COMBINING ECOSYSTEM GREEN ENGINEERING AND EARLY LIFE HISTORY PROCESSES TO ENHANCE THE INTERTIDAL BIODIVERSITY IN THE PORT OF EAST LONDON, SOUTH AFRICA

A thesis submitted in fulfilment of the requirement for the degree of

MASTER OF SCIENCE

of

RHODES UNIVERSITY

by

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April 2020

ABSTRACT

Marine coastal ecosystems are highly impacted by anthropogenic activities, including the development of, and practices within, harbours and/or ports. Artificial structures associated with harbours have a different chemical composition, texture and orientation than that of the natural benthic habitats they have replaced, and are therefore not generally favourable for the settlement and occurrence of indigenous species. Attempts are being made to identify what structures and materials can be used to aid in the rehabilitation of native species within harbours. The aim of this study was to investigate the effects of utilising environmentally-friendly artificial structures (tiles) with varying complexity (crevices and ridges with different depths) with ecological engineers (the indigenous bivalve *Perna perna*), on the associated benthic biodiversity within an international port in South Africa (Port of East London). The objectives of the study were to test the effects of artificial habitat complexity and the presence of bivalves on 1) the growth, mortality and biomass of a selected model species of ecosystem engineer (*P. perna*), and 2) the associated intertidal biodiversity. Tiles seeded with bivalves (*P. perna*) were deployed at two sites in the Port of East London and monitored monthly over a period of 12 months (November 2016-October 2017) to assess survival, growth and associated biodiversity. Environmental variables were also measured every month. The results of the three-way repeated measures ANOVAs indicated that tile treatment (especially high complexity of 2.5 and 5 cm) had an effect on the diversity of mobile species, length, height and biomass of the bivalves used as model ecosystem engineer, indicating the potentials for protection from wave dislodgement and refuge provision. Treatment (especially flat tiles) also had an effect on sessile/sedentary species diversity, indicating the greater proportion of space provided by these non-complex tiles. In addition, month had an effect on the mortality, height and biomass of the bivalves. Mortality was highest in October 2017, while the growth in height and biomass of *P. perna* were largest in January and October 2017 respectively. The use of artificial tiles also had a positive effect on the survival, growth, and biomass of bivalves (especially the length, weight and dry weight in 2.5 cm and 5 cm complexity). Additionally, this research investigated patterns of settlement and recruitment of the local bivalve population (*P. perna*) in the Port of East London and adjacent natural coastline to understand the early life history temporal and spatial dynamics of this model ecosystem engineer species. Settlement and recruitment were assessed every month by deploying and replacing artificial collectors for a total period of 19 months (November 2016-May 2018). The results of the two-way ANOVAs indicated that month and site (port vs natural) had an effect on settlement and recruitment of bivalves. Settlement and recruitment of bivalves were highest in July 2017 (port) and March 2018 (natural rocky shore). This study has highlighted that the use of artificial concrete tiles with increased complexity, as well as the investigation of the early stages of mussel populations could be important to consider in a framework of rehabilitation of urban coastal environments such as the Port of East London. Ecological engineering (in terms of increased complexity and heterogeneity) has indeed the potentials to be incorporated in South African programmes aiming at improving natural biodiversity in coastal urban environments. Nonetheless, the spatio-temporal variability of early driver of mussel populations (settlement and recruitment) is also an important feature to be closely monitored if biodiversity in South African coastal armouring is to be enhanced effectively and in the long term.

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ACKNOWLEDGEMENTS

I would like to thank God for giving me the opportunity, strength and knowledge to do this work. I would like to thank the South African Institute for Aquatic Biodiversity for affording me the opportunity to use their facilities, expertise and funding together with the National Research Foundation to conduct this research. I would also like to express my gratitude to my supervisor Dr Francesca Porri for uncovering the potential that I never noticed I had, being patient with me and also for being the greatest supervisor. I would also like to give thanks to my co-supervisor Dr Paula Pattrick for her patience, advice and comments which made my work a success. Thank you to Transnet Port Terminals in the Port of East London and the Department of Environment, Forestry and Fisheries (previously known as the Department of Agriculture, Forestry and Fisheries) for granting me the permit to conduct research in the port. I also want to thank Nozuko Litile (Transnet National Ports Authority) for always being so willing to assist whenever I needed help in the port and also assisting with fieldwork whenever possible. I would like to thank Andre Bok for providing accommodation during this study. I would like to thank Garth Sampson from the South African Weather Service for assisting me with providing wind, air temperature and rain data for the region. I would also like to thank Christian Schulz, Leopold Fouquet, Gabriele Manzottu, Francesca Porri, Paula Pattrick, Siphelele Dyantyi, Olwethu Duna, Zizipho mnyaka, Aseeqah Davids, Sethu Mnqotho, Zinzi Somana, Zipho Canda, Tholoana Ntokoane, Nonkoliseko Mgibantaka, Asive Nyoka and Samantha Ockhuis for assisting with the fieldwork; without your help this project would have been impossible. I would like to thank Ferdy Jacobs for assisting with the driving and fieldwork. I thank Maditaba Maltaf and Sally Schramm for being patient with me in the use of the library and always coming to my rescue every time I was in need. I thank Mauricio Orostica for assisting me with the write up. I thank Lulama Makana for assisting me with the vehicle

and accommodation bookings during this study. Most importantly, to my mom, Fundiswa Tyekela, your support, words of wisdom, encouragement and your love have made me come this far and complete this degree.

1. GENERAL INTRODUCTION

Biodiversity encompasses the variety of all organisms living in both terrestrial and aquatic ecosystems (Spellerberg and Hardes, 1992; Noss and Cooperrider, 1994; Delong, 1996). Biodiversity involves taxonomic diversity which only accounts for species composition and abundance (Magurran, 1988) and functional diversity that accounts for the ecological traits of species responsible for ecosystem functions and the ecological complexes of which they are part (Diaz and Cabido, 2001). In light of the above definition, biodiversity in this study is considered to be the species composition and abundance in a particular area and their roles within that ecosystem (Wilson, 1988; McCann, 2007). Biodiversity has played a major role in mankind's existence through time, providing ethical, aesthetic, and ecological value (Gaston, 1996; Mutia, 2009). Ethical values emphasise the importance of all species in nature irrespective of their functional use to humans (Kassas, 2002; Mutia, 2009). Ecological values relate to the maintenance of the environment by factors that support species (Sayer *et al.,* 2004) such as the regulation of carbon emissions and nutrient cycling by seagrass and mangroves in marine systems (Gray, 1997; Duarte, 2000).

In the coastal realm, ecological values such as improved species diversity in rocky shores include the colonisation of these shores by sessile organisms, which may serve as a source of nutrients for mobile species as well as create habitats for other organisms. In addition, a greater diversity of sessile indigenous species reduces the survival and richness of invasive species (Sala and Knowlton, 2006; Stachowicz *et al.,* 2002; Stachowicz *et al*., 2007), as these organisms increase resistance to disturbance and biological invasion (Elton, 1958). Reduced biodiversity negatively affects ecosystem functions and services that provide for human well-being (Lubchenco, 1998; Boulton *et al*., 2008).

Ecosystem services are the processes whereby a natural ecosystem fulfils human needs while maintaining biodiversity and its functioning (Daily, 1997). Diverse ecosystems support functional and healthy environments, often facilitated by ecosystem engineers, aided by the provision of nursery habitats (e.g. seagrass; Heck *et al*., 2003; Kamermans *et al*., 2016) as well as the filtering of water and detoxification functions by suspension feeders such as bivalves (Worm *et al.,* 2006). Ecosystem engineers are organisms that modify, maintain or create habitats through their ability to self-design and/ or self-organise in order to protect other organisms from abiotic forces in order to increase species diversity (Jones *et al*., 1994; Jones *et al*., 1997; Jones *et al*., 2010; Watt and Scrosati 2013).

Although biodiversity changes with time (Margalef, 1963; Odum, 1969) and species do become extinct naturally as a result of natural physical disturbances such as storms (Connell and Slatyer, 1977; Sousa, 1979) increased anthropogenic activities due to coastal urbanisation have resulted in a rapid loss of biodiversity (Chapin III *et al.,* 2000) due to habitat loss (Gray 1997). Coastal urbanisation can result in habitat fragmentation (Fischer and Lindenmayer, 2007) and aid in more man-made structures that replace natural habitats worldwide being created in the marine environment (Connell and Glasby, 1999; Glasby and Connell, 1999). Habitat loss is regarded as one of the greatest threats to diversity globally especially in the marine environment where there are intense human activities (Sih *et al*., 2000; Moberg and Rönnbäck, 2003; Lotze, 2004; Knottnerus, 2005; Lotze *et al*., 2006; Valiela, 2006). Habitat loss involves a complete removal of the structural and functional space and its associated services

(Lotze *et al.* 2006). One of the main sources of habitat loss in the marine systems includes the conversion of coastal and intertidal habitats into hardened shorelines (Crain *et al*., 2009).

Human development at the coast, including harbours, marinas, seawalls and railway lines (Griffiths *et al.,* 2004), coupled with climate change related issues such as sea-level rise and stormier seas, has resulted in the development of coastal defence structures such as vertical seawalls within the intertidal zone (Borsje *et al.,* 2011; Nicholls *et al.,* 2015). While a natural intertidal zone can generally accommodate a high number of species and density of both plants and animals (Bertness *et al.,* 1999; Branch, 2001; Mouritsen and Poulin, 2002; Denny, 2007; Branch and Branch, 2018), coastal armouring, such as seawalls is featureless and lacks microhabitats, which results in a reduced native biodiversity (Chapman and Blockley, 2009). Coastal armouring substitutes the shoreline and reduce water filtration, ecosystem functions and connectivity among habitats (Airoldi and Beck, 2007).

The presence of artificial structures, such seawalls within harbours and ports is generally designed to reduce wave energy, water flow and shore erosion (Gedan *et al*., 2011; Cooke *et* al., 2012; Pires *et al*., 2013). Such alteration of the physical properties on the coastline though often favours the introduction of opportunistic and non-native species, reducing the diversity of native benthic organisms associated with rocky shores (Airoldi, 1998; Clark and Johnson, 2011). Within ports and harbours, the presence of artificial structures can also change the light availability, water flow and wave energy within the intertidal zone (Dugan *et al.,* 2011; Dafforn *et al.,* 2015Gaston *et al*., 2015, Davies *et al*., 2015). Altered lighting can increase the abundance of some species within a restricted zone (Depledge *et al.,* 2010; Becker *et al.,* 2012) as well as alter the dominance of macroalgal diversity (Dafforn *et al*., 2012).

'Blue growth' and 'blue economy' are recently introduced (or re-introduced) terms referring to the economic and innovative development of the ocean by using sustainable practices and preserving marine ecosystems from overexploitation and degradation (Eikeset *et al.,* 2018). In line with these principles, many countries are seeking ways to mitigate loss and protect and preserve marine biodiversity within urbanised coastal areas by investigating and inventing new environmental strategies (Chapman and Underwood, 2011; Mitsch, 2012; Steinberg *et al.,* 2016; Perkol-Finkel *et al.,* 2017). Countries such as Australia (Browne and Chapman, 2014), the USA (Toft *et al.,* 2013), Norway, UK and Ireland (Firth *et al.,* 2014a) have recently started testing new eco-friendly materials to be used in the construction of vertical seawalls for the improvement of biodiversity.

Disturbed coastal urban systems often require mitigation interventions to reverse them to their natural state and re-establish many lost important functions and services (Suding *et al.* 2004; Airoldi and beck, 2007) they provide such as nutrient cycling, food production, provision of habitat, disturbance regulation, natural barriers to erosion, control of water quality, and nursery grounds.

Ecological restoration has been used to mitigate the impact of anthropogenic disturbance while improving natural biodiversity (Young, 2000; Kardol and Wardle, 2010). Restoration, rehabilitation and reconciliation are major concepts that are often used in urban ecology

(Elliott et al. 2007; Abelson *et al*., 2016). Restoration is the process of restoring damaged or changed ecosystems to their original state (Bradshaw, 2002; Bird, 2005; Livingston, 2006; Andel and Aronson, 2012), while rehabilitation actions involve the replacement and improvement of structural and functional characteristics of a disturbed ecosystem which may/may not return to its original state (Aronson et al., 1993; Bradshaw, 2002; Mitsch and Jørgensen, 2004). Reconciliation ecology is the process where new habitats are created and maintained to conserve species diversity and to provide for human benefits (Rosenzweig, 2003; Mitch 2012). The term rehabilitation is the one that mostly encompasses the topic of this study and reference to it is made to contextualise this research.

Terrestrial environments have generally received more attention in the ecological frame of restoration, rehabilitation, reconciliation due to world-wide efforts to counteract deforestation (Young, 2000). Some examples of rehabilitation programmes of natural forests aim to improve carbon sequestration, reduce pollution, regulate runoff and increase wildlife diversity (Twilley *et al*., 1998). In the coastal environment, examples of rehabilitation programmes include the use of oysters to increase water quality and reduce eutrophication (Newell, 2004; Pomeroy *et al*., 2006; Coen, 2007; Fulford *et al.,* 2010) and the use of alternative structures (Chapman, 2003; Chapman and Blockley, 2009; Firth *et al*., 2016) through green engineering (Chapman and Underwood, 2011; Strain *et al.,* 2018) to increase benthic marine biodiversity.

Ecological engineering has been re-defined as the designing and construction of artificial structures that not only accommodate the needs of human society, but the natural environment too (Schulze 1996, Bergen *et al*. 2001, Mitsch 2012). This scope is achieved by operating on systems disturbed by human activities and developing new manageable eco-networks that preserve ecological and human values (Mitsch 1993). Structurally, ecological engineering can be identified as "soft (hybrid)" or "hard", with the "soft" approach involving complete removal of existing structures, while the "hard" approach involves restoring existing artificial walls which cannot be removed (Russell *et al.* 1983). These structures aid in the rehabilitation of ecosystem functions and services (Beatley, 2011; Francis and Lorimer, 2011) as human-made marine infrastructures that are similar to that of adjacent natural rocky shores can provide a unique habitat to support ecological communities (McKinney, 2006). These infrastructures can support an increased diversity of filter-feeders (e.g., oysters) that can help improve water quality (Rivero *et al.,* 2013). Enhanced diversity and biomass of filter-feeders supported by artificial structures can further assist in carbon storage (Dehon, 2010).

Environmental parameters, such as salinity, dissolved oxygen, temperature, turbidity and current speed can all differ between artificial and natural habitats (Cavraro *et al.,* 2003; Mizutani *et al*., 2000). Wave action and dissolved oxygen are reduced, while salinity, temperature and turbidity generally increase in harbours, due to the large man-made structures that surround a body of coastal water, creating a physical barrier to the adjacent outside environment (Bulleri and Chapman, 2010; Dafforn *et al.,* 2015). Reduced wave action by the surrounding artificial structures generally results in a decrease of water mixing within a harbour, creating stressful conditions for organisms (Dafforn, 2015) as the limited flow leads to decreased oxygen concentrations in the water column, and the nutrient influx from the nearby rivers into the port can cause eutrophication (Xu *et al*., 2010).

This thesis specifically aims to explore the use of green engineering to enhance intertidal biodiversity in a port, conducting two experimental studies. First, the study was conducted in a harbour using engineered structures, presenting increased spatial complexity and ecosystem engineers (organisms that create favourable habitats for other organisms; Jones *et al*., 1994), to provide more suitable habitats for benthic intertidal organisms to improve overall biodiversity. Secondly, the study investigated the spatio-temporal patterns of bivalve settlement/recruitment in both natural and artificial habitats to shed light on the early drivers of population dynamics of the ecosystem engineers chosen for this study. The ultimate goal of this research was to contribute towards the understanding of the role of of spatial complexity and heterogeneity in ecological engineering in enhancing marine biodiversity in South African harbours, and to provide information useful to urban planners and restoration ecologists working on the preservation of natural biodiversity in anthropogenised coastal systems.

This thesis consists of four chapters. Chapter 1 is an overall general introduction defining marine biodiversity and discussing its loss due to human coastal development and the potential application of ecological engineering for coastal rehabilitation. Chapter 2 focuses on the use of artificial complex structures in combination with ecosystem engineers, to improve intertidal biodiversity. Chapter 3 compares the spatial and temporal patterns of the settlement and recruitment of bivalves between natural rocky shores and man-made structures within a harbour to estimate and understand the early dynamics of adult mussel populations. Chapter 4 discusses the main results of this study, putting them in a context for the potential application of artificial structures (green engineering) in developed urbanised coastal areas in South Africa for the rehabilitation of intertidal biodiversity.

2. THE EFFECTS OF ECOLOGICAL ENGINEERING ON THE INTERTIDAL BIODIVERSITY IN THE PORT OF EAST LONDON

2.1. Introduction

The growth in the human population, which is estimated to reach 10 billion by 2050 (Lutz and Samir, 2010, Bloom, 2011), has resulted in the increase of manufactured goods and services which causes the need for not only larger, but more harbours for the transportation of such goods (Creel, 2003). With more than 27 000 harbours worldwide, coastal development is only expected to further increase (Airoldi and Beck 2007; Bulleri and Chapman, 2010). Urbanisation and coastal development will ultimately result in the acceleration of issues related to shoreline degradation as ports and harbours and other conglomerates of infrastructures replace natural habitats (Bulleri and Chapman, 2010; Aguilera *et al*., 2018).

In the intertidal zone, artificial structures are built in place of the natural habitat in order to prevent damage to nearshore developments, to prevent soil erosion in harbours, and for the development of aquaculture activities (Gilbert *et al*., 1997; Bulleri and Chapman, 2004; Chapman and Underwood, 2011). These structures replace the natural substrate completely and thereby disrupt intertidal biodiversity (Chapman and Underwood, 2011; Strain *et al.,* 2018). Microhabitats that provide refuge for mobile species from predation and desiccation are therefore absent on artificial structures (Chapman, 2003; Chapman and Bulleri, 2003; Firth *et al.,* 2013), resulting in both reduced diversity and abundance of species (Chapman, 2003, 2006), and often an increased abundance of alien species (Bulleri and Airoldi, 2005; Moreira *et al*., 2007; Firth *et al.,* 2011; Firth *et al.,* 2016). Artificial structures such as seawalls along the coastline are known to alter the distribution and assemblages of native marine fauna and flora by providing habitat consisting of hard, non-complex substrates which seem to facilitate invasive opportunistic species not present prior to the urban development (Glasby and Connell, 1999; Glasby *et al.,* 2007; Chapman and Blockley, 2009).

Artificial structures generally have steep sides, reducing the amount of available surface area within the intertidal zone, and influencing species distribution at small spatial scales (Gabrielle *et al.,* 1999). These steep sides result in an increase in water movement causing dislodgment of organisms, as well as accelerating water runoff during low tide, promoting desiccation (Hayward, 1971). The surface texture of man-made structures also differs from that of natural rocks. These surfaces are smooth and therefore reduce the chances of attachment of native organisms to the substrate, further contributing to the loss of habitat for local species (Chapman, 2003; Chapman and Bulleri, 2003).

Harbours and marinas are heavily influenced by human activity and are more often subjected to transformed conditions than natural adjacent coastal systems. An example of such alteration is the increase or decrease in freshwater flow facilitated by storm water piping systems which drain into harbours and can be unfavourable for marine life, compounded by the related increased pollution that often result in harmful algal blooms (Bax *et al*., 2003). The benthic sediments and nutrients in harbours are often disturbed repeatedly and this contaminates the water column (Nilsson *et al.,* 2005). Vertical structures such as seawalls within harbours have a negative impact on local biodiversity due to a suite of altered and often detrimental physical and biological factors (light alteration, wave action and increased presence of alien species) (Glasby and Connell, 2001; Bulleri and Airoldi, 2005; Farrell and Fletcher, 2006; Marchini *et al.,* 2007). In the marine environment, the presence of artificial structures affect primary production through by altering light, also water quality and nutrient cycling are affected due because of reduced wave action (Dugan, 2018).

The biodiversity of urban coastal areas can, however, be enhanced by using specific technologies and materials to replace traditional human-made structures (Firth et al., 2012; Aguilera *et al*., 2014; Perkol-Finkel and Sella, 2015; Ido and Shimrit, 2015; *Evans et al*., 2016) These technologies can improve habitat complexity (Gilinsky, 1984; Telleria and Carrascal, 1994; Hull, 1997; William *et al.,* 2002) by providing pits, grooves, crevices, and pools on surfaces, which are important to increase the structural heterogeneity typical of rocky shore systems (McGuinness and Underwood, 1986; Astles, 1993; Benedetti-Cecchi and Cinelli, 1995).

Intertidal heterogeneity and complexity facilitate recruitment (Strain *et al.,* 2017) and growth of species which occupy such habitats, and also reduce predator-driven mortality, leading to a general increase in biodiversity (Chapman and Underwood, 1994; Johnson, 2007). Structural complexity is defined as the physical constructing of a rough surface made of different structures such as crevices and holes (McCoy and Bell, 1991). Structural complexity, serves as a booster of biodiversity (Huston, 1979; Pianka, 2000) and ecologists have often considered this to be an important factor in environmental management (Hobbs and Huenneke, 1992) as well as in the mitigation and rehabilitation of biodiversity (Matias *et al*., 2010; Kovalenko *et al.,* 2012). The absence of protective microhabitats on man-made structures can, nevertheless be recreated by artificially developing ‘flowerpots’ and artificial water-retaining features on blocks (rock pools) (Chapman and Blockley, 2009; Firth *et al.,* 2013, 2014), tiles with added complexity (ridges and crevices) (Strain *et al.,* 2017) and seawall stairs (Dyson and Yocom, 2015).

Following from this, mussels are considered ecosystem engineers (Jones *et al*., 1997; Arribas *et al.,* 2014) because they create interstitial spaces for other associated species to hide from predation and physical stress such as desiccation and waves (Borthagaray and Carranza, 2007; Ward and Ricciardi, 2010; Arribas *et al.,* 2014). Marine mussels are sedentary bivalves which occur on many natural and artificial coastal hard substrates where they form large beds (Vakily, 1989; Ysebaert *et al*., 2009). Mussels stay attached by means of byssal threads to a large variety of man-made vertical substrata, such as piers, pipes, buoys, harbour seawalls (Tsuchiya, 2002) and even building rubble (Vakily, 1989) where their beds can increase local biodiversity by creating unique habitats for associated species (Palomo *et al.,* 2007; Arribas *et al.,* 2014). Because of the general ease (on natural and anthropogenised systems) in which mussels can favour dense and diverse invertebrate assemblages and additional service provided of improved water quality (Wilkie *et al.,* 2013), there is a growing interest in enhancing and rehabilitating ecosystems in urban coastal areas using bivalves (Gillies *et al*., 2018; Strain *et al.,* 2018). Their biological features make mussels an ideal model species to test how they can improve biodiversity in harbours, especially when in conjunction with material and structural engineering.

Intertidal mussel species are exposed to increased predation and competition pressure (Jackson, 2009; Martins *et al*., 2010) on vertical seawalls due to the absence of microhabitat heterogeneity which act as refuges (Bulleri and Chapman, 2010; Bishop *et al*., 2017). By constructing artificial microhabitats on seawalls however, competition and mortality can be reduced (Bulleri and Chapman, 2010; Bishop *et al.,* 2017), favouring the growth and survival of mussels (Strain *et al.,* 2018). Reduced mortality results in increased growth due to the direct positive correlation between growth and survival of mussels, with large individuals having a better chance of survival due to their enhanced byssal attachment strength (Bayne and Worrall, 1980). Decreased mortality of large adults (Leeb, 1995; Tomalin, 1995) further positively increases density (McQuaid and Lindsay, 2000), biomass and associated biodiversity (Dornelas, 2010).

This study forms part of the World Harbour Project (WHP), a global project aiming to enhance coastal biodiversity using a combination of natural and artificial ecological engineering to add structural complexity to otherwise flat seawalls (Steinberg *et al.,* 2016; Strain *et al.,* 2019). The WHP operates in 17 countries with the aim of developing productive global ports and harbours which service both mankind and the environment. The project also aims to assist research platforms through the innovation of shared values and threats in international harbours around the world using a network of collaborating scientists, to address the issues of ecosystem functioning of ports and harbours (Steinberg *et al.,* 2016).

In this study, the effects of engineered structures presenting different levels of complexity on associated benthic biodiversity of seawalls were investigated in the Port of East London, South Africa (though mistakenly listed in the official WHP map as Port Elizabeth). Specifically, the effects of complexity on the survival, growth and biomass of the seeded mussels and the biodiversity associated with the seeded indigenous brown mussel (*Perna perna*) were assessed. Adults of *Perna perna* (being an ecosystem engineer; Borthagaray and Carranza, 2007; Ward and Ricciardi, 2010; Arribas *et al.,* 2014) that are seeded onto artificial structures (tiles in the present study) could potentially attract other organisms by providing moisture, shelter and protection and therefore could instigate a greater overall benthic species diversity. On flat tiles with no complexity, *P. perna* could be exposed to both wave action, desiccation and predation and could, therefore, have a high probability of being dislodged by the waves and/or being threatened by predators. These circumstances may also affect the growth rate of mussels, thereby reducing mussel biomass and overall associated biodiversity. This study was therefore based on the following hypotheses:

1. Associated biodiversity and richness would be greater on complex tiles seeded with *P. perna* due to the increase structural complexity and heterogeneity, especially in summer/spring, when there is high primary productivity.
2. Growth and biomass of *P. perna,* would be greater on complex tiles. The complexity effect would be especially evident in summer/spring, when most mussels are expected to increase growth.
3. The mortality of *P. perna* would be greater on flat tiles with no complexity due to increase potential of dislodgement, especially in winter, when wave action is maximal.
4. The tiles (non-complex) deployed would favour an increase of native rather than invasive species, due to the urban setting.

2.2 Methodology

2.2.1 Study area

This study was conducted at two duplicated sites within the Port of East London (33˚ 01’ 26’’ S, 27˚ 54’ 50’’E), on the south east coast of South Africa (Figure 2.1). This port, formerly known as Port Rex, was established at the mouth of the Buffalo River in 1848 due to the presence of a military fort (Gordon, 1932) and it is currently the only river port in South Africa. Towards the turn of the 18th century, the port became an international link for South Africa and other countries (Gordon, 1932). Today this port is owned by the National Ports Authority (NPA) of South Africa and is one of seven commercial harbours in South Africa. In the Port of East London, the Buffalo River waste waters cause an increased nutrient availability in the harbour (Fatoki and Mathabatha, 2001; Helson and Gardner, 2004; Humphreys, 2005).

East London is on the south coast, is a warm temperate region (Emanuel *et al*., 1992) and the dominant mussel species is an indigenous warm-water *P. perna* which is threatened by invasive cooler mussel *M. galloprovincialis* (van Erkom Schurink and Griffiths, 1990). *M. galloprovincialis* is found in lower density on the far east of the Port of East London and is a stronger competitor in the indigenous mussel *P. perna* (van Erkom Schurink and Griffiths, 1990; Hockey and van Erkom Schurink, 1992; Branch and Steffani 2004). These two mussels compete for space in the intertidal zone with *P. perna* domination the low shore, *M. galloprovincialis* the high shore and they co-exist intertidally (Bownes and McQuaid, 2010).

Figure 2. 1: Map of South Africa showing the sampling site (black circle in the insert map) of the Port of East London located on the south east coast of South Africa. Sampling sites (stars) are located on the East and West banks of the Buffalo River (triangle) within the Port of East London and also two locations (1 and 2) within the Wintertrand natural rocky shores. The white circle on the satellite map represents the natural rocky shore habitat where mussels for this study were collected.

2.2.2 Sampling and data collection

The study was set up in October 2016 (month 0), with monthly sampling of mussel mortality, growth and associated biodiversity beginning in November 2016 (month 1), and was completed by October 2017 (month 12). Monthly sampling was carried out at both sides (East bank 33° 01′ 23.1′′ S 27° 54′ 08.0′′ E; West bank 33° 01′ 32.3′′ S 27° 54′ 19.0′′ E) of the Buffalo River, close to the mouth region of the Port of East London (Figure 2.1). On each site (~400 m apart), sampling was conducted within the low intertidal zone, which was comprised of building rubble, and consisted of concrete and brick sections (Figure 2.2). Each site presented an established population of the native brown mussel, *Perna perna* (Family: Mytilidae).

Figure 2. 2: The two sites in the port of East London used for tile attachment.

Artificial tiles (25 x 25 cm) were used as experimental units to mimic vertical seawalls for this study. The tiles were manufactured from hard wearing concrete made by the Reef Design Lab in Sydney, Australia. Three main structural complexities (flat, 2.5 cm ridged and 5 cm ridged (crevice and ledge) tiles) were used to investigate the effects of micro-complexity on biodiversity. Adults (~35mm in height) of the indigenous mussel *Perna perna* were collected (2500 individuals) from Kayser's Beach (33° 12' 31.9" S 27° 36' 50.1" E), close (<50 km) to the Port of East London (Figure 2.1). After collection, mussels were cleaned by scraping off all epibionts on their shell using a 28 mm chisel. Mussels were then attached on the tiles in groups of 4-5 individuals using Splash Zone underwater 2-part epoxy (A-788). The number of mussels seeded/attached on each tile corresponded to a cover of ~35% of the tile surface. Tiles with ridges (2.5 cm and 5 cm) had mussels equally distributed on both the bottom of the crevices and the top of the ridges (Figure 2.3). At each site, 30 tiles were placed which included fifteen (5 x flat; 5 x 2.5 cm; and 5 x 5 cm tiles) with mussels attached (seeded) and fifteen (5 x flat; 5 x 2.5 cm and 5 x 5 cm tiles) with no mussels attached (unseeded). In addition, at each site, five control areas were created on the rocks as 30 x 30 cm quadrats cleared of all biota.

Figure 2. 3: Assortment of mussels attached on crevices and ledges of tiles. Starting from left, a flat tile, 2.5 cm ridged tile and 5 cm ridged tile.

For tile placement at two duplicate sites, 30 selected areas (30 x 30 cm) in the intertidal zone on the seawall were cleared of any living organism using chisels, metal brushes and tile scrapers, in order to avoid edge effects (Fletcher *et al.,* 2007) and to assist with the attachment of the tile to an even vertical surface. The cleared areas for tile attachment were at least 3 m apart. The location of tile deployment followed a pre-random assignment of tiles. A Hilti TE 6-A36 drill, with an 8 mm masonry SDS drill bit, was used to drill a hole in each corner of the 25 x 25 cm tiles so as to secure onto the vertical walls. Tiles were fastened to the substrate with 8 x 65 mm stainless steel dynabolts and 8 mm nylon washers.

To determine the average size and biomass at month 0 of the once-off collected mussels used to prepare the seeded treatments, a subset of 180 individuals were randomly selected and their maximal length (from umbo to opposite tip of the shell) measured to the nearest 0.01 mm. Mussels were then cut open to separate soft tissue from the shell (Figure 2.4) to measure biomass. The shell and soft tissue were dried in a Memmert UN30 oven at 60°C for 24 hours and then weighed using a PGL 303 weighing balance. The same procedure was followed at the end of the study, upon retrieval of all seeded tiles (see details below) to determine the biomass of mussels at the end of the experiment (month 12). This procedure was also performed in month 12 for any other organisms (dry weight) which had settled on the seeded and unseeded tiles. As these mussels were collected outside the port, a pre-random assignment allocation to site and treatment, in which tile details (soft tissue and dry shell with the site, treatment and time) were uploaded and automatically randomised.

Figure 2. 4: Shell (on the right) and soft tissue (on the left) of a dissected mussel, placed on pre-weighed aluminium foil which was then dried in the oven.

Gross estimates of water motion on each site was monitored monthly, over a 24-hour period, using clod cards fabricated according to Doty (1971). A mixture of 500 g of plaster of Paris and 450 ml water was made at room temperature to obtain a homogenous, semi-liquid paste. The mixture was then poured into an ice cube tray (12 cubes) with a plastic straw inserted into the middle of each cube to create a hole which would allow a screw (8 mm stainless steel) to be inserted over a washer and fastened onto the rock (Figure 2.5).

Figure 2. 5: Clod card fastened to the rock, used to quantify water motion over a 24-hour period.

The plaster of Paris mixture was allowed to dry, removed from the tray and then placed in an oven at 60°C for 24 hours. Each dry clod card was weighed prior to deployment. Three clod cards were placed in line with the first, middle and last tile on each site for a period of 24 hours. After 24 hours, the clod cards were removed by loosening the screws, individually placed into a zip lock bag (labelled according to the place where clod card was originally deployed) and transported to the South African Institute for Aquatic Biodiversity (SAIAB) laboratory in Grahamstown, South Africa (33°18ˈ37.1ˈˈS 26°31ˈ11.1ˈˈE). Once back in the laboratory, clod cards were dried in an oven at 60°C for 24 hours and weighed again. Relative water motion was determined by calculating the difference in weight prior to, and after deployment.

Turbidity (NTU), salinity, pH and dissolved oxygen (mg/L) were monitored once, every month over the 12-month period, using a Sea-Bird Electronics (SBE 19 plus V2) conductivity temperature depth (CTD) profiler. At two positions on each site (the most upstream and the most downstream), the CTD was placed in the water column at a depth of 1.5 m and kept there for at least 10 minutes. Data were downloaded from the CTD on return from the field, using the SBE software. Additionally, water temperature (°C) was measured monthly, using iButton thermal loggers (Figure 2.5). These loggers, once set using the iButton Cold Chain Thermodynamics software (Fairbridge Technologies, 4.9), provided real time integrated *in situ* measurements of temperature. The iButtons were waterproofed by individually casing them with perfomix PLAST DIP Junior, to ensure that while deployed in the water for a period of one month, data would not be compromised. At each site, three iButtons were secured onto the rocks using cable ties and eye bolts (8 mm) (Figure 2.6). The iButtons were retrieved and replaced every month when datum was downloaded and the logger re-set.

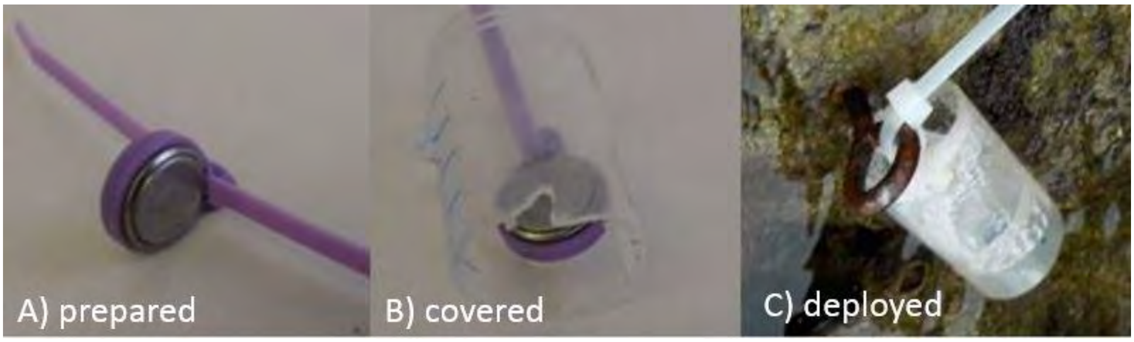

Figure 2. 6: iButton (used to monitor temperature) during setting and deployment in the field.

After the tiles were deployed in October 2016 (Month 0), the survival, growth and position (either in ridge or crevice) of seeded mussels were recorded monthly, for a period of one year. The morphology of a mussel is largely described by the shell length (maximum dorso-ventral axis), width (maximum lateral axis) and height (maximum anterior-posterior axis) (Seed, 1968). Monthly growth was established by measuring the difference in length, width and height (Figure 2.7) of each seeded mussel among measurements taken over two consecutive months, (e.g size month 2 - size month 1)/2 (King, 2007).

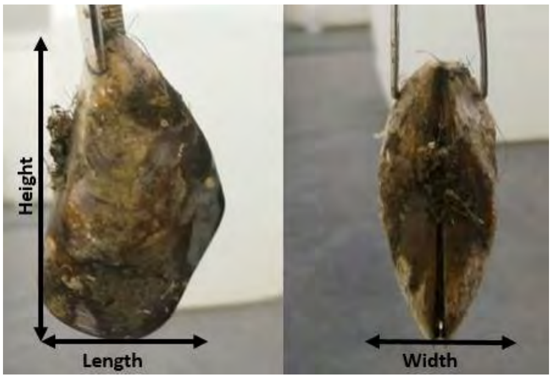

Figure 2. 7: Morphometric parameters of the seeded bivalves which were recorded monthly, for the period of 12 months.

To estimate mortality, every month, missing mussels, drilled shells, specimens with missing internal tissues or intact shells without tissue were cumulatively counted for each of the seeded tiles.

Biodiversity associated with the tiles was monitored monthly by means of *in situ* estimates by taking a photograph of each tile. In order to determine biodiversity, counting and identification to the lowest possible taxon were conducted for both mobile species as well as the percentage cover of sessile and sedentary species and algal cover. The intercept, point quadrat method was used to estimate percentage cover of sessile/sedentary invertebrates and algae in the field, and by projecting photos taken during sampling over a grid of 100 dots (Dethier *et al.,* 1993; Drummond and Connell, 2005). The presence of a specific sessile/sedentary and mobile organisms under each intercept were recorded (Foster *et al.,* 1991; Leonard and Clark, 1993; Drumond and Connell, 2005). At the end of the experiment (October 2017), all tiles were removed from the field, transported to the South African Institute for Aquatic Biodiversity (SAIAB) laboratory in Grahamstown, South Africa (33°18ˈ37.1ˈˈS 26°31ˈ11.1ˈˈE) and individually stored in a freezer at -10°C. Total species composition and mussel biomass from the seeded and unseeded tiles was determined in the laboratory. Mussels were removed from the tiles by gently separating the body from the epoxy using a chisel and hammer and rinsed with tap water into a 75 µm sieve, with the content preserved for further analysis of biodiversity. Mussels were then dissected following the same procedure as for the freshly collected mussels, weighed and dried at 60°C for 24 hours. After the mussels were removed, each empty tile was also rinsed of all other organisms attached into a 75 µm sieve with tap water, and the contents collected in a 250 ml jar and preserved in ethanol. The collected invertebrates (from both the mussels and tiles) were examined by eye and/or viewed under a Leica dissecting microscope (Model Z45V). Field guides and identification keys were used to identify all invertebrates collected for the biodiversity component (Branch *et al*., 1994; Day, 1969, 1967, 1974).

Adult mussel cover was assessed at each location, using ten 50 x 50 cm quadrats which were randomly deployed within the mid to low intertidal zone, known to be dominated by mussels (McQuaid *et al.,* 2000) at each site. The intercept, point method (used as per the method for assessing biodiversity) was applied to assess mussel adult cover. It should be noted that at the beginning of the study, a greater mussel abundance was observed in the port (specifically the East bank) compared to the natural rocky shores (pers. obs.). Due to heavy dislodgement during the study, adult mussels on the shore were mostly washed off during the sampling for mussel cover.

2.2.3 Statistical analysis

As multiple analyses were carried out for mortality, growth (in relation to height, width, length), biomass (dry shell, soft tissue and dry weights), species diversity (Shannon-Wiener and Simpson's indices for both mobile and sessile species) and mussel adult cover (*Perna perna* and *Mytilus galloprovincialis*), the Benjamini-Hochberg (B-H) false discovery rate correction on a posteriori results of the multiple analyses was applied to reduce the probability of incurring type I errors or false positives (Benjamini and Hochberg, 1995). The p-values from all tests were ranked in ascending order, i.e., the lowest p-value ranked as the second was 2 and the third was 3 and so on, as shown in Table 2.1. The B-H was calculated using the formula: B-H = (i/m)Q, where:

i = p-value rank,

m = number of tests,

Q = 0.05

Calculated (B-H) p-values were compared to the original p-values; the p-value smaller than the calculated B-H p-value was considered to be the new cut-off for significance (0.01; Table 2.1).

Table 2. 1: Calculations for the Benjamini-Hochberg procedure of false discovery rate, to reduce probability of type 1 errors. Bold represents the cut-off significant value.

