Temporal Interactions with Flamingo Foraging Plasticity:

Ecological effects on basal resources and benthic heterogeneity

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Abstract

The role of predation as a structuring agent of communities has been a focal area of research in marine ecology. Conversely, studies focusing on foraging plasticity, particularly by shorebirds, and consequences for benthic community structure, heterogeneity and ecosystem functioning have been limited in marine soft-sediments. Temporal interactions with foraging plasticity is an even greater knowledge gap. The primary goal of this dissertation was to expand on current understanding of foraging plasticity and the broader ecological role of Greater Flamingos as predators in marine sedimentary ecosystems. The specific aim was to test the long-term effects of different foraging structure sizes (which is a subtle form of foraging plasticity) on sedimentary assemblages following foraging disturbances. *In situ* comparisons of large and small foraging structures created by the flamingos with adjacent non-foraged sediments (controls) indicated that small channels had greater concentrations of sediment organic matter relative to large channels following feeding. Additionally, small feeding structures supported greater abundances of the burrowing amphipod *Urothoe grimaldii* and the grazing gastropod *Assiminea globulus* along with elevated size-specific sediment deposition rates. These results shed light on the differential time-dependent impacts flamingo foraging plasticity can generate on basal trophic resources and higher consumers. Results also showed that irrespective of size, feeding channels made by flamingos generally became enriched with microalgae following foraging, with this enrichment effects spilling over into non-foraged controls sediments. This indicates that foraging by flamingos has the potential to create resource islands that become enriched with microalgae over time, with effects spilling over into adjacent non-foraged areas. Importantly, these positive effects may oppose the negative effects of bioturbation by burrowing sandprawns on productivity, which is a dominant process in the study area. This study emphasizes the importance of Greater Flamingos in regulating basal resource supply, community structure and spatio-temporal heterogeneity and has highlighted the need for predation models within sedimentary environments to incorporate time-dependent effects of foraging plasticity into current thinking.

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Chapter 1: Introduction

1.1 Predation, competition and disturbance

A major goal of ecology is to understand the dominant forces involved in structuring communities and how such forces determine community stability, structure and broader ecological functioning (Peterson 1977). Three dominant forces considered to be important determinants of community organisation are predation, competition and disturbance (Reise 2002).

Predation refers to interactions involving the consumption of one animal by another, resulting in various direct and indirect biotic interactions (Estes & Palmisano 1974; Paine 1980; Baum & Worm 2009). A classic indirect effect of predators is encapsulated in the concept of top-down trophic cascades, which describes a decrease in abundance of prey but an associated rise in abundance of components consumed by prey (Carpenter *et al*. 1985; Shears & Babcock 2002; Ripple & Beschta 2012). This is well-demonstrated by Estes & Palmisano (1974), who showed that overexploitation of sea otter populations off the Near Islands through hunting by humans, led to major faunal and floral differences compared to the Rat Islands, an island in close proximity. Specifically, overexploitation of sea otters leads to decreased predation on sea urchins (important prey item of otters), which consequently caused overgrazing of the surrounding kelp forests.

A number of studies have shown that ecosystem functioning, structure and resilience are dependent on the relative abundance of predators within an ecosystem, and that changes in abundance can have important consequences for community organisation (Paine 1969; Quammen 1981; Quammen 1984; Wilson 1990; Thrush *et al.* 1994; Glassom & Branch 1997; Baum & Worm 2009; Ripple & Beschta 2012). Such effects of predators are often mediated through alterations in intra- and interspecific competitive interactions. For example, Gurevitch *et al.* (2000), using a factorial meta-analysis on results of 20 peer-reviewed articles, highlighted the importance of predator presence in decreasing competitive intensity. Therefore, predator declines or removal magnifies competition for a limiting resource (space or food; Connell 1983), thus altering community organisation and lowering diversity, principally by promoting competitive exclusion (Paine 1966; Paine 1974; Lubchenco 1986). Exclusion essentially refers to the displacement of an inferior competitor from a local patch and hence a community. This process has been demonstrated in Paine's (1974) experimental study examining the interactions between a predatory starfish (*Pisaster ochraceus*) and a competitively dominant mussel species (*Mytilus californianus*) in Washington. Predation restricted the distribution of the mussel to a well-defined band in the mid-littoral zone of a rocky shore. Following experimental removal of the starfish, mussels expanded their vertical range and dominated the lower shore. In addition, displacement of inferior competitors by mussels lower down the shore lead to a reduction in species diversity through reduction in coexistence.

Although competition effects driven by predation do affect community organization, disturbance related effects are also important pathways responsible for regulating community structure in ecosystems (Thistle 1981; Picket & White 1985; Brey 1991; Wynberg & Branch 1994; Glassom & Branch 1997; Helmus *et al*. 2010). Broadly, disturbance events are typical of many ecosystems, but they vary in frequency, intensity and the strength to which it impacts resident communities (van der Maarel 1993). A disturbance event can be defined as any event that initiates a change in species population either through removal or mortality or by changing the basal resources of the community (Zajac and Whitlatch 1982a). Consequently, these disturbances can have different effects on communities which vary over different temporal and spatial scales (Hall *et al.* 1994; Watling & Norse 1998). Disturbances act on communities by inducing mortality or by physically damaging organisms or impairing their physiology (Connell 1978; Collins and Gibson 1990; Thrush *et al.* 1996; Olff and Ritchie 1998). Disturbances can generate a diverse array of consequences following removals of individuals, including a reduction in competition intensity, increasing substrate-availability for recruitment and enhancing resource availability for opportunistic colonisers (Thistle 1981; VanBlaricom 1982; Glassom & Branch 1997; Pringle 2008).

There are two main types of disturbances that impact ecosystems (Probert 1984). Physical disturbances typically occur at large spatial scales (km^2) and are generally caused by large physical processes such as storms (McCall 1978), fire (Taylor 1973; Collins and Gibson 1990), pycnocline associated internal waves (Carter 1976) and tidal sand movement (Grant 1983). The second disturbance type is biologically generated and typically smaller in scale (either cm^2 or m^2). These disturbances are caused biotically either through feeding (e.g. rays feeding on benthic communities (Gregory *et al.* 1979); elephants damage through feeding (Laws 1970; Pringle 2008) or through the creation of structures and burrows, for example dams made by beavers (Naiman 1988) or mounds made by burrowing *Callianassa* (Aller & Dodge 1974). Whether large- or small-scale, biological disturbances are critical for maintaining spatio-temporal heterogeneity, community organisation and ecological function (Pettex *et al.* 2012).

1.2 Foraging disturbance and Succession

In shallow marine sediments, which is the focus of this dissertation, benthic predators impact ecological processes through trophic (consumption) and non-trophic (ecosystem engineering – altered abiotic conditions) disturbances, thereby providing new space and resources for recolonization and larval recruitment through a series of ecological stages termed succession (Wilson 1990; Thrush *et al.* 1991; Glassom & Branch 1997). For example, dugongs frequently feed on seagrasses in eastern Africa and as a result disturb the benthos (Wake 1975; VanBlaricom 1982). Gray whales forage in the Benthic Sea for benthic invertebrates and create large pits as a result (VanBlaricom 1982) and sea otters dig for echiurids and clams resulting in excavation structures (Shimek 1977; VanBlaricom 1982). Specifically, succession can be defined as the change in sequence of assemblages colonising a disturbed patch following a disturbance (Zajac & Whitlatch 1982b; Wilson 1990).

Margalef (1968) provided some generalisations on the commencement of succession and the sequence of change that follow. He argued that a disturbance is followed by an initial biomass increase, and a subsequent elevation in primary production, resulting in increased diversity. This initial phase is followed by growth of biogenic structures, increases in inactive organic matter levels, declining population/community variability and increases in long-term efficiency. Close to the end point of succession, there is stability in organismal abundance at the patch-scale.

There have been various other studies that have proposed models of succession over a wide range of ecosystems (Johnson 1970; Johnson 1972; Grassle & Sanders 1973; Connell & Slatyer 1977; Thistle 1981; Rhoads & Boyer 1982; Zajac 2001). However, it is important to note these conceptual models are based on different communities with distinct differences in migration and emigration constraints, which determine assemblage responses to disturbances (Thrush *et al.*

1991). It is therefore likely that a combination of elements from these models likely predicts community responses to disturbance (Johnson 1970). Irrespective of variation in models thought to drive succession, it is understood that general ecological factors influence the course of successional dynamics. These factors include resource availability and quality, life history traits of colonisers, the scale of the disturbance as well as the local hydrodynamics in the case of marine sediments (Thrush *et al.* 1991).

Resource availability affects succession because disturbances enhance the availability of trophic resources for other consumers that would otherwise be unavailable (Thrush *et al.* 1991). In marine sediments, depression pits that are formed by foraging predators typically accumulate organic matter due to changes in local hydrodynamics that dampen flow and facilitate deposition; This higher organic matter, reduced flow and increased deposition tend to increase the attractiveness for colonisers (VanBlaricom 1978; VanBlaricom 1982; Thistle 1980; Thistle 1981; Thrush *et al.* 1991).

However, it has been suggested that temporal changes in resource quality may be more important than resource availability in driving patterns of succession. VanBlaricom's (1982) study examining ray foraging and its effect on infaunal communities demonstrated that only certain early-colonizing organisms are able to readily utilize the detrital carbon in ray pits. The next stage of succession occurred once microfloral and bacterial populations developed in pits and converted detrital carbon into a more attractive state.

Predicting how succession proceeds following a disturbance in marine sediments requires an appreciation that there are two major ways in which recolonization may occur, viz. through adult macrofauna invading from adjacent patches or through larval recruitment from the water column (Probert 1984). Probert (1984) argued that the potential for recolonization to occur through adult macrofaunal immigration is inversely related to the size of the disturbed patch. Thus, smaller disturbed patches have a greater likelihood of recolonization predominately by adult macrofauna immigration (Probert 1984). This model however, may not hold true for larvae of micro, meio and macrofauna, as it has been suggested that these groups will colonize any given patch size provided that settlement cues are adequate and/or that local hydrodynamics are strong enough to transport larvae to disturbed patches (Probert 1984; Snelgrove 1994).

The above-mentioned points highlight the need to understand traits of assemblages in order to understand how succession proceeds following a disturbance. This is further underscored by conceptual models of succession, which suggest that opportunistic species with *r*-selected traits are first to colonise after disturbances, which are then followed later by less opportunistic, longer lived *K*-selected species (Zajac and Whitlatch 1982b). In Thistle's review (1981) of responses of soft-bottom communities to disturbances, he suggested that *r*-selected species colonize first due to them being resource specialists that spend a small portion of their lives in a disturbed patch. As such, these individuals exploit a number of disturbed patches throughout their lifetimes (Whitlatch 1980). He further suggested that the decline of opportunists from disturbed patches is not driven by displacement by *K*-selected colonists, which are better resource competitors, but rather by resource exhaustion, which prompts emigration and exploitation of other disturbed patches.

The third factor determining community responses is the spatial scale over which disturbances occurs, mainly due to different sized structures created by disturbances having different morphological traits and therefore interact differently with local hydrodynamic processes. A summary of research showing speed of recolonization of benthic fauna to large and small disturbances is reported in Table 1. Smith and Brumsickle (1989), for example, showed that post-larval immigration varies inversely with the size of the disturbed patch in intertidal sediment, with colonization occurring more rapidly in smaller experimental plots (50 cm^2) than in larger ones (1750 cm^2). Therefore, recolonization may occur rapidly in smaller disturbance patches (<1 m^2) but may occur over a period of months for larger patches (Sherman & Coull 1980; Zajac and Whitlatch 1982b; Zajac & Whitlatch 2003).

Lastly, effects of local hydrodynamics are highly influential in determining community succession, particularly in fluid sedimentary systems. (Eckman 1979; Eckman 1983; Emerson & Grant 1991; Turner *et al.* 1995). Hydrodynamics play an important role in trophic resource distribution and retention (Thistle 1981) as well as in the dispersal of adults and larvae (Zajac *et al*. 1998). Hydrodynamic processes indirectly influence resource supply and provides a means of immigration for adults and larvae. Importantly, local currents act on each disturbance structure differently, depending on morphological attributes (Zajac *et al*. 1998). Thus, community response and succession following disturbances are complex and numerous.

Table 1: Summary of research showing speed of recolonization of benthic fauna for large and small disturbances.

Reference	Disturbance Source	Location	Disturbance size	Colonisation Speed to disturbances
Grant 1981	Experimentally defaunated plots	Debidue Flat, South Carolina	Small (0,089m^2)	Rapid recolonization (24 days)
Zajac and Whitlatch 1982b	Experimentally defaunated plots	Alewife Cove, Connecticut	Small (0,229m^2)	Rapid recolonization (14-30 days)
Smith and Brumsickle 1989	Experimentally defaunated plots	Barnstable Harbor, Massachusetts	Small (0,005m^2) Large (0,175m^2)	Small plots were colonized faster than large
Thrush *et al* . 1991	Feeding eagle rays	Manukau Harbour, Auckland	Small (Largest being 95cm ± 37 cm)	Rapid recolonization (12 days)
Thrush *et al* . 1996	Experimentally defaunated plots	Manukau Harbour, Auckland	Large (3.24m^2) Small (0,203m^2)	Small recovered faster than Large
Beukema *et al* . 1999	Experimentally defaunated plots	Balgzand, Wadden Sea	Large (120m^2)	Slow recolonization (≈3-4 years)
Zajac and Whitlatch 2003	Experimentally defaunated plots	Poquonock River estuary, Groton	Large (1m^2)	Slow recolonization (4,5 months)

1.3 Foraging plasticity and Flamingos as epibenthic predators

Foragers spend a significant amount of time on acquiring food resources (Drent & Daan 1980). This is necessitated by the need to acquire energy in order to ensure survival and reproductive success (Lemon 1991). However, foraging is constrained by the abundance, distribution and predictability of food resources in space and time (Bell 1991; Otto *et al.* 2008). Due to these constraints, foragers compensate by optimizing their net energy intake by adjusting foraging behaviours and selection of food resources that enhance their reproductive fitness (Pyke 1984; Stephens and Krebs 1986; Pettex *et al.* 2012). Foragers overcome variability in resource availability, quality and its distribution by employing plastic foraging strategies in accordance to available food resources (Greeff & Whiting 2000; Lewis *et al.* 2008; Paiva *et al.* 2010; Delclos & Rudolf 2011; Katano 2011).

