Benthic Metrics as Indicators of Human Disturbance in a Marine-dominated Lagoon

By

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TABLE OF CONTENTS

LIST OF FIGURES

LIST OF TABLES

PLAGARISM DECLARATION

I understand the definition of plagiarism and declare that the work presented in this minor dissertation is that of my own, unless otherwise acknowledged accordingly.

Amy M. Jones

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ABSTRACT

Expanding anthropogenic developments along with the added stress of climate change, are negatively influencing coastal ecosystems. Because of their many benefits to mankind, it is important to identify key bioindicators that can detect disturbance-induced ecosystem change. Benthic metrics are an excellent example of disturbance indicators in soft sediment based aquatic systems, and are directly applicable to one of South Africa's most economically and ecologically significant marine-dominated lagoons; Langebaan lagoon. This lagoon is managed through the designation of three zones (A, B and C) with contrasting human presence. Public access, recreation and bait-collecting is permitted in A, but no bait colleting is permitted in B. Human presence is completely restricted in Zone C. This study thus aimed to test the level of impact of human disturbance on two zones of the lagoon (A and C), using benthic metrics as bioindicators. Macrofaunal community metrics (abundance, species richness, Shannon-Weiner diversity, evenness, and community structure), performance of a key ecosystem engineer (sandprawn abundance and condition factor), organic matter content and microphytobenthic biomass were compared between the two sites, comprising multiple subsites. Results showed minimal differences between disturbed and undisturbed sites, with the exception of organic matter content and Shannon-Weiner diversity comparisons, which were greater in undisturbed subsites. There was however, a general trend of increasing dominance by sandprawns (*Callichirus kraussi*) from undisturbed to disturbed subsites, whilst the undisturbed subsites were numerically dominated by a several co-dominant polychaetes (*Euclymene* spp., *Notomastus latericeus* and *Marphysa sanguinea*). Interestingly, there were more significant differences at the subsite level, suggesting that localized conditions are more important in shaping macrobenthic communities than disturbance impacts, as supported by

previous literature. Despite limitations, this study does provide important baseline data relevant to optimizing sampling designs for detecting human disturbance impacts in Langebaan Lagoon.

Key Words: Benthic metrics, bioindicator, macrobenthos, disturbance, trampling, coastal lagoon.

INTRODUCTION

Coastal ecosystems

Our planet's most dominant habitat is the marine environment. Thus, it comes as no surprise that salt water ecosystems support the highest levels of biodiversity, representing a vast richness of life, most of which is yet to be discovered (Teixeira 2010). Recent research suggests that only 1% of the total marine benthic species is currently discovered (May 1992, Briggs 1994, Snelgrove 1999). Coastlines are regions of biodiversity hotspots, and include salt marshes, coral reefs, seagrass beds, mangroves, sedimentary habitats, algal meadows, and kelp forests (Duarte & Cebrián 1996, Teixeira 2010). Together these ecosystems contribute enormously to direct primary production, comparable to those of tropical forests (Duarte & Cebrián 1996). In addition, productive environments enhance nutrient cycling, which indirectly facilitate the productivity of marine and terrestrial primary producers (Teixeira 2010). In turn, a high local biodiversity is sustained, and secondary production is enhanced to provide nearshore ecosystems with important nursery functions for many species (Beck et al. 2001, Martinho et al. 2009). Vegetated coastal habitats are particularly critical sites for carbon sequestration, sediment stabilization, as well as protection from physical disturbances such as wave energy (Smith 1981, Duarte 2009). These attributes place coastal environments among the most ecologically and socio-economically important on the planet, providing essential goods to humankind. The benefits of coastal ecosystem functions to mankind, direct or indirect, include the basic provision of water, food and raw materials, gas and climate regulation, disturbance regulation, flood and erosion resilience, nutrient cycling, waste detoxification, biological control, tourist income, habitat and genetic resources, recreation and cultural uses (Costanza et al. 1997, Worm et al. 2006). However, these marine coastal habitats are disappearing globally up to 10 times faster than rainforests (Lotze et al. 2006).

Ecosystem function and resilience in the face of anthropogenic disturbance and climate change

Anthropogenic activities account for accelerated rates of destruction of marine ecosystems worldwide, contributing the greatest threat to biodiversity (Gray 1997, Airoldi & Beck 2007, Airoldi et al. 2008). Increased coastal development, unmanaged tourism, destructive fishing methods, introduction of alien species, climate change and pollution are the major causes of damage to the abovementioned ecosystem functions (Gray 1997, Airoldi & Beck 2007, Airoldi et al. 2008). These human impacts have serious negative implications for coastal environments at every level, from individual species to entire habitats. At the individual level, reproduction and growth is impaired, resulting in lower adult fitness by carcinogenicity, exposure to toxins, and endocrine interference (Teixeira 2010). At the habitat level, pollutants and destruction impair the nursery function of the environment, resulting in losses to biodiversity (Teixeira 2010). Other consequences include alteration of global nutrient cycles, and the promotion of coastal eutrophication, leading to ecosystem destruction and homogenization, which includes the reduction of species richness and energetic resources, altogether proceeding to weaken ecosystem resilience (McKinney & Lockwood 1999, Airoldi et al. 2008, Teixeira 2010). Ecosystem resilience is the response capacity to resist perturbation before (initial resistance) and after (ability to recovery quickly) disturbance. Stresses of sufficient magnitude or duration can breach ecological thresholds, forcing an ecosystem to fall into an alternative state (Boesch 1999). This alternate ecosystem could be completely devoid of appropriate ecosystem function, or merely shifted to support an alternate community predominated by different regimes of processes and structures (Folke et al. 2004). Often, these altered ecosystems shift from more complex to less complex states (Airoldi et al. 2008), and are less desirable, performing poorly in terms of effective ecosystem functioning, and recovery may be irreversible (Boesch 1999).

In addition to direct human-induced disturbance, climate change is also a contributor to coastal habitat endangerment al. 2007). There is an expected sea surface temperature increase of 1.0 – 3.7˚C by 2081-2100 (IPCC 2014). This is expected to directly affect organismal morphology, behavior and physiology at any point in their life history cycle by intensifying the rate of biochemical reactions, which drain energy reserves (Pörtner et al. 2005, Harley et al. 2006). This is particularly alarming as it implies a constant exposure to stress. Hypoxic conditions are also amplified, whilst elevating respiratory demands and reducing oxygen solubility. Ultimately coastal ventilation suffers, leading to unwanted stratification (Vaquer-Sunyer & Duarte 2008). The build-up of carbon dioxide in our atmosphere from anthropogenic activity is constantly absorbed by oceans, resulting in the ongoing decrease in oceanic pH. Whilst this is helpful in moderating atmospheric CO_2 levels, the transfer of this gas to the marine world poses a severe stress to calcifying organisms and may also interfere with migratory sensors of certain fish species (Fabry et al. 2008, Guinotte & Fabry 2008, Hall-Spencer et al. 2008). Sea level rise, the elevated frequency of risk to flooding, changing ocean currents and other related occurrences, can also impose disturbances that threaten biodiversity (Worm et al. 2006). Lagoons that provide nursing grounds may flood, vegetated areas that prevent erosion may no longer be able to do so, wetlands which buffer salinity against terrestrial habitats will become ineffective, and currents may cease to distribute resources and the recruitment of species (Boesch 1999, Danielsen et al. 2005).

In summary, all these anthropogenic-induced impacts, including climate change, lead toward an overall loss in ecosyste the globe. This is a great example of 'ecological integrity' which suggests a holistic approach of ecosystem management beyond what is considered to be of human interest, areas completely cut off from human access (Karr 1996, Borja et al. 2008). Of course, appropriate management efforts cannot be implemented without proper assessment of disturbance of current and future ecosystem condition.

Assessment of disturbance and ecosystem condition

One of the most effective ways of quantifying disturbance effects to an ecosystem would be to analyse the response of the ecosystem itself (Karr 1991). Measures of biotic integrity in index development permits biological communities to simply 'tell the story' as it is observed along a continuum from disturbed to undisturbed environmental conditions (Diaz et al. 2004, Chapman 2007). The realization that these communities could reflect every environmental event or unusual change in a 'story,' gave rise to the identification of ecological indicators - either biological, chemical or physical attributes that can sufficiently indicate a measure of change (Teixeira 2010). Ecological indicators are now one of the most commonly-used approaches in providing synoptic information about the state of ecosystems (NRC 2000, Fisher et al. 2001, Marques et al. 2009). An appropriate indicator should bridge a conceptual link between the stressor-response relationship, include the ability to quantify change with confidence, be sensitive enough to anticipate potential future problems, be applicable locally and globally over a variety of conditions, communities and environments, be straightforward to measure, integrative, non-destructive and ideally easy to interpret, as well as convey meaningful information such as the identification of thresholds, that will lead to effective management decision-making (O'Connor &

Dewling 1986, Cairns et al. 1993, Dale & Beyeler 2001, Fisher et al. 2001, ICES 2001, 2005, UNESCO 2003, 2006, EEA 2005, Magni et al. 2005, Rees et al. 2006, 2008).

The selection of successful key indicators will then lead to the expansion of a collection of relevant indices which can be used as operational tools. Because the benthic environment makes up the foundation of most coastal ecosystems, it hosts enormous ecological processes and functions. It's overall significance to the ecosystem is unquestionable, and any disturbance brought upon the coastal environment will most likely affect not only the overlying waters but also accumulate into the sediment (Elliott 1994, Diaz et al. 2004, McLusky & Elliott 2004, Dauvin 2007, Pinto et al. 2009). Thus, benthic metrics are often applied as ecological indicators for several marine environments. Macrobenthos, microphytobenthic biomass and organic matter content are frequently used as biological indicators because of their ease of access and their direct dependency to local sediments where exposure to disturbance is frequent (Elliott 1994, Diaz et al. 2004, McLusky & Elliott 2004, Dauvin 2007, Pinto et al. 2009). These benthic metrics will be discussed in detail hereafter.

Macrobenthos

Many studies have shown that benthic macrofaunal organisms respond rapidly to both human-induced and natural stresses (Pearson & Rosenberg 1978, Bustos-Baez & Frid 2003). There are several reasons for their use in disturbance studies. Firstly, they are relatively immobile, resulting often in direct impacts by local effects. Secondly, macrobenthos are easy to sample quantitatively (Warwick 1993, Chandrasekara & Frid 1996). Lastly, macrofauna are short lived, and any change to the environment can result in a rapid response in macrofaunal community structure (Warwick 1993, Chandrasekara & Frid 1996, Thompson & Lowe 2004). Because of these qualities, macrofauna have become one of the most well-researched biological components of benthic habitats and have proven to be a viable assessment of anthropogenic influence (Pearson & Rosenberg 1978, Warwick 1993, Chandrasekara & Frid 1996, Bustos-Baez & Frid 2003).

Alterations in community composition can provide the first indications of anthropogenic disturbance, as particular species are known to be more sensitive or resilient to specific stresses (Warwick 1993). Therefore, resilient species will likely increase in abundance in response to disturbance and outcompete less resilient ones (Warwick 1993). It has also been shown that species with increased fecundity, higher growth rates and short-life cycles will be the most successful in terms of invading and colonising disturbed areas (Newell et al. 1998). These species are coined '*r*-strategists' or the pioneer species, which become opportunistic in frequently disturbed environments. In contrast, '*K*-strategists' are those that thrive in stable environments and accumulate in abundance by being better competitors for resources (Gheskiere et al. 2005). These organisms are generally longer living, larger, and reproduce later due to lower mortality rates (Gheskiere et al. 2005). Macrofaunal community compositions in these stable conditions are thus predominantly defined by biological interactions, as opposed to fluctuations in environmental conditions (Warwick 1993). Of course, there are intermediate environments which host an array of *r*- and *K*-strategists (Warwick 1993, Gheskiere et al. 2005).

Macrofaunal community composition also provides insight into local physico-chemical conditions and furthermore reflects an environment's capacity to recover from disturbance (Boesch 1999, Teixeira 2010). It is widely accepted that habitats with higher species diversity have an enhanced ability to recover from disturbances, thus resulting in a stronger, more resilient ecosystem (Warwick 1993, Boesch 1999, Teixeira 2010). Similarly, an environment subjected to higher levels of disturbance will likely have decreased biodiversity levels (Warwick 1993, Wynberg & Branch 1994, 1997).

Biodiversity indices, such as the Shannon-Weiner diversity index (H'), are quantifiable measures of biodiversity that can be used to evaluate, compare and analyse changes in community compositions due to disturbance. There are two aspects that contribute to assessing community diversity, viz. species richness (total number of different species) and evenness (how evenly represented each species is). These metrics as well as macrofaunal abundance (total number of individual organisms) are often considered in macrobenthic studies that focus on disturbance effects (Wynberg & Branch 1994, 1997).

