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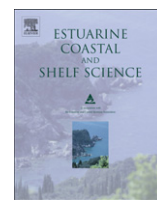
Short-term response of estuarine sandflat trophodynamics to pulse anthropogenic physical disturbance: Support for the Intermediate Disturbance Hypothesis

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ABSTRACT

Many anthropogenic activities physically disturb urbanised coastal habitats. The functional response of ecosystems to physical disturbances remains largely unknown due to the lack of suitable quantitative tools for assessing impacts. We conducted a manipulative field experiment to investigate the short-term (i.e. temporally sensitive) response of estuarine sandflat trophodynamics to pulse anthropogenic physical disturbance, using combined chemical tracer (^{13}C), compartmental modelling and network analysis techniques. Pulse physical disturbance, as sediment pumping for an infaunal bait species, was applied at two disturbance intensities at the commencement of the experiment, in 0.09 m^2 quadrats. Six compartments and three trophic levels in the estuarine sandflat food web were sampled, including the microphytobenthos, four meiofaunal groups, and soldier crabs (*Mictyris longicarpus*). Compared with undisturbed controls, in the low disturbance intensity treatment: 1) carbon flow rates between compartments increased, 2) carbon cycling increased, 3) more carbon was retained in the food web, and 4) system indices reflecting ecosystem functioning and resilience were higher. Low disturbance intensity facilitated carbon transfer between organisms and apparently increased resilience. Conversely, high disturbance intensity reduced carbon flow among compartments and carbon cycling, thus lowering resilience. This is the first study with field data quantifying structural and functional changes of sandflat food webs in response to physical disturbance and showed that both ecosystem structure and processes may support the Intermediate Disturbance Hypothesis. This alternative approach to assessing the immediate functional response of estuarine trophic interactions to physical disturbances allows impact detection not possible using conventional approaches.

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1. Introduction

Food web structure and the strength of trophic interactions are important in determining ecosystem functioning and resilience (Neutel et al., 2002; Thrush et al., 2009). Resilience is a key component of ecosystem health (Mageau et al., 1995). It indicates the amount of disturbance that a system can absorb and still remain within the same state or general condition (Holling, 1973) and the degree to which a system is capable of self-organisation in response to disturbance (Gunderson, 2000). Ecosystem functioning depends not only on species abundance and assemblage composition but also trophic interactions (Duffy et al., 2005; Ings et al., 2009).

Healthy ecosystems have more energy reserve (as indicated by the system index 'overhead') to combat disturbance, and hence greater resilience (Costanza and Mageau, 1999). However, when an ecosystem moves from one state to another as a result of disturbance, it may lose resilience as well as some of the ecosystem services available in the desired state (Elmqvist et al., 2003). One approach to understanding how ecosystems respond to anthropogenic disturbance is through the study of food web dynamics (Folke et al., 2004).

The empirical approach to measuring ecosystem resilience mainly focuses on the relationship between diversity, magnitude of ecosystem process and variability of ecological processes (Tilman et al., 2001; van Ruijven and Berendse, 2005). However, few studies have examined both ecosystem structure and functioning across multiple trophic levels (Mulder et al., 1999; Duffy et al., 2005). The understanding of ecosystem resilience in response to disturbance will help develop a predictive framework for avoiding changes associated with loss of essential ecosystem functions.

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Previous studies of disturbance effect on ecosystem structure led to the Intermediate Disturbance Hypothesis (IDH) (Grime, 1973). The IDH states that diversity and abundance of organisms are higher when disturbance is intermediate in frequency and intensity. This level of disturbance allows the coexistence of more species since the disturbance may mediate periodic reductions of competitive dominant species, and may favour the colonisation of opportunistic species (Huston, 1979). However, the IDH may not apply in all ecological situations (see review Mackey and Currie, 2000), and whether the IDH applies to ecosystem function as well as structure is yet to be examined.

Linking ecological theories of ecosystem structure and functioning has become an important aspect of ecosystem-based management (Olff et al., 2009). Physical disturbance is one key factor controlling the spatial and temporal composition of communities (Schratzberger et al., 2009). Anthropogenic activities cause physical disturbances on coastal areas mainly through activities such as bait collection (Contessa and Bird, 2004), boating (Herbert et al., 2009), trampling (Bowles and Maun, 1982) and dredging (Somerfield et al., 1995). Harvesting of invertebrates for bait by recreational fishers is a widespread phenomenon worldwide. For example, live bait shrimp production in Texas, USA, is valued at US$33 880 per ha (Gandy, 2007). The most common harvesting activity on Australian estuarine sandflats targets the infaunal thalassinidean shrimp (*Trypea australiensis*) known as a yabby (McPhee and Skilleter, 2002).

Previous studies have assessed the impact of recreational yabby harvesting by measuring changes in the densities and assemblage composition of the benthic infauna (Skilleter et al., 2005). Yabby pumping not only removes target invertebrates but also turns the sediment over, transporting the underlying organically-enriched sediment to the surface and changing the prevailing biogeochemical pathways (Jordan et al., 2009). It is also expected that yabby pumping would have prolonged effects on the recruitment and settlement of benthic fauna (Wynberg and Branch, 1997; Skilleter et al., 2005).

Yabby pumping has significant immediate consequences on the structure of intertidal benthic communities (Skilleter et al., 2005). Since fluctuations in ecosystem structure could crucially influence ecosystem functioning and resilience (Yaragina and Dolgov, 2008), physical disturbances such as yabby pumping are expected to affect ecological processes such as trophodynamics. However, yabby collection is largely unregulated, and there are no background data on ecosystem function to support the development of appropriate management strategies. This deficiency impedes our understanding of sandflat resilience to common but moderate anthropogenic physical disturbances such as bait collection.

