Interactions between ecosystem engineering by burrowing sandprawns (*Callichirus kraussi*) and nutrients: consequences for benthic community structure and ecosystem functioning

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Dissertation

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This PhD thesis demonstrates to me that through education poverty can be transmuted to success. As a black student from underprivileged rural community, achieving this work indicates to me that it is our choice to remain embraced by the shadow of poverty, otherwise, a choice to be formally educated is surely the key route to a more lucrative and civilized lifestyle. My best advice to anyone contemplating on embarking on a similar journey would be not to leave God behind, and to understand that challenges incurred in the process are an indelible price required to be paid in exchange for success.

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ABSTRACT

Non-trophic interactions are significant structuring agents of ecological communities. Knowledge of how this process drives ecosystem functioning and community structure either individually, or interactively with other processes, is however, limited, particularly in shallow soft- littoral ecosystems. At a local level, such systems are dominated by allogenic engineers such as the burrowing axiid sandprawn *Callichirus kraussi* Stebbing, which has important effects on macro- and meiobenthic assemblages. *C. kraussi* is distributed across the South African coastline, from the subtropical Mozambican border to the temperate west coast borders with Namibia. Bioturbation — the principal mechanism by which *C. kraussi* engineers influence associated biota in sedimentary systems, also has significant effects on sediment properties, biofilms, microalgal and microbial composition. However, theory suggests that ecosystem engineering effects are contextually dependent and contingent upon processes that are temporally and spatially variable.

In South Africa, variations in background nutrient levels across the coastline is significant, with the West coast being dominated strong upwelling, which increases biological productivity. Within the west coast, upwelling is also seasonally variable, being strongest in summer. In view of this natural variability in nutrient levels across the coast, seasonal variability within the west coast and the fact that the sandprawn *C. kraussi* dominates across these conditions, the central focus of this PhD thesis was to investigate how ecosystem engineering by sandprawns *C. kraussi* and nutrient levels individually or interactively influence assemblages and ecological processes in coastal soft-sediment ecosystems. The study was carried out in Langebaan Lagoon, which is a marine lagoonal system on the west

coast of South Africa that is dominated by sandprawns and subjected to seasonal upwelling that is a feature of the west coast.

This thesis was based on the two principal approaches, viz. a field comparative study and *in situ* experiments. The field observational study investigated the responses of macro- and meiofaunal communities to sandprawn bioturbation impacts between upwelling and non-upwelling seasons, with the aim of understanding how upwelling nutrient pulses modify these benthic assemblages. Benthic and water column chlorophyll-*a* (chl-*a*) levels were also measured, while meiofaunal communities were investigated within sandprawn burrows (burrow-walls) and at the sediment surface. It was hypothesized that chl-*a* levels, and community metrics would be lower in winter (non-upwelling) but increase in summer upwelling season due to nutrient pulses. It was also hypothesized that community metrics would be negatively correlated with sandprawn density due to bioturbatory effects (sediment turnover) in winter (non-upwelling) but this relationship would become neutral or positive increased in summer, due to increased productivity offsetting negative bioturbative effects.

Clear, non-intuitive and ecologically interesting outcomes emerged from the field study. Firstly, benthic chl-*a* concentrations appeared to be lower in summer relative to winter in 2015, although, this pattern disappeared in 2016. In contrast, water column chl-*a* concentrations within the lagoon channel conformed to the posed hypothesis, being consistently greater in summer relative to winter. Even though both macro- and meiofaunal assemblages differed significantly between seasons, the hypothesis that community metrics would be greater in summer relative to winter season was not overwhelmingly supported by these findings. Pearson correlation analyses revealed that sandprawn effects were generally weaker within seasons but stronger when winter and summer data were combined and investigated per year. In terms of the latter, most community metrics and benthic chl-*a* levels were generally negatively correlated with sandprawn abundances, but this varied seasonally and spatially. Overall, results of the comparative study suggest that increases in water column chl-*a* levels do not necessarily translate into increases in benthic chl-*a* and community metric levels. One possible reason for this is that increasing bioturbation by *C. kraussi* overrides nutrient enrichment effects. This conclusion though is spatially dependent, given that results of correlation analyses were site-specific.

The factorial field experiment employed in this dissertation manipulated nutrients (fertilizer capsules, Plantacote N: P: K) and sandprawns (*C. kraussi* densities) to investigate their individual and interactive effects on benthic assemblages. I hypothesized within the context of the grazer-reversal hypothesis of Proulx and Mazumder (1998) that, responses of diversity metrics should alter from a linear decrease at the ambient nutrient level to a unimodal hump-shaped response at the intermediate nutrient level and then to a linear increase at highest nutrients. Generally, emerging patterns for meiofaunal diversity metrics and individual morphotypes were inconsistent with the prediction of the grazer-reversal model. Instead, responses were of an increasing and decreasing nature. The outcomes of this investigation, however, revealed that meiofaunal community structure at the sediment surface was significantly affected by the main effect of sites and sandprawn densities, while within burrow-walls, the interaction between sites and nutrients, but also sandprawn densities alone, significantly affected meiofaunal community structure. Overall, meiofaunal results of this investigation showed limited support for the grazer-reversal hypothesis.

Although the findings of this investigation also indicated limited support for the grazer-reversal hypothesis on the macrofauna community, interactive effects of nutrient enrichment and sandprawn densities emerged to influence the macrofaunal community structure and abundances of certain individual species/taxa. Generally, macrofaunal

community metrics exhibited both increasing and decreasing patterns in response to experimental treatments, however, in some instances unimodal hump-shaped patterns emerged. There was evidence of macrofaunal functional groups (i.e. suspension feeders) conforming to the hypothesis posed, but this was site-specific. Overall, I conclude that an interplay between nutrients and sandprawns does not exert strong influences on the benthic communities of Langebaan Lagoon. However, sandprawn ecosystem engineering, mainly in the form of bioturbation overrides nutrient enrichment effects in regulating benthic assemblages.

CHAPTER 1

INTRODUCTION AND LITERATURE REVIEW

1.1 The ecosystem engineering concept

Understanding biodiversity and community structure and factors that influence them over space and time has been a central subject in ecological research. In this regard, organismal interactions have received major interest (Sueiro *et al.* 2013, Bouma *et al.* 2009, Connell and Orias 1964, Jones *et al.* 1994, Tilman *et al.* 1997, Hastings *et al*. 2007). Research has shown the importance of both trophic and non-trophic interactions in driving biodiversity and community patterns, through intricate direct or indirect networks (Cardinale *et al.* 2002, Goudard and Loreua 2012). Trophic interactions typically involve consumptive interactions, such as predation and grazing, while non-trophic interactions do not involve consumption.

Of the non-trophic interactions, Jones *et al.* (1994) have highlighted the importance of species in creating, altering and maintaining habitats. These processes are broadly referred to as ecosystem engineering. More specifically, this term describes the activities or structures created by organisms (engineers) that indirectly modulate the availability of resources for other species. Two broad classes of ecosystem engineers have been identified by Jones *et al.* (1994), i.e. allogenic and autogenic engineers. Allogenic engineers alter ecosystems by changing living and non-living materials from one physical state to another via mechanical means. A classic example of an allogenically engineered structure is a dam constructed by beavers (Jones *et al.* 1994, Wright *et al.* 2003, Crain and Bertness 2006). In this case, beavers utilize wood to build dams and in so doing create wetlands and ponds that may remain in the ecosystem for several years. These wetlands and ponds significantly alter ecological processes in surrounding environments, resulting in changes to local hydrology, sedimentology and organic matter cycling, nutrient fluxes and decomposition dynamics. These alterations can exert considerable impacts on plant and animal communities and hence overall biodiversity (Jones *et al.* 1994). Apart from beavers, other examples of allogenic engineers with significant impacts on environments include prairie dogs (*Cynomys* spp) and elephants (*Loxodonta africana).* Prairie dogs are known to disturb soil surfaces by creating surface sand mounds through extensive digging of burrows (Van Nimwegen *et al.* 2008). The presence of the forest elephant *(L. africana)* in tropical regions can potentially transform forested areas to grassland ecosystems by trampling of vegetation (Dublin *et al.* 1990, Ruggiero and Fay 1994).

Autogenic engineers modify their environments because of the presence of their own physical structures such as living and dead tissues (Jones *et al.* 1994). Typical examples of autogenic engineers are trees, coral reefs and microbial biofilms (Jones *et al.* 1994, 2010). Trees modify hydrology, soil stability, nutrient cycle, wind speed and temperature (Jones *et al.* 1994), while corals provide important habitats for associated organisms, and also transform organic and inorganic materials (Wild *et al*. 2011). Cordgrass is known to facilitate some benthic species by stabilizing sediment through rooting structures (Altieri *et al.* 2007). Most autogenic engineers are generally sedentary, but some are mobile (e.g. the shells of live crabs which provide epibiont living space).

1.2 Development and controversies regarding the concept of ecosystem engineering

Impacts of organisms on physical and chemical processes in the environment had long been recognized before the concept of ecosystem engineering was introduced. For example, Darwin (1881) published a book focusing on the effects of earthworms on soil formation, while other studies provided further details and examples of organisms with major impacts on ecosystem properties (Naiman *et al.* 1988, Thayer 1979, Dayton 1972). However, an integrative understanding of how organisms structure biotic assemblages through habitat modification only emerged when the refined concept of ecosystem engineering was introduced by Jones *et al.* (1994). The concept gained its strength through substantial models, illustrative examples and postulations. Within its first year of inception, it was cited more than 470 times in the peer-reviewed literature. However, the concept generated significant controversy as well (Wright and Jones 2006).

One of the major criticisms of the concept of ecosystem engineering was that it would simply lead to more "buzzwords" in ecology, of which there are many (Jones *et al.* 1997b, Power 1997a, 1997b). Some authors have also raised concerns about the resemblance of the ecosystem engineering concept to the "keystone species" concept. Significant effort in the form of discussions and seminars has been dedicated to clarifying these two ecological terminologies (Wright and Jones 2006). Keystone species are defined by their effects on associated biota, which are mainly derived from trophic interactions (Van Nimwegen *et al.* 2008). Keystone species (e.g. top predators) influence food web structure through top-down control; their suppression or removal in the ecosystems can therefore result in significant alterations to food-web structure, species composition and nutrient cycling (Jones *et al.* 1994). On the other hand, ecosystem engineers regulate communities by modifying environmental states. A recent definition of keystone species emphasizes that species should have disproportionate effects relative to their abundance or biomass (Power *et al.* 1996). This definition also qualifies many engineering species with large community effects relative to their biomass to be regarded as keystone species (Wright and Jones 2006). Therefore, keystone species may exert effects on communities and ecosystems either by consumption or as a result of ecosystem engineering (Jones *et al.* 1994, 1997a, Wright and Jones 2006).

1.3 Ecosystem engineering in intertidal soft-sediment habitats

Soft-sediment, the unconsolidated substrate that ranges in size from silt to pebbles (0.0039 mm – 64 mm), is one of the largest ecosystems on earth (Snelgrove 1999). It is a key component of coastal (e.g estuaries, beaches and bays) and offshore habitats (continental shelf, slope and deep sea). These ecosystems not only provide living space for organisms, but support organisms through a variety of key ecological functions such as food provision to higher trophic levels (Hines *et al.* 1990), maintenance of nutrient and organic matter fluxes (Raffaelli *et al.* 2003), and sustaining important connections between benthic and pelagic processes (Lohrer *et al.* 2004a, 2004b).

In marine coastal sedimentary ecosystems, ecosystem engineering by allogenic and autogenic engineers are amongst the most influential of processes influencing ecosystem functioning. Generally, soft-sediment habitats are three-dimensional spaces, which allows organisms to partition the habitat both vertically and horizontally (Wilson 1991, Little 2000). Soft-sediment engineers are therefore classified into two broad divisions depending on where they live (Bouma *et al.* 2009). Epibenthic ecosystem engineers inhabit the sediment surface and typically impact environments through their own physical structures (autogenic engineers). Commonly reported impacts of epibenthic ecosystem engineers include alterations of local sediment dynamics, particle trapping, increased accretion of sediment and attenuation of hydrodynamic energy from current and waves (Fonseca and Fisher 1986, Gambi *et al.* 1990, Gacia *et al.* 1999, Bouma *et al.* 2005). The most widely distributed examples of epibentic engineers in temperate ecosystems are seagrasses, salt marsh species and certain taxa of macroalgae (Bouma *et al.* 2009).

Endobenthic invertebrates are mostly allogenic engineers inhabiting deeper sections of sediments, with some species being able to burrow to depths greater than 1 m, such as burrowing axiid sandprawns and/or ghost shrimps (Branch and Pringle 1987, Pillay and Branch 2011). They modify sediment resources mainly via bioturbation (Biles *et al.* 2002, Meysman *et al.* 2006, Bouma *et al.* 2009), which is defined as the process by which animals directly or indirectly affect sediment matrices through both particle reworking and burrow ventilation (Kristensen *et al.* 2012). Both of these processes can shape environments and significantly influence soft-sediment ecosystem functioning. For example, ecosystem engineering by burrowing lugworms (Arenicola marina) has been reported to reduce sediment chlorophyll content and concentrations of ammonium, phosphate, silicate, and sulphide relative to patches without lugworms, due to sub-surface irrigation and burrowing activity (Volkenborn *et al.* 2007a). Changes in habitat properties created by lugworms have also been reported to cause functional shifts in benthic community structure from assemblages dominated by mixed suspension- and surface-deposit feeding tube worms to subsurface deposit-feeding motile worms (Volkenborn *et al.* 2007a).

The role of ecosystem enginnering by shrimp has not only been investigated in marine but also in freshwater ecosystems. For example, in Peurto Rico, Crowl *et al.* (2001) manipulated the presence/absence of shrimp species (*Atya lanipes* and *Xiphocaris elongata*) in six fenced pools of a headwater stream and reported that both shrimp species alter nutrient composition and influence detrital processing in different ways. Yee *et al.* (2005) illustrated through laboratory macrocosms that tadpole shrimp can act as important determinants of macroinvertebrate communities in Playa Lake through both direct and indirect effects. Direct effects of tadpole shrimp include the removal of prey species abundance, which in turn may alter biotic interactions among other taxa, while indirect effects include physical alteration of the environment during foraging through surface sediments. Ghost shrimps species are known to exert negative influences on seagrass plants, seeds and/or seedlings through sediment disturbance (Suchanek 1983, Duarte *et al.* 1997, Dumbauld and Wyllie-Echeverria 2003). Indirect adverse effects of ghost shrimp bioturbation might be linked to the impairment of photosynthetic processes due to increased sedimentation and resuspension of fine particles reducing available sunlight and smothering of plants (Suchanek 1983).

Other examples of endobenthic engineers with considerable impacts in soft-sediment communities are mangrove sesarmid (Grapsidae) and fiddler (Ocypodidae) crabs (Smith *et al.* 1991, Stieglitz *et al.* 2000, Thongtham and Kristensen 2003, Kristensen 2008). These mangrove crabs create and maintain their burrows for various purposes (Skov and Hartnoll 2002, Micheli 1993). Burrows provide an important facilitatory role for other species in providing refuges from predation, increasing availability of trophic resources and protection from adverse abiotic conditions (Warren 1990, Kristensen 2008, Thongtham and Kristensen 2003). Burrows created by crabs modify biogeochemistry, transport conditions and physical structures, thereby altering the availability of important resources for communities (Stieglitz *et al.* 2000, Kristensen 2008).

Burrowing engineer impacts on soft-sediment ecosystems differ substantially, and are largely dependent on habitat features and those of the engineering species. In terms of the latter, burrow morphology, sediment type (Volkenborn *et al.* 2012) and the behavior of the burrowing species (Biles *et al.* 2002) have been shown to be highly influential. Blind-ending and poorly lined burrows like those created by arenicolid polychaetes are characterized by ventilation which increases advective flow of water (Volkenborn *et al.* 2012). Burrow flushing and ventilation can generate intense pore-water movements depending on (1) burrow morphology (one or more than one opening) and (2) sediment permeability and cohesiveness. However, in muddy areas, pore-water advection is low, resulting in high resistance to flow within burrows. This is usually observed in a situation where more than two burrow openings are formed (Kristensen *et al.* 2012, Mermillod-Blondin and Rosenberg 2006).

Burrow structures also provide important functions for the infauna. Generally, burrows are enriched by organic matter (Volkenborn and Reise 2006), derived from phytoplankton, microphytobenthos and detritus (Papaspyrou *et al.* 2005). In addition, several microhabitats for microbes and meiofauna may occur in a single burrow, due to niche diversity. For example, sesarmid crab burrows vary from basic to complex morphologies. Conspicuous features of these burrows include vertical shafts (5 to 25 cm long) with various connecting branches that provide living spaces for the associated crustacean fauna. These branches also have their own surface openings which enable increased exchange rates of fluxes of organic matter, nutrients and gases between the sediment and overlying water column. The most prominent factors that determine the quality of services provided by burrows include age and type of burrow, sediment characteristics and associated faunal abundance.

Generally, the burrowing activities of axiidean crustaceans can alter important ecosystem features and functions such as community structure (Dittmann 1996, Berkenbusch *et al.* 2000, Berkenbusch and Rowden 2003, Berkenbusch and Rowden 2007, Berkenbusch *et al.* 2007, Pillay *et al.* 2007b, Siebert and Branch 2007, Henninger and Froneman 2013), biogeochemical cycling, nutrient and gaseous exchange (Branch and Pringle 1987, Rowden and Jones 1993, Hughes *et al.* 2000, Webb and Eyre 2004) and physical properties of sediments (Suchanek and Colin 1986). Axiid prawns can positively influence bacteria and benthic microalgae, particularly within their burrow walls and exert negative effects on macro- and meiofaunal communities (Branch and Pringle 1987, Pillay and Branch 2011, Henninger and Froneman 2013). Bacterial densities have been shown to be enhanced between 30 to 100% by axiid prawns along the burrow-walls (Branch and Pringle 1987). In contrast, some studies have documented a reduction in bacteria and microalgae in the presence of axiid prawns particularly at the surface sediment (Pillay *et al.* 2007b, Pillay and Branch 2011, Henninger and Froneman 2013). Pillay *et al.* (2007b) illustrated that carbohydrate exuded by microalgae and bacteria on the sediment surface is lower in areas where axiid prawns are absent or less dominant. Studies have consistently reported negative influence of axiid prawns on particular faunal functional groups that are most vulnerable to environmental changes created by axiids. As illustrated by Pillay *et al.* (2007b), in Durban Bay lower abundance of surface feeders were found to be associated with the presence of sandprawns at high densities. A recent study of axiid prawns as ecosystem engineers undertaken in a South African temporarily open/closed estuary has also reported high abundances of surface feeders in the absence of sandprawns (Henninger and Froneman 2013).

1.4 The burrowing sandprawn *Callichirus kraussi*: the focal organism of this study

Callichirus kraussi (**Fig.1.1**) is a conspicuous macrofaunal species and a permanent member of benthic ecosystems in South Africa (Siebert and Branch 2005a, Siebert and Branch 2005b). In general, axiid crustaceans (including the *C. kraussi* species) are distributed worldwide from cold temperate climates to tropical environments but excluding polar regions north of 70°N and south of 55°S (Dworschak 2004). They inhabit intertidal sand flats and estuaries (either temporarily open/close or permanently open systems) and sheltered marine environments (Whitfield 1992). In southern Africa, the distribution of *C. kraussi* ranges from

Namibia on the west coast, up to Mozambique on the east coast (Day 1981, Branch *et al.* 2010; **Fig 1.2**), with densities of up to 602 ind.m^{-2} in certain locations (**Table. 1.1**).

Fig.1.1: Lateral view of male (**A**) and female (**B**) burrowing sandprawns *(Callichirus kraussi*).

Table.1.1: Abundances of the sandprawn (*Callichirus kraussi*) reported in selected shallow water coastal environments and estuaries along the southern African coastline.

Location	Sandprawns abundance (ind. m^{-2})	Source
Langebaan Lagoon, Western Cape	190-330	Nel and Brach 2013
Durban Bay, KwaZulu-Natal	0-264	Pillay *et al*. 2007
Langebaan Lagoon, Western Cape	2-602	Nel 2006
Swartkops Estuary, Eastern Cape	>400	Hanekom 1980
Great Brak Estuary, Western Cape	22-419	DWAF 2001

Unlike estuarine dependent or migratory species, sandprawns in South Africa (*C. kraussi*) are able to complete their entire lifecycle within an estuary. Their life cycles consist of a short larval life cycle that has no planktonic stages (Forbes 1973b). At high salinity (> 20 PSU), larvae are retained within burrows until hatched (Forbes 1978), while adult *C. kraussi* are capable of withstanding salinity values as low as 1 PSU.

Generally, *C. kraussi* has two breeding seasons viz. in winter and summer. A peak of breeding occurs in winter, between May and August, followed by November and December in summer, which is regarded as a minor breeding period. The overall life span of sandprawns is roughly two years. Breeding usually occurs between the age of 16 and 19 months when adults reach a carapace length of 8mm. However, males have a different growth phase to females as they attain a carapace length of 8-9 mm in their first year of living and 11-13 mm by the time they reach 18 months (Forbes 1977b).

Sandprawns are influential bioturbators in soft-sediment ecosystems in South Africa (Pillay *et al.* 2007b). They occur in very high densities (**Table 1.1**) and occupy beds that can extend several kilometers in length (Pillay and Branch 2011). Through their burrowing activities, they produce sand mounds on the sediment surface at very high rates (Siebert and

Branch 2005a), ranking them amongst the most prominent bioturbating species in aquatic soft-bottom ecosystems (Pillay *et al.* 2007b). Both the vertical and horizontal mixing of sediment are important mechanisms by which sandprawns, like other axiid prawns structure soft-sediment communities (Van Nes *et al.* 2007a, Pillay *et al.* 2007b). These activities can modify sedimentary environments and thus modulate resource availability for other benthic species. By the original definition of ecosystem engineering (Jones *et al.* 1994), such activities qualify axiid prawns to be regarded as ecosystem engineers (Siebert and Branch 2006, Pillay and Branch 2011).

Many processes have been suggested to account for the reduction in the abundances of surface feeders due to the presence of axiid prawns (Pillay *et al.* 2007b, Henninger and Froneman 2013). These include low food availability on surface sediment due to burial by ejected sediment, burial of surface feeders through sediment expulsion and elevated sediment erodibility (Amaro *et al.* 2007, Henninger and Froneman 2013).

Worldwide, axiid crustaceans have a high important economic value, mainly due to their use for baiting by fishermen (Wynberg and Branch 1994, 1997, Abrunhosa *et al.* 2008, Nel and Branch 2013). In Langebaan Lagoon where this study was undertaken, collection of sandprawns is regulated and prohibited in certain areas of the lagoon. Their harvesting, however, still is a major concern given the integral ecological role sandprawns play in the ecosystem (Nel and Branch 2013).

1.5 Ecosystem engineering and contextual dependencies

Previous studies have highlighted the need to understand the environmental contexts which determine community responses to ecosystem engineering (Hastings *et al.* 2007, Badano *et al.* 2010), particularly the role of spatial and temporal processes. Both factors are integral determinants of ecosystem dynamics and are likely to be the most influential broad-scale factors responsible for determining community responses to ecosystem engineers. For example, it has been indicated that for many ecosystem engineers, their effects on biodiversity are contingent on spatial scale (Crooks 2001, Crooks and Khim 1999, Bouma *et al.* 2009).

In terms of aquatic soft-bottom ecosystems, one of the most influential contextual dependencies likely to influence responses to ecosystem engineering is spatio-temporal variability in productivity and nutrient levels (Pillay 2019). This is of particular importance in the South African context from two perspectives. Firstly, along the South African coastline, productivity varies between the warm Aghulas and cold Benguela current (**Fig.1. 2**). The Algulhas current located along the Indian Ocean side (east and south coasts) is strongly influenced by warm, fast flowing current (2 ms^{-1}), with temperatures ranging between 16 to 22 °C (Lutjeharms *et al.* 1996). Generally, this is a well-defined western boundary current arising from the Mozambique Channel. The Algulhas current flows very close to the shelf edge of South Africa, and as a result of the Mozambique eddy, a single meander referred to as Natal pulse occurs in this current (Schouten *et al.* 2002). Primary productivity is moderately enhanced on the Algulhas current particularly where the current passes from a narrow to a wider shelf (Lutjeharms *et al.* 1996**,** 2000, Meyer 2002).

On the other hand, the Western Coast is distinctive, being dominated by the cold and productive Benguela upwelling system with temperatures ranging between 8 to 17 °C (Branch and Branch 1981). This current is characterized by high primary and secondary production. The outer shelf of this current is largely influenced by cool and moderately slow north-ward flowing water (0.25-0.50 m $^{s-1}$). Langebaan Lagoon, which is the focal system in this PhD study, is located on the west coast of South Africa, in the Benguela current - one of the four major upwelling systems in the world (Blanchette *et al.* 2009). Upwelling systems are regions of high biological productivity fuelled by coastal, wind-driven upwelling of cold, nutrient-rich subsurface waters (Brown 1992, Blanchette *et al.* 2009). Along the west coast of South Africa, dynamic upwelling occurs in summer (Blanchette *et al.* 2009, Bustamante *et al.* 1995). During this period, ecological functioning in coastal ecosystems is influenced by offshore upwelling (Bustamante *et al.* 1995).

As previous studies have indicated, increased nutrient levels can modify community patterns (Kondoh 2001, Posey *et al.* 1999), increase microalgal biomass (Pitta *et al.* 1998), enhance growth rates and abundances of certain macrofaunal species (Posey *et al.* 1999, Wolfrath 1992), and enhance trophic resource availability on surface sediments (Posey *et al.* 1999). However, nutrients can also alter ecological processes by modifying the outcome of biotic interactions (Posey *et al.* 1999, 2002, 2006), though little is known on the topic.

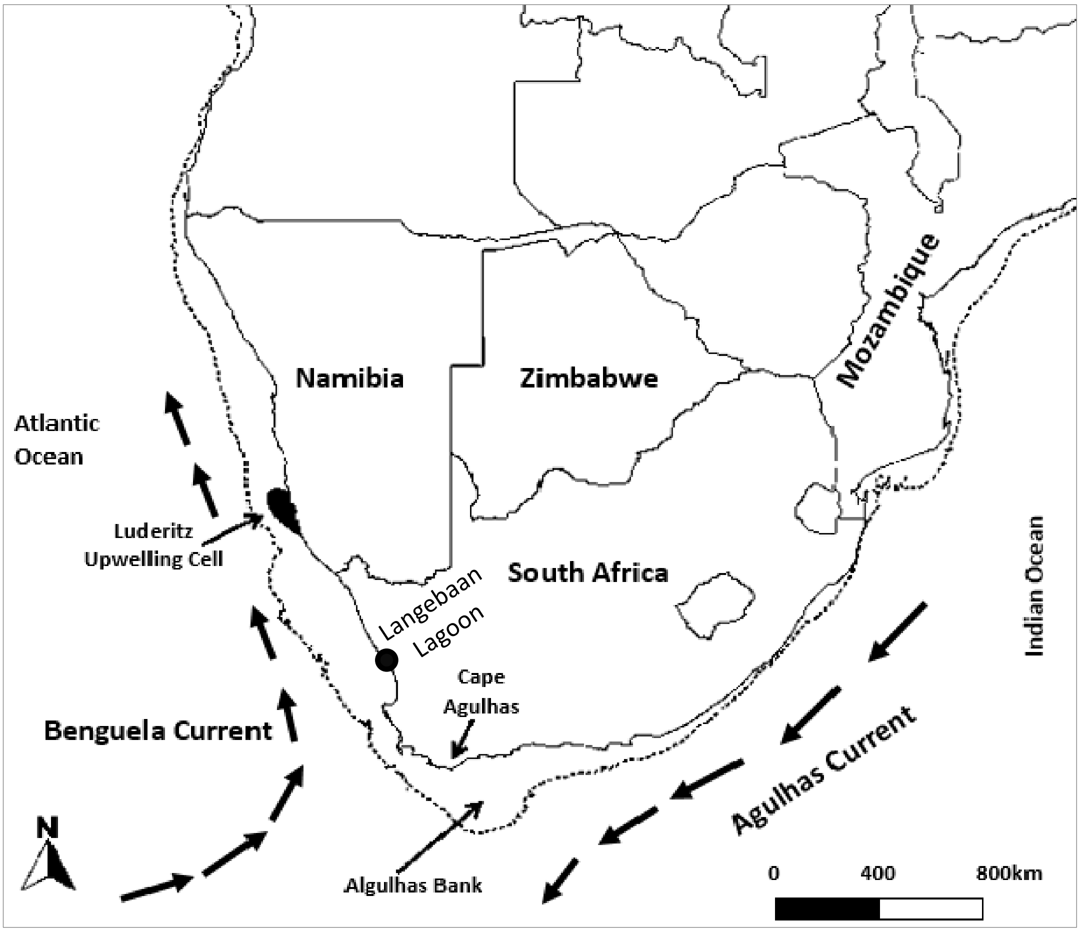

Fig.1. 2: Map of Southern Africa displaying two major currents along the South African coast line. i.e., the Agulhas Current in the Indian Ocean and the Benguela Current along the Atlantic Ocean. The latter system is characterized by summer upwelling. The axiid sandprawn *Callichirus kraussi* is distributed along the South African coastline, from Mozambique on the east coast to Namibia on the west coast.

1.6 Objectives and outline of this dissertation

This study broadly aims to determine if ecosystem engineering by burrowing sandprawns (*Callichirus kraussi*) interacts with productivity to influence benthic community structure. Although these ecological processes are well-recognized individually, little information exists currently on their interactive role in structuring soft-sediment ecosystems both at a local or global level. Based on ecological theories and models such as Huston's Dynamic Equilibrium Model (DEM; Huston 1979, 1994) and grazer-reversal hypothesis (Proulx and Mazumder 1998) that make predictions about the relationship between disturbance and species richness at different productivity levels, it is expected that sandprawns (proxy for disturbance) and nutrients (proxy for productivity) in this study will interact to structure benthic communities of Langebaan Lagoon. These models are discussed in detail in chapter 5 of this thesis. Generally, these models predict that disturbance-diversity relationships should change from a linear decrease at ambient levels of nutrients to unimodal hump-shaped at the intermediate nutrient levels and then to a linear increase at the highest nutrient level. Sandflats of Langebaan Lagoon are expose to both the influence of upwelling and sediment turnover (bioturbation) by burrowing sandprawns. For this reason, community responses to bioturbation impacts of sandprawns should be influenced by the availability of nutrients, which is derived from upwelling on the west coast.

Following this introduction and literature review chapter, chapter two describes the methods and materials on which this thesis is based. Two distinct approaches were undertaken to meet the objectives of this study. The first approach entailed field surveys aimed at understanding the effects on summer upwelling on benthic assemblages in sandprawn-sandflats in Langebaan Lagoon. A secondary objective was to determine whether the strength of ecosystem engineering by sandprawns on intertidal soft-sediment communities was altered by upwelling. The results of this component are covered in chapters three and four. The second approach used in this thesis was a factorial experiment conducted *in situ* in Langebaan Lagoon that examined the effects of ecosystem engineering by sandprawns and nutrient enrichment on benthic assemblages. The experiment was designed to test for the main and interactive effects of both nutrient enrichment and sandprawn densities on communities. Chapters five and six report the results of this investigation. Chapter seven concludes the thesis by providing a synthesis of major findings emerging from the thesis. Chapter 8 presents the references used in this thesis, while chapter 9 is an appendix. The general structure of this thesis is presented in Fig. 1.3.

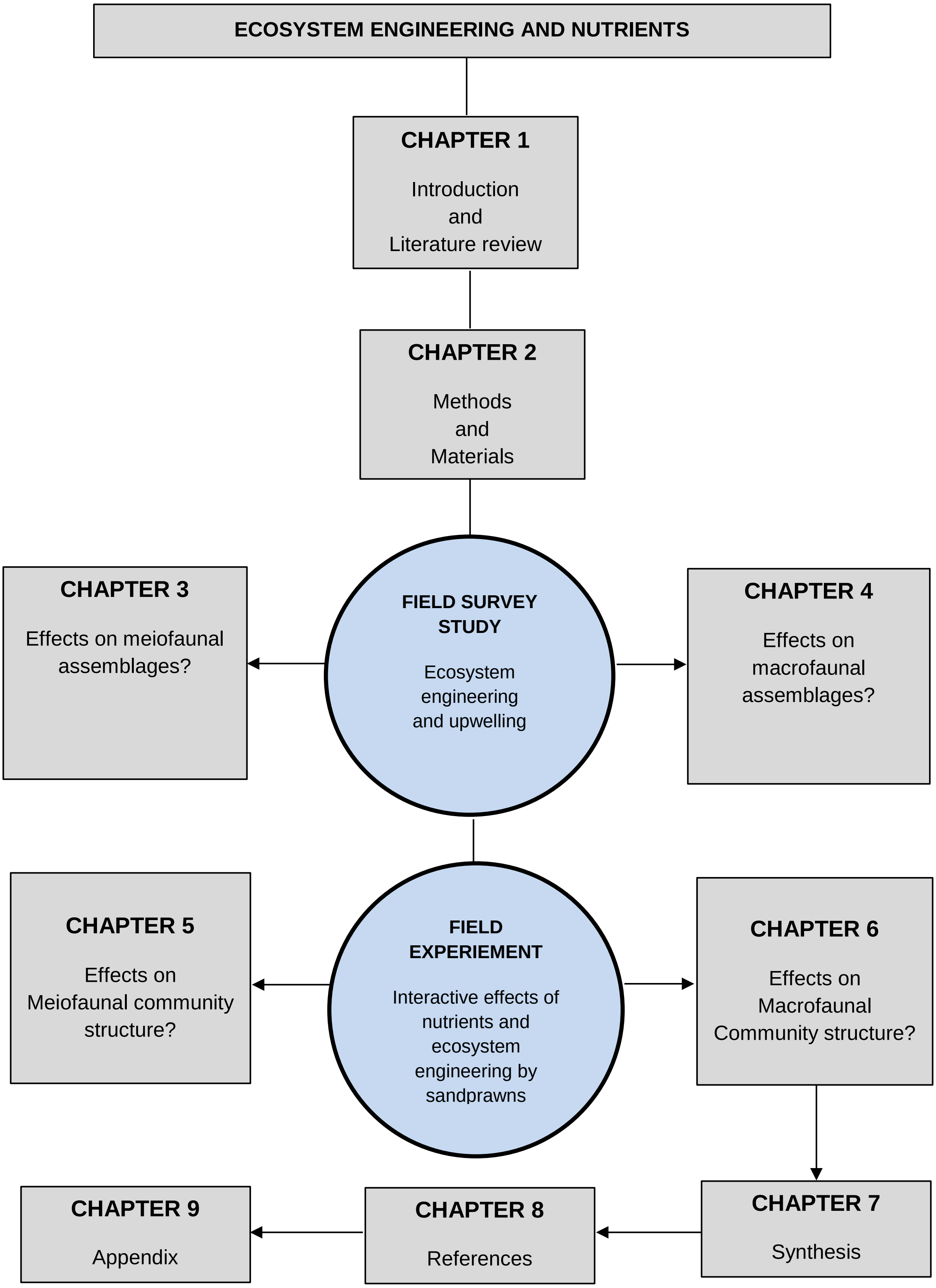

Fig. 1.3: General structure of thesis illustrating chapter contents in relation to the central objectives.

CHAPTER 2

METHODS AND MATERIALS

2.1 Study site

This PhD study was based on field work and *in situ* experiments conducted in Langebaan Lagoon, which forms part of a National Park on the West Coast of South Africa (**Fig.2.1**: 33° 11’ 27’’ S; 180 07’ 37’’E). Langebaan Lagoon is approximately 15 km in length and is divided into three management sections: (Zone A) a multipurpose recreational area, which permits access and resource exploitation (bait collecting) by the public, (Zone B) a restricted recreational area with public access but where no harvesting is allowed, and (Zone C) a sanctuary area in which no access is permitted (Wynberg and Branch 1997). The sanctuary area is however accessible for activities related to scientific research. These major zones were demarcated by the park management to reduce anthropogenic impacts on the system. Such impacts include disturbance and removal of ecologically important species like sandprawns, which are commonly collected for bait by the local fishermen (Nel and Branch 2013).

Langebaan Lagoon is distinctive from most lagoons that have been created as a result of river flow into the sea. Langebaan was formed over millions of years through massive fluctuations in sea level and is thus, permanently connected to the sea (Shaefer and Shaefer 1993). It is influenced strongly by marine tidal regimes that transport waters from the Atlantic Ocean into the system. Fringing salt marshes and seagrass beds are likely to be an important source of primary production in the lagoon, however, a large fraction of nutrients in the system are derived from summer upwelling events prevalent on the west coast (Wynberg and Branch 1994). Because of the prominence of seasonal upwelling, Langebaan Langoon was an ideal location to test the hypotheses of this study. Comparisons between the east and west coasts would have been unsuitable to test the hypothesis posed in this study mainly because temperature varies between these coasts and would likely (1) confound nutrient effects and

(2) significantly influence the burrowing activities of sandprawns, as shown by studies elsewhere (White *et al.* 1987, Berkenbusch and Rowden 1999, Rowden *et al.* 1998, Canal *et al.* 2015, Stanzel and Finelli 2004, Pillay 2019).

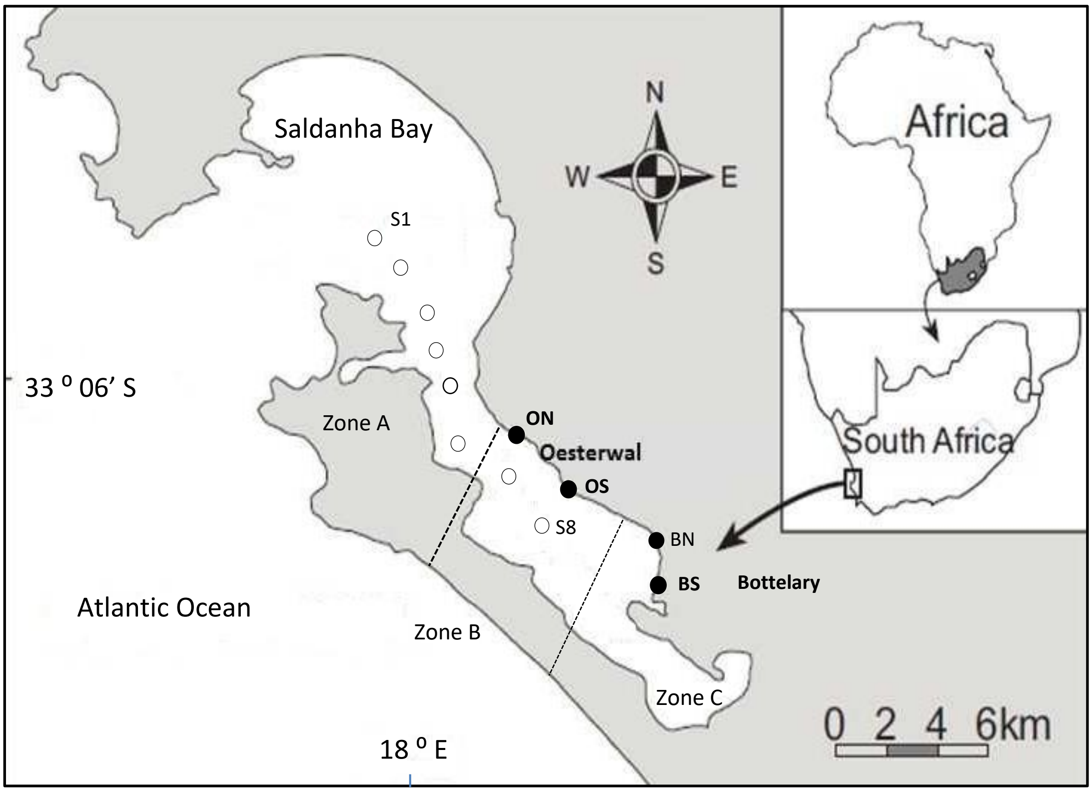

Fig. 2.1: Map of Langebaan Lagoon showing the positions of study sites for the field survey (Oesterwal North and South [ON & OS]) and *in situ* experiment (Bottelary North and South [BN & BS]). NB: white circles indicate sampling stations (S1to S8) for water column chlorophyll-*a* concentrations within the lagoon.

2.2 Field Survey

As indicated in Chapter 1, this thesis is built upon *in situ* surveys and experiments, which will be described in detail here. Field surveys, which form the basis of Chapters 3 and 4, were conducted in a mid-shore position in the lagoon, over two winter (down-welling periods) and two summer (up-welling) seasons between 2015 and 2016. Biological community and abiotic data were collected and analysed to quantify the role of upwelling on meio- and macrofaunal communities in sandprawn dominated sandflats. Two sampling sites, each with three sub-sites as replicates, were selected for the purposes of the study: Oesterwal North (ON; sub-sites ON1, ON2 and ON3) and Oesterwal south (OS; sub-sites: OS1, OS2, and OS3) (**Fig. 2.1**, **Fig. 2.2**). These sites were roughly 0.5 km apart with sub-sites being separated by a distance of roughly 50 - 100m. These sampling sites were chosen on the basis that they were relatively undisturbed by human activity.

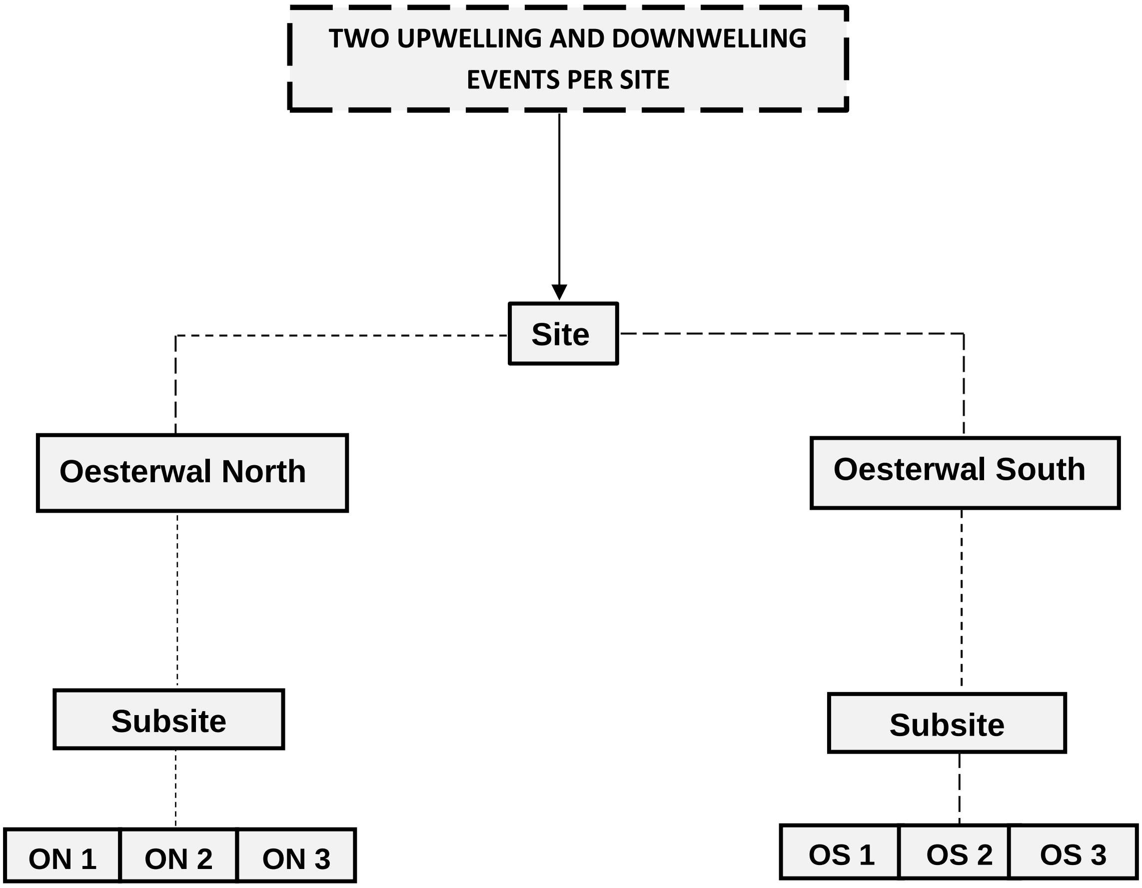

Fig. 2. 2: Overview of study design for field surveys on which chapters 3 and 4 were based. Data were collected over 2 up-welling (summer) and 2 down-welling (winter) periods in accordance with this design.

2.3 Sample collection

2.3.1 Water column chlorophyll-a (chl-*a*)

Water column chl-*a* biomass was measured (depth = 0.7 m) using a Conductivity-Temperature-Depth Profiler (CTD; YSI 6600 Multi-parameter probe) at eight stations along the main channel of the lagoon from the mouth to Oesterwal (**Fig 2.1**). Chl-*a* was measured as LED incident light (Marcelli *et al.* 2014). Of the stations in Chl-*a* was measured, stations 6 to 8 were in the vicinity of areas where community and other environmental data were collected, as indicated in **Figs 2.1 - 2.2**. *In situ* surface chl-*a* biomass was measured once every spring tide during a three month period in summer and winter seasons. Water column chl-*a* biomass was collected to (a) quantify seasonal differences in upwelling intensity among seasons and to relate this to benthic community dynamics and (b) identify spatial gradients in water column chl-*a* biomass from the mouth of the lagoon to the location of the field survey study sites.

Dissolved inorganic nutrient concentrations were measured in pore-water samples (10 cm sediment depth) using a plastic syringes (50ml) fitted with a fine mesh (63µm) over the extraction opening. A single pore-water sample was collected from each sub-site and was immediately filtered (0.45 µm Whatman GF/F) to remove particulates and then stored in a freezer at – 6 °C before the analysis in the lab which took about a month. Using a flow injection auto-analyzer (QuickChem. FIA+8000 series auto-analyzer) and by following a guide for brackish and seawater provided by Lachat instruments, silicate (SiO_4), phosphate (PO_4), nitrate (NO_3), nitrite (NO_2) and ammonium (NH_4) concentrations were determined.

2.3.2 Macrofaunal community structure

Samples for macrofauna were collected from each subsite using a stainless steel corer (N = 5, internal diameter 10 cm, Depth 20 cm). Sandprawn densities were also determined from this sampling procedure. Samples were sieved through a mesh of 500 µm and stored in jars containing a 70% ethanol solution blended with the biological stain Rose Bengal. Using a light microscope (Leica EZ4) and macrofaunal identification guides (Day 1969, Branch *et al.* 2010), organisms were identified to the lowest possible taxonomic level. Where identification of polychaetes was unfeasible due to their small sizes, they were classified as juvenile polychaetes. With the exception of copepods and juvenile polychaetes, all organisms were further assigned into functional groups based on published and expert knowledge.

Functional group classification in this study was supplemented by direct observations of depth distributions and feeding behaviours of species sampled. This was achieved by following the methods used by Moyo *et al.* (2017), in which groups of individuals of each species were placed into a narrow glass tank (50cm (length) X 30cm (height) X 0.7cm (width) that limited the three dimensional movement of macrofauna to two dimensions. The water in the tanks were oxygenated using an Elite 802 air pump. The temprature inside the tanks ranged between 18 and 19 ^{0}C. The dominant feeding strategy of numerically dominant organisms was then observed for two hours at 20 min intervals and thereafter classified as surface suspension feeders, surface deposit feeders, burrowing deposit feeders, burrowing deposit feeders and predators, surface deposit feeders and predators. The latter two functional groups comprised omnivorous taxa but were differentiated on the basis of their occurance within the sediment (epifaunal vs infaunal). For this component of the study, benthic sediment samples were randomly collected separately from the main field study, species identified, and then observed as described above.

2.3.3 Meiofaunal community structure

Two sets of five meiofaunal samples were collected from each subsite. The first set was collected from the sediment surface (0 to 2 cm depth), while the second set was collected from sandprawn burrow-walls, roughly 10 cm deep. The method for sampling meiofauna within sandprawn burrows used by Branch and Pringle (1987) was modified (an Oostenbrink apparatus was not used) and employed in this study. First, burrows were randomly chosen and cautiously sectioned using a fine blade. Sediment from one section of the opened burrow was gently removed to expose only a single section of the burrow-wall, from which sediment samples (± 10 g) were gently scraped from top and buttom sections of the burrow. Sampled burrows were roughly 10cm apart. Samples were then stored in 30 ml vials containing a 70% ethanol and Rose Bengal solution. Using a dissecting microscope (Leica EZ4), meiofaunal morphotypes were identified, counted and classified as into broad taxonomic groups, due to the lack of local taxonomic expertise on meiofauna (Pillay *et al.* 2009).

2.3.4 Benthic chl-*a* concentrations

Samples for benthic chl-*a* determinations were collected from each sub-site in the exact manner as described for meiofaunal communities (including surface and burrow sections). Samples were then stored in 100 ml test tubes filled with 30 ml of a 90% acetone solution. Samples were refrigerated for 48 h before chl-*a* concentrations were determined from homogenised supernatant subsamples using a Turner Designs Trilogy fluorometer (wavelength = 440nm) and after conversion to biomass using a standard curve.

2.3.5 Sediment particle size

To ascertain sediment particle size distribution, single samples of surface sediments were collected at each subsite in 30 ml vails from a depth of 5cm. Using a series of sieves with geometrically decreasing mesh sizes (2000 µm, 1000 µm, 500 µm, 250 µm, 125 µm, 63 µm and 38 µm), samples were sieved while a shaker was applied to agitate the pot sieves for about 20 min (Gee and Or 2002). Sediment fractions retained by each sieve were oven-dried at 70 °C overnight and weighed. For each sediment sample, plots of cumulative particle size against sediment phi values were produced. Median phi values were calculated as the phi value corresponding to 50 % of the cumulative mass of sediment.

2.4 Factorial experiment

2.4.1 Design and set-up

Building on from correlative field surveys, a six month field factorial experiment was undertaken to further quantify effects of nutrients and ecosystem engineering by sandprawns (*Callichirus kraussi*) in driving benthic community structure. Results of this experiment form the basis of Chapters 5 and 6. The experiment was conducted at mid-shore positions within two sites (Bottelary North [BN] and Bottelary South [BS], Fig. 2.1), with a 1 km distance separating the two sites. Time between high and low tide was approximately six hours. Experimental sites and tidal positions were chosen on the basis of ease of access and because of relatively stable abiotic conditions.

Three levels of sandprawn densities were used in the experiment: Level 1 had no sandprawns added to cages, Level 2 had 60 sandprawns added to cages and Level 3 had 120 sandprawns per cage (**Table 2.1**). Sandprawn densities used in this experiment were based on density ranges recorded in the field prior to commencing the experiment. For this component, sandprawn densities were assessed using the hole count method at experimental study sites (N = 5; quadrat length = 0.74 m, breadth = 0.53 m and height = 0.46; area, 0.3922 m^2). Prior work in Langebaan Lagoon showed a virtual 1 to 1 relationship between sandprawn holes and their abundance (Wynberg and Branch 1994), suggesting that hole counts are an effective and accurate means of estimating sandprawn abundance. Adult sandprawns ranging between 60 and 80 mm in total length were used for the experiment.

Nutrient levels were manipulated in this experiment using controlled slow released fertilizer capsules (Plantacote-Plus™ 12M Aglukon; N: P: K, 14: 9: 15), with a release duration of eight months. Three treatment levels were established (**Table 2.1**). For the background nutrient level (no nutrient capsules added), nine centrifuge tubes (50 ml) were filled with inert gravel and pushed into the sediment until tube caps were at the same level as surface sediment within each cage. Gravel particle sizes were similar to those of fertilizer pellets used for nutrient enrichment treatments. The same number and size of centrifuge tubes were half filled with fertilizer capsules for the intermediate nutrient treatment level, but were filled completely with fertilizer for the high nutrient level. Roughly 200 holes were drilled into each tube to facilitate nutrient dispersion.

Table 2.1: Illustration of the factorial field experimental design with three replicates of increasing sandprawn density levels (0P, 60P and 120P) within each nutrient treatment level (Background 0N, Intermediate 1N, and High 2N). NB: In the field all treatment cages were randomly interspersed and not blocked as shown below. This design was followed at two sites viz. Bottelary North and Bottelary South.

BACKGROUND (0N)			**INTERMEDIATE (1N)**			**HIGH (2N)**		
0N-0P	0N-60P	0N-120P	1N-0P	1N-60P	1N-120P	2N-0P	2N-60P	2N-120P
0N-0P	0N-60P	0N-120P	1N-0P	1N-60P	1N-120P	2N-0P	2N-60P	2N-120P
0N-0P	0N-60P	0N-120P	1N-0P	1N-60P	1N-120P	2N-0P	2N-60P	2N-120P

The quantity of nutrient capsules used in the experiment were determined from a pilot study undertaken two months prior to the main experiment (**Table 2.2**). Results emanating from this component are presented in Appendix 1 (Fig 9.1). In this preliminary study, the same type of fertilizer capsules described above were used to establish four increasing nutrient levels. The first level (background) had no nutrient capsules added to sediment plots, four centrifuge tubes (50 ml) were filled with nutrient capsules for the second nutrient level, the third level had 8 tubes while the fourth had 16 centrifuge tubes filled with fertilizer capsules.

Plastic creates (Length = 0.58 m, breadth = 0.45 m and Height = 0.43 m; Area = 0.261 m^2) were used to designate independent sediment plots for this pilot study, and were positioned in the mid-shore position of Oesterwal North, spaced 2m from each other. Each nutrient level comprised five replicate plots, as illustrated in **Table 2.2**. After 6 weeks, two pore-water samples were collected from each replicate plot, so that volume of fertiliser could be related to pore-water nutrient levels. Thus, the maximum mass of nutrient pellets used in the final experiment was determined by scaling up maximum masses used in the trial experiment to the dimensions of the cages used in the experiment, which were larger. Based on the results of the trial experiment, masses of nutrients used in the final experiment resulted in a total mean nitrate + nitrite vale of 32.5μg/L, which was 2-3 times greater than maximum pore-water summer values. This mass was used for the 2N nutrient level in the final experiment, and was halved for the N treatment.

Table 2.2: Illustration of the layout of the field trial experimental testing the relationship between mass of fertilizer capsules and pore-water nutrient concentrations. Four nutrient treatments were established, which were replicated five times. Duplicate samples were collected per replicate.

Level 0 (background)		**Level 1**		**Level 2**		**Level 3**	
0N	0N	4N	4N	8N	8N	16N	16N
0N	0N	4N	4N	8N	8N	16N	16N
0N	0N	4N	4N	8N	8N	16N	16N
0N	0N	4N	4N	8N	8N	16N	16N
0N	0N	4N	4N	8N	8N	16N	16N

Cages used in the main experiment to test the effects of sandprawns and nutrients on benthic community structure were constructed from black plastic crates (N = 54; length = 0.74 m, breadth = 0.53 m and height = 0.46; area, 0.3922 m^2), in which bottoms and sides were cut out. The frame remaining was covered by mesh (1 mm). Cages were unroofed since the roofing is known to cause fouling (Pillay *et al.* 2007b) and would have also obstructed benthic colonization from the water column. The roofing was also not important since sandprawns are obligate sediment dwellers and would therefore not have left the sediment or recruited into exclusion cages through immigration. Sandprawns also lack a planktonic larval stage; therefore a meshed top was not required to exclude newly settled larvae (Pillay *et al.* 2007b).

Prior to cage installation, a metal frame exceeding the size of experimental cages (length = 79 cm, breadth = 69 cm and height = 37 cm) was pressed into the sediment. The sediment within the frame was removed and experimental cages inserted into the space created. The frame was then gently removed, resulting in adjacent sediments infilling the space surrounding cages. Sediment that was initially removed was sieved (1mm mesh) to ensure an absence of sandprawns in all cages. All cages were installed 4 m apart to ensure independence (**Fig. 2.3**). Treatments were randomly interspersed in cages to avoid small scale benthic features from confounding treatment effects.

Sandprawns were introduced into the cages according to designated density treatments after a period of one week following fertilizer addition and activation. Throughout the duration of the experiment, cages were constantly monitored to ensure that both nutrient and sandprawn density treatments were stable as desired. For sandprawn treatments, the holes on the surface sediment were counted in each cage during monitoring periods. Where the holes did not match the original number, sandprawns were either added or removed from the treatment cages depending on the situation. A plastic suction pump was gently employed to remove sandprawns from the cages. No removals in controls were necessary after an initial two-week period. Over the duration of the experimental, a maximum of four sandprawns per cage were either removed or added.

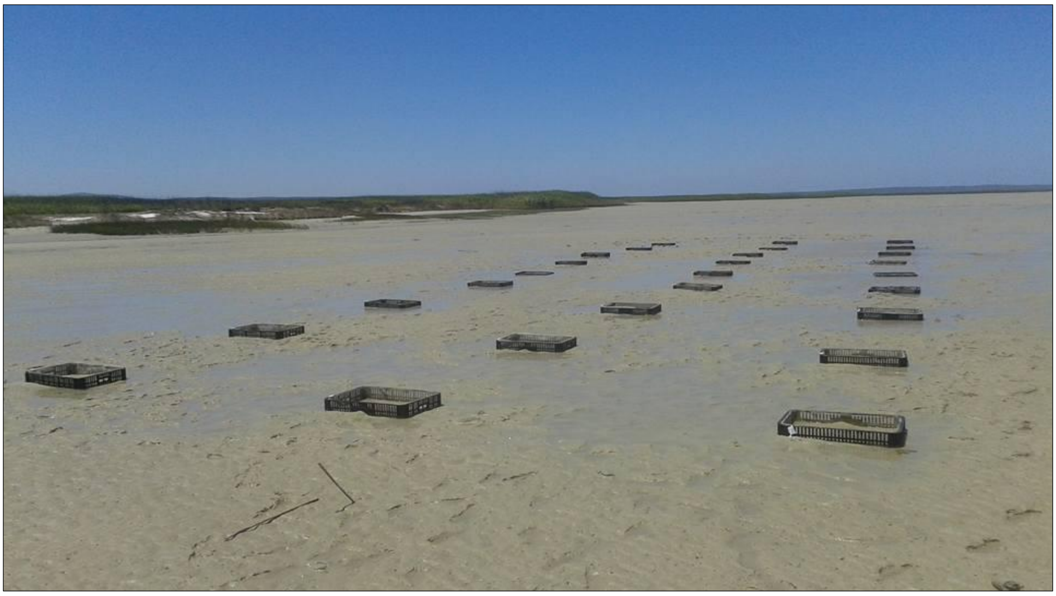

Fig. 2.3: Layout of cages in Bottelary South for the experiment testing the effects of sandprawns (*Callichirus kraussi*) and nutrient enhancement on benthic communities.

2.4.2 Data collection and analyses

The following sets of data were collected at the termination of the six month field experiment. Apart from sample sizes, procedures used to collect and analyze these samples were similar to those used in the field survey (see Section 2.2).

For macrofaunal community structure, three sediment cores were collected from each cage, while three sets of three samples were collected per cage for meiofauna. Each set of samples comprised samples from the sediment surface, within burrow-walls (10cm below the sediment surface) and 10cm adjacent to the burrow-wall (hereafter referred to as "reference" samples). The latter samples were collected to ascertain if any differences exist in assemblages between burrow-wall environments and non-burrow areas, and how these compared with assemblages associated with the sediment surface. Three sets of three sediment samples were also collected for chl-*a* biomass determinations from sediment surfaces, burrow-walls and adjacent to burrow-walls.

Sediment turnover was estimated using the sediment trap method (Ellis *et al.* 2002) in order to quantify differences in sediment turnover in response to sandprawns and nutrients. This was achieved by inserting three centrifuge tubes (aperture = $0.78 cm^2$, length = 10 cm) without caps into the sediment within each cage. Centrifuge tubes were left protruding 0.5cm above the sediment surface. After 24 h, tubes were removed and the sediment they contained was measured and expressed per unit area. This was conducted once off, 1 week prior to the termination of the experiment.

2.5 Statistical analyses

2.5.1 Multivariate analysis: survey and experimental data

Macro-and meiofaunal assemblages for the experimental and survey components were analysed at the community level using statistical routines with PRIMER (Plymouth Routines In Multivariate Ecological Research) 6.1.11 with PERMANOVA + 1.01 (Clarke and Gorley 2006). (PRIMER) is as statiscal programme with a variety of multivariate, univariate and graphical routines for analyzing species data for community analysis. Multivariate routines incorporated in PRIMER include Multidimesional Scallinmg (MDS), Similarity Percentage (SIMPER), grouping cluster, Principal component and others. For example, MDS which is one of the functions used in this study is a technique that allows visualization of similarity within and between groups of data. It is generally used to interpret information about the pairwise 'distances' among a set of species or objects into points displayed in a map format. SIMPER is a type of data analysis that quantifies the contribution of each species or variable to dissimilarity using similarity indices. Permutation Multivariate Analysis of Variance (PERMANOVA), is used to statistically determine differences in multivariate datasets in accordance with an ANOVA design, with p-values achieved using an appropriate, distribution-free permutation technique (Anderson 2017).

Meiofaunal data were analysed separately based on sandprawn burrow positions, i.e. sediment surface (surface-burrow), burrow-wall and reference (no burrow areas). The reference position was only included for the experimental study. The DIVERSE function was applied to determine various community descriptors for macro- and meiofaunal communities (total species richness [S], species evenness [J’], abundance [N] and Shannon-Wiener diversity

[H’]). These community descriptors were calculated based on untransformed and unstandardized abundance data.

The data were then square root transformed for further multivariate community analysis. This was done in order to down-weight extreme values and outliers. Using PERMANOVA with sites as a fixed factor and nutrients and sandprawns as random factors, interactive and main effects of nutrient and sandprawn treatments on macro- and meiofaunal communities were examined. As for the field survey data, community responses to main and interactive effects of seasons, sites and subsites were examined. Where necessary, ordination plots were produced using a multidimensional scaling (MDS). This analysis was undertaken to visually discern spatial variation in communities due to factors of interest. PERMANOVA and ordination analyses were based on the resemblance matrices generated from Bray Curtis similarities. The SIMPER routine was employed to identify the dominant macrofaunal species that cumulatively accounted for 90 % of community structure. SIMPER analysis was not applied for meiofaunal communities due to the small number of meiofaunal taxa recorded. Each taxon was analysed independently using univariate techniques.

2.5.2 Univariate analysis

2.5.2.1 Survey data

Using R statistics, Pearson correlation analysis was used to examine the relationship between sandprawn abundances and macro-and meiofaunal community metrics and the abundance of species/taxa and functional groups. This approach was used to test the relationship between sandprawn abundance and various community measures and if this was altered between upwelling and non-upwelling seasons. Sandprawn abundance data that were collected from macrofaunal samples (Section 2.3.2) were used in correlation analyses for both macro- and meiofauna. Water column chl-*a* data was analysed using ANOVA in R statistics.

2.5.2.2 Experimental data

Generalised Linear Models (GLMs) were employed to test for the effects of nutrients and sandprawn densities on macro- and meiofaunal diversity indices, individual species/taxa, macrofaunal functional groups, chlorophyll-*a* and sediment turnover. GLMs are a mathematical extension of linear models that permit the modelling of non–normal response distribution through transformation to a linear form (Venables and Ripley 2002). More information on the background to GLMs are provided in Appendix 9.2. They are based on the presumed relationship between the mean of a response variable and a group of linear predictors (Guisan *et al.* 2002).

Generalised linear models were performed on the data analysis platform R (version 3.4.2) and fitted using the MASS package (Venables and Ripley 2002). The GLMs allowed univariate descriptors of macro- and meiofaunal communities to be tested as response variables against assigned predictor variables. For example, in the case of the experiment, sites, nutrients and sandprawn densities were the main predictor variables examined for their main and interactive effects. Meiofaunal data were analysed separately based on the habitat position (i.e. surface-burrow, burrow-wall and reference).

Three general linear models were generated against each response variable; (1) a model that examined interactive effects of sites, nutrients and sandprawns, (2) interaction between nutrients and sandprawns but not sites and (3) main effects of sites, nutrients and sandprawns. Before the models were run, data normality assumption tests were conducted graphically following the approach of Zuur *et al.* (2010) and numerically by employing the

Shapiro-Wilk Tests ($p < 0.05$). Where possible, outliers in the data were retained for the model fit, however they were also checked for transcription and calculation errors. Where the possibility of rectifying outliers resulting from calculation and transcription errors was not feasible, those outliers were excluded from the dataset. All link function fits applied in the models were visually assessed by plotting a linear predictor variable against the estimated link function before there were selected for the model fit. The homogeneity of variance assumption was also tested by plotting the residuals against the fitted values. The likelihood ratio test and Chi-square test were both employed to examine the model fit. Each model summery was generated along with lower and upper limits coefficient intervals.

As for the graphical representation, trellis plots from the lattice packages in R (Sarkar 2008) were applied for visualizing data. The advantage of using trellis plots is that they are an appropriate statistical tool to demonstrate effects of factorial and continuous covariates on a response variable. They also enable illustration of a replicate plot for sub-sets of data that correspond to the chosen intervals of a numerical variable or to different levels of a categorical variable (Becker and Cleveland 1996).

2.6 Methodological considerations

2.6.1 Cage experiment

In marine ecology, cages are frequently utilized in experiments as exclosure or enclosure tools to manipulate densities of organisms such as grazer and predators. Cage experiments have often been conducted in inter-tidal rocky and soft-sediment shores, generally with the goal of examining biological interactions (Hindell *et al.* 2001, Menge *et al.* 2004). However, the use of cage experiments has the disadvantage of introducing artifacts into the study, which can influence the results of the experiment (Miller and Gaylord 2007). In particular, it has been argued that cages may provide refuge from wave actions, alter densities of consumers (Kennelly 1983, Berlow 1997) and alter sedimentation rates, all of which alters community structure within the cages over and above the factor/s being tested (Virnstein 1977, Menge *et al.* 1986).

Nevertheless, problems associated with cage artefacts can often be overcome by various alterations to the basic exclusion/inclusion design. One commonly used approach is to use a cage control that mimics physical effects of the cage without obstructing the movement of mobile organisms (Miller and Gaylord 2007). Although this approach can effectively reduce artifacts, an inevitable challenge is that a cage control can never be perfectly designed to capture the full spectrum of physical attributes of experimental cages and yet not be a cage (Miller and Gaylord 2007). In some instances, artifacts are minimized by increasing the mesh size and plot, or by lowering cage profile (Miller and Gaylord 2007).

Another approach is to use multiple densities in experiments such that binary exclusions and inclusions are not the outcome of the experiment (Pillay *et al.* 2009, 2010). Here, the rationale is that whatever artefact is present in the experiment, it is held constant over a range of densities of the factor/s being manipulated so that ecological responses can be gauged across a density range. This is particularly advantageous when cage attributes cause minimal alterations to abiotic conditions. In this study testing the interactive effects of ecosystem engineering by sandprawns and nutrient enrichment on benthic communities, the latter approach was adopted. Cage artefacts in this study were reduced by frequently monitoring and cleaning the algal growth around cages. In addition, since cages were buried almost flush with the sediment surface, physical alterations of flow patterns were minimal. In addition, when collecting samples from cages, cores were collected 10cm away from cage margins to avoid edge effects interfering with results.

2.6.2 Modelling approach

This study adopted a generalised linear modelling approach in order to understand effects of nutrients and ecosystem engineering by sandprawns on benthic communities. The most important statistical constraint that needs consideration in modelling techniques is sample size. The sample size should be neither too large nor small but adequate to cover data variability. If the sample size is too large, assumptions of independence of observations may be easily violated due to spatial autocorrelation (Heckman *et al.* 2014). On the other hand, smaller sample sizes reduce confidence for population parameters by producing large standard errors and wide confidence intervals. For regression parameters, a small sample size can lead to an incoherent estimation, and if the respective confidence interval comprises zero values, coefficients are likely to be insignificant (Heckman *et al.* 2014). On the other hand, large sample sizes reduce confidence intervals and standard errors in the estimation of parameters.

Restrictions relating to sample size are to be carefully considered as they can result in overfitting of the model and over-parameterisation (Venables and Ripley 2002, Hjort and Marmion 2008). The risk of over-parameterisation can be noticed in a stepwise model selection that is based on the level of significance, and where large samples in a model facilitate the inclusion of a number of variables. Overfitting - the inclusion of many variables in a model does not necessary imply a better model performance, instead it may result in a poor model performance. A model that precisely fits to a specific set of data may not always perform well in a new set of data (Stockwell and Townsend Peterson 2002). When a statistical model starts to describe the random error in the data rather than actual relationships between variables/factors, it is usually due to model overfitting, which results in a complex model. The problem with overfitting is that it can produce innacurate outputs. An overfitted regression model consists of many terms for the number of observations (sample size) and as a result, regression coefficients represent noise and not relationships within the data cloud.

In the context of sample size, some of the data in this study were strongly affected by sample size limitations during the modelling process. Very little variability was also observed in some of the response data (e.g. meio-and macro-faunal abundances between cages in the experiment). Given the limited available data, an arbitrary rules was applied to restrict the fitting of the models. In case where very little variability or a large number of zeros (80 % counts are zeros) was observed in the data, no models were fitted for such variables, e.g. experiment data; polychaetes *Ceratonereis erythraeensis, Marphysa elitueni* and bivalve *Carditella rugosa*. The decision to exclude these species from the modelling process was made followed by an extensive stepwise data exploration, i.e. first, each response variable against a combination of predictor variables and also against individual predictors. However, some variables showed normal distribution pattern with minimal variability, thus creating a challenge in determining an adequate sample size. Overall, more samples could have been collected to minimize the variability of data, and also for the simplification of model performance. This maybe be necessary in future studies to ensure that clear ecological patterns are revealed. Another important consideration in this study was the exclusion of predictor independent variables that had little impact or did not directly influence the response variable in the model, i.e. pore-water nutrients, sediment trap, sediment particle size.

