

## Artificial rockpools create habitat refugia on seawalls at high tide

Jessica R. Bone<sup>a,b,\*</sup>, Alice E. Hall<sup>c</sup>, Rick Stafford<sup>a</sup>, Nazish F. Mir<sup>a</sup>, Jeesa Benny<sup>a</sup>, Roger J. H. Herbert<sup>a</sup>

<sup>a</sup> Bournemouth University, Poole, Dorset, United Kingdom

<sup>b</sup> Natural England, Eastbrook, Cambridge, United Kingdom

<sup>c</sup> University of Plymouth, Drake Circus, Plymouth, United Kingdom

### ARTICLE INFO

#### Keywords:

Ecological enhancement  
Nature-based solutions  
Greening the grey  
Nature inclusive design

### ABSTRACT

Rockpools are fundamental habitats on natural rocky shores that provide refugia for marine life at low and high tide. Yet, artificial coastal structures lack the topographical complexity seen in these natural habitats. Eco-engineering, that may include the deployment of artificial rockpools, attempts to address the lack of suitable habitat on coastal infrastructure but most studies focus on species abundance metrics at low tide. It is important to understand how eco-engineering interventions may provide habitat at high tide compared to the surrounding artificial substrate.

In this study, we demonstrate how groups of rockpools (1, 3 or 5 rockpools) add habitat complexity at high tide to a concrete seawall in Poole Harbour, UK. Between April and October 2022, eighteen GoPro cameras were deployed to record species richness and abundance in artificial rockpools and the adjacent concrete sea wall. Additionally, the length of time the most abundant fauna (the shanny fish *Lipophrys pholis* and the European shore crab *Carcinus maenas*) spent engaging in different behaviour (resting, feeding, moving) was recorded.

Overall, there was no significant difference in the abundance and species richness of mobile fauna using the artificial rockpools versus the seawall. However, both the shanny and shore crab generally spent more time in the rockpools than on the seawall. Both crabs and shanny preferentially engaged in feeding behaviours on the seawall, which has been attributed to the high percentage cover of barnacle prey. Crabs and shanny spent more time resting in the rockpools than the seawall and the only reproductive behaviour observed occurred within the rockpools. Our work suggests that artificial rockpools support the habitat needs and multiple life history requirements of these species at high tide. Both the seawall and rockpools provide valuable resources, which further emphasises the need for variety in eco-engineering feature designs.

### 1. Introduction

The intertidal zone interfaces the land and sea, and emersion of the intertidal at low tide exposes fauna to risk of mortality through desiccation stress and predation (Little et al., 2007). Species richness on intertidal rocky shores can be largely attributed to the heterogenous nature of the substratum, which can include rough and smooth surfaces, pools, overhangs and a variety of aspects and steepness of slope. Rockpools are shallow water-retaining depressions (Metaxas and Scheibling, 1993) that are found on intertidal rocky shores that provide refuge and resources at low and high tide (Martins et al., 2007; Firth et al., 2013; Legrand et al., 2018). The patchiness of rockpools and other microhabitats are crucial to the connectivity and survival of mobile fauna (Noel et al., 2009) on rocky shores.

Artificial coastal structures, such as seawalls, piers, groynes and breakwaters, often lack the structural and topographical complexity seen in natural rocky shores (Moschella et al., 2005; Chapman and Underwood, 2011; Aguilera et al., 2014). As a result, they usually fail to support diverse intertidal benthic communities, and often have lower abundance, species richness and biodiversity (Connell and Glasby, 1999; Chapman, 2003; Moschella et al., 2005; McKinney, 2006; Glasby et al., 2007; Vaselli et al., 2008; Pister, 2009; Firth et al., 2013; Earp et al., 2023). Artificial coastal structures provide poorer attachment capabilities for seaweeds (Drakard et al., 2021) and alter reproductive states and outputs of gastropods (Moreira et al., 2006; Thompson et al., 2023) compared to natural substrates.

Intertidal eco-engineering involves the integration of habitat features in construction (Bergen et al., 2001; Mitsch and Jorgensen, 2003;

\* Corresponding author at: Bournemouth University, Poole, Dorset, United Kingdom.

E-mail address: [jbone@bournemouth.ac.uk](mailto:jbone@bournemouth.ac.uk) (J.R. Bone).

<https://doi.org/10.1016/j.ecoleng.2024.107318>

Received 5 January 2024; Received in revised form 3 June 2024; Accepted 7 June 2024

Available online 12 June 2024

0925-8574/© 2024 The Authors. Published by Elsevier B.V. This is an open access article under the CC BY license (<http://creativecommons.org/licenses/by/4.0/>).

Odum and Odum, 2003), and can increase benthic species richness on artificial coastal structures (Firth et al., 2014; Naylor et al., 2017; Strain et al., 2017; O'Shaughnessy et al., 2019; Evans et al., 2021). However, the majority of studies are conducted at low tide and only capture data for half of the story. Understanding how eco-engineered habitats are used at high tide is crucial for ensuring the habitat needs of organisms are met throughout the tidal cycle and for further demonstrating how interventions may improve ecosystem provision and functionality of artificial coastal structures (Bishop et al., 2022).

Research on mobile fauna associated with artificial structures has predominantly concentrated on offshore subtidal natural and artificial reefs (Baine, 2001; Reis et al., 2021), with a recent focus on industrial subtidal structures, such as renewable energy installations (Wilhelmsson et al., 2006; Reubens et al., 2013; Krone et al., 2013; Reubens et al., 2014; Langhamer et al., 2016; Bender et al., 2020; Glarou et al., 2020; Sheehan et al., 2020) and oil rigs (Claisse et al., 2014, 2015). Investigations into the behaviour of intertidal mobile species have been limited by the availability of suitable equipment. Yet the advent of cheaper, robust underwater cameras has increased the possibilities of simultaneously comparing assemblages of different habitats. For example, using GoPro cameras, Ng et al. (2021) found that the feeding rate of algal turf-feeding fishes was greater on granite seawalls than adjacent reef flats on the coast of Singapore, and the functional composition of algal turf-feeding fishes also differed between seawall and reef habitats. The authors postulated that this was due to the greater algal turf coverage on the seawall habitat.

Using cameras, intertidal ecological enhancements have been shown to have varying impacts when surveying fish and crab abundance, species richness and assemblage composition at high tide (Sheehan et al., 2010; Morris et al., 2017; Morris et al., 2018a, 2018b; Ushiyama et al., 2019; Strain et al., 2020; Taira et al., 2020). Results are generally species poor compared to studies conducted at low tide surveying epilithic and sessile biota on ecological enhancements. Morris et al. (2017) found no consistent effect of artificial rockpools (flowerpots) on pelagic and benthic fish assemblages and few effects on diversity and abundance over the year of their study in Sydney Harbour, Australia. Ushiyama et al. (2019) found similar results, with no significant difference in pelagic and cryptobenthic fish abundance between complex tiles, flat tiles, and seawall in Sydney Harbour. However, the length of time cryptobenthic fish spent interacting with complex tiles was greater than flat tiles and the seawall, though this difference was not apparent for pelagic fish. Strain et al. (2020) found species density and MaxN of cryptobenthic fish was positively influenced by tiles seeded with oysters in Sydney Harbour, though the complexity of the tiles had little effect. Again, there were no detectable effects in the species diversity or MaxN of pelagic fish between seeded and unseeded, and complex and flat tiles after 1 month. Conversely, Taira et al. (2020) found that enhanced granite riprap in Singapore significantly increased species richness of epibenthic fish, as well as influencing their assemblage composition, likely due to the increase in trophic food provision through enhanced algal growth.

As part of the Marineff Project, forty-five artificial rockpools were installed on an intertidal seawall in Poole Harbour, UK. Experimental data collected from the rockpools at low tide demonstrated their success at increasing the species richness of the overall seawall, as well as increasing the abundance of mobile fauna such as crabs, prawns and benthic fish (unpublished data). At the time of writing, all existing studies using video analysis of eco-engineering interventions at high tide have been conducted in warm temperate or tropical locations in the southern hemisphere, and there is a need to investigate the effects of ecological interventions in colder temperate waters in the northern hemisphere. To determine how the artificial rockpools affected local benthic and demersal mobile species compared to the seawall at high tide, video footage of both the artificial rockpools and sections of seawall was recorded. To our knowledge, this is the first study of its kind that examines the individual behaviours of mobile fauna interacting with artificial rockpools at high tide. We hypothesised that:

- As a structurally complex feature, abundance of fauna would be greater in the artificial rockpools, than on seawall controls.
- As an ecologically complex feature, organisms would interact with the artificial rockpools for longer than the seawall controls.
- Organisms would interact more with groups of artificial rockpools, which add more local complexity and potential habitat connectivity, than single rockpools.

## 2. Method and materials

### 2.1. Location

References to seasons hereafter will refer to boreal seasons. The study site is in Poole Harbour (50.691798, -1.9353187) Dorset, UK (Fig. 1). Poole Harbour is a microtidal estuary with a double high tide, where for ~16 h a day the water is above mean tide level (Humphreys, 2005). Salinity ranges between 26.3 PSU to 34.5 PSU in this area of the harbour (Humphreys, 2005). The Peninsula, known as Sandbanks, is highly developed and a very popular area for tourism and water sports activities, particularly during the summer.

The study site was on a north-west facing vertical concrete seawall which was characterised by an existing species poor community, consisting of 75% mean percentage cover of barnacles and 20% mean percentage cover of fucoid algae. The site consisted of ~180 m of contiguous seawall, which included an 85 m stretch of seawall between two concrete boat slipways on which forty-five retrofitted artificial rockpools were fixed, and an additional 60 m of seawall the other side of one of the slipways where 6 of the control replicates were installed. The additional seawall was necessary as not all control camera replicates would fit between rockpool treatments.

Artificial rockpools were installed at High Water Neap tidal level in July 2020. The rockpools were made from low-carbon Vicat Prompt cement and sharp sand by Artecology Ltd. and fixed to the seawall using marine-grade stainless steel brackets (Fig. 2). The pool interior and rim had a rough, stippled texture and the exterior was covered in concave hemispherical pockets created using bubble wrap to line the rockpool moulds. The rockpools were arranged in three different treatments as part of a wider experiment through the Marineff Project: five rows of five, five rows of three and five single rockpools. In each row, the rockpools were separated by 15 cm of seawall (Fig. 2) and were fully immersed when the tidal height exceeded ~2 m (high water springs maximum 2.5 m) and retained approximately 1.5 l of seawater at low tide. At the commencement of the experiment in April 2022, the rockpools were characterised by 60% mean percentage cover of fucoids and 6% mean percentage cover of barnacles. Species on the rockpools and seawall included *Fucus spiralis*, *Ulva* spp., red turf algae, littorinid snails, patellid limpets, the native barnacle *Semibalanus balanoides* and the non-native barnacle *Austrominius modestus*.

### 2.2. Experimental design

Three replicates of each rockpool treatment (groups of five, groups of three, single rockpools) were randomly selected for filming. For the grouped rockpools, only the central rockpool was filmed with the assumption that this position would be representative of species activity and abundance within each pool of the array (Fig. 3). In addition to the nine rockpools being filmed, nine sections of the seawall without rockpools were also filmed as controls. Each rockpool treatment and control section was at least >2 m from the next camera to help maintain independence and avoid spatial autocorrelation. Morris (2016) showed that little spatial correlation in the diversity or abundance of fish between adjacent cameras on seawalls occurs.

