

An endangered seahorse selectively chooses an artificial structure

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Abstract The development of a residential marina estate within the Knysna estuary, South Africa, introduced Reno mattresses (horizontal wire cages filled with rocks) as a novel habitat for the endangered Knysna seahorse Hippocampus capensis. Consistently high seahorse densities on these artificial structures, despite the availability of seagrass habitat, begged the question of whether this habitat was chosen by the seahorse in preference to natural vegetation. An in situ habitat choice experiment was conducted which focused on the choice made by adult H. capensis between natural vegetation (Zostera capensis) and artificial (Reno mattress) habitat within a choice chamber. Seahorses were significantly more likely to move away from Z. capensis onto a Reno mattress structure or remain on this structure. This study concludes that higher H. capensis densities on Reno mattresses within Thesen Islands Marina are owing to some positive feature of this habitat and the underlying processes responsible for the choice made by this species (additional food, holdfasts, protection) can now be investigated.

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Introduction

The coastal zone is known for its high population density and development pressures (Nicholls and Small 2002), and a major challenge for conservationists is to conserve despite these pressures. Specifically, urban sprawl has spread into our coastal and estuarine environments and this phenomenon has been dubbed 'ocean sprawl' (Firth et al. 2016a). Ocean sprawl can be defined as: "the proliferation of artificial structures associated with coastal protection, shipping, aquaculture, and other coastal industries (coastal and marine infrastructure (CMI))" (Firth et al. 2016a). The impact from ocean sprawl is extensive (Dafforn et al. 2015), but one of the most pertinent is the loss and alteration of natural aquatic habitat (Firth et al. 2016b; Perkol-Finkel et al. 2017) and the related impact on species diversity.

Some coastal and marine infrastructure can, however, have a positive impact through habitat creation or the protection of vulnerable species (Garcia-Gomez et al. 2011; Perkol-Finkel et al. 2012), and in the case of Artificial Water Bodies (terminology European Commission 2003) provide completely novel habitat (Waltham and Connolly 2013). With the extent of ocean sprawl, the challenge of the conservationist today is to be able to conserve within this heavily modified and artificial environment. In particular, scenarios where altered and artificial habitats result in conservation opportunities should be realised (Clynick 2008; Garcia-Gomez et al. 2011; Perkol-Finkel et al. 2012; Garcia-Gomez et al. 2015). For example, higher abundances of the endangered limpet, *Patella ferruginea*, were found on artificial harbour stones and these structures were established as Artificial Marine Micro-Reserves (Guerra-Garcia et al. 2004; Garcia-Gomez et al. 2011). Use of artificial habitat as a conservation tool is particularly applicable in areas devoid of natural habitat (Clynick 2008; Correia et al. 2013; Correia et al. 2015a).

Seahorses (Syngnathidae) are generally found in shallow coastal and estuarine environments, prone to developmental pressure and ocean sprawl (Foster and Vincent 2004). The distribution of these fish, along with their biology (e.g., small home ranges and limited distribution, lack of mobility, monogamy, low population sizes), make them vulnerable to anthropogenic impacts (Foster and Vincent 2004). Seahorses are threatened by habitat loss (Harasti 2016), and many species have shown population declines owing to the destruction and/or alteration of their natural complex habitats (Marcus et al. 2007; MasonJones et al. 2010). There is a growing need to understand how habitat alteration and loss impacts seahorses, to be better able to conserve this genus (Vincent et al. 2011).

The Knysna seahorse, Hippocampus capensis Boulenger, 1900 is South Africa's only endemic seahorse species and is found in only three adjacent estuaries situated on the southern Cape coast (Knysna, Keurbooms and Swartvlei estuaries) (Bell et al. 2003; Lockyear et al. 2006). Hippocampus capensis was the first (and is still the only) seahorse species to be listed as endangered on the IUCN Red Data List of Threatened species (Czembor and Bell 2012), with habitat loss identified as a major threat (Whitfield 1995). Zostera capensis, an important habitat of H. capensis (Teske et al. 2007), is threatened within the Knysna estuary owing to a lengthy Ulva lactuca bloom, known to displace Z. capensis (Adams 2016; Allanson et al. 2016; Human et al. 2016). The loss of important natural habitat can potentially have a major negative effect on H. capensis within this system.

A recent investigation into the abundance and distribution of *H. capensis* within a residential marina estate in the Knysna Estuary, found significantly higher densities of seahorses on artificial Reno mattresses (rock filled wire cages) compared to adjacent vegetation (Claassens 2016). The Reno mattress habitat, one of four habitat types identified within this Artificial Water Body (terrestrial habitat converted into aquatic habitat;

European Commission 2003) (Claassens 2016), was located within a 2 m wide section from the side of the canal walls. Could the observed distribution pattern of *H. capensis* be explained by the location of the artificial habitat in the marina canals (sides vs middle), some negative feature of other available habitats in the marina, or rather by the positive features of the Reno mattress habitat itself? To answer these questions, an in situ choice experiment was conducted between two microhabitats (definition by Morris 1987): a Reno mattress structure and Zostera capensis (eelgrass). The aim of this experiment was to understand the underlying process responsible for the observed distribution of H. capensis previously found by Claassens (2016). This study will assess the usefulness of artificial structures as potential novel habitat for the endangered Knysna seahorse.

