Flamingo foraging activity as a driver of spatial heterogeneity in Langebaan Lagoon, South Africa

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Abstract

Numerous studies have attempted to quantify the effect of epifaunal predation and its co-occurring disturbance on macrofaunal communities with the aid of exclosure experiments. However, no attention has been paid to the possible impacts of different foraging methods used by flamingos on benthic communities. Multivariate and univariate analyses were carried out in order to determine the effects of two different flamingo feeding strategies (pit and channel foraging) on sediment penetrability and macrofaunal community structure in Langebaan Lagoon. The two foraging strategies appear only to differ with regards to prey removal and recolonisation. The more energy intensive, pit-forming foraging enables the flamingo to obtain higher quantities of *Urothoe grimaldii* in addition to bivalves, while promoting recolonisation by opportunists. On the other hand, channel-foraging enables the attainment of various polychaete and nematode species. These small-scale differences, as well as the spatial (and possibly temporal) variation in structures generate habitat complexity. Thus, this preliminary study supports the notion that flamingo foraging activity is a key driver of spatial heterogeneity in Langebaan Lagoon and highlights the need for further research.

Key words: heterogeneity, flamingo, predation, disturbance, *Phoenicopterus minor*, *Phoenicopterus roseus*

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1. Introduction

Soft - sediment communities are regulated by various biological and physical processes that operate over a range of spatial and temporal scales (Ellis et al. 2000).Consequently, complex species abundance and distribution patterns are governed by a set of interacting factors that include hydrodynamic and sediment properties as well as predation and competition, with the latter two operating predominantly on a local (as opposed to regional) scale (Thrush 1991; Ellis et al. 2000).

In sheltered soft-sediment environments, the effects of organisms on their physical surroundings increase, producing small-scale habitat complexity (Probert 1984; Reise 1985). This effect is often in the form of short-lived, localized biogenic structures that modify the environment (Woodin 1981; Wilson 1991; Hewitt et al. 2005) and act as frequent biological disturbances that are predominantly the result of mobile epifaunal predation and the movement through, or processing of, sediment by large infauna (Probert 1984). With these disturbance events occurring at varying spatial and temporal scales, as well as at different frequencies and

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intensities, the result is a mosaic of macrobenthic community patches that differ according to their stage of recovery or recolonization (Johnson 1970). In this way, epifaunal predation and its co-occurring disturbance can facilitate the maintenance of spatio-temporal heterogeneity in soft-sediment communities (Probert 1984).

Flamingos are large filter-feeding aquatic birds that often occur at high densities (Glassom and Branch 1997) and have a considerable impact on the dynamics of both subtidal and intertidal prey populations. A few studies have attempted to quantify the impact of their predation and foraging-related disturbance on macrofaunal community structure via exclusion experiments. One of the first studies was conducted by Hurlbert and Chang (1983), who found that the exclusion of the Andean flamingo (*Phoenicopterus andinus*) from a salt lake in the Andes resulted in an increase in microorganismal biomass. An increase in macrofaunal abundance, change in sediment properties and unaffected diversity indices were reported by Glassom and Branch (1997) when partially excluding the greater flamingo (*Phoenicopterus roseus*) from two lagoons along the Namibian coastline. Rodríguez-Pérez et al. (2007) found that the same flamingo species caused a significant reduction in chironomid abundance and an increase in the proportion of larger larvae in a temporary marsh. The greater flamingo has also been found to negatively affect certain aquatic (Rodríguez-Pérez and Green 2006; Guillaume et al. 2012) and semi-aquatic plants via mechanical disturbance (Tourenq et al. 2001). Overall, the ecological role of the flamingo has largely been neglected (Glassom and Branch 1997; Bildstein et al. 2000), with observational and descriptive studies far outweighing experimental ones.

Both the greater and lesser flamingo (*Phoenicopterus roseus* and *Phoenicopterus minor* respectively) occur in South Africa and are frequently found along the coast and in estuaries (Rodríguez-Pérez et al. 2007). The former feeds predominantly on the sediment surface for small invertebrates, algae and plant material, (Jenkin 1957; Glassom and Branch 1997; Johnson 1997), while the latter has a finer filter and feeds on cyanobacteria and diatoms from the water column (Jenkin 1957) or sediment surface film (Vareschi 1978), but rotifers can act as a partial substitute.

Out of the several feeding behaviours that have been described for flamingos (Brown and King 2005), two are observed frequently in Langebaan Lagoon. The first behaviour is described as the flamingo sweeping its inverted bill horizontally back and forth in a semicircle while walking, creating an elongated channel-like structure with little disturbance (Figure1a). The other behaviour gives rise to large round pits of considerable disturbance, approximately 1m in diameter (Figure 1b) due the circular jogging motion of the flamingo while retaining its inverted bill in a central position (Glassom and Branch 1997; Rodríguez-Pérez et al. 2007). Although these behaviours are typically exhibited by greater flamingos (Glassom and Branch 1997; Rodríguez-Pérez et al. 2007), Brown and King (2005) suggest that it is unknown to what extent feeding

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behaviour may be shared among species. Thus, the impact of both foraging behaviours will be attributed collectively to ‘flamingos’.

The aim of this study was to determine the role flamingos play in generating spatial heterogeneity via predation and foraging-related disturbance in Langebaan Lagoon. This was done by quantifying the effects of pit and channel foraging on sediment penetrability and macrofaunal community structure. As flamingos usually occur in high densities (Glassom and Branch 1997) and with population numbers on the rise (R. Summers, personal communication), it is important to understand their impact on soft-sediment systems and how this is influenced by their foraging method. Overall, this study will provide a better understanding of the role of flamingos as predators and agents of biological disturbance in soft-sediment marine systems (Bildstein et al. 2000), while possibly improving understanding into their use of different foraging behaviours.

It is expected that the two different foraging structures will contain sediment that is more penetrable than their respective controls due to forging associated disturbance. Both structures will have fewer species, greater species evenness and a lower overall macrofaunal abundance in comparison to controls as foraging is anticipated to remove specific, possibly dominant, prey items. Pits will consist of sediment that is more penetrable when compared to channel sediments as they seem to have an observable greater disturbance. Consequently, if pit foraging is more energy intensive, requiring more prey items to offset this energy cost, it is expected that pits will contain fewer species, a greater species evenness value and a lower overall macrofaunal abundance when compared to channels. With regards to changing species abundance, richness and evenness, a change in community structure is implied. Thus community structure will differ between structures and their controls, as well as between pits and channels.

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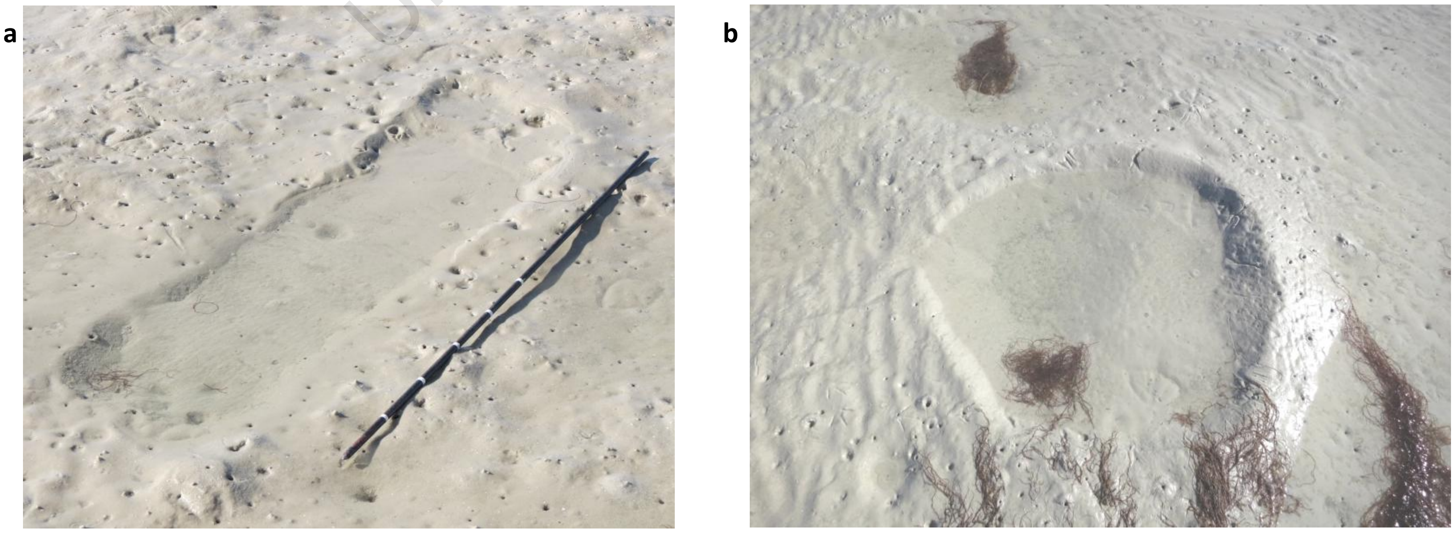

Figure 1: Flamingo foraging structures generated from two different feeding behaviours: (a) channel (©Alexa Prinsloo; pole = 1m) and (b) pit (© Jessica Dawson).