Treatment	Effect	p	Rank	B-H
Mobile Shannon	Month	0,000	1	0,000
Dry shell	Month	0,000	2	0,001
Sessile Shannon	Month	0,000	3	0,001
Length	Treatment	0,000	4	0,001
Sessile Simpson	Month	0,000	5	0,002
Height	Month	0,000	6	0,002
Dry tissue	Month	0,000	7	0,002
Mortality	Month	0,000	8	0,003
Height	Treatment	0,000	9	0,003
Mobile Simpson	Month	0,000	10	0,003
Sessile Shannon	Month*Seeding	0,000	11	0,004
Sessile Shannon	Site	0,001	12	0,004
Mobile Primer	Site	0,001	13	0,005
Mobile Primer	Treatment	0,001	14	0,005

Mobile Primer	Seeding	0,001	15	0,005
Mobile Primer	Month	0,001	16	0,006
Mobile Primer	Seeding*Site	0,001	17	0,006
Mobile Primer	Site*Month	0,001	18	0,006
Mobile Primer	Treatment*Seeding	0,001	19	0,007
Mobile Primer	Treatment*Seeding*Site	0,001	20	0,007
Sessile/sedentary Primer	Site	0,001	21	0,007
Sessile/sedentary Primer	Seeding	0,001	22	0,008
Sessile/sedentary Primer	Month	0,001	23	0,008
Sessile/sedentary Primer	Site*Month	0,001	24	0,008
Dry weight	Seeding	0,001	25	0,009
Sessile Simpson	Month*Seeding	0,002	26	0,009
Mobile Shannon	Month*Seeding	0,002	27	0,009
Sessile/sedentary Primer	Treatment*Seeding*Site	0,002	28	0,010
Dry weight	Treatment	0,002	29	0,010
Sessile Shannon	Month*Treatment*Seeding*Site	0,004	30	0,010
Width	Month*Site	0,004	31	0,011
Mobile Primer	Treatment*Site	0,007	32	0,011
Sessile Simpson	Month*Treatment*Seeding*Site	0,007	33	0,012
Sessile/sedentary Primer	Treatment*Seeding	0,008	34	0,012
Length	Treatment*Site	0,009	35	0,012
Mobile Shannon	Treatment	0,010	36	0,013
Sessile Simpson	Month*Site	0,010	37	0,013
Length	**Month*Treatment**	**0,011**	**38**	**0,013**
Sessile Shannon	Month*Site	0,013	39	0,014
Dry weight	Site	0,018	40	0,014
Mobile Simpson	Month*Treatment*Seeding	0,022	41	0,014
Sessile/sedentary Primer	Seeding*Site	0,031	42	0,015
Mobile Shannon	Treatment*Seeding	0,032	43	0,015
Sessile/sedentary Primer	Treatment*Month	0,032	44	0,015
Height	Month*Site	0,034	45	0,016
Mobile Simpson	Month*Treatment	0,037	46	0,016
Sessile/sedentary Primer	Treatment	0,041	47	0,016
Dry tissue	Site*Month	0,042	48	0,017
Dry weight	Treatment*Site	0,051	49	0,017
Sessile/sedentary Primer	Treatment*Site	0,052	50	0,017
Length	Month	0,055	51	0,018
Width	Month	0,055	52	0,018
Sessile/sedentary Primer	Seeding*Site*month	0,056	53	0,019
Mobile Shannon	Month*Site	0,064	54	0,019
Dry weight	Treatment*Site*Seeding	0,086	55	0,019
Mobile Shannon	Month*Treatment	0,087	56	0,020

Length	Month*Treatment*Site	0,111	57	0,020
Mortality	Month*Treatment	0,120	58	0,020
Mobile Primer	Seeding*Month	0,125	59	0,021
Mobile Primer	Treatment*Month	0,136	60	0,021
Mortality	Month*Site	0,142	61	0,021
Dry tissue	Site*Treatment	0,147	62	0,022
Sessile/sedentary Primer	Treatment*Seeding*Site*Month	0,166	63	0,022
Mobile Shannon	Seeding*Site	0,169	64	0,022
Sessile Shannon	Month*Treatment	0,176	65	0,023
Mortality	Treatment*Site	0,179	66	0,023
Width	Treatment*Site	0,188	67	0,023
Mobile Simpson	Site	0,191	68	0,024
Sessile Simpson	Month*Treatment*Site	0,208	69	0,024
Height	Site	0,208	70	0,024
Sessile Shannon	Seeding*Site	0,226	71	0,025
Dry shell	Treatment	0,228	72	0,025
Mobile Simpson	Month*Site	0,239	73	0,026
Length	Site	0,262	74	0,026
Mobile Simpson	Month*Treatment*Seeding*Site	0,262	75	0,026
Length	Month*Site	0,275	76	0,027
Sessile/sedentary Primer	Treatment*Site*Month	0,277	77	0,027
Mobile Simpson	Month*Seeding	0,298	78	0,027
Mobile Shannon	Month*Seeding*Site	0,325	79	0,028
Width	Site	0,330	80	0,028
Mobile Simpson	Treatment	0,335	81	0,028
Mortality	Treatment	0,337	82	0,029
Width	Month*Treatment*Site	0,342	83	0,029
Sessile Simpson	Month*Treatment	0,369	84	0,029
Dry tissue	Site*Treatment*Month	0,413	85	0,030
Sessile Simpson	Treatment*Seeding	0,431	86	0,030
Dry shell	Site*Treatment*Month	0,435	87	0,030
Mobile Shannon	Month*Treatment*Site	0,447	88	0,031
Mobile Simpson	Month*Seeding*Site	0,475	89	0,031
Mobile Shannon	Treatment*Site	0,485	90	0,031
Mobile Shannon	Month*Treatment*Seeding	0,486	91	0,032
Dry weight	Site*Seeding	0,502	92	0,032
Sessile Simpson	Treatment	0,508	93	0,033
Sessile Simpson	Treatment*Seeding*Site	0,511	94	0,033
Width	Month*Treatment	0,533	95	0,033
Sessile Simpson	Site	0,546	96	0,034
Sessile Shannon	Month*Treatment*Site	0,551	97	0,034
Mobile Shannon	Month*Treatment*Seeding*Site	0,564	98	0,034

Dry tissue	Treatment	0,572	99	0,035
Dry shell	Site	0,578	100	0,035
Sessile Shannon	Seeding	0,582	101	0,035
Mobile Simpson	Treatment*Seeding	0,595	102	0,036
Mobile Shannon	Seeding	0,619	103	0,036
Dry weight	Treatment*Seeding	0,625	104	0,036
Sessile Shannon	Treatment*Site	0,627	105	0,037
Mobile Simpson	Seeding	0,642	106	0,037
Sessile Simpson	Seeding	0,646	107	0,037
Sessile Simpson	Month*Seeding*Site	0,664	108	0,038
Height	Treatment*Site	0,667	109	0,038
Sessile Shannon	Treatment*Seeding	0,670	110	0,038
Width	Treatment	0,682	111	0,039
Sessile Simpson	Month*Treatment*Seeding	0,718	112	0,039
Mobile Simpson	Seeding*Site	0,720	113	0,040
Mobile Simpson	Treatment*Site	0,721	114	0,040
Sessile Shannon	Month*Seeding*Site	0,728	115	0,040
Sessile Simpson	Treatment*Site	0,733	116	0,041
Mobile Shannon	Site	0,737	117	0,041
Height	Month*Treatment	0,743	118	0,041
Mobile Simpson	Treatment*Seeding*Site	0,756	119	0,042
Sessile Shannon	Month*Treatment*Seeding	0,762	120	0,042
Dry shell	Site*Month	0,796	121	0,042
Sessile Shannon	Treatment*Seeding*Site	0,822	122	0,043
Mobile Primer	Treatment*Seeding*Month	0,837	123	0,043
Mobile Simpson	Month*Treatment*Site	0,846	124	0,043
Sessile/sedentary Primer	Treatment*Seeding*Month	0,858	125	0,044
Dry tissue	Treatment*Month	0,859	126	0,044
Sessile Simpson	Seeding*Site	0,864	127	0,044
Dry tissue	Site	0,865	128	0,045
Mortality	Month*Treatment*Site	0,891	129	0,045
Dry shell	Site*Treatment	0,914	130	0,045
Sessile/sedentary Primer	Seeding*Month	0,917	131	0,046
Sessile Shannon	Treatment	0,927	132	0,046
Height	Month*Treatment*Site	0,940	133	0,047
Mortality	Site	0,946	134	0,047
Mobile Shannon	Treatment*Seeding*Site	0,950	135	0,047
Mobile Primer	Treatment*Site*Month	0,981	136	0,048
Mobile Primer	Seeding*Site*month	0,990	137	0,048
Mobile Primer	Treatment*Seeding*Site*Month	0,994	138	0,048
Dry shell	Treatment*Month	0,996	139	0,049
Mytilus cover	Site	0.000	140	0,049

Perna cover	Location (Site)	0.003	141	0,049
Mytilus cover	Location (Site)	0.010	142	0,050
Perna cover	Site	0.080	143	0,050

Mussel cover

A one-way ANOVA was performed to test the effect of site on the adult mussel cover (*Perna perna* and *Mytilus galloprovincialis*). This analysis was performed to check for differences in the distribution of adult mussels among sites used for this study. Normality of the adult abundance was tested using a Shapiro-Wilk test. Homogeneity of the datum was tested using Cochran's C, the grouping of homogenous significant groups was done using Fisher LSD post-hoc test.

Environmental data

Environmental factors including turbidity (NTU), salinity, pH, dissolved oxygen (mg/L) and water motion were analysed using Primer v6. There was no correlation ($r < 0.7$) among factors after performing the Draftsman plots to assess the multi-collinearity of data, and no transformation of datum was therefore considered (Zuur *et al*., 2007; Anderson *et al*., 2008). Data were then normalised (Clarke and Gorley, 2006), and a resemblance matrix was calculated using the Euclidean distance similarity measures, and a principle component analysis (PCA) was performed to assess patterns of environmental variables.

Biodiversity data

All the species observed during the course of the study were categorised according to functional groups; mobile species (abundance) were grouped together separately from sessile/sedentary species (percentage cover) (Underwood and Skilleter, 1996). Data were

Log(x+1) transformed and the resemblance matrix calculated using the Bray-Curtis similarity, with an addition of a dummy value (0.01) due to low variability in the dataset (zero-adjusted Bray Curtis measure) (Clarke *et al.*, 2006). Permutational multivariate 4-way analyses of variance (PERMANOVAs), based on 999 permutations of residuals, were used to assess the partitioning of the Log(x+1) biodiversity data cloud in response to the factors of site, treatment, seeding and month. Relationships between environmental variables and biodiversity data were assessed using distance-based linear modelling (DistLM) and the relationships were visualised using distance-based redundancy analysis ordination (dbRDA).

The Shannon-Wiener index assumes that all individuals in a large population are included in samples taken randomly, while Simpson's index assumes that two individuals selected randomly from a large sample community are the same (Clarke and Warwick, 2001). The diversity indices were calculated according to the equations: Shannon-Wiener index H = $-(\sum Pi\ x\ lnPi)$ and Simpson's index of diversity $D = 1 - (\sum Pi^2)$, where; **Pi** is the proportion of individuals of a particular species divided by the total number of individuals, **ln** is the natural log and **Σ** is the sum of the calculations.

In order to assess the spatio-temporal differences in the species diversity indices according to treatment, two four-way repeated measures ANOVAs (F-value) were performed, both to test the effect of site (2 levels, random; East and West banks), seeding (2 levels; fixed, seeded and unseeded) and treatment (3 levels, fixed; flat, 2.5 cm tiles and 5 cm tiles) with month (12 levels, continuous repeated; November 2016-October 2017).

Mortality and Growth of seeded mussels

The variability in mortality and on the three indicators of mussel growth (shell length, height and width) of seeded mussels were assessed in relation to time (months), bank (site) and micro-complexity (treatment). Normality of the datum was tested using a Shapiro-Wilk test (Razali and Wah, 2011). Homogeneity of variance was assessed using a Cochran's C test. Heterogeneous right-skewed (Jones, 2012) datasets for mortality were transformed using Log(x+1) because the data had numerous zeros and growth datasets were transformed using square-root (Osborne, 2002; Yamamura, 1999). In order to evaluate possible differences in the mortality and growth of mussels according to time, site and complexity, a parametric three-way repeated measures ANOVA (F-value) was performed to test the effects of month (12 levels, continuous, repeated; November 2016-October 2017), site (2 levels, random; East and West banks) and treatment (3 levels, fixed; flat, 2.5 cm tiles and 5 cm tiles) on the mortality and on the three indicators of mussel growth (shell length, height and width) of seeded mussels. During month 2 (November 2016), the shell morphometrics of height and width could not be measured due to rough sea conditions and mussels were therefore not accessible, which hampered the completion of data collection during this particular month. Post-hoc tests were performed on significant results, using Fisher LSD to further explore the differences relevant to the specific hypothesis of the study, that is, the effect of complexity on mussel mortality.

Biomass of seeded mussels

Normality of the biomass data was determined using a Shapiro-Wilk test. Homogeneity was tested using Cochran's C, and heterogeneous data were Log (x+1) transformed. A three-way

ANOVA (F-value) was performed to test the effects of month (2 levels, October 2016 and October 2017), site (2 levels, random; East and West banks) and treatment (3 levels, fixed; flat, 2.5 cm tiles and 5 cm tiles) on the biomass (soft and shell dry weights) of mussels. An additional three-way ANOVA was performed to test the effects of site (2 levels, random; East and West banks), seeding (2 levels, fixed; seeded and unseeded) and treatment (3 levels, fixed; flat, 2.5 cm tiles and 5 cm tiles) on the biomass of the dry weight of other organisms on the tiles. Post-hoc tests were performed using Fisher LSD to explore the differences relevant to the specific hypothesis of the study, that is, the effects of complexity on mussel biomass.

The software package Statistica (v13.2), (StatSoft Inc. 2018), was used for all statistical analyses performed, except for the multivariate analyses of the environmental parameters and biodiversity, which were performed using Primer v6 (Clarke and Gorley, 2006).

2.3. Results

Mussel cover

One-way nested ANOVAs performed on the adult cover of *P. perna* and *M. gallogrovincialis* showed that there was a significant difference between locations within the sites for both species and an effect of site for the mussel *M. galloprovincialis* (Table 2.2). The East bank in the port had higher *P. perna* cover than the West bank, and, on the natural rocky shore, Winterstrand site 1 had a higher *P. perna* cover than Winterstrand site 2 (Figure 2.8). The West bank in the port had higher *M. galloprovincialis* cover than the East bank, with this species being completely absent on the natural rocky shore (Figure 2.9).

Table 2. 2: Results of the one-way (ANOVA) testing the effect of location nested in site on the abundance of *Perna perna* and *Mytilus galloprovincialis* adult mussel percent cover at two sites (natural rocky shores (Winterstrand 1 and 2), port (East and West banks)). SS = Sum of squares, df = degrees of freedom, MS = Mean squares, F= f-ratio, p = p-value. The level of significance is represented by asterisks with p≤0.01 = *, p≤0.001 = ** and non-significant (n.s.). Significant results are highlighted in bold.

	P. perna					***M. galloprovincialis***				
Effect	df	SS	MS	F	p	df	SS	MS	F	p
Site	1	0,07	0,07	0,06	n.s.	**1**	**15,72**	**15,72**	**15,78**	******
Location(Site)	**2**	**17,19**	**8,60**	**7,01**	******	**2**	**10,48**	**5,24**	**5,26**	*****
Error	36	44,14	1,23			36	35,87	1,00		

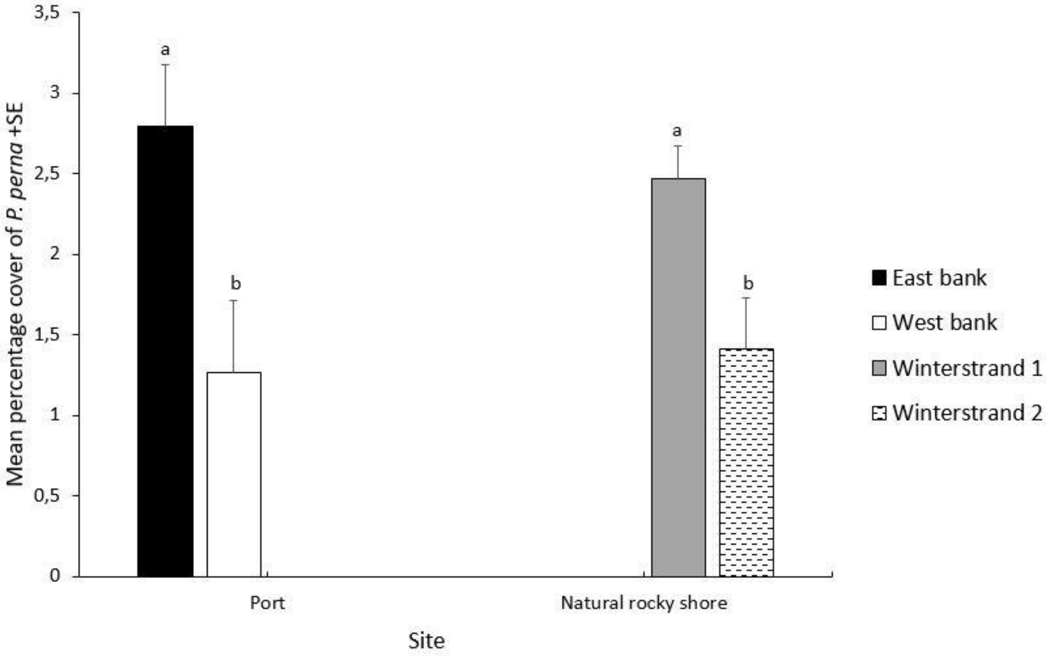

Figure 2. 8: Mean abundance of adult *P. perna* percentage cover at two different sites on the East London coastline, South Africa. Error bars represent standard error. The letters above the graphs indicate the homogenous groups according to Fisher LSD post-hoc for the factor location*site

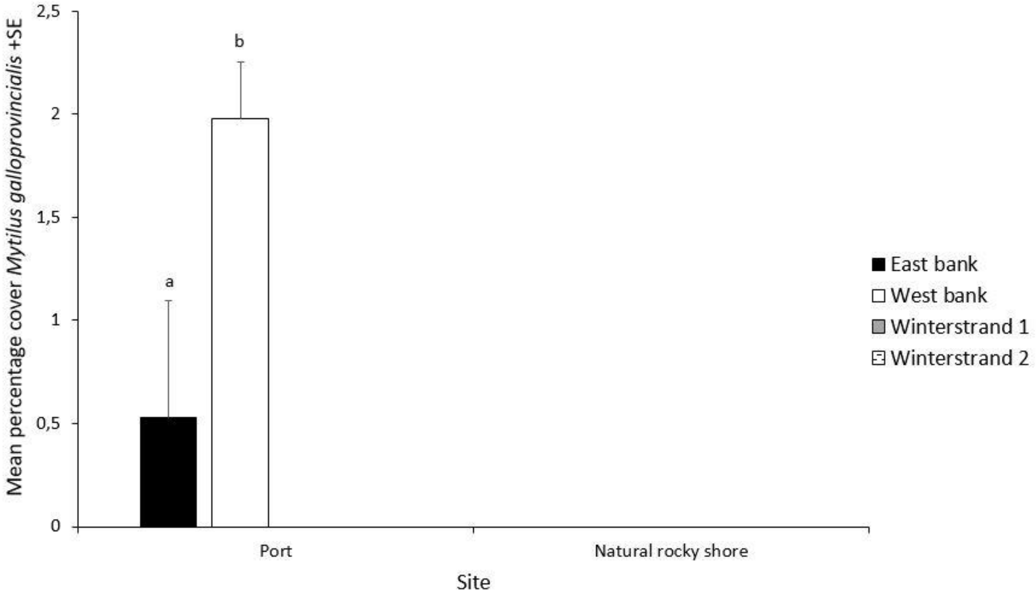

Figure 2. 9: Mean abundance of adult *M. galloprovincialis* percentage cover at two different sites on the East London coastline, South Africa. Error bars represent standard error. The letters above the graphs indicate the homogenous groups according to Fisher LSD post-hoc for the factor location*site.

Biodiversity data

A total of 21 mobile species from several classes including Gastropoda, Polychaeta, Echinodermata, Malacostraca and Polyplacophora were identified over the duration of the study, with the abundance of species differing across months, sites, seeding and treatments (Figures A.1-A.12 shown in the Appendix). The results of the four-way PERMANOVA on the effects of seeding, site, time and treatment on the community composition of mobile species showed significant results for the interaction between treatment, seeding and site (Table 2.3). Highest species diversity was observed on seeded tiles in east bank, however, mobile species on complex seeded treatments (2.5 cm and 5 cm) were significantly higher than on flat treatments at all the sites except the west bank of the seeded tiles (Figure 2. 10).

Table 2. 3: Four-way PERMANOVA for treatment, site, seeding and month over the sampling period (November 2016-October 2017) for mobile species. SS = Sum of squares, df = Degrees of freedom, MS = Mean squares, F = F-ratio, p = p-value. The level of significance is

represented by asterisks with p ≤ 0.001 = * and non-significant (n.s.). Significant results are in bold.

Treatment	df	SS	MS	F	p
Site	**1**	**1,04E+05**	**1,04E+05**	**40,75**	*******
Treatment	**2**	**7,22E+04**	**3,61E+04**	**14,09**	******
Seeding	**1**	**1,94E+04**	**1,94E+04**	**7,57**	******
Month	**11**	**3,01E+05**	**2,74E+04**	**10,69**	******
Site*Treatment	**2**	**1,11E+04**	**5,56E+03**	**2,17**	*****
Site*Seeding	**1**	**3,59E+04**	**3,59E+04**	**14,02**	******
Site*Month	**11**	**7,39E+04**	**6,71E+03**	**2,62**	******
Treatment*Seeding	**2**	**3,15E+04**	**1,58E+04**	**6,15**	******
Treatment*Month	22	6,41E+04	2,91E+03	1,14	n.s.
Seeding*Month	11	3,35E+04	3,04E+03	1,19	n.s.
Site*Treatment*Seeding	**2**	**1,81E+04**	**9,04E+03**	**3,53**	*******
Site*Treatment*Month	22	4,23E+04	1,92E+03	0,75	n.s.
Site*Seeding*Month	11	1,77E+04	1,61E+03	0,63	n.s.
Treatment*Seeding*Month	22	5,01E+04	2,28E+03	0,89	n.s.
Site*Treatment*Seeding*Month	22	4,17E+04	1,89E+03	0,74	n.s.
Res	554	1,42E+06	2,56E+03		
Total	697	2,35E+06			

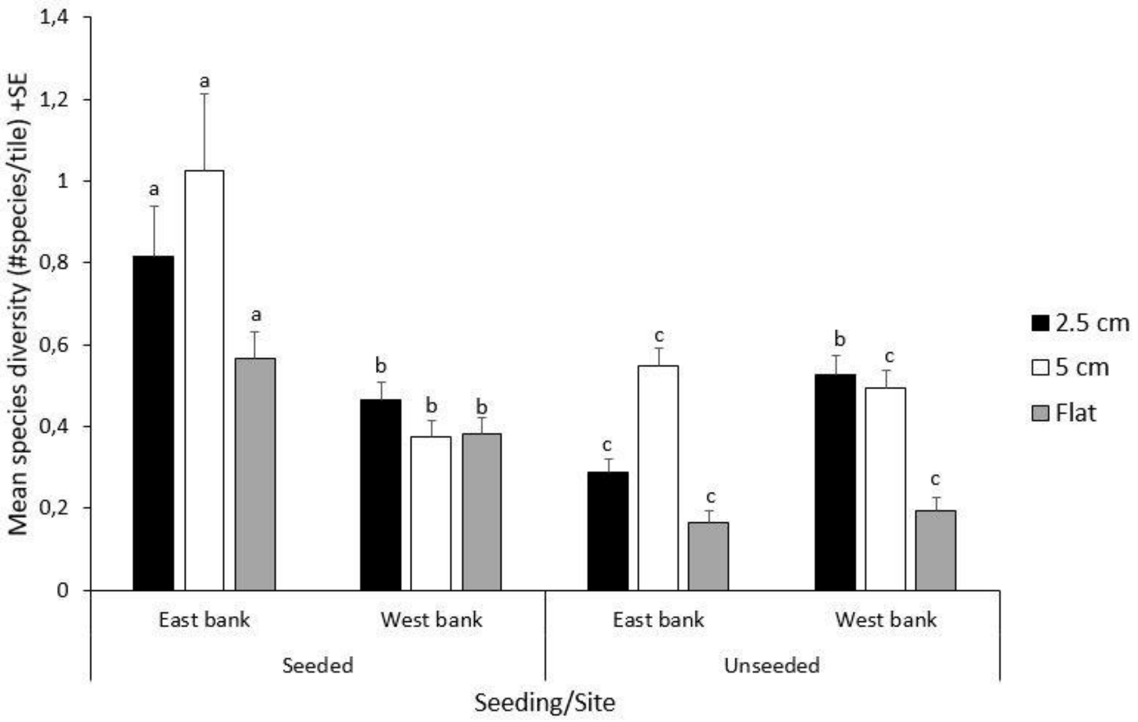

Figure 2. 10: Mean mobile species diversity on seeding (seeded and unseeded) for each treatment (flat, 2.5 cm tiles and 5 cm tiles) at both sites (East and West banks) pooled over the 12-month sampling period (November 2016-October 2017). Error bars represent standard error. The letters above the graphs symbolise homogenous groups identified be the 'interaction seeding*site*treatment' pairwise test.

The dissimilarity of percentages was calculated to identify the species that contributed most to the dissimilarities for factors seeding, sites, months and treatments. The species listed in (Tables 2.4-2.6) are those contributing substantially to the differences among the seeding, sites, months and treatments. A percentile value was used to report the average dissimilarity in species diversity between seeding (Table 2.4), sites (Table 2.5) and treatment (Table 2.6). The higher the value, the less similar the groups were.

Table 2. 4: Average dissimilarity percentages between seeding groups and the percentage contributions of key species to the total dissimilarity of communities (mobile) in each month. The cut off for low contributions is 90%.

Seeding	**Seeded/Unseeded**
Average dissimilarity %	79.62
Species	**Percentage contribution to community abundance (%**
C. oculus	19,14
O. sinensis	14,65
S. concinna	12,12
S. longicosta	11,47
S. capensis	11,27
S.serrata	9,2
O. tabularis	5,95
O. tigrina	3,74
A. garnoti	3,14

Table 2. 5 Average dissimilarity percentages between site groups and the percentage contributions of key species to the total dissimilarity of communities (mobile) in each month. The cut off for low contributions is 90%.

Site	East/West
Average dissimilarity %	80.72
Species	**Percentage contribution to community abundance (%**
C. oculus	19,15
O. sinensis	14,81
S. longicosta	11,84
S. concinna	11,83
S. capensis	11,43

S.serrata	8,45
O. tabularis	6,06
O. tigrina	3,8
S. granularis	3,11

Table 2. 6: Average dissimilarity percentages between treatment groups and the percentage contributions of key species to the total dissimilarity of communities (mobile) in each month. The cut off for low contributions is 90%.

Treatment	**Flat/2.5 cm**	**Flat/5 cm**	**2.5 cm/5 cm**
Average dissimilarity %	81.22	78.73	74.59
Species	**Percentage contribution to community abundance (%)**		
C. oculus	17,56	23,06	18,99
S. longicosta	12,75	9,32	11,76
S. concinna	12,67	11,88	12,84
O. sinensis	12,38	15,54	14,55
S. capensis	11,55	10,19	10,65
S.serrata	10,16	7,83	7,92
O. tabularis	5,09	6,73	6,95
S. granularis	4,13		3,6
O. tigrina	3,68	4,23	
H. pruinosus	2,91		
A. garnoti		3,39	3,69

The DistLM marginal test results showed that all the environmental variables contributed significantly towards the distribution of species' biodiversity (Table 2.7). The first two axes of the fitted model visualised by the dbRDA plot explained almost 80% of the fitted variation, and 6.2% of the total variation in species' composition over the 12 months. Turbidity, pH, and temperature (minor) had positive correlations with the first axis, while water motion, dissolved oxygen and salinity (minor) had negative correlations with the second dbRDA axis (Figure 2.11).

Table 2. 7: DistLM marginal test for the 12-month sampling period (November 2016-October 2017) on mobile species at two different sites (East and West banks) for each treatment (flat, 2.5 cm tiles and 5 cm tiles). SS = Sum of squares, F = F-ratio, p = p-value, Prop = proportion of

variance explained by each variable. The level of significance is represented by asterisks with p ≤ 0.01 = *, p ≤ 0.001 = **. Significant results are in bold.

Variable	SS	F	p	Prop.
DO	**65830,00**	**20,09**	*	**0,03**
Salinity	**25027,00**	**7,50**	*	**0,01**
Temp	10900,00	3,25	n.s.	0,00
pH	**54656,00**	**16,60**	*	**0,02**
Turbidity	**25405,00**	**7,62**	*	**0,01**
Water motion	**66618,00**	**20,34**	*	**0,03**

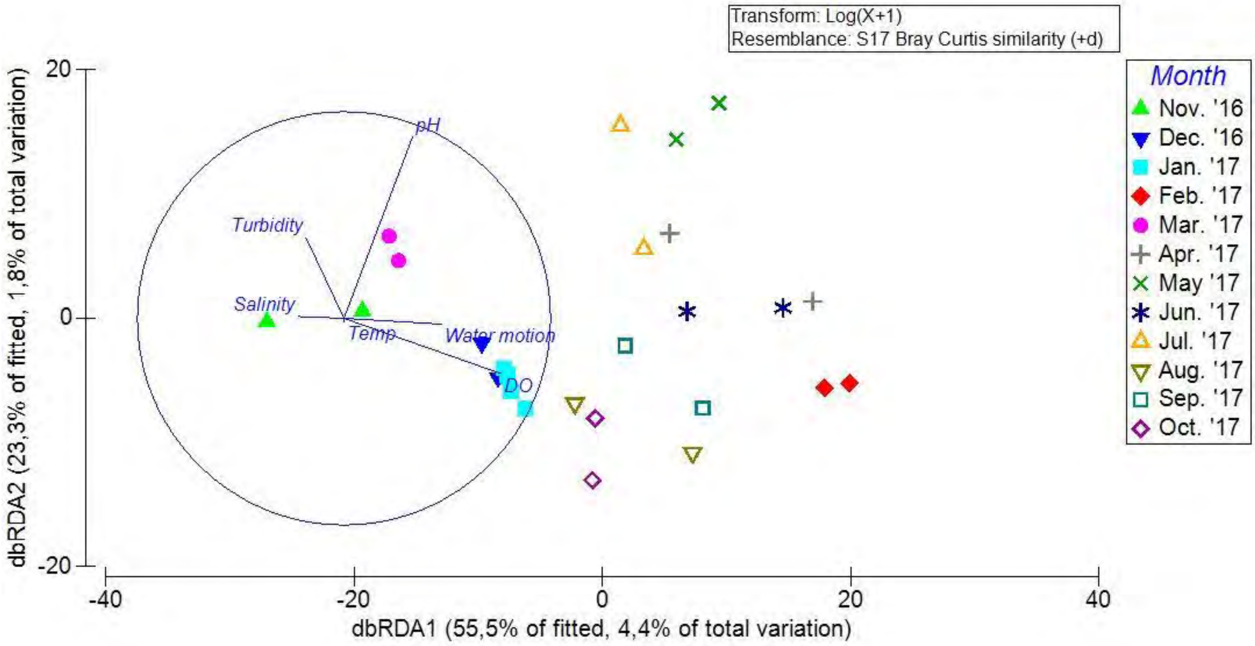

Figure 2. 11: RDA ordination biplot for the 12-month sampling period of mobile species diversity and the explanatory environmental variables (as vectors).

The results of the four-way repeated measures ANOVA on the effect of site, treatment, seeding and month on mobile species on the Shannon- Wiener diversity index showed a significant effect of treatment and the interaction between month and seeding (p < 0.001) (Table 2. 8). Species diversity was significantly higher on 2.5 cm and 5 cm tiles than flat tiles (Figure 2.12). In February 2017 and March 2017 species diversity on seeded tiles was significantly higher than that on unseeded tiles, however, the pattern was reversed in July 2017 and August 2017 where species diversity on unseeded tiles was significantly higher than that on seeded tiles for mobile species (Figure 2.13). There was a significant effect of month on the Simpson’s species diversity index (Table 2.8), highest species diversity was observed in November 2016, a month after the setup of the project (Figure2.14).

Table 2. 8: Four-way repeated measures ANOVA testing the effect of treatment, seeding, site and month on the biodiversity of mobile species calculated by Shannon-Wiener and Simpson's diversity indices in the Port of East London, South Africa, over the sampling period (November 2016—October 2017). SS = Sum of squares, df = degrees of freedom, MS = Mean squares, F = F-ratio, p = p-value. The level of significance is represented by asterisks with p ≤ 0.01 = *, p ≤ 0.001 = **, p ≤ 0.0001 = *** and non-significant (n.s.). Significant results are in bold.

	Shannon-Wiener mobile					Simpson mobile				
Effect	df	SS	MS	F	p	df	SS	MS	F	p
Month	**11**	**52,615**	**4,783**	**33,882**	**	**11**	**3,15**	**0,29**	**3,69**	**
Site	1	0,098	0,098	0,114	n.s.	1	0,32	0,32	1,76	n.s.
Treatment	**2**	**8,746**	**4,373**	**5,111**	*	2	0,41	0,21	1,12	n.s.
Seeding	1	0,215	0,215	0,251	n.s.	1	0,04	0,04	0,22	n.s.
Error	48	41,07	0,856			48	8,84	0,18		
Month*Site	11	2,686	0,244	1,729	n.s.	11	1,08	0,10	1,27	n.s.
Month*Treatment	22	4,491	0,204	1,446	n.s.	22	2,77	0,13	1,62	n.s.
Month*Seeding	**11**	**4,285**	**0,39**	**2,76**	**	11	1,01	0,09	1,18	n.s.
Seeding*Site	1	1,67	1,67	1,951	n.s.	1	0,02	0,02	0,13	n.s.
Treatment*Site	2	1,258	0,629	0,735	n.s.	2	0,12	0,06	0,33	n.s.
Treatment*Seeding	2	6,337	3,169	3,703	n.s.	2	0,19	0,10	0,52	n.s.
Month*Treatment*Site	22	3,142	0,143	1,012	n.s.	22	1,19	0,05	0,70	n.s.
Month*Seeding*Site	11	1,775	0,161	1,143	n.s.	11	0,83	0,08	0,97	n.s.
Month*Treatment*Seeding	22	3,049	0,139	0,982	n.s.	22	2,94	0,13	1,72	n.s.
Treatment*Seeding*Site	2	0,088	0,044	0,051	n.s.	2	0,10	0,05	0,28	n.s.
Month*Treatment*Seeding*Site	22	2,866	0,13	0,923	n.s.	22	2,01	0,09	1,18	n.s.
Error	528	74,539	0,141			528	40,97	0,08		

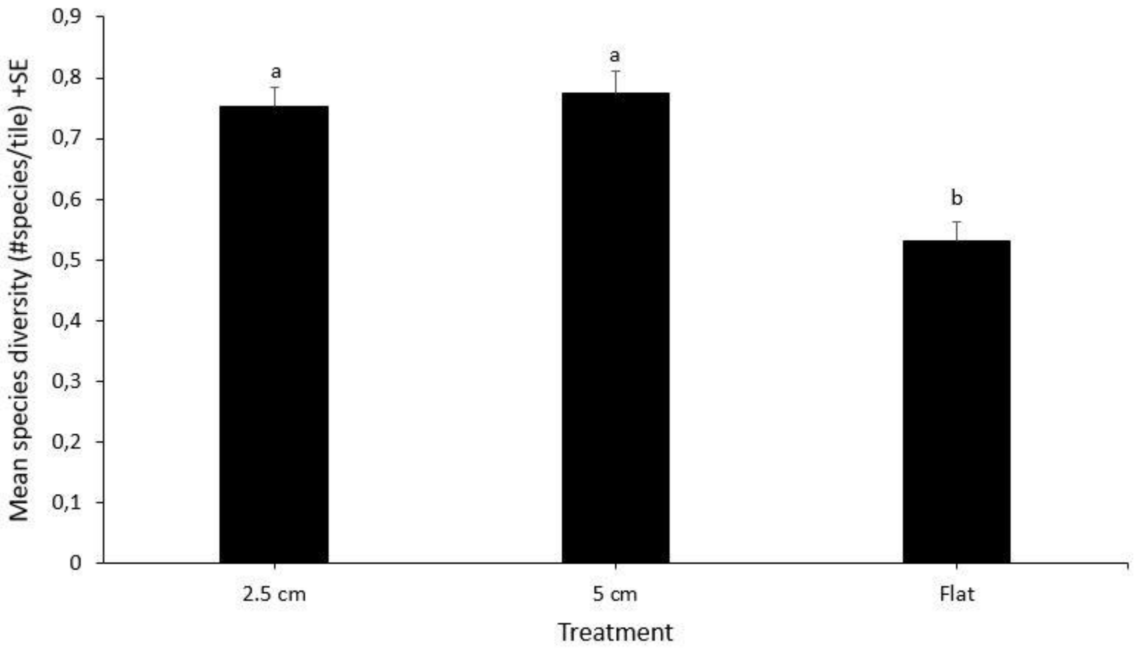

Figure 2. 12: Mean mobile species diversity (Shannon-Wiener) over the 12-month sampling period (November 2016-October 2017) on seeding (seeded and unseeded) pooled for both sites (East and West banks) and for all treatments (flat, 2.5 cm tiles and 5 cm tiles). Error bars represent standard error. The letters above the graphs symbolise homogenous groups according to the Fisher LSD post-hoc test for the interaction of month*seeding.

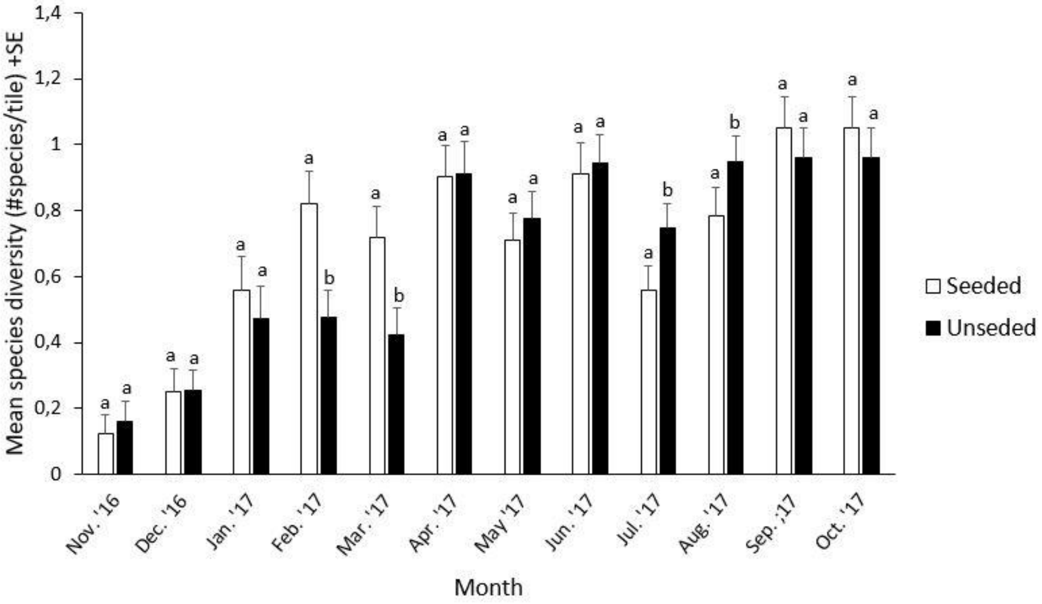

Figure 2. 13: Mean mobile species diversity (Shannon-Wiener) over the 12-month sampling period (November 2016-October 2017) on seeding (seeded and unseeded) pooled for both sites (East and West banks) and for all treatments (flat, 2.5 cm tiles and 5 cm tiles). Error bars represent standard error. The letters above the graphs symbolise homogenous groups according to the Fisher LSD post-hoc test for the interaction of month*seeding.

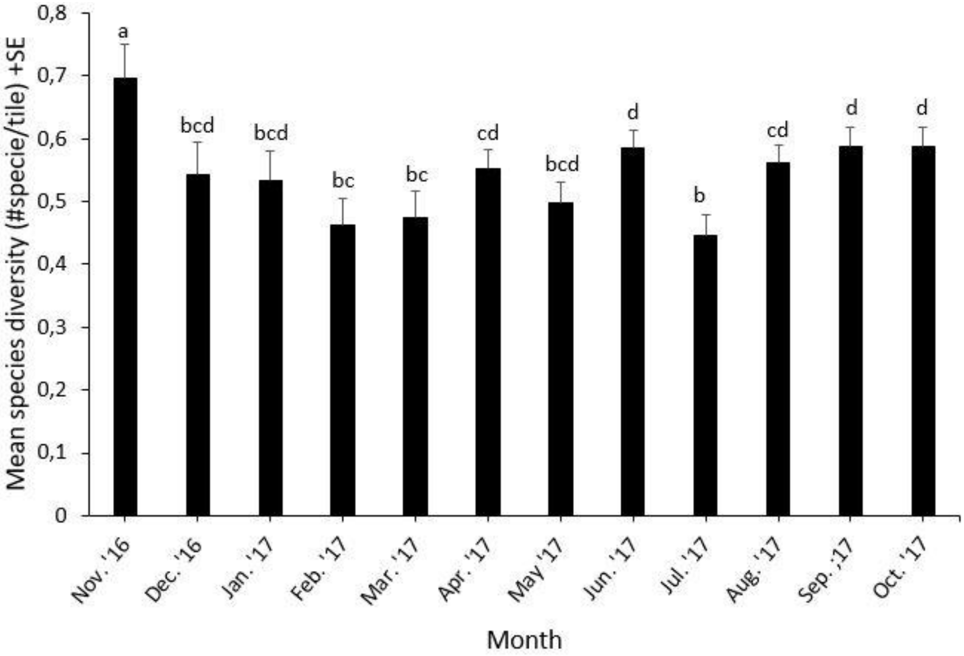

Figure 2. 14: Mean mobile species diversity (Simpson's) over the 12-month sampling period (November 2016-October 2017) pooled for both sites (East and West banks), for all treatments (flat, 2.5 cm tiles and 5 cm tiles) and for seeding (seeded and unseeded). Error bars represent standard error. The letters above the graphs symbolise homogenous groups according to the Fisher LSD post-hoc test for the interaction of month.

Sessile/sedentary

A total of six sessile and sedentary species, including bivalves, seaweeds and crustaceans, were also identified over the study period (Figures A.13-A.24). The results of the four-way PERMANOVA on the effects of site, seeding, treatment and month on species composition of sessile/sedentary species indicated a significant effect for the interaction between treatment, seeding and site (Table 2.9). Sessile/sedentary species composition was significantly highest on flat, unseeded tiles on the East bank (Figure 2.15).

Table 2. 9: Four-way PERMANOVA for treatment, site, seeding and month over the sampling period (November 2016-October 2017) for sessile/sedentary species. SS = Sum of squares, df = degrees of freedom, MS = Mean squares, F = F-ratio, p = p-value. The level of significance is represented by asterisks with p≤0.01 = *, p≤0.001 = ** and non-significant (n.s.). Significant results are in bold.