In addition to disturbance effects, biological interactions between species are a major determinant of organismal abundance and distribution (Jones et al. 1994). In particular, key species are capable of creating, modifying and maintaining habitats (Thayer 1979, Naiman et al. 1988). Jones et al. (1994) have coined these species 'ecosystem engineers.' One of the most obvious examples of an engineering species are beavers, where their activities modify water characteristics and distribution of organic matter, sediments, and nutrients, to ultimately influence animal and plant community structure and diversity (Naiman et al. 1988). Gophers, ants, and termites that move soil, alligators that create wallows, woodpeckers that puncture holes and burrowing crustaceans that move marine sediments are just a few more examples of ecosystem engineers (Jones et al. 1994, Wynberg & Branch 1997). Assessments of disturbance effects on ecosystem engineers are thus of great importance as they highlight potential cascading effects for the entire ecosystem arising from alterations of engineer function.

Microphytobenthic biomass

Microphytobenthic organisms consist of unicellular, photosynthetic eukaryotic algae and cyanobacteria that reside within the upper millimetres of shallow, seafloor sediments (MacIntyre et al. 1996). Their presence is practically unnoticeable, save for a subtle shade of brownish-green. Despite their invisibility to our naked eyes, “the secret garden” of the microphytobenthos plays key roles within marine ecosystems (MacIntyre et al. 1996), including their ability to modulate nutrient exchanges between the water-sediment interface (Krom 1991, Sundbäck et al. 1991, Rizzo et al. 1992), fix carbon dioxide into organic matter (MacIntyre et al. 1996) as well as to stabilize the sediment surface from resuspension via mucilaginous film secretion (Holland et al. 1974, Delgado 1989, Paterson et al. 1990).

In exposed, intertidal ecosystems, microphytobenthos are almost consistently attached to particles, exhibiting a diel rhythm of vertical migration, being exposed on the surface at low tide, and typically descending to 10 mm or in extreme cases as far as 20 cm during the flooding tides (Hopkins 1963, Heckman 1985, Pinckney & Zingmark 1993, MacIntyre & Cullen 1995). This behaviour is speculated to avoid either suspension into the overlying water column (Heckman 1985), or predation by marine benthic-surface feeders (Joint et al. 1982). Despite their movements being extremely slow, moving at 10 - 27 mm h^{-1} (Hopkins 1963), this behaviour has significant implications for rates of photosynthesis and measurements of microalgal abundance (Pinckney & Zingmark 1993). In more sheltered habitats, microphytobenthos may form stratified mats a few millimetres thick, which contrary to algal bloom-induced mats, provide rapid oxygen production with increased density (Jorgensen et al. 1983).

The vertical and horizontal distribution of microphytobenthos is also determined by sediment properties, location, wave strength, benthic macrofauna, season and other physical and chemical gradients on scales of tenths of a millimetre (MacIntyre et al. 1996). For example, in low energy, organic enriched habitats, microphytobenthos are limited to the upper millimetres of oxic sediments. Conversely, in high-energy, highly-mixed sandy sediments, their distribution extends uniformly to depths of up to 20 cm (Steele & Baird 1968, Fenchel & Straarup 1971, Fielding et al. 1988). In contrast to exposed sandy ecosystems, microphytobenthic biomass is higher in sheltered muddy habitats (Cadée & Hegeman 1977, Colijn & Dijkema 1981, Tett 1982, Delgado 1989, Sundbäck et al. 1991).

Chlorophyll-a is the photosynthetic pigment present in microphytobenthic organisms, and is used to estimate microphytobenthic biomass, giving an insightful index into the photosynthetic potential of the population (MacIntyre et al. 1996). This is important because the more photosynthetic activity, the more primary production and the more carbon is fixed into the sediments, creating an organically rich environment (MacIntyre et al. 1996). Primary production is promoted by strong irradiance and limited by respiration, however in oxygen-rich, shallow-water ecosystems there is a tendency for net production. In unvegetated habitats, microphytobenthos are not in competition for nutrients with other photosynthetic organisms, and are therefore not limited by nitrogen or phosphorous, which are constantly available due to the remineralization of sediment thanks to the activity of burrowing macrofaunal organisms (Admiraal et al. 1982, Granéli & Sundbäck 1985).

One of the most significant impacts of human disturbance on microphytobenthos is displacement by beach trampling, bait collection and general recreational uses of beaches, resulting specifically in cell resuspension and submergence. The act of resuspension, either natural or human-induced, is a very important flux in shallow-water ecology (MacIntyre et al. 1996). It is likely that a resuspension of the top few millimetres could account for all water column chlorophyll (Baillie & Welsh 1980). In almost all cases, primary production is not lost and instead displaced into the water column (Roman & Tenore 1978, Shaffer & Sullivan 1988). However, the magnitude to which disturbance-induced resuspension occurs and to furthermore determine subsequent primary production alteration is difficult to determine, simply because other factors outside of anthropogenic influence such as tide strength, wind velocity and animal activity, all interlace (MacIntyre et al. 1996). In addition, the time scale at which resuspension and resettling occur could vary from minutes after a disturbance, to hours or even months (MacIntyre et al. 1996). Trampling and other similar activities may result in increased submergence of microphytobenthos. The act of depressing these organisms into deeper, anoxic conditions may result in organism asphyxia and ultimately loss of primary production, and a decrease in photosynthetic potential (MacIntyre et al. 1996). Despite these complexities, microphytobenthic biomass can be used to indicate levels of human disturbance, as previous studies show significant loss of biomass by disturbance-induced displacement (Contessa & Bird 2004, Rossi et al. 2007).

Organic Matter Content

Organic matter is a critical food source for benthic organisms and ensures physical, chemical and biological integrities of sediments (Sanders 1958, Gray 1974, Pearson & Rosenberg 1978, Snelgrove & Butman 1994). Lopez & Levinton (1987), Sediment structure, compressibility, strength, water holding capacity, nutrient flux contributions, biological activity as well as water and air exchange rates, are all influenced by organic matter contents (Reddy 2002). However, excessive organic matter becomes a major pollutant of marine life and promotes eutrophication. This phenomenon has the capacity to deplete oxygen and produce toxic by-products, which in turn weakens the ecosystem by causing negative changes in community structure. Specifically, and most frequently observed in static, sheltered bays, extreme eutrophication causes losses of species richness, abundance and biomass (Pearson & Rosenberg 1978, Diaz & Rosenberg 1995, Gray et al. 2002). Often, organic matter increases are associated with increases in other chemical contaminants, implying that macrofauna endure multiple concurring stressors (Landrum & Robbins 1990, Lamberson et al. 1992, Thompson & Lowe 2004). A study conducted by Hyland et al. in 2005 used organic matter content and total organic carbon (TOC) concentrations as an indicator of stress in marine benthos and identified critical thresholds for ecosystem functioning that can be applied to a broad range of coastal sediment systems. Organic matter concentrations can therefore be compared to the work of Hyland et al. (2005), or other similar studies to estimate the degree of disturbance and quantify ecosystem risk to organic pollution. At the other end of the spectrum, Gheskiere et al. (2005) showed that beach trampling and mechanical beach clean-up was the main cause of losses of organic matter, which limited the richness of infaunal communities. Gheskiere et al. (2005) further confirmed that total organic matter was the single most important factor for observed differences between infaunal community structure between tourist verses non-tourist beaches.

Langebaan Lagoon

The effects of human-induced disturbances such as beach trampling have been successfully quantified in several soft-sediment benthic ecosystems using benthic metrics as bioindicators (Hailstone & Stephenson 1961, Wynberg & Branch 1991, Contessa & Bird 2004). In South Africa, as in many other parts of the world, lagoonal and estuarine ecosystems face significant pressure in the form of trampling and bait collecting, given the popularity of these habitats for tourism and recreational users.

Langebaan lagoon is a prime example of a coastal ecosystem that requires effective management in the face of growing human pressure and direct physical disturbance. Located on the west coast of South Africa, it stretches 15km inland, with a maximum width of 4km, and opens into Saldanha Bay before connecting to the Atlantic Ocean (Figure 1). The lagoon is not estuarine and therefore displays no significant salinity gradient (Shannon & Stander 1977). It does however, experience seasonal temperature changes, with a considerably warmer Summer temperature within the southernmost regions, reaching up to 30˚C in comparison to the adjacent open ocean at 16˚C (Flemming 1977). The lagoon itself is divided into three recreational zones; A, B and C. Spilling out from Saldanha Bay, zone A (14.15 km^2) hosts the highest levels of human disturbance. It supports most types of recreational sports including motor boats, fishing, bait collecting and kitesurfing. Zone B (16.37 km^2) is in the middle of the lagoon and hosts intermediate levels of human disturbance. Although angling and other fishing activities as well as motor-boats are prohibited, this area is still open to the public for kitesurfing, sailing and general beach recreation. Zone C (10.58 km^2) is the furthest inland, and nests under the protection of the West Coast National Park (WCNP). Here, access is completely restricted to those without a permit, which is only granted for research or educational outreach programs. This zone therefore has the lowest levels of direct human impact. As a result of this zonation, Langebaan lagoon has evolved to host a gradient of human disturbance, making it an ideal model to understand disturbance effects.

The Saldanha Bay – Langebaan lagoon system is one of the most ecologically and economically important areas in southern Africa, and is the only natural harbour on South Africa's west coast (Kerwath et al. 2009). Human development surrounding Saldanha Bay and Langebaan lagoon has increased dramatically in recent years, with tourist visitations to in the WCNP reaching an average of 16% per annum (Clark et al. 2016). Unsurprisingly, associated developments have increased to accommodate the influx of people, and as a result, environmental impacts have increased. Pollutants, waste, oil spillage, metal ore exposures, dredging dislodgements, industrial emissions and the presence of other human activities are infiltrating the natural integrity of the ecosystem (Krug 1999, Cloern 2001). Disturbance effects may lead to permanent loss of biodiversity as well as species and sediment composition changes, depending on distance from disturbance sources (Krug 1999). For example, previous research has brought to light the consequences from the Port construction within Saldanha Bay. The sediment used to build the part of the Port, was obtained from the historic ebb tide delta, a natural mound of sediment that had been accumulating for millennia (Weeks et al. 1991). The destruction of this feature, so critically located at the mouth of the Bay, now refracts the incoming wave energy to the shoreline at a level 50% greater than before, causing massive beach erosion (Weeks et al. 1991). The dislodgement also caused the drift of fine sediment into Langebaan Lagoon, leading to sediment composition change which in turn lead to direct and indirect distress on birds of the lagoon (Weeks et al. 1991) and often lead to the detriment of seagrasses (Hemminga & Duarte 2000, Baden et al. 2003, Waycott et al. 2009). The cumulative impacts brought upon Langebaan Lagoon from human disturbance originating from Saldanha Bay demand the necessity for sustainable development with environmental consideration.

There are three main habitats that make-up Langebaan lagoon viz. seagrass beds (dominated by the seagrass *Zostera capensis* (Setchell) Tomlinson & Posluzny), saltmarshes (dominated by the cordgrass *Sarcocornia perennis* (Miller) Scott and *Spartina maritima* (Curtis) Fernald) as well as unvegetated sandflats (dominated by the sandprawn *Callichirus kraussi* Stebbing). The seagrass and saltmarsh habitats are the most valuable as they provide shelter, food and increase sediment stability, altogether supporting the highest levels of species richness, biodiversity, abundance and biomass across a range of animal taxa, from invertebrates, to fish, to birds (Gray 1997, Puttick 1977, Hemminga & Duarte 2000, Orth et al. 2006). There is a North to South energy-gradient, with tidal disturbance forming a large central channel that separates medium-grain sands to western regions, and fine-grain sands to the East of the lagoon (Flemming 1977). This channel does not migrate due to underlying fossil oyster reefs, and eventually slackens towards the southern end, where seagrass and saltmarshes start to emerge, with saltmarshes dominating the sheltered-most southern coastline (Flemming 1977). Seagrass beds however, have been on a dramatic decline, with an estimated loss of 38% coverage since the 1960s (Pillay et al. 2010). Macrofaunal communities associated with seagrass presence have also disappeared accordingly as have some seagrass-depended birds such as the Terek Sandpiper (Pillay et al. 2010). The fall of seagrass beds is a convincing indication that the lagoon is experiencing an alteration of state, and it is speculated that anthropogenic disturbance is the main driver. Whilst there is plentiful research regarding saltmarshes and seagrass beds within Langebaan, including their comparisons to sandflats, the unvegetated sandflats themselves are lesser studied.

