MAPPING ECOSYSTEM PROCESSES AND FUNCTION ACROSS SHALLOW SEASCAPES

D Maher¹, B Eyre¹ Southern Cross University, Lismore, NSW

Abstract

Benthic habitat mapping is an important component of the assessment of shallow aquatic resources due to the recognised link between flora, fauna and habitat. Benthic habitat mapping is commonly undertaken using remotely sensed acoustical techniques that only map the physical features of the seafloor. Some studies may include ground-truthing of physical and chemical data such as grain size, organic carbon content and current velocities and at the highest level of detail the relationship between physical and chemical parameters and biological communities may be considered. However, biodiversity, the parameter we want to conserve, is more than just biological communities as it also include components of structure, function, and processes of species, communities, ecosystems. Despite processes and function being part of biodiversity, benthic maps of ecosystem function and functional value maps of benthic ecosystem processes have never been produced for shallow coastal systems. Shallow subtropical and warm temperate east Australian coastal lagoons and estuaries were used as case studies to develop a system for assigning functional value to shallow seascapes and to construct functional value maps of benthic ecosystem processes and overall functional value of benthic habitats. Eight habitat classes (Mangroves, Sands/ Muds with Large Burrowing Macrofauna, Stable Seagrass Communities, Ephemeral Seagrass Communities, Channels, Subtidal Shoals, Intertidal Shoals, Depositional Mud Basins,) and ten ecosystem processes (gross benthic production, gross benthic respiration, net benthic production, net benthic respiration, benthic dissolved organic and inorganic nitrogen fluxes, denitrification, denitrification efficiency and secondary production) were used to assign functional values and construct the maps. These functional value maps of ecosystem processes and overall functional value will be used to identify "hot spots" of functional value that have high conservation value. A case study from southern Moreton Bay will also be used to illustrate the application of the process functional value and overall functional maps by comparing with a map of impact (decrease in light) associated with the discharges from a wastewater treatment facility.

Introduction

A fundamental requirement in assessing the way in which shallow aquatic ecosystems function is the mapping of benthic habitats due to the intrinsic linkage between habitat, flora, fauna and biogeochemical cycles. In shallow coastal systems these relationships are complicated due to the complex mosaic of habitats often found in these ecosystems (eg Eyre and Maher, in press, Eyre et al. under review a,b), with habitat complexity and connectivity determining the composition of ecological communities (Hosack et al., 2006), and the flow of nutrients and energy through the food chain (Cloern, 2007). For example it is the balance between production and respiration (or net ecosystem metabolism, NEM)

that determines the amount of organic matter that is available to sustain secondary production and subsequently higher order (including fisheries) production (Kemp et al., 1997). This balance between production and respiration varies markedly across different habitat types (Santos et al. 2004), thus an integrated approach incorporating habitat coverage should be used to elucidate controls on ecosystem-wide organic matter cycling. NEM is also determining factor as to whether an aquatic ecosystem is a net sink or source of carbon (Gazeau et al 2005).

Benthic habitat mapping has become a critical component in managing and conserving coastal areas (Aswani & Lauer 2006, Godet et al. 2009) due to the increasing use of benthic habitats as surrogates for biodiversity (Ward et al.,1999). Coupled to the increased awareness of the importance of benthic habitats to the functioning of shallow water aquatic ecosystems is an advance in the technologies available to produce benthic habitat maps, including satellite and aerial photograph imagery and shipboard acoustic techniques (eg. multibeam ecosounder, side-scan sonar) (Blondel, 2002). These remotely sensed techniques are excellent at defining the physical structure of the benthos (Blondel and Murton, 1997, Fish and Carr, 2001), however significant assumptions and/or extensive ground-truthing are required to produce accurate benthic habitat maps. Whilst accurate habitat maps are a powerful tool in managing the aquatic environment, it is biodiversity that we are trying to conserve, and biodiversity is dependent upon not only habitat, but the structure, function and processes of an ecosystem (Marcot et al., 2002).

Despite biodiversity incorporating processes and functioning of an ecosystem, to our knowledge only one study has incorporated ecosystem function into a benthic map (Harbone et al., 2006), and functional value maps of benthic processes have never been produced. The importance of different benthic habitats to the overall ecosystem function has been reported (Eyre et al under review a,b, Eyre and Maher in press,) however functional values of each habitat were not defined and ecosystem processes were not mapped. As such the importance of conserving and restoring these habitats remains unknown.