Treatment	df	SS	MS	F	p

Site	1	8,03E+04	8,03E+04	117,09	**
Treatment	2	3,64E+03	1,82E+03	2,65	n.s.
Seeding	1	7,71E+03	7,71E+03	11,25	**
Month	11	4,77E+04	4,33E+03	6,32	**
Site*Treatment	2	3,39E+03	1,69E+03	2,47	n.s.
Site*Seeding	1	2,65E+03	2,65E+03	3,86	n.s.
Site*Month	11	1,87E+04	1,70E+03	2,48	**
Treatment*Seeding	2	5,31E+03	2,66E+03	3,87	**
Treatment*Month	22	2,28E+04	1,04E+03	1,51	*
Seeding*Month	11	4,26E+03	3,87E+02	0,57	n.s.
Site*Treatment*Seeding	2	9,18E+03	4,59E+03	6,70	**
Site*Treatment*Month	22	1,71E+04	7,77E+02	1,13	n.s.
Site*Seeding*Month	11	1,20E+04	1,09E+03	1,59	n.s.
Treatment*Seeding*Month	22	1,12E+04	5,11E+02	0,75	n.s.
Site*Treatment*Seeding*Month	22	1,85E+04	8,40E+02	1,22	n.s.
Res	554	3,80E+05	6,86E+02		
Total	697	6,43E+05			

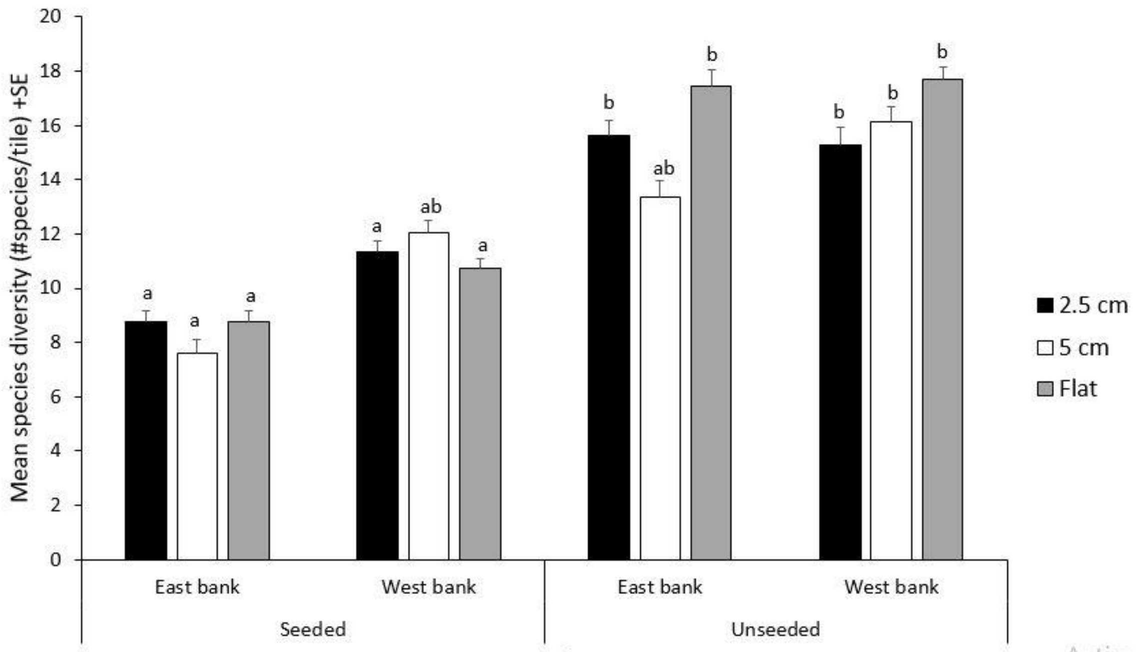

Figure 2. 15: Mean sessile/sedentary species diversity on seeding (seeded and unseeded) for each treatment (flat, 2.5 cm tiles and 5 cm tiles) at both sites (East and West banks) pooled over the 12-month sampling period (November 2016-October 2017). Error bars represent standard error. The letters above the graphs symbolise homogenous groups identified be the ‘interaction seeding*site*treatment’ pairwise test.

The dissimilarity of percentages was calculated to identify the species that contributed most to the dissimilarities for factors seeding, sites, months and treatments. The species listed in

(Tables 2.10-2.12) are those contributing substantially to the differences among the seeding, sites, months and treatments. A percentile value was used to report the average dissimilarity in species diversity between seeding (Table 2.10), site (Table 2.11) and treatment (Table 2.12). The higher the value, the less similar the groups were.

Table 2. 10: Average dissimilarity percentages between seeding groups and the percentage contributions of key species to the total dissimilarity of communities (sessile) in each month. The cut off for low contributions is 90%.

Seeding	**Seeded/Unseeded**
Average dissimilarity %	36
Species	**Percentage contribution to community abundance (%)**
H. rubra	44,94
Ulva spp	34,6
H. lecanellieri	10,35
G. pristoides	6,81

Table 2. 11: Average dissimilarity percentages between site groups and the percentage contributions of key species to the total dissimilarity of communities (sessile) in each month. The cut off for low contributions is 90%.

Site	**East/West**
Average dissimilarity %	38.07
Species	**Percentage contribution to community abundance (%)**
H. rubra	46,52
Ulva spp	33,41
H. lecanellieri	10,18

Table 2. 12: Average dissimilarity percentages between treatment groups and the percentage contributions of key species to the total dissimilarity of communities (sessile) in each month. The cut off for low contributions is 90%.

Treatment	**Flat/2.5 cm**	**Flat/5 cm**	**2.5 cm/5 cm**
Average dissimilarity %	34,12	34.34	36.49
Secies	**Percentage contribution to community abundance (%)**		
H. rubra	47,21	47,23	42,9
Ulva spp	32,76	33,51	33,3
H. lecanellieri	10,09	8,61	12,83
G. pristoides		7,54	6,54

The DistLM marginal test results showed that dissolved oxygen, salinity, temperature and water motion contributed significantly towards the distribution of species biodiversity (Table 2.13). The first two axes of the fitted model visualised by the dbRDA plot explained 91.3% of the fitted variation and 5.7% of the total variation in species composition over the 12 months. Dissolved oxygen, temperature and pH (minor) had positive correlations with the first axis, while water motion had negative correlations with the second dbRDA axis (Figure 2.16).

Table 2. 13: DistLM marginal test for the 12-month sampling period (November 2016-October 2017) on sessile/sedentary species at two different sites (East and West banks) for each treatment (flat, 2.5 cm ridged tiles and 5 cm ridged tiles). SS = Sum of squares, F = F-ratio, p = p-value, Prop = proportion of variance explained by each variable. The level of significance is represented by asterisks with $p \leq 0.01$ = *, $p \leq 0.001$ = **. Significant results are in bold.

Variable	SS (trace)	F	p	Prop
DO	**17402,00**	**19,36**	**	**0,03**
Salinity	**9992,30**	**10,98**	**	**0,02**
Temp	**6175,90**	**6,75**	*	**0,01**
pH	**2764,80**	**3,00**	*	**0,00**
Turbidity	1944,70	2,11	n.s.	0,00
Water motion	**16098,00**	**17,87**	**	**0,03**

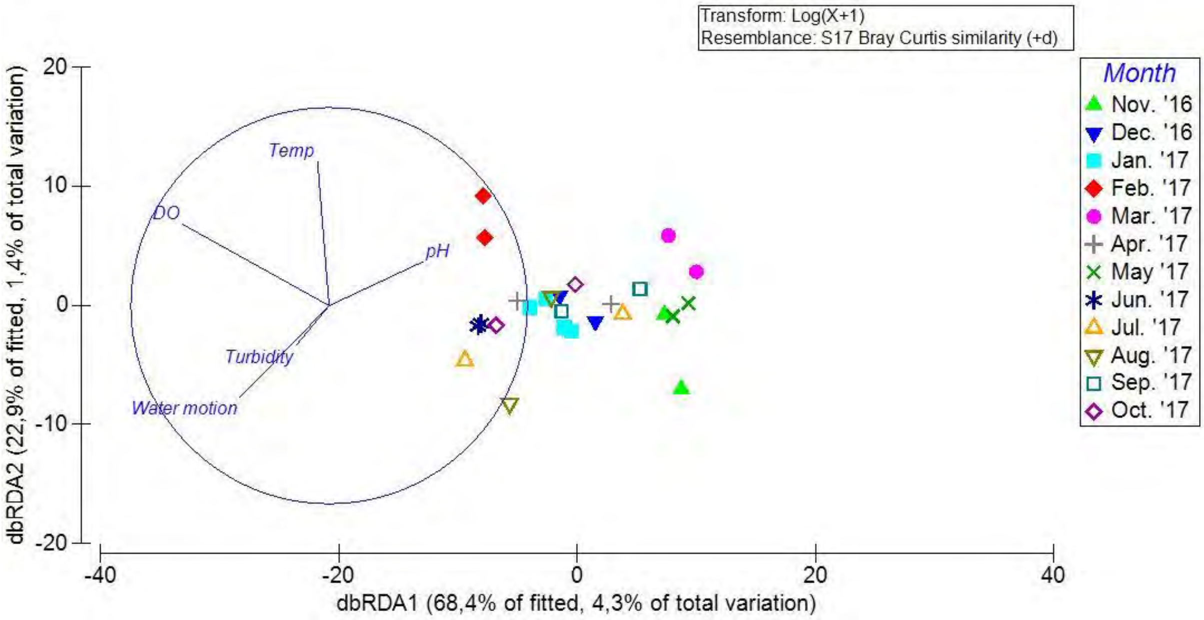

Figure 2. 16: RDA ordination biplot for the 12-month sampling period of sessile/sedentary species diversity and the explanatory environmental variables (as vectors).

The analysis of the four-way repeated measures ANOVA on the effect of site, treatment, seeding and month on sessile/sedentary species showed that the interaction between month and seeding ($p < 0.001$) had a significant effect on the Shannon-Wiener diversity index (Table 2. 14). In November 2016 and December 2016, species diversity on seeded tiles was significantly higher than that on unseeded tiles, however, the pattern was reversed in February 2017, September 2017 and October 2017 where species diversity on unseeded tiles was significantly higher than that on seeded tiles (Figure 2.17). The interaction between month and site ($p < 0.001$) had a significant effect on Simpson's diversity index (Table 2. 14). In December 2016 and July 2017, species diversity on the East bank was significantly higher than that observed on the West bank, however, the pattern was reversed in September 2017 and October 2017 and there were no other differences observed amongst the months (Figure 2. 18).

Table 2. 14: Four-way repeated measures ANOVA testing the effect of treatment, seeding, site and month on the biodiversity of sessile/sedentary species calculated by Shannon-Wiener and Simpson's diversity indices in the Port of East London, South Africa, over the sampling period (November 2016—October 2017). SS = Sum of squares, df = degrees of freedom, MS = Mean squares, F = F-ratio, p = p-value. The level of significance is represented by asterisks with p ≤ 0.01 = *, p ≤ 0.001 = **, p ≤ 0.0001 = *** and non-significant (n.s.). Significant results are in bold.

	Shannon-Wiener Sessile/sedentary					Simpson Sessile/sedentary				
Effect	df	SS	MS	F	p	df	SS	MS	F	p
Month	**11**	**4,774**	**0,434**	**7,938**	**	**11**	**0,267**	**0,024**	**6,505**	**
Site	1	2,055	2,055	13,167	**	1	0,009	0,009	0,37	n.s.
Treatment	2	0,024	0,012	0,076	n.s.	2	0,034	0,017	0,687	n.s.
Seeding	1	0,048	0,048	0,307	n.s.	1	0,005	0,005	0,214	n.s.
Error	47	7,336	0,156			47	1,167	0,025		
Month*Site	11	1,324	0,12	2,202	n.s.	**11**	**0,094**	**0,009**	**2,281**	*
Month*Treatment	22	1,543	0,07	1,282	n.s.	22	0,088	0,004	1,076	n.s.
Month*Seeding	**11**	**1,97**	**0,179**	**3,275**	**	11	0,115	0,01	2,792	n.s.
Seeding*Site	1	0,235	0,235	1,508	n.s.	1	0,001	0,001	0,03	n.s.
Treatment*Site	2	0,147	0,073	0,471	n.s.	2	0,016	0,008	0,313	n.s.
Treatment*Seeding	2	0,126	0,063	0,404	n.s.	2	0,043	0,021	0,857	n.s.
Month*Treatment*Site	22	1,122	0,051	0,933	n.s.	22	0,102	0,005	1,24	n.s.
Month*Seeding*Site	11	0,428	0,039	0,712	n.s.	11	0,032	0,003	0,777	n.s.
Month*Treatment*Seeding	22	0,928	0,042	0,771	n.s.	22	0,066	0,003	0,807	n.s.
Treatment*Seeding*Site	2	0,062	0,031	0,197	n.s.	2	0,034	0,017	0,681	n.s.
Month*Treatment*Seeding*Site	**22**	**2,436**	**0,111**	**2,025**	**	**22**	**0,158**	**0,007**	**1,926**	**
Error	517	28,27	0,055			517	1,929	0,004		

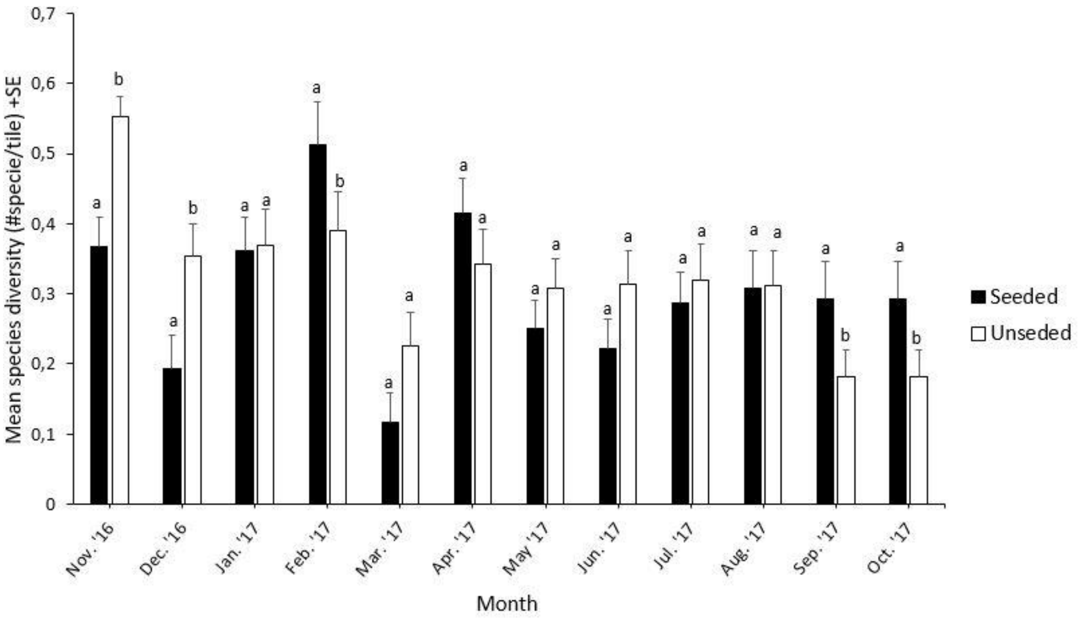

Figure 2. 17: Mean sessile/sedentary species diversity (Shannon-Wiener) over the 12-month sampling period (November 2016-October 2017) on seeding (seeded and unseeded) pooled for both sites (East and West banks) and for all treatments (flat, 2.5 cm tiles and 5 cm tiles). Error bars represent standard error. The letters above the graphs symbolise homogenous groups according to the Fisher LSD post-hoc test for the interaction of month*seeding.

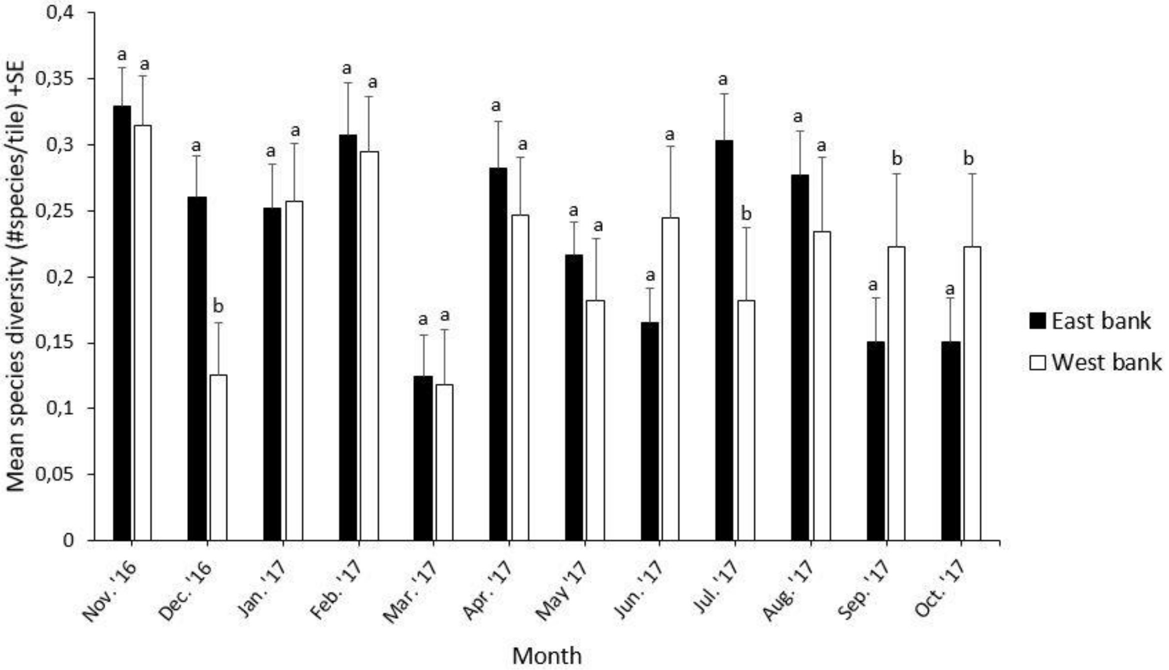

Figure 2. 18: Mean sessile/sedentary species diversity (Simpson's) over the 12-month sampling period (November 2016-October 2017) at both sites (East and West banks) pooled for seeding (seeded and unseeded) and for all treatments (flat, 2.5 cm tiles and 5 cm tiles). Error bars represent standard error. The letters above the graphs symbolise homogenous groups according to the Fisher LSD post-hoc test for the interaction of month*site.

Growth and mortality of seeded mussels

The analysis of the three-way repeated measures ANOVA on the effect of site, treatment and month on length growth showed a significant effect on the interaction between month and treatment ($p < 0.01$), and treatment and site ($p < 0.001$) had (Table 2.15). Throughout the sampling period, growth in length of mussels seeded on the 2.5 cm and 5 cm tiles was significantly higher compared to flat tiles (Figure 2. 19). During some months however, length growth significantly differed between complex tiles. In March 2017, 2.5 cm had a significantly higher length growth as compared to 5 cm and in April 2017 and June 2017 the pattern was reversed. At both banks, 2.5 cm and 5 cm tiles length growth was higher than on flat tiles, however, length growth in 2.5 cm tiles differed between the banks, with east bank having higher length growth than the west bank (Figure 2.20).

Table 2. 15: Three-way repeated measures ANOVA testing the effect of treatment, site and month on the height, length and width growth of mussels in the Port of East London, over the 12-month sampling period (November 2016-October 2017). SS = Sum of Squares, df = degrees of freedom, MS = Mean Squares, F = F-ratio, p = p-value. The level of significance is represented by asterisks with p≤0.001 = *, p≤0.0001 = ** and non-significant (n.s.). Significant results are in bold.

	HEIGHT					LENGTH					WIDTH				
Effect	df	SS	MS	F	p	df	SS	MS	F	p	df	SS	MS	F	p
Month	**10**	**0,86**	**0,09**	**7,41**	**	10	9,25	0,93	1,84	n.s.	10	0,29	0,03	1,84	n.s.
Site	1	0,13	0,13	1,68	n.s.	1	0,77	0,77	1,32	n.s.	1	0,02	0,02	0,99	n.s.
Treatment	**2**	**3,01**	**1,50**	**19,82**	**	**2**	**120,89**	**60,44**	**103,38**	**	2	0,02	0,01	0,39	n.s.
Error	23	1,75	0,08			23	13,45	0,58			23	0,55	0,02		
Month*Site	10	0,23	0,02	2,00	n.s.	10	6,18	0,62	1,23	n.s.	**10**	**0,42**	**0,04**	**2,67**	**
Month*Treatment	20	0,18	0,01	0,77	n.s.	**20**	**19,53**	**0,98**	**1,94**	*	20	0,29	0,01	0,94	n.s.
Treatment*Site	2	0,06	0,03	0,41	n.s.	**2**	**6,78**	**3,39**	**5,80**	*	2	0,09	0,04	1,80	n.s.
Month*Treatment*Site	20	0,13	0,01	0,55	n.s.	20	14,36	0,72	1,43		20	0,35	0,02	1,11	n.s.
Error	230	2,68	0,01			230	115,79	0,50			230	3,60	0,02		

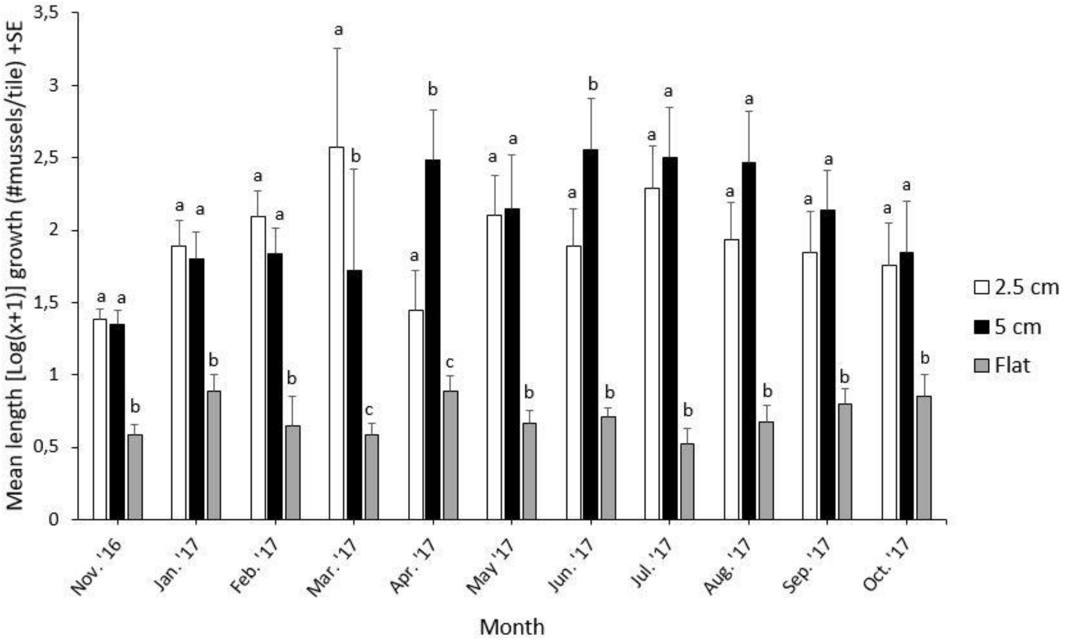

Figure 2. 19: Mean monthly growth in length of mussels for each treatment (flat, 2.5 cm tiles and 5 cm tiles) over the 12-month sampling period (November 2016-October 2017) pooled for both sites (East and West banks). Error bars represent standard errors. The letters above the graphs indicate the homogenous groups according to the Fisher LSD post-hoc test for the significant factor month*treatment interaction.

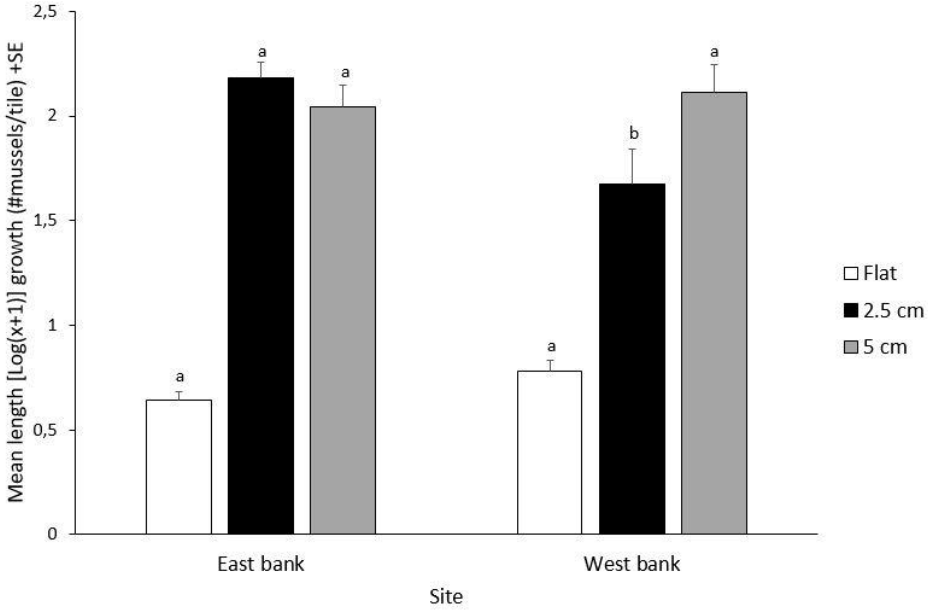

Figure 2. 20: Mean monthly growth in length of mussels for each treatment (flat, 2.5 cm tiles and 5 cm tiles) at both sites (East and West banks) pooled for the 12-month sampling period (November 2016-October 2017). Error bars represent standard errors. The letters above the graphs indicate the homogenous groups according to the Fisher LSD post-hoc test for the significant factor site*treatment interaction.

There was a significant effect of treatment on the height growth (Table2.15), being significantly higher in 2.5 and 5 cm tiles than flat tile (Figure 2. 21). There was also a significant effect of month on the height growth ($p < 0.0001$) (Table 2.15). The growth rate for height of the mussels was significantly higher in January 2017, one month after the experiment started, than any other month. The lowest height growth rate was observed in November 2016, one month after the start of the study (Figure 2.22).

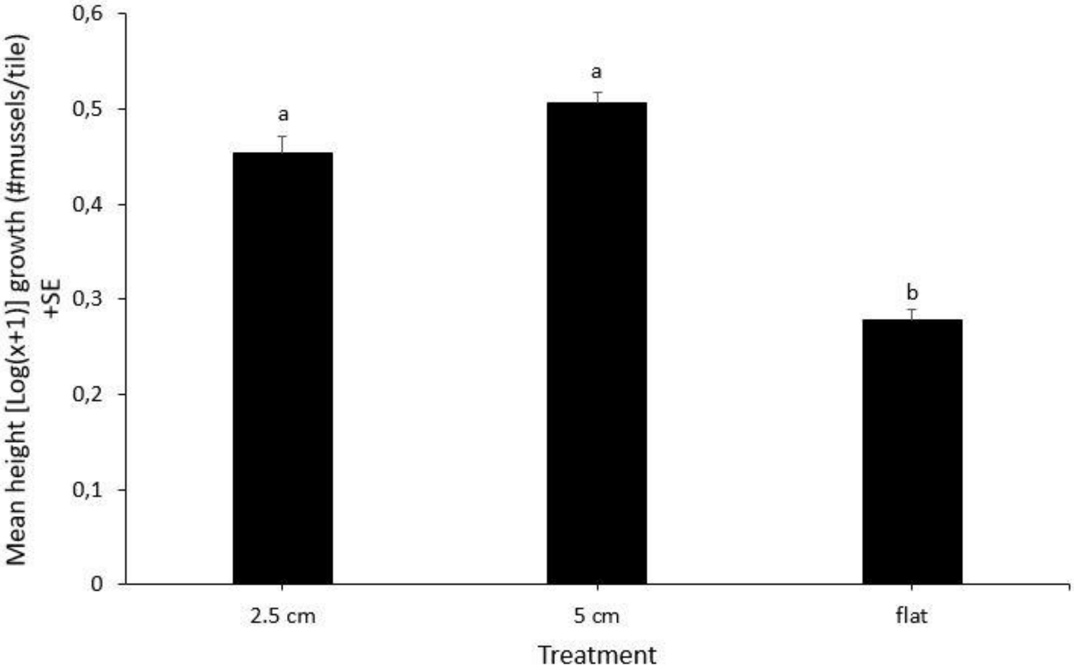

Figure 2. 21: Mean monthly growth in height of mussels for each treatment (flat, 2.5 cm tiles and 5 cm tiles) pooled for the 12-month sampling period (November 2016-October 2017) and both sites (East and West banks). Error bars represent standard errors. The letters above the graphs indicate the homogenous groups according to the Fisher LSD post-hoc test for the factor treatment.

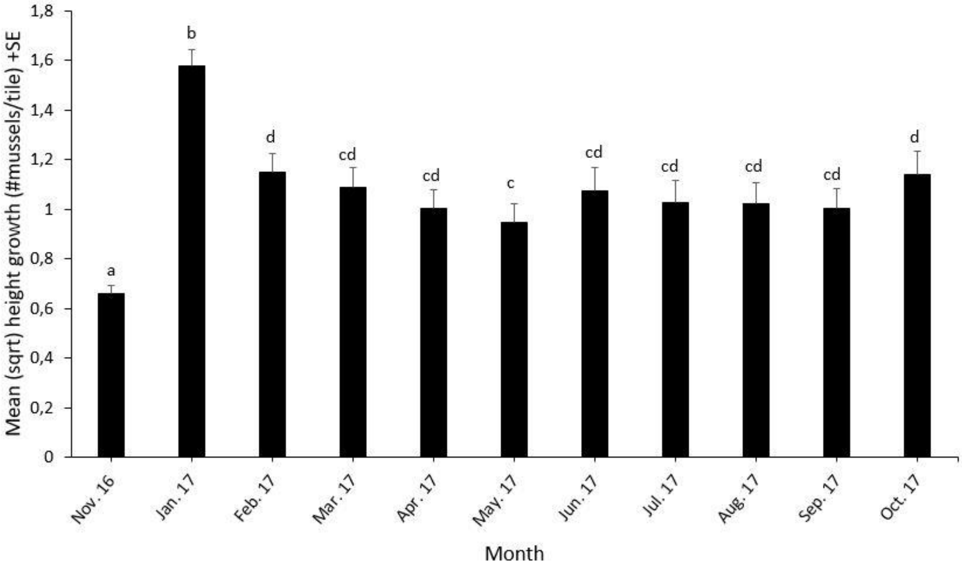

Figure 2. 22: Mean monthly growth in height of mussels over the 12-month sampling period (November 2016-October 2017) pooled for all treatments (flat, 2.5 cm tiles and 5 cm tiles) and both sites (East and West banks). Error bars represent standard errors. The letters above the graphs indicate the homogenous groups according to the Fisher LSD post-hoc test for the factor month.

The interaction between month and site had a significant effect on the growth of mussel width ($p < 0.001$) (Table 2.15). In January and February 2017, mussels on the West bank were significantly larger in width than mussels on the East bank. In July 2017 however, mussels on the East bank were significantly larger in width than those on the West bank (Figure 2.23). No significant difference was observed in mussel width during all other months between those of the two banks.

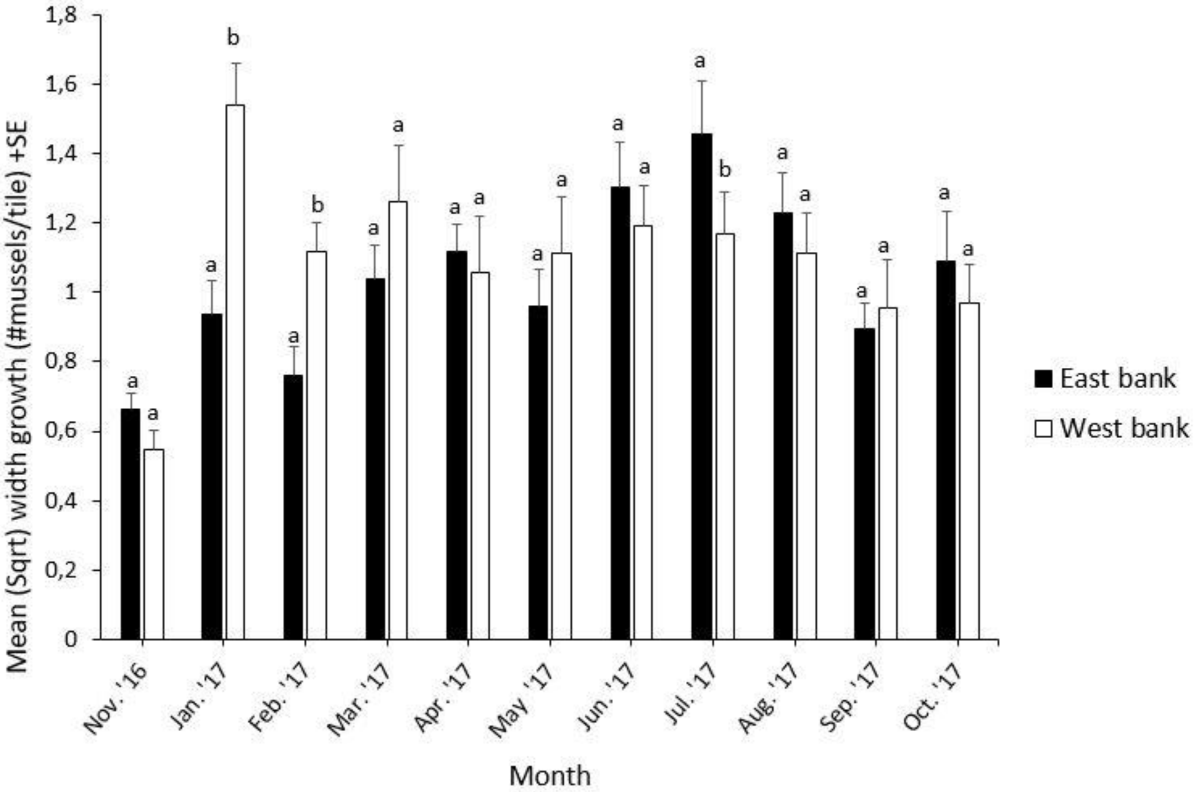

Figure 2. 23: Mean monthly growth in width of mussels over the 12-month sampling period (November 2016-October 2017) at the two different sites (East and West banks) pooled for all treatments (flat, 2.5 cm tiles and 5 cm tiles). Error bars represent standard error. The letters above the graphs symbolise homogenous groups according to the Fisher LSD post-hoc test for the significant factor month*site interaction.

There was a significant effect of month on the mortality ($p < 0.0001$) of mussels seeded on the tiles deployed on either bank of the Port of East London (Table 2.16). Over the 12-month study period, the lowest mortality occurred in May and June 2017, while the highest mortality was recorded in October 2017 (Figure 2.24).

Table 2. 16: Three-way repeated measures ANOVA testing the effect of treatment, site and month on the mortality (Log(x+1) transformed) of mussels in the Port of East London, over the 12-month sampling period (November 2016-October 2017). SS = Sum of Squares, df = degrees of freedom, MS = Mean Squares, F = F-ratio, p = p-value. The level of significance is represented by asterisks with p≤0.0001 = * and non-significant (n.s.). Significant results are in bold.

Effect	df	SS	MS	F	p
Month	**11**	**5,78**	**0,53**	**4,43**	*****

Site	1	0,00	0,00	0,00	n.s.
Treatment	2	0,41	0,21	1,14	n.s.
Error	24	4,33	0,18		
Month*Site	11	1,92	0,17	1,47	n.s.
Month*Treatment	22	3,62	0,16	1,39	n.s.
Treatment*Site	2	0,67	0,33	1,85	n.s.
Month*Treatment*Site	22	1,68	0,08	0,64	n.s.
Error	264	31,31	0,12		

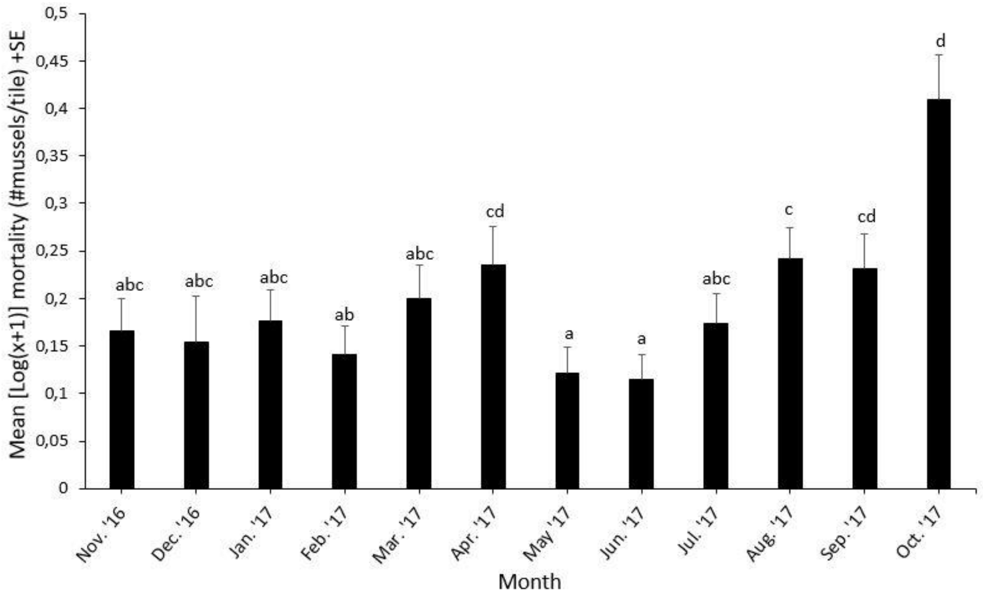

Figure 2. 24: Mean mortality of mussels over the 12-month sampling period (November 2016-October 2017) pooled for all treatments (flat, 2.5 cm tiles and 5 cm tiles) and both sites (East and West banks). Error bars represent standard errors. The letters above the graphs indicate the homogenous groups according to the Fisher LSD post-hoc test for the factor month.

Biomass of the seeded mussels

There was a significant effect of treatment ($p < 0.001$) on the biomass of the dry weight (other organisms; Table 2.17). Biomass on the 5 cm tiles was significantly higher than that on 2.5 cm tiles and flat tiles (Figure 2.25).

Table 2. 17: Three-way ANOVA testing the effect of treatment, site and seeding on the biomass of the dry weight in the Port of East London, South Africa. SS = Sum of squares, df = degrees of freedom, MS = Mean squares, F = F-ratio, p = p-value. The level of significance is represented by asterisks with $p \leq 0.001$ =* and non-significant (n.s.). Significant results are in bold.

Effect	SS	df	MS	F	p
Site	0,11	1	0,11	6,01	n.s.
Seeding	**0,22**	**1**	**0,22**	**11,88**	*****
Treatment	**0,26**	**2**	**0,13**	**6,91**	*****
Site*Seeding	0,01	1	0,01	0,46	n.s.
Site*Treatment	0,12	2	0,06	3,17	n.s.
Seeding*Treatment	0,02	2	0,01	0,47	n.s.
Site*Seeding*Treatment	0,10	2	0,05	2,58	n.s.
Error	0,90	48	0,02		

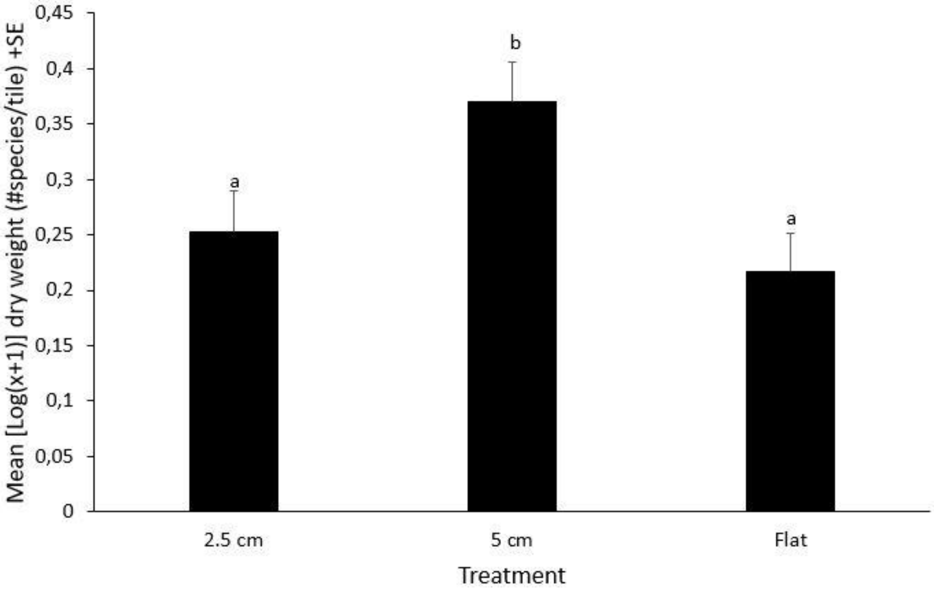

Figure 2. 25: Mean biomass (g) of dry weight for each treatment (flat, 2.5 cm ridged tiles and 5 cm ridged tiles) pooled for seeding (seeded and unseeded) and both sites (East and West banks). Error bars represent standard error. The letters above the graphs symbolise homogenous groups according to the Fisher LSD post-hoc test for the significant factor treatment.

There was a significant effect of seeding ($p < 0.01$) on the biomass of the dry weight (other organisms; Table 2.17). Biomass of the dry weight was significantly higher on seeded than unseeded tiles (Figure 2.26).