The main scope of this study was to assess structural and functional changes in estuarine sandflat food webs to physical disturbance. We hypothesised that meiofaunal abundance and C flow rates among organisms at the lower trophic levels of the estuarine sandflat food web would be maximised by low intensity of yabby pumping. We conducted a field manipulative experiment on the impact of pulse physical disturbance employing an innovative approach combining an in-situ stable isotope enrichment experiment and ecological modelling (Lee et al., 2011), in parallel with empirical ecological measurements of animal abundance and assemblage composition. The short-term impact of yabby pumping on C flow and resilience was assessed in a simple food web comprising six compartments and three trophic levels: the microphytobenthos (MPB), four dominant meiofaunal groups and soldier crabs (*Mictyris longicarpus*). While we had strong a priori reasons for expecting intermediate disturbance (in our case, LD) to maximise meiofaunal abundances (structure), our test of effect on C flow rates (process) was exploratory; we set up the test to confirm or refute that the pattern in our process measures would match those on structure.

2. Materials and methods

2.1. Field site

The experiment was conducted on an intertidal estuarine sandflat ∼ 2 km upstream from the mouth of Tallebudgera Creek in southeast Queensland, Australia (28°06′29″S, 153°26′57″E). The sandflat is about 220 m long and runs parallel to the shore at ∼ 1 m above mean low water.

2.2. Experimental design: short-term dynamic response of sandflat trophodynamics to yabby pumping

Three weeks prior to the commencement of the experiment, 90 cages (mesh size: 8 mm × 8 mm, diameter: 0.2 m, height: 0.4 m) were randomly placed 3–5 m apart on the sandflat, at around +2 m from extreme low tide, within the aggregation zone of soldier crabs in an overall belt of ∼ 4 × 200 m. Refer to Lee et al. (2011) for details on cage design and deployment. Adult soldier crabs (*M. longicarpus*) with similar carapace lengths were collected locally by hand. Two weeks after cage establishment (day 14, to allow settlement of the sand after initial disturbance), one crab was put into each cage to simulate natural field density, estimated to be 1.5 ± 0.2 individuals per 0.0625 m^2. Crabs were allowed to acclimatise in the cage for one week before the sediment was physically disturbed.

Sediment was disturbed in an effective area of $0.3 \times 0.3 \text{ m}^2$ centred around each cage, using a "yabby pump", a manual suction device consisting of a stainless-steel pipe with a handle and plunger ($L = 0.75$ m, $\varnothing = 0.05$ m) on day 21 (between 3 and 1 h prior to high tide). This device is popular among local bait-collectors for collecting yabbies. There were two treatments and two controls, each with 30 replicates. Cages were assigned to one of the following categories: (1) low disturbance intensity (LD) with one 'burrow' per disturbance area and four pumps per 'burrow'; (2) high disturbance intensity (HD) with three burrows, and four pumps per 'burrow', resulting in a total of 12 pumps in total; (3) cage controls where sediment in the cages was undisturbed (UD); and (4) controls where sediment was collected randomly outside the cages (but within the effective area) without disturbance ('in-between' samples) (Fig. 1). Yabbies were collected after pumping, in order to simulate the actual yabby pumping activity. Disturbance intensity applied in the present study was generalised from previous studies (McPhee and Skilleter, 2002; Rotherham and West, 2003) and our observation that bait collectors usually pump three to four times from the same yabby burrow and occasionally up to 12 times in a confined area similar to that in the present study. The disturbance was applied five hours before high tide, allowing for sediment settlement before the tide returned.

Chl *a* concentration and organic content of treatments and controls were monitored before the experiment began (day 0), on day 7 and 14 and when the sediment was finally harvested (day 21–26), to monitor changes throughout the experiment. Preliminary work showed that abundance and assemblage composition of meiofauna at high-intensity disturbance returned to the pre-disturbance level within seven days. In order to assess carbon flow, on day 21 of the experiment, $\text{NaH}^{13}\text{CO}_3$ (1 g L^{-1}) enrichment solution was sprayed evenly over the sediment surface in each cage. At an application rate of 2 g $\text{NaH}^{13}\text{CO}_3 \text{ m}^{-2}$ ($= 0.306 \text{ g }^{13}\text{C m}^{-2}$), this is enough to act as a tracer but is low enough to avoid stimulating additional productivity. Cages were randomly allocated for destructive sampling 0 (before), 1, 2, 4 and 6 days after enrichment (i.e. day 21–26 of the experiment), with six replicates for each treatment × time combination. On each sampling date, 24 sediment samples (18 from the cages and six randomly from the sandflat between cages – the 'in-between' samples), were collected
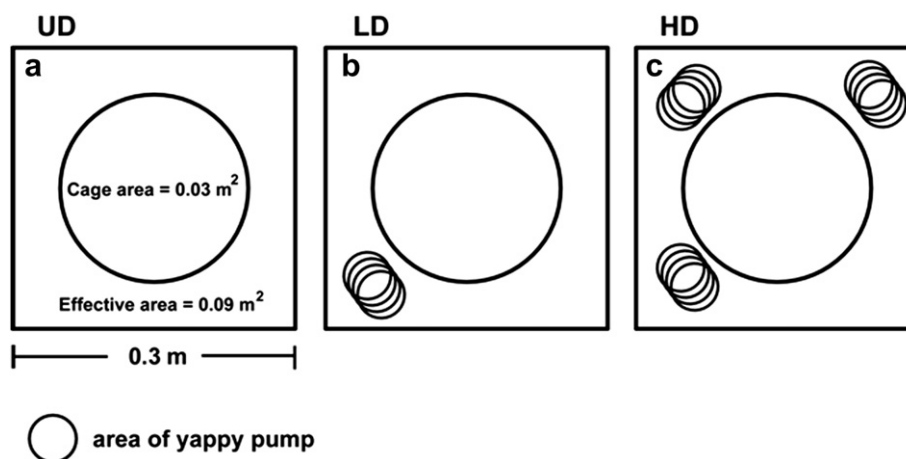
Fig. 1. Top-view of the experimental setup of this study, (a) cage controls where sediment in the cages was un-disturbed (UD); (b) low density disturbance (LD) with one 'burrow' per disturbance area and four pumps per 'burrow'; and (c) high disturbance intensity (HD) with three burrows and four pumps per 'burrow'. Sediment was disturbed outside the cage wherever a visible yabby hole or burrow was found inside the effective area. Overlapping of ○ represents how the actual yabby pumping was performed at the same visible burrow.

from the top 10 cm of sediment within the cages (using a 10-cm diameter corer). Soldier crabs inside the allocated cages, where the sediment samples were collected, and six crabs freely wandering on the shore were collected. The crabs were put in ice-slurry and transported back to the laboratory and stored at −20 °C before analysis. Refer to Lee et al. (2011) for details of the standard processing procedures for the microphytobenthos (MPB), extraction of the dominant meiofaunal taxa from the sediment and removal of soldier crab hepatopancreas for stable isotope analysis. Crab hepatopancreas tissue was used for stable isotope analysis because it takes up ^{13}C label faster than leg muscle (Oakes et al., 2010), and is thus quicker to reflect changes.