The purpose of this paper is to present a system for assigning functional values to shallow water benthic habitats and to provide examples of functional value maps of benthic ecosystem processes and maps of overall functional value. These maps are then used to identify "hot spots" of functional value and thus areas of high conservation value. We used a subtropical (southern Moreton Bay) and three warm-temperate estuaries (Hastings River, Camden Haven and Wallis Lake) as case studies, however when assigning functional values to each habitat literature from a wide range of coastal ecosystems was considered to make the results more broadly applicable. Ecosystem processes considered included: gross benthic production (GPP), gross benthic respiration, net benthic production (NPP), net benthic respiration, benthic nitrogen fluxes (inorganic - DIN and organic - DON), denitrification, denitrification efficiency and secondary production. To illustrate a potential use for this system a case study from southern Moreton Bay is presented in which an impact map (modelled light decrease associated with a future wastewater discharge strategy) is compared to the functional value maps.

Methods

Habitats

Habitats were classified based on a modified version of the benthic habitat classes used previously for warm-temperate and subtropical estuaries (Eyre et al., under review, Eyre and Maher, in press). Habitats were classified based on depth, hydrodynamics and sediment type (intertidal shoals, subtidal shoals, channel, depositional basins), presence of burrowing macrofauna (predominantly the marine shrimp, *Trypaea australiensis*) and vegetation type (mangroves, stable seagrass community and ephemeral seagrass community). Habitats were then classified into the following classes, mangroves, sand/mud shoals with large burrowing macrofauna, stable seagrass community, ephemeral seagrass community, channel, subtidal sand/mud shoals, intertidal sand/mud shoals and depositional mud basins. Habitats were defined through a combination of aerial photograph interpretation, underwater video transects, diver transects, hydrodynamic data and benthic grab samples.

Functional values

A modification of the approach used by Harbone et al (2006) was used to assign functional values to each of the eight habitat types in the four study estuaries. Ten key processes were identified based on the availability of data and the importance of these processes to ecosystem function. The processes used were gross benthic productivity (GPP), gross benthic respiration (R), net benthic production (NPP), net benthic respiration (NR), denitrification, benthic dissolved inorganic nitrogen (DIN) fluxes, benthic dissolved organic nitrogen (DON) fluxes, denitrification efficiency and secondary production. The functional importance of each habitat to the total ecosystem in terms of each process was quantified using measured rates and habitat areas. This is seen as a better method than just incorporating process rates (eg Harbone et al 2006) as it also incorporates the aerial extent of each habitat. The habitat with the largest contribution to the ecosystem was assigned a value of 1.0. Each other habitat was then assigned a functional value based on its contribution to the ecosystem relative to the largest contributor. Table 1 gives an example for GPP calculations in the Hastings River estuary. Functional value was classed as high for habitats with a contribution relative to the largest contributor of 0.75 to 1.0, medium for 0.5 to 0.74, low for 0.01 to 0.25 and nil for <0.01.

	000		-		- J -	
Habitat	GPP	% Contribution	Functional		Value	Functional
	(tCyr⁻¹)	To Ecosystem	(Proportion	of	largest	Value
			contributor)			
Mangrove	764.0	18	0.49			Medium
Sand/muds with						Medium
burrowing macrofauna	523.9	12	0.34			
Stable seagrass						High
community	1563.4	36	1.00			
Ephemeral seagrass						Low
community	102.0	2	0.07			
Channel	518.0	12	0.33			Medium
Subtidal shoals	498.3	12	0.32			Medium
Intertidal shoals	115.4	3	0.22			Low
Depositional mud basin	206.2	5	0.39			Low

Table 1 Example of process functional value calculations for the Hastings River estuary

Denitrification efficiency was not area weighted but was based on its % value (>75% = High; 25% to 74% = Medium; 1 to 24% = Low; <1% = nil). Overall functional value was calculated by assigning each process functional value 3 for High, 2 for medium, 1 for low and 0 for nill, and summing the individual process values. Overall functional values were ranked and presented as a gradient of colours (red for high value green for low) on overall functional value maps. Maps were generated by incorporating benthic habitat data and functional values into a geographic information system (GIS) using a combination of MapInfo and ArcGIS software packages.

