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Natural dynamics overshadow anthropogenic impact on marine fauna at an urbanised coastal embayment

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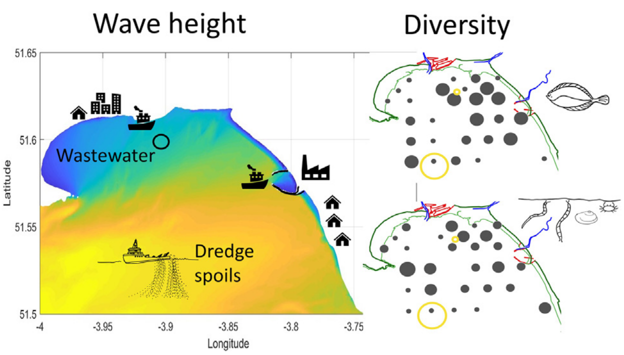
HIGHLIGHTS

- In an urbanised, industrial coastal area, the balance of anthropogenic and natural impacts on benthos and fish was assessed.
- Wave and tidal current models and measured environmental factors were used to explain variation in faunal communities.
- Anthropogenic use of the coastal areas was overshadowed by the impact of wave and tidal currents on biota.
- Infauna, epifauna and fish showed different sensitivities to individual anthropogenic and natural factors

GRAPHICAL ABSTRACT



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ABSTRACT

Understanding vulnerabilities of coastal ecosystems facing anthropogenic use is a precondition for management decisions and development planning. This can be challenging in urbanised areas with multiple activities affecting different faunal communities. The aim of this study was to provide a holistic understanding of the relative importance of anthropogenic and natural variables for macroinfauna, epifauna and fish in a heavily modified waterbody (HMWB) designated under the EU Water Framework Directive (WFD). The study area, Swansea Bay (Wales, UK), had two regularly dredged industrial ports, three estuaries, a wastewater discharge point and a dredge-spoil disposal site. Wave and tidal current models were constructed, and environmental data were gathered by field studies. Biota were assessed by grab sampling and dredging. Modelled and empirical data were combined in a Distance-based Linear Model (DistLM) that quantified how much of the faunal variation was explained by wave exposure and tidal currents, sediment characteristics and other environmental factors, and by anthropogenic usage. Wave and tidal current parameters explained over 50% of the variation in all biota. Infauna communities were further linked with sediment properties and epibenthos with distance to estuaries. Fish and epibenthos were affected by a dredge-spoil disposal site, but none of the faunal communities was affected by the wastewater outfall. Biota were predominantly driven by the natural hydrodynamic regime while

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Abbreviations: max(x), maximum value of a parameter x; $\bar{x}$, mean value of a parameter x; σ(x), standard deviation of a parameter x; $\frac{d}{dt}(x)$, rate of change of a parameter x; BL, bed level; H_s, significant wave height; H_{max}, maximum wave height; T_p, peak wave period; T_z, mean wave period; TL, total load sediment transport; $U_{w,\, z=-h}$, horizontal component of wave driven orbital velocity at the seabed; *U, tidal flow velocity computed from* $U = \sqrt{u^2 + v^2}$; *u*, x-component tidal flow velocity; *v*, y-component tidal flow velocity; max(U_{mag}), maximum tidal flow velocity (magnitude); max(U_{dir}), maximum tidal flow velocity (direction); $\overline{U}_{mag}$, mean tidal flow velocity (magnitude); $\overline{U}_{dir}$, mean tidal flow velocity (direction); R_{mag}, mean tidal residual flow velocity (magnitude); R_{dir}, mean tidal residual flow velocity (direction).

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anthropogenic factors had secondary influence. The study highlighted that ecosystems driven by a strong hydrodynamic regime can be relatively resistant to human activities.

1. Introduction

Understanding the impact of anthropogenic use and alterations on coastal ecosystems is crucial for environmental managers and ecologists to effectively and sustainably manage future development. This includes evaluating biodiversity, resistance to disturbance and the long-term recovery potential of an area. In heavily urbanised areas with prolific maritime economic activities this may be challenging due to habitats being modified by harbours, ports and navigation infrastructure, flood protection, wastewater discharge, toxic chemical pollutants and dredging, which can impact natural ecosystem resources through single, cumulative or synergistic processes (Adams, 2005; McLusky and Elliott, 2004). These anthropogenic activities and coastal modifications are integral to nationally and internationally important economies. There are over 120 commercial ports in the UK alone, and globally there are currently at least 166 seaport cities with over 1 million people (Wales Marine Evidence Report, 2015; Siegel, 2019). The total quantity of freight handled in EU ports is about 3600 million tonnes, and 400 million maritime passengers travel in or out of EU ports (Eurostat, 2013). Severely altered coastal habitats are categorised under the EU Water Framework Directive (WFD) as Heavily Modified Water Bodies (HMWB) required to achieve Good Ecological Potential (GEP) (Reyjol et al., 2014). Over 150 coastal and estuarine areas were designated as HMWB in the UK (Defra, 2012). While it is generally acknowledged that humans profoundly impact marine ecosystems, the consequences of widespread coastal urbanization are yet poorly understood (Madricardo et al., 2019).

Faunal communities adapt to environmental disturbances, and the impact of anthropogenic factors has to be measured against the background of natural forces; an anthropogenic factor can be detected if its impact exceeds intensity and frequency of natural physical disturbance (Kaiser et al., 2006). Anthropogenic pressures altering natural ecosystems are largely the result of societal and economic development (Borja and Dauer, 2008). Detrimental effects of specific factors such as sewage discharge are evidenced (Borja et al., 2006; Borja et al., 2010), but it is challenging to disentangle and quantify the relative importance of individual anthropogenic and natural factors in environments with competing activities, permanent alterations and persistent usage (Kenny et al., 2009; Large et al., 2015; Kenny et al., 2018).

Assessments evaluating the severity of anthropogenic impact often focus on specific faunal groups. Macrobenthic infauna is generally used as an indicator group for disturbance measures and ecological condition (Bertocci et al., 2019; Wetzel et al., 2015). This is based conceptually on their ability to integrate long-term environmental conditions at a particular site (Warwick, 1993). The group is sensitive to characteristics and changes in upper sediment surface layers, such as sewage impacts or heavy metal contamination (Borja et al., 2006). Other groups such as epibenthos and fish are by definition less directly dependent on the sea floor and respond more sensitively to factors operating above the bottom in the water column, but these groups are often ignored in coastal anthropogenic impact studies and play a greater role in offshore impact research (Dutertre et al., 2013; Sheehan et al., 2018).

The aim of this study was to provide a holistic understanding of a heavily modified coastal system by simultaneously assessing multiple anthropogenic and natural environmental drivers on multiple segments of the fauna, namely macroinfauna, epifauna and fish. Due to the complexity of the system we combined diverse sources of data: two models were constructed for waves and tidal currents providing fine-scale hydrodynamic information; environmental and anthropogenic usage data were gathered either by field studies or taken from existing databases and maps; biota were assessed directly by grab sampling and dredging, appropriate for the relevant faunal groups.

The objectives of this study were

1. Combining models for wave climate and tidal currents with empirical faunal and environmental studies.
2. Quantifying the relative importance of natural and anthropogenic variables for the diversity of marine fauna within this heavily anthropogenically modified coastal embayment.
3. Identifying differences between macrobenthic infauna, epifauna and fish in their response to natural and anthropogenic drivers.

2. Study area: natural environment and anthropogenic usage

Swansea Bay is a designated ‘Heavily Modified Waterbody’ as a result of extensive coastal defence measures (HMWB) (EU Water Framework Directive WFD, Directive 2000/60/EC). It is a shallow embayment on the northern coastline of the Bristol Channel (Wales, UK) with depth generally <-20 m Ordnance Datum (OD) (Pye and Blott, 2014) (Fig. 1). It is exposed to severe hydrodynamic forces due to strong winds and tides generated in the Bristol Channel, as well as North Atlantic swells (Allan et al., 2009). The tide increases in amplitude as the Bristol Channel reduces in width before becoming the Severn Estuary. The tidal range in Swansea Bay is hyper-tidal (>6 m); the mean spring tidal ranges at Mumbles Head and Port Talbot are 8.46 m and 8.60 m respectively (Horrillo-Caraballo et al., 2019).

