FLAMINGO FORAGING PLASTICITY: ECOLOGICAL DRIVERS AND IMPACTS

Kirti Narendra Gihwala

Supervisor: [1]Dr. Deena Pillay
Co Supervisor: [2]Dr. Melvin Varughese

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[1] *Department of Biological Sciences, University of Cape Town, Private Bag Rondebosch, 7701 Cape Town, South Africa*

[2] *Department of Statistical Sciences, University of Cape Town, Private Bag Rondebosch, 7701 Cape Town, South Africa*

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Kirti Narendra Gihwala

23 December 2016

gihwalakirti@yahoo.co.uk

ABSTRACT

The consequences of predation have become a central focus of marine ecological research. Numerous studies have emphasized the importance of apex predators in structuring assemblages at various organisational levels and in determining how ecosystems function. However, less appreciated currently is the fact that predators display multiple foraging behaviours, thereby allowing them to overcome problems associated with unpredictability of food resources in space and time. The primary goal of this dissertation is to contribute to growing understanding of the ecological causes and consequences of foraging plasticity displayed by Greater Flamingo *Phoenicopterus ruber roseus* in intertidal sandflat ecosystems in Langebaan Lagoon, South Africa. *P. roseus* feeds by either (1) creating pits, which involves flamingos stirring up deep sediments with their feet or (2) creating channels, in which their inverted bills are swept from side-to-side on the sediment surface. The first objective of the study was to quantify the ecological drivers of decisions made by flamingos to feed, and to implement either pit- or channel-foraging strategies. The latter was achieved through *RandomForest* modelling techniques that identified the prominent ecological drivers from a suite of biotic and abiotic variables. Results indicate that biotic variables, i.e. those associated with flamingo prey assemblages, were key in driving choices made by flamingos to forage and to implement either pit- or channel-foraging strategies. The second aim of this dissertation was to quantify the repercussions of the two different foraging behaviours on benthic assemblages. Comparisons of benthic assemblages in flamingo foraging structures (pits and channels) with adjacent non-foraged sediments (controls) indicated differential effects of both flamingo foraging methods on benthic communities, with channel-foraging eliciting a greater negative impact compared to pit-foraging, for which impacts were negligible. Abundance of macrofauna and surface-dwelling taxa such as micro-algae and the amphipod *Urothoe grimaldii* were all negatively impacted by channel-foraging. Sizes of channels constructed by flamingos were inversely related to their impacts, with impacts on macrofaunal abundance being greater in smaller channels. Overall, this study has shed light on the differential effects of foraging plasticity on prey assemblages and its importance in enhancing spatio-temporal heterogeneity in intertidal sandflats. The study also emphasizes the need to incorporate foraging plasticity into current thinking and conceptual models of predation in marine soft sediments, in order to appreciate the full spectrum of predation effects on assemblages.

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CHAPTER 1: INTRODUCTION

1.1 Predation

Understanding processes that are responsible for structuring ecological assemblages is one of the major goals of ecology (Miller 2002; Molles 2015). Organismal interactions have been shown to be particularly important and powerful determinants of spatio-temporal patterns in biotic assemblages in various ecosystem types (Ricklefs 2008; Wisz *et al.* 2013). The major type of organismal interaction that has often been cited as a key driver of community structure is predation (Paine 1971; Putman & Wratten 1984; Glassom & Branch 1997). A wealth of research has demonstrated the various impacts of predators through consumptive and non-consumptive pathways that span different spatial scales and ecological organisational levels as illustrated in Figure 1.

The lowest class at which predators influence assemblages is at the individual level in the form of sub-lethal predation (Zajac 1985; Harvell & Suchanek 1987, Figure 1). The latter involves partial consumption by a predator in which prey lose part of their body tissue but survive encounters with predators (Wilson 1990; Lawrence & Vasquez 1996; Pape-Lindstrom *et al.* 1997). Loss of organismal tissue can have significant effects on individuals, with reductions in growth (Smith 1990; Kamermans & Huitema 1994), feeding (Woodin 1984; Lawrence & Vasquez 1996) and reproductive fitness being commonly reported (Zajac 1985). In the long-term, sub-lethal predation can be critical in regulating population size (Harris 1989).

PREDATION IMPACTS

INDIVIDUAL

Consumptive effects
- Sublethal predation
  - Growth reduction
  - Feeding reduction
  - Reproductive success reduction

Non-consumptive effects
- Anti-predator behaviour
  - Feeding reduction
  - Habitat shift (rich to poor)
  - Reproductive success reduction

POPULATION

Consumptive effects (direct)
- Post-settlement mortality
- Competition, resource limitation altered

Consumptive effects (indirect)
- Create space-free patches
  - Displace existing residents
  - Colonization opportunities

Non-consumptive effects
- Altered settlement cues for recruits

COMMUNITY

Indirect effects
- Trophic cascades
  - Density-mediated
  - Trait-mediated
- Competitive exclusion altered
- Top-down cascade
  - Primary producers decrease
  - Ecosystem functioning impaired

ECOSYSTEM

Consumptive effects
- Altered trophic transfers
  - Affect productivity in recipient ecosystem
- Diminished nutrient transport

Non-consumptive effects
- Anti-predator behaviour
  - Induce shift in herbivore foraging behaviour (diet)
  - Alter plant community and nutrient flow

Figure 1: Conceptual diagram illustrating the consumptive and non-consumptive effects of predators on different ecological organisational levels.

While consumptive effects of predators have been well researched in many ecosystems (Lima 1998), behaviourally induced non-consumptive effects of predators also have the potential to impact ecological systems and should therefore not be ignored (Lima 1998). The mere presence of predators induces alterations to prey behaviour in ways that fundamentally reduce the risk of predation and prolong their survival (Lima 1998, Figure 1), but with important fitness consequences for prey. The majority of studies in aquatic systems suggest that prey undergo reductions in growth rates, due to predator avoidance behaviour indirectly reducing feeding activities (Skelly & Werner 1990) or causing spatial shifts from resource rich (but perilous) to poorer (but safer) habitats (Werner *et al.* 1983; Persson & Eklov 1995). Ultimately, predator avoidance behaviour can reduce prey reproductive output due to reductions in foraging rate (Peckarsky *et al.* 1993; Scrimgeour & Culp 1994; Lima 1998).

At the population level, predators directly interact with prey and cause mortality through direct consumption (Paine 1966; Connell 1975; Sih *et al.* 1985; Preisser *et al.* 2005), resulting in reductions of prey population sizes (Sih *et al.* 1985). Various studies in marine systems have demonstrated reductions in prey population sizes by predation increasing post-settlement mortality (Hixon 1991; Sweatman 1993; Carr & Hixon 1995; Albins & Hixon 2008, Figure 1). Predators consuming newly settled recruits, juveniles and adults can severely shrink population sizes to a level where other ecological processes such as resource limitation and competition are inhibited and become negligible in structuring populations (Hixon 1991). Consequences of predation on post-settlement recruits can potentially have large ecosystem impacts if predators remove ecologically important species (Williams & Polunin 2001; Mumby *et al.* 2006).

Despite the negative effects of predators on newly settled recruits at the population level, these effects can also induce indirect positive effects for other recruit populations (Figure 1). In marine soft-sediment ecosystems, epibenthic predators displace or increase mortality of residents, or alter colonization patterns, by providing resources through alterations of sediment properties while feeding (Thrush *et al*. 1991). In addition, the presence of predators can facilitate recruitment of sympatric species by providing settlement cues (Raimondi 1988).

The presence of apex predators has impacts that extend beyond the population level, with effects being able to influence community structure and spatio-temporal dynamics (Paine 1980; Carpenter *et al.* 1985; Power 1992; Menge 1995; Estes *et al.* 2001; Baum & Worm 2009, Figure 1). Apex predators exert top-down control on intermediate consumers (usually herbivores) through direct consumption, resulting in indirect positive effects on lower trophic levels (usually plants). This positive indirect effect of apex predators mediated through changes in herbivore density are generally referred to as a density-mediated indirect interaction (DMII, Abrams 1995; Werner & Peacor 2003). However, ecologists have also recognized another class of indirect interaction initiated by engineers mediated by predator altering prey behaviour, which commonly results in reduced feeding activities (Abrams 1992); greater investment in defensive strategies (Preisser *et al.* 2005) or spatial shifts to safer, low quality habitats (Power *et al*. 1985; McIntosh & Townsend 1996; Turner *et al.* 1999). Overall, these predator induced effects lower foraging rates and intermediate consumer impacts on primary producers. Such effects are broadly known as a trait-mediated indirect interaction (TMII, Kerfoot & Sih 1987; Abrams 1995; Werner & Peacor 2003).

Studies have shown that trophic-level effects of predators can span a spectrum of positive and negative effects, and are contingent on many factors, including environmental contexts

(Schmitz *et al.* 2004), resource abundance (Abrams 1991; Peacor 2002), predator foraging behaviour (Preisser *et al.* 2007), prey traits and life history characteristics (Abrams 1991) as well as the spatial and temporal scales at which these interactions are quantified (Peacor & Werner 2004; Abrams 2008). The role predators play in regulating community structure also influences ecosystem functioning and resilience (Paine 1969; Duffy 2002; Heithaus *et al.* 2008) by indirectly impacting the ecological functions provided by prey assemblages.

Predator effects can also influence competitive interactions between species (Figure 1), as demonstrated in Paine's (1974) study of sea star *Pisaster ochraceous* predation on California mussels *Mytilus californianus*. This classical work highlighted the ability of predatory species to prevent competitively dominant mussels from monopolising primary space (which is a limiting resource in the ecosystem), thereby indirectly allowing weaker competitors to co-exist. Subsequent studies have highlighted the ability of predators to prevent competitive exclusion in both terrestrial and freshwater ecosystems (Inouye *et al.* 1980; Morin 1983; Hambäck 1998).

The loss of predators can also elicit cascading changes to food webs (Figure 1). Estes & Palmisano (1974) showed that human overexploitation of sea otters in Alaska led to an increase in abundance of sea urchins (otter prey), which in turn reduced the biomass of kelp forests due to overgrazing. This cascading effect resulted in a shift in productivity and local assemblage structure. The ecosystem returned to its original state once sea otter populations had recovered over time (Estes & Duggins 1995). Such cascading effects of predator removals and introductions have been quantified in several ecosystem types, suggesting that these processes are ubiquitous (Power 1990; Pace *et al.* 1999; Menge 2000; Halaj & Wise 2001; Myers *et al.* 2007; Carpenter *et al.* 2010).

While there is substantial evidence of predators influencing ecological communities by regulating food webs (Wootton & Emmerson 2005; Dobson *et al.* 2006), research has also revealed the potential for predatory impacts to alter ecosystem level processes, such as resource flows (Costanza *et al.* 1997; Dobson *et al.* 2006, Figure 1). For example, studies have shown that anadromous fish in fresh water are a vital trophic resource for predators (Hansen 1987; Willson 1993; Willson & Halupka 1995) and serve as an ecologically significant link between freshwater and terrestrial ecosystems (Willson & Halupka 1995). However, marine predators hunting these fish during their migrations (Fiscus 1980) effectively lower trophic transfers to terrestrial ecosystems, causing a weakening of bottom-up interactions, and altering terrestrial productivity and biodiversity (Willson & Halupka 1995). Similarly, studies have demonstrated the ability of predators to negatively impact guano inputs into ecosystems by consuming prey, thereby lowering productivity and altering community structure (Croll *et al.* 2005; Fukami *et al.* 2006). Non-consumptive effects of predators can also generate key impacts at the ecosystem scale. By inducing foraging behaviour shifts in prey, predators indirectly alter producer nutrient levels (Schmitz *et al.* 2010, Figure 1), which ultimately alters nutrient availability in ecosystems (Schmitz 2006).

1.2 Predator foraging plasticity

Ecosystems often experience changes to biotic and abiotic processes (Putman & Wratten 1984; Molles 2015). Such effects enhance spatial and temporal variability in the distribution and abundance of resident organisms (Pettex *et al.* 2012), which in turn poses significant problems for predators, by effectively reducing the predictability of food resources available in space and time (Bell 1991). Studies have shown that consumers dedicate a significant proportion of their activity budgets to foraging (Drent & Daan 1980), in order to acquire sufficient nutritional and energetic resources to maintain or improve reproductive fitness (Lemon 1991). Due to the latter, and the need to overcome constraints associated with variable habitat conditions and the unpredictability of food resources, several predators have evolved plastic phenotypes (Paiva *et al.* 2010; Pettex *et al.* 2012; Cherel *et al.* 2014). A summary of studies reporting plastic foraging strategies employed by consumers is reported in Table 1. More specifically, predators have evolved multiple foraging behaviours that are adaptable to rapid environmental changes, allowing them to overcome variability in prey distribution, quality and quantity (Paiva *et al.* 2010). Foraging plasticity therefore allows predators to broaden their dietary niches based on profitability of prey resources, thereby reducing fitness costs associated with modifications in resource availability (Greeff & Whiting 2000).

Despite the widespread use of plastic foraging strategies in nature (Miner *et al.* 2005), little is known about this aspect of predation, particularly in marine ecosystems. The majority of the studies on predation have focused generally on quantifying the effects of predators across different trophic positions (Pace *et al.* 1999; Silliman & Bertness 2002). Studies have also investigated the subtleties of predator-prey relationships, in the form of trait-mediated indirect interactions (indirect interactions transmitted by predators modifying prey behaviour) and density-mediated indirect interactions (indirect interactions transmitted by predators modifying prey densities through consumption) in driving trophic cascades (Grabowski 2004; Siddon & Witman 2004). While predator impacts on prey assemblages have been well researched in marine ecosystems, the consequences of plastic foraging strategies employed by predators have rarely been quantified. Studies that have dealt with foraging plasticity have focused more on the factors that drive consumers to switch between foraging behaviours (McCafferty *et al.* 1998; Hamer *et al.* 2007; Paiva *et al.* 2010).

Table 1: Summary of studies showing varying degrees of foraging plasticity employed by consumers.

Reference	Consumer	Location	Foraging plasticity
Duval *et al.* 1984	Cuttlefish (*Sepia officinalis*)	Luc-sur-Mer, France	(1) Capture small crabs by ejection of tentacles (2) Capture large crabs by jumping on prey
Peterson & Skilleter 1994	Baltic clam (*Macoma balthica*)	Neuse River estuary, North Carolina	(1) Deposit feeds when current flow decreases (2) Suspension feeds when current flow increases or when siphon-cropping fish present
Craig *et al.* 1996	Golden silk spider (*Nephila clavipe*)	Barro Colorado Island, Panama	(1) Spin webs that appear golden to attract insects in bright light (2) Spin webs that appear white in dim light for camouflage
Sutherland *et al.* 2000	Western sandpiper (*Calidris mauri)*	Fraser River estuary, British Columbia	(1) Pecking for epibenthic copepods and cumaceans (2) Probing for large infaunal polychaetes
Bowen *et al.* 2002	Harbour seal (*Phoca vitulina*)	Sable Island, Canada	(1) Digging/cruising in sand bottom for cryptic prey (2) High speed pursuit of conspicuous schools of prey
Tso *et al.* 2007	Giant wood spider (*Nephila pilipes*)	Forests of central Taiwan	(1) Stiffer webs when feeding on crickets (2) Limp webs when feeding on flies
Paiva *et al.* 2010	Cory's shearwater (*Calonectris diomedea*)	4 archipelagos, North Atlantic	(1) Shallower and shorter dives in productive neritic areas (2) Deeper and longer dives in less productive pelagic areas

Prior research has revealed a growing appreciation of the ecological consequences of phenotypic plasticity, including effects on direct and indirect interactions between organisms and their surrounding environments in ways that can influence local biodiversity and ecosystem functioning (Miner *et al.* 2005). Miner *et al.* 2005 highlighted the need for further research in understanding the consequences of plasticity for community structuring and fundamental ecological processes. Although a few studies have demonstrated that shifts in predator foraging behaviour can alter the outcome of predator-prey interactions, the quality and distribution of food resources within a community (Otto *et al.* 2008), the strength of competition (Relyea 2000), facilitation (Sih *et al.* 1998) and trophic cascades (Katano 2011), such knowledge is limited for marine soft-sediment ecosystems, despite the fact that many foragers in marine soft-sediments do actually employ multiple foraging behaviours in response to variable ecosystem conditions (Hall *et al.* 1991; Thrush *et al.* 1991; Johnson & Cézilly 2007).

1.3 Flamingos and plastic foraging

Flamingos are well known shorebird predators that are highly adaptable to environmental changes, allowing them to exploit a large diversity of trophic resources. These charismatic predators are well known for executing a wide range of feeding behaviours (Brown *et al.* 2005), allowing them to feed on a variety of habitats including land, water surfaces, water column and benthic sands/muds (Allen 1956; Jenkin 1957). Numerous studies have demonstrated flamingos altering their foraging behaviour in order to consume prey with varying distribution in aquatic environments (Arengo & Baldassarre 1999; Brown *et al.* 2005; Johnson & Cézilly 2007).

The Greater Flamingo *Phoenicopterus ruber roseus* which commonly occurs in coastal and estuarine zones (Rodríguez-Pérez *et al.* 2007), is the primary subject of investigation in this study, which focuses specifically on understanding the ecological causes and consequences of foraging plasticity employed by Greater Flamingos in Langebaan Lagoon, on the west coast of South Africa. *P. roseus* are filter feeders, feeding off small-invertebrates through different foraging techniques. In Langebaan Lagoon, two major behaviours have been observed. The first involves *P. roseus* sweeping their inverted bills in a semi-circular arc as they walk, creating a channel-like structure in the sediment (Figure 2A). The second behaviour involves flamingos retaining their inverted bills in a central position near the substrate, while stamping in a circular motion around it. This behaviour creates a pit-like foraging structure with a sediment mound in the centre (Figure 2B, Glassom & Branch 1997; Brown *et al.* 2005; Johnson & Cézilly 2007).

Flamingos are colonial shorebirds that can occur at high densities in marine sedimentary habitats and can therefore exert considerable impacts on these systems (Glassom & Branch 1997; Rodríguez-Pérez *et al.* 2007). A few studies have quantified the impact of flamingo predation on macrofaunal community structure via exclusion experiments. Hurlbert and Chang (1983) conducted one of the first field experiments quantifying flamingo impacts and demonstrated an increase in micro-organism biomass following exclusion of Andean Flamingo *Phoenicoparrus andinus*. Glassom and Branch (1997) also recorded an increase in macrofaunal abundance and altered sediment properties when excluding the Greater Flamingo from two lagoons in Namibia. Rodríguez-Pérez *et al.* (2007) found that Greater Flamingos significantly reduced chironomid abundance and increased the density of larger larvae in an ephemeral marsh ecosystem. Apart from these quantitative studies, the majority of research on flamingos has been descriptive and observational, resulting in little attention being paid to understanding the ecological role flamingos play in marine soft-sediment ecosystems (Glassom & Branch 1997; Bildstein *et al.* 2000).

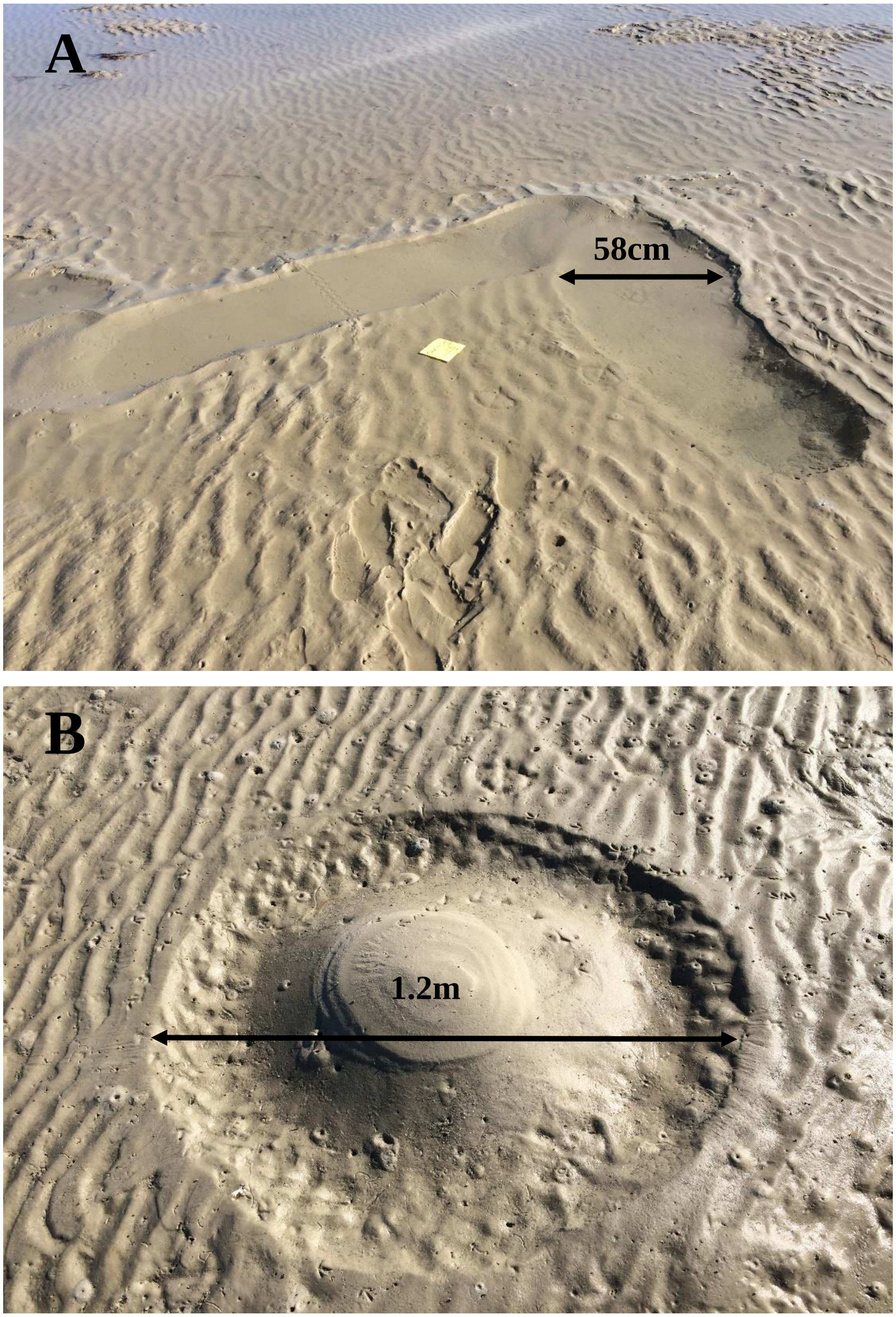

Figure 2: Foraging structures (A: channel, B: pit) produced by Greater Flamingos. Photos taken at low tide, Oesterwal, Langebaan Lagoon.