2. Methods

2.1. Study area

Langebaan Lagoon, which is situated between 33°11’27’’S, 18°07’37’’E and 33°03’54’’S, 17°58’07’’E (Pillay et al. 2011), lies along the west coast of South Africa (Figure 2) and constitutes the core of the West Coast National Park (Schils et al. 2001). Connected to the ocean via Saldanha Bay by means of a narrow tidal inlet (Compton 2001), this marine-dominated lagoon experiences little freshwater input and is approximately 15km long, with a maximum width of 4km and a tidal range of 1.8m during spring tide (Day 1959; Flemming 1988). Expansive supratidal saltmarsh and intertidal sandflat systems exist, with the latter separated by tidal channels that reach an estimated 4-11m depth at low tide (Flemming 1977; Compton 2001; Kerwath et al. 2009).

The lagoon is recognised as an Important Bird Area by BirdLife International (Pillay et al. 2010), supporting approximately 50 000 birds in summer and 13 000 in winter (Clark et al. 2009). Flamingos comprise roughly 2% of the total bird population in the summer, rising to 38% in winter.

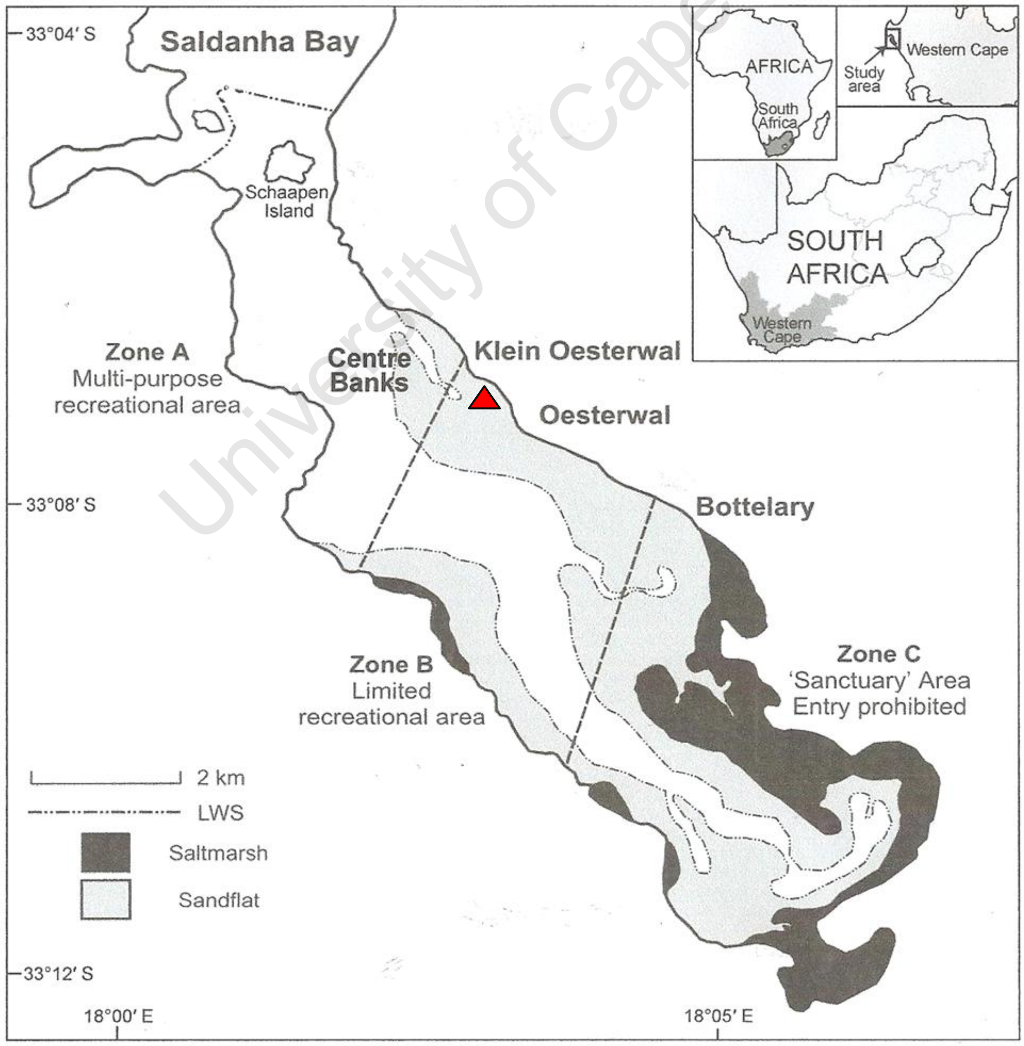

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Figure 2: Map of Langebaan Lagoon depicting geographical position, the sample site and park zones. LWS: low water spring (adapted after Nel and Branch 2013).

Samples were collected at mid-shore during low tide on the eastern sandflat of the lagoon at Oesterwal. Restricted access is permitted in this area but bait collection is prohibited (Nel and Branch 2013). Consequently, flamingo foraging tracks were conspicuous and well preserved.

Seven pits and seven channels were sampled, as were their respective controls, defined as areas less than 1m away from the feeding structure where no foraging had occurred. An attempt was made to sample the most recent foraging structures (less than 24 hours since foraging occurred) of similar size.

2.2 Sediment penetrability

To assess the degree of sediment disturbance generated by flamingo foraging, sediment penetrability was measured per structure and respective control by dropping a steel rod (length =1m, diameter =1cm) from a height of 1m above the substratum and recording penetration depth to the nearest centimetre.

2.3. Macrofauna sampling

Three cylindrical sediment cores (depth =15cm, diameter =10cm) were collected and pooled per foraging structure and per respective control (Figure 3). The sediment obtained was then sieved through a 500µm mesh, followed by a 2mm mesh and retained material was preserved in 70% ethanol with Rose Bengal for staining. Using a microscope, macrofauna were identified to the lowest taxonomic level possible and counted. Finally all specimens were preserved in 70% ethanol.

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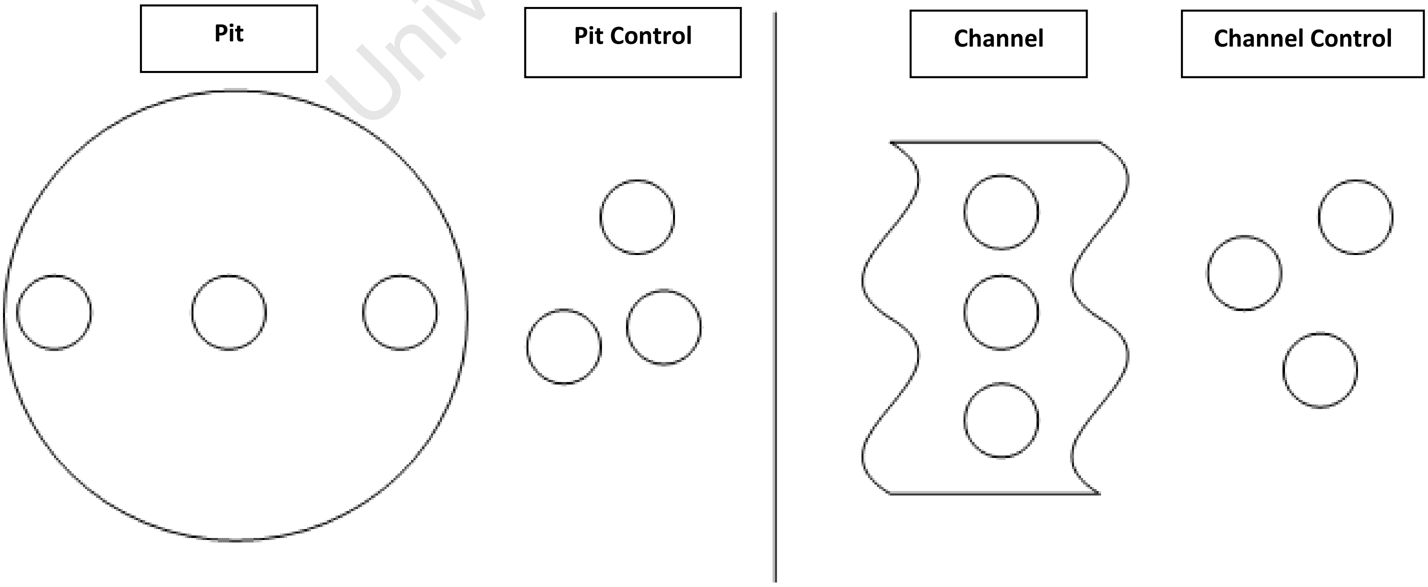

Figure 3: Sampling design used to collect sediment cores from foraging structures and respective controls.

