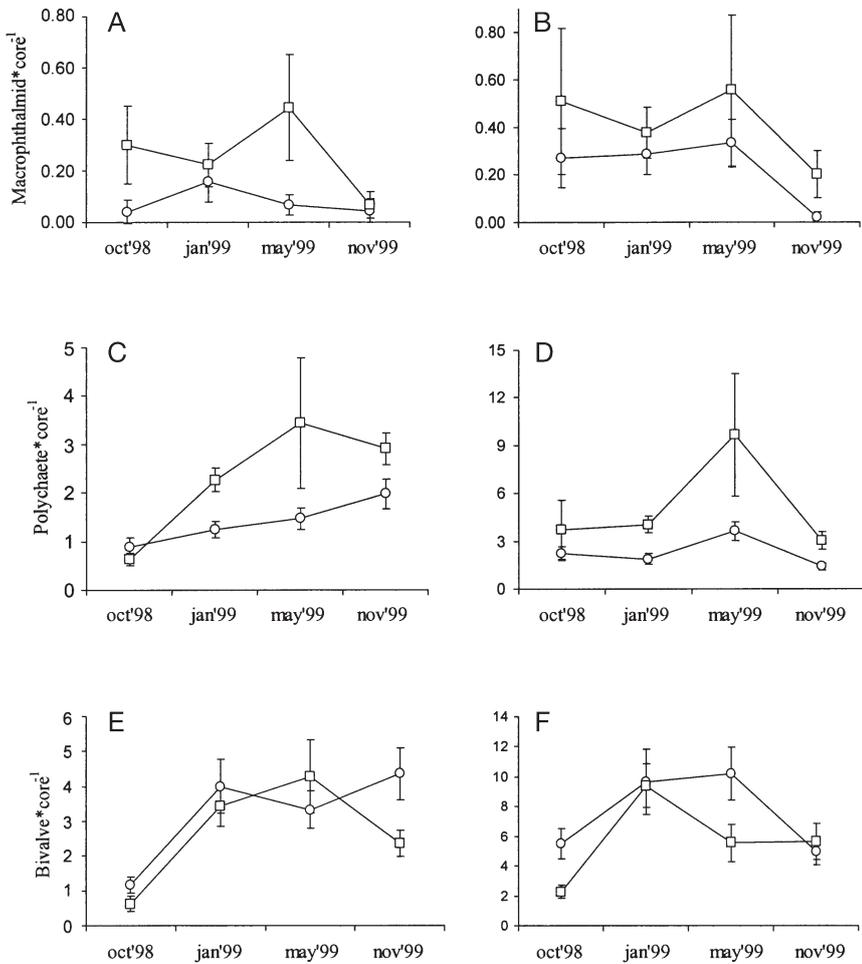
Fig. 3. Mean (±SE) abundances of macrophthalmid crabs, polychaetes and bivalves in control (square) and experimental (circle) plots estimated per 5 cm deep (A, C, E) and 15 cm deep cores (B, D, F). First *Trypaea* removal took place between the October and November 1998 sampling sessions

Godwit responses to the experimental manipulations

Habitat disturbance due to *Trypaea* removal had a rather dramatic effect on the godwits. All 3 variables (density, capture rate and foraging success) examined with ANOVA showed significantly lower values in the experimental plots (Table 1). All the variables started off being roughly equal between the treatments but then showed a strong response to the experimental manipulations. However, the strength of the response apparently diminished over time (Fig. 4). The density, capture rate and foraging success were respectively 58.5, 22.2 and 17.6 % lower in the plots from which *Trypaea* were being removed than in the controls. The time of sampling contributed significantly to the overall variability in the capture rate and foraging success. Both behavioural parameters gradually decreased over time. The density of godwits remained unchanged within and between the seasons, but varied considerably at the scale of Plots within Treatment.

Relationship between prey densities and capture rates

If the godwit capture rates were determined directly by the prey densities, a strong linear relationship between these 2 variables would have been expected. At first, linear regression of the mean monthly in-plot godwit capture rate against *Mictyris* density (15 cm cores) produced a poor relationship ($R^2 = 0.12$, p = 0.08, n = 24). However, when the October 1998 data, collected at the time of godwit arrival from their breeding grounds, i.e. before any depletion

The temporal patterns of abundance of bivalves were similar in the 5 and 15 cm cores (Period, $F_{3,12}$-values > 5.70, p-values < 0.011) and between the treatments with an increase in density over time (Fig. 3E–F). These molluscs showed no response to the *Trypaea*-harvesting activities (all p-values > 0.23).

