

**The use of gabions as a tool for ecological engineering: evidence from a South
African temperate estuary**

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Abstract

Anthropogenic activities are centred in coastal ecosystems, including the development of harbours and/or marinas. The artificial structures used in coastal development typically has a different composition, orientation and level of complexity to that of natural ecosystems contributing to loss of biodiversity and increased incidence of invasive species. Ecological engineering research is attempting to identify different types of structures and materials that can increase species diversity and target species of conservation concern in coastal systems. The aim of this study was to investigate the efficacy of gabions (rock filled structures) as an ecological engineering tool by comparing community structure on these structures with pre-existing seawall structures within a small harbour and marina in South Africa (Knysna Harbour). The objectives of the study were to compare the differences in; 1) fish and; 2) colonising organisms' diversity and composition between two artificial structures. Thirteen gabion boxes were deployed in Knysna Harbour and together with corresponding seawalls, monitored quarterly over a period of 12 months (August 2020 – August 2021) to assess taxon and functional richness, diversity, abundance and composition of fish, invertebrate and algal species. Physico-chemical characteristics of the water body were also monitored quarterly. Remote underwater video systems were used to quantify MaxN (maximum number of a fish species in the frame at any one time during each set that gives an indication of relative abundance) and identify fish species. The results of the two-way crossed ANOVAs indicated that gabion habitats recruited greater numbers and more types of fish species and from more functional groups than the seawalls, especially omnivorous and carnivorous fish. Additionally, photoquadrats were used to quantify percentage cover, counts and to identify colonising taxa. The results of the two-way crossed ANOVAs indicated

that gabions hosted greater numbers of species resulting in a higher overall diversity and abundance of colonising organisms than seawalls. By contrast, the seawalls supported more types of functional groups of colonising organisms than gabions, largely due to abundances of different algal species. The results from the crossed PERMANOVAs indicated that the composition of fish and colonising organisms were vastly different from one another, and that each habitat was supporting very different functional groups. Results indicate that whilst both gabions and seawalls contain several alien species, that the ratio of native to alien species is higher in gabion habitats. Additionally, this research observed that gabion structures hosted four species listed on the IUCN Red List of Threatened Species. This study has highlighted that the use of gabions (with their natural increased complexity) could be important to consider for the future of urban coastal development in harbours such as in Knysna Harbour. Ecological engineering projects using gabions have the potential to be used in South Africa in projects that aim at increasing biodiversity in urban coastal environments. As well as increasing the settlement and abundance of habitat-forming ecosystem engineers to ensure the long-term stability of these ecosystems. They can be used both in the development of new coastal development projects as well as in an ad-hoc fashion where they can be interspersed on seawalls in harbours. Additionally, gabions have the potential to be used in projects that target species of conservation concern such as the endangered Knysna Seahorse (*Hippocampus capensis*). It is, however, important to monitor the invasion by non-native species in future ecological engineering projects in South Africa as well as their potential for creating ecological traps (a situation in which an organism may be convinced to settle in a low-quality habitat) for certain species.

Keywords: artificial structures, ecological engineering, harbours, estuary, gabions

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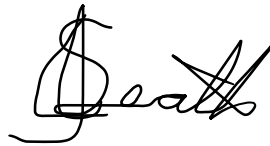
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Declaration

This thesis is the result of the author's own work, except where acknowledged or specifically stated in the text. It has not been submitted for any other degree or examination at any other university or academic institution.

A handwritten signature in black ink, appearing to read 'J. Seath', with a stylized flourish at the end.

Jessica Seath

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Chapter 1

General Introduction

1.1. Coastal development

The Earth's population is estimated to reach 9.4 billion by 2050 (Gerland *et al.*, 2014), of whom approximately 40 % currently live within 100 km of the coastline (Tibbetts, 2002; Firth *et al.*, 2016b). There are currently between 600 million and 1 billion people living in coastal areas < 10 m above the current sea level (McGranahan *et al.*, 2007; Kulp & Strauss, 2019; Kirezci *et al.*, 2020). It is anticipated that with sea level rise, some 630 million people will be living below sea level by the year 2100 (Kulp & Strauss, 2019). Climate change poses one of the greatest threats to the ocean and its coastline with phenomena such as sea-level rise (Kirby *et al.*, 2021), ocean acidification (Greenhill *et al.*, 2020), and an increase in frequency and intensity of storms (Webster *et al.*, 2005; FitzGerald *et al.*, 2008; IPCC, 2023). Rising sea levels will cause changes to ocean currents, tides and wave action (Mimura, 2013), leading to increased coastal erosion and flooding along sedimentary shorelines (Masselink *et al.*, 2020; IPCC, 2023). Future population growth and continued relocation to coastal cities (Nicholls & Cazenave, 2010), together with the impacts of climate change, will exacerbate the need to concentrate humans in high rise buildings or expand urban environments via urban and ocean sprawl (Evans *et al.*, 2019; Theodora & Spanogianni, 2022).

Coastlines around the world have seen the proliferation of artificial structures for millennia (Airolidi *et al.*, 2005; Dugan *et al.*, 2011). For example, seawalls were used in the Middle Ages in

23 Europe, although they might have existed earlier in the Far East, while Groynes were used in
24 Europe as early on as the 1850s (Dugan *et al.*, 2011). Coastal development includes the erection
25 of a variety of perpendicular (breakwaters, groynes and jetties) and parallel (seawalls, and
26 revetments) structures (Bulleri & Chapman, 2010; Firth *et al.*, 2016b; Fig. 1.1.) built for a range
27 of purposes including transport (docks, harbours), coastal erosion prevention (rock armouring,
28 groynes, breakwaters), redirection of rivers or currents (training walls), and protection of
29 property (Chapman & Bulleri, 2003; Cooper *et al.*, 2016). The materials used to construct these
30 structures vary widely, as does their life span and costs (Jones, 1994; Griggs, 1998). The
31 construction materials may include stone, wood, concrete, steel, wool or geotextile. There is
32 also a great demand for property near the shore where houses, waterfront commercial
33 properties and parking lots are built for their aesthetic value (Airoldi & Beck, 2007) and as a
34 cultural ecosystem service (Rodrigues *et al.*, 2017). It is estimated that over 70 % of the world's
35 coastal cities have been artificially engineered, the types of structures and extent of this
36 development is summarised in Table 1.1 (Lai *et al.*, 2015, Chee *et al.*, 2017; Firth *et al.* (under
37 review)). More recently land reclamation has seen the construction of entire artificial islands in
38 areas such as Asia and the Middle East (Burt *et al.*, 2010; Chee *et al.*, 2017; Firth *et al.*, 2020;
39 Chee *et al.*, 2021).



40

41 Figure 1.1: Images showing different types of artificial structures along South Africa's coastlines
 42 including; (a) a seawall in Knysna, South Africa; (b) a restaurant, parking lot and seawall in
 43 Ramsgate, South Africa; (c) a wooden harbour wall in Knysna, South Africa; (d) a man-made
 44 tidal pool in Ramsgate, South Africa; (e) a slipway in Knysna, South Africa; and (f) a breakwater
 45 in Mossel Bay, South Africa (a structure that absorbs wave-action before reaching a port).

46 Table 1.1: Summary of the extent of coastal artificial structures around the world.

Area	Extent	References
Australia	32 - 49 % of shorelines are modified with seawalls. Raby Bay (Southeast Queensland) has > 19 km of concrete structures. Pontoons, break walls and jetties line 10 % of the Great Barrier Reef coastline.	Chapman, 2003; Creese <i>et al.</i> , 2009; Dugan <i>et al.</i> , 2011; Waltham & Sheaves, 2015.
Europe	4 700 km is artificially stabilized. 22 000 km ² of coastline is armoured.	EC, 2004; Airoidi & Beck, 2007; Dugan <i>et al.</i> , 2011.
Japan	27 % (9 400 km) of the coast is hardened.	Koike, 1993.
Malaysia	21.3 % of Penang Island's shoreline is artificial.	Chee <i>et al.</i> , 2017.
Mediterranean coastlines	An estimated 1 500 km of the coast is hardened by concrete with 1 250 km being harbours and ports; the North Adriatic Sea has more than 190 km of artificial structures.	EEA, 1999; Airoidi & Beck, 2007; Dafforn <i>et al.</i> , 2015a.
Singapore	63 % of the shoreline is hardened with 319 km of seawalls.	Lai <i>et al.</i> , 2015.
South Africa	2.86 % of the coastline is armoured.	Claassens <i>et al.</i> , 2022;
United States of America	Just over 50 % of coastlines in California, Virginia and Maryland are hardened; 17 % of New Jersey coastline is altered, Florida is 21 %, California is 12 %.	Griggs, 1998; Living Shoreline Summit Steering Committee, 2006; Lathrop & Love, 2007; Bulleri & Chapman, 2011.
Globally	4 000 km of residential canal estates, 4 700 ports around the world.	Waltham & Connolly, 2011; World Port Source, 2022.

47

48

49 The increasing domination of coastal environments by artificial structures is known as ocean
50 sprawl (Duarte *et al.*, 2012, Firth *et al.*, 2016b). Ocean sprawl replaces natural habitats
51 (beaches, rocky shores, mangroves and salt marshes) with artificial ‘habitats’ such as seawalls,
52 harbours, marinas and jetties (Airoidi *et al.*, 2009, Bulleri & Chapman, 2015, Dafforn *et al.*,
53 2015b; Bulleri *et al.*, 2020). These artificial habitats often lead to biotic homogenization
54 (McKinney, 2006; Bulleri & Chapman, 2010; Olden *et al.*, 2016); the process by which increasing
55 species invasions or species extinctions leads to the increased genetic, taxonomic or functional
56 similarity between populations across different locations within a specified time interval
57 (McKinney & Lockwood, 1999). Biotic homogenisation of marine fauna and flora threatens
58 ocean biodiversity (Firth *et al.*, 2016a), by forming ecological traps (reducing fitness of
59 colonising organisms) and contributing to increased mortality, which results in increasing
60 opportunistic and invasive species and competition for important native species (McKinney,
61 2006; Komyakova *et al.*, 2022). Coastal development can be so extensive that it replaces entire
62 natural shores as seen in Singapore where between the 1920s and 1990s entire stretches of
63 mangroves, coral reefs and sand/mudflats were removed to reclaim land (Lai *et al.*, 2015). The
64 loss of natural habitats as a result of ocean sprawl leads to the loss of important ecosystem
65 services and connectivity between the terrestrial and oceanic zones (Bulleri & Chapman, 2010,
66 Bishop *et al.*, 2017), which causes a reduction in the exchange of organic and inorganic
67 materials, nutrient uptake and water filtration (Bilkovic & Roggero, 2008). Furthermore,
68 artificial habitats often do not support the same community composition and species
69 assemblages as neighbouring natural rocky shores. For example, in the Southwest Atlantic
70 Ocean, compared to natural areas, artificial habitats were characterised by a reduction in

71 calcareous algae and declines in sediment carbonate content, likely caused by nutrient enriched
72 water (Sherner *et al.*, 2013).

73 The loss of structural complexity and habitat types also directly impacts the diversity and
74 abundance of fauna in these modified coastal ecosystems (Airoldi *et al* 2005; Martin *et al* 2005;
75 Moschella *et al* 2005; Dugan *et al.*, 2011; Grasselli & Airoldi, 2021). The materials used in the
76 construction of coastal development often lacks the complexity of natural coastal ecosystems
77 (Lawrence *et al.*, 2021), limiting attachment opportunities, the provision of habitats for
78 vertebrates and invertebrate species and limited refugia from predators and environmental
79 stressors (Dugan *et al.*, 2008; Firth *et al.*, 2016a). Moreover, these structures are commonly
80 built vertically which limits the distribution of space available for diverse and competing species
81 (Strain *et al.*, 2018; Hall *et al.*, 2019). Natural rocky shores are typically more gently sloping
82 whereas seawalls are steeper and often vertical (Andersson *et al.*, 2009). This orientation limits
83 the distribution of species needing to live at different tidal heights, affecting biotic interactions
84 and species biodiversity (Perkol-Finkel *et al.*, 2006; Chapman & Underwood, 2011), and
85 reducing light needed for photosynthesis in vegetation to occur and a reduced opportunity for
86 the support of nurseries for fishes (Bulleri & Chapman 2010; Dyson & Yacom, 2015).

87 The hardening of shorelines can also lead to both scouring and sedimentation (Waltham and
88 Sheaves, 2018; Hall *et al.*, 2019; Bone *et al.*, 2022b), which can significantly impact the available
89 habitat for benthic organisms such as those typically found in soft substrates (Dyson & Yacom,
90 2015; Firth *et al.*, 2016b; Bone *et al.*, 2022b). Moreover, when infrastructure is constructed on
91 sedimentary substrates, it exacerbates the reduction of habitat available for selected benthic
92 organisms (Heery *et al.*, 2017), leading to habitat fragmentation, loss of ecological connectivity

(Bishop *et al.*, 2017), and ultimately, habitat degradation (Dafforn *et al.*, 2019). The loss of sedimentary habitats has been shown to have negative effects on biodiversity, animal community assemblages, and ecosystem functioning (Airoldi & Beck, 2007; Heery *et al.*, 2017). Such changes may occur due to a higher abundance of primary producers than consumers, although the specific mechanisms underpinning this response is not well understood (Ryser *et al.*, 2019). However, Bone *et al.* (2022b), found that sediment that had accrued in artificial rockpools in the United Kingdom contained infauna characteristic of the surrounding estuarine benthos. The sedimentation occurring in artificial structures may therefore, provide an additional habitat in altered urban areas.

Harbours and marinas are coastal structures built to provide safe anchorage and facilities for marine vessels, are a transition zone between the land and the sea and are important in local economies (Chatzinikolau & Arvanitidis, 2016). However, their development can have significant environmental impacts (Firth *et al.*, 2016b). These include amongst others, the alteration of natural shoreline processes, changes in water circulation and sedimentation patterns, and the introduction of pollutants and proliferation of non-native species (Dafforn *et al.*, 2015b; O'Shaughnessy *et al.*, 2022; Bulleri *et al.*, 2022). Harbours and marinas are typically created by excavating canals and continuous dredging of bays or estuaries which is disruptive to natural habitats (Baird *et al.*, 1981). These structures are some of the most heavily modified environments (Lotze *et al.*, 2006), and their construction leads to the linearisation of coastlines (Firth *et al.*, 2016b). Because they can be impacted and polluted by both the surrounding terrestrial and marine environment, they can impact surrounding coastal ecosystems

(Chatzinikolau & Arvanitidis, 2016). Ships are responsible for bringing in non-native species causing the biotic homogenisation of species (Firth *et al.*, 2016b), where small harbours that support yachts are known for supporting more non-native alien species than other harbours (Peters *et al.*, 2014).

The prevalence of harbours and marinas in estuaries varies depending on the region and local development patterns. In some areas, such as heavily urbanized coastal regions, there may be a high concentration of harbours and marinas in estuaries. For example, in Australia, around 70 % of marinas are located in estuaries and sheltered bays (James *et al.*, 2010). The construction and presence of harbours and marinas in estuaries can have significant impacts on these ecosystems. One of the most notable impacts is the alteration of water flow and sediment transport, which can affect the distribution of nutrients and organic matter in the estuary (Bilkovic & Rogerro, 2008). These changes can have cascading effects on the biology within these systems. Overall, harbours and marinas in estuaries often contribute to ecosystem degradation and the loss of biodiversity (Parker *et al.*, 1999; Beck *et al.*, 2001).

Heavily-modified environments are deemed as ‘novel’ or ‘emerging’ ecosystems because they’re not likely to be reversible in their current state (Hobbs *et al.*, 2009, 2013). They are characterised by non-natural compositions of species with no recent ‘natural’ state. They can either be left untouched to preserve them or these novel habitats (e.g. bridges, buildings, jetties, harbours, etc.) can be modified to retain their original function by providing habitat for species whose natural habitat has been entirely lost or severely damaged (Rosenzweig, 2003).

The construction of harbours and marinas can be used over and above their role for transportation and may offer habitat to aquatic organisms (Dyson & Yacom, 2015), by acting as

an avenue for ecological restoration and therefore, urban conservation (Clynick, 2007). The adverse impacts of harbours and marinas can be mitigated using ecologically sensitive design and management practices. With careful planning and management, harbours and marinas can serve as vital economic and recreational resources while also minimizing their impact on the coastal and marine environment (Aguilera *et al.*, 2023).

1.2. Ecological Engineering as a solution

Whilst restoration typically aims to return compromised ecosystems back to a more natural state or at least a target state (Geist & Hawkins, 2016), this is not always possible in heavily-modified environments (Chapman & Blockley, 2009; Hawkins *et al.*, 2020). Engineering projects that have the potential to increase biodiversity in artificial habitats should be the focus of future research. This is known as reconciliation ecology which aims to diversify urban habitats and to increase biodiversity in these human-dominated spaces (Rosenzweig, 2003). This is achieved through ecological engineering (Mitsch, 1996). Ecological engineering focuses on enhancing novel ecosystems to promote biodiversity and maintain ecosystem functioning (Dyson & Yacum, 2015; Dafforn *et al.*, 2015a). The process involves designing ecologically resilient systems that can self-organise and evolve under situations of unanticipated environmental stress (Bergen *et al.*, 2001).

There are many examples of multifunctional structures that are offsetting biodiversity. This includes manipulating building materials, adding topographical complexity and transplanting organisms onto substrate (see O' Shaughnessy *et al.*, 2020 for full review). An example of a soft

engineered approach was the removal of a seawall in Chesapeake Bay which was replaced with marsh plants to control coastal erosion (Davis *et al.*, 2006). Transplantation was employed to restore canopy-forming algae through biological interventions in the North Adriatic (Italy) where juvenile *Cystoseira barbata* (Stackhouse) were transplanted into four habitats and showed a greater rate of species survival than the original site (Firth *et al.*, 2014b). Adams *et al.* (2021), assessed the effectiveness of transplanting seeded mussels (*Mytilus galloprovincialis*) onto artificial structures in a marina to reduce colonisation by invasive taxa and found varying results amongst applications. They described how further research needed to be conducted to determine how the study could be upscaled to improve native biodiversity in marinas. Marinas can be easily contaminated and are often characterised by poor water quality. Bulleri *et al.* (2022), employed sponges on floating installations in the Mediterranean to act as a tool for biomonitoring of inorganic and organic pollutants. This is a nature-based solution that could improve the ecological value of urban environments. By contrast, a study conducted in the Sydney Harbour demonstrated an example of a hard retrofitting approach where cavities were added to a seawall at three different tidal heights (Chapman & Blockley, 2009). Although this approach did contribute to enhanced diversity at each level and a greater vertical range of species, the overall community was different from neighbouring natural rock pools because of a supposed difference in slope and aspect as well as wave-action. More recently, Bishop *et al.* (2022), demonstrated the importance of habitat heterogeneity to maximise biodiversity. They also tested a few retrofitting approaches at patch and site scales and observed increases in unique species based on the niche of their target species and the chosen eco-engineering intervention.

180 In general, ecological engineering approaches to existing structures aim to increase the
181 complexity of the infrastructure at different spatial scales (Moschella *et al.*, 2005; Moreira *et*
182 *al.*, 2007; Chapman & Blockley, 2009; Chee *et al.*, 2021; Strain *et al.*, 2021; O'Shaughnessy *et al.*,
183 2021; Bishop *et al.*, 2022; Mayer-Pinto *et al.*, 2022). At the micro-scale, pits and crevices are
184 drilled into concrete walls to increase the micro-habitat availability (Chapman, 2003; Moreira *et*
185 *al.*, 2007; Bender *et al.*, 2020). These small-scale interventions can increase the numbers of
186 species found on these modified units (Firth *et al.*, 2014b; Strain *et al.*, 2018; Burt &
187 Bartholomew, 2019). Chapman & Underwood (2011), found that adding pits to seawalls
188 resulted in an increased number of limpets due to enhanced recruitment and immigration. Hall
189 *et al.* (2019), designed 'vertipools' and retrofitted them onto seawalls across the intertidal zone
190 to mitigate the effects of sea-level rise on the geographical distribution of invertebrates. The
191 results showed a significantly greater species richness in the vertipools than seawalls. 'The
192 URBANE project' which ended in 2014 tested the use of BIOBLOCKS; precast habitat enhancing
193 units that mimic multiple different habitats (Firth *et al.*, 2014b), to enhance the biodiversity.
194 The BIOBLOCKS can be used on a small, medium and macro-scale if implemented at the design
195 phase. Whilst the initial results of this project demonstrated the success of these units,
196 returning to the project a few years later, in 2019, it was discovered that after various storms
197 the BIOBLOCKS were covered in sand and buried (Firth *et al.*, 2020). Whilst many of these
198 projects initially had positive outcomes, the interventions did not always persist time, which
199 highlights the importance for reporting unintended outcomes so as to not oversell ecological
200 engineering (Firth *et al.*, 2020; Hsiung *et al.*, 2020; Strain *et al.*, 2021).

While many of these projects are assessing different structures and materials to enhance habitat availability, there may be value in testing the efficacy of existing structures such as gabions in ecological engineering projects. Gabions are rock-filled wire cages (Maccaferri, 1915), that are often used as erosion control structures along coastlines and in sheltered bays and estuaries, particularly in South Africa (Claassens, 2016). Gabions have subsequently been used in other applications such as stabilisation of riverbanks and as weirs due to their ecological and economic advantages over solid weirs – they are relatively cheap, in South Africa, to construct and porous which not only allows fish to swim through them but the increased flow of water increases the available dissolved oxygen which is beneficial for the biota in these systems (Shariq *et al.*, 2022). An understanding of the impact of these structures on the natural shores that they are replacing is lacking although, it is believed that they provide a suitable habitat to biotic communities because their structure is similar to natural boulders (Firth *et al.*, 2014b). In South Africa, gabions have been found to provide suitable habitat for the Endangered Knysna Seahorse *Hippocampus capensis* (Claassens *et al.*, 2018; Claassens & Hodgson, 2018). Similarly, Reno-mattresses (flat gabions) used for erosion control in estuaries have also been found to support fish and invertebrate communities typically associated with rocky shores (de Villiers *et al.*, 2021). The manipulation of the sizes of rocks used in the construction of the gabions can further potentially enhance the diversity and abundances of epibiotic assemblages of invertebrates and offer protection from predators (Firth *et al.*, 2014b). These case studies highlight the potential of gabions in ecological engineering projects.

1.3. South African coastal development

South African coastline is characterised by 290 estuaries and 42 micro-estuaries (Whitfield, 2000; van Niekerk & Turpie, 2012). In addition to their ecological importance, estuaries provide a vast number of ecosystem services to coastal communities including provision of natural resources, buffering against floods and carbon sequestration (Turpie *et al.*, 2002; van Niekerk *et al.*, 2013). Estuarine systems are estimated to have an annual subsistence harvesting value of R 35.7 million (Turpie *et al.*, 2018), and a nursery value of R 803 million since they serve as an important nursery for many commercially important line fish (Whitfield, 1983; 1990). The ecosystem functioning and services that estuaries provide are under threat due to urbanisation, overexploitation of resources, habitat loss and development within these systems (Turpie *et al.*, 2002).