CHAPTER 3

EFFECTS OF COASTAL UPWELLING ON **MEIOFAUNAL** COMMUNITIES IN SANDPRAWN-DOMINATED SANDFLATS

3. Introduction

3.1 Environmental contexts

Understanding the contextual dependencies that influence ecosystem functioning is a central goal in ecology (Boyer *et al.* 2009, Stachowicz *et al.* 2008b, Reich *et al.* 2012, O'Connor and Donoheu 2013, Ford *et al.* 2016). Generally, environmental contexts refer to local processes and characteristics of the habitat in question, be they abiotic or biotic in nature (Menge 2003b). Examples of abiotic contextual features include environmental stress, disturbance, and productivity, whereas biotic features include aspects such as species traits, diversity and community composition within habitats under investigation (Menge 2003b). Importantly, these contextual dependencies are well-known in ecology for determining the strength and direction of outcome of species interactions (Chamberlain *et al.* 2014) and hence drive spatio-temporal variability in community patterns (McCreadie and Adler 2012, Heneash *et al.* 2015, Gerwing *et al.* 2016). For instance, studies have shown that contextual processes can alter the relationship between species diversity and disturbance (Johnson *et al.* 1996, Cardinale *et al.* 2000, Badano *et al.* 2010, Reich *et al.* 2012).

A major challenge underlying studies on environmental contexts is that it is dependent on spatial scale (Levin 1992). Processes that occur over large scales are logistically challenging to investigate, resulting in limitations to understanding of these processes (Levin 1992, Roughgarden *et al.* 1994, Link *et al.* 2010). Nevertheless, ecologists have prioritized the need to understand how ecological processes are influenced by environmental contexts that are erratic and often hard to determine (Levin 1992, Gough *et al.* 1994, Cardinale *et al.* 2000, Hastings *et al*. 2007).

3.2 Primary productivity: an important contextual dependence in marine ecosystems

Primary production, the amount of organic material produced per unit area over a temporal cycle (Wetzel 1975, Cloern *et al.* 2014), plays a fundamental role in determining ecological processes of aquatic ecosystems (Vargas *et al.* 2006, Ask *et al.* 2016). Primary production is driven predominantly by a variety of autotrophs, which are commonly photosynthetic plants (Oliveira *et al.* 2005, Duarte *et al.* 2005). In marine coastal ecosystems such as lagoons and estuaries, phytoplankton and benthic micro- and macroalgae are the most dominant primary producers (Nozais *et al.* 2001, Cloern *et al.* 2014, Tania *et al.* 2015). Phytoplankton are microscopic, photosynthetic organisms that drift in the water column within the pelagic zone (Francisco *et al.* 2011). They constitute a central component of food webs (Vargas *et al.* 2006, Tania *et al.* 2015), contributing in excess of 90 % to total marine primary production (Duarte and Cebrain 1996). As a result, phytoplankton fulfils a fundamental ecological role in marine ecosystems by supporting bottom-up processes (Irwin *et al.* 2012, Tania *et al.* 2015, Brun *et al.* 2015). Given optimal growth conditions (e.g. light availability and nutrients), autotrophic primary production may proliferate (Underwood and Kromkamp 1999, Ask *et al.* 2016), and influence food webs and community structure significantly. For example, aquatic ecosystems that are characterised by high autotrophic primary production typically display higher secondary production with increased food web efficiency (Berglund *et al.* 2007).

Benthic primary producers are also important contributors to productivity in littoral ecosystems, which they dominate due to high nutrient and light levels associated with shallow conditions (Cahoon 1999, Gazeau *et al.* 2004). Most of this benthic primary production is generated by sediment microalgae, also known as microphytobenthos (Cahoon 1999), which are benthic unicellular, eukaryotic algae, mainly diatoms and certain cyanobacteria and dinoflagellates (MacIntyre *et al.* 1996). They proliferate in the upper millimetres of sediment in sub-tidal coastal ecosystems (MacIntyre *et al.* 1996), but also as epiphytes on aquatic plants such as seagrasses and macroalgae (Duarte *et al.* 2005). Microphytobenthos are considered important ecosystem modifiers that also fuel estuarine food webs due to their consumption by groups such as snails, annelids, copepods and amphipods. When suspended, microphytobenthos increase microalgal biomass in the water column, thereby increasing availability of trophic resources for consumers (MacIntyre *et al.* 1996). Microphytobenthos do not only contribute towards primary production, but also perform several other key ecological functions, including stabilizing of sediment by producing extracellular carbohydrates (MacIntyre *et al.* 1996, Underwood and Paterson 1993, de Brouwer *et al.* 2003), prevention of nutrient release to the overlying water column and oxygenation of underlying waters (Sundback 1986, Sundback and Snoeijs 1991, Wiltshire 1992, Ní Longphuirt *et al.* 2009). Microphytobenthos also facilitate nutrient recycling by assimilation of surface nutrients (Kromkamp *et al.* 1995, Kristensen *et al.* 1997, Underwood 2001).

3.3 Coastal upwelling

Upwelling generally describes the vertical movement of cold, nutrient-rich bottom waters to the surface in coastal ecosystems (Schumann *et al.* 1982, Merino and Moreal-Gomez 2009, Rossi *et al.* 2013, Hu and Wang 2016). By mobilising nutrients, upwelling plays a critical role in driving ecological processes in marine ecosystems, (Blanchette *et al.* 2009, Barth *et al.* 2007, Gonzalez *et al.* 2012) essentially by increasing biological productivity (Blanchette *et al.* 2009, Capone and Hutchins 2013). Generally, upwelling systems are classified as either permanent or sporadic (Merino and Moreal-Gomez 2009, Rossi *et al.*

2013). Permanent upwelling systems are often defined as systems where upwelling events always occur, but have seasonality (Alvarez *et al.* 2008a, Herrera *et al.* 2008). The four major permanent upwelling current systems are, (i) Benguela, (ii) Canary, (iii) California and (iv) Humboldt currents (Merino and Moreal-Gomez 2009, Aristegui *et al.* 2009**,** Fuchs *et al.* 2013, Benazzouz *et al.* 2014). These current systems are all situated on eastern boundaries and are maintained by prevailing winds (Menna *et al.* 2016). Sporadic upwelling systems (e.g. Western Australian coast) are littoral and limited in spatial and temporal scales (Nykjaer and Van Camp 1994, Alvarez *et al.* 2008, Rossi 2013). As a result, productivity is relatively lower in sporadic upwelling systems than in permanent upwelling cells.

Although upwelling systems are generally characterized by analogous geographical features and mechanisms driving upwelling, they also display significant variability (Fuchs *et al.* 2013). Both spatial and temporal variance in relation to wind and topographic features (e.g. canyons and headlands) create variability within and among upwelling systems (Graham and Largier 1997, Chavez and Messie 2009). These factors also determine the efficiency and scale of upwelling events (Schumann *et al.* 1982, Carr and Kearns 2003, Rossi *et al.* 2013). In terms of temporal scales, variation in wind intensity and velocity with change of seasons can significantly influence upwelling strength and its occurrence (Merino and Moreal-Gomez 2009). For example, in the north-west of Africa (north of Cape Blanc), upwelling occurs throughout the year, whereas, south of this region, it occurs predominantly in winter and spring (Merino and Moreal-Gomez 2009). The summer Azores high pressure cell is known to drive equatorward winds northwards, which improves upwelling conditions in the north-west compared to the southern region (Mittelstaedt 1991, Mason *et al.* 2011). The Benguela upwelling also occurs throughout the year, with the highest peak in summer from the southern regions, i.e., Cape Town and Lüderitz. Prevailing south easterly winds drive the Benguela upwelling system (Andrews and Hutchings 1980, Field and Shillington 2006).

Biological and physical characteristics within and between upwelling systems determine nutrient levels, primary production and community structure and variability in these variables (Merino and Moreal-Gomez 2009). For instance, both the Peru and California upwelling systems display elevated nutrient concentrations (e.g. nitrate) compared to the Benguela upwelling system (**Table 3.1**). The location of these upwelling systems is one of the reasons that causes differences in nutrient levels (Merino and Moreal-Gomez 2009). The Peru and California upwelling systems are situated in the Pacific Ocean, where the thermocline circulation enables a greater movement of deep, nutrient-rich waters whereas, in the Benguela, upwelling is limited by circulation (Merino and Moreal-Gomez 2009). In terms of total productivity among permanent upwelling systems, estimates indicate highest productivity in the Benguela system followed by the Canary and Humboldt, while the California current displays the lowest value of productivity (Carr 2002). Species richness in inter-tidal rocky shores within these upwelling systems does not appear to correlate with productivity estimates, with richness being higher in the California and New Zealand systems, and surprisingly very low in the Benguela system, despite it having highest productivity levels (Blanchette *et al.* 2009). This paradox can be explained by (1) differences in spatial scales over which richness was measured relative to the area of upwelling and (2) differences in sensitivity of techniques used to measure productivity. Regarding the latter, satellite data, which are used by many studies to quantify productivity, do not provide realistic representations of intertidal productivity because of chlorophyll patchiness in the nearshore (Blanchette *et al.* 2009).

Elevated nutrient levels in upwelled regions may not necessarily lead to increases in productivity in shallow water coastal ecosystems. Prevailing winds for example, may deflect nutrient-transporting currents away from shores and effectively limit productivity within coastal environments. Upwelling current deflection has been reported to influence planktonic larvae by redirecting them offshore, resulting in larval mortality and lower recruitment (Morgan 2014). Major changes in ecological functioning, spanning individual species to whole communities can materialize as a result of limitations on productivity in space and time in upwelling regions. For example, Ware (1992) noted that variability in winds reduced the productivity of the California current, resulting in lower hake stocks compared to Peru and Benguela systems (Ware 1992). Barth *et al.* (2007) also showed how a delay in upwelling influenced inter-tidal rocky shore communities. They documented a significant temporal decrease in chlorophyll-*a* and nutrient levels of up to 50% and 30%, respectively, which was associated with reductions in mussel recruits and barnacles. These upwelling anomalies were associated with a month delay in spring transition to upwelling-favourable winds (Barth *et al.* 2007).

Table 3.1: Mean values of nutrients and primary productivity of global permanent upwelling systems (Merino and Moreal-Gomez 2009).

Upwelling systems	**Nitrate concentration (μm. L^{-1})**	**chlorophyll-*a* concentration (mg. m^{-2})**	**Total primary productivity (g C m^{-2}. d^{-1})**	**New primary productivity (g C m^{-2}. d^{-1})**
Peru current	25	118	2.8	0.6
California current	23	154	2.6	1.8
Benguela current	20	106	3.5	2.5
Equatorial Atlantic	10	33	Undefined	Undefined
Equatorial Pacific	>12	Undefined	8.0	0.2
Somalia Coast	20	58	2.1	1.9

The mean productivity within upwelling ecosystems has been previously estimated to reach 300 g C. m^{-2}.year $^{-1}$, which is six times greater than the predicted average for the open ocean (Merino and Moreal-Gomez 2009). This high level of productivity thus reinforces the importance of upwelling for supporting marine biodiversity and driving ecological processes. Although upwelling represents only 1% of the global ocean's surface and 5% of global marine productivity (Carr 2002), its impacts on the functioning of marine ecosystems from individual species to whole communities is disproportionately large.

Major differences exist between upwelling and non-upwelling ecosystems in terms of community organization (De Leo and Pires-Vanin 2006). Studies have shown that upwelling ecosystems are characterized by having simpler and shorter trophic chains, comprising herbivores, primary producers and secondary consumers (Duarte and Garcia 2004). Increased primary production in upwelling regions is also associated with lower species diversity but an increase in organism abundance (Field and Griffiths 1991). Greater trophic resource availability in upwelled regions generate positive effects on important commercial fish species (Schumann *et al.* 1982), with approximately 17% of commercial fish species supported by upwelling across the globe (Pauly and Christensen 1995). On the other hand, non-upwelling ecosystems have relatively low biomass but higher species diversity (Bolton and Levitt 1987, Field and Griffiths 1991).

In the South African context, distinct spatial patterns in marine diversity and community attributes exist along the coastline, with the west coast being influenced by higher productivity as a result of the Benguela upwelling current, whereas both east and south coasts are characterized by lower productivity (Bustamante *et al.* 1995, Griffiths *et al.* 2010). Previous studies have summarized knowledge of South Africa's marine littoral diversity and identified a conspicuous pattern of low species richness along the west coast and relatively higher species richness on the east and south coasts (Field and Griffiths 1991, Awad *et al.* 2002, Griffiths *et al.* 2010). Also, noticeable is the dominance of commercial fisheries on the west and south coasts compared to east coast (Griffiths *et al.* 2010).

This chapter focuses on meiofaunal community composition in an inter-tidal soft-sediment ecosystem. Meiofauna are defined as small metazoan organisms that range between 100 to 1000 µm in size (Heip *et al.* 1988). Specifically, meiofauna pass through a 0.5 or 1 mm mesh sieve, but retained by a 63 µm (Heip *et al.* 1988). This study seeks to provide insights into whether meiofaunal communities in sandprawn-dominated sandflats are influenced by seasonal upwelling in Langebaan Lagoon. Specifically, this chapter determines spatial variability in water column productivity from the mouth of the system to inter-tidal sandflats in the middle- to upper reaches of the system. Secondly, it quantifies whether meiofaunal community structure in sandprawn dominated sandflats is altered by upwelling. Thirdly, the study makes use of corelative techniques to determine the relationship between sandprawn abundance and meiofaunal community metrics to determine whether the strength of sandprawn engineering effects are altered by upwelling. In terms of the latter, upwelling can influence benthic meiofaunal composition by altering quantities and quality of food resource within sediments (Quintana *et al.* 2015). On the other hand, sandprawn densities can influence benthic faunal composition by inducing negative effects on epifaunal organisms through rapid sediment turnover (Pillay *et al.* 2007a). While other studies documented negative sandprawn impacts on meiofauna and several other benthic communities (Colin *et al.* 1986, Branch and Pringle 1987, Pillay *et al.* 2011, Pillay and Branch 2011, Henninger and Froneman 2013), others have reported positive relationship between sandprawns and bacterial community within burrow walls (Branch and Pringle 1987). Thus, it is possible that with increased availability of trophic resources associated with upwelling, negative effects of sediment turnover by sandprawns may be dampened.

3.4 Aims and hypotheses

The general aim of this chapter was to investigate the effects of upwelling, as an important environmental context, on the meiofaunal community structure in sandprawn-dominated inter-tidal sandflats in Langebaan Lagoon. Based on this aim, it was hypothesized that:

H1: Meiofaunal community metrics, water column and sediment chlorophyll-*a* (chl-*a*) levels within Langebaan Lagoon should be lower in winter (non-upwelling season) but increase during summer.

H2: Values for meiofaunal community metrics would be negatively related to sandprawn abundance in winter (non-upwelling) but this relationship may weaken or become positive in summer upwelling seasons due to higher trophic resource levels offsetting negative effects of sediment turnover.

- **METHODS AND MATERIALS**

Please refer to chapter 2 for the methods used in this chapter.

3.5 RESULTS

3.5.1 Water column chlorophyll–*a* concentrations

Water column chl-*a* concentrations (**Fig 3.1**) within Langebaan Lagoon differed significantly between the winter (non-upwelling) and summer upwelling seasons (ANOVA, $F_{3, 21} = 12.888$; $p < 0.0001$), and also between stations (ANOVA, $F_{7, 21} = 8.204$; $p < 0.0001$). Generally, chl-*a* concentrations were higher in summer relative to winter during both sampling periods (2015 and 2016). The stations closer to the mouth of the lagoon (S1, S2 and S3) displayed higher chl-*a* values during both seasons, however, levels decrease towards the upper reaches of the lagoon (S4—S8). Also evident was that the latter stations showed minor differences in summer and winter chl-*a* levels relative to stations S1-S3, where summer chl-*a* values were much greater that winter values.

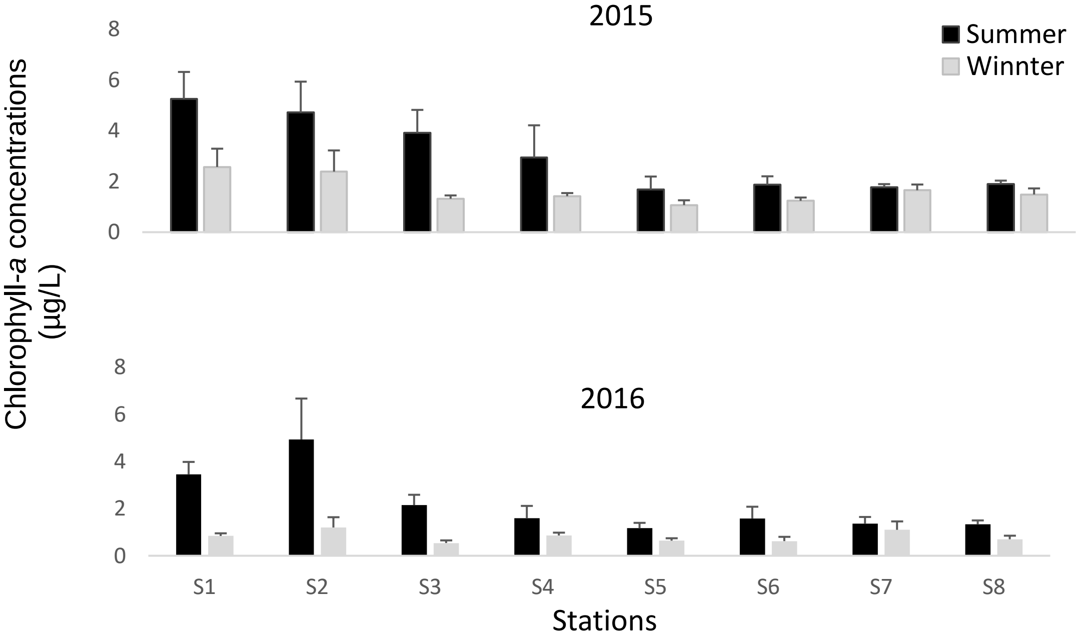

Fig. 3.1: Spatio-temporal variability in chlorophyll-*a* concentrations (mean ± 1SE) in Langebaan Lagoon from the mouth (S1) to the upper reaches of the lagoon (S8).

3.5.2 Sediment chlorophyll-*a* concentrations

The likelihood ratio test (LRT) approved both seasons and sites as predictor variables for sediment surface chl-*a* concentrations ($p = 0.0188$, **Table 3.2A**), while at the burrow-wall, these variables were disapproved by the LRT ($p = 0.0825$). The Akaike's information criterion (AIC) confirmed that the model of an interaction between sites and seasons was the most parsimonious model for sediment surface chl-*a* (**Table 3.2B**).

The correlation test performed on sediment chl-*a* per site during each season (**Table 3.3**) generally indicated weak sandprawn effects, with one case of a negative sandprawn effect on burrow-wall chl-*a* in Oesterwal South during winter of 2015 ($r = -0.58$, $p = 0.02$). In Oesterwal North there were no sandprawn effects on sediment chl-*a* concentrations ($p > 0.05$, in all cases). However, when summer and winter data per year were explored, sandprawn effects appeared to be much stronger on chl-*a* concentrations, generally, negatively affecting surface sediment chl-*a* in both sites ($p = 0.05$, in all cases, **Table: 3.4**), but not in 2016 in Oesterwal North ($r = 0.0005$, $p = 0.99$). On the other hand, sandprawn effects on burrow-wall chl-*a* were minimal, with a negative correlation observed once for Oesterwal South in 2015 ($r = -0.58$, $p < 0.0001$).

At the site and subsite level, sediment chl-*a* concentrations were greater in 2015 winter compared to summer in both Oesterwal North and South (**Fig 3.2A** and **B**). However, this pattern disappeared during the 2016 sampling periods, with both sites showing relatively similar chl-*a* levels within subsites.

Table 3.2A: Likelihood ratio test (LRT) results examining if seasons and sites were important predictors in models for chlorophyll-*a* concentrations at the sediment surface and burrow-wall. Statistical descriptions: LRT = test statistic, df = degrees of freedom, *p* – value = significance level. Values in bold indicate statistical significance.

	Sediment surface			**Burrow-wall**		
	LRT	**df**	***p*-value**	**LRT**	**df**	***p*-value**
Chlorophyll-*a*	16.7485	7	**0.0188**	12.591	7	0.0825

Table 3.2B: Generalised linear mixed effects models conducted on chlorophyll-*a* concentrations, investigating effects of sites and seasons. Statistical descriptions: AIC = Akaike's information criterion, df = degrees of freedom. Values in bold indicate the most parsimonious model.

Sediment surface		
Model	**df**	**AIC**
Null	10	2164.335
Sites	13	2166.301
Seasons	15	2163.113
Site + Seasons	16	2165.055
Sites x Seasons	19	**2161.544**

Table 3.3: Summary statistics of Pearson correlation analysis testing the relationship between chlorophyll-*a* concentrations and sandprawn abundances in Oesterwal North (ON) and South (OS). Statistical descriptions: r = goodness of fit, t = test statistic, df = degrees of freedom, and *p*— value = significance level. Values in bold indicate statistical significance. NB: where correlations are statistically significant, scatter plots are provided on the appendix **(Fig 9.2**).

Oesterwal North (ON)																
Sediment Chlorophyll-*a*	**Winter 2015**				**Summer 2015**				**Winter 2016**				**Summer 2016**			
	r	**t**	**df**	***p*-value**	**r**	**t**	**df**	***p*-value**	**R**	**T**	**df**	***p*-value**	**r**	**t**	**df**	***p*-value**
Sediment surface	-0.123	-0.44	13	0.66	0.06	0.22	13	0.82	0.33	1.29	13	0.21	-0.03	-0.11	13	0.9
Burrow-wall	-0.11	-0.41	13	0.68	0.24	0.91	13	0.37	0.28	1.07	13	0.3	-0.04	-0.15	13	0.87
Oesterwal South (OS)																
Sediment surface	-0.09	-0.33	13	0.74	-0.31	-1.16	13	0.26	0.33	1.29	13	0.21	0.21	0.8	13	0.43
Burrow-wall	-0.58	-2.6	13	**0.02**	-0.42	-1.66	13	0.11	0.28	1.07	13	0.3	0.27	1.03	13	0.31

Table 3.4: Summary statistics of Pearson correlation analysis testing the relationship between chlorophyll-*a* concentrations and sandprawn abundances in Oesterwal North (ON) and South (OS) based on combined summer and winter data per year (2015 and 2016). Statistical descriptions: r = goodness of fit, t = test statistic, df = degrees of freedom, and *p*— value = significance level. Values in bold indicate statistical significance. NB: where correlations are statistically significant, scatter plots are provided on the appendix (**Fig 9.3**).

	Oesterwal North (ON)								**Oesterwal South (OS)**							
Sediment Chlorophyll-*a*	**2015**				**2016**				**2015**				**2016**			
	r	**t**	**df**	***p*-value**	**r**	**T**	**df**	***p*-value**	**r**	**t**	**df**	***p*-value**	**r**	**t**	**df**	***p*-value**
Sediment-surface	-0.47	-2.82	28	**0.008**	0.0005	-0.0002	28	0.99	-0.51	-3.21	28	**0.003**	0.45	2.69	28	**0.012**
Burrow-wall	-0.04	-0.24	28	0.81	-0.14	-0.78	28	0.43	-0.65	-4.5	28	**<0.0001**	0.1	0.56	28	0.57

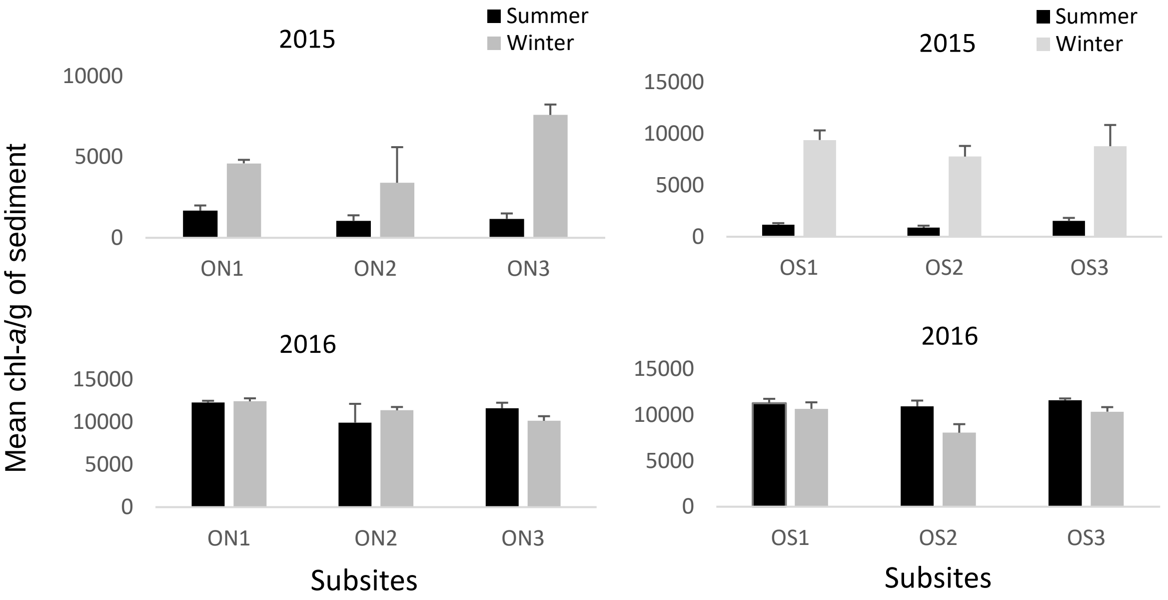

Fig. 3.2A: Spatio-temporal variability in sediment surface chlorophyll-*a* concentrations (means ± 1SE) at three subsites in Oesterwal North (ON1-3) and Oesterwal South (OS1-3).

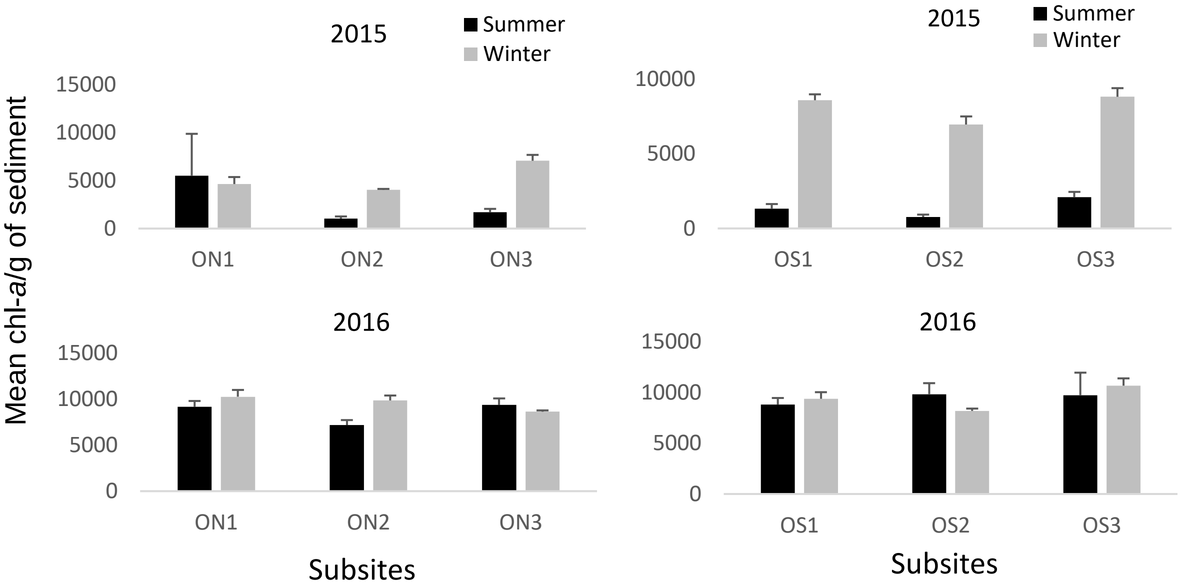

Fig. 3.2B: Spatio-temporal variability in burrow-wall chlorophyll-*a* concentrations (means ± 1SE) at three subsites in Oesterwal North (ON1-3) and Oesterwal South (OS1-3).

3.5.3 Meiofaunal community structure: Overall composition

Meiofaunal community structure was significantly influenced by seasons at the sediment surface (PERMANOVA, *Pseudo*-$F_{1,\ 119}$ = 33.538, p = 0.001) and burrow-wall (PERMANOVA, *Pseudo*-$F_{1,\ 119}$ = 25.026, p = 0.001) positions (**Table 3.5**). Communities at the surface and burrow-wall habitats did not vary among sites or subsites. An interaction between seasons and sites significantly affected the burrow-wall meiofaunal community (PERMANOVA, *Pseudo*-$F_{1,\ 119}$ = 3.1378, p = 0.029).

Table 3.5: PERMANOVA summary statistics testing for variability in meiofaunal community structure among seasons, sites and subsites. Statistical descriptions: *Pseudo-F* = test statistics, df = degrees of freedom, *p* – value = significance level. Values in bold indicate statistical significance.

	Sediment surface			**Burrow-wall**		
Factors	***Pseudo-F***	**df**	***p*-value**	***Pseudo-F***	**df**	***p*-value**
Seasons	33.538	1	**0.001**	25.026	1	**0.001**
Sites	0.571	1	0.715	2.733	1	0.054
Sub-sites	1.096	2	0.355	0.880	2	0.543
Seasons X Sites	1.540	1	0.166	3.137	1	**0.029**
Seasons X Sub-sites	1.125	2	0.329	9.765	2	0.573
Sites X Sub-sites	1.794	2	0.058	0.778	2	0.560
Seasons X Sites X Sub-sites	1.651	2	0.084	0.815	2	0.550

3.5.4 Community metrics

With the exception of abundance, all meiofaunal community metrics at the sediment surface habitat were predicted by seasons and sites, as indicated by the likelihood ratio test ($p < 0.05$, for all cases, **Table 3.6A**). Of these metrics, the Akaike's information criterion (AIC) value indicated that evenness was best predicted by the model investigating interactive effects between sites and seasons (**Table 3.6B**), while species richness was best predicted by main effects of sites and season. Shannon-Wiener diversity was the only metric predicted by a single factor, viz. the main effect of sites. No meiofaunal community metric was predicted by sites or seasons at the burrow-wall ($p > 0.05$, for all cases, **Table 3.6A**), suggesting that variability in burrow-wall metrics was neither site nor season dependent.

Sandprawn abundances recorded over the duration of this study ranged between 0-102 ind.m^{-2}. Based on the correlation test performed on the meiofaunal community metrics per site during each season, sandprawn impacts on metrics were limited, positively affecting species richness ($r = 0.69$, $p = 0.03$) at the sediment surface in winter in Oesterwal South (**Table 3.8**), while negatively affecting evenness at the burrow-wall in summer ($r = -0.084$, $p = 0.002$). No sandprawn effects on meiofaunal diversity metrics were recorded in Oesterwal North ($p > 0.05$, in all cases; **Table 3.7**) in both seasons. Interestingly, when the summer and winter data were combined and examined per year, results indicated robust sandprawn effects on meiofaunal diversity metrics, negatively influencing all metrics at both sediment surface and burrow-wall in Oesterwal South during 2016 ($p < 0.0001$, in all cases; **Table 3.9**). On the other hand, these relationships were variably observed in Oesterwal North, with negative effects on the abundance, evenness and Shannon-Weiner at the sediment surface ($p < 0.05$, in all cases), while within the burrow-walls, richness and abundance were both negatively influenced by sandprawn abundances ($p < 0.05$, for both cases). In 2015, sandprawn effects were observed in Oesterwal South for both sediment surface and burrow-wall meiofaunal abundance ($p < 0.05$, for both cases), with meiofaunal abundance being negatively related to sandprawn abundances.

Strong seasonal variation on the meiofaunal diversity metrics was observed at the site and subsite level, with most diversity metrics being elevated during the 2016 winter sampling period compared to summer and winter of 2015 (**Fig 3.3A – H**). During 2015, some diversity metrics appeared to be enhanced either in winter or summer depending on the subsite, e.g. species richness (**Fig.3.3A** and **B**), evenness (**Fig.3.3E** and **F**) and Shannon-Wiener diversity (**Fig 3.3G** and **H**).

Table 3.6A: Likelihood ratio test (LRT) results examining if seasons and sites were important predictors in the models for meiofaunal community metrics. Statistical descriptions: LRT = test statistic, df = degrees of freedom, p – value = significance level. Values in bold indicate statistical significance.

Meiofaunal Diversity matrices	**Burrow-surface**			**Burrow-wall**		
	LRT	**df**	***p*-value**	**LRT**	**df**	***p*-value**
Richness (S)	16.0171	7	**0.0249**	7.2518	7	0.4031
Abundance (N)	5.7087	7	0.5741	6.6233	7	0.4917
Evenness (J’)	14.9562	7	**0.0365**	5.5609	7	0.5860
Shannon-Wiener-diversity (H’)	26.3861	7	**0.0004**	3.6785	7	0.8159

Table 3.6B: Generalised linear mixed effects models conducted on meiofaunal community metrics, investigating effects of sites and seasons. Statistical descriptions: AIC = Akaik’es information criterion, df = degrees of freedom. Values in bold indicate the most parsimonious model.

Sediment surface	**Richness (S)**		**Evenness (J’)**		**Shannon-Wiener-diversity (H’)**	
Models	**Df**	**AIC**	**df**	**AIC**	**Df**	**AIC**
Null	10	353.24	10	-61.50	10	0.11
Sites	11	352.79	11	-60.54	11	**-2.29**
Seasons	13	353.18	13	-60.85	13	1.29

Table 3.7: Summary statistics of Pearson correlation analysis testing the relationship between meiofaunal community metrics (sediment surface and burrow-wall) and sandprawn abundances in Oesterwal North (ON). Statistical descriptions: r = goodness of fit, t = test statistic, df = degrees of freedom, and *p*— value = significance level. Values in bold indicate statistical significance.

Community metrics	**Oesterwal North (ON)**															
	Winter 2015				**Summer 2015**				**Winter 2016**				**Summer 2016**			
Sediment surface	**r**	**t**	**df**	***p*-value**	**r**	**T**	**Df**	***p*-value**	**R**	**T**	**df**	***p*-value**	**r**	**t**	**df**	***p*-value**
Richness (S)	0.18	-0.66	13	0.51	0.12	0.44	13	0.66					0.39	1.55	13	0.14
Abundance (N)	-0.33	-1.29	13	0.21	0.21	0.76	13	0.45	-0.03	-0.11	13	0.91	-0.14	-0.52	13	0.6
Evenness (J’)	-0.19	-0.7	13	0.49	0.11	0.43	13	0.62	-0.29	-1.09	13	0.29	-0.07	-0.24	13	0.81
Shannon-Wiener-diversity (H’)	-0.39	-1.57	13	0.14	0.21	0.77	13	0.45	-0.29	-1.09	13	0.29	0.18	0.66	13	0.51
Burrow-wall																
Richness (S)	0.37	1.43	13	0.17	-0.08	-0.31	13	0.76					0.21	0.77	13	0.45
Abundance (N)	-0.11	-0.43	13	0.67	-0.05	-0.18	13	0.85	-0.23	-0.86	13	0.41	-0.15	-0.55	13	0.58
Evenness (J’)	0.06	0.17	13	0.86	-0.21	-0.66	13	0.52	-0.01	-0.07	13	0.94	-0.01	-0.05	13	0.95
Shannon-Wiener-diversity (H’)	0.37	1.47	13	0.16	-0.12	-0.46	13	0.64	-0.01	-0.08	13	0.94	0.09	0.32	13	0.74

Table 3.8: Summary statistics of Pearson correlation analysis testing the relationship between meiofaunal community metrics (sediment surface and burrow-wall) and sandprawn abundances in Oesterwal South (OS). Statistical descriptions: r = goodness of fit, t = test statistic, df = degrees of freedom, and *p*— value = significance level. Values in bold indicate statistical significance. NB: where correlations are statistically significant, scatter plots are provided on the appendix (**Fig 9.4**).

Community metrics	**Oesterwal South (OS)**															
	Winter 2015				**Summer 2015**				**Winter 2016**				**Summer 2016**			
Sediment surface	**r**	**t**	**df**	***p*-value**	**r**	**T**	**df**	***p*-value**	**R**	**t**	**df**	***p*-value**	**r**	**t**	**df**	***p*-value**
Richness (S)	0.69	3.48	13	**0.03**	0.07	0.28	13	0.78					-0.12	-0.47	13	0.64
Abundance (N)	-0.28	-1.1	13	0.3	0.11	0.42	13	0.67	-0.03	-0.11	13	0.91	-0.27	-1.04	13	0.31
Evenness (J’)	-0.3	-1.1	13	0.27	0.0005	0.002	13	0.99	-0.29	-1.1	13	0.29	0.02	0.09	12	0.92
Shannon-Wiener-diversity (H’)	0.2	0.76	13	0.45	0.03	0.13	13	0.89	-0.29	-1.08	13	0.28	-0.14	-0.56	13	0.58
Burrow-wall																
Richness (S)	0.05	0.21	13	0.83	0.049	2.07	13	0.051					0.01	0.05	13	0.95
Abundance (N)	-0.36	-1.42	13	0.17	-0.07	-0.26	13	0.79	-0.23	-0.86	13	0.4	0.22	0.85	13	0.4
Evenness (J’)	0.05	0.16	13	0.86	0.37	0.8	13	0.46	-0.01	-0.07	13	0.94	-0.84	-4.48	8	**0.002**
Shannon-Wiener-diversity (H’)	0.03	-0.13	13	0.89	0.46	1.87	13	0.08	-0.01	-0.068	13	0.94	-0.35	-1.38	13	0.18

Table 3.9: Summary statistics of Pearson correlation analysis testing the relationship between meiofaunal community metrics (sediment surface and burrow-wall) and sandprawn abundances in Oesterwal North (ON) and South (OS) based on combined summer and winter data per year (2015 and 2016). Statistical descriptions: r = goodness of fit, t = test statistic, df = degrees of freedom, and *p*— value = significance level. Values in bold indicate statistical significance. NB: where correlations are statistically significant, scatter plots are provided on the appendix (**Fig 9.5A-D**).

Community metrics	**Oesterwal North (ON)**								**Oesterwal South (OS)**							
	2015				**2016**				**2015**				**2016**			
Sediment surface	**r**	**t**	**df**	***p*-value**	**r**	**T**	**Df**	***p*-value**	**r**	**T**	**df**	***p*-value**	**r**	**t**	**df**	***p*-value**
Richness (S)	-0.07	-0.4	28	0.68	-0.03	-0.2	28	0.83	0.21	1.16	28	0.24	-0.71	-5.48	28	**<0.0001**
Abundance (N)	-0.18	-1.07	28	0.29	-0.42	-2.46	28	**0.019**	-0.39	-2.27	28	**0.03**	-0.67	-4.83	28	**<0.0001**
Evenness (J’)	0.07	-0.38	28	0.7	-0.36	-2.06	28	**0.048**	-0.07	-0.51	28	0.61	-0.51	-3.08	28	**<0.0001**
Shannon-Wiener-diversity (H’)	-0.13	-0.71	28	0.48	-0.34	-1.92	28	**0.064**	0.08	0.42	28	0.67	-0.73	-5.62	28	**<0.0001**
Burrow-wall																
Richness (S)	0.04	0.21	28	0.83	-0.36	-2.06	28	**0.048**	-0.18	-0.98	28	0.33	-0.75	-5.92	28	**<0.0001**
Abundance (N)	0.27	-1.53	28	0.13	-0.46	-2.74	28	**0.009**	-0.47	-2.82	28	**0.008**	-0.74	-5.89	28	**<0.0001**
Evenness (J’)	0.09	0.4	28	0.69	0.08	0.42	28	0.67	0.22	0.94	28	0.35	-0.55	-3.17	28	**<0.0001**
Shannon-Wiener-diversity (H’)	0.17	0.91	28	0.36	-0.18	-1.005	28	0.32	-0.11	-0.61	28	0.54	-0.77	-6.42	28	**<0.0001**

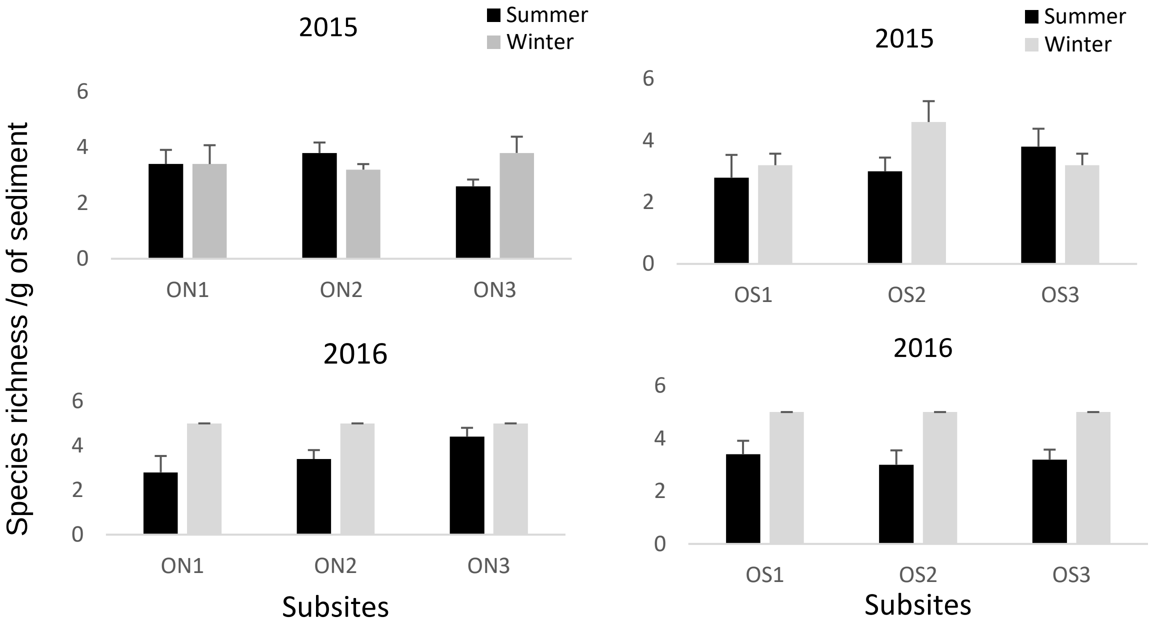

Fig. 3.3A: Spatio-temporal variability in meiofaunal sediment surface richness (means ± 1SE) at three subsites in Oesterwal North (ON1-3) and Oesterwal South (OS1-3).

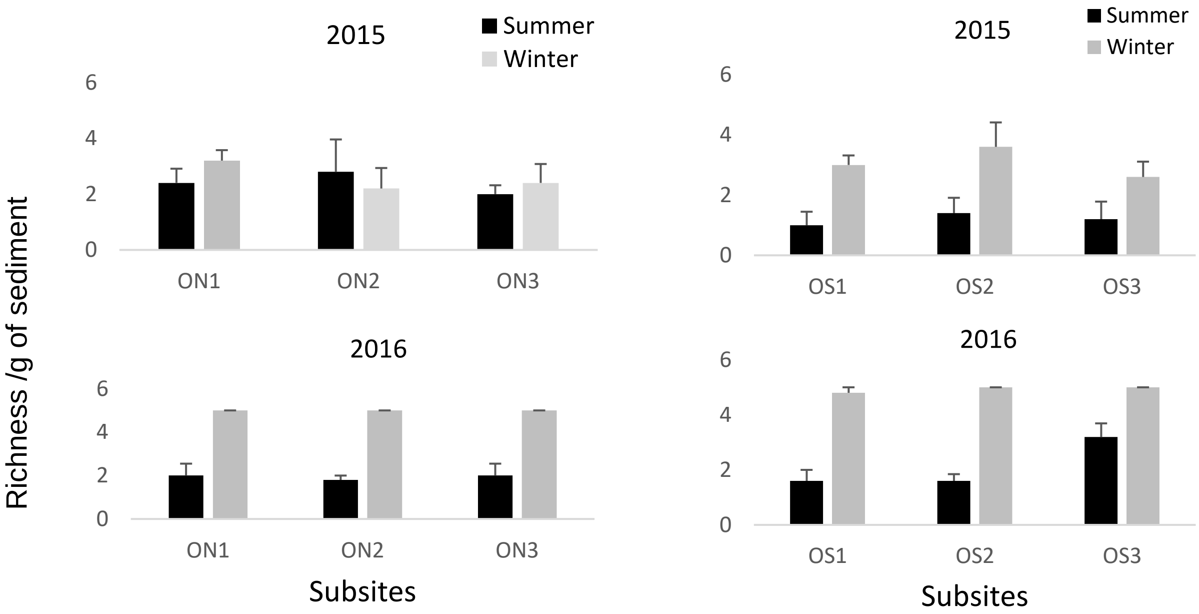

Fig. 3.3B: Spatio-temporal variability in meiofaunal burrow-wall richness (means ± 1SE) at three subsites in Oesterwal North (ON1-3) and Oesterwal South (OS1-3).

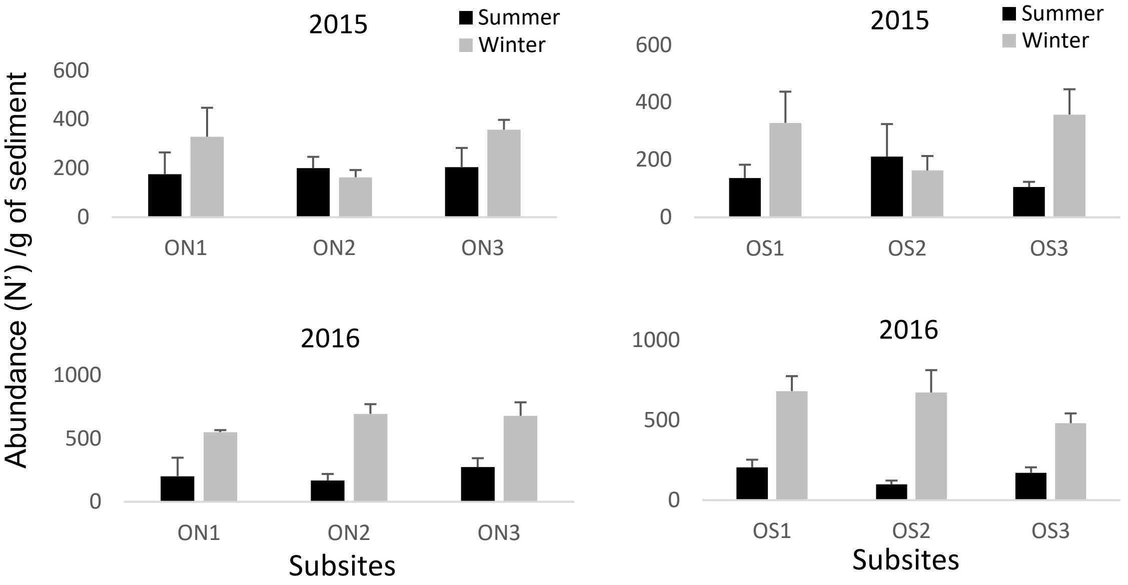

Fig. 3.3C: Spatio-temporal variability in meiofaunal sediment surface abundance (means ± 1SE) at three subsites in Oesterwal North (ON1-3) and Oesterwal South (OS1-3). NB: Y axis scales are different to show the trend in the data.

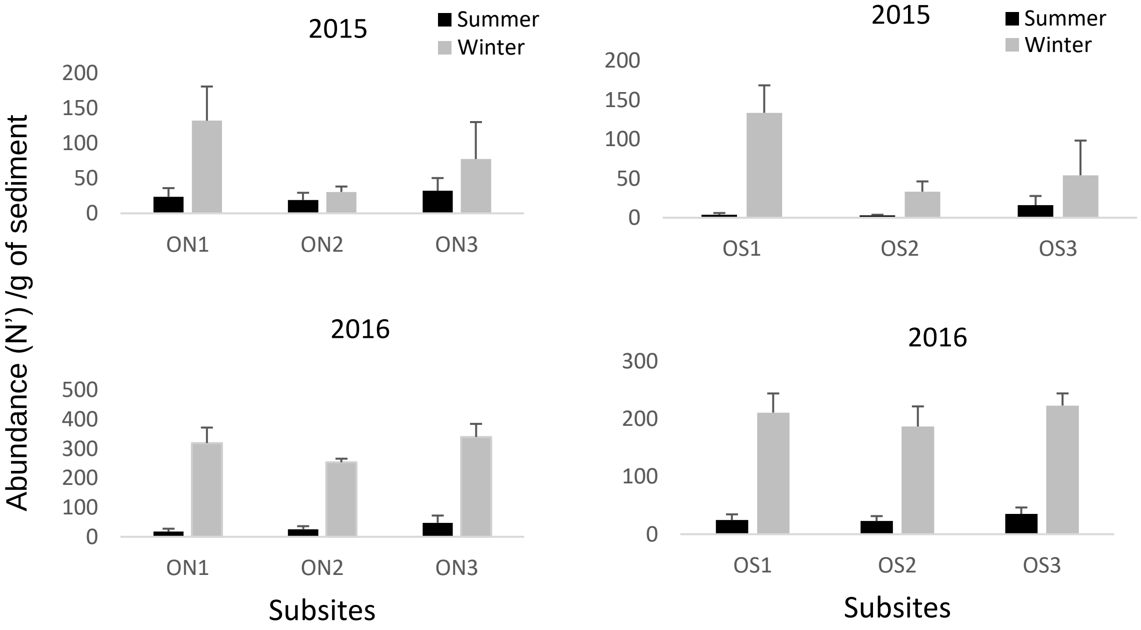

Fig. 3.3D: Spatio-temporal variability in meiofaunal burrow-wall abundance (means ± 1SE) at three subsites in Oesterwal North (ON1-3) and Oesterwal South (OS1-3). NB: Y axis scales are different to show the trend in the data.

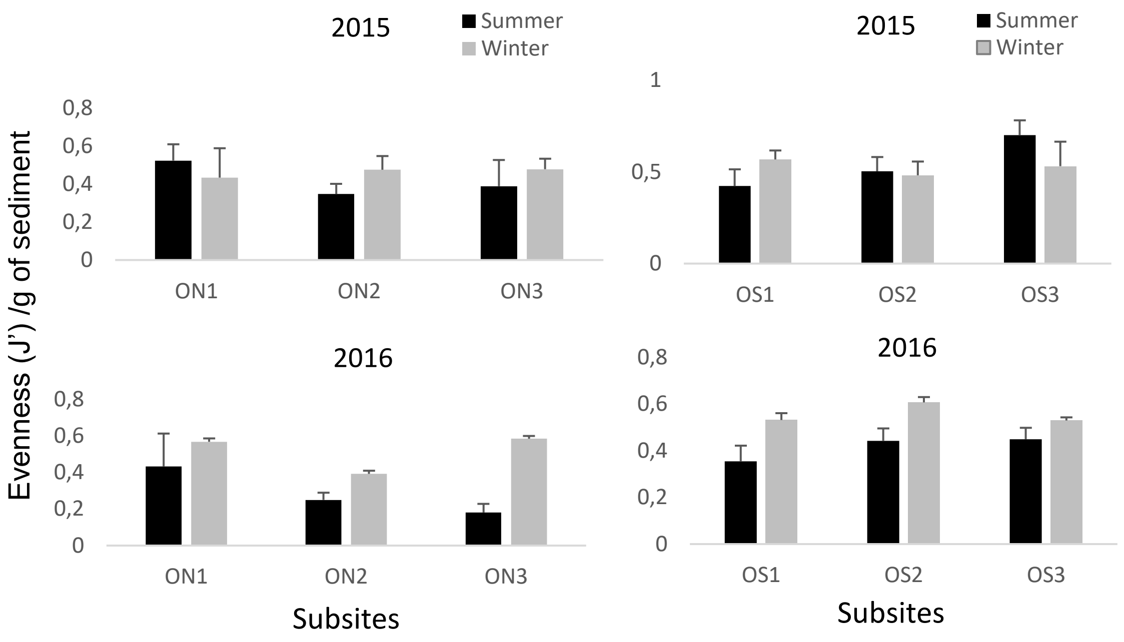

Fig. 3.3E: Spatio-temporal variability in meiofaunal sediment surface evenness (means ± 1SE) at three subsites in Oesterwal North (ON1-3) and Oesterwal South (OS1-3). NB: Y axis scales are different to show the trend in the data.

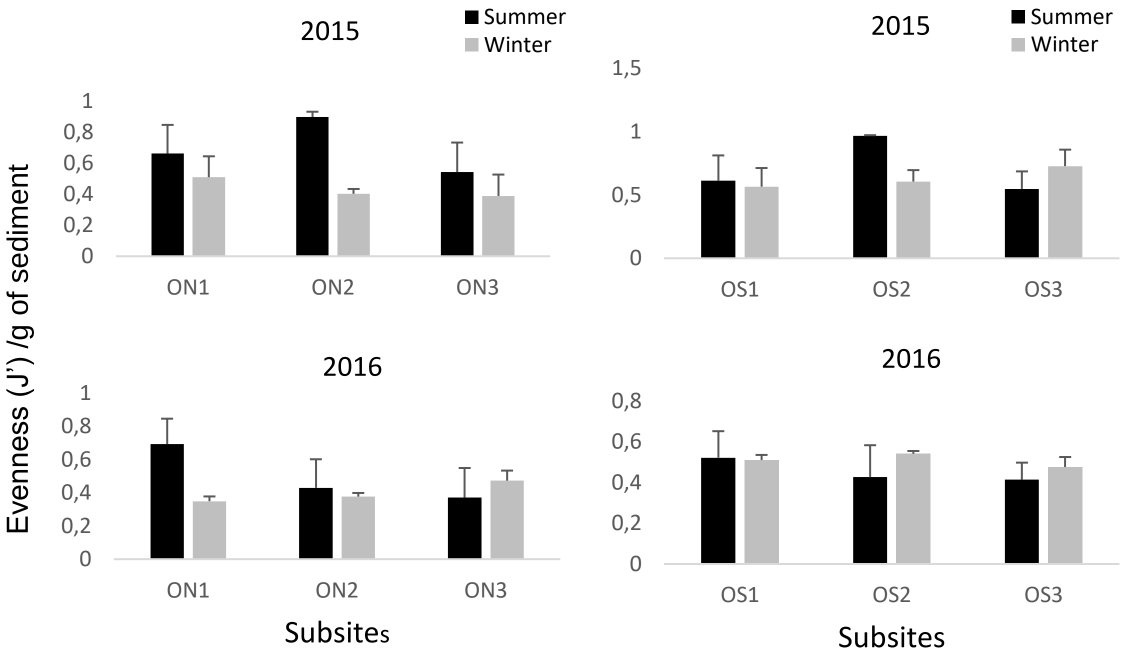

Fig. 3.3F: Spatio-temporal variability in meiofaunal burrow-wall evenness (means ± 1SE) at three subsites in Oesterwal North (ON1-3) and Oesterwal South (OS1-3). NB: Y axis scales are different to show the trend in the data.

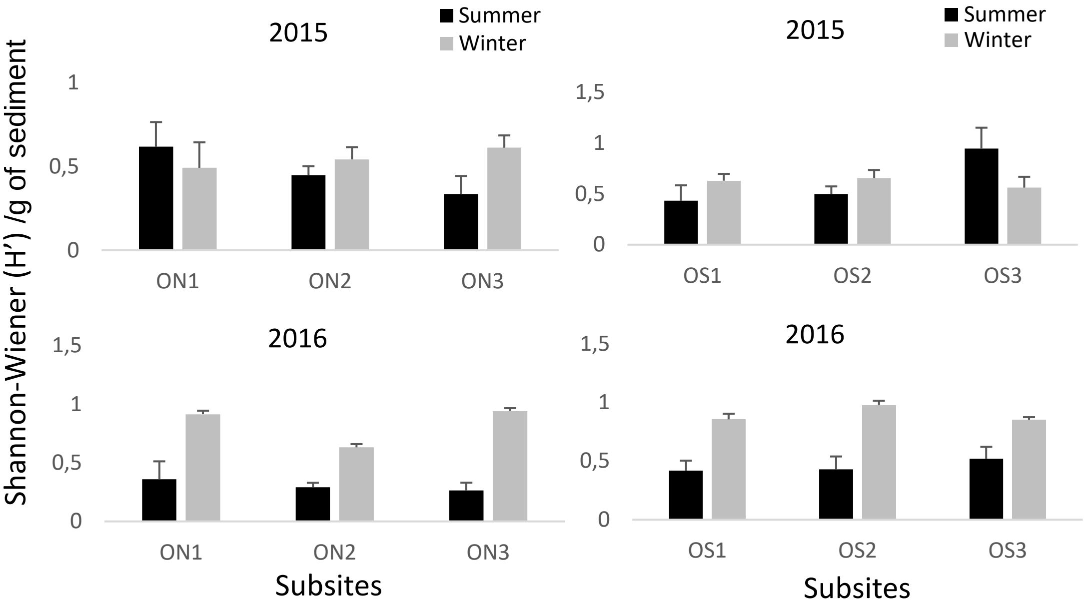

Fig. 3.3G: Spatio-temporal variability in meiofaunal sediment surface Shannon-Wiener diversity (means ± 1SE) at three subsites in Oesterwal North (ON1-3) and Oesterwal South (OS1-3).

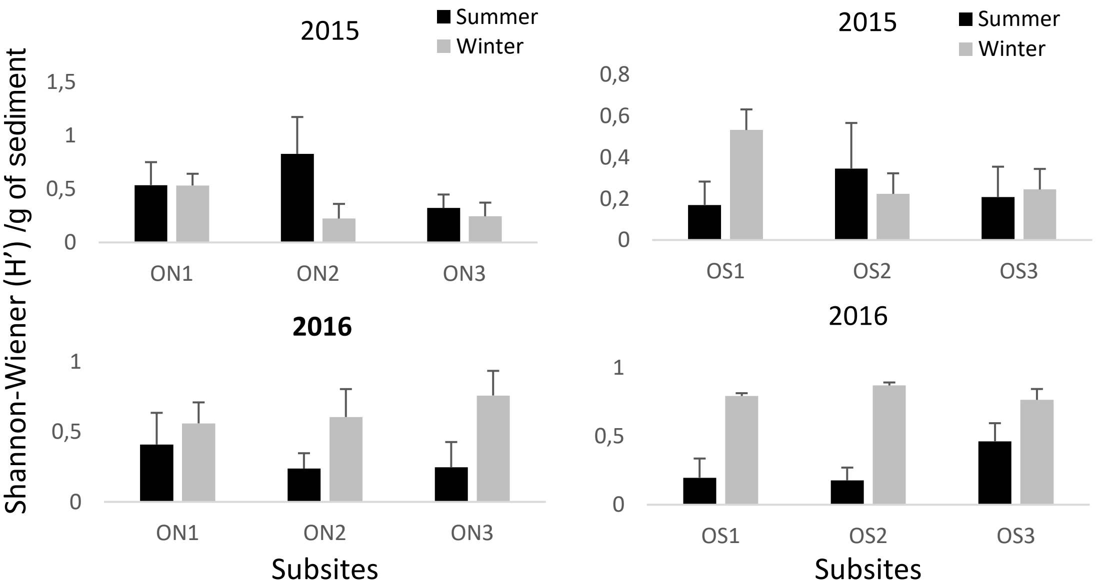

Fig. 3.3H: Spatio-temporal variability in meiofaunal burrow-wall Shannon-Wiener diversity (means ± 1SE) at three subsites in Oesterwal North (ON1-3) and Oesterwal South (OS1-3). NB: Y axis scales are different to show the trend in the data.

3.5.5 Meiofaunal morphotypes

Three out of five meiofaunal morphotypes displayed sufficient variability for the data to meet the modelling assumptions. Of these morphotypes, both copepods and bivalves were predicted by sites and season at the surface sediment ($p < 0.05$ for all cases, **Table 3.10A**), while these factors also predicted nematode abundances at the burrow-wall ($p = 0.042$). Based on the AIC model selection, all these morphotypes were explained by the interactive model between sites and seasons, being the most parsimonious model for them (**Table 3.10B**).

Based on the correlation analysis, with the exception of copepods, all meiofaunal morphotypes were not significantly affected by sandprawn abundances within seasons at both study sites ($p > 0.05$ for all cases, **Table 3.11** and **Table 3.12**). Surface copepod abundances were negatively correlated with sandprawn abundances in both sites ($r = -0.54$, $p = 0.03$, in both cases). Combined winter and summer data analysed per year indicated greater sandprawn impacts on meiofaunal individual morphotypes (**Table 3.13**), particularly in 2016 for Oesterwal South, in which all morphotypes recorded within the surface and burrow-wall positions were strongly influenced by sandprawn abundances ($p < 0.05$, in all cases). Also in 2016, sandprawn abundances significantly affected copepods, bivalves, foraminifera and ostracods at the sediment surface and nematodes and foraminifera within burrow-walls in Oesterwal North ($p < 0.05$, in all cases). In 2015, sandprawn abundances did not influence meiofaunal morphotypes ($p > 0.05$, in all cases) in Oesterwal North, while in Oesterwal both copepods and nematodes at the burrow-wall were significantly affected by sandprawns, along with surface copepods ($r = -0.44$, $p = 0.012$). Most interestingly, sandprawn impacts were negative for all meiofaunal morphotypes (**Table 3.13**).

The overriding pattern that emerged from morphotype responses was a major increase in their abundances in winter for both 2015 and 2016 sampling periods (e.g. copepods and bivalves, and nematodes; **Fig 3.4A and F**). On rare occasions, meiofaunal abundances were enhanced in summer relative to winter. For example, abundances of bivalves (**Fig. 3.4D**) and ostracods (**Fig. 3.4G**) were higher in summer 2015 relative to winter in Oesterwal North of the same year.

Table 3.10A: Likelihood ratio test (LRT) results examining if seasons and sites were important predictors in the models for meiofaunal morphotypes. Statistical descriptions: LRT = test statistic, df = degrees of freedom, *p* – value = significance level. Values in bold indicate statistical significance.

	Sediment surface			**Burrow-wall**		
Response variable	**LRT**	**Df**	***p*-value**	**LRT**	**df**	***p*-value**
Copepods	14.189	7	**0.047**	3.219	5	0.704
Bivalves	21.467	7	**0.003**	5.289	6	0.530
Nematodes	4.496	7	0.721	14.643	7	**0.042**

Table 3.10B: Generalised linear mixed effects models conducted on meiofaunal mophortypes, investigating effects of sites and seasons. Statistical descriptions: Statistical descriptions: AIC = Akaik'es information criterion, df = degrees of freedom. Values in bold indicate the most parsimonious model.

	Sediment surface				**Burrow-wall**	
Models	**Copepods**		**Bivalves**		**Nematodes**	
	Df	**AIC**	**df**	**AIC**	**Df**	**AIC**
Null	10	1178.461	10	403.394	10	1154,985
Sites	11	1179.576	11	399.247	11	1156,971
Seasons	13	1179.032	13	404.333	13	1156,666
Site + Seasons	14	1179.771	14	400.571	14	1158,622
Sites x Seasons	17	**1178.272**	17	**395.927**	17	**1154,525**

Table 3.11: Summary statistics of Pearson correlation analysis testing the relationship between meiofaunal morphotypes (sediment surface and burrow-wall) and sandprawn abundances in Oesterwal North (ON). Statistical descriptions: r = goodness of fit, t = test statistic, df = degrees of freedom, and *p*— value = significance level. Values in bold indicate statistical significance. NB: where correlations are statistically significant, scatter plots are provided on the appendix (**Fig 9.6**).

	Oesterwal North (ON)															
Morphotypes	**Winter 2015**				**Summer 2015**				**Winter 2016**				**Summer 2016**			
Sediment surface	**r**	**t**	**df**	***p*-value**	**R**	**T**	**df**	***p*-value**	**R**	**t**	**df**	***p*-value**	**r**	**t**	**df**	***p*-value**
Copepods	-0.18	-0.66	13	0.51	0.44	1.81	13	0.09	-0.54	-2.3	13	**0.03**	-0.03	-0.12	13	0.9
Nematodes	-0.24	0.91	13	0.37	0.16	0.6	13	0.55	0.24	0.92	13	0.37	-0.14	-0.52	13	0.6
Foraminifera	-0.3	-1.36	13	0.19	0.32	1.22	13	0.24	0.07	0.25	13	0.81				
Ostracods	-0.39	-1.52	13	0.15	-0.22	-0.82	13	0.42	0.12	0.44	13	0.66	-0.32	-1.22	13	0.24
Bivalves					0.23	0.84	13	0.4	0.32	1.24	13	0.23	-0.26	-0.104	13	0.33
Burrow-wall																
Copepods	-0.18	-0.67	13	0.51	0.19	0.72	13	0.48	-0.24	-0.89	13	0.38	-0.26	-0.99	13	0.33
Nematodes	-0.11	-0.42	13	0.67	0.09	0.35	13	0.73	-0.36	-1.42	13	0.17	-0.15	-0.54	13	0.59
Foraminifera					-0.44	-1.7	13	0.09	-0.33	-1.3	13	0.21				
Ostracods					-0.49	-2.01	13	0.06	0.09	0.33	13	0.74				
Bivalves					-0.45	-1.82	13	0.09	0.19	0.71	13	0.48				

Table 3.12: Summary statistics of Pearson correlation analysis testing the relationship between meiofaunal morphotypes (sediment surface and burrow-wall) and sandprawn abundances in Oesterwal South (OS). Statistical descriptions: r = goodness of fit, t = test statistic, df = degrees of freedom, and *p*— value = significance level. Values in bold indicate statistical significance. NB: where correlations are statistically significant, scatter plots are provided on the appendix (**Fig 9.6**).

Oesterwal South (OS)																
Morphotypes	**Winter 2015**				**Summer 2015**				**Winter 2016**				**Summer 2016**			
Sediment surface	**r**	**t**	**df**	***p*-value**	**R**	**t**	**df**	***p*-value**	**R**	**t**	**df**	***p*-value**	**r**	**t**	**df**	***p*-value**
Copepods	-0.28	-1.1	13	0.3	0.11	0.41	13	0.69	-0.54	-2.33	13	**0.03**	-0.12	-0.44	13	0.66
Nematodes	-0.17	-0.62	13	0.54	0.12	0.43	13	0.66	0.24	0.92	13	0.37	-0.29	-1.05	13	0.29
Foraminifera	0.43	1.74	13	0.1	0.32	1.22	13	0.24	0.07	0.25	13	0.8	0.44	1.76	13	0.1
Bivalves					0.31	1.17	13	0.25	0.32	1.24	13	0.23	0.11	0.41	13	0.68
Ostracods									0.12	0.44	13	0.66	0.01	0.04	13	0.96
Burrow-wall																
Copepods	-0.2	-0.74	13	0.46					-0.24	-0.89	13	0.38	0.1	0.39	13	0.7
Nematodes	-0.39	-1.57	13	0.14	-0.09	-0.35	13	0.72	-0.36	-1.41	13	0.17	0.25	0.95	13	0.35
Foraminifera									-0.33	-1.3	13	0.21				
Ostracods									0.09	0.3	13	0.74	-0.39	-1.5	13	0.14
Bivalves									0.19	0.71	13	0.48	0.38	1.49	13	0.15

Table 3.13: Summary statistics of Pearson correlation analysis testing the relationship between meiofaunal morphotypes (sediment surface and burrow-wall) and sandprawn abundances in Oesterwal North (ON) and South (OS) based on combined summer and winter data per year (2015 and 2016). Statistical descriptions: r = goodness of fit, t = test statistic, df = degrees of freedom, and *p*— value = significance level. Values in boldindicate statistical significance. NB: where correlations are statistically significant, scatter plots are provided on the appendix (**Fig 9.7A-G**).