Foraging plasticity has been demonstrated, for example, in Cory's shearwater - *Calonectris diomedea* (Paiva *et al.* 2010). Birds that foraged along the neritic shelf used shorter dives compared to those feeding in pelagic areas. This was due to pelagic environments being less profitable in resources compared to nutrient-rich coastal shelf areas, resulting in the pelagic shearwaters investing more effort per unit foraging time to make up for the scarce food resources. This study illustrates the adaptability of shearwaters to forage in environments in which prey resources are variable.

Another predatory group of birds that displays plasticity in foraging are flamingos. Flamingos are charismatic predatory shorebirds that are capable of modifying their feeding behaviours to feed on diverse aquatic prey (Allen 1956; Jenkin 1957; Arengo & Baldassarre 1999; Brown *et al.* 2005). The Greater Flamingo (*Phoenicopterus ruber roseus*), which are known to occur in wetlands and coastal areas (McCulloch *et al.* 2003), is the focal predator under investigation in this study. Greater Flamingos are filter-feeders that consume small invertebrates in subtidal and intertidal zones. There are accounts of *P. ruber roseus* employing two main foraging behaviours (Glassom & Branch 1997). The first technique can be described as ‘walk-feeding’, which involves flamingos walking while sweeping their bills in an arc over surface sediments, thereby creating channel like structures in the benthos (Figure 1A). The second foraging technique involves flamingos ‘stamp-feeding’, in which they stamp on the sediment while walking in a circle; this results in pit-like structures being formed in the sediment (Figure 1B) (Bildstein *et al.* 1991; Glassom & Branch 1997; Brown *et al.* 2005). However, there are more subtle aspect to their plastic foraging behaviour that has been observed in the field but rarely studied. This involves flamingos producing foraging structures of different sizes, presumably in response to variability in prey quantity and quality (Gihwala *et al.* 2017).

Flamingos are known to flock to wetlands in large densities in order to feed. Their high densities in marine soft-sediment habitats imply that they could generate significant impacts on benthic processes and communities (Glassom & Branch 1997; Rodríguez-Pérez *et al.* 2007). In this context, some studies have used exclusion experiments to quantify the predation effects of flamingos on benthic communities. Glassom and Branch (1997), for example, found that macrofaunal abundance increased 3 fold in subtidal exclusion sites and 1.5 times in intertidal exclusion sites compared to controls following flamingo exclusion. Similarly, Rodríguez-Pérez *et al.* (2007) reported reduced chironomid abundance but a greater proportion of large chironomid larvae in a temporary marsh in the presence of the Greater Flamingo in the Doñana National Park. With the exception of these studies, however, there have been very few studies quantifying the ecological effects of flamingos on marine sandflat ecosystems (Glassom & Branch 1997; Bildstein *et al*. 2000; Gihwala et al. 2017).

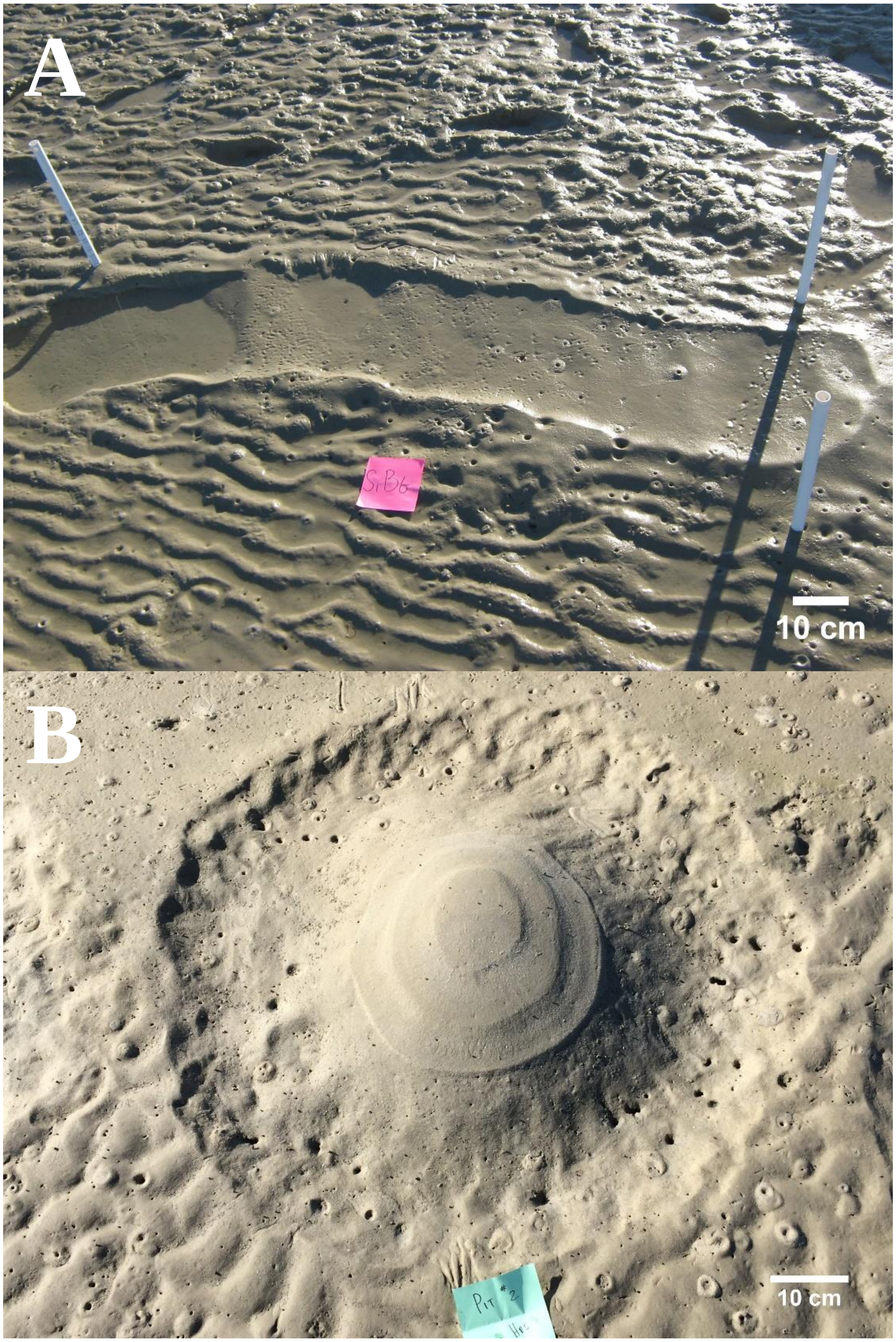

Figure 1: Example of the channels (A) and pits (B) produced via the two main foraging behaviours of Greater Flamingos. Photos were taken during low tide at Oesterwal, Langebaan Lagoon. Photo B credits: Kirti Gihwala.

Flamingos, like other epibenthic predators, impact ecological process and community structure through direct consumption of prey and by modifying abiotic properties of sediments (Thrush *et al.* 1991; Thrush 1999). Modification of surficial sediment changes local topography and hydrodynamics (Nowell & Jumars 1984), which result in biotic displacement, greater exposure to secondary predation, and more opportunities for recolonization (Thrush *et al.* 1991). Furthermore, flamingos are capable of altering benthic ecosystems by enhancing nutrient fluxes across the sediment-water interface through bioturbation (sediment disturbance; Comin *et al.* 1997; Meysman *et al.* 2006; Pillay & Branch 2011; Green & Elmberg 2014). The combined trophic and non-trophic effects of flamingos foraging, particularly in dense aggregations, probably results in these shorebirds having a significant impact on the structure and functioning of marine soft-sediment ecosystems. This is made more significant by their activities being of different intensities and frequencies, which likely create a mosaic of benthic patches that are in different stages of succession (Johnson 1970; VanBlaricom 1982; Thrush *et al.* 1996; Gihwala et al. 2017).

This study focuses on temporal interactions with channel foraging plasticity exhibited by Greater Flamingos within intertidal sandflats of Langebaan Lagoon, a marine-dominated lagoon along the west coast of South Africa. This study builds on prior work that quantified the instantaneous effects of flamingo foraging plasticity on benthic assemblages. The specific aim of this dissertation however is to test the long-term effects of different channel sizes (a subtle form of foraging plasticity; Gihwala *et al.* 2017) on sedimentary assemblages following foraging disturbances. I hypothesise that channel-foraging plasticity would affect basal trophic resources and prey assemblages in contrasting ways over time due to structures having different morphological traits and hence contrasting hydrodynamic forcing.

Chapter 2: Materials and Methods

2.1 Study site

The study took place in intertidal sandflats of Langebaan Lagoon, a marine lagoon situated on the west coast of South Africa (33°11’27’’S, 18°07’37’’E and 33°03’54’’S, 17°58’07’’E; Pillay *et al* 2011; Figure 1). The system is 4 km wide and 15 km long and connects to the Atlantic Ocean via a thin tidal inlet near Saldanha Bay (Compton 2001). Langebaan Lagoon has semi-diurnal tides, with a spring tidal range of 1.8m (Flemming 1977; Compton 2001). The lagoon receives negligible sediment or freshwater inputs, experiences a semi-arid Mediterranean climate and an annual rainfall of 240mm (Compton 2001). The lagoon is considered a key wetland for waders within South Africa and has been identified by BirdLife International to be an important bird area, accounting for 10% of the South African coastal wader populations (Underhill 1987; Pillay *et al.* 2010).

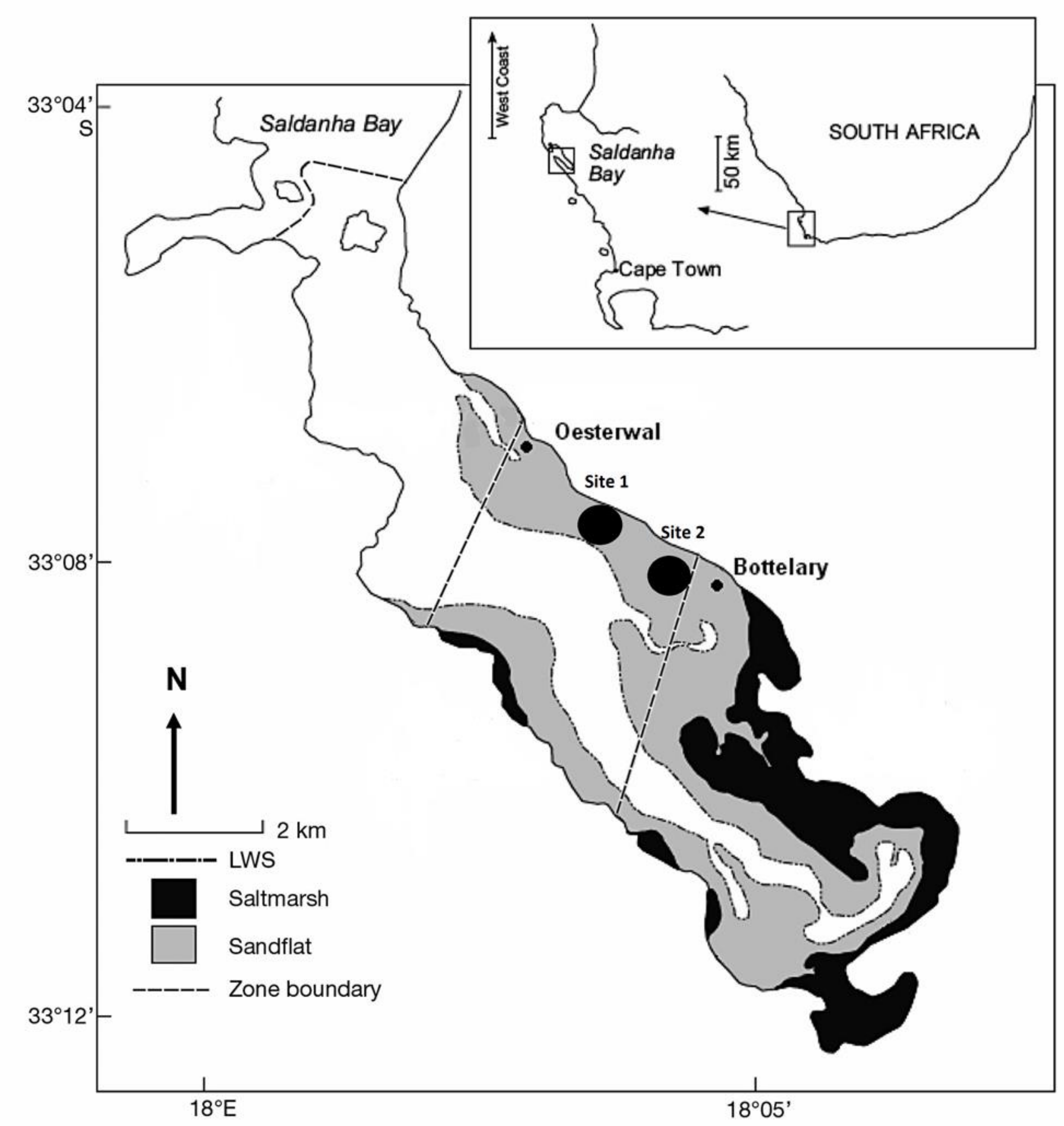

Figure 2: Map showing the geographical position of Langebaan Lagoon along the South African coastline together with the park zones and sampling sites. LWS: low water spring (modified from Pillay *et al.* 2010)

2.2 Structure age standardization

A preliminary field study was conducted prior to the onset of sampling in order to (A) confirm the appearance of newly formed channels (Gihwala *et al.* 2017) and (B) determine the number of days that channels persist in sediments. These steps were crucial for the identification of newly created channels and for identifying the time-period over which to assess the temporal change occurring in the channels. For the preliminary study, two $25m^2$ mid-shore plots were marked during low tide within flamingo feeding areas at the two sampling sites for the main study (Figure 2) and the sediment raked to smooth out previous foraging structures. Channels that were produced one day after the plots were raked were marked, staked (to prevent additional flamingo disturbance) and photographed. Marked channels were photographed again after 1, 2, 3, 5 and 8 days. This resulted in the creation of a photographic library of changes in appearance of channels from creation to disappearance in response to wave and tidal action (Figure 4 and 5; channels disappeared by day 8).