Approximately one third of South Africa's population reside within 100 km of the coastline (Theron & Rossouw, 2008). Presently, South Africa is regarded as the most urbanized and globalized region in Sub Saharan Africa (Salahuddin *et al.*, 2019). Like many other countries, the region is experiencing increased incidence of extreme weather events (storm activity and droughts), rapid urban development and intensifying food pressures (Theron & Rossouw, 2008; Blekking *et al.*, 2022). Two of the major pressures on the South African coastline include development and mining with the Indian Ocean Coastal Belt (south-east coastline of South Africa) experiencing an estimated 22 % loss of natural habitat due to coastal development (Harris *et al.*, 2019). Coastal armouring are the most common structure found along the coastline with parking lots and bridges also routinely recorded (Claassens *et al.*, 2022). The Western Cape Province of South Africa has the greatest concentration of coastal armouring

(Claassens *et al.*, 2022), with most structures being found in proximity to and within the major coastal cities.

A large part of the coastal development taking place along the South African coastline is found in the immediate vicinity of estuaries (Midgely *et al.*, 2005; van Niekerk & Turpie, 2012).

Skowno *et al.*, (2019), estimated that 29 % of South African estuaries have been severely altered due to development. More recently Claassens *et al.* (2022), estimated that 51.74 km of estuarine shores in South Africa have been hardened with armouring structures together with a number of other artificial structures. The study further found that jetties were the most common artificial structure recorded in estuaries and suggested that the large number of jetties and slipways were developed prior to the *Integrated Coastal Management (ICM) Act 24* (RSA, 2009), when private property development was less regulated. Presently, a total of 14 harbours and nine marinas are present in South African estuaries, covering an estimated area of 34.82 km² (Claassens *et al.*, 2022). The construction and development of harbours and marinas in estuaries has resulted in habitat fragmentation, biodiversity loss and changes to natural processes such as nutrient regulation, carbon sequestration and water flow dynamics (Harris *et al.*, 2019; van Niekerk *et al.*, 2019).

1.4. Study area: The Knysna Estuary

The Knysna Estuary (34.0351° S, 23.0465° E) is situated in the Western Cape province of South Africa (Fig. 1.2). This system can be described as an Estuarine Bay (Whitfield, 1992), and is one of the 42 permanently open estuaries along the South Africa coastline (Van Niekerk *et al.*,

2020). The subtidal area of the bay is $\sim 10 \text{ km}^2$ (Bell *et al.*, 2003), and is characterized by three hydrological regimes: the lower 'bay regime' adjoining the Indian Ocean which is influenced by tidal flows, the upper 'estuary regime' influenced by the river inflow and the middle 'lagoon regime' which lies between the two and is less influenced by tidal or river inflows (Largier *et al.*, 2000). The physico-chemical characteristics of the estuary were described in detail by Allanson *et al.* (2000), suggesting no change in salinity patterns since 1952, an 82 – 97 % oxygen saturation of the water column throughout the estuary (which increases in the event of upwellings) and a pH below 7 after high flooding and reaching a high of 8.2 in the areas of high salinity.

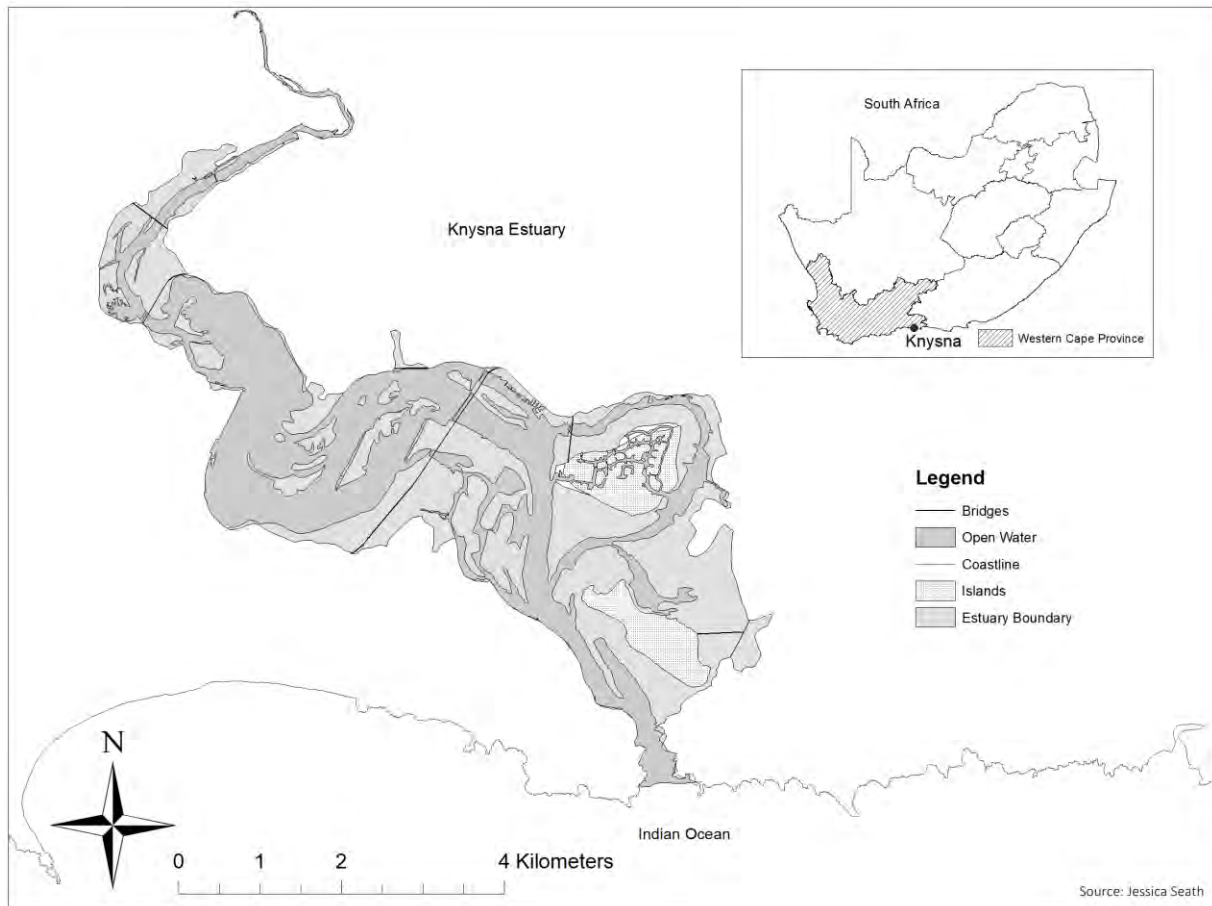


Figure 1.2: Map showing the Knysna Estuary situated with the town of Knysna on the southern coast of South Africa.

The Knysna Estuary lies within a protected area and is considered as South Africa's most important estuary in terms of biodiversity, range of habitats and hence conservation importance (Turpie *et al.*, 2002). The estuary is therefore an essential location in conservation efforts and species protection studies. The Recommended Ecological Category of the estuary is (B) "Largely natural with few modifications" (DWA, 2009). These modifications include a few marinas, an extensive waterfront development and island residential properties which are largely situated in the lower bay and lagoon sections within the system. In the highly developed and modified ecologically important Knysna estuary reconciliation ecology rather than

restoration ecology may be an option to consider to combat the negative effects of coastal development.

1.5. Rationale and Aims

Few studies have attempted to investigate the potential ecological benefits of ecological engineering in South Africa (but see Strain *et al.*, 2021; de Villiers *et al.*, 2021; Porri *et al.*, 2023).

With the continued movement of humans to coastal cities and accelerated coastal development, the need/desire for coastal modification, including harbours and marinas, is on the increase. Engineers and local stakeholders need to be aware of the consequences of altering these shallow water ecosystems and have options available to them that can mitigate these impacts. Whilst infrastructure can provide novel habitats, an ecological engineering approach can increase their capacity for enhancing biodiversity, improving water quality, targeting species of conservation and commercial importance and adding topographical complexity to these ecosystems to make them more like natural rocky habitats. There is a lack of information available on the capacity of different building materials' y to provide habitat for both fish and invertebrates in novel environments.

I tested an ecological engineering approach to share with coastal developers and stakeholders by comparing two different artificial structures that are readily used in South Arica: a concrete seawall and gabion boxes. Most of the research on the impact that gabion installations have on marine biodiversity has been conducted in South Africa. This research has largely been limited to the role they play in providing alternative habitat for the endangered Knysna Seahorse

(Claassens, 2016; Claassens & Hodgson, 2018; Claassens *et al.*, 2018), as well as a comparative study between faunal assemblages in reno mattresses and neighbouring seagrass beds (de Villiers *et al.*, 2021). A knowledge gap exists on the scope of using gabions to provide habitat for a range of different species as well functional groups that may have important structuring roles (e.g. predators or habitat-formers) in these ecosystems. There is currently no information available on the type of faunal assemblages that may arise when adding gabions to an existing harbour constructed of seawalls.

The aim of this research was to fill this knowledge gap. This was achieved by comparing gabion and seawall habitats in Knysna Harbour in the Knysna Estuary in South Africa over a period of 1 year. An in-depth analysis was conducted in Chapter 2 on fish assemblages in the two habitats. Fish were identified and grouped into their relevant functional feeding groups and using the measurement MaxN, taxon and functional richness, diversity, relative abundance and composition were determined. As well as the identification of species listed in the IUCN Red List of Threatened Species and a brief description of feeding behaviour. This was used to assess how assemblages of fish species differed between the two habitats and how gabions might help increase the biodiversity in Knysna Harbour as well as potentially offer a habitat for species of conservation concern. An in-depth analysis was conducted in Chapter 3 on colonising organisms (algae and invertebrates) assemblages in the two habitats. Colonising organisms were identified and grouped into their relevant functional groups and using percentage cover, counts and presence/absence data, taxon and functional richness, diversity, relative abundance and composition were determined. Using these data, we tested whether gabions could provide habitat for more native than invasive species and what types of functional groups were present

329 in the different habitats. Chapter 4 outlines what the overarching findings of the study were in
330 the greater context of South Africa and globally and how gabions possess the potential for
331 being used in future ecological engineering projects.

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Chapter 2

A comparison of fish assemblages between gabion and seawall habitats

2.1. Introduction

Habitat degradation associated with urbanisation represents one of the largest threats to global biodiversity (Suchanek, 1994; Gray, 1997; Sih *et al.*, 2000; Bulleri & Chapman, 2010). This urbanisation in coastal cities leads to proliferating infrastructure along these coastlines and further into the ocean (Bugnot *et al.*, 2021). This resultant loss of biodiversity has been exacerbated by dredging which results in sedimentation and turbid waters (Chou *et al.*, 2004; Hoeksema & Koh, 2009). Moreover, the urbanisation of coastlines often facilitates the invasion by alien fauna which poses a threat to native species, by out-competing them, and threatens the local biodiversity (Airoldi *et al.*, 2005; Bulleri & Airoldi, 2005; Airoldi & Bulleri, 2011; Firth *et al.*, 2011), as seen when opportunistic invasive fish species and the loss of endemic fish species in urban headwater streams in China caused fish assemblages to become functionally homogenised (Qiao *et al.*, 2022). Also, urbanisation has been shown to be one of the causes of biotic and functional homogenisation (Chapman, 2003; McKinney, 2006), where natural rocky shores are supporting > 50 % more unique taxa than urban artificial structures (Mayer-Pinto *et al.*, 2018), as well as these novel habitats increasing the niche availability for native invasive species spread (Glasby *et al.*, 2007; Dafforn *et al.*, 2012; Airoldi *et al.*, 2015).

Ecological engineering is the development of man-made ecosystems that integrate ecological, economic and social needs (Mitsch, 1996). Ecological engineering methods have been shown to

374 be effective in enhancing the native biodiversity inhabiting artificial structures (see Firth *et al.*,
375 2013a for more details on ecological engineering methods). Many of the approaches used
376 assume that greater habitat complexity leads to greater species richness (Moschella *et al.*,
377 2005; Chapman & Clynick, 2006; Chapman & Blockley, 2009; Firth *et al.*, 2014a), with examples
378 including deploying artificial structures on breakwaters at different tidal heights and with
379 increased complexity (grooves, pits and surface roughness) supporting higher biodiversity
380 (Borsje *et al.*, 2011).

381 Gabion boxes and reno mattresses (hereafter ‘gabions’) are rock-filled wire cages, employed
382 globally in coastal infrastructure for the purposes of land retention, erosion control and as a
383 more aesthetically appealing alternative to concrete, block or sheet metal seawalls (Maccaferri,
384 1915; Toprak *et al.*, 2016). Like any hard substrate placed in the marine environment, gabions
385 inevitably become colonized by fouling organisms (Firth *et al.*, 2014b; Adams *et al.*, 2021), and
386 can provide habitat and food for mobile species. For instance, as seahorses require a ‘holdfast’
387 to grasp using their prehensile tail while resting and feeding (James & Heck, 1994), gabions and
388 other cage- and mesh-like structures can provide valuable substrate for attachment in
389 degraded habitats (Simpson *et al.*, 2020). Research from South Africa has not only revealed that
390 gabions support high densities of seahorses in urban waterways (Claassens 2016; Claassens &
391 Hodgson 2018; Claassens & Harasti 2020), but behavioural experiments have also revealed that
392 seahorses selectively ‘choose’ gabion mesh over natural vegetation (Claassens *et al.*, 2018).

393 Fish are routinely observed interacting with flat and featureless seawalls, but many species are
394 more commonly attracted to features that provide potential refugia from predators (Morris *et*
395 *al.*, 2017). A study conducted in Keurbooms, a permanently open estuary in South Africa, found

396 that fish diversity and abundances were greater on gabions compared to natural eelgrass in an
397 estuarine system (de Villiers *et al.*, 2021). Whilst it is clear that gabions have the potential to
398 support diverse marine life, a major knowledge gap remains on their ability to enhance habitat
399 for fish compared to concrete walls conventionally used in coastal development.

400 Estuaries are the interface between rivers and oceans (Day *et al.*, 1989; Whitfield & Elliot,
401 2011), and are responsible for linking marine, terrestrial and freshwater ecosystems, leaving
402 them vulnerable to human pressures (van Niekerk & Turpie, 2012). These systems play a vital
403 role as nursery habitats for juvenile fish (Whitfield, 1994a; Strydom *et al.*, 2003). To survive and
404 make their journey seaward juvenile fish need habitats that offer them a refuge from predators
405 (Mittlebach, 1981; Beck *et al.*, 2001), and feeding grounds (Werner *et al.*, 1983). In natural
406 estuarine environments this may look like salt marshes or seagrass beds where there is shelter
407 and food available, or rocky shores that offer cryptobenthic fish species protection from wave
408 action (Kimirei, 2012; Troyer *et al.*, 2018).

409 Coastal systems worldwide have experienced hardening of their shorelines particularly in
410 lagoons, estuaries and bays (Sempere-Valverde *et al.*, 2023). This development has contributed
411 to the loss of habitat available for fish species, permanently altering their community
412 assemblages (Connel & Jones, 1991; Piko & Szedlmayer, 2007). South African estuarine
413 environments are threatened by development and mining (Harris *et al.*, 2019), with the
414 National Biodiversity Assessment reporting that 29 % of estuaries are subject to land-use
415 pressures and habitat modification (van Niekerk *et al.*, 2019), with a total of 1 679 artificial
416 structures being present in these systems (Claassens *et al.*, 2022).

417 The Knysna Estuary is a warm temperate estuarine bay in South Africa (Whitfield, 1992), and
418 the most important to conserve in terms of its biodiversity (Turpie *et al.*, 2002). It consists of
419 the largest area of seagrass *Zostera capensis* in South Africa (Grindley, 1985; Russel *et al.*, 2012;
420 Wasserman *et al.*, 2020), which supports a diverse macrobenthic community of high
421 conservation value (Barnes & Ellwood, 2012). This plays an important role in the food webs
422 structure within the system and sustains an important fishery (Napier *et al.*, 2009; Barnes,
423 2010), with an estimated economic value of R 167.6 million per annum (Turpie & Clark, 2007).
424 The eelgrass is particularly important as a nursery ground for juvenile fishes (Wallace & van der
425 Elst 1975, Adams 1976, Beckley 1983, Whitfield *et al.*, 1989), which provides important habitat
426 and food for a myriad of fish including the Endangered Knysna seahorse *Hippocampus capensis*
427 (Bell *et al.*, 2003; Lockyear *et al.*, 2006; Claassens *et al.*, 2018). An estimated 490 ha of the
428 estuary is developed (Claassens *et al.*, 2020); including concrete walls, bank erosion control
429 structures and the N2 highway along the westbank of the system altering an estimated 80 % of
430 the estuarine banks (Claassens *et al.*, 2020), and the loss of intertidal salt marshes which consist
431 of a perimeter of artificial structures of 20.7 km in length (Raw *et al.*, 2020).

432

433 In this chapter, I assessed the potential of gabion boxes as an alternative habitat to seawalls for
434 fish in an urban estuary using remote underwater video cameras. Specifically, I tested the
435 hypotheses that: i) taxon and functional diversity, richness and relative abundances of fish
436 would be higher in gabion compared to seawall habitats; ii) more threatened species (including
437 the Endangered Knysna Seahorse, *Hippocampus capensis*) would be present in gabion than

seawall habitats; iii) that taxon and functional composition would significantly differ between gabion and seawall habitats and that iv) patterns would vary across time. By making observations of the feeding behaviour of individual fishes, I also noted the difference in feeding behaviour between the gabions and seawall habitats. This information will help inform environmentally sensitive urban coastal design in the future.

2.2. Methods and Materials

2.2.1 Study site

Research was conducted in the Knysna Waterfront Harbour and Knysna Marina Quays (34.04°,23.04°; further referred to as Knysna Harbour) (Fig. 2.1) in the Knysna Estuary. The development of a small boat harbour was approved in 1993 (Watermeyer Prestedge Retief [WPR], 1995). The development consisted of a looped canal developed above the high-water mark to provide residential accommodation, with a connection to the small boat harbour (WPR, 1995). The quayside around the small boat harbour was developed as a public waterfront with stores, restaurants and accommodation. The site for this small craft harbour was developed by dredging 16 500 m² of salt marsh to a depth of 3.5 m below the mean spring low mark (WPR, 1995). It consists of 108 floating moorings, a double deck bascule bridge and is constructed out of a 1.4km long steel sheet pile quay wall covered with concrete (Fig. 2.2). The small craft harbour has a wooden wave screen separating it from the main channel of the estuary with an opening of approximately 25 m for boats to enter and exit. The bed of the harbour consists

mainly of bare sediment with some rubble and lacks any other major vegetation (pers. obs).
The canals are between 30 - 50 m wide and the depth at a neap high tide ranges from 3 - 4.5 m.

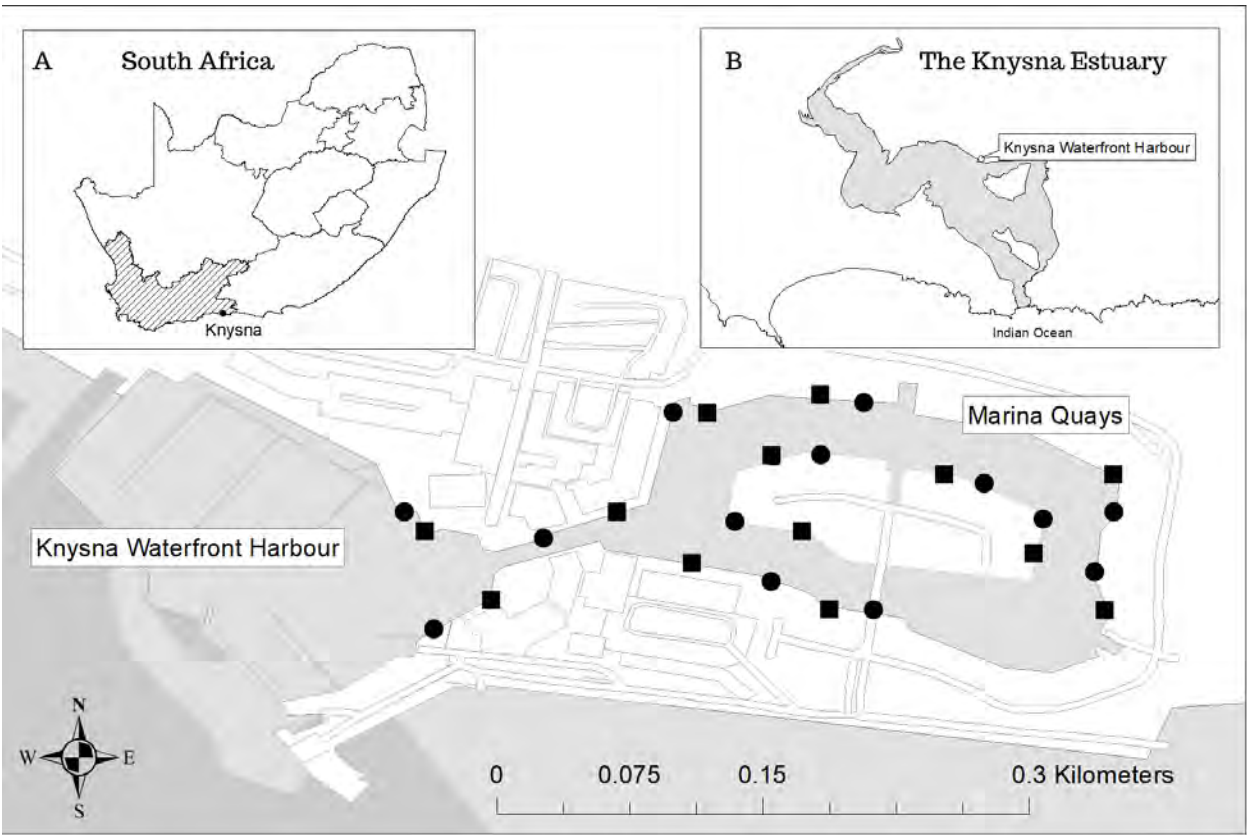


Figure 2.1: Knysna Harbour study site within the; (a) Knysna Estuary in (b) Knysna, South Africa; indicating the position of 13 replicates for both gabion and control seawall habitats used for fish surveys at times T₂, T₆, T₁₀, T₁₂; square: seawall habitat, circle: gabion habitat.



Figure 2.2: Concrete vertical seawalls along the edges of Knysna Harbour within the Knysna Estuary (view from the water).

2.2.2 Gabion deployment and setup

To assess whether the relative abundance, diversity and assemblages of fish differed between gabion and seawall habitats, gabion boxes were deployed subtidally in Knysna Harbour. Each gabion habitat and corresponding control seawall habitat was replicated 13 times (Fig. 2.1). Between each gabion habitat, control patches of vertical seawall were selected < 15m away (Fig. 2.4). There was an average distance of 45 m between a gabion and seawall habitat and the next set of replicate gabion and seawall habitats (Fig. 2.1). One gabion habitat consisted of three gabion boxes; one box stacked on top of two other boxes. The bottom boxes were not used in fish surveys as they were intended to elevate the gabions off the seafloor due to low visibility in the bottom section of the harbour and to protect them from sinking into the

sediment. The control seawall sites were also selected 0.5 m above the seafloor to ensure sites were sampled at the same tidal height.