Arguably the most important species of macrofauna living in unvegetated sediments of Langebaan Lagoon is the sandprawn *C. kraussi*. This is because of its high numerical and ecological dominance within the ecosystem (Nel & Branch 2013), so much so that it has been termed an ecosystem engineer (Siebert & Branch 2006, Pillay et al. 2008, 2012, Pillay & Branch 2011). These sandprawns build deep, ever-changing burrows that continuously displace sediment (Aller & Dodge 1974, Roberts et al. 1981, Suchanek et al. 1986, Pillay et al. 2008, 2012, Pillay & Branch 2011). This process, known as bioturbation, oxygenates sediments, alters organic matter distribution, increases mineralization, promotes nutrient exchange, encourages bacterial growth and influences communities of meiofauna, seagrass, and microalgae (Forbes 1973, Yingst & Rhoads 1980, Brenchley 1981, 1982, Hines & Jones 1985, Posey 1986, Branch & Pringle 1987). Sandprawn population size is also suggested to influence communities at higher trophic levels, such as benthic-feeding fish and birds (Hanekom & Erasmus 1988, Pillay et al. 2008). Pillay et al. (2012) furthermore experimentally determine that the microphagous fish species *Liza richardsonii,* is negatively affected with large sandprawn densities, as they decrease microbial biomass. Ecosystem engineering by sandprawns also promotes selective evolution of unique morphology, behavior and social interactions in co-occurring species (Pillay & Branch 2011).

What is of concern is the act of sediment trampling and disturbance associated with the collection of these sandprawns as bait within zone A of the lagoon, which may have consequential, unintended effects on other species. These activities can be more detrimental to the ecosystem than the removal of the sandprawns themselves (Wynberg & Branch 1997). This physical-disturbance could also lead to changes in sandprawn activity, with cascading effects to all sandprawn dependent processes and co-occurring communities (Pillay & Branch 2011). The intensity at which the shoreline of zone A is used for sandprawn collection and recreational purposes has thus led to major concern for the preservation and protection of biodiversity and ecosystem function in the area (Wynberg & Branch 1997), highlighting the importance for regulating bait-collection and zonation. Previous surveys have shown that sandprawn densities living in similar sedimentary conditions, differ between harvested and protected areas within Langebaan lagoon (Nel & Branch 2013). Nel & Branch (2013) furthermore determine that the harvest restriction within zones B and C protects 90.2% of sandprawn stocks.

In this study, macrofaunal assessments (diversity, evenness, abundance, species richness, and community structure), including those of the ecosystem engineer (sandprawn abundance and condition factor), microphytobenthic biomass and organic matter content, will be evaluated for their applicability as indicators of human disturbance associated with bait collection and trampling, in Langebaan Lagoon, South Africa. Furthermore, whichever ecological indicator represented the most profound difference between disturbed and undisturbed areas would be considered the most effective metric. This will allow managers to better understand ecosystem dynamics of a changing environment that may otherwise go unnoticed until too late. An assessment of these benthic metrics will also provide a status of current condition, which may be applied to predict future conditions, as well as offer a baseline dataset which future conditions can be compared. It is hypothesized that all metrics will be significantly lower in disturbed sites (zone A) of the lagoon, in comparison to undisturbed sites (zone C). A hierarchical sampling design will be implemented such that these metrics can be analysed not only at the disturbance level, but also within-sites such that levels of site heterogeneity can be assessed. As the time-frame given to complete this study was very limited, sampling took place during the first two weeks of December 2017 (transition of Spring into Summer). The overarching goal is to provide information to park managers that could ultimately be used to develop long-term assessment plans in detecting and managing impacts of human associated disturbance.

METHODS & MATERIALS

Sampling Location & Study Design

This study took place at two sites within Langebaan Lagoon, viz. Shark Bay and Gravity (Fig. 1). Shark Bay is located in zone A of the lagoon, where beach access is permitted for multi-recreational activities such as motor-boat use, sailing, kitesurfing, swimming, bait-collecting, fishing and other general beach activity. Gravity is located further south, within zone C, where human access is strictly prohibited to those without a permit. Such concessions are granted mainly for purposes of research or educational outreach programs. Within each site, two subsites were selected at mid-tide positions, roughly 50m from the highwater mark and 150m apart (Fig. 1). For convenience, disturbed subsites will be denoted as D1 & D2 and undisturbed subsites as U1 & U2 in this dissertation. During the first two weeks of December 2017 (transition of Spring into Summer), multiple benthic samples were collected to assess effects of disturbance, as detailed in the following sections.

Data Collection

A: Microphytobenthic Biomass

Microphytobenthic biomass was estimated at each of the four subsites using chlorophyll-a biomass as a proxy (MacIntyre 1995, MacIntyre et al. 1996). Sediment samples were collected using a 2.7cm diameter custom-built corer, which sampled the top 1cm layer of sediment, giving a total sediment volume of 5.73×10^{-6} m^3 per sample. Six cores were randomly extracted during low tide per subsite, within an area of 5 m^2. Each core sample was immediately placed into a test tube containing 30ml of 90% acetone,

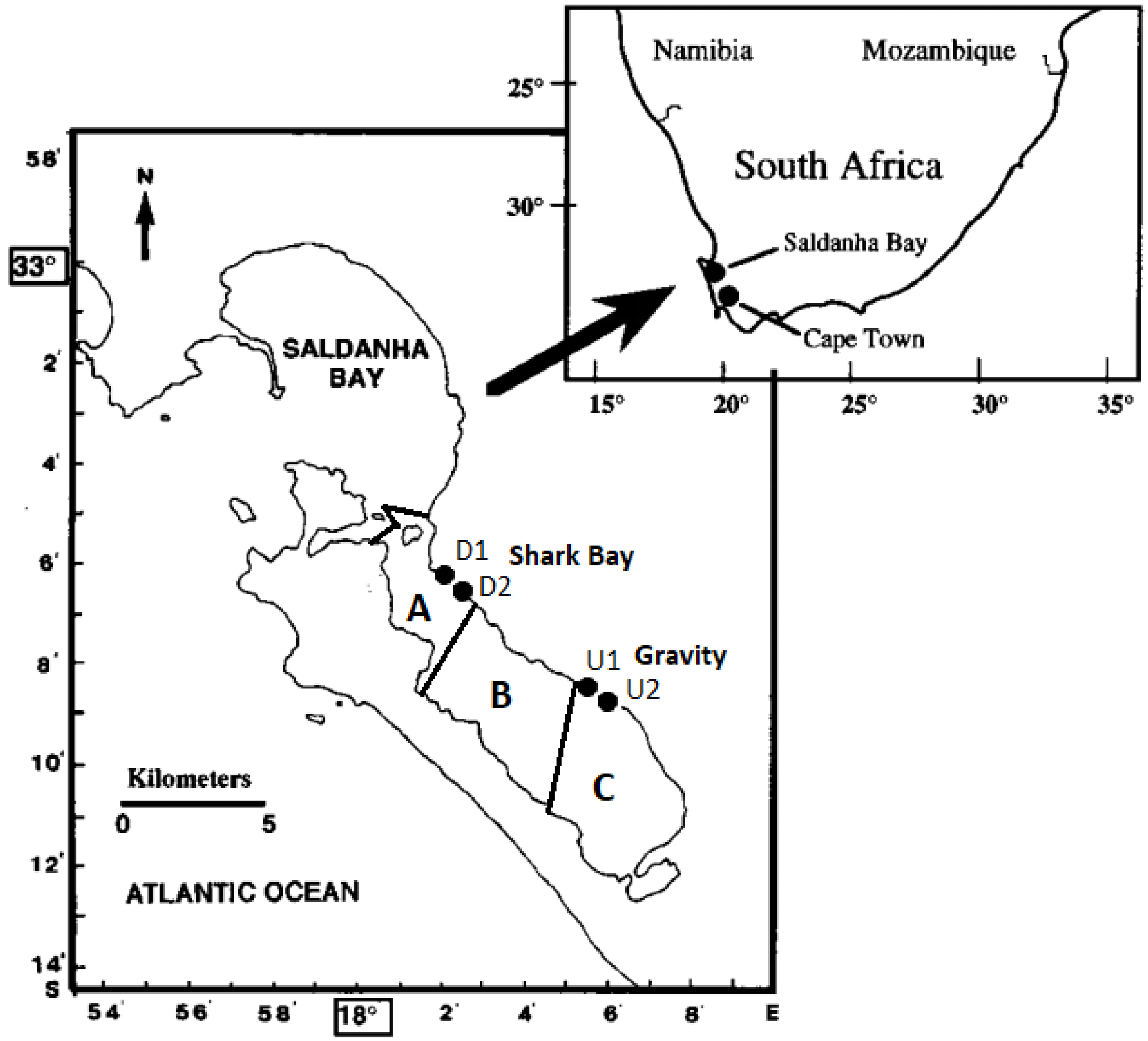


Figure 1: Map of Saldanha Bay and Langebaan Lagoon (including zones A, B and C), South Africa, showing positions of sampling stations D1, D2, U1 and U2. D1 & D2: disturbed sites 1 & 2; U1 & U2: undisturbed sites 1 & 2.

and kept in a cool bag and in darkness until transported back to the laboratory located at the University of Cape Town (UCT) later the same day where it was refrigerated in darkness (1.6˚C for 48 hours for chlorophyll-a extraction). A 5ml acetone subsample was withdrawn and chlorophyll-a content measured using a Turner Designs Trilogy fluorometer. The raw fluorescence (RFU) absorbance readings were then converted into chl-a biomass (mg chl-a m^{-2}) using a calibration curve comprising three known chl-a concentrations. (See Appendix for method of calculations).

B: Organic Matter content

Organic matter content (%) at each of the four subsites, was determined using a protocol similar to that used for microphytobenthic biomass determinations. In brief, replicate sediment cores (2.7cm diameter, depth = 1cm, n = 6) were extracted during low tide per subsite. Cores were placed in air-tight plastic jars and kept in a cool bag, and then frozen (-18˚C) in the laboratory. Samples were thawed and weighed following Reddy (2002). Cores were dried overnight (105˚C) and then ignited in a muffle-furnace for a second overnight period at 440˚C. Organic matter was expressed as the change in mass following ignition relative to the dry sediment mass.

C: Macrofauna and Sandprawns

Benthic cores were collected at each of four subsites using a cylindrical hand-held prawn pump, which was 5cm in diameter, and penetrated a specified 50cm of sediment. This depth was clearly marked, and the extraction was carefully observed such that no sediment 'slipped out.' If this was the case, cores were discarded and re-done. Cores were collected during a flooding tide, at a water depth of 0.5m. Five sediment cores collected randomly within 1m of each other were pooled (combined in a bucket) to produce a single sample per subsite, with a total sediment volume of 0.01965m^3 (volume calculated from pump dimensions, multiplied by 5). Each sample was sieved in the field through a 1mm mesh and all retained organisms emptied into appropriately labelled sample jars containing an ethanol (70%)-Rose Bengal (biological stain) solution. In total, six samples (comprising of 5 cores each) were collected per subsite with each sample being randomly collected within 5-10m proximity to each other. Once at the laboratory, samples were sieved through a 1mm mesh and emptied into a sorting tray with water, where stained macrofaunal organisms were counted. These are listed in Table 2.

Sandprawns *(C. kraussi)* from sorted sediment cores were further investigated for physical condition determination. This involved first measuring the body length (tip of rostrum to end of tail; Fig. 2), and oven drying at 60˚C overnight to obtain dry weight. The condition index was expressed as the dry mass: length ratio (g mm^{-1}). Only whole sandprawns were included in condition index determinations.

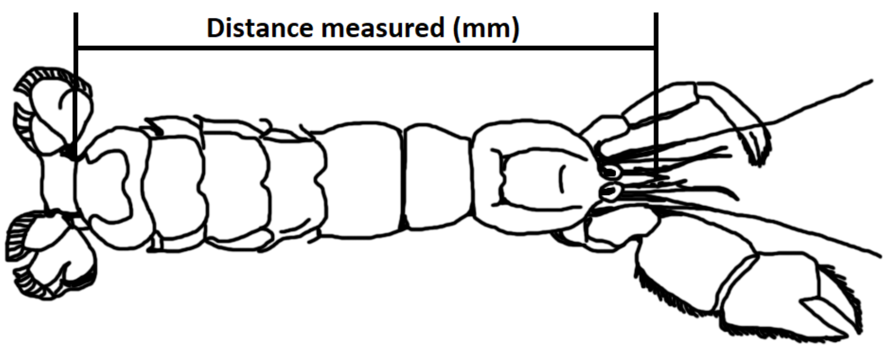


Figure 2: Length determination in sandprawns. Note: Tail fans were excluded from length determinations as these were frayed and damaged on some individuals.