Swansea Bay is exposed to large waves originating from the North Atlantic and propagating along the Bristol Channel; fetch length in the direction of the prevailing west and south west winds exceed 6500 km. The combination of strong waves and tides mean wave-current interaction is an important process in the region (Fairley et al., 2014). Around 49% of the waves in the area are <1 m in height, and 85% <2 m. At the Turbot bank buoy, situated to the west of the study site, 50-year return period extreme wave height values have been calculated as 11.7 m (Fairley et al., 2016). Typical wave periods are 7 to 9 s. The ocean exposure means long period swell waves with periods up to around 20 s are not uncommon. The waves inside Swansea Bay are mostly influenced by the headland Mumbles Head (Fig. 1), which offers shelter to the area. Waves moving inside the bay are affected by shoaling and refraction due to waves moving to shallower areas reducing their energy. The western part of the bay is protected by the headland, but beaches in the eastern part of the bay are more exposed to the swell waves and more prone to erosion and are a popular destination for surfers.

Swansea Bay is characterised by a complex patchwork of bottom substrata (Collins and Banner, 1980) and consists of depositions of poorly sorted, consolidated glacial boulder clay (glacial till), pebbles and cobbles, sometimes mixed with unconsolidated mud and silt as well as mixed sand, silts and clays with associated peats (Culver and Bull, 1980). Marine sediments in the eastern Swansea Bay area are mixed with re-distributed dredge spoils from the Swansea and Port Talbot docks (Culver and Bull, 1980). Generally, surface sediments are highly temporarily variable depending on storminess, with an increase in the proportion of sand and the exposure of relic gravel deposits after periods of wave exposure and deposition of mud following calm weather.

There are two urban centres, the cities of Swansea (population 250,000) and Port Talbot (population 38,000). The natural drainage

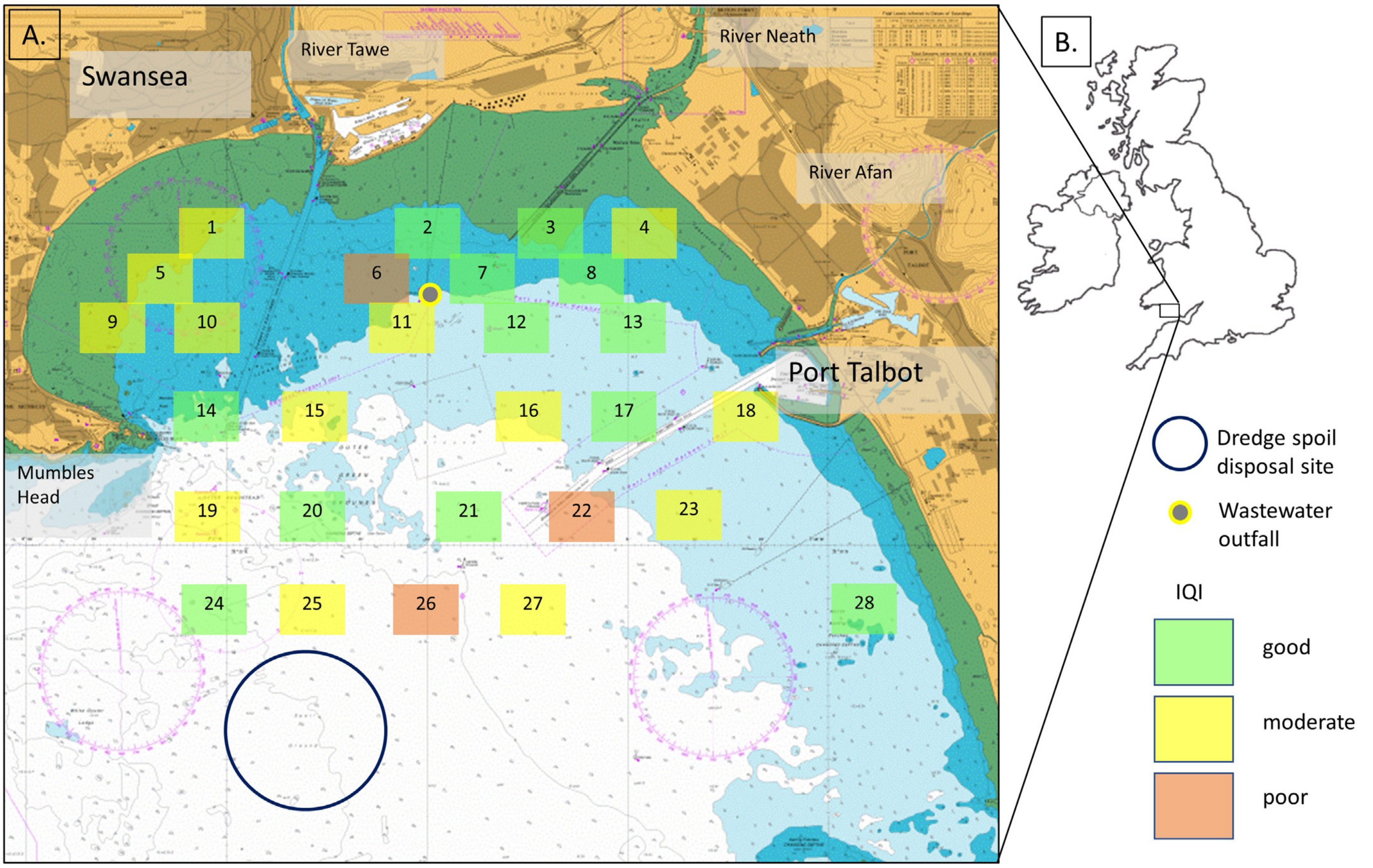

Fig. 1. Swansea Bay area, Wales, UK. A. Admiralty chart 1161 showing coastal infrastructure, anthropogenic usage and faunal survey positions (1–28). Survey position coloured according to WFD Infauna Quality Index (IQI) (adapted from Callaway, 2016); B. Outline of the UK and Ireland, with the sampling area marked.

catchment surrounding the bay is highly urbanised with light industries in the lower reaches of the rivers Tawe, Neath and Afan, and agricultural use in the upper reaches. The main wastewater outfall for the wider Swansea area is located in the centre of the inner bay. Local authorities aspire to achieve bathing water quality for Swansea Bay and discharges from wastewater treatment works have improved substantially since the 1980s (NRW, 2019). Disinfection through ultraviolet treatment of the effluent protects the quality of the bathing waters.

Shipping lanes are dredged inside the bay to Swansea Docks and Port Talbot Docks as well as the approach channel to the River Neath. A tidal harbour is located next to Port Talbot Steelworks at the River Afan, handling vessels importing iron ore and coal; the harbour is also regularly dredged. All dredge spoils are discarded at a designated dredge spoil disposal site in the outer Swansea Bay approximately 13 km from Swansea, which covers an area of 6 ha.

3. Methods

3.1. Wave and tidal current models

Modelled wave conditions and sediment transport were taken from simulations of storm events in the region over the winter of 2013/14 (Fairley et al., 2016). The winter of 2013/2014 is recognised as one of the most energetic on record (Scott et al., 2016) and is the winter prior to the ecological sampling. Two very similar storms, one over a neap tidal cycle (27/12/2013) and one over a spring tidal cycle (03/01/2014) are simulated.