Given the calls for greater understanding of phenotypic plasticity in driving ecological processes (Miner *et al.* 2005) and the scarcity of quantified data on flamingo foraging, the central goal of this study was to contribute to growing understanding of the causes and consequences of plastic foraging strategies employed by Greater Flamingos in intertidal soft-sediments. The investigation consisted of two main components, an outline of which is summarised, overleaf in Figure 3. The first utilised modelling techniques to identify ecological factors that drive decisions made by flamingos to initiate foraging or to execute pit- or channel-foraging. The second component focused on quantifying the effects of flamingo foraging plasticity (channel- or pit-foraging) on benthic assemblages. For the first component, it was hypothesized that biotic factors (prey characteristics) would be the main drivers of flamingo foraging plasticity. Three hypotheses were tested for the second component. The first was that foraging plasticity would generate differential impacts on benthic assemblages. The second was that the magnitude of predation impact would be greater when flamingos undertake pit-foraging relative to channel-foraging. It was reasoned that since pit-foraging involved disturbance of sediments to greater depths, this technique should impose a greater fitness cost (compared to channel-foraging) and would thus need to be compensated for by the energy gained from this foraging method (Pyke *et al.* 1997). Lastly, it was hypothesized that increasing sizes of flamingo foraging structures (pits or channels) would result in a greater predation impact on prey assemblages relative to non-foraged sediments, based on the rationale presented in the previous hypothesis.

This dissertation consists of four Chapters. Following this introductory chapter, Chapter 2 outlines the methods employed to test the hypotheses that were highlighted above. Chapter 3 presents the findings of the two main components of the study (Figure 3), which are then discussed critically in Chapter 4.

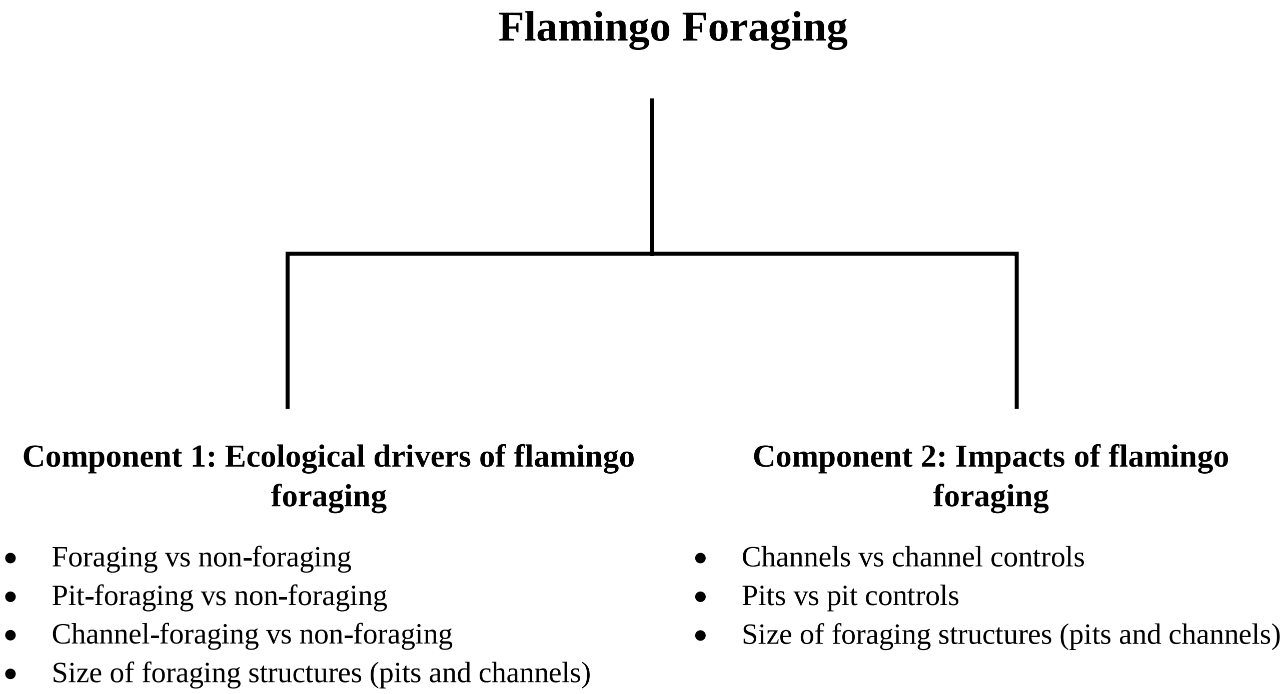

Figure 3: Diagram illustrating the two central components carried out in the investigation. Component 1 uses modeling techniques to identify the ecological drivers of flamingo decisions to (1) feed or not feed, (2) employ pit- or channel-foraging and (3) create foraging structures of different sizes. Component 2 tests the consequences of flamingo foraging plasticity (in the form of different structure types (pits or channels) and their sizes) on benthic assemblages.

CHAPTER 2: MATERIALS AND METHODS

2.1 Study area

Langebaan Lagoon (located between 33°11’27’’S, 18°07’37’’E and 33°03’54’’S, 17°58’07’’E, Figure 4) is a marine-dominated lagoonal system located on the west coast of South Africa (Pillay *et al.* 2011). The lagoon is 15km long and 4km wide with a connection to the Atlantic Ocean via a narrow tidal inlet passing through Saldanha Bay (Flemming 1977; Compton 2001). Langebaan Lagoon receives minimal freshwater runoff (Siebert & Branch 2005) and experiences an average spring tidal range of 1.8m and 1.5m at the mouth and head of the system (Day 1959; Flemming 1977). Langebaan experiences a Mediterranean, semi-arid climate with hot and dry summers, winter rainfall and an annual precipitation below 300mm (Day 1959; Flemming 1977). The ecosystem supports a rich diversity of marine invertebrates that potentially exceeds all other lagoonal and estuarine systems in South Africa (Day 1959; Christie & Moldan 1977). BirdLife International has also classified Langebaan Lagoon as an Important Bird Area (Pillay *et al.* 2010), due to it supporting approximately 37 500 birds in summer and 10 500 in winter, with flamingos comprising approximately 1% of the total bird population in summer, rising to 40% in winter (Underhill 1987). Management authorities divided this ecosystem into three recreational zones as a conservation measure. The first is a multi-purpose recreational area (Zone A) used for fishing, bait collection and water sports. Zone B is a limited recreational zone where bait collection is prohibited, however non-destructive recreational activities are allowed. Lastly, there is a marine sanctuary (Zone C) which is a prohibited area that is closed off to public use and all activities are ceased (Hanekom *et al.* 2009).

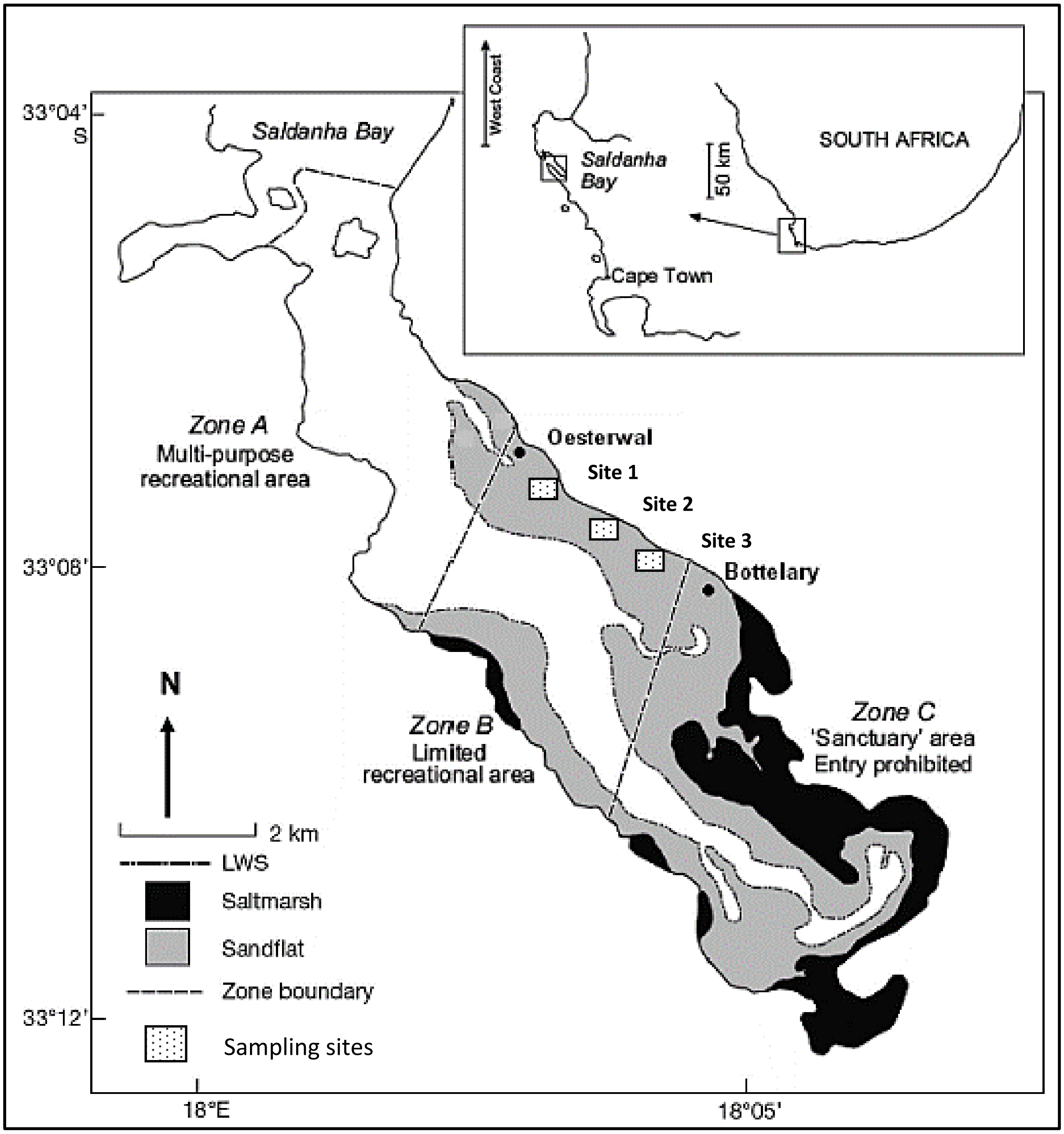

Figure 4: Map of Langebaan Lagoon, with its geographical position, sampling sites and park zones on the South African coastline. LWS: low water spring (adapted from Pillay *et al.* 2010).

2.2 Sampling design

A nested hierarchical sampling design was employed for the study. Samples were collected in the middle of winter (middle of flamingo season) during spring low tide across three sites, between Oesterwaal and Bottelary (Figure 5). At each of the three sites, three shore positions (high-, mid- and low-water mark) were sampled, with each shore position sample comprising six quadrats (10m x 10m) with three covering areas where flamingos fed and three where they did not feed. Feeding quadrats were chosen with areas that were abundant of flamingo foraging structures (pits or channels). Non-feeding quadrats were positioned where sediments were undisturbed to flamingo predation (no foraging structures present). A minimum of three and maximum of five foraging structures were sampled per feeding quadrat along with an equivalent number of controls. Control samples were collected between 0.5 -1m from foraged structures to reduce variability. Pit - and channel-foraging structures were spatially segregated (0.5m – 1m) thereby preventing any overlap between these foraging structures and their controls. In addition, five non-feeding controls (substantial feeding-free spaces with no evidence of flamingo foraging) were sampled per non-feeding quadrat. Only freshly created pit- and channel-foraging structures (within 24 hours of foraging activity) were sampled in the study to avoid confounding foraging effects with structure age.

2.3 Standardizing structure age

A preliminary field study was undertaken one month before final sampling in order to identify newly created flamingo foraging structures in Langebaan Lagoon. Two plots ($25m^2$; at the high- and mid-water mark, Site 1) of sediment were raked during low tide to smooth out any existing flamingo foraging structures. After a tidal cycle, freshly (within 24 hours) formed flamingo foraging structures were marked and photographed. Marked foraging structures were photographed again 24 hours later. Photographs were used to generate a photographic library (Figure 6) of appearances of newly formed channels and pits and their subsequent changes after 24 hours in response to wave action.

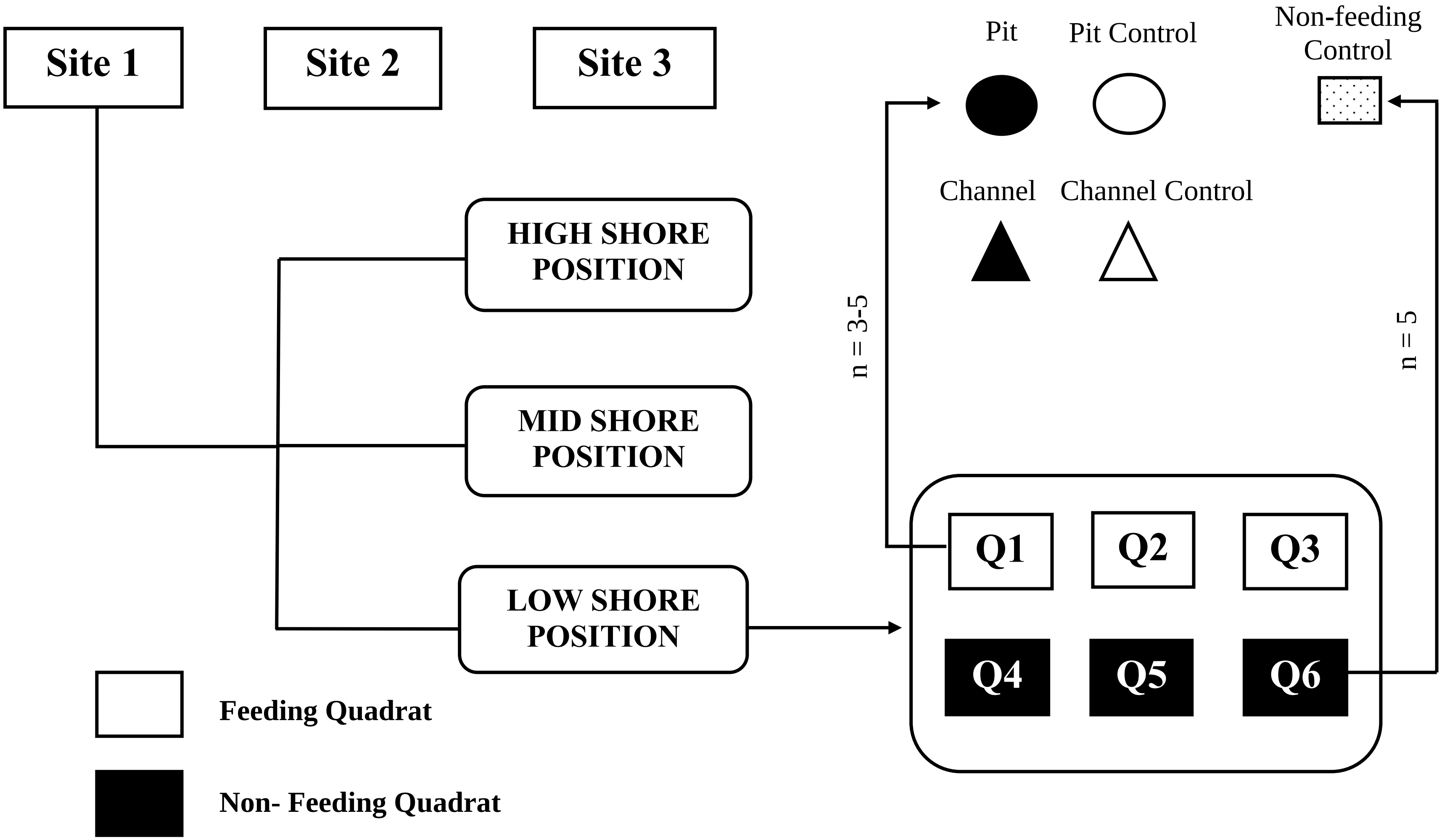

Figure 5: Schematic overview of nested sampling design used in the study. Three sites were sampled (Sites 1-3), comprising high-, mid- and low- water samples. Three feeding (Q1-3) and non-feeding quadrats (Q4-6) were sampled per shore position.

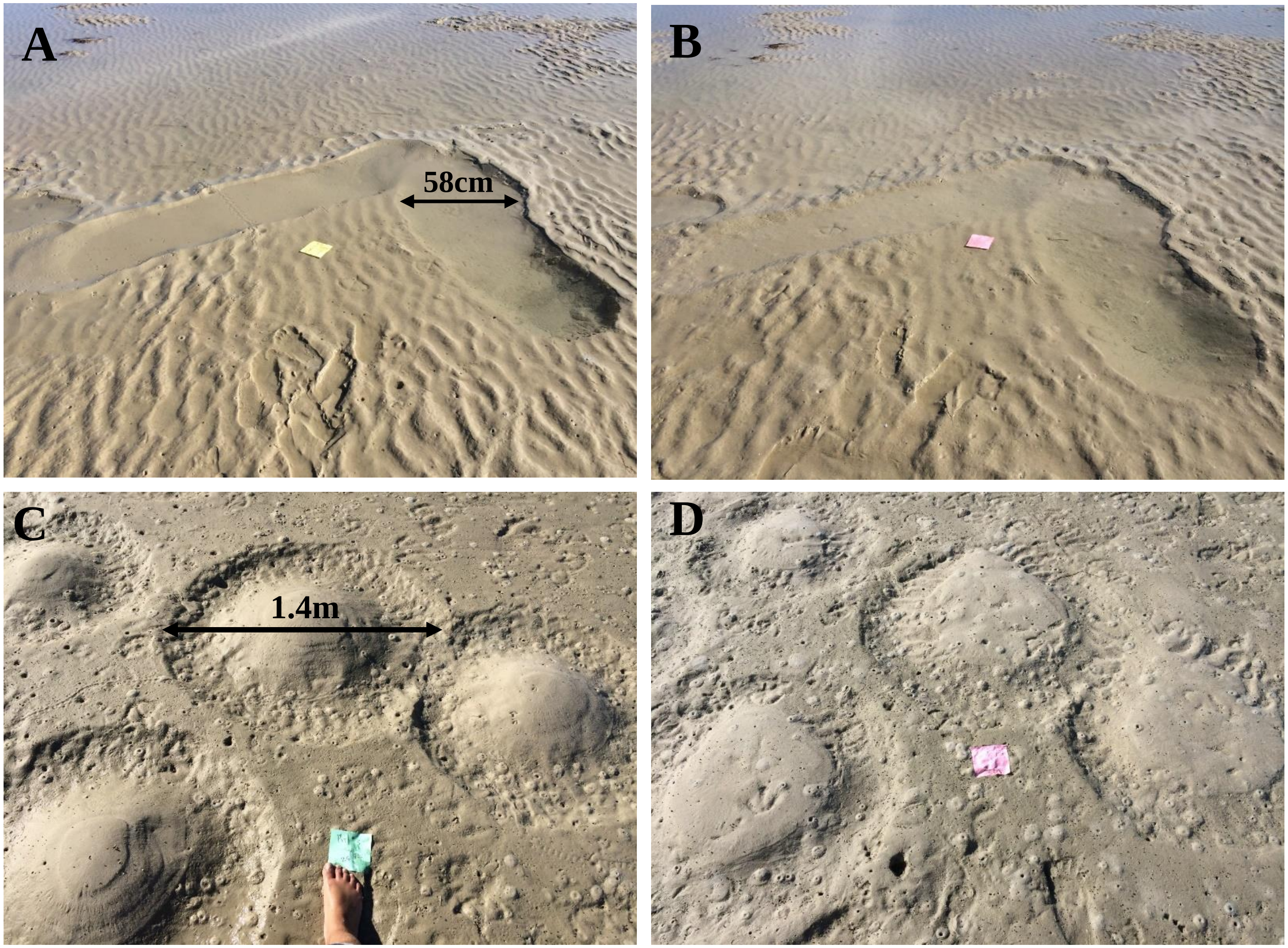

Figure 6: Photos of flamingo foraging structures within 24 (A: channel, C: pits) and 48 hours (B: channel, D: pits) of foraging. Photos taken at low tide, Oesterwal, Langebaan Lagoon.

2.4 Abundance and size of foraging structures

Prior to sampling, the abundance of every foraging structure within each feeding quadrat was counted. Photographs were only taken of the freshly created foraging structures that were going to be sampled using a digital camera (Canon IXUS 130). All photographs were taken from a standard distance (1m) perpendicular to structures. ImageJ (version 1.48, 2014) was used to quantify the area of each foraging structure.

2.5 Macrofauna

For macrofauna samples, three cylindrical sediment cores (depth = 15cm, diameter = 10cm) were collected and pooled from each of the foraging structures, their controls and non-feeding controls. For pit-foraging structures, a single core was collected from the central mound and two cores collected from the depression on either side. In the case of channels, three cores were collected across the length of the structure. Cores were then churned in a bucket before being sieved through a 500μm mesh. This procedure was repeated five times before being sieved in a 2mm mesh, and retained material preserved in 70% ethanol with Rose Bengal for staining. Macrofauna were counted and identified to the lowest taxonomic level possible in the laboratory. The biomass of individual species within samples were calculated using two different approaches. For large macrofaunal organisms (e.g. sandprawns, mudprawns, crabs), ten individuals were weighed (wet weight) on a Sartorius balance (5 decimal places) after blotting on tissue paper for one minute; and a mean individual biomass was calculated per species. Secondly, for smaller organisms (e.g. amphipods, polychaetes, isopods), thirty individuals were weighed and a mean generated. For molluscs (mainly gastropods and bivalves), organisms were removed from shells prior to weighing. To estimate biomass per species per sample, mean biomass for each species was multiplied by their abundance.

2.6 Micro-algal biomass

Chlorophyll-*a* (chl-*a*) was extracted from sediment cores (diameter = 2cm, depth = 1cm; n = 3 per foraging structure/control and non-feeding control) and placed in 20ml 90% acetone. Cores were kept in darkness in a refrigerator for 24 hours. A sub-sample of the homogenised acetone sample was analysed using a fluorometer (Turner Designs Trilogy) to determine chl-*a* concentration, which served as a proxy for micro-algal biomass.

2.7 Soil moisture content & sediment particle size

To quantify soil moisture content, a single sediment core (20ml vial) was collected per feeding and non-feeding quadrat and frozen. After defrosting, the weight of individual sediment cores was measured (to the nearest 0.0001g), then dried at 105ºC for 24 hours and re-weighed. Soil moisture content was expressed as the difference in initial and final mass of sediment samples divided by the final mass of dry sediment. In addition, these dry sediment samples were also analysed with a Malvern Analyser (Mastersizer 2000), in which laser diffraction calculated sediment particle size (µm) at a 50% cumulative distribution per sample.