	Oesterwal North (ON)								**Oesterwal South (OS)**							
Morphotypes	**2015**				**2016**				**2015**				**2016**			
Sediment surface	**r**	**t**	**df**	***p*-value**	**r**	**T**	**df**	***p*-value**	**R**	**T**	**df**	***p*-value**	**r**	**t**	**df**	***p*-value**
Copepods	-0.34	-1.95	28	0.06	-0.43	-2.59	28	**0.014**	-0.44	-2.6	28	**0.012**	-0.46	-2.78	28	**0.009**
Bivalves	-0.17	-0.91	28	0.34	-0.37	-2.11	28	**0.043**	0.29	1.63	28	0.11	-0.55	-3.52	28	**0.0014**
Nematodes	-0.05	-0.28	28	0.77	-0.29	-1.62	28	0.11	-0.26	-1.4	28	0.15	-0.71	-5.42	28	**<0.0001**
Foraminifera	0.31	1.77	28	0.08	-0.39	-2.3	28	**0.028**	0.31	1.71	28	0.09	-0.78	-6.71	28	**<0.0001**
Ostracods	0.08	0.45	28	0.64	-0.38	-2.17	28	**0.038**	0.07	0.42	28	0.67	-0.46	-2.78	28	**0.009**
Burrow-wall																
Copepods	-0.11	-0.61	28	0.54	-0.31	-1.76	28	0.088	-0.36	-2.06	28	**0.048**	-0.51	-3.13	28	**0.004**
Bivalves	-0.11	-0.58	28	0.55	-0.25	-1.39	28	0.17					-0.64	-4.48	28	**<0.0001**
Nematodes	-0.26	-1.44	28	0.15	-0.48	-2.96	28	**0.006**	-0.47	-0.82	28	**0.007**	-0.71	-5.35	28	**<0.0001**
Foraminifera	0.17	-0.93	28	0.36	-0.45	-2.7	28	**0.01**	0.007	0.04	28	0.96	-0.72	-5.6	28	**0.001**
Ostracods	-0.12	-0.65	28	0.52	-0.09	-0.48	28	0.63					-0.69	-5.06	28	**0.001**

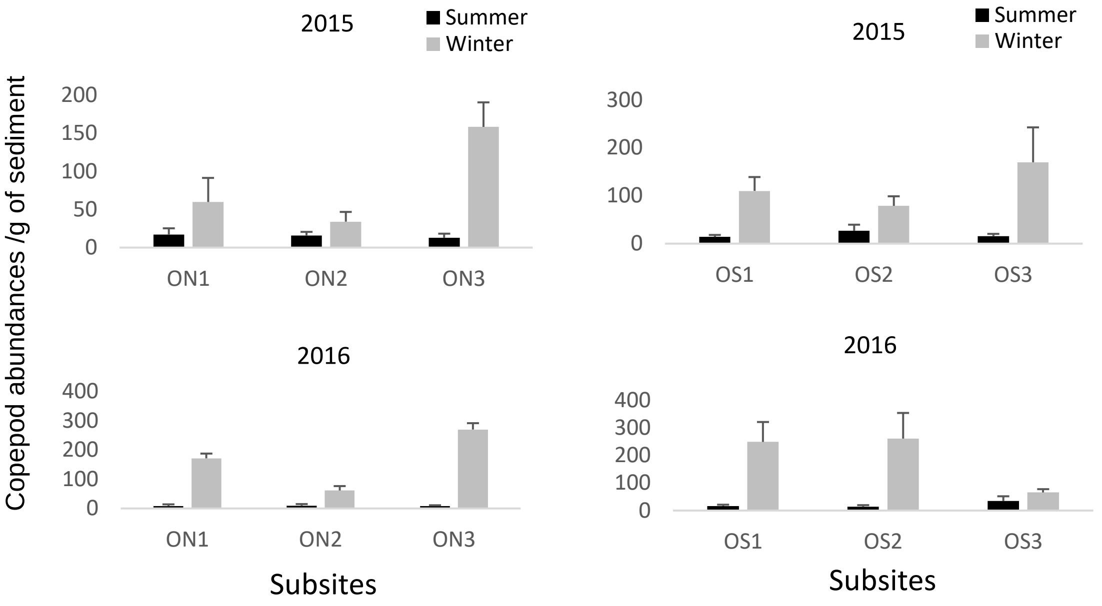

Fig. 3.4A: Spatio-temporal variability in meiofaunal copepod abundances (sediment surface, means ± 1SE) at three subsites in Oesterwal North (ON1-3) and Oesterwal South (OS1-3). NB: Y axis scales are different to show the trend in the data.

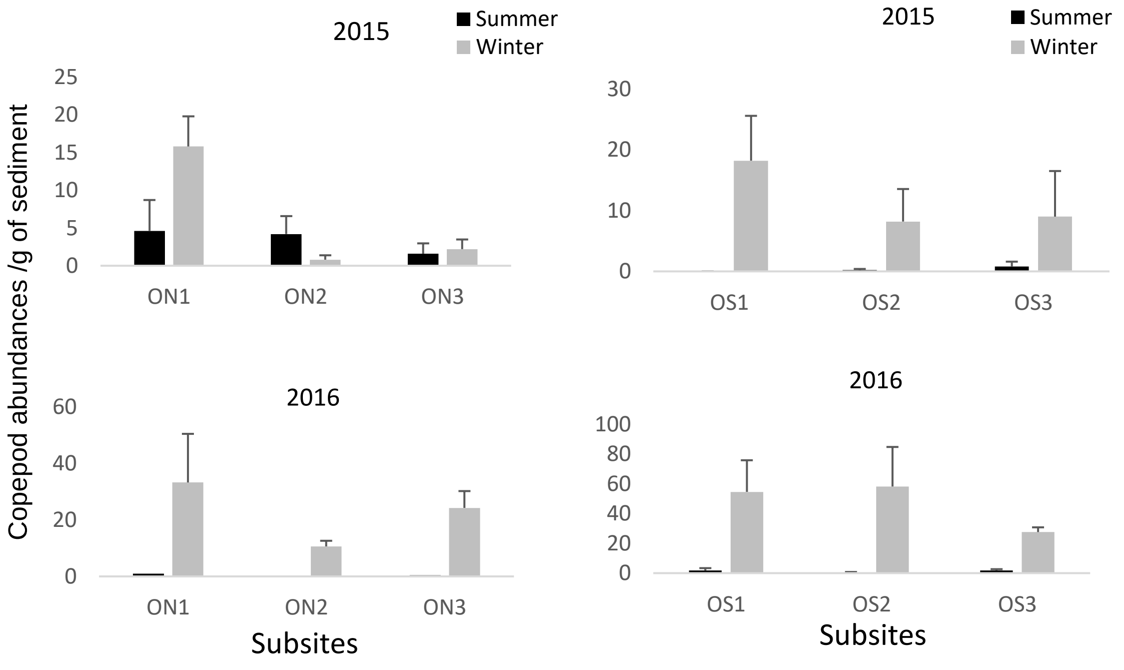

Fig. 3.4B: Spatio-temporal variability in meiofaunal copepod abundances (burrow-wall, means ± 1SE) at three subsites in Oesterwal North (ON1-3) and Oesterwal South (OS1-3). NB: Y axis scales are different to show the trend in the data.

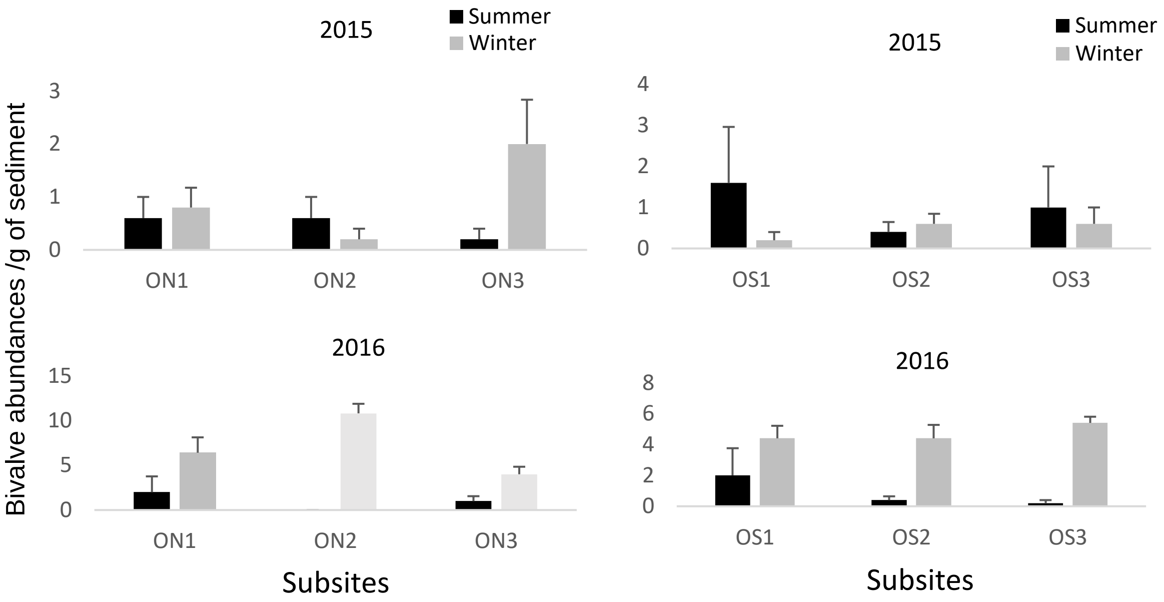

Fig. 3.4.3C: Spatio-temporal variability in meiofaunal bivalve abundances (sediment surface, means ± 1SE) at three subsites in Oesterwal North (ON1-3) and Oesterwal South (OS1-3). NB: Y axis scales are different to show the trend in the data.

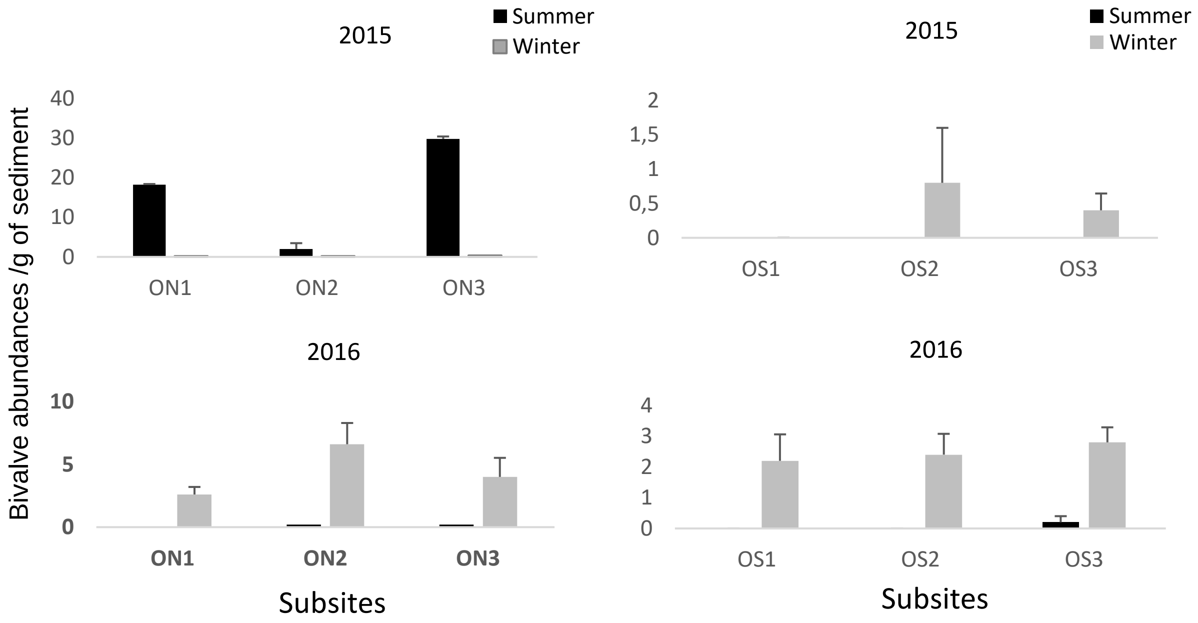

Fig. 3.4D: Spatio-temporal variability in meiofaunal bivalve abundances (burrow-wall, means ± 1SE) at three subsites in Oesterwal North (ON1-3) and Oesterwal South (OS1-3). NB: Y axis scales are different to show the trend in the data.

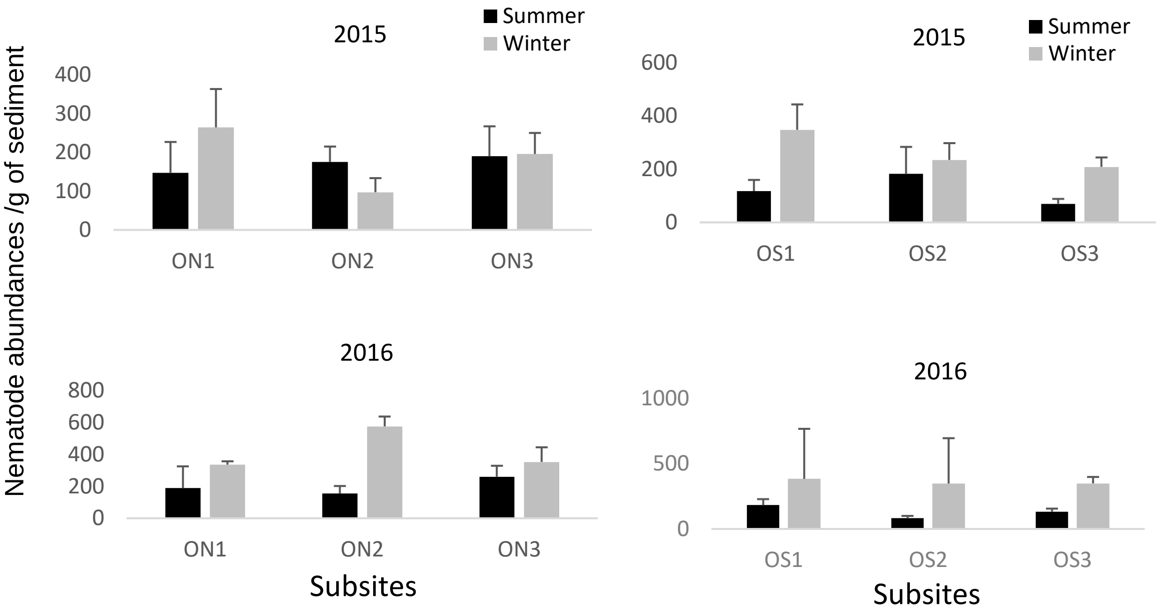

Fig. 3.4E: Spatio-temporal variability in nematode abundances (sediment surface, means ± 1SE) at three subsites in Oesterwal North (ON1-3) and Oesterwal South (OS1-3). NB: Y axis scales are different to show the trend in the data.

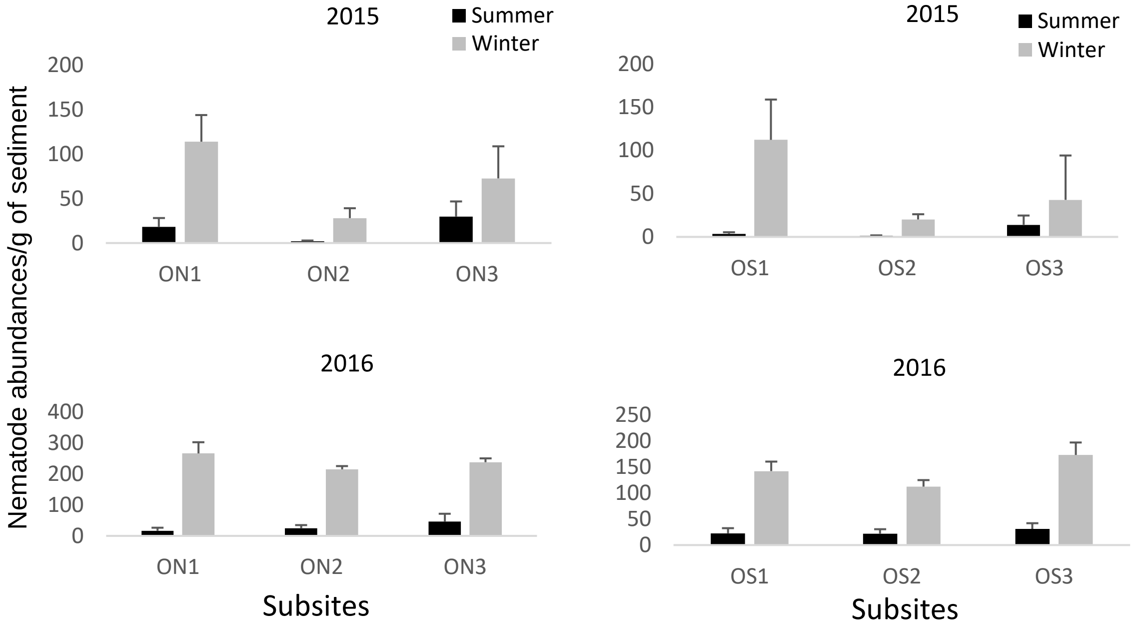

Fig. 3.4F: Spatio-temporal variability in nematode abundances (burrow-wall, means ± 1SE) at three subsites in Oesterwal North (ON1-3) and Oesterwal South (OS1-3). NB: Y axis scales are different to show the trend in the data.

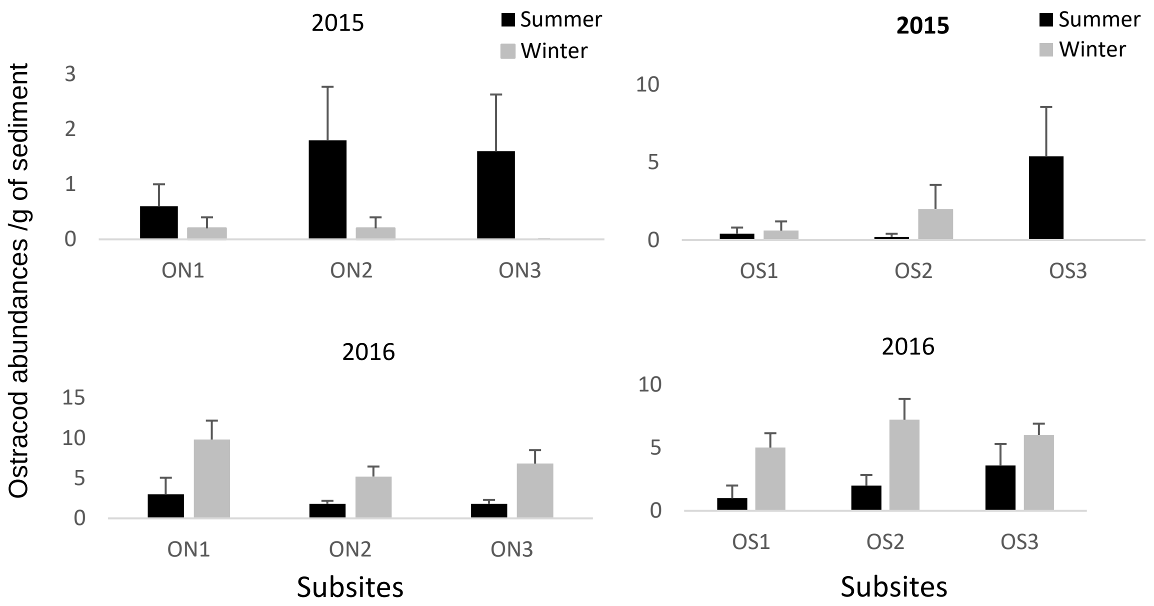

Fig. 3.4G: Spatio-temporal variability in ostracod abundances (sediment surface, means ± 1SE) at three subsites in Oesterwal North (ON1-3) and Oesterwal South (OS1-OS3). NB: Y axis scales are different to show the trend in the data.

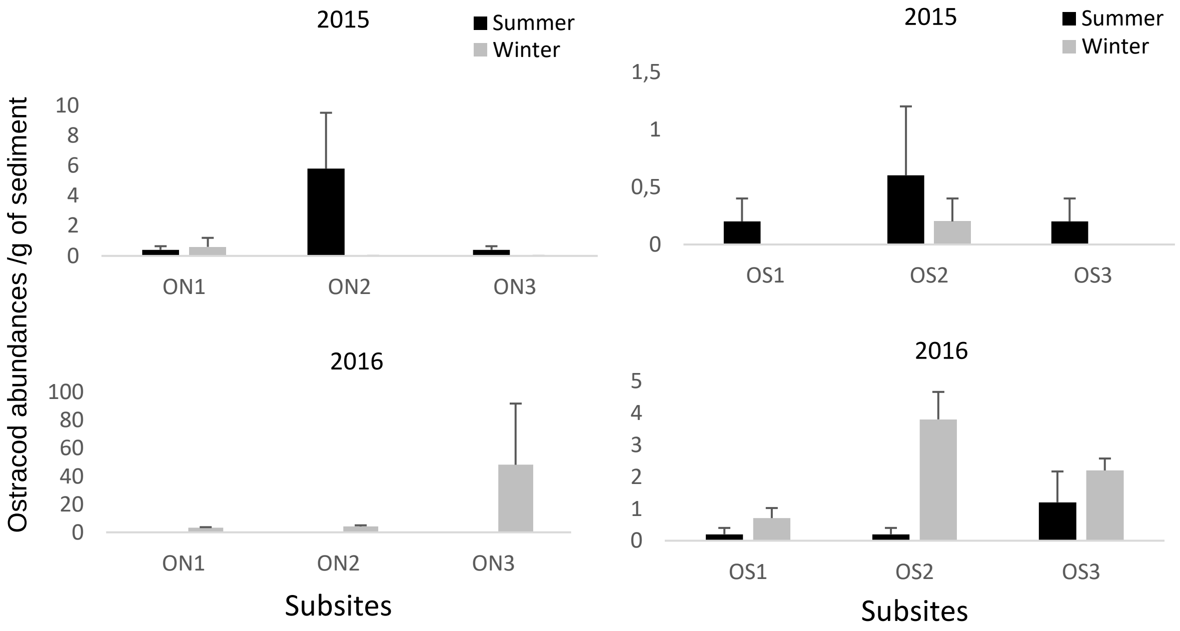

Fig. 3.4H: Spatio-temporal variability in ostracod abundances (burrow-wall, means ± 1SE) at three subsites in Oesterwal North (ON1-3) and Oesterwal South (OS1-3). NB: Y axis scales are different to show the trend in the data.

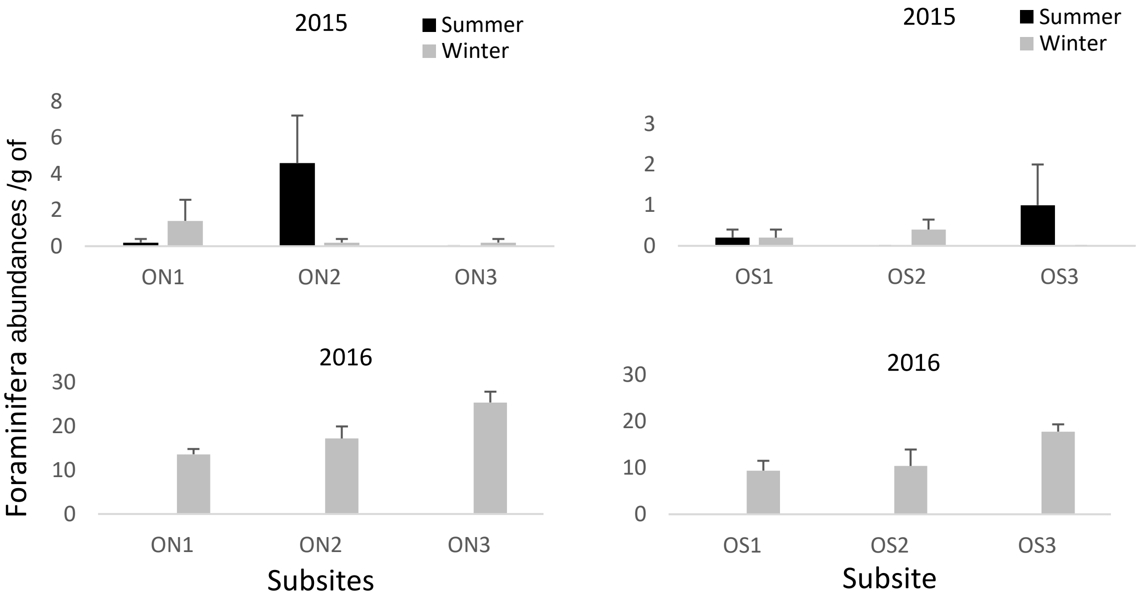

Fig. 3.4I: Spatio-temporal variability in foraminifera abundances (sediment surface, means ± 1SE) at three subsites in Oesterwal North (ON1-3) and Oesterwal South (OS1-3). NB: Y axis scales are different to show the trend in the data.

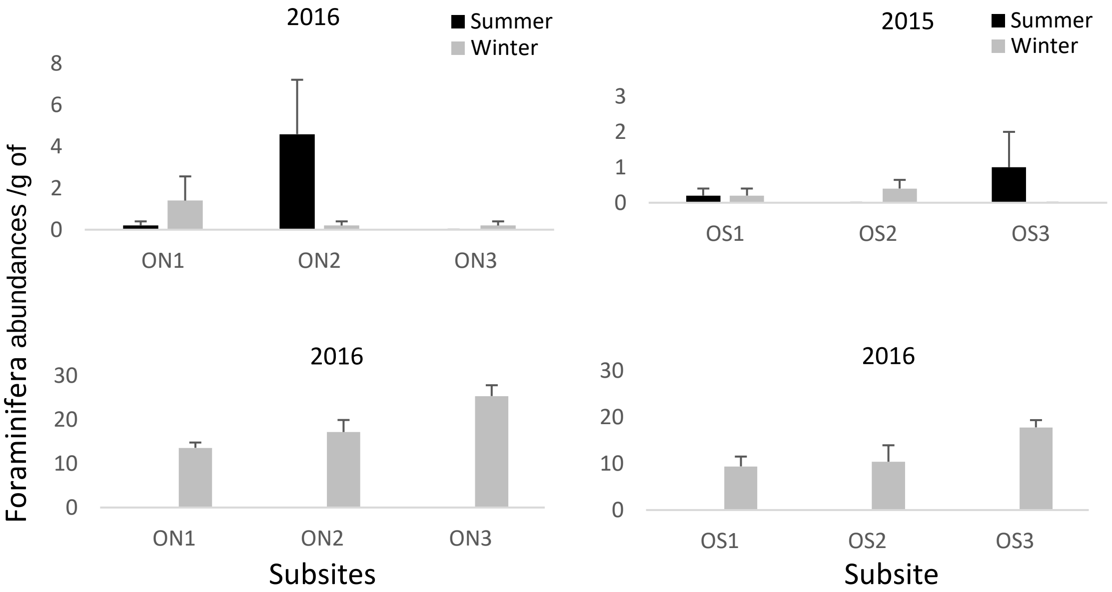

Fig. 3.4J: Spatio-temporal variability in foraminifera abundances (burrow-wall, means ± 1SE) at three subsites in Oesterwal North (ON1-3) and Oesterwal South (OS1-3). NB: Y axis scales are different to show the trend in the data

3. 6 DISCUSSION

The central aim of this chapter was to investigate effects of upwelling on the benthic meiofaunal assemblages in sandprawn-dominated inter-tidal sandflats in Langebaan Lagoon. This aim was based on the potential for season upwelling to act as an important contextual variable that could determine how meiofauna respond to sandprawn (*Callichirus kraussi*) engineering impacts, as outlined in the introduction to this chapter. Based on this aim, I hypothesized that meiofaunal community metrics and water column and sediment chl-*a* would be lower in winter (non-upwelling) but increase in summer in response to upwelling events. The results of this study supported the hypothesis posed for the water column but not sediment chl-*a* concentrations*.* Although the whole community structure of meiofauna was significantly influenced by seasons, community metrics failed to adhere to the hypothesis proposed in this study, which may relate to the low taxonomic resolution at which meiofauna were identified. Nevertheless, Pearson correlation analysis employed to examine the relationship between sandprawn abundances and meiofaunal diversity metrics and individual morphotypes in this study revealed interesting findings, highlighting a potentially important regulatory role for sandprawns on meiobenthic community structure in Langebaan Lagoon sandflats.

3.6.1 Water column chlorophyll-*a* concentrations

Seasonal variation in water column chl-*a* concentrations within the lagoon was an important finding of this study. Generally, chl-*a* levels were markedly higher in summer but lower in winter season (**Fig 3.1**), which supported the hypothesis that chl-*a* concentrations would increase in summer in response to upwelling events. However, an ecologically interesting finding was the steep gradient in column chl-*a* values, being greater close to the mouth (Saldanha Bay) of the lagoon, but becoming progressively diminished toward the middle to upper reaches of the lagoon.

Several processes may explain this gradient pattern of chl-*a* concentrations. Generally, the Langebaan Lagoon system obtains upwelling nutrients via two mechanisms. The firstly involves inflow of cold upwelled Atlantic Ocean waters into Saldanha Bay; this is regulated by the baroclinic pressure gradient between the coastal and embayment domains. The second involves active tidal pumping that transports water from Saldanha Bay through the narrow channels to the Langebaan Lagoon system (Monterio and Largier 1999). Generally, the bay receives phytoplankton limiting nitrate ($N0_3$) directly from the ocean through a density-driven intrusion process that involves rising of the cold upwelled water to about 5m depth. Advected $N0_3$ rich water reaches equilibrium between density-driven force, surface mixing and heating triggered by winds when the upper layer of the thermocline is virtually at 5m depth. Since this is depth regulated process, areas shallower than 5m, which includes the oligotrophic Langebaan Lagoon system, which is on average between 1-2m deep (Flemming 1977) are limited to $N0_3$, consequently resulting in bottleneck in phytoplankton production (Monterio and Largier 1999).

The oceanographic processes described above are therefore critical considerations in understanding temporal patterns in phytoplankton biomass in Langebaan Lagoon. Importantly, while, these processes supply nutrients into the Saldanha Bay-Langebaan Lagoon complex, limitations in the strength of these processes impose constraints on new primary productivity within the lagoon system (Monterio and Largier 1999). Nevertheless, the findings of this study correspond with those of Christie (1981) and Henry *et al.* (1977) who also indicated higher chl-*a* levels in the Langebaan Lagoon in summer. However, the decreasing trend in chl-*a* levels from the mouth to upper reaches of the lagoon suggest that strong oceanic upwelling may not necessarily be translated to equally strong positive effects on phytoplankton biomass through much of the intertidal sandflats of Langebaan Lagoon.

3.6.2 Sediment chlorophyll-*a* concentrations

Patterns in sediment chl-*a* content measured within sandprawn-dominated subsites in this study were unexpected. Firstly, the Likelihood Ratio Test (LRT) confirmed seasons and sites as explanatory variables for chl-*a* concentrations at the sediment surface, with the generalised linear mixed effect model analysis further confirming that an interaction between season and sites affected chl-*a* concentrations. However, the pattern of chl-*a* (**Fig 3.2A** and **B**) was surprizing in that in the first year of sample collection (2015), both surface and burrow-wall chl-*a* levels were markedly higher in winter relative to summer, while this pattern disappeared in 2016, with both summer and winter displaying little variation. Surprisingly, seasons and sites were disapproved by the LRT analysis as predictor variables for chl-*a* concentrations within sandprawn burrow-walls, possibly suggesting that these variables were not responsible for the observed variability in chl-*a* levels.

The results of this study did not conform to the hypothesis posed that, sediment chl-*a* concentrations would increase in response to upwelling in summer on the west coast. Seasonal discrepancies in sediment chl-*a* patterns in this study could in theory be explained by differences in consumer pressure (e.g. grazer densities) on sediment microalgal biomass. Grazers have been reported in several studies to greatly suppress microalgal biomass through grazing pressure in marine soft-sediment ecosystems (Davis and Lee 1983, Underwood and Paterson 1993, Posey *et al.* 1995, Carman *et al.* 1997, Cahoon 1999, Jackson *et al.* 2009, Webb and Eyre 2004, Baggett *et al.* 2010, Dawson and Pillay 2011). However, there was limited evidence of increased grazer abundance in this study either from meiofaunal or macrofaunal data in summer that could explain low benthic chl-*a* levels in this season.

Secondly, sediment chl-*a* concentrations may have proliferated in winter in response to sandprawn abundances, which were generally lower in this season than in summer (see chapter 4**, Fig 4.2A**). This is supported by correlation analyses, which generally showed a negative effect of sandprawns on benthic chl-*a* levels across summer-winter data (**Table 3.4**). These findings potentially reflect the susceptibility of chl-*a* to sandprawn bioturbation (sediment turnover), although, this interpretation is not empirically testable in this study, given that sediment turnover was not explicitly measured. The previous study undertaken by Pillay *et al.* (2007c) observed significant differences in chl-*a* levels between the sites dominated by high densities of *C. kraussi* and those in which sandprawns were rare or absent. Their study revealed that high sandprawn density sites had up to 10 times lower chl-*a* concentrations relative to sites where sandprawns were less dominant. Other studies that have also demonstrated negative relationships between sediment microalgal biomass and sandprawn densities include the work undertaken by Wynberg and Branch (1994), Contessa and Bird (2004) and Pillay *et al.* (2007a, 2007b).

However, it must be pointed out that on occasion, sandprawns have been reported to have positive influences on microalgal biomass (Katrak and Bird 2003, Papaspyrou *et al.* 2005). The latter occurs mainly due to sandprawn burrow-walls being enriched by microalgae and other trophic resources such as bacteria and mucopolysaccharides. This enrichment is mainly facilitated by mucus on the burrow-walls and excretion of nutrients, which promotes microbial and chl-*a* biomass (Papaspyrou *et al.* 2005, Pillay *et al.* 2011).

3.6.3 Meiofaunal community structure, diversity metrics and morphotypes: sediment surface and burrow-walls.

Although the meiofaunal community structure in this study differed significantly between seasons, the hypothesis that diversity metrics will be higher in summer in response to upwelling was not upheld by these findings. Upwelling on the west coast was expected to enhance meiofaunal community diversity metrics in this study with the reverse pattern anticipated to occur during winter (down-welling). Meiofaunal community structure was studied within the context of sediment surface and burrow-wall habitats with the view that communities would differ between these two burrow environments due to sandprawn ecosystem engineering that differentially influences these microhabitats. However, an interesting outcome of this study was that all models performed for the burrow-wall community metrics were refuted by the LRT analysis, indicating that both seasons and sites were unimportant predictors for any of the burrow-wall response variables, suggesting that the above-mentioned factors are not important determinants of variability in burrow-wall metrics. On the other hand, an interaction between sites and seasons influenced sediment surface evenness, while the main effects of sites and season affected surface richness and sites individually affected surface Shannon-Wiener diversity. Thus, for surface meiofauna, site and seasonal variability were significant in regulating meiofaunal community metrics. Taken collectively, findings suggest that the burrow-wall and sediment surface meiofauna may be influenced by different ecological processes.

Meiofaunal diversity metrics generally increased in winter (e.g. richness and Shannon-Weiner diversity; **Fig 3.3 A, B, G** and **H**). This enhancement was not only restricted to metrics, but was apparent for certain individual morphotypes of meiofauna (e.g. copepods, bivalves and nematodes; **Fig. 3.4A-F**). Statistically, copepod and bivalve abundances were predicted by sites and seasons at the sediment surface, while within the burrow-walls, nematode abundances were the only groups to be predicted by these factors. All of these meiofaunal morphotypes were predicted by the interactive model between sites and seasons.

Two possible mechanisms may explain the enhancement of meiofaunal diversity metrics and some individual morphotypes in winter (e.g. nematodes and bilvalves). The firstly mechanism is trophic in nature. In this regard, greater availability of food resources on the sediment in the form of microalgal biomass, which generally, was higher in winter (particularly in 2015), may have led to a strengthening of bottom-up trophic interactions, resulting in higher meiofaunal abundance. This mechanism is supported by several studies that have documented positive relationships between meiofaunal abundances and benthic microalgae in shallow water littoral ecosystems (Decho and Castenholz 1986, Decho and Fleeger 1988, Pinckney and Sandulli 1990).

The second mechanism that can explain higher diversity metrics and abundance of some taxa is based on ecosystem engineering by the sandprawn *Callichirus kraussi*, in the form of sediment turnover. As indicated in the previous section on benthic chl-*a*, sandprawn abundances were generally lower in winter than in summer (see chapter 4**, Fig 4.2A**). Lower winter sandprawn abundance could have indirectly resulted in an increase in meiofaunal metrics and morphotype abundances, due to an attenuation of sediment turnover rates. This could imply that sandprawn impacts on meiofauna in this study were density dependent, and as such, resulted in meiofaunal colonization and proliferation in winter. This interpretation is supported by correlation analyses, indicating that sandprawn abundances exerted weak effects on both these variables within seasons, positively effecting surface sediment richness in winter in Oesterwal South, while negatively affecting burrow-wall evenness in summer. In contrast, when data from summer and winter seasons were combined and investigated annually, correlations were much stronger, indicating strong and negative effects of sandprawn abundance on diversity metrics and morphotypes. However, it must be noted that these effects were site-specific, with strong effects in Oesterwal South in 2016 for diversity metrics (**Table.3.9**) and morphotypes (**Table 3.13**). Such findings are likely to be ascribed to certain unknown local ecological processes and site-specific characteristics.

The findings of correlation analyses are broadly consistent with other studies that have previously indicated negative impacts of sandprawns on an array of benthic communities, including meiofauna (Colin *et al.* 1986, Branch and Pringle 1987, Pillay *et al.* 2011, Pillay and Branch 2011, Henninger and Froneman 2013). However, other studies have reported that burrowing shrimp induce not only adverse but also positive effects on fauna and flora (Posey 1986, Dittmann 1996, Berkenbusch *et al.* 2000, Dumbauld and Wyllie-Echeverria 2000, Berkenbusch and Rowden 2003, Berkernbusch *et al.* 2007). Branch and Pringle (1987) demonstrated positive sandprawn impacts particularly on bacteria, but with negative influences upon meiofauna (Branch and Pringle 1987). Promotive sandprawn effects generally occur within burrow-walls, while negative effects occur on the sediment surface (Branch and Pringle 1987). Generally, burrows are enriched with nutrients and organic matter, which serves as an important food resource for benthic infauna (Waslenchuk *et al.* 1983, Hughes *et al.* 2000, Volkenborn and Reise 2006, Pillay and Branch 2011). Furthermore, burrows provide diverse microclimates below the sediment-water interface for meiofauna, while also providing important niches for microbes. As such, burrow environments are thought to be more favorable habitats for meiobenthic communities than the overlying water column (Volkenborn and Reise 2006, Pillay and Branch 2011).

3.7 CONCLUSION

In conclusion, results of this chapter provide strong evidence that west coast summer upwelling enhances water column chlorophyll-*a* levels in Langebaan Lagoon, but this does not apparently lead to corresponding positive bottom-up effects on meiofauna. In addition, sediment chlorophyll-*a* patterns were inversely related to those of the water column, which consistently followed the prediction of higher values in the summer upwelling season. Thus it is very possible that in Langebaan Lagoon and similar systems, upwelling processes do not necessarily enhance benthic primary and secondary production (in the form of meiofaunal abundance). It is likely that complex and intricate ecological processes lead the mismatch in chl-*a* and microphytobenthic and meiofaunal metrics that were recorded. While explicit identification of these processes was beyond the scope of this chapter, it did shed light on one potential biotic mechanism that could explain this mismatch viz. ecosystem engineering. Based on correlation analysis, it appears that sandprawns may induce negative impacts on benthic meiofauna and chlorophyll-*a*, potentially overriding potential bottom-up effects of upwelling.

CHAPTER 4

EFFECTS OF UPWELLING ON **MACROFAUNAL** COMMUNITIES IN SANDPRAWN-DOMINATED SEDIMENTS

4. Introduction

4.1 Habitat complexity and ecosystem engineering

The repercussions of ecosystem engineering for ecological functioning, biodiversity and community composition are well addressed in the literature (Jones *et al.* 1994, 1997b, Bouma *et al.* 2009, Sueiro *et al.* 2013, Passarelli *et al.* 2014). Engineering organisms modify the physical structure of ecosystems by their actions (allogenic) or presence (autogenic), thereby altering local heterogeneity, complexity and consequently, biotic use of habitats (Jones *et al.* 1994, 1997b, Crooks 2002). Of the above-mentioned ecological aspects, studies have shown that habitat complexity plays a particularly influential role in structuring biotic communities (McCoy and Bell 1991, Lassau and Hochuli 2004). Habitat complexity generally refers to the level of heterogeneity in the structural attributes of a habitat (Lassau and Hochuli 2004, Taniguchi and Tokeshi 2004, Tokeshi and Arakaki 2012). It therefore indicates the quantity, assortment and traits of structural components of a habitat (McCoy and Bell 1991). In the context of ecosystem engineering, alterations of habitat complexity through abiotic modification is a significant mechanism by which organisms (engineers) modify community structure and ecosystem functioning (Hastings *et al.* 2007, Bouma *et al.* 2009).

Studies have generally shown that increasing environmental complexity is often associated with increases in particular community metrics or descriptors, such as species richness or diversity (Dean and Connell 1987a, Crooks 2002, Bouma *et al.* 2009, Matias *et al.* 2010). The underlying mechanism thought to drive this facilitative effect is that compound habitat structures increase niche availability and diversity (e.g. microhabitats), while increasing levels of trophic and non-trophic resources (Connor and McCoy 2001, Eckman *et al.* 2003, Lejart and Hily 2011, Kovalenko *et al.* 2012). While several studies have reported facilitative effects of habitat complexity on community metrics, others have reported neutral effects, with habitat structure not resulting in expected increases in abundance or diversity (Bourget *et al.* 1994, Kelaher 2003, Lassau and Hochuli 2004). Failure to detect positive effects of complexity on community metrics suggests that the relationship between habitat structure and assemblage descriptors is not simple, and is likely dependent on biotic and abiotic contexts.

The relationship between habitat structure and benthic communities has received much attention in marine coastal ecosystems (Gray and Elliott 2009, Lu *et al.* 2008, Van der Zee *et al.* 2015, Carvalho *et al.* 2017). Consistent with general trends in the literature, different findings have been reported, with some studies failing to detect positive influences of habitat complexity on sympatric communities. For example, a recent study by Carvalho *et al.* (2017) found no positive response of macrofaunal species diversity, richness and abundance as a result of increasing habitat complexity due to differences in sediment fractions. Their findings were consistent with those of Bourget *et al.* (1994), who also reported no positive response of benthic macrofaunal diversity due increases in the number and types of crevices on rock reefs. Similarly, on rocky substrate, Kelaher (2003) manipulated densities of carolline algal fronds and detected no positive influence on gastropods diversity. However, Sueiro *et al.* (2011) reported that species richness and diversity were positively related to increasing habitat complexity provided by cordgrass-mussel, mussel and barnacle-engineered habitats.

A number of factors are likely to account for discrepancies in results of the different studies. One of the most important contributors is the variation in scales and measurements used to quantify habitat structural components (Tews *et al.* 2004). The use of different terminologies, e.g. spatial heterogeneity, habitat architecture and structural complexity, also creates ambiguity in describing and quantifying habitat structure. Some of these terminologies are subjective and thus have different meanings, which further makes comparisons and synthesis between different studies difficult (Tews *et al.* 2004).

In marine sedimentary ecosystems, sediment stabilisation and destabilisation are key processes that influence heterogeneity, complexity and community dynamics. For example, extracellular polymeric substances (EPS) produced by microalgae and bacteria play a significant role in stabilizing sediment (Wotton 2004b) and promoting laminar flow of over-lying water (Paterson and Hagerthey 2001). EPS is known to coat the sediment surface, create biofilms and facilitate recruitment (Pillay *et al.* 2007). Sediment stabilisation can also largely achieved by autogenic structures, which are commonly produced by plants. For example, complexity in seagrass meadows has been shown to influence both meiofaunal behaviour and colonization (Palmer 1988, Cummings and Ruber 1987, Bell and Hicks 1991, Guerrini *et al.* 1998), while also enhancing bivalve settlement (Wilson 1990, Reusch and Chapman 1995, Grizzle *et al.* 1996, Reusch *et al.* 1999). Both active dispersal and passive recruitment are important mechanisms by which seagrass meadow structure communities (Moore 2004, Van der Heide *et al.* 2008). Active dispersal involves migration of organisms within and between seagrass patches, which allows them to select suitable habitat for settlement (Sogard 1989), while passive recruitment is associated with hydrodynamic forces being attenuated by seagrass meadows, which allows for settlement of benthic organisms (Ward *et al.* 1984, Fonseca and Fisher 1986, Bos *et al*. 2007, Eklof *et al*. 2011). Similarly, mussels are known for increasing habitat complexity and biodiversity through provision of important trophic and non-trophic resources from microalgal growth on their shells, attenuating currents speeds for the settlement of organisms and also for providing refuge for many other organisms (Suchanek 1992, Bertness *et al.* 2006, Sadchatheeswaran *et al.* 2015).

Sediment stabilisation can also be achieved through burrow construction by invertebrates, due to the binding effects of mucus secretions that hold burrows together. Burrows also increase habitat complexity for the infauna with specific components of burrow structures functioning as microhabitats that harbour unique microbes and meiofauna (Volkenborn and Reise 2006, Kristensen 2008). A classic example of this would be the burrows of sesarmid (*Grapsidae*) and fiddler (*Ocypodidae*) crabs, which are known for their complex morphologies (Volkenborn and Reise 2006). These burrows have an important facilitatory effect on other species in providing refuge from predation, increasing availability of trophic resources and functioning as refugia from adverse environmental conditions (Branch and Pringle 1987, Warren 1990, Kristensen 2008, Volkenborn and Reise 2006, Bouma *et al.* 2009). Furthermore, sediment sorting, which is affected by burrowing invertebrates (Pillay and Branch 2011), can also influence habitat complexity (Lu *et al.* 2008). Sediment with a large number of sediment fractions is therefore considered complex and would likely provide several niches to support a large number of macrofaunal species and functional groups, compared to sediments that are well sorted (Gray and Elliott 2009).

Axiidean crustaceans are a ubiquitous group of decapod crustaceans that have long been known for their substantial influence on intertidal and shallow subtidal soft sediment ecosystems (Swif 1993, Cade´e 2001). For example, Berkenbusch and Rowden (2003) described ghost shrimp, *Callianassa filholi* as a key allogenic ecosystem engineer with major influences on macrofaunal assemblages over a small spatial scale through its large per capita bioturbation activity. Loverock *et al.* (2010) illustrated that bioturbating shrimp *Upegebia deltaura* and *Callianassa subterranea* can modify the structure and diversity of marine bacteria communities.

In Southern Africa, burrowing sandprawns (*Callichirus kraussi*) dominate soft-sediment habitats in estuaries and shallow water coastal systems (Branch *et al*. 2010). These macro-faunal benthic organisms generate striking effects on resident biota through their bioturbative activities (Pillay *et al*. 2007a, 2007c). Like other endobenthic engineers, sandprawns increase habitat complexity by creating burrows in which they live, which in turn offers several new microhabitats in sediments (Pillay *et al.* 2007b), but also potentially food availability for associated benthic infauna (Branch and Pringle 1987). For example, organic matter derived from detritus and micro-benthos often accumulates within sandprawn burrows, and thus becomes trophic resource for benthic infauna (Papaspyrou *et al*. 2005). Elevated bacterial biomass has also been linked with burrow walls relative to areas without burrows (Branch and Pringle 1987, Pillay and Branch 2011). However, while burrow construction increases below-ground complexity, sediment turnover to the sediment-water interface may reduce complexity by homogenising the sediment and eliminating autogenic structures (Bouma *et al.* 2009). Thus the net effects of burrowing sandprawns on community structure depends on the strength of habitat creation and destruction.

Effects of ecosystem engineering by sandprawns are also contigent upon wider environmental contexts that are temporally and spatial variable (Lawton 1983). The environmental context of interest in this study was the variation in background nutrient levels modulated by seasonal upwelling. In view of the background ideas about habitat complexity created by sandprawns, the primary goal of this chapter was to investigate, based on field observations, how macrofaunal communities respond to sandprawn effects within an area influenced by seasonal upwelling. While habitat complexity is not directly tested or quantified in this chapter, it is inferred from sandprawn abundance, which determines the level of below-ground complexity present in benthic systems, mainly though the abundance of burrows constructed. It is expected that variation in background nutrients levels will determine how macrofaunal assembleges respond to sandprawn engineering. Specifically, upwelling in Langebaan Lagoon should enhance macrofaunal community metrics through food provision (mainly chlorophyll-*a*). This should counteract any negative sandprawn impacts due to sediment turnover. The secondary goal was to understand whether the strength of engineering by sandprawns on community metrics, functional groups and individuals was altered by nutrient pulses. This was achieved using a correlative *in situ* approach.

4.2 Hypotheses

The following broad hypotheses were tested.

> **H1:** Macrofaunal community structure in *C. kraussi* dominated sandflats should differ between upwelling and non-upwelling seasons. In particular, community metrics (e.g. abundance, richness) should be greater during upwelling events due to increased availability of trophic resources.
>
> **H2**: Macrofaunal community metrics (such as diversity) would be reduced with increasing *C. kraussi* densities due to sediment turnover during non-upwelling seasons (when nutrients are low) but this trend would weaken or reverse during summer upwelling seasons due to increased trophic resources offsetting sediment turnover effects.

- **METHODS AND MATERIALS**

Please refer to chapter 2 for the methods used in this chapter.

4.3 RESULTS

4.3.1 Macrofaunal community structure: overall composition

Macrofaunal community structure differed significantly between upwelling and non-upwelling seasons (PERMANOVA, Pseudo-$F_{3,\,119}$ = 10.695, *p* = 0.001: **Table 4.1**). There was a highly significant effect of sites on macrofaunal community structure (PERMANOVA, Pseudo-$F_{1,\,119}$ = 9.7764, *p* = 0.001), while at the subsite level, macrofaunal community structure did not differ significantly (PERMANOVA, Pseudo-$F_{2,\,119}$ = 1.6338, *p* = 0.067). PERMANOVA also detected a strong interactive effect of seasons and sites on the macrofaunal community structure (Pseudo-$F_{3,\,119}$ = 2.3133, *p* = 0.001). On the other hand, seasons, sites and subsites failed to interact and significantly influence macrofaunal community structure (PERMANOVA, Pseudo-$F_{6,\,119}$ = 1.4264, *p* = 0.058). Similarly, sites and subsites interaction had no significant effect on macrofaunal community structure (PERMANOVA, Pseudo-$F_{2,\,119}$ = 1.7453, *p* = 0.062).

Table 4.1: Summary statistics of PERMANOVA analysis testing macrofaunal community structure responses to seasons, sites and subsites as well as interactions. Statistical descriptions: *Pseudo-F* = test statistic, df = degrees of freedom, *p* – value = significance level. Values in bold indicate statistical significance.

Factors	***Pseudo-F***	**Df**	***p*-value**
Seasons	10.695	3	**0.001**
Sites	9.7764	1	**0.001**
Subsites	1.6338	2	0.067
Seasons x Sites	2.3133	3	**0.001**
Seasons x Subsites	1.087	6	0.293
Sites x Subsites	1.7453	2	0.062
Seasons x Sites x Subsites	1.4264	6	0.058

4.3.2 Community metrics

The likelihood ratio test (LRT) performed on the macrofaunal community metrics indicated that evenness (J') variation was predicted by effects of sites and seasons ($p = 0.030$, **Table 4.2A**). All other metrics were refuted by the LRT procedure ($p > 0.05$, for all cases), suggesting that variability in these metrics were not site or season dependent. For evenness, the model with sites only was identified by the Akaike's Information Criterion (AIC) model base selection to be the best predicting model for macrofaunal evenness (**Table 4.2B**). Visual trends in the data suggest a strong seasonal variation in diversity metrics, being higher in winter 2015 than in summer, especially for abundance, richness and Shannon-Wiener diversity (**Fig 4.1A and B and D**). This pattern was not strong in 2016 though.

The correlation test performed on the macrofauna community metrics per site during each season indicated evenness (J') and abundance (N) to be the only diversity metrics affected by sandprawn abundances (**Table 4.3**). Evenness was influenced by sandprawn abundance in Oesterwal North in summer 2016, with the correlation analysis suggesting a negative relationship between these variables (r = -0.66, $p = 0.006$), while abundance was positively affected by sandprawns in Oesterwal South in winter 2016 (r = 0.52 $p = 0.045$). On the other hand, sandprawn abundances had a marginally non-significant effect on evenness (r = -0.5, $p = 0.051$) in Oesterwal North in summer 2015 and Shannon-Wiener diversity (r = -0.49, $p = 0.051$) in Oesterwal South in winter 2015. All other metrics were unaffected by sandprawn abundances ($p > 0.05$, in all cases, **Table 4.3**). When summer and winter data per year were explored, sandprawn effects on macrofaunal diversity metrics were only detected in 2015 for both sites (**Table 4.4**). Richness (r = -0. 45, $p = 0.012$) and abundance (r = -0.37, $p = 0.04$) were both negatively influenced by sandprawn abundances in Oesterwal North, while evenness (r = 0. 44, $p = 0.013$) and richness (r = -0.5, $p = 0.004$) were affected in Oesterwal

South. In the former case, sandprawn effects were positive, but negative effects were recorded in the latter case.

Table 4.2A: Likelihood ratio test (LRT) results examining if seasons and sites were important predictors in the models for macrofaunal community metrics. Statistical descriptions: LRT = test statistic, df = degrees of freedom, *p* – value = significance level Values in bold indicate statistical significance.

Macrofaunal diversity matrices	LRT	Df	*p*-value
Richness (S)	10.134	6	0.149
Abundance (N)	2.120	6	0.911
Evenness (J’)	14.778	6	**0.030**
Shannon Wiener diversity (H’)	12.338	6	0.056

Table 4.2B: Generalised linear mixed effects models conducted on the macrofaunal community metrics, investigating effects of sites and seasons. Statistical descriptions: AIC = Akaike’s information criterion, df = degrees of freedom. Values in bold indicate the most parsimonious model.

	Evenness (J’)	
Candidate models	**Df**	**AIC**
Null	10	-166.162
Sites	11	**-164.360**
Seasons	13	-170.445
Site + Seasons	14	-168.489
Sites x Seasons	17	-167.856

Table 4.3: Summary statistics of Pearson correlation analysis testing the relationship between macrofaunal community metrics and sandprawn abundances in Oesterwal North (ON) and South (OS). Statistical descriptions: r = goodness of fit, t = test statistic, df = degrees of freedom, and *p*— value = significance level. Values in bold indicate statistical significance. NB: where correlations are statistically significant, scatter plots are provided on the appendix (**Fig 9.8**).

								Oesterwal North (ON)								
Community metrics	**Winter 2015**				**Summer 2015**				**Winter 2016**				**Summer 2016**			
	r	**t**	**df**	***p*-value**	**R**	**t**	**df**	***p*-value**	**R**	**t**	**df**	***p*-value**	**r**	**t**	**df**	***p*-value**
Richness (S)	0.21	0.8	13	0.43	-0.34	-0.33	13	0.2	0.2	0.75	13	0.46	0.29	1.1	13	0.29
Abundance (N)	-0.2	-0.75	13	0.46	0.001	0.0006	13	0.99	0.47	1.9	13	0.07	0.25	0.94	13	0.36
Evenness (J’)	0.12	0.46	13	0.65	0.5	2.1	13	0.051	-0.07	-0.26	13	0.79	-0.66	-3.21	13	**0.006**
Shannon-Wiener-diversity (H’)	0.21	0.77	13	0.45	0.11	0.41	13	0.62	-0.002	-0.01	13	0.99	-0.36	-1.39	13	0.18
								Oesterwal South (OS)								
Richness (S)	0.0005	0.021	13	0.98	-0.36	-1.4	13	0.18	0.29	1.17	13	0.28	0.34	1.31	13	0.21
Abundance (N)	0.06	0.24	13	0.81	0.144	0.5	13	0.6	0.52	2.21	13	**0.045**	0.49	2.05	13	0.06
Evenness (J’)	0.36	1.47	13	0.17	0.43	1.73	13	0.1	-0.03	-0.13	13	0.89	0.13	0.49	13	0.62
Shannon-Wiener-diversity (H’)	0.49	2.06	13	0.051	-0.12	-0.44	13	0.66	0.33	1.27	13	0.22	0.21	0.78	13	0.44

Table 4.4: Summary statistics of Pearson correlation analysis testing the relationship between macrofaunal community metrics and sandprawn abundances in Oesterwal North (ON) and South (OS) based on combined summer and winter data per year (2015 and 2016). Statistical descriptions: r = goodness of fit, t = test statistic, df = degrees of freedom, and *p*— value = significance level. Values in bold indicate statistical significance. NB: where correlations are statistically significant, scatter plots are provided on the appendix (**Fig 9.9**).

Oesterwal North (ON)								
Community metrics	**Year 2015**				**Year 2016**			
	r	**t**	**df**	***p*-value**	**r**	**T**	**df**	***p*-value**
Richness (S)	-0.45	-2.6	28	**0.012**	0.17	0.96	28	0.34
Abundance (N)	-0.37	-2.1	28	**0.04**	0.03	0.17	28	0.86
Evenness (J’)	0.18	0.99	28	0.32	-0.07	-0.38	28	0.74
Shannon-Wiener diversity (H’)	-0.22	-1.2	28	0.22	0.0001	0.0003	28	0.99
Oesterwal South (OS)								
Richness (S)	-0.5	-3.01	28	**0.004**	0.12	0.63	28	0.52
Abundance (N)	-0.31	-1.78	28	0.08	0.28	1.6	28	0.12
Evenness (J’)	0.44	2.64	28	**0.013**	-0.14	-0.8	28	0.43
Shannon-Wiener diversity (H’)	-0.11	-0.61	28	0.54	0.02	0.13	28	0.89

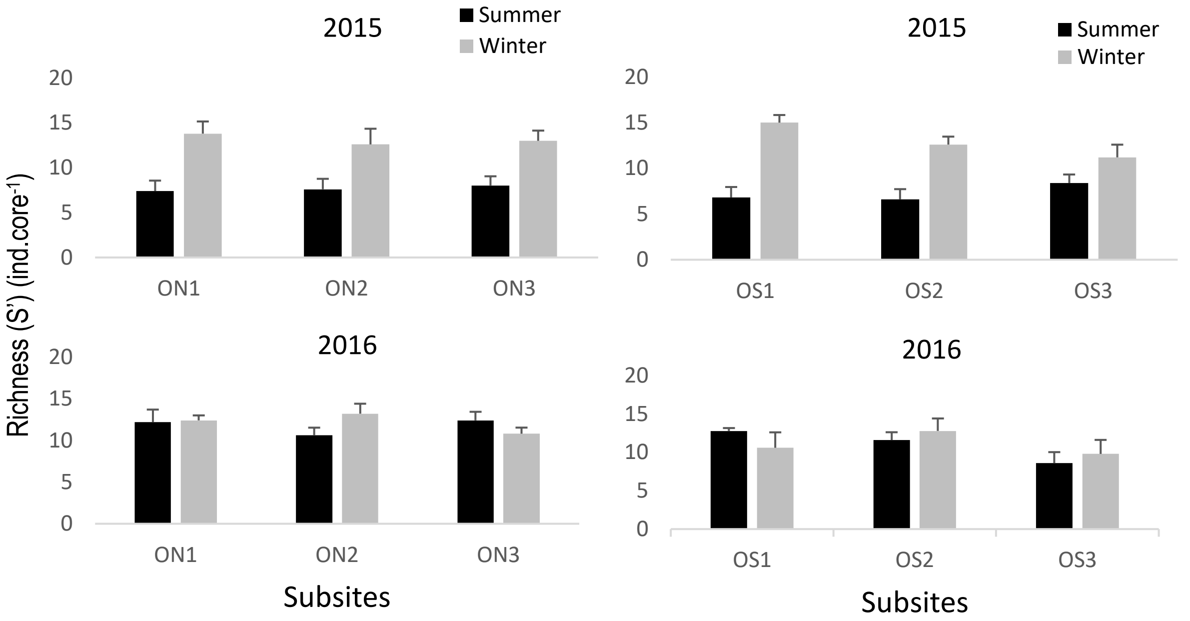

Fig.4.1A: Spatio-temporal variability in macrofaunal richness (means ± 1SE) at three subsites in Oesterwal North (ON1-3) and Oesterwal South (OS1-3).

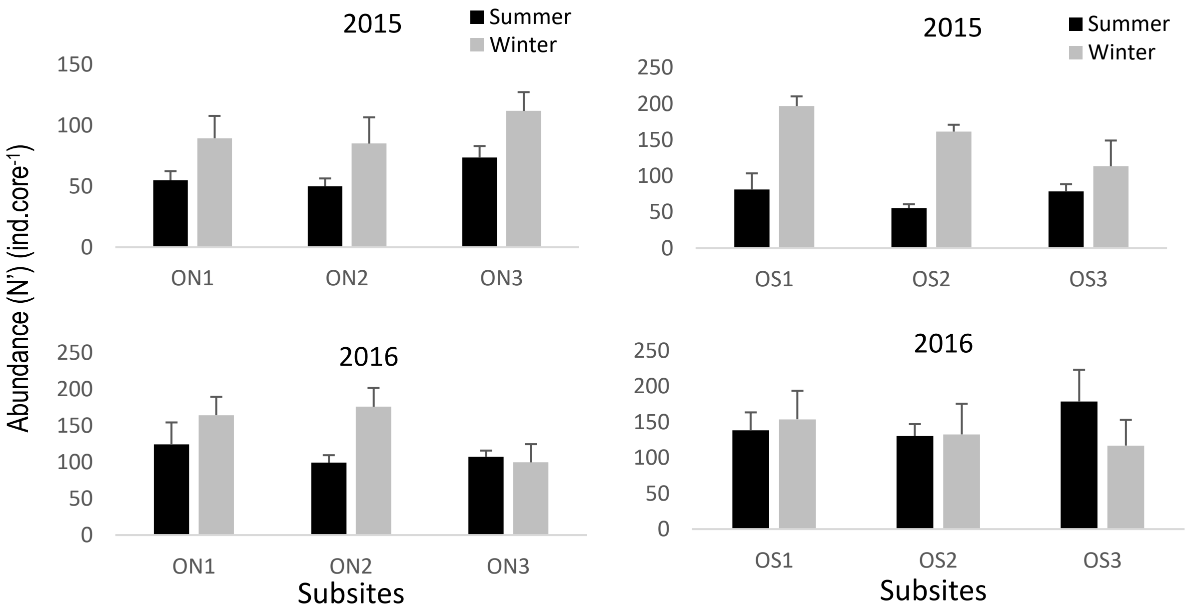

Fig.4.1B: Spatio-temporal variability in macrofaunal abundance (means ± 1SE) at three subsites in Oesterwal North (ON1-3) and Oesterwal South (OS1-3).

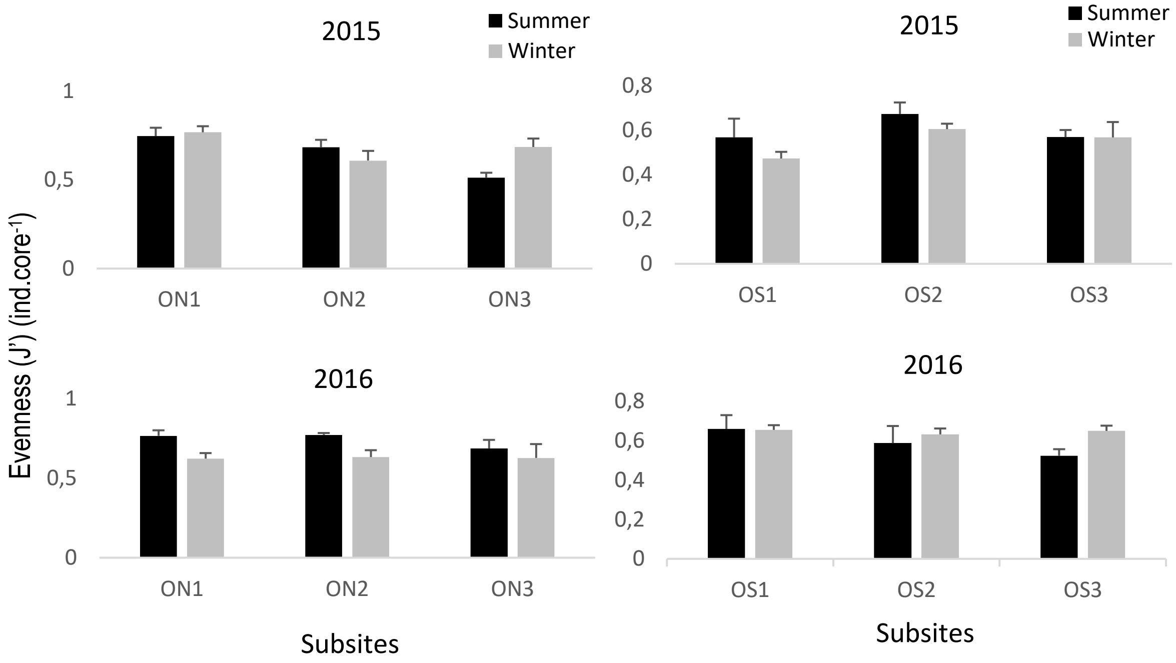

Fig.4.1C: Spatio-temporal variability in macrofaunal evenness (means ± 1SE) at three subsites in Oesterwal North (ON1-3) and Oesterwal South (OS1-3). NB: Y axis scales are different to show the trend in the data.

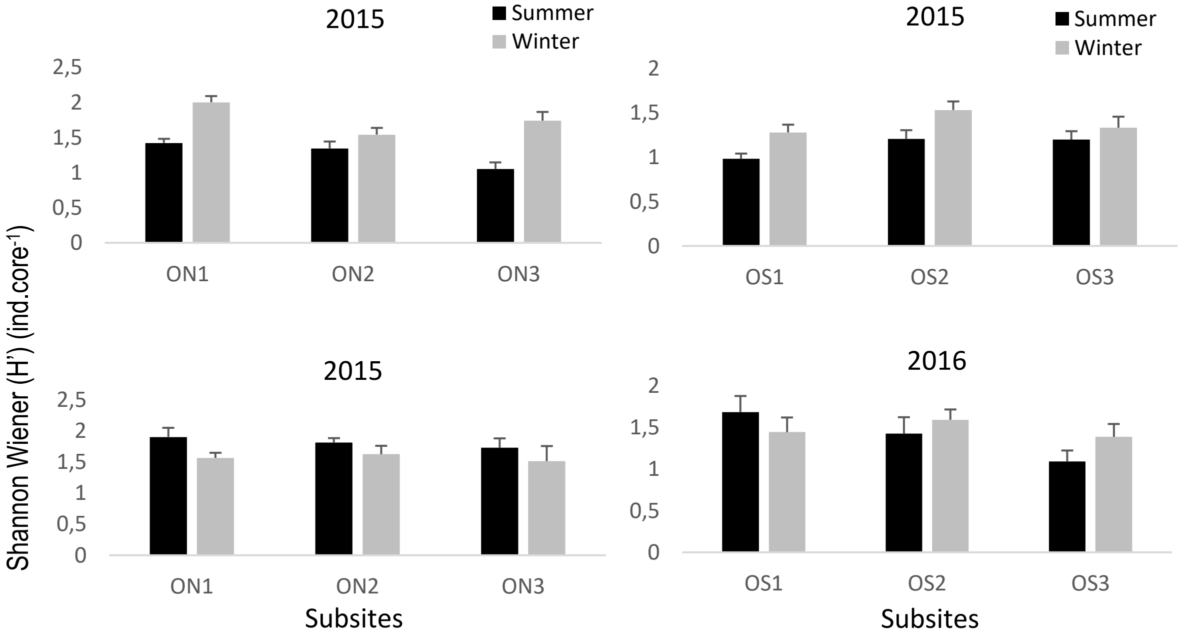

Fig.4.1D: Spatio-temporal variability in macrofaunal Shannon-Wiener diversity (means ± 1SE) at three subsites in Oesterwal North (ON1-3) and Oesterwal South (OS1-3).

4.3.3 Dominant macrofaunal species

Ten species were identified by SIMPER analysis to contribute 90 % towards macrofaunal community structure (**Table 4.5**). Of these species, the amphipod *Urothoe grimaldii* was the most dominant, contributing more than 50 % to overall community structure across all seasons in both sites. The crown crab *Hymenosoma orbiculare,* the polychaete *Marphysa elitueni* and copepods contributed least to community structure, occurring only once within the dominant community members for the entire sampling period.

Of the dominant species, the bivalve *Tellimya trigona*, juvenile polychaetes and copepods were excluded from the modelling analyses as they displayed too little variability to meet the modelling assumptions. Of the remaining species that showed sufficient variability, the likelihood ratio test (LRT) revealed the importance of seasons and sites in predicting three macrofaunal species, i.e., *Callichirus kraussi* (sandprawn)*, Ampelisca palmata* (amphipod) and *H. orbiculare* (crab; $p < 0.05$, for all cases, **Table 4.6A**). Of these species, both the amphipod *A. palmata* and crown crab *H. orbiculare* were predicated by a model with seasons only, while *C. kraussi* was best predicted by an interactive model between seasons and sites as indicted by the lowest AIC model based selection (**Table 4.6.5B**).

The seasonal variation in macrofauna species was prominent with some species/taxa being more abundant in the summer upwelling than in winter (e.g., sandprawn *C. kraussi* and bivalve *T. trigona,* **Fig. 4.2A** and **H**), while others showed an increase in abundances mostly in winter (*A. palmata* and *H. orbiculare,* **Fig. 4.2C** and **G**). For some species, (e.g. amphipod *A. palamata*) this pattern seemed to be subsite dependent. For example, the mean abundance of amphipod *A. palamata* at ON1 was higher in winter, whereas at OS1, it was higher in summer.

As for sandprawn effects, the amphipod *U*. *grimaldii* was the only species that appeared to be positively significantly affected by sandprawn abundances in Oesterwal North ($r = 0.68$, $p = 0.04$, **Table 4.7**) within summer and winter of both sampling years. In Oesterwal South, five species were affected positively by sandprawn abundances ($p < 0.05$, in all cases, **Table 4.8**). Despite few dominant species/taxa recorded in summer 2015 in both sites, sandprawn abundances failed to influence any of those species/taxa during this season ($p > 0.05$, in all cases, **Table 4.7** and **4.8**). When summer and winter data were combined, for 2015 and 2016, sandprawn effects were clearly detected (**Table 4.9**). In Oesterwal North, three species were negatively influenced by sandprawn abundances in 2015 ($p < 0.05$, in all cases) while no species appeared to be affected in 2016 ($p > 0.05$, in all cases). In contrast, no species was affected by sandprawn abundances in 2015 in Oesterwal South, but five species were affected in 2016 ($p < 0.05$, in all cases), with all but one case showing positive relationships.