One gabion basket measured 0.5 m height x 0.5 m length x 0.5 m width (Fig. 2.3), the mesh was made from a zinc-coated wire with PVC coating of 0.3 cm in diameter and had openings of 7.6 x 7.6 cm. The gabions were filled with a variety of unusually-shaped rocks which were both sloping and rectangular in shape, the rocks were rough and measured between 70 mm – 400 mm in length. The gabions were filled with rocks so that some interval remained between the rocks.

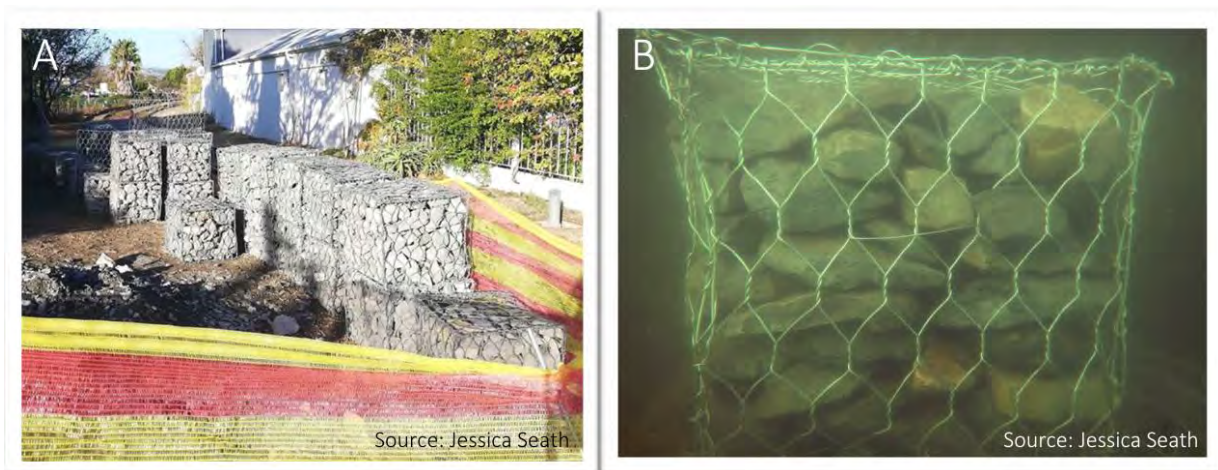
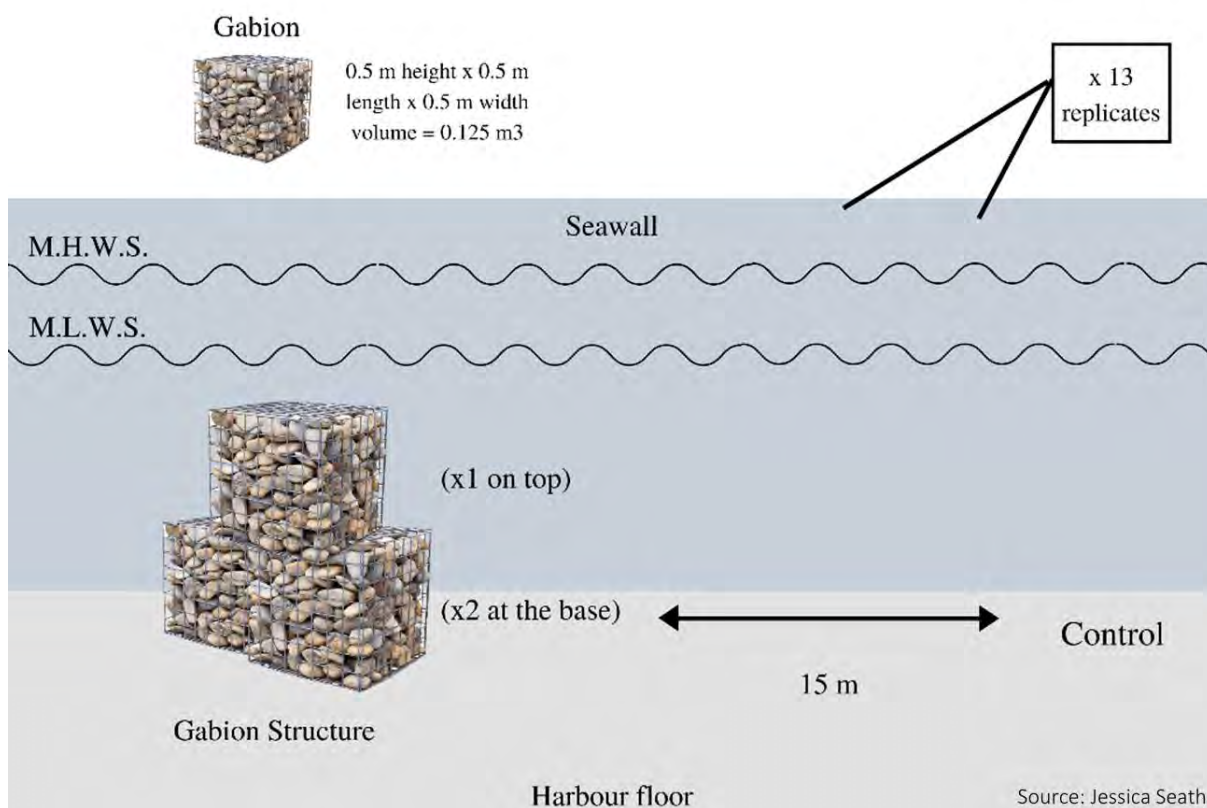


Figure 2.3: Gabion boxes built for this study: a) during the construction phase before deployment, b) one gabion basket of 0.5 x 0.5 x 0.5 m stacked on top of two gabion boxes, against the seawall, immediately after deployment in Knysna Harbour.

The gabion boxes were deployed using a barge and a scuba diver, the boxes were placed onto the harbour floor and maneuvered into position against the seawall with the barge and a pulley

495 system to create the stacked gabion habitats. The seawall sites were 0.5 length x 0.5 m width
 496 and 0.5 m height above the seafloor. The area behind the gabions and the control seawall sites
 497 were scraped clean of all biota with a metal scraper prior to commencement of the experiment,
 498 to ensure both habitats were clear of any fauna (Fig. 2.4). Both gabions and seawalls were
 499 permanently submerged by water at depths between 2 – 4.5 m. Fish were surveyed on the
 500 gabions and seawalls two months after deployment.



501
 502 Figure 2.4: Schematic diagram of the layout of a gabion habitat on the harbour floor against the
 503 seawall 15 m away from a control seawall habitat in Knysna Harbour. Replicated 13 times with
 504 45 m distance between the replicates. (MHWS: mean high water spring; MLWS: mean low
 505 water spring).

506 2.2.3 *Physico-chemical characteristics*

507 The replicates within Knysna Harbour may be subject to spatio-temporal variability of physico-
508 chemical characteristics so to ensure this was not a confounding factor, these were (bottom
509 temperature, DO, pH and salinity), sampled for the same above sampling periods on incoming
510 tides, with a calibrated (prior to every sampling period) multiprobe (OTT Hach HL4 handheld
511 sonde) held off the side of a boat with a tether and real-time surveyor. Three sets of readings
512 were taken at each site to determine the average reading at each sampling station.

513

514 2.2.4 *Fish Surveys*

515 Fish surveys were carried out four times: two months, six months, 10 months and 12 months
516 post deployment (hereafter referred to as times T_2 , T_6 , T_{10} and T_{12}). Each of these months were
517 chosen from a different season in the year as numerous studies have highlighted the
518 differences in fish populations across seasons (Fennessy *et al.*, 1998; Clark *et al.*, 1996). The two
519 habitat types defined as gabion and seawall were spatially replicated 13 times (Fig. 2.1).

520 Remote Underwater Video Systems (RUVS) are routinely used to successfully study fish
521 assemblages in marine environments (Cappo *et al.*, 2004; Watson *et al.*, 2005), specifically in
522 low visibility and turbid estuaries (Becker *et al.*, 2010; Keur *et al.*, 2019). This method is useful
523 for studying fish assemblages where traditional methods (such as seine netting) may not be
524 possible in small specific habitats (Becker *et al.*, 2010), and can include behavioural
525 observations to better understand what drive fish assemblage patterns (Adams *et al.*, 2006).

526 One RUV deployment was made at each site, resulting in 26 deployments per month, 10

cameras were used which meant sampling took place over the period of 3 days. One RUV consisted of a GoPro Hero camera mounted to the top of a metal stand measuring 1 m in height (Fig. 2.5). The camera was deployed via snorkelling and placed 30 cm in front of the habitat with the camera pointing into the habitat (Fig. 2.5). A distance of 30 cm was selected since it allowed the full habitat to be in the field of view whilst still being close enough to see the fish clearly in this low visibility environment. All cameras were deployed at each unit for a period of 65 minutes, 5 minutes was allowed for an acclimation period (Bouchet *et al.*, 2018) which is deemed a suitable time for the deployment of RUVS in fish survey studies (Bernard & Götz, 2012; Harasti *et al.*, 2015). Cameras were set at a video setting of 1080p wide at 60 fps (frames per second) to ensure the lowest possible taxonomic identification of fish possible (Perkol-Finkel *et al.*, 2017). All deployments were carried out on the incoming tide between 09:00 and 15:00. Deployments were not conducted on very low visibility days. During deployment of cameras, fish seen within the habitats were recorded and included as present in the species list.

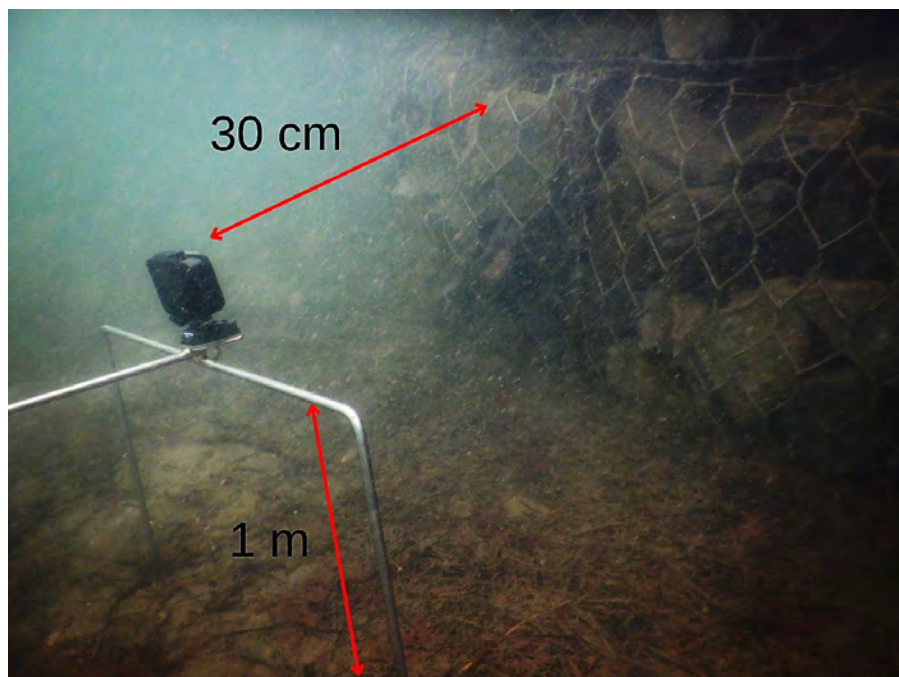


Figure 2.5: GoPro cameras attached to a metal stand (measuring 1 m in height) placed 30 cm away from the gabion, used to sample fish in Knysna Harbour (the image is just for illustrative purposes and not true to actual distances used).

Videos were analysed using SeaGIS Eventmeasure 5.61 software (www.seagis.com.au), to record MaxN of each fish species. MaxN is the maximum number of a fish species in the frame at any one time during each set that gives an indication of relative abundance (Cappo *et al.*, 2004; Campbell *et al.*, 2018) and is commonly used for quantifying fish species (Harasti *et al.*, 2015; Morris *et al.*, 2017; Taira *et al.*, 2020). Fish that swam into the field of view were counted and identified to the lowest possible operational taxonomic unit. The identification of individuals from the families Mugilidae, Clinidae, Blennidae and Gobiidae to the species level were not possible from video footage so all individuals were referred to at the family level. Fish were then grouped into functional feeding groups (Carnivorous, Omnivorous, Herbivorous, Zoobenthic Predator and Planktivorous) as listed in Smith's Sea Fishes (Smith & Heemstra, 1988). All fish species observed were checked against the IUCN Red List of Threatened Species (www.iucnredlist.org).

A quantitative comparison of feeding behaviour was compared between gabion and seawall habitats. Every individual fish seen in the cameras field of view was recorded for each habitat, if the fish was seen feeding (taking a bite) from the habitat, they were counted and the number of fish feeding were totalled.

2.2.5 Statistical analyses

A range of univariate and multivariate metrics were employed using the statistical program R studio (R Development Core Team, 2014). A two-way crossed ANOVA with fixed factors Habitat (Gabion and Seawall) and Time (T_2 , T_6 , T_{10} and T_{12}) was used to compare taxon and functional richness, Shannon diversity [H'], and relative abundance; and physico-chemical comparisons (temperature, salinity, pH, DO). Normality was tested using Shapiro-Wilks test, when data were non-normal a non-parametric test was used. Cochran's test (using the GAD package; Sandrini-Neto & Camargo, 2021), was used to test for homogeneity of variances, where variances were heterogeneous, data was transformed using square-root transformations. Tukey honest significance tests (TukeyHSD) were used to make post-hoc comparisons.

To investigate differences in taxon and functional compositions between gabions and seawalls and across time, multivariate analysis of variance (PERMANOVA; Anderson *et al.*, 2008) were conducted on Bray-Curtis transformed community data, with 9999 unrestricted permutations. The multivariate data analyses were based on a two-way crossed design with fixed factors Habitat and Time. The SIMPER (Clarke, 1993), function in R was used to determine the dissimilarities between habitats and which taxon or functional groups were contributing to these differences.

2.3. Results

In total, 18 fish taxa (classified to the lowest possible taxa) were observed across habitats and time periods (Table 2.1). An additional two species (*Petrus rupestris*, *Amblyrhynchotes honckenii*) were observed in the water during sampling events. A total of 20 and 7 fish taxa were observed on the gabions and seawalls, respectively. Fish that were unique to gabions were *Blenniidae* sp., *Chaetodon marleyi*, *Chirodactylus brachydactylus*, *Caffrogobius* sp., *Apletodon Pellegrini*, *Monodactylus falciformis*, *Cheilodactylus pixi*, *Boopsoidea inornate*, *Chrysoblephus laticeps*, *Sarpa salpa* and *Hippocampus capensis* (Table 2.1). No species were unique to seawalls. Four species were listed as either Endangered: *H. capensis* (Czembor & Bell, 2012), and *P. rupestris* (Mann *et al.*, 2014a,) or Near Threatened: *D. chrysonota* (Pollom *et al.*, 2020), and *C. laticeps* (Mann *et al.*, 2014b), on the IUCN Red List (IUCN, 2022). Three of the four species were observed in gabion habitats only, and a single *D. chrysonota* was observed in seawall habitats.

Table 2.1: Fish taxa recorded in the Knysna estuary by RUVS within gabion and seawall habitats for 13 replicates of each habitat per time periods T₂, T₆, T₁₀ and T₁₂ and the (a) total number of times each fish taxa was recorded across the full set of sampling replicates and; (b) the total (sum of) MaxN of fish observed. Fish taxa's functional feeding groups included. Symbols denote Endangered (*) and Near Threatened (§) species.

Family	Species	(a)		(b)		Functional group
		Gabion	Seawall	Gabion	Seawall	
Blenniidae	spp.	2	0	2	0	Omnivore
Chaetodontidae	<i>Chaetodon marleyi</i>	14	0	16	0	Carnivore
Cheilodactylidae	<i>Chirodactylus brachydactylus</i>	6	0	6	0	Carnivore
Clinidae	sp.	7	3	7	4	Carnivore
Dasyatidae	<i>Dasyatis chrysonota</i> §	4	1	4	1	Carnivore
Gobiidae	<i>Caffrogobius</i> sp.	6	0	6	0	Omnivore
	spp.	36	31	59	44	Omnivore
Gobiesocidae	<i>Apletodon pellegrini</i>	1	0	1	0	Carnivore
Monodactylidae	<i>Monodactylus falciformis</i>	4	0	10	0	Planktivore
Morwong	<i>Cheilodactylus pixi</i>	3	0	3	0	Carnivore
Mugilidae	spp.	5	1	30	6	Zoobenthic Predator
Sparidae	<i>Diplodus capensis</i>	40	15	182	47	Omnivore
	<i>Diplodus hottentotus</i>	36	15	79	31	Carnivore
	<i>Boopsoidea inornata</i>	4	0	6	0	Omnivore
	<i>Chrysoblephus laticeps</i> §	1	0	2	0	Carnivore
	<i>Petrus rupestris</i>	-	-	-	-	Carnivore
	<i>Rhabdosargus</i> sp.	33	7	174	21	Carnivore
	<i>Sarpa salpa</i>	1	0	3	0	Herbivore
Syngnathidae	<i>Hippocampus capensis</i> *	3	0	4	0	Carnivore
Tetraodontidae	<i>Amblyrhynchotes honckenii</i>	-	-	-	-	Carnivore

2.3.1 *Physico-chemical characteristics*

There were no significant differences in water temperature (ANOVA, $F = 1.62$, $p = 0.2$), salinity (ANOVA, $F = 1.5$, $p = 0.23$), dissolved oxygen (ANOVA, $F = 0.62$, $p = 0.43$), or pH (ANOVA, $F = 0.08$, $p = 0.77$) between gabion and seawall habitats. Temperature (ANOVA, $F = 3523.77$, $p < 0.01$), salinity (ANOVA, $F = 623.31$, $p < 0.01$) dissolved oxygen (ANOVA, $F = 10.07$, $p < 0.01$) and pH (ANOVA, $F = 286.29$, $p < 0.01$) differed significantly among time periods. The physico-chemical characteristics of the water body were similar across replicates within each habitat. These measurements were taken to ensure that there was no significant variation amongst each habitat's replicates and that there was uniformity between habitats, which is important because fish are affected by changes in temperature and salinity (Whitfield, 1996; Le Quesne, 2000; Harrison & Whitfield, 2006), for comparison's sake.

2.3.2 *Taxon and functional richness*

There was a significant interaction between Habitat and Time for taxon richness (Table 2.2a, Fig. 2.6a). Gabions supported greater mean taxon richness than seawalls in all four sampling periods but this was only significant at times T_6 (5.54 ± 1.71 vs 1.46 ± 1.51), T_{10} (5.15 ± 1.41 vs 2.62 ± 1.04) and T_{12} (3.23 ± 1.48 vs 1 ± 0.82) (Fig. 2.6a). Taxon richness peaked at time T_6 and T_{10} in gabion and seawall habitats, respectively (Fig. 2.6a).

Gabions supported greater mean functional richness than seawall habitats when pooled over all sampling times (1.69 ± 0.88 vs 1.08 ± 0.76); Table 2.2a, Fig. 2.6b).

2.3.3 *Taxon and functional diversity*

There was a significant interaction between Habitat and Time for mean taxon diversity (Table 2.2b, Fig. 2.6c). The diversity of fish on gabion habitats (1.03 ± 0.07) was significantly greater than on the seawall habitats (0.34 ± 0.06) in all sampling periods except T_2 when diversity in the two habitats was not significantly different (Table 2.2b, Fig. 2.6c). Taxon diversity peaked at time T_6 and T_{10} in gabion and seawall habitats, respectively (Fig. 2.6c).

There was a significant interaction between Habitat and Time for mean functional diversity (Table 2.2b, Fig. 2.6d). Gabions supported greater mean functional diversity in all four sampling periods but this was only significant in T_6 (0.81 vs 0.22 ; Fig. 2.6d). Functional diversity peaked at time T_6 and T_{10} in gabion and seawall habitats, respectively (Fig. 2.6d).

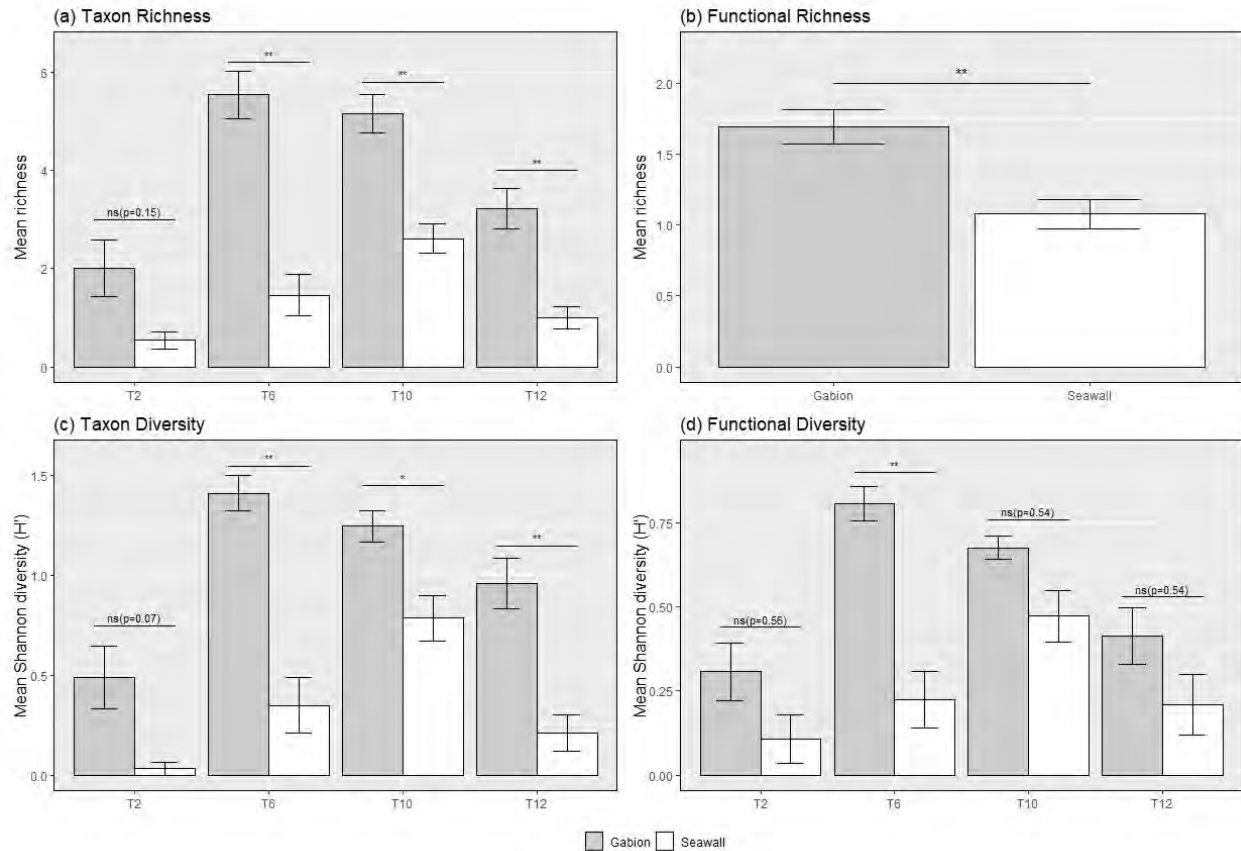


Figure 2.6: Comparison of mean ($n = 13$, $\pm$ SE) (a) taxon richness in gabion (grey bars) and seawall (white bars) habitats amongst times T₂, T₆, T₁₀ and T₁₂; (b) functional richness in gabion (grey bars) and seawall (white bars) habitats at combined times T₂, T₆, T₁₀ and T₁₂; (c) taxon and (d) functional shannon-weiner diversity indices (H') of fish in gabion (grey bars) and seawall (white bars) habitats amongst times T₂, T₆, T₁₀ and T₁₂ recorded in Knysna Harbour. **P < 0.01; *P < 0.05.