2.8 Statistical analyses

The package *RandomForest* was utilized in R (Liaw & Wiener 2002; James *et al.* 2013) to quantify ecological factors determining flamingo decisions to 1) feed or not feed (by comparing foraging vs non-foraging samples) and 2) using channels or pits to forage. Regression analyses were undertaken using *RandomForest* to identify key determinants of sizes of pits and channels created by flamingos. Predictor variables were obtained from biological data from non-feeding controls and foraging structure controls and consisted of community metrics (macrofaunal abundance, species richness and biomass), abundance and biomass of dominant macrofaunal species and chl-*a* concentrations. For community biomass, data with and without sandprawn *Callichirus kraussi* biomass were used as predictor variables in order to assess whether *C. kraussi* biomass disproportionately affected statistical outcomes. Macrofaunal species were classified into three functional groups (surface feeders (0-5cm), infauna (5-10cm) and deep burrowing feeders (>10cm)) based on their depth distribution sediments (Branch *et al.* 2010). Soil moisture content and sediment particle size were only used as predictor variables when assessing factors driving flamingo foraging/non-foraging. Each of the *RandomForest* analyses consisted of a model with 500 classification trees. Accuracy was evaluated based on the out-of-bag estimation of error (classification analysis) and the percentage of variance explained in a given dataset (regression analysis, Liaw & Wiener 2002). Variable importance plots were extracted from the models to identify the top ranked predictor variables. Partial dependence plots were created from the important variables identified, in order to model the predictions of interest (James *et al.* 2013).

Multivariate analyses were performed on unstandardized and transformed (fourth root) abundance data in PRIMER v.6.1.5 (Plymouth Routines in Multivariate Ecological Research; Clarke and Gorley 2006). Non-metric multidimensional scaling (MDS) ordinations (based on resemblance matrices generated from Bray-Curtis similarities) were used to visually assess macrofaunal community structure between flamingo foraging structures and their controls. PERMANOVA (Permutational Analysis of Variance, nesting hierarchy: Site, Shore Position(Site), Quadrat(Shore Position)) was used to determine whether macrofaunal community structure differed between flamingo foraging structures and their controls, with pair-wise tests being used to identify significant within-treatment differences per site and tidal position. W-statistics were calculated for each foraging structure and their controls in order to numerically quantify the magnitude of difference in community biomass and abundance using the Cumulative Abundance-Biomass Curve function. The DIVERSE function was utilised to calculate macrofaunal abundance (N) and species richness (total number of S) per feeding structure, feeding structure control and non-feeding control. SIMPER (similarity percentage analysis) was used to identify dominant species that accounted for 90% of overall community abundance and biomass structure in pits, channels and their corresponding controls per tidal position per site.

Univariate analyses and parametric tests were conducted in SPSS (Statistical Package for Social Sciences) v 21. Levene's and Kolmogorov-Smirnov tests were used to test for normality and homogeneity of variance in data. In cases where data did not meet the required assumptions for parametric testing, data were transformed ($\ln(x + 1)$). A nested analysis of variance (ANOVA) with post-hoc Tukey tests were applied to determine whether macrofaunal community measures differed between 1) flamingo foraging structure controls and non-feeding controls, 2) flamingo foraging structures and their controls. Nested ANOVA and post-hoc Tukey tests were also applied to determine whether the abundance and size of flamingo foraging structures differed spatially across sites and tidal positions.

A linear mixed-model analysis (LMM) was conducted in R (package *lme4*) in order to investigate the strength of the relationship between the size of the flamingo foraging structures and the impacts on macrofaunal community measures along with dominant macrofaunal species. Flamingo impact was expressed as the difference in macrofaunal community measures or abundance of dominant species between foraging structures and respective controls. A nested hierarchical structuring was employed in the linear mixed model, with shore position nested in site and quadrat nested in shore position as random effects. Size of the foraging structures (pits and channels) remained as fixed effects and were standardized (see equation 1 below). Response variables were transformed ($L(x) = \text{sign}(x) * \log(|x| + 1)$: where x = data point) in order to normalize the data (John & Draper 1980). The package *MuMIn* was utilized to calculate the coefficient of determination (R^2) for linear mixed models.

$$x' = \frac{x - \mu}{\sigma} \qquad \textbf{(1)}$$

x' = new data point

x = original data point

μ = mean of data set

σ = standard deviation of data set

CHAPTER 3: RESULTS

3.1 Spatial variation in the abundance and size of flamingo foraging structures

Shore position was the only spatial variable to significantly affect the size ($F_{1,47}$ = 6.57, p = 0.01, Table 2) and abundance ($F_{2,8}$ = 6.72, p = 0.02) of channel-foraging structures. Sizes of channel-foraging structures appeared to decline from the high- to the low-water mark at Site 3 (Figure 7A). On the other hand, abundance of channel-foraging structures increased from the high- to low-water mark at Site 2 (Figure 7B). The size of pit-foraging structures varied significantly among quadrats ($F_{2,33}$ = 3.67, p = 0.04, Table 2). Channel-foraging structures ranged from 380.64 - 6096.57cm^2, with an average size of 2756.24 ± 159.93cm^2. Pits ranged from 2254.76 - 6329.93cm^2, with an average size of 4112.38 ± 186.36cm^2.

Table 2: Results of nested ANOVA testing for differences in the abundance and size of flamingo foraging structures between spatial levels. Degrees of freedom are indicated in brackets below the *F*- value. * = significant difference; - = no statistic computed.

Factor	**Channel Abundance**		**Pit Abundance**		**Channel Size**		**Pit Size**	
	F	p	*F*	p	*F*	p	*F*	p
Site	0.44 (2,2)	0.70	-	-	0.13 (2,1)	0.89	-	-
Shore Position	6.72 (2,8)	0.02*	-	-	6.57 (1.47)	0.01*	-	-
Quadrat	0.63 (4,8)	0.66	0.47 (2,4)	0.66	1.84 (4,47)	0.14	3.67 (2,33)	0.04*

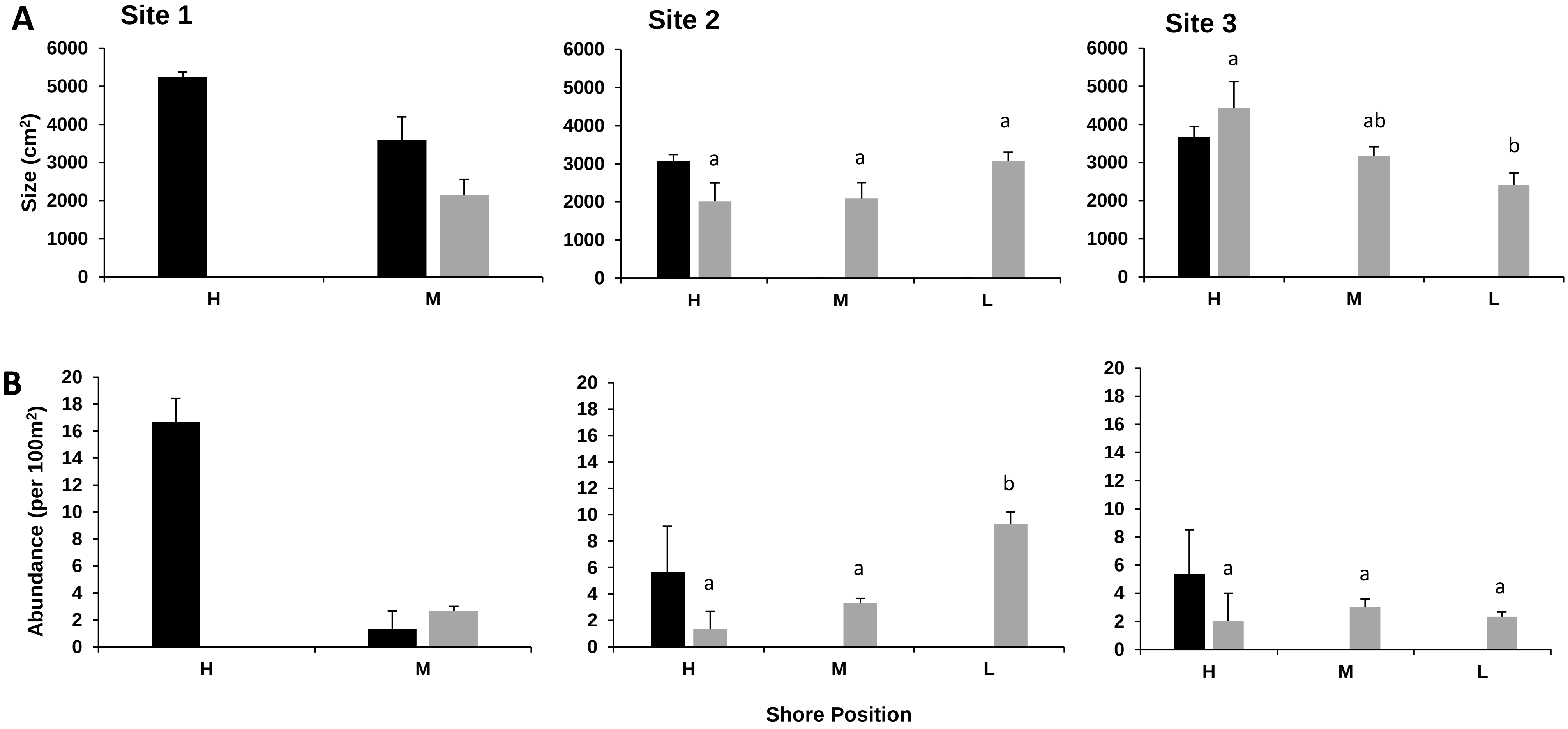

Figure 7: Differences in (A: size, B: abundance) of flamingo pit (■) and channel (▨) foraging structures across the three sites and shore positions (H: high, M: mid, L: low). Different letters denote significant differences between shore positions. Means ± 1SE are shown.

3.2 Part A: Drivers of flamingo foraging

3.2.1 Foraging vs non-foraging

RandomForest modelling revealed that species richness and macrofaunal biomass excluding *Callichirus kraussi* along with the abundance of infauna, were the primary predictors of flamingo foraging (Figure 8). For richness, the probability of feeding was high when richness was between six and eight, but then declined followed by an increase. The probability of feeding was greatest when macrofaunal biomass was low between 0.0 and 0.05g, but thereafter decreased as the biomass increased. For infauna, the probability of feeding was low when infauna was between 0 and 20; but then increased rapidly before reaching a steady state after 23.

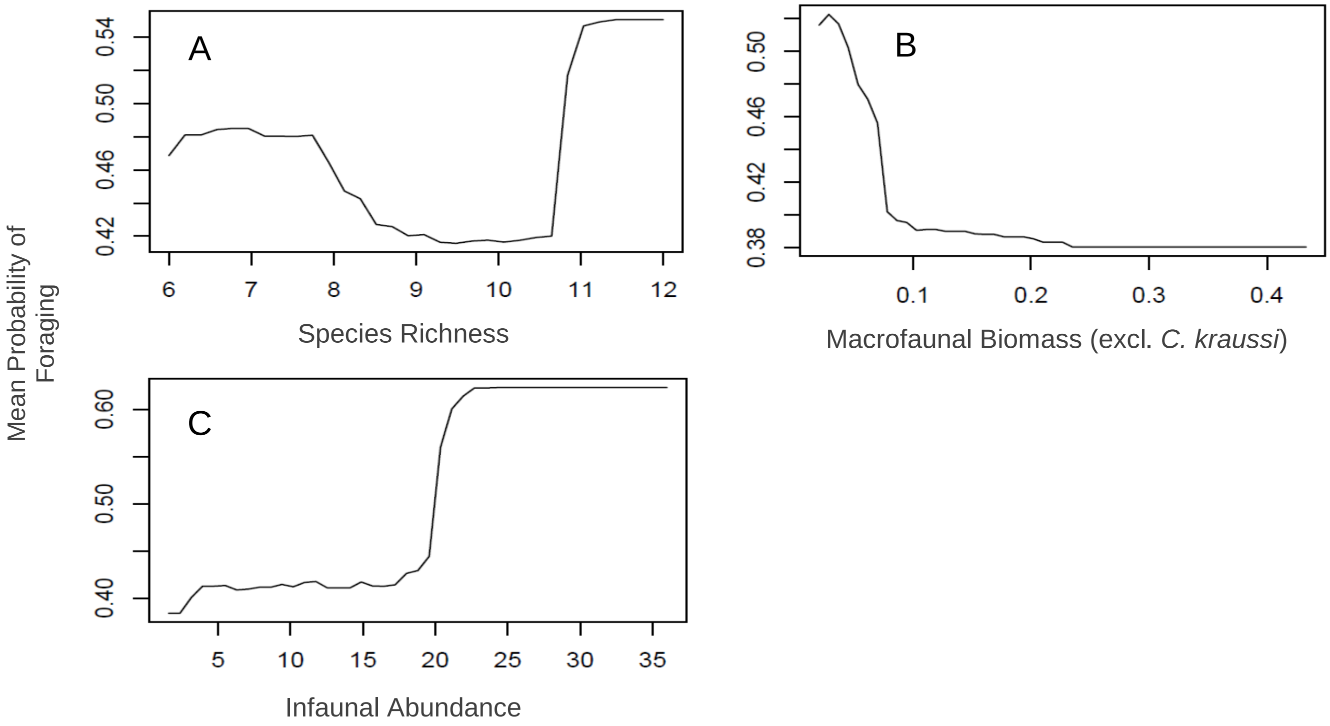

Figure 8: Best predictors (A: Species Richness, B: Macrofaunal Biomass (excl. *C. kraussi*), C: Infaunal Abundance) of flamingo foraging.

Visual trends in variables identified by *RandomForest* modelling to drive flamingo feeding are illustrated in Figures 9-11. Macrofaunal richness did not vary among flamingo foraging treatments (Nested ANOVA: $F_{3,39} = 1.85$, p = 0.15, Figure 9) nor did infaunal abundance (Nested ANOVA: $F_{3,39} = 2.06$, p = 0.12, Figure 11).

Macrofaunal biomass excluding *C. kraussi* was significantly affected by flamingo foraging treatment (Nested ANOVA: $F_{3,39} = 6.48$, p = 0.001). Feeding quadrats generally held a lower biomass than non-feeding quadrats across the sites, of which two out of eight comparisons were statistically supported (Figure 10).

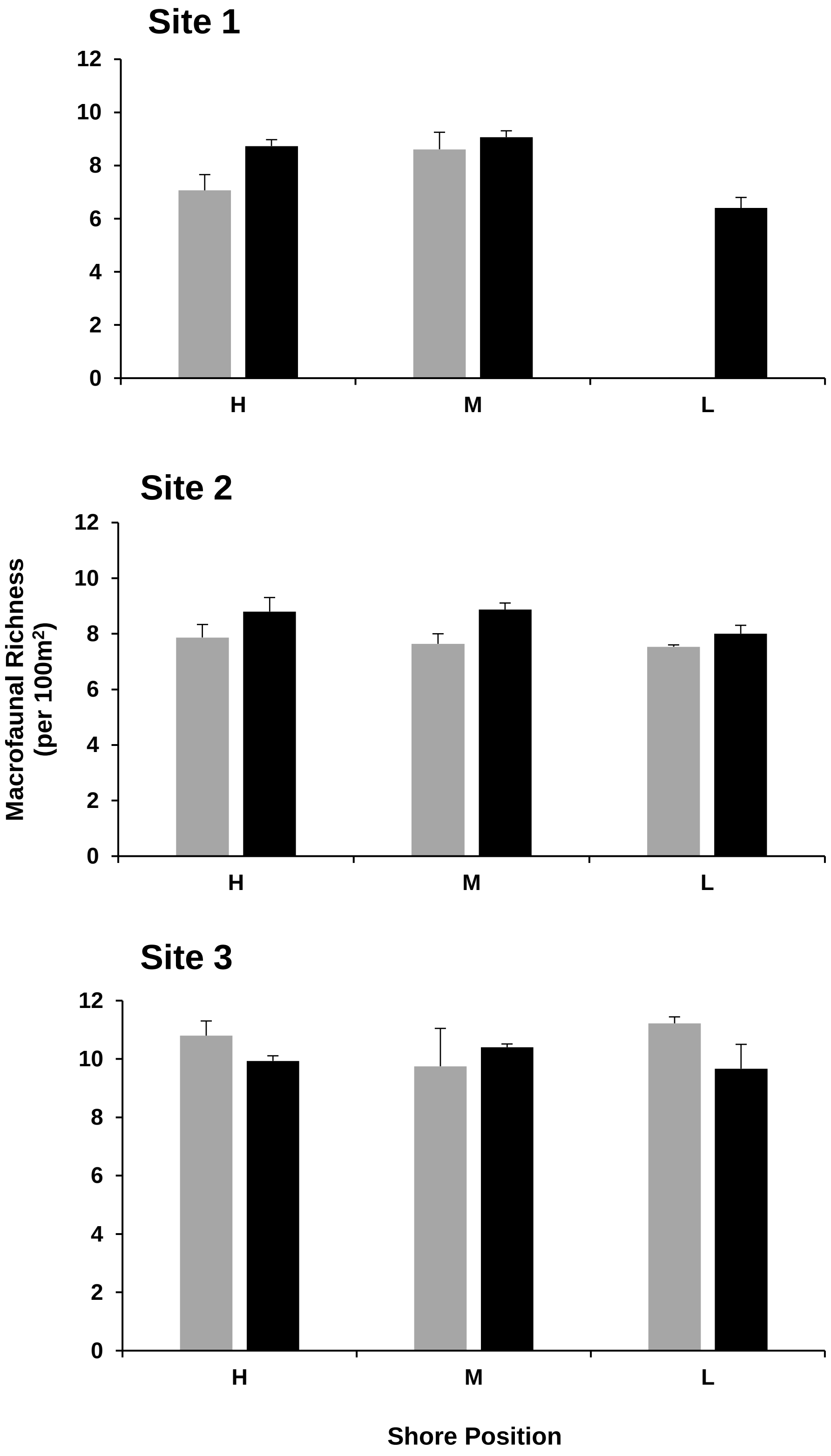

Figure 9: Differences in macrofaunal richness between feeding (▨) and non-feeding quadrats (■) across the three sites and shore positions (H: high, M: mid, L: low). Means ± 1SE are shown.

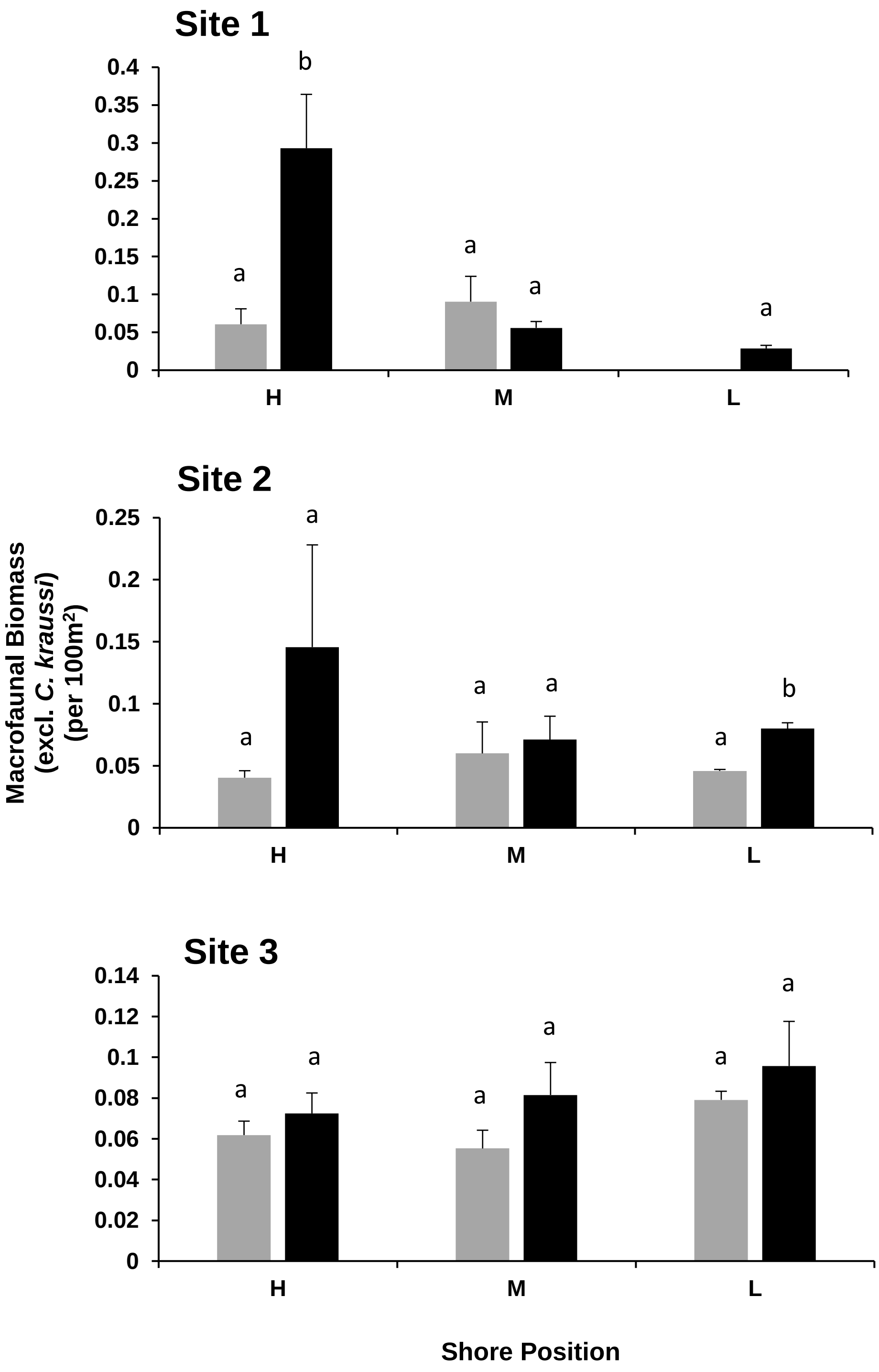

Figure 10: Differences in macrofaunal biomass (excl. *C. kraussi*) between feeding (■) and non-feeding quadrats (■) across the three sites and shore positions (H: high, M: mid, L: low). Different letters denote significant differences of biomass between treatments within a shore position. Means ± 1SE are shown.