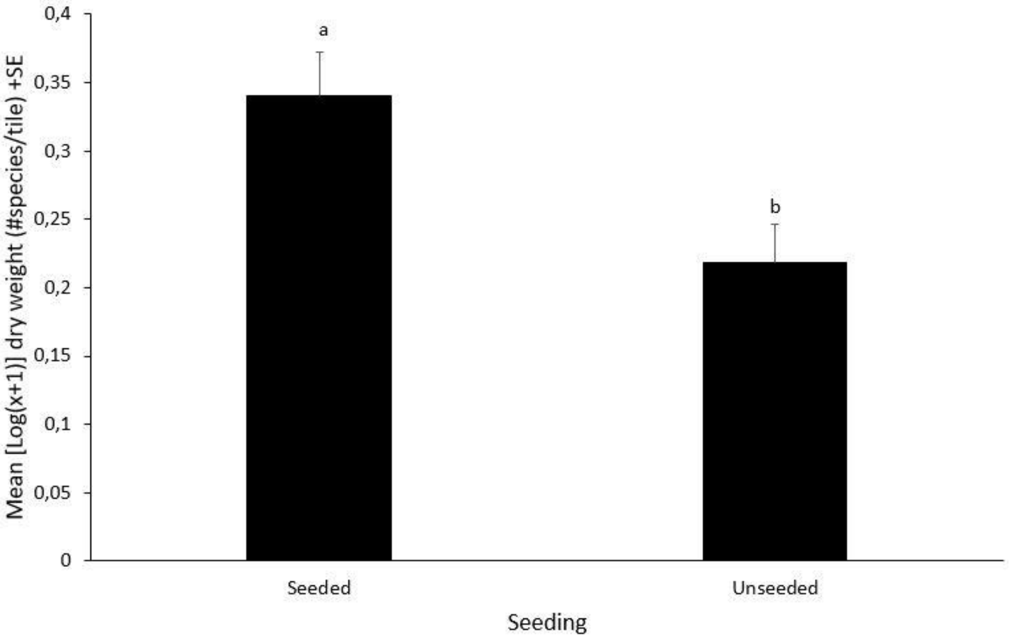

Figure 2. 26: Mean biomass (g) of dry weight on seeding (seeded and unseeded) pooled for all treatments (flat, 2.5 cm ridged tiles and 5 cm ridged tiles) and both sites (East and West banks). Error bars represent standard error. The letters above the graphs symbolise homogenous groups according to the Fisher LSD post-hoc test for the significant factor seeding.

There was a significant effect of month on the weight of dry shell (p < 0.0001) and weight of soft tissue (p < 0.0001) of mussels seeded on the tiles deployed on either bank of the Port of East London (Table 2.18). In October 2017, the weight of both the dry shell and soft tissue were significantly higher than that of October 2016 (Figure 2. 27).

Table 2. 18: Three-way repeated measures ANOVA testing the effect of treatment, site and month on tissue and shell weight (Log(x+1) transformed) of mussels in the Port of East London, over the 12-month sampling period (November 2016-October 2017). SS = Sum of Squares, df = degrees of freedom, MS = Mean Squares, F = F-ratio, p = p-value. The level of significance is represented by asterisks with p≤0.0001 = * and non-significant (n.s.). Significant results are in bold.

	Shell					**Tissues**				
Effect	df	SS	MS	F	p	df	SS	MS	F	p
Treatment	2	0,01	0,00	1,54	n.s.	2	0,00	0,00	0,57	n.s.
Site	1	0,00	0,00	0,32	n.s.	1	0,00	0,00	0,03	n.s.
Month	**1**	**0,23**	**0,23**	**119,86**	*****	**1**	**0,01**	**0,01**	**39,40**	*****
Site*Treatment	2	0,00	0,00	0,09	n.s.	2	0,00	0,00	2,02	n.s.

Site*Month	1	0,00	0,00	0,07	n.s.	1	0,00	0,00	4,44	n.s.
Treatment*Month	2	0,00	0,00	0,00	n.s.	2	0,00	0,00	0,15	n.s.
Site*Treatment*Month	2	0,00	0,00	0,85	n.s.	2	0,00	0,00	0,91	n.s.
Error	37	0,07	0,00			37	0,01	0,00		

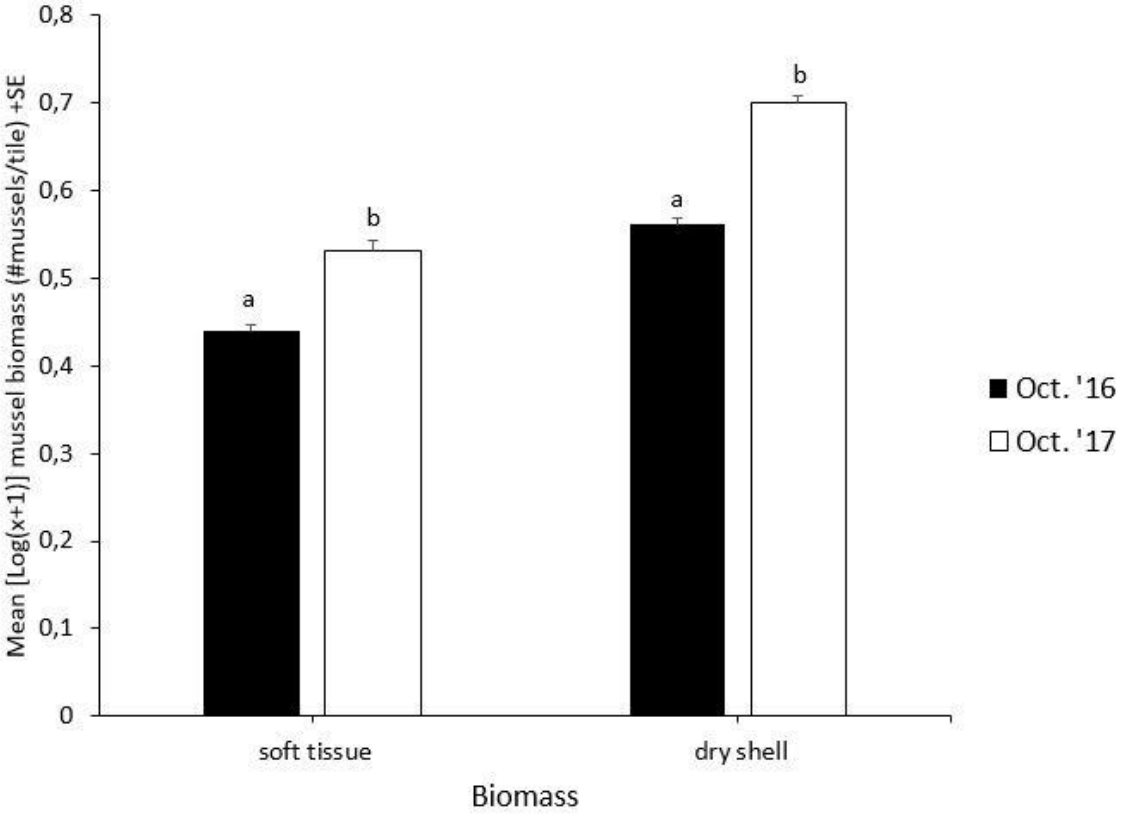

Figure 2. 27: Mean (Log(x+1) transformed) biomass (g; soft tissue and dry shell) of mussels at the start (October 2016) and end of 12-month study (October 2017) pooled for all treatments (flat, 2.5 cm tiles and 5 cm tiles) and both sites (East and West banks). Error bars represent standard error. The letters above the graphs symbolise homogenous groups according to the Fisher LSD post-hoc test for the significant factor month.

2.4. Discussion

Increased complexity can improve species diversity (Loke *et* al., 2015). In this study, complexity treatments to the various structures (2.5 cm and 5 cm) increased the growth in height and the length of the seeded mussels and the abundance of the associated mobile species diversity, while simple tiles (flat) with seeded bivalves increased the assemblages of sessile/sedentary species. Mobile species diversity increased with complexity (2.5 cm and 5 cm tiles), with seeded tiles being mostly colonised by limpets, chitons and sea snails, while only a few of these species colonised the flat, non-complex treatments, at least for the first 5 months of the study. The simple treatments (flat) were poorly colonised by mobile species, likely due to the risk of dislodgment from wave and predation (Strain *et al.,* 2017). Mobile organisms were found in seeded complex treatments, possibly seeking refuge from predation and desiccation (Chapman and Underwood, 2011).

Contrary to the natural rocky shores (e.g., rock pools, pits, grooves and crevices) (Underwood and Chapman, 1989; Erlandsson *et al*., 1999; Aguilera *et* al., 2014), the absence of complex structures on artificial structures can result in a reduced number of species as compared to substrates with plenty complex structures (like in the natural rocky shores), due to high levels of stress, caused by factors such as desiccation at low tide (Underwood and Chapman, 1998, Chapman, 2003, Kostylev *et al*., 2005). In those rocky shores where complex habitat such as rock pools and crevices are absent, species diversity is indeed reduced (Dafforn *et al*., 2015). An increase in structurally complex habitats appears to favour species diversity and/or survivorship of benthic organisms (Strain *et al.,* 2018). A similar study to this one, conducted in Singapore using tiles of varying structural complexity, reported a greater mobile species diversity due to microhabitat availability (Loke *et al*., 2015) confirming the importance of complexity on artificial structures (Firth *et al*., 2014). Similarly, a study conducted in Australia on an urbanised coastline also reported the positive effect of the complexity of artificial structures on mobile assemblages (Lavender *et al*., 2017).

The richness of mobile species did not differ between the 2.5 cm and 5 cm treatment tiles, likely because the micro scale complexity is most successful for encouraging colonisation (Moschella *et al*. 2005). Nevertheless, it has been noticed that micro scale complexity of depth can have some limited effects if monitoring period is relatively short-term (Evans *et al*., 2015).A small-sized crevices (1-100 cm) have been shown to affect species richness, as early colonisers tend to occupy all the available surface area, with little surface area available for colonisation of organisms that arrive later (Chapman and Underwood, 2011; Loke *et al*., 2015). This study confirms this trend, as mobile species filled the 2.5 cm and 5 cm treatments of seeded tiles. High mobile species diversity within mussel patches/beds has been recorded (Tsuchiya, 2002; Borthagaray and Carranza, 2007) and this study confirms such a positive correlation, as an increase of mobile species diversity occurred on tiles with seeded mussels.

The high diversity of mobile species on seeded tiles is possibly due to the fact that mussels, as ecosystem engineers (Thompson *et al.,* 1996; Borthagaray and Carranza, 2007), facilitate biodiversity by providing habitat complexity and ameliorating the conditions of the primary substrate for small mobile invertebrates (Crooks and Khim, 1999; Gutiérrez *et al*., 2003). This has also been confirmed by the higher dry weight (weight of the organisms left on the tiles after mussels were removed) on seeded than unseeded tiles in this study to indicate the importance of *Perna perna* (ecosystem engineer) (O'Connor *et al*., 2006).

Increased complexity can also positively affected sessile/sedentary diversity. It has been suggested that deeper complex structures support more sessile/sedentary species (Ranta, 1982; Fairweather and Underwood, 1991; Moschella *et al*. 2005). Nonetheless, this was not the case for this study as the species composition was higher on flat unseeded tiles compared to other treatments, likely because flat empty tiles offer a greater proportion of available surface area to "encrusting" species (Birdsey *et al.,* 2012). Sessile/sedentary species have in fact been found to colonise treatments lacking high complexity due to increased availability of space (Lavender *et al*., 2017). This trend has been observed elsewhere, where species richness has been found to be slightly higher in shallow than deep habitats (Browne and Chapman 2014; Firth et al. 2014).

Another possible reason that sessile/sedentary species may have avoided complexity could have been the increased presence of mobile predators on complex treatments, likely seeking refuge from wave effects while looking for food (Chapman and Blockley, 2009). High colonisation by mobile organisms on crevices might have also had an impact on the low availability of sedentary species due to a lack of space (William *et al*., 2013). Marine sessile/sedentary species such as marine algae tend to colonise and dominate artificial bare structures (Chapman, 2003; Bulleri *et al*., 2005; Strain *et al*., 2017) and this was the case in this study, where *Ulva* sp and *Hildenbrandia rubra* were the most contributing sessile species throughout the study at both sites (although with spatio-temporal differences in patterns).

Due to the pioneering nature of the most dominant sessile species, the diversity of this group during this study was highest (though not significantly) in November 2016, possibly due to the increased surface area available to colonise during the first month of the study (Birdsey *et al*., 2012). Increased species diversity of sessile/sedentary species during the first month of a successional study is common due to the sudden availability of additional space for colonisation (Smith *et al*., 2014).

Species diversity in the marine algal community is influenced by mobile grazers (Williams *et al*., 2013). In this study, mobile grazers such as limpets were present throughout the sampling period and may have limited the algal colonisation on the complex tiles. Despite being grazed upon, algae have been observed to grow beyond a 'grazeable' size to thrive on tiles (Bayne, 1999; Nandakumar, 1996) and stabilise through time (Benedetti-Cecchi, 1995). Availability of nutrients such as nitrates is one of the factors that contribute to the species diversity of primary producers (Quin *et al*., 2007). In this study, nutrient availability from the upstream section of the estuarine harbour may have influenced algal colonisation, although this component was not measured.

Site variability in the diversity of species associated with mussel beds is common (Commito *et al*., 2005) and this study confirms this trend in that species diversity, particularly in the mobile species, was greater on the East than the West bank, most likely due to the increased mussel abundance. In this study, the West bank is located closest to the area where ships dock, which indicates that the low species diversity observed could also be due to the impact of boat-generated waves which might consistently dislodge the organisms (Bishop, 2008), although there was no clear trend between the sites regarding water motion.

Two indices were used to calculate species diversity and yielded to different results, as their assumption to sample community differed (Clarke and Warwick, 2001). The Shannon-Wiener diversity index provided positive results for the diversity of mobile species in relation to the complex seeded tiles as compared to non-complex tiles.

In this study, mussels from the complex tiles were longer and higher than those from non-complex tiles. In sheltered areas, mussels are observed to experience reduced growth and become small and long due to limited water circulation and associated low nutrient availability (Baird, 1966). Nevertheless, the opposite effect has also been observed (McQuaid and Phillips, 2006; Rius and McQuaid, 2006). The height and length of mussels in complex tiles, in this study, were larger than those on flat tiles, likely because the crevices provided insufficient space for mussel "sideways" growth (width) (Moschella *et al.,* 2005; Moriera *et al.,* 2007). Maximum growth (mussel height in this study), was observed during summer (January 2017). This is in line with the fact that food availability in summer is the most abundant due to the seasonal increase in heavy rains, run-off and primary productivity (Griffiths, 1980; Tomalin, 1995; Dekker and Beukema, 1999; Beal *et al.,* 2001; Wong and Cheung, 2001).

Food availability is key for growth (Seed, 1968; Hawkins *et al.,* 1992), and ports tend to have plenty (phytoplankton) for mussel growth compared to the open coast (Karayücel and

Karayücel, 2000; Helson *et al.,* 2007). East London, the city where the port of this study is located, experiences intense tourism during summer (ASCLME, 2012), as well as heavy run-off into the Buffalo River, with three dams connected to this river (Weaver, 1982). The increased mussel growth (determined by shell height and length) during the summer months could, therefore, be linked to increased nutrients from waste waters released into the Buffalo River (Seed, 1968; Fatoki and Mathabatha, 2001). Mussels are suspension feeders and in South Africa are not limited by a low availability of nutrients due to high water circulation, and so they can potentially reach maximum growth under favourable conditions (van Erkom Schurink and Griffiths, 1993; Steffani and Branch, 2003). Nevertheless, chlorophyll-*a,* which is generally higher in harbours than on the coast (Helson *et al.,* 2007), is regarded as the key to productivity and an important component for the growth of mussels (Steele, 1962; Cullen, 1982; Boyer, 2009).

Perna perna can also feed opportunistically on crustacean nauplii, harpacticoid copepods (Lehane and Davenport, 2006) and mussel larvae (Davenport *et al.,* 2000; Alfaro, 2006; Porri *et al.,* 2008) which further favours growth due to the variability in their diet (Alber and Valiela, 1994; Helson *et al.,* 2007). The growth of mussels, in terms of width, varied at the two sites during specific months. The increased width of mussels observed in summer (January and February 2017) may have been influenced by the seasonal variation in the food supply, as its availability is generally greater in summer than in winter (Rodhouse *et al*., 1984; Helson *et al*., 2007). The West bank of the study site was closest to the area where ships dock, and mussel growth may have been higher here because of increased food availability, made possible by the wave action generated by the ships (Bishop, 2008).

Biomass of both soft tissue and dry shell differed according to season (both highest in October 2017, at the end of the study), however, there was no change in biomass regarding the effect of treatment. As the size of a mussel increases it is known that so does the weight (biomass) (Franz, 1993), as its mass is mostly made up of shell (Hickman, 1979). The positive correlation between the shell and soft tissue weight of the mussel can be further reinforced under favourable conditions, such as increased food availability and optimal temperatures (Seed, 1973). This positive relationship however did not match the otherwise treatment effect and positive influence of complexity on growth. For this study, the increase in shell weight and soft tissue could be the result of increased nutrient content in the harbour (Helson *et al.,* 2007), however, this study did not have access to data regarding nutrient availability in the Port of East London over this time period. An increase in mussel weight due to increased nutrient availability has been observed in harbours (Rodhouse *et al.,* 1984) as well as in natural systems (Diehl *et al.,* 1986; Bustnes and Erikstad, 1989).

Mussel mortality fluctuated throughout the 12-month sampling period, with the highest mortality recorded in October 2017 (spring, and end of the study) and lowest mortality in May and June 2017 (winter). Seasonality seems to have therefore influenced the mortality of the seeded mussels during this study. Variations in environmental conditions such as temperature, wave action and risk of desiccation are known to influence mortality of mussels on a seasonal basis in the region (McQuaid and Lindsay, 2000; Zardi *et al.,* 2008). High mortality of mussels (*Mytilus edulis*) in spring has also been recorded in temperate regions of the northern hemisphere after a bloom of the *Phaeocystis globosa* (Prymnesiophyceae) harmful alga (Verity *et al.*, 1991) resulted in depletion of oxygen in the water column (Peperzak and Poelman, 2008). In this study, some seeded mussels were entirely missing from the tiles, and this could have been a result of dislodgement by waves (Seed, 1993; Denny, 1995; McQuaid and Lindsay, 2005; Bownes and McQuaid, 2010), as strong inshore hydrodynamics (in terms of strength of flow and turbulence) can displace mussels (Denny 1987). Wave action is greatest in winter and summer during rainy and intense storm events (Goschen and Schumann, 2011), with the largest waves in the study region originating from strong winter westerly winds that blow consistently over long periods of time (Goschen and Schumann, 1988; Garstang *et al.,* 1996; Hauck and Sowman, 2003).

In contrast, however, wave action seems to have had limited effect on the survival of mussels, as lowest mortality was observed in winter. An expected increase in mortality in winter could derive from mussel energy generally invested in the production of byssal threads for increased attachment onto the substrate (Griffiths and King, 1979; Hawkins and Bayne, 1985; Zardi *et al.,* 2006). Mussel mortality was highest in October 2017, during spring. The high mortality observed in October could be due to the extended reproductive season of *P. perna* in South Africa (from winter to summer; van Erkom Schurink and Griffiths, 1991), when byssal thread production is weakened due to the large investment in gonad development (Seed and Suchanek, 1992; Zardi *et al.,* 2007), causing mussels to be vulnerable to dislodgement by wave action (Carrington, 2002). Some mussels shells were intact, but had no tissue, particularly in summer (December 2016 and February 2017) and spring (September and October 2017), suggesting that heat stress also could have contributed to desiccation, leading to mortality

(Rius and McQuaid, 2006) and providing proof of the vulnerability of *P. perna* to heat (Hockey and Van Erkom Schurink, 1992; Zardi *et al.,* 2006).

In this study, some mortality could have been caused by parasites and/or desiccation (Kennedy, 1976; Calvo-Ugarteburu and McQuaid, 1998). Additional source of mortality could have resulted from individuals that did not cope with manipulation. This is however unlikely given the low mortality at the start of the study (month 1). Mussels infected by parasites are easy to open and are thus vulnerable to predation (Calvo-Ugarteburu and McQuaid, 1998). Nevertheless, parasites can also prevent mortality against heat stress (Zardi *et al.,* 2016), as mussels tend to lose water (body) through evaporation, when exposed to extreme temperatures (Branch and McQuaid, 1985; Branch, 2001). Parasites cause a lowering of body heat of mussels by whitening the outer layer of the shell, which reduces the ability of organisms to absorb solar energy (Zardi *et al*., 2016). High mussel mortality during the warmer seasons has been observed before in harbours (Lachowicz, 2005) and at local rocky shores (Kennedy, 1976; Rius and McQuaid, 2006) and it has mostly been attributed to high temperatures causing desiccation (Lachowicz, 2005).

Some mussel shells were cracked, while others were drilled, suggesting predation by birds, crabs (Elner, 1978; Griffiths and Hockey, 1987) and gastropods (Seed, 1993) respectively. The gastropod *Nucella* spp. feeds by secreting chemicals (Seed, 1993) and making small circular holes of approximately 40 mm on mussel shells (Griffiths and Blaine, 1994). Similar holes on mussels were observed in this study, concurring with local literature indicating that *Nucella* spp. do prey on mussels (McQuaid, 1985), including *Perna perna* (Lindsay, 1998).

Nevertheless, whelks, octopus and crabs seemed to have a weak effect in terms of predation on mussels (Seed, 1993; Plass-Johnson *et al.,* 2010). In this study, the presence of increased structural complexity did not have an effect on mortality of the seeded mussels, and the hypothesis # 3 was rejected.

The study also examined the possible influence of the tested tiles on the presence of invasive species, as artificial structures within harbours have been known to favour colonisation by alien species (Bulleri and Chapman, 2004; Bulleri and Airoldi, 2005; Chapman and Blockley, 2009). Also in this study the results of adult cover showed a higher abundance of one of the most common invasive species in the country *Mytilus galloprovincialis* in the port compared to natural habitat. No records of alien species were found on the tiles. The same study carried out by partners from the World Harbour Project in Sydney Harbour, Australia, confirmed the positive effect of artificial structure on local biodiversity, with only local indigenous species colonising the artificial structures (Strain *et al*., 2017). Although updates from other partners from this international project are still emerging, this positive response of only local species colonisation, supporting a zero presence of alien species, might make the Port of East London an ideal location for the use of these novel eco-engineering artificial structures.

To conclude, complexity of artificial structures can have an influence on local marine mussel growth (height and length). The additional seeding of mussels on these structures can further improve the presence of algal propagules and colonisation by mobile species. Seeded mussels are likely to have provided additional habitat, moisture and refuge from predation for mobile and sessile/sedentary species. Overall, the use of these simple treatments had a positive effect on the growth (height and length) of mussels, diversity of mobile species and richness of sessile communities. For a more comprehensive and long-term inference of the enhancing nature of these complex structures, the time frame of this type of study could be increased to 3-5 years. This will effectively measure the durability of changes brought about by these engineered structures on the presence of mobile and sessile/sedentary species, as well as the long-term wellbeing of the ecosystem engineers used (in this case, mussels).

3. COMPARING SETTLEMENT AND RECRUITMENT OF BIVALVES BETWEEN THE PORT OF EAST LONDON AND THE ADJACENT INTERTIDAL COASTLINE

3.1. Introduction

Coastal human-made structures can create barriers to the movement of organisms and resources and change the trophic dynamics (Hodgson *et al.,* 2012), thus influencing the genetic, population and community structures (Bishop *et al.,* 2017). Reduced hydrodynamics (as strength of flow and circulation) in harbours and enhanced growth of propagules due to availability of nutrients could nevertheless result in increased connectivity towards adjacent open coastlines for some taxa (Shima and Swearer, 2010). Artificial structures however, generally act as barriers to recruitment of propagules, especially of those taxa that are patchily distributed on hard substrata and naturally require structural complex habitats with the presence of rock pools and crevices (Chapman, 2003). In addition, high anthropogenic activities within the harbour can lead to increased pollution which may reduce recruitment, compared to natural rocky shores (Chueng, 1993). Adult benthic invertebrates can in fact tolerate high levels of pollution (Lee, 1985), however, increased contaminants concentration can be toxic to larvae, resulting in increased mortality due to their sensitivity to high pollution levels (Beiras *et al*., 2002).

Alternatively, vertical walls in ports and harbours, with the shading they provide (Chan and Williams, 2003), can reduce heat stress and positively affect settlement and recruitment of invertebrates like mussels, compared to the thermally challenging conditions on natural rocky shores (Lam *et al.,* 2009), . Organisms settled on these vertical structures during warmer times (especially at midday to early afternoon spring low tides) are shaded for extended periods (Chan *et al*., 2006). Nevertheless, horizontal natural rocky shores also can offer protective microhabitats such as crevices, pits and pools to provide similar conditions (Garrity, 1984).

Settlement and recruitment of mussels differ between human-made structures and natural rocky shores due to their physical and chemical characteristics of these environments, with implications on weathering and heterogeneity of habitat (Walters and Wethey, 1996; Abelson and Denny, 1997). Generally, fragmentation, the separation of large patches of habitat into smaller ones, negatively affects connectivity in rocky shores (Goodshell *et al*., 2007). Habitat fragmentation in harbours as a result of human disturbance (anthropogenic fragmentation) is widespread and continuous (Taylor *et al*., 1993; Ricketts, 2001). As a result, anthropogenic fragmentation in harbours may have a larger impact on connectivity than natural fragmentation, due to large patches of featureless structures replacing the complex rocky shores and determining altered patterns of larval settlement (Goodshell *et al*., 2007).

The ecology of marine benthic populations is largely determined by their early life history processes (Gaines and Roughgarden, 1985; Grosberg and Levitan, 1992; Hughes *et al*., 2000). Many marine invertebrates such as mussels have a complex life cycle that involves sedentary adult broadcast spawners producing pelagic larvae (Menge, 1991; Commito *et al*., 1995; Dobretsov and Wahl, 2001; Pineda, 2000). The larvae of mussels can remain for up to five-six weeks in the water column before arriving back at shore, with their pelagic duration influencing survival and settlement success (Kautsky, 1982). Benthic population dynamics and the population structure of sedentary and sessile species is therefore largely regulated by the availability of settlers and their successful recruitment (Connell, 1985; Menge, 1991; Grosberg and Levitan, 1992; Hunt and Scheibling, 1996). An understanding of the mechanisms that regulate sessile/sedentary benthic populations requires the investigation of several early life history processes, including spawning, dispersal, settlement, successful recruitment into the adult habitats (Gaines and Bertness, 1992; Morgan, 2001) and overall connectivity. Ecological connectivity is the exchange of individuals among geographically separated subpopulations (Webster *et al*., 2002; Cowen *et al*., 2016) and, among other factors, it is influenced by coastal urbanisation (Shima and Swearer, 2010; Bishop *et al*., 2017).

Reduced wave action and increased nutrient input are key factors that positively affect connectivity within harbours (Garder, 2000; Helson, 2001; Helson *et al*., 2004) through an enhancement of larval conditions, growth and retention (Shima and Swearer, 2010). Artificially protected, shallow habitats such as harbours and marinas (Arenas *et al*., 2006) are closely influenced by human activity and are therefore subjected to different conditions to those of the adjacent natural coastal systems (Healy *et al*., 1996; Bax *et al*., 2003). An example of such an anthropogenic impact is the discharge of sewage and contaminants into harbours, which can alter the composition of nutrients within the water and sediments (Nilsson *et al.,* 2005), with cascading effects on the diversity (Helson *et al.,* 2004) and reproductive connectivity of coastal populations (which encompasses larval dispersal to recruitment and successful gonadal maturation; Pineda, 2007). Estuarine harbours (such as the Port of East London) have a mixed water column towards the mouth, due to the input of freshwater from a river (Buffalo River), which can create a strong diversity of nutrients and food particles in the water (Xu *et al*., 2010; Humphreys, 2005).

When dealing with larval and supply side ecology of mussels, it is necessary to distinguish between settlement and recruitment, the two fundamental processes that end the dispersal phase of mussels (Pineda, 2007). Settlement describes the initial attachment of pelagic-competent larvae onto the substrate and in the past, it was further divided into a primary and secondary settlement (Bayne, 1964; Seed, 1969; Du Plessis, 1977; Beckley, 1979). Primary settlement would involve the attachment of competent planktonic larvae to filamentous substrates such as algae, in order to be fit enough to settle with the adults (Thorson, 1957; Berry, 1978). Secondary settlement comprises one or multiple detachments of the recently settled larvae from the initial substrate and reattachment onto another substrate and eventually the adult habitat (Thorson, 1957). Follow up research has, however, established that after the primary settlement, larvae can attach directly within adult beds (McGrath *et al*., 1988; King *et al*., 1990; Lasiak and Bernard, 1995). Recruitment describes the permanent joining to the adult populations by the recent settlers which have survived a period of post-settlement mortality (Keough and Downes, 1982; Lasiak and Barnard, 1995; Pineda, 2000).

Pelagic larvae can travel considerable distances (Thorson, 1950), but they must either remain close to the shore or return after offshore dispersal, in order to successfully complete their life cycle (McQuaid and Phillips, 2000; Dobretsov and Wahl, 2001). The colonisation by larvae on a favourable location or substrate where adults occur (Knowlton and Keller, 1986; Roegner, 1991) relies on a number of bio-physical factors that promote onshore transport (Seed, 1969; Bertness *et al*., 1996; Shanks, 1998). Physical factors include current dynamics, local winds, temperature and salinity, while biologically, food supply, chemical cues and larval behaviour are key (Gaines *et al*., 1985; Minchinton and Scheibling, 1991; Pineda, 1994). Wind plays an important role in the ecology of intertidal populations as it drives alongshore currents that supply larvae, causing a change in the distribution of zooplankton (Shanks *et* al., 2003).

Wind is also an important factor in upwelling, the process where strong equatorial wind cause the upward movement of water from deeper to shallower reaches of the ocean and brings nutrients into the euphotic zone (Boje and Tomezak, 1978; Morgan *et al*., 2009). Upwelling can influence settlement and recruitment by acting directly on the larval pool (Pineda, 2000; Morgan, 2001; Underwood and Keough, 2001; Menge *et al*., 2003). The process of upwelling transporting the larvae near the coast and when the equatorial wind relaxes the process is reversed and larvae is transported shoreward (Wing *et al*., 1995; Shanks et al. 2000, Garland *et al*., 2002).

Settlement, and ultimately recruitment, relies upon the availability of larvae (Gaines and Bertness, 1992). The conditions that provide a nearshore supply of larvae, however, may differ among sites, seasons and taxa (Keough, 1983; McQuaid and Phillips, 2006). Nevertheless, settlement and recruitment success within the same biogeographic region can differ across kilometres to just a few centimetres (Petraitis, 1991; Bertness *et al*., 1992; Hunt and Scheibling, 1996). In addition, coastline topography is known to be significant in the distribution of the adult populations (Mace and Morgan, 2006; von der Meden *et al.,* 2008). Coastal topography influences the movement of water and wind, which are ultimately responsible for the transport and delivery of larvae (Wolanski and Hamner, 1988; Bertness *et al.,* 1992; Shanks *et al.,* 2003; Tackenberg, 2003).

Wind also plays a role in the spatial and temporal retention of zooplankton (Roughan *et al*., 2005). Semi-enclosed areas such as harbours, can be effective in tetaining propagules and plankton and further reducing along shore dispersal (Largier *et* al., 1997; Wing *et al*., 1998).

The aim of this study was to investigate the local patterns of settlement and recruitment of mussels and other benthic bivalves within an anthropogenic system (Port of East London) and adjacent natural rocky shore, on the south east coast of South Africa, in order to understand the early temporal and spatial processes driving the structuring of populations of model ecosystem engineers (bivalves) that occur in the region where the harbour is located. This study makes it a one-to-one comparison, with one site in the harbour and one on the natural shores and it was designed to locally address the feasibility of the Port of East London for a possible urban (harbour) site to rehabilitate artificial habitats and enhance natural biodiversity. A decision was made to add within site replication to enhance the robustness of the outcome of this study, based on the local nature of this study and the impossibility to find another harbour in the area. As a first hypothesis, the rates of settlement and recruitment of mussels and other benthic bivalves within the harbour were expected to be higher than at the adjacent natural rocky shores due to increased input of organic nutrients in the urban system (Cheung 1993) and possible more benign hydrodynamics driven by wind speed and direction. Secondly, as the spawning of mussels in the region occurs during summer/autumn, the rates of settlement and recruitment of mussel larvae were expected to increase during those periods (Lasiak and Barnard, 1995; Porri *et al.*, 2006; Zardi *et al.,* 2007). Lastly, settlement and recruitment rates were expected to be highest where the cover (patches) of mussel adult beds was largest due to enhanced settlement and recruitment within the adult populations (Harris *et al.,* 1998, Lawrie and McQuaid, 2001; von der Meden *et al.,* 2008).

3.2. Methodology

3.2.1 Study site

Monthly settlement and recruitment of benthic bivalves were investigated at two replicate locations within the Port of East London and at two replicate locations outside the port, at a natural rocky shore habitat named Winterstrand (Location 1 33°05ˈ34.7ˈˈS 27°48ˈ02.5ˈˈE and location 2 33°05ˈ28.3ˈˈS 27°48ˈ07.2ˈˈE), approximately 21 km west of the port (Figure 3.1). At each site (Port of East London and Winterstrand), the two locations were approximately 400 m apart.

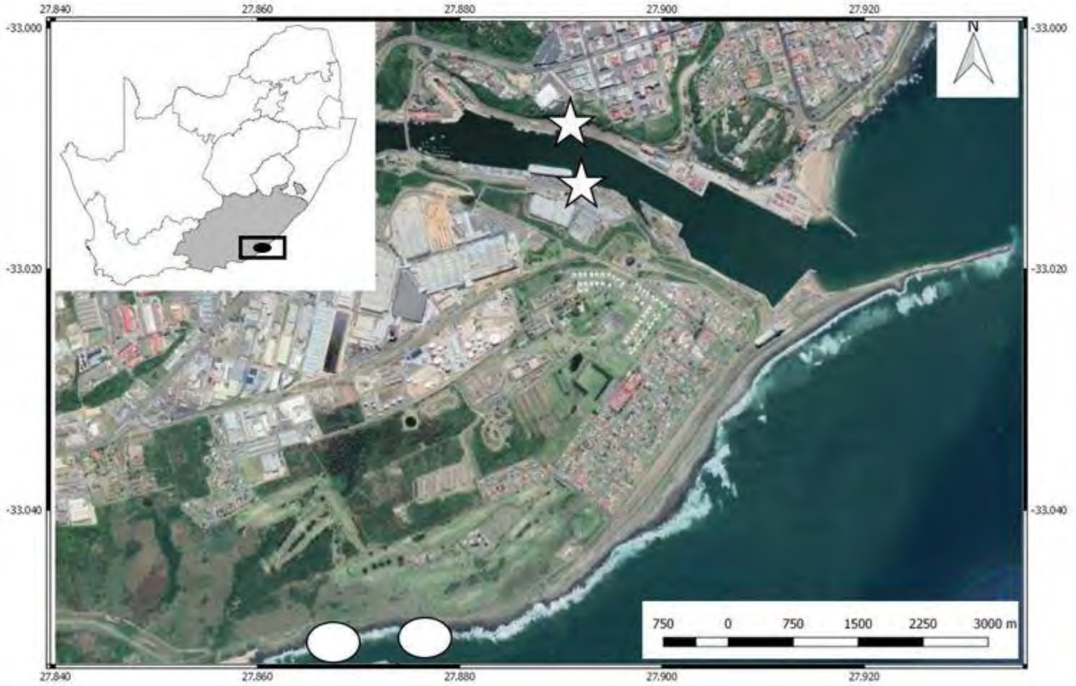

Figure 3. 1: Map of South Africa showing the sampling sites at Winterstrand (west) and the Port of East London (east) located on the south coast of South Africa. Sampling locations within the port (stars) are positioned on the East and West banks of the Buffalo River while locations at Winterstrand (circles) were on natural rocky shores.

3.2.2 Sampling and data collection

Plastic scouring pads were used as collectors for settlers and recruits. This method has been proven suitable to estimate recruitment of mussels (Menge, 1992; Porri *et al.,* 2006). Eyebolts (8 mm) were placed into drilled rock within the lower intertidal area, where the mussel *Perna*

perna is known to be the dominant species, followed by coralline algae including *Gelidium pristoides* (McQuaid *et al.,* 2000) and limpets such as *Scutellastra cochlear* (van Erkom Schurink and Griffiths, 1990; Bownes and McQuaid, 2010). The plastic scouring pads were attached to the eyebolts by four cable ties each. Scouring pads were collected and replaced monthly for a total sampling period of 19 months (November 2016-May 2018). Every month, the scouring pads were collected and stored in 250 ml plastic jars with absolute ethanol. In the laboratory, at the South African Institute for Aquatic Biodiversity (SAIAB), Grahamstown, South Africa, three scouring pads out of the total 10 deployed each month were selected randomly and processed. Bleach (10 ml) was added to each jar containing a scouring pad and left to soak for five minutes to allow for the detachment of any organic material, including bivalve settlers and recruits, without damaging their shell structures (Davies, 1974). The scouring pads were then rinsed thoroughly with tap water onto a 75 µm sieve to collect all bivalve settlers and recruits. Samples were sorted under a microscope (Leica ZOOM 2000 model No. Z45V) to separate bivalve recruits from bivalve settlers and stored in Eppendorf tubes (2 ml) for further taxonomic identification. Bivalves were identified to the lowest possible taxonomic level (Bownes *et al.,* 2008). Bivalves less than 360 µm in length were referred to as settlers and those larger than 360 µm in length as recruits (Porri *et al.,* 2007, Bownes *et al.,* 2008, von der Meden *et al.,* 2008). Bivalve settlers and recruits grouped together that could not be identified were referred to collectively as ‘others’. Adult mussel cover measurements were conducted in a similar manner to that described in Chapter 2 (please refer to Chapter 2 for the methodology of adult mussel cover).

Wind data were obtained from the East London weather station (0059572B8, Latitude: 33.0350, Longitude: 27.8160) every month for the entire study period. Mean monthly wind speeds (m/s) before the time collectors were deployed were calculated and wind roses were produced from the raw data using the formula by Hsu *et al.,* (1994):

$$V_{1m} = V_h*(1/h)^{0.11}$$

where V_{1m} is the wind velocity at a height of 1 m (adjusted height from the anemometer height at the East London weather station), V_h is the wind velocity measured at height h (the actual height of the anemometer at the East London weather station), and h is the height of the anemometer from the sea surface. Due to the low abundance of bivalve settlers and recruits, the effects of wind speed and direction was tested only on recruitment of *P. perna,* as this was the model species of ecosystem engineer used for this study. Wind direction between 45° and 135° was classified as easterly, and that between 225° and 315° as westerly.

3.2.3 Statistical analysis

Given the multiple tests performed over the different taxa, the Benjamini-Hochberg false discovery rate (FDR) was applied to reduce the probability of incurring Type I errors or false positives (Benjamini and Hochberg, 1995) (Table 3.1). Nine three-way nested ANOVAs (Underwood, 1981) were performed to test the effect of site (2 levels, Port of East London and natural rocky shore in Winterstrand, fixed), location (2 levels, nested in site, random) and month (19 levels, October 2016-May 2018, random) on settlement and recruitment of bivalves (*Perna perna, Mytilus galloprovinciallis, Lasaea adansonii*, *Hiatella* sp and 'other bivalves'). A dummy value of 0.01 was used for the analysis of settlement of *M. galloprovincialis* due to very low numbers of settlers. Multiple regressions were performed to test the effect of speed of the prevailing easterly and westerly winds on recruitment of *P.*

perna in the port and natural rocky shore. The software package Statistica (v13.2) (StatSoft Inc. 2018) was used for the statistical analyses.

Table 3. 1: Calculations for the Benjamini-Hochberg procedure of false discovery rate, to reduce the probability of type 1 errors. Bold represents the cut-off significant value.

Treatment	**Effect**	**p**	**Rank**	**B-H**
Perna recruits	Month	0.00	1	0.00
Perna settlers	Month	0.00	2	0.00
Perna recruits	Site*Month	0.00	3	0.00
Perna settlers	Site*Month	0.00	4	0.00
Hiatella settlers	Month	0.00	5	0.01
Hiatella settlers	Site*Month	0.00	6	0.01
'Other bivalves'	Month	0.00	7	0.01
Mytilus settlers	Site*Month	0.00	8	0.01
Mytilus recruits	Site*Month	0.00	9	0.01
Hiatella recruits	Month	0.00	10	0.01
Mytilus settlers	Month	0.01	11	0.01
Lasaea recruits	Location(Site*Month)	0.01	12	0.01
Lasaea recruits	Month	0.01	13	0.01
Lasaea recruits	Location(Site)	0.01	14	0.02
'Other bivalves'	**Location(Site)**	**0.01**	**15**	**0.02**
'Other bivalves'	LocationMonth(Site)	0.02	16	0.02
Lasaea recruits	Site	0.03	17	0.02
Mytilus recruits	Site	0.03	18	0.02
Mytilus recruits	Month	0.04	19	0.02
Lasaea settlers	Site	0.04	20	0.02
'Other bivalves'	Site*Month	0.04	21	0.02
Lasaea settlers	Location(Site*Month)	0.05	22	0.02
Hiatella settlers	Site	0.05	23	0.03
Perna recruits	Location(Site)	0.07	24	0.03
Perna recruits	Site	0.07	25	0.03
Hiatella recruits	Location(Site*Month)	0.10	26	0.03
'Other bivalves'	Site	0.13	27	0.03
Mytilus recruits	LocationMonth(Site)	0.15	28	0.03
Lasaea recruits	Site*Month	0.15	29	0.03
Hiatella recruits	Site	0.15	30	0.03
Hiatella recruits	Location(Site)	0.18	31	0.03

Hiatella recruits	Site*Month	0.22	32	0.04
Lasaea settlers	Location(Site)	0.24	33	0.04
Perna settlers	Site	0.26	34	0.04
Mytilus settlers	Site	0.29	35	0.04
Lasaea settlers	Site*Month	0.33	36	0.04
Perna settlers	Location(Site)	0.34	37	0.04
Mytilus settlers	Location(Site)	0.38	38	0.04
Lasaea settlers	Month	0.40	39	0.04
Hiatella settlers	Location(Site)	0.50	40	0.04
Hiatella settlers	LocationMonth(Site)	0.63	41	0.05
Mytilus recruits	Location(Site)	0.73	42	0.05
Perna recruits	LocationMonth(Site)	0.90	43	0.05
Perna settlers	Location(Site*Month)	0.99	44	0.05
Mytilus settlers	LocationMonth(Site)	0.99	45	0.05

3.3 Results

Settlement

The interaction between site and month had a significant effect on the average abundance of settlers of *P. perna* ($p < 0.001$), *M. galloprovincialis* ($p < 0.001$) and *Hiatella* sp ($p < 0.0001$) (Table 3.2). In December 2016 and July 2017, *P. perna* settlement was significantly higher in the port than the on natural rocky shore, whereas in March 2018 the pattern was reversed, with the natural rocky shore having a higher settlement than the port (Figure 3.2). In November 2016, May 2017, October 2017 and February 2018 settlers were completely absent at both sites. In the Port of East London, settlers were absent in January 2017 and April 2017 and at the Winterstrand natural rocky shore they were absent in March 2017, April 2017, June 2017, August 2017, September 2017, November 2017, December 2017 and January 2018. Settlement of *M. galloprovinciallis* only occurred in December 2016 at the natural rocky shore and in January 2018 and April 2018 in the port, always showing high variability (Figure 3.3). Similarly, *Hiatella* sp settlers occurred exclusively at the port (Figure 3.4), but were generally very rare throughout the 19-month study period, only being observed during the summer months in November 2017, January 2018 and February 2018.