In each of the nine rockpools, a 10 mm diameter hole was drilled into the rim of the rockpool, adjacent to the seawall. A small amount of resin mortar was injected into the hole and a 24 mm stainless steel connector (or coupling) nut was set into the resin mortar. This was used as a point



Service Layer Credits: Esri, HERE, Garmin, (c) OpenStreetMap contributors, and the GIS user community  
 Source: Esri, Maxar, Earthstar Geographics, and the GIS User Community

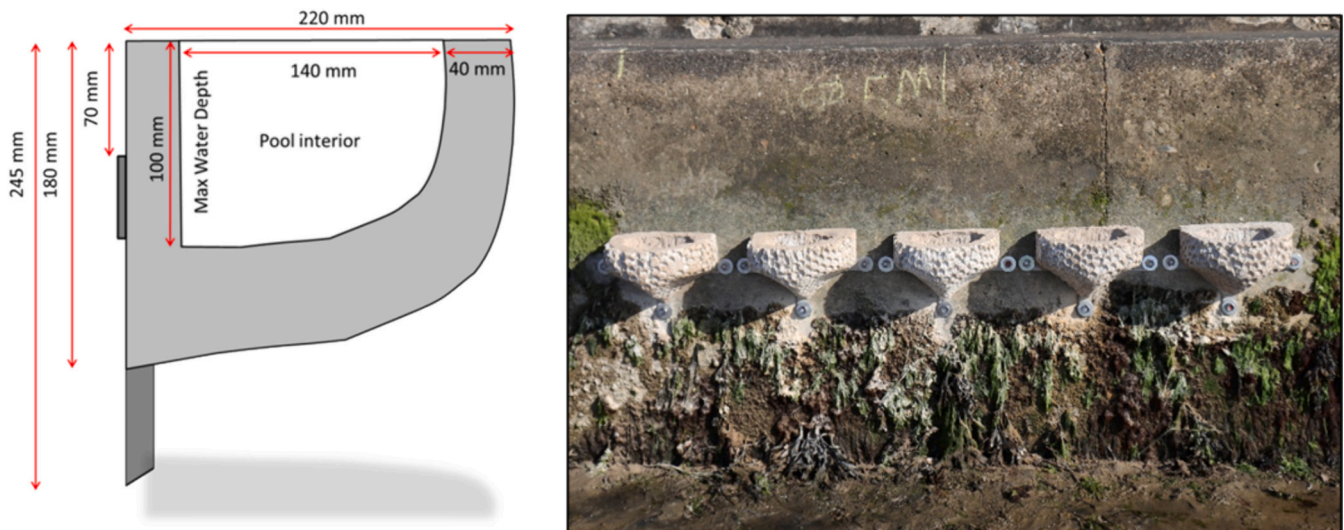
**Fig. 1.** The location of the study site in Poole Harbour on the south coast of the UK. Polygons denote approximate study site location in each map and are not to scale with subsequent map.

of attachment for a stainless-steel threaded bar which was screwed into the nut, and a tripod mount screwed onto the other end. A GoPro® Hero9 camera in a dive housing was fixed to the tripod mount (1080 progressive resolution, 24 frames per second, wide lens, vertical field of view  $94.4^\circ$ , horizontal field of view  $122.6^\circ$ ). The camera was then angled to face down at the top elevation of the rockpool (Fig. 4, Morris et al., 2017; Strain et al., 2020). This was replicated for the seawall, where the holes were drilled into the concrete facing, ensuring the same distance from the sea wall. The control cameras on the seawall were fixed and angled to capture the same tidal height as the cameras above the rockpools (Fig. 4). No bait was used to prevent bias in the organisms attracted to the cameras (Whitmarsh et al., 2017), particularly as there were a high number of camera replicates on the same structure, and so

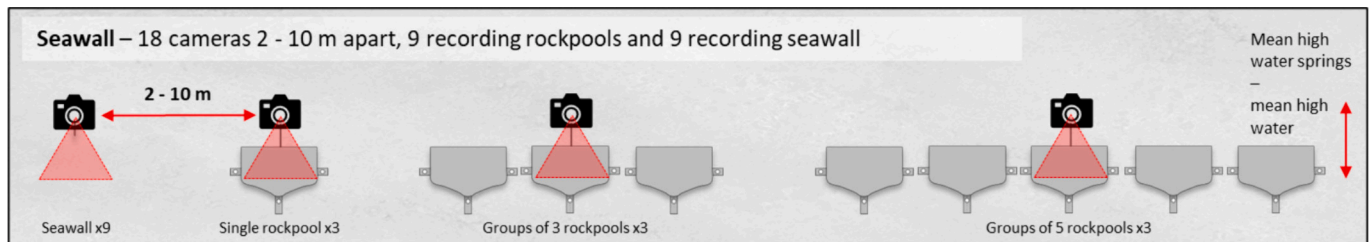
bait plumes may have overlapped into neighbouring habitats (Hannah and Blume, 2012) and disrupted independence. Additionally, unbaited remote underwater video is sufficient at capturing the intertidal species likely to appear at this estuarine site (Rhodes et al., 2020).

The height of the cameras above the rockpools was constrained by the maximum tidal height of high spring water above the rockpools (maximum 40 cm above the rockpool rim). For the rockpool cameras, the rockpool rim was within the camera frame. To ensure an equivalent and comparable spatial area an equivalent tidal depth was recorded on the seawall, the seawall was marked with a thin line of paint to prevent recording of organisms beyond the limit of the rockpool depth.

From April to October 2022, continuous footage was recorded simultaneously on all replicates (total 18 cameras) for two diurnal high



**Fig. 2.** The profile view of an artificial rockpool showing approximate dimensions (left) and a group of 5 rockpools at low tide shortly after installation in July 2020 (right).



**Fig. 3.** Experimental set up (not to scale).

tides each month during late morning. Where possible, these were consecutive diurnal high tides. Footage began recording on a flooding tide as the cameras were immersed (Becker et al., 2012; Espadero et al., 2020) at 2.1 m above Chart Datum and was recorded for 60 min (Whitmarsh et al., 2017). Due to the microtidal regime of the harbour, it was often not possible to record >60 min of immersed footage. For one tide in July and both tides in August and September only two replicates of the single rockpools were filmed as a nut broke away from one of the single rockpools.

### 2.3. Data collection and analysis

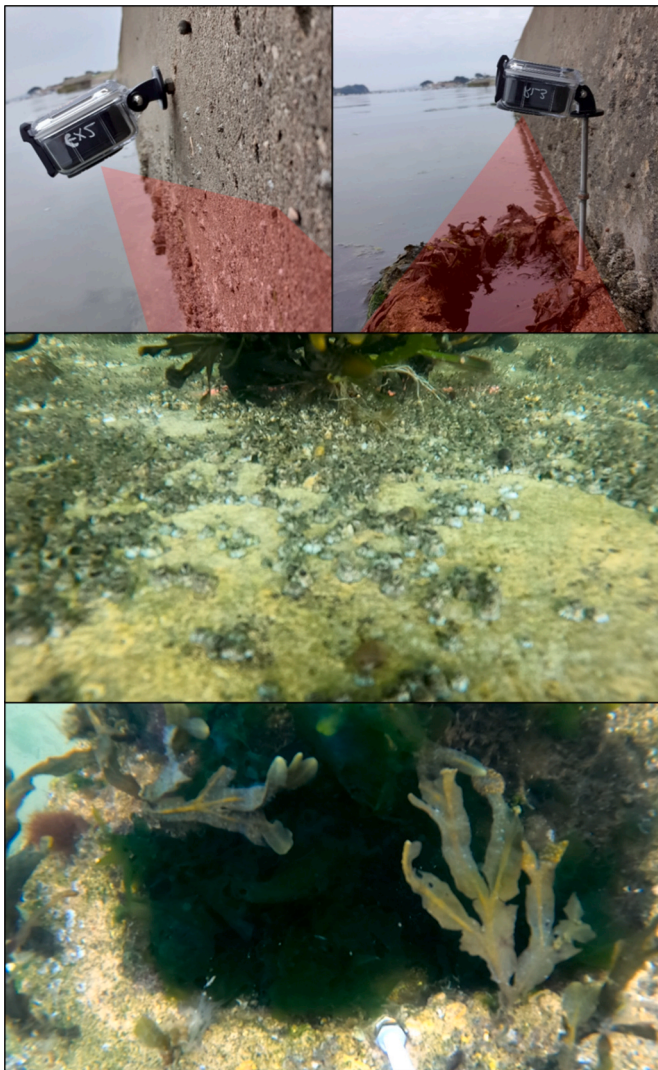
Sixty minutes of footage were reviewed from each camera from each tide, totalling 252 h of footage filmed across seven months. The 60 min began and finished at the same time across all cameras ( $\pm 5$  min as recording was started manually and therefore not simultaneous). The relative abundance of species (MaxN) and the number of species (S) was recorded for each 60 min. MaxN is the maximum number of individuals observed in a single frame (Cappo et al., 2004; Cappo et al., 2007; Erickson et al., 2023) over 60 min and avoids repeat counts of individuals. The number of species (S) was determined as the total number of species recorded over 60 min.

In addition to MaxN and S, the following was also recorded for each organism: total length of observed interaction with rockpool/ seawall, and type and length of behaviour within the interaction (e.g., locomotion, resting, Martinez-Baena et al., 2022, feeding Espadero et al., 2020). Observation began when an organism entered the frame and came within 50 mm of the substrate surface (Campbell et al., 2018; Ushiyama et al., 2019) or the seaweed growing on the substrate and ended when the organism left the frame or was out of sight (i.e., behind seaweed) for

more than thirty seconds. Organisms that remained in the water column >50 mm away from the substrate surface for the duration of time they were in the field of view and did not make tactical contact with the rockpool/ seawall, were not included in analysis (sensu Ng et al., 2021). This was to ensure all behaviours recorded were connected to the rockpool/ seawall.

Types of behaviour included locomotion, resting, feeding and conspecific (Tables 1 and 2). Conspecific behaviour was observed as either reproductive or aggressive in nature. It was not possible to infer exact behaviour other than physical contact for some instances and as conspecific behaviour was relatively infrequent, all conspecific behaviour was pooled into the same category. Feeding for grazing organisms (crabs, prawns) was measured in length of time, whereas feeding for benthic fish was measured as number of bites observed (quantified by contact with mouth to substrate/ seaweed Ushiyama et al., 2019; Ng et al., 2021; Taira et al., 2020). Length of behaviour was determined as time spent performing that behaviour for at least 30 s.

To test for statistically significant differences in abundance (MaxN), species richness, and species behaviour between rockpool and seawall habitats over time, linear mixed effect models were run using the “nlme” package (Pinheiro et al., 2020) in R Studio (Version 1.2.1335). For behavioural analyses, only shanny and crabs were used as they were the most frequently observed species in both habitats throughout the study. Assumptions of statistical tests were verified by examination of residuals against fitted model plots, as per Zuur et al. (2009). Where clear lack of normality or heteroskedasticity were identified, transformations were made to the data (log+1 transformations) before further statistical analysis. Habitat (rockpool and seawall) and month (April – October) were fixed factors. To account for repeated measures within the rockpool and seawall, as the same rockpool and seawall sections were



**Fig. 4.** The installation of the GoPro Hero 9 s above the seawall (top left) and above the rockpools (top right) with the red shaded area showing the field of view, and the view underwater of the seawall cameras (middle) and the rockpool cameras (bottom). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

**Table 1**

Ethogram of state behaviours (recorded by length of time, one state begins when another has ended if multiple states observed).

Feeding (crabs, prawns)	Organism uses of claws/ chelate legs to gather food items from the benthic environment
Locomotion	Organism swims or crawls around environment
Resting	Organism remains immobile, either on the substrate or in the water column
Conspecific	Organism makes physical contact with a member of the same species. Nested within this are reproductive, predatory and competitive behaviours due to infrequency observed.

**Table 2**

Ethogram of event behaviours (recorded by number of events, events can occur during state behaviours).