Materials and methods

Study site

The Knysna Estuary (Fig. 1) is an estuarine bay (Whitfield 1992) situated on the southern Cape coast of South Africa. Thesen Islands Marina (34° 2' 47.16"S, 23° 3'18.84"E) is a 90.6 ha residential marina estate located on Thesen Island (Fig. 1) in the bay regime (see Largier et al. 2000; Switzer 2003) of the estuary. The marina development commenced in 2000 and was completed in 2005. This development can be classified as an artificial water body (European Commission 2003) as it transformed terrestrial habitat into aquatic habitat and added 25 ha of new and additional aquatic habitat to the Knysna estuary. The marina is connected to the estuary by two wide access entrances; one at the western end connected to the main channel of the Knysna Estuary, the other at the eastern end located off the Ashmead Channel. The marina canals, excavated to 1.75 m below mean sea level, were made out of gabions (wire boxes filled with rocks, Maccaferri 1915) and lined with Reno mattresses. Four major habitat types have been identified within the marina canals: i) artificial Reno mattress; ii) Codium tenue; iii) mixed vegetation (Zostera capensis, Caulerpa filliformis, Asparagopsis taxiformis) on sediment; and iv) barren canal floor (Claassens 2016). Habitat types i (artificial Reno mattress), and iii (mixed vegetation on sediment)

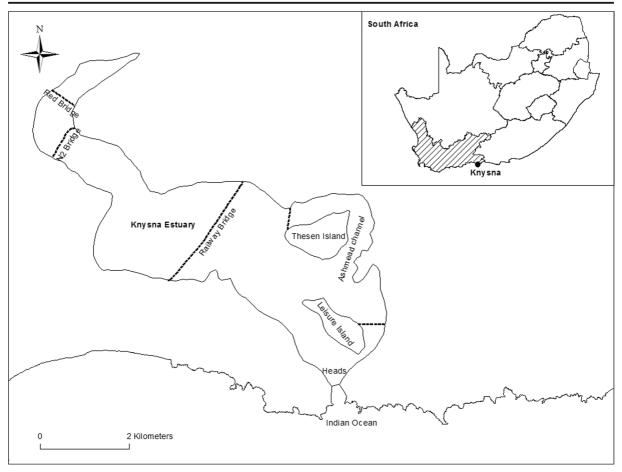


Fig. 1 Location of Knysna (insert – hatched area shows the Western Cape and the town of Knysna) and the layout of the Knysna Estuary. The bay regime stretches from the Heads to the railway bridge; the lagoon regime from the railway bridge to the

were used in the habitat choice experiment described in section Habitat choice experiment.

Habitat choice experiment

Choice experiments took place within the western section of Thesen Islands Marina (Fig. 2) during the austral summer from November 2015 to March 2016. Throughout the experimental period, temperature, dissolved oxygen, pH and salinity measurements were recorded by a permanently fixed Hydrolab MS5 multiparameter mini sonde (OTT Hydromet, Colorado), as part of the Knysna Estuarine Monitoring Platform (KEMP) project, located about 200 m from the experimental site (Fig. 2). This real-time water quality monitoring undergoes calibration every six weeks.

N2 Bridge and the estuary regime from the N2 Bridge up to the Knysna River (Largier et al. 2000). The Ashmead channel lies on the eastern side of Thesen Island (Switzer 2003). Both Thesen and Leisure Islands are situated within the bay regime

Ten replica Reno mattresses (30 cm \times 25 cm \times 10 cm) were constructed from double twisted galvanised PVC coated wire mesh and filled with rocks (Fig. 3a). These materials were similar to those used in the construction and lining of the marina canals. The replica Reno mattresses were placed within the marina on 17 August 2015 for maturation.

Ten choice chambers (50 cm \times 30 cm \times 30 cm) were constructed out of wood and wrapped with green plastic mesh (1 cm diameter). The bottom and top of the chambers were left unlined. Two sandbags were used to submerge and stabilize the chambers. The chambers were placed within a 45 m stretch of marina canal (Fig. 4) and positioned 2–3 m from the canal side wall to ensure protection from passing boats.

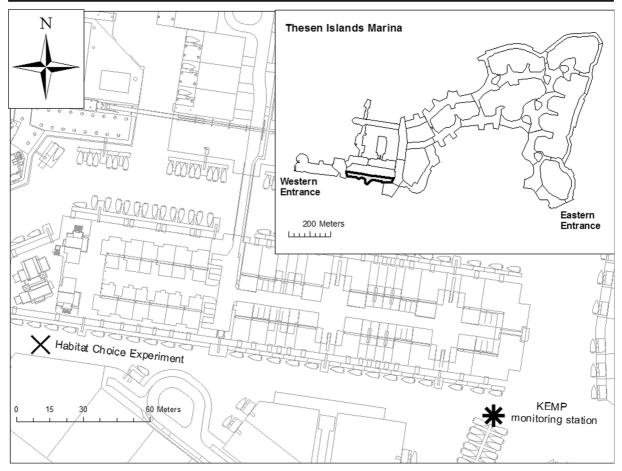


Fig. 2 The location of the habitat choice experiment, conducted on *H. capensis*, within Thesen Islands Marina and the water quality monitoring station. Insert shows the location of the experiment within the marina (bold and shaded area)