Table 3. 2: Three-way nested ANOVA testing the effect of site, location nested in site and month on the abundance of *Perna perna*, *Mytilus galloprovincialis* and *Hiatella* sp settlement (Log(x+1) transformed) in the Port of East London, South Africa, over the sampling period (November 2016-May 2018). SS = Sum of squares, df = Degrees of freedom, MS = Mean squares, p = p-value. The level of significance is represented by asterisks with p ≤ 0.001 = *, p ≤ 0.0001 = ** and non-significant (n.s.). Significant results are in bold.

		P. perna					***M. galloprovincialis***					***Hiatella* sp**				
Treatment	Effect	SS	df	MS	F	p	SS	df	MS	F	p	SS	df	MS	F	p
Month	**Fixed**	**11.81**	**18**	**0.66**	**27.39**	**	**0.04**	**18**	**0.02**	**2.49**	*	**0.54**	**18**	**0.03**	**5.48**	*
Site	Fixed	0.06	1	0.06	2.39	n.s.	0.00	1	0.00	1.87	n.s.	0.08	1	0.08	20.71	n.s.
Location(Site)	Random	0.05	2	0.03	1.12	n.s.	0.00	2	0.00	1.00	n.s.	0.01	2	0.00	0.70	n.s.
Site*Month	**Fixed**	**2.46**	**18**	**0.14**	**5.71**	**	**0.04**	**18**	**0.01**	**2.79**	*	**0.54**	**18**	**0.03**	**0.90**	*
Location(Site*Month)	Random	0.86	36	0.02	0.51	n.s.	0.03	36	0.00	0.49	n.s.	0.2	36	0.01	0.00	n.s.
Error		7.15	152	0.05			0.24	152	0.00			0.92	152	0.01		

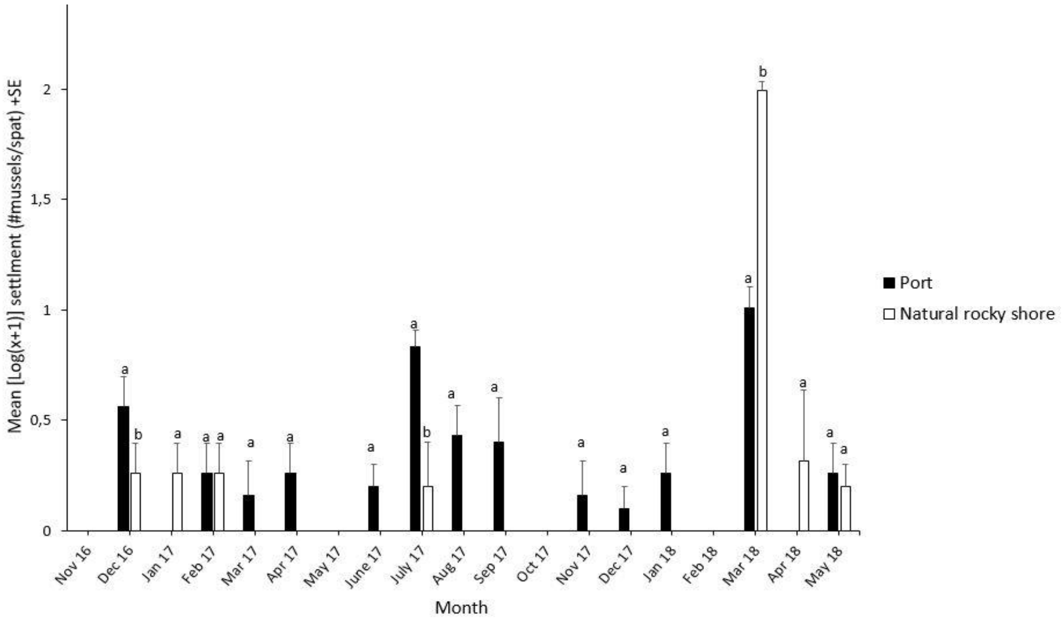

Figure 3. 2: Mean *Perna perna* settlement over the 19-month (November 2016-May 2018) sampling period at 2 different sites (port and natural rocky shore) on the East London coastline, South Africa. Error bars represent standard errors. The letters above the graphs indicate the homogenous groups according to Fisher LSD post-hoc test for the factor month*site.

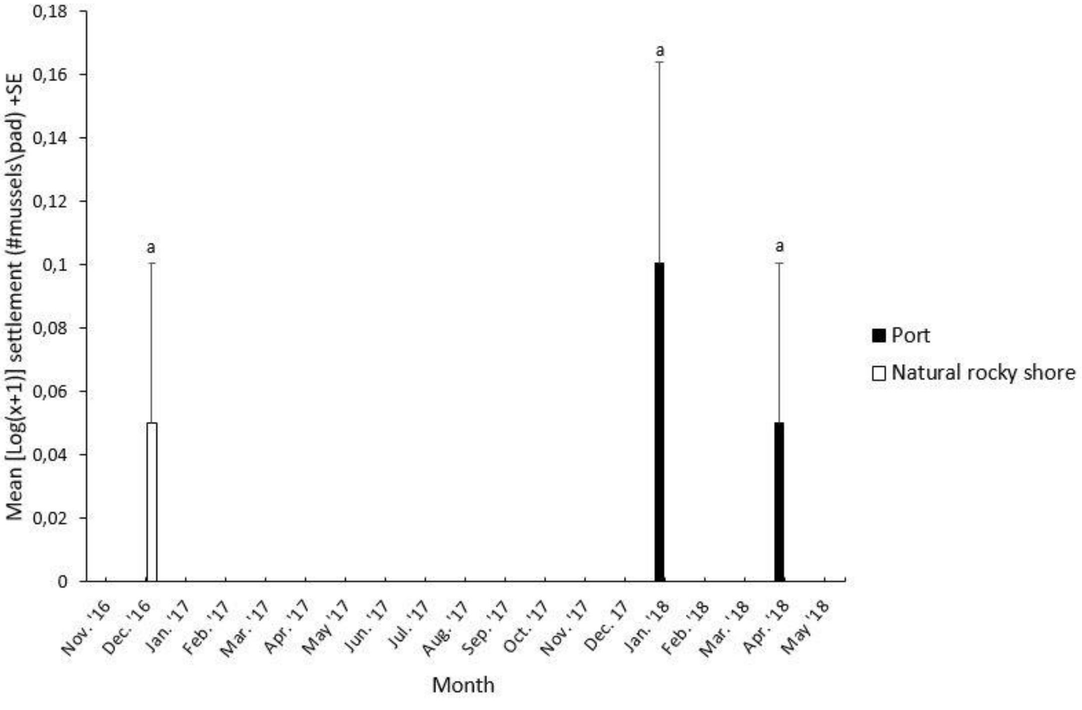

Figure 3. 3: Mean *Mytilus galloprovincialis* settlement over the 19-month (November 2016-May 2018) sampling period at 2 different sites (port and natural rocky shore) on the East London coastline, South Africa. Error bars represent standard errors. The letters above the graphs indicate the homogenous groups according to Fisher LSD post-hoc test for the factor month*site.

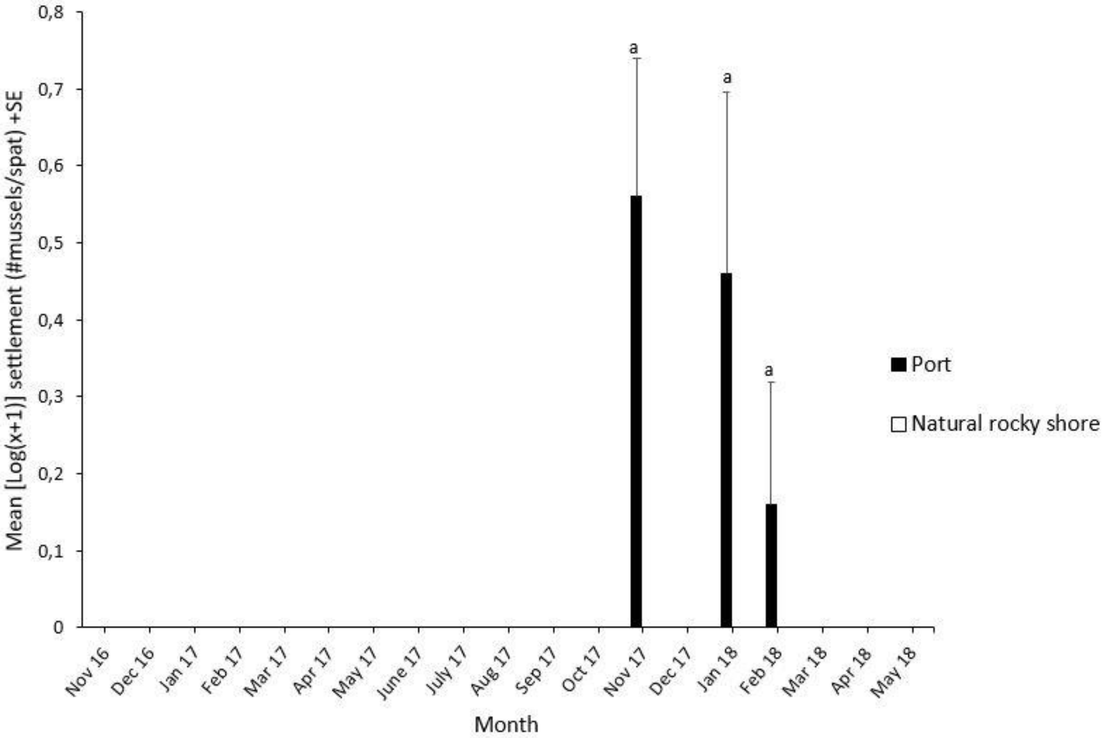

Figure 3. 4: Mean *Hiatella* sp settlement over the 19-month (November 2016-May 2018) sampling period at different sites (port and natural rocky shore) on the East London coastline, South Africa. Error bars represent standard errors. The letters above the graphs indicate the homogenous groups according to Fisher LSD post-hoc test for the factor month*site.

Recruitment

There was a significant effect of interaction between site and month on recruitment of *P. perna* ($p < 0.001$) and *M. galloprovincialis* ($p < 0.0001$) (Table 3.3). In December 2016, March 2017, April 2017 and June 2017 to September 2017, recruitment of *P. perna* was significantly higher within the port than at the natural rocky shore (Figure 3.5). The pattern was, however, consistently reversed in March 2018, April 2018 and May 2018 (Figure 3.5). In February 2017 and December 2017 to February 2018, *P. perna* recruits were absent at the Winterstrand natural rocky shore. *Mytilus galloprovincialis* recruits were generally limited and were found mostly at the Winterstrand natural rocky shore (Figure 3.6), with the abundance of recruits at its highest, yet not significantly different from other months, in autumn (March 2018). There was a significant effect of month on the abundance of *Hiatella* sp ($p < 0.001$) (Table

3.3). In January 2018, the abundance of *Hiatella* sp recruits was significantly the highest, but there were no other noticeable differences observed amongst the months (Figure 3.7). Lastly, there was a significant effect on the interaction of month and location nested in site on recruitment of *L. adansonii* ($p < 0.001$) (Table 3.3). In the port, for January 2017, February, June 2017, February 2018, March 2018 and April 2018, the abundance of recruits was significantly higher on the East bank than on the West bank, and in September 2017 the pattern was reversed, with the West bank having a higher abundance of recruits than the East bank. At the natural rocky shore site in April 2017, June 2017, July 2017, September 2017, February 2018, March 2018 and April 2018, the abundance of recruits was significantly higher at Winterstrand site 1 than Winterstrand site 2 (Figure 3.8).

Table 3. 3: Three-way nested ANOVA testing the effect of site, location nested in site and month on *Perna perna*, *Lasaea adansonii*, *Hiatella* sp and *Mytilus galloprovincialis* recruitment (Log(x+1) transformed) in the Port of East London, South Africa, over the sampling period (November 2016-May 2018). SS = Sum of squares, df = Degrees of freedom, MS = Mean squares, p = p-value. The level of significance is represented by an asterisk with p ≤ 0.05 = *, p ≤ 0.01 = **, p ≤ 0.001 = *** and non-significant (n.s.). Significant results are in bold.

		P. perna					***L. adansonii***					***Hiatella sp***					***M. galloprovincialis***				
Treatment	Effect	SS	df	MS	F	p	SS	df	MS	F	p	SS	df	MS	F	p	SS	df	MS	F	p
Month	**Fixed**	**23.99**	**18**	**1.33**	30.01	***	**5.73**	**18**	**0.32**	2.49	*	**1.26**	**18**	**0.07**	2.85	**	0.69	18	0.04	2.02	n.s.
Site	Fixed	1.59	1	1.59	12.49	n.s.	24.47	1	24.47	36.69	n.s.	0.23	1	0.23	5.07	n.s.	0.18	1	0.18	29.80	n.s.
Location(Site)	Random	0.26	2	0.13	2.87	n.s.	**1.33**	**2**	**0.67**	5.21	*	0.09	2	0.05	1.82	n.s.	0.01	2	0.01	0.32	n.s.
Site*Month	**Fixed**	**8.61**	**18**	**0.48**	10.77	***	3.42	18	0.19	1.49	n.s.	0.59	18	0.03	1.37	n.s.	**1.00**	**18**	**0.06**	2.92	**
Location(Site*Month)	Random	1.60	36	0.04	0.69	n.s.	**4.61**	**36**	**0.13**	1.83	**	0.89	36	0.03	1.34	n.s.	0.69	36	0.02	1.29	n.s.
Error		9.74	152	0.06			10.66	152	0.07			2.73	152	0.02			2.26	152	0.02		

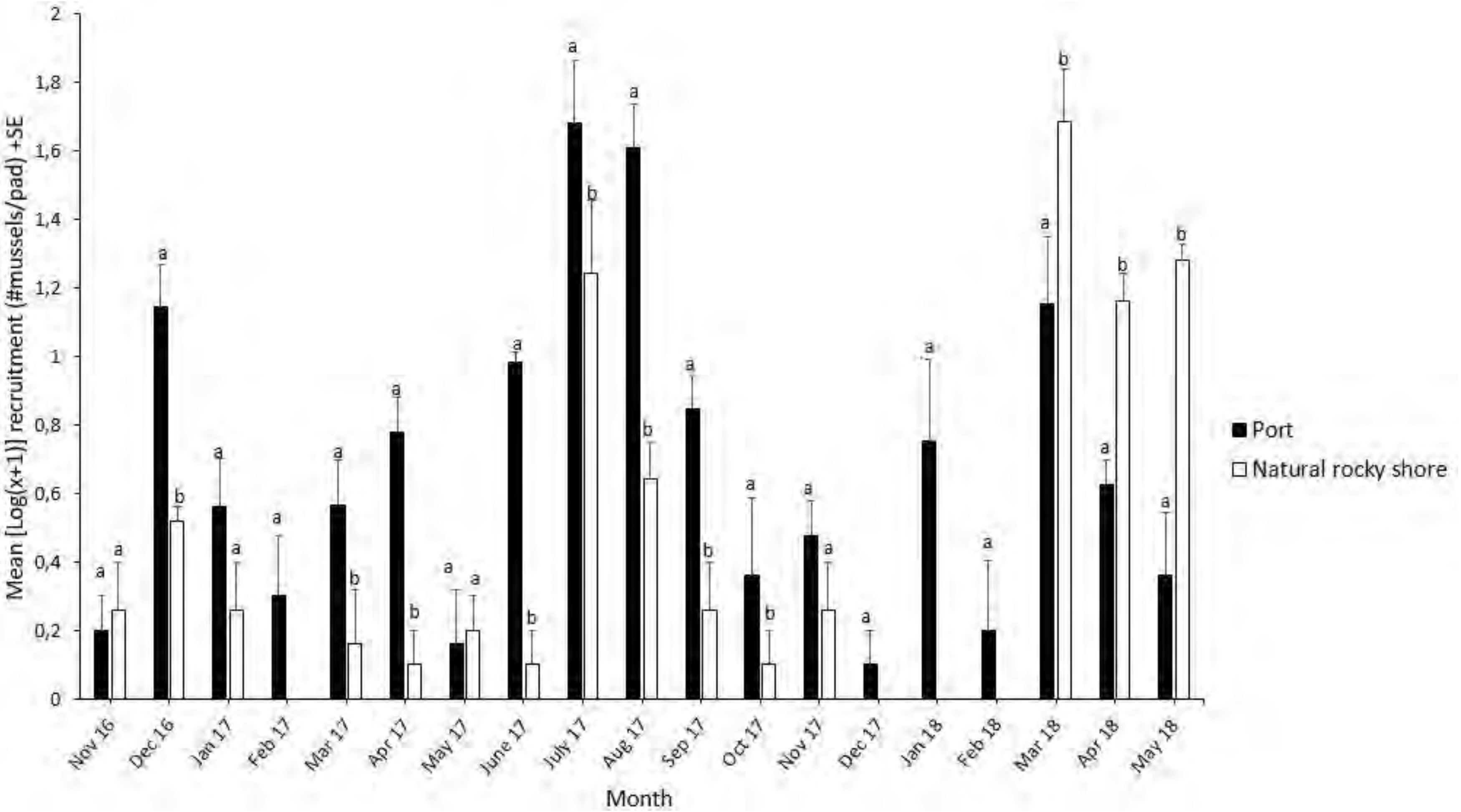

Figure 3. 5: Mean recruitment of *Perna perna* over the 19-month (November 2016-May 2018) sampling period at two different sites (port and natural rocky shore on the East London coastline, South Africa. Error bars represent standard error. The letters above the graphs indicate the homogenous groups according to Fisher LSD post-hoc test for the factor month*site.

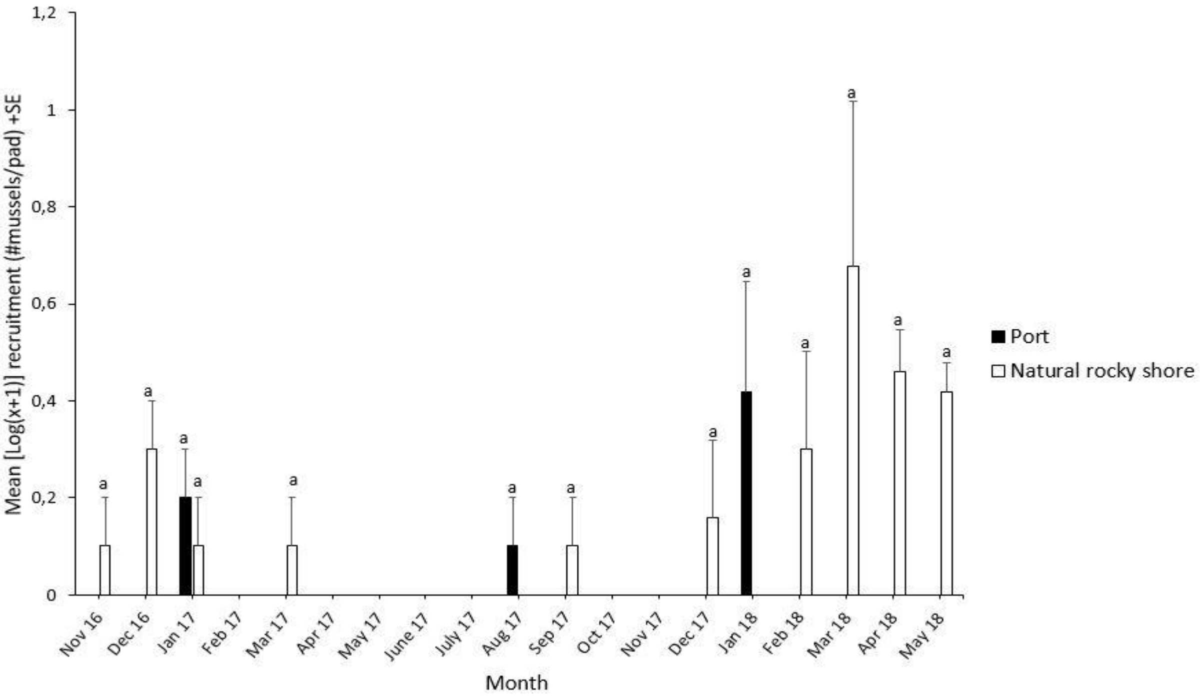

Figure 3. 6: Mean recruitment of *Mytilus galloprovincialis* over the 19-month (November 2016 - May 2018) sampling period at two different sites (port and natural rocky shore) on the East London coastline, South Africa. Error bars represent standard error. The letters above the graphs indicate the homogenous groups according to Fisher LSD post-hoc test for the factor month*site.

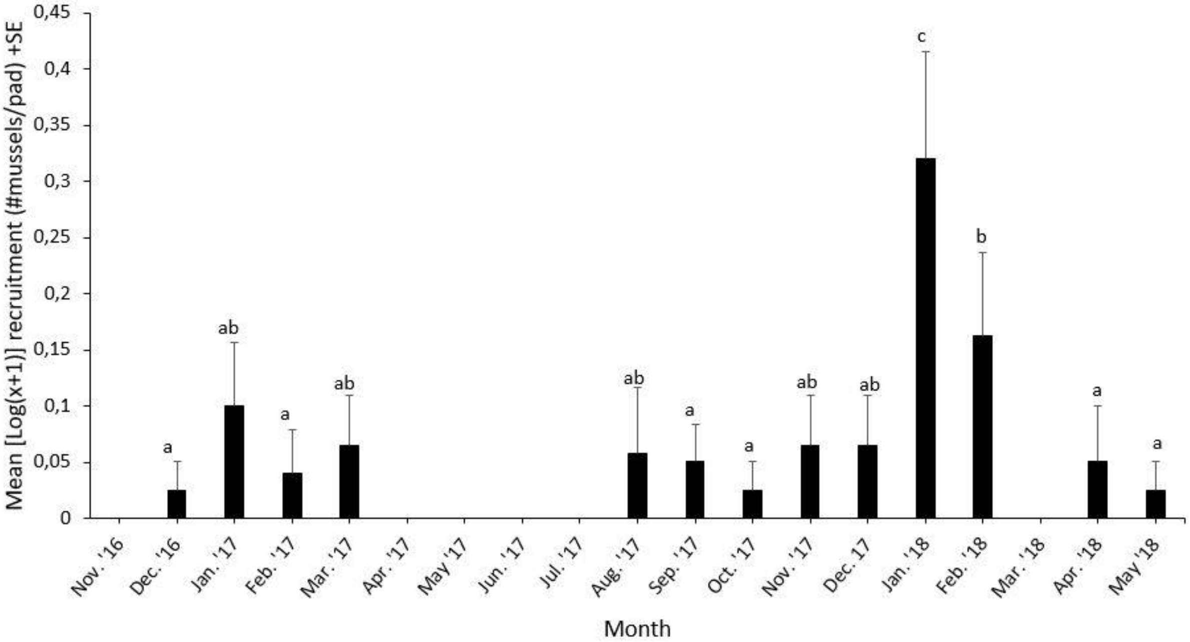

Figure 3. 7: Mean recruitment of *Hiatella* sp over the 19-month (November 2016-May 2018) sampling period on the East London coastline, South Africa. Error bars represent standard error. The letters above the graphs indicate the homogenous groups according to Fisher LSD post-hoc test for the factor month.

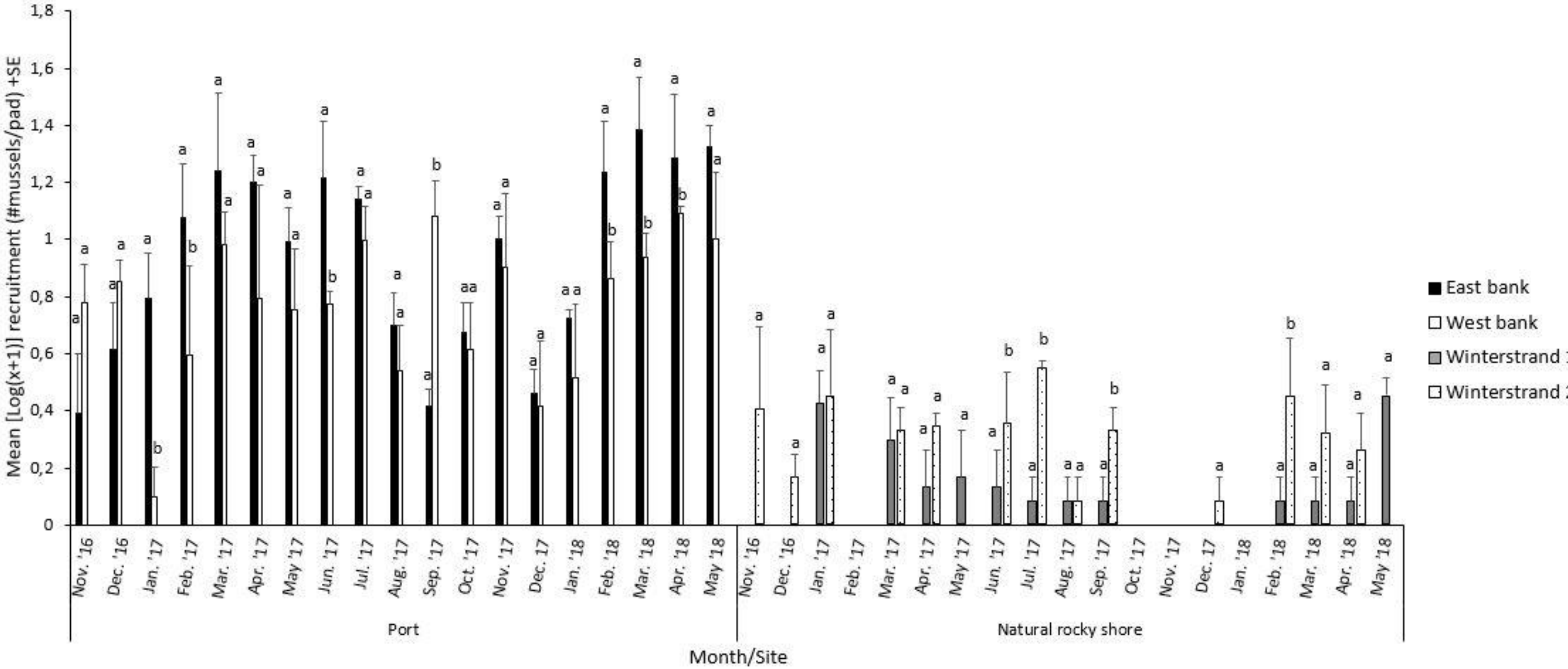

Figure 3. 8: Mean recruitment of *Lasaea adansonii* over the 19-month (November 2016-May 2018) sampling period at two different sites (port and natural rocky shore on the East London coastline, South Africa. Error bars represent standard error. The letters above the graphs indicate the homogenous groups according to Fisher LSD post-hoc test for the factor month*location nested in site.

'Other bivalves'

A three-way nested ANOVA performed on the settlement/recruitment of the group of unidentified bivalves, labelled 'other bivalves', indicated that there was a significant effect of month and location, nested in site, on their abundance (Table 3.4). There was no clear pattern on the effect of month on settlement/recruitment of this group (Figure 3.9). There was a significant difference between locations within the sites, with the West bank in the Port of East London having a higher abundance of these unidentified bivalves than the East bank, and Winterstrand site 2 on the natural rocky shore having a higher abundance than Winterstrand site 1 (Figure 3.10).

Table 3. 4: Three-way nested ANOVA testing the effect of site, location nested in site and month on 'other bivalves' (Log(x+1) transformed) recruitment in the Port of East London, South Africa, over the sampling period (November 2016-May 2018). SS = Sum of squares, df = degrees of freedom, MS = Mean squares, p = p-value. The level of significance is represented by asterisks with p≤0.01 = *, p≤0.001 = ** and non-significant (n.s.). Significant results are highlighted in bold.

Treatment	Effect	SS	df	MS	F	p
Month	**Fixed**	**6.26**	**18**	**0.35**	**4.10**	**
Site	Fixed	2.83	1	2.83	6.42	n.s.
Location(Site)	**Random**	**0.88**	**2**	**0.44**	**5.19**	*
Site*Month	Fixed	2.97	18	0.17	1.94	n.s.
Location*Month(Site)	Random	3.06	36	0.09	1.63	n.s.
Error		7.90	152	0.05		

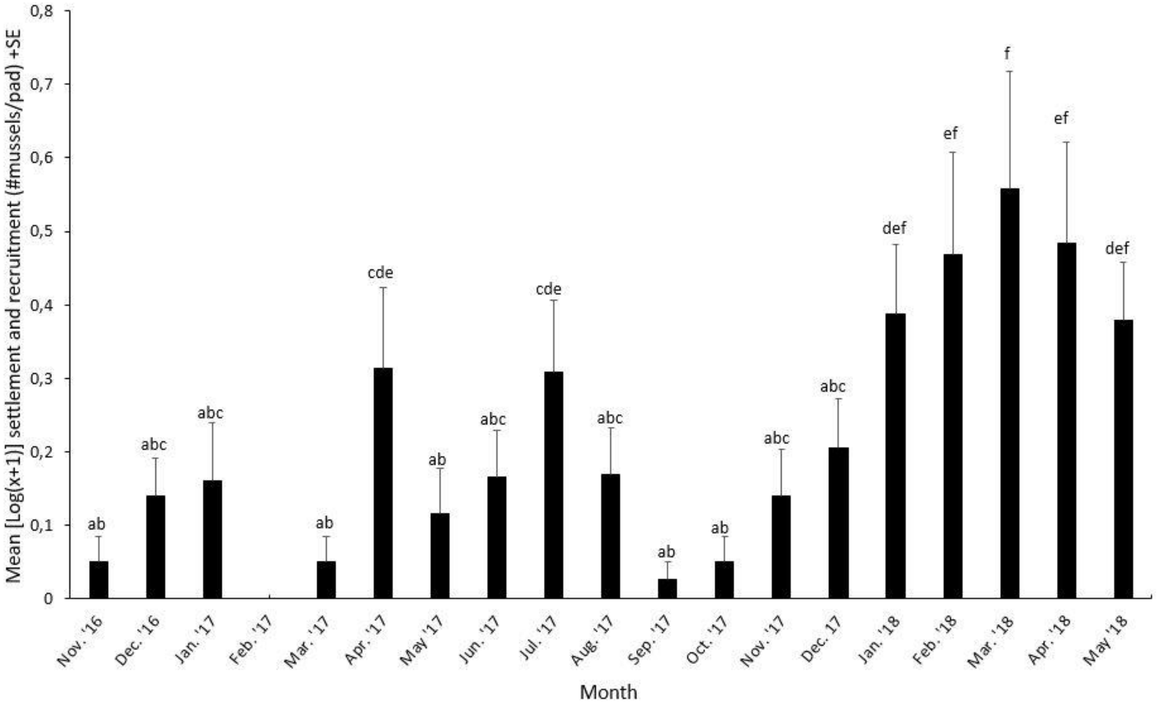

Figure 3. 9: Mean settlement/recruitment of unidentified bivalves, labelled ‘other’, over the 19-month (November 2016-May 2018) sampling period on the East London coastline, South Africa. Error bars represent standard error. The letters above the graphs indicate the homogenous groups according to Fisher LSD post-hoc for the factor month.

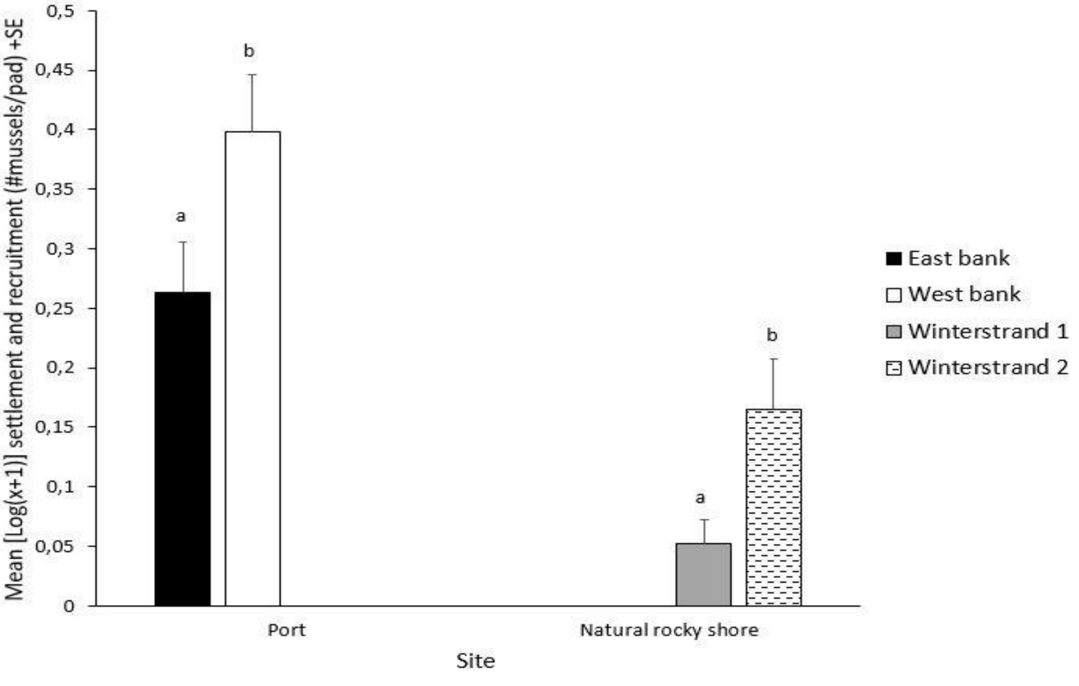

Figure 3. 10: Mean settlement/recruitment of unidentified bivalves, labelled ‘other’, over the 19-month (November 2016-May 2018) sampling period at two different sites on the East London coastline, South Africa. Error bars represent standard error. The letters above the graphs indicate the homogenous groups according to Fisher LSD post-hoc for the factor location*site.

The monthly wind patterns, overlapped with monthly means of *P. perna* recruits, suggest that mussel recruitment for the two summer and autumn periods was related to easterly winds, whereas in winter and spring, mussel recruitment was related to westerly winds (Figures B1 to B3 in the Appendix). The increase of mussel recruits followed after a drop in the westerly wind speed (Figure 3.11). Despite these qualitative trends, there was, however, no correlation between easterly wind and recruitment (Table 3.5), with easterly winds explaining merely 5% and 11% of recruitment in the port and natural rocky shores, respectively (Figure 3.12). There was, however, a significant negative correlation between westerly wind and recruitment on the natural rocky shore, while there was no such correlation for the port (Table 3.5), with the westerly wind speeds explaining 1% and 30% of recruitment in the port and natural rocky shores, respectively (Figure 3. 13).

Table 3. 5: Results of correlations between the wind speed (easterly and westerly) and *P. perna* recruitment for the 19-month (November 2016-May 2018) sampling period. r = correlation, p = p-value.

Wind	Recruitment	r	p
Easterly	Port	-0.225	n.s.
Easterly	Natural rocky shore	-0.344	n.s.
Westerly	Port	-0.035	n.s.
Westerly	Natural rocky shore	-0.549	*

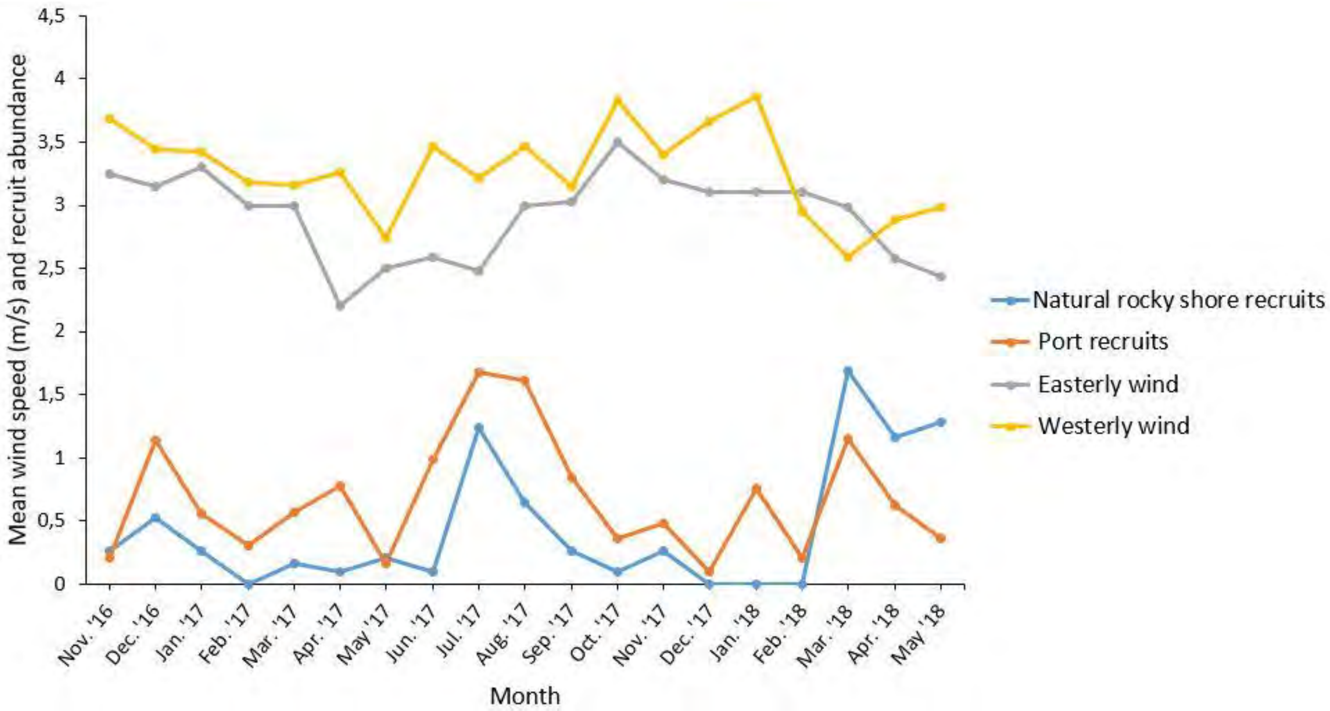

Figure 3. 11: Mean wind speed (easterly and westerly) and *P. perna* recruit abundance at two sites (port and natural rocky shore).

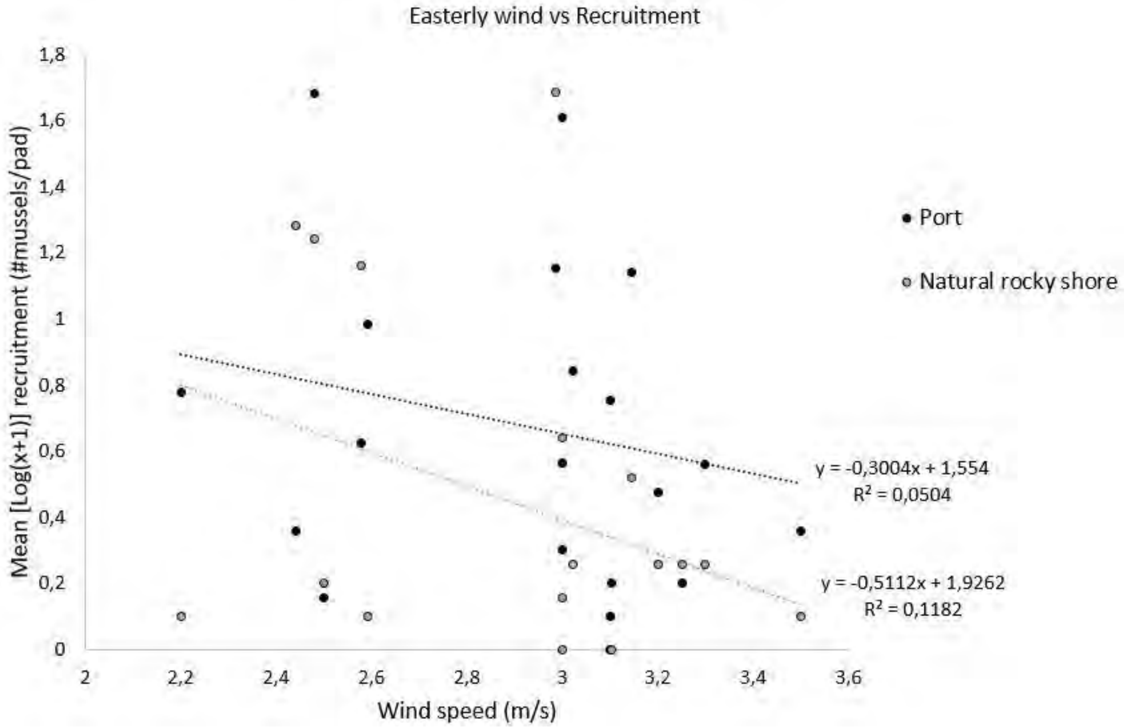

Figure 3. 12: Correlation between easterly wind speed (m/s) and recruitment of *P. perna* on the East London coastline (Port of East London and natural rocky shore).