2.3 Sampling design

A comparative approach involving assessments of benthic assemblages from freshly created channels and adjacent non-foraged sediments (Gihwala *et al.* 2017) was used to test hypothesis. Sampling took place during spring low tide along the mid-shore position of two sites between Oesterwal and Bottelary (Figure 3) in winter (July-August) when Greater Flamingos are found to be at their most abundant (Liversidge *et al.* 1958; Underhill 1987). At each site 20 large and 20 small (differences in mean areas are shown in Tables 5 and 6) newly formed foraging structures (created via flamingo foraging activity within a 24-hour period) were marked using plastic stakes (width = 1.8cm; height = 61cm, n_{small} = 4 per structure, n_{large} = 8 per structure) in order to remove confounding foraging effects that could occur with structure age. This marking allowed for foraging structures to be delineated while simultaneously preventing further disturbances by flamingos (feeding or trampling) to the marked structures. The preliminary study has shown that these stakes function effectively as barriers due to flamingos being suspicious of them thus avoiding them. In order to track temporal changes, five large and five small channels were sampled 1, 3, 5 and 8 days following flamingo foraging activities at each site, along with an equivalent number of controls. Control samples were collected between 0.3 – 1m from their relative foraging structure, where the sediments had not been previously disturbed by foraging activity. Due to the sampling of channels being destructive, individual channels could not be repeatedly sampled in order to quantify temporal changes.

2.4 Foraging structure size

Photographs of freshly created channels were taken with a digital camera (Canon Powershot A470) at an angle perpendicular to the channels and at a standardised height of 1m. Channel areas were calculated from photographs using ImageJ (version 1.50i, 2016) which was used to relate channel size to benthic responses (both resources and assemblages).

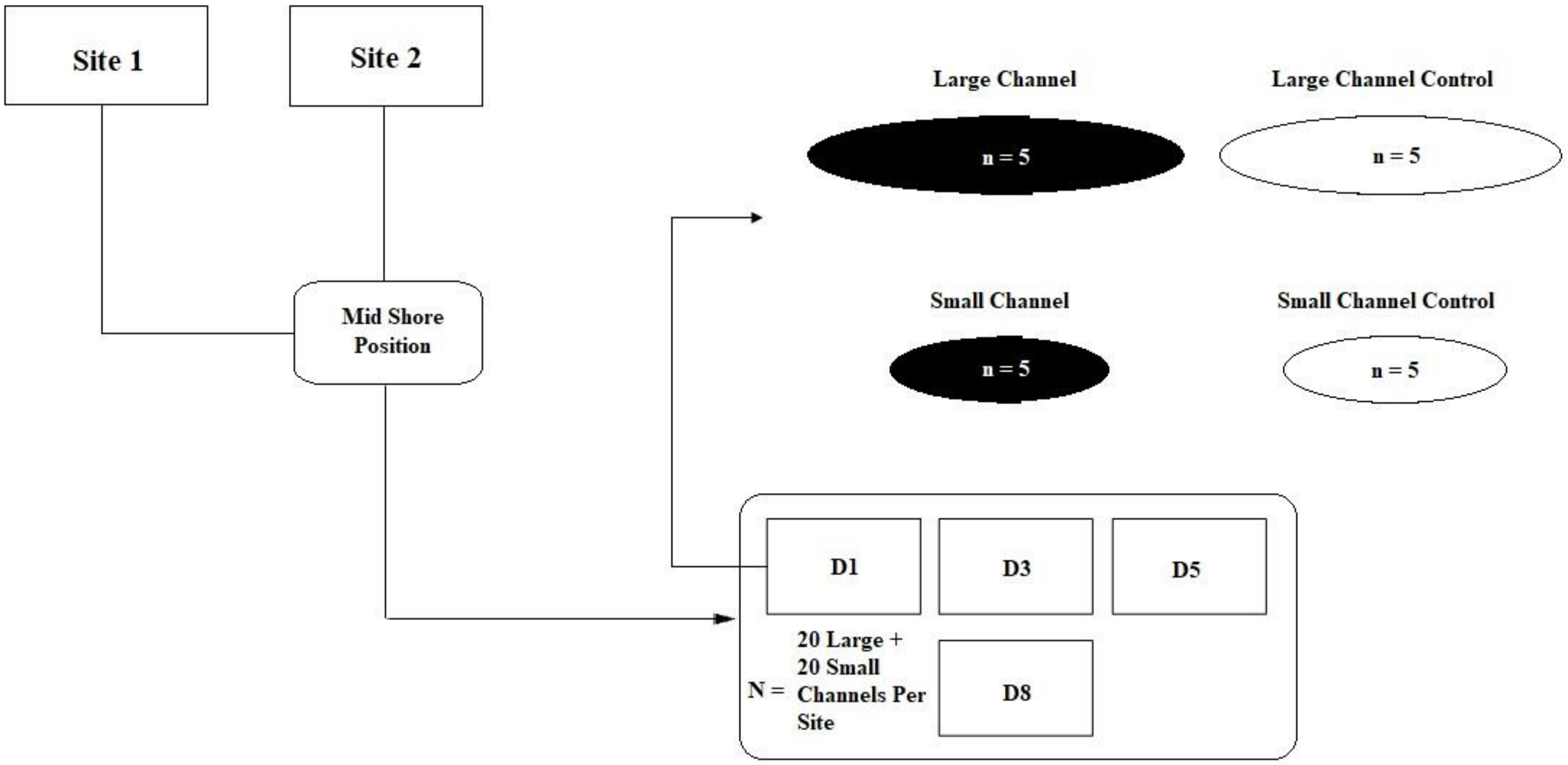

Figure 3: A schematic overview showing the sampling design used in this study. Two sites (Sites 1 and 2) were sampled at the mid shore position. Five large and five small along with their controls were sampled per day (D1-8).

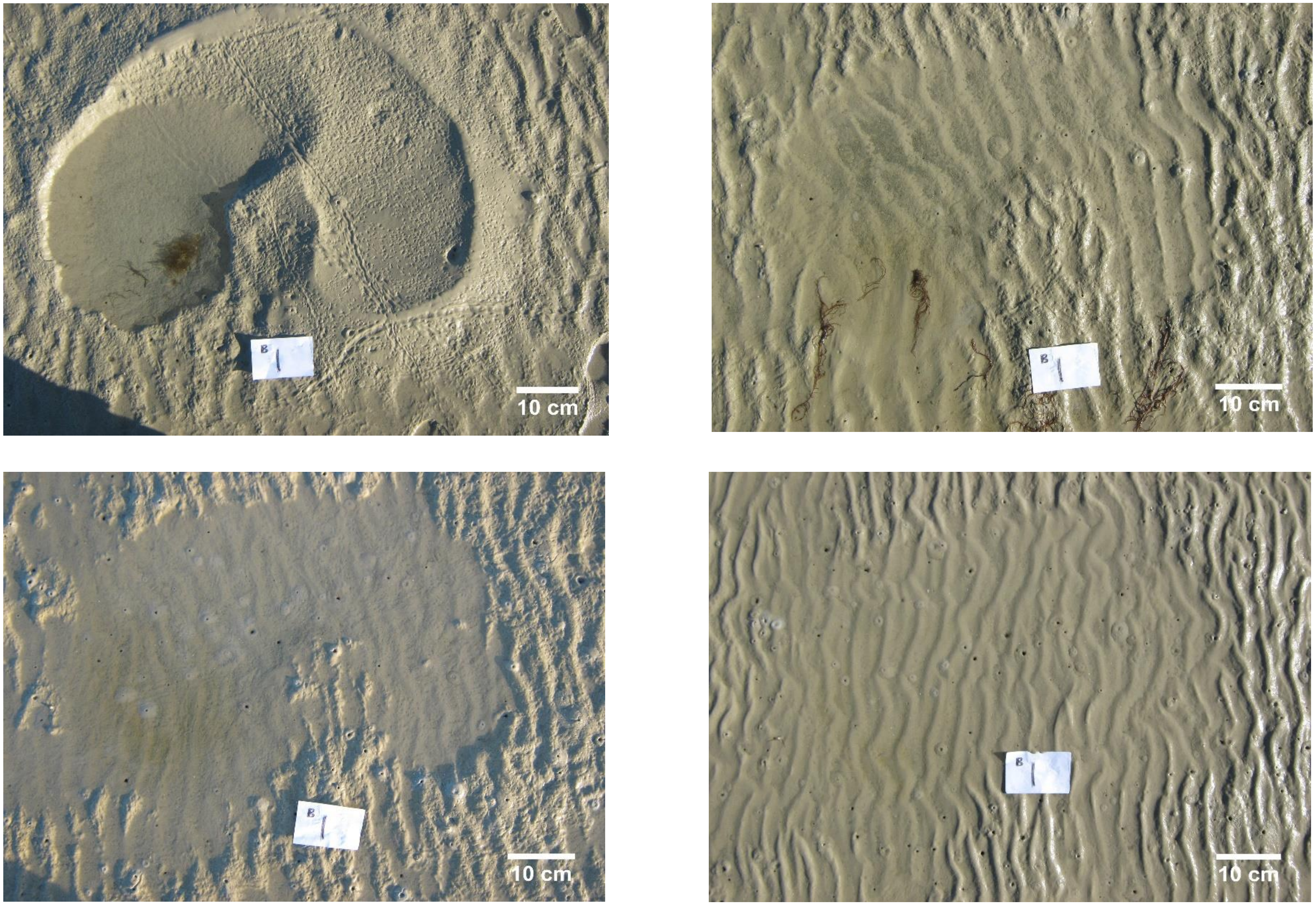

Figure 4: Photos of Large Flamingo foraging channels within days 1 (A), 2 (B), 3 (C) and 5 (D) of foraging. Photos were taken during low tide, at Site 1 between Oesterwal and Bottelary.

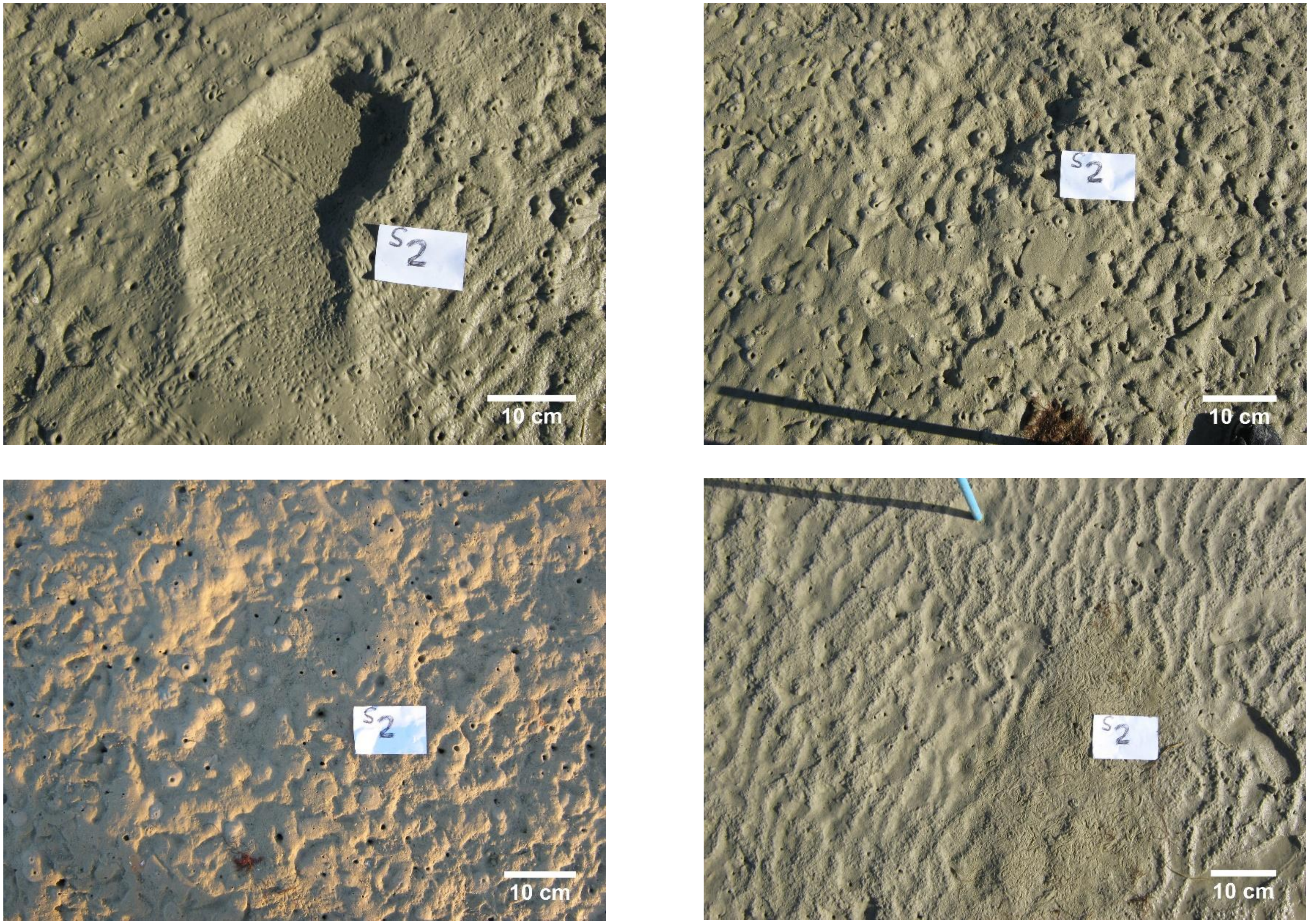

Figure 5: Photos of Small Flamingo foraging channels within days 1 (A), 2 (B), 3 (C) and 5 (D) of foraging. Photos were taken during low tide, at Site 1 between Oesterwal and Bottelary.