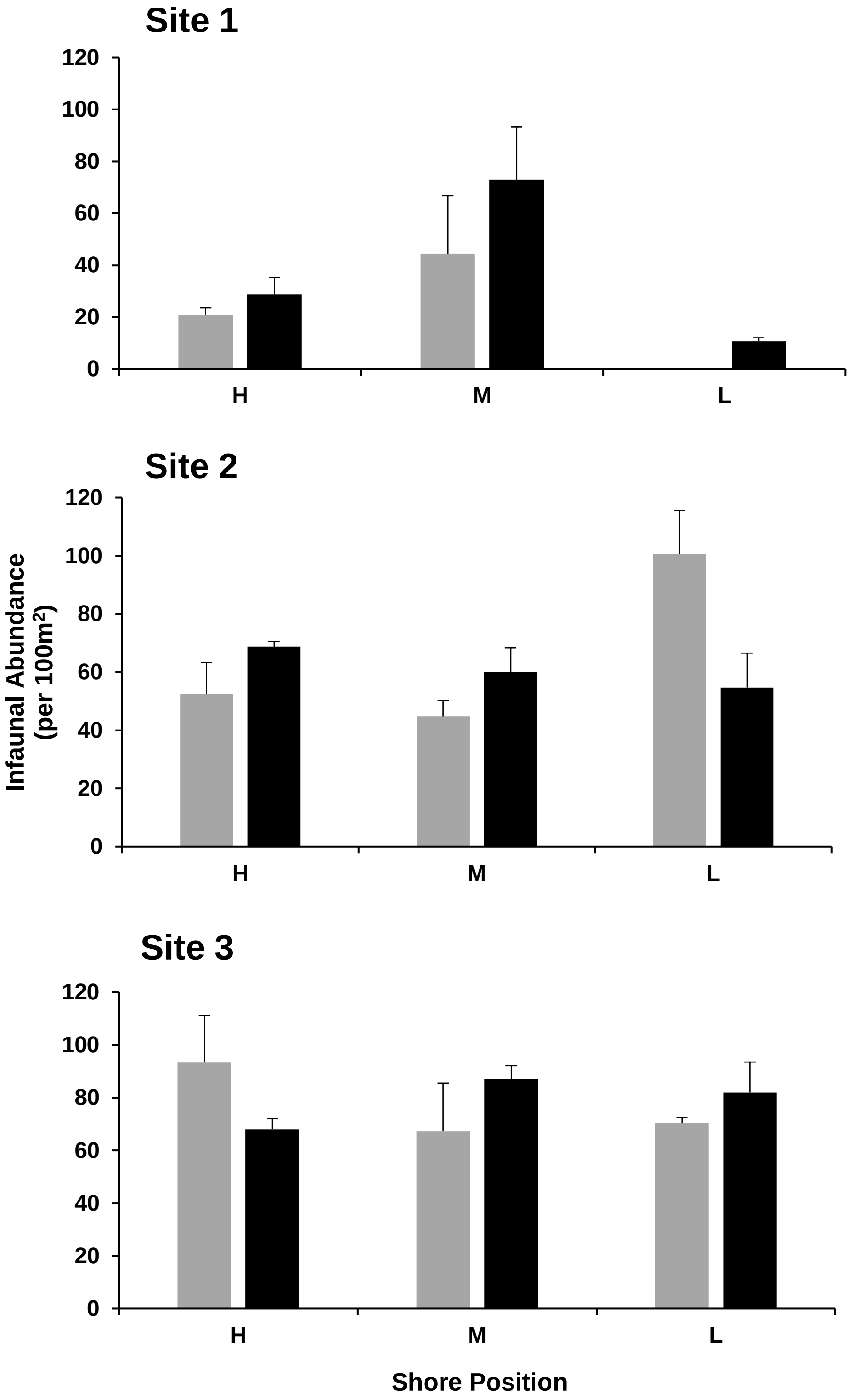

Figure 11: Differences in infaunal abundance between feeding (▨) and non-feeding quadrats (■) across the three sites and shore positions (H: high, M: mid, L: low). Means ± 1SE are shown.

3.2.2 Pit-foraging vs non-foraging

Chl-*a* concentrations, total biomass of macrofauna (including *C. kraussi)* and biomass of surface feeders were identified as the primary drivers of pit-foraging by flamingos (Figure 12). The chl-*a* model predicted low probabilities of pit-foraging between 0.2 and 0.4 mg L^{-1}, but thereafter probability increased steadily as chl-*a* concentrations increased. On the other hand, probability of pit-foraging was predicted to be related to both biomass of macrofauna and surface feeders in an inversely exponential relationship, with pit-feeding being likely to occur when both predictor variables are low in magnitude.

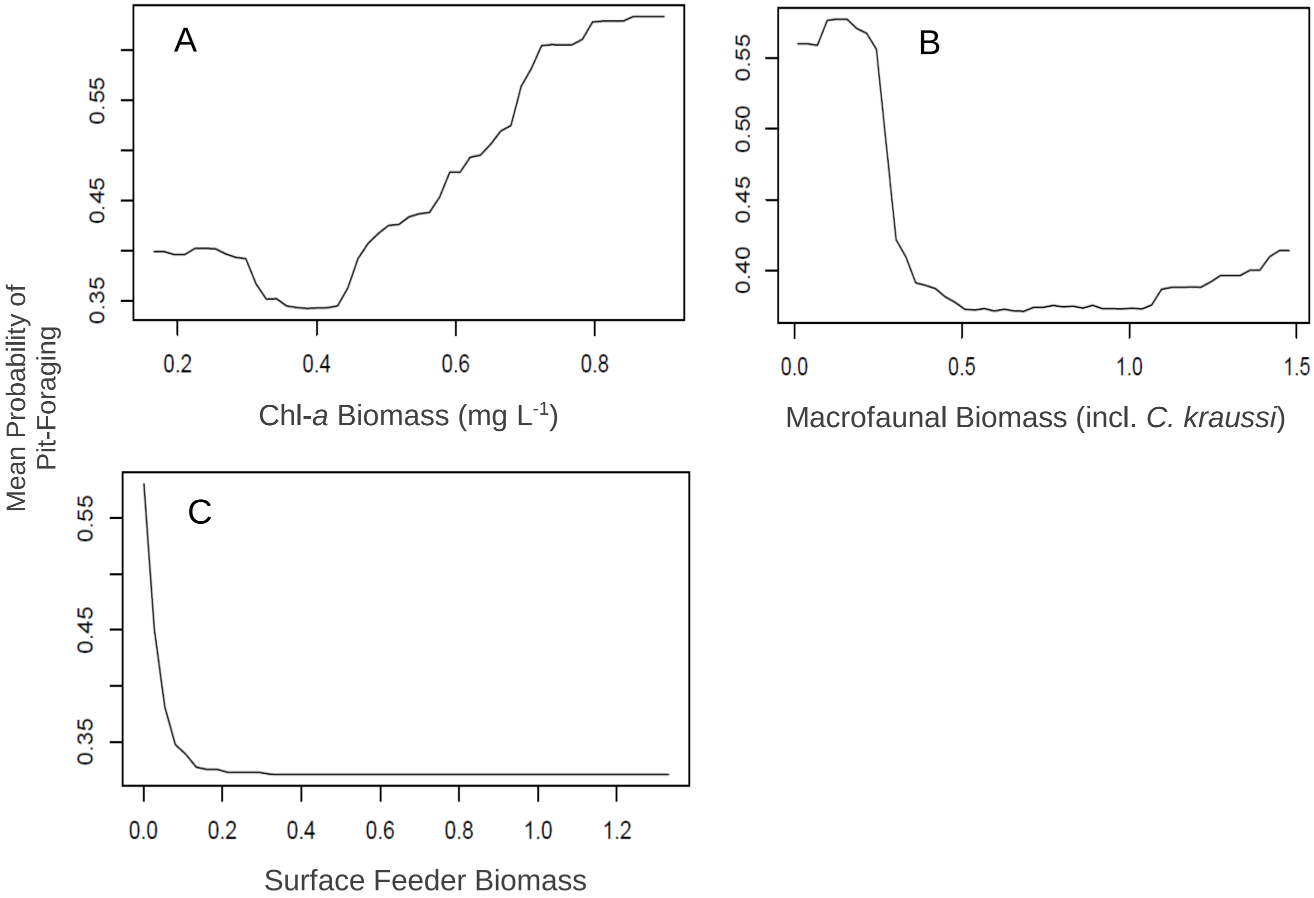

Figure 12: Best predictor variables (A: Chl-*a* Biomass, B: Macrofaunal Biomass (incl. *C. kraussi*), C: Surface Feeder Biomass) of flamingo pit-foraging.

Spatial patterns of the predictor variables identified by *RandomForest* in driving flamingo pit-foraging activities are illustrated in Figures 13-15. Concentration of chl-*a* differed statistically between pit-foraging controls and non-feeding controls (Nested ANOVA: $F_{3,156} = 4.08$, $p = 0.01$) with values in pit controls generally being higher than non-feeding controls, with two out of four comparisons being statistically supported (Figure 13).

Biomass of surface feeders varied significantly among flamingo pit-foraging treatments (Nested ANOVA: $F_{3,156} = 5.00$, $p = 0.002$). Generally, pit-foraging controls were lower in biomass compared to non-feeding controls, with one out of four comparisons being statistically significant at the high-water mark of Site 1 (ANOVA Post - hoc Tukey: $p = 0.001$, Figure 14).

Total biomass of macrofauna including *C. kraussi* differed statistically across flamingo foraging treatments (Nested ANOVA: $F_{6,211} = 3.10$, $p = 0.01$, also mentioned in section 3.2.3). Pit-foraging controls were generally lower in biomass compared to non-feeding controls, however none of these comparisons were significant (Figure 15). Channel-foraging controls also revealed similar patterns in comparison to non-feeding controls, however, only one out of seven comparisons were statistically supported at the low-water mark of Site 2 (ANOVA Post Hoc Tukey: $p = < 0.001$).

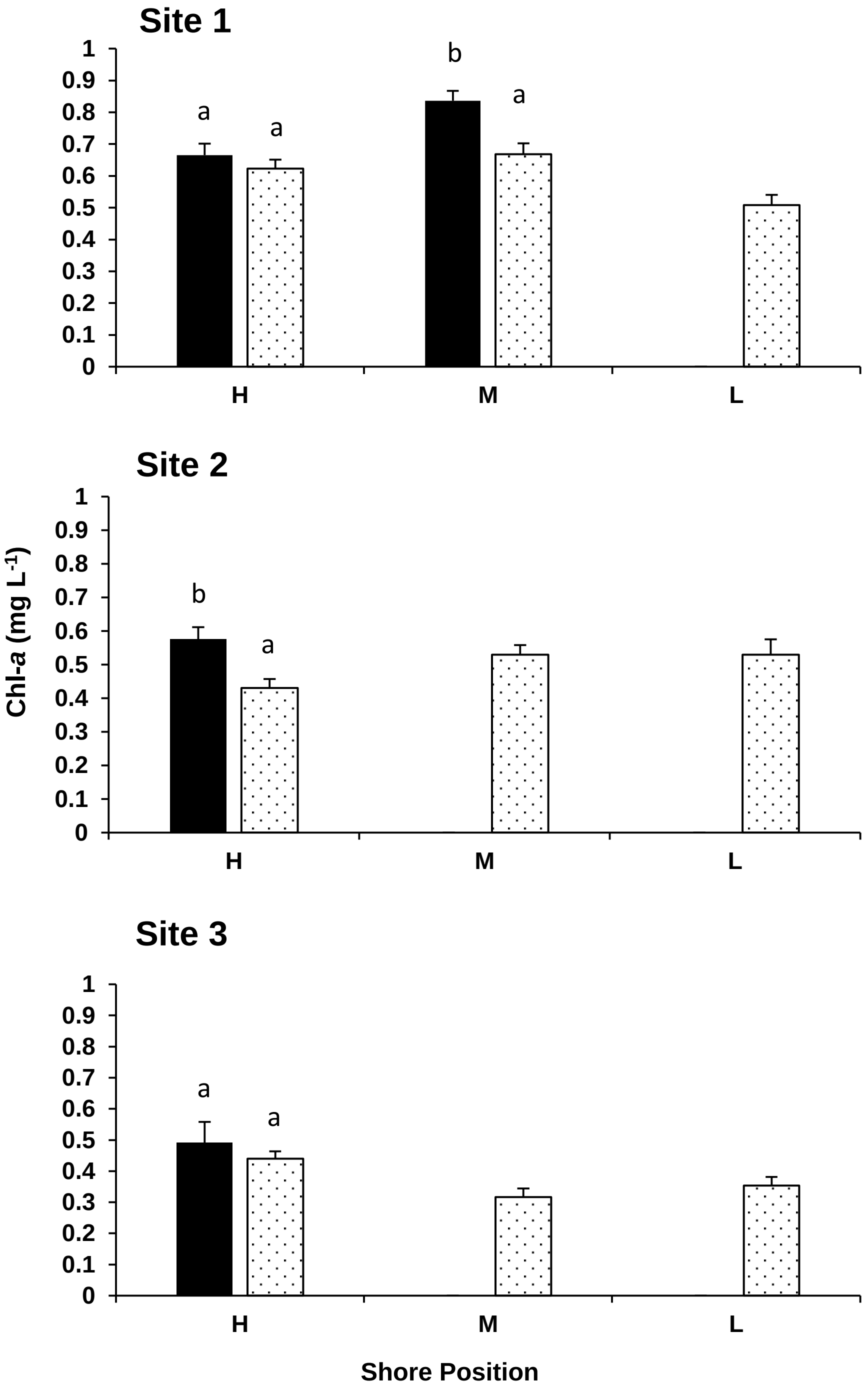

Figure 13: Differences in chl-*a* concentrations between flamingo pit-foraging controls (■) and non-feeding controls (⬚) across the three sites and shore positions (H: high, M: mid, L: low). Different letters denote significant differences of chl-*a* between pit-foraging controls and non-feeding controls within a shore position. Means ± 1SE are shown.

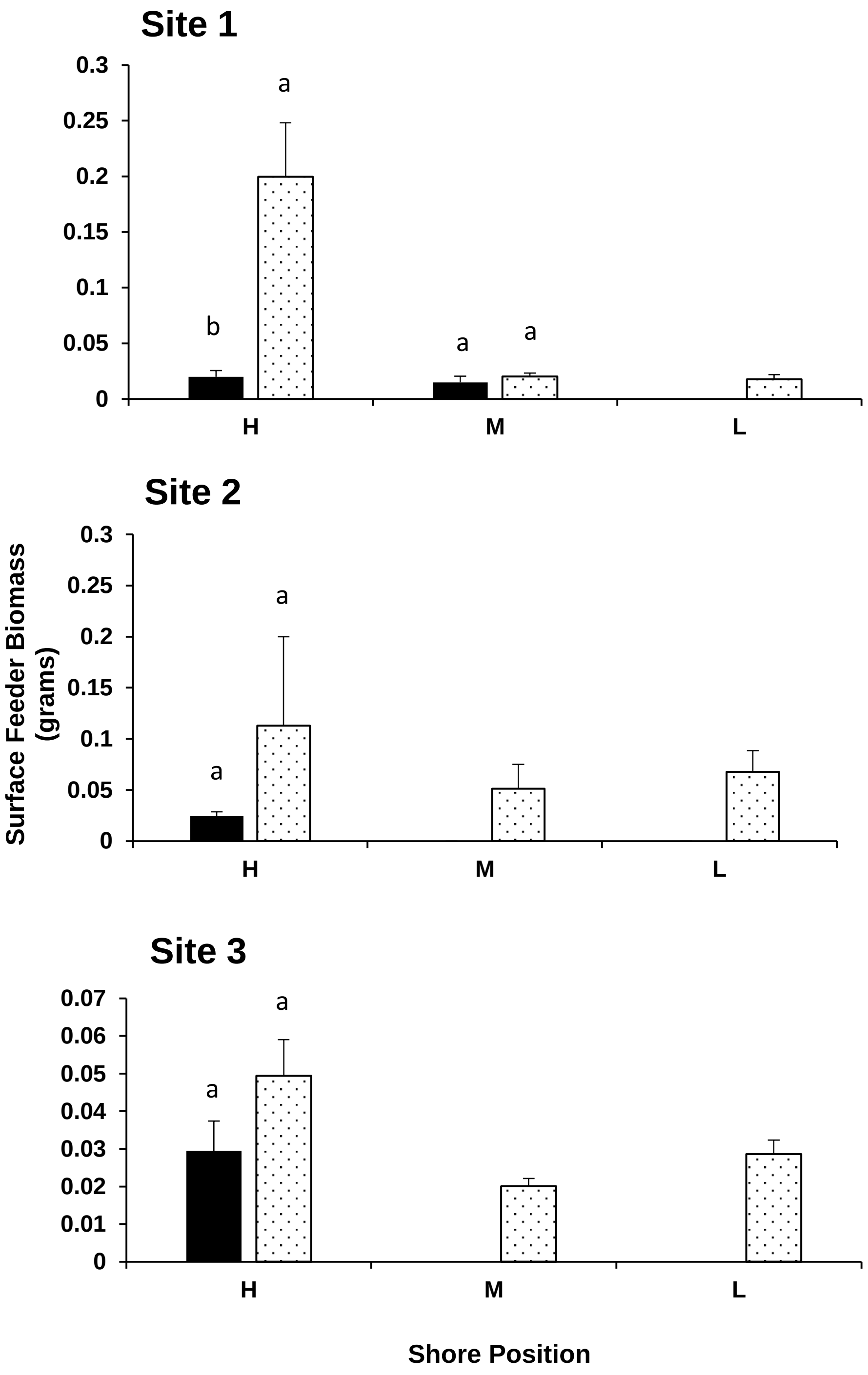

Figure 14: Differences in surface feeder biomass between flamingo pit-foraging controls (■) and non-feeding controls (▒) across the three sites and shore positions (H: high, M: mid, L: low). Different letters denote significant differences between pit-foraging controls and non-feeding controls within a shore position. Means ± 1SE are shown.

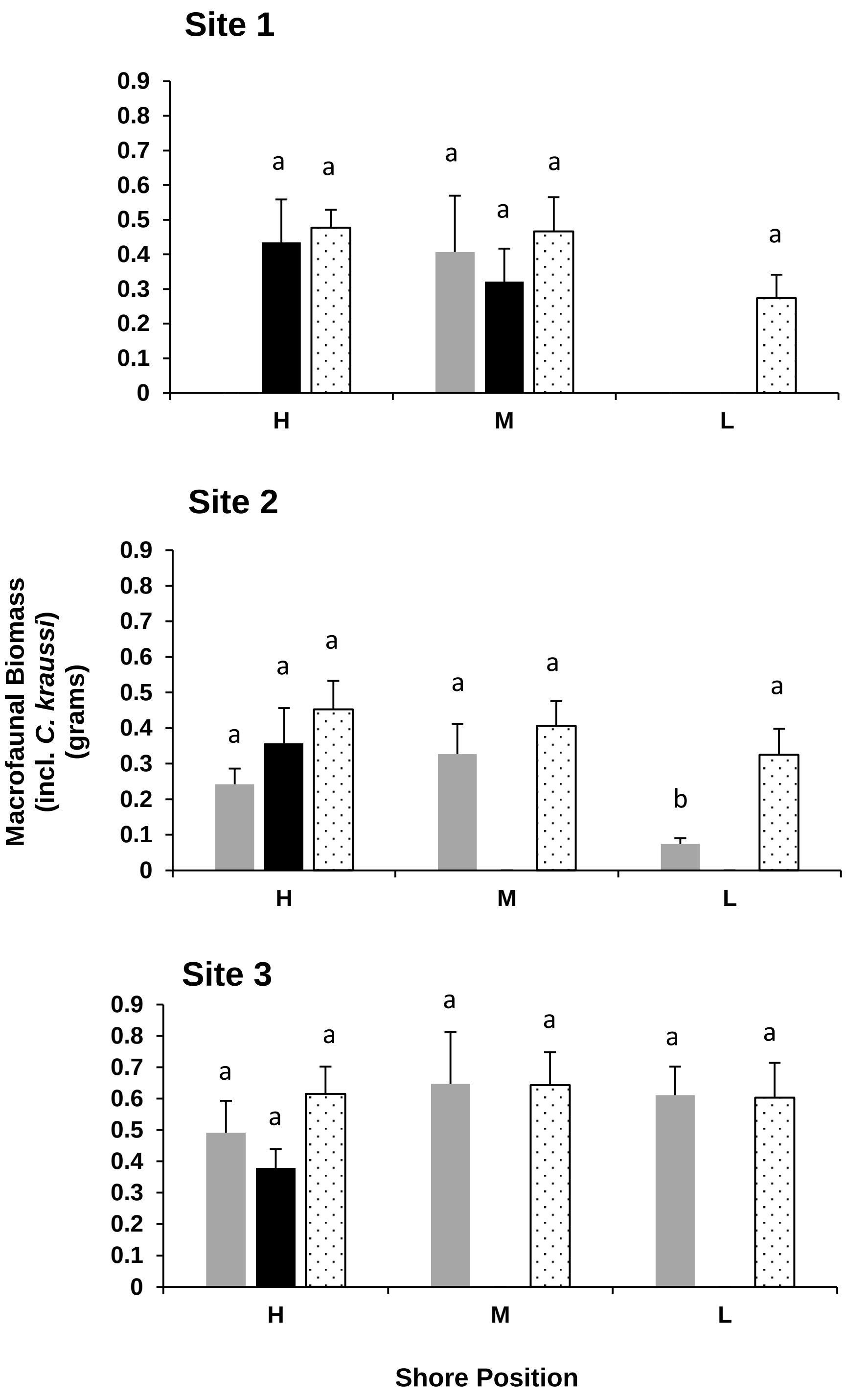

Figure 15: Differences in macrofaunal biomass (incl. *C. kraussi*) between flamingo foraging structure controls (channels:▨, pits:■) and non-feeding controls (⬚) across the three sites and shore positions (H: high, M: mid, L: low). Different letters denote significant differences of biomass between a foraging structure control and non-feeding control within a shore position. Means ± 1SE are shown.

3.2.3 Channel-foraging vs non-foraging

Abundance of all macrofauna, infauna and surface feeders along with macrofaunal biomass (including *C. kraussi*) were the main determinants of flamingo channel-foraging (Figure 16). Models predicted high probabilities of channel-foraging when biomass of macrofauna was low, followed by a decline that reached a steady state as biomass increased. Probability of channel-foraging was predicted to be related to abundances of macrofauna, infauna and surface feeders in a sigmoidal relationship. The latter initially had low probabilities at low abundance values before reaching a threshold beyond which likelihood of channel-foraging increased rapidly before reaching a steady state.