Table 2.2: Two-Way ANOVA comparing (a) taxon and functional richness and (b) taxon and functional shannon diversity between gabion and seawall habitats amongst times T₂, T₆, T₁₀ and T₁₂. **P < 0.01; *P < 0.05; ns, not significant.

(a) Univariate ANOVA of richness							
Source	Taxon				Functional		
	<i>df</i>	<i>MS</i>	<i>F</i>	<i>P</i>	<i>MS</i>	<i>F</i>	<i>P</i>
Habitat (Ha)	1	172.65	86.88	<0.01**	9.85	18.12	<0.01**
Time (Ti)	3	38.41	19.33	<0.01**	5.23	9.63	<0.01**
Ha x Ti	3	7.83	3.94	<0.01**	0.31	0.57	0.64ns
Residuals	96	1.99			0.54		

(b) Univariate ANOVA of Shannon diversity index							
Source	Taxon				Functional		
	<i>df</i>	<i>MS</i>	<i>F</i>	<i>P</i>	<i>MS</i>	<i>F</i>	<i>P</i>
Habitat (Ha)	1	12.18	77.73	<0.01**	2.31	31.59	<0.01**
Time (Ti)	3	2.93	18.71	<0.01**	0.77	10.58	<0.01**
Ha x Ti	3	0.54	3.44	<0.05*	0.23	3.21	<0.05*
Residuals	96	0.16			0.07		

2.3.4 Taxon and functional relative abundance

Total relative abundance of fish combining T₂, T₆, T₁₀ and T₁₂ was 594 and 154 in the gabion and seawall habitat, respectively. Sparidae were the most frequently observed family due to the presence of six taxa including large numbers of *Diplodus capensis* being the most abundant fish at 182 and 47 on gabion and seawall habitats respectively (Table 2.1).

Gabions supported a significantly greater taxon relative abundance of fish than seawalls ((11.38 ± 1.44) vs (2.96 ± 0.58); Fig. 2.7).

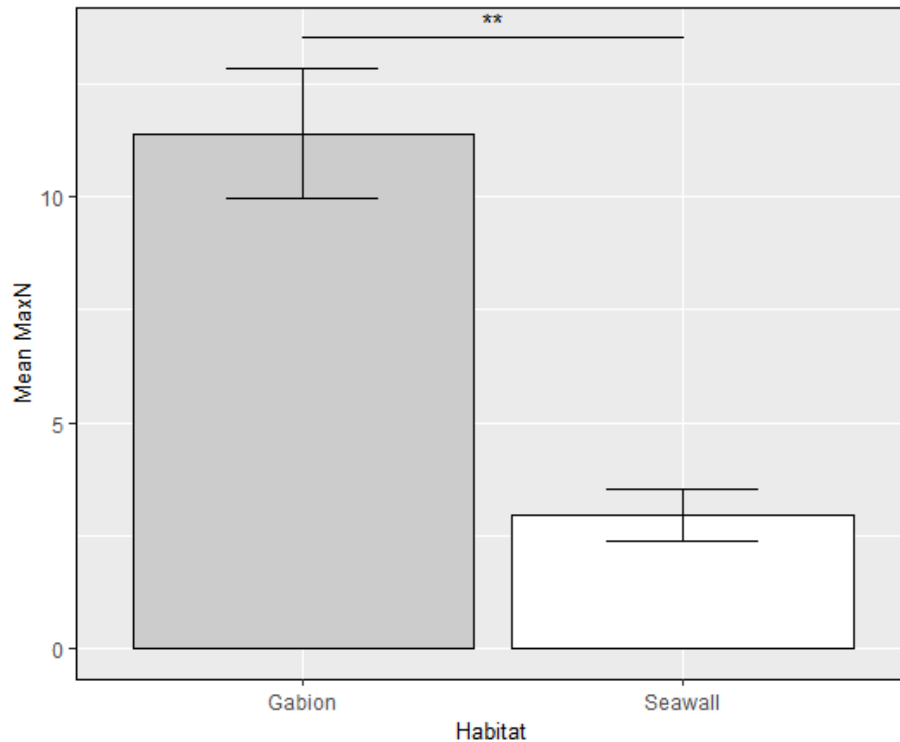


Figure 2.7: Mean ($n = 13$, $\pm$ SE) relative abundance (MaxN) of fish taxa in gabion (grey bars) and seawall (white bars) habitats at combined times T_2 , T_6 , T_{10} and T_{12} recorded in Knysna Harbour. $**P < 0.01$; $*P < 0.05$.

A total of five functional feeding groups were observed in the two habitats, five in gabion habitats and three in seawall habitats (see table 2.1 for more information). Both gabions and seawall habitats were dominated by carnivores and omnivores (Fig. 2.8). Gabions supported a significantly greater relative abundance of carnivores (5.69 vs 1.1; Fig. 2.8a), and omnivores (4.9 vs 1.75; Fig. 2.8b) than seawalls.

656 Table 2.3: Two-Way ANOVA results for relative abundance (MaxN) comparison in; (a) taxon and
657 (b) functional groups: carnivores, omnivores, herbivores, zoobenthic predators and
658 planktivores, between gabion and seawall habitats amongst times T₂, T₆, T₁₀ and T₁₂. **P < 0.01;
659 *P < 0.05; ns, not significant.

(a) Univariate ANOVA of taxon relative abundance

Source	<i>df</i>	<i>MS</i>	<i>F</i>	<i>P</i>
Habitat (Ha)	1	73.87	58.40	<0.01**
Time (Ti)	3	22.11	17.48	<0.01**
Ha x Ti	3	2.38	1.88	=0.14ns
Residuals	96	1.26		

(b) Univariate ANOVA of functional relative abundance

Source	Carnivores				Omnivores			Herbivores		
	<i>df</i>	<i>MS</i>	<i>F</i>	<i>P</i>	<i>MS</i>	<i>F</i>	<i>P</i>	<i>MS</i>	<i>F</i>	<i>P</i>
Habitat (Ha)	1	48.99	61.33	<0.01**	23.36	34.8	<0.01**	0.87	1	0.32ns
Time (Ti)	3	15.99	20.01	<0.01**	9.50	14.1	<0.01**	0.87	1	0.40ns
Ha x Ti	3	1.95	2.44	0.07ns	1.42	2.12	0.10ns	0.87	1	0.40ns
Residuals	96	0.80			0.67			0.87	1	

Source	Zoobenthic Predators				Planktivores		
	<i>df</i>	<i>MS</i>	<i>F</i>	<i>P</i>	<i>MS</i>	<i>F</i>	<i>P</i>
Habitat (Ha)	1	5.54	1.36	0.25ns	0.96	3.33	0.07ns
Time (Ti)	3	3.54	0.87	0.46ns	0.73	2.53	0.06ns
Ha x Ti	3	3.39	0.83	0.48ns	0.73	2.53	0.06ns
Residuals	96	4.08			2.89		

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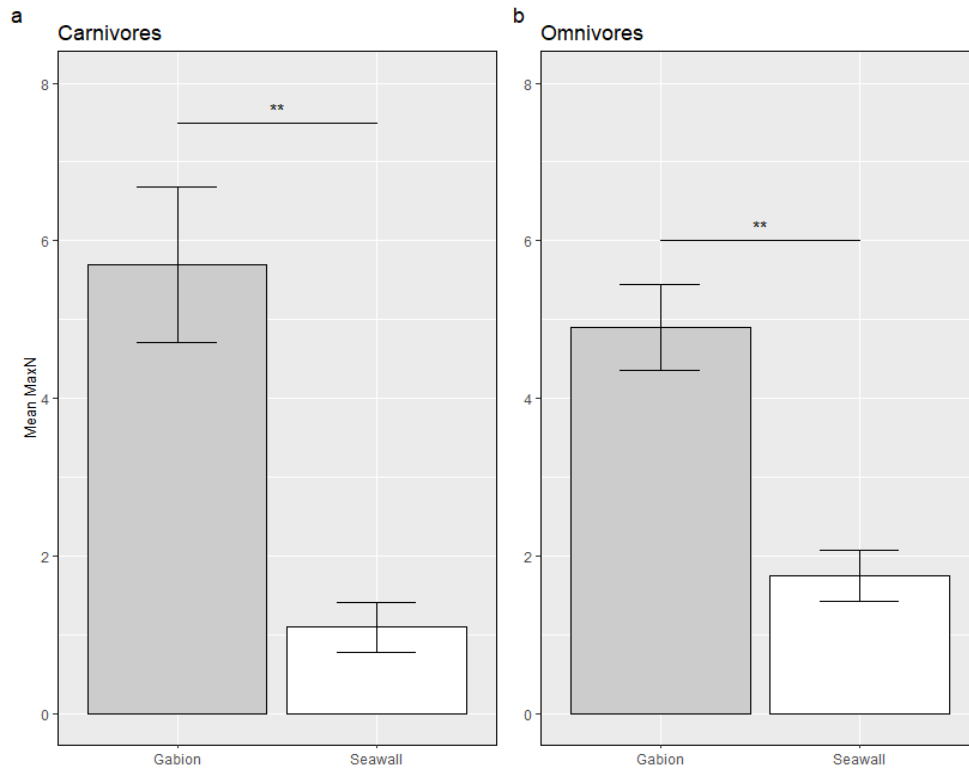


Figure 2.8: Comparison of mean ($n = 13$, $\pm$ SE) relative abundance (MaxN) of fish species in different functional groups in gabion (grey bars) and seawall (white bars) habitats amongst times T_2 , T_6 , T_{10} and T_{12} recorded in Knysna Harbour for (a) carnivorous and (b) omnivorous feeding groups. ** $P < 0.01$; * $P < 0.05$.

2.3.5 Taxon and functional composition

Taxon composition differed significantly between habitats and among time periods (Table 2.4, Fig. 2.9a,b). The composition of fish varied between habitats such that the MDS plot suggests the species on the seawall habitat are a subset of those on the gabion habitat (Fig. 2.9a). It is clear that there was little difference in fish populations between times T_2 and T_{12} but there was

much more difference between times T_6 and T_{10} (Fig. 2.9b). SIMPER analysis identified seven fish taxa that were influential in separating taxon compositions between habitats (Table 2.5a). *Diplodus capensis* and *Rhabdosargus* sp. contributed to the greatest dissimilarity between habitats, being significantly more abundant on gabion than seawall habitats (Table 2.5a). There was also a significantly greater abundance of *Diplodus Hottentotus* and *Chaetodon Marleyi* on gabions than seawall habitats (Table 2.5a).

There was a significant interaction between Habitat and Time for functional compositions (Table 2.4). *Post-hoc* pairwise tests revealed significant differences in functional compositions between gabion and seawall habitats (Table 2.4, Fig. 2.10). Similarly, pairwise tests revealed significant differences between habitats for times T_2 , T_6 and T_{12} (Fig. 2.10a,b,d), and slightly less difference in time T_{10} (Fig. 2.10c). SIMPER analysis identified five functional groups that were influential in separating functional compositions between habitats (Table 2.5b). Carnivores and omnivores contributed to the greatest dissimilarity between habitats but abundances were also significantly greater for zoobenthic predators, planktivores and herbivores in gabion habitats (Table 2.5b).

Table 2.4: Results of permutational multivariate analysis of variance (PERMANOVA) for differences in taxon and functional fish composition between gabion and seawall habitats across times T₂, T₆, T₁₀ and T₁₂ recorded in Knysna Harbour. **P < 0.01; *P < 0.05; ns, not significant.

Multivariate PERMANOVA of community composition							
Source	Taxon				Functional		
	df	R ²	F	P	R ²	F	P
Habitat (Ha)	1	0.15	24.56	<0.01**	0.25	50.01	<0.01**
Time (Ti)	3	0.23	12.56	<0.01**	0.24	16.29	<0.01**
Ha x Ti	3	0.03	1.84	0.07ns	0.04	2.56	<0.04*
Residuals	96	0.59			0.47		
Total	103	1.00			1.00		

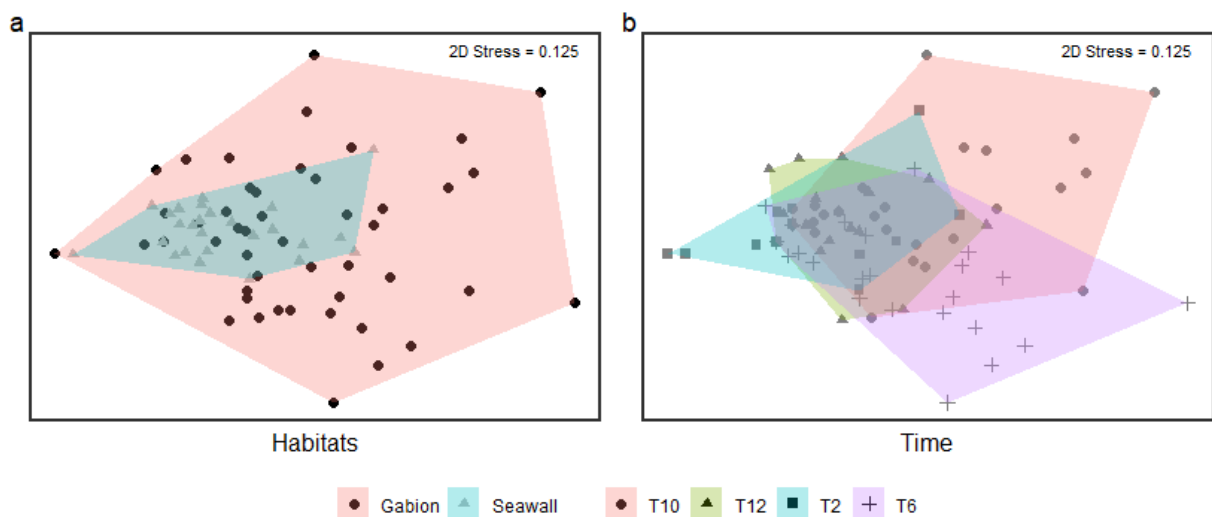


Figure 2.9: Non-metric multidimensional scaling (nMDS) ordination displaying the fish composition (MaxN) on Bray-Curtis transformed data with a polygon to display groups of data as (a) seawall (pink) and gabion (blue) habitats; and (b) the time of sampling (blue – T₂, purple – T₆, pink – T₁₀, green – T₁₂).

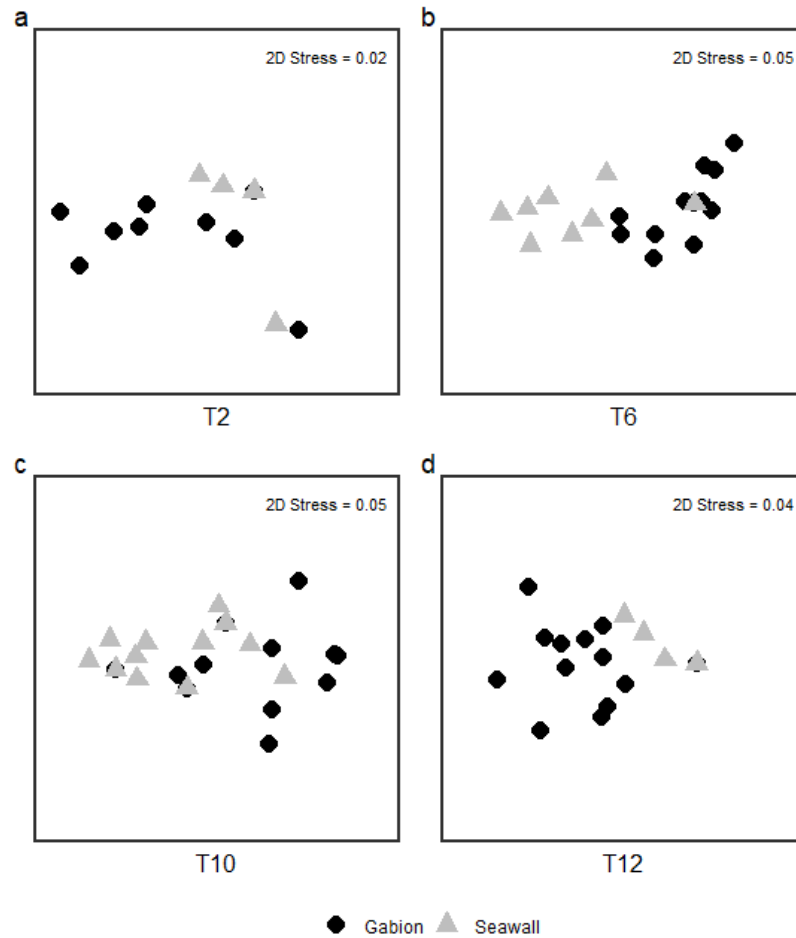


Figure 2.10: nMDS ordination plots of functional composition at times; (a) T₂; (b) T₆; (c) T₁₀ and; (d) T₁₂ compared between the gabion (black circle) and seawall (grey triangle) habitats on Bray-Curtis transformed data.

Table 2.5: SIMPER analysis outputting the contribution of dissimilarity between gabion and seawall habitats of (a) fish taxa and (b) fish functional feeding groups. Av.Abund: average abundance, Cont. %: contribution percentage, Cum. % cumulative percentage contribution. Cumulative contributions below 90% left out. ***P < 0.01; *P < 0.05; ns, not significant.

	Gabion	Seawall			
(a) Taxon	<i>Av.abund A</i>	<i>Av.abund B</i>	<i>Cont. %</i>	<i>Cum. %</i>	<i>P</i>
<i>Diplodus Capensis</i>	1.97	1.28	28.00	0.28	<0.01**
<i>Rhabdosargus</i> sp.	1.79	1.12	24.00	0.52	<0.01**
<i>Diplodus Hottentotus</i>	1.52	1.21	16.00	0.68	<0.01**
<i>Gobbiidae</i> sp.	1.42	1.32	11.00	0.79	0.31ns
<i>Mugilidae</i> sp.	1.13	1.03	5.00	0.84	0.06ns
<i>Chaetodon Marleyi</i>	1.12	1.00	3.00	0.87	<0.01**
<i>Clinidae</i> sp.	1.06	1.03	3.00	0.90	0.12ns
	Gabion	Seawall			
(b) Functional	<i>Av.abund A</i>	<i>Av.abund B</i>	<i>Cont. %</i>	<i>Cum. %</i>	<i>P</i>
Carnivorous	2.34	1.34	48.00	0.48	<0.01**
Omnivorous	2.29	1.55	42.59	0.91	<0.01**
Zoobenthic Predator	1.13	1.03	6.03	0.97	<0.03*
Planktivorous	1.06	1.00	2.40	0.99	<0.01**
Herbivorous	1.02	1.00	0.73	1.00	<0.01**

2.3.6 Fish feeding behaviour

Of the 2731 fish counted utilizing the gabion habitats, 539 (19.74 %) were observed feeding while on the seawall habitat, 106 of the 506 fish counted were feeding (Table 2.6). The greater majority of fish feeding on the gabion habitats were carnivores (67 %; Table 2.6); whereas on the seawall habitat, the greater majority of fish feeding were omnivores (58 %; Table 2.6).

724 Table 2.6: The total number of fish counted in the field of view of the cameras in Knysna
 725 Harbour across times T₂, T₆, T₁₀ and T₁₂ and the number of fish recorded feeding with the
 726 percentage of these classified into functional groups: omnivorous and carnivorous.

Habitat	Total	Feeding	Omnivore %	Carnivore %
Gabion	2731	539	33	67
Seawall	506	106	58	42

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2.4. Discussion

Despite gabions and seawalls having many fish species in common, gabions supported greater numbers of individuals and species than the seawall habitats. No fish species were unique to the seawalls. In addition, a larger relative abundance of fish was found within the gabion habitats than seawall habitats which suggests that these more complex structures may be increasing habitat and space availability for fish (Clynick, 2007; Mercador *et al.*, 2017), compared to the flatter, less topographically complex seawall. The combination of relative abundance and diversity data was supported by the analyses of fish assemblages having more variation in gabion than seawall habitats. The gabions were associated with a number of species listed on the IUCN Red List of Threatened Species that were not present on the seawalls.

The increased three-dimensional structural complexity and microhabitat availability provided by the gabions are likely to have provided fish with many benefits including provisions of a refuge for cryptobenthic fish from predators, protection from environmental stressors and food availability (Rilov & Benayahu, 2000; Bulleri, 2005; Kovalenko *et al.*, 2012; Morris *et al.*, 2018). The difference in complexity of the gabion and seawalls has a direct impact on fish abundance and diversity which may be influenced by body size, foraging preferences, mobility and life-history traits (Bozec *et al.*, 2013; Morris *et al.*, 2018), as well as resource partitioning (Risk, 1972). Selfati *et al.* (2018), found that by increasing habitat complexity with the addition of biohuts in a marina in the Marchica Lagoon on the Mediterranean coast of Morocco, densities of juvenile dusky and comb groupers were higher than the natural sandbar habitats. Moreover, their study suggested that the addition of hard complex structures assisted in mitigating the

762 loss of natural habitats to fishes. While the increase in abundance and diversity of fish may be
763 in part due to increased habitat complexity, Sawyer *et al.* (2020), suggests that an increase in
764 food (prey) availability may also drive the observed increase in fish density. The link between
765 food availability and fish density in this study will be explored in the discussion chapter (Chapter
766 4) of the thesis. It is important to note that whilst there may be surface area/complexity
767 differences between the gabion and seawall habitats, these were difficult to standardise using
768 GoPros, however the increase in surface area, crevices and topographical complexity proved to
769 be valuable in increasing the diversity and abundance of fish in the gabion habitats in Knysna
770 Harbour.