Table 4.5: Seasonal variation in contribution of dominant macrofaunal species/taxa collected from Oesterwal North (ON) and South (OS), as identified by the SIMPER routine based on 90% cut off limit. Letters in brackets after species names denote broader taxonomic grouping: A = amphipod, Ax = axiid crustacean, P = polychaete, C = copepod, Cr = crab, B = bivalve.

	% contribution							
	Oesterwal North (ON)				**Oesterwal South (OS)**			
	2015		**2016**		**2015**		**2016**	
Macrofaunal Species	**Summer Season 1**	**Winter Season 1**	**Summer Season 2**	**Winter Season 2**	**Summer Season 1**	**Winter Season 1**	**Summer Season 2**	**Winter Season 2**
Urothoe grimaldii (A)	70.01	66.82	59.20	52.21	67.77	77.93	69.94	58.46
Callichirus kraussi (Ax)	19.00	4.37	9.63	5.34	16.01		12.21	
Notomastus latericeus (P)	5.01	3.15			11.88	3.57	4.10	8.74
Ampelisca palmata (A)		10.94	12.16	16.94		2.50		2.83
Griffithsia latipes (A)		4.47		3.16				
Juvenile polychaetes (P)		3.23		13.93				18.59
Copepods (C)								3.68
Hymenosoma orbiculare (Cr)						8.29		
Tellimya trigona (B)			5.99				5.94	
Marphysa elitueni (P)			4.30					

Table 4.6A: Likelihood ratio test (LRT) results examining if seasons and sites were important predictors in the models for macrofaunal dominant species. Statistical descriptions: LRT = test statistic, df = degrees of freedom, *p* – value = significance level. Letters in brackets after species names denote broader taxonomic grouping: A = amphipod, Ax = axiid crustacean, P = polychaete, C = copepod, Cr = crab, B = bivalve. Values in bold indicate statistical significance.

Macrofaunal species	**LRT**	**df**	***p*-value**
Urothoe grimaldii (A)	3.483	7	0.836
Callichirus kraussi (Ax)	33.192	7	**<0.0001**
Griffithsia latipes (A)	3.513	7	0.833
Ampelisca palmata (A)	22.794	8	**0.003**
Marphysa elitueni (P)	5.713	6	0.528
Notomastus latericeus (P)	9.459	7	0.292
Hymenosoma orbiculare (Cr)	26.732	7	**<0.0001**

Table 4.6B: Generalised Linear Mixed effects Models (GLMM) conducted on the dominant species of macrofauna, investigating the effect of sites and seasons. Statistical descriptions: AIC = Akaike's information criterion, df = degrees of freedom. Letters in brackets after species names denote broader taxonomic grouping: Ax = axiid crustacean, A = amphipod, Cr = crab. Values in bold indicate the most parsimonious model.

species	***C. kraussi* (Ax)**		***A. palmata* (A)**		***H. orbiculare* (Cr)**	
Candidates models	**Df**	**AIC**	**df**	**AIC**	**Df**	**AIC**
Null	10	627.05	11	697.80	10	436.61
Sites	11	622.58	12	698.30	11	434.57
Seasons	13	624.30	15	**689.22**	13	**423.05**
Site + Seasons	14	614.51	16	691.24	14	424.53
Sites x Seasons	17	**607.86**	19	691.29	17	423.88

Table 4.7: Summary statistics of Pearson correlation analysis testing the relationship between sandprawn abundance and dominant macrofaunal species/taxa in Oesterwal North (ON) per season. Statistical descriptions**:** r = goodness of fit, t = test statistic, df = degrees of freedom, and *p*—value = significance level. Letters in brackets after species names denote broader taxonomic grouping: A = amphipod, P = polychaete, C = copepod, Cr = crab. Values in bold indicate statistical significance. NB: where correlations are statistically significant, scatter plots are provided on the appendix (**Fig 9.10A-B**).

Species	**Oesterwal North (ON)**															
	Winter 2015				**Summer 2015**				**Winter 2016**				**Summer 2016**			
	r	**t**	**df**	***p*-value**	**R**	**t**	**df**	***p*-value**	**R**	**t**	**df**	***p*-value**	**r**	**t**	**df**	***p*-value**
Urothoe grimaldii (A)	-0.13	-0.47	13	0.64	-0.18	-0.67	13	0.51	0.18	0.68	13	0.5	0.68	3.4	13	**0.004**
Griffithsia latipes (A)					0.03	0.13	13	0.89	-0.1	-0.39	13	0.7	0.11	0.42	13	0.67
Ampelisca palmata (A)	-0.32	-0.12	13	0.23	0.27	1.02	13	0.32	-0.02	-0.09	13	0.92	-0.09	-0.33	13	0.74
Paratylodiplax edwardsi (Cr)					-0.04	-0.15	13	0.88								
Maphysa elitueni (P)	0.46	1.87	13	0.061					0.17	0.65	13	0.51	-0.29	-1.11	13	0.28
Notomastus latericeus (P)	0.04	0.17	13	0.86					0.46	1.9	13	0.07	-0.02	-0.08	13	0.92
Hymenosoma orbiculare (Cr)	0.03	0.12	13	0.92					-0.03	-0.13	13	0.89	0.19	0.7	13	0.49
Tellimya trigona (B)									-0.15	-0.57	13	0.57	-0.33	-1.27	13	0.22
Juvenile polychaetes (P)	-0.31	-1.1	13	0.26					0.34	0.32	13	0.2	-0.1	-0.38	13	0.7
Copepods (C)	0.03	0.14	13	0.89					0.37	1.45	13	0.16	-0.03	-0.12	13	0.9

Table 4.8: Summary statistics of Pearson correlation analyses testing the relationship between sandprawn abundances and dominant macrofaunal species/taxa in Oesterwal South (OS) per season. Statistical descriptions: r = goodness of fit, t = test statistic, df = degrees of freedom, and *p*— value = significance level. Letters in brackets after species names denote broader taxonomic grouping: A = amphipod, P = polychaete, C = copepod, Cr = crab, O = Ostracod. Values in bold indicate statistical significance. NB: where correlations are statistically significant, scatter plots are provided on the appendix (**Fig 9.10A-B**).

Species/taxa	**Oesterwal South (OS)**															
	Winter 2015				**Summer 2015**				**Winter 2016**				**Summer 2016**			
	r	**T**	**df**	***p*-value**	**r**	**T**	**Df**	***p*-value**	**r**	**t**	**df**	***p*-value**	**r**	**t**	**df**	***p*-value**
Urothoe grimaldii (A)	-0.09	-0.34	13	0.73	0.17	0.65	13	0.52	0.68	3.35	13	**0.005**	0.34	-0.21	13	0.2
Griffithsia latipes (A)	0.51	2.1	13	**0.047**	-0.11	-0.7	13	0.47	0.31	1.19	13	0.25	0.58	2.61	13	**0.02**
Ampelisca palmata (A)	0.78	4.5	13	**0.0001**					-0.06	-0.23	13	0.82	-0.29	-1.1	13	0.28
Maphysa elitueni (P)	0.016	0.058	13	0.95					-0.02	0.1	13	0.91	0.39	1.56	13	0.14
Notomastus latericeus (P)	0.19	0.71	13	0.49					0.73	3.9	13	**0.0017**	0.49	2.02	13	0.06
Hymenosoma orbiculare (Cr)					-0.26	-0.9	13	0.34	-0.001	-0.005	13	0.99	0.07	0.26	13	0.79
Tellimya trigona (B)									0.42	1.85	13	0.071	0.08	0.31	13	0.75
Copepods (C)	-0.24	-0.92	13	0.37					0.56	2.49	13	**0.02**	-0.009	0.03	13	0.97
Ostracods (O)	0.33	1.27	13	0.22					0.04	0.14	13	0.88				
Juvenile polychaetes (P)	-0.14	-0.52	13	0.61												

Table 4.9: Summary statistics of Pearson correlation analysis testing the relationship between macrofaunal species/taxa and sandprawn abundances in Oesterwal North (ON) and South (OS) based on combined summer and winter data per year (2015 and 2016). Statistical descriptions: r = goodness of fit, t = test statistic, df = degrees of freedom, and *p*— value = significance level. Letters in brackets after species names denote broader taxonomic grouping: A = amphipod, P = polychaete, C = copepod, B = bivalve, Cr = crab. Values in bold indicate statistical significance. NB: where correlations are statistically significant, scatter plots are provided on the appendix (**Fig 9.11A-B**).

			Oesterwal North (ON)					
Species/taxa	**Year 2015**				**Year 2016**			
	R	**T**	**df**	***p*-value**	**r**	**t**	**df**	***p*-value**
Urothoe grimaldii (A)	-0.24	-1.34	28	0.18	0.17	0.91	28	0.36
Griffithsia latipes (A)	-0.42	-2.4	28	**0.02**				
Ampelisca palmata (A)	-0.39	-0.4	28	**0.03**	0.009	0.04	28	0.96
Maphysa elitueni (P)	0.11	0.58	28	0.56	0.08	0.47	28	0.64
Notomastus latericeus (P)	0.05	0.3	28	0.76	0.15	0.78	28	0.44
Hymenosoma orbiculare (Cr)	-0.31	-1.7	28	0.08	0.09	0.51	28	0.6
Tellimya trigona (B)	-0.009	-0.04	28	0.96	-0.03	-0.2	28	0.83
Juvenile polychaetes (P)	-0.38	-2.1	28	**0.03**	-0.18	-0.99	28	0.33
Copepods (C)	-0.18	-0.98	28	0.33	-0.05	-0.29	28	0.76
			Oesterwal South (OS)					
Urothoe grimaldii (A)	-0.32	-1.8	28	0.07	0.49	3.01	28	**0.005**
Griffithsia latipes (A)	-0.1	-0.55	28	0.58	0.52	3.29	28	**0.002**
Ampelisca palmata (A)	-0.01	-0.05	28	0.95	-0.14	-0.75	28	0.45
Maphysa elitueni (P)	-0.08	-0.4	28	0.67	0.52	3.21	28	**0.003**
Notomastus latericeus (P)	0.07	0.37	28	0.7	0.29	1.65	28	0.1
Tellimya trigona (B)	0.007	0.04	28	0.96	0.48	2.9	28	**0.006**
Juvenile polychaetes (P)	-0.32	-1.68	28	0.11	-0.47	-2.83	28	**0.008**
Copepods (C)	-0.34	-1.92	28	0.06	-0.17	-0.91	28	0.36
Hymenosoma orbiculare (Cr)					-0.13	-0.73	28	0.46

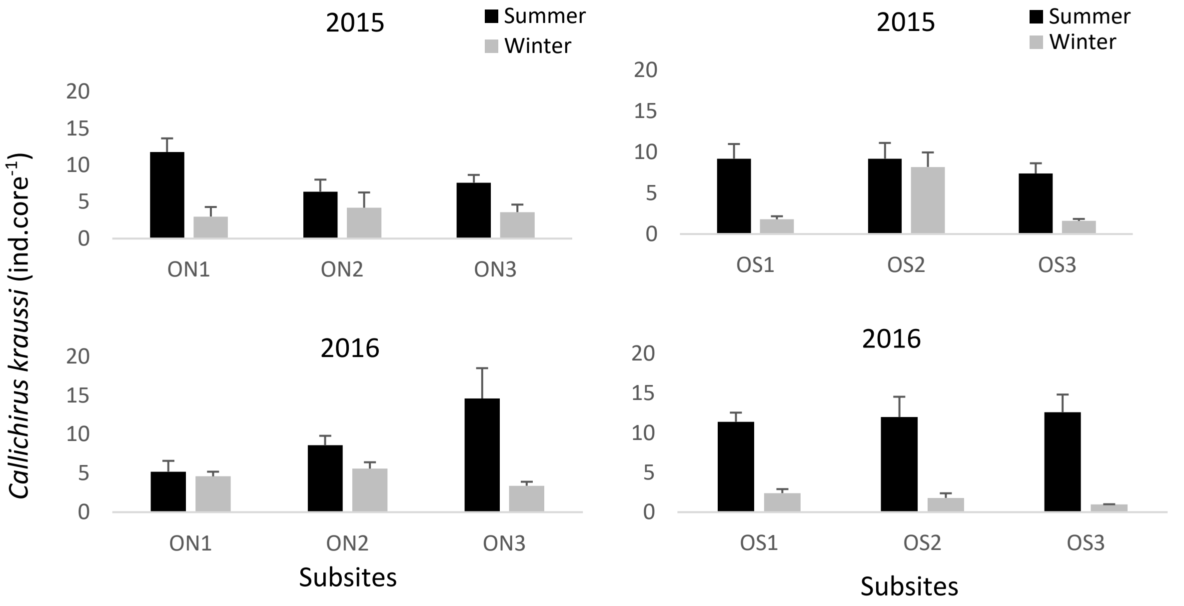

Fig. 4.2A: Spatio-temporal variability in *Callichirus kraussi* (thalassinid crustacean, means ± 1SE) at three subsites in Oesterwal North (ON1-3) and Oesterwal South (OS1-3).

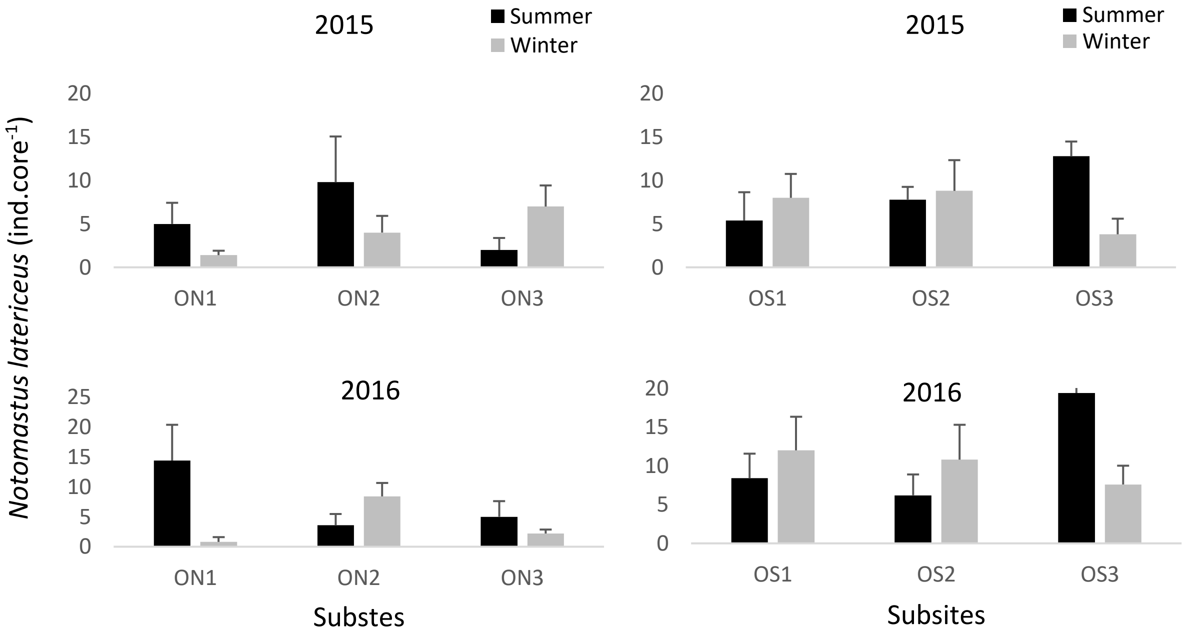

Fig. 4.2B: Spatio-temporal variability in *Notomastus latericeus* (*polychaete*, means ± 1SE) at three subsites in Oesterwal North (ON1-3) and Oesterwal South (OS1-3).

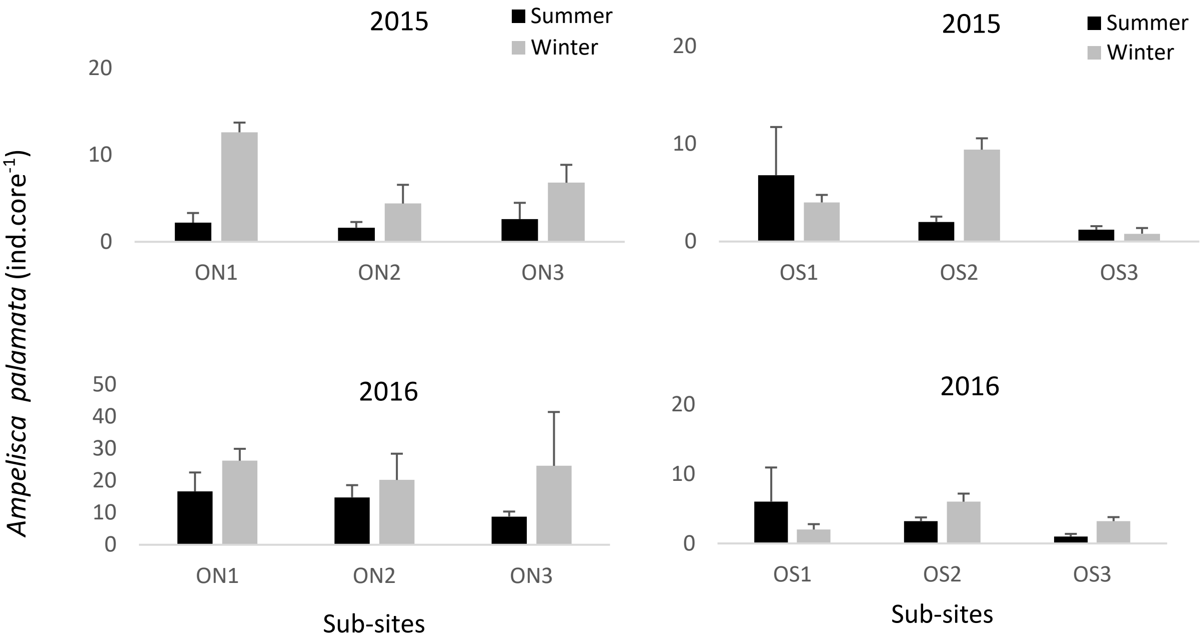

Fig. 4.2C: Spatio-temporal variability in *Ampelisca palmata* (*amphipod*, means ± 1SE) at three subsites in Oesterwal North (ON1-3) and Oesterwal South (OS1-3).

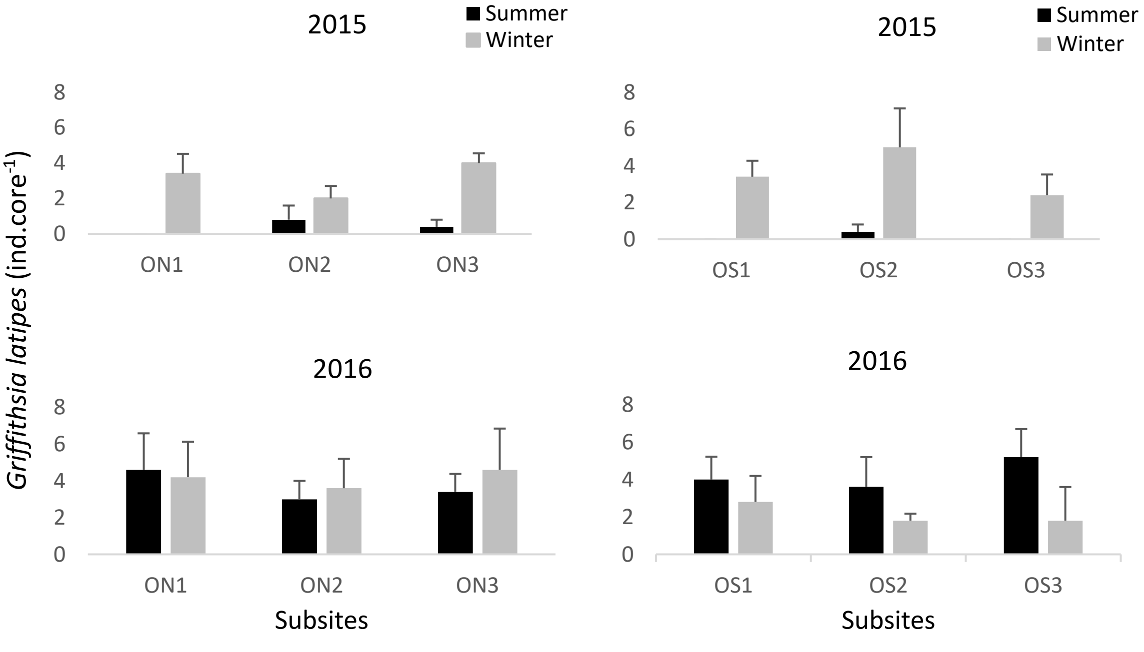

Fig. 4.2 D: Spatio-temporal variability in *Griffithsia latipes* (*amphipod*, means ± 1SE) at three subsites in Oesterwal North (ON1-3) and Oesterwal South (OS1-3).

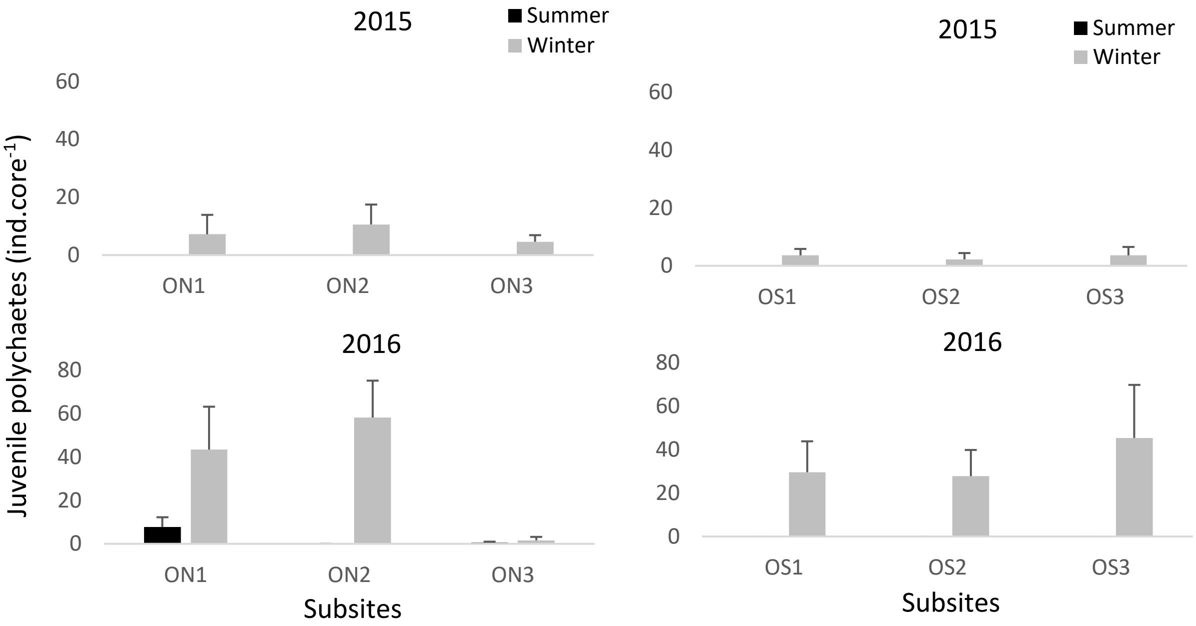

Fig. 4.2 E: Spatio-temporal variability in *juvenile polychaetes* (means ± 1SE) at three subsites in Oesterwal North (ON1-3) and Oesterwal South (OS1-3). NB: Y axis scales are different to show the trend in the data.

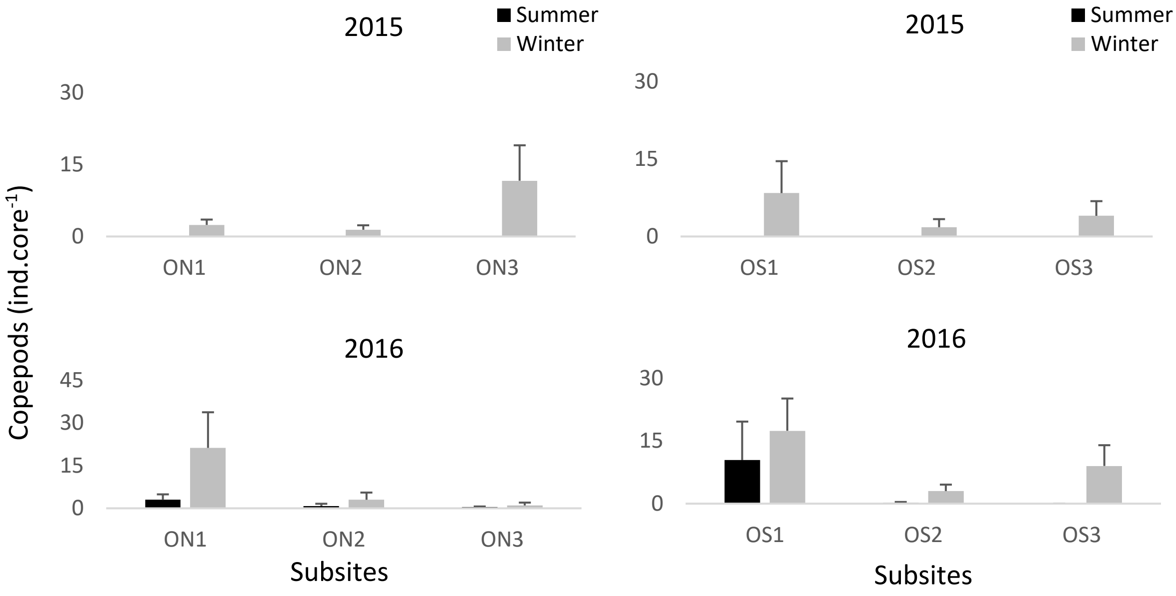

Fig 4.2F: Spatio-temporal variability in *copepods* (means ± 1SE) at three subsites in Oesterwal North (ON1-3) and Oesterwal South (OS1-3). NB: Y axis scales are different to show the trend in the data.

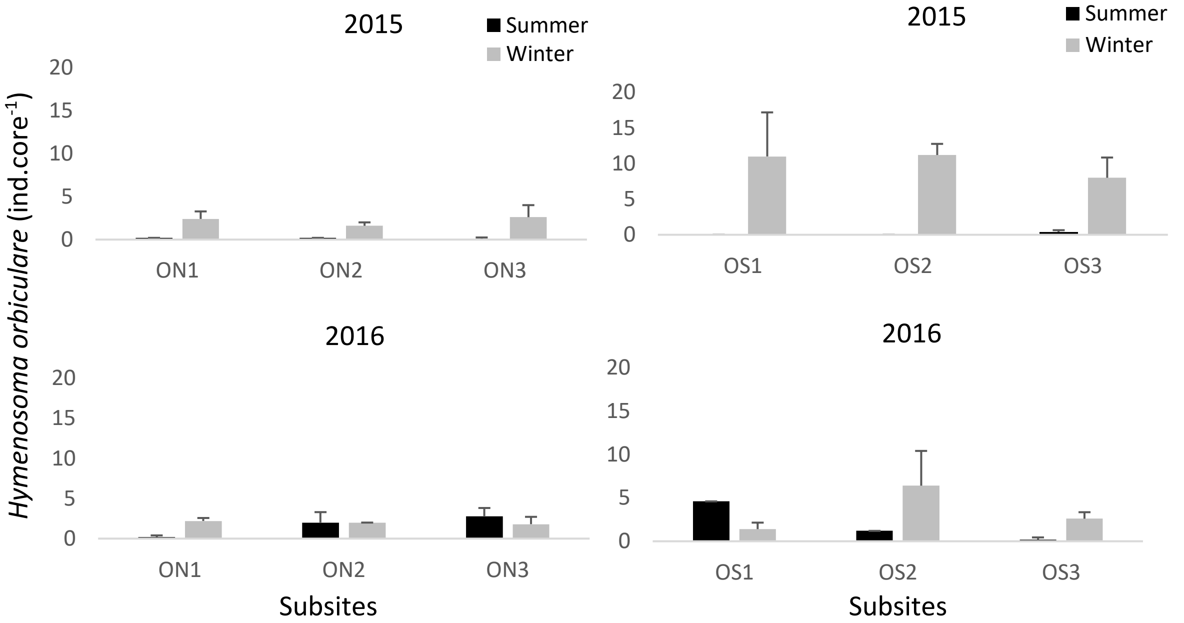

Fig 4.2G: Spatio-temporal variability in *Hymenosoma orbiculare* (crab, means ± 1SE) at three subsites in Oesterwal North (ON1-3) and Oesterwal South (OS1-3).

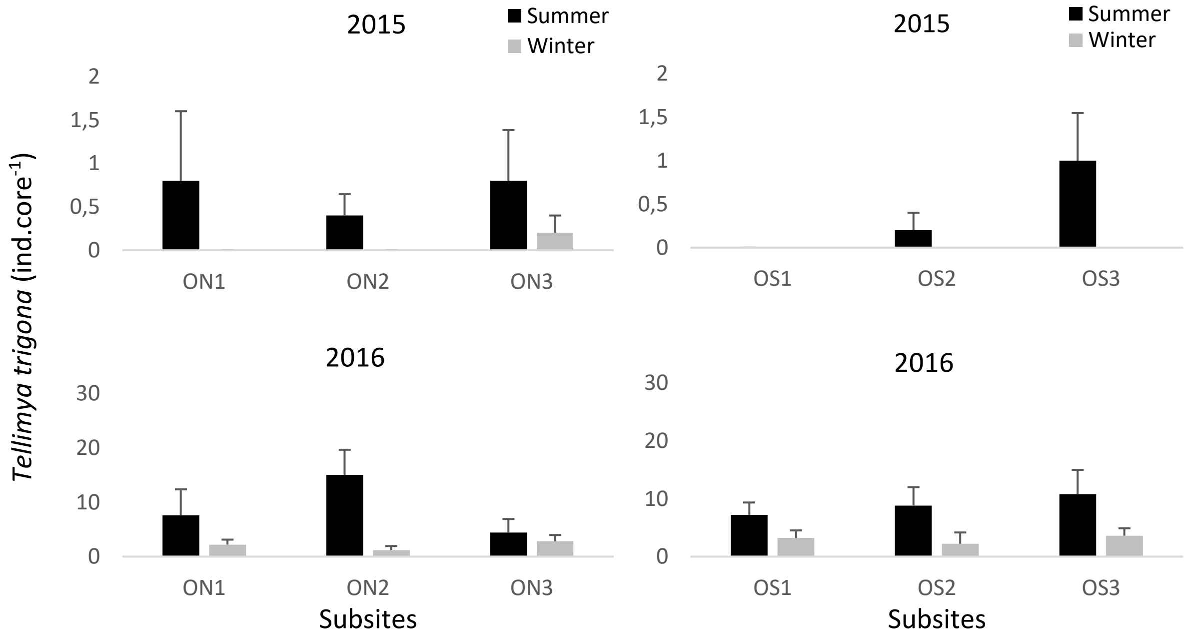

Fig 4.2H: Spatio-temporal variability in *Tellimya trigona* (*bivalve*, means ± 1SE) at three subsites in Oesterwal North (ON1-3) and Oesterwal South (OS1-3). NB: Y axis scales are different to show the trend in the data.

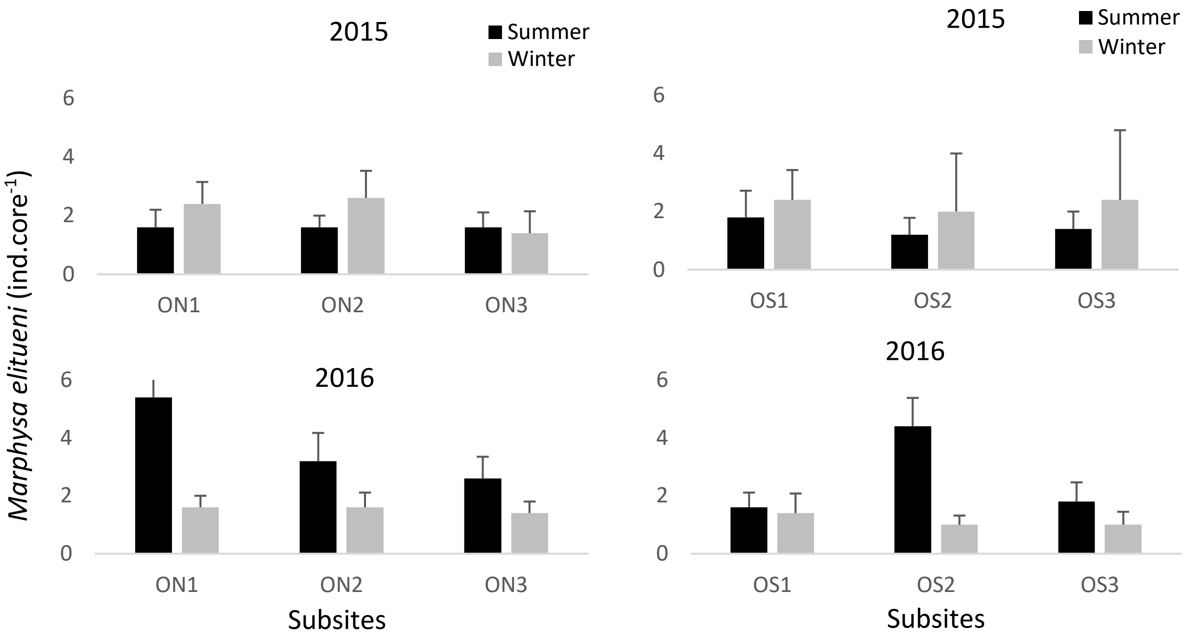

Fig 4.2I: Spatio-temporal variability in *Marphysa elitueni* (*polychaete*, means ± 1SE) at three subsites in Oesterwal North (ON1-3) and Oesterwal South (OS1-3).

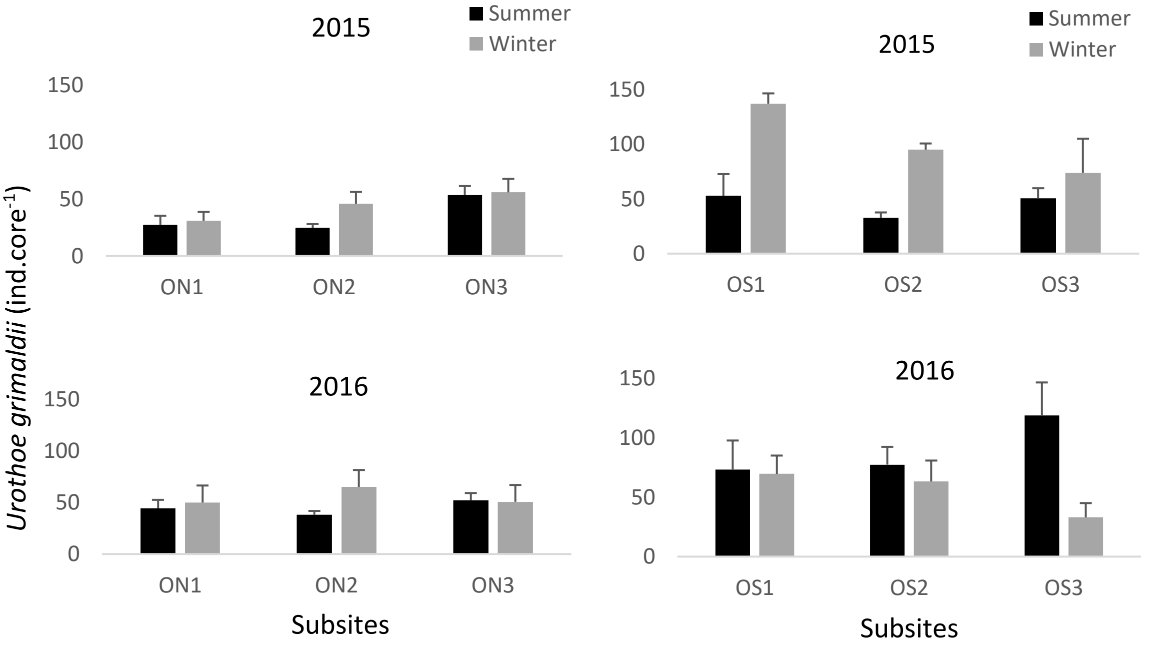

Fig 4.2J: Spatio-temporal variability in *Urothoe grimaldii* (Amphipod, means ± 1SE) at three subsites in Oesterwal North (ON1-3) and Oesterwal South (OS1-3).

4.3.4 Functional groups

Seasons and sites were suitable predictors of three macrofauna functional group abundances as indicated by the likelihood ratio test ($p < 0.05$, for all cases, **Table 4.10A**). Of these three functional groups, surface deposit feeders were predicted by an interactive model between sites and seasons, while both surface deposit feeders and predators, and suspensions feeders were predicted by the main effect of sites and seasons. However, suspension feeders were also predicted by an interactive effect of sites and seasons (**Table 4.10B**).

The prominent pattern displayed by macrofaunal functional groups was that their abundance increased in winter season (**Fig 4.3B, D** and **E)**. For suspension feeders, this pattern was observed during both 2015 and 2016 sampling periods at both sites (**Fig 4.3E**). On the other hand, summer increases were observed for surface deposit feeders and surface deposit feeder and predators in 2016. Noticeably, surface deposit feeders and predators revealed a distinctive spatial pattern with its abundance being site dependent. For examples, in 2016 the abundance of the surface deposit feeders and predators was enhanced in both winter and summer seasons, particularly appeared to be higher at the ON1, OS2 and OS3 in winter, while in summer it was higher at both ON3 and OS1 (**Fig 4.3E**).

Based on the Pearson correlation analysis, both surface and burrowing deposit feeders were affected by sandprawn abundances in Oesterwal North, within particular seasons (**Table 4.11**). Burrowing deposit feeders were positively affected by sandprawn abundance in summer of 2016 (r = 0.66, p = 0.007). Surface deposit feeders were negatively affected by sandprawn abundance in summer 2015 (r = -0. 51, p = 0.04). On the other hand, in Oesterwal South, burrowing deposit feeders were positively affected by sandprawn abundance in winter 2016 (r = 0. 69 p = 0.004), while surface deposit feeders and predators were also positively affected by sandprawn abundance in winter 2015 (r = 0. 5, p = 0.047). Surprisingly, no sandprawn effects were detected for suspension feeders group within seasons at each site (p > 0.05, for all cases).

When summer and winter data were combined for each of the two sampling years, statistically significant effects of sandprawn abundance on macrofaunal functional groups in each year were clearly detected (**Table 4.12**). Four functional groups were affected by sandprawn abundances in 2015 (p < 0.05, in all cases), three in Oesterwal North (surface deposit feeders, surface deposit feeders and predators, and suspension feeders), while in Oesterwal South, surface deposit feeders and predators was the only functional group that was affected by sandprawn abundance (r = -0. 33, p = 0.031). In all cases, negative relationships were recorded between the above-mentioned functional groups and sandprawns abundance. In 2016, no macrofaunal functional groups were influenced by sandprawn abundances in Oesterwal North (p > 0.05, for all cases). With the exception of surface deposit feeders and predators (r = 0.14, p = 0.45), all functional groups in Oesterwal South were significantly influenced by sandprawn abundance (p < 0.05, in all cases) in 2016. Of these, suspension feeders were negatively related to sandprawn abundance, but the remaining functional groups (surface deposit feeders, burrowing deposit feeders, and burrowing deposit feeders and predators) were positively related to sandprawn abundance.

Table 4.10A: Likelihood ratio test (LRT) results examining if seasons and sites were important predictors in the models for macrofaunal functional groups. Statistical descriptions: LRT = test statistic, df = degrees of freedom, *p* – value = significance level. Values in bold indicate statistical significance.

Macrofaunal functional groups	LRT	df	*p*-value
Burrowing deposit feeders	2.814	7	0.901
Surface deposit feeders	15.783	7	**0.027**
Burrowing deposit feeders and predators	5.523	7	0.596
Surface deposit feeders and predators	26.438	7	**0.000**
Suspension feeders	17.964	7	**0.023**

Table 4.10B: Generalised linear mixed effects models conducted on macrofaunal functional groups, investigating the effect of sites and seasons. Statistical descriptions: AIC = Akaike's information criterion, df = degrees of freedom. Values in bold indicate the most parsimonious model.

	Surface deposit feeders		Surface deposit feeders and predators		Suspension feeders	
Candidate models	Df	AIC	df	AIC	Df	AIC
Null	10	614.69	10	496.52	10	829.81
Sites	11	615.40	11	490.81	11	831.06
Seasons	13	615.63	13	481.80	13	829.47
Site + Seasons	14	614.00	14	**481.46**	14	**828.15**
Sites x Seasons	17	**612.91**	17	484.08	17	**828.15**

Table 4.11: Summary statistics of Pearson correlation analysis testing the relationship between sandprawn abundance and macrofaunal functional groups in Oesterwal North (ON) and South (OS) per season. Statistical descriptions: r = goodness of fit, t = test statistic, df = degrees of freedom, and *p*— value = significance level. Values in bold indicate statistical significance. NB: where correlations are statistically significant, scatter plots are provided on the appendix (**Fig 9.12**).

Oesterwal North (ON)																
Functional Groups	**Winter 2015**				**Summer 2015**				**Winter 2016**				**Summer 2016**			
	r	**t**	**df**	***p*-value**	**r**	**T**	**df**	***p*-value**	**r**	**t**	**df**	***p*-value**	**r**	**t**	**df**	***p*-value**
Burrowing deposit feeders	-0.03	-0.13	13	0.89	0.01	0.04	13	0.6	0.28	1.06	13	0.31	0.66	3.16	13	**0.007**
Surface deposit feeders	-0.25	-0.93	13	0.36	-0.51	-2.1	13	**0.04**	-0.34	-1.31	13	0.21	-0.37	-1.45	13	0.17
Burrowing deposit feeders and predators	0.36	1.41	13	0.18	0.22	0.8	13	0.42	0.11	0.65	13	0.52	-0.23	-0.86	13	0.4
Surface deposit feeders and predators	-0.29	-1.15	13	0.28	-0.33	-1.3	13	0.21	-0.25	-0.95	13	0.35	0.06	0.24	13	0.81
Suspension feeders	-0.2	-0.73	13	0.47	0.27	1.02	13	0.32	-0.08	-0.31	13	0.75	-0.03	-0.12	13	0.9
Oesterwal South (OS)																
Burrowing deposit feeders	0.03	0.11	13	0.9	0.22	0.83	13	0,41	0.69	3.45	13	**0.004**	0.46	1.91	13	0.07
Surface deposit feeders	0.28	1.06	13	0.307	-0.28	-1.08	13	0,29	0.44	1.78	13	0.1	0.13	0.49	13	0.62
Burrowing deposit feeders and predators	-0.11	-0.4	13	0.68	0.12	0.46	13	0,64	-0.01	-0.03	13	0.96	0.49	2.04	13	0.06
Surface deposit feeders and predators	0.5	2.08	13	**0.047**	-0.44	-1.8	13	0,09	-0.007	-0.02	13	0.97	0.05	0.18	13	0.85
Suspension feeders	0.27	1.01	13	0.32	-0.4	-1.6	13	0.13	-0,11	-0.43	13	0.67	-0.21	-0.71	13	0.44

Table 4.12: Summary statistics of Pearson correlation analysis testing the relationship between macrofaunal functional groups and sandprawn abundances in Oesterwal North (ON) and South (OS) based on combined summer and winter data per year (2015 and 2016). Statistical descriptions: r = goodness of fit, t = test statistic, df = degrees of freedom, and *p*-value = significance level. Values in bold indicate statistical significance. NB: where correlations are statistically significant, scatter plots are provided on the appendix (**Fig 9.13A-B**).

Oesterwal North (ON)								
Functional Groups	**Year 2015**				**Year 2016**			
	r	**t**	**df**	***p*-value**	**r**	**t**	**df**	***p*-value**
Burrowing deposit feeders	-0.08	-0.4	28	0.64	0.34	1,97	28	0.058
Surface deposit feeders	-0.46	-2.78	28	**0.009**	-0.02	-0,12	28	0.9
Burrowing deposit feeders and predators	0.03	0.21	28	0.83	0.16	0,85	28	0.39
Surface deposit feeders and predators	-0.43	-2.54	28	**0.015**	-0.009	-0,05	28	0.95
Suspension feeders	-0.37	-2.1	28	**0.03**	-0.26	-1,42	28	0.16
Oesterwal South (OS)								
Burrowing deposit feeders	-0,23	-1,2	28	0.22	0.54	3.48	28	**0.001**
Surface deposit feeders	-0,19	-1,06	28	0.29	0.52	3.23	28	**0.003**
Burrowing deposit feeders and predators	-0,26	-1,4	28	0.15	0.57	3.73	28	**0.0008**
Surface deposit feeders and predators	-0,33	-1,86	28	**0.031**	0.14	-0.76	28	0.45
Suspension feeders	-0,28	-1,54	28	0.12	-0.32	-2.01	28	**0.041**

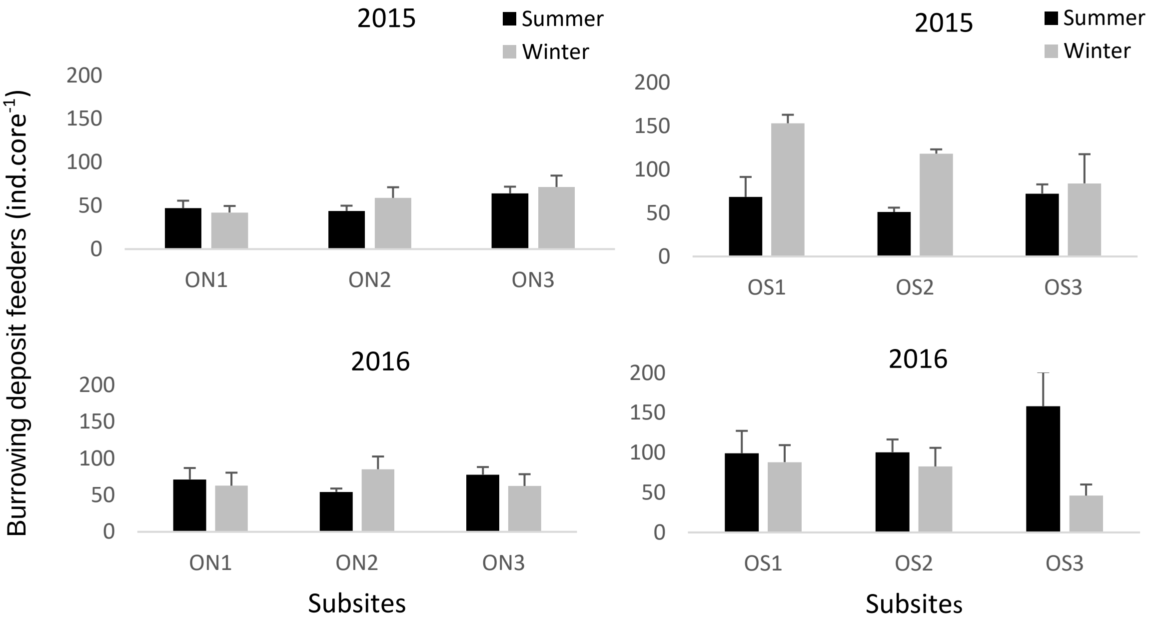

Fig 4.3A: Spatio-temporal variability in burrowing deposit feeders of macrofaunal functional groups (means ± 1SE) at three subsites in Oesterwal North (ON1-3) and Oesterwal South (OS1-3).

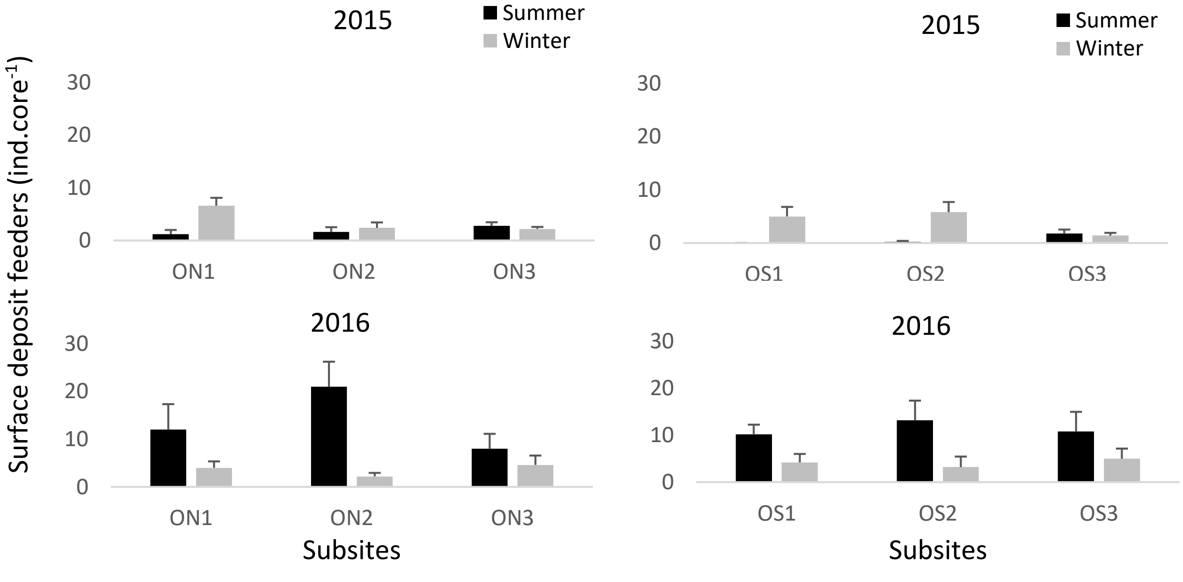

Fig 4.3B: Spatio-temporal variability in surface deposit feeders of macrofaunal functional groups (means ± 1SE) at three subsites in Oesterwal North (ON1-3) and Oesterwal South (OS1-3).

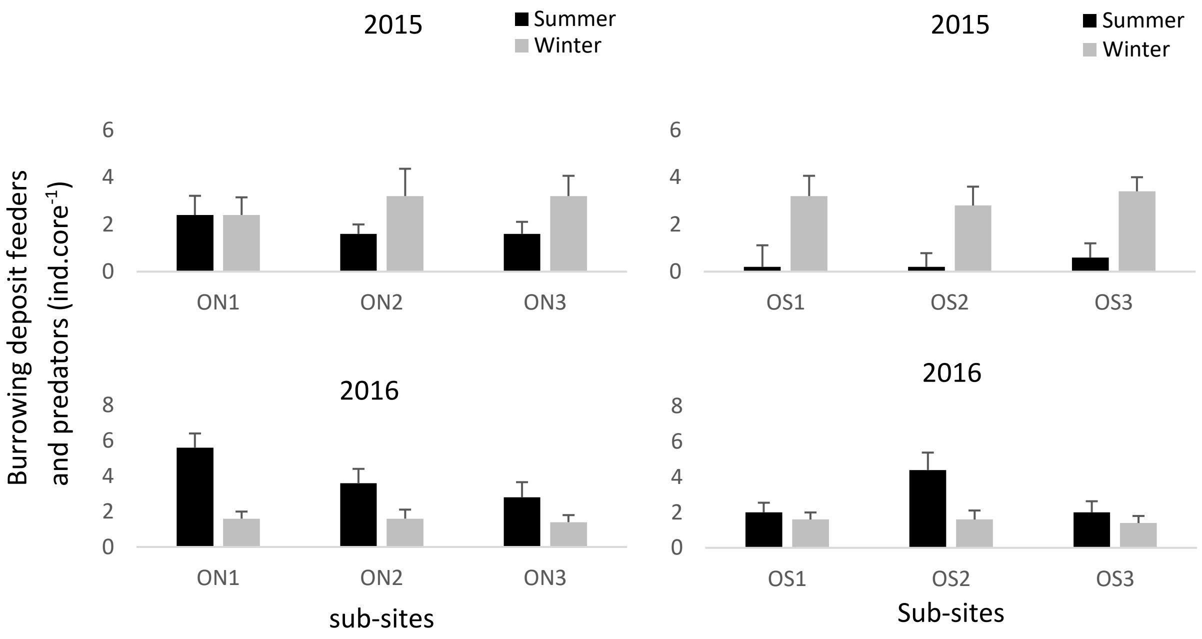

Fig 4.3C: Spatio-temporal variability in burrowing deposit feeders and predators of macrofaunal functional groups (means ± 1SE) at three subsites in Oesterwal North (ON1-3) and Oesterwal South (OS1-3). NB: Y axis scales are different to show the trend in the data.

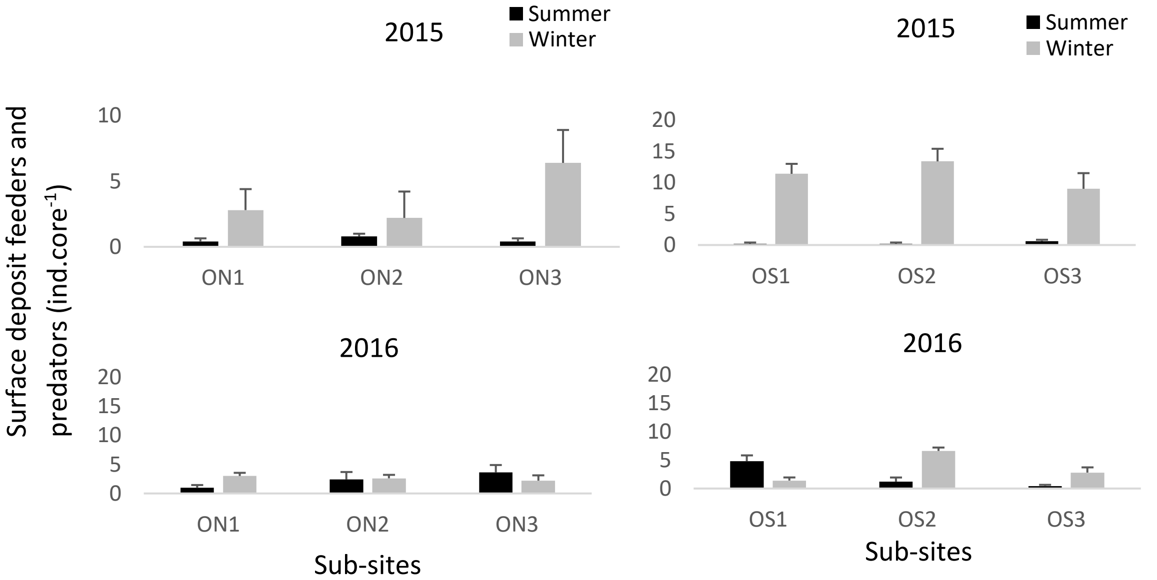

Fig 4.3D: Spatio-temporal variability in surface deposit feeders and predators of macrofaunal functional groups (means ± 1SE) at three subsites in Oesterwal North (ON1-3) and Oesterwal South (OS1-3). NB: Y axis scales are different to show the trend in the data.

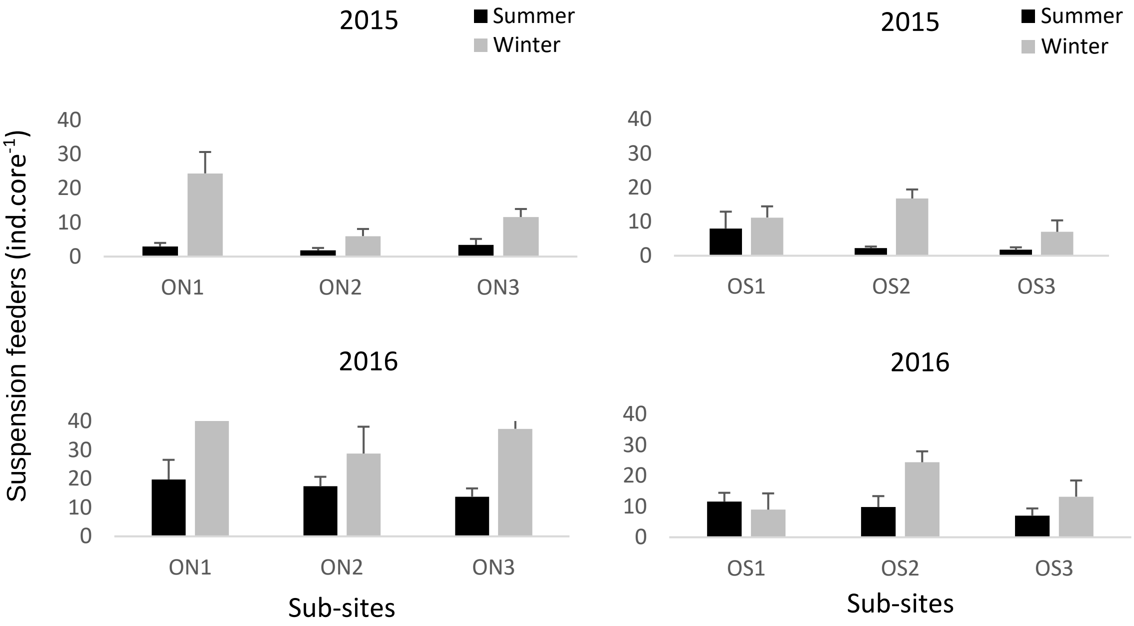

Fig 4.3E: Spatio-temporal variability in suspension feeders of macrofaunal functional groups (means ± 1SE) at three subsites in Oesterwal North (ON1-3) and Oesterwal South (OS1-3).

4.4 DISCUSION

This chapter extends the questions of the preceding chapter, but focusses on macrofaunal community structure. More specifically, this chapter made use of *in situ* surveys to study the influence of upwelling on benthic macrofaunal assemblages in Langebaan Lagoon, while seeking to understand how upwelling modifies sandprawn effects using a correlative approach. The rationale for this chapter was that sandprawn bioturbation is dominant in the system, but at a broader level, temporal upwelling is key feature of the system. I thus anticipated that effects of sandprawns on macrofaunal assemblages would be contingent upon seasonal inputs of nutrients through upwelling. I specifically hypothesized that macrofaunal diversity metrics will be lower in winter (non-upwelling) but higher in summer during upwelling events. I also hypothesized that the strength of sandprawn effects on macrofauna would be reduced by nutrient input, due to bottom-up processes overcoming negative sandprawn effects. Specifically, upwelling should enhance primary productivity (chl-*a*) and therefore counteract negative impacts of sandprawn bioturbation on macrofaunal community. Surprisingly, findings of this study did not generally overwhelmingly support the hypothesis put forward, however, they did broaden understanding of seasonal upwelling in sandprawn dominated sediments.

4.4.1 Macrofauna: overall community composition, diversity metrics

Although macrofaunal community structure was strongly affected by the main and interactive effects of seasons and sites over the whole study, the hypothesis that community metrics will be enhanced in response to summer upwelling season was not upheld in this study. This particular result leads to an idea that macrofaunal assemblages of Langebaan Lagoon are possibly not highly influenced by variability in productivity related to seasonal upwelling. Such a finding was unexpected, but ecologically important, given the positioning of Langebaan Lagoon within the Benguela current, which is regarded as one of the most world's productive upwelling system (Schumann *et al.* 1982, Carr 2002, Puccinelli *et el.* 2016).

An interesting observation emerging from this study is that the general elevation of macrofaunal community metrics in winter coincided with increased winter sediment chlorophyll-*a* concentrations (see chapter 3). This general pattern could suggest that availability of trophic resources on the surface sediment in the form of microalgae does generate positive bottom up effects. However, variability in chl-*a* in the study as a whole, does not appear to manifest consistently as would be expected by upwelling. Therefore, it is possible that variability in benthic chl-*a* levels and macrofaunal community metrics in this study is influenced by other processes that are unrelated directly to upwelling. One such factor could be spatial variability in the distribution and abundance of the sandprawn *C.*

kraussi. This bioturbator was generally amongst the most numerically dominant species and highly abundant in summer, particularly in the first year of study. In winter, however, *C. kraussi* was not as numerically dominant, which could, at least in part, explain the observed enhancement of individual macrofaunal species and the community structure in winter. This is based on local studies in which sandprawn bioturbation has been shown to reduce benthic chl-*a* levels and macrofaunal community metrics (Branch and Pringle 1987, Pillay *et al.* 2007c).

Based on the GLMM model output, sites was the only factor that appeared to influence macrofauna evenness (**Table 4.2B**). This result is perhaps an indication that at the level of community metrics, spatio-temporal variability is not a major determinant of macrofauna. However, correlation analysis indicated that sandprawn abundance is a significant explanation of variability in community metrics. More specifically, correlation tests within particular seasons of the study showed positive relationships between macrofauna abundance and sandprawns (in Oesterwal North); graphically, this pattern was obvious, with abundance generally being higher in winter 2015 relative to summer of the same year (**Fig.4.1B**, **Fig 4.2A**). On the other hand, macrofauna evenness was negatively related to sandprawn abundances in winter of 2016 at Oesterwal South, although, graphically this pattern was less clear. Overall, interannual variability in responses was evident, which is possibly linked to variation in the strength of upwelling, which is a feature of the South African west coast (Branch and Branch 1981, Awad *et al.* 2002, Griffiths *et al.* 2010).

When data from summer and winter were investigated annually, correlation test identified interesting relationships between sandprawn abundances and macrofaunal community metrics (**Table 4.4**), with trends differing from those observed within seasons. Generally, in 2015, sandprawn impacts on macrofaunal diversity metrics were much stronger, affecting both richness and abundance in Oesterwal North, while evenness and richness were influenced in Oesterwal South. These effects were generally negative, except for evenness. These results suggest that potential sandprawn effects on macrofaunal assemblages in Langebaan Lagoon are site-specific.

4.4.2 Dominant species

Among species/taxa that dominated the study sites, the amphipod *Urothoe grimaldii* was the most prevalent species in both summer and winter seasons, with more than 50 % contribution in both sites, while the sandprawn *Callichirus kraussi* was the second most dominant species in summer. As for the winter seasons, the dominant species/taxa after the amphipod *U. grimaldii* was the crown crab *Hymenosoma orbiculare*, copepods and the amphipod *Ampelisca palmata*. However, the amphipod *A. palmata* was also prevalent in summer 2016 in the Oesterwal North. Only three species met the modelling assumptions in terms of data variability. Of these species, the sandprawn *C. kraussi* was affected by an interaction between sites and seasons, while both the amphipod *A. palmata* and crown crab *H. orbiculare* abundances were influenced by seasons. Graphically, impacts of seasons were clear on the abundances of the amphipod *A. palmata* and crown crab *H. orbiculare*, with both these species being more abundant in winter compared to summer upwelling seasons (**Fig. 4.2C** and **Fig 4.2G**). One possible reason for this trend is the elevation of sediment chl-*a* levels in winter, particularly in 2015. Though, the expected increase in abundances of particular species during summer upwelling did not manifest.

The findings relating to species abundance in this chapter are consistent with those of Quintana *et al.* (2015), who documented lower densities of macrofaunal abundances during upwelling than in non-upwelling periods. One possible reason for such this finding could be the weakness of upwelling nutrients in enhancing benthic productivity, which is key to the elevation of typically generated positive bottom-up effects on abundances of associated benthic species. However, the dominance of sandprawns in summer in this study could also mean that most species were suppressed by bioturbation sediment-turnover impacts of this engineer. Generally, coastal upwelling areas have typically been reported to show striking upwelling-related increases in nutrient variability, associated with high densities (74,000 ind.m^{-2}) of macrofaunal species (Sellanes *et al.* 2007). Productive upwelling systems are generally acknowledged for their effects on marine coastal habitats by elevating nutrients and availability of trophic resources for consumers (Pennington *et al.* 2006, Chavez and Messié 2009), with very strong effects on benthic faunal communities (Bustamante *et al.* 1995, Levin *et al.* 2009).

The results of this study further indicated that macrofauna species/taxa that dominated the study sites were mostly positively influenced by sandprawn abundances within individual seasons, and that strongest effects were recorded in Oesterwal South. This result further reinforces the notion that sandprawn effects on individual species/taxa are site-specific. The amphipod *U. grimaldii* was the only species affected by sandprawn abundances in Oesterwal North, while in Oesterwal South, the amphipods *A. palmata*, *G. latipes* and *U. grimaldii*, the polychaete *N. latericeus* and the bivalve *T. trigona* were all positively affected by sandprawn abundance within seasons. Interestingly, results further indicated strong sandprawn impacts in winter than in summer in Oesterwal South. Given that sandprawn abundances were generally higher in summer than in winter, one potential explanation of the above finding (strong positive effects on macrofaunal species/taxa in winter in Oesterwal South) is that the magnitude and direction of sandprawn effects are not only site-specific, but also density-dependant, which could also be site specific. At low abundance, positive effects emerge, while at higher abundance, positive effects disappear. These results point to the important role played by sandprawns in regulating macrofaunal assemblages. It is likely that higher sediment turnover related to increased sandprawn numbers negatively impacts benthic species.

When data from summer and winter were combined, annual trends showed that sandprawn abundance was both positively and negatively related to species abundance. For example, the amphipods *G. palmata* and *G. latipes* in 2015 and juvenile polychaetes in 2016 were all negatively related to sandprawn abundances, while the polychaete *M. elitueni*, and amphipods *U. grimaldii* and *G. latipes* in 2016 were positively impacted by sandprawn abundances. These results therefore suggest that sandprawn impacts on macrofauna in this study were species/taxa dependent, which may be an important indication that sandprawn ecosystems engineering effects are not always antagonistic for macrofauna assemblages. It is likely that the species that were negatively correlated to sandprawn abundances (e.g. amphipods *A. palmata* and *G. latipes,* and juvenile polychaetes) exhibited biological traits that negatively pre-disposed them to sediment turnover by sandprawns, which either hindered feeding or settlement behaviour (Pillay and Branch 2011). For example, the amphipod *A. palmata* is a surface suspension feeder that extracts organic particles from the water column. High concentrations of suspended sediment particles caused by sandprawns bioturbation may directly interfere with the food intake by clogging filter-feeding appendages of this species thus, potentially hindering its growth and the condition and hence abundance (Rhoads and Young 1970, Pillay *et al.* 2007a). Sandprawns burrowing activities affect benthic communities through an immense amount of sediment being turned over to the sediment-water interface (Colin *et al.* 1986, Branch and Pringle 1987, Pillay *et al.* 2007a, 2007b, Pillay *et al.* 2011). Turned over sediment can negatively affect macrofauna species through burial, which may also impede their feeding and metabolic processes (Ellis *et al.* 2002, Pillay *et al.*

2007c). Sandprawns bioturbation can also increase sediment erodibility at the sediment-water interface, consequently impairing the settlement of larvae and macrofaunal growth (Rhoads and Young 1970, Pillay and Branch 2011). Furthermore, sediment erodibility can lead to re-suspension of macrofauna to the water column, subsequently increasing their vulnerability to predation (Flach 1993).

Promotive sandprawn impacts on some of the species documented in this study (e.g. amphipods *U. grimaldii* and *G. latipes* and bivalvia *T. trigona*) suggests that they perhaps have a high tolerance to sediment reworking by sandprawns, which in turn is likely due to inherent biological and life-history traits. This could imply that these species are able to withstand bioturbation impacts, and benefit from resource provision by sandprawn ecosystem engineering.

4.4.3 Functional groups

At a functional group level, surface deposit feeders, surface deposit feeders and predators, and suspension feeders were predicted by effects of seasons and sites. Both surface deposit feeders and suspension feeders were influenced by an interaction between sites and seasons, while, surface deposit feeders and also suspension feeders were influenced by the main effects of sites and seasons. Generally, the dominant pattern displayed by these functional groups was an increase in their abundances in winter season (**Fig 4.3B, D** and **E**), which was contrary to the posed hypothesis, although in 2016, both surface deposit feeders (**Fig 4.3B**) and burrowing deposit feeders and predators (**Fig 4.3C**) seemed to have somewhat followed this prediction in both sites. Correlation analysis revealed that within seasons, abundance of both burrowing and surface deposit feeders, and surface deposit feeders and predators were all variably influenced by sandprawn abundances, with burrowing deposit-feeders and surface deposit feeders and predators being positively affected while surface deposit feeders were negatively influenced.

Interestingly, when summer and winter data were combined per year, sandprawn abundances appeared to influence functional groups differently. In 2015, surface deposit feeders, surface deposit feeders and predators, and suspension feeders were all negatively impacted by sandprawn abundances in Oesterwal North. On the other hand, in Oesterwal South, most functional groups were affected by sandprawn abundances in a positive manner, except for suspension feeders, which were negatively related to sandprawn abundances. Generally, abundances of surface deposit feeder were higher in winter 2015, but this pattern was reversed in 2016, with abundances of surface deposit feeders being elevated in summer relative to winter. Surface deposit feeders and predators increased in winter 2015 and 2016 but also showed a peak in summer at some subsites (OS1 and ON3. **Fig 4.3D**). Suspension feeders were generally more abundant in winter season throughout the duration of the study.

Findings of this chapter did not conform to the hypothesis of this study that macrofauna should increase in response to upwelling, although, surface deposit feeders and predators seemed to have somewhat followed this hypothesis. Extending the discussion proposed earlier, increases in abundances of certain functional groups in winter may be due to increased food availability in the form of chlorophyll-*a*. Suspension feeders for example are known to feed predominantly on microalgae (Pillay *et al.* 2007a), which in this study, was elevated in winter, particularly in 2015 (see chapter 3). It is therefore very likely that the winter increase in suspension feeders was attributed to increased chlorophyll-*a* concentrations as a food resource. Secondly, lower abundance of sandprawns in winter could also provide an explanation for the overall increase exhibited by some functional groups in winter, due to the bioturbatory impacts of *C. kraussi* being reduced. In support for this interpretation, Pillay *et al.* 2007a, reported high densities of suspension feeders, subsurface feeding polychaetes and bivalves in sediment areas where the *C. kraussi* was either rare or absent compared to areas where *C. kraussi* was abundant. Moreover, both Pillay *et al.* (2007a) and Rhoads and Young (1970) have illustrated that suspension feeders are susceptible to high rates of bioturbation as the suspended sediment particles clog their filtration apparatus and decrease their feeding rate which then affect their body condition.