Table 1. Analyses of variance of the bar-tailed godwit density, capture rate and foraging success (all $\log_e [x+1]$-transformed except for success, see 'Materials and methods' for design details) in control and experimental plots. Degrees of freedom for *F*: Treatment = 1,4; Plot (Treatment) = 4,161; Period = 2,8; Period × Treatment = 2,8; and Period × Plot(Treatment) = 8,161. Significant p-values in bold

Factor	Treatment		Plot(Tr)		Period		Period × Tr		Period × Pl(Tr)	
	F	p	*F*	p	*F*	p	*F*	p	*F*	p
Density	8.11	**0.046**	2.32	0.06	0.70	0.53	2.20	0.17	0.92	0.50
Capture rate	11.43	**0.028**	0.80	0.53	14.92	**0.002**	0.68	0.53	2.56	**0.011**
Foraging success	17.10	**0.014**	0.19	0.94	12.94	**0.003**	1.07	0.39	1.92	0.06

of prey density could take place, were taken out of the equation, the linear fit ($y = 1.18x + 1.75$) improved greatly ($R^2 = 0.52$, p = 0.001, n = 18). Addition of other prey types (Bivalve, Macrophthalmid crab, Polychaete) into the equation did not improve the fit.
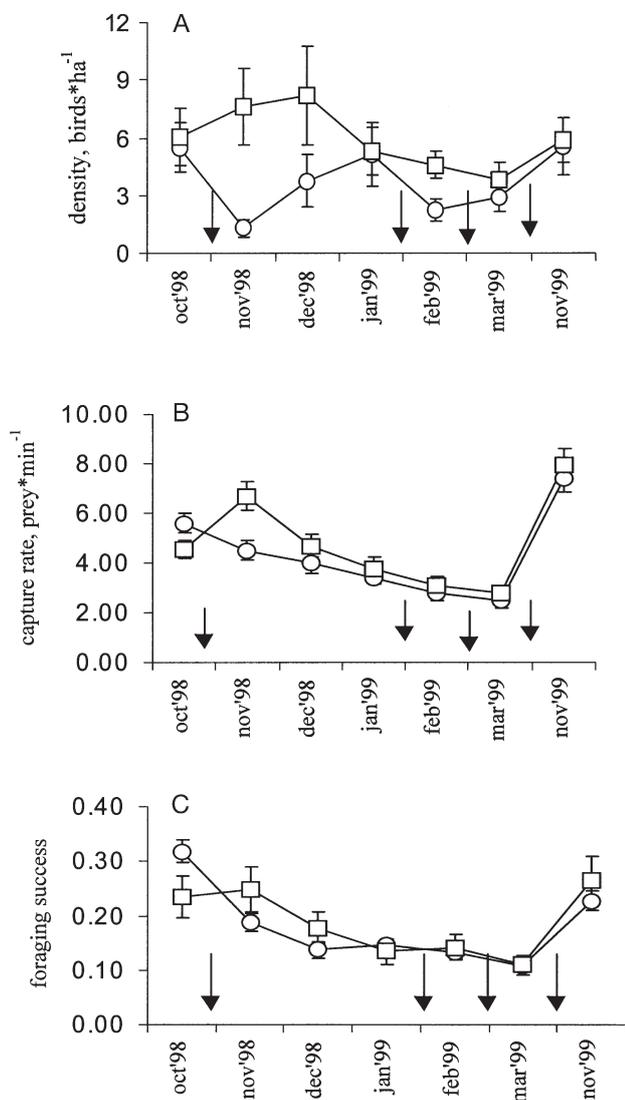

Fig. 4. Mean (±SE) density (A) capture rate (B) and foraging success (C) for bar-tailed godwits *Limosa lapponica* in control (square) and experimental (circle) plots throughout the study period. Arrows indicate the points of experimental impacts. (A) Density sample sizes for each month for control and experimental plots respectively were: October 98 – 30, 55; November 98 – 27, 28; December 98 – 8, 30; January 99 – 29, 31; February 99 – 33, 28; March 99 – 32, 31; October–early November 99 – 32, 27; and February 2000 – 28, 28. (B, C) Capture rate and foraging success sample size for each month × treatment combination equalled 36. Within-season (1998/99) correlations were: month and density: $r_p = -0.01$, p = 0.88, n = 382; capture rate: $r_s = -0.42$, p = 0.000, n = 432, and foraging success: $r_s = -0.46$, p = 0.000, n = 432