The placement of choice chambers depended on the presence of Z. capensis [a habitat used by H. capensis (Teske et al. 2007)], and consistency of percentage eel grass cover in each chamber could not be ensured owing to natural seagrass variability. Each chamber was pushed down into the sediment to ensure no gaps or crevices were located along the bottom. At the start of the experimental period, one matured replica Reno mattress was placed within each choice chamber. Half of the chamber area (0.075 m^2) was covered by a Reno mattress structure and the other half by Z. capensis (Fig. 3b). Teske et al. (2007) concluded that H. capensis will use any holdfast that is available, regardless of vegetation height, and most seahorse species require some sort of holdfast within their habitat (Harasti et al. 2014; Correia et al. 2015a). As a consequence, choice chambers with no microhabitat type or only one microhabitat type available to a seahorse that would act as a control, were considered superfluous. To ensure that the position of the Reno mattress within the chamber had no effect on the direction of movement of seahorses when introduced to the experimental chambers, the Reno mattresses in four of the chambers were positioned towards the canal middle, in another four chambers they were positioned towards the canal wall and in two of the chambers they were parallel to the canal wall (Fig. 4). Experimental trials were conducted during neap tides to ensure that the choice chambers were submerged throughout the experiment, and consequently consecutive trials were conducted a minimum of 14 days apart.

At the start of the trial, the top of each cage was covered with a Perspex lid attached with cable ties. The surrounding area ($\approx 900 \text{ m}^2$) was then searched for ten seahorses using SCUBA. Seahorse sex was

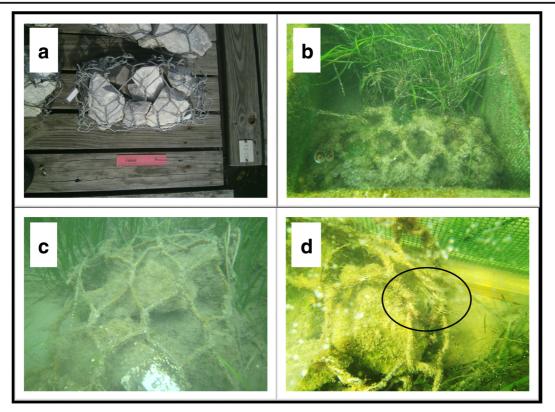


Fig. 3 An example of a replica Reno mattress used in the habitat choice assessment of H. *capensis* (a); the choice chamber used in the experiment with a matured Reno mattress structure and

established, the brood pouch status assessed, and their heights measured (to the nearest 0.5 cm) using the method of Lourie (2003) before placing one seahorse in each chamber. Only adult seahorses (> 4 cm, Lockyear et al. 2006) were used in the trials. At the onset of an experiment, a seahorse was held parallel between the two microhabitats facing downward within the chamber by the diver. The seahorse was released by the diver. The initial choice (Reno mattress or *Z. capensis*) made by the seahorse was recorded. The seagrass abundance of each chamber was recorded as percentage cover.

After a 48-h acclimation period (Correia et al. 2013), an initial search for the seahorse within each cage was conducted without the removal of the Perspex lid or the disturbance of the choice chamber. If a seahorse was visible, the microhabitat in which it was located and holdfast used were recorded. If it was not possible to locate the seahorse, the lid was removed, and the vegetation section of the cage searched. If the seahorse was not found in the vegetation section, the Reno mattress

Z. capensis (**b**); a matured Reno mattress structure (**c**); a seahorse holding on to the wire of the Reno mattress structure within the choice chamber (**d**)

was searched and if needed moved to search behind and under the structure. Once a seahorse was located, the microhabitat in which it was located and the holdfast used was recorded. After each trial, seahorses were released at the site of collection. Seahorses were collected and placed inside the choice chambers and released after 48 h during morning periods between 08:00 and 11:00. One trial consisted of ten choice chambers and only one trial was conducted per neap tide period. Seahorses were not tagged and the possibility exists that seahorses were resampled. The probability of resampling an animal was deemed to be low owing to the relatively high seahorse density recorded for this site in previous seasonal population surveys (Claassens 2018), the size of the area searched (900 m²) and, the period between consecutive surveys (> 14 days). Seahorses found as pairs were not used. Seven trials were conducted between November 2015 and March 2016 with 67 recordings made. During Trial 6, only seven seahorses were found and used in the experiment.