2.4. Statistical analyses

Multivariate analyses were performed on unstandardised and untransformed abundance data using PRIMER v.6.1.5 (Plymouth Routines in Multivariate Ecological Research; Clarke and Gorley 2006). Non-metric multidimensional scaling (MDS) ordinations, based on a resemblance matrix generated from Bray-Curtis similarities, were used to visually assess macrofaunal community structure among and between foraging structures and their respective controls. Thereafter PERMANOVA (permutational analysis of variance) and pairwise tests were used to determine whether there was a significant difference in community structure according to foraging type and control and if so, between which structures or controls these differences exist.

The DIVERSE function was utilised in order to obtain the total macrofaunal abundance (N), the total number of species (S) and species evenness (J') per structure type and respective control. Thereafter, SIMPER (similarity percentage analysis) was used to determine the average abundance of each species that contributes to at least 90% of the difference among and between foraging structures and their controls.

After employing Levene's and the Shapiro-Wilk test for normality and homogeneity of variance, univariate analyses were carried out using SPSS v. 21. Heteroscedastic data were square-root transformed to achieve equality of variance and the significance of statistical tests was assigned at the 5% level. T-tests for independent samples were carried out to ascertain whether significant differences occurred between structures and their respective controls with regards to sediment penetrability and diversity indices. When heteroscedastic data could not be transformed to meet parametric test assumptions, Mann-Whitney U-tests were carried out, as was the case when investigating macrofaunal response to structure-forming foraging and the controls at the class and species level.

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3. Results

3.1 Sediment penetrability

The sediment was significantly more penetrable in the pit structure than in its control (4.2cm ± 0.6 SD and 3.0cm ± 0.7 SD respectively, t =3.53, df =12, p<0.01) with the difference between them, excluding standard error, approximately two times the difference between the channel structure and its control (Figure 4). However, there was no significant difference in sediment penetrability between the channel structure and its respective control (4.0 ± 0.9 SD and 3.4 ± 0.4 SD respectively; t =1.61, df=8.145, p>0.05) or between pits and channels (t =0.50, df =12, p>0.05).

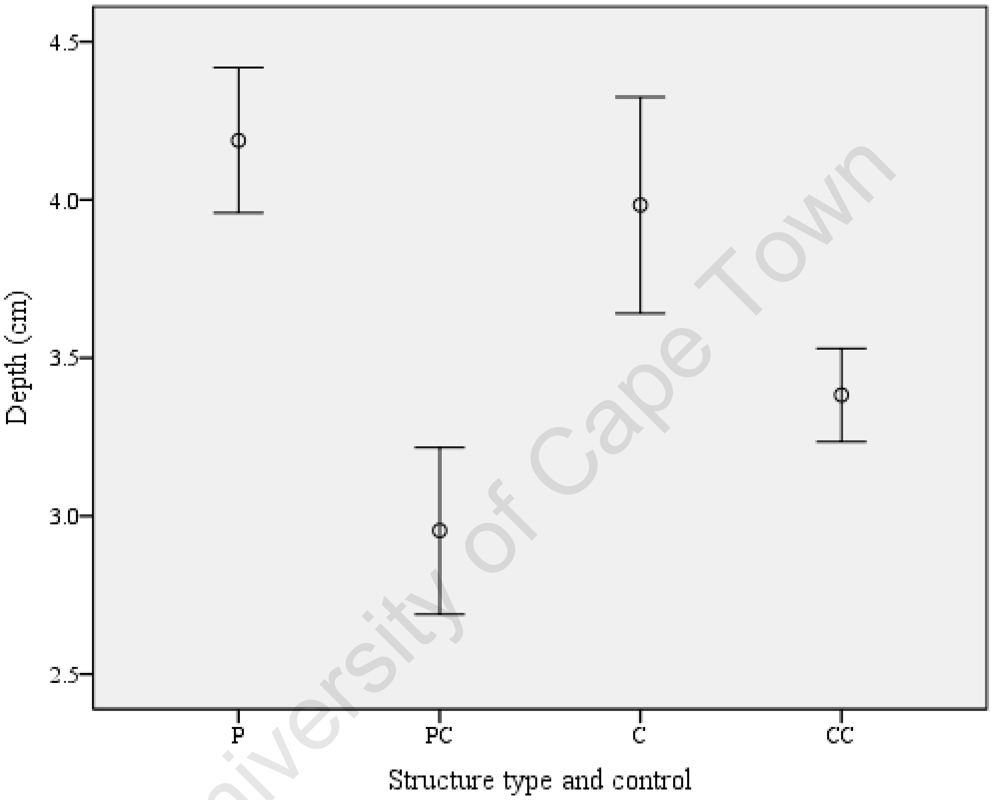

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Figure 4: Square-root transformed mean penetration depth per structure type and control, with error bars. Foraging structures include pits (P) and channels (C), with controls (PC and CC respectively).

3.2 Macrofauna

MDS ordinations visually demonstrate a separation in macrofaunal community structure between pits and their controls (Figure 5b; average similarity 33.7%) as well as between channels and their respective controls (Figure 5c; average similarity 45.3%). Overall, pit and channel controls overlap (Figure 5a; average similarity of 43.0% and 42.1% respectively), while channel foraging appears to produce a rather homogenous macrofaunal community structure, with an average similarity of 58.6%. In contrast, pit foraging seems to generate a rather heterogeneous macrofaunal community structure, with an average similarity of 34.5%.

Macrofaunal community structure was significantly influenced by foraging structure type (df_1 =3, df_2 =24, F =1.74, p=0.048). Community structure differed significantly between the pits and their controls (p=0.053) as well as between channels and their controls (p=0.046) but not between pits and channels (p>0.05).