2.3. Gut content analysis

In order to confirm that the relevant meiofaunal groups were chosen in the model, gut content analysis of local soldier crabs was performed. Carapace length (CL) of thawed crabs was measured to the nearest mm using Vernier callipers and the crabs were then dissected. The stomach contents were homogenized in 1 mL of Milli-Q water, and food items identified and scored using a 1-mL Sedgwick rafter counting chamber (S50) under a light microscope (Olympus CX31) at 100× magnification. The relative abundance of each food item was calculated as:

$$\frac{\text{Total number of points scored for food item A}}{\text{Total number of intersections with a food item}} \times 100\%$$

Food items were placed into the following categories: MPB, harpacticoid copepods, amphipods, polychaetes and nematodes. Feeding activity of crabs at different enrichment levels was assessed by their relative stomach fullness, calculated as:

$$\frac{\text{Total number of intersections with a food item}}{\text{Total number of intersections on counting chamber}} \times 100\%$$

2.4. Modelling

2.4.1. WinSAAM

The compartmental modelling software WinSAAM (available at http://www.winsaam.org) was used to determine the carbon transfer rate between organisms based on temporal changes in the amount of tracer in the organisms throughout the experiment,

without the need for the levels to reach equilibrium (Stefanovski et al., 2003). Use of the program is described generally in Wastney et al. (1999) and specifically for the purposes of food web experiments by Lee et al. (2011). Compartments within the model were: (1) microphytobenthos (MPB, C source); (2) juvenile polychaetes; (3) harpacticoid copepods; (4) nematodes; (5) amphipods; and (6) soldier crabs. Transfer of ^{13}C label to each compartment was described in terms of a differential equation:

$$\int (^{13}\text{C in compartment}) \, dt \ = \ \int (^{13}\text{C input} - \ ^{13}\text{C output}) \, dt$$

The fractional transfer rate, $L_{i,j}$, describes the fraction of material in compartment j that moves to compartment i per unit time. $L_{i,j}$ was estimated from the initial fractional slope of each compartment through time, derived from the temporal changes of the δ^{13}C signature of each compartment. Data were weighted using fractional standard deviation (FSD), one of the data sensitivity parameters in WinSAAM, to estimate how well the model fitted the observed values. Data are considered well-described by the model if FSD is <0.5 and none of the adjusted parameters has an estimated value equal to the boundary condition value (supplementary information Table 1).

2.4.2. EcoNet modelling

The carbon transfer rates between compartments as determined using the ^{13}C tracer and WinSAAM were entered into EcoNet, and food web structure and energy cycling analysed. EcoNet is a simulation and network analysis software package for studying food

Table 1
Summary of two-factor ANOVA results on Chl a concentration and organic content of sediment, with disturbance intensity and sampling day as factors. p values in bold indicate significance at $\alpha = 0.05$.

Independent variable	df	F	p
Dependent variable - Chl a concentration			
Disturbance intensity	3	5.88	**0.001**
Sampling day	4	2.91	**0.025**
Interaction (Disturbance intensity × sampling day)	12	0.66	0.784
Residual	100		
Dependent variable - Organic content			
Disturbance intensity	3	3.57	**0.017**
Sampling day	4	3.23	**0.015**
Interaction (Disturbance intensity × sampling day)	12	0.48	0.923
Residual	100		

web structure of ecosystems (available at http://eco.engr.uga.edu/index.html). It was chosen because it can handle non-linear models and it features fast stochastic simulation algorithms based on Langevin equations and Gillespie's Stochastic Algorithm, apart from deterministic methods (Kazanci, 2007). EcoNet uses Network Environ Analysis to quantify the actual relation among compartments, environmental inputs and outputs (Kazanci, 2007; Tollner and Kazanci, 2007).

The selected method was fixed time-step (4th order Runge-Kutta), with step size at 0.001 and iterated until the system reached steady-state. Quantitative indices on ecosystem functioning, namely, ascendency (A), overhead (O), Finn Cycling Index (FCI), total system throughput (T), throughflow analysis matrix (N), storage analysis matrix (S) and utility analysis matrix (U), were compared between