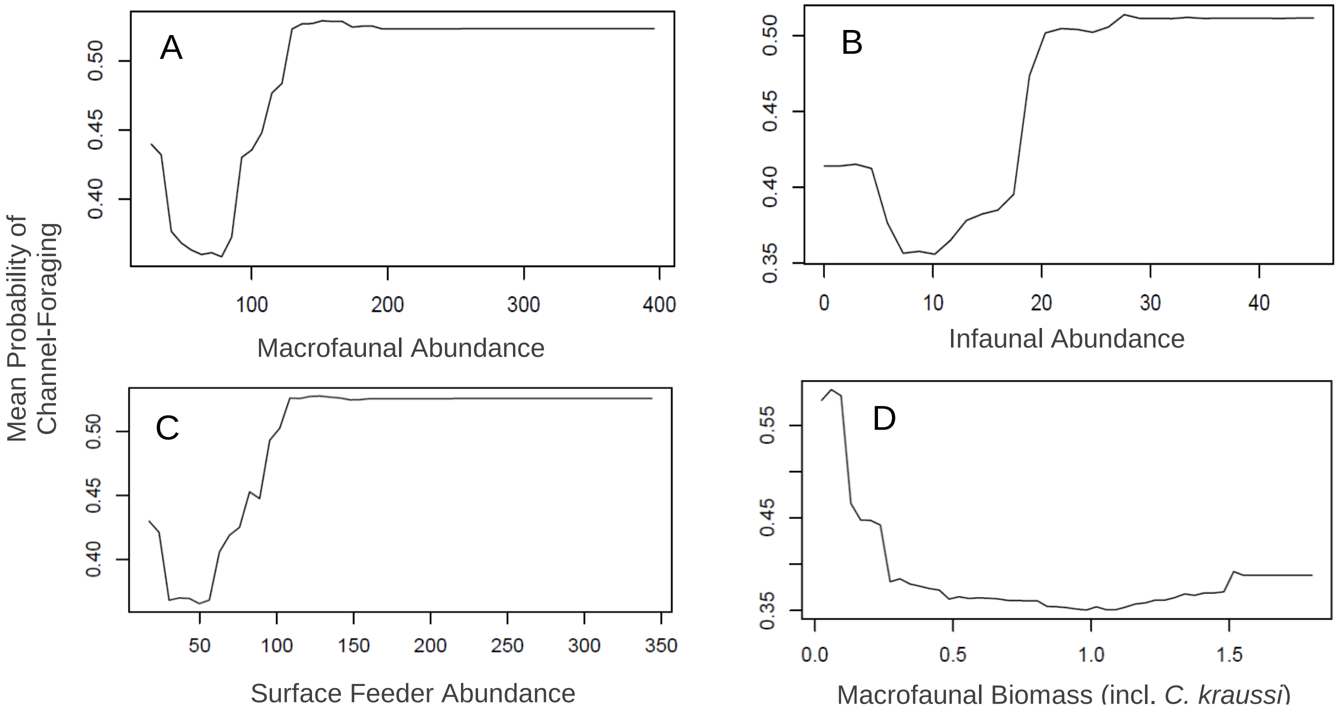

Figure 16: Best predictor variables (A: Macrofaunal Abundance, B: Infaunal Abundance, C: Surface Feeder Abundance, D: Macrofaunal Biomass (incl. *C. kraussi*)) of flamingo channel-foraging.

Visual trends in predictor variables to drive flamingo channel-foraging are illustrated in Figures 17-19. Abundance of macrofauna was significantly affected by flamingo channel-foraging treatment (Nested ANOVA: $F_{3,175} = 6.79$, $p < 0.001$). Channel controls were significantly greater than non-feeding controls, with four out of seven comparisons being statistically validated, with the exception being the high-water mark of Site 2, where channel controls were significantly lower than non-feeding controls (ANOVA Post Hoc Tukey: $p = 0.004$, Figure 17).

Surface feeder abundance varied significantly among flamingo channel-foraging treatments (Nested ANOVA: $F_{3,175} = 5.44$, $p = 0.001$), with surface feeder abundance generally being greater in channel-foraging controls compared to non-feeding controls, with two out of seven comparisons being statistically supported (Figure 18). However, there was one comparison of abundance being significantly lower in channel-foraging controls than non-feeding controls at the high-water mark of Site 2 (ANOVA Post Hoc Tukey: $p = 0.003$).

Infaunal abundance was significantly affected by flamingo channel-foraging treatments (Nested ANOVA: $F_{3,175} = 6.34$, $p = < 0.001$), where channel-foraging structure controls had greater infaunal abundances than non-feeding controls, with three out of seven comparisons being statistically supported (Figure 19).

For macrofaunal biomass (incl. C. kraussi) refer to section 3.2.2 and Figure 15

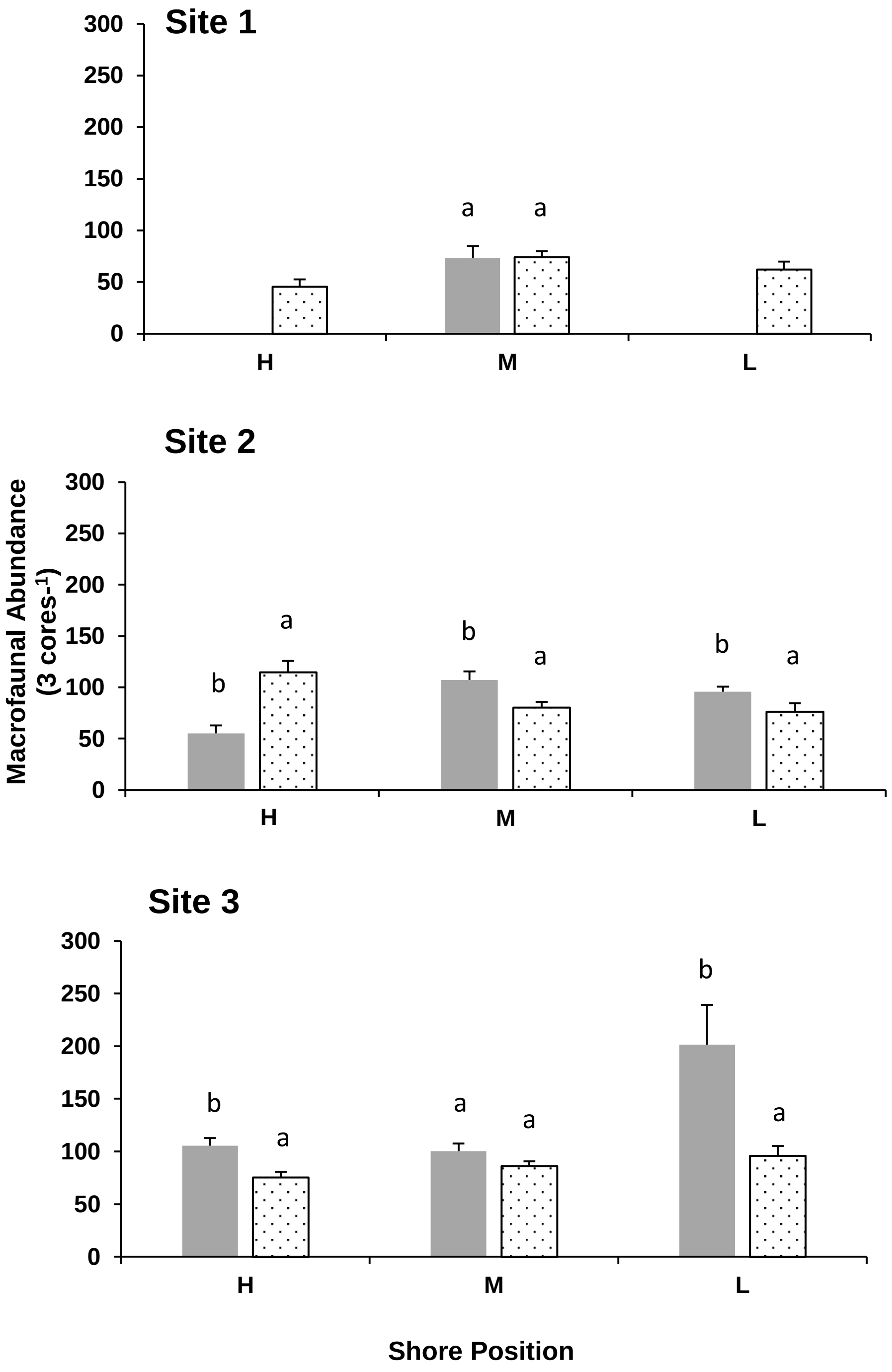

Figure 17: Differences in macrofaunal abundance between flamingo channel-foraging controls (■) and non-feeding controls (⬚) across the three sites and shore positions (H: high, M: mid, L: low). Different letters denote significant differences of abundance between channel-foraging controls and non-feeding controls within a shore position. Means ± 1SE are shown

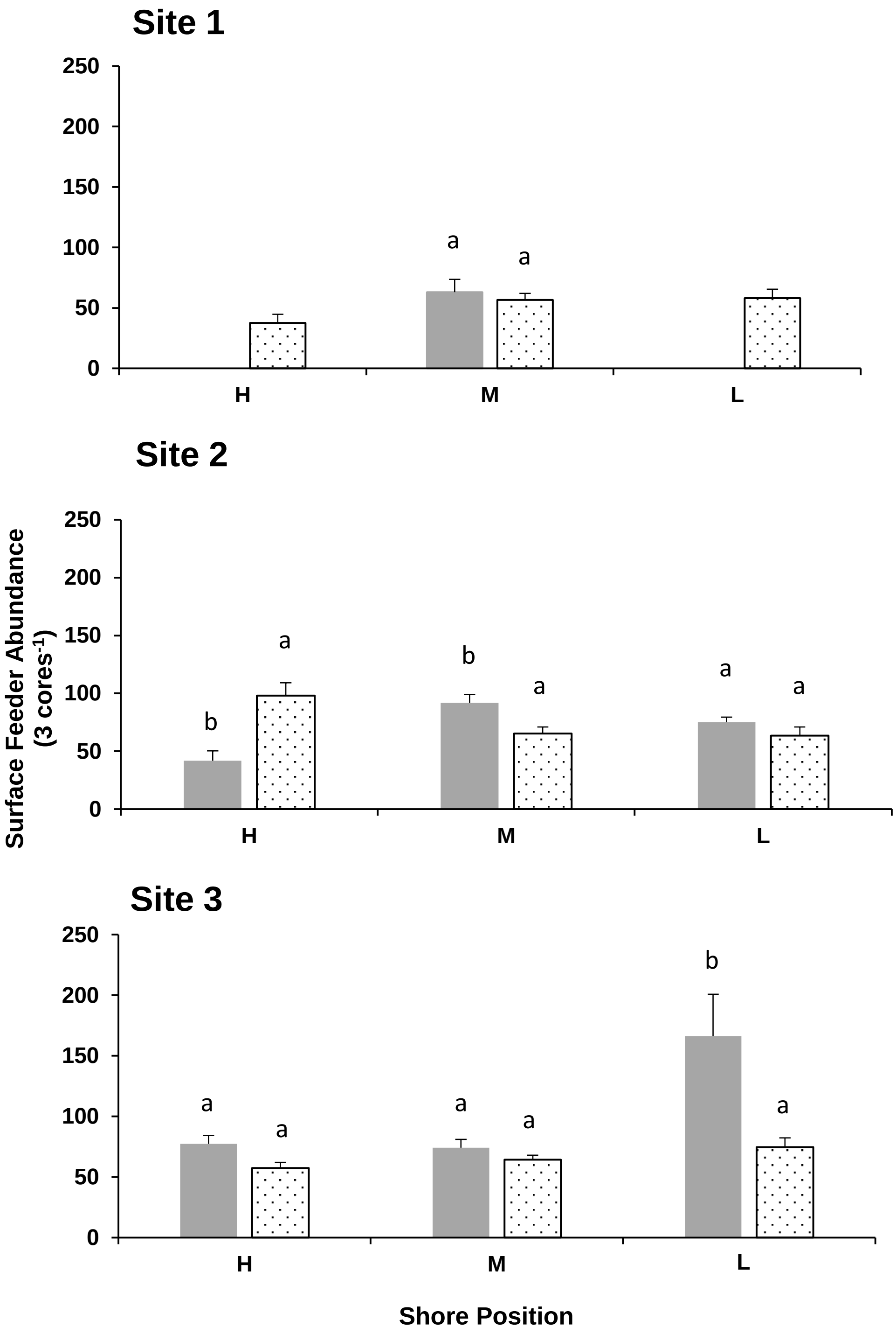

Figure 18: Differences in surface feeder abundance between flamingo channel-foraging controls (■) and non-feeding controls (⬚) across the three sites and shore positions (H: high, M: mid, L: low). Different letters denote significant differences of abundance between channel-foraging controls and non-feeding controls within a shore position. Means ± 1SE are shown.

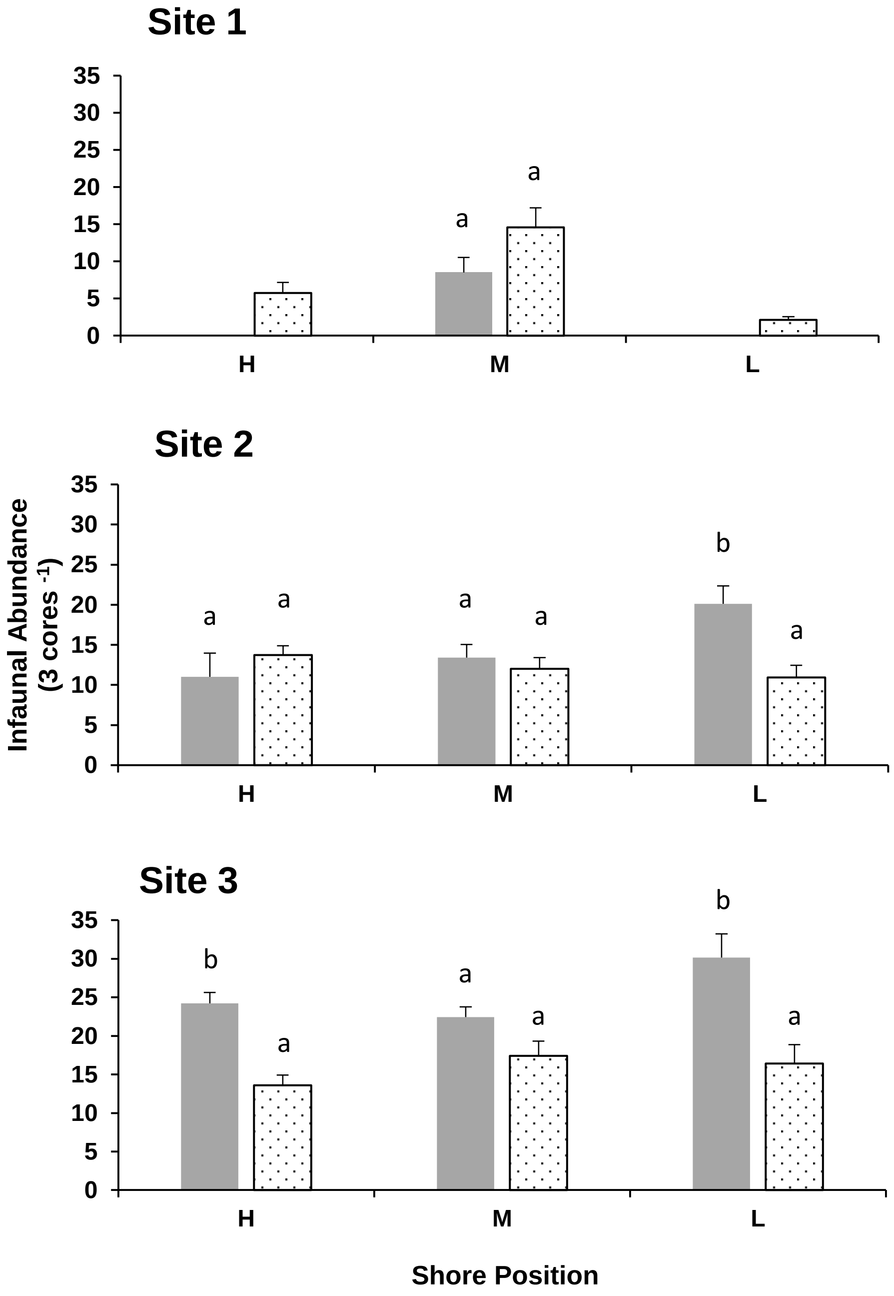

Figure 19: Differences in infaunal abundance between flamingo foraging structure controls (channels:■, pits:■) and non-feeding controls (⬚) across the three sites and shore positions (H: high, M: mid, L: low). Different letters denote significant differences of abundance between a foraging structure control and non-feeding control within a shore position. Means ± 1SE are shown.

3.2.4 Variability in sizes of flamingo foraging structures

The abundance of *Urothoe grimaldii* (Amphipoda) and *Notomastus latericeus* (Polychaeta) were the only variables driving variability in sizes of pits created by flamingos (Figure 20). Pit sizes were predicted by inversely exponential relationships for both species, with large pit sizes being predicted at low abundances. Thereafter, the pit sizes are predicted to drop rapidly with increasing abundances of the latter two species.

RandomForest did not produce a model for the size of channel-foraging structures, as there was a low percentage of variation explained in the data. Thus, none of the variables were recognized as predictors of channel sizes.

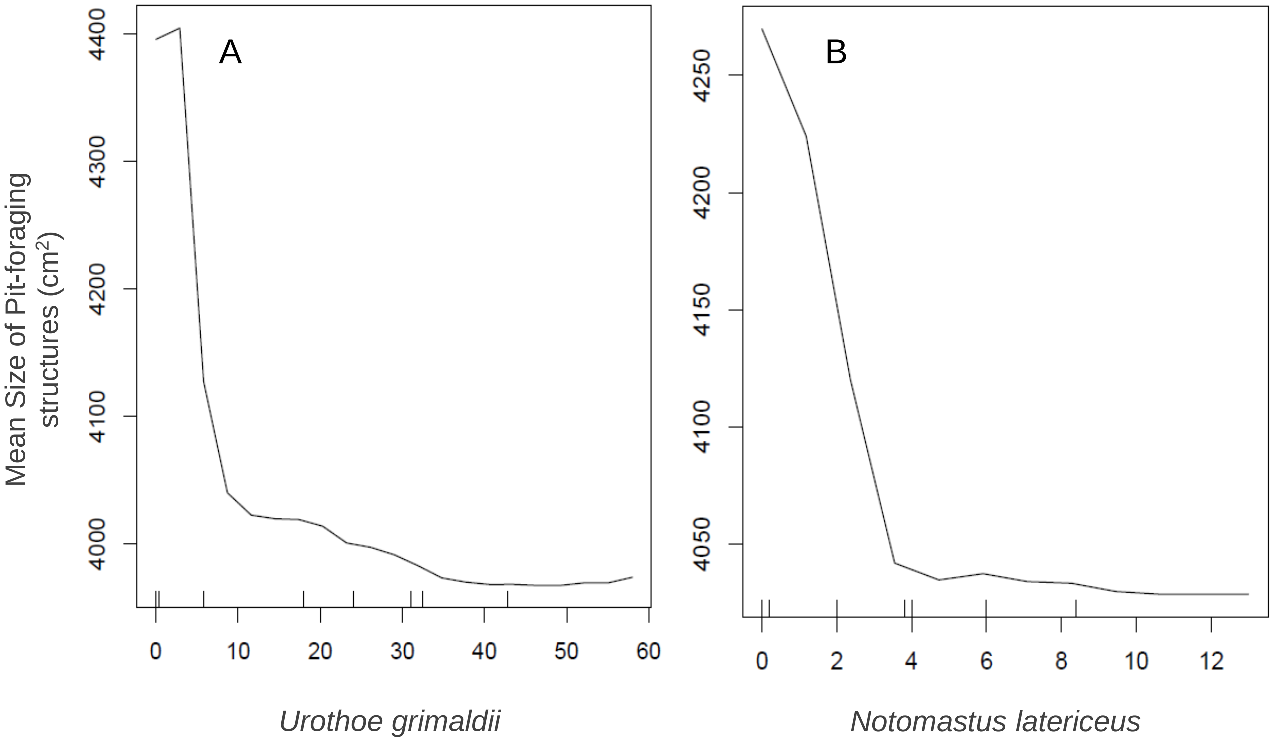

Figure 20: The abundance of (A: *Urothoe grimaldii*, B: *Notomastus latericeus*) were the best predictor variables in driving the size variability of flamingo pit-foraging structures.

3.3 Part B: Impacts of flamingo foraging plasticity on benthic assemblages

3.3.1 Micro-algal biomass

Chl-*a* concentrations differed significantly among quadrats (Nested ANOVA: $F_{3,172} = 2.79$, $p = 0.04$, Table 3) and flamingo foraging treatments (Nested ANOVA: $F_{8,172} = 12.31$, $p < 0.001$). At Site 2, chl-*a* concentrations decreased from the high- to both the mid- and low-water mark as well as from the low- to the mid-water mark (Figure 21). Chl-*a* levels were generally lower in channels relative to their controls, and were statistically supported at the mid- and low-water marks across all sites. However, pits and their controls had similar chl-*a* levels.

Table 3: Nested ANOVA results testing for differences in macrofaunal community metrics and chl-*a* biomass between flamingo foraging structures and controls. * = significant difference.