Data Analysis

All data were tested for normality and homogeneity of variance using Q-Q plot and Levene's tests prior to univariate testing. Due to high variability, all data failed to meet the assumptions required for parametric testing. This problem persisted even after data were transformed (log x + 1). Because of this, non-parametric Kruskal-Wallis tests were applied to test the main effects of disturbance level (disturbed vs undisturbed) and subsite (D1, D2, U1, U2) on benthic metrics. Dunn's *post-hoc* test was used to identify statistically significant within-treatment differences where applicable. All univariate statistical analyses were performed using the data analysis platform R Studio.

All multivariate analyses were undertaken using PRIMER 6 (Plymouth Routines In Multivariate Ecological Research). Abundance data were transformed (fourth root) and converted to a similarity matrix using the Bray-Curtis similarity coefficient (Warwick & Clarke 1993). The transformation was applied to downweigh the contributions of numerically dominant species to the similarities calculated between samples, such that rare species become more prominent (Warwick & Clarke 1993). This is especially useful when using the Bray-Curtis similarity index, as it does not include any form of scaling of each species. A non-metric Multidimensional Scaling (nmMDS) ordination was used to visualize spatial variability in assemblages across factors tested. Similarity Percentages (SIMPER) analysis was used to identify diagnostic species principally responsible for the clustering of samples. Analysis of Similarities (ANOSIM) was used to test for statistically significant differences among groups, testing the null hypothesis of no differences among spatial factors.

Three diversity indices were calculated to estimate spatial variability in diversity among factors tested. The Shannon-Weiner diversity index (H') was calculated using equation 1:

$$H = -\sum_{i=1}^{s} p_i \ln p_i \qquad (1)$$

where the proportion of species (i) relative to the total number of species (p_i) is calculated, and then multiplied by the natural logarithm of this proportion ($\ln p_i$). The resultant product is then summed across species and multiplied by -1. The Shannon-Wiener index incorporates both abundance and evenness of species present in estimating diversity. Evenness (E) was calculated according to Equation 2:

$$E = \frac{H'}{\ln S} \qquad (2)$$

where the Shannon-Weiner diversity (H') is divided by the natural logarithm of the total number of species per subsite (S). It assumes a value between 0 and 1 with 1 being complete evenness. Macrofaunal richness was estimated as the total count of species per sample while macrofaunal abundance was expressed as the sum of all individuals (across all species) in samples.

RESULTS

Microphytobenthic Biomass

Although there was no significant difference in chlorophyll-a content between disturbed and undisturbed sites (Kruskal-Wallis $\chi^2 = 2.0833$, df = 1, p = 0.09407; Table 1a), a statistically significant difference was observed between subsites (Kruskal-Wallis $\chi^2 = 18.62$, df = 3, p = 0.0003276; Table 1a; Fig. 3a). *Post-hoc* analysis revealed that differences occurred between subsites (1) U2 and D1 and (2) U2 and U1, (Table 1a). Undisturbed site number 2 (U2) had the highest chlorophyll-a content (33.4 ± 0.81 mg chl-a m^{-2}), with the remaining three sites (D1, D2 and U1) having means of 18.6 ± 1.18, 23.7 ± 0.61 and 20.8 ± 0.68 mg chl-a m^{-2}, respectively. Low variability was evident across the four subsites, as indicated by the small standard error bars (Fig. 3a).

Organic Matter Content

There were significant differences in organic matter contents between disturbed and undisturbed sites (Kruskal-Wallis $\chi^2 = 4.8133$, df = 1, p = 0.02824; Table 1b) as well as across the four subsites (Kruskal-Wallis $\chi^2 = 8.6067$, df = 3, p = 0.035; Table 1b; Fig. 3b), with mean values of 0.51 ± 0.025, 0.47 ± 0.022, 0.54 ± 0.046 and 0.61 ± 0.035 % for subsites D1, D2, U1 and U2, respectfully. More specifically, a significant difference was recorded between subsites D2 and U2 (Table 1b). Subsite U1 had the highest variability levels. In general, organic matter was lower in disturbed than undisturbed subsites.

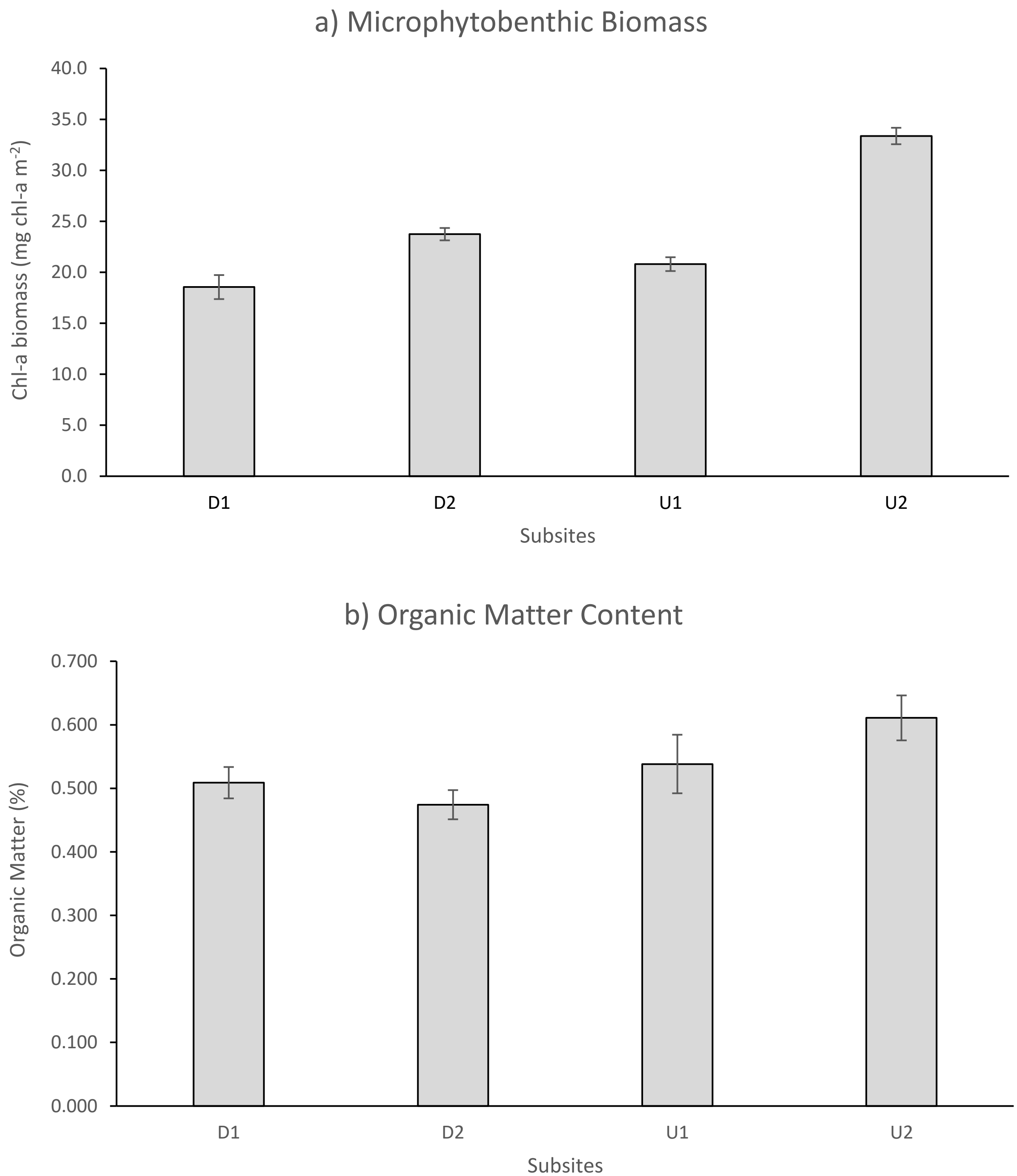


Figure 3: Spatial variability in mean (± SE) a) microphytobenthic biomass and b) organic matter content.

Table 1: Results of Kruskal-Wallis χ^2 tests determining effects of disturbance and subsite on a) microphytobenthic biomass, and b) organic matter content. df = degrees of freedom; p = significance level. Results of Dunn's *post-hoc* subsites show within-treatment comparisons where relevant. Obs = observed statistic, Crit = critical value.

a) Microphytobenthic Biomass

Kruskal-Wallis Sites Test: Disturbed vs undisturbed

Kruskal-Wallis chi-squared = 2.0833, df = 1, p-value = 0.09407

Kruskal-Wallis Subsites Test: D1, D2, U1, U2

Kruskal-Wallis chi-squared = 18.62, df = 3, p-value = 0.0003276

Dunn's *Post-hoc* Subsites Test

Sites comparison	Obs	Crit	p = 0.05
D1-D2	9.50000	10.77064	>0.05
D1-U1	3.00000	10.77064	>0.05
D1-U2	16.16777	10.77064	<0.05
D2-U1	6.50000	10.77064	>0.05
D2-U2	6.66670	10.77064	>0.05
U1-U2	13.16667	10.77064	<0.05

b) Organic Matter Content

Kruskal-Wallis Sites Test: Disturbed vs undisturbed

Kruskal-Wallis chi-squared = 4.8133, df = 1, p-value = 0.02824

Kruskal-Wallis Subsites Test: D1, D2, U1, U2

Kruskal-Wallis chi-squared = 8.6067, df = 3, p-value = 0.035

Dunn's *Post-hoc* Subsites Test

Sites comparison	Obs	Crit	p=0.05
D1-D2	4.33	10.77064	>0.05
D1-U1	0.83	10.77064	>0.05
D1-U2	7.50	10.77064	>0.05
D2-U1	5.17	10.77064	>0.05
D2-U2	11.83	10.77064	<0.05
U1-U2	6.67	10.77064	>0.05

Table 2: Abundance of macrofaunal species (per 0.01965 m^{-3}) across the four sampling subsites in Langebaan Lagoon (D1, D2: disturbed subsites 1 & 2; U1, U2: undisturbed subsites 1 & 2). Six classes were observed, totalling 21 species. Crustacea and Polychaeta were the dominant classes, dominating disturbed and undisturbed subsites, respectively.

Species Name	**Common Name**	**D1**	**D1**	**D1**	**D1**	**D1**	**D1**	**D2**	**D2**	**D2**	**D2**	**D2**	**D2**	**U1**	**U1**	**U1**	**U1**	**U1**	**U1**	**U2**	**U2**	**U2**	**U2**	**U2**	**U2**
Crustacea																									
Callichirus kraussi	Common Sandprawn	2	4	3	-	-	1	7	2	-	2	1	2	3	2	4	1	4	1	2	4	6	2	6	-
Ostracoda	Seed shrimp	-	-	-	12	-	-	-	-	-	23	-	1	-	-	-	-	-	-	-	-	-	-	-	-
Hymenosoma orbiculare	Crown crab	-	-	-	-	1	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Betaeus jucundus	Commensal Shrimp	-	-	-	-	-	-	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Spiroplax spiralis	Three legged crab	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Upogebia africana	Estuarine mud prawn	-	-	1	-	3	1	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	1	-	1
Unknown juvenile crab	Unknown juvenile crab	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2
Gastropoda																									
Turritella capensis	Waxy screw shell	-	-	-	-	1	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Littorina saxatilis	Common periwinkle	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1
Polychaeta																									
Marphysa sanguinea	Estuarine wonder-worm	-	-	-	1	-	-	1	-	3	-	-	-	2	1	2	1	2	3	2	1	2	3	-	1
Glycera tridactyla	Glycerine worm	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Notomastus latericeus	Club worm	-	-	-	-	-	-	-	-	-	-	-	-	3	1	1	-	2	-	3	3	-	-	2	-
Euclymene spp.	Bamboo worm	-	-	-	-	-	-	-	-	-	-	1	1	2	2	1	1	2	1	-	-	-	-	-	-
Orbinia angrapequensis	Woolly worm	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	1
Thelepus spp.	Tangle worm	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-
Arabella iricolor	Arabella iricolor	-	2	-	1	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	3
Unknown Polychaeta	Unknown Polychaeta	1	-	-	1	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Bivalvia																									
Carditella capensis	Cockle	-	-	-	-	-	1	-	-	-	5	-	-	-	-	-	-	-	-	-	1	-	2	-	-
Venerupis corrugata	Corrugated venus	1	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Arthropoda																									
Nymphon signatum	Scarlet sea spider	-	-	-	-	-	-	-	-	-	-	-	-	2	-	-	2	1	-	-	-	-	-	-	-
Amphipoda																									
Ampelisca palmata	Four-eyed amphipod	-	-	-	-	-	-	10	6	2	6	1	10	1	3	2	3	1	2	-	-	-	-	-	-

Multivariate Analysis

Lack of clustering between disturbed and undisturbed samples (Fig. 4) suggests negligible effect of disturbance at the assemblage level. There does however, appear to be evidence of clustering at the subsite level, especially for undisturbed subsites.