Estimated proportion of prey removed by the godwits

Bar-tailed godwits, foraging for 96% of the low tide time available to them at a rate of 4.54 prey min^{-1} and at a density of 4.85 bird ha^{-1} (Zharikov & Skilleter 2002), would have removed 116 *Mictyris* m^{-2} season^{-1} assuming that 38% of the prey taken were these crabs, and the godwits' wintering season lasted from early October to mid-April. The density of *Mictyris* in 15 cm cores at the start of the season in October 1998 was 132 crabs m^{-2}. Therefore, 88% of the initial stock would have been removed by the godwits. The *in situ Mictyris* density decreased by 90% over the same period (Fig. 2).

DISCUSSION

During a wintering season in the north temperate region, depletion of stocks of benthic organisms by shorebirds on average does not exceed 25 to 40% of the initial, start-of-the-season levels (Székely & Bamberger 1992, Meire et al. 1994, Zwarts & Ens 1999) and appears to be independent of production/standing stock (van der Meer et al. 2001). Due to the high local densities of prey at the onset of a season, intake rates can remain invariable across a range of prey densities and such a level of depletion may not be sufficient to affect intake rates noticeably (e.g. Dolman & Sutherland 1997). When depletion in excess of these values occurs, it is usually brought about by cold spells (e.g. Camphuysen et al. 1996, Zwarts et al. 1996), prey infestation (Jonsson & André 1992) causing considerable background mortality or by a decrease in the area available for foraging (Evans et al. 1979). In the near absence of benthic production in the northern estuaries during boreal winter, a large (≫50%) decrease in the density of food stocks leads to emigration of shorebirds from the heavily depleted sites/estuaries (e.g. Zwarts et al. 1996) into areas where comparatively higher intake rates can be achieved. The relatively frequent occurrence of high background prey mortality events in the northern estuaries (Camphuysen et al. 1996, cf. Moverley et al. 1986 for a subtropical site) coupled with generally irregular recruitment patterns of benthos (Beukema 1982, Beukema et al. 1993, 2000) necessitates the maintenance of a high ratio between benthic stock and shorebird consumption to insure against prey overexploitation in poor years (Wolff 1991). How do the results of this study compare?

Disturbance experiment

Physical perturbation of intertidal sediment often leads to a decrease in the densities of benthic fauna

(e.g. Wynberg & Branch 1994, Beukema 1995, Ambrose et al. 1998) and can be used to assess the relationship between shorebird intake rate, densities and prey abundance. In one published study a decrease in the density of a benthic amphipod *Corophium volutator* caused by sediment disturbance reduced capture rates and foraging success of a flock-foraging shorebird, the semipalmated sandpiper *Calidris pusilla* (Shepherd & Boates 1999). Unfortunately, no information on the densities of the sandpipers in control and disturbed areas was available, precluding any insight into whether or not the birds emigrated out of the impacted areas. The present study provides such an example in a warm subtropical estuary.

Sediment disturbance significantly reduced *in situ* densities of 2 important godwit prey, *Mictyris* and polychaetes, which comprise 73% and <5% of godwit dry weight intake in the sandy habitat respectively (Zharikov & Skilleter 2002). The numeric and functional responses of the godwits associated with the impact were in agreement with the original prediction. The initial decrease in godwit density, capture rate and foraging success in the experimental plots occurred soon after an impact event (Fig. 4). The significance of ANOVA tests that used only the data obtained shortly after impacts also attests to the rapidity of shorebird response. This suggests that prey density in the plots was limiting intake rates of the birds throughout the non-breeding season. As discussed earlier, this is often not the case in the north temperate region, where prey densities may vary broadly without affecting shorebird intake rates.

Godwits leaving the experimental plots appeared to forage, at least partially, in the control plots, suggesting that moving farther away would not improve their feeding conditions. Otherwise, it seems likely the birds would have left the general study area. Also, bar-tailed godwits that were colour-flagged in a different study appeared to use the same sites (100s of m scale) within the study area day after day for the duration of a wintering season (6 months) (author's pers. obs). Both observations contrast with many north temperate estuaries, where non-territorial shorebirds use areas of >1 to 10 km² in search of suitable foraging sites, e.g. red knot *Calidris canutus* (e.g. Zwarts et al. 1992, Piersma et al. 1993b), western sandpiper *C. mauri* (Warnock & Takekawa 1996), dunlin *C. alpina* (Shepherd 2001) and black-tailed godwit *Limosa limosa* (Shubin 1999). In the absence of prey reproduction this roaming may be caused by local prey depletion, but one should keep in mind that northern estuaries are usually much larger and thus have more surface area available (e.g. Hockey et al. 1992).