Factor		**Chl-*a***		**Macrofaunal Abundance**		**Species Richness**		**Macrofaunal Biomass**		**W - statistics**	
	Degrees of freedom	*F*	p	*F*	p	*F*	p	*F*	p	*F*	p
Site	2,33	3.08	0.19	3.45	0.17	5.61	0.10	2.73	0.21	3.50	0.16
Shore Position	3,172	8.74	<0.001*	9.11	<0.001*	7.27	<0.001*	2.53	0.06	7.19	<0.001*
Quadrat	3,172	2.79	0.04*	0.08	0.97	1.19	0.32	0.99	0.40	2.23	0.09
Treatment	8,172	12.31	<0.001*	9.35	<0.001*	1.12	0.35	0.83	0.58	6.33	<0.001*

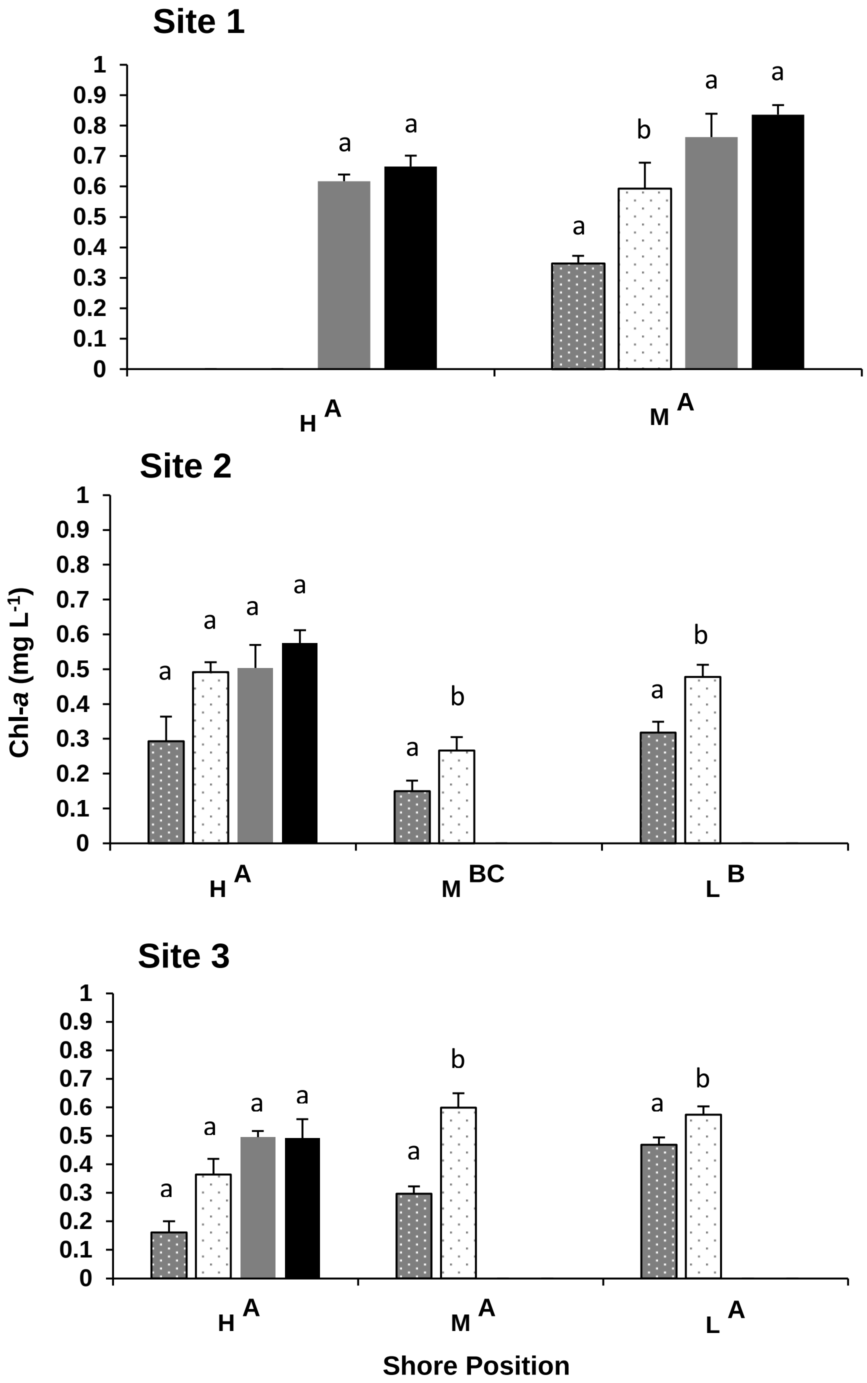

Figure 21: Differences in chl-*a* concentrations between flamingo foraging structures (channels: ▩, pits: ◼) and controls (channel controls: ⬚, pit controls: ■) across the three sites and shore positions (H: high, M: mid, L: low). Different letters denote significant differences of total chl-*a* biomass between shore positions (in uppercase) and between a feeding structure and its control within a shore position (in lowercase). Means ± 1SE are shown.

3.3.2 Macrofaunal community structure

PERMANOVA indicated that macrofaunal community structure was significantly affected by shore position ($F_{5,193}$ = 8.90, p = 0.001) and flamingo foraging treatments ($F_{26,193}$ = 2.17, p = 0.001), but not by site ($F_{2,193}$ = 1.70, p = 0.188) nor quadrat ($F_{16,193}$ = 0.97, p = 0.538). Pair-wise tests generally indicated differences in community structure between flamingo channels and their controls, with seven out of eight comparisons being statistically supported; but no differences were evident between pits and controls. MDS visually confirmed differences in community structure between flamingo channels and controls (Figure 22) as well as similarities between pits and their controls (Figure 23).

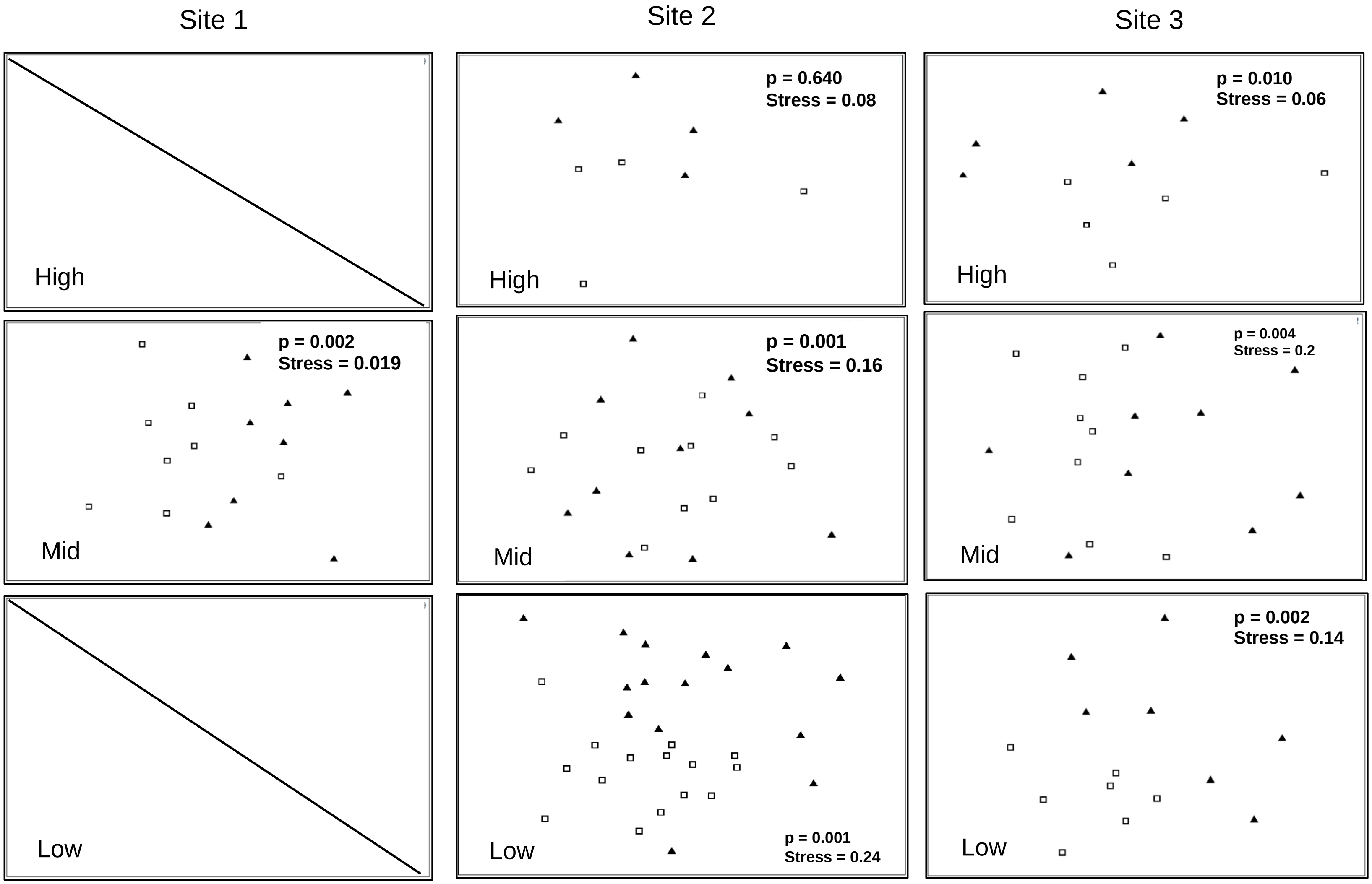

Figure 22: MDS ordinations showing differences in macrofaunal community structure between channels (▲) and channel controls (☐) across the three sites and shore positions. Pair-wise testing with p values provided.

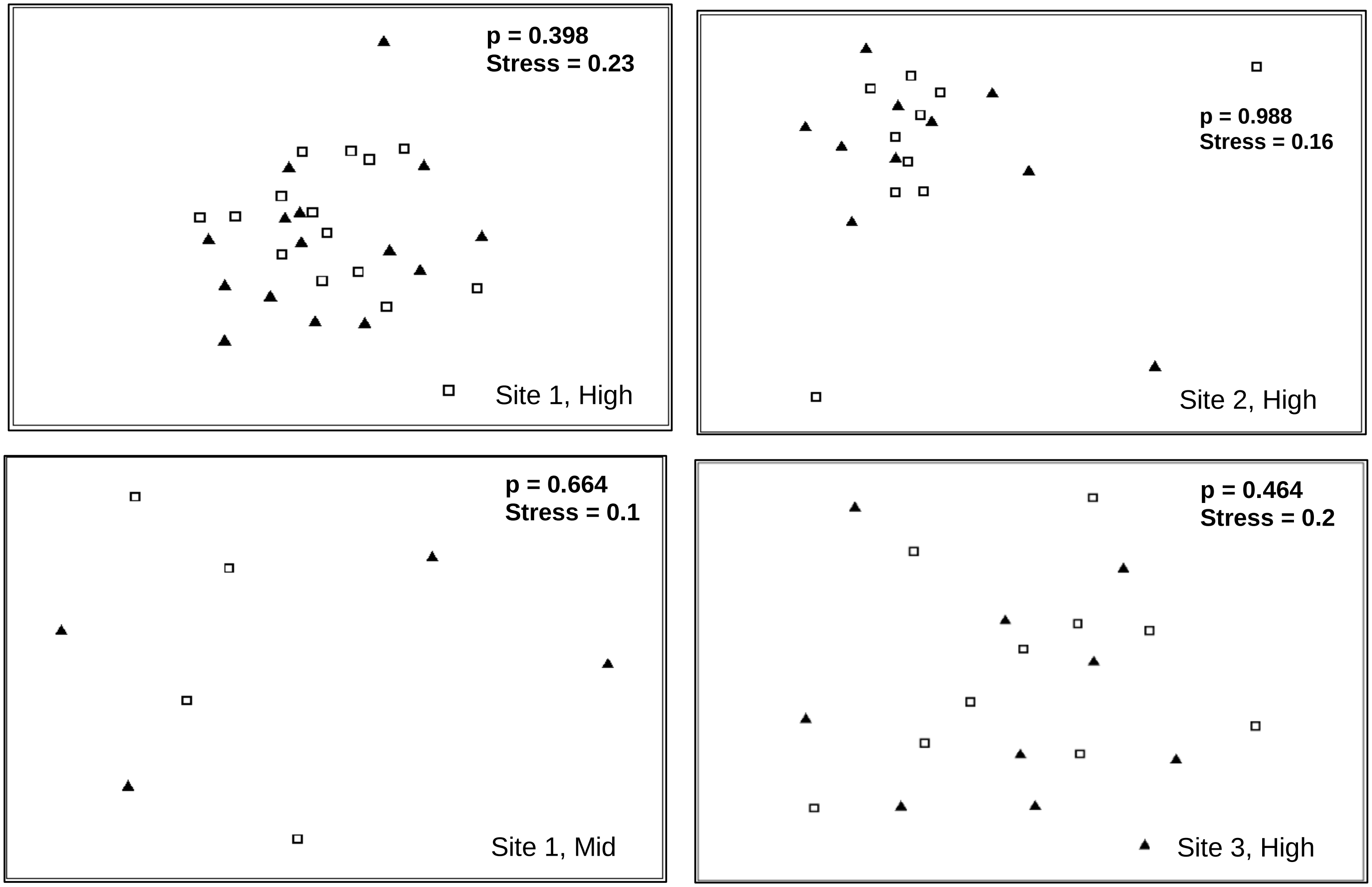

Figure 23: MDS ordinations showing differences in macrofaunal community structure between pits (▲) and pit controls (□) across the three sites at the high-and mid-shore position. Pair-wise testing with p values provided.

3.3.3 Macrofaunal community metrics

Nested ANOVA revealed that all macrofaunal community metrics (except total biomass) differed statistically across shore position ($p < 0.001$, Table 3) but not sites ($p > 0.1$). Differences between flamingo foraging treatments were only evident for macrofaunal abundance (Nested ANOVA: $F_{8,172} = 9.35$, $p < 0.001$, Table 3) and not for species richness (Nested ANOVA: $F_{8,172} = 1.12$, $p = 0.35$, Table 3) or total biomass (Nested ANOVA: $F_{8,172} = 0.83$, $p = 0.58$, Table 3, Figure 26). Macrofaunal abundance was lower at the high- compared to the mid-water mark at Site 1 (Figure 24). At Site 2, both the high- and low- were lower than the mid-water mark; whereas at Site 3, the high- and mid- were lower than the low-water mark. Abundance was lower in flamingo channels relative to their controls with five out of seven comparisons being statistically significant, but not between pits and their controls, with the exception being the high-shore position of Site 1 (ANOVA Post - hoc Tukey: $p = 0.025$). Macrofaunal richness was higher at the mid- compared to the high-water mark at Site 1 (ANOVA Post – hoc Tukey: $p = < 0.001$, Figure 25). W-statistics were significantly affected by flamingo foraging treatment (Nested ANOVA: $F_{8,172} = 6.33$, $p = < 0.001$, Table 3). W-statistics were consistently greater in flamingo channels relative to their controls with four out of seven comparisons being statistically upheld (Figure 27). None of the comparisons of W-statistics between pits and their controls were statistically significant.

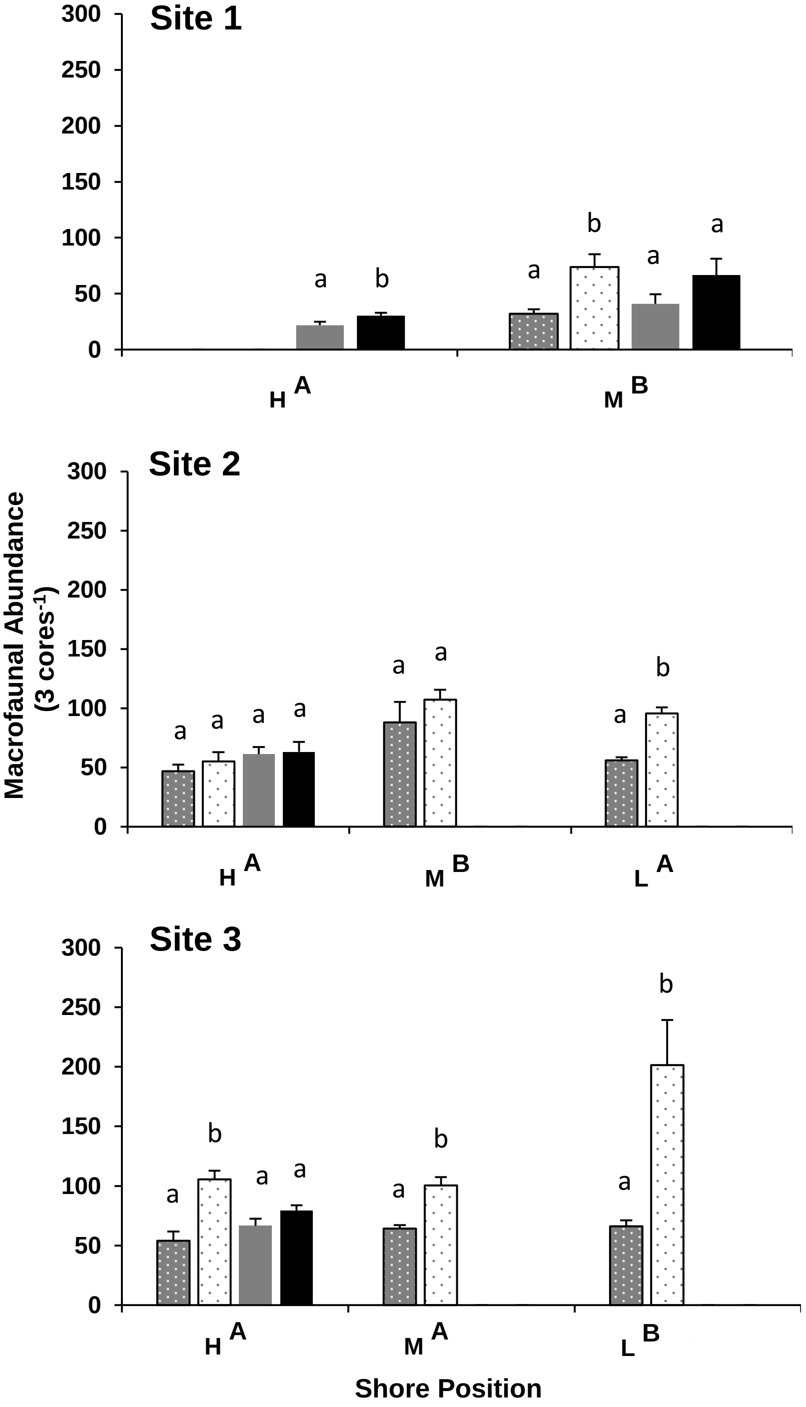

Figure 24: Differences in macrofaunal abundance between flamingo foraging structures (channels: ▨, pits: ▩) and controls (channel controls: □, pit controls: ■) across the three sites and shore positions (H: high, M: mid, L: low). Different letters denote significant differences of total abundance between shore positions (in uppercase) and between a feeding structure and its control within a shore position (in lowercase). Means ± 1SE are shown.

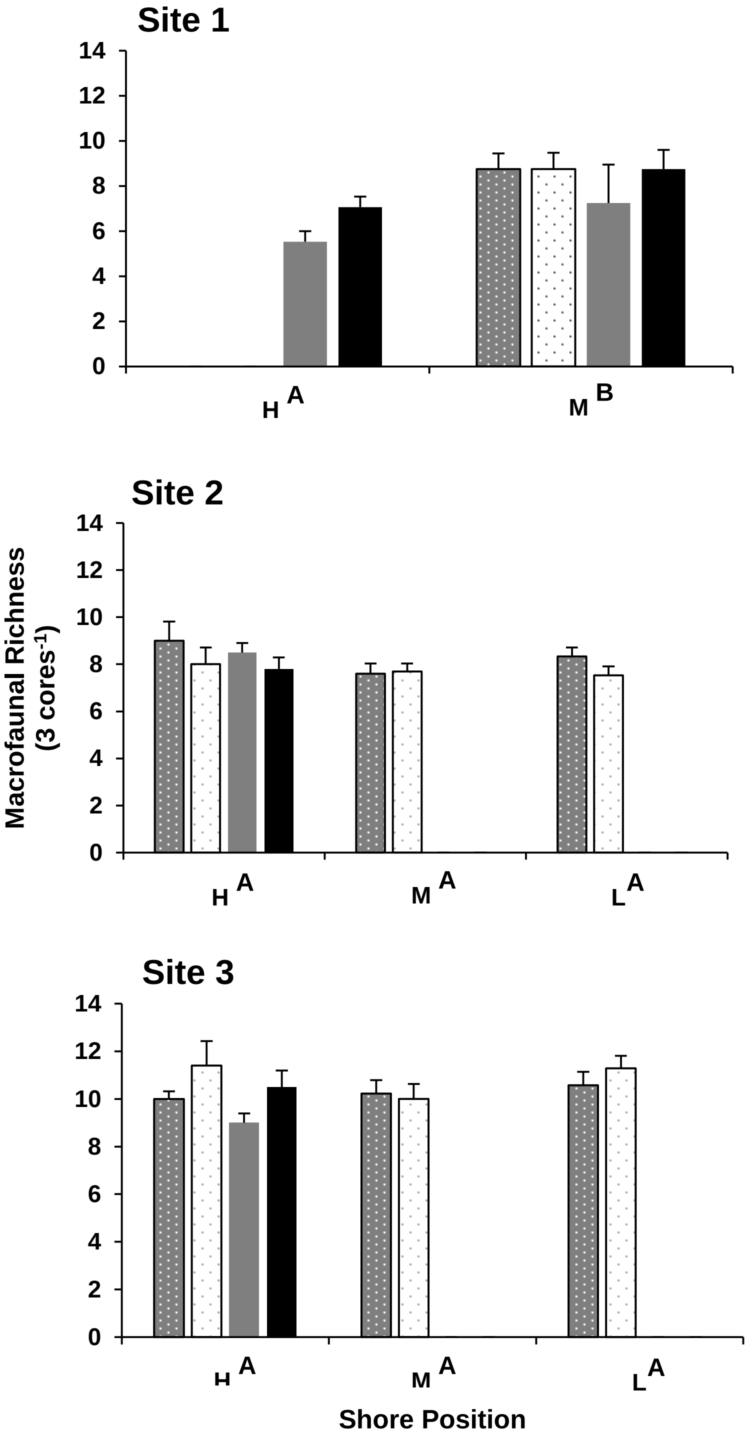

Figure 25: Differences in macrofaunal richness between flamingo foraging structures (channels: ▩, pits : ▨) and controls (channel controls: ☐, pit controls: ■) across the three sites and shore positions (H: high, M: mid, L: low). Different letters denote significant differences of total richness between shore positions (in uppercase). Means ± 1SE are shown.