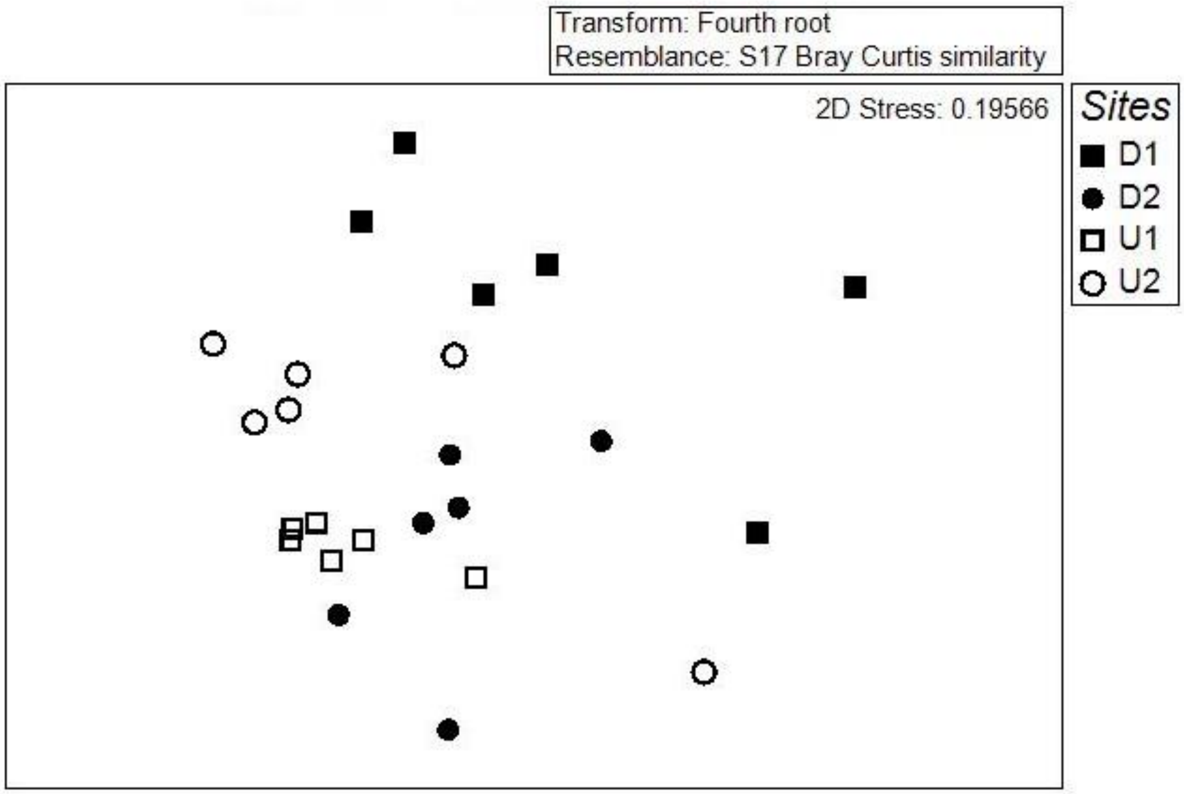


Figure 4: Non-metric multidimensional scaling (nmMDS) plot visually depicting similarity in macrofaunal community structure in two-dimensional space.

In support of the nmMDS ordination, ANOSIM indicated no difference in macrofaunal community structure between disturbed and undisturbed areas (R = 0.410, significance level = 66.7%) but significant differences among subsites (R = 0.494, Significance level = 0.1%) (Table 3).

Table 3: Results of ANOSIM tests quantifying effects of spatial variables on macrofaunal assemblage structure. Pair-wise tests (equivalent of univariate *post-hoc* tests) are presented for within-treatment differences where relevant. Significance of less than 5% indicates significant R statistic.

	R Statistic	**Significance Level %**	**Possible Permutations**	**Actual Permutations**	**Number ≥ Observed**
Two-Way Nested test between:					
Sites: Disturbed vs undisturbed	0.410	66.7	3	3	2
Subsites: D1, D2, U1, U2	0.494	0.1	213444	999	0
Pairwise tests					
D1, D2	0.413	0.2	462	462	1
D1, U1	0.629	0.2	462	462	1
D1, U2	0.185	4.1	462	462	19
D2, U1	0.424	0.2	462	462	1
D2, U2	0.531	0.2	462	462	1
U1, U2	0.575	0.2	462	462	1

SIMPER indicated an average dissimilarity between disturbed and undisturbed sites of 68.30% and that four species contribute to 50% dissimilarity (Table 4). These were *Marphysa sanguinea* (polychaete), *Ampelisca palmata* (amphipod), *Notomastus latericeus* (polychaete) and *Callichirus kraussi* (endobenthic crustacean), each contributing 13.73, 11.68, 11.05 and 8.16%, respectively to dissimilarity (Table 4). It is noticeable that crustaceans were more abundant in disturbed subsites with polychaetes dominating numerically in undisturbed subsites. For example, *M. sanguinea,* the dominating polychaete across all samples, has an average abundance of 1.05 per 0.01965 m^{-3} in the undisturbed subsites but 0.28 per 0.01965 m^{-3} in the disturbed subsites (Table 4). SIMPER furthermore revealed average similarities in community structure among subsites to be 27.48, 46.94, 76.62 and 49.10 % for subsites D1, D2, U1 and U2, respectively (Table 5).

Table 4: Results of SIMPER dissimilarity tests showing dominant species that cumulatively accounted for 90% of the dissimilarity between disturbed and undisturbed sites. Av. Abund = average abundance; Av. Diss = average dissimilarity, Diss/SD = dissimilarity/standard deviation, Contrib% = percentage contribution, Cum.% = cumulative percentage contribution.

Species	**Av.Abund**	**Av.Abund**	**Av.Diss**	**Diss/SD**	**Contrib%**	**Cum.%**
Disturbed and Undisturbed			**Average dissimilarity = 68.30**			
	Disturbed	Undisturbed				
Marphysa sanguinea	0.28	1.05	9.38	1.52	13.73	13.73
Ampelisca palmata	0.74	0.58	7.97	1.1	11.68	25.4
Notomastus latericeus	0	0.69	7.55	1.07	11.05	36.46
Callichirus kraussi	0.93	1.19	5.57	1	8.16	44.62
Euclymene spp.	0.17	0.55	5.43	0.98	7.95	52.57
Upogebia africana	0.28	0.25	4.45	0.74	6.51	59.08
Ostracoda	0.42	0	3.71	0.55	5.43	64.51
Carditella capensis	0.21	0.18	3.49	0.62	5.11	69.62
Arabella iricolor	0.27	0.11	3.23	0.62	4.73	74.35
Unknown Polychaeta	0.25	0	2.56	0.56	3.75	78.09
Nymphon signatum	0	0.28	2.46	0.57	3.61	81.7
Venerupis corrugatus	0.17	0	1.87	0.44	2.74	84.44
Hymenosoma orbiculare	0.17	0	1.77	0.44	2.59	87.03
Turritella capensis	0.17	0	1.77	0.44	2.59	89.62
Orbinia angrapequensis	0	0.17	1.55	0.44	2.26	91.88

The numerically dominant species contributing most to community structure are listed accordingly in Table 5. *Callichirus kraussi* dominated subsite D1, contributing 50.28% to community structure; *A. palmata* dominated subsite D2, contributing 58.05%; subsite U1 was evenly dominated by *C. kraussi, A. palmata, M. sanguinea* and *Euclymene* spp., whose individual contributions were approximately 22% each; and finally, *M. sanguinea* dominated subsite U2, contributing 33.36% to community structure.

Table 5: Results of SIMPER similarity tests showing dominant species that cumulatively accounted for 90% of the similarity between subsites D1, D2, U1 and U2. Av. Abund = average abundance; Av. Sim = average similarity, Sim/SD = similarity/standard deviation, Contrib% = percentage contribution, Cum.% = cumulative percentage contribution.

Species	**Av.Abund**	**Av.Sim**	**Sim/SD**	**Contrib%**	**Cum.%**
Group D1		**Average similarity: 27.48**			
Callichirus kraussi	0.82	13.82	0.77	50.28	50.28
Upogebia africana	0.55	6.34	0.48	23.07	73.35
Unknown Polychaeta	0.5	4.2	0.48	15.3	88.65
Venerupis corrugatus	0.33	1.71	0.26	6.23	94.87
Group D2		**Average similarity: 46.94**			
Ampelisca palmata	1.48	27.25	4.31	58.05	58.05
Callichirus kraussi	1.03	15.74	1.27	33.54	91.59
Group U1		**Average similarity: 76.62**			
Callichirus kraussi	1.22	17.3	7.08	22.58	22.58
Ampelisca palmata	1.17	17.05	5.89	22.25	44.82
Marphysa elityeni	1.15	16.93	5.92	22.09	66.91
Euclymene spp.	1.09	16.22	9.92	21.17	88.08
Notomastus latericeus	0.75	6.19	0.79	8.08	96.16
Group U2		**Average similarity: 49.10**			
Marphysa elityeni	0.95	16.38	1.26	33.36	81.13
Notomastus latericeus	0.64	6.66	0.48	13.56	94.69

Univariate Analysis

Macrofauna: Shannon-Weiner Diversity, Evenness, Abundance and Species Richness

Shannon-Weiner diversity (H') differed between disturbed and undisturbed sites (Kruskal-Wallis χ^2 = 4.4641, df = 1, p = 0.03461; Table 6a) and among all four sampling subsites (Kruskal-Wallis Test; χ^2 = 10.597, df = 3, p = 0.01412; Table 6a; Fig. 5a). Dunn's *post-hoc* subsite comparisons indicated differences between (1) subsites U1 and D1 and (2) subsites U1 and D2 (Table 6a; Fig. 5a). In terms of general patterns, disturbed subsites had lower diversity relative to undisturbed ones, but this trend was due to subsite U1 having highest mean diversity (1.6 ± 0.083), whilst values for remaining subsites were similar (1.02 ± 0.11, 1.03 ± 0.11 and 1.07 ± 0.18 for subsites D1, D2 and U2, respectively; Fig. 5a). Conversely, there was no significant difference in evenness between disturbed and undisturbed sites (Kruskal-Wallis χ^2 = 0.18799, df = 1, p = 0.6646; Table 6c) or among subsites (Kruskal-Wallis χ^2 = 4.7073, df = 3, p = 0.1945; Table 6c; Fig. 5b). Except for that of U1, there was a high level of variance within the evenness dataset, as indicated by the sizeable standard errors bars (Fig. 5b).

No difference in macrofaunal abundance was recorded between disturbed and undisturbed sites (Kruskal-Wallis χ^2 = 1.1539, df = 1, p = 0.2827; Table 6d) or among subsites (Kruskal-Wallis χ^2 = 5.8275, df = 3, p = 0.1203; Table 6d; Fig. 5c). Despite this, it is noticeable that the disturbed sites hosted both the smallest and largest total number of individuals, with greater data variability (Fig. 5c). Whilst species richness did not differ significantly between disturbed and undisturbed sites (Kruskal-Wallis χ^2 = 2.1741, df = 1, p-value = 0.1404; Table 6b), there was a significant difference among subsites (Kruskal-Wallis χ^2 = 8.8563, df = 3, p = 0.03126; Table 6b; Fig. 5d). However, *post-hoc* subsite comparisons tests were unable to detect significant differences between any subsites (Table 6b). It is worth noting however, that mean richness was greatest at undisturbed site U1. (U1 with 5.67 ± 0.42 species, and subsites D1, D2 and U2 with 3.5 ± 0.42, 3.83 ± 0.48 and 3.5 ± 0.62 species) (Fig. 5d).