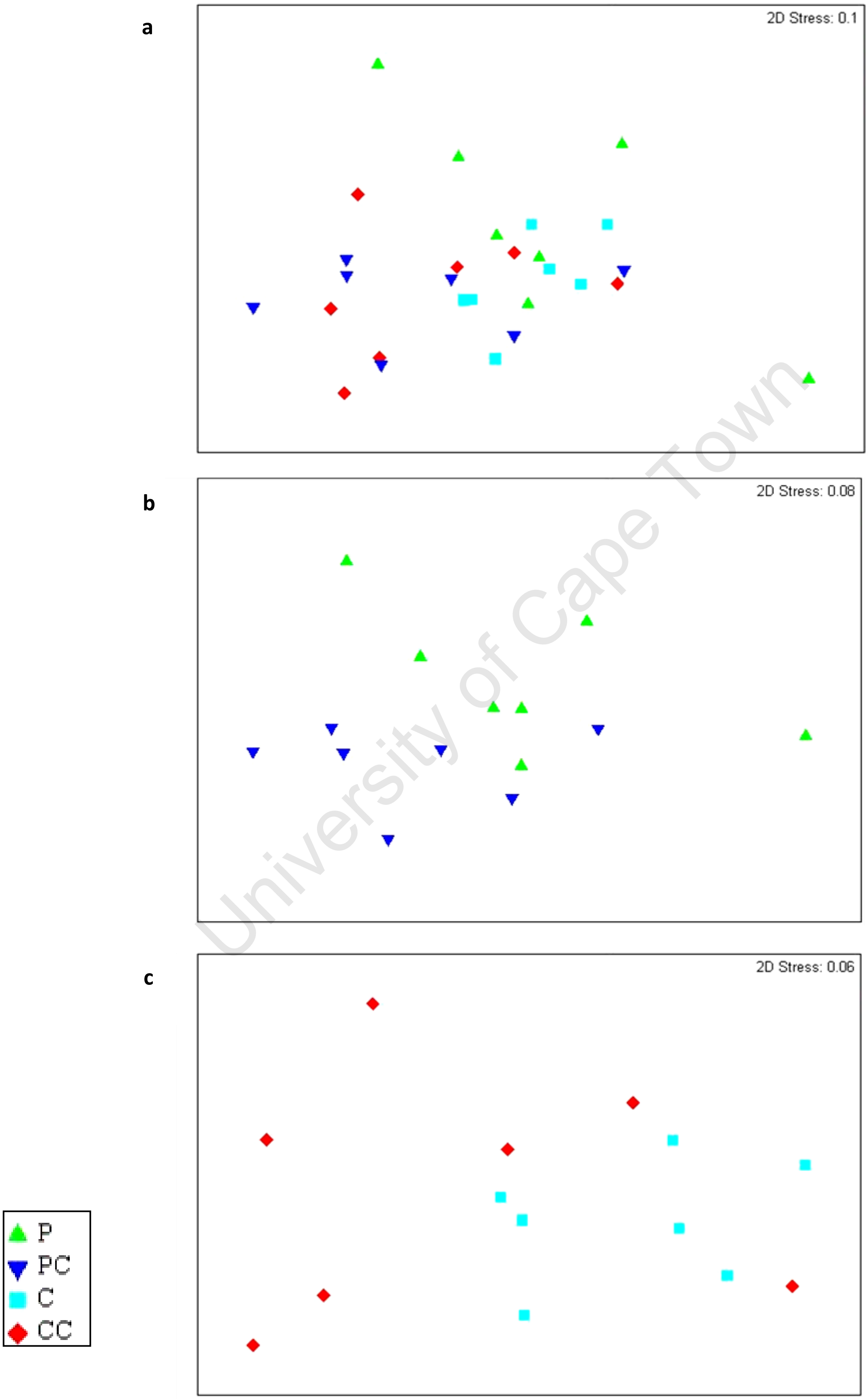

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Figure 5: Non-metric multidimensional scaling plots demonstrating macrofaunal community structure between (a) both foraging structure types and controls, (b) pits and their controls (c) channels and their controls.

Table 1: Results of independent samples t-tests regarding diversity indices, where n.s. = not significant. Foraging structures include pits (P) and channels (C), with controls (PC and CC respectively).

Structure type	Diversity index	Mean ± SD	t	df	p
P / PC	N	7.1±3.2 / 10.3±4.3	-1.64	12	n.s.
	S	10.7±5.3 / 12.9±5.1	-0.77	12	n.s.
	J’	0.8±0.1 / 0.6±0.2	2.13	12	n.s. (0.054)
C / CC	N	6.7±1.3 / 10.2±3.3	-2.59	7.97	0.024
	S	9.9±2.0 / 13.7±4.1	-2.26	12	0.043
	J’	0.7±0.1 / 0.6±0.2	0.97	12	n.s.
P / C	N	7.1±3.2 / 6.7±1.3	0.25	12	n.s.
	S	10.7±5.3 / 9.9±2.0	0.40	12	n.s.
	J’	0.8±0.1 / 0.7±0.1	0.67	12	n.s.

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Total macrofauna abundance and species richness was significantly higher in channel controls when compared to channels, but not between pits and their controls or pits and channels. Species evenness was higher in pits when compared to their controls, but was only marginally significant (Table 1).

Individuals of the classes Malacostraca, Bivalvia and Polychaeta appear to dominate this soft-sediment environment (Figure 6; Table 2). Both channel and pit foraging largely target the class Malacostraca, with pits having a significantly lower average number of individuals when compared to their controls (U=6.00, Z=-2.36, n_{pc}=7, n_p=7, p=0.017). Pits appear to remove more individuals from this class when compared to channels, but this is not significant (U=18.00, Z=-0.83, n_p=7, n_c=7, p>0.05), as is the difference in the removal of individuals in Malacostraca between channels and their controls (U=11.00, Z=-1.73, n_{cc}=7, n_c=7, p>0.05). Although insignificant, pit foraging seems to remove bivalves (U=23.00, Z=-0.19, n_{pc}=7, n_p=7, p>0.05), which is in contrast to the relatively similar bivalve abundance seen in channels and their controls (Table 2). Polychaetes are more abundant in pits than in their respective control, with channel foraging removing them from the environment, but both results are insignificant. On a smaller scale, both foraging methods enable the flamingo to remove copepods and nematodes, with more success when creating channels. Nematode average abundance experiences a marginally significantly decrease from channel controls to channels (U=9.00, Z=-2.21, n_{cc}=7, n_c=7, p=0.054), but the other results regarding nematode and copepod abundance between foraging structures and with their respective controls was insignificant. Few individuals of the class Oligochaeta and Ostracoda are obtained during pit and channel foraging respectively, but average abundances are not significantly different from their controls, or each other (Figure 6, Table 2).

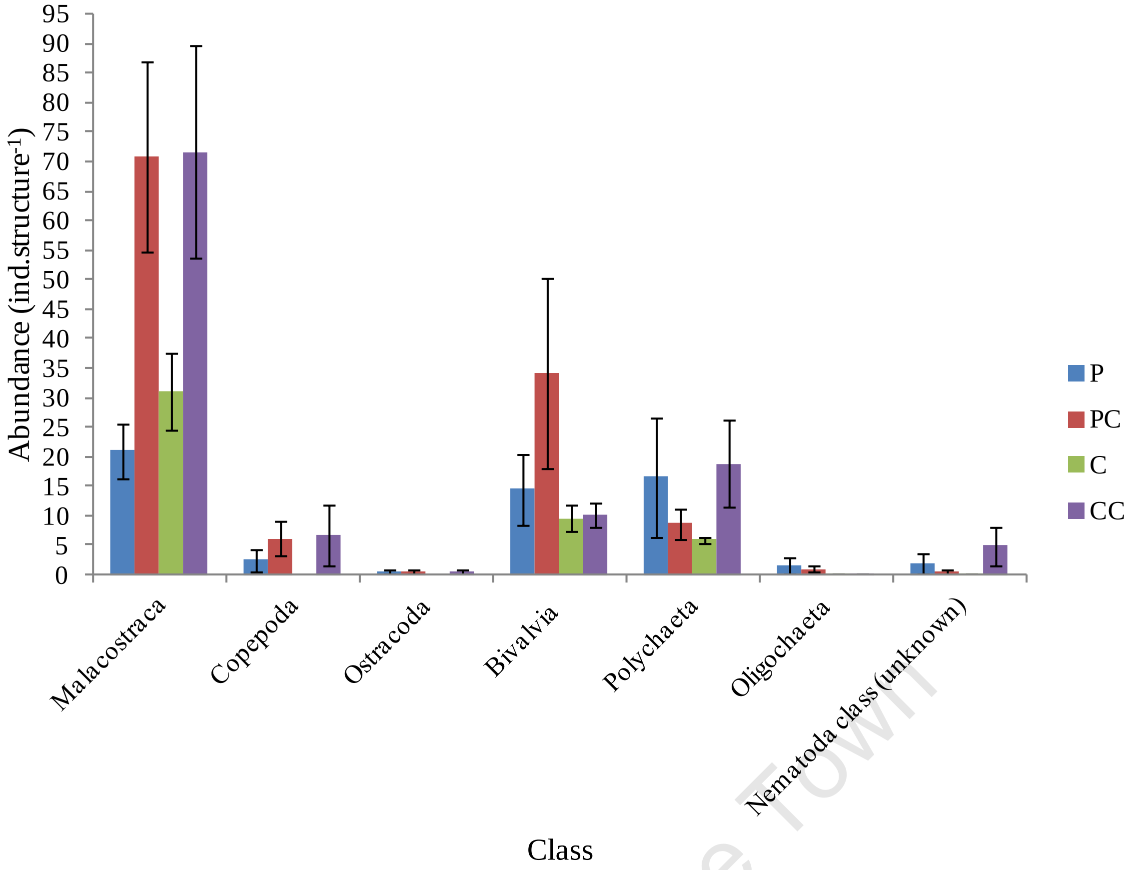

Figure 6: Average number of individuals per class according to structure type and respective control, with error bars. Foraging structures include pits (P) and channels (C), with controls (PC and CC respectively).