2.5 Macrofauna

Macrofaunal samples were collected per channel and adjacent non-foraged control by using a cylindrical stainless-steel corer (diameter = 10cm, depth = 15cm). Each sample consisted of three sediment cores that were collected along the length of each channel or control (Totalling 160 samples across the two sites; with each treatment comprising of 20 samples per site). Cores were pooled in a bucket before seawater was added, followed by the supernatant being stirred and sieved (500µm) five times. The remaining sediments were further sieved through a 2mm mesh to extract larger fauna (typically bivalves and gastropods). The resultant material collected by sieves were preserved and stained using a mixture of 70% ethanol and Rose Bengal. All individuals found in the samples were identified to the lowest taxonomic level possible and enumerated in the laboratory. The amphipod *Urothoe grimaldii*, which was found to be the most dominant macrofaunal organism in the samples, was categorized into juvenile (1 – 3.5mm) and adult life stages (3.6 - 7mm) in order to determine if different life stages are impacted differentially by channel-foraging plasticity. The biomass of individuals of the same species per sample were calculated using two different methods depending the sizes of the species. For smaller macrofaunal organisms (e.g. isopods, amphipods, and polychaete), thirty individuals of the same species were weighed and had their mean biomass calculated. For larger organisms (e.g. hermit crabs, mudprawns and sandprawns), ten individuals of the same species were weighed from which a mean biomass was calculated. In order to estimate species specific biomass per sample, each species had their mean biomass multiplied by their relative abundances in each sample (Gihwala *et al.* 2017). Biomass for molluscs (mainly bivalves and gastropods) was determined once the individuals were removed from their shells. A Sartorius Balance was used to take biomass measurements with a precision of 4 decimal places.

2.6 Chlorophyll-a

Chlorophyll-*a* (chl-*a*) concentrations were measured from sediment cores (depth = 1cm, diameter = 2cm; n = 3 per channel and control) that were placed in 20ml of 90% acetone and kept in darkness within a refrigerator for 48 hours. Chl-*a* concentrations were determined by measuring a homogenized sub-sample of the refrigerated acetone sample by using a fluorometer (Turner Designs Trilogy).

2.7 Sediment Organic Matter

Sediment organic matter content was estimated from sediment cores (depth = 1cm, diameter = 3.5cm; n = 3 per channel and control) by using the weight loss on ignition method. Each sample was homogenized before a sub-sample was taken from it and dried in an oven (100°C for 24h) after which it was combusted in a muffle furnace (400°C for 8 hours).

2.8 Sediment deposition & sediment particle size

Sediment deposition within structures was estimated by gently placing 50ml centrifuge tubes (diameter = 3cm; n = 3 per channel and control) into the sediment (centrifuge tube openings flush with sediment surface) where they were left for 24 hours for each of the different sampling times. The sediment collected in the centrifuge tubes after 24 hours was oven dried (100°C for 24h), weighed and expressed as a mass relative to the area of each channel. In addition, sub-samples of the dried sediments from the centrifuge tubes were later analysed for particle size via laser diffraction using a Malvern Analyser (Mastersizer 2000).

2.9 Statistical analyses

PRIMER v.6.1.5 (Plymouth Routines in Multivariate Ecological Research; Clarke & Gorley 2006) was used to perform all multivariate analyses, based on unstandardized and untransformed abundance data. Permutational analysis of variance (PERMANOVA) was conducted to test for differences in the macrofaunal community structure between flamingo foraging channels as well as their respective controls, with pair-wise tests being conducted in order to find significant within-treatment differences per day and site.

IBM SPSS (Statistical Package for Social Sciences) ver 24 (IBM, 2016) was used to conduct univariate analyses and parametric tests. Normality and homogeneity of variance were tested through the use of Kolmogorov-Smirnov and Levene's tests respectively. Analysis of Variances (ANOVA) with Tukey post-hoc analyses were applied to determine whether biotic and abiotic metrics differed spatio-temporally.

Chapter 3: Results

3.1 Spatial-temporal variation in the area of flamingo foraging channels

Channel Area was found to be uniform across all tested spatial factors ($p > 0.05$, Table 2) except for treatment where Area was found to differ between small and large channels ($F_{1,79} = 84.84$, $p < 0.001$) where the latter was roughly 300% bigger than small channels.

Table 2: ANOVA results testing for spatial-temporal differences in area and sediment depositional characteristics of flamingo foraging channels. Treatment refers to the small and large channels as well as each of their controls.

Factor	**Channel Area**				**Area Specific Sediment Deposition**				**Sediment Particle Size**			
	Type III Sum Of Square / [N]	*df*	*F*	p	Type III Sum Of Square / [N]	*df*	*F*	p	Type III Sum Of Square / [N]	*df*	*F*	p
Site	[80]	1	2.75	0.102	[180]	1	0.63	0.427	[20]	1	0.01	0.919
Day	-	-	-	-	[180]	2	55.73	<0.001	-	-	-	-
Treatment	[80]	1	84.84	<0.001	[180]	1	57.89	<0.001	[20]	1	0.23	0.640
Site*Day	-	-	-	-	-	2	3.22	0.043	-	-	-	-
Site*Treatment	-	1	2.00	0.162	-	1	0.60	0.441	-	1	0.002	0.964
Day*Treatment	-	-	-	-	-	2	8.93	<0.001	-	-	-	-
Site*Day*Treatment	-	-	-	-	-	2	1.35	0.263	-	-	-	-
Error	88121929.37	76	-	-	0.03	168	-	-	70131.41	16	-	-

3.2 Spatial-temporal variation in area-specific sediment deposition

Area-specific sediment deposition (ASSD) was significantly affected by time ($F_{2,179}$ = 55.73, p < 0.001, Table 2, Figure 6) and treatment ($F_{1,179}$ = 57.89, p < 0.001). Sediment deposition generally declined over the sampling period following flamingo foraging where deposition tended to be greater in small channels relative to large ones. ASSD was also influenced by interactions between site and day ($F_{2,179}$ = 3.217, p = 0.043) and day and treatment ($F_{2,179}$ = 8.931, p < 0.001). Sediment particle size was found to be uniform across all tested spatial factors (p > 0.05, Table 2).

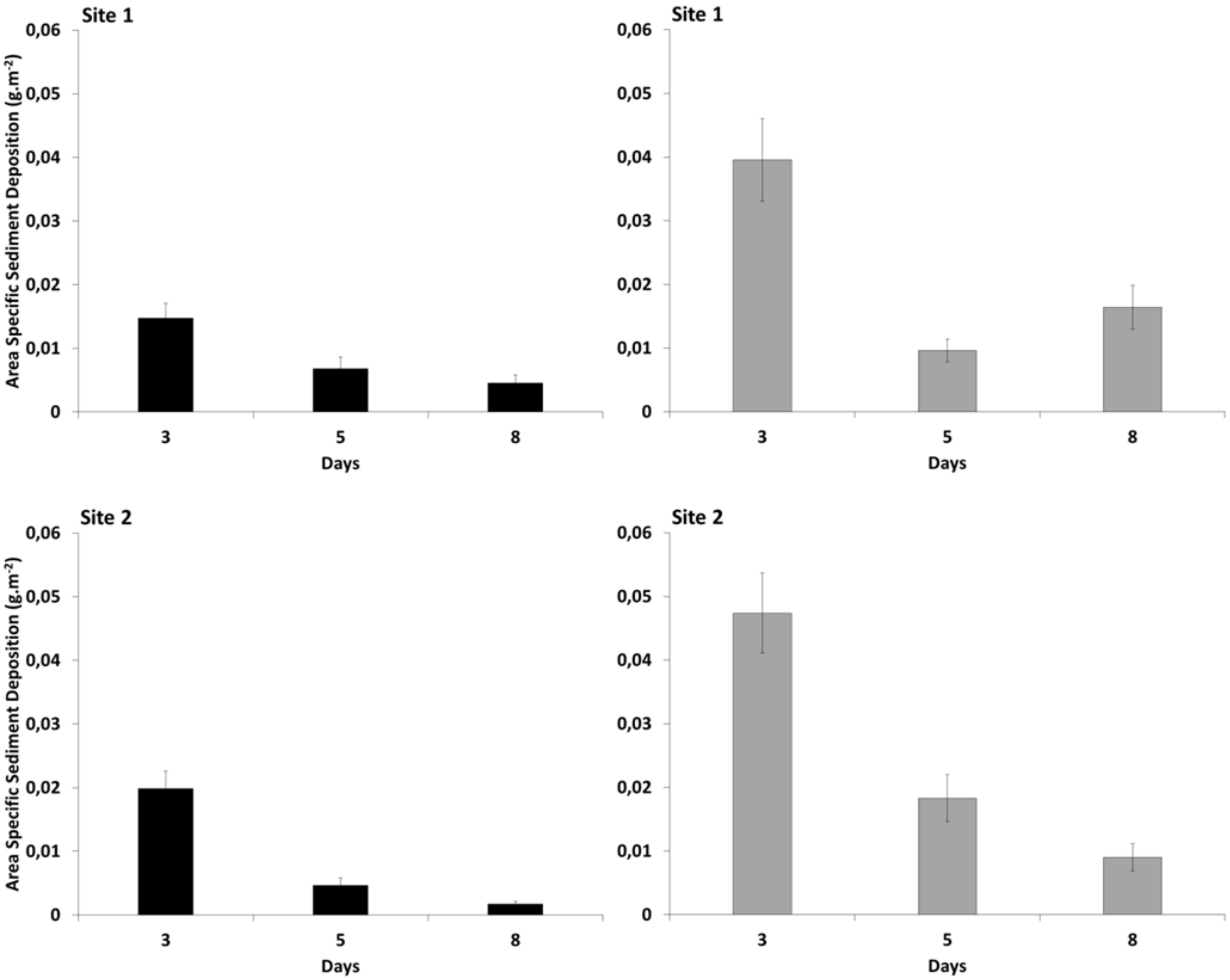

Figure 6: Differences in area-specific sediment deposition between flamingo channels (large: ■, small: ▨) across two sampling sites on days 3, 5 and 8 following flamingo foraging. Means ± SE are displayed.

3.3 Chlorophyll-a

Chl-*a* concentrations differed significantly between sites ($F_{1,157}$ = 45.69, $p < 0.001$, Table 3, Figure 7), where Site 2 had a greater concentration than Site 1, and days ($F_{3,157}$ = 32.82, $p < 0.001$) with values tending to either (1) increase then stabilize over time or (2) conform to a unimodal trend. These patterns observed were evident for both channels and controls. Chl-*a* concentrations were also found to be affected by flamingo foraging treatment ($F_{3,157}$ = 16.08, $p < 0.001$) where chl-*a* biomass in small channels tended to be greater than large channels following foraging (Post – hoc Tukey $p < 0.001$) at Site 1. This pattern was evident at Site 2 but was not statistically upheld (Post – hoc Tukey $p = 0.068$). Interactions between site and day ($F_{3,157}$ = 2.97, $p = 0.040$, Table 3) and day and treatment ($F_{9,157}$ = 3.42, $p = 0.001$, Table 3) also influenced chl-*a* concentrations.

Table 3: ANOVA results testing for spatial-temporal differences in chl-*a* biomass, sediment organic matter and macrofaunal community metrics.