Feeding (fish)	Organism makes brief, rapid contact with mouth to a food item (Morris et al., 2017). This behaviour is recorded regardless of whether the attempt was successful.
----------------	---

surveyed each time, rockpool and seawall ‘ID’ was included as a random factor. To account for pseudo replication, as two consecutive tidal cycles were surveyed each month, ‘replicate’ was also included as a random factor, with ‘ID’ nested within it. Pairwise tests were run using the “emmeans” package (Lenth, 2021). To test for similarity between assemblages, a SIMPER analysis was run using Plymouth Routines in Multivariate Ecological Research (Primer-e v.7). To determine any relationship between algae cover and mean interaction time of shanny (*Lipophrys pholis*) and shore crabs (*Carcinus maenas*), two way ANOVAs were run with Algae Percentage Cover and Habitat as factors.

### 3. Results

A total of 8 mobile taxa were observed between April and October 2022 at the study site, including four invertebrates, three cryptobenthic fish and one demersal fish (Table 3). Of these, six were recorded in the rockpools and seven were recorded on the seawall. Three species were only recorded once: the sea slater *Idotea granulosa*, a sea spider (pycnogonida), and the three-spined stickleback fish *Gasterosteus aculeatus*. Two species, European bass *Dicentrarchus labrax* (Fig. 5) and the goby *Pomatoschistus* sp., were recorded most months.

#### 3.1. Species richness

Within the three artificial rockpool treatments (1, 3, 5 rockpool array), there was very little variation in species richness and no significant difference between treatments ( $p = 0.8501$ ). Pairwise tests revealed a weak significant difference in species richness between 3 and 5 rockpool treatments in June ( $p = 0.0496$ ). As a result, all rockpool treatments have been pooled.

The maximum species richness recorded was 5 on a single occasion in June on the control seawall. No species (0) were recorded on one tidal replicate in April and another in May, and this occurred predominantly in the rockpool habitat in the April tidal replicate and evenly in both habitats in the May tidal replicate. In both habitats, mean species richness remained relatively low throughout the study period, peaking at 3 species in June on the seawall (Fig. 6). There was a significant difference between the species richness in habitats over time ( $p = 0.0003$ ). The seawall was significantly more species rich than the rockpools in June, and the rockpools were significantly more species rich than the seawall in September (Table 4, Fig. 6).

#### 3.2. Abundance

There was no significant difference in species abundance between the three rockpool treatments ( $p = 0.4388$ ), though pairwise tests showed a significant difference in MaxN between single and 5 rockpool treatments ( $p = 0.0111$ ) in October. As a result, all rockpool treatments have been pooled.

**Table 3**

Mean MaxN per 60 min (standard deviation in brackets) of observed species within rockpool and seawall habitats observed at high tide between April and October 2022.

Common name	Taxonomic name	Rockpool	Seawall
Green shore crab	<i>Carcinus maenas</i>	0.98 (±0.92)	1.03 (±1.37)
Sea slater	<i>Idotea granulosa</i>	0	0.009 (±0.09)
Sea spider	Pycnogonid	0.008 (±0.09)	0
Prawn	<i>Palaemon</i> sp.	0.5 (±1.13)	0.4 (±0.56)
Three-spined stickleback	<i>Gasterosteus aculeatus</i>	0	0.009 (±0.09)
Shanny	<i>Lipophrys pholis</i>	1.26 (±0.97)	1.11 (±0.92)
Goby	<i>Pomatoschistus</i> sp.	0.02 (±0.13)	0.23 (±0.46)
European bass	<i>Dicentrarchus labrax</i>	0.13 (±0.33)	0.04 (±0.2)
<b>Total</b>		<b>6</b>	<b>7</b>



Fig. 5. A crab (*Carcinus maenas*) on a control section of seawall (left) and a bass (*Dicentrarchus labrax*) and crab (*C. maenas*, partially obscured by seaweed) in a rockpool (right).

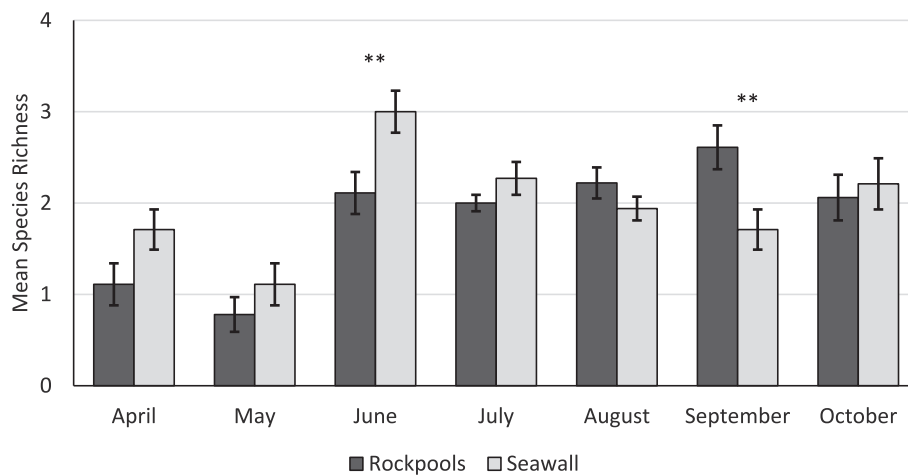


Fig. 6. Mean species richness over time. Statistically significant interactions indicated by \* (<0.05), \*\* (<0.01) and \*\*\* (<0.001). Error bars show standard error.

Table 4

Pairwise results for species richness (habitat\*month). Bold values indicate significant result.

Factor	Estimate	SE	df	t.ratio	p.value
April	-0.5591	0.304	17	-1.838	0.0836
May	-0.3662	0.304	17	-1.204	0.245
June	-0.9005	0.304	17	-2.962	<b>0.0087</b>
July	-0.2908	0.317	17	-0.917	0.3719
August	0.2979	0.308	17	0.967	0.3472
September	0.9423	0.308	17	3.059	<b>0.0071</b>
October	-0.1805	0.324	17	-0.557	0.5846

The maximum abundance recorded was 12 organisms in October, which can be attributed to an aggregation of prawns in the rockpool basin. Mean abundance remained low in the spring months (April, May) before peaking in June for the seawall with 3.9 organisms and peaking in August for the rockpools with 2.9 organisms (Fig. 7). There was a significant difference for MaxN between months and habitats and months (Table 9 Appendix). The abundance in both habitat changes over time, with little difference between abundance in habitats in April, May and July, but in June the abundance on the seawall is significantly higher. Conversely, from August to October the reverse is true, with abundance in the rockpools significantly higher (Table 5).

### 3.3. Assemblages

Shanny, prawns and crabs were recorded throughout the study period, and formed the predominant mobile assemblage associated with both the seawall and the rockpools. Gobies first appeared in the seawall habitat in June and were then occasionally observed on the seawall until the end of the study period. One goby was observed on two consecutive tides in September using the same rockpool, but gobies were otherwise absent from the rockpools. Juvenile bass were rarely observed in July in the seawall habitats, before appearing more frequently in both habitats in August, September and October. While their infrequent appearances in the earlier part of the study period were exclusively in seawall habitat, their increased presence in the latter months can be attributed to their visitations of the rockpools.

A SIMPER analysis revealed an average similarity of 43.10% and 45.05% within the seawall and within the rockpools respectively. Between the seawall and rockpools, there was an average dissimilarity of 57.05%, with shannies, crabs and prawns contributing 85.5% to the dissimilarity, and all other species contributing to the remainder. Average similarity between habitats ranged from 58% (September) to 84% (July) over the study period.

### 3.4. Behaviour

At the end of the study period, the mean length of interaction for all organisms at the study site was 101 s and ranged between 81 s (August)

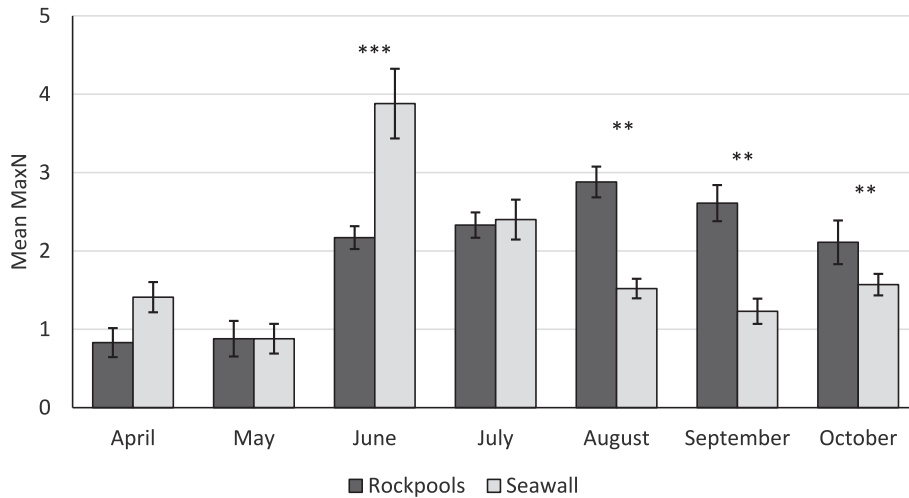


Fig. 7. Mean abundance over time. Statistically significant interactions indicated by \* (<0.05), \*\* (<0.01) and \*\*\* (<0.001). Error bars show standard error.

Table 5

Pairwise results for MaxN (habitat\*month). Bold values indicate significant result.

Factor	Estimate	SE	df	t.ratio	p.value
April	-0.57848	0.39	17	-1.483	0.1565
May	0.00902	0.39	17	0.023	0.9818
June	-1.7317	0.39	17	-4.435	<b>0.0004</b>
July	-0.05928	0.402	17	-0.147	0.8846
August	1.36115	0.391	17	3.486	<b>0.0028</b>
September	1.39223	0.391	17	3.565	<b>0.0024</b>
October	1.19755	0.411	17	2.914	<b>0.0097</b>

to 194 s (October). Apart from June, organisms spent more time interacting with the rockpools than the seawall each month, significantly so between August and October. Only in April and May was there little difference between the rockpools and seawall (Fig. 8).

The longest time an organism spent interacting with a habitat was the full hour, and this occurred on four occasions exclusively with shore crabs resting in the rockpools. The longest time an organism spent interacting with the seawall was a crab resting for 2884 s, or just over 48 min.

3.5. Crabs

There were no significant differences between the three rockpool (1,

3 or 5 rockpools) treatments for all crab behaviours. Pairwise tests found weakly significant differences between single and 3 rockpools in October for crab movement ( $p = 0.0309$ ). As a result, all rockpool treatments have been pooled. There was no relation between algae percent cover and the mean interaction time for crabs ( $p \geq 0.05$ ).

Total time crabs spent interacting with the habitats was significantly different (Table 9 Appendix) across the study period (habitat\*month,  $p = 0.0030$ ). In every month except June, crabs spent on average more time in the rockpools, significantly so from July onwards (Fig. 9).

Over the study period, crabs spent on average 43% of time resting, 28% of time feeding, 26% of time moving, and 3% of time engaging in conspecific behaviours. Crabs spent over double the amount of time resting in rockpools than they did on the seawall. Conversely, crabs spent almost triple the amount of time engaging in locomotive behaviour on the seawall than in the rockpools. Conspecific behaviour, notably pre-copulatory behaviour, was only observed in the rockpools.