771 The groups of fish that were largely responsible for driving the differences in assemblages
772 between the gabion and seawall habitats were from the Sparidae family which included
773 *Rhabdosargus* spp. and *D. capensis*. *Diplodus capensis* inhabits rocky and sandy substrates
774 (Coetzee & Baird, 1981), with its juveniles and sub-adults usually being found in estuaries
775 (Winter, 1979; Beckley, 1983), and tidal pools (Beckley, 1985). *Rhabdosargus globiceps* spawns
776 inshore (Biden, 1930), and its juveniles spend their nursery years in estuaries, bays and in the
777 surf zone (Whitfield & Kok, 1992; Griffiths *et al.*, 2002). *Rhabdosargus holubi* is endemic to
778 South Africa and is regarded as an estuary-dependent fisheries species (Heemstra & Heemstra,
779 2004). The gabion habitats appeared to promote the presence of a larger abundance of these
780 commonly occurring fish species within the present study. *Diplodus capensis* are marine teleost
781 fish typically associated with reef habitats and rocky shores (van der Elst, 1981; Mann, 1992),
782 and have been found inhabiting structurally complex artificial reefs and structures (Fennessy *et*
783 *al.*, 1998; Lechanteur & Griffiths, 2015). These results suggest habitat provided by the gabion

784 may be more comparable with natural reefs than the seawalls. *Rhadosargus* spp. are associated
785 with seagrass and submerged macrophyte habitats (James *et al.*, 2019). This habitat type shows
786 no obvious resemblance to the present studies' two habitat types, other than the greater
787 complexity and more cryptic habitat of gabions, however Folpp *et al.* (2013), conducted a study
788 on the post-deployment fish assemblages of artificial reefs in Lake Macquarie, Australia and
789 found *R. sarba* to be one of the four key colonising species. Fennessy *et al.* (1998), also found *R.*
790 *sarba* on the Vetch's Pier on the Durban beachfront. The underlying reasons for these fish taxa
791 being associated with gabion habitats may need to be further studied, with particular reference
792 to the ages of these fish and the food availability.

793 The presence of a number of fish within the gabion habitat that were absent from the seawall
794 habitats, indicates that the gabions supported unique composition of fish. Those species that
795 were only recorded in gabion habitats included *Blenniidae*, *Chaetodon marleyi*, *Chirodactylus*
796 *brachydactylus*, *Caffrogobius* sp., *Apletodon pellegrini*, *Monodactylus falciformis*, *Cheilodactylus*
797 *pixi*, *Boopsoidea inornata*, *Chrysoblephus laticeps*, *Sarpa salpa* and *Hippocampus capensis*.
798 These species have been documented to be associated with both coral reefs and rocky shores
799 (van der Elst, 1988; Heemstra & Heemstra, 2004), and in the case of *Hippocampus capensis*;
800 macrophytes and artificial structures (Bell *et al.*, 2003; Claassens, 2016). The fish assemblages
801 associated with the gabion habitats are therefore akin to those found on natural coral reefs and
802 rocky shores (Burcharth *et al.*, 2007). These similarities with natural reefs may include; the
803 number and sizes of shelters to support larger and more groups of fish and the vertical range
804 and rugosity index (Risk, 1972; Morris *et al.*, 2018).

805

806 Of the 22 fish taxa that were recorded in gabion habitats, seven are endemic, and classified as
807 estuary-utilising species, in South Africa (Whitfield, 1994b). These species have previously been
808 found in the Knysna Estuary in other studies (Le Quesne, 2000; Griffiths *et al.*, 2002; Day *et al.*,
809 2010). Wallace *et al.* (1984), categorised South African estuarine fish fauna into four categories
810 based on their dependence on estuaries for their life histories. A number of species recorded
811 fall into category III (species whose juveniles occur mainly in estuaries, but are also found at
812 sea) and category I (truly estuarine species, dependent on estuaries for entire life cycle)
813 including *Monodactylidae falciformis*, *Rhabdosargus* sp., some *Mugilidae* and *Hippocampus*
814 *capensis*, respectively (Wallace *et al.*, 1984). These results suggest that the gabions have the
815 potential to fulfil a more important nursery function than seawall habitats within the estuary
816 and in part, may mitigate the loss and degradation of habitats due to anthropogenic activities
817 within the system. Three taxa identified in this study are important angling species (Wallace *et*
818 *al.*, 1984; Whitfield, 1994a) and the taxa of fish that fall into categories III and V contribute to
819 adult fish stocks (Wallace *et al.*, 1984). This is particularly important in the Knysna Estuary
820 where there are 30 full-time and 200 part-time subsistence fishers involved in bait collection
821 and fishing (Napier *et al.*, 2009). Gabions may be a better engineering approach to choose from
822 when development is planned to take place. Such approaches should not be used to promote
823 development of semi-pristine natural habitat (Airoidi *et al.*, 2005; Firth *et al.*, 2020). The
824 saltmarsh previously present in the study area, should be protected and preserved before
825 choosing an artificial approach.

826 Of the species found in the present study, *P. rupestris* and *H. capensis* are listed as Endangered
827 on the IUCN Red List of Threatened Species (Mann *et al.*, 2014a; Pollom, 2017), while *C. laticeps*

828 and *D. chrysonota* are listed as Near Threatened (Mann *et al.*, 2014b; Pollom *et al.*, 2020).
829 Gabion structures appear therefore, to be playing a role in protecting threatened and
830 endangered fish within this highly modified and urbanised ecosystem which may aid in their
831 long-term recovery (Afonso *et al.*, 2011). Seahorses and in particular, *H. capensis* have been
832 found to commonly make use of artificial holdfasts and there is some evidence to suggest
833 preference for artificial over natural habitats (Curtis & Vincent, 2005; Rosa *et al.*, 2007; Clynick,
834 2008). Claassens (2016), found that *H. capensis* was able to make use of gabions in the Thesen
835 Island Canals, Knysna – the present study used the same type of material as those in Thesen
836 Islands, however these canals were built on an old island and habitat was added to the estuary,
837 unlike the Knysna Harbour. With continued coastal development and increased pressures on
838 the marine environment moving into the future, careful planning and the integration of eco-
839 engineering principles into the coastal region need to be applied (Chapman & Underwood,
840 2011; Morris *et al.*, 2018; Firth *et al.*, 2020; O’Shaughnessy *et al.*, 2020).

841 The numerical dominance of fish carnivores and omnivores within the gabion and seawall
842 habitats, suggest that these habitats provide sufficient food (invertebrates and algae) to sustain
843 these feeding modes. The presence of planktivores and herbivores in the gabion habitats that
844 were absent from the seawall habitat, indicate that gabions are offering either a specific food
845 source or habitat-niche that the seawalls are not offering (Becker *et al.*, 2010), such as
846 increased grazing surface area and nutritional resource availability (Eggertsen *et al.*, 2019;
847 Oakley-Cogan *et al.*, 2020).

848 My study has shown that gabions appear to provide a more suitable habitat for fish than the
849 pre-existing concrete seawall in Knysna Harbour. Many studies, report higher abundances and

850 diversity of fishes in artificial reefs compared to adjacent natural habitats (Claisse *et al.*, 2014;
851 Bartholomew *et al.*, 2022). Whilst such habitats may indeed support greater numbers of
852 species, they may also be functioning as ecological traps (Schlaepfer *et al.*, 2002), through
853 reducing the fitness of inhabitants, or in the case of fish, concentrating them in an area where
854 they are more susceptible to mortality through fishing and other anthropogenic stressors
855 (Komyakova *et al.*, 2021; Swearer *et al.*, 2021; Bartholomew *et al.*, 2022). In the case of looking
856 to enhance already-modified coastal environments, the focus should rather lie in improving
857 nursery function and habitat availability than attempting to mimic the natural fish assemblages.
858 Gabions have the potential to be used for more targeted projects such as targeting
859 commercially important species to enhance their stocks, or to increase the biodiversity in
860 harbours to promote ecosystem services such as water filtration or aesthetic value. They offer
861 an alternative to seawalls that could greatly improve the habitat in coastal environments for
862 local fish species.

863

864

Chapter 3

A comparison of colonising organism assemblages between gabion and seawall habitats

3.1. Introduction

The highly complex and productive ecosystems of salt marshes, sandy and rocky shores, and mangroves offer a myriad of ecological benefits. They serve as vital habitats and nurseries, providing food, shelter, and a nurturing environment for a diverse array of marine organisms, as documented in studies by Whitfield (1990, 1998), Blaber (1997), Potter & Hyndes (1999), and Henseler *et al.* (2019). These ecosystems contribute significantly to coastal resilience, protecting shorelines from erosion and storm surges (Day *et al.*, 2007; Koch *et al.*, 2009; Marois & Mitch, 2015), while supporting the overall productivity and biodiversity of coastal regions (Suchanek, 1994; Gray, 1997). Marine fauna and flora, which are responsible for underpinning ecosystem services (Spalding *et al.*, 2007; Beck *et al.*, 2011), occur in the highest abundances and have the greatest diversity in these shallow water habitats (Henseler *et al.*, 2019), making them highly vulnerable to anthropogenic pressures (Spalding *et al.*, 2007).

The concept of 'ocean sprawl', referring to the proliferation of artificial structures associated with coastal industries has gained attention as a major threat to marine ecosystems (Airoidi & Beck, 2007; Dafforn *et al.*, 2015a; Firth *et al.*, 2016b). These structures alter the physical environment, disrupt natural coastal processes, and fragment habitats, posing significant challenges to the biodiversity and ecological functioning of marine ecosystems (Airoidi & Beck 2007; Firth *et al.*, 2013a; Dafforn *et al.*, 2015a).

886 Artificial marine structures can provide important ecosystem services for commercially
887 important species and species of conservation concern (Toft *et al.*, 2013; Firth *et al.*, 2015;
888 García-Gómez *et al.*, 2015). However, they may be poor surrogates for natural ecosystems;
889 supporting lower biodiversity of benthic communities (Firth *et al.*, 2016a), changes in natural
890 abundances (Chapman, 2003), mixes of species (Moschella *et al.*, 2005; Buller *et al.*, 2005),
891 reproductive output and size-structures of populations (Moreira *et al.*, 2006).

892 Concrete which is largely used to manufacture seawalls and other artificial marine structures is
893 known to provide a poor substrate for marine invertebrates and algae to attach and provides a
894 high likelihood of marine invasives and supports a poor biodiversity of species (Lukens &
895 Selberg, 2004; McManus *et al.*, 2017). Seawalls typically exhibit flat, vertical configurations,
896 lacking the three-dimensional features commonly found in natural rocky shores (Birkemeier,
897 1985; Chen *et al.*, 2013). Natural rocky shores exhibit complex three-dimensional
898 configurations, including crevices, ledges, and tidal pools, providing diverse habitats for a wide
899 range of marine organisms (Sousa, 1979; Menge & Sutherland, 1987; Bertness & Gaines, 1993).

900 Another popularly-used building material in coastal environments of South Africa are gabion
901 boxes (rock-filled cages), a three-dimensional configuration which may be more topographically
902 similar to natural rocky shores than seawalls. Gabions are used in a variety of applications,
903 including erosion control, slope stabilisation, riverbank protection, and retaining walls (Toprak
904 *et al.*, 2016). Additionally, gabions have been utilised in the construction of dams for sediment
905 control and in stream restoration projects to enhance aquatic habitats (Mohamed, 2010).

906 Previous investigations have demonstrated that gabions host a myriad of invertebrate species

907 (Firth *et al.*, 2014b; de Villiers *et al.*, 2021), although further studies are required to assess their
908 suitability as a habitat for other marine organisms such as fish.

909 Ecological engineering has been developed to off-set the adverse effects of artificial coastal
910 structures on natural habitats by promoting biodiversity. Ecological engineering projects have
911 included retrofitting microhabitats such as pits and crevices (Martins *et al.*, 2010; Bishop *et al.*,
912 2017), installing 'tidal' pools (Chapman & Blockley, 2009; Firth *et al.*, 2016a; Evans *et al.*, 2016),
913 and transplanting habitat-forming species (such as oysters) onto artificial structures (Grabowski
914 *et al.*, 2012; Ushiyama *et al.*, 2019). There has been a surge of new research on eco-engineering
915 tools that offer coastal engineers a wide range of options to mitigate the impacts of coastal
916 development on natural habitats (Elliott *et al.*, 2016; Strain *et al.*, 2018; O'Shaughnessy *et al.*,
917 2020). However, some of these options can create the superficial appearance of improving
918 ecological aspects of artificial habitats, but are primarily utilised as a means of gaining approval
919 for potentially harmful coastal development projects (Airoldi *et al.*, 2015; Firth *et al.*, 2016a,
920 2020).

921 In some cases instead of reinventing the wheel, there is scope for exchanging featureless
922 structures, such as cement seawalls, with three-dimensional structures that are already used
923 and readily available as building material – such as gabion boxes. Whilst the viability of gabion
924 boxes as habitat for marine organisms has been briefly studied (e.g. Firth *et al.*, 2014;
925 Claassens, 2016; de Villiers *et al.*, 2021), they have not been tested as an alternative to seawalls.
926 The aim of this study was to trial gabion boxes as an eco-engineering approach in comparison
927 to seawalls to determine patterns of biodiversity and composition of invertebrates and algae
928 (furthermore known as colonising organisms); to inform future harbour design.

929 Specifically, I tested the hypotheses: i) that taxon and functional richness, diversity and
930 abundance of colonising organisms would be greater in gabion than seawall habitats; and ii)
931 that taxon and functional composition would be different between gabion and seawall habitats.
932 The results from this study are important for policy-makers and coastal engineers wanting to
933 make informed decisions about coastal development, if their goal is increased biodiversity of
934 organisms then they have a knowledge base to back up choosing gabions instead of seawalls.

935

936 **3.2. Methods and materials**

937 *3.2.1 Experimental setup*

938 The same experimental setup used for fish sampling was used for colonising organism surveys
939 as seen below. Refer to Chapter 2 for information on study site, gabion deployment and
940 experimental setup as well as physico-chemical characteristics of the water body.

941

942 *3.2.2 Invertebrate and algal surveys*

943 All colonising organisms (which includes all sessile, encrusting and mobile invertebrates and
944 algae) were sampled on four occasions: two months, six months, 10 months and 12 months
945 post deployment (July 2020) (known as times T₂, T₆, T₁₀ and T₁₂). Surveys were conducted using
946 a 0.2 x 0.2 m quadrat to determine percentage cover of encrusting species (colonising ascidians,
947 sponges, bryozoans) and algae and counts of solitary species (solitary tunicates, polychaete
948 worms, barnacles, mussels). One quadrat was haphazardly placed on the vertical surface of

each top gabion box (Fig. 3.1), and two quadrats placed on the corresponding seawall habitat (Fig. 2.4). The reason for using one and two quadrats on the gabion and seawall, respectively, was to account for the difference in surface area based on the 2-dimensional and 3-dimensional nature of the seawall and gabions. Species at each seawall replicate were totalled across the two quadrats. Each quadrat was photographed using a NIKON Coolpix W300. In total 26 seawall and 13 gabion quadrats were photographed at each sampling event. It must be noted that this approach was a visual inspection of the vertical surface of the gabion and did not consider the biota hidden outside of view.



Figure 3.1: The 0.2 x 0.2 m stainless-steel metal quadrat lined with yellow tape used for conducting invertebrate and algae surveys, shown on the vertical surface of a gabion habitat in Knysna Harbour.

The photographic images were analysed using PhotoQuad software (Trygonis & Sini, 2012), to determine percentage cover and counts of all colonising organisms; percentage cover was determined for encrusting species (colonising ascidians, sponges, bryozoans) and algae while solitary (solitary tunicates, polychaete worms, barnacles, mussels) and mobile species were individually counted for analysis. Species that were not able to be identified down to species level were given morphotypes based on their higher taxonomic classification (eg. Bryozoa 1), Invertebrates and algae were grouped into functional groups based on morphological features (Steneck & Dethier, 1994; Macdonald *et al.*, 2010), and feeding strategies.

3.2.3 Statistical Analysis

For statistical analyses a variety of different univariate and multivariate metrics were employed using the statistical program R studio (R Development Core Team, 2014). A two-way crossed ANOVA with fixed factors Habitat and Time was used to test for the comparisons of taxon and functional richness, Shannon diversity [H'] and abundance. Cochran's test (GAD R package; Sandrini-Neto & Camargo, 2021), was used to test for homogeneity of variances, where variances were heterogeneous, data was transformed using square-root transformations. Data were tested for normality, non-parametric tests were used for non-normal data. Tukey honest significance tests (TukeyHSD) were used to make post-hoc comparisons.

To investigate differences in taxon and functional compositions between gabions and seawall habitats over time, multivariate analysis of variance (PERMANOVA; Anderson & Clarke, 2008), were conducted on Bray-Curtis transformed community data, with 9999 unrestricted

permutations. These were calculated using presence/absence data. The multivariate data analyses was based on a two-way crossed design with fixed factors Habitat and Time. SIMPER (Clarke, 1993) analysis in R of individual taxon and functional groups were used to determine the dissimilarities between treatments and which taxa or groups were contributing to these differences.

3.3. Results

In total, 37 different taxa of invertebrates and algae (classified to the lowest possible taxonomic group) were recorded across all habitats and time periods (Table 3.1). There were 28 and 21 invertebrate taxa and 4 and 5 algal taxa recorded within the gabion and seawall habitats, respectively. Seven functional groups were identified (filter feeders, carnivores, detritivores, herbivores, turf algae, foliose algae, encrusting algae). Eleven invertebrates were unique to gabion habitats: the flatworm, *Planocera gilchristi*; the polychaete worm, *Pseudobranchiomma longa*; the barnacle, *Amphibalanus* sp.; the shrimp, *Palaemon peringueyi*; the bryozoan, *Watersipora subtorquata*; the mussel, *Perna perna*; the nudibranch, *Polycera capensis*; the octopus, *Octopus vulgaris*; the brittlestar, *Ophiothrix* sp.; the urchin, *Parechinus angulosus* and; the solitary tunicate, *Ciona intestinalis*. Four invertebrates were unique to the seawall habitat: the sponge, *Sponge* sp.1.; the bryozoan, *Bryozoa* sp2.; the seahares, *Bursatella leachii* and *Aplysia oculifera*. A single algal species (*Algal* sp.) was unique to the seawalls.

1005 Table 3.1: Invertebrate and algal taxa recorded in gabion and seawall habitats in Knysna

1006 Harbour across four sampling times T₂, T₆, T₁₀ and T₁₂; “+” indicates presence and “-” indicates

1007 absence of taxon; and the functional group they belong to. Symbols denote known non-native

1008 species (*).

Taxa	Gabion	Seawall	Functional group
<u>PORIFERA</u>			
<i>Leucosolenia</i> sp.	+	+	Filter feeder
Sponge sp.	+	+	Filter feeder
Sponge sp.1.	-	+	Filter feeder
Sponge sp.2.	+	+	Filter feeder
<u>PLATYHELMINTHES</u>			
<u>Polycladida</u>			
<i>Planocera gilchristi</i>	+	-	Carnivore
<u>ANNELIDA</u>			
<u>Polychaeta</u>			
<i>Pseudobranchiomma longa</i>	+	-	Filter feeder
<u>Serpulidae</u>			
<i>Spirorbis</i> sp.	+	+	Filter feeder
<i>Serpulid</i> 1	+	+	Filter feeder
<u>ARTHROPODA</u>			
<u>Crustacea</u>			
<u>Thecostraca</u>			
<i>Amphibalanus</i> sp.	+	-	Filter feeder
<u>Decopoda</u>			
<i>Palaemon peringueyi</i>	+	-	Detritivore
<u>BRYOZOA</u>			
Bryozoa sp.1.	+	+	Filter feeder
Bryozoa sp.2.	-	+	Filter feeder
<i>Bowerbankia</i> sp.	+	+	Filter feeder
<i>Watersipora subtorquata</i> *	+	-	Filter feeder
<u>MOLLUSCA</u>			
<u>Bivalvia</u>			
<i>Perna perna</i>	+	-	Filter feeder
<u>Gastropoda</u>			
<i>Bursatella leachii</i>	-	+	Herbivore
<i>Aplysia oculifera</i>	-	+	Carnivore
<i>Polycera capensis</i>	+	-	Carnivore

Cephalopoda

<i>Octopus vulgaris</i>	+	-	Carnivore
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ECHINODERMATA**Ophiuroidea**

<i>Ophiothrix</i> sp.	+	-	Detritivore
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Echinoidea

<i>Parechinus angulosus</i>	+	-	Herbivore
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CHORDATA**Urochordata****Ascidacea**

<i>Clavelina lepadiformis</i> *	+	+	Filter feeder
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<i>Ciona intestinalis</i> *	+	-	Filter feeder
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<i>Styela plicata</i> *	+	+	Filter feeder
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<i>Pyura herdmanni</i>	+	+	Filter feeder
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<i>Ascidia</i> sp.	+	+	Filter feeder
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<i>Ascidia</i> sp.2.	+	+	Filter feeder
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<i>Microcosmus squamiger</i> *	+	+	Filter feeder
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<i>Trididemnum cerebriforme</i>	+	+	Filter feeder
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<i>Diplosoma listerianum</i> *	+	+	Filter feeder
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<i>Botryllus magnicoecus</i>	+	+	Filter feeder
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<i>Botryllus</i> sp. 1	+	+	Filter feeder
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OCHROPHYTA

<i>Colpomenia</i> sp.	+	+	Foliose algae
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Algal sp.	-	+	Turf algae
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RHODOPHYTA

<i>Asparagopsis taxiformis</i> *	+	+	Turf algae
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Alga sp.2.	+	+	Encrusting algae
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<i>Plocamium</i> sp.	+	+	Foliose algae
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1009

1010 **3.3.1 Taxon and functional richness**

1011 There was a significant interaction between Habitat and Time for taxon richness (Table 3.2a,

1012 Fig. 3.2a). Gabions supported greater mean taxon richness than seawalls ((6.12 ± 4.12) vs (4.96

1013 ± 2.71)) in three out of the four sampling periods but times T₆ and T₁₀ were not significant (Fig.1014 3.2a); whilst in T₁₂ gabions supported significantly greater mean taxon richness than seawalls

1015 ((8.3 ± 3.25) vs (5.2 ± 1.86); Fig. 3.2a). Taxon richness peaked at time T_{10} in both gabion and
1016 seawall habitats (Fig. 3.2a).