treatments and controls. These indices were chosen because of their relevance to ecosystem attributes that are sensitive to disturbance (Odum, 1985). Ascendency measures both the size and the structure of flows and is taken as a product of growth and development, serving as a measure of a network's performance in processing material. Overhead is the difference between capacity of ecosystem development and ascendency (Ulanowicz, 1986), which gives a useful measure of resilience (Costanza and Mageau, 1999). A high overhead indicates a high proportion of parallel pathways in the system (Allesina et al., 2005). The amount of energy cycling is reflected by FCI, which has been used to determine the degree of maturity and resilience of a system (Vasconcellos et al., 1997; Ray, 2008). FCI is derived from the fraction of total flow that is devoted to cycling, and is defined as the ratio of the energy recycled to the
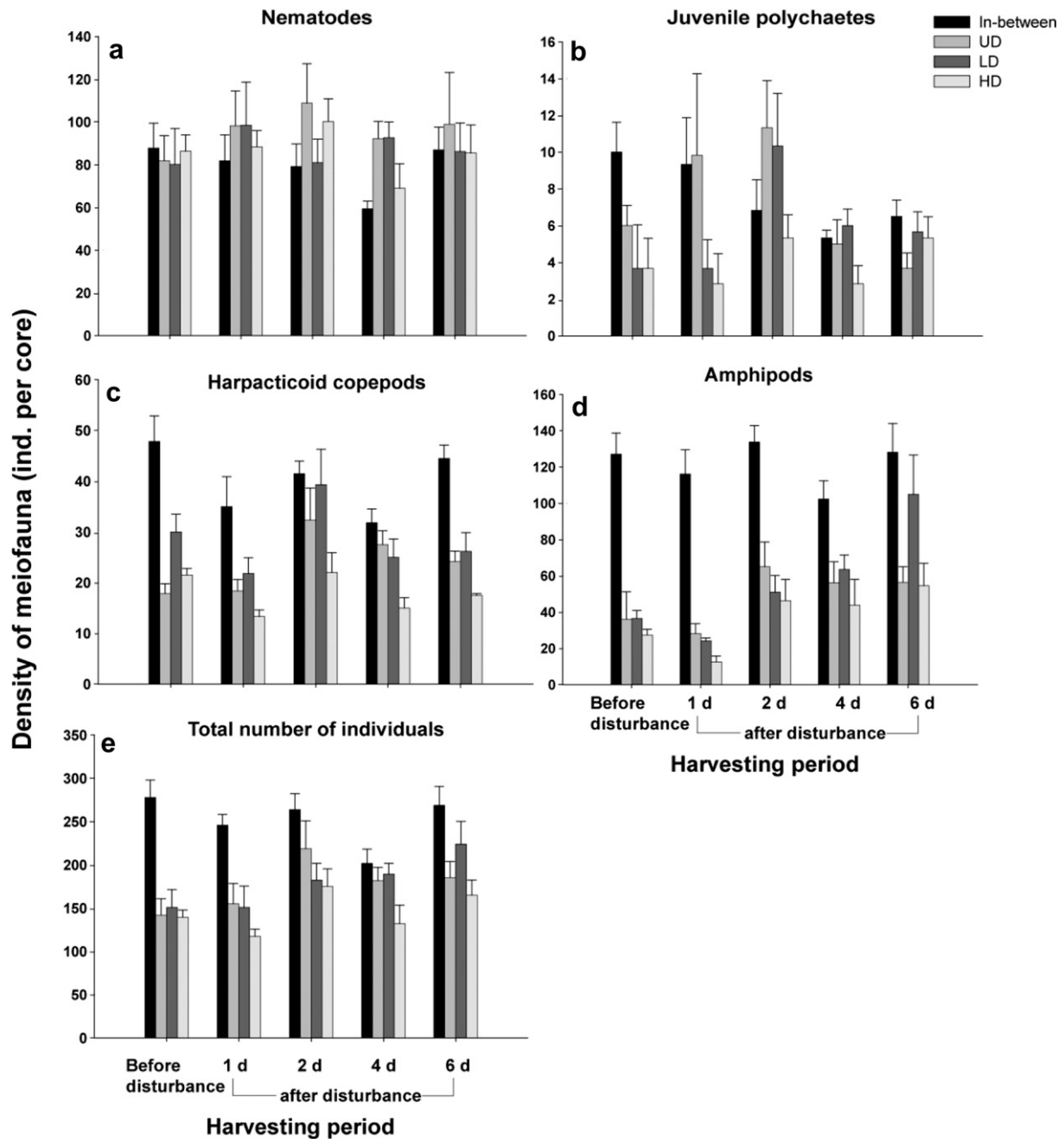

Fig. 2. Abundance of the taxa at different disturbance intensities initially after the disturbance and on day 21–26 during the course of the experiment: (a) nematodes; (b) juvenile polychaetes; (c) harpacticoid copepods; (d) amphipods; and (e) total number of individuals (mean + SE). Core volume = 785 cm³.

sum of all flows in the ecosystem. T reflects the size of the system in terms of the sum of flows through all the individual compartments (Baird and Ulanowicz, 1993). N represents how much environmental input to one compartment is received by another. S represents the relationship between input flow rates and compartment storage values and U indicates the interaction strengths between compartments. A negative value of U between compartments indicates that an increase in abundance of one compartment will decrease the C flow to the other compartments. Sensitivity analysis was performed by calculating new solutions of the model after changing the input value of the MPB by $\pm$ 10%. A brief explanation and citation of system indices are given in Table 1 of the supplementary information. Refer to Kazanci (2007) for further details of EcoNet system indices.

2.5. Statistical analysis

Stomach fullness and CL of the crabs for isotopic analysis were tested separately using one-way ANOVA with disturbance treatment as a fixed factor, to ensure that the crabs tested had similar body size and thus could be expected to show similar dietary composition and consistent response to ^{13}C labelling. Differences in the Chl a concentration and organic content of sediment, abundance of individual meiofauna taxa and total abundance of meiofauna in the harvesting period were assessed separately using two-way ANOVA, with treatment and sampling day as fixed factors and planned contrasts separately for each time period when the interaction between treatment and sampling day was significant (Quinn and Keough, 2002). Similarity of meiofauna assemblage composition among treatments was analysed, with temporal data on abundance of each meiofauna at each treatment, using ANOSIM (Primer v.6, Clarke and Gorley, 2006), with intensity of disturbance as the treatment factor. In order to account for natural variability in the system, meiofaunal assemblage composition was compared among 'in-between' sediment samples throughout the harvesting period using ANOSIM (Primer v.6); Chl a concentration and organic content of in-between' sediment samples were compared separately throughout the harvesting period using one-way ANOVA, with sampling day as a fixed factor. All statistical analyses were conducted using SPSS v.17.0.

3. Results

3.1. Physical conditions and assemblage structure

Natural variability of the system was low during the harvesting period (Chl a concentration: df = 4, 25; p = 0.414; organic content: df = 4, 25; p = 0.120; meiofaunal assemblage composition: ANO-SIM: R = 0.03; p = 0.259). The organic content and Chl a concentration of LD and HD sediments decreased after disturbance. However, these two variables were similar to post-disturbance level by the end of the sampling period (Table 1). Chl a concentration did not differ between 'in-between' and UD sediments (df = 3, 116, ANOVA interaction Time*Treatment p = 0.784). Chl a concentration was similar between 'in-between' and 'background' sediment at all times (all planned contrasts non-significant), suggesting that deployment of cages did not have any effect on MPB or C abundance, e.g. by reducing light availability. However, density of meiofauna and abundance of individual meiofaunal taxa at UD were lower than 'in-between' sediment (Fig. 2). This may indicate some caging effect on the colonisation and recruitment of meiofauna.