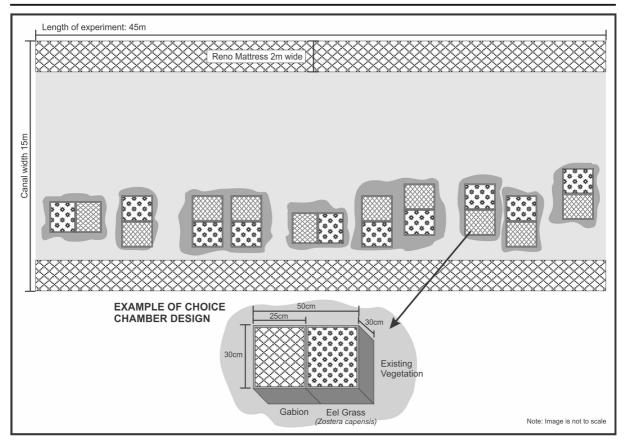


Fig. 4 Experimental layout of the habitat choice experiment conducted on *H. capensis* from November 2015 to March 2016. The experiment was conducted within the western section of Thesen Islands Marina

Statistical analysis

The statistical programme R (R Development Core Team 2014) was used in all analyses. The Plyrpackage was used for all basic descriptive statistics (Wickham 2011). A Chi-square test was used to assess the sex ratio of seahorses used in the experiment and to compare holdfasts used.

Microhabitat choice was investigated by the assessment of movement, if any, by seahorses from the microhabitat type initially chosen to that occupied 48 h later. Movement was coded with a (0) if the seahorse was found on the same microhabitat initially chosen; and a (1) if the seahorse was found in another microhabitat than that originally chosen. A Binomial Generalized Linear Mixed Model was used to assess the likelihood of a seahorse moving from the habitat type initially chosen using the assigned codes (see McCullagh and Nelder 1989; Venables and Ripley 2002; Dobson and Barnett 2008). Water quality features (pH, dissolved oxygen, temperature), seahorse sex, location of the replica Reno mattress in the chamber and percentage seagrass cover in each chamber were treated as fixed effects in the model and the variable 'choice chamber' controlled for by treating it as a random effect (each choice chamber was repeatedly sampled). The lme4 package (Bates et al. 2015) was used for the generalised linear mixed effects model.

Results

After the three-month maturation period, all replica Reno mattresses were covered by biofilm and colonized by a number of animals which included fish (Gobiidae, Gobiesocidae, Clinidae), feather stars and sea stars (Crinoidea, Asteroidea), urchins (Echinoidea), barnacles (Balanidae), shrimps (Caridae) and snails (Nassaridae) (Fig. 3c). Within 7 days of deployment *H. capensis* was noted on the artificial structures (n = 7). At the end of the maturation phase, a total of 14 seahorses were noted on the structures and the maximum number of seahorses found on a single Reno mattress structure during the maturation phase was five.

Temperature ranged from 11.6 °C to 26.4 °C during the experimental period with a mean (\pm sd) of 21.2 \pm 2.7 °C. An upwelling event occurred during the third trial (16–18 January 2016) of the experiment with a \approx 7 °C drop in temperature over one tidal cycle. Dissolved oxygen ranged from 27.5% to 127.5% with a mean (\pm sd) of 86.4 \pm 17.2%. Salinity ranged from 32.2 to 35.4 with a mean (\pm sd) of 34.8 \pm 0.6 and pH ranged from 7.7 to 8.5.

Zostera capensis coverage ranged from 10% to 90% among the choice chambers and over the experimental period. For the trials, 60% of seahorses were collected from adjacent mixed vegetation habitat, 36% from Reno mattress habitat, and 4% were found holding onto the outside of the choice chambers. Seahorse height ranged from 4.5 to 9.0 cm with a mean (\pm sd) of 6.8 \pm 1.1 cm. The sex ratio of seahorses used in the experiment was female biased ($\chi 2 = 4.3$; df = 1; P = 0.04) with 42 females and 25 males, of which 13 males had an inflated brood pouch, indicative of breeding (Curtis and Vincent 2005).

The original microhabitat choice and the microhabitat choice after the 48-h trial period are summarized in Table 1. Instances where seahorses were found swimming around in the cage, no habitat choice was logged. Neither the sex of the seahorse, the location of the replica Reno mattress within the choice chambers, physico-chemical water quality features nor percentage vegetation cover had a significant effect on seahorse microhabitat choice and were excluded from the final model. Seahorses were significantly (Z = 3.0, p < 0.01) more likely to move away from *Z. capensis* towards the Reno mattress structure, or remain on the Reno mattress structure, if given a choice (Table 1). Significantly ($\chi 2 = 29.6$; df = 3; p = < 0.01) more seahorses used the wire of the Reno mattress structures (48%) (Fig. 3d) as a holdfast compared to vegetation (31%), the green plastic mesh (12%) or nothing (7%) after the 48-h period.

Discussion

This study found that adult *H. capensis* were significantly more likely to move towards or remain on a Reno mattress structure compared to *Z. capensis*. This behavioural choice made by *H. capensis* suggests that it is the particular features of the Reno mattress structures (e.g., specific materials used to construct a Reno mattress, availability of holdfasts, increased protection provided by crevices, food availability) responsible for the observed distribution pattern as discussed in Claassens (2016).