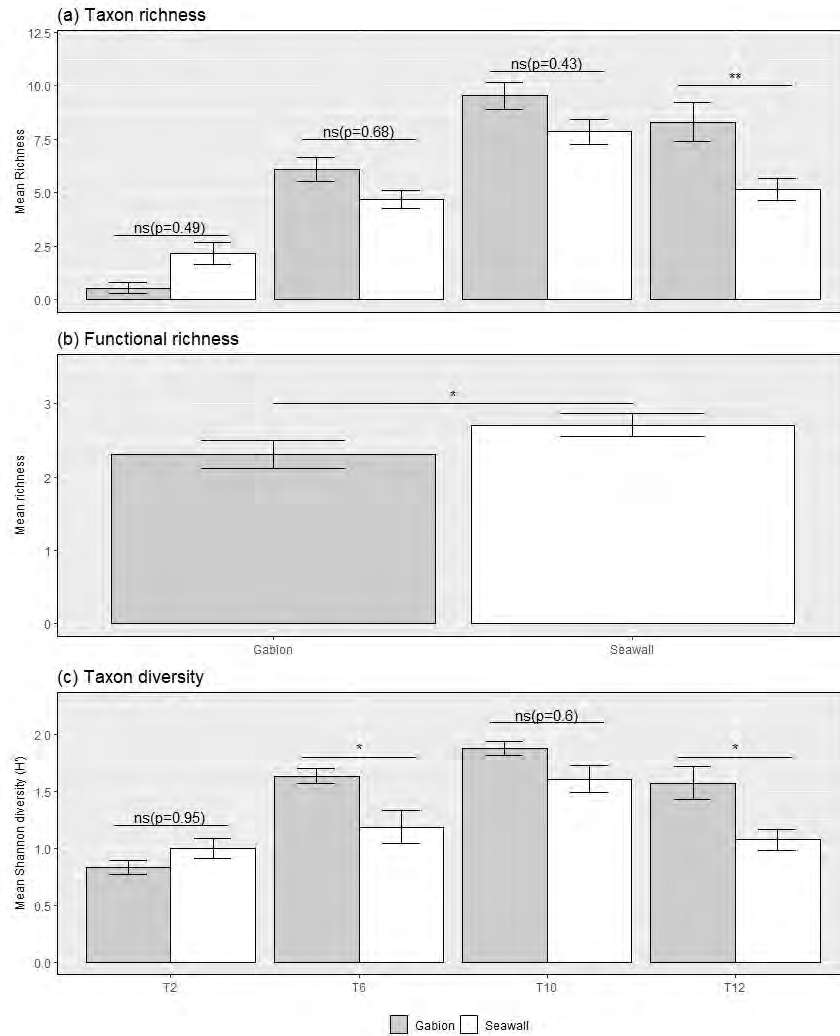
1017 Seawalls supported significantly greater mean functional richness than the gabions ((2.7 ± 1.16)
1018 vs (2.3 ± 1.36); Table 3.2a, Fig. 3.2b).

1019

1020 3.3.2 Taxon and functional diversity

1021 There was a significant interaction between Habitat and Time for taxon Shannon diversity
1022 (Table 3.2b, Fig. 3.2c). Gabions supported greater mean taxon diversity than seawalls (($1.48 \pm$
1023 0.51) vs (1.21 ± 0.47)) on three out of the four sampling periods, but this was only significant in
1024 time periods T_6 and T_{12} (Fig. 3.2c). Taxon diversity peaked at time T_{10} in both gabion and seawall
1025 habitats (Fig. 3.2c).

1026 There was no significant difference in mean functional Shannon diversity between the gabions
1027 and seawalls (Table 3.2b).



1028

1029 Figure 3.2: Comparison of mean ($n = 13$, $\pm$ SE) (a) taxon richness in gabion (grey bars) and
 1030 seawall (white bars) habitats amongst time periods T_2 , T_6 , T_{10} and T_{12} ; (b) functional richness in
 1031 gabion (grey bars) and seawall (white bars) habitats at combined times T_2 , T_6 , T_{10} and T_{12} ; (c)
 1032 functional shannon-weiner diversity indices (H') of colonising organisms in gabion (grey bars)
 1033 and seawall habitats (white bars) amongst time periods T_2 , T_6 , T_{10} and T_{12} , recorded in Knysna
 1034 Harbour. (ns = not significant; ** $P < 0.01$; * $P < 0.05$).

Table 3.2: Two-way ANOVA comparing (a) taxon and functional richness and (b) shannon diversity between gabion and seawall habitats across a range of time periods T₂, T₆, T₁₀ and T₁₂.
 **P < 0.01; *P < 0.05; ns, not significant.

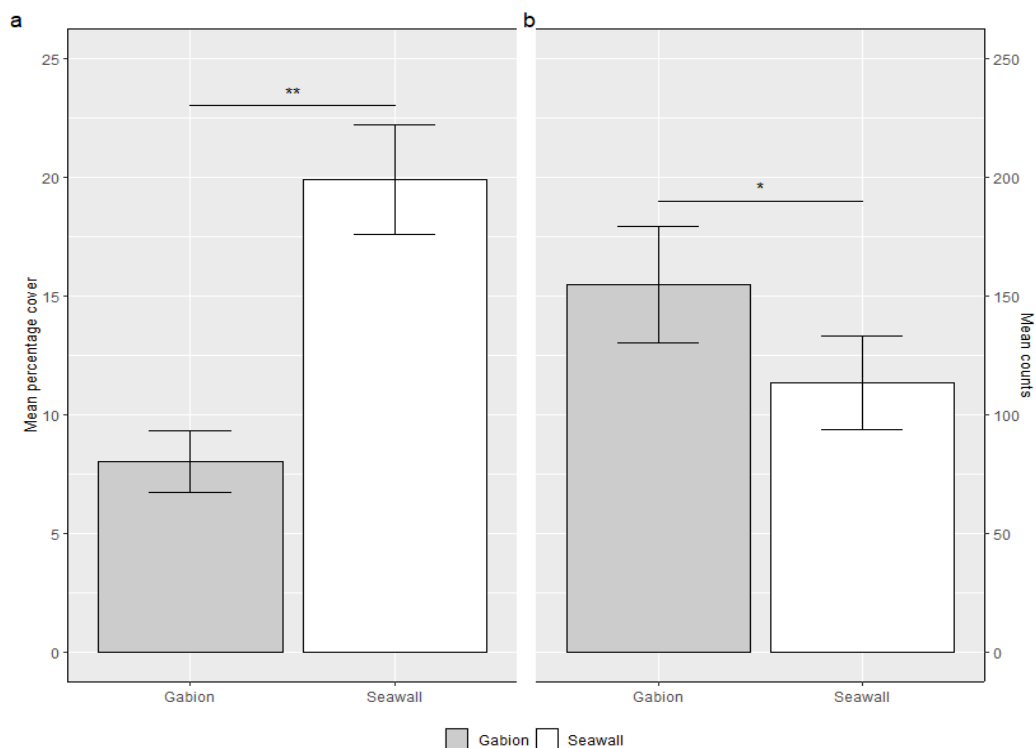
(a) Univariate ANOVA of richness							
Source	Taxon				Functional		
	<i>df</i>	<i>MS</i>	<i>F</i>	<i>P</i>	<i>MS</i>	<i>F</i>	<i>P</i>
Habitat (Ha)	1	34.62	8.11	<0.01**	3.12	5.1	<0.03*
Time (Ti)	3	251.05	58.78	<0.01**	15.35	25.13	<0.01**
Ha x Ti	3	26.03	6.09	<0.01**	0.53	0.86	0.46ns
Residuals	96	4.27			0.61		

(b) Univariate ANOVA of Shannon diversity index							
Source	Taxon				Functional		
	<i>df</i>	<i>MS</i>	<i>F</i>	<i>P</i>	<i>MS</i>	<i>F</i>	<i>P</i>
Habitat (Ha)	1	1.78	12.68	<0.01**	0	0.03	0.86ns
Time (Ti)	3	3.01	21.41	<0.01**	1.04	13.78	<0.01**
Ha x Ti	3	0.59	4.22	<0.01**	0.14	1.86	0.14ns
Residuals	96	0.14			0.08		

3.3.3. Taxon and functional abundance

Sampling identified 13 978 solitary invertebrates of which 8 055 were found on gabions and 5 923 on the seawalls. Of these, 13 959 were filter feeders; 8 041 and 5 918 identified on gabions and seawalls, respectively. In total, three carnivores, two detritivores and 14 herbivores (ten and four on gabions and seawalls, respectively) were recorded.

Seawalls had significantly greater mean taxon percentage cover than gabions ((19.9 % ± 16.61 %) vs (8.03 % ± 9.38 %) average cover; Table 3.3a, Fig. 3.3a). By contrast, there were significantly greater mean taxon counts from amongst gabions than from seawalls ((154.9 ± 175.88) vs (113.44 ± 141.03) average counts; Table 3.3b, Fig. 3.3b).



1048

1049 Figure 3.3: Comparison of mean ($n = 13$, $\pm$ SE) taxon abundance of colonising organisms on 13

1050 replicate gabion (grey bars) and 13 replicate seawall (white bars) habitats across times T_2 , T_6 ,

1051 T_{10} and T_{12} expressed as (a) percentage cover and (b) counts; recorded in Knysna Harbour. (ns =

1052 not significant; ** $P < 0.01$; * $P < 0.05$).

Table 3.3: (a) Two-way ANOVA comparing taxon abundance (expressed as percentage cover) and (b) two-way ANOVA comparing taxon abundance (expressed as counts) between gabion and seawall habitats across a range of time periods T₂, T₆, T₁₀ and T₁₂. **P < 0.01; *P < 0.05; ns, not significant.

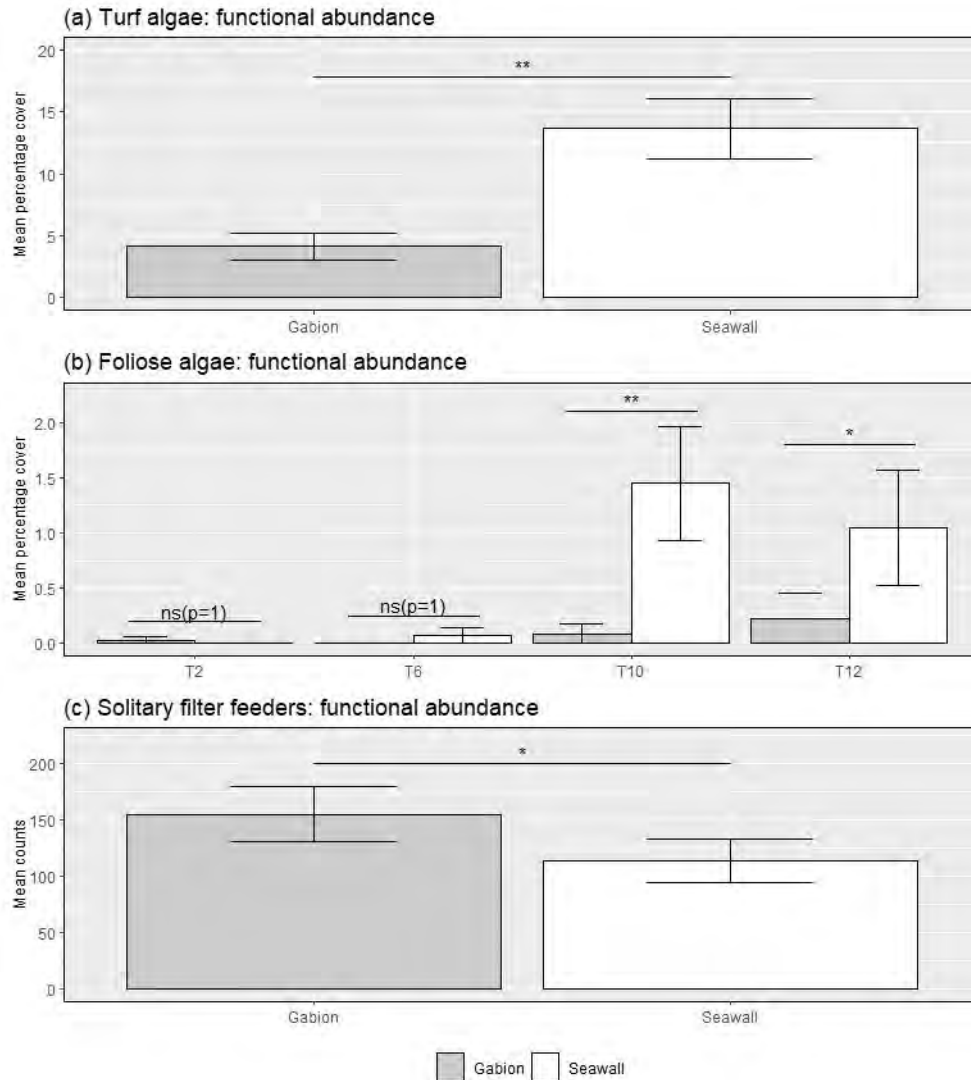
Univariate ANOVA of taxon abundance							
Source	(a) Percentage cover				(b) Counts		
	<i>df</i>	<i>MS</i>	<i>F</i>	<i>P</i>	<i>MS</i>	<i>F</i>	<i>P</i>
Habitat (Ha)	1	72.04	36.70	<0.01**	108.20	4.47	<0.04*
Time (Ti)	3	70.76	36.08	<0.01**	1088.50	45.01	<0.01**
Ha x Ti	3	3.44	1.76	0.16ns	51.90	2.15	0.09ns
Residuals	96	1.96			24.20		

Turf algae were significantly more abundant on seawall (13.62 % ± 17.7 % average cover) than gabion (4.15 % ± 7.88 % average cover) habitats (Table 3.4a, Fig. 3.4a).

There was a significant interaction between habitat and time for the foliose algae (Table 3.4a, Fig. 3.4b). There was significantly greater foliose algae abundance on seawalls at times T₁₀ ((1.44 % ± 1.85 %) vs (0.09 % ± 0.32 %) average cover) and T₁₂ ((1.05 % ± 1.88 %) vs (0.22 % ± 0.81 %) average cover) than on and amongst gabion habitats (Fig. 3.4b).

In contrast, gabions supported greater abundance of solitary filter feeders than seawalls ((154.63 ± 175.76) vs (113.36 ± 141.01) average counts; Table 3.4b, Fig. 3.4c).

There was no significant difference in abundance of encrusting filter feeders, encrusting algae, carnivores, herbivores and detritivores between gabion and seawall habitats (Table 3.4a,b).



1074

1075 Figure 3.4: Comparison of mean ($n = 13$, $\pm$ SE) functional abundance of (a) turf algae between
 1076 gabion (grey bars) and seawall (white bars) habitats at combined times T₂, T₆, T₁₀ and T₁₂; (b)
 1077 foliose algae between gabion (grey bars) and seawall (white bars) habitats amongst times T₂, T₆,
 1078 T₁₀ and T₁₂; and (c) solitary filter feeders in gabion (grey bars) and seawall (white bars) habitats
 1079 at combined times T₂, T₆, T₁₀ and T₁₂ recorded in Knysna Harbour. (ns = not significant; **P <
 1080 0.01; *P < 0.05.)

1081 Table 3.4: Two-Way ANOVA results for comparison of percentage cover abundance of (a) encrusting filter feeders, encrusting algae,
 1082 turf algae and foliose algae; and count abundance of (b) solitary filter feeders, carnivores, herbivores, detritivores between gabion
 1083 and seawall habitats across time periods T₂, T₆, T₁₀ and T₁₂. **P < 0.01; *P < 0.05; ns, not significant.

(a) Univariate ANOVA of functional group percentage cover

Source	Encrusting filter feeders				Encrusting algae			Turf algae			Foliose Algae		
	<i>df</i>	<i>MS</i>	<i>F</i>	<i>P</i>	<i>MS</i>	<i>F</i>	<i>P</i>	<i>MS</i>	<i>F</i>	<i>P</i>	<i>MS</i>	<i>F</i>	<i>P</i>
Habitat (Ha)	1	2.07	1.54	0.22ns	0.5	2.33	0.13ns	48.04	14.08	<0.01**	3.0	13.24	<0.01**
Time (Ti)	3	24.31	18.97	<0.01**	0.4	1.86	0.14ns	53.6	15.71	<0.01**	1.47	6.47	<0.01**
Ha x Ti	3	1.98	1.47	0.23ns	0.4	1.89	0.14ns	5.17	1.52	0.22ns	0.98	4.32	<0.01**
Residuals	96	1.35			0.21			3.41			0.23		

(b) Univariate ANOVA of functional group counts

Source	Solitary filter feeders				Carnivores			Herbivores			Detritivores		
	<i>df</i>	<i>MS</i>	<i>F</i>	<i>P</i>	<i>MS</i>	<i>F</i>	<i>P</i>	<i>MS</i>	<i>F</i>	<i>P</i>	<i>MS</i>	<i>F</i>	<i>P</i>
Habitat (Ha)	1	104.9	4.34	<0.04*	0.09	3.18	0.08ns	0.11	0.81	0.37ns	0.01	1	0.32ns
Time (Ti)	3	1095.7	45.38	<0.01**	0.04	1.29	0.28ns	0.14	1.1	0.35ns	0.01	1	0.4ns
Ha x Ti	3	52.7	2.18	0.09ns	0.04	1.29	0.28ns	0.02	0.18	0.91ns	0.01	1	0.4ns
Residuals	96	24.1			0.03			0.13			0.01		

3.3.4 Taxon and functional composition

There was a significant interaction between Habitat and Time for both taxon and functional compositions (Table 3.5). *Post-hoc* pairwise tests showed significant differences in taxon community composition (Table 3.5, Fig. 3.5) between gabion and seawall habitats. Similarly, pairwise tests revealed significant differences between habitats for times T₆, T₁₀ and T₁₂ (Fig. 3.5b,c,d), but not for time T₂ (Fig. 3.5a). Taxon composition within habitats became more varied over time (Fig. 3.5). SIMPER analysis identified fifteen taxa that were influential in separating taxon compositions between the gabion and seawall habitats (Table 3.6a). *Asparagopsis taxiformis* contributed to the greatest dissimilarity between habitats, being significantly more abundant on the seawall than gabion habitats (Table 3.6a). There was a significantly greater abundance of *Spirorbis*.sp, *Leucosolenia* sp., *Ciona intestinalis*, *Styela plicata* and *Amphibalanus* sp. on gabion than seawall habitats (Table 3.6a). There was a significantly greater abundance of *Trididemnum cerebriforme*, Serpulid sp.1, *Plocamium* sp., Alga sp.1., Sponge sp.3 on seawall than gabion habitats (Table 3.6a).

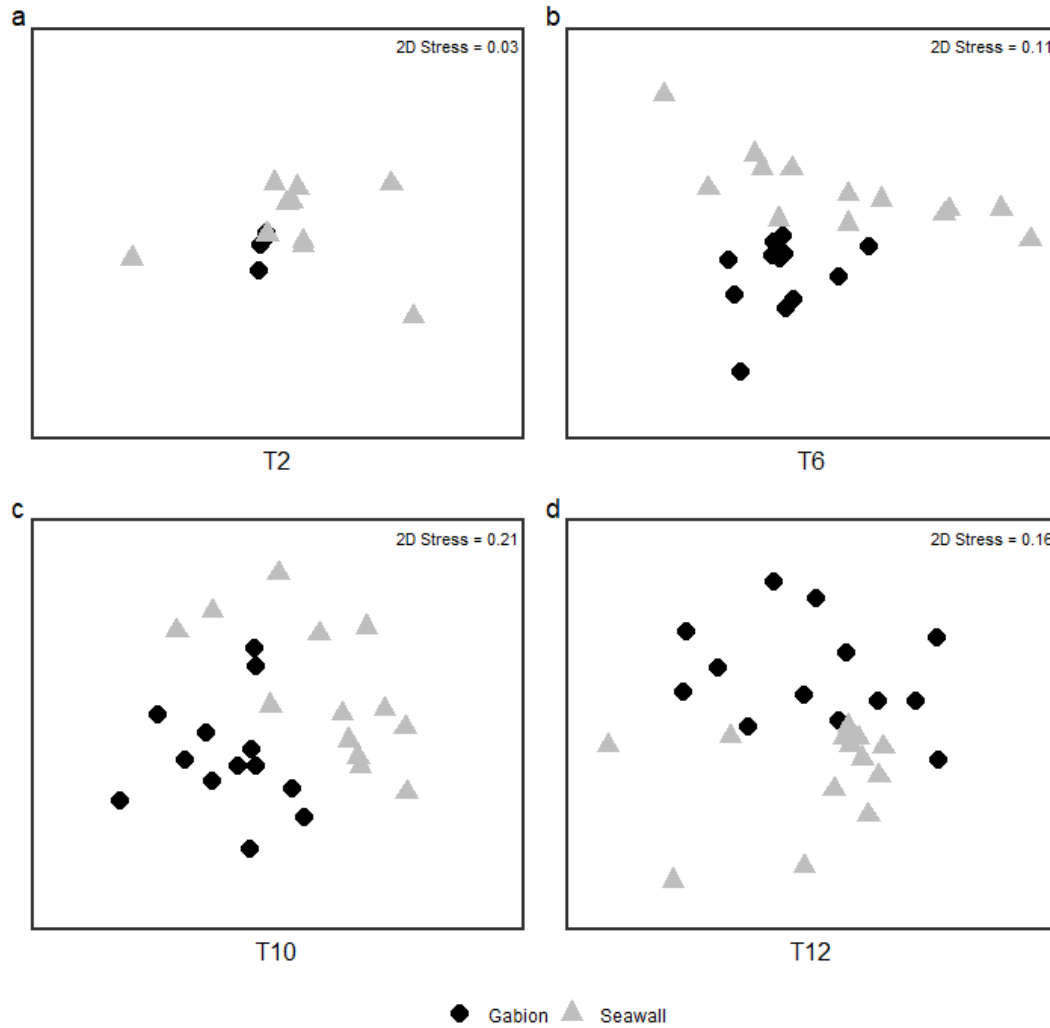
Post-hoc pairwise tests showed significant differences in functional community composition (Table 3.5; Fig. 3.6) between gabion and seawall habitats. There was little variance between habitats at times T₂ and T₁₀ (Fig. 3.6a,c), but functional composition varied more significantly at time T₆ and even more at time T₁₂ (Fig. 3.6b,d). SIMPER analysis identified four functional groups that were influential in separating functional compositions between habitats (Table 3.6b) of which only foliose algae was significantly different.

1105 Table 3.5: Results of permutational multivariate analysis of variance (PERMANOVA) for
 1106 differences in taxon and functional colonising organisms between gabion and seawall habitats
 1107 across a range of periods T₂, T₆, T₁₀ and T₁₂ recorded in Knysna Harbour. **P < 0.01; *P < 0.05;
 1108 ns, not significant.