Factor	**Chl-*a***				**Sediment Organic Matter**				**Macrofaunal Abundance**				**Species Richness**				**Macrofaunal Biomass**			
	Type III Sum Of Square / [N]	*df*	*F*	p	Type III Sum Of Square / [N]	*df*	*F*	p	Type III Sum Of Square / [N]	*df*	*F*	p	Type III Sum Of Square / [N]	*df*	*F*	p	Type III Sum Of Square /	*df*	*F*	p
Site	[158]	1	45.69	<0.001	[158]	1	3.79	0.054	[160]	1	0.01	0.928	[160]	1	23.81	<0.001	[160]	1	4.45	0.037
Day	[158]	3	32.82	<0.001	[158]	3	0.50	0.686	[160]	3	24.76	<0.001	[160]	3	15.08	<0.001	[160]	3	2.76	0.045
Treatment	[158]	3	16.08	<0.001	[158]	3	102.84	<0.001	[160]	3	9.10	<0.001	[160]	3	0.19	0.901	[160]	3	0.37	0.772
Site*Day	-	3	2.97	0.040	-	3	3.29	0.023	-	3	9.59	<0.001	-	3	7.56	<0.001	-	3	2.55	0.059
Site*Treatment	-	3	0.66	0.577	-	3	1.39	0.249	-	3	0.42	0.742	-	3	1.02	0.386	-	3	0.11	0.955
Day*Treatment	-	9	3.42	0.001	-	9	0.75	0.660	-	9	0.60	0.792	-	9	0.92	0.508	-	9	0.42	0.921
Site*Day*Treatment	-	9	1.36	0.212	-	9	0.83	0.589	-	9	1.33	0.229	-	9	1.53	0.143	-	9	1.42	0.185
Error	145488649.50	126	-	-	0.38	126	-	-	911152.40	128	-	-	38550.00	128	-	-	224.58	128	-	-

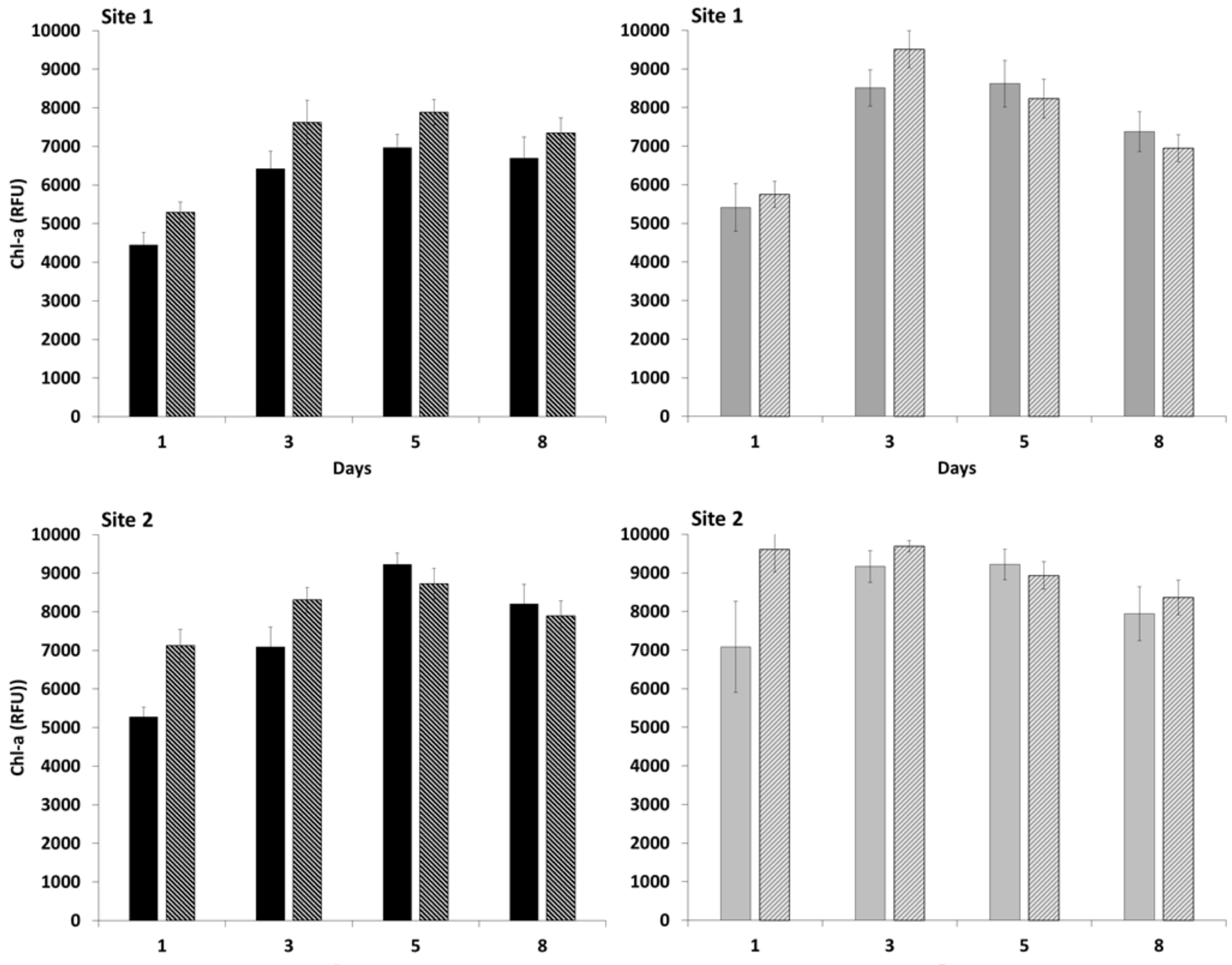

Figure 7: Differences in chl-*a* concentrations between flamingo channels (large: ■, small: □) and controls (large channel control: ▧, small channel control: ▨) across two sampling sites on days 1, 3, 5 and 8 following flamingo foraging. Means ± SE are displayed.

3.4 Sediment organic matter

Sediment organic matter content differed considerably across foraging treatments ($F_{3,157}$ = 102.84, $p < 0.001$, Table 3, Figure 8), with the organic matter content of large channels being diminished by 93.3% relative to its controls and by 92.9% relative to the small channels (Post – hoc Tukey $p < 0.001$). In contrast, small channels had a 17.1% reduction in its organic matter content relative to their controls. The interaction between site and day ($F_{3,157}$ = 3.29, $p = 0.023$) significantly affected organic matter levels.

3.5 Macrofaunal community structure

PERMANOVA revealed that macrofaunal community structure was significantly affected by site ($F_{9,159}$ = 2.12, $p = 0.001$), day ($F_{9,159}$ = 2.12, $p = 0.001$) and flamingo foraging treatments ($F_{9,159}$ = 2.12, $p = 0.001$). Pairwise tests indicated that there was a difference in the community structure between large and small channels as well as between channels and controls. Interactions between site and day ($F_{3,159}$ = 5.01, $p = 0.001$), day and treatment ($F_{9,159}$ = 2.12, $p = 0.001$) and site, day and treatment ($F_{9,159}$ = 1.59, $p = 0.006$) was also found to influence macrofaunal community structure.

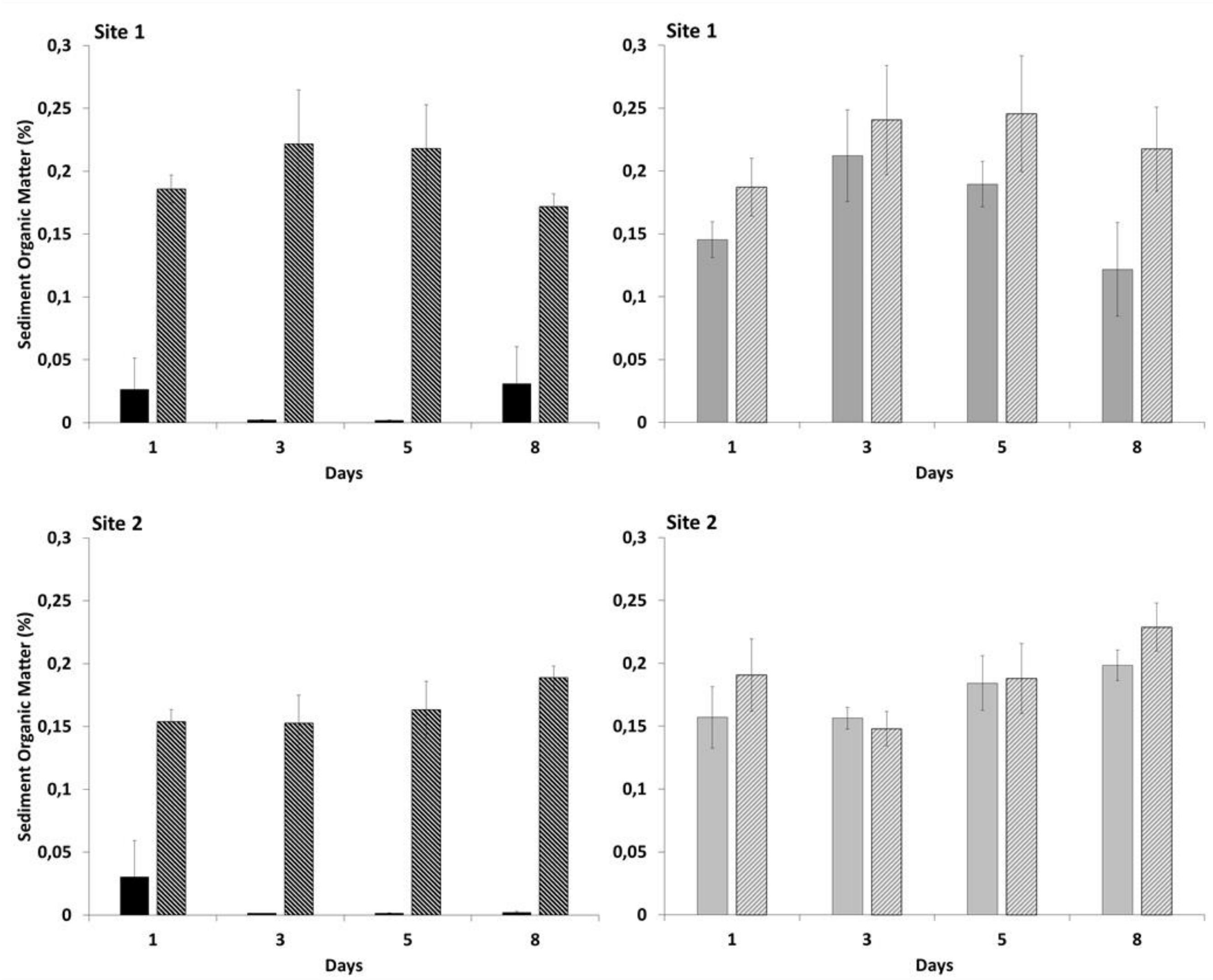

Figure 8: Differences in sediment organic matter levels between flamingo channels (large: ■, small: □) and controls (large channel control: ▧, small channel control: ▨) across two sampling sites on days 1, 3, 5 and 8 following flamingo foraging. Means ± SE are displayed.

3.6 Macrofaunal community metrics

ANOVA indicated that all macrofaunal community metrics were significantly affected by site ($p < 0.001$, Table 3; except for macrofaunal abundance) and day ($p < 0.05$, Table 3). It also revealed that flamingo foraging treatment significantly influenced macrofaunal abundance ($F_{3,159} = 9.10$, $p < 0.001$, Table 3, Figure 9) but not species richness ($F_{3,159} = 0.19$, $p = 0.901$, Table 3, Figure 10) nor macrofaunal biomass ($F_{3,159} = 0.37$, $p = 0.772$, Table 3, Figure 11). Abundance was generally found to be lower in foraging channels relative to controls and also tended to increase over time in both channels and their respective controls. However, no major differences in macrofaunal abundance between large and small channels were recorded. Species richness was found to be greater at Site 1 than Site 2 and was influenced by time although obvious temporal patterns could not be detected. Macrofaunal biomass was lower in Site 1 than Site 2 and generally increased as time progressed, though specific trends were erratic. The interaction between site and day was found to significantly influence both macrofaunal abundance ($F_{3,159} = 9.10$, $p < 0.001$, Table 3, Figure 9) and species richness ($F_{3,159} = 7.56$, $p < 0.001$, Table 3, Figure 10).

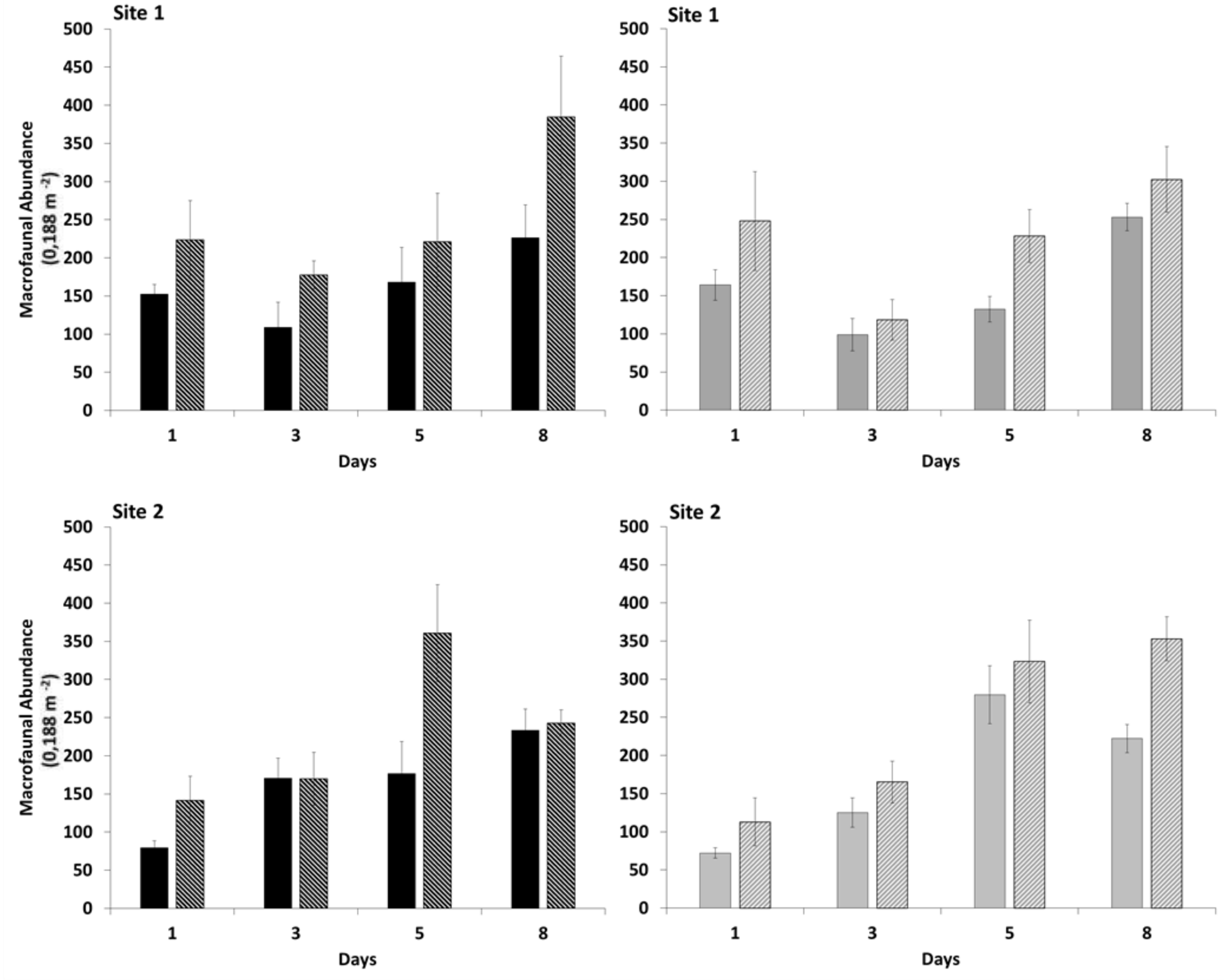

Figure 9: Differences in macrofaunal abundance between flamingo channels (large: ■, small: □) and controls (large channel control: ▧, small channel control: ▨) across two sampling sites on days 1, 3, 5 and 8 following flamingo foraging. Means ± SE are displayed.