An unexpected outcome of the experiment was that godwit densities in the harvested and control plots merged after 3 months without further *Trypaea* harvesting. One explanation for this pattern could be that the stocks of benthic prey recovered from such disturbance rather quickly (McLusky et al. 1983, van den Heiligenberg 1987, but see Wynberg & Branch 1994). Whereas this suggestion was not supported by the benthic sampling data, unfortunately benthic sampling occurred on a coarser temporal scale than shorebird observations. Therefore, short-term pulses in benthos abundance could be missed. Alternatively, godwits could learn to use different prey in the impacted plots, e.g. bivalves, densities of which did not differ between the treatments, thus offsetting the decrease in the density of the other prey (*Mictyris*, polychaetes). Although visual observations cannot help in resolving this suggestion (>95% of prey items could not be identified), it appeared that godwits, for example, were capturing 10 times more large surface-dwelling *Penaeus* shrimp in control (1.1% of visual diet) as opposed to the experimental plots (0.1% of visual diet) following the start of the experiment—no shrimp were taken in October.

The godwits not only achieved a lower capture rate in the experimental plots, but their foraging success was also lower than in the controls. Temporal fluctuations in foraging success showed a pattern similar to that of the density (Fig. 4A,C). It is possible the birds were attempting to compensate for a drop in prey density by increasing their probing rate. As the increase in the probing rate did not fully cancel out the decrease in foraging success, immigration of godwits out of the impacted plots occurred. Also, it can be suggested that godwits were making more mistakes while foraging. This could either be due to obliteration of some important visual cues on the surface (Velasquez & Navarro 1993) or a change in the spatial aggregation of prey (Warwick & Clarke 1993).

Small-scale spatial aggregation of benthos is commonly associated with microrelief features of the flats (e.g. Hogue & Miller 1987, Sun & Fleeger 1994) and topography may be used by shorebirds as foraging cues (e.g. Sutherland et al. 2000). Therefore, a disruption of this spatial arrangement even without a decrease in the overall density of prey would result in a drop in foraging success until the new spatial distribution of prey is memorised by the predators. If the new pattern persists over time, obviously its effect on the predator foraging efficiency will decline. Unpublished data (G. A. Skilleter) indicate that *Trypaea*-pumping decreased the degree of spatial aggregation in the small-scale distribution of *Mictyris*, which may have resulted from changes to the topography and sediment structure of the substratum caused by this type of harvesting (Curley 1996). If the *in situ* aggregation of *Mictyris* is linked to any microrelief features, then their obliteration may lead to both removal of important visual cues used by the godwits and a less

clumped, i.e. predictable distribution of prey (e.g. Fauchald 1999), causing the godwits to have to travel greater distances between successive captures (e.g. Sutherland et al. 2000). In either case, the rate of prey capture will be compromised.

Functional response in bar-tailed godwits and estimated depletion of *Mictyris* stocks

In addition to the rapid functional and numerical responses of bar-tailed godwits to the experimental decrease in their prey density, there were 2 more lines of evidence pointing to the birds' capture rate being directly limited by the instantaneously available stocks of the prey. First, regression of mean monthly in-plot godwit capture rates against mean *Mictyris* density initially produced a poor relationship, but when the October 1998 data were taken out of the equation, the linear fit improved greatly. This suggests that if an excess of prey for these birds existed in the system, it was only for a short period soon after their arrival in October, and subsequent removal of this excess took place very quickly. Second, estimated seasonal depletion of *Mictyris* stocks was 88% of the initial (October) level. Indeed, between the start and the end of a shorebird wintering season densities of *Mictyris* in the substratum decreased by a similar value (90%). This suggests that even if the *in situ* stocks of *Mictyris* were being replenished through recruitment (Cameron 1966), predation pressure coupled with other factors was exceeding it. However, to show that godwit predation controls *in situ* density of *Mictyris* would require an appropriately designed (Sewell 1996) exclosure experiment (e.g. Quammen 1984, Székely & Bamberger 1992).