The Danish Hydraulic Institute's MIKE3 suite was used for the wave modelling. The rectangular model domain, with limits at 50^0 – 53^0N and 10^0–2.5^0W, covered the entire Bristol Channel and parts of the Celtic and Irish Seas. A triangular unstructured grid was used to ensure computational efficiency while maintaining sufficient resolution in the area of interest; node spacing was <200 m in the Swansea Bay area. The wave model, MIKE21SW, was forced over the entire domain with wind and surface pressure fields from the ECMWF ERA-interim reanalysis dataset. Wave forcing was applied at the model boundaries from the same dataset. A 3-dimensional model was run in MIKE3 HD covering the same domain to provide tidal elevation and current forcing for the spectral wave model. Total load sediment transport and bed level change was then calculated within the MIKE3 suite using a look-up table approach.

Validation of the wave model against the nearby Cefas Wavenet wavebuoy at Scarweather Sands (51^0 25.99′N, 3^0 55.99′ W) was undertaken for both neap (25/12/2014–31/12/2013) and spring (01/01/2014–06/01/2014) storm events showed good performance (Fig. 2). The model slightly underpredicts the peak of the storm events; root mean squared error in significant wave height (H_s) was 0.33 m for both simulated storms and r^2 values were 0.8 for the spring tide event and 0.9 for the neap tide event. A range of wave model parameters were included in the statistical testing. Parameters were temporally averaged over both storms; the aim being to reduce tidal influence on spatial distribution of wave parameters. Significant wave height, maximum wave height (H_{max}), mean wave periods (T_z), peak wave period (T_p) and the horizontal component of the wave induced orbital water particle velocity at the seabed ($U_{w,\, z=-h}$), were all included. Rate of change of seabed level ($\frac{d}{dt}(BL)$) and total load sediment transport (TL) were also tested. Further details of the model set-up and validation can be found in Fairley et al. (2016).

The numerical model used for the tidal modelling was DELFT3D-FLOW, which is capable of simulating flow in three dimensions but may also be configured to run for two-dimensional flow (Horrillo-

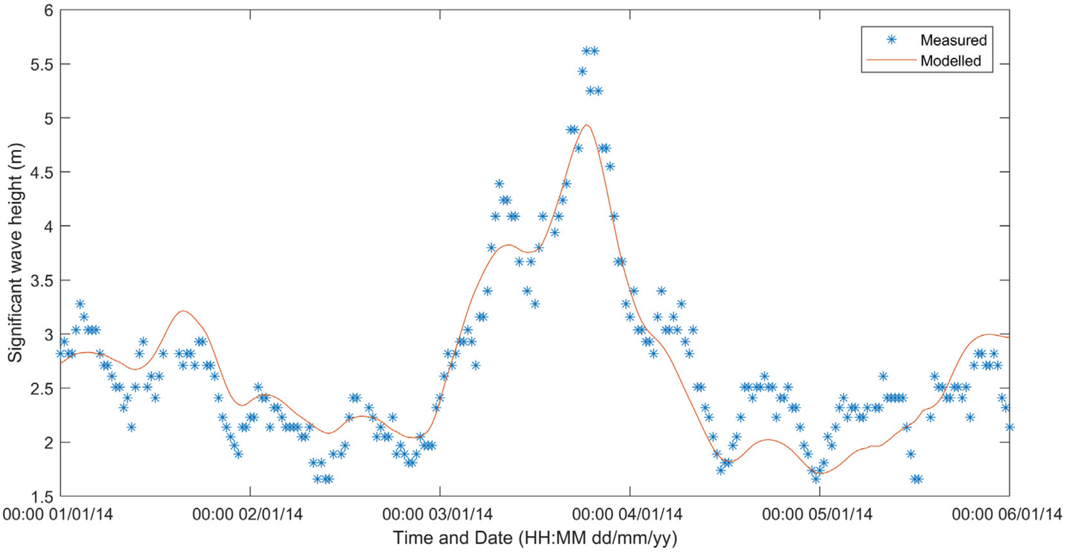

Fig. 2. Comparison between modelled and measured significant wave heights at the Scarweather Sands buoy (Wales UK) for the spring tide event (01/01/2014–06/01/2014).

Caraballo et al., 2019). It was developed by WL|Delft Hydraulics in close cooperation with Delft University of Technology. Its 2DH version (depth-averaged) solves the unsteady shallow-water equations in one-layer (vertically homogeneous) fluids and has been applied in a large number of studies around the world (Deltares, 2014).

The tidal model (DELFT3D) covered the continental shelf region in order to accurately capture the progression and transformation of the tide in the coastal region. Tidal flow around the UK can be approximated by two-dimensional flow with the assumption that the sea is well-mixed and not strongly stratified. The modelling solution was performed on a nested grid: a coarse grid that covers the UK continental shelf, a grid that covers the Irish Sea, a grid that covers the Severn Estuary and the fine grid that covers Swansea Bay region in more detail. The Swansea Bay grid contained 220 × 124 cells and the grid spacing is around 200 m (0.00167°). It was calibrated against available tide gauge and other published information. The boundary conditions selected satisfied the condition that there are tidal stations which can provide data for comparison with the model results. Harmonic constant was imposed along the open boundaries. Data were taken from the TPXO database (Egbert and Erofeeva, 2002). Calibration and validation were performed for the Swansea Bay model and the overall performance is considered good with root mean square error (RMSE) $< 5\%$ for all the area. Details of the calibration and validation of the model can be found in Horrillo-Caraballo et al. (2019). The values used for this study correspond to the maximum velocity, mean velocity and residual velocity; for all of them magnitude and directions are considered. The direction is defined in degrees clockwise from North (assuming the nautical convention) and magnitude is measured in m/s. Nonlinear effects on the tidal harmonics can cause flow asymmetries which can produce tidal residual currents over the model domain and these residual currents are indicative of how sediments move (Horrillo-Caraballo et al., 2019).

3.2. Fish, macrobenthic infauna and epifauna

In 2014, macrobenthos and fish were surveyed in the inner and outer Swansea Bay area. These faunal communities consist of a large range of taxonomic and functional groups, and they respond to environmental change in physical, chemical and ecological characteristics of ecosystems (Warwick, 1993; Sheehan et al., 2018). They were sampled at 28 positions; bedrock, boulders, or large shells prohibited successful sampling in some areas of Swansea Bay, but the majority of the wider bay was covered (Fig. 1).

Macrobenthic epifauna and demersal fish were sampled with a 2-m steel beamtrawl over a distance of 200 m (400 m^2) at 1 knot. Epifauna was defined as invertebrates living on top of the seafloor. The beamtrawl was fitted with a 20 mm stretched mesh (10 mm knot to knot) and a cod-end liner of 4 mm knotless mesh (2 mm "knot" to "knot") (Jennings et al., 1999). Samples were washed through a 5 mm sieve (internal mesh size) and epibenthic fauna and fish were separated from other material. Species that could not be identified at sea were preserved in 4% buffered formalin solution for later identification in the laboratory. All animals were identified to the lowest possible taxonomic level.

Macrobenthic infauna samples were taken with a 0.1m^2 Day grab. Infauna species are invertebrates >1 mm living inside seafloor sediments. They are generally less mobile than epifauna and have a limited capacity to escape from unfavourable environmental conditions. Samples were washed through a 1 mm sieve. The sieve residue was fixed in 4% formaldehyde and stained with Rose Bengal. All benthic species were sorted from the samples, identified to species level and counted. Benthos and fish species names were standardized to the nomenclature of the World Register of Marine Species (WoRMS).

Fifteen species occurred in both grab as well as beamtrawl samples, mainly because trawls occasionally dig into softer sediments and sample infauna, or species generally living inside sediment come to the surface. Grabs on the other hand can pick up the occasional epibenthic species. Eight of the species could be classified as infauna species since they live in upper sediment layers, such as the bivalves *Corbula gibba* and *Spisula elliptica* or the polychaete *Lagis koreni*, while seven species were classified as epibenthos, such as the bryozoan *Flustra foliacea* or the sea urchin *Echinocardium cordatum*. For pragmatic reasons species from grab samples are referred to as macrobenthic infauna, and species sampled with the beamtrawl are referred to as epifauna (and fish).