Overall total abundance of meiofauna was highest at LD, followed by UD and HD during the course of the experiment (LD: 185 $\pm$ 10; UD: 176 $\pm$ 11; HD: 147 $\pm$ 8 ind. per core). Density of meiofauna at LD and HD was depressed initially after disturbance

and then increased back to the level at the commencement of the enrichment experiment by the end of the harvest period (Fig. 2). Meiofaunal taxa had a different response to yabby pumping though the overall interaction terms between harvesting period and treatment were insignificant for all dominant meiofaunal taxa (Table 2). Nematodes were the least affected by the level of physical disturbance, followed by juvenile polychaetes, amphipods and harpacticoid copepods. Assemblage composition of meiofauna was similar across treatments at the conclusion of the experiment, suggesting that meiofauna had recolonised the sediment by the end of the harvest period (ANOSIM, R = 0.007; p = 0.297).

The crabs added to cages had similar body sizes across treatments (one-way ANOVA on CL, df = 3, 100; p = 0.292) and thus could be expected to show similar dietary composition and a consistent response to ^{13}C labelling. Stomach fullness of crabs was the lowest at HD (one-way ANOVA, df = 3, 100; p < 0.001), due to the decrease in meiofaunal abundance and/or inability of the crabs to feed at elevated disturbance intensity. The composition of crab diets was consistent among the disturbance intensity levels, with nematodes being the major food item, mirroring the high abundance of nematodes in the sediments.

3.2. Modelling

There was a clear difference in ^{13}C labelling between MPB, meiofauna and soldier crabs (Fig. 3). Rates of ^{13}C transfer among compartments were derived from the temporal changes in the δ^{13}C values of the compartments. All adjusted parameters in WinSAAM had FSD values < 0.5 and no adjustable parameter had an estimated value equal to the boundary condition values, suggesting that data were well defined by the model. The best fit of the compartmental model was achieved using the transfer rates between compartments shown beside the arrows in the C flow network of each treatment (Fig. 4). Meiofaunal assimilation of MPB C was highest in LD, followed by UD and then HD. Nematodes were the least

Table 2
Summary of two-factor ANOVA results on the abundance of nematodes, juvenile polychaetes, harpacticoid copepods, amphipods, and total abundance of meiofauna with disturbance intensity and sampling day as factors. p values in bold indicate significance at α = 0.05.

Independent variable	df	F	p
Dependent variable − abundance of nematode			
Disturbance intensity	3	1.34	0.266
Sampling day	4	0.77	0.546
Interaction (Disturbance intensity × sampling day)	12	0.51	0.905
Residual	100		
Dependent variable − abundance of juvenile polychaetes			
Disturbance intensity	3	4.11	**0.009**
Sampling day	4	2.79	**0.030**
Interaction (Disturbance intensity × sampling day)	12	1.55	0.120
Residual	100		
Dependent variable − abundance of harpacticoid copepods			
Disturbance intensity	3	28.78	**<0.001**
Sampling day	4	5.15	**0.001**
Interaction (Disturbance intensity × sampling day)	12	1.37	0.194
Residual	100		
Dependent variable − abundance of amphipods			
Disturbance intensity	3	57.04	**<0.001**
Sampling day	4	7.73	**<0.001**
Interaction (Disturbance intensity × sampling day)	12	1.77	0.066
Residual	100		
Dependent variable - Total abundance of meiofauna			
Disturbance intensity	3	25.40	**<0.001**
Sampling day	4	4.25	**0.003**
Interaction (Disturbance intensity × sampling day)	12	1.37	0.195
Residual	100		

affected, followed by harpacticoid copepods, amphipods and juvenile polychaetes across treatments. Juvenile polychaetes were the most sensitive and their ability to assimilate MPB C decreased by 92% from LD to HD. The order of meiofaunal assimilation of MPB C was: amphipods (87%) > nematodes (77%) > harpacticoid copepods (53%), all of which showed a negative response to disturbance from LD to HD. Soldier crabs assimilated more C from nematodes in HD, followed by UD and then LD; whereas their assimilation of amphipod C was highest in UD, followed by LD and then HD (Fig. 4).

The total amount of energy (indicated by T), C cycling (indicated by FCI) in the food webs, ascendency and system overhead were greatest in LD, followed by UD and HD (Fig. 5d–e). This indicated that the degree of organisation and resilience of sandflat food webs were greatest at the intermediate level of disturbance but decreased at the high level of disturbance. $N_{MPB, MPB}$ was >1 in all treatments, indicating that MPB C was recycled through the sandflat food web and re-entering the MPB compartment before leaving the system. The diagonal values of meiofaunal groups in throughflow analysis matrix (N) were >1 in all treatments, suggesting that the above compartments had the potential to cycle energy within

themselves (Fig. 5a). The soldier crabs received more C generated by MPB indirectly in HD ($N_{crabs, MPB} = 0.73$) than in LD ($N_{crabs, MPB} = 0.58$) and UD ($N_{crabs, MPB} = 0.59$) but there was no direct flow from MPB to soldier crabs in any treatments or the control ($N_{crabs, MPB} = 0$).

The storage analysis matrix S traces the amount of C storage in each compartment. There was no direct environmental input of C into the soldier crab compartment. Further, the environmental input to soldier crabs will not affect the amount of C stored in other compartments since the $S_{polychaetes,crabs} = S_{copepods,crab} = S_{nematodes,crabs} = S_{amphipods,crabs} = 0$. The C storage value of meiofaunal compartments was greatest at LD, followed by UD and HD (Fig. 5b). Juvenile polychaetes and harpacticoid copepods gained more C when the abundance of soldier crabs increased in HD followed by UD and LD. However, an increase in soldier crab abundance was more detrimental for nematodes in HD followed by UD and LD. Amphipods gained less C in the presence of soldier crabs in UD, following those in LD and HD (Fig. 5c). Time-course figures of each simulation with MPB stocks changed by ± 10%, resulting in overlapping solutions for each compartment. Hence the models were considered to be stable.