Crabs spent more time feeding in the rockpools than the seawall except for June and October, though this was not significant. There was no significant difference in time spent feeding over the study period (habitat\*month,  $p = 0.1080$ ) or between habitats ( $p = 0.9198$ , Table 9 Appendix). Time spent resting peaked in August with 976 s in rockpools and 313 s on the seawall in June, and time spent feeding peaked in April for the rockpools 847 s and 722 s in June for the seawall. Crabs spent significantly more time (habitat,  $p = 0.0006$ ) resting in the rockpools compared to the seawall (Fig. 10), including over the study period (habitat\*month,  $p = 0.0055$ , Table 9 Appendix). Time crabs spent

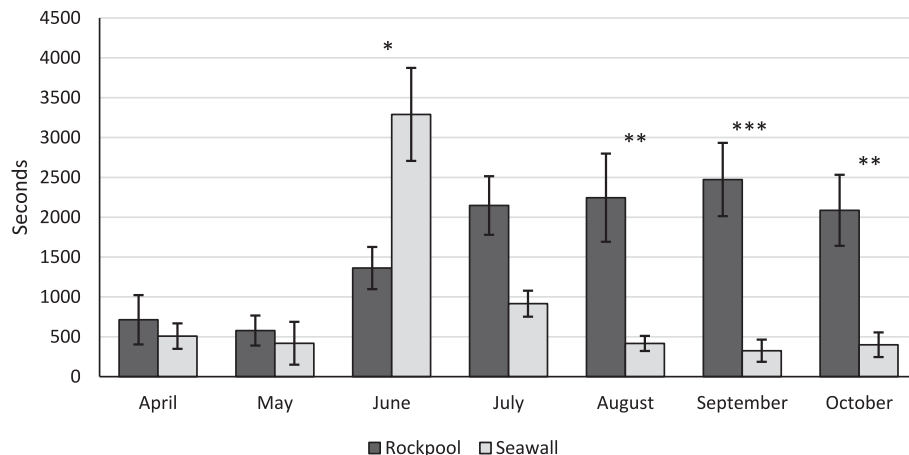
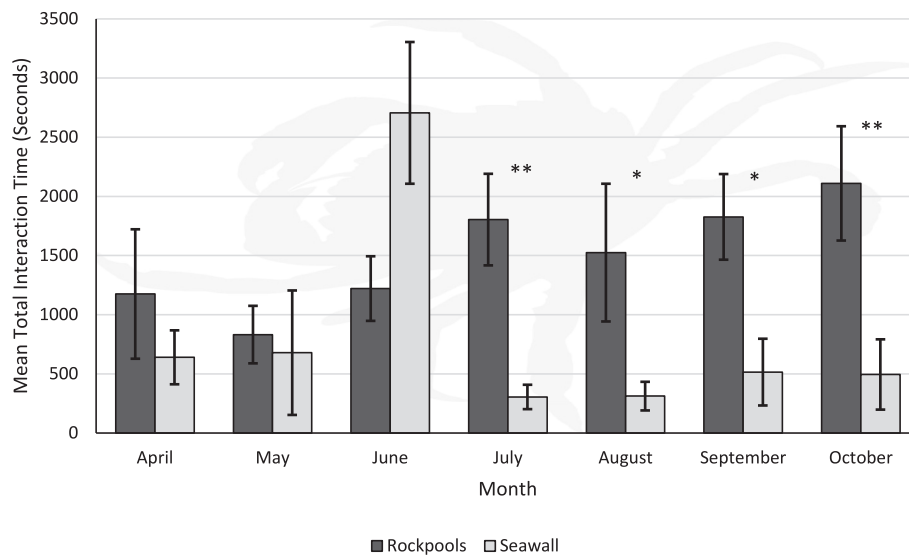


Fig. 8. Mean total interaction times in the rockpools and the seawall across the study period. Error bars show standard error.



**Fig. 9.** Mean length of interaction crabs had with both habitats (rockpools, seawall). Statistically significant interactions indicated by \* (<0.05), \*\* (<0.01) and \*\*\* (<0.001). Error bars show standard error.

moving in both habitats remained below 200 s in May, July, August and September, but peaked in the rockpools in October with 299 s and on the seawall in June with 1084 s. There was no significant difference in time spent moving (habitat,  $p = 0.0531$ ) between habitats (Fig. 10), including over the study period (habitat\*month,  $p = 0.2325$ , Table 9 Appendix), though crabs spent significantly more time moving on the seawall than the rockpools in June (Table 6). June was particularly notable, as large numbers of small crabs were observed on the seawall and is reflected in overall MaxN trends (Fig. 7).

### 3.6. Shanny

There were no significant differences between the three rockpool (1, 3 or 5 rockpools) treatments for all shanny behaviours, except for treatment\*month for moving behaviour. Analyses for shanny behaviour omitted data from June as shanny did not interact with 3 rockpool treatments during this month. For shanny movement between single and 3 rockpools in April ( $p = 0.0449$ ) and between 3 and 5 rockpools in September ( $p = 0.0137$ ), there were weak significant differences. Total interaction time for shanny was also significantly different between 3 and 5 rockpools in October ( $p = 0.0088$ ). As a result, all rockpool treatments have been pooled. There was a weakly significant relationship between algae percent cover and mean interaction time for shanny ( $p = 0.012$ ) compared to a moderately significant relationship between habitat and mean interaction time ( $p = 0.0043$ ).

Total time shanny spent interacting with the habitats was significantly different (habitat,  $p = 0.0042$ ) (Figure x), including across the study period (habitat\*month,  $p \leq 0.0001$ , Table 9 Appendix). Except for April, August and September, where mean shanny interaction time was significantly greater in the rockpools than the seawall (Table 7), there is little difference in shanny interaction time between the habitats (Fig. 11).

Over the study period, shanny spent on average 73% of time moving, 26% of time resting, and only 2% of time engaging in conspecific behaviours. Shanny spent 72% and 75% of their time moving on the rockpools and the seawall respectively. Similarly, there is little difference in the time spent resting in both habitats, with 27% and 24% of resting time spent on the rockpools and seawall respectively. Conspecific behaviour was only observed in the rockpools.

Shanny spent significantly more time resting in the rockpools than the seawall in August (Fig. 12, Table 7). Time spent resting peaked in September with 521 s in rockpools and 228 s on the seawall in June.

Time shanny spent resting within the habitats was not significantly different (habitat,  $p = 0.1508$ , Table 9 Appendix), but time spent resting was weakly significant when factoring in month (habitat\*month,  $p = 0.0339$ ).

Time spent engaging in locomotive behaviour in both habitats increased in the summer months but declined to pre-summer levels in September and October. Locomotive behaviour peaked in the rockpools in August with 629 s and on the seawall in June with 228 s. Time shanny spent moving within the habitats was significantly different (habitat,  $p = 0.0086$ , Table 9 Appendix), including over the study period (habitat\*month,  $p \leq 0.001$ ), with significantly more time spent moving in the rockpools in August and October than the seawall (Fig. 12, Table 7).

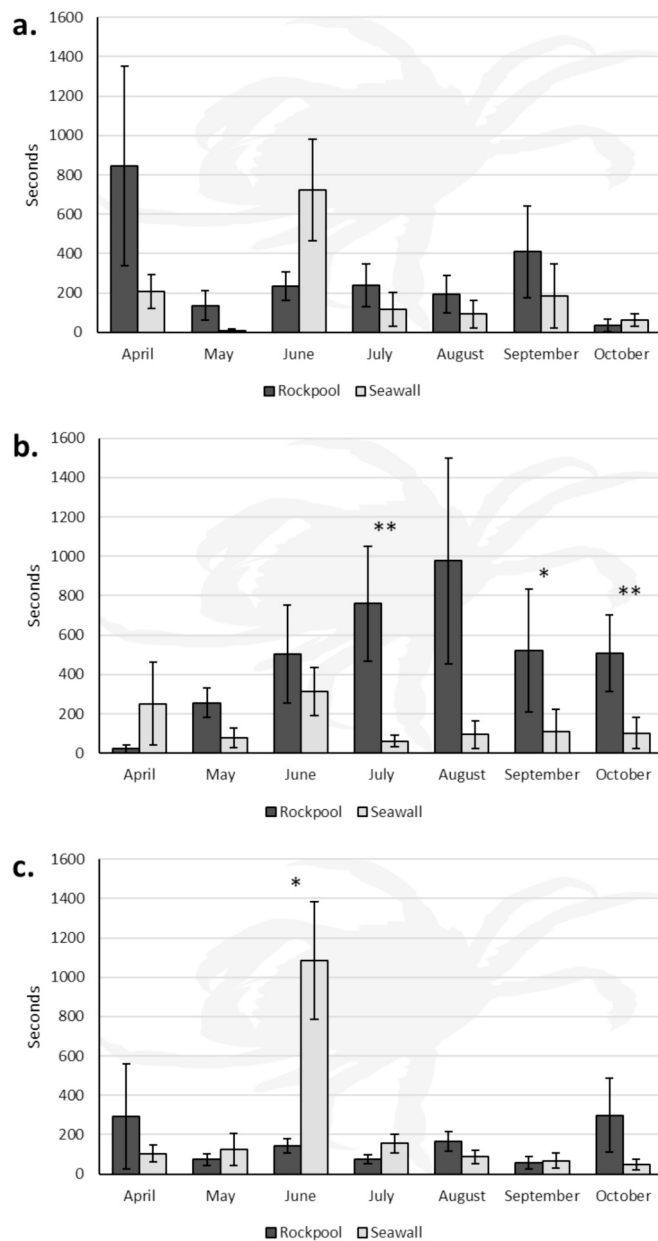
The mean number of bites observed peaked in September, and throughout the study period more bites were observed on the seawall than the rockpool, with no bites observed on the rockpools during April and May. Shanny bites differed significantly between habitats ( $p = 0.0425$ ) and between rockpools and seawall over time (habitat\*month  $p \leq 0.0001$ , Table 9 Appendix). Significantly more bites were observed in June, July and September on the seawall than on the rockpools (Fig. 13, Table 8). Shanny were observed to be feeding predominantly on barnacles, though on a handful of occasions were observed to pluck small littorinid snails from the substrate before dropping them. On one occasion, a shanny preyed on a small crab in the rockpool.

## 4. Discussion

The abundance and species richness of mobile fauna utilising both the rockpools and seawall at high tide is not significantly different overall, which is consistent with the existing literature (Mercader et al., 2017; Morris et al., 2017). Yet, organisms generally spent more time in the rockpools than on the seawall, but this was not consistent over the study period, or consistent within crabs or shannies.

Crabs spent more time throughout the study period in the rockpools than the seawall, particularly to rest. Although determining size of organisms was beyond the scope of this study, crabs that used the rockpools were generally of a larger size than the crabs that predominantly used the seawall. This was particularly evident in June, when a relatively high abundance of small crabs (< 2 cm) was recorded on the seawall, both feeding and moving over the extensive coverage of barnacles. Juvenile crabs in lab experiments have shown to preferentially feed on barnacle cirri over littorinid snails (Rangeley and Thomas, 1987) and the partial predation on barnacles in this study is consistent with





**Fig. 10.** Mean length of time crabs spent feeding (a), resting (b), and moving (c) in both habitats (rockpools, seawall). Statistically significant interactions indicated by \* (<0.05), \*\* (<0.01) and \*\*\* (<0.001). Error bars show standard error.

that observed by Burrows et al. (1999). Although barnacles have been recorded inside the rockpools, their coverage is comparatively minimal. Consequently, the rockpools may not have provided sufficient food for the high abundance of juvenile crabs compared to the barnacle-covered seawall during June. In addition, the high percentage cover of canopy-forming furoid algae on the rockpools may have obscured organisms from view, leading to an underestimation of smaller crabs in the rockpools. Juvenile crab carapaces often feature white pigmentation that aids camouflage on a light-coloured, barnacle-dominated substrate (Todd et al., 2006; Stevens et al., 2014). This pigmentation usually disappears in older, larger crabs (Bedini, 2002; Todd et al., 2006) that prefer dark, macroalgal-dominated habitats (Hogarth, 1975; Orlosk et al., 2011; Barr and Elwood, 2011; Twort and Stevens, 2023) which has been shown to provide spatial refuge from predation by gulls (Dumas and Witman, 1993). The dimly lit rockpool basins shadowed by the overlying algae canopy would have provided such spatial refuge and

**Table 6**

Pairwise results for crab behaviour in artificial rockpool versus seawall for each month. Bold values indicate significant result.