Results

Habitat classification

Benthic habitat maps for each estuary are presented in Figure 1. Each estuary displays a distinctly different composition of benthic habitat types. In the southern Moreton Bay estuary, the benthic habitat is dominated by mangroves, (~ 43 %) with substantial areas of subtidal shoals (~17%) and burrowing macrofauna (~14%). In the Hastings River estuary the dominant benthic habitat is comprised of channel (~43%), with only small isolated patches of stable seagrass beds (~5%). Both the Camden Haven and Wallis Lake estuaries have substantial areas of stable seagrass beds (~24% and ~29% respectively) with significant areas of depositional muds (~31% and ~21% respectively).

Ecosystem Processes

Gross Primary Production

Figure 1 displays the GPP functional value map for each system. In all estuaries, the stable seagrass communities were assigned a high functional value, and a high functional value was also assigned to mangroves in southern Moreton Bay, and ephemeral seagrass communities in the Wallis Lake estuary. Stable seagrass communities have also been found to be the contribute the highest GPP in the shallow Mississippi Sound (USA) and Ria Formosa (Portugal) (Moncreiff et al. 1992, Santos et al. 2004). Medium functional values were assigned to subtidal shoals in southern Moreton Bay and Hastings River, depositional muds in the Camden Haven and Hastings River systems, and ephemeral seagrass communities in the Camden Haven and southern Moreton Bay estuaries and the channel habitats of the Hastings River (primarily due to the proportionally large aerial coverage $\sim 43\%$).



Figure 1 Benthic habitat maps of the four study estuaries (A – southern Moreton Bay, B – Hastings River estuary, C – Camden Haven estuary and D – Wallis Lake estuary).

Respiration

Respiration follows the same general trend as GPP within each estuary however channel habitat in the Hastings River was assigned a high functional value (24% of total ecosystem respiration) and mangroves in southern Moreton Bay a medium functional value. Stable seagrass communities generally were the largest contributor to system wide respiration in each system, ranging from 28% in southern Moreton Bay to 65% in Wallis Lake. Sands and muds with burrowing macrofauna also contributed significantly to system wide respiration in most systems.

Net Primary Production

NPP is probably more critical than GPP and respiration in terms of trophic dynamics within an aquatic ecosystem as it is NPP that is available to sustain secondary production. NPP also determines the magnitude and direction of carbon flux into or out of an estuary. NPP functional values are presented in Figure 3. Stable seagrass communities were assigned a high functional value in the three warm temperate estuaries with a contribution of between 30 and 60% (Eyre and Maher, in press). In the subtropical southern Moreton Bay system the stable seagrass beds were net heterotrophic over an annual cycle (Eyre et al., under review) and were thus given a nil functional value in this estuary.

Nitrogen cycling

Nitrogen fluxes (DON, DIN and N₂) were only available for the southern Moreton Bay system and functional values for each process are presented in Figure 4. The functional value for each habitat varies across the range of processes, however in general the seagrass habitats (stable and ephemeral) subtidal shoals, and burrowing macrofauna habitats are nitrogen cycling "hot spots" with the channel and intertidal areas less important. Webb and Eyre (2004) found that the presence of the burrowing marine yabbie (*Trypaea australiensis*) increased denitrification rates by 4 times over non-colonised sediments, and the role of seagrasses in nitrogen cycling is well documented (Blackburn et al., 1994, Kemp & Cornwell, 2001, Eyre & Ferguson, 2002, Ferguson et al., 2004). The relative role of subtidal shoals in ecosystem-wide nitrogen cycling is less well defined, and the importance of this habitat to in terms of this ecosystem process may not be missed using conventional environmental assessment techniques.



Figure 2 Gross primary production functional value for each estuary (A – southern Moreton Bay, B – Hastings River estuary, C – Camden Haven estuary and D – Wallis Lake estuary).



Figure 3 NPP functional value in each estuary (A – southern Moreton Bay, B – Hastings River estuary, C – Camden Haven estuary and D – Wallis Lake estuary).



Figure 4 Functional value maps of nitrogen cycling processes in southern Moreton Bay (A-Benthic DON Flux, B – Benthic DIN Flux, C – Denitrification and D – Denitrification Efficiency).