Seahorse populations have been found to decline owing to habitat damage caused by anthropogenic activity (Marcus et al. 2007; MasonJones et al. 2010), and a 97% decline in H. whitei numbers at one site in Port Stephens, Australia, was attributed to a major decline of the preferred habitat of this species (Harasti 2016). Habitat loss was identified as a specific threat to H. capensis, and the last IUCN Red Data List of Threatened Species assessment (Czembor and Bell 2012) indicated that this species has an area of occupancy of only 27 km². The authors of this assessment concede that the estimate is probably too liberal, particularly when one considers that only 2.4 km² of the Knvsna estuary's subtidal area (the largest system occupied by H. capensis) is covered by vegetation (Adams 2016). In addition, a recent threat to subtidal vegetation (in

Table 1Summary of the original
habitat choice and the habitat
choice after the 48-h experimental
period made by 10 adult Knysna
seahorses per replicate. In in-
stances where the seahorse was
found swimming around in the
choice chamber no habitat choice
was recorded

Trial	Initial habitat choice		48 Hour habitat choice		
	Reno mattress	Vegetation	Reno mattress	Vegetation	None
1	4	6	5	4	1
2	4	6	6	3	1
3	4	6	4	5	1
4	4	6	6	3	1
5	7	3	7	3	0
6	3	4	6	1	0
7	6	4	8	2	0

particular *Z. capensis*) within the bay regime of the Knysna estuary is an extensive and lengthy *Ulva lactuca* bloom (Allanson et al. 2016). *Ulva* spp. have been found to displace saltmarsh vegetation (Watson et al. 2015) and *Z. capensis* (Human et al. 2016), and the available natural habitat within the Knysna estuary is mostly likely decreasing. In some instances, the alteration and loss of natural habitats goes together with an increase in artificial structures (Gristina et al. 2015; Otero-Ferrer et al. 2015), and a number of seahorse species have been observed to use these artificial structures [*H. guttulatus*, Curtis and Vincent 2005; Gristina et al. 2015; *H. whitei*, Hellyer et al. 2011; Harasti et al. 2012]. Therefore, the potential exists to use artificial structures in areas devoid of natural habitat (Correia et al. 2015a) as a remediation method.

Habitat loss and alteration is one of the three major threats to syngnathid populations worldwide (Vincent et al. 2011). The protection of natural seahorse habitat is integral in successful conservation, but novel conservation solutions are needed in situations where natural habitats are inevitably lost or altered, particularly within urban environments (Savard et al. 2000). The role of artificial water bodies (European Commission 2003) in conservation actions show particular promise, as these developments provide novel habitats with no loss of natural habitats (Waltham and Connolly 2013). Thesen Islands Marina provided an additional 25 ha of aquatic habitat which was readily used by *H. capensis*, specifically, the artificial Reno mattresses found in the marina canals.

This study found that adult H. capensis moved towards a Reno mattress structure in the presence of Z. capensis. By contrast, H. guttulatus and H. hippocampus in the Ria Formosa, Portugal, tended to maintain a preference for natural sea grass habitat over Artificial Holdfast Units (AHU) (Correia et al. 2015a). The usefulness of this specific AHU design was found to be limited in assisting seahorse population recovery in damaged areas only. In Sydney Harbour, Australia, H. whitei was found to utilize protective swimming nets, but the temporary nature of seasonal nets and maintenance activities of the permanent nets left seahorses vulnerable within this habitat (Clynick 2008). Seahorses on swim nets were, however, exclusively found in areas with epiphytic growth and generally within a meter of the bottom that allowed management and conservation actions to be implemented (Harasti et al. 2010). According to Clynick (2008), permanent artificial habitat located in close proximity to the seafloor may be beneficial in the provision of suitable, alternative habitat for H. whitei.

Perhaps the deployment of Reno mattress structures, or similar, in Sydney Harbour would provide this permanent surrogate habitat for *H. whitei*, which has been found to be in decline owing to the loss of essential habitat (Harasti 2016)?

An alternative view is that artificial structures (and the Reno mattresses in Thesen Islands Marina) might act as fish aggregation devices (Correia et al. 2015a) and may not increase populations per se. This seemed to be the case in the Ria Formosa, as highest seahorse densities on the AHUs deployed were found in areas with limited alternative natural habitat (Correia et al. 2015a). Many studies find that artificial reefs and structures concentrate fish populations, rather than increasing biomass (see Grossman et al. 1997; Pickering and Whitmarsh 1997). The concept of a successful artificial reef relies on the assumption that it would provide additional habitat and increase the environmental carrying capacity and thus also increase the abundance and biomass of the surrounding biota (see Bohnsack 1989). The increase in carrying capacity can be owing to increased food availability and feeding efficiency, increased shelter and higher recruitment opportunities (see Bohnsack 1989). Distribution patterns alone are not enough to confirm the suitability of a particular habitat and it is crucial to understand the underlying process responsible for the observed distribution using an experimental approach. Only then can insightful conclusions be made with regards to habitat use by a species and its usefulness in conservation actions. The higher densities of seahorses found on the Reno mattress structures do not necessarily equate to an increase in population biomass and ongoing research is needed to establish if these structures increase the environmental carrying capacity or merely attract seahorses from adjacent natural habitats.