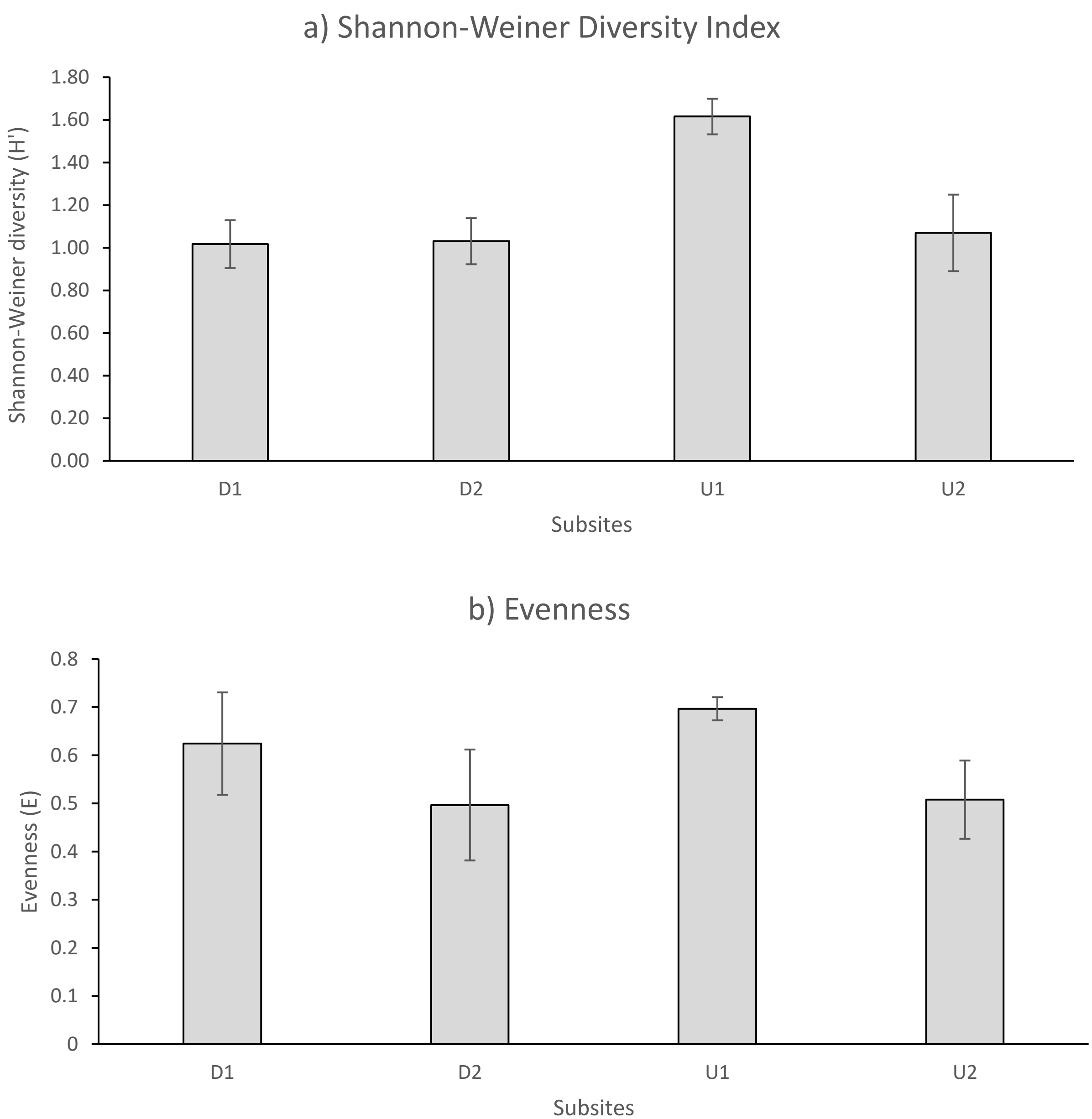
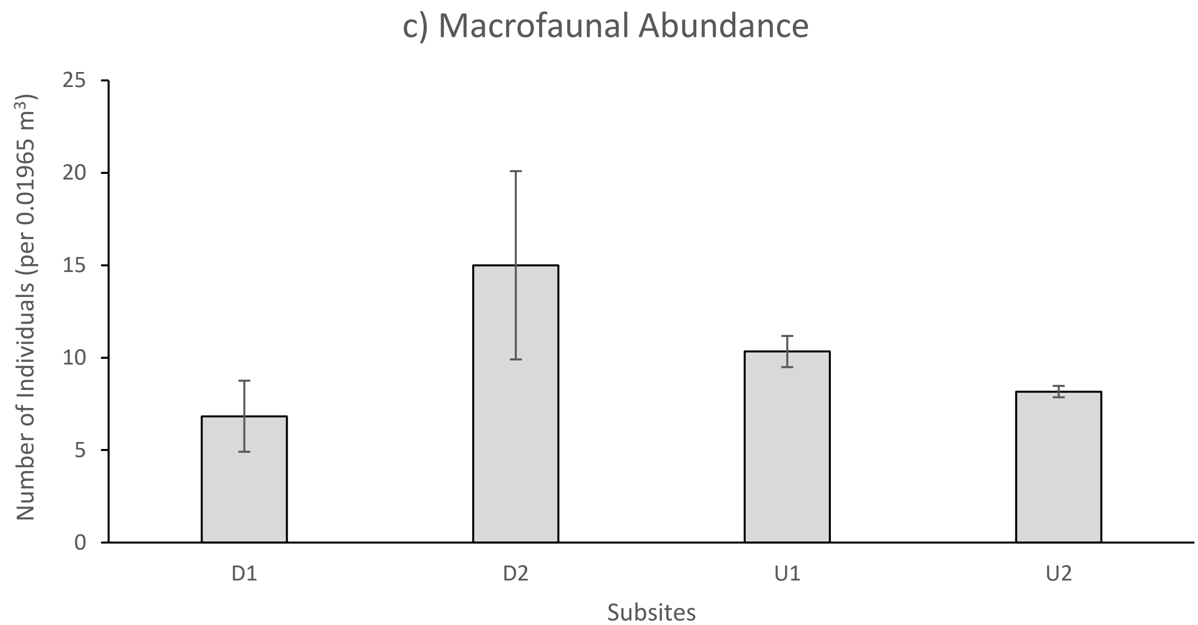


Figure 5: Spatial variability in mean (±SE) a) Shannon-Weiner diversity (H'), b) evenness, c) macrofaunal abundance, and d) species richness.



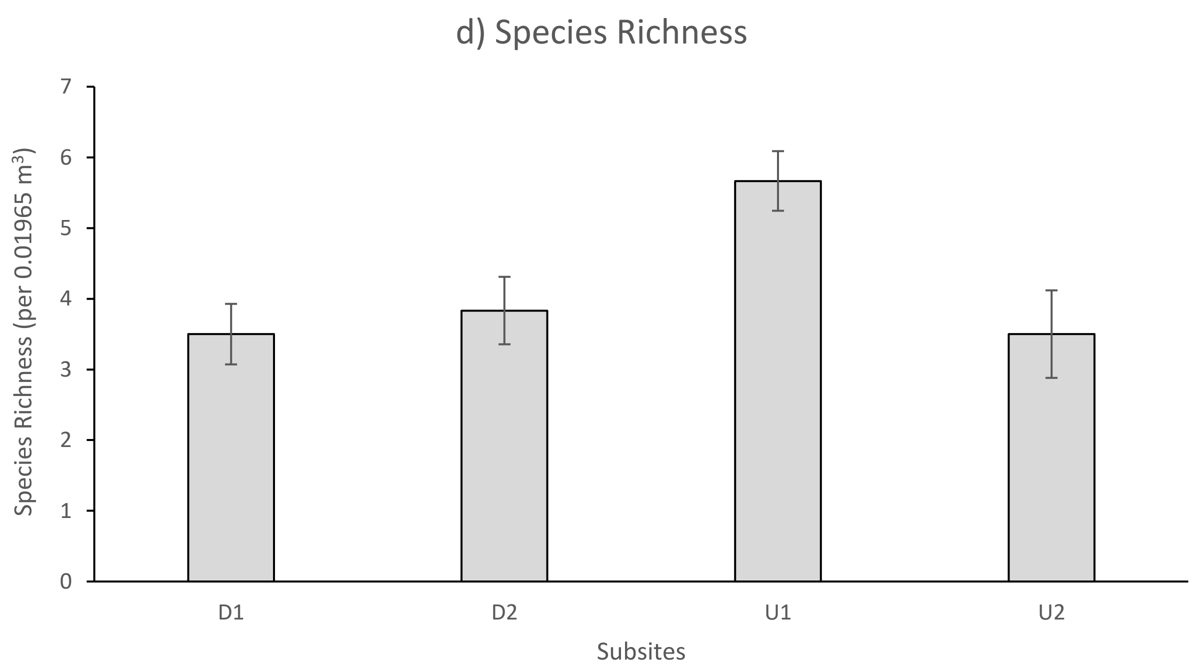


Figure 5. (Continued)

Table 6: Results of Kruskal-Wallis χ^2 tests determining effects of disturbance and subsite on a) Shannon-Weiner diversity (H'), b) species richness, c) evenness and d) macrofaunal abundance. df = degrees of freedom; p = significance level. Results of Dunn's *post-hoc* subsites show within-treatment comparisons where relevant. Obs = observed statistic, Crit = critical value.

a) Shannons's Diversity				b) Species Richness			
Kruskal-Wallis Sites Test: Disturbed vs undisturbed				**Kruskal-Wallis Sites Test: Disturbed vs undisturbed**			
Kruskal-Wallis chi-squared = 4.4641, df = 1, p-value = 0.03461				Kruskal-Wallis chi-squared = 2.1741, df = 1, p-value = 0.1404			
Kruskal-Wallis Subsites Test: D1, D2, U1, U2				**Kruskal-Wallis Subsites Test: D1, D2, U1, U2**			
Kruskal-Wallis chi-squared = 10.597, df = 3, p-value = 0.01412				Kruskal-Wallis chi-squared = 8.8563, df = 3, p-value = 0.03126			
Dunn's *Post-hoc* Subsites Test				**Dunn's *Post-hoc* Subsites Test**			
Sites comparison	Obs	Crit	p = 0.05	Sites comparison	Obs	Crit	p=0.05
D1-D2	0.08333	10.77064	>0.05	D1-D2	1.83333	10.77064	>0.05
D1-U1	11.08333	10.77064	<0.05	D1-U1	10.16667	10.77064	>0.05
D1-U2	1.00000	10.77064	>0.05	D1-U2	0.00000	10.77064	>0.05
D2-U1	11.16667	10.77064	<0.05	D2-U1	8.33333	10.77064	>0.05
D2-U2	1.08333	10.77064	>0.05	D2-U2	1.83333	10.77064	>0.05
U1-U2	10.08333	10.77064	>0.05	U1-U2	10.16667	10.77064	>0.05
c) Evenness				**d) Macrofaunal Abundance**			
Kruskal-Wallis Sites Test: Disturbed vs undisturbed				**Kruskal-Wallis Sites Test: Disturbed vs undisturbed**			
Kruskal-Wallis chi-squared = 0.18799, df = 1, p-value = 0.6646				Kruskal-Wallis chi-squared = 1.1539, df = 1, p-value = 0.2827			
Kruskal-Wallis Subsites Test: D1, D2, U1, U2				**Kruskal-Wallis Subsites Test: D1, D2, U1, U2**			
Kruskal-Wallis chi-squared = 4.7073, df = 3, p-value = 0.1945				Kruskal-Wallis chi-squared = 5.8275, df = 3, p-value = 0.1203			
Dunn's *Post-hoc* Subsites Test				**Dunn's *Post-hoc* Subsites Test**			
N/A				N/A			

Sandprawn: Abundance and Condition Factor

While mean sandprawn abundance appears to increase along a disturbance level, this trend was not statistically supported between disturbed and undisturbed sites (Kruskal-Wallis $\chi^2 = 1.6021$, df = 1, p = 0.2056; Table 7a) as well as at the subsite level (Kruskal-Wallis $\chi^2 = 1.9496$, df = 3, p = 0.5829; Table 7a; Fig. 6a). Similarity, physical condition of sandprawns were not significantly different between disturbed and undisturbed sites (Kruskal-Wallis $\chi^2 = 0.34286$, df = 1, p-value = 0.5582; Table 7b) or among subsites (Kruskal-Wallis $\chi^2 = 2.2934$, df = 3, p = 0.5138; Table 7b; Fig. 6b) but appeared to be more variable in disturbed subsites.