Multivariate PERMANOVA of community composition

Source	Taxon				Functional		
	<i>df</i>	<i>R</i> ²	<i>F</i>	<i>P</i>	<i>R</i> ²	<i>F</i>	<i>P</i>
Habitat (Ha)	1	0.10	14.42	<0.01**	0.02	3.57	<0.04*
Time (Ti)	3	0.17	7.83	<0.01**	0.46	30.58	<0.01**
Ha x Ti	3	0.05	2.46	<0.01**	0.03	2.30	<0.04*
Residuals	96	0.68			0.58		
Total	103	1.00			1.00		

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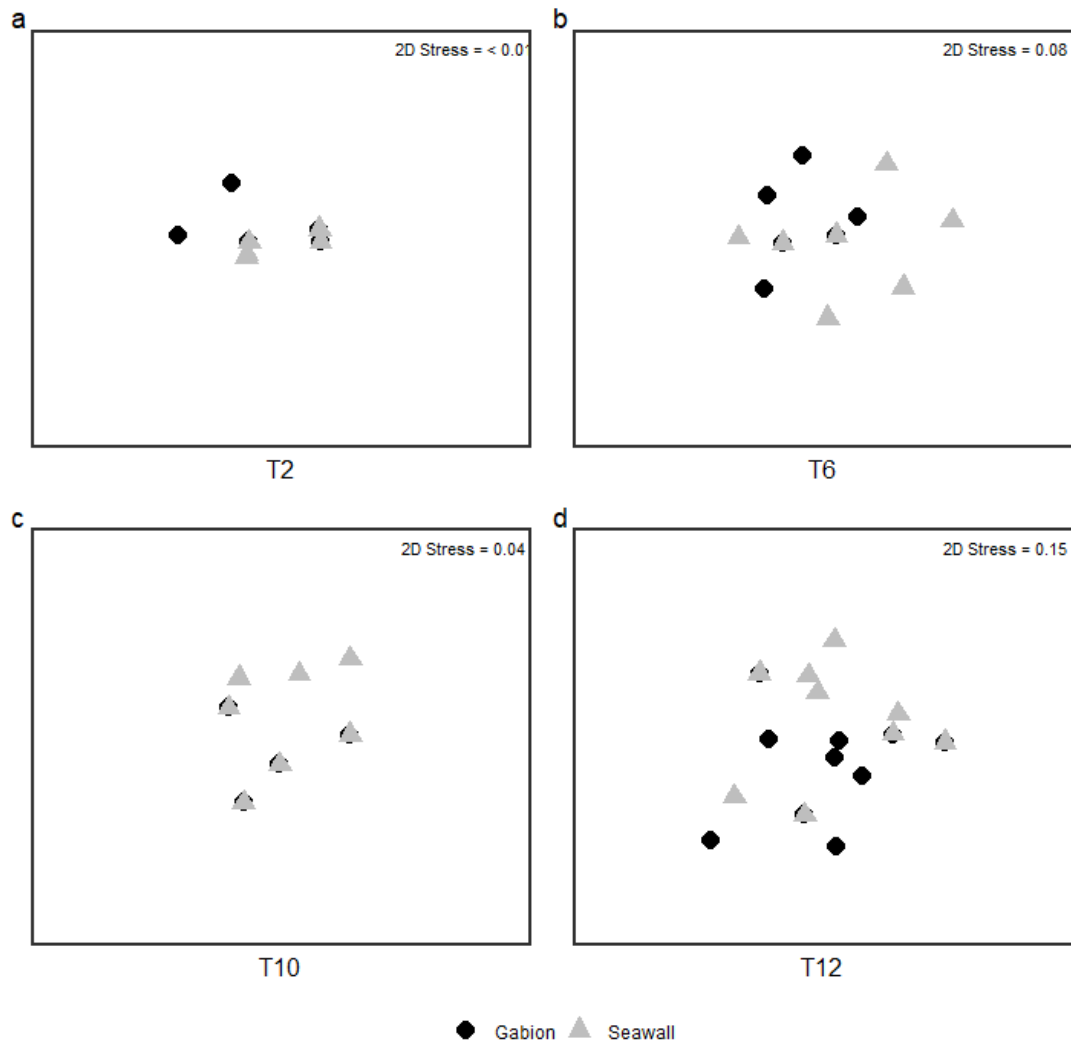
1111 Figure 3.5: nMDS ordination plots of taxon composition at times (a) T₂; (b) T₆; (c) T₁₀ and; (d)

1112 T₁₂ compared between the gabion (black circle) and seawall (grey triangle) habitats on Bray-

1113 Curtis transformed data.

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1117 Figure 3.6: nMDS ordination plots of functional composition at times (a) T₂; (b) T₆; (c); T₁₀ and;

1118 (d) T₁₂ compared between the gabion (black circle) and seawall (grey triangle) habitats on Bray-

1119 Curtis transformed data.

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1123 Table 3.6: SIMPER analysis outputting the contribution of dissimilarity between gabion and
 1124 seawall habitats of (a) taxon and (b) functional composition. Av.Abund: average abundance,
 1125 Cont.-%: contribution percentage, Cum.-% cumulative percentage contribution. Cumulative
 1126 contributions below 90% left out. **P < 0.01; *P < 0.05; ns, not significant.

SIMPER table of results of invertebrate and algae taxa groups					
	Gabion	Seawall			
(a) Taxon	<i>Av.abund A</i>	<i>Av.abund B</i>	<i>Cont.-%</i>	<i>Cum.-%</i>	<i>P</i>
<i>Asparagopsis taxiformis</i>	1.85	2.97	27.00	0.27	<0.01**
<i>Spirorbis</i> sp.	1.72	1.26	11.00	0.36	<0.01**
<i>Trididemnum cerebriforme</i>	1.08	1.51	8.00	0.44	<0.01**
<i>Serpulid</i> 1	1.13	1.59	7.00	0.51	<0.01**
<i>Leucosolenia</i> sp.	1.41	1.08	6.00	0.57	<0.01**
<i>Ciona intestinalis</i>	1.34	1.00	4.00	0.61	<0.01**
<i>Styela plicata</i>	1.31	1.06	5.00	0.66	<0.05*
Sponge.sp1.	1.07	1.25	4.00	0.70	0.09ns
<i>Clavelina lepadiformis</i>	1.23	1.15	4.00	0.74	0.54ns
<i>Diplosoma listerianum</i>	1.10	1.19	4.00	0.78	0.24ns
<i>Amphibalanus</i> sp.	1.23	1.00	2.00	0.80	<0.01**
<i>Plocamium</i> sp.	1.01	1.20	3.00	0.83	<0.01**
Alga.sp.1	1.00	1.16	3.00	0.86	<0.05*
<i>Parechinus angulosus</i>	1.14	1.00	1.00	0.87	0.056ns
Sponge.sp.3	1.01	1.12	2.00	0.89	<0.01**
	Gabion	Seawall			
(b) Functional	<i>Av.abund A</i>	<i>Av.abund B</i>	<i>Cont.-%</i>	<i>Cum.-%</i>	<i>P</i>
Turf algae	1.21	1.24	26.00	0.26	0.44ns
Solitary filter feeders	1.29	1.26	23.00	0.49	0.44ns
Encrusting filter feeders	1.31	1.33	18.00	0.67	0.53ns
Foliose algae	1.02	1.28	17.00	0.84	<0.01**

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3.4. Discussion

In this experiment we deployed 13 gabion habitats throughout Knysna Harbour alongside the concrete seawall in the subtidal zone of the system. We hypothesised that gabions would support greater diversity of colonising organisms than the seawalls, due to increased habitat complexity (in the form of added surface area). The study found that after 12 months a total of 37 species had colonised the habitats (32 on gabions and 26 on seawalls) and that there was a greater taxon richness and diversity of colonising organisms on gabions than seawall habitats (as hypothesised). The gabions had a major effect on the subtidal taxon diversity by increasing the number of species of invertebrates that are found colonising the Knysna Harbour, which is typical of complex artificial structures (Chapman & Blockley, 2009; Perkol-Finkel *et al.*, 2018). The effect on the diversity of functional groups between the two habitats was less significant than predicted.

Many other studies have also investigated the invertebrate diversity on artificial structures in estuaries, for example, Chapman & Clynick (2006), demonstrated that waste materials in estuaries sustained diverse faunal assemblages. Similarly, Barnes *et al.* (2022), studied the macrobenthic biodiversity between natural channels and marina canals in Knysna, South Africa and reported higher species richness and abundance within the artificial canals. Results of which were in line with the present study where the gabions were covered by a variety of polychaetes, sponges, tunicates, bryozoans while the seawalls were covered in a similar but lower diversity composition of species. Similar diversities of species have also been recorded colonising artificial structures (Chapman & Clynick, 2006), pilings and natural reefs in Sydney

1151 Harbour (Connell & Glasby, 1999). Diversity of polychaetes, crustaceans and the bivalve *Perna*
1152 *perna* was greater on the gabions which therefore had the desired effect of increasing the
1153 diversity of species to those on the seawalls. This is similarly seen in other studies that
1154 compared various altered structures to seawalls (Chapman, 2003; Martins *et al.*, 2007;
1155 Chapman & Blockley, 2009; Firth *et al.*, 2014b). In order to combat biotic homogenisation and
1156 biodiversity loss in coastal development projects, it is important to consider interventions that
1157 promote higher diversities of species such as these gabions.

1158 The gabions were also characterised by a larger number of habitat-forming species such as
1159 barnacles, these organisms act as ecosystem engineers (Jones *et al.*, 1994), by increasing the
1160 complexity and habitat availability for fish and other mobile invertebrates (Perkol-Finkel &
1161 Sella, 2015). Results from chapter 2 suggest that the types of crypto-benthic fish utilising these
1162 structures may be benefiting from the habitat-forming species and increased habitat
1163 complexity that the colonised organisms on the gabions provided.

1164 It is common for encrusting invertebrates (such as sponges and some ascidians) to settle and
1165 survive on artificial structures, such as flat seawalls, whilst species such as solitary filter feeders
1166 need more complex surfaces to survive (Walter & Wetthey, 1996). Many of the species that
1167 recruited onto the gabion habitats were solitary tunicates, these are filter feeding organisms
1168 which are known to contribute to the improved quality of water (Perkol-Finkel & Sella, 2015).
1169 Suggesting that the increase in habitat complexity promoted the settlement of species that
1170 filter water and provide an ecosystem service. While seawalls were characterised by greater
1171 abundance of encrusting organisms (which are also filter feeders), this was largely attributed to
1172 the cover of algae, particularly *Asparagopsis taxiformis*. *Asparagopsis taxiformis* is known to

1173 have inhibitory properties against fouling organisms (Manilal *et al.*, 2010), which would have
1174 impacted settlement by other invertebrates on the seawalls.

1175 The gabion community consisted of more carnivores, detritivores and herbivores than the
1176 seawall habitats. A notable carnivore found only in the gabions was the common octopus
1177 (*Octopus vulgaris*) which is typically found seeking refuge in sheltered areas such as rocky
1178 shores (Kayes, 1973), suggesting that the gabions provided safe habitat. The other functional
1179 groups are species that do not require such a specific habitat type but may have been found on
1180 the gabions due to higher availability of food. For example, the detritivores (*Palaemon*
1181 *peringueyi* and *Ophiothrix fragilis*) which were only found on the gabions due to the structure
1182 possibly acting as a sink for detritus compared to the flat seawalls.

1183 Chapman & Clynick (2006), suggested that the number and type of species observed within
1184 different artificial habitats are influenced by the quantity and type of microhabitats that these
1185 habitats/structures provide. Invertebrates that have small areas of attachment, including
1186 solitary tunicates and barnacles, are likely to be associated with complex habitats that offer pits
1187 and crevices whereas encrusting invertebrates are able to settle onto a wider variety of
1188 structures (Walters & Wethey, 1996), which was observed in the present study. The lower
1189 number of taxa recorded on the seawalls can therefore, likely be attributed to a lack of
1190 available microhabitats (Connor & McCoy, 1979). The porosity and three-dimensional structure
1191 of the gabions likely translates into a much larger area available to colonise which may provide
1192 better habitat for species than the non-porous seawall (Sherrard *et al.*, 2016). Hunter & Sayer
1193 (2009), found higher abundances of crustacean species in complex artificial modules in

1194 comparison with simple modules. Complexity aids in determining composition on artificial
1195 structures (Andersson *et al.*, 2009; Coombes *et al.*, 2015), and the current study is no exception.
1196 Gabions offer more complexity than seawalls and already consist of rock pools, pits and
1197 crevices which are absent from the seawalls. Although the structural complexity plays an
1198 important role in determining the community composition of epibiotic communities, biotic
1199 factors such food availability, interaction between species (Jones, 1948; Southward, 1964), and
1200 competition (Connell, 1961; Paine, 1974), also influencing their structure.

1201 A total of seven non-native species were observed on the gabion and five on the seawall
1202 habitats. Overall, the ratio of native to non-native species on the gabion habits (7 out of 32) was
1203 lower than that recorded on the seawall (5 out of 26). It is well documented that alien
1204 invertebrates colonise artificial structures, in particular, harbours and marinas where they are
1205 transported via boat and ship ballast water (Firth *et al.*, 2011; Airoidi & Bulleri, 2011; Firth *et al.*,
1206 2016a). There were a number of common invasives between the habitats; *C. lepadiformis*, *M.*
1207 *squamiger*, *S. plicata* and *D. listerianum*, all of which are ascidians. The introduction of non-
1208 indigenous ascidians is common and is increasing in coastal areas around the world, often
1209 establishing themselves in harbours (Lambert & Lambert, 1998; Coles *et al.*, 1999), and at rapid
1210 rates due to them attaining sexual maturity within a few weeks of establishment, minimising
1211 Allee effects (Lambert, 2001, 2002). Their presence may cause problems by competing and
1212 interfering with native fauna that do not settle as rapidly (Lambert & Lambert, 1998; Lambert,
1213 2001).

1214 Despite the greater ratio of alien species to native species on the seawalls, a number of alien
1215 species were only found on the gabions (*W. subtorquata* and *C. intestinalis*). *Watersipora*
1216 *subtorquata* is a highly successful cryptic invader common along coastlines around the world
1217 (Ryland *et al.*, 2009). It has been found on settlement collectors in Sri Lanka where it facilitates
1218 the settlement of other biofoulers and poses a significant threat to native biota through
1219 interspecific competition (Marasinghe *et al.*, 2018). Blum *et al.* (2007), found that higher
1220 abundances of *Ciona intestinalis* was correlated with lower species richness of sessile
1221 invertebrates. Although these two species were only present on the gabions, they were not
1222 associated with lower diversities of invertebrates.

1223 Mancuso *et al.* (2021), found that *A. taxiformis* in the Mediterranean Sea caused an entire
1224 habitat shift in rocky shore habitats through a bottom-up effect by reducing the biodiversity
1225 and ecosystem services provided by the habitat after invasion. *Asparagopsis taxiformis*, first
1226 noted in the Knysna Estuary in 2009 (Bolton *et al.*, 2011), covers an area of 41.3 ha in the
1227 Knysna Estuary (Wasserman *et al.*, 2020), and is an extremely successful invader that may be
1228 placing high pressure on the natural *Zostera capensis* seagrass beds (Williams & Smith, 2007;
1229 Maggi *et al.*, 2015). The high abundance of this species on the seawalls indicates the potential
1230 for this habitat assisting in the reproduction and continued successful invasion of *A. taxiformis*
1231 in the Knysna Estuary as well as limiting attachment opportunities for native invertebrates.

1232 Several studies have observed a greater ratio of non-native species on control seawall plots
1233 compared to eco-engineered solutions (Perkol-Finkel *et al.*, 2017; Hall *et al.*, 2019). The
1234 colonisation by non-native species on artificial structures is a major driver of biotic
1235 homogenisation and loss of biodiversity within these systems (Mineur *et al.*, 2012; Simkanin *et*

1236 *al.*, 2013). Eco-engineering may, therefore, mitigate biological invasions since they sustain a
1237 more biodiverse community of species (Firth *et al.*, 2016a), than sea walls (Stachowicz *et al.*,
1238 2002; Arenas *et al.*, 2006). The gabions in the present study, while still being hosts to invasive
1239 species, are hosting more numbers of native species thus promoting greater biodiversity of
1240 colonising organisms. Adding gabion structures to harbours could be beneficial for the
1241 conservation of native species in artificial habitats but may not fully mitigate biological
1242 invasions.

1243 Species richness was lower on gabions in the beginning of the study (time T₂) but increased and
1244 superseded that of the seawalls later into the study. Perkol-Finkel *et al.* (2017), observed this to
1245 be the opposite in their study where recruitment occurred to their control sites at a slower rate
1246 than to their ECO panels. Colonisation to the seawalls and gabions may have been differently
1247 affected by the influence of recruitment from their proximity to the unscraped seawall, the
1248 gabion boxes were next to but not touching the seawall whilst the seawall habitats were
1249 directly touching, indicating that there was less spatial connectivity between gabions and
1250 surrounding seawalls which may influence patterns of recruitment (Cowen & Sponaugle, 2009;
1251 Herbert *et al.*, 2017). Despite this, the gabions still supported a greater taxon richness and
1252 diversity. Chapman *et al.* (2008), observed that artificial structures placed directly on
1253 substratum or placed on a rack on substratum may slightly influence the animals recruited to
1254 these structures. Colonisation takes place either through the water column, over the
1255 substratum or through a combination of both (Negrello Filho *et al.*, 2006; Chapman *et al.*,
1256 2008). Recruitment patterns to the gabion habitats followed similarly known trends where the
1257 first colonisers were biofilms followed by later colonisers being barnacles, mussels and foliose

1258 algae, while the seawalls were initially colonized by biofilms and followed by the colonization of
1259 algae and encrusting species. These early successional processes and settlement of early
1260 taxonomic groups may be what causes temporal differences in species assemblages and
1261 diversity (Moschella *et al.*, 2005; Perkol-Finkel *et al.*, 2018).

1262 Gabions are a millenia-old invention that have stood the test of time as an engineering
1263 approach in coastal habitats and are a well-researched structure that are relatively cheap to
1264 develop and widely available (Brand, 1992; Mohamed, 2010; Chen & Tang, 2012; Toprak *et al.*,
1265 2016). So instead of reinventing the wheel, why not focus ecological engineering projects on
1266 structures that already exist and can be utilised to increase biodiversity and protect species of
1267 commercial and conservation concern in harbours and other coastal development projects?
1268 Whilst they may be commonly used in engineering, there have been very few studies that have
1269 tested them as an ecological engineering approach. Firth *et al.* (2014b), tested the use of
1270 different sized rocks in gabions for invertebrate colonisation. Claassens *et al.* (2018), found that
1271 gabions and reno mattresses offered an alternative habitat for the Knysna Seahorse in Thesen
1272 Islands canals and de Villers *et al.* (2021), compared faunal assemblages between reno
1273 mattresses, used as erosion control structures, to natural seagrass beds; reporting that they
1274 hosted species analogous to rocky shore habitats. Chapter 2 of the present study found that
1275 gabions supported higher diversity and abundance of fish species than seawalls and hosted
1276 more species of conservation concern compared to seawalls. These few examples demonstrate
1277 the possibility for considering gabions in future ecological engineering practices to achieve
1278 reconciliation ecology.

1279 This study demonstrates the possibility for achieving various management goals through
1280 ecological engineering projects that enlist the collaboration of ecologists, engineers and local
1281 government to produce cheap engineering that can add value to artificial habitats. Results of
1282 this study suggest that gabion structures have the potential to increase the biodiversity of
1283 marine species in harbours and promote a more holistic approach to harbour design. The more-
1284 complex gabion habitats can create a variety of habitats which are otherwise absent from
1285 seawalls. This study showcases the potential for replacing seawall habitats with gabions to
1286 promote reconciliation ecology whilst maintaining the structural integrity of coastal marine
1287 structures for urban waterfronts. It is important to consider what ecological engineering
1288 interventions can be applied to sustain biodiversity in urban environments where there is no
1289 hope of returning a habitat to its pristine state (Chapman & Blockley, 2009; Hawkins *et al.*,
1290 2020). Gabions should be considered in maintenance or extension of existing, and new coastal
1291 development projects, where there is a similar environmental setting, as an alternative to
1292 seawalls.

1293

Chapter 4

General discussion

4.1. Synthesis

Coastlines and estuaries are focal points for development worldwide (Ma *et al.*, 2014; Popkin, 2015; Waltham & Sheaves, 2015). The increased use of artificial structures can have both positive and negative impacts on the fauna and flora living within these coastal zones (Duarte *et al.*, 2012; Bishop *et al.*, 2017; Heery *et al.*, 2017). Estuarine ecosystems are continually being developed with soft-bottomed ecosystems, such as saltmarshes, often being converted into hard artificial habitats (Able *et al.*, 1999; Airoidi & Beck, 2007; Lai *et al.*, 2015). Harbours and marinas in estuaries typically host different invertebrate and vertebrate communities compared to neighbouring natural ecosystems (Chapman, 2003; Moreira, 2006; Chapman *et al.*, 2018). Moreover, these structures typically sustain higher abundances of invasive and non-native species (Floerl & Inglis, 2005; Floerl *et al.*, 2009). The present study investigated the taxonomic and functional differences in fish and colonising organism diversity and composition between a pre-existing seawall and several deployed gabion boxes in Knysna Harbour in the Knysna Estuary in South Africa. It was assumed that differences in the habitat structure of the gabions and existing seawall would provide very different habitat opportunities for marine organisms. The present study found distinct differences in richness, diversity, abundance and composition in the fauna between gabion and seawall habitats (see Fig. 4.1 summary). Moreover, gabions also supported a few species of fish listed in the IUCN Red List of Endangered Species that were not present in the seawall habitats (Fig. 4.1).

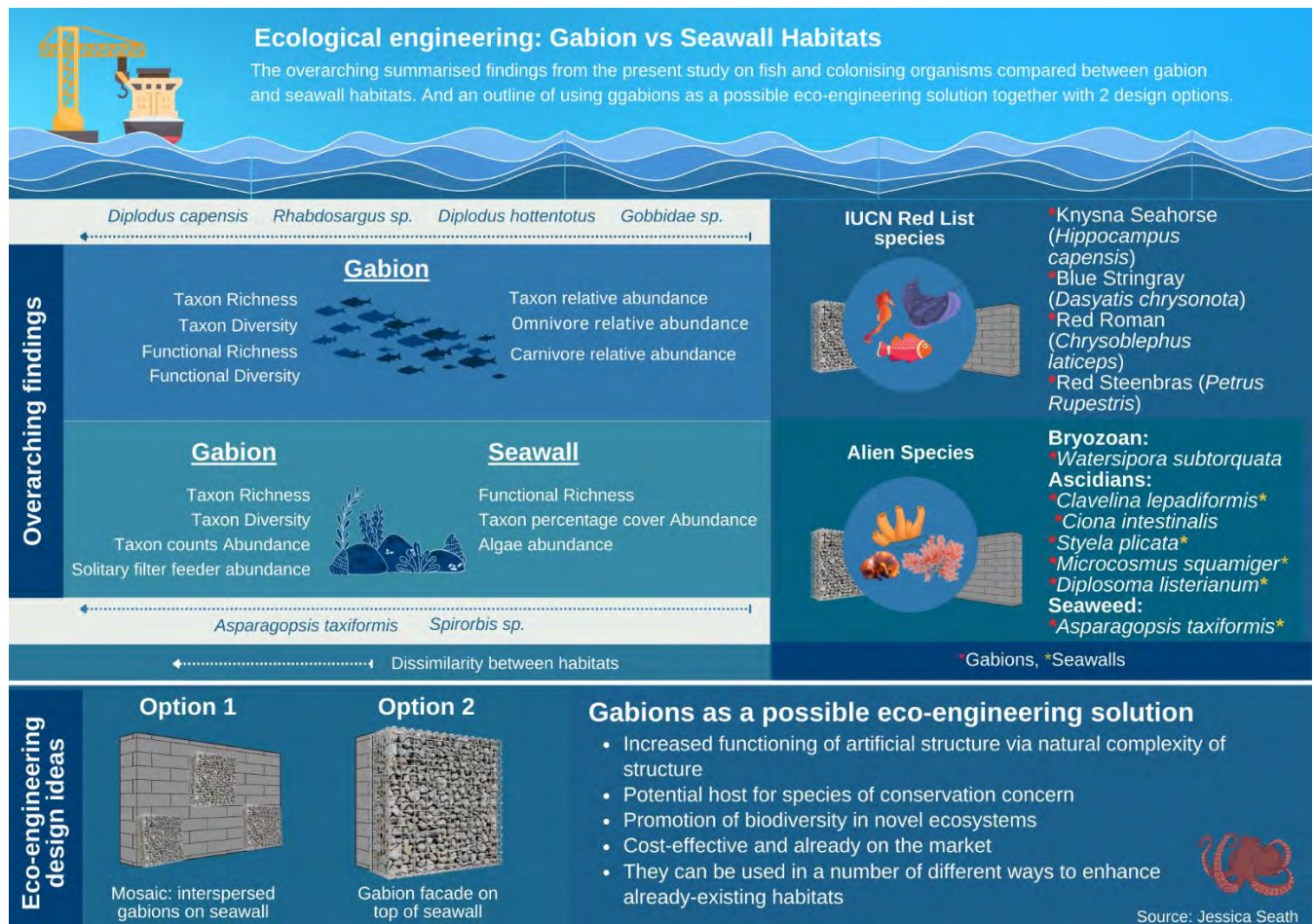


Figure 4.1: A graphical representation of the overarching findings from chapters 2 and 3 of the present study. The summarised results of univariate parameters shows whether measures were more significant on gabion or seawall habitats. Multivariate measures show which taxa contribute the most to dissimilarity between the habitats. Included is the species found on the IUCN Red Data List of Threatened Species and the alien species observed. At the bottom is a summary of the potential for using gabions and an eco-engineering solution.