About 200 g of sediment per grab sample were removed for particle size analysis. Sediment samples were air dried and passed through a series of sieves from 2 mm to 63 μm according to the Wentworth-Udden classification scale to determine particle-size distribution. The sediment parameters mean grain size ($\bar{x}$), sorting (σ), skewness (Sk) and kurtosis (K) were calculated with GRADISTAT (Blott and Pye, 2001).

3.3. Data analysis

Variation in environmental conditions within the sampling area were analysed using normalized principal component analysis (PCA) to determine which variables differed the most between sampling stations (PRIMER6 software; Clarke and Warwick, 2001). SIMPER was carried out for the entire sampling area for fish, macrobenthic epifauna and infauna to examine the contribution of individual species to the average similarity among samples (PRIMER6, Clarke and Warwick, 2001). The extent to which environmental variables explained the community structure of fish, macrobenthic epifauna an infauna was explored by Distance-based linear models (DistLM) (Anderson et al., 2008; PERMANOVA+ for PRIMER software). The routine allows analysing and modelling the relationship between a multivariate data cloud, as described by a resemblance matrix, and one or more predictor variables. The resemblance matrix was constructed by calculating the Bray-Curtis index between samples from fourth-root transformed species/abundance data. DistLMs provided quantitative measures and tests of the faunal variation explained by the predictor variables. These were measured variables for depth, sediment characteristics and distance to three rivers (Rivers Tawe, Neath and Afan), of which two had a port (Swansea, Port Talbot). The distance to the wastewater outfall was entered to quantify the impact of nutrient enrichment and point-source pollution, and distance to the dredgespoil disposal site as a measure for anthropogenic sediment disturbance and sedimentation. Modelled variables of the wave and tidal current regime were entered to evaluate the impact of the natural hydrodynamic environment on biota. Wave climate parameters tested included both storm averaged values and maximum values over the storms: average maximum wave height ($\overline{H_{max}}$), mean of significant wave height (($\overline{H_s}$), mean of peak wave period ($\overline{T_p}$), Maximum value of mean wave period over simulation duration (max(T_z)), Maximum wave induced horizontal velocity of particles at seabed (max($U_{z=-h}$)), standard deviation of Horiz Vel maX (σ($U_{w,\, z=-h}$)), Mean value of total load sediment transport ($\overline{TL}$), Rate of bed-level change ($\frac{d}{dt}(BL)$). Tidal current parameters: magnitude of maximum current velocity (max(U_{mag})), direction of the maximum current velocity (max(U_{dir})), magnitude of the mean velocity ($\overline{U}_{mag}$), direction of mean velocity ($\overline{U}_{dir}$), magnitude of the residual current (R_{mag}), direction of residual current (R_{dir}).

Before the DistLM regression was carried out a Draftsman plot was evaluated for multi-collinearity and skewness of data. If variables were highly correlated one of them was excluded from the analysis. Marginal tests were carried out for each variable to assess how well they individually correlated with the community data. The number of explanatory variables was large in comparison with the number of samples and therefore R^2 approaches 1.0, meaning the percentage variation explained approached 100%. For that reason, the amount of explained variation should be viewed with caution (Anderson et al., 2008). Predictor variables were partitioned into sets representing depth, sediment, rivers, outfalls, waves and currents. This allowed examining the proportion of variation explained by different categories of impacts. Each of the six groups was then tested individually and in a sequential test (DistLM) (Anderson et al., 2008; PERMANOVA+ for PRIMER software).

4. Results

PCA revealed that environmental conditions distinguished sampling stations according to the wave environment, sediments, the dredge spoil disposal site and the wastewater outfall (Fig. 3). The separation along principal component axis 1 (PC1), explaining 38.6% of the total variation, mainly reflected wave properties and the distance to the dredge spoil disposal site. Separation along axis 2 (PC2), explaining 19.1%, was driven by sediment properties and the distance to the wastewater outfall.

4.1. Waves and tidal currents

Maximum wave height averaged over the two storms is shown in Fig. 4. Under the simulated storm conditions, maximum wave height exceeded 5 m. Waves are incident from the WSW and the western portion of Swansea Bay is sheltered by a headland, Mumbles Head, where even under storm conditions wave heights are low. Refraction and diffraction mean wave heights increase towards the east of the embayment. There are areas of wave focussing and de-focussing caused by the presence of the dredged river channels. The calibrated tidal model (DELFT3D) was set up to derive the tidal circulations and the residual flows in the Swansea Bay area. The modelled residual circulation agreed broadly with past measurements while providing considerable additional detail (Collins and Banner, 1980) (Fig. 5). The model suggested a residual flow field with an anticlockwise gyre at the western side of Swansea Bay in the area of Mumbles Head, and another clockwise gyre in the East near Port Talbot. The concurrence of these two gyres flows towards the mouth of river Neath. They divert the flow in two direction, one towards the west and the other in the east direction.

4.2. Faunal communities

A total of 177 species were identified from beamtrawl and grab samples. In beamtrawls 24 fish and 88 epibenthic invertebrate species were found, in grabs 80 infauna invertebrate species (15 invertebrate species occurred in beamtrawls as well as grabs).

Among sampling stations, the similarity of the fish community was greater than among the benthic communities; the average similarity (SIMPER) among all sampling positions was: fish 40.7, epibenthos

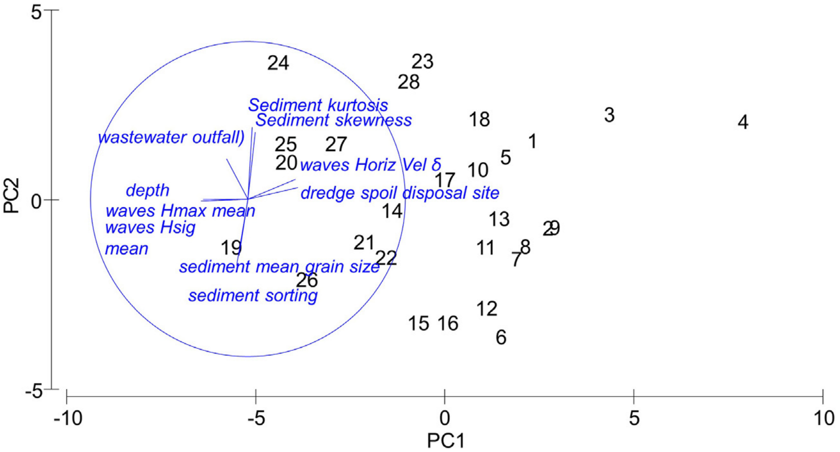

Fig. 3. PCA of environmental variables in Swansea Bay (Wales, UK) at 28 sampling points (Fig. 1). PC1 explained 38.6% of the variation in the data, PC2 19.1% (collectively 57.7%). The main contributing factors to PC 1 and PC2 are superimposed.

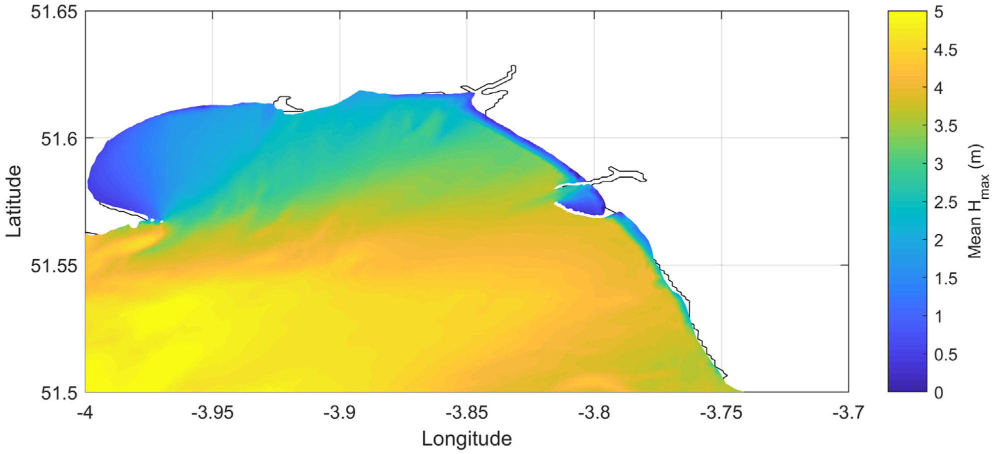

Fig. 4. Maximum wave height averaged over two storm events ($\overline{H_{max}}$).