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Five species, specifically *Urothoe grimaldii* (Malacostraca), *Kellia rotunda*, *Carditella rugosa* (Bivalvia), cyclopoid copepods (Copepoda) and the unidentified worm species one (Polychaeta) contribute largely to the difference between pits and their controls (Figure 7; Table 3). Flamingos appear to specifically target *U. grimaldii*, with a significant decrease in average abundance after pit-forming foraging had occurred (U=4.00, Z=-2.62, n_{pc}=7, n_p=7, p=0.007). Bivalves and copepods, as well as the syllid spp. (Polychaeta), *Hymenosoma orbiculare* and *Paraphoxus oculatus* (both Malacostraca) are all removed to a lesser, non-significant extent (Table 3). However, *K. rotunda* does experience a three-fold non-significant decrease, excluding standard error, after pit foraging. Several species, predominantly members of the Polychaeta (*Notomastus latericeus*, *Marphysa elitueni*, unidentified worm species one) and Nematoda classes (oligochaete species, unidentified worm species two) with the exception of *Callichirus kraussi* and the eurydice species (both Malacostraca) show a non-significant increase in pit structures when compared to their controls. All these increases are slight, with the exception of the unidentified worm species one, which demonstrates a nine-fold increase, excluding standard error, in the pit structure.

Table 2: Results of Mann-Whitney U-tests regarding taxonomic class, where n.s. = not significant and n=7 per structure type and/or control. Foraging structures include pits (P) and channels (C), with controls (PC and CC respectively).

Class	Structure type comparison	Mean ± SD	U	Z	p
Malacostraca	PC/P	70.9±43.0 / 21.0±12.2	6.00	-2.36	0.017
	CC/C	71.7±47.4 / 31.0±17.1	11.00	-1.73	n.s.
	P/C	21.0±12.2 / 31.0±17.1	18.00	-0.83	n.s.
Copepoda	PC/P	6.1±7.5 / 2.4±5.2	17.00	-1.06	n.s.
	CC/C	6.7±13.8 / 0.0±0.0	14.00	-1.87	n.s.
	P/C	2.4±5.2 / 0.0±0.0	17.50	-1.47	n.s.
Ostracoda	PC/P	0.4±0.8 / 0.4±0.8	24.50	0.00	n.s.
	CC/C	0.4±1.1 / 0.0±0.0	21.00	-1.00	n.s.
	P/C	0.4±0.8 / 0.0±0.0	17.50	-1.47	n.s.
Bivalvia	PC/P	34.3±42.6 / 14.4±15.5	23.00	-0.19	n.s.
	CC/C	10.1±5.7 / 9.6±5.7	22.50	-0.26	n.s.
	P/C	14.4±15.5 / 9.6±5.7	22.00	-0.32	n.s.
Polychaeta	PC/P	8.7±6.7 / 16.6±26.7	23.50	-0.13	n.s.
	CC/C	18.9±19.2 / 5.9±1.2	13.50	-1.42	n.s.
	P/C	16.6±26.7 / 5.9±1.2	17.50	-0.90	n.s.
Oligochaeta	PC/P	1.0±1.5 / 1.6±3.7	21.50	-0.45	n.s.
	CC/C	0.1±0.4 / 0.1±0.4	24.50	0.00	n.s.
	P/C	1.6±3.7 / 0.1±0.4	20.5	-0.71	n.s.
Nematoda class (unknown)	PC/P	0.4±1.1 / 2.0±4.5	21.00	-0.62	n.s.
	CC/C	4.9±8.7 / 0.1±0.4	9.00	-2.21	n.s. (0.054)
	P/C	2.0±4.5 / 0.1±0.4	20.00	-0.80	n.s.

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Similarly, *U. grimaldii*, cyclopoid copepods and *K. rotunda* predominantly contribute to the difference between channels and their controls, but individuals in the class Polychaeta (syllid species) and Nematoda (unidentified worm species two) also play a role (Figure 8, Table 4). Although *U. grimaldii* is the main prey item removed via channel foraging and in similar quantities to pit foraging, this is not significant (U=11.00, Z=-1.73, n_{cc}=7, n_c=7, p>0.05).The syllid species (Polychaeta), unidentified worm species two and *N. latericeus* (Nematoda) significantly decrease after channel foraging has occurred (Table 4), while cyclopoid copepods, *H. orbiculare* and the unidentified worm species one are also removed to a lesser, non-significant extent. Both *C. kraussi* and *P. oculatus* (Malacostraca) demonstrated a non-significant increase when compared to the channel control, while *K. rotunda*, *C. rugosa* (Bivalves) and *M. elitueni* showed no real difference between channels and their controls.

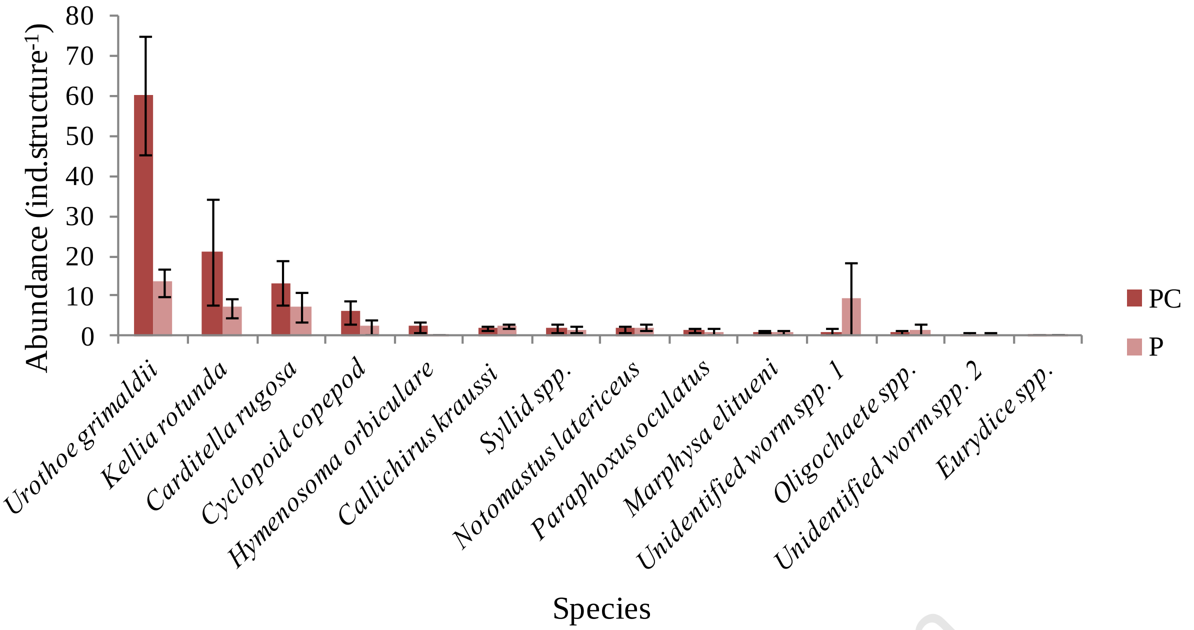

Figure 7: Average abundance of species, with error bars, that contributed to at least 90% of the difference between pits (P) and their controls (PC).

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Table 3: Results of Mann-Whitney U-tests regarding species that contributed to at least 90% of the difference between pits and their controls, where n.s. = not significant and n=7 per pit (P) and control (PC).