4. Discussion

Anthropogenic physical disturbance is expected to exert influence on benthic trophodynamics, but quantitative assessment of such impacts is almost non-existent. In highly disturbed environments, ecosystem processes are driven by the colonisation ability and growth rate of individual species (Loreau et al., 2001). Physical disturbance leads to unstable food web structure, and causes the food web to become less resilient to subsequent disturbances (Worm and Duffy, 2003; de Ruiter et al., 2005). It is important to identify ecosystem resilience in response to physical disturbances in order to sustain beneficial ecosystem services (Balmford and Bond, 2005).

4.1. Physical factors, meiofaunal abundance and behaviour of soldier crabs in relation to bait collection

Compared to previous studies (e.g. Wynberg and Branch, 1994, 1997), organic content and Chl a concentration of the sediment and the abundance of the meiofauna recovered from disturbance in a short time (six days) at Tallebudgera Creek. Rapid recovery of the meiofauna following physical disturbance was also reported for crab tiling (Johnson et al., 2007). The high recolonisation rate of the benthic fauna might be a result of the rapid turnover rate of the meiofauna (Coull and Chandler, 1992). Meiofauna were able to re-establish their original position after brief periods of disturbance, due to the ease with which benthic fauna re-distribute by water movement (Gheskiere et al., 2006).

Bait collection inflicts a broad range of direct and indirect impacts on target species and other components of the ecosystem (Herbert et al., 2009). The actual yabby pumping activity does not only disturb the sediment, but also remove the target species, which may have implications for other species (Skilleter et al., 2005). However, the main scope of this study was to investigate the impact of pumping activity on the trophodynamics of sandflats. Yabby pumping has immediate strong impacts on sandflat trophodynamics: the meiofaunal assimilation rate of MPB C changed in response to the intensity of yabby pumping. Soldier crabs do not have fixed home-range, so the only way to track C flows on the sandflats is to confine the crabs in the sampling area. We chose the mesh size of cages carefully in order to minimise caging effect. Although relatively low abundance of organisms in the 'background' may suggest an artefact of caging, this effect on the
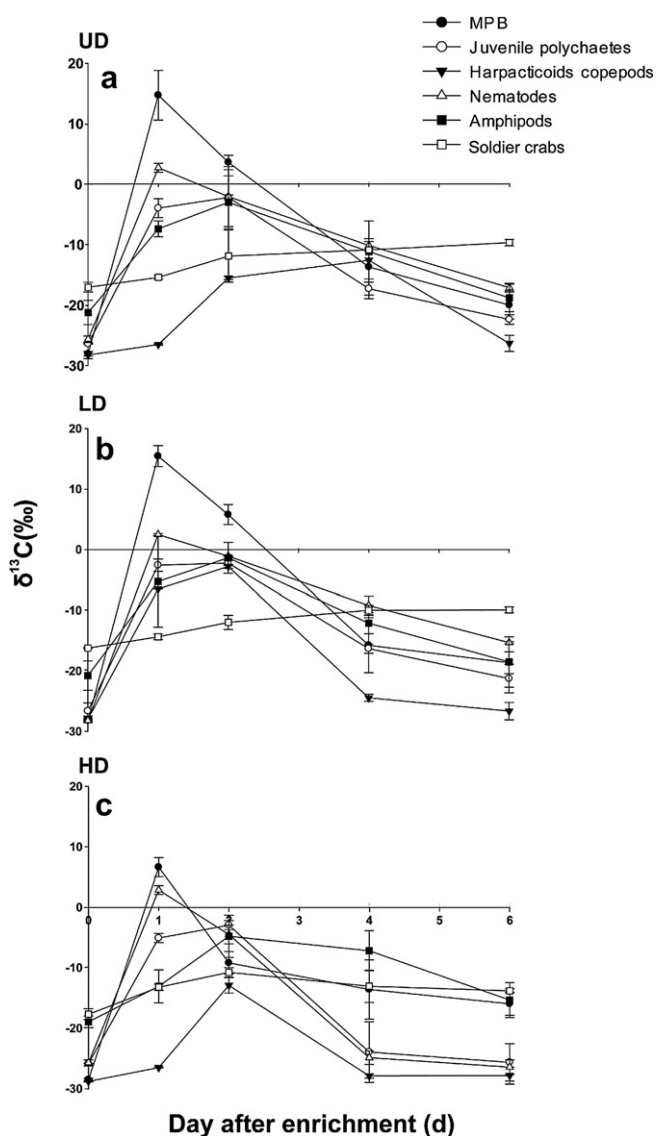