29.5, benthic infauna 17.3. The result indicated greatest spatial heterogeneity in the infauna community.

4.2.1. Fish

Fish species contributing most to the similarity within the samples (SIMPER analysis) and therefore typifying this faunal group were the sand goby *Pomatoschistus minutus*, juveniles of flatfish, gadoids and gurnards (Table 1). Adults of other naturally small demersal fish were present (as opposed to juveniles of larger species), such as solonetts *Buglossidium luteum*, dragonets *Callionymus lyra* and pog *Agonus cataphractus*.

On average 5.5 ± 2.5 fish species (mean ± sd 400 m^{-2}) were recorded and 38.6 ± 32.5 individuals (mean ± sd 400 m^{-2}). Highest species richness and abundances were recorded in eastern areas of Swansea Bay with up to 10 species and over 100 individuals per breamtrawl (Fig. 6).

Wave and tidal current parameters explained over 70% of the variation in the fish community (DistLM, Tables 2 & 3). Distance to rivers and seafloor sediments had no significant influence. When factors were tested separately (Marginal tests, Table 2), the structure of the fish community was also significantly linked to depth and the dredge spoil disposal site. However, when factors were added sequentially into DistLM, which indicated the additional faunal variation explained with each added predictor variable, only wave and tidal current parameters were significantly linked with the community structure, with wave parameters explaining 47% of the variation (Table 3).

4.2.2. Macrobenthic Epifauna

Epibenthic fauna was mainly characterised by nine invertebrate species of diverse phyla: shrimps, swimming and hermit crabs, spider crabs, sea and brittle stars, Bryozoa, Cephalopoda and Bivalvia (Table 1). The brown shrimp *Crangon crangon* was present almost throughout the bay. The brittle star *Ophiura ophiura* was the most abundant species present at about half of the sampling positions, but it was extremely patchily distributed with densities of over 3000 individuals per trawl.

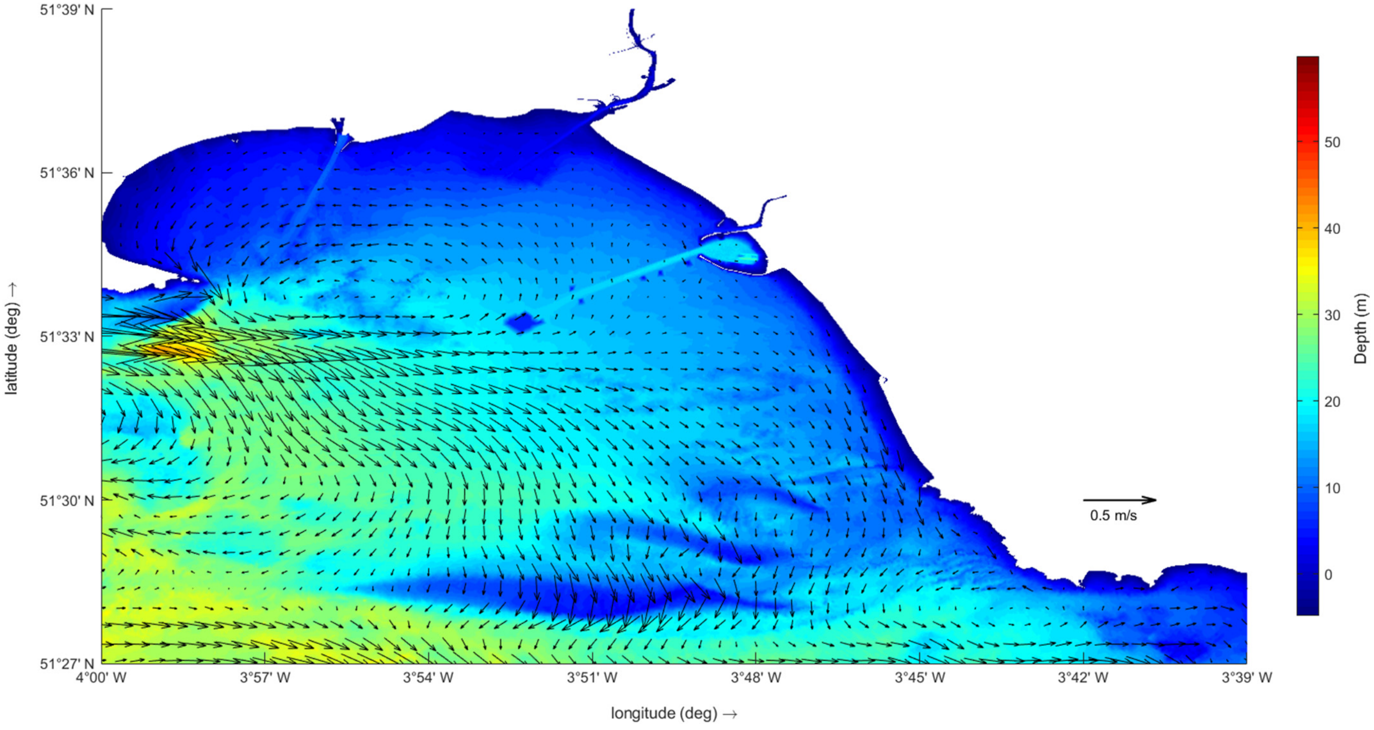

Fig. 5. Computed residual currents for the Swansea Bay area model. Arrows show direction and strength of currents.

Table 1
Species contributing to >90% of the similarity within faunal communities (SIMPER) in Swansea Bay; the three faunal groups were separately analysed.

		# No of positions	Total individuals	Mean ± sd	SIMPER Contrib. %	SIMPER Cum. %
Fish	*Pomatoschistus minutus*	22	420	15.0 ± 19.5	28.2	28.2
	Solea solea	21	120	4.3 ± 5.4	19.7	47.9
	Trisopterus minutus	17	101	3.6 ± 4.7	15.0	63.0
	Limanda limanda	15	163	5.8 ± 10.8	11.2	74.2
	Eutrigla gurnardus	17	61	2.2 ± 3.7	10.3	84.6
	Trisopterus luscus	15	37	1.3 ± 1.7	7.7	92.4
Epifauna	*Crangon crangon*	24	2241	80.0 ± 224.4	27.0	27.0
	Liocarcinus holsatus	20	540	19.3 ± 36.3	15.8	42.5
	Asterias rubens	20	435	15.5 ± 31.4	12.8	55.7
	Ophiura ophiura	15	5176	184.9 ± 628.0	8.0	63.7
	Alcyonidium diaphanum	16	207	7.4 ± 12.8	7.6	71.3
	Macropodia rostrata	16	97	3.5 ± 6.2	6.3	77.7
	Sepiola atlantica	14	27	1.0 ± 1.2	5.5	83.3
	Pagurus bernhardus	15	203	7.3 ± 22.7	5.2	88.5
	Mactra stultorum	9	1008	36.0 ± 96.0	2.0	90.6
Infauna	*Nephtys hombergii*	15	81	2.9 ± 4.4	20.3	20.3
	Nucula nitidosa	16	1116	39.9 ± 94.9	18.7	39.6
	Diastylis rathkei	12	42	1.5 ± 3.1	13.1	52.3
	Nototropis falcatus	11	42	1.5 ± 3.5	11.2	63.5
	Spiophanes bombyx	10	111	4.0 ± 10.2	7.4	70.9
	Glycera tridactyla	10	26	0.9 ± 1.7	6.0	77.0
	Nephtys cirrosa	6	15	0.5 ± 1.3	3.8	80.8
	Notomastus latericeus	8	14	0.5 ± 1.1	3.4	84.2
	Spisula elliptica	9	82	2.9 ± 9.5	2.6	86.8
	Phoronis muelleri	6	10	0.4 ± 0.7	2.2	89.1
	Magelona mirabilis	6	11	0.4 ± 0.9	2.0	91.2

On average 11.3 ± 6.6 species (mean ± sd 400 m^{-2}) were recorded and 421.3 ± 789.4 individuals (mean ± sd 400 m^{-2}). Highest species richness was recorded in eastern areas of Swansea Bay and one position off Mumbles Head (Fig. 6). Abundances varied considerably with highest numbers in the inner eastern bay with almost 4000 individuals per trawl, driven mostly by *C. crangon*, *O. ophiura* and the bivalves *Mactra stultorum* and *Nucula nitidosa*.