Species	**Taxonomic Class**	**Mean ± SD PC / P**	**U**	**Z**	**p**
Urothoe grimaldii	Malacostraca	60.3±39.2 / 13.6±9.2	4.00	-2.62	0.007
Kellia rotunda	Bivalvia	21.0±35.4 / 7.1±6.6	21.00	-0.45	n.s.
Carditella rugosa	Bivalvia	13.3±14.8 / 7.3±9.4	19.00	-0.70	n.s.
Cyclopoid copepod	Copepoda	6.1±7.5 / 2.4±5.2	17.00	-1.06	n.s.
Hymenosoma orbiculare	Malacostraca	2.4±3.2 / 0.1±0.4	12.00	-1.86	n.s.
Callichirus kraussi	Malacostraca	2.1±1.8 / 2.6±1.6	19.50	-0.67	n.s.
Syllid spp.	Polychaeta	2.0±2.8 / 1.7±2.2	23.50	-0.14	n.s.
Notomastus latericeus	Polychaeta	1.9±1.7 / 2.1±1.9	22.50	-0.26	n.s.
Paraphoxus oculatus	Malacostraca	1.7±1.3 / 1.1±1.9	15.50	-1.20	n.s.
Marphysa elitueni	Polychaeta	1.1±0.7 / 1.4±1.3	22.00	-0.33	n.s.
Unidentified worm spp.1	Polychaeta	1.1±2.0 / 9.4±24.5	24.50	0.00	n.s.
Oligochaete spp.	Nematoda class	1.0±1.5 / 1.6±3.7	21.50	-0.45	n.s.
Unidentified worm spp.2	Nematoda class	0.4±1.1 / 2.0±4.5	21.00	-0.62	n.s.
Eurydice spp.	Malacostraca	0.3±0.8 / 1.7±2.4	16.00	-1.36	n.s.

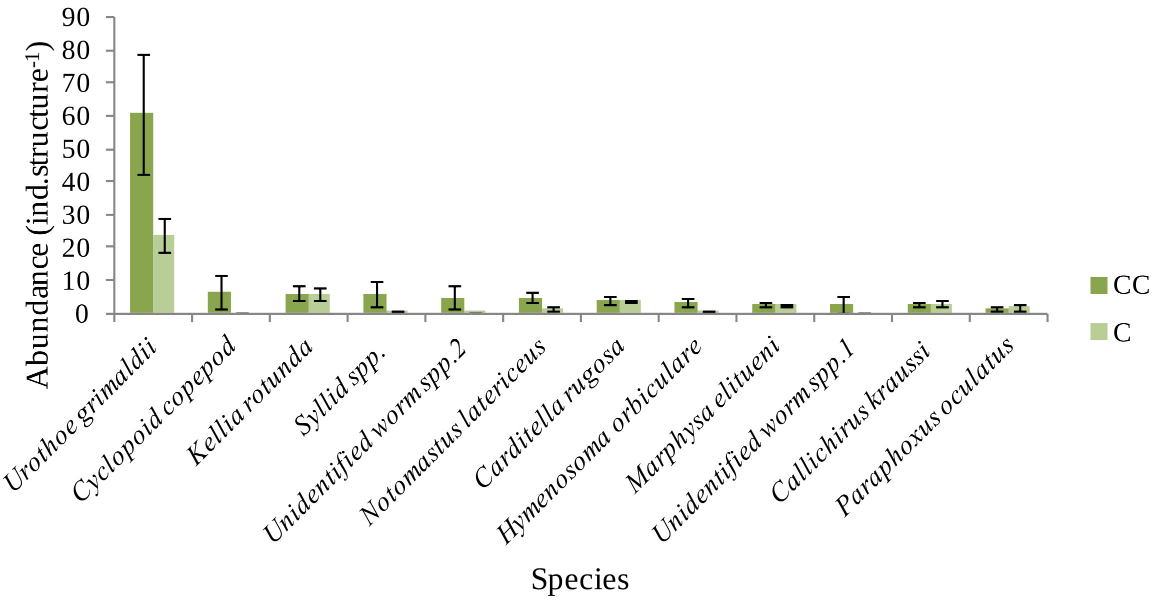

Figure 8: Average abundance of species, with error bars, that contributed to at least 90% of the difference between channels (C) and their controls (CC).

Table 4: Results of Mann-Whitney U-tests regarding species that contributed to at least 90% of the difference between channels and their controls, where n.s. = not significant and n=7 per channel (C) and control (CC).

Species	**Taxonomic Class**	**Mean ± SD CC / C**	**U**	**Z**	**p**
Urothoe grimaldii	Malacostraca	60.9±48.2 / 24.0±13.6	11.00	-1.73	n.s.
Cyclopoid copepod	Copepoda	6.7±13.8 / 0.0±0.0	14.00	-1.87	n.s.
Kellia rotunda	Bivalvia	6.1±5.4 / 5.9±4.6	23.00	-0.19	n.s.
Syllid spp.	Polychaeta	6.1±10.2 / 0.3±0.5	7.50	-2.32	0.040
Unidentified worm spp.2	Nematoda class	4.9±8.7 / 0.1±0.4	9.00	-2.21	n.s. (0.054)
Notomastus latericeus	Polychaeta	4.7±4.2 / 1.4±1.6	9.00	-2.12	0.041
Carditella rugosa	Bivalvia	4.0±3.3 / 3.7±1.4	20.00	-0.59	n.s.
Hymenosoma orbiculare	Malacostraca	3.3±3.5 / 0.6±0.8	12.50	-1.61	n.s.
Marphysa elitueni	Polychaeta	2.9±2.1 / 2.6±1.0	23.50	-0.13	n.s.
Unidentified worm spp.1	Polychaeta	2.9±7.1 / 0.0±0.0	17.50	-1.47	n.s.
Callichirus kraussi	Malacostraca	2.4±1.6 / 3.0±2.2	22.00	-0.35	n.s.
Paraphoxus oculatus	Malacostraca	1.4±1.3 / 2.0±2.4	23.50	-0.13	n.s.

Finally, the difference between pits and channels arises predominantly due to *U. grimaldii*, the unidentified worm species one and the two bivalve species (Figure 9, Table 5). Although there was no significant difference between pits and channels, the former appeared to remove more *U. grimaldii*, *M. elitueni*, *P. oculatus*, *O. angrapequensis* and euclymene species. On the other hand, channel foraging seemed to remove copepods and the bivalve and eurydice species, as well as several polychaetes (unidentified worm species one, *N. Latericeus*, syllid species) and nematodes (unidentified worm species two, oligochaete species). *C. kraussi* demonstrated a similar average abundance in both pits and channels.

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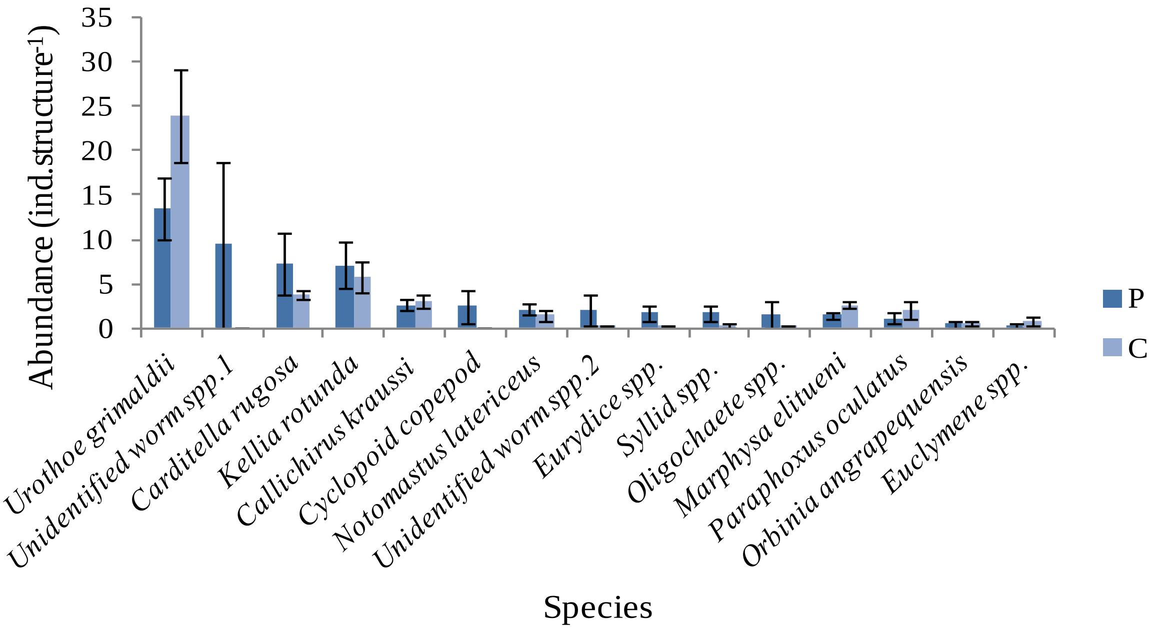

Figure 9: Average abundance of species, with error bars, that contributed to at least 90% of the difference between pits (P) and channels (C).