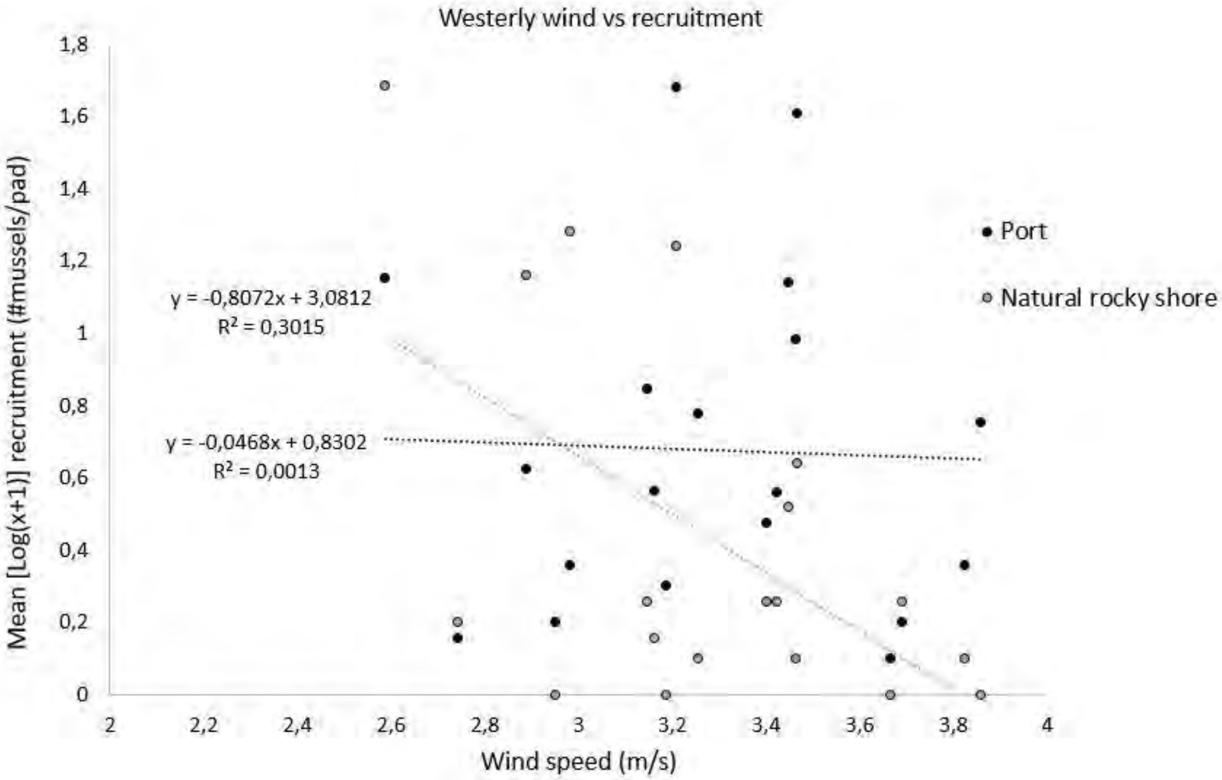

Figure 3. 13: Correlation between westerly wind speed (m/s) and recruitment of *P. perna* on East London coastline (Port of East London and natural rocky shore).

3.4 Discussion

The repeated occurrence of the significant effect of month (interaction with site/location) highlighted the temporal variability of settlement and recruitment of bivalves both in the Port of East London and the adjacent natural rocky shore on the south east coast of Southern Africa. Recruitment and settlement of bivalves were significantly higher in either summer or winter, depending on the taxon, with generally higher settlement and recruitment at the port than the natural rocky shores. There were, however, some months in which the spatial patterns were reversed.

The results of this study suggest that the Port of East London has conditions that favour the settlement and recruitment of the indigenous mussel *P. perna*. This study is in line with the studies conducted in polluted areas of Hong Kong (Victoria Harbour; Lee, 1985) and (Tolo Harbour; Cheung, 1993), where mussel densities were found to be higher in harbours as compared to natural rocky shores. High mussel density was also observed in Wellington Harbour (New Zealand) due to high food availability (Helson *et al.*, 2004). Nonetheless, the results from this study did not conform to studies on urbanised areas where smaller densities of mussels were observed due to competition (Airoldi and Bulleri, 2010; Veiga *et al.*, 2020). These results also suggest that the abundance of adults could be directly linked to the availability of settlers and recruits.

The patterns of settlement and recruitment of the mussel *P. perna* differed between the harbour (Port of East London) and adjacent natural rocky shore (Winterstrand). Settlement of mussels was limited on the natural rocky shore and mostly dense in the port, however, the highest peak in settlement was observed at the natural rocky shore for *P. perna*. The generally higher settlement and recruitment observed in the port compared to that of the natural rocky shore could be due to the higher abundance of adult mussels occurring in the port, although the measured patterns did not differ significantly (2.9% port and 2.5% natural rocky shore). High recruitment related to high adult cover has been reported on natural rocky shores in the Dwesa Nature Reserve (~120km east of the Port of East London) on the south east coast of South Africa (Lasiak and Barnard, 1995), and also in other parts of the world (McGrath *et al.,* 1988; Connolly and Roughgarden, 1998). Another study which reported low mussel recruitment rates due to the effect of human exploitation, observed that this resulted in decreased adult mussel populations (Harris *et al.,* 1998).

Mussel settlement and recruitment in the region of the south coast where this study was carried out is indeed known to vary in both time and space (McQuaid and Lawrie, 2005; Porri *et al.,* 2006). Summer to autumn trends have been generally identified due to the positive effects of benign temperature fluctuations and stable wind patterns (McQuaid and Lawrie, 2005). Nevertheless, this study also showed recruitment peaks in the middle of winter. Warm temperatures are associated with seasonal rainfall, which results in run-off and increases primary productivity (Tomalin, 1995; Dekker and Beukema, 1999; Beal *et al.,* 2001; Wong and Cheung, 2001). The increased food levels in the water column influence the feeding, metabolism, growth, development and dispersal of the larvae (Somero, 2002; Harley, 2003), which in turn improves the recruitment of mussels (Strathmann, 1985, 1993. An autumn and summer recruitment trend in mussels due to the positive effect of increased temperature, has also been recorded at the Tsitsikamma National Park natural rocky shore, in the same warm temperature region of the south east coast of South Africa (Crawford and Bower, 1983) where this study was carried out. Winter recruitment of both indigenous and non-indigenous mussels on natural rocky shores has also been observed in other regions of South Africa, such as False Bay in the Western Cape (van Erkom Schurink and Griffiths, 1991) and Plettenberg Bay in the Eastern Cape, (Zardi *et al*., 2007).

The winter pattern of increased settlement/recruitment was consistent for the indigenous species, *P. perna* and *L. adansonii* within the port, confirming an extended spawning season (Lasiak, 1986; Porri *et al*., 2008). Favourable thermal conditions might have played a role in the increased mussel settlement and recruitment (Seed, 1969; Kautsky, 1982; Seed and Suchanek, 1992; Zardi *et al.,* 2007) observed in winter, as warm temperatures can favour gonad production (van Erkom Schurink and Griffiths, 1991; Helson, 2001; Zardi *et al*., 2007). Nevertheless, although temperature favours gonad development, spawning in mussels is species-dependant (Wilson and Hodgkin, 1967), with *P. perna* preferring a range of 16˚C-22˚C, while *M. galloprovincialis* favours a range of 16˚C-20˚C (Zardi *et al.,* 2007). In ports, under favourable water temperatures conditions (10˚C-20°C) gonadal development can occur (Kennedy, 1977), resulting in a prolonged reproductive season with year-round reproduction (Helson, 2001) and persistent settlement and recruitment of mussels. Temperature can also be related to food quality and availability, which further translates to improved and fast gonad maturation, spawning and general turnover (Bayne and Worrall, 1980; Newell *et al.,* 1982; Seed, 1969). In the northern hemisphere, high settlement and recruitment of mussels have been recorded in autumn following a phytoplankton bloom, which would suggest an increased supply of food having been available for the mussel larvae (Kautsky, 1982). A continuous food supply occurring throughout the year in harbours (Helson *et al.,* 2007; Burford *et al.,* 2008; Yin *et al.,* 2010) could also be the reason for the winter peak of settlement/recruitment observed in this study, as food availability favours the increase of growth and survival (Loosanoff and Davis, 1963). Food availability in the water column where a mussel larva feeds can improve growth, settlement and recruitment. Spawning in mussels, however, can also be delayed due to low concentrations of food in the water column (Lenihan *et al.,* 1996).

Limited export of larvae due to decreased wave forcing (Hunt and Scheibling, 1996) had no effect during this study, as mussel settlement and recruitment observed in the port was high. High settlement and recruitment of mussels in areas with reduced wave action, such as in the port in this study, could be caused by local retention of larvae in the nearshore waters (Morgan and Fisher, 2010; Porri *et al*., 2014), associated with high abundance of local adult stocks (Roughan *et al*., 2005; Mace and Morgan, 2006). The effect of larval retention on settlement and recruitment of mussels has been observed in warm temperate Wellington Harbour, New Zealand (Helson and Gardner, 2004), but this trend has also been recorded locally, on the south coast of Southern Africa (von der Meden *et al*., 2008). Additionally, the natural rocky shore may have higher chances of settlers or recruits being dislodged due to high wave action (Hunt and Scheibling, 1996) which would explain the low settlement and recruitment patterns of mussels observed in this study in those areas.

Wind can affect water circulation (especially at the surface) (Bertness *et al.,* 1996), sea temperatures and food availability (Griffiths, 1977), especially during periods of upwelling

(Goschen and Schumann, 1994). High recruitment of mussel larvae during spring through to early autumn when wind frequency increases have been recorded (Pfaff *et al.,* 2011; Shanks *et al.,* 2018). The results of this study, however, did not follow such trends. The easterly winds had no effect on the recruitment of mussels, while the westerly winds negatively influenced mussel recruitment in winter only on the natural rocky shore, possibly due to the prolonged strong winter prevalence of this feature (Goschen and Schumann, 1988; Garstang *et al.,* 1996; Hauck and Sowman, 2003). The strong westerly winds on natural rocky shores might have produced strong waves that could have prevented mussel larvae from settling and recruiting. The sheltered nature of the harbour may have prevented this negative effect of wind on mussel recruitment in the port.

The presence of food particles (chlorophyll-*a*) in the water column increases adult mussel growth, which also aids in gonad development (Loosanoff and Davis, 1963) and most likely spawning (Griffiths and King 1979). In this study, food availability may have played a role in the increased abundance of larvae observed in the port compared to the natural rocky shore, due to the higher availability of nutrients in the port (Fakoti and Mathabatha, 2010). The positive effect of increased food supply does not only apply to adults, but also to larvae (Loosanoff and Davis, 1963), as high settlement and recruitment of mussel larvae have been attributed to increased phytoplankton concentrations in the water column (Helson and Gardner, 2004). High larval densities in the water column adjacent to natural rocky shores in the same region as this study have also been linked to increased levels of chlorophyll-*a* (McQuaid and Philips, 2006), possibly having a bearing on the relatively higher rate of settlement and recruitment.

High mussel recruitment recorded just south (Port Alfred, 32 km) of the area where this study was carried out coincided with a phytoplankton bloom (McQuaid and Lawrie, 2005), while increases in settlement have also been associated with the presence of biofilm containing chlorophyll-*a* (von der Meden *et al*., 2010) and to large adult mussel populations (Wainman *et al.,* 1996). Although at the start of this study the port had a visually higher abundance of adult mussels compared to the natural rocky shore sites, other studies conducted in South Africa on natural rocky shores observed a greater recruitment abundance compared to the ports (McQuaid and Lawrie, 2005; Porri *et al.,* 2006). While the visual patterns did not match with the calculated mussel adult cover, variability in recruitment exists even where stable mussel beds go through limited temporal adjustment (von der Meden, 2008).

Although the calculated percentage cover of adult *M. galloprovincialis* was slightly higher in the port than on the adjacent natural rocky shores, with a mean percentage of 2% and 0% respectively, settlement and recruitment by this species within the port were very low. The low abundance of *M. galloprovincialis* implies that there may be an increased chance of the indigenous *P. perna* establishing itself within the port, therefore, supporting a good community of indigenous ecosystem engineers. Low settlement and recruitment of mussel larvae, coupled with a high percentage cover of the adult population, have been linked to the mechanism of post-settlement mortality (Menge, 2000), but the adult percentage cover finally recorded cannot fully explain the low numbers of recruitment by *M. galloprovincialis* in the port. In addition, there is still no clear explanation of the higher recruitment than settlement of the *M. galloprovincialis* species, especially at Winterstrand sites. The invasive opportunistic *M. galloprovincialis* can occupy the spaces made available by physical disturbances in natural shores, whereas *P. perna* has more chances of settling on less disturbed shores (Rius and McQuaid, 2006; Steffani and Branch, 2004) and this may have contributed to the increased abundance of recruitment by *M. galloprovincialis* in the natural rocky shores during the last few months of the study.

The abundance of mussel recruits in this study did not only differ between the natural rocky shore and the port, but also between the locations within these areas. The same trend was observed in a study by Porri *et al.* (2006), where the abundance of mussel settlers differed over scales of just a few hundred meters, due to the settlers consistently being delivered in different directions from a common pool of larvae offshore. Small scale effects on mussel recruits have been observed on the south coast of South Africa, with differences recorded at the mere centimetre scale (Lawrie and McQuaid, 2001). The delivery of larvae within the same location is influenced by wave action (Jeffery and Underwood, 2000; Pineda, 2000), which varies over small spatial scales (Bertness *et al*., 1992; Hunt and Scheibling, 1996), therefore influencing the variability of settlement and recruitment within a few hundred meters (Jenkins *et al.,* 2000; Pineda *et al.,* 2002; Porri et al., 2006). One of the striking results of this study was the low overall abundance of the invasive *M. galloprovincialis*. This species is one of the most abundant species to be transported and introduced into harbours by ships (Bax *et al.,* 2003) and range expansion from introduction for aquaculture purposes in Port Elizabeth in the 80’s (Hockey and van Erkom Schurink, 1992), however, warmer sea temperatures in this region may minimise the invasion of this species (Steffani and Branch, 2004).

4. GENERAL DISCUSSION

In order to provide environmental management support for the rehabilitation of biodiversity of human-impacted urbanised ports, it is important to understand the factors that drive the establishment of coastal invertebrate communities within them (Beatley, 2011; Lai *et al*., 2015). Biodiversity and other coastal services can be improved by providing added microhabitats on the artificial structures (Chapman and Blockley, 2009; Chapman and Underwood, 2011; Firth *et al*., 2014; Perkol-Finkel and Sella, 2015; Evans *et al*., 2016). In ecological engineering and rehabilitation projects, improving microhabitats in artificial structures has been shown to be effective (Chapman and Blockley, 2009; Bulleri and Chapman, 2010).

The overall aim of this research was to investigate whether the combination of artificial structures made of eco-friendly concrete material, the increased structural complexity and the presence of indigenous ecosystem engineers enhanced the intertidal biodiversity within the Port of East London on the south east coast of South Africa. The patterns of settlement and recruitment of the indigenous ecosystem engineers (*Perna perna*) between urbanised and natural locations were also investigated. Based on this framework, survival, growth and biodiversity associated with the indigenous mussel *Perna perna* were measured, as well as the patterns of settlement and recruitment of mussels and other benthic bivalves within the artificial anthropogenic system and adjacent natural rocky shores.

The complexity of the eco-friendly concrete structures had a positive effect on the height and length of mussels, biomass and the diversity of the benthic mobile (and somewhat sessile) species. The maximum height and length of mussels and the highest diversity of benthic mobile rocky shore species was observed in the complex (2.5 cm and 5 cm) tiles. The improved growth of mussels could have assisted in the enhancement of biodiversity of the mobile species, with larger mussels being able to support and accommodate a greater number of species and individuals (Lwasaki, 1995; Tsuchiya, 2002). This study has also shown that as the mussels grow in size, the substrate complexity they create increases and accommodate a wider range of species composition (Murray *et al*., 2007). This aspect reinforces the ecosystem engineering role mussels have as they provide habitat for other organisms thereby improving biodiversity (Montes *et al*., 2012; Gundersen *et al*., 2016). The results of this study indicate that creating complex microhabitats such as crevices on artificial structures in the Port of East London may be an effective strategy in restoring native biodiversity within an urbanised area.

Tiles with seeded mussels supported a greater mobile species diversity than unseeded tiles, with a clear bias towards native rather than non-indigenous species. Complexity, which creates microhabitats of otherwise featureless artificial structures, proved to be key in enhancing biodiversity in this case, but only in combination with the presence of natural ecosystem engineers. Nonetheless, the seeding of *P. perna*, together with the presence of mobile species, ensured occupation on all the available space on the tile and thereby reduced the chances of sessile/sedentary species colonisation due to the limited surface area (Gabriel *et al.,* 1999). Sessile species such as barnacles were in fact limited to only the edges (pers. obs.) of the seeded tiles. The diversity of sessile/sedentary organisms should, however, be improved as they provide important ecological functions (Vermeij and Gronsberg, 2010) and create space for other organisms (Sala and Knowlton, 2006).

The favourable conditions conducive to increased biodiversity provided by ecosystem engineers attached to the eco-friendly structures with increased complexity favoured mobile species diversity, while had a minimal, in any, effect on sessile species. With continuous change of marine biodiversity changes over time (Margalef, 1963; Odum, 1969), ecosystem engineers on the eco-friendly artificial structures with increased complexity may also favour sessile species diversity depending on the successional stage of the intertidal community. Sessile organisms, such as canopy-forming algae could become dominant during the later stages and remove the turf-forming algae that appeared early in succession (Bennedetti-Cecchi 2000).

Many studies have reported the negative impacts of seawalls, and the fact that they seem to favour the introduction of alien species (Glasby *et al*., 2007;Dafforn *et al*., 2012), reducing the natural intertidal biodiversity (Chapman, 2003; Chapman and Bulleri, 2003; Moschella *et al*., 2005; Firth *et al*., 2013; Aguilera *et al*., 2014; Firth *et al*., 2016). This study, however, highlighted the general positive impacts of a well-structured, eco-friendly artificial structures, not only on diversity as a whole, but on the enhancement of the natural invertebrate intertidal communities. In this study, it should be noted that the tiles were deployed on vertical seawalls comprised of building rubble (consisting of concrete and brick sections) which may have contributed to the dissimilar results to other studies, as they may have provided a more complex substrate than the common concrete, flat seawalls. Throughout this study, I particularly showed that crevices of any size are an improved microhabitat for coastal invertebrate intertidal species, which could serve as bottom-up drivers in the rehabilitation of natural resources in urban, as well as natural, degraded systems (Goodshell *et al.,* 2007).

An additional overall bottom-up improvement of ecosystem functioning comes from the fact that the Port of East London had higher mussel recruitment than the natural rocky shore during the 19-month study period. In South Africa, as is the case worldwide, there is a general lack of long term monitoring studies, which evaluate the role of early life stages in affecting intertidal communities within urbanised coasts (Bulleri, 2005). The studies in settlement/recruitment of ecosystem engineers have mainly focused on natural rocky shore habitats (von der Meden, 2009; Pfaff *et al.,* 2011; von der Meden *et al.,* 2012), but the source of recruits to these habitats could be coming from nearby harbours (Shima and Swearer, 2009). As settlement and recruitment are fundamental processes, which regulate population dynamics (Hunt and Scheibling, 1998; Balch and Scheibling, 2000), the inclusion of monitoring of such early processes would make any rehabilitation scheme more effective to establish if the populations of the ecosystem engineers are replenished locally and naturally, becoming a self-sustaining system.

Enhancement of structural complexity has great potentials in improving biodiversity and artificial designs derived from ecological engineering have been effective for rehabilitation efforts (Chapman and Blockley, 2009; Bulleri and Chapman, 2010). In the Port of East London, a rehabilitation programme involving the use of eco-friendly artificial structures would be easy to sustain, and the within-port larval retention dynamics observed in this project would favour a natural replenishment of the local mussel populations (Morgan and Fisher, 2010; Porri *et al*., 2014).

In conclusion, a combination of ecological engineering, complexity and the selection of the correct ecosystem engineers have to be considered in a framework of rehabilitation of urban coastal environments such as the Port of East London, as they appear to favour a biodiverse invertebrate intertidal community. Nonetheless, extensive research should still be carried out on long-term rehabilitation and monitoring, paying particular attention to the increased size of crevices, as the small-sized crevices were only used on a short-term basis. Further work needs to focus on the search for more self-sustainable eco-friendly materials to improve intertidal biodiversity of ports. The type of eco-engineering used for this study could contribute to further contribute to the framework of rehabilitation ecology and can improve our ability to conserve and manage harbours.

The South African government has identified the need for increase in ecological rehabilitation of marine artificial structures in the coastal areas due to the ever increasing pressure to convert natural coastal assets into human-made structures (Lochner, 2005). In countries like South Africa, where erosion, increased colonisation of invasive species and land degradation has an impact on the coastline, the management of artificial marine infrastructures is very important (Chevallier, 2015). Effective management through ecological engineering, enhancement and rehabilitation of biodiversity is however still lacking (Lochner, 2005; Chevallier, 2015). My study is a once off unique opportunity to fulfil possible implementation management plans. This case study on the work on eco-engineering in the Port of East

London can be taken as a model for similar implementation plans, using eco-engineering in other urban coastal areas in South Africa for rehabilitating urban coastal systems. Ecological engineering (in terms of increased complexity and heterogeneity) has indeed the potentials to be incorporated in South African programmes aiming at improving the natural biodiversity in coastal urban environments to drive local coastal economic development without causing an ecological collapse of the functioning of these urbanised systems.

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APPENDIX: Pie charts for both mobile and sessile/sedentary species diversity.

Table A. 1: Legends for the mobile species list in two sites and three treatments through time

Species	Colour
Nerididae	🟦
Sipuncula	🟪
Cymbula oculus	🟦
Siphonaria concinna	🟦
Siphonaria capensis	🟦
Siphonaria serrata	🟫
Helcion concolor	🟩
Helcion pruinosus	🟧
Oxystele sinesis	🟧
Oxystele tigrina	🟨
Oxystele tabularis	▒
Scutelastra longicosta	🟩
Scutelastra argenville	🟦
Scutelastra granularis	🟪
Acanthochitona garnoti	🟥
Leucothoe spinicarpa	⬛
Cymodocella pustulata	🟩
Perna perna	🟥
Mytilus galloprovincialis	🟪
Branchidontes semistruatus	🟩
Lasaea adansoni	🟪
Cyclograpsus punctatus	▦
Parvulastra exigua	⬜

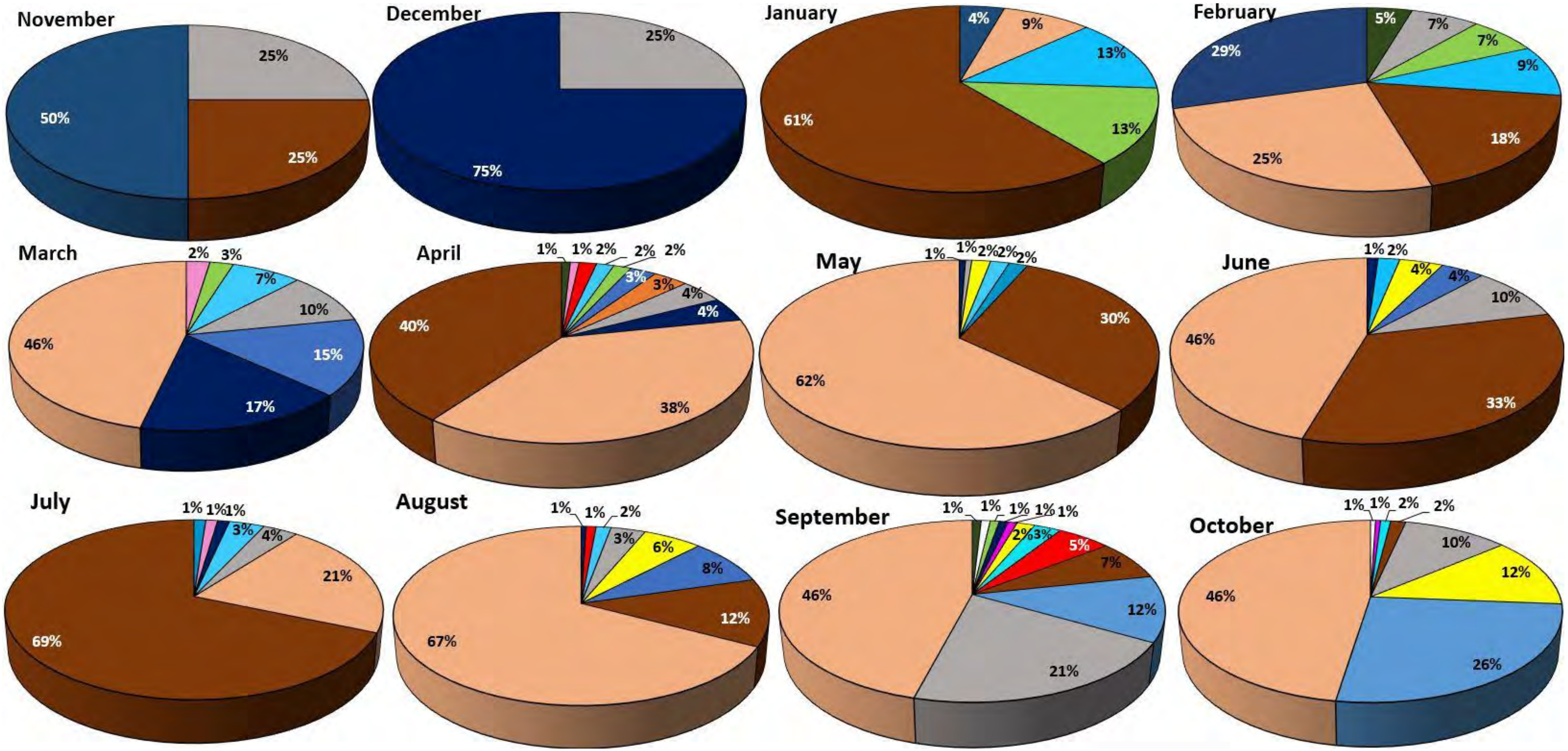


Figure A. 1: Mobile species diversity on the East bank of the Port of East London over the 12-month period on flat seeded tiles.

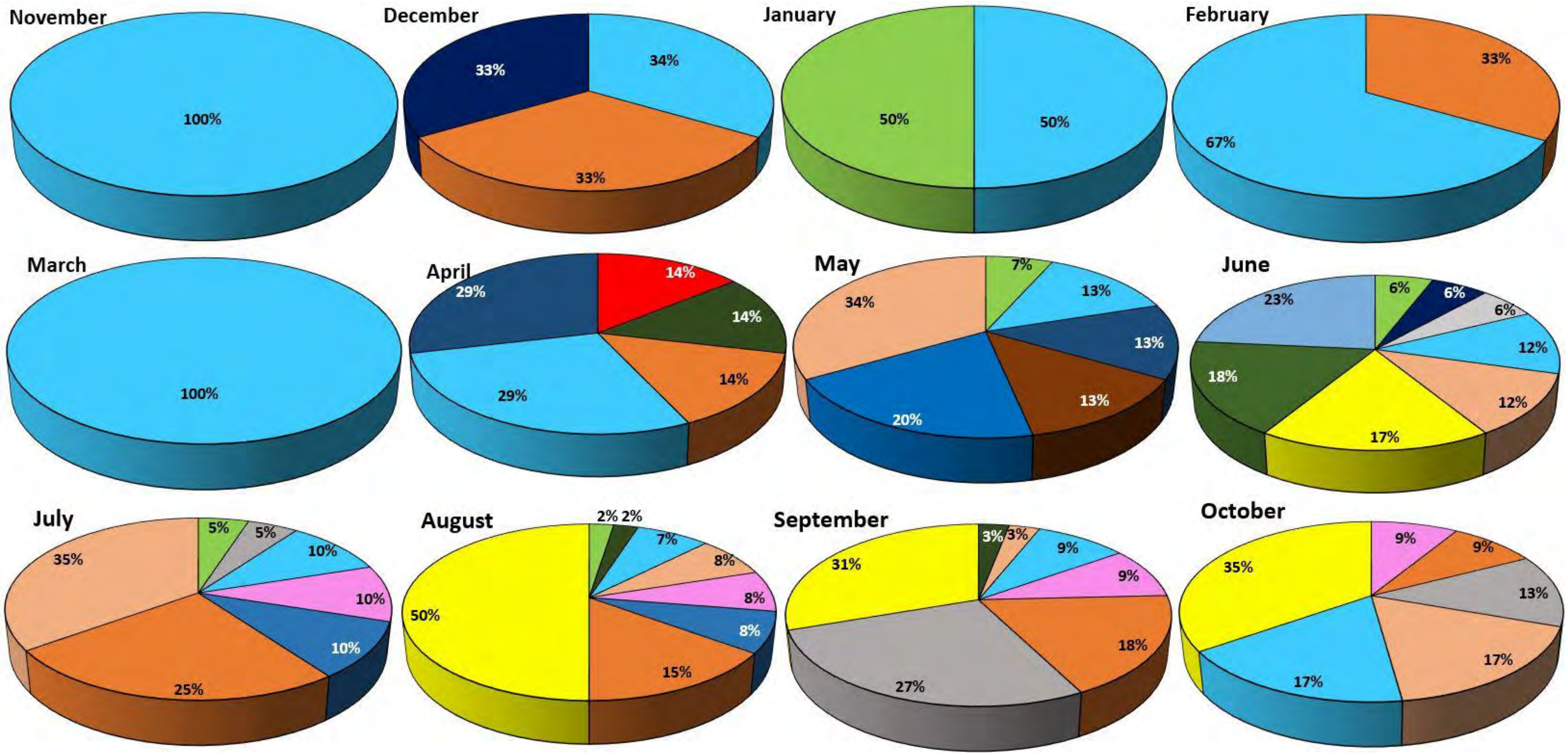


Figure A. 2: Mobile species diversity on the East bank of the Port of East London over the 12-month period on flat unseeded tiles.

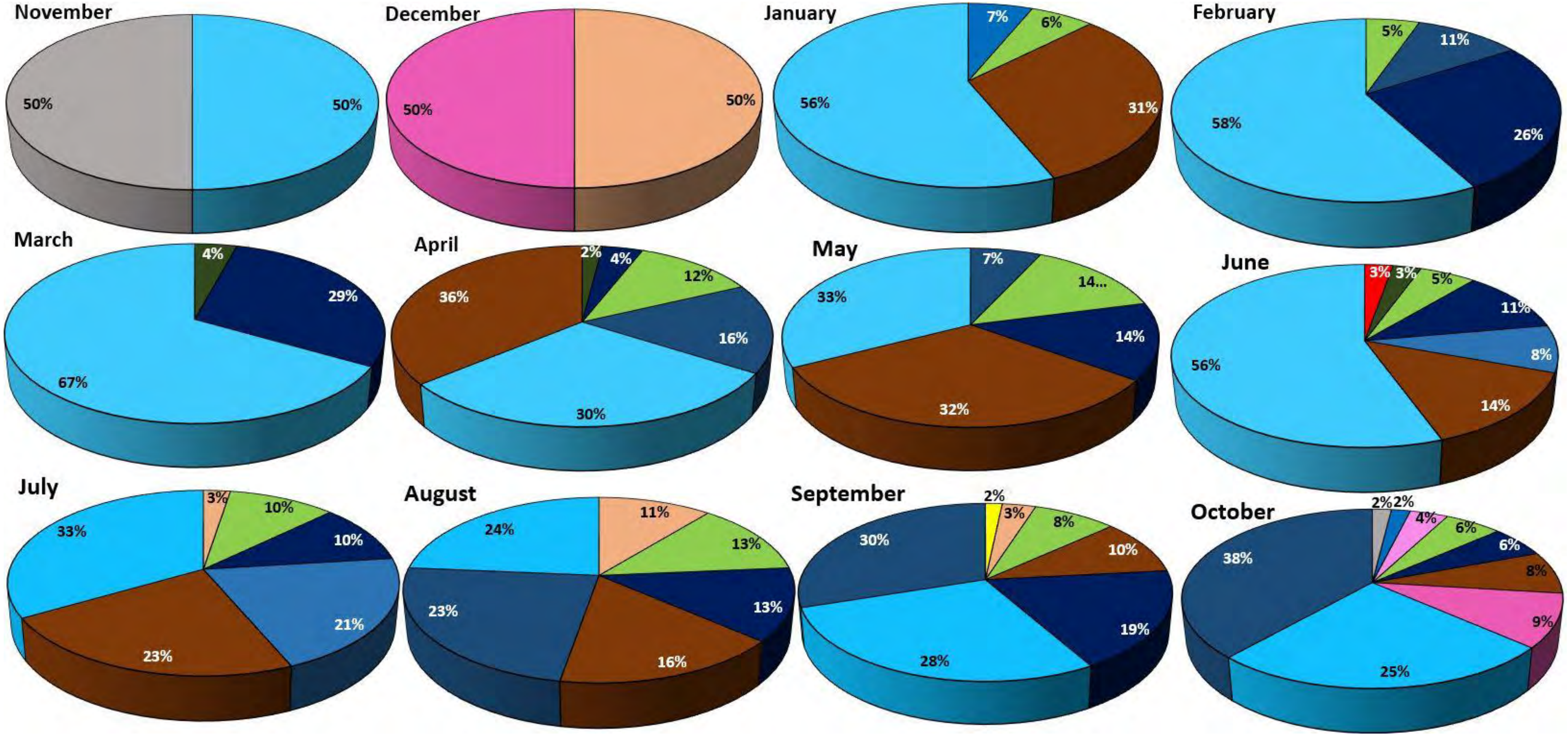


Figure A. 3: Mobile species diversity on the West bank of the Port of East London over the 12-month period on flat seeded tiles.

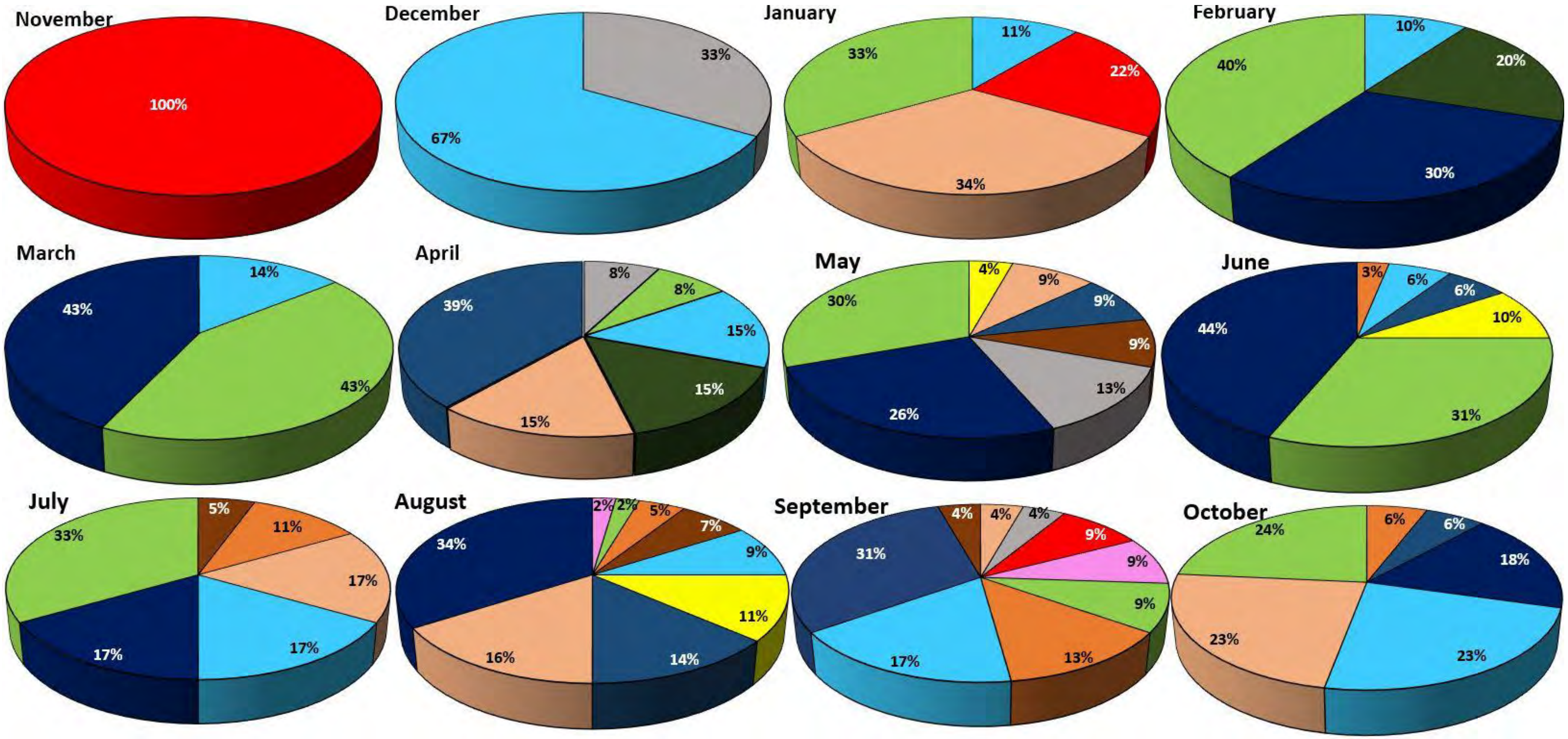


Figure A. 4: Mobile species diversity on the West bank of the Port of East London over the 12-month period on flat unseeded tiles.