It is however, very important to note that *C. kraussi* does not necessarily induce only negative responses on functional groups (Pillay and Branch 2011). In this study, surface deposit feeders **(Fig 4.3B)** appeared to be elevated when sandprawns were abundant, which could be an indicative of a promotive role played by *C. kraussi* on this functional group of macrofauna.

4.5 CONCLUSION

Overall, this study highlighted spatial and seasonal variation displayed by macrofaunal community composition, diversity metrics, species and functional groups. Although macrofaunal community patterns differed between seasons, these results strongly suggest that summer upwelling in Langebaan Lagoon does not play a fundamental role in influencing these patterns as would be expected by nutrient enrichment (i.e. strengthening of bottom-up pathways). This outcome is similar to that reported for meiobenthos (detailed in the previous chapter), which differed significantly between sites and seasons, but without any obvious bottom up effects. Community metrics for both assemblages were enhanced during the winter non-upwelling season, possibly due to high benthic chl-*a* concentrations and lower sandprawn abundances (and potentially lower sediment turnover). These results therefore suggest that responses of macro- and meiofauna to sandprawn ecosystem engineering in the Langebaan Lagoon are unlikely to be influenced greatly by upwelling productivity, and do not display predicted positive responses relative to non-upwelling seasons. These results therefore suggest that sandprawn engineering may be stronger than bottom-up pathways (productivity) in regulating benthic community dynamics in this system.

CHAPTER 5

INTERACTIVE EFFECTS OF SANDPRAWNS AND NUTRIENT ENRICHEMENT ON **MEIOFAUNAL** COMMUNITY STRUCTURE: AN INTER-TIDAL EXPERIMENTAL APPROACH

5.1 Introduction

Physical, biological and chemical processes interact in complex ways to determine ecosystem functioning (Daly and Smith 1993), including the regulation of biological production, food web dynamics and interactions and biogeochemical cycling (Daly and Smith 1993). The importance of these biological-physico-chemical interplays in driving ecosystem processes is reflected and addressed in several seminal hypotheses such as Hubbell's Neutral Theory of Biodiversity (Hubbell 2001), the Intermediate Disturbance Hypothesis (IDH; Connell 1978) and Huston's Dynamic Equilibrium Model (DEM; Huston 1979, 1994). These models and others not only provide valuable conceptual frameworks that develop generalised ideas on the relationships between biological metrics and environmental variability, but are also highly relevant to conservation and management of ecosystems (Wootton 1998, Olff and Ritchie 1998, Svesson *et al.* 2012).

Huston's (1994) dynamic equilibrium model emphasizes the importance of competition as a structuring force for communities, especially at high productivity levels. It proposes that: (**i**) species diversity would be minimal at low productivity due to insufficient resources that maintain and promote species diversity; (**ii**) as the level of productivity increases, resource availability would allow more species to coexist and ultimately increase diversity and (**iii**) under high productivity, population growth of dominant competitors first grows exponentially without any limits but eventually collapses. The latter occurs as a result of rapid population expansion utilizing much of the available resources, thereby indirectly removing rival species and ultimately reducing diversity. Overall, the dynamic equilibrium model captures explicitly the idea that community structure is an unstable equilibrium between resource supply and its exploitation. Therefore, equilibrium between community structure and resources is continuously influenced by a different degree of perturbation.

The IDH predicts a unimodal relationships between species diversity and disturbance, with the highest diversity occurring at an intermediate level of disturbance (Connell 1978). Co-existence of rapid colonizers (*r*-selected) and competitively dominant (*K*-selected) species is generally thought to be facilitated by an intermediate level of disturbance. On the other hand, competitive exclusion and local species extinctions are hypothesised mechanisms thought to drive patterns of low diversity at high disturbance levels. At low disturbance, competitively dominant species outcompete those with weak competitive abilities, but at high disturbance, only the most tolerant species survive (Connell 1978).

Huston's dynamic equilibrium model has been strongly supported by other authors. For example, Proulx and Mazumder (1998) examined the interaction between grazing (which is a dominant type of biotic disturbance) and nutrients on plant species richness and developed the grazer-reversal hypothesis (**Fig.5.1**). This hypothesis proposes that (**i**) under low nutrient regimes, grazing reduces richness due to stress imposed by low productivity (i.e. there is insufficient resources); (**ii**) at intermediate nutrient levels, richness increases at intermediate grazing pressure and **(iii**) at high nutrient regimes, an increase in grazing pressure increases richness by offsetting the competition intensity.

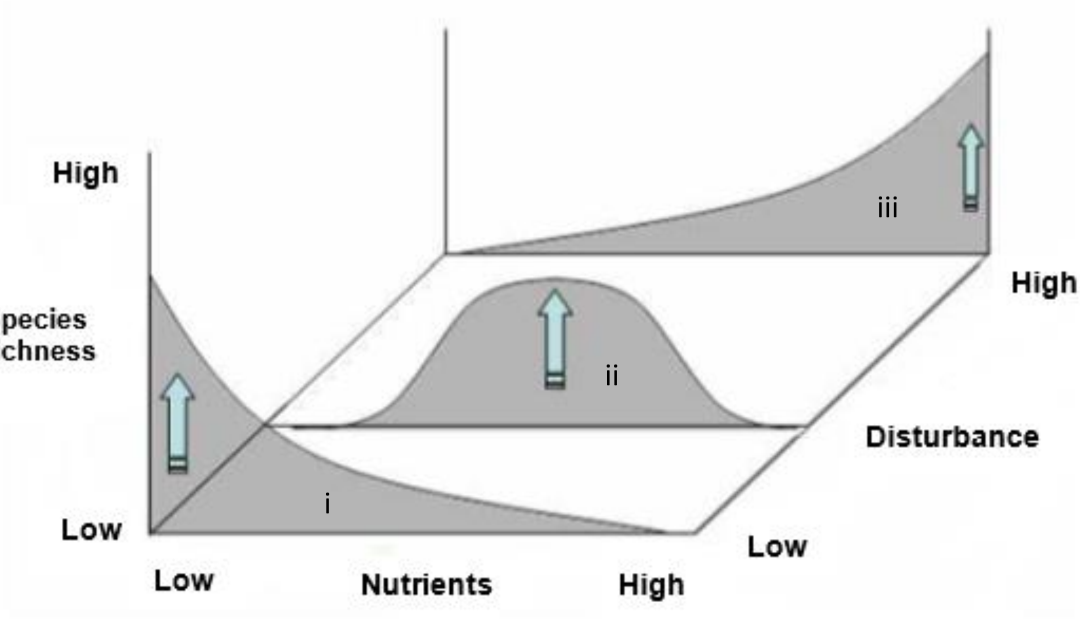

Fig.5.1. Schematic illustrating the response of species richness (y – axis) to interactions between nutrients (x - axis) and disturbance (z –axis) after Proulx and Mazumder (1998).

Although both the IDH and DEM models are considered important tools in ecological science and management (Svensson *et al.* 2012), they have been criticized through both empirical and theoretical studies for their simplistic nature (Huxham *et al*. 2000b, Shea *et al.* 2004). For example, Violle *et al.* (2010) illustrated strong competition along a disturbance gradient and showed that the maximum disturbance level observed did not weaken the intensity of competition. Their findings thus challenge the assumption of the IDH, in which emphasis is placed on the principle of competitive exclusion mediating low diversity at both low and high disturbance levels. Mackey and Currie (2001), based on a meta-analysis, argued that no single pattern appears to be common in global studies of diversity and disturbance, instead multiple patterns are found in nature, including decreasing and U-shaped diversity responses. Their findings are consistent with those of Miller *et al.* (2011) who indicated that in areas where species coexistence is high and in which diversity peaks, increasing diversity can be in a form of U-shaped pattern. A recent review of the IDH model in terrestrial systems by Kershaw and Mallik (2013) has revealed that 22 of 48 examined studies supported the IDH. Despite such findings, a call to abandon the IDH model due to its refutation on both empirical and theoretical grounds has recently emerged in the literature (Fox 2013). According to Sheil and Burslem (2013) and Huston (2014) criticisms on the IDH occur as a result of misrepresentation of the theory. They argued that studies often attempt to examine the IDH inappropriately by conducting experiments in regions where both population growth rates and productivity are beyond intermediate range desired by the IDH. As for soft-sediment systems, a recently study by Gerwing *et al.* (2017) argued that communities do not respond to disturbance in a manner predicted by the IDH model. They reported species richness to be unaffected by mechanical disturbance of sediment at different intensity levels.

Nevertheless, criticisms of the IDH and DEM have not dampened interest in applying these models in ecological sciences. A high volume of citations and published scientific papers are an evidence for the latter (Svensson *et al.* 2012, Fox 2013). Furthermore, the evaluation of these models has occurred across a wide range of ecosystems, i.e. in terrestrial (Molino and Sabatier 2001), fresh water (Padisak 1993, Mackey and Currie 2001, Hughes *et al.* 2007) and marine soft-sediment ecosystems for the IDH (Sousa 1979, Austen and Widdicombe 1998, Cowie *et al.* 2000), and for the DEM in terrestrial and aquatic ecosystems (Worm *et al.* 2002, Svensson *et al.* 2012).

Several studies have examined interactions between nutrients and disturbance on communities (Proulx and Mazumder 1998, Kondoh 2001, Worm *et al.* 2002, Wilson and Tilman 2002), with nutrients generally being a proxy for productivity and disturbance being depicted through various means depending on the study. For example, some studies have use allogenic engineers which are also grazers, to test disturbance effects (Liess *et al.* 2009, Hlillebrand 2003, Wilson and Tilman 2002, Worm *et al.* 2002). In general, studies of relevance have reported little reported evidence for an interaction between productivity and disturbance (Warren and Spencer 1996, Nielsen 2003, Hillebrand 2003, Contardo-Jara *et al.* 2006). In some instances, main effects but not an interaction between productivity and disturbance have been found to be important for regulating community patterns (Hillebrand 2003). On the other hand, Wilson and Tilman (2002) showed that increased nutrients within disturbance regimes reduced species richness, thus showing evidence supporting interactions between productivity and disturbance.

Different diversity metrics that are applied to test community response analyses are viewed as an important reason causing discrepancies among studies. For example, Svensson *et al.* (2012) highlights the fact that richness and evenness are considered important aspects of diversity, yet it is unclear if both these indices respond in a similar way to different levels of disturbance. Different productivity levels and spatial scales at which the experiments are conducted could also explain the inconsistent results among studies (Mackey and Currie 2001, Violle *et al.* 2010).

5.2 Sandprawns, disturbance and nutrients

In view of the preceding background in this chapter about disturbance and productivity, as well as the grazer-reversal model proposed by Proulx and Mazumder 1998, this chapter aims to determine the relative importance of an interaction between disturbance generated by burrowing sandprawns (*Callichirus kraussii*) through sediment bioturbation and productivity (by nutrient enrichment) on meiofaunal community structure. This chapter also aims to ascertain if meiofaunal responses follow the predictions of the grazer-reversal hypothesis. To date, this question has not been addressed but is an important research area in marine soft-sediment ecology. Grazing effects can be somewhat analogous to bioturbation by sandprawns in a sense that the activities of both organism groups create disturbances, which can result in reductions of biomass and/or abundance (Cadée 2001, Dawson and Pillay 2011). However, these organisms differ in the mechanisms by which their effects are derived. Grazers alter biomass primarily through consumption (Levinton and Stewart 1982) whereas sandprawns modify biomass by overturning sediment and smothering surface dwellers amongst other effects (Branch and Pringle 1987).

Apart from generating information relevant to fundamental ecology, the questioned posed in this chapter are also of applied relevance. Both background nutrient levels and sand-pawn densities are significantly altered by anthropogenic activities (Mork *et al*. 2009, Nel and Branch 2013). Humans are renowned for their considerable impacts in coastal ecosystems, often through high rate of nutrient inputs (Michener *et al*. 1997, Espinosa *et al.* 2007, Diaz and Rosenberg 2008, Shin and Cheung 2010) and over-harvesting of ecologically important species (Duffy 2003, Mork *et al*. 2009). Such activities can have drastic impacts in marine ecosystems, leading to major shifts in ecosystem functioning and the quality of goods and services provided (Mork *et al*. 2009). In Langebaan Lagoon, sandprawns are the main target for recreational and commercial bait-collectors, with the collection of 50 sandprawns per person per day being permitted subject to appropriate licenses being held.

5.3 Hypotheses

This study investigated the following hypotheses as part of the study objectives:

H1: At the low nutrient levels, increasing sandprawn densities should reduce surface meiofaunal species diversity.

H2: At the intermediate nutrient levels, increasing sandprawn densities should induce unimodal, hump-shaped responses in surface meiofaunal diversity.

H3: At high nutrient levels, surface meiofaunal diversity should increase with increasing sandprawn densities.

H4: Meiofaunal diversity should be lower at the sediment surface and higher along the burrow-walls, due to increased surface instability created by sediment reworking.

- **METHODS AND MATERIALS**

Please refer to chapter 2 for the methods used in this chapter.

5.4 RESULTS

5.4.1 Microalgal biomass (chl-*a*)

Nutrient treatments and sandprawn densities did not significantly influence microalgal biomass as indicated by the Likelihood ratio Test (LRT), revealing no parsimonious candidate model for chl-*a* concentrations at all habitat positions ($p > 0.05$, in all cases, **Table 5.1**). At the site level, the chl-*a* concentrations showed no clear pattern either in response to increasing sandprawn densities or nutrient treatments. The latter trend was observed for all sandprawn habitat positions (**Fig 5.2**).

Table 5.1: Generalized linear models reporting candidate models that were parsimonious and statistically significant for sediment microbial biomass (chl-*a*) at three different sandprawn habitat positions within experimental cages. The experiment investigated effects of nutrients and sandprawn densities on meiofaunal communities. NB: full model = interaction between all factors, model 2 = interaction between nutrients and sandprawns, model 3 = main effects.

Habitat positions											
		Burrow-wall					**Surface sediment**				
Candidate models		**RDF**	**RD**	**Deviance**	**DF**	**Pr(>Chi)**	**RDF**	**RD**	**Deviance**	**DF**	**Pr(>Chi)**
Full model	S X N X P	36	5538	3629	17	0.131	36	3922	2589	17	0.125
Model 2	S + (N X P)	44	6386	-8478	-8	0.701	44	5355	-1432	-8	0.106
Model 3	S + N+ P	48	7579	-1192	-4	0.101	48	5711	-3567	-4	0.513
Null		53	9168				53	6511			
Reference											
Full model	S X N X P	36	1563	6843	17	0.541					
Model 2	S + (N X P)	44	1866	-3035	-8	0.537					
Model 3	S + N +P	48	2043	-1764	-4	0.397					
Null		53	2247								

1: s sites
2: N = Nutrients
3: P = Prawns
5: RD = Residual deviance
6: DF = Degrees of freedom
7: Pr (> Chi) = Measure of the *p*-value

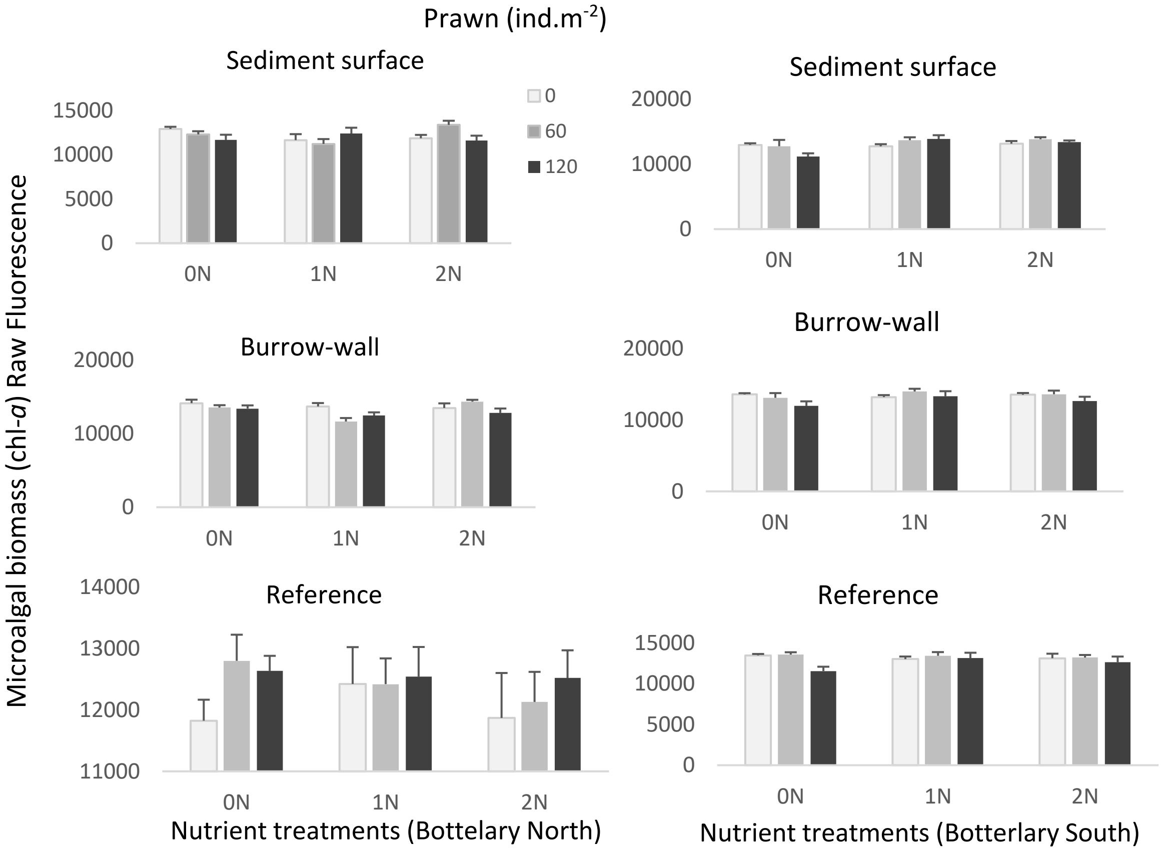

Fig 5.2: Variation in microalgal biomass (chl-*a*, ± 1SE) at the three habitat positions, in response to increasing sandprawn densities, within each nutrient treatment level at the two experimental sites. NB: Y axis scales are different to show the trend in the data.

5.4.2 Sediment turnover

Sediment turnover was best predicted by model 3 predicting the main effect of sites, nutrient enrichment and sandprawn densities ($p = 0.039$; **Table 5.2**). Neither an interaction between sites, nutrient enrichment and sandprawn densities (full model) nor the interaction between nutrient enrichment and sandprawn (model 2) predicted the sediment turnover within experimental cages ($p > 0.05$, for all cases). The GLM model analysis indicated that sediment turnover differed significantly between sites ($p = 0.017$), and that a sandprawn density of 120 (ind.m^{-2}) was main level responsible for within-treatment differences in sediment turnover (*p* = 0.014). The rate of sediment turnover was generally elevated in the presence of sandprawns in both sites, with the exception of the 1N treatment in Bottelary South (**Fig 5.3**).

Table 5.2: Generalized linear models reporting candidate models that were parsimonious and statistically significant for sediment turnover within experimental cages. Values in bold indicate statistical significance.

Sediment turnover						
Candidate models		**RDF**	**RD**	**Deviance**	**DF**	**Pr(>Chi)**
Full model	S X N X P	36	42.206	480.18	4	0.5307
Model 2	S + (N X P)	44	43.15	577.33	4	0.510
Model 3	S + N+ P	48	83.877	620.49	2	**0.039**
Null		53	798.08			

1: S sites
2: N = Nutrients
3: RD = Residual deviance
4: DF = Degrees of freedom
5: P = Prawns
6: Pr (> Chi) = Measure of the *p*-value

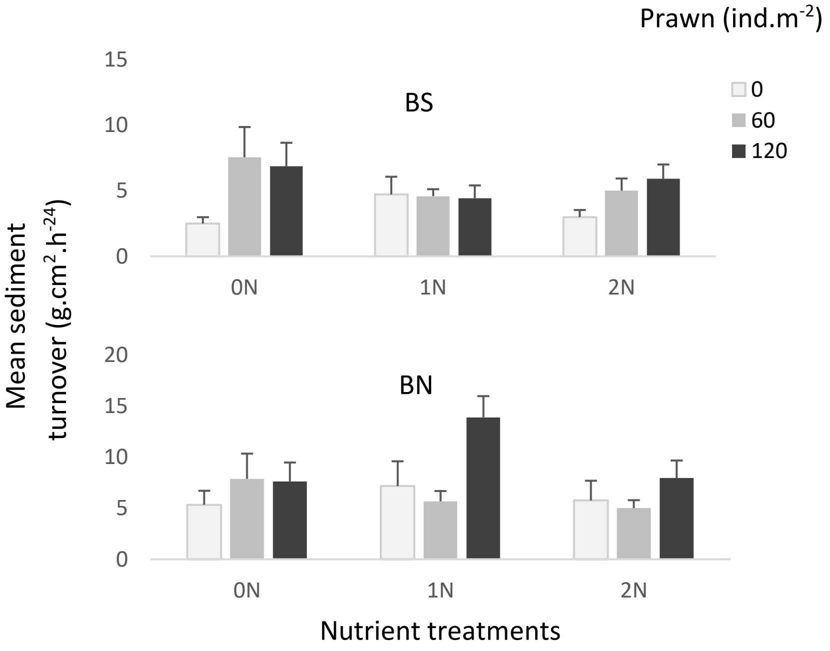

Fig 5.3: Mean sediment turnover levels (± 1SE) in Bottelary South (**BS**) and North (**BN**) within experimental cages manipulating nutrient and sandprawn levels.

5.4.3 Meiofaunal community structure: Overall composition

5.4.3.1 Sediment surface

Meiofaunal community structure at the sediment surface was not significantly affected by an interaction between sites, nutrient treatments and sandprawn densities (PERMANOVA, Pseudo-$F_{4, 161}$ = 1.384, p = 0.181, **Table 5.3**). However, sites (PERMANOVA, Pseudo-$F_{1, 161}$ = 7.092, p= 0.017) and sandprawn densities (PERMANOVA, Pseudo-$F_{2, 161}$ = 5.859, p = 0.034) as individual factors had a significant influence on the surface meiofauna. Nutrient treatments did not significantly influence the structure of surficial meiofaunal communities (PERMANOVA, Pseudo-$F_{2, 161}$ = 0.773, p = 0.654).

5.4.3.2 Burrow-wall

The burrow-wall meiofaunal community was significantly influenced by an interaction between sites and nutrient treatments (PERMANOVA, Pseudo-$F_{2, 161}$ = 2.776, p = 0.028), and also by sandprawn densities (PERMANOVA, Pseudo-$F_{2, 161}$ = 34.755, p = 0.033, **Table 5.3**). However, the combination of sites, nutrient treatments and sandprawn densities failed to influence burrow-wall meiofaunal communities (PERMANOVA, Pseudo-$F_{4, 161}$ =1.494, p = 0.151). Similarly, nutrients and sandprawn densities did not interact to influence meiofaunal communities at the burrow-wall habitat position (PERMANOVA, Pseudo-$F_{4, 161}$ =1.527, p = 0.123). Moreover, sites (PERMANOVA, Pseudo-$F_{1, 161}$ =3.1591, p = 0.177) and nutrient treatments (PERMANOVA, Pseudo-$F_{2, 161}$ = 0.499, p = 0.791) as individual factors failed to influence burrow-wall meiofaunal community structure.

5.4.3.3 Reference

PERMANOVA revealed a strong interactive effect of sites, nutrients and sandprawn densities on reference meiofaunal community assemblages (Pseudo-$F_{4, 161}$ = 2.414, p = 0.009, **Table 5.3**). For the main effects, sites significantly influenced the reference meiofaunal community structure (PERMANOVA, Pseudo-$F_{1, 161}$ = 6.089, p = 0.013), but neither nutrient treatments (PERMANOVA, Pseudo-$F_{2, 161}$ = 1.654, p = 0.261) nor sandprawn densities (PERMANOVA, Pseudo-$F_{2\ 161}$ = 0.881, p = 0.499) significantly affected reference meiofaunal community structure.

Table 5.3: PERMANOVA summary statistics reporting the responses of meiofaunal community structure to nutrient treatments, sandprawn densities, sites and the interaction among all factors. Statistical descriptions: *Pseudo-F* = test statistics, df = degrees of freedom, *p*— value = significance level. Values in bold indicate statistical significance.

Habitat position	**Sediment surface**			**Burrow-wall**			**Reference**		
Factors	***Pseudo-F***	**df**	***p*-value**	***Pseudo-F***	**df**	***p*-value**	***Pseudo-F***	**df**	***p*-value**
Sites	7.092	1	**0.017**	3.159	1	0.177	6.089	1	**0.013**
Nutrients	0.773	2	0.654	0.499	2	0.791	1.654	2	0.261
Prawns	5.859	2	**0.034**	34.755	2	**0.033**	0.881	2	0.499
Nutrients X Prawns	1.253	4	0.241	1.527	4	0.123	1.613	4	0.094
Sites X Nutrients	0.898	2	0.506	2.776	2	**0.028**	0.296	2	0.813
Sites X Prawns	0.559	2	0.695	1.375	2	0.318	1.183	2	0.388
Sites X Nutrients X Prawns	1.384	4	0.181	1.494	4	0.151	2.414	2	**0.009**

5.4.4 Diversity metrics

5.4.4.1 Sediment surface

Based on the likelihood ratio (LRT) and Chi-square tests, species richness and abundance at the sediment surface were the only meiofaunal diversity metrics influenced by the candidate models (**Table 5.4A**). Species richness was significantly influenced by both the full model of an interaction between site, nutrients and sandprawns and by model 3 examining main effects (p <0.05, for all cases, **Table 5.4A**). Meiofaunal abundance was also significantly affected by the model 3 ($p < 0.001$).

For the model 2, effects on species richness were significant at the level 1N treatment and 120 ind.m^2 ($p = 0.017$), while for the main effects model 3, richness differed significantly between sites *(*$p = 0.025$). A significant effect of 60 and 120 (ind.m^2) sandprawns occurred on abundance at the sediment surface ($p < 0.0001$, for all cases, **Table 5.4B**).

Table 5.4A. Generalized linear models reporting candidate models that were parsimonious and statistically significant for meiofaunal diversity metrics at the sediment surface. The experiment investigated effects of nutrients and sandprawn densities on meiofaunal communities. NB: only parsimonious and significant models ($p < 0.05$) were selected for further analysis. Statistical descriptions: full model = interaction between all factors, model 2 = interaction between nutrients and sandprawns, model 3 = main effects. Values in bold indicate statistical significance.

Sediment surface habitat position											
				Species richness (S)					**Evenness (J')**		
Candidate models		**RDF**	**RD**	**Deviance**	**DF**	**Pr(>Chi)**	**RDF**	**RD**	**Deviance**	**DF**	**Pr(>Chi)**
Full model	S X N X P	36	5.259	5.646	17	**0.002**	36	0.814	0.140	17	0.991
Model 2	S + (N X P)	44	7.522	-2.263	-8	0.050	44	0.835	-0.020	-8	0.099
Model 3	S + N +P	48	8.987	-1.465	-4	**0.039**	48	0.904	-0.069	-4	0.547
Null		53	10.905				53	0.955			
				Shannon-Wiener diversity (H')					**Abundance (N)**		
								Theta Res.	**LR stat.**	**DF**	**Pr(>Chi)**
Full model	S X N X P	36	1.042	0.301	17	0.885	36	9.926	8.230	8	0.411
Model 2	S + (N X P)	44	1.089	-0.046	-8	0.990	44	8.558	0.952	4	0.916
Model 3	S + N +P	48	1.269	-0.179	-4	0.185	48	8.413	19.151	5	**0.001**
Null		53	1.344				53	5.985			

1: S = Site
2: N = Nutrients
3: P = Prawns
4: RDF = Residual degrees of freedom
5: RD = Residual deviance
6: DF = Degrees of freedom
7: Pr(>Chi) = Measure of the *p*-value

Table 5.4B: Summary of parsimonious generalized linear models investigating effect of nutrients and sandprawn densities on the meiofaunal diversity metrics from the sediment surface habitat position. Statistical descriptions: full model = interaction between all factors, model 2 = interaction between nutrients and sandprawns, model 3 = main effects. Values in bold indicate statistical significance.

Sediment surface habitat position					
		Species richness (S)			
Models		**Term level**	**Estimate**	**95 % Coefficient Intervals (Lower and upper limits)**	**Pr(>/t/)**
Full model	S X N X P	S X 1N X 120P	0.833	0.171 1.495	**0.017**
Model 3	S + N +P	S	0.271	0.040 0.502	**0.025**
		Abundance (N)			
Model 3	S + N +P	60P	-0.404	-0.630 -0.177	**<0.0001**
		120P	-0.469	-0.696 -0.243	**<0.0001**

1: S = Site
2: N = Nutrients
3: P = Prawns
4: Pr (>/t/) = Measure of the *p*-value

5.4.4.2 Burrow-wall

The full model that examined an interaction between sites, nutrients and sandprawn densities was identified as the most parsimonious model for all diversity metrics at the burrow-wall position ($p < 0.05$ for all cases, **Table 5.5A**). The interactive model 2 was only parsimonious for Shannon-Wiener diversity ($p = 0.049$). On the other hand, evenness, abundance and Shannon-Wiener diversity were all best predicted by the smallest parsimonious model 3, examining main effects of the sites, nutrients and sandprawns ($p = 0.05$, for all cases).

Of the interactive models, the full model significantly influenced evenness, abundance and Shannon-Wiener diversity ($p < 0.05$ for all cases, **Table 5.5B**). For evenness, interactive effects were significant between sites, 2N treatment and 60 ind.m^2 ($p = 0.019$) and between sites, 2N and 120 ind.m^2 ($p = 0.004$). For abundance, the interaction was significant between sites, 2N and 60 ind.m^2 treatments ($p = 0.003$), while for Shannon-Wiener diversity, it was between sites, 2N and 120 ind.m$^{2.}$ ($p = 0.019$). As for the interactive model 2, two separate interactions were identified by the GLM model analysis for Shannon-Wiener diversity (**Table 5.5B).** The first interaction occurred between the 1N treatment and level 120 ind.m^{2} (p = 0.002), while the second interaction was observed between the 2N and 120 ind.m^{2} ($p = 0.006$).

Based on the model 3 GLM analysis, there was a significant effect of sandprawn densities on burrow-wall meiofaunal evenness, Shannon-Wiener diversity, and abundance ($p < 0.05$, for all cases, **Table 5.5B**). Evenness was significantly influenced by the sandprawn level 120 ind.m$^{2.}$ ($p = 0.0005$). Shannon-Wiener diversity was significantly affected by both 60 and 120 ind.m$^{2.}$ ($p < 0.0001$, for both cases), while abundance was significantly affected by both level 60 and 120 (ind.m^{2}) sandprawn densities ($p < 0.0001$, for both cases).

Table 5.5A. Generalized linear models reporting the candidate models that were parsimonious and significant for meiofaunal diversity metrics from the sandprawn burrow-walls within experimental cages. The experiment investigated an interactive effect of nutrients and sandprawn densities on the meiofaunal communities. NB: full model = interaction between all factors, model 2 = interaction between nutrients and sandprawns, model 3 = main effects. Values in bold indicate statistical significance.

Burrow-wall habitat position											
Candidate Models				**Species richness (S)**					**Evenness (J')**		
		RDF	**RD**	**Deviance**	**DF**	**Pr(>Chi)**	**RDF**	**RD**	**Deviance**	**DF**	**Pr(>Chi)**
Full model	S X N X P	36	5.4074	5.541	17	**0.003**	36	0.327	0.455	17	**<0.0001**
Model 2	S + (N X P)	44	6.238	-0.831	-8	0.699	44	0.458	-0.130	-8	0.073
Model 3	S + N +P	48	7.098	-0.860	-4	0.220	48	0.623	-0.164	-4	**0.001**
Null		53	10.948				53	0.783			
				Shannon-Wiener diversity (H')					**Abundance (N)**		
								Theta Res.	**LR stat.**	**DF**	**Pr(>Chi)**
Full model	S X N X P	36	0.388	0.470	17	**<0.0001**	36	8.112	17.756	8	**0.023**
Model 2	S + (N X P)	44	0.556	-0.168	-8	**0.049**	44	5.907	0.716	4	0.949
Model 3	S + N +P	48	0.783	-0.226	-4	**<0.0001**	48	5.832	71.059	5	**0.001**
Null		53	0.858				53	5.985			

1: S = Site
2: N = Nutrients
3: P = Prawns
4: RDF = Residual degrees of freedom
5: RD = Residual deviance
6: DF = Degrees of freedom
7: Pr (> Chi) = Measure of the *p*-value

Table 5.5B: Summary of parsimonious generalized linear models investigating interactive effect of nutrients and sandprawn densities on the meiofaunal diversity metrics, sampled from the sandprawn burrow-walls within experimental cages. Statistical descriptions: full model = interaction between all factors, model 2 = interaction between nutrients and sandprawns, model 3 = main effects. Values in bold indicate statistical significance.

				Burrow-wall habitat position					
			Species richness (S)				**Evenness (J')**		
Models		**Term level**	**Estimate**	**95 % Coefficient Intervals (Lower and upper limits)**	**Pr(>/t/)**	**Term level**	**Estimate**	**95 % Coefficient Intervals (Lower and upper limits**	**Pr(>/t/)**
Full model	S X N X P	S X 1N X 60P	5.556	-0.684 1.795	0.3858	S X 2N X 60P	0.382	0.076 0.6875	**0.019**
Model 2	S + (N X P)					S X 2NX 120	0.320	0.015 0.6258	**0.047**
Model 3	S + N +P					120P	0.111	0.036 0.1857	**0.005**
			Shannon-Wiener diversity (H')				**Abundance (N)**		
Full model	S X N X P	S X 2N X 120P	0.416	0.028 0.748	**0.019**	S X 2N X 60P	-1.710	-2.842 -0.5784	**0.003**
Model 2	S + (N X P)	1N X 120P	0.292	0.112 0.472	**0.002**				
		2N X 120P	0.264	0.084 0.444	**0.006**				
Model 3	S + N +P	60P	-0.404	-0.630 -0.177	**<0.0001**	60P	-1.287	-1.559 -1.015	**<0.0001**
		120P	-0.469	-0.696 -0.243	**<0.0001**	120P	-1.351	-1.625 -1.077	**<0.0001**

1: S = Site 3: P = Prawns
2: N = Nutrients 4: Pr (>/t/) = Measure of the *p*-value

5.4.4.3 Reference

As indicated by the likelihood ratio (LRT) and Chi-square tests, species richness and abundance were the only diversity metrics at the reference position to be predicted by sites, nutrients and sandprawn densities (**Table 5.6A**). The full model was parsimonious for both these diversity metrics (p <0.05, for both cases). However, species richness was further predicted by model 2 (p = 0.005), which examined an interaction between nutrients and sandprawn densities, and by model 3 (p = 0.003), testing for the main effects of the experimental treatments.

As for the full model, species richness was significantly influenced by an interaction between sites, 2N treatment and 60 ind.m^2 (p = 0.007, **Table 5.6B**), while abundance was significantly affected by an interaction between sites, 1N treatment and 60 ind.m^2 (p < 0.0001), sites, 2N treatment and 60 ind.m^2 (p = 0.030), sites, 1N treatment and 120 ind.m^2 (p < 0.0001), and sites, 2N treatment and 120 ind.m^2 (p = 0.008). The GLM model analysis indicated that model 2 of an interaction between nutrients and sandprawns but not site had a significant influence on species richness, particularly between the 1N treatment and 120 ind.m^2 (p = 0.026). A sandprawn density of 120 ind.m^2 was identified by the GLM for model 3 analysis as the density level that significantly affected species richness (p = 0.0252, **Table 5.6B**).

Table 5.6A. Results from generalized linear models reporting the candidate models that were parsimonious and significant for meiofaunal diversity metrics collected from the cage experiment within the reference position adjacent to sandprawn burrows. The experiment investigated an interactive effects of nutrients and sandprawn densities on meiofaunal communities. Statistical descriptions: full model = interaction between all factors, model 2 = interaction between nutrients and sandprawns, model 3 = main effects. Values in bold indicate statistical significance.

				Reference habitat position							
				Species richness (S)					**Evenness (J')**		
Models		**RDF**	**RD**	**Deviance**	**DF**	**Pr(>Chi)**	**RDF**	**RD**	**Deviance**	**DF**	**Pr(>Chi)**
Full model	S X N X P	36	3.481	4.923	17	**<0.0001**	36	0.625	0.200	17	0.826
Model 2	S + (N X P)	44	5.592	-2.111	-8	**0.005**	44	0.694	-0.068	-8	0.864
Model 3	S + N +P	48	7.107	-1.5144	-4	**0.003**	48	0.770	-0.076	-4	0.355
Null		53	8.405				53	0.826			
				Shannon-Wiener diversity (H')					**Abundance (N)**		
								Theta Res.	LR stat.	DF	Pr(>Chi)
Full model	S X N X P	36	0.888	0.3610	17	0.622	36	11.222	17.000	8	**0.030**
Model 2	S + (N X P)	44	1.019	-0.1314	-8	0.722	44	8.262	1.5015	4	0.826
Model 3	S + N +P	48	1.141	-0.1220	-4	0.293	48	8.043	7.5062	5	0.185
Null		53	1.249				53	7.036			

1: S = Site
2: N = Nutrients
3: P = Prawns
4: RDF = Residual degrees of freedom
5: RD = Residual deviance
6: DF = Degrees of freedom
7: Pr (>Chi) = Measure of the *p*-value

Table 5.6B. Summary of parsimonious generalized linear models investigating effects of nutrients and sandprawn densities on the meiofaunal diversity metrics collected from the cage experiment within the reference position adjacent to sandprawn burrows. Statistical descriptions: full model = interaction between all factors, model 2 = interaction between nutrients and sandprawns, model 3 = main effects. Values in bold indicate statistical significance.

Reference habitat position									
		Species richness (S)				**Abundance (N)**			
Models		**Term level**	**Estimate**	**95 % Coefficient Intervals (Lower and upper limits)**	**Pr(>/t/)**	**Term level**	**Estimate**	**95 % Coefficient Intervals (Lower and upper limits)**	**Pr(>/t/)**
Full model	S X N X P	S X 2N X 60P	0.014	0.449 2.439	**0.007**	S X 1N X 60P	1.450	0.490 2.409	**0.003**
Model 2	S + (N X P)	1N X 120P	0.666	0.096 1.237	**0.026**	S X 2N X 60P	1.053	0.094 2.012	**0.030**
Model 3	S + N +P	120P	-0.296	-0.547 -0.044	**0.025**	S X 1N X 120P	1.701	0.742 2.660	**<0.0001**
						S X 2NX 120P	1.2919	0.332 2.250	**0.008**

1: S = Site	4: P = Prawns
2: N = Nutrients	5: Pr (>/t/) = Measure of the *p*-value

5.4.5. Diversity metrics: overall patterns

Nutrient treatment effects on meiofaunal diversity were unclear for all diversity metrics in both sites, and also across all sandprawn habitat positions (**Fig. 5.4A-D**). However, strong patterns that dominated most diversity metrics were largely due to sandprawn densities, in which the metrics were either reduced or enhanced in response to increasing sandprawn densities.

At the sediment surface position, meiofaunal abundance decreased against increasing sandprawn densities (**Fig.5.4B:** 1N and 2N treatment in Bottelary North, and also at the ON and 2N treatment in Bottelary South). On the other hand, a hump-shaped pattern in response to increasing sandprawns was observed for the abundance at the ON treatment in Bottelary North.

Most meiofaunal diversity metrics were significantly affected by sandprawn densities at the burrow-wall habitat position, with the exception of species richness. Abundance decreased with increasing sandprawn densities (e.g. Bottelary North: 1N and 2N, and Bottelary South: ON, 1N and 2N, **Fig.5.4B**), while evenness displayed mostly a linear increase against increasing sandprawns (e.g. Bottelary North and South: 1N and 2N nutrient treatment, **Fig.5.4C**). In Bottelary South, an interesting pattern appeared in which Shannon-Wiener diversity, was first reduced against increasing sandprawns at the ON treatment, slightly enhanced at the 1N and eventually followed a linear increase pattern at the 2N treatment (**Fig. 5.4D**). At the reference position, species richness, being the only meiofaunal diversity metric that was statically influenced by sandprawns, showed a hump-shaped pattern at the 0N and 2N treatment in Bottelary North and 1N in Bottelary South. A reduction in species richness due to increasing sandprawn densities was also observed at the 2N treatment (**Fig. 5.4A**).

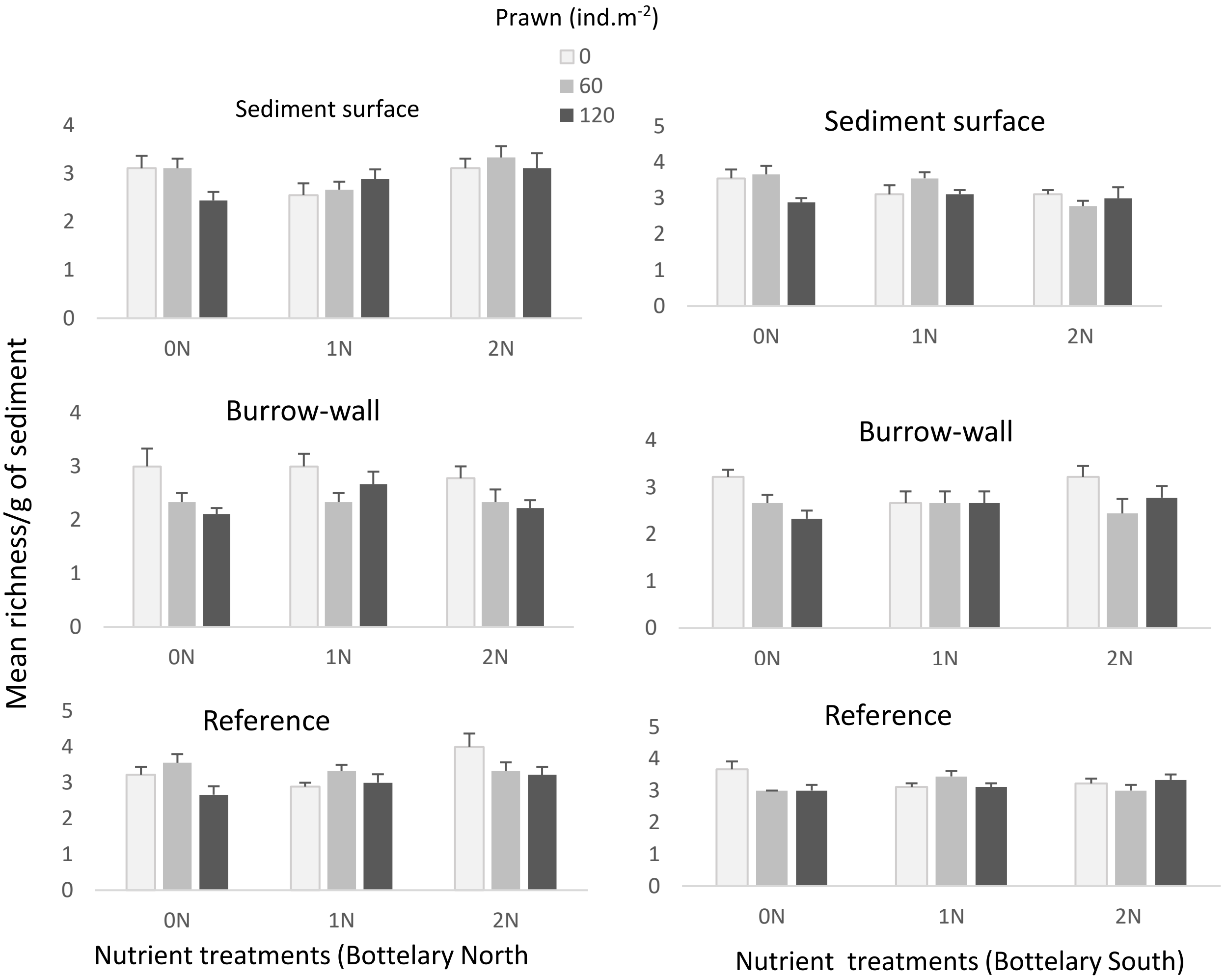

Fig. 5.4A: Variation in mean meiofaunal species richness (± 1SE) at the three sandprawn habitat positions, in response to increasing sandprawn densities within each nutrient treatment level at the two experimental sites.

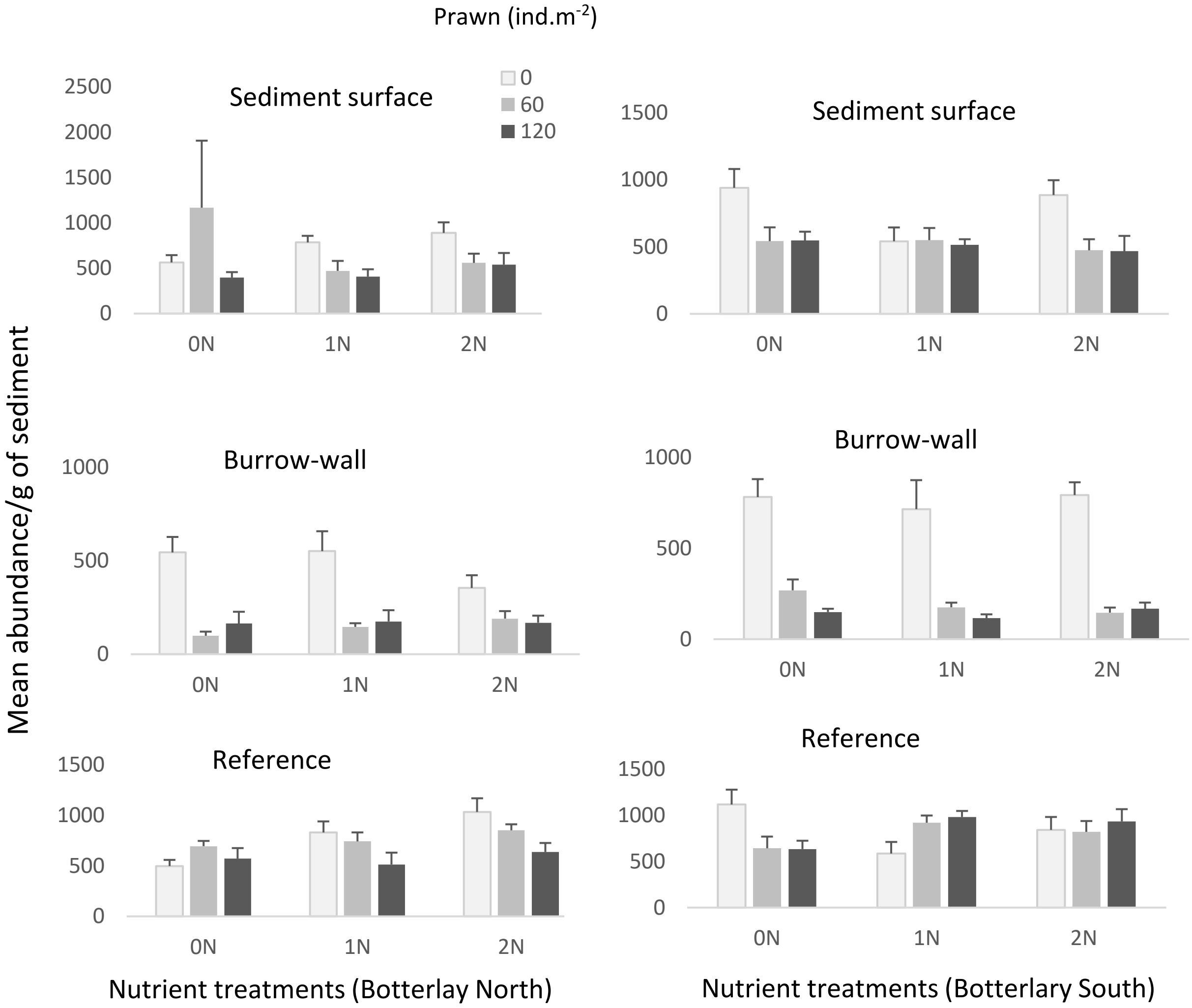

Fig. 5.4B: Variation in mean meiofaunal abundance (± 1SE) at each sandprawn habitat position, in response to increasing sandprawn densities within each nutrient treatment level at the two experimental sites. NB: Y axis scales are different to show the trend in the data.

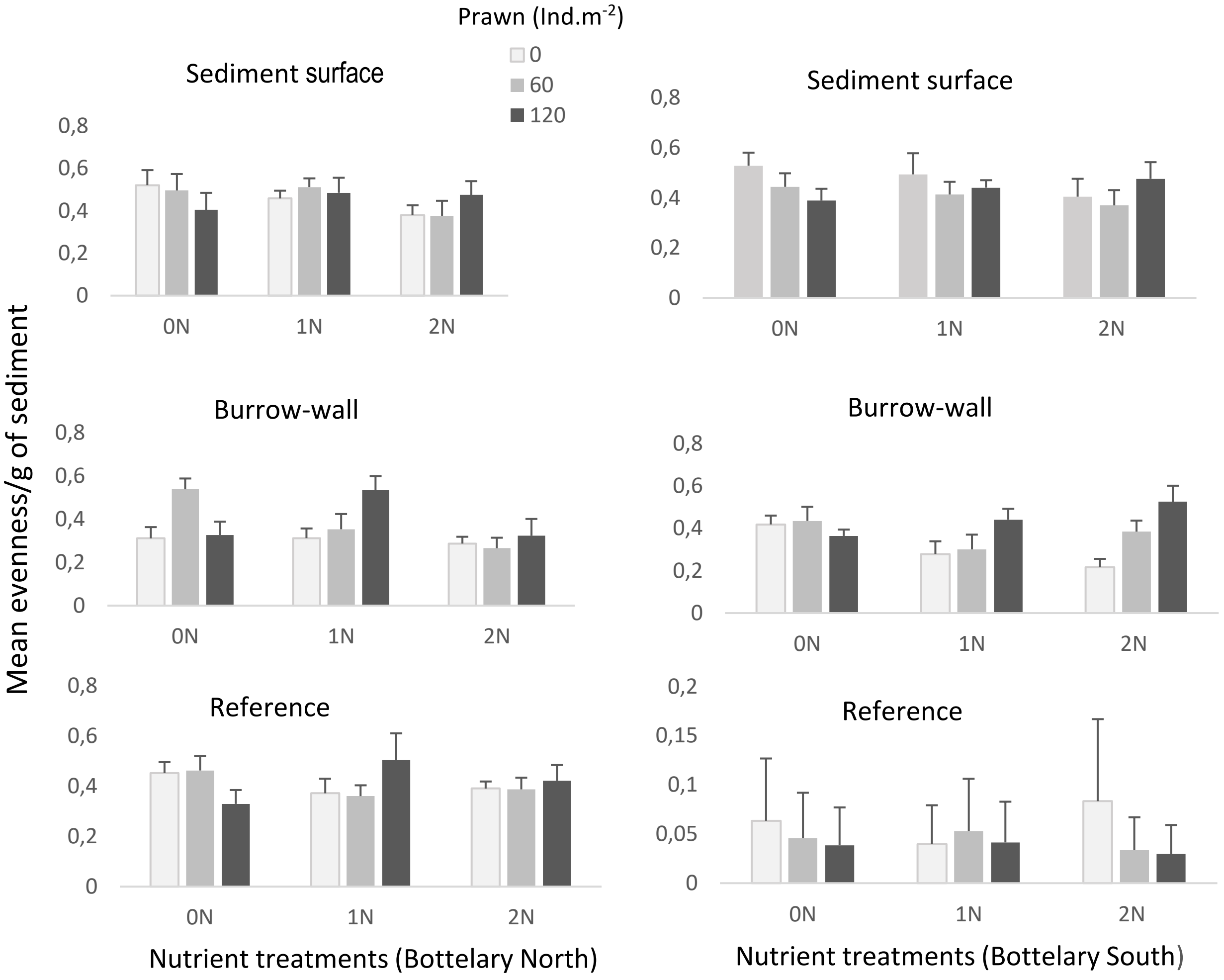

Fig. 5.4C: Variation in mean meiofaunal evenness of (± 1SE) at each sandprawn habitat position, in response to increasing sandprawn densities within each nutrient treatment level at the two experimental sites. NB: Y axis scales are different to show the trend in the data.

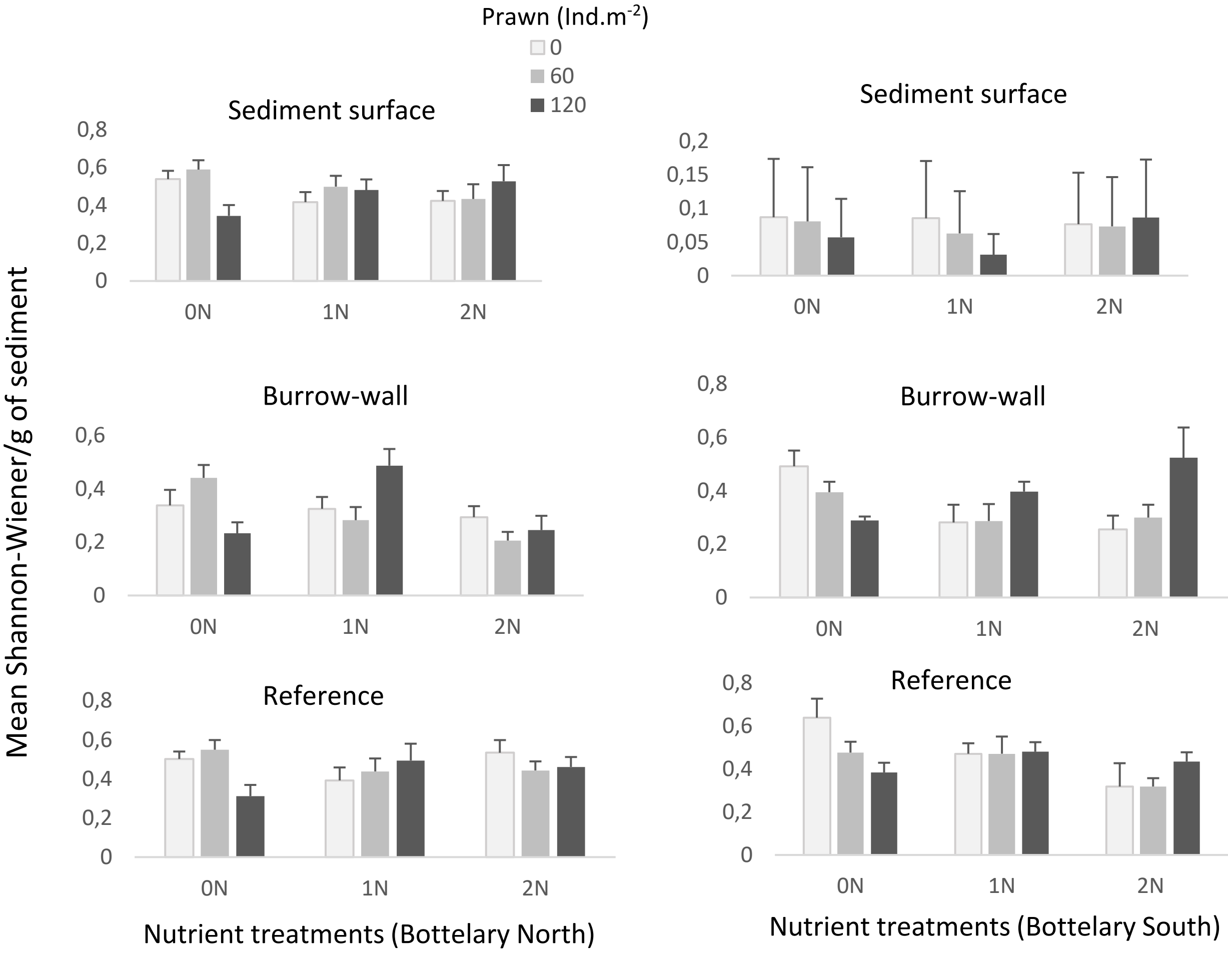

Fig. 5.4D: Variation in meiofaunal Shannon-Wiener diversity (± 1SE) at each sandprawn habitat position, in response to increasing sandprawn densities within each nutrient treatment level at the two experimental sites. Y axis scales are different to show the trend in the data.

5.4.6 Meiofaunal morphotypes

5.4.6.1 Sediment surface

Three of the four meiofaunal morphotypes met the modelling assumptions in terms of data robustness and variability viz: nematodes, copepods and ostracods. Of these morphotypes, only models 2 and 3 were parsimonious for ostracod abundances at the sediment surface position (p < 0.05, for all cases, **Table 5.7A**). The GLM model analysis indicated that interactive model 2 significantly affected ostracod abundance between 1N treatment and 120 (ind.m^2) sandprawn density (p = 0.012), while for model 2, the 120 (ind.m^2) density was responsible for the observed significant effect on stracods (p = 0.047, **Table 5.7B**).

Table 5.7A: Results from generalized linear models reporting the candidate models that were parsimonious and significant for the meiofaunal morphotypes from the sediment surface habit position within experimental cages. The experiment investigated an interactive effect of nutrients and sandprawn densities on the meiofaunal communities. Statistical descriptions: full model = interaction between all factors, model 2 = interaction between nutrients and sandprawns, model 3 = main effects. Values in bold indicate statistical significance.

		Sediment surface habitat position									
		Nematodes					**Copepods**				
Models		**RDF**	**Theta Res.**	**LR stat.**	**DF**	**Pr(>Chi)**	**RDF**	**Theta Res.**	**LR stat.**	**DF**	**Pr(>Chi)**
Full model	S X N X P	36	6.197	11.130	8	0.194	36	2.998	6.793	8	0.559
Model 2	S + (N X P)	44	5.096	4.508	4	0.341	44	2.672	3.091	4	0.542
Model 3	S + N +P	48	4.712	10.906	5	0.053	48	2.537	10.470	5	0.062
Null		53	3.904				53	2.135			
				Ostracods							
Full model	S X N X P	36	1.699	4.427	8	0.186					
Model 2	S + (N X P)	44	1.546	8.022	4	**0.009**					
Model 3	S + N +P	48	1.316	43.620	5	**<0.0001**					
Null		53	0.615								

1: S = Site
2: N = Nutrients
3: P = Prawns
4: RDF = Residual degrees of freedom
5: RD = Residual deviance
6: DF = Degrees of freedom
7: Pr (>Chi) = Measure of the *p*-value

Table 5.7B: Results from the parsimonious generalized linear models investigating effects of nutrients and sandprawn densities on the meiofaunal ostracods from the sediment surface. Statistical descriptions: full model = interaction between all factors, model 2 = interaction between nutrients and sandprawns, model 3 = main effects. Values in bold indicate statistical significance.

Sediment surface habitat position Ostracods					
Models		**Term level**	**Estimate**	**95 % Coefficient Intervals (Lower and upper limits)**	**Pr(>/t/)**
Full model	S X N X P				
Model 2	S + (N X P)	1N X 120P	0.724	0.367 3.078	**0.012**
Model 3	S + N +P	120P	-0.592	-1.199 0.015	**0.047**

1: S = Site 3: P = Prawns
2: N = Nutrients 4: Pr (>/t/) = Measure of the *p*-value

5.4.6.2 Burrow-wall

The full model comprising an interaction between sites, nutrients and sandprawns densities was parsimonious for nematode and copepod abundances ($p < 0.05$ for all cases, **Table 5.8A**). Model 2 of an interaction between nutrient treatments and sandprawn densities, but not sites, was parsimonious for copepod and ostracod abundances ($p < 0.05$, for all cases), while the main effects model 3 affected the ostracod and nematode abundances ($p < 0.0001$). As for the full model, the interaction between sites, the 2N treatment and 60 ind.m^2 was significant for nematode abundances as identified by the GLM model analysis ($p = 0.001$, **Table 5.8B**), while for copepods, a strong significant interaction was identified between sites, 1N treatment and 120 ind.m^2 ($p < 0.0001$). For model 2, both copepod and ostracod abundances were significantly influenced by an interaction between 1N and 120 ind.m^2, and also between 2N and 120 ind.m^2 ($p < 0.05$, for all cases). For model 3, nematode, copepod, and ostracod abundances were all significantly influenced by 60 and 120 (ind.m^2) sandprawn densities ($p < 0.0001$, for all cases).

Table 5.8A: Results from generalized linear modelling reporting the candidate models that were parsimonious and significant for the meiofaunal morphotypes collected from the burrow-wall habit position within experimental cages. The experiment investigated effects of nutrients and sandprawn densities on the meiofaunal communities. Statistical descriptions: full model = interaction between all factors, model 2 = interaction between nutrients and sandprawns, model 3 = main effects. Values in bold indicate statistical significance.

		Burrow-wall habitat position									
		Nematodes					**Copepods**				
Candidate models		**RDF**	**Theta Res.**	**LR stat.**	**DF**	**Pr(>Chi)**	**RDF**	**Theta Res.**	**LR stat.**	**DF**	**Pr(>Chi)**
Full model	S X N X P	36	7.869	18.021	8	**0.021**	36	4.401	15.771	8	**0.005**
Model 2	S + (N X P)	44	5.703	0.812	4	0.936	44	3.302	12.759	4	**0.001**
Model 3	S + N +P	48	5.621	69.474	5	**<0.0001**	48	2.639	35.395	5	**<0.0001**
Null		53	1.749				53	1.465			
		Ostracods									
Full model	S X N X P	36	1.506	6.759	8	0.562					
Model 2	S + (N X P)	44	1.248	11.779	4	**0.021**					
Model 3	S + N +P	48	0.937	40.425	5	**<0.0001**					
Null		53	0.396								

1: S = Site
2: N = Nutrients
3: P = Prawns
4: RDF = Residual degrees of freedom
5: RD = Residual deviance
6: DF = Degrees of freedom
7: Pr (>Chi) = Measure of the *p*-value

Table 5.8B: Results from the parsimonious generalized linear models investigating effects of nutrients and sandprawn densities on the meiofaunal morphotypes collected from the cage experiment within burrow-wall positions. Statistical descriptions: full model = interaction between all factors, model 2 = interaction between nutrients and sandprawns, model 3 = main effects. Values in bold indicate statistical significance.

				Burrow-wall habitat position					
				Nematodes				**Copepods**	
Models		**Term level**	**Estimate**	**95 % Coefficient Intervals (Lower and upper limits)**	**Pr(>/t/)**	**Term level**	**Estimate**	**95 % Coefficient Intervals (Lower and upper limits**	**Pr(>/t/)**
Full model	S X N X P	S X 2N X 60P	-1.855	-3.004 -0.705	**0.001**	S X N1X 120P	-1.570	-3.164 0.023	0.052
Model 2	S + (N X P)					S + (1N X 120P)	1.259	0.3462 2.173	**0.006**
						S + (2N X 120P)	1.352	0.442 2.2625	**0.003**
Model 3	S + N +P	60P	-1.266	-1.543 -0.989	**<0.0001**	60P	-1.343	-1.757 -0.929	**<0.0001**
		120P	-1.373	-1.653 -1.093	**<0.0001**	120P	-1.949	-1.370 -0.529	**<0.0001**
				Ostracods					
Full model	S X N X P								
Model 2	S + (N X P)	S +(1N X 120P)	2.081	0.391 3.780	**0.015**				
		S +(2N X 120P)	2.074	0.413 3.735	**0.014**				
Model 3	S + N +P	60P	-1.501	-2.241 -0.764	**<0.0001**				
		120P	-1.534	-2.296 -0.779	**<0.0001**				

1: S = Site 3: P = Prawns
2: N = Nutrients 4: Pr (>/t/) = Measure of the *p*-value

5.4.6.3 Reference

At the reference habitat position, nematodes were the only morphotype to be predicted by the full interactive model (*p* = 0.030, **Table 5.9A**), which identified significant interactions between sites, 1N treatment and 60 ind.m^2 (*p* = 0.007) and also between sites, 1N treatment and 120 ind.m^2 (*p* = 0.015, **Table 5.9B**). On the other hand, both ostracod and copepod abundances were best predicted by model 3 ($p < 0.05$, **Table 5.9A**), in which the GLM model summary identified level 120 ind.m^2 as the sandprawn density responsible for a significant effect on both of these morphotypes ($p < 0.05$, for all cases, **Table 5.9B**).

5.4.7 Meiofauna morphotypes: overall patterns

All meiofaunal morphotypes that were statically significant showed a strong response to increasing sandprawn density (**Fig.5.5A**-**C**). Nutrient treatment impacts were not clearly demonstrated for these meiofaunal morphotyps, which was also confirmed by GLM candidate model analyses.

At the sediment surface, copepod abundance at Bottelary North showed a clear hump-shaped pattern in response to increasing sandprawn densities at the ON treatment (**Fig.5.5B**). On the other hand, the copepod abundance declined due to increasing sandprawns at the ON treatment in Bottelary South. This pattern of decreasing copepod abundance was also observed at the 2N treatment in both sites. Furthermore, increasing sandprawn densities at the 1N treatment revealed two distinctive patterns of copepod abundance at both sites, being a unimodal U-shape pattern in the Bottelary North, while in the Bottelary South, abundances conformed to a hump-shaped pattern.

At the burrow-wall, the common pattern displayed by all meiofaunal morphotypes was a decrease in their abundances in response to increasing sandprawn densities (**Fig. 5.5A-C**). Interestingly, this pattern was observed to be stronger in Bottelary South, with all nutrient treatment showing a reduction in nematode abundance against increasing sandprawn densities (**Fig 5.5A**). Copepod responses were similar, with reductions in abundance at both sites being recorded in the 0N treatment with increasing sandprawn density, but with unimodal U-shaped- patterns at 1N and 2N. A unimodal response pattern was also observed for ostracod abundance at the 1N treatment in Bottelary North and 2N treatment in the Bottelary South (**Fig. 5.5C**).

Responses at the reference position were distinct from those recorded at the burrow-wall and sediment surface. For the reference position, a hump-shaped pattern was observed for both ostracod and copepod abundances at the 0N treatment in Bottelary North with increasing sandprawn densities, but abundance declined in the 1N and 2N treatments with increasing sandprawn densities (**Fig. 5.5B**-**C**). The most interesting pattern for ostracod abundances occurred in Bottelary South, with ostracod abundances apparently being reduced by increasing sandprawn densities at the ON treatment, but exponentially enhanced at the 1N treatment and responding in a unimodal U-shaped pattern at the 2N level (**Fig.5.5C**).

Table 5.9A: Results from parsimonious generalized linear modelling investigating effects of nutrients and sandprawn densities on the meiofaunal morphotypes collected from the cage experiment within the reference position adjacent to sandprawn burrows. Statistical descriptions: full model = interaction between all factors, model 2 = interaction between nutrients and sandprawns, model 3 = main effects. Values in bold indicate statistical significances.

Reference habitat position											
		Nematodes					Copepods				
Models		**RDF**	**Theta Res.**	**LR stat.**	**DF**	**Pr(>Chi)**	**RDF**	**Theta Res.**	**LR stat.**	**DF**	**Pr(>Chi)**
Full model	S X N X P	36	11.434	16.972	8	**0.030**	36	3.475	7.349	8	0.499
Model 2	S + (N X P)	44	8.416	0.759	4	0.943	44	3.063	5.720	4	0.221
Model 3	S + N +P	48	8.302	8.276	5	0.141	48	2.780	12.291	5	**0.031**
Null		53	7.162				53	2.266			
		Ostracods									
Full model	S X N X P	36	1.3831	8.411	8	0.341					
Model 2	S + (N X P)	44	1.1794	2.734	4	0.603					
Model 3	S + N +P	48	1.1211	31.395	5	**<0.0001**					
Null		53	0.6588								

1: S = Site
2: N = Nutrients
3: P = Prawns
4: RDF = Residual degrees of freedom
5: RD = Residual deviance
6: DF = Degrees of freedom
7: Pr (>Chi) = Measure of the *p*-value

Table 5.9B: Results from generalized linear models reporting the candidate models that were parsimonious and significant for the meiofaunal morphotypes collected from the cage experiment within the reference position adjacent to sandprawn burrows. The experiment investigated effects of nutrients and sandprawn densities on the meiofaunal communities. Statistical descriptions: full model = interaction between all factors, model 2 = interaction between nutrients and sandprawns, model 3 = main effects.