The spatial variation in the epibenthic community was significantly linked with all variables: distance to rivers/ports, the dredge spoil disposal site, wave characteristics, tidal currents and sediments (Table 2). However, similar to the fish community, the sequential DistLM indicated that wave and tidal current parameters alone explained significant amounts of the variation in the data (Table 3).

4.2.3. Macrobenthic Infauna

Infauna was characterised by mobile Polychaeta such as Nephtys spp., sedentary polychaetes such as Spionidae and the phoronid *Phoronis muelleri*. Other typifying phyla were Bivalvia, Cumacea and Amphipoda (Table 1).

On average 7.8 ± 6.2 species (mean ± sd 0.1 m^{-2}) were recorded and 36.6 ± 47.0 individuals (mean ± sd 0.1 m^{-2}). Highest species richness was recorded off Mumbles Head with up to 30 species 0.1 m^{-2}, followed by positions in the inner eastern bay (Fig. 6). The pattern was mirrored and exacerbated by abundances. Numbers of species and individuals were poor in the inner western and outer parts of the bay.

Variation in the macrobenthic infauna community was significantly linked to wave characteristics and sediment, although none of the tested factors were highly significant ($p < .01$) (Table 2). The sequential DistLM confirmed that both the wave climate and sediments explained significant amounts of infauna variation.

5. Discussion

In this study hydrodynamic forces exceeded the impact of anthropogenic factors on faunal communities, suggesting that the system is predominantly driven by waves and tidal currents and relatively resistant to changes through anthropogenic activities. Biota in this system may be less vulnerable to anthropogenic pressures compared with more sheltered environments (Borja et al., 2006). On the flip side, this implies that improvements in anthropogenic interference would in contrast to other areas not necessarily manifest in a measurably improved ecological status. The study illustrates the value for environmental management to understand the relative importance of natural and anthropogenic factors in order to gage the change-potential of specific coastal ecosystems, both in terms of deterioration and recovery. Further, the study highlights that a designation as ‘Heavily Modified Waterbody’ (WFD) has to be interpreted with caution and the specific criteria for the designation need to be considered. Here, the bay was designated due to extensive coastal protection infrastructure, which carries little information about the wider impact of anthropogenic usage on the system or its ecological status.

Waves and tidal currents form the physical habitat in sedimentary coastal environments by shaping the seafloor topography, driving the stability or fluidity of sediments and determining the composition of grain sizes (Dalyander et al., 2013; Heath et al., 2017). Hydrodynamic forces thereby affect the suitability of the seafloor as habitat for benthic organisms (Bolam et al., 2008) and are main drivers for infauna community composition (Kröncke et al., 2018). Impact of anthropogenic activities is difficult or impossible to quantify in areas of high natural disturbance and they have limited effects on the faunal communities in wave and current exposed environments (Van Denderen et al., 2015). A strong link between tidal stress and faunal community structure had been established in the wider Bristol Channel outside Swansea Bay by a much coarser hydrodynamic model over the entire region (Warwick and Uncles, 1980). The high correlation between both hydrodynamic models of this study and each of the surveyed faunal communities confirmed that validated three-dimensional environmental models can be useful tools in understanding the distribution of benthos and fish, and that they are important tools to support ecosystem management (Gogina and Zettler, 2010), particularly in areas with complex, highly variable hydrodynamic patterns.

Sediment properties were an important factor for benthic fauna, a relationship that is well-established (Hily et al., 2008). Hydrodynamic forces and sediment characteristics are closely linked (Ghinassi et al., 2019; King et al., 2019) and it can be difficult to separate their impact.

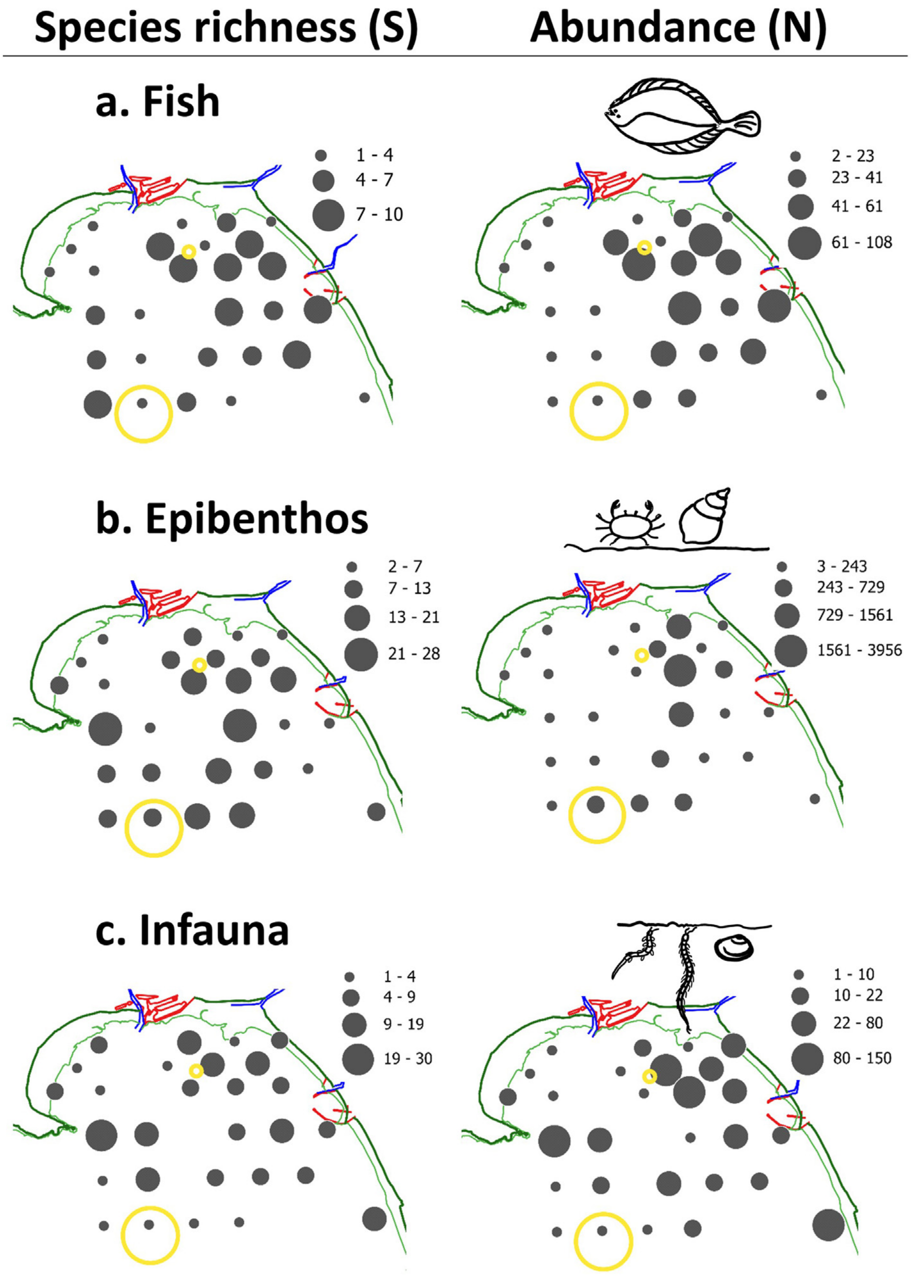

Fig. 6. Diversity of marine fauna in Swansea Bay. Species richness (left) and abundance of individuals (right) of benthic and fish fauna; a. fish sampled with 2 m-breamtrawl (5 min at 1knot, Jennings et al., 1999), b. epibenthic fauna sampled as fish (a.), c. macrobenthic infauna based on 0.1m^2 Day-grab samples. Map: MHW line (dark green), MLW line (light green), rivers and estuaries (blue), docks and breakwaters (red), wastwater diffuser (small yellow circle), dredge spoil disposal site (large yellow circle). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