The underlying process behind the choice for the artificial structure made by *H. capensis* is still to be determined, but it is hypothesised that the complexity of the Reno mattress structure with its numerous crevices and wire sides could provide more security and a greater number of rigid holdfasts to seahorses. Density of *H. whitei* populations on nets increased when the structural complexity of the net was increased by the addition of frayed net material (Hellyer et al. 2011). *Hippocampus guttulatus* numbers were greater when more holdfast structures were available (Correia et al. 2015b). Holdfast use by *H. capensis* is non-specific and, therefore, it is perhaps not surprising that they would take advantage of the holdfast opportunities presented

by the Reno mattress (Teske et al. 2007). However, holdfast availability may not be the only reason for seahorse habitat choice as Hellyer et al. (2011) found more complex artificial habitats supported greater numbers of small mobile epifauna (amphipods and copepods) and *H. whitei* abundance on swim nets were positively correlated to epibenthic growth which provided structural complexity, and the colonization of swim nets by epifauna seems to be an important requirement for seahorse colonization (Harasti et al. 2010). The rate of maturation of Reno mattresses, and the colonization by epibenthic organisms might also play a role in the use of these structures by seahorse, and should be considered in future research.

Seahorse densities on artificial structures have been found to be higher compared to natural vegetation habitats (Clynick 2008; Harasti et al. 2012; Correia et al. 2015a). These higher densities could leave populations vulnerable to human impacts (Correia et al. 2015a), particularly owing to the fact that artificial structures are usually located close to human activities (Clynick 2008), and undergo regular maintenance activities which may reduce the diversity of epibiota on these structures (Bulleri and Chapman 2010). It is thus important to include these structures in management and conservation actions and even in reserves (Harasti et al. 2010; Garcia-Gomez et al. 2015). Artificial Marine Micro-Reserves can be used to protect artificial habitats utilized by vulnerable and endangered species (Garcia-Gomez et al. 2015). In the case of *H. capensis*, if Reno mattress habitats within Thesen Islands Marina are given formal protection, it would assist in the conservation of this endangered species.

It is concluded from the current study that *H. capensis* is found in higher densities on artificial Reno mattress habitat owing to the nature of the artificial structure as opposed to the specific location of these structures within the marina canals. The Reno mattress structure was chosen by *H. capensis* and the reasons responsible for this choice (positive or negative (Underwood et al. 2004)) can now be investigated.

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References

- Adams JB (2016) Distribution and status of *Zostera capensis* in south African estuaries – a review. S Afr J Bot 107:63–73. https://doi.org/10.1016/j.sajb.2016.07.007
- Allanson BR, Human LRD, Claassens L (2016) Observations on the distribution and abundance of a green tide along an intertidal shore, Knysna estuary. S Afr J Bot 107:49–53. https://doi.org/10.1016/j.sajb.2016.02.197
- Bates D, Maechler M, Bolker B, Walker S (2015) Fitting linear mixed-effects models using lme4. J Stat Softw 67:1–48
- Bell EM, Lockyear JF, McPherson JM, Marsden AD, Vincent ACJ (2003) First field studies of an endangered south African seahorse, *Hippocampus capensis*. Environ Biol Fish 67(1): 35–46. https://doi.org/10.1023/A:1024440717162
- Bohnsack JA (1989) Are high densities of fishes at artificial reefs the result of habitat limitation or behavioural preference? Bull Mar Sci 44(2):631–645
- Bulleri F, Chapman MG (2010) The introduction of coastal infrastructure as a driver of change in marine environments. J Appl Ecol 47(1):26–35. https://doi.org/10.1111/j.1365-2664.2009.01751.x
- Claassens L (2016) An artificial water body provides habitat for an endangered estuarine seahorse species. Estuar Coast Shelf Sci 180:1–10. https://doi.org/10.1016/j.ecss.2016.06.011
- Claassens L (2018) Aspects of the Population ecology, habitat use and behaviour of the endangered Knysna seahorse (*Hippocampus capensis* Boulenger, 1900) in a residential marina estate, Knysna, South Africa: implications for conservation. PhD Thesis, Rhodes University, Grahamstown, pp 220. http://hdl.handle.net/10962/54789
- Clynick BG (2008) Harbour swimming nets: a novel habitat for seahorses. Aquatic Conserv Mar Freshw Ecosyst 18(5):483– 492. https://doi.org/10.1002/aqc.856
- Correia M, Palma J, Koldewey H, Andrade JP (2013) Can artificial holdfast units work as a habitat restoration tool for longsnouted seahorse (*Hippocampus guttulatus* Cuvier, 1829)? J Exp Mar Biol Ecol 448:258–264. https://doi.org/10.1016/j. jembe.2013.08.001
- Correia M, Koldewey H, Andrade JP, Palma J (2015a) Effects of artificial holdfast units on seahorse density in the Ria Formosa lagoon. Portugal J Exp Mar Biol Ecol 471:1–7. https://doi.org/10.1016/j.jembe.2015.05.012
- Correia M, Caldwell IR, Koldewey HJ, Andrade JP, Palma J (2015b) Seahorse (Hippocampinae) population fluctuations in the ria Formosa lagoon, south Portugal. J Fish Biol 87(3): 679–690. https://doi.org/10.1111/jfb.12748
- Curtis JMR, Vincent ACJ (2005) Distribution of sympatric seahorse species along a gradient of habitat complexity in a seagrass-dominated community. Mar Ecol Prog Ser 29:81–91
- Czembor CA, Bell EM (2012) *Hippocampus capensis* The IUCN Red List of Threatened Species 2012
- Dafforn KA, Glasby TM, Airoldi L, Rivero NK, Mayer-Pinto M, Johnston EL (2015) Marine urbanization: an ecological framework for designing multifunctional artificial structures.