Factor	Estimate	SE	df	t.ratio	p.value
<b>Total Time</b>					
April	0.2617	0.794	17	0.329	0.7458
May	1.6483	0.86	17	1.916	0.0723
June	-0.6981	0.55	17	-1.269	0.2216
July	1.7983	0.571	17	3.148	<b>0.0059</b>
August	1.3841	0.644	17	2.149	<b>0.0463</b>
September	1.999	0.763	17	2.621	<b>0.0179</b>
October	2.2595	0.72	17	3.138	<b>0.006</b>
<b>Moving</b>					
April	-1.03001	1.121	17	-0.919	0.3709
May	0.90739	1.216	17	0.746	0.4656
June	-1.98587	0.766	17	-2.593	<b>0.0189</b>
July	-0.80305	0.796	17	-1.009	0.327
August	0.53638	0.902	17	0.595	0.5597
September	-1.3505	1.075	17	-1.257	0.2259
October	0.02023	1.013	17	0.02	0.9843
<b>Resting</b>					
April	-1.8627	1.58	17	-1.179	0.2548
May	2.5707	1.73	17	1.486	0.1557
June	-0.1682	1.07	17	-0.158	0.8764
July	3.8463	1.11	17	3.472	<b>0.0029</b>
August	2.4374	1.27	17	1.925	0.0712
September	4.3246	1.52	17	2.841	<b>0.0113</b>
October	4.7558	1.43	17	3.332	<b>0.0039</b>
<b>Feeding</b>					
April	1.9113	1.47	17	1.3	0.211
May	2.6792	1.602	17	1.672	0.1128
June	-1.5002	0.995	17	-1.508	0.1498
July	1.505	1.034	17	1.455	0.1638
August	0.9449	1.178	17	0.802	0.4336
September	0.224	1.412	17	0.159	0.8758
October	-1.5747	1.327	17	-1.186	0.2518

**Table 7**

Pairwise results for shanny behaviour in artificial rockpool versus seawall for each month. Bold values indicate significant result.

Factor	Estimate	SE	df	t.ratio	p.value
<b>Total Time</b>					
April	1.4712	0.622	17	2.365	<b>0.0302</b>
May	0.3504	0.685	17	0.512	0.6155
June	-0.792	0.486	17	-1.628	0.1219
July	-0.286	0.44	17	-0.65	0.5245
August	1.5373	0.427	17	3.596	<b>0.0022</b>
September	2.2539	0.48	17	4.691	<b>0.0002</b>
October	0.1966	0.477	17	0.412	0.6852
<b>Moving</b>					
April	0.8006	0.652	17	1.229	0.236
May	0.0478	0.716	17	0.067	0.9476
June	-0.8584	0.514	17	-1.671	0.1131
July	-0.4353	0.466	17	-0.934	0.3633
August	1.6732	0.453	17	3.692	<b>0.0018</b>
September	2.5729	0.507	17	5.071	<b>0.0001</b>
October	0.4916	0.504	17	0.976	0.3428
<b>Resting</b>					
April	0.583	1.205	17	0.484	0.6346
May	0.0402	1.326	17	0.03	0.9762
June	-0.7726	0.945	17	-0.818	0.4247
July	0.6162	0.855	17	0.721	0.481
August	3.0775	0.831	17	3.704	<b>0.0018</b>
September	0.9101	0.933	17	0.976	0.3429
October	-0.4944	0.926	17	-0.534	0.6002

supports the observations in this study of smaller, lighter crabs generally being observed on the barnacle-dominated seawall and the larger, darker crabs on the macroalgae-dominated rockpools. Crabs spent significantly more time resting in the rockpools than the seawall. This was usually in the basin, below the relief of the rockpool rim, or occasionally on the rim but lodged in the interstices between furoid hold-fasts. This suggests that the rockpools, through enhanced epilithic

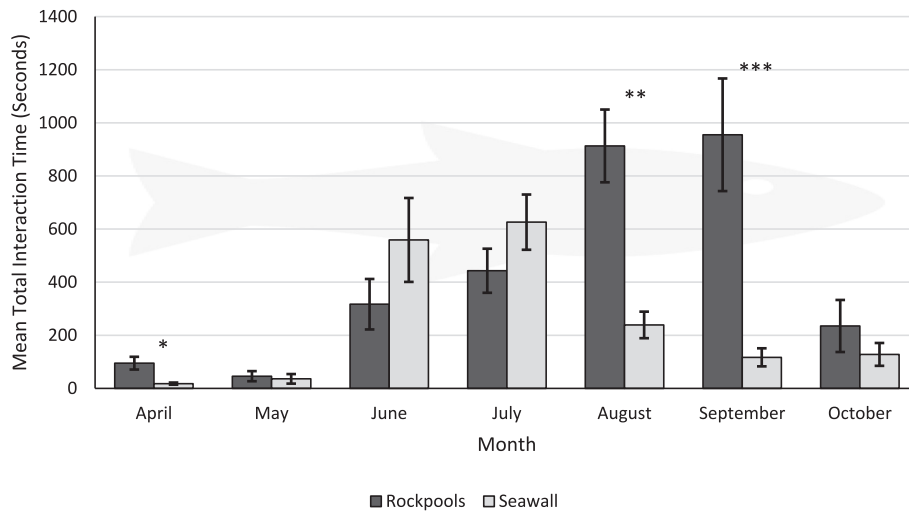


Fig. 11. Mean total length of interaction shanny had with both habitats (rockpools, seawall). Error bars show standard error. Statistically significant interactions indicated by \* (<0.05), \*\* (<0.01) and \*\*\* (<0.001).

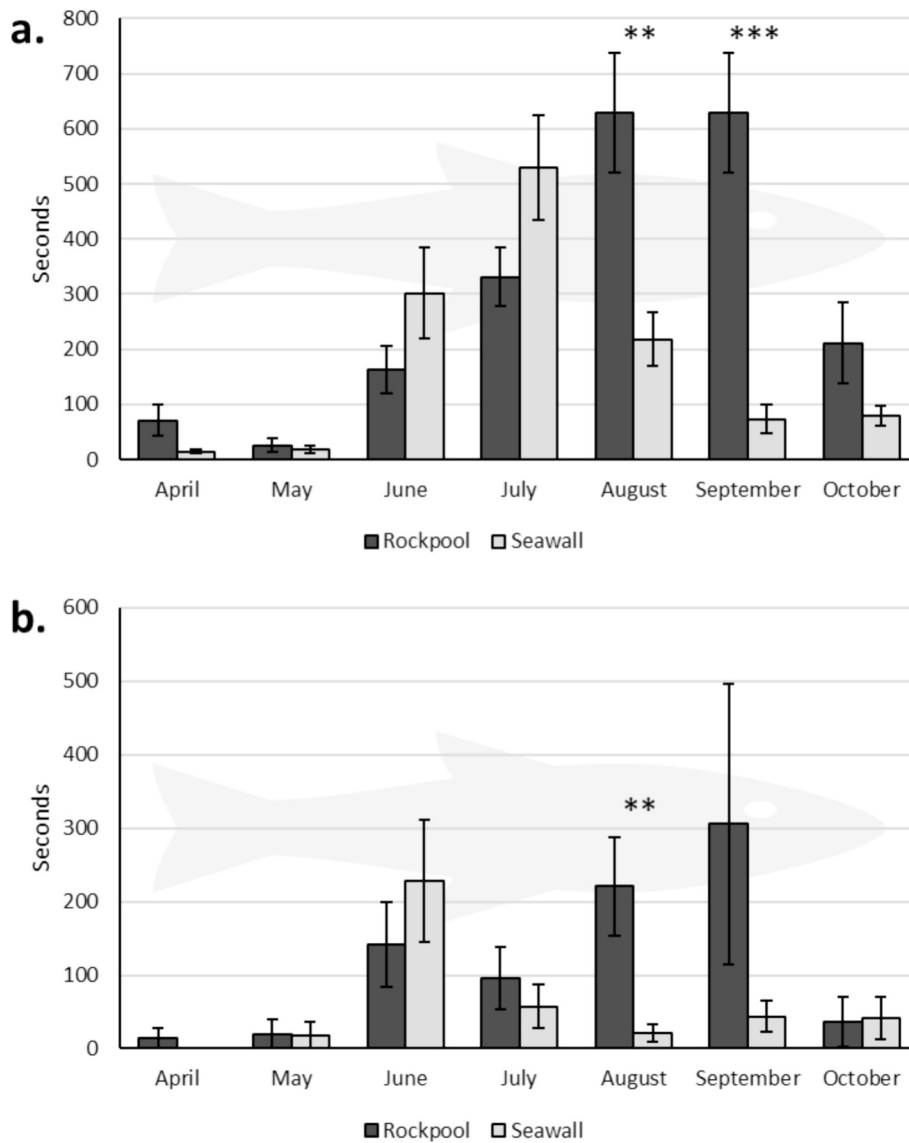
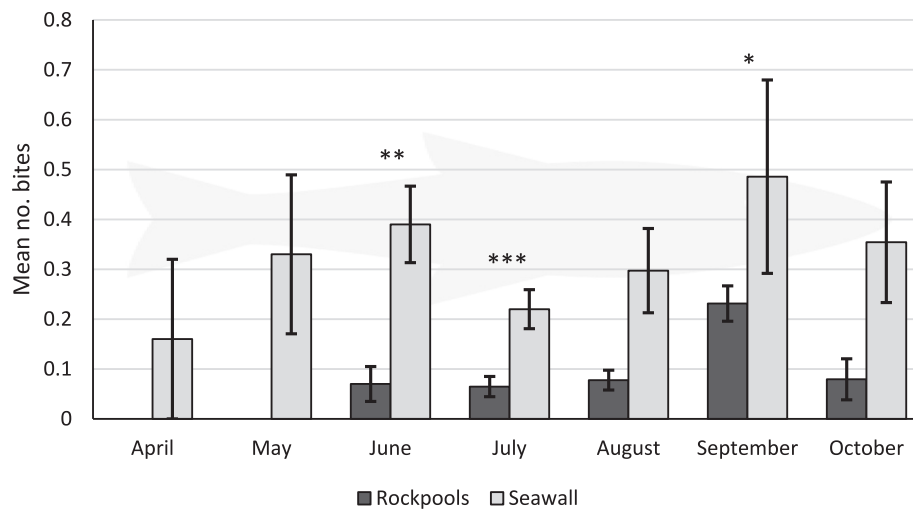


Fig. 12. Mean length of time shanny spent moving (a) and resting (b) in both habitats (rockpools, seawall). Statistically significant interactions indicated by \* (<0.05), \*\* (<0.01) and \*\*\* (<0.001). Error bars show standard error.



**Fig. 13.** The mean number of bites performed by shanny fish in a 60 min period in both habitats over time. Error bars show standard error. Statistically significant differences indicated by \* (<0.05), \*\* (<0.01) and \*\*\* (<0.001).

**Table 8**

Pairwise results for total number of shanny bites in artificial rockpool versus seawall for each month. Bold values indicate significant result.