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Table 5: Results of Mann-Whitney U-tests regarding species that contributed to at least 90% of the difference between pits and channels, where n.s. = not significant and n=7 per pit (P) and channel (C).

Species	**Taxonomic Class**	**Mean ± SD P / C**	**U**	**Z**	**p**
Urothoe grimaldii	Malacostraca	13.6±9.2 / 24.0±13.6	16.00	-1.09	n.s.
Unidentified worm spp.1	Polychaeta	9.4±24.5/ 0.0±0.0	17.50	-1.47	n.s.
Carditella rugosa	Bivalvia	7.3±9.4 / 3.7±1.4	22.50	-0.26	n.s.
Kellia rotunda	Bivalvia	7.1±6.6 / 5.9±4.6	23.50	-0.13	n.s.
Callichirus kraussi	Malacostraca	2.6±1.6 / 3.0±2.2	24.00	-0.07	n.s.
Cyclopoid copepod	Copepoda	2.4±5.2 /0.0±0.0	17.50	-1.47	n.s.
Notomastus latericeus	Polychaeta	2.1±1.9 / 1.4±1.6	20.00	-0.61	n.s.
Unidentified worm spp.2	Nematoda class	2.0±4.5 / 0.1±0.4	20.00	-0.80	n.s.
Eurydice spp.	Malacostraca	1.7±2.4 / 0.1±0.4	16.00	-1.36	n.s.
Syllid spp.	Polychaeta	1.7±2.2 / 0.3±0.5	14.50	-1.42	n.s.
Oligochaete spp.	Nematoda class	1.6±3.7 / 0.1±0.4	20.50	-0.71	n.s.
Marphysa elitueni	Polychaeta	1.4±1.3 / 2.6±1.0	12.00	-1.65	n.s.
Paraphoxus oculatus	Malacostraca	1.1±1.9 / 2.0±2.4	17.50	-0.94	n.s.
Orbinia angrapequensis	Polychaeta	0.4±0.8 / 0.6±0.8	21.50	-0.45	n.s.
Euclymene spp.	Polychaeta	0.3±0.5 / 0.7±1.3	22.50	-0.32	n.s.

Discussion

By quantifying the difference in disturbance and macrofaunal community structure between the two foraging methods (pits and channels), this study was able to determine the impact of flamingos on macrofaunal communities in Langebaan Lagoon.

As expected, pit-forming foraging produces a significant disturbance when compared to its control, suggesting considerable energy input by the flamingo. On the other hand, channel sediment penetrability was not significantly different to its control, which could be due to a number of reasons. The channel-forming disturbance may just be very small and thus not different from a non-foraging area, or could be attributed to the large standard error observed in channel structure sediment penetrability (seen most clearly in untransformed data). This may have arisen due to variation in channel length that was seen in the field (as opposed to pits that exhibit a relatively consistent diameter) or even different rates of recovery of the two foraging structures. This is explained as follows: when channels are first formed they may be associated with a small, but significant disturbance when compared to their control, but the sediment 'recovers' faster than in pits due to the small size of the disturbance. It is even possible that flamingos may aid this channel compaction by trampling over these structures. They would not really be able to have the same effect on pits as they would probably avoid deep craters. This introduces a temporal 'recovery' component that was not taken into account.

Tentatively, this overlooked component could be suggested as a key idea explaining the results obtained. The study area consisted of numerous channels interspersed by large pits that had to be actively sought out. It could be possible that in this location, foraging structures recover over different time scales. When a pit is produced, considerable disturbance (as well as the shape of the structure) may inhibit both methods of flamingo foraging for a certain time period at that exact location as flamingos would probably be unable to make channel structures while walking backwards through a 'new' pit. Channels are not always straight (personal observation) and so the surrounding pit control may be fed on due to disturbance-related nutrient release and the associated attraction of macrofauna leading to the variability seen in the pit control. On the other hand, channels display a rather small disturbance and it is consequently suspected that these structures recover quickly, allowing the flamingo to revisit the exact location more often than is the case with pits, possibly leading to the lower variability seen in the channel control. In this case, the sediment would be reworked repeatedly, leading to homogeneity and could be a possible explanation of the slightly higher channel control sediment penetrability when compared to the pit control.

This theory is supported by the similarity values demonstrated between foraging structures and their respective controls. Channels share a higher percentage similarity with their respective controls and demonstrate a homogenous community structure, while pits have a lesser percentage similarity with their controls, suggesting a heterogeneous community structure. This would support the idea that channels often

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get reworked repeatedly, while pits remain somewhat disconnected from their controls and separated by distance as observed.

There was a significant difference in community structure when pits and channels were compared to their respective controls implying that flamingos do have an impact on macrofaunal communities as expected. Total macrofaunal abundance and species richness was significantly higher in channel controls, partially supporting the original hypothesis and the studies done by Glassom and Branch (1997) and Rodríguez-Pérez et al. (2007). This may be due to repetitive channelling causing a constant slight disturbance that releases nutrients into the surrounding control area encouraging macrofauna (Glassom and Branch 1997 found that organic content was higher in sediment worked by flamingos). On the other hand, these two diversity indices showed no significant difference between pits and their controls, which may be attributed to this method of foraging, with the considerable pit-forming foraging related disturbance negatively affecting its surroundings via sedimentation. Another further explanation could be that when pits are originally created, they release nutrients into the system, but only over a short time frame when compared to the repeated reworking and releasing of nutrients by channel foraging. It is important to note though, that Glassom and Branch (1997) found very similar diversity indices in their study across treatments. Finally, species evenness was greater in pits as expected. This could be attributed to the removal of *Urothoe grimaldii*, a dominant species in this system and/or recolonisation as described below.

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There was no significant difference in sediment penetrability, macrofaunal community structure, diversity indices or prey removal between the two foraging strategies, disproving the original hypothesis. Non-significant sediment penetrability differences may again be attributed to the reasons discussed previously. Community structure results suggest that both pits and channels have a similar impact on macrofaunal communities, but recolonisation may play a role, with opportunistic species that recolonise pit structures (discussed below) removing difference from the structures. Again, the homogeneity with regards to macrofaunal community in channels may be attributed to the re-working of the sediments. The heterogeneous community structure seen in pits could also be induced by bird size variability: birds of different sizes and weights could have an effect on the depth of the pit made (channel width should be similar as bill size is probably relatively consistent). This could also have arisen due to erroneous methodology with regards to core sampling, with variability being introduced as a core was taken from the centre of each pit, and two were taken from the outer edges.

Both channel and pit foraging largely target *Urothoe grimaldii*, a species in the class Malacostraca (probably due to their abundance), but only pits have a significantly lower average number of individuals when compared to their controls. Although non-significant, pits seem to remove more malacostracans, while possibly also targeting bivalves (predominantly *Kellia rotunda*). This could suggest a need for a greater abundance, or more energy rich food when pit-forming foraging is performed, probably due to the high energy expense associated with considerable disturbance. Channel foraging allows for the additional feeding of flamingos on polychaetes, and this method has greater success with regards to the removal of copepods and nematodes (as seen in Hurlbert and Chang (1983)). Polychaetes and nematodes were also seen to increase in pits when compared to their controls, acting as opportunistic colonisers of disturbed sediment. In both foraging structures, there was a slight non-significant increase of *Callichirus kraussi* as this species is too large to act as a prey item for flamingos. Although the majority of these results were insignificant, Kneib (1985) noted that it is often difficult to statistically detect changes in macrofaunal abundance. Glassom and Branch (1997) also found that the proportions of species hardly changed in their study.

With regards to flamingo choice of foraging activity at the study site, channels seemed to be preferred. It is suggested that in this particular location, flamingos periodically ‘test’ the environment to determine whether or not to use the more energy-intensive pit foraging, but often chose rather to create channels. Due to this, one has to wonder whether the two foraging methods can accurately be compared at a site where one is obviously preferred.

Limitations of this study could include the small area studied and the few samples taken which may have resulted in the data obtained being not enough to capture the variability of the system. Error may have also arisen with regards to species identification, especially when differentiating between juveniles and adults or working with undescribed species. Finally, no observational work was done and so the above theory rests on a large number of assumptions. As noted by Hulbert and Change (1983), the macrobenthic community may also be influenced by defecation, which was not considered. Finally, biomass and/or size class studies, which may have revealed further insight (Glassom and Branch 1997; Rodríguez-Pérez et al. 2007) into the impact that the foraging strategies have on macrofaunal communities were not carried out.