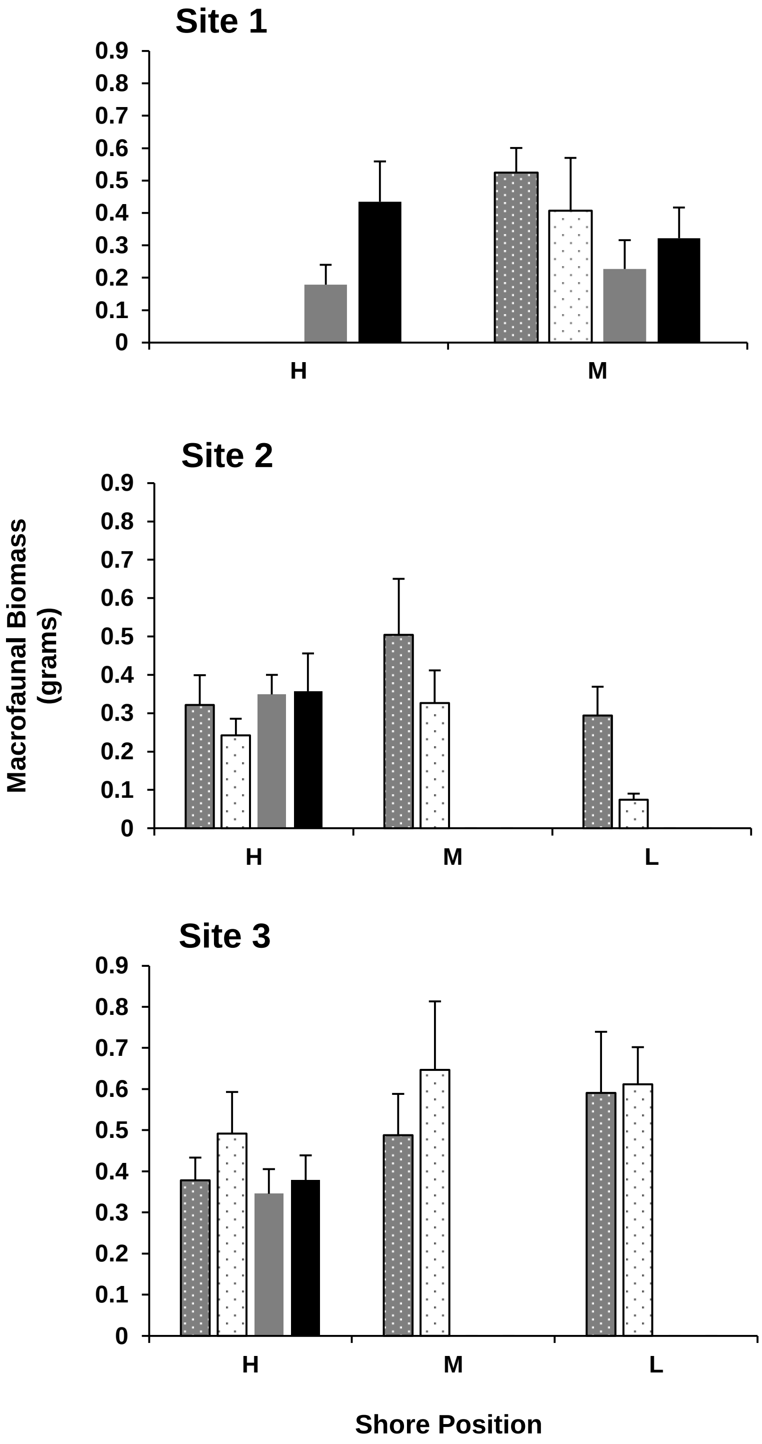

Figure 26: Differences in macrofaunal biomass between flamingo foraging structures (channels: ▩ , pits : ▨) and controls (channel controls: ⬚ , pit controls: ■) across the three sites and shore positions (H: high, M: mid, L: low). Means ± 1SE are shown.

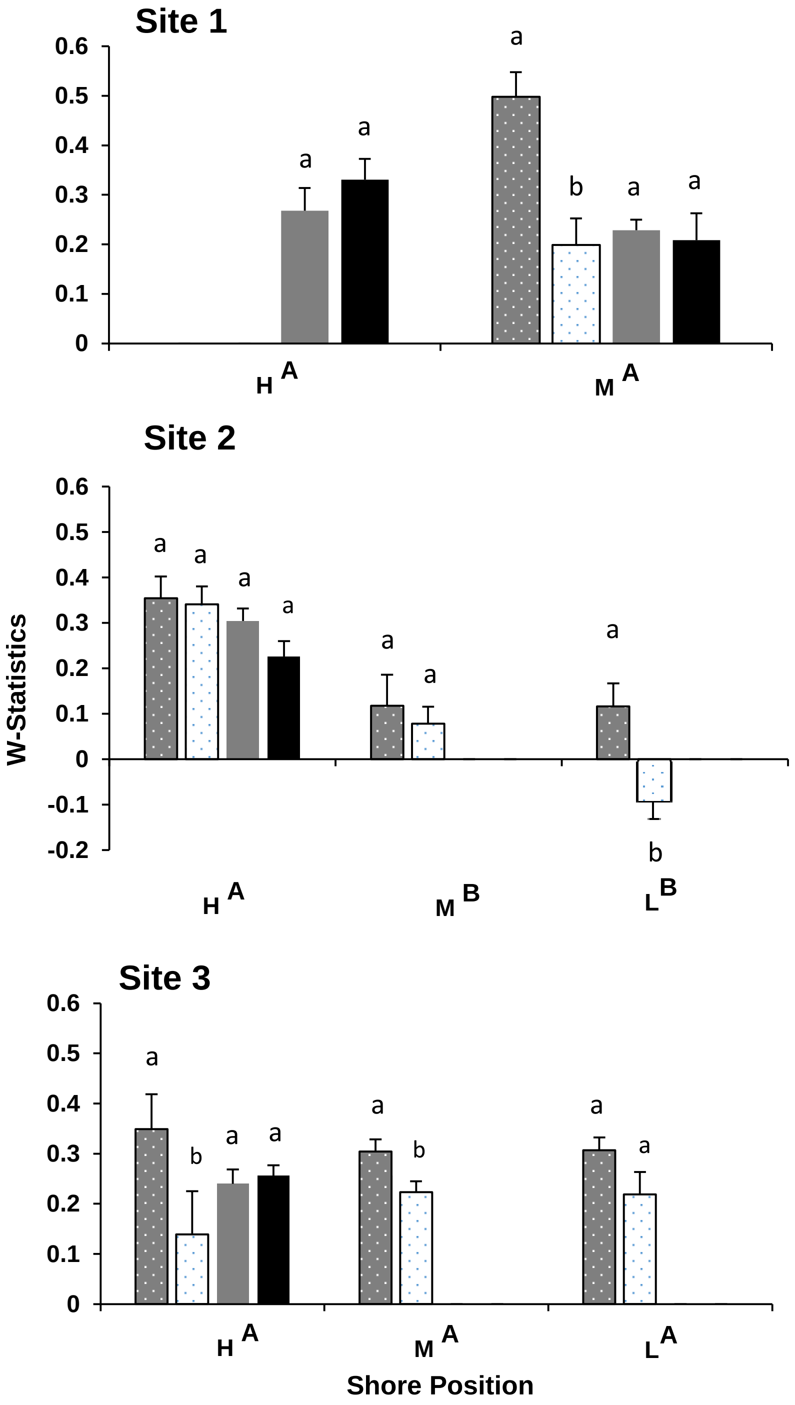

Figure 27: Differences in W-statistics between flamingo foraging structures (channels: ▨ , pits: ▩) and controls (channel controls: ⬚ , pit controls: ■) across the three sites and shore positions (H: high, M: mid, L: low). Different letters denote significant differences of total W-statistics between shore positions (in uppercase) and between a feeding structure and its control within a shore position (in lowercase). Means ± 1SE are shown.

3.3.4 Dominant macrofaunal species

Of the 43 species identified from samples, 21 were identified by SIMPER to distinguish flamingo foraging structures from their controls based on the abundance data (Table 4). The most dominant macrofaunal species, which was the amphipod *Urothoe grimaldii*, was reduced in pits by 20% and in channels by 63%, indicating that this species is likely one of the main prey items of flamingos. Calanoid copepods, *Notomastus latericeus*, *Eurydice kensleyi*, *Orbinia angrapequensis*, *Hymenosoma orbiculare*, *Leucothoe spinicarpa*, *Heterocuma africanum* and *Griffithsia latipes* were additional species that were generally significantly reduced in abundance in channels relative to their controls. *Callichirus kraussi* was the only macrofaunal species to increase in abundance in channels relative to their controls at the mid-shore position of Site 1 and the low-shore position of Site 2 (Table 4). The polychaete *Perinereis nuntia vallata*, the crab *Paratylodiplax blephariskios* and *C. kraussi* showed similar response patterns, with their abundances being reduced significantly in pits relative to their controls at the high shore position of Site 1 (Table 4). SIMPER analyses based on biomass data identified 14 species that distinguished flamingo foraging structures from their controls (Table 5). However, only four species (*U. grimaldii*, *E. kensleyi*, *H. orbiculare* and *O. angrapequensis*) had their biomasses significantly reduced in channels compared to their controls (Table 5). The biomass of *C. kraussi* was significantly higher in channels than controls at the low-shore position of Site 2.

Table 4: Abundance of macrofaunal species that cumulatively accounted for 90% of community structure in flamingo foraging structures (P = pits, C =channels) and controls (PC = pit controls, CC = channels controls). Different superscript letters denote significant differences.

Taxon	Species	Site 1						Site 2								Site 3							
		High		*Mid*				*High*				*Mid*		*Low*		*High*				*Mid*		*Low*	
		P	PC	P	PC	C	CC	P	PC	C	CC	C	CC	C	CC	P	PC	C	CC	C	CC	C	CC
Amphipoda	*Urothoe grimaldii*	0.13	0.33	23.3	36	10.1^{a}	38.9^{b}	28.3	32.4	19.3	20.25	24.6^{a}	65.8^{b}	20.47^{a}	41.8^{b}	24.3	26.5	18.2^{a}	45.8^{b}	15.89^{a}	41.67^{b}	14.29^{a}	77.71^{b}
Copepoda	*Calanoid copepods*	11.4	13.73	4.25	9	4.63^{a}	16^{b}	9.1	10	7.75	15.75	45.4	23.1	22.33^{a}	31.47^{b}	21.1	26.7	13.6	22.6	16.56	23.33	21.86	58.71
Polychaeta	*Notomastus latericeus*	0	0.07	2.5	6.5	4.63	3.5	7.9	6.3	5.75	6	7.4	6.9	2.4	3.4	2.6	3.4	7^{a}	15.6^{b}	16.89	15.67	12.71	18.71
Thalassinidea	*Callichirus kraussi*	0.67^{a}	1.4^{b}	1.5	2.5	4^{a}	1.63^{b}	2.9	2.4	2.75	2	2.2	2	1.53^{a}	0.27^{b}	2.6	3	3.2	4	3.56	3.78	3.43	5
Polychaeta	*Ceratonereis erythraeensis*	0.33	0.33	3.25	6.75	1.75	2.75	0.8	0.6	3	2.25	2.5	3.1	1.6	1.73	7.5	7.8	0.6	0.8	0	0	0	0.11
Isopoda	*Eurydice kensleyi*	0.8	0.73	1.25	0.25	0.5	2.5	5.9	10	1.5	2.75	1	0.9	0.8	0.73	1.2	1.7	1.8^{a}	4.6^{b}	2.11	3	0.86^{a}	0.14^{b}
Polychaeta	*Marphysa elitueni*	0.4	0.53	2	1	1.75	1.63	1.9	3	1.75	1.75	1.1	1.2	0.73	1	0.1	0.4	2.4	1.6	2.56	3.11	3.29	4
Polychaeta	*Orbinia angrapequensis*	0	0	0.75	0.75	0	0.25	1.6	0.9	3	1	1.4	2	3.67^{a}	10.47^{b}	1.8	0.9	0.8	2.4	0.22	0.11	1.29	2.43
Brachyura	*Hymenosoma orbiculare*	0	0	0	0	0.25	0	0.1	0.2	0.25	0	0	0	0.53^{a}	3.33^{b}	0.9	1.5	1.4	3	1.56^{a}	3.22^{b}	2.57	4.43
Amphipoda	*Leucothoe spinicarpa*	0	0	0	0	0	0	0	0	0	0	0	0	0.13	0	0	0	0	0	0.67	0.78	2.86^{a}	16.29^{b}
Cumacea	*Heterocuma africanum*	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.3	0.4	0.2	0.2	0.89	3	1.29^{a}	11^{b}
Gastropoda	*Assiminea globulus*	3.6	6.07	0	0.5	0.5	0	0.6	0.2	0	0.25	0	0	0	0	0.7	2.2	0.2	0.6	0.11	0.44	0	0
Gastropoda	*Hydrobia* spp	0.6	0.6	0.75	0.25	0	0.13	0.9	0	0.25	1.75	0	0	0	0	0.4	0.7	1.2	1.2	0.56	0.33	0	0
Amphipoda	*Griffithsia latipes*	0	0.07	0.25	0.5	0.88^{a}	3^{b}	0.2	0	0.75	0	0.8	0.9	0	0.07	0	0	0^{a}	0.40^{b}	0.44	0.11	0.29	0.57
Polychaeta	*Perinereis nuntia vallata*	0.93^{a}	2.47^{b}	0.25	0	0.13	0	0.4	0.1	0	0	0	0	0	0	1.2	1.7	0	0	0	0	0	0
Polychaeta	*Thelepus* spp	0.47	0.2	0	0.25	0.63	0.13	0	0	0	0	0	0.1	0.47	0.47	0.9	1	0.4	0.6	0.11	0.78	0	0.29
Polychaeta	*Cirriformia capensis*	1.67	1.67	0	0	0	0	0	0	0	0	0	0	0.13	0	0.2	0.4	0.2	0.2	1	0	0	0
Isopoda	*Paridotea ungulate*	0.07	0.13	0	0	0.25	2	0.3	0.6	0.5	1	0.3	0	0	0.07	0	0.1	0	0	0	0	0	0
Brachyura	*Paratylodiplax blephariskios*	0.13^{a}	0.8^{b}	0.25	1.25	0	0.375	0.1	0	0	0	0	0.2	0	0	0.2	0.1	0	0.4	0	0	0	0.14
Bivalvia	*Macoma* spp	0.07	0.33	0	0	0	0	0	0	0	0	0	0	0	0.07	0.1	0	2.4	0	0	0	0	0
Bivalvia	*Tellimya trigona*	0.07	0.47	0	0	1.25	0.13	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

Table 5: Biomass of macrofaunal species that cumulatively accounted for 90% of community structure in flamingo foraging structures (P = pits, C =channels) and controls (PC = pit controls, CC = channels controls). Different superscript letters denote significant differences.

Taxon	Species	Site 1						Site 2								Site 3							
		High		*Mid*				*High*				*Mid*		*Low*		*High*				*Mid*		*Low*	
		P	PC	P	PC	C	CC	P	PC	C	CC	C	CC	C	CC	P	PC	C	CC	C	CC	C	CC
Thalassinidea	*Callichirus kraussi*	0.146	0.374	0.159	0.266	0.496	0.314	0.308	0.311	0.292	0.213	0.459	0.269	0.238^{a}	0.028^{b}	0.276	0.319	0.34	0.425	0.441	0.589	0.525	0.531
Amphipoda	*Urothoe grimaldii*	<0.001	<0.001	0.007	0.011	0.003^{a}	0.012^{b}	0.009	0.010	0.006	0.006	0.007^{a}	0.020^{b}	0.006^{a}	0.013^{b}	0.007	0.008	0.006^{a}	0.014^{b}	0.005^{a}	0.013^{b}	0.004^{a}	0.023^{b}
Isopoda	*Cirolana hirtipes*	0	0	0.041	0	0	0.041	0	0	0	0	0.016	0.016	0	0	0	0	0	0	0	0	0	0
Brachyura	*Hymenosoma orbiculare*	0	0	0	0	0.0006	0	<0.001	0.001	0.001	0	0	0	0.001^{a}	0.009^{b}	0.02	0.004	0.004	0.008	0.004^{a}	0.008^{b}	0.034	0.011
Polychaeta	*Marphysa elitueni*	0.001	0.002	0.006	0.003	0.005	0.005	0.005	0.008	0.005	0.005	0.003	0.003	0.002	0.003	<0.001	0.001	0.007	0.005	0.009	0.011	0.007	0.009
Isopoda	*Eurydice kensleyi*	0.002	0.002	0.003	0.001	0.001	0.006	0.014	0.014	0.004	0.007	0.002	0.002	0.002	0.002	0.003	0.004	0.004^{a}	0.011^{b}	0.005	0.007	0.002^{a}	$<0.001^{b}$
Brachyura	*Paratylodiplax blephariskios*	0.002	0.0311	0.003	0.016	0	0.015	0.001	0	0	0	0	0.003	0	0	0.003	0.001	0	0.005	0	0	0	0.013
Polychaeta	*Thelepus* spp	0.006	0.003	0	0.003	0.008	0.002	0	0	0	0	0	0.001	0.006	0.006	0.011	0.013	0.005	0.008	0.001	0.010	0	0.004
Polychaeta	*Ceratonereis erythraeensis*	0.001	0.001	0.006	0.012	0.003	0.005	0.001	0.001	0.005	0.004	0.004	0.005	0.003	0.003	0.013	0.013	0.001	0.001	0	<0.001	0	0
Polychaeta	*Cirriformia capensis*	0.015	0.015	0	0	0	0	0	0	0	0	0	0	0.001	0	0.002	0.004	0.002	0.002	0.009	0	0	0
Brachyura	*Spiroplax spiralis*	0	0	0	0.007	0.003	0	0	0.005	0.003	0.003	0	0.001	0.005	0.001	0	0.001	0.005	0	0	0	0	0
Eumalacostraca	*Betaeus jucundus*	0.003	0.005	0	0	0.002	0.005	0	0.001	0	0	0.003	0	0.001	0	0.003	0.004	0	0	0.006	0	0	0
Polychaeta	*Orbinia angrapequensis*	0	0	0.001	0.001	0	<0.001	0.001	0.001	0.002	0.001	0.001	0.001	0.002^{a}	0.006^{b}	0.001	0.001	0.001	0.002	<0.001	<0.001	0.0008	0.0015
Polychaeta	*Euclymene* spp	0	0	0	0	0	0	0	0	0	0	0	0	0.021	0	0	0	0	0	0	0	0	0

3.3.5 Size of foraging structures in relation to flamingo predation impact

Linear mixed models revealed that the impact of flamingo foraging on macrofaunal abundance was negatively related to the size of channels (t = -2.605, p = 0.012, R^2 = 0.507, Table 6), suggesting that smaller channels induce greater impacts on macrofaunal abundance. There was evidence that the abundance of the polychaete *N. latericeus* also displayed a negative relationship with channel size, although the latter was marginally non-significant (t = -1.762, p = 0.084, R^2 = 0.440). There were no significant relationships with the impacts of flamingo foraging on the community variables in relation to the size of pits.

Table 6: Results of linear mixed effects modelling testing the effects of sizes of flamingo foraging structures against various community metrics. * = significant effect.

Response variable	Pits			Channels		
	R^2	Slope	p	R^2	Slope	p
Macrofaunal Abundance	0.207	1.895	0.588	0.507	-17.95	0.012*
Species Richness	0.207	0.122	0.813	0.085	-0.033	0.547
Chl-*a*	0.014	0.003	0.917	0.158	0.031	0.231
Macrofaunal Biomass	0.065	0.105	0.114	0.089	0.019	0.764
Urothoe grimaldii	0.001	-0.032	0.816	0.453	-4.440	0.173
Notomastus latericeus	0.267	0.017	0.855	0.440	-1.330	0.084
Ceratonereis erythraeensis	0.304	-0.547	0.296	0.042	0.310	0.208
Eurydice kensleyi	0.019	0.066	0.412	0.297	0.048	0.343
Callichirus kraussi	0.042	0.291	0.301	0.225	0.264	0.437

CHAPTER 4: DISCUSSION

The overarching goal of this study was to contribute to expanding knowledge of the causes and consequences of the plastic foraging strategies employed by Greater Flamingos in Langebaan Lagoon. Results of statistical modelling indicated that biotic variables were the main determinants of flamingo foraging, and that different aspects of prey assemblages influenced choices made by flamingos to employ particular foraging methods. Results also indicate that the various strategies employed by flamingos when foraging result in differential impacts on soft sediment assemblages. However, contrary to the hypothesis made, pit-foraging did not result in a greater impact on prey assemblages relative to channel-foraging. Taken collectively, the results obtained broaden the understanding of foraging plasticity displayed by predators in marine soft-sediment ecosystems, which to date, have been rarely investigated.

4.1 Ecological determinants of flamingo foraging

A summary of variables predicting flamingo foraging is presented in Table 7. Macrofaunal richness was identified as one of the primary variables driving flamingo decisions to feed. High probabilities of feeding were predicted when richness was between six and eight species. This was followed by a decline in predicted foraging as richness approached ten species, and an increase when richness approached eleven species. Although few studies have demonstrated the link between prey richness and consumer foraging choices, inferences on the latter have been made based on the consumer foraging behaviour. For example, Mori *et al.* (2005), using dive profile data, showed that Weddell seals foraged for longer when prey index, a proxy for prey richness, was high. This suggests that prey richness may be an important driver of seal feeding behaviour, resulting in increased foraging effort when prey diversity is high. Similar trends have been reported for herbivores. Wang *et al.* (2010) demonstrated that increases in plant species richness, through field and indoor experiments, resulted in sheep increasing their time spent foraging, resulting in a greater protein and energy intake.

Table 7: Summary of the ecological factors predicting flamingo foraging behaviour.

Flamingo foraging behavior	**Predictor**	**Relationship**
Foraging vs non-foraging	1. Macrofaunal Richness 2. Macrofaunal Biomass (excl. *C. kraussi*) 3. Infaunal Abundance	1. Bimodal (High probabilities of feeding between 6-8 and 11-12 species) 2. Exponential decay (High probabilities of feeding between 0 and 0.05g) 3. Sigmoidal (High probabilities of feeding after 23 counts of infauna)
Pit-foraging vs non-foraging	1. Chl-*a* biomass 2. Macrofaunal Biomass (incl. *C. kraussi*) 3. Surface Feeder Biomass	1. Linear (High probabilities of pit-foraging with increases in chl-*a* concentrations after 0.4 mg L^{-1}) 2. Exponential decay (High probabilities of pit-foraging between 0 and 0.25g) 3. Exponential decay (High probabilities of pit-foraging when biomass is < 0.01g)
Channel-foraging vs non-foraging	1. Macrofaunal Abundance 2. Infaunal Abundance 3. Surface Feeder Abundance 4. Macrofaunal Biomass (incl. *C. kraussi*)	1. Sigmoidal (High probabilities of channel-foraging after 150 counts of macrofauna) 2. Sigmoidal (High probabilities of channel-foraging after 23 counts of infauna) 3. Sigmoidal (High probabilities of channel-foraging after 110 counts of surface feeders) 4. Exponential decay (High probabilities of channel-foraging when biomass is < 0.1g)

It must be noted that in the present study, models did not identify a linear relationship between richness and probability of feeding; models instead predicted a bimodal response. A possible reason for the latter was that it reflects spatial variability in richness among the sampling sites. For example, at Sites 1 and 2, feeding patches consisted on average seven to eight species (which may correspond to the first peak predicted by models; Figure 8), whereas at Site 3, macrofaunal richness increased to approximately ten. Another reason for the models producing a bimodal response was that flamingo feeding comprised of pooled data for both pit- and channel-foraging. The first predicted peak of foraging could therefore reflect pit-foraging, whereas the second predicted peak may correspond to channel-foraging or vice-versa. While modelling techniques did identify macrofaunal richness as a predictor of flamingo foraging, the fact that predicted foraging increased only by 7% across the ranges of richness observed, suggests that richness may not be a very strong determinant of foraging. The latter is supported by results showing that no significant differences were detected between flamingo feeding and non-feeding patches.