This study provided evidence that sediments were of direct importance to infauna and to a lesser degree to epifauna. Fish communities, even the demersal ones studied here, were not directly affected by sediment properties. This aligns with the broader ecology of the studied groups. Infauna organisms require specific sediment characteristics, for example for feeding, burrowing or tube building (Pinedo et al., 2000). Epibenthos and demersal fish are by definition in direct contact with the water column and thereby with hydrodynamic forces, and direct impact of sediment characteristics on these communities is less evident. Individual species or groups of species of these faunal groups depend, however, also on sediment properties (Callaway et al., 2002).

While wave exposure and tidal currents were the dominant drivers of community composition, the presence of a dredge spoil disposal ground contributed significantly to the variation in fish and epibenthic communities. Spoil disposal generally changes sediment composition, increases turbidity, and mobilises toxic materials such as heavy metals (Marmin et al., 2014). The nature and magnitude of the impact of dredge spoil disposal on the fauna varies with site specific environmental factors (Roberts and Forrest, 1999; Bolam et al., 2010). In Swansea Bay there are indications of a severe localised negative effect: the site itself is almost deprived of epifauna (Powell-Jennings and Callaway, 2018) and the ecological status according to the WFD Infaunal Quality Index (IQI) was poor or bad in close proximity to the disposal site (Callaway, 2016) (Fig. 1). This study suggests that there may also be a wider spatial effect on fish and epibenthic communities.

In contrast, the wastewater outfall seemed to have no impact on any of the three faunal groups. Generally, wastewater discharge and catchment inputs in coastal areas are known to impact benthic systems (Bertocci et al., 2019; Munroe et al., 2018). Possible impacts may have been overshadowed by the wave and current regime, but it may equally

Table 2
Variables explaining faunal communities in Swansea Bay (DistLM). The table shows significance levels for each predictor variable (significance level $p \le .05$ marked with *, p ≤ .01 in bold) and the proportion of variation in the communities explained.

		Fish		Epifauna		Infauna	
		p	Prop. %	p	Prop. %	p	Prop. %
Depth	Depth	**.004***	12	.013*	8	.111	5
Sediment characteristics	Mean	.498	3	.209	5	.158	5
	Sorting	.486	3	.018*	7	.013*	8
	Skewness	.537	3	.050*	6	.073	6
	Kurtosis	.573	3	**.003***	9	.033*	6
Rivers (distance to mouth)	Tawe	.872	2	.472	4	.554	3
	Neath river	.104	6	**.010***	8	.136	5
	Afon	.207	5	**.000***	11	.273	4
Outfalls (distance)	Wastewater outfall	.238	5	.065	6	.054	6
	Dredge-spoil disposal site	**.005***	11	**.008***	8	.472	4
Waves (modelled parameters)	$\overline{H_{max}}$	**.002***	13	**.005***	8	.032*	7
	$\overline{H_s}$	**.001***	13	**.004***	8	.037*	6
	$\overline{T_p}$	.156	6	.361	4	.038*	6
	$\max(T_z)$	**.005***	11	**.000***	11	.069	6
	$\max(U_{w,\, z=-h})$	.683	3	**.005***	9	.335	4
	$\sigma(U_{w,\, z=-h})$	.205	5	.081	6	.153	5
	$\overline{TL}$	.241	5	.556	3	.570	4
	$\frac{d}{dt}(BL)$	.466	3	.277	4	.364	4
Tidal currents (modelled parameters)	$\max(U_{mag})$	**.008***	12	.061	6	.568	3
	$\max(U_{dir})$	.455	4	.335	4	.113	5
	$\overline{U}_{mag}$	**.003***	13	**.003***	9	.515	4
	$\overline{U}_{dir}$	.362	4	.149	5	.051	6
	R_{mag}	.036*	8	.090	6	.719	3
	R_{dir}	.193	5	.051	6	.480	4

indicate the high technical standard of the wastewater treatment plant including sophisticated UV treatment of wastewater (NRW, 2019). The IQI was though poor at one position in direct proximity to the outfall, and therefore very localised negative impacts upon infauna seem possible (Callaway, 2016; Fig. 1).

This study assessed a number of anthropogenic factors that potentially influence the composition of fauna, but there are others that are common in heavily modified waterbodies and would be desirable to include in a comprehensive study. For example, the study area has a long industrial history of organic and heavy metal pollution, which enriches in sediments and may have individual and synergistic impacts on biota (Dachs and Méjanelle, 2010; Jones et al., 2019). However, sediments at shallow coasts are dynamic due to the exposure to hydrodynamic forces (Ghinassi et al., 2019), prohibiting the long-term storage of pollutants in surface sediments which are in direct contact with benthic and fish fauna. Although contaminants may be present in deeper sediment layers, they are unlikely to have profound impact on current surface-dwelling biota. Further, marine ecosystem research on anthropogenic impact often focuses on fisheries, which is seen as a major driver for ecosystem change (Hiddink et al., 2006; Kenny et al., 2009; Large et al., 2015). There was some whelk potting activity in the study area and some low-level fishing cannot be ruled out, but it was difficult to quantify and was regarded as negligible for the purpose of this study. It seems, however, plausible that commercial fishing in the wider off-shore area impacts the composition and traits of near-shore biota (Bolam et al., 2014).

In terms of ecosystem resilience, recovery and improved ecological status, it has been suggested that dynamic marine systems with highly variable hydrodynamics may recover more quickly than non-dynamic low-energy ones (Borja et al., 2010). This study confirmed that

Table 3
Grouped variables explaining faunal communities in Swansea Bay (DistLM). A. test results for each group alone (marginal test); B. test results for sequentially added factors indicating the additional variation explained with each added predictor factor. The sequence of factors in descending order based on results of marginal tests (A.).

	Fish			Epifauna			Infauna	
A. Marginal tests for individual factors								
	P	Proportion %		**P**	Proportion %		**P**	Proportion %
depth	**.002***	12		.011*	8		.112	5
sediment	.991	7		.042*	20		.016*	20
rivers	.285	13		**.004***	18		.069	14
outfalls	**.005***	17		**.003***	14		.144	9
waves	**.001***	47		**.000***	47		.023*	36
currents	**.000***	40		**.001***	33		.017*	29
B. Sequential tests								
	P	Proportion % (cumulative)		**P**	Proportion % (cumulative)		**P**	Proportion % (cumulative)
waves	**.001***	47	waves	**.000***	47	waves	0.024*	36
currents	.032*	24 (71)	currents	**.008***	23 (70)	currents	0.574	20 (56)
outfalls	.103	7 (78)	sediment	.443	10 (80)	sediment	0.026*	20 (76)
rivers	.914	1 (79)	rivers	.637	6 (86)	rivers	0.434	9 (85)
depth	.341	3 (82)	outfalls	.617	2 (88)	outfalls	0.326	4 (89)
sediment	.353	10 (92)	depth	.492	2 (90)	depth	0.364	3 (92)

ecosystems shaped predominantly by waves and tidal currents will not deteriorate to the degree a low-energy system would under similar anthropogenic pressure. Consequently, a need to recover would be less likely to arise. For Swansea Bay, historical comparisons with the 1980s suggested little change in infauna community structure, despite, for example, reduced nutrient input through improvements in wastewater treatment (Callaway, 2016) (Fig. 6). This must, however, not be confused with the potential to remain or attain historical ecosystem status and historic environmental homeostasis, defined as the inherent variability and resilience in the ecosystem required to mitigate or buffer anthropogenic change (Elliott and Quintino, 2007). Evidence from the 19th century indicates that the Swansea Bay area was characterised by expansive estuarine sand and mudflats and prolific oyster beds (Fig. 7). The hardening of the coastline by coastal infrastructure such as ports, breakwaters and coastal defences as well as the obliteration of the oyster beds through overfishing in the late 19th and early 20th century may have made the most profound impact to the ecosystem. It is though difficult to assess where an ecosystem is positioned along a trajectory to destruction or recovery without detailed understanding of historical human activities (Latimer et al., 2003).