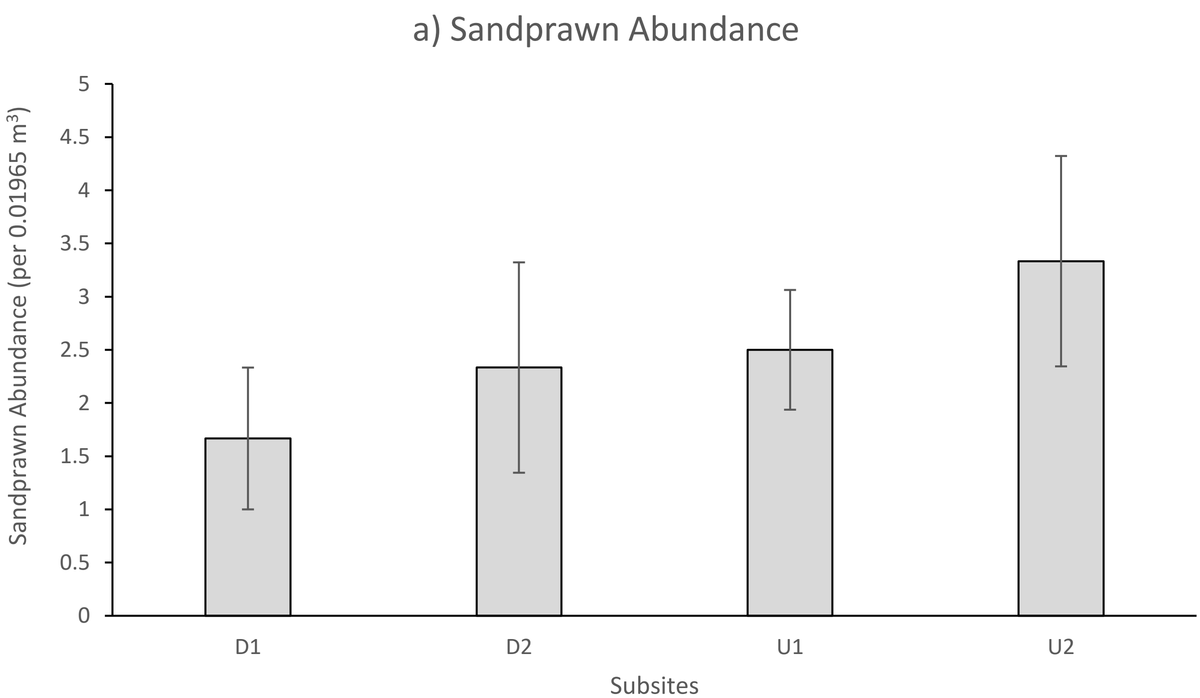


Figure 6: Spatial variability in mean (±SE) a) sandprawn abundance and b) sandprawn condition.

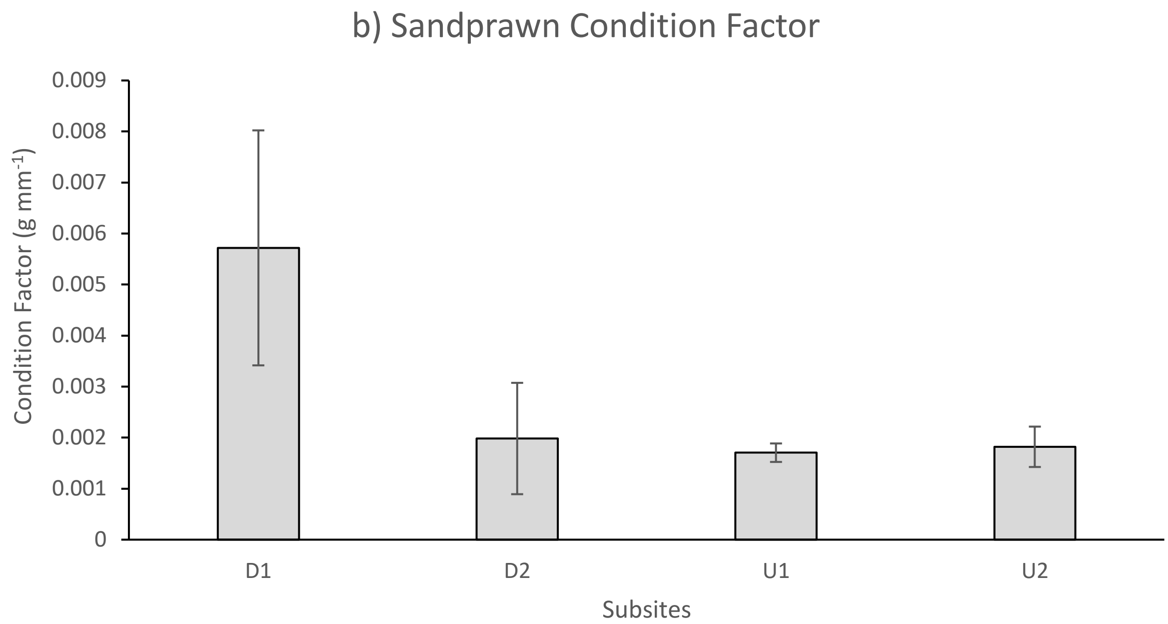


Figure 6: (Continued)

Table 7: Results of Kruskal-Wallis χ^2 tests determining effects of disturbance and subsite on a) sandprawn abundance and b) Sandprawn condition. df = degrees of freedom; p = significance level. Results of Dunn's *post-hoc* subsites show within-treatment comparisons where relevant.

a) Sandprawn Abundance
Kruskal-Wallis Sites Test: Disturbed vs undisturbed
Kruskal-Wallis chi-squared = 1.6021, df = 1, p-value = 0.2056
Kruskal-Wallis Subsites Test: D1, D2, U1, U2
Kruskal-Wallis chi-squared = 1.9496, df = 3, p-value = 0.5829
Dunn's *Post-hoc* Subsites Test
N/A

Table 7: (Continued)

b) Sandprawn Condition Factor
Kruskal-Wallis Sites Test: Disturbed vs undisturbed
Kruskal-Wallis chi-squared = 0.34286, df = 1, p-value = 0.5582
Kruskal-Wallis Subsites Test: D1, D2, U1, U2
Kruskal-Wallis chi-squared = 2.2934, df = 3, p-value = 0.5138
Dunn's *Post-hoc* Subsites Test
N/A

DISCUSSION

The broad purpose of this study was to evaluate the use of several benthic metrics in quantifying any potential impacts of human disturbance associated with bait collection and trampling within Langebaan Lagoon. It was initially hypothesised that subsites under stress of human impacts (D1 and D2) will have lower levels of benthic metrics relative to undisturbed areas (U1 and U2). The secondary objectives were to (1) test the sensitivity and robustness of different benthic metrics to assess human disturbance and (2) provide baseline information on spatial variability in these metrics to optimise future sampling designs dealing with disturbance impacts. It is thus proposed that the ecological indicator that represented the most profound difference between disturbed and undisturbed areas would be the most effective metric. The overarching goal was to provide information to park managers that could ultimately be used to develop long-term assessment plans in detecting and managing impacts of human associated disturbance.

Results obtained from this study indicate minimal effects of disturbance between the two sites of contrasting human activity in Langebaan Lagoon. Contrary to expectation, both locations hosted comparable abundance of macrofaunal organisms, including sandprawns. Although there was in general, an elevated number of sandprawns across the disturbed-undisturbed gradient, this trend was statistically insignificant. Within-treatment variability in sandprawn abundance was also high, resulting in large standard errors relative to means. Whilst sandprawn abundance was generally higher in undisturbed sites, their physical condition factor was generally lower, thus disagreeing with initial hypotheses posed. This trend was again statistically insignificant, however it does follow the work of Christie & Moldan (1977), who found that macrofauna living in the southern end of the lagoon are relatively smaller. It is proposed that because the distance from the lagoon entrance is greater, and currents are slower, incoming food material settles before it reaches the outskirt sandbanks (Christie & Moldan 1977).

The lack of a significant difference in sandprawn abundance between disturbed and undisturbed sites is supported by the assertion that sandprawns are currently being sustainably harvested, with <0.01% of total stock (approximately 800 million) being removed from Langebaan Lagoon per year (Nel & Branch 2014). However, a previous study has shown that despite only a small percentage of sandprawns being removed from the total Langebaan Lagoon population, further mortalities of sandprawns and benthic macrofauna are observed with the concomitant disturbance associated with trampling and sediment-sucking, with slow recovery as a result of sediment compaction (Wynberg & Branch 1994, 1997).

Trampling is estimated to cover a surface area of approximately 562 800m^2 of zone A's intertidal region, displacing around 6189 tonnes of sediment per year (Nel & Branch 2014), making the effects of trampling just as detrimental as the removal of sandprawns themselves (Wynberg & Branch 1997, Nel & Branch 2014). Because sandprawns are ecosystem engineers, they disproportionately contribute to ecosystem function, mainly through the activity of bioturbation, which includes the extraction of organic matter (Forbes 1973), maintenance of microphytobenthic biomass (Branch & Pringle 1987), sediment modification (Aller & Dodge 1974, Roberts et al. 1981, Suchanek et al. 1986), oxygenation and mineralization promotion (Hines & Jones 1985), as well as shaping benthic community structure (Branch & Pringle 1987). Trampling therefore indirectly impacts all these functions through direct sandprawn removal, as well as directly causing the collapse of sandprawn burrows, decreasing oxygen circulation as well as water penetration (Contessa & Bird 2004), and increasing sediment compaction (Wynberg &

Branch 1997), ultimately restricting organic matter, nutrient exchange and impairing local biodiversity (Wynberg & Branch 1997). It has been formerly documented that these sandprawns are well adapted to conditions of hypoxia (Hill 1967, Baird & Hanekom 1987), and this quality may be one reason for their persistence in sediment-compacted, disturbed areas.

Trampling has furthermore been shown to physically cause losses of microphytobenthos from the sediment into flooding tides, but also create uneven surfaces that capture pockets of overlying waters at low tide, decreasing the exposure of the remaining microphytobenthos to atmospheric CO_2 for photosynthesis (Rossi et al. 2007). This has previously been observed to cause an overall loss of local primary productivity, as seen by a reduction in microphytobenthic biomass, which is a main food source for several macrofaunal species (Rossi et al. 2007). Losses in microphytobenthic biomass may explain to some degree the decreases in macrofaunal abundance, biomass, and species richness associated with disturbance (Wynberg & Branch 1994, 1997, Rossi et al. 2007). A former study by Fielding et al. (1988) looked at surface chl-a concentrations at two comparable sites within Langebaan lagoon (Klein Oesterwal, 2km South of Shark Bay; and Bottelary, another name for Gravity) and found that at low tide, there was a similar concentration of 30 and 35 mg chl-a m^{-2} at Klein Oesterwal and Bottelary, respectively. The averaged results in this study also show no significant difference between sites, (21 and 27 mg chl-a m^{-2} for Shark Bay and Gravity respectively), however seem to display a decreased shift of value, perhaps reflecting a consequence of disturbance affecting the entire lagoon (e.g. climate change) or a simple result of time sampled (e.g. seasonal difference, as Fielding et al. (1988) did not specify the season that sampling took place). What is of importance, is the further investigation carried-out by Fielding et al. (1988), to sample areas below the immediate surface, and at more locations throughout the lagoon. Fielding el al. (1988) discovered large diatom biomasses at depts of up to 30 cm below the surface, and whilst the highest concentration of active chl-a resides in the top 1mm, this deeper population forms an important pool of potential primary producers which may resume photosynthesis given their appearance to the surface. As the sites in question experience high rates of sediment turnover, with sandprawn bioturbation bringing up to 12 kg m^{-2} of sediment to the surface per day (Branch & Pringle 1987), study of these diatom populations assumes some importance (Fielding et al. 1988). It was found that at low tide, most of the diatom biomass at Klein Oesterwal remained buried between 20 – 30cm, whereas at Bottelary, diatoms stayed within the top 10 cm, increasing the chance of upheaval and thus photosynthetic potential at the undisturbed site (Fielding et al. 1988). This finding, combined with additional sampling locations, determined that there was a general North to South increase in benthic primary production (Fielding et al. 1988). What is of additional interest is the fact that benthic primary production within Langebaan is independent of water-column nutrient concentrations, as seen by a contrasting (North to South) decline in phytoplankton and nitrates (Christie 1981, Fielding et al. 1988). The results from this study, which show no significant difference in microphytobenthic biomass, species richness, evenness, macrofaunal abundance, sandprawn abundance or sandprawn condition between disturbed and undisturbed areas, are therefore somewhat surprising.

Despite the unexpected findings, results are consistent with the study of Chandrasekara & Frid (1996), who showed that overall, macrofauna did not respond to trampling, with the exception of two benthic deposit-feeders that decreased in abundance and a few species that actually benefited from the disturbance. Wynberg & Branch (1994) also found that a species of hermit crab (*Diogenes brevirostris)* increased its abundance in response to trampling. This is because trampling, like other forms of disturbance, changes population distributions and dynamics of certain species depending on their tolerance to disturbances (Wynberg & Branch 1994, Chandrasekara & Frid 1996, Rossi et al. 2007). Also worth considering is that trampling can have contrasting effects at different life stages, as has been observed for a species of bivalve (*Macoma balthica*) that is apparently negatively impacted at adulthood but promoted as juveniles by way of beach trampling improving recruitment (Rossi et al. 2007). Wynberg & Branch's (1994) study, also conducted within Langebaan Lagoon, identified that the most sensitive species to trampling are "sedentary, shallow-dwelling, tubiculous deposit feeders," specifically drawing attention to the fragile polychaetes *Euclymene* spp. and *Notomastus latericeus.* In the present study, both species were almost exclusively found in undisturbed subsites, except for two *Euclymene* spp. individuals found in the disturbed subsite D2. This study also shows that the polychaete *Marphysa sanguinea* has a disproportionately higher abundance in undisturbed subsites versus disturbed ones. This is because trampling compacts the sediment, displacing trapped water and reducing sediment penetrability, thus making it difficult for soft-bodied, shallow-burrowing polychaetes to survive (Wynberg & Branch 1994).