Fig. 3. Temporal changes in the δ^{13}C signatures of MPB, juvenile polychaetes, harpacticoid copepods, nematodes, amphipods and soldier crabs, for the (a) UD; (b) LD; (c) HD treatments.
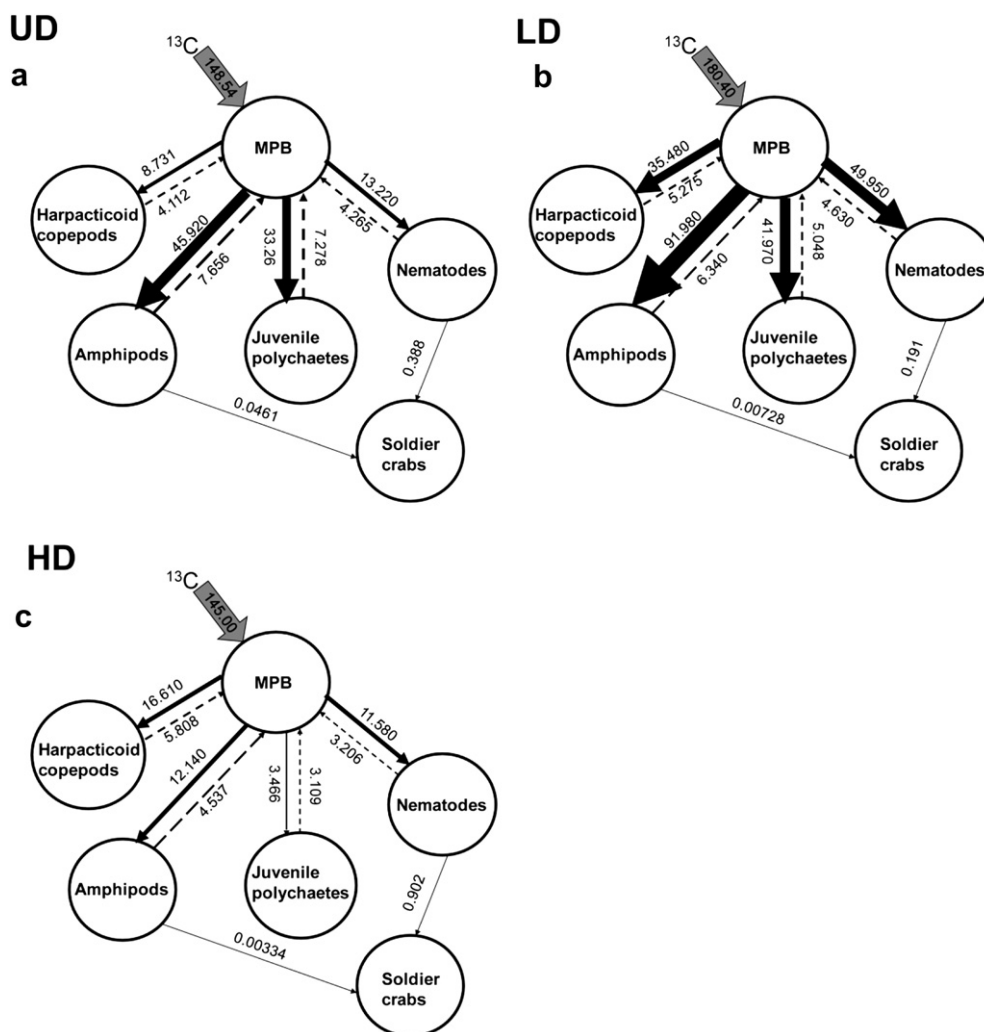
Fig. 4. The C transfer rate (μg ^{13}C d^{-1}) estimated by WinSAAM modeling between the food web compartments for the (a) UD; (b) LD; and (c) HD treatments. Solid lines represent the direction of C flow from lower to higher trophic levels, whereas dashed lines represent the return pathway. Line thickness represents the relative magnitude of the C flow rate. The numbers associated with the arrows represent the amount of MPB-assimilated ^{13}C label (μg) transferred via the various flow paths.

abundance of meiofauna should be equal while comparing the C flow rates between treatments and control. The C flow rates among compartments might, however, be higher for the 'in-between' controls. Harpacticoid copepods assimilated the greatest amount of MPB C at higher disturbance intensity. This was supported by previous studies, which showed that among the major meiofaunal groups, copepods were most resilient to the effects of strong physical disturbance (Warwick et al., 1990). Furthermore, the amount of meiofaunal C available to MPB (as indicated by the backflow of meiofaunal C to MPB) decreased at high-intensity disturbance. The net flow of MPB C by meiofauna was therefore greatest at LD, followed by UD and HD. This resulted in a decrease in C cycling at HD, implying that the system at HD was under most stress.

Survival rate and dietary composition of soldier crabs were consistent regardless of disturbance intensity. However, the amount of meiofaunal C assimilated was different among the treatments. Soldier crabs assimilated the least total amount of meiofaunal C at LD but the greatest amount at HD. Further, a reversed pattern in feeding activity of soldier crabs was apparent, i.e. fullest at UD and least full at HD. This inconsistency might be because soldier crabs assimilated more meiofaunal C in a stressed and more food-limiting environment, to compensate for the

depurated meiofauna available in the sediment and also the inability of the crabs to feed properly under stress. This inverse relationship between assimilation and feeding rates is commonly observed in some invertebrates, such as marine mussels (Pessatti et al., 2002) and sea urchins (Lawrence et al., 2003). This pattern also indicates that not all the food items present in the gut of soldier crabs were assimilated (Rudnick and Resh, 2005), again suggesting that snapshot approaches reporting ingestion (e.g. gut contents analysis) could be misleading in trophic studies.