Overall Functional Value

The highest overall functional value was assigned to the stable seagrass community as it was assigned a high functional value for most ecosystem processes. Ephemeral seagrass communities where more important in nitrogen cycling processes however had lower benthic metabolism, and were therefore assigned the second overall highest functional. Sands and muds with burrowing macrofauna were assigned the third highest overall functional value due to its contribution to nitrogen cycling processes and benthic respiration. Subtidal shoals had similar contributions to metabolism as the ephemeral seagrass community but were less significant in system wide nitrogen cycling and were ranked fourth overall. Ranked fifth were the mangrove habitats, as they played a significant only in the southern Moreton Bay. Depositional mud basins were ranked sixth as they were of a medium significance for most processes in the Camden Haven estuary and had a medium functional value for benthic DON cycling and denitrification efficiency in southern Moreton Bay. Intertidal shoals were assigned a low to nil functional value for most processes and were ranked seventh. Channel habitats generally displayed a nil functional value for most processes across most systems and were hence ranked eighth. Figure 5 presents the overall functional value map for southern Moreton Bay.

Discussion

To our knowledge this study represents the first attempt to map functional values of ecosystem processes in aquatic ecosystems, and only one of two (see also Harbone et al., 2006) to quantify and map the overall functional value of benthic habitats in shallow water coastal ecosystems. The study by Harbone et al. (2006) was specific to Caribbean coral reefs, mangrove and seagrass habitats however the results from this study are broadly applicable to most coastal lagoons and estuaries. Variations on habitat classification, the way in which functional values are assigned and the types of ecosystem processes assessed would increase the specificity of the technique to a particular estuary or coastal lagoon.

Habitat Classification and Assigning Overall Functional Value

The habitat classification scheme used in this study was chosen due to the availability of data on both distribution of these habitat classes and ecosystem process measurements for each habitat (Eyre et al under review a; Eyre and Maher, in press). The habitat classes were similar to those of Harris and Heap (2003) in their geomorphic assessment of Australian coastal systems and thus broadly applicable to a wide range of shallow coastal systems. Additional habitat classes could be added if required, or the habitat classes used could be further divided. For example Eyre and Maher (in press) analysed the contribution of each individual seagrass species to total ecosystem production, however in this current study seagrass habitat was defined only as stable or ephemeral communities. Obviously habitat classification is linked to the scale at which benthic habitats are mapped.



Figure 5 Overall functional value map of southern Moreton Bay.

Whilst the functional value of the habitats for the various ecosystem processes presented in this study are broadly applicable across a range of systems some caution is required when applying these values to a particular estuary or lagoon. For example, in southern Moreton Bay, we assigned a high functional value to stable seagrass communities for denitrification (Figure 4). Whilst high rates of denitrification have been measured in tropical seagrass communities (Blackburn et al., 1994, Kemp and Cornwell, 2001, Ferguson et al., 2004), moderate denitrification rates have been found in warm temperate seagrass communities (Eyre and Ferguson, 2002) and low rates have been measured in temperate seagrass communities (Rysgaard et al., 1996, Risgaard-Petersen et al., 1998, Welsh et al. 2000). Similarly the relative aerial extent of each habitat class will vary in each ecosystem (for example mangrove coverage, Figure 1) thus likely changing the functional value. For example the functional value of mangroves for ecosystem GPP varied from high in southern Moreton Bay to nil in Wallis Lake, commensurate with coverage. Interestingly however the relative proportion of seagrass across the four study ecosystems varied widely (from 5% to 29%) yet the importance of this habitat for ecosystem wide metabolism was high for all four estuaries.

The weighting of each process was given equal value in determining the overall functional value of each habitat in this study, however this system could be modified depending on the management problem wanting to be addressed. For example if an ecosystem was impacted by nitrogen enrichment and subsequent eutrophication, a higher weighting may be attributed to denitrification and denitrification efficiency, or in the case of declining fish stocks a higher weighting may be given to NPP.

Application of the Functional Value Maps – A Case Study from southern Moreton Bay

The most apparent application of ecosystem function maps is to determine areas of high functional value for conservation purposes (Harbone et al., 2006). For example stable seagrass communities in each of the study areas had a high overall functional value and thus efforts should be made to ensure these habitats are conserved. More importantly, these maps can be used to highlight the importance of each habitat to individual ecosystem processes, something that can easily be overlooked utilising traditional environmental assessment methods. For example, the sand and muds with large burrowing macrofauna habitat in southern Moreton Bay were the second largest contributor to ecosystem respiration and the largest contributor to the system wide DIN flux, and were the second highest contributor to ecosystem-wide respiration (data not shown).