Bites	Estimate	SE	df	t.ratio	p.value
April	-0.1244	0.366	17	-0.34	0.7382
May	-0.3161	0.403	17	-0.784	0.4439
June	-0.9742	0.286	17	-3.404	<b>0.0034</b>
July	-1.0584	0.259	17	-4.087	<b>0.0008</b>
August	0.0532	0.251	17	0.211	0.8351
September	0.7236	0.283	17	2.559	<b>0.0203</b>
October	-0.4713	0.28	17	-1.68	0.1112

complexity, provide sufficient shelter that is otherwise not present on the seawall. Crothers (1968) determined that crabs are unlikely to be found resting in open and homogenous habitat, such as the seawall, and are more likely to be sheltering in crevices. Rockpools were the only habitat where reproductive behaviour was observed, with male crabs gripping females in a pre-copulatory position in the rockpool basin. The mobility of male crabs in pre-copulation is limited (Adams and Greenwood, 1985; Van der Meeren, 1994) and so the more sheltered nature of rockpools may permit pre-copulatory pairs to minimise movement that would otherwise be necessary to prevent dislodgement on a turbulent and exposed seawall. As retrofitted rockpools can disrupt hydrodynamics on a vertical seawall (Salaudin et al., 2021), this may benefit crab foraging efficiency where flow rates are reduced (Robinson et al., 2011). As observed by Sheehan et al. (2010) with crab-tiles, artificial crab habitats on intertidal soft sediment, crabs may spend more time in rockpool habitats at high tide to guard it for their use as refugia at low tide.

Shanny spent significantly more time in the rockpools for three of the months. Goncalves and Almada (1998) found that shanny minimized the time spent outside of their nest territories, which reduces the time spent in turbulent intertidal conditions, such as on the seawall, where the risk of physical injury and dislodgement is high. Conversely, shanny fed significantly more on the seawall than the rockpools. It is clear in this study that the cryptobenthic shanny use the rockpools as shelter but prefer the feeding opportunities of the seawall. This is consistent with the results of Ushiana et al. (2019) which found that feeding activity of cryptobenthic fish was greater on flat tiles than structurally complex tiles. The prey available on the seawall better supports the preferred shanny diet (Maze et al., 1999), particularly for the relatively small shannies observed during this study (Faria and Almada, 2008). Shanny are visual feeders (Gibson, 1970; Davenport et al., 2023), and so feeding

on the well-illuminated seawall may explain their preference. Fish predation pressure on sessile invertebrates increases in areas of lower structural complexity (Bolton et al., 2018). There was a weakly significant relationship between algae cover and mean interaction time with shanny, but as high algae cover was strongly associated with the rockpools, it is not possible to disentangle which factor is most responsible, though it is likely a combination. Shanny were observed navigating the relatively flat and featureless surface of the seawall by resting in the interstices of barnacle tests where the concrete substrate was exposed or on the leeward side of limpets, as the majority of those observed were relatively small.

Shanny will navigate to dark, shadowy crevices when threatened (Dodd et al., 2000). Indeed, the greater algal canopy cover and structural complexity of the rockpools offers cryptobenthic fish enhanced predator avoidance (Schofield, 2003; Gregor and Anderson, 2016), and the crevices and interstices that occur on the rockpool substrate provide habitat more suited for shanny body size (Randall, 1963; Hixon and Beets, 1989; Nunes et al., 2019). It was observed in this study, though not formally recorded, that shanny would squeeze into the narrow gap between the back of the rockpool and the seawall. It has been suggested that shanny activity is greatest at flooding or high tide in the morning, when shanny are likely to be hungriest as they do not feed at night (Burrows et al., 1999; Faria and Almada, 2006). Therefore, later diurnal high tides may bring about differences in the drivers of shanny activity and consequently their interactions with the rockpools and the seawall. Shanny show fidelity to a network of shelter sites and will access them based on a hierarchy of dominance mediated by body size (Almada et al., 1983; Faria and Almada, 2006). The majority of shanny observed in this study were relatively small, with very few incidences of agonistic behaviour which suggests that although the rockpools may increase the likelihood of intraspecific interaction through provision and concentration of shelter spaces, shelter spaces are not so few that competition is fierce.

The recording of these behaviours in the rockpool demonstrate the importance of habitat provision on habitat-poor artificial coastal structures, particularly when it may boost mating opportunities and reduce predation risk. However, it is evident that the seawall also provides habitat resources, such as food provision for juvenile crabs and shanny, which highlights the importance of habitat heterogeneity and patchiness of habitat features and complexity (Paxton et al., 2017; Ushiana et al., 2019; Hall et al., 2021; Bishop et al., 2022) to support species' different requirements throughout their life history. Canopy-forming fucoid growth was strongly associated with the rockpool habitat, while high coverage of barnacles was strongly associated with the seawall. The high

abundance of furoid algae on the rockpools was likely by virtue of the rugose texture and horizontal orientation on the rockpool rim, where furoid holdfasts were predominantly fixed, providing a sufficient settlement surface (Fletcher and Callow, 1992) and adequate sun exposure. This topside algal colonisation has been observed with artificial rockpools of a similar commercial model elsewhere in the UK (Drakard et al., 2023) and artificial reefs (Herbert et al., 2017). Vegetated/ complex and non-vegetated/ less complex habitats are important for shore crabs at different life history stages (Amaral et al., 2009) and so the vegetated complexity of the rockpools mixed with the comparatively structurally simple seawall may support shore crabs from juveniles to adults.

Further study should focus on the connectivity between ecological enhancement habitats and the substrate they are on. This study was limited by the camera orientation that only permitted recording of the topside of the rockpools, when it was evident that mobile fauna was moving back and forth over the rim and potentially using the underside of the rockpools and gaps between closely grouped rockpools. The set-up also potentially excluded interactions from demersal fish which may have been attracted to the rockpools or interacted with the rockpool underside but did not appear on camera. Replication at a larger scale, for example filming away from but looking back at the rockpool and the surrounding seawall, would provide a greater understanding as to the wider spatial impact of the rockpools. We did not pursue this due to logistical challenges and the very public nature of the study site. It is clear from existing literature that shanny and shore crab behaviour may differ between day and night (Davenport et al., 2023). Therefore, elucidating habitat use of the seawall and rockpools at night would be beneficial as to date no behavioural studies of ecological enhancements have been performed at night.

Lack of significant differences between the rockpool treatments (1, 3 or 5 rockpools) may have been due to the camera recording only a single, central rockpool, whereas there may have been greater activity at the edges of the array. Yet it may also indicate that these multiple-pool arrays do not offer any additional habitat benefits other than replicating that of individual pools. Therefore, the array, as designed, may not create habitat complexity above that of the sum of the individual component pools.

Intertidal ecological enhancement often focuses on shelter provision at low tide and incorporates features that are skewed to that requirement. However, some of the features seen in subtidal artificial reefs (deep holes, tunnels and other 'swim-through' features) have relevance in the intertidal at high tide, despite their potentially lower habitat value at low tide. It was noted by Faria and Almada (2008) that crevices and holes for larger adult shanny (15–20 cm) were usually absent from natural rocky shores, and so there may be value in providing larger holes to support individual taxa throughout their life histories. As demersal fish also use artificial coastal structures, as observed in this study and others (Herbert et al., 2017; Hall et al., 2021), there is justification for enhancement features that cater to their habitat needs (see Morris et al., 2018a, 2018b). Providing enhancement that encourages epilithic complexity, such as canopy-forming macroalgae, will provide additional habitat value that the enhancement alone cannot. For cryptobenthic fish, holes and cracks that match their body sizes would benefit their survival. With artificial rockpools, this could be achieved by varying the space between the back of the rockpools and the seawall, as has been incorporated in Sydney by Bishop et al. (2022) and *Artecology Ltd.* (personal communication) creating different habitat spaces. Other design choices can be made to avoid undesirable abiotic conditions, such as increased temperatures at low tide, for example by adding overhangs to create shaded areas and by creating a deeper basin that retains a greater volume of water. Features such as these may ameliorate extreme temperature values exacerbated by climate change. It is important any ecological enhancement design and deployment is implemented with the advice and recommendation of a local ecologist, particularly on urbanised coasts. Enhancement should be considered on a site-by-site basis, as features are not one-size-fits-all, and enhancement should not

be used to greenwash construction schemes (Firth et al., 2020).

## 5. Conclusion

Our study has shown that while intertidal ecological enhancements can sometimes have limited impact on the abundance and species richness of mobile fauna at high tide, they provide crucial habitat that allow organisms such as crabs and cryptobenthic fish, to rest, mate and find refuge. It is evident that both flat seawalls predominantly covered in barnacles and artificial rockpools predominantly covered in macroalgae are both important for the survival of intertidal mobile fauna. A patchwork of different surfaces and features would therefore best support these species at high tide, in addition to adding features more commonly seen on subtidal artificial reefs, such as deep crevices, holes and tunnels.

## CRedit authorship contribution statement

**Jessica R. Bone:** Writing – review & editing, Writing – original draft, Visualization, Validation, Supervision, Software, Resources, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Alice E. Hall:** Writing – review & editing, Supervision, Methodology, Formal analysis, Conceptualization. **Rick Stafford:** Writing – review & editing, Supervision, Funding acquisition, Formal analysis, Conceptualization. **Nazih F. Mir:** Data curation, Investigation, Methodology. **Jeesa Benny:** Data curation, Investigation, Methodology. **Roger J.H. Herbert:** Writing – review & editing, Supervision, Resources, Methodology, Funding acquisition, Formal analysis, Conceptualization.

## Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

## Data availability

Data will be made available on request.

## Acknowledgements

This research formed part of the Marineff Project, selected by Interreg France Channel England which was co-funded by the European Regional Development Fund. We are grateful to the students and staff who assisted with fieldwork (Sam Greenhill and Peter Lewis).

## Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.ecoleng.2024.107318>.

## References

- Adams, A., Greenwood, P.J., 1985. Environmental constraints on mate choice in *Gammarus pulex*. *Crustaceana* 50, 45–52.
- Aguilera, M.A., Broitman, B.R., Thiel, M., 2014. Spatial variability in community composition on a granite breakwater versus natural rocky shores: lack of microhabitats suppresses intertidal biodiversity. *Mar. Pollut. Bull.* 87 (1–2), 257–268. <https://doi.org/10.1016/j.marpolbul.2014.07.046>.
- Almada, V.C., Dores, J., Pinheiro, A., Pinheiro, M., Santos, R.S., 1983. Contribuicao para o estudo do comportamento de *Coryphoblennius galerita* (L.) (Pisces: Blenniidae). *Mem. Mus. Mar. Ser. Zool.* 2 (24), 1–166.
- Amaral, V., Cabral, H.N., Jenkins, S., Hawkins, S., Paula, J., 2009. Comparing quality of estuarine and nearshore intertidal habitats for *Carcinus maenas*. *Estuar. Coast. Shelf Sci.* 83 (2), 219–226.
- Baine, M., 2001. Artificial reefs: a review of their design, application, management and performance. *Ocean Coast. Manag.* 44, 241–259.