				Reference habitat position					
			Nematodes					**Copepods**	
Models		**Term level**	**Estimate**	**95 % Coefficient Intervals (Lower and upper limits)**	**Pr(>/t/)**	**Term level**	**Estimate**	**95 % Coefficient Intervals (Lower and upper limits**	**Pr(>/t/)**
Full model	S X N X P	S X 1N X 60	1.295	0.344 2.245	**0.007**	120P	-0.486	-0.887 -0.084	**0.015**
		S X 1N X 120P	1.783	0.832 2.734	**0.015**				
			Ostracods						
Model 3	S + N +P	120P	-0.607	-1.245 0.031	**0.057**				

1: S = Site
2: N = Nutrients
3: P = Prawns
4: Pr (>/t/) = Measure of the *p*-value

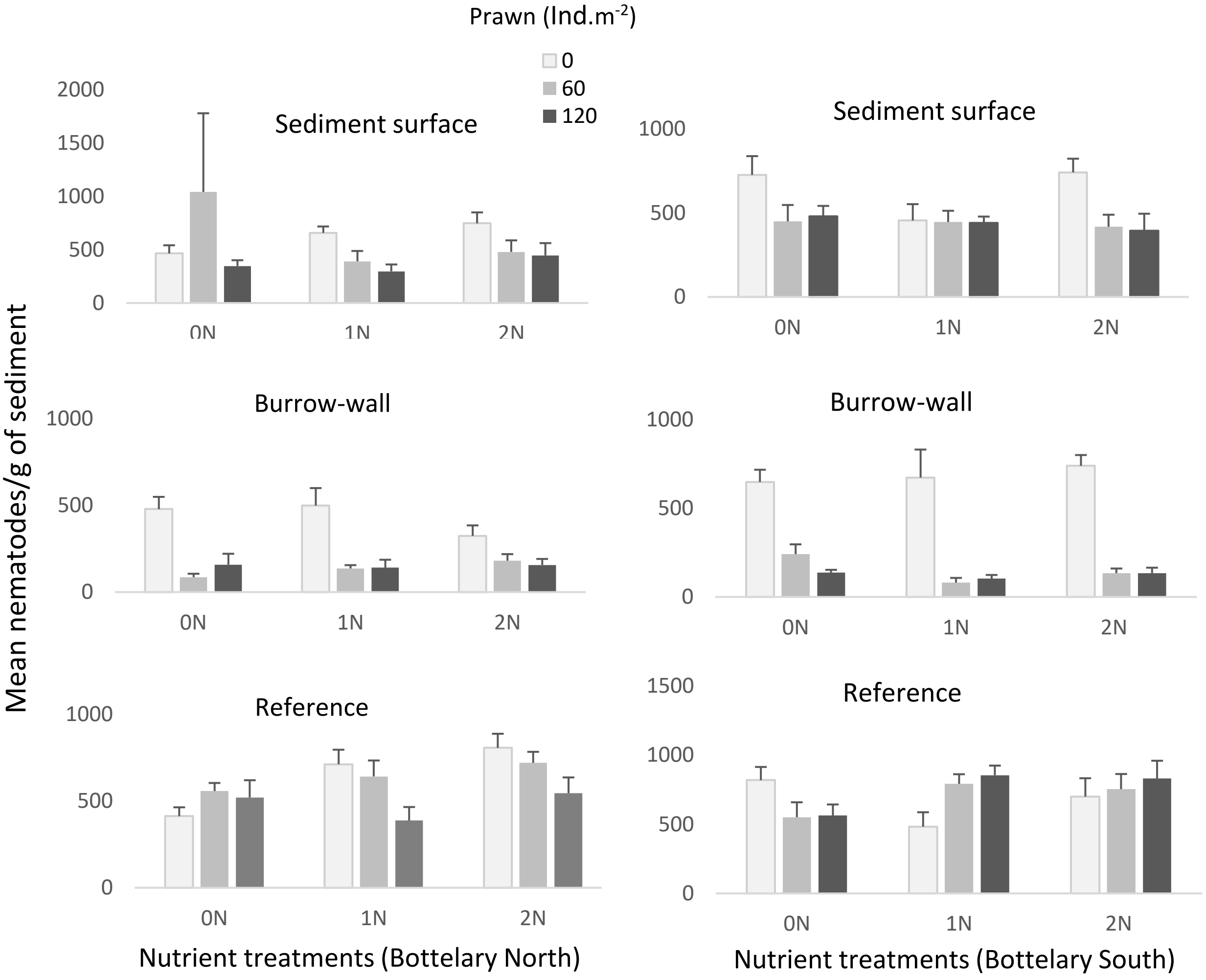

Fig.5.5A: Variation in mean nematode abundances (± 1SE) within each burrow habitat position in response to increasing sandprawn densities and nutrient treatment levels at the two experimental sites. Y axis scales are different to show the trend in the data.

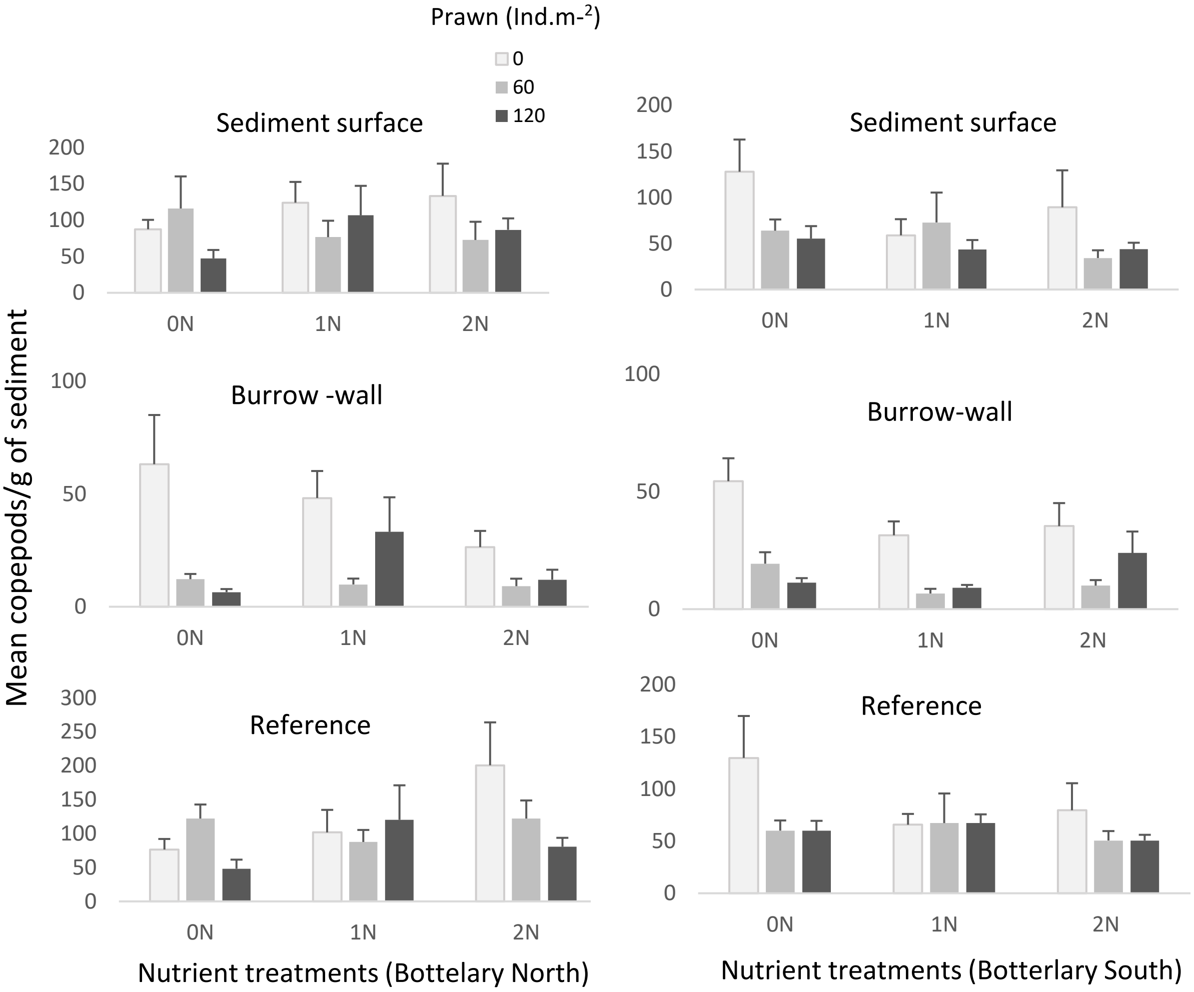

Fig.5.5B: Variation in mean copepod abundances (± 1SE) within each sandprawn habitat position in response to increasing sandprawn densities and nutrient treatment levels at the two experimental sites. Y axis scales are different to show the trend in the data.

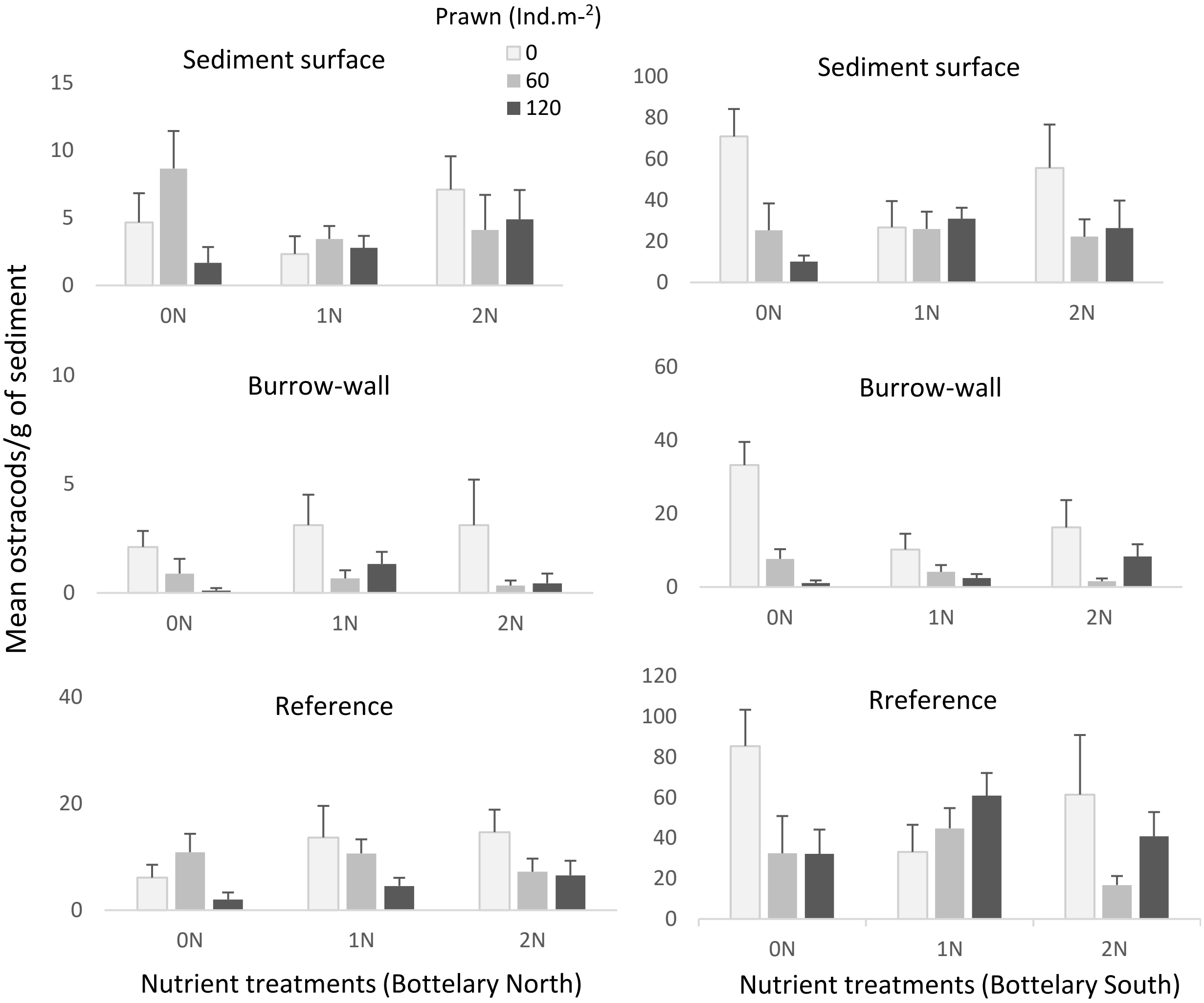

Fig.5.5C: Variation in mean ostracod abundances (± 1SE) within each sandprawn habitat position in response to increasing sandprawn densities and nutrient treatment levels at the two experimental sites. Y axis scales are different to show the trend in the data.

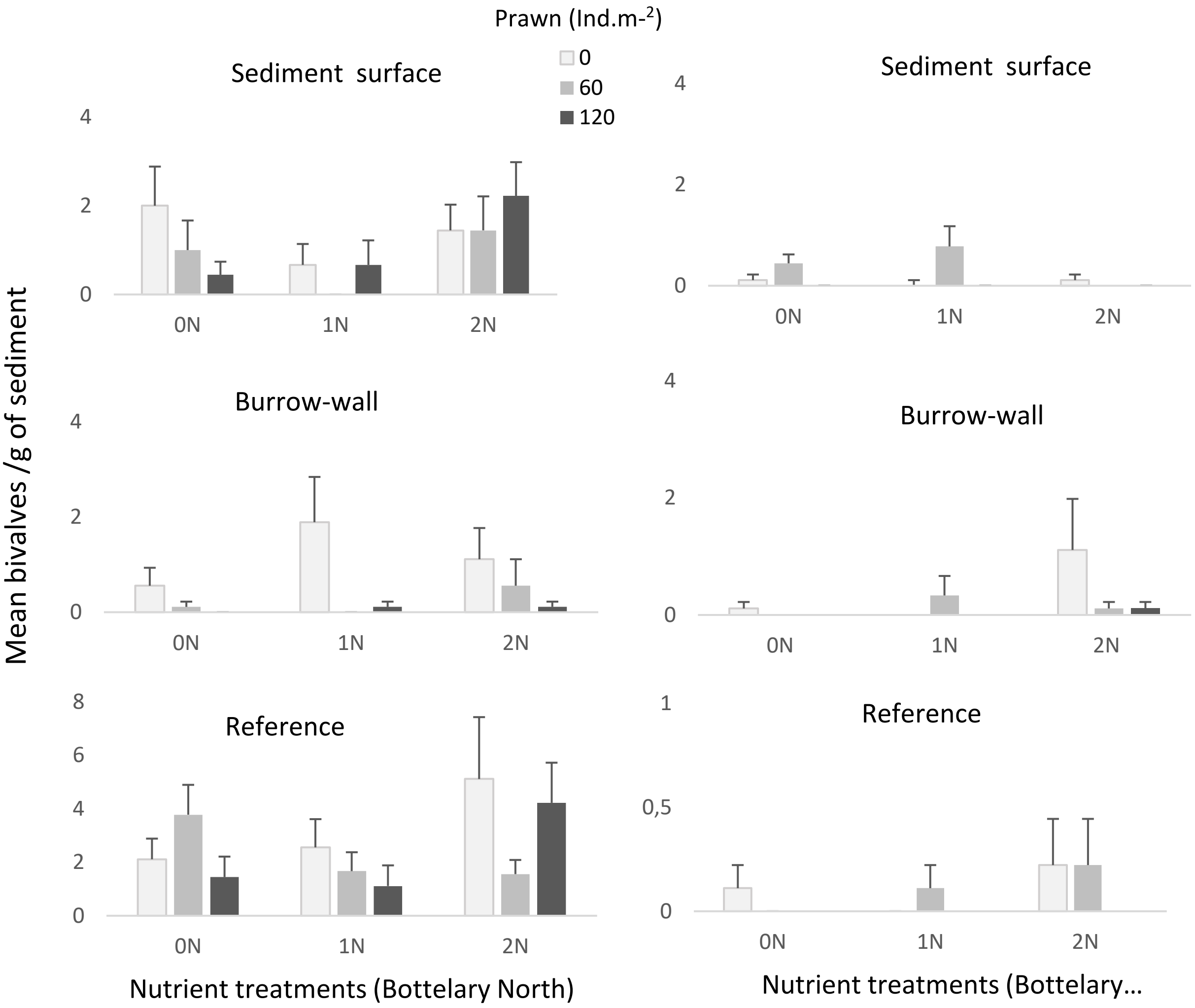

Fig.5.5D: Variation in mean bivalve abundances (± 1SE) within each burrow habitat position in response to increasing sandprawn densities and nutrient treatment levels. Y axis scales are different to show the trend in the data.

5.5 DISCUSSION

This chapter provides insights into the interactive effects of nutrient enrichment (proxy for productivity) and sandprawn density (proxy for disturbance) on meiofaunal assemblages in intertidal soft-sediments of Langebaan Lagoon. Using an *in situ* factorial experiment that manipulated nutrients (fertilizer capsules) and sandprawn (*Callichirus kraussi*) densities, I predicted that meiofaunal community responses to sandprawn bioturbation will be altered by nutrient enhancement. More specifically, I hypothesize based on the predictions of the grazer-reversal hypothesis of Proulx and Mazumder (1998) that the form of disturbance-diversity relationship (sandprawn-meiofaunal diversity metrics) should change from a linear decrease at the ambient nutrient level (0N treatment) to unimodal hump-shaped at the intermediate nutrient enrichment level (1N) and then to a linear increase at the highest nutrient treatment (2N). The same predictions were made for the benthic microalgal biomass (chl-*a*) within the experimental cages. Overall, the results indicated limited support for the grazer-reversal hypothesis on the meiofaunal community metrics, while no effects of experimental treatments were detected for microalgal biomass. However, *C. kraussi* emerged to be a prominent regulator of meiofaunal community assemblages, arguably an important indication for ecosystem-engineer induced community control.

5.5.1 Benthic microalgal biomass (chl-*a*)

One of the most significant outcomes of this *in situ* factorial experiment was the similarity of sediment chl-*a* concentrations across nutrient and sandprawn treatments, resulting in neither of these factors explaining variability in sediment chl-*a* levels. It is possible that the variability exhibited in microalgal biomass in this study obscured chl-*a* patterns.

Therefore, studies of this nature in future may need greater sample sizes to adequately detect chl-*a* responses.

The limited nutrient enrichment effects on sediment chl-*a* concentrations in this study was unexpected given that in shallow water coastal ecosystems, microalgal growth is generally stimulated by nutrient inputs (Beukema 1991, Cahoon and Nearhoof 1999, Downing *et al.* 1999, Rosemond *et al.* 2000, Thornton *et al.* 2002, Gattuso *et al.* 2006, Garcia-Robledo *et al.* 2016). It would therefore be anticipated that chl-*a* would increase in response to increasing nutrient enrichment. Findings of the current experiment contrasts with several other studies that have reported microagal biomass to increase in response to nutrient enrichment in marine coastal habitats (Beukema 1991, Pitta *et al.* 1998, Posey *et al*. 2002, Canning-Clode *et al.* 2008, Bucolo *et al.* 2008) and fresh water ecosystems (Power 1992, Deegan *et al.* 1997). For instance, Hillebrand *et al.* (2003) detected strong effects of nutrient enrichment on microalgae, showing an increase in biomass within nutrient enhancement treatments. Posey *et al.* (2002) indicated higher chl-*a* levels in nutrient addition treatments relative to control plots. More recently, Santos *et al.* (2009) through an *in situ* experiment, demonstrated increasing surface sediment chl-*a* concentrations in response to the addition of inorganic fertilizer.

The findings of this study are however in agreement with previous results documented by Sullivan (1981) in salt marshes and O'Brien *et al.* (2009) in intertidal sandflats of the Wadden Sea. O'Brien *et al.* (2009) argued that abiotic factors such as light availability, sediment characteristics and hydrodynamic forces were the reasons for the lack of nutrient enrichment effects on microalgae in their experimental study. Light availability is the most important factor known for limiting benthic microagal biomass (Grant 1986, Kromkamp *et al.* 1995, Blanchard *et al.* 1997), but it is unlikely to have contributed to the limited of chl-*a* response to nutrient enrichment in this study, given that shading of sediment by cages was negligible due to cages being uncovered on the top.

Pore-water samples collected from the field trial experiment (see appendix; **Fig. 9.1**) indicated that the fertilizer capsules (Plantacote N: P: K) used in this study effectively increased pore-water nutrient levels. Thus, the lack of nutrient effects on chl-*a* is somewhat surprising. It is possible that nutrients used in this study were unable to spike chl-*a* concentrations or that chl-*a* within experimental cages was supprerssed by grazers. In theory, producer and consumer biomass are constantly oscillating, with producer blooms being followed by grazer increases. However, this is then succeeded by consumer proliferation, resulting in increased top-down pressure and a decline in producer biomass. Thus, it is possible that nutrient-induced chl-*a* blooms in this study were supressed by grazing within cages.

It is also possible that microalgal biomass could not have been affected by nutrient enrichment in this study due to sedimentary characteristics. It is known that sediment porosity influences pore-water retention capacity, with highly porous sediment being least retentive (Raffaelli and Hawkins *et al.* 2012). Thus, in highly porous bioturbated sediments, which is feature of the study site, high nutrient levels in pore-water may not results in benthic algal blooms because of low retention. Thus sediment characteristics can influence whether it functions as either a sink or source of nutrients for the water column, which in turn influences the strength of benthic-pelagic coupling (Raffaelli *et al.* 2003).

While bioturbation is known to influence benthic chl-*a*, bioturbation is unlikely to account for the limited chl-*a* response in this experiment. For instance, inclusion cages had greater sediment deposition values relative to exclusions (**Fig 5.3**); if microalgal biomass was limited by sediment bioturbation, statistically significant differences would have manifested between exclusions and exclusion cages. Results for sediment deposition correspond to those reported by Henninger and Froneman (2013), in which higher levels of bioturbation occurred in inclusion compared to exclusion cages in an *in situ* experiment that manipulated sandprawn densities.

The lack of a sandprawn effect on chl-*a* concentrations in this study contrasts with various studies that have documented negative impacts of *C. kraussi* on surface sediment microalgal biomass (Rowden and Jones 1993, Wynberg and Branch 1994, Pillay *et al.* 2007a, 2007b, 2012). For example, Pillay *et al.* (2007c) indicated that chl-*a* varied spatially between sediments densely populated by sandprawns and those in which sandprawns were rare. They showed that sediments uninhabited by *C. kraussi* had a 2- to 4-fold greater microalgal biomass compared to areas occupied by sandprawns. Furthermore, they demonstrated experimentally that increasing *C. kraussi* density resulted in 2- to 3-fold attenuations in microalgal biomass. Bioturbation by the lugworm *Arenicola marina*, has also been reported to cause substantial reductions in surface sediment microalgal biomass in intertidal sandflats of the Wadden Sea (Volkenborn *et al.* 2007a).

The results of the present study correspond with several previous studies that have not detected sandprawn effects on chl-*a* concentrations. For example, Henninger and Froneman (2013) reported no statically differences in sediment chl-*a* concentrations between exclusions and inclusion experimental cages. Similarly, Branch and Pringle (1987) found no effect of *C. kraussi* on microalgal biomass in a cage experimental study, also undertaken in Langebaan Lagoon. In their study (Branch and Pringle 1987), they argued that the small cage size used (cylinders cages; internal diameter = 25 cm, depth = 30 cm) for manipulating sandprawn densities was the reason for the lack of effect on chl-*a* concentrations. However, cages utilized in the current study were larger. Therefore, it is unlikely that sandprawn effects on chl-*a* concentrations could have been contingent upon the cage size artefact. Taken collectively, the studies reporting conflicting effects of sandprawns on chl-*a* highlight the complexity of processes underlying sandprawn-chl-*a* relationships. Such conflicting outcomes are potentially mediated by differences in sedimentary contexts in which studies were carried out.

5.5.2 Meiofaunal community structure: Overall composition, diversity and individual morphotypes

The unresponsiveness of surface meiofaunal community composition to nutrient enrichment was another striking result of this study. However, nutrient enrichment did emerge to be important for burrow-wall meiofaunal community structure when interacting with sites, while at the reference position, meiofaunal assemblages were regulated by the interaction between sites, nutrients and sandprawns. Meiofaunal community composition at the sediment surface was not governed by any interaction but was, however, affected by the main effect of sites and sandprawn densities. Similarly, sandprawn impacts were apparent at the burrow-wall but not reference positions. The lack of sandprawn impacts on the meiofaunal community composition in reference areas was an unsurprising result. In reference positions, meiofauna were not directly exposed to sandprawn burrows and therefore, would be anticipated to be less affected or unaffected by sandprawn ecosystem engineering/trophic impacts. Statistically, these findings indicated that sandprawn impacts at the burrow-wall and sediment surface manifested mostly at higher densities of 120 ind.m^2.

Even though the interaction between nutrient enrichment and sandprawn densities affected a few of the diversity metrics, the hypothesis that this interaction would result in affected community metrics conforming to the predictions of the grazer-reversal hypothesis was not overwhelmingly supported in this study. Generally, prevailing patterns in this study were of an increasing and decreasing nature. For instance, sediment surface meiofaunal abundances at both 1N and 2N treatments decreased against increasing sandprawn densities in Bottelary North and also at the 0N and 2N treatments in Bottelary South (**Fig.4B**). Similarly, burrow-wall species richness (**Fig 3.4A**) and surface evenness (**Fg.5.4C**) were both reduced in response to increasing sandprawn densities at the ambient nutrient treatment (0N). This particular trend partially conformed to the predictions of the grazer-reversal hypothesis (Proulx and Mazumder 1998) or Dynamic Equilibrium Model (DEM; Kondoh 2001), which assert that disturbance-diversity relationship should follow a decreasing pattern when productivity is low. On the other hand, at the highest nutrient treatment level (2N), both burrow-wall evenness (**Fig.5.4C**) and Shannon-Wiener diversity (**Fig. 5.4D**) in Bottelary South increased in response to increasing sandprawn densities. Shannon-Wiener diversity at the sediment surface in Bottelary North also increased with increasing sandprawn densities at the 2N treatment (**Fig.5.4D**). This positive relationship also follows the predictions of the grazer-reversal hypothesis, asserting that when productivity is high, disturbance-diversity relationship should follow an increasing pattern.

The third pattern of the grazer-reversal hypothesis which predicts disturbance-diversity relationship to conform to the hump-shaped form at intermediate levels of productivity was limited, occurring only for the species richness in the reference position at both sites but was, however, not as clear in Bottelary South (**Fig.5.3A**). Notably, meiofaunal diversity metrics at the intermediate nutrient level were either enhanced (e.g. burrow-wall evenness [**Fig.5.4C**] and Shannon-Wiener diversity [**Fig. 5.4D**]) or reduced (e.g. burrow-wall abundance, **Fig 5.4B**) by increasing sandprawn densities. It is also important to indicate that some of the patterns documented in this study were opposite to the prediction of the grazer-reversal hypothesis. For example, species richness at the burrow-wall and reference positions in Bottelary North appeared to be reduced by increasing sandprawn densities at the highest nutrient level (**Fig.5.4A**). Similarly, total abundance at the burrow-wall was substantially reduced by sandprawn densities at the 2N treatment in both sites (**Fig 5.4B**).

Another point worth mentioning regarding patterns documented in this study is that they occurred idiosyncratically across nutrient treatment levels and habitat positions, suggesting that (**i**) meiofaunal diversity metrics respond differently to both nutrient enrichment and sandprawn bioturbation, and this could be largely attributed to differences in which these community metrics are calculated, (**ii**) sandprawn bioturbation effects on these diversity metrics do differ with the habitat position (i.e., burrow-wall, surface and reference as used in this study) due to different environmental conditions and resources modulated by sandprawns between these habitat positions, and (**iii**) productivity does not play a fundamental role in mediating responses of meiofaunal community metrics to sandprawn ecosystem engineering, which implies that sandprawn impacts are much stronger than bottom up (nutrients) effects on the meiofaunal community.

Previous experimental studies testing the effects of simulated productivity on meiofauna have produced varied responses including density reductions with nutrient enrichment (Schratzberger and Warwick 1998, La Rosa *et al.* 2001, Fraschetti *et al.* 2006, Armenteros *et al.* 2010), while others observed this pattern specifically for nematode abundances (Sutherland *et al.* 2007). The *in situ* experimental study undertaken by Santos *et al.* (2009) has also provided some evidence of reductions in estuarine meiofauna abundances in response to inorganic fertilizer. On the other hand, Widbom and Elmgren (1988) documented mixed effect of nutrient enrichment on meiofauna, with response directions being taxon specific. This study found that abundances of nematode and juvenile polychaetes were enhanced by increasing nutrients while foraminiferans and juvenile bivalves were substantially reduced.

Sandprawn impacts on meiofaunal community metrics and individual morphotypes in this study provided important evidence to suggest that in the sandflats of Langebaan Lagoon, meiofauna are greatly regulated by ecosystem engineering in the form of bioturbation. However, it is surprizing that meiofauna responded to sandprawn densities while microalgal biomass did not. This could suggest that the two differ with the sensitivity degree to sandprawn ecosystem engineering impacts, with the meiofauna appearing more sensitive than microalgae, possibly due to particular biological traits leading to a negative predisposition to sandprawn bioturbation. Generally, *C. kraussii* has been reported to similarly influence both meiofauna and chl-*a*, largely mediated by sediment turnover (Branch and Pringle 1987, Pillay and Branch 2011), often with negative impacts reported at the sediment-water interface relative to burrow-walls (Pillay *et al.* 2007a, 2007c, 2012). The mechanical disturbance of the biofilm and increasing porosity (and therefore retention capacity) of the sediment are important mechanisms by which sandprawns affect settlement of microalgae and meiofauna. Rapid turnover rate of sediment from burrows to the surface sediment is likely to limit surface colonization (Branch and Pringle 1987, Pillay *et al.* 2007c). Generally, sediments with poorly developed biofilms are more erodible and prone to resuspension, which may increase erosion of these colonizers to the water column.

Despite detected effects of *C. kraussii* on meiofaunal diversity metrics and morphotypes in this study, there was no discernible evidence of meiofauna being enhanced within burrow-walls relative to surface sediments. This refutes the hypothesis posed in this study that greater meiofaunal abundances would be recorded from burrow-wall areas. Meiofaunal individual morphotypes showed varied patterns but with a negative trend generally being prevalent. For instance, burrow-wall nematode abundances were substantially reduced in response to increasing sandprawn densities across all nutrient treatment levels in both sites (**Fig.5.5A**). Similarly, copepods (**Fig.5.5B**) and ostracods (**Fig.5.5C**) all displayed reductions in their abundances against sandprawn densities, though patterns were not always consistent.

The prevalence of the negative pattern between meiofauna and sandprawn densities observed in this study is in line with other studies that have related *C. kraussi* effects to reductions in meiofauna abundances (Branch and Pringle 1987, Kinoshita *et al.* 2003, Pillay and Brach 2011). For instance, Branch and Pringle (1987) showed that bioturbation by *C. kraussi* induces negative effects on surface meiofaunal abundances and within burrows between 10–20 cm depths. They showed that nematodes were mostly affected by bioturbation compared to both copepods and juvenile polychaetes, which appeared to be either less affected or unaffected. Similarly, Alongi (1985) reported a decline in meiofaunal densities in burrows of several species of axiid prawns in a subtidal lagoon. In contrast, a study undertaken by Dittmann (1996) on a different species of axiid prawns, revealed promotive effects within burrow-walls versus non-burrow areas. Generally, meiofauna at the sediment-water interface are more susceptible to bioturbation due to burial by turned over sediment. However, promotive effects usually occur within burrow-walls due to sediment oxygenation and elevation of food availability in the form of organic matter (Dobbs and Guckert 1988, Branch and Pringle 1987, Kinoshita *et al.* 2003).

5.6 CONCLUSION

The manipulation of sandprawn densities and nutrients in this study did not reveal overwhelming evidence supporting the grazer-reversal hypothesis as a mechanism responsible for regulating meiofaunal community structure. Instead, the patterns documented were of an intricate nature, illustrating varied relationships between sandprawn densities and meiofaunal community metrics or morphotypes at each nutrient enhancement level. On very few occasions, meiofaunal diversity metrics appeared to be enhanced at the high nutrient level in response to sandprawn ecosystem engineering effects (e.g. evenness and Shannon-Weiner **Fig. 5.4C** and **D**).

Based on these findings, I infer that meiofaunal community composition is strongly regulated by sandprawn ecosystem engineering in Langebaan Lagoon rather than an interaction between sandprawn densities and nutrients, or by nutrients alone. However, for the diversity metrics, interaction between productivity and disturbance emerged to be stronger especially within burrow-wall areas, although, results suggest that this interaction does not be simply adhere to the predictions of the grazer-reversal hypothesis. It is very likely that the patterns observed in this study were due to site-specific contextual dependencies that determine the net outcome of interaction between nutrients and sandprawns on the meiobenthos. This reinforces the idea that in order to achieve the patterns postulated by the grazer-reversal hypothesis in the intertidal soft-sediment such as Langebaan Lagoon, certain requisite factors may be required. For instance, concepts such as the intermediated disturbance hypothesis (Connell 1978) and dynamic equilibrium model (Kondoh 2001) are explicitly based upon competitive exclusion. However, these factors are difficult to quantify using *in situ* experiments, which then makes it difficult to empirically test these generalized models. Nevertheless, the results of this experiment shed light on the important role of sandprawn ecosystem engineering in determining meiofaunal community structure.

CHAPTER 6

INTERACTIVE EFFECTS OF SANDPRAWNS AND NUTRIENT ENRICHEMENT ON **MACROFAUNAL** COMMUNITY STRUCTURE: AN INTER-TIDAL EXPERIMENTAL APPROACH

6.1 Introduction

Marine soft-sediments are one of the largest ecosystems on earth, occupying approximately 80 % of the sea floor (Lenihan and Micheli 2001, Lohrer *et al.* 2004a, Nybakken and Bertness 2005). These habitats have therefore been the focus of much research aimed at understanding the ecological processes that drive their functioning (Lenihan and Micheli 2001, Gray 2002). Soft-sediments provide key habits for benthic infauna (Little 2000, Coblentz *et al.* 2015), which are organisms that dwell within the sediment matrix (Fairweather and Quinn 1995). In coastal sediments, benthic fauna are at particular risk to anthropogenic impacts and climate change (Gray 1997, Snelgrove *et al.* 1997), given their proximity to human settlements and associated disturbances. Such activities can significantly alter biotic composition in soft-sediments, consequently having large and unanticipated ramifications for ecosystem functioning (Hatcher *et al.* 1994, Balmford *et al.* 2003, Hooper and Dukes 2003a, Chou *et al.* 2004, Barbier *et al.* 2008).

Benthic species perform a variety of ecological functions, including regulating processes that determine energy flow through food webs. For example, benthic organisms provide important services relevant to trophic interactions by mediating productivity, detrital decomposition and nutrient recycling (Wallace and Webster 1996, Lohrer *et al.* 2004a). Such processes are thus central to the feeding activities of benthic species in littoral habitats (Hutchinson 1993, Wallace and Webster 1996, Bishop and Kelaher 2007), which may augment growth rates of microbes, algae and macrophytes, which in turn serve as important food source for herbivorous and omnivorous benthic invertebrates (Lodge *et al.* 1994, Nystrom *et al.* 1996). Thirdly, benthic organisms serve as food source for vertebrate consumers such as fishes, turtles, and birds (De Léo and Pires-Vanin 2006, Rocha *et al.* 2003).

Generally, benthic fauna comprise two dominant, yet distinctive groups, i.e. meio- and macrofauna (Ólafsson 2003). A major feature that differentiates these two groups is their size; meiofaunal are retained by a 63 µm sieve (Heip *et al.* 1988), while macrofauna are retained by a 500 µm mesh (Gray 2002). Macrofauna are commonly distinguished by function in addition to taxonomic groupings, based on feeding guilds, which are often utilized to derive a mechanistic understanding of ecological responses (Bolam *et al.* 2002) and ecosystem functioning (Blackford 1997, Bolam *et al.* 2002). Typical functional classifications include surface deposit feeders, sub-surface deposit feeders, herbivores and carnivores and suspension feeders (Rosenberg 2001). It is not only size-related traits that differentiate meiofauna from macrofauna, as it has been shown that these two benthic faunal groups often have different life history characteristics. Meiofauna typically undergo direct benthic development while most macrofauna species have pelagic larvae (Ólafsson 2003). Meiofauna are also characterized by much shorter generation times relative to macrofauna (Warwick 1984).

Soft-sediment macrobenthos display significant diversity in traits such as taxonomy, mobility, morphology and functionality, and also influence meiofauna in diverse and intricate ways (Ólafsson 2003). For example, endobenthic crustaceans (e.g. sandprawns or lugworms) may induce striking negative and/or positive effects on meiobenthos (Pillay *et al.* 2007a, Volkenborn *et al.* 2007a). Effects of macrofauna on meiofauna have been quantified using both observational and experimental studies; such effects materialise through multiple mechanisms, including food competition, the construction of biogenic structures, predation and disturbance (Ólafsson 2003). Experimental studies have particularly shown the important effects of endobenthic crustaceans (Branch and Pringle 1987, Dobbs and Gucker 1988, Dittmann 1996), epibenthic crustaceans (Ólafsson and Ndaro 1997, Dittmann 1993) polychaetes (Kennedy 1993, Volkenborn *et al.* 2007a) and bivalves (Austen and Thrush 2001) in regulating meiofaunal assemblage dynamics.

Sandprawns (also referred to as ghost-shrimps) are conspicuous members of benthic infaunal assemblages and are well-known for critically influencing benthic processes and assemblages (Peterson 1977, Siebert and Branch 2007, Pillay and Branch 2011). For instance, sandprawns through bioturbation can alter the habitat topography, increase turbidity, influence nutrient cycling and secondary productivity (Graf and Rosenberg 1997). The resuspension of sediment by burrowing sandprawns can also elevate erodibility of sediments which in turn affects the recruitment and susceptibility of macrofauna to predation (Amaro *et al.* 2007, Pillay and Branch 2011). Sandprawns are deposit feeders, i.e. they ingest sediment to obtain trophic resources composed of mainly microalgae and particulate organic matter (Pillay and Branch 2011). However, the deposition of residual sediments at the sediment - water interface and “loosening” of sediments can generate significant effects on sympatric assemblage, including burial of associated epifauna and alterations in availability of trophic resources such as microalgae and microbial biofilms (Flach 1993, Pillay and Branch 2011). Biofilms are a compound mixture of microalgae, fungi and bacteria coated in extracellular polymeric substances (EPSs), which are exuded by microorganisms (Wotton 2011, Dawson and Pillay 2011) and mucus discharge by larger invertebrates (Underwood and Paterson 1995). Biofilms therefore play a significant ecological role in marine soft-sediment ecosystems by (1) binding the surface sediment layer and promoting laminar flow of overlaying water (Paterson and Hagerthey 2001, Pillay *et al.* 2007c), (2) serving as food source for invertebrates (Decho 1990), and (3) stabilizing sediment that facilitates the settlement and recruitment of associated benthic infauna (Pillay *et al.* 2007c, Dawson and Pillay 2011).

Generally thalassinidean shrimps have been reported to exert positive or neutral impacts on benthic deposit feeders (Dobbs and Gucker 1988, Kinoshita *at al.* 2003, Siebert and Branch 2005a, 2007). For example, Dittmann (1996) reported high nematode and turbellarian abundances in burrowed areas relative to adjacent sediment. In contrast, thalassinidean shrimps are hypothesised to exert negative impacts on suspension feeders (Pillay *et al.* 2007c, 2008), based on the predictions of the trophic amensalism hypothesis of Rhoads and Young (1970), which argues that sediment-reworking by deposit feeders interferes with filtration ability of suspension feeders. Suspension feeders general occur at the sediment-water interface and are therefore prone to sediment resuspension effects, which can obstruct their filtering apparatus and negatively affect growth (Siebert and Branch 2007, Pillay and Branch 2011). In South Africa, high densities of the burrowing sandprawn *Callichirus kraussi* have been linked to alterations in sediment granulometry from muddy sand to sand following major transformations of sand flats in an estuarine embayment, resulting in reductions in abundances of suspension feeders, but also surface associated grazers and deposit feeders (Pillay and Branch 2011).

This chapter extends the questions posed in the previous chapter, but aims to understand how benthic macrofauna respond to experimental manipulation of nutrients and sandprawns. Comparisons between this and the previous chapter would thus provide important information on how sedimentary ecosystems respond to these factors, which have received little research attention, despite the potential for human activities to significantly affect them (Espinosa *et al.* 2007, Sugden *et al.* 2008). Of particularly interest in this study, is the question of how nutrient addition may alter effect strength of ecosystem engineering on suspension feeders through trophic resource enhancement. I therefore anticipate bottom up control (productivity) to override sandprawn negative impacts and thereby increase abundances of suspension feeders, as result of nutrients increasing trophic resource (microalgal biomass) for suspensions feeders.

It is broadly hypothesised that macrofaunal community structure will be significantly influenced by the interactive effects of ecosystem engineering by sandprawn densities and nutrient enrichment. In line with this broad hypothesis, there was also interest in understanding whether macrofaunal assemblages respond to the experimental treatments in a manner predicted by the grazer-reversal hypothesis (Proulx and Mazumder 1998). This hypothesis and background theory has been discussed in detail in the previous chapter.

6.2 Hypotheses:

H1: At low nutrient levels, increasing sandprawn densities should reduce macrofaunal species diversity.

H2: At intermediate nutrient levels, increasing sandprawn densities should impact diversity of macrofauna in a unimodal humped-shape pattern.

H3: At high nutrient levels, macrofaunal diversity should increase with increasing sandprawn densities.

H4: At background nutrient levels, increasing sandprawn densities should positively impact burrowing macrofaunal abundances but negatively affect abundances of suspension feeders. However, both of these functional groups should be positively affected by nutrient addition.

- **METHODS AND MATERIALS**

Please refer to chapter 2 for the methods used in this chapter.

6.3 RESULTS

6.3.1 Macrofaunal community structure: Overall composition

Macrofaunal community structure was significantly influenced by an interaction between nutrient treatments and sandprawn densities (PERMANOVA, Pseudo-$F_{4,\,53}$ = 1.716, *p* = 0.044), and also by sites (PERMANOVA, Pseudo-$F_{1,\,53}$ = 5.663, *p* = 0.008, **Table 6.1**). An interaction between sites and nutrient treatments, sites and sandprawn densities or the combination of all three factors failed to influence the macrofaunal community structure (*p* < 0.05, for all cases, **Table 6.1**). Site effects on macrofauna were obvious on MDS ordination (**Fig.6.1**), showing a clear separation of samples between sites. The lack of significant effect on macrofaunal community structure either by nutrient treatments (Pseudo-$F_{2,\,53}$ = 0.774, *p* = 0.062) or sandprawn densities (Pseudo-$F_{2,\,53}$ = 0.7911, *p* = 0.621) was clearly revealed by a PERMANOVA test, and visually supported by MDS ordinations (**Fig.6.2**), illustrating no clear separation of samples based on the sandprawn densities or nutrient treatments.

Table 6.1: PERMANOVA summary statistics reporting responses of macrofaunal community structure to sites, nutrients, sandprawn densities, and their interactions. Statistical descriptions: *Pseudo-F* = test statistics, df = degrees of freedom. Values in bold indicate statistical significance.

Source	***Pseudo-F***	**df**	***p*-value**
Sites	5.6635	1	**0.008**
Nutrients	0.77444	2	0.062
Prawns	0.79118	2	0.621
Nutrients X Prawns	1.7169	4	**0.044**
Sites X Nutrients	0.68599	2	0.677
Sites X Prawns	1.0623	2	0.456
Sites X Nutrients X Prawns	0.91672	4	0.581

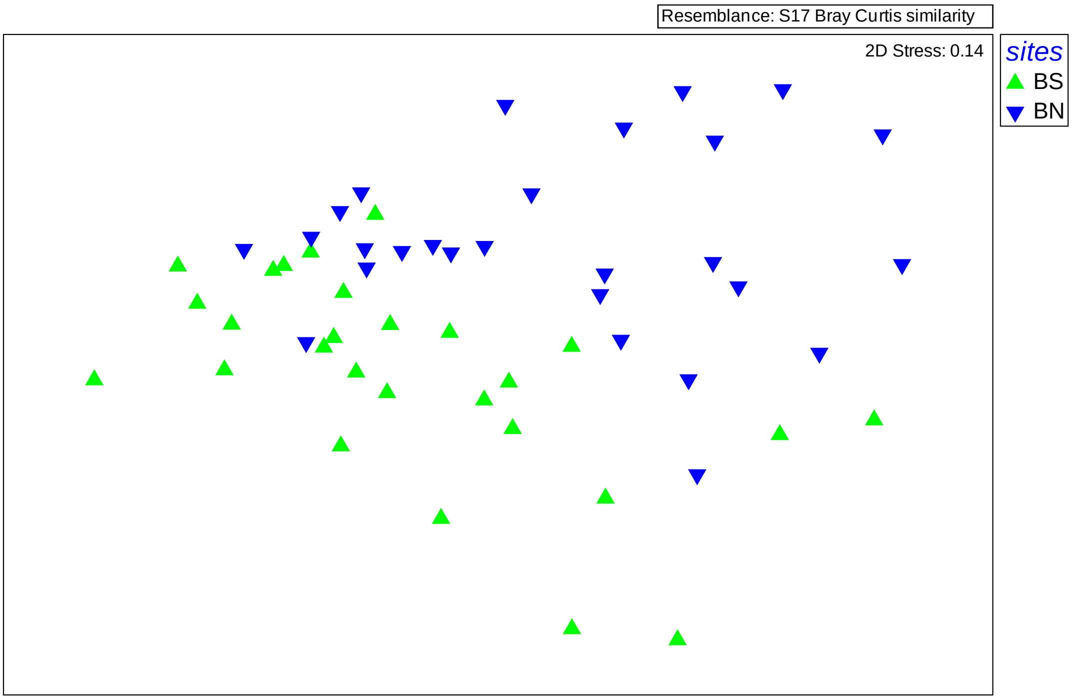

Fig. 6.1: Multidimensional Scaling (MDS) ordination showing spatial variability in macrofaunal community structure in response to sites, based on the *in situ* experiment manipulating sandprawn densities and nutrient levels.

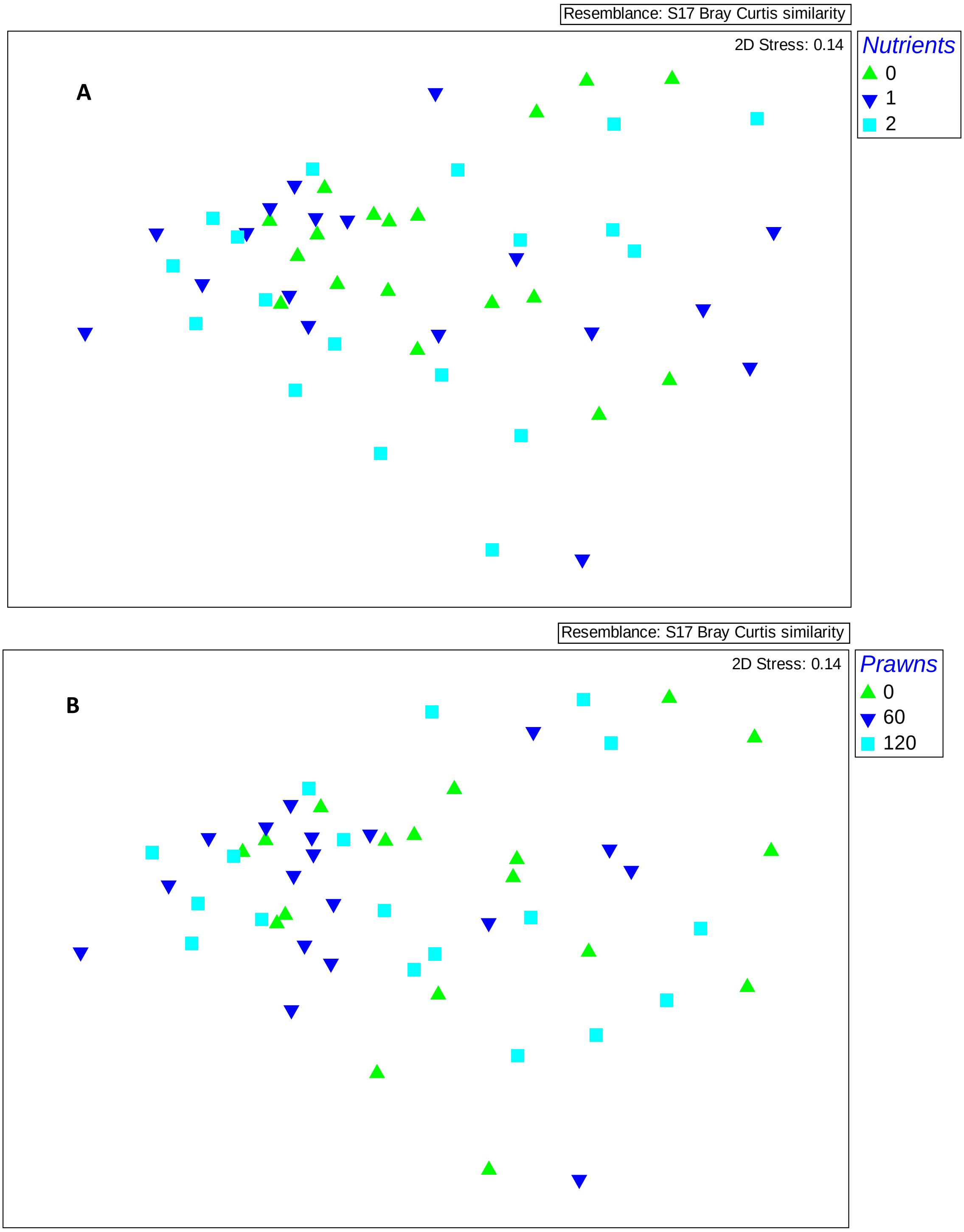

Fig. 6.2: Multidimensional Scaling (MDS) ordination illustrating spatial variability in macrofaunal community structure in response to increasing nutrient levels (**A**) and sandprawn densities (**B**), based on *in situ* manipulation of sandprawn densities and nutrient levels.

6.3.2 Diversity metrics

Macrofaunal diversity metrics were not statistically predicted by the candidate models ($p > 0.05$, for all cases), except for the abundance model 3, which examined main effects of sites, nutrients and sandprawn densities ($p = 0.001$, **Table 6.2A**). The GLM model analysis indicated that abundance differed significantly between sites ($p < 0.0001$) and was significantly influenced by the level 60 (ind.m^2) sandprawn density ($p = 0.015$, **Table 6.2B**).

The variation in macrofaunal abundance due to sites and sandprawn densities was generally clear (**Fig 6.3B**). In Bottelary North, increasing sandprawn densities resulted in macrofaunal abundance responding in a hump-shaped pattern at both ON and 1N treatments, while at the 2N treatment, abundance increased in response to increasing sandprawn densities. On the other hand, in Bottelary South, abundance first decrease with increasing sandprawn densities at the 0N treatment, followed a hump-shaped response at the 1N treatment, and subsequently increased at the 2N treatment (**Fig 6.3A**)

Table 6.2A: Generalized linear models reporting candidate models for macrofaunal diversity metrics based on *in situ* manipulation of sandprawn densities and nutrient levels. NB: only parsimonious and significant models ($p < 0.05$) were selected for further analysis. Statistical descriptions: full model = interaction between all factors, model 2 = interaction between nutrients and sandprawns, model 3 = main effects. Values in bold indicate statistical significance.

				Species richness (S)					Evenness (J')		
Candidate models		**RDF**	**RD**	**Deviance**	**DF**	**Pr(>Chi)**	**RDF**	**RD**	**Deviance**	**DF**	**Pr(>Chi)**
Full model	S X N X P	36	92.593	42.519	17	0.486	36	0.613	0.324	17	0.326
Model 2	S + (N X P)	44	104.214	-11.621	-8	0.807	44	0.716	-0.103	-8	0.641
Model 3	S + N +P	48	105.621	-1.407	-4	0.968	48	0.814	-0.097	-4	0.219
Null		53	135.111				53	0.937			
				Shannon Wiener diversity (H')					**Abundance (N)**		
							RDF	**Theta Res.**	**LR stat.**	**DF**	**Pr(>Chi)**
Full model	S X N X P	36	2.929	1.333	17	0.496	36	7.370	4.009	8	0.856
Model 2	S + (N X P)	44	3.441	-0.511	-8	0.614	44	6.829	4.833	4	0.304
Model 3	S + N +P	48	3.885	-0.444	-4	0.243	48	6.236	20.366	5	**0.001**
Null		53	4.263				53	4.292			

1: S = Site 4: RDF = Residual degrees of freedom 7: Pr (>Chi) = Measure of the *p*-value
2: N = Nutrients 5: RD = Residual deviance
3: P = Prawns 6: DF = Degrees of freedom

Table 6.2B: Summary of generalized linear models reporting the parsimonious model (model 3) for macrofaunal abundance, based on *in situ* manipulation of sandprawn densities and nutrient levels.

Abundance (N)					
Models		**Term level**	**Estimate**	**95 % Coefficient Intervals (Lower and upper limits**	**Pr(>/t/)**
Model 3	S + N +P	S	0.4106	0.190 0.630	<0.0001
		60P	0.3313	0.061 0.600	0.015

1: S = Site
2: N = Nutrients
3: P = Prawns
4: Pr (>/t/) = Measure of the *p*-value

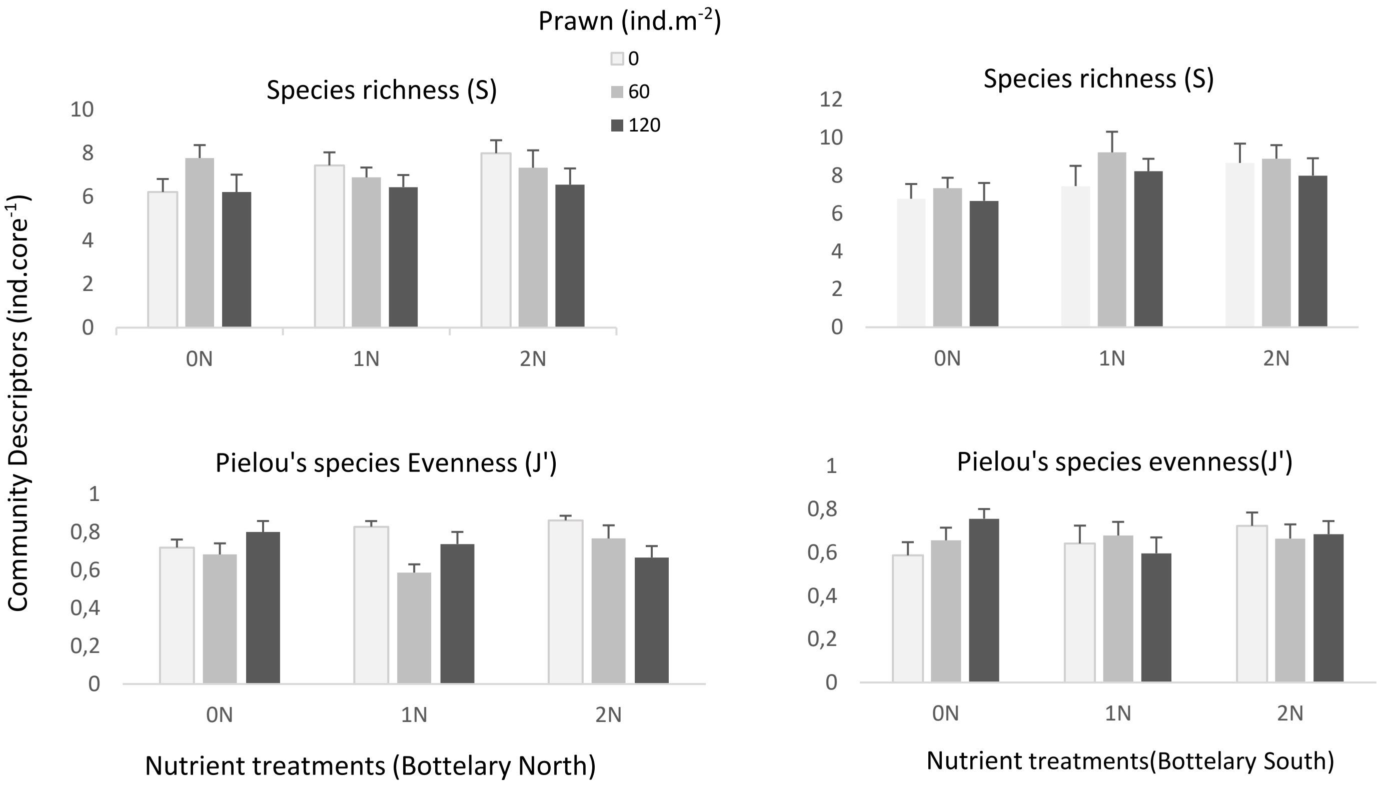

Fig.6.3A: Variation in mean macrofaunal community metrics (± 1SE) at the Bottelary North and South sites, in response to increasing sandprawn densities at each nutrient treatment level. NB: Y axis scales are different to show the trend in the data.

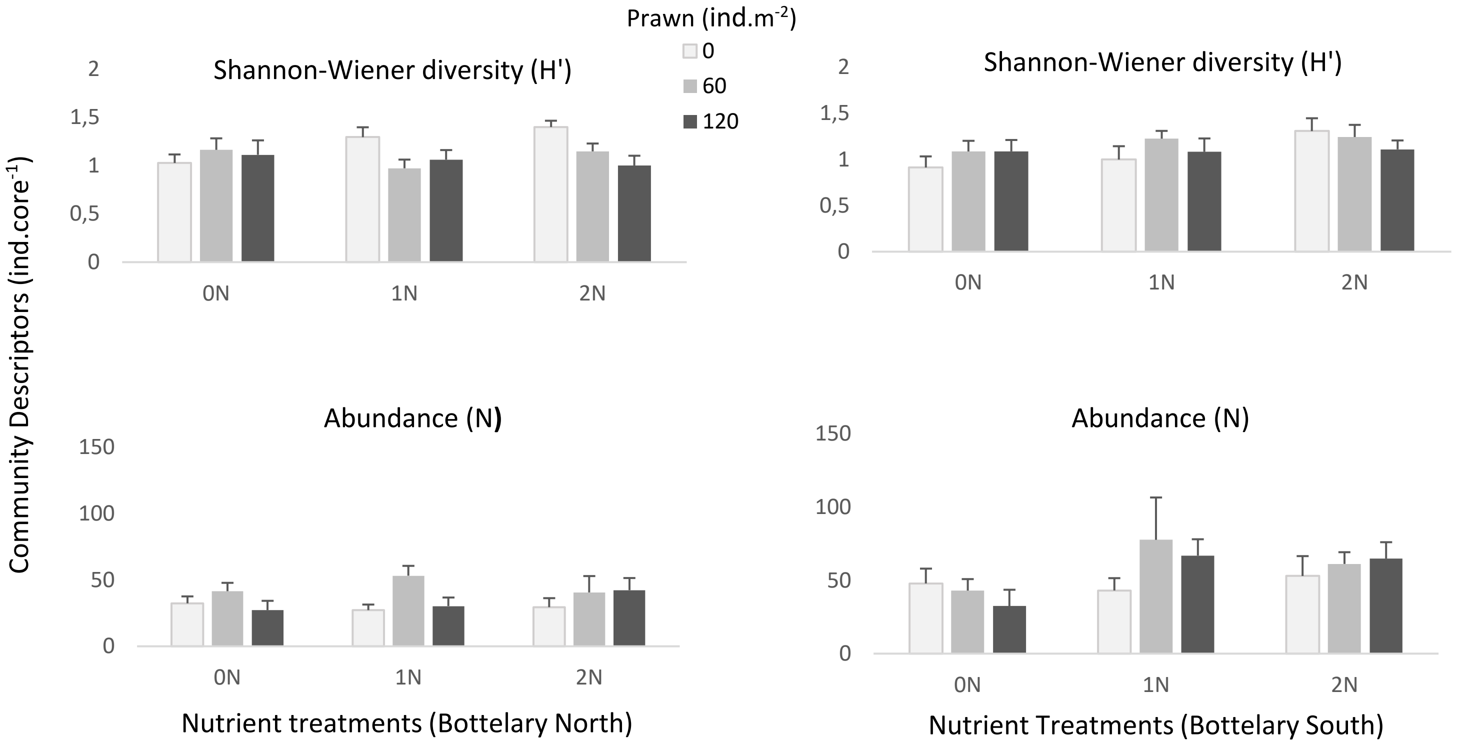

Fig.6.3B: Variation in mean macrofaunal community metrics (± 1SE) at the Bottelary North and South sites, in response to increasing sandprawn densities at each nutrient treatment level. NB: Y axis scales are different to show the trend in the data.

6.3.3 Dominant species

In terms of percentage contribution, SIMPER analysis identified nine out of 40 species/morphotypes to contribute 90 % towards macrofaunal community structure (**Table 6.3, Fig.6.4)**. Juvenile polychaetes were the main contributors to community structure in Bottelary North (60.25 %) and South (60.67 %), while the polychaete *Marphysa elitueni* and bivalves *Tellimya trigona* and *Carditella rugosa* were the smallest contributors.

Table 6.3: Dominant macrofaunal taxa identified by SIMPER (based on 90 % cut off limit) at each of the experimental sites. Letters in brackets after species names denote broader taxonomic grouping: P = polychaete, A = amphipod, C = copepod, B = bivalve.

	% contribution	
Macrofauna	**Bottelary North**	**Bottelary South**
Juvenile polychaetes (P)	60.25	60.67
Urothoe grimaldii (A)	8.49	12.29
Copepods (C)	3.97	4.35
Tellimya trigona (B)	3.20	3.87
Carditella rugosa (B)		3.30
Ampelisca palmata (A)		5.63
Ceratonereis erythraeensis (P)	6.59	
Notomastus latericeus (P)	5.41	
Marphysa elitueni (P)	3.32	

Six of the nine macrofaunal dominant species met the modelling assumptions in terms of data variability. However, of these species, models for the polychaete *Notomastus latericeus* and bivalve *Tellimya trigona* were not parsimonious as indicated by the model selection procedure performed by the likelihood ratio test (p > 0.05, **Table 6.4A**), while amphipods *Ampelisca palmata*, copepods and juvenile polycheates were all best predicted by the candidate models (p< 0.05 **Table 6.4A**). The full model of an interaction between sites, nutrient treatments and sandprawn densities predicted the abundance of the amphipod *A.*

palmata ($p = 0.045$); model 2 of an interaction between nutrient and sandprawns but not sites predicted juvenile polychaetes ($p = 0.019$), while the main effect model 3 predicted *A. palmata,* copepods and juvenile polychaetes ($p < 0.05$**,** for all cases).

For the interactive model 2, the GLM analysis revealed that juvenile polychaetes were significantly affected by the interaction between the 1N treatment and 120 ind.m^2 ($p = 0.008$) and by the 2N and 120 ind.m^2 treatments ($p < 0.0001$, **Table 6.4B**). Although abundance of the amphipod *A. palmata* was predicted by the full model, the GLM model analysis failed to locate any interaction between all combination levels of nutrients and sandprawn density ($p > 0.05$). For the main effect model, juvenile polychaetes differed significantly between sites ($p = 0.006$) and were significantly affected by level 60 (ind.m^2) sandprawns ($p = 0.010$). Similarly, copepod abundances differed significantly between sites ($p = 0.004$) and were strongly influenced by the 2N nutrient treatment ($p = 0.002$). Sandprawn densities also appeared to have an influence on the copepods, with the level 0 ind.m^2 being significantly different from both 60 ($p = 0.014$) and 120 ($p = 0.008$) ind.m^2. Sites also had a strong influence on the abundance of *A. palmata* ($p < 0.0001$).

Dominant macrofaunal taxa showed clear patterns relating to effects of sites, nutrients and sandprawns (**Fig.6.4A - B**). First, juvenile polychaetes abundance in Bottelary North showed hump-shaped patterns against increasing sandprawn densities at both 0N and 1N treatments, while at the 2N treatment adopted a linear increase against increasing prawn densities (**Fig.6.4A**). A similar pattern occurred for juvenile polychaetes in Bottelary South, but with abundances first declining in response to increasing sandprawn densities at the 0N treatment (**Fig.6.4A**). Copepod abundances at Bottelary North first increased with increasing sandprawn densities at low nutrient levels followed by a hump-shaped pattern at the 1N treatment and a linear increase against increasing sandprawns densities at the 2N treatment

(**Fig.6.4B**). On the other hand, this pattern changed slightly in Bottelary South, as copepod abundances declined at the 0N treatment in response sandprawn density increase. *A. palmata* (amphipod) showed different response patterns between the sites, with abundance in Bottelary North displaying a hump-shaped response at both 0N and 2N treatments but followed a unimodal U-shape pattern at the 1N treatment (**Fig.6.4A**). In Bottelary South, copepod abundances were reduced by increasing sandprawn densities at the 0N but followed a hump-shaped pattern at both 1N and 2N treatments.

Table 6.4A: Generalized linear models reporting candidate models for dominant macrofaunal taxa from experimental manipulation of nutrients and sandprawn densities. NB: only parsimonious and significant models ($p < 0.05$) were selected for further analysis. Statistical descriptions: full model = interaction between all factors, model 2 = interaction between nutrients and sandprawns, model 3 = main effects. Letters in brackets after species names denote broader taxonomic grouping: P = polychaete, A = amphipod, C = copepod, B = bivalve. Values in bold indicate statistical significance.

		Juvenile polychaetes (P)					***Urothoe grimaldii* (A)**				
Models		**RDF**	**Theta Res.**	**LR stat.**	**DF**	**Pr(>Chi)**	**RDF**	**Theta Res.**	**LR stat.**	**DF**	**Pr(>Chi)**
Full model	S X N X P	36	3.183	4.9560	8	0.762	36	2.510	11.393	8	0.180
Model 2	S + (N X P)	44	2.914	11.696	4	**0.019**	44	1.836	9.115	4	0.058
Model 3	S + N +P	48	2.379	14.047	5	**0.015**	48	1.459	10.371	5	0.065
Null		53	1.877				53				
		Copepods (C)					***Tellimya trigona* (B)**				
Full model	S X N X P	36	3.7930	7.799	8	0.453	36	2.328	7.482	8	0.485
Model 2	S + (N X P)	44	2.816	5.310	4	0.256	44	1.878	8.857	4	0.064
Model 3	S + N +P	48	2.222	21.520	5	**<0.0001**	48	1.517	9.234	5	0.100
Null		53	1.172				53	1.193			
		***Ampelisca palmata* (A)**					***Notomastus latericeus* (P)**				
Full model	S X N X P	36	2.004	15.813	8	**0.045**	36	1.309	4.202	8	0.838
Model 2	S + (N X P)	44	1.263	3.179	4	0.528	44	1.154	5.243	4	0.263
Model 3	S + N +P	48	1.195	27.283	5	**<0.0001**	48	0.995	6.988	5	0.221
Null		53	0.597				53	0.830			

1: S = Site
2: N = Nutrients
3: P = Prawns
4: RDF = Residual degrees of freedom
5: RD = Residual deviance
6: DF = Degrees of freedom
7: Pr (>chi) = Measure of the *p-value*

Table 6.4B: Summary of generalized linear models reporting effects of experimental treatments (nutrients and sandprawn densities) on dominant macrofaunal taxa based on the parsimonious model selection process. Statistical descriptions: model 2 = interaction between nutrients and sandprawns, model 3 = main effects. Letters in brackets after species names denote broader taxonomic grouping: P = polychaete, A = amphipod, C = copepod.

		Juvenile polychaetes (P)				***Urothoe grimaldii* (A)**			
Models		Term level	Estimate	95 % Coefficient Intervals (Lower and upper limits)	Pr(>/t/)	Term level	Estimate	95 % Coefficient Intervals (Lower and upper limits	Pr(>/z/)
Model 2	S + (N X P)	1N X 120P	1.297	1.393 9.623	0.008	2N X 120P	-1.898	0.040 0.550	0.003
		2N X 120P	1.641	1.958 13.627	<0.0001				
Model 3	S + N +P	S	0.490	1.144 2.331	0.006				
		60P	0.560	1.125 2.723	0.010				
			Copepods (C)						
Model3	S + N +P	S	0.632	1.212 2.924	0.004				
		2N	0.836	1.343 3.973	0.002				
		60P	0.681	1.143 3.432	0.014				
		120P	0.726	1.192 3.596	0.008				
			***Ampelisca Palmata* (A)**						
Model 3	S + N +P	S	1.541	2.581 8.520	<0.0001				

1: S = Site
2: N = Nutrients
3: P = Prawns
4: Pr (>/t/) and Pr(>/z/) = Measure of the *p-value*

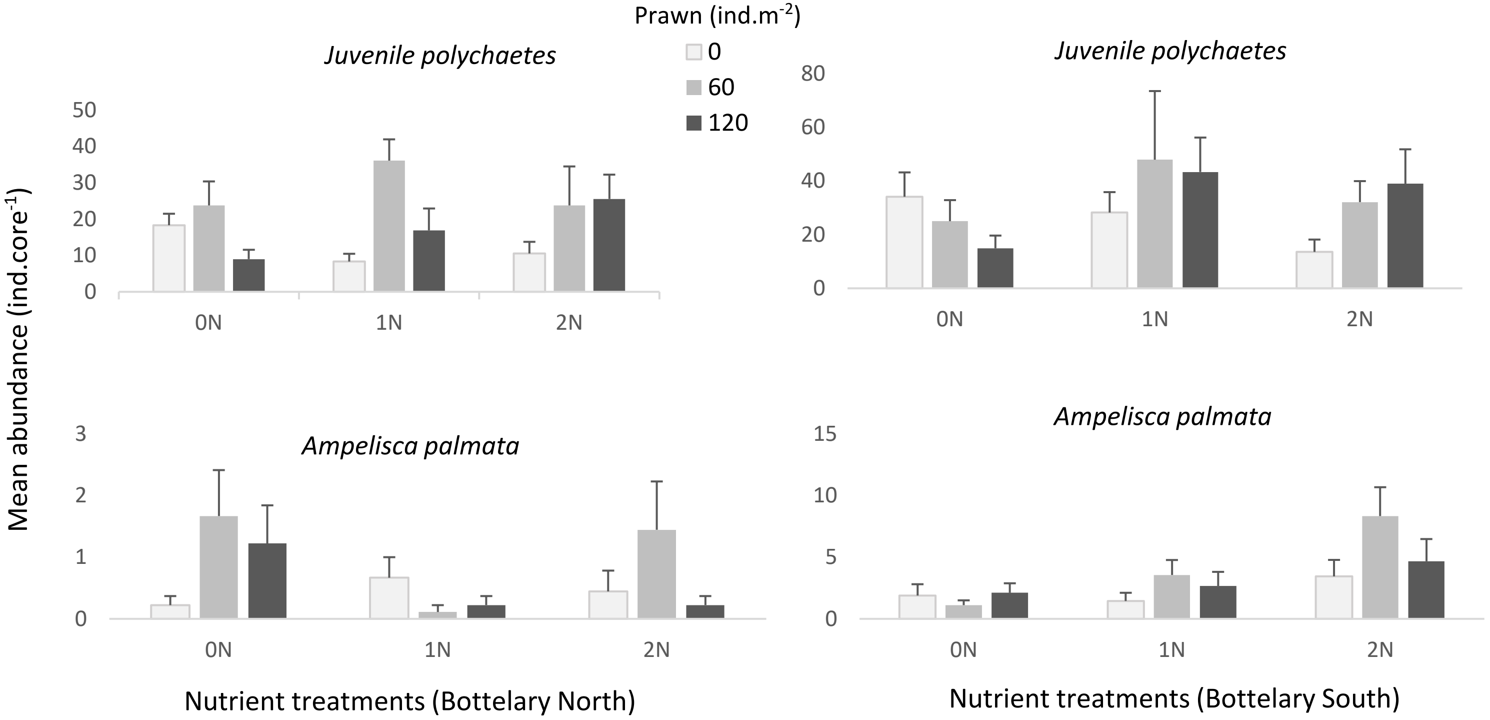

Fig.6.4A: Variation in mean macrofaunal abundances (± 1SE) at Bottelary North and South, in response to increasing sandprawn densities at each nutrient treatment level. NB: Y axis scales are different to show the trend in the data.