The biomass of macrofauna, either including or excluding *Callichirus kraussi*, was consistently identified as an important driver of choices made by flamingos to feed and implement either pit- or channel-foraging (Table 7). All three feeding models predicted an exponential decline in probability of flamingo feeding/pit- or channel-foraging with increasing macrofaunal biomass. Interestingly, similar patterns were predicted for surface feeder biomass, which was identified as a predictor of pit-foraging. Collectively, the models highlighted above would suggest that flamingos preferentially target prey with low biomass for consumption. Greater Flamingos have been shown to feed optimally on prey between 2-4mm in size (Zweers *et al.* 1995), which supports the idea that flamingos may target smaller organisms when feeding. The latter is also supported by

(1) low macrofaunal biomass recorded in feeding patches and channel structure controls and (2) low surface feeder biomass in pit controls in comparison to the non-feeding controls. The above findings suggest that areas foraged by flamingos in the field have lower biomass than areas where no feeding occurs. Therefore, statistical models reveal that irrespective of the feeding strategy employed by Greater Flamingos, these shorebird predators target smaller prey for consumption.

Models predicted that increases in surface feeder, macrofaunal and infaunal abundances would lead to greater probabilities of flamingos employing channel-foraging (Table 7). Holme (1964) pointed out that the majority of benthic fauna resides within the top 10cm of sediment. In addition, many infaunal species are found in the upper 15cm (Johnson 1967) whereas amphipods, crustaceans and isopods are generally found in the upper 5cm sediment layer (Hines & Comtois 1985). Taxa that were sampled in the present study were collected from a depth of 15cm and their abundances were significantly higher in channel controls compared to non-feeding controls within particular shore positions. Therefore, the likelihood of creating channels are greatest when surface-associated prey is available. This is intuitive given that this foraging method essentially involves the bill being swept from side-to-side on the surface of sediments (Glassom & Branch 1997; Johnson & Cézilly 2007). Surface feeders contributed approximately 80% to overall macrofaunal abundance in channel-foraging controls and non-feeding controls, which may explain why macrofaunal abundance was highlighted as a predictor of channel-foraging. The greater probability of channel-foraging with increasing macrofaunal abundance may be a reflection of flamingos employing channel-foraging behaviour to target surface organisms.

Infaunal abundance was also identified as a primary predictor of flamingo feeding (Table 7), with increases in infaunal abundance leading to increases in probabilities of feeding. However, significant differences in infaunal abundances were detected only between channel controls and non-feeding controls and not between feeding and non-feeding quadrats. It is important to note that of the 97 structures sampled in the study, 60% were channels. Thus, the selection of infaunal abundance as an ecological driver of flamingo feeding may be due to a disproportionate number of data points for channel-foraging in the data set. At the same time, the pooling of pit- and channel-foraging samples into one feeding dataset for ANOVA analysis, potentially lowered the statistical power of the test due to the large biological variance in the feeding data. This lead to comparisons between feeding and non-feeding treatments being statistically insignificant. Studies have raised awareness of the potential problems associated with analysing pooled datasets statistically, particularly that large variances in datasets were potentially hidden, resulting in false confidence in rejecting a true null hypothesis (Machlis *et al.* 1985; Zhang & Gant 2005). In my study, I had to pool data from all quadrats spanning different foraging methods in order to differentiate probabilities of foraging and not foraging.

Micro-algal biomass (chl-*a*) was highlighted as a predictor of pit-foraging by flamingos, with increases in this trophic resource predicted to increase probabilities of flamingos employing pit-foraging (Table 7). This model prediction was supported by chl-*a* being significantly greater in pit controls than non-feeding controls. However, considering this feeding technique involves flamingos using their feet to dig up prey items from deep sediments (Glassom & Branch 1997; Johnson & Cézilly 2007), it would not be intuitive for this feeding strategy to be employed to target benthic micro-algae, which are generally found on the surface sediment layer (MacIntyre *et al.* 1996). Although few studies have demonstrated Greater Flamingos feeding on algae and plant material (Johnson 1997), the flamingo species *Phoenicoparrus andinus*, *P. jamesi*, and *Phoeniconaias minor* specialize in algal diets. This is due to fine lamellae in their beaks allowing them to strain finer organisms (Jenkin 1957; Vareschi 1978; Hurlbert & Chang 1983). In contrast, members of the genus *Phoenicopterus* have coarser lamellae to filter comparatively larger items, thus allowing them to have a broader diet breadth (Jenkin 1957). Based on the latter, micro-algal biomass may not necessarily be a direct driver of Greater Flamingo pit-foraging. Given that pit-foraging behaviour was predicted when biomass of both macrofauna and surface feeders were low, and the suggestion that Greater Flamingos target smaller macrofaunal prey when employing this feeding method, the selection of micro-algal biomass as a driver of pit-foraging may thus be a consequence of small consumers being removed by flamingo pit-foraging facilitating micro-algal biomass. This idea is supported by several field experiments conducted in marine systems that have demonstrated stimulation of blooms of algal biomass following reductions in mesograzers (Whalen *et al.* 2013; Ebrahim *et al.* 2014; Reynolds *et al.* 2014; Duffy *et al.* 2015).

Unexpectedly, the abundances of the amphipod *Urothoe grimaldii* and the polychaete *Notomastus latericeus* were the main determinants of the sizes of pit-foraging structures. The model predicted an increase in pit size with decreasing abundances of the two species listed above, indicating that when these prey were rare, the pits were bigger. Several studies have documented various consumers increasing their foraging effort as well their time spent foraging during periods of low prey abundance (Boyd *et al.* 1994; Monaghan *et al.* 1994; Suryan *et al.* 2000; Ronconi & Burger 2008). Based on the above, it is plausible that Greater Flamingos exert greater effort in foraging (larger pit size) when *U. grimaldii* and *N. latericeus* are rare. The latter could indicate that these species are targeted while pit-foraging, although, this is not intuitive since (1) both species have been recorded in the upper sediment layers of various sandflats (Christie 1976;

Pienkowski 1983; Desroy *et al.* 2002) and (2) deeper-dwelling prey items would have been expected to better predict pit-foraging given that the strategy was thought to target deep-dwelling organisms (Glassom & Branch 1997; Johnson & Cézilly 2007). This paradox of surface-dwelling taxa predicting the variability in the size of pit-foraging structures is possibly due to these taxa being consumed incidentally while targeting deeper-dwelling prey.

The inability of *RandomForest* modelling to identify drivers of variability of flamingo channel sizes may be due to the predictor variables not being fully informative in explaining channel size. Although *RandomForest* can handle a large number of input variables (de Edelenyi *et al.* 2008), variable selection ultimately reduces the statistical noise emerging from uninformative variables, allowing more informative variables to be identified (de Edelenyi *et al.* 2008; Touw *et al.* 2012). However, since the same predictor variables were input for pit size, and *RandomForest* did successfully identify the most informative variables, the other possibility was that there was a greater variance in the channel size data compared to the pit size data, hindering the detection of the underlying relationship between channel size and the predictor variables (Abu-Mostafa *et al.* 2012). The low proportion of variation explained in the channel size data does suggest a poor fit to the dataset leading to the model becoming unpredictable.

4.2 Differential effects of flamingo foraging plasticity

As is evident in Table 8, the different foraging strategies employed by flamingos generated contrasting impacts on benthic assemblages. The differential impacts of pit- and channel-foraging behaviours on benthic assemblages were likely to be driven by each of these feeding strategies serving distinct foraging functions (Brown *et al.* 2005). Based on visual observations of how each foraging strategy was executed, channel-foraging was likely to be a strategy aimed at consuming

Table 8: Summary of differences in macrofaunal community structure, community metrics, chl-*a* biomass and dominant species between flamingo foraging structures and controls.

Response variable	Impact	
	Pits vs Pit controls	*Channels vs Channel controls*
Macrofaunal community structure	No difference	Significant difference (6/7 comparisons supported)
Chl-*a*	No difference	Significant difference (lower in channels relative to controls with 5/7 comparisons supported)
Macrofaunal Abundance	Significant difference (lower in pits relative to controls with 1/4 comparisons supported)	Significant difference (lower in channels relative to controls with 5/7 comparisons supported)
Macrofaunal Richness	No difference	No difference
Macrofaunal Biomass	No difference	No difference
W-statistics	No difference	Significant difference (higher in channels relative to controls with 4/7 comparisons supported)
Dominant macrofaunal species (abundance)	3 species significantly lower in pits relative to controls	• 9 species significantly lower in channels relative to controls • 1 species significantly higher in channels relative to controls
Dominant macrofaunal species (biomass)	No difference	• 4 species significantly lower in channels relative to controls • 1 species significantly higher in channels relative to controls

organisms associated with the sediment surface; whereas pit-foraging may be a strategy aimed at acquiring deeper-dwelling prey. Therefore, the differential impacts on benthic assemblages observed in this investigation was likely reflective of each of these foraging methods targeting prey from different depth strata in the benthos. This may explain the greater impact of channel-foraging on micro-algae (chl-*a*), which are surface-associated organisms (MacIntyre *et al.* 1996). In addition, the negative effect of channel-foraging on the amphipod, *U. grimaldii* (Christie 1976), along with other species identified by SIMPER that were largely surface feeders and upper surface infauna, support the idea of channel-foraging impacting predominantly surface-associated fauna. Lastly, the results of modelling have shown that channel-foraging was predicted when the abundance of infauna and surface feeders increases, which provides further support of channel-foraging being associated with surface-dwelling taxa. Given that *U. grimaldii* was the most numerically dominant macrofaunal species in the study, contributing roughly 39% to total macrofaunal abundance, the strong negative impact of this channel-foraging on overall macrofaunal abundance may be a reflection of flamingos targeting *U. grimaldii* and potentially other surface-dwelling organisms while channel-foraging.

It could be argued that pit-foraging by flamingos could be more energetically costly than channel-foraging, given that flamingos use their feet to dig into sediment to greater depths than channel-foraging. Therefore, the expectation would be that the fitness cost involved may need to be offset by foraging on larger organisms with greater energetic value than smaller surface-dwelling taxa. Taxa that fulfil the latter in Langebaan Lagoon are bivalves. Given that bivalves are often found deep within benthic substrates (Puttick 1977; Hines & Comtois 1985), they are potentially the targets of flamingos when employing pit-foraging. In addition, these prey items could potentially compensate for the energy invested by flamingos, as large amounts of tissue are found in bivalves in comparison to other macrofaunal taxa such as polychaetes (Blanchard & Knowlton 2013). In addition, various studies have shown bivalves to have a greater calorific content relative to other benthic organisms (Stoker 1978; Wilt *et al.* 2014). The present data revealed patterns of some bivalve species (*Macoma* spp and *Tellimya trigona*) being reduced in pits relative to pit controls, but these were weak and statistically insignificant. The latter trend however could be due to the low abundance of bivalves in the study site – a trend commonly reported in South African systems (Day 1951).

Another possible reason for pit-foraging not eliciting a greater impact on prey assemblages is that this method may target a trophic resource different to benthic macrofauna. Johnson & Cézilly (2007) describe Greater Flamingos using pit-foraging to either feed on buried invertebrates or mud that they sieve from pits. By swallowing the finer mud particles, flamingos can extract fine organic matter (Jenkin 1957; Johnson & Cézilly 2007). Thus, the extraction of fine organic material could be a secondary resource that flamingos target while pit-foraging, a variable that was not measured in this study.

It is also possible that pit-foraging may not be a primary method of feeding for flamingos. Schmitz & Baldassarre (1992) reported a high frequency of pit-foraging activities in American Flamingos following a hurricane, and argued that the switch from channel- to pit-feeding was driven by the reduction of primary resources (gastropods) and submerged vegetation. It was argued that flamingos would need to feed on secondary resources (seeds and tubercles) in bottom sediments following the hurricane, which were most likely to be obtained by pit-foraging. In this investigation, it is likely that channel-foraging is the primary method of feeding employed by Greater Flamingos, with pit-foraging fulfilling a secondary role. This was supported by data showing that channels occurred predominantly across mid- and low-shore positions, whereas pits, in contrast, were recorded mainly in high-shore positions (see Figure 7B).

In contrast to the negative effects of channel-foraging by flamingos on macrofaunal abundance, there were no significant effects of either channel- or pit-foraging on macrofaunal richness (Table 8). The similarity in richness across foraging treatments would suggest that Greater Flamingos were selecting a narrow spectrum of the prey available for consumption and that they were potentially targeting particular prey items. It is well known that flamingos have the ability to switch between foraging strategies in response to changes in habitat conditions (Brown *et al.* 2005). However, these shorebird predators are also capable of searching and consuming preferred prey items (Jenkin 1957; Zweers *et al.* 1995). Studies have shown that flamingos can select particular food items within desired size ranges by adjusting the distances between their bill lamellae. Favourable prey sizes are retained in the mesh and consumed, whereas prey sizes that are too small or large are rejected and returned to the sediment (Jenkin 1957; Zweers *et al.* 1995). The lack of statistically significant effects of flamingo foraging on macrofaunal biomass (Table 8) also suggests that flamingos were targeting a very narrow spectrum of available prey for consumption.

There were no significant reductions in micro-algal biomass in pits relative to their controls, whereas channel-foraging generated a strong impact on this trophic resource (Table 8). Interestingly though, micro-algal biomass was similar in both pit- and channel-foraging structure controls within particular shore positions. Two possible mechanisms may explain pit-foraging not eliciting a greater impact on benthic micro-algal biomass. Firstly, if flamingos were intending to select large, deep-dwelling organisms through pit-foraging, they would need to increase the distances between their bill lamellae (Zweers *et al.* 1995). A consequence of the latter would be that fine particles such as micro-algal cells would pass through the mesh and be returned to the sediment. Secondly, pit-foraging may generate net positive feedbacks on surface micro-algae by stimulatory effects of this foraging technique countering consumptive impacts. Several studies have highlighted the effects of bioturbation (sediment reworking, Meysman *et al.* 2006; Pillay & Branch 2011) in increasing fluxes of nutrients from deep sediment layers and indirectly promoting productivity at the sediment-water interface (Ziebis *et al.* 1996; Lohrer *et al.* 2004; Mermillod-Blondin *et al.* 2004; D'Andrea & DeWitt 2009). A study by Comin *et al.* (1997) revealed that flamingos, through their prolonged stamping behaviour, have the potential to release nutrients from the sediment into the water column. Therefore, the upward-conveyer belt bioturbation (Francois *et al.* 2001) employed by flamingos during pit-foraging may elicit a positive effect on nutrient fluxes and productivity, thereby enhancing micro-algal biomass. The latter could potentially explain why chl-*a* concentration was chosen as a predictor variable for pit-foraging, as areas surrounding pit-foraging structures generally had greater micro-algal biomass.

W-statistics (obtained from abundance-biomass comparison curves) revealed overall that species ranked biomass was greater than abundance in channel-foraging structures compared to their controls, with four out of seven comparisons being statistically upheld. The greater species ranked biomass in channels in comparison to controls relative to pits and their controls, is most likely due to flamingos selectively removing smaller organisms for consumption and avoiding larger ones. The greater impact of flamingo channel-foraging on the small, surface-dwelling amphipods *U. grimaldii*, *Griffithsia latipes, Leucothoe spinicarpa*; along with the isopod *Eurydice kensleyi* supports the idea of selective removal of smaller prey by flamingos during channel-foraging. The latter was also corroborated by all flamingo feeding models predicting that flamingos were most likely to feed (pit- and channel-forage) when prey biomass was low. The greater abundance and biomass of the sandprawn *C. kraussi* in some channels relative to controls may also provide support for the latter. Considering that sandprawns can grow up to 60mm in length (head to tail; Branch *et al.* 2010), they fall beyond the preferred prey size spectrum for flamingos (Zweers *et al.* 1995) and are therefore most likely rejected from the bill and returned to the sediment. The greater abundance of *C. kraussi* in channels could also indicate active selection by flamingos for sediments with dense aggregates of *C. kraussi*, given the various studies demonstrating the potential for engineering effects of burrowing sandprawns to elevate abundances of various organisms (Branch & Pringle 1987; Siebert & Branch 2005; Pillay & Branch 2011).

It was hypothesized that increasing sizes of flamingo foraging structures would increase impacts on prey assemblages relative to non-foraged sediments. However, none of the response variables were significantly affected by the size of pit-foraging structures. In contrast, size of channels was inversely related to impacts on macrofaunal abundance. Results also indicated that channel size was significantly affected by shore position, where at Site 3, channel size reduced significantly from the high- to low-water mark (see Figure 7A). Generally, there was also a decline of macrofaunal abundance from the high- to low-water mark at Site 3 (see Figure 24). The difference in channel size across the shore positions may be an indication of the different levels of food available for flamingos to feed on. An increase in prey abundance can alter a predator's response to increase or decrease its foraging effort, depending on the constraints imposed by changes in food availability (Abrahams & Dill 1989). Lubin & Henschel (1996) experimentally demonstrated that desert spiders decreased their foraging activity (reduced the dimensions of their prey capture web) when their food supply increased as prey-handling costs (digestive constraints) prevented spiders from fully utilizing the prey available. Therefore, it can be argued that flamingos create smaller channels in abundantly rich areas to maximize their prey intake, but reserve energy devoted to handling prey (Johnson & Cézilly 2007). This may explain why there was a greater impact on macrofaunal abundance with small channels.

Given the wealth of literature documenting the patchy distributions of organisms dwelling in marine sediments (Barry & Dayton 1991; McIntosh 1991; Thrush 1991; Ólafsson 1992; Legendre *et al.* 1997), the possibility exists that if preferred prey items (potentially *U. grimaldii*) were distributed in small patches, Greater Flamingos could increase their foraging rate and intensity to maximise prey capture from these patches. This results in smaller channels having greater impacts on prey. Santos *et al.* (2009) demonstrated that waders rely on probing techniques rather than visual cues to detect enriched patches of buried prey. A single contact with a prey would induce further probing, eventually leading to patch recognition. Therefore, the low impact of larger channels made by flamingos could be a consequence of larger structures being created during random probing behaviour, and not as part of a feeding event.

4.3 Methodological considerations

While this study has provided important insights on the role of flamingo foraging plasticity in intertidal sedimentary systems, it is important to acknowledge the limitations inherent in this study. The main limitation was that the study was based on field measurements and relied on a correlative approach to understand causal relationships. As such, there was significant potential for external factors to influence findings. In this study, it was assumed that foraging structure controls represented un-impacted states and were unaffected by flamingo feeding at the time of sampling. This was based largely on visual indications of no foraging activity within the immediate vicinity of foraging controls. However, the possibility does exist that flamingos may have disturbed these controls at some point in time, or that controls may have been impacted by other disturbances in the past. In addition, it was also assumed that the sedimentary environment between feeding structures and controls was homogenous, though it is possible for habitat characteristics to vary even at the relatively small spatial scales (1meter). The points raised above would suggest that future studies of this nature would benefit, by rigorously standardising comparisons between foraging structures and controls. A second point worth noting is that in a field study of the type I conducted, direct and indirect effects cannot be explicitly quantified directly, suggesting that drivers highlighted through statistical testing may not be ultimate drivers. For example, sediment characteristics were not identified to be drivers of flamingo foraging plasticity; prey traits were apparently stronger predictors. However, it is possible for sediment traits to directly determine prey abundance and distribution, thereby indirectly influencing flamingo foraging plasticity.

4.4 Implications of the study for marine ecology: Flamingo foraging plasticity – a key driver of heterogeneity in marine sediments

One of the primary ramifications of the study was that the differential effects of flamingo foraging plasticity can act as key sources of spatio-temporal heterogeneity in intertidal sandflats, by essentially creating patches that are dissimilar to non-foraged sediments at the community level. Findings indicate that communities in pit-foraging structures were similar to surrounding environments; whereas channels in contrast, were highly dissimilar to non-foraged sediments. Additionally, smaller channels, exerted a greater impact on macrofaunal abundance; which in turn may amplify over time and enhance heterogeneity. The differing degrees to which flamingos remove consumers from sediments will most likely determine the rate at which basal resources accumulate in structures over time. Several studies have documented the effects of top-down control exerted by various predators on intermediate consumers in marine sediments, which collectively influence the recovery and accumulation of basal trophic resources (Van Blaricom 1982; Thrush *et al.* 1991; Lewis & Anderson 2012). Therefore, based on the latter, the greater impact of flamingos on consumers from smaller channels, will most likely allow resources to increase at a relatively high rate compared to larger channels, potentially exceeding levels occurring in pre-foraged sediments. However, the latter may be less prominent in pits. If the latter hypothesis is validated, positive feedbacks will most likely occur where the dissimilarity in channels (of different sizes) against pits in relation to non-foraged sediments will strengthen over time. The accumulation of basal resources such as bacterial assemblages are vital elements for ecosystem functioning (Blackburn 1987; Deming & Baross 1993), along with release of micro-algae and carbohydrate matrices that serve as important attractants for sediment recruitment (Pillay *et al.* 2007), resulting in short-term increases in community metrics. In addition to spatial heterogeneity, flamingo foraging can also drive temporal variability in benthic assemblages over seasonal time scales, given that flamingo predation is probably greatest in winter due to the larger over-wintering flamingo populations (Underhill 1987). Taken collectively, continual impacts of flamingo foraging and associated successional change over multiple time-scales (days, weeks and seasons) can therefore create a mosaic of patches that are at different stages of succession depending on the type and size of the structure created.

CONCLUSION

Overall, the study has provided insight on the ecological roles played by a charismatic and iconic shorebird predator that has received little attention in marine systems (Glassom & Branch 1997; Bildstein *et al.* 2000). The study has shed light on the importance of biotic drivers of flamingo foraging behaviour, which in turn determines the strength of flamingo impacts on prey assemblages. The latter is particularly important and highlights the need to incorporate foraging plasticity into broader conceptual models of predation in marine systems. Furthermore, the feeding structures produced by Greater Flamingos have differential effects on macrofaunal communities, altering spatio-temporal heterogeneity in soft-sediment ecosystems at various scales. Based on the above, predation impact cannot be assumed to be uniform across habitats since subtle changes in foraging behaviour can determine the strength of top-down control exerted by predators. Future predation studies need to focus more on quantifying factors that drive predator foraging behaviours as the strength of predation is tightly linked to foraging behaviour.

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