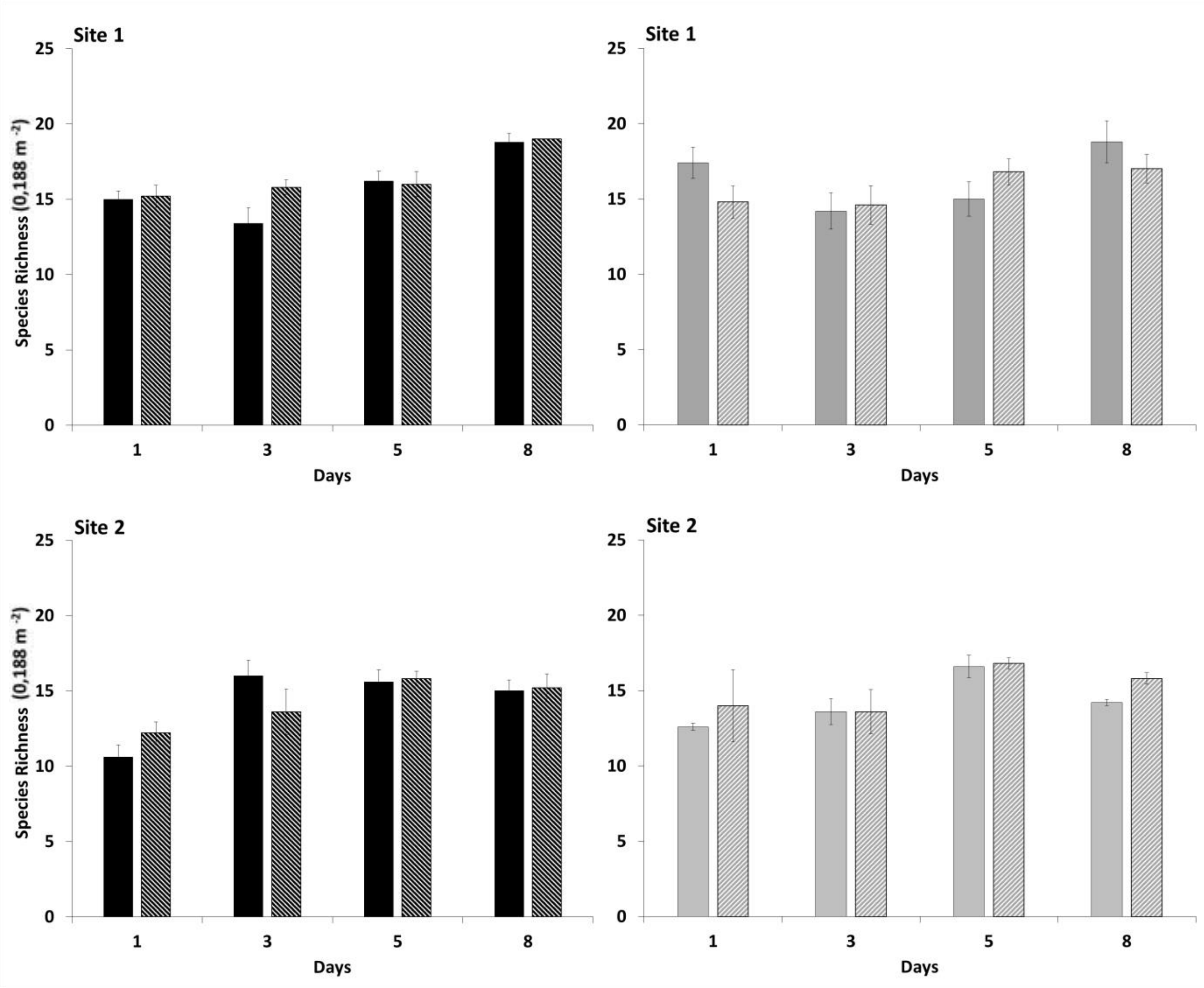

Figure 10: Differences in species richness between flamingo channels (large: ■, small: □) and controls (large channel control: ▧, small channel control: ▨) across two sampling sites on days 1, 3, 5 and 8 following flamingo foraging. Means ± SE are displayed.

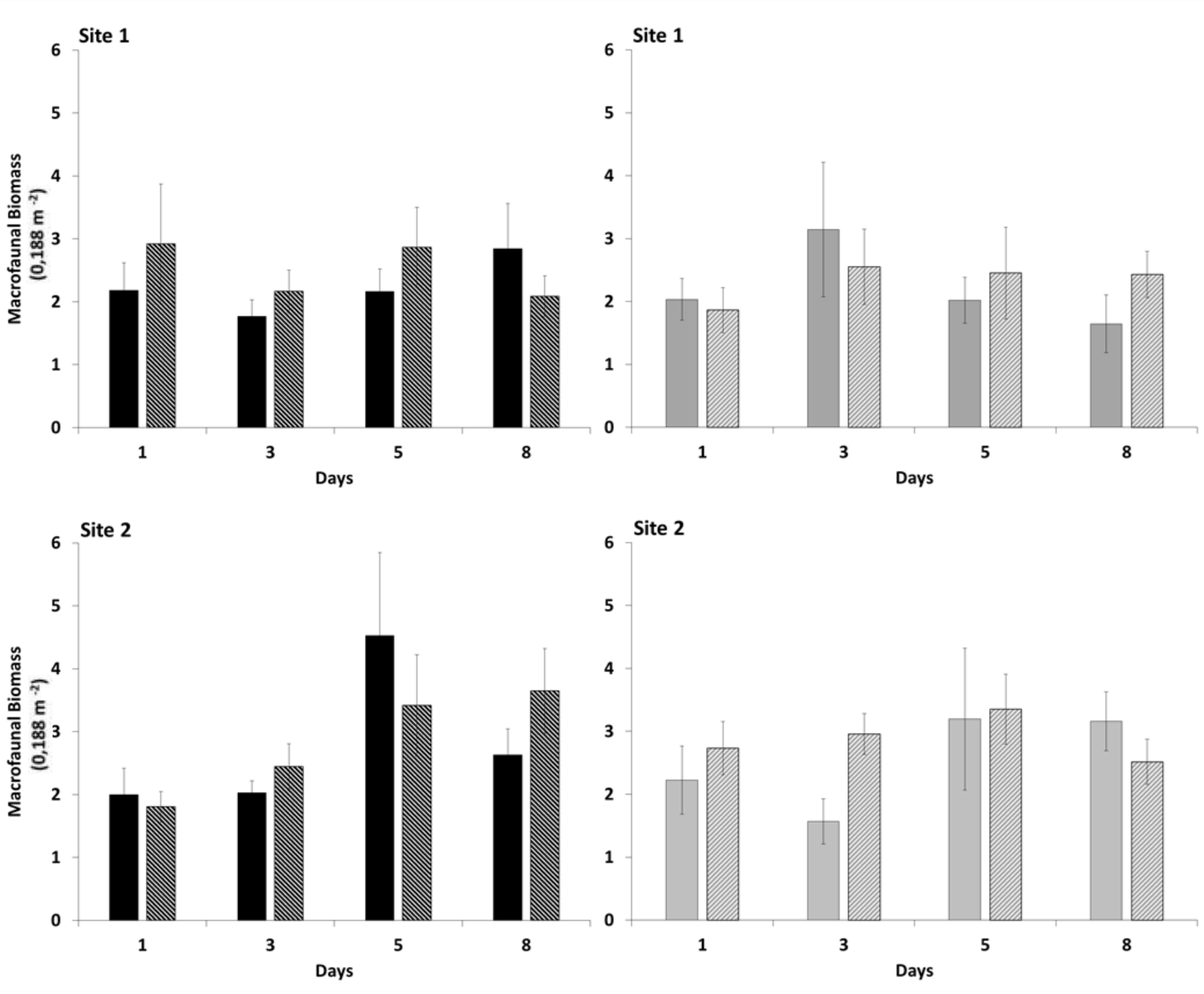

Figure 11: Differences in macrofaunal biomass between flamingo channels (large: ■, small: □) and controls (large channel control: ▨, small channel control: ▨) across two sampling sites on days 1, 3, 5 and 8 following flamingo foraging. Means ± SE are displayed.

3.7 Dominant macrofaunal taxa

The abundance of most of the dominant macrofaunal species differed significantly among sites ($p < 0.05$, Table 4, Fig 12-13; except for *Tellimya trigona*) and days ($p < 0.05$, Table 4, Fig 12-13; except for calanoid copepods) with values tending to either increase and stabilizing over time, fitting a unimodal trend or not conforming to any temporal pattern. The gastropod *Assiminea globulus* was significantly affected by flamingo foraging treatment ($F_{3,159} = 8.28$, $p < 0.001$, Table 4, Fig 12), with small channels and their controls having a greater abundance than large channels and controls, particularly near the end of the study period. Flamingo foraging effects were also significant for the abundance of juvenile *Urothoe grimaldii* (Amphipoda; $F_{3,159} = 11.88$, $p < 0.001$, Table 4, Fig 13), which was found to be reduced in large channels relative to controls, but similar in small channels relative to controls. Flamingo foraging also affected the abundance of the polychaete *Orbinia angrapequensis* ($F_{3,159} = 3.24$, $p = 0.024$, Table 4), with large channels having on average greater densities than small channels, particularly near the end of the study period at Site 1. The abundance of juvenile polychaetes was also significantly affected by flamingo foraging treatment ($F_{3,159} = 4.71$, $p = 0.004$, Table 4), with levels being lower in channels relative to their controls and large channels having a greater abundance than small ones, most notably at Site 1.

Interactions between site and day significantly affected *Assiminea globulus* ($F_{3,159} = 4.24$, $p = 0.007$, Table 4), *Orbinia angrapequensis* ($F_{3,159} = 3.80$, $p = 0.012$, Table 4), *Tellimya trigona* ($F_{3,159} = 2.90$, $p = 0.038$, Table 4) and juvenile polychaetes ($F_{3,159} = 4.37$, $p = 0.006$, Table 4). Site x treatment interactions affected the abundance of juvenile *Urothoe grimaldii* ($F_{3,159} = 2.82$, $p = 0.041$, Table 4) and *Tellimya trigona* ($F_{3,159} = 2.81$, $p = 0.042$, Table 4). The interaction between day and treatment affected the abundance of *A. globulus* ($F_{9,159} = 5.73$, $p < 0.001$, Table 4), juvenile ($F_{9,159} = 2.12$, $p = 0.033$, Table 4) and adult *Urothoe grimaldii* ($F_{9,159} = 2.82$, $p = 0.005$, Table 4).

The interaction between site, day and treatment significantly affected juvenile polychaetes abundance ($F_{9,159}$ = 2.79, p = 0.005, Table 4).

Table 4: ANOVA results testing for spatial-temporal differences in the abundance of the dominant macrofaunal species.