Another application for functional value maps is to use them to assess how an activity might impact upon an ecosystem by overlaying an impact map on the functional value map. To demonstrate this application a case study from southern Moreton Bay will be presented. In response to high population growth in the southern Moreton Bay region a major wastewater treatment facility is being built, which will discharge effluent in to the oligotrophic southern Moreton Bay. An intensive modelling exercise was carried out to determine the effect of different discharge options (quality and quantity of effluent) on the receiving waters (Szylkarski et al. 2005; SKM 2006). Among the parameters modelled was decrease in secchi depth (primarily associated with phytoplankton biomass increase linked to nutrient enrichment). Figure 6 displays the decrease in secchi depth associated with one of the discharge options (adapted from SKM, 2006). By comparing the areas of high

impact in Figure 6 to the overall functional value of the habitats in this area it can easily be shown that there will be some impact upon areas of medium overall functional value.



Figure 6 Impact map of decreased secchi depth from modelled wastewater discharge options in southern Moreton Bay (adapted from SKM, 2006).

When compared to the NPP functional value (Figure 3) it can also be seen that areas of high impact are also located in habitats of medium NPP functional value, indicating a potential loss of net production in southern Moreton Bay associated with this discharge option. This may in turn impact upon secondary production including recreational and commercially significant fish species. This case study gives one example of how ecosystem process functional value maps can be used to enhance current environmental assessment techniques. This environmental assessment technique also serves an important purpose as a conduit of information from scientists to managers, with the visual representation, and functional value classification scheme easily interpreted by people with no specific training in the complex field of coastal biogeochemistry.

References

Aswani S & Lauer M (2006) Benthic mapping using local aerial photo interpretation and resident taxa incventories for designing marine protected areas. *Environmental Conservation 33*, 263-273

Blackburn, T. H., Nedwell, D. B. & Wiebe, W. J. (1994). Active mineral cycling in a Jamaica seagrass sediment. *Marine Ecology Progress Series 110*, 233-239.

Blondel, P. (2002) Seabed classification at continental margins. In Wefer, G., Billet, D., Hebbeln, D., Jørgensen, B. B. & Van Weering, T. (Eds), *Ocean Margin Systems*. (pp. 125-141) Berlin: Springer

Blondel, P. & Murton B. J. (1997). *Handbook of Seafloor Sonar Imagery.*, Chichester U.K.: John Wiley and Sons

Cloern, J. E. (2007). Habitat connectivity and ecosystem productivity: Implications from a simple model. *American Naturalist*. *169*, E21-E33.

Eyre, B. D. & Ferguson, A. J. P. (2002). Comparison of carbon production and decomposition, benthic nutrient fluxes and denitrification in seagrass, phytoplankton, benthic microalgal and macroalgal dominated warm temperate Australian lagoons. *Marine Ecology Progress Series 229*, 43-59.

Eyre, B. D., Ferguson, A. J. P., Webb, A. & Maher, D. (Under review a.) Metabolism of different benthic habitats and their contribution to the carbon budget of a shallow oligotrophic sub-tropical coastal system (southern Moreton Bay, Australia). *Biogeochemistry*

Eyre, B. D., Ferguson, A. J. P., Webb, A. & Maher, D. (Under review b.) Denitrification, Nfixation and nitrogen and phosphorus fluxes in different benthic habitats and their contribution to the nitrogen and phosphorus budgets of a shallow oligotrophic sub-tropical coastal system (southern Moreton Bay, Australia). *Biogeochemistry*

Eyre, B. D. & Maher, D. (In press.) Structure and function of warm temperate east Australian coastal lagoons: implications for natural and anthropogenic change, In Kennish, M. & Paerl, H. (Eds.), *Coastal Lagoons: Systems of Natural and Anthropogenic Change*. CRC Press, pp. xx to xx.

Ferguson, A. J. P., Eyre, B. D. & Gay, J. (2004). Benthic nutrient fluxes in euphotic sediments along shallow sub-tropical estuaries, northern NSW, Australia. *Aquatic Microbial Ecology.* 37, 219-235.