4.2. Effects of bait collection on ecosystem function

System indices, C flow rates between compartments and C cycling in the system decreased significantly more at HD compared to UD and LD, suggesting that observations of the differences in abundance and in the faunal assemblage composition in response to disturbance (the conventional approach) are not sufficient for identifying impacts on ecosystem function. Further, the present system has a low resilience in response to physical disturbance, since the system attributes and C flow rates between compartments decreased significantly under the HD treatment. High intensity yabby pumping greatly suppressed C cycling in the system. The system at HD became more 'leaky' (less capable of
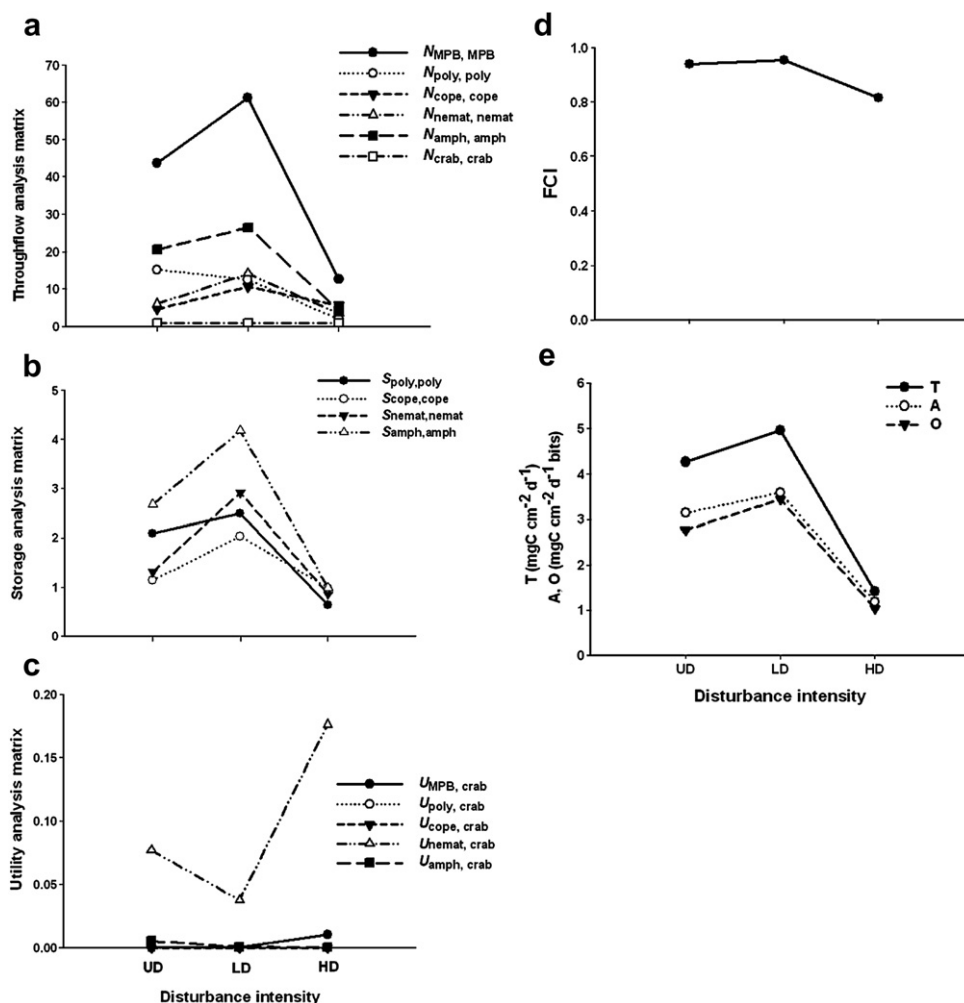
Fig. 5. Comparison of system indices across treatments: diagonal values of (a) throughflow analysis and (b) storage analysis of meiofaunal compartments; (c) magnitude of utility analysis matrix between meiofaunal compartments and soldier crab; (d) Finn Cycling Index (FCI); and (e) total system throughput (T), ascendency (A) and system overhead (O). The lines are put in to demonstrate the pattern of change in the system indices. The negative sign of $U_{nemat,crabs}$ and $U_{amph,\ crabs}$ is removed to improve clarity. MPB − micro-phytobenthos; poly- juvenile polychaetes; cope − harpacticoid copepods; nemat − nematodes; amph − amphipods; and crab − soldier crabs. Note that maximum or minimum values of the indices occur almost exclusively with the LD treatment.

retaining C through recycling in the system), as the system at HD had lower ascendency and FCI, which would ultimately result in system dysfunction.

The IDH has been used to explain the role of non-equilibrium conditions for the maintenance of species diversity in ecological communities (Grime, 1973). Although the recolonisation rate of meiofauna in the present study was fast (diversity and assemblage composition returned to post-disturbance level within a week), C flow rates between compartments (as shown by N, S and U matrices among compartments) and C cycling (as indicated by FCI) in the sandflat food webs were greatest at the intermediate intensity of yabby pumping (Fig. 5). This pattern may be potential support for the IDH from the ecosystem function perspective. The IDH predicts coexistence of many species and maximal productivity at intermediate levels of disturbance (Kadmon and Benjamini, 2006). Further, Jørgensen and Padisák (1996) demonstrated that IDH complies with thermodynamic predictions on ecosystems. Findings of this study showed that an intermediate level of physical disturbance intensity would facilitate the organisation and functioning of sandflat food webs.

Our findings could potentially support predictions of the IDH. Although we could not compare the changes in system indices statistically, consistent patterns in the changes of magnitude of C

flow rates and system indices were observed in this study, i.e., the magnitudes were greatest at intermediate levels (LD in our case) of disturbance. From a theoretical perspective, low levels of disturbance facilitate the colonisation of opportunistic species and hence lead to greater species diversity and abundance. This increase in species abundance can lead to an increase in species biomass, which in turn causes an increase in system organisation, utilisation of food sources and hence C flow rates in the system. This increase in species diversity can lead to an increase in species interaction in the systems, which in turn causes an increase in utilisation of food sources and hence C flow rates in the system (Bukovinszky et al., 2008). Therefore, the magnitude of system indices was greatest at LD (brief explanation in the system indices is given in supplementary information Table 1).

Trophic interaction plays an important role in maintaining ecosystem stability after disturbance (Worm and Duffy, 2003). Human use of ecosystems results in changes to ecosystem structure and hence may have profound effects on ecosystem functioning (Balmford and Bond, 2005). There are limitations to exploring ecological changes in response to disturbance over large spatial scales and long time spans. Nevertheless, this study successfully investigated a small system experimentally with the integrated use of ENA and empirical ecological measurement tools, including

changes in diversity and assemblage composition. Although we only disturbed the sediment once, and the meiofauna were able to recolonise within a period of time, we found that C flow among compartments and C cycling in the sandflat food web demonstrated significant changes in response to yabby pumping. Therefore it is expected that the impacts from yabby pumping on sandflat food web trophodynamics may be magnified if disturbances occur repeatedly. Findings of this study could potentially provide support for the relation between IDH and ecological processes and are expected to have generic implications for sustainable management of estuarine resources. Although meiofauna have high turnover rates and may colonise the disturbed area within a short period, findings of this study suggested that impacts of bait collection on ecosystem function could be severe. Future management plans for recreational harvest of estuarine invertebrates, including frequency and volume of bait collection, should be cognizant of the impacts of bait collection on both structural and functional changes of the communities.

Acknowledgements

Appendix. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.ecss.2011.03.003

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