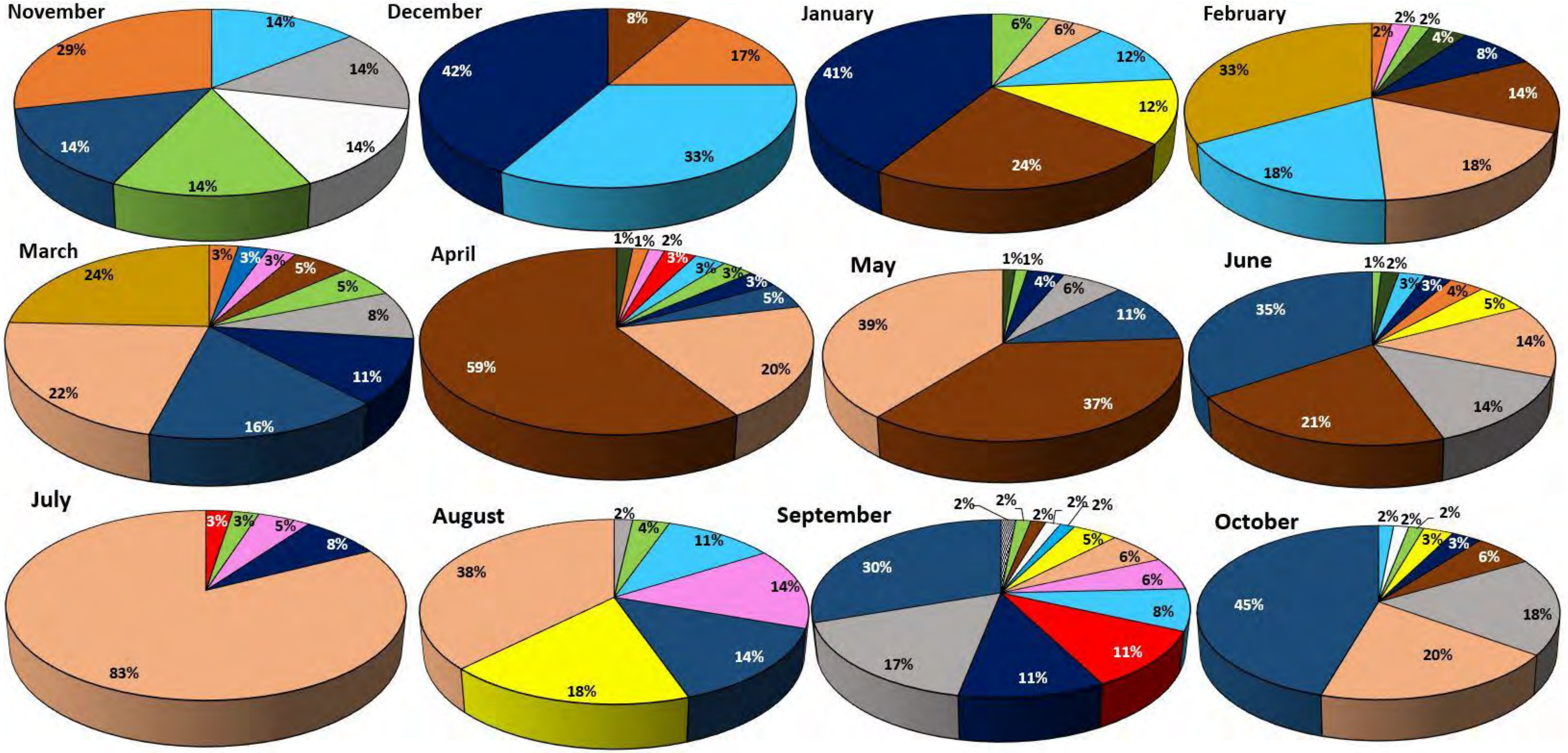


Figure A. 5: Mobile species diversity on the East bank of the Port of East London over the 12-month period on 2.5 cm seeded tiles

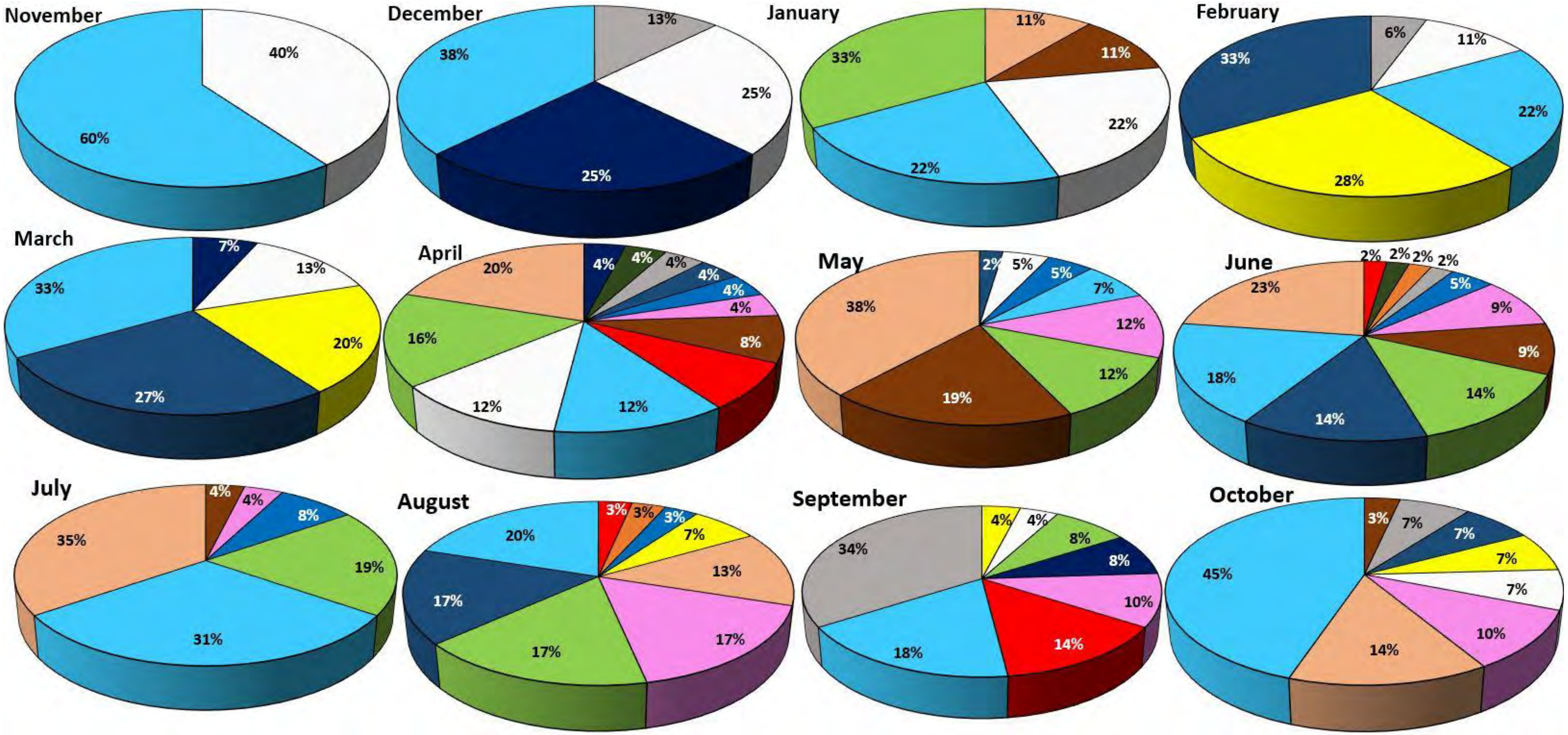


Figure A. 6: Mobile species diversity on the East bank of the Port of East London over the 12-month period on 2.5 cm unseeded tiles

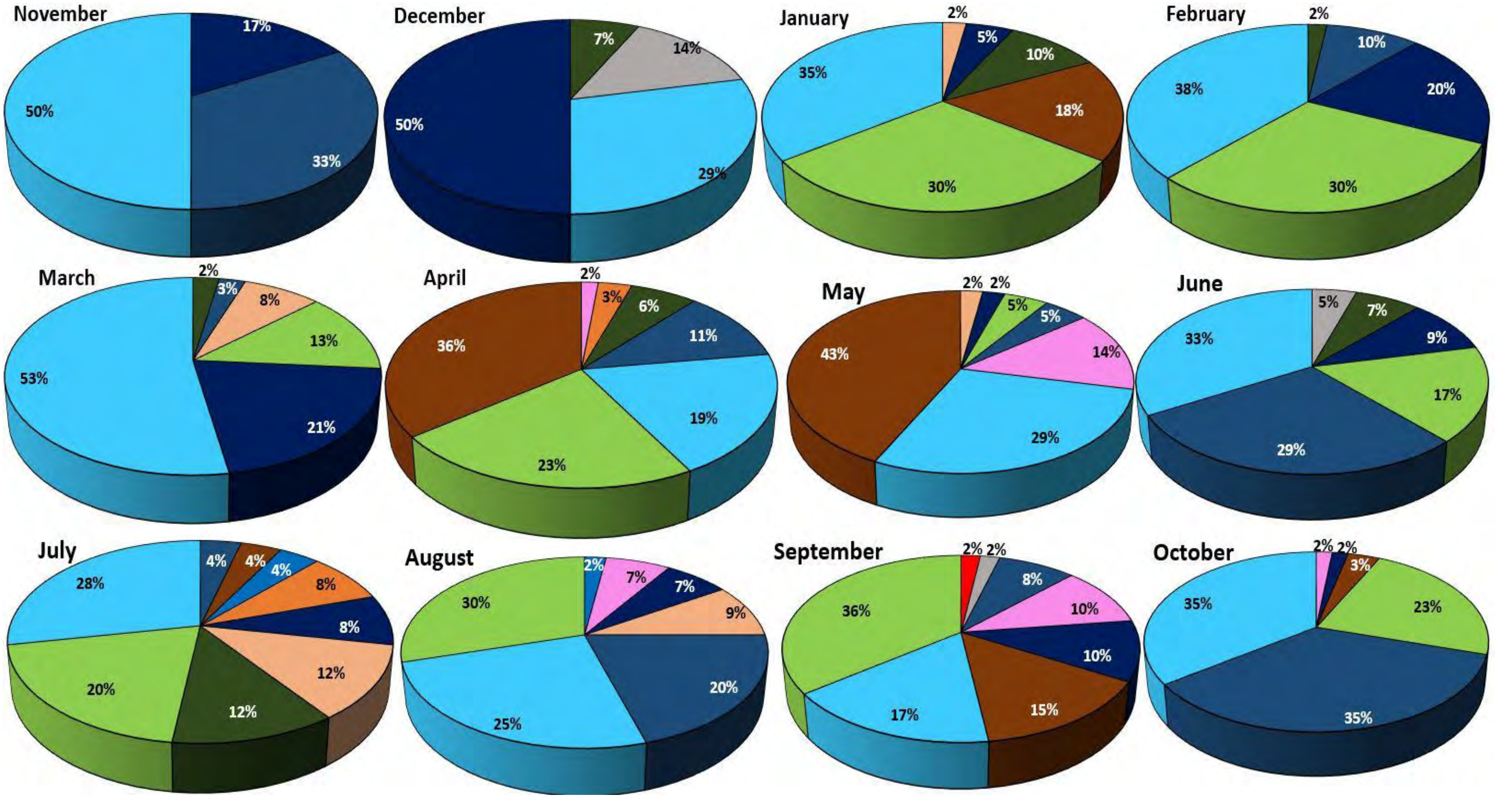


Figure A. 7: Mobile species diversity on the West bank of the Port of East London over the 12-month period on 2.5 cm seeded tiles

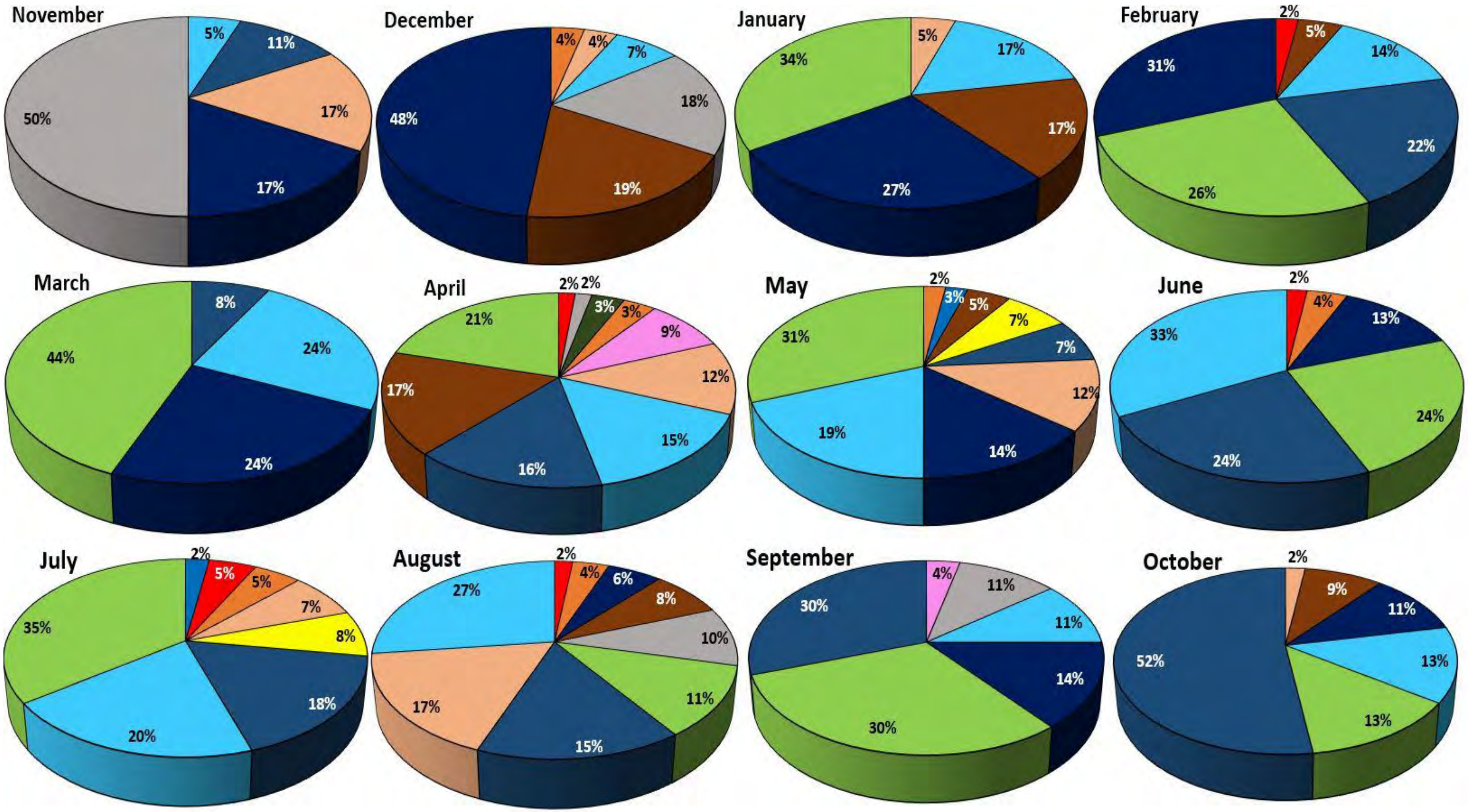


Figure A. 8: Mobile species diversity on the West bank of the Port of East London over the 12-month period on 2.5 cm unseeded tiles

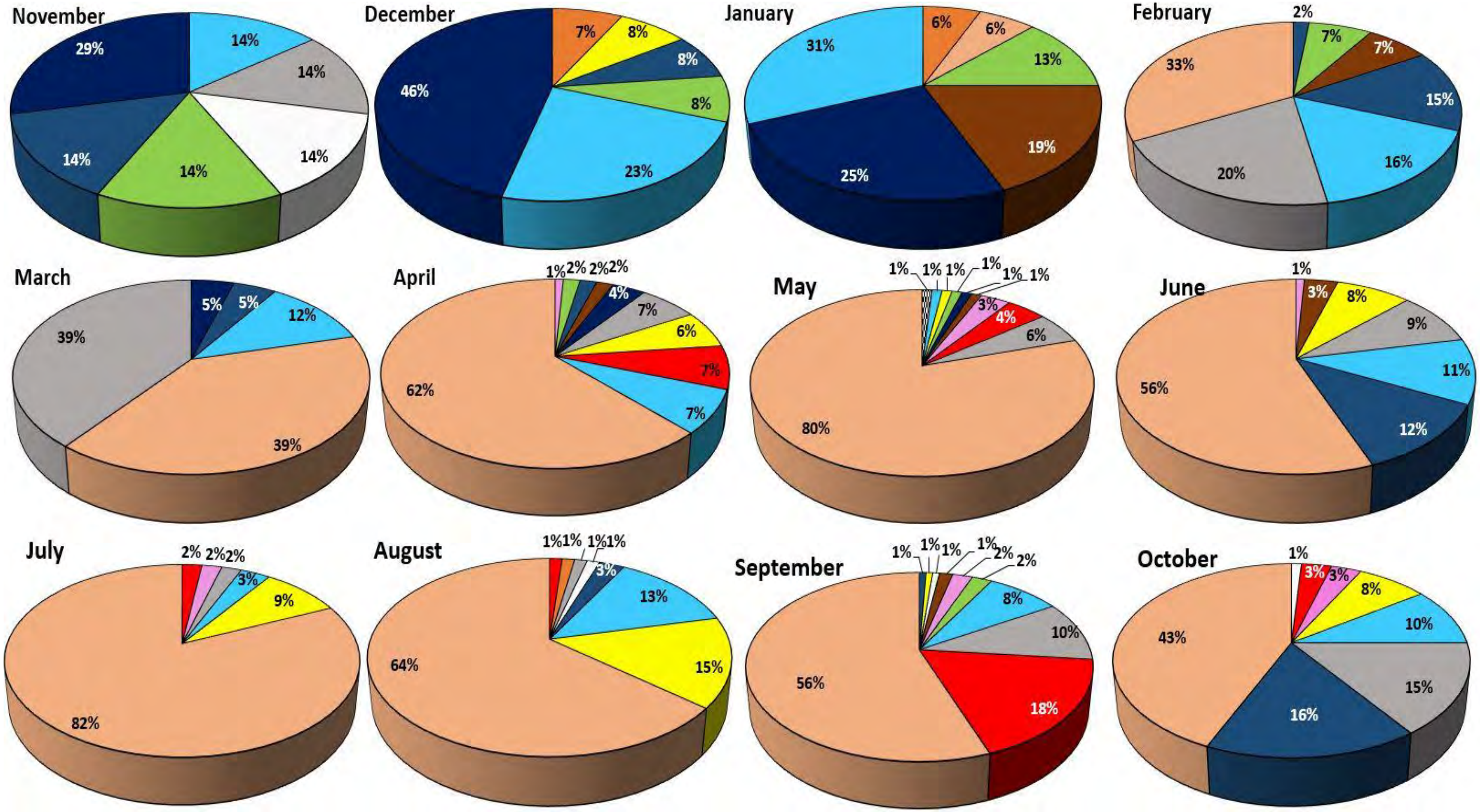


Figure A. 9: Mobile species diversity on the East bank of the Port of East London over the 12-month period on 5 cm seeded tiles

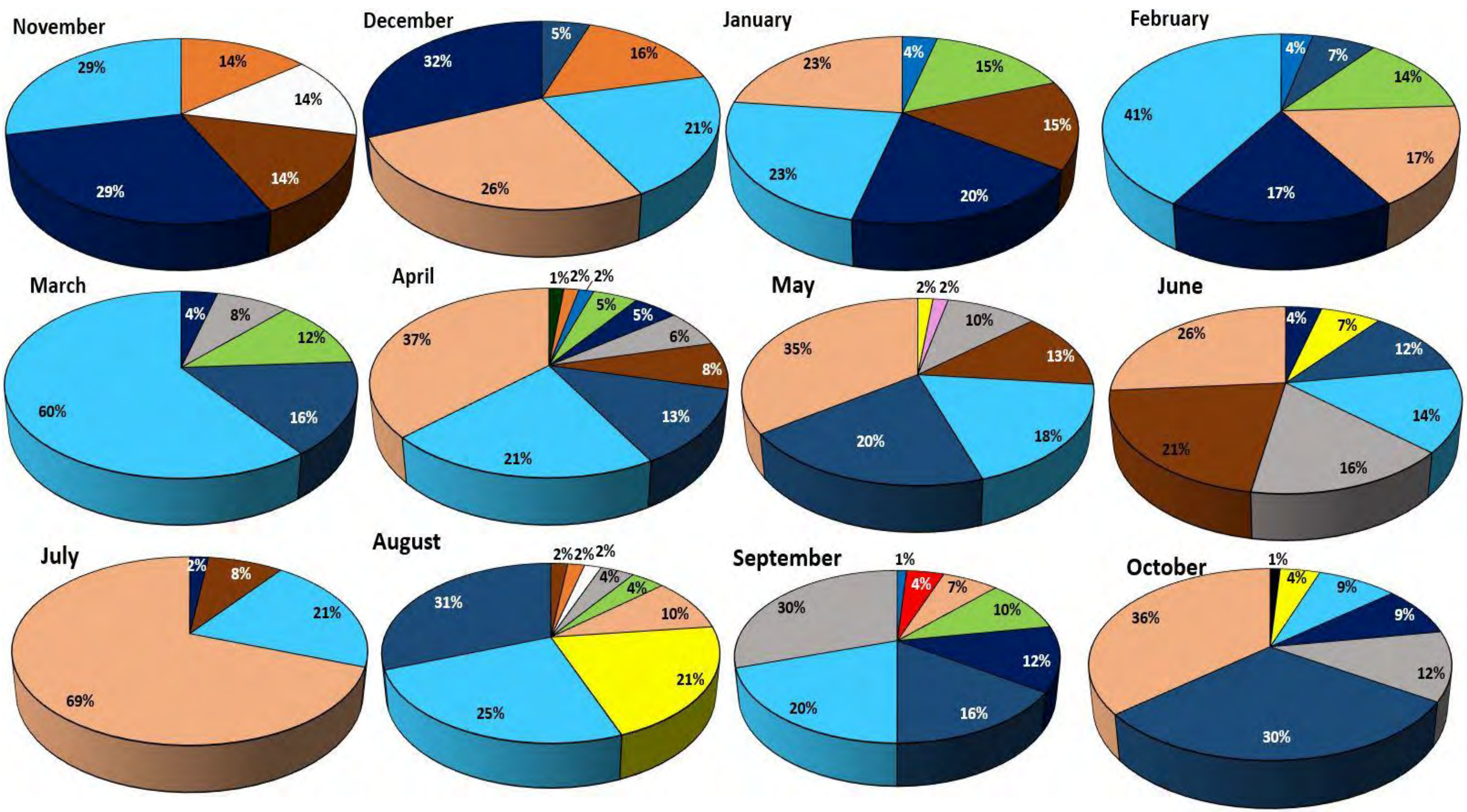


Figure A. 10: Mobile species diversity on the East bank of the Port of East London over the 12-month period on 5 cm unseeded tiles

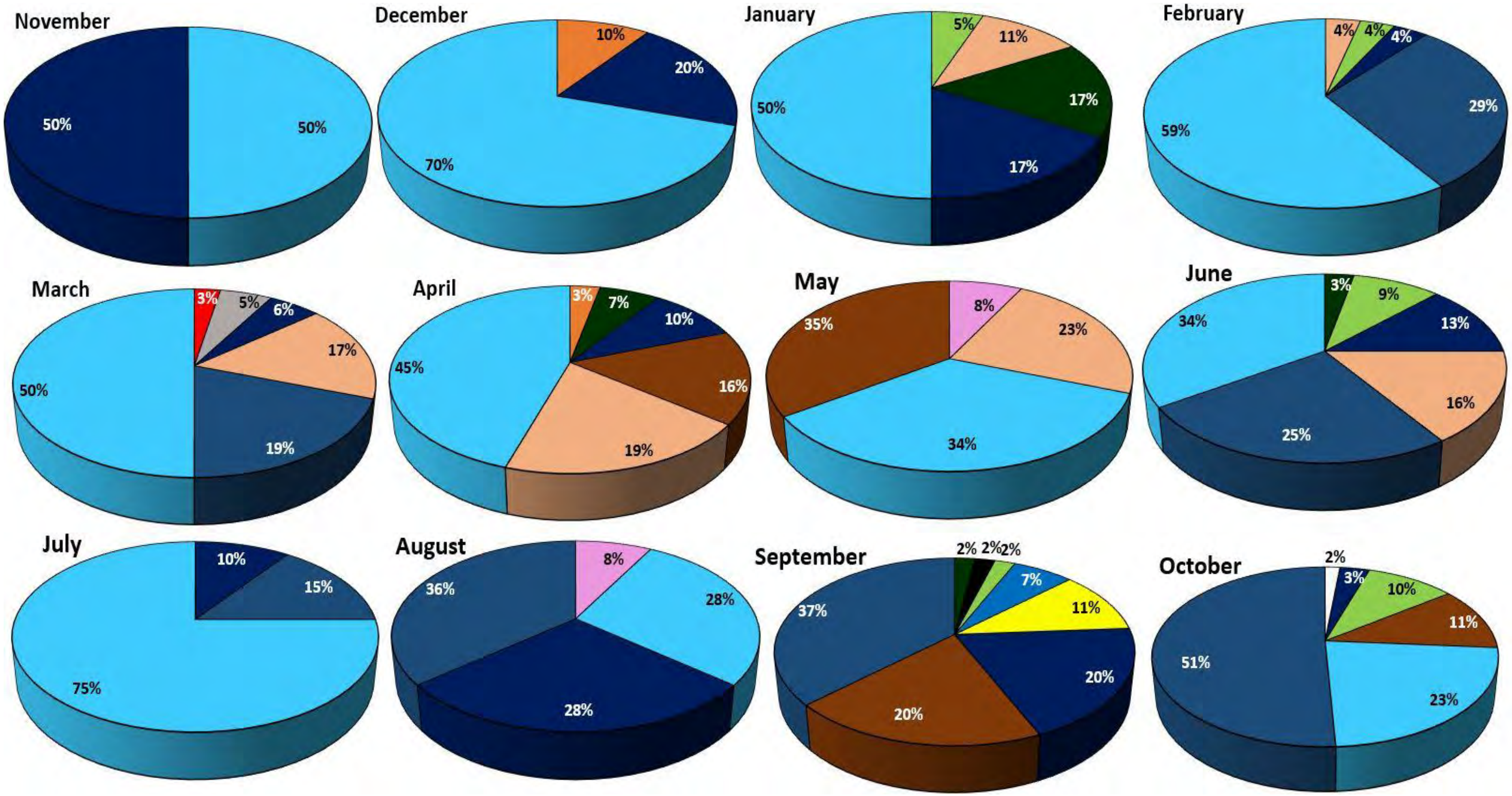


Figure A. 11: Mobile species diversity on the West bank of the Port of East London over the 12-month period on 5 cm seeded tiles

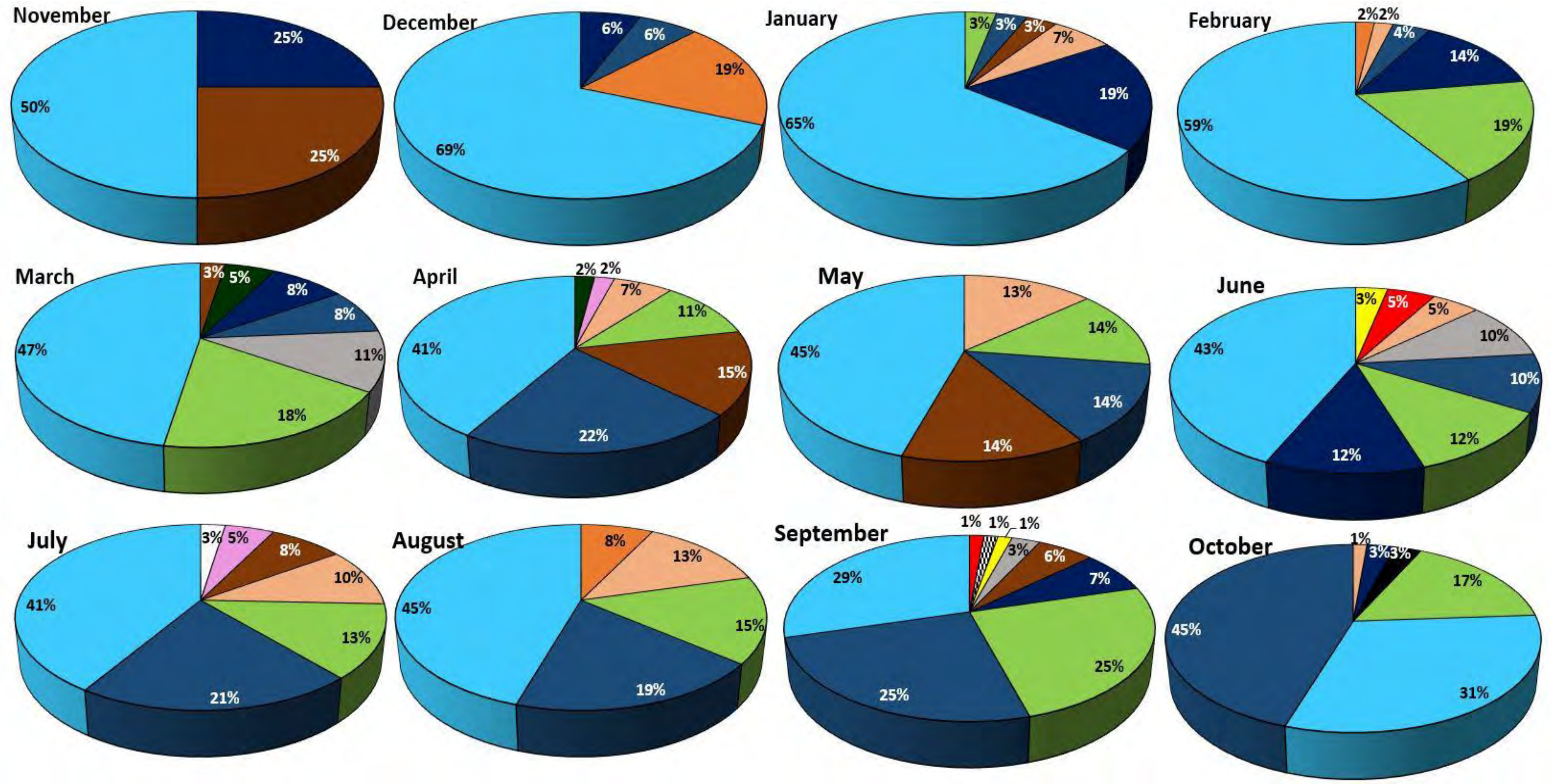


Figure A. 12: Mobile species diversity on the West bank of the Port of East London over the 12-month period on 5 cm unseeded tiles

Table A. 2: Legend for sessile species list in two sites and three treatments through time

Species	Colour
Ulva	🟨
Gelidium	⬜
Hildernbrandia rubra	▨
Hildernbrandia lecanellieri	⬛
Amphibalanus amphritrite	🟦

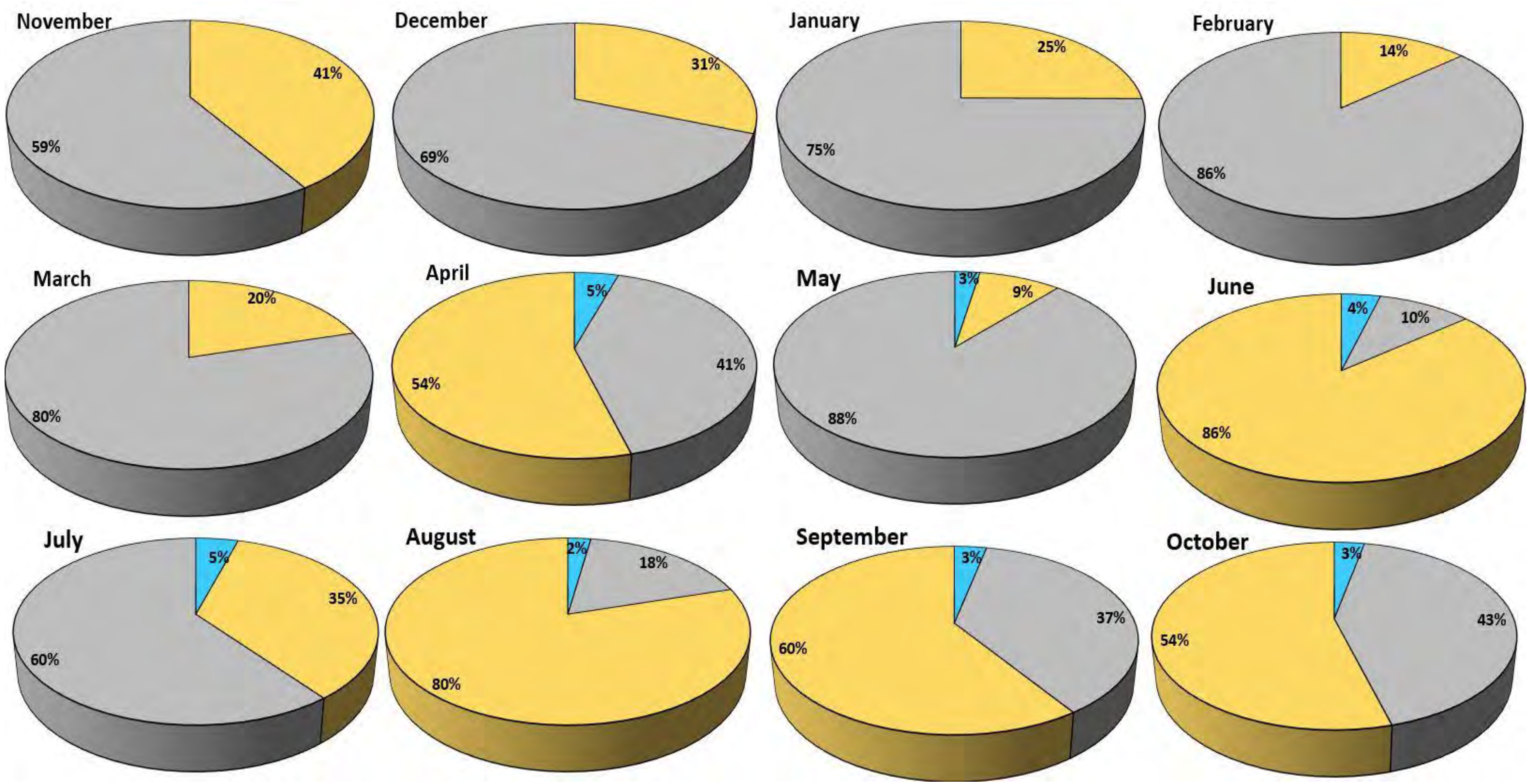


Figure A. 13: Sessile species percentage cover on the East bank of the Port of East London over the 12-month period on flat seeded tiles

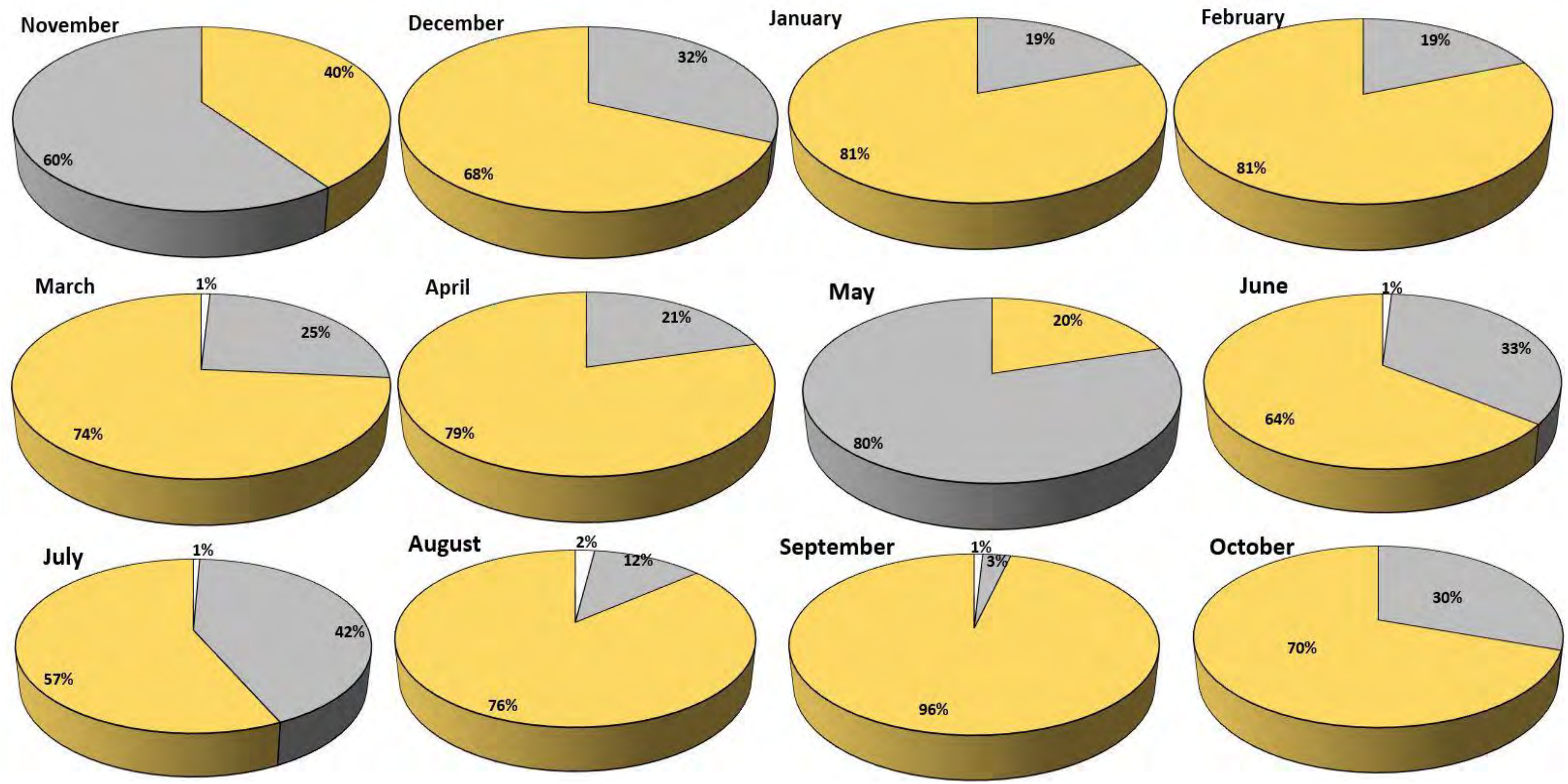


Figure A. 14: Sessile species percentage cover on the East bank of the Port of East London over the 12-month period on flat unseeded tiles

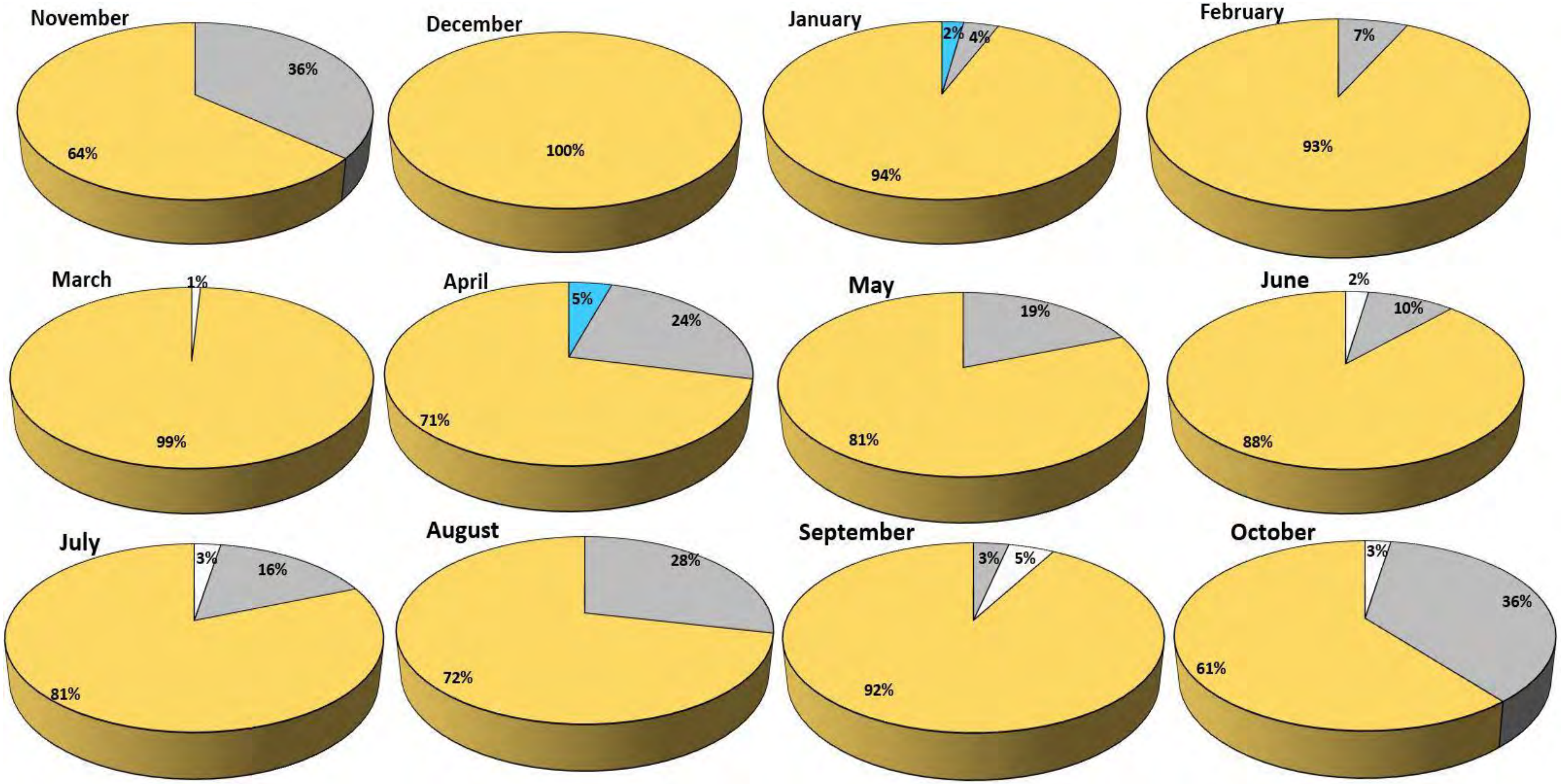


Figure A. 15: Sessile species percentage cover on the West bank of the Port of East London over the 12-month period on flat seeded tiles

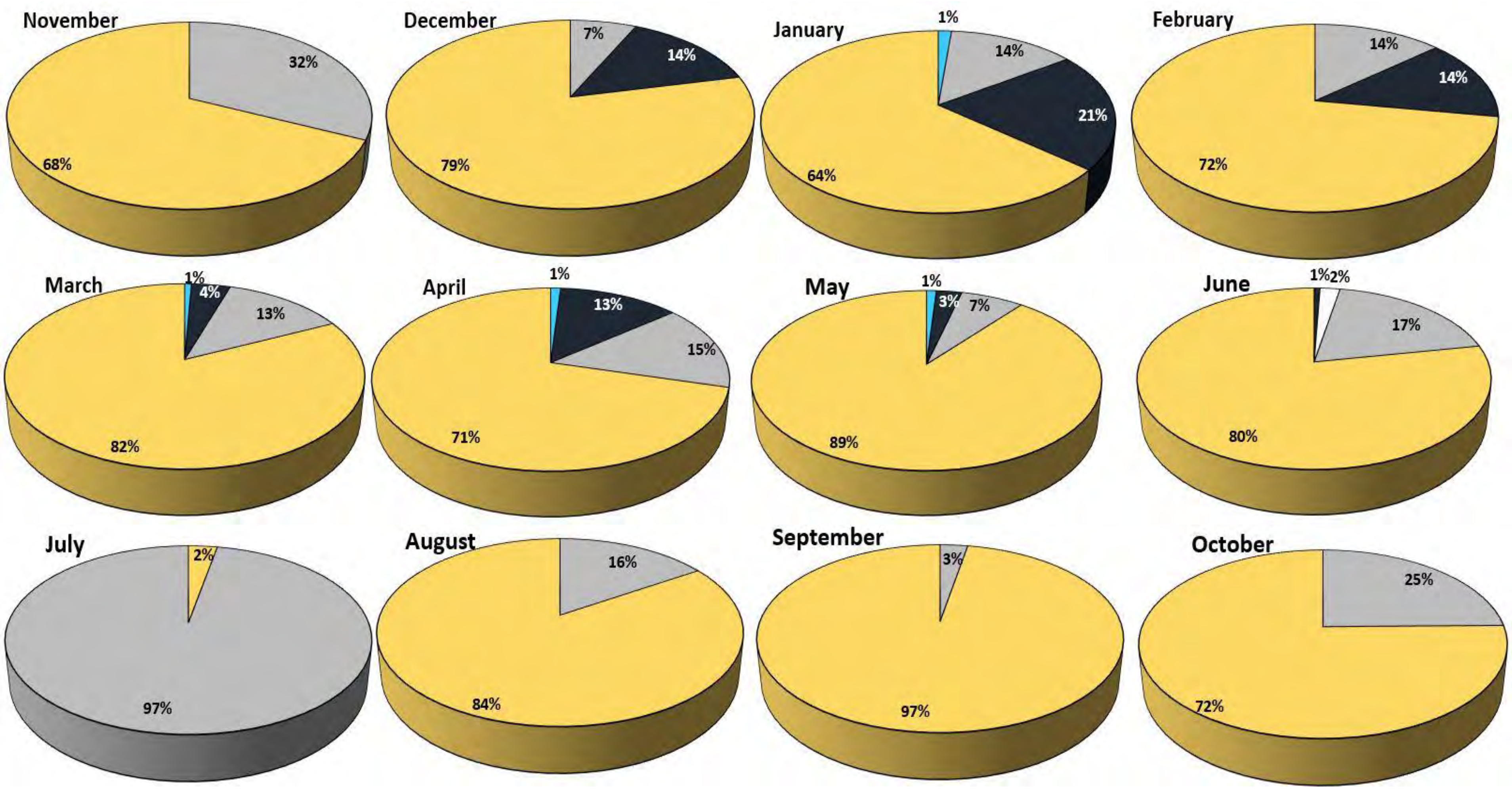


Figure A. 16: Sessile species percentage cover on the West bank of the Port of East London over the 12-month period on flat unseeded tiles