Front Ecol Environ 13(2):82–90. https://doi.org/10.1890 /140050

- Development Core Team R (2014) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna
- Dobson AJ, Barnett A (2008) An introduction to generalized linear models, 3rd edn. CRC Press, Boca Raton, p 320
- European Commission (2003) Commission implementation strategy for the water framework directive (2000/60/EC). Working group 2.2 HMWB. Guidance document no 4. Identification and Designation of Heavily Modified and Artificial Water Bodies. European Commission, Luxembourg, p 109
- Firth LB, Knights AM, Bridgers D, Evans AJ, Mieszkowska N, Moore PJ, O'Connor NE, Sheehan EM, Thompson RC, Hawkins SJ (2016a) Ocean sprawl: challenges and opportunities for biodiversity management in a changing world. Oceanogr Mar Biol 54:193–269
- Firth LB, Browne KA, Knights AM, Hawkins SJ, Nash R (2016b) Eco-engineered rock pools: a concrete solution to biodiversity loss and urban sprawl in the marine environment. Environ Res Lett 11(9):094015. https://doi.org/10.1088 /1748-9326/11/9/094015
- Foster SJ, Vincent ACJ (2004) Life history and ecology of seahorses: implications for conservation and management. J Fish Biol 65(1):1–61. https://doi.org/10.1111/j.0022-1112.2004.00429.x
- Garcia-Gomez JC, Lopez-Fe CM, Guerra-Garcia JM, Rivera-Ingraham GA (2011) Marine artificial micro-reserves: a possibility for the conservation of endangered species living on artificial substrata. Mar Ecol 32(1):6–14. https://doi. org/10.1111/j.1439-0485.2010.00409.x
- Garcia-Gomez JC, Guerra-Garcia JM, Espinosa F, Maestre MJ, Rivera-Ingraham G, Fa D, Conzalez AR, Ruiz-Tabares AR, Lopez-Fe CM (2015) Artificial marine micro-reserves networks (AMMRNs): an innovative approach to conserve marine littoral biodiversity and protect endangered species. Mar Ecol 36(3):259–277. https://doi.org/10.1111/maec.12167
- Gristina M, Cardone F, Carlucci R, Castellano L, Passarelli S, Corriero G (2015) Abundance, distribution and habitat preference of *Hippocampus guttulatus* and *Hippocampus hippocampus* in a semi-enclosed central Mediterranean marine area. Mar Ecol 36(1):57–66. https://doi.org/10.1111 /maec.12116
- Grossman GD, Jones GP, Seaman WJ (1997) Do artificial reefs increase regional fish production? A review of existing data. Fisheries 22(4):17–23. https://doi.org/10.1577/1548-8446 (1997)022<0017:DARIRF>2.0.CO;2
- Guerra-Garcia JM, Corzo J, Espinosa F, Garcia-Gomez JC (2004) Assessing habitat use of the endangered marine mollusc *Patella ferruginea* (Gastropoda, Patellidae) in northern Africa: preliminary results and implications for conservation. Biol Conserv 116(3):319–326. https://doi.org/10.1016 /S0006-3207(03)00201-5
- Harasti D (2016) Declining seahorse populations linked to loss of essential marine habitats. Mar Ecol Prog Ser 546:173–181. https://doi.org/10.3354/meps11619
- Harasti D, Glasby TM, Martin-Smith KM (2010) Striking a balance between retaining populations of protected seahorses and maintaining swimming nets. Aquat Conserv 20(2):159– 166. https://doi.org/10.1002/aqc.1066