1327 Gabions employed to stabilise foreshore environments are structurally more complex than
 1328 seawalls and can be effective in providing habitat for fish and invertebrate communities as
 1329 demonstrated in the present study. One of the key considerations in selecting the type of
 1330 artificial structure to develop with, if the goal is also the ecological efficacy of a development, is
 1331 the complexity of a structure (Knott *et al.*, 2004; Moschella *et al.*, 2005; Chapman &
 1332 Underwood, 2011). de Villiers *et al.* (2021), found that the reno mattresses (flattened gabions)
 1333 used to combat coastal erosion in the nearby Keurbooms Estuary in South Africa supported reef
 1334 associated fish and rocky shore invertebrates. The present study found a number of fish species
 1335 unique to the gabion habitat (blennies, double-sash butterfly fish, two-tone fingerfin, a goby,
 1336 chubby clingfish, cape moony, barred fingerfin, fransmadam, red roman, streepie and the
 1337 Knysna seahorse), which are also typically associated with rocky shores and coral reefs; habitats
 1338 characterised by their natural complexity. No unique fish taxa were observed on the seawall,
 1339 suggesting that the gabions may have complexity similar to that of natural ecosystems which
 1340 seawalls lack.

1341 Selfati *et al.* (2018), demonstrated how they could use their 'biohuts' to create small marine
 1342 reserves and assist in the long-term recovery of the endangered dusky grouper as well as acting
 1343 as ready-made nursery areas for this species' conservation. Lai *et al.* (2015), undertook a study
 1344 to describe the effects of urbanisation on the extensively developed Singapore coastline, which
 1345 is extensively altered, and are using ecological engineering concepts to guide urban marine
 1346 conservation in these areas. There are many other examples of artificial structures being
 1347 deployed/constructed which support species of conservation concern including fucoid
 1348 macroalgae ((e.g. *C. barbata* (Perkol-Finkel *et al.*, 2012), molluscs (e.g. *P. ferruginea* (Garcia-

Gomez *et al.*, 2014)), and fish (e.g. *H. brevirostris* (Garcia-Gomez *et al.*, 2014)). Further to this, a number of ecological engineering projects have had unintended positive outcomes for species of conservation concern. Seawalls in the port of Ceuta, North Africa have become an important refuge for the endangered limpet, *Patella ferruginea* from human harvesting (Rivera-Ingraham *et al.*, 2011). Similarly, Claassens & Hodgson (2018), found that the reno mattresses in Thesen Islands canals in the Knysna Estuary were beneficial for the Knysna seahorse (*H. capensis*) as they provided an important additional habitat for this species. In the present study, a number of endangered species including the Knysna seahorse, were making use of the gabion habitats (Fig. 4.1). This study has thus added to the growing body of evidence in South Africa for gabions supporting seahorse populations. Further, it has demonstrated the potential for using gabions to promote species of conservation concern. Coastal infrastructure that supports species of conservation concern (see Firth *et al.*, 2016a and Ostalé-Valriberas *et al.*, 2022 for reviews), should be used to for the enhancement of populations (e.g. Martins *et al.*, 2010; Langhamer & Wilhelmsson 2009).

It is vital to consider the potential for creating ecological traps when using artificial structures for conservation of habitats and specific species (Komyakova *et al.*, 2022; Marangoni *et al.*, 2022). Ecological traps are a phenomenon where animals become more attracted to poor-quality habitats which may eventually affect their fitness (Komyakova & Swearer, 2019; Swearer *et al.*, 2021). This may be more common in the marine environment than previously thought, Komyakova *et al.* (2021), assessed artificial reefs as ecological traps and demonstrated how a number of species associated with artificial reefs experiencing increased mortality rates and

1371 higher fitness. Swearer *et al.* (2021), discusses methods to be used to understand ecological
1372 traps and how this information can be used to improve management of marine environments. It
1373 is imperative to consider the impact of using artificial habitats for conservation purposes and
1374 the effect on the fitness of organisms. The present study did not directly study ecological traps
1375 but notes that the threatened species utilising the gabions may be selecting these sites over
1376 their natural habitats which could possibly lead to reduced fitness in these already vulnerable
1377 species. The Knysna Seahorse, for example, could experience greater exposure to predators
1378 because they do not camouflage into the gabions the same way they would their natural
1379 eelgrass habitats. Whilst endangered fish might choose this habitat whose poor water quality,
1380 for instance, may endanger the fish's reproductive capability. Therefore, it is important to note
1381 that gabion habitats cannot act as a surrogate for natural habitats and should only be
1382 considered when development has already been approved (Firth *et al.*, 2020), ideally only in
1383 ecosystems that have already been highly modified (O'Shaughnessy *et al.*, 2020), or as part of
1384 restoration of redundant structures and basins post-industrialisation (Geist & Hawkins *et al.*,
1385 2016; Hawkins *et al.*, 2020).

1386

1387 Whilst the current study did not consider/compare the food web structure, the functional
1388 feeding group composition, particularly the fish, does provide insights into trophic interactions
1389 between the two habitats. The most represented functional feeding group of fish in the gabion
1390 habitats were carnivores, suggesting that the structural complexity of the gabions can sustain
1391 high numbers of potential prey including zooplankton, polychaete worms and solitary tunicates.
1392 By contrast, the most common functional feeding groups of fish in the seawall habitats were

1393 omnivores which were likely sustained by algae and encrusting species. Pointing to functional
1394 differences in the two habitats being compared. Algae was more prevalent on seawalls which
1395 suggests greater primary production taking place in this habitat. Generally, however, algae do
1396 better on horizontal or gently sloping surfaces due to propagule attachment, but this was not
1397 observed in the present study. Several studies have demonstrated the complex nature of
1398 predator-prey relationships in marine food webs in natural ecosystems (Orth *et al.*, 1984;
1399 Fernandez-Betelu *et al.*, 2022), but the abundance of predators may differ between natural and
1400 artificial habitats (Forrest *et al.*, 2013a,b), thus impacting grazing pressure and the successful
1401 establishment of certain epibiotic communities in artificial habitats. When considering the
1402 success of different eco-engineering interventions, one may only focus on the functional value
1403 of organisms or assemblages (Strain *et al.*, 2018a), or the focus on individual target species of
1404 conservation (Perkol-Finkel *et al.*, 2012), or commercial concern (Langhamer & Wilhelmsson,
1405 2009). But it may also be important to consider the multi-functional objectives that include a
1406 mixture of community-level and species-specific targets (Evans *et al.*, 2021), to achieve
1407 reconciliation ecology.

1408

1409 The proliferation of invasive species is a key anthropogenic driver of global biotic
1410 homogenisation (Glasby *et al.*, 2007; Dafforn *et al.*, 2012; Airoidi *et al.*, 2015), loss of
1411 biodiversity and economic loss (Pimental *et al.*, 2005). It is, therefore, imperative to consider the
1412 possible role of eco-engineering projects in promoting biological invasions (Dafforn, 2017). It is
1413 now well-known that artificial structures support higher numbers of invasive species than
1414 neighbouring natural habitats (Glasby *et al.*, 2007; Dafforn *et al.*, 2009, 2012; Mayer-Pinto *et al.*,

2018). In the present study, the ratio of invasive colonising organisms to native species on the seawall habitat was greater than that on the gabions. This finding is in agreement with the study by Perkol-Finkel *et al.* (2018), who observed a lower ratio of invasive to native species on their ECO panels than control seawall plots. Artificial structures lacking structural complexity such as seawalls often have lower abundances of natural predators (Chapman, 2003; Chapman & Blockley, 2009), which may facilitate the establishment of non-indigenous species (Perkol-Finkel *et al.*, 2018).

There is a data-deficiency on alien invertebrate species in South African estuaries (van Wilgen & Wilson, 2018). However, Griffiths *et al.* (2009), documented 22 marine alien species with well-established populations along the South African coastline. The majority of these species are found in sheltered areas such as bays and harbours. Of these species, only three are known as invasive, having spread significantly beyond their point of origin. One of these being the North-east Atlantic and Mediterranean mussel, *Mytilus galloprovincialis*, which has been found in the Knysna Estuary extending from the mouth up to 12 km up stream on rocky shores and man-made structures (Pollard & Hodgson, 2016). However, this species was not present on either seawalls or gabions in Knysna Harbour, despite the low wave action and sheltered nature of this habitat. Of the 22 marine alien species documented by Griffiths *et al.* (2009), four were found in the present study; *Ciona intestinalis*, *Clavelina lepadiformis*, *Diplosoma listerianum* and *microcosmos squamiger* (Fig. 4.1). All were already present and previously described in the Knysna Estuary. The only species with a known significant economic impact is *C. intestinalis* which reduces the growth rate of mussels and fouls equipment (Griffiths *et al.* 2009). It's presence in the gabion structures (Fig. 4.1), may proliferate into nearby equipment and ropes

1437 and impact maritime processes. The present study found much higher abundances of the
1438 invasive algal species *A. taxiformis* in the seawall habitats, which is also present throughout the
1439 Thesen Island canals in Knysna Estuary (Claassens, 2016). It's impact on the ecology of this
1440 system is not known. There needs to be more monitoring and control of introduced and alien
1441 species along South African coastlines (Van Wilgen & Wilson, 2018), as well as a review of the
1442 extent of these invasions on artificial structures. An understanding of their impact on native
1443 species can be used to guide ecological engineering design if looking to mitigate biological
1444 invasions and promote native species establishment in coastal development projects. The
1445 gabions deployed in Knysna Harbour have shown that adding/replacing these structures in
1446 place of seawalls will not fully help mitigate biological invasions but by promoting the
1447 colonisation of more native species might promote greater biodiversity in an artificial system.
1448 The absence of *M. galloprovincialis* on the gabions, meant that there was more available space
1449 for the brown mussel *Perna perna* which settled only on the gabion habitats. *Perna perna* is an
1450 engineer species that provides vital ecosystem services, sustains high diversity of associated
1451 organisms and participates in the food web as prey (Lathlean & McQuaid, 2017; Vaughn &
1452 Hoellein, 2018). It helps form substrate so that it can act as a biodiversity hotspot, and nursery
1453 ground for a variety of species (Lathlean & McQuaid, 2017). It is an important filter feeder and
1454 regulates nutrient availability control (Lathlean & McQuaid, 2017; Vaughn & Hoellein, 2018).
1455 While not enough is known from this particular study about the organisms associated with *P.*
1456 *perna* patches, the presence of the mussel only on the gabion habitats would have had bottom-
1457 up effects on the establishment of the more diverse communities of both fish and invertebrate
1458 species observed within the gabion habitats. It was one of the many habitat-forming species

1459 found on the gabions (including barnacles and tube-sponges), which contribute to biogenic
1460 buildup, both strengthening the structure it is attached to and speeding up succession (Strain *et*
1461 *al.*, 2017).

1462

1463 The interpretation of ecological engineering studies are often limited due to small sample size,
1464 absence in the consideration of geographic variability, short duration, and lack of on-going
1465 monitoring (Perkol-Finkel *et al.*, 2012; Sheehan *et al.*, 2013; Ng *et al.*, 2015; Firth *et al.*, 2020).
1466 Because one eco-engineering study may have worked using one approach, does not always
1467 mean it is going to work in another setting. Firth *et al.* (under review), recommends that in
1468 order to address these concerns, experiments need to be bigger and better going forward; this
1469 includes going beyond measuring simple biodiversity metrics (O'Shaughnessy *et al.*, 2023), and
1470 starting to measure ecosystem functioning together with socio-economic metrics. There have
1471 been very few studies that have focused on ecological functional traits which includes fitness
1472 and reproduction (but see Espinosa *et al.*, 2020; Sedano *et al.*, 2020a; Raoux *et al.*, 2022). In the
1473 present study, observations were made of functional responses related to reproduction. There
1474 was evidence of invertebrate eggs (e.g. nudibranch and sea hare eggs) on both gabion and
1475 seawall habitats, with more being observed in the gabion habitat, which might result from the
1476 increased amount of surface area available for mobile species to lay eggs. Of the eggs observed
1477 only in the gabions, cuttlefish (from the patchwork cuttlefish *Sepia vermiculata*) eggs were
1478 found on a number of different gabion boxes. Additionally, a few of the Knysna Seahorses were
1479 observed to be pregnant. This might point to the gabions' capacity to enhance multiple facets of
1480 biodiversity, population processes such as reproductive output of target species as well

1481 ecosystem functioning in general, thereby supporting ecosystem services, whilst also mitigating
1482 common impacts and stressors in urban coastal environments (Pioch & Souche, 2021). These
1483 multiple of gabions benefits require further holistic research.

1484 Furthermore, Firth *et al.* (under review), recommends returning to projects after the initial
1485 intended lifespan, repeating them in the same location under different environmental
1486 conditions as well as in different locations. There is therefore not always sufficient information
1487 available to make recommendations in certain areas and on a large scale, however, you can
1488 draw on the information that is available (Evans *et al.*, 2019). A growing number of studies have
1489 included repetition in a number of environmental and geographic settings that have led to large-
1490 scale interventions (see World Harbour Project, 2018; Ecostructure, 2019; Living Seawalls, 2019;
1491 Strain *et al.*, 2021; Clifton *et al.*, 2022). Experiments that have been replicated across different
1492 spatial scales have found that interventions are very context dependant and produce results
1493 that range from positive to negative (Strain *et al.*, 2021; O'Shaughnessy *et al.*, 2021; Clifton *et*
1494 *al.*, 2022). For example, Perkol-Finkel & Sella (2014), found the pH of concrete to play an
1495 important role in determining biodiversity in the Red Sea and Mediterranean Sea near Ashdod,
1496 Israel, whilst Hsiung *et al.* (2020), found this not to be the case in Plymouth in the UK and at
1497 Pulau Hantu and Pulau Seringat in Singapore. The present study, although conducted over the
1498 period of a year (four seasons), was limited to a small harbour in South Africa. These data can
1499 be used to guide future research but is insufficient to recommend using gabions instead of
1500 seawalls in other harbour settings. Further than the environmental and geographical
1501 considerations, different legislation for development occurs in different countries.

1502

4.2. Management

South Africa has introduced a wide range of environmental legislation around coastal development practices including the National Environmental Management Act (Act No. 107 of 1998) & Integrated Coastal Management Act, 2008 (ICM Act No. 24). The legislation aims to stop unwarranted, unsustainable development of the coastal environment (i.e. development must ensure social and ecological sustainability). Further to this, each estuary must have a location specific Estuarine Management Plan. Despite these regulations, there is still a lack of enforcement and compliance at a national level (Adams *et al.*, 2020). The implementation of the *Integrated Management Act* (RSA, 2009), has had both positive and negative impacts; it has improved the way construction is implemented, however, because landowners cannot carry out their own maintenance, their properties are at risk; there has also been continued encroaching of the coastal environment by development despite the *Integrated Management Act* (RSA, 2009). This points to the need for holistic management to be regarded in both small and large-scale future coastal development projects.

O'Shaughnessy *et al.* (2020), proposed several steps that need to be followed when a decision about building, modifying or removing a structure in the marine environment occurs. This includes consultation with local government and stakeholders, conducting an Environmental Impact Assessment (if necessary), obtaining a licence for the work, checking if water quality monitoring is in place, considering the secondary management goals, scheduling maintenance work around ecologically sensitive seasons and determining the type of artificial structure to be used. It is, therefore, critical when selecting an eco-engineering intervention that the physical (e.g. storm frequency, wave action, tidal difference, sediment loading, turbidity), biological (e.g.

1525 larval supply, proximity to invasive species, potential colonising species) and chemical factors
1526 (e.g. pollution loading, nutrient supply and salinity regime) (O'Shaughnessy *et al.*, 2020) be
1527 considered. This procedure is a requirement in South Africa, but there is a lack of follow-
1528 through. To maximise the outcomes of the eco-engineering installations, it is important for
1529 engineers and developers to engage with ecologists, oceanographers and relevant experts to
1530 ensure successful deployment and ecological success of the structures. These guidelines need
1531 to be considered when designing environmentally sensitive developments in coastal regions. In
1532 order to inform sound eco-engineering practice, wider testing in different environmental
1533 settings needs to occur (Airoidi *et al.*, 2005; Evans, 2016), there needs to be informed decision-
1534 making and the setting of secondary management goals to maximise the benefits to society and
1535 the ecological efficacy (Russell *et al.*, 1983; Hawkins *et al.*, 1992; Geist & Hawkins, 2016;
1536 Hawkins *et al.*, 2020).

1537

1538 Claassens *et al.* (2020), estimates that nearly 20 % of the banks of the Knysna Estuary
1539 Functional Zone have been developed. This included an upgrade of the N2 road which did
1540 undergo an EIA process, although no post-construction monitoring has been conducted (CES,
1541 2009). In 2018, the Knysna Estuary was characterised by the presence of 51 artificial structures
1542 extending into the subtidal zone, including bank stabilisation structures, jetties, slipways,
1543 bridges etc. and two harbours and three marina estates covering 103 ha of estuary
1544 (Wasserman, 2018). Although a requirement of the EIA is that post-development monitoring
1545 occurs, there is an evident gap on the impact of these artificial habitat developments on the
1546 ecology of the Knysna Estuary (Allanson *et al.*, 2014; Claassens, 2016; Hodgson *et al.*, 2018).

Together with the lack of post-development monitoring, little-to-no consideration was given to the types of structures used and how they could in fact be used to create habitats. In future development projects, the EIA process as well as research and design needs to consider taking the ecological engineering route instead of the conventional route.

4.3. Future research and development

Whilst the present study largely achieved its aim of comparing the faunal assemblages of gabions to seawalls in a small boat harbour, it was conducted on a small-scale within a single system. Since ecosystems differ ecologically, hydrologically and physically, replication of this study needs to take place in alternative systems to get a more holistic and well-replicated understanding of their impact in different environments. Gabions are used for the purposes of erosion control, silt blocking, damming up rivers, and in the Knysna Estuary, to build the artificial canals of Thesen Island (Claassens & Hodgson, 2018). There have been no studies that have compared the structural integrity of seawalls and gabions. However, gabions have been thoroughly studied in many different localities and settings. Two of their main advantages are their flexibility and permeability, they are not prone to cracking and are an ideal solution to drainage systems (Toprak *et al.*, 2016). In addition, these structures are considered to be environmentally friendly and aesthetically pleasing, and most importantly they are a low-cost building solution with wires that last between 30 – 100 years (Toprak *et al.*, 2016; Salmasi & Abraham, 2020).

1567 The life span of gabions on Thesen Islands was estimated at 50 years although in some areas
1568 these structures show early signs of deterioration after two decades (pers. Obs). The structural
1569 integrity and life span of gabions may be compromised in areas with higher current velocities
1570 although they seem to have stood the test of time for reducing erosion, being durable,
1571 permeable and reducing construction costs (Salmasi & Abraham, 2020). While preliminary data
1572 suggest that these structures are a viable eco-engineering approach, particularly in low water
1573 velocity environments, future ecological engineering studies need to continue testing how they
1574 can enhance habitat, help conserve species and their potential for acting as an ecological trap.

1575 The current research is not proposing that the existing seawalls in harbours and marinas that
1576 are in good structural condition should be removed and replaced with gabions. It is suggesting
1577 that at the design phase of a new harbour, marina or coastal defence project that gabions
1578 should be considered as a viable alternative to vertical seawalls in appropriate settings, such as
1579 external seawalls without any berthing. Alternatively, there may be scope for using gabions in
1580 existing novel habitats as demonstrated in this study (see Fig. 4.1 for visual). Using a variety of
1581 different structures can increase landscape heterogeneity and hence beta diversity
1582 (O'Shaughnessy *et al.*, 2023), with implications for more effective ecosystem functioning in
1583 coastal systems by creating mosaics of habitats with different functional roles (Hawkins, 2004;
1584 Giller *et al* 2004; Geist & Hawkins, 2016; Firth *et al.*, 2016). Gabions can be added over existing
1585 seawalls to create a gabion façade, albeit this does take up a larger footprint, or the gabions can
1586 be interspersed around harbours to form a mosaic and add some complexity to these systems
1587 (Frost *et al.*, 2005).

1588 This is the first field-based study both locally and internationally, to compare the ecological
1589 efficiency of gabion boxes to seawall structures. Gabions may present an alternative and even
1590 superior ecological engineering option for harbour and marina development, but further
1591 research needs to be conducted across a greater biogeographical scale where different systems
1592 (estuaries and coastlines) are compared. The ecological efficacy, cost, time taken to build,
1593 structural integrity and longevity of this engineering option also needs to be thoroughly
1594 researched (Chapman *et al.*, 2018). However, this research has provided an initial basis of
1595 knowledge to work from and in many ways has proven the value in attempting to choose to use
1596 gabions, together with, or as well as concrete seawalls in projects going forward.

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Chapter 5

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Appendix A

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2671 Photographs of the installation of the gabions into Knysna Waterfront Harbour via a barge.

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2676 Photographs of a few different Knysna Seahorses (*Hippocampus capensis*) and a Red Roman
 2677 (*Chrysoblephus laticeps*; bottom right) on the gabion habitats in Knysna Harbour.

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