- Barr, S., Elwood, R.W., 2011. No evidence of morphine analgesia to noxious shock in the shore crab, *Carcinus maenas*. *Behav. Process.* 86 (3), 340–344.
- Becker, A., Coppinger, C., Whitfield, A.K., 2012. Influence of tides on assemblages and behaviour of fishes associated with shall seagrass edges and bare sand. *Mar. Ecol. Prog. Ser.* 456, 187–199.
- Bedini, R., 2002. Colour change and mimicry from juvenile to adult: *Xantho poressa* (Olivieri, 1792) (Brachyura, Xanthidae) and *Carcinus maenas* (Linnaeus, 1758) (Brachyura, Portunidae). *Crustaceana* 75, 703–710.
- Bender, A., Langhamer, O., Sundberg, J., 2020. Colonisation of wave power foundations by mobile mega- and macrofauna—a 12 year study. *Mar. Environ. Res.* 161, 105053.
- Bergen, S.D., Bolton, S., Fridley, J., 2001. Design principles for ecological engineering. *Ecol. Eng.* 18 (2), 201–210. [https://doi.org/10.1016/S0925-8574\(01\)00078-7](https://doi.org/10.1016/S0925-8574(01)00078-7).
- Bishop, M.J., Vozzo, M.L., Mayer-Pinto, M., Dafforn, K.A., 2022. Complexity–biodiversity relationships on marine urban structures: reintroducing habitat heterogeneity through eco-engineering. *Philos. Trans. R. Soc. B* 377, 20210393.
- Bolton, D.K., Johnston, E.L., Coleman, M.A., Clark, G.F., 2018. Caught between a rock and a hard place: fish predation interacts with crevice width and orientation to explain sessile assemblage structure. *Mar. Environ. Res.* 140, 31–40.
- Burrows, M.T., Kawai, K., Hughes, R.N., 1999. Foraging by mobile predators on a rocky shore: underwater TV observations of movements of blennies *Lipophrys pholis* and crabs *Carcinus maenas*. *Mar. Ecol. Prog. Ser.* 187, 237–250.
- Campbell, M.D., Salisbury, J., Caillouet, R., Driggers, W.B., Kilfoil, J., 2018. Camera field-of-view and fish abundance estimation: a comparison of individual-based model output and empirical data. *J. Exp. Mar. Biol. Ecol.* 501, 46–53.
- Cappo, M., Speare, P., De'Ath, G., 2004. Comparison of baited remove underwater video stations (BRUVS) and prawn (shrimp) trawls for assessments of fish biodiversity in the inter-reefal areas of the Great Barrier Reef Marine Park. *J. Exp. Mar. Biol. Ecol.* 302, 123–152.
- Cappo, M., Harvey, E., Shortis, M., 2007. Counting and measuring fish with baited video techniques – an overview. In: Furlani, D., Beumer, J.P. (Eds.), *Proceedings of the Australian Society for Fish Biology Workshop*, Hobart, August 2007. Australian Society of Fish Biology, Australia, pp. 101–114.
- Chapman, M.G., 2003. Paucity of mobile species on constructed seawalls: effects of urbanisation on biodiversity. *Mar. Ecol. Prog. Ser.* 264, 21–29. <https://doi.org/10.3354/meps264021>.
- Chapman, M.G., Underwood, A.J., 2011. Evaluation of ecological engineering of “armoured” shorelines to improve their value as habitat. *J. Exp. Mar. Biol. Ecol.* 400 (1–2), 302–313. <https://doi.org/10.1016/j.jembe.2011.02.025>.
- Claissie, J.T., Pondella, D.J., Love, M., Zahn, L.A., Williams, C.M., Williams, J.P., Bull, A.S., 2014. Oil platforms off California are among the most productive marine fish habitats globally. *Proc. Natl. Acad. Sci. USA* 111, 15462–15467.
- Claissie, J.T., Pondella, D.J., Love, M., Zahn, L.A., Williams, C.M., Bull, A.S., 2015. Impacts from partial removal of decommissioned oil and gas platforms on fish biomass and production on the remaining platform structure and surrounding Shell mounds. *PLoS One* 10, 1–19.
- Connell, S.D., Glasby, T.M., 1999. Do urban structures influence local abundance and diversity of subtidal epibiota? A case study from Sydney Harbour, Australia. *Mar. Environ. Res.* 47 (4), 373–387. [https://doi.org/10.1016/S0141-1136\(98\)00126-3](https://doi.org/10.1016/S0141-1136(98)00126-3).
- Crothers, J.H., 1968. The biology of the shore crab *Carcinus maenas* (L.) 2. The life of the adult crab. *Field Stud.* 2, 579–614.
- Davenport, J., Jessopp, M., Harman, L., Micaroni, V., McAllen, R., 2023. Feeding, agonistic and cooperative behavioural responses of shallow-water benthic marine scavengers. *J. Nat. Hist.* 57 (17–20), 1049–1065.
- Dodd, J., Gibson, R.N., Hughes, R.N., 2000. Use of cues by *Lipophrys pholis* L. (Teleostei, Blenniidae) in learning the position of a refuge. *Behav. Process.* 49 (2), 69–75.
- Drakard, V.F., Brooks, P.J., Crowe, T.P., Earp, H.S., Thompson, B., Bourke, N., George, R., Piper, C., Moore, P.J., 2021. *Fucus vesiculosus* populations on artificial structures have potentially reduced fecundity and are dislodged at greater rates than on natural shores. *Mar. Environ. Res.* 168, 105324.
- Drakard, V.F., Evans, A.J., Crowe, T.P., Moore, P.J., Coughlan, J., Brooks, P.R., 2023. Artificial rockpools: Seaweed colonisation and productivity vary between sites but are consistent across environmental contexts. *Mar. Environ. Res.* 188, 106022.
- Dumas, J.V., Witman, J.D., 1993. Predation by Herring Gulls [*Larus argentatus* (Coles)] on two rocky intertidal crab species [*Carcinus maenas* (L.) and *Cancer irroratus* (Say)]. *J. Exp. Mar. Biol. Ecol.* 169 (1), 89–101.
- Earp, H.S., George, R., Brooke, P.R., Drakard, V.F., Thompson, B.J., Fisher, B., Hayden, R., Crowe, T.P., Moore, P.J., 2023. The population structure, sex ratio and reproductive potential of limpets (*Patella* spp.) on natural shores and artificial structures in the Irish Sea. *Mar. Environ. Res.* 184, 105853.
- Erickson, K.R., Bugnot, A.B., Figuiera, W.F., 2023. Optimising sampling of fish assemblages on intertidal reefs using remote underwater video. *PeerJ* 11, e15426.
- Espadero, A.D.A., Nakamura, Y., Uy, W.H., Tongnunui, P., Horinouchi, M., 2020. Tropical intertidal seagrass beds: an overlooked foraging habitat for fishes revealed by underwater videos. *J. Exp. Mar. Biol. Ecol.* 526, 151353.
- Evans, A.J., Moore, P.J., Firth, L.B., Smith, R.K., Sutherland, W.J., 2021. Enhancing the Biodiversity of Marine Artificial Structures: Global Evidence for the Effects of Interventions. In: *Conservation Evidence Series Synopses*. University of Cambridge, Cambridge, UK.
- Faria, C., Almada, V.C., 2006. Patterns of spatial distribution and behaviour of fish on a rocky intertidal platform at high tide. *Mar. Ecol. Prog. Ser.* 316, 155–164.
- Faria, C., Almada, V.C., 2008. Temporal asymmetries in the feeding patterns along the tidal cycle in two sympatric littoral blennies. *Estuar. Coast. Shelf Sci.* 79, 566–568.
- Firth, L.B., Thompson, R.C., White, F.J., Schofield, M., Skov, M.W., Hoggart, S.P.G., Jackson, J., Knights, A.M., Hawkins, S.J., 2013. The importance of water-retaining features for biodiversity on artificial intertidal coastal defence structures. *Divers. Distrib.* 19, 1275–1283.
- Firth, L.B., Schofield, M., White, F.J., Skov, M.W., Hawkins, S.J., 2014. Biodiversity in intertidal rock pools: informing engineering criteria for artificial habitat enhancement in the built environment. *Mar. Environ. Res.* 102, 122–130. <https://doi.org/10.1016/j.marenvres.2014.03.016>.
- Firth, L.B., Airoidi, L., Bulleri, F., Challinor, S., Chee, S., Evans, A.J., Hanley, M.E., Knights, A.M., O’Shaughnessy, K., Thompson, R.C., Hawkins, S.J., 2020. Greening of grey infrastructure should not be used as a Trojan horse to facilitate coastal development. *J. Appl. Ecol.* 00, 1–7.
- Fletcher, R.L., Callow, M.E., 1992. The settlement, attachment and establishment of marine algal spores. *Br. Phycol. J.* 27 (3), 303–329.
- Gibson, R.N., 1970. The vertical distribution and feeding relationships of intertidal fish on the Atlantic Coast of France. *J. Anim. Ecol.* 41 (1), 189–207.
- Glarou, M., Zrust, M., Svendsen, J.C., 2020. Using artificial-reef knowledge to enhance the ecological function of offshore wind turbine foundations: implications for fish abundance and diversity. *J. Marine Sci. Eng.* 8, 332.
- Glasby, T.M., Connell, S.D., Holloway, M.G., Hewitt, C.L., 2007. Nonindigenous biota on artificial structures: could habitat creation facilitate biological invasions? *Mar. Biol.* 151, 887–895.
- Goncalves, E.J., Almada, V.C., 1998. A comparative study of territoriality in intertidal and subtidal blennioids (Teleostei, Blenniidae). *Environ. Biol. Fish.* 51, 257–264.
- Gregor, C.A., Anderson, T.W., 2016. Relative importance of habitat attributes to predation risk in a temperate reef fish. *Environ. Biol. Fish.* 99 (6), 539–556.
- Hall, A.E., Herbert, R.J.H., Stafford, R., 2021. Temporal and spatial variation in adult and juvenile mobile fauna associated with natural and artificial coastal habitats. *Mar. Biol.* 168 (19).
- Hannah, R.W., Blume, M.T.O., 2012. Tests of an experimental unbaited video lander as a marine fish survey tool for high-relief Deepwater rocky reefs. *J. Exp. Mar. Biol. Ecol.* 430–431, 1–9.
- Herbert, R.J.H., Collins, K., Mallinson, J., Hall, A.E., Pegg, J., Ross, K., Clarke, L., Clements, T., 2017. Epibenthic and mobile species colonisation of a geotextile artificial surf reef on the south coast of England. *PLoS One* 12 (9), e0184100.
- Hixon, M., Beets, J., 1989. Shelter characteristics and Caribbean fish assemblages: experiments with artificial reefs. *Bull. Mar. Sci.* 44, 666–680.
- Hogarth, P.J., 1975. Pattern polymorphism and predation in the shore crab, *Carcinus maenas* (L.). *Crustaceana* 28 (3).
- Humphreys, J., 2005. Salinity and Tides in Poole Harbour: Estuary or Lagoon. In: Humphreys, J., May, V. (Eds.), *The Ecology of Poole Harbour*. Elsevier, London.
- Krone, R., Gutow, L., Brey, T., Dannheim, J., Schroder, A., 2013. Mobile demersal megafauna at artificial structures in the German Bight – likely effects of offshore wind farm development. *Estuar. Coast. Shelf Sci.* 125, 1–9.
- Langhamer, O., Holand, H., Rosenqvist, G., 2016. Effects of an Offshore Wind Farm (OWF) on the common shore crab *Carcinus maenas*: tagging pilot experiments in the Lillgrund Offshore Wind Farm (Sweden). *PLoS One* 11, 1–17.
- Legrand, E., Riera, P., Pouliquen, L., Bohner, O., Cariou, T., Martin, S., 2018. Ecological characterization of intertidal rockpools: seasonal and diurnal monitoring of physico-chemical parameters. *Reg. Stud. Mar. Sci.* 17, 1–10.
- Lenth, R.V., 2021. Emmeans: Estimated Marginal Means, aka Least-Squares Means. R package version 1.6.3. <https://CRAN.R-project.org/package=emmeans>.
- Little, C., Williams, G.A., Trowbridge, C.D., 2007. *The Biology of Rocky Shores*, Second edition. Oxford University Press, New York, United States.
- Martinez-Baena, F., Lanham, B.S., McLeod, I., Taylor, M.D., McOrrie, S., Bishop, M.J., 2022. De novo reefs: fish habitat provision by oyster aquaculture varies with farming method. *Aquac. Environ. Interact.* 14, 71–84.
- Martins, G.M., Hawkins, S.J., Thompson, R.C., Jenkins, S.R., 2007. Community structure and functioning in intertidal rock pools: effects of pool size and shore height at different successional stages. *Mar. Ecol. Prog. Ser.* 329, 43–55.
- Maze, R.A., Dominguez, J., Perez-Cardenal, D., 1999. Diet of *Lipophrys pholis* (L.) (Teleostei, Blenniidae) in Cantabrian coastal waters (Spain). *Acta Oecol.* 20 (4), 435–448.
- McKinney, M.L., 2006. Urbanisation as a major cause of biotic homogenization. *Biol. Conserv.* 127 (3), 247–260. <https://doi.org/10.1016/j.biocon.2005.09.005>.
- Mercader, M., Merciere, A., Saragoni, G., Cheminee, A., Crech’hriou, R., Pastor, J., Rider, M., Dubas, R., Lecaillon, G., Boissery, P., Lenfant, P., 2017. Small artificial habitats to enhance the nursery function for juvenile fish in a larger commercial port of the Mediterranean. *Ecol. Eng.* 105, 78–86.
- Metaxas, A., Scheibling, R.E., 1993. Community structure and organisation of tidepools. *Mar. Ecol. Prog. Ser.* 98, 187–198.
- Mitsch, W.J., Jorgensen, S.E., 2003. Ecological engineering: a field whose time has come. *Ecol. Eng.* 20 (5), 363–377. <https://doi.org/10.1016/j.ecoleng.2003.05.001>.
- Moreira, J., Chapman, M.G., Underwood, A.J., 2006. Seawalls do not sustain viable populations of limpets. *Mar. Ecol. Prog. Ser.* 322, 179–188.
- Morris, R.L., 2016. *Retrofitting biodiversity: Ecological engineering for management of urbanised systems*. University of Sydney. PhD Thesis.
- Morris, R.L., Chapman, M.G., Firth, L.B., Coleman, R.A., 2017. Increasing habitat complexity on seawalls: investigating large- and small-scale effects on fish assemblages. *Ecol. Evol.* 7, 9567–9579. <https://doi.org/10.1002/ece3.3475>.
- Morris, R.L., Golding, S., Dafforn, K.A., Coleman, R.A., 2018a. Can coir increase native biodiversity and reduce colonisation of non-indigenous species in eco-engineered rock pools? *Ecol. Eng.* 120, 622–630.
- Morris, R.L., Porter, A.G., Figueira, W.F., Coleman, R.A., Fobert, E.K., Ferrari, R., 2018b. Fish-smart seawalls: a decision tool for adaptive management of marine infrastructure. *Front. Ecol. Environ.* 16 (5), 278–287.
- Moschella, P.S., Abbiati, M., Aberg, P., Airoidi, L., Anderson, J.M., Bacchiocchi, F., Bulleri, F., Dinesen, G.E., Frost, M., Gacia, E., Granhag, L., Jonsson, P.R., Satta, M.P., Sundelof, A., Thompson, A.C., Hawkins, S.J., 2005. Low-crested coastal defence