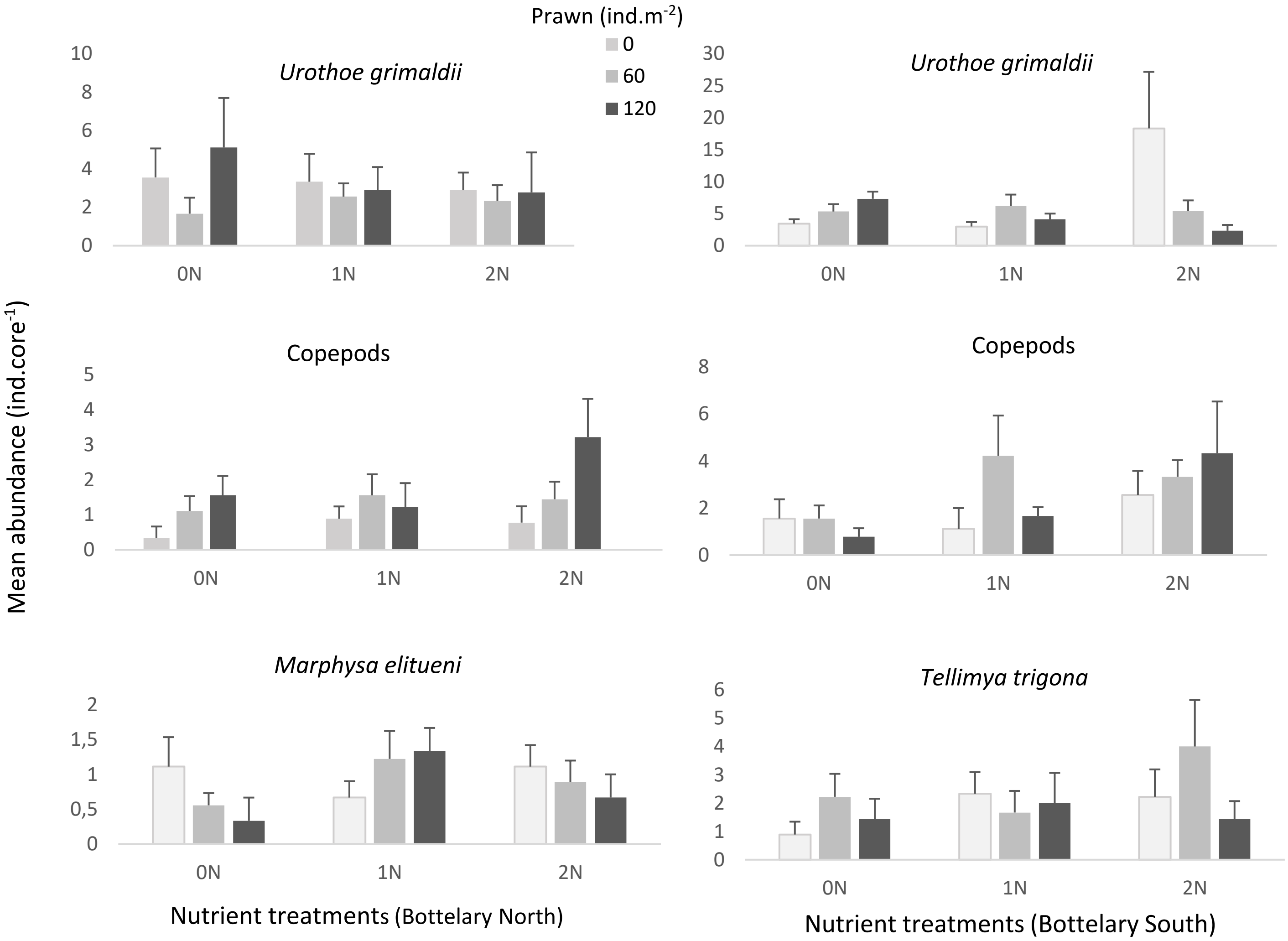

Fig.6.4B: Variation in mean macrofaunal abundances (± 1SE) in response to increasing sandprawn densities at each nutrient treatment level within two experimental sites. NB: Y axis scales are different to show the trend in the data.

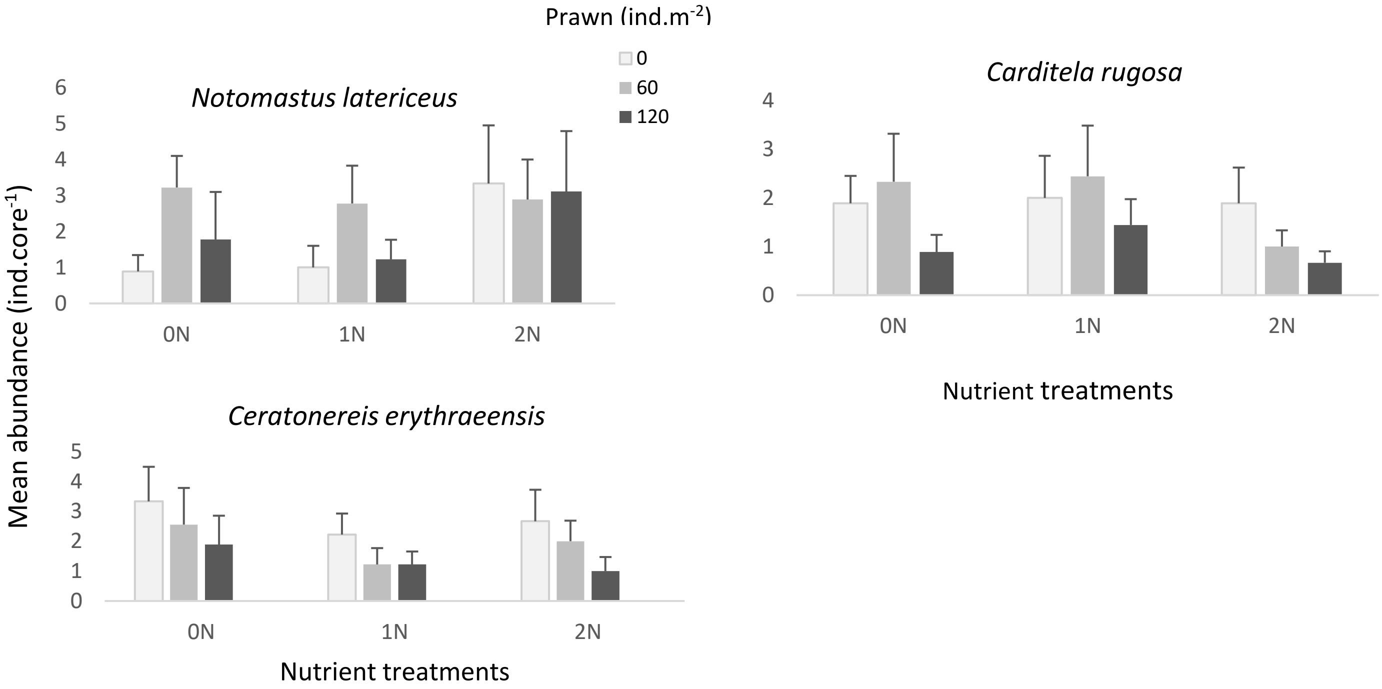

Fig.6.4C: Variation in mean macrofaunal abundances (± 1SE) in response to increasing sandprawn densities at each nutrient treatment level within two experimental sites.

6.3.4 Functional groups

Three out five macrofaunal functional groups met the modelling assumptions in term of data variability. Of these groups, both burrowing deposit feeders and suspension feeders were the only groups predicted by the experimental factors ($p > 0.05$, for all cases, **Table 6.5A**). Burrowing deposit feeders were best predicted by model 2 of an interaction between nutrient treatments and sandprawn densities ($p = 0.016$), while suspension feeders were best predicted by the full model of an interaction ($p = 0.014$) and very strong effects of model 3 main effects ($p < 0.0001$).

As for the interactive model, burrowing deposit feeders were significantly influenced by the interaction between the 1N treatment and 120 ind.m^2 ($p = 0.024$) and between the 2N treatment and 120 ind.m^2 ($p = 0.003$, **Table 6.5B**). The interactive effect of sites, nutrients and sandprawn densities on suspension feeders occurred between the 1N treatment and 60 ind.m^2 ($p = 0.012$), and 2N treatment and 120 ind.m^2 ($p = 0.042$), but was stronger between the 1N treatment and 120 ind.m^2 ($p < 0.0001$). For the main effect model 3, abundances of suspension feeders differed significantly between sites ($p < 0.0001$), and were significantly influenced by nutrients, particularly the 1N ($p = 0.019$) and 2N treatments ($p = 0.002$).

Both study sites displayed distinctive patterns of suspension feeders and burrowing deposit feeders (**Fig. 6.5A - B**). Generally, in Bottelary North burrowing deposit feeders showed increasing abundances at the 0N treatment, but at both 1N and 2N treatments, abundances decreased in response to increasing sandprawn densities. In Bottelary South, the difference was that no burrowing deposit feeders were recorded at the 0 sandprawn densities for both 0N and 1N treatments. However, the abundances showed an increase at the 0N, a slightly decrease at the 1N and the obvious reduction of the abundances at the 2N treatment in response to increasing sandprawn densities (**Fig. 6.5A**). In Bottelary South, the abundance of suspension feeders increased in response to increasing sandprawn densities, especially at the 1N and 2N nutrient treatments, whereas in Bottelary North, a decline in abundance was observed at the 1N while at the 2N treatment the abundance followed a hump-shaped pattern (**Fig.6.5B**).

Table 6.5A: Generalized linear models reporting candidate models for macrofaunal functional groups from experimental manipulation of nutrients and sandprawn densities. NB: only parsimonious and significant models (*p* < 0.05) were selected for further analysis. Full model = interaction between all factors, model 2 = interaction between nutrients and sandprawns, model 3 = main effects. Values in bold indicate statistical significance.

		Burrowing deposit feeders				
Models		**RDF**	**Theta Res.**	**LR stat.**	**DF**	**Pr(>Chi)**
Full model	S X N X P	36	5.141	9.141	8	0.330
Model 2	S + (N X P)	44	4.166	12.050	4	**0.016**
Model 3	S + N +P	48	3.244	3.626	5	0.604
Null		53	3.016			
		Surface deposit feeders and predators				
Full model	S X N X P	36	2.921	11.060	8	0.198
Model 2	S + (N X P)	44	2.172	4.616	4	0.328
Model 3	S + N +P	48	1.932	4.307	5	0.506
Null		53	1.737			
		Suspension feeder				
Full model	S X N X P	36	6.329	19.138	8	**0.014**
Model 2	S + (N X P)	44	3.868	3.217	4	0.522
Model 3	S + N + P	48	3.732	47.302	5	**<0.0001**
Null		53	1.289			

1: S = Site
2: N = Nutrients
3: P = Prawns
4: RDF = Residual degrees of freedom
5: DF = Degrees of freedom
6: Pr (> Chi) = Measure of the *p*-value

Table 6.5B: Summary of generalised linear models reporting effects of the experimental treatments on macrofaunal functional groups based on the parsimonious model selection process. Full model = interaction between all factors, model 2 = interaction between nutrients and sandprawns, model 3 = main effects.

			Burrowing deposit feeders			
Models		**Term level**	**Estimate**	**95 % Coefficient Intervals (Lower and upper limits)**		**Pr(>/z/)**
Model 2	S + (N X P)	1N X 120P	-0.966	0.162	0.889	0.024
		2N X 120P	-1.265	0.120	0.659	0.003
			Suspension feeder			
Full model	SXNXP	1N X 60P	2.294	1.689	64.133	0.012
		1N X 120P	4.010	8.650	391.639	<0.0001
		2N X 120P	1.912	1.101	45.479	0.042
Model 3	S + N +P	S	1.320	2.713	5.174	<0.0001
		1N	0.470	1.076	2.384	0.019
		2N	0.595	1.225	2.687	0.002

1: S = Site
2: N = Nutrients
3: P = Prawns
4: Pr(>/z/) = Measure of *p*-value

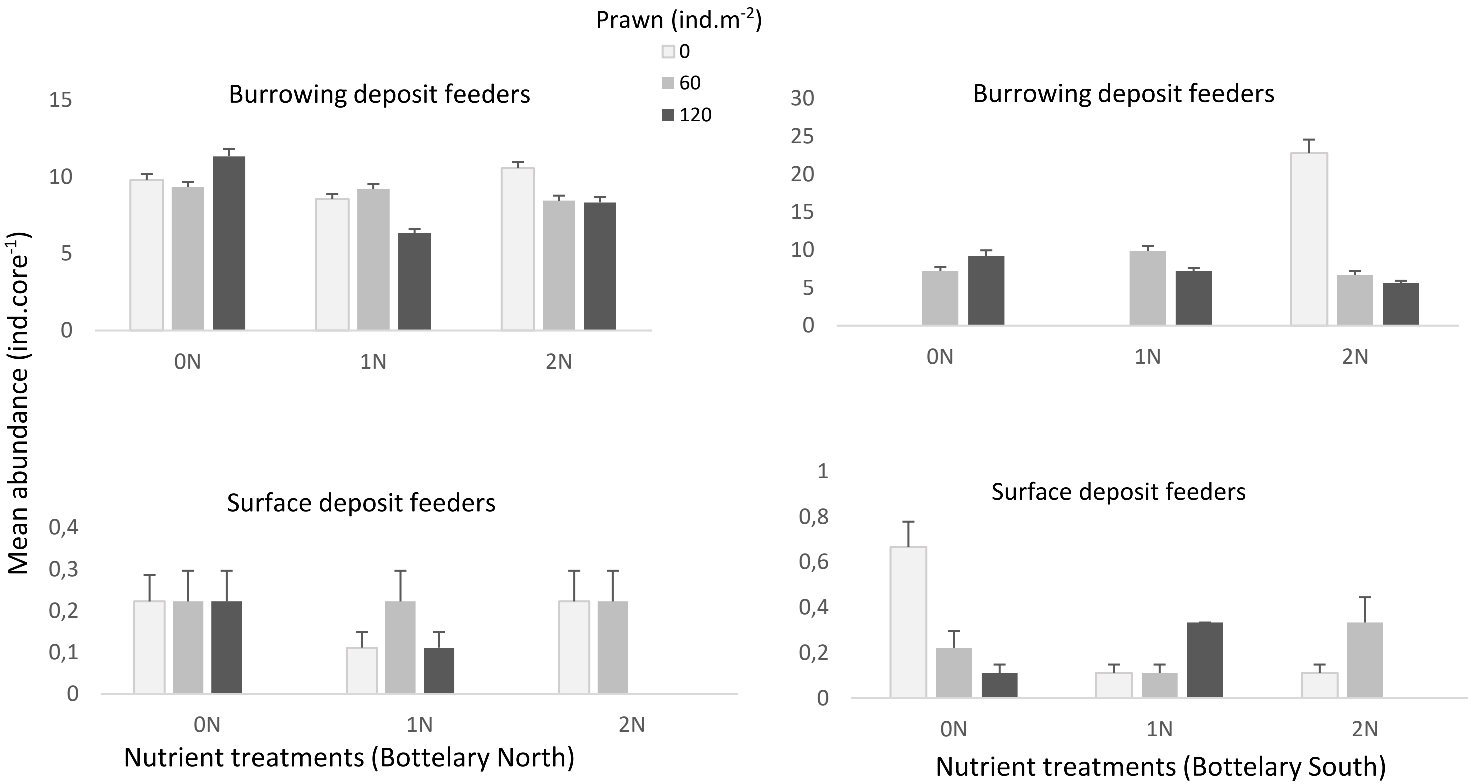

Fig.6.5A: Variation in mean macrofaunal functional group abundances (± 1SE) in response to increasing sandprawn densities at each nutrient treatment level within two experimental sites. NB: Y axis scales are different to show the trend in the data.

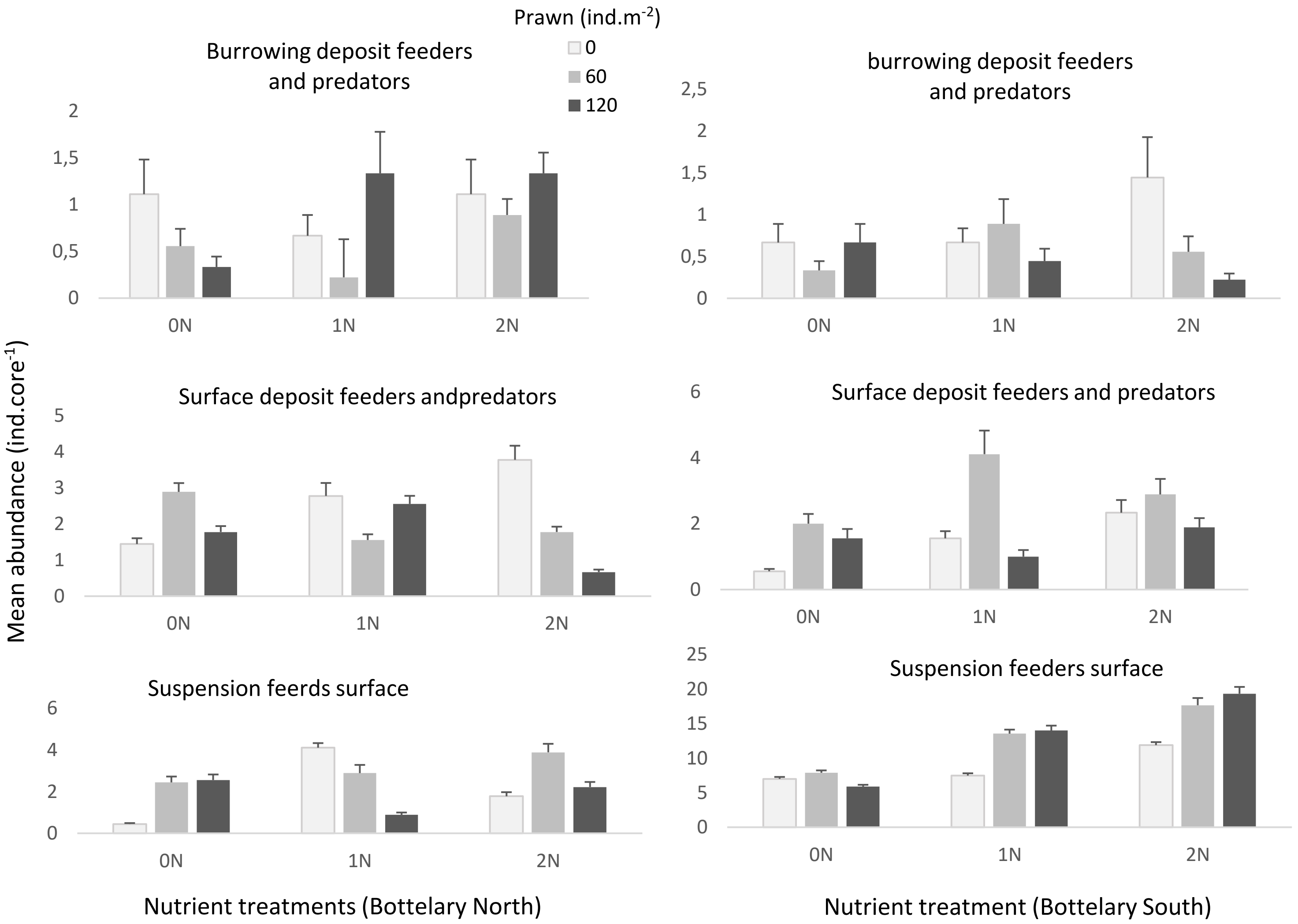

Fig.6.5B: Variation in mean macrofaunal functional group abundances (± 1SE) in response to increasing sandprawn densities at each nutrient treatment level within two experimental sites. NB: Y axis scales are different to show the trend in the data.

6.4 Discussion

This chapter builds on the previous chapter, but with the central aim being to understand how macrofaunal assemblages in inter-tidal sandflats respond to experimental manipulation of nutrients and sandprawns. Findings of this chapter were meant to complement those of the preceding chapter on meiofauna, to provide a holistic understand of biotic responses to sandprawns and nutrients. I specifically hypothesized that macrofaunal diversity metrics would respond to the manipulated factors in a manner predicted by the grazer-reversal hypothesis (Proulx and Mazumder 1998), which is detailed in chapter 5 (**Fig.5.1**). In addition, macrofaunal suspension feeders were hypothesized to be negatively influenced by increasing sandprawn densities at ambient nutrient levels but to increase in abundance in nutrient addition treatments, while burrowing macrofaunal abundances were expected to increase despite nutrient edition. Despite limited support for the patterns predicted by the grazer-reversal hypothesis in results of this chapter, interactive effects of nutrient enrichment and sandprawn densities emerged to influence macrofaunal community composition and the abundance of certain individual species/taxa (i.e., juvenile polychaetes and amphipod *Ampelisca palmata*). Both sandprawn densities and sites as separate factors appeared to play an important role in regulating the macrobethos of Langebaan Lagoon. Suspension feeders did conform to the hypothesis posed, but this was site-specific.

6.4.1 Macrofaunal community structure: overall composition, diversity metrics and dominant species

The most striking result of this experiment was that at the community level, macrofauna were affected by the interactive effects of nutrients and sandprawns, but not by their main effects. This was an important finding given that productivity and disturbance were hypothesized to interact and structure the macrofaunal assemblage, but, in a manner predicted by the grazer-reversal hypothesis (Proulx and Mazumder 1998). Macrofaunal community structure also emerged to differ between sites, with the latter being evident using ordination techniques (**Fig.6.1**). The observed spatial distinction in macrofaunal community is likely a product of unique environmental characteristics present within each site, which in turn has important implications for how resident macrofaunal communities respond to the factors manipulated in this experiment.

Surprisingly, macrofaunal abundance was the only community metric that responded to treatments, being significantly affected by both sites and sandprawns, particularly at intermediate density levels (60 ind.m^{-2}). This result suggests that the majority of macrofaunal diversity metrics were insensitive to treatments. In the case of nutrient enrichment, this insensitivity of macrofaunal community metrics could be due to the lack of a positive response of benthic microalgal biomass to enrichment (**Chapter 5**). It was anticipated that nutrient addition to sediments in this study would enhance benthic microalgal growth and in turn increase the abundances of macrofaunal species. This was based on previous studies indicating that macrofaunal abundance can be enhanced by food availability, mainly in the form of benthic microalgae (Huxham *et al.* 2006), which is considered an important source of benthic primary production in shallow water littoral ecosystems (Underwood and Paterson 1993, MacIntyre *et al.* 1996, Cahoon 1999, Gazeau *et al.* 2004).

The results of the current study differ considerably from previously studies that have tested the singular effects of sandprawns, which have documented promotive effects, particularly on species richness and evenness (Siebert and Branch 2005b). At the species level, forty macrofaunal species/taxa were recorded in this study, with only nine of them being dominant, as indicated by SIMPER (**Table 6.3**). Juvenile polychaetes were the most dominant group at both sites, followed by amphipod *Urothoe grimaldii,* while the third dominant was the amphipod *Ampelisca palmata* in Bottelary South and the polychaete *Ceratonereis erythraeensis in* Bottelary North. *Urothoe grimaldii* was unaffected by the experimental treatments, which may indicate insensitivity of this species to nutrient enrichment and sandprawn densities. For instance, in the *in situ* survey carried out in **Chapter 4**, a model with sites and seasons failed to predict amphipod *U. grimaldii*, suggesting that these variable were unimportant for *U. grimaldii* despite it being the most prevalent macrofaunal species. It is therefore very possible that *U. grimaldii* is a generalist in the sandflats of Langebaan Lagoon and capable of tolerating varying biotic and abiotic factors.

Of the dominant species/taxa recorded, juvenile polychaetes, copepods and the amphipod *A. palmata* responded to treatments. Both juvenile polychaetes and *A. palmata* were affected by the interaction between nutrients and sandprawn densities and also by the main effects of sites and sandprawn densities. On the other hand, an interesting outcome was that copepod abundances were strongly affected by the main effects of nutrient enrichment and sandprawn densities but not their interaction (**Table 6.4A**). Visually, nutrient effects on copepods were apparent at the highest enrichment level (2N), with copepod abundances increasing with sandprawn densities in both sites (**Fig.6.4B**). The responses of copepod abundances to nutrient enrichment in this study may be explained by treatment effects on food availability. As such, this could imply that nutrient addition in this study had a positive influence on diatom biomass, thereby promoting copepod abundance. Although copepods often display specialized diets (Rzeznik-Orignac *et al.* 2008), their feeding strategies are plastic in response to availability of food resource (Hicks and Coull 1983, Heip *et al.* 1995, De Troch *et al.* 2003, Hyndes and Lavery 2005).

Sandprawn effects were clearly demonstrated for both copepod and juvenile polychaete abundances, with both groups responding in a hump-shaped pattern to sandprawns at the intermediate nutrient level. Copepods are generally classified functionally as suspension feeders - organisms that feed by straining suspended food particles from the water column, mainly phytoplankton (Cloern 1982, Underwood and Kromkamp 1999). Given the unremitted nature of sandprawn bioturbation, copepods may be susceptible to sediment resuspension, given its classification as a suspension feeder; a group that has been shown to be negatively affected by bioturbation (Siebert and Branch 2005a, Pillay *et al.* 2007c). This may be supported at least in part by the observed decreasing trend in copepod abundances at the 1N treatment (**Fig.6.4B**). Resuspended sediment particles induced by sandprawns can potentially affect copepods by impeding the functioning of their filtration apparatus, thereby reducing feeding rates and reductions in their abundances (Siebert and Branch 2005a, Ellis *et al.* 2002, Pillay *et al.* 2007c).

6.4.2 Limited evidence for grazer-reversal hypothesis

The response of macrofaunal abundance and that of individual species/taxa to nutrient enrichment (productivity) and sandprawn bioturbation (disturbance) were variable in this study. Generally, these patterns were of an increasing and decreasing nature, but in some occasions, unimodal hump-shaped patterns emerged. Patterns as such conform to the grazer-reversal hypothesis (Proulx and Mazumder 1998), an extension of the Dynamic Equilibrium Model (DEM, Kondoh 2001), which asserts that disturbance–diversity relationship deviates in response to different productivity levels resulting in (**i**) negative patterns when productivity is low, (**ii**) unimodal hump-shaped when productivity is at the intermediate level, and (**iii**) a linear increase when productivity is high. In addition, unimodal U-shaped responses, which are not explicitly predicted by the grazer-reversal hypothesis was also among the response patterns documented in this study.

There was, however, very little similarity in patterns documented in this study and with those predicted by the grazer-reversal hypothesis or the dynamic equilibrium model. For instance, macrofaunal abundance in Bottelary North was structured in a hump-shaped manner at both 0N and 1N treatments, while at the 2N treatment, abundance was elevated by increasing sandprawn densities (**Fig.6.3B**). On the other hand, contrasting trends emerged for macrofaunal abundance in Bottelary South, in which increasing sandprawn densities at ambient nutrient levels (0N) resulted in reductions of species abundance, while at the 1N treatment, abundance followed a hump-shaped pattern. Abundance subsequently increased at the highest nutrient level (2N) with increasing sandprawn densities (**Fig 6.3B**). These patterns were not only restricted to species abundance as they were also apparent for juvenile polychaete and copepod abundances at Bottelary South. However, in Bottelary North juvenile polychaetes followed a unimodal hump-shaped response in the ambient nutrient treatment (0N), while copepod abundances were elevated against increasing sandprawn densities. Trends for both groups at the 0N treatment in Bottelary North did not conform to the grazer-reversal hypothesis (**Fig 6.3B)**.

Macrofaunal abundance and that of copepods conformed somewhat to the predictions of the grazer-reversal hypothesis, despite the lack of an interaction between nutrients and sandprawn densities. However, these outcomes cannot be regarded as strong support for the grazer-reversal model due to the fact that main but not interactive effect of nutrients and sandprawn treatments on these community measures were recorded (**Table 6.4A**). One important requirement for the grazer-reversal model is that both productivity and disturbance should interact to influence response variables (Proulx and Mazumder 1998).

Given that juvenile polychaetes were affected by the interaction between nutrients and sandprawn densities and displayed patterns similar to those predicted by the grazer-reversal model **(Fig.6.4A**), responses of this group can therefore be affirmed as a potential grazer reversal outcome. The abundance of the amphipod *A. palmata* also conformed to the grazer-reversal model but only in Bottelary South (**Fig.6.4A**).

In comparison with the other studies that have previously examined interactions between disturbance and productivity on communities, grazer-reversal (Proulx and Mazumder 1998) and/or dynamic equilibrium models (Kondoh 2001) have not been overwhelmingly supported in the majority of studies. For instance, Wilson and Tilman (2002) examined old-field species richness along a gradient of disturbance and increased nutrients and reported decreasing trends for all cases. Hillebrand (2003) observed a slight increase in species richness of freshwater periphyton against increasing grazing intensity within productivity, but no hump-shaped pattern was documented. Sugden *et al.* (2008) found that the interaction between nutrient enrichment and disturbance frequency on benthic communities contradicted Kondoh's DEM prediction. They reported that both low and high disturbance frequencies increased species evenness at the ambient productivity levels, with the same pattern observed when nutrients were enhanced.

Sugden *et al.* (2008) indicated that eight analogous experiments conducted in four different locations across the Northern Hemisphere failed to follow the predictions of Kondoh's model. It must be mentioned however, that in one of the experiments comprising the latter study (Italy), the interaction between disturbance and nutrients was successfully detected, but did not yield hypothesized patterns. Furthermore, an experiment performed in Sweden conformed to the predictions of the Intermediate Disturbance Hypothesis (IDH), however, no interaction between disturbance and productivity was detected (Svensson *et al.* 2007).

Kondoh's model has been in rare occasions successfully demonstrated. For example, Kassen *et al.* (2004) showed a peak in bacterial diversity at an intermediate disturbance level with increasing productivity levels. A mesocosm experimental study undertaken by Austen and Widdicombe (2006) investigating disturbance and nutrient enrichment on macrofaunal communities revealed an increase in diversity in response to high disturbance and enrichment treatment levels. A study undertaken by Jara *et al.* (2006) manipulating both nutrient enrichment and disturbance levels in the Brazilian oligotrophic system indicated evidence of Kondoh's (2001) model. They reported macrofaunal species richness to decline with increasing disturbance at the ambient nutrient level.

Numerous reasons may account for the observed discrepancies between patterns documented in this study and that of the grazer-reversal hypothesis or Kondoh's model. First and foremost, with the exception of macrofaunal species abundance, patterns that apparently conformed to grazer-reversal hypothesis in this study arose from responses of particular species, but both the Kondoh (2001) and Proulx and Mazumder (1998) models are based on disturbance–diversity relationships, not disturbance–species abundance interplays. Extreme caution is therefore essential when interpreting results of this nature. It has been stressed in the literature that the application of different diversity descriptors when examining ecological theories such as intermediate disturbance hypothesis (IDH; Connell 1978) often result to major discrepancies among studies. For instance, Svensson *et al.* (2012) indicated that richness and evenness are regarded key aspects of diversity, yet it is unclear if both these indices yield similar responses to different levels of perturbation.

Secondly, it may be possible that varied patterns observed in this study were due to nutrient enrichment being insufficient to influence macrofaunal diversity metrics and individual species/taxa. As a result, these patterns did not overwhelmingly conform to the predictions of the grazer-reversal hypothesis, but instead, followed inconsistent trends relating to the interaction between nutrient and sandprawn treatments, which were site dependent in some cases. Interactions between nutrients and sandprawns on the overall macrofauna assemblages highlights that nutrients used in this study were effective, which was also indicated by the outcome of the field experimental trail (see appendix, **Fig.9.1**). However, it is likely that nutrients within the cage experiment were mostly used by microalgal biomass, which was possibly subsequently grazed by the macrofauna. A few studies have investigated nutrient enrichment impacts on macrofauna, but have reported varying responses (Posey *et al.* 2002), including increase in growth and abundances of macrofauna (Beukema 1991, Posey *et al.* 1995, 1999), while in some instance no responses have been detected (Wiltse *et al.* 1984). The lack of consensus between these studies has been previously attributed to background productivity levels in which studies were conducted. For instance, in areas characterized by low background nutrient availability, species diversity and richness are likely to increase with nutrient enrichment, while in areas with high ambient nutrient loadings there is likely to be a decrease in these community measures (Morris and Keough 2003, Posey *et al.* 2006).

6.4.3 Functional groups

Even though both burrowing deposit feeders and suspension feeders were strongly affected by an interaction between nutrients and sandprawn treatments, graphically, these functional groups did not overwhelmingly exhibit patterns predicted by the grazer-reversal model (**Fig.6.5A-B**). These findings therefore suggest that disturbance-productivity interaction on macrofaunal functional groups in sandflats may be idiosyncratic and not necessarily conform to the grazer-reversal model. In Bottelary South, the highest level of productivity (2N) enhanced abundances of suspension feeders against increasing sandprawn densities (**Fig.6.5B**). This was the only macrofaunal functional group pattern that emerged to partially conform to the grazer-reversal hypothesis, suggesting that under high productivity, suspension feeders can proliferate despite increased disturbance levels. A similar trend was observed at the 1N treatment in Bottelary South, conforming to the hypothesis under investigation in this study that suspension feeder abundance should be enhanced in nutrient addition treatments despite increasing sandprawn densities. This pattern highlights the potential for productivity to reverse sandprawn ecosystem engineering impacts for suspension feeders. However, in Bottelary North, at an intermediate nutrient level (1N), increasing sandprawn densities caused negative impacts on suspension feeders (**Fig.6.5B**). The inverse pattern of responses of suspension feeders observed at the 1N treatment between sites highlights the influence of spatial variability of the sandflats of Langebaan Lagoon sandflats in contextually determining how particular functional groups such as suspension feeders respond to sandprawns and nutrients. Sediment destabilization by deposit feeders that elevate sediment resuspension have long been known to negatively influence sympatric surface suspension feeders (Rhoads and Young 1970, Thrush *et al.* 2008, Pillay and Branch 2011). Such effects manifest mainly by turned over sediment clogging feeding apparatus (Ellis *et al.* 2002, Pillay and Branch 2011). However, the findings of this study suggest that such amensalistic relationships between deposit- and suspension feeders may be contextually dependant, with site characteristics and background productivity being important determinants of the direction and magnitude of interactions.

The hypothesis that burrowing deposit feeders will be positively affected by increasing sandprawn densities was not confirmed in this study. Instead, intricate trends were observed with the deposit feeder abundances showing distinctively different patterns between sites. For example, In Bottelary North, abundances of deposit feeders were generally greater than in Bottelary South, but a decreasing pattern against sandprawn densities, particularly at the 1N and 2N treatments was recorded in the former site (**Fig.6.5A**). However, in Bottelary South, no burrowing deposit feeders were recorded at the ambient and 1N nutrient treatments, but at the highest nutrient level, increasing sandprawn densities appeared to reduce abundance of burrowing deposit feeders. Discrepancies in burrowing deposit feeders observed between the two experimental sites may be explained by abiotic or biotic characteristics unique to each site. The negative trend displayed by deposit feeders in this study is similar to that reported by Pillay *et al.* (2008). However, as indicated by Pillay and Branch (2011), bioturbation by sandprawns can either exert negative or positive effects on macrofauna depending on the mobility of species. Generally, macrofauna with restricted mobility are negatively influenced by sandprawn bioturbation (Posey 1986, Flach and Tamaki 2001), while mobile taxa such as ostracods, amphipods and burrowing infauna are usually positively enhanced by sandprawn burrowing effects (Siebert and Branch 2005b, 2007).

6.5 CONCLUSION

Although the results of this study confirmed the interactive effect of nutrient enrichment and sandprawn densities on macrofaunal assemblages, the hypothesis that this interaction impact communities in a manner predicted by the grazer-reversal model (Proulx and Mazumder 1998) was not overwhelmingly supported. In fact, macrofaunal diversity metrics were generally unresponsive to experimental treatments, though macrofaunal abundance partially conformed to the grazer-reversal hypothesis, despite the lack of a statistical interaction between nutrients and sandprawns. Results suggest that macrofaunal responses to productivity and sandprawns occur mainly at the level of individual species. Inconsistencies between these findings and grazer-reversal hypothesis may be attributed to complex local ecological process and characteristics within sandflat ecosystems, including the minor importance of competition as a structuring force in these systems. It has been previously suggested that when investigating models involving productivity and diversity relationships focus needs to be more on the interactive effects of several mechanisms (Kondoh 2001, Worm *et al.* 2002, Duffy 2003, Michalet *et al.* 2006). However, the common challenged when undertaking *in situ* experiments of this nature is that some factors cannot be simply quantified or isolated thus, making it difficult to empirically examine these ecological theories (Sugden *et al.* 2008).

Owing to these findings, it appears that ecosystem engineering by the sandprawn does alter macrofaunal community compositions and that productivity plays a role mainly by interacting with sandprawns. This suggest that macrofaunal communities of Langebaan Lagoon are regulated mainly by ecosystem engineering and secondarily through interactions between engineering and nutrients at the individual taxon level. The lack of nutrient effects may also indicate that macrofaunal communities are not limited by primary production and/or nutrient availability in the system.

CHAPTER 7

FINAL SUMMATION

7.1 Conclusion

Axiid crustaceans are well known for their modification of abiotic and biotic processes in benthic ecosystems (Wynberg and Branch 1991, Berkenbusch and Rowden 2003, Pillay and Branch 2011). The intensity at which these engineers modulate resource flows and associated benthic fauna has resulted in them receiving substantial research attention (Pillay and Branch 2011, Pillay 2019). However, research to date has focused on particular species and how they influence community organisation and ecosystem functioning. There has therefore been little attention paid to contextual dependencies that are likely to influence the strength of their engineering effects. A recent review by Pillay (2019) discussed in detail some of these contextual process and dependencies on ecosystem engineering by thalassinidean crustaceans. Such dependencies for axiid engineers encompass engineer traits and density, sediment type, wave action, temperature, productivity and nutrients. It is in this context this PhD contributes to growing our understanding of contextual processes and how they impact biotic responses to ecosystem engineering by axiid crustaceans.

The environmental context of interest in this PhD dissertation was productivity and/or nutrients levels in determining how benthic community respond to ecosystem engineering by axiid sandprawn *Callichirus kraussi*. This engineer is a dominant member of macrofauna in South African sandflats and estuaries with significant structuring effects on sympatric biota (Forbes 1973b, Day 1981, Siebert and Branch 2006, 2007, Pillay and Branch 2011). Broadly, this PhD thesis aimed to ascertain how nutrient levels (as a contextual variable) interact with sandprawns to determine macro- and meiofaunal community responses. Nutrient levels were the focal contextual process in this PhD because variation in background nutrients across the South African coastline is significant, with the west coast being dominated by strong upwelling, which increases biological productivity. Within the west coast, upwelling is also seasonally variable, being strongest in summer. This PhD thesis was based on work carried out in Langebaan Lagoon, which is a lagoonal system on the west coast of South Africa that is dominated by sandprawns and subjected to seasonal upwelling.

7.2 Field observational study

In chapter 3 of this dissertation, I presented results from an observational study testing the effects of upwelling on meiofaunal community structure in sandprawn-dominated sandflats. The hypothesis tested was that community metrics, water column and sediment chlorophyll-*a* (chl-*a*) would all be lower in winter (non-upwelling) but higher in summer in response to upwelling. The findings of this study supported the hypothesis posed for the water column but not sediment chl-*a* concentrations. Spatio-temporal variability in water column chl-*a* concentrations was clear within the lagoon, with high chl-*a* values at stations near the mouth compared to those in the upper reaches, with this trend generally being magnified in summer than winter (**Fig. 3.1**). Results indicated that sites and seasons were best explanatory variables for sediment chl-*a* at the sediment surface but not within the walls of burrows produced by sandprawns (**Table 3.2A, Fig. 3.2A**-**B**). The refutation of sites and seasons within sandprawn burrow-walls by the Likelihood Ratio Test (LRT) suggested that these factors affected the sediment surface chl-*a*, but not that of burrow-walls. Interestingly, chl-*a* levels at the sediment surface increased in winter compared to summer in 2015, which was a reversion of the pattern observed for water column chl-*a*. This trend disappeared in 2016, with chl-*a* levels appearing similar between seasons (**Fig. 3.2A**-**B**). Chl-*a* concentrations were generally negatively correlated with sandprawn abundance (**Table 3.4**), which could explain to some degree the mismatch between water column and sediment surface chl-*a* levels, given that sandprawns were more abundant in summer than winter. The finding that chl-*a* concentrations were negatively related to sandprawn abundance is consistent with several previous studies that have reported substantial reductions in chl-*a* levels in response to sediment reworking by burrowing axiid crustaceans (Wynberg and Branch 1994, Contessa and Bird 2004, Pillay *et al.* 2007b).

Even though the community structure of meiofauna differed significantly between seasons, the hypothesis that community metrics would be higher in summer in response to upwelling was not upheld. Meiofaunal diversity metrics and individual morphotypes were generally higher in winter relative to summer (e.g. abundance [**Fig. 3.3C**-**D**], Evenness [**Fig. 3.3F**], Shannon-Wiener diversity [**Fig. 3.3G**-H] and morphotypes [**Fig. 3.4A**-**H**]). Surprisingly, sites and seasons were disapproved by the Likelihood Ratio Test (LRT) as predictor variables for community metrics within sandprawn burrow-walls (**Table 3.6A**), which could indicate that these factors were not important determinants of meiofaunal community patterns within sandprawn burrows. This may indicate that finer-scale processes are more influential in determining burrow meiofaunal community patterns. In contrast, sites and seasons did influence some community metrics (e.g. evenness and Shannon-Wiener diversity) at the sediment surface, suggesting that these variables play an important role in governing meiofaunal assemblages in this microhabitat.

Correlations again indicated negative effects of increasing sandprawn abundance on meiofaunal community metrics and morphotypes when summer and winter data were combined and investigated annually (**Table 3.9**). These findings again accentuate the importance of sandprawns in regulating meiofaunal communities, mainly through sediment turnover and habitat (burrows) creation. This was not a surprising outcome, given that sediment reworking by sandprawns has been shown to play an important role in structuring benthic communities in marine littoral ecosystems worldwide (see review by Pillay and

Branch 2011), with negative impacts observed on meiofauna in some cases (Branch and Pringle 1987, Alongi 1986). However, it must be emphasised that the negative correlations between sandprawn abundance and meiofaunal community metrics and morphotypes were site-specific, suggesting that sandprawn bioturbation impacts were not general, but contingent on specific localized conditions.

In chapter 4, I tested the hypothesis that macrofaunal diversity metrics would be lower in winter (non-upwelling) but higher in summer in response to upwelling. In this chapter, I also hypothesized that community metrics would be negatively associated with increasing *C. kraussi* densities due to sediment reworking during winter (non-upwelling season), but that this trend would weaken or reversed during upwelling in summer as a result of enhanced trophic resources counteracting sediment turnover effects. Although, the whole community structure of macrofauna was strongly affected by the main and interactive effects of seasons and sites, the hypotheses posed were not overwhelmingly supported by these findings.

There were limited responses of macrofaunal community metrics to sites and seasons (**Table 4.2A**), which may indicate that the macrobenthic assemblages of Langabaan Lagoon are not substantially regulated by spatio-temporal variability. However, at the species level, seasons and sites emerged to be important for certain species (e.g. amphipod *Ampelisca palmata* and crown crab *Hymenosoma orbiculare,* sandprawn *C. kraussi,* **Fig. 4.2A** - **4.2I**). Sandprawn effects on macrofaunal species within seasons were clear, but only for certain species, with their abundances generally being positively correlated with sandprawn abundances (**Table 4.7**, **Table 4.8**). Interestingly, combined winter and summer data examined per year showed that some of these species/taxa (e.g. amphipods *A. palmata*, *Griffithsia latipes* and juvenile polychaetes) were negatively correlated with sandprawn abundances, but this trend was site-specific (**Table 4.9)**. Another interesting outcome of this study was that dominant species (i.e. amphipods *A. palmata*, *G. latipes* and *U. grimaldii*, polychaete *N. latericeus*, copepods and juvenile polychaetes, **Fig. 4.2C**-**G**) were generally enhanced in winter seasons relative to summer. The abundance of *C. kraussi* (**Fig. 4.2A**) was generally greater in summer throughout the duration of the study, which could explain temporal patterns observed for dominant taxa.

Sandprawn effects on macrofaunal functional groups within seasons were minimal, site-specific and mostly positive. However, when summer and winter data were integrated and explored per year, impacts were much stronger, generally negatively influencing surface deposit feeders, surface deposit feeders and predators, and suspension feeders in Oesterwal North in 2015 (**Fig 4.3B, 4.3D** and **4.3E)**. On the other hand, in Oesterwal South most functional groups were positively influenced by sandprawn abundances in 2016, except for suspension feeders, which were negatively related to sandprawn abundances. In general, findings for suspension feeders were consistent with those elsewhere in the literature that show their susceptibility to sandprawn bioturbation, with sediment resuspension likely to obstruct their filter feeding (Rhoads and Young 1970, Pillay *et al.* 2007a, Pillay and Brand 2011).

Although the outcomes of chapters 3 and 4 did not generally overwhelmingly support the hypotheses put forward, they did broaden understanding of the functioning of sandprawn dominated sediments in the context of seasonal upwelling. Both macro- and meiofaunal communities responded similarly to seasons and sandprawn abundances in this study, but with responses generally being site-specific. An important difference in responses of these benthic communities was that, at species or morphotype level, meiofauna were strongly affected by sandprawn abundances in a negative manner, while for macrofauna, responses to sandprawn abundances were both positive and negative. This difference is likely due to their distinctive biological traits.

Given the findings of the observational components (chapters 3 and 4), I conclude that in Langebaan Lagoon sandflats, benthic community patterns are to a large extent regulated by the strength of sandprawn bioturbation and that bottom-up processes associated with upwelling are weak. This result was unexpected, but ecologically important, given the position of Langebaan Lagoon within the Benguela current, which is regarded as one of the most world's productive upwelling system (Carr 2002, Puccinelli *et al.* 2016). Upwelling systems are well recognized world-wide for their influence on benthic fauna in marine shallow water coastal ecosystem, generally by enhancing levels of trophic resources (Levin *et al.* 2009, Quintana *et al.* 2014).

7.3 Field factorial experiment

The experimental approach on which chapters 5 and 6 of this PhD thesis was based allowed for the main and interactive effects of sites, nutrient enrichment and sandprawn densities to be tested on macro- and meiofaunal communities. The first general hypothesis tested in this study was based on the grazer-reversal hypothesis, which is a well-known model proposed by Proulx and Mazumder (1998), which argues that the response of diversity to disturbance would vary with productivity (see chapter 5), with a reversal of patterns likely at the ends of a productivity spectrum. I therefore hypothesized that diversity metrics for macro- and meiofauna should display the following responses with increasing sandprawn densities: a linear-decreasing pattern at ambient nutrient levels, a unimodal hump-shaped pattern at intermediate nutrient levels, and lastly a linear increase at the highest nutrient level (2N). The second hypothesis examined in this study was that in the presence of sandprawns, meiofaunal diversity metrics should be reduced at the sediment surface and increased within the burrow-walls, due to turned over sediment by sandprawns increasing surface instability and burrows being enriched in trophic resources (e.g. chl-*a*).

One of the most surprising outcomes of the experiment was the unresponsiveness of microalgal biomass (chl-*a*) to treatments (**Table 5.1**), with values being similar between nutrients and sandprawn levels (**Fig 5.2**). This was an unexpected finding given that microalgal biomass is generally known to be enhanced by nutrients in shallow water coastal habitats (Downing *et al.* 1999, Rosemond *et al.* 2000, Thornton *et al.* 2002). The lack of sandprawn effects on chl-*a* concentrations was another surprising outcome of this investigation, given that these results differed from a number of studies that have reported sandprawns to negatively influence microalgal biomass in marine soft-sediment ecosystems (Rowden and Jones 1993, Wynberg and Branch, 1994, Pillay *et al.* 2007a, 2007b, 2012). That being said, other studies have also failed to detected effects of sandprawns on microalgal biomass (Branch and Pringle 1987, Henninger and Froneman 2013).

The overall community structure of meiofauna within burrow-walls (presented in chapter 5) was significantly affected by the interaction between nutrient enrichment and sites, while within the reference position (non burrowed areas), community structure was significantly affected by the interaction between nutrients, sites and sandprawn densities (**Table 5.3**). At the sediment surface, meiofaunal community structure was governed by the main effects of sites and sandprawn densities. The hypothesis that the interaction between nutrients and sandprawns would result in diversity metrics responding in the manner predicted by the grazer-reversal models was not overwhelmingly supported by findings of this chapter. However, results were nevertheless ecologically interesting, and shed light on the interplay between sandprawn ecosystem engineering and nutrient levels in regulating the meiobenthos. Nevertheless, both decreasing and increasing patterns predicted by the grazer-reversal model at low and high nutrient levels were detected for some community metrics. For example, burrow-wall species richness (**Fig 5.4A**) and surface evenness (**Fg.5.4C**) reductions occurred at the ambient nutrient treatments in Oesterwal North and South, while burrow-wall evenness (**Fig.5.3C**) and Shannon-Wiener diversity (**Fig. 5.3D**) in Bottelary South conformed to the increasing pattern predicted by the grazer-reversal hypothesis at highest level of productivity.

Individual morphotypes of meiofauna displayed diverse responses to nutrients and sandprawn densities but with a negative trend generally being prevalent (**Fig.5.5A**-**D**), with trends deviating from the postulations of Proulx and Mazumder (1998). Broadly, these results agreed with other studies that have reported sandprawn densities to negatively affect meiofaunal abundances (Branch and Pringle 1987, Kinoshita *et al.* 2003, Pillay and Brach 2011). It is worth noting that, sandprawn effects on meiofauna in this study were generally strongest at densities of 120 ind.m^2.

Despite detected effects of *C. kraussi* on meiofaunal diversity metrics and morphotypes, there was no clear evidence of meiofauna being enhanced within burrow -walls relative to sediment surfaces. This repudiates the hypothesis posed in this study that meiofaunal abundances should be greater in burrow-wall environments compared to sediment surface.

The results presented in chapter 6 indicate that macrofaunal community structure was significantly affected by the interaction between nutrient treatments and sandprawn densities, but also by sites (**Table 6.1**). However, this interaction did not appear to affect macrofaunal community metrics. As a result, the hypothesis that the interaction between nutrients and sandprawn densities should result in community metrics conforming to the grazer-reversal models of Proulx and Mazumder (1998) was repudiated. With the exception of abundance, which was affected by sites and sandprawn densities (60 ind.m^{-2}), macrofaunal community metrics were unresponsive to treatments (**Table 6.2A**). The insensitivity of most diversity metrics in this study could possibly be ascribed to the lack of response of microalgal biomass to experimental treatments.

Although varied trends of increasing, decreasing and unimodal hump-shaped responses were detected for macrofaunal taxa and functional groups, they did not convincingly conform to the grazer-reversal models of Proulx and Mazumder (1998) predicted in this study. These findings agree with several studies that have previously examined interactions between disturbance and productivity on communities and report little or no support for the grazer-reversal models (Wilson and Tilman 2002, Hillebrand 2003, Svensson *et al*. 2007, Sugden *et al.* 2008). While other studies suggest that inconsistent application of diversity metrics is likely to cause discrepancies between findings, lack of consensus could also be ascribed to nutrient enrichment having little influence on metrics.

Interestingly, the hypothesis that the abundance of suspension feeder should increase in nutrient addition treatments against increasing sandprawn densities was upheld by these results, but this was site-specific (**Fig.6.5B**). Burrowing deposit feeder abundance however, was not enhanced in response to increasing sandprawn densities as hypothesized. The former outcome is likely an indication of potential effects of productivity in reversing sandprawn ecosystem engineering impacts for suspension feeders. Overall, I conclude that ecosystem engineering by sandprawns modifies benthic community composition in Langebaan Lagoon and that productivity plays a role mainly by interacting with sandprawns. However, this interaction does not influence community patterns in a manner predicted by the grazer-reversal models of Proulx and Mazumder (1998). This therefore suggest that benthic communities of Langebaan Lagoon are structured mainly by sandprawn ecosystem engineering and secondarily by interactions between ecosystem engineering and productivity.

Overall, findings of this study provide important information that enhances understanding of ecosystem engineering and nutrients in mediating biotic responses in marine soft-sediment ecosystems. The main findings of this study are conceptualised in Fig 7.1, which is smiliar to heuristic models proposed by Berkensbuch and Rowdwen (2003, 2007), based on ghostshrimp and seagrass interactions. It was expected in my study that the interaction between sandprawn densities and nutrient enrichment would interact to influence macro-and meiofaunal communities. However, this was not the case in many cases, with results additionally indicating a weak nutrient effect and a stronger sandprawn effect overall. Based on this, it is probable that in sandprawn dominated habitats, engineering by sandprawns outweighs nutrient effects (**Fig 7.1**). In non-engineered states, sediments are likely to be characteristed predominantly by relatively undisturbed benthic habitats. However, a shift to a sandprawn-dominated state, results in extensive habitat modification, principally by sediment turnover and burrow construction. In this state, sandprawn engineering is a dominant structuring force and nutrient availability is potentially weaker as a driver of biotic assemblages.

7.4 Perspective on future research

While this study has generated new knowledge on ecological processes occurring in sandprawn-dominated ecosystems, limitations in this study have to be acknowledged, as they provide considerations relevant to future research. A particularly important issue that needs addressing is why nutrients had limited effects in this study. This may relate to sediment characteristics, which influence porosity and nutrient-retention (Christensen *et al.* 1984, Lohse *et al.* 1996, Huettel *et al.* 1998, Adaba 2013). Future research thus needs to understand the role of sediment particle size in influencing nutrient retention and biotic responses. It needs to be undertood that findings of this study may differ under conditions in which sediments are finer, with a greater nutrient retention capacity (Pillay 2019). Of course, where possible, attention needs to be paid to ensuring that sample sizes are adequate to detect responses. In my study, there were cases were data were highly variable, suggesting a need for a larger sample size. Thus, expansion of future studies to increase spatial and temporal replication is imperative, which apart from allowing for robust tests of hypotheses, also improves ability to generalise findings and extrapolate to a wider set of ecological conditions.

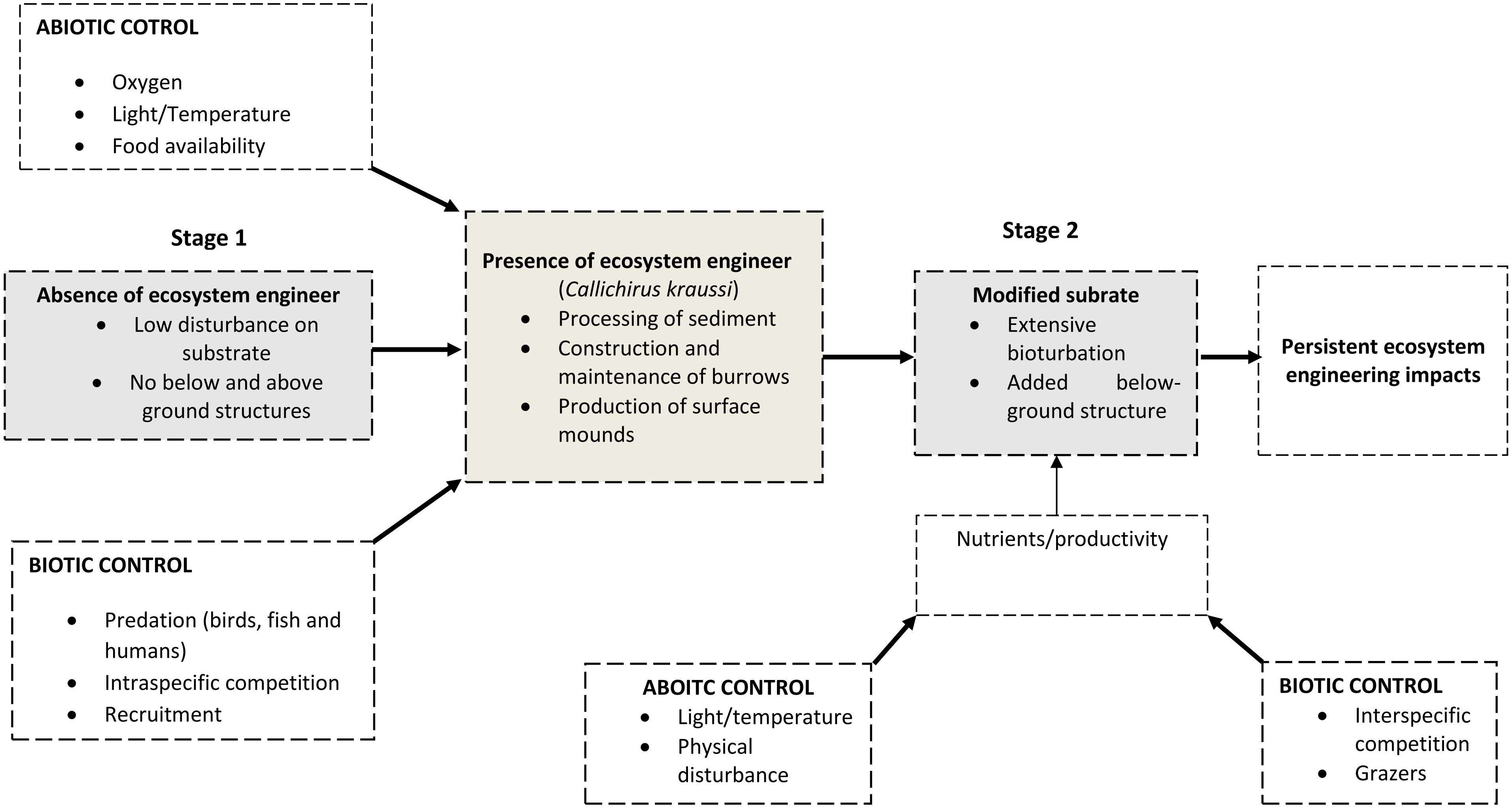

Fig.7.1: Conceptual model illustrating the relative strength of ecosystem engineering by the burrowing sandprawn (*Callichirus kraussi*) and nutrients in intertidal sandflats of Langebaan Lagoon. NB: error thickness denotes the perceived strength of engineering and nutrients based on study findings. Stages 1 and 2 show non-engineered and engineered states respectively and expected effects on sediments characteristics. In Stage 2, engineering strength outweighs the effects of nutrients in structuring benthic communities. Abiotic and biotic processes influence engineer populations and productivity levels.

CHAPTER 8

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CHAPTER 9

APPENDIX

9.1 Pore-water nutrients

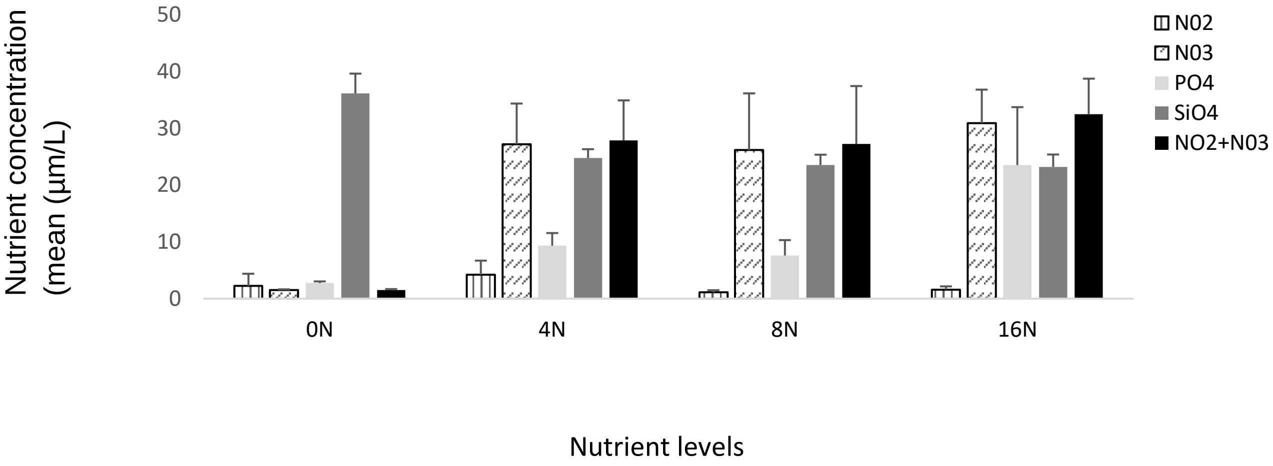


Fig 9.1: Variation in sediment pore-water nutrients from the experimental trial determining nutrient levels that were used for the *in situ* field experiment.

9.2 Generalised linear models used in this thesis

GLM models are defined as:

$$g(E[y]) = \beta_0 + \sum_k \beta_k X_k \qquad (equ.2.1)$$

where g (.) represents link function = equivalent to an assumed relationship between the predator variable and response variable, *E[y]* is the expected value of the response variable *y* and $\beta_0 + \sum_k \beta_k X_k$ represent the linier predictor, in which the $\beta0$ is grouped with the sum of predictor variables (X_k) and the regression coefficients (β_k). In the case of the adopted generalised linear model approach for the experimental study, both Gaussian and negative binomial distributions were applied. The Gaussian distribution was used with an identity link where data were in the form of normal distribution, whereas the negative binomial was applied with a log-link function for non-normal distribution data, which was in the form of proportions and presence/absence.

Gaussian distribution can be defined as:

$Yi \sim N (\mu_i, \sigma^2)$ *(equ.2.2)*

$E(Yi) = \mu_i$ and $var\ (Yi\dot{n}) = \sigma^2$, where *Yi* is a response variable assumed to be normally distributed with a mean μ_i and variance σ^2 (Zuur *et al.* 2009).

The equation for the binomial distribution can be simplified as:

$Y_i \sim B(\pi_i, n_i)$ (equ.2.3)

$E(Y_i) = \pi_i \times n_i$ and $var(Y_i) = \pi_i \times n_i \times (1 - \pi_i)$ (equ.2.4)

, where the response variable $E(Y_i)$ is expected to be binomially distributed with the probability of π_i and n_i as independent trials. In case of the proportional data, n_i equals the total number of trials while for the presence/ absence data n_i equals 1.

Table.9.1: List of macofaunal functiomal groups

Species name	Common name	Functional group
Urothoe grimaldii	Burrowing amphipod	Deposit feeders-burrowers
Griffithsia latipes	Spade foot ampipod	Deposit feeders-burrowers
Paratylodiplax edwardsii	Sandflat crab	Deposit feeders-burrowers
Notomastus latericeus	Club worm	Deposit feeders-burrowers
Orbinia angrapequensis	Woolly worm	Deposit feeders-burrowers
Betaeus jucundus	Commensal Shrimp	Deposit feeders-burrowers
Spiroplax spiralis	three legged crab	Deposit feeders-burrowers
Ceratonereis erythraeensis	estuarine nereid worm	Deposit feeders-burrowers
Perinereis nuntia vallata		Deposit feeders-burrowers
Heterocum africanum	Sandbankcumacean	Deposit feeders-burrowers
Upogebia Africana	Estuarine mud prawn	Deposit feeders-burrowers
Arabella iricolor		Deposit feeders-burrowers
C. Kraussi		Deposit feeders-burrowers
Ostracods	Seed shrimp	Deposit feeders-surface
Euclymene spp	Bamboo worm	Deposit feeders-surface
Sipunculindea	peanut worm	Deposit feeders-surface
Tellimya trigona		Deposit feeders-surface
A.gracilis	Slender tenaid	Deposit feeders-surface
Gastrosaccus psarumodytes	surf mysid	Deposit feeders-surface
Marphysa elitueni	Estuarinewonder-worm	Predators and scaverngers-burrowers

Glycera tridactyla	Glycerine worm	Predators and scaverngers-burrowers
Nephtys spp	Nephty's sand worm	Predators and scaverngers-burrowers
Predator and scavenger- surface		Predator and scavenger- surface
Cirolana hirtipes	Hairy-legged cirolanid	Predator and scavenger- surface
Hymenosoma orbiculare	Crown crab	Predator and scavenger- surface
Excirolana natalensis	Natal beach louse	Predator and scavenger- surface
Nassarius Kraussianus	Tick shell	Predator and scavenger- surface
Volvarina capensis	Cape marginella	Predator and scavenger- surface
Eurydice barnardi		Predator and scavenger- surface
Ampelisca palmata	four-eyed amphipod	Suspension feerds-surface
Carditella rugosa	Rough false cockle	Suspension feerds-surface
Tellimya trigona	dwarf triangular clam	Suspension feerds-surface
Thelepus spp	Tangle worm	Suspension feerds-surface
Nebalia capensis	Cape leaf shrimp	Suspension feerds-surface
Euphausia Lucens		Suspension feerds-surface
Kellia rotunda		Suspension feerds-surface
Copepods		Suspension feerds-surface
Protomella capensis		Suspension feerds-surface
Assiminea globulus		Grazers
Idotea balthica (grazer)		Grazers
Exosphaeroma truncatitelson		Grazers
Protomella capensis	Waxy screw shell	*filter feeder- burrowers*

9.3 Scatterplots

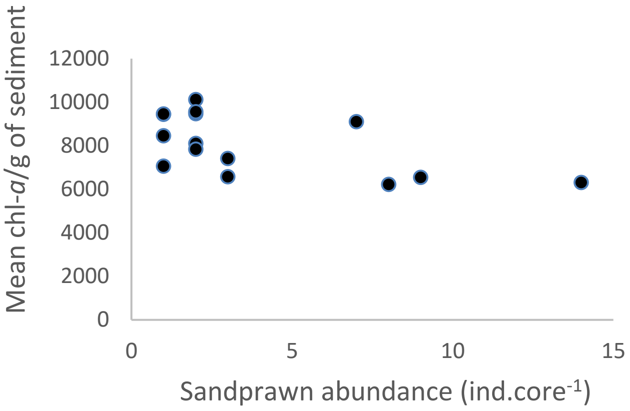
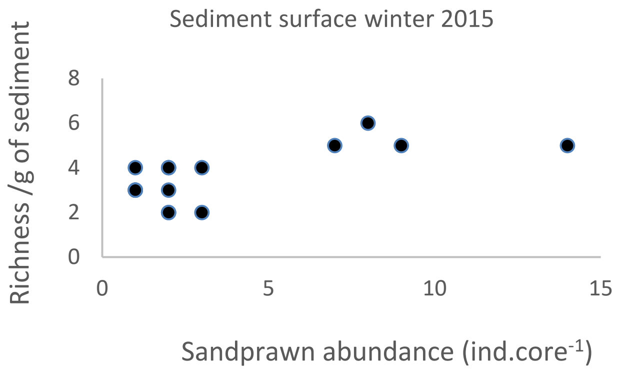


Fig 9.2: The relationship between burrow-wall chl-*a* concentrations and sandprawn abundances in Oestewal South based data per season (winter 2015).

Fig 9.3: Relationships between chlorophyll-*a* concentrations and sandprawn abundances in Oesterwal North (ON) and South (OS) based on combined summer and winter data per year (2015 and 2016). NB: Y axis scales are different to show the trend in the data.