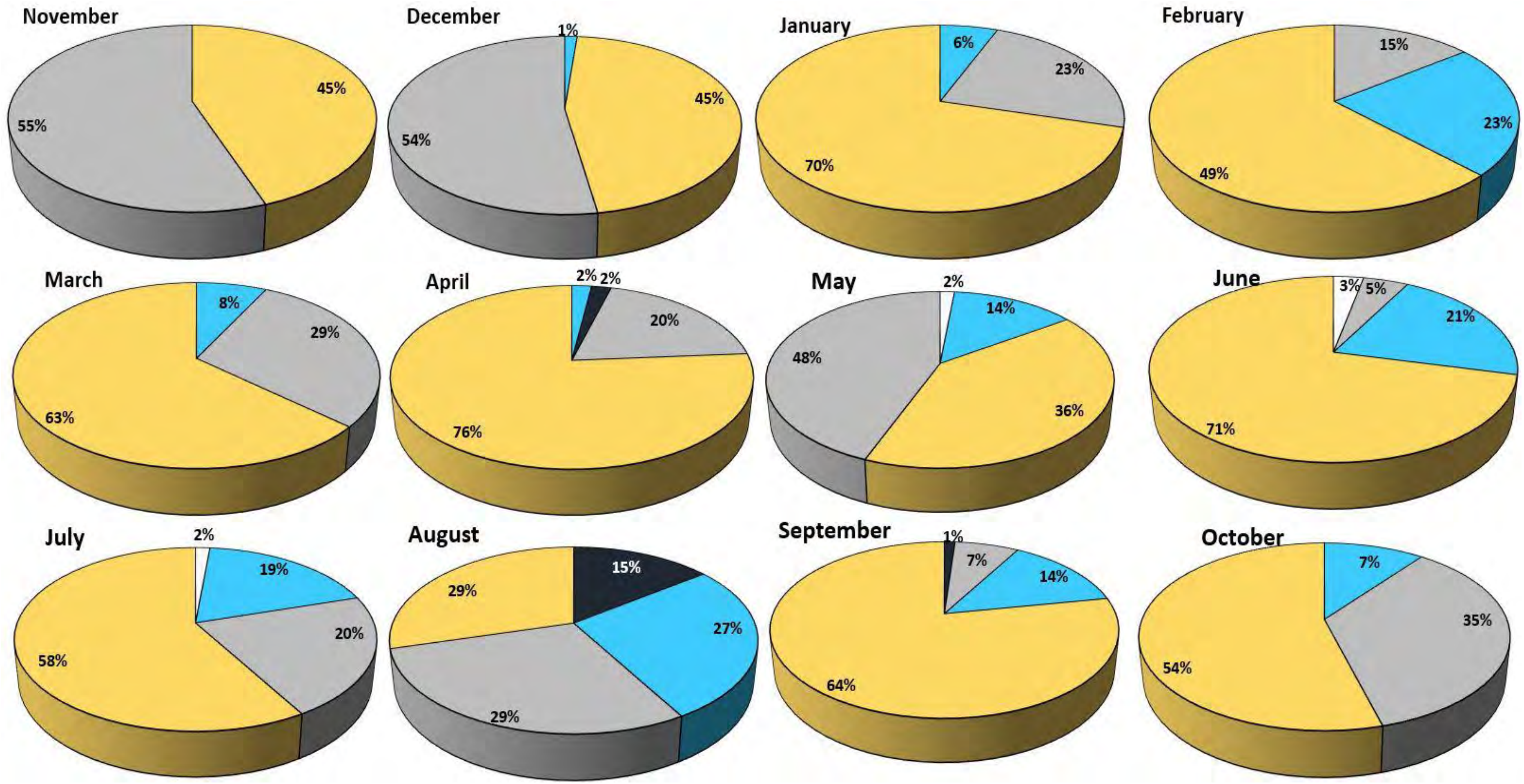


Figure A. 17: Sessile species percentage cover on the East bank of the Port of East London over the 12-month period on 2.5 cm seeded tiles

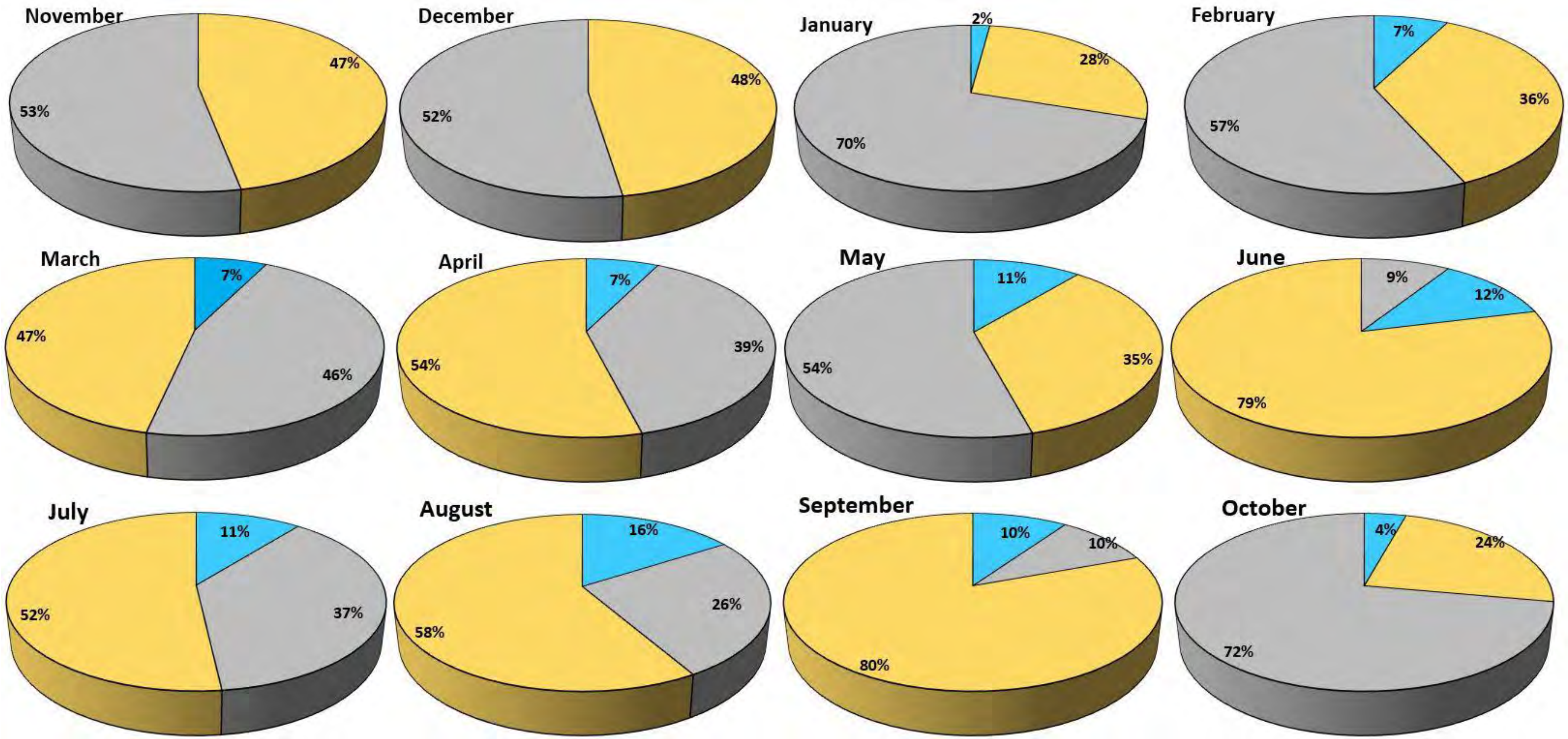


Figure A. 18: Sessile species percentage cover on the East bank of the Port of East London over the 12-month period on 2.5 cm unseeded tiles

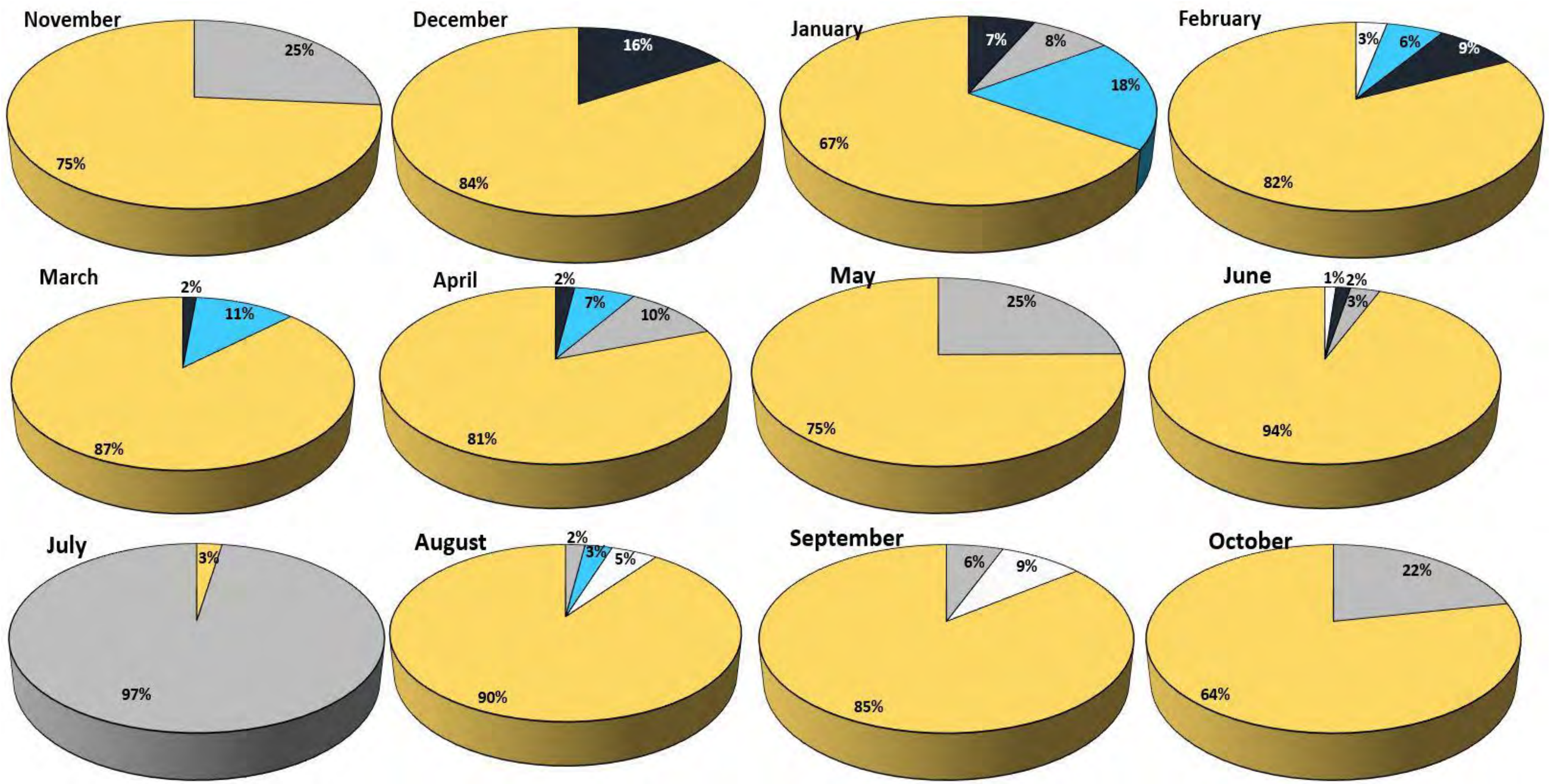


Figure A. 19: Sessile species percentage cover on the West bank of the Port of East London over the 12-month period on 2.5 cm seeded tiles

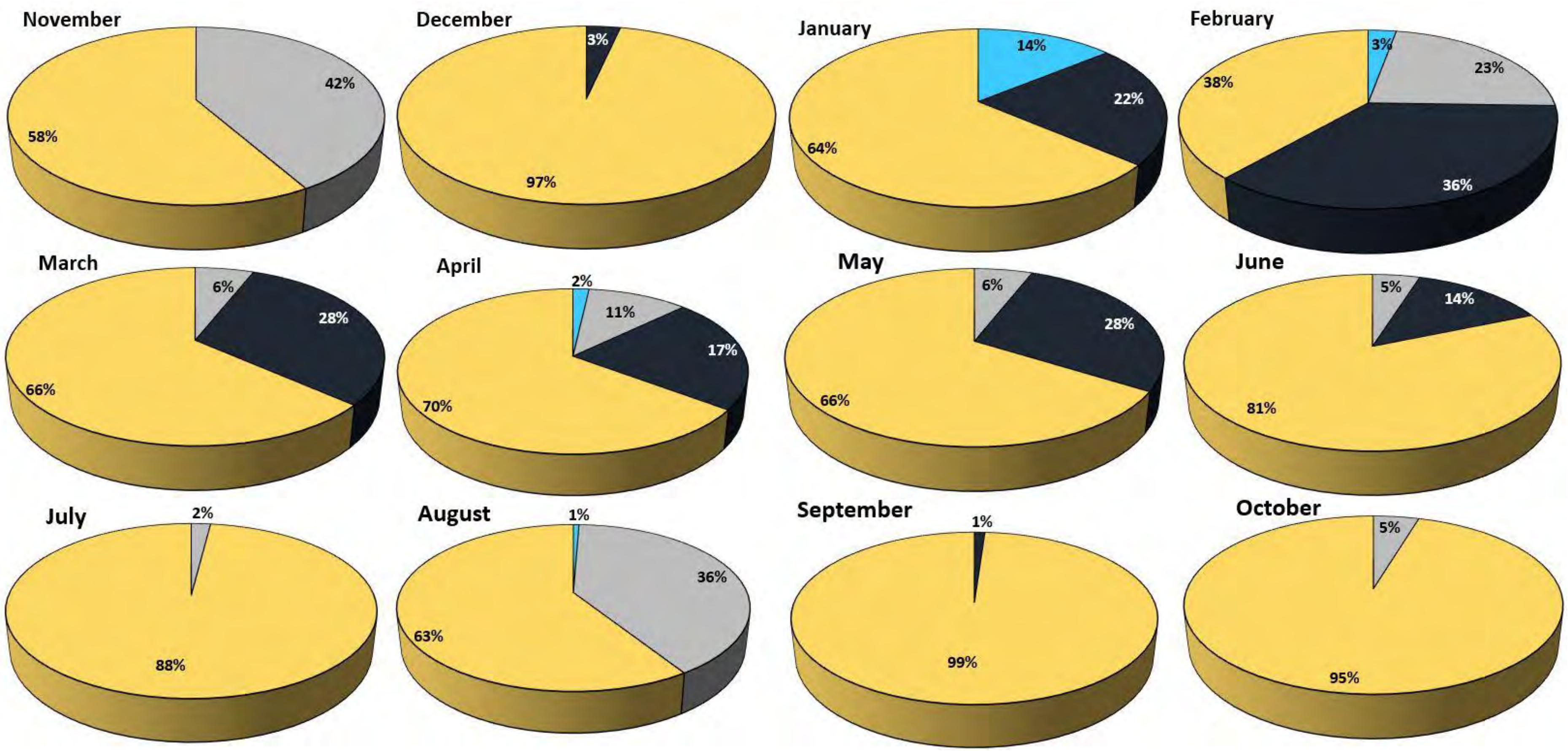


Figure A. 20: Sessile species percentage cover on the West bank of the Port of East London over the 12-month period on 2.5 cm unseeded tiles

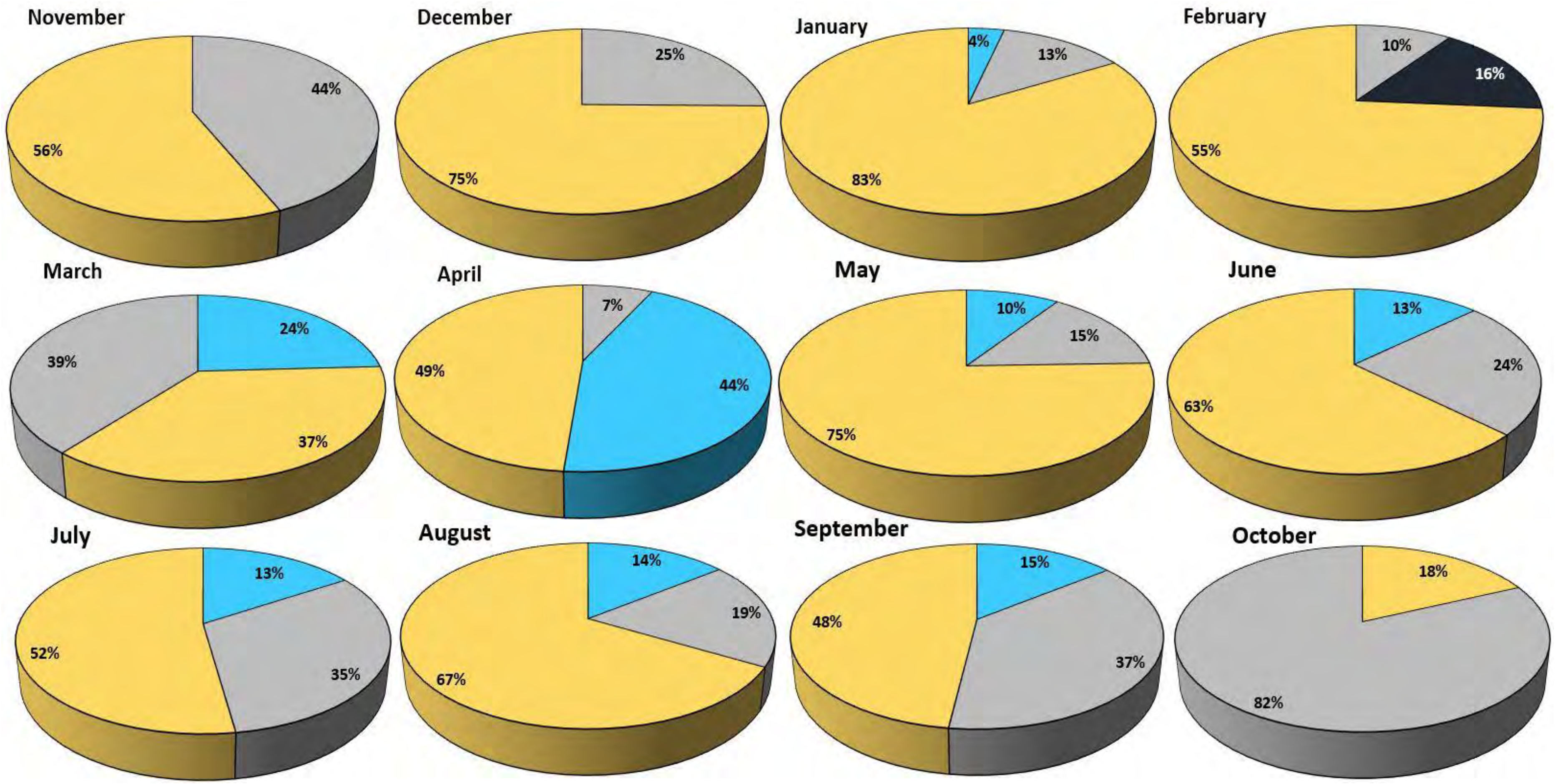


Figure A. 21: Sessile species percentage cover on the East bank of the Port of East London over the 12-month period on 5 cm seeded tiles.

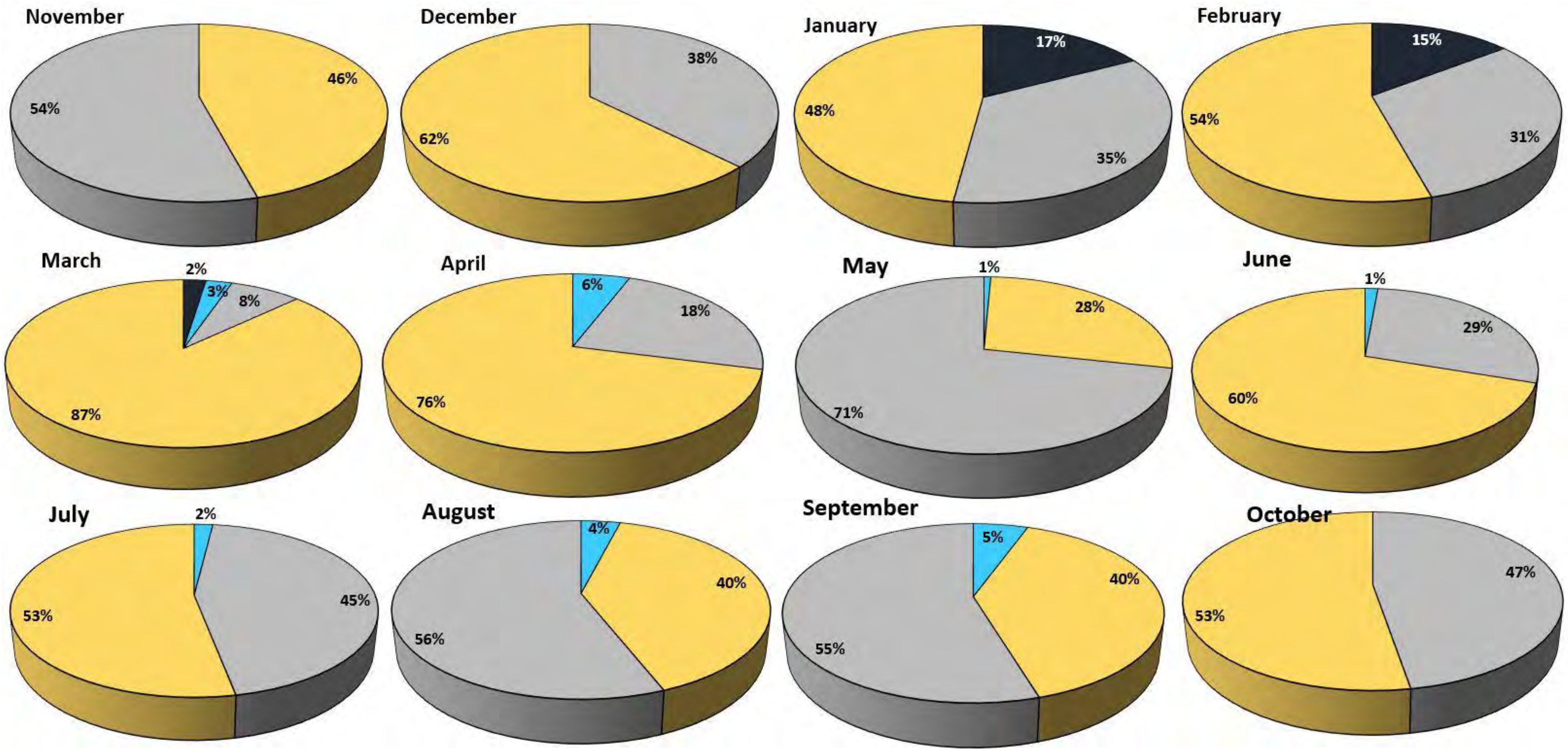


Figure A. 22: Sessile species percentage cover on the East bank of the Port of East London over the 12-month period on 5 cm unseeded tiles.

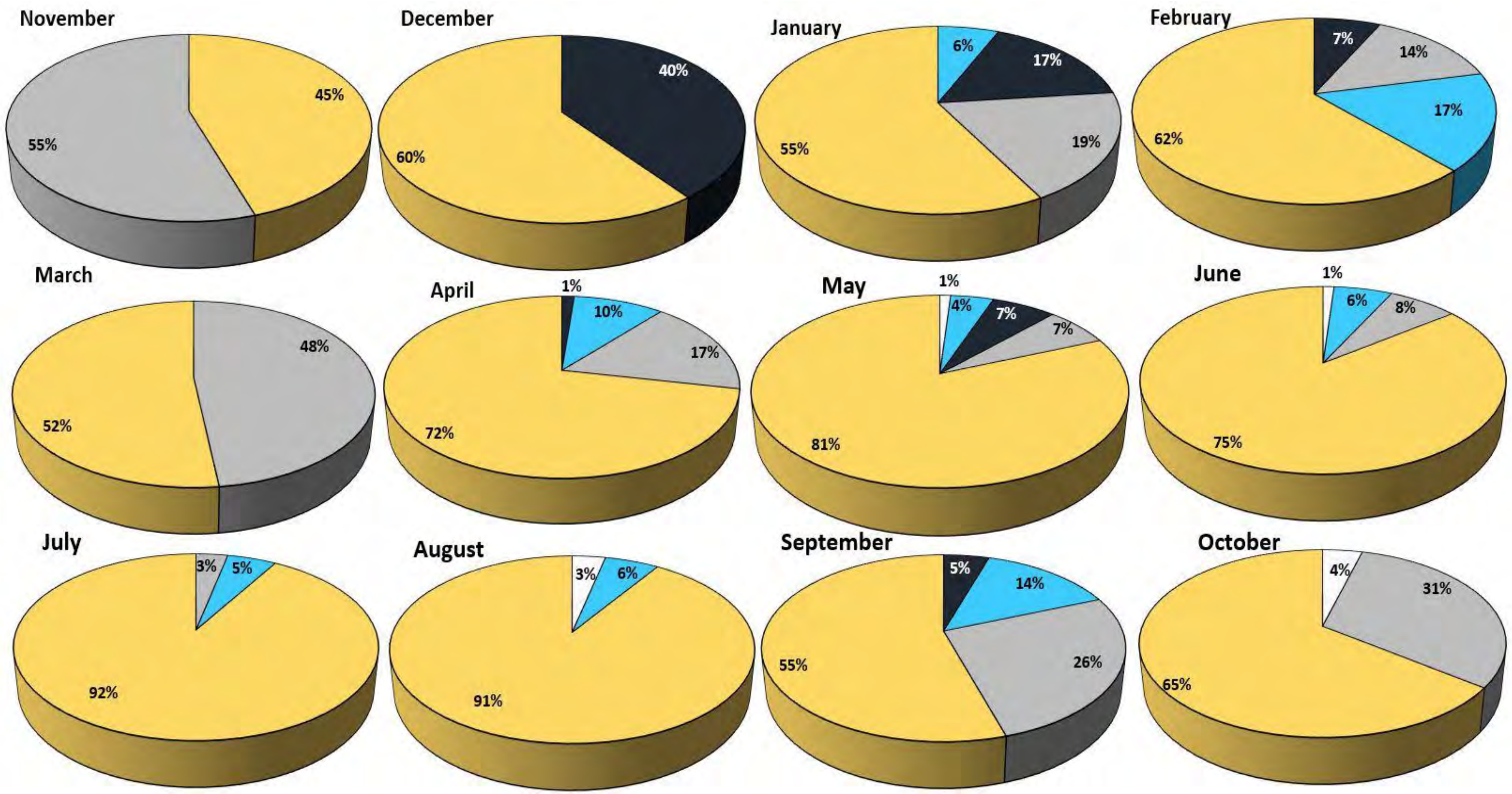


Figure A. 23: Sessile species percentage cover on the West bank of the Port of East London over the 12-month period on 5 cm seeded tiles.

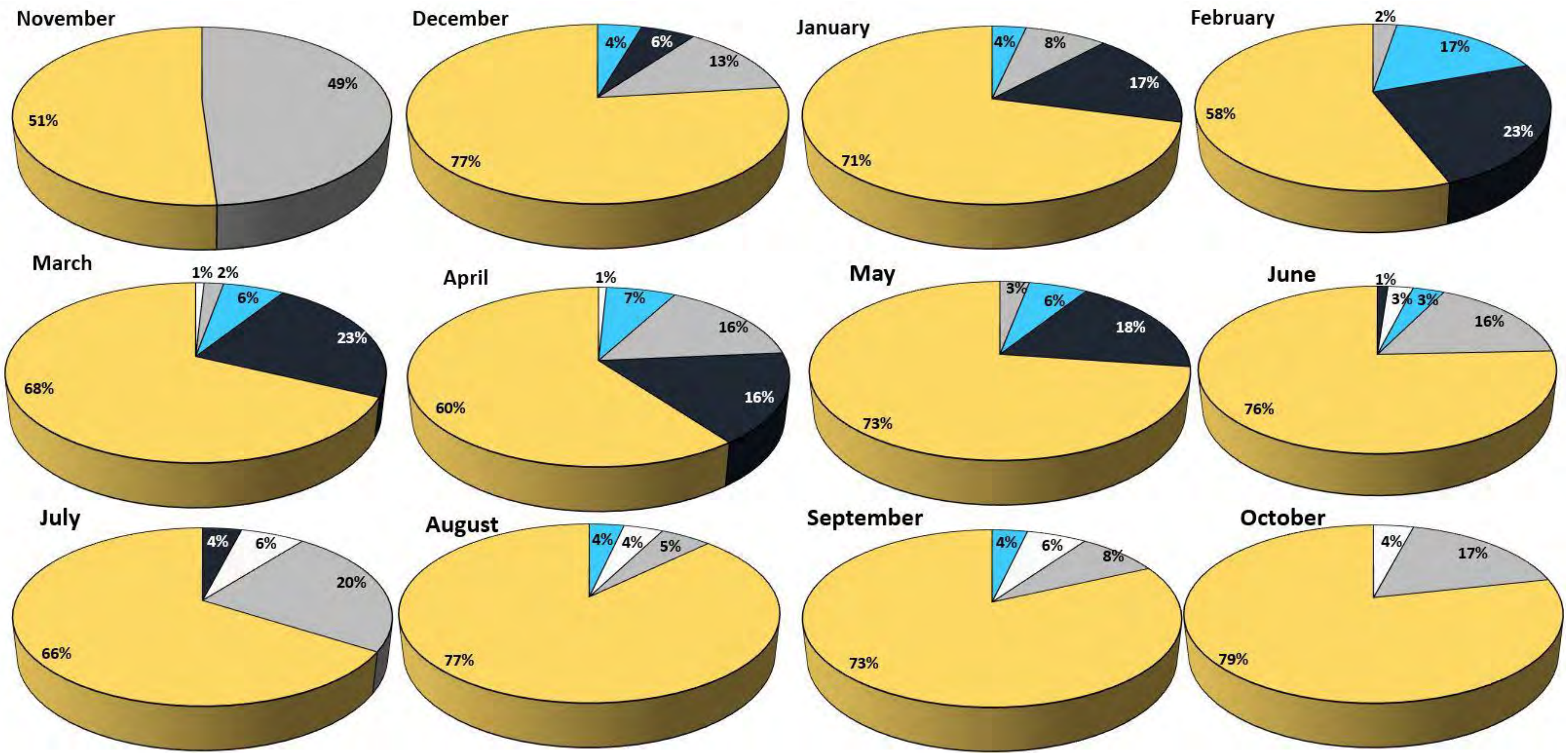


Figure A. 24: Sessile species percentage cover on the West bank of the Port of East London over the 12-month period on 5 cm unseeded tiles.

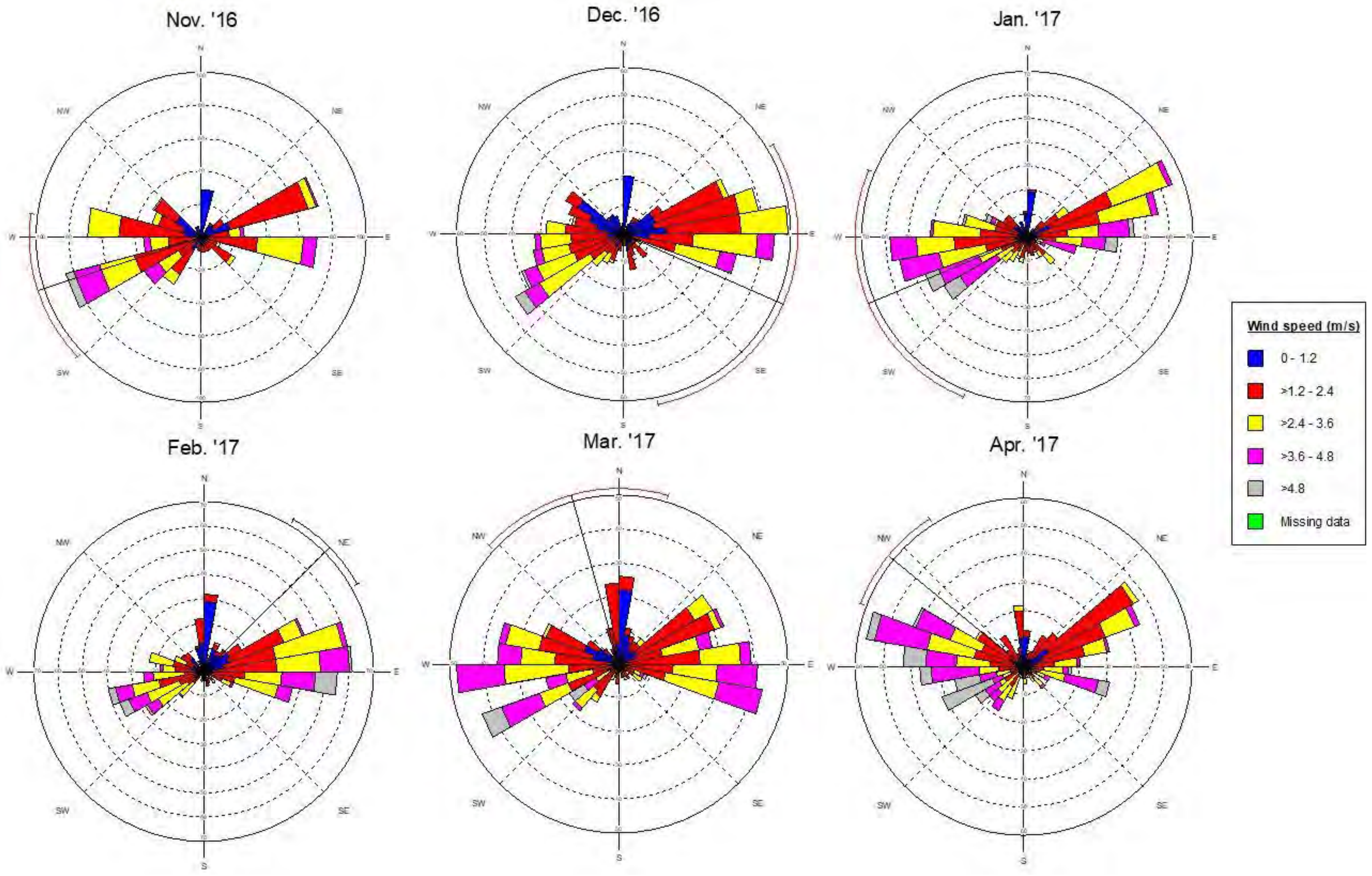
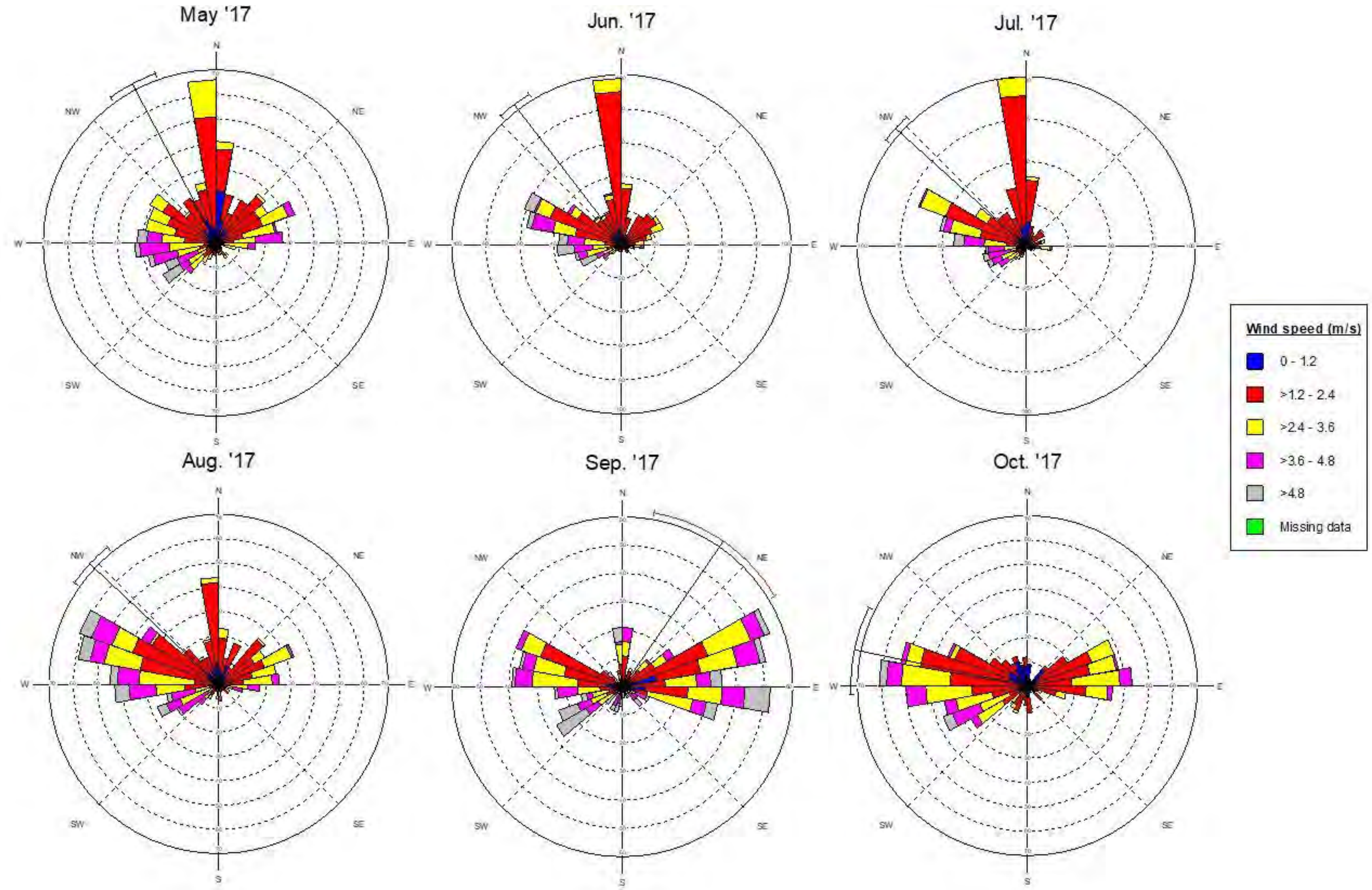


Figure B. 1: Wind roses showing the direction of the wind effect for the months November 2016-April 2017.


May '17

Jun. '17

Jul. '17

Aug. '17

Sep. '17

Oct. '17

Figure B. 2: Wind roses showing the direction of the wind effect for the months May 2017-October 2017.

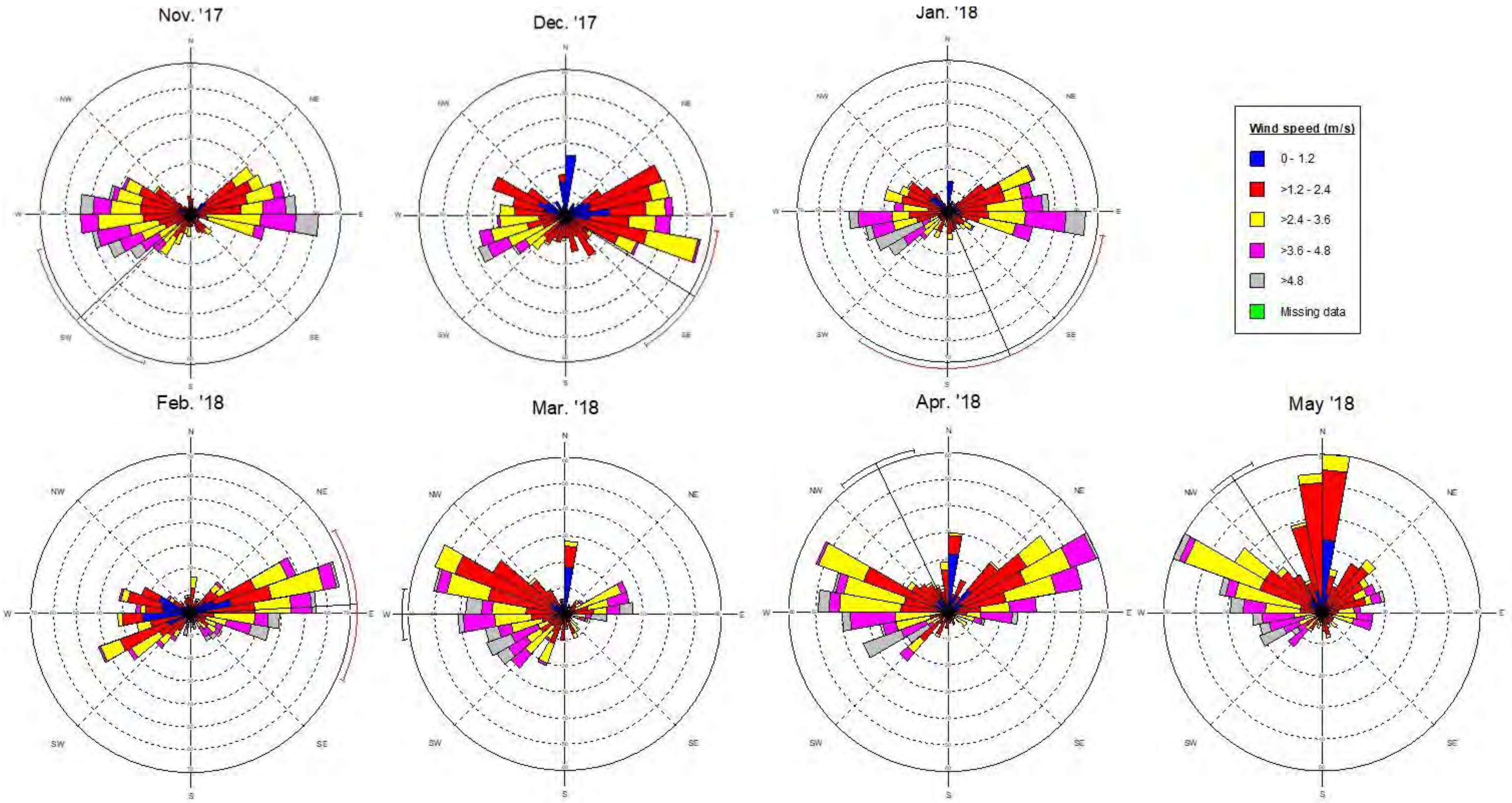


Figure B. 3: Wind roses showing the direction of the wind effect for the months November 2017-May 2018.