- structures as artificial habitats for marine life: using ecological criteria in design. *Coast. Eng.* 52 (10–11), 1053–1071.
- Naylor, L.A., Kippen, H., Coombes, M.A., Horton, B., MacArthur, M., Jackson, N., 2017. *Greening the Grey: A Framework for Integrated Green Grey Infrastructure (IGGI)*. University of Glasgow, Glasgow.
- Ng, D., Daisuke, T., Heery, E.C., Todd, P.A., 2021. Antagonistic effects of seawalls and urban sedimentation on epilithic algal matrix (EAM)-feeding fishes. *Mar. Pollut. Bull.* 173, 113098.
- Noel, L.M.-L.J., Hawkins, S.J., Jenkins, S.R., Thompson, R.C., 2009. Grazing dynamics in intertidal rockpools: connectivity of microhabitats. *J. Exp. Mar. Biol. Ecol.* 370 (1–2), 9–17.
- Nunes, J.A.C.C., Leduc, A., Miranda, R.J., Cipresso, P.H., Alves, J.P., Mariano-Neto, E., Sampaio, C.L.S., Barros, F., 2019. Refuge choice specificity increases with predation risk in a rocky reef fish. *J. Exp. Mar. Biol. Ecol.* 520, 151207.
- Odum, H.T., Odum, B., 2003. Concepts and method of ecological engineering. *Ecol. Eng.* 20, 339–361.
- Orlosk, J.L., Walker, J.M., Morrison, A.L., Atema, J., 2011. Conditioning the crab *Carcinus maenas* against instinctive light avoidance. *Mar. Freshw. Behav. Physiol.* 44 (6), 375–381.
- O'Shaughnessy, K.A., Hawkins, S.J., Evans, A.J., Hanley, M.E., Lunt, P., Thompson, R.C., Francis, R.A., Hoggart, S.P.G., Moore, P.J., Iglesias, G., Simmonds, D., Ducker, J., Firth, L.B., 2019. Design catalogue for eco-engineering of coastal artificial structures: a multifunctional approach for stakeholders and end-users. *Urban* 23, 431–443.
- Paxton, A.B., Pickering, E.A., Adler, A.M., Taylor, J.C., Peterson, C.H., 2017. Flat and complex temperate reefs provide similar support for fish: evidence for a unimodal species-habitat relationship. *PLoS One* 12 (9), e0183906.
- Pinheiro, J., Bates, D., DebRoy, S., Sarkar, D., the R Core Team, 2020. *nlme: Linear and Nonlinear Mixed Effects Models*. R package version 3.1-144, URL: <https://CRAN.R-project.org/package=nlme>.
- Pister, B., 2009. Urban marine ecology in southern California: the ability of riprap structures to serve as intertidal rocky habitat. *Mar. Biol.* 156 (5), 861–873.
- Randall, J., 1963. An analysis of the fish populations of artificial and natural reefs in the Virgin Islands. *Caribb. J. Sci.* 3, 31–47.
- Rangeley, R.W., Thomas, M.L.H., 1987. Predatory behaviour of juvenile shore crab *Carcinus maenas* (L.). *J. Exp. Mar. Biol. Ecol.* 108 (2), 191–197.
- Reis, B., van der Linden, P., Sousa Pinto, I., Almada, E., Teresa Borges, M., Hall, A.E., Stafford, R., Herbert, R.J.H., Lobo-Arteaga, J., Jose Gaudencio, M., Tuaty-Guerra, M., Ly, O., Georges, V., Audo, M., Sebaibi, N., Boutouil, M., Blanco-Fernandez, E., Franco, J.N., 2021. Artificial reefs in the North–East Atlantic area: present situation, knowledge gaps and future perspectives. *Ocean Coast. Manag.* 213, 105854.
- Reubens, J.T., Braeckman, U., Vanaverbeke, J., Van Colen, C., Degraer, S., Vincx, M., 2013. Aggregation at windmill artificial reefs: CPUE of Atlantic cod (*Gadus morhua*) and pouting (*Trisopterus luscus*) at different habitats in the Belgian part of the North Sea. *Fish. Res.* 139, 28–34.
- Reubens, J.T., De Rijcke, M., Degraer, S., Vincx, M., 2014. Diel variation in feeding and movement patterns of juvenile Atlantic cod at offshore windfarms. *J. Sea Res.* 85, 214–221.
- Rhodes, N., Wilms, T., Baktoft, H., Ramm, G., Bertelsen, J.L., Flavio, H., Stottrup, J.G., Kruse, B.M., Svendsen, J.C., 2020. Comparing methodologies in marine habitat monitoring research: an assessment of species-habitat relationships as revealed by baited and unbaited remote underwater video systems. *J. Exp. Mar. Biol. Ecol.* 526, 151315.
- Robinson, E.M., Smee, D.L., Trussell, G.C., 2011. Green crab (*Carcinus maenas*) foraging efficiency reduced by fast flows. *PlosOne* 6 (6), e21025.
- Salauddin, Md., O'Sullivan, J.J., Abolfathi, S., Pearson, J.M., 2021. Eco-engineering of seawalls – an opportunity for enhanced climate resilience from increased topographic complexity. *Front. Mar. Sci.* 8, 674630.
- Schofield, P.J., 2003. Habitat selection of two gobies (*Microgobius gulosus*, *Gobiosoma robustum*): influence of structural complexity, competitive interactions, and presence of a predator. *J. Exp. Mar. Biol. Ecol.* 335, 167–176.
- Sheehan, E.V., Coleman, R.A., Attrill, M.J., Thompson, R.C., 2010. A quantitative assessment of the response of mobile estuarine fauna to crab-tiles during tidal immersion using remote underwater video cameras. *J. Exp. Mar. Biol. Ecol.* 387 (1–2), 68–74.
- Sheehan, E.V., Cartwright, A.Y., Witt, M.J., Attrill, M.J., Vural, M., Holmes, L.A., 2020. Development of epibenthic assemblages on artificial habitat associated with marine renewable infrastructure. *ICES J. Mar. Sci.* 77, 1178–1189.
- Stevens, M., Lown, A.E., Wood, L.E., 2014. Color change and camouflage in juvenile shore crabs *Carcinus maenas*. *Front. Ecol. Evol.* 2 (14).
- Strain, E.M.A., Olabarria, C., Mayer-Pinto, M., Cumbo, V., Morris, R.L., Bugnot, A.B., Dafforn, K.A., Heery, E., Firth, L.B., Brooks, P.R., Bishop, M.J., 2017. Eco-engineering urban infrastructure for marine and coastal biodiversity: which interventions have the greatest ecological benefit? *J. Appl. Ecol.* 55, 426–441. <https://doi.org/10.1111/1365-2664.12961>.
- Strain, E.M.A., Cumbo, V.R., Morris, R.L., Steinberg, P.D., Bishop, M.J., 2020. Interacting effects of habitat structure and seeding with oysters on the intertidal biodiversity of seawalls. *PLoS One* 15 (7), e0230807. <https://doi.org/10.1371/journal.pone.0230807>.
- Taira, D., Heery, E.C., Loke, L.H.L., Teo, A., Bauman, A.G., Todd, P.A., 2020. Ecological engineering across organismal scales: trophic-mediated positive effects of microhabitat enhancement on fishes. *Mar. Ecol. Prog. Ser.* 656, 181–192. <https://doi.org/10.3354/meps13462>.
- Thompson, B., Brooks, P.R., Drakard, V.F., Kubin, F., Earp, H.S., Alvarez-Cienfuegos, I., Moore, P.J., Crowe, T.P., 2023. Population structures and reproductive states of the dogwhelk *Nucella lapillus* differ between artificial and natural rocky shores. *Mar. Environ. Res.* 189, 106058.
- Todd, P.A., Briers, R.A., Ladle, R.J., Middleton, F., 2006. Phenotype-environment matching in the shore crab (*Carcinus maenas*). *Mar. Biol.* 148, 1357–1367.
- Twort, L., Stevens, M., 2023. Active background selection facilitates camouflage in shore crabs, *Carcinus maenas*. *Anim. Behav.* 203, 1–9.
- Ushiyama, S., Mayer-Pinto, M., Bugnot, A.B., Johnston, E.L., Dafforn, K.A., 2019. Eco-engineering increases habitat availability and utilisation of seawalls by fish. *Ecol. Eng.* 138, 403–411.
- Van der Meeren, G.I., 1994. Sex- and size-dependent mating tactics in a natural population of shore crabs *Carcinus maenas*. *J. Anim. Ecol.* 63, 307–314.
- Vaselli, S., Bulleri, F., Benedetti-Cecchi, L., 2008. Hard coastal-defence structures as habitats for native and exotic rocky-bottom species. *Mar. Environ. Res.* 66 (4), 395–403.
- Whitmarsh, S.K., Fairweather, P.G., Huvener, C., 2017. What is big BRUVver up to? Methods and uses of baited underwater video. *Rev. Fish Biol. Fish.* 27, 53–73.
- Wilhelmsson, D., Malm, T., Ohman, M.C., 2006. The influence of offshore windpower on demersal fishes. *ICES J. Mar. Sci.* 63, 775–784.
- Zuur, A.F., Ieno, E.N., Walker, N., Saveliev, A.A., Smith, G.M., 2009. *Mixed Effects Models and Extensions in Ecology with R*. Springer.