The implication here is that although abundance and richness data may not change significantly between disturbed and undisturbed sites, there could be subtle changes in community composition. In this study, even though there was a higher abundance of polychaetes in undisturbed subsites, and a numerical dominance of crustaceans at disturbed subsites, multivariate analysis showed no species assemblage differences between disturbed and undisturbed sites. Fraschetti et al. (2001) also applied a hierarchical design testing bait collection along shallow subtidal hard substratum assemblages and found considerable sources of macrofaunal community variation within sites of the same treatment. Multivariate analyses from this study indeed showed that assemblages differed between subsites, whilst failing to detect differences between disturbed and undisturbed sites.

The ability of macrobenthos to indicate human disturbance can therefore be a rather complex and time-consuming approach if population dynamics of species within the system are to be considered.

In this study, the only significant differences recorded between disturbed and undisturbed areas were organic matter content and Shannon-Weiner diversity, both of which were higher in undisturbed areas, suggesting that most macrofaunal assessments (macrofaunal abundance, species richness, evenness, sandprawn abundance and sandprawn condition) utilized were ineffective in signalling human disturbance under conditions in which the study was conducted.

The possibility does exist that other factors unrelated to disturbance may offset or contribute to variability in metrics and confound human disturbance effects in Langebaan Lagoon. Potential confounding factors include spatial variability in productivity, site-specific ecological factors, and/or a result of inter-community species composition and interaction. It is possible that the dominant species (*C. kraussi,* with >50% abundance) is more responsible for the community structure than disturbance effects in disturbed sites, and that the combination of higher diversity and heterogeneity explains community structures in undisturbed sites. Superimposed upon this is the effect of time, with timing of the study and temporal resolution impacting the direction and magnitude of differences among disturbed and undisturbed areas likely to be detected. A previous study examining effects of trampling on unvegetated tidal flat infauna showed that abundances of dominant taxa were higher in the peak of summer in concurrence with increased tourism and trampling, ultimately changing (species either increased, decreased or remained the same in abundance) the macrofaunal community structure for the season (Chandrasekara & Frid 1996). These changes however, were not apparent in winter when the trampling intensity was lower, nor were they recorded in less trampled sites throughout the year (Chandrasekara & Frid 1996). In my study, the sampling period took place during the transitionary period of spring into summer. Perhaps differences observed in benthic community structure relates to the commencement of the summer season, where the significant results of lower organic matter content and Shannon-Weiner diversity show the first signs of disturbance-induced community shift. This is likely given that human disturbance typically increases during peak summer months in the lagoon.

Within Saldanha Bay, the discharge of wastewater effluents still contributes to local elevated nutrient concentrations, specifically nitrates and phosphates used in fertilizers (Cloern 2001). These nutrients stimulate growth and primary production of rapid-growing phytoplankton and ephemeral macroalgae at the expense of slower-growing vascular plants such as seagrasses (Cloern 2001). In extreme cases, large amounts of nutrient enrichment can pollute surrounding conditions, creating an oxygen-depleted environment leading to increased species asphyxia and mortality. In addition to anthropogenic inputs, Saldanha Bay is located in the Benguela upwelling zone, which brings in critical influxes of nutrient rich waters that sustain primary production within the bay. However, because of an existing thermocline seldom shallower than 5m, these nutrient rich waters enter rather slowly, if not at all, to the shallow waters of Langebaan Lagoon (Cloern 2001). It is possible that this influx of nutrients into zone A of Langebaan Lagoon may provide a nutrient pulse locally, just enough to offset potential disturbance-related losses in zone A, thus explaining the comparable macrofaunal metrics between disturbed and undisturbed sites. This idea though is complicated by the significantly lower quantities of organic matter located at disturbed sites. Although Gheskiere et al. (2005) showed that beach trampling and mechanical beach clean-up was discovered to be the main cause for losses to organic matter, their study also showed that this decrease in organic matter limited the richness of infaunal communities, which was not evident in this present study. Gheskiere et al. (2005) further confirmed that total organic matter was the single most important factor for observed differences between infaunal community structure between tourist verses non-tourist beaches. With the complex dynamics of organic matter distributions, use and displacements throughout the ecosystem, not to mention the influence of Langebaan's current velocity and direction, this metric alone becomes impractical in indicating measures of disturbance, and can rather be used as a supportive tool for quantifying ecosystem condition in relation to disturbance. A globally applicable study conducted by Hyland et al. in 2005, showed that benthic organic matter concentrations of approximately 10 mg g^{-1} support the most diverse coastal sediment ecosystems. Whilst organic matter is a vital food source for benthic fauna, Hyland et al. (2005) found that over a critical threshold abundance of 35 mg g^{-1}, detrimental effects to the ecosystem are observed, specifically causing reductions in macrofaunal species richness, abundance and biomass, as a result of organic matter build-ups that deplete oxygen and promote toxic by-products. With appropriate conversions, (organic matter % appropriately converted to mg organic matter/g sediment, and increased by a factor of 3 to correct for the underestimation of organic carbon associated with CHN analyser methodology; Leong & Tanner 1999) the data collected from Langebaan translates into approximately 15.27, 14.23, 16.15 and 18.33 mg g^{-1} for sites D1, D2, U1 and U2, respectively. These quantities relative to Hyland et al. (2005) findings suggest that all subsites are well below the threshold of exposure to the dangers of organic matter overabundance.

The focus of discussion thus far has, for the most part, addressed the unexpected similarities in benthic metrics between disturbed and undisturbed areas. Interestingly, there were more significant differences recorded at the subsite level than in relation to disturbed and undisturbed sites. Univariate analysis showed significant differences between microphytobenthic biomass, organic matter content, Shannon-Weiner diversity and species richness between subsites. The significant differences in Shannon-Weiner diversity between subsites arises from one of the undisturbed sites (U1) displaying a much higher value relative to the other subsites. Shannon-Weiner diversity results suggest that disturbed areas support lower, yet rather similar levels of macrofaunal diversity, yet undisturbed sites are more variant in their diversity, indicating the possibility of undisturbed areas being more heterogenous. Multivariate analysis further supported the observed pattern of subsite differences, and the breakdown of species contributions within-subsites revealed that each subsite comprised a unique macrofaunal community. Previous work done to investigate the macrofaunal species composition of intertidal sandbanks within Langebaan have therefore become incomparable. The work of Puttick (1977) and Christie & Moldan (1977) are excellent documentations that record insights of Langebaan lagoon's historical macrofaunal communities, however these findings again show high localized variations between sites, and because the sampling locations in these historical studies are kilometres away from the subsites used in this study, become unrealistic comparisons. Despite this, it may be worth mentioning that *A. palmata* was a dominating species found at both northern and southern regions within Langebaan within my study as well as that of Christie and Moldan (1977). These findings support the ideas that the effects of disturbance are minimal, and differences are a result of localised subsite conditions.

A major find emanating from the study is that sample sizes used were too small, and that the areas of disturbed and undisturbed sites sampled was low. However, this statement must be viewed in the context of time-constraints associated with a course-work degree. Problems with low sample size or area are evident upon examination of high variability in data in some cases. This is a major disadvantage that may explain to some degree why datasets failed to pass tests of normality and homogeneity of variance. It is therefore critical that future studies quantifying disturbance effects deal with the issue of sample size and sampling area to avoid problems relating to high data variance. In this regard, data collected from this study may be usefully incorporated into future analyses (e.g. power analyses; MacCallum et al. 1966) to determine appropriate sample sizes required to answer questions related to disturbance impacts.

To summarize the different benthic metrics for their respective advantages and disadvantages, it becomes clear that macrofaunal assessments are the most informative, given the various ways to analyse the data. Additionally, there was a higher source of literature to comparatively review results, in comparison to microphytobenthic and organic matter content. All benthic metrics are cost-friendly, easy to sample and ecologically non-invasive, and show very little disadvantages. The disadvantages in this study mainly arose from lack of sample size, both spatially and temporally.

In conclusion, the benthic metrics applied in this study to investigate the effects of human disturbance revealed minimal disturbance effects yet supported more significant subsite differences. This implies either (1) human disturbance is sustainable in the face of increased surrounding developments, (2) other factors unrelated to disturbance are offsetting the impacts of human influence, (3) the metrics themselves were inadequate in detecting disturbance due to low sample size or more likely (4) an interlace of all three. Despite low sample size and areas sampled, this study has provided important baseline data that can be used to optimise future study designs. It also compares the advantages and disadvantages of benthic metrics used, and highlights key considerations in developing further studies on disturbance impacts in Langebaan Lagoon.

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APPENDIX

Solving for chlorophyll-a concentration per sample

A calibration curve was made using three known concentration of chlorophyll-a (x = 0, 0.1 and 1 mg chla L^{-1}) and the resultant absorbance readings measured by the Turner Designs Trilogy fluorometer were 2.83, 1485.3 and 15860.25 RFU, respectively. The calibration curve was then plotted graphically with a trendline (Fig. A).

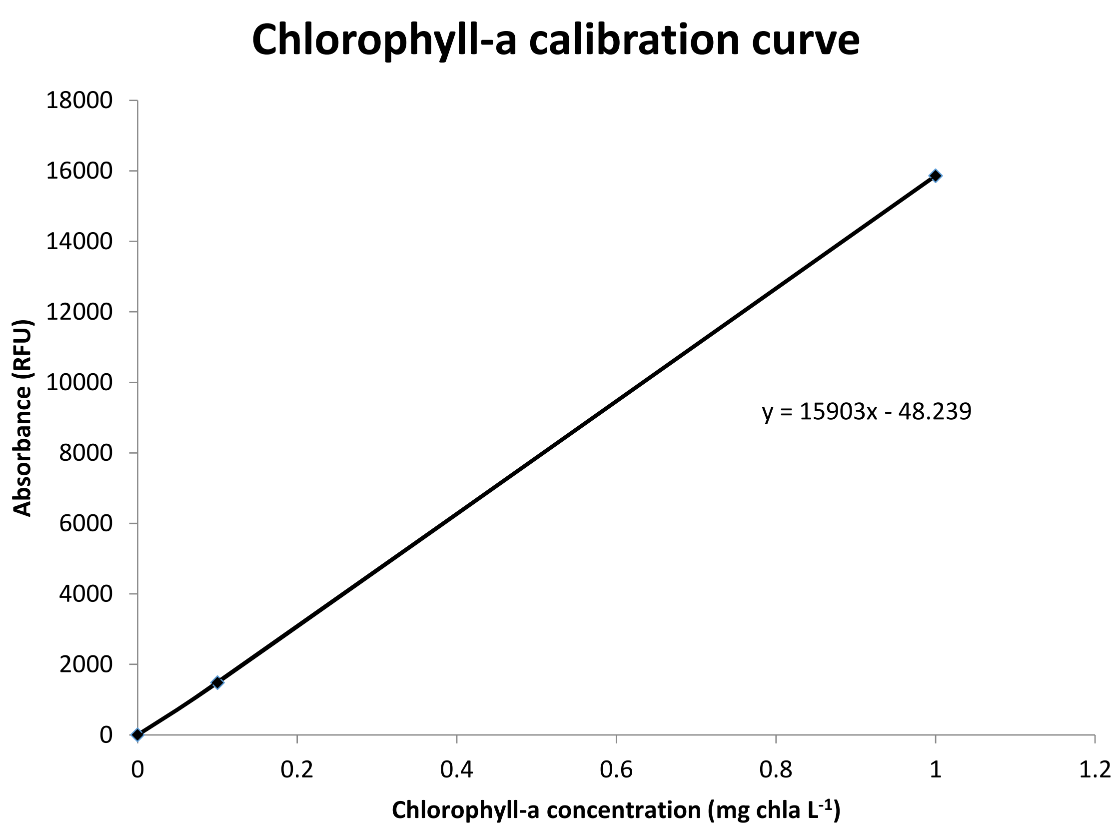

Fig. A: Calibration curve of chlorophyll-a, where three known chl-a concentrations were plotted against resultant absorbance readings to obtain trendline equation.

The resultant trendline equation was then rearranged ($X = (y - 48.23)/ 15903$) such that any new sample's absorbance readings (y) (RFU) can be inputted to solve for the unknown concentration of chlorophyll-a (x). It is assumed that chlorophyll-a is only at the surface as this is where photosynthesis occurs, thus the resultant x values were then converted from liters to meters squared, given the following equation:

$$\text{Concentration (mg chla m}^{-2}\text{)} = x * 0.03 / \pi r^2$$

Where x = concentration of chlorophyll-a as solved from the calibration curve, 0.03 = volume of acetone solution used in the sample in litres, and r = radius of the sample core in metres.