Even though this is a preliminary study, it has still provided a better understanding into the role of flamingos as predators and agents of biological disturbance in soft-sediment marine systems (Bildstein et al. 2000). However, extensive further research is needed. Studies need to be carried out to delineate the effects of predation and disturbance on macrofaunal community structure with regards to the two different foraging methods and the impact of flamingos in this system needs further study on larger temporal and spatial scales. Rodríguez-Pérez et al. (2007) note that the impact of flamingos is highly context dependent and largely influenced by bird density. Thus, the explanation that seems to fit in this study may be void in another system or even in a different area of Langebaan Lagoon. Therefore between system comparisons would also be useful.

In conclusion, pit and channel foraging are not as different as originally hypothesised. Both pit and channel foraging target the amphipod *Urothoe grimaldii*, but pit-forming structures enable the flamingo access to a

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higher quantity of this species in addition to bivalves, both of which are important with regards to the flamingo being able to offset the cost of higher energy input. The considerable disturbance caused enables the recolonisation of opportunistic polychaete and nematode species, both of which are important prey items accessed by the flamingo via channel foraging. These small-scale differences in recolonisation and prey-removal, as well as the spatial (and possibly temporal) variation in structures generate habitat complexity. Thus flamingo foraging activity does act as a driver of spatial heterogeneity in Langebaan Lagoon and possibly in every other system in which they occur.

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University of Cape Town

References

- **Brown**, C., & King, C. (Eds.). (2005). Flamingo husbandry guidelines. American Zoo and Aquarium Association. Silver Spring: Maryland.
- **Bildstein**, K. L., Baldassarre, G. A., & Arengo, F. (2000). Flamingo science: current status and future needs. Waterbirds, 206-211.
- **Compton**, J. S. (2001). Holocene sea-level fluctuations inferred from the evolution of depositional environments of the southern Langebaan Lagoon salt marsh, South Africa. The Holocene, 11(4), 395-405.
- **Clarke**, K.R., Gorley, R.N. (2006). PRIMER v6: User Manual/Tutorial. PRIMER-E, Plymouth.
- **Clark**, B. M., Orr, K.K., Hutchings, K., Steffani, N., Angel, A., & Turpie, J. (2009).State of the Bay 2008: Saldanha Bay and Langebaan Lagoon. Anchor Environmental.
- **Day**, J. H. (1959). The biology of Langebaan Lagoon: a study of the effect of shelter from wave action. Transactions of the Royal Society of South Africa,35(5), 475-547.
- **Dernie**, K. M., Kaiser, M. J., Richardson, E. A., & Warwick, R. M. (2003). Recovery of soft sediment communities and habitats following physical disturbance. Journal of Experimental Marine Biology and Ecology, 285, 415-434.
- **Ellis**, J. I., Norkko, A., & Thrush, S. F. (2000). Broad-scale disturbance of intertidal and shallow sublittoral soft-sediment habitats; effects on the benthic macrofauna. Journal of Aquatic Ecosystem Stress and Recovery, 7(1), 57-74.
- **Flemming**, B. W. (1977). Distribution of recent sediments in Saldanha Bay and Langebaan Lagoon. Transactions of the Royal Society of South Africa, 42(3-4), 317-340.
- **Flemming**, B. W. (1988). Process and pattern of sediment mixing in a microtidal coastal lagoon along the west coast of South Africa. In Tide-Influenced Sedimentary Environments and Facies (pp. 275-288). Springer: Netherlands.
- **Guillaume**, G., Nicolas, C., Patrick, G., Carole, N., Clémence, D., & Pierre, D. D. R. (2012). Expected and unexpected effects of waterbirds on Mediterranean aquatic plants. Aquatic Botany.
- **Glassom**, D., & Branch, G. M. (1997). Impact of predation by greater flamingos *Phoenicopterus ruber* on the macrofauna of two southern African lagoons.Marine Ecology Progress Series, 149(1), 1-12.
- **Hewitt**, J. E., Thrush, S. F., Halliday, J., & Duffy, C. (2005). The importance of small-scale habitat structure for maintaining beta diversity. Ecology, 86(6), 1619-1626.
- **Hurlbert**, S. H., & Chang, C. C. (1983). Ornitholimnology: effects of grazing by the Andean flamingo (*Phoenicoparrus andinus*). Proceedings of the National Academy of Sciences, 80(15), 4766-4769.
- **Jenkin**, P. M. (1957). The filter-feeding and food of flamingoes (Phoenicopteri).Philosophical Transactions of the Royal Society of London. Biological Sciences, 401-493.
- **Johnson**, R. G. (1970). Variations in diversity within benthic marine communities. American Naturalist, 285-300.
- **Johnson**, A. R. (1997). Long-term studies and conservation of Greater Flamingos in the Camargue and Mediterranean. Colonial Waterbirds, 306-315.
- **Kerwath**, S. E., Thorstad, E. B., Naesje, T. F., Cowley, P. D., Økland, F., Wilke, C., & Attwood, C. G. (2009). Crossing invisible boundaries: the effectiveness of the Langebaan Lagoon Marine Protected Area as a harvest refuge for a migratory fish species in South Africa. Conservation Biology, 23(3), 653-661.

University of Cape Town

- **Kneib**, R. T. (1985). Predation and disturbance by grass shrimp, *Palaemonetes pugio* Holthuis, in soft-substratum benthic invertebrate assemblages. Journal of Experimental Marine Biology and Ecology,93(1), 91-102.
- **Nel**, P., & Branch, G. M. (2013). Assessment of the abundance and distribution of burrowing sandprawns and mudprawns (*Callichirus* and *Upogebia* species) in Langebaan Lagoon, South Africa. African Journal of Marine Science, 1-14.
- **Pillay**, D., Branch, G. M., Griffiths, C. L., Williams, C., & Prinsloo, A. (2010). Ecosystem change in a South African marine reserve (1960-2009): role of seagrass loss and anthropogenic disturbance. Marine Ecology Progress Series,415, 35-48.
- **Pillay**, D., Branch, G. M., Dawson, J., & Henry, D. (2011). Contrasting effects of ecosystem engineering by the cordgrass *Spartina maritima* and the sandprawn *Callianassa kraussii* in a marine-dominated lagoon. Estuarine, Coastal and Shelf Science, 91(2), 169-176.
- **Probert**, P. K. (1984). Disturbance, sediment stability, and trophic structure of soft-bottom communities. Journal of Marine Research, 42(4), 893-921.
- **Reise**, K. (1985). Tidal flat ecology. An experimental approach to species interactions. Springer-Verlag.
- **Rodríguez-Pérez**, H., & Green, A. J. (2006). Waterbird impacts on widgeongrass *Ruppia maritima* in a Mediterranean wetland: comparing bird groups and seasonal effects. Oikos, 112(3), 525-534.
- **Rodríguez-Pérez**, H., Green, A. J., & Figuerola, J. (2007). Effects of greater flamingo *Phoenicopterus ruber* on macrophytes, chironomids and turbidity in natural marshes in Donana, SW Spain. Fundamental and Applied Limnology/Archiv für Hydrobiologie, 170(2), 167-175.
- **Schils**, T., De Clerck, O., Leliaert, F., Bolton, J. J., & Coppejans, E. (2001). The change in macroalgal assemblages through the Saldanha Bay/Langebaan Lagoon ecosystem (South Africa). Botanica Marina, 44(3), 295-305.
- **Thrush**, S. F. (1991). Spatial patterns in soft-bottom communities. Trends in Ecology & Evolution, 6(3), 75-79.
- **Tourenq**, C., Aulagnier, S., Durieux, L., Lek, S., Mesléard, F., Johnson, A., & Martin, J. L. (2001). Identifying rice fields at risk from damage by the greater flamingo. Journal of Applied Ecology, 38(1), 170-179.
- **Turner**, J. S. (2003). Trace fossils and extended organisms: a physiological perspective. Palaeogeography, Palaeoclimatology, Palaeoecology, 192(1), 15-31.
- **Vareschi**, E. (1978). The ecology of Lake Nakuru (Kenya). I. Abundance and feeding of the lesser flamingo. Oecologia, 11-35.
- **Wilson**, W. H. (1991). Competition and predation in marine soft-sediment communities. Annual Review of Ecology and Systematics, 21, 221-241.
- **Woodin**, S. A. (1981). Disturbance and community structure in a shallow water sand flat. Ecology, 1052-1066.

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