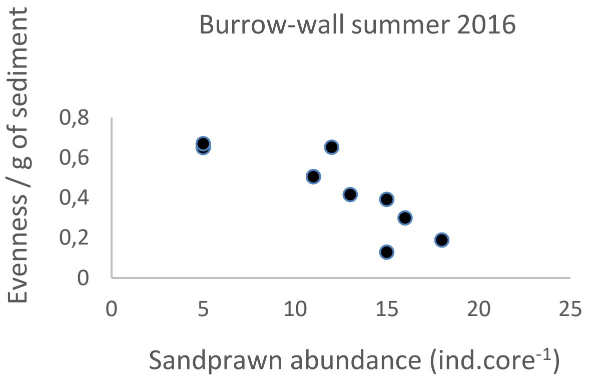


Fig 9.4: Relationships between meiofaunal community metrics and sandprawn abundances in Oesterwal South (OS) based on data per season.

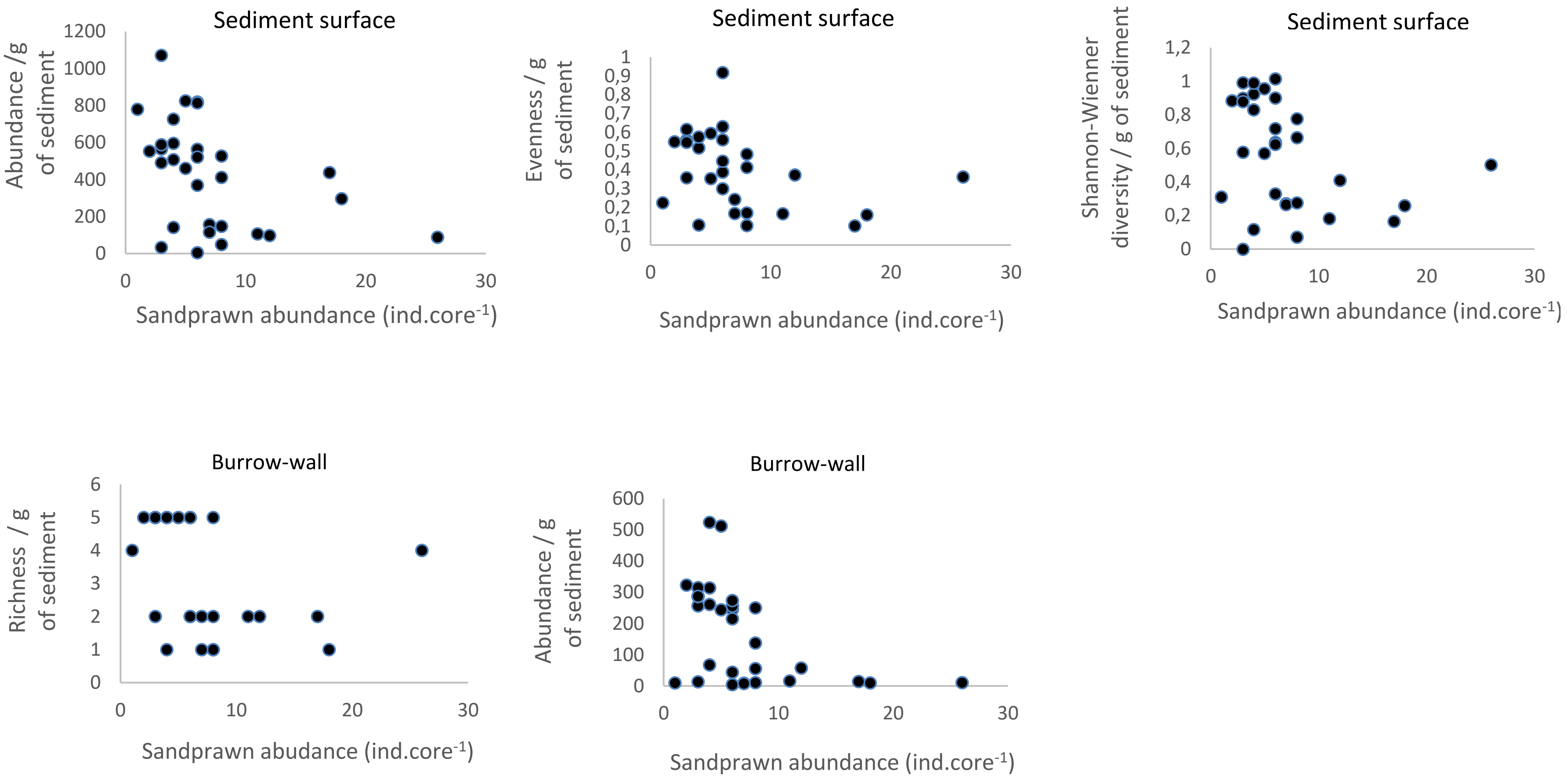


Fig 9.5 A: Relationships between meiofaunal community metrics and sandprawn abundances in Oesterwal North (ON) based on combined summer and winter data per year (2016).

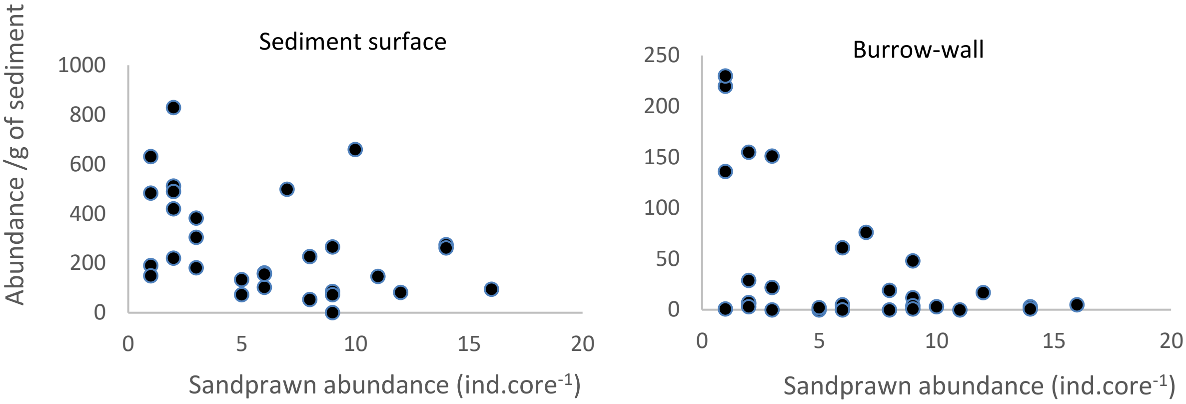


Fig 9.5B: Relationships between meiofaunal community metric (abundance) and sandprawn abundances in Oesterwal South (OS) based on combined summer and winter data per year (2015). NB: Y axis scales are different to show the trend in the data.

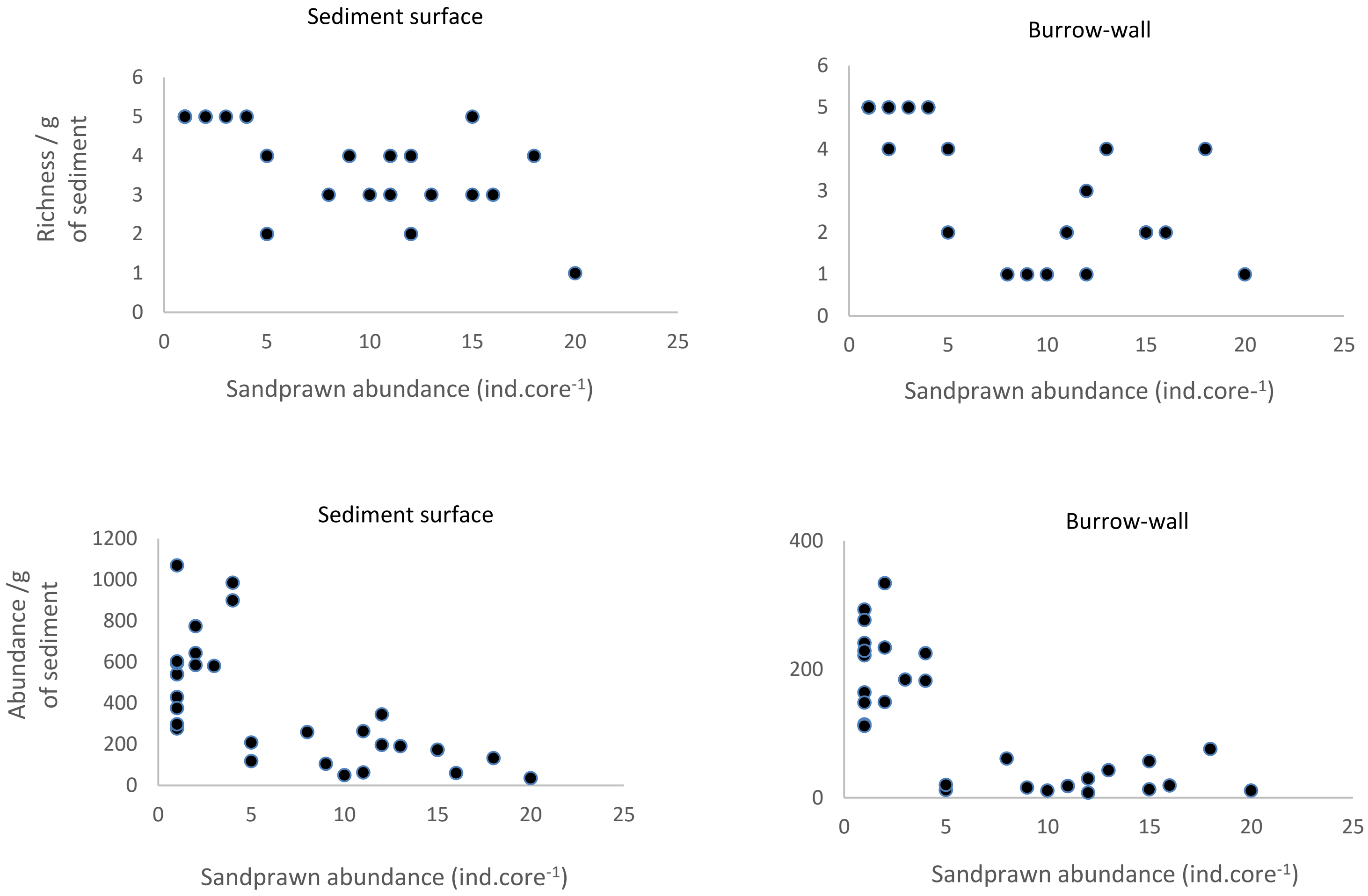


Fig 9.5C: Relationships between meiofaunal community metrics and sandprawn abundances in Oesterwal South (OS) based on combined summer and winter data per year (2016).

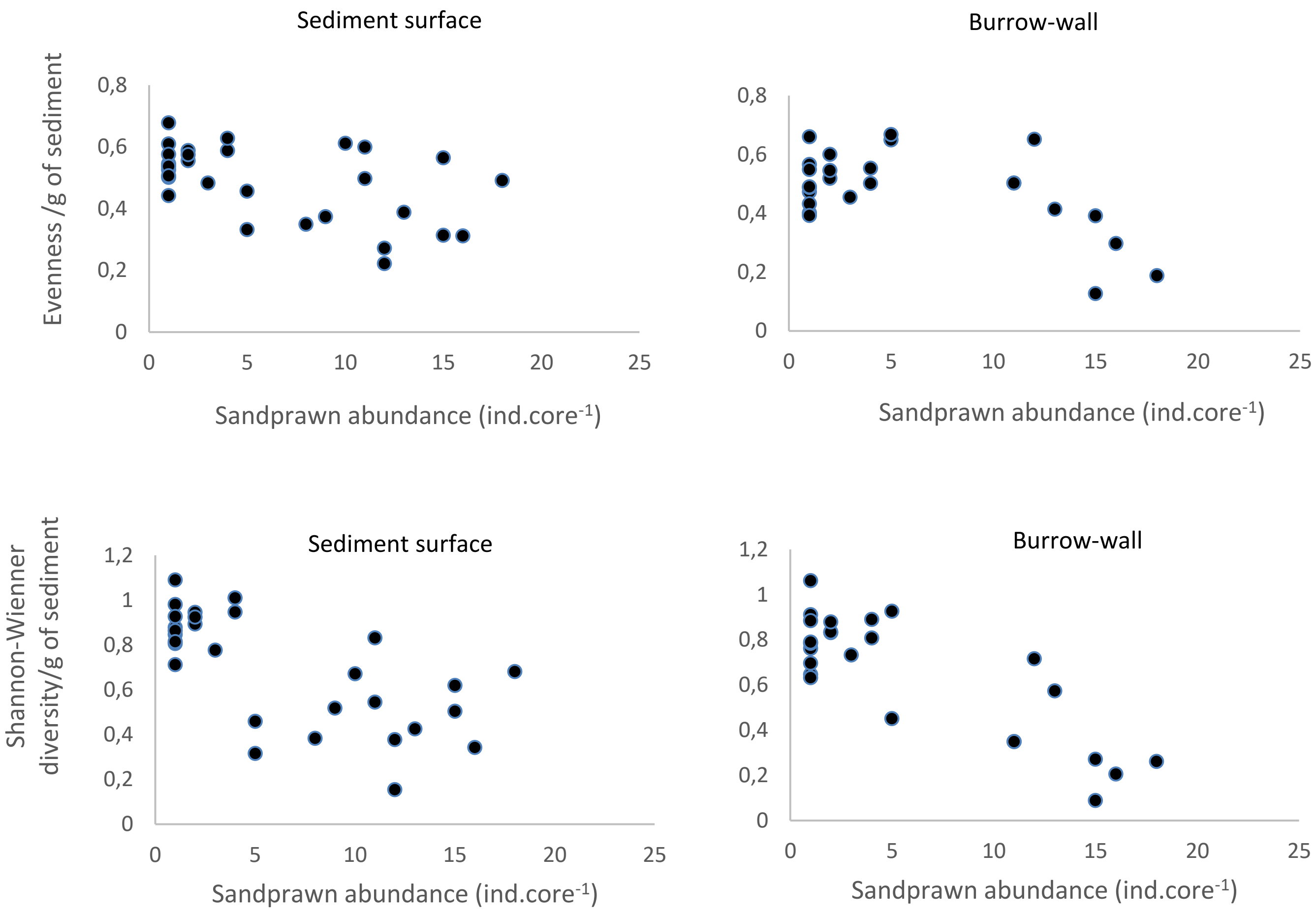


Fig 9.5D: Relationships between meiofaunal community metrics and sandprawn abundances in Oesterwal South (OS) based on combined summer and winter data per year (2016).

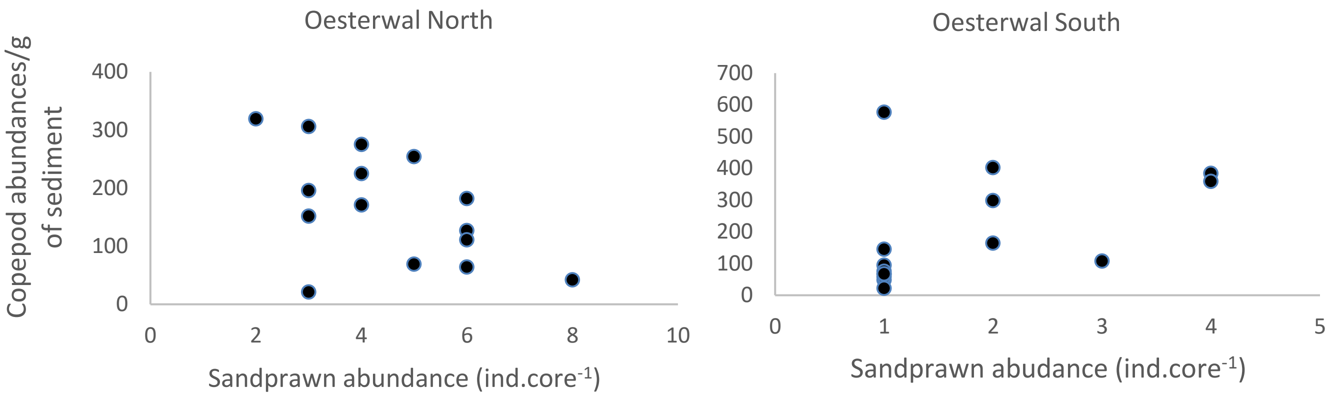


Fig 9.6: Relationships between sediment surface copepod abundances and sandprawn abundances in Oesterwal North (ON) and Oesterwal South based on data per season (winter 2016).

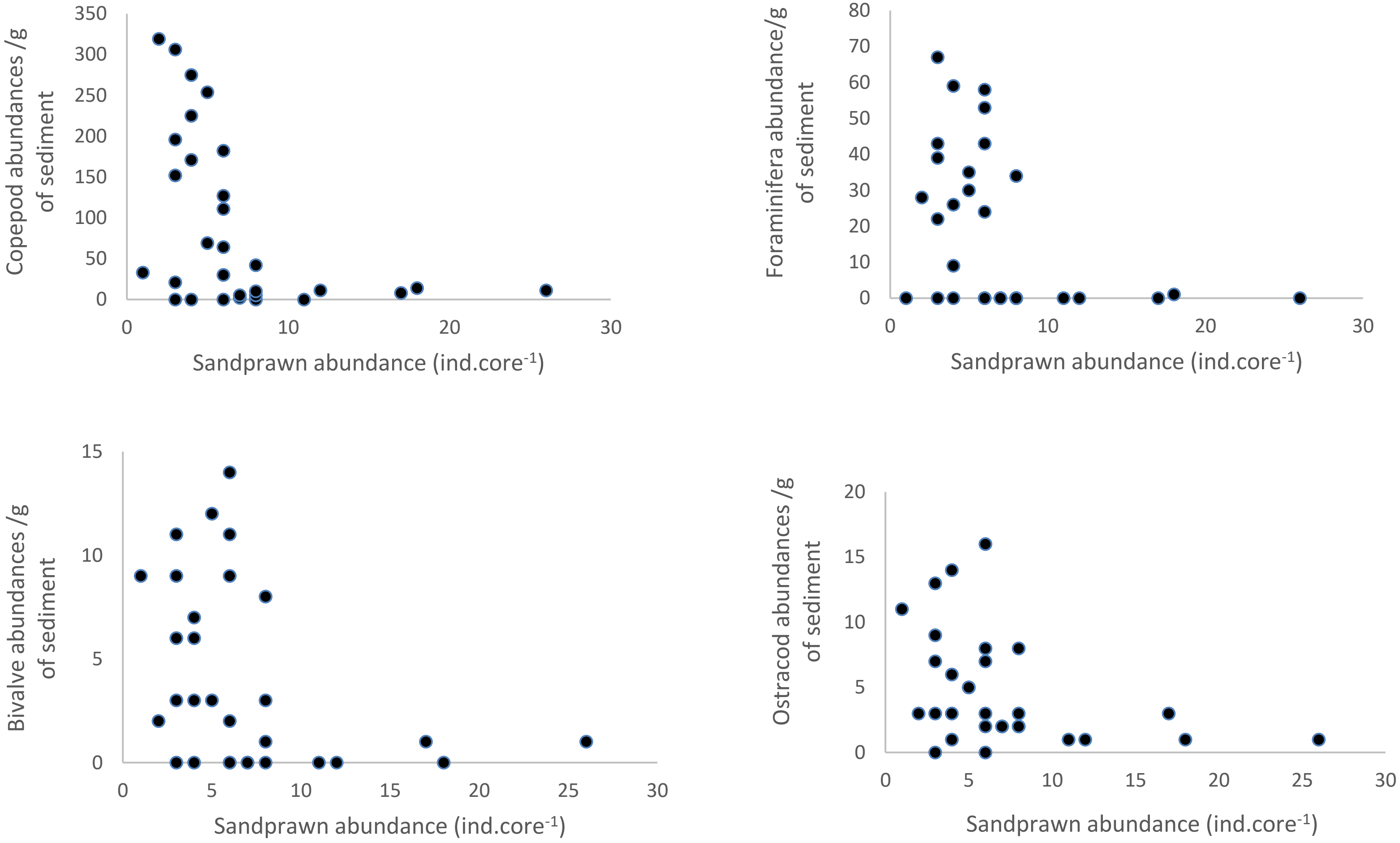


Fig 9.7A: Relationships between sediment surface meiofaunal morphotypes and sandprawn abundances in Oesterwal North (ON) based on combined summer and winter data per year (2016). NB: Y axis scales are different to show the trend in the data.

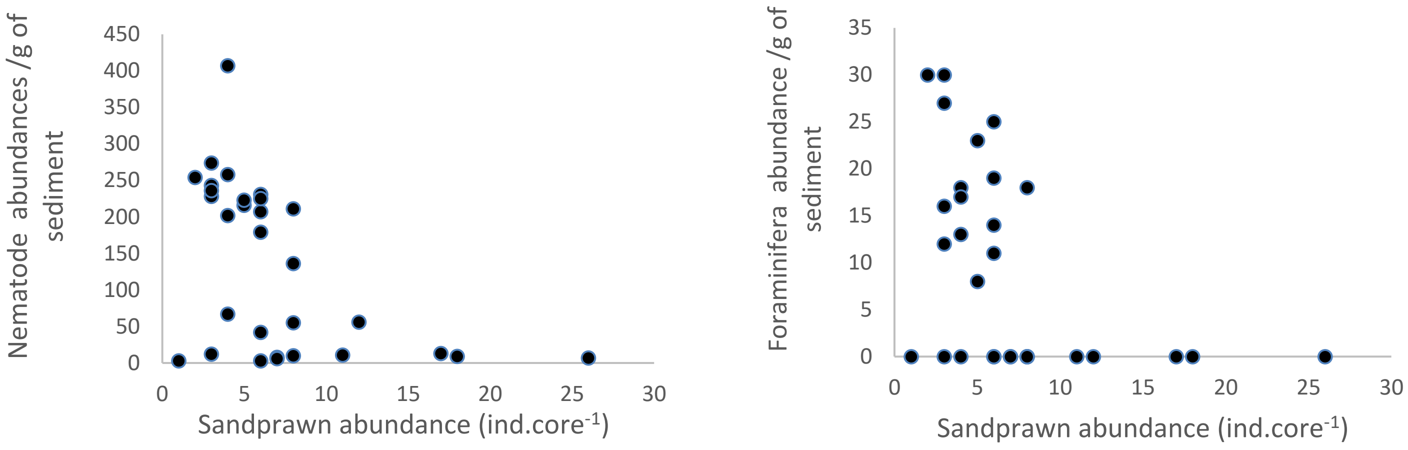


Fig 9.7B: Relationships between burrow-wall meiofaunal morphotypes and sandprawn abundances in Oesterwal North (ON) based on combined summer and winter data per year (2016). NB: Y axis scales are different to show the trend in the data.

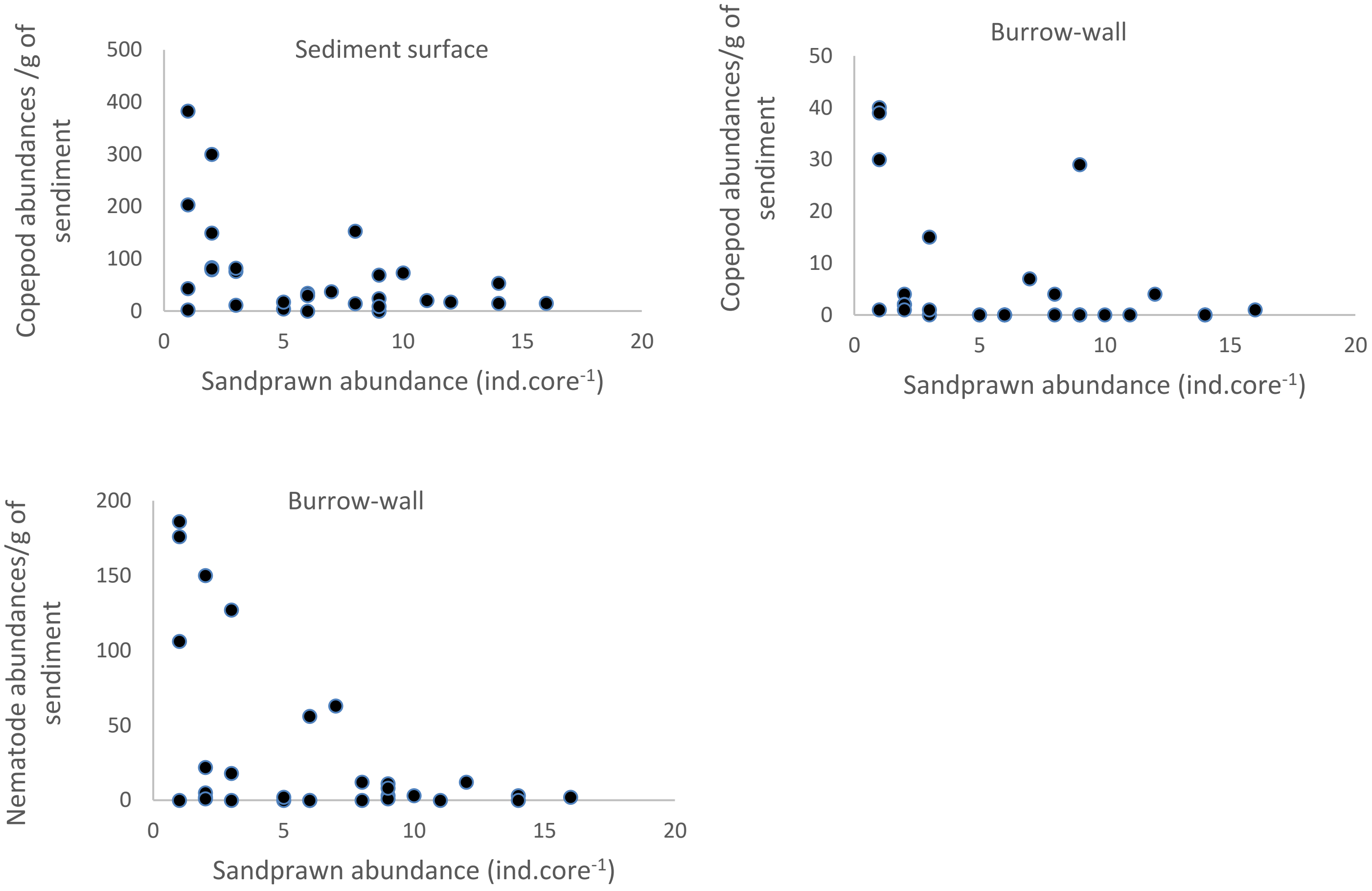


Fig 9.7C: Relationships between meiofaunal morphotypes and sandprawn abundances in Oesterwal South (OS) based on combined summer and winter data per year (2015). NB: Y axis scales are different to show the trend in the data.

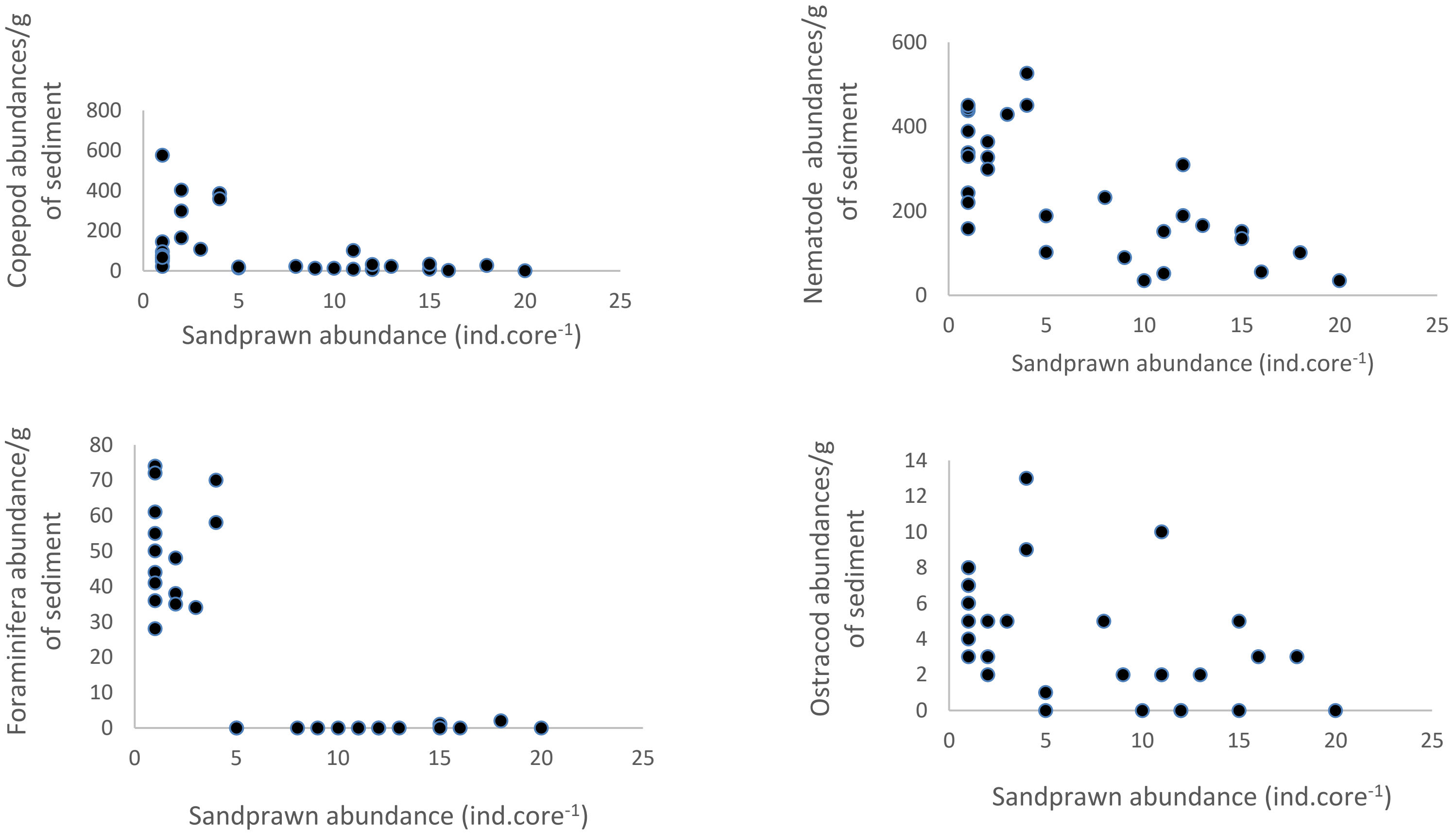


Fig 9.7D: Relationships between sediment surface meiofaunal morphotypes and sandprawn abundances in Oesterwal South (OS) based on combined summer and winter data per year (2016). NB: Y axis scales are different to show the trend in the data.

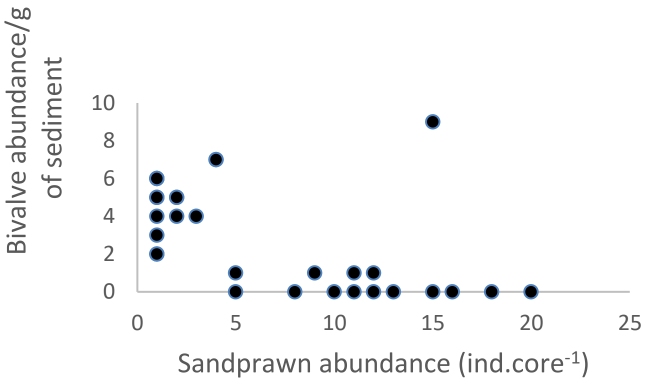


Fig 9.7E: The relationship between sediment surface meiofaunal morphotype (bivalves) and sandprawn abundances in Oesterwal South (OS) based on combined summer and winter data per year (2016).

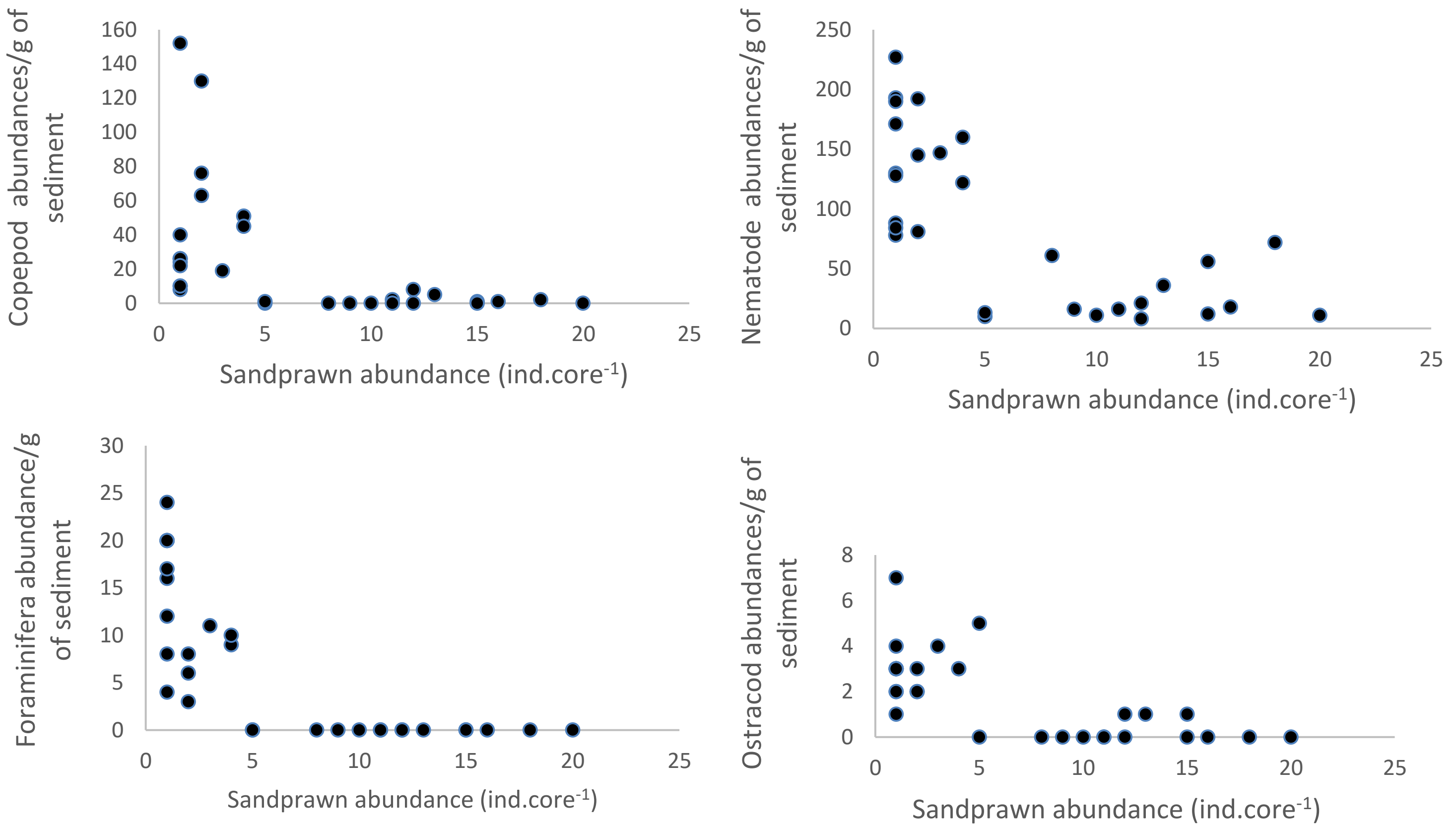


Fig 9.7F: Relationships between burrow-wall meiofaunal morphotypes and sandprawn abundances in Oesterwal South (OS) based on combined summer and winter data per year (2016). NB: Y axis scales are different to show the trend in the data.

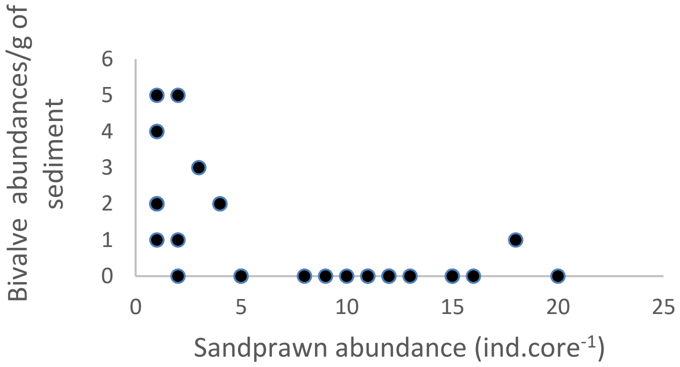
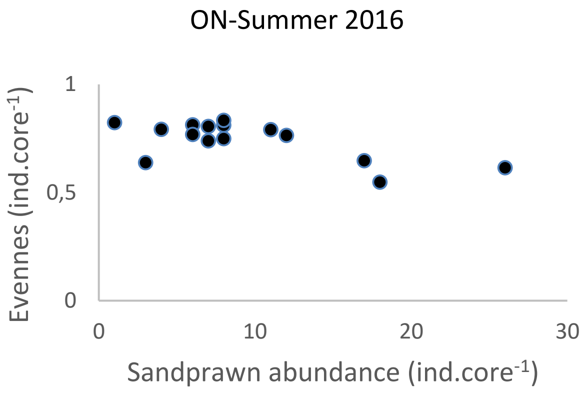


Fig 9.7G: The relationship between burrow-wall meiofaunal morphotype (bivalves) and sandprawn abundances in Oesterwal South (OS) based on combined summer and winter data per year (2016).



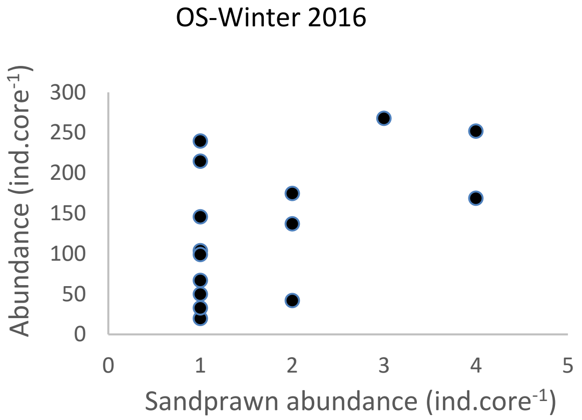


Fig 9.8: Relationships between macrofaunal community metrics and sandprawn abundances in Oesterwal North (ON) and Oesterwal South (OS) based on data per season.

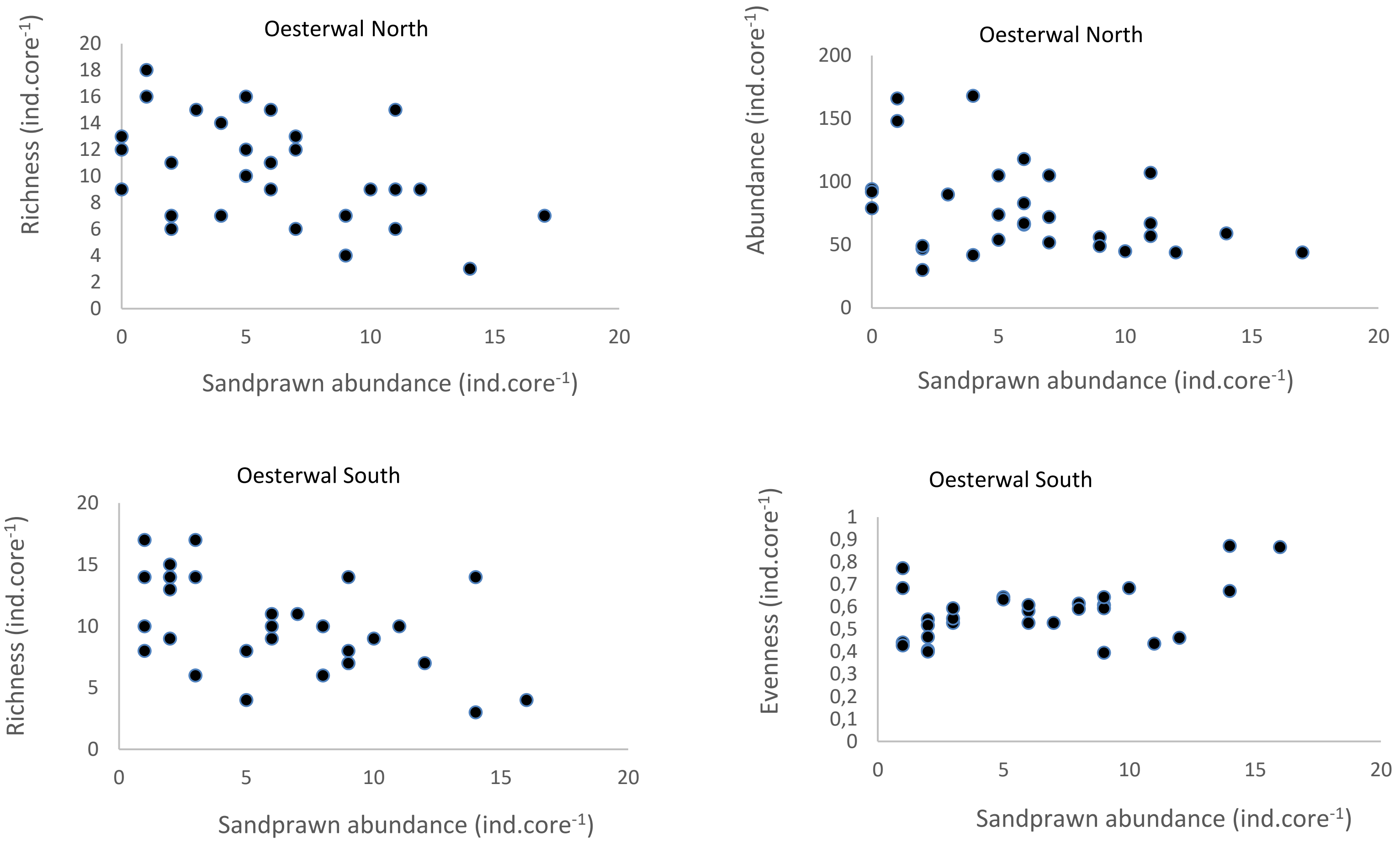


Fig 9.9: Relationships between macrofaunal community metrics and sandprawn abundances in Oesterwal North (ON) and South (OS) based on combined summer and winter data per year (2015).

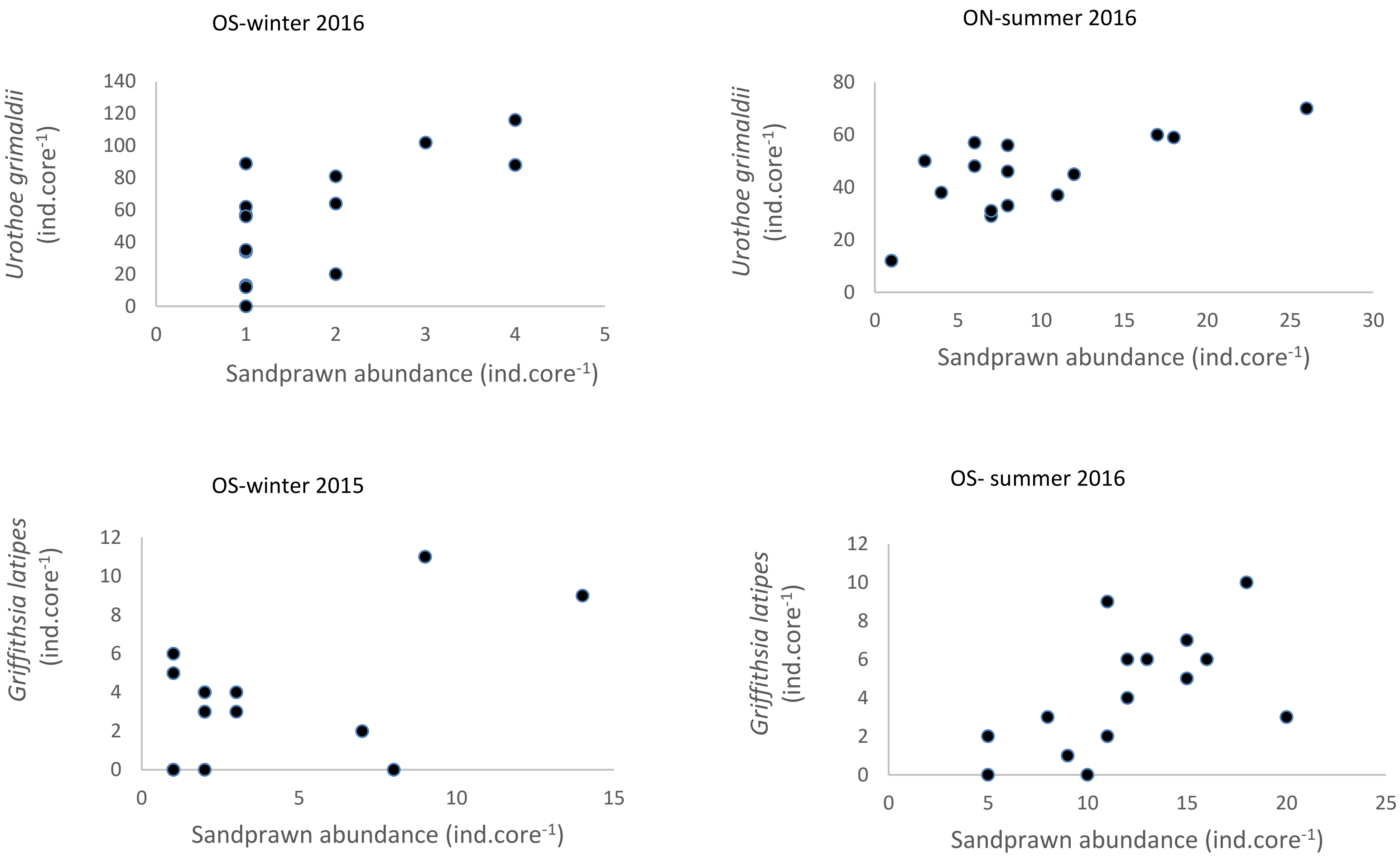


Fig 9.10A: Relationships between macrofaunal species abundances and sandprawn abundances in Oesterwal North (ON) and South (OS) based on data per season. NB: Y axis scales are different to show the trend in the data.

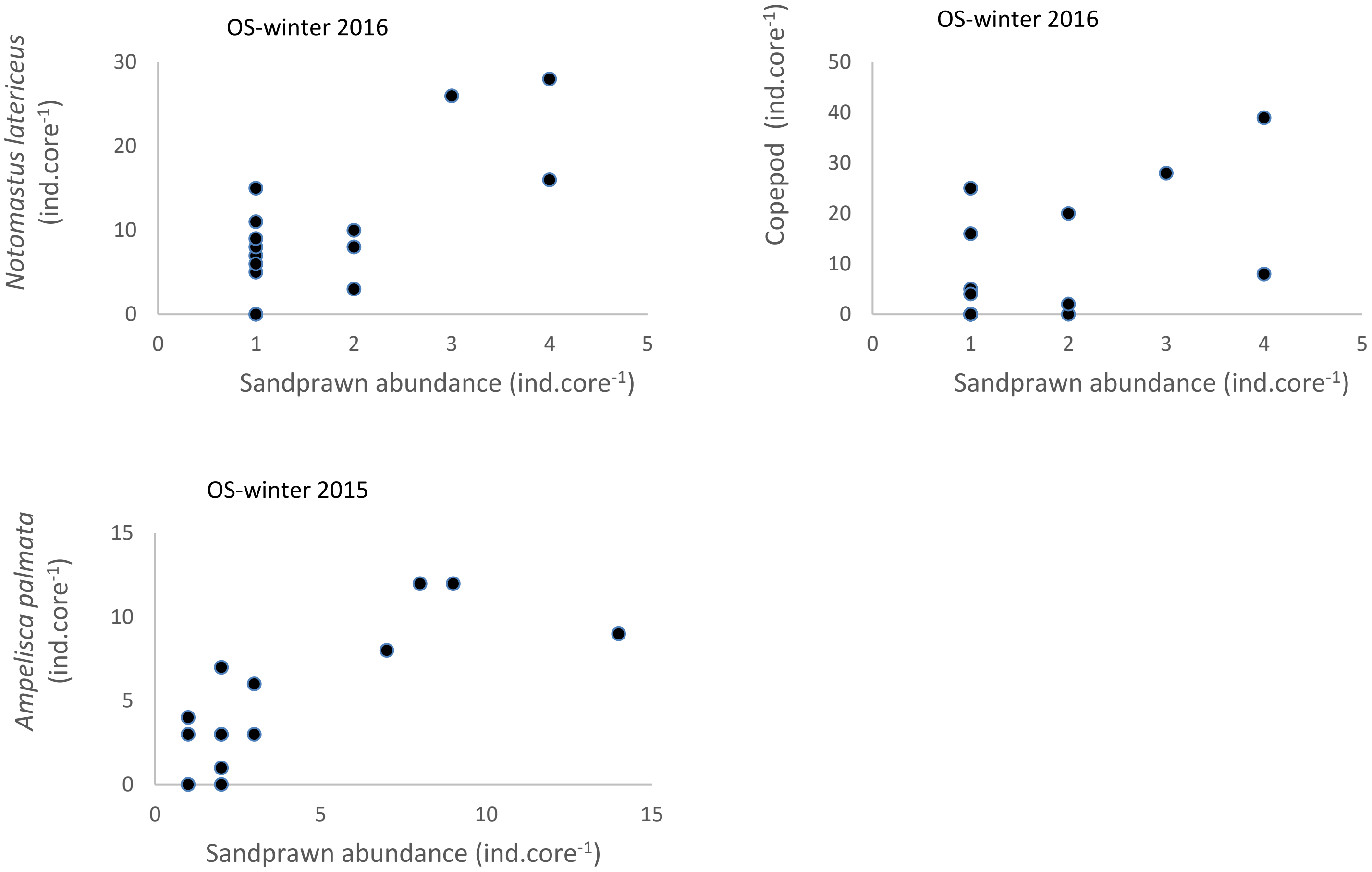


Fig 9.10B: Relationships between macrofaunal species abundances and sandprawn abundances in Oesterwal South (OS) based on data per season. NB: Y axis scales are different to show the trend in the data.

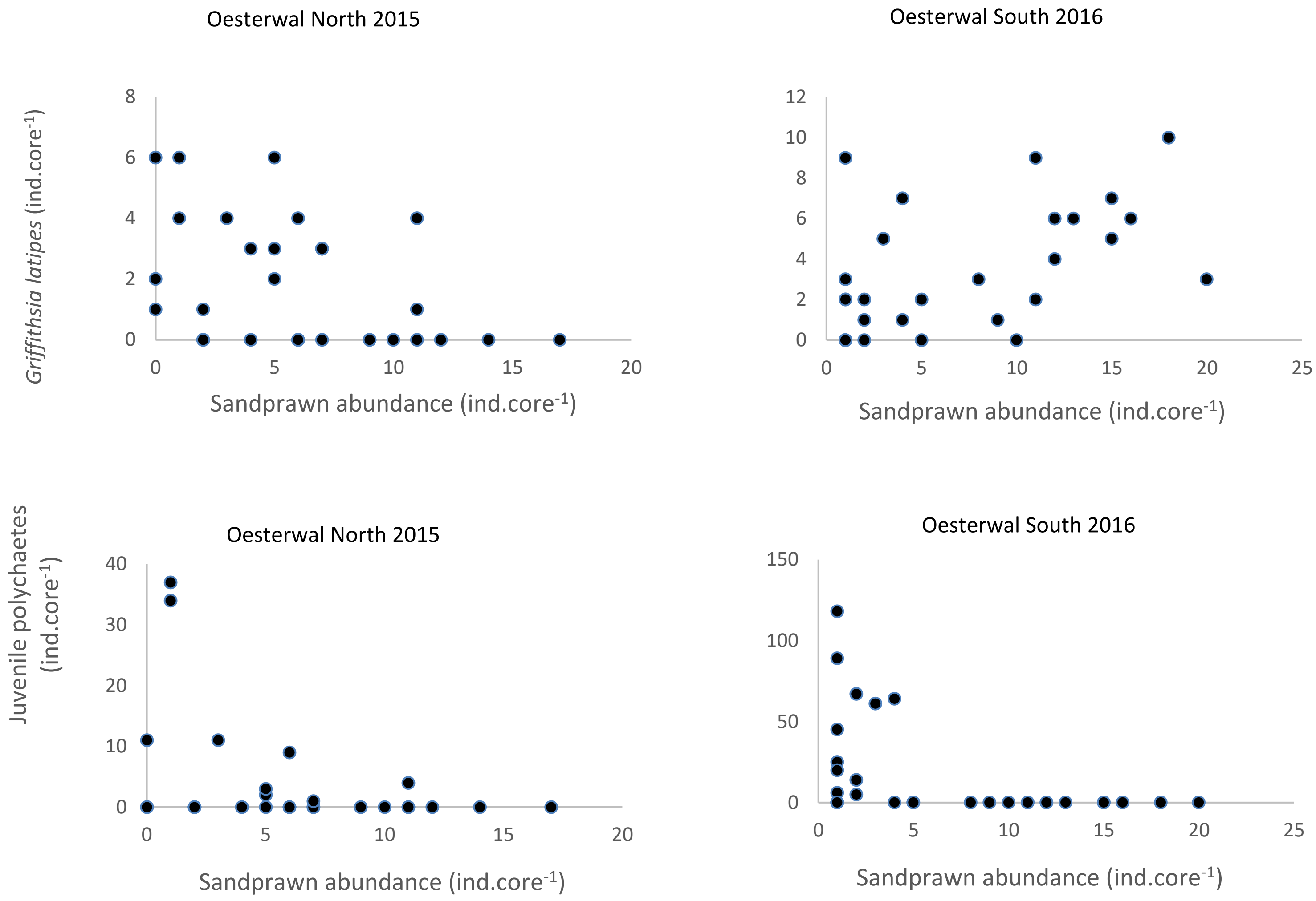


Fig 9.11A: Relationships between macrofaunal species/morphotype abundances and sandprawn abundances in Oesterwal North (ON) and Oesterwal South (OS) based on combined summer and winter data per year (2015 and 2016). NB: Y axis scales are different to show the trend in the data.

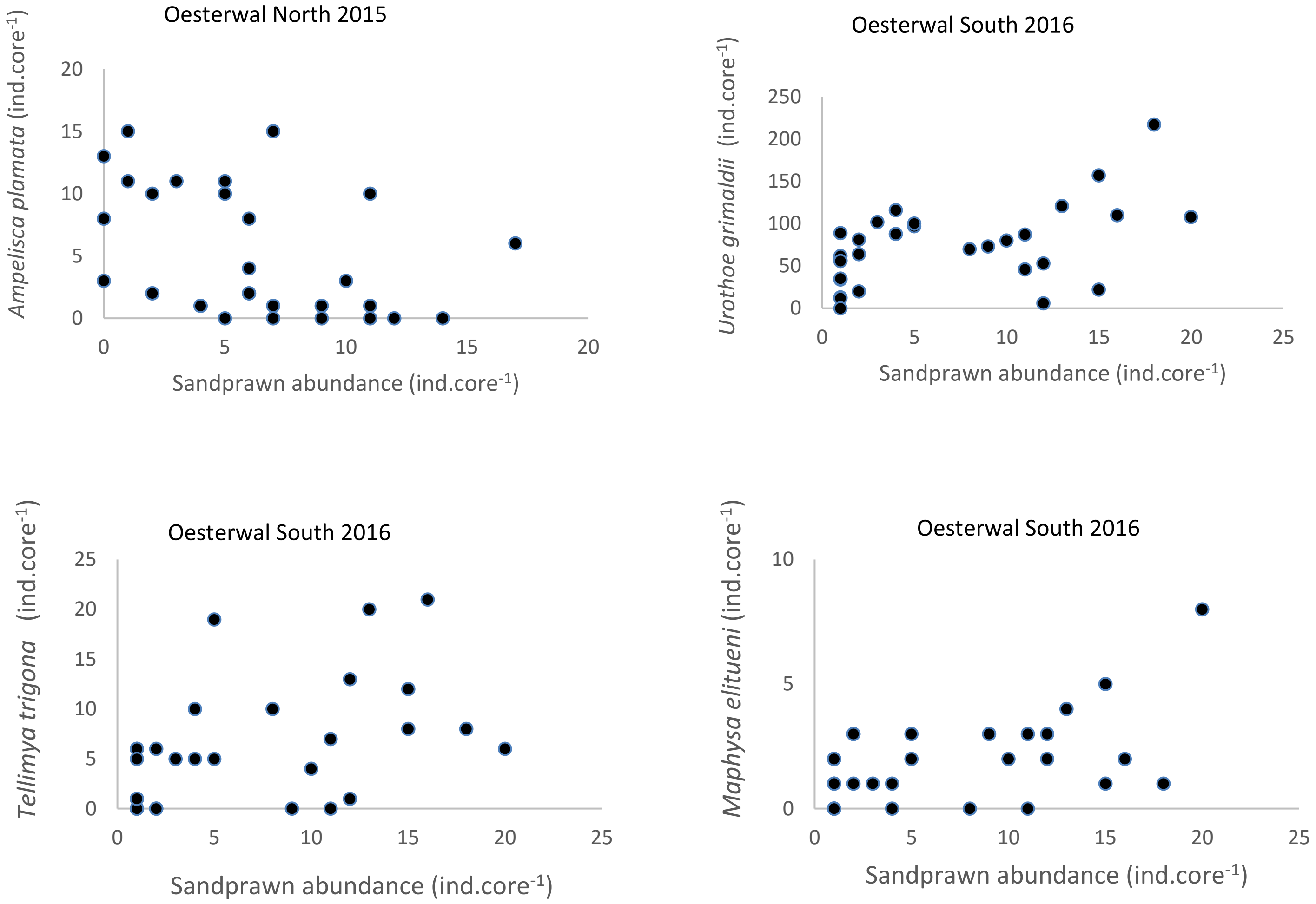


Fig 9.11 B: Relationships between macrofaunal species abudances and sandprawn abundances in Oesterwal North (ON) and Oesterwal South (OS) based on combined summer and winter data per year (2015 and 2016). NB: Y axis scales are different to show the trend in the data.

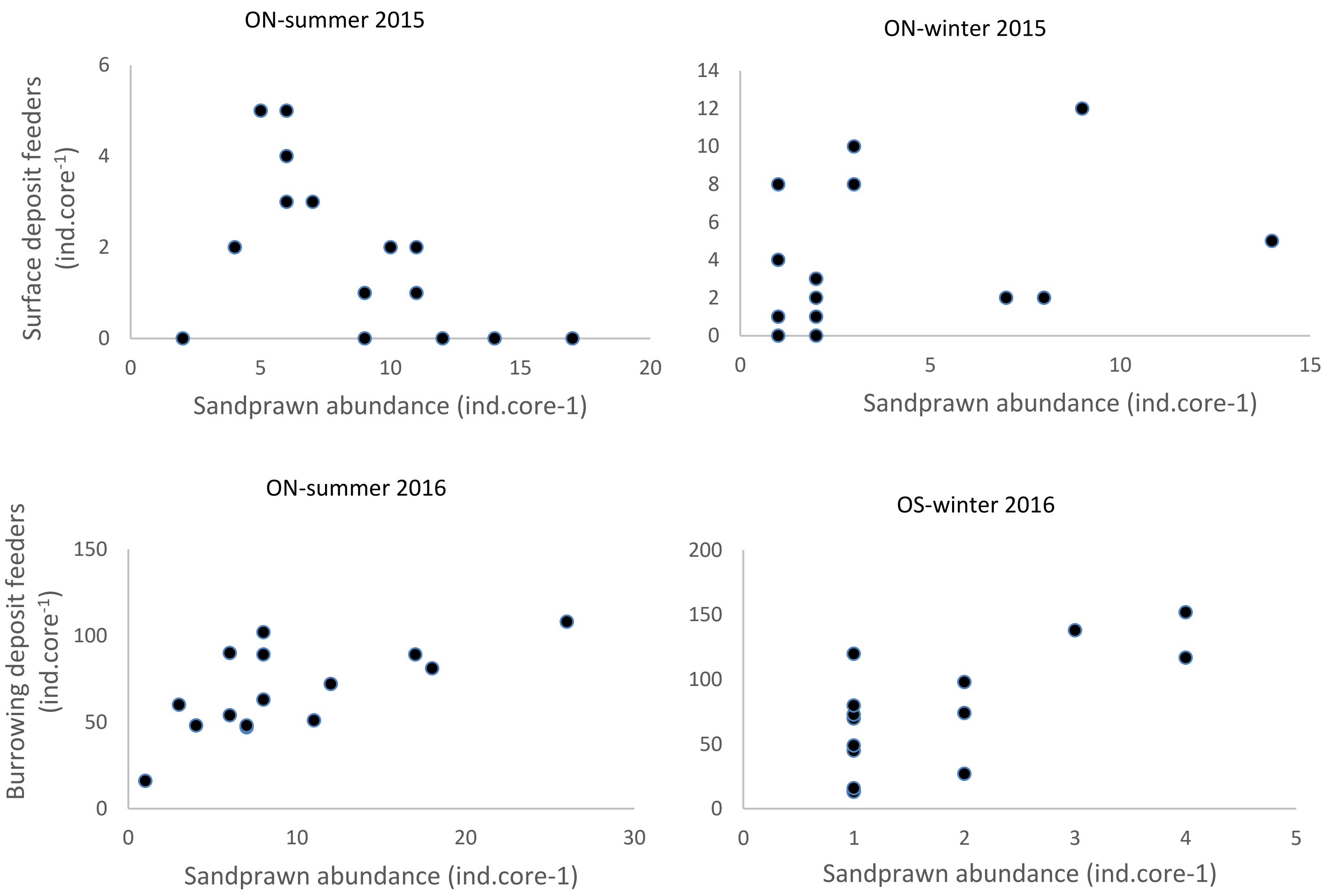


Fig 9.12: Relationships between macrofaunal functional group abundances and sandprawn abundances in Oesterwal North (ON) and Oesterwal South (OS) based on data per season. NB: Y axis scales are different to show the trend in the data.

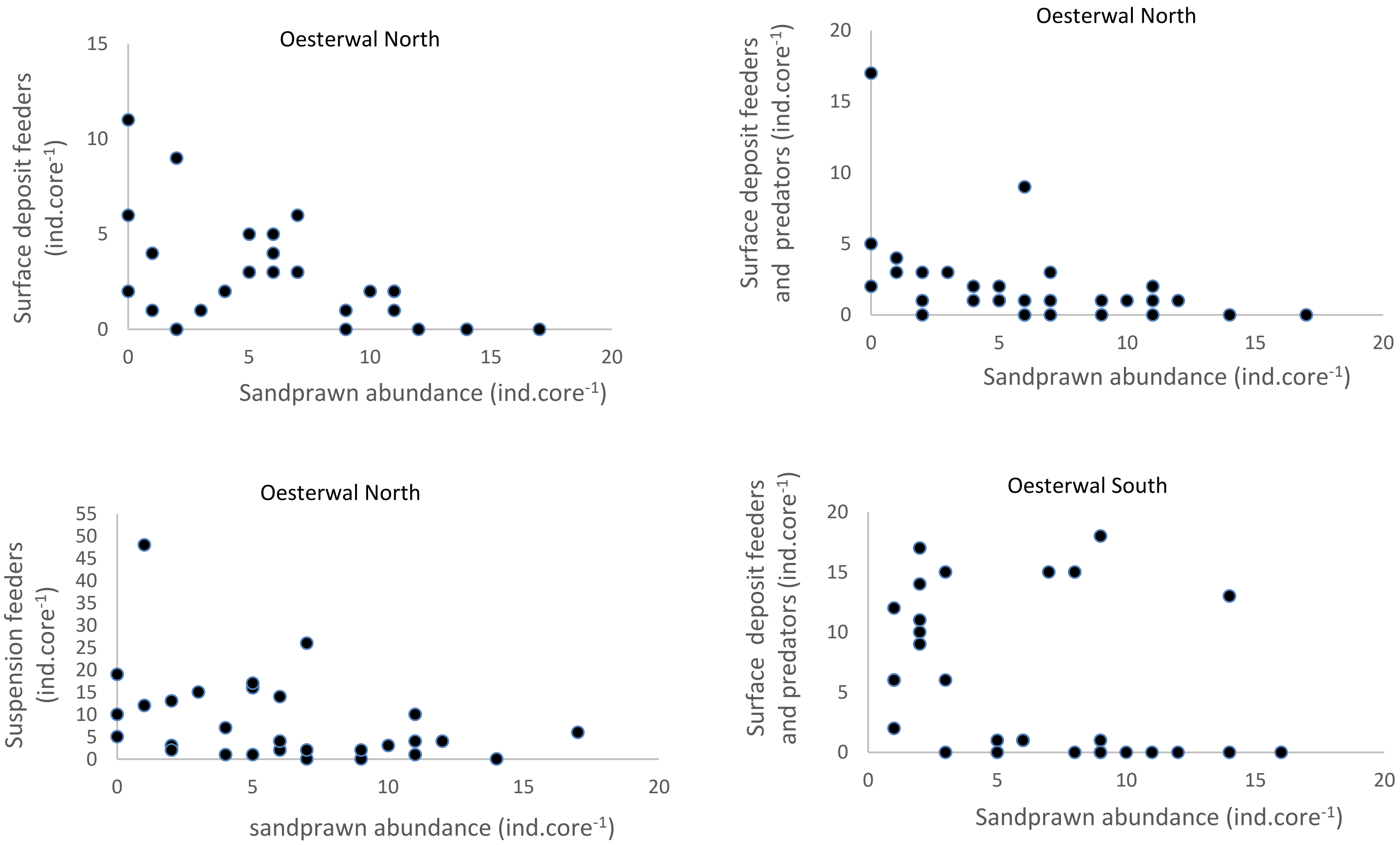


Fig 9.13A: Relationships between macrofaunal functional group abundances and sandprawn abundances in Oesterwal North (ON) and Oesterwal South (OS) based on combined summer and winter data per year (2015).

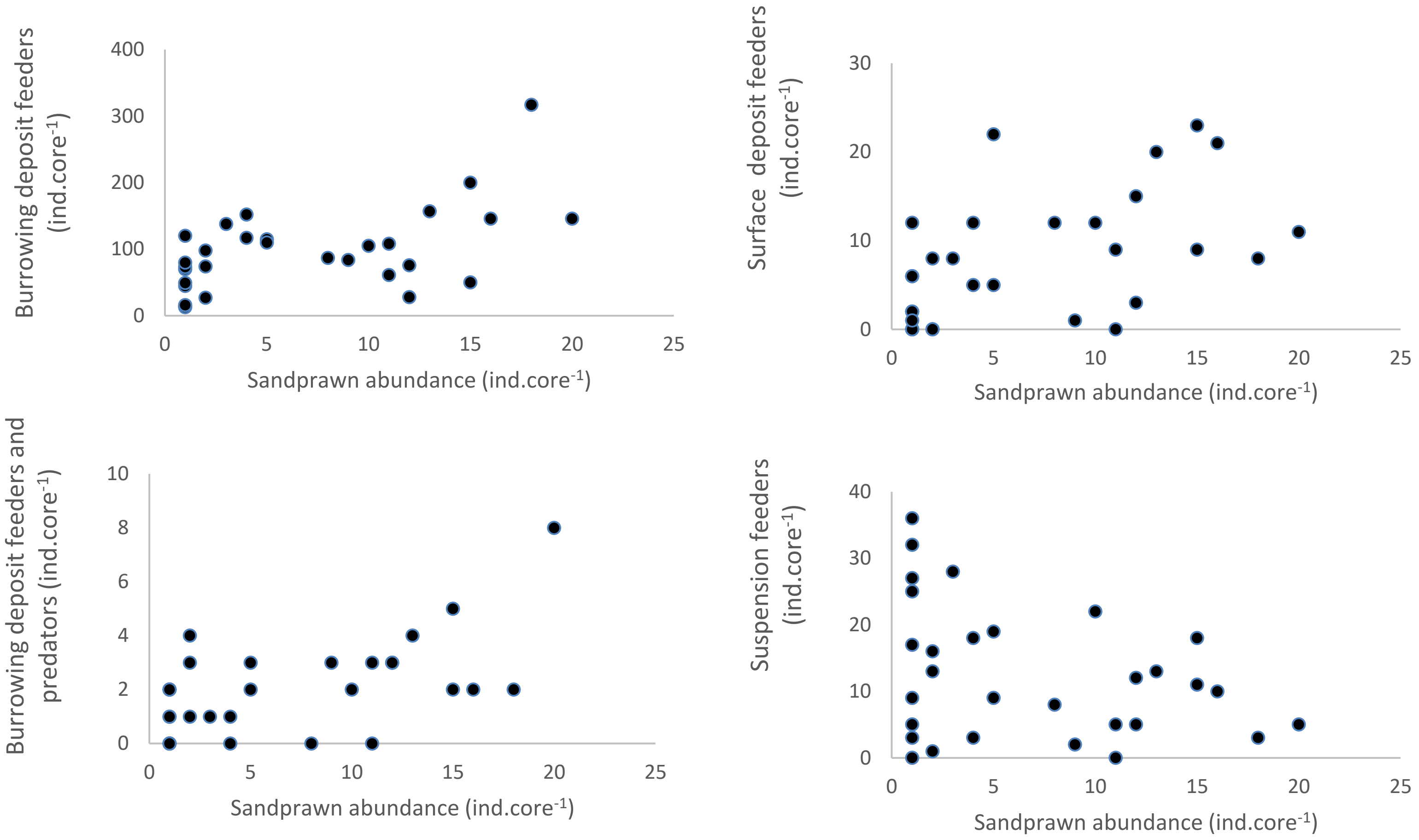


Fig 9.13B: Relationships between macrofaunal functional group abundances and sandprawn abundances in Oesterwal South (OS) based on combined summer and winter data per year (2016). NB: Y axis scales are different to show the trend in the data.