Seasonal trends in godwit density, foraging behaviour and prey densities

A significant seasonal decrease in the capture rate and foraging success suggest that fewer prey were becoming available to the godwits as the time progressed. However, neither the density of godwits in the plots nor the total mudflat population, ca. 2400 individuals per 250 ha mudflat, decreased between October (1998/99) and April (1999/2000) (author's pers. obs.). This has been explained by a seasonal increase in the size of consumed prey, which resulted in an apparent increase in the intake rate (sandy habitat: 0.88 kJ min^{-1} in December to 1.20 kJ min^{-1} in March, Zharikov & Skilleter 2002) despite a lower capture rate.

The explanation to the paradoxical situation: virtual disappearance of *Mictyris* from sediment samples versus the stable local godwit population size, and apparently, small contributions of the other prey types to the energy intake of the birds (Zharikov & Skilleter 2002) may lie in the life history of *Mictyris*.

Cameron (1966) reported that reproduction in *Mictyris longicarpus* takes place year-round. However, further north on the Queensland coast Dittmann (1998) reported a large peak in the number of juvenile (<7 mm CL) individuals only in September 1989, about the same time of the year as our samples containing high *Mictyris* densities were collected, but not during other months of the year. Furthermore, pilot samples of surface-active *Mictyris* collected in the study area in October 2000 and March 2001 had 67 and 27% of juvenile *Mictyris* respectively. These observations do not exclude year-round reproduction because in this study juvenile individuals were found in all sets of benthic samples (Fig. 2). However, they do suggest that regular recruitment events may take place in September to October, the time of mass arrival of Pale- and Nearctic shorebirds to the east Australian coast (Thompson 1992).

Mictyris forage on the mudflat surface (Quinn 1983, Dittmann 1993). Although the exact relationship between the body size of the crabs and the proportion of time they spend foraging remains unknown, adult individuals forage for longer and move over larger distances than juveniles (Cameron 1966, Quinn 1983). Therefore, while on the one hand the small individual fraction of the population present in the sediment is reduced by predators, on the other hand *Mictyris* grow and recruit into the surface-active population, which is not effectively sampled by benthic cores. The combination of these 2 processes may explain the steep seasonal decrease in the *in situ* density of these crabs. However, as stated above, it needs to be determined experimentally whether predation by the godwits, which typically consume *Mictyris* <10 mm CL (Zharikov 2002), plays an important role in the decline.

To conclude, the observed functional and numerical responses to the experimental reduction of prey density, the strong linear relationship between prey densities and capture rate and the high estimated depletion of the initial stock of *Mictyris* demonstrate that: (1) bar-tailed godwits wintering in subtropical Moreton Bay may achieve a high exploitation level of their food resources and (2) the rate of intake achieved by these birds is limited by prey density. This finding may tie together (1) the low intake rates observed in this population (0.88 to 1.62 kJ min^{-1}, Zharikov & Skilleter 2002) as compared to the populations wintering and/or staging in Europe (1.21 to 2.38 kJ min^{-1}, Smith 1975; 1.5 to 1.8 kJ min^{-1}, Scheiffarth et al. 2002) with (2) the low rate of body mass gain (2.9 g d^{-1}) and the generally prolonged period of pre-migratory preparations reported in bar-tailed godwits elsewhere in Australia (M. Barter & J. Wilson pers. comm.).

Utility of large-scale experiments in shorebird–prey interaction studies

When an experiment directed at studying spatial distribution of a mobile predator is to be conducted, its scale has to correspond to the scale of movements of the study species (e.g. Cummings et al. 1997). Otherwise, any potentially important interactions may be overshadowed by the background variability. Shorebirds frequently range over large distances (e.g. Zwarts et al. 1992, Piersma et al. 1993b) but generally respond numerically to the densities of their prey from scales of 100s of m and up (Colwell & Landrum 1993). In this study area, bar-tailed godwits appeared to range over distances of 100s of m. Therefore, the scale of 1 ha was chosen to investigate responses of the shorebirds to manipulations of their prey densities. This choice was appropriate for the godwits as can be seen from the significant correlations between the shorebird capture rates and densities of their principal prey and the near-significant variability in their density at the level of plots (Table 1). We propose that the optimal approach to studies of shorebird predator–benthic prey interactions in the intertidal habitats is application of large-scale controlled manipulative experiments, which would account for both large-scale shorebird movements and small-scale spatial and temporal variability in benthos (Thrush 1991, Sewell 1996) distribution irrelevant to the distribution of the birds.

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