Fish J. P. & Carr H. A. (2001). *Sound Reflections, Advanced Applications of Side Scan Sonar.* Orleans, MA.: Lower Cape Publishing,

Gazeau, F., Duarte, C. M., Gattuso, J.-P., Barron, C., Navarro, N., Ruiz, S., Prairie, Y. T., Calleja, M., Delille, B., Frankignoulle, M. & Borges, A. V. (2005). Whole-system metabolism and CO₂ fluxes in a Mediterranean Bay dominated by seagrass beds (Palma Bay, NW Mediterranean). *Biogeosciences 2* 43-60

Godet L, Fournier J, Toupoint N & Olivier F (2009) Mapping and monitoring intertidal benthic habitats: A review of techniques and a proposal for a new methodology for the European coasts. *Progress in Physical Geography 33*, 378-402

Harborne, A. R., Mumby, P. J., Micheli, F., Perry, C. T., Dahlgren, C. P., Holmes, K. E. & Brumbaugh, D. R. (2006). The functional value of Caribbean coral reef, seagrass and mangrove habitats to ecosystem processes. *Advances in Marine Biology. 50*, 57-189.

Harris, P. T. & Heap, A. D. (2003). Environmental management of clastic coastal depositional environments: inferences from an Australian geomorphic database. *Ocean and Coastal Management.* 46, 457-478.

Hosack, G. R., Dumbauld, B. R., Ruesink, J. L. & Armstrong, D. A. (2006). Habitat associations of estuarine species: Compositions of intertidal mudflat, seagrass (*Zostera marina*), and oyster (*Crassostrea gigas*) habitats. *Estuaries and Coasts 29*, 1150-1160

Kemp, W. M. & Cornwell, J. C. (2001). *Role of benthic communities in the cycling and balance of nitrogen in Florida Bay*. Final report to the US EPA, Region 4, Atlanta, GA. 53pp.

Kemp, W. M., Smith, E. M., Marvin-DiPasquale, M. & Boynton, W. R. (1997). Organic carbon balance and net ecosystem metabolism in Chesapeake Bay. *Marine Ecology Progress Series.* 150, 229-248.

Marcot, B. G., McConnaha, W. E., Whitney, P. H., O'Neil, T. A., Paquet, P. J., Mobrand, L., Blair, G. R. Lestelle, L. C., Malone, K. M. & Jenkins, K. I. (2002). *A multi-species framework approach for the Columbia River Basin: integrating fish, wildlife, and ecological functions.* Northwest Power Planning Council, Portland, Oregon.

Moncreiff, C. A., Sullivan, M. J. & Daehnick, A. E. (1992). Primary production dynamics in seagrass beds of Mississippi Sound: The contributions of seagrass, epiphytic algae, sand microflora, and phytoplankton. *Marine Ecology Progress Series 87*, 161-171.

Risgaard-Petersen, N., Dalsgaard, T., Rysgaard, S., Christensen, P. B., Borum, J., McGlathery, K. J. & Nielsen, L. P. (1998). Nitrogen balance of a temperate eelgrass *Zostera* marine bed. *Marine Ecology Progress Series* 174, 281-291.

Rysgaard, S., Risgaard-Petersen, N. & Sloth, N. P. (1996). Nitrification, denitrification and nitrate ammonification in sediments of two coastal lagoons in Southern France. *Hydrobiologia 329*, 133-141.

Santos, R., Silva, J. Alexandre, A. Navarro, N. Barron, C. & Duarte, C. M. (2004). Ecosystem metabolism and carbon fluxes of a tidally-dominated coastal lagoon. *Estuaries* 27, 977-985.

SKM. (2006). Pimpama River Estuary Ecological Study- Final report. SKM, Brisbane.

Szylkarski, S., Dorge, J. & Toomey, D. (2005). *Hydraulic and ecological modelling of the Pimpama River Estuary.* Proceedings of the Australian Water Association 05 Ozwater Conference, Brisbane, Australia.

Ward, T. J., Vanderklift, M. A., Nicholls, A. O. & Kenchington, R. A. (1999). Selecting marine reserves using habitats and species assemblages as surrogates for biological diversity. *Ecological Applications 9*, 691-698.

Welsh, D. T., Bartoli, M., Nizzoli, D., Castaldelli, G., Riou, S. A. & Viaroli, P. (2000). Denitrification, nitrogen fixation, community productivity and inorganic-N and oxygen fluxes in an intertidal *Zostera noltii* meadow. *Marine Ecology Progress Series 208*, 65-77.

Webb, A. P. & Eyre, B. D. (2004). Effect of natural populations of burrowing thalassinidean shrimp on sediment irrigation, benthic metabolism, nutrient fluxes and denitrification." *Marine Ecology Progress Series 268*, 205-220.