The aspiration under legislation such as Water Framework Directive (WFD) and the Marine Strategy Framework Directive (MSFD) in Europe is to ensure sustainable ecosystems that integrate human society with the natural environment for the benefit of both, acknowledging that sensitivity and resilience vary substantially across ecosystems (Bergen et al., 2001; Lewis, 2005). An innovative aspect of this legislation is to base management decisions on the ecological effects of pressures while being responsive to the fact that sensitivity and resilience vary substantially across ecosystems. Coastal ecosystems may never attain the technical definition of being restored, but end up irreversibly in an alternative state (Borja et al., 2006). Swansea Bay may fall into that category.

6. Conclusion

The integration of biological survey data, fine-scale hydrodynamic models and anthropogenic impact data greatly improved our understanding of the relationship between faunal communities and environmental factors in an industrialised environment at the spatial scale of management concerns. In this urban embayment wave and tidal current parameters explained over half of the variation in all biota. This would be of interest for future development in the area, in particular for anthropogenic alterations that impact the local wave and tidal current environment. Given the important role of these factors for fish and benthic communities it seems plausible that any infrastructure changing the current hydrodynamic climate would significantly alter the marine fauna. This would, for example, be relevant for a proposed tidal lagoon development in the inner Swansea Bay (TLP, 2017).

Importantly, different faunal groups were assessed in this study (benthic infauna, epifauna and fish) which differ in their dependency on sediments and the water column. The community structure of all groups was predominantly shaped by the same hydrodynamic forces, despite some differences in sensitivity between groups. This could have practical implications. Benthic infauna is generally used to assess biodiversity and ecological quality and to determine change, but infauna grab samples are time consuming to process and requires a high level of taxonomic expertise. In contrast, epibenthos and fish beam-trawl samples are less demanding to obtain, process and identify. If the aim of a study is to identify spatial variation in biodiversity over a large area or

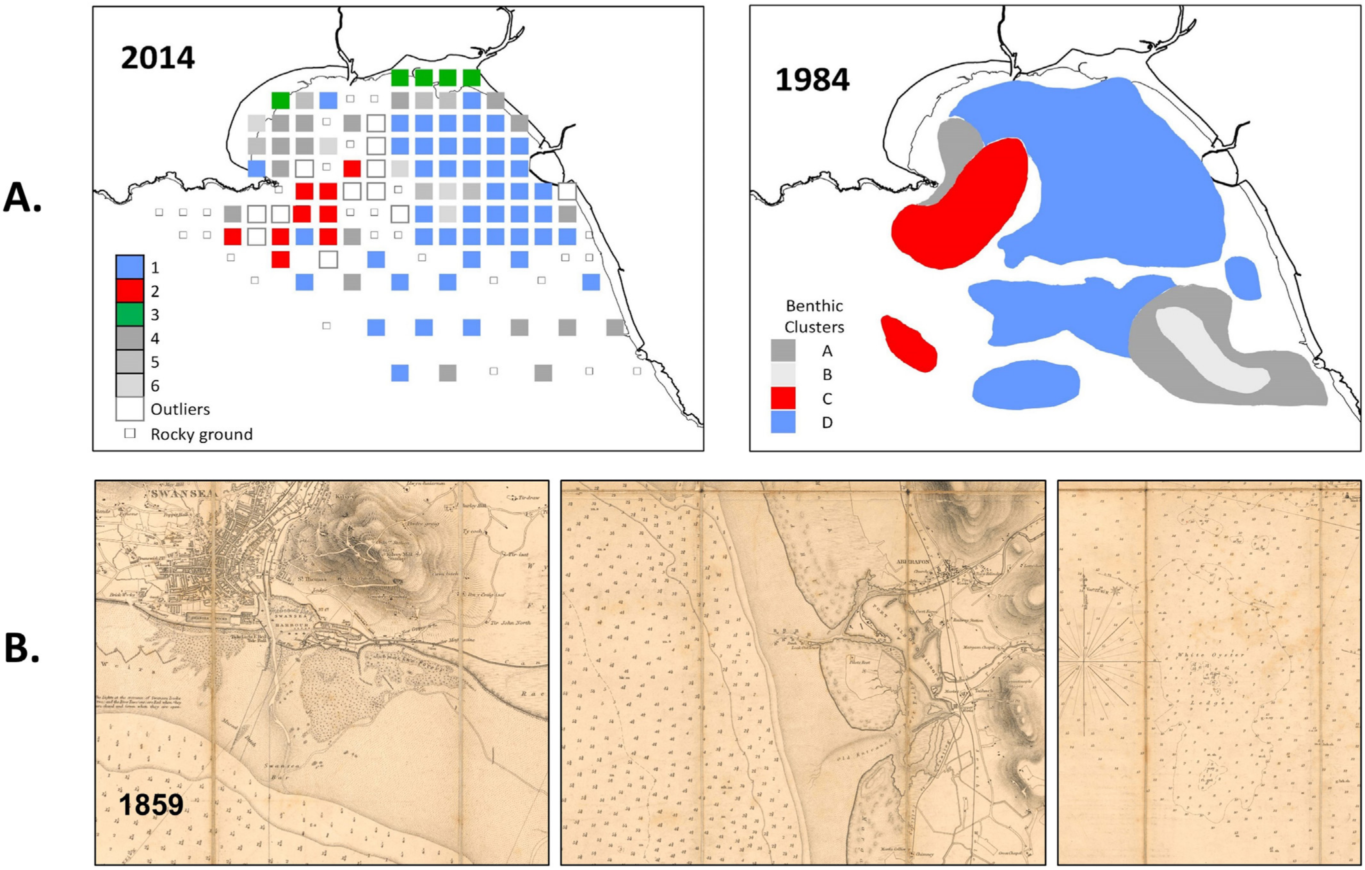

Fig. 7. Historical environment of Swansea Bay. A. Benthic infauna community patterns in 1984 and 2014 (adapted from Callaway, 2016). Colours identify clusters of similar species composition, indicating similar spatial patterns in both studies. B. Sections of Admiralty Chart from 1859 showing expansive intertidal, transitional habitats at Swansea (left) and Port Talbot (middle), and indications of large oyster beds in the central bay (right).

to sample frequently to establish short-term change, 2 m beam-trawl sampling may prove to be a reliable, cost-effective alternative.

This study focused on a specific location and results cannot be readily extrapolated to other urban embayments. It does, however, highlight that ecosystems driven by a strong hydrodynamic regime can be relatively resistant to human activities. The quantification of such biota–environment relationships represents the core of predictive modelling (Gogina and Zettler, 2010), and this study of an urban embayment provides key data for predictive modelling of biodiversity in challenging coastal environments. Predictive modelling of a static tidal barrage in the Severn Estuary east of the studied Swansea Bay area indicated impacts on the distribution and food web dynamics of benthic and fish species (Baker et al., 2020). The approach outlined here forms the basis for further studies that aspire to provide a holistic understanding of natural variation versus anthropogenic impact in complex, highly used marine areas.

Declaration of competing interest

All authors confirm that there are no known conflicts of interest associated with this publication and there has been no significant financial support for this work that could have influenced its outcome.

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