Factor	***Assiminea globulus***				**Juvenile *Urothoe grimaldii***				***Orbinia angrapequensis***				**Juvenile Polychaetes**			
	Type III Sum Of Square / [N]	*df*	*F*	p	Type III Sum Of Square / [N]	*df*	*F*	p	Type III Sum Of Square / [N]	*df*	*F*	p	Type III Sum Of Square / [N]	*df*	*F*	p
Site	[160]	1	5.72	0.018	[160]	1	55.82	<0.001	[160]	1	5.43	0.021	[160]	1	4.73	0.031
Day	[160]	3	19.40	<0.001	[160]	3	6.56	<0.001	[160]	3	4.15	0.008	[160]	3	7.28	<0.001
Treatment	[160]	3	8.28	<0.001	[160]	3	11.88	<0.001	[160]	3	3.24	0.024	[160]	3	4.71	0.004
Site*Day	-	3	4.24	0.007	-	3	2.29	0.082	-	3	3.80	0.012	-	3	4.37	0.006
Site*Treatment	-	3	0.44	0.726	-	3	2.82	0.041	-	3	1.02	0.385	-	3	0.95	0.419
Day*Treatment	-	9	5.73	<0.001	-	9	2.12	0.033	-	9	1.90	0.058	-	9	1.70	0.095
Site*Day*Treatment	-	9	1.45	0.172	-	9	0.71	0.701	-	9	0.73	0.680	-	9	2.79	0.005
Error	84371.60	128	-	-	39872.40	128	-	-	13341.20	128	-	-	446438.00	128	-	-

Table 5: Continued ANOVA results testing for spatial-temporal differences in the abundance of the dominant

Factor	***Tellimya trigona***				***Notomastus latericus***				**Adult *Urothoe grimaldii***				**Calanoid copepods**			
	Type III Sum Of Square / [N]	*df*	*F*	p	Type III Sum Of Square / [N]	*df*	*F*	p	Type III Sum Of Square / [N]	*df*	*F*	p	Type III Sum Of Square / [N]	*df*	*F*	p
Site	[160]	1	1.08	0.301	[160]	1	12.76	0.001	[160]	1	36.84	<0.001	[160]	1	39.12	<0.001
Day	[160]	3	24.15	<0.001	[160]	3	11.27	<0.001	[160]	3	3.51	0.017	[160]	3	0.58	0.629
Treatment	[160]	3	0.90	0.443	[160]	3	1.79	0.152	[160]	3	1.59	0.196	[160]	3	0.86	0.463
Site*Day	-	3	2.90	0.038	-	3	4.99	0.003	-	3	2.51	0.062	-	3	0.54	0.659
Site*Treatment	-	3	2.81	0.042	-	3	0.22	0.881	-	3	1.46	0.230	-	3	0.29	0.833
Day*Treatment	-	9	0.45	0.905	-	9	2.23	0.024	-	9	2.82	0.005	-	9	1.61	0.120
Site*Day*Treatment	-	9	0.84	0.583	-	9	2.03	0.041	-	9	0.57	0.823	-	9	1.28	0.253
Error	4179.20	128	-	-	10956.80	128	-	-	8950.40	128	-	-	5657.60	128	-	-

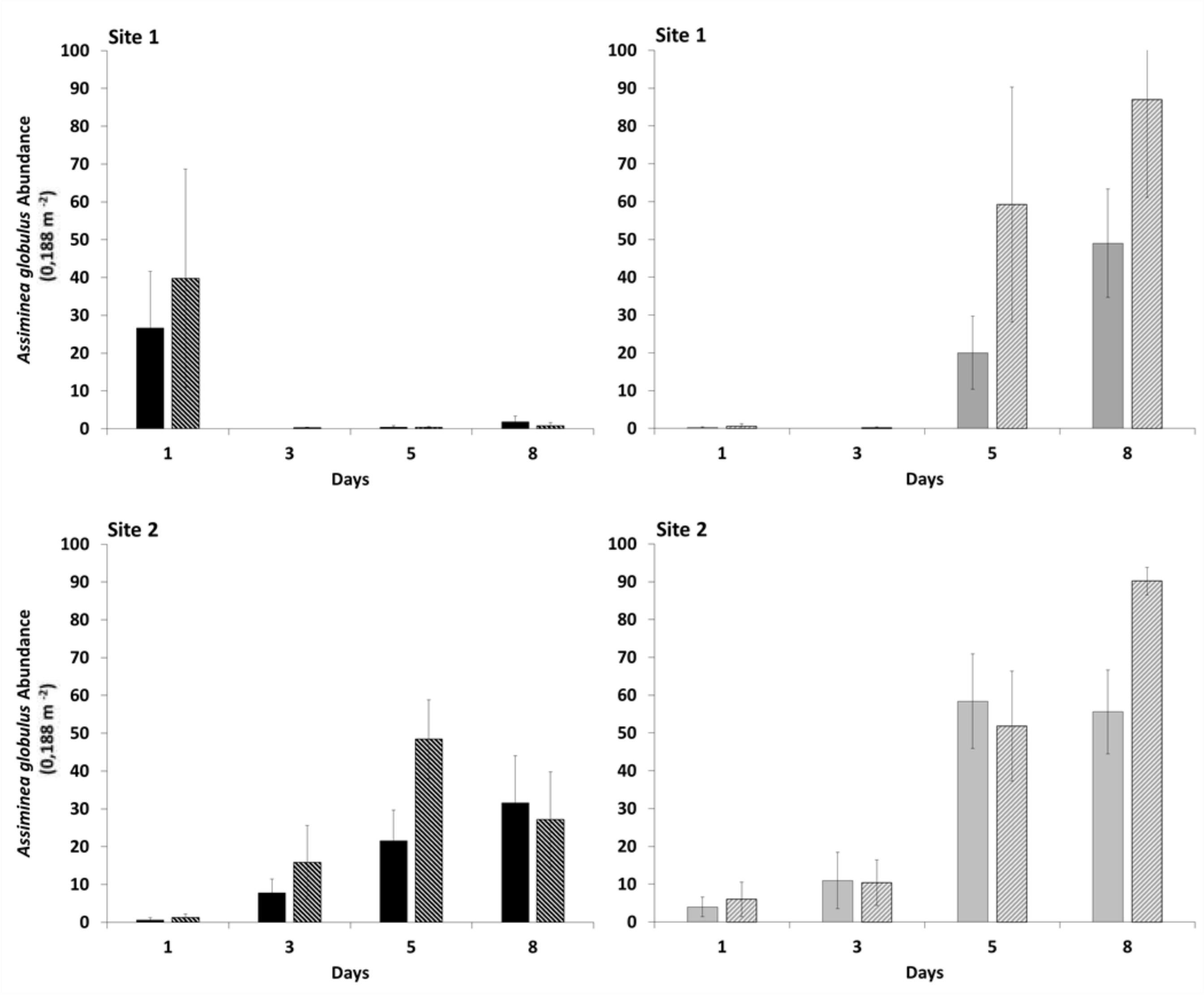

Figure 12: Differences in *Assiminea globulus* abundance between flamingo channels (large: ■, small: ▒) and controls (large channel control: ▨, small channel control: ▨) across two sampling sites on days 1, 3, 5 and 8 following flamingo foraging. Means ± SE are displayed.

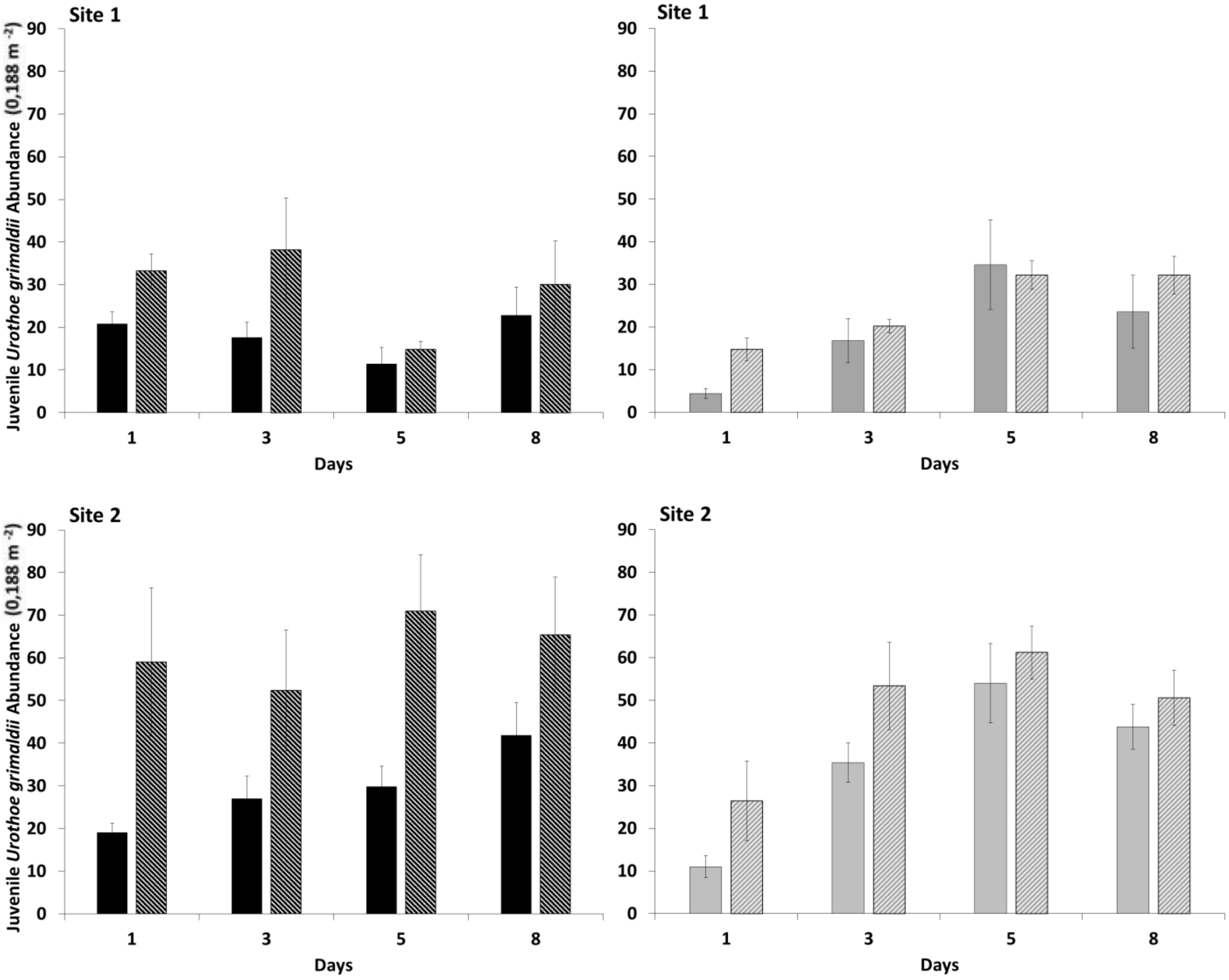

Figure 13: Differences in juvenile *Urothoe grimaldii* abundance between flamingo channels (large: ■, small: ▢) and controls (large channel control: ▧, small channel control: ▨) across two sampling sites on days 1, 3, 5 and 8 following flamingo foraging. Means ± SE are displayed.

Chapter 4: Discussion

The overarching goal of this dissertation was to expand current understanding of foraging plasticity and the ecological role Greater Flamingos play as predators in marine sediments, given the lack of research in these fields thus far (Glassom & Branch 1997; Bildstein et al. 2000; Miner et al. 2005; Gihwala et al. 2017). The central objective was to determine the individual and interactive effects of channel-foraging plasticity displayed by Greater Flamingos in driving spatial-temporal variability of basal resources and broader community structure. Results indicate that channel-foraging employed by flamingos interacted differentially with time to evoke contrasting responses on trophic resources (chl-*a* and organic matter) and some taxa (*Assiminea globulus* and juvenile *Urothoe grimaldii*). However, similar evidence was absent for community-level metrics. Taken collectively, results obtained expand on understanding of foraging plasticity exhibited by predators and identify a subtler form of feeding plasticity (size variation) that has rarely been investigated.

Various studies have documented the potential of biotic factors to indirectly impact food chain dynamics and ecosystem functioning by impacting basal trophic resource levels (Gutiérrez & Iribarne 2004; Eldridge & Mensinga 2007). In this regard, my results highlight a novel and previously unappreciated role of flamingos as ecosystem engineers in marine sediments. Firstly, results indicated that foraging channels created by flamingos become enriched with benthic microalgae over time; to levels greater than recorded in fringing non-foraged sediments at the start of sampling. Secondly, it was also demonstrated (Figure 7) that chl-*a* levels in the controls surrounding channels increased over time, suggesting that the stimulation caused by flamingos on benthic microalgal biomass is not only restricted to the foraging structures produced, but could possibly spill-over into the surrounding benthos.

Studies have shown the importance of microalgal biofilms in marine ecosystems in impacting food web dynamics (Moore *et al.* 1993; Pillay *et al.* 2007; Raffaelli & Hawkins 2012), particularly by influencing sediment stability (Paterson & Hagerthey 2001), trophic resource availability (Decho & Lopez 1993) and settlement cues for invertebrate larvae (Pillay *et al.* 2007; Pillay *et al.* 2009). Overall, findings suggest that flamingo foraging may be key in creating networks of microalgal hotspots that are spatially and temporally dispersed in sedimentary habitats, which are likely to significantly influence fundamental ecological processes and therefore reinforce spatial-temporal heterogeneity (MacIntyre *et al.* 1996; Pillay *et al.* 2007). An example of this is Langebaan over winter, where approximately 4200 flamingos can be seen in the system all creating patches of succession at different times therefore creating a significant network of microalgal hotspots (Underhill 1987).

There are a number of potential reasons for microalgal blooms following flamingo foraging. The most obvious is that flamingos being predators, likely consume key macroinvertebrate grazers that feed on microalgae. This is supported by the data collected which demonstrated a reduction in macrofaunal abundance as well as that of other taxa in flamingo channels immediately following the feeding event. In addition, various studies have demonstrated an elevation in sedimentary microalgal levels following the removal of grazers (Daborn *et al.* 1993; Morrisey 1988; Uthicke 1999; Pillay *et al.* 2009; 2010). In this regard, it is likely that trophic cascades may be initiated following foraging by flamingos through a reduction in top-down pressure on producers (microalgae) by intermediate consumers (grazers). The post-foraging microalgal blooms experienced may also be driven by flamingos enhancing nutrient fluxes from deep within the sediments to the surface through feeding, thereby mobilising nutrients that would be otherwise unavailable and potentially limit microalgal productivity, as suggested by Comin *et al.* (1997). Flamingo feeding may thus be functionally analogous to infaunal bioturbation, which has been shown to stimulate primary production at the sediment-water interface (Ziebis *et al.* 1996; Mermillod-Blondin *et al.* 2004; Lohrer *et al.* 2004; D'Andrea & DeWitt 2009). Channels could be enriched with microalgae following feeding due to their three-dimensional structural attributes causing passive deposition of particles through the reduction of hydrodynamic flow. However, it is important to note that it is possible that this increase in chl-a levels may be due to unknown temporal processes that were not measured in this study.