- Harasti D, Martin-Smith K, Gladstone W (2012) Population dynamics and life history of a geographically restricted seahorse, *Hippocampus whitei*. J Fish Biol 81:1297–1314
- Harasti D, Martin-Smith K, Gladstone W (2014) Ontogenetic and sex-based differences in habitat preferences and site fidelity of White's seahorse *Hippocampus whitei*. J Fish Biol 85: 1413–1428
- Hellyer CB, Harasti D, Poore AGB (2011) Manipulating artificial habitats to benefit seahorses in Sydney harbour, Australia. Aquat Conserv 21(6):582–589. https://doi.org/10.1002 /aqc.1217
- Human LRD, Adams JB, Allanson BR (2016) Insights into the causes of an *Ulva lactuca* bloom and its impact in South Africa's most important estuary. S Afr J Bot 107:55–62. https://doi.org/10.1016/j.sajb.2016.05.016
- Largier JL, Attwood C, Harcourt-Baldwin J-L (2000) The hydrographic character of the Knysna estuary. Trans Roy Soc S Afr 55(2):107-122. https://doi.org/10.1080 /00359190009520437
- Lockyear JF, Hecht T, Kaiser H, Teske PR (2006) The distribution and abundance of the endangered Knysna seahorse *Hippocampus capensis* (Pisces: Syngnathidae) in south African estuaries. Afr J Aquat Sci 31(2):275–283. https://doi.org/10.2989/16085910609503897
- Lourie S (2003) Measuring seahorses. Project seahorse technical report no.4, version 1.0. Fisheries Centre, University of British Columbia, Project Seahorse, p 15
- Maccaferri (1915) Gabion for protective waterwork: US patent 1165194A. Washington, DC
- Marcus JE, Samoilys MA, Meeuwig JJ, Villongco ZAD, Vincent ACJ (2007) Benthic status of near-shore fishing grounds in the central Philippines and associated seahorse densities. Mar Pollut Bull 54(9):1483–1494. https://doi.org/10.1016/j. marpolbul.2007.04.011
- MasonJones HD, Rose E, McRae LB, Dixson DL (2010) An examination of the population dynamics of syngnathid fishes within Tampa Bay, Florida, USA. Current Zoology 56(1):118–133
- McCullagh P, Nelder JA (1989) Generalized Linear Models. Chapman and Hall, London. https://doi.org/10.1007/978-1-4899-3242-6
- Morris DW (1987) Ecological scale and habitat use. Ecology 68(2):362–369. https://doi.org/10.2307/1939267
- Nicholls RJ, Small C (2002) Improved estimates of coastal population and exposure to hazards released. Earth Space Sci 83(28):301–305
- Otero-Ferrer F, Herrera R, Tuset VM, Socorro J, Molina L (2015) Spatial and seasonal patterns of European short-snouted seahorse *Hippocampus* distribution in island coastal environments. Afr J Mar Sci 37(3):395–404
- Perkol-Finkel S, Ferrario F, Nicotera V, Airoldi L (2012) Conservation challenges in urban seascapes: promoting the growth of threatened species on coastal infrastructures. J Appl Ecol 49(6):1457–1466. https://doi.org/10.1111/j.1365-2664.2012.02204.x
- Perkol-Finkel S, Hadary T, Rella A, Shirazi R, Sella I (2017) Seascape architecture – incorporating ecological considerations in design of coastal and marine infrastructure. Ecol Eng. https://doi.org/10.1016/j.ecoleng.2017.06.051
- Pickering H, Whitmarsh D (1997) Artificial reefs and fisheries exploitation: a review of the 'attraction versus production' debate, the influence of design and its significance for policy.

Fish Res 31(1-2):39–59. https://doi.org/10.1016/S0165-7836 (97)00019-2

- Savard J-PL, Clergeau P, Mennechez G (2000) Biodiversity concepts and urban ecosystems. Landsc Urban Plan 48(3-4): 131–142. https://doi.org/10.1016/S0169-2046(00)00037-2
- Switzer TB (2003) The role of water column and benthic communities in the spatial and temporal production and uptake of nutrients in controlling the trophic status of the Knysna River Estuary, South Africa. PhD Thesis, University of Cape Town, Cape Town, pp 188. http://hdl.handle.net/11427/8617
- Teske PR, Lockyear JF, Hecht T, Kaiser H (2007) Does the endangered Knysna seahorse, *Hippocampus capensis*, have a preference for aquatic vegetation type, cover or height? Afr Zool 42(1):23-30. https://doi.org/10.1080 /15627020.2007.11407373
- Underwood AJ, Chapman MG, Crowe TP (2004) Identifying and understanding ecological preferences for habitat or prey. J Exp Mar Biol Ecol 300(1-2):161–187. https://doi. org/10.1016/j.jembe.2003.12.006
- Venables WN, Ripley BD (2002) Modern applied statistics with S. Springer, New York. https://doi.org/10.1007/978-0-387-21706-2

- Vincent ACJ, Foster SJ, Koldewey HJ (2011) Conservation and management of seahorses and other Syngnathidae. J Fish Biol 78: 1681–1724, 6, doiI: https://doi.org/10.1111/j.1095-8649.2011.03003.x
- Waltham NJ, Connolly RM (2013) Artificial tidal lakes: built for humans, home for fish. Ecol Eng 60:414–420. https://doi. org/10.1016/j.ecoleng.2013.09.035
- Watson EB, Wigand C, Oczkowski AJ, Sundberg K, Vendettouli D, Jayaraman S, Saliba K, Morris JT (2015) Ulva additions alter soil biogeochemistry and negatively impact Spartina alterniflora growth. Mar Ecol Prog Ser 532:59–72
- Whitfield AK (1992) Characterization of southern African estuarine systems. S. Afr J Aquat Sci 18(1-2):89–103. https://doi. org/10.1080/10183469.1992.9631327
- Whitfield AK (1995) Threatened fishes of the world: *Hippocampus capensis* Boulenger, 1900 (Syngnathidae). Environ Biol Fish 44(4):362. https://doi.org/10.1007 /BF00008251
- Wickham H (2011) The split-apply-combine strategy for data analysis. J Stat Softw 40(1):1–29 http://www.jstatsoft. org/v40/i01/