The creation of sediment patches enhanced with microalgae through Greater Flamingo foraging is of particular relevance at a local level. Langebaan Lagoon is dominated by benthic sandy habitats that support high densities of burrowing sandprawns (*Callichirus kraussi*). Previous studies have highlighted the remarkable rates at which these bioturbators turn over sediment and its strong negative effects on epibenthic microalgal biomass (Pillay *et al.* 2007; Pillay & Branch 2011). For example, field observations and experiments indicated that microalgal biomass was roughly 2 to 4 times greater when *C. kraussi* was rare or absent (Pillay *et al.* 2007). Therefore, the creation of spatially dispersed channels that are enriched with microalgae by flamingos may be key in suppressing deleterious bioturbation effects that would otherwise normally spatially homogenise and reduce epibenthic microalgal biomass.

Flamingo foraging plasticity was found to have very strong impacts on sedimentary organic matter levels in this study. Results illustrate that at both sites, large channels had organic matter levels consistently depleted relative to controls; on the other hand, organic matter concentrations were generally similar between small channels and their controls. This observation would suggest that small channels are somehow able to better facilitate the accumulation and retention of organic matter than large channels. It is plausible that large channels increases resistance to water flow, thereby preventing organic matter deposition. On the other hand, small channels are likely to be less hydrodynamically turbulent, thus resulting in them becoming enriched over time. This idea of feeding structures with different structural traits inducing differential hydrodynamic effects is supported by my results which indicate size-specific effects on sediment deposition, where small channels accumulated more sediment than large channels. Previous research has also demonstrated the potential for structures with contrasting attributes to interact differently with local hydrodynamics (Table 1; VanBlaricom 1982; Zajac & Whitlatch 1982b; Oliver *et al.* 1985; Savidge & Taghon 1988; Snelgrove 1994). However, the results obtained could potentially have been impacted by unknown temporal processes such as the transition from spring to neap tide, which could have affected sedimentation rates and the hydrodynamics of each structure. Irrespective of the mechanisms at play, it is clear that foraging plasticity differentially impacts the accumulation of organic matter into foraged areas, which adds another dimension through which Greater Flamingos are able to reinforce the spatio-temporal heterogeneity observed in ecological processes in benthic ecosystems.

In contrast to the noticeable effects of foraging plasticity on organic matter levels (and benthic microalgal biomass to a lesser degree), there was no commensurate bottom-up effects observed on the community metrics. It would be expected, based on the linkage between organic matter (as an important basal resource and recruitment cue) and consumer metrics (Reise 1985; Levin & Gage 1998; Pillay *et al.* 2007), that a rise in organic matter levels associated with small foraging channels would lead to facilitative effects on benthic macrofaunal abundance, richness and/or biomass. One potential interpretation for this unexpected effect of rising organic matter levels not evoking a positive effect on community descriptors, is that the magnitude of organic matter increases was not sufficient to reach the necessary threshold for effects to manifest. This idea is supported by data which showed that while the relative increase of organic matter from large to small channels was 92.9%, the absolute increase was not as impressive, since total organic matter content seldom reached 0.3%.

Despite the effects channel foraging plasticity had on trophic resource levels (mainly organic matter) not transferring to macrofaunal community metrics, there was evidence of bottom-up effects at the level of individual macrofaunal species. More specifically, the gastropod *Assiminea globulus* was one species that showed the most noticeable response to increases in chl-*a* and organic matter content near the end of the study period, where its abundance in small channels increased on average by 96.3% and 43.2% at sites 1 and 2 relative to the large channels. Similar responses were reported for the juveniles of the amphipod *Urothoe grimaldii*, where their abundance was found to be reduced by up to 61.4% in large channels relative to their controls, but was negligible between the small channels and their controls after the first sampling day. These trends suggest that although the surplus of chl-*a* and organic matter reported in these channels did not meet the threshold magnitude required to have a positive impact on community metrics, it was sufficient to generate bottom-up effects at the individual macrofaunal species level. VanBlaricom (1982) found that only certain species actively selected recently formed foraging pits of the rays *Urolophus halleri* and *Myliobatis californica*, which were sites of organic matter accumulation.

While it was suggested that the positive effects exhibited by *A. globulus* and juvenile *U. grimaldii* in small channels was primarily driven by the elevated levels of chl-*a* and organic matter content, it is also conceivable that these differential responses are a result of the structural attributes of each channel having contrasting hydrodynamic interactions. Prior studies have highlighted how macrofaunal settlement can be influenced by small-scale variability in hydrodynamics, which is often a product of disturbance structure traits and substrate properties. For example, Snelgrove (1994) conducted field experiments in which colonization trays of differing trapping properties (one flush with sediment and another forming a depression) were placed in sediment to test effects of near-bed hydrodynamics on larval settlement and distribution. Results indicated that depression trays had a greater density of settlers than flush trays probably due to passive entrainment. For this reason, it is possible that recruitment of *A. globulus* and juvenile *U. grimaldii* into small channels may be facilitated through effects on local hydrodynamic environments. At the same time, there is a wealth of studies that have linked benthic microalgae and organic matter to the settlement and recruitment of benthic larvae (VanBlaricom 1982; Oliver *et al*. 1985; Pillay *et al.* 2007; Gu *et al*. 1996; Huang & Hadfield 2003; Van Colen *et al*. 2009), thus suggesting that the above-mentioned accumulation of basal resources could also be involved in the selective attraction, settlement and recruitment of *A. globulus* and juvenile *U. grimaldii*.

The greater *A. globulus* abundance in small channels compared to large ones towards the end of sampling emphasizes a secondary mechanism by which Greater Flamingos foraging plasticity may potentially reinforce heterogeneity in soft-sediment ecosystems. Grazing by *A. globulus* can strongly determine community structure in intertidal sedimentary systems at my study sites, having important density-dependent effects on basal resources (chl-*a* & extracellular polymeric substances) and the abundance and diversity of organisms through trophic and non-trophic pathways (Pillay *et al.* 2009). The results of this study and prior work (Pillay *et al.* 2009) have demonstrated the potential for flamingo foraging structures with differential structural traits to impact key consumers differentially, which may generate different strengths of secondary top-down regulation within structures.

Conclusion

The findings of this study have provided insight on the ecological importance of a charismatic shorebird predator within intertidal soft-sedimentary ecosystems, for which surprisingly little information exists (Glassom & Branch 1997; Bildstein et al. 2000; Gihwala et al. 2017). Previous research, through the use of exclusion experiments, has highlighted the negative impacts high densities of Greater Flamingos can impose on benthic communities through their bioturbation and consumptive activities (Glassom & Branch 1997). The results of this study however, with time explicitly superimposed as a factor, has highlighted that at low population densities, Greater Flamingos are capable of generating significant positive impacts on prey assemblages. In particular, findings indicated that flamingo foraging channels became enriched with microalgae over time, with effects spilling over into fringing non-foraged sediments. These effects are capable of enhancing short-term productivity at small spatial scales (m^2 in scale), which could potentially have very large cumulative spatial effects (km^2 in scale), considering Greater Flamingos are known to feed across a large expansion of shallow and intertidal sediments within Langebaan Lagoon. Additionally, the results demonstrated that foraging behaviour plasticity differentially impacted benthic chl-*a* (to a lesser degree), sediment organic matter, sediment deposition as well as key consumers and juvenile stages. More broadly, these findings underscore the importance of Greater Flamingos as ecosystem engineers that enhance benthic productivity and heterogeneity in soft-sediment ecosystems. Prior studies have demonstrated the importance of these latter factors in determining key ecological processes such as local diversity, food-web dynamics and ecosystem resilience (Reise 1985; Moore et al. 1993). With this in mind, predation and foraging plasticity displayed by Greater Flamingos may be a key regulator of the benthic ecosystems functioning within Langebaan Lagoon as well as in similar ecosystems elsewhere.

Taken collectively, this study adds to a growing body of literature that emphasizes the importance of predator foraging plasticity in marine ecosystems (Micheli 1997; Gihwala et al. 2017), by explicitly linking foraging plasticity with temporal processes. As has been demonstrated in past and present work, immediate (Gihwala et al. 2017) and delayed effects of foraging plasticity by Greater Flamingos are capable of generating very different magnitude and directional effects. It is therefore imperative that such effects be incorporated into models of predation in order to develop a predictive and mechanistic understanding of shorebird predation within heterogeneous marine ecosystems.

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Appendix A:

Table 6: Time-dependant differences in channel area, sediment particle size and abundance of macrofaunal taxa in large and small channels relative to controls at Site 1.

	Site 1															
	Large Structures								**Small Structures**							
Day	**1**		**3**		**5**		**8**		**1**		**3**		**5**		**8**	
	Channel	**Control**	**Channel**	**Control**	**Channel**	**Control**	**Channel**	**Control**	**Channel**	**Control**	**Channel**	**Control**	**Channel**	**Control**	**Channel**	**Control**
Channel Area (m^2)	5323.0 ± 610.1	-	3090.5 ± 609.7	-	2828.9 ± 662.0	-	3567.8 ± 702.4	-	1306.0 ± 79.7	-	1168.8 ± 166.1	-	972.0 ± 137.8	-	1130.9 ± 154.7	-
Sediment Particle Size (µm)	-	-	310.4 ± 53.4	-	-	-	-	-	-	-	294.9 ± 17.0	-	-	-	-	-
Species																
Adult *Urothoe grimaldii*	10.6 ± 2.0	24.8 ± 2.7	10.6 ± 2.1	13.6 ± 3.9	9.8 ± 2.5	9.6 ± 1.5	12.6 ± 4.1	13.2 ± 4.9	5.2 ± 0.7	11.4 ± 2.3	13.4 ± 3.1	15.6 ± 4.2	16.2 ± 3.2	17.6 ± 4.2	20.6 ± 3.0	13.8 ± 2.5
Orbinia angrapequensis	6.4 ± 1.4	14.8 ± 4.6	9.4 ± 6.1	28.2 ± 10.7	9.4 ± 3.7	14.4 ± 5.9	25.8 ± 3.5	26.4 ± 5.5	17.0 ± 5.6	19.8 ± 7.7	9.6 ± 5.2	11.0 ± 4.6	7.2 ± 1.8	13.0 ± 4.6	11.4 ± 4.4	9.6 ± 2.9
Juvenile Polychaetes	31.8 ± 6.9	41.0 ± 17.1	19.6 ± 17.1	24.4 ± 10.4	77.2 ± 38.2	107.0 ± 42.5	77.0 ± 37.6	216.8 ± 81.8	63.6 ± 14.0	134.8 ± 51.9	4.2 ± 2.6	16.0 ± 13.0	10.2 ± 3.3	41.2 ± 18.9	51.0 ± 17.6	67.8 ± 20.3
Tellimya trigona	6.6 ± 1.9	10.0 ± 3.3	2.2 ± 1.0	10.8 ± 2.5	6.8 ± 2.1	5.0 ± 1.7	15.8 ± 2.2	15.8 ± 2.6	4.8 ± 1.1	2.6 ± 1.6	4.0 ± 1.4	6.2 ± 1.4	3.2 ± 1.6	3.8 ± 1.6	17.4 ± 4.5	10.0 ± 4.8

Appendix B:

Table 7: Time-dependant differences in channel area, sediment particle size and abundance of macrofaunal taxa in large and small channels relative to controls at Site 2.

	Site 2															
	Large Structures								**Small Structures**							
Day	**1**		**3**		**5**		**8**		**1**		**3**		**5**		**8**	
	Channel	**Control**	**Channel**	**Control**	**Channel**	**Control**	**Channel**	**Control**	**Channel**	**Control**	**Channel**	**Control**	**Channel**	**Control**	**Channel**	**Control**
Channel Area (m^2)	3848.1 ± 870.8	-	2816.2 ± 567.2	-	2782.6 ± 349.1	-	2405.5 ± 385.8	-	1090.9 ± 57.0	-	1178.4 ± 96.5	-	1049.8 ± 135.8	-	1024.1 ± 148.4	-
Sediment Particle Size (µm)	-	-	306.0 ± 17.8	-	-	-	-	-	-	-	293.3 ± 7.4	-	-	-	-	-
Species																
Adult *Urothoe grimaldii*	17.2 ± 3.7	26.2 ± 5.0	15.8 ± 1.2	20.8 ± 5.6	27.0 ± 4.5	24.0 ± 3.6	28.8 ± 3.0	28.4 ± 3.4	13.6 ± 1.7	14.6 ± 3.4	18.2 ± 4.1	17.0 ± 2.3	30.0 ± 5.9	26.4 ± 3.7	23.0 ± 8.0	16.0 ± 4.2
Orbinia angrapequensis	2.4 ± 0.6	4.0 ± 0.5	9.8 ± 1.1	10.6 ± 4.5	10.4 ± 5.0	18.8 ± 5.5	20.2 ± 5.1	16.2 ± 4.0	2.8 ± 0.6	6.4 ± 3.9	6.4 ± 3.0	6.8 ± 2.5	11.8 ± 2.0	20.2 ± 7.0	12.0 ± 1.7	14.4 ± 2.1
Juvenile Polychaetes	5.8 ± 5.8	18.4 ± 13.8	58.4 ± 23.8	24.8 ± 9.7	22.0 ± 8.4	122.6 ± 37.0	46.2 ± 23.8	36.8 ± 17.8	6.4 ± 4.2	12.4 ± 6.2	8.0 ± 6.2	22.4 ± 15.7	53.4 ± 23.3	95.6 ± 33.9	27.4 ± 13.8	98.0 ± 25.1
Tellimya trigona	3.6 ± 1.9	1.0 ± 1.0	7.4 ± 2.9	1.8 ± 1.1	7.8 ± 5.0	7.0 ± 3.0	15.8 ± 4.3	11.8 ± 4.2	1.6 ± 0.5	2.8 ± 1.2	2.8 ± 0.7	4.6 ± 1.9	8.0 ± 2.2	9.8 ± 2.8	11.4 ± 1.